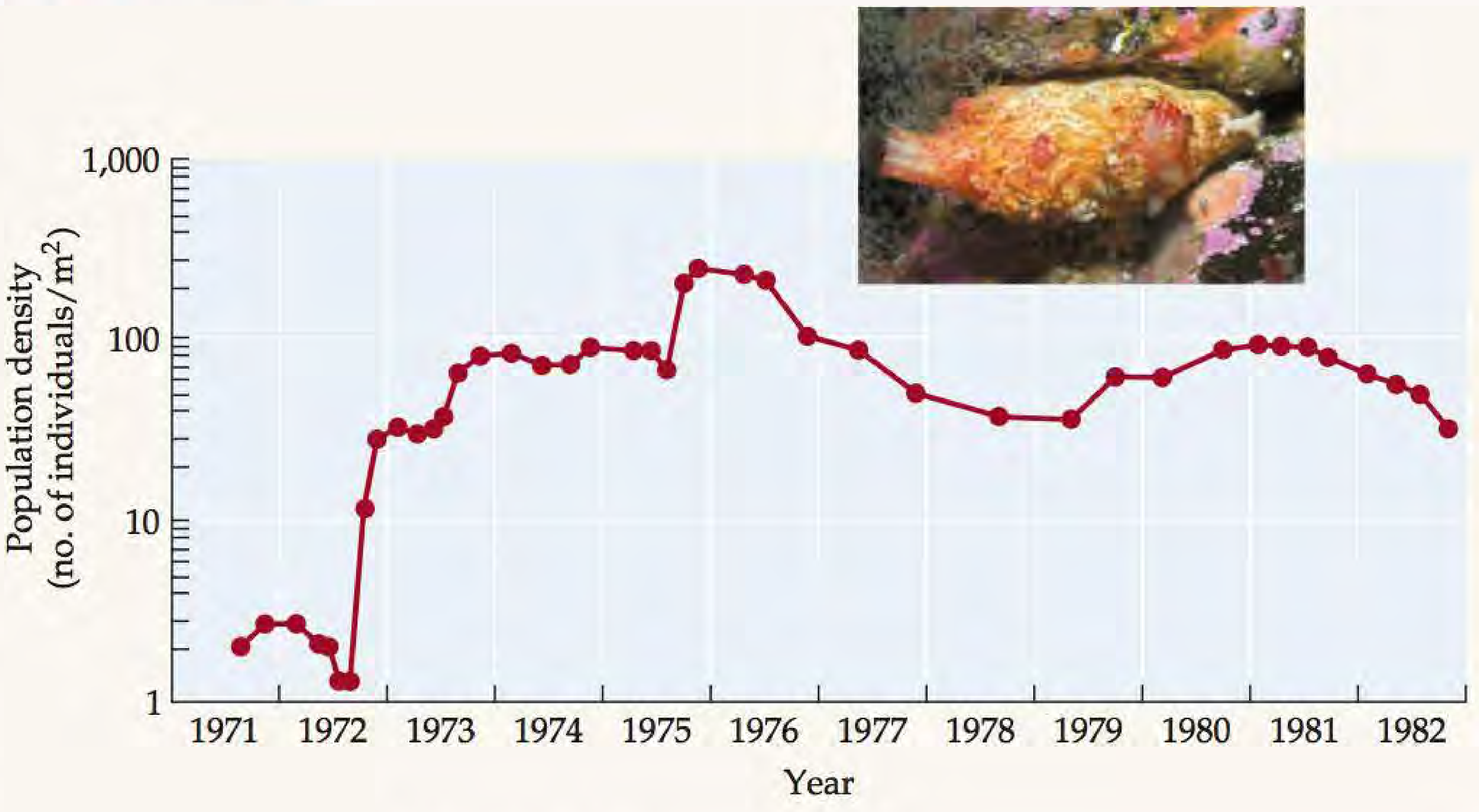
Review Questions

1. Describe a factor that can cause a time lag in the response of a natural population to a change in population density. How do such time lags affect changes in abundance over time?
2. Summarize how chance events can threaten small populations.
3. A population consists of four unrelated individuals, two females (F1 and F2) and two males (M1 and M2). Individuals live only one year, and they mate only once, producing two offspring (one female, one male) from each mating. Individuals avoid mating with relatives if possible.
   - **a.** Starting with individuals F1, F2, M1, and M2 as the parent generation, can the first two generations of offspring be born to parents that are not related to each other? You may find it helpful to construct a diagram to illustrate the two generations of parents and their offspring.
   - **b.** If the second generation of offspring become parents, how many of the matings in this third generation of parents can occur between unrelated individuals? Generalizing from your results, is inbreeding likely to be common or uncommon in small populations?
4. **a.** Explain how a metapopulation can become extinct while suitable habitat remains.
   - **b.** Imagine that human actions created a metapopulation from what was once continuous habitat. If many small and two large habitat patches remained, what arrangement of those patches would make it most likely that the metapopulation would *not* persist?

Hone Your Problem-Solving Skills

Svane (1984) studied population dynamics in the tunicate (or "sea squirt") *Ascidia mentula*, a filter-feeding marine invertebrate. The figure shows population densities over time for one of six study populations, and the table provides data (averaged across the six study populations) on how per capita birth and death rates are related to population density.



POPULATION DENSITY (NO. INDIV/M²)	BIRTH RATE (OFFSPRING/INDIV/YR)	DEATH RATE (DEATHS/INDIV/YR)
38	0.40	0.38
60	0.39	0.32
75	0.56	0.51
105	0.47	0.36
180	0.44	0.48
230	0.30	0.32

1. Estimate the minimum and maximum density observed for the population whose densities are shown in the figure. Which of the four population growth patterns described in Concept 11.1 best represents the results shown in the figure? Explain.
2. Use the data in the table to graph the birth rate versus population density. To do this, first plot each data point and then draw an approximate "best-fit" curve that goes through those points. Are birth rates density-dependent or density-independent? Explain. (See Concept 10.4 to review density independence and density dependence.)
3. Use the data in the table to graph the death rate versus population density; to do this, first plot each data point and then draw an approximate best-fit curve that goes through those points. Are death rates density-dependent or density-independent? Explain.
4. Draw a graph (similar to that in Figure 11.5B) showing how at any given density, both the birth rate and the death rate vary over time; one way to draw this graph would be to begin with the best-fit curves that you produced in questions 2 and 3 and then add broad bands around each curve that represent the variation observed in the data points plotted in questions 2 and 3. Does your graph indicate that a sea squirt population with these birth and death rates should reach a steady carrying capacity (*K*)? Explain.

ON THE COMPANION WEBSITE
ecology4e.sinauer.com

The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

- **11.1** Bamboo, Rats, and Famine in the Far East: Population Overshoots and Carrying Capacity

Web Extensions

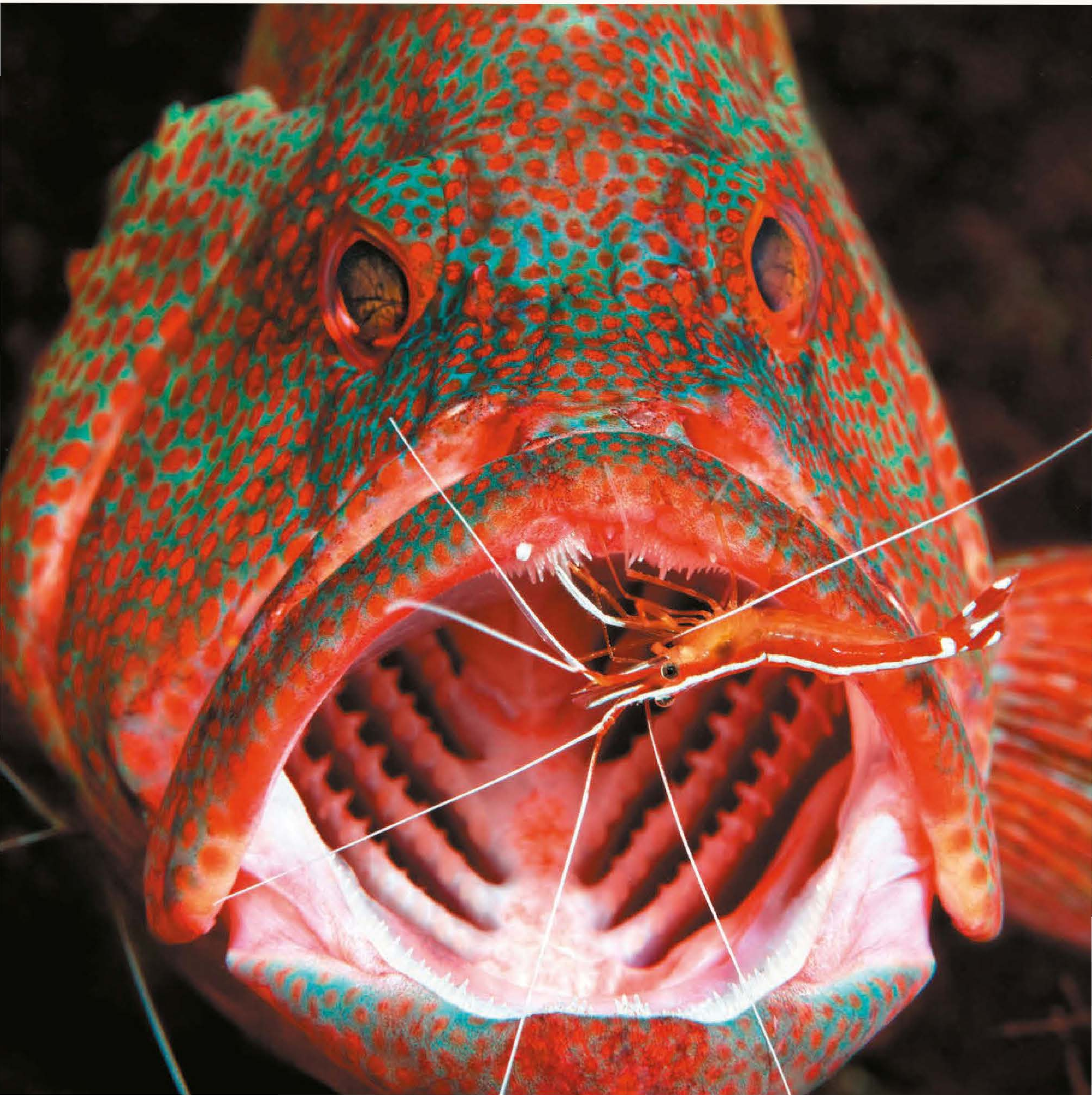
- **11.1** The Meaning and Use of the Geometric Mean
- **11.2** Deriving Levins's Rule for Persistence

Online Climate Change Connection

- **11.1** Climate Warming and Collapsing Population Cycles

Unit 4

Species Interactions



12 Predation

KEY CONCEPTS

CONCEPT 12.1 Most carnivores have broad diets, whereas a majority of herbivores have relatively narrow diets.

CONCEPT 12.2 Predation results in a wide range of capture and avoidance mechanisms.

CONCEPT 12.3 Predator populations can cycle with their prey populations.

CONCEPT 12.4 Predation can affect prey distribution and abundance, in some cases causing a shift from one community type to another.

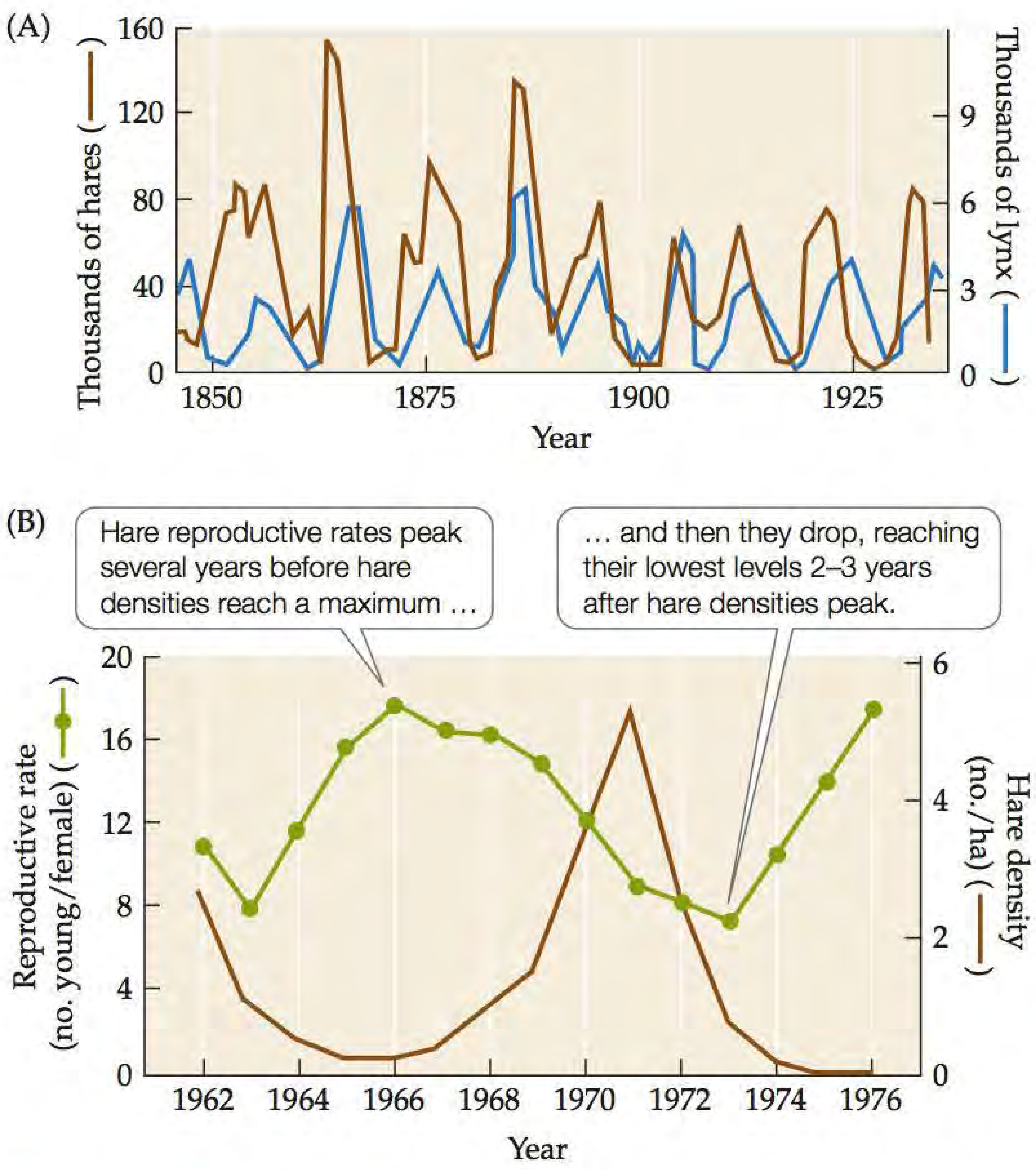
Snowshoe Hare Cycles: A Case Study

In 1899, a fur trader in northern Ontario reported to the Hudson's Bay Company that "Indians are bringing poor hunts. They have been starving all spring. Rabbits being scarce" (Winterhalder 1980). The "hunts" referred to were pelts of beavers and other fur-bearing animals trapped by members of the Ojibwa tribe, and the "rabbits" were actually snowshoe hares (*Lepus americanus*) (**Figure 12.1**). Collectively, 200 years of such reports show that hare populations increased and decreased regularly. When hares were abundant, the Ojibwa had enough food to spend time trapping for pelts, which they then traded to the Hudson's Bay Company. But when hares were scarce, tribal members concentrated on gathering food, rather than trapping animals that provided pelts, but little meat.

Beginning in the early 1900s, wildlife biologists used the careful records of the Hudson's Bay Company to estimate abundances of snowshoe hares and their Canada lynx predators (*Lynx canadensis*). Both species exhibited regular population cycles, with abundances peaking about every 10 years and then falling to low levels (**Figure 12.2A**). Snowshoe hares constitute a major portion of the lynx diet, so it was not surprising that numbers of lynx should rise and fall with numbers of hares. But what drove the cyclic fluctuations in the hare population? Adding to the mystery, hare population sizes rose and fell in synchrony across broad regions of the Canadian forest, so explanations of hare cycles had to account for the large-scale synchrony as well.

One approach to finding the factors important to hare population cycles is to document the changes in birth, death, and dispersal rates that are associated with increasing or declining numbers of hares. Dispersal plays a relatively small role: it may alter local population sizes, but hares do not move far enough to account for the simultaneous changes in their abundance seen across broad geographic regions. In contrast, consistent patterns of birth and death rates have been found across different regions of Canada. Snowshoe hares can raise up to three or four litters over the summer, with an average of five young per litter. Hare reproductive rates reach their highest levels (ca. 18 young per female) several years before hare density reaches a maximum. Reproductive rates then begin to fall, reaching their lowest levels 2–3 years after hare density peaks (**Figure 12.2B**). Hare survival rates show a similar pattern:

Figure 12.1 Predator and Prey A snowshoe hare (*Lepus americanus*) flees from its specialist predator, the Canada lynx (*Lynx canadensis*).



Hare reproductive rates peak several years before hare densities reach a maximum …

… and then they drop, reaching their lowest levels 2–3 years after hare densities peak.

Figure 12.2 Hare Population Cycles and Reproductive Rates (A) Historical trapping data from the Hudson's Bay Company indicate that numbers of both hares and lynx fluctuated in a 10-year cycle. (B) The highest hare reproductive rates do not coincide with the highest hare densities. (A after MacLulich 1937; B after Cary and Keith 1979.)

? In (A), does the peak abundance of one species typically occur after the peak abundance of the other species? Describe the observed pattern and hypothesize why it might occur.

they are highest several years before hare density peaks; then they fall and do not rise again until several years after hare density peaks.

Together, the changes over time in hare birth and survival rates drive the hare population cycle. But what causes these rates to change? Several hypotheses have been proposed, one of which focuses on food supplies. Large numbers of hares consume prodigious amounts of vegetation, and studies have shown that food can be limiting at peak hare densities (up to 2,300 hares/km^2). Two observations, however, indicate that food alone does not drive the hare cycle: first, some declining hare populations do not lack food, and second, the experimental addition of high-quality food does not prevent hare populations from declining.

A second hypothesis focuses on predation. Many hares (up to 95% of those that die) are killed by predators such as lynx, coyotes, and birds of prey. In addition, lynx and coyotes kill more hares per day during the peak and decline phases of the hare cycle than during the increase phase. But questions remain. The killing of hares by predators explains the drop in survival rates as hare numbers decline, but by itself it does not explain (1) why hare birth rates drop during the decline phase of the cycle or (2) why hare numbers sometimes rebound slowly after predator numbers plummet. Nor does it explain other observations, such as why the physical condition of hares worsens as hares decrease in numbers. What other factors are at work?

Introduction

Over half the animals on Earth sustain themselves by feeding on other organisms. Some kill other organisms, then eat them, while others "graze" on living organisms by eating their tissues or internal fluids. As we will see, those millions of species interact with the organisms they eat in a rich variety of ways. But all these interactions share a common feature: they are all forms of **predation**, a **trophic interaction** in which an individual of one species, a **predator**, consumes individuals (or parts of individuals) of another species, its **prey**.

Over the course of this and the next chapter, we will consider the three broad categories of predation: carnivory, herbivory, and parasitism (**Figure 12.3**). Predation includes **carnivory**, in which the predator (a **carnivore**) and prey are both animals; **herbivory**, in which the predator (an **herbivore**) is an animal and the prey is a plant or alga; and **parasitism**, in which the predator (a **parasite**) lives in **symbiosis** (close physical and/or physiological contact) with its prey (a **host**) and consumes certain tissues without necessarily killing the host. Some parasites are **pathogens** that cause disease in their hosts.

These definitions seem simple, and it is easy to think of examples: a lion that kills and eats a zebra, an insect that eats a plant leaf, a tapeworm that robs a dog of nutrients in its digestive tract. But the natural world defies such simple categorization. Consider those prototypical herbivores, sheep: they get most of their food from plants, but they have also been known to eat the helpless young of ground-nesting birds. Conversely, carnivores can act like herbivores: wolves, for example, will eat berries, nuts, and leaves. And some organisms do not fit neatly into any category. **Parasitoids** are insects that typically lay one or a few eggs on or in another insect (the host) (**Figure 12.4**). After they hatch from their eggs, the parasitoid larvae remain with the host, which they eat and usually kill. Parasitoids can be considered unusual parasites (because they consume most or all of their host, almost always killing it) or unusual carnivores (because over the course of their lives they eat only one individual, killing it slowly).

Figure 12.3 Three Ways to Eat Other Organisms (A) Some dragonfly larvae are carnivores that kill and consume other animals. This larva is eating a worm. (B) Herbivores such as elephants eat grasses, leaves, or other plant parts. (C) This marine isopod is a parasite that has attached to and is feeding on the tissues of its host, a creole fish (*Paranthias furcifer*) of the Caribbean coral reefs.

Figure 12.4 Are Parasitoids Carnivores or Parasites? Parasitoids such as the wasp *Aphidius colemani*, shown here depositing an egg into an aphid, can be considered unusual carnivores because during their lifetime they eat and slowly kill only one prey individual. Parasitoids can also be viewed as unusual parasites that eat all or most of their host, thereby killing it.

Despite these and other complications, we will approach the rich variety of trophic interactions in two chapters: this chapter will cover carnivory and herbivory, and Chapter 13 will focus on parasitism. We will begin by exploring some aspects of carnivores and herbivores that define and characterize their dietary preferences.

CONCEPT 12.1

Most carnivores have broad diets, whereas a majority of herbivores have relatively narrow diets.

Carnivore and Herbivore Dietary Preferences

Although they share some similarities, carnivores and herbivores differ from each other in many aspects. The most obvious difference is that carnivores invariably kill their prey (it is hard to eat only part of an animal without killing it), while herbivores usually do not kill the plants they eat, at least not immediately. Another difference is that animal prey can usually move away or hide from their predators but most plant prey cannot. Finally, even though plant prey are often more abundant, their body tissues have much lower nitrogen content, and thus are less nutritious, than animal prey (**Figure 12.5**). These three factors have important consequences for the dietary preferences of carnivores versus herbivores.

As we learned in Concept 8.2, optimal foraging and dietary preferences are thought to be dependent on two

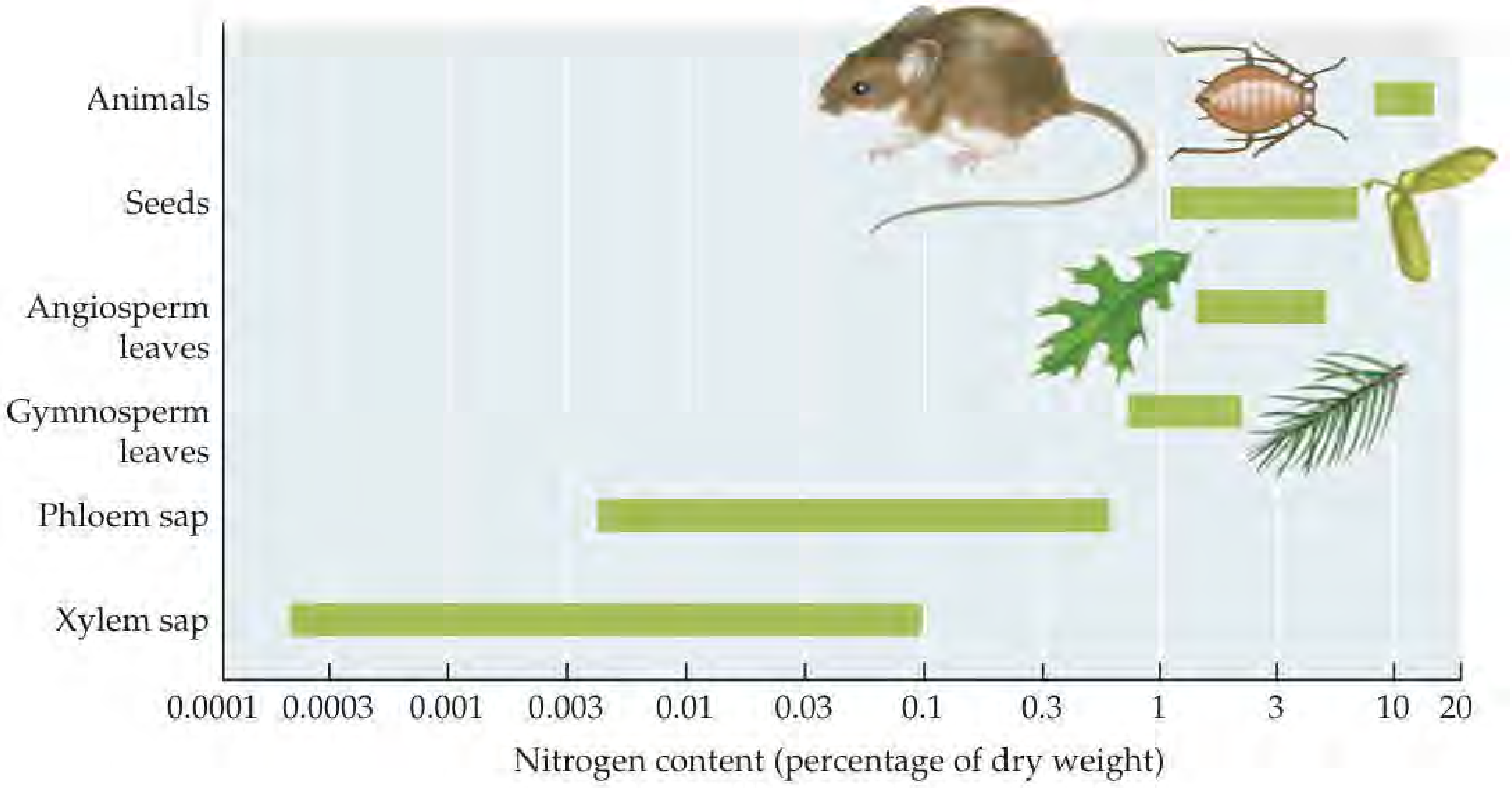


Figure 12.5 The Nitrogen Contents of Plants and Animals Differ Nitrogen is an essential component of any animal's diet. Body tissues of animals have much higher nitrogen content than those of plants. Of plant tissues, leaves tend to have the highest nitrogen content of any plant parts other than seeds. (After Mattson 1980.)

factors: (1) encounter rate, a function of search time, or the time it takes to search and find prey, and (2) handling time, or the time it takes to subdue and consume the prey. If the encounter rate for prey is low, as would be the case for predators searching for mobile animal prey, then the prediction is that the predators should not be too narrow in their prey choices. As a consequence, these predators (carnivores) should be *generalists* and have fairly broad diets. On the other hand, if prey are relatively easy to search for but their handling times are longer, as is the case for immobile but less nutritious plants, then the predators (herbivores) should be *specialists* and have narrow diets. Let's consider these predictions in more detail below.

Many carnivores have broad diets

Most carnivores eat prey in relation to their availability without showing a preference for any particular prey species. This lack of preference is likely a result of a generalist strategy. A predator can be said to show a preference for a particular prey species if it eats that species more often than would be expected based on that prey's availability.

Some carnivores do show a strong preference for certain prey species. Lynx and coyotes, for example, eat more hares than would be expected based on their availability; even when hares constitute only 20% of the available food, they constitute 60%–80% of the diet of lynx and coyotes.

Some carnivores concentrate their foraging on whatever prey is most plentiful. When researchers provided guppies with two kinds of prey, fruit flies (floating on the water surface) and tubificids (aquatic worms found on the bottom), the guppies ate disproportionate amounts of whichever prey was most abundant (**Figure 12.6**). Predators like these guppies that focus on abundant prey tend to "switch" from one prey species to another. Such switching may occur because the predator forms a search image of the most common prey type and hence tends to orient toward that prey, or because learning enables it to become increasingly efficient at capturing the most common prey type. As we saw in Concept 8.2, in some cases predators switch from one type of prey to another in a manner consistent with the predictions of optimal foraging theory.

Most herbivores have relatively narrow diets

While most predators eat a broad range of prey species, the majority of herbivores feed on comparatively restricted sets of plant parts or plant species.

SPECIALIZATION ON PARTICULAR PLANT PARTS As we saw in Figure 12.5, the tissues of plant parts differ in their nitrogen content and thus their nutritional value. While

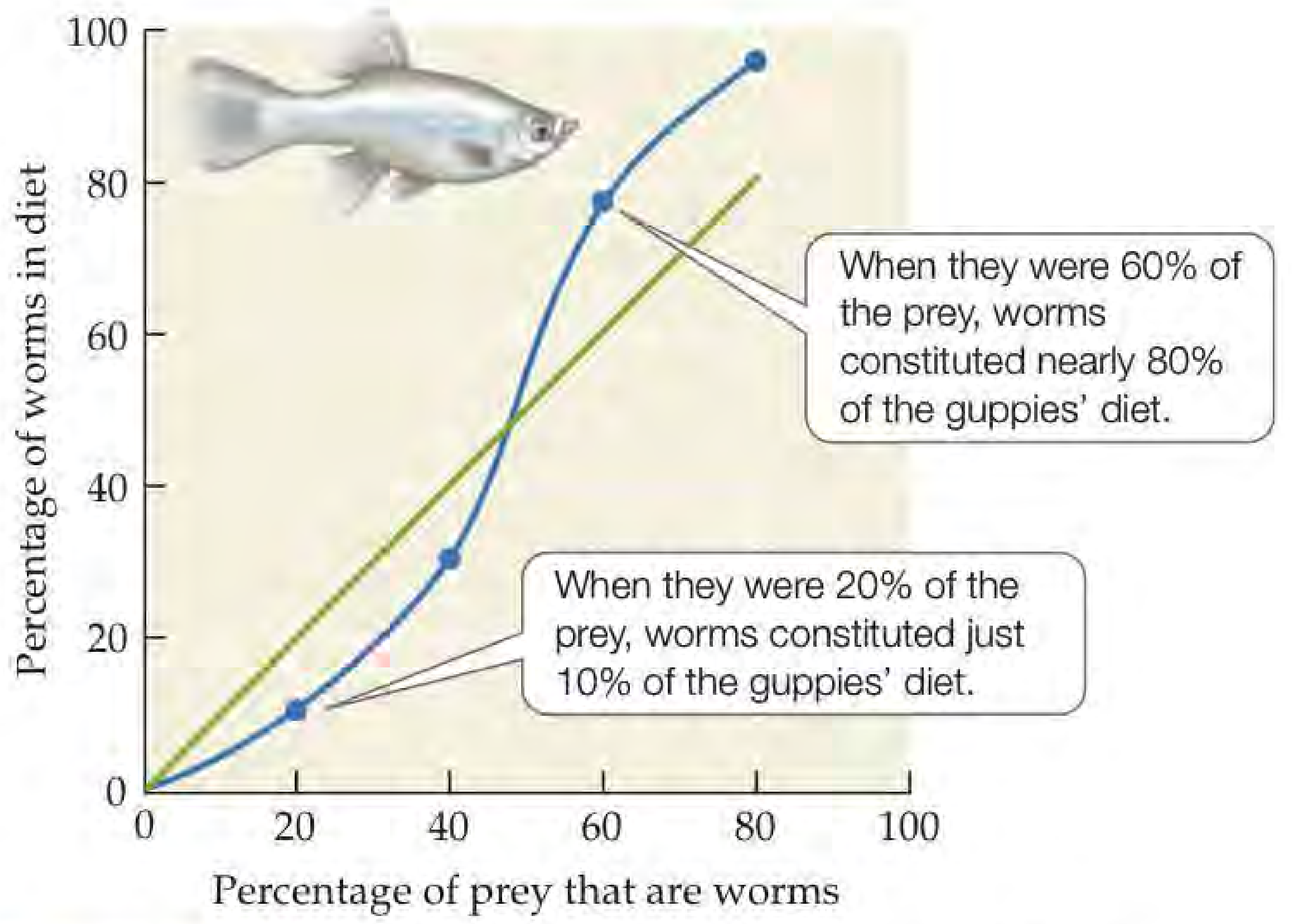


Figure 12.6 A Predator That Switches to the Most Abundant Prey Guppies focused their foraging efforts on whichever prey species was most common in their habitat: aquatic worms (tubificids) or fruit flies. The solid green line indicates the results that would have been expected if the guppies had captured worms according to their availability instead of switching to whichever prey species was more abundant. (After Murdoch et al. 1975.)

some herbivores that are large relative to their food plant eat all parts of the plant, most herbivores tend to specialize on particular parts of plants. They can be grouped according to whether they eat leaves, stems, roots, seeds, or internal fluids (e.g., nutrient-containing sap).

More herbivores eat leaves than any other plant part. Leaves are abundant, and they are available year-round in many places; leaves are also more nutritious than other plant parts (except for seeds) (see Figure 12.5). Herbivores that eat leaves range from large browsers, such as deer or giraffes, to grasshoppers and herbivorous fishes, to tiny "leaf miners" such as fly larvae that enter a leaf and eat it from the inside. By removing photosynthetic tissues, leaf-eating herbivores can reduce the growth, survival, or reproduction of their food plants.

Belowground herbivory can also have major effects on plants, as illustrated by the 40% reduction in growth observed in bush lupine plants after 3 months of herbivory by caterpillars of the root-killing ghost moth *Hepialus californicus*. Similarly, herbivores that eat seeds can have large effects on plant reproductive success, sometimes reducing it to zero. The effects of herbivores that feed on internal fluids are not always obvious (because visible plant parts are not removed), but they too can be considerable. For example, Dixon (1971) showed that although the lime aphid (*Eucallipterus tiliae*) did not reduce aboveground growth in lime trees during the year of infestation, the roots of trees infested with aphids did not grow that year, and a year later, their leaf production dropped by 40%.

SPECIALIZATION ON PLANT SPECIES Most herbivores also specialize on particular plant species. This statement is true largely because of insects: there is an enormous number of herbivorous insect species, and most of them live on and eat only one (or a few) plant species. For example, most species of agromyzid flies, whose larvae are leaf miners, feed on only one or a few plant species (**Figure 12.7**). Similar results have been found for leaf-feeding beetles in the genus *Blepharida*: among 37 species of these beetles, 25 feed on a single plant species, 10 feed on 2–4 plant species, and only 2 feed on a relatively broad suite of plants (12–14 species) (Becerra 2007).

There are numerous examples of herbivores that eat many plant species, however. Grasshoppers, for example, graze on a broad range of plant species, and even among the leaf miners in Figure 12.7, several species eat more than ten different plants. Large browsers, such as deer, often switch from one tree or shrub species to another; in addition, they eat all or most of the aboveground parts of many herbaceous plant species. The golden apple snail (*Pomacea canaliculata*) is a voracious generalist herbivore, capable of removing all the large plants from wetlands; the snail then survives by eating algae and detritus.

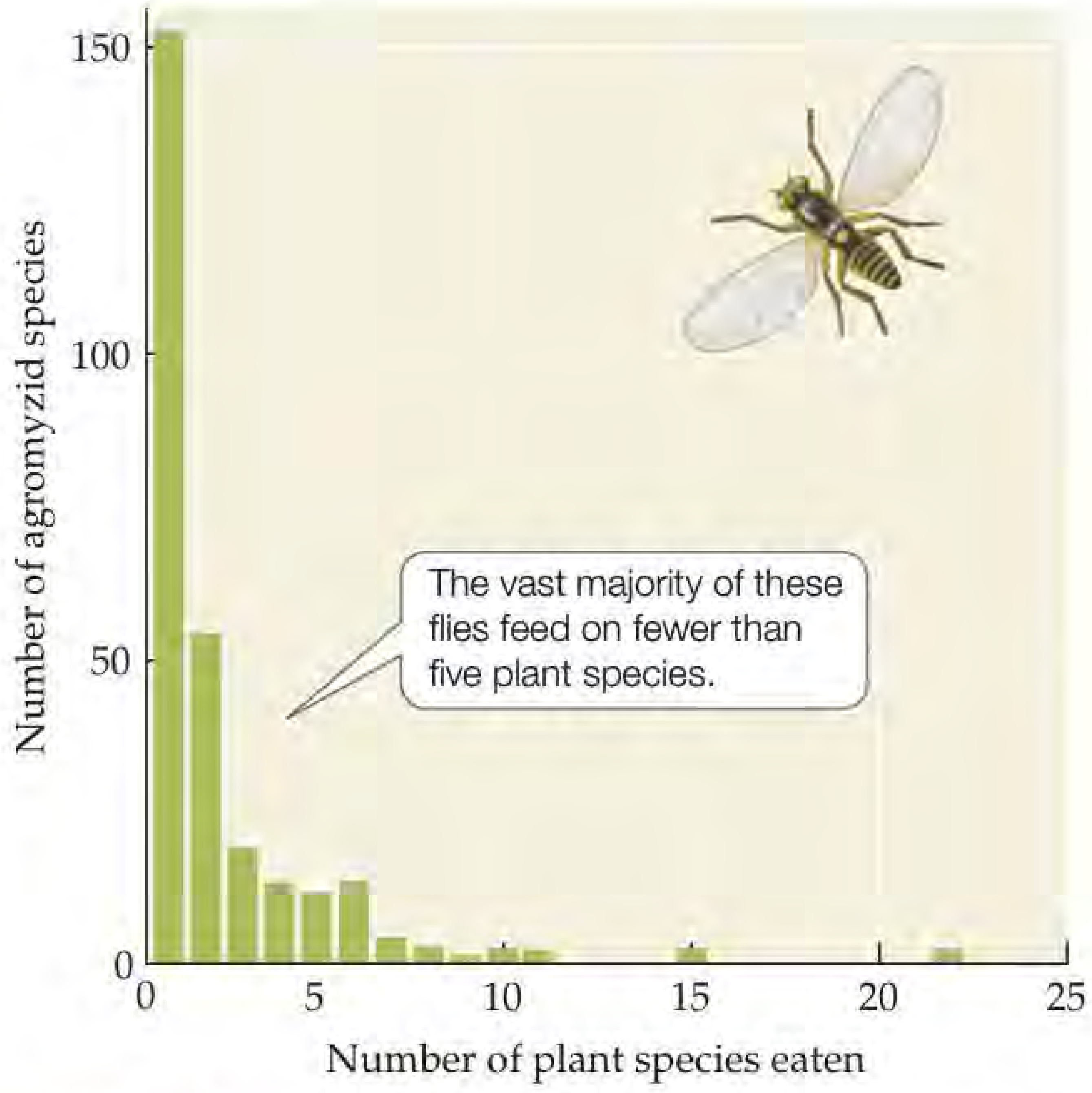


Figure 12.7 Most Agromyzid Flies Have Narrow Diets The larvae of agromyzid flies are leaf miners that live inside leaves and feed on leaf tissue. (After Spencer 1972.)

? Using the data in the graph, make a rough estimate of the percentage of agromyzid fly species that feed on fewer than five host plant species.

Now that we have considered diet preferences, we'll next focus on adaptations of predators and prey to either obtain food or avoid being eaten.

CONCEPT 12.2
Predation results in a wide range of capture and avoidance mechanisms.

Mechanisms Important to Predation

Among the other challenges they face, all animals must obtain food while striving to avoid being eaten themselves. As we have seen in Concepts 5.4 and 8.2, this ongoing drama has resulted in the evolution of a dazzling array of morphological and behavioral mechanisms in both predator and prey. Let's consider some of them here.

Some carnivores move in search of prey, while others sit and wait

Many carnivores forage throughout their habitat, moving about in search of prey. Examples of species that hunt in this way include wolves, sharks, and hawks. Other carnivores remain in one place and attack prey that move within striking distance (as do moray eels and some snakes, such as mambas and vipers) or enter a trap (such as a spider's web or the modified leaf of a carnivorous plant).

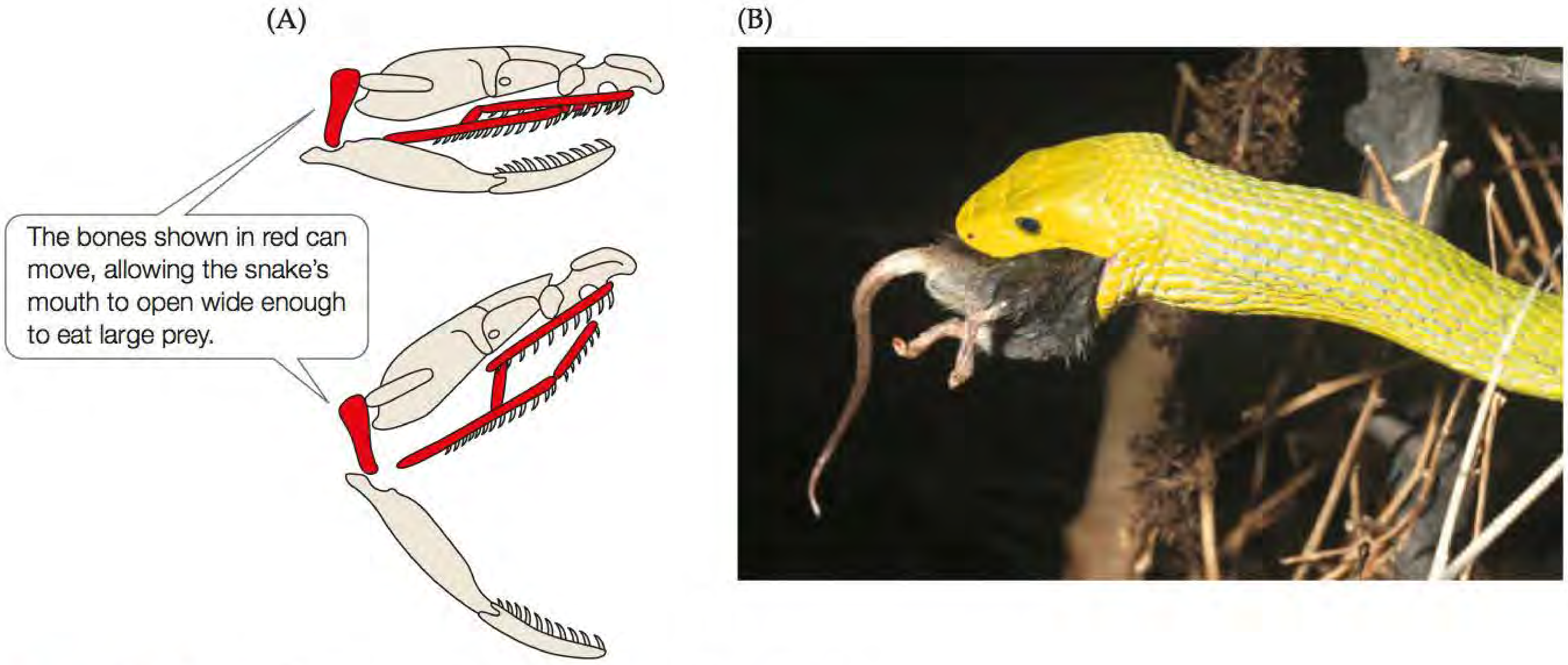


Figure 12.8 How Snakes Swallow Prey Larger Than Their Heads (A) Snakes have movable skull bones that allow them to swallow surprisingly large prey. (B) This eastern green mamba snake (*Dendroaspis angusticeps*) is swallowing a mouse larger than its head.

Many carnivores have unusual physical features that help them capture prey. The body form of the cheetah, for example, enables great bursts of speed that allow it to catch gazelles and other rapidly fleeing prey. In another example, most snakes can swallow prey that are considerably larger than their heads (**Figure 12.8**). Unlike those of other terrestrial vertebrates, the bones of a snake's skull are not rigidly attached to one another. This unique feature allows the snake to open its jaws to a seemingly impossible extent. Curved teeth mounted on bones that can move inward then help to pull prey items down the throat. A person with similar adaptations would be able to swallow a watermelon whole.

While some carnivores depend primarily on their physical structure, others subdue prey with poison (e.g., venomous spiders). Still others use mimicry: ambush bugs, scorpionfishes, and many other predators blend into their environment so well that prey may be unaware of their presence until it is too late. Some predators have inducible traits that improve their ability to feed on specific prey species. The predatory ciliate protist *Lembadion bullinum* has such an inducible offense: individuals gradually adjust their size to match the size of the available prey. Thus, if a ciliate is small but the available prey in its environment are large, the ciliate increases in size. Similarly, if a ciliate is large but available prey are small, the ciliate decreases in size. Finally, some predators can detoxify or tolerate prey chemical defenses, as the following example shows.

The garter snake (*Thamnophis sirtalis*) is the only predator known to eat the toxic rough-skinned newt (*Taricha granulosa*). In some of its populations, the skin of this newt contains large amounts of tetrodotoxin (TTX), an extremely potent neurotoxin. TTX binds to sodium channels in nerve and muscle tissue, thus preventing nerve signal transmission and causing paralysis and death. A single newt can contain enough TTX to kill 25,000 mice—far more than enough to kill a person, as was tragically demonstrated in 1979 when a 29-year-old man died after eating a rough-skinned newt on a dare.

The garter snakes in some populations, however, can eat rough-skinned newts because they can tolerate TTX. These snakes have TTX-resistant sodium channels (Geffeney et al. 2005). Although these garter snakes are protected from the lethal effects of TTX, those individuals that can tolerate the highest concentrations of TTX move more slowly than less resistant individuals—a trade-off between tolerance for the poison and speed of locomotion. In addition, once they swallow a poisonous newt, the snakes are immobilized for up to 7 hours. During that time, the snakes are vulnerable to predation themselves and may also suffer from heat stress.

Escaping carnivores: Physical defenses, toxins, mimicry, and behavior

Many prey species have physical features that reduce their chances of being killed by predators. Such physical defenses include large size (e.g., elephants), a body plan designed for rapid or agile movement (e.g., gazelles), and body armor (e.g., snails and armored mammals such as the pangolin in **Figure 12.9A**).

Other species use poisons to defend themselves against predators. Species that contain powerful toxins are often brightly colored (**Figure 12.9B**). Such **warning (aposematic) coloration** can itself provide protection from predators, which may instinctually avoid prey that are brightly colored or may learn from experience not to eat them.

Other prey species use **mimicry** as a defense: by resembling less palatable organisms or physical features of their environment, they cause potential predators to mistake

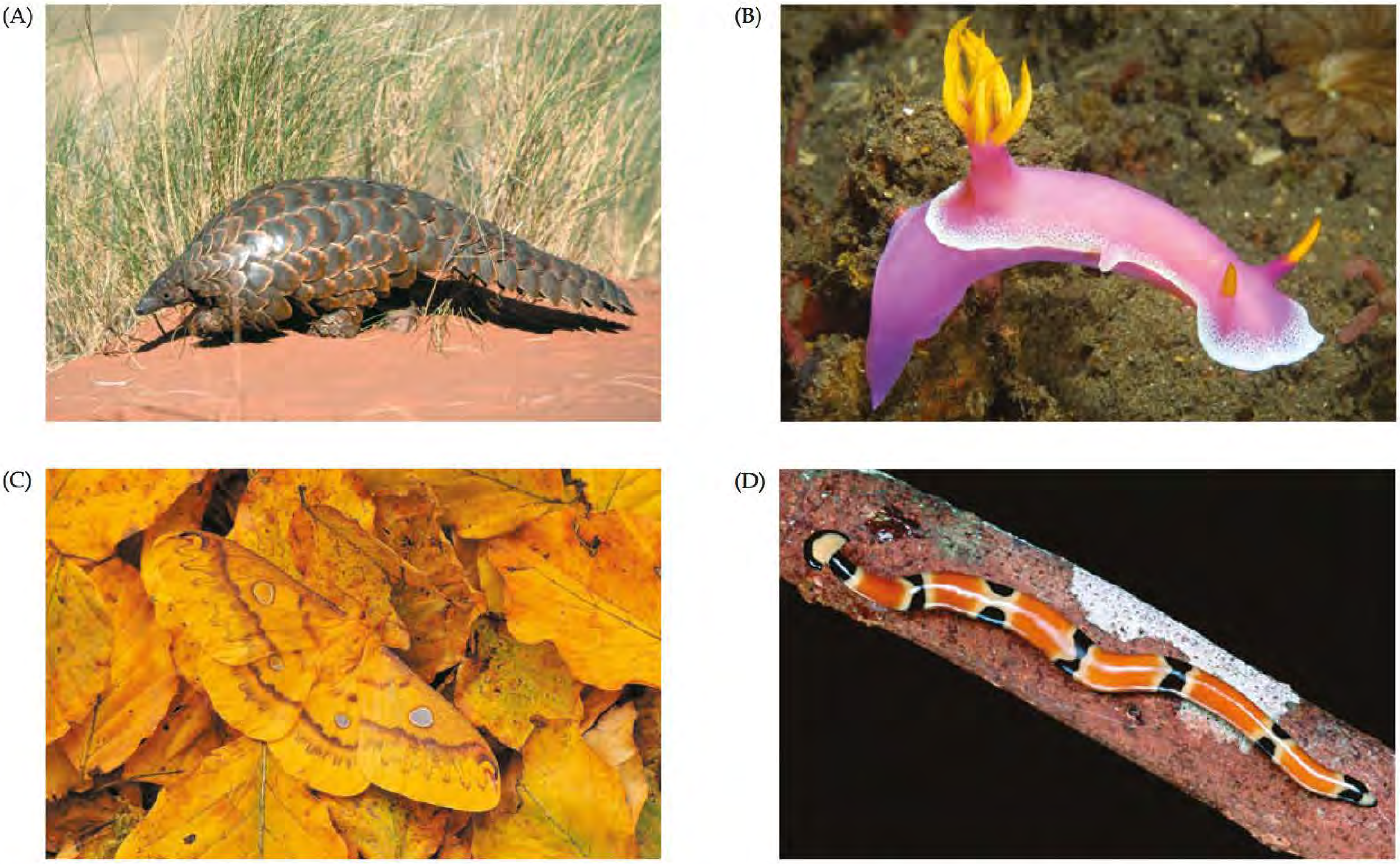


Figure 12.9 Adaptations to Escape Being Eaten Prey have evolved a wide range of mechanisms to escape from predators, including (A) physical features, such as the armor of the ground pangolin of South Africa (*Manis temmenickii*); (B) toxins, advertised by bright warning colors such as those of the nudibranch *Hypselodoris bullockii*; (C) crypsis, or camouflage, as in this female Saturniid Moth (*Rhodinia fugax*), which blends in with the leaf litter on the forest floor; and (D) mimicry, as in this terrestrial flatworm (*Bipalium everetti*) that resembles a snake.

them for something less desirable to eat. There are many forms of mimicry. Some species have a shape or coloration that provides camouflage, allowing them to avoid detection by predators (**Figure 12.9C**); this form of mimicry is called **crypsis** (from *cryptic*, "hidden"). Other prey species use mimicry as a form of "false advertising": their shape and coloration mimic those of a species that is fierce or that contains a potent toxin (**Figure 12.9D**). Finally, many prey species change their behavior when predators are present. When predators are abundant, snowshoe hares, like the elk described in Concept 8.2, forage less in open areas (where they are most vulnerable to attack). When threatened, musk oxen form a defensive circle, which makes them a difficult target (see Figure 8.19).

In some cases, there may be a trade-off between different types of defenses. For example, among four species of marine snails eaten by the green crab (*Carcinus maenas*), the species whose shells could be crushed most rapidly by crabs were the quickest to take refuge when crabs were detected, and vice versa (**Figure 12.10**). The exact negative correlation between resistance to crushing and predator avoidance behavior suggests that there may be a trade-off between a snail's physical and behavioral defenses.

Reciprocal plant–herbivore interactions

As we have learned, herbivores generally consume only parts of their food plant and usually do not kill them. Moreover, because most plants are not mobile and thus unable to escape herbivory in space, they employ defenses to reduce being eaten. Let's first consider plant responses to reduce herbivory and then ways that herbivores can respond.

REDUCING HERBIVORY: AVOIDANCE, TOLERANCE, AND DEFENSES Some plants avoid herbivory by producing great numbers of seeds in some years and few or no seeds in other years. For example, up to 100 years may pass between bouts of seed production, as in the mass flowering of bamboos in China. This phenomenon, known as *masting*, allows plants to hide (in time) from seed-eating herbivores, then overwhelm them by sheer numbers. Plants can also avoid herbivores in other ways, such as by producing leaves at times of the year when herbivores are scarce.

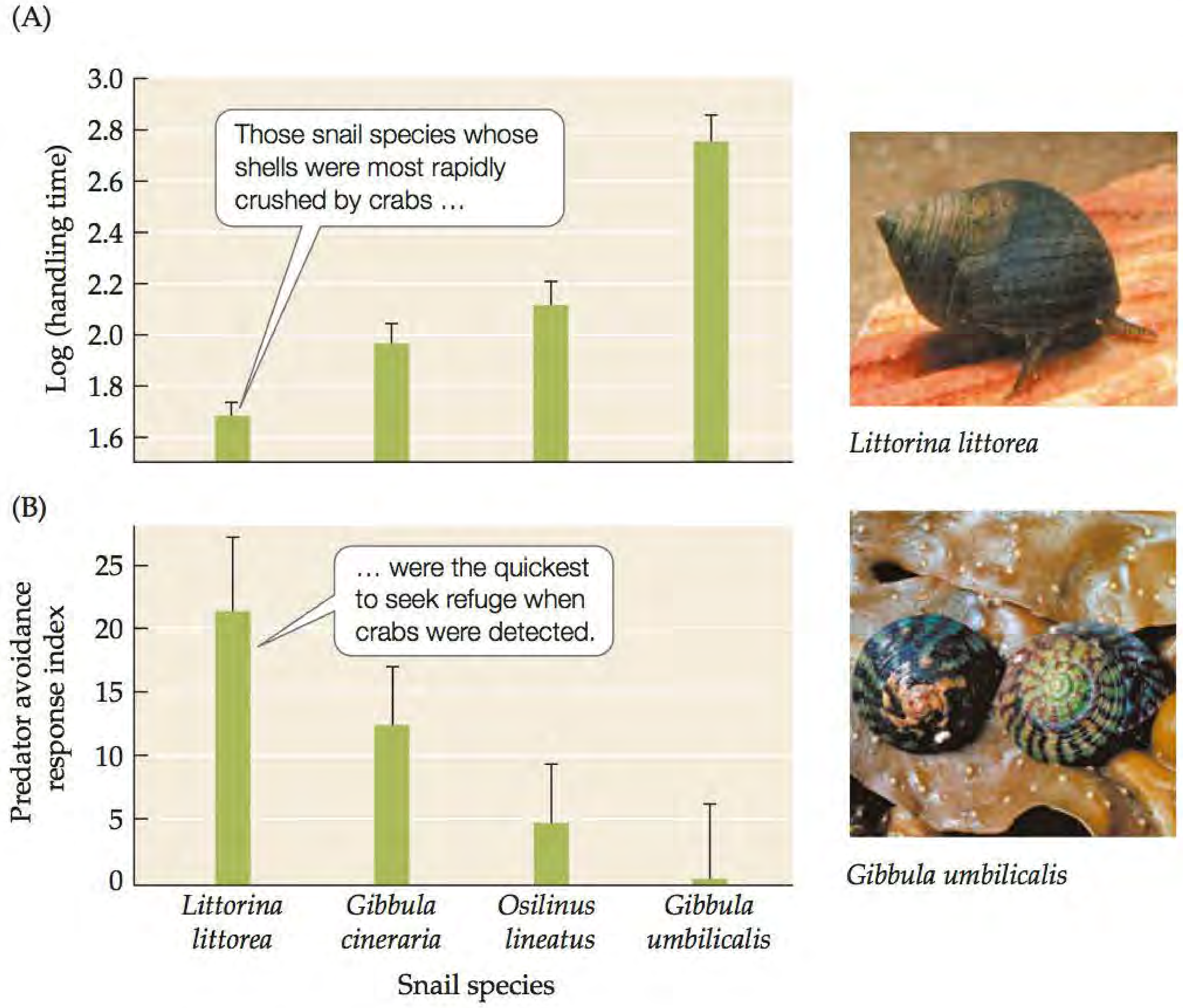
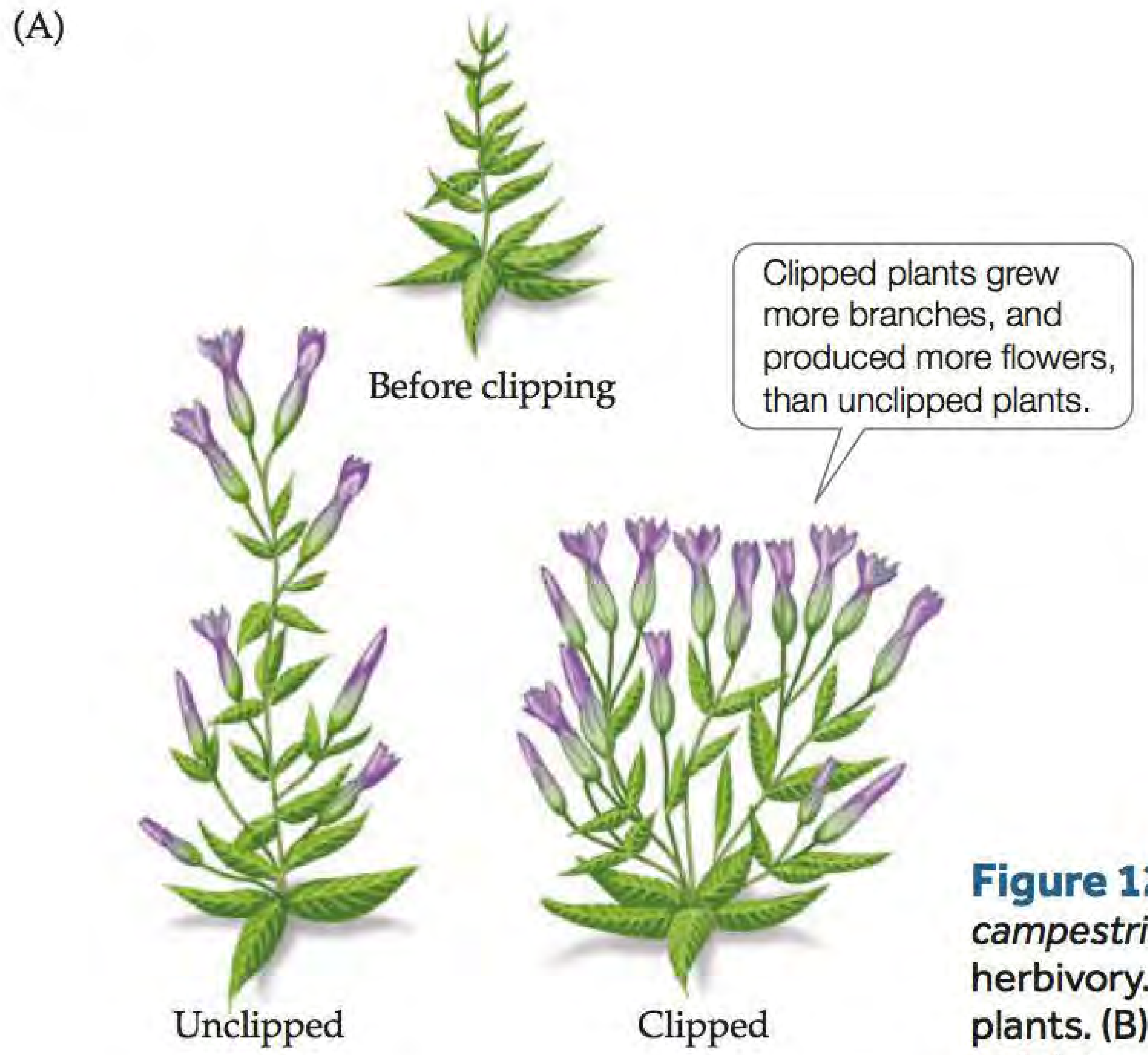


Figure 12.10 A Trade-Off in Snail Defenses against Crab Predation? (A) Handling time taken by green crabs (*Carcinus maenas*) to manipulate and crush the shells of each of four snail species. (B) Index of the strength of the predator avoidance response of each of four snail species; larger values indicate a more rapid behavioral response to crabs. Error bars show one SE of the mean. (After Cotton et al. 2004.)

Other plants have adaptive growth responses that allow them to compensate for, and hence tolerate, the effects of herbivory—at least up to a point. **Compensation** occurs when removal of plant tissues stimulates a plant to produce new tissues, allowing for relatively rapid replacement of the material eaten by herbivores. When *full compensation* occurs, herbivory causes no net loss of plant tissue. Compensation may occur when, for example, removal of leaf tissue decreases self-shading, resulting in increased plant growth, or when removal of apical buds (those at the end of a branch or shoot) allows lower buds to open and grow. Beech trees respond to simulated herbivory (clipping) by increasing both their leaf production and their photosynthetic rate. Similarly, moderate to high levels of herbivory may benefit field gentians (*Gentianella campestris*) under some circumstances (**Figure 12.11**). In this case, the timing of herbivory is critical: early in the growing season (up to July 20), the plant more than fully compensates for the lost tissue, but later in the season (July 28), it does not. If the amount of material removed from a field gentian—or any other plant—is



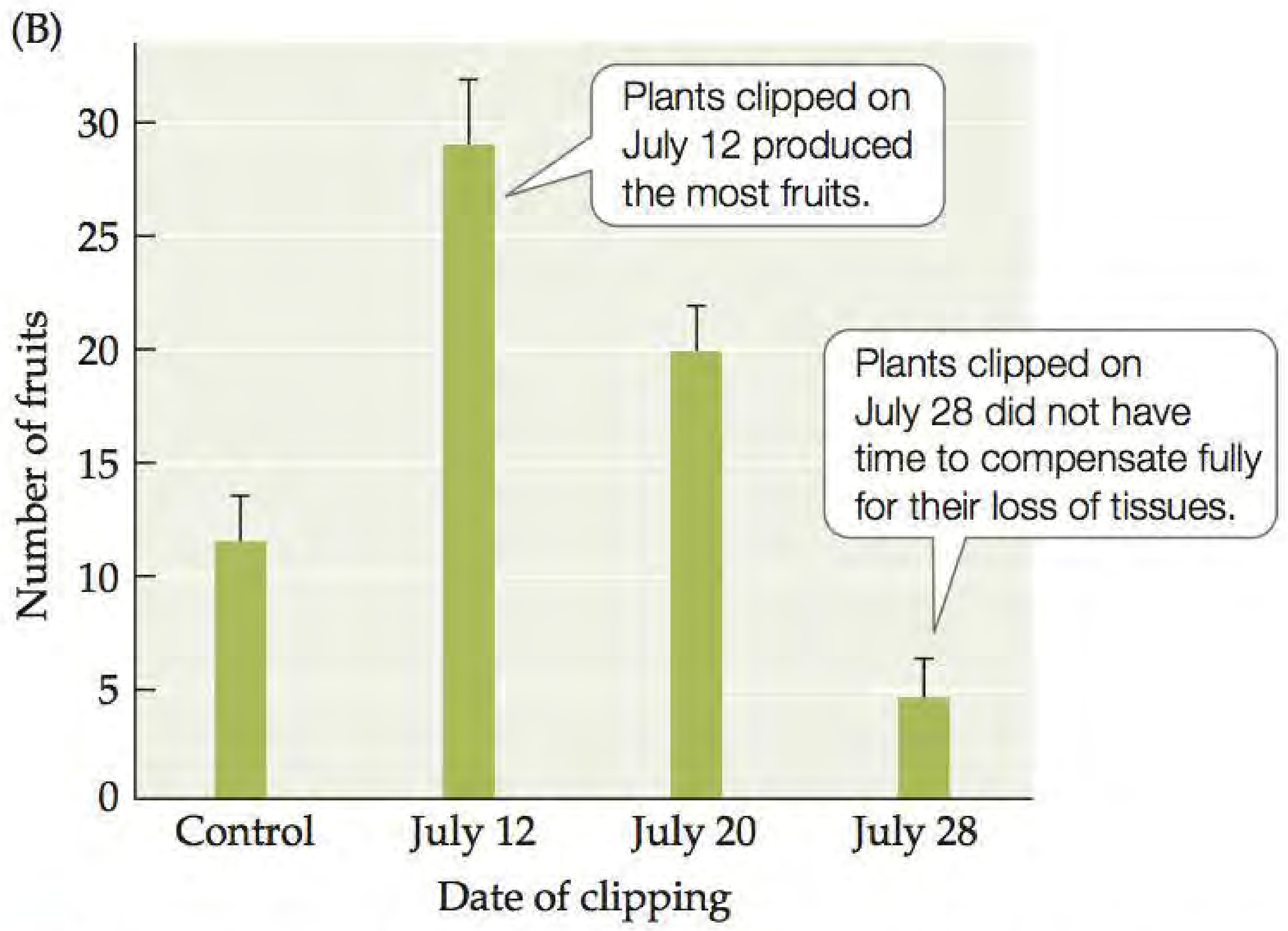


Figure 12.11 Compensating for Herbivory Field gentians (*Gentianella campestris*) were clipped at different times during the growing season to simulate herbivory. (A) The shape and production of flowers in unclipped (control) and clipped plants. (B) Numbers of fruits produced by control plants and plants clipped on different dates. Error bars show one SE of the mean. (After Lennartsson et al. 1998.)

? How many fruits would you expect to be produced by a field gentian that compensates fully for clipping? Explain your reasoning.

large enough, however, or if insufficient resources are available for growth, the plant cannot fully compensate for the damage.

Finally, plants use an enormous array of structural and chemical defenses to ward off herbivores (Pellmyr et al. 2002; Agrawal and Fishbein 2006). A stroll through many plant communities makes this readily apparent: the leaves of many plants are tough, and many plant bodies are covered with spines, thorns, sawlike edges, or pernicious (nearly invisible) hairs that can pierce the skin like miniature porcupine quills. In some cases, such structures are an **induced defense** (stimulated by herbivore attack), as illustrated by individual cacti that increase their production of spines only after they have been grazed (Myers and Bazely 1991).

Plants also produce a wide variety of chemicals, called **secondary compounds**, that function to reduce herbivory. Some secondary compounds are toxic, protecting the plant from all but the relatively small number of herbivore species that can tolerate them. Others serve as chemical cues that attract predators or parasitoids to the plant, where they attack herbivores (Schnee et al. 2006).

Some plant species, such as oak trees, produce secondary compounds constantly, regardless of whether herbivores have attacked the plant. In other species, the production of secondary compounds is an induced defense. For example, when attacked by herbivores, a North American tobacco species, *Nicotiana attenuata*, produces two induced defenses: toxic secondary compounds that deter herbivores directly, and volatile compounds that deter herbivores indirectly by attracting predators and parasitoids. Acting together, these defenses are very effective in reducing losses of tissue to herbivores. In one experiment, the application of compounds that are normally induced by herbivory to the stems of *N. attenuata* caused the numbers of a leaf-feeding herbivore on the plants to drop by more than 90% (Kessler and Baldwin 2001).

OVERCOMING PLANT DEFENSES: STRUCTURAL, CHEMICAL, AND BEHAVIORAL ADAPTATIONS The defenses used by plants prevent most herbivores from eating most plants. But for any given plant species, there are some herbivores that can cope with its defensive mechanisms. A plant covered with spines may be attacked by an herbivore that can avoid or tolerate those spines. Many herbivores have evolved digestive enzymes that enable them to disarm or tolerate plant chemical defenses. Such herbivores may gain a considerable advantage: they can eat plants that other herbivores cannot and thereby have access to an abundant food resource.

Some herbivores use behavioral responses to circumvent an otherwise effective plant defense. For example, some beetles use a behavioral response to cope with the defenses of tropical plants in the genus *Bursera*. These plants combine the production of toxic secondary compounds with a high-pressure delivery system: they store a toxic, sticky resin in a network of canals that runs through their leaves and stems (**Figure 12.12**). If an insect herbivore chews through one of these canals, the resin squirts from the plant under high pressure and may repel or even kill the insect (the resin hardens after it is exposed to air, so if an insect is drenched in resin, it can be entombed). Yet some tropical beetles in the genus *Blepharida* have evolved an effective counterdefense (Becerra 2003). Their larvae chew slowly through the leaf veins where the resin canals are located, releasing the pressure so gradually that the resin does not squirt from the plant. It often takes a beetle larva more than an hour to "disarm" a leaf in this manner; once that job is done, the larva eats the leaf in 10–20 minutes.

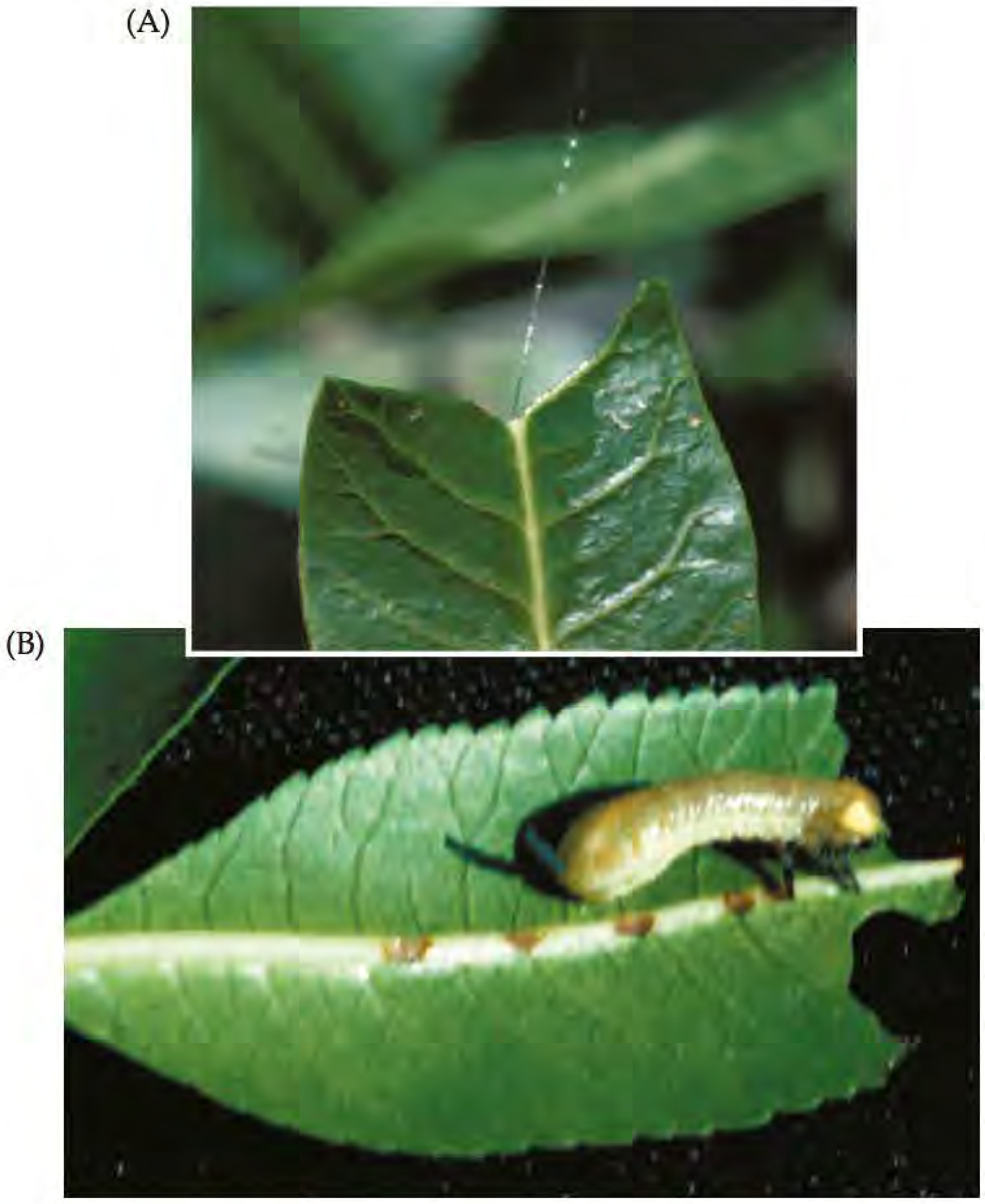


Figure 12.12 Plant Defense and Herbivore Counterdefense Some plants in the genus *Bursera* store toxic resin under high pressure in leaf canals. (A) When herbivores eat the leaves, they chew through these canals, causing the resin to be squirted up to 2 m from the leaf. (B) The larvae of some beetles in the genus *Blepharida* can disable this defense by chewing slowly through the canals, releasing the pressure in a gradual and harmless way.

Evolution can influence plant–herbivore interactions

The variety of antiherbivore defenses seen in plants suggests that herbivores represent a strong source of selection

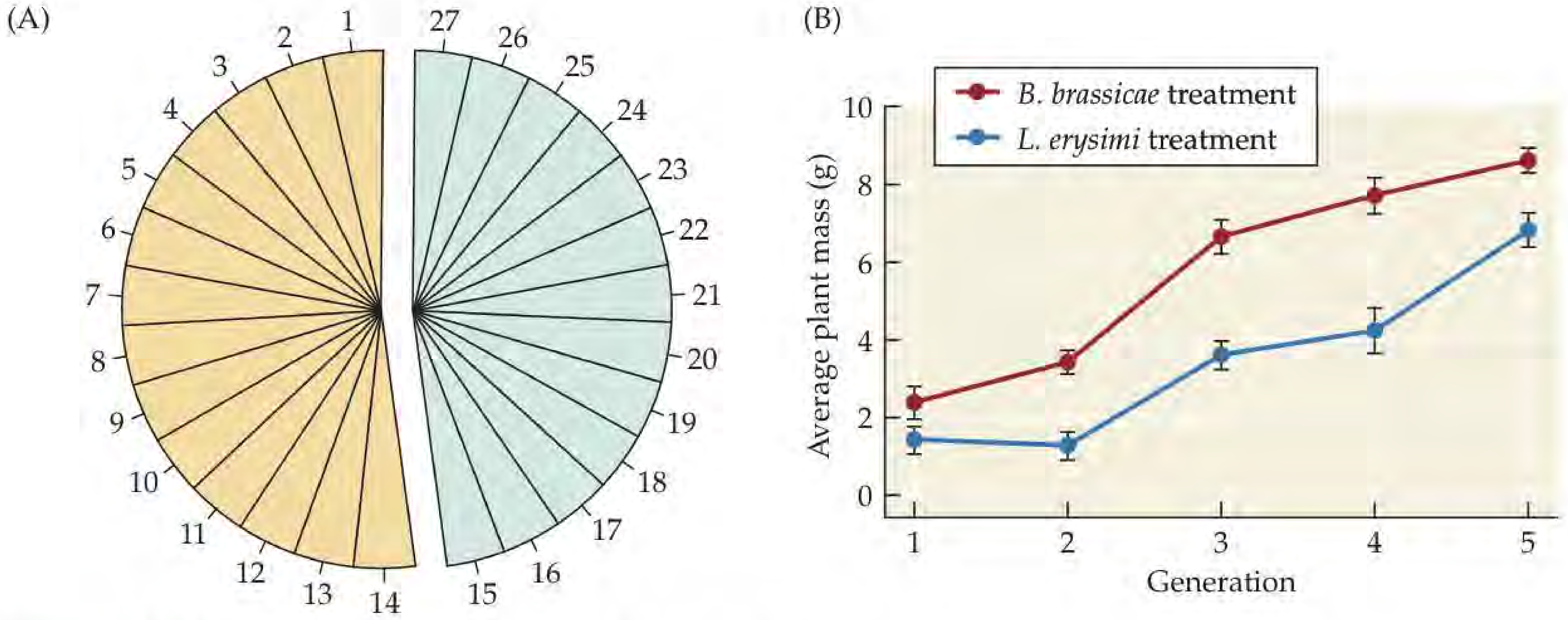


Figure 12.13 Does Herbivory Cause Evolution in Plant Populations? (A) This pie chart shows the equal proportions of 27 *Arabidopsis thaliana* genotypes used at the start of an experiment testing the hypothesis that herbivory by aphids caused evolution in experimental plant populations. Orange indicates plant genotypes that encode defensive compounds that have three-carbon side chains (3C defensive compounds), while green indicates plant genotypes that encode defensive compounds that have four-carbon side chains (4C defensive compounds). (B) The herbivory by aphids (two species were used, *Brevicoryne brassicae* and *Lipaphis erysimi*) caused the average mass of *A. thaliana* plants to increase from generation to generation, indicating an evolutionary response by plant populations. Error bars show ± one SE of the mean. (After Züst et al. 2012.)

on plant populations. Several recent studies have tested this claim. For example, in an experiment lasting five plant generations, Züst et al. (2012) tested the hypothesis that aphid herbivores cause evolution by natural selection in populations of the annual plant *Arabidopsis thaliana*, a small plant in the mustard family that is often used in laboratory experiments and genetic studies. They began their experiment with equal mixtures of 27 different *Arabidopsis* genotypes obtained from natural populations (**Figure 12.13A**). Typically, any one plant genotype expresses a subset of the full chemical arsenal of a species; collectively, however, the 27 genotypes used in this study were chosen to represent the full diversity of *Arabidopsis* chemical defenses.

Züst and colleagues found that feeding by aphids (two species were used, *Brevicoryne brassicae* and *Lipaphis erysimi*) reduced average plant size by up to 82% compared with a no-aphid (control) treatment, indicating that herbivory has a cost. However, they also found that the average sizes of plants exposed to the two species of aphids rose steadily over the course of the experiment (**Figure 12.13B**), suggesting that rapid evolution may have occurred in these populations. These increases in average plant size were associated with considerable changes in the genotypic composition of the plant populations. For example, ten plant genotypes were lost completely, and different aphid species selected for different plant genotypes. You can explore the extent to which different aphid species caused different plant genotypes to be favored by natural selection in **Analyzing Data 12.1**. Overall, Züst et al.'s results provide clear experimental evidence that herbivores can cause evolution by natural selection in plant populations.

CONCEPT 12.3

Predator populations can cycle with their prey populations.

Predator–Prey Population Cycles

We introduced population cycles in Chapter 11 (see Figure 11.9), and in the Case Study at the opening of this chapter, we described the most famous one of all: the hare–lynx cycle. Cyclic fluctuations in abundance are one of the most intriguing patterns in nature. After all, what could cause populations to change so considerably in size over time, yet in such a regular manner? We will return to the mechanisms that underlie the hare–lynx cycle in the Case Study Revisited, but first we'll describe some insights into the causes of population cycles that have come from models, experiments, and field observations of predator–prey interactions.

Predator–prey cycles can be modeled mathematically

One way to evaluate possible causes of population cycles is to investigate the issue mathematically. In the 1920s, Alfred Lotka and Vito Volterra independently represented the dynamics of predator–prey interactions with what is now called the **Lotka–Volterra predator–prey model**:

$$\frac{dN}{dt} = rN - aNP$$

$$\frac{dP}{dt} = baNP - mP \qquad \textbf{(12.1)}$$

ANALYZING DATA 12.1 Do Different Herbivore Species Select for Different Plant Genotypes?

As a graduate student, Tobias Züst (Züst et al. 2012)* examined how herbivory by aphids affected evolution by natural selection in plant populations. Six replicate populations of the annual plant *Arabidopsis thaliana* were established for each of three experimental treatments: a control (no aphids), herbivory by the aphid *Brevicoryne brassicae*, and herbivory by the aphid *Lipaphis erysimi*. Each replicate population was initiated from 27 natural genotypes, and plants were grown at high densities (over 8,000 plants/m^2) in each of the three treatments.

At the start of the experiment, each replicate population contained equal proportions of the 27 plant genotypes (see Figure 12.13A). The experiment was conducted for five generations. At the end of the experiment, the frequencies of all surviving genotypes were determined.

The table shows the average plant genotype frequencies at the end of the selection experiment; in addition to the genotypes shown here, genotypes 12, 14, and 21 occurred at low frequencies (less than 1.5%) in one or two treatments. Other genotypes not shown in the table did not survive.

1. In total, how many plant populations were established in this experiment? In each of these populations, what was the initial frequency of each plant genotype?
2. Did evolution occur in the control populations? If so, what factor or factors may have caused evolution by natural selection in these populations? Explain your answers.
3. Did evolution occur in the populations exposed to aphid herbivores? If so, what factor or factors may have caused evolution by natural selection in these populations? Explain your answers.
4. Compare results for the *B. brassicae* treatment with those for the *L. erysimi* treatment, focusing on whether selection favored genotypes that code for 3C or 4C defensive compounds (see Figure 12.13A). To what extent do the plant genotypes favored by selection differ between these two treatments?

See the companion website for a similar ANALYZING DATA exercise.

	FREQUENCY (%) OF SURVIVING PLANT GENOTYPES													
TREATMENT	**1**	**2**	**3**	**4**	**5**	**6**	**8**	**9**	**10**	**15**	**16**	**22**	**25**	**27**
Control	0.7	4.9	0	2.8	0	42.3	2.8	8.5	6.3	0	1.4	1.4	26.1	0.7
B. brassicae	2.8	3.5	0	0.7	0.7	0	0	9.9	3.5	1.4	2.1	1.4	67.4	2.8
L. erysimi	0.7	0	5.6	0	9.7	0	0	63.2	4.2	9.7	0	0.7	6.3	0

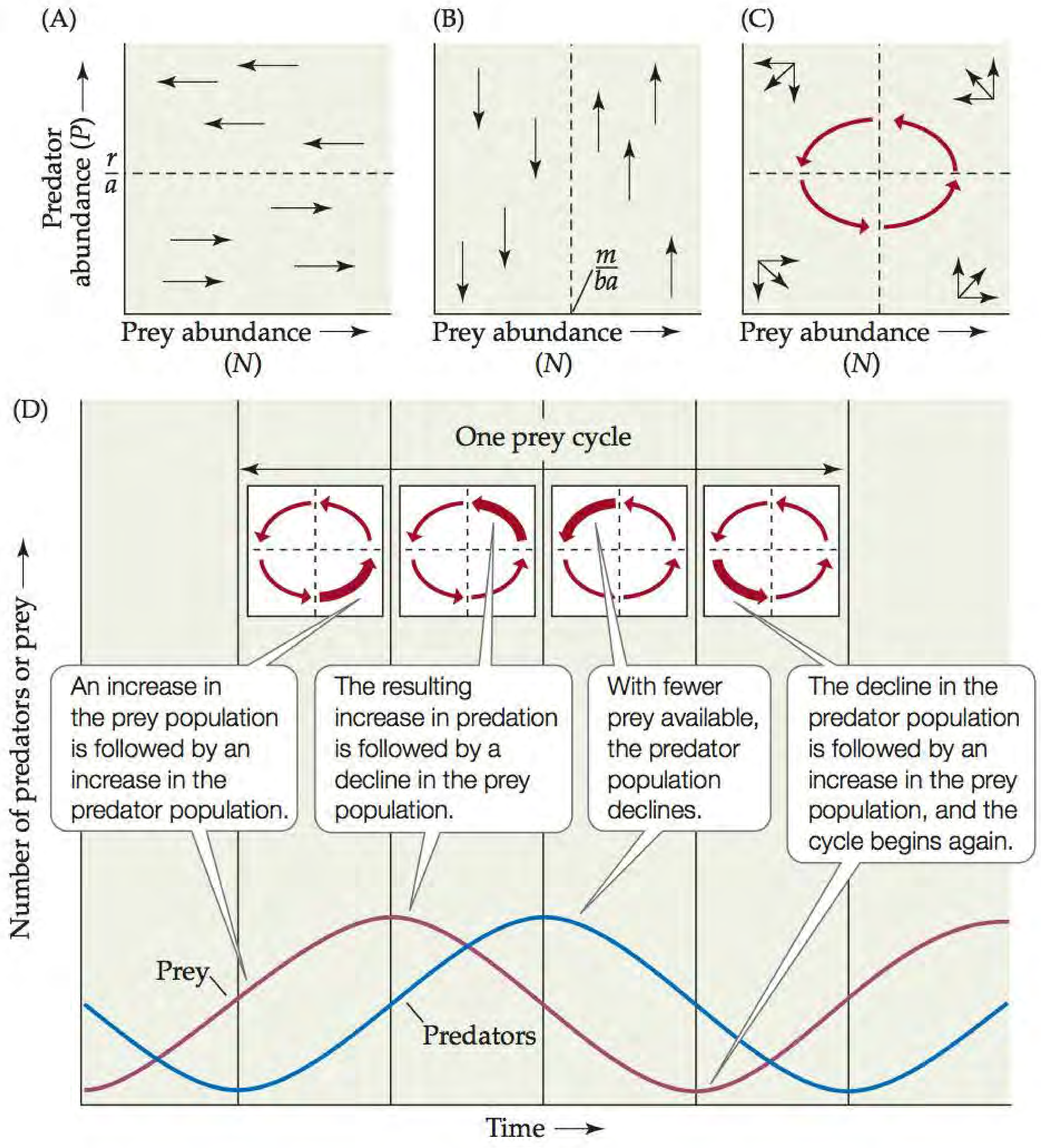
---

*Züst, T., C. Heichinger, U. Grossniklaus, R. Harrington, D. J. Kliebenstein and L. A. Turnbull. 2012. Natural enemies drive geographical variation in plant defenses. *Science* 338: 116–119.

In these equations, N represents the number of prey individuals and P represents the number of predator individuals. The equation for change in the prey population over time (dN/dt) assumes that when predators are absent ($P = 0$), the prey population grows exponentially (i.e., $dN/dt = rN$, where r is the exponential growth rate; see Concept 10.3). When predators are present ($P \neq 0$), the rate at which they kill prey depends in part on how frequently predators and prey encounter one another. This frequency is expected to increase with the number of prey (N) and with the number of predators (P), so a multiplicative term (NP) is used in the equation for dN/dt. The rate at which predators kill prey also depends on the efficiency with which predators capture prey; this capture efficiency is represented by the constant a, so the overall rate at which predators remove individuals from the prey population is aNP.

Predators starve when there are no prey. Thus, the equation for change in the predator population over time (dP/dt) assumes that in the absence of prey ($N = 0$), the number of predators decreases exponentially with a mortality rate of m (i.e., $dP/dt = -mP$). When prey are present ($N \neq 0$), individuals are added to the predator population according to the number of prey that are killed (aNP) and the efficiency with which prey are converted into predator offspring (represented by the constant b). Thus, the rate at which individuals are added to the predator population is $baNP$.

We can determine the relationship between prey and predator populations by solving for the population growth equation of each species (Equation 12.1) when they stop changing in size (or reach an equilibrium). This approach involves determining the zero population growth isocline for both prey and predator. The zero population growth isocline (or simply **isocline**) is the condition in which the population size of the prey (or the predator) does not change in size for a given number of predators (or prey). For prey, their abundance does not change when $dN/dt = 0$, which occurs when $P = r/a$. Similarly, the abundance of predators does not change when $dP/dt = 0$, which occurs when $N = m/ba$.



An increase in the prey population is followed by an increase in the predator population.

The resulting increase in predation is followed by a decline in the prey population.

With fewer prey available, the predator population declines.

The decline in the predator population is followed by an increase in the prey population, and the cycle begins again.

Figure 12.14 The Lotka–Volterra Predator–Prey Model Produces Population Cycles (A) Considering the prey population first, the abundance of prey does not change when $dN/dt = 0$, which occurs when $P = r/a$ (see Equation 12.1). (B) Similarly, considering the predator population, the abundance of predators does not change when $dP/dt = 0$, which occurs when $N = m/ba$. Combining the results in parts (A) and (B) shows that the combined abundances of predator and prey populations (represented by the red vectors) have an inherent tendency to cycle (C). These cycles are shown here in two ways: (C) by plotting the abundances of predators and prey populations together, and (D) by plotting the abundance of both predators and prey versus time; the four inset diagrams in (D) show the combined effect of prey and predator abundance. In (D), note that the predator abundance curve is shifted one-fourth of a cycle behind the prey abundance curve.

Once we determine r/a and m/ba, we can then plot the isocline for both the prey (x axis) and predators (y axis) in graphical form. For the prey, the isocline will be a horizontal line originating at the value $P = r/a$ (**Figure 12.14A**). This line represents the number of predators needed to keep the prey population from changing (or at equilibrium). If the predator abundance is below the line, the prey population will increase in size. If the predator abundance is above this line, then the prey population will decrease in size. Similarly, for the predator, the isocline will be a vertical line originating at the value $N = m/ba$ (**Figure 12.14B**). This line represents the number of prey needed to maintain the predator population at zero growth. If the prey abundance is to the left of the line, the predator population will decrease in size. If the prey abundance is to the right of the line, then the predator population will increase in size.

Combining the isoclines in Figure 12.14A,B shows that the isoclines cross at 90° angles and divide the graph into four regions (**Figure 12.14C**). We can then follow the population growth of both predator and prey in each of these regions and find that both cycle over time, with the predators lagging behind the prey by one-fourth of a cycle (**Figure 12.14D**). Starting in the lower right corner, both prey and predator populations are growing but the increasing numbers of predators cause the prey abundance to level off and eventually reach zero population growth at its isocline. As the populations move into the upper right corner, predator abundance is still increasing but prey abundance is in decline. This causes the predator population to slow its growth and eventually reach its isocline. Now the prey population has declined to the point that the predator population cannot sustain itself and it declines as well (upper left corner). Finally, in the lower left corner, the prey population rebounds because of low predator numbers and begins to increase. This increase eventually leads to an increase in predators when the cycle starts all over again.

The Lotka–Volterra predator–prey model thus yields an important result: it suggests that predator and prey populations have an inherent tendency to cycle because the abundance of one population is dependent on the abundance of the other population. The only condition in which the two populations do not cycle is when the predator and prey isoclines intersect. Here, by definition, both populations do not change in size. But the model also has a curious and unrealistic property: the *amplitude* of the cycle (the magnitude by which predator and prey numbers rise and fall) depends on the initial numbers of predators and prey. If the initial numbers shift even slightly, the amplitude of the cycle will change (see **Web Extension 12.1** to find out what features of the model cause this change). More complex predator–prey models (e.g., Harrison 1995) still produce cycles but do not show this unrealistic dependence on initial population sizes. The same general conclusion emerges from all of these models, however: predator–prey interactions have the potential to cause population cycles.

Predator–prey cycles can be reproduced under laboratory conditions

Can the cycling behavior of predator–prey models be reproduced in the laboratory? Experiments show that such cycles can be difficult to achieve. When prey are easy for predators to find, predators typically drive prey to extinction, then go extinct themselves. Such was the case in C. B. Huffaker's experiments with the herbivorous six-spotted mite (*Eotetranychus sexmaculatus*) and the predatory mite, *Typhlodromus occidentalis*, that eats it (Huffaker 1958). In an initial set of experiments, Huffaker released 20 six-spotted mites on a tray with 40 positions, a few of which contained oranges, which these herbivorous mites could eat (**Figure 12.15A**). At first, the six-spotted mite population increased, in some cases reaching densities of 500 mites per orange. Eleven days after the start of the experiment, Huffaker released two predatory mites on the tray. Both prey and predator populations increased for a time, then declined to extinction (**Figure 12.15B**).

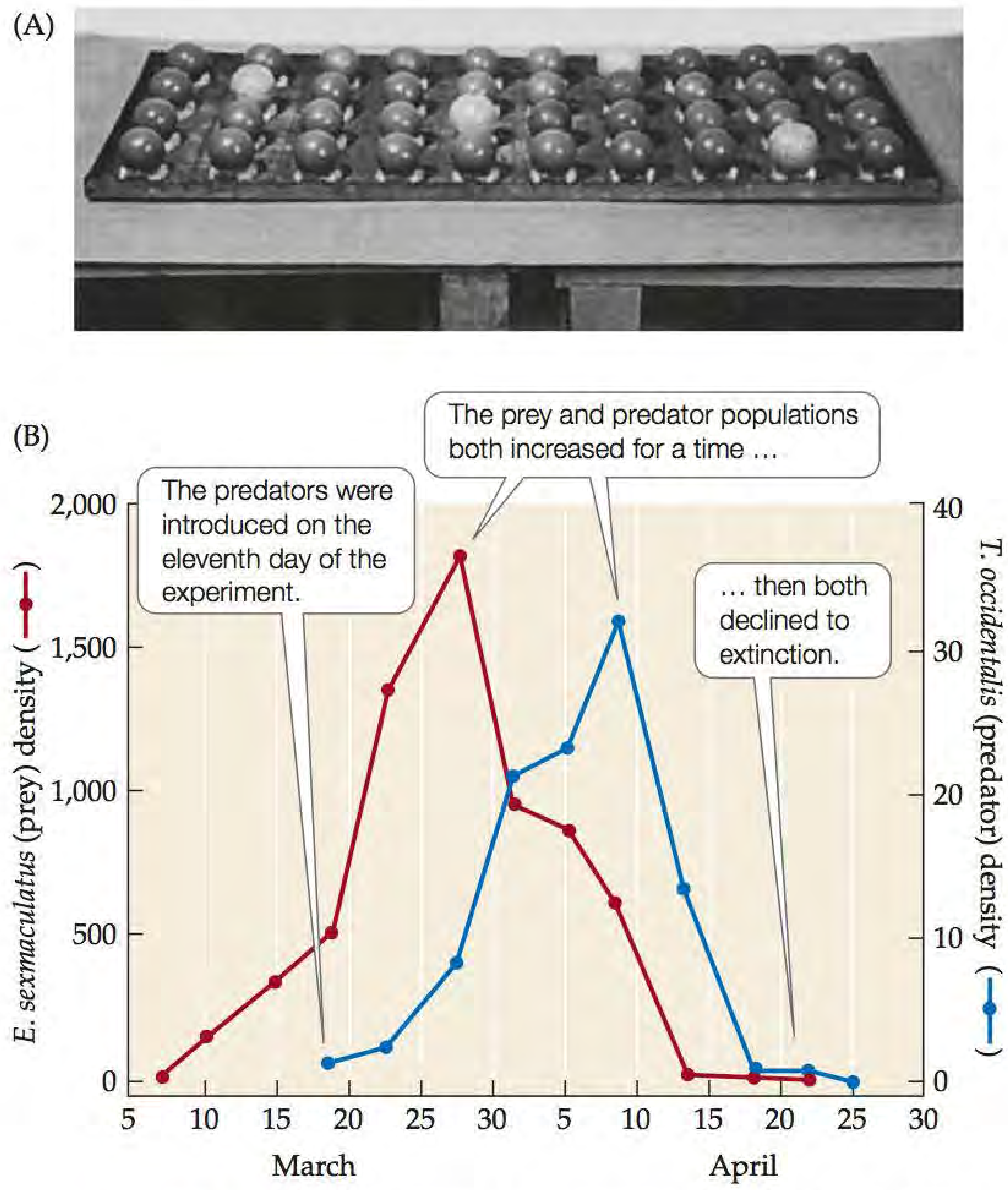


Figure 12.15 In a Simple Environment, Predators Drive Prey to Extinction (A) C. B. Huffaker constructed a simple laboratory environment to test for conditions under which predators and prey would coexist and produce population cycles. He placed oranges in a few positions in an experimental tray to provide food for the herbivorous six-spotted mite (*Eotetranychus sexmaculatus*); the remainder of the positions contained inedible rubber balls. (B) When a predatory mite (*Typhlodromus occidentalis*) was introduced into this simple environment, it drove the prey to extinction, causing its own population to go extinct as well. (After Huffaker 1958.)

Huffaker observed that the prey persisted longer if the oranges were widely spaced—presumably because it took the predators more time to find their prey. He tested this idea in a follow-up experiment in which he increased the complexity of the habitat in the following way: First, he added strips of Vaseline that partially blocked the predatory mites as they crawled from one orange to another. Then he placed small wooden posts in an upright position on some of the oranges; these posts allowed the six-spotted mites to take advantage of their ability to spin a silken thread and float on air currents over the Vaseline barriers. Thus, he altered the experimental environment to favor dispersal of the six-spotted mite and impede dispersal of the predatory mite. Under these conditions, the prey and the predators both persisted, illustrating a form of "hide-and-seek" dynamics that produced population cycles (**Figure 12.16).** The six-spotted mites dispersed to unoccupied oranges, where their numbers increased. Once the predators found an orange with six-spotted mites, they ate them all, causing both prey and predator numbers on that orange to plummet. In the meantime, however, some six-spotted mites dispersed to other portions of the experimental environment, where they increased in number until they too were discovered by the predators.

Predator–prey cycles can persist in the field

Natural populations of predators and prey can coexist and show dynamics similar to those of Huffaker's mites. Clumps of mussels off the coast of California, for example, can be driven to local extinction by predatory sea stars. However, mussel larvae float in ocean currents and hence disperse more rapidly than the sea stars. As a result, the mussels continually establish new clumps that flourish until they are discovered by sea stars. Thus, like the six-spotted mites in Huffaker's experiments, the mussels persist because portions of their population escape detection by predators for a time.

Field studies have also shown that predators influence population cycles in species such as southern pine beetles, voles, collared lemmings, snowshoe hares, and moose (Gilg et al. 2003; Turchin 2003). But predation is not the only factor that causes population cycles in these species. The supply of food plants for the herbivorous prey can also play an important role, and in some cases, social interactions are important as well. Thus, reality is not as simple as implied by the results of predator–prey models (in which cycles are maintained purely by predator–prey interactions). In the field, some population cycles may be caused by three-way feeding relationships—by the effects of predators and prey on each other, coupled with the effects of prey and their food plants on each other.

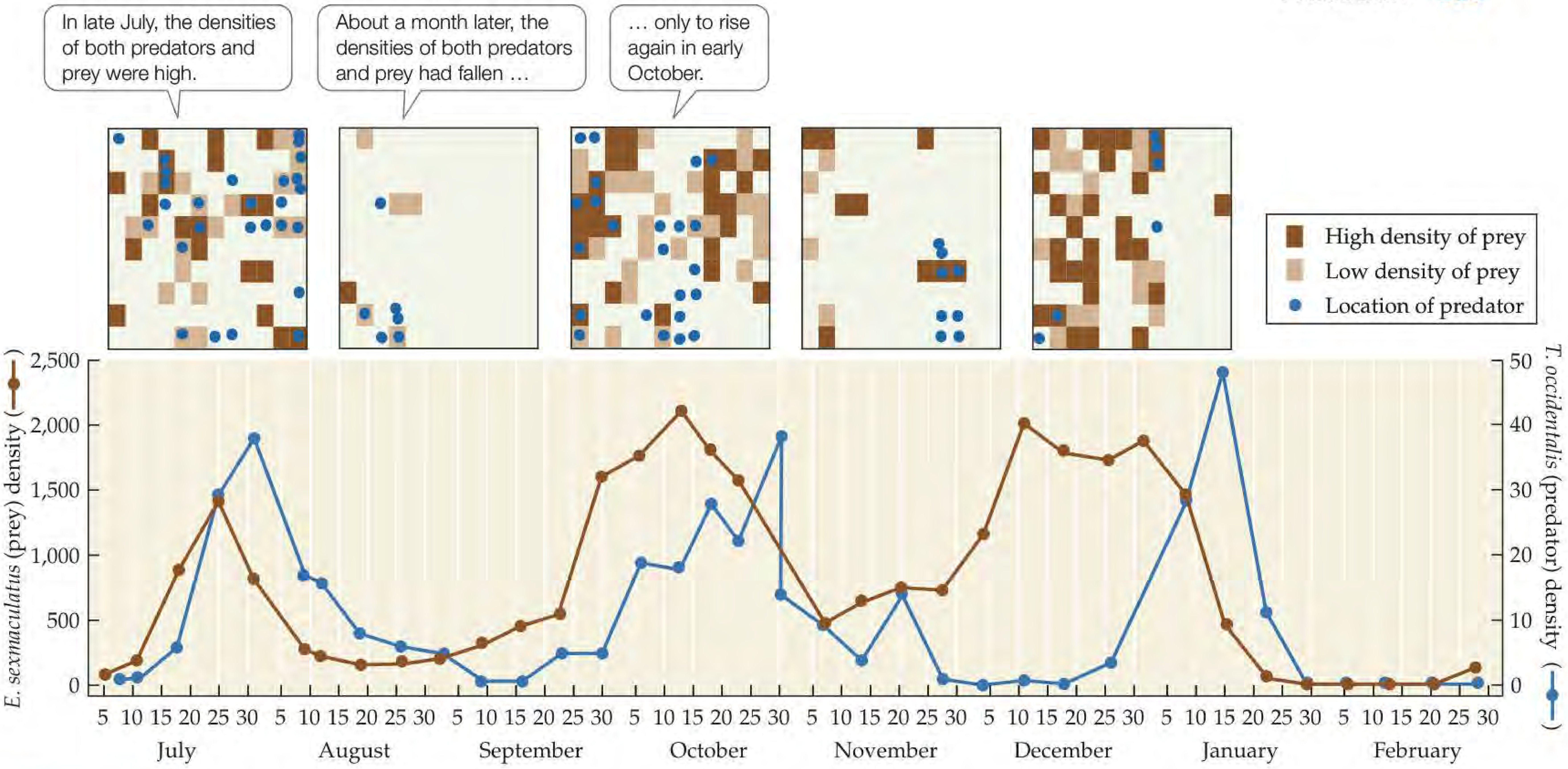


Figure 12.16 Predator–Prey Cycles in a Complex Environment Huffaker modified the simple laboratory environment shown in Figure 12.15 to create a more complex environment that aided the dispersal of the prey species but hindered the dispersal of the predator. Under these conditions, predator and prey populations coexisted, and their abundances cycled over time. The top panels show the locations within the environment of prey (shaded regions) and predators (circles) at five different points in time. (After Huffaker 1958.)

Whether their populations cycle or not, a variety of factors can prevent predators from driving prey to extinction. Such factors include habitat complexity and limited predator dispersal (as in Huffaker's mites), prey switching in predators (see Figure 12.6), spatial refuges (i.e., areas in which predators cannot hunt effectively), and, as we will see next, evolutionary changes in the prey population.

Evolution can influence predator–prey cycles

In laboratory studies of an algal prey species and its predator, a rotifer, Nelson Hairston Jr. and colleagues obtained a puzzling result: they observed predator–prey cycles, but the predator populations tended to peak when the prey populations reached their lowest levels, and vice versa (**Figure 12.17**). The researchers knew that predator–prey interactions alone could not produce such a pattern (see Figure 12.14D). They suggested four mechanisms that might do so: (1) rotifer egg viability might increase with prey density; (2) algal nutritional quality might increase

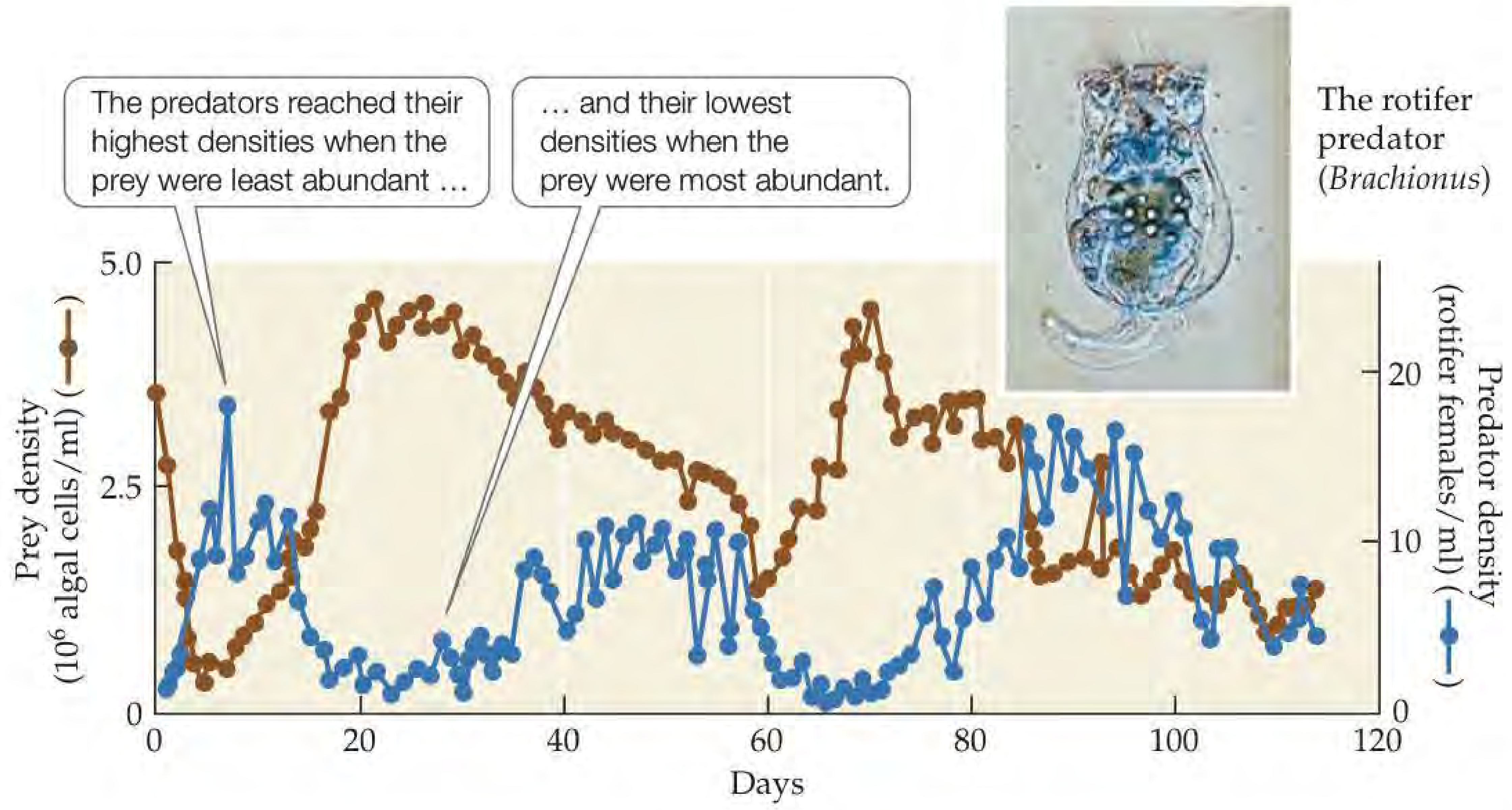


Figure 12.17 Evolution Causes Unusual Population Cycles In laboratory experiments, the abundances of a rotifer predator (*Brachionus calyciflorus*) and its algal prey (*Chlorella vulgaris*) fluctuated over time, but their population cycles differed from the typical predator–prey cycle (see Figure 12.14D). Results from further experiments indicated that these unusual population cycles were driven by evolutionary changes in the prey population. (After Yoshida et al. 2003.)

with nitrogen concentrations; (3) accumulation of toxins might alter algal physiology; and (4) the algae might evolve in response to predation.

Hairston and colleagues tested these four hypotheses in two ways. First, they compared their data with results from four mathematical models (one for each mechanism). Only the model that included evolution in the prey population provided a good match to their data. Second, they performed an experiment in which they manipulated the ability of the prey population to evolve; the idea was to see whether the puzzling results of Figure 12.17 would be duplicated only when the prey population could evolve freely. That is exactly what happened (Yoshida et al. 2003). In treatments in which prey evolution was restricted (because only a single algal genotype was used), they observed typical predator–prey cycles; that is, predator abundance peaked shortly after prey abundance peaked (as in Figure 12.14D). In contrast, when the prey population could evolve freely (because multiple genotypes were used), they observed cycles similar to those in Figure 12.17: predators were most abundant when prey were scarce.

Yoshida et al. (2003) also found that the algal genotypes that were most resistant to predators were poor competitors. The puzzling results shown in Figure 12.17 are hypothesized to be a consequence of the following: When predator density is high, resistant algal genotypes have an advantage, and they increase in abundance. Eventually, the prey population consists mostly of resistant genotypes, and predator numbers drop and remain low, even though algae are abundant. Because there are now few predators, the nonresistant but competitively superior algal genotypes outcompete the resistant genotypes and increase in abundance. This increase in edible prey allows the predator population to increase, thus initiating another cycle. Yoshida et al.'s results suggest an important lesson: ongoing evolutionary changes can have a powerful effect on predator–prey interactions (an illustration of maxim 5 in Table 1.1: "Evolution matters").

In this section, we have seen how predation can alter the population size of predator and prey, resulting in population cycles. We turn next to how predators can have major effects on ecological communities.

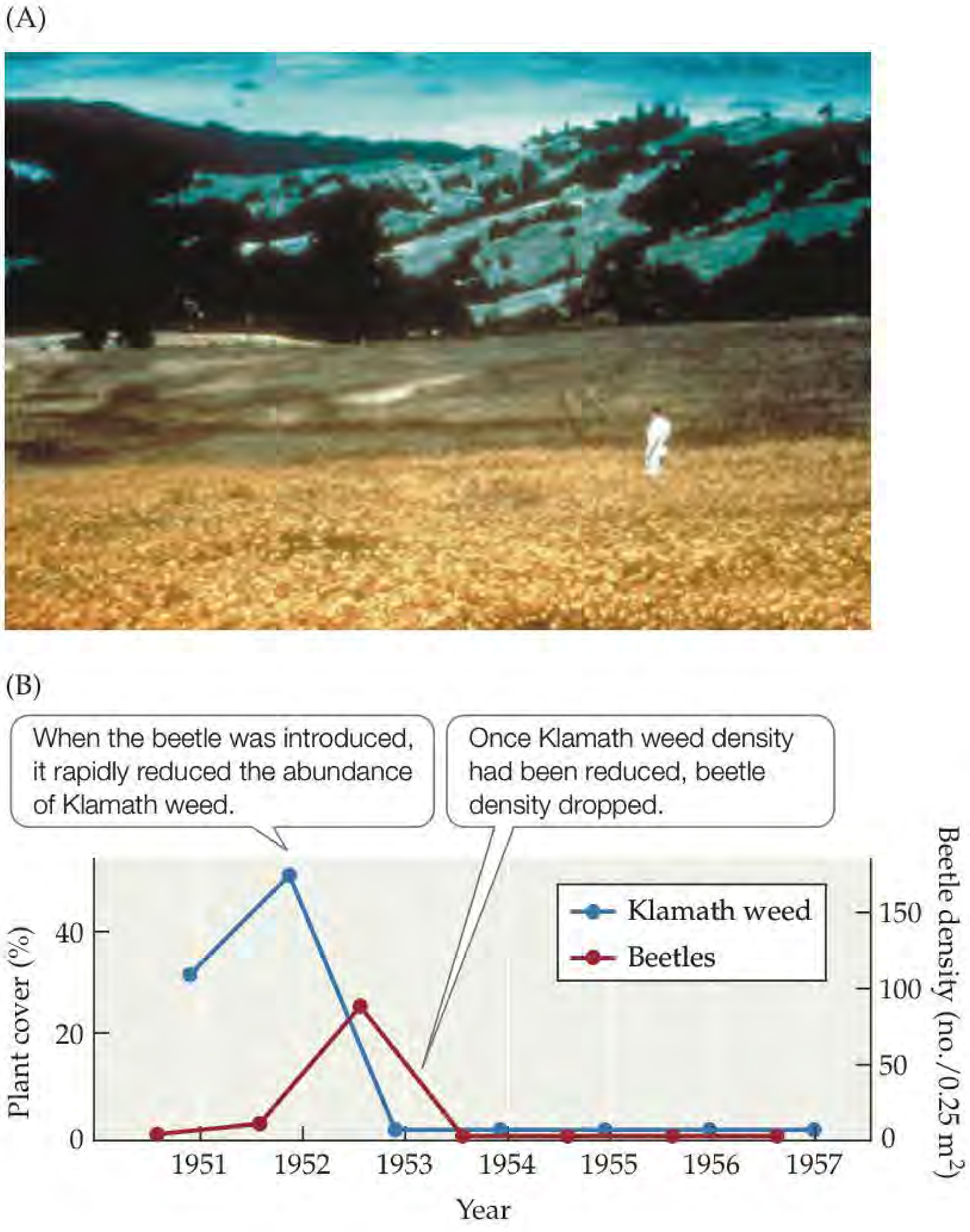
CONCEPT 12.4

Predation can affect prey distribution and abundance, in some cases causing a shift from one community type to another.

Effects of Predation on Communities

A general theme that runs through this book is that ecological interactions can affect the distributions and abundances of species, affecting communities and ecosystems. The community-level consequences of predation can be profound, in some cases causing major shifts in the types of organisms found at a given location.

All trophic interactions have the potential to reduce the growth, survival, or reproduction of the organisms that are eaten. These effects can be dramatic, as demonstrated in the case of a leaf-feeding beetle, *Chrysolina quadrigemina*, that rapidly reduced the density of Klamath weed, an invasive plant that is poisonous to livestock (**Figure 12.18**). Predators and parasitoids can also have dramatic effects when they are introduced as biological pest controls. In six cases, introductions of wasps that



When the beetle was introduced, it rapidly reduced the abundance of Klamath weed.

Once Klamath weed density had been reduced, beetle density dropped.

Figure 12.18 A Beetle Controls a Noxious Rangeland Weed Klamath weed (*Hypericum perforatum*), which poisons cattle, once covered about 4 million acres of rangeland in the western United States. (A) This photograph, taken in 1949, shows a field completely covered with flowering Klamath weed. (B) The leaf-feeding beetle *Chrysolina quadrigemina* was introduced in 1951 in the hope of controlling Klamath weed. This graph tracks densities of beetles and of Klamath weed (as a percentage of plant cover) in plots after the beetle's introduction. (After Huffaker and Kennett 1957.)

? Explain how a plant community might change after *C. quadrigemina* reduced the density of Klamath weed.

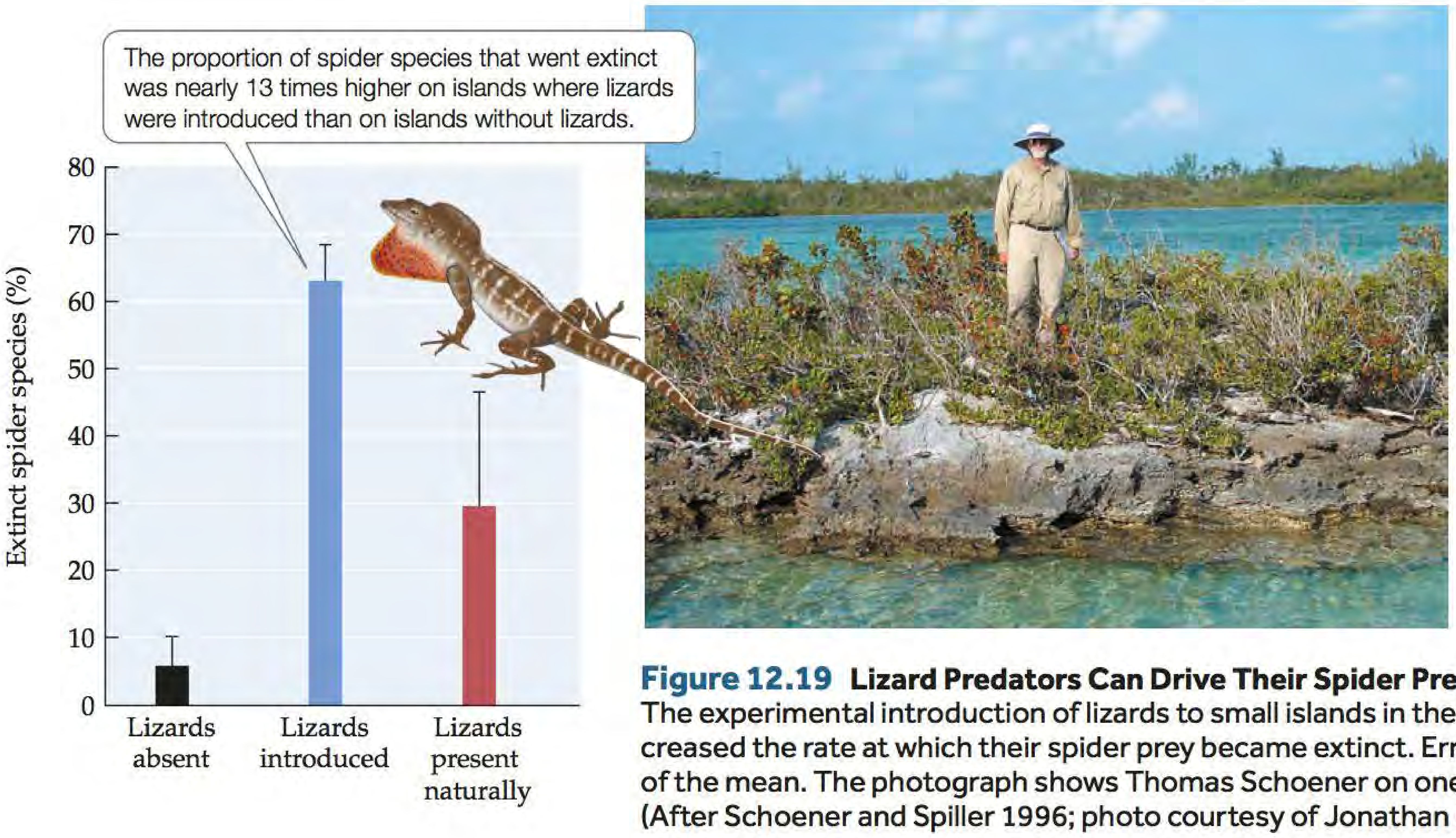


Figure 12.19 Lizard Predators Can Drive Their Spider Prey to Extinction The experimental introduction of lizards to small islands in the Bahamas greatly increased the rate at which their spider prey became extinct. Error bars show one SE of the mean. The photograph shows Thomas Schoener on one of the study islands. (After Schoener and Spiller 1996; photo courtesy of Jonathan Losos.)

preyed on crop-eating insects decreased the herbivores' densities by more than 95%, thus greatly reducing the economic damage caused by those pests.

As we've seen, predators and herbivores can change the outcome of competition (see Concept 14.4), thereby affecting the distributions or abundances of competitor species. In particular, inferior competitors may increase in abundance when they are in the presence of a predator that decreases the abundance or performance of a dominant competitor. Paine (1974) found such a result: he showed that the removal of a predatory sea star (*Pisaster*) led to the local extinction of all large invertebrates but one, a mussel. The mussel was a dominant competitor that, in the absence of the sea star, drove all the other large invertebrates to local extinction.

We turn now to examples of how trophic interactions can affect communities: first for carnivores and second for herbivores.

Carnivores can alter communities in dramatic ways

Anolis lizards are predators that eat a broad range of prey species, including spiders. Thomas Schoener and David Spiller studied the effects of lizard predators on their spider prey in the Bahamas. They selected 12 small islands and divided them into four groups of 3 islands each that were similar in size and vegetation. Initially, each group of 3 islands contained an island with lizards and 2 without. One of the latter 2 islands was then chosen at random to have two male and three female adult *Anolis sagrei* lizards introduced to it; the other island was left as a control where lizards were absent naturally.

The introduced lizards greatly reduced the distributions and abundances of their spider prey (Schoener and Spiller 1996). Before the experiment began, the numbers of spider species and the overall densities of spiders were similar among the 8 islands that lacked lizards. By the end of the experiment, however, the introduction of lizards to 4 islands had reduced the numbers and densities of spider species to the levels found on the 4 islands where lizards were present naturally. The proportion of spider species that went extinct was nearly 13 times higher on islands where lizards were introduced than on islands without lizards (**Figure 12.19**). Similarly, the density of spiders was about 6 times higher on islands without lizards than on islands that had lizards (either naturally or experimentally). The introduction of lizards reduced the densities of both common and rare spider species, and most of the rare species went extinct. Similar experimental results have been obtained for beetles eaten by rodents and grasshoppers eaten by birds.

Schoener and Spiller's work on the effects of predatory lizard on spiders shows that the direct effects of a predator can greatly reduce the number of prey species in a community. In other cases, a predator that suppresses a dominant competitor can (indirectly) cause the number of species in a community to increase (as in the sea star and mussel example). Indirect effects of predators can also alter ecological communities by affecting the transfer of nutrients from one ecosystem to another, as the following study on arctic foxes illustrates.

In the late nineteenth and early twentieth centuries, humans introduced arctic foxes (*Vulpes lagopus*) to some of the Aleutian islands off the coast of Alaska. Other islands remained fox-free, either because foxes were never introduced there or because the introductions failed. Taking advantage of this inadvertent large-scale experiment, Croll et al. (2005) determined that, on average, the introduction of foxes to an island reduced the density of breeding seabird populations nearly 100-fold. The decrease in seabird numbers, in turn, reduced the input of guano (bird feces) to an island from roughly 362 to 6 g per square meter. Seabird guano, which is rich in phosphorus and nitrogen, transfers nutrients from the ocean (where seabirds feed) to the land. By reducing the amount of guano that fertilized the (nutrient-limited) plant communities on the islands, the introduction of foxes caused dwarf shrubs and forbs to increase in abundance at the expense of grasses. As a result, the introduction of foxes had the unexpected effect of transforming the island communities from grasslands to communities characterized by small shrubs and forbs.

Herbivores can alter communities in dramatic ways

Herbivores can have equally large effects. Lesser snow geese (*Chen caerulescens caerulescens*) migrate from their overwintering grounds in the United States to breed in salt marshes that border Canada's Hudson Bay. During the summer, the geese graze on marsh grasses and sedges. Historically, although the geese removed considerable plant matter, their presence benefited the marshes by adding nitrogen, which is a limiting resource for plant growth. As they eat, the geese defecate every few minutes, thereby adding nitrogen to the soil (nitrogen moves into the soil from goose feces more rapidly than it does from the decomposing leaves of marsh plants). The plants absorb the added nitrogen, which allows them to grow rapidly after being grazed. Overall, low to intermediate levels of grazing by geese lead to increased plant growth (Jefferies et al. 2003). For example, net primary production (NPP, measured as the amount of new aboveground plant growth) was higher in lightly grazed plots than in ungrazed plots (**Figure 12.20A**).

About 40 years ago, however, the situation described in the previous paragraph started to change. Beginning around 1970, lesser snow goose densities increased exponentially. This increase probably occurred because increased crop production near their overwintering sites provided the geese with a superabundant supply of food. The ensuing high densities of geese no longer benefited marsh plants. The geese completely removed the vegetation, drastically changing the community of marsh plant species (**Figure 12.20B**). Of an original 54,800 hectares (135,400 acres) of intertidal marsh in the Hudson Bay region, geese are estimated to have destroyed 35% (19,200 ha or 47,400 acres). An additional 30% (16,400 ha or 40,500 acres) of the original marsh has been badly damaged by the geese. Controlled hunts (from 1999 on) have slowed goose population growth; this strategy may eventually lead to marsh recovery.

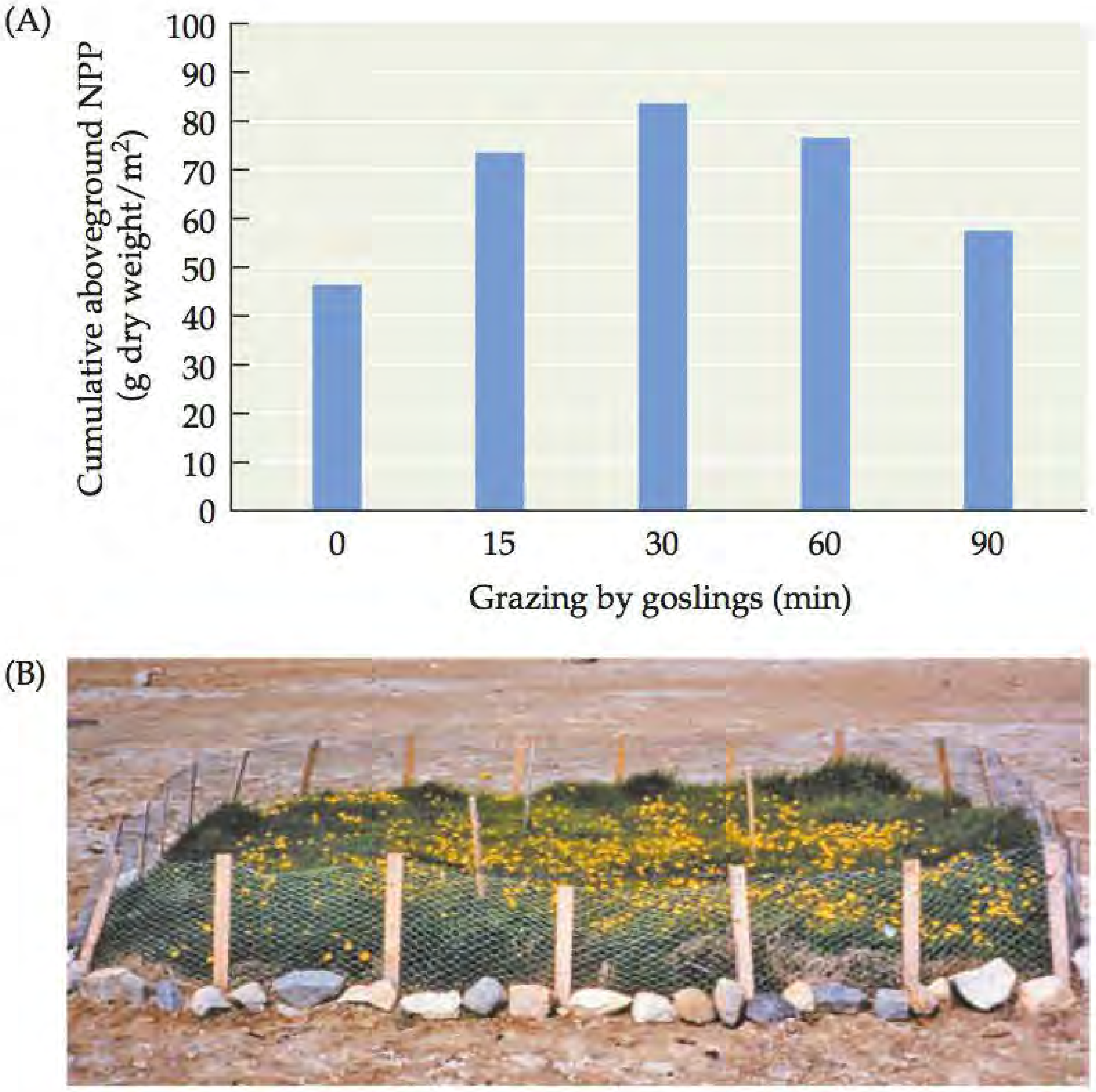


Figure 12.20 Snow Geese Can Benefit or Decimate Marshes (A) When lightly grazed (for a single 15- to 90-minute episode) by snow goose goslings, salt marsh plants increased their subsequent cumulative production of new biomass compared with no grazing, because of the nitrogen added by the defecating geese. (B) Heavy grazing by high densities of snow geese can convert salt marshes to mudflats, as seen by comparing this small remnant of marsh (protected from geese) with the surrounding mudflat (a former marsh that was grazed heavily by geese). (A after Hik and Jefferies 1990.)

In *The Origin of Species*, Darwin (1859) noted the speed with which Scotch fir trees replaced heaths after regions of heathland were enclosed to prevent grazing by cattle. When he observed heathlands grazed by cattle, "on looking closely between the stems of the heath, I found a multitude of seedlings and little trees, which had been perpetually browsed down by the cattle. In one square yard … I counted thirty-two little trees; and one of them, judging from the rings of growth, had during 26 years tried to raise its head above the stems of the heath, and had failed." Darwin concluded that seeds dispersed from trees located at the edge of the heath would germinate and overgrow the heath if not for grazing by cattle. Thus, the very existence of the heath community in that area depended on grazing.

Herbivores can also have pronounced effects in aquatic environments. The golden apple snail was introduced into Taiwan from South America in 1980 for local consumption and export. The snail escaped from cultivation

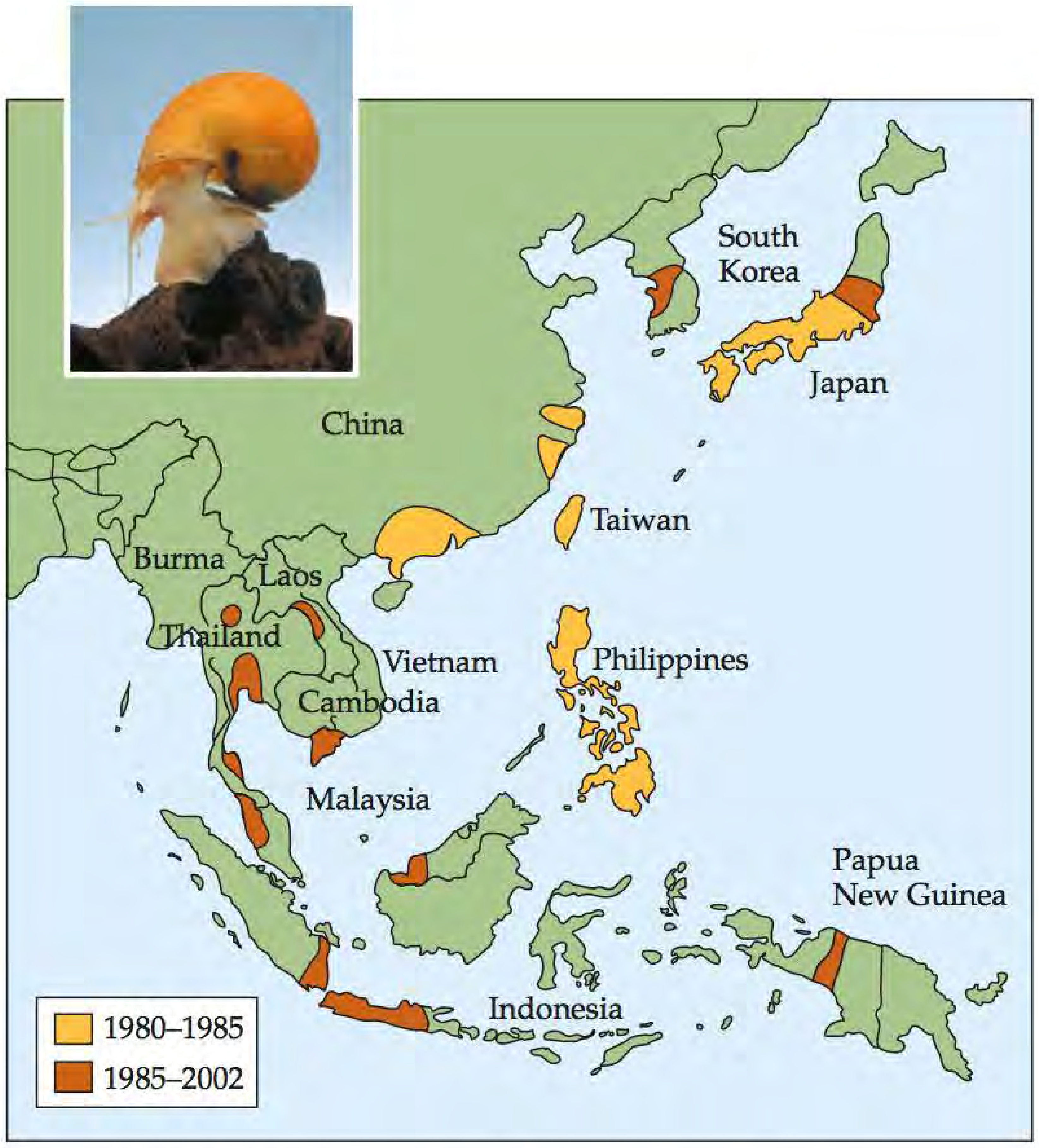
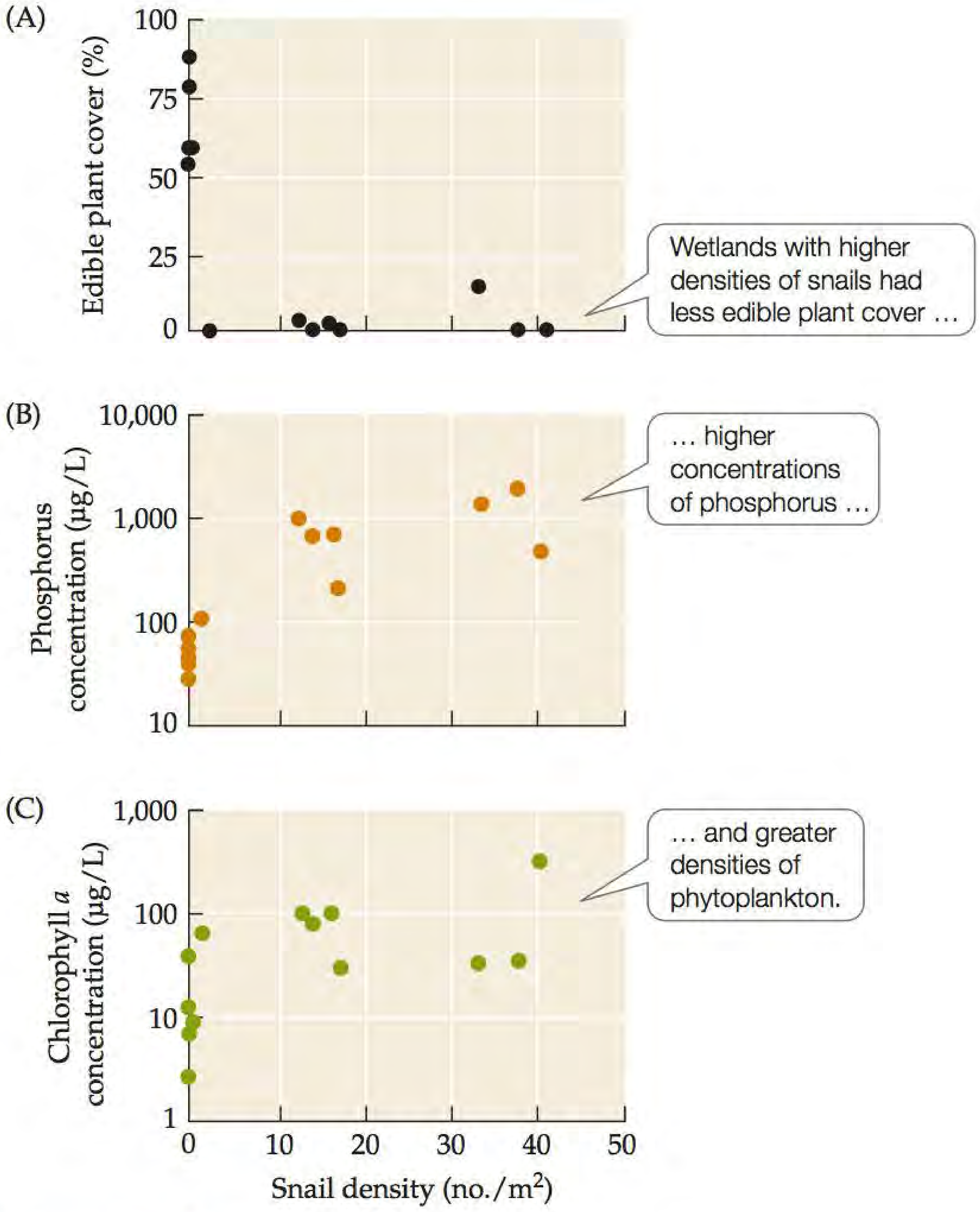


Figure 12.21 The Geographic Spread of an Aquatic Herbivore Since its introduction to Taiwan in 1980, the golden apple snail (*Pomacea canaliculata*) has spread rapidly across parts of Southeast Asia, threatening rice crops and native plant species. The map shows the regions the snail had occupied by 1985 and by 2002.



Wetlands with higher densities of snails had less edible plant cover …

… higher concentrations of phosphorus …

… and greater densities of phytoplankton.

Figure 12.22 A Snail Herbivore Alters Aquatic Communities Nils Carlsson and colleagues measured characteristics of 14 natural wetlands in Thailand that differed in their densities of golden apple snails (*Pomacea canaliculata*). (A) Percentage of the wetlands covered by edible plant species. (B) Concentrations of phosphorus in the water. (C) Chlorophyll *a* concentrations (an indicator of phytoplankton biomass). Note the log scale in (B) and (C). Experiments conducted separately indicated that all the trends shown here could have been caused by the snail. (After Carlsson et al. 2004.)

? In (B), compare the average total phosphorus concentration in wetlands without snails with that in wetlands with snails.

and spread rapidly through Southeast Asia (**Figure 12.21**). Its spread caught the attention of researchers and government officials because it proved to be a serious pest of rice. The snail has also been found in Hawaii, the southern United States, and Australia and is expected to reach Bangladesh and India (Carlsson et al. 2004).

Most freshwater snails eat algae, but the golden apple snail prefers to eat aquatic plants, including those that float on the water surface and those that attach themselves to the bottom. However, as mentioned in Concept 12.1, golden apple snails are generalists, and if plants are not available, they can survive on algae and detritus. As a result, these snails are resilient and hard to get rid of.

As a first step toward assessing how the snail had affected natural communities, Nils Carlsson and colleagues surveyed 14 wetlands in Thailand with varying densities of snails. They found that wetland communities with high densities of snails were characterized by few plants, high nutrient concentrations in the water, and a high biomass of algae and other phytoplankton (**Figure 12.22**).

To test whether the trends observed in their survey could have been caused by the snail, Carlsson et al. (2004) placed 24 1 × 1 × 1 m enclosures in a wetland in which snail densities were low. To each enclosure, they added about 420 g of water hyacinth (*Eichhornia crassipes*), one of the most abundant plant species in many Southeast Asian wetlands. Next, they added 0, 2, 4, or 6 snails to the enclosures; there were six replicates of each of the four snail density treatments. Carlsson and colleagues then measured the effects of the snails on plant biomass and phytoplankton biomass. Water hyacinth biomass increased in the enclosures where no snails were present but decreased in all the other enclosures. At the highest snail density tested (6 snails/m^2), phytoplankton biomass increased.

The results of the survey and the experiment concur in suggesting that the golden apple snail can have an enormous effect on wetland communities, causing a shift from a wetland with clear water and many plants to a wetland with turbid water, few plants, high nutrient concentrations, and high phytoplankton biomass. It is likely that this shift occurs because the snails suppress plants directly (by eating them) and because they release the nutrients they obtain from the plants into the water, thus providing improved growth conditions for algae and other phytoplankton.

A CASE STUDY REVISITED
Snowshoe Hare Cycles

What is the cause of snowshoe hare population cycles? As we saw in the Case Study, neither the food supply hypothesis nor the predation hypothesis alone can explain these cycles. However, much of the variation in hare densities can be explained when we combine these two hypotheses—and add even more realism with a few new twists.

Charles Krebs and colleagues (1995) performed an experiment designed to determine whether food, predation, or their interaction caused population cycles in hares. The sheer scope of the experiment was impressive: the experimental treatments were performed in seven 1 × 1 km blocks of forest located in an isolated region of Canadian wilderness. Three blocks were not manipulated and were used as controls. Food for hares was added to two blocks (the "+Food" treatment). In 1987, an electric fence 4 km in length was constructed to exclude predators from one block of forest (the "–Predators" treatment). In the following year, a second 4 km fence was built; in the block of forest enclosed by this fence, food was added and predators were excluded (the "+Food/–Predators" treatment). The two fences (with a total length of 8 km) had to be monitored daily during the winter, when temperatures could plummet to –45°C (–49°F); this monitoring required so much time that the researchers could not replicate either fenced treatment. The survival rates and densities of hares in each block of forest were observed for 8 years.

Compared with the control blocks, hare densities were considerably higher in the +Food, the –Predators, and the +Food/–Predators blocks (**Figure 12.23**). The most pronounced effects were seen in the +Food/–Predators block, where, on average, hare densities were 11 times those in the control blocks. The strong effect of jointly adding food and removing predators suggests that hare population cycles are influenced by both food supply and predation.

This conclusion was supported by results from a mathematical model that examined feeding relationships across three levels: vegetation (the hares' food), hares, and predators (King and Schaffer 2001). Field data were used to estimate the model parameters, and the model's predictions were compared with the actual results for Krebs et al.'s four treatments. Although the match was not exact, there was reasonably good agreement between the model and the results, again suggesting that both food and predators influence hare population cycles (**Figure 12.24**).

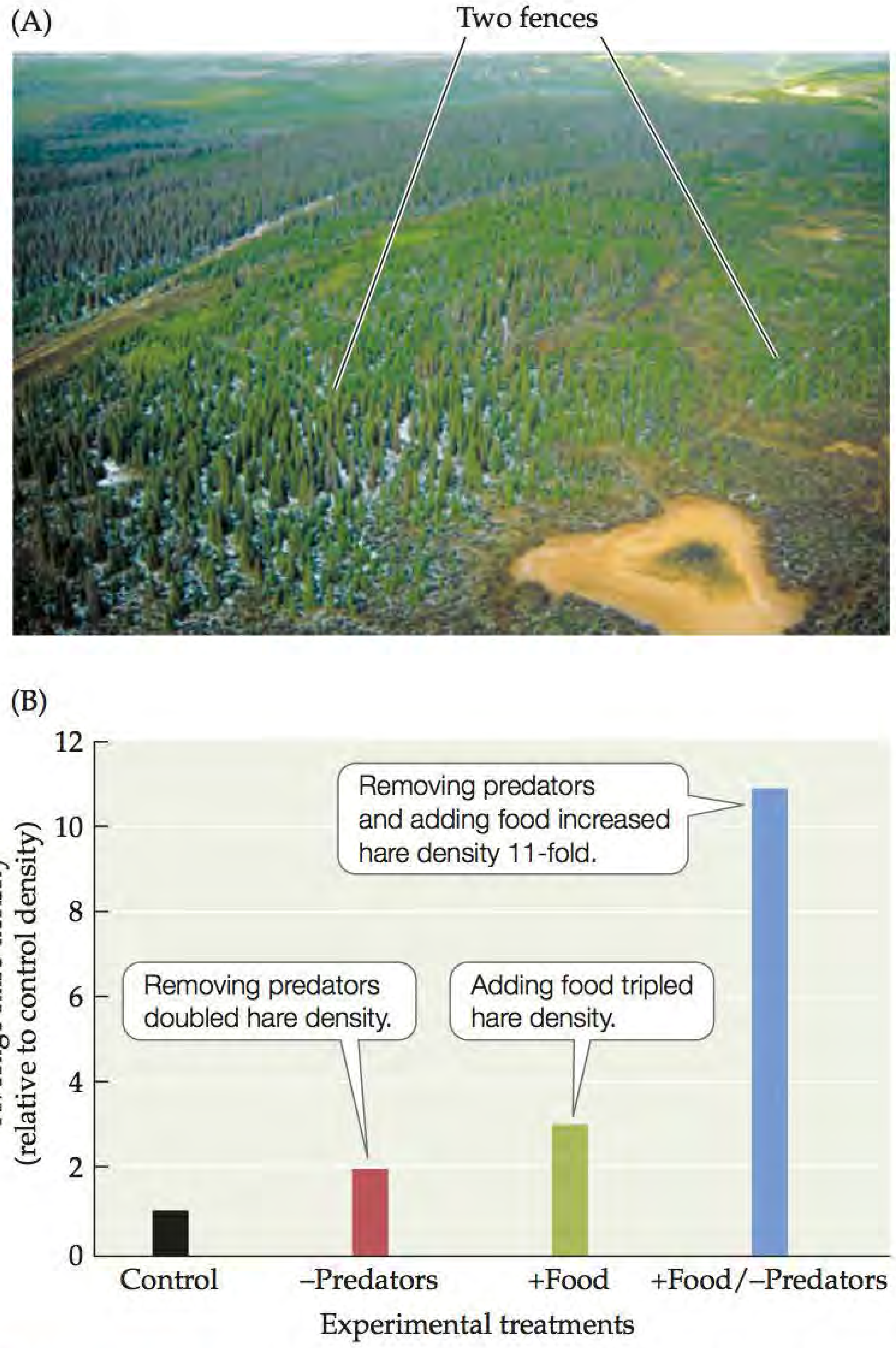


Figure 12.23 Both Predators and Food Influence Hare Density (A) This aerial photograph shows one of the 1 km^2 snowshoe hare study sites described in the text. (B) Average hare densities relative to their densities in control blocks of forest. (B after Krebs et al. 1995.)

While much progress has been made in the study of snowshoe hare population cycles, some questions remain. We do not yet have a complete understanding of the factors that cause hare populations across broad regions of Canada to cycle in synchrony. Lynx can move from 500 to 1,100 km. If lynx move from areas with scarce prey to areas with abundant prey on a scale of hundreds of kilometers, their movements might be enough to cause geographic synchrony in hare cycles. In addition, large geographic regions in Canada experience a similar climate, and that may also affect the synchrony of hare population cycles.

Finally, the Krebs et al. experiment provided a test of whether the addition of food or the removal of predators (or both) could stop the hare population cycle. Although hare densities declined less in the +Food/–Predators block than in the control blocks, they did decline at the usual point in the hare cycle. Why did the +Food/–Predators treatment fail to stop the cycle? One possible reason

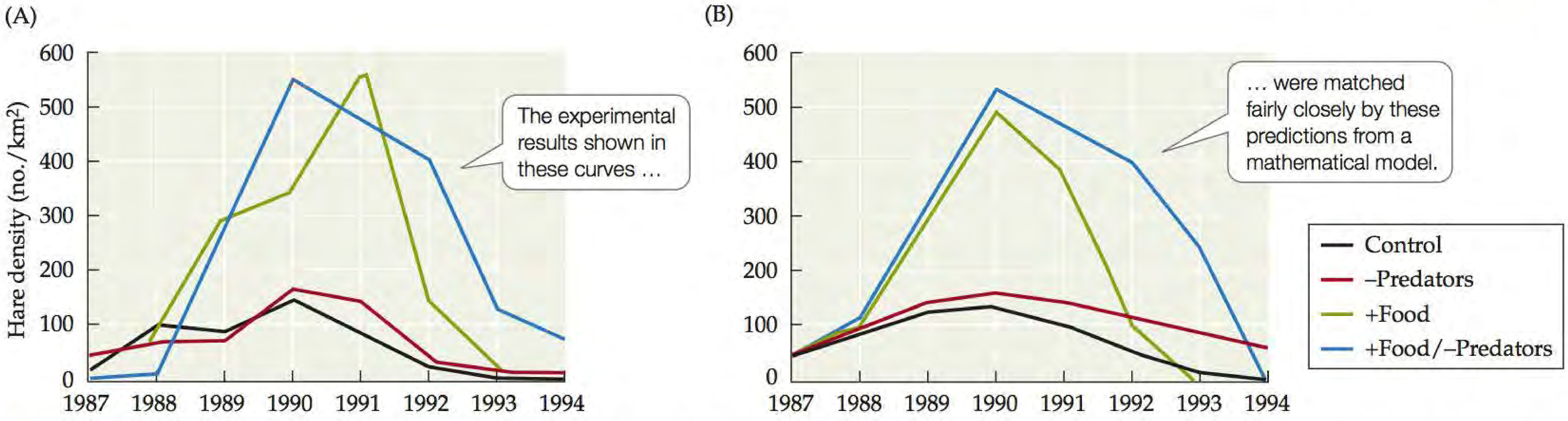


Figure 12.24 A Vegetation–Hare–Predator Model Predicts Hare Densities Accurately The model assumes that hare population densities are influenced by feeding relationships across three levels: vegetation (the hares' food), hares, and predators. Parameters for the model were estimated from field data. When the investigators compared the predictions of their model with the experimental results of Krebs et al. (1995), they found a reasonably good match between (A) the experimental results and (B) the model's predictions. (After King and Schaffer 2001.)

is that the fences excluded lynx and coyotes but did not exclude owls, goshawks, and other birds of prey. Collectively, these bird predators accounted for about 40% of snowshoe hare deaths and thus could have contributed to the onset of the decline phase of the hare cycle in the +Food/–Predators block. Next we'll explore another possible explanation: stress caused by fear of predator attack.

CONNECTIONS IN NATURE

From Fear to Hormones to Population Dynamics

Predators not only affect their prey directly (by killing them), but also influence them indirectly (e.g., by altering their foraging behavior, as described for elk in Concept 8.2). Boonstra et al. (1998) tested snowshoe hares for another possible indirect effect of predators: fear. Their results hint at a fascinating way in which predation might influence the decline phase of the hare cycle.

When humans are in a dangerous situation, we often engage a set of fight-or-flight responses that can produce rapid and sometimes astonishing results (such as the ability to move unusually heavy weights). Snowshoe hares have a similar stress response. A hormone called cortisol stimulates the release of stored glucose into the blood, where it becomes available to the muscles; cortisol also suppresses body functions that are not essential for immediate survival, including growth, reproduction, and immune system function (**Figure 12.25**).

The stress response works well for immediate, or *acute*, forms of stress, such as an attack by a predator. Energy is provided to the muscles rapidly to help the animal deal with the threatening situation. Shortly thereafter, the response is shut down by a negative feedback process. The stress response works less well for long-term, or *chronic*, stress, however. In such cases, the negative feedback signals are weak, and the stress response is maintained for a long time. A failure to "turn off" the stress response can have

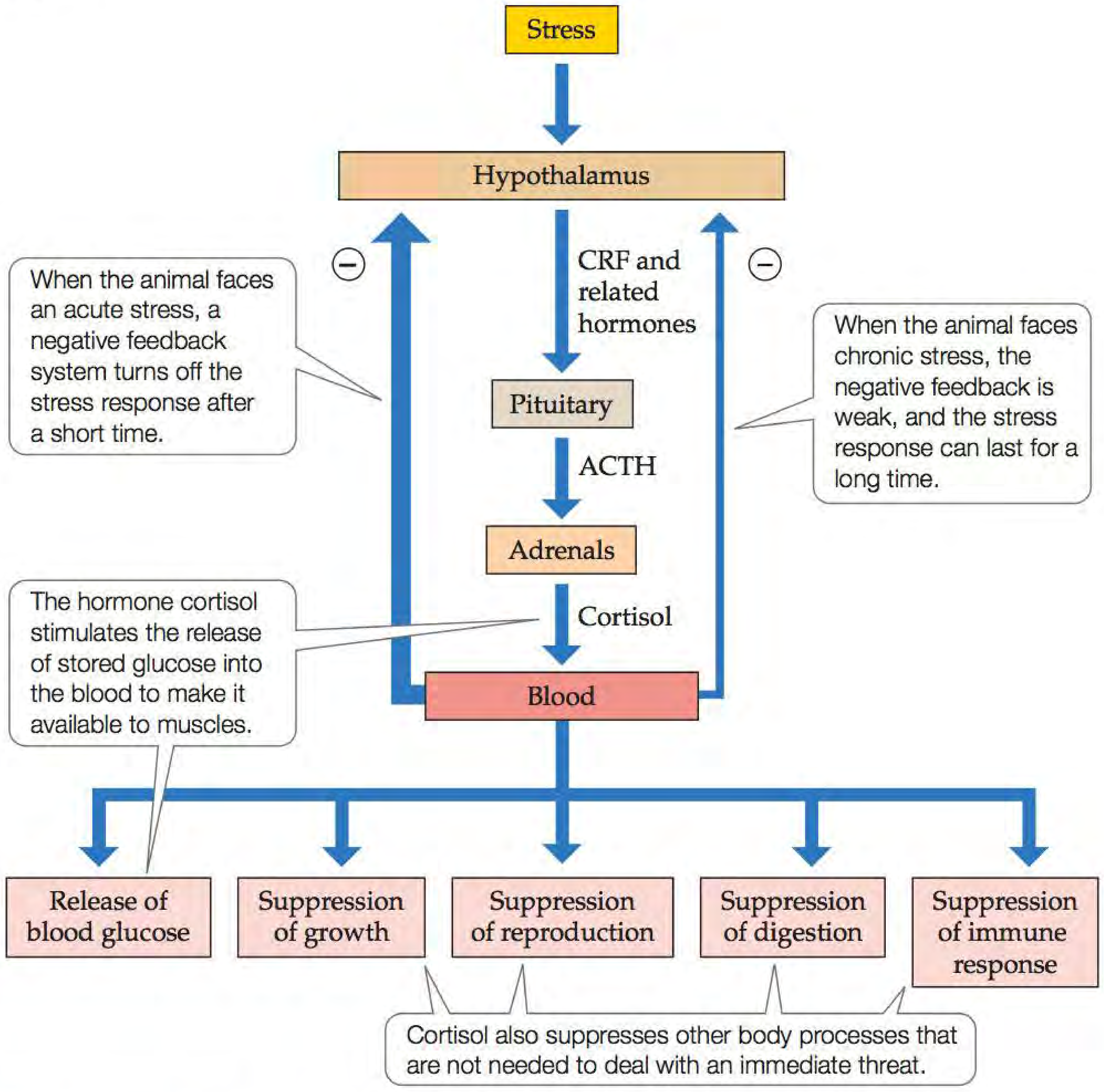


Figure 12.25 The Stress Response When an animal is stressed, the hypothalamus releases a hormone called CRF, which stimulates a cascade of reactions that affect a number of body processes. (After Boonstra et al. 1998.)

harmful effects, including decreased growth and reproduction and increased susceptibility to disease. Collectively, such effects can reduce a population's survival and reproductive rates.

When predators are abundant, as we have seen, they can cause up to 95% of snowshoe hare deaths. At such times, hares are at increased risk of encountering predators; hares would also be likely to see or hear predators killing other hares and to find the remains of hares that had been killed by predators. Reasoning that the fear provoked by such events could trigger chronic stress, Boonstra and colleagues measured the hormonal and immune responses of hares exposed in the field to high versus low numbers of predators. During the decline phase of the hare cycle (when hares are exposed to many predators), cortisol levels increased, blood glucose levels increased, reproductive hormone levels decreased, and overall body condition worsened—as expected for hares experiencing chronic stress (see Figure 12.25). Further experiments showed that a predator-induced increase in cortisol levels led to a drop in the number and size of offspring produced by female snowshoe hares (Sheriff et al. 2009). In addition, female hares with high cortisol levels (caused by exposure to predators) transmitted high cortisol levels to their offspring, who also had reduced reproductive rates (Sheriff et al. 2010).

Overall, chronic stress induced by predation may help to explain some of the puzzling observations mentioned in the Case Study, including the drop in birth rates during the decline phase of the hare cycle and the slow rebound of hare numbers after predator numbers plummet. If future studies confirm the results of Boonstra et al. (1998) and Sheriff et al. (2009, 2010), their work will provide a clear example of how predation risk can alter the physiology of individual prey, thereby changing prey population dynamics and influencing predator–prey cycles.

Summary

CONCEPT 12.1 Most carnivores have broad diets, whereas a majority of herbivores have relatively narrow diets.

- Predation is a trophic interaction in which an individual of one species (a predator) kills and/or consumes individuals (or parts of individuals) of another species (its prey).
- Predation includes carnivory, in which the predator and prey are both animals; herbivory, in which the predator is an animal and the prey is a plant or alga; and parasitism, in which the predator (a parasite) lives symbiotically on or in the prey (its host) and consumes certain tissues without necessarily killing the host.
- Most carnivores do not specialize on particular prey species; instead, they typically eat prey in relation to their availability across a broad range of prey species.
- Many herbivores specialize on particular plant parts, such as leaves (the most common food source), roots, stems, seeds, or internal fluids.
- Herbivorous insects, which constitute a majority of herbivore species, tend to have relatively narrow diets, feeding on only one or a few plant species.

CONCEPT 12.2 Predation results in a wide range of capture and avoidance mechanisms.

- Many predators move about their habitat in search of prey; others remain in one place and attack or trap prey that move within striking distance.
- In response to strong selection pressure exerted by carnivores, prey have evolved a rich variety of defensive mechanisms, including physical defenses, toxins, mimicry, or behavioral responses to escape predation.
- Plants cope with herbivory via masting and other forms of avoidance, compensation (a form of tolerance), and secondary chemicals that deter herbivores.
- Although a plant's defensive mechanisms prevent most herbivores from eating it, typically some herbivores can overcome the plant's defenses by structural, chemical, or behavioral means.

CONCEPT 12.3 Predator populations can cycle with their prey populations.

- Results from mathematical predator–prey models, laboratory experiments, and field observations show that population cycles can be caused by trophic interactions.
- The Lotka–Volterra predator–prey model suggests that predator and prey populations have an inherent tendency to cycle because the abundance of one population is dependent on the abundance of the other population.
- In reality, whether predators and prey cycle may depend on several factors, including habitat complexity and dispersal rates.
- Evolutionary change can affect predator–prey population dynamics, in some cases producing unusual population cycles.

CONCEPT 12.4 Predation can affect prey distribution and abundance, in some cases causing a shift from one community type to another.

- Predators can affect the distribution and abundance of their prey as well as having indirect effects on other species in their communities.
- Carnivores can cause dramatic declines in their prey; similarly, herbivores can decimate their food plants.
- Predation can dramatically alter the composition of ecological communities, in some cases changing one community type to another.

Review Questions

1. Compare and contrast the diet breadth of carnivores and herbivores, and hypothesize why these differences exist.
2. Summarize the effects that carnivores and herbivores have on their prey, as well as the effects that prey have on the carnivores and herbivores that eat them. Explain why these effects are pervasive and pronounced.
3. In this chapter, we claim that predation can have strong effects on ecological communities.
   - a. Provide a logical argument to support this claim.
   - b. Does the scientific evidence support or contradict this claim? Explain.

Hone Your Problem-Solving Skills

In the Case Study of this chapter, we considered a nearly 100-year record of the Hudson's Bay Company to estimate abundances of snowshoe hares and their Canada lynx predators (*Lynx canadensis*). Both species exhibited regular population cycles, with abundances peaking about every 10 years and then falling to low levels (see Figure 12.2A). Suppose for the purposes of this problem that you know the following components of the relationship between snowshoe hare and lynx:

$r = 0.4$, $m = 0.9$

$a = 0.01$, $ba = 0.01$

1. Using the values above, calculate the isoclines for prey and predator. Then, graph the isoclines for each species. Label all your axes and isoclines.
2. You are given the following abundance data for prey and predator for two different time periods where the prey or predators cross their respective isoclines:

   Time 1: 90 prey, 30 predators

   Time 2: 100 prey, 40 predators

   Plot the population abundances of both species for Time 1 and Time 2 on your graph. Now, given Lotka–Volterra model assumptions, determine the abundances for Time 3 (predator crosses its isocline) and Time 4 (prey crosses its isocline). Describe, and draw on the graph, what will happen to both populations over time.
3. Now, plot the abundance of both prey and predators over time, starting with Time 1 and ending at Time 5.
4. Suppose the population sizes of prey and predators at Time 1 were those values where the isoclines cross. Plot the abundances of both prey and predators over time starting with Time 1 and ending at Time 5. Describe what will happen to both populations over time.

ON THE COMPANION WEBSITE

ecology4e.sinauer.com

The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

12.1 Wolves, Willows, and the Ecology of Fear: Cascading Effects of Predators

12.2 The Ups and Downs of Predators: Predator–Prey Cycles

Web Extensions

12.1 Modifying the Lotka–Volterra Predator–Prey Model

13 Parasitism

KEY CONCEPTS

CONCEPT 13.1 Parasites typically feed on only one or a few host species, but host species have multiple parasite species.

CONCEPT 13.2 Hosts have mechanisms for defending themselves against parasites, and parasites have mechanisms for overcoming host defenses.

CONCEPT 13.3 Host and parasite populations can evolve together, each in response to selection pressure imposed by the other.

CONCEPT 13.4 Hosts and parasites can have important effects on each other's population dynamics.

CONCEPT 13.5 Parasites can alter the outcomes of species interactions, thereby causing communities to change.

Enslaver Parasites: A Case Study

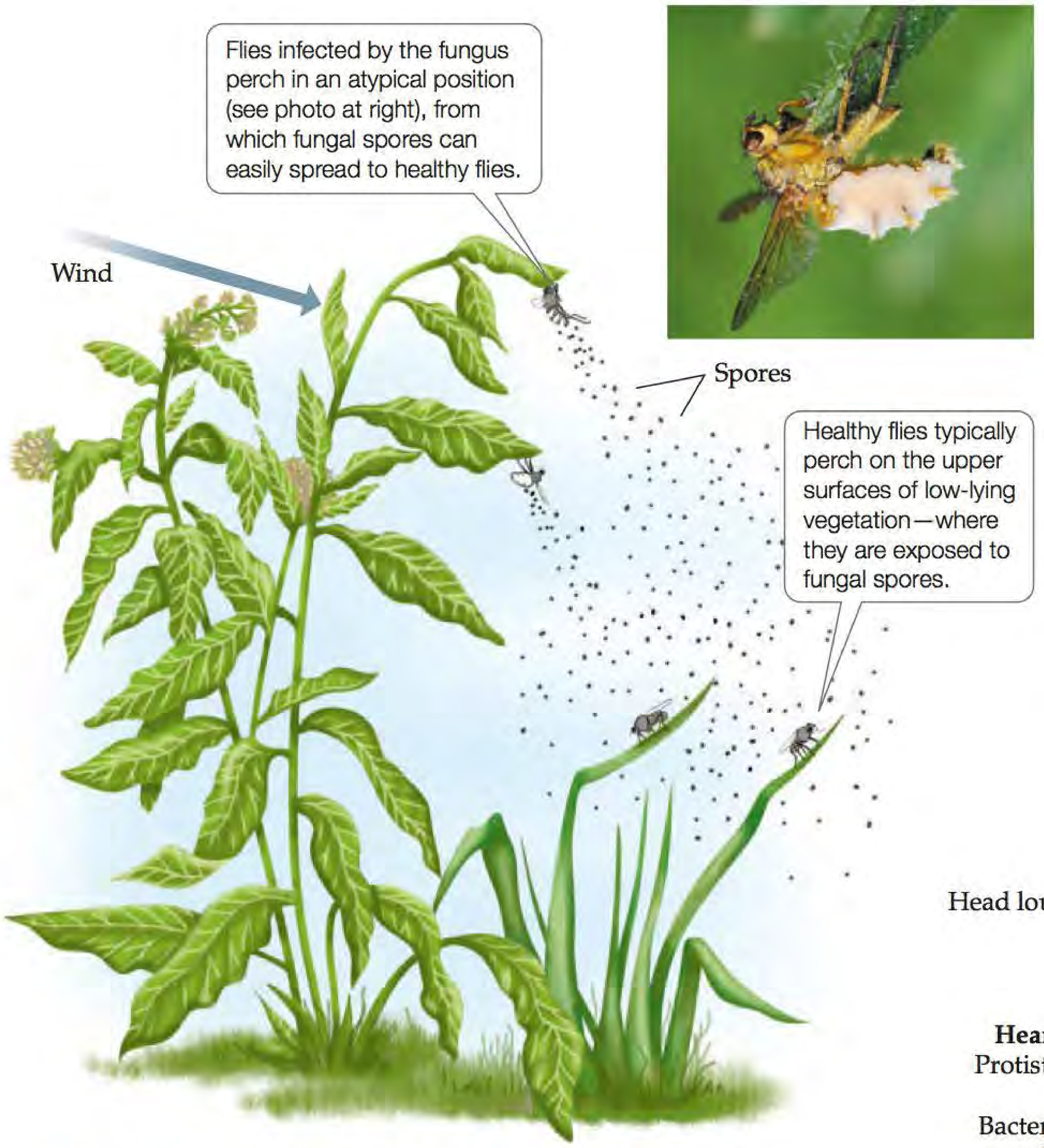
In science fiction books and movies, villains sometimes use mind control or physical devices to break the will and control the actions of their victims. In these stories, people may be forced to perform strange or grotesque actions, or to harm themselves or others—all against their will.

Real life can be just as strange. Consider the hapless cricket shown in the video in **Web Extension 13.1**. This cricket does something that a cricket ordinarily would never do: it walks to the edge of a body of water, jumps in, and drowns. Shortly afterward, a hairworm begins to emerge from the body of the cricket (**Figure 13.1**). For the worm, this is the final step in a journey that begins when a terrestrial arthropod—such as a cricket—drinks water in which a hairworm larva swims. The larva enters the cricket's body and feeds on its tissues, growing from microscopic size into an adult that fills all of the cricket's body cavity except its head and legs. When fully grown, adult hairworms must return to the water to mate. After the adults mate, the next generation of hairworm larvae are released to the water, where they will die unless they are ingested by a terrestrial arthropod host.

Has the hairworm "enslaved" its cricket host, forcing it to jump into the water—an act that kills the cricket but is essential for the hairworm to complete its life cycle? The answer appears to be yes. Observations have shown that when crickets infected with hairworms are near water, they are much more likely to enter the water than are uninfected crickets (Thomas et al. 2002). Furthermore, in ten out of ten trials, when infected crickets were rescued from the water, they immediately jumped back in. Uninfected crickets do not do this.

Hairworms are not the only parasites that enslave their hosts. Maitland (1994) coined the term "enslaver parasites" for several fungal species that alter the perching behavior of their fly hosts in such a way that fungal spores can be dispersed more easily after the flies die (**Figure 13.2**). The fungus *Ophiocordyceps unilateralis* also manipulates the final actions of its host, the ant *Camponotus leonardi*. First, an infected ant climbs down from its home in the upper branches of trees and selects a leaf in a protected environment about 25 cm above the soil (Andersen et al. 2009). Then, just before the fungus kills it, the ant bites into the selected leaf with a "death grip" that will hold its body in place after it is dead. The fungus grows well in such protected environments, but it cannot survive where the ant usually lives—at the tops of trees, where the temperature and humidity are more variable. Thus, while the ant's final actions do not benefit the ant, they do allow the fungus to complete its life cycle in a favorable environment.

Figure 13.1 Driven to Suicide The behavior of this wood cricket (*Nemobius sylvestris*) was manipulated by the hairworm (*Paragordius tricuspidatus*) emerging from its body. By causing the cricket to jump into water (where it drowns), the parasite is able to continue its life cycle.



Flies infected by the fungus perch in an atypical position (see photo at right), from which fungal spores can easily spread to healthy flies.

Healthy flies typically perch on the upper surfaces of low-lying vegetation—where they are exposed to fungal spores.

Figure 13.2 Enslaved by a Fungus Shortly before they die from the infection, yellow dung flies infected by the fungus *Entomophthora muscae* move to the downwind side of a relatively tall plant and perch on the underside of one of its leaves. This position increases the chance that fungal spores released by *Entomophthora* will land on healthy yellow dung flies. (After Maitland 1994.)

Even vertebrates can be enslaved by parasites. Rats typically engage in predator avoidance behaviors in areas that show signs of cats. However, rats infected with the protist parasite *Toxoplasma gondii* behave abnormally: they do not avoid cats, and in some cases they are actually attracted to cats. While such a behavioral change can be a fatal attraction for the rat, it benefits the parasite because it increases the chance that the parasite will be transmitted to the next host in its complex life cycle—a cat.

How do some parasites enslave their hosts? Can the hosts fight back? More generally, what can these remarkable interactions tell us about host–parasite relationships?

Introduction

More than half of the millions of species that live on Earth are **symbionts**, meaning that they live in or on other organisms. To begin to understand how many symbionts there are, we need look no further than our own bodies (**Figure 13.3**). Our faces are home to mites that feed on exudates from the pores of our skin and on secretions at the base of our eyelashes. There are bacteria and fungi that grow on our skin and under our toenails. Arthropods such as lice may live on our heads, pubic regions, and other parts of our bodies. Moving inward, our tissues, organs, and body cavities can be infested with a rich variety of organisms, from bacteria to worms to fungi to protists.

These symbionts can be mutualists (as we will see in Chapter 15) or parasites. A **parasite** consumes the tissues or body fluids of the organism on or within which it lives, called its **host**; some parasites, called **pathogens**, cause diseases. Unlike carnivores but similar to herbivores, parasites typically harm, but do not immediately kill, the organisms they eat. The negative effects

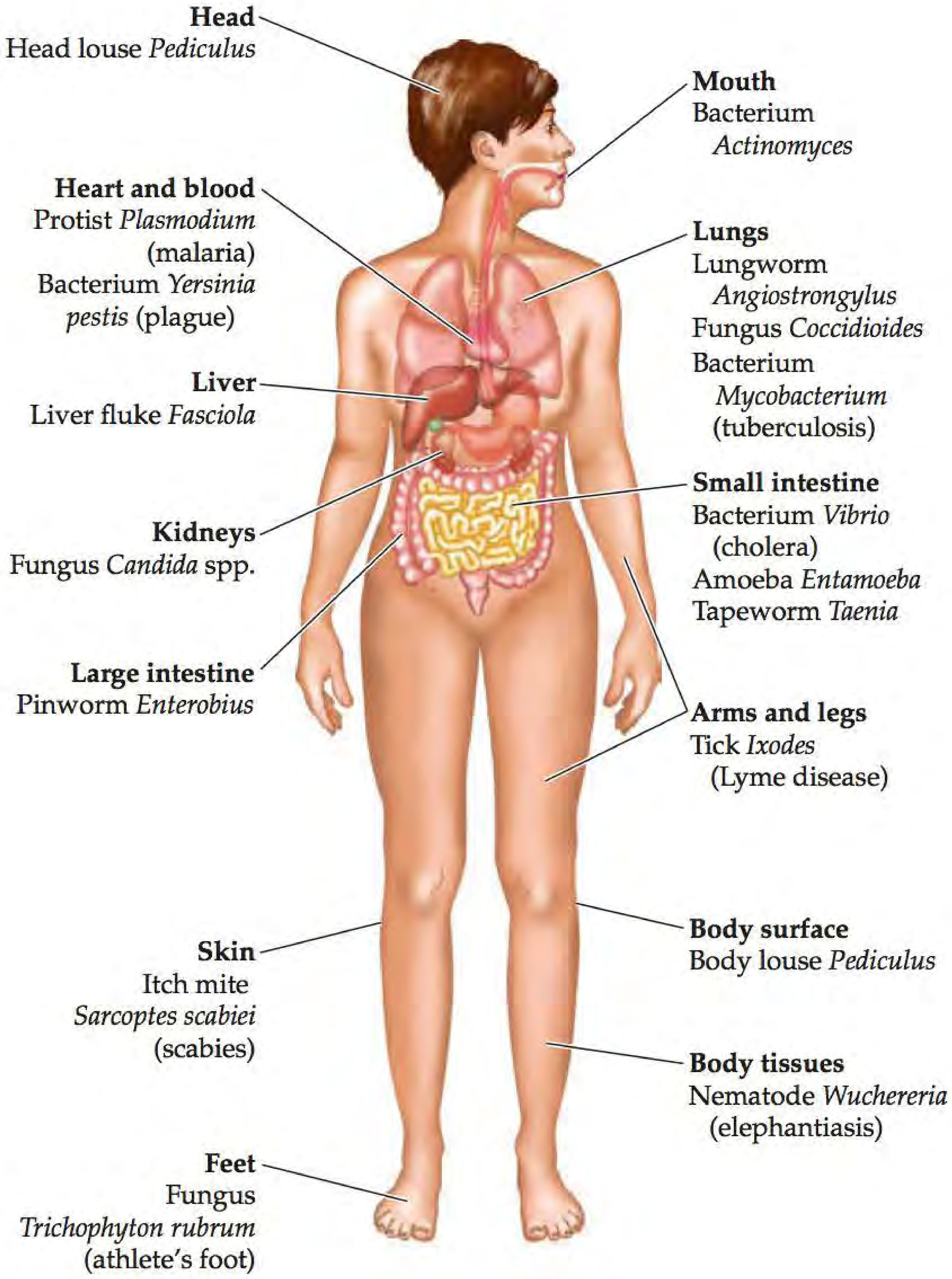


Figure 13.3 The Human Body as Habitat for Symbionts Different parts of our bodies provide suitable habitat for a wide range of symbionts, many of which are parasites; only a few examples are shown here. Some of these organisms are pathogens that cause disease.

of parasites on their hosts vary widely, from mild to lethal. We see this variation in our own species, for which some parasites, such as the fungus that causes athlete's foot, are little more than a nuisance. Others, such as the protist *Leishmania tropica*, can cause disfigurement, and still others, such as *Yersinia pestis*, the bacterium that causes the plague, can kill. There is similar variation in the degree of harm caused by parasites that infect other species. Parasites vary in many other ways, as we'll see next as we examine their basic biology.

CONCEPT 13.1

Parasites typically feed on only one or a few host species, but host species have multiple parasite species.

Parasite Natural History

Parasites vary in size from relatively large species (**macroparasites**), such as arthropods and worms, to species too small to be seen with the naked eye (**microparasites**), such as bacteria, protists, and unicellular fungi. But whether they are large or small, parasites typically feed on only one or a few host individuals over the course of their lives. Thus, defined broadly, parasites include herbivores, such as aphids or nematodes, that feed on only one or a few host plants, as well as **parasitoids**, insects whose larvae feed on a single host, almost always killing it.

Most species are attacked by more than one parasite (**Figure 13.4**), and even parasites have parasites. Because parasites spend their lives feeding on one or a few host individuals, they tend to have a close relationship to the organisms they eat. For example, many parasites are closely adapted to particular host species, and many attack only one or a few host species. This specialization at the species level helps to explain why there are so many species of parasites—many host species have at least one parasite that eats *only* them. Overall, although the total number of parasite species is not known, a rough estimate is that 50% of the species on Earth are parasites (Windsor 1998).

Parasites are also specialized for living on or eating certain parts of the host's body. We'll focus next on this aspect of parasite specialization by describing both ectoparasites and endoparasites.

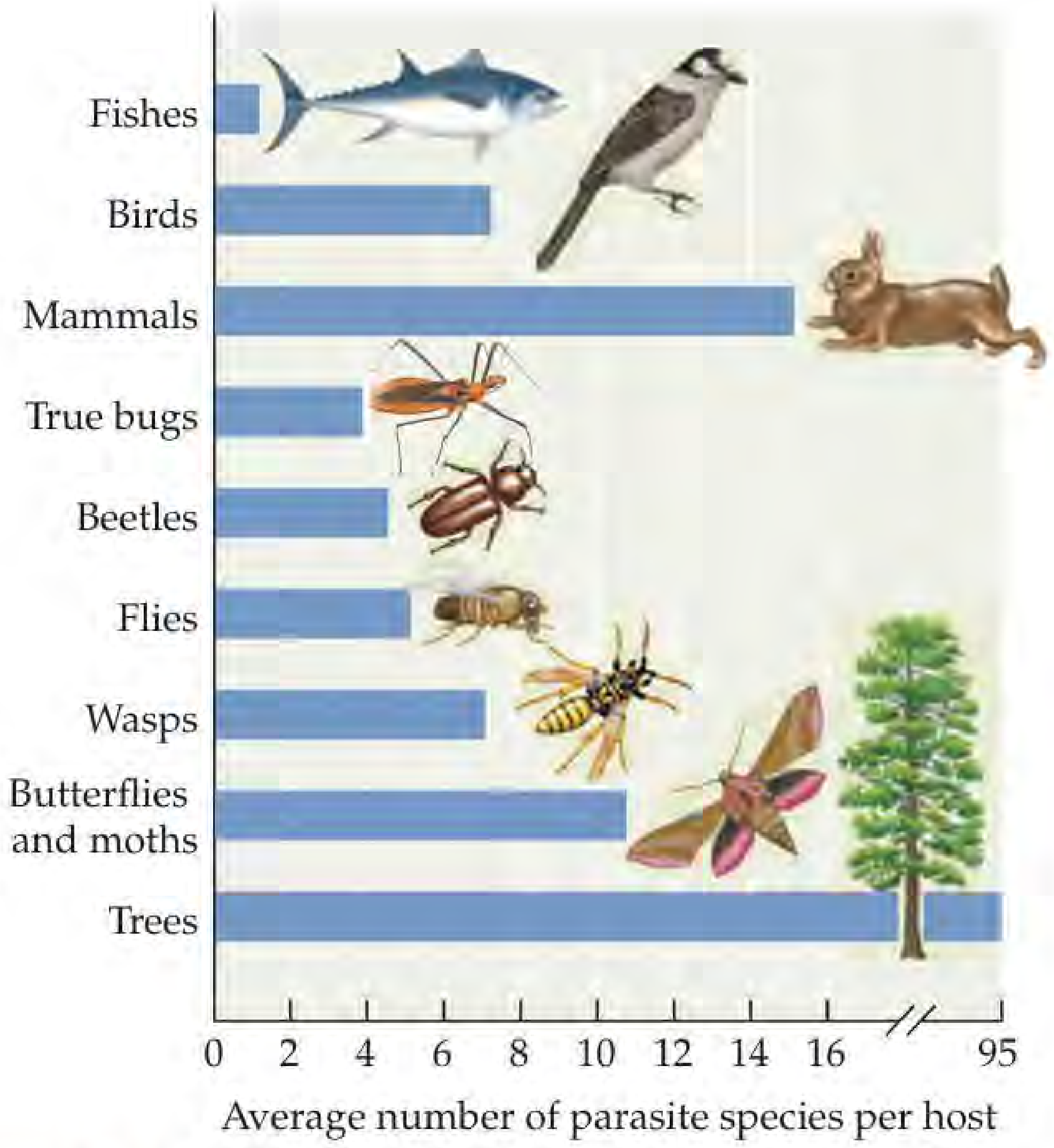


Figure 13.4 Many Species Are Host to More Than One Parasite Species In a study conducted in Britain, most host species were found to harbor more than one parasite species. The number of parasite species shown here for fishes, birds, and mammals includes only helminth worm parasites and hence is an underestimate of the actual number of parasite species found in these vertebrates. (After Poulin and Morand 2004.)

? Averaging across the six groups of organisms other than vertebrates (which we exclude because the data underestimate the true number of parasites), what is the average number of parasite species per host? Suppose the number of parasite species was determined for a previously unstudied host from one of the six groups. Is it likely that the number of parasites in that host would be close to the average you calculated? Explain.

Ectoparasites live on the surface of their host

An **ectoparasite** lives on the outer body surface of its host (**Figure 13.5**). Ectoparasites include plants such as dodder and mistletoe that grow on, and obtain water and food from, another plant (see Figure 5.3). As described in Concept 5.1, such parasitic plants use modified roots called *haustoria* to penetrate the tissues of their host. Dodder cannot photosynthesize and hence depends on its host for both mineral nutrients and carbohydrates. In contrast, mistletoes are *hemiparasitic*: they extract water and mineral nutrients from their hosts, but since they have green leaves and can photosynthesize, they do not rely exclusively on their hosts for carbohydrates.

There are also many fungal and animal parasites that live on the surfaces of plants, feeding on their hosts' tissues or body fluids. More than 5,000 species of fungi attack important crop and horticultural plants, causing billions of dollars of damage each year. Some fungi that attack plants, including mildews, rusts, and smuts, grow on the surface of the host plant and extend their hyphae (fungal filaments) within the plant to extract nutrients from its tissues (see Figure 13.5A). Plants are also attacked by numerous animal ectoparasites, including aphids, whiteflies, and scale insects, which are found on stems and leaves, and nematode worms, beetles, and (juvenile) cicadas, which are found on roots. Animal ectoparasites that eat plants and live on their outer surfaces can sometimes be thought of both as herbivores (because they eat

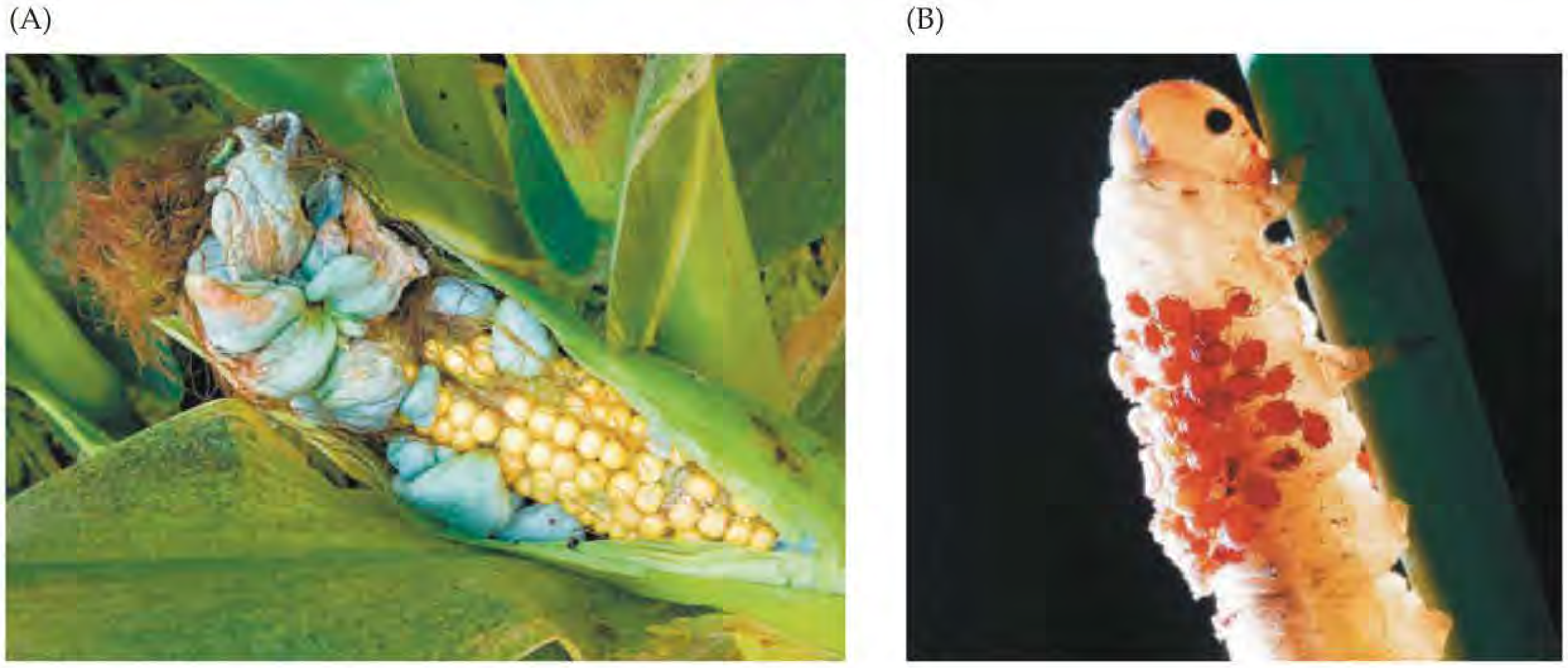


Figure 13.5 Ectoparasites A wide range of parasites live on the outer surfaces of their hosts, feeding on host tissues. Examples include (A) the corn smut fungus (*Ustilago maydis*), seen here growing on an ear of corn, and (B) the velvet mite (*Trombidium* spp.), which in its larval form feeds parasitically on the blood of insects, such as this sawfly larva.

plant tissues) and as parasites (especially if they remain on a single host plant for much of their lives).

A similar array of fungal and animal ectoparasites can be found on the surfaces of animals. Familiar examples include *Trichophyton rubrum*, the fungus that causes athlete's foot, and fleas, mites, lice, and ticks, which feed on the tissues or blood of their hosts (see Figure 13.5B). Some of these parasites also transmit diseases to their hosts, including fleas that spread the plague and ticks that spread Lyme disease.

Endoparasites live inside their host

If we ignore the details of their shape, we can think of people and most other animals as being constructed in a similar way: their bodies consist of tissues that surround an open tube called the *alimentary canal*. The alimentary canal runs through the middle of the body, from the mouth to the anus. Parasites that live inside their hosts, called **endoparasites**, include species that inhabit the alimentary canal as well as species that live within host cells or tissues.

The alimentary canal provides excellent habitat for parasites. The host brings in food at one end (the mouth) and excretes what it cannot digest at the other (the anus). Parasites that live within the alimentary canal often do not eat host tissues at all; instead, they rob the host of nutrients. A tapeworm, for example, has a *scolex*, a structure with suckers (and sometimes hooks) that it uses to attach itself to the inside of the host's intestine (**Figure 13.6A**). Once it is attached, the tapeworm simply absorbs food that the host has already digested. Tapeworms that infect humans can grow up to 10–20 m (33–66 feet) long; large tapeworms such as these can block the intestines and cause nutritional deficiencies.

Many other endoparasites live within the cells or tissues of animal hosts, causing a wide range of symptoms

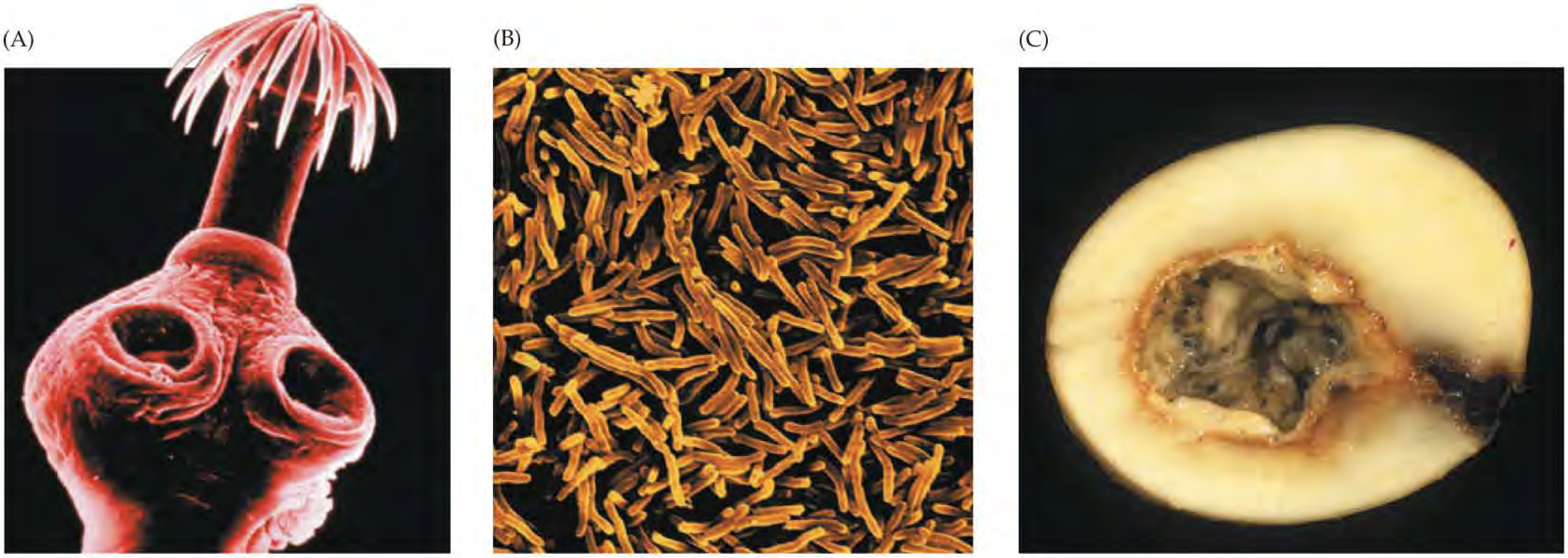


Figure 13.6 Endoparasites Many parasites live within the body of their host, feeding on the host's tissues or robbing it of nutrients. (A) The tapeworm *Taenia taeniaeformis* uses the suckers and hooks shown here to attach to the intestinal wall of its mammalian host, often a rodent, rabbit, or cat. Once attached, an adult can grow to over 5 m (16 feet) in length. (B) The bacterium *Mycobacterium tuberculosis* causes the lung disease tuberculosis, which kills 1 to 2 million people each year. (C) This section of a potato tuber shows the destruction wrought by *Erwinia carotovora*, a bacterium that causes soft rot. Affected areas become soft with decay and develop a distinctive foul odor.

as they reproduce or consume host tissues. Examples in humans include *Yersinia pestis*, the bacterium that causes the plague, and *Mycobacterium tuberculosis*, the bacterium that causes tuberculosis (TB) (**Figure 13.6B**). TB is a potentially fatal lung disease, aptly referred to as the "Captain of Death"; with the possible exception of malaria, it has killed more people than any other disease in human history. TB continues to kill 1 to 2 million adults each year (a number comparable to the roughly 2 million that currently die each year from AIDS).

Plants too are attacked by a wide variety of endoparasites, including bacterial pathogens that cause soft rot in various plant parts, such as fruits (e.g., tomatoes) or storage tissues (e.g., potatoes; **Figure 13.6C**). Other plant pathogens include fungi that cause plant parts to rot from the inside out. Some bacteria invade plant vascular tissues, where they disrupt the flow of water and nutrients, causing wilting and often death. Plant pathogens can have large effects on natural communities, as illustrated by the protist *Phytophthora ramorum*, which causes sudden oak death, a disease that has recently killed more than a million oaks and other trees in California and Oregon (see also the chestnut blight in Figure 13.14).

Endoparasitism and ectoparasitism have advantages and disadvantages

There are advantages and disadvantages to living in or on a host (**Table 13.1**). Because ectoparasites live on the surface of their host, it is relatively easy for them or their offspring to disperse from one host individual to another. It is much more difficult for endoparasites to disperse to new hosts. Endoparasites solve this problem in a variety of ways. Some, like the enslaver parasites discussed in the Case Study at the opening of this chapter, alter the physiology or behavior of their host in ways that facilitate their dispersal. Other examples include the bacterium, *Vibrio cholerae*, that causes cholera and the amoeba, *Entamoeba histolytica*, that causes amoebic dysentery. People with cholera and dysentery have diarrhea, a condition that increases the chance that the parasite will contaminate drinking water and thereby spread to new hosts. Other endoparasites have complex life cycles that include stages that are specialized for dispersing from one host species to another (see Figure 13.9).

TABLE 13.1 Advantages and Disadvantages of Living in or on a Host

	ECTOPARASITISM	ENDOPARASITISM
Advantages	Ease of dispersal	Ease of feeding
	Safe from host's immune system	Protected from external environment
		Safer from natural enemies
Disadvantages	Vulnerability to natural enemies	Vulnerability to host's immune system
	Exposure to external environment	
	Feeding more difficult	Dispersal more difficult

Although dispersal is relatively easy for ectoparasites, there are costs to life on the surface of a host. Compared with endoparasites, ectoparasites are more exposed to natural enemies such as predators, parasitoids, and parasites. Aphids, for example, are attacked by ladybugs, birds, and many other predators, as well as by lethal parasitoids and by parasites such as mites that suck fluids from their bodies. Endoparasites, in contrast, are safe from all but the most specialized predators and parasites. Endoparasites are also relatively well protected from the external environment, and they have relatively easy access to food—unlike an ectoparasite, an endoparasite does not have to pierce the host's protective outer surfaces to feed. But living within the host does expose endoparasites to a different sort of danger: attack by the host's immune system. Some parasites have evolved ways to tolerate or overcome immune system defenses, as we will see in the following section.

CONCEPT 13.2
Hosts have mechanisms for defending themselves against parasites, and parasites have mechanisms for overcoming host defenses.

Defense and Counterdefenses

As we saw in Chapter 12, carnivores and herbivores exert strong pressure on their food organisms, and vice versa. The prey species and plants eaten by carnivores and herbivores have mechanisms that help them avoid being eaten. Similarly, carnivores and herbivores have mechanisms that help them to overcome the defenses of their prey or food plants. The same is true of parasites and their hosts: hosts have ways to protect themselves against parasites, and parasites have countermeasures to circumvent host defenses.

Immune systems, biochemical defenses, and symbionts can protect hosts against parasites

Host organisms have a wide range of defensive mechanisms that can prevent or limit the severity of parasite attacks. For example, a host may have a protective outer covering, such as the skin of a mammal or the hard exoskeleton of an insect, that can keep ectoparasites from piercing its body or make it difficult for endoparasites to enter. Endoparasites that do manage to enter the host's body are often killed or rendered less effective by the host's immune system, biochemical defenses, or defensive symbionts.

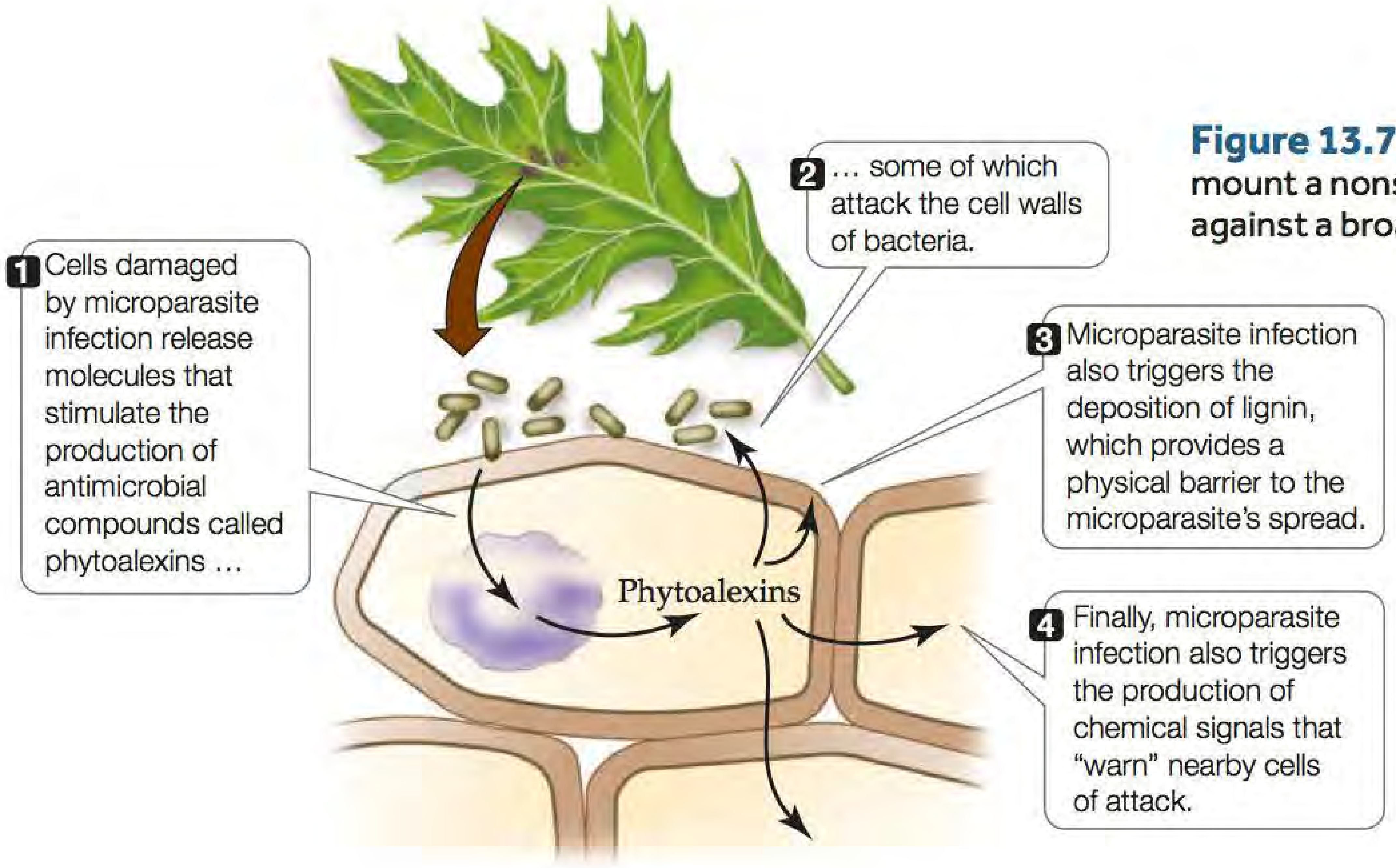


Figure 13.7 Nonspecific Plant Defenses Plants can mount a nonspecific defensive response that is effective against a broad range of fungal and bacterial microparasites.

IMMUNE SYSTEMS The vertebrate immune system includes specialized cells that allow the host to recognize microparasites to which it has been previously exposed; in many instances, the "memory cells" of the immune system are so effective that the host has lifelong immunity against future attack by the same microparasite species. Other immune system cells engulf and destroy parasites or mark them with chemicals that target them for later destruction.

Plants can also mount highly effective responses to invasion by parasites. Some plants have resistance genes, the different alleles of which provide protection against microparasites with particular genotypes; we will describe this defense system in more detail in Concept 13.3. Plants are not helpless, however, even when they lack alleles that provide resistance to a specific attacker. In such a case, the plant relies on a nonspecific immune system that produces antimicrobial compounds, including some that attack the cell walls of bacteria and others that are toxic to fungal parasites (**Figure 13.7**). The plant may also produce chemical signals that "warn" nearby cells of imminent attack, and still other chemicals that stimulate the deposition of lignin, a hard substance that provides a barricade against the invader's spread.

BIOCHEMICAL DEFENSES Hosts have ways of regulating their biochemistry to limit parasite growth. Bacterial and fungal endoparasites, for example, require iron to grow. Vertebrate hosts—including mammals, birds, amphibians, and fishes—have a protein called transferrin that removes iron from their blood serum (where parasites could use it) and stores it in intracellular compartments (where parasites cannot get to it). Transferrins are so efficient that the concentration of free iron in mammalian blood serum is only $10^{-26}\,M$—so low that parasites cannot grow in vertebrate blood unless they can somehow outmaneuver the host. To do this, some parasites steal iron from the transferrin itself and use it to support their own growth.

Similar biochemical battles occur between plants and their parasites. As we saw in Concept 12.2, plants use a rich variety of chemical weapons to kill or deter the organisms that eat them. Plant defensive secondary compounds are so effective that some animals eat specific plants in order to treat or prevent parasite infections. For example, when parasitic flies lay eggs on the bodies of woolly bear caterpillars, the caterpillars switch from their usual food plant (lupines) to a diet of poisonous hemlock (Karban and English-Loeb 1997). The new diet does not kill the parasites, but it does increase the chance that the caterpillar will survive the attack and metamorphose into an adult tiger moth (*Platyprepia virginalis*). Chimpanzees infected with the nematode *Oesophagostomum stephanostomum* specifically seek out and eat a bitter plant that scientists have learned contains compounds that kill or paralyze the nematodes and can also deter many other parasites (Huffman 1997). Humans do essentially the same thing: we spend billions of dollars each year on pharmaceuticals that are based on compounds originally obtained from plants.

DEFENSIVE SYMBIONTS Some organisms are aided in their defense against parasites by mutualistic symbionts such as bacteria and fungi. For example, fungal symbionts living within leaves protect grasses and plants such as cacao trees (the source of the beans used to make chocolate) from attack by pathogens. Growing evidence also indicates that bacterial symbionts living within the human digestive tract can protect us against disease-causing organisms (Britton and Young 2012).

Many such "defensive symbionts" are heritable, meaning the symbiont is reliably transmitted from a host to its offspring. We might expect that hosts harboring heritable defensive symbionts should increase in frequency in a population when parasites are common—and indeed, that frequently happens. For example, in a laboratory experiment, the frequency of pea aphids (*Acyrthosiphon pisum*) harboring the bacterial symbiont *Hamiltonella defensa* increased rapidly in the presence of a lethal wasp parasite (Oliver et al. 2008). This was expected, because the symbiont is heritable and because pea aphids harboring the symbiont survived at higher rates than did pea aphids lacking the symbiont. In another study on pea aphids, the bacterial symbiont

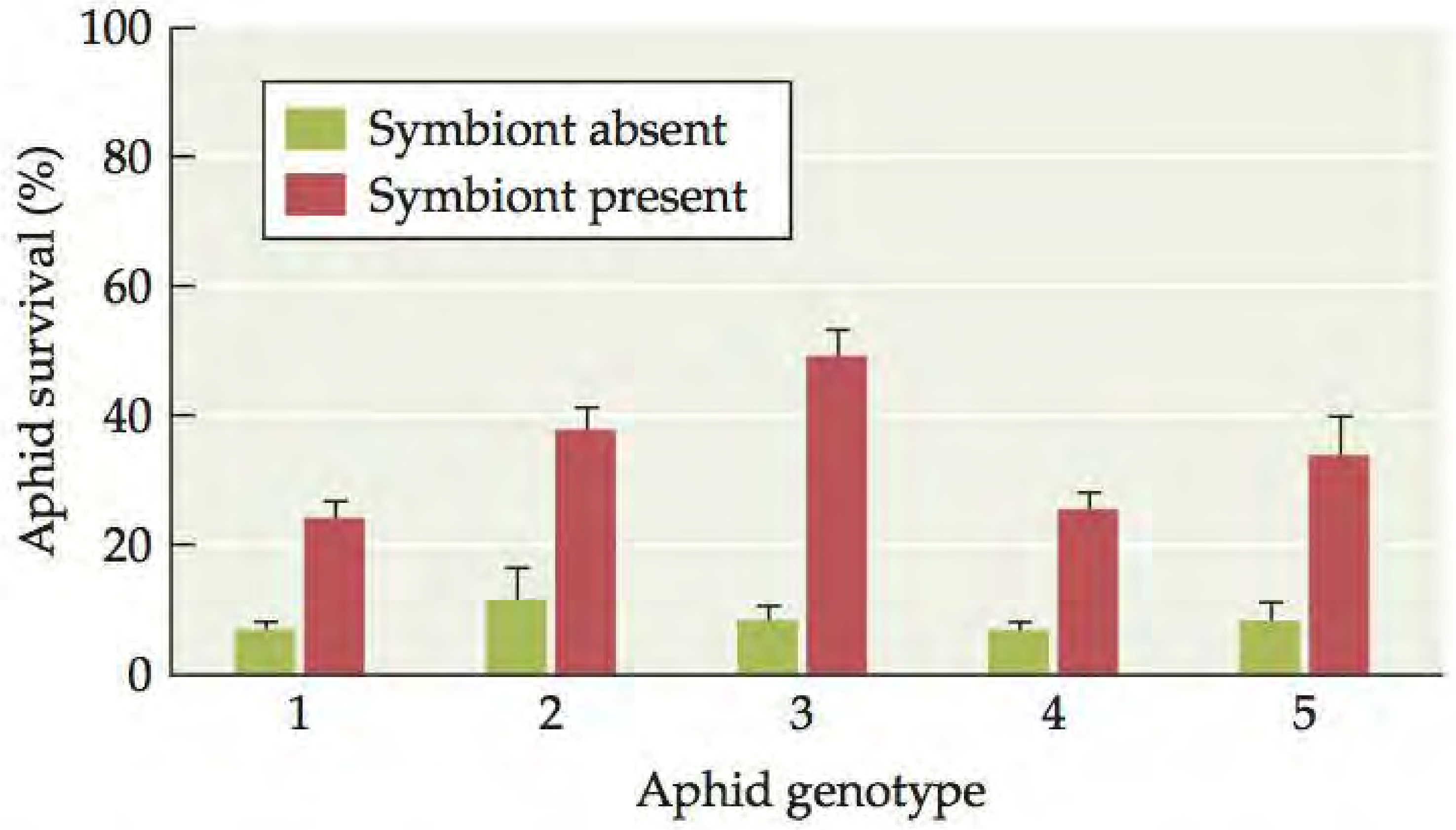


Figure 13.8 Protected by a Symbiont Pea aphids (*Acyrthosiphon pisum*) of five different genotypes were exposed to the pathogenic fungus *Pandora neoaphidis*. For each of these genotypes, some aphids were inoculated with the bacterial symbiont *Regiella insecticola*, while other aphids lacked the symbiont. Aphids harboring the symbiont survived at higher rates than did aphids lacking the symbiont. Error bars show one SE of the mean. (After Scarborough et al. 2005.)

Regiella insecticola was found to protect against attack by a deadly fungal parasite (**Figure 13.8**). Defensive symbionts have also been shown to protect against attack by nematode parasites, as you can explore in **Analyzing Data 13.1**.

Parasites have mechanisms that circumvent host defenses

To survive and reproduce, a parasite must be able to tolerate or evade its host's defensive mechanisms. Aphids and other ectoparasites, for example, must be able to pierce the protective outer covering of the host, and they must be able to tolerate whatever chemical compounds are present in the host tissues or body fluids that they eat. Viewed broadly, the challenges faced by ectoparasites are similar

ANALYZING DATA 13.1

Will a Defensive Symbiont Increase in Frequency in a Host Population Subjected to Parasitism?

Although we would expect heritable defensive symbionts to increase in frequency in host populations subjected to parasitism, few studies have tested this hypothesis. Jaenike and Brekke (2011)* performed such a test, using laboratory populations of the fruit fly *Drosophila neotestacea*. These flies harbor a bacterial symbiont of the genus *Spiroplasma*, which protects flies from the nematode parasite *Howardula aoronymphium*. *Howardula* can sterilize female flies and reduce the mating success of male flies.

Jaenike and Brekke established five replicate populations in which flies were exposed every generation to the nematode parasite and five replicate populations in which the parasite was absent. Initially, each population had a 50:50 mixture of *Spiroplasma*-infected and uninfected adult flies. In a second experiment, the researchers established five replicate populations in which all flies were infected with *Spiroplasma* and five replicate populations in which all flies were uninfected. All populations in this second experiment were exposed to *Howardula* parasites (but not necessarily infected by *Howardula*) in the first generation only. Both experiments were run for seven fly generations. The results for each experiment are shown in the tables.

Experiment 1 Percentage of Fruit Fly Individuals Harboring *Spiroplasma* Symbionts

	GENERATION						
TREATMENT	1	2	3	4	5	6	7
Howardula absent	54	65	52	65	59	65	39
Howardula present	49	52	86	92	97	99	96

Experiment 2 Percentage of Fruit Fly Individuals Infected by the Nematode Parasite *Howardula*

	GENERATION						
TREATMENT	1	2	3	4	5	6	7
Spiroplasma absent	30	59	95	92	87	—	—
Spiroplasma present	25	15	7	2	1	0	0

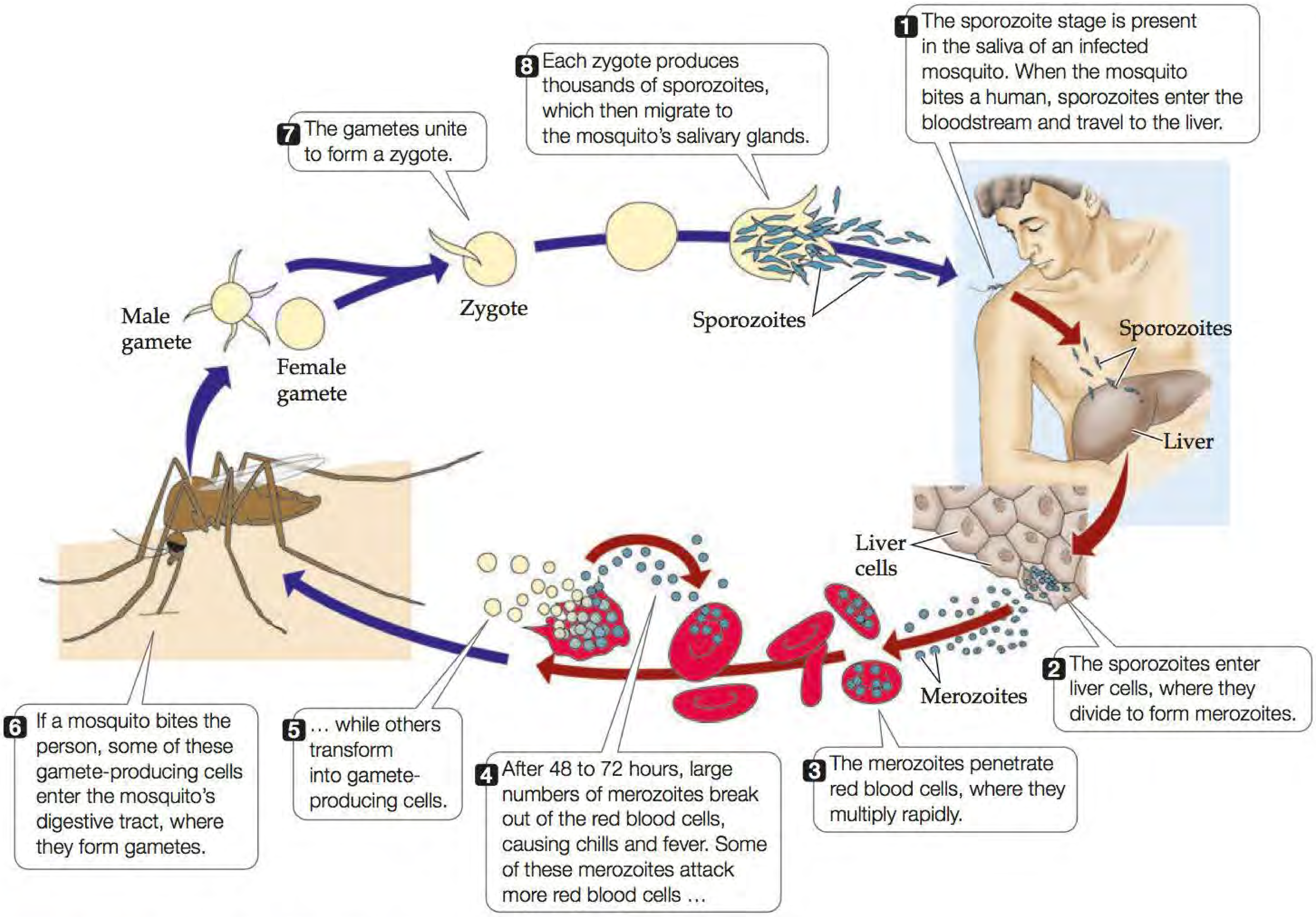
By generation 6, all fly populations were extinct because *Howardula* had sterilized the flies it parasitized.

1. Plot the percentage of flies harboring *Spiroplasma* (*y* axis) versus generation (*x* axis) for both treatments in Experiment 1. Describe the hypothesis tested by this experiment. Which treatment represents the control? Do the results support the hypothesis?
2. Plot the percentage of flies infected by *Howardula* (*y* axis) versus generation (*x* axis) for both treatments in Experiment 2. Describe the hypothesis tested by this experiment. Which treatment represents the control? Do the results support the hypothesis?
3. Examine the graphs you made for Questions 1 and 2. Do the results indicate that there is a cost to flies for harboring *Spiroplasma*? Explain.

See the companion website for a similar ANALYZING DATA exercise.

---

*Jaenike, J. and T. D. Brekke. 2011. Defensive endosymbionts: A cryptic trophic level in community ecology. *Ecology Letters* 14: 150–155.



1 The sporozoite stage is present in the saliva of an infected mosquito. When the mosquito bites a human, sporozoites enter the bloodstream and travel to the liver.

2 The sporozoites enter liver cells, where they divide to form merozoites.

3 The merozoites penetrate red blood cells, where they multiply rapidly.

4 After 48 to 72 hours, large numbers of merozoites break out of the red blood cells, causing chills and fever. Some of these merozoites attack more red blood cells …

5 … while others transform into gamete-producing cells.

6 If a mosquito bites the person, some of these gamete-producing cells enter the mosquito's digestive tract, where they form gametes.

7 The gametes unite to form a zygote.

8 Each zygote produces thousands of sporozoites, which then migrate to the mosquito's salivary glands.

Figure 13.9 Life Cycle of the Malaria Parasite The life cycle of the protist *Plasmodium falciparum* includes specialized stages that facilitate the dispersal of this endoparasite from one host to another. The sporozoite stage, for example, enables the parasite to disperse from an infected mosquito to a human host.

? Which stage in the life cycle enables the parasite to disperse from a human host to a mosquito?

to those faced by herbivores and carnivores as they attempt to cope with the toxins and physical structures that their prey use to defend themselves. We discussed such challenges in Concept 12.2, so here we focus on how endoparasites cope with defenses found inside the host.

COUNTERDEFENSES AGAINST ENCAPSULATION Endoparasites face formidable challenges from host immune systems and related aspects of host biochemistry. Host species typically have a number of ways to destroy parasite invaders. In addition to the strategies we have already described, some hosts can cover parasites or parasite eggs with capsules that kill them or render them harmless, a process called *encapsulation*.

Encapsulation is used by some insects to defend themselves against macroparasites. Insect blood cells can engulf small invaders, such as bacteria, but they cannot engulf large objects, such as nematodes or parasitoid eggs. However, some insects have *lamellocytes*, which are blood cells that can form multicellular sheaths (capsules) around large objects. When an insect mounts such an encapsulation defense, most or all of the attacking parasites may be destroyed. As a result, the parasites are under strong selection to develop a counterdefense.

For example, *Drosophila* fruit flies have an effective defense against wasp parasitoids: they encapsulate (and hence kill) their eggs. Parasitoid wasps that attack fruit flies avoid encapsulation in several different ways. When wasps in the genus *Leptopilina* lay their eggs inside a fruit fly host, they also inject virus-like particles into the host. These particles infect the host's lamellocytes and cause them to self-destruct, thus weakening the host's resistance and increasing the percentage of wasp eggs that survive (Rizki and Rizki 1990). Other parasitoid wasps, such as *Asobara tabida*, lay eggs covered with filaments. These filaments cause the eggs to stick to and become embedded in fat cells and other host cells, where they are not detected by circulating lamellocytes.

COUNTERDEFENSES INVOLVING HUNDREDS OF GENES Some endoparasites have a complex set of adaptations that allows them to thrive inside their host. One such endoparasite is *Plasmodium falciparum*, a protist that causes malaria, a disease that kills 1 to 2 million people each year (**Figure 13.9**). *Plasmodium*, like many endoparasites, has a complex life cycle with specialized stages that allow it to alternate between a mosquito and a human host.

Infected mosquitoes contain one specialized *Plasmodium* stage, called a *sporozoite*, in their saliva. When an infected mosquito bites a human, sporozoites enter the victim's bloodstream and travel to the liver, where they divide to form another stage, called a *merozoite*. The merozoites penetrate red blood cells, where they multiply rapidly. After 48–72 hours, large numbers of merozoites break out of the red blood cells, causing the periodic chills and fever that are associated with malaria. Some of the offspring merozoites attack more red blood cells, while others transform into gamete-producing cells. If another mosquito bites the victim, it picks up some of the gamete-producing cells, which enter its digestive tract and form gametes. After fertilization occurs, the resulting zygotes produce thousands of sporozoites, which then migrate to the mosquito's salivary glands, where they await their transfer to another human host.

Plasmodium faces two potentially lethal challenges from its human host. First, red blood cells do not divide or grow, and hence they lack the cellular machinery needed to import nutrients necessary for growth. A *Plasmodium* merozoite inside a red blood cell would starve if it did not have a way to obtain essential nutrients. Second, after 24–48 hours, a *Plasmodium* infection causes red blood cells to have an abnormal shape. The human spleen recognizes and destroys such deformed cells, along with the parasites inside.

Plasmodium addresses these challenges by having hundreds of genes whose function is to modify the host red blood cell in ways that allow the parasites to obtain food and escape destruction by the spleen (Hiller et al. 2004; Marti et al. 2004). Some of these genes cause transport proteins to be placed on the surface of the red blood cell, thereby enabling the parasite to import essential nutrients into the host cell. Other genes guide the production of unique knobs that are added to the surface of the red blood cell. These knobs cause the infected red blood cell to stick to other human cells, thereby preventing it from traveling in the bloodstream to the spleen, where it would be recognized as infected and then destroyed. The proteins on these knobs vary greatly from one parasite individual to another, making it difficult for the human immune system to recognize and destroy the infected cells.

CONCEPT 13.3

Host and parasite populations can evolve together, each in response to selection pressure imposed by the other.

Parasite–Host Coevolution

As we have just seen, *Plasmodium* has specific mechanisms that enable it to live inside a red blood cell. When a parasite and its host each possess such specific mechanisms, that observation suggests that the strong selection pressure that hosts and parasites impose on each other has caused their populations to evolve. Such changes have been directly observed in Australia, where the myxoma virus was introduced to control populations of the European rabbit (*Oryctolagus cuniculus*).

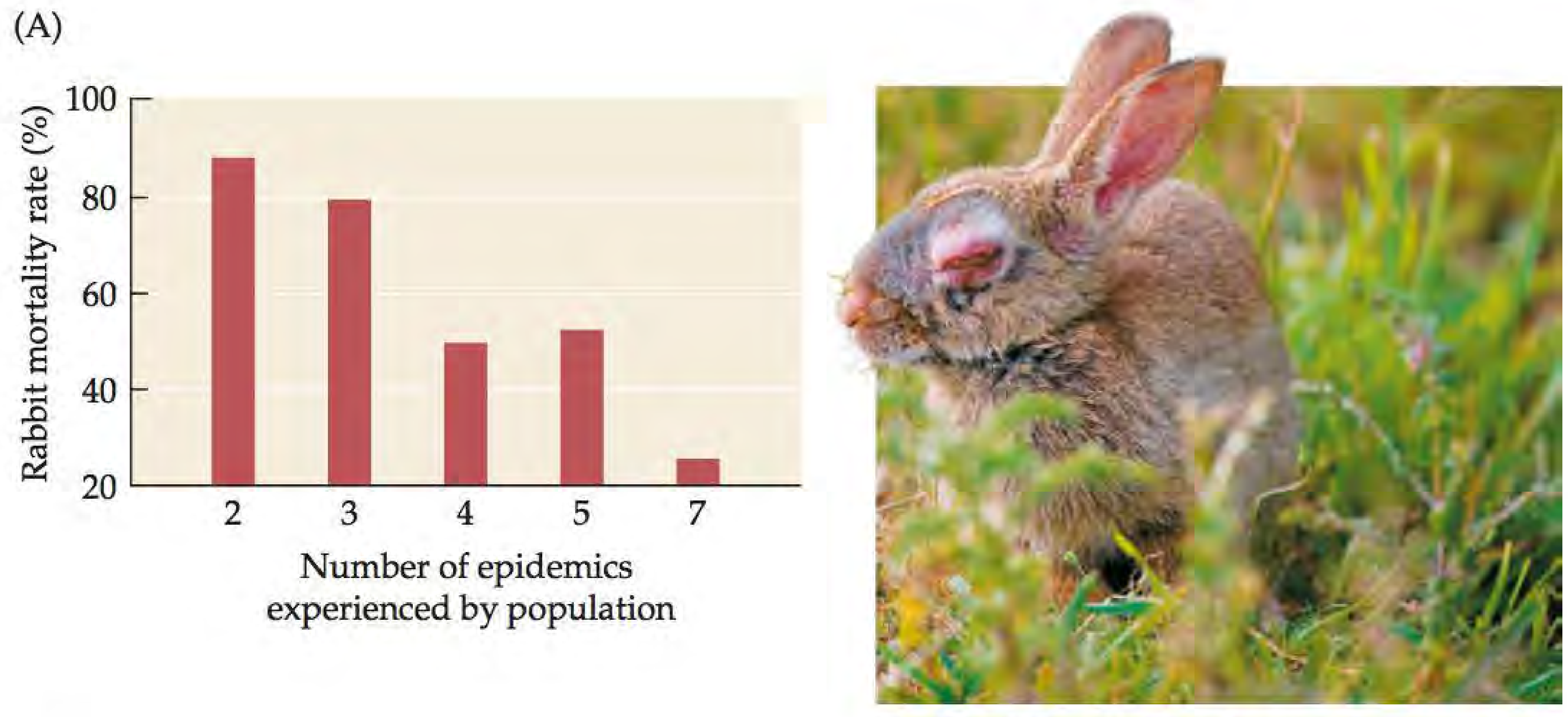
European rabbits were first introduced to Australia in 1859, when 24 wild rabbits were released at a ranch in Victoria. Within a decade, rabbit populations had grown so large, and were consuming so much plant material, that they posed a threat to cattle and sheep pasturelands and wool production. Several control measures were enacted, including introductions of predators, shooting and poisoning of rabbits, and the building of fences to limit the spread of rabbits from one region to another (Fenner and Ratcliffe 1965). None of these methods worked. By the 1900s, hundreds of millions of rabbits had spread throughout much of the continent.

After years of investigation, Australian government officials settled on a new control measure: introduction of the myxoma virus. A rabbit infected with this virus may suffer from skin lesions and severe swellings, which can lead to blindness, difficulty with feeding and drinking, and death (usually within 2 weeks of infection). The virus is transmitted from rabbit to rabbit by mosquitoes. In 1950, when the virus was first used to control rabbit populations, 99.8% of infected rabbits died. In the ensuing decades, millions of rabbits were killed by the virus, and the sizes of rabbit populations dropped dramatically throughout the Australian continent. Over time, however, rabbit populations evolved resistance to the virus, and the virus evolved to become less lethal (**Figure 13.10**). The myxoma virus is still used to control rabbit populations, but doing so requires a constant search for new, lethal virus strains to which the rabbit has not evolved resistance.

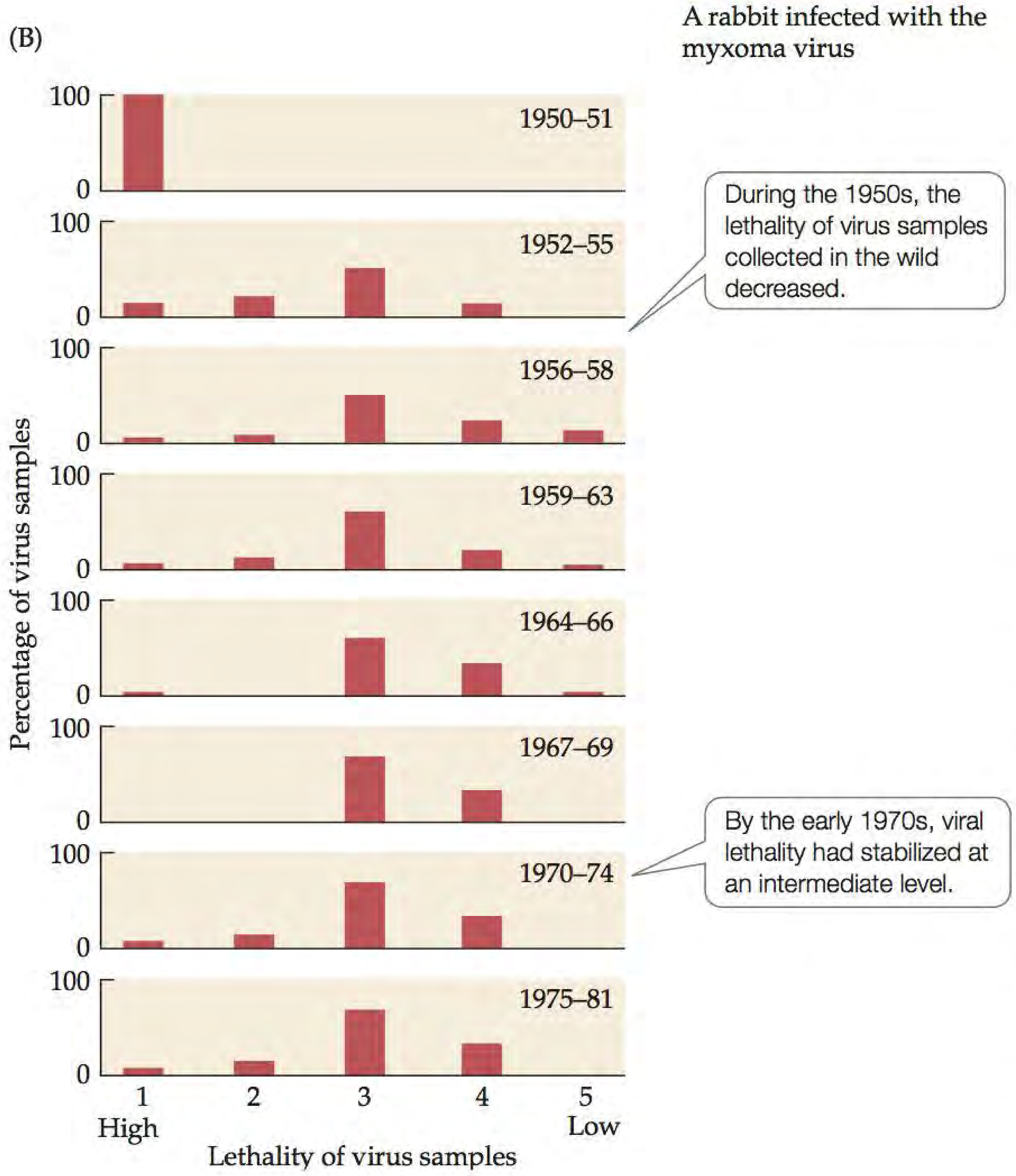
The increased resistance of the rabbit and the reduced lethality of the virus illustrate **coevolution**, which occurs when populations of two interacting species evolve together, each in response to selection pressure imposed by the other. The outcome of coevolution can vary greatly depending on the biology of the interacting species. In the European rabbit, selection favored the evolution of increased resistance to viral attack, as you might expect. In addition, viral strains of intermediate lethality predominated, perhaps because such strains allowed rabbits to live long enough for one or more mosquitoes to bite them and transmit the virus to another host (mosquitoes do not bite dead rabbits). In other cases of host–parasite coevolution, the parasite evolves counterdefenses to overcome host resistance mechanisms, as the following examples illustrate.

Selection can favor a diversity of host and parasite genotypes

As mentioned earlier, plant defense systems include a specific response that makes particular plant genotypes



A rabbit infected with the myxoma virus



During the 1950s, the lethality of virus samples collected in the wild decreased.

By the early 1970s, viral lethality had stabilized at an intermediate level.

Figure 13.10 Coevolution of the European Rabbit and the Myxoma Virus (A) After the introduction of the myxoma virus to Australia, researchers periodically tested its lethality by collecting rabbits from a wild population and exposing them to a standard strain of the virus that killed 90% of naive (unselected) laboratory rabbits. Over time, mortality in those wild rabbits declined as the population evolved resistance to the virus. (B) The lethality of virus samples collected in the wild also declined, as was determined when they were tested against a standard (unselected) line of rabbits. (A after Kerr and Best 1998; B after May and Anderson 1983.)

resistant to particular parasite genotypes. Such *gene-for-gene interactions* are well documented in a number of plant species, including wheat, flax, and *Arabidopsis thaliana*. Wheat has dozens of different genes for resistance to fungi such as wheat rusts (*Puccinia*). Different wheat rust genotypes can overcome different wheat resistance genes, however, and periodically, mutations occur in wheat rusts that produce new genotypes to which wheat is not resistant. Studies have shown that the frequencies of wheat rust genotypes vary considerably over time as farmers use different resistant varieties of wheat. For example, a rust variety may be abundant in one year because it can overcome the resistance genes of wheat varieties planted that year, yet less abundant the following year because it cannot overcome the resistance genes of the different wheat varieties planted that year.

Changes in the frequencies of host and parasite genotypes also occur in natural systems. In the lakes of New Zealand, a trematode worm (*Microphallus* sp.) parasitizes the snail *Potamopyrgus antipodarum*. The worm has serious negative effects on its snail hosts: it castrates the males and sterilizes the females. The parasite has a much shorter generation time than its host, and hence we might expect that it would rapidly evolve the ability to cope with the snail's defensive mechanisms. Lively (1989) tested this idea in an experiment that pitted parasites from each of three lakes against snails from the same three lakes. He found that parasites infected snails from their home lake more effectively than they infected snails from the other two lakes (**Figure 13.11**). This observation suggests that the parasite genotypes in each lake had evolved rapidly enough to overcome the defenses of the snail genotypes found in that lake.

The snails also evolved in response to the parasites, albeit more slowly. Dybdahl and Lively (1998) documented the abundances of different snail genotypes over a 5-year period in another New Zealand lake. The snail genotype that was most abundant changed from one year to the next. Moreover, roughly a year after a snail genotype was the most abundant one in the population, snails of that genotype had a higher than typical number of parasites. Together with Lively's earlier study (1989), these results suggest that parasite populations evolve to exploit the snail genotypes found in their local environment. Refining this idea further, Dybdahl and Lively hypothesized that as a result of evolution by natural selection, parasites would be able to infect snails with a common genotype at a higher rate than they could

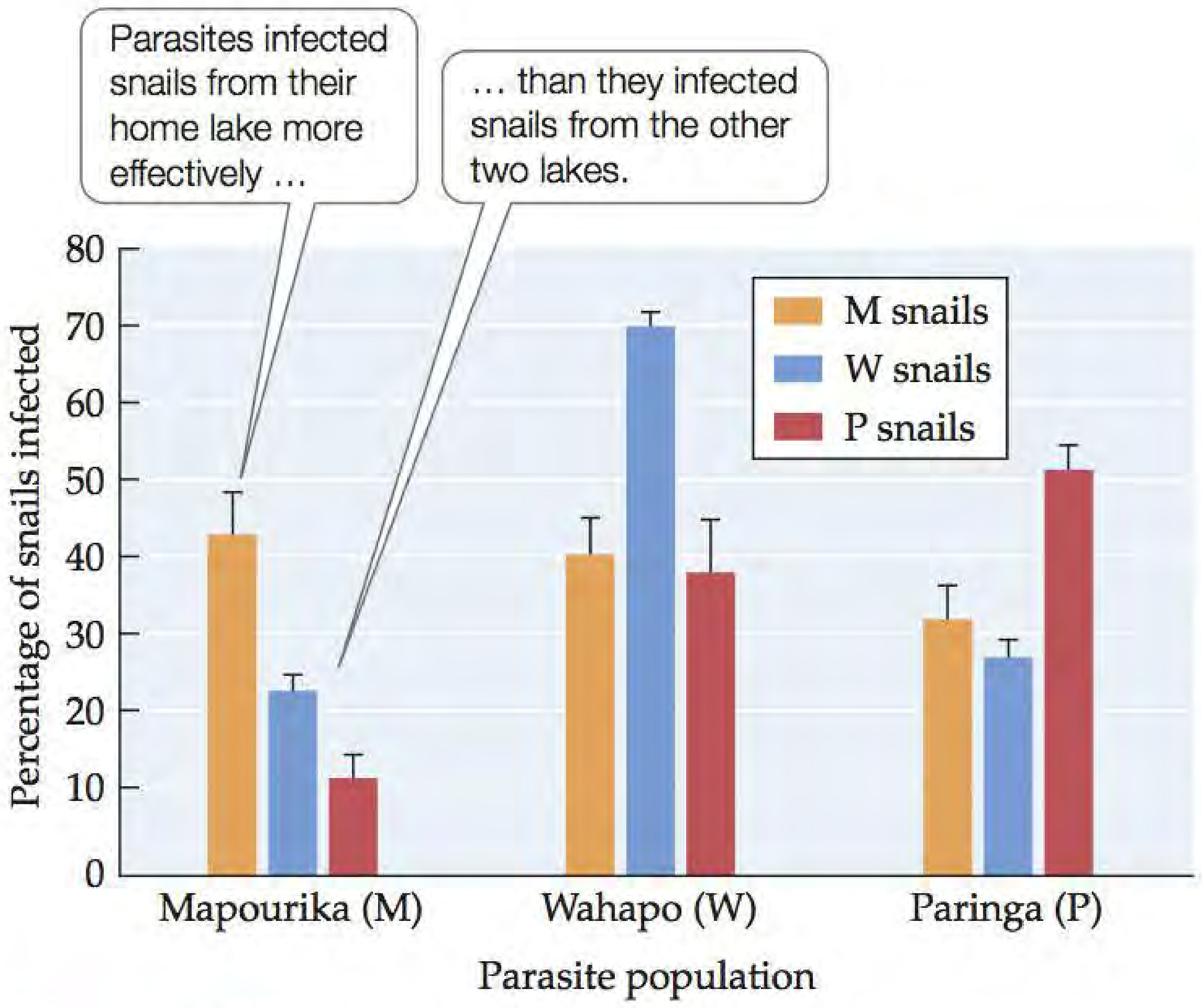


Figure 13.11 Adaptation by Parasites to Local Host Populations The graph shows the frequencies with which *Microphallus* parasites from three lakes in New Zealand (Lake Mapourika, Lake Wahapo, and Lake Paringa) were able to infect snails (*Potamopyrgus antipodarum*) from the same three lakes. Error bars show one SE of the mean. (After Lively 1989.)

? Do snails with poor defenses against parasites from their own lake also have poor defenses against parasites from other lakes? Explain.

Lake Paringa

infect snails with a rare genotype. That is exactly what they found in a laboratory experiment (**Figure 13.12**). Hence, snail genotype frequencies may change from year to year because common genotypes are attacked by many parasites, placing them at a disadvantage and driving down their numbers in future years.

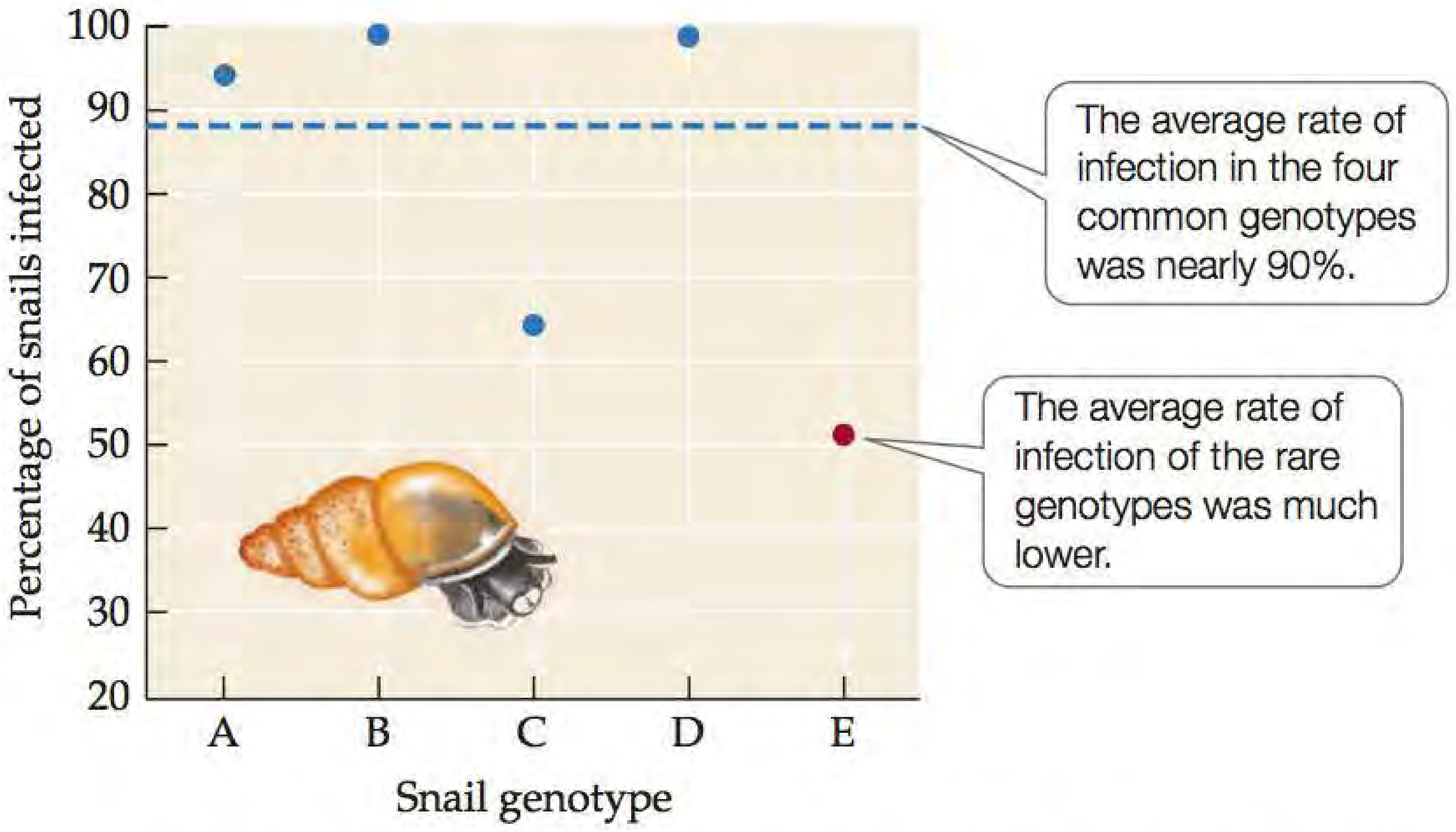


Figure 13.12 Parasites Infect Common Host Genotypes More Easily Than Rare Genotypes In a laboratory experiment, Dybdahl and Lively compared rates of *Microphallus* infection in four common snail genotypes (A–D, represented by blue dots) and in a group of 40 rare snail genotypes (E, represented by a red dot). The parasites and snails in this experiment were all taken from the same lake. (After Dybdahl and Lively 1998.)

Host defenses and parasite counterdefenses both have costs

Parasites and hosts have such a powerful effect on each other that we might expect an ever-escalating "arms race" in which host resistance and parasite counterdefenses both get stronger and stronger over time. But such an outcome rarely occurs. In some cases—as in Dybdahl and Lively's snails and trematodes—host genotypes that are common decrease in frequency because they are attacked by many parasites, leading to an increase in the frequency of a previously rare genotype, and the arms race continually begins anew. An arms race may also stop because of trade-offs: a trait that improves a host's defenses or a parasite's counterdefenses may have costs that reduce other aspects of the organism's growth, survival, or reproduction.

Such trade-offs have been documented in a number of host–parasite systems, including *Drosophila* fruit flies and the parasitoid wasps that attack them (described on p. 301). Alex Kraaijeveld and colleagues (2001) have shown that selection can increase both the frequency with which fruit fly hosts encapsulate wasp eggs (from 5% to 60% in five generations) and the ability of wasp eggs to avoid encapsulation (from 8% to 37% in ten generations). But they have also shown that there are costs to these defenses and counterdefenses. For example, fruit flies from lineages that can mount an encapsulation defense have lower larval survival rates when they compete for food with flies of the same species that cannot. Similarly, wasp eggs that avoid encapsulation by becoming embedded in host tissues take longer to hatch than do other eggs.

The evolutionary changes in host and parasite populations that we've discussed in this section reflect the profound effects these organisms have on each other. Next, we'll focus on some of the ecological consequences of host–parasite interactions.

CONCEPT 13.4

Hosts and parasites can have important effects on each other's population dynamics.

Host–Parasite Population Dynamics

As we've seen, parasites can reduce the survival, growth, or reproduction of their hosts—an observation that is illustrated clearly by the large drop in reproductive success that a sexually transmitted mite can inflict on its beetle host (**Figure 13.13**). At the population level, the harm that parasites cause host individuals translates into a reduction of the host population growth rate, λ (see Concept 10.2). As we will see in this section, the reduction in λ can be drastic: parasites may drive local host populations extinct or even reduce the geographic range of the host species. In other, less extreme cases, parasites may reduce host abundances or otherwise alter host population dynamics without causing the extinction of host populations.

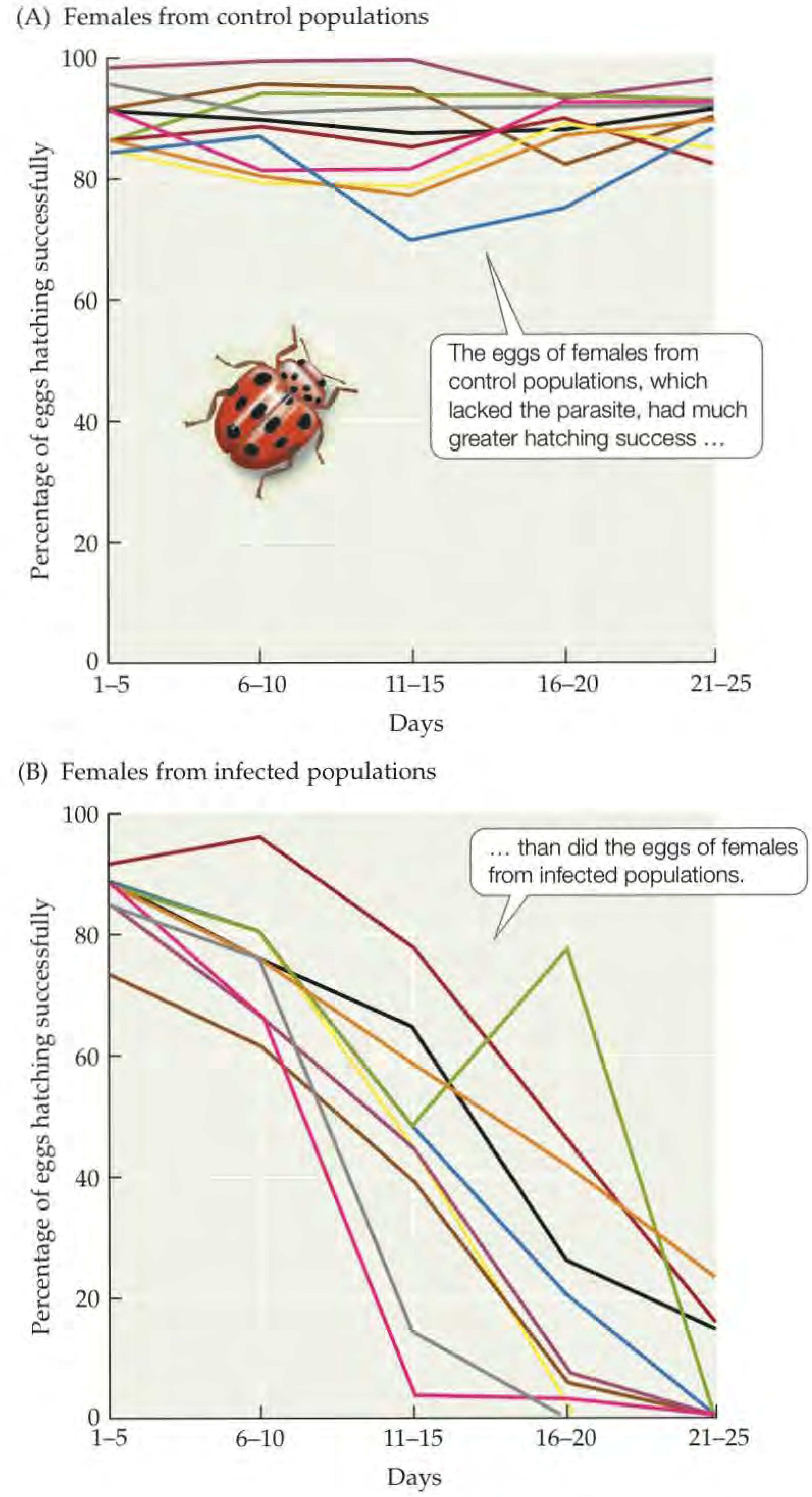


Figure 13.13 Parasites Can Reduce Host Reproduction Researchers infected experimental populations of the beetle *Adalia decempunctata* with a sexually transmitted mite parasite (*Coccipolipus hippodamiae*). Over the next 25 days, they monitored the proportions of the eggs laid by female beetles from (A) control and (B) infected populations that hatched. Each curve represents the eggs laid by a single female. (After Webberley et al. 2004.)

Parasites can drive host populations to extinction

The amphipod *Corophium volutator* lives in North Atlantic tidal mudflats. *Corophium* is small (1 cm long) and often very abundant, reaching densities of up to 100,000 individuals per square meter. *Corophium* builds tubular burrows in the mud, from which it feeds on plankton suspended in the water and on microorganisms found in sediments near the burrow opening. It is eaten by a wide range of organisms, including migratory birds and trematode parasites. The parasites can reduce the size of *Corophium* populations greatly, even to the point of local extinction. For example, in a 4-month period, attack by trematodes caused the extinction of a *Corophium* population that initially had 18,000 individuals per square meter (Mouritsen et al. 1998).

Parasites can also drive host populations to extinction over a large geographic region. The American chestnut (*Castanea dentata*) once was a dominant member of deciduous forest communities in eastern North America (**Figure 13.14**), but the parasitic fungus *Cryphonectria parasitica* changed that completely. This fungal pathogen causes chestnut blight, a disease that kills chestnut trees. The fungus was introduced to New York City from Asia in 1904 (Keever 1953). By midcentury, the fungus had wiped out most chestnut populations, greatly reducing the geographic range of this once-dominant species.

Isolated chestnut trees still can be found in North American forests, and some of these trees show signs of resistance to the fungus. But it is likely that many of the standing trees simply have not yet been found by the fungus. Once the fungus reaches a tree, it enters the tree through a hole or wound in the bark, killing the aboveground portion of the tree in 2–10 years. Before they die, infected trees may produce seeds, which may germinate and give rise to offspring that live for 10–15 years before they are killed by the fungus in turn. Some infected trees also produce sprouts from their roots, but these are usually killed a few years after they appear aboveground.

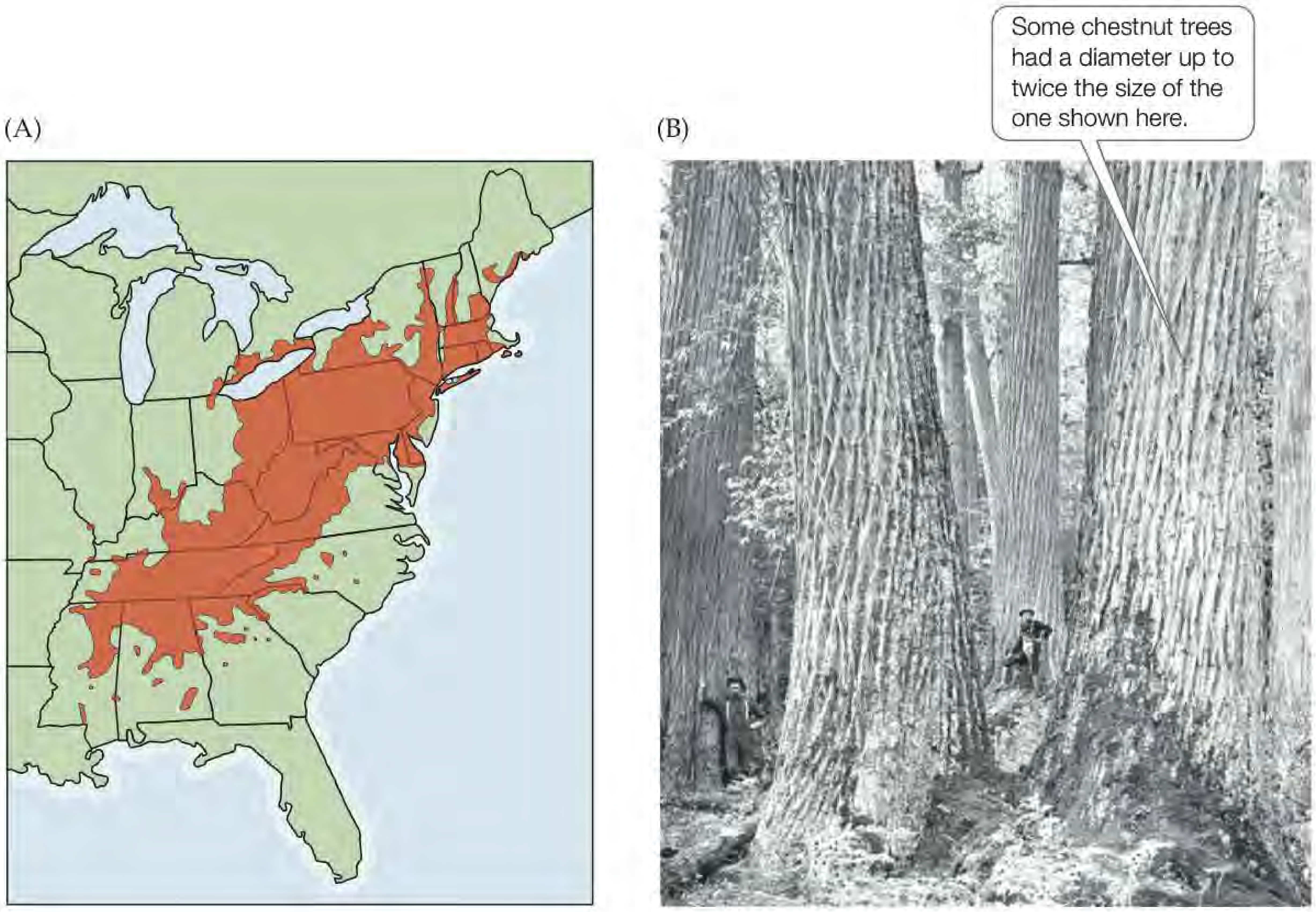


Figure 13.14 Parasites Can Reduce Their Host's Geographic Range (A) The original distribution of the American chestnut (*Castanea dentata*) is shown in red. Although a few chestnut trees remain standing, a fungal parasite drove this once-dominant species virtually extinct throughout its entire former range. (B) Chestnuts were once important timber trees (note the two loggers shown in the photograph). (Photo courtesy of the Forest History Society, Durham, NC.)

Efforts are under way to breed resistant chestnut varieties, but at present it is not known whether chestnut populations will ever recover from the onslaught of the chestnut blight fungus.

Parasites can influence host population cycles

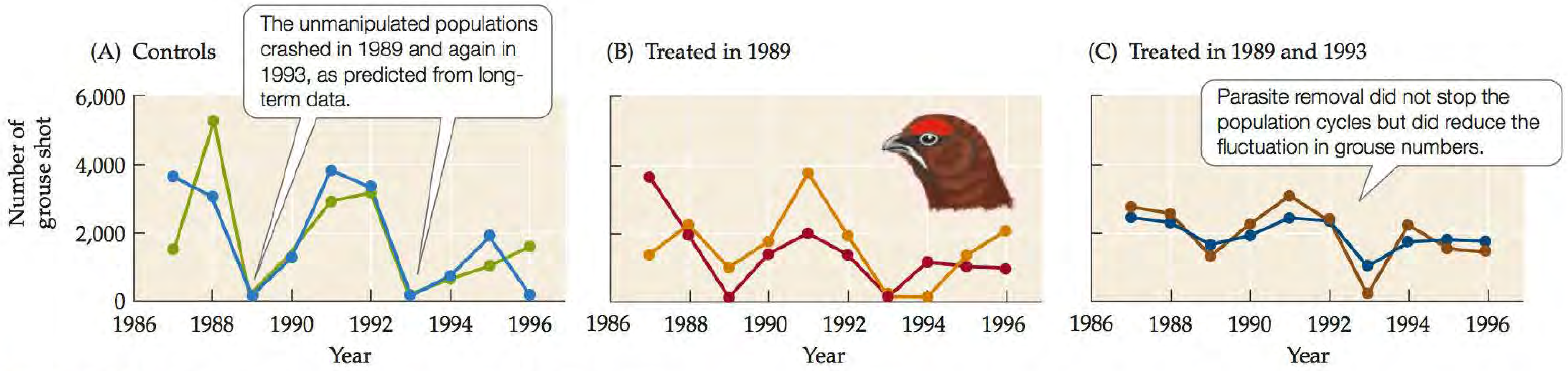
Ecologists have long sought to determine the causes of population cycles. As we saw in Concept 12.3, such cycles may be caused by three-way feeding relationships—by the effects that predators and herbivorous prey have on each other, coupled with the effects that those prey and their food plants have on each other.

Population cycles can also be influenced by parasites. Consider the work of Peter Hudson and colleagues, who manipulated the abundances of parasites in red grouse (*Lagopus lagopus*) populations on moors in northern England. In this region, red grouse populations tend to crash every 4 years. Previous studies had shown that a parasitic nematode, *Trichostrongylus tenuis*, decreased the survival and reproductive success of individual red grouse. Hudson et al. (1998) investigated whether this parasite might also cause grouse populations to cycle.

The researchers studied changes in red grouse numbers in six replicate populations over the course of two population cycles. Long-term data on grouse population cycles indicated that these populations were likely to crash in 1989 and again in 1993. In two of the six study populations, the researchers treated as many grouse as they could catch in 1989 and 1993 with a drug that killed the parasitic nematodes. In two of the other study populations, grouse were caught and treated for parasites in 1989 only. The remaining two populations served as unmanipulated controls. Because each replicate population covered a very large area (17–20 km^2), it was not possible to count red grouse directly. Instead, Hudson and colleagues used the number of red grouse shot by hunters as an index of the actual population size.

In the control populations, red grouse numbers crashed as predicted in 1989 and 1993 (**Figure 13.15**). Although parasite removal did not completely stop the red grouse population cycle, it did reduce the fluctuation in grouse numbers considerably; this was particularly true for the populations that were treated for parasites in both 1989 and 1993. Thus, the experiment provided strong evidence that parasites influence—and may be the primary cause of—red grouse population cycles.

As we've seen, parasites that cause diseases (pathogens) can greatly affect the population dynamics of both wild and domesticated plant and animal species. Pathogens also have large effects on human populations—so much so that they are thought to have played a major role in the rise and fall of civilizations throughout the course of human history (McNeill 1976; Diamond 1997). One example is the European conquest of North America, where up to 95% of the native population (19 million of the original 20 million) were killed by new diseases brought to the continent by European trappers, missionaries, settlers, and soldiers. Even with such massive mortality, the conquest took roughly 400 years; without it, the conquest would certainly have taken longer, and might have failed. Pathogens continue to be a major source of human mortality today. Despite medical advances, millions of people die each year from diseases such as AIDS, tuberculosis, and malaria.


(A) Controls

The unmanipulated populations crashed in 1989 and again in 1993, as predicted from long-term data.

(B) Treated in 1989

(C) Treated in 1989 and 1993

Parasite removal did not stop the population cycles but did reduce the fluctuation in grouse numbers.

Figure 13.15 Parasite Removal Reduces Host Population Fluctuations Hudson et al. studied the effects of parasites on the cycling of six red grouse populations subjected to three treatments: (A) two control populations, (B) two populations treated for nematode parasites in 1989, and (C) two populations treated for parasites in 1989 and 1993. The six replicate populations are designated by different colors. (After Hudson et al. 1998.)

? If parasite removal completely stopped the population cycles, how might the results in (C) differ from those actually obtained?

Simple models of host–pathogen dynamics suggest ways to control the establishment and spread of diseases

Considerable effort has been devoted to the development of mathematical models of host–pathogen population dynamics. These models often differ in three ways from those we have seen in earlier chapters. First, the host population is subdivided into categories, such as susceptible individuals, infected individuals, and recovered and immune individuals. Second, it is often necessary to keep track of both host and pathogen genotypes because, as we have seen, host genotypes may differ greatly in their resistance to the pathogen, and pathogen genotypes may differ greatly in their ability to cause disease. Third, depending on the pathogen, it may be necessary to account for other factors that influence its spread, such as (1) differences in the likelihood that hosts of different ages will become infected; (2) a latent period, in which a host individual is infected but cannot spread the disease; and (3) vertical transmission, the spread of the disease from mother to newborn, as can occur in AIDS.

Models that include all of these factors can be very complicated. Here we'll consider a simple model that does not incorporate most of these complicating factors, yet still yields a key insight: a disease will spread only if the density of susceptible hosts exceeds a critical **threshold density**.

To develop a model that can be used to estimate the threshold density, we must determine how to represent the transmission of the disease from one host individual to the next. We'll denote the density of susceptible individuals by S and the density of infected individuals by I. For a disease to spread, infected individuals must encounter susceptible individuals. Such encounters are assumed to occur at a rate that is proportional to the densities of susceptible and infected individuals; here, we'll assume that this rate is proportional to the product of their densities, SI. Diseases do not spread with every such encounter, however, so we multiply the encounter rate (SI) by a transmission coefficient (β) that indicates how effectively the disease spreads from infected to susceptible individuals. Thus, an essential feature of the model—disease transmission—is represented by the term βSI.

The density of infected individuals increases when the disease is transmitted successfully (at the rate βSI) and decreases when infected individuals die or recover from the disease. If we set the combined death and recovery rate equal to m, these assumptions yield the equation

$$\frac{dI}{dt} = \beta SI - mI \tag{13.1}$$

where dI/dt represents the change in the density of infected individuals at each instant in time.

A disease will become established and spread when the density of infected individuals in a population increases over time. As explained in more detail in **Web Extension 13.2**, this occurs when dI/dt is greater than zero, which, according to Equation 13.1, occurs when

$$\beta SI - mI > 0$$

We can rearrange this equation to get

$$S > \frac{m}{\beta}$$

Thus, a disease will become established and spread when the number of susceptible individuals exceeds m/β; this number of susceptible individuals is the threshold density, denoted by S_T. In other words,

$$S_T = \frac{m}{\beta}$$

For some diseases that affect people or animals, the transmission rate β and the death and recovery rate m are known, permitting estimation of the threshold density.

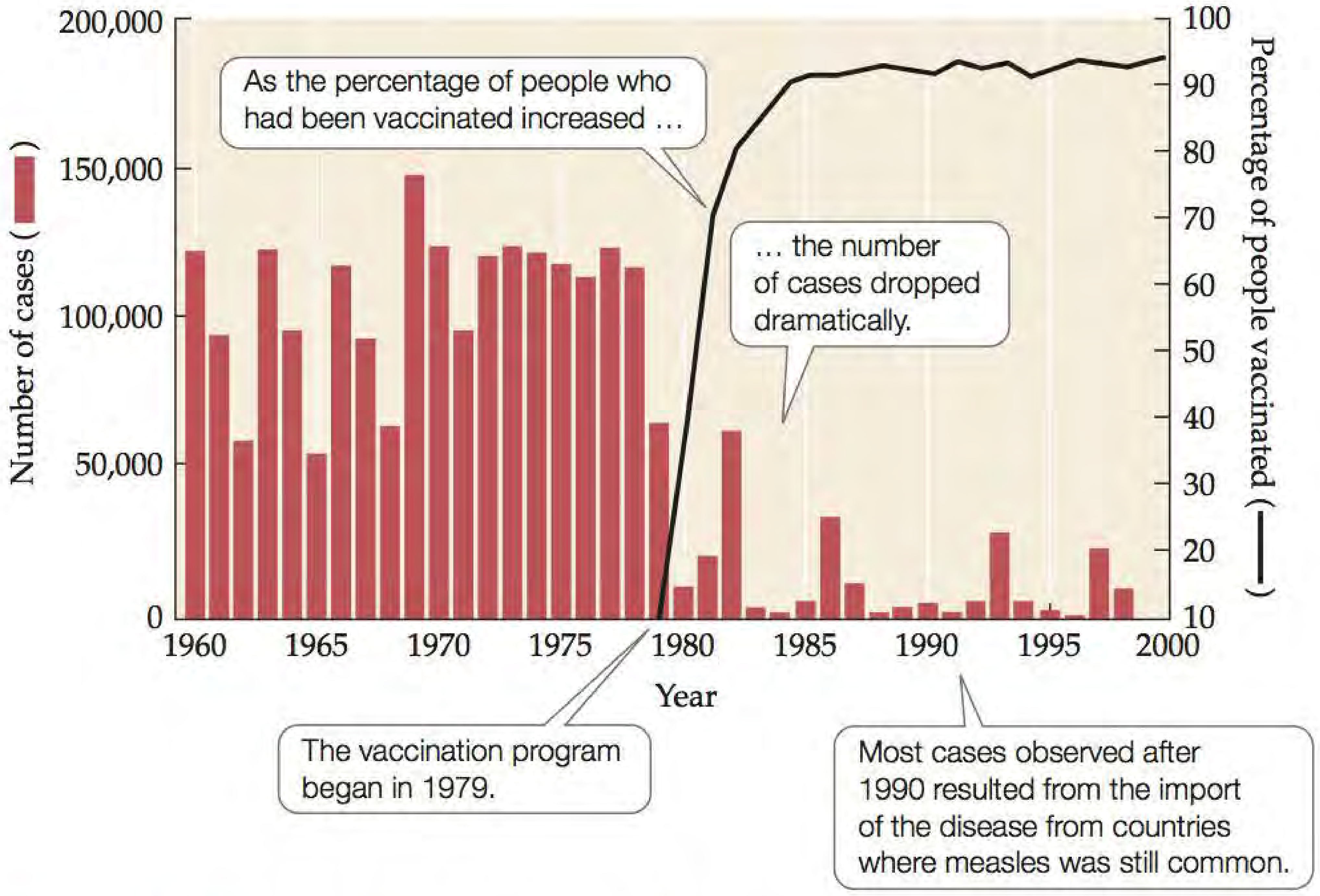


Figure 13.16 Vaccination Reduces the Incidence of Measles in Humans The results of a measles vaccination program in Romania show that lowering the density of susceptible individuals can control the spread of a disease. Measles often kills (especially in populations that are poorly nourished or that lack a history of exposure to the disease) and can cause severe complications in survivors, including blindness and pneumonia. (After Strebel and Cochi 2001.)

CONTROLLING THE SPREAD OF DISEASES As Equation 13.1 suggests, to prevent the spread of a disease, the density of susceptible individuals must be kept below the threshold density (S_T). There are several ways of achieving this goal. People sometimes slaughter large numbers of susceptible domesticated animals to reduce their density below S_T and hence prevent disease spread. This is typically done when the disease in question can spread to humans, as in highly virulent forms of bird flu. In human populations, if an effective and safe vaccine is available, the density of susceptible individuals can be reduced below S_T by a mass vaccination program. Such programs work, as illustrated by the dramatic results of a measles vaccination program in Romania (**Figure 13.16**).

Other public health measures can also be taken to raise the threshold density, thereby making it more difficult for the disease to become established and spread. For example, the threshold density can be raised by taking actions that increase the rate at which infected individuals recover and become immune (thereby increasing m and hence increasing $S_T = m/\beta$). One way to increase the recovery rate is to improve the early detection and clinical treatment of the disease. The threshold density can also be raised if β, the disease transmission rate, is decreased. This can be achieved by quarantining infected individuals or by convincing people to engage in behaviors (such as hand washing or condom use) that make it more difficult for the disease to be transmitted from one person to the next.

The same principles can be applied to wild populations. Dobson and Meagher (1996) studied bison populations to determine how best to prevent the spread of the bacterial disease brucellosis. Using data from previous studies in which 16 bison herds in six national parks in Canada and the United States had been tested for exposure to the disease, they found that the threshold density (S_T) for disease establishment appeared to be a herd size of 200–300 bison (**Figure 13.17**). This field-based estimate of S_T was very similar to the estimated threshold density of 240 individuals calculated from a model similar to Equation 13.1. Many of the herds in the six national parks had 1,000–3,000 individuals, so reducing herd sizes below a threshold value of 200–300 individuals would require implementing a vaccination program or killing large numbers of bison. An effective vaccine was not available, and killing many bison was not acceptable, either politically or ecologically (since herds as small as 200 individuals

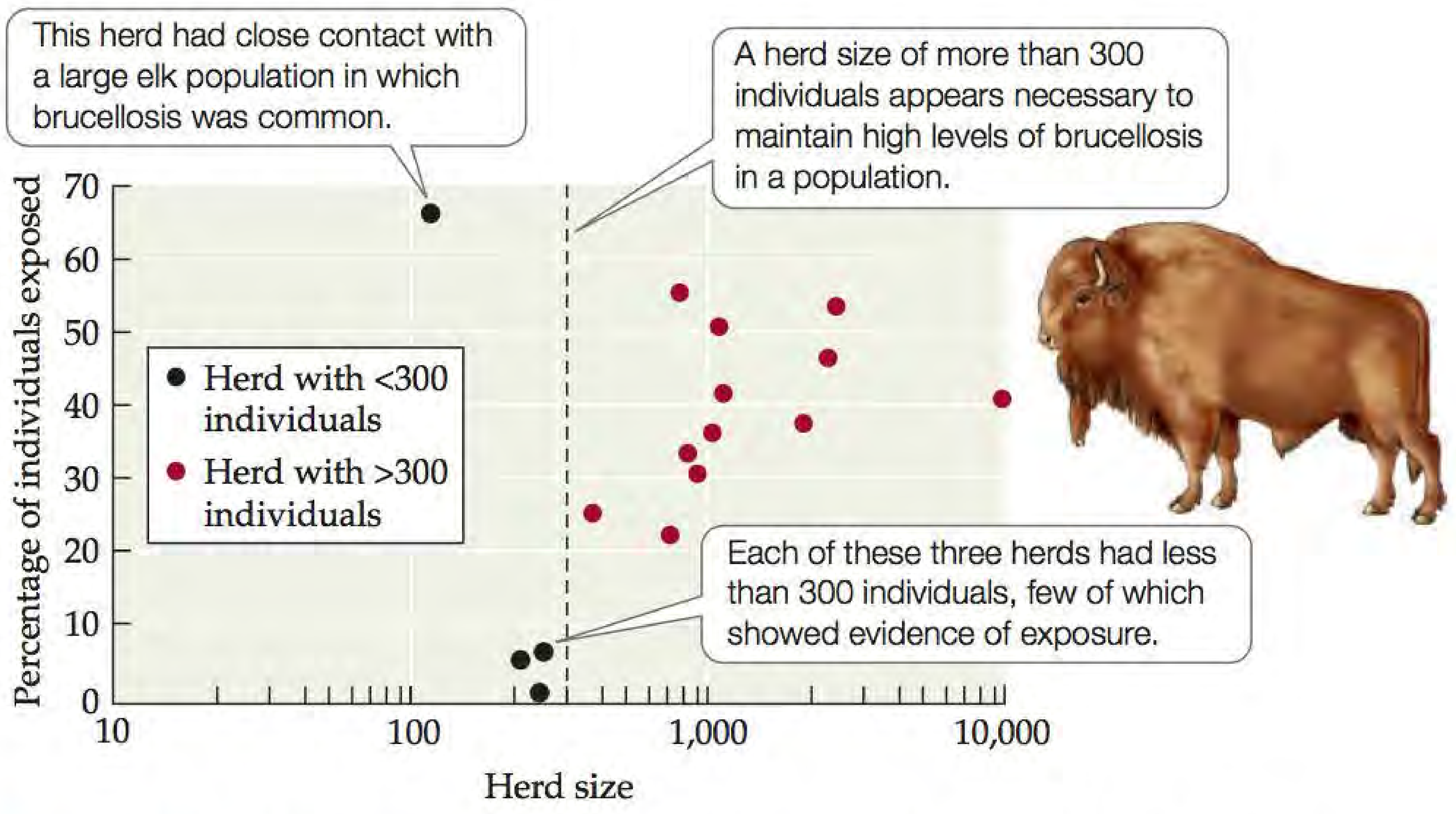


Figure 13.17 Determining Threshold Population Densities for Disease Control The percentage of bison that showed evidence of previous exposure to brucellosis was monitored in six national parks in the United States and Canada. By plotting this percentage versus the size of each of 16 bison herds, researchers obtained a rough estimate of the threshold density for establishment of the disease (200–300 individuals, the upper bound of which is shown by the dotted line). (After Dobson and Meagher 1996.)

would face an increased risk of extinction). Thus, Dobson and Meagher concluded that it would be difficult to prevent the establishment of brucellosis in wild bison populations.

CONCEPT 13.5

Parasites can alter the outcomes of species interactions, thereby causing communities to change.

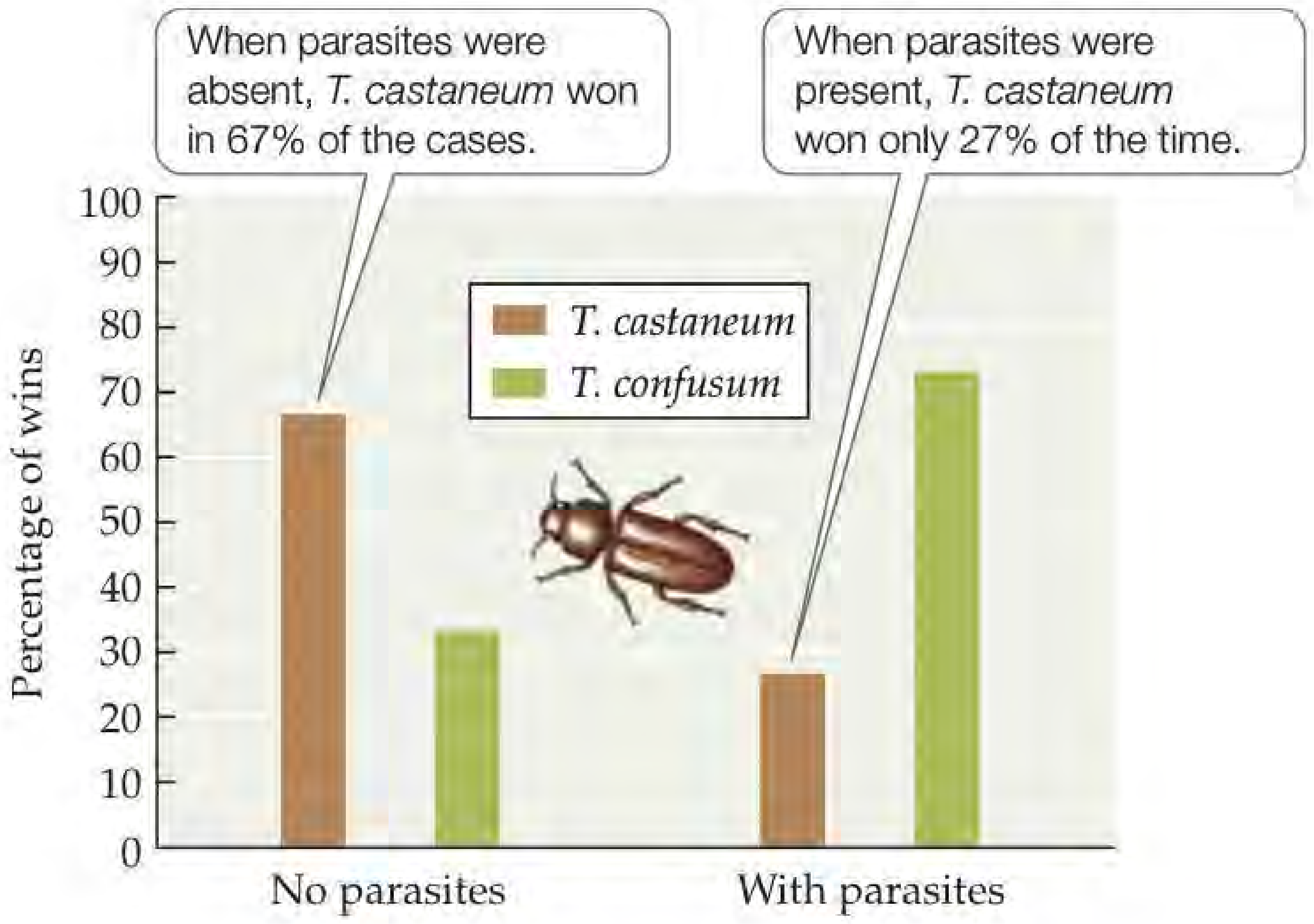
Parasites Can Change Ecological Communities

The effects of parasites on their hosts can have ripple effects on communities: by reducing the performance of host individuals and the growth rates of host populations, parasites can change the outcome of species interactions, the composition of ecological communities, and even the physical environment in which a community is found.

Changes in species interactions

When two individual organisms interact with each other, the outcome of that interaction depends on many features of their biology. An individual predator that is young and healthy may be able to catch its prey—even though the prey organism literally "runs for its life"—whereas a predator that is old or sick may go hungry. Similarly, an individual that is in good condition may be able to compete effectively with others for resources, while an individual in poor condition may not.

Because they can affect host performance, parasites can affect the outcome of interactions between their hosts and other species. Thomas Park conducted a series of experiments on factors that influenced the outcome of competition between flour beetle species. In one of those experiments, Park (1948) examined how the protist parasite *Adelina tribolii* affected the outcome of competition experiments using two species of flour beetles, *Tribolium castaneum* and *T. confusum*. In the absence of the parasite, *T. castaneum* usually outcompeted *T. confusum*, driving it to extinction in 12 of 18 cases (**Figure 13.18**). The reverse was true when the parasite was present: *T. confusum* outcompeted *T. castaneum* in 11 of 15 cases. The outcome of competition was reversed because the parasite had a large negative effect on *T. castaneum* individuals, but virtually no effect on *T. confusum*. Parasites can also affect the outcome of competition in the field, as when the malaria parasite *Plasmodium azurophilum* reduced the competitive superiority of the lizard *Anolis gingivinus* over its smaller counterpart, *A. wattsi* (Schall 1992). Finally, parasites can alter the outcome of predator–prey interactions: by decreasing the physical condition of infected individuals, parasites may make predators less able to catch their prey, or prey less able to escape predation.



When parasites were absent, *T. castaneum* won in 67% of the cases.

When parasites were present, *T. castaneum* won only 27% of the time.

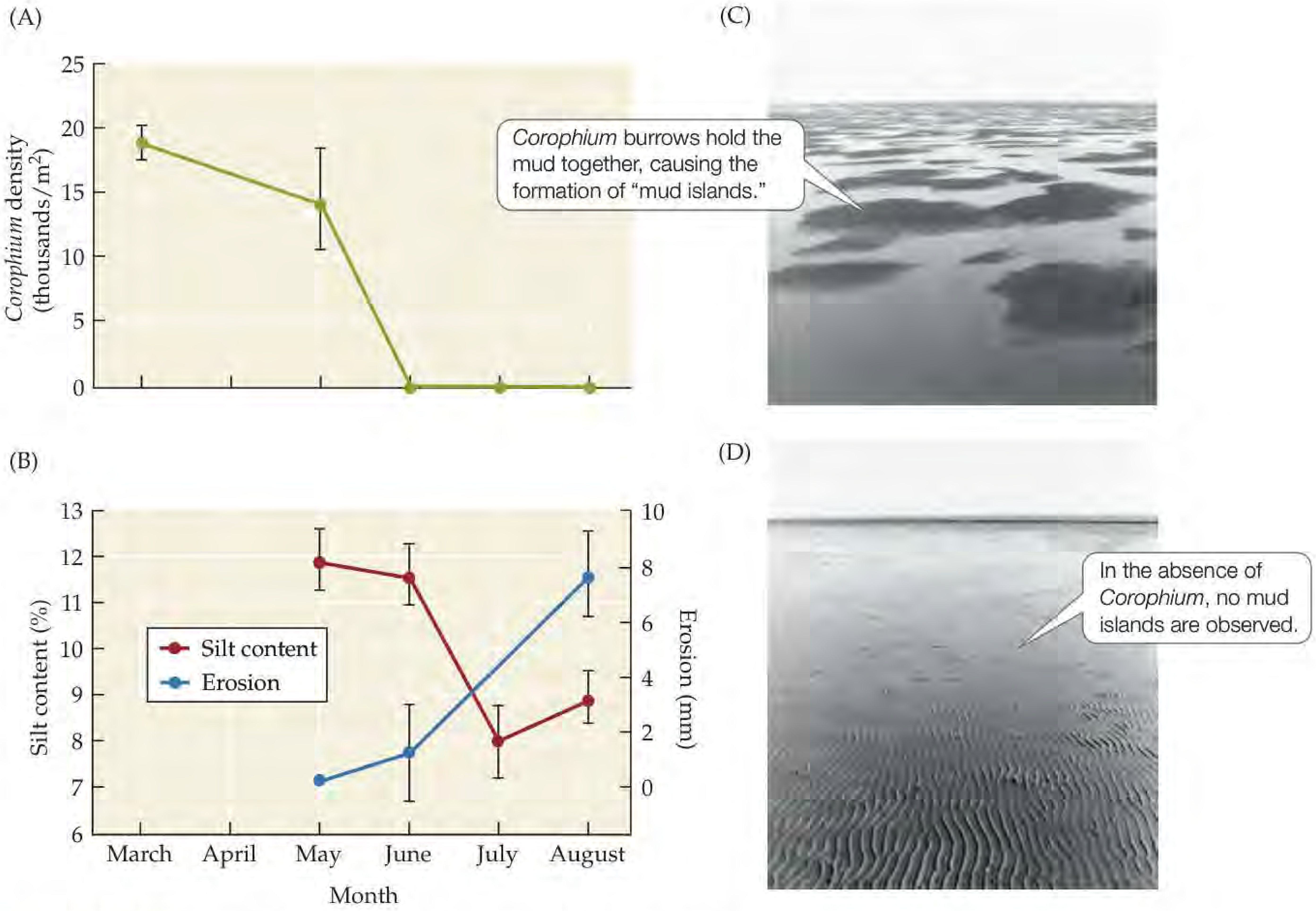
Figure 13.18 Parasites Can Alter the Outcome of Competition Thomas Park performed competition experiments using populations of the flour beetles *Tribolium castaneum* and *T. confusum* that were or were not infected with a protist parasite. (After Park 1948.)

In the examples described in the previous paragraph, parasites affected the outcome of species interactions by altering the physical condition of their host. Parasites can also alter the outcome of species interactions by changing host behavior. For example, when infected by a parasite, the host may behave in an unusual manner that makes it more vulnerable to predation. There are numerous examples of this phenomenon, including protist parasites making rats less wary of cats, as described in the Case Study. Some worm parasites cause amphipods to move from sheltered areas to areas of relatively bright light, where the amphipods are more likely to be seen and eaten by fish or bird predators. In both of these cases, the parasite induces a change in host behavior that makes the host more likely to be eaten by a species that the parasite requires to complete its life cycle.

Changes in community structure

As we'll discuss in Chapter 16, ecological communities can be characterized by the number and relative abundances of the species they contain as well as by physical features of the environment. Parasites can alter and be altered by each of these aspects of communities.

In this chapter, we have seen several cases in which a parasite reduced the abundance, or even the geographic range, of its host, and we have also seen that parasites can change the outcome of species interactions. Such changes can have profound effects on the composition of communities. For example, a parasite that attacks a dominant competitor can suppress that species, causing the abundances of inferior competitors to increase. Such an effect was observed in six stream communities studied by Kohler and Wiley (1997). Prior to recurrent outbreaks of a fungal pathogen, the caddisfly *Glossosoma nigrior* was



Corophium burrows hold the mud together, causing the formation of "mud islands."

In the absence of *Corophium*, no mud islands are observed.

Figure 13.19 Parasites Can Alter the Physical Environment Infection of the amphipod *Corophium volutator* by a trematode parasite affects not only the host, but its entire tidal mudflat community. (A) The trematode can drive amphipod populations to local extinction. (B) In the absence of *Corophium*, the erosion rate increases and the silt content of the mudflats decreases. (C,D) The overall physical structure of the mudflats also changes [compare (C) with (D)]. Error bars show ± one SE of the mean. (A,B after Mouritsen and Poulin 2002; C,D from Mouritsen et al. 1998.)

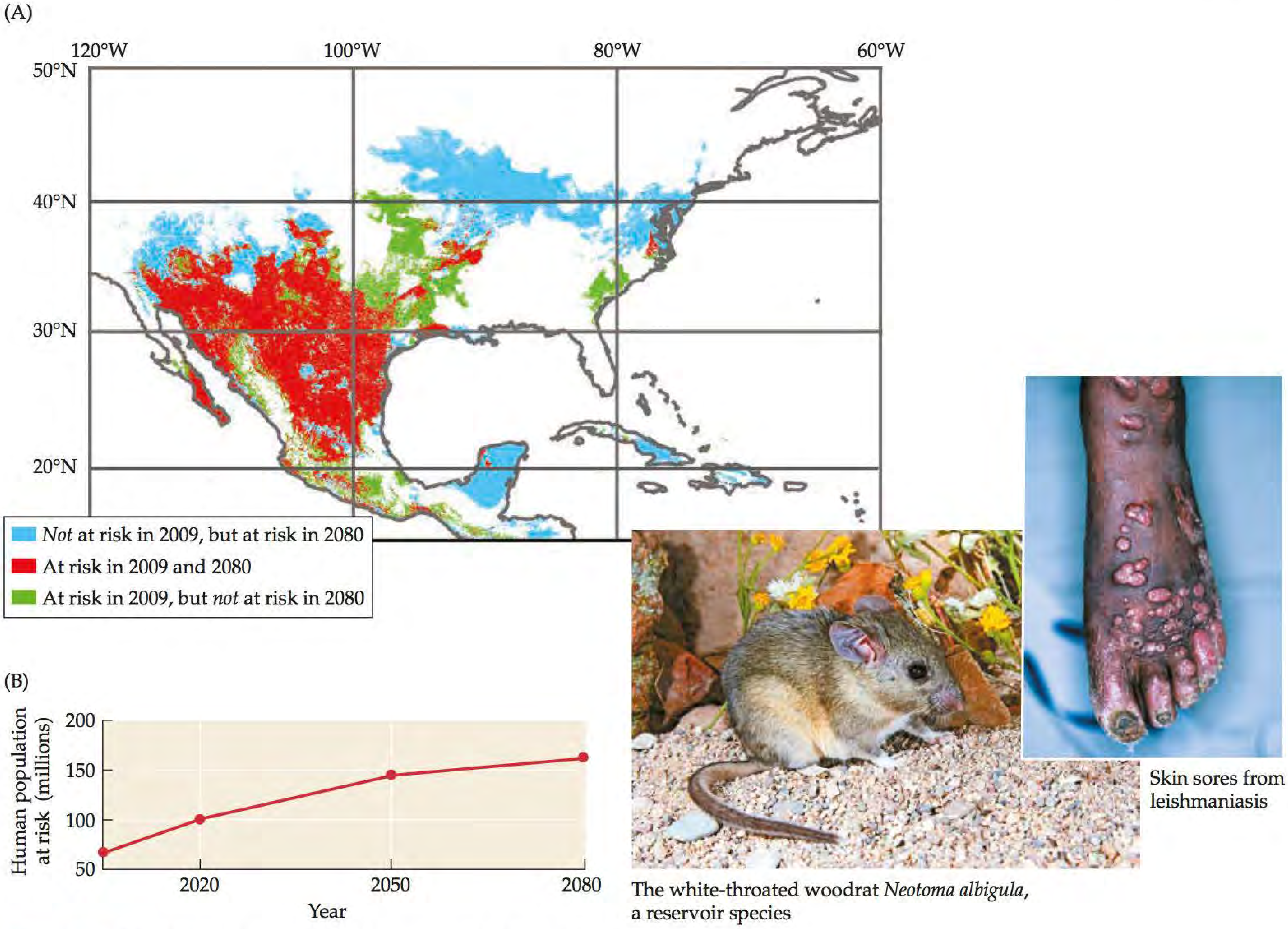
the dominant herbivore in each of the six communities. The fungus devastated *Glossosoma* populations, reducing their densities nearly 25-fold, from an average of 4,600 individuals per square meter to an average of 190 individuals per square meter. This drastic reduction in *Glossosoma* density allowed increases in the abundances of dozens of other species, including algae, grazing insects that ate algae, and filter feeders such as blackfly larvae. In addition, several species that previously were extremely rare or absent from the communities were able to establish thriving populations, thus increasing the diversity of the communities.

Parasites can also cause changes in the physical environment. This can happen when a parasite attacks an organism that is an *ecosystem engineer*, a species whose actions change the physical character of its environment, as when a beaver builds a dam (see Concept 16.3). As we learned earlier in Concept 13.4, the amphipod *Corophium volutator* can function as an ecosystem engineer in its tidal mudflat environment: in some circumstances, the burrows it builds hold the mud together, preventing the erosion of silt and causing the formation of "mud islands" that rise above the surface of the water at low tide. As described earlier, trematode parasites can drive local *Corophium* populations to extinction (**Figure 13.19A**). When this happens, erosion rates increase, the silt content of the mudflats decreases, and the mud islands disappear (**Figure 13.19B–D**). Along with these physical changes, in one instance, the abundances of ten large species in the mudflat community changed considerably in the presence of the parasite, including one species (a ribbon worm) that was driven to local extinction (K. N. Mouritsen, personal communication).

Finally, certain aspects of a community can be important in pathogen success and disease transmission. As we will learn in the Case Study in Chapter 19, the species diversity within a community can reduce the emergence and transmission of infectious diseases in wildlife and humans.

CLIMATE CHANGE CONNECTION

Climate Change and Disease Spread Climate affects the physiology of organisms, the distribution and abundance of populations, and the outcome of interactions between species (see Chapter 2). As a result, changes in climate are expected to have wide-ranging effects on ecological



The white-throated woodrat *Neotoma albigula*, a reservoir species

Skin sores from leishmaniasis

Figure 13.20 Climate Change May Increase the Risk of Leishmaniasis in North America Leishmaniasis can cause severe skin sores, difficulty breathing, immune system impairment, and other complications that can lead to death. There are currently 2 million new cases each year. Leishmaniasis is caused by protists in the genus *Leishmania* and spread by sand flies (blood-sucking insects in the genera *Lutzomyia* and *Phlebotomus*). In addition to infecting humans, the pathogen can persist in several reservoir species (rodents in the genus *Neotoma*). (A) Change in the geographic regions in which people are predicted to be at risk from leishmaniasis due to the presence of at least one vector and reservoir species. (B) Change in numbers of people predicted to be at risk due to the presence of at least one vector and reservoir species. (After González et al. 2010.)

communities. For example, because mosquitoes and other *vectors* (organisms that transmit pathogens from one host to another) are often more active or produce more offspring under warm conditions, scientists have predicted that ongoing climate change may cause the incidence of some diseases to rise in human and wildlife populations (Epstein 2000; Harvell et al. 2002).

A growing body of evidence supports this prediction. In one such study, increases in ocean temperatures were strongly correlated with increases in coral diseases along Australia's Great Barrier Reef (Bruno et al. 2007). Similar results have been found in corals at other locations, as well as in a variety of amphibian and shellfish populations (Harvell et al. 2009).

Climate change is also expected to change the distributions of some pathogens and their vectors by changing the locations where conditions are suitable for those organisms. For example, González et al. (2010) found that climate change is likely to increase the risk of leishmaniasis in North America by increasing the geographic ranges of its reservoir species (rodents in the genus *Neotoma* that can harbor the pathogen) and its sand fly vectors (**Figure 13.20**). Similarly, the number of people at risk from malaria, cholera, and the plague may increase as global temperatures continue to warm (see citations in Ostfeld 2009).

In addition to the direct effects that climate change has on individual species, interactions between species have the potential to alter how organisms respond to climate change (Gilman et al. 2010). For example, in a review of over 600 articles, Tylianakis et al. (2008) found that climate change affected the strength and frequency of a wide range of ecological interactions (**Figure 13.21**). Collectively, these results suggest that species interactions are

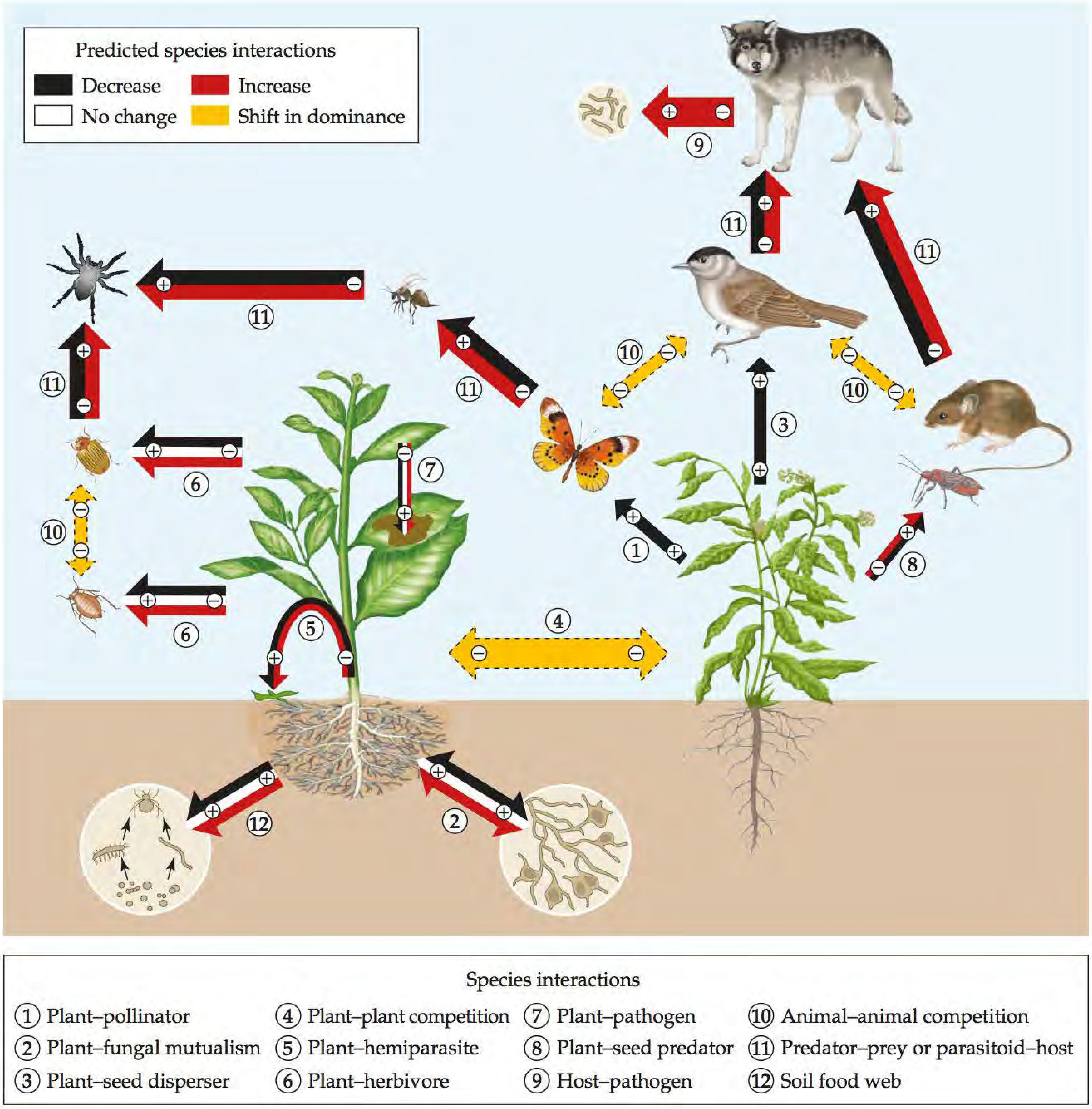


Figure 13.21 Climate Change Alters Species Interactions This diagram provides an overview of a literature review of how climate change is predicted to alter species interactions in terrestrial systems, including some with parasites, in studies that tested for the effects of increased temperature, changing rainfall patterns, or increased frequency of extreme weather events. Arrows with solid outlines indicate nutrient and energy flow; double-headed arrows with dotted outlines indicate competition. A + or – symbol within an arrow indicates benefit or cost to each participant. (After Tylianakis et al. 2008.)

likely to complicate efforts to predict how climate change will affect the prevalence and severity of disease. For example, although the direct effects of climate on the vectors or hosts of a pathogen might suggest that these species would extend their ranges in response to climate change, competition with other species could prevent this from occurring. If competition had this effect, then interactions with other organisms would have caused the actual distribution of a species under climate change to be smaller than its potential distribution (see Figure 4.3). In other circumstances, however, a very different result might be observed. For example, as discussed in Concept 25.2, changes in climate can lead to the formation of new types of communities that contain collections of species that differ from those found in current communities. In such a new community type, a pathogen might interact with new vectors or hosts and hence might expand its geographic range farther than would otherwise be expected. In this case, over time the actual distribution of the pathogen would become larger than its (predicted) potential distribution, because of changes in community structure that resulted from climate change.

Overall, results in Tylianakis et al. (2008) and Gilman et al. (2010) indicate that ecological interactions will influence how future climate change will affect the incidence of disease in humans and many other species. Likewise, Costello et al. (2009) outlined major threats to human health from direct and indirect effects of climate change on disease incidence, food and water insecurity, and extreme climate events (such as hurricanes and floods that create conditions that favor the spread of diseases). It is highly likely that climate change will also have direct and indirect effects on the incidence of disease in the populations of many species other than humans, contributing to the ongoing biodiversity crisis.

A CASE STUDY REVISITED

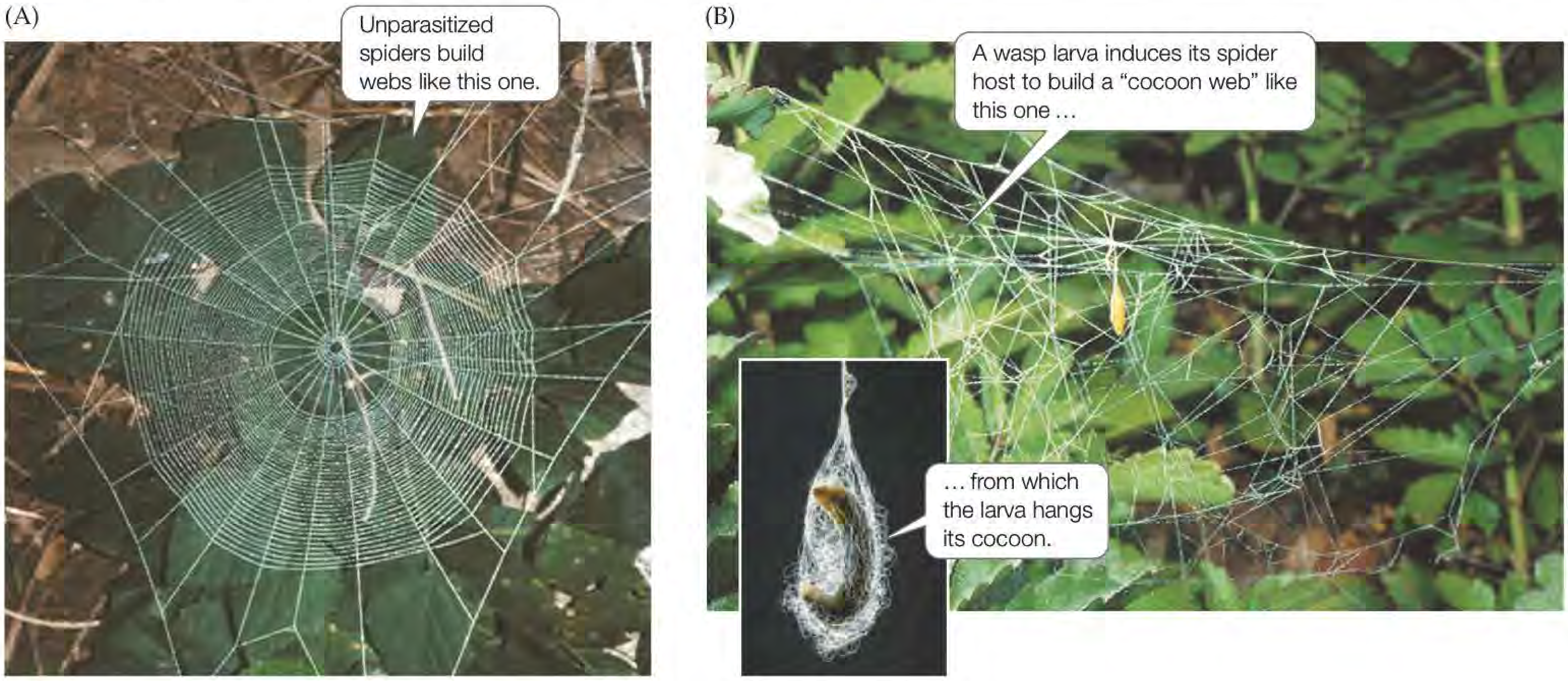
Enslaver Parasites

Returning to a question that we posed in the Case Study, how do enslaver parasites manipulate the behavior of their hosts? In some cases, we have hints of how they do this. Consider the tropical parasitoid wasp *Hymenoepimecis argyraphaga* and its host, the orb-weaving spider *Plesiometa argyra*. The larval stage of this wasp attaches to the exterior of a spider's abdomen and sucks the spider's body fluids. When fully grown, the wasp larva induces the spider to make a special "cocoon web" (**Figure 13.22**). Once the spider has built the cocoon web, the larva kills and eats the spider. The larva then spins a cocoon and attaches it to the cocoon web. As the larva completes its development within the cocoon, the cocoon web serves as a strong support that protects the larva from being swept away by torrential rains.

A parasitized spider builds normal webs right up to the night when the wasp induces it to make a cocoon web. This sudden change in the spider's web-building behavior suggested that the wasp might inject the spider with a chemical that alters its behavior. To test this idea, William Eberhard (2001) removed wasp larvae from spider hosts several hours before the time when a cocoon web would usually be made. Wasp removal sometimes resulted in the construction of a web that was very similar to a cocoon web, but more often resulted in the construction of a web that was intermediate in form but differed substantially from both normal and cocoon webs. In the days that followed the removal of the parasite, some spiders partially recovered the ability to make normal webs. These results are consistent with the idea that the parasite induces construction of a cocoon web by injecting a fast-acting chemical into the spider. The chemical appears to act in a dose-dependent manner; otherwise, we would expect spiders exposed to the chemical to build only cocoon webs, not webs that are intermediate in form. Spiders build cocoon webs by repeating the early steps of their normal web-building sequence a large number of times; thus, the chemical appears to act by interrupting the spiders' usual sequence of web-building behaviors.

Other enslaver parasites also appear to manipulate host body chemistry. In the Case Study, we described hairworm parasites that cause crickets to commit suicide by jumping into water. Thomas and colleagues (2003) have shown that the hairworm causes biochemical and structural changes in the brain of its cricket host. The concentrations of three amino acids (taurine, valine, and tyrosine) in the brains of parasitized crickets differ from those in crickets that have not been parasitized. Taurine,

Figure 13.22 Parasites Can Alter Host Behavior The parasitoid wasp *Hymenoepimecis argyraphaga* dramatically alters the web-building behavior of the orb-weaving spider *Plesiometa argyra*. (A) The web of an uninfected spider. (B) The "cocoon web" of a parasitized spider.



Unparasitized spiders build webs like this one.

A wasp larva induces its spider host to build a "cocoon web" like this one …

… from which the larva hangs its cocoon.

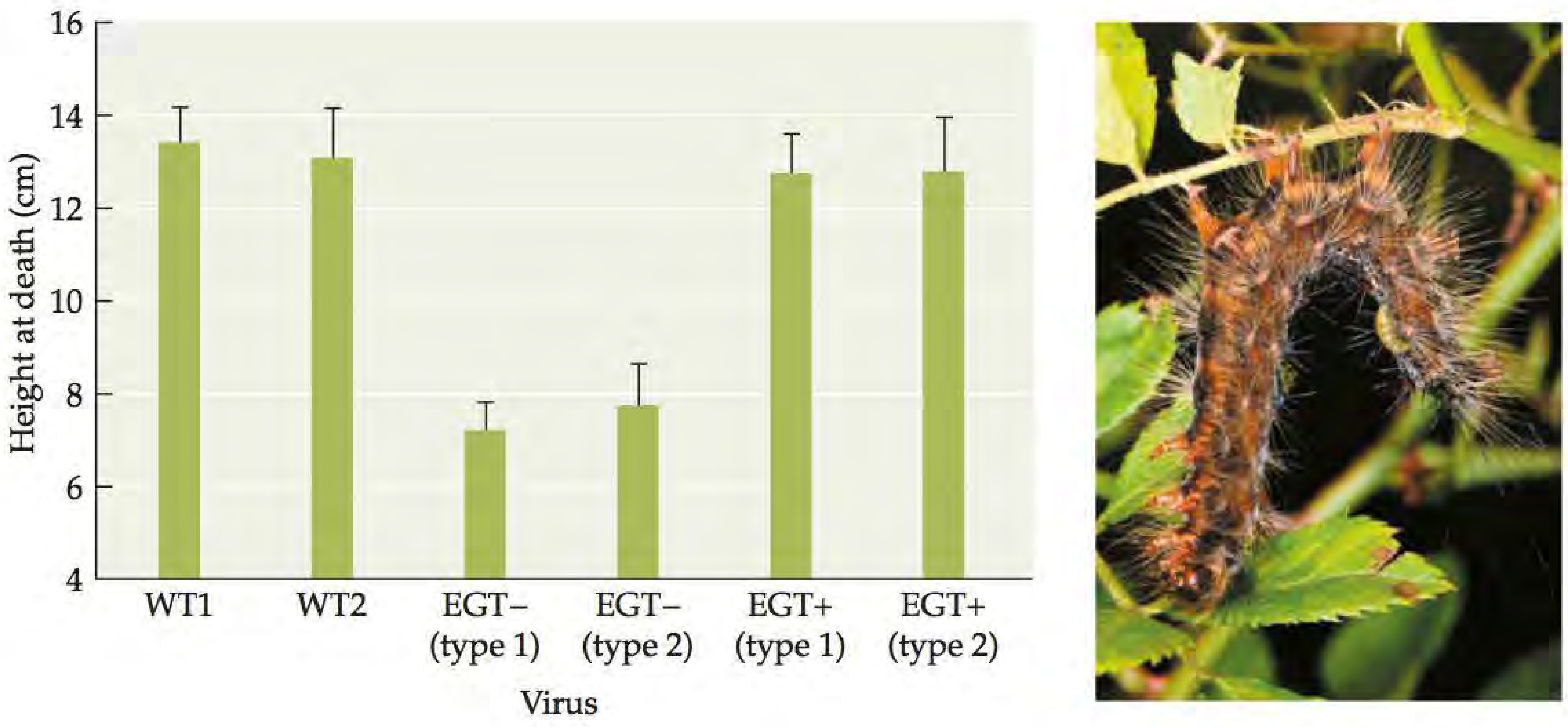


Figure 13.23 A Parasite Gene That Enslaves Its Host Gypsy moths infected by a virus (*Lymantria dispar* nucleopolyhedrovirus, or LdMNV) climb to high locations before they die—a behavior that benefits the virus but not the moth. To test the hypothesis that a particular viral gene (the *egt* gene) affects this behavior, researchers reported the height at death of gypsy moth caterpillars reared in cages and subjected to the following treatments: WT viruses (two different natural, or wild-type, viruses); EGT– viruses (two different experimental viruses from which the *egt* gene had been removed); and EGT+ viruses (two different experimental viruses from which the *egt* gene was first removed, then replaced). Error bars show one SE of the mean. (After Hoover et al. 2011.)

? Explain why the researchers included the WT and EGT+ treatments.

in particular, is an important neurotransmitter in insects, and it also regulates the brain's ability to sense a lack of water. Hence, it is possible that the parasite induces its host to commit suicide by causing biochemical changes in its brain that alter the host's perception of thirst.

The papers by Eberhard (2001) and Thomas et al. (2003) suggest that some parasites enslave their hosts by manipulating them chemically. But even in Eberhard's work, which indicates that the wasp injects a chemical into its spider host, the chemical in question has not been found. If this chemical were known, it could be injected into unparasitized spiders; if those spiders constructed cocoon webs, we would have a clear understanding of how the parasite manipulates the spider.

Although a definitive chemical experiment such as this has yet to be performed, a similar genetic experiment was performed for gypsy moths (*Lymantria dispar*) enslaved by a virus (Hoover et al. 2011). Gypsy moths infected with this virus move to the tops of trees shortly before they die; after death, the bodies of the moths liquefy and release millions of infective viral particles. Uninfected gypsy moths do not exhibit this climbing behavior before death. Based on previous work, Hoover and colleagues hypothesized that the expression of a particular viral gene (the *egt* gene) caused infected moths to move to treetops shortly before death. In a laboratory test of this hypothesis, they found that moths infected with the typical, or wild-type, virus strain died at higher positions than did moths infected by viruses from which the suspect gene had been removed (**Figure 13.23**)—strong evidence that they had succeeded in identifying the first known "enslaver gene."

CONNECTIONS IN NATURE
From Chemicals to Evolution and Ecosystems

Enslaver parasites that manipulate their hosts exert strong selection pressure on host populations, so resistance to the manipulations of enslaver parasites might be expected to evolve in host populations. For example, selection would favor host individuals with the ability to recognize and destroy chemicals that a parasite uses to alter host behavior. Likewise, enslaver parasites might be expected to evolve the ability to overcome host resistance mechanisms.

To date, we know of no such evidence of ongoing host–enslaver parasite coevolution. However, interactions between enslaver parasites and their hosts do provide evidence of previous evolutionary change. Like any parasite, an enslaver parasite has adaptations that allow it to cope with host defenses (otherwise it would not survive). More specifically, an enslaver parasite that uses a chemical to manipulate a specific host behavior is beautifully adapted to take advantage of the body chemistry of its host. Such evolutionary links between enslaver parasites and their hosts illustrate a central feature of both ecology and evolution: ecological interactions affect evolution, and vice versa, at times making it difficult to distinguish one from the other (see Concept 6.5). As we've seen in this chapter, the outcome of such ecological and evolutionary interactions can have profound effects on individuals, populations, communities, and ecosystems. As evolutionary change tips the balance back and forth, first in favor of the host, then in favor of the parasite, we can expect concomitant changes in the population dynamics of other species, such as those that compete with or eat the host or the parasite. Viewed in this way, communities and ecosystems are highly dynamic, always shifting in response to the ongoing ecological and evolutionary changes that are occurring within them.

Summary

CONCEPT 13.1 Parasites typically feed on only one or a few host species, but host species have multiple parasite species.

- Parasites usually feed on only one or a few host individuals during the course of their lives. Most host species are attacked by more than one parasite.
- Some parasites are ectoparasites that live on the surface of their host; others are endoparasites that live within the body of their host.
- Endoparasitism and ectoparasitism each have advantages and disadvantages. It is easier for ectoparasites or their offspring to disperse from one host individual to another; however, ectoparasites are at greater risk from natural enemies than are endoparasites.

CONCEPT 13.2 Hosts have mechanisms for defending themselves against parasites, and parasites have mechanisms for overcoming host defenses.

- Many host organisms have immune systems that allow them to recognize and defend against endoparasites. Biochemical conditions inside the host's body can also provide protection against parasites, as can defensive symbionts such as fungi and bacteria.
- Parasites have a broad suite of mechanisms that allow them to circumvent host defenses, from relatively simple counterdefenses against encapsulation to more complex counterdefenses that involve hundreds of genes.

CONCEPT 13.3 Host and parasite populations can evolve together, each in response to selection pressure imposed by the other.

- Host–parasite interactions can result in coevolution, in which populations of the host and parasite evolve together, each in response to selection pressure imposed by the other.
- Selection can favor a diversity of host and parasite genotypes. A rare host genotype may increase in frequency because few parasites can overcome its defenses; as a result, parasite genotypes that can respond to the new host genotype's defenses may also increase in frequency.
- Host–parasite interactions can exhibit trade-offs in which a trait that improves host defenses or parasite counterdefenses has costs that reduce other aspects of the organism's growth, survival, or reproduction.

CONCEPT 13.4 Hosts and parasites can have important effects on each other's population dynamics.

- Parasites can reduce the abundances of host populations, in some cases driving local host populations to extinction or changing the geographic distributions of host species.
- Evidence suggests that parasites can influence host population cycles.
- Some models of host–pathogen population dynamics subdivide the host population into susceptible individuals, infected individuals, and recovered and immune individuals; track different host and pathogen genotypes; and take into account factors such as host age, latent periods, and vertical transmission.
- A simple mathematical model of host–pathogen dynamics yields an important insight: for a disease to become established and spread, the density of susceptible hosts must exceed a critical threshold density.
- To control the spread of a disease, efforts may be made to lower the density of susceptible hosts (by slaughtering domesticated animals or undertaking vaccination programs) or to raise the threshold density (by increasing the recovery rate or decreasing the transmission rate).

CONCEPT 13.5 Parasites can alter the outcomes of species interactions, thereby causing communities to change.

- Parasites can affect the outcomes of interactions between their hosts and other species; for example, a species that is a dominant competitor may become an inferior competitor when infected by a parasite.
- The effects of parasites can alter the composition of ecological communities and change features of the physical environment.
- Ongoing climate change will likely cause the incidence of diseases to rise through both direct and indirect changes in the abundances and distributions of pathogens.

Review Questions

1. Define endoparasites and ectoparasites, giving an example of each. Describe some advantages and disadvantages associated with each of these two types of parasitism.
2. Given the effects that parasites can have on host individuals and host populations, would you expect that parasites could also alter the outcomes of species interactions and the composition of ecological communities? Explain.
3. a. Summarize the mechanisms that host organisms use to kill parasites or reduce the severity of their attack.
   b. With your answer to (a) as background material, do you think the following statement from a news report could be true?

      The parasite has a mild effect on a plant species in Australia, but after it was introduced for the first time to Europe, it had devastating effects on European populations of the same plant species.

   Explain your reasoning, and illustrate your argument with an example of how a plant defensive mechanism might work—or fail to work—in a situation such as this.

Hone Your Problem-Solving Skills

As we learned in Concept 13.5, leishmaniasis is a serious disease caused by protists that reside in and are spread by sand flies. The disease is found both in humans and in rodents in the genus *Neotoma* (see Figure 13.20). Suppose a control program is being designed to reduce new cases of leishmaniasis in humans that involves reducing the infection by leishmaniasis in *Neotoma* rodents. You are asked to consult on the program and answer the following questions.

1. Why would you expect that reducing the infection by leishmaniasis of *Neotoma* rodents would have an effect on similar infection in humans?
2. To reduce the spread of leishmaniasis in *Neotoma* rodents, the control program recommends reducing the threshold density, S_T, in rodent populations. What is meant by the concept of a threshold density for the establishment and spread of a disease? Why is this concept important?
3. Suppose the control program determines that the threshold density (S_T) of leishmaniasis in *Neotoma* populations is 5,000 individuals. Using the data in the table, determine which *Neotoma* rodent populations will need to be reduced, and by how much, to decrease leishmaniasis infection?
4. What other measures besides reducing the host population sizes of both rodents and sand flies can be proposed to decrease the infection prevalence in humans?

POPULATION	1	2	3	4	5	6	7	8
Number of rodent individuals	9,000	1,200	5,500	4,000	8,000	1,000	4,000	10,000

ON THE COMPANION WEBSITE
ecology4e.sinauer.com

The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

13.1 The Animal That Changed the World: Fleas, Rats, and the Black Death

Web Extensions

13.1 Enslaved by a Hairworm Parasite

13.2 When Will a Disease Become Established and Spread?

Competition

14

Competition in Plants That Eat Animals: A Case Study

Despite repeated reports that plants could eat animals, early scientists were skeptical of those claims. Charles Darwin (1875) laid their doubts to rest by providing clear experimental evidence of carnivory by plants. Today, more than 600 species of plants that eat animals have been identified, including bladderworts, sundews, pitcher plants, and the well-known Venus flytrap.

Plants use a variety of mechanisms to eat animals. The Venus flytrap has modified leaves that look like fanged jaws yet attract insects with a sweet-smelling nectar (**Figure 14.1**). The inner surface of the leaf has touch-sensitive hairs; if an insect trips those hairs, the leaf snaps shut in less than half a second. Once the insect is captured, the trap tightens further, forming an airtight seal around its victim, which is then digested over the course of 5–12 days. Some plants can capture animals at truly blinding speeds. For example, aquatic bladderworts (*Utricularia* spp.) have a trapdoor that springs inward when touched, creating a suction that pulls in prey in less than half a millisecond.

Other plants lack moving parts yet still can eat animals. Consider the pitcher plants, which can use nectar or visual cues to lure insects into a pitcher-shaped trap. The inside of the pitcher often has downward-facing hairs, which make it easy for the insect to crawl in, but hard to crawl out. What's more, in many pitcher plants, once it is about halfway down, the insect encounters a layer of flaky wax. An insect that steps onto this wax is doomed: the wax sticks to its feet, causing it to lose its grip and tumble into a vat that contains either water (in which it drowns) or deadly digestive juices.

Why do some plants eat animals? The answer may relate to the subject of this chapter: competition. Because plants are immobile, competition for limiting resources such as nutrients or water can be intense. Many carnivorous plants are found in environments with nutrient-poor soils. Furthermore, evolutionary relationships among plants reveal that in nutrient-poor environments, carnivory has evolved multiple times, in a variety of independent plant lineages. Overall, these observations suggest that carnivory in plants is an adaptation for life in nutrient-poor environments—perhaps providing a way to avoid competing with other plants for soil nutrients.

Does eating animals allow plants to better deal with competition for nutrients? Typically, the root systems of carnivorous plants are less extensive than those of noncarnivorous plants that live in the same area, which suggests that the

KEY CONCEPTS

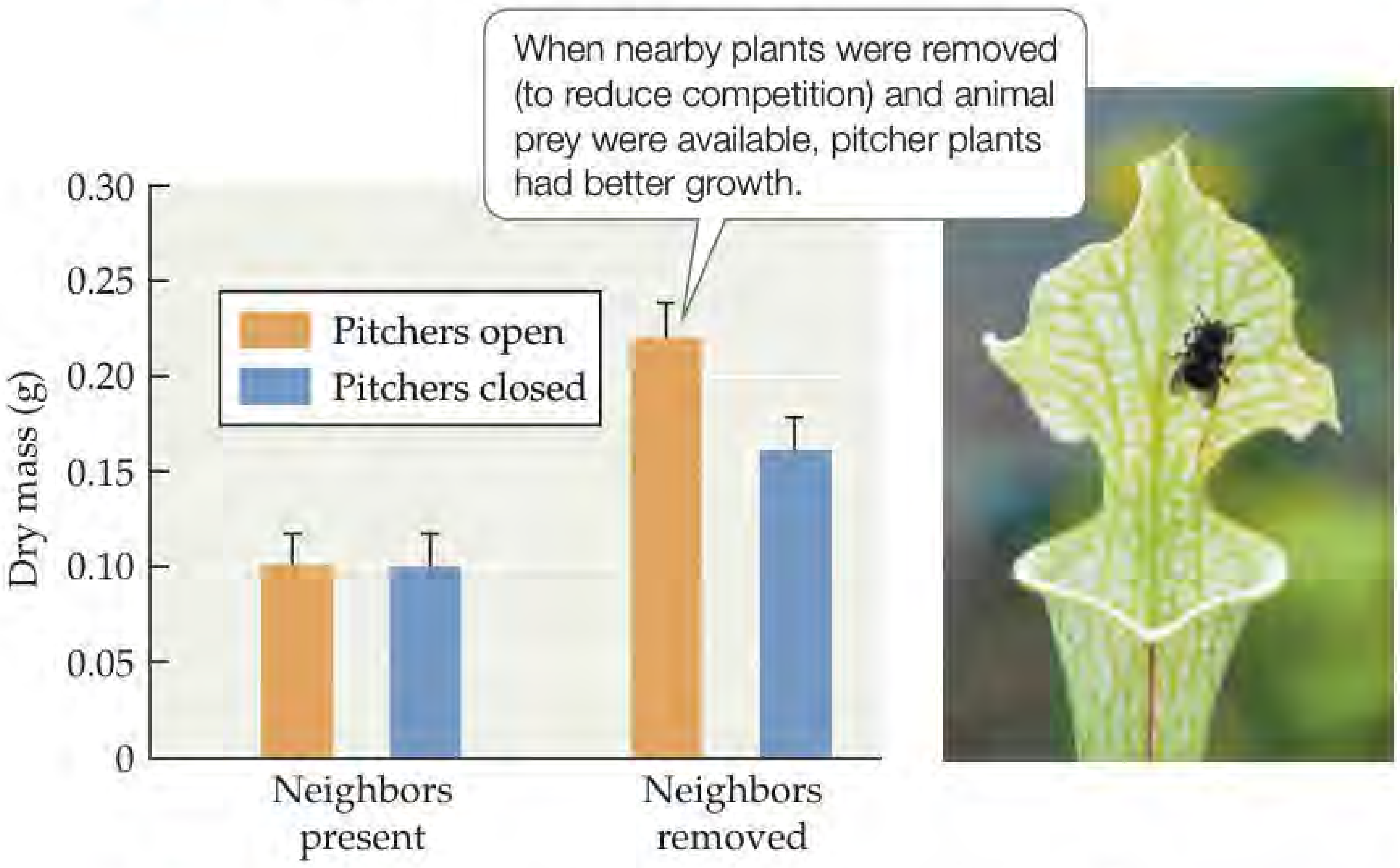
CONCEPT 14.1
Competition can be direct or indirect, vary in its intensity, and occur between similar or dissimilar species.

CONCEPT 14.2
Competing species are more likely to coexist when they use resources in different ways.

CONCEPT 14.3
Competitive interactions can be modeled using the logistic equation.

CONCEPT 14.4 The outcome of competition can be altered by the physical environment, disturbance, and predation.

Figure 14.1 A Plant That Eats Animals Attracted to the plant's sweet-smelling nectar, this fly is about to become a meal. Although the Venus flytrap typically captures insects, it can also feed on other animals, such as slugs and small frogs.



When nearby plants were removed (to reduce competition) and animal prey were available, pitcher plants had better growth.

Figure 14.2 Competition Decreases Growth in a Carnivorous Plant To test the effects of competition on the carnivorous pitcher plant *Sarracenia alata*, the growth of control plants ("neighbors present") was compared with the growth of plants whose noncarnivorous competitors were weeded and clipped ("neighbors removed"). Neighbor removal increased plant growth, especially when animal prey were available. Error bars show one SE of the mean. (After Brewer 2003.)

carnivorous plants may be poorer competitors for soil resources. Hence, carnivorous plants could use animal prey as an alternative source of nutrients when competition is intense.

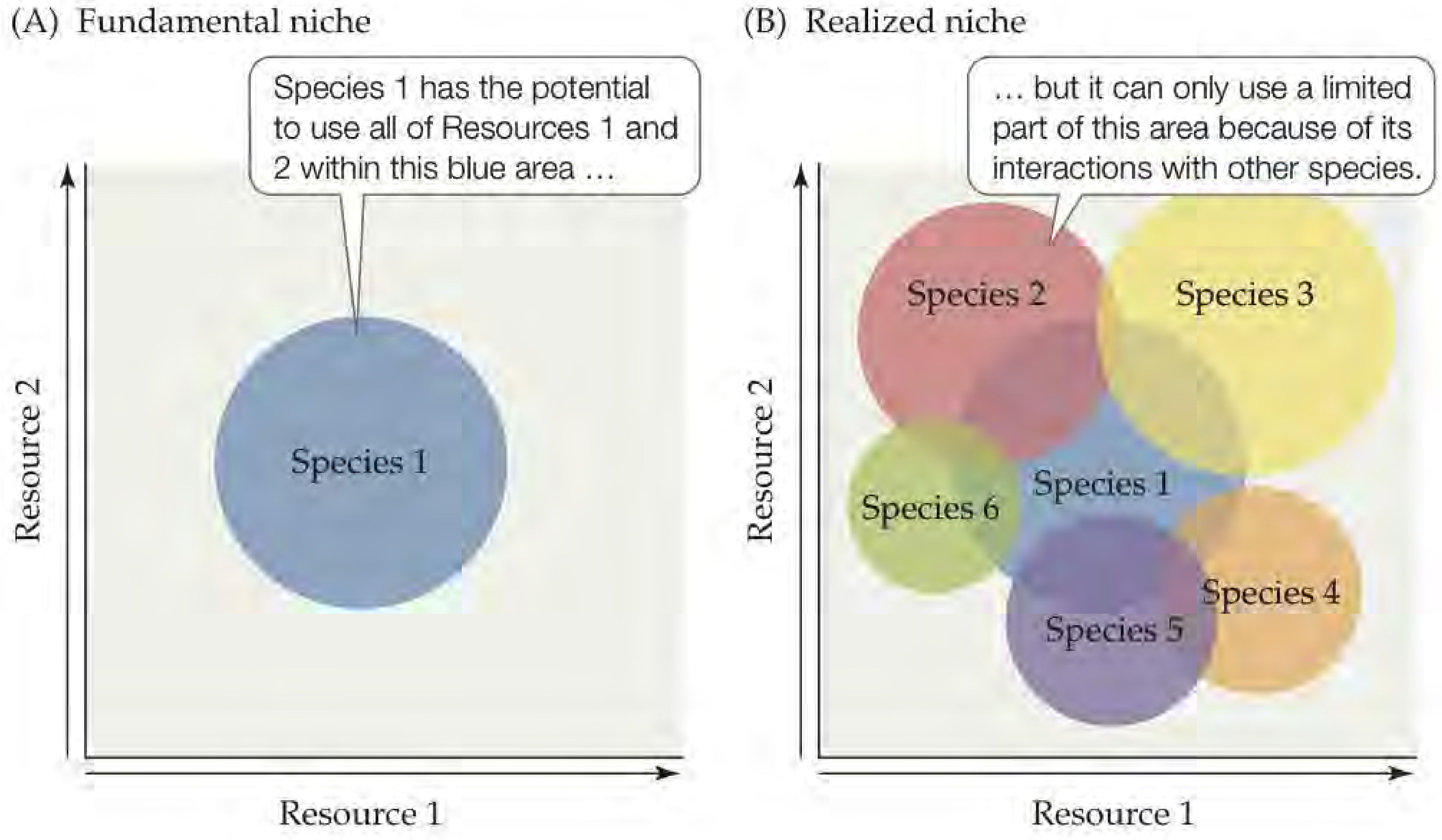
To test this idea, Stephen Brewer measured how the growth of the pitcher plant *Sarracenia alata* was affected when he cut off its access to prey (by covering the pitchers) and when he reduced noncarnivorous competitor plant species ("neighbors") by weeding and clipping. His results show that biomass in *Sarracenia* increased when neighbors were reduced (**Figure 14.2**), suggesting that competition had an important effect on growth. But further examination of Figure 14.2 reveals that matters are not as simple as they may at first appear. Although the growth of pitcher plants with competition was expected to decline when they were deprived of prey, that did not happen. Instead, it seems that pitcher plants were only able to benefit from animal prey when neighbors were removed. Why is this so?

Introduction

In 1917, A. G. Tansley reported results from a series of experiments designed to explain the distribution in Britain of two species of bedstraw plants, *Galium hercynicum* and *G. pumilum* (then known as *G. sylvestre*). *Galium hercynicum* was restricted to acidic soils, *G. pumilum* to calcareous soils. Even in places where the two species grew within inches of each other, each remained confined to its characteristic soil type. In his experiments, Tansley found that when grown alone, each species could survive on both acidic and calcareous soils. However, when he grew the species together on acidic soils, only *G. hercynicum* survived, and if he grew them together on calcareous soils, only *G. pumilum* survived. Tansley concluded that the two species competed with each other and that when grown on its native soil type, each species drove the other to extinction.

Tansley's work on bedstraws is one of the first experiments ever performed on **competition**, a non-trophic interaction between individuals of two or more species in which all species are negatively affected by their shared use of a resource that limits their ability to grow, reproduce, or survive. In this chapter, we specifically focus on **interspecific competition** (between individuals of different species) as opposed to **intraspecific competition** (between individuals of a single species), as in *density dependent growth*, a topic we addressed in Chapter 10.

What are some of the resources that species compete for? **Resources** are simply the components of the environment, such as food, water, light, and space, that are required by species. Food is an obvious example—when food is scarce, population growth rates fall unless individuals can successfully compete. In terrestrial ecosystems—especially arid ones—water is also a resource. But an organism does not need to consume a substance for it to be a resource. Plants "consume" light in the sense that they use it to fix carbon, and they can deplete the


(A) Fundamental niche

(B) Realized niche

Species 1 has the potential to use all of Resources 1 and 2 within this blue area ...

... but it can only use a limited part of this area because of its interactions with other species.

Figure 14.3 The Concept of a Fundamental and a Realized Niche In this conceptual representation of Species 1's use of two resources, (A) its fundamental niche is contained within the entire blue area, but (B) the use of resources in that area is limited by interactions with other species, which set the limits of its realized niche.

supply available to other plants by shading them. Space is also an important resource. Plants, algae, and sessile animals require space to attach and grow, and competition for space can be intense. Mobile animals also compete for space as they seek access to foraging grounds, territories to attract mates, or refuges from heat, cold, or predators.

Finally, as we learned in Concept 9.5, the full set of resources, along with other biotic and abiotic requirements, is what is known as the ecological or **fundamental niche** of a species (**Figure 14.3A**). But, within the context of species interactions, no one species has exclusive access to all the resources within its fundamental niche. Thus, ecologists recognize a more restricted set of conditions that a species is limited to, in large part, because of species interactions. These more restricted conditions form the **realized niche** of a species (**Figure 14.3B**). We will consider the niche concept later in Concept 14.2 and in Chapter 19 when we discuss resource partitioning. For now, let's begin our exploration of competition by considering some of its general characteristics.

CONCEPT 14.1

Competition can be direct or indirect, vary in its intensity, and occur between similar or dissimilar species.

General Features of Competition

The simple definition of competition as two or more species negatively affecting one another because of shared resources belies the complicated ways in which species actually compete with one another. Because resources are the mitigating factor in the interaction, and each species requires and obtains resources in different ways, the mechanisms used to compete and the intensity and ultimate outcome of competition can vary widely among species. Let's next consider some of the ways in which species compete.

Species may compete directly or indirectly

Species often compete indirectly through their mutual effects on the availability of a shared resource. Known as **exploitation competition**, this type of competition occurs simply because individuals reduce the supply of a shared resource as they use it. We have already considered an example of exploitation competition in the Case Study on pitcher plants.

The other kind of competition is **interference competition**, a case in which one species directly interferes with the ability of its competitors to use a limiting resource. Such interactions are perhaps most familiar in mobile animals, as when carnivores fight with one another over animal prey. Similarly, herbivores such as voles may aggressively exclude other vole species from preferred habitat, and members of warring ant colonies may kidnap and slaughter one another. Interference competition can also occur among sessile animals. For example, as it grows, the acorn barnacle *Semibalanus balanoides* often crushes or smothers nearby individuals of another barnacle species, *Chthamalus stellatus*. As a result, *Semibalanus* directly prevents *Chthamalus* from living in most portions of the rocky intertidal zone (we'll describe competition between these barnacles in more detail in Concept 14.4).

Interference competition also occurs in plants, as when one plant species grows over another, reducing its access to light (**Figure 14.4**). There is also circumstantial evidence that interference competition can take the form of **allelopathy**, in which individuals of one species release toxins that harm other species. Although allelopathy appears to be important in some crop systems (Minorsky 2002; Belz 2007), there is little experimental evidence for it in natural communities. One reason for this lack of evidence is that in a species in which allelopathy is suspected, all members can usually produce the chemical that is thought to act as a toxin—hence, it has not been possible to compare the performance of individuals that can produce the toxin with that of individuals that cannot. In a promising new line of research, genes that code for allelopathic toxins have been identified in some plant species, which has allowed researchers to develop genetic varieties in which these genes are disabled, or "silenced." In current experiments, both plants in which the production of allelopathic toxins has been silenced and plants able to produce these toxins are being grown with members of other species, thus providing a rigorous test of the effects of allelopathy in competitive environments.

Figure 14.4 Interference Competition in Plants A formidable competitor, the kudzu vine (*Pueraria montana*) has grown over and completely covered these Georgia trees and shrubs, outcompeting them for light.

Competition can vary in intensity depending on resource availability and type

Plants can compete for aboveground resources, such as light, as well as for belowground resources, such as soil nutrients. Researchers have suggested that the relative importance of aboveground and belowground competition in plants might change depending on whether aboveground or belowground resources are more scarce: belowground competition, for example, might be expected to increase in intensity when the competing plants are growing in nutrient-poor soils. Scott Wilson and David Tilman tested this idea by performing transplant experiments with *Schizachyrium scoparium*, a perennial grass species native to their study site in Minnesota.

Wilson and Tilman selected a series of 5 × 5 m plots of natural vegetation growing in sandy, nitrogen-poor soils. For 3 years, they treated half of the plots with high-nitrogen fertilizer each year. This 3-year period gave the plant communities in the fertilized plots time to adjust to the experimentally imposed change in soil nitrogen levels. At the end of the 3-year period, they planted *Schizachyrium* individuals in all the plots.

Once they were added to the high-nitrogen (fertilized) and low-nitrogen (unfertilized) plots, *Schizachyrium* individuals were grown under three treatments: (1) with neighbors present (competition), (2) with neighbor roots present but neighbor stems tied back (which prevented aboveground competition with *Schizachyrium*), or (3) with neighbor roots and stems both removed (no competition). Wilson and Tilman found that while total competition (the sum of belowground and aboveground competition) did not differ between the low- and high-nitrogen plots, belowground competition was most intense in the low-nitrogen plots (**Figure 14.5A**). They also found that aboveground competition increased when light levels were low (**Figure 14.5B**). Thus, their work demonstrates that the intensity of competition can increase when the particular resource being competed for is scarce.

Competition is often asymmetrical

When two species compete for a resource that is in short supply, each obtains less of the resource than it could if the competitor were not present. Because competition reduces the resources available for the growth, reproduction, and survival of both species, the abundance of each species is reduced to some extent. In many cases, however, the effects of competition are unequal, or asymmetrical: one species is harmed more than the other. This asymmetry is especially clear in situations in which one competitor drives another to extinction.

For example, in a laboratory experiment, Tilman et al. (1981) examined competition for silica (SiO_2) between species of freshwater diatoms, which use silica to construct their cell walls. Tilman and colleagues grew two diatom species, *Synedra ulna* and *Asterionella formosa*, alone and in competition with each other. They measured how the population densities of the diatoms and silica concentrations in the water changed over time. When grown alone, each species reduced silica (the resource) to a low and approximately constant concentration; each species also reached a stable population size (**Figure 14.6**). *Synedra* had a lower stable population size than *Asterionella*, and it reduced silica to lower levels than did *Asterionella*. When the two species competed with each other, *Synedra* drove *Asterionella* to extinction, apparently because it reduced silica to such low levels that *Asterionella* could not survive.

As this example suggests, before the inferior competitor goes extinct, the superior competitor typically loses potential resources to its competitor or invests energy in the competitive interaction. Hence, even when one species drives the other to extinction, both the superior and the inferior competitor are harmed to some extent. However, the effect of the superior competitor is still greater

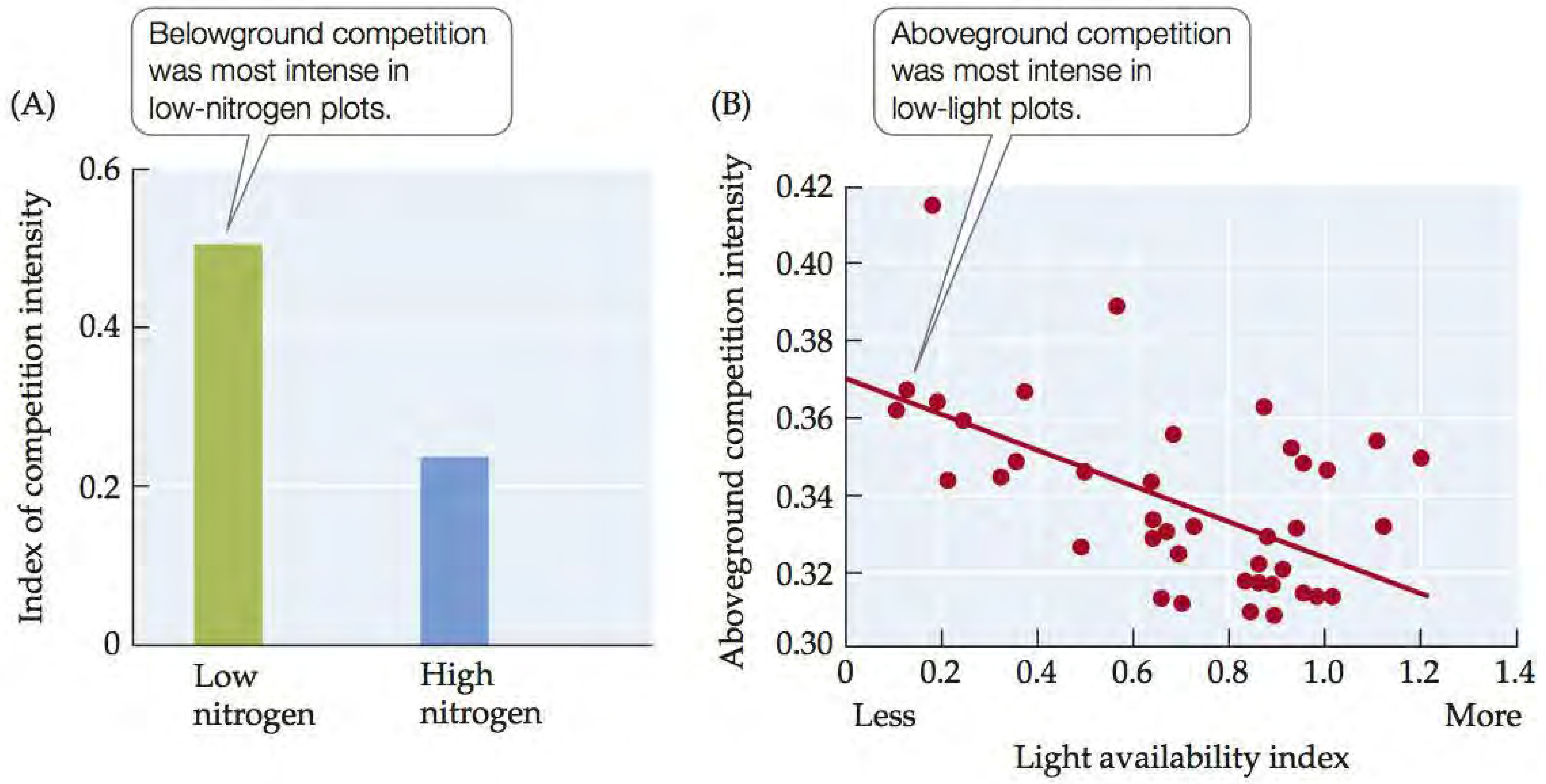


Figure 14.5 Resource Availability Affects the Intensity of Competition (A) In transplant experiments with the grass *Schizachyrium scoparium*, belowground competition between plant species for nutrients increased in intensity when soil nutrients were scarce. (B) Similarly, aboveground competition for light increased as light levels decreased. (After Wilson and Tilman 1993.)

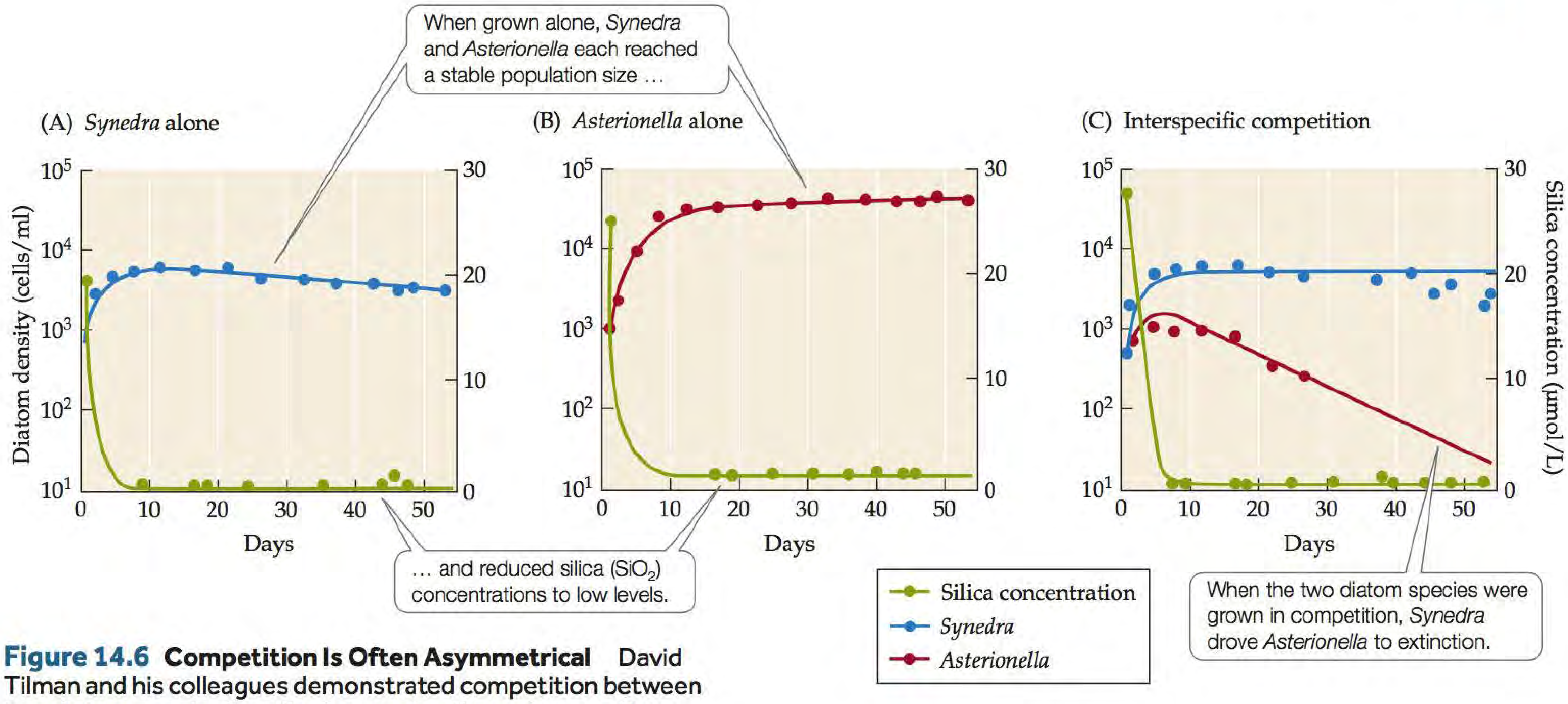


Figure 14.6 Competition Is Often Asymmetrical David Tilman and his colleagues demonstrated competition between two diatom species for silica by growing them alone and in competition with each other. *Synedra* (A) reduced silica concentrations to lower levels than did *Asterionella* (B). This result may explain why *Synedra* outcompeted *Asterionella* when the two species were grown together (C). (After Tilman et al. 1981.)

? Suppose a third diatom species reduced the concentration of silica to 5 µmol/L when grown alone. Predict what would happen if this species were grown in competition with *Asterionella*.

than the effect of the inferior competitor. Indeed, in general, there is a continuum in how strongly each competitor affects the other (**Figure 14.7**). Note that the two ends of this continuum do not represent competitive (–/–) interactions. Instead, such interactions are referred to as **amensalism**, –/0 interactions in which individuals of one species are harmed while individuals of the other species are not affected at all. Possible examples of amensal interactions include small woody plants that grow beneath towering trees, or corals in which the individuals of one species can grow over those of another, depriving them of light.

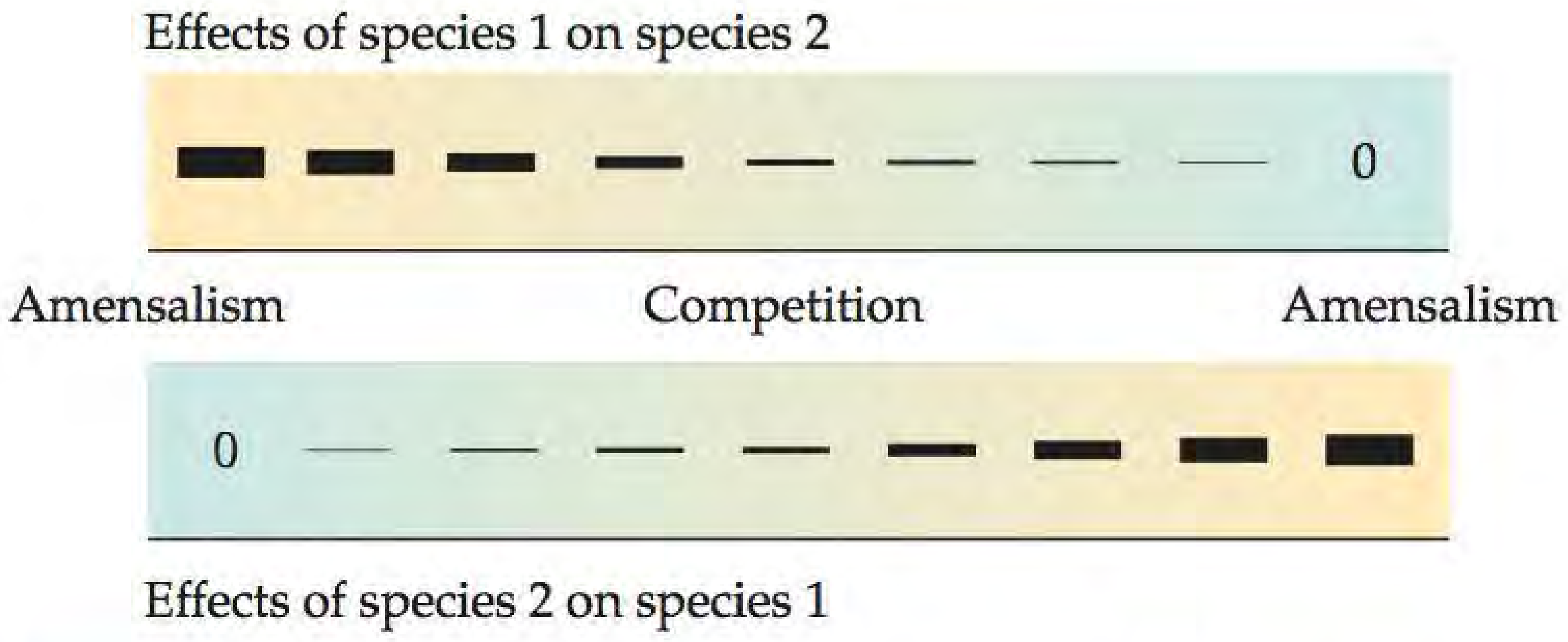


Figure 14.7 A Continuum of Competitive Effects Competition may affect members of both species equally, or the members of one species may be harmed more than are members of the other species. Bars that are thick indicate strong competitive effects.

? Circle the interactions that represent asymmetrical competition.

Competition can occur between closely or distantly related species

We've seen that competition can occur between pairs of closely related species, such as the diatom species studied by Tilman. Brown and Davidson (1977) examined whether competition also occurs between groups of more distantly related species. In particular, they suspected that rodents and ants might compete because both eat the seeds of desert plants, and the sizes of the seeds they eat overlap considerably (**Figure 14.8**).

Brown and Davidson established experimental plots (each about 1,000 m^2) in a desert region near Tucson, Arizona. Their experiment lasted 3 years and used four treatments: (1) plots in which a ¼-inch wire mesh fence excluded seed-eating rodents and from which rodents within the fence were removed by trapping; (2) plots in which seed-eating ants were excluded by applying insecticides; (3) plots in which both rodents and ants were excluded by fencing, trapping, and insecticides; and (4) plots in which both rodents and ants were left undisturbed (control plots).

The results indicated that rodents and ants do compete for food. Relative to the control plots, the number of ant colonies increased by 71% in the plots from which rodents were excluded, and rodents increased by 18% in number and 24% in biomass in the plots from which ants were excluded. In the plots from which both rodents and ants were excluded (treatment 3), the density of seeds increased by 450% compared with all other plots.

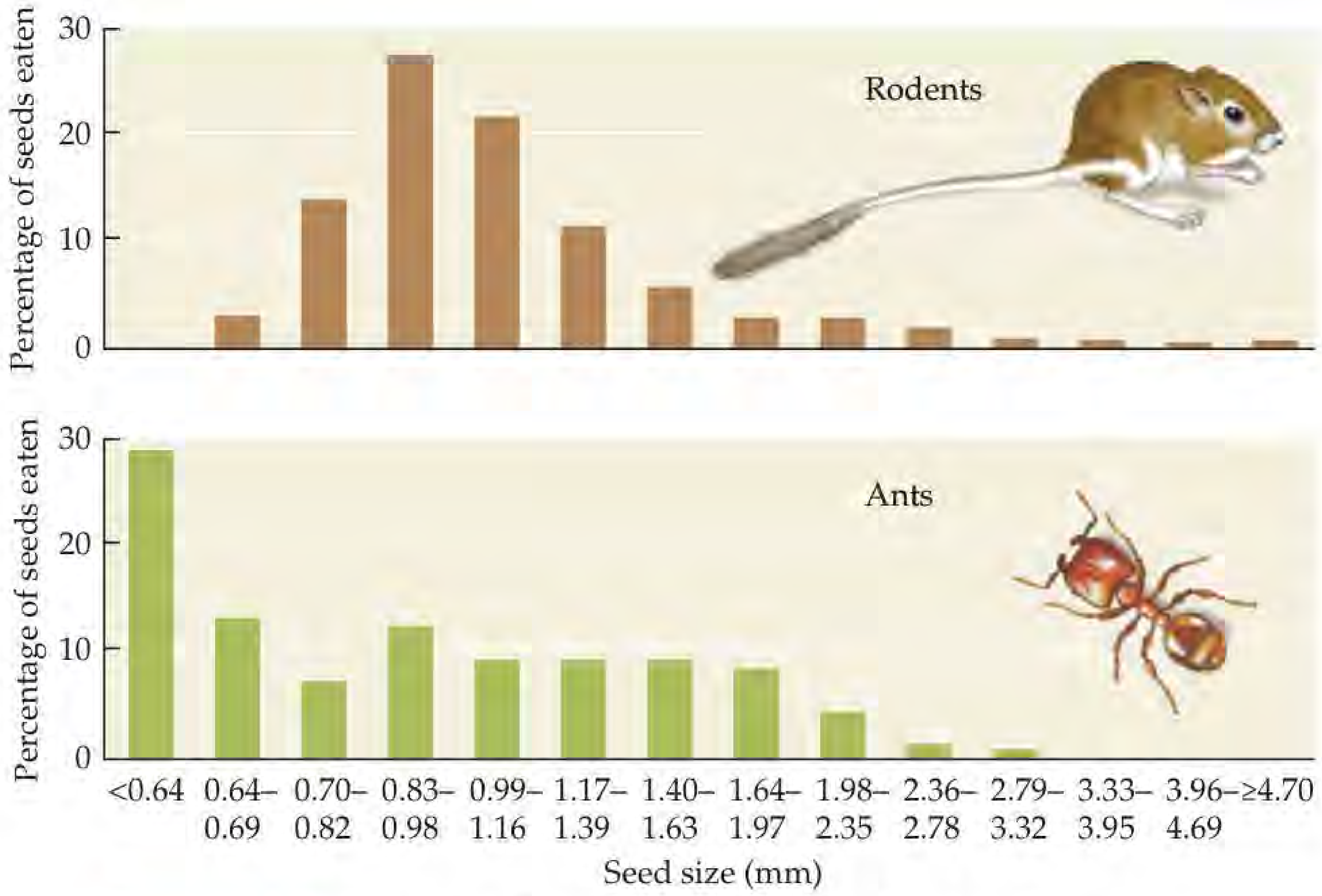


Figure 14.8 Ants and Rodents Compete for Seeds There is extensive overlap in the sizes of seeds eaten by ants and by rodents. Removal experiments showed that these two distantly related groups compete for this food source. (After Brown and Davidson 1977.)

Treatments 1 (no rodents), 2 (no ants), and 4 (the control plots, with both rodents and ants present) all resulted in similar densities of seeds. These results suggest that when either rodents or ants were removed, the group that remained ate roughly as many seeds as rodents and ants combined ate in the control plots. Thus, under natural conditions, each group would be expected to eat fewer seeds in the presence of the other group than it could eat when alone.

It is not surprising that species as different as ants and rodents compete. After all, people differ greatly from bacteria, fungi, and insects, yet we compete with these organisms for food in farm fields, in grain storage bins—even in our refrigerators. Overall, whether they are closely or distantly related, organisms can compete if they share the use of a limiting resource.

Competition for resources is common in natural communities

How important is competition in natural communities? To answer this question, results from many field studies must be compiled and analyzed. The findings of three such analyses indicate that competition has important effects on many species. For example, Schoener (1983) examined the results of 164 published studies on competition and found that of 390 species studied, 76% showed effects of competition under some circumstances, and 57% showed effects of competition under all circumstances tested. Connell (1983) examined the results of 72 studies and found that competition was important for 50% of the 215 species studied. Gurevitch et al. (1992) took a different approach: they did not report the percentage of species for which competition was important, but rather analyzed the magnitude of competitive effects found for 93 species in 46 studies published between 1980 and 1989. They showed that competition had significant (though variable) effects on a wide range of organisms.

Surveys such as those by Schoener, Connell, and Gurevitch et al. face potential sources of bias, including investigators' failure to publish studies that show no significant effects and the tendency for investigators to study "interesting" species (i.e., those they suspect will show competition). Despite such potential sources of bias, the fact that hundreds of studies have documented effects of competition makes it clear that competition is common—though not ubiquitous—in nature. We explore the relative importance of competition to community structure in Chapter 19.

CONCEPT 14.2

Competing species are more likely to coexist when they use resources in different ways.

Competitive Coexistence

As indicated above, ecologists have long thought that competition between species was important in communities. For example, although he often focused on competition within species, Darwin (1859) also argued that competition between species could influence both ecological and evolutionary processes. Darwin recognized that interspecific competition could lead to two possible outcomes. At one extreme, if a dominant species prevents another species from using essential resources, the inferior species may become locally extinct, a process known as **competitive exclusion**. We saw this result in the diatom example tested in a laboratory setting (see Figure 14.6). However, in reality, most species show some sort of **competitive coexistence**, or the ability to coexist with one another despite sharing limiting resources. Let's consider some general features of competition that lead to either competitive exclusion or competitive coexistence.

Competitors that use limiting resources in the same way cannot coexist

In the 1930s, the Russian ecologist G. F. Gause performed laboratory experiments on competition using three species of the single-celled protist group *Paramecium*. He constructed miniature aquatic ecosystems by growing paramecia in tubes filled with a liquid medium that contained bacteria and yeast cells as a food supply. He found that populations of each of the three *Paramecium* species reached a stable

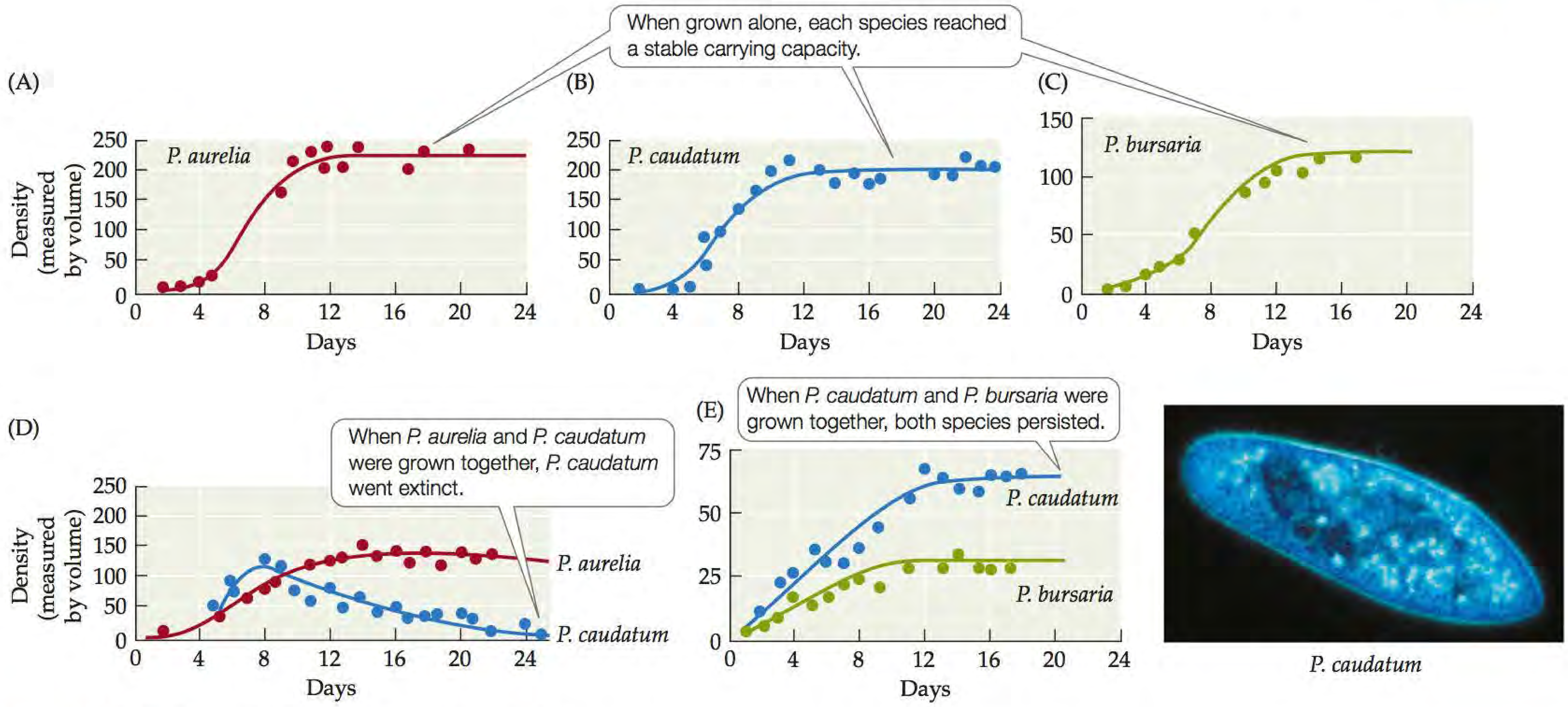


Figure 14.9 Competition in *Paramecium* G. F. Gause grew *Paramecium* species in tubes filled with a liquid medium containing bacteria and yeast cells. *Paramecium aurelia* and *P. caudatum* both fed mainly on floating bacteria, while *P. bursaria* fed mainly on yeast cells. (After Gause 1934a,b.)

? Predict what would happen if *P. aurelia* and *P. bursaria* were grown together. Explain.

carrying capacity when grown alone (**Figure 14.9A–C**). But when pairs of these species competed with each other, several different outcomes were obtained. When *P. aurelia* was grown in competition with *P. caudatum*, *P. aurelia* drove *P. caudatum* to extinction (**Figure 14.9D**). These two species may have been unable to coexist because they both fed primarily on bacteria floating in the medium, which led to considerable overlap in their food requirements. In contrast, when *P. caudatum* was grown with *P. bursaria*, neither species drove the other to extinction (**Figure 14.9E**). Although *P. caudatum* and *P. bursaria* coexisted, it was clear that they competed for one or more resources because the carrying capacity of each was lowered by the presence of the other. Gause suggested that *P. caudatum* and *P. bursaria* could coexist because *P. caudatum* usually ate bacteria floating in the medium, while *P. bursaria* usually fed on yeast cells that settled to the bottom of the tubes.

Experiments with a wide range of other species (e.g., algae, flour beetles, plants, and flies) have yielded similar results: one species drives the other to extinction unless the two species use the available resources in different ways. Such results led to the formulation of the **competitive exclusion principle**, which states that two species that use a limiting resource in the same way cannot coexist indefinitely. As we'll see next, field observations are consistent with this explanation of why competitive exclusion occurs in some situations but not others.

Competitors may coexist if they use resources differently

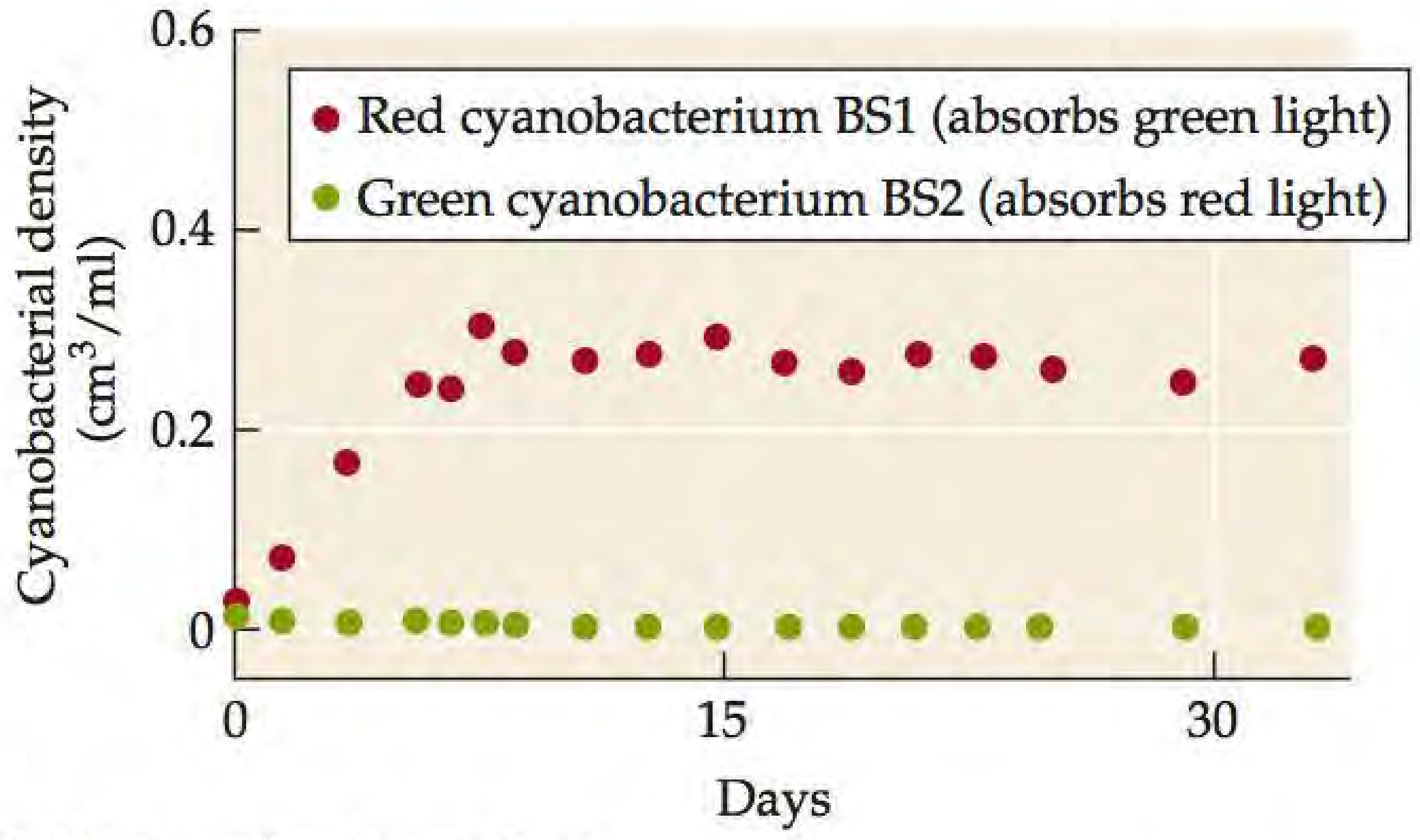
In natural communities, many species use the same limiting resources yet manage to coexist with one another. This observation does not violate the competitive exclusion principle, because a key point of that principle is that species must use limiting resources in the same way. Field studies often reveal differences in how species use limiting resources. Such differences are referred to as **resource partitioning** (or sometimes, **niche partitioning**).

Thomas Schoener studied resource partitioning in four lowland *Anolis* lizard species that live on the West Indian island of Jamaica. Although these species all live together in trees and shrubs and eat similar foods, Schoener (1974) found differences among them in the height and thickness of their perches and in the time they spent in sun or shade. As a result of these differences, members of the different *Anolis* species competed less intensely than they otherwise would. (We explore this example in more detail in **Web Extension 14.1**.)

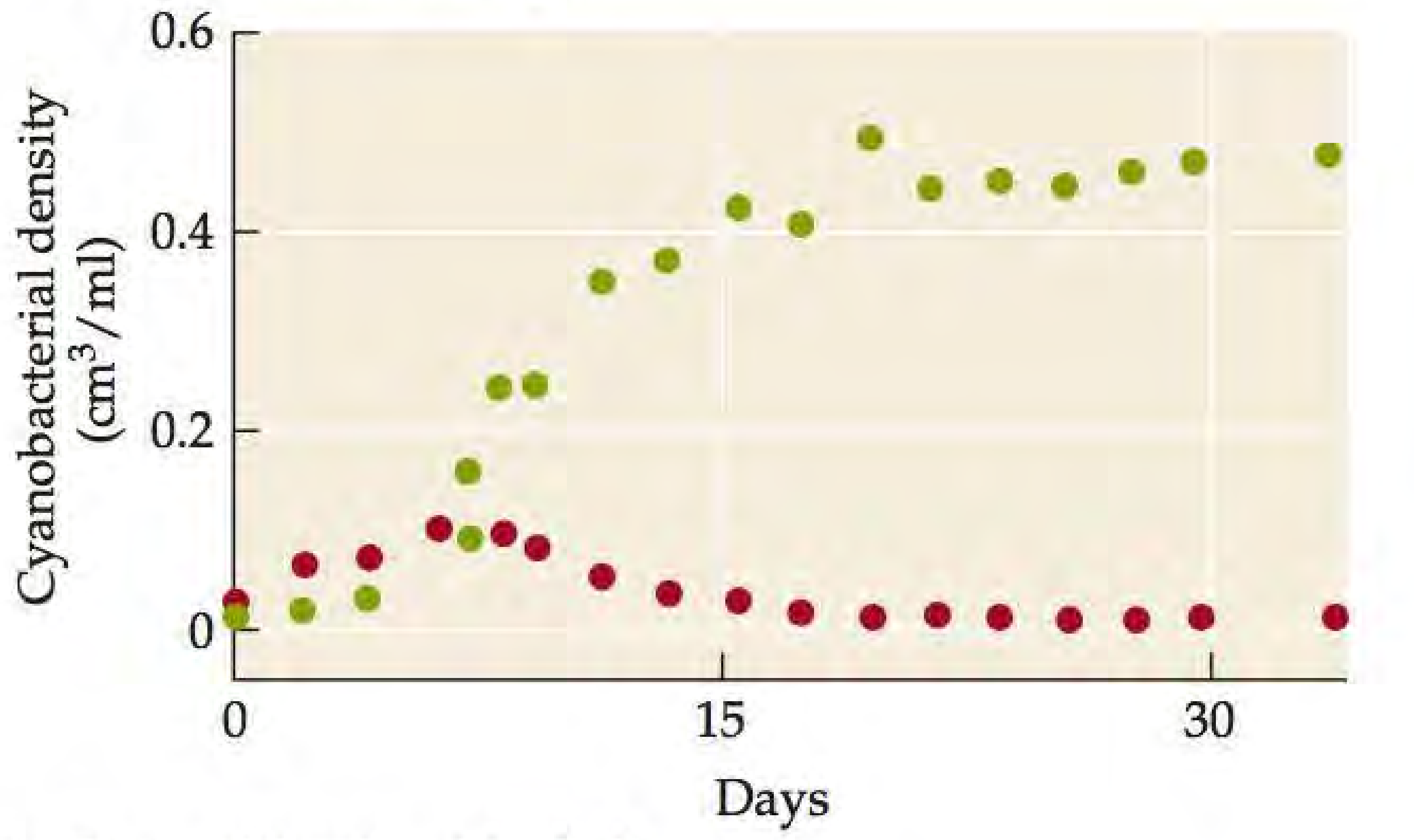
In a marine example, Stomp et al. (2004) studied resource partitioning in two types of cyanobacteria collected from the Baltic Sea. The species identities of these cyanobacteria are unknown, so we will refer to them as BS1 and BS2 (standing for Baltic Sea 1 and Baltic Sea 2). BS1 absorbs green wavelengths of light efficiently, which it uses in photosynthesis. However, BS1 reflects most of the red light that strikes its surface; hence, it uses red wavelengths inefficiently (and is red in color). In contrast, BS2 absorbs red light and reflects green light; hence, BS2 uses green wavelengths inefficiently (and is green in color).

Stomp and colleagues explored the consequences of these differences in a series of competition experiments. They found that each species could survive when grown

(A) Competition in green light



(B) Competition in red light



(C) Competition in white light

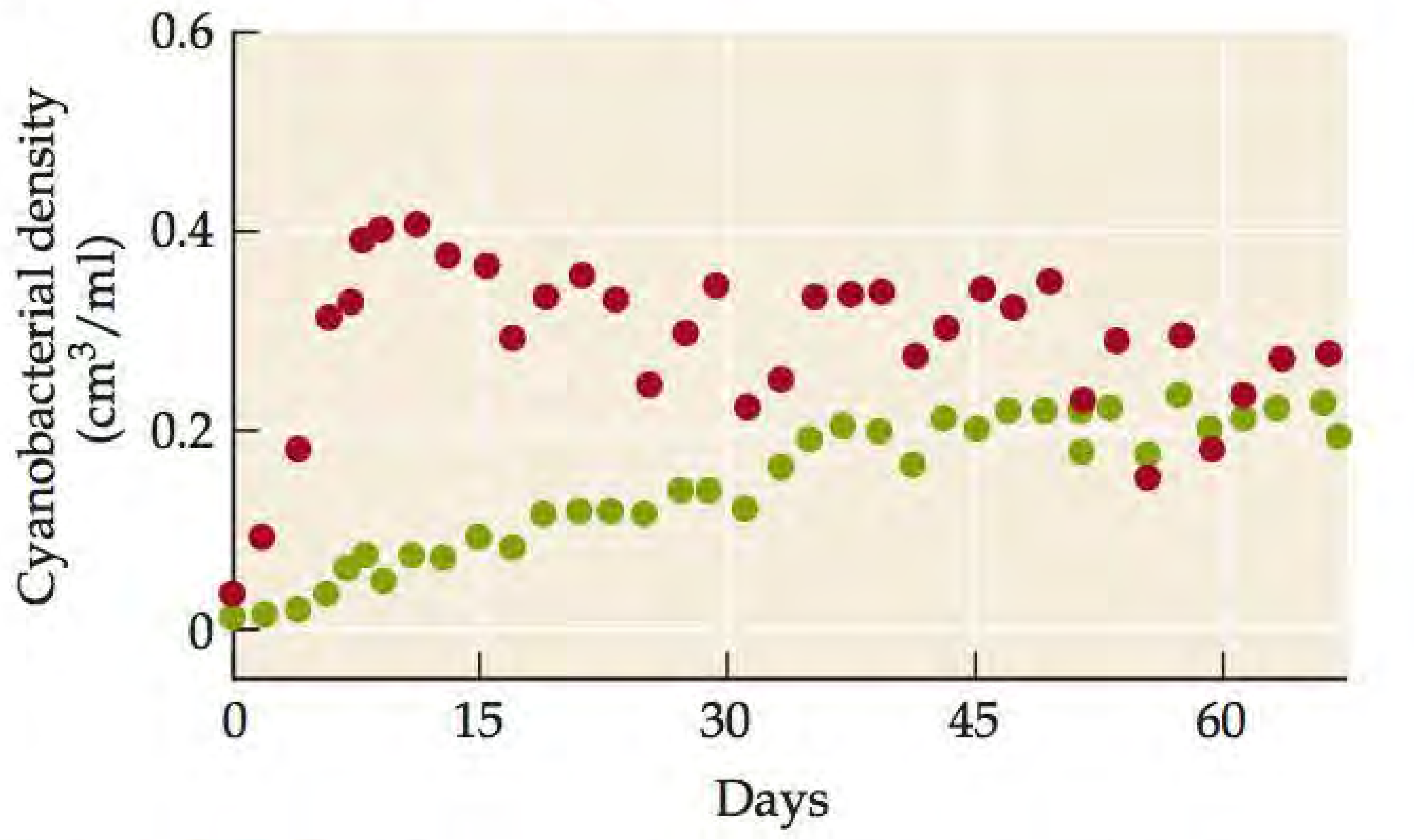


Figure 14.10 Do Cyanobacteria Partition Their Use of Light? Two types of cyanobacteria, BS1 and BS2, were grown together under (A) green light (550 nm), (B) red light (635 nm), and (C) "white" light (the full spectrum, which includes both green and red light). BS1 absorbs green light more efficiently than it absorbs red light; the reverse is true for BS2. Only BS1 persists when the two types are grown together under green light, and only BS2 persists when they are grown under red light. However, both types persist under white light, suggesting that BS1 and BS2 coexist by partitioning their use of light. (After Stomp et al. 2004.)

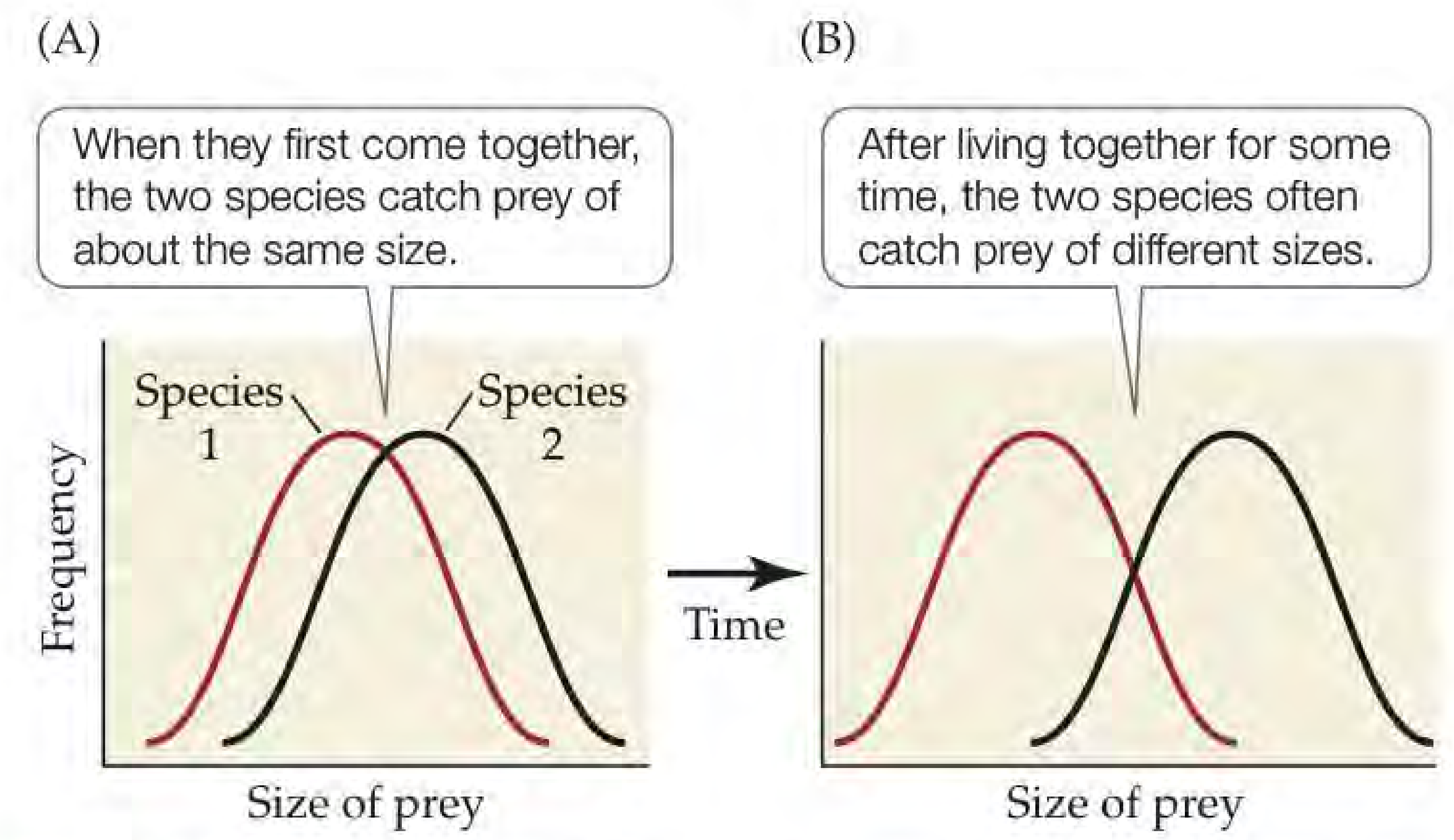
alone under green or red light. However, when they were grown together under green light, the red cyanobacterium BS1 drove the green cyanobacterium BS2 to extinction (**Figure 14.10A**)—as might be expected, since BS1 uses green light more efficiently than does BS2. Conversely, under red light, BS2 drove BS1 to extinction (**Figure 14.10B**), as also might be expected. Finally, when grown together under "white light" (the full spectrum of light, including both green and red light), both BS1 and BS2 persisted (**Figure 14.10C**). Taken together, these results suggest that BS1 and BS2 coexist under white light because they differ in which wavelengths of light they use most efficiently in photosynthesis.

Following up on their laboratory experiments, Stomp et al. (2007) analyzed the cyanobacteria present in 70 aquatic environments that ranged from clear ocean waters (where green light predominates) to highly turbid lakes (where red light predominates). As could be predicted from Figure 14.10, only red cyanobacteria were found in the clearest waters and only green cyanobacteria were found in highly turbid waters—but both types were found in waters of intermediate turbidity, where both green and red light were available. Thus, the laboratory experiments and field surveys conducted by Stomp and colleagues suggest that red and green cyanobacteria coexist because they partition the use of a key limiting resource: the underwater light spectrum.

Competition can lead to character displacement and resource partitioning

When two species compete for resources, natural selection may favor individuals whose phenotype either (1) allows them to outcompete their competitors, resulting in competitive exclusion (see **Web Extension 14.2** for an example using flies) or (2) allows them to partition their limiting resources, thus decreasing the intensity of competition. For example, when two fish species live apart from each other (each in its own lake), the two species may catch prey of similar size. If some factor (such as dispersal) were to cause members of these two species to live in the same lake, their use of resources would overlap considerably (**Figure 14.11A**). In such a situation, natural selection might favor individuals of species 1 whose morphology was such that they ate smaller prey, hence reducing competition with species 2; similarly, selection might favor individuals of species 2 that ate larger prey, hence reducing competition with species 1. Over time, such selection pressures could cause species 1 and species 2 to evolve to become different when they live together than when they live apart (**Figure 14.11B**). Such a process illustrates **character displacement**, which occurs when competition causes the phenotypes of competing species to evolve to become different over time.

Character displacement appears to have occurred in two species of finches on the Galápagos archipelago. Specifically, the beak sizes of the two species, and hence the sizes of the seeds the birds eat, are different on islands where both species live than on islands that have only one of the two species (**Figure 14.12**). Field observations suggest that these two finch species probably differ when



When they first come together, the two species catch prey of about the same size.

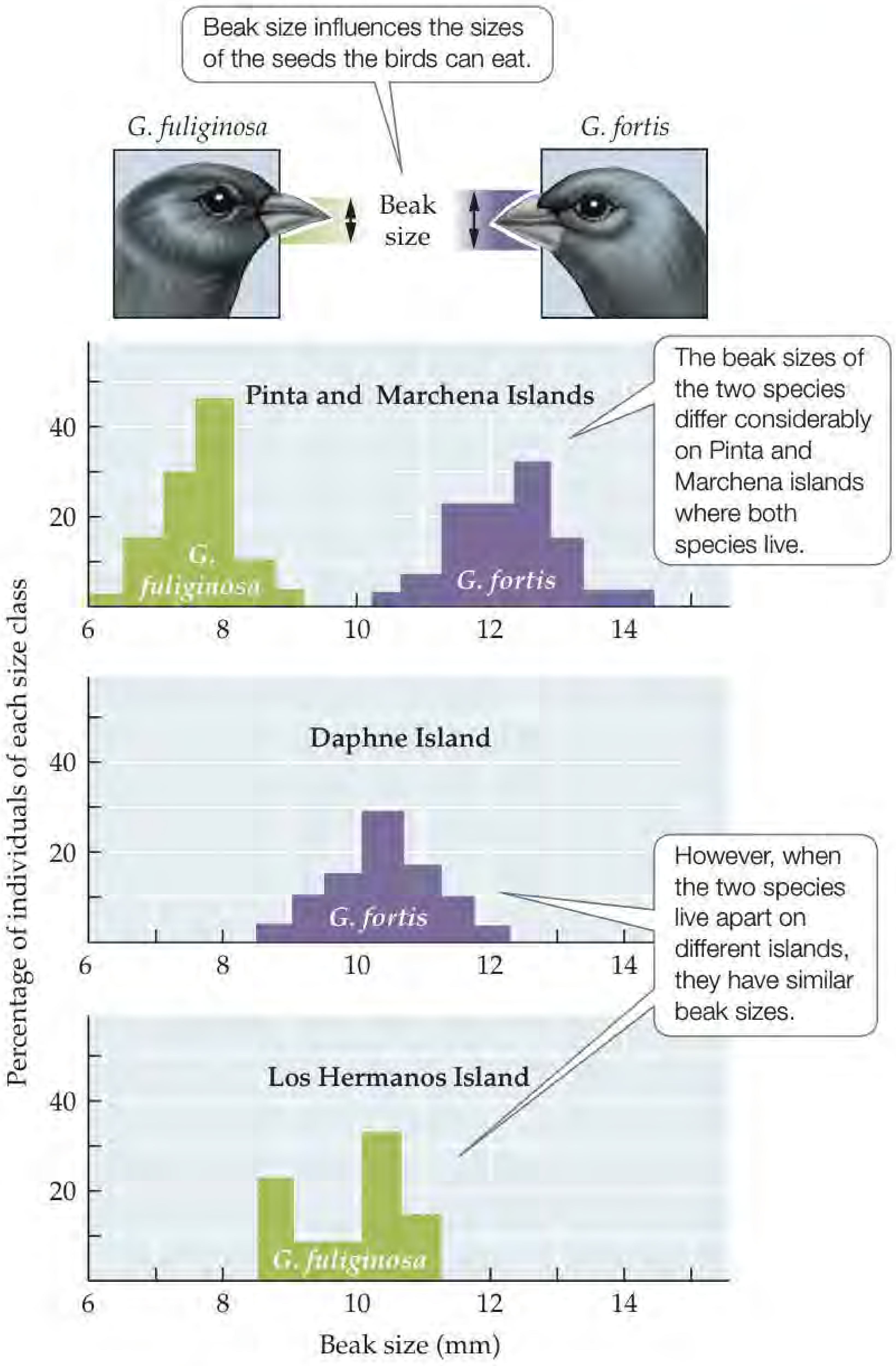
After living together for some time, the two species often catch prey of different sizes.

Figure 14.11 Character Displacement Competition for resources can cause competing species to change over time. Imagine that two fish species that once lived apart and tended to catch prey of about the same size are brought together in a single lake. (A) When the two species first come together, there is considerable overlap in the resources they use. (B) As the two species interact over time, the characteristics they use to obtain prey may evolve such that they tend to catch prey of different sizes.

they live together because of competition, not because of other factors, such as differences in food supplies (Schluter et al. 1985; Grant and Grant 2006).

Data suggestive of character displacement have also been observed in plants, frogs, fishes, lizards, birds, and crabs: in each of these groups, there are pairs of species that consistently differ more where they live together than where they live apart. Additional evidence is needed, however, if we are to make a strong argument that such differences result from competition (as opposed to other factors). Strong support for the role of character displacement can come from experiments designed to test whether competition occurs and has a selective effect on morphology. Such experiments were conducted on sticklebacks of the genus *Gasterosteus*, a group of fish species whose morphology varies most when different species live in the same lake (Schluter 1994). The results indicated that individuals whose morphology differed the most from that of their competitors had a selective advantage: they grew more rapidly than did individuals whose morphology was more similar to that of their competitors. Support for character displacement has also been found in field experiments with spadefoot toad tadpoles (Pfennig et al. 2007) and in laboratory experiments with the bacterium *Escherichia coli* (Tyerman et al. 2008). In each of these studies, experimental results suggest that competition caused the observed morphological differences—that is, that character displacement occurred—and the species were better able to partition their resources as a result.

Evidence for resource partitioning has been used as an explanation for the patterns of species diversity found in communities, as we will see in Chapter 19. For now, let's next turn to mathematical models designed to predict whether the outcome of competition results in competitive exclusion or competitive coexistence.



Beak size influences the sizes of the seeds the birds can eat.

The beak sizes of the two species differ considerably on Pinta and Marchena islands where both species live.

However, when the two species live apart on different islands, they have similar beak sizes.

Figure 14.12 Competition Shapes Beak Size On islands harboring both *Geospiza fuliginosa* and *G. fortis*, competition between these two species of Galápagos finches may have had a selective effect on the sizes of their beaks. (After Lack 1947b.)

CONCEPT 14.3
Competitive interactions can be modeled using the logistic equation.

The Lotka–Volterra Competition Model

Working independently of each other, A. J. Lotka (1932) and Vito Volterra (1926) both modeled competition by modifying the logistic equation. Recall from the discussion under Concept 10.5 that in the logistic equation, the rate at which a population changes in size (dN/dt) is

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

or alternatively,

$$\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right)$$

where N is the population size, r is the intrinsic rate of increase (the maximum possible growth rate for the species, achieved only under ideal conditions), and K is the number at which the population stops increasing in size (which can be interpreted as the carrying capacity of the population).

As we have seen in Concept 14.2, competition deprives species of resources and hence reduces population growth rates. Thus, the presence of a competitor should reduce the growth rate of the original population. To incorporate the effects of the competitor species on one another, we can modify the logistic equation of each species by subtracting a **competition coefficient**, which is a constant used to indicate how strong the competitive effect of one species is on another. The new equations, known as the **Lotka–Volterra competition model**, can be written as

$$\frac{dN_1}{dt} = r_1N_1\left(\frac{K_1 - N_1 - \alpha N_2}{K_1}\right)$$
$$\frac{dN_2}{dt} = r_2N_2\left(\frac{K_2 - N_2 - \beta N_1}{K_2}\right) \qquad \textbf{(14.1)}$$

In these equations, N_1 is the population density of species 1, r_1 is the intrinsic rate of increase of species 1, and K_1 is the carrying capacity of species 1; N_2, r_2, and K_2 are similarly defined for species 2. The competition coefficients (α and β) are constants that describe the effect of one species on the other: α is the effect of species 2 on species 1, and β is the effect of species 1 on species 2. For example, if $\alpha = 1$, then individuals of the two species have the same effect in depressing the growth of species 1. If $\alpha = 5$, each individual of species 2 decreases the growth of species 1 by the same amount as five additional individuals of species 1. Thus, the competition coefficient α is a measure of the effect, on a per individual basis, of species 2 on the population growth of species 1, measured relative to the effect of species 1. Similar reasoning applies to β, which is the effect, on a per individual basis, of species 1 on the population growth of species 2.

We can also think of α and β as "translation terms," each of which converts the number of individuals of one species into the number of individuals of the other species that has an equivalent effect on population growth rates. For example, if $\alpha = 3$, each individual of species 2 decreases the growth of species 1 by the same amount as would three individuals of species 1. Thus, if there are 100 individuals of species 2, it would take 300 individuals of species 1 to decrease the growth rate of species 1 by the same amount as do the 100 individuals of species 2 (i.e., $\alpha = 3$ and $N_2 = 100$, so it takes $\alpha N_2 = 3 \times 100 = 300$ individuals of species 1 to have an equivalent effect).

In the remainder of this section, we'll see how Equation 14.1 can be used to predict the outcome of competition; then we'll explore how competitive coexistence is affected by species interaction strength.

Predicting the outcome of competition

The outcome of competition can be predicted if we know how the population sizes of species 1 and species 2 are likely to change over time. For example, if the population size of species 2 is likely to increase while that of species 1 is likely to decrease to zero, then species 2 should drive its competitor to extinction, thus "winning" the competitive interaction. A computer can be programmed to solve Equation 14.1, thereby predicting the population sizes of species 1 and 2 at different times. Here, however, we'll use a graphical approach to examine the conditions under which each species would be expected to increase or decrease in population size.

We begin by determining when the population size of each competing species would stop changing in size. This approach, which we also used for the Lotka–Volterra predator–prey model (see Concept 12.3), is based on the idea that the population size (N) does not change when the population growth rate (dN/dt) equals zero (or reaches an equilibrium). For example, based on the Lotka–Volterra competition model (Equation 14.1), the population size of species 1 does not change when $dN_1/dt = 0$. When we set dN_1/dt equal to zero, we find that the population size of species 1 (N_1) does not change when

$$N_1 = K_1 - \alpha N_2 \qquad \textbf{(14.2)}$$

Likewise, the population size of species 2 (N_2) does not change when

$$N_2 = K_2 - \beta N_1 \qquad \textbf{(14.3)}$$

Notice that Equations 14.2 and 14.3 are straight lines, written with N_1 as a function of N_2 and N_2 as a function of N_1, respectively. Each of these lines is called the zero population growth isocline (or simply **isocline**), so named because a population does not increase or decrease in size for any combination of N_1 and N_2 that lies on these lines. For species 1, the abundance does not change when $dN_1/dt = 0$, which occurs when $N_2 = K_1/\alpha$ and $N_1 = K_1$. Similarly, for species 2, the abundance does not change when $dN_2/dt = 0$, which occurs when $N_1 = K_2/\beta$ and $N_2 = K_2$.

Once we determine K_1/α and K_2/β, we can then plot the isoclines for both species 1 (x axis) and species 2 (y axis) in graphical form. For species 1, the isocline will be a diagonal line originating at the value $N_2 = K_1/\alpha$ and

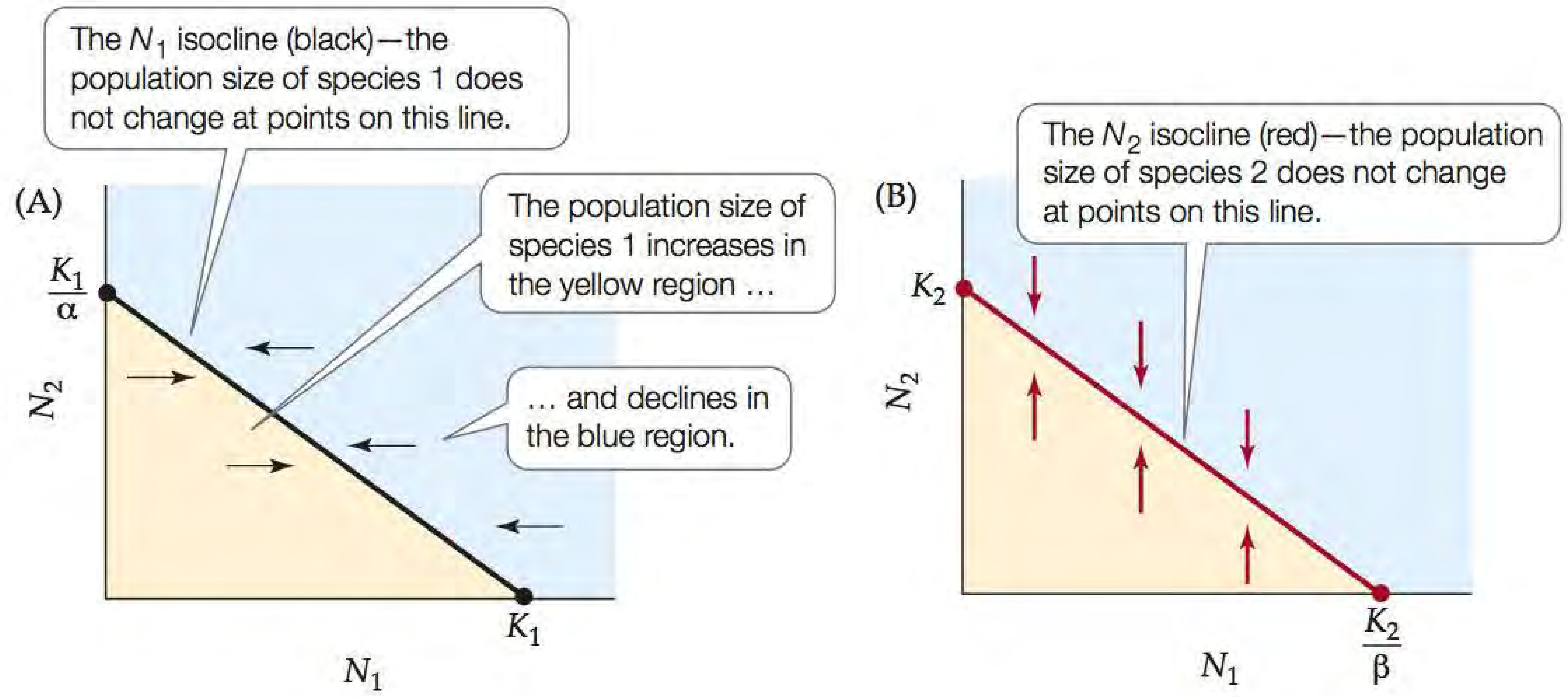


Figure 14.13 Graphical Analyses of Competition The zero population growth isoclines from the Lotka–Volterra competition model can be used to predict changes in the population sizes of competing species. (A) The N_1 isocline. The change in population size of species 1 (indicated by black arrows or vectors) increases in the yellow region and decreases in the blue region. (B) The N_2 isocline. The change in population size of species 2 (indicated by red arrows or vectors) increases in the yellow region and decreases in the blue region.

ending at the value $N_1 = K_1$ (**Figure 14.13A**). This isocline represents the number of individuals of species 2 that would keep species 1's population from changing (or at equilibrium). For example, in Figure 14.13A, because a point to the right of the N_1 isocline represents more individuals than zero population growth will allow, the population size of species 1 will decrease until it reaches the isocline. This is true for the entire region shaded in blue: the population size of species 1 decreases for all points to the right of the N_1 isocline. In contrast, when the population size of species 1 is to the left of the N_1 isocline, the population size of species 1 increases. Similar reasoning applies to species 2's isocline, which can be plotted as the diagonal line originating at the value $N_1 = K_2/\beta$ and ending at the value $N_2 = K_2$ (**Figure 14.13B**). This isocline represents the number of individuals of species 1 that would keep species 2's population from changing (or at equilibrium). Here the population size of species 2 decreases in regions above the N_2 isocline and increases in regions below the N_2 isocline.

The graphical approach we have just described can be used to predict the end result of competition between species. To do this, we plot the N_1 and N_2 isoclines together. Because there are four possible ways that the N_1 and N_2 isoclines can be arranged relative to each other, we must make four different graphs. In two of these graphs, the isoclines do not cross, and competitive exclusion results: depending on which isocline is above the other, either species 1 (**Figure 14.14A**) or species 2 (**Figure 14.14B**) always drives the other to extinction. Note that in the regions shaded in blue, the population sizes of both species are greater than the population sizes on their isoclines, and hence both species *decrease* in number (as indicated by the thick black arrows). Similarly, in the regions shaded in yellow, the population sizes of both species are less than those on their isoclines, and hence both species *increase* in number. In the regions shaded in light or dark gray, one species increases in number (because its population sizes are less than those on its isocline) while the other decreases until the species that increases reaches its carrying capacity (K) and the species that decreases reaches zero and becomes extinct.

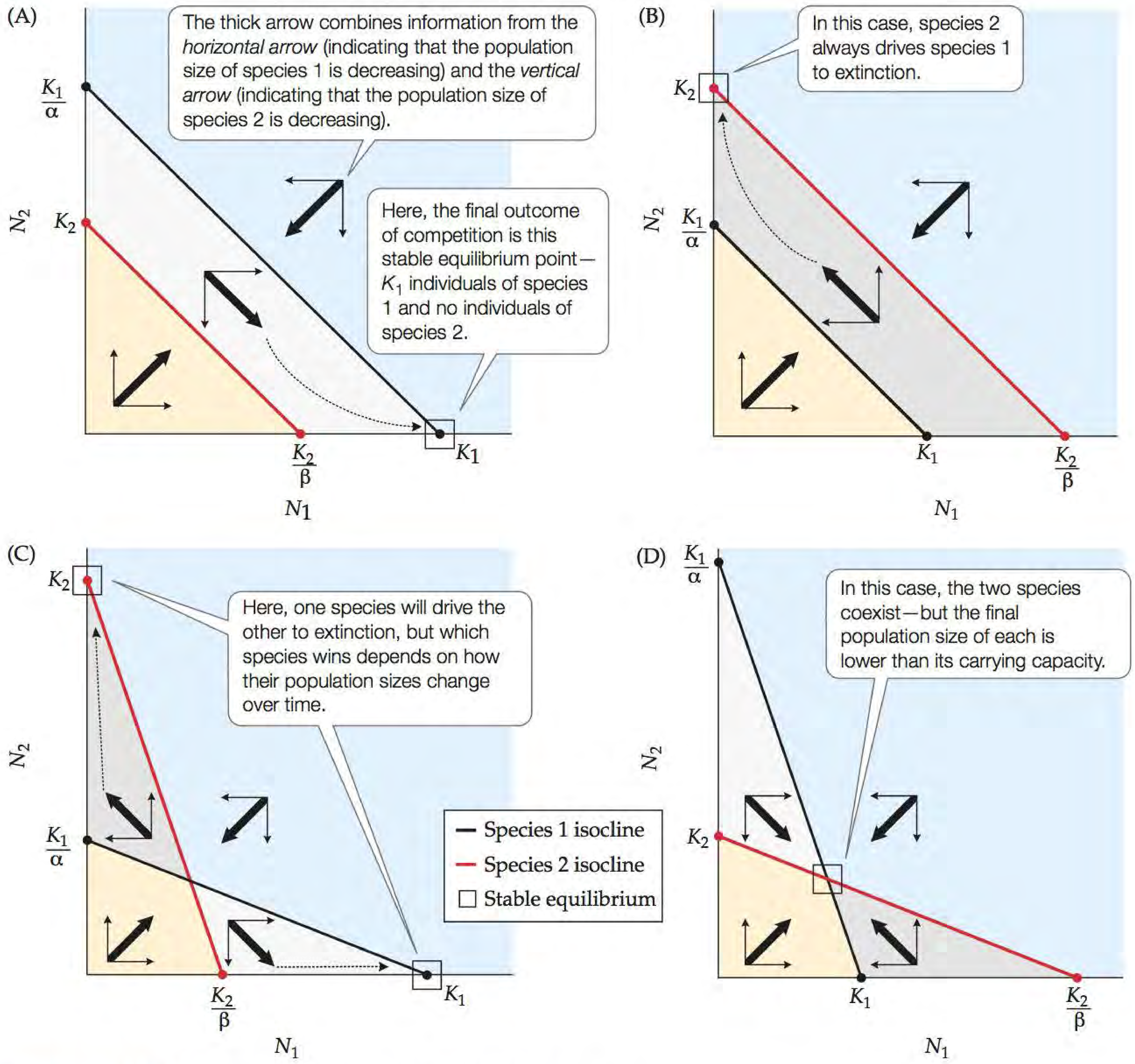
Competitive exclusion also occurs in the third graph (**Figure 14.14C**), but which species "wins" depends on whether the changing population sizes of the two species first enter the region shown in dark gray (in which case, species 2 drives species 1 to extinction) or the region shown in light gray (in which case, species 1 drives species 2 to extinction). Finally, **Figure 14.14D** shows the only case in which the two species coexist, and hence competitive exclusion does not occur. Although in this case neither species drives the other to extinction, competition still has an effect: the final or equilibrium population size of each species (indicated by the box in the figure) is lower than its carrying capacity, as in Gause's experiments with *Paramecium* (compare Figure 14.9B, C, and E).

Researchers have used the graphical approach described in Figure 14.14 to predict the outcome of competition under different ecological conditions. For example, Livdahl and Willey (1991) used this approach to predict whether competition with a native species of mosquito could prevent the invasion of an introduced mosquito species. You can explore their results in **Analyzing Data 14.1**.

The strength of competitive interactions affects coexistence

Now that we've seen the four possible outcomes predicted by the Lotka–Volterra competition model, let's focus on the single case in which competitive coexistence occurs. As described in **Web Extension 14.3**, we can use Figure 14.14D to show that coexistence occurs when the values of α, β, K_1, and K_2 are such that the following inequality holds:

$$\alpha < \frac{K_1}{K_2} < \frac{1}{\beta} \qquad \textbf{(14.4)}$$



The thick arrow combines information from the *horizontal arrow* (indicating that the population size of species 1 is decreasing) and the *vertical arrow* (indicating that the population size of species 2 is decreasing).

Here, the final outcome of competition is this stable equilibrium point—K_1 individuals of species 1 and no individuals of species 2.

In this case, species 2 always drives species 1 to extinction.

Here, one species will drive the other to extinction, but which species wins depends on how their population sizes change over time.

In this case, the two species coexist—but the final population size of each is lower than its carrying capacity.

Figure 14.14 Outcome of Competition in the Lotka–Volterra Competition Model The outcome of competition depends on how the N_1 and N_2 isoclines are positioned relative to one another. (A) Competitive exclusion of species 2 by species 1; species 1 always wins. (B) Competitive exclusion of species 1 by species 2; species 2 always wins. (C) The two species cannot coexist; either species 1 or species 2 wins depending on population sizes of both species. (D) Species 1 and species 2 coexist. The box in each graph indicates a *stable equilibrium point*—a combination of population sizes of the two species that once reached, does not change over time.

? In (B), if K_2 = 1,000 and if species 1 went extinct when N_2 = 1,200, how would the population size of species 2 change after the extinction of species 1?

To see what we can learn from this inequality, consider a situation in which the competing species are equally strong competitors, indicating that α = β. If the two species are also very similar in how they use resources, an individual of species 1 will have nearly the same effect on the growth rate of species 2 as would an individual of species 2 (and vice versa). Thus, when the two species use resources in very similar ways and thus strongly compete, α and β should both be close to 1.

Suppose, for example, that $\alpha = \beta = 0.95$. If we substitute these values for α and β into Equation 14.4, we obtain

$$0.95 < \frac{K_1}{K_2} < 1.05$$

This result suggests that when species strongly compete, coexistence is predicted only when the two species also have similar carrying capacities.

In contrast, if the competing species do not compete strongly but rather differ greatly in how they use resources, α and β will be much lower than 1. To illustrate this case, suppose that $\alpha = \beta = 0.1$. In this situation, coexistence is predicted even if the carrying capacity of one species is nearly 10 times that of the other species, namely,

$$0.1 < \frac{K_1}{K_2} < 10$$

ANALYZING DATA 14.1 Will Competition with a Native Mosquito Species Prevent the Spread of an Introduced Mosquito?

The mosquito *Aedes albopictus* breeds in small volumes of water, such as those in tree holes (cavities in trees that can hold water) and in abandoned tires. Introduced from Asia to North America in the 1980s, this species is a public health concern because it can transmit diseases such as dengue fever. Once in North America, *A. albopictus* colonized tree holes and tires, where it encountered thriving populations of several different native species of mosquitoes.

Livdahl and Willey (1991)* sought to predict the outcome of competition between *A. albopictus* and the native mosquito *A. triseriatus*, a predominant member of tree hole communities. To do this, they estimated competition coefficients and carrying capacities for *A. albopictus* and *A. triseriatus* mosquito larvae developing in water obtained from tree holes and from tires. Their results are shown in the table.

WATER OBTAINED FROM TREE HOLES	WATER OBTAINED FROM TIRES
Competition coefficients	
$\alpha = 0.43$	$\alpha = 0.84$
$\beta = 0.72$	$\beta = 0.25$
Carrying capacities (no. individuals/100 ml of water)	
$K_1 = 42.5$	$K_1 = 33.4$
$K_2 = 53.2$	$K_2 = 44.7$

1. Using Equation 14.1, designate *A. triseriatus* as species 1 and *A. albopictus* as species 2. Use the data in the table to plot the N_1 and N_2 isoclines (see Equations 14.2 and 14.3) for these two species competing in tree hole communities. Predict the equilibrium population density (no. individuals per 100 ml of water) for each species. Describe the likely outcome of competition between these two species in tree hole communities.
2. On a separate graph, plot the N_1 and N_2 isoclines for these two species competing in tires. Predict the equilibrium population density (no. individuals per 100 ml of water) for each species. Describe the likely outcome of competition between these two species in tires.
3. Is it likely that competition with the native species (*A. triseriatus*) will prevent the spread of the introduced species (*A. albopictus*)? Explain.

See the companion website for a similar ANALYZING DATA exercise.

---

*Livdahl, T. P. and M. S. Willey. 1991. Prospects for an invasion: Competition between *Aedes albopictus* and native *Aedes triseriatus*. *Science* 253: 189–191.

As you can demonstrate on your own, other values for the competition coefficients α and β yield similar results. Taken together, such analyses of the Lotka–Volterra competition model suggest the following refinement of the competitive exclusion principle: competing species are more likely to coexist (and hence competitive exclusion is *less* likely) when they do not compete strongly but rather use resources in different ways.

A variety of factors can influence how species divide their use of resources, thereby preventing one competitor from driving the other to extinction. As we'll see in the next section, some of these factors can alter the outcome of competition entirely, turning the inferior competitor into the superior one.

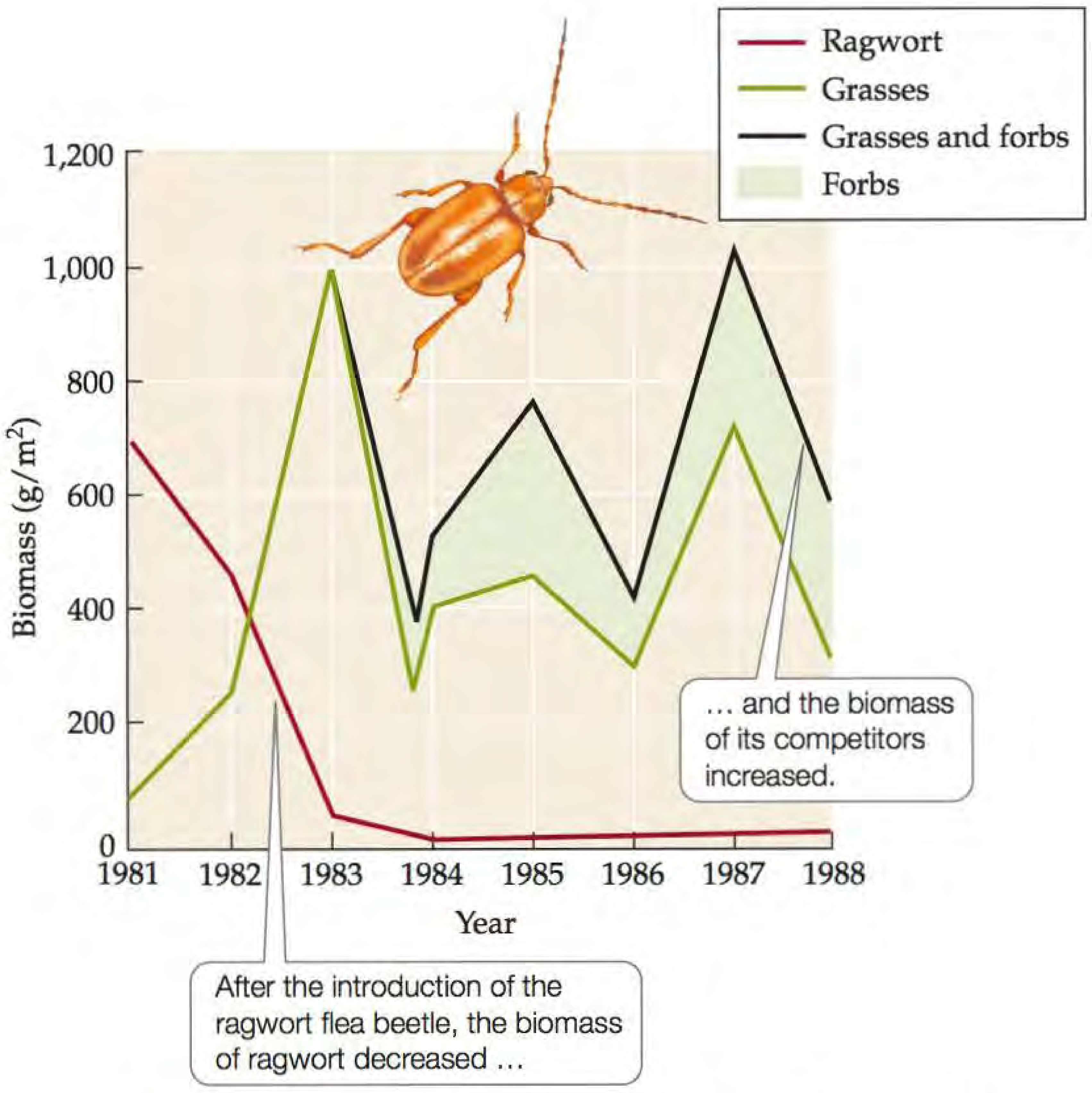
CONCEPT 14.4

The outcome of competition can be altered by the physical environment, disturbance, and predation.

Altering the Outcome of Competition

The outcome of competition between species can be changed by a broad suite of factors, including features of the physical environment, disturbance, and interactions with other species. For example, a difference in abiotic conditions—as might occur from one place to another—can cause a competitive reversal, in which the species that was the inferior competitor in one habitat becomes the superior competitor in another. Cases in which the outcome of competition is different under different abiotic conditions include Tansley's bedstraws, described in the Introduction, and *Semibalanus balanoides* in North America (see Figure 9.9).

Interactions with other species can have similar effects on the outcome of competition between species. The presence of herbivores has been shown to reverse the outcome of competition between species of encrusting marine algae (Steneck et al. 1991) and between ragwort (*Senecio jacobaea*) and other plant species (**Figure 14.15**). Herbivores can have this effect if they prefer to feed on the superior competitor, thereby reducing the growth, survival, or reproduction of that species. What is true of herbivores is also true of predators, pathogens, and mutualists: an increase or decrease in the abundance of such species can change the outcome of competition among the species with which they interact.



... and the biomass of its competitors increased.

After the introduction of the ragwort flea beetle, the biomass of ragwort decreased ...

Figure 14.15 Herbivores Can Alter the Outcome of Competition Ragwort flea beetles are herbivores that feed on ragwort (*Senecio jacobaea*), an invasive plant species. The graph tracks the biomasses of ragwort, grasses, and forbs (broad-leaved herbaceous plants) at a site in western Oregon after the flea beetle was introduced there in 1980. The results show that in the absence of the flea beetle, ragwort was a superior competitor, but it declined precipitously when the beetle was introduced. (After McEvoy et al. 1991.)

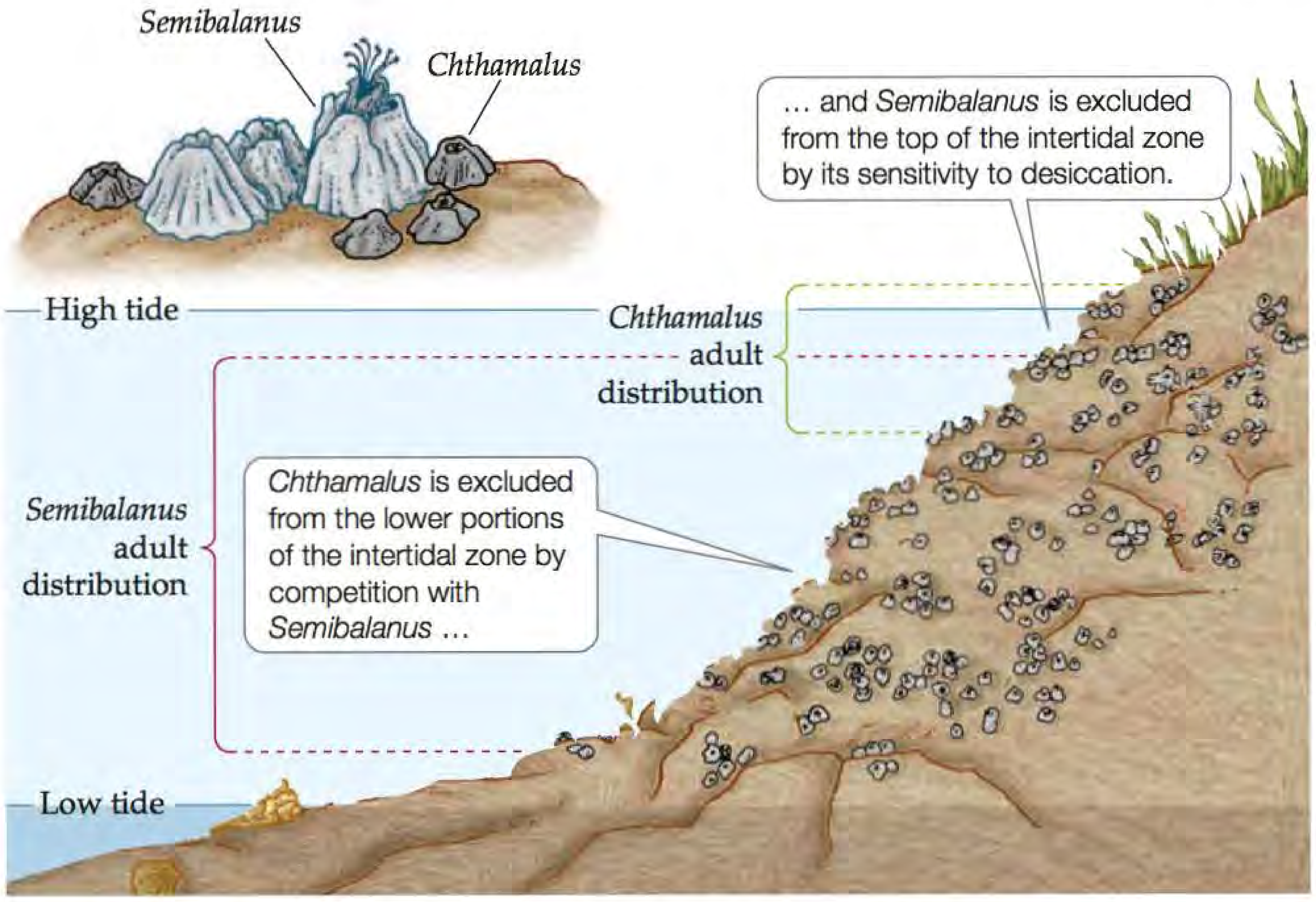
In later chapters, we'll explore many examples in which species interactions alter competitive outcomes—sometimes preventing a superior competitor from driving other species to extinction. Here, we'll focus on the effects of the physical environment and disturbance.

The physical environment can affect competition and ultimately the distribution of species

In a series of classic experiments, Joseph Connell (1961a,b) examined factors that influenced the local distribution, survival, and reproduction of two barnacle species, *Chthamalus stellatus* and *Semibalanus balanoides*. The larvae of barnacles drift through ocean waters, then settle on rocks or other surfaces (such as boat hulls), where they metamorphose into adults, forming a hard outer shell.

At Connell's study site along the coast of Scotland, the distributions of *Chthamalus* and *Semibalanus* larvae overlapped considerably: the larvae of both species were found throughout the upper and middle intertidal zones. However, adult *Chthamalus* were usually found only near the top of the intertidal zone, whereas adult *Semibalanus* were not found there but were found throughout the rest of the intertidal zone (**Figure 14.16**). What accounted for these differences in distribution?

To answer this question, Connell examined the effects of competition and of abiotic features of the environment, such as the risk of desiccation (drying out because of exposure to air, which is greatest in the upper intertidal zone). To test the importance of competition under different abiotic conditions, he chose some individual young barnacles of each species that had settled in each zone and removed all nearby members of the other species. For other focal individuals, he left nearby members of the other species in place. He found that competition with *Semibalanus* excluded *Chthamalus* from all but the top of the intertidal zone, where *Chthamalus* was able to thrive under reduced competition. As they grew, *Semibalanus* smothered (by growing on top of), removed (by growing underneath, hence prying off the rocks), and crushed the *Chthamalus* in the middle intertidal but not in the upper intertidal zone. Averaging across all regions of the intertidal zone, only 14% of *Chthamalus* survived their



... and *Semibalanus* is excluded from the top of the intertidal zone by its sensitivity to desiccation.

Chthamalus is excluded from the lower portions of the intertidal zone by competition with *Semibalanus* ...

Figure 14.16 Squeezed Out by Competition Removal experiments at a field site in Scotland showed that competition mediated by the physical environment determines the local distribution of two species of barnacles, *Chthamalus stellatus* and *Semibalanus balanoides*.

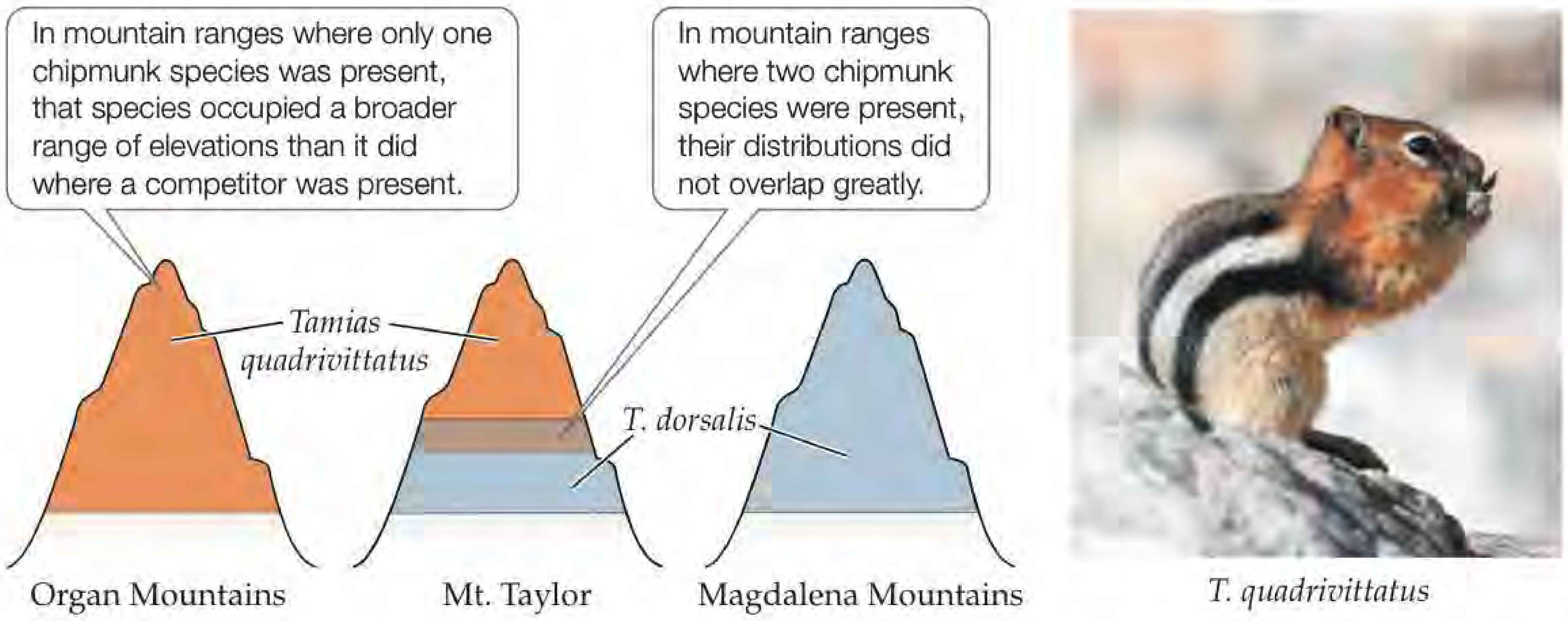


Figure 14.17 A Natural Experiment on Competition between Chipmunk Species Observations of the distributions of *Tamias* chipmunks on mountain ranges in New Mexico suggest that competition may restrict the habitats in which they live. Similar results were obtained for *Tamias* species living in Nevada.

first year when faced with competition from *Semibalanus*, whereas 72% survived where Connell had removed *Semibalanus*. *Chthamalus* individuals that survived a year of competition with *Semibalanus* were small and reproduced poorly.

Semibalanus, in contrast, was not affected strongly by competition with *Chthamalus*. However, whether *Chthamalus* was removed or not, *Semibalanus* dried out and survived poorly near the top of the intertidal zone. Thus, *Semibalanus* appears to have been excluded from that zone by its sensitivity to desiccation rather than its interactions with *Chthamalus*.

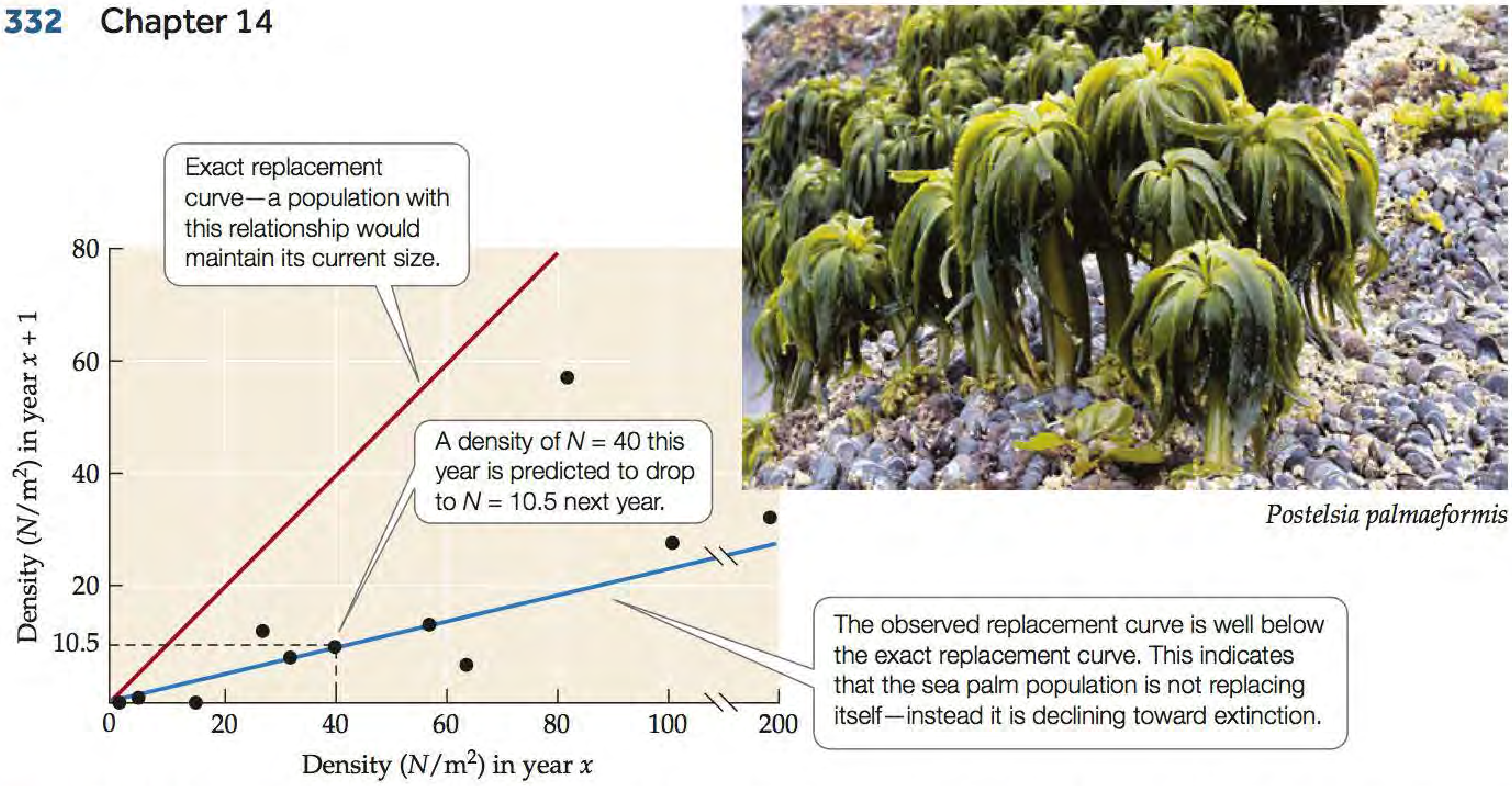
As observed for Tansley's bedstraw plants and Connell's barnacles, competition can restrict the local distribution of a species to a particular set of environmental conditions—the bedstraws, for example, could be growing inches away from each other, but each species was restricted to a particular soil type. Competition has also been shown to prevent a wide range of species, including mammals, marine invertebrates, birds, and plants, from occupying geographic regions in which they would otherwise thrive.

In some cases, a "natural experiment"—a situation in nature that is similar in effect to a controlled removal experiment—provides evidence that competition can vary depending on environmental conditions and ultimately affect geographic distributions. Such a situation was found for chipmunks in the genus *Tamias* (previously known as *Neotamias* or *Eutamias*). These chipmunks live in forests on mountains in the southwestern United States, where mountain ranges are separated from one another by desert flatlands. Patterson (1980, 1981) studied the distributions of *Tamias* chipmunks and found that when a species lived alone on a mountain range because it preferred those environmental conditions, it consistently occupied a broader range of habitats and elevations than when it lived with a competitor species (**Figure 14.17**). As in Connell's removal experiments, this result suggests that competition may have prevented some *Tamias* chipmunk species from living in areas of otherwise suitable habitat.

Disturbance can prevent competition from running its course

As we saw in Concept 9.2, a disturbance such as a fire or major storm may kill or damage some individuals while creating opportunities for others. Some species can persist in an area only if such disturbances occur regularly. Forests, for example, contain some herbaceous plant species, such as the primroses described in Concept 11.4, that require abundant sunlight and are therefore found only in areas where wind or fire has created an opening in the tree canopy. Over time, a population of such plants is doomed: as trees recolonize the area, shade increases to the point at which the species are competitively excluded. Such species are called **fugitive species** because they must disperse from one place to another to take advantage of disturbances that open up resources and allow them to avoid competitive exclusion.

Robert Paine, a marine ecologist from the University of Washington, has described how periodic disturbance allows a fugitive algal species, the sea palm (*Postelsia palmaeformis*), to coexist with a competitively dominant species, the mussel *Mytilus californianus*. The sea palm is a brown alga that lives in the intertidal zone and must attach itself to rocks to grow. It competes for attachment space with mussels. Although a sea palm can outcompete an individual mussel (by growing on top of it), the sea palm is eventually displaced by other mussels that grow in from the side. Competition with mussels causes sea palm populations to decline over time (**Figure 14.18**). Hence, if competition ran its course, mussels would drive sea palm populations to extinction. That is exactly what happens on low-disturbance shorelines (with a mean rate of 1.7 disturbances per year), where waves only occasionally tear patches of mussels from the rocks. However, sea palms can persist in shoreline areas where high-energy



Exact replacement curve—a population with this relationship would maintain its current size.

A density of N = 40 this year is predicted to drop to N = 10.5 next year.

The observed replacement curve is well below the exact replacement curve. This indicates that the sea palm population is not replacing itself—instead it is declining toward extinction.

Figure 14.18 Population Decline in an Inferior Competitor Lacking Disturbance In this graph, each point represents an observed change in density (N, the number of individuals per square meter) from one year (year x) to the next (year x + 1) at sites where sea palms are growing in competition with mussels and lack disturbance. These points can be used to estimate a *replacement curve* (blue line), which shows the extent to which sea palm individuals replace themselves over time without disturbance. The exact replacement curve (red line) shows the densities at which the population size would not change from one year to the next. (After Paine 1979.)

? Based on the observed replacement curve (the blue line), how many years would it take for a sea palm population to decline from 100 individuals to fewer than 20 individuals?

waves remove mussels more frequently (with a mean rate of 7.7 disturbances per year), thereby creating temporary openings for sea palm individuals.

A CASE STUDY REVISITED

Competition in Plants That Eat Animals

In plants, competition for nutrients can be especially important (see Figure 14.5), but other resources, such as light and water, can also be in short supply. Carnivorous plants live in nutrient-poor soils, and their root systems are usually less well developed than the root systems of their noncarnivorous neighbors. As noted in the Case Study, these observations suggest that carnivorous plants may be poor competitors for soil nutrients and hence may rely on eating animals to obtain the nutrients they need for growth. These observations suggest that carnivorous plants might be especially hard-hit by belowground competition if they were denied access to their unique, alternative source of nutrients (animal prey).

Instead, contrary to what would be expected if competition for nutrients were important, *Sarracenia alata* was not especially hard-hit when neighbors were present and pitchers were deprived of prey (see Figure 14.2). In fact, when neighbors were present, pitcher plants had the same biomass regardless of whether they had access to prey. These results suggest that there was relatively little competition between *Sarracenia* and noncarnivorous plants for soil nutrients and that some other factor was driving the positive response these plants had to neighbor removal.

Further investigation revealed that competition for light appeared to be more important to pitcher plants. Brewer found that neighbors reduced the availability of light to *Sarracenia* by a factor of 10. When neighbors were removed, *Sarracenia* responded by greatly increasing its growth, especially if pitchers were open and the plants could capture prey (see Figure 14.2). Hence, *Sarracenia* responded to higher light levels when neighbors were removed by growing more rapidly—but only if prey were available to supply the extra nutrients they needed for such growth.

Overall, it appears that pitcher plants compete with their neighbors for light but avoid competition for soil nutrients by eating animals and by using changes in light levels as a cue for growth. When light levels are low—as would be the case when it is shaded by competitors—*Sarracenia* grows little and hence requires few nutrients. In such a situation, prey deprivation has little effect because the plant does not need extra nutrients. When light levels are high, however—as would occur after a fire or whenever few competitors are present—*Sarracenia* is stimulated to grow. Under these circumstances, prey deprivation has a major effect because animal prey supply most of the nutrients that it uses for growth.

CONNECTIONS IN NATURE
The Paradox of Diversity

As we've seen, some field data show that superior competitors can drive inferior competitors extinct—which is exactly what the competitive exclusion principle states should happen whenever two or more species use the same set of limiting resources. Natural communities, however, contain many species that share the use of scarce resources without driving one another to extinction. Pitcher plants, for example, coexist with a diverse group of other species (**Figure 14.19**), even though they were predicted to be inferior competitors for soil nutrients. In the context of Brewer's experiments on pitcher plants, let's reconsider why superior competitors do not always drive inferior competitors to extinction.

The concept of resource partitioning suggests that a number of species could coexist in nutrient-poor environments if they avoided competition for scarce nutrients by acquiring them in different ways. This idea helped to motivate Brewer's study: he wanted to know whether differences in their means of nutrient acquisition could explain the coexistence of carnivorous and noncarnivorous plants. To find out, Brewer deprived carnivorous plants of their unique source of nutrients (animal prey), thus increasing the overlap between the ways in which carnivorous and noncarnivorous plants acquired nutrients. If competition for nutrients was important, pitcher plants that were deprived of prey should have experienced more severe competitive effects, or they should have compensated for reduced nutrient intake by increasing their production of roots or pitchers. Neither of these outcomes occurred, so Brewer sought other explanations of species coexistence.

As we'll see in Concept 19.3, environmental variation provides a second mechanism for the coexistence of species in communities: if environmental conditions fluctuate over space or time (or both), species may coexist if different species are superior competitors under different environmental conditions. Tansley's bedstraw example (given in the Introduction) illustrates how differences in soils can alter the outcome of competition, thus promoting coexistence in environments that vary over space. With respect to variation over time, an inferior competitor may persist whenever competition fails to run its course. Consider a species such as the sea palm (see Figure 14.18), which competes poorly but tolerates disturbance well. Such a species may persist if a disturbance periodically "resets the clock" by decreasing the abundance of a superior competitor before that species drives the inferior competitor to extinction. Such a scenario may also apply to the pitcher plant *Sarracenia alata*. The habitat in which it lives is prone to fire; pitcher plants tolerate fire well, and they use changes in light levels as a cue for growth. As a result, *Sarracenia* grows primarily when its competitors are reduced by fire. This growth strategy may allow it to escape competition for nutrients by reducing its demand for scarce nutrients when competition is potentially most intense (i.e., in years without fire) and increasing its demand for nutrients when competitors have been reduced (years with fire).

Figure 14.19 Coexistence in a Nutrient-Poor Environment The pitcher plant *Sarracenia alata*, seen in the close-up at the left, coexists with noncarnivorous plants that can outcompete it for both nutrients and light. (Landscape photo courtesy of Chase Bailey.)

Summary

CONCEPT 14.1 Competition can be direct or indirect, vary in its intensity, and occur between similar or dissimilar species.

- The most common form of competition is exploitation competition, which occurs when species compete indirectly as they share the use of a limiting resource. Another form of competition, called interference competition, occurs when species compete directly for access to resources.
- If resource levels become sufficiently low, the intensity of competition can increase.
- Competition is often asymmetrical, affecting one competitor more strongly than the other.
- Competition can occur between closely or distantly related species.
- Competition for resources is common—though not ubiquitous—in natural communities.

CONCEPT 14.2 Competing species are more likely to coexist when they use resources in different ways.

- The competitive exclusion principle states that if competing species use the same limiting resource in the same way, they cannot coexist.
- In reality, most species show competitive coexistence, or the ability to coexist with one another despite sharing limiting resources.
- Field studies have revealed many examples of resource partitioning, in which competing species use one or more shared resources in different ways.
- In character displacement, competition causes the phenotypes of competing species to evolve to become different from each other over time, thereby reducing the intensity of competition and allowing resource partitioning.

CONCEPT 14.3 Competitive interactions can be modeled using the logistic equation.

- Lotka and Volterra modeled the effects of interspecific competition by modifying the logistic equation.
- The Lotka–Volterra competition model includes a competition coefficient, which is a constant used to indicate how strong the competitive effect of one species is on another.
- Graphical analyses of the Lotka–Volterra competition model allows four predictions for the outcome of competition—three lead to competitive exclusion, and one leads to competitive coexistence.

CONCEPT 14.4 The outcome of competition can be altered by the physical environment, disturbance, and predation.

- Herbivores or predators can change or reverse the outcome of a competitive interaction if they prefer to feed on the superior competitor.
- The physical environment can affect the outcome of competition and ultimately the distribution of species.
- Periodic disturbances that remove a superior competitor can allow an inferior competitor to persist.

Review Questions

1. Plant species require nitrogen to grow and reproduce. Assume that a single application of high-nitrogen fertilizer is added to a low-nitrogen, sandy soil in which two plant species are found. Predict how the intensity of competition for soil nitrogen will change over time, and explain your prediction.
2. List four general features of competition described in Concept 14.1, and provide an example of each.
3. Suppose that each of 20 meadows contains a population of plant species 1, a population of plant species 2, or populations of both plant species. Species 1 and 2 are known to compete with each other. Each meadow is separated from the others by areas in which neither species 1 nor species 2 can grow or survive.
    a. List three possible reasons why the meadows contain different combinations of the two plant species.
    b. Describe an experiment that would help to evaluate one or more of the reasons you have listed.

Hone Your Problem-Solving Skills

As described in Concepts 14.2 and 14.3, laboratory experiments, field observations, and mathematical models have been used to explain why competing species coexist in some situations but not others.

1. From *each* of these three approaches, describe a result that helps to explain when competing species are likely to coexist. Taken together, do these three approaches to studying competition yield similar or different explanations for why coexistence occurs in some situations but not others?
2. If $\alpha = 0.8$, $\beta = 1.6$, $N_1 = 140$, and $N_2 = 230$, are individuals of species 1 or species 2 having a greater effect on the growth rate of species 2?
3. Based on graphical analyses of the Lotka–Volterra competition model, evaluate the following statement: if $\alpha < \beta$, species 1 will always drive species 2 to extinction. Explain your answer.

ON THE COMPANION WEBSITE
ecology4e.sinauer.com

The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

14.1 **If You Can't Beat 'em, and You Can't Join 'em, Move Away: Competition-Induced Character Displacement**

Web Extensions

14.1 **Resource Partitioning in *Anolis* Lizards**

14.2 **Evolution of a Competitive Reversal**

14.3 **Deriving the Conditions for Coexistence in the Lotka–Volterra Competition Model**

15 Mutualism and Commensalism

KEY CONCEPTS

CONCEPT 15.1 In positive interactions, no species is harmed and the benefits are greater than the costs for at least one species.

CONCEPT 15.2 Each partner in a mutualistic interaction acts in ways that serve its own ecological and evolutionary interests.

CONCEPT 15.3 Positive interactions affect the abundances and distributions of populations as well as the structure of ecological communities.

The First Farmers: A Case Study

Humans first began to farm about 10,000 years ago. Agriculture was a revolutionary development that led to great increases in the size of our population as well as to innovations in government, science, the arts, and many other aspects of human societies. But people were far from the first species to farm. That distinction goes to ants in the tribe Attini, a group of 210 species, most of which live in tropical forests of South America. These ants, known informally as the attines or fungus-growing ants, started cultivating fungi for food at least 50 million years before the first human farmers (**Figure 15.1**).

Like human farmers, the ant farmers nourish, protect, and feed on the species they grow, forming a relationship that benefits both the farmer and the crop. The attines cannot survive without the fungi they cultivate; many of the fungi depend on the ants as well. When a virgin queen ant leaves her mother's nest to mate and begin a new colony, she carries in her mouth some of the fungi from her birth colony. The fungi are cultivated in subterranean gardens (**Figure 15.2**). An ant colony may contain hundreds of gardens, each roughly the size of a football; these gardens can provide enough food to support 2–8 million ants. Some attines occasionally replace the fungi in their gardens with new, free-living fungi that they gather from surrounding soils. Other species, such as leaf-cutter ants in the genera *Atta* and *Acromyrmex*, do not cultivate fungi found in the environment. Instead, the fungi in their gardens come only from propagules passed from a parent ant colony to each of its descendant colonies.

As their name suggests, leaf-cutter ants cut portions of leaves from plants and feed them to the fungi in their gardens. Back at the nest, the ants chew the leaves to a pulp, fertilize them with their own droppings, and "weed" the fungal gardens to help control bacterial and fungal invaders. In turn, the cultivated fungi produce specialized structures, called *gongylidia*, on which the ants feed. The partnership between leaf-cutter ants and fungi has been called an "unholy alliance" because each partner helps the other to overcome the formidable defenses that protect plants from being eaten. The ants, for example, scrape a waxy covering from the leaves that the fungi have difficulty penetrating, while the fungi digest and render harmless the chemicals that plants use to kill or deter insect herbivores.

Figure 15.1 Collecting Food for Their Fungi Fungus-growing ants (*Atta cephalotes*) in Costa Rica carry leaf segments to their colony, where the leaves will be fed to the fungi the ants cultivate for food.

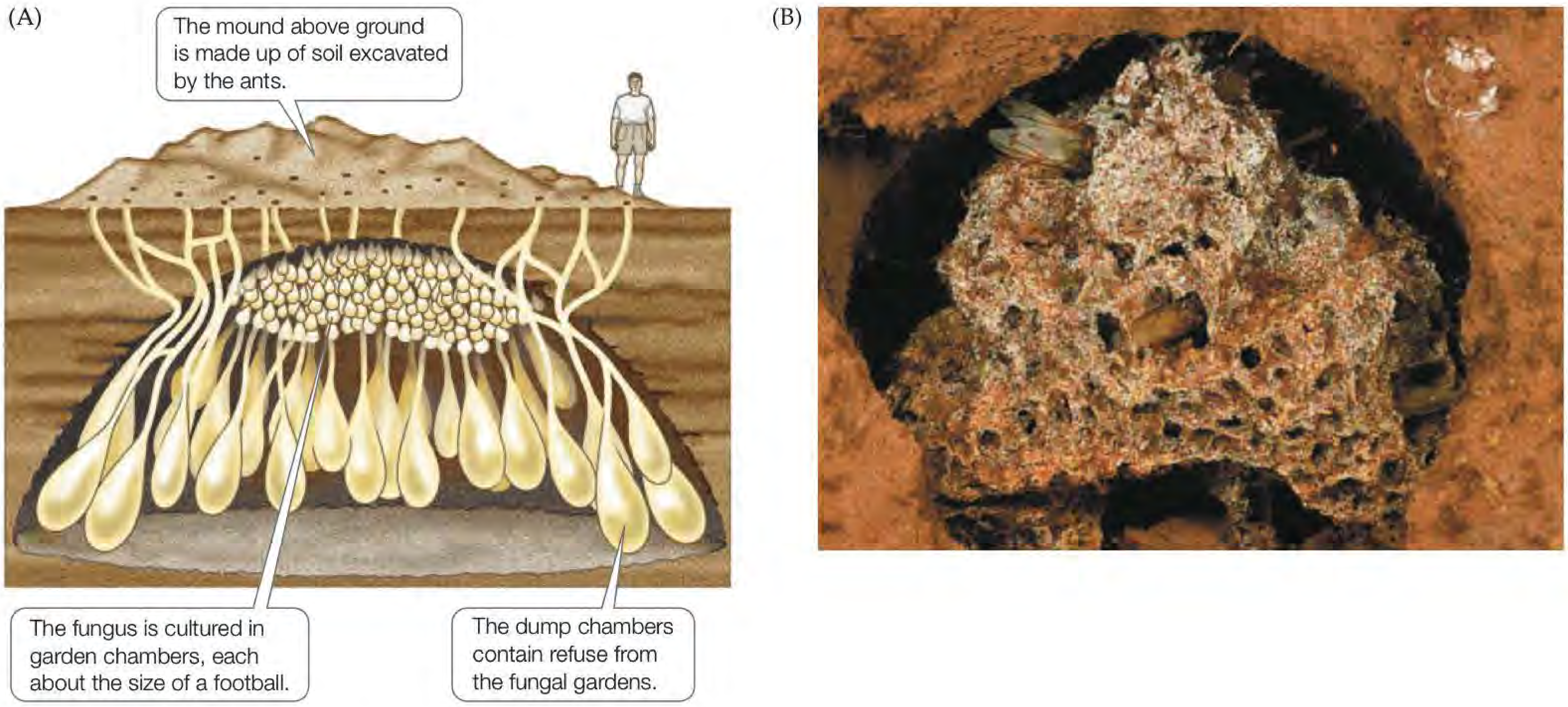


Figure 15.2 The Fungal Garden of a Leaf-Cutter Ant (A) A diagrammatic representation of a large *Atta* leaf-cutter ant colony. (B) This photo shows a cutaway view of a garden chamber in a central Paraguay colony of the leaf-cutter ant *Atta laevigata*. Inside the chamber is a specialized structure called a gongylidia, which is produced by the cultivated fungi and eaten by the ants.

But all is not perfect in the gardens. Nonresident fungi, which themselves would benefit from ant cultivation, periodically invade leaf-cutter ant colonies. Furthermore, pathogens and parasites that attack the cultivated fungi occasionally outstrip the ants' ability to weed them out. What prevents such unwanted guests from destroying the gardens?

Introduction

Chapters 12–14 emphasized interactions between species in which at least one member is harmed (predation, herbivory, parasitism, and competition). But life on Earth is also shaped by **positive interactions**, those in which one or both species benefit and neither is harmed. Most vascular plants, for example, form beneficial associations with fungi that improve the growth and survival of both species. In fact, fossil evidence indicates that the earliest vascular plants formed similar associations with fungi more than 400 million years ago (Selosse and Le Tacon 1998). These early vascular plants lacked true roots, so their interactions with fungi may have increased their access to soil resources and aided their colonization of land.

As this example suggests, positive interactions have influenced key events in the history of life as well as the growth and survival of organisms living today. As we'll see in this chapter, positive interactions can also influence the outcome of other types of interactions among organisms, thus shaping communities and influencing ecosystems. We will begin our study of positive interactions with definitions of some key terms and an overview of the scope of these interactions in ecological communities.

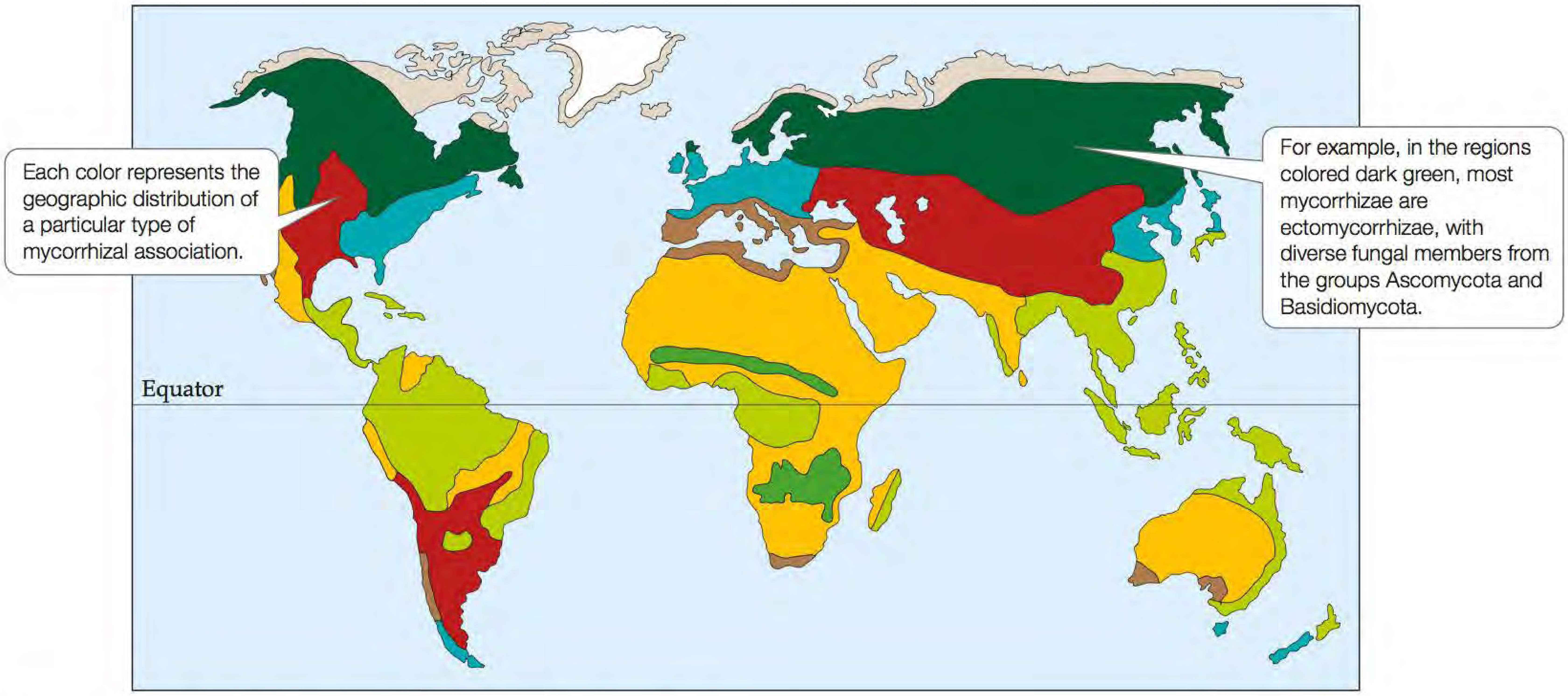
CONCEPT 15.1

In positive interactions, no species is harmed and the benefits are greater than the costs for at least one species.

Positive Interactions

There are two fundamental types of positive interactions: mutualism and commensalism. **Mutualism** is a mutually beneficial interaction between individuals of two or more species (+/+ relationship). **Commensalism** is an interaction in which individuals of one species benefit, while those of the other species do not benefit and are not harmed (+/0 relationship). Many ecologists refer to mutualism and commensalism collectively as **facilitation**.

In some cases, the species involved in a positive interaction form a **symbiosis**, a relationship in which individuals of the two species live in close physical and/or physiological contact with each other. Examples include the relationships between pea aphids and their bacterial symbionts (see Concept 13.2) and between humans and bacteria (we have a diverse set of bacteria living in our guts, many of which are beneficial). However, parasites



Each color represents the geographic distribution of a particular type of mycorrhizal association.

For example, in the regions colored dark green, most mycorrhizae are ectomycorrhizae, with diverse fungal members from the groups Ascomycota and Basidiomycota.

Figure 15.3 Mycorrhizal Associations Cover Earth's Land Surface Each color on the map shows the region in which one of eight major types of mycorrhizal associations is found (see Fitter 2005 to learn which fungi are involved in each of these eight mycorrhizal associations). Notice that the locations of the different types of mycorrhizal associations correspond fairly closely to the locations of major terrestrial biomes (see Figure 3.5A). (After Fitter 2005.)

? What types of plants are likely to be involved in the mycorrhizal association shown in light green? (Hint: Refer to Figure 3.5A.)

also form symbiotic associations with their hosts (see Figure 13.3). Thus, symbiotic relationships can range from parasitism (+/–) to commensalism (+/0) to mutualism (+/+).

In mutualism and commensalism, the growth, reproduction, or survival of individuals of one or multiple species is increased by their interaction with other species (and no species is harmed). The benefits can take a variety of forms. A species may provide its partner with food, shelter, or a substrate to grow on; it may transport its partner's pollen or seeds; it may reduce heat or water stress; or it may decrease the negative effects of competitors, herbivores, predators, or parasites. In a mutualism, there can be costs to an organism that provides a benefit to its partner, as when supplying food to its partner reduces its own opportunity for growth. Nevertheless, the net effect of the interaction is positive because the benefits are greater than the costs for each of the partners.

In the remainder of this section, we will discuss some general observations that apply to both mutualism and commensalism; in Concept 15.2, we'll examine some characteristics that are specific to mutualism.

Mutualism and commensalism are ubiquitous

Mutualistic associations literally cover the land surface of Earth. For example, most vascular plant species, including those that dominate terrestrial ecosystems, form **mycorrhizae**, symbiotic associations between plant roots and various types of fungi that are usually mutualistic (**Figure 15.3**). About 80% of angiosperms (flowering plants) and all gymnosperms (e.g., conifers, cycads, and the ginkgo) form mycorrhizal associations. Mycorrhizae provide clear benefits to the plants, improving their growth and survival in a wide range of habitats (Smith and Read 2008; Booth and Hoeksema 2010). One way in which mycorrhizal fungi benefit plants is by increasing the surface area over which the plants can extract water and nutrients from the soil; in some cases, over 3 m of fungal filaments, known as *hyphae*, may extend from 1 cm of plant root. The fungi may also protect the plants from pathogens, while the plants typically benefit the fungi by supplying them with carbohydrates.

There are two major types of mycorrhizae (**Figure 15.4**). In **ectomycorrhizae**, the fungal partner typically grows between root cells and forms a mantle around the exterior of the root; hyphae in the mantle often extend varying distances into the soil. In **arbuscular mycorrhizae**, the fungal partner also grows into the soil, and it grows between some root cells while penetrating the cell walls of others. Hyphae of arbuscular mycorrhizae that penetrate a root cell form a branched network, called an *arbuscule*. Since their hyphae can penetrate root cells, arbuscular mycorrhizae once were called "endomycorrhizae" (from the Greek *entos*, "in"). However, most researchers no longer

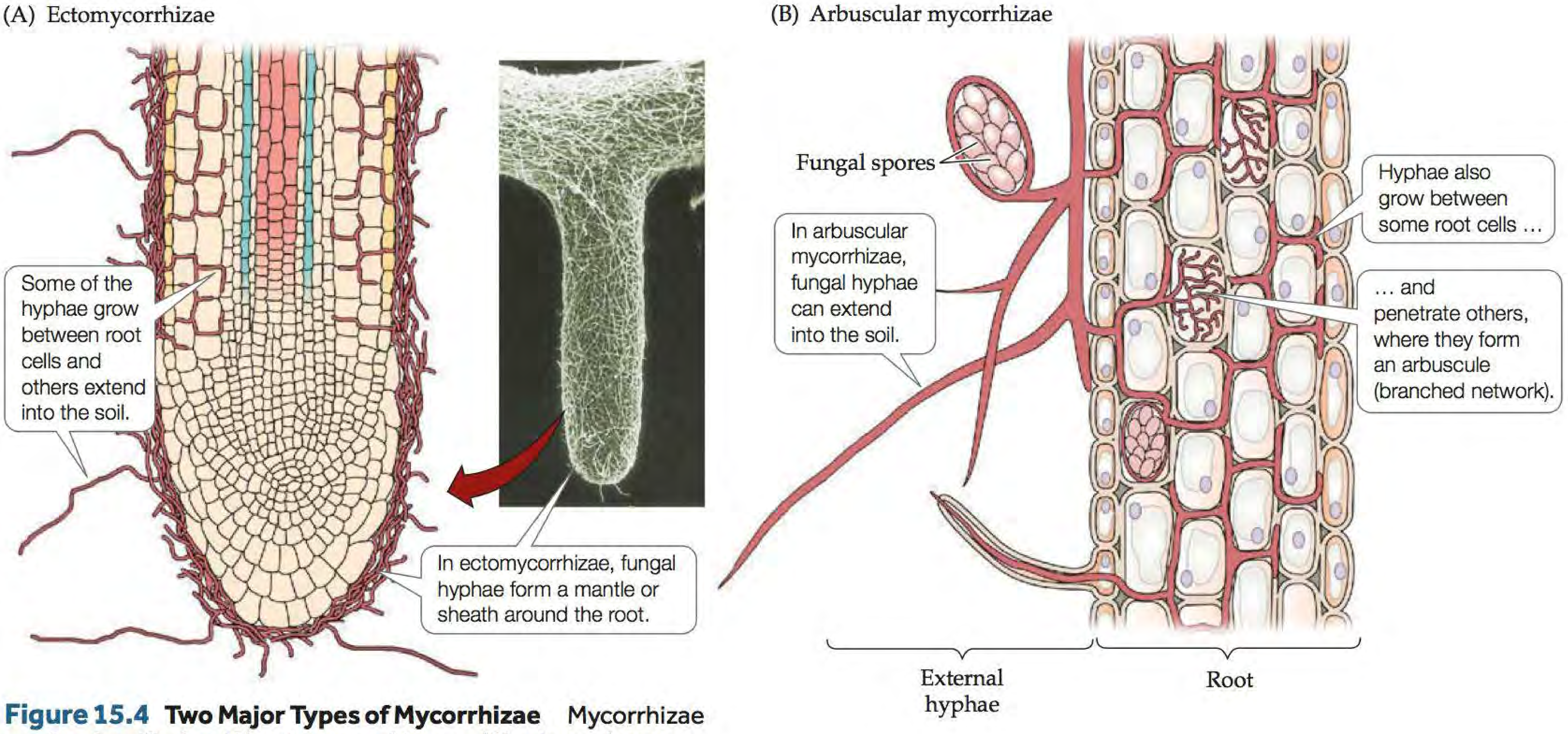


Figure 15.4 Two Major Types of Mycorrhizae Mycorrhizae can be classified as (A) ectomycorrhizae or (B) arbuscular mycorrhizae. In arbuscular mycorrhizae, hyphae that enter root cells penetrate the cell wall, but not the cell membrane. (A after Rovira et al. 1983; B after Mauseth 1988.)

? Describe morphological features that distinguish ectomycorrhizae from arbuscular mycorrhizae.

use the term "endomycorrhizae," because the hyphae of some ectomycorrhizae can also penetrate root cells.

Mutualistic associations can be found in many other organisms and habitats. In the oceans, corals form mutualisms with symbiotic algae, as mentioned in Concept 3.3. The corals provide the algae with habitats, nutrients (nitrogen and phosphorus), and access to sunlight; the algae provide the corals with carbohydrates produced by photosynthesis. All the numerous invertebrate and vertebrate species that live in and on coral reefs depend directly or indirectly on the coral–alga mutualism. On land, mammalian herbivores such as cattle and sheep depend on bacteria and protists that live in their guts and help them metabolize otherwise indigestible plant material, such as cellulose. Similarly, insects rely on mutualisms with a number of other species, including plants (e.g., pollination mutualisms, fungi, protists (**Figure 15.5**), and bacteria.

Commensalism, like mutualism, is everywhere—the ecological world is built on it. As we'll see in Concept 16.3, millions of species form +/0 relationships with so-called foundation species, which provide the habitat in which they live. In these relationships, a species that depends on the habitat provided by another species often has little or no effect on the species that provides that habitat. Examples include species that live on other species, such as lichens found on the bark of a tree or the harmless bacteria that grow on the surface of your skin. Many algae, invertebrates, and fishes found in marine kelp forests go locally extinct if the kelp are removed (see Case Study Chapter 9); such species depend on the kelp for a home, but most of them do not harm or benefit the kelp. Likewise, although the numbers are quite uncertain, there may be more than a million insect species and thousands

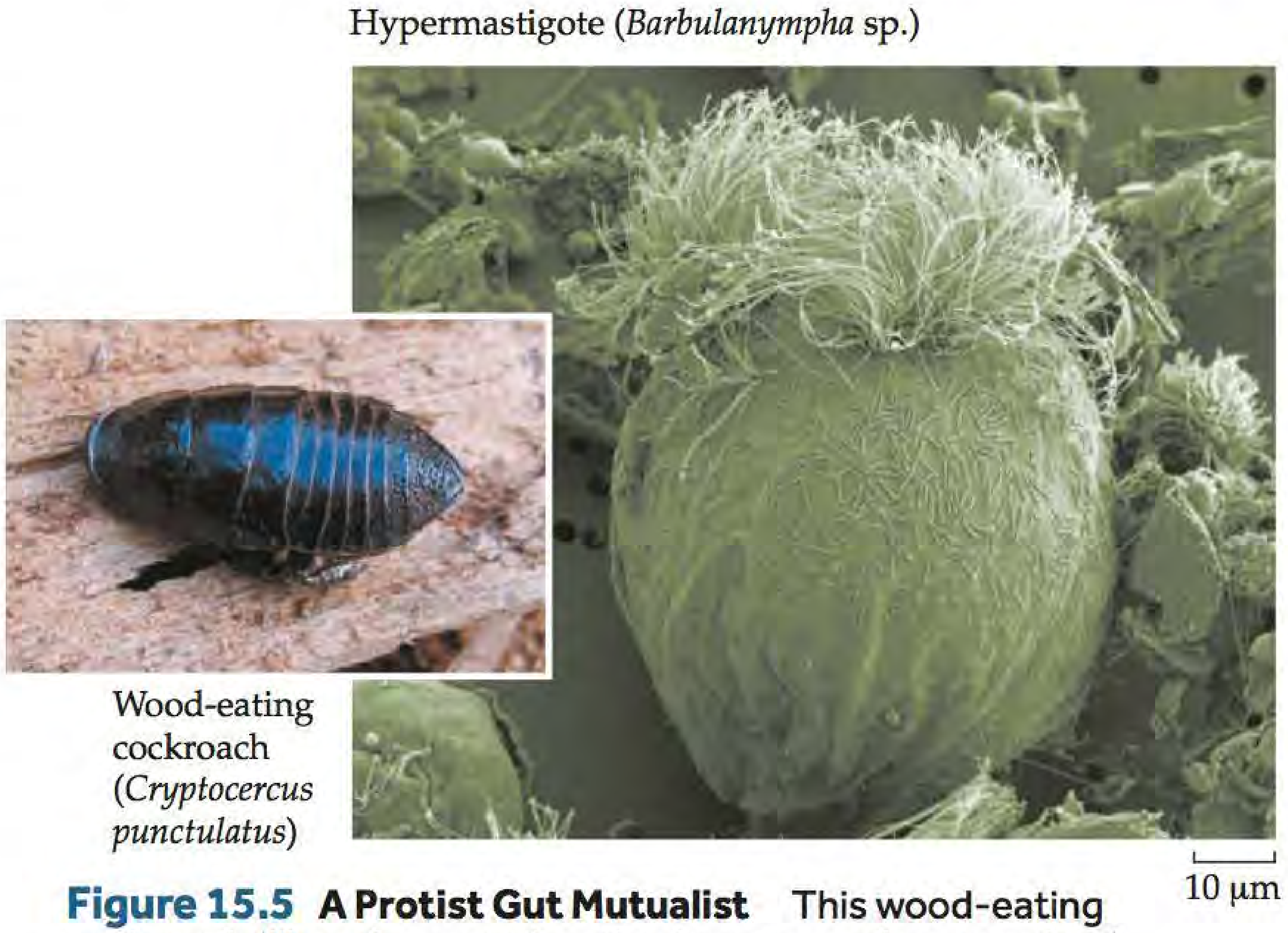


Figure 15.5 A Protist Gut Mutualist This wood-eating cockroach (like other wood-eating insects, such as termites) would starve if gut mutualists such as the protist shown here (a hypermastigote) did not help it to digest wood. The hypermastigote can break down cellulose, a major structural component of wood that the cockroach cannot digest on its own.

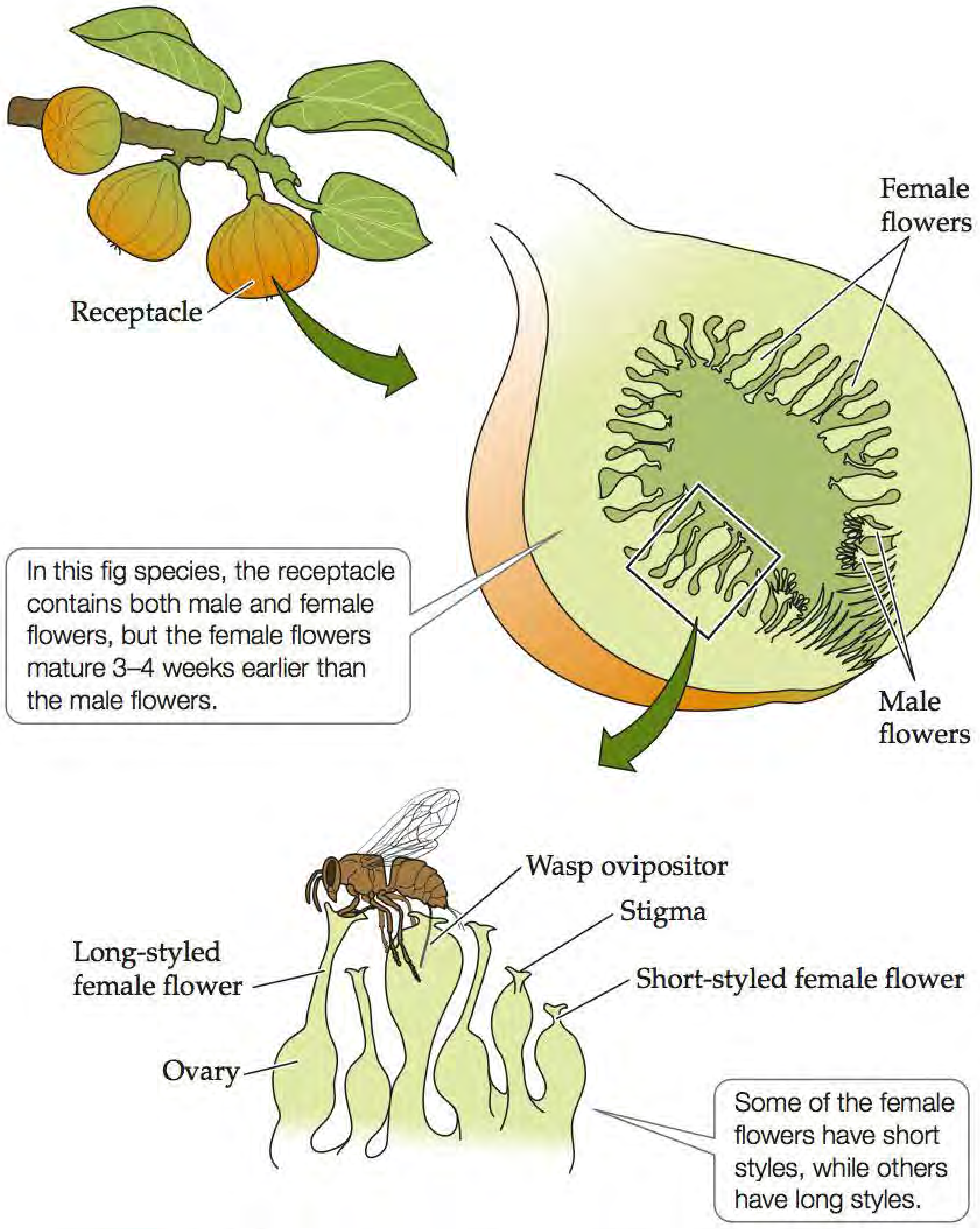


Figure 15.6 Fig Flowers and the Wasp That Pollinates Them The receptacle and flowers of a typical monoecious fig tree, *Ficus sycomorus*. (After Bronstein 1992.)

of understory plant species that live in tropical forests and nowhere else. These insects and small plants depend on the forest for their habitat, yet many have little or no effect on the trees that tower above them.

Positive interactions can be obligate or facultative and loosely structured

Mutualism and commensalism include a broad set of interactions, ranging from those that are *obligate* (that is, required for species) to those that are *facultative* (not required). The leaf-cutter ant–fungus mutualism discussed in the Case Study illustrates one end of this spectrum: the ants and the fungi they cultivate have a highly specific, obligate relationship in which neither partner can survive without the other, and their interaction has led each partner to evolve unique features that benefit the other species.

Similarly, many tropical fig trees are pollinated by one or a few species of fig wasps. These relationships are mutually beneficial and obligate for both species in that neither species can reproduce without the other. Fig–fig wasp interactions also show clear signs of coevolution (Bronstein 1992). Fig flowers are contained within structures of fleshy stem tissue known as *receptacles* (**Figure 15.6**). In monoecious figs (those in which each tree has separate male and female flowers), the male and female flowers are located in different parts of the receptacle, and the male flowers mature after the female flowers. The forms of female flowers range from those with short styles to those with long styles.

A female fig wasp enters the receptacle, carrying pollen she collected from male flowers in another receptacle. Once inside, the wasp inserts her ovipositor through the styles of the female flowers to lay eggs in the ovaries (see Figure 15.6). She then deposits pollen on the stigmas of those flowers. The wasp pollinates both long-styled and short-styled flowers, and hence both flower types develop seeds. Perhaps because wasp ovipositors are not long enough to reach the ovaries of long-styled flowers, wasp larvae typically develop within short-styled flowers and feed on some of their seeds.

When the young wasps complete their development, they mate, the males burrow through the receptacle, and the females exit through the passageway the males have made. Before the females leave the receptacle, however, they visit male flowers (which are now mature), collect pollen from them, and store it in a specialized sac for use when they lay their eggs in another receptacle. The wasp's reproductive behavior is a remarkable example of a specialization that provides a benefit to another species.

Unlike the ant–fungus and fig–fig wasp mutualisms, many mutualisms and commensalisms are facultative. In desert environments, for example, the soil beneath an adult plant is often cooler and moister than the soil of an adjacent open area. These differences in soil conditions may be so pronounced that the seeds of many plant species can germinate and survive only in the shade provided by an adult plant; such adults are called *nurse plants* because they "nurse" or protect the seedlings. A single species of nurse plant may protect the seedlings of many different species. Desert ironwood (*Olneya tesota*), for example, serves as a nurse plant for 165 different species, most of which can also germinate and grow under other plant species. This situation is typical of facultative interactions: a species that requires "nursing" may be found under a variety of nurse plant species (and hence has a facultative relationship with each of them), and the nurse plant and the beneficiary species may evolve little in response to one another.

Facultative positive interactions also occur in forest communities. For example, large herbivores such as deer or moose may inadvertently eat the seeds of small herbaceous plants whose leaves they feed on. The seeds may pass unharmed through the herbivore's digestive tract and be deposited with its feces, often far from the parent

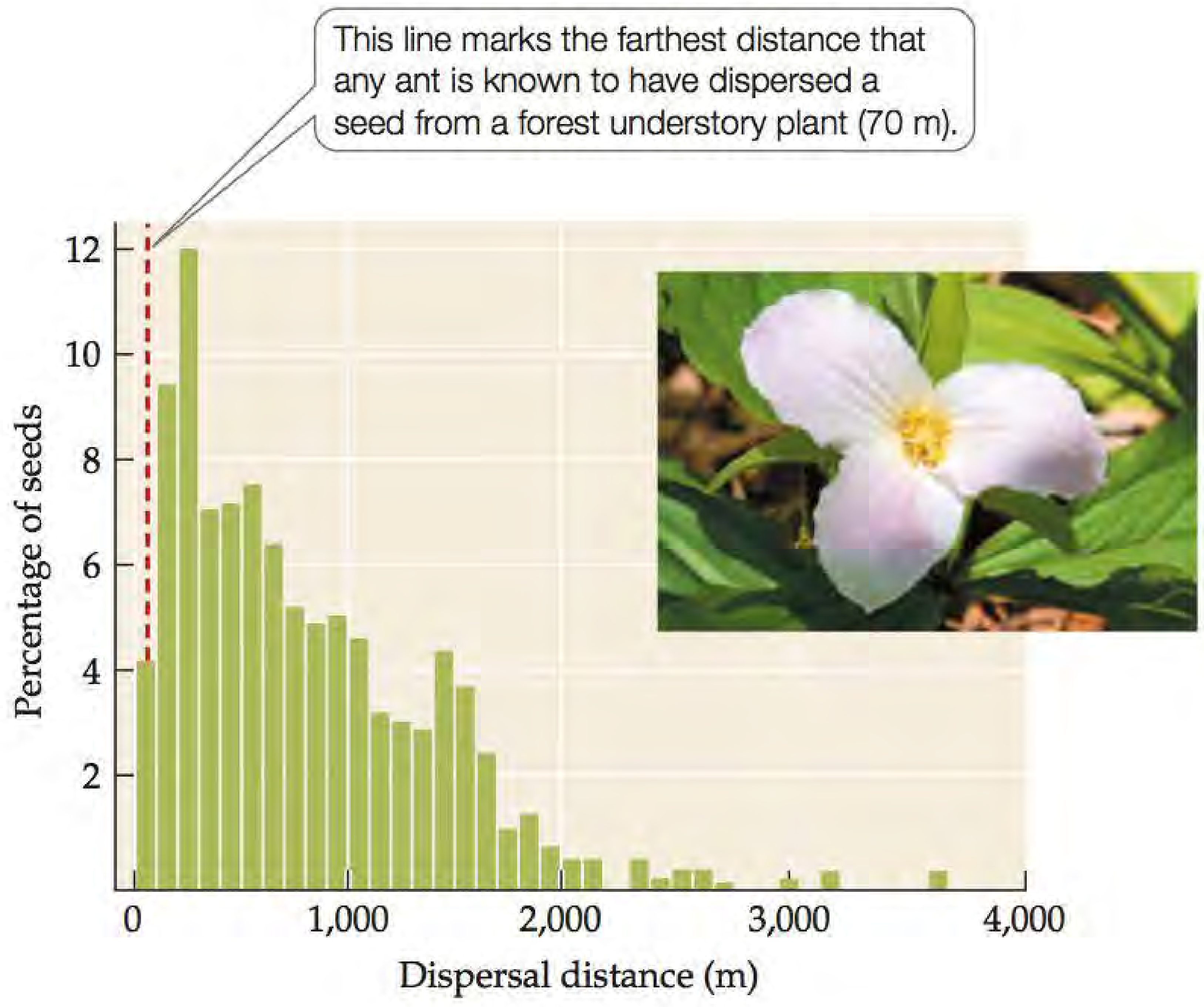

This line marks the farthest distance that any ant is known to have dispersed a seed from a forest understory plant (70 m).

Figure 15.7 Deer Can Move Plant Seeds Long Distances These estimates of the distances that white-tailed deer disperse the seeds of the forest understory plant *Trillium grandiflorum* are based on observations of deer movements and of the length of time that deer retain plant seeds in their digestive tracts (from the time they eat the seeds until they defecate them). Although *T. grandiflorum* seeds are also dispersed by ants, deer move the seeds much farther. (After Vellend et al. 2003.)

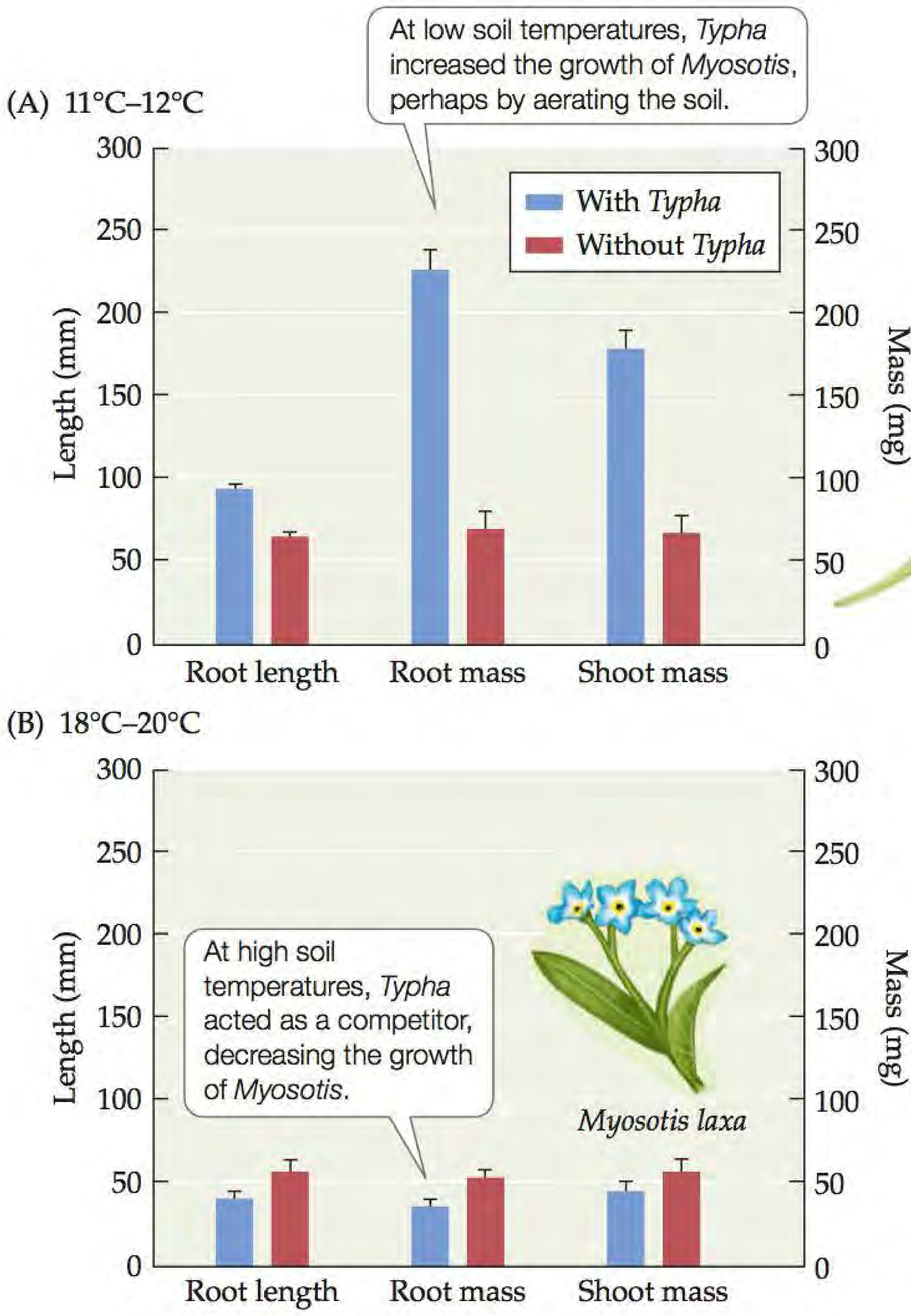
plant (**Figure 15.7**). As we saw in Concept 7.4, dispersal of offspring away from parents may be advantageous, so benefits may accrue to both the plant (whose seeds are dispersed) and the herbivore (which feeds primarily on leaves).

Positive interactions can cease to be beneficial under some circumstances

Interactions between two species can be categorized by determining for each species whether the outcome of the interaction is positive (benefits > costs), negative (costs > benefits), or neutral (benefits = costs). However, the costs and benefits experienced by interacting species can vary from one place and time to another (Bronstein 1994). Thus, depending on the circumstances, an interaction between two species may have either positive or negative outcomes.

Soil temperature, for example, influences whether a pair of wetland plant species interact as commensals or competitors (Callaway and King 1996). Some wetland plants aerate hypoxic soils by passively transporting oxygen through air channels in their leaves, stems, and roots. Oxygen leaked into the soil from the roots of such plants can become available to other plant species, thereby reducing the negative effects of the hypoxic soil conditions. In a greenhouse experiment, Ragan Callaway and Leah King grew the cattail *Typha latifolia*, a species that has extensive air channels, together with the small-flowered forget-me-not *Myosotis laxa*, a species that lacks air channels. They grew these plants under two different temperature regimes (11°C–12°C and 18°C–20°C) in pots filled with a mix of natural pond soil and peat, with the soil in the pots submerged under 1–2 cm of water to make it hypoxic. They also grew some pots of *Myosotis* without *Typha* under the same conditions.

At the low soil temperatures, the dissolved-oxygen content of the soil increased when *Typha* was present, but that did not happen at the high soil temperatures. How did these different oxygen levels affect the outcome of the *Myosotis*–*Typha* interaction? At the low soil temperatures, the growth of *Myosotis* roots and shoots increased when *Typha* was present (**Figure 15.8A**). At the high soil


At low soil temperatures, *Typha* increased the growth of *Myosotis*, perhaps by aerating the soil.

At high soil temperatures, *Typha* acted as a competitor, decreasing the growth of *Myosotis*.

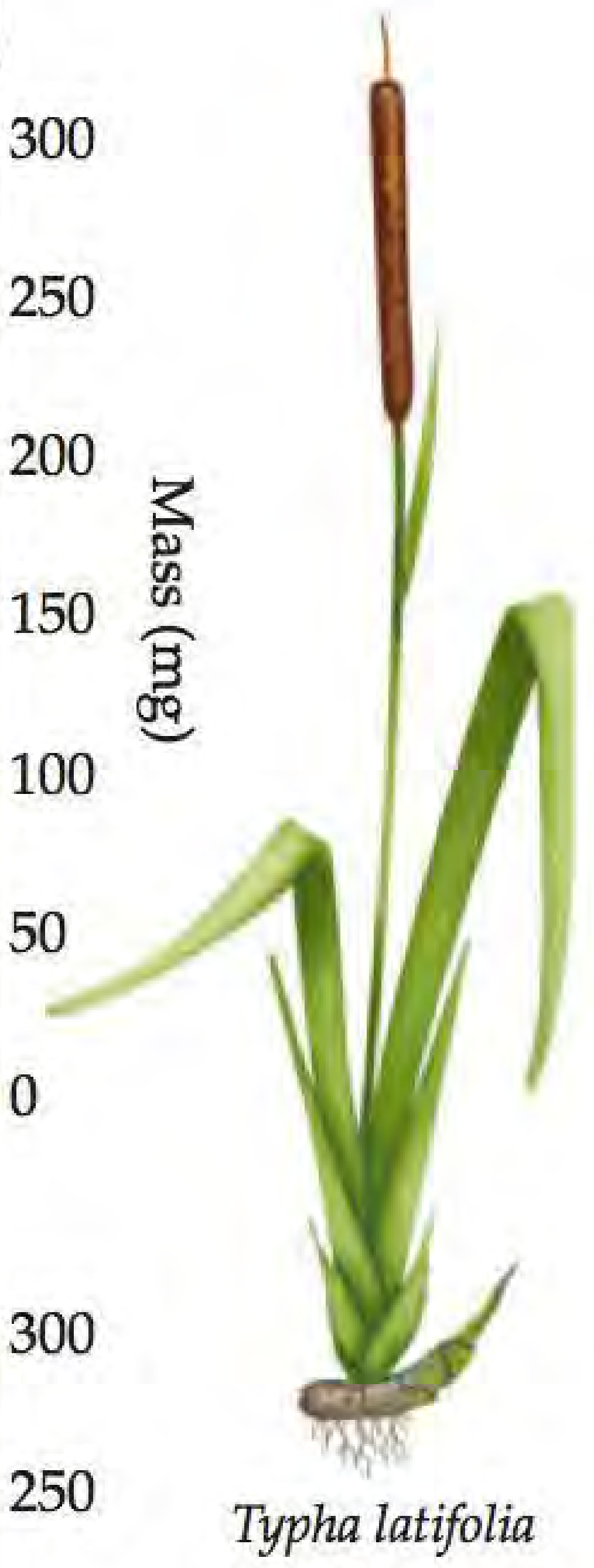


Figure 15.8 From Benefactor to Competitor The growth of the small-flower forget-me-not *Myosotis laxa* under (A) low soil termperatures (11°C–12°C), and (B) high soil temperatures (18°C–20°C) in the presence and absence of the cattail *Typha latifolia* was measured by changes in three parameters: root length (left *y* axis), root mass (right *y* axis), and shoot mass (right *y* axis). Error bars show one SE of the mean. (After Callaway and King 1996.)

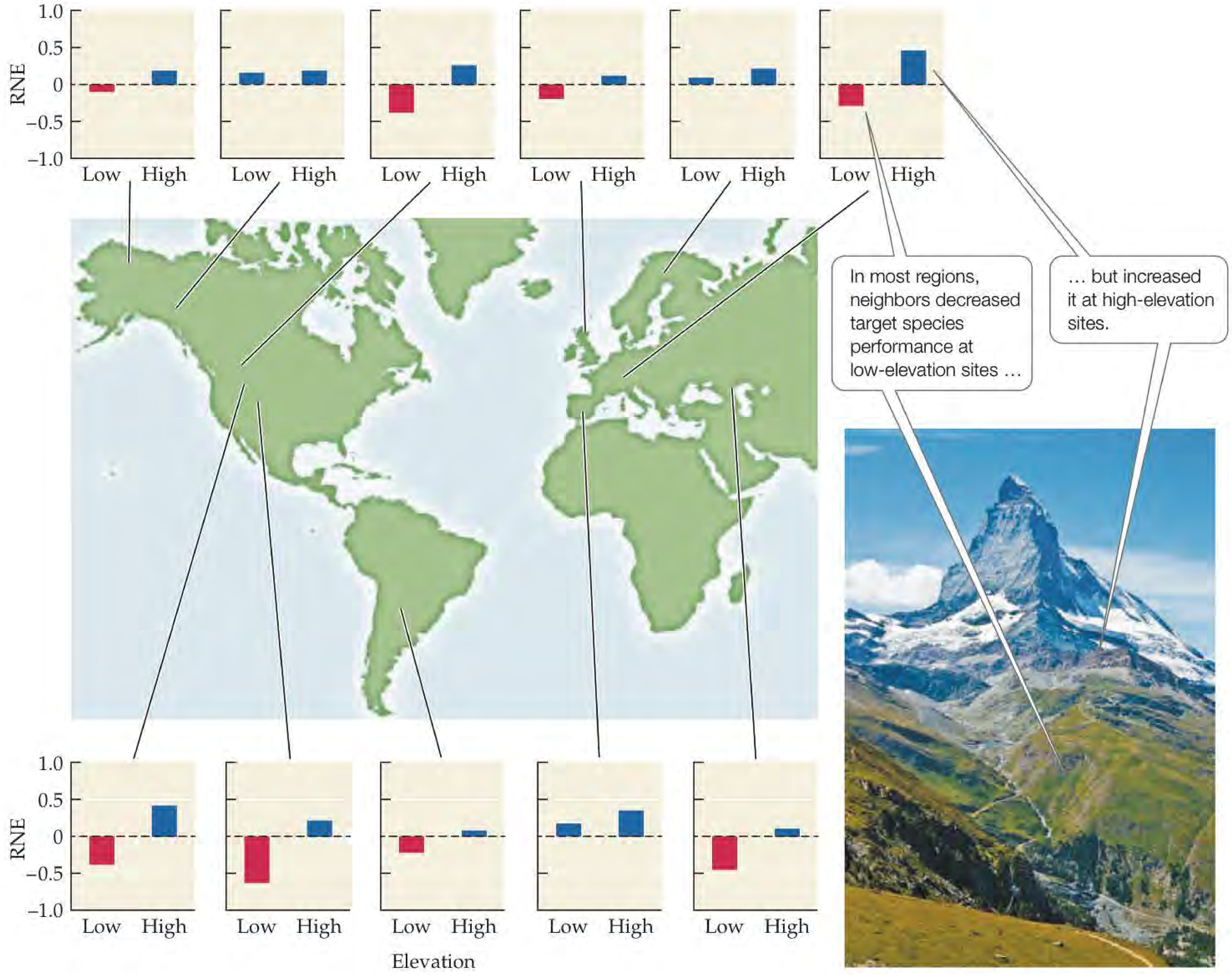
? Under what conditions does *Myosotis laxa* best grow? Explain.

temperatures, however, *Myosotis* growth decreased when *Typha* was present (**Figure 15.8B**). Overall, these results suggest that at the low soil temperatures, *Typha* provided benefits to *Myosotis* (perhaps by aerating the soil), while at the high temperatures, *Typha* had a negative effect on *Myosotis*—just one example of how a change in environmental conditions can alter the outcome of an ecological interaction (other examples are discussed in Concepts 16.3 and 17.3 and in Bronstein 1994).

Positive interactions may be more common in stressful environments

In recent decades, studies have shown that positive interactions are important in a number of ecological communities, such as oak woodlands, coastal salt marshes, and marine intertidal communities. Many of these studies have focused on how individuals of a target species are affected by nearby individuals of one or more other species. These effects can be assessed by comparing the performance of the target species when neighbors are present with its performance when neighbors are removed. Although results from such studies cannot be used to determine whether mutualism, commensalism, or competition is occurring (because two-way interactions are not examined), they do provide a rough assessment of whether positive interactions are common in ecological communities.

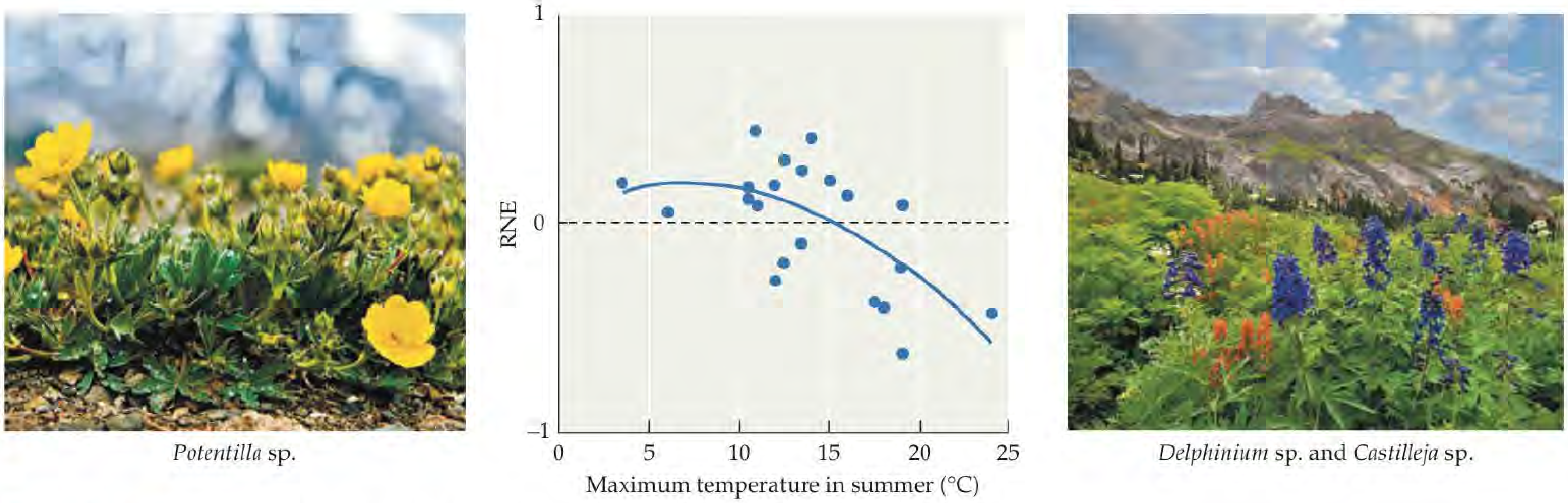
In one of the most comprehensive studies of this type, an international group of ecologists tested the effects that neighboring plants had on a total of 115 target plant species in 11 regions worldwide (Callaway et al. 2002). In 8–12 replicate plots for each treatment of each target species, neighbors were either left in place or removed from the vicinity



In most regions, neighbors decreased target species performance at low-elevation sites …

… but increased it at high-elevation sites.

Figure 15.9 **Neighbors Increase Plant Growth at High-Elevation Sites** The relative neighbor effect (RNE, defined as the growth of the target plant species when neighboring plants are present minus its growth when neighbors are removed) of alpine plants was measured in plots at high and low elevations in 11 regions. Plant growth was measured as change in biomass (for most sites) or in leaf number. RNE values greater than zero (in blue) indicate that neighbors increased the growth of target species; RNE values less than zero (in red) indicate that neighbors decreased the growth of target species. (After Callaway et al. 2002.)


Potentilla sp.

Delphinium sp. and *Castilleja* sp.

Figure 15.10. Neighbors Ameliorate Cold Temperatures in Alpine Plants The relative neighbor effect (RNE, defined in Figure 15.9) of alpine plants changes from positive (above zero) to competitive (below zero) as temperature increases at lower elevations. (After Callaway et al. 2002.)

of the target species. The "relative neighbor effect" (RNE, defined as the growth of the target species with neighbors present minus its growth when neighbors were removed) was then measured. The researchers found that RNE was generally positive at high-elevation sites, indicating that neighbors had a positive effect on the target species, but negative at low-elevation sites (**Figure 15.9**). In addition, neighbors tended to reduce the survival and reproduction of target species individuals at low-elevation sites, but to increase their survival and reproduction at high-elevation sites. Callaway et al. determined that the RNE was negatively related to the maximum temperature in the summer, suggesting that positive interactions were more common in colder, more stressful environments and competition was more common in warmer, less stressful environments (**Figure 15.10**). Similar results have been found in salt marsh communities (see Figure 16.14) and intertidal communities (Bertness 1989; Bertness and Leonard 1997).

With this discussion of positive interactions as background, let's examine some of the characteristics that are unique to mutualism. Our discussion will place special emphasis on what can be learned from studies that document the costs and benefits of mutualistic interactions.

CONCEPT 15.2

Each partner in a mutualistic interaction acts in ways that serve its own ecological and evolutionary interests.

Characteristics of Mutualism

In the previous section, we discussed some features that apply to both mutualism and commensalism: these two types of positive interactions are ubiquitous, they can evolve in many ways, and they can cease to be beneficial under some conditions. However, because mutualism is a reciprocal relationship in which both parties benefit, some of its characteristics differ from those of commensalism. A mutualism has costs as well as benefits, and if the costs exceed the benefits for one or both partners, their interaction will change. Before we describe the special characteristics of mutualism, however, we'll begin with a discussion of how mutualisms are classified.

Mutualisms can be categorized according to the benefits they provide

Mutualisms are often categorized by the types of benefits that the interacting species provide to each other, such as food or a place to live. As we'll see, one partner in a mutualism may receive one type of benefit (such as food) while the other receives a different benefit (such as a place to live). In such cases, the mutualism could be classified in two different ways.

There are many **trophic mutualisms**, in which a mutualist receives energy or nutrients from its partner. In the leaf-cutter ant–fungus mutualism described in this chapter's Case Study, each partner feeds the other. (Recall that the ant and the fungus also help each other to overcome plant defenses, so each also provides the other with an ecological service.) In other trophic mutualisms, one organism may receive an energy source while the other receives limiting nutrients. In mycorrhizae, for example, the fungus receives energy in the form of carbohydrates and the plant may get help in taking up water or a limiting nutrient such as phosphorus. An exchange of energy for limiting nutrients also occurs in the coral–alga symbiosis, in which the coral receives carbohydrates and the alga receives nitrogen.

In **habitat mutualisms**, one partner provides the other with shelter, a place to live, or favorable habitat. Alpheid (pistol) shrimps form a habitat mutualism with some gobies (fishes of genera *Cryptocentrus* and *Vanderhorstia*) in environments with abundant food but little protective

Figure 15.11 A Seeing-Eye Fish In environments with little protective cover, a habitat mutualism between an alpheid (pistol) shrimp and a goby benefits both partners.

cover. The shrimp digs a burrow in the sediments, which it shares with a goby, thus providing the fish with a safe haven from danger. For its part, the goby serves as a "seeing-eye fish" for the shrimp, which is nearly blind. Outside the burrow, the shrimp keeps an antenna on the fish (**Figure 15.11**); if a predator or some other form of disturbance causes the fish to move suddenly, the shrimp darts back into the burrow.

In other habitat mutualisms, a species may provide its partner with favorable habitat by altering local environmental conditions or by improving its partner's tolerance of existing conditions. The grass *Dichanthelium lanuginosum* grows next to hot springs in soils whose temperatures can be as high as 60°C (140°F). Regina Redman, Russell Rodriguez, and colleagues performed laboratory and field experiments in which this grass was grown with and without *Curvularia protuberata*, a symbiotic fungus that grows throughout the plant body (such fungi are called *endophytes*). In the laboratory, 100% of the grass plants that had the *Curvularia* endophyte survived intermittent soil temperatures of 60°C, while none of the plants without the endophyte survived (Redman et al. 2002). In field experiments in which soil temperatures reached up to 40°C (104°F), plants with endophytes had greater root and leaf mass than plants without endophytes. In soils above 40°C, the grass plants with endophytes continued to grow well, but all the plants without endophytes died. Thus, *Curvularia* increased the ability of its grass host to tolerate high soil temperatures. *Curvularia* is not alone: many other fungal endophytes can increase the tolerance of their host plants for soils that are high in temperature or salinity (Rodriguez et al. 2009), as can some mycorrhizal fungi (Bunn et al. 2009).

Mutualists are in it for themselves

Although both partners in a mutualism benefit, that does not mean that a mutualism has no costs for the partners. In the coral–alga mutualism, for example, the coral receives benefits in the form of energy, but it incurs the costs of supplying the alga with nutrients and space. Likewise, the alga gains limiting nutrients, but it provides the coral with energy that it could have used to support its own growth and metabolism. The costs of mutualism may be especially clear when one species provides the other with a "reward" such as food for a service such as pollination. For example, during flowering, milkweeds use up to 37% of the energy they gain from photosynthesis to produce the nectar that attracts insect pollinators such as honeybees.

For an ecological interaction to be a mutualism, the net benefits must exceed the net costs for both partners. However, neither partner in a mutualism is in it for altruistic reasons. Should environmental conditions change so as to reduce the benefits or increase the costs for one of the partners, the outcome of the interaction may change. This is especially true if the interaction is not obligate. Ants, for example, often form facultative relationships in which they protect other insects from competitors, predators, and parasites. In one such case, ants protect treehoppers from predators, and the treehoppers secrete honeydew (a sugar syrup substance), which the ants feed on (**Figure 15.12**). Treehoppers always secrete honeydew, so the ants always have access to this food source. However, in years when predator abundances are low, the treehoppers may receive no benefit from the ants. In such years, the outcome of the interaction may shift from +/+ (a mutualism) to either +/0 (a commensalism) or +/– (parasitism), depending on whether the consumption of honeydew by ants reduces treehopper growth or reproduction.

Finally, under certain conditions, a mutualist may withdraw or modify the reward that it provides to its partner. In high-nutrient environments, for example, some plants reduce the carbohydrate rewards that they usually provide to mycorrhizal fungi. In such environments, the plant can obtain ample nutrients on its own, and hence the fungus is of little benefit. Thus, when nutrients are plentiful, the plant may cease to reward the fungus because the costs of supporting fungal hyphae are

Figure 15.12 A Facultative Mutualism Ants often form facultative mutualisms with insects that secrete honeydew, a sugar syrup substance on which the ants feed. The ants shown here will protect these Equadorian treehoppers from predators and parasites in exchange for honeydew.

greater than the benefits the fungus can provide. Moreover, a recent study found that the plant *Medicago truncatula* can discriminate among mycorrhizal fungi, allocating more carbohydrate rewards to those fungal hyphae that are supplying the most nutrients (**Figure 15.13**). You can explore this relationship further in **Analyzing Data 15.1**, where you will examine whether the fungus also modifies its provision of nutrients to the plant depending on the rewards it receives from the plant.

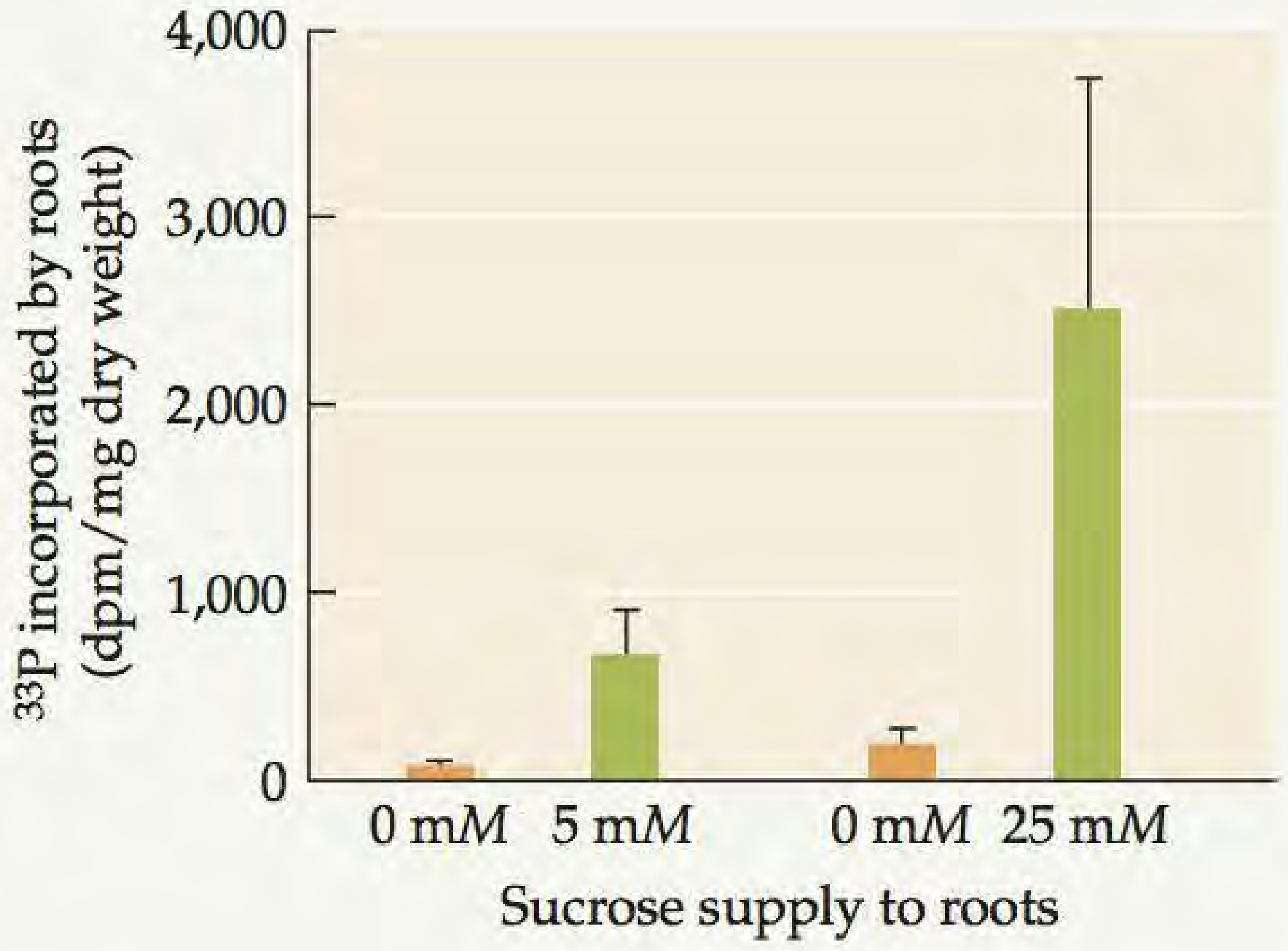
Some mutualists have mechanisms to prevent overexploitation

As we've seen, there is an inherent conflict of interest between the partners in a mutualism: the benefit to each species comes at a cost to the other. In such a situation, natural selection may favor **cheaters**, individuals that increase their production of offspring by overexploiting

ANALYZING DATA 15.1 Does a Mycorrhizal Fungus Transfer More Phosphorus to Plant Roots That Provide More Carbohydrates?

As seen in Figure 15.13, Kiers et al. (2011)* found that the plant *Medicago truncatula* transfers more carbohydrates to those fungal hyphae that have greater access to phosphorus. The researchers also tested the reciprocal interactions: whether the plant's mycorrhizal partner, the fungus *Rhizophagus irregularis* (previously known as *Glomus intraradices*), behaves in a similar manner, transporting more phosphorus to roots that have greater access to carbohydrates.

To do this, Kiers et al. used a split-plate experimental design similar to that in Figure 15.13. They provided fungal hyphae with radioactively labeled phosphorus (^{33}P) and monitored the transfer of phosphorus to plant roots differing in access to carbohydrates (sucrose). Some plant roots had no access to sucrose, while other plant roots were supplied with either 5 or 25 m*M* of sucrose. In the results shown in the figure, "dpm" refers to disintegrations per minute, a measure of radiation intensity; error bars show one SE of the mean.



1. Draw and label a sketch of the split-plate experimental design, modeling your diagram on the photograph in Figure 15.13A.
2. Interpret the results shown in the figure.
3. Compare the results in the figure here with those in Figure 15.13B. Does the plant or the fungus control the exchange of materials, or do both partners play a role? Explain.

See the companion website for a similar ANALYZING DATA exercise.

---

* Kiers, E. T. and 14 others. 2011. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science* 333: 880–882.

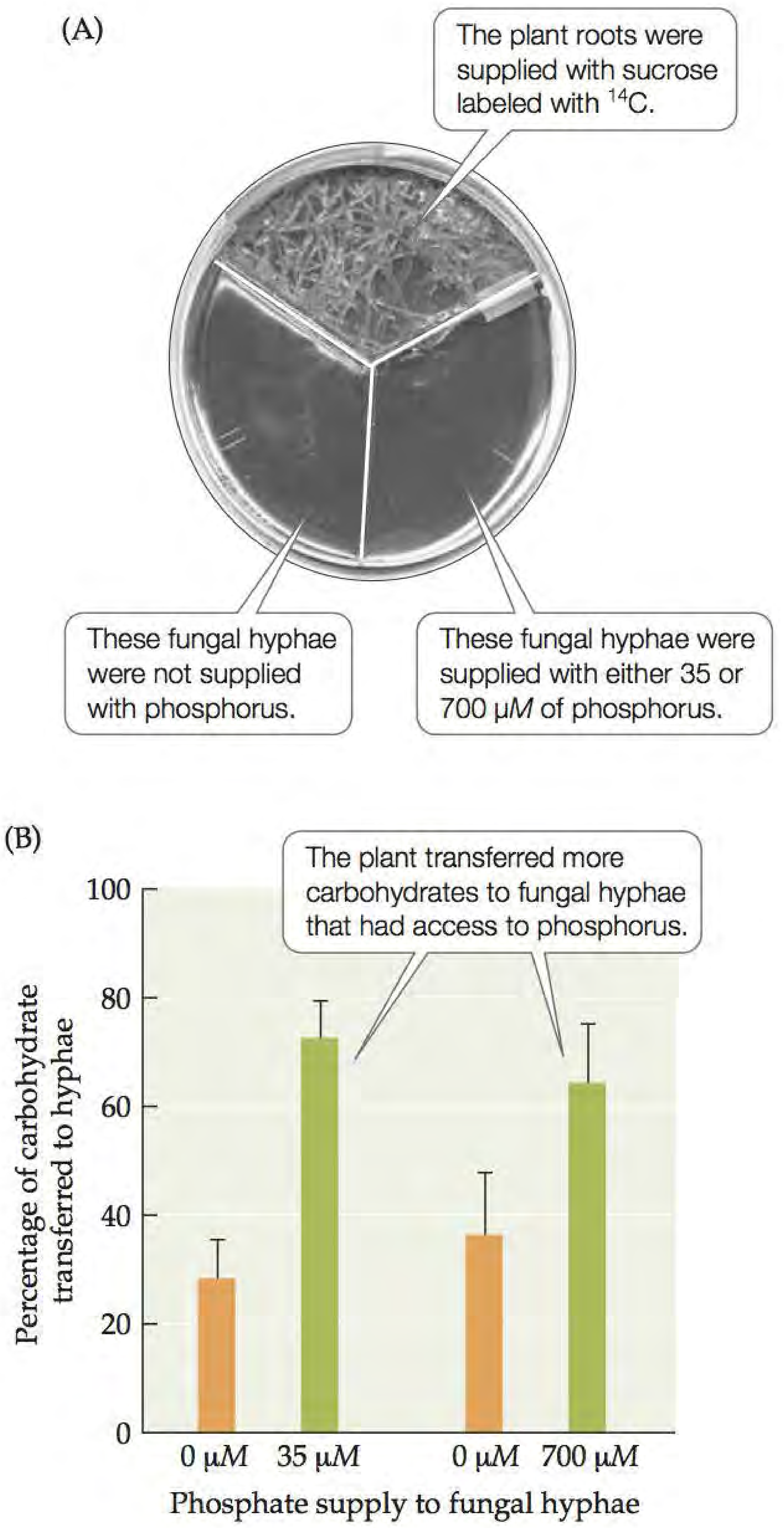


Figure 15.13 Rewarding Those Who Reward You Researchers tested the hypothesis that *Medicago truncatula* plants allocate more carbohydrates to those mycorrhizal fungi that provide them with higher concentrations of phosphorus, a key plant nutrient. (A) They used a split-plate design to separate the fungal hyphae into two groups. Some fungal hyphae lacked access to phosphorus, while other fungal hyphae were supplied with either 35 or 700 μ*M* of phosphorus. (B) They then tracked the proportion of sucrose (labeled with ^{14}C) that the plant provided to each group of hyphae. Error bars show one SE of the mean. (After Kiers et al. 2011.)

their mutualistic partner. When one of the partners in a mutualism overexploits the other, it becomes less likely that the mutualism will persist. But mutualisms do persist, as the 50 million-year association between fungus-growing ants and the fungi they cultivate readily attests. What factors allow a mutualism to persist in spite of the conflict of interest between the partners?

One answer is provided by "penalties" imposed on individuals that overexploit a partner. If those penalties are high enough, they can reduce or remove any advantage gained by cheating. Olle Pellmyr and Chad Huth documented such a situation in an obligate, coevolved mutualism between the yucca plant *Yucca filamentosa* and its exclusive pollinator, the yucca moth *Tegeticula yuccasella* (Pellmyr and Huth 1994). Female yucca moths collect pollen from yucca plants with their unique mouthparts (**Figure 15.14A**). After collecting pollen, a female moth typically moves to another plant, lays eggs in the ovary of a flower, and then walks up to the top of the style. There, the moth deliberately places some of the pollen she carries on the stigma, thus pollinating the plant (**Figure 15.14B**). The larvae that hatch from the moth's eggs complete their development by eating some of the seeds that develop in the ovary of the flower.

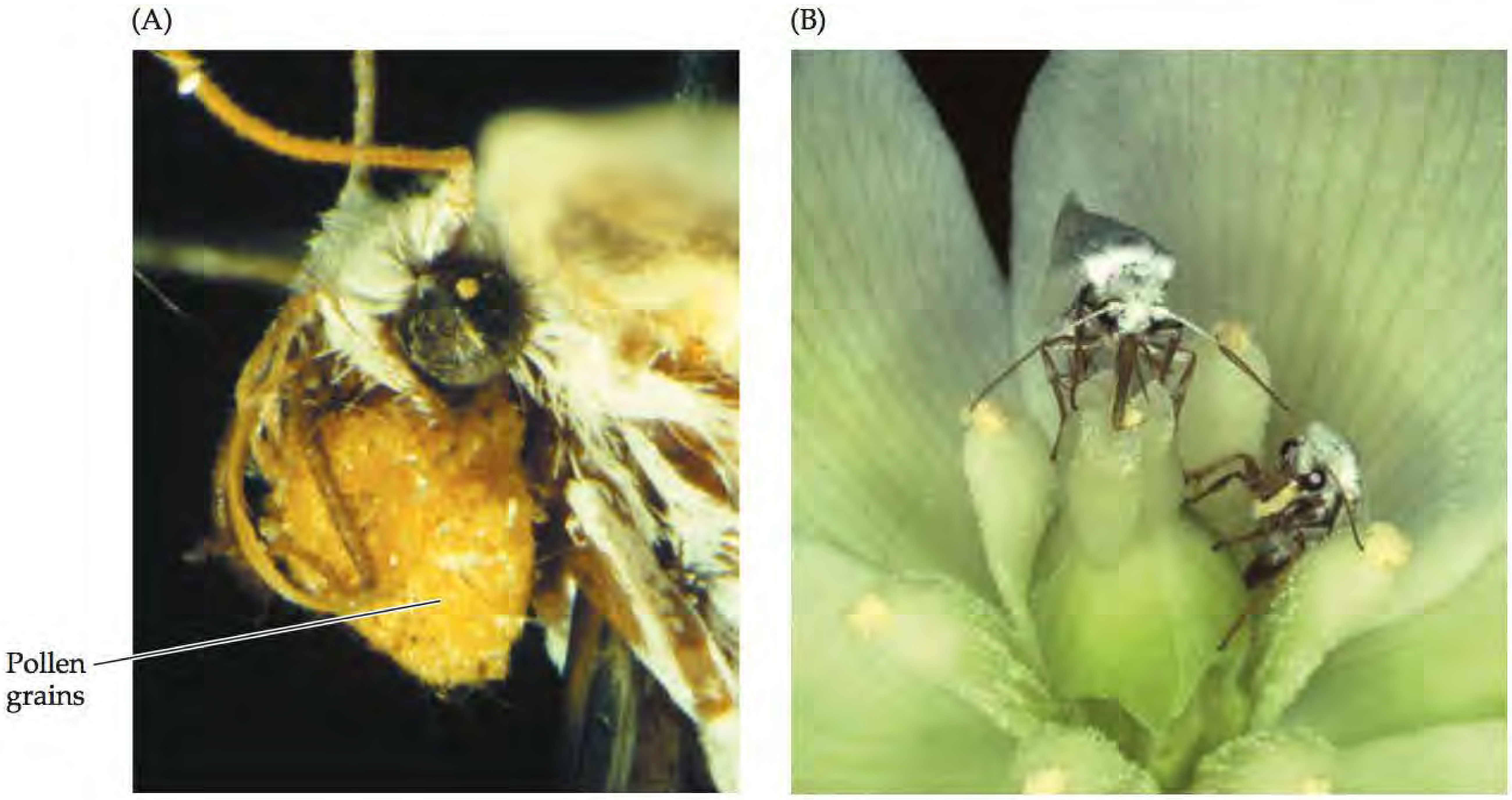


Figure 15.14 Yuccas and Yucca Moths *Yucca filamentosa* has an obligate relationship with its exclusive pollinator, the yucca moth *Tegeticula yuccasella*. (A) The female moth collects pollen from a yucca flower using specialized mouthparts. She may carry a load of up to 10,000 pollen grains, nearly 10% of her own weight. (B) The moth at the lower right of this photo is laying eggs in the ovary of a yucca flower; the moth at the top is placing pollen on the stigma. (From Pellmyr 2003; photos courtesy of O. Pellmyr.)

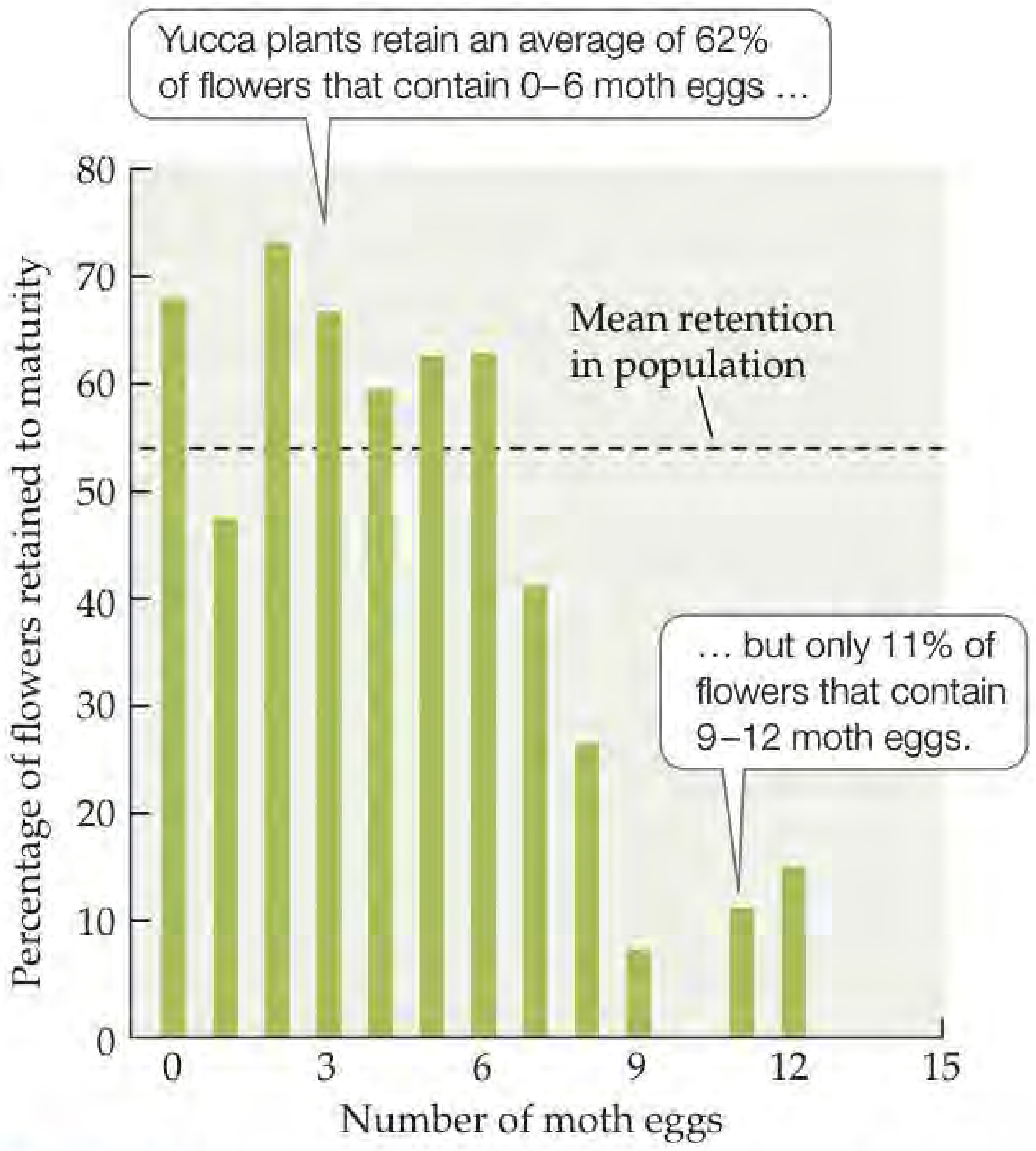


Figure 15.15 A Penalty for Cheating Yucca plants selectively abort flowers in which yucca moths have laid too many eggs. (After Pellmyr and Huth 1994.)

The moth and the plant depend absolutely on each other for reproduction. However, the mutualism is vulnerable to overexploitation by moths that lay too many eggs and hence consume too many seeds. Yuccas have a mechanism to prevent such overexploitation: they selectively abort flowers in which female moths have laid too many eggs (**Figure 15.15**). On average, yuccas retain 62% of the flowers that contain up to six moth eggs, but only 11% of the flowers that contain nine or more eggs. When the yucca aborts a flower, it does so before the moth larvae hatch from their eggs. Although the cue that determines flower abortion is not known, it is clear that it is a powerful mechanism for reducing overexploitation: all the moth larvae in an aborted flower die.

Few other clear cases of penalties for cheating have been documented, so we do not yet know whether such penalties are common in nature. Be that as it may, the yucca–yucca moth interaction illustrates the theme that runs throughout this section: the partners in a mutualism are not altruistic. Instead, the yucca takes actions that promote its own interests, and the yucca moth does the same. In general, a mutualism evolves and is maintained because its net effect is advantageous to both parties. If the net effect of a mutualism were to impair the growth, survival, or reproduction of one of the interacting species, the ecological interests of that species would not be served, and the mutualism might break down, at least temporarily. Should such a situation continue, the longer-term or evolutionary interests of that species might also fail to be served, and the mutualism might break down on a more permanent basis.

Although it is possible for a mutualism to break down, we've also seen that mutualism and commensalism are very common and that some of these interactions have been maintained for millions of years. Let's turn now to the ecological effects of these pervasive interactions.

CONCEPT 15.3

Positive interactions affect the abundances and distributions of populations as well as the structure of ecological communities.

Ecological Consequences of Positive Interactions

So far in this chapter, we've discussed features that are common to commensalism and mutualism as well as characteristics that are unique to mutualism. At various points in these discussions, we've mentioned some ecological consequences of positive interactions, including increased survival rates and the provision of habitats. In this section, we'll take a closer look at how positive interactions affect populations of organisms and the communities in which they are found.

Positive interactions influence the abundances and distributions of populations

As examples earlier in this chapter suggest, mutualism and commensalism can provide benefits that increase the growth, reproduction, or survival of individuals in one or both of the interacting species—a point that was demonstrated recently for a defensive bacterial symbiont that increased the reproductive success of its fruit fly host (**Figure 15.16**). As a result, mutualism and commensalism can affect the abundances and distributions of the interacting species. To explore these issues further, we will first examine how an ant–plant mutualism affects the abundances of its members. We will then consider how mutualism and commensalism influence the distributions of organisms.

EFFECTS ON ABUNDANCE The effects of mutualism on abundance can be seen in the mutualistic relationship between ants in the genus *Pseudomyrmex* spp. and the bullhorn acacia (*Acacia* spp.). This plant has unusually large thorns, which provide a home for the ants (**Figure 15.17A**). The thorns have a tough, woody covering but a soft, pithy interior that is easy for the ants to excavate. A queen ant establishes a new colony by burrowing into a green thorn, removing some of its pithy interior, and laying eggs inside the thorn. As the colony grows, it eventually occupies all of the acacia's thorns.

The ants feed on nectar, which the plant secretes from specialized nectaries, and on modified leaflet tips called Beltian bodies, which are high in protein and fat (**Figure 15.17B**). The ants aggressively attack insect and even

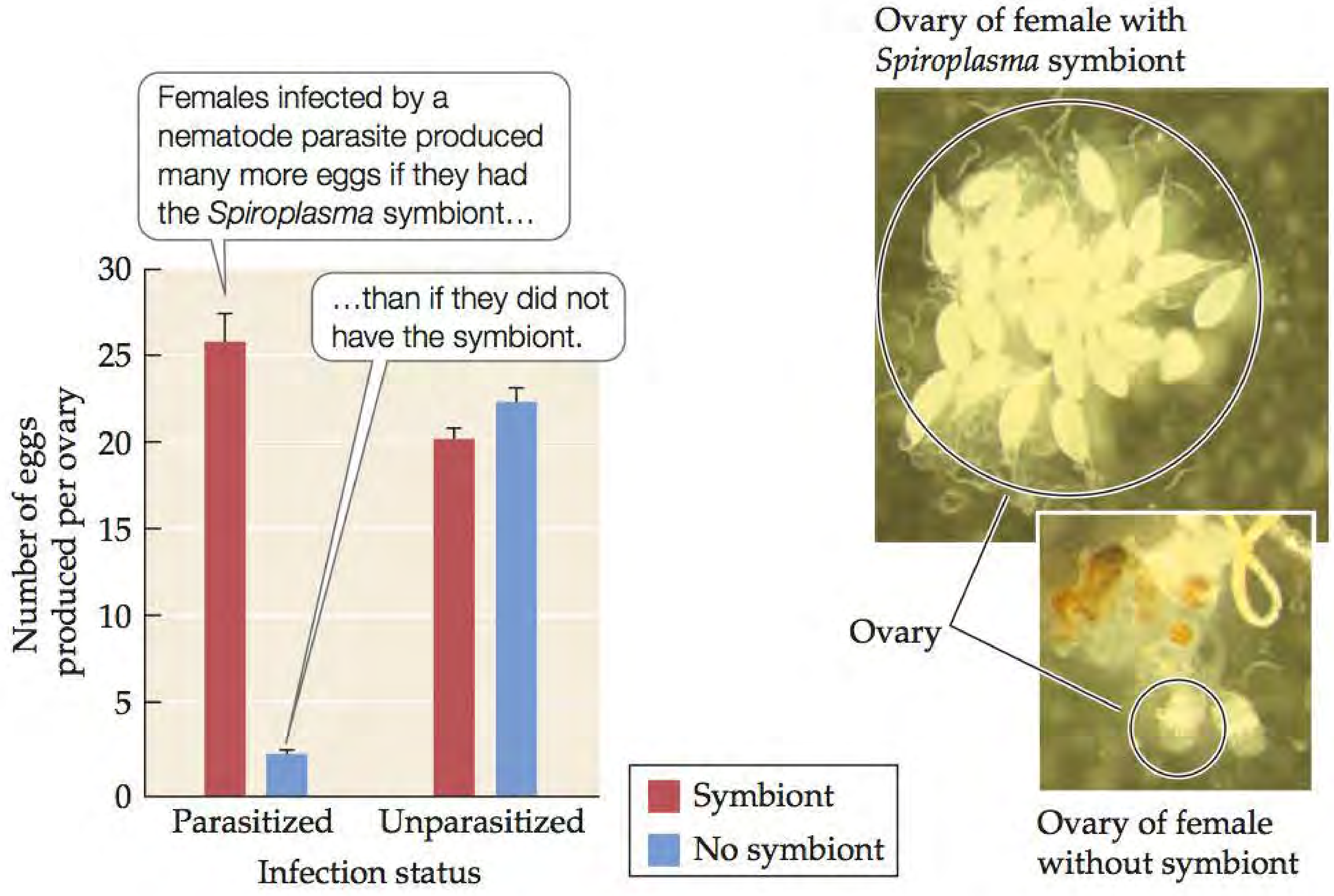


Figure 15.16 A Symbiont Increases the Fertility of Its Host Bacteria in the genus *Spiroplasma* are obligate symbionts that live within the cells of their host, the fruit fly *Drosophila neotestacea*. The graph shows the number of eggs produced by laboratory-reared female flies that either had *Spiroplasma* symbionts (red bars) or did not have *Spiroplasma* symbionts (blue bars), and that either were infected by the nematode parasite *Howardula* (Parasitized) or were not infected by it (Unparasitized). *Howardula* can sterilize female flies and reduce the mating success of male flies. Error bars show one SE of the mean. (After Jaenike et al. 2010; photos courtesy of J. Jaenike.)

mammalian herbivores (such as deer) that attempt to eat the plant. The ants also use their mandibles to maul other plants that venture within 10–150 cm of their home acacia, thus providing the acacia with a competitor-free zone in which to grow (**Figure 15.17C**).

Do the services provided by the ants benefit the acacias? To find out, Dan Janzen removed ants from some acacia plants and compared the growth and survival of those plants with those of plants that had ant colonies. The results were striking. On average, bullhorn acacias with ant colonies weighed over 14 times as much as acacias that lacked colonies; acacias with ants also had higher survival rates (72% vs. 43%) and were attacked by insect herbivores much less frequently (Janzen 1966).

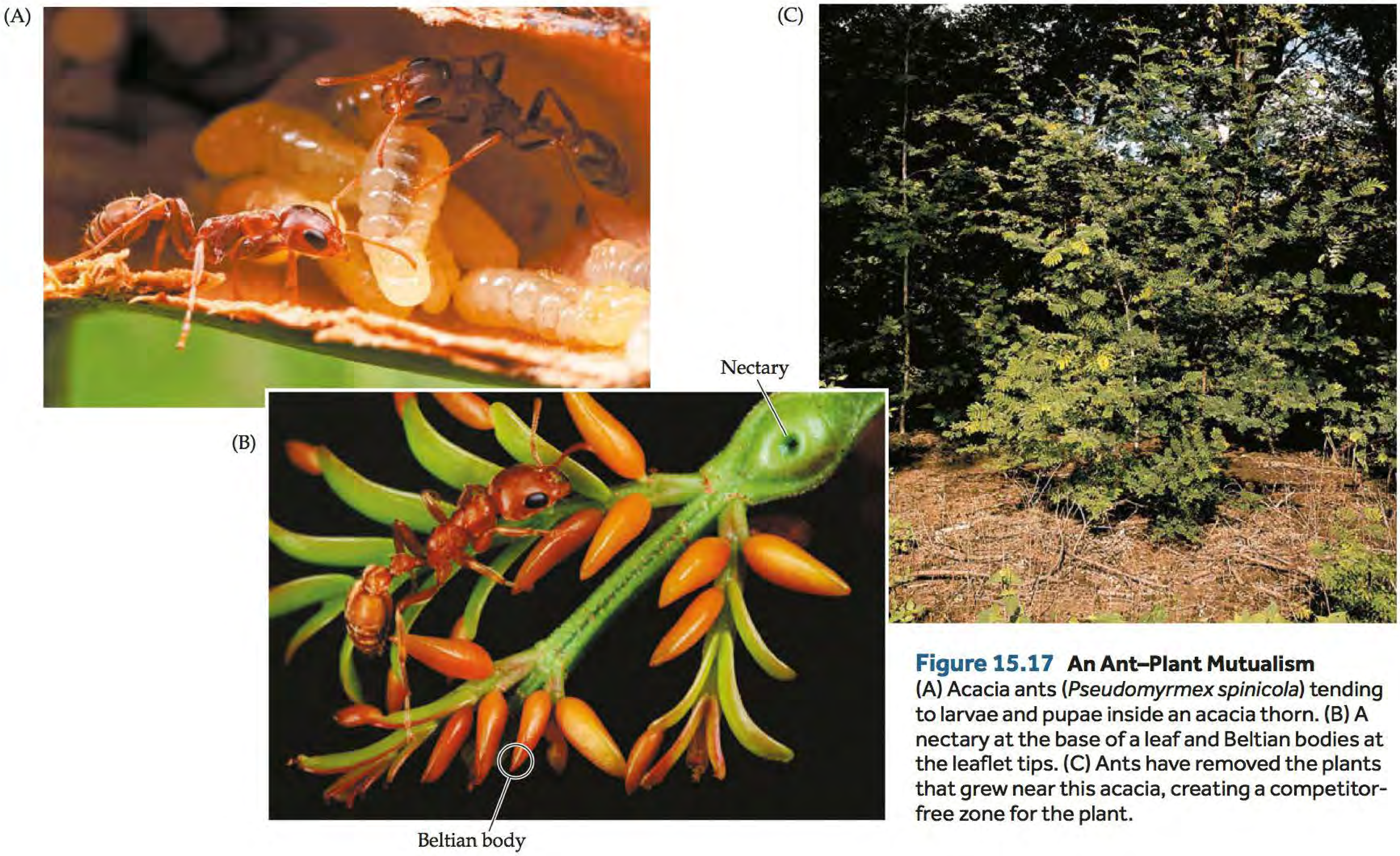


Figure 15.17 An Ant–Plant Mutualism (A) Acacia ants (*Pseudomyrmex spinicola*) tending to larvae and pupae inside an acacia thorn. (B) A nectary at the base of a leaf and Beltian bodies at the leaflet tips. (C) Ants have removed the plants that grew near this acacia, creating a competitor-free zone for the plant.

If a bullhorn acacia lacks an ant colony, the repeated loss of its leaves and growing tips to herbivores often kills the plant in 6 to 12 months. The ants, in turn, depend on the acacias for food and a home, and they cannot survive without these plants. Thus, the ant–acacia mutualism has considerable effects on the abundance of each partner. Furthermore, both the ant and the plant have evolved unusual characteristics that benefit their partners. For example, *Pseudomyrmex* ants that depend on acacias are highly aggressive, remain active for 24 hours a day (patrolling the plant surface), and attack vegetation that grows near their home plants; *Pseudomyrmex* species that do not form mutualisms with acacias show none of these traits. Similarly, acacias that form mutualisms with ants have enlarged thorns, specialized nectaries, and Beltian bodies on their leaves; few nonmutualistic acacia species show these traits. Overall, both the ants and the acacias appear to have evolved in response to their partners, making the ant–acacia partnership an example of an obligate and coevolved mutualism.

EFFECTS ON DISTRIBUTION There are literally millions of positive interactions in which one species provides another with favorable habitat and thus influences its distribution. Specific examples include corals that provide their algal symbionts with a home and fungal symbionts that enable plants to live in environments they otherwise could not tolerate (such as the *Curvularia protuberata* fungi that enable the grass *Dichanthelium lanuginosum* to live in high-temperature soils). Of course, obligate mutualisms, such as the fig–fig wasp mutualism discussed earlier, have a profound influence on the geographic distribution of the interacting species because neither can live where its partner is absent.

It is very common for a group of dominant species, such as the trees in a forest, to determine the distributions of other species by physically providing the habitat on which they depend. Many plant and animal species are found only in forests. Such "forest specialists" either cannot tolerate the physical conditions of more open areas (such as a nearby meadow) or are prevented from living in those open areas by competition with other species. Similarly, at low tide in marine intertidal communities, many species (e.g., crabs, snails, sea stars, sea urchins, barnacles) can be found under the strands of seaweeds that are attached to the rocks. The seaweeds provide a moist and relatively cool environment that enables some species to live in higher regions of the intertidal zone than they otherwise could. Finally, many sandy and cobblestone beaches are stabilized by grasses such as *Ammophila breviligulata* and *Spartina alterniflora*. By holding the substrate together, these species enable the formation of entire communities of plants and animals.

Many forest specialists have little direct effect on the trees under which they live; hence, they have a commensalism with the trees of the forest. The same is true of many marine species that seek shelter under seaweeds and of many of the organisms that depend on substrate stabilization by grasses. In each of these cases, a positive interaction (often a commensalism) allows one species to have a larger distribution than it otherwise would.

Positive interactions can alter communities and ecosystems

The effects that commensalism and mutualism have on the abundances and distributions of species can affect interactions among species, and those effects, in turn, can have a large influence on a community. For example, if a dominant competitor depends on a mutualist, loss of the mutualist may reduce the performance of that dominant species and increase the performance of other species—thus changing the mix of species in the community or their relative abundances. As we'll see, when the structure of a community changes, properties of the ecosystem may also change.

COMMUNITY DIVERSITY Coral reefs are known for their astonishing beauty, and they are exceptional ecologically in that their fish communities are the most diverse vertebrate communities in the world. One of the most common interactions among these diverse coral reef fish is a service mutualism in which a small species (the "cleaner") removes parasites from a larger fish (the "client"). The cleaner often ventures into the mouth of the client (**Figure 15.18A**). What prevents the client from simply eating the cleaner?

The answer appears to be that the benefit a client receives from cleaning (parasite removal) is greater than the energy benefit it could gain by eating the cleaner. In the Great Barrier Reef of Australia, individuals of the cleaner species *Labroides dimidiatus* were visited by an average of 2,297 clients each day, from which the cleaner removed (and ate) an average of 1,218 parasites per day (0.53 parasites per client). To determine whether the activities of cleaners were translated into a reduction in the number of parasites found on clients, Alexandra Grutter experimentally removed *L. dimidiatus* from three of five small reefs. After 12 days, on the reefs from which the cleaners had been removed, there were 3.8 times more parasites on *Hemigymnus melapterus* fish than on the control reefs. In follow-up studies, Grutter and colleagues (2003) examined the effect of *L. dimidiatus* on the number of species and the total abundance of fish found on coral reefs. The results were dramatic: removal and exclusion of *L. dimidiatus* for a period of 18 months caused large drops in both the number of fish species and the total abundance of fish found on the reefs (**Figure 15.18B,C**).

Grutter's work shows that a mutualism can have a major effect on the diversity of species found in a

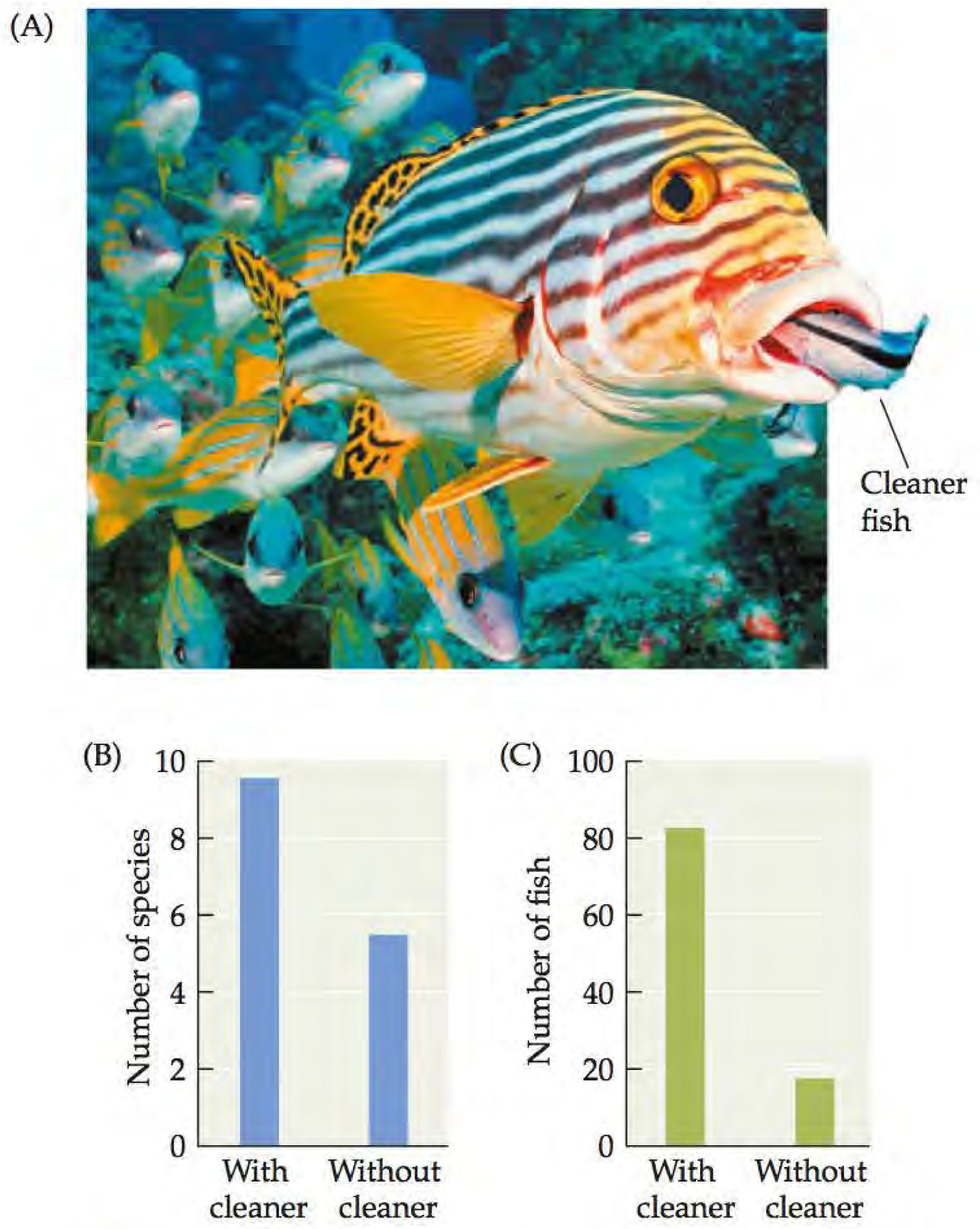


Figure 15.18 Ecological Effects of the Cleaner Fish *Labroides dimidiatus* (A) Looking for parasites, a cleaner fish places its head within the mouth of a much larger client fish, this sweetlips. The experimental removal of *L. dimidiatus* from small reefs within the Great Barrier Reef of Australia led to (B) a drop in the number of fish species found on the reefs and (C) a decrease in the total abundance of fish on the reefs. (B,C after Grutter et al. 2003.)

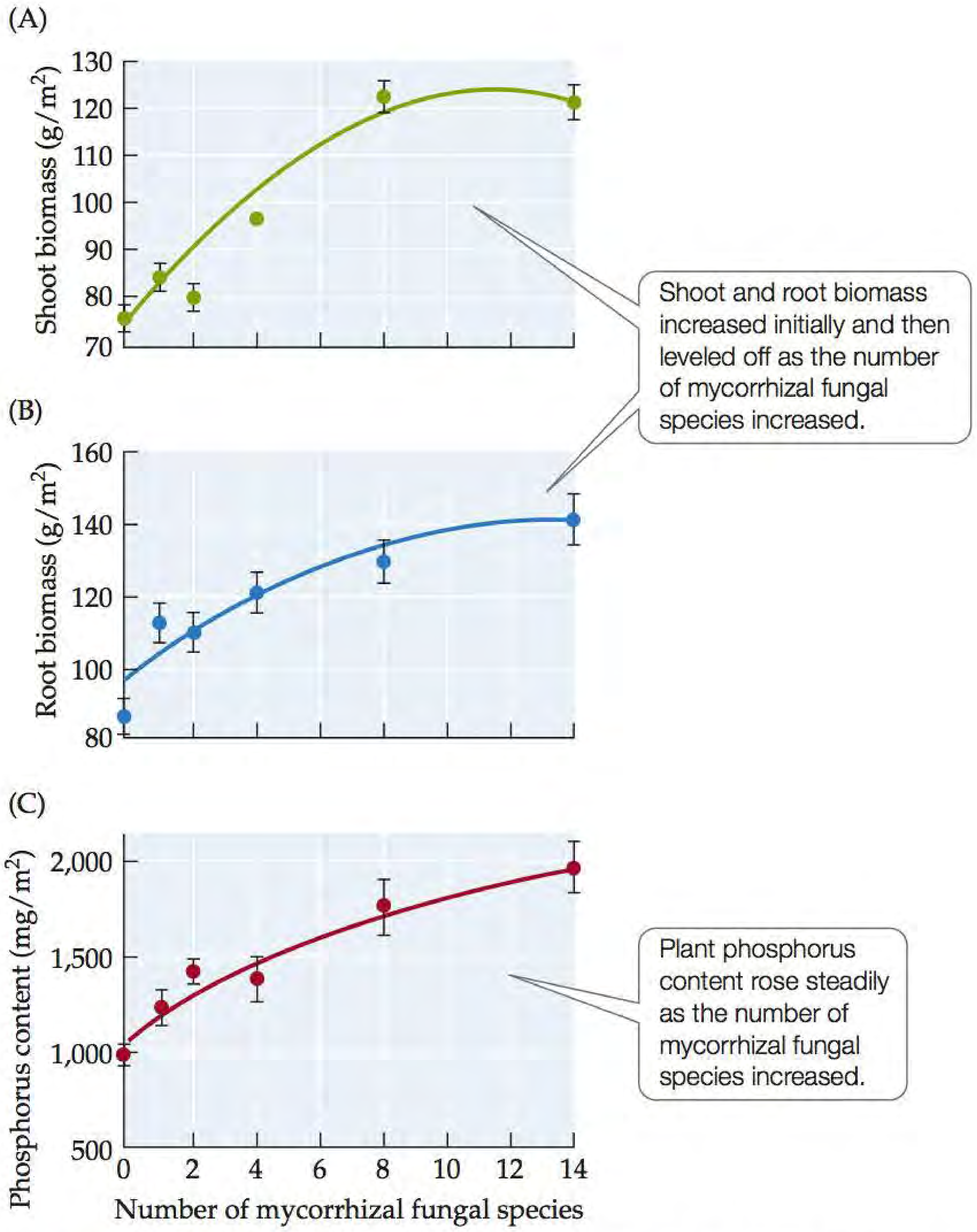


Figure 15.19 Mycorrhizal Fungal Species Richness Affects Ecosystem Properties Researchers measured the effects of the number of mycorrhizal fungal species in the soil on (A) average shoot biomass, (B) average root biomass, and (C) phosphorus content in mixtures of 15 species of plants grown from seed in a field experiment. Error bars show ± one SE of the mean. (After van der Heijden et al. 1998.)

community. Most of the species lost from the reefs without cleaners were species that typically move among reefs, including some large predators. Large predators can themselves affect the diversity and abundance of species, so the removal of cleaner fish could also result in further, but difficult to predict, long-term changes to the community.

SPECIES INTERACTIONS AND ECOSYSTEM PROPERTIES

Barbara Hetrick and colleagues (1989) performed greenhouse experiments in which the presence of mycorrhizal fungi altered the outcome of competition between two prairie grasses, big bluestem (*Andropogon gerardii*) and junegrass (*Koeleria macrantha*). They found that big bluestem dominated when mycorrhizal fungi were present and that junegrass dominated when they were not. In a natural prairie community of which big bluestem was a dominant member, when David Hartnett and Gail Wilson (1999) suppressed mycorrhizal fungi with a fungicide, the performance of big bluestem decreased. At the same time, the performance of a variety of other plant species, including both grasses and wildflowers, increased. Hartnett and Wilson suggested that big bluestem's dominance may have come from a competitive advantage conferred by its association with mycorrhizal fungi and that removal of those fungi removed that advantage and released the inferior competitors from the negative effects of competition.

Mycorrhizal associations can affect other features of ecosystems in addition to diversity, as shown in a 1998 study by Marcel van der Heijden, John Klironomos, and colleagues. In a large-scale field experiment, these scientists manipulated the number of species of mycorrhizal fungi (from 0 to 14 species) found in soils in which identical mixtures of the seeds of 15 plant species had been sown. After one growing season, plant dry weights and phosphorus content were measured. Plant root and shoot biomass increased as the number of species of fungi increased (**Figure 15.19A,B**), as did the efficiency of phosphorus uptake by plants (**Figure 15.19C**). These results show that mycorrhizal fungal species richness can influence key features of ecosystems such as net primary production (measured as the amount of new plant growth over one growing season) and the supply and cycling of nutrients such as phosphorus.

A CASE STUDY REVISITED

The First Farmers

The fungal gardens of leaf-cutter ants represent an enormous food resource for any species able to overcome the ants' defenses. As we saw in Chapter 13, roughly half the world's species are parasites, and many of them have remarkable adaptations for evading host defenses. Are there any parasites that specialize in attacking fungal gardens?

Although you might expect that the answer would be yes, for more than 100 years after the fungus-growing role of leaf-cutter ants was discovered (Belt 1874), no such parasites were known. That changed in the early 1990s, when Ignacio Chapela observed that leaf-cutter ant gardens were plagued by a virulent parasitic fungus of the genus *Escovopsis* (see also Currie et al. 1999a). This parasite can spread from one garden to the next, and it can rapidly destroy the gardens it invades, leading to the death of ant colonies. Leaf-cutter ants respond to *Escovopsis* by increasing the rate at which they weed their gardens (**Figure 15.20**) and, in some cases, by increasing how often they dose the garden with antimicrobial toxins, which they produce in specialized glands (Fernández-Marín et al. 2009).

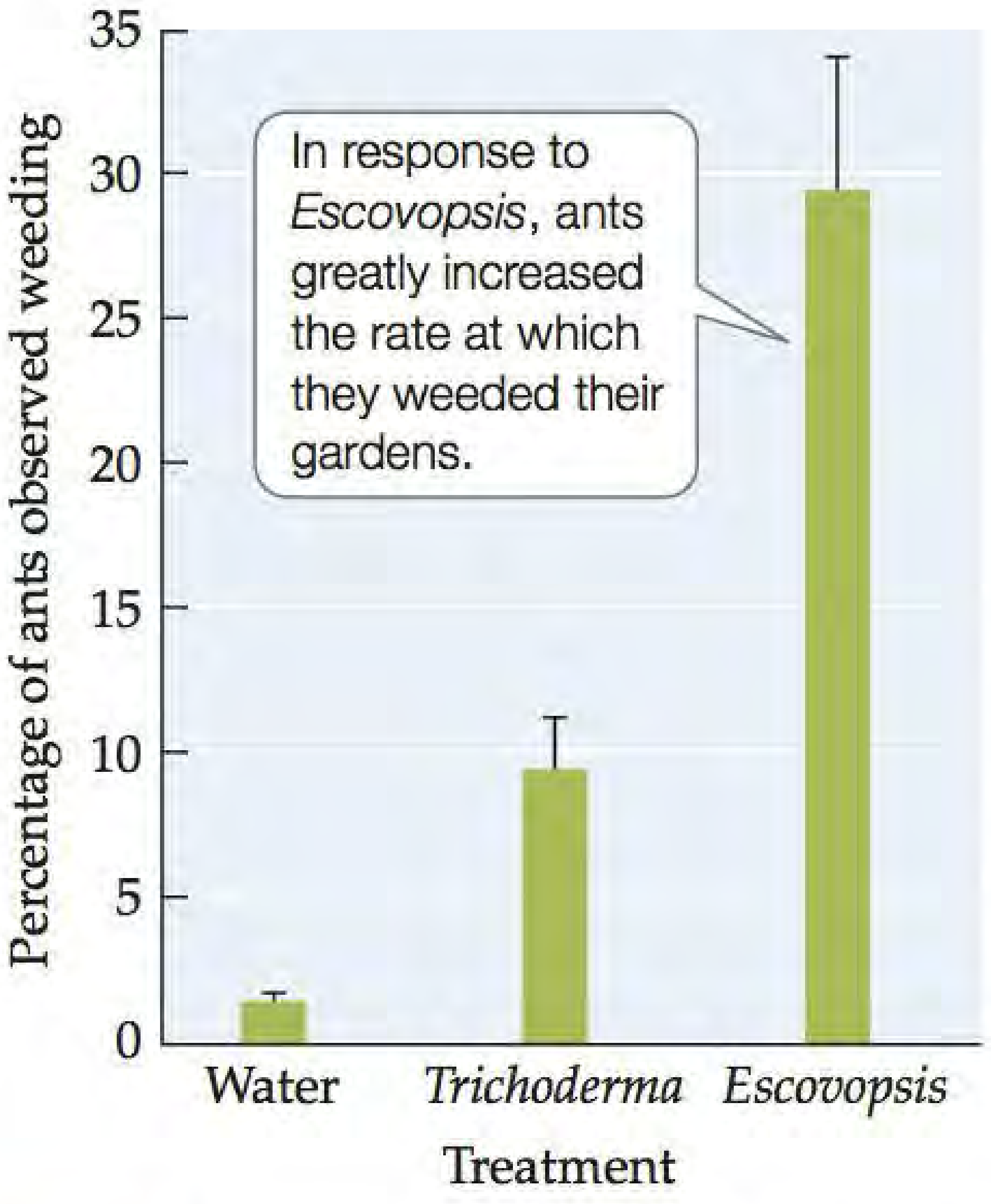


Figure 15.20 A Specialized Parasite Stimulates Weeding by Ants Currie and Stuart measured the frequency with which the leaf-cutter ant *Atta colombica* weeded its fungal gardens after colonies were exposed to water, *Trichoderma viride* (a generalist fungal parasite), and the specialized fungal parasite *Escovopsis*. Error bars show one SE of the mean. (After Currie and Stuart 2001.)

Suppose 2% of ants were observed weeding in colonies exposed to water, 20% in colonies exposed to *Trichoderma* and 20% in colonies exposed to *Escovopsis*. Propose a hypothesis that might explain these results.

The ants also enlist the help of other species in combatting *Escovopsis* (Currie et al. 1999b). On the underside of the ant's body lives a bacterium that produces chemicals that inhibit *Escovopsis*. The queen carries this bacterium on her body when she begins a new colony. While the ants clearly benefit from the use of these fungicides, what of the bacterium? Recent work (Currie et al. 2006) indicates that the bacterium also benefits: the ant provides it with both a place to live (it is housed in specialized structures called *crypts* that are located on the ant's exoskeleton) and a source of food (glandular secretions). Thus, the bacterium appears to be a third mutualist that benefits from, and contributes to, these unique fungal gardens.

CONNECTIONS IN NATURE

From Mandibles to Nutrient Cycling

While you have been reading this chapter, billions of pairs of leaf-cutter ant mandibles have been removing leaves from the forests of the Americas. The workers of a single colony can harvest as much plant matter each day as it would take to feed a cow. People have long known that leaf-cutter ants are potent herbivores. Weber (1966) describes reports—the earliest from 1559—of leaf-cutter ants destroying the crops of Spanish colonists, and they still plague farmers today. In tropical regions, these ants tend to increase in abundance after a forest is cut down. Anecdotal evidence suggests that the thriving ant colonies found in deforested areas are one of the reasons why farms in some tropical regions are often abandoned just a few years after trees have been removed to make room for them (other reasons relate to a point made in Chapters 3 and 22: some tropical soils are nutrient-poor).

In addition to their effects on human farmers, leaf-cutter ants introduce large amounts of organic matter into tropical forest soils. As a consequence, they affect the supply and cycling of nutrients in the forest ecosystem (a topic we will discuss in more detail in Concept 22.3). Normally, nutrients in the leaf litter that falls to the forest floor enter the soil when the leaves decompose. Bruce Haines (1978) compared the amounts (g/m^2) of 13 mineral nutrients contained in leaf litter with the amounts of the same nutrients found in aboveground areas where colonies of the leaf-cutter ant *Atta colombica* deposit their refuse (other *Atta* species deposit refuse belowground, as shown in Figure 15.2A). Averaged across the 13 nutrients, the ants' refuse areas contained about 48 times the nutrients found in the leaf litter. Plants respond to this concentration of nutrients by increasing their production of fine roots in the *Atta* refuse areas. Furthermore, the activities of leaf-cutter ants have the effect of tilling the soil near their nests, making it easier for plant roots to penetrate the soil (Moutinho et al. 2003). Moutinho and colleagues also found that the leaf material ants bring into their colonies fertilizes the soil, causing soils beneath ant colonies to be 3 to 4 times richer in calcium and 7 to 14 times richer in potassium than are soils that are 15 m away from the nest. Finally, recent evidence suggests that the fungal gardens tended by ants may also house nitrogen-fixing bacteria (**Figure 15.21**). These bacteria may be part of yet another mutualism found in the gardens—a mutualism that may prove to be an important source of nitrogen in tropical ecosystems.

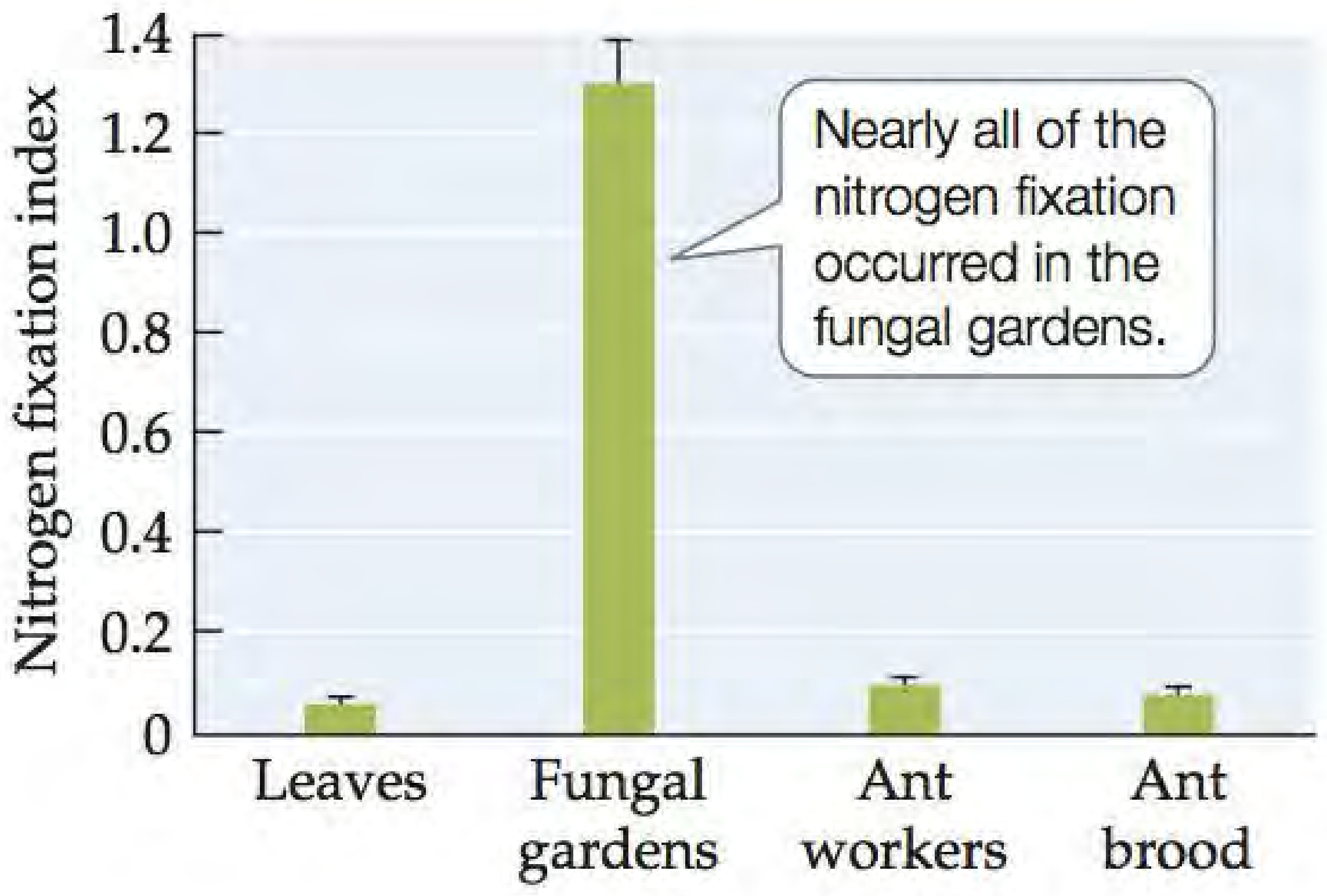


Figure 15.21 Nitrogen Fixation in Fungal Gardens When researchers measured nitrogen fixation activity in different parts of the colonies of leaf-cutter ants, they found that most of it was taking place in the fungal gardens. In addition, bacteria from genus *Klebsiella* were isolated from the fungal gardens and shown to fix nitrogen. Error bars show one SE of the mean. (After Pinto-Tomás et al. 2009.)

The overall effects of leaf-cutter ants on the ecosystems in which they live are complex. In forest ecosystems, net primary production (NPP) is usually measured as new aboveground plant growth (see Concept 20.1); root growth is often ignored, since it is difficult to measure in trees. Although leaf-cutter ants reduce NPP by harvesting leaves, some of the other activities of ants (e.g., tillage, fertilization) may increase NPP. As a result, the net effect of the ants on the NPP of their ecosystem is difficult to estimate. While it may prove possible to disentangle such effects in future studies, there is no doubt that the ants and their partners have considerable effects on the ecosystems in which they are found.

Summary

CONCEPT 15.1 In positive interactions, no species is harmed and the benefits are greater than the costs for at least one species.

- Mutualism is a mutually beneficial interaction between species, and commensalism occurs when one species benefits but the other is not affected.
- Mutualism and commensalism are ubiquitous interactions that are important in both terrestrial and aquatic communities.
- Mutualism and commensalism can evolve from other kinds of ecological interactions; for example, over time, a host–parasite interaction may evolve to become a mutualistic interaction.
- The costs and benefits of a positive interaction can vary from one place and time to another; as a result, a positive interaction may cease to be beneficial under some circumstances.
- Positive interactions may be more common in stressful environments.

CONCEPT 15.2 Each partner in a mutualistic interaction acts in ways that serve its own ecological and evolutionary interests.

- Mutualisms can be categorized by whether one partner provides the other with food (a trophic mutualism) or a place to live (a habitat mutualism).
- The partners in a mutualism are in it for themselves—it is not an altruistic interaction.
- Some mutualists have mechanisms to prevent overexploitation by cheaters.

CONCEPT 15.3 Positive interactions affect the abundances and distributions of populations as well as the structure of ecological communities.

- Positive interactions can provide benefits that increase the growth, reproduction, or survival of one or both of the interacting species.
- As a result of such demographic effects, positive interactions can determine the abundances and distributions of populations of the interacting species.
- Positive interactions can also affect interactions among organisms and hence the structure of ecological communities as well as the properties of the ecosystems of which those communities are a part.

Review Questions

1. Summarize the key features of positive interactions described in Concept 15.1.
2. Researchers who study mutualism do not think of it as an altruistic interaction. Explain why.
3. High water temperature is one of several stressors that can cause coral bleaching, in which a coral expels its algal mutualists and hence loses its color. If bleaching occurs repeatedly, coral death may result. Some corals are more sensitive than others to high water temperatures. If a reef containing a mixture of coral species were exposed to increasingly high water temperatures over a series of years, how might the community change over time?

Hone Your Problem-Solving Skills

The survival rates of small seedlings of the Scotch pine tree (*Pinus sylvestris*) growing in open areas and shaded beneath *Salvia* shrubs are given in the table below, as are mean values for certain abiotic conditions.

	UNDER *SALVIA*	OPEN AREAS
Seedling survival		
Pinus sylvestris	55%	22%
Abiotic conditions (means)		
Light level (W/m^2)	473	917
Soil moisture (%)	12	9
Soil temperature (°C)	15	19

Source: Castro et al. 2002.

1. How would you characterize the relationship between *Pinus sylvestris* seedlings and *Salvia* shrubs?
2. What factors may lead to the increased survival of *Pinus sylvestris* seedlings that live under *Salvia* shrubs?
3. How might the relationship between these species change over time?

ON THE COMPANION WEBSITE
ecology4e.sinauer.com

The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

15.1 A Double-Edged Sword: Costs and Benefits of Mutualisms

Unit 5

Communities

16 The Nature of Communities

KEY CONCEPTS

CONCEPT 16.1 Communities are groups of interacting species that occur together at the same place and time.

CONCEPT 16.2 Species diversity and species composition are important descriptors of community structure.

CONCEPT 16.3 Communities can be characterized by complex networks of direct and indirect interactions that vary in strength and direction.

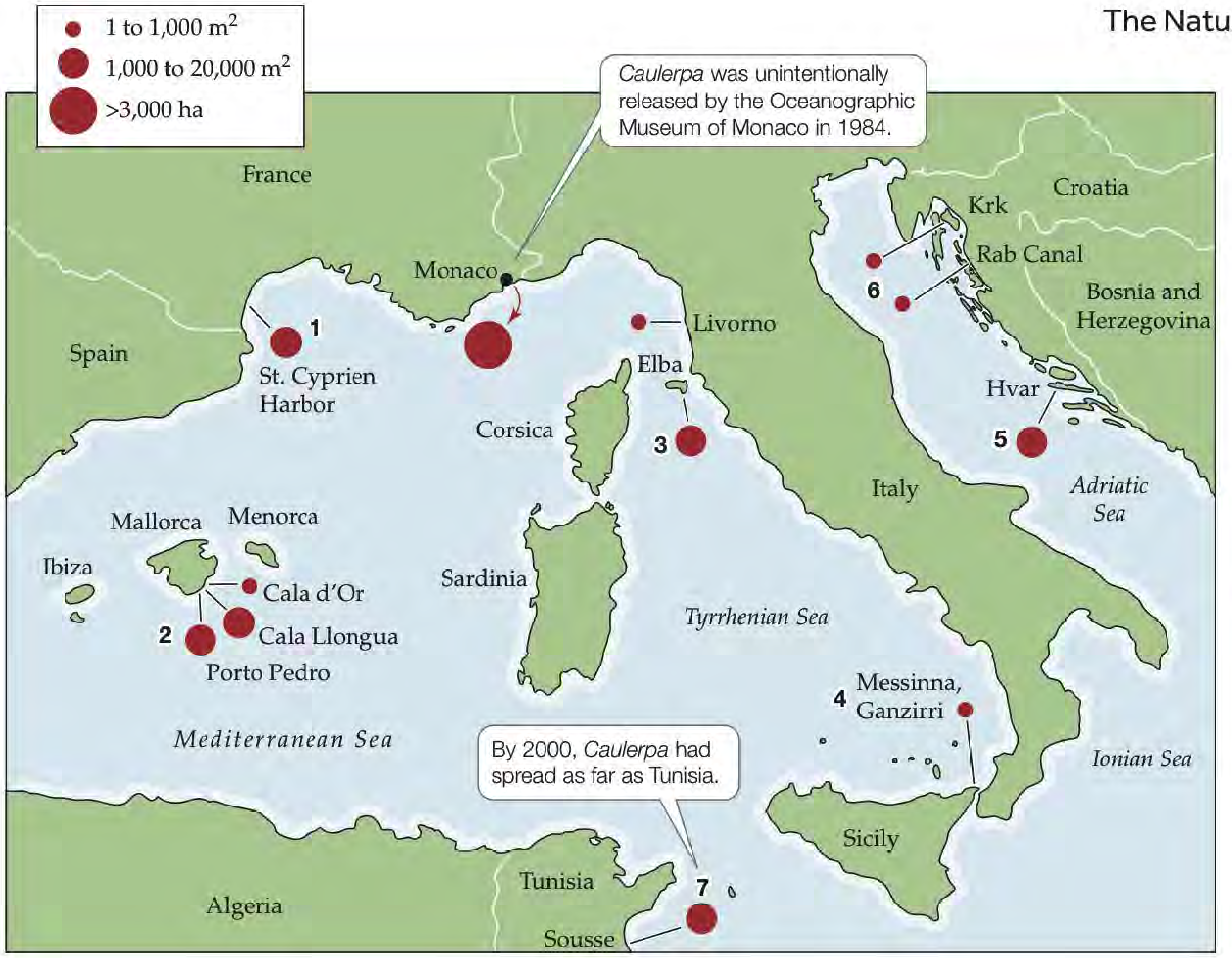
"Killer Algae!": A Case Study

In 1988, a French marine biology student dove into the crystal clear water of the Mediterranean Sea and made an unusual discovery. On the seafloor, just below the cliffs on which stood the palatial Oceanographic Museum of Monaco, grew an unusual seaweed, *Caulerpa taxifolia* (**Figure 16.1**), a native of the warm tropical waters of the Caribbean. The student told Alexandre Meinesz, a leading expert on tropical algae and a professor at the University of Nice, about the unusual species. Over the following year, Meinesz confirmed its presence and determined that its feathery fluorescent green fronds, interconnected by creeping underground stems called rhizomes, carpeted an underwater area in front of the museum.

Meinesz was astonished because this species had never been seen in such cold waters, and it had certainly never reached the high densities he recorded. As it later turned out, earlier sightings from 1984 allowed Meinesz to calculate a spread of more than 1 hectare (ha) in 5 years. Over the next few months, he asked himself and his colleagues some important questions. First, how did the seaweed get to the Mediterranean in the first place, and how could it survive in temperatures as cold as 12°C–13°C (54°F–55°F), given that its normal temperature range is 18°C–20°C (64°F–68°F)? Second, did this species occur anywhere else in the Mediterranean, and was it spreading beyond the soft-sediment habitats found in front of the museum? Most importantly, at such high population densities, how was it interacting with native algae and seagrasses, both of which are critical habitats and sources of food for fish and invertebrate species?

A definitive answer to the second question came in July 1990, when the alga was found 5 km east of the museum, at a popular fishing location. Evidently, fragments had been caught on the gear and anchors of fishing vessels and transported to new sites of colonization. The find generated media coverage that included information on the toxicity of the seaweed, which produces a peppery secondary compound to deter the fish and invertebrate herbivores that abound in the tropics. The press sensationalized *Caulerpa*'s natural toxicity with headlines such as "Killer algae!"—a misleading title that suggested that the seaweed was toxic to humans (it is not). As the news spread, so did the sightings of *Caulerpa*. By 1991, 50 sightings had been reported in France alone. The fluorescent green alga indiscriminately colonized muddy, sandy, and rocky bottoms at 3 to 30 m water depth. By 2000, the alga had moved from France to Italy, then to Croatia to the east and Spain to the west, eventually spreading as far as Tunisia (**Figure 16.2**). It had

Figure 16.1 Invading Seaweed *Caulerpa taxifolia* rapidly invaded and dominated marine communities in the Mediterranean Sea.



Caulerpa was unintentionally released by the Oceanographic Museum of Monaco in 1984.

By 2000, *Caulerpa* had spread as far as Tunisia.

Figure 16.2 Spread of *Caulerpa* in the Mediterranean Sea *Caulerpa taxifolia* first invaded the waters off Monaco and France. By 2000, this algal species had reached Croatia and Tunisia. (After Meinesz 2001.)

? Using the order of appearance on the map, describe the possible invasion pathways of *Caulerpa* within this region.

invaded thousands of hectares, despite frantic but futile efforts to remove it.

From the very beginning, Meinesz suspected that the answer to his first question lay with the museum. In 1980, a cold-resistant strain of *Caulerpa taxifolia* had been discovered and propagated in the tropical aquariums at the Wilhelma Zoo in Stuttgart, Germany. Cuttings were sent to other aquariums, including the one in Monaco, to be grown as aesthetically pleasing backdrops to tropical fish displays. The museum admitted to unintentionally releasing *Caulerpa* in the process of cleaning tanks but believed the alga would die in the cold waters of the Mediterranean.

Given that *Caulerpa* did not die, but instead quickly invaded and overtook shallow areas of the Mediterranean, scientists and fishermen alike wanted to understand how this abundant and fast-spreading seaweed would affect marine habitats and the fisheries dependent on them. How do interactions with one very abundant species influence the hundreds of other species with which it shares a community?

Introduction

We have emphasized throughout this book that species are connected with one another and with their environment. Ecology is, at its very essence, the study of these interconnections. In Unit 4, we looked at interactions between species as two-way relationships, with one species eating, competing with, or facilitating another species. For ease of mathematical modeling, we considered these pairwise interactions in isolation, even though we have emphasized that, in reality, species experience multiple interactions. In this chapter, we will explore multiple-species interactions and how they shape the nature of communities. We will consider the various ways in which ecologists have defined communities, the metrics used to measure community structure, and the types of species interactions that characterize communities.

CONCEPT 16.1

Communities are groups of interacting species that occur together at the same place and time.

What Are Communities?

Ecologists define **communities** as groups of interacting species that occur together at the same place and time. Interactions among multiple species and their physical environment give communities their character and function. Whether we are dealing with a desert, a kelp forest, or the gut of an ungulate, the existence of the community is dependent on the individual species that are present and on how they interact with one another and their physical surroundings. As we will see in this chapter and others in this unit, the relative importance of species interactions and the physical environment, which can vary among communities, is a major focus of research for community ecologists.

Ecologists often delineate communities by their physical or biological characteristics

The technical definition of a community given above is more theoretical than operational. In practical terms, ecologists often delineate communities using physical or biological characteristics as a guide (**Figure 16.3**). A community may be defined by the physical characteristics of its environment; for example, a physically defined community might encompass all the species in a sand dune, a mountain stream, or a desert. The biomes and aquatic biological zones described in Chapter 3 are based largely on the physical characteristics thought to be important in defining communities. Similarly, a biologically defined community might include all the species associated with a kelp forest, a freshwater bog, or a coral reef. This way of thinking uses the presence and implied importance of abundant species, such as kelp, wetland plants, or corals, as the basis for community delineation.

In most cases, however, communities end up being defined somewhat arbitrarily by the ecologists who are studying them. For example, if ecologists are interested in studying aquatic insects and their amphibian predators, they are likely to restrict their definition of the community to that particular interaction. Unless they broaden their question, researchers are unlikely to consider the roles of birds that forage in wetlands or other inherently important aspects of the wetland in which they are working. Thus, is it important to recognize that ecologists typically define communities based on the questions they are posing.

Regardless of how a community is defined, ecologists interested in knowing which species are present in a community must contend with the difficult issue of accounting for them. Merely creating a species list for a community is a huge undertaking, and one that is essentially impossible to complete, especially if small or relatively unknown species are considered. Taxonomists have

(A) Desert

(B) Hot springs

(C) Tropical rainforest

(D) Coral reef

Figure 16.3 Defining Communities Ecologists often delineate communities based on their physical attributes or their biological attributes.

? Of the four communities shown in this figure, which are mostly defined by physical attributes and which are mostly defined by biological attributes?

officially described about 1.9 million species, but we know from sampling studies of tropical insects and microorganisms that this number greatly underestimates the actual number of species on Earth, which could be closer to 9 million or even more. For this reason, and because of the difficulty of studying many species at one time, ecologists usually consider a subset of species when they define and study communities.

Ecologists may use subsets of species to define communities

One common way of subdividing a community is based on taxonomic affinity–that is, by groups of species classified together because of evolutionary lineage (**Figure 16.4A**). For example, a study of a forest community might be limited to all the bird species within that community (in which case an ecologist might speak of "the forest bird community"). Another useful subset of a community is a **guild**, a group of species that use the same resources, even though they might be taxonomically distant (**Figure 16.4B**). For example, some birds, bees, and bats feed on flower pollen, thus forming a guild of pollen-eating animals. Finally, a **functional group** is a subset of a community that includes species that function in similar ways but may or may not use similar resources (**Figure 16.4C**). For example, nitrogen-fixing plants (legumes) can be placed in the same functional group.


(A) Taxonomic affinity


(B) Guild


(C) Functional group

Figure 16.4 Subsets of Species in Communities Ecologists may use subsets of species to define communities. These examples show three ways in which such subsets could be designated. (A) All the bird species in a community could be grouped together by taxonomic affinity. (B) All the species that use pollen as a resource could be grouped together as a guild. (C) All the plant species in a community that have nitrogen-fixing bacteria (e.g., legumes) could be placed in the same functional group.

There are other subsets of communities that allow ecologists to organize species based on their *trophic*, or energetic, interactions (**Figure 16.5A**). Species can be organized in a **food web**, a representation of the trophic or energetic connections among species within a community. Food webs can be further organized into **trophic levels**, or groups of species that have similar ways of interacting and obtaining energy. The lowest trophic level contains *primary producers*, which are autotrophs such as plants. The primary producers are fed on by organisms at the second level, the *primary consumers*, which are herbivores. The third level contains *secondary consumers*, which are carnivores, or animals that eat animals. Secondary consumers are fed on in turn by *tertiary consumers*, also carnivores.

Traditionally, food webs have been used as a descriptive or idealized method of understanding the trophic relationships among the species in a community. Food webs tell us little, however, about the strength of those interactions or their importance in the community. In addition, the use of trophic levels can create confusion for a number of reasons: for example, some species span two trophic levels (e.g., corals can be classified as both carnivores and herbivores because they eat zooplankton and they have symbiotic algae), some species change their feeding status as they mature (e.g., amphibians can be herbivores as tadpoles and carnivores as adults), and some species are *omnivores*, feeding on more than one trophic level (e.g., some fish feed on both algae and invertebrates). Moreover, idealized food webs often do not include certain important resources and consumers that are common within communities. For example, all organisms that die without being consumed become organic matter known as *detritus* and can be consumed by *detritivores* (mostly fungi and bacteria) through a process known as *decomposition*; see Concept 22.2. Another example is symbionts, including parasites and mutualists, which are present at almost all trophic levels (see Chapters 13 and 15).

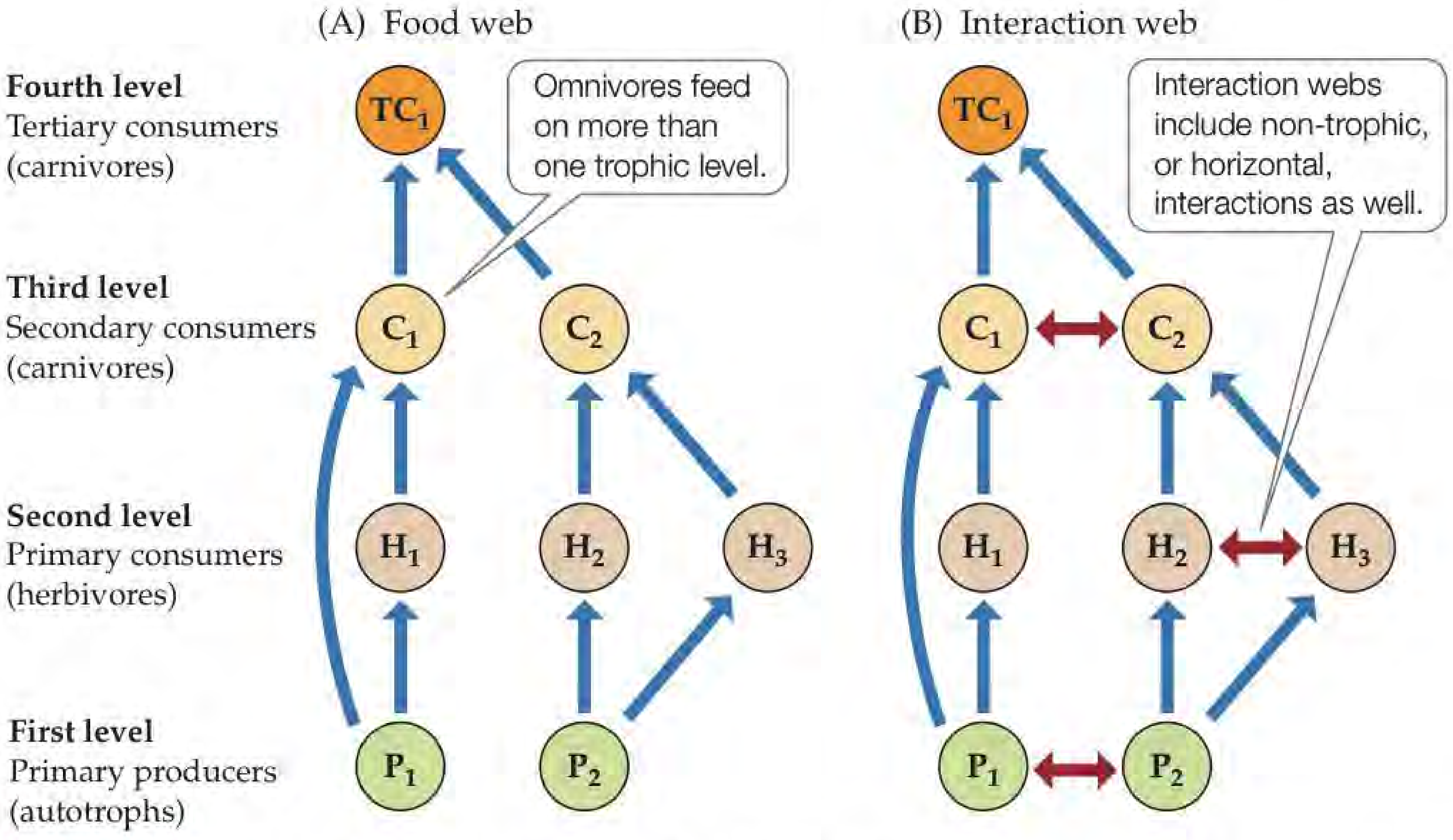


Figure 16.5 Food Webs and Interaction Webs (A) Food webs describe trophic or energetic connections among species within a community. (B) Interaction webs include both trophic interactions (vertical arrows) and non-trophic (horizontal) competitive and positive interactions.

Another characteristic of food webs is that they do not include non-trophic interactions (so-called **horizontal interactions**, such as competition and some positive interactions), which, as we have seen in Unit 4, can also influence community character. The concept of an **interaction web** has been introduced to more accurately describe both the trophic (vertical) and non-trophic (horizontal) interactions among the species in a traditional food web (**Figure 16.5B**). Despite these drawbacks, the food web concept remains a strong one, if only for its visual representation of important consumer relationships within a community.

We will learn much more about food webs in Chapter 21. Next let's consider the important properties of communities that allow us to characterize them and to distinguish one from another.

CONCEPT 16.2

Species diversity and species composition are important descriptors of community structure.

Community Structure

We have seen that communities vary greatly in the number of species they contain. A tropical rainforest, for example, has many more tree species than a temperate rainforest, and a midwestern prairie has many more insect species than a New England salt marsh. Ecologists have devoted substantial effort to measuring this variation at a number of spatial scales. Species diversity and species composition are important descriptors of **community structure**, the set of characteristics that shape a community. Community structure is descriptive in nature but provides the necessary quantitative basis for generating hypotheses and experiments directed at understanding how communities work.

Species diversity is an important measure of community structure

Species diversity is the most commonly used measure of community structure. Even though the term is often used generally to describe the number of species within a community, it has a more precise definition. **Species diversity** is a measure that combines the number of species (species richness) and their abundances compared with those of the other species (species evenness) within the community. **Species richness** is the easiest metric to determine: one simply counts all the species in the community. **Species evenness**, which tells us about the commonness or rarity of species, requires knowing the abundance of each species relative to those of the other species within the community, a harder value to obtain. (See Ecological Toolkit 9.1 for methods of estimating abundances in terms of number, biomass, or percentage of cover.)

The contributions of species richness and species evenness to species diversity can be illustrated using a hypothetical example (**Figure 16.6**). Let's imagine two meadow communities, each containing four species of butterflies. Both communities have the same butterfly species richness, but their species evenness differs. In community A, one species constitutes 85% of the individuals in the community, while the other four species constitute only 5% of the individuals in the community; thus, species evenness is low. In community B, the number of individuals are evenly divided among the four species (25% each), so species evenness is high. In this case, even though each community has the same species richness (four species), community B has the higher species diversity because it has higher species evenness.

A number of species diversity indices can be used to describe species diversity quantitatively. By far the most commonly used is the **Shannon index**,

$$H = -\sum_{i=1}^{s} p_i \ln(p_i)$$

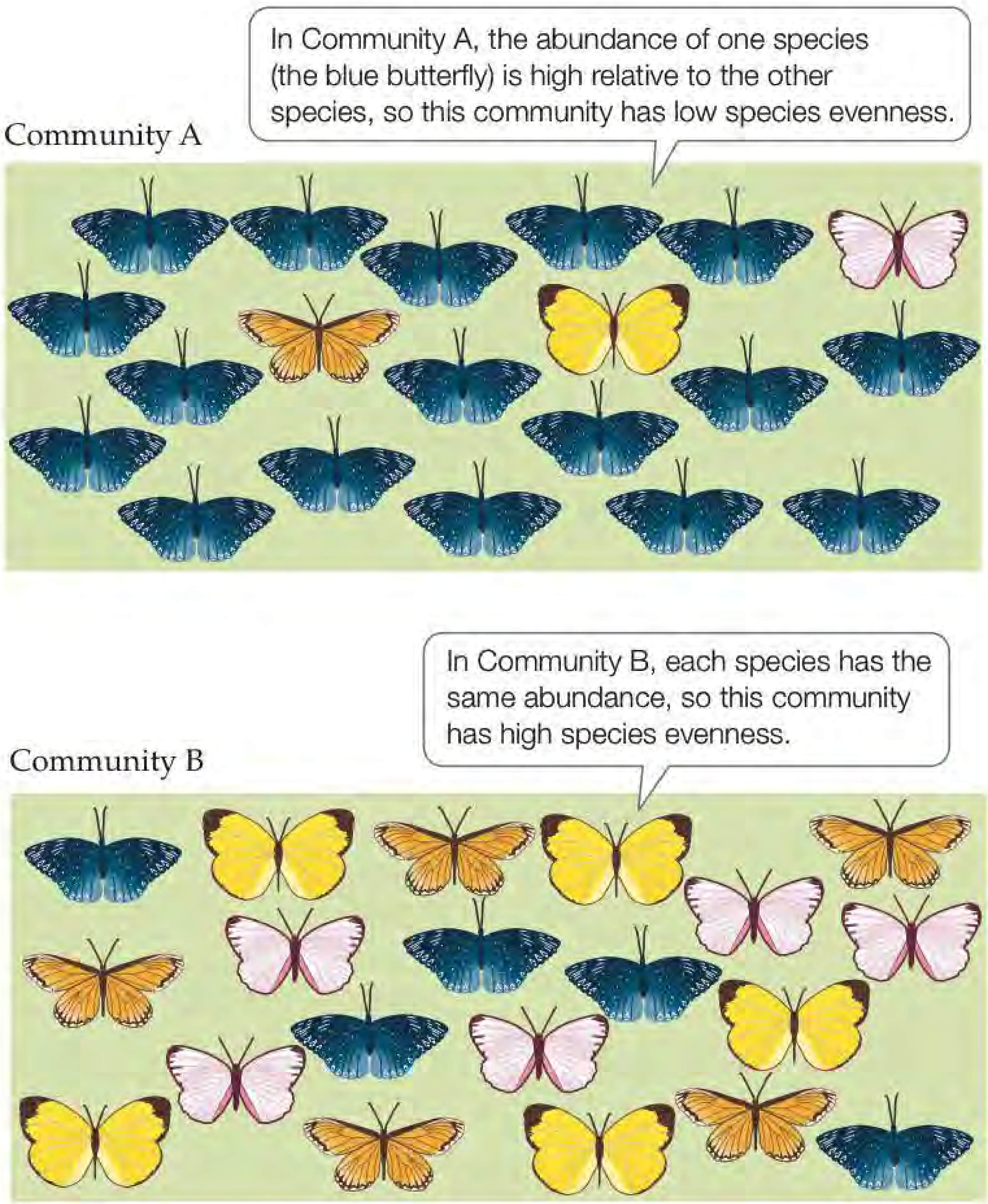
where

H = the Shannon index value

p_i = the proportion of individuals found in the ith species

ln = the natural logarithm

s = the number of species in the community



In Community A, the abundance of one species (the blue butterfly) is high relative to the other species, so this community has low species evenness.

In Community B, each species has the same abundance, so this community has high species evenness.

Figure 16.6 Species Richness and Species Evenness These two hypothetical butterfly communities have the same number of species (species richness) but different relative abundances (species evenness). Species diversity, as measured using the Shannon index, is lower in community A (see Table 16.1).

The lowest possible value of H is zero. The higher a community's H value, the greater its species diversity. **Table 16.1** calculates the Shannon index for the two butterfly communities in Figure 16.6. These calculations show that community A has the lower Shannon index value (H), confirming mathematically that this community has lower species diversity than community B. Given that both communities have the same species richness, the difference in species diversity is driven by the lower species *evenness* in community A. You can practice calculating the Shannon index in **Analyzing Data 16.1**, which explores how an invasive plant affects community structure in central European grasslands.

As we mentioned earlier, the term "species diversity" is often used imprecisely to describe the number of species in a community without regard to the relative abundances of species or species diversity indices. For example, one commonly hears the assertion that "species diversity" is higher in tropical communities than in temperate communities, without any accompanying information about the actual relative abundances of species in the two community types. Another term that is often used interchangeably with "species diversity" is "biodiversity." Technically, **biodiversity** is a term used to describe the diversity of important ecological entities that span multiple spatial scales, from genes to species to communities (**Figure 16.7**). Implicit in the term is the interconnectedness of genes, individuals, populations, species, and even community-level components of diversity. As we saw in Chapter 11, the genetic variation among individuals within a population influences that population's

TABLE 16.1 Calculation of Species Diversity Using the Shannon Index for Communities A and B

COMMUNITY A

SPECIES	ABUNDANCE	PROPORTION (p_i)	ln (p_i)	p_i ln (p_i)
Blue	17	0.85	−0.163	−0.139
Yellow	1	0.05	−2.996	−0.150
Pink	1	0.05	−2.996	−0.150
Orange	1	0.05	−2.996	−0.150
Total	**20**	**1.00**		**−0.589**

COMMUNITY B

SPECIES	ABUNDANCE	PROPORTION (p_i)	ln (p_i)	p_i ln (p_i)
Blue	5	0.25	−1.386	−0.347
Yellow	5	0.25	−1.386	−0.347
Pink	5	0.25	−1.386	−0.347
Orange	5	0.25	−1.386	−0.347
Total	**20**	**1.00**		**−1.388**

To calculate the Shannon Index (H), the natural logarithm (ln) is applied to p_i for each species (i)…

…and then this value is multiplied by p_i once again.

All the values are summed for all the species in the community and multiplied by −1 to get H.

$$H = -\sum_{i=1}^{s} p_i \ln(p_i) = 0.589$$

Community B has higher species diversity than community A.

$$H = -\sum_{i=1}^{s} p_i \ln(p_i) = 1.388$$

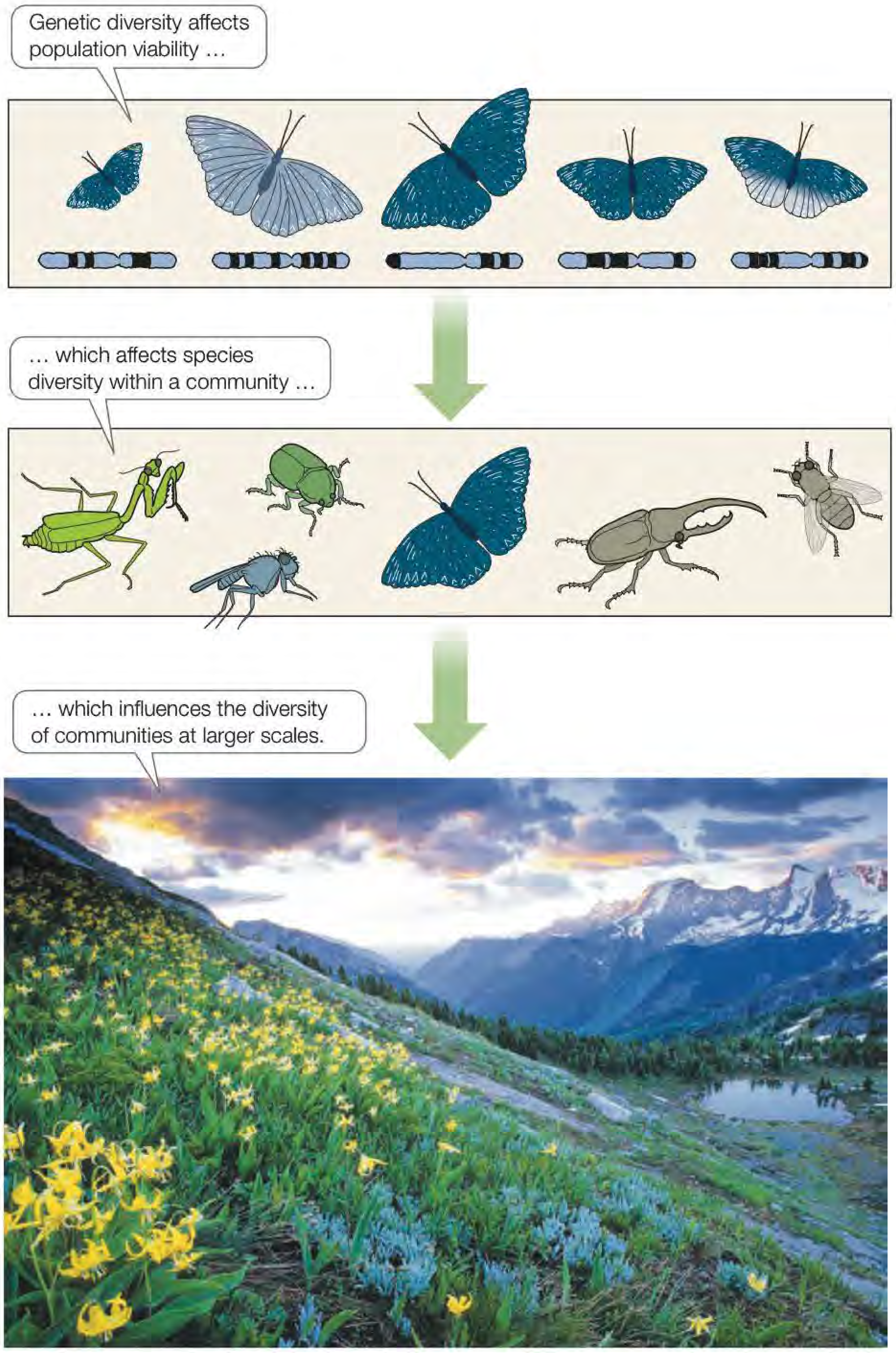


Figure 16.7 **Biodiversity Considers Multiple Spatial Scales** Diversity can be measured at spatial scales that range from genes to species to communities. The term "biodiversity" encompasses diversity at all of these scales.

viability (its chance of persistence). Population viability, in turn, has important consequences for species persistence, and ultimately for species diversity within communities. Moreover, the number of different kinds of communities in a region is critical to diversity at larger regional and latitudinal scales (see Figure 18.5). We will discuss the importance of spatial scale and biodiversity in chapters to come, but it is worth understanding some of the ways in which the term "diversity" is used, as a starting point for those later discussions.

Species within communities differ in their commonness or rarity

Although species diversity indices allow ecologists to compare different communities, graphical representations of species diversity can give us a more explicit view of the commonness or rarity of the species in communities. Such graphs, called **rank abundance curves**, plot the proportional abundance of each species (p_i) relative to the others in rank order, from most abundant to least abundant (**Figure 16.8**). If we use rank abundance curves to compare our two butterfly communities from Figure 16.6, we can see that community A has one abundant species (i.e., the blue butterfly) and three rare species (i.e., the yellow, pink, and orange butterfly species), whereas in community B, all the species have the same abundance.

These two patterns could suggest the types of species interactions that might occur in these two communities. For example, the dominance of the blue butterfly in community A might indicate that it has a strong effect on one or more of the other species in the community. In community B, where all the species have the same abundance, their interactions might be fairly equivalent, with no one species dramatically affecting the others. To test these hypotheses, we can design manipulative experiments to explore relationships between species abundances and

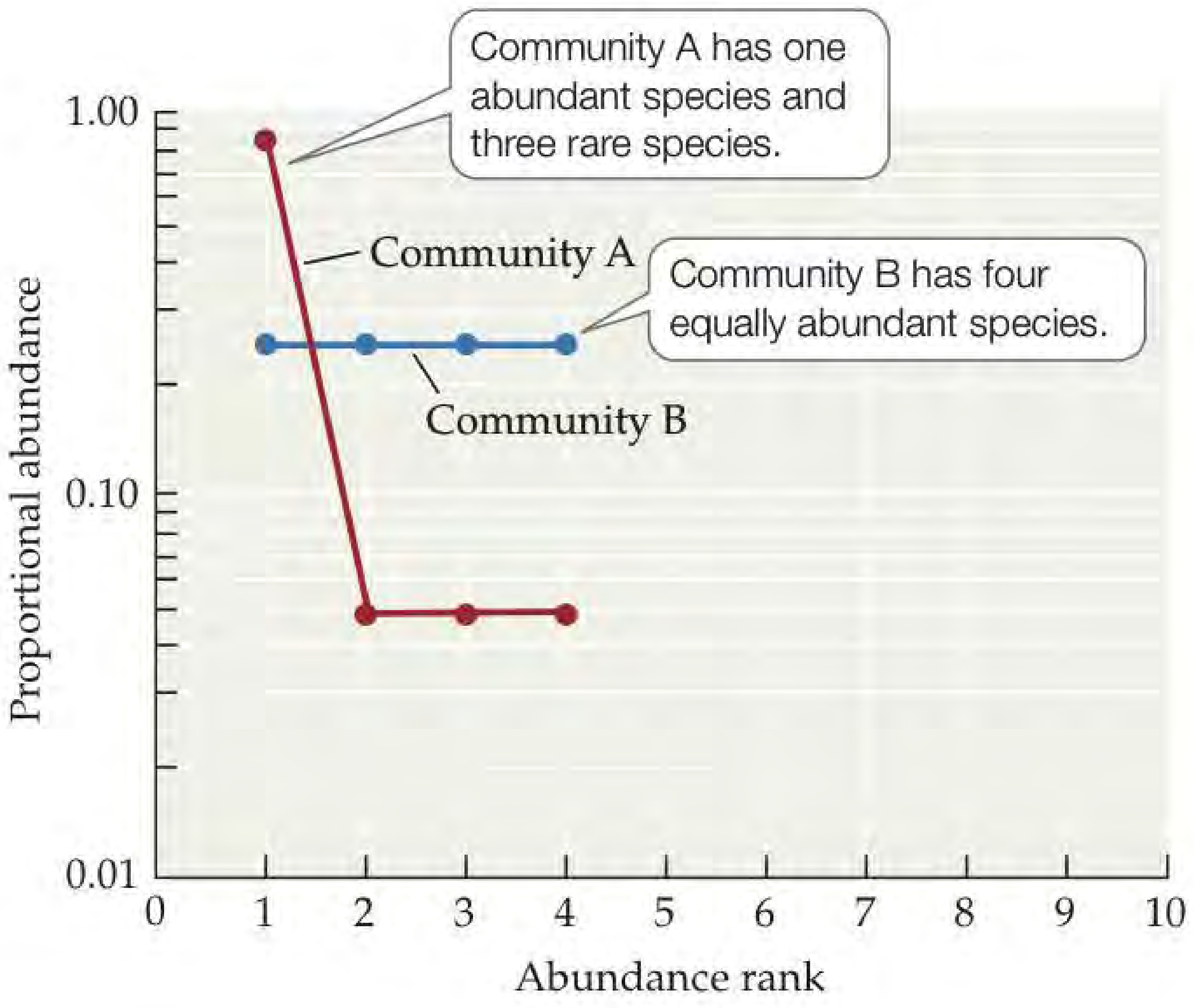


Figure 16.8 **Are Species Common or Rare?** Using rank abundance curves, we can see that the two hypothetical butterfly communities in Figure 16.6 differ in the commonness and rarity of the same four species.

ANALYZING DATA 16.1 What Are the Effects of Invasive Species on Species Diversity?

Invasions of non-native species have been implicated in both increases and decreases of species diversity within communities. One study looked at the effects of 13 "neophyte" plant species (i.e., those introduced since 1500) on the species diversity of a variety of plant communities in the Czech Republic in Central Europe (Hejda et al. 2009).* To understand the importance of species invasions to species diversity, the researchers measured species richness and abundance (percent plant cover) in plots with similar site conditions that differed in whether they had been invaded or not (i.e., native) by particular invasive species. They then subtracted the species richness of the invaded plots from that of the native plots, averaged the resulting values, and obtained an average change in species richness (*y* axis) for each species invasion (*x* axis). The results are shown in **Figure A**. The researchers also calculated the Shannon index (*H*) for each of the plots and conducted the same analysis: they calculated an average change in species diversity (*y* axis) for each invasive species (*x* axis). These values are given in **Figure B**. Error bars show one SE of the mean.

Figure A

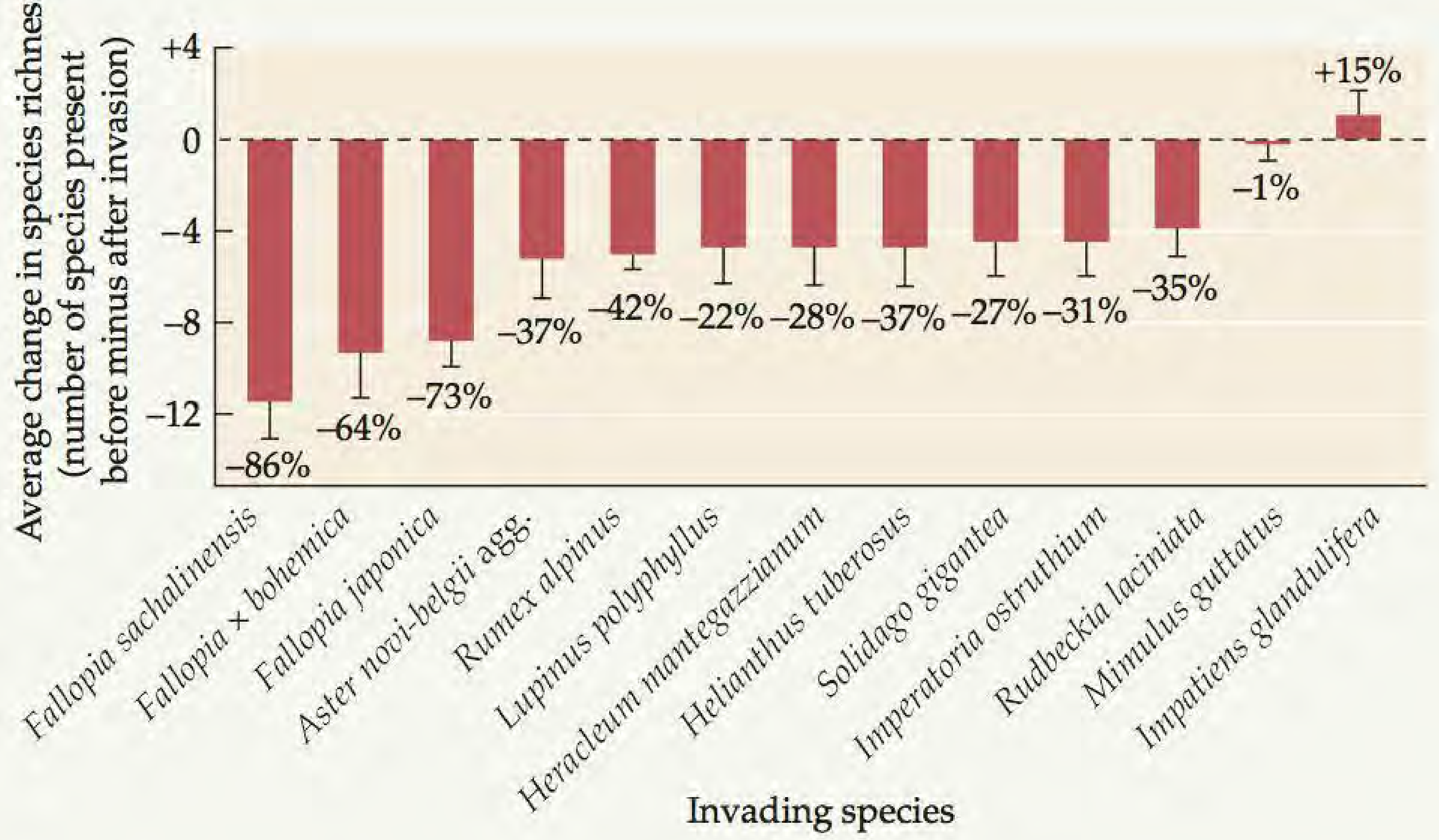
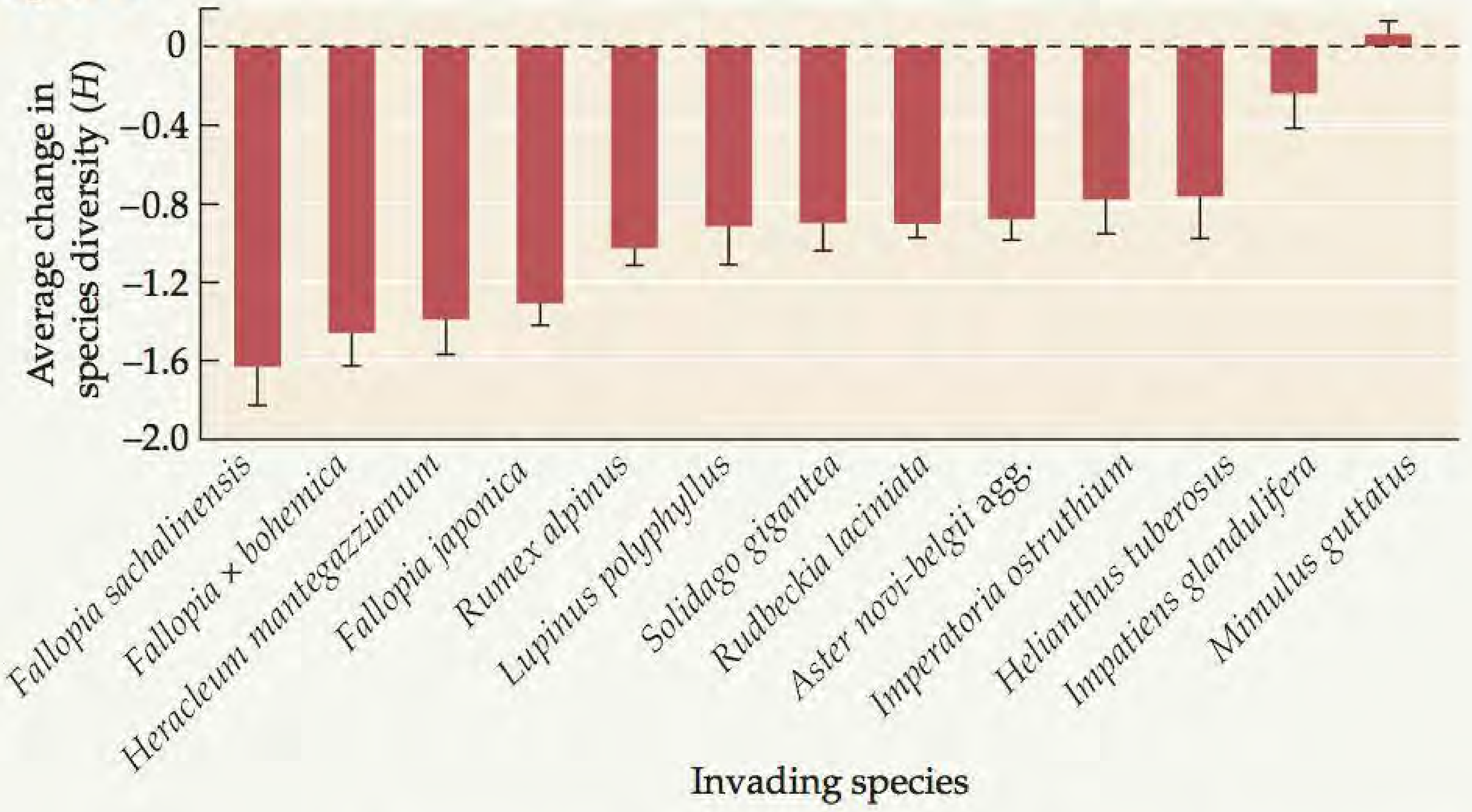


Figure B



1. Based on the average changes in species richness in Figure A, how many invasive species probably had negative effects on species richness, how many probably had positive effects on species richness, and how many probably had no effect on species richness?
2. Above (or below) each bar in Figure A is the percentage change in species richness for that invader. What do these percentages tell you about the likely direction and strength of the effect of invasive species on native community richness?
3. Compare the rank order of the magnitude of the average change in species richness from Figure A with that of the change in species diversity (*H*) in Figure B. Does the order differ between the two measures and, if so, why?

See the companion website for a similar ANALYZING DATA exercise.

---

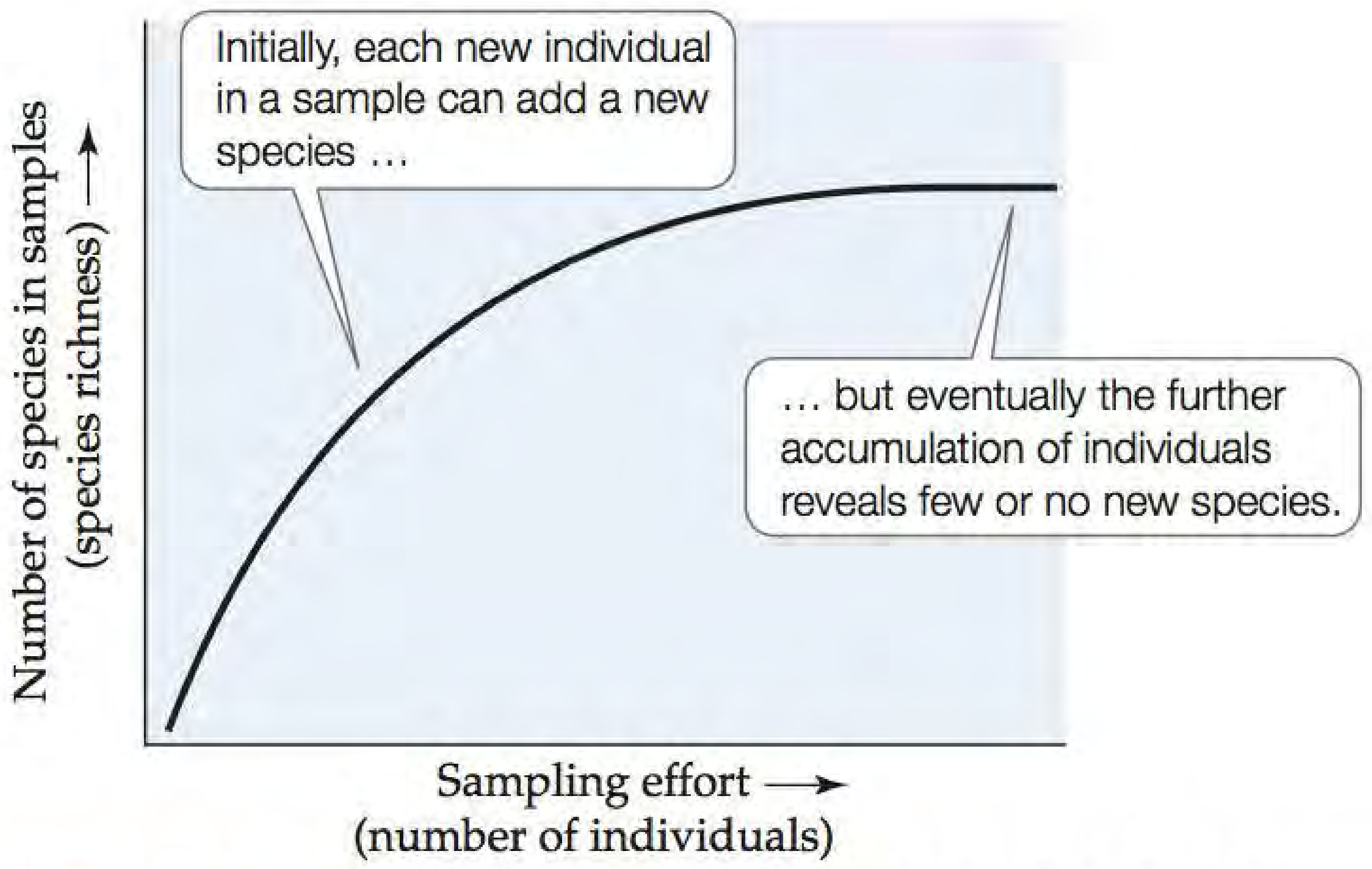
*Hejda, M., P. Pysek and V. Jorosik. 2009. Impact of invasive plants on the species richness, diversity, and composition of invaded communities. *Journal of Ecology* 97: 393–403.

the types of interactions that occur among the species in a community. As we will see in the next section, experiments of this kind typically involve adding or removing a species and measuring the responses of other species in the community to the manipulation.

For simplicity, we have considered a hypothetical example of species diversity patterns in butterfly communities. What do real communities reveal in this regard? An example from soil bacterial communities in Scotland can be found in **Web Extension 16.1**.

Species diversity estimates vary with sampling effort and scale

Let's imagine that you are sampling your backyard for insect species. It makes sense that the more samples you collect, the more species you are likely to find. However, eventually you reach a point in your sampling effort at which any additional sampling will reveal so few new species that you could stop sampling and still have a good notion of the species richness of your backyard. That point of "no significant return" for your effort can be determined using a **species accumulation curve** (**Figure 16.9**). These curves are calculated by plotting species richness as a function of sampling effort. In other words, each data point on a species accumulation curve represents the total number of species and the sampling effort up to that point. The more samples taken, the more individuals will be added, and the more species will be found. In theory, one could imagine, a threshold could be reached at which no new species would be added by additional sampling. In reality, this never occurs in natural systems, because new species are constantly being found.

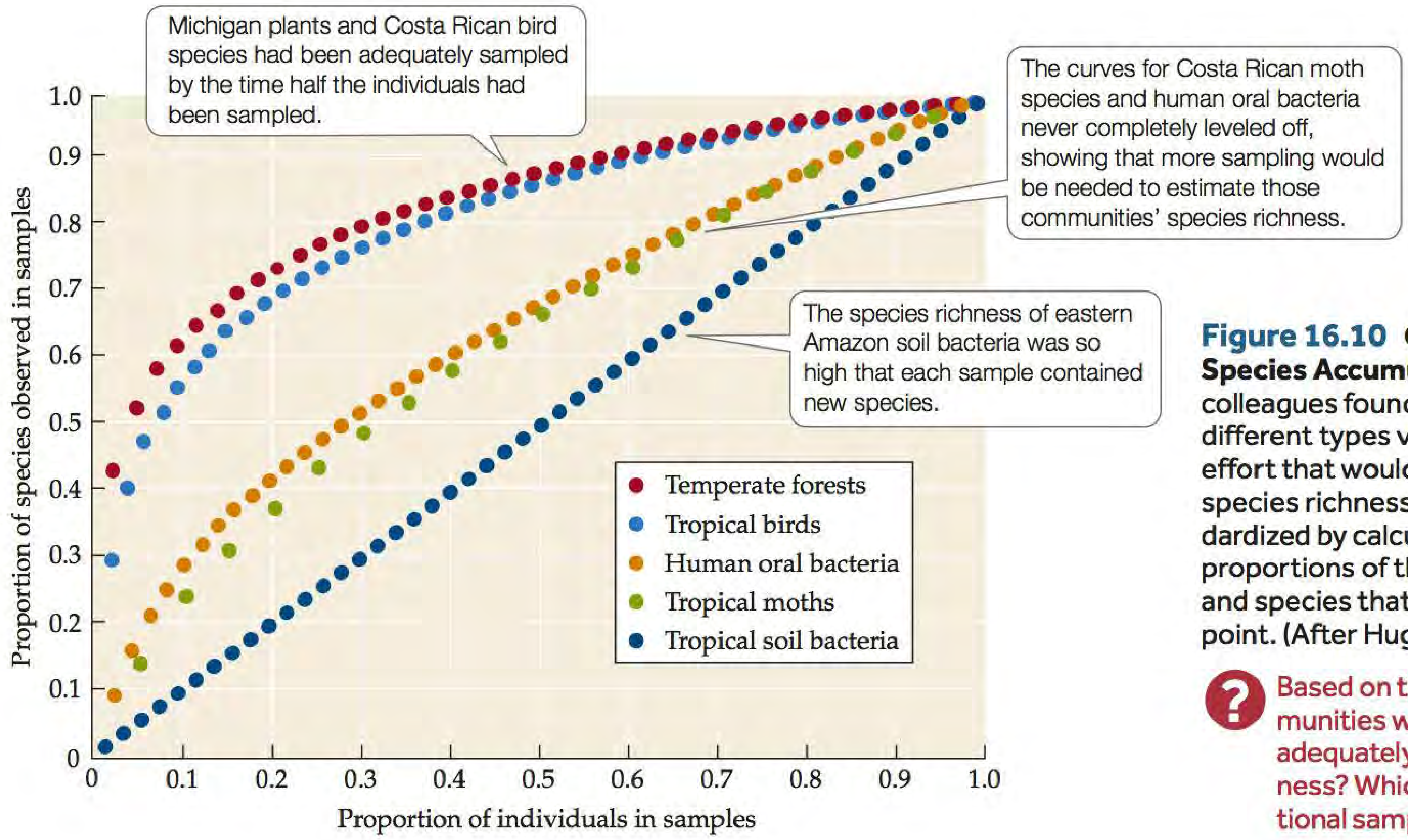


Initially, each new individual in a sample can add a new species …

… but eventually the further accumulation of individuals reveals few or no new species.

Figure 16.9 When Are All the Species Sampled? Species accumulation curves can help us determine when most or all of the species in a community have been observed. In this hypothetical example, the number of new species observed in each sample decreases after about half the individuals in the samples have accumulated.

Jennifer Hughes and colleagues (2001) used species accumulation curves to ask how communities differ in the relationship between species richness and sampling effort. Are there some very diverse communities in which we are unable to estimate species richness accurately despite intensive sampling? Hughes and colleagues calculated species accumulation curves for five different communities: a temperate forest plant community in Michigan, a tropical bird community in Costa Rica, a tropical moth community in Costa Rica, a bacterial community from the human mouth, and a bacterial community from tropical soils in the eastern Amazon (**Figure 16.10**). To compare the curves properly, given that the communities differed substantially in organismal abundance and species richness, the data sets were standardized by calculating for each data point the proportions of the total number of individuals and species that had been sampled up to that point. The results showed that the species richnesses of the Michigan forest plant and Costa Rican bird communities were adequately represented well before half the individuals



Michigan plants and Costa Rican bird species had been adequately sampled by the time half the individuals had been sampled.

The curves for Costa Rican moth species and human oral bacteria never completely leveled off, showing that more sampling would be needed to estimate those communities' species richness.

The species richness of eastern Amazon soil bacteria was so high that each sample contained new species.

Figure 16.10 Communities Differ in Their Species Accumulation Curves Hughes and colleagues found that communities of five different types varied greatly in the sampling effort that would be needed to estimate their species richness. The data sets were standardized by calculating for each data point the proportions of the total number of individuals and species that had been sampled up to that point. (After Hughes et al. 2001.)

? Based on the graph, which of these communities would require more sampling to adequately estimate their species richness? Which would require very little additional sampling?

were sampled. Human oral bacteria and Costa Rican moth communities had species accumulation curves that never completely leveled off, suggesting that their species richness was high and that additional sampling would be required to achieve an approximation of that richness. Finally, the eastern Amazon soil bacterial community had a linear species accumulation curve, demonstrating that each new sample resulted in the observation of many new bacterial species. Based on this analysis, it is clear that the sampling effort for tropical bacteria was well below that needed to adequately estimate species richness in these hyperdiverse communities.

A comparison of species accumulation curves not only provides valuable insight into the differences in species richness among communities, but also demonstrates the influence of the spatial scale at which sampling is carried out. For example, if we were to sample the richness of bacteria in tropical soils at the same scale at which we sampled Costa Rican moths, the bacterial richness would be immense in comparison. But such comparisons do suggest that our ability to sample all the bacteria in the human mouth is roughly equivalent to our ability to sample all the moth species in a few hundred square kilometers of tropical forest. The work of Hughes et al. also reminds us how little we know about the community structural characteristics of rarely sampled assemblages, such as microbial communities.

Species composition tells us who is in the community

A final element of a community's structure is its **species composition**: the identity of the species present in the community. Species composition is an obvious but important characteristic that is not revealed in species diversity indices. For example, two communities might have the same species diversity value but have completely different members. In the case of the bacterial communities in Scottish pastures that we considered in Web Extension 16.1, although diversity indices for two communities were nearly identical, their composition differed. Five taxonomic groups of bacteria out of the 20 the researchers found were present in one or the other pasture, but not in both.

In many ways, community structure is the starting point for more interesting questions: How do species in the community interact with one another? Do some species play greater roles in the community than others? How is species diversity maintained? How does this information shape our view of communities in terms of conservation and the services they provide to humans? Let's move from the rather static view of communities as groups of species occurring together in space and time to a more active view of them as complex networks of species with connections and interactions that vary in strength, direction, and significance.

CONCEPT 16.3

Communities can be characterized by complex networks of direct and indirect interactions that vary in strength and direction.

Interactions of Multiple Species

The way we think about species interactions changes dramatically when we consider that they are embedded in a community of multiple interactors. Instead of a particular species experiencing a single, direct interaction with another species, we are now dealing with multiple species interactions that generate a multitude of connections—some direct, but many indirect (**Figure 16.11**). **Direct interactions** occur between two species and include trophic and non-trophic interactions—the interactions we explored in Unit 4. **Indirect interactions** occur when the relationship between two species is mediated by a third (or more) species. The simple addition of a third species to a two-species interaction creates many more effects, both direct and indirect, which have the potential to change the outcome of the original interaction dramatically.

A social interaction analogy fits well here. Consider Figure 16.11B. Let's say you are person A and you have a good friend (person B) with whom you interact well. Now, suppose this friend meets another person (person C) who dominates your friend's time. They go to dinner, the movies, and bowling—all things you and your friend enjoyed together—without you. At some point, this new friend might begin to interfere with your friendship, possibly compromising it to the point at which it becomes antagonistic. Sadly, the indirect effect of person C changes your friendship irreparably. You might say that "the friend of my friend is my enemy." Likewise, one could imagine gaining a friend indirectly, if your foe had a foe (in this case, "the enemy of my enemy is my friend"). The point is that simply adding another person to the

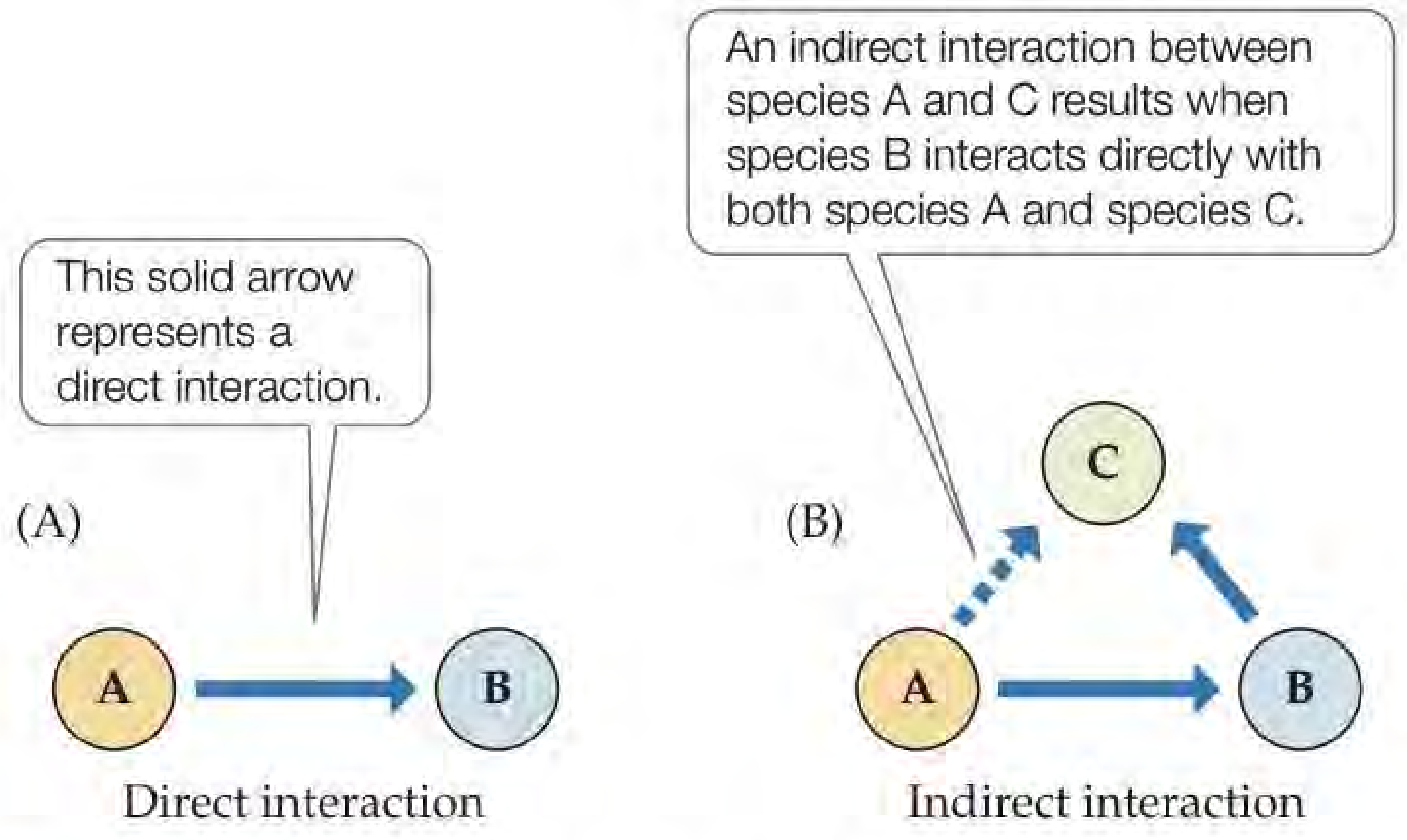


Figure 16.11 Direct and Indirect Species Interactions (A) A direct interaction occurs between two species. (B) An indirect interaction (dashed arrow) occurs when the direct interaction between two species is mediated by a third species.

social circle can change the outcome of your relationship completely. The same is true of species interactions when we view them in the community context, rather than as isolated entities.

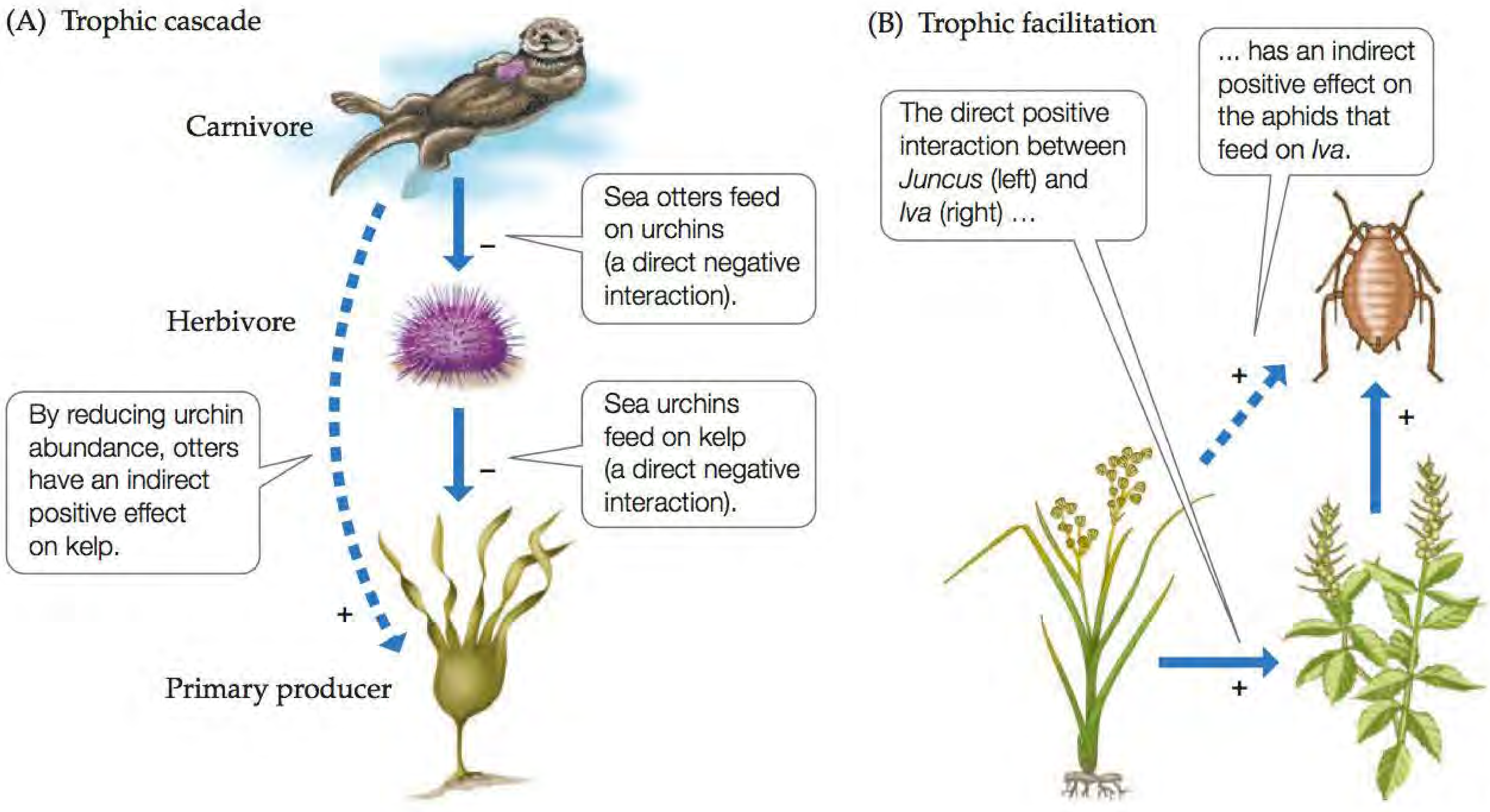
Indirect species interactions can have large effects

Charles Darwin was one of the first to convey the importance of indirect interactions. In *The Origin of Species* (1859), Darwin set the scene by describing the role of bees in flower pollination, and hence in seed production, among native plants in the region of England where he lived. In the book, he established the hypothesis that the number of bees is dependent on the number of field mice, which prey on the combs and nests of bees. Mice, in turn, are eaten by cats, leading Darwin to muse, "Hence it is quite credible that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district!" (Darwin 1859, p. 59).

It is only recently that the sheer number and variety of effects of indirect interactions have been documented (Menge 1995). In many cases, indirect effects are discovered almost by accident when species are experimentally removed to study the strength of a direct negative interaction such as predation or competition. A good example of this type of indirect effect comes in the form of an interaction web called a trophic cascade (**Figure 16.12A**). A **trophic cascade** occurs when the rate of consumption at one trophic level results in a change in species abundance or composition at lower trophic levels. For example, when a carnivore eats an herbivore (having a direct negative effect on the herbivore) and decreases its abundance, there may be an indirect positive effect on a primary producer that was eaten by that herbivore. One of the best-known examples is the indirect regulation of kelp forests by the sea otter (*Enhydra lutris*) through its direct interaction with sea urchins (*Strongylocentrotus* spp.) along the west coast of North America (see the Case Study Revisited in Chapter 9) (Simenstad et al. 1978). Two direct trophic interactions, those of sea otters feeding on sea urchins and sea urchins feeding on kelp, generate indirect positive effects, including that of sea otters on kelp (via their reduction of urchin abundance) and that of kelp on sea otters (via the food they provide for the urchins). Furthermore, the kelp can positively affect the abundances of other seaweeds, which serve as habitat and food for many marine invertebrates and fishes. The indirect effects generated in this simple food web are just as important as the direct effects in determining whether the ecosystem will be a kelp forest or an urchin barren (see Figure 9.20). We will explore the effects of indirect interactions on species diversity (Chapter 19), food webs (Chapter 21), and ecosystem management (Chapter 24) in more detail later in the book.

Indirect effects can also emerge from direct positive interactions called trophic facilitations. A **trophic facilitation** occurs when a consumer is indirectly helped by a positive interaction between its prey and another species (**Figure 16.12B**). An example of this type of indirect effect was demonstrated by Sally Hacker (Oregon State University) and Mark Bertness (Brown University), who studied salt marsh plant and insect interaction webs in New England. Their research showed that a commensal interaction between two salt marsh plants—a rush, *Juncus gerardii*, and a shrub, *Iva frutescens*—has important indirect effects on aphids feeding on *Iva* (Hacker and Bertness 1996).

To explore these findings in greater detail, let's first consider the commensal interaction between the two



(A) Trophic cascade

Sea otters feed on urchins (a direct negative interaction).

Sea urchins feed on kelp (a direct negative interaction).

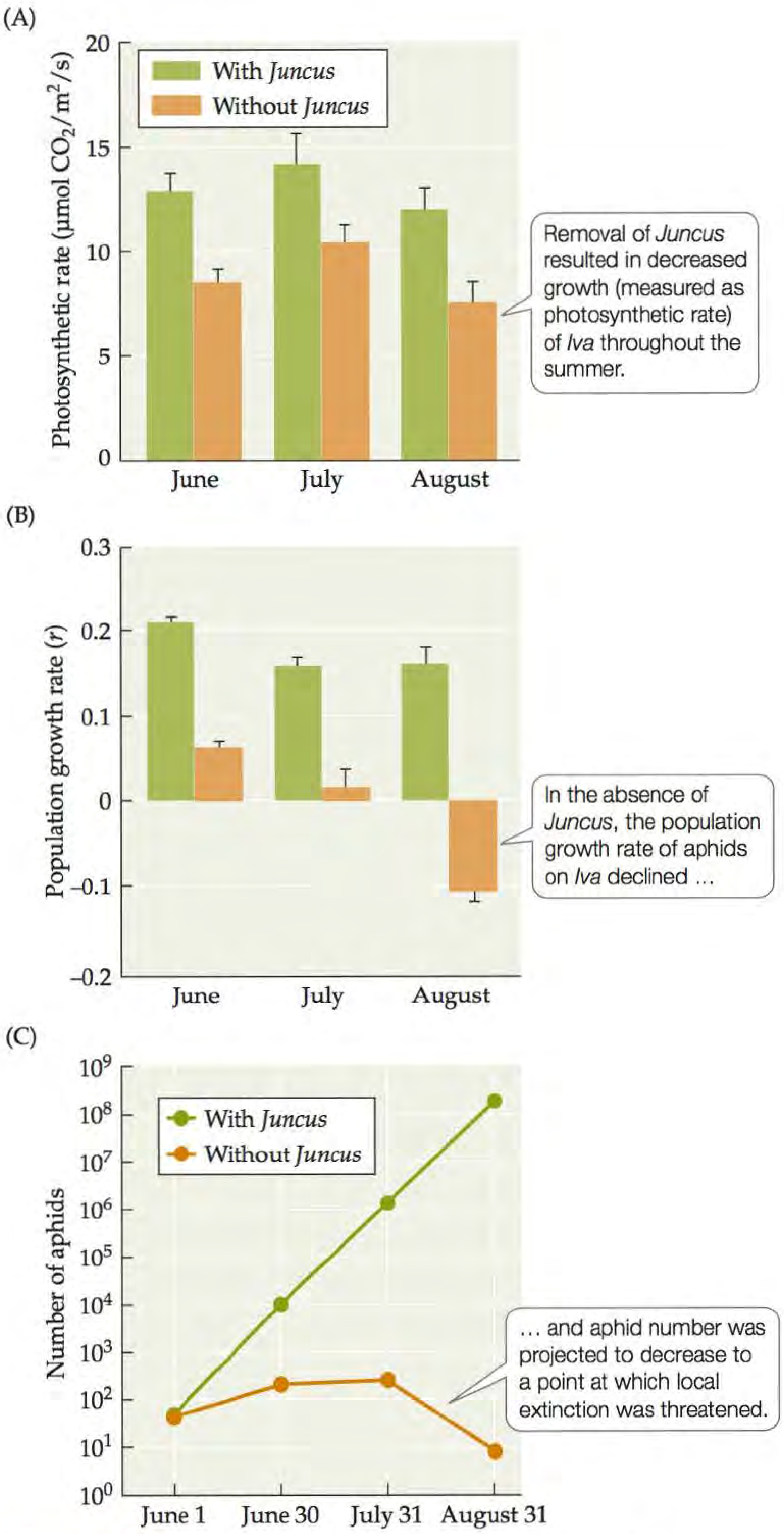
By reducing urchin abundance, otters have an indirect positive effect on kelp.

(B) Trophic facilitation

The direct positive interaction between *Juncus* (left) and *Iva* (right) …

… has an indirect positive effect on the aphids that feed on *Iva*.

Figure 16.12 Indirect Effects in Interaction Webs (A) A trophic cascade occurs when a carnivore feeds on an herbivore and thus has an indirect positive effect on a primary producer that is eaten by that herbivore. (B) Trophic facilitation occurs when a consumer is indirectly helped by a positive interaction between its prey and another species.



Removal of *Juncus* resulted in decreased growth (measured as photosynthetic rate) of *Iva* throughout the summer.

In the absence of *Juncus*, the population growth rate of aphids on *Iva* declined …

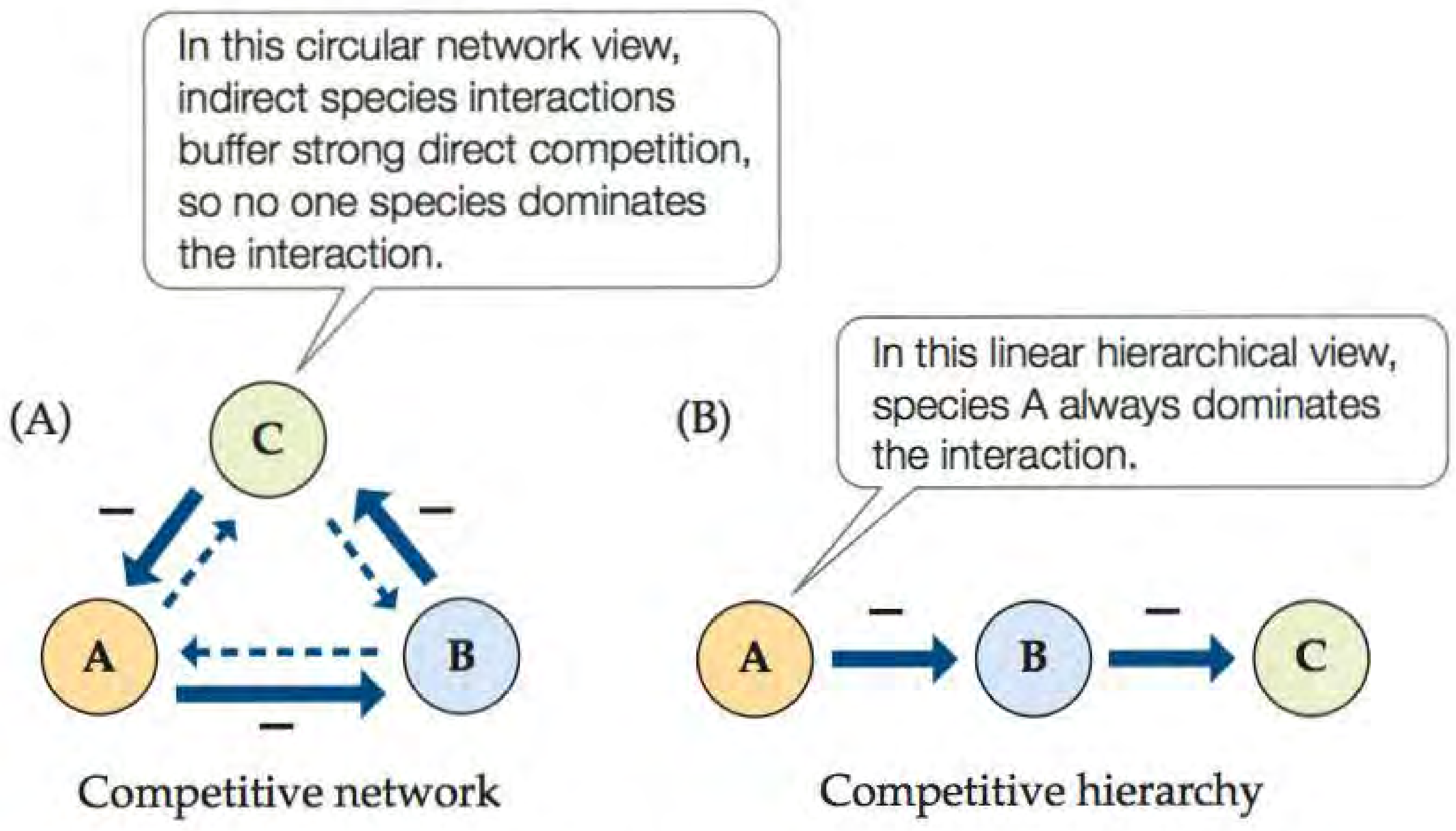
… and aphid number was projected to decrease to a point at which local extinction was threatened.

Figure 16.13 Results of Trophic Facilitation in a New England Salt Marsh Removal experiments demonstrated that aphids are indirectly facilitated by the rush *Juncus gerardii*, which has a direct positive effect on the shrub *Iva frutescens*, on which the aphids feed. (A) Photosynthetic rate of *Iva* with and without *Juncus*. (B) Growth rate of aphid populations with and without *Juncus*. (C) Projected numbers of aphids with and without *Juncus*. Error bars show one SE of the mean. (After Hacker and Bertness 1996.)

plant species. When *Juncus* was experimentally removed, the growth rate of *Iva* decreased (**Figure 16.13A**). In contrast, removing *Iva* had no effect on *Juncus*. In the absence of *Juncus*, soil salinity increased and oxygen content decreased considerably around *Iva*, suggesting that the presence of *Juncus* ameliorated harsh physical conditions for *Iva*. *Juncus*, by shading the soil surface and thus decreasing water evaporation from the surface of the marsh, decreases salt buildup. *Juncus* also has specialized tissue called aerenchyma, through which oxygen can move into the belowground parts of the plant, thus keeping it from "drowning" during daily high tides. Some of the oxygen "leaks" out of the plant and can be used by other neighboring plants, such as *Iva*.

To understand the importance of this direct positive interaction, Hacker and Bertness (1996) measured the population growth rate of aphids on *Iva* growing with and without *Juncus*. They found that aphids had a much harder time finding shrubs in the presence of the rush but that once they did, their population growth rates were significantly higher (**Figure 16.13B**). Using the exponential growth equation, they predicted that aphids would become locally extinct in the salt marsh without the indirect positive effects of *Juncus* (**Figure 16.13C**). It is clear from this example that interactions in trophic facilitation webs can have both positive effects (as when *Juncus* improves soil conditions for *Iva*) and negative effects (as when *Juncus* facilitates aphids that feed on *Iva*), but it is the sum total of these effects that determines whether the interaction is beneficial or not. Given that the ultimate fate of *Iva* without *Juncus* is death, the positive effects greatly outweigh the negative.

Finally, important indirect effects can arise from interactions among multiple species at one trophic level (i.e., the horizontal interactions in Figure 16.5B). Buss and Jackson (1979), looking for an explanation for the coexistence of competitors, hypothesized that **competitive networks**—competitive interactions among multiple species in which every species has a negative effect on every other species—might be important in maintaining species richness in communities. A network, as opposed to a hierarchy, is an interaction web that is circular rather than linear (**Figure 16.14A**). The idea is that networks



In this circular network view, indirect species interactions buffer strong direct competition, so no one species dominates the interaction.

In this linear hierarchical view, species A always dominates the interaction.

Competitive network

Competitive hierarchy

Figure 16.14 Competitive Networks versus Competitive Hierarchies

of interacting species indirectly buffer strong direct competition, thus making competitive interactions weaker and more diffuse. So, for example, species A may have the potential to outcompete species B, and species B may have the potential to outcompete species C, but because species C also has the potential to outcompete species A, no one species dominates the interaction. This is clearly an example of the "enemy of my enemy is my friend" effect described earlier. All else being equal, a hierarchical view of competition, with species A outcompeting B and B outcompeting C (**Figure 16.14B**), always results in species A dominating the interaction.

Buss and Jackson tested this hypothesis using encrusting invertebrates and algae that live on the undersides of coral reefs in Jamaica (**Figure 16.15**). These species compete for space by growing over one another. The researchers collected samples at the margins between species, where one species overgrows another, for as many pairs of individuals of different species as possible to determine the proportion of wins (species on top) to losses (species on the bottom) for each interaction. Their results showed that every species both overgrew and was overgrown by at least one other species and that no one species consistently won the competition. The species interacted in a circular network rather than a linear hierarchy. These observations demonstrate how competitive networks, by fostering diffuse and indirect interactions, can promote diversity in communities.

Figure 16.15 Competitive Networks in Coral Reef Communities Encrusting invertebrates and algae compete for space on coral reefs by overgrowing one another, but no one species consistently "wins" this competition.

Species interactions vary greatly in strength and direction

It should be clear by now that species interactions in a community vary greatly in their strength and direction. Some species have a strong negative or positive effect on the community, while others probably have little or no effect. **Interaction strength**, the effect of one species on the abundance of another species, can be measured experimentally by removing one species (referred to as the *interactor species*) from the community and looking at the effect on the other species (the *target species*, as described in **Ecological Toolkit 16.1**). If the removal of the interactor species results in a large decrease in the target species, we know that the interaction is strong and positive. However, if the abundance of the target species increases significantly after removal, we know that the interactor species has a strong negative effect on the target species.

The interaction strength "dynamic" (i.e., the relative proportion of strong to weak interactions or positive to negative interactions) is not well understood for any community, because of the numbers of species involved and the many indirect interactions that emerge. As you will see throughout Unit 5, however, we can get an idea of what species are "in charge" of communities through both observations and experiments.

There are some large or abundant species, such as trees, that are likely to have large community-wide effects by virtue of providing habitat or food for other species. They may also be good competitors for space, nutrients, or light. These species, known as **foundation species** (Dayton 1971), have large effects on other species, and thus on the species diversity of communities, by virtue of their considerable size and abundance (**Figure 16.16**).

Some foundation species act by "bioengineering" their environment. These species, known as **ecosystem**

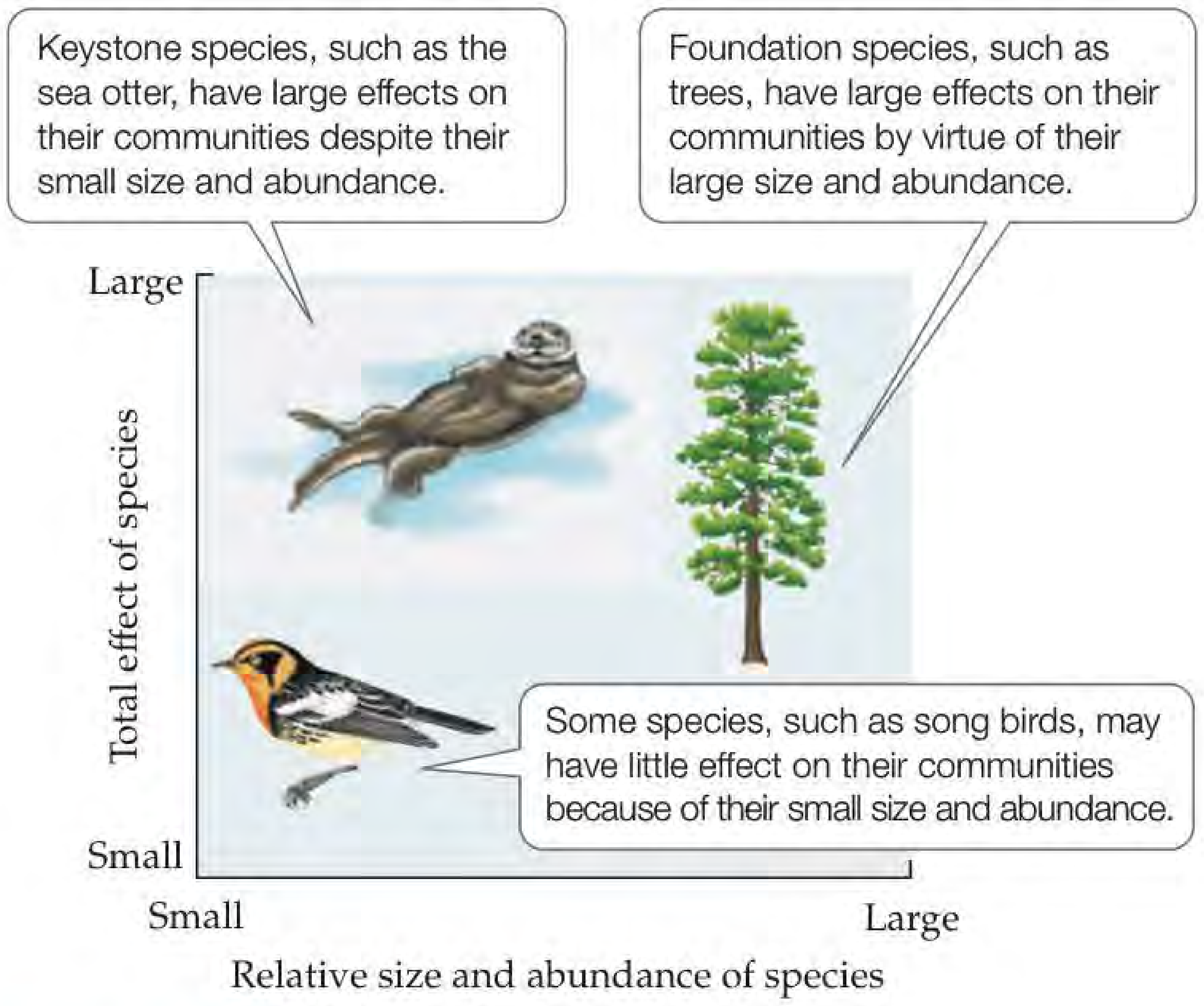


Figure 16.16 Foundation versus Keystone Species Species that have large effects on their communities may or may not do so by virtue of their large size and abundance. Some species (lower left-hand corner) have little overall effect relative to their size and abundance, especially if they are redundant in the community. (After Power et al. 1996b.)

ECOLOGICAL TOOLKIT 16.1 Measurements of Interaction Strength

We can measure interaction strength by experimentally manipulating species interactions. The usual procedure involves the removal (or sometimes the addition) of one of the species involved in the interaction (the interactor species) and measurement of the response of the other species (the target species). There are several different ways to calculate interaction strength, but the most common is to determine the per capita interaction strength using the following equation:

$$\text{per capita interaction strength} = \ln\frac{\left(\frac{C}{E}\right)}{I}$$

where

ln = the natural logarithm

C = the number of target individuals in the presence of the interactor

E = the number of target individuals in the absence of the interactor

I = the number of interactor individuals

Interaction strength can vary depending on the environmental context in which the interaction is measured. For example, Menge et al. (1996) measured the interaction strength of sea star (*Pisaster ochraceus*) predation on mussels (*Mytilus trossulus*) in wave-exposed versus wave-protected areas of the shoreline at Strawberry Hill on the coast of Oregon (see figure). Sea stars were excluded from some mussel beds by cages in both exposed and protected areas. At the end of the experiment, the numbers of mussels in the cages (*E*) were compared with the numbers of mussels in control plots (*C*) that had been exposed to sea star predation (see figure). The value of *I* was determined by counting all the sea stars near the plots in each type of mussel bed (exposed and protected). An equation similar to the one above was used to calculate the per capita interaction strength of sea star predation on mussels. The results (see figure) showed that interaction strength was greater in wave-protected than in wave-exposed areas. Sea stars probably cannot feed as efficiently when subjected to the crashing waves characteristic of wave-exposed areas. Thus, this study demonstrates the importance of environmental context (in this case, wave exposure) to the strength of species interactions. It also shows how those interactions can change over relatively small spatial scales (e.g., between wave-exposed and wave-protected areas of the Strawberry Hill shoreline).

How Much Does Predation by Sea Stars Matter? It Depends (Top left) The shoreline at Strawberry Hill, Oregon. Plots with (bottom left) and without (middle) cages that excluded sea stars were set up in both wave-exposed and wave-protected areas along the shoreline. (Bottom right) When mussels were counted and interaction strengths calculated, the results showed that interaction strength was greater in protected than in exposed areas. Error bars show one SE of the mean. (Graph after Menge et al. 1996.)

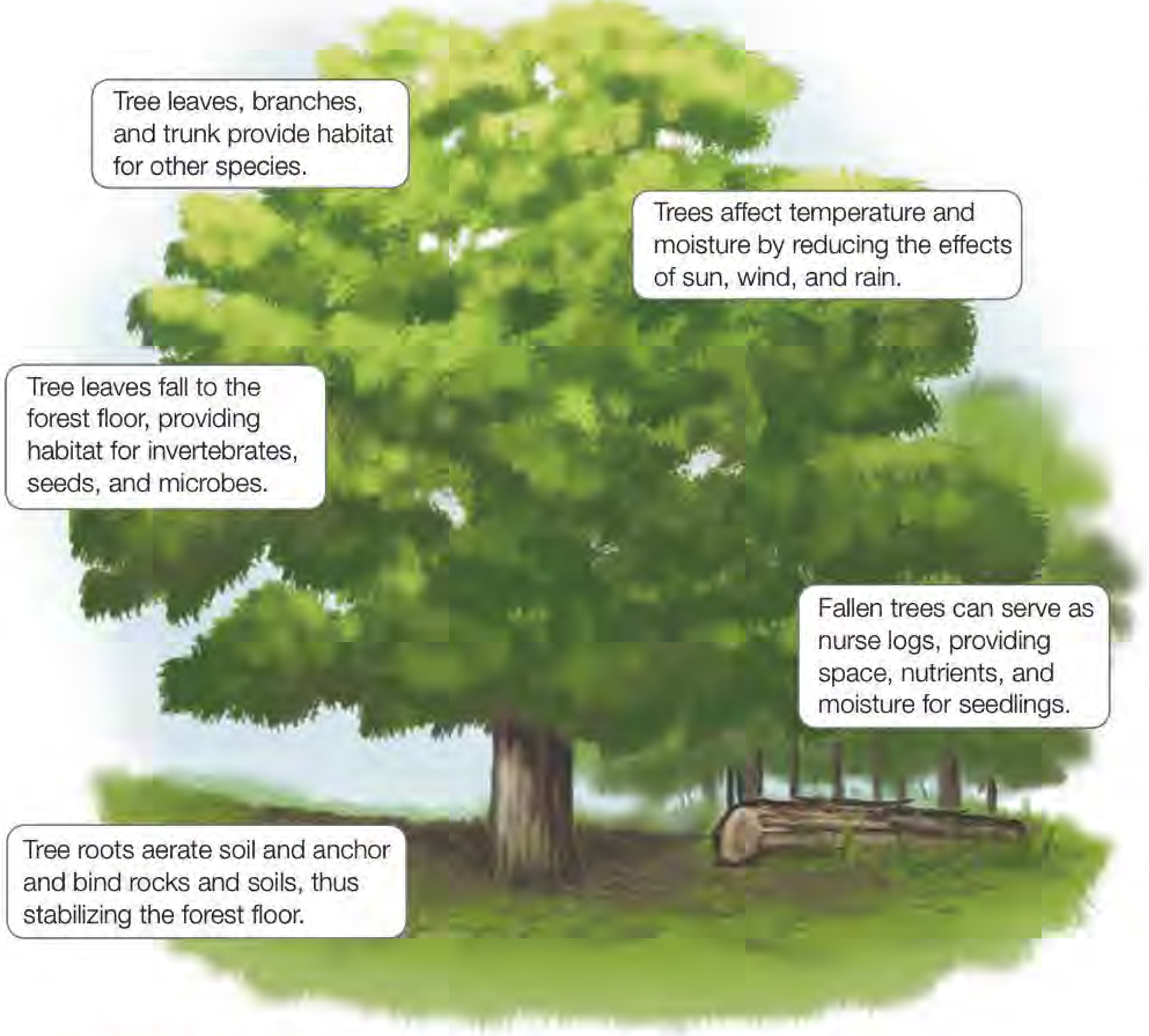


Figure 16.17 Trees Are Foundation and Ecosystem Engineering Species Trees not only provide food for and compete with other species, but also act as ecosystem engineers by creating, modifying, or maintaining physical habitat for themselves and other species. (After Jones et al. 1997.)

engineers (Jones et al. 1994), are able to create, modify, or maintain physical habitat for themselves and other species. Consider the simple example of the trees mentioned above. Just like any other species, trees provide food for other organisms and compete for resources. However, trees also engineer their environment in subtle but important ways (**Figure 16.17**). The trunk, branches, and leaves of a tree provide habitat for a multitude of species, from birds to insects to lichens. The physical structure of the tree reduces sunlight, wind, and rainfall, influencing temperature and moisture levels in the forest. The roots of the tree can increase weathering and aeration of the soil, and they can stabilize surrounding substrates. The tree's leaves fall to the forest floor, where they add moisture and nutrients to the soil and provide habitat for soil-dwelling invertebrates, seeds, and microorganisms. If the tree falls, it can become a "nurse log," providing space, nutrients, and moisture for tree seedlings. Thus, trees can have a large physical influence on the structure of a forest community, which obviously changes over time as trees grow, mature, and die.

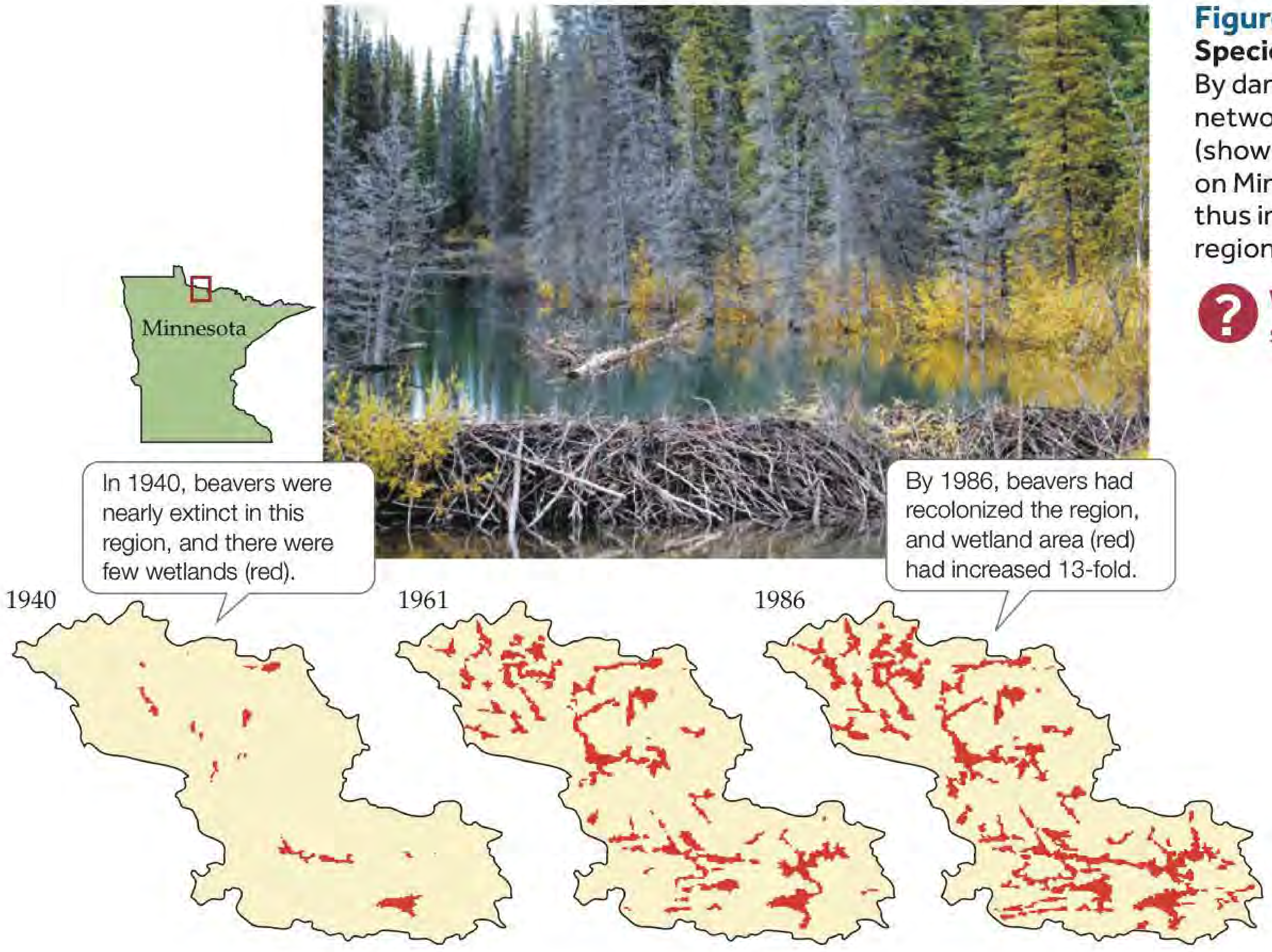
Other strong interactors, so-called **keystone species**, have large effects not because of their abundance, but because of the vital roles they play in their communities. They differ from foundation species in that their effect is large in proportion to their size and abundance (see Figure 16.16). Keystone species usually influence community structure indirectly, via trophic means, as we saw in the case of sea otters (see Figure 16.12A and Chapter 9). Sea otters are considered keystone species because, by preying on sea urchins, they indirectly enhance the presence of kelp, which provides important habitat for many other species. We will consider the role of keystone species in more detail in Chapter 21 and the Case Study Revisited in Chapter 24.

There are also keystone species that act as ecosystem engineers. A great example is the beaver, a species in which just a few individuals can have dramatic effects on the landscape. Beavers dam streams with cut trees and woody debris. Very quickly, flooding ensues and sediment accumulates as the increasing number of woody obstacles slows the water flow. Eventually, the once swiftly flowing stream is replaced by a wetland, containing plants that can deal with flood conditions; plants that cannot do so, such as trees, are lost from the community. At the landscape level, by creating a mosaic of wetlands within a larger forested community, beavers can increase regional species diversity significantly (**Figure 16.18**). Naiman et al. (1988) showed that there was a 13-fold increase in wetland area in one region of Minnesota (from roughly 200 to 2,600 ha) when beavers were allowed to recolonize areas where they had been hunted nearly to extinction some 60 years previously.

Finally, it is worth mentioning that there are species that play only a small role in a community's structure and function. Rather than being keystone species or ecosystem engineers, these species are more like bit players: they contribute to the overall diversity of the community, but their presence or absence has little significance for the ultimate regulation of the community (see Figure 16.16). Some of these species may be **redundant**—that is, they may have the same function in the community as other species within a larger functional group (see Figure 16.4C). Their loss from a community might have little effect as long as other species within the same functional group remain present. We will discuss the role of species in community regulation in more detail in Chapter 19.

Environmental context can change the outcome of species interactions

As we have seen in this section, interactions among species can vary in strength and direction, and their outcomes are highly dependent on the influence of each of the species in the community. As we saw in Unit 4 and Ecological Toolkit 16.1, another important factor in the



In 1940, beavers were nearly extinct in this region, and there were few wetlands (red).

By 1986, beavers had recolonized the region, and wetland area (red) had increased 13-fold.

Figure 16.18 **Beavers Are Keystone Species and Ecosystem Engineers** By damming streams, beavers created networks of different types of wetlands (shown in red) in a 45 km^2 watershed on Minnesota's Kabetogama Peninsula, thus increasing biodiversity within the region. (After Naiman et al. 1988.)

? Why are beavers both keystone species and ecosystem engineers?

outcome of species interactions is the environmental context in which they occur. For example, under benign environmental conditions that are favorable for population growth, it makes sense that species will thrive and be limited by resources and will therefore engage in negative interactions such as competition or predation. Under harsh environmental conditions, species will naturally be more strongly limited by physical factors and will therefore interact either weakly or positively with other species.

This view of species interactions as *context-dependent*, or changeable under different environmental conditions, is relatively new to ecology, but a number of important examples of context dependence exist. Most of these examples involve keystone or foundation species that play important roles in their communities in one context, but not in another. Mary Power, a professor at the University of California, Berkeley, who works on stream communities in Northern California, has shown that the role of fish predators [roach (*Hesperoleucas symmetricus*) and steelhead (*Oncorhynchus mykiss*)] changes from year to year. The role of these predators shifts from that of keystone species following winters of scouring floods to that of weak interactors during years with winter droughts and in places where flood control is operating (Power et al. 2008).

In the Northern California rivers where Power works, there is a natural winter flood regime that produces dramatic population cycles of the green filamentous alga *Cladophora glomerata*. In most years, scouring winter floods remove most of the inhabitants—particularly armored herbivorous insects such as large caddisfly larvae—from the river bottom. In the following spring, there are large blooms of *Cladophora*. Increased light and nutrients and the lack of invertebrate herbivores allow *Cladophora* mats to grow profusely over the rocks, producing filaments up to 8 m (26 feet) long. By midsummer, these mats detach from the rocks and cover large portions of the river, at which time midge larvae, which feed on the floating alga and use it to weave small homes, increase in number. The midges are fed on by small fish and damselfly larvae, which in turn are eaten by steelhead and roach (a trophic cascade with four levels; **Figure 16.19A**). The steelhead and roach are able to decrease the size of the algal mats by eating small fish and damselfly larvae, which feed on midge larvae, which feed on the mats. The roach also feed on the algae directly, but only to a small degree.

During drought years, however, and in rivers where flood control is operating, flooding and scouring of the river bottom do not occur. In those years, *Cladophora* persists but does not form large, lush mats. Power and colleagues showed that this change was due to the presence of more armored herbivorous insects, which were not removed by floods and which ate the *Cladophora* while it was still attached to the rocks. This interaction led to declines in *Cladophora* and the loss of the detachment phase of the alga. The armored insects are much less susceptible

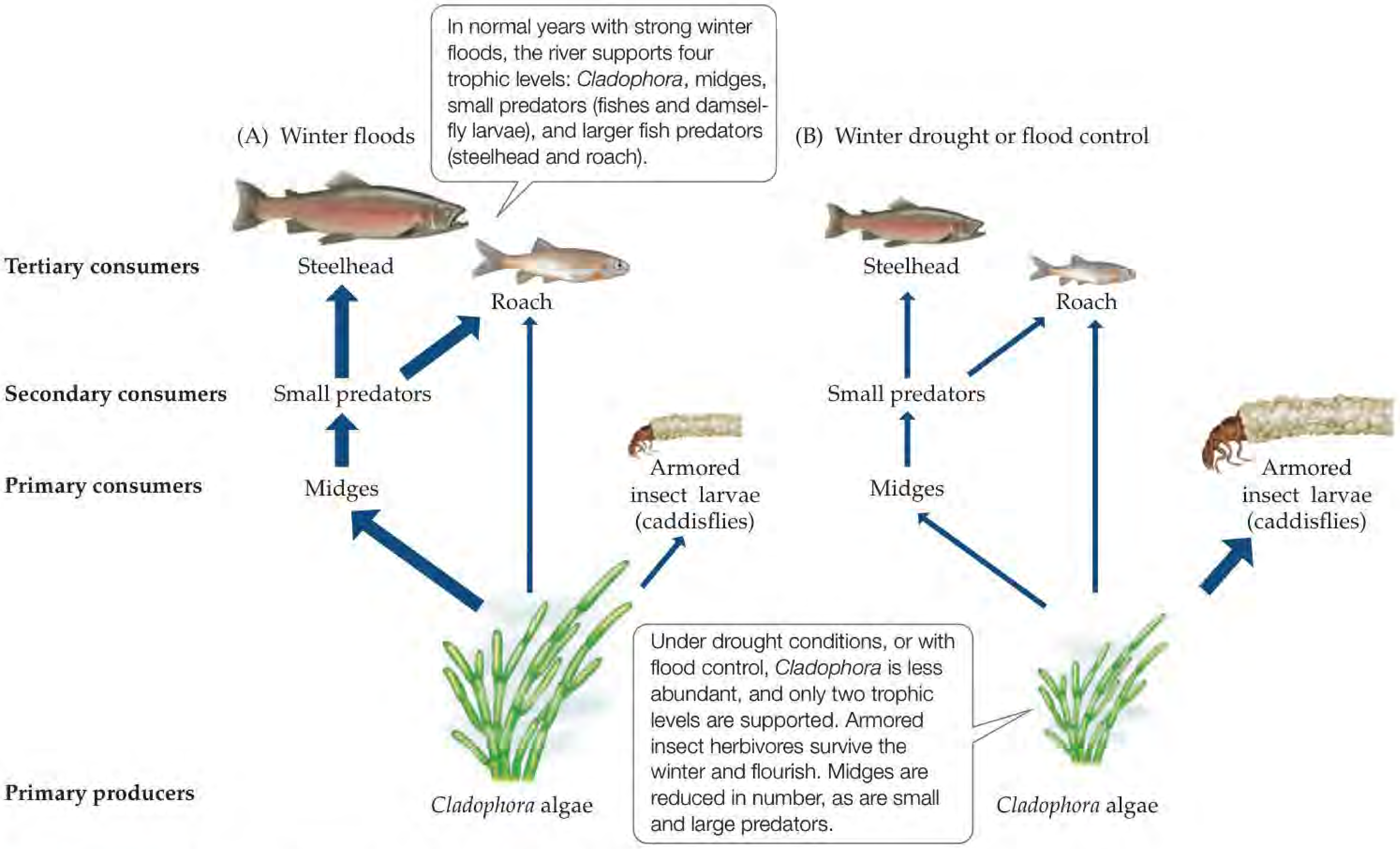


Figure 16.19 Context Dependence in River Food Webs Environmental changes alter the relative importance of different trophic levels in the Eel River of Northern California during winter floods (A) and winter drought or flood control conditions (B). Wider arrows represent stronger interactions. (After Power et al. 1996a.)

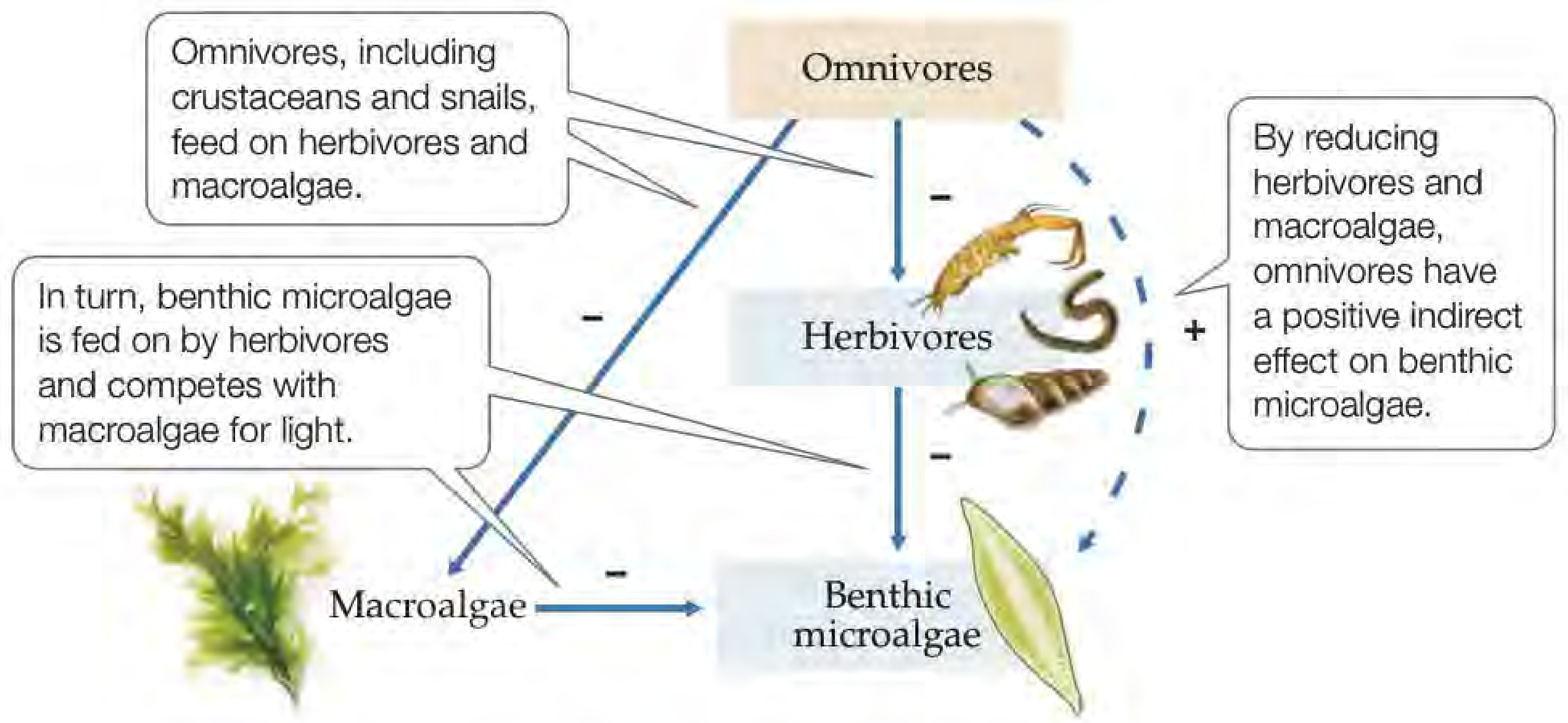
to predation than the midges and thus are not controlled by higher trophic levels. In essence, the typical river food web with four trophic levels is converted into a two-level food web during drought years, and the steelhead and roach, which in flood years are keystone predators, become minor players in the food web (**Figure 16.19B**).

CLIMATE CHANGE CONNECTION

Context Dependence of Ocean Acidification One emerging environmental context that will affect communities is ocean acidification. Estimates show that oceans are absorbing about 48% of all atmospheric CO_2. Marine primary producers use some of the human-created CO_2 in photosynthesis, but the remainder reacts chemically with seawater, lowering its pH and causing oceans to become more acidic (see Concept 25.1). Ocean acidification can have negative effects on calcifying organisms such as corals, mollusks, and crustaceans, which rely on calcium carbonate for the accretion and maintenance of their external shells. But the negative effects of increasing CO_2 and acidification are not universal. For example, primary producers such as seagrasses, algae, and phytoplankton are known to increase their productivity under elevated CO_2. Although the effects of ocean acidification on the physiology of single species is a growing field of study, much less is known about how a world with a lower pH will affect the structure and function of communities. Moreover, along with the acidification of oceans, temperatures are increasing, creating multiple stressors. As a result, marine ecologists are asking, How will species interactions, both direct and indirect, be influenced by ocean acidification?

Christian Alsterberg and his colleagues (2013) considered how a food web in an estuarine community on the western coast of Sweden was influenced by ocean acidification and warming. The researchers chose to focus on single-celled microalgae living in the sediments and their interactions with macroalgae and consumers. Under normal conditions in this estuarine system, omnivores (i.e., a guild of medium-sized crustaceans and snails that feed on two trophic levels) increase the productivity of benthic microalgae in two ways: (1) they increase the light available to microalgae by feeding on macroalgae, and (2) they prey on herbivores of microalgae (i.e., a guild of small crustaceans, snails, and worms) (**Figure 16.20A**). To estimate the importance of ocean acidification and increased warming in a multispecies food web, the researchers conducted an experiment in which

(A) Food web under ambient conditions



(B) Food web under ocean acidification and warming

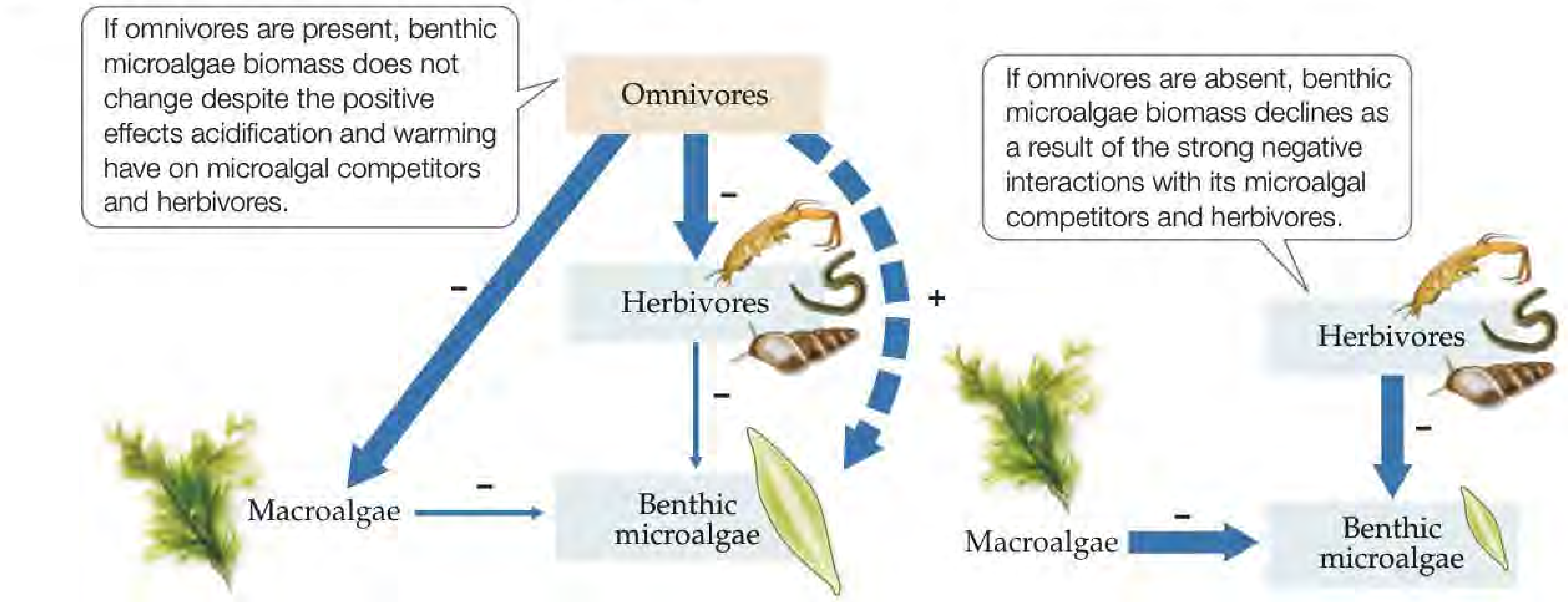


Figure 16.20 Food Webs in an Acidic and Warming World (A) The interaction web of species in an estuarine community off the western coast of Sweden. (B) The effects of ocean acidification and warming on the interaction web with (left) and without (right) omnivores. The biomass of benthic microalgae did not change with omnivores (left) but declined without them (right). Thicker arrows represent stronger interactions. (After Alsterberg et al. 2013.)

CO_2 and temperature, as well as omnivores, were manipulated in mesocosms (in this case, large aquariums). After a 5-week period, the experiment showed that with elevated CO_2 and temperature, macroalgae and herbivores increased in biomass. When omnivores were present, this greater biomass was consumed by omnivores, resulting in a stronger negative interaction between them and their food sources (**Figure 16.20B**). The stronger negative interaction lead to a stronger indirect positive effect for benthic microalgae. As a result, there was no change in benthic microalgae abundance despite the elevated CO_2 and temperature conditions. However, when omnivores were absent, macroalgae and herbivores were not kept in check, and their negative interactions with benthic microalgae grew even stronger, resulting in the decline of benthic microalgae. Thus, this experiment showed that consumers were able to modulate the negative effects of elevated CO_2 and temperature on primary producers in this estuarine system. This study highlights the importance of understanding how organisms, placed within the context of their food web communities, gain some resilience against the effects of climate change.

In upcoming chapters, we will consider in much more detail the effects of physical and biological factors on the outcome of species interactions and ultimately on the diversity of communities.

A CASE STUDY REVISITED

“Killer Algae!”

The introduction of *Caulerpa taxifolia* into the Mediterranean Sea in the early 1980s set in motion a series of unfortunate events that resulted in large carpets of fluorescent green algae dominating formerly species-rich nearshore marine communities. *Caulerpa* thrived because humans facilitated its dispersal and its physiological tolerance. Even in the early stages of the invasion, Meinesz documented the seaweed in at least three types of communities, with different species compositions, on rocky, sandy, and muddy substrates. Together, these communities are home to several hundred species of algae and three marine flowering plants, as well as a number of animal species. Once *Caulerpa* arrived, native competitor and herbivore species were unable to keep it from spreading.

The invasion of *Caulerpa* has changed the ways in which native species interact with one another, and thus the structure and function of the native communities. One obvious consequence of the presence of *Caulerpa* is the

Figure 16.21 A Mediterranean Seagrass Meadow Native communities like this one, dominated by the seagrass *Posidonia oceanica*, can be replaced by invasive *Caulerpa taxifolia*. Compare this photograph with Figure 16.1.

decline of seagrass meadows dominated by *Posidonia oceanica* (**Figure 16.21**). This seagrass has been likened to an "underwater tree" because of its long life span and slow growth (patches grow to 3 m in diameter in 100 years). Just like forests, seagrass meadows support a multitude of species that use the vegetation as habitat. Research showed that *Posidonia* and *Caulerpa* have different growth cycles: *Posidonia* loses blades in summer, when *Caulerpa* is most productive. Over time, these asynchronous growth patterns result in *Caulerpa* overgrowing the existing seagrasses and establishing itself as the foundation species. Additional research has shown that *Caulerpa* acts as an ecosystem engineer, accumulating sediments around its roots more readily than *Posidonia*, which can change the species composition of the small invertebrates that live on the seafloor. Some surveys have revealed a significant drop in the numbers and sizes of fish using the communities invaded by *Caulerpa*, suggesting that these habitats may be less suitable for some commercially important species.

Future changes in Mediterranean seagrass meadows, and in the species dependent on them, will be difficult to predict, given the sheer number of species that are potentially affected by *Caulerpa*, the indirect effects that will be generated by changing interactions, and the relatively short time that has elapsed since the invasion began. A scientific approach, guided by a combination of theory and real-world observations, will be necessary if future predictions are to be made about the ultimate effect of *Caulerpa* on this potentially vanishing underwater community.

CONNECTIONS IN NATURE
Stopping Invasions Requires Commitment

Even though it may be too late to stop the invasion of *Caulerpa taxifolia* in the Mediterranean, the lessons learned there have been important in other regions of the world. In 2000, just as Meinesz was making progress in banning international trade of the alga, he received an e-mail from an environmental consultant in San Diego, California. While surveying eelgrass in a lagoon, she had noticed a large patch of what was later identified as *Caulerpa taxifolia*. Acting on Meinesz's recommendation, a team of scientists and managers from county, state, and federal agencies immediately assembled to design an eradication plan. This plan involved treating the alga with chlorine gas injected under tarps placed on top of algal patches. More than $1 million was initially budgeted for the project in 2000, but it eventually took 6 years and $7 million to eradicate the alga. The invasion was widely publicized, resulting in the discovery of another patch of *Caulerpa* in another lagoon near Los Angeles, which was also eradicated. The California experience is a rare success story only because immediate action was taken by scientists, managers, and policymakers to deal with the invasion before eradication became an ecological and fiscal impossibility.

To determine the origin of the *Caulerpa* that invaded California, molecular evidence was needed. This shift in the team's focus from communities to genes illustrates a point made in Chapter 1: ecologists must study interactions in nature across many levels of biological organization. The team sent specimens of the alga to geneticists at two universities, who analyzed the sequences of its ribosomal DNA and quickly determined that they were identical to those of *Caulerpa* from the Mediterranean, the Wilhelma Zoo (where the strain was first cultivated), and many other public aquariums around the world (Jousson et al. 2000). Unfortunately, it is still unknown how the species was introduced into the two California lagoons, but hypotheses range from amateur aquarists cleaning their tanks in the lagoons to an accidental release from aquariums on board a Saudi Arabian prince's yacht, which was being repainted in San Diego at about the time the alga probably arrived. Through the use of DNA analysis, it has been determined that the *Caulerpa* algae involved in subsequent invasions in Australia and Japan are genetically identical to the original German *Caulerpa taxifolia* strain. The molecular evidence makes it clear that the trade of this alga in aquarium circles poses a global threat to nearshore temperate marine environments. Legislation is now in place to ban the "killer alga" from a number of other countries where it has a good chance of invading successfully.

Summary

CONCEPT 16.1 Communities are groups of interacting species that occur together at the same place and time.

- Communities can be delineated by the characteristics of their physical environment or by biological characteristics, such as the presence of abundant species.
- Ecologists often use subsets of species to define and study communities because it is impractical to count or study all the species within a community, especially if they are small or undescribed.
- Subsets of species used to study communities include taxonomic groups, guilds, functional groups, and food and interaction webs.

CONCEPT 16.2 Species diversity and species composition are important descriptors of community structure.

- Species diversity, the most commonly used measure of community structure, is a combination of the number of species (species richness) and the abundances of those species relative to one another (species evenness).
- Communities can differ in the commonness or rarity of their species. Rank abundance curves allow one to plot the proportional abundance of each species relative to the others, from most abundant to least abundant.
- Species richness increases with increased sampling effort up to a certain point, at which additional samples reveal few or no new species.
- Species composition—the identity of the species present in a community—is an obvious but important characteristic of community structure that is not revealed in measures of species diversity.

CONCEPT 16.3 Communities can be characterized by complex networks of direct and indirect interactions that vary in strength and direction.

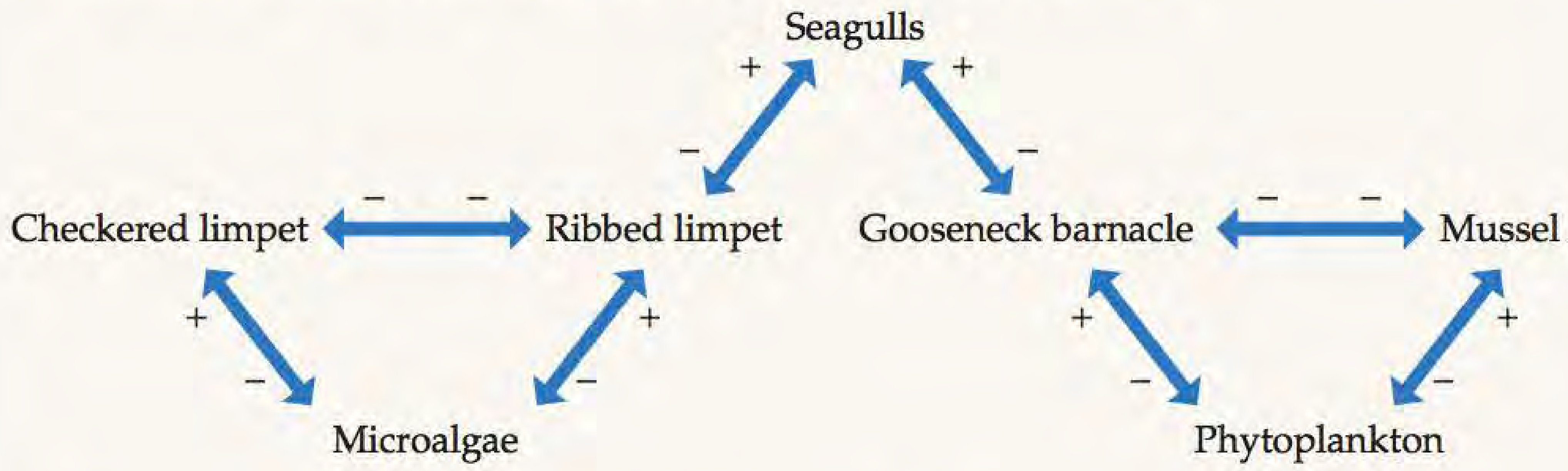
- Indirect species interactions, in which the relationship between two species is mediated by a third (or more) species, can have large effects on the outcomes of direct species interactions.
- Some species have a strong negative or positive effect on their communities, but others probably have little or no effect.
- Species that have large effects on their communities by virtue of their size and abundance are known as foundation species. Those that have large effects due to the roles they play in their communities are known as keystone species.
- Ecosystem engineers create, modify, or maintain physical habitat for themselves and other species.
- The environmental context, including climate change, can modify species interactions enough to change their outcome.

Review Questions

1. What is the formal definition of a community? Why is incorporating species interactions into that definition important?
2. Species diversity measurements take into account both species richness and species evenness. Why would these measurements be preferred to species richness alone? What do rank abundance curves add to one's knowledge about community structure?
3. Species vary in the strength of their interactions with other species. Species that interact strongly with other species include foundation species, keystone species, and ecosystem engineers. Describe the differences among these three types of species and give some examples. Can foundation and keystone species also be ecosystem engineers?

Hone Your Problem-Solving Skills

The interaction web shown in the figure is common in the rocky intertidal zone of Washington and Oregon. The arrows and their signs (+ or –) represent interactions that occur between species in the food web.



Suppose an ecologist wants to know the influence of seagulls on other members of the food web. She conducts a seagull removal experiment along a stretch of rocky shoreline to determine the interaction strength between seagulls and other members of the food web (with the exception of phytoplankton). The results are shown in the table. Determine the per capita interaction strength (IS) values between seagulls and each of the five species given in the table, using the equation in the Ecological Toolkit 16.1.

TARGET SPECIES	CONTROL (*C*) NUMBER OF INDIVIDUALS WITH SEAGULLS	EXPERIMENTAL (*E*) NUMBER OF INDIVIDUALS WITHOUT SEAGULLS	INTERACTORS (*I*) NUMBER OF SEAGULLS
Ribbed limpet	10	100	10
Gooseneck barnacle	500	3,000	10
Checkered limpet	100	50	10
Mussel	3,000	2,500	10
Microalgae	500	100	10

1. Based on your per capita interaction strength calculations, which species of prey is most negatively affected by seagulls? Which nonprey species is most affected by seagulls, and what is that affect?
2. Determine the four indirect effects that occur when seagulls are removed from the community. How does each species respond (i.e., does it increase, decrease, or not change in abundance) and through what type of interaction (i.e., herbivory or competition)?
3. Would the effect of seagulls be stronger or weaker on microalgae and phytoplankton if the mussel and checkered limpet were excluded from the food web? Explain.

ON THE COMPANION WEBSITE
ecology4e.sinauer.com

The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

16.1 "Rich without Wealth": Richness and Diversity in Marine Sediments

16.2 Diversity, the Spice of Life: Calculating Species Diversity

Web Extensions

16.1 Measuring Community Structure in Soil Bacterial Communities in Scotland

Change in Communities

17

A Natural Experiment of Mountainous Proportions: A Case Study

The eruption of Mount St. Helens was a defining moment for ecologists interested in natural catastrophes. Mount St. Helens, located in Washington State, is part of the geologically active Cascade Range, located in the Pacific Northwest region of North America (**Figure 17.1**). The once frosty-topped mountain had a rich diversity of ecological communities. If you had visited Mount St. Helens in the summer, you could have seen alpine meadows filled with colorful wildflowers and grazing elk. At lower elevations, you could have hiked across the cool fern- and moss-covered forest floor under massive old-growth trees. You could have swum in the blue, clear water of Spirit Lake, or fished along its shores. But a few minutes after 8:30 A.M. on May 18, 1980, all that was living on Mount St. Helens would be gone. On the north side of the mountain, a huge magma-filled bulge had been forming for months. The bulge gave way that morning in an explosive eruption and the largest avalanche in recorded history.

Photos of the eruption show that mud and rock flowed down the face of Mount St. Helens and were deposited tens of meters deep in some areas (**Figure 17.2**). The wave of debris that passed over Spirit Lake was 260 m (858 feet) deep and decreased the lake's water depth by 60 m (200 feet). The bulk of the avalanche traveled 23 km (14 miles) in about 10 minutes to the North Fork Toutle River, where it scoured the entire valley, from floor to rim, with material from the volcano and left a truly massive pile of tangled vegetation at its tail end. In addition to the avalanche, the blast produced a cloud of hot air that burned forests to ash near the mountain, blew down trees over a large area, and left dead but standing trees stretching for miles away from the mountain. Ash from the explosion blanketed forests, grasslands, and deserts located hundreds of kilometers away.

The destruction that ensued on that day created whole new habitats on Mount St. Helens, some of which were completely devoid of any living organisms. At one extreme, there was the Pumice Plain, a large, gently sloping moonscape of a place below the volcano, that had been pelted with hot, sterilizing pumice (see Figure 17.2). This harsh and geologically monotonic environment lacked life, or even organic matter, of any form. All life in Spirit Lake was extinguished, and huge amounts of woody debris were deposited there, some of which still floats on top of the lake today. But, not surprisingly, given the large forests that had surrounded the mountain, the majority of the landscape consisted of downed or denuded trees covered with rock, gravel, and mud tens of meters deep in some places (see Figure 17.2). Compared with the Pumice Plain, this blowdown zone had some hope of a biological legacy buried under the piles of trees and ash.

KEY CONCEPTS

CONCEPT 17.1 Agents of change act on communities across all temporal and spatial scales.

CONCEPT 17.2 Succession is the process of change in species composition over time as a result of abiotic and biotic agents of change.

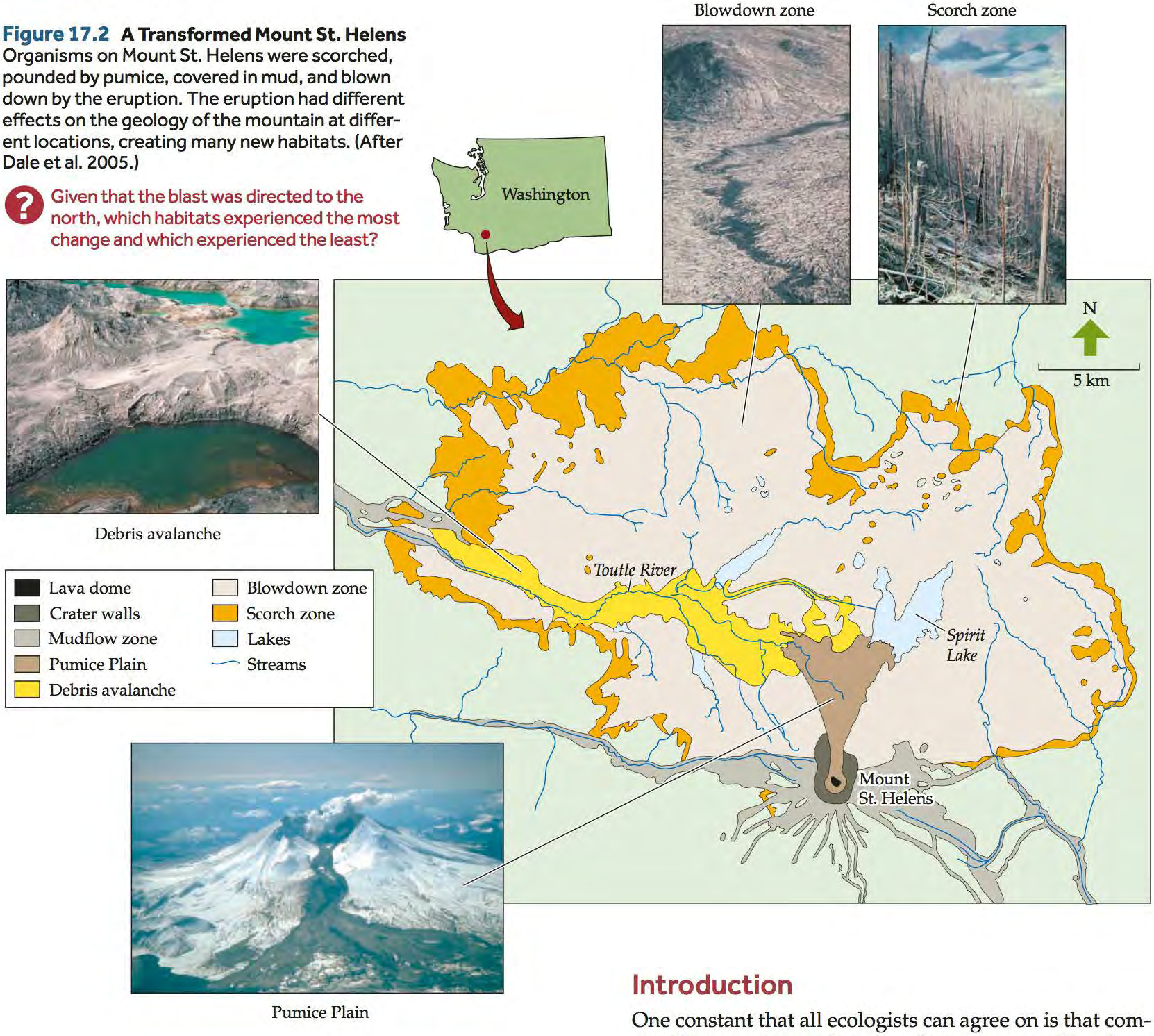
CONCEPT 17.3 Experimental work on succession shows its mechanisms to be diverse and context-dependent.

CONCEPT 17.4 Communities can follow different successional paths and display alternative states.

Figure 17.1 Once a Peaceful Mountain Before the eruption on May 18, 1980, Mount St. Helens, in southwestern Washington State, had a diversity of communities, including alpine meadows, old-growth forests, and lakes and streams.

Figure 17.2 A Transformed Mount St. Helens Organisms on Mount St. Helens were scorched, pounded by pumice, covered in mud, and blown down by the eruption. The eruption had different effects on the geology of the mountain at different locations, creating many new habitats. (After Dale et al. 2005.)

? Given that the blast was directed to the north, which habitats experienced the most change and which experienced the least?



Shortly after the eruption, helicopters delivered the first scientists to the mountain to begin studying what was essentially a natural experiment of epic proportions. A few lucky ecologists recorded the first observations of the sequence of biological changes that began soon after the eruption. Field excursions in the summers of 1980 and 1981 were organized, and valuable baseline data were collected. Now, more than 35 years later, hundreds of ecologists have studied the reemergence of life on Mount St. Helens. For many, the experience has been life-changing, and their careers have been consumed by research on this fascinating study system. Much of what has been learned has been unexpected and has changed the way we view the recovery of communities and the persistence of life on Earth.

Introduction

One constant that all ecologists can agree on is that communities are always changing. Some communities show more dynamism than others. For example, it is hard to imagine that desert communities, with their large, stoic cacti, have changed much over time. This is especially true if you compare deserts with, for example, high mountain streams or rocky intertidal zones, where species are coming and going on a regular basis. But community change is relative, and there is no question that even deserts change, though at a much slower pace than we might realize on the basis of one visit, or even one ecological study. In the words of one of the ecological maxims presented in Table 1.1, time matters.

Unfortunately, we humans cannot deny that our actions are becoming one of the strongest forces of change in communities, and that we are taking those actions with an imperfect understanding of their consequences. In this chapter, we will consider the agents of change in communities, from subtle to catastrophic, and their effects on community structure over time.

CONCEPT 17.1

Agents of change act on communities across all temporal and spatial scales.

Agents of Change

Let's imagine for a moment that you have the ability to look back in time and follow the change in a typical coral reef community in the Indian Ocean (**Figure 17.3**). Over the last few decades, you might have seen considerable change, both subtle and catastrophic. Subtle changes might include the slow rise to dominance of certain coral species, and the slow decline of others, due to the effects of competition, predation, and disease. More catastrophic changes might include the massive deaths of corals in the last decade due to bleaching (loss of symbiotic algae, as described in Concept 3.3) and the great tsunami of 2004, resulting in the replacement of some coral species with other species, or no replacement at all. Taken together, these changes make the community what it is today: a community that has fewer coral species than it did a few decades ago, the effect of a combination of natural and human-caused agents of change.

Succession is change in the species composition of communities over time. Succession is the result of a variety of abiotic (physical and chemical) and biotic agents of change. In Concepts 17.2–17.4, we will consider the theory behind succession and examples that illustrate how it works in a variety of systems. But first, in this section, we will identify and define the agents of change that are most responsible for driving succession.

Agents of change can be abiotic or biotic

Communities, and the species contained within them, change in response to a number of abiotic and biotic factors (**Table 17.1**). We have considered many of these factors in previous chapters. In Unit 1, we learned that abiotic factors, in the form of climate, soils, nutrients, and water, vary over daily, seasonal, decadal, and even 100,000-year time scales. This variation has important implications for community change. For example, in Indian Ocean coral reef communities (see Figure 17.3), unusually high water temperatures driven by large-scale climate change have been implicated in recent losses of symbiotic algae from corals, resulting in coral bleaching. If the symbiotic algae do not return, the corals will eventually die, thus creating the conditions for species replacement. Likewise, increases in sea level can decrease the amount of light that reaches the corals. If light availability falls below the physiological limits of some coral species, they could slowly be replaced by more tolerant species, or even by macroalgae (seaweeds). Finally, increasing ocean acidification can dissolve the skeletons of corals, hindering their growth (see Chapter 25 and Chapter 16's Climate Change Connection for more information on climate change and ocean acidification). Because these abiotic conditions are constantly changing, communities are doing the same, at a pace consistent with their environment.

Abiotic agents of change can be placed into two categories, both of which can have either natural or human origins, but which differ in the effects they have on species: disturbances and stresses. A **disturbance** is an abiotic

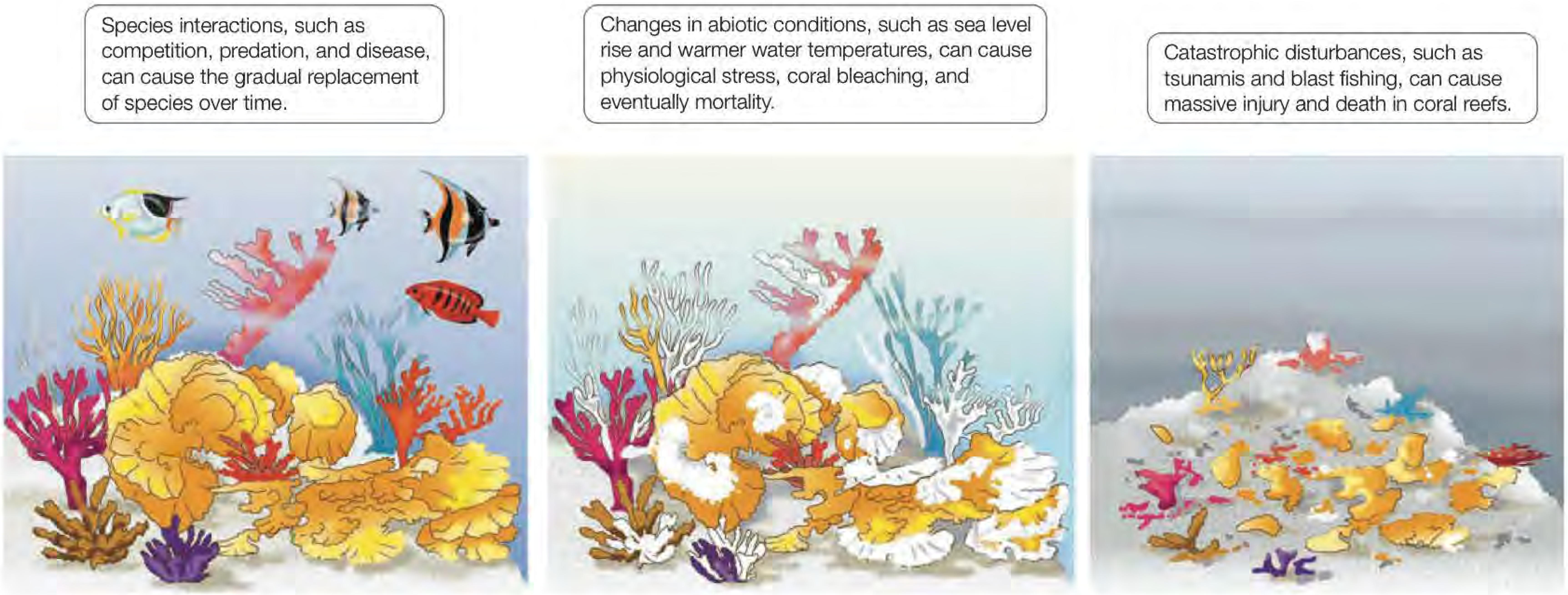


Figure 17.3 Change Happens Coral reef communities in the Indian Ocean have experienced large changes over the last few decades. The agents of change have been both subtle and catastrophic, natural and human-caused.

TABLE 17.1 Examples of Abiotic and Biotic Agents of Stress, Disturbance, and Change in Communities

AGENT OF CHANGE	EXAMPLES
Abiotic factors	
Waves, currents	Storms, hurricanes, floods, tsunamis, ocean upwelling
Wind	Storms, hurricanes and tornados, wind-driven sediment scouring
Water supply	Droughts, floods, mudslides
Chemical composition	Pollution, acid rain, high or low salinity, high or low nutrient supply
Temperature	Freezing, snow and ice, avalanches, excessive heat, fire, sea level rise or fall
Volcanic activity	Lava, hot gases, mudslides, flying rocks and debris, floods
Biotic factors	
Negative interactions	Competition, predation, herbivory, disease, parasitism, trampling, digging, boring

Source: Adapted, with additions, from Sousa 2001.

event that physically injures or kills some individuals and creates opportunities for other individuals to grow or reproduce. Some ecologists also consider biotic events such as digging by animals to be disturbances. In our coral reef example, the 2004 tsunami can be viewed as a disturbance because the force of water passing over the reef injured and killed many coral individuals. Likewise, the outlawed practice of blast fishing, which involves using dynamite to stun or kill fish for easy collection, can cause massive injury and death in coral reefs. Even biotic events such as coral boring by snails or predation by parrot fishes can be considered disturbances because they remove coral tissue and weaken coral skeletons. *Stress*, on the other hand, occurs when some abiotic factor reduces the growth, reproduction, or survival of individuals and creates opportunities for other individuals. A stress in our coral reef might be the effect of warmer water temperatures or sea level rise on the growth, reproduction, or survival of corals. Examples of other stresses and disturbances are included in Table 17.1. Both disturbance and stress are believed to play critical roles in driving succession.

How do biotic factors influence community change? In Unit 4, we saw that species interactions, both negative and positive, can result in the replacement of one species with another through stress and disturbance. In our coral reef (see Figure 17.3), change might be driven by competition between, for example, platelike corals and branched corals, with the platelike forms eventually dominating over time. Coral diseases are another example of a species interaction that can initiate change in communities by causing particular coral species to grow more slowly or eventually die. Equally common agents of change are the actions of ecosystem engineers and keystone species (see Figures 16.16 and 16.17). Both types of species have large effects on other species that result in community change.

Finally, it is important to realize that abiotic and biotic factors often interact to produce change in communities. We can see this interaction in the case of ecosystem engineers such as beavers, which cause changes in abiotic conditions that in turn cause species replacement (see Figure 16.18). Similarly, abiotic factors such as wind, waves, or temperature can act by modifying species interactions, either positively or negatively, thus creating opportunities for other species. We have seen examples of this kind of effect on sea palms in the rocky intertidal zone (see Figure 14.18), plants in alpine regions (see Figure 15.9), and stream insects in Northern California (see Figure 16.19).

Agents of change vary in their intensity, frequency, and extent

As you might guess, the tempo of succession is largely determined by how often, at what magnitude, and to what areal extent agents of change act. For example, when the avalanche produced by Mount St. Helens ripped through the alpine community back in 1980, it produced a disturbance that was larger and more severe than any others that had occurred that year, that decade, or that century. The *intensity*, or severity, of that disturbance—the amount of damage and death it caused—was huge, both because of the massive physical force involved and because of the area covered. In contrast, the *frequency* of that kind of disturbance is low because such eruptive episodes are so rare (occurring once every few centuries). Extremely intense and infrequent events, such as the eruption of Mount St. Helens, are at the far end of the spectrum of disturbances organisms experience in communities (**Figure 17.4**). In this case, the entire community is affected, and recovery involves the complete reassembly of the community over time. We will consider the mechanisms of that reassembly in Concepts 17.2–17.4.

At the other end of the spectrum are weak and frequent disturbances that may have more subtle effects or affect a smaller area (see Figure 17.4). Prior to the eruption of Mount St. Helens, such disturbances might have included wind blowing down old trees living in the Douglas fir forests surrounding the mountain. These more frequent disturbances open up patches of resources that can be used by individuals of the same or different species. A mosaic of disturbed patches can promote species diversity in communities over time, but may not lead to much successional change. We will learn more about these smaller disturbances and their effects on species diversity in Chapter 19. For now let's turn our attention from the agents of change to their consequences for community succession.

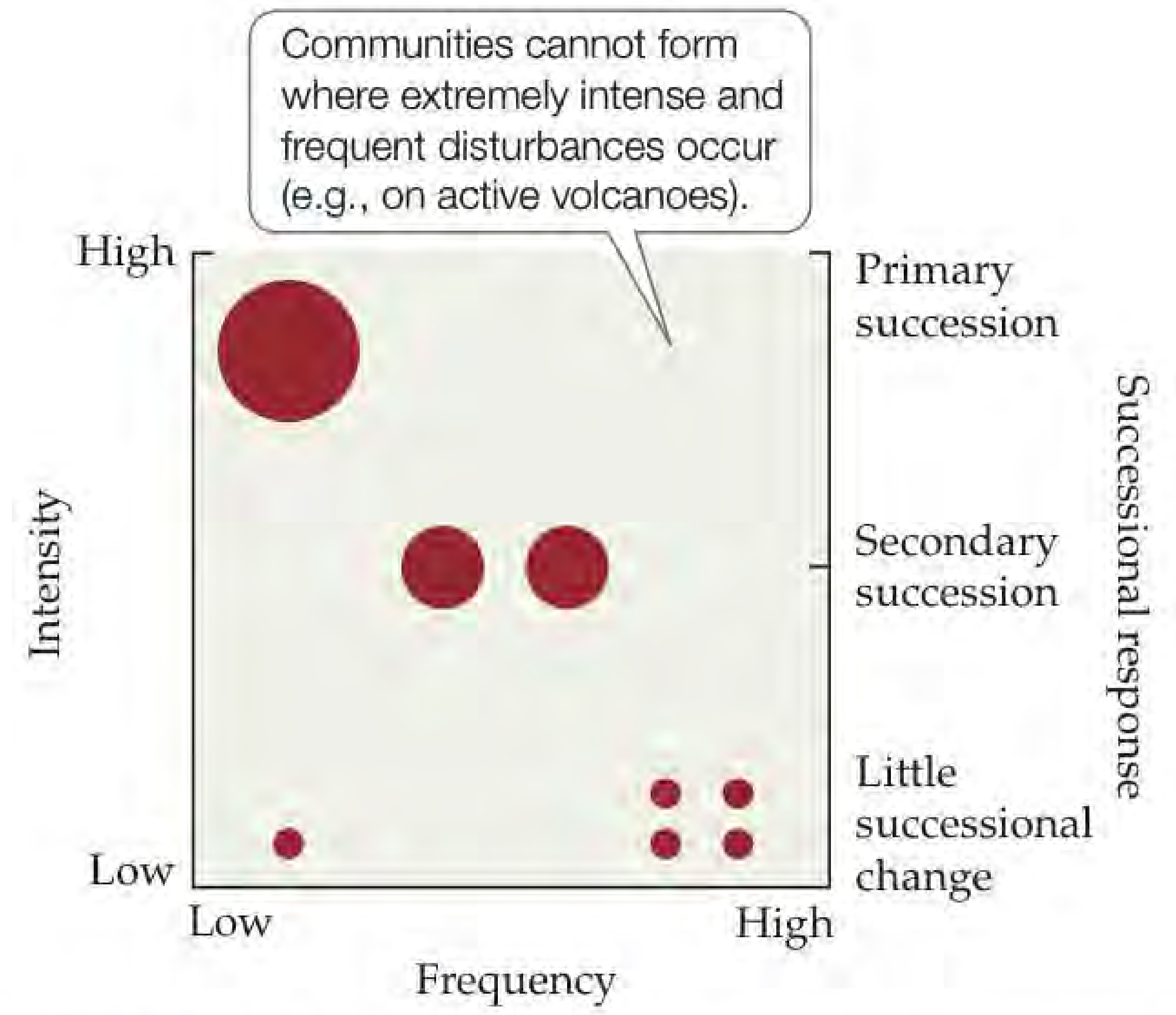


Figure 17.4 The Spectrum of Disturbance How much biomass is removed (the intensity, or severity, of disturbance) and how often it is removed (the frequency of disturbance) can influence the amount of change (represented by the size of the red circles) that occurs and the type of succession that is possible afterward (right side of the graph).

Describe how the type of organism being studied might influence whether we classify a disturbance as being intense or frequent.

CONCEPT 17.2

Succession is the process of change in species composition over time as a result of abiotic and biotic agents of change.

The Basics of Succession

At the most basic level, the term "succession" refers to the process by which the species composition of a community changes over time. Mechanistically, succession involves colonization and extinction due to abiotic and biotic agents of change. Even though studies of succession often focus on changes in vegetation, the roles of animals, fungi, bacteria, and other microbes are equally important.

Theoretically, succession progresses through various stages that include a **climax stage** (**Figure 17.5**). The climax is thought to be a stable end point that experiences little change until a particularly intense disturbance sends the community back to an earlier stage.

As we will see in Concepts 17.3 and 17.4, there is some argument about whether succession can ever lead to a stable end point.

Primary succession and secondary succession differ in their initial stages

Ecologists recognize two types of succession that differ in their initial stages. The first type, **primary succession**, involves the colonization of habitats that are devoid of life (see Figure 17.5), either as a result of catastrophic disturbance, as we see on the Pumice Plain at Mount St. Helens, or because they are newly created habitats, such as volcanic rock. As you can imagine, primary succession can be very slow because the first arrivals (known as *pioneer* or *early successional* species) typically face extremely inhospitable conditions. Even the most basic resources needed to fuel life, such as soil, nutrients, and water, may be lacking. The first colonizers, then, tend to be species that are capable of withstanding great physiological stress and transforming the habitat in ways that benefit their further growth and expansion (and that of other species, as we will see).

The other type of succession, known as **secondary succession**, involves the reestablishment of a community in which most, but not all, of the organisms or organic constituents have been destroyed (see Figure 17.5). Agents of change that can create such conditions include fire, hurricanes, logging, and herbivory. Despite the catastrophic effect of the eruption on Mount St. Helens, there were many areas, such as the blowdown zone, where some organisms survived and secondary succession took place. As you might expect, the legacy of the preexisting species and their interactions with colonizing species can play a large role in the trajectory of secondary succession.

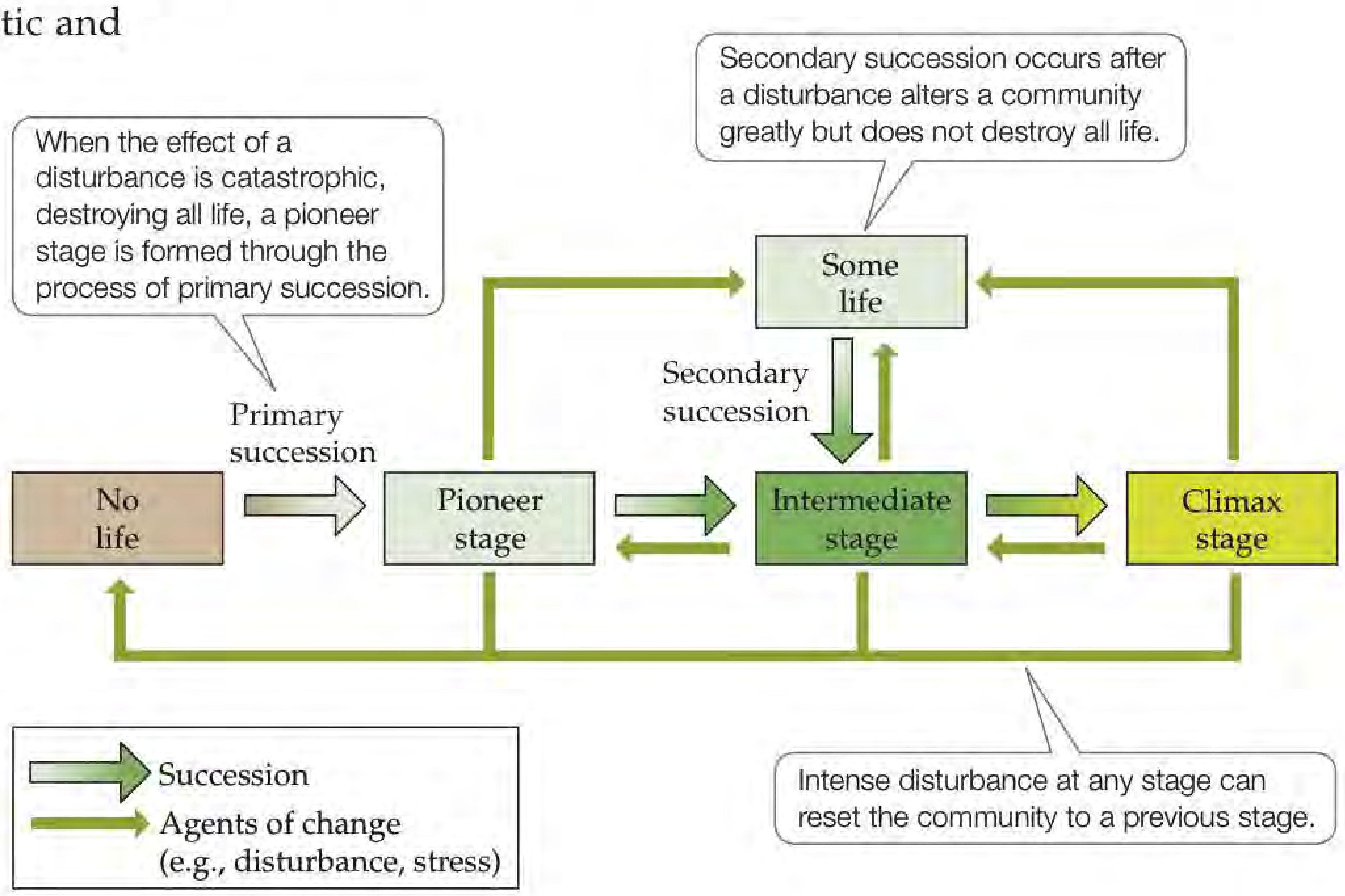


Figure 17.5 The Trajectory of Succession A simple model of succession involves transitions between stages driven by species replacements over time. Theoretically, these changes ultimately result in a climax stage that experiences little change. There is some argument, however, about whether succession can ever lead to a stable end point.

The early history of ecology is a study of succession

The modern study of ecology had its beginnings at the turn of the twentieth century. At that time, it was dominated by scientists who were fascinated with plant communities and the changes they undergo over time. One of these pioneers was Henry Chandler Cowles, who studied the successional sequence of vegetation in sand dunes on the shore of Lake Michigan (**Figure 17.6**). In this ecosystem, the dunes are continually growing as new sand is deposited at the shoreline. This new sand is blown onshore when shorelines are exposed during droughts. Cowles was able to infer the successional pattern along a dune by assuming that the plant assemblages farthest from the lake's edge were the oldest and that the ones nearest the lake, where new sand was being deposited, were the youngest. As you walked from the lake to the back of the dune, he believed, you were traveling forward in time and able to imagine what the areas you had just passed through would look like in centuries to come. The first stages were dominated by a hardy ecosystem engineer, American beach grass (*Ammophila breviligulata*). *Ammophila* (whose genus name literally means "sand lover") is excellent at trapping sand and creating hills, which provide refuge on their leeward side for plants less tolerant of the constant burial and sand scouring experienced on the beachfront.

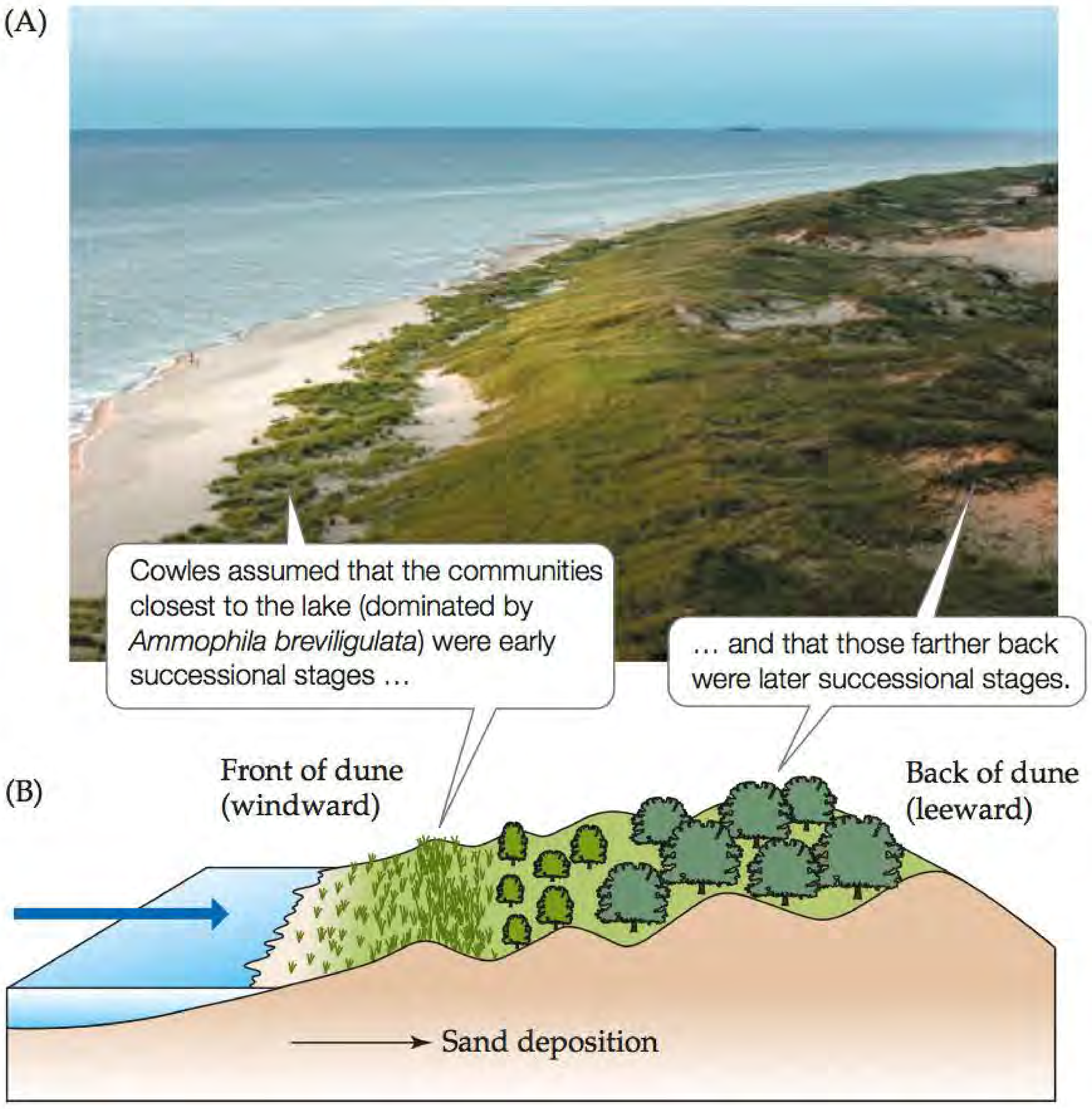


Figure 17.6 Space for Time Substitution (A) The portion of a dune nearest the shoreline on Lake Michigan is covered with *Ammophila*. (B) When Henry Chandler Cowles studied succession on these dunes, he assumed that the earliest successional stages occurred on the newly deposited sand at the front of the dune, and that later successional stages occurred at the back of the dune.

Cowles (1899) made the assumption that the different plant assemblages—or "societies," as he called them—that he saw in different positions on a dune represented different successional stages. That assumption allowed him to predict how a community would change over time without actually waiting for the pattern to unfold, which would have taken decades to centuries. This idea, known as the "space for time substitution" (Pickett 1989), is used frequently as a practical way to study communities over time scales that exceed the life span of an ecologist. It assumes that time is the main factor causing communities to change and that unique conditions in particular locations are inconsequential. These are big assumptions, and they have fueled a debate about the predictability of community dynamics over time. We will discuss this debate in more detail in Concept 17.4, when we deal with alternative stable state theory.

Henry Cowles was not alone in his interest in plant succession. His peers included Frederick Clements and Henry Gleason, two men who had completely different and contentious views on the mechanisms driving succession (Kingsland 1991). Clements, one of the first to write a formal book in 1907 on the new science of ecology, believed that plant communities were like "superorganisms," groups of species that worked together in a mutual effort toward some deterministic end. Succession was similar to the development of an organism, complete with a beginning (embryonic stage), middle (adult stage), and end (death). Clements (1916) thought that each community had its own predictable life history and, if left undisturbed, ultimately reached a stable end point. This "climax community" was composed of species that dominated and persisted over many years and provided the type of stability that could potentially be maintained indefinitely.

Gleason (1917) thought that viewing a community as an organism, with various interacting parts, ignored the responses of individual species to prevailing conditions. In his view, communities were not the predictable and repeatable result of coordinated interactions among species, but rather the random product of fluctuating environmental conditions acting on individual species. Each community was the product of a particular place and time, and was thus unique in its own right.

Looking back, it is clear that Gleason and Clements had extreme views of succession. As we will see in the next section, we can find elements of both theories in the results of studies that have accumulated over the last century.

(A)

(B)

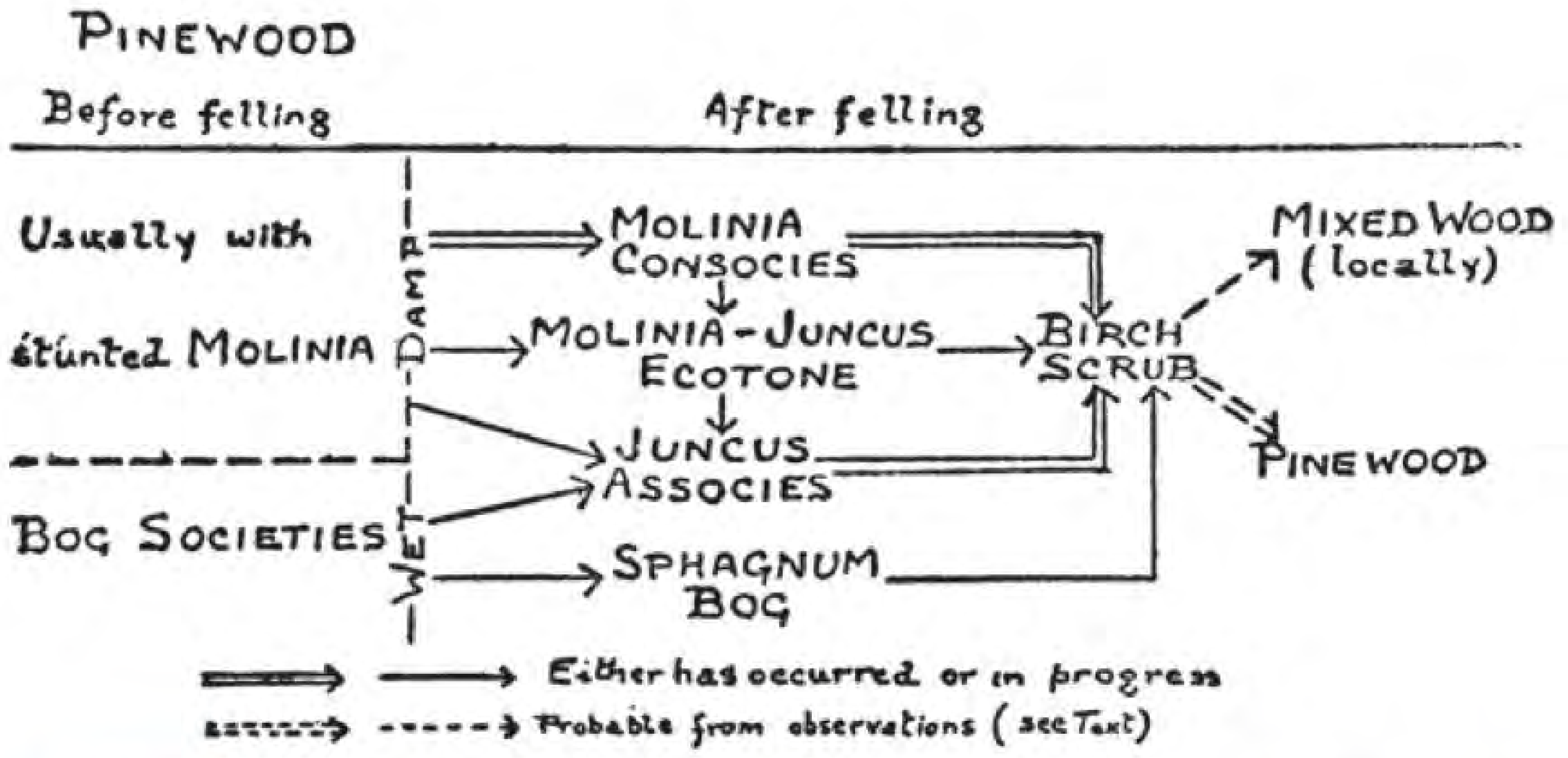


Figure 17.7 Elton's Trajectory of Pine Forest Succession (A) Charles Elton at the age of 25, a year before the publication of his first book, *Animal Ecology* (1927). (B) Elton's book contained this diagram of succession in pine forests after logging. The successional trajectory differed depending on the moisture content of a particular area: wetter areas became sphagnum bogs, while slightly drier areas became wetlands containing rushes (*Juncus*) and grasses (*Molinia*). Eventually, these communities all became birch scrub but then ultimately diverged into pine woods or mixed woods, again depending on moisture. (B from Elton 1927.)

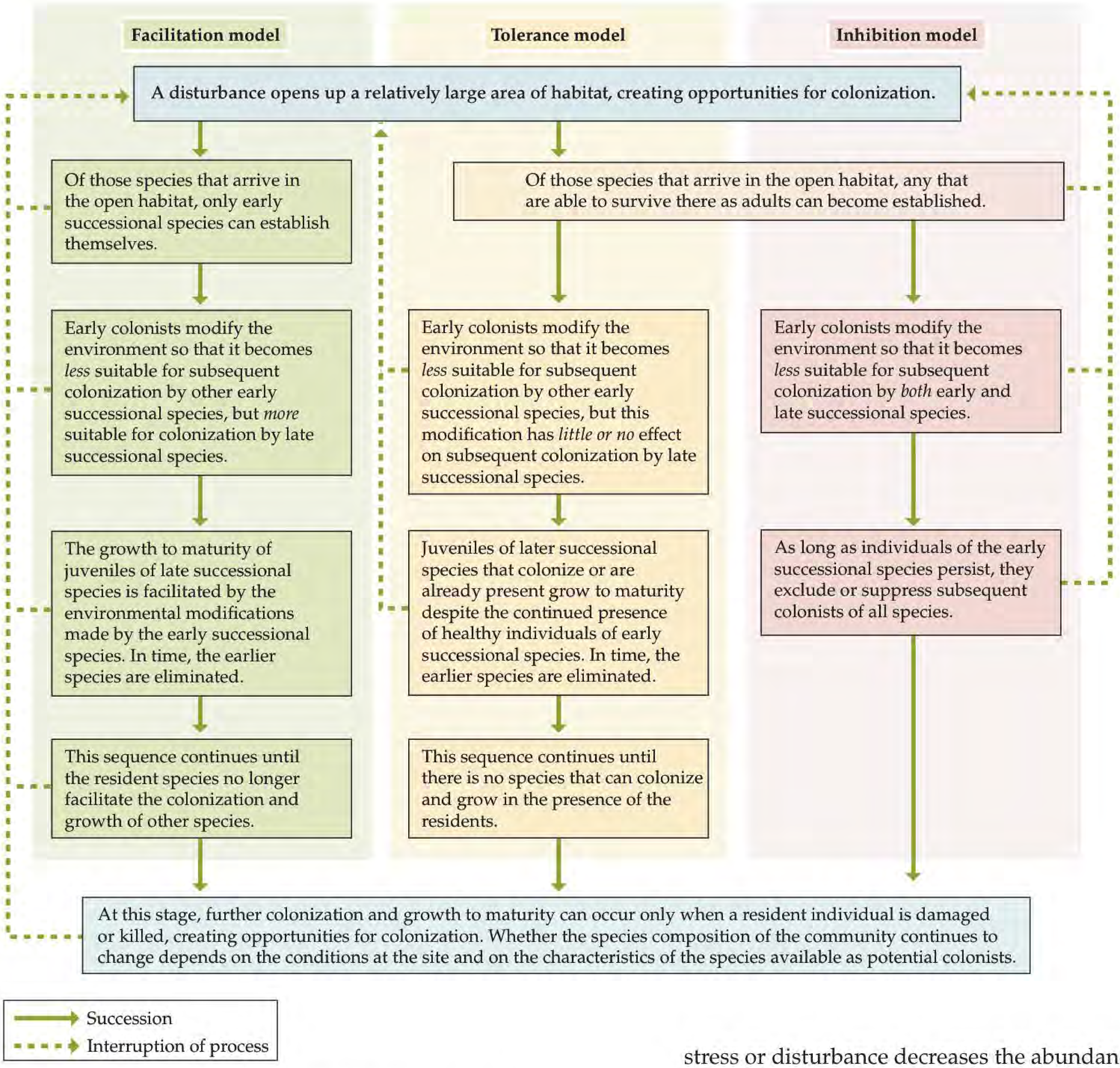
First, however, it is important to mention one last ecologist, Charles Elton (**Figure 17.7A**), whose perspective on succession was shaped not only by those of the botanists who came before him, but also by his interest in animals. He wrote his first book, *Animal Ecology* (1927), in 3 months' time at the age of 26. The book addresses many important ideas in ecology, including succession. Elton believed that organisms and the environment interact to shape the direction succession will take. He presented an example from pine forests in England that were being subjected to deforestation. After the felling of the pines, the trajectory of succession varied depending on the moisture content of the environment (**Figure 17.7B**). Wetter areas developed into sphagnum bogs, while slightly drier areas developed into wetlands containing rushes and grasses. Eventually, these communities all became birch scrub, but then ultimately diverged into two types of forest. Through these observations, Elton demonstrated that the only way to predict the trajectory of succession was to understand the biological and environmental context in which it occurred.

Elton's greatest contribution to the understanding of succession was his acknowledgment of the role of animals. Up to that point, most ecologists believed that plants drove succession, while animals were passive followers. Elton provided many examples showing how animals could create successional patterns by eating, dispersing, trampling, and destroying vegetation in ways that greatly affected the sequence and timing of succession. We will review some examples of animal-driven succession in the next section, but it is clear that the observations and conclusions Elton made 90 years ago still hold today.

Multiple models of succession were stimulated by lack of scientific consensus

Fascination with the mechanisms responsible for succession, and attempts to integrate the controversial theories of Clements, Cowles, and Elton, led ecologists to use more scientifically rigorous methods to explore succession, including comprehensive reviews of the literature and manipulative experiments. Joseph Connell and his collaborator Ralph Slatyer (1977) surveyed the literature and proposed three models of succession that they believed to be important (**Figure 17.8**).

- The *facilitation model*, inspired by Clements, describes situations in which the earliest colonizers modify the environment in ways that ultimately benefit later-arriving species but hinder their own continued dominance. These early successional species have characteristics that make them good at colonizing open habitats, dealing with physical stress, growing quickly to maturity, and ameliorating the harsh physical conditions often characteristic of early successional stages. Eventually, however, a sequence of species facilitations leads to a climax community composed of species that no longer facilitate other species and are displaced only by disturbances.
- The *tolerance model* also assumes that the earliest colonizers modify the environment, but in neutral ways that neither benefit nor inhibit later species. These early successional species have life history strategies that allow them to grow and reproduce quickly. Later species persist merely because they



A disturbance opens up a relatively large area of habitat, creating opportunities for colonization.

Of those species that arrive in the open habitat, only early successional species can establish themselves.

Of those species that arrive in the open habitat, any that are able to survive there as adults can become established.

Early colonists modify the environment so that it becomes *less* suitable for subsequent colonization by other early successional species, but *more* suitable for colonization by late successional species.

Early colonists modify the environment so that it becomes *less* suitable for subsequent colonization by other early successional species, but this modification has *little or no* effect on subsequent colonization by late successional species.

Early colonists modify the environment so that it becomes *less* suitable for subsequent colonization by *both* early and late successional species.

The growth to maturity of juveniles of late successional species is facilitated by the environmental modifications made by the early successional species. In time, the earlier species are eliminated.

Juveniles of later successional species that colonize or are already present grow to maturity despite the continued presence of healthy individuals of early successional species. In time, the earlier species are eliminated.

As long as individuals of the early successional species persist, they exclude or suppress subsequent colonists of all species.

This sequence continues until the resident species no longer facilitate the colonization and growth of other species.

This sequence continues until there is no species that can colonize and grow in the presence of the residents.

At this stage, further colonization and growth to maturity can occur only when a resident individual is damaged or killed, creating opportunities for colonization. Whether the species composition of the community continues to change depends on the conditions at the site and on the characteristics of the species available as potential colonists.

Figure 17.8 Three Models of Succession Connell and Slatyer proposed three conceptual models—the facilitation, tolerance, and inhibition models—to describe succession. (After Connell and Slatyer 1977.)

have life history strategies such as slow growth, few offspring, and long life that allow them to tolerate increasing environmental or biological stresses that would hinder early successional species.

- The *inhibition model* assumes that early successional species modify the environment in ways that hinder later successional species. For example, these early colonizers may monopolize resources needed by subsequent species. This suppression of the next stage of succession is broken only when stress or disturbance decreases the abundance of the inhibitory species. As in the tolerance model, later species persist merely because they have life history strategies that allow them to tolerate environmental or biological stresses that would otherwise hinder early successional species.

CONCEPT 17.3

Experimental work on succession shows its mechanisms to be diverse and context-dependent.

Mechanisms of Succession

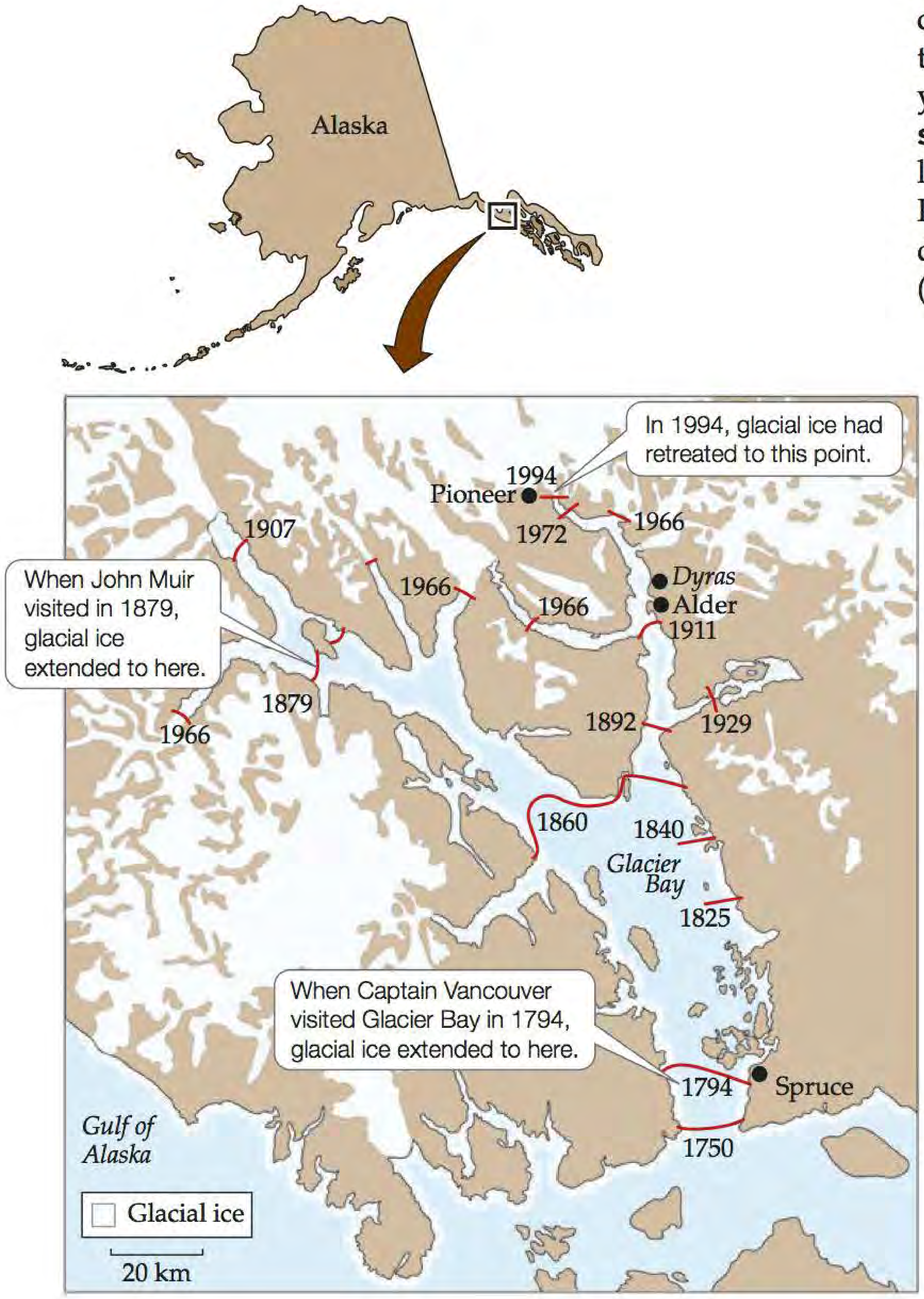
More than 30 years have gone by since Connell and Slatyer wrote their influential theoretical paper on succession. Since that time, there have been a number of experimental tests of their three models. Those studies show that the mechanisms driving succession rarely conform to any one model, but instead are dependent on the community and the context in which experiments are conducted.

No one model fits any one community

To illustrate the types of successional mechanisms that have been revealed by experiments, we will focus on three studies: communities that form (1) after glacial retreat in Alaska, (2) after vegetation disturbance in salt marshes in New England, and (3) after wave disturbance in the rocky intertidal zone of the U.S. Pacific coast.

PRIMARY SUCCESSION IN GLACIER BAY, ALASKA One of the best-studied examples of primary succession occurs in Glacier Bay, Alaska, where the melting of glaciers has led to a sequence of community change that reflects succession over many centuries (**Figure 17.9**). Captain George Vancouver first recorded the location of glacial ice there in 1794, while exploring the west coast of North America. Over the last 200 years, the glaciers have retreated up the bay, leaving behind bare, broken rock (known as *glacial till*). John Muir, in his book *Travels in Alaska* (1915), first noted how much the glaciers had melted since Vancouver's time. When he visited Glacier Bay in 1879, he camped among ancient tree stumps that had once been covered by ice and saw forests that had grown up in previously glaciated areas. He was impressed with the dynamic nature of the landscape and how the plant community responded to the changes.

Muir's book sparked the interest of William S. Cooper (1923a), who began his studies of Glacier Bay in 1915. A former student of Henry Chandler Cowles, Cooper saw Glacier Bay as an example of the "space for time substitution" so well documented by his advisor in the Lake Michigan dunes. He established permanent plots (Cooper 1923b) that have allowed researchers to observe the pattern of community change along the bay from Vancouver's time to today. This pattern is generally characterized by an increase in plant species richness and a change in plant species composition with time and distance from the melting ice front (**Figure 17.10**). In the first years after new habitat is exposed, a primary or **pioneer stage** develops, dominated by a few species that include lichens, mosses, horsetails, willows, and cottonwoods. Roughly 30 years after exposure, a second community develops, named the *Dryas* stage after the small shrub (*Dryas drummondii*) that dominates this community. In



In 1994, glacial ice had retreated to this point.

When John Muir visited in 1879, glacial ice extended to here.

When Captain Vancouver visited Glacier Bay in 1794, glacial ice extended to here.

Figure 17.9 Glacial Retreat in Glacier Bay, Alaska Over more than 200 years, the melting of glaciers has exposed bare rock to colonization and succession. (After Chapin et al. 1994.)

? Based on the locations of the glaciers over time, describe where the oldest and youngest communities are located.

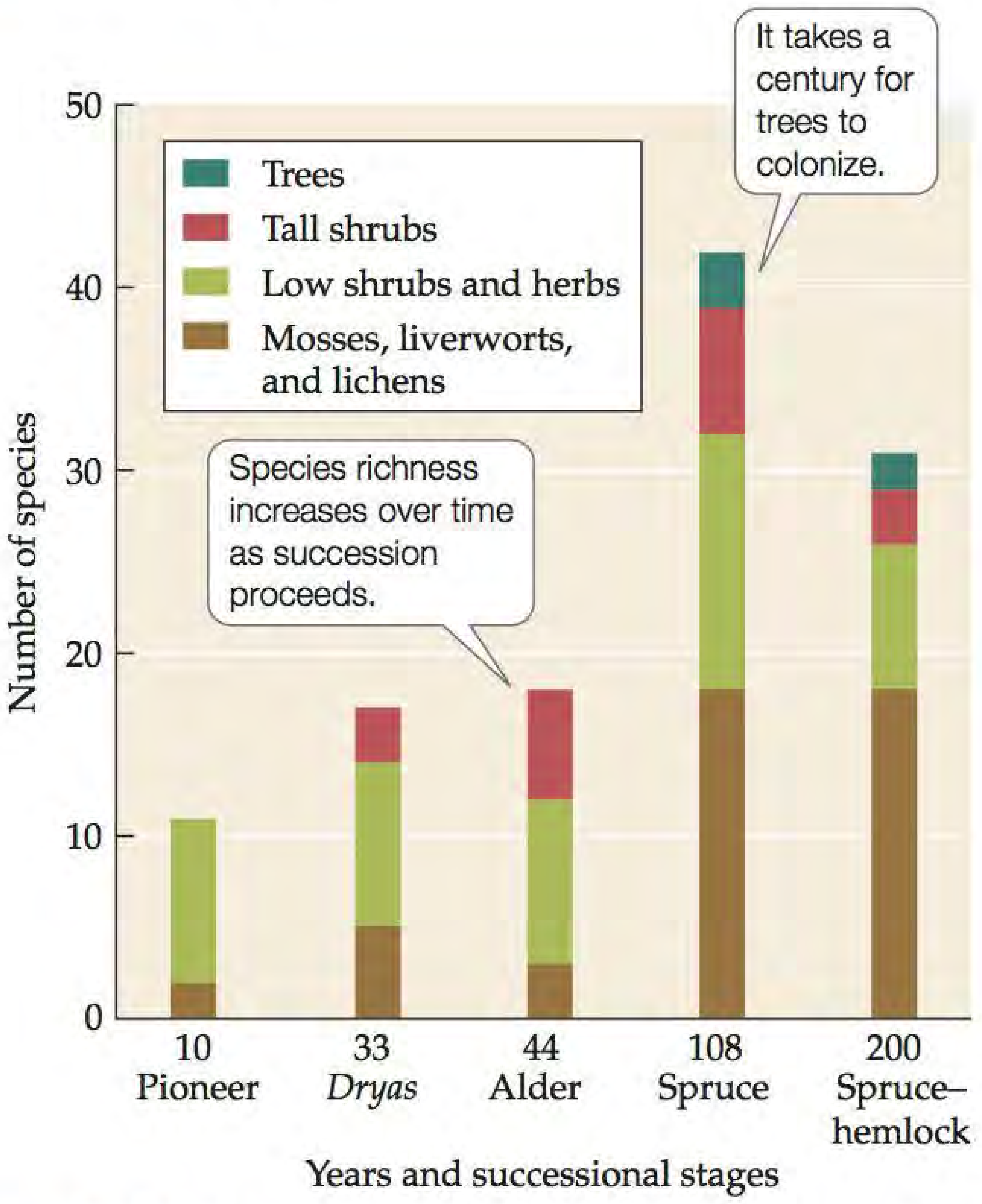


Figure 17.10 Successional Communities at Glacier Bay, Alaska Plant species richness has generally increased over the 200 years following glacial retreat. (After Reiners et al. 1971.)

this stage, species richness increases, with willows, cottonwoods, alders (*Alnus sinuata*), and Sitka spruce (*Picea sitchensis*) sparsely distributed among the carpet of *Dryas*. After about 50 years (or some 20 km from the ice front), alders dominate, forming the third community, referred to as the alder stage. Finally, a century after glacial retreat, a mature Sitka spruce forest (the spruce stage) is in place, which fosters a diverse array of lichens, low shrubs, and herbs. Reiners et al. (1971) documented that 200 years after exposure, species richness decreases somewhat as Sitka spruce forests are transformed into forests of longer-living western hemlocks.

The mechanisms underlying succession in this system have been studied extensively by F. Stuart Chapin and colleagues (1994). They wondered, given the harsh physical conditions experienced by most species in the pioneer stage, whether the facilitation model could explain the pattern of succession observed by Cooper and Reiners et al. First, they analyzed the soils of the different successional stages. They found significant changes in soil properties that were coincident with the increases in plant species richness (**Figure 17.11**). Not only were there increases in soil organic matter and soil moisture in later stages of succession, but nitrogen increased more than fivefold from the alder stage to the spruce stage. (This increase resulted from the action of nitrogen-fixing bacteria associated with plant roots, which we'll describe in more detail in this chapter's Connections in Nature.) Chapin hypothesized that the assemblage of species at each stage of succession was having effects on the physical environment that largely shaped the pattern of community formation. The question remained, however, whether those effects were facilitative or inhibitory, and how they varied across the different successional stages.

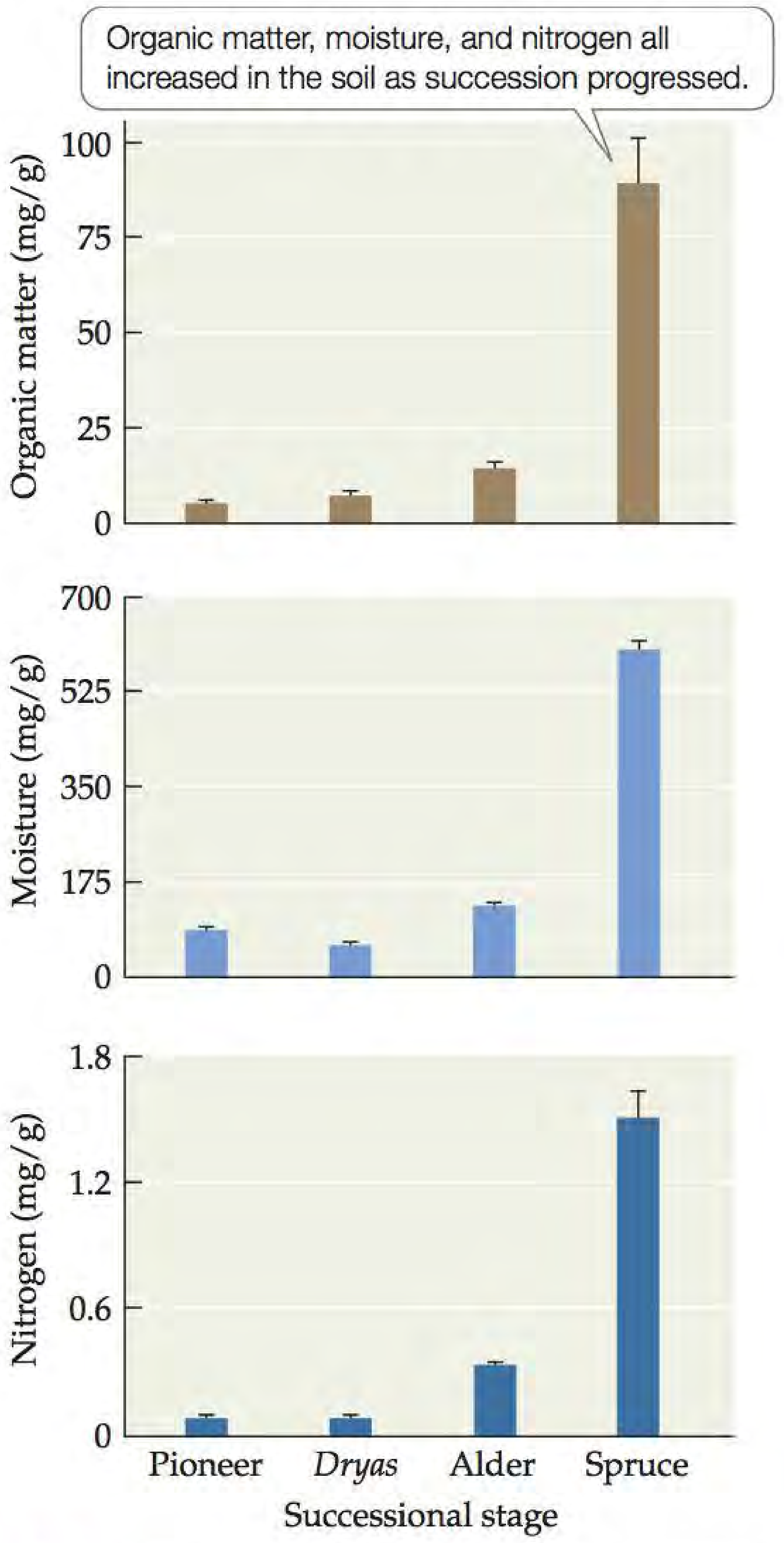
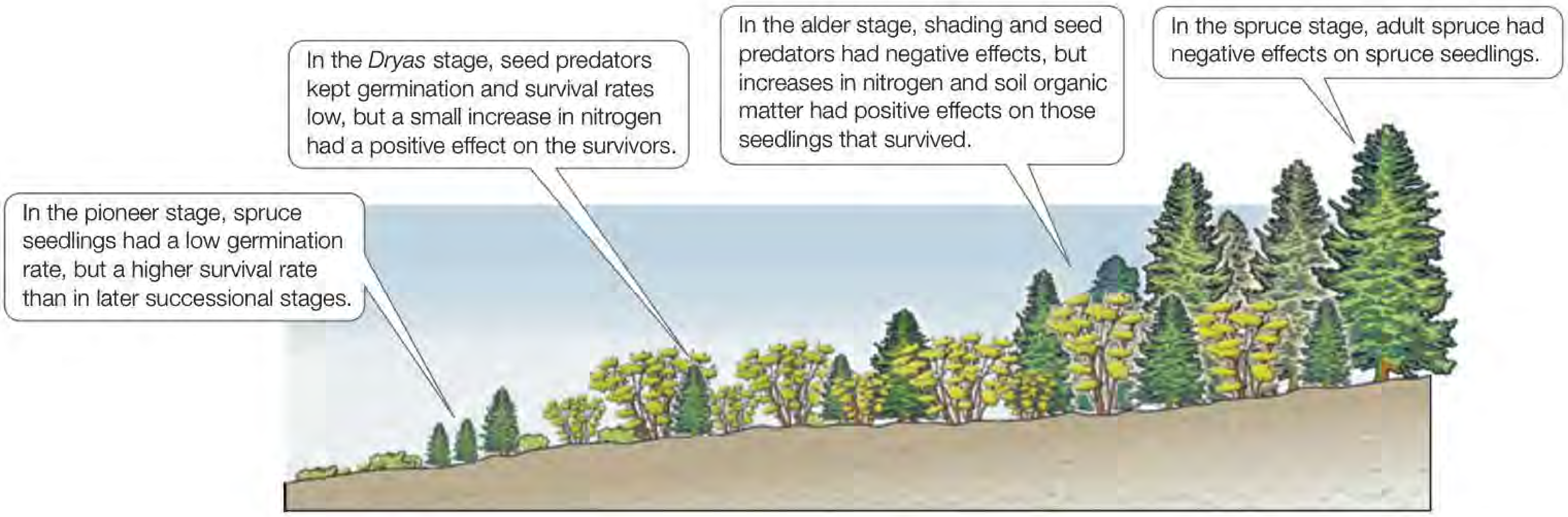


Figure 17.11 Soil Properties Change with Succession Chapin and colleagues studied the properties of the soils in each of four successional stages at Glacier Bay. Error bars show one SE of the mean. (After Chapin et al. 1994.)

To test their facilitation hypothesis, Chapin et al. (1994) conducted manipulative experiments. They added spruce seeds to each of the successional stages and observed their germination, growth, and survival over time. These experiments, along with observations of unmanipulated plots, showed that neighboring plants had both facilitative and inhibitory effects on the spruce seedlings but that the directions and strengths of those effects varied with the stage of succession (**Figure 17.12**). For example, in the pioneer stage, spruce seedlings had a low germination rate, but a higher survival rate, than in later successional stages. In the *Dryas* stage, spruce seedlings had low germination and survival rates due to increases in seed predators, but those individuals that did



	Successional stage			
Effects on spruce seedlings	Pioneer	*Dryas*	Alder	Spruce
Positive	Higher survival	Higher nitrogen level Higher growth	Higher soil organic matter Higher nitrogen level More mycorrhizae Higher growth	Higher germination
Negative	Lower germination	Lower germination Lower survival Higher seed predation and seed mortality	Lower germination Lower survival Higher seed predation and seed mortality Root competition Competition for light	Lower growth Lower survival Higher seed predation and seed mortality Root competition Competition for light Lower nitrogen level

Figure 17.12 Both Positive and Negative Effects Influence Succession The relative contributions of positive and negative effects of other species on spruce seedling establishment changed across successional stages in Glacier Bay, Alaska. Positive effects equaled or outweighed negative effects in the first three stages, but the opposite was seen in the last spruce stage. (After Chapin et al. 1994.)

survive grew better because of the presence of nitrogen fixed by symbiotic bacteria associated with *Dryas*. In the alder stage, a further increase in nitrogen (alders also host nitrogen-fixing bacteria) and an increase in soil organic matter had positive effects on spruce seedlings, but shading and seed predators led to overall low germination and survival rates. In this stage, alders had a net positive effect on spruce seedlings that germinated before alders were able to dominate. Finally, in the spruce stage, the effects of large spruce on spruce seedlings were mostly negative and long-lasting. Growth and survival rates were low because of competition with adult spruce for light, space, and nitrogen. Interestingly, seed production by adults was enhanced, which led to relatively high seedling numbers merely as a consequence of the many more seeds available for germination.

Thus, in Glacier Bay, the mechanisms outlined in Connell and Slatyer's models were operating in at least some stages of succession. Early on, aspects of the facilitation model were seen as plants modified the habitat in positive ways for other plants and animals. Species such as alders had negative effects on later successional species unless they were able to colonize early, supporting the inhibition model. Finally, some stages—such as the spruce stage, in which dominance was a result of slow growth and long life—were driven by life history characteristics, a signature of the tolerance model.

SECONDARY SUCCESSION IN A NEW ENGLAND SALT MARSH

What do other studies show with regard to Connell and Slatyer's three models? Mark Bertness and Scott Shumway studied the relative importance of facilitative versus inhibitory interactions in controlling secondary succession in a New England salt marsh. Salt marshes are characterized by different species compositions and physical conditions at different tidal elevations. The shoreline border of the marsh is dominated by the cordgrass *Spartina patens*, whereas dense stands of the black rush *Juncus gerardii* are found between the shoreline and the terrestrial border. A common natural disturbance in salt marsh habitats is the deposition of tidally transported dead plant material

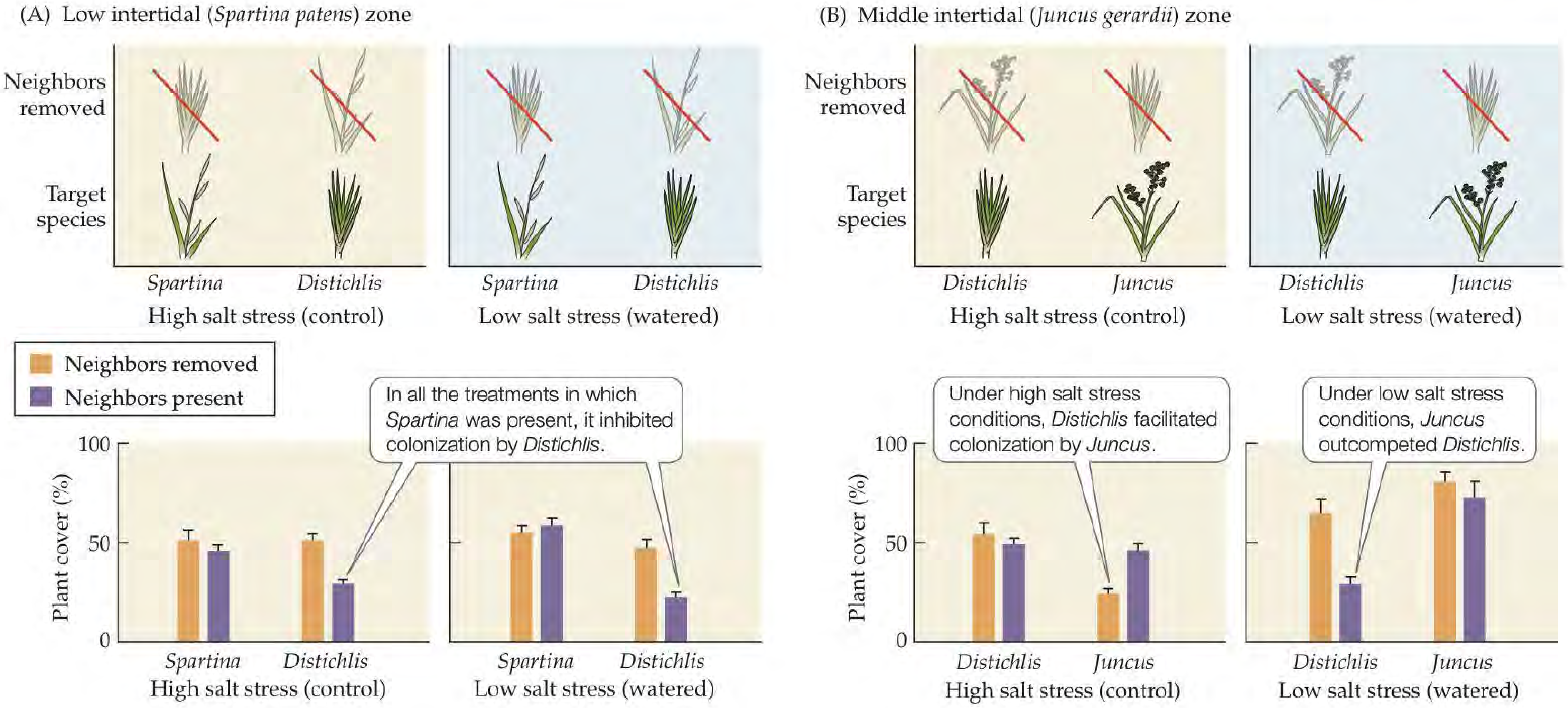
Figure 17.13 Wrack Creates Bare Patches in Salt Marshes A tidal deposit of wrack at Rumstick Cove, Rhode Island, where Bertness and Shumway conducted their research on secondary succession. This dead plant material smothers living plants, creating bare patches with high soil salinity.

known as *wrack* (**Figure 17.13**). The wrack smothers and kills plants, creating bare patches where secondary succession takes place. Soil salinity is high in these patches because, without shading by plants, water evaporation increases, leaving behind salt deposits. The patches are initially colonized by the spike grass *Distichlis spicata*, an early successional species that is eventually outcompeted by *Spartina* and *Juncus* in their respective zones.

Bertness and Shumway (1993) hypothesized that *Distichlis* could either facilitate or inhibit later colonization by *Spartina* or *Juncus* depending on the salt stress experienced by the interacting plants. To test this idea, they created bare patches in two zones of a marsh and manipulated plant interactions shortly after the patches had been colonized (**Figure 17.14**). In the low intertidal zone (the *Spartina* zone, close to the shoreline), they removed *Distichlis* from half the newly colonized patches, leaving *Spartina*, and removed *Spartina* from the other half, leaving *Distichlis*. In the middle intertidal zone (the *Juncus* zone, closer to the terrestrial border of the marsh), they performed similar manipulations, with *Juncus* and *Distichlis* as the target species. Control patches, in which the colonization process was not manipulated, were maintained in both zones. In addition, they watered half the patches in each treatment group with fresh water to alleviate salt stress, and left half as controls.

After observing the patches for 2 years, Bertness and Shumway found that the mechanisms of succession differed depending on the level of salt stress experienced by the plants and the species interactions involved. In the low intertidal zone, *Spartina* always colonized and dominated the plots, whether or not *Distichlis* was present or watering occurred (Figure 17.14A). *Distichlis* was able to dominate only if *Spartina* was removed from the plots, so it was clearly inhibited by *Spartina*, the dominant

Figure 17.14 New England Salt Marsh Succession Is Context-Dependent The trajectory of succession in salt marshes depends on soil salinity and the physiological tolerances of plant species. The kinds of interactions observed differed between the low intertidal zone (A) and the middle intertidal zone (B). Error bars show one SE of the mean. (After Bertness and Shumway 1993.)



In all the treatments in which *Spartina* was present, it inhibited colonization by *Distichlis*.

Under high salt stress conditions, *Distichlis* facilitated colonization by *Juncus*.

Under low salt stress conditions, *Juncus* outcompeted *Distichlis*.

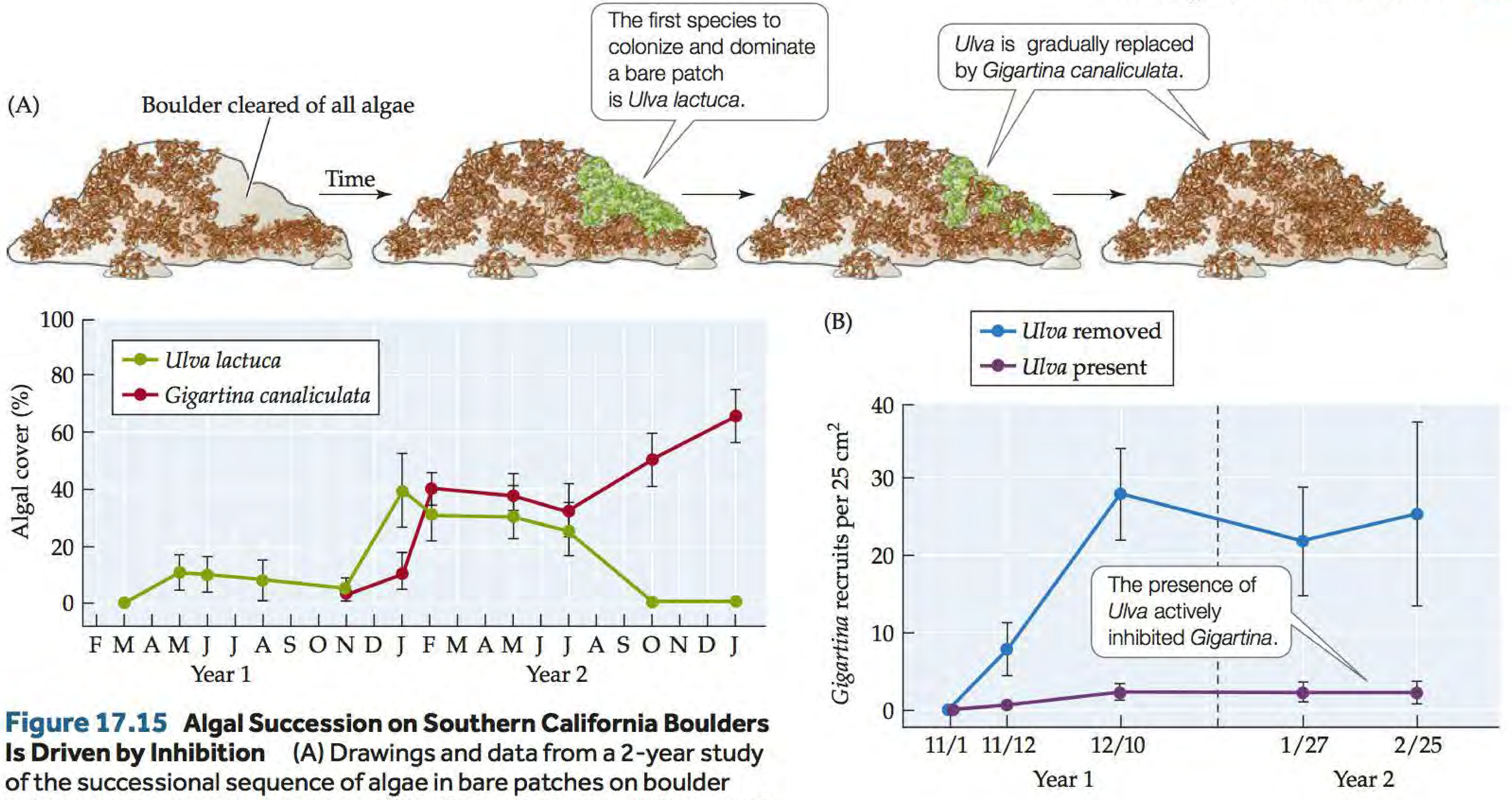


Figure 17.15 Algal Succession on Southern California Boulders Is Driven by Inhibition (A) Drawings and data from a 2-year study of the successional sequence of algae in bare patches on boulder fields in the rocky intertidal zone of Southern California. (B) In a study that lasted 4 months, Sousa performed removal experiments on concrete blocks to understand the mechanisms of succession in this ecosystem. Error bars show ± one SE of the mean. (After Sousa 1979b.)

competitor. In the middle intertidal zone, *Juncus* was able to colonize only if *Distichlis* was present or watering occurred (Figure 17.14B). Measurements of soil salinity confirmed that the presence of *Distichlis* helped to shade the soil surface, thus decreasing salt accumulation and reducing stress for *Juncus*. *Distichlis*, however, was able to colonize plots with *Juncus* only when salt stress was high—that is, under the control conditions. If plots were watered, *Distichlis* was easily outcompeted by *Juncus*.

These experimental manipulations confirmed that the mechanisms important to succession are context-dependent. No single model is sufficient to explain the underlying causes of succession. In the middle intertidal zone, *Distichlis* was a strong facilitator of colonization by *Juncus*. Once this facilitation occurred, the balance was tipped in favor of *Juncus*, which outcompeted *Distichlis* (see Figure 17.14B). In the low intertidal zone, *Distichlis* and *Spartina* were equally able to colonize and grow in salty patches. If *Spartina* arrived first, it inhibited *Distichlis* colonization. If *Distichlis* arrived first, it persisted only if *Spartina* did not arrive and displace it (see Figure 17.14A).

PRIMARY SUCCESSION IN ROCKY INTERTIDAL COMMUNITIES

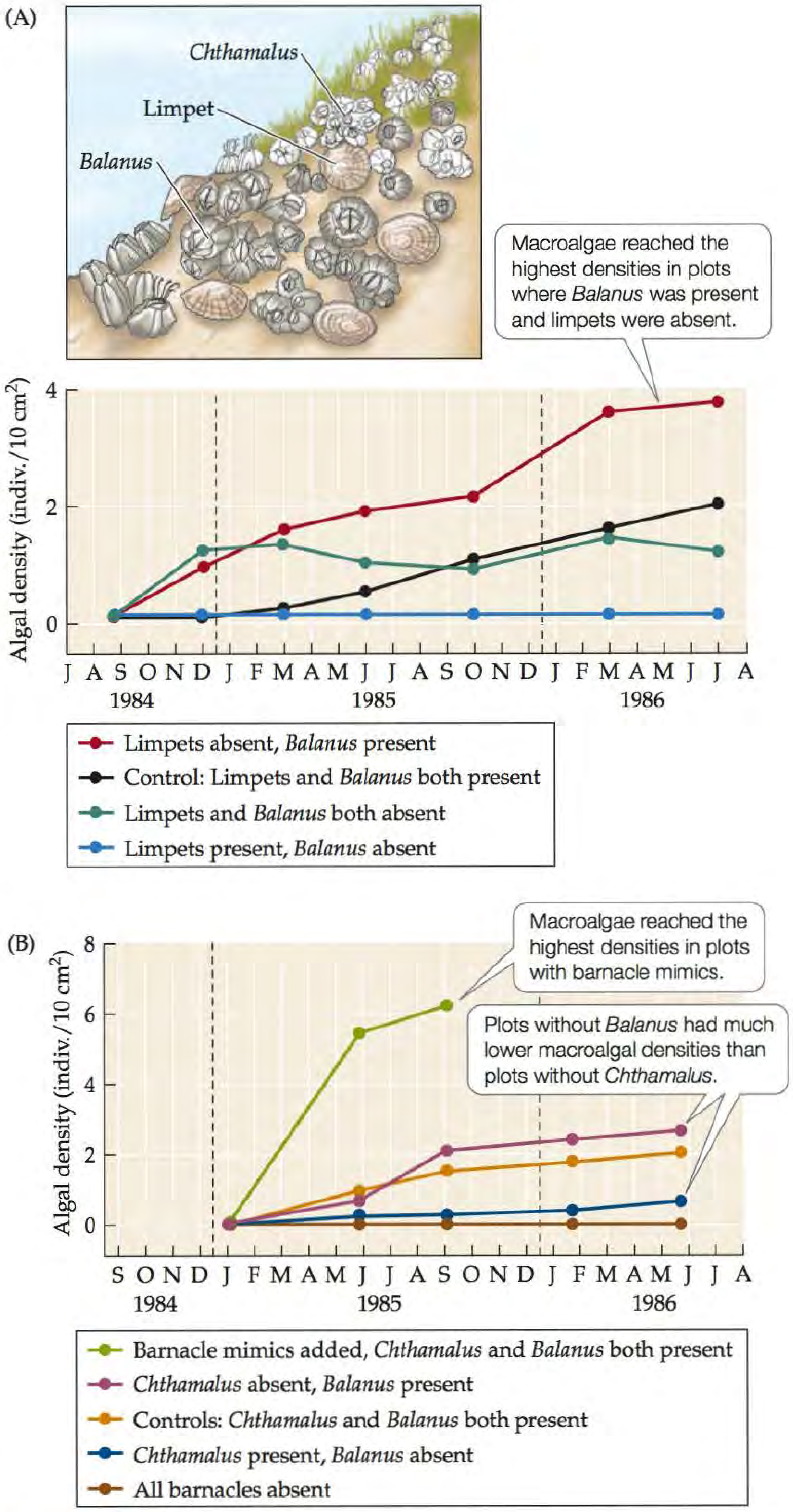
Our final examples come from an environment where succession has been studied extensively: the rocky intertidal zone. Here, disturbances are created mainly by waves, which can tear organisms from the rocks during storms or propel objects such as logs or boulders into them. In addition, stresses caused by low tides that expose organisms to high or low air temperatures can easily kill them or cause them to lose their attachment to the rocks. The resulting bare rock patches become active areas of colonization and succession.

Some of the first experimental work on succession in the rocky intertidal zone was done on boulder fields in Southern California by Wayne Sousa, a graduate student at the time. Sousa (1979b) noticed that the algae-dominated communities on these boulders experienced disturbance every time the boulders were overturned by waves. When he cleared some patches on the boulders and observed succession in those patches over time, he found that the first species to colonize and dominate a patch was always the bright green alga *Ulva lactuca* (**Figure 17.15A**). It was followed by the red alga *Gigartina canaliculata*. To understand the mechanisms controlling this successional sequence, Sousa performed removal experiments on concrete blocks that he had allowed *Ulva* to colonize. He found that colonization by *Gigartina* was accelerated if *Ulva* was removed (**Figure 17.15B**). This result suggested inhibition as the main mechanism controlling succession, but a question remained: if *Ulva* is able to inhibit other seaweed species, why doesn't it always dominate? Through a series of further experiments, Sousa found that grazing crabs preferentially fed on *Ulva*, thus initiating a transition from the early *Ulva* stage to other mid-successional algal species. In turn, the mid-successional species were more susceptible to the effects of stress and parasitic algae than the late successional *Gigartina*. *Gigartina* dominated because it was the least susceptible to stress and consumer pressures.

This view of rocky intertidal succession as driven by inhibition was the accepted paradigm for many years. Facilitation and tolerance were thought to be much less important in a system where competition for space was strong. More recent work by Terence Farrell and others (e.g., Berlow 1997) demonstrated that the relative importance of inhibition is probably much more context-dependent than previously thought. In the more productive rocky intertidal zone of the Oregon coast, the communities include many more sessile invertebrates, such as barnacles and mussels, than Sousa's communities of the Southern California coast, where seaweeds dominate. In the high intertidal zone of Oregon, Farrell (1991) found that the first colonizer of bare patches was a barnacle, *Chthamalus dalli*. It was replaced by another, larger barnacle species, *Balanus glandula*, which was then replaced by three species of macroalgae, *Pelvetiopsis limitata*, *Fucus gardneri*, and *Endocladia muricata*. A series of removal experiments showed that *Chthamalus* did not inhibit colonization by *Balanus*, but that *Balanus* was able to outcompete *Chthamalus* over time, thus supporting the tolerance model. Likewise, *Balanus* did not hinder macroalgal colonization, but in fact facilitated it, lending credibility to the facilitation model.

But why and how would *Balanus* facilitate macroalgal colonization? Farrell suspected that *Balanus* protected the algae in some way, possibly from desiccation stress or grazing by limpets (herbivorous marine snails). To test this idea, Farrell created experimental plots from which *Balanus*, limpets, or both were removed, then observed macroalgal colonization in those plots. He found that macroalgae colonized all of the plots without limpets but had a much higher density in the plots with barnacles than in those without barnacles (**Figure 17.16A**). These results suggested that *Balanus* did indeed act to impede limpets from grazing on newly settled macroalgal sporelings.

You might be asking yourself, Why doesn't *Chthamalus* have the same facilitative effect on macroalgae that *Balanus* does? Farrell suspected that the reason was *Balanus*'s larger size (it is nearly three times wider than *Chthamalus*). By using plaster casts to mimic barnacles that were slightly larger than *Balanus*, Farrell found that these barnacle mimics had an even more positive effect on macroalgal colonization than did smaller-sized live barnacles of either species (**Figure 17.16B**). It seems likely that the smaller and smoother *Chthamalus* does not retain as much moisture, or block as many limpets, as the larger and more sculpted *Balanus*—or the mimics, for that matter.



Macroalgae reached the highest densities in plots where *Balanus* was present and limpets were absent.

Macroalgae reached the highest densities in plots with barnacle mimics.

Plots without *Balanus* had much lower macroalgal densities than plots without *Chthamalus*.

Figure 17.16 Algal Succession on the Oregon Coast Is Driven by Facilitation (A) Changes in macroalgal densities over time were measured in plots from which *Balanus* barnacles, limpets, or both had been removed. The results suggested that *Balanus* facilitates macroalgae by reducing limpet grazing. (B) To understand the mechanisms of the facilitation, large barnacle mimics were added to some plots and compared with plots from which the real barnacle species—*Balanus*, *Chthamalus*, or both—had been removed. The results suggested that the larger the barnacle species, the better it protects macroalgae against limpet grazing and desiccation. (After Farrell 1991.)

Experiments show facilitation to be important in early stages

A number of experimental studies like the ones we have just described, initially stimulated by Connell and Slatyer's 1977 paper, suggest that succession in any community is driven by a complex array of mechanisms (see **Analyzing Data 17.1**). No one model fits any one community; instead, each community is characterized by elements of all three of Connell and Slatyer's models. In most successional sequences, especially those in which a pioneer stage is exposed to physically stressful conditions, facilitative interactions are important drivers of early succession.

ANALYZING DATA 17.1 What Kinds of Species Interactions Drive Succession in Mountain Forests?

We learned in Concept 17.3 that successional patterns are often the result of complex species interactions. Such interactions are exemplified in a study investigating the patterns of succession in mountain forests in Utah dominated by quaking aspen (*Populus tremuloides*) and subalpine fir (*Abies lasiocarpa*) (Calder and St. Clair 2012).* In some cases, aspen can form stable and self-sustaining populations, but more commonly these trees occur in mixed stands with firs. Observations show that aspen initiate the earliest stage of secondary succession in open meadows created by fire or deforestation, using root suckers (underground shoots that produce clonal plants; see Figure 9.5) to colonize open meadows. Over time, mixed aspen–fir stands are formed as the shade-tolerant firs become established and increase in abundance while aspen decline. The stands are eventually dominated by firs, which are more susceptible to fire than pure stands of aspen, thus increasing the chance of starting the successional cycle anew.

To understand the transition from one successional stage to another, Calder and St. Clair counted the aspen suckers and fir seedlings in four successional stages—meadow, aspen, mixed aspen–fir, and fir—with the results shown in **Figure A**. To test for the type of interaction important in the transition from one stage to another, the researchers then measured the mortality of canopy aspen and subalpine fir trees as a function of their distance from the nearest neighboring tree of the other species. These results are given in **Figure B**. Error bars show one SE of the mean.

1. Based on the data in Figure A, what is the pattern of aspen abundance over the four successional stages? How does the abundance pattern of subalpine fir differ? Do these patterns of abundance of aspen and fir support the successional sequence described in the first paragraph above?
2. What type of interspecific interaction would you hypothesize could account for the difference between the number of fir seedlings in the aspen stage and in the meadow stage in Figure A? What type of interspecific interaction might explain the difference between the number of aspen suckers in the mixed and the fir stages?

Figure A

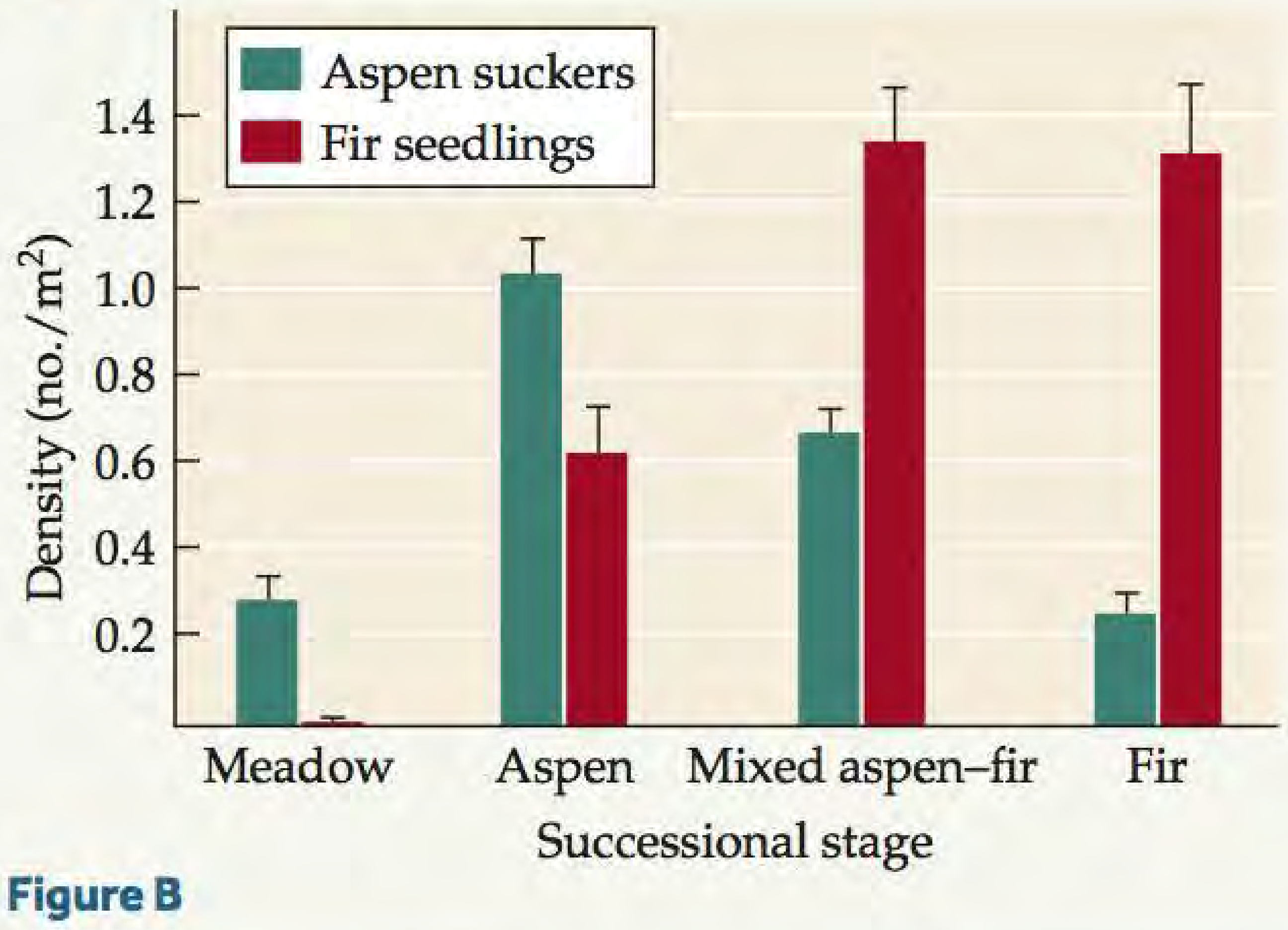
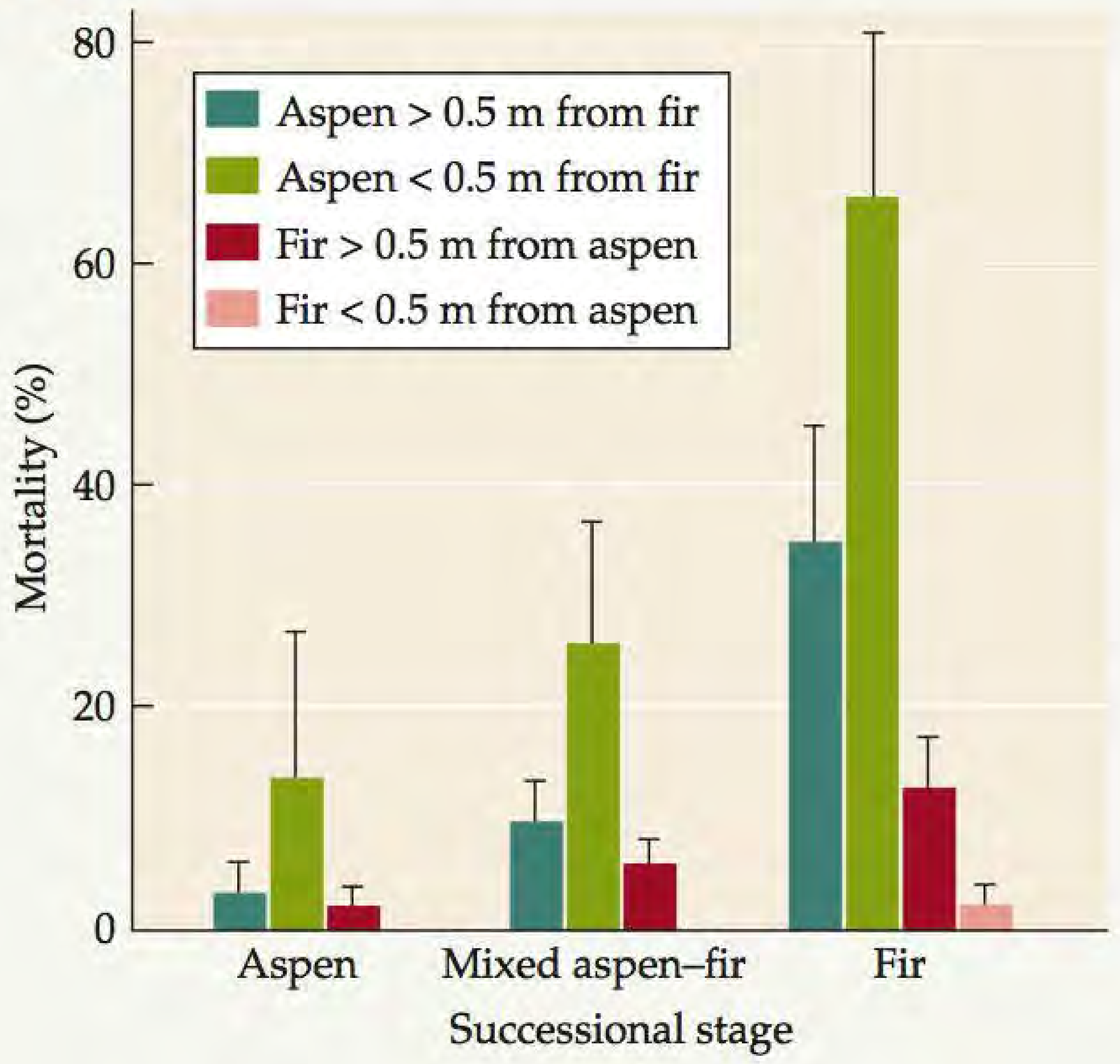


Figure B



3. Now consider Figure B. What happens to fir trees when they live close (<0.5 m) to aspen trees? What happens to aspen when they live close (<0.5 m) to fir trees? Do these data support your previous hypotheses (from question 2) about the types of species interactions driving succession?
4. Which of Connell and Slatyer's three models (see Figure 17.8) best fits the results of this study? Why?

See the companion website for a similar ANALYZING DATA exercise.

---

*Calder, W. J. and S. B. St. Clair. 2012. Facilitation drives mortality patterns along successional gradients of aspen-conifer forest. *Ecosphere* 3: 1–11.

Organisms that can tolerate and modify these physically challenging environments will thrive and facilitate other organisms that lack those capabilities. As succession progresses, slow-growing and long-lived species begin to dominate. Those species tend to be larger and more competitively dominant than early successional species. For this reason, one might expect competition to play a more dominant role than facilitation later in succession.

As succession proceeds, species richness typically increases (see Figure 17.10); thus, we must recognize that vast arrays of both positive and negative interactions are operating in mid- to late successional stages. We will learn more about the mechanisms responsible for controlling species diversity in Chapter 19, but let's turn our attention next to the question of whether succession always takes one predictable path, as Clements believed, or whether other paths are possible.

CONCEPT 17.4

Communities can follow different successional paths and display alternative states.

Alternative Stable States

Up to this point, we have assumed that the trajectory of succession is repeatable and predictable. But what if, for example, a boulder in the rocky intertidal zone of Southern California turns over and, instead of a seaweed community forming, as Sousa (1979b) observed, a sessile invertebrate community forms instead? Or what if *Dryas* never colonizes the till left behind by a glacier at Glacier Bay, but is replaced by a grass that competes with, rather than facilitates, later successional species such as Sitka spruce? Might spruce forests never develop? Possibly. There are cases in which different communities develop in the same area under similar environmental conditions. Ecologists refer to such alternative scenarios as **alternative stable states**. Richard Lewontin (1969) was one of the first to formally define and model alternative stable states in natural communities.

A community is said to have **stability**, or to be stable, when it remains in or returns to the original structure and function after some perturbation. How stable are natural communities? This question has perplexed ecologists for some time, partly because the notion of stability depends on spatial and temporal scale. At a small spatial scale, such as a 1 m^2 plot in a midwestern prairie, there might be considerable change or instability over time. If all the plants were removed from the plot, it is unlikely that all the same species would recolonize that particular plot, and certainly not in the exact same locations. However, if a larger area is considered (e.g., a 100 m^2 plot), the chance of finding the same species increases. Similarly, if one followed the plot for a short time, the chance that its species composition would change would be low. But the longer you observed it, the more likely it would be that the community would change and thus appear unstable. With these caveats in mind, let's take a closer look at examples of communities that, once disturbed, do not revert to previous states, but instead show alternative stable states.

Alternative states are controlled by strong interactors

John Sutherland (1974) studied alternative states in marine fouling communities: the sponges, hydroids, tunicates, and other invertebrates that encrust ships, docks, and other hard surfaces in bays and estuaries. He suspended ceramic tiles from the dock at Duke University Marine Lab in Beaufort, North Carolina, in early spring and allowed them to be colonized by planktonic invertebrate larvae (**Figure 17.17A**). At the end of 2 years, even though a handful of species had colonized the tiles, most of them were dominated by a solitary tunicate species, *Styela*. Its dominance was not universal, however. *Styela* actually declined on Sutherland's tiles during the first winter and was replaced by the hydroid species *Tubularia*. This effect was due to the annual nature of *Styela*, which dies off in winter, and the tunicate quickly regained dominance the following spring when larvae started to settle.

By placing new tiles out periodically, Sutherland also showed that *Styela* was able to persist despite the existence of other potential colonizers. These colonizers fouled the new tiles but were unable to colonize those dominated by *Styela*. For this reason, Sutherland viewed this fouling community as stable. Within a few months, he also identified what he believed to be another stable fouling community, this one dominated by *Schizoporella*, an encrusting bryozoan (see Figure 17.17A). This community developed on new tiles suspended from the dock in late summer and was also impervious to colonization by other species, including *Styela*.

To understand what might be controlling these two alternative outcomes of succession, Sutherland submerged new tiles at the same spot on the dock but excluded fish predators from half of the tiles by surrounding them with cages (**Figure 17.17B**). After a year, Sutherland found that the tiles protected from fish predation had formed communities dominated by *Styela*, while those exposed to fish predation had formed communities dominated by *Schizoporella*. He also noticed that the abundances of both species on the tiles protected from predators were reversed when *Styela* began to die off in the winter. These results suggested that *Styela* is competitively dominant if left undisturbed, but is outcompeted by *Schizoporella* when disturbed. Sutherland explained his original observations of *Styela* dominance by suggesting that fish predation was spotty and that the tunicates themselves, once they reached a certain large size, might have acted as a natural "cage" or predator exclusion mechanism.

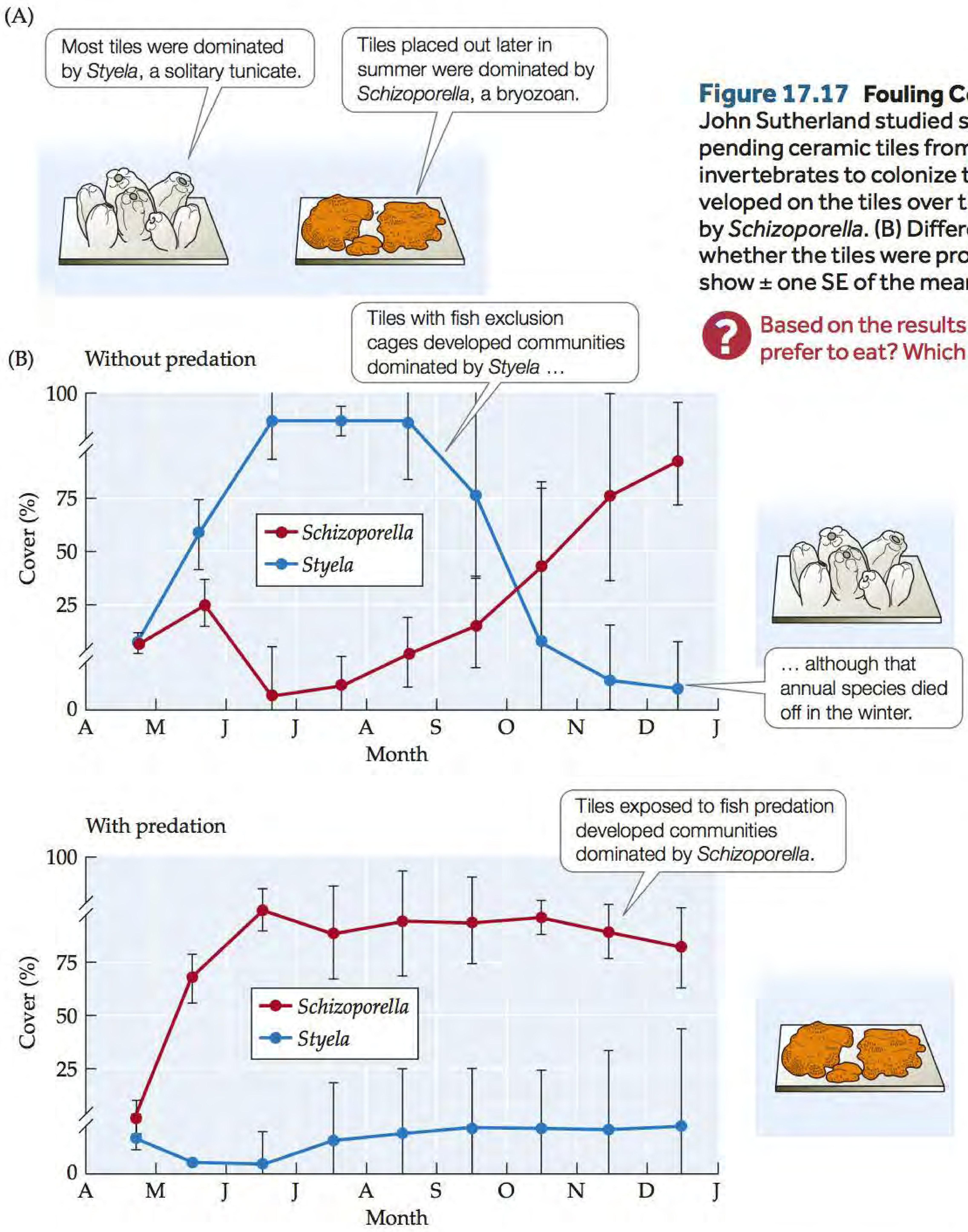
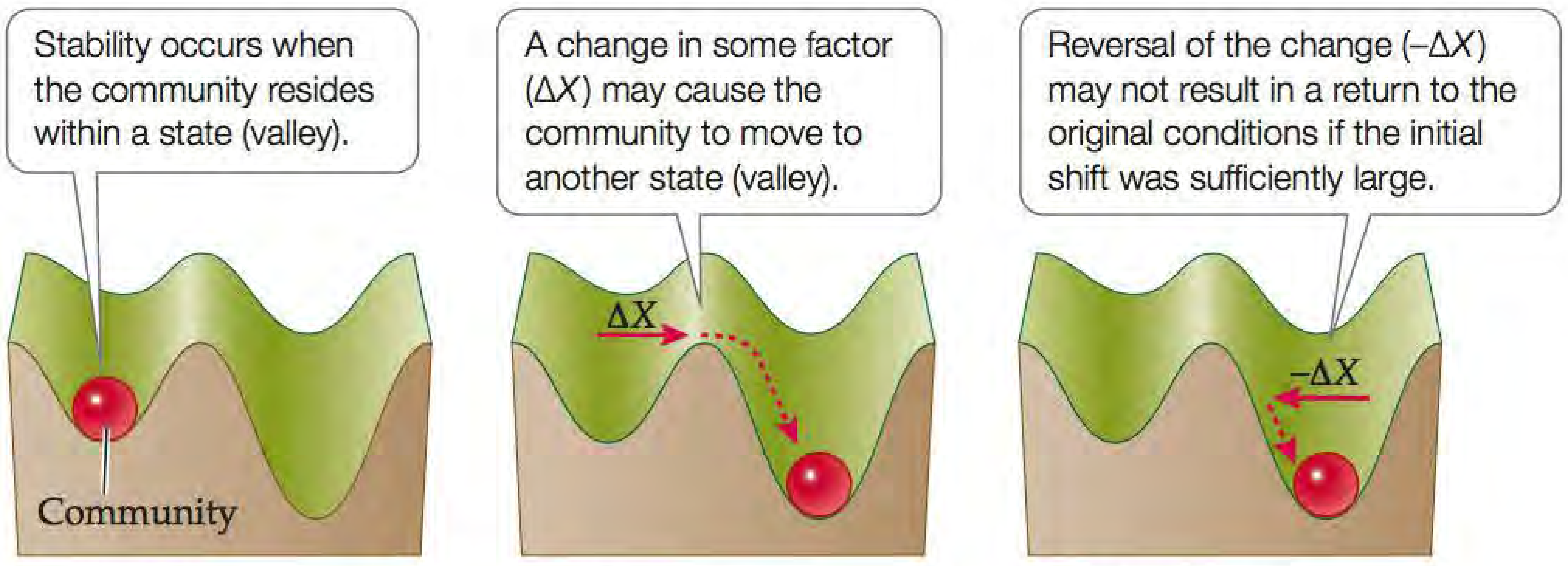


Figure 17.17 Fouling Communities Show Alternative States John Sutherland studied succession in fouling communities by suspending ceramic tiles from a dock in North Carolina and allowing invertebrates to colonize them. (A) Two types of communities developed on the tiles over time, one dominated by *Styela* and another by *Schizoporella*. (B) Different communities developed depending on whether the tiles were protected from fish predation. Error bars show ± one SE of the mean. (After Sutherland 1974.)

? Based on the results shown in (B), which fouling species did fish prefer to eat? Which species was the competitive dominant?

Lewontin (1969) and Sutherland (1974) both believed that multiple stable states existed in communities and could be driven by the addition or exclusion of particularly strongly interacting species. If those species were missing or ineffective, communities could follow alternative successional trajectories that might never lead back to the original community type (state) but might instead form a new community type. We can visualize the theory behind alternative stable states by imagining a landscape in which different states are represented by valleys and in which a community is represented by a ball (**Figure 17.18A**). Just as the ball can move from one valley to another, the community can move from one state to another, depending on the presence or absence of strongly interacting species and how they effect the community (**Figure 17.18B**). For example, it may take only a slight change in the abundance of one or more dominant species to force the community (ball) into an alternative state (valley), or it may require complete removal of a species to cause this change. If we use Sutherland's work as an example, we can think of the *Styela* and *Schizoporella* community types as two different valleys. Whether the ball resides in the *Schizoporella* valley or the *Styela* valley depends on the presence of fish predators. Interestingly, in this system, the ball may not simply move back to the *Schizoporella* valley if access is restored to fish predators (**Figure 17.18C**). As Sutherland noted, *Styela* is able to escape predation once it reaches a certain size. Thus, this system might show **hysteresis**, an inability to shift back to the original community type even when the original conditions are restored.

Connell and Sousa (1983) were skeptical that Sutherland had demonstrated the existence of alternative stable states, for several reasons. First, they thought that his tile communities did not persist long enough, or have a spatial scale large enough, to be considered stable. If the tiles could be followed over multiple years, they asked, would they not all end up being dominated by one or the other species? In addition, they wondered whether the fouling communities could have been sustained outside of an experimental setting in which predators were removed. Their final argument, although it was not a criticism of Sutherland's study per se, was that alternative stable states could be driven only by species interactions and not by physical changes in the community. They argued that many of the examples Sutherland had used to bolster the importance of alternative stable states fell into the latter category. Their requirement that the physical environment not change is problematic because it excludes as drivers of succession all species that interact with other species



(A) Stability (B) Change (C) Hysteresis

Figure 17.18 A Model of Alternative Stable States (A) A community is represented by a ball that moves within a landscape of community states (valleys). (B) Note that some valleys can be deeper than others, suggesting the magnitude of change (ΔX) needed to shift the community from one state to another. (C) Hysteresis occurs when reversal of the change ($-\Delta X$) does not return the community to its original state. (After Beisner et al. 2003.)

by modifying their physical environment—that is, all ecosystem engineers. We know that ecosystem engineers can have strong effects on communities, so excluding them is unrealistic to most ecologists.

Human actions have caused communities to shift to alternative states

The stringent requirements suggested by Connell and Sousa had the effect of delaying alternative stable state research for 2 decades. Recently, however, there has been renewed interest in alternative stable states, spurred by the increasing evidence that human activities, such as habitat destruction, species introductions, and overharvesting of wild species, are shifting communities to alternative states. We have already seen examples of such changes in several of the Case Studies in this book, including the change from kelp forests to urchin barrens due to the decline of sea otters (see Chapter 9), the crash of the anchovy fishery in the Black Sea due to the introduction of *Mnemiopsis* (see Chapter 11), and the invasion of the aquarium strain of *Caulerpa taxifolia* in the Mediterranean, Australia, Japan, and North America (see Chapter 16). These so-called *regime shifts* are caused by the removal or addition of strongly interacting species that maintain one community type over others. Ecologists are uncertain whether the results can be reversed or whether hysteresis will occur once communities have been "manipulated" by human activities and new regimes are in place. Will recolonization by sea otters rejuvenate kelp forests? Will the cessation of nutrient enrichment in the Black Sea revitalize the anchovy fishery? And will the removal of *Caulerpa* restore seagrass communities? These are all questions whose answers may be found in a better understanding of the factors that drive alternative stable states and of the role restoration of the original conditions can play in reversing the effects of those factors.

A CASE STUDY REVISITED

A Natural Experiment of Mountainous Proportions

On the twentieth anniversary of the eruption of Mount St. Helens, in 2000, a group of ecologists gathered on the once smoking and ash-covered volcano to participate in a week-long field camp. They gathered their gear, including tape measures, quadrat frames, and maps, and visited the same sites they had explored 2 decades earlier. This visit, termed a "pulse," was an opportunity to establish a 20-year benchmark of data comparable to those first collected in 1980 and 1981. Many of the participants had spent the past 20 years—for some, their entire careers—studying recolonization and succession patterns in those once-devastated landscapes. When they departed, they agreed to write a book, the chapters of which would contain all that was known about the extraordinary ecology of this ecosystem, with the hope that young ecologists would be motivated to continue the research and carry on their legacy. The book, *Ecological Responses to the 1980 Eruption of Mount St. Helens* (Dale et al. 2005), was published 5 years later.

What does the book tell us about succession on Mount St. Helens? First, the eruption created disturbances that varied in their effects depending on distance from the volcano and habitat type (e.g., aquatic versus terrestrial). Although areas close to the summit, such as the Pumice Plain, were literally sterilized by the heat of the eruption, ecologists were surprised to discover how many species actually survived on the mountain (**Table 17.2**). Because the eruption occurred in spring, many species had been still dormant under the winter snows. Survivors included plants with underground buds or rhizomes, animals such as rodents and insects with burrows, and fish and other aquatic species in ice-covered lakes. In the blowdown zone, large trees and animals perished while smaller organisms survived in the protection of their larger neighbors. The opposite was true in areas outside the blowdown zone, where falling rocks and ash smothered smaller plants and animals, but not larger organisms.

A second important research discovery from Mount St. Helens is the role survivors have played in controlling the pace and pattern of succession. In many cases, these species were thrust into novel physical environments and species assemblages without time to adapt over evolutionary time scales. Some species thrived, while others fared poorly, but their adaptability and unpredictability were surprising. Unlikely alliances were formed that

TABLE 17.2 Surviving Organisms Found on Mount St. Helens within a Few Years after the Eruption

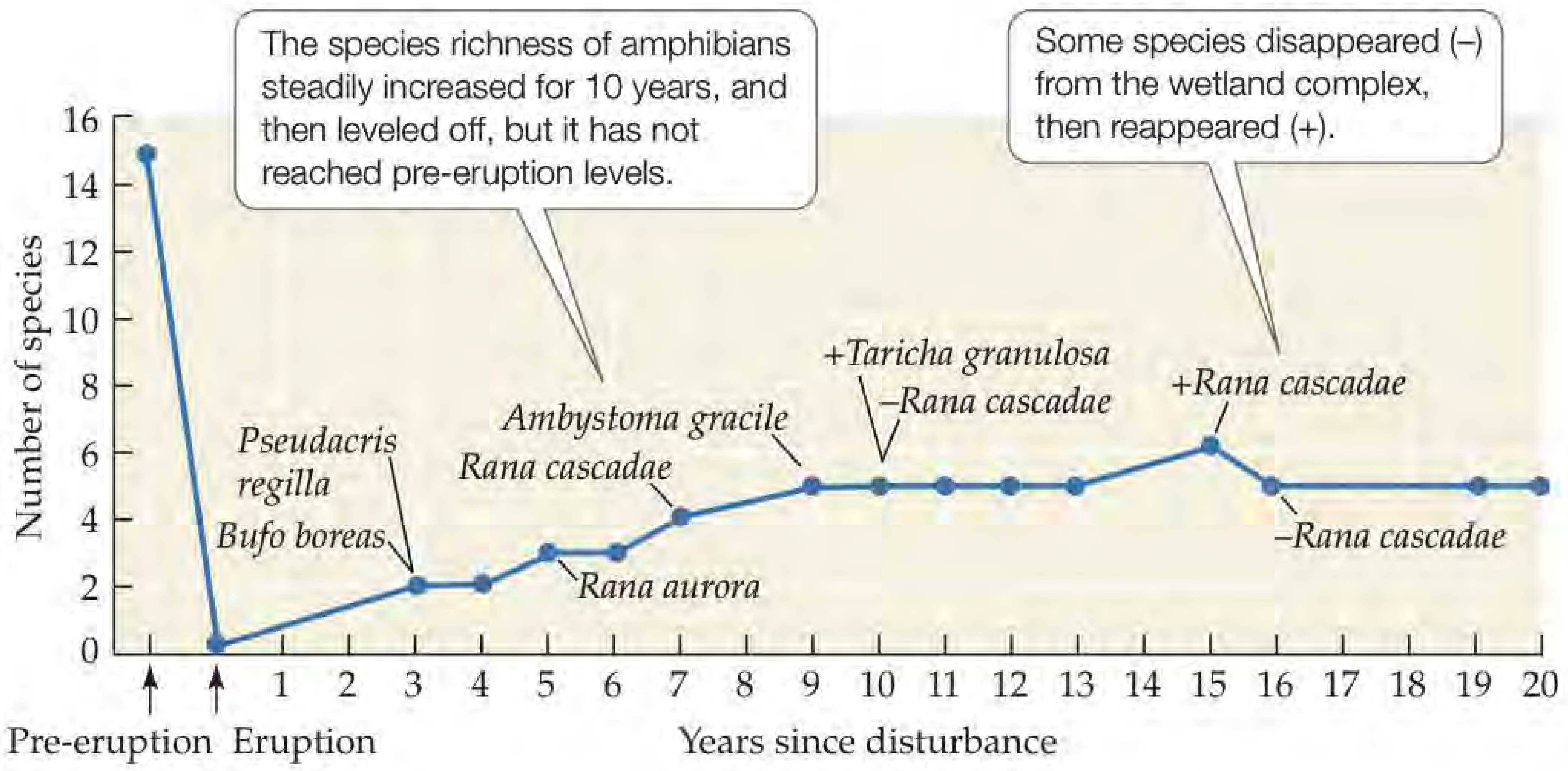
DISTURBANCE ZONE	MEAN VEGETATION COVER (%)	AVERAGE NUMBER OF PLANT SPECIES/m^2	ANIMALS					
			SMALL MAMMALS	LARGE MAMMALS	BIRDS	LAKE FISH	AMPHIBIANS	REPTILES
Pumice Plain	0.0	0.0	0	0	0	0	0	0
Mudflow zone	0.0	0.0	0	0	0	N/A	0	0
Blowdown zone			8	0	0	4	11	1
Pre-eruption clear-cut	3.8	0.0050						
Forest without snow	0.06	0.0021						
Forest with snow	3.3	0.0064						
Scorch zone	0.4	0.0039	0	0	0	2	12	1

Source: Crisafulli et al. 2005.

hastened succession in particular habitats. For example, newly formed and isolated ponds and lakes were colonized by amphibians much faster than had been thought possible (**Figure 17.19**). Scientists discovered that frogs and salamanders were using tunnels created by northern pocket gophers (*Thomomys talpoides*) to make their way from one pond to another across the arid landscape (Crisafulli et al. 2005). The gophers were particularly successful on Mount St. Helens, both because they survived the eruption in their tunnels and because grassy meadows—their preferred habitat—expanded greatly after the eruption. Interestingly, the gophers were also responsible for facilitating plant succession: their burrowing activity brought to the soil surface organic matter, seeds, and fungal spores buried deep under the volcanic rock and ash (Crisafulli et al. 2005) (**Figure 17.20**).

A third important discovery was the realization that multiple mechanisms were responsible for primary succession on Mount St. Helens. Facilitation on the Pumice Plain was exemplified by the dwarf lupine (*Lupinus lepidus*), the first plant to arrive there. Dwarf lupines trapped seeds and detritus and increased the nitrogen content of the soil though their symbiotic association with nitrogen-fixing bacteria (del Moral et al. 2005). The lupines, in turn, were inhibited by multiple insect herbivores, which essentially controlled the pace of primary succession (Bishop et al. 2005). Tolerance was evident in some primary successional habitats, where Douglas fir lived in concert with annual herbs. The diversity of strategies species used, and the resulting community compositions, never ceased to amaze ecologists, who up to that point had been guided mostly by the models of Connell and Slatyer (1977).

Despite decades of data and a treasure trove of novel discoveries, research on Mount St. Helens has only just begun. Another "pulse" visit occurred in 2010 to establish a 30-year benchmark since the eruption. Will communities there follow paths of succession that lead to predictable and repeatable outcomes? Or will they form alternative states that are highly dependent on their historical legacies? Geologic studies suggest that Mount St. Helens erupts roughly every 300 years.



The species richness of amphibians steadily increased for 10 years, and then leveled off, but it has not reached pre-eruption levels.

Some species disappeared (–) from the wetland complex, then reappeared (+).

Figure 17.19 Rapid Amphibian Colonization Frog and salamander species rapidly colonized a wetland complex in the Pumice Plain on Mount St. Helens. (After Crisafulli et al. 2005.)

Figure 17.20 Pocket Gophers to the Rescue The burrowing activity of northern pocket gophers, some of which survived the eruption underground, brought organic matter, seeds, and fungal spores to the soil surface, creating microhabitats, like this one in the Pumice Plain, where plants could grow. (Left from C. Crisafulli.)

The life span of its community succession thus greatly exceeds our own life span by hundreds of years, so we must be content with the limited knowledge we have gained from studying what is arguably the most interesting phase of succession on Mount St. Helens and with the hope that ecologists will continue their research there for years to come.

CONNECTIONS IN NATURE

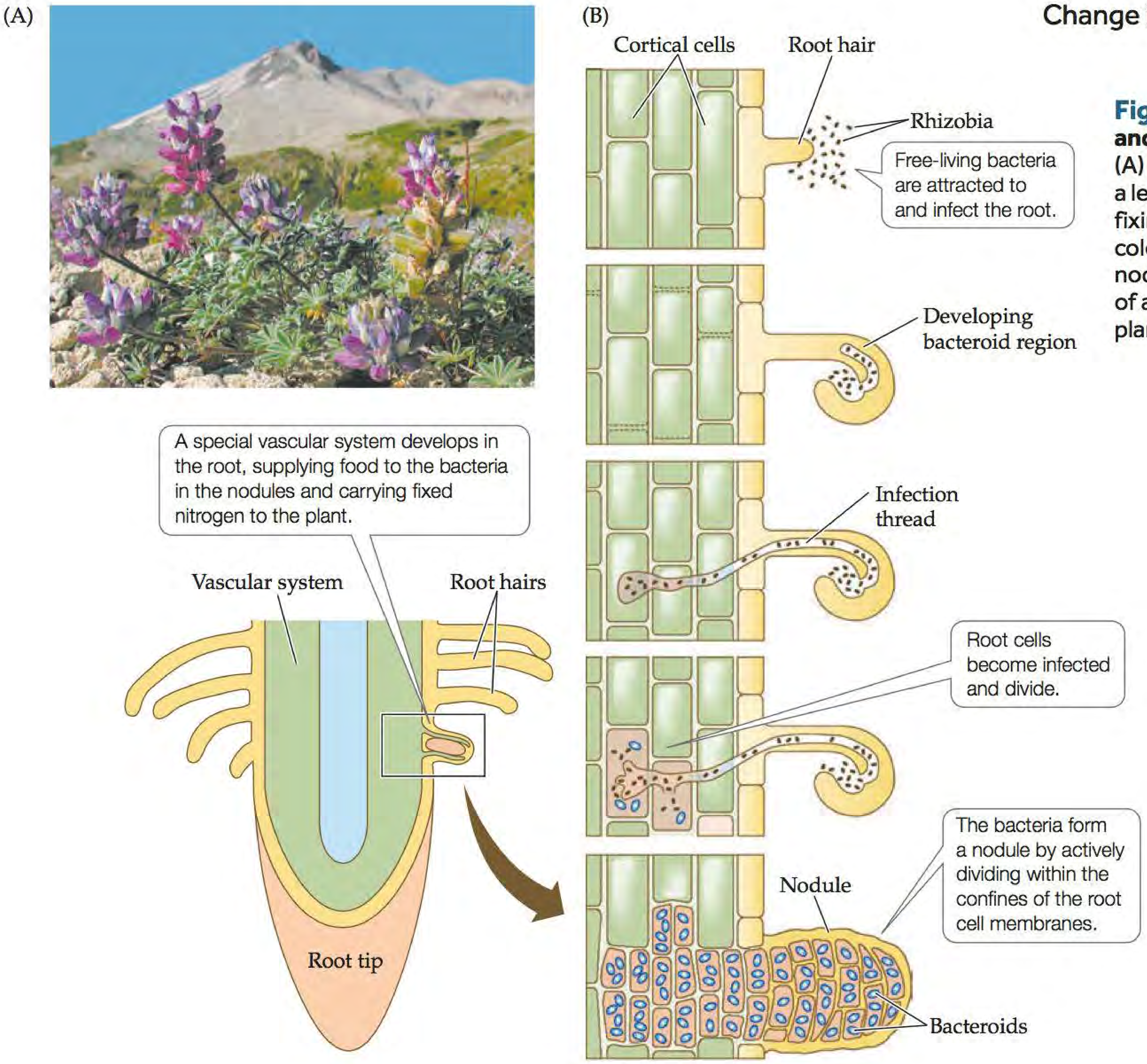
Primary Succession and Mutualism

We saw in Chapter 15 that positive relationships can alter communities, and that they may be particularly important in stressful environments. Primary succession in terrestrial environments illustrates both of these effects: some of the examples presented in this chapter involve plants that interact in a mutualistic way with symbiotic nitrogen-fixing bacteria. These bacteria form nodules in the roots of their plant hosts, where they convert nitrogen gas from the atmosphere (N_2) into a form that is usable by plants [ammonia (NH_4^+)]. The plants provide the bacteria with sugars produced by photosynthesis. This interaction appears to be extremely important for plants and animals colonizing completely sterile environments. We have seen that *Dryas* and alders, both species that form tight mutualisms with nitrogen-fixing bacteria, were some of the first species to colonize the till left behind by glaciers at Glacier Bay, Alaska. Similarly, *Lupinus lepidus* was able to use the nitrogen produced by its bacterial symbionts to colonize the sterile Pumice Plain of Mount St. Helens after the eruption. Lupines were the major source of nitrogen for subsequent plants and herbivorous insects for many years. Thus, lupines and their symbiotic bacteria play a large role in controlling the rate of primary succession on Mount St. Helens.

The nitrogen-fixing bacteria involved in symbioses are extremely diverse. Only a few groups of bacteria live in root nodules; all the rest are associated with either the surfaces of roots or the guts of ruminants. The nodule-forming bacteria include the rhizobia, a taxonomic group associated with legumes (such as lupines), and actinomycetes of the genus *Frankia*, which are associated with woody plants such as alders and *Dryas*. Nodule formation involves a complex series of chemical and cellular interactions between the root and the bacteria (**Figure 17.21**). Free-living bacteria are attracted to root exudates that cause the microbes to attach to the roots and multiply. Sets of genes are activated in both bacterial and root cells that allow the bacteria to enter the root, the root cells to divide, and the nodule to be formed.

The enzyme involved in nitrogen fixing (nitrogenase) is highly sensitive to oxygen and requires anaerobic conditions. Thus, wherever nitrogen-fixing symbioses occur, there are structural components to the interaction (such as membranes within the root nodules) that produce anaerobic conditions. The bacteria, however, need oxygen to metabolize, so a hemoglobin protein known as leghemoglobin, which has a high affinity for oxygen, is produced in the nodules to deliver oxygen to the bacteria in an essentially anaerobic environment. The nodules often have an eerie pink color that is associated with the leghemoglobin. In addition, the nodule develops a specialized vascular system that supplies sugars to the bacteria and carries fixed nitrogen to the plant.

Maintaining a symbiosis with nitrogen-fixing bacteria is costly to plants. Estimates suggest that creating and maintaining the nodules alone costs a plant 12%–25% of its total photosynthetic output. Plants may be able to shoulder this cost, especially if it allows them to live in environments free of competitors and herbivores. But as they increase the nitrogen content of the soils in which they live, plants with symbionts make conditions better for other plant species as well—some of which are likely to be competitors. Thus, these plants face a trade-off between improving the environment for themselves and competing with other species, which makes their role in early successional environments important, if somewhat ironic.



Free-living bacteria are attracted to and infect the root.

A special vascular system develops in the root, supplying food to the bacteria in the nodules and carrying fixed nitrogen to the plant.

Root cells become infected and divide.

The bacteria form a nodule by actively dividing within the confines of the root cell membranes.

Figure 17.21 Dwarf Lupines and Nitrogen-Fixing Bacteria (A) Dwarf lupine (*Lupinus lepidus*), a legume with symbiotic nitrogen-fixing bacteria, was the first plant to colonize Mount St. Helens. (B) Root nodule development is the result of a strong interaction between the plant and the bacteria.

Summary

CONCEPT 17.1 Agents of change act on communities across all temporal and spatial scales.

- Agents of change include both abiotic and biotic factors.
- Abiotic agents of change can act as disturbances (injuring or killing organisms) or as stresses (reducing the growth, reproduction, or survival of organisms).
- Biotic agents of change include negative species interactions such as competition, predation, and trampling. Ecosystem engineers and keystone species are common agents of change.
- Agents of change vary in their intensity, frequency, and areal extent.

CONCEPT 17.2 Succession is the process of change in species composition over time as a result of abiotic and biotic agents of change.

- Succession involves a series of stages that theoretically include a stable end point, or climax stage.
- Primary succession involves the colonization of habitats that are devoid of life.
- Secondary succession involves the reestablishment of a community in which most, but not all, of the organisms or organic constituents have been destroyed.
- Early ecologists were fascinated with succession but disagreed about whether it proceeded in deterministic or random ways.
- Connell and Slatyer proposed three models of succession in 1977, known as the facilitation model, tolerance model, and inhibition model.

CONCEPT 17.3 Experimental work on succession shows its mechanisms to be diverse and context-dependent.

- Multiple studies of succession have shown that no one model fits any one community. Aspects of the facilitation, tolerance, and inhibition models can be seen in almost all systems studied.
- Generally, experiments show that facilitation tends to be important in early stages of succession, and competition in later stages of succession.

(Continued)

Summary (Continued)

CONCEPT 17.4 Communities can follow different successional paths and display alternative states.

- Alternative stable states occur when different communities develop in the same area under similar environmental conditions.
- In communities that experience alternative states, succession is typically controlled by strongly interacting species.
- Human activities have caused regime shifts in communities that may or may not be reversible.

Review Questions

1. List some abiotic and biotic agents of change in communities. Describe the intensities and frequencies with which they are likely to act.
2. Describe the differences between primary and secondary succession and what those differences mean for colonizing species.
3. Connell and Slatyer proposed three separate models of succession: the facilitation model, the tolerance model, and the inhibition model. Choose a hypothetical community and describe the different circumstances that would be required to support each of the models.
4. Why is it hard to determine whether a community is stable? Do you think John Sutherland was able to demonstrate alternative stable states on his ceramic tiles? Why or why not?

ON THE COMPANION WEBSITE

ecology4e.sinauer.com

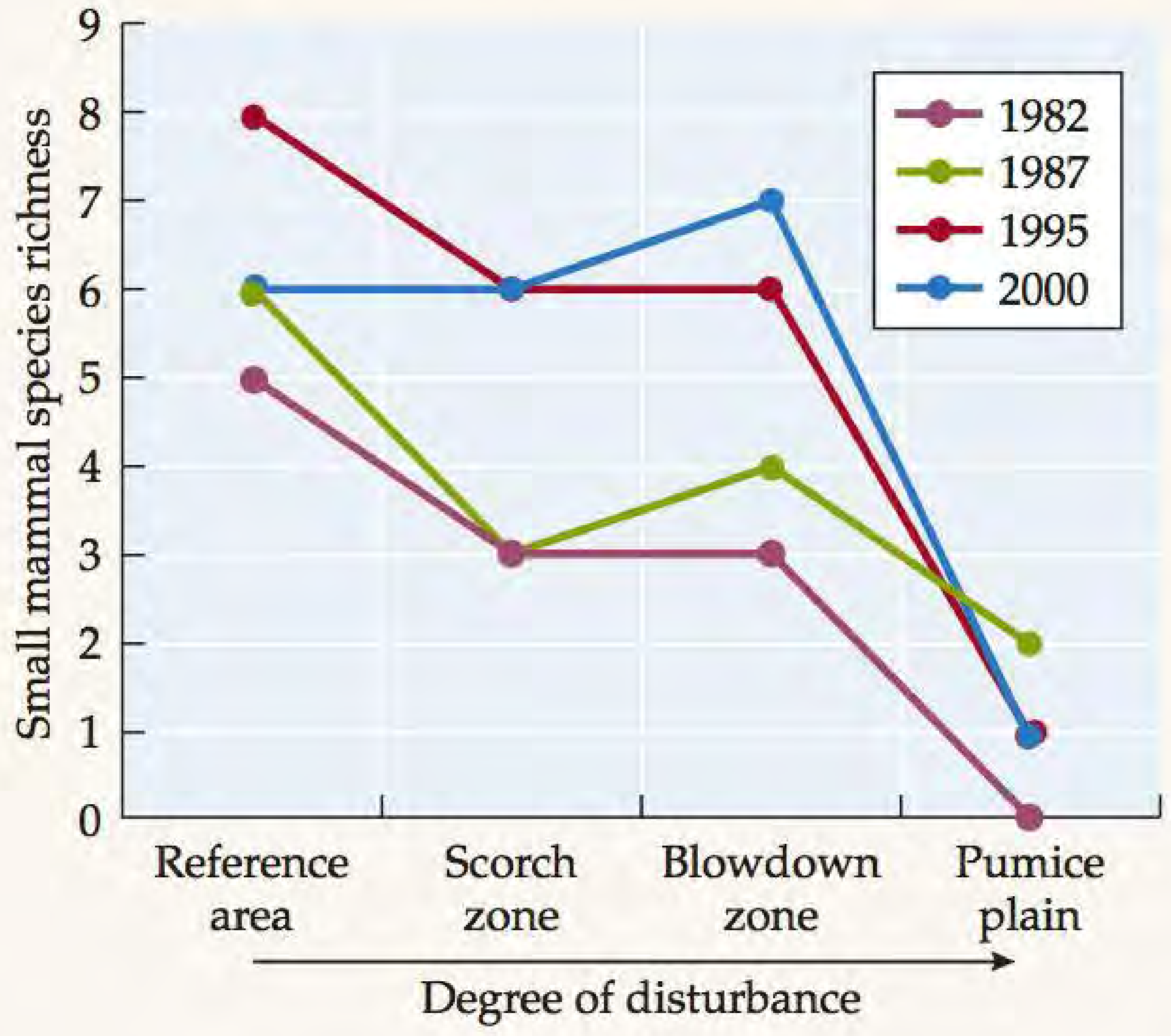
The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

17.1 Starting Over in a Tropical Rainforest: Succession in Ants and Plants

Hone Your Problem-Solving Skills

The eruption of Mount St. Helens created a number of successional communities including primary, secondary, and climax stages. One study by Charles Crisafulli and colleagues (2005) considered the pace of recovery of small mammals in four of these successional communities: the Pumice Plain (primary succession), the blowdown zone (secondary succession), the scorch zone (secondary succession), and an undisturbed reference area 21 km away from the mountain (climax stage). To compare the recovery of small mammals in these successional communities, the researchers conducted extensive trapping between 1982 and 2000. Below is a graph of small mammal species richness over time in different successional communities, organized according to the degree of disturbance the communities experienced from the eruption:



1. What happened to small mammal species richness over time and within the different successional habitats?
2. Did small mammals recover in all or some of the successional habitats, if you use the reference area as a standard for recovery? Describe what you think may have controlled recovery (or lack thereof).
3. The researchers recorded species composition of the small mammals they caught. They found that the deer mouse (*Peromyscus maniculatus*) was the only species present in all four communities. What does this suggest about the deer mouse and its role in succession?
4. The reference area, which served as a control for the small mammal surveys, increased in species richness over time. Give some plausible reasons for this increase.

Biogeography

18

The Largest Ecological Experiment on Earth: A Case Study

There is probably only one place on Earth where a person can hear the calls of 100 species of birds or smell the fragrances of 1,000 species of flowering plants or see the leaf patterns of 300 species of trees, all in 1 hectare (2.5 acres) of land. That place is the Amazon, where half the world's remaining tropical rainforests and species reside. Just 1 hectare (ha) of rainforest in the Amazon contains more plant species than all of Europe! Of course, not all of the species diversity of the Amazon is confined to the rainforest itself. The Amazon Basin contains the largest watershed in the world; one-fifth of all the fresh water on Earth falls on its slopes, collects in over 1,000 forested tributaries, and eventually flows into the Amazon River and out to sea. A trip to a fish market in Manaus, Brazil, would reveal the amazing diversity of aquatic life in these rivers (**Figure 18.1**). The number of fish species in the Amazon Basin exceeds that of the entire Atlantic Ocean.

Ironically, with this incredible species diversity can come devastating species losses when these ecosystems are disturbed. The main destructive force in the Amazon Basin has been deforestation, which began in earnest with the building of roads in the 1960s (Bierregaard et al. 2001). Before then, most of the region had no roads and was relatively isolated from the rest of society. Within 50 years, however, 20% of the rainforest has been converted to pastureland, towns, roads, and mines. Although this percentage might seem modest, it is deceiving, both because of the sheer number of species involved and because of the pattern of deforestation. Logging practices have caused extreme *habitat fragmentation*, sometimes resulting in a "fishbone" pattern in which thin linear fragments of rainforest are surrounded by strips of nonforested land. As we will see, habitat fragmentation can have serious consequences for species diversity.

The fragmentation of the Amazon rainforest motivated Thomas Lovejoy and his colleagues to initiate one of the largest and longest-running ecological experiments ever conducted. The Biological Dynamics of Forest Fragments Project (BDFFP) began in 1979, and Lovejoy seized a unique opportunity to find out what was happening to the species diversity of the Amazon as logging eliminated

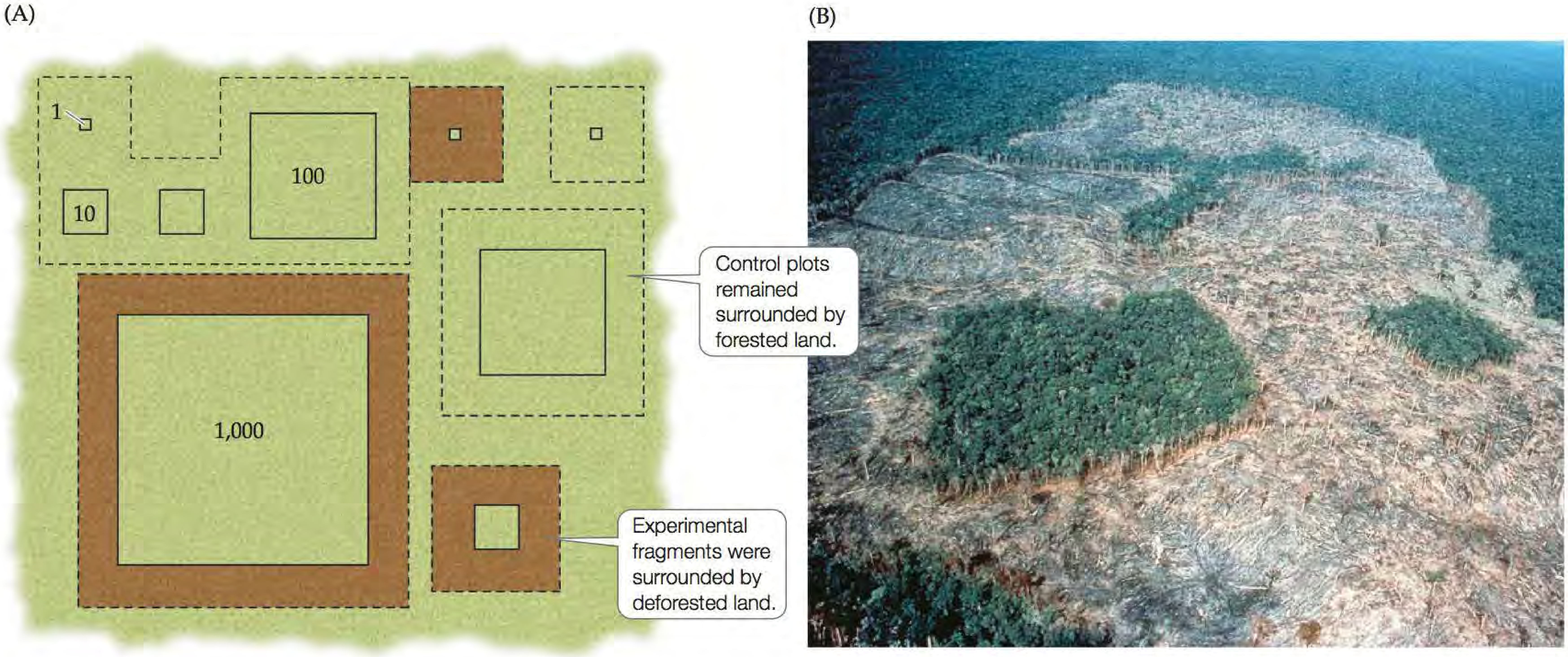
KEY CONCEPTS

CONCEPT 18.1 Patterns of species diversity and distribution vary at global, regional, and local spatial scales.

CONCEPT 18.2 Global patterns of species diversity and composition are influenced by geographic area and isolation, evolutionary history, and global climate.

CONCEPT 18.3 Regional differences in species diversity are influenced by area and distance, which determine the balance between immigration and extinction rates.

Figure 18.1 Diversity Abounds in the Amazon Freshwater fish caught in the Amazon River on display in a market in Manaus, Brazil.



Control plots remained surrounded by forested land.

Experimental fragments were surrounded by deforested land.

Figure 18.2 Studying Habitat Fragmentation in Tropical Rainforests The Biological Dynamics of Forest Fragments Project (BDFFP) near Manaus, Brazil, was designed to study the effects of habitat fragment size on species diversity. (A) Plots of four sizes (1, 10, 100, and 1,000 ha) were designated before logging took place, then either isolated by logging or left surrounded by forest as controls. (B) Aerial photo of a 10 ha and a 1 ha fragment isolated in 1983. (A after Bierregaard et al. 2001.)

? Why didn't the experimental manipulation involve removing forest from the fragments?

more and more of the forest. He was guided by an elegant model in Robert MacArthur and Edward O. Wilson's 1967 book *The Theory of Island Biogeography*, which presents an explanation for the observation that more species are found on large islands than on small islands. By taking advantage of a Brazilian law requiring landowners to leave half of their land as forest, Lovejoy arranged to designate different-sized forest plots that would be surrounded by either forested land (control plots) or deforested land (fragments) (**Figure 18.2**). The control plots and fragments were designated before logging took place and were either 1, 10, 100, or 1,000 ha in size. Baseline data collected immediately after logging showed little difference in species diversity between control plots and fragments.

By the mid-1980s, the ecologists had a fully replicated experiment at a scale unimaginable in the past. Over the last 38 years, the BDFFP has evolved from a study that asks the simple question, What is the minimum area of rainforest needed to maintain species diversity? to one that asks, What roles do the shape, configuration, and connectivity of forest fragments play in maintaining species diversity? How does the surrounding habitat influence that diversity? And what is the prognosis for the Amazon rainforest, one of the most deforested but species-rich terrestrial biomes on Earth?"

Introduction

Looking out over a community such as a rocky intertidal zone on the Northern California coast, it is obvious that the locations of species on the shoreline are influenced not only by physical factors, such as tide height and wave action, but also by a variety of biological interactions. Sea stars eat sessile mussels in the low intertidal zone, thus limiting them to the higher intertidal zones. In those zones, the crevices between mussels provide habitat for many species that otherwise would be absent. Local conditions such as these are important regulators of species distributions. However, as important as these conditions appear to us, we must always be cognizant of the influence of processes operating at larger geographic scales. Oceanographic processes, such as currents and ocean upwelling, regulate the delivery of invertebrate larvae to rocky shorelines. At a global scale, oceanic circulation patterns control current direction. By limiting dispersal, those patterns can isolate species over ecological and evolutionary time. As a result, the local assemblage of species on the Northern California coast is ultimately based on a foundation of global and regional processes. In this chapter, we will consider the effects of these large-scale geographic processes on one of the most recognizable ecological patterns known: the distribution and diversity of species on Earth.

CONCEPT 18.1

Patterns of species diversity and distribution vary at global, regional, and local spatial scales.

Biogeography and Spatial Scale

One of the most obvious ecological patterns on Earth is the variation in species composition and diversity among geographic locations. The study of this variation is known as **biogeography**. Pretend for a moment that you have a lifelong desire to see all the forest biomes on Earth. In this imaginary scenario, you have the ability to move from one geographic region on Earth to another. Think Google Earth, but with the ability to fly down into a community and see species up close. You start in the tropics at 4°S latitude and 60°W longitude and fly into the Amazon rainforest, the most species-rich forest on Earth (**Table 18.1**). At 20 m altitude, you fly through the middle of the humid forest, and as you travel over each hectare, you see new tree species (**Figure 18.3A**). You may have encountered half of them in the previous hectare, but at least half are completely new. The more area you cover, the more tree species you see. The richness is almost overwhelming, and the heat and humidity are stifling, so you decide to head north to drier climes.

You arrive at 35°N, 125°W. This is the southern coast of California, where the forests are oak woodland—a dry biome, as we learned in Chapter 3. Most of the trees and shrubs are evergreen, but they are not conifers. Instead, they are flowering plants with small, tough (*sclerophyllous*) leaves. The woodlands are interspersed with grasslands (**Figure 18.3B**). Flying down through the vegetation, you

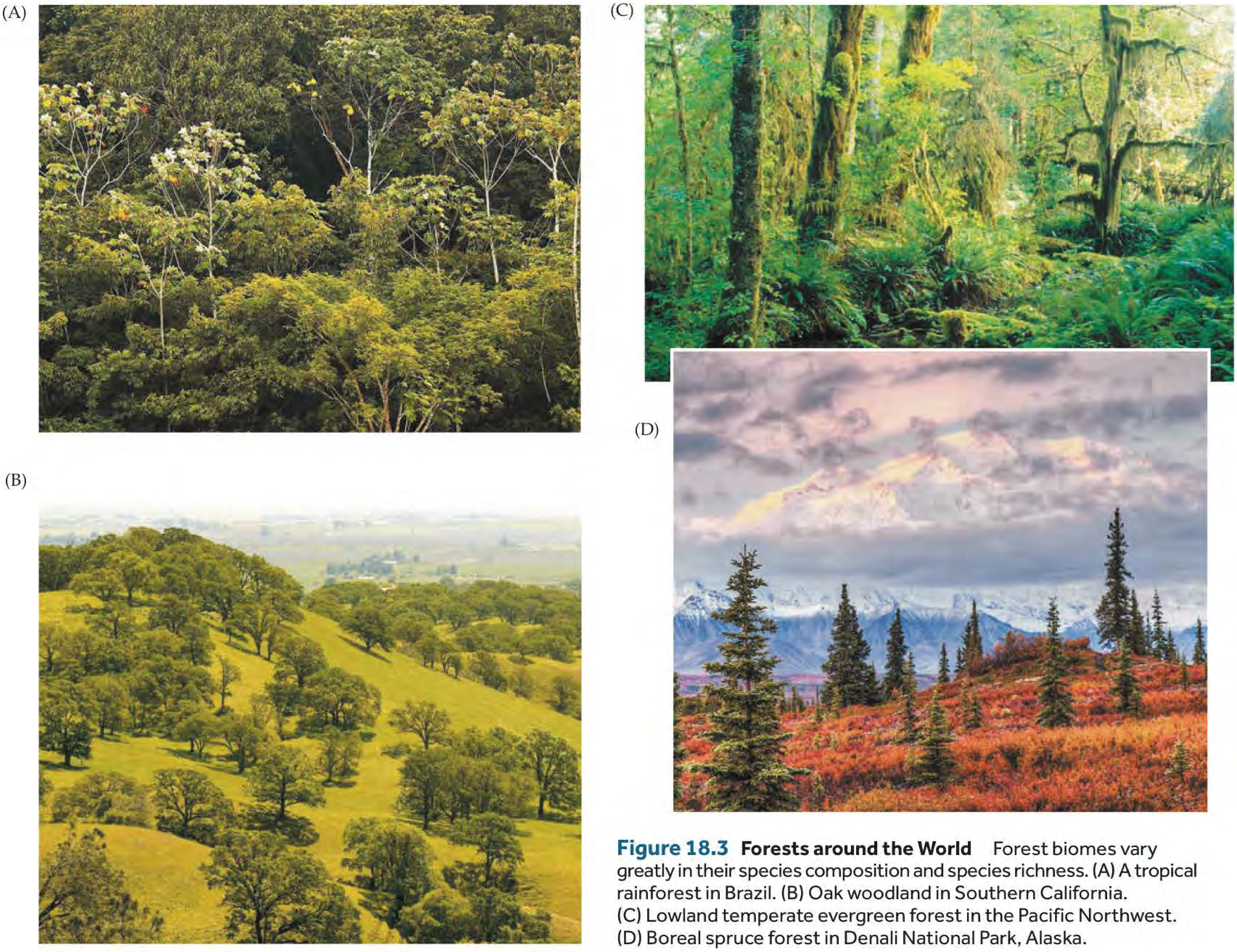


Figure 18.3 Forests around the World Forest biomes vary greatly in their species composition and species richness. (A) A tropical rainforest in Brazil. (B) Oak woodland in Southern California. (C) Lowland temperate evergreen forest in the Pacific Northwest. (D) Boreal spruce forest in Denali National Park, Alaska.

TABLE 18.1 Tree Species Richness in Different Forests around the World

FOREST LOCATION/TYPE	LATITUDE, LONGITUDE	APPROXIMATE TREE SPECIES RICHNESS	SOURCE
Amazon, Brazil	4°S, 60°W	1,300	Laurance 2001
Southern California, USA	35°N, 125°W	57	Allen et al. 2007
Pacific Northwest, USA			Franklin and Dyrness 1988
Douglas fir forest	45°N, 123°W	7	
Garry oak forest	45°N, 123°W	4	
Boreal forest, Canada	64°N, 125°W	2	Kricher 1998
New Zealand			Dawson and Lucas 2000
Beech forest	45°S, 170°E	20	
Flowering tree forest	35°S, 170°E	100	

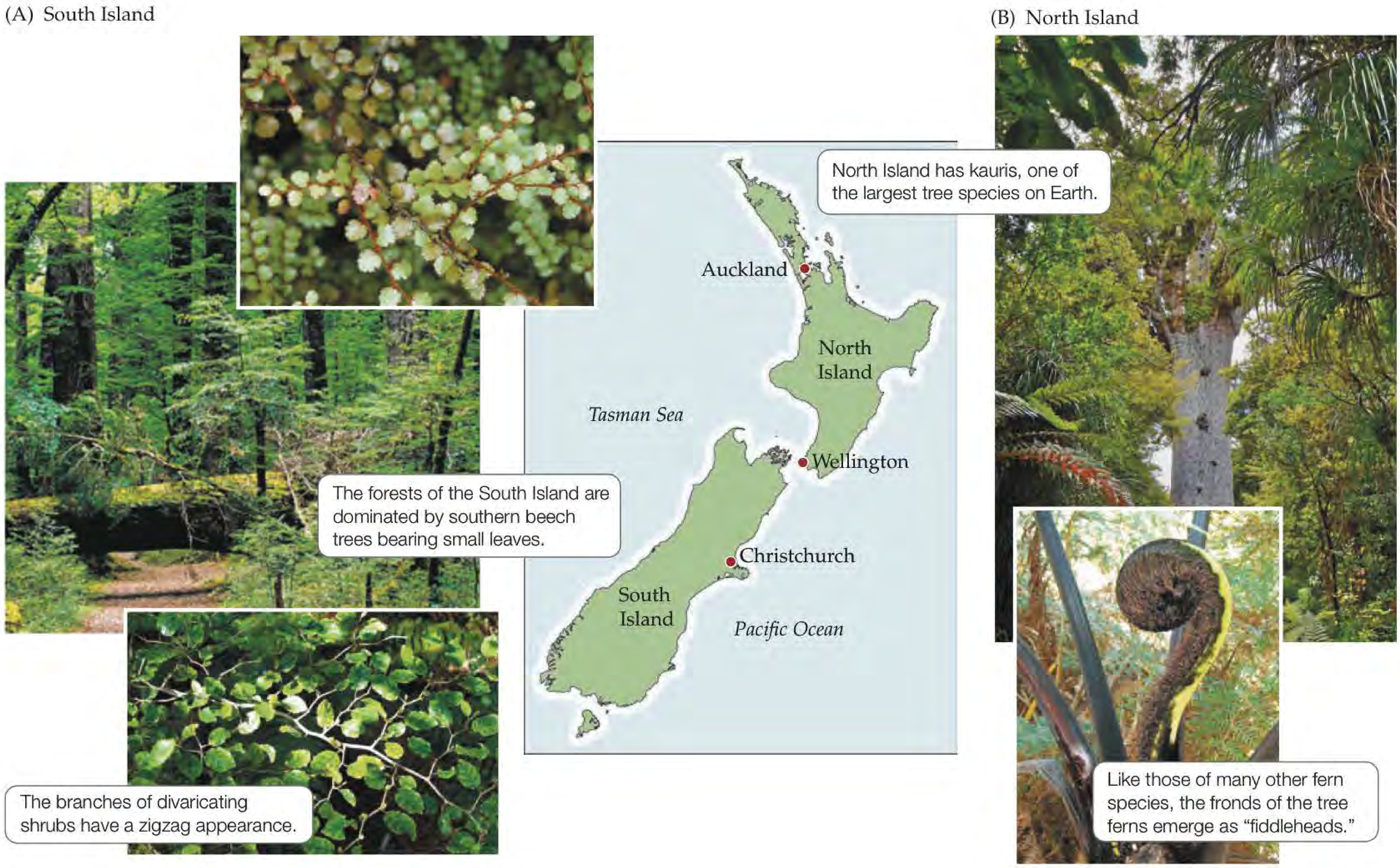
notice the many kinds of trees and shrubs, all with small leaves and thick bark. The woodland is aromatic because of the volatile oils contained in the shrubs and herbaceous plants. Plant species richness is high, but just a fraction of that in the Amazon (see Table 18.1).

It's still warm, so you decide to head north to 45°N, 123°W, where the forest is cool and very wet. You are in the Pacific Northwest region of North America, where the forests are dominated by large conifers. As you fly through, you notice the lushness of the forest, with its lichen-filled canopy and fern-covered floor (**Figure 18.3C**). Tree species richness in these lowland temperate evergreen forests is a fraction of that in the two previous forests you've visited (see Table 18.1). There are only a handful of tree species: Douglas fir, western hemlock, western red cedar, red alder, and big leaf maple. What these forests lack in species richness, however, is made up by their huge biomass.

You want to see the extremes in species richness, so your next stop is 64°N, 125°W, in the boreal forests of Canada. Flying over the cold landscape, you notice rows and rows of identical spruce trees, broken once in a while by large wetlands (**Figure 18.3D**). Dipping down into the canopy, you are struck by the dense and monotonous nature of the forest. It's dark down under those spruce boughs, but low-lying berry bushes are a reminder that light does penetrate the canopy, especially in the summer months. You continue to fly north, and the forests thin until the landscape is one long expanse of treeless tundra.

Your trip could end here, but you have always wanted to visit New Zealand, so you take the time to fly back to the Southern Hemisphere. New Zealand was separated from the ancient continent of Gondwana roughly 80 million years ago, and since that time, evolution has produced unique forests there (**Figure 18.4**). Roughly 80% of the species in New Zealand are **endemic**, meaning that they occur nowhere else on Earth. Dialed into 45°S, 170°E, on the South Island of New Zealand, you fly through the Southern Hemisphere equivalent of the Pacific Northwest. Instead of conifers, the forests are dominated by four species of southern beech trees with billowy layers of twisted branches (see Figure 18.4A). Below the canopy are "divaricating shrubs," whose multiple-angled branches give them a zigzag appearance. Plants with this growth form are found in highest abundance in New Zealand. Although temperate evergreen forests in the Northern and Southern Hemispheres are similar in some ways (e.g., each has low tree species richness compared with forests in the tropics), they are made up of completely different species assemblages with very different evolutionary histories.

Even within New Zealand, over a distance that extends from 35°S to 47°S (a latitudinal distance identical to that from Southern California to British Columbia in the Northern Hemisphere), there are big differences in tree species richness and composition. The North Island is warmer (closer to the equator) than the South Island and has more diverse forests, consisting of many flowering tree species with a few tall emergent conifers (see Figure 18.4B). These forests have a tropical feel to them because of all the flowering trees and the multitude of vines and epiphytes (plants and lichens that live on larger plants). The tree ferns growing here are similar to those that were dominant 100 million years ago, during the age of the dinosaurs. One of the most extraordinary trees is the kauri (*Agathis australis*), which is among the largest tree species on Earth (interestingly, the largest is the giant sequoia, *Sequoiadendron giganteum*, which occurs at roughly the same latitude in the Northern Hemisphere). Some kauri trees are 60 m (200 feet) high and 7 m (23 feet) in diameter. Unfortunately, like redwoods, kauris have been extensively logged, and they exist in a forest community



North Island has kauris, one of the largest tree species on Earth.

The forests of the South Island are dominated by southern beech trees bearing small leaves.

The branches of divaricating shrubs have a zigzag appearance.

Like those of many other fern species, the fronds of the tree ferns emerge as "fiddleheads."

Figure 18.4 Forests of the North and South Islands, New Zealand The two islands of New Zealand span a large latitudinal gradient (35°S–47°S) and thus have different forest types. (A) The forests of the South Island are dominated by beeches. (B) The forests of the warmer North Island have greater tree species diversity and a different species composition than those on the South Island (see Table 18.1).

in only two small reserves, 100 km^2 in total size. Given that old-growth stands of kauris take 1,000–2,000 years to generate, these forests are virtually irreplaceable. If we contrast the tree species richness of the forests characteristic of the North Island with those on the South Island, we find more than 100 tree species in the warmer northern forests, compared with the 10–20 species in the less diverse beech forests characteristic of the temperate south (see Table 18.1).

With our world forest tour at its end, what can we conclude about biogeographic patterns on Earth, assuming that forest communities are good global representatives?

- First, species richness and composition vary with latitude: the lower tropical latitudes have many more, and different, species than the higher temperate and polar latitudes.
- Second, species richness and composition vary from continent to continent, even where longitudes or latitudes are roughly similar.
- Third, the same community type or biome can vary in species richness and composition depending on its location on Earth.

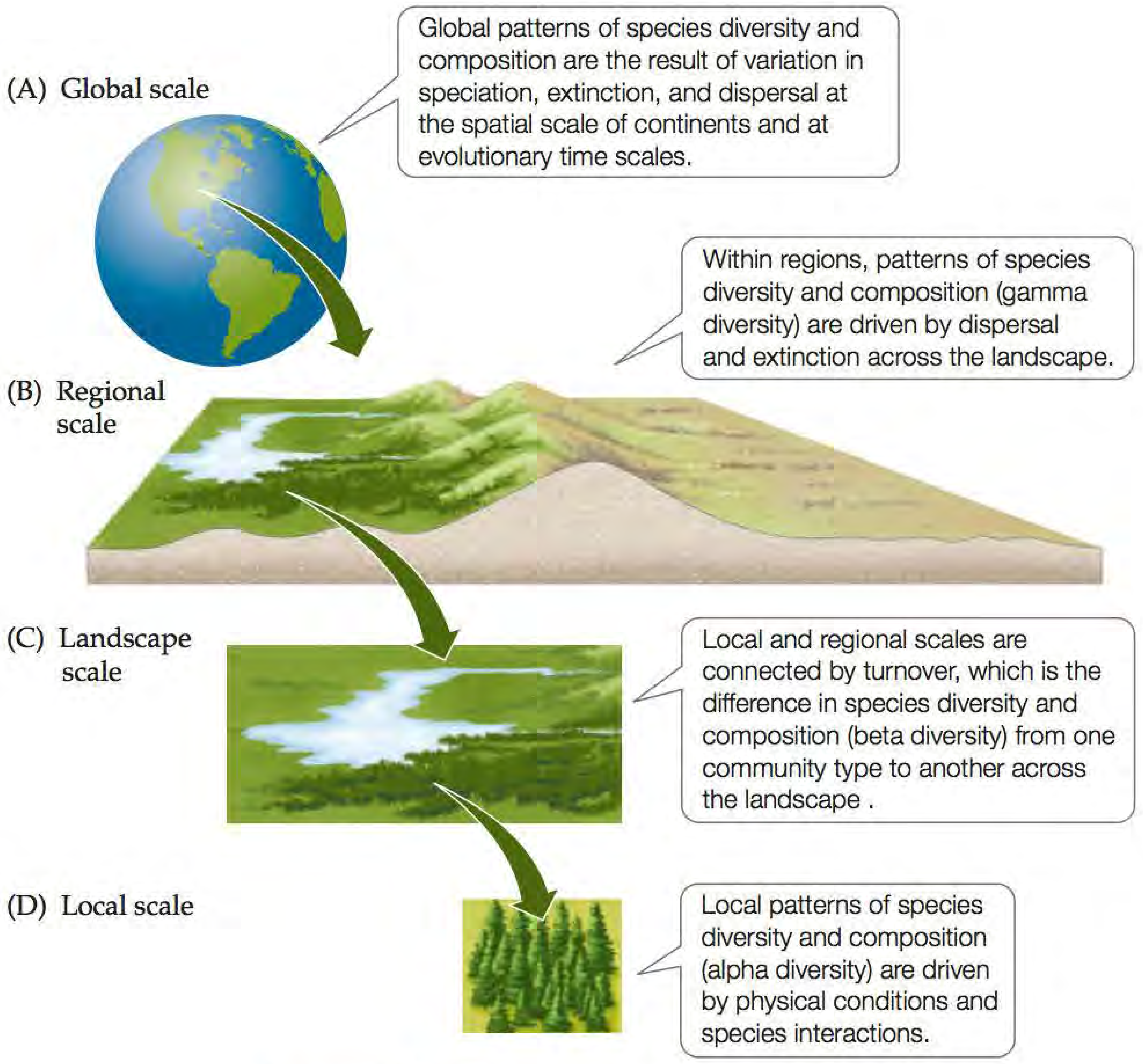
As we will see in the rest of this chapter, these are reliable patterns that have been demonstrated over and over again for many regions of the world and many community types. What has puzzled naturalists for centuries is just what processes control these biogeographic patterns. Why are more species found in some areas than in other areas? Why do some regions harbor species assemblages that are not found anywhere else on Earth?

A number of hypotheses have been proposed to explain biogeographic variation in species composition and diversity. As we'll see, these hypotheses are highly dependent on the spatial scale at which they are applied. In other words, as one of the ecological maxims presented in Table 1.1 states, space matters, so let's deal with the issue of spatial scale.

Patterns of species diversity at different spatial scales are interconnected

On our world forest tour, we saw that patterns of species diversity and composition varied at global, regional, and local spatial scales. We can think of these spatial scales as interconnected in a hierarchical way, with patterns of species diversity and composition at one spatial scale setting the conditions for patterns at smaller spatial scales (Whittaker et al. 2001). Let's start with the largest spatial scale and work downward.

The *global scale*, as the term suggests, includes the entire world, a huge geographic area over which there are major variations with changes in latitude and longitude (**Figure 18.5A**). Species have been isolated from one another, often on different continents or in different oceans, by long distances and over long time periods. Differences in the rates of three processes—speciation, extinction, and dispersal—help determine differences in species diversity and composition at the global scale. We will consider these processes in more detail in the following section.



Global patterns of species diversity and composition are the result of variation in speciation, extinction, and dispersal at the spatial scale of continents and at evolutionary time scales.

Within regions, patterns of species diversity and composition (gamma diversity) are driven by dispersal and extinction across the landscape.

Local and regional scales are connected by turnover, which is the difference in species diversity and composition (beta diversity) from one community type to another across the landscape .

Local patterns of species diversity and composition (alpha diversity) are driven by physical conditions and species interactions.

Figure 18.5 Interconnected Spatial Scales of Species Diversity The arrows represent the relationships between, and processes important to, species diversity and composition at (A) global, (B) regional, (C) landscape, and (D) local scales.

The **regional scale** encompasses smaller geographic areas in which the climate is roughly uniform and to which species are restricted by dispersal limitation (see Concept 9.2). All the species contained within a region are known as the **regional species pool**, sometimes called the **gamma diversity** of the region (**Figure 18.5B**). Earth's regions differ in species diversity and composition because of differences in the rates of speciation, extinction, and dispersal at the global scale, as mentioned above. The Amazon, for example, has many more species, and thus a larger species pool, than the Canadian boreal forest.

The physical geography of a region, such as the number, area, and distance from one another of mountains, valleys, deserts, islands, and lakes—referred to collectively as the *landscape*—is critical to within-region biogeography. Species composition and diversity vary within a region depending on how the landscape shapes the rate of extinction in, and the rates of immigration to and emigration from, local habitats (**Figure 18.5C**). Ecologists consider within-region biogeography in two related ways:

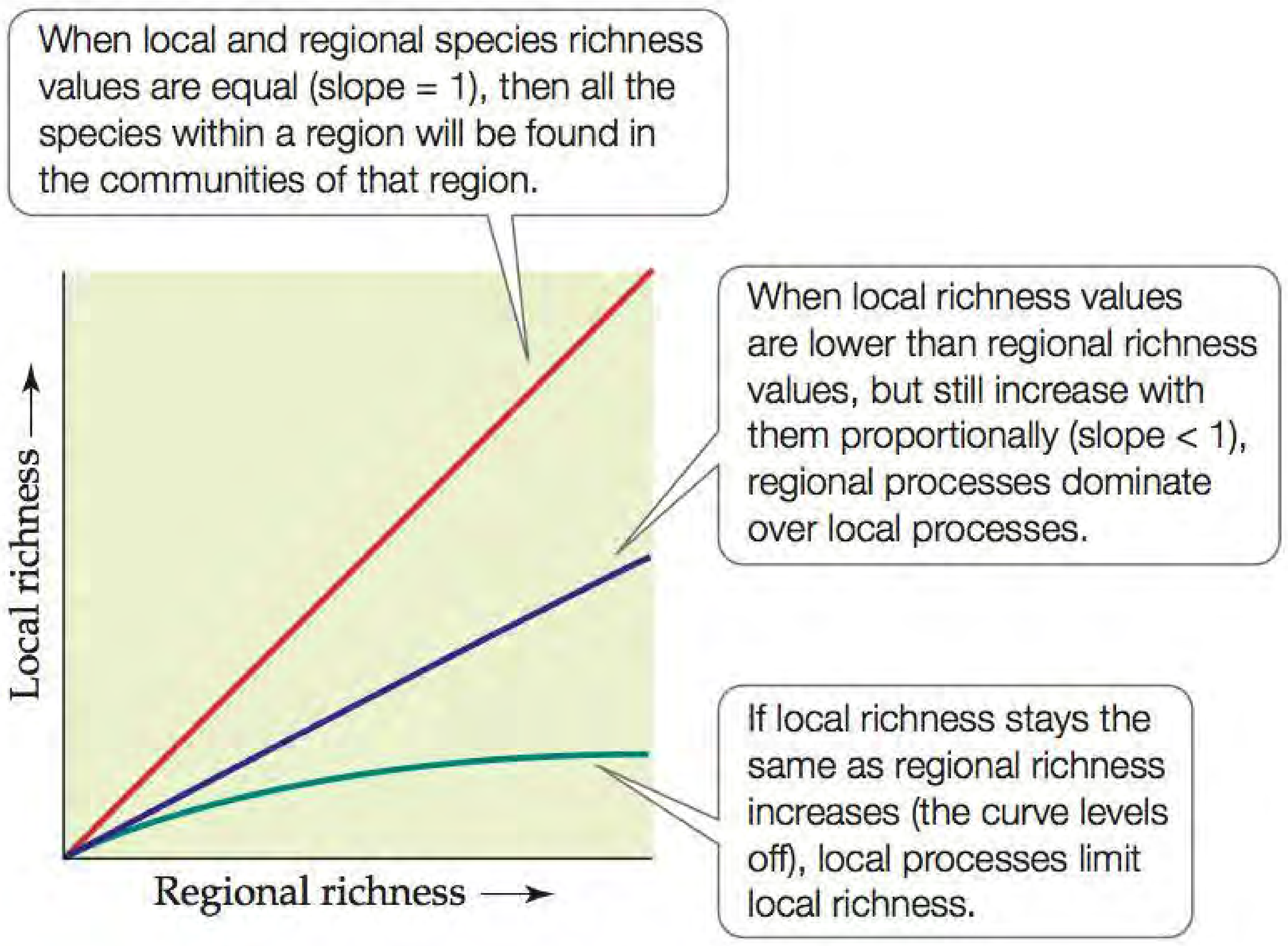
- The **local scale**, which is essentially equivalent to a community, reflects the suitability of the abiotic and biotic characteristics of habitats for species from the regional species pool once they reach those habitats through dispersal (**Figure 18.5D**). Species physiology and interactions with other species both influence species diversity at the local scale (sometimes called **alpha diversity**).
- The connection between local and regional scales of species diversity is expressed by a measurement known as **beta diversity**. Beta diversity tells us the change in species diversity and composition, or **turnover** of species, as one moves from one community type to another across the landscape (see Figure 18.5C).

Knowing how spatial scales are related to one another in a hierarchical way is important, but are there actual area values one could apply to local and regional spatial scales? For example, how much area does a region or locality encompass? The answer is highly dependent on the species and communities of interest. For example, Shmida and Wilson (1985) suggest that terrestrial plants might have a local scale of 10^2–10^4 m^2 and a regional scale of 10^6–10^8 m^2. But for bacteria, the local scale might be something more like 10^2 cm^2. As we will see, the actual area we use to define species diversity measurements can be critical to our interpretation of the processes controlling biogeographic patterns.

Local and regional processes interact to determine local species diversity

Figure 18.5 shows that patterns of species diversity, and the processes that control them, are interconnected across spatial scales. Given these interconnections, ecologists are interested in knowing just how much variation in species diversity at the local scale is dependent on larger spatial scales. The regional species pool provides the raw material for local species assemblages and sets the theoretical upper limit on species richness for communities in the region. But is local species richness also determined by local conditions, including species interactions and the physical environment?

One way we can consider this question quantitatively is by plotting the local species richness for a community against the regional species richness for that community (**Figure 18.6**). Three basic types of relationships can be seen in such plots. First, if local species richness and regional species richness are equal (slope = 1), then all the species within a region will be found in the communities of that region. Although this pattern is theoretically possible, we would not expect to find it in the real world, for the simple reason that all regions have varying landscape and habitat features that exclude some species from some communities (e.g., lowland tree species will not be found in alpine forests). Second, if local species richness is simply proportional to regional species richness (i.e., local species richness increases with increasing regional species richness, but the relationship is not 1:1), then we can assume that local species richness is largely determined by the regional species pool, with local processes such as species interactions and physical conditions playing a more minor role. Finally, if local species richness levels off despite an increasing regional species pool, then local processes can be assumed to limit local species richness. The degree to which local richness levels off can tell us something about how important species interactions and physical conditions are in setting a *saturation point*—a limit on species richness—for communities.



When local and regional species richness values are equal (slope = 1), then all the species within a region will be found in the communities of that region.

When local richness values are lower than regional richness values, but still increase with them proportionally (slope < 1), regional processes dominate over local processes.

If local richness stays the same as regional richness increases (the curve levels off), local processes limit local richness.

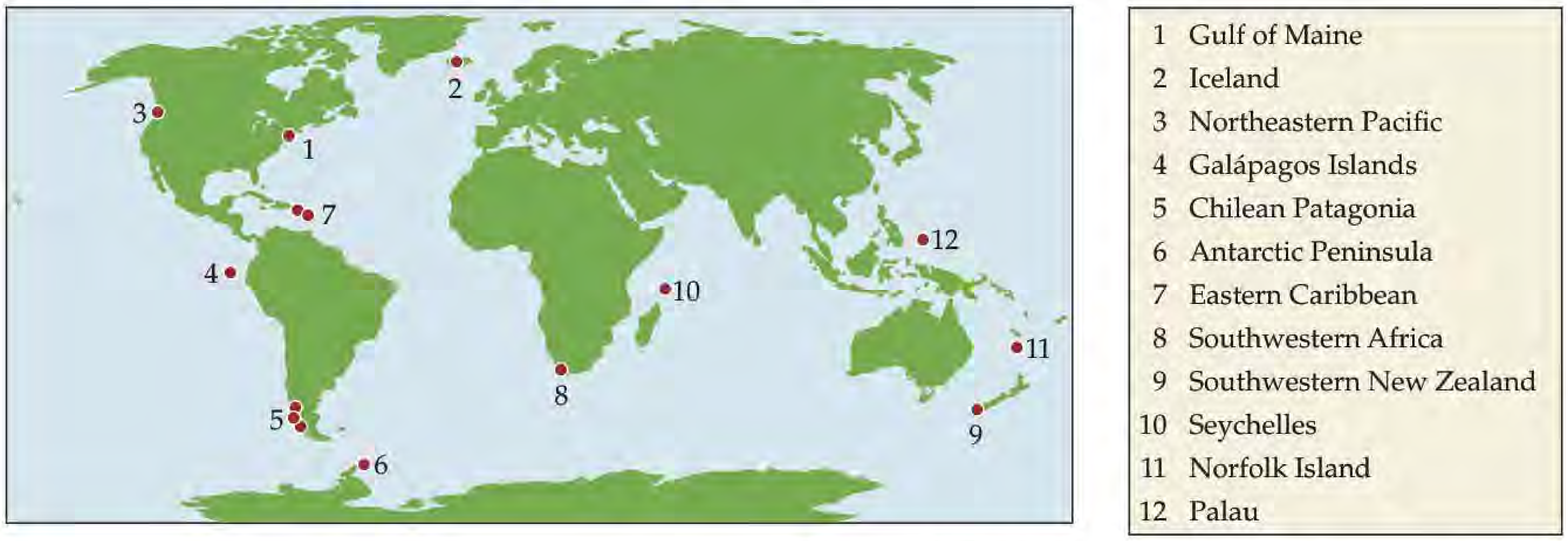
Figure 18.6 What Determines Local Species Richness? The relative influences of local and regional processes in a community can be determined by plotting local species richness against regional species richness.

? Would you ever have a local to regional species richness relationship that had a slope of more than 1? Why or why not?

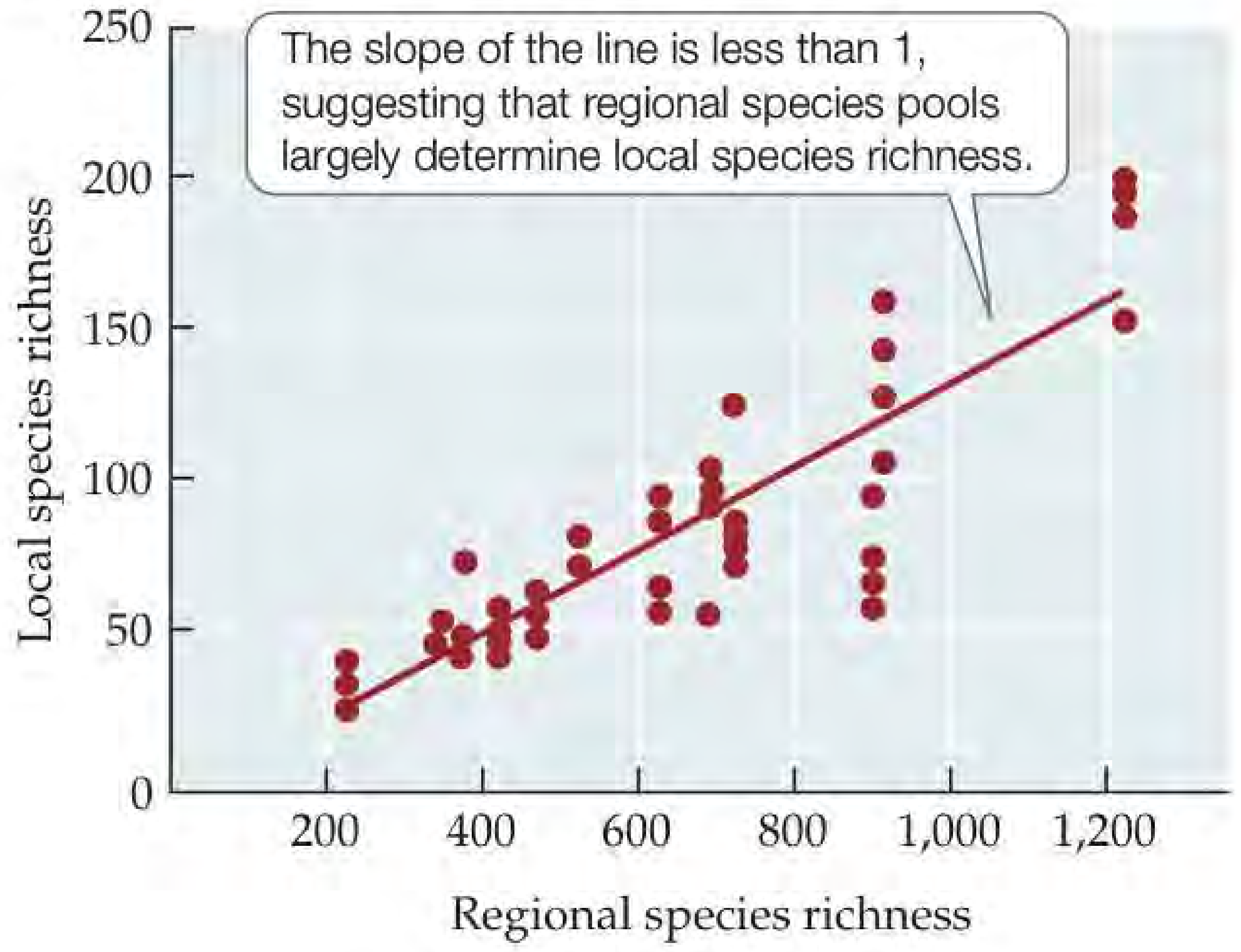
Let's move away from these theoretical constructs and look at what real data show us about the relationship between local and regional species richness. Witman and colleagues (2004) considered this relationship for marine invertebrate communities living on subtidal rock walls at a variety of locations throughout the world (**Figure 18.7A**). At 49 local sites in 12 regions, they surveyed species richness in 0.25 m^2 plots on rock walls at a 10–15 m (33–50 feet) water depth. They then compared the local species richness values they found at the sites with regional species richness values from published lists of invertebrate species capable of living on hard substrates at similar depths. A plot of local versus regional species richness at all the sites (**Figure 18.7B**) showed that local species richness was always proportionally lower than regional species richness. Furthermore, local species richness never leveled off—that is, the communities never became saturated—at high regional richness values. Instead, regional species richness explained approximately 75% of the variation in local species richness. The results of this study suggest that regional species pools largely determine the number of species present in these marine invertebrate communities.

Does the lack of saturation detected in this study and others indicate that local processes are unimportant in determining local species richness? The answer is no, for at least two reasons. First, there was still considerable unexplained variation among local communities within regions, which could be attributable to the effects of local processes such as species interactions, abiotic conditions, or dispersal limitation (see Figure 19.1). Second, the effects of species interactions, in particular, are likely to be highly sensitive to the local spatial scale chosen. Although the small spatial scale of Witman and colleagues' study is probably appropriate for species interacting on subtidal rock walls, other studies have used inappropriate (usually too large) spatial scales that were unlikely to detect local effects. Nevertheless, the strong influence of regional-scale processes on local species richness suggests that both marine and terrestrial communities are likely to be much more susceptible to changes such as species invasions from outside their regions than previously thought.

(A) Study sites



(B) Local versus regional species richness



The slope of the line is less than 1, suggesting that regional species pools largely determine local species richness.

Figure 18.7 Marine Invertebrate Communities May Be Limited by Regional Processes Among shallow subtidal marine invertebrate communities, regional species richness explains approximately 75% of the local species richness. (A) The 12 regions of the world where the 49 sampling sites were located. (B) A plot of local species richness against regional species richness. Each dot represents one of the 49 sampling sites. (After Witman et al. 2004.)

In the remainder of this chapter, we will explore the factors controlling variation in species diversity at global and regional biogeographic scales. Chapter 19 will delve in more detail into the causes and consequences of species diversity differences at the local scale.

CONCEPT 18.2

Global patterns of species diversity and composition are influenced by geographic area and isolation, evolutionary history, and global climate.

Global Biogeography

It must have been incredible to be a European scientific explorer 200 years ago. You would have left the safety of your home to travel by ship to a destination largely unknown. You would have had to endure seasickness, disease, accidents of all kinds, and years away from your family, friends, and colleagues. You might have had many years of financial debt to repay unless you were independently wealthy or could sell your collections. But you would have been the first scientist to document and collect animal and plant species of beauty, novelty, and rarity. It was under these circumstances that the science of biogeography was born and many important discoveries were made. Up to that point, European scientists had very little information about the natural history and ecology of other parts of the world; most was secondhand or anecdotal. What these early naturalists were able to bring back were specimens and, most of all, theories to help make sense of their observations.

Although not the first in his field, Alfred Russel Wallace (1823–1913) rightly earned his place as the father of biogeography (**Figure 18.8**). Inspired by naturalists such as Alexander von Humboldt, Charles Darwin, and Joseph Hooker, Wallace came on the scene with considerably less wealth or education, but his intellect and motivation more than made up for what he lacked in financial resources and training. Wallace is best known, along with Charles Darwin, as the codiscoverer of the principles of natural selection, although he has always stood in the shadow of Darwin in that regard. But his main contribution was the study of species distributions across large spatial scales.

Wallace left England for Brazil in 1848 and explored the Amazon rainforest for 4 years. On his way back, the ship he was traveling on burned in the middle of the Sargasso Sea, destroying all his specimens and most of his notes and illustrations. After 10 days in a lifeboat, he was rescued and made his way back to England, where he published an impressive six papers on his observations.

Even though he had vowed never to travel again, in 1852 Wallace left England for the Malay Archipelago

Figure 18.8 **Alfred Russel Wallace and His Collections** (A) A photograph of Wallace taken in Singapore in 1862, during his expedition to the Malay Archipelago. (B) Part of Wallace's rare beetle collection from the Malay Archipelago, found in an attic by his grandson in 2005.

(present-day Indonesia, the Philippines, Singapore, Brunei, East Malaysia, and East Timor). It was here that he made the puzzling observation described in his 1869 book *The Malay Archipelago*: that the mammals of the Philippines were more similar to those in Africa (5,500 km away) than they were to those in New Guinea (750 km away). Wallace was the first to notice the clear demarcation between these two faunas, which came to be known as *Wallace's line*. It turns out, as we'll see shortly, that these separate groups of mammals evolved on two different continents that have come into close proximity only within the last 15 million years.

Wallace's biogeographic research culminated in the publication of a two-volume work called *The Geographical Distribution of Animals*, published in 1876. In this book, Wallace overlays species distributions on top of geographic regions and reveals two important global patterns:

- Earth's land masses can be divided into six recognizable **biogeographic regions** containing distinct biotas that differ markedly in species composition and diversity.
- There is a gradient of species diversity with latitude: species diversity is greatest in the tropics and decreases toward the poles.

These two patterns are necessarily interrelated; the latitudinal gradient is superimposed over the biogeographic regions. For ease of explanation, we'll begin by exploring the biogeographic regions described by Wallace and the underlying forces that created them. We will then consider some of the processes likely to be responsible for the latitudinal gradient in species diversity.

The biotas of biogeographic regions reflect evolutionary isolation

The six biogeographic regions described by Wallace are the Nearctic (North America), Neotropical (Central and South America), Palearctic (Europe and parts of Asia and Africa), Ethiopian (most of Africa), Oriental (India, China, and Southeast Asia), and Australasian (Australia, the Indo-Pacific, and New Zealand) (**Figure 18.9**). It is no coincidence that these regions correspond roughly to Earth's six major tectonic plates. These plates are sections of Earth's crust that move across Earth's surface through the action of currents generated deep within its molten rock mantle (**Figure 18.10**). Before scientists understood the processes driving the movement of these plates, they hypothesized that the continents drifted over Earth's surface, thus the name **continental drift** was given to the early theory describing these movements. There are three major types

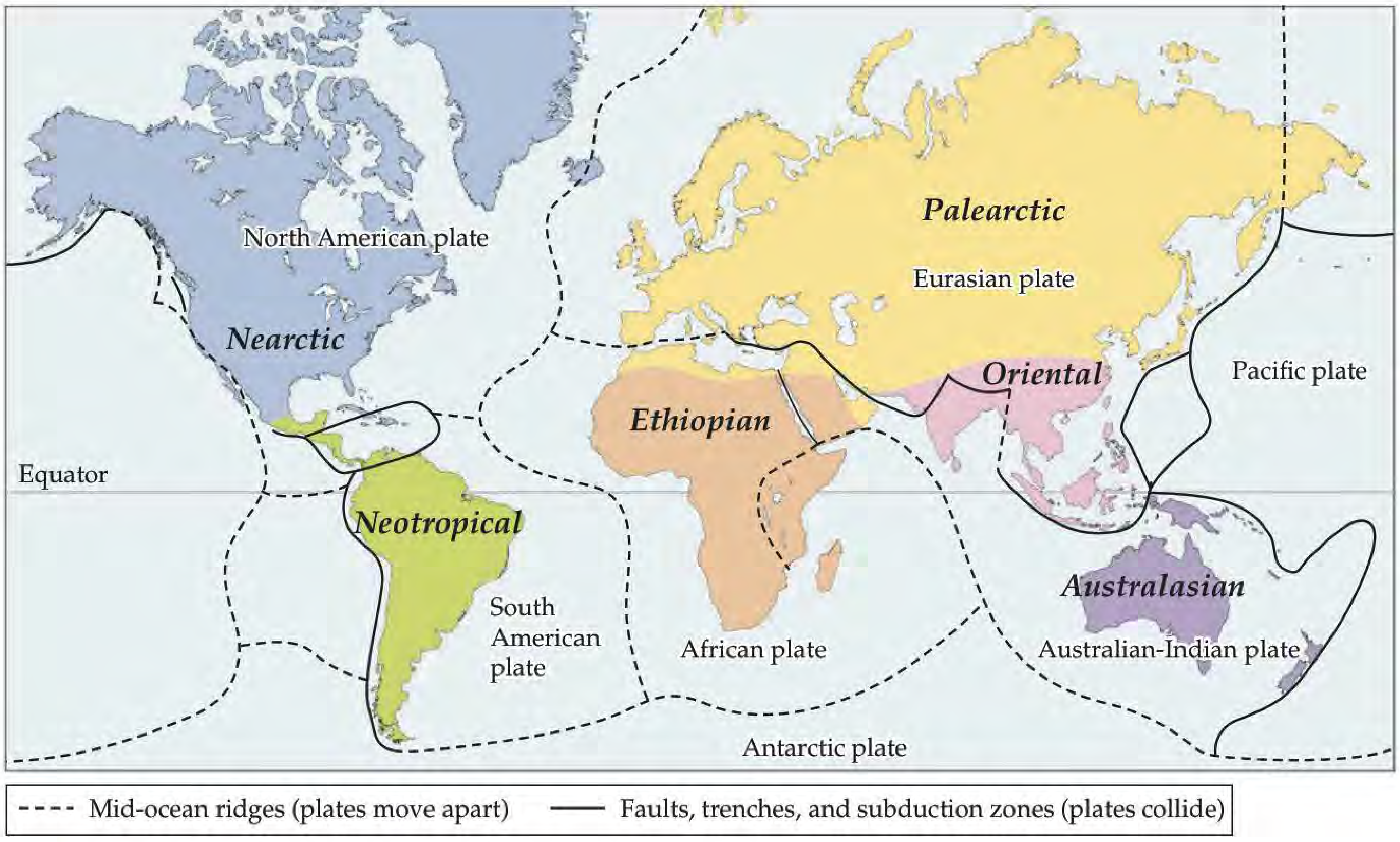
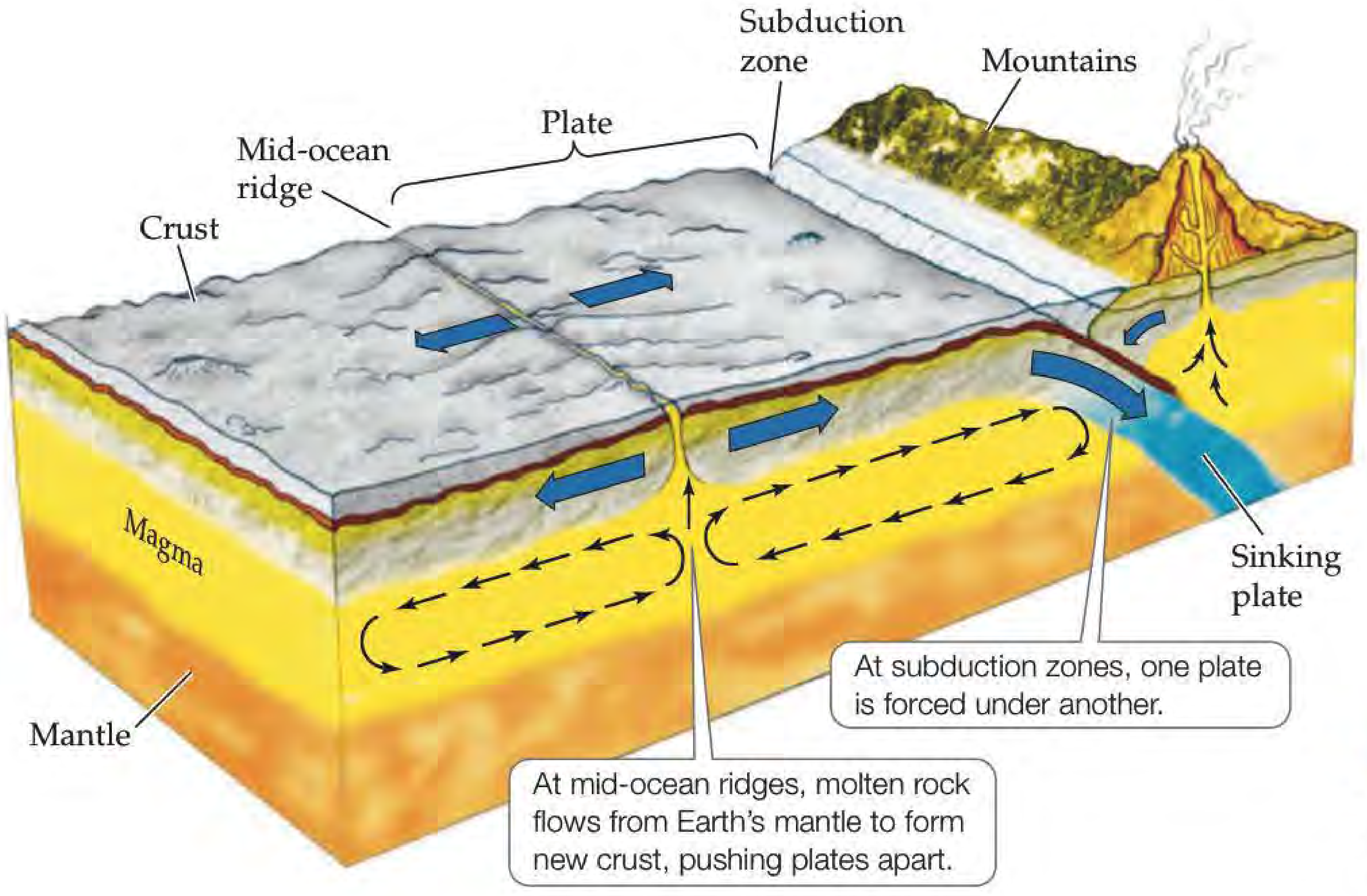


Figure 18.9 Six Biogeographic Regions Wallace identified six biogeographic regions using the distributions of terrestrial animals. These six regions roughly correspond to Earth's major tectonic plates.

? Compare Wallace's 6 regions with the 11 biogeographic divisions shown in Figure 1.2. What types of data were used to expand the number of regions to 11?

of boundaries between tectonic plates. In areas known as *mid-ocean ridges*, molten rock flows out of the seams between plates and cools, creating new crust and forcing the plates apart in a process called *seafloor spreading*. In some areas where two plates meet, known as *subduction zones*, one plate is forced downward under another plate. These areas are associated with strong earthquakes, volcanic activity, and mountain range formation. In other areas where two plates meet, the plates slide sideways past each other, forming a *fault*.

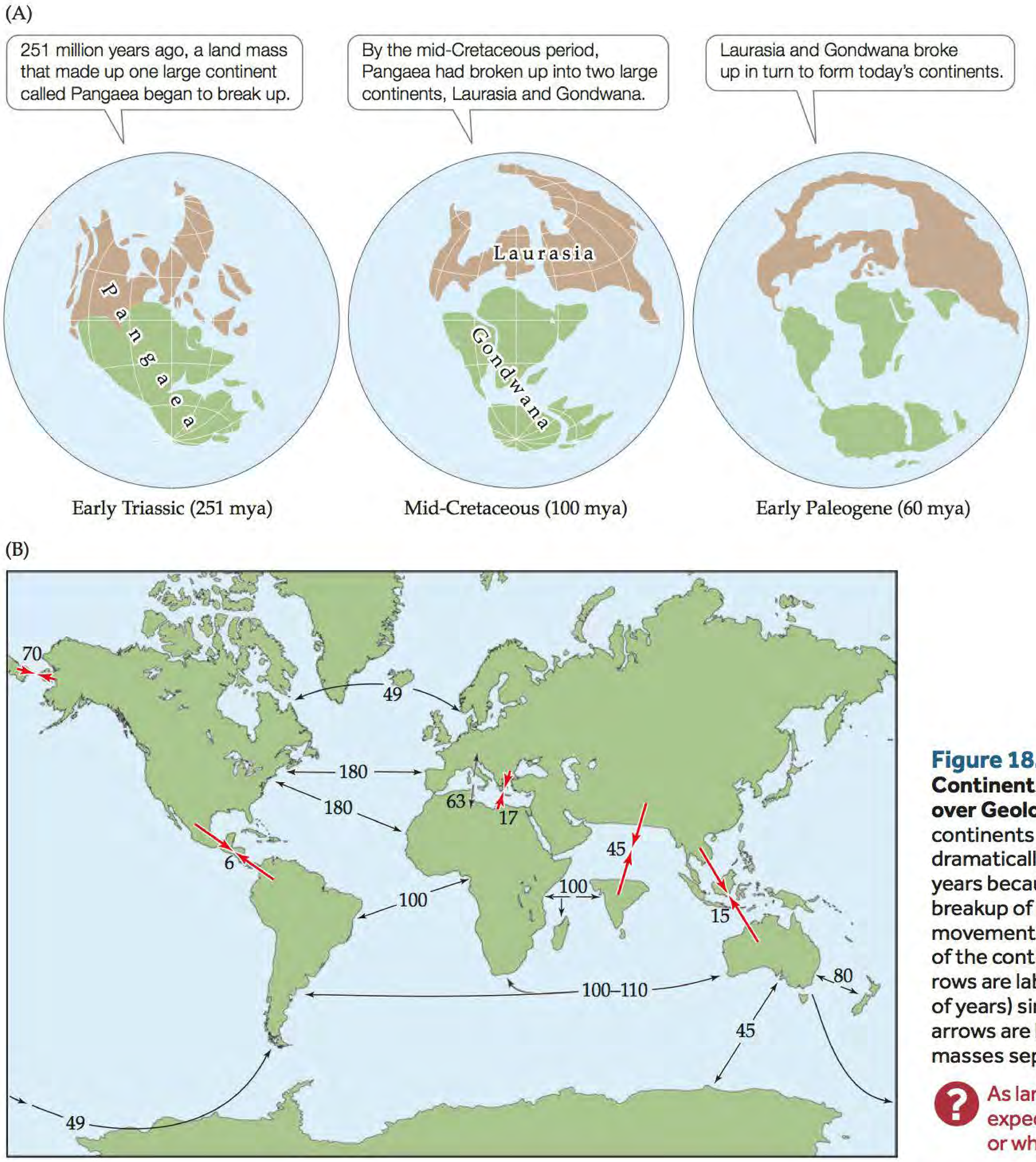
As a result of processes such as seafloor spreading and subduction, the positions of the plates, and of the continents that sit on them, have changed dramatically over geologic time (for a video, see **Web Extension 18.1**). For our purposes, let's consider the movements of the major tectonic plates since the early Triassic period (251 million years ago), when all of Earth's land masses, a single continent named Pangaea, began to break up (**Figure 18.11A**). At that time, there was a mass extinction (see Figure 6.18), which eventually led to the rise of the first archosaurs (precursors to dinosaurs) and the cynodonts (precursors to mammals). About 100 million years ago, during the mid-Cretaceous period, Pangaea had split into Laurasia to the north and Gondwana to the south. During that time, dinosaurs were in their heyday and



At subduction zones, one plate is forced under another.

At mid-ocean ridges, molten rock flows from Earth's mantle to form new crust, pushing plates apart.

Figure 18.10 Mechanisms of Continental Drift Over geologic time, currents generated deep within Earth's molten rock mantle move sections of Earth's crust across its surface.



251 million years ago, a land mass that made up one large continent called Pangaea began to break up.

By the mid-Cretaceous period, Pangaea had broken up into two large continents, Laurasia and Gondwana.

Laurasia and Gondwana broke up in turn to form today's continents.

Early Triassic (251 mya)

Mid-Cretaceous (100 mya)

Early Paleogene (60 mya)

Figure 18.11 The Positions of Continents and Oceans Have Changed over Geologic Time The locations of continents and oceans have changed dramatically over the last 251 million years because of continental drift. (A) The breakup of Pangaea. (B) A summary of the movements that led to the configuration of the continents we know today. Red arrows are labeled with the time (in millions of years) since land masses joined; black arrows are labeled with the time since land masses separated.

? As land masses separated, would you expect speciation to increase? Why or why not?

mammals were small and a relatively minor component of the fauna. The end of the Cretaceous period was marked by another mass extinction, which resulted in the disappearance of dinosaurs. By the early Paleogene period (60 million years ago), Gondwana had separated into the present-day continents of South America, Africa, India, Antarctica, and Australia. Laurasia eventually split apart to form North America, Europe, and Asia. Most of these movements resulted in the separation of continents from one another, but some continents were brought together (**Figure 18.11B**). For example, North and South America joined at the Isthmus of Panama, India collided with Asia to create the Himalayas, Africa and Europe united at the Mediterranean Sea, and a land bridge formed between North America and Asia at the Bering Strait (for a video, see **Web Extension 18.2**).

The movement of Earth's tectonic plates thus separated the terrestrial biota of Pangaea, united by geography and phylogeny, into biogeographically distinct groups of species by isolating them on different continents. The sequence and tempo of the continental movements has resulted in some biogeographic regions having very different flora and fauna than others. For example, the Neotropical, Ethiopian, and Australian regions, all once part of Gondwana, have been isolated for quite some time and have very distinctive forms of life. In other cases, however, distinct groups of species have been united. For example, the biota of the Nearctic region differs substantially from that of the Neotropical region despite their modern-day proximity. Because North America was part of Laurasia while South America was part of Gondwana, North and South America had no contact until about 6 million years ago. Within that time, however, many species have moved from one continent to the other (e.g., mountain lions, wolves, and the precursors of llamas spread to South America, while armadillos and opossums spread to North America), somewhat homogenizing the biotas of the two regions. Interestingly, there is also evidence that several families of terrestrial mammals went extinct once the two continents merged, suggesting that ecological coexistence was not possible for some species (Flessa 1975). Finally, the Nearctic and Palearctic, both part of ancient Laurasia, have similarities in biota across what is now Greenland as well as across the Bering Strait, where a land bridge has intermittently allowed exchanges of species over the last 100 million years.

The legacy of continental movements can be found in a number of existing taxonomic groups as well as in the fossil record. The evolutionary separation of species due to barriers such as those formed by continental drift is known as **vicariance**. Tracing the threads of vicariance over large geographic areas and long periods provided important evidence for early theories of evolution. For example, as Wallace began to amass knowledge of the distributions of more and more species and make geographic connections between them, his ideas about the origin of species started to solidify. In an 1855 paper titled "On the law which has regulated the introduction of new species," he wrote, "Every species has come into existence coincident both in space and time with a pre-existing closely allied species." Despite the biogeographic evidence of evolutionary connections among species, it took a few more years for one mechanism of evolution (i.e., natural selection) and its role in the origin of new species to be formally proposed by both Wallace (1858) and Darwin (1859).

Before we move on, it is important to consider contemporary research that updates and expands on the biogeographic regions first identified by Wallace. One recent study (Holt et al. 2013) used phylogenetic information acquired from DNA analysis and recent observations of global species distribution patterns to test whether Wallace's original biogeographic regions are supported by modern data. The researchers identified more biogeographic regions (a total of 11), some of which were the same and others of which were different from Wallace's original 6 regions (compare Figure 18.9 with Figure 1.2). This new analysis suggests that additional isolation mechanisms beyond continental drift are responsible for the different regions. Interestingly, New Guinea and the Pacific Islands, separated from the Philippines by Wallace's line, emerge as a new biogeographic region, completely separate from the Australian or Oriental regions.

Another recent analysis of biogeographic regions involved mapping the distribution of species in the oceans. After all, the oceans make up 71% of Earth's surface area and, just as we have seen for continents, they are dynamic, in the sense that they are created, merged, and destroyed by the movements of Earth's tectonic plates (see Figure 18.11). The main question, then, is whether there are barriers to dispersal between oceans as there are between continents. Despite their appearance of connectivity, oceans do have significant impediments to the exchange of biotas: these impediments take the form of continents and currents; thermal, salinity, and oxygen gradients; and differences in water depth. Oceanographic discontinuities have isolated species from one another, allowed for evolutionary change, and created unique oceanic biogeographic regions (Briggs 2006). Unfortunately, delineation of marine biogeographic regions has been hindered by the extra complicating factor of water depth and by our basic lack of natural history and taxonomic knowledge of the deep oceans. One recent model by Adey and Steneck (2001) identifies 24 recognizable biogeographic regions for intertidal benthic marine macroalgae. Although it is hard to compare these macroalgal regions with terrestrial biogeographic regions, the analysis does suggest that the marine realm has much more biogeographic variation than previously realized.

Species diversity varies with latitude

If you recall our Google Earth–style tour of the globe in the previous section, it was clear that plant species diversity and community composition changed dramatically with latitude: species diversity was highest at tropical latitudes and decreased toward the poles. Wallace and other nineteenth-century European scientific explorers became keenly aware of this pattern as they collected thousands of species in the tropics and compared them with their more meager European collections. As more data have accumulated over the last 200 years, the latitudinal gradient in species diversity has been more firmly established (**Figure 18.12**). Willig and colleagues (2003) tallied the results of 162 studies on a variety of taxonomic groups extending over broad spatial scales (20° latitude or more) that considered whether diversity and latitude showed a negative relationship (with diversity decreasing toward the poles), a positive relationship (increasing toward the poles), a unimodal relationship (increasing toward mid-latitudes and then declining toward the poles), or no relationship. Negative relationships were by far the most often seen.

In addition to this undeniably strong latitudinal gradient, biogeographers have observed an important pattern of longitudinal variation. Gaston et al. (1995) measured

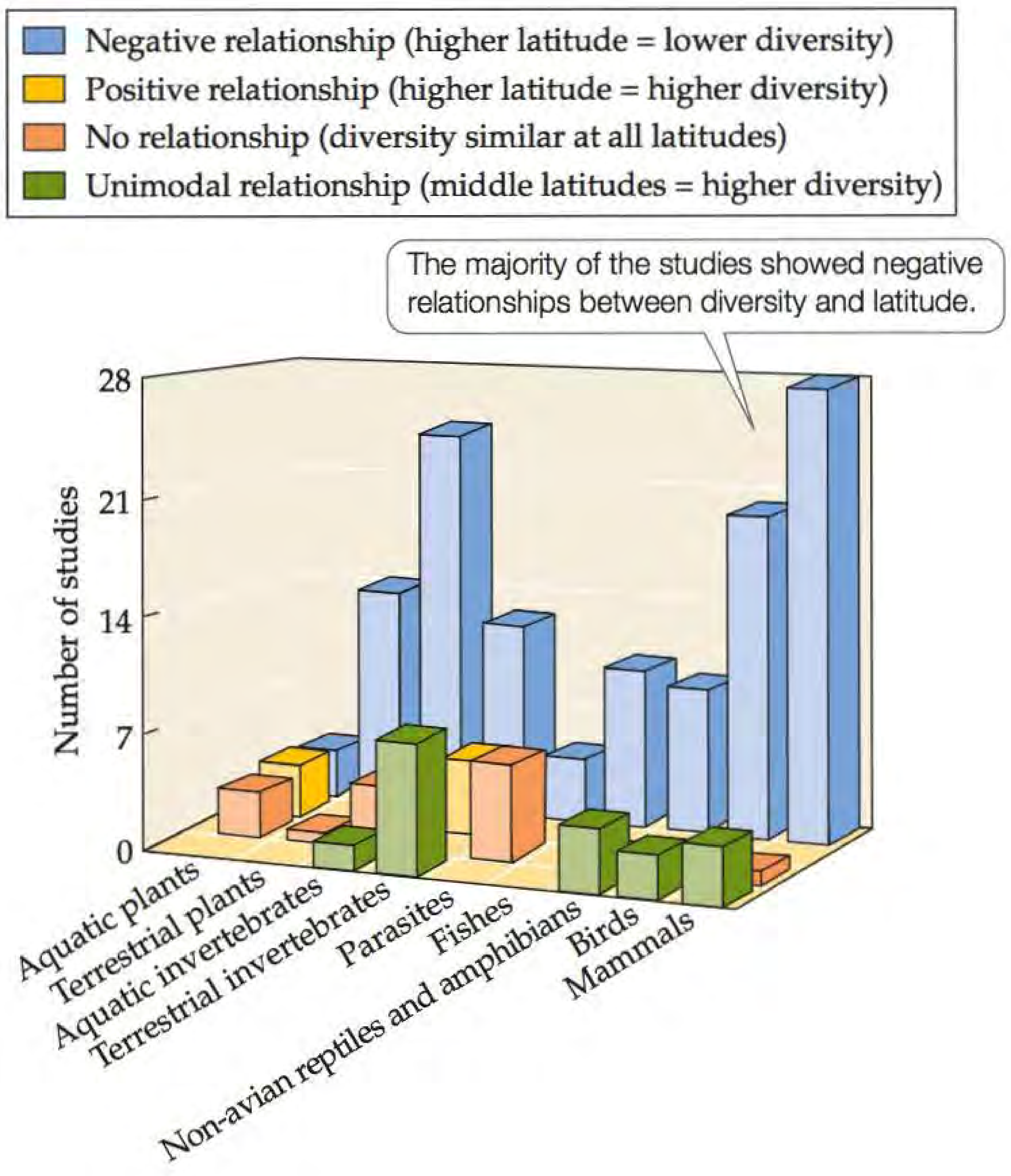


Figure 18.12 Studies of Latitude and Species Diversity Confirm Conventional Wisdom The relationship between species diversity and latitude (measured at 20° increments), tallied for a variety of taxonomic groups, shows that most are negative correlations (i.e., increasing species diversity with decreasing latitude). (After Willig et al. 2003.)

the numbers of families along multiple transects running north to south and separated by 10° longitude. Families of seed plants, amphibians, reptiles, and mammals all increased in number toward the equator and declined at higher latitudes in both the Northern and Southern Hemispheres. These researchers determined, however, that the number of families also depended on the longitude chosen. Their observations showed that there were areas of particularly high species richness at some locations, sometimes secondary to latitude. These areas are known as *biodiversity hot spots* in situations in which they are under threat from humans.

Of course, not all groups of organisms show decreases in species richness at higher latitudes. Some groups display the opposite pattern. Seabirds, for example, have their highest diversity at temperate and polar latitudes (Harrison 1987) (**Figure 18.13A**). Seabirds of the Antarctic and subantarctic include penguins, albatrosses, petrels, and skuas (**Figure 18.13B**). In the Arctic and subarctic, auks replace penguins, and gulls, terns, and grebes are common. In the tropics and subtropics, seabird diversity declines: the seabird community there is composed mostly of pelicans, boobies, cormorants, and frigatebirds. This pattern of seabird diversity correlates well with marine productivity, which is substantially higher in temperate and polar oceans than in the tropics (see Figure 20.10). The same pattern of diversity has been observed in marine benthic communities, which also experience much higher productivity at higher latitudes.

As we will see, productivity differences are one possible cause of latitudinal gradients in species diversity. Let's turn now to some other possible explanations.

Latitudinal gradients have multiple, interrelated causes

As we have seen, global patterns of species richness are ultimately controlled by the rates of three processes: speciation, extinction, and dispersal. Let's assume here, for simplicity's sake, that the rate of species dispersal is roughly the same worldwide. We can then predict that the number of species at any particular location will reflect a balance, or equilibrium, between the rates of two fundamental processes: speciation and extinction. Subtracting the extinction rate from the speciation rate gives us the

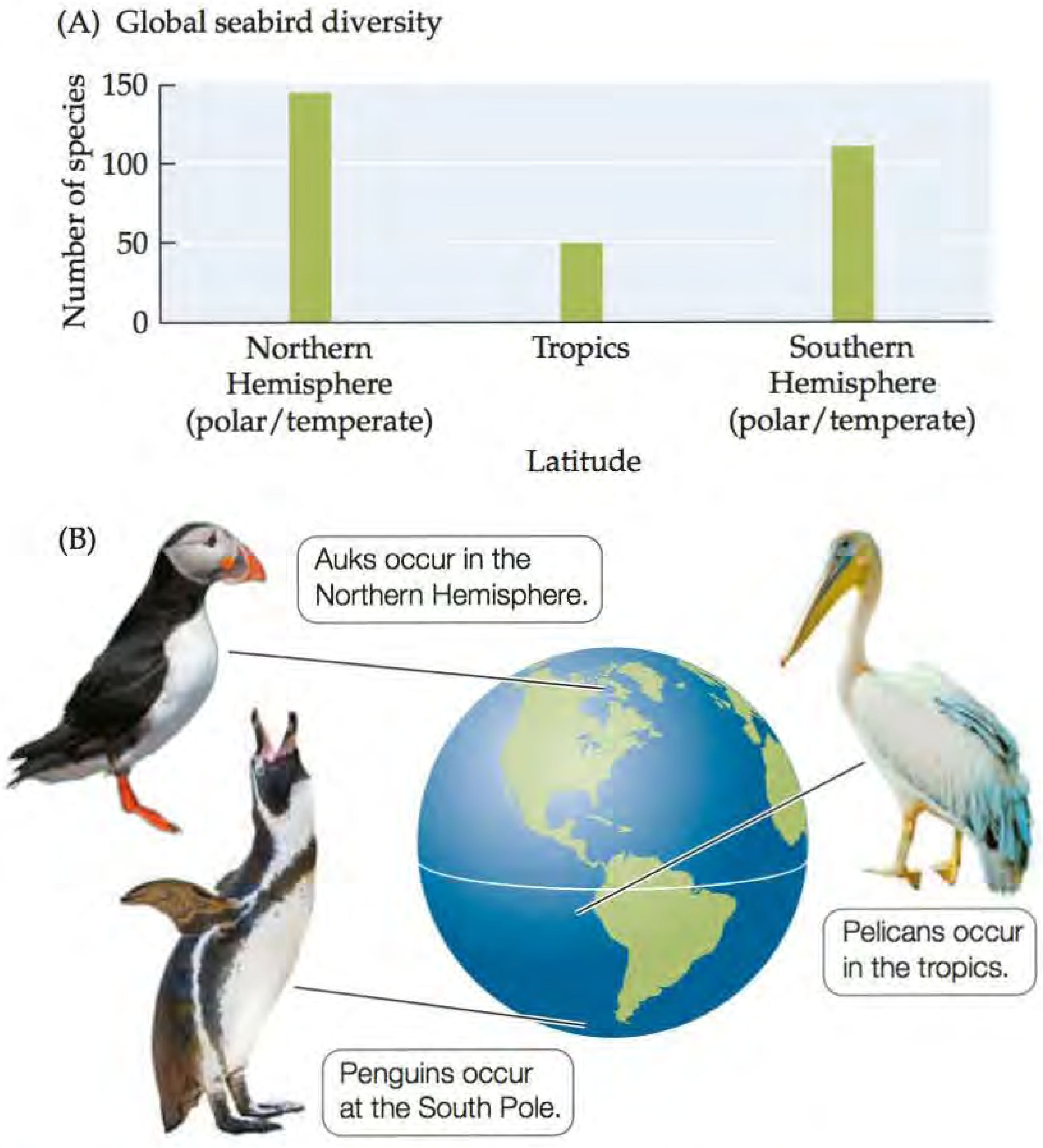


Figure 18.13 Seabirds Defy Conventional Wisdom Global seabird species richness shows a latitudinal pattern opposite to that of most faunas. (A) Species richness among seabirds is high in temperate and polar regions and much lower in the tropics. (B) Species composition also shows strong latitudinal differences. (A after Harrison 1987.)

rate of *species diversification*: the net increase or decrease of species diversity over time. What ultimately controls this rate? Dozens of hypotheses have been proposed to explain species diversification with latitude, but there is very little agreement among biogeographers and ecologists. Part of the reason lies in the fact that there are multiple and confounding latitudinal gradients in area, evolutionary age, and climate that are correlated with species diversity gradients. In addition, because speciation and extinction occur at a global spatial scale and over evolutionary time scales, it is impossible to conduct manipulative experiments to isolate various factors and separate correlation from causation.

In an effort to summarize the most convincing ideas, Gary Mittelbach and colleagues (2007) suggested that hypotheses proposed to explain latitudinal gradients in species richness fall into three broad categories. The first category of hypotheses is based on the assumption that the rate of species diversification in the tropics is greater than that in temperate regions (**Figure 18.14A**). The second category of hypotheses suggests that the rates of diversification in the tropics and at higher latitudes are similar, but that the evolutionary time available for diversification has been much greater in the tropics (**Figure 18.14B**). The third category of hypotheses suggests that resources are more plentiful in the tropics because of higher productivity, and thus that species there have higher carrying capacities and a greater ability to coexist (**Figure 18.14C**). Let's take a look at each category of hypotheses in more detail.

SPECIES DIVERSIFICATION RATE There are a number of hypotheses that seek to explain why species diversification might be higher in the tropics. One hypothesis relates diversification to geographic area and temperature. John Terborgh (1973) and Michael Rosenzweig (1992) proposed that terrestrial species diversity is highest in the tropics because the tropics have the largest land area (**Figure 18.15A**). Rosenzweig calculated that the region between 26° N and S has 2.5 times more land area than any other latitude range on Earth. This makes intuitive sense, given that this latitude range is at the middle, and thus at the widest part, of the planet. Equally interesting are data showing that this very large area is also the most thermally homogeneous region on Earth (**Figure 18.15B**). A plot of average annual temperature against latitude by Terborgh showed that land temperatures are remarkably uniform over a wide area between 25°N and S, but then drop off rapidly at higher latitudes.

Why would a larger land area and more constant temperatures foster greater species diversity? Rosenzweig suggested that these two factors combine to decrease extinction rates and increase speciation rates in tropical regions. He argued that a larger and more thermally stable area should decrease extinction rates in two ways: first, by increasing the population sizes of species (assuming that their densities are the same worldwide), and thus decreasing their risk of extinction due to chance events, and second, by increasing the geographic ranges of species, and thus decreasing their chances of extinction by spreading the risk over a larger geographic area (see Concept 11.3). He further suggested that speciation should increase in larger areas because species should have larger geographic ranges, and thus should have a greater chance of reproductive isolation of populations (see Concept 6.4). Rosenzweig's theory is controversial for a number of reasons, however. **Web Extension 18.3** describes several alternative hypotheses proposed to explain species diversification rates in the tropics.

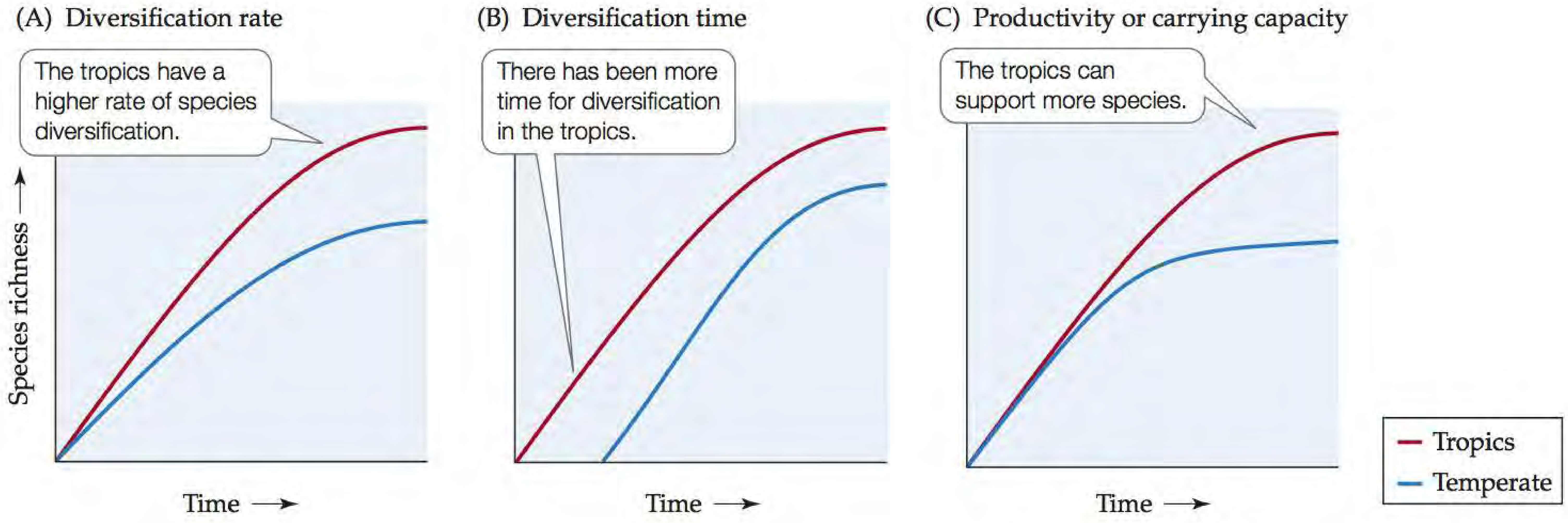


Figure 18.14 Hypotheses Proposed to Explain the Latitudinal Gradient in Species Richness (A) The tropics have a higher diversification rate (speciation rate – extinction rate) than temperate areas do, so they have accumulated species faster. (B) The tropics have had more time for diversification than temperate areas have, so they have accumulated more species. (C) Because their productivity is higher, the tropics have a higher carrying capacity than temperate areas, so more species can coexist there. (After Mittelbach et al. 2007.)

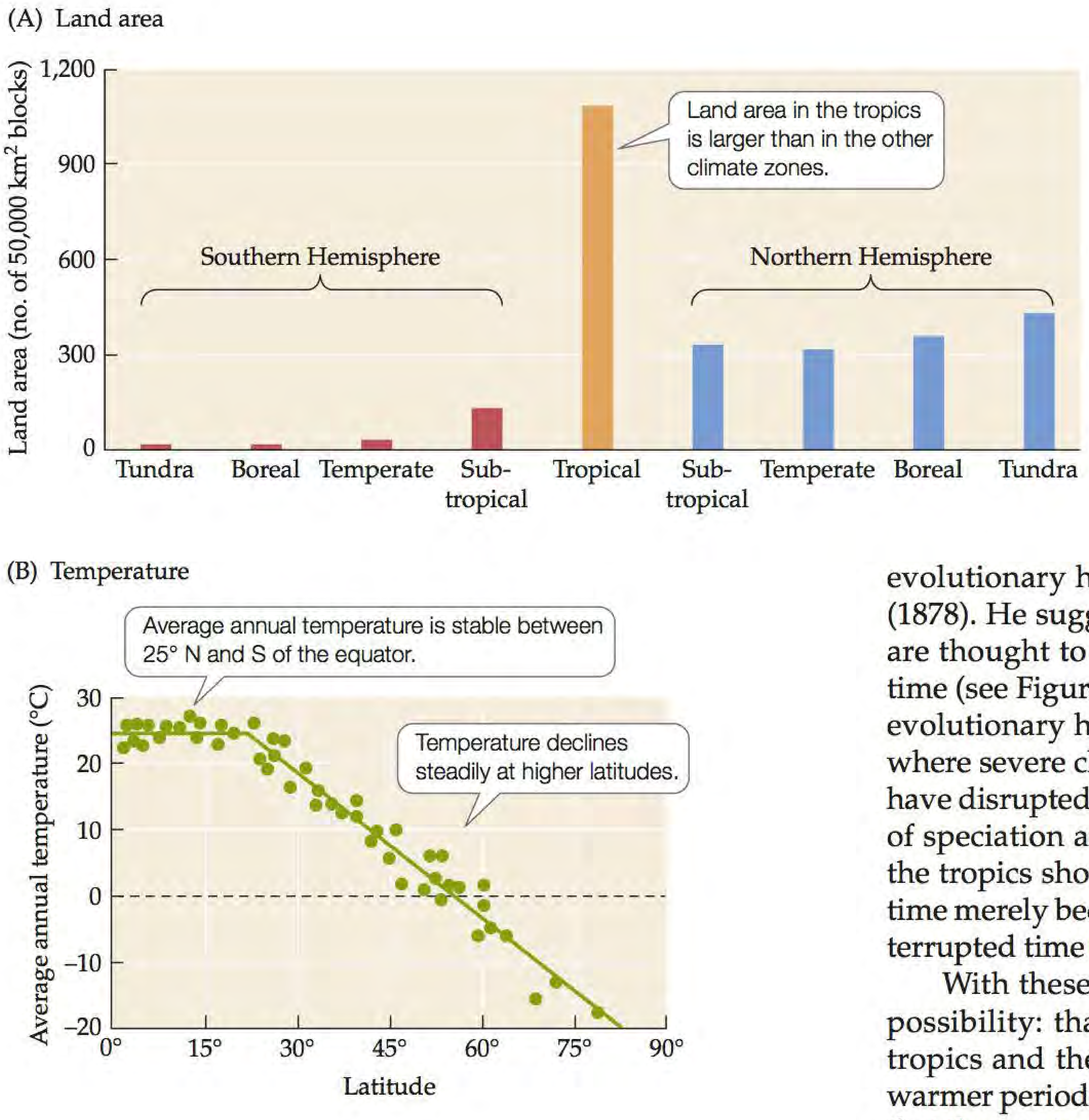


Figure 18.15 Do Land Area and Temperature Influence Species Diversity? Michael Rosenzweig hypothesized that two characteristics of the tropics lead to high speciation rates and low extinction rates: (A) their land area and (B) their stable temperatures. (After Rosenzweig 1992.)

SPECIES DIVERSIFICATION TIME The second category of hypotheses, which proposes that latitudinal gradients in species diversity are influenced by evolutionary history, was first championed by Wallace (1878). He suggested that tropical regions, because they are thought to have been more climatically stable over time (see Figure 18.15B), could have considerably longer evolutionary histories than temperate or polar regions, where severe climate conditions (such as ice ages) might have disrupted species diversification. Thus, even if rates of speciation and extinction were the same worldwide, the tropics should have accumulated more species over time merely because species should have had more uninterrupted time to evolve there.

With these ideas in mind, we can consider another possibility: that most species actually originate in the tropics and then disperse to temperate regions during warmer periods of greater climate homogeneity. The idea that the tropics serve as a “cradle” for diversity was originally proposed by Stebbins (1974). Jablonski et al. (2006) recently examined this hypothesis by comparing modern marine bivalve faunas with marine bivalve fossils from as far back as 11 million years ago. They found that the majority of extant marine bivalve taxa originated in the tropics (**Figure 18.16A**) and spread toward the poles (**Figure 18.16B**), but without losing their tropical presence. Thus, in this particular case, we can think of the tropics as a cradle of species diversity because the majority of extant taxa originated there. But, as Jablonski and colleagues also pointed out, the tropics can serve as a “museum” as well as a cradle. If extinction rates in the tropics are low, then species that diversify there will tend to stay there “on

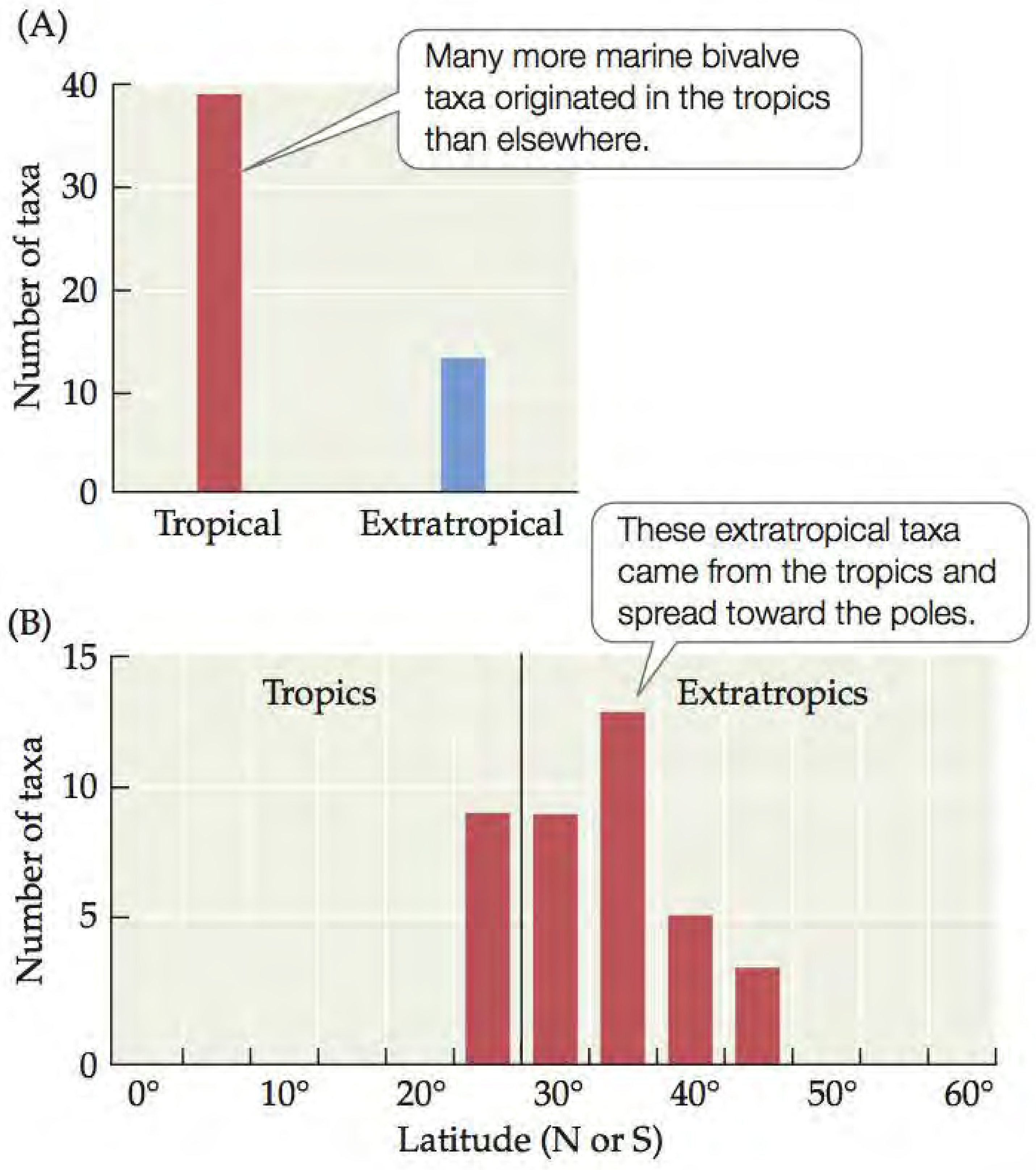


Figure 18.16 The Tropics Are a Cradle and a Museum for Speciation Extant and fossil marine bivalve taxa were examined to evaluate the hypothesis that longer evolutionary histories in the tropics contribute to the latitudinal gradient in species diversity. (A) Climate zones of first occurrence of marine bivalve taxa (based on families of fossils). (B) Range limits of modern marine bivalve taxa with tropical origins. (After Jablonski et al. 2006.)

? What is meant by the tropics being a cradle and a museum for diversity?

display," if you will. Jablonski and colleagues suggested that the current loss of biodiversity in the tropics is likely to have profound effects because it not only compromises species richness today, but also could conceivably cut off the supply of new species to higher latitudes in the future.

PRODUCTIVITY The final category of hypotheses for the latitudinal gradient in species diversity that we will consider is based on resources—in particular, productivity. The productivity hypothesis, proposed as long ago as 1959 by G. E. Hutchinson, posits that species diversity is higher in the tropics because that is where productivity is highest, at least for terrestrial systems (see Figure 20.7). The thought is that higher productivity promotes larger population sizes because species will have higher carrying capacities. This higher productivity will lead to lower extinction rates, greater species coexistence, and overall higher species richness. The productivity hypothesis might explain why we see a reversal in the latitudinal gradient for some marine organisms, such as seabirds (see Figure 18.13), given that productivity is generally higher in temperate coastal marine habitats than in tropical regions (see Figure 20.10). But we also know that some of the most productive habitats on Earth, such as estuaries, typically have very low species diversity. Suffice it to say, the productivity hypothesis is complex and unsatisfactory in many cases. In Chapter 19, we will consider how productivity influences diversity at local scales, where manipulative experiments can give us more insight into its effects.

CLIMATE CHANGE CONNECTION

Latitudinal Gradients in Diversity under Climate Change

One way to explore the potential causes of latitudinal gradients in species diversity is to consider them over evolutionary time and with major changes in climate. We can ask, Did the fundamental pattern of increasing species diversity toward the tropics exist in the past, and if not, why? Philip Mannion and colleagues (2014) used the fossil record and fluctuations in past global temperatures as a window into past latitudinal and species diversity gradients and their potential causes. Their analysis showed that a tropical peak in species diversity has not been a universal pattern but has been restricted to particular intervals of time throughout the Phanerozoic when the Earth experienced colder, "icehouse" conditions (**Figure 18.17**). Likewise, they found that during warmer, "greenhouse" conditions, species diversity peaked in temperate latitudes, exhibiting a more unimodal relationship. These switches from temperate to tropical peaks in species diversity corresponded to transitions in greenhouse to icehouse climate conditions, lending support for the notion that polar to temperate glaciations could drive species to the tropics where extinctions would be lower. Conversely, during greenhouse conditions, the tropics might become too hot for many organisms, leading to increased extinction rates and dispersal out of the tropics. One might

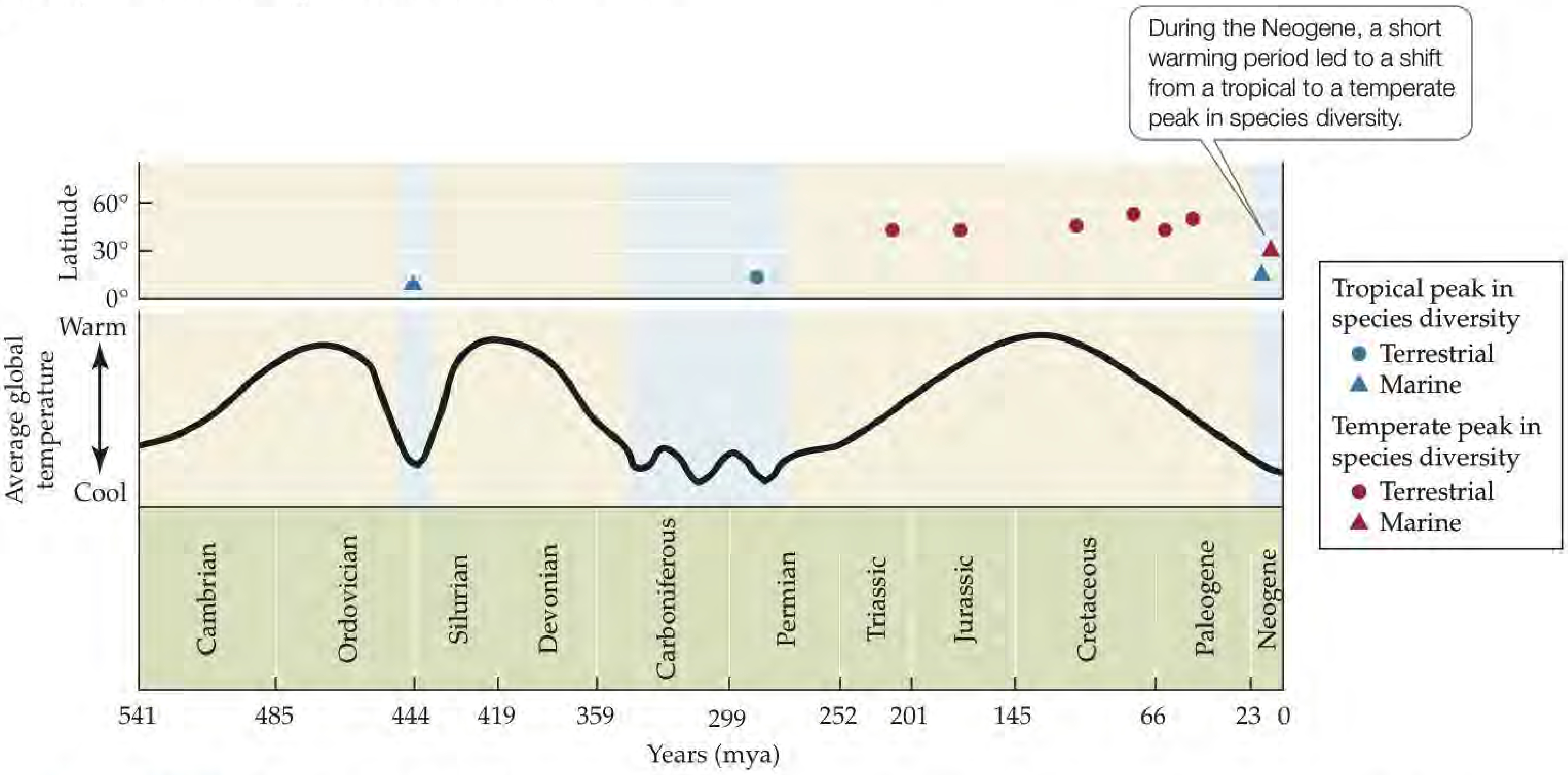

During the Neogene, a short warming period led to a shift from a tropical to a temperate peak in species diversity.

Figure 18.17 Latitudinal Species Diversity Gradients Vary with Climate The latitudinal species diversity gradients under fluctuating global temperature through the Phanerozoic. Tropical peaks in species diversity (blue symbols) are restricted to cold, "icehouse" conditions, whereas temperate peaks in diversity (red symbols) occur during warm, "greenhouse" intervals. Note that during the icehouse conditions of the Neogene, a short warming period during the Pleistocene interglacial period led to a peak in diversity at temperate latitudes. Circles are terrestrial examples, and triangles are marine examples. (After Mannion et al. 2014.)

speculate, in fact, that with global warming, latitudinal gradients in species diversity could become shallower or more unimodal as warming causes species to disperse poleward or become increasingly extinct within tropical latitudes.

As we have seen, biogeographic patterns have motivated and inspired some of the best and brightest scientists of modern times. Their fascination with the differences in the numbers and kinds of species at the global scale and their overwhelming drive to understand why these differences exist have resulted in some of the most influential scientific theories of all time, including that of the origin of species. In the next section, we will consider another important theory that strives to understand species diversity at smaller spatial scales.

CONCEPT 18.3

Regional differences in species diversity are influenced by area and distance, which determine the balance between immigration and extinction rates.

Regional Biogeography

An important thread that runs through this chapter, and through biogeography generally, is the relationship between species richness and geographic area. We saw in the Case Study that large fragments of Amazon rainforest had greater species richness than smaller fragments. In our global tour of the world's forests, we saw that species diversity was greatest in the tropics (see Table 18.1), the climate zone whose geographic area is largest (see Figure 18.15A). This so-called **species–area relationship**, in which species richness increases with the area sampled, has been documented at a variety of spatial scales, from small ponds to whole continents. Most studies of species–area relationships have been targeted at regional spatial scales, where these relationships tend to be good predictors of differences in species richness.

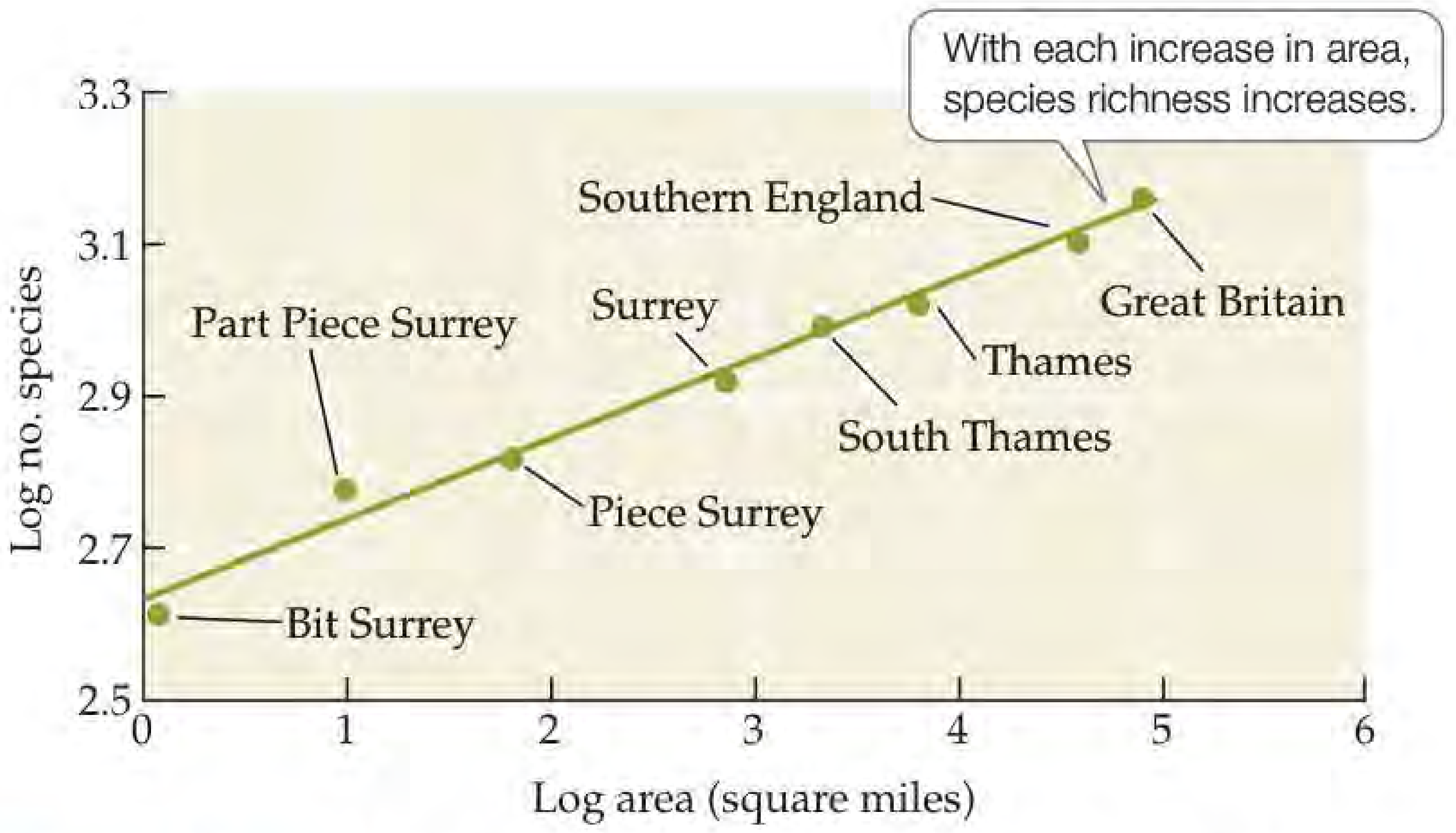


Figure 18.18 The Species–Area Relationship The first species–area curve, for British plants, was constructed by H. C. Watson in 1859. (After Williams 1943.)

Species richness increases with area and decreases with distance

In 1859, H. C. Watson plotted the first curve showing a quantitative species–area relationship—in this case, for plants within Great Britain (**Figure 18.18**) (Williams 1943). The curve starts with a small "bit" of Surrey County and expands to ever-increasing areas that eventually encompass all of Surrey County, southern England, and finally Great Britain. With each increase in area, species richness increases until it reaches a maximum number bounded by the largest area considered. (**Ecological Toolkit 18.1** and **Analyzing Data 18.1** provide further insight on how species–area curves are plotted and interpreted.)

Most species–area relationships have been documented for islands (**Figure 18.19**). Islands, in this case, include

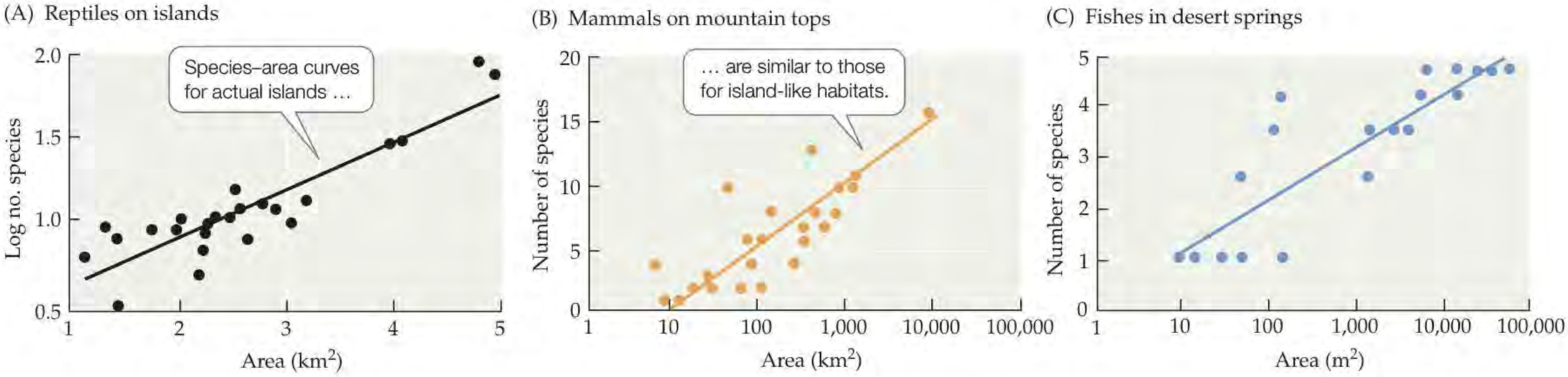


Figure 18.19 Species–Area Curves for Islands and Island-Like Habitats Species–area curves plotted for (A) reptiles on Caribbean islands, (B) mammals on mountaintops in the American Southwest, and (C) fishes living in desert springs in Australia all show a positive relationship between area and species richness. (A after Wright 1981; B after Lomolino et al. 1989; C after Kodric-Brown and Brown 1993.)

ECOLOGICAL TOOLKIT 18.1 Species–Area Curves

Species–area curves are the result of plotting the species richness (*S*) of a particular sample against the area (*A*) of that sample. A linear regression equation estimates the relationship between *S* and *A* in the following manner:

$$S = zA + c$$

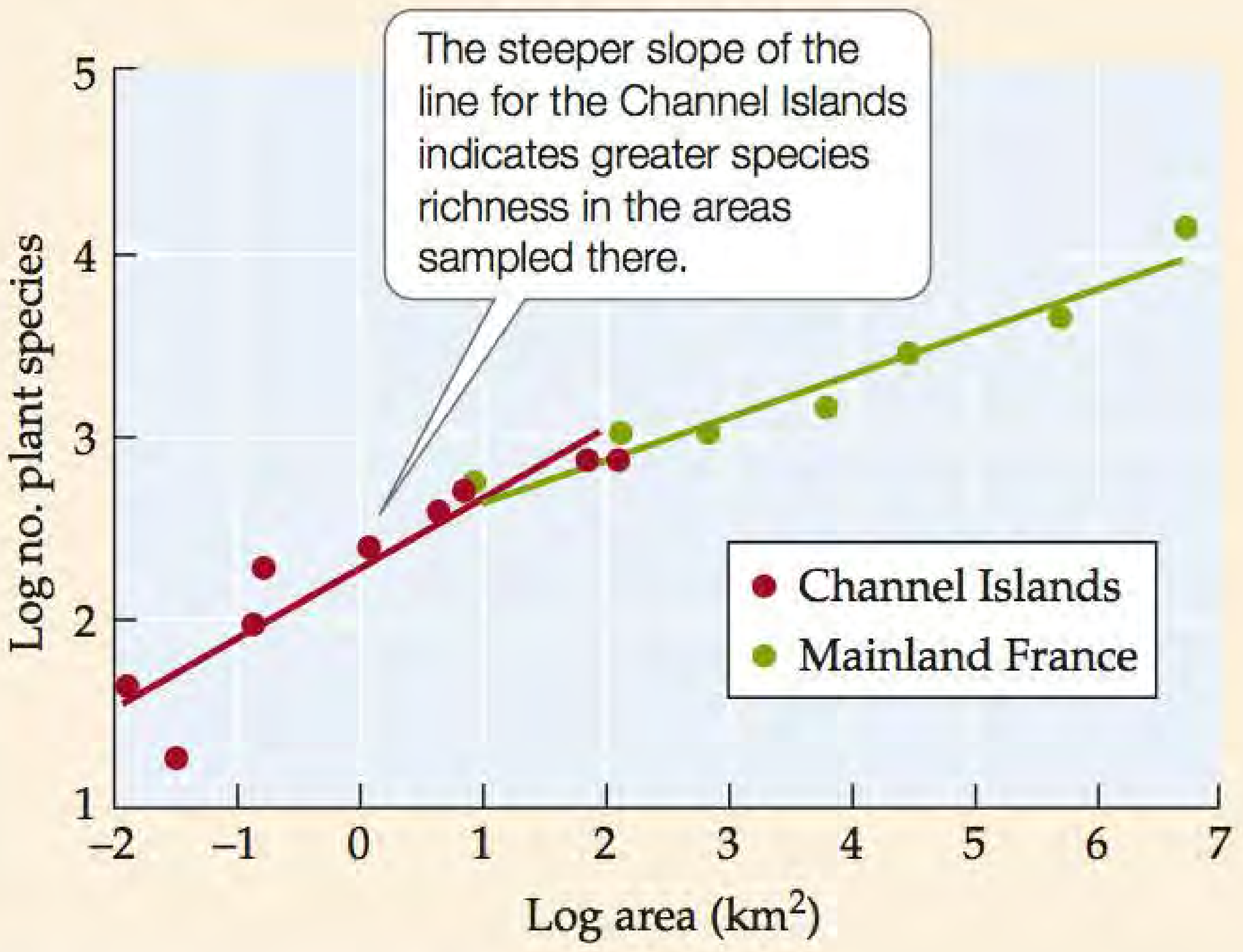
where *z* is the slope of the line and *c* is the *y* intercept of the line.

Because species–area data are typically nonlinear, ecologists transform *S* and *A* into logarithmic values so that the data fall along a straight line and conform to a linear regression model.

The figure shows species–area curves for plants on the Channel Islands (off the coast of France) and on the French mainland (Williams 1964). Log transformations were conducted on both the island and mainland data, the two data sets were plotted separately, and a linear model was used to estimate the best-fit curve for each of the data sets.

An important characteristic of species–area curves is evident in this figure: the steeper the slope of the line (i.e., the greater the *z* value), the greater the difference in species richness among the sampling areas. The Channel Islands have a much steeper slope than the French mainland areas, for the reasons outlined at the end of Concept 18.3.

Species–Area Relationships of Island versus Mainland Areas Species–area curves for plant species on the Channel Islands and in mainland France show that the slope of a linear regression equation (*z*) is greater for the islands than for the mainland areas. (After Williams 1964.)



all kinds of isolated areas surrounded by a "sea" of dissimilar habitat (referred to as *matrix* habitat). So "islands" can include real islands surrounded by ocean, lake "islands" surrounded by land, or mountain "islands" surrounded by valleys. They can also include habitat fragments, like those produced by the deforestation of the Amazon (see Figure 18.2). Nonetheless, all of these islands and island-like habitats display the same basic pattern: large islands have more species than small islands.

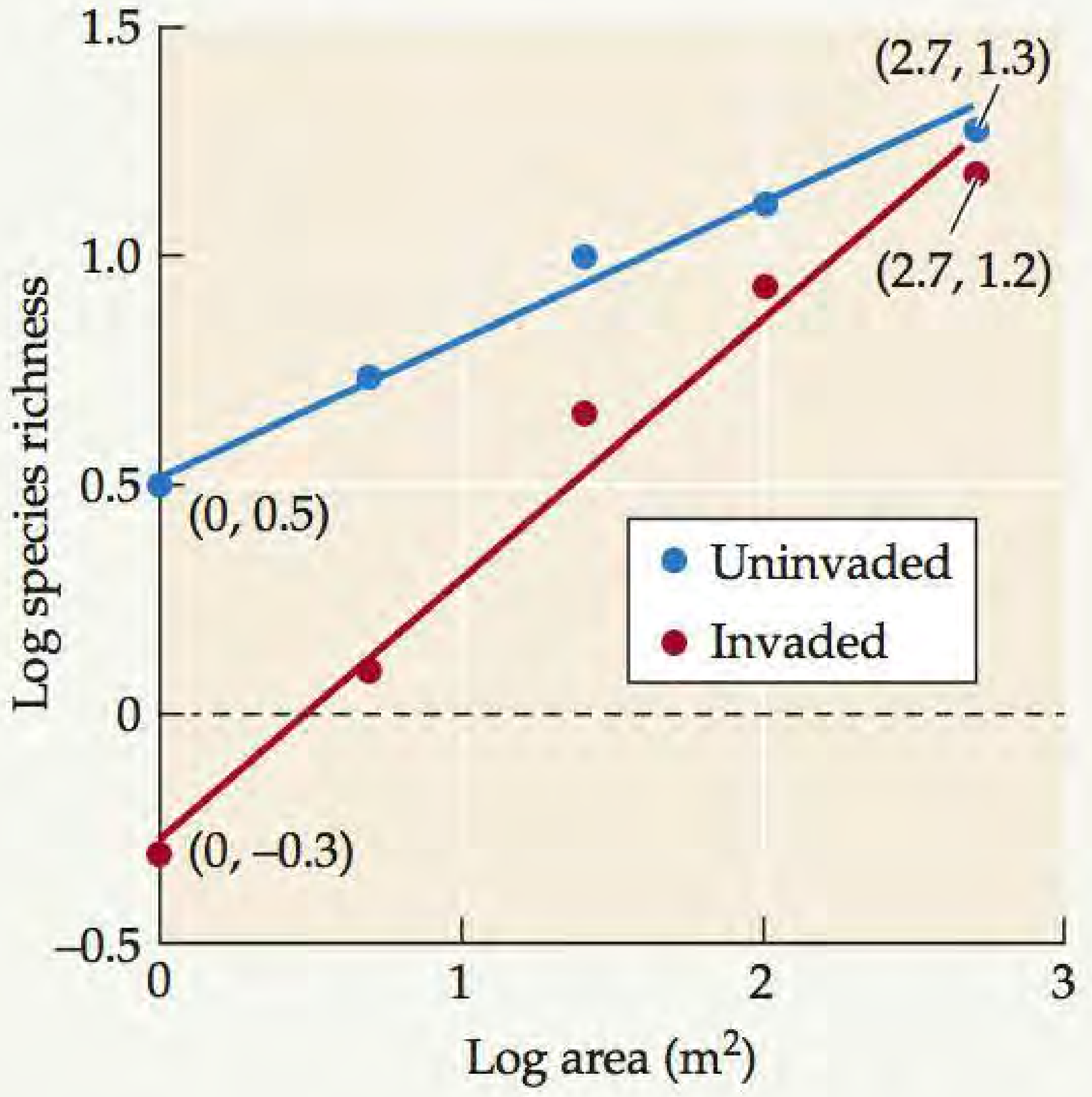
In addition, because of the isolated nature of islands, species diversity on islands shows a strong negative relationship to distance from the main source of species. For example, Lomolino et al. (1989) found that mammal species richness on mountaintops in the American Southwest decreases as a function of the distance from the main source of species—in this case, two large mountain ranges in the region. This and other examples generally show that islands more distant from source populations, such as those in mainland areas or unfragmented habitats, have fewer species than islands of roughly the same size closer to source populations.

Almost always, however, island isolation and size are confounded. Robert MacArthur and Edward O. Wilson (1963) illustrated this problem by plotting the relationship between bird species richness and island area for a group of islands in the Pacific Ocean off New Guinea (**Figure 18.20**).

ANALYZING DATA 18.1 Do Species Invasions Influence Species–Area Curves?

As we learned in Analyzing Data 16.1, the invasion of non-native species has been implicated in both increases and decreases of species diversity within communities. In the study we considered in that exercise, the majority of the non-native species had negative effects on species diversity at relatively small scales (16 m^2). Does this pattern hold as we increase the spatial scale over which we sample species diversity?

Kristin Powell and colleagues (2013)* considered this question by comparing the effect of native and non-native plants on forest communities at different spatial scales. They used species–area curves to plot the number of plant species versus the area sampled for three separate tree communities across the United States: tropical forests in Hawaii being invaded by the fire tree (*Morella faya*), oak–hickory forests in Missouri being invaded by Amur honeysuckle *(Lonicera maackii*), and hardwood hammock forests in Florida being invaded by the cerulean flax lily (*Dianella ensifolia*). In each of the forests, they identified multiple pairs of sites on opposite sides of an invasion front that had been ongoing for at least 30 years. At invaded sites, more than 90% of the plant cover was invaders, while the second site remained uninvaded. Powell et al.'s results for the Florida forest community are shown in the figure. (Their studies of forests in Hawaii and Missouri are explored in the Analyzing Data 18.1 Online Exercise.)



1. How do the slope (*z*) and *y* intercept (*c*) of the curve differ for invaded and uninvaded sites? What does this difference tell us about the effect of invaders on species richness at small versus large spatial scales?
2. Convert the log area (m^2) and log species richness to non-log values at the smallest and largest spatial scales for invaded and uninvaded sites. What is the approximate range in spatial extent and in species richness for invaded and uninvaded plots?
3. Provide a hypothesis that could explain the difference between the species–area curves for invaded versus uninvaded areas.

See the companion website for a similar ANALYZING DATA exercise.

---

*Powell, K. I., J. M. Chase and T. M. Knight. 2013. Invasive plants have scale-dependent effects on diversity by altering species–area relationships. *Science* 339: 316–318.

Here, the islands varied in both size and degree of isolation from the mainland, but some patterns were evident. For example, if we compare islands of equivalent size, the island farthest from source populations (on New Guinea) has fewer bird species than the island closest to source populations.

Let's turn now to the question of how island area and isolation could together act to produce these commonly observed species diversity patterns.

Species richness is a balance between immigration and extinction

The Theory of Island Biogeography (1967) represented one of the most important breakthroughs in the science of

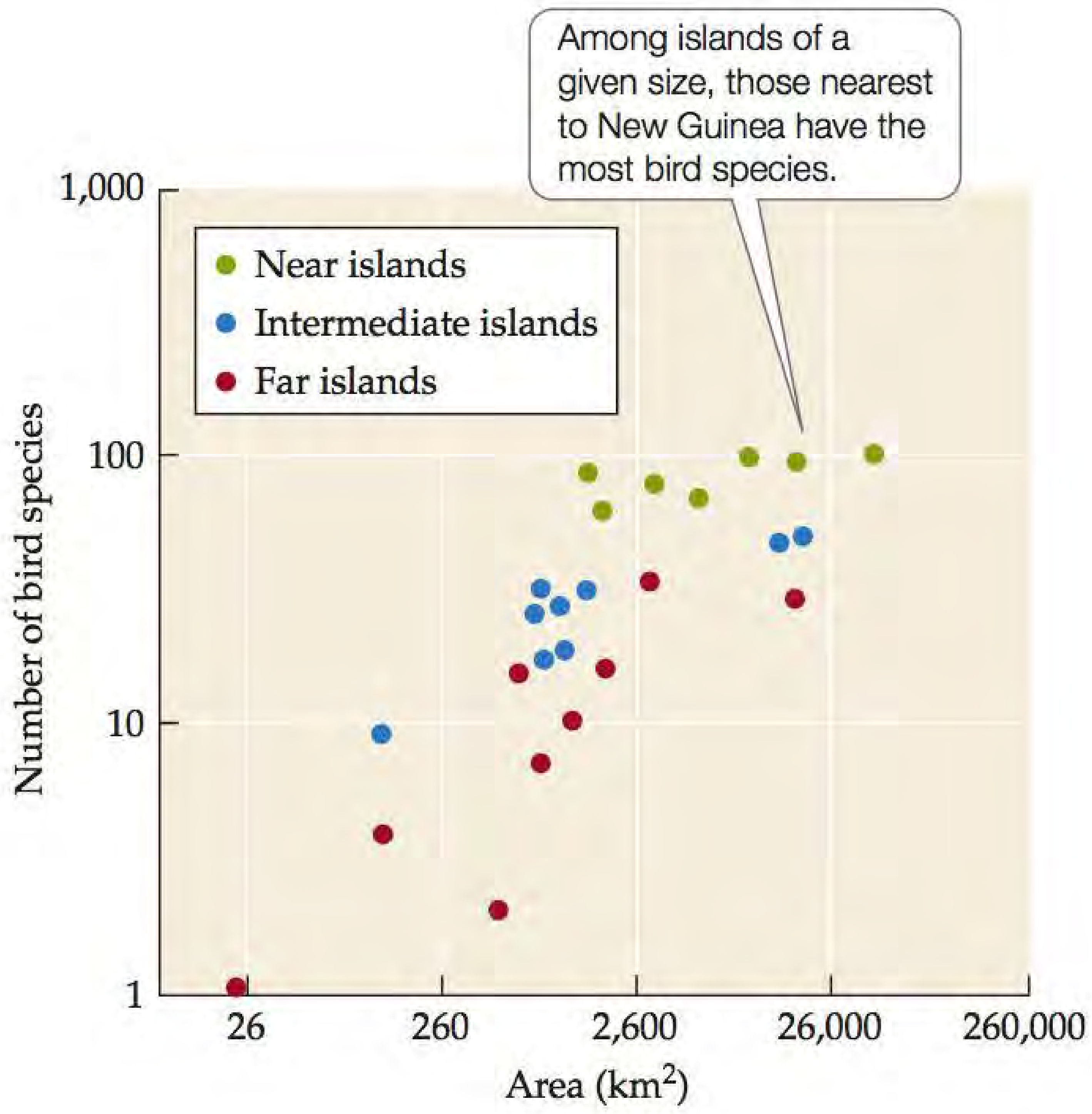
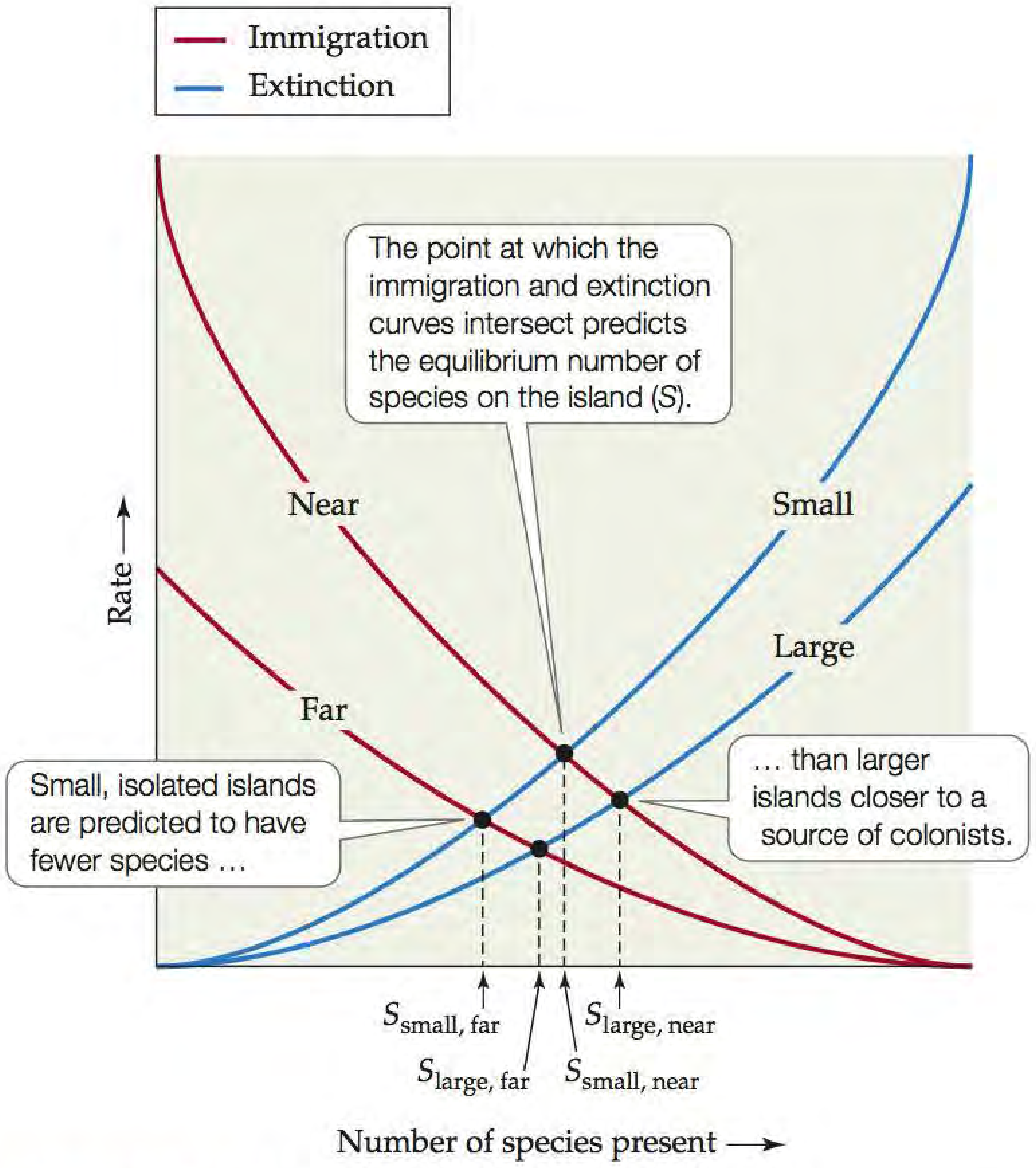

Among islands of a given size, those nearest to New Guinea have the most bird species.

Figure 18.20 Area and Isolation Influence Species Richness on Islands MacArthur and Wilson plotted species–area relationships for birds on islands of different sizes and at different distances from source populations (on New Guinea). (After MacArthur and Wilson 1963.)

biogeography since Wallace's time. The book was born out of the common interests of two scientists: an ecologist, Robert MacArthur, and a taxonomist and biogeographer, Edward O. Wilson. Wilson, who had studied the biogeography of ants for his Ph.D. thesis work, had made a few key observations about islands in the South Pacific, which he found himself discussing with MacArthur when they met at a scientific meeting (Wilson 1994). The first observation was that for every tenfold increase in island area, there was a rough doubling of ant species richness. The second was that as ant species spread from mainland areas to islands, the new species tended to replace the existing species, but there was no net gain in species richness. There appeared to be an equilibrium number of species on the islands, which was dependent on their size and distance from the mainland, but species composition on the islands could, and did, change over time.

MacArthur, a gifted mathematical ecologist, was just 31 years old when he and Wilson developed these observations into the beginnings of a simple but elegant theoretical regional biogeographic model. The model, published in their book 5 years later, became more commonly known as the **equilibrium theory of island biogeography**. The theory is based on the idea that the number of species on an island, or in an island-like habitat, depends on a balance between immigration or dispersal rates and extinction rates. The theory works something like this: Imagine an empty island open for colonization by species from mainland, or source, populations. As new species arrive on the island, by whatever means necessary, the island starts to fill up. The rate of immigration (the number of new species arriving) decreases over time as more and more species are added, eventually reaching zero when the entire pool of new species that could reach the island and be supported there is exhausted. But as the number of species on the island increases, there should also be an increase in the rate of extinction. This assumption makes sense according to the simple principle of balance mentioned above: with more species, there are more species extinctions. Additionally, as the number of species increases, the population size of each species should get smaller. Conceivably, this could occur for two reasons. First, competition may increase, thus decreasing the population sizes of species as they vie for the same space and resources. Second, predation may increase as more consumer species are added to the island. The result of either interaction is smaller population sizes and thus a greater risk of species extinction. If we plot the immigration rate against the extinction rate, the actual number of species on the island should fall where the two curves intersect, or where species immigration and extinction are in balance (**Figure 18.21**). This equilibrium number is the number of species that should theoretically "fit" on the island, irrespective of the turnover, or replacement of one species with another, that occurs on the island over time.



The point at which the immigration and extinction curves intersect predicts the equilibrium number of species on the island (*S*).

Small, isolated islands are predicted to have fewer species …

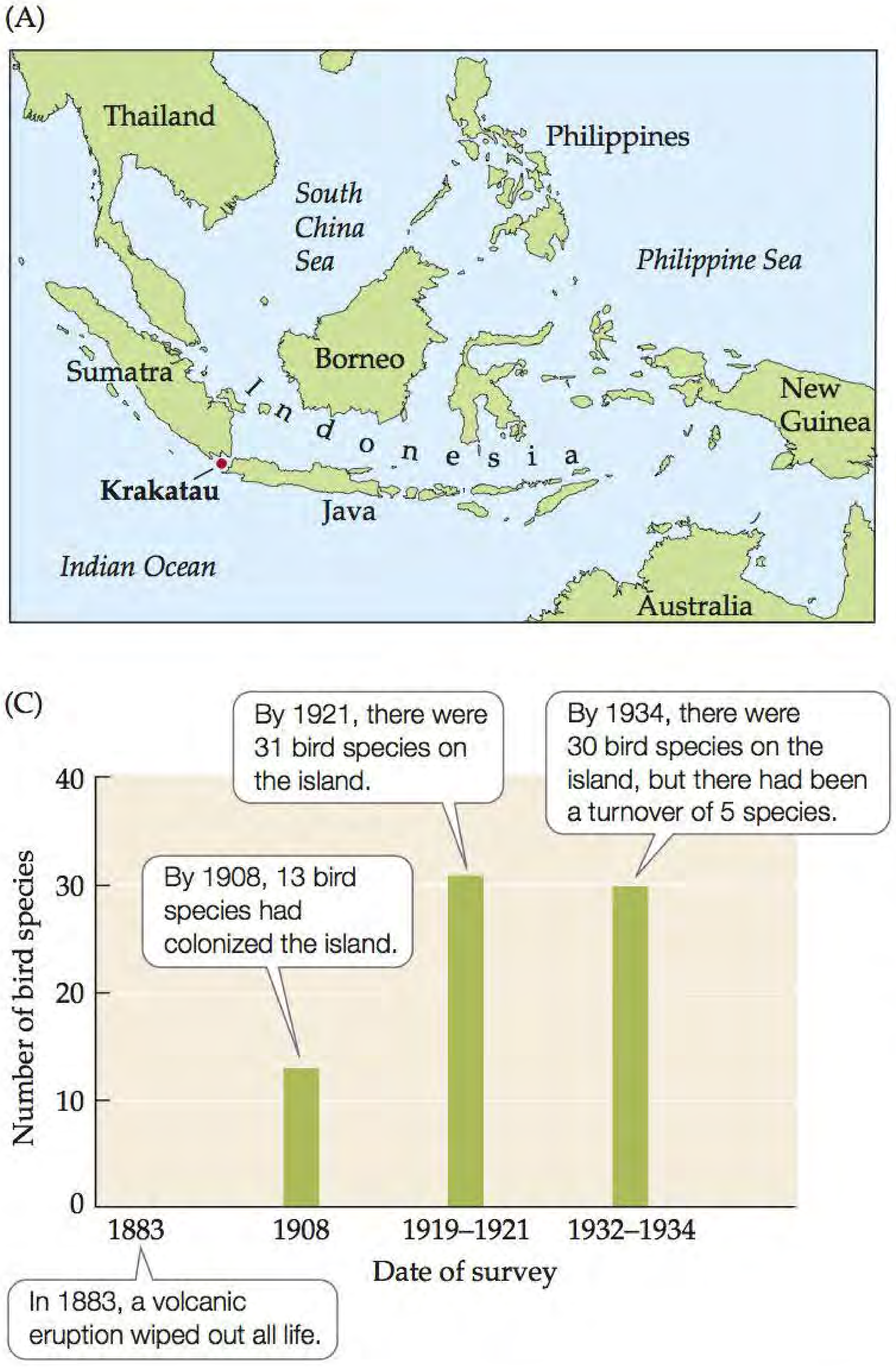
… than larger islands closer to a source of colonists.

Figure 18.21 The Equilibrium Theory of Island Biogeography MacArthur and Wilson's theory emphasized the balance between species immigration rates and species extinction rates for islands of different sizes and at different distances from a source of colonizing species. (After MacArthur and Wilson 1967.)

To understand the influence of island size and isolation on island species richness, MacArthur and Wilson simply adjusted their curves up or down to reflect their effects (see Figure 18.21). They assumed that island size mainly controls the extinction rate. They reasoned that small islands should have higher extinction rates than large islands, for the same two reasons described above, resulting in an extinction curve for small islands that is higher than that for large islands. Likewise, they reasoned that the distance of an island from the mainland mainly controls the immigration rate. Distant islands should have lower rates of immigration than islands near the mainland, resulting in an immigration curve for distant islands that is lower than that for islands near the mainland.

To test their theory, MacArthur and Wilson (1967) applied it to observations from the small volcanic island of Krakatau, between Sumatra and Java, which erupted violently in 1883, wiping out all life on the island (**Figure 18.22**). Surprisingly, animal and plant species began returning to what little remained of the island within a year of the explosion. MacArthur and Wilson used data from three surveys at various times since the eruption to calculate the immigration and extinction rates of birds on the island. Based on these rates, they predicted that the

(A)



By 1921, there were 31 bird species on the island.

By 1934, there were 30 bird species on the island, but there had been a turnover of 5 species.

By 1908, 13 bird species had colonized the island.

In 1883, a volcanic eruption wiped out all life.

(B)

Figure 18.22 The Krakatau Test (A) The eruption of the small volcanic island of Krakatau, near Sumatra and Java, in 1883 provided a natural test of the equilibrium theory of island biogeography. (B) Krakatau is still an active volcano, as this recent photo shows. (C) By 1921, the number of bird species had reached 31, and in 1934, it was at 30—the equilibrium number predicted by MacArthur and Wilson's theory. Turnover, however, was five times higher than the theory had predicted. (C after MacArthur and Wilson 1967.)

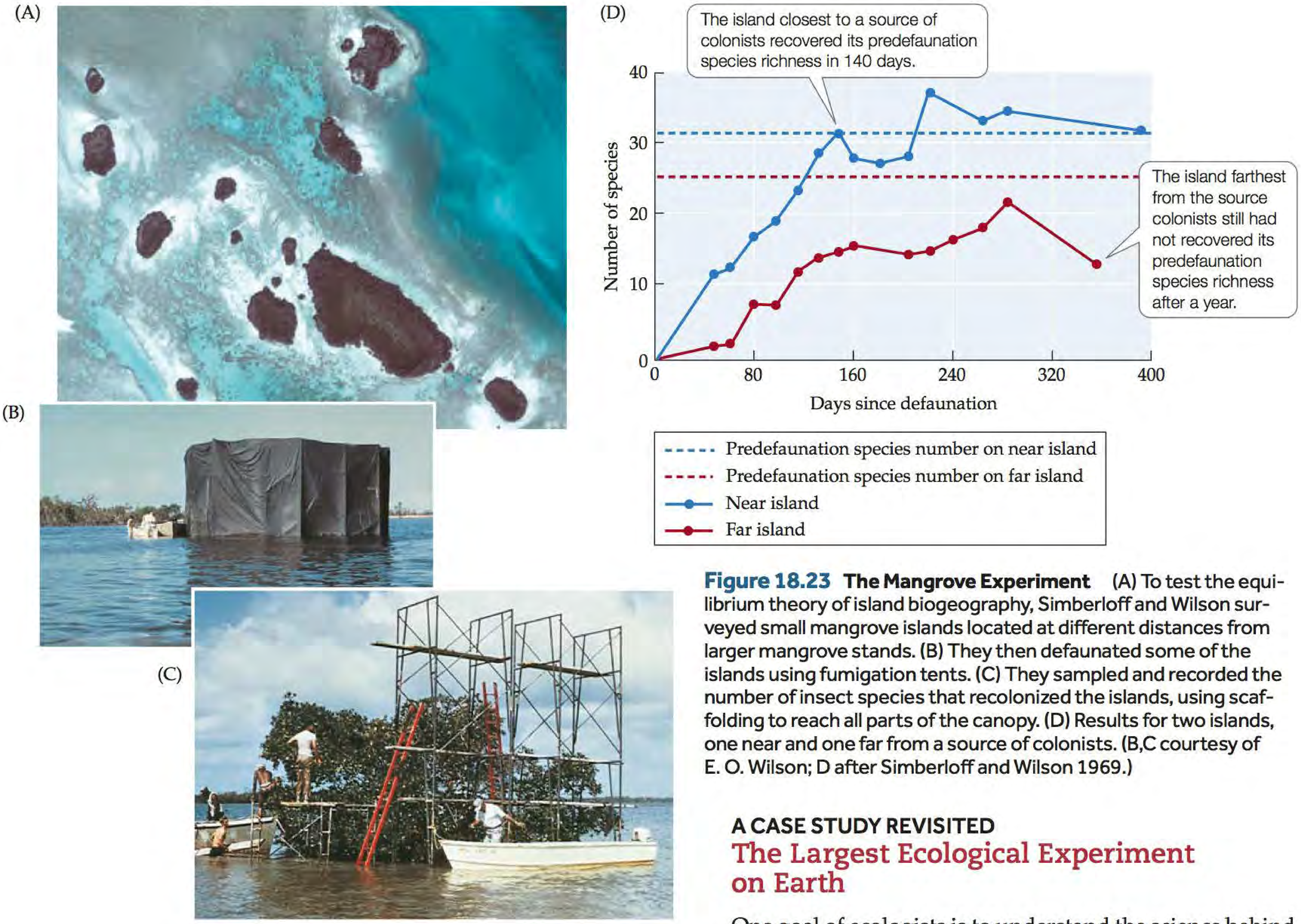
island should sustain roughly 30 bird species at equilibrium, with a turnover of 1 species. The data showed that bird species richness on the island had indeed reached 30 species within 40 years after the eruption and had remained close to that number thereafter. However, they also found that turnover was much higher, at 5 species. Whether this difference was due to a sampling error or a problem with the model is unknown, but this example motivated Wilson and others (e.g., the BDFFP researchers whose work is described in this chapter's Case Study) to start testing the model using manipulative experiments.

One of the best-known experiments to test the equilibrium theory of island biogeography was conducted by Daniel Simberloff and his advisor, Edward O. Wilson, on small mangrove islands and their arthropod inhabitants in the Florida Keys (Simberloff and Wilson 1969; Wilson and Simberloff 1969). These islands were scattered at various distances from large "mainland" mangrove stands (**Figure 18.23A**). After surveying species richness on the islands, Simberloff and Wilson manipulated a handful of them by fumigating them with an insecticide to remove all of their insects and spiders (**Figure 18.23B**). They then surveyed the defaunated islands over a year-long period (**Figure 18.23C**). By the end of the year, species numbers on the islands were similar to those before the defaunation; furthermore, the island closest to a source of colonists had the most species, and the farthest island had the least (**Figure 18.23D**). Interestingly, the farthest island had not quite regained its original species richness even after 2 years. All the islands showed considerable turnover of species, as might be expected for small islands where extinction rates are predicted to be high (see Figure 18.21).

The equilibrium theory of island biogeography holds true for mainland areas

Do the effects of area and isolation influence differences in species richness in mainland areas as well as on islands? As we saw in Watson's graph of plant species richness in Great Britain (see Figure 18.18), the species–area relationships observed on islands can also hold for mainland areas. How, then, does the biogeography of mainland areas differ from that of islands and island-like areas?

Let's consider a plot of plant species richness in mainland areas of France and on the Channel Islands in the English Channel (see Ecological Toolkit 18.1). Williams (1964) showed that plant species richness increases with area in both locations but that the slope of the line representing the increase is steeper for the Channel Islands than for the French mainland (i.e., the z value was greater on the islands). How can we interpret this difference? In mainland areas, just as on islands, species richness is theorized to be controlled by rates of immigration and extinction. In mainland areas, however, these rates are likely to be different from those on islands. Immigration rates



The island closest to a source of colonists recovered its predefaunation species richness in 140 days.

The island farthest from the source colonists still had not recovered its predefaunation species richness after a year.

Figure 18.23 **The Mangrove Experiment** (A) To test the equilibrium theory of island biogeography, Simberloff and Wilson surveyed small mangrove islands located at different distances from larger mangrove stands. (B) They then defaunated some of the islands using fumigation tents. (C) They sampled and recorded the number of insect species that recolonized the islands, using scaffolding to reach all parts of the canopy. (D) Results for two islands, one near and one far from a source of colonists. (B,C courtesy of E. O. Wilson; D after Simberloff and Wilson 1969.)

should be greater in mainland areas because the barriers to dispersal are lower. Species can move from one area to the next, presumably through continuous, non-island habitat. In addition, extinction rates should be much lower in mainland areas because of the continual immigration of new individuals from the larger mainland population. The idea is that species will always have a good chance of being "rescued" from local extinction by other population members. The end result of these higher immigration and lower extinction rates in mainland areas is a lower rate of increase in species richness with increasing area, and thus a gentler slope, than in island areas.

We have seen over and over again in this chapter that geographic area has a large influence on species diversity at global and regional spatial scales. This effect takes on heightened significance as more habitats become "island-like" because of human influences. As we will see in the Case Study Revisited, the theory and practice of island biogeography is timely and relevant to the issues of conservation that we deal with today.

A CASE STUDY REVISITED

The Largest Ecological Experiment on Earth

One goal of ecologists is to understand the science behind the conservation of species threatened by habitat destruction and fragmentation. As we set aside more and more reserves to protect species diversity, the areas around those reserves continue to be changed by human activities, leaving many of them islands in a matrix of degraded habitat that is unsuitable for the species they contain. Thus, it is critical that we understand reserve design if we are to meet our conservation goals. When Lovejoy and his colleagues embarked, almost 40 years ago, on the Biological Dynamics of Forest Fragments Project in the Amazon, one of their goals was to study the effects of reserve design on the maintenance of species diversity (Bierregaard et al. 2001). As it turned out, they learned that habitat fragmentation had even more negative and complicated effects than they had originally anticipated.

One of the first things they learned was that forest fragments needed to be large and close together to effectively maintain their original species diversity. For example, in a study of forest understory birds, Ferraz et al. (2003) found that even the largest fragments they surveyed (100 ha) lost 50% of their species within 12 years. Given that regeneration time for these tropical rainforests ranges from several decades to a century, they projected that even fragments of 100 ha would be ineffective at maintaining bird species richness until forest regeneration could "rescue" species surviving within the fragments. The ecologists calculated that over 1,000 ha would be needed to maintain bird species richness until the forests could be regenerated, an area far greater than the average Amazon rainforest fragment in existence today (Gascon et al. 2000). If forest regeneration did not occur—as is likely when the land around a forest fragment is developed or used for agriculture—the fragment would have to contain 10,000 ha or more to maintain most of its bird species over more than 100 years of isolation (although even a fragment of that size could not sustain them all).

The researchers of the BDFFP were also surprised at how even minimal distances between fragments resulted in almost complete isolation of species. Clearings even 80 m (265 feet) wide hindered the recolonization of fragments by birds, insects, and arboreal (tree-dwelling) mammals (Laurance et al. 2002). It seemed that animals avoided entering the clearings for a number of interrelated reasons, the most obvious of which is that they have no innate reason to do so, having evolved within large, continuous, and climatically stable habitats that lacked the fragmentation imposed on them by deforestation. Moreover, even if some animals were inclined to venture into the clearings, specific requirements for their movement, such as trees for arboreal mammals, would not be present to facilitate their travel to other forest patches.

A second major finding of the BDFFP was that habitat fragmentation exposes the species within a fragment to a wide variety of potential hazards, including harsh environmental conditions, fires, hunting, predators, diseases, and invasive species. These *edge effects*, which occur at the transition between forest and nonforested matrix habitat, can act together to increase local species extinctions. Trees, for example, can be killed or damaged by their sudden exposure to brighter light, higher temperatures, wind, fire, and diseases (**Figure 18.24**). Over time, depending on the surrounding matrix habitat, the ultimate influences of edge effects are revealed. If the matrix habitat is left undisturbed, secondary succession occurs, as described in Chapter 17, reducing edge effects. If the matrix habitat continues to be disturbed, however, then the area subjected to edge effects may increase in size. For example, Gascon et al. (2000) describe forest fragments in the southern Amazon that are embedded in huge non-native sugarcane and *Eucalyptus* plantations where burning is used regularly for crop rotation. The burning keeps the forest edges in a constant state of disturbance. Fire-tolerant plant species, many of them non-native, become more common at the edges and act as conduits for more fires. This positive feedback loop ends up decreasing the effective size of the forest fragments and continually increasing the area subjected to edge effects. Some edge effects can extend a kilometer or more into a fragment, essentially influencing the entire area of a 1,000 ha fragment.

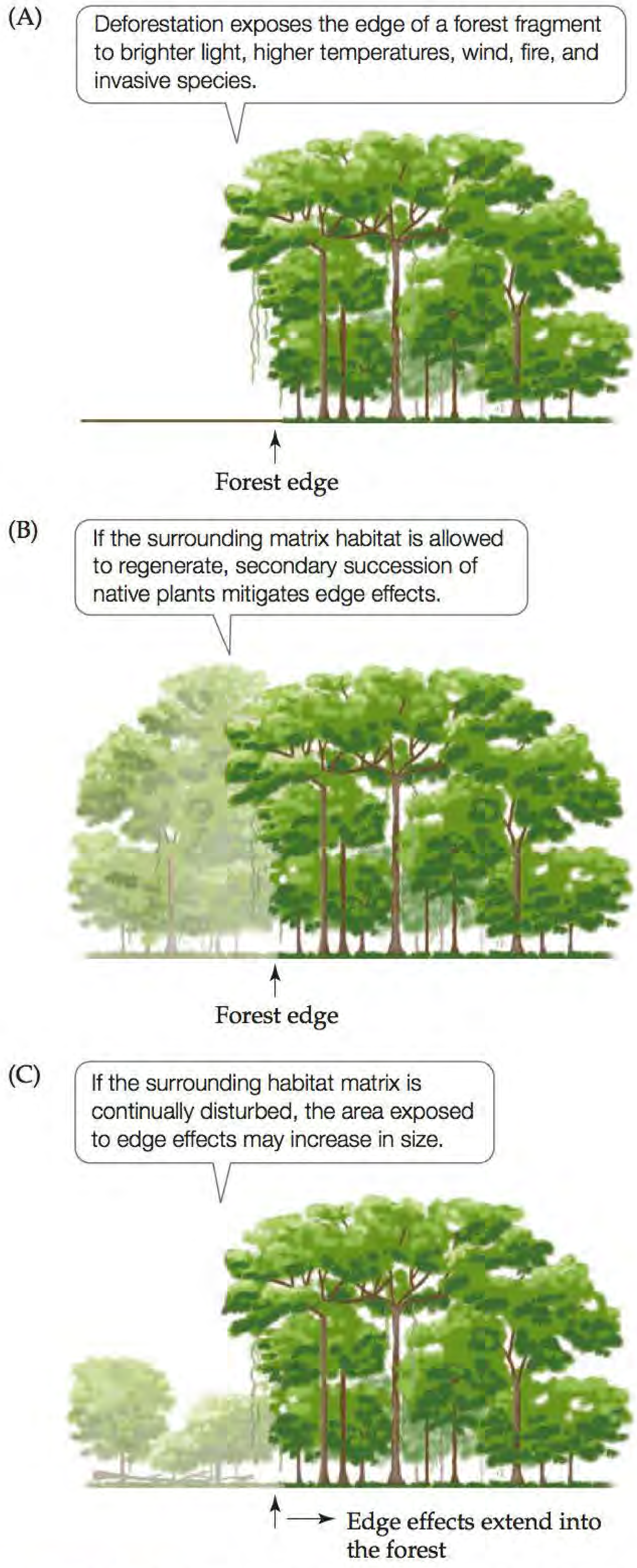


Figure 18.24 Tropical Rainforests on the Edge The BDFFP's research showed that deforestation subjects the forest fragments that remain to negative edge effects. (After Gascon et al. 2000.)

The results of the BDFFP have made an immense and sobering contribution to our understanding of forest fragmentation. As Laurance et al. (2002) point out, the BDFFP is a controlled experiment that probably provides a conservative estimate of species losses. The BDFFP has shown us that most of the forest fragments human activities are creating are too small to maintain all their original species; thus, habitat fragmentation is likely to result in the loss of many species. We'll see how the BDFFP's findings are being applied to reserve design and other conservation efforts when we discuss habitat fragmentation and edge effects in more detail in Concept 24.2.

CONNECTIONS IN NATURE
Tropical Rainforest Diversity Benefits Humans

Why do we care when species go extinct in a rainforest far away? As we will see in Concept 23.1, such extinctions raise ethical and aesthetic concerns similar to those that arise when great works of art or antiquities are lost to society. In addition, there are economic concerns about the loss of important *ecosystem services* produced by natural systems, which help sustain human health and well-being. For example, tropical deforestation raises concerns about losses of important foods and medicines that have their origins in rainforests. At least 80% of the developed world's diet originated in tropical rainforests, including corn, rice, squash, yams, oranges, coconuts, lemons, tomatoes, and nuts and spices of many kinds. Twenty-five percent of all commercial pharmaceuticals are derived from tropical rainforest plants, but less than 1% of tropical rainforest plants have been tested for their potential medical uses.

These statistics raise the question, How does the economic value of tropical rainforest plants used for nontimber purposes compare with the value of deforestation? It turns out that there have been very few economic analyses of this type. A few studies come from the Millennium Ecosystem Assessment (2005), a synthesis of studies on the use of the environment and its relationship to human needs, created by leading scientists from around the world. An example comes from Cambodia, where the total economic value of traditional forest products (e.g., fuelwood, rattan and bamboo, malva nuts, and medicines) was compared with that of unsustainable forest harvesting. The value of traditional forest products is four to five times greater ($700–$3,900 per hectare) than that of unsustainable forest harvesting ($150–$1,100 per hectare).

Recognition of the economic benefits of changing our resource management practices has only just begun. Why is this? Part of the answer lies in our not formally recognizing the economic value of the services provided to humans by species or whole communities. Tropical rainforests provide food, medicine, fuel, and a destination for tourists, all of which can be obtained without complete deforestation. Rainforests also regulate water flow, climate, and atmospheric CO_2 concentrations. Assigning a value to any of these important services is difficult compared with setting the market price of timber or agricultural products. For that reason, it is easier to justify the use of rainforest timber and land (and even some sustainable forest products) for private profit than to press for the conservation of rainforests based on the ecological services they provide to society in general. If private landowners are not given incentives to value the larger social benefits of ecological services, maximization of personal gain often drives their decisions. Given the importance of ecological services to our planet, we can no longer afford to ignore these economic trade-offs.

Summary

CONCEPT 18.1 Patterns of species diversity and distribution vary at global, regional, and local spatial scales.

- Biogeography is the study of variation in species composition and diversity among geographic locations.
- Patterns of species composition and diversity at different spatial scales are connected to one another in a hierarchical way.
- The regional spatial scale encompasses a smaller geographic area in which the climate is roughly uniform and the species contained therein are bound by dispersal limitation to that region.
- The local spatial scale encompasses the smallest geographic area and is essentially equivalent to a community.
- Beta diversity is the change in species number and composition, or turnover of species, across the landscape from one local community to another.
- Studies show that regional species pools largely determine the numbers of species present in local communities but that local conditions are also important.

CONCEPT 18.2 Global patterns of species diversity and composition are influenced by geographic area and isolation, evolutionary history, and global climate.

- Earth's land mass can be divided into biogeographic regions that vary markedly in species diversity and composition.
- The biotas of the biogeographic regions reflect an evolutionary history of isolation due to continental drift caused by the movements of Earth's tectonic plates.
- Tracing the threads of vicariance over large geographic areas and long time periods provided important evidence for early theories of evolution.
- Species diversity is greatest in the tropics and declines at higher latitudes.
- A number of hypotheses, involving species diversification rate, species diversification time, and productivity, have been proposed to explain the latitudinal gradient in species diversity.

(Continued)

Summary (Continued)

CONCEPT 18.3 Regional differences in species diversity are influenced by area and distance, which determine the balance between immigration and extinction rates.

- Species richness tends to increase with the area sampled and decrease with distance from a source of species.
- Most species–area relationships have been documented for "islands," which include all kinds of isolated areas surrounded by dissimilar habitat.
- The equilibrium theory of island biogeography predicts that a balance between immigration and extinction rates controls species diversity on islands or in island-like areas.
- According to the theory, larger islands closer to a source of species have more species than smaller islands that are more distant from a source of species, because they have higher immigration rates and lower extinction rates.
- In some cases, the same species–area relationship observed on islands also holds for mainland areas, but the rate of increase in species richness with increasing area is lower than on islands and in island-like areas.

Review Questions

1. Spatial scale is important to the biogeographic patterns of species diversity and composition that we see on Earth. Define the various spatial scales that are important to biogeography, and describe how they are related to or interconnected with one another.
2. Describe the factors that Alfred Russel Wallace believed created biogeographic regions on land and in the oceans.
3. Latitudinal gradients in species diversity and composition are strong global features of biogeography. Describe three hypotheses proposed to explain why species diversity is higher in the tropics and decreases toward the poles for the majority of taxonomic groups.

ON THE COMPANION WEBSITE

ecology4e.sinauer.com

The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

18.1 Shining Light on the Swiss Family Robinson: Diversity and Dynamics on Islands

18.2 Why Size Matters: Island Size and Ecosystem Function

Web Extensions

18.1 Animation of Continental Drift

18.2 Animation of the Bering Land Bridge after Glaciers Retreated

18.3 Alternative Hypotheses Posed for the Species Diversification Rate in the Tropics

Hone Your Problem-Solving Skills

One study from the Biological Dynamics of Forest Fragments Project (BDFFP) considered the number of understory bird species living in different-sized forest fragments surrounded by deforested land (see the Ferraz et al. 2003 study in Case Study Revisited). This study involved counting the number of bird species in the fragments at the start of the experiment and then over a handful of years afterward. A scaling factor was estimated to determine the time it takes to lose half of the bird species (t_{50}) in the different fragment sizes. Below is a table with the results of the study, organized by the fragment area:

FRAGMENT AREA (HA)	BIRD SPECIES RICHNESS INITIAL COUNT	t_{50} (YR)
1	83	5
10	92	8
100	113	12

1. Graph the initial numbers of bird species by fragment area. Do the fragments follow the species–area relationship?
2. Assuming that the species loss is linear over time, use the table to calculate the percentage loss of species per year in the 1, 10, and 100 ha fragments. Which fragment has the greatest species loss per year, and which has the least?
3. Now use the percentage loss per year to calculate the number of species in each of the fragment sizes 9 years after the start of the experiment. Graph the number of species by fragment area on the graph you developed for Question 1.
4. If you were to draw linear regressions for the species–area data points at the start of the experiment and 9 years after fragmentation, which species–area relationship would have the steepest slope (z)? Explain why.

19 Species Diversity in Communities

KEY CONCEPTS

CONCEPT 19.1 Species diversity differs among communities as a consequence of regional species pools, abiotic conditions, and species interactions.

CONCEPT 19.2 Resource partitioning is theorized to reduce competition and increase species diversity.

CONCEPT 19.3 Processes such as disturbance, stress, predation, and positive interactions can mediate resource availability, thus promoting species diversity.

CONCEPT 19.4 Many experiments show that species diversity affects community function.

Can Species Diversity Suppress Human Diseases? A Case Study

On May 14, 1993, a 19-year-old cross-country track star, riding in the backseat of his family's car, began struggling to breathe. The family immediately stopped at a convenience store to call for help, and the young man was rushed to a hospital in Gallup, New Mexico. The ambulance crew tried to revive him, but he died soon after reaching the emergency room. A chest X ray showed that his lungs were filled with fluid. The deputy medical investigator based in Gallup was called in, and over the course of 2 weeks, he determined that at least five other residents of the area, which included members of the Navajo Nation living in the Four Corners region (where New Mexico, Arizona, Colorado, and Utah intersect), had also mysteriously died in the same sudden manner. After interviewing families of the victims, the medical examiner determined that all had experienced flu-like symptoms and then acute respiratory distress as a result of their lungs being filled with fluid. The disease appeared to be infectious and viral.

By early June 1993, the Viral Special Pathogens Branch of the Centers for Disease Control and Prevention had determined that the culprit was a previously unknown species of hantavirus, a pathogen carried by rodents. It was given the name Sin Nombre virus (SNV) or "the nameless virus." The virus is carried by rodents, which shed the virus in their urine, feces, and saliva. If those sources are disturbed, the virus can become aerosolized and inhaled by humans. It was subsequently determined that the new viral strain was carried by a species of deer mouse (*Peromyscus maniculatus*) whose populations had recently boomed in the Four Corners region (**Figure 19.1**). Research showed that deer mouse populations had increased 20-fold in some locations, triggering the transmission of SNV infections in humans (see Concept 9.5 and Figure 9.17).

Over the last 60 years, the number of emerging diseases affecting humans has substantially increased. Of these diseases, 62% are zoonotic—hosted by wildlife and infectious to humans. Diseases such as the Zika virus, Ebola virus, and avian influenza are all zoonotic diseases that have emerged over the last few decades. The factors that affect zoonotic disease emergence are complex and sometimes disease-specific but often include human-caused events such as

Figure 19.1 Deer Mice Trigger Hantavirus Infection in Humans Can the number of small-mammal species affect the transmission of hantavirus by the deer mouse?

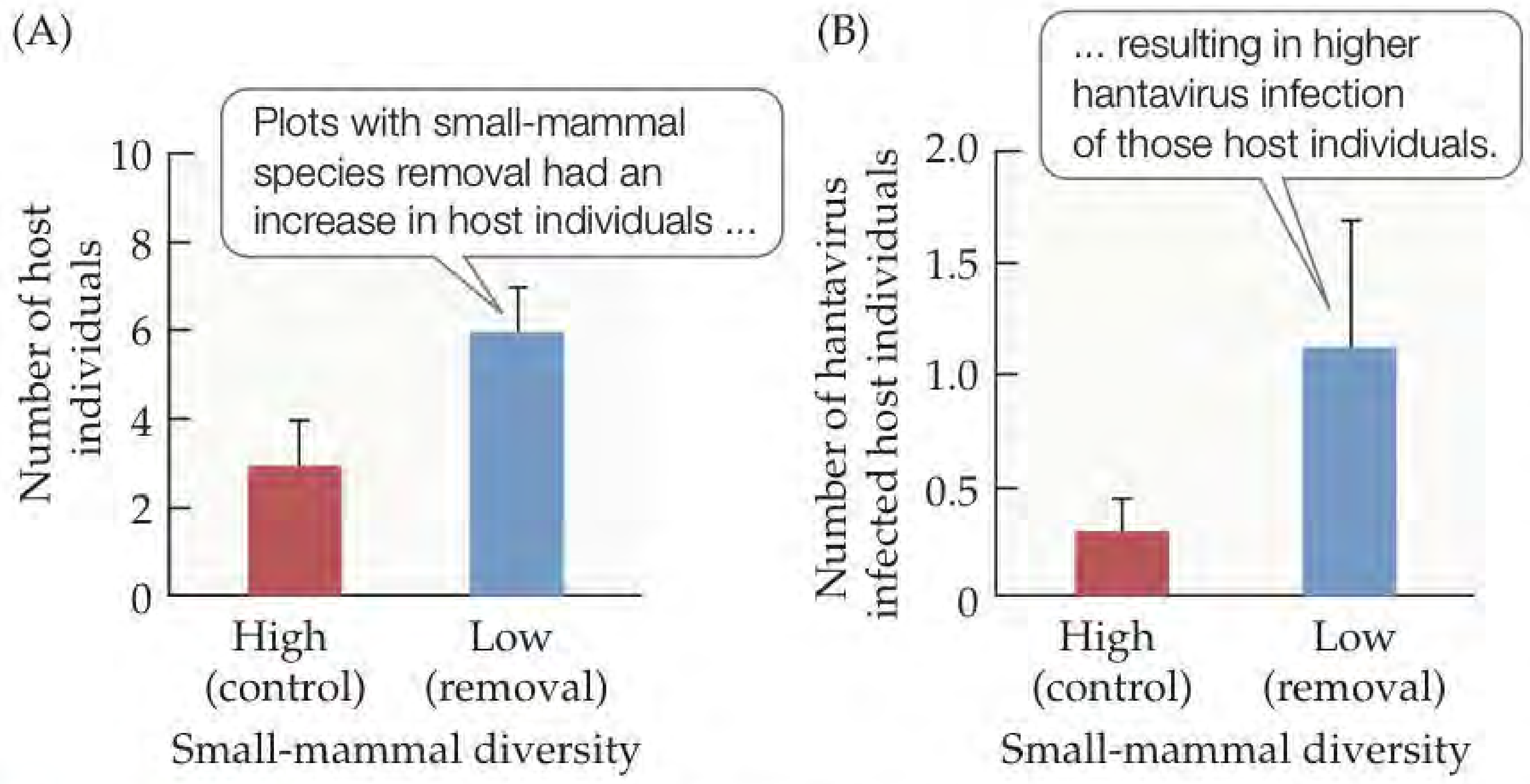


Figure 19.2 Disease Transmission Increased with Species Diversity Loss An experiment in Panama showed that plots with small-mammal diversity removal (low diversity plots) increased in (A) the number of rodent host individuals and (B) the number of hosts infected with the hantavirus compared to the control (high diversity plots). Error bars show one SE of the mean. (After Keesing et al. 2010).

species invasions, climate change, pollution, and land use conversion. One seemingly unlikely factor, that of declining species diversity, is starting to be recognized as an important mechanism that may facilitate the emergence and transmission of zoonotic diseases.

It turns out that hantaviruses provide a nice model system for studying how the loss of species diversity within a community may affect disease emergence and transmission. A number of observational studies have linked hantavirus infection prevalence in deer mouse host populations with declining small-mammal species diversity. For example, in a field study in Oregon, the one variable that was significantly linked to SNV infection prevalence was small-mammal species diversity, with the prevalence of SNV rising from 2% to 14% as species diversity declined (Dizney and Ruedas 2009). A similar study in Utah came to the same conclusion. They too found a negative correlation between small-mammal diversity and SNV infection prevalence in deer mice (Clay et al. 2009).

These observational studies are supported by an experimental study of hantaviruses in rodent communities of Panama. In their study, Gerardo Suzàn and colleagues (2009) conducted a small-mammal removal experiment in replicate field plots, where zoonotic hantaviruses are native and common. Small-mammal diversity was reduced through trapping of species that were not host to the virus. They found that plots with reduced small-mammal diversity had both an increase in rodent host individuals and that more of those individuals were infected by hantavirus (**Figure 19.2**).

The observational and experimental evidence presented here point to the role of species diversity in buffering the transmission of zoonotic pathogens to wildlife and ultimately humans. But what explains the effect of species diversity in disease transmission? As we will see, the response of the host to changes in species diversity makes all the difference in the answer to this question.

Introduction

Communities vary tremendously in the numbers and kinds of species they contain. In Chapter 18, our worldwide tour of forest communities demonstrated the wide variation in species diversity that occurs both globally and regionally. We saw that communities in the tropics (such as the Amazon rainforest) had many more tree species than those at higher latitudes (such as the forests of the Pacific Northwest or New Zealand). Moreover, we found that regional species pools had an important, but not an exclusive, influence on the number of species within a community.

In this chapter, we will focus on species diversity at the local scale. We will ask two important questions: First, what are the factors that control species diversity within communities? Second, what effects does species diversity have on the functioning of communities?

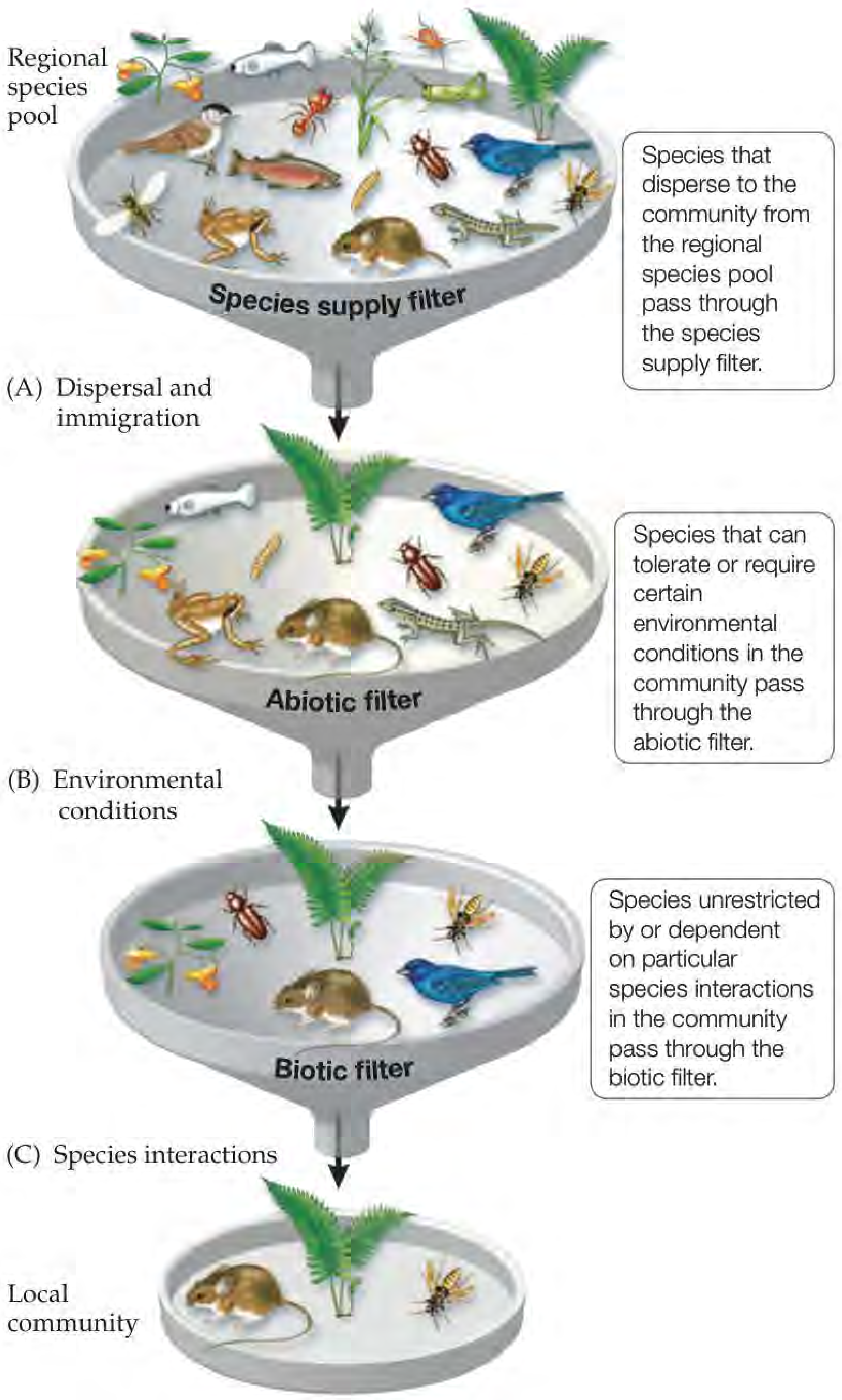
CONCEPT 19.1

Species diversity differs among communities as a consequence of regional species pools, abiotic conditions, and species interactions.

Community Membership

If you looked across a landscape from the top of a mountain, you would see a patchwork of different communities that might consist of, say, forests, meadows, lakes, streams, and marshes (**Figure 19.3**). You could be sure that

Figure 19.3 A View from Above Looking at these mountains in Glacier National Park, Montana, it is easy to see that the landscape is made up of a patchwork of communities of different types.



Species that disperse to the community from the regional species pool pass through the species supply filter.

Species that can tolerate or require certain environmental conditions in the community pass through the abiotic filter.

Species unrestricted by or dependent on particular species interactions in the community pass through the biotic filter.

Figure 19.4 Community Membership: A Series of Filters Species end up in a local community by passing through a series of "filters" that determine community membership. Species are lost at each filter, so local communities contain a fraction of the species in the regional pool. In practice, all the filters work at the same time, rather than in series as the figure suggests. (After Lawton 2000.)

Would it make sense for the fish and frog species in the regional pool to be present in the local community shown in the figure? Explain.

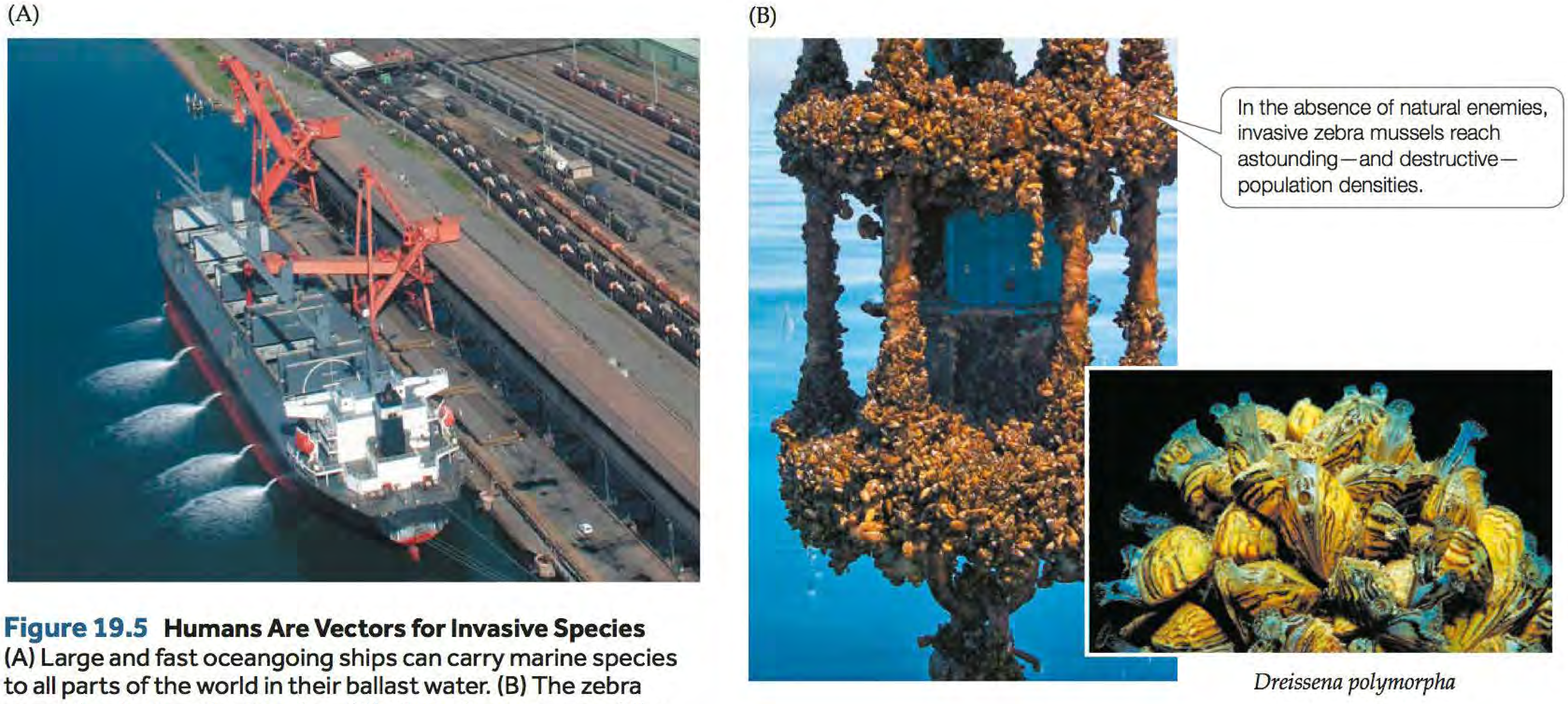
each of those communities would have a different species richness and composition. The meadow would be dominated by a variety of grasses, herbs, and terrestrial insects. The lake would be filled with various species of fish, plankton, and aquatic insects, and it might possibly harbor as many species as the meadow. Even though some species would be able to move from one community to another (such as amphibians), the two communities would still be highly distinct.

How do collections of species end up coming together to form different communities? One way to answer this question is to consider the factors that control species membership in communities. If you think about the sheer number of species that coexist within any community, it is clear that no one process is responsible for all the species we find there. As we saw in Concepts 9.2 and 18.1 the distributions and abundances of organisms are dependent on three interacting factors: (1) regional species pools and dispersal ability (species supply), (2) environmental conditions, and (3) species interactions. We can think of these three factors as "filters" that act to exclude species from (or include them in) particular communities (**Figure 19.4**). Let's briefly consider each of them in more detail.

Species supply is the "first cut" to community membership

In Concept 18.1, we saw that the regional species pool provides an absolute upper limit on the numbers and types of species that can be present within communities (see Figure 18.6). Not surprisingly, we saw that regions of high species richness tend to have communities of high species richness (see Figure 18.7). This relationship is due to the role of the regional species pool and, more specifically, the role of dispersal in "supplying" species to communities (see Figure 19.4A). Nowhere is the controlling effect of dispersal on community membership more evident than in the invasion of communities by non-native species.

As ecologists are beginning to learn, humans have greatly expanded the regional species pools of communities by serving as vectors of dispersal. For example, we know that many aquatic species travel to distant parts of the world, which they could not otherwise reach, in the ballast water carried by ships (**Figure 19.5A**). Seawater is pumped into and out of ballast tanks, which serve to balance and stabilize cargo-carrying ships, all over the world. Most of the time, the water—along with the organisms it contains (from bacteria to planktonic larvae to fish)—is taken up and released close to ports, where some of the organisms have the opportunity to colonize nearshore communities. An estimated 10,000 marine species are transported in the ballast water of oceangoing vessels each day. Ballast water introductions have increased substantially over the past few decades because ships are larger and faster, so more species can be taken up and more survive the trip. In 1993, Carlton and Geller listed 46 known examples of ballast water–mediated invasions in the previous 20 years. One species, the zebra mussel (*Dreissena polymorpha*), arrived in North America in the late 1980s in ballast water discharged into the Great Lakes (**Figure 19.5B**). It has had community-changing effects on inland waterways and native species. Another example of a ballast water introduction with negative ecological



In the absence of natural enemies, invasive zebra mussels reach astounding—and destructive—population densities.

Figure 19.5 Humans Are Vectors for Invasive Species (A) Large and fast oceangoing ships can carry marine species to all parts of the world in their ballast water. (B) The zebra mussel, a destructive invader of the inland waterways of the United States, was carried there from Russia in ballast water.

consequences, which we learned about in the Case Study in Chapter 11, was the release of the comb jelly *Mnemiopsis leidyi* into the Black Sea.

Next let's turn our attention to the role of local conditions, particularly the abiotic and biotic characteristics of communities that help determine their structure.

Environmental conditions play a strong role in limiting community membership

A species may be able to get to a community but fail to become a member of the community because it is physiologically unable to tolerate the environmental or abiotic conditions there (see Figure 19.4B). Such physiological constraints can be quite obvious. For example, if we return to our thought experiment of viewing a landscape from the top of a mountain, it is reasonable to assume that the abiotic attributes of the lakes we see make them good places for fishes, plankton, and aquatic insects, but not for terrestrial plants. Similarly, lakes might be good habitat for certain species of fish, plankton, and aquatic insects, but not for all of them. Some of these species depend on fast-flowing water and are thus restricted to streams. These differences among abiotic environments are obvious constraints (or requirements, depending on how you look at it) that largely determine where particular species can and cannot occur within a region. There are many examples throughout this book that demonstrate how physiological constraints can control the distributions and abundances of species [see, for example, the discussions of aspen (Concept 4.1), creosote bush and saguaro cactus (Concept 9.2), and the barnacle *Semibalanus balanoides* (Concept 9.2)].

In our earlier discussion of species introductions by ballast water, it was clear that humans transport many more species than can actually survive in the new locations to which they are carried. For example, the majority of organisms released with ballast water find themselves in coastal waters that do not have the temperature, salinity, or light regimes they need to survive or grow. Luckily, many of these individuals die before they can become a threat to the native community. But ecologists know, based on examples such as the *Caulerpa taxifolia* invasion in the Mediterranean (see the Case Study in Chapter 16), that it is not wise to rely on physiological constraints to exclude potential invaders from a community. It may be that, with multiple introductions, particular individuals with slightly different physiological capabilities can survive and reproduce in an environment once thought uninhabitable by individuals of their species.

Who interacts with whom makes all the difference in community membership

Even if species can disperse to a community and cope with its potentially restrictive abiotic conditions, the final cut to community membership is coexistence with other species (see Figure 19.4C). Clearly, if a species depends on other species for its growth, reproduction, and survival, those other species must be present if it is to gain membership in a community. Equally importantly, some species may be excluded from a community by competition, predation, parasitism, or disease. For example, returning to our thought experiment, we might assume that lakes are suitable habitats for many fish species, but could those species all live together in one lake, given

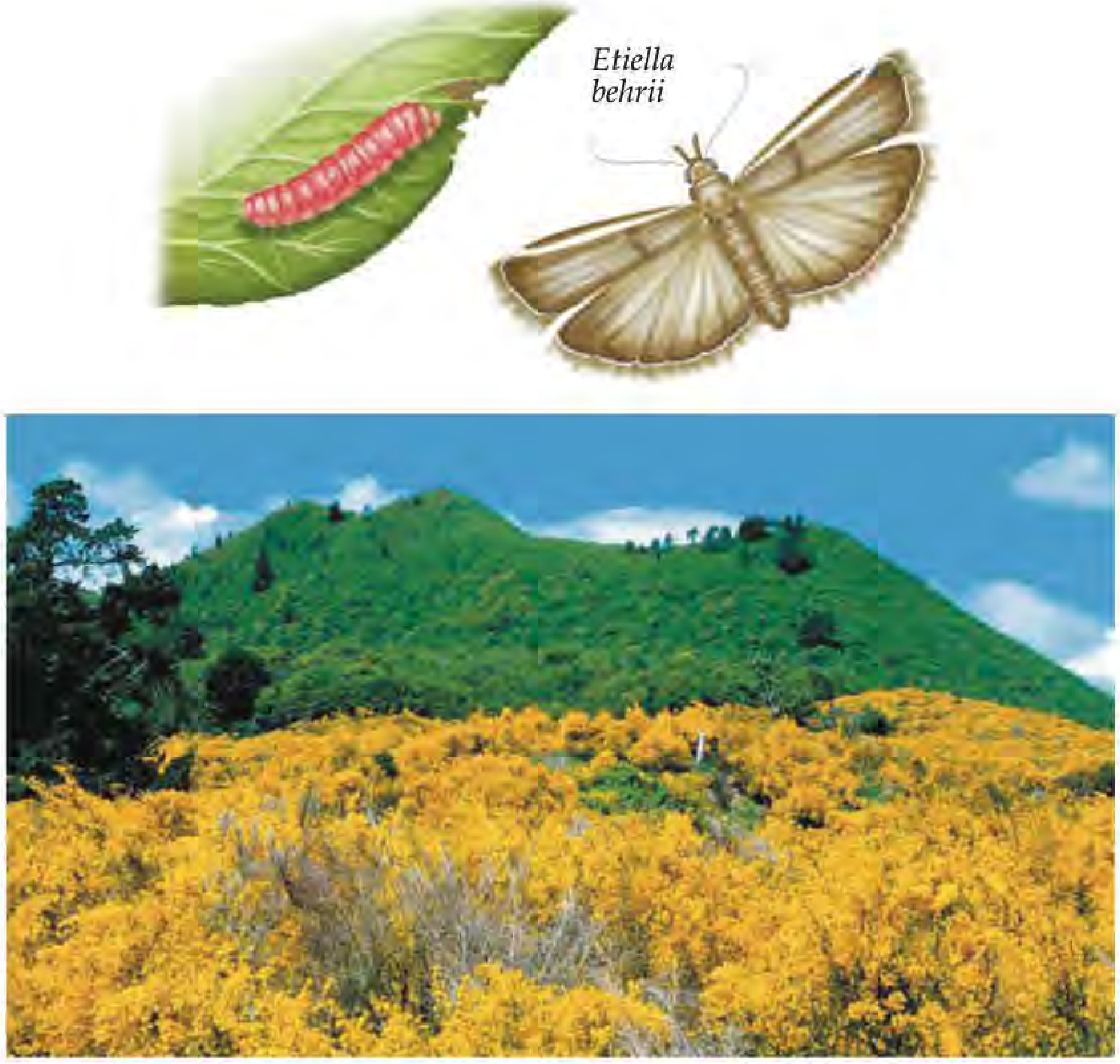


Figure 19.6 Stopping Gorse Invasion? Herbivory by adults and larvae of the native lucerne seed web moth (*Etiella behrii*) has slowed, but not stopped, an invasion of the non-native gorse shrub *Ulex europaeus* (the plants with yellow flowers) in Australia.

that resources are limiting? A simple view suggests that the best competitors or predators should dominate the lake, thus excluding weaker competitors and resulting in a low-diversity community. But we know that most communities are full of species that are actively interacting and coexisting. So what allows this coexistence? There are many important mechanisms that allow species to coexist, and we will spend the next two sections considering them. But first, let's ask how species might be excluded from communities by biological interactions—a question that is a bit different, but equally relevant.

The invasive species literature provides some of the best tests of whether species interactions can exclude species from communities. The failure of some non-native species to become incorporated into communities has been attributed to interactions with native species that exclude, or slow the population growth of, the non-native species—a phenomenon that ecologists call **biotic resistance**. Multiple studies in a variety of communities have shown that native herbivores have the ability to reduce the spread of non-native plants in substantial ways. Maron and Vila (2001) found that mortality of non-native plants due to native herbivores can be quite high (about 60%), especially at the seedling stage (up to 90% in some studies). But while native herbivores can kill individual non-native plants, it is still unknown how important native species are in completely excluding non-native species from a community. For example, Faithfull (1997) found that in Australia, adults and larvae of the native lucerne seed web moth (*Etiella behrii*) breed and feed on the seedpods of the invasive gorse shrub *Ulex europaeus*, but the plant still continues to spread (**Figure 19.6**). This lack of knowledge about biotic resistance may be an artifact of ecologists being more likely to study why a particular non-native species does or does not spread once it becomes a provisional member of the community than to study all the cases in which it is unable to gain a foothold because of interactions with native species. It may also be true that most failed introductions of non-native species go completely undetected.

CLIMATE CHANGE CONNECTION

How Are Species Invasions Enhanced by Climate Change?

There is growing evidence that climate change—and, in particular, rising temperatures—may facilitate the invasions of species that would be unable to survive under cooler conditions. As you might guess, climate change can play a role in mediating the ability of species to pass through the three filters described in Figure 19.4, thus potentially exacerbating the arrival, spread, impact, and management of invasive species.

Hellmann et al. (2008) outlines five potential consequences of climate change for invasive species (**Figure 19.7A**). The first consequence arises when climate change alters the pathways (transport and introduction) of non-native species (see Figure 19.7A, consequence 1). Such alterations could occur if climate change better links areas that are geographically separate prior to climate change. For example, Sylvia Behrens Yamada and colleagues (2005) have shown that non-native European green crabs (*Carcinus maenas*) (**Figure 19.7B**), originally introduced to San Francisco Bay from the east coast of North America, were able to colonize northern Pacific estuaries during warm El Niño years. At these times, crab larvae were transported in stronger, warmer northward-flowing coastal currents to new estuarine locations in Oregon and Washington, where they were able to survive as adults. Thus, changes in coastal currents caused by global warming could create new pathways of dispersal for other non-native species.

A second consequence of climate change is the alteration of environmental constraints on non-native species that allows some species to overcome physiological or biotic constraints on their persistence outside of their native range (see Figure 19.7A, consequence 2). For example, in the green crab invasion mentioned above, it was predicted that green crabs would become locally extinct in northern estuaries once El Niño subsided, because of their intolerance of cold winter ocean temperatures (they are unable to molt and reproduce at temperatures below 10°C). In fact, the researchers found that green crabs persist as invaders where they experience occasional warm winters,

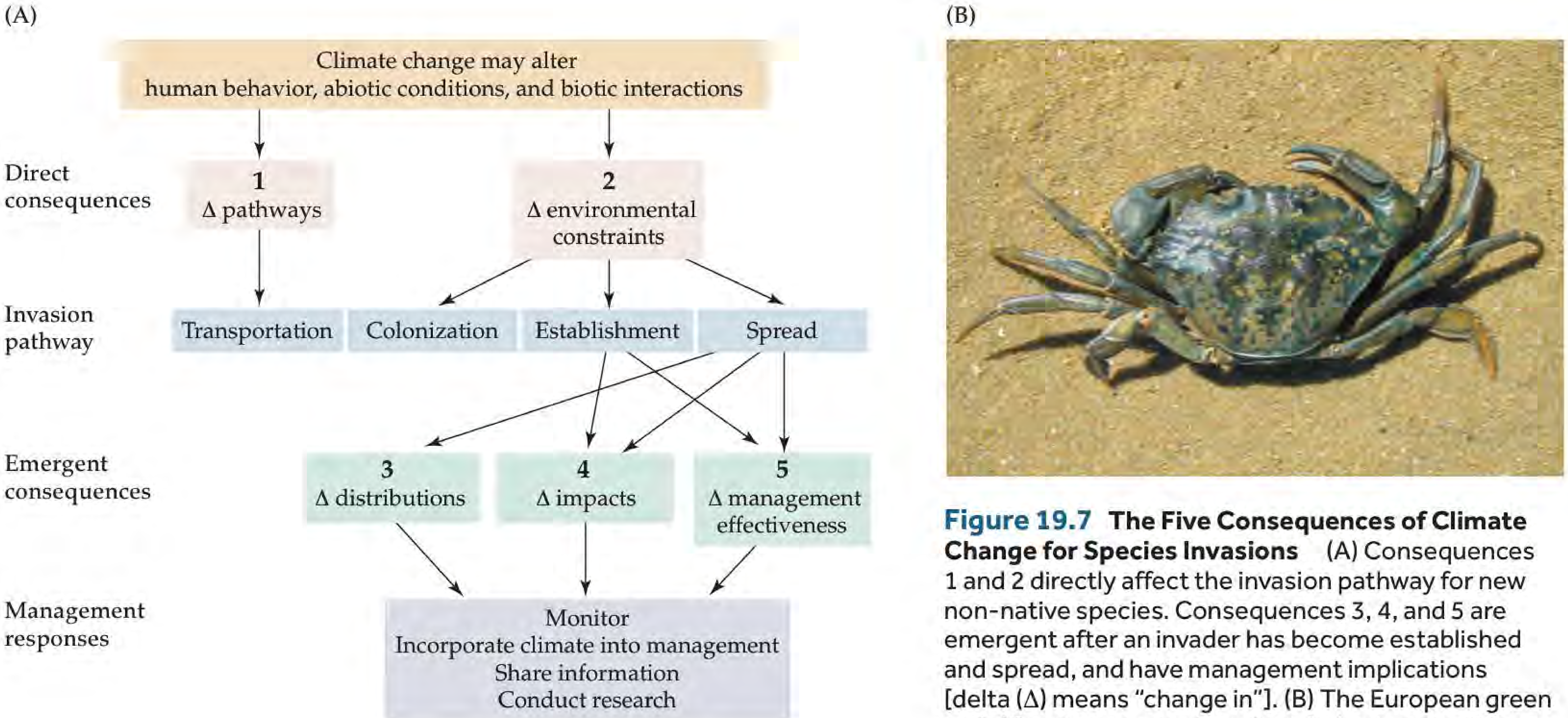


Figure 19.7 The Five Consequences of Climate Change for Species Invasions (A) Consequences 1 and 2 directly affect the invasion pathway for new non-native species. Consequences 3, 4, and 5 are emergent after an invader has become established and spread, and have management implications [delta (Δ) means "change in"]. (B) The European green crab (*Carcinus maenas*) has invaded estuaries along the U.S. Pacific coast. (A after Hellmann et al. 2008).

during which they have much greater survival, growth, and reproduction.

A third consequence of climate change is the alteration of the distributions of existing invasive species (see Figure 19.7A, consequence 3). For non-native species that have gained a foothold outside of their biogeographic range, climate change could expand (or contract) their new range in dramatic ways. For example, one could imagine that with warming of estuarine water temperatures above 10°C, green crabs would not merely exist in small populations but, instead, increase their numbers through enhanced survival and reproduction.

The fourth consequence of climate change occurs when the impacts of non-native species are altered (see Figure 19.7A, consequence 4). The impacts of the green crab under the climatic conditions of today are minimal. Hunt and Behrens Yamada (2003) observed very little overlap in the distribution and resource use of the green crab and the larger native red rock crab (*Cancer productus*). The red rock crab is dominant in the colder and more saline portions of estuaries, while the invasive green crab occurs in warmer and less saline areas. With climate change, increased temperatures or more rainfall could lead to warmer and less saline estuarine conditions, thus favoring green crabs over red rock crabs and having a greater impact on the estuarine community as a result.

The fifth and final consequence of climate change is its effects on the management of non-native species (see Figure 19.7A, consequence 5). Current management, whether it involves removal of invasive species or restoration of habitats impacted by these species, will need to adapt to changing climate in ways that maintain its control and efficacy. In the green crab example, management has been minimal beyond destroying individuals found in traps. If green crabs expand in population size and range in response to climate change, however, active management may be required to keep this invasive species from becoming a pest to shellfishery and aquaculture operations. As you can see, climate change can act on invasive species in a multitude of ways that may be hard to predict in advance.

Studying invasions gives us valuable insights into how species are included or excluded from communities, but how species coexist can be complicated. In the next two sections, we will consider theories of species coexistence and ultimately species diversity. We will start by revisiting the concept of **resource partitioning** (also known as **niche partitioning**), which relies on ecological and evolutionary "compromises" that result in divergence in resource use as a mechanism for coexistence (see Concept 14.3). We will then explore alternative theories and studies that consider the importance of disturbance, stress, predation, and even positive interactions to the coexistence of species and, ultimately, the species diversity of communities.

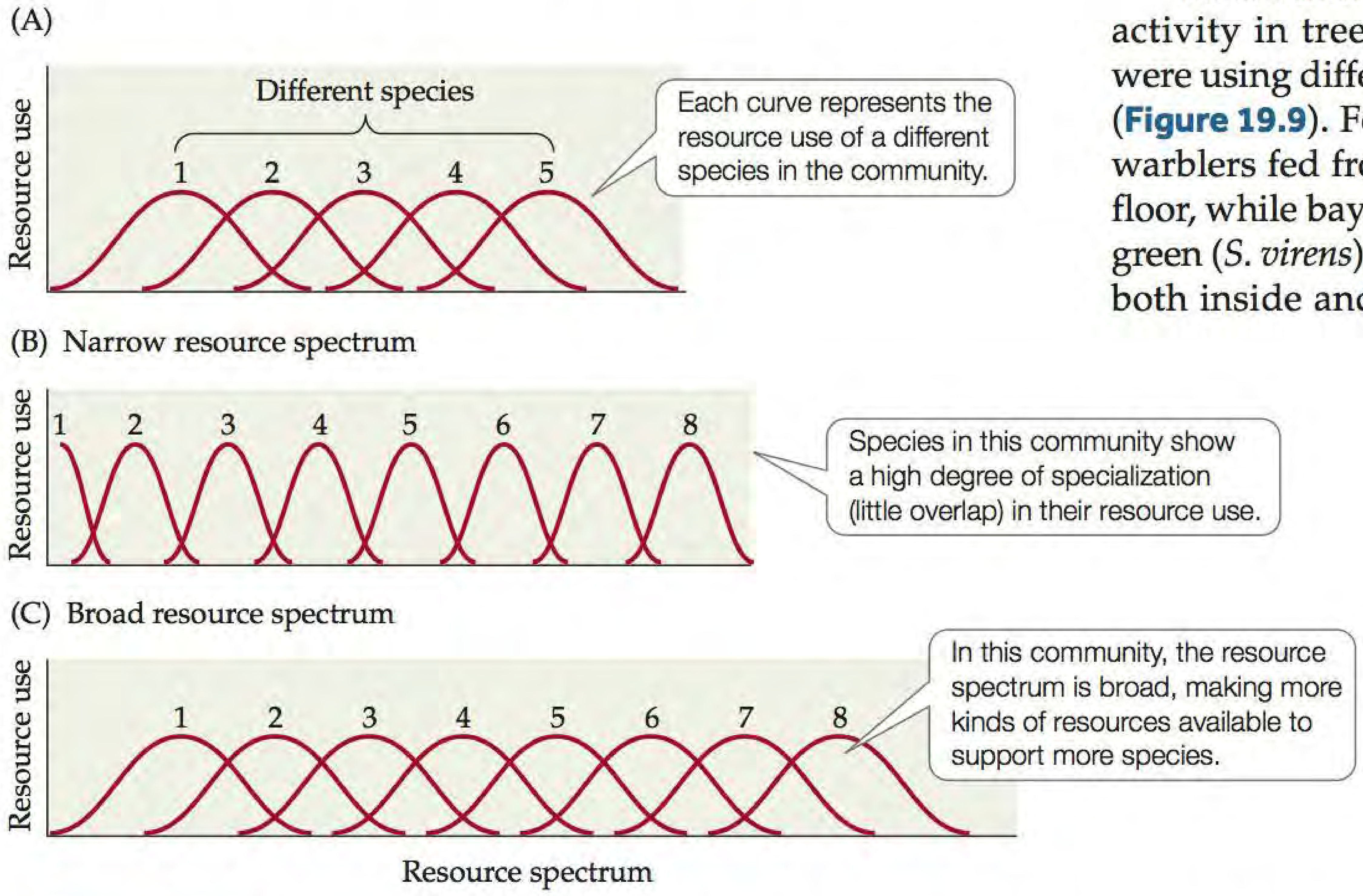
CONCEPT 19.2

Resource partitioning is theorized to reduce competition and increase species diversity.

Resource Partitioning

A simple model of resource partitioning envisions each type of resource available in a community as varying along a "resource spectrum." This spectrum could represent, for example, different nutrients, prey sizes, or habitat types; note that such a spectrum represents the *variability* of an available resource, not the amount. We can assume that the resource use of each species falls somewhere along this spectrum and overlaps with the resource uses of other species to varying degrees (**Figure 19.8A**). The assumption is that the more overlap, the more competition between species, with the extreme being complete overlap and competitive exclusion. The less overlap, the more partitioning of resources has occurred, and the less strongly the species will compete with one another.

Using this guiding theory, we can consider some of the possible ways in which resource partitioning might result in higher species richness in some communities than in others. First, species richness could be high in some communities because species show a high degree of partitioning along the resource spectrum (**Figure 19.8B**). More species could be "packed" into a community if the overlap in resource use among the species is low, leading to less competition and ultimately higher species richness. This lower overlap could be due to the evolution of specialization or character displacement (see Figure 14.12, which may reduce competition over time. Second, species richness could be high in some communities because the resource spectrum is broad (**Figure 19.8C**). Presumably, a broader resource spectrum would make a greater diversity of resources available to be used by a wider variety of species, resulting in higher species richness.



Each curve represents the resource use of a different species in the community.

Species in this community show a high degree of specialization (little overlap) in their resource use.

In this community, the resource spectrum is broad, making more kinds of resources available to support more species.

Figure 19.8 Resource Partitioning Species coexistence within communities may depend on how the species divide resources. (A) The principle of resource partitioning along a resource spectrum. (B,C) Two characteristics of communities that can result in higher species richness.

? Which panel shows the most resource partitioning? Which shows the least?

At this point, let's turn our attention away from models and take a look at some real communities to see how resource partitioning might work in practice.

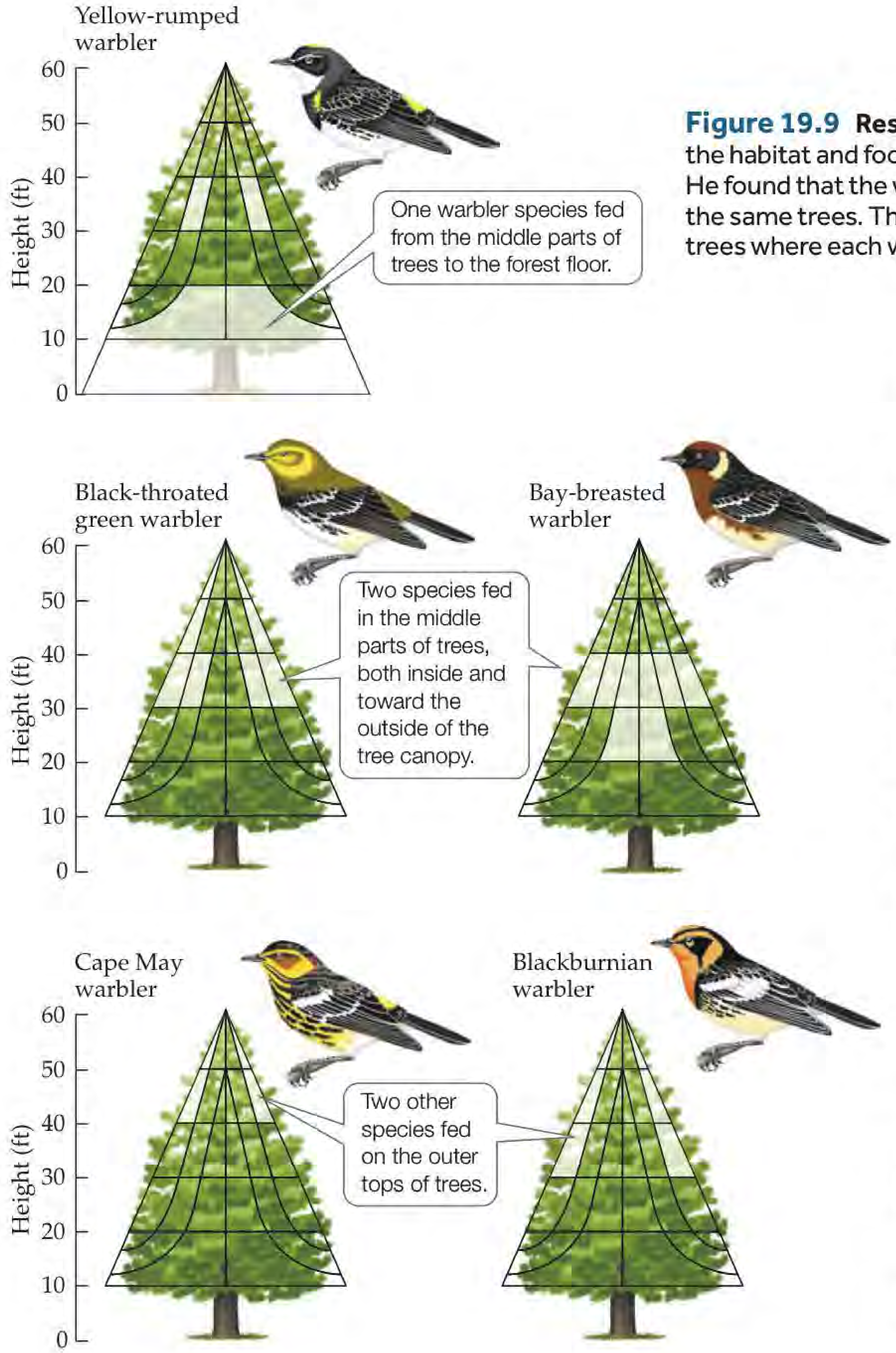
Early studies suggested that resource partitioning was the main mechanism of coexistence

As we learned earlier from the two-species studies of Gause (1934a) on *Paramecium* (see Concept 14.3) and Connell (1961a,b) on barnacles (see Concept 14.2), species that compete with each other may coexist by using slightly different resources. Robert MacArthur, whose work on the equilibrium theory of island biogeography we described in Concept 18.3, played a pioneering role in understanding how this principle might be applied to whole communities, where multiple species interactions are occurring all at once.

MacArthur studied warblers, small and brightly colored birds that co-occur in the forests of northern North America. The idyllic New England forests that MacArthur studied are home to an array of warbler species *Setaphaga* spp. (renamed from *Dendroica* spp.) that migrate from the tropics each spring to breed and feed on insects. Through a series of detailed natural history observations in the summers of 1956 and 1957 in Maine and Vermont, MacArthur (1958) recorded the feeding habits, nesting locations, and breeding territories of five species of warblers to find out how they might coexist in the face of very similar resource needs.

MacArthur began mapping the locations of warbler activity in tree canopies and found that the warblers were using different parts of the habitat in different ways (**Figure 19.9**). For example, yellow-rumped (*S. coronata*) warblers fed from the middle parts of trees to the forest floor, while bay-breasted (*S. castanea*) and black-throated green (*S. virens*) warblers fed more in the middle of a tree, both inside and toward the outside of the tree canopy. Blackburnian (*S. fusca*) and Cape May (*S. tigrina*) warblers both fed on the outside tops of trees, often catching their prey in midflight. MacArthur found that the nesting heights of the five warbler species also varied, as did their use of breeding territories. Taken together, these observations supported his hypothesis that the warblers, although using the same habitat and food resources, were able to coexist by partitioning those resources in slightly different ways. MacArthur's work, which was part of his Ph.D. thesis, earned him the prestigious Mercer Award, bestowed each year for the best paper in ecology.

MacArthur, along with his brother John MacArthur (MacArthur and



One warbler species fed from the middle parts of trees to the forest floor.

Two species fed in the middle parts of trees, both inside and toward the outside of the tree canopy.

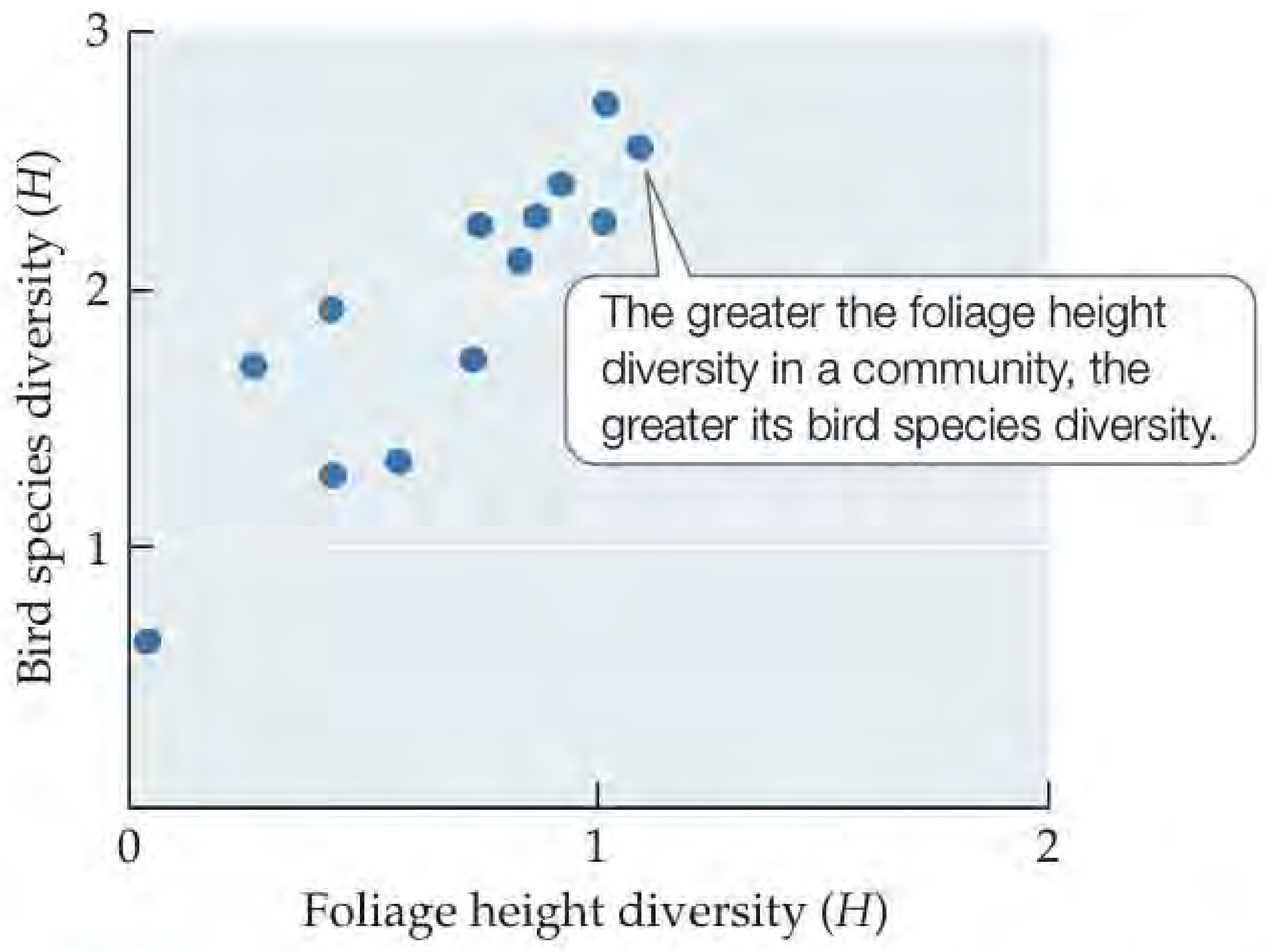
Two other species fed on the outer tops of trees.

Figure 19.9 Resource Partitioning by Warblers Robert MacArthur studied the habitat and food choices of five species of warblers in New England forests. He found that the warblers partition resources by feeding in different parts of the same trees. The shaded areas in each tree diagram represent the parts of trees where each warbler species fed most often. (After MacArthur 1958.)

MacArthur 1961), extended these ideas about resource partitioning in a study of the relationship between bird species diversity (calculated using the Shannon index; Concept 16.2) and foliage height diversity (a measure of the number of vegetation layers in a community that serves as an indication of habitat complexity, also calculated using the Shannon index). They found a positive relationship between the two in 13 tropical and temperate bird habitats from Panama to Maine (**Figure 19.10**). Interestingly, bird species diversity was not related to plant diversity per se, beyond the effects of foliage height diversity, suggesting that tree species identity was less important than the structural complexity of the habitat.

Another important resource partitioning study comes from phytoplankton communities. In Concept 14.1, we learned about David Tilman and colleagues' (1981) study of two species of diatoms that competed for silica (which diatoms use to build their cell walls). When the two species were grown together in a laboratory environment with limited supplies of silica, one outcompeted and excluded the other (see Figure 14.6). How, then, do diatom species coexist in nature? Tilman (1977) proposed what has become known as the **resource ratio hypothesis**, which posits that species coexist by using resources in different ratios or proportions. He predicted that diatoms would be able to coexist, despite using the same set of limiting nutrients, by acquiring those nutrients in different ratios. By growing two diatom species, *Cyclotella* and *Asterionella*, in laboratory environments that differed in their ratios of silica (SiO_2) to phosphorus (PO_4), Tilman found that *Cyclotella* was able to dominate only when the ratio of silica to phosphorus was low (approximately 1:1). When the ratio of silica to phosphorus was high (more like 1,000:1), *Asterionella* outcompeted *Cyclotella*. Only when the ratios of silica and phosphorus were limiting to both species (in the range of 100:1 to 10:1) could they coexist. Even though both species needed the same set of nutrients, it was the way in which they partitioned those resources that allowed them to coexist.

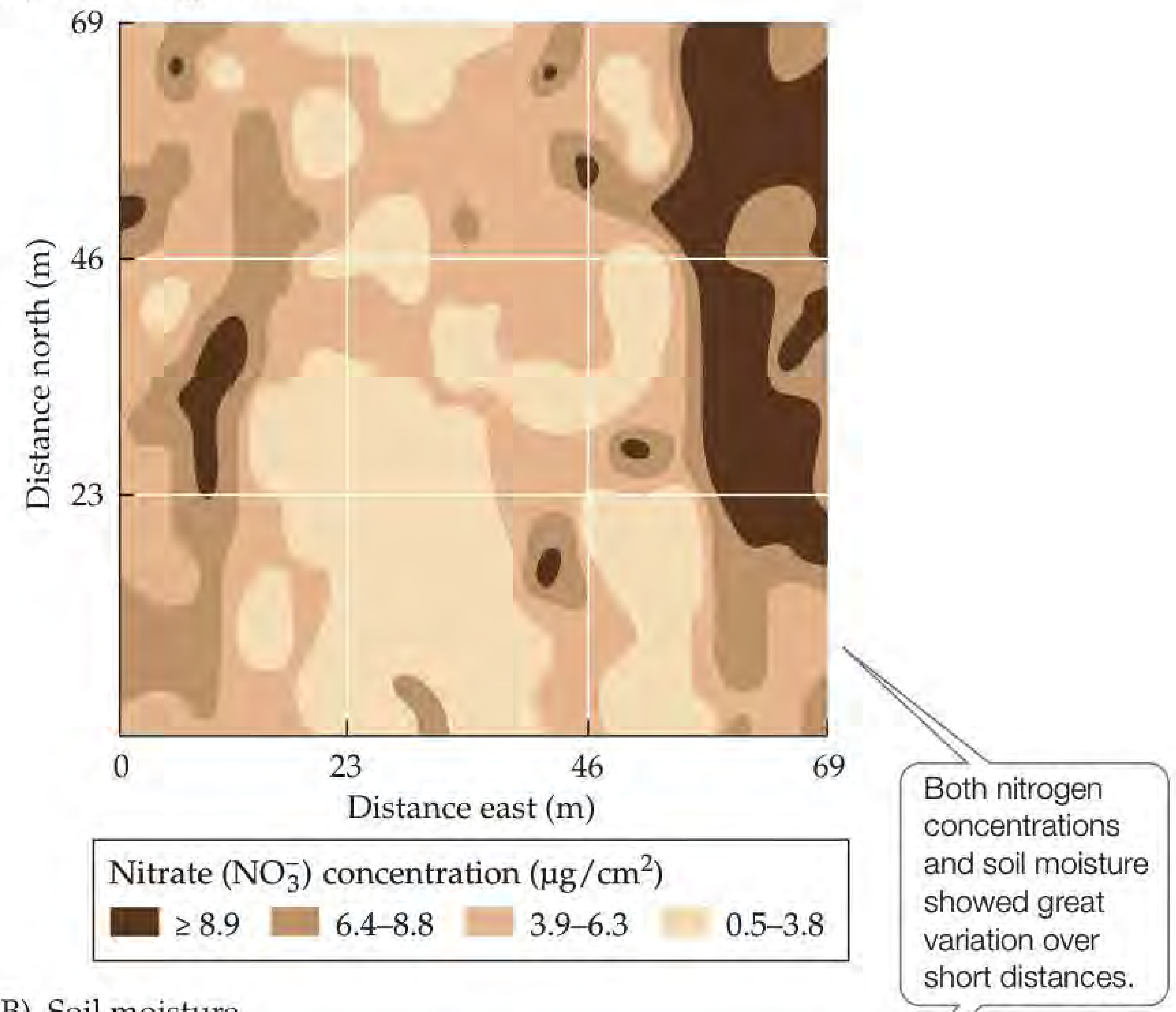
Outside of a laboratory setting, this type of partitioning would work best if resources naturally varied within the environment. What is the support for this possibility in the field? In a detailed survey, Robertson and colleagues (1988) mapped resource distribution in an abandoned agricultural field in



The greater the foliage height diversity in a community, the greater its bird species diversity.

Figure 19.10 Bird Species Diversity Is Higher in More Complex Habitats MacArthur and MacArthur plotted bird species diversity against foliage height diversity (a measure of habitat complexity) for 13 different communities. Both kinds of diversity were calculated for each community, using the Shannon index (*H*). (After MacArthur and MacArthur 1961.)

(A) Soil nitrogen concentrations



Both nitrogen concentrations and soil moisture showed great variation over short distances.

(B) Soil moisture

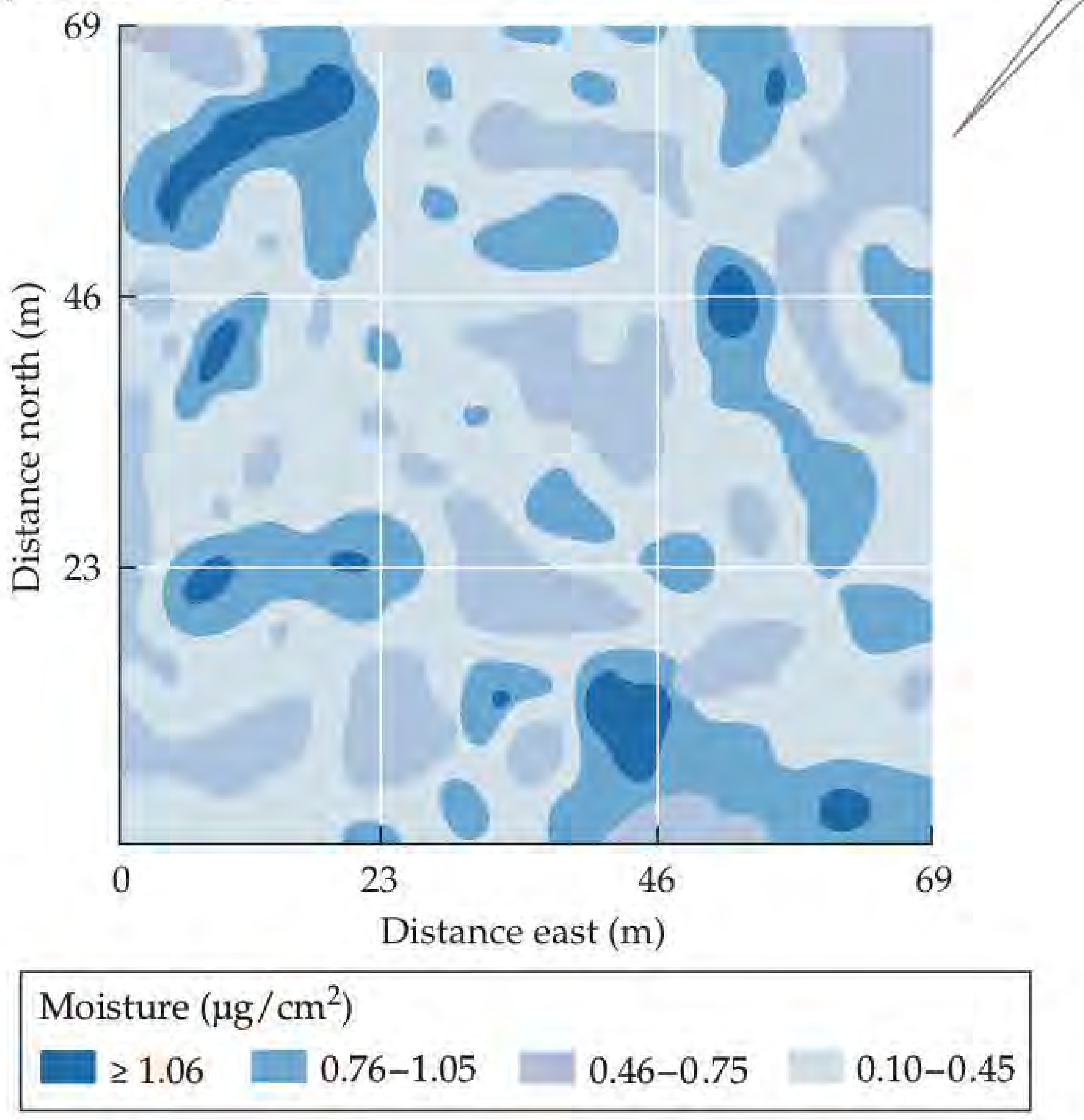


Figure 19.11 Resource Distribution Maps Mapping of (A) nitrogen concentrations and (B) soil moisture in an abandoned agricultural field revealed considerable small-scale variation. (From Robertson et al. 1988.)

Michigan that had been colonized by grassland plants. They found considerable variation in soil nitrogen and moisture at spatial scales of a meter or less (**Figure 19.11**). These patches of nitrogen and water resources did not necessarily correspond to topographic differences, and they were not correlated with each other. If we were to overlay the nitrogen map on the water map, we would find even smaller patches corresponding to different proportions of these two resources. Some of the best evidence of resource partitioning in plants comes from experiments that manipulate species richness and measure productivity, as we will explore in more detail in Concept 19.4.

The theory of resource partitioning relies on the assumption that species have evolved mechanisms for using resources in different, but complementary, ways, thus increasing their ability to coexist. As we learned in our discussion of species interactions in Unit 4, there are numerous other processes that can alter the outcome of species interactions and allow coexistence. In the next section, we will consider how those processes control species diversity at the local scale.

CONCEPT 19.3

Processes such as disturbance, stress, predation, and positive interactions can mediate resource availability, thus promoting species diversity.

Resource Mediation and Species Diversity

We have seen in previous chapters that disturbance, stress, and predation can modify species interactions and allow for species coexistence. We saw that when two species are competing with each other for the same resource, as in the case of the sea palms and mussels competing for space in the rocky intertidal zone (see Concept 14.4), coexistence can be achieved if the population growth of the dominant species is disrupted. In that example, mussels are the dominant competitors, and sea palms can coexist with them only where the mussels are disturbed frequently enough by wave action to allow the sea palms to acquire space. In this and many other examples in this book, as long as disturbance, stress, or predation keeps the dominant competitor from reaching its own carrying capacity, competitive exclusion cannot occur, and coexistence will be maintained (**Figure 19.12**).

We have also explored the effect of positive interactions between species in ameliorating extreme conditions and allowing coexistence. For example, we saw in the cases of salt marsh plants (Figure 17.14) and plants at high elevations (Figure 15.9) that species that might normally be unable to tolerate stressful conditions can maintain viable populations under those conditions because of the facilitative effects of other species.

Let's expand these ideas about modification of species interactions to whole communities and ask how processes that mediate resources influence species diversity.

Processes that mediate resources can allow species to coexist

There is an old adage among ecologists that goes something like this: "If you think it's a new idea, check Darwin.

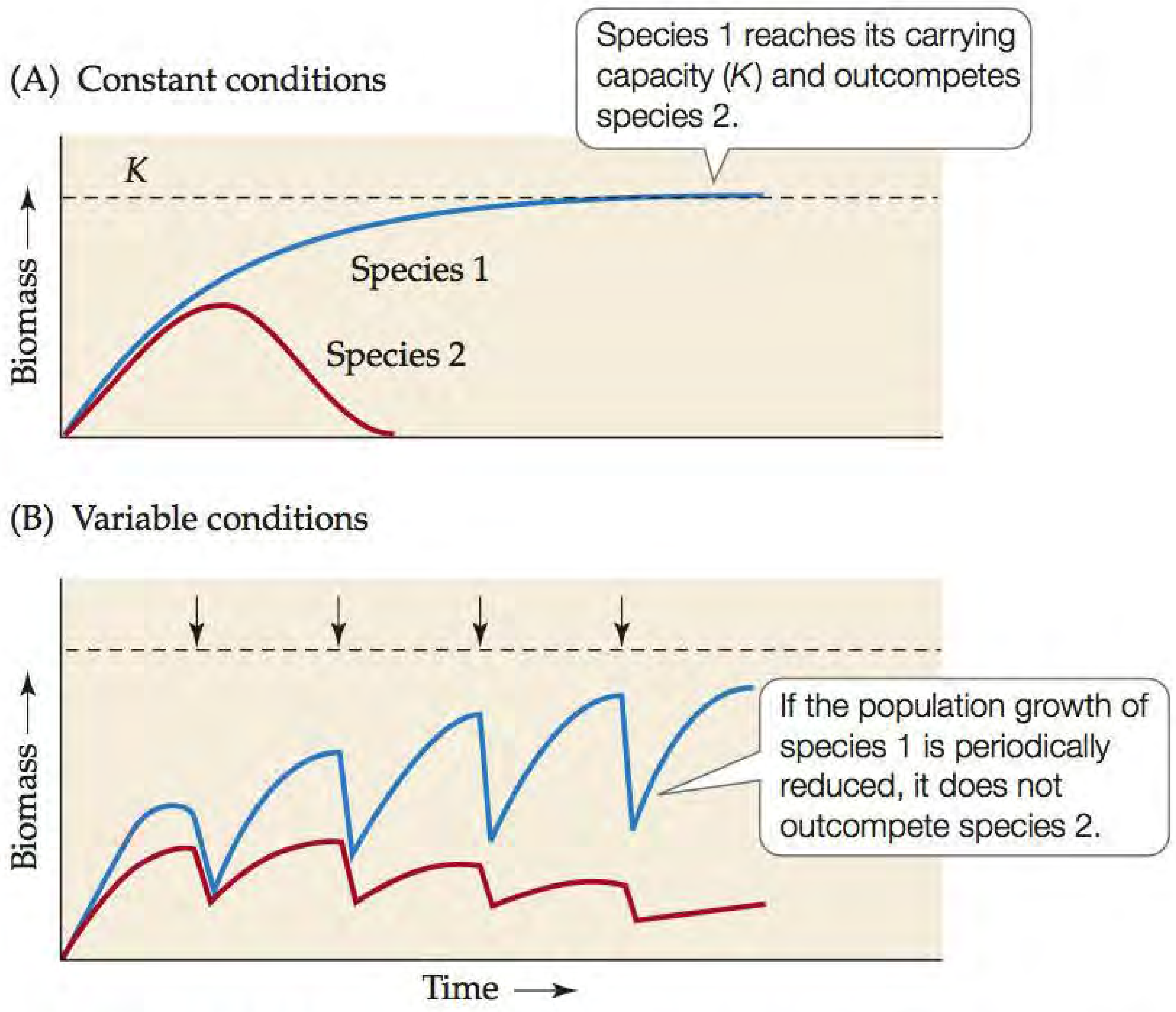


Figure 19.12 The Outcome of Competition under Constant and Variable Conditions (A) Under constant conditions, species 1 (the dominant competitor) outcompetes species 2 when it reaches its own carrying capacity (*K*). (B) If disruptive processes such as disturbance, stress, or predation (represented by the arrows) reduce the population growth of species 1, it will not reach its carrying capacity and will not outcompete species 2, thus allowing coexistence. (After Huston 1979.)

He probably proposed it first." In fact, when it comes to theories that explain coexistence, Darwin was the first to formally recognize disturbance as a mechanism for the maintenance of species diversity. In *The Origin of Species* (1859, p. 55), he noted the following results after an impromptu experiment in which he left a meadow on his property undisturbed by mowing: "Out of twenty species growing on a little plot of mown turf (three feet by four) nine species perished, from the other species being allowed to grow freely." Without mowing, the dominant competitors in the meadow community competitively excluded weedy plants and cut species richness nearly in half. Darwin used this example, along with a multitude of others, to support the argument that nature applies limits to the tendency of species to increase in abundance and outcompete other species. His hypothesis was that species struggle for existence, a necessary first piece to his theory of natural selection.

In 1961, G. E. Hutchinson revived this idea in a paper titled "The Paradox of the Plankton." Hutchinson, an influential community ecologist from Yale University (and major professor to Robert MacArthur), provided one of the first mechanistic descriptions of how coexistence could be maintained under fluctuating environmental conditions. He focused on phytoplankton communities in temperate freshwater lakes (**Figure 19.13**). The simple idea behind Hutchinson's model was the seeming paradox of the presence of 30–40 species of phytoplankton given the relatively limited resources at their disposal. He reasoned that all of the phytoplankton compete for the same array of resources, including carbon dioxide, nitrogen, phosphorus, sulfur, and trace elements, which are likely to be evenly distributed in lakes. How could so many species manage to coexist with so few resources and in such a structurally simple environment as a lake? Hutchinson hypothesized that the conditions in the lake changed seasonally and over longer periods, and that those changes kept any one species from outcompeting the others. As long as conditions in the lake changed before the competitively superior species eliminated others, coexistence would be possible.

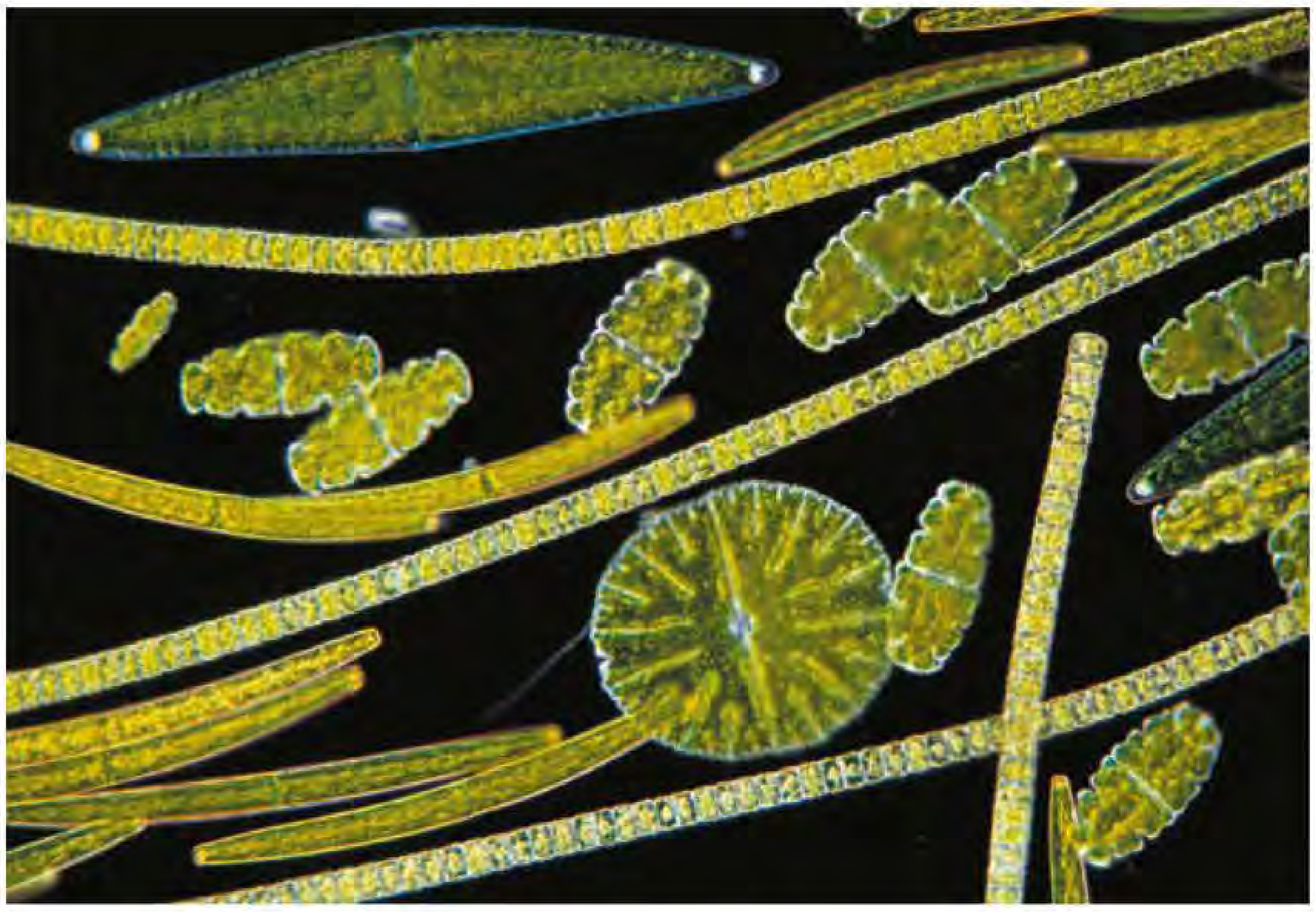


Figure 19.13 Paradox of the Plankton Phytoplankton from a freshwater lake. How can so many species coexist using the same set of basic resources? G. E. Hutchinson suggested that the answer is the influence of environmental variation over time.

Hutchinson's model has two components that interact to control coexistence among species. One is the time required for one species to competitively exclude another species (t_c), which depends on the population growth rates of the two competing species. The second is the time it takes for environmental variation to act on the population growth of the two competing species (t_e). Hutchinson predicted that when competitive exclusion occurs more rapidly than environmental conditions can change ($t_c << t_e$), coexistence cannot be achieved. One could imagine this occurring in communities where there is little environmental change or where the dominant competitor has very rapid growth rates. Conversely, in a fluctuating environment to which the competitors are adapted (where $t_c >> t_e$), environmental variation does not affect the competitive interactions, and competitive exclusion occurs. One could imagine this pattern in environments with frequent, low-intensity environmental fluctuations and long-lived species. Hutchinson argued that it is only when the time it takes for competitive exclusion to occur is roughly equal to the time it takes for environmental variation to interrupt the competitive interaction (when $t_c = t_e$) that competitive exclusion is thwarted and coexistence occurs. Hutchinson argued that this condition is likely to be met often in lake phytoplankton communities; otherwise, very few species, rather than tens of species, would coexist.

Hutchinson proposed the idea that competitive exclusion is rare in nature, but did not test it. It was Robert Paine's work in the rocky intertidal zone of the west coast of North America in the late 1960s that provided some of the most rigorous and convincing evidence that coexistence could be maintained by disruptive processes such as predation or disturbance. Paine (1966) manipulated population densities of *Pisaster*, a predatory sea star that feeds preferentially on the mussel *Mytilus californianus*. In plots from which *Pisaster* was removed, species richness decreased as mussels outcompeted barnacles and other competitively inferior species. In plots where *Pisaster* was present, species richness was enhanced. There are several important aspects to Paine's work, including the keystone species concept and the effects of indirect interactions, but we will consider those aspects in more detail in Concept 21.4 when we discuss food webs. For now, let's concentrate on an idea that arose from the work of Darwin, Hutchinson, and Paine: the intermediate disturbance hypothesis.

The intermediate disturbance hypothesis considers species diversity under variable conditions

The **intermediate disturbance hypothesis** was proposed to explain how gradients in disturbance (although we can easily include stress and predation in this model) affect species diversity in communities (**Figure 19.14**). This hypothesis was first formally proposed by Joseph Connell, Paine's contemporary and an author of the classic work on barnacle competition (see Figure 14.16). Connell (1978) recognized that the level of disturbance (its frequency and intensity; see Figure 17.4) experienced by a particular community could have dramatic effects on its species diversity. He hypothesized that species diversity would be greatest at intermediate levels of disturbance and lowest at high and low levels of disturbance. Why would this be the case? At low levels of disturbance, competition would regulate species diversity because dominant species would be free to exclude competitively inferior species. At high levels of disturbance, on the other hand, species diversity would decline because many individuals would die and some species would become locally extinct as a result. At intermediate levels of disturbance, species diversity would be maximized simply by the balance between disruption of competition and mortality due to disturbance.

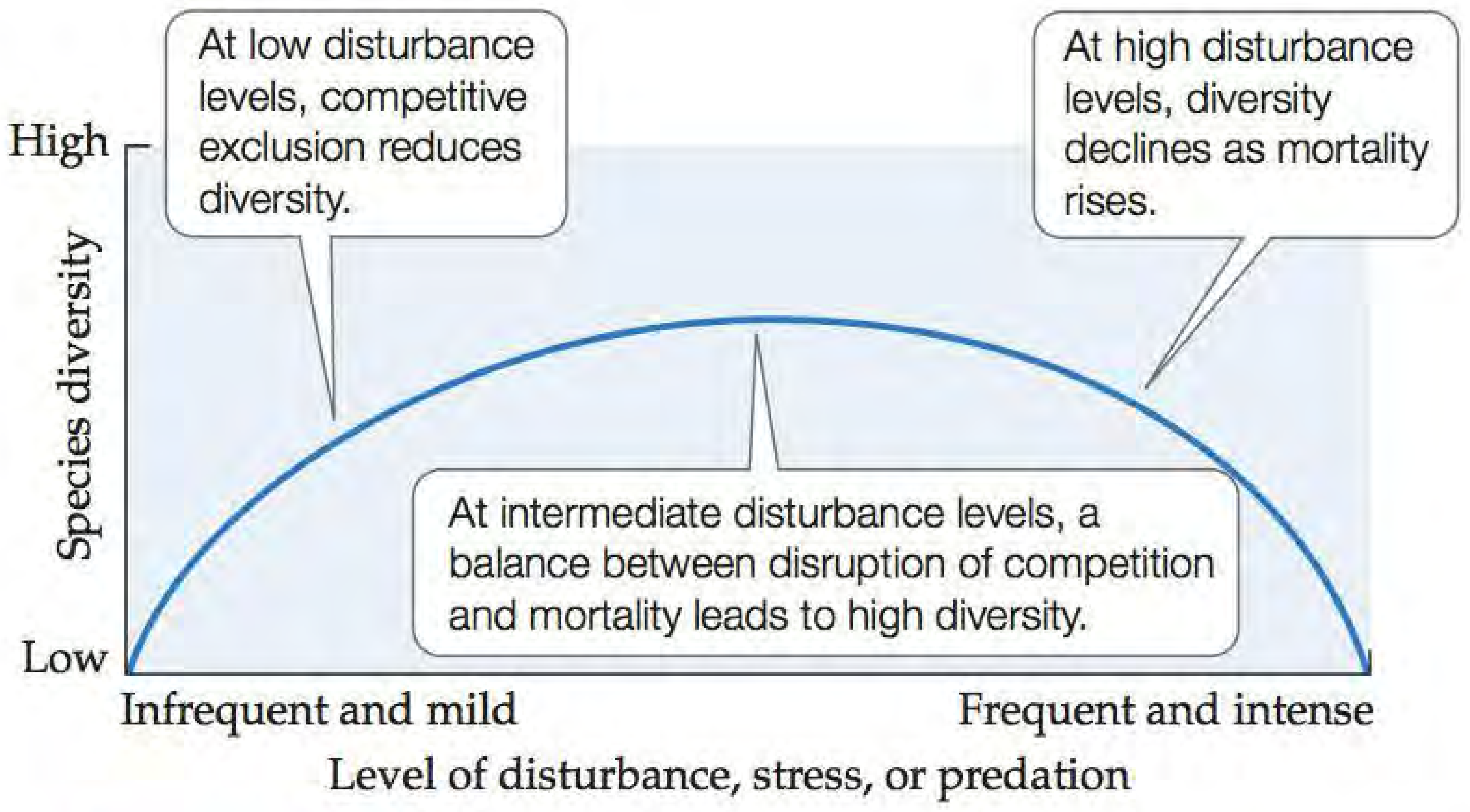
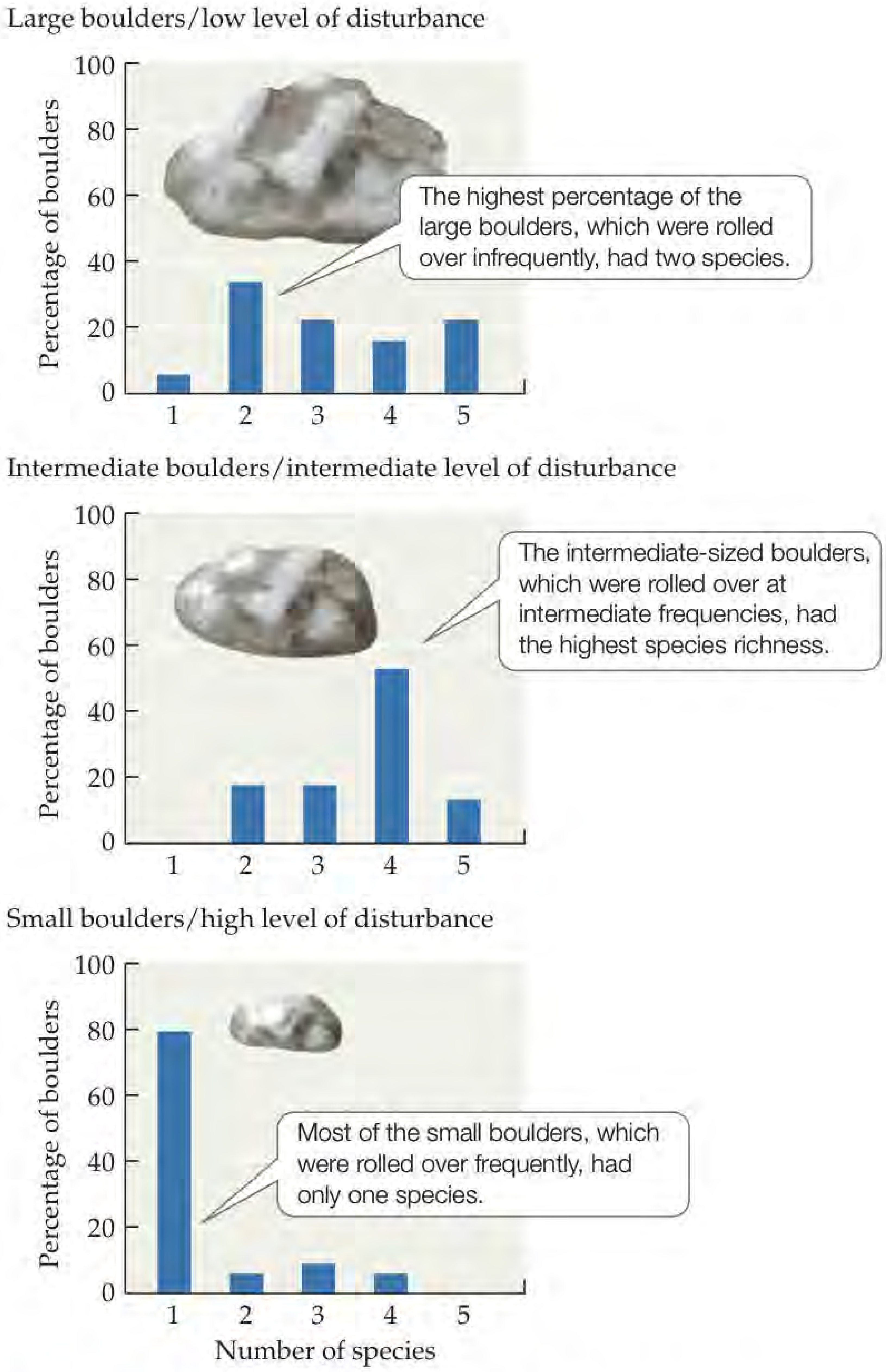


Figure 19.14 The Intermediate Disturbance Hypothesis Species diversity is expected to be greatest at intermediate levels of disturbance, stress, or predation. (After Connell 1978.)

The intermediate disturbance hypothesis is highly amenable to testing. One such test was carried out by Wayne Sousa (1979a), who studied succession in intertidal boulder fields in Southern California (see Figure 17.15). In a different but related study, Sousa measured the rate of disturbance of communities living on the boulders and documented their species richness (**Figure 19.15**). Small boulders were rolled over frequently by waves and thus constituted highly disturbed environments for the marine algae and invertebrate species that lived on them. The opposite was true for large boulders, which rarely experienced wave forces large enough to dislodge them. Intermediate-sized boulders, of course, were rolled over at intermediate frequencies. After 2 years, Sousa found that most of the small boulders had only one species (early successional species: the macroalga *Ulva* or the barnacle *Chthamalus*), while the greatest percentage of the large boulders had two species (late successional species: the macroalga *Gigartina canaliculata* and others). The greatest percentage of the intermediate-sized boulders had four species, but some had up to seven species (a mixture of early, mid-, and late successional species). Sousa's study is just one of many that have demonstrated the highest diversity at intermediate disturbance levels.

There have been several elaborations on the intermediate disturbance hypothesis

The intermediate disturbance hypothesis is a simple model that relies on variation in disturbance levels to explain species diversity in communities. A handful of ecologists have used it as a foundation for adding more complexity and realism to their theories. One of the first to elaborate on the model was Michael Huston (1979), who acknowledged the effect of disturbance on competition but reasoned that a second process, competitive displacement, could be an important mediating factor. **Competitive displacement** occurs when the best competitor uses limiting resources that the weaker competitor requires,



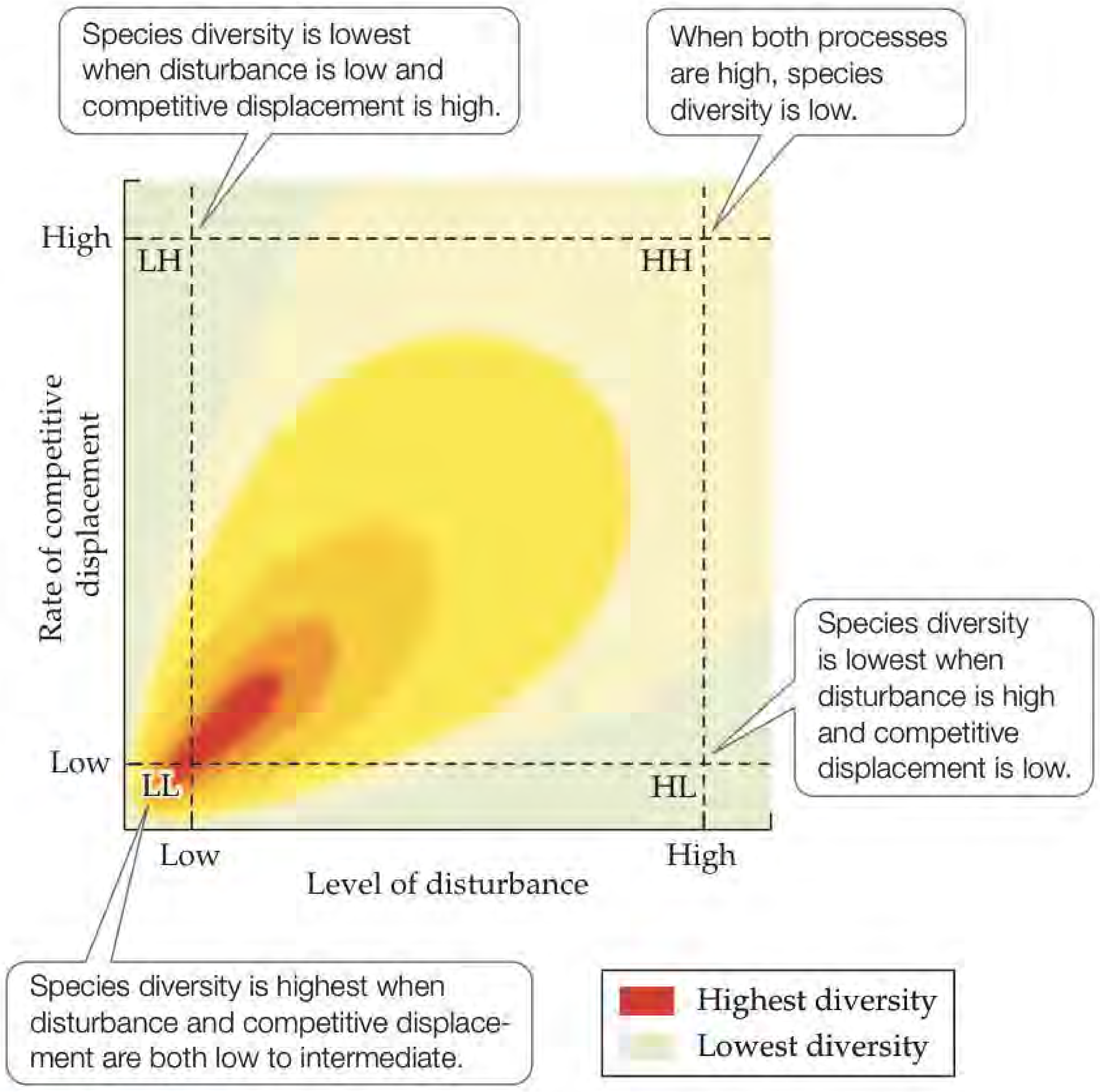
The highest percentage of the large boulders, which were rolled over infrequently, had two species.

The intermediate-sized boulders, which were rolled over at intermediate frequencies, had the highest species richness.

Most of the small boulders, which were rolled over frequently, had only one species.

Figure 19.15 A Test of the Intermediate Disturbance Hypothesis Marine intertidal communities were surveyed on boulders that differed in the level of disturbance they experienced from being rolled over by wave action. After Sousa 1979a.)

? Which size boulder had the lowest species richness, and why?



Species diversity is lowest when disturbance is low and competitive displacement is high.

When both processes are high, species diversity is low.

Species diversity is lowest when disturbance is high and competitive displacement is low.

Species diversity is highest when disturbance and competitive displacement are both low to intermediate.

Figure 19.16 The Dynamic Equilibrium Model The dynamic equilibrium model predicts that species diversity will be highest when the frequency and intensity of disturbance and the rate of competitive displacement are both low to intermediate. (After Huston 1979.)

ultimately causing a decline in the weaker competitor's population growth to the point of extinction. Huston's **dynamic equilibrium model** considers how the frequency or intensity of disturbance and the rate of competitive displacement combine to determine species diversity (**Figure 19.16**). Like Hutchinson's model, Huston's model predicts maximum species diversity when the level of disturbance and the rate of competitive displacement are roughly equivalent (hence the term "equilibrium" in the model name). Species diversity will be highest when the frequency or intensity of disturbance and the rate of competitive displacement are both at low to intermediate levels (see Figure 19.16, point LL). Moreover, species diversity will be lowest either when disturbance is high and competitive displacement is low (see point HL) or when competitive displacement is high and disturbance is low (see point LH). When both processes are high and roughly similar (point HH), we expect species diversity to be relatively low because both high mortality and competitive displacement will be acting to reduce species diversity. Perhaps because of its added complexity, there have been few observational or experimental studies of the dynamic equilibrium model. One example, which comes from an observational study of riparian wetlands in Alaska by Pollock et al. (1998), can be found in **Web Extension 19.1**.

Another elaboration of the intermediate disturbance hypothesis comes from Hacker and Gaines (1997), who incorporated positive interactions into their model. If we think back to Chapters 15, 16, and 17, we learned that species interactions are highly context-dependent, varying in direction and strength depending on certain physical and biological factors. Theory and experiments both suggest that positive interactions should be more common under relatively high levels of disturbance, stress, or predation—all circumstances in which associations among species could increase their growth and survival. Hacker and Gaines reasoned that positive interactions might be

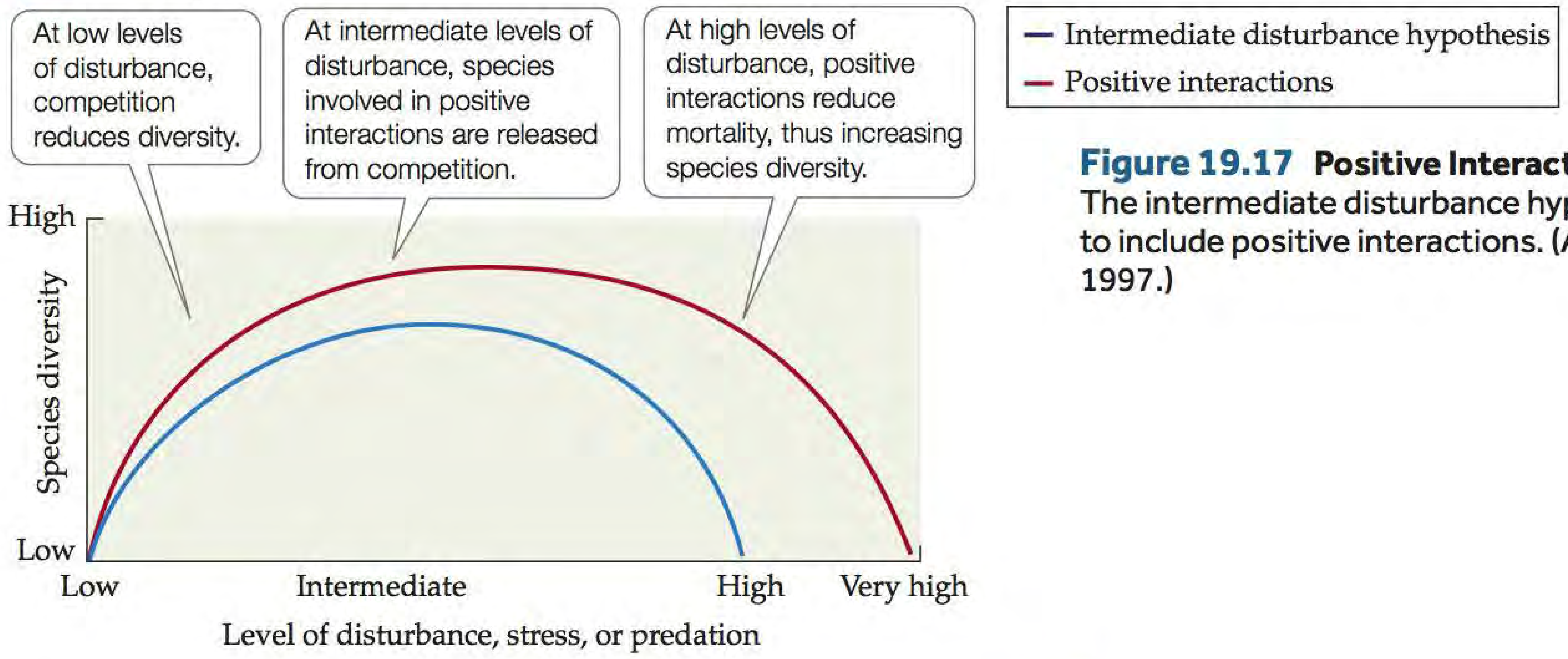


Figure 19.17 Positive Interactions and Species Diversity The intermediate disturbance hypothesis has been elaborated to include positive interactions. (After Hacker and Gaines 1997.)

particularly important in promoting species diversity at intermediate to high levels of disturbance (or stress or predation) for two reasons (**Figure 19.17**). First, at high levels of disturbance, positive interactions should increase the survival of individuals of the interacting species through both the amelioration of harsh conditions and associational defenses. Second, at intermediate levels of disturbance, species will be released from competition and thus are more likely to engage in positive interactions, an effect that should further increase species diversity.

Hacker and Gaines used studies of a New England salt marsh to support their theory. In this community, there is a strong gradient of physical stress due to saltwater inundation. The highest stress occurs closest to the shoreline, where the tides inundate the plants most frequently. A survey of plants, insects, and spiders across the marsh revealed three distinct intertidal zones, each with a different species composition, and showed that the middle intertidal zone had a higher species richness than the high or low intertidal zones (**Figure 19.18A**). The researchers then conducted transplant experiments in which all the plant species were moved to all three zones, with or without the most abundant plant of their own zone: the tall shrub *Iva frutescens* in the high intertidal zone, and the rush *Juncus gerardii* in the middle and low intertidal zones (Bertness and Hacker 1994; Hacker and Bertness 1999). The results revealed that competition with *Iva* in the high intertidal zone led to the competitive exclusion of most plant species transplanted there, whether or

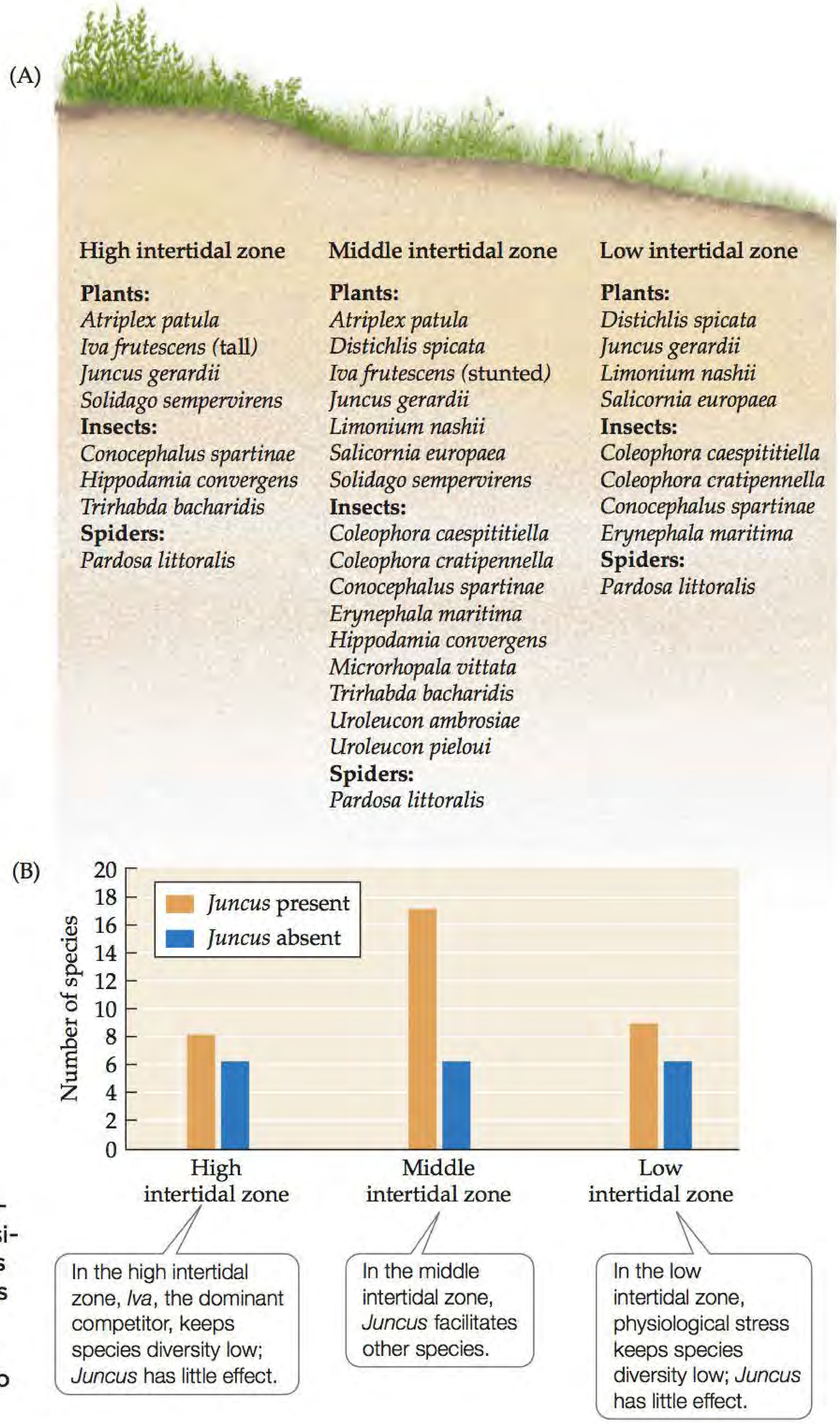


Figure 19.18 Positive Interactions: Key to Diversity in Salt Marsh Communities? (A) Surveys of plant and arthropod species diversity in a New England salt marsh show diversity to be greatest in the middle intertidal zone. (B) Experiments suggest that the high diversity of plants and arthropods in this zone is controlled by the direct and indirect effects of the facilitating rush species *Juncus gerardii* as well as by a decrease in the effect of the dominant competitor, *Iva frutescens*, due to physical stress. (After Hacker and Gaines 1997.)

not *Juncus* was also present. In the low intertidal zone, physiological stress was the main factor in controlling population numbers, as many individuals died whether *Juncus* was present or absent. In the middle intertidal zone, however, *Juncus* facilitated other plant species. Without *Juncus*, mortality was 100% for most species by the end of the summer. The mechanism of facilitation, described in Concept 16.3, was amelioration of both hypoxia and salt stress by *Juncus*. Additionally, as we saw in that discussion, *Juncus* indirectly facilitates an aphid herbivore that depends on *Iva* for survival (see Figures 16.12 and 16.13). It turns out that such indirect interactions affect a number of insect herbivores that feed on a variety of other plants facilitated by *Juncus* in the marsh. Hacker and Gaines (1997) concluded, based on these studies, that positive interactions are critically important in maintaining species diversity, especially at intermediate levels of physical stress (**Figure 19.18B**). They recognized that physical stress in the middle intertidal zone of the New England salt marsh both decreased the competitive effect of *Iva* and increased the facilitative effect of *Juncus* (and its indirect effects on insects), thus providing ideal conditions for enhanced species coexistence and diversity.

The Menge–Sutherland model separates the effects of predation from those of disturbance and stress

The intermediate disturbance hypothesis assumes that disturbance, stress, and predation all have similar effects on interspecific competition, and thus on species diversity (see Figure 19.14). In particular, it considers disturbance and predation to be similar processes—that is, processes that act to kill or damage dominant competitors and thereby create opportunities for subordinate species. This equating of disturbance and predation ignores an important difference between them: disturbance is a physical process, whereas predation is a biological one. Menge and Sutherland (1987) have argued that because predation is a biological interaction, it is independently affected by physical disturbance and stress and thus should be considered separately.

The Menge–Sutherland model predicts that predation should be relatively important in maintaining species richness at low levels of stress (or disturbance), at which predators can most easily feed on, and thus limit the abundance of, competitively dominant species (**Figure 19.19**). As stress increases, the effect of predation decreases as predators become less able to inflict damage on their prey at lower trophic levels. These prey, which are predicted by the model to be more tolerant of physical stress or disturbance, are more likely to compete for resources, especially at intermediate levels of stress or disturbance. But as environmental stress increases to high levels, both predation and competition become less important as more and more species are excluded from the community by their physiological limitations. As with the intermediate disturbance hypothesis, the influences of positive interactions, which are especially important at either extreme of predation or physical stress, have since been incorporated into the Menge–Sutherland model (Bruno et al. 2003), leading to conclusions similar to those of Hacker and Gaines (1997) (see Figure 19.17).

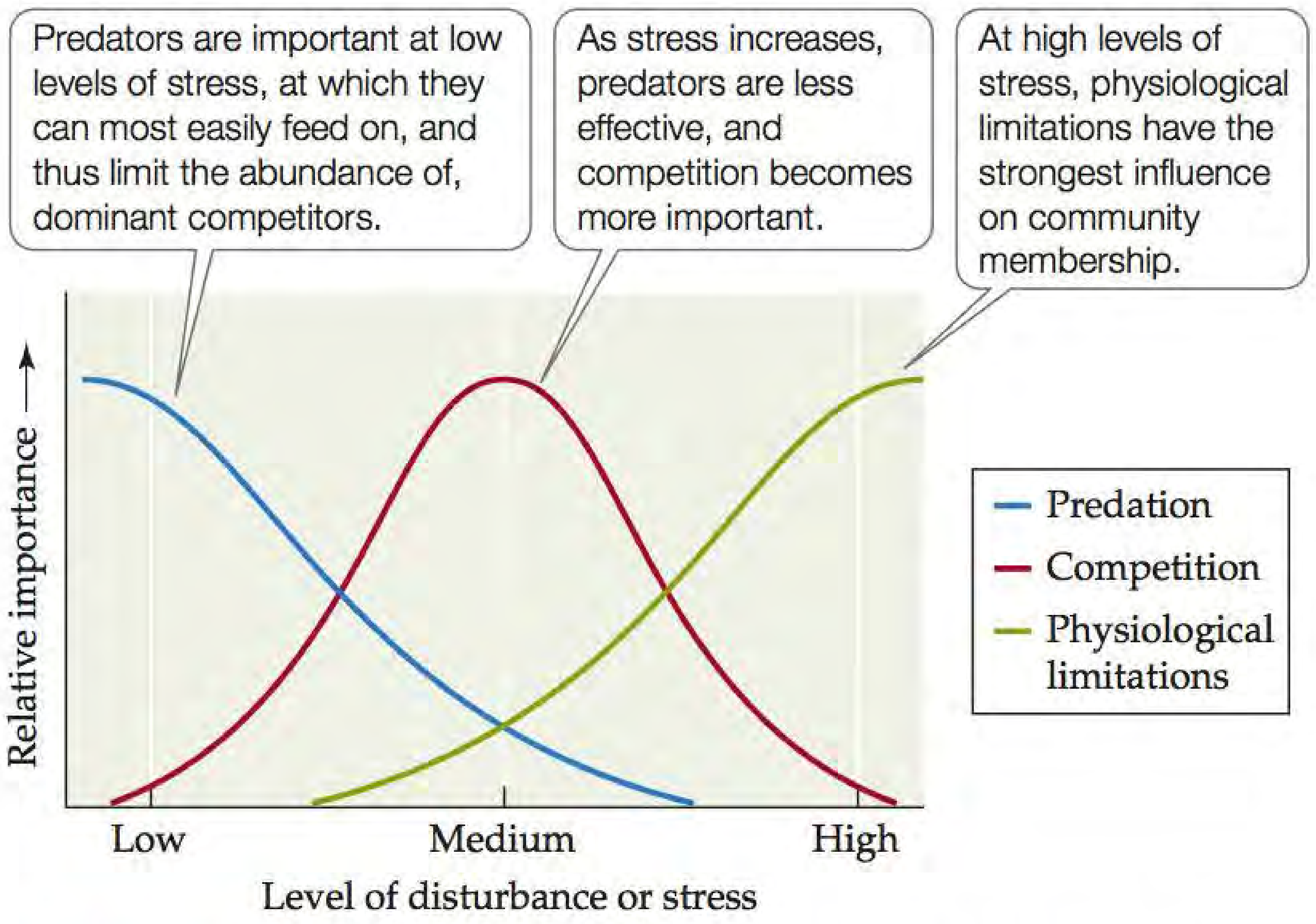


Figure 19.19 The Menge–Sutherland Model Menge and Sutherland's model of influences on community diversity is similar to the intermediate disturbance hypothesis (see Figure 19.14), but it accounts for the effect of predation separately from that of stress or disturbance. (After Menge and Sutherland 1987.)

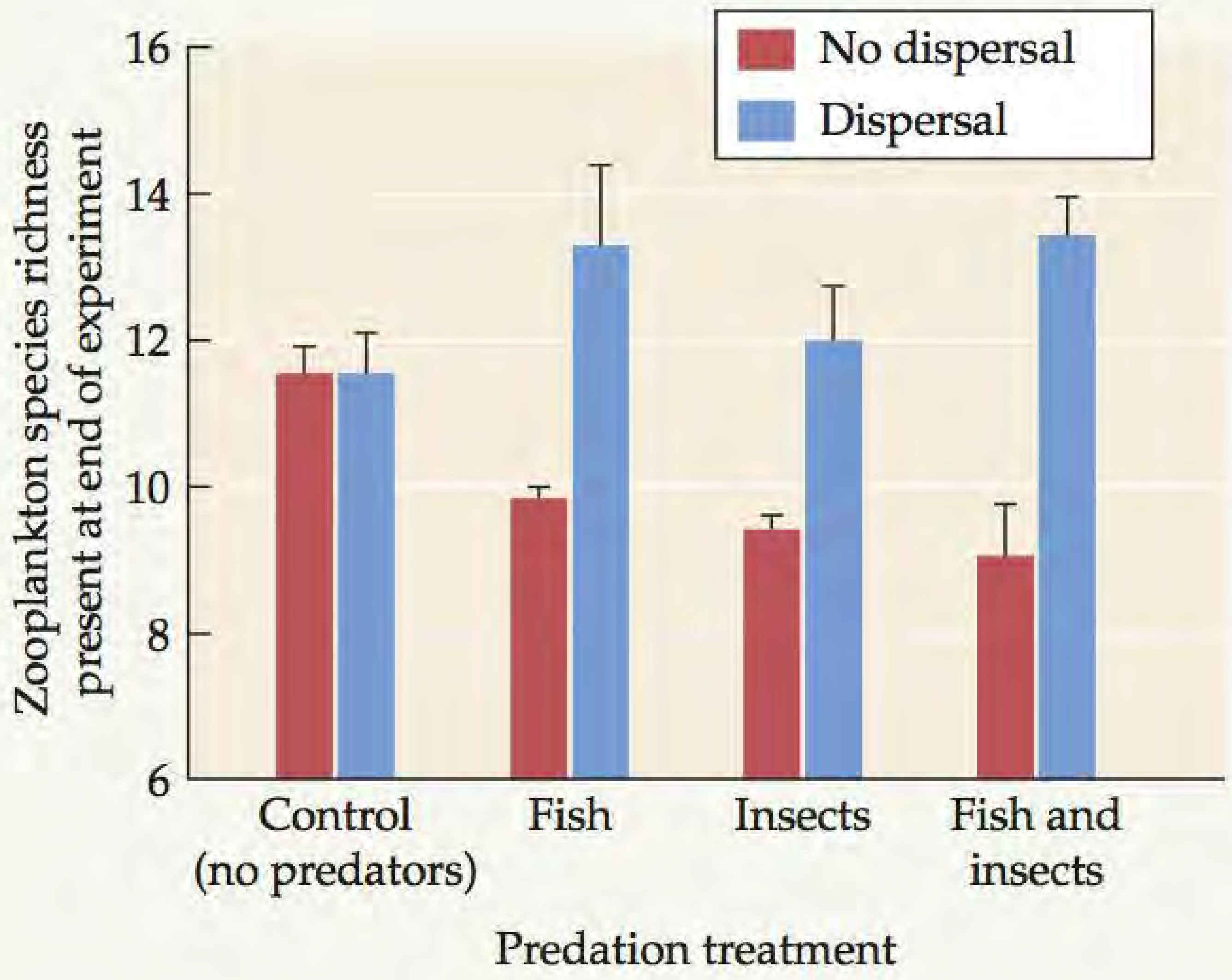
Another important factor that Menge and Sutherland considered in their model was the influence of a particular kind of dispersal known as *recruitment*: defined as the addition of young individuals to a population. They predicted that if recruitment was low, competition might not be particularly important in determining species diversity, because resources would be less likely to be limiting. Instead, the interplay between predation under benign environmental conditions and physical stress under extreme conditions would be the most influential factor regulating community membership. If recruitment increased, however, the role of competition would also increase, ultimately resulting in predictions similar to those in Figure 19.19. Thus, Menge and Sutherland suggest that dispersal (in the form of recruitment) can be another important influence on species diversity and species composition, as shown in Figure 19.4 and demonstrated in **Analyzing Data 19.1**.

The intermediate disturbance hypothesis and the Menge–Sutherland model assume that there is an underlying competitive hierarchy among species—that is, that some species are much stronger competitors than others and thus dominate communities if they are not kept in check by disruptive processes. What happens if we assume that there is no competitive hierarchy among

ANALYZING DATA 19.1 How Do Predation and Dispersal Interact to Influence Species Richness?

A prominent theme in this chapter is that processes such as disturbance, stress, and predation can mediate resource availability, thus promoting species coexistence and species diversity. Another important theme in this and the previous chapter is that regional species pools and the dispersal abilities of species can play important roles in supplying new species to communities. What happens when we combine these concepts in an attempt to explain the factors important to species coexistence within local communities? That was the goal of research on zooplankton communities conducted by Jonathan Shurin (2001),* who explored the effects of predation and dispersal on the species diversity of local zooplankton communities. He used experimental ponds made from plastic cattle watering tanks, which he stocked with a diversity of local zooplankton to create individual zooplankton communities. Next, he imposed one of four predation treatments on each pond: (1) no predators, (2) fish predators only (juvenile bluegill sunfish, *Lepomis macrochirus*), (3) insect predators only (the backswimmer bug *Notonecta undulata*), and (4) both fish and insect predators. Finally, Shurin applied a second type of treatment: either the ponds received dispersers of a large number of zooplankton species from the regional pool (which Shurin repeatedly added to the ponds at low densities throughout the experiment), or they received no dispersers. The experiment ran over a summer, after which time Shurin counted the number of zooplankton species in each of the pond communities. His results are shown in the graph.

1. How did predation alone affect the species richness of zooplankton within the ponds? Give a plausible explanation for why this occurred. Did fish and insect predators have different effects on local species richness?



2. How does species richness change with the addition of zooplankton dispersal into the ponds? Without knowing anything about the species composition of the ponds, can you say what these results suggest about the dual effects of predation and dispersal on local species richness?
3. Suppose an additional treatment, that of doubling the number of predators, was added to this experiment. Suppose the results showed a decline in zooplankton richness (let's say six species without dispersal and ten species with dispersal). What would these results suggest about the role of dispersal in pond communities subjected to heavy predation? Considering the entire range of predation intensity, from none to intermediate to heavy, do the results fit the intermediate disturbance hypothesis? Why or why not?

See the companion website for a similar ANALYZING DATA exercise.

---

*Shurin, J. B. 2001. Interactive effects of predation and dispersal of zooplankton communities. *Ecology* 82: 3404–3416.

species? If species have equivalent effects on one another, then the ability of any one species to live in a community will depend more on chance than on "conflict resolution." Let's spend a moment discussing this alternative theory of species diversity.

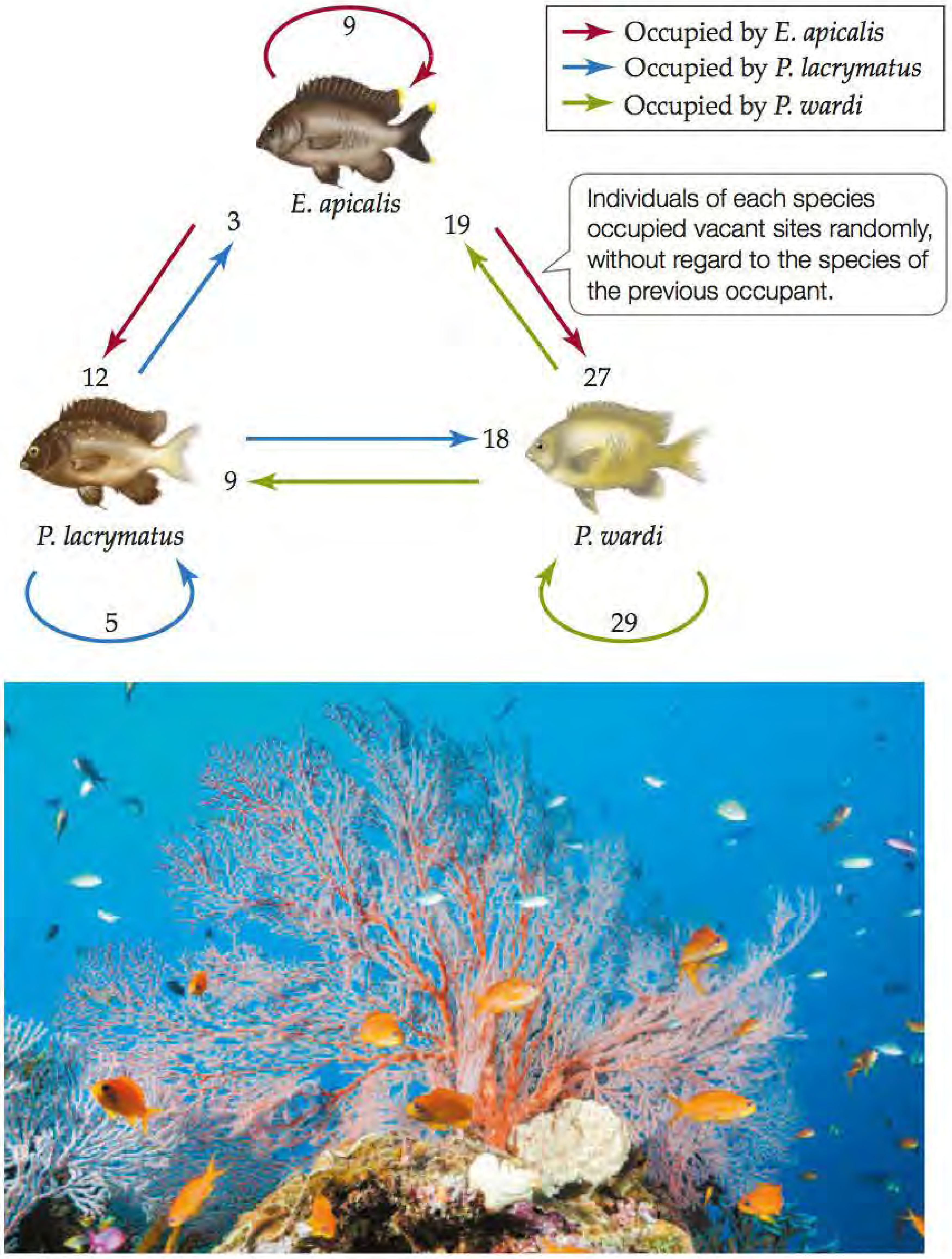
Lottery and neutral models rely on equality and chance

A final group of models proposed to explain species coexistence are so-called **lottery models** and **neutral models** (Sale 1977; Chesson and Warner 1981; Hubbell 2001). As their names suggest, these models emphasize the role of chance in the maintenance of species diversity. Lottery and neutral models assume that resources in a community made available by the effects of disturbance, stress, or predation are captured at random by recruits from a larger pool of potential colonists. For this mechanism to work, species must have fairly similar interaction strengths and population growth rates, and they must have the ability to respond quickly, by dispersing, to disturbances that free up resources. If there is a large disparity in competitive abilities among species, the dominant competitor will have a greater chance of obtaining resources and eventually monopolizing them. In lottery and neutral models, it is the equal chance of all species to obtain resources that allows species coexistence.

Lottery and neutral models have most often been applied to highly diverse communities. Peter Sale (1977, 1979) conducted one of the earliest and best-known tests of the lottery model on fishes of the Great Barrier Reef of Australia. Fish species diversity on this reef ranges from 1,500 species in the north to 900 species in the south. On any one small patch of reef (about 3 m, or 10 feet, in diameter), up to 75 species might be recorded. In the reef ecosystem, there is strong habitat fidelity and severe space limitation, and many individual fish spend their entire adult lives in roughly the same spot on the reef. Given these conditions, Sale asked the obvious question: How could so many species coexist in such a small space for so long?

Sale reasoned that only a portion of the coexistence among these fishes could be explained by resource partitioning, because the species tended to have very similar diets. He noted that vacant sites or territories were highly desirable and were made available rather unpredictably by the deaths of individual occupants (due, for example, to predation, disturbance, starvation, or disease). To look at this system in more detail, Sale observed losses of occupants and recruitment to newly vacated sites among three species of territorial pomacentrid fishes (*Eupomacentrus apicalis*, *Plectroglyphidodon lacrymatus*, and *Pomacentrus wardi*). He found the pattern of occupation to be random (**Figure 19.20**)—the identity of the species that had previously occupied a site had no bearing on which species was recruited to that site when it became vacant. One species, *P. wardi*, both lost and occupied sites at a greater rate than the other two species, but this had no effect on its overall ability to coexist with the other two species. Sale noted that one important component of this lottery system is that fishes produce many, highly mobile juveniles that can saturate a reef and take advantage of open space made available (as described for clownfish in Chapter 7's Connections in Nature). As Sale put it, "The species of a guild are competing in a lottery for living space in which larvae are tickets and the first arrival at a vacant site wins that site" (Sale 1977, p. 351).

The role of chance in maintaining species diversity, especially in unpredictable environments, has intuitive appeal. As long as species win the lottery every once in a while, they will continue to reproduce (i.e., buy more tickets) and be able to enter the lottery once again. It is easy to see how this mechanism might be particularly relevant in highly diverse communities such as tropical rainforests and grasslands, where so many species overlap in their resource requirements. Its relevance decreases, however, in communities where species have large disparities in interaction strength. In those communities, it appears that the "great equalizers" are processes that decrease competitive exclusion, such as disturbance, stress, or predation, or increase inclusion, such as positive interactions.



Individuals of each species occupied vacant sites randomly, without regard to the species of the previous occupant.

Figure 19.20 A Test of the Lottery Model Peter Sale tested the lottery model using coral reef fishes living on the Great Barrier Reef of Australia. By counting the individuals of three fish species (*Eupomacentrus apicalis*, *Plectroglyphidodon lacrymatus*, and *Pomacentrus wardi*) that occupied vacated sites, he found that the species of the new occupant was random and unrelated to the species that had previously occupied the site. The drawings represent the original occupants of vacated sites, and the colored arrows pointing to each drawing show the number of individuals of each species that took over those sites when they became vacant. (Data from Sale 1979.)

Ecologists are a long way from agreeing on any one theory to explain why certain species end up coexisting in space and time. Instead, they continue to strive for generalities while recognizing that the relative importance of different mechanisms of species diversity may depend on the characteristics of the community in question.

Up to this point in the chapter, we have focused on the causes of species diversity at the community level. We have asked, Why and how does species diversity differ among communities? In the next section, we will shift gears and instead ask what might be considered the flip side of that question. We want to know, given the variation in species diversity among communities (and the current losses of species diversity due to human activities), whether species diversity matters. In other words, what do species do in communities? Does species diversity have functional significance?

CONCEPT 19.4

Many experiments show that species diversity affects community function.

The Consequences of Diversity

In the Case Study at the opening of this chapter, we saw reduced hantavirus prevalence in small-mammal communities with higher species diversity compared with those with lower species diversity (see Figure 19.2). These results support the notion that species diversity can control certain ecological functions of a community. These **community functions**, or processes that control community structure, are numerous and include not only disease suppression, but also plant productivity, water quality and availability, atmospheric gas exchange, and even resistance to disturbance (and recovery afterward). Many of these functions of communities provide valuable ecosystem services to humans, such as food and fuel production, water purification, O_2 and CO_2 exchange, and protection from catastrophic events such as floods or tsunamis (see Concept 23.1). The Millennium Ecosystem Assessment (2005), a synthesis of studies produced under the auspices of the United Nations, details the importance of these ecosystem services to humans. The assessment predicts that if the current losses of species diversity continue, the world's human populations will be severely affected by the loss of the services those species, and the communities in which they live, provide.

What evidence underlies these dire predictions? Recent research has attempted to look at the connections between species diversity and community function, not only to seek basic insights into community ecology, but also because of concerns over species losses and the services that may be affected as a result.

Some relationships between species diversity and community function are positive

The consequences of species diversity to communities were first proposed by both Robert MacArthur (1955) and Charles Elton (1958), who theorized that species richness should be positively related to **community stability**. A community is thought to have stability when it remains, or returns, to its original structure and function after some perturbation (see Concept 17.4). The diversity–stability theory remained "conventional wisdom" until the mid-1970s, when it was tested mathematically using food web models that varied in species richness and complexity. We will consider those models in more detail in Concept 21.4. But it was not until 40 years later that the theory was first tested experimentally.

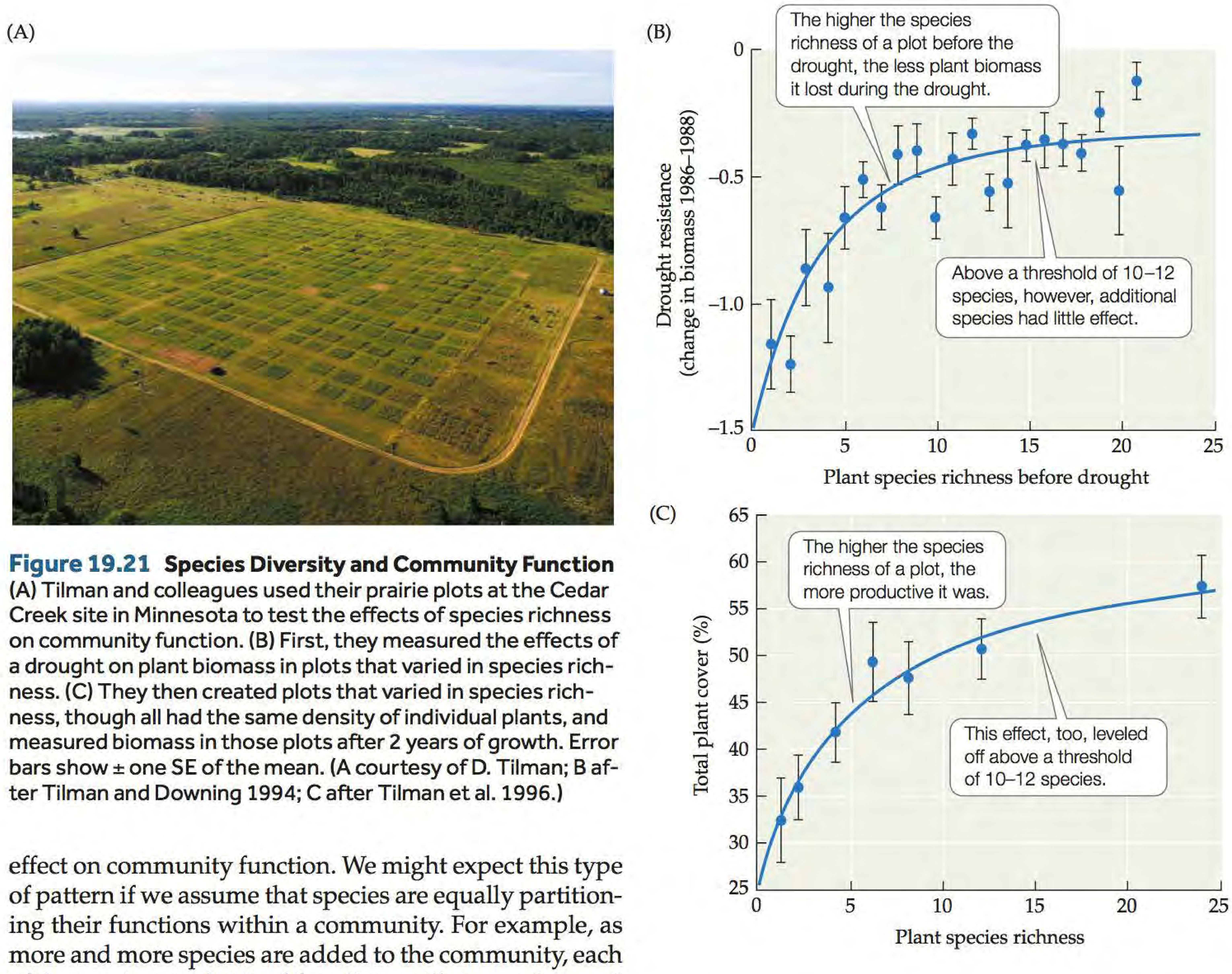
David Tilman and colleagues used a set of experimental plots on abandoned agricultural land at Cedar Creek, Minnesota, to explore the relationship between plant species richness and measures of community function (**Figure 19.21A**). In the first study, Tilman and Downing (1994) noticed that some of their experimental plots at Cedar Creek seemed to be responding to a drought differently from others. A survey of their plots showed that plots with higher species richness were better able to withstand the drought than plots with lower species richness (but the same density of plants) (**Figure 19.21B**). Drought-induced total plant biomass decrease was less in species-rich plots than in species-poor ones, resulting in a positive, curvilinear relationship between species richness and drought resistance (measured as the difference between biomass before and after the drought). Tilman and Downing reasoned that a curvilinear relationship would be expected if additional species beyond some threshold (the point at which the curve levels off; roughly 10–12 species in this study) had little additional effect on drought resistance. These species could be considered redundant in the sense that they had essentially the same effects on drought resistance as other species. Tilman and Downing suggested, however, that once the number of species in a plot declined below that threshold, each additional species lost from the plot would result in a progressively greater negative effect of drought on the community.

To test this idea more rigorously, Tilman et al. (1996) conducted a well-replicated experiment in which species diversity was directly manipulated. In the same prairie ecosystem, a series of plots that differed in plant species richness, but not in the number of individual plants, was created by randomly selecting sets of species from a pool of 24 species. Each plot was provided with the same amounts of water and nutrients. When biomass in the plots was measured after 2 years of growth, the results confirmed the curvilinear effect of species richness on biomass (**Figure 19.21C**) and additionally showed that nitrogen was more efficiently used as species richness increased.

There is debate over diversity–function relationships and their explanations

Although experiments documenting the relationships between species diversity and community function continue to increase in their sophistication, ecologists have debated over the generality of the relationships and their underlying mechanisms. Naeem and colleagues (1995) summarized at least three possible relationships between species diversity and community function and their corresponding hypotheses. Two variables distinguish these hypotheses: the degree of overlap in the ecological functions of species, and variation in the strength of the ecological functions of species.

The first hypothesis, known as the **complementarity hypothesis**, proposes that as species richness increases, there will be a linear increase in community function (**Figure 19.22A**). In this case, each species added to the community will have a unique and equally incremental



The higher the species richness of a plot before the drought, the less plant biomass it lost during the drought.

Above a threshold of 10–12 species, however, additional species had little effect.

The higher the species richness of a plot, the more productive it was.

This effect, too, leveled off above a threshold of 10–12 species.

Figure 19.21 Species Diversity and Community Function (A) Tilman and colleagues used their prairie plots at the Cedar Creek site in Minnesota to test the effects of species richness on community function. (B) First, they measured the effects of a drought on plant biomass in plots that varied in species richness. (C) They then created plots that varied in species richness, though all had the same density of individual plants, and measured biomass in those plots after 2 years of growth. Error bars show ± one SE of the mean. (A courtesy of D. Tilman; B after Tilman and Downing 1994; C after Tilman et al. 1996.)

effect on community function. We might expect this type of pattern if we assume that species are equally partitioning their functions within a community. For example, as more and more species are added to the community, each of their unique individual functions will accumulate and increase the overall community function.

The second hypothesis, known as the **redundancy hypothesis**, relies on assumptions similar to those of the complementarity hypothesis, but it places an upper limit on the effect of species richness on community function (**Figure 19.22B**). This model best fits the results of Tilman and colleagues described above (see Figure 19.21), in which the functional contribution of additional species reaches a threshold. This threshold is reached because as more species are added to the community, there is overlap in their function—essentially, there is redundancy among species. In this model, species can be thought of as belonging to certain functional groups (see Figure 16.4C). As long as all the important functional groups are represented, the actual species composition of the community is of little importance to its overall function.

The third hypothesis, known as the **idiosyncratic hypothesis**, proposes that the ecological functions of some species have stronger effects than others do and that they vary dramatically (**Figure 19.22C**). Some species have a large effect on community function, while other species have a minimal effect. The addition of dominant species to a community will therefore have a large effect on community function, producing a curve with an idiosyncratic shape, as shown in Figure 19.22C. If communities are assembled in such a way that there are only a few dominant species (e.g., keystone or foundation species; see Figure 16.16), then one would expect community function values to vary dramatically with species richness, that is, there would be peaks and valleys in community function values, depending on whether the dominant species are present or not. As species richness increases, however, the chance that the dominant species will be present also increases. As a result, the variation in community function values should eventually stabilize.

Although these models provide a theoretical foundation for understanding how species contribute to community function, testing them is logically challenging because of the number of species involved and the variety of community functions that could be considered. In many ways, these models and tests are at the heart of modern community ecology, not only because they tell us something about how communities work, but also because they may be able to tell us what the future holds

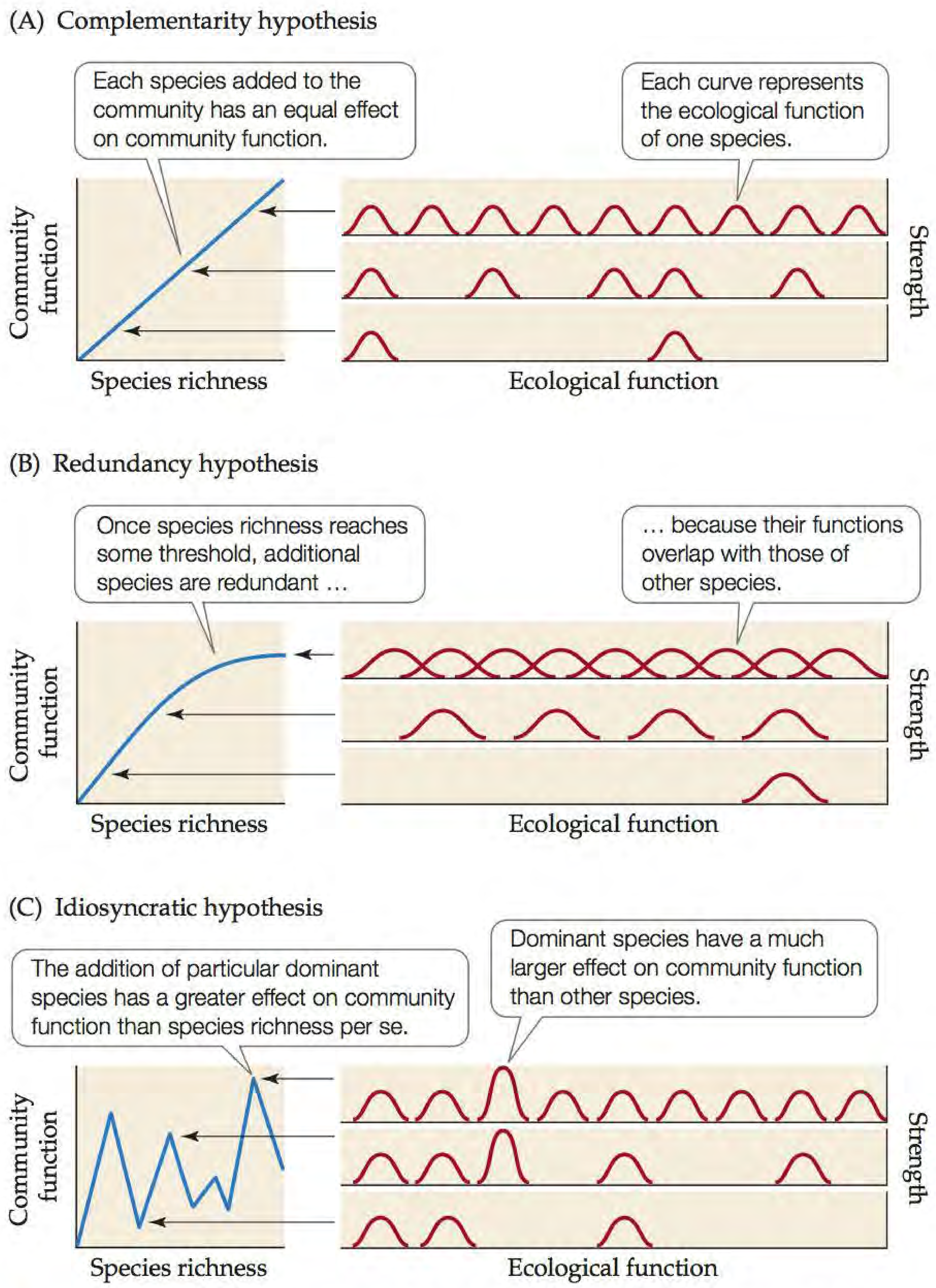


Figure 19.22 Hypotheses on Species Richness and Community Function At least three possible relationships between species diversity and community function and their corresponding hypotheses have been proposed. Two variables distinguish these hypotheses: the degree of overlap in the ecological functions of species, and variation in the strength of the ecological functions of species. (After Naeem et al. 1995.)

for communities that are both losing (by extinction) and gaining (by invasions) species through human influence.

A CASE STUDY REVISITED

Can Species Diversity Suppress Human Diseases?

The potential value of understanding how species diversity controls community function is limitless when we consider the services communities provide to humans. As we have seen, these services are numerous and diverse. One potential service that has been overlooked until recently is the role species diversity plays in infectious disease emergence and transmission. As we saw in the Case Study at the opening of this chapter, Suzàn and colleagues (2009) showed that plots with reduced small-mammal diversity increased in both host rodent species abundance and the number of SNV-infected rodent individuals (see Figure 19.2). How can species diversity have this effect on disease transmission? Several hypotheses have been proposed. First, if the species that are lost within the community compete with or prey on the host species, then their loss can lead to an increase in the population density of the host and the pathogen. Second, it might be that hosts in more species diverse situations are simply more likely to come into contact with individuals of other species than their own species (conspecifics), reducing the probability of transmission. Finally, it may be that more diverse communities allow hosts to build up greater resistance to diseases because those hosts are exposed to similar pathogens in other species within the community.

The research to date on the effects of species diversity on hantavirus transmission best supports the first two hypotheses. In the case of the experimental plots in Panama, the data support the first hypothesis; there was an increase in the number of rodent indivudals that led to an increase in the number of SNV-infected hosts (see Figure 19.2). Presumably, as the number of small-mammal competitors declined, the rodent host species were able to take advantage of greater resources and their numbers increased. More host individuals then lead to greater hantavirus disease transmission. However, the results from the observational studies in Utah and Oregon showed a different pattern that more closely supports the second hypothesis. In those studies, the lower small-mammal diversity increased infection prevalence by simply increasing the encounter rate, rather than density, of individuals of the same host species.

Disentangling the effect of higher density from the effect of reduced species diversity can be difficult. One study, using the trematode parasite *Schistosoma mansoni* and its snail host, manipulated species richness while keeping density constant (Johnson et al. 2009). The researchers showed that the presence of other snail species reduced parasite transmission even when the density of the host remained constant. In this case, the multispecies treatments reduced the encounter rate of the snail host with its trematode parasite by providing alternative but suboptimal host species. Other studies have shown that which species are lost within a community can make a difference in disease transmission, supporting principles of the idiosyncratic hypothesis (see Figure 19.22C). It is clear that the number of examples of species diversity loss and disease transmission is increasing, but the generalities that can be drawn from these examples are still unfolding.

By applying basic principles of ecology to zoonotic disease transmission, we can see that we cannot underestimate the role of species diversity in regulating community integrity. We must consider what might seem like inconsequential and esoteric details, such as the number of species that coexist within communities. In this case, species richness makes all the difference, not only in protecting humans from disease transmission, but also in thwarting emerging and potentially dangerous diseases in the future.

CONNECTIONS IN NATURE

Managing Pathogens by Managing Biodiversity

As more evidence accumulates that changes in biodiversity can trigger infectious diseases, there is interest in managing for these outbreaks. Management can come in many forms depending on the pathogen in question. Beyond the obvious recommendation that genetic and species diversity be maintained within ecosystems, there are other management suggestions that can help provide early warning signs or reduce the risk of emerging pathogens altogether.

First, it is critical to survey potential "emergence hotspots" where land use changes and agricultural intensification reduce diversity and have the potential to trigger endemic wildlife pathogens, potentially causing them to jump to new host species, including livestock and humans. In fact, research shows that almost half of the zoonotic diseases that have emerged since 1940 have occurred in regions where major changes in land use, agriculture, or wildlife hunting practices have occurred (Jones et al. 2008).

Second, the research also suggests that another 20% of diseases emerging since the 1940s have arisen through the widespread use of antibiotics and the production of resistant strains of microbes. Antibiotics are thought to select for resistant microbes by both eliminating the diversity of nonresistant microbial strains and by eliminating species that suppress those strains. The observation that a more diverse microbiome can suppress strains that are resistant to antibiotics suggests that avoiding the overuse of these pharmaceuticals in medicine and agriculture is critical in preventing emerging diseases.

Finally, managing emerging diseases will involve considering the complex ways that factors such as climate change, invasive species, and pollution interact with biodiversity loss to increase the emergence and transmission of diseases. Despite the many questions that remain, it is clear that managing for biodiversity is a critical component in protecting human populations from potential disease epidemics.

Summary

CONCEPT 19.1 Species diversity differs among communities as a consequence of regional species pools, abiotic conditions, and species interactions.

- The regional species pool and the dispersal abilities of species play important roles in supplying species to communities.
- Humans have greatly expanded the regional species pools of communities by serving as vectors for the dispersal of non-native species.
- Local environmental or abiotic conditions act as a strong "filter" for community membership.
- When a species depends on other species for its growth, reproduction, and survival, those other species must be present if it is to gain membership in a community.
- Species may be excluded from communities by competition, predation, parasitism, or disease.

CONCEPT 19.2 Resource partitioning is theorized to reduce competition and increase species diversity.

- Resource partitioning theory predicts that species must use resources slightly differently if they are to avoid competitive exclusion.
- One model of resource partitioning states that the less overlap there is among species in their use of resources, along a resource spectrum, the more species can coexist in the community.
- The resource ratio hypothesis posits that species that use the same set of resources are able to partition them by using them in different proportions.

CONCEPT 19.3 Processes such as disturbance, stress, predation, and positive interactions can mediate resource availability, thus promoting species diversity.

- If disturbance, stress, or predation keeps dominant competitors from reaching their carrying capacity, competitive exclusion will not occur and coexistence will be maintained.
- The intermediate disturbance hypothesis states that intermediate levels of disturbance, stress, or predation promote species diversity by reducing competitive exclusion. At low levels of disturbance, competitive exclusion reduces species diversity, and at high levels of disturbance, high mortality reduces species diversity.
- The dynamic equilibrium model predicts that species diversity will be highest when the level of disturbance and the rate of competitive displacement are roughly equivalent.

(Continued)

Summary (Continued)

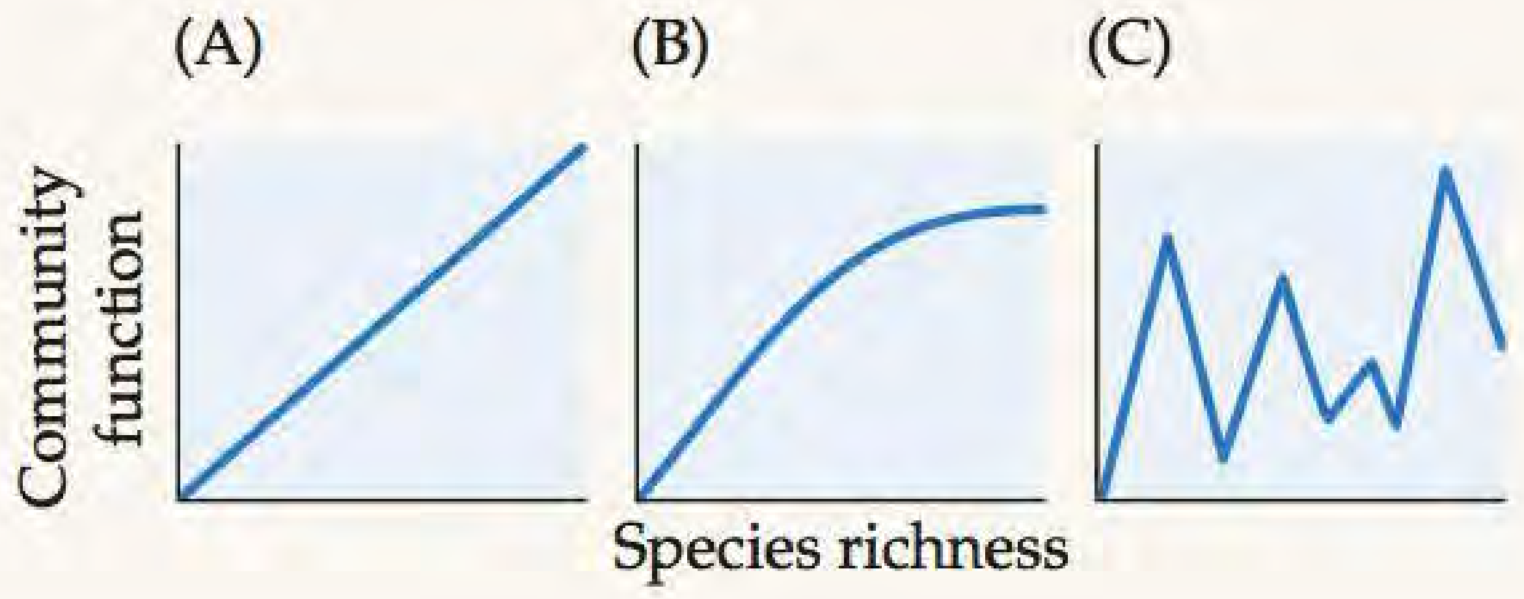
- Positive interactions can promote species diversity, particularly at intermediate to high levels of disturbance, stress, or predation.
- The Menge–Sutherland model is similar to the intermediate disturbance hypothesis except that it separates the effect of predation from that of physical disturbance.
- Lottery and neutral models assume that resources in a community made available by disturbance, stress, or predation are captured at random by recruits from a larger pool of potential colonists, whose chances for capturing resource are equal.

CONCEPT 19.4 Many experiments show that species diversity affects community function.

- Evidence suggests that species diversity can control numerous functions of communities, including productivity, soil fertility, water quality and availability, atmospheric gas exchange, and responses to disturbance.
- Some manipulative experiments in different communities have shown that as species diversity increases, so does community function.
- Hypotheses proposed to explain the positive relationship between species diversity and community function fall into three general categories, which include different assumptions about the degree to which individual species vary in their contribution to community function.

Review Questions

1. Suppose you are an ecologist studying prairie grassland communities in Minnesota. As you are doing your fieldwork, grass seeds with hooked spines attach themselves to your shoes. You then travel to New Zealand to study the grasslands on the South Island. When you enter the customs area in the Auckland airport, the officers in charge ask if you have visited a natural area or farm recently. You say yes, and they tell you to take off your shoes and wait while they disinfect them with bleach. Given what you know about the mechanisms important to community membership, is it worth the time and money required to clean all that footwear before allowing it into New Zealand?
2. We know that species diversity varies greatly among communities. Describe how some of the models proposed to explain this variation differ in their explanations of the mechanisms involved.
3. Suppose you are studying a tropical rainforest community in Panama. You obtain a 50-year data set for the forest that records both the mortality of adult trees and the emergence of new tree seedlings. As you analyze the data, you try to determine whether there is a pattern of species replacement, in which individuals of one species generally replace one another in the same sites, rather than individuals of other species establishing. After much work, you are convinced that no pattern of replacement exists in this forest—instead, sites are colonized in an entirely random fashion, with no one species having an advantage. What general set of models of species diversity best describes your observations, and why?
4. Recent experimental work in communities has shown positive relationships between species diversity and community function. We learned that there is considerable debate about the relationships and their controlling mechanisms and that at least three hypotheses have been developed to explain them. Below are three graphs (A, B, and C) of species richness–community function relationships that vary in the shapes of their curves. Describe which hypothesis best fits each curve, and why.



Hone Your Problem-Solving Skills

In the Case Study of this chapter, we explored the results of a study that considered the relationship between species diversity and disease transmission of the Sin Nombre virus in deer mouse populations in Oregon (Dizney and Ruedas 2009). Suppose a similar study is conducted in six parks in or around a city that vary in their degree of human disturbance. The researchers record the number of small-mammal species, the density of deer mice, and the number of deer mouse individuals infected with the Sin Nombre virus. Below is a table with the results of this hypothetical study, organized by the degree of human disturbance at the trapping locations:

PARK	DEGREE OF HUMAN DISTURBANCE (LOWEST TO HIGHEST)	SMALL-MAMMAL SPECIES RICHNESS	DEER MOUSE DENSITY	SIN NOMBRE VIRUS INFECTION PREVALENCE
1	1	12	5	0.045
2	2	14	6	0.045
3	3	16	6.5	0.04
4	4	13	6.5	0.04
5	5	9	5.5	0.08
6	6	6	6	0.12

1. Graph the relationship between degree of human disturbance and small-mammal species richness. What species diversity model do your data best describe and why?
2. Now graph the relationship between species richness and deer mouse density. What does the graph show? Do the data support the theory that species richness is a consequence of resource partitioning in this small-mammal community?
3. Graph both the relationship of species richness with Sin Nombre virus infection prevalence in the deer mouse and the relationship of deer mouse density with Sin Nombre virus infection prevalence in the deer mouse. Which factor seems to be more important in spreading infection in deer mice—species richness or deer mouse density? Explain why this might be so, based on theory.

ON THE COMPANION WEBSITE
ecology4e.sinauer.com

The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

19.1 What Goldilocks Can Teach Us about Coexistence: The Intermediate Disturbance Hypothesis

19.2 Does It Really Matter? Diversity and Productivity in Grasslands

Web Extensions

19.1 Testing the Dynamic Equilibrium Model

Unit 6
Ecosystems

20 Production

KEY CONCEPTS

CONCEPT 20.1 Energy in ecosystems originates with primary production by autotrophs.

CONCEPT 20.2 Net primary production is constrained by both physical and biotic environmental factors.

CONCEPT 20.3 Global patterns of net primary production reflect climate constraints and biome types.

CONCEPT 20.4 Secondary production is generated through the consumption of organic matter by heterotrophs.

Life in the Deep Blue Sea, How Can It Be? A Case Study

Ecologists once considered the deep sea to be the marine equivalent of a desert. The physical environment at depths between 1,500 and 4,000 m (5,000–13,000 feet) did not seem conducive to life as we knew it. It is completely dark, so photosynthesis is not possible. The water pressure reaches values 300 times greater than those at the surface of the ocean, similar to the pressure used to crush cars at a junkyard. Organisms living on the floor of the deep sea were thought to obtain energy exclusively from the sparse rain of dead material falling from the upper layers of the ocean where sunlight is sufficient for phytoplankton to carry out photosynthesis. Most of the known deep-sea organisms were detritus feeders such as echinoderms (e.g., sea stars), mollusks, crustaceans, and polychaete worms.

Our view of deep-sea life was changed dramatically in 1977, when an expedition led by Robert Ballard of the Woods Hole Oceanographic Institution used the submersible craft *Alvin* to dive to a mid-ocean ridge near the Galápagos archipelago (**Figure 20.1**). The team aboard the *Alvin* was in search of the deep-sea hot springs thought to occur along mid-ocean ridges. These ridges lie at the junctions of tectonic plates, where the seafloor spreads as the plates are pushed apart by molten rock rising from Earth's mantle (see Figure 18.10). Because mid-ocean ridges are volcanically active, geologists and oceanographers had hypothesized that seawater seeping into cracks in the ocean floor near the ridges would be superheated by pockets of magma, chemically transformed, and ejected as hot springs. These hot springs were considered potential sources of chemicals for the ocean system as well as sources of heat. Despite their hypothesized existence, no such hot springs had ever been located.

Ballard's group did indeed find hot springs, known as *hydrothermal vents*. However, this geochemical finding paled in comparison with their biological discovery: the areas around the hydrothermal vents were teeming with life. Dense assemblages of tube worms (e.g., *Riftia* spp.), giant clams (e.g., *Calyptogena* spp.), shrimps, crabs, and polychaete worms were found in the areas surrounding the vents (**Figure 20.2**). The density of organisms was unprecedented for the deep, dark seafloor.

The discovery of these diverse and productive hydrothermal vent communities posed an immediate question: How did the organisms obtain the energy needed to sustain themselves in such

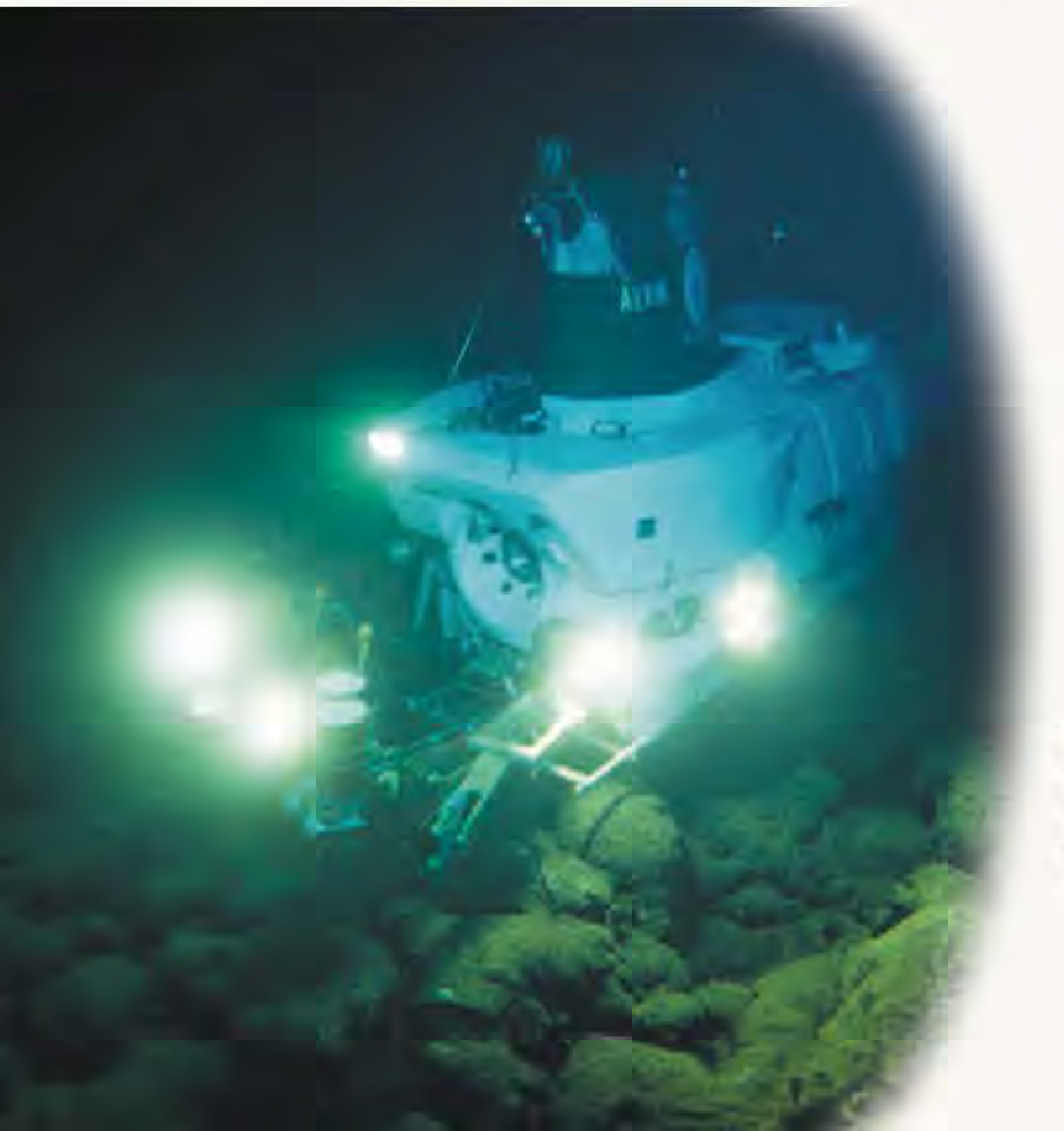


Figure 20.1 ***Alvin* in Action** The deep-sea submersible craft *Alvin* was instrumental in locating and exploring the first known hydrothermal vent site in 1977. The *Alvin* can carry two scientists and is equipped with video cameras and robotic arms for collecting specimens from the seafloor.

Figure 20.2 Life around a Hydrothermal Vent Tube worms more than 2 m long surround a hydrothermal vent. The vent spews superheated water as hot as 400°C, which contains high concentrations of dissolved metals and chemicals, particularly hydrogen sulfide.

abundance? The rate at which dead organisms from the upper zones of the ocean accumulate on the seafloor is very low (0.05–0.1 mm/year). The newly formed areas of seafloor where the vents are located are only decades old, and thus the amount of organic material that would have accumulated should not be enough to sustain these high densities of organisms. Photosynthesis in the surface waters therefore did not appear to be the energy source supporting these hydrothermal vent communities.

The water being emitted from the hydrothermal vents also constitutes a problem for life: its chemical composition is toxic to most organisms. The water emitted by the vents is rich in sulfides as well as heavy metals such as lead, cobalt, zinc, copper, and silver, which inhibit metabolic activity in most organisms.

Hydrothermal vent communities thus pose two mysteries: first, what is the source of energy that sustains them, and second, how do the organisms tolerate the high concentrations of potentially toxic sulfides in the water? As we shall see, the answers to these two questions are intimately related.

Introduction

In 1942, the journal *Ecology* published a controversial paper authored by Raymond Lindeman, describing energy flow in a Minnesota lake. Lindeman had studied the energy relationships among the organisms and nonliving components in a lake ecosystem. Rather than grouping its component plants, animals, and bacteria according to their taxonomic categories, Lindeman grouped them into categories based primarily on how they obtained their energy (**Figure 20.3**). His views on the importance of the energy base of the system—an "ooze" of particulate and dissolved dead organic matter—and on the efficiency of energy transfer among the system's biological components were groundbreaking. Lindeman's treatment of energy flow in the lake was considered too theoretical at the time, and his paper was initially rejected. The publishers later reconsidered after Lindeman's mentor, the prominent limnologist G. E. Hutchinson, advocated its acceptance. Lindeman's paper was among the first in the area of ecosystem science, and it is now considered a fundamental paper in the discipline.

The term **ecosystem** was first coined by A. G. Tansley, a plant ecologist, to refer to all of the components of an ecological system, biotic and abiotic, that influence the flow of energy and elements (Tansley 1935). The "elements"

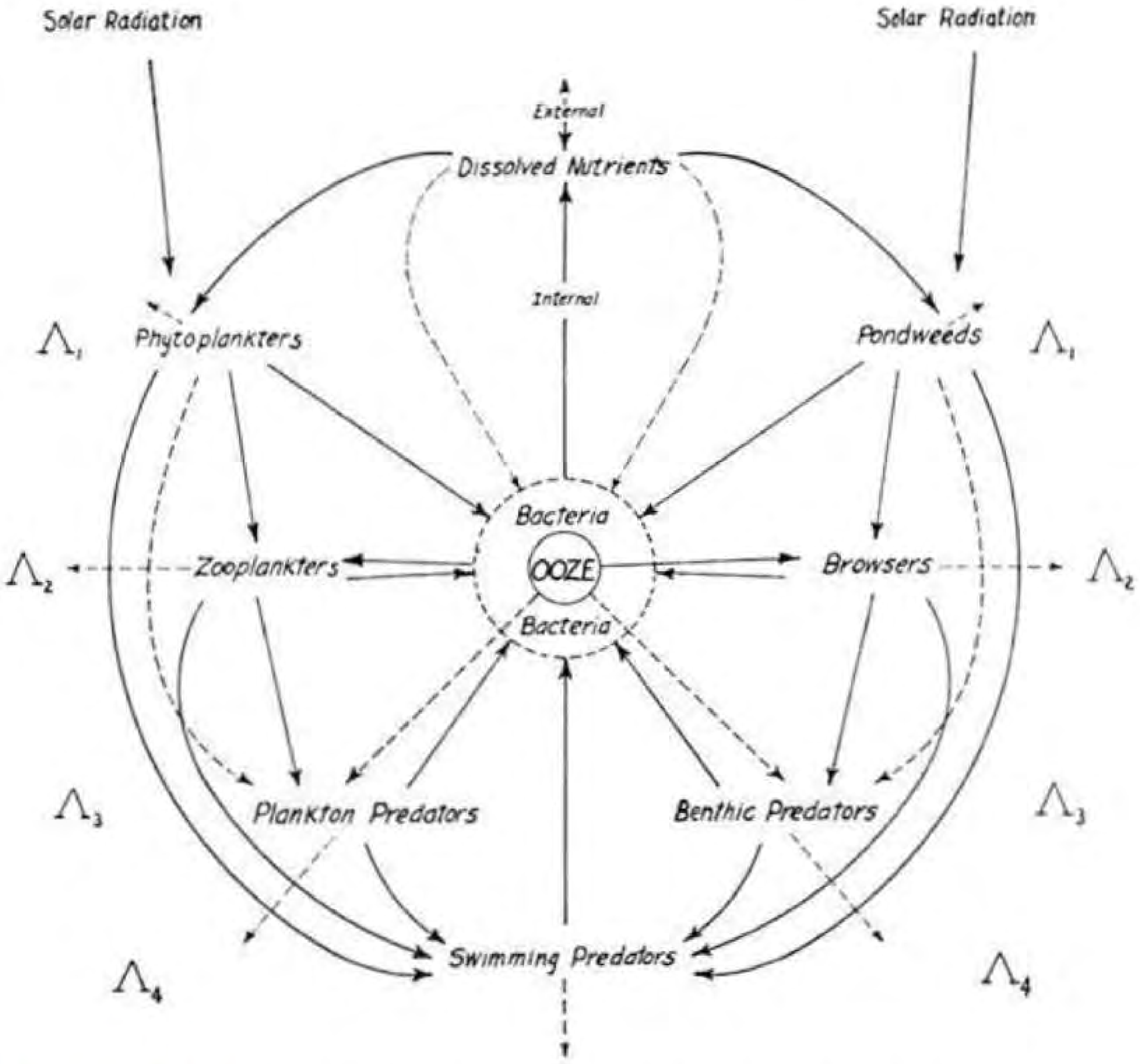


Figure 20.3 Energy Flow in a Lake Raymond Lindeman's diagram describes the movement of energy among groups of organisms at Cedar Bog Lake, Minnesota. Note the general functional categories of organisms Lindeman used, as well as the central position of "ooze" (organic matter) in the diagram. The subscripts next to the uppercase Greek lambdas represent trophic levels. (From Lindeman 1942.)

considered in ecosystem studies are primarily nutrients, but they also include pollutants; the movements of those elements through ecosystems are the topic of Chapter 22. The ecosystem concept is now well established and has become a powerful tool for integrating ecology with other disciplines such as geochemistry, hydrology, and atmospheric science.

In Chapter 5, we described the physiological basis for the capture of energy through photosynthesis and chemosynthesis by autotrophs, and we explained how heterotrophs obtain that energy by consuming autotrophs. In this chapter, we return to the topic of energy as we review how energy enters ecosystems, how it is measured, and what controls rates of energy flow through ecosystems.

CONCEPT 20.1

Energy in ecosystems originates with primary production by autotrophs.

Primary Production

The generation of chemical energy by autotrophs, known as **primary production**, is derived from the fixation of carbon during photosynthesis and chemosynthesis (see Chapter 5). Chemosynthesis can be the main source of energy in some rare circumstances, as we will see at the end of this chapter. However the majority of energy on Earth comes from photosynthesis, and thus primary production derived from photosynthesis will be the focus of the this section. Primary production represents an important energy transition: the conversion of light energy from the sun into chemical energy that can be used by autotrophs and consumed by heterotrophs. Primary production is the source of energy for all organisms, from bacteria to humans; even the fossil fuels we use today are derived from primary production. Primary production also accounts for the largest movement of carbon dioxide between Earth and the atmosphere, and it is therefore an important influence on global climate (see Chapters 2 and 25).

The energy assimilated by autotrophs is stored as carbon compounds in plant and phytoplankton tissues; therefore, carbon (C) is the currency used for the measurement of primary production. The *rate* of primary production is sometimes referred to as *primary productivity*.

Gross primary production is total ecosystem photosynthesis

The amount of carbon fixed by the autotrophs in an ecosystem is called **gross primary production** (**GPP**). The GPP in most terrestrial ecosystems is equivalent to the total of all plant photosynthesis.

The GPP of an ecosystem is controlled by climate through its influence on rates of photosynthesis, as we saw in Concept 5.2, and by the leaf area of the plants per unit of ground area, known as the **leaf area index,** a metric that lacks units, since it is an area divided by an area. The leaf area index varies among biomes, from less than 0.1 in tundra (i.e., less than 10% of the ground surface has leaf cover) to 12 in boreal and tropical forests (i.e., on average, there are 12 layers of leaves between the canopy and the ground). Shading of the leaves below the uppermost layer increases with the addition of each new leaf layer, so the incremental gain in photosynthesis for each added leaf layer decreases (**Figure 20.4**). Eventually, the respiratory costs associated with adding leaf layers outweigh the photosynthetic benefits. Plants generally match their leaf area index to the climate conditions and the supplies of resources, particularly water and nutrients, in order to maximize carbon gain.

A plant uses approximately half of the carbon it fixes by photosynthesis in cellular respiration to support biosynthesis and cellular maintenance. All living plant tissues lose carbon via respiration, but not all of them acquire carbon via photosynthesis. Thus, plants that have a large proportion of nonphotosynthetic stem tissue, such as trees and shrubs, tend to have higher overall respiratory carbon losses than herbaceous plants. Plant respiration rates increase with increasing temperatures, and as a result, respiratory carbon losses are higher in tropical forests than in temperate and boreal forests.

Net primary production is the energy remaining after respiratory losses

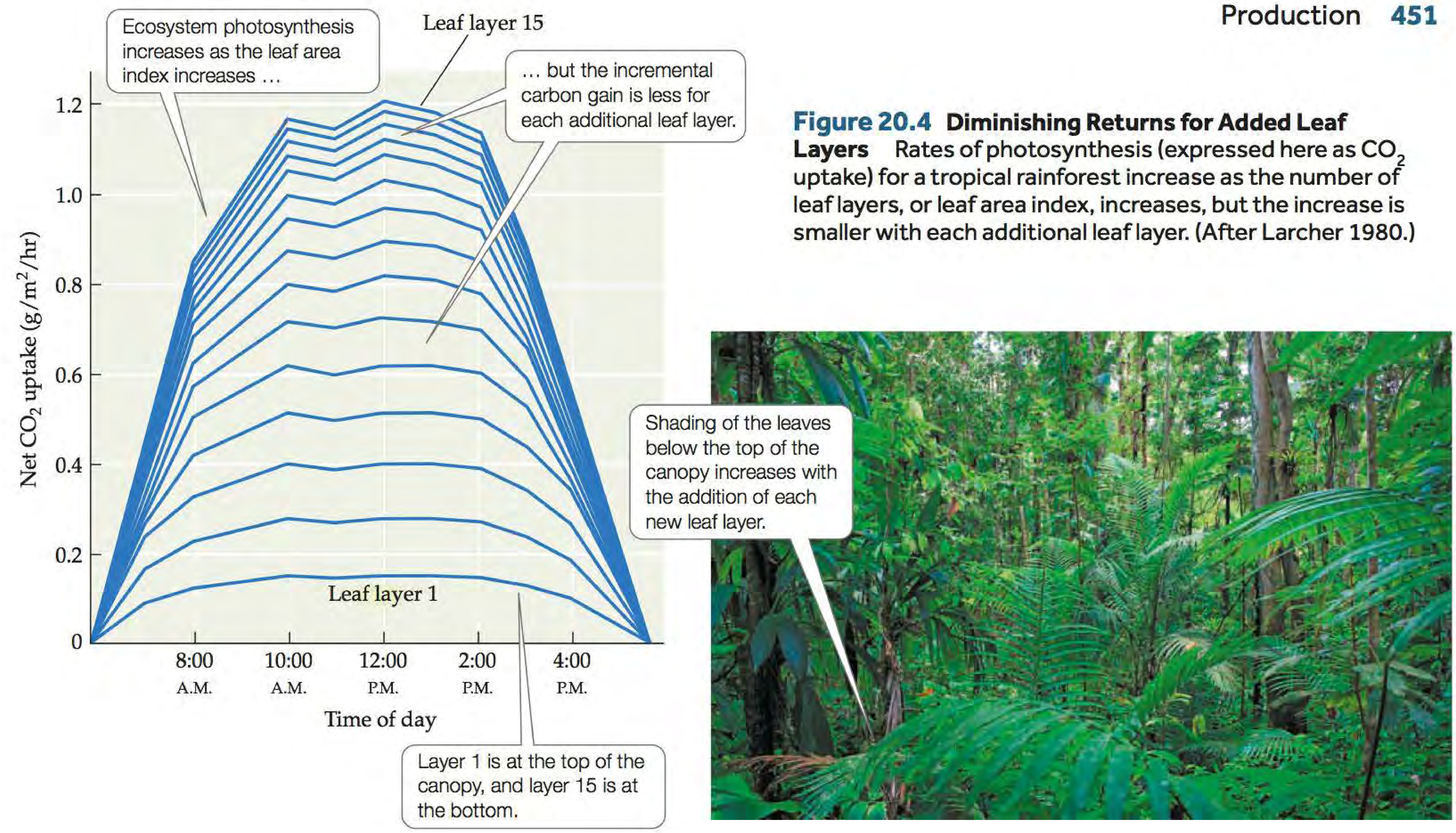
The balance between GPP and autotrophic respiration is called **net primary production** (**NPP**):

$$\text{NPP} = \text{GPP} - \text{respiration}$$

The NPP of a terrestrial ecosystem is the amount of energy captured by autotrophs that results in an increase in living plant matter, or **biomass**. In other words, NPP is the energy left over for plant growth, plant reproduction, and consumption by herbivores and detritivores. It also represents the total net input of carbon into ecosystems.

Carbon not used in respiration is used for growth and reproduction, storage, and defense against herbivory. Plants respond to varying environmental conditions by allocating carbon to the growth of different tissues. The allocation of carbon within a plant varies considerably according to the species, the availability of resources, and the climate. Allocation of carbon to photosynthetic tissues is an investment in potential future NPP, but the demands of the plant for other resources, particularly water and nutrients, as well as biological interactions such as herbivory influence whether that investment pays off.

A plant's allocation of NPP to the growth of leaves, stems, and roots is generally balanced so as to maintain supplies of water, nutrients, and carbon to match the plant's requirements. For example, plants growing in desert, grassland, and tundra ecosystems are regularly exposed to shortages of water or nutrients. Plants in these



Ecosystem photosynthesis increases as the leaf area index increases …

… but the incremental carbon gain is less for each additional leaf layer.

Layer 1 is at the top of the canopy, and layer 15 is at the bottom.

Shading of the leaves below the top of the canopy increases with the addition of each new leaf layer.

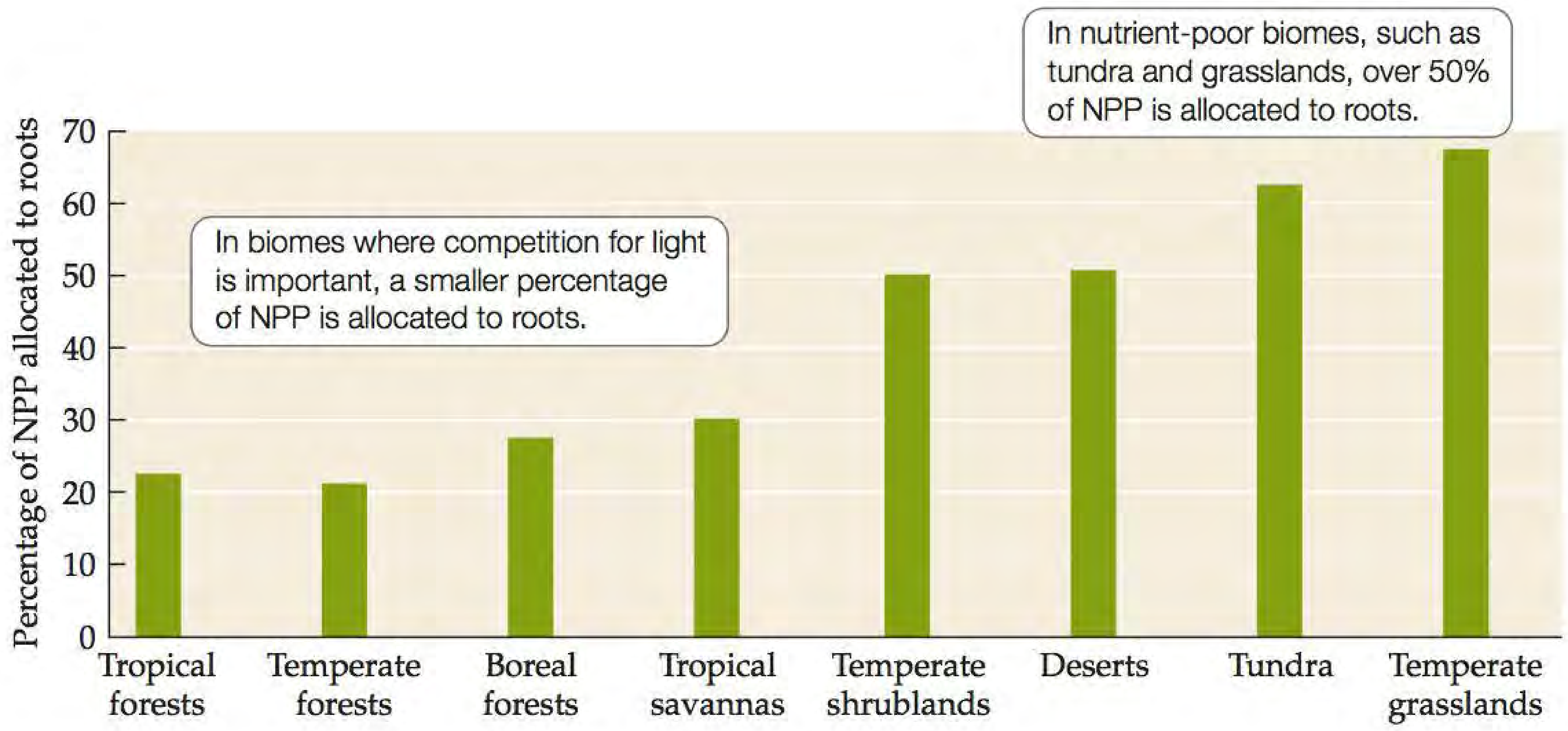
Figure 20.4 Diminishing Returns for Added Leaf Layers Rates of photosynthesis (expressed here as CO_2 uptake) for a tropical rainforest increase as the number of leaf layers, or leaf area index, increases, but the increase is smaller with each additional leaf layer. (After Larcher 1980.)

ecosystems may allocate a greater proportion of NPP to root growth, relative to the growth of shoots (leaves and stems), than plants growing in ecosystems with higher soil water and nutrient availability (**Figure 20.5**). This greater allocation to root growth facilitates their acquisition of the resources that are in short supply. In contrast, plants growing in dense communities, with neighbors that may shade them, may allocate NPP preferentially to stems and leaves in order to capture more sunlight for photosynthesis. In other words, plants tend to allocate the most NPP to those tissues that acquire the resources that limit their growth.

Allocation of NPP to storage compounds such as starch and carbohydrates provides insurance to compensate for losses of tissues to herbivores, disturbances such as fire, and weather events such as frost. These compounds are usually stored in the stems of woody plants or in belowground stems and roots of herbaceous plants. Where levels of herbivory are high, plants may allocate a substantial amount of NPP (up to 20%) to defensive secondary compounds, such as tannins or terpenes, that inhibit grazing.

NPP changes during ecosystem development

As ecosystems develop during primary or secondary succession (see Concept 17.2), NPP changes as the leaf area index, the ratio of photosynthetic to nonphotosynthetic tissue, and plant species composition all change.



In nutrient-poor biomes, such as tundra and grasslands, over 50% of NPP is allocated to roots.

In biomes where competition for light is important, a smaller percentage of NPP is allocated to roots.

Figure 20.5 Allocation of NPP to Roots The proportion of NPP that plants allocate to roots varies with the resources available to them. (After Saugier et al. 2001.)

? In addition to low supplies of resources in the soil, what other factors might favor greater allocation of NPP to tissues below the soil surface?

Disturbance and succession can therefore influence gains or losses of CO_2 from ecosystems, thereby affecting atmospheric CO_2 concentrations.

Most ecosystems have their highest NPP at mid-successional stages. Several factors contribute to this pattern, including the tendency for the proportion of photosynthetic tissues, plant diversity, and nutrient supply to be highest at mid-successional stages. In forest ecosystems, the leaf area index and the photosynthetic rates of leaves decrease in old-growth stands, lowering GPP and thus NPP. In some grasslands, such as the tallgrass prairies of the central United States, the accumulation of dead leaves near the ground surface and the development of a closed upper canopy of leaves decrease light availability to short plants, lowering the photosynthetic carbon gain of the ecosystem. However, the decrease in NPP over time is far less pronounced in grasslands than in forest ecosystems. Although NPP may decrease in late successional stages, lowering the uptake of CO_2 from the atmosphere, these old-growth ecosystems contain large pools of stored carbon and nutrients and provide habitat for late successional animal species.

NPP can be estimated by a number of methods

There are several reasons why it is important to be able to measure NPP in an ecosystem. As we have seen, NPP is the ultimate source of energy for all organisms in an ecosystem and thus determines the amount of energy available to support that ecosystem. It varies tremendously over space and time. Year-to-year variation in NPP provides a metric for examining ecosystem health, because changes in primary productivity can be symptomatic of stresses such as drought or acid rain. Finally, as noted earlier, NPP is intimately associated with the global carbon cycle, and it is therefore an important influence on global climate change (see Chapters 2 and 25). For all these reasons, scientists have put great effort into improving techniques for estimating NPP over the past 3 decades.

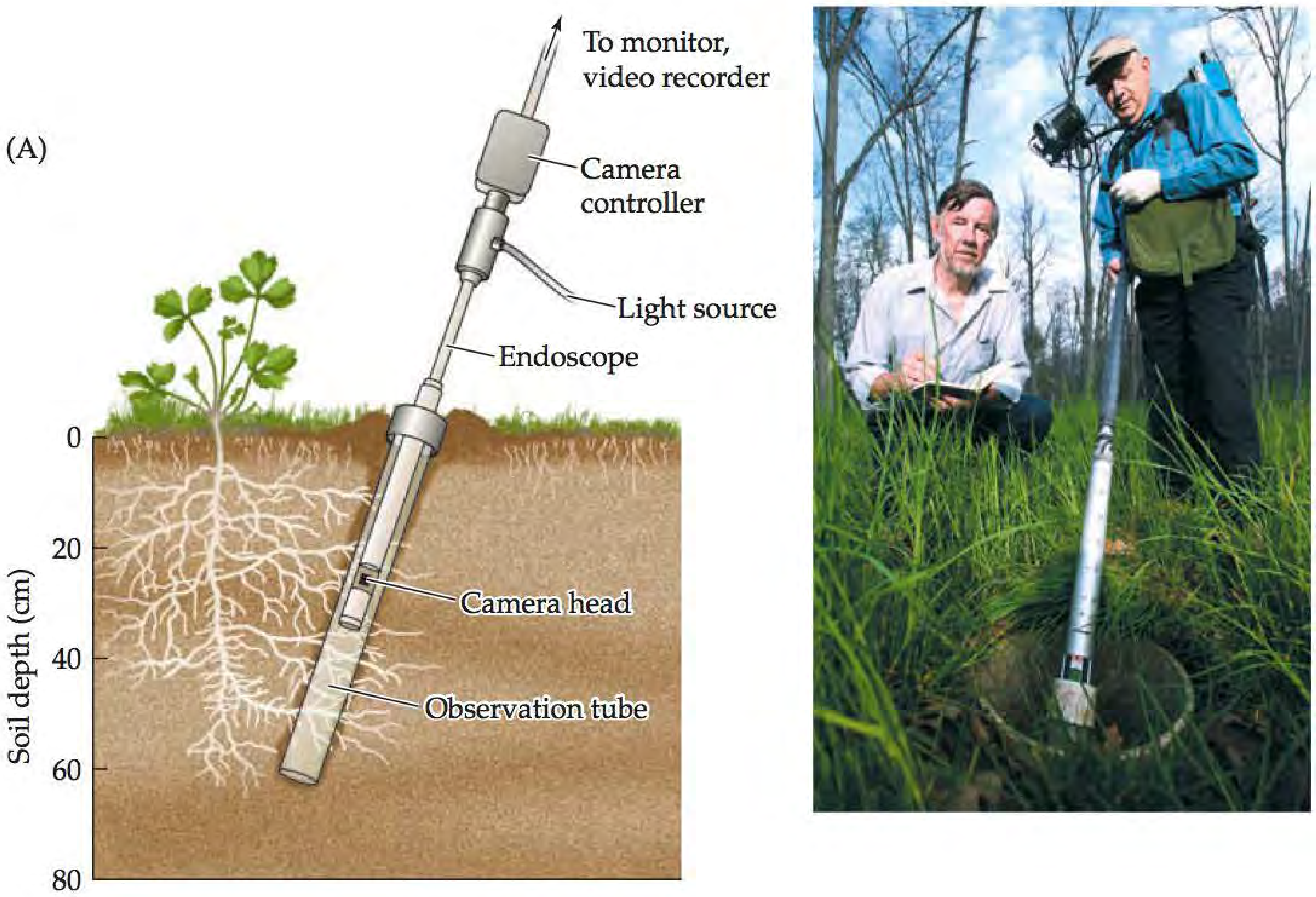
TERRESTRIAL ECOSYSTEMS Methods for estimating NPP in forest and grassland ecosystems are the best developed because of the economic importance of these ecosystems for wood and forage production. Traditional techniques measure the increase in plant biomass during the growing season by harvesting plant tissues in experimental plots, measuring biomass, and scaling the results up to the ecosystem level. For example, in temperate grassland ecosystems, the aboveground biomass can be harvested from plots at the start of the growing season and again when the amount of plant biomass reaches its maximum. The difference in plant biomass between the two harvests is used as an estimate of NPP. In forests, the radial growth of wood must be included in estimates of NPP. In the tropics, plants may continue to grow throughout the year, and tissues that die decompose rapidly, making the use of harvest techniques problematic. Despite these shortcomings, harvest techniques still provide reasonable estimates of aboveground NPP, particularly if corrections are made for tissue loss to herbivory and mortality.

Measuring the allocation of NPP to growth belowground is more difficult because root growth is more dynamic than the growth of leaves and stems. The proportion of NPP in roots exceeds that in aboveground tissues in some ecosystems: in grassland ecosystems, for example, root growth may be twice that of aboveground leaves, stems, and flowers combined. The finest roots *turn over* more quickly than shoots; that is, more roots are "born" and die during the growing season than stems and leaves. In addition, roots may exude a large amount of carbon into the soil, and they may transfer carbon to mycorrhizal or bacterial symbionts. Therefore, harvests for measuring root biomass must be more frequent, and additional correction factors must be used when estimating belowground NPP. Proportional relationships correlating aboveground to belowground NPP have been developed for some forest and grassland ecosystems so that measurements of aboveground NPP can be used to estimate whole-ecosystem NPP. The use of *minirhizotrons*, underground viewing tubes outfitted with video cameras, has led to advances in the understanding of belowground production processes (**Figure 20.6**).

The labor-intensive and destructive nature of harvest techniques makes them impractical for estimating NPP over large areas or in biologically diverse ecosystems. Several nondestructive techniques have been developed that allow more frequent estimation of NPP over much larger spatial scales, although with lower precision than harvest techniques. Some of these techniques, which include remote sensing and atmospheric CO_2 measurements, provide a quantitative index rather than an absolute measure of NPP. Some techniques use a combination of data collection and modeling of plant physiological and climate processes to estimate the actual fluxes of carbon associated with NPP.

The concentration of the photosynthetic pigment chlorophyll in a plant canopy provides a proxy for photosynthetic biomass that can be used to estimate GPP and NPP. Chlorophyll concentrations can be estimated using remote sensing techniques that rely on the reflection of solar radiation (**Ecological Toolkit 20.1**). Remote sensing allows NPP to be measured frequently, at spatial scales up to the entire globe, using satellite-based sensors (**Figure 20.7**). Indicators of NPP that are based on chlorophyll concentrations can overestimate NPP if the vegetation is not physiologically active, as in boreal forests in winter, but remote sensing generally provides the best estimate for NPP at regional to global scales.

NPP can also be estimated from direct measurements of its components: GPP and plant respiration. This approach typically involves measuring the change in CO_2



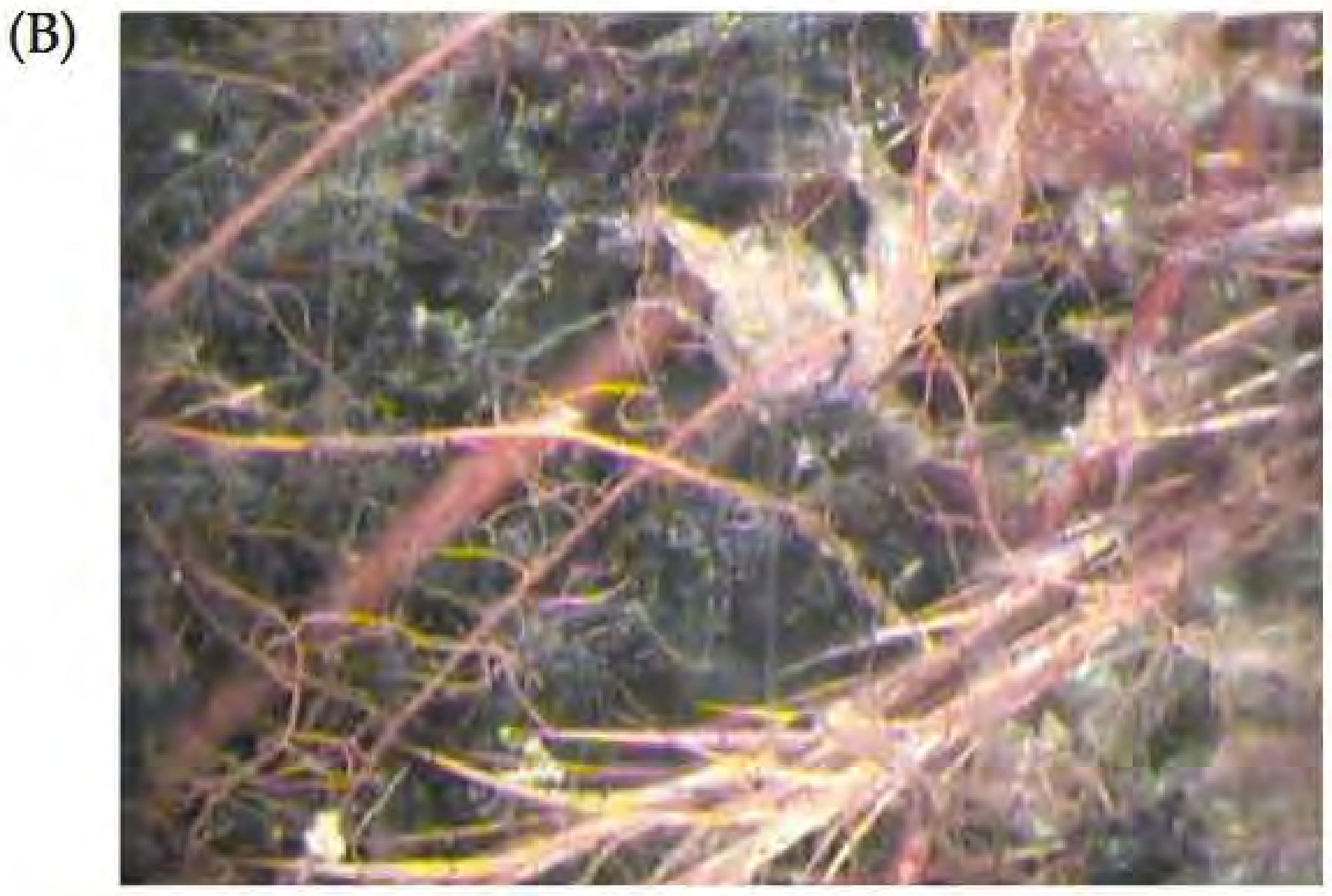
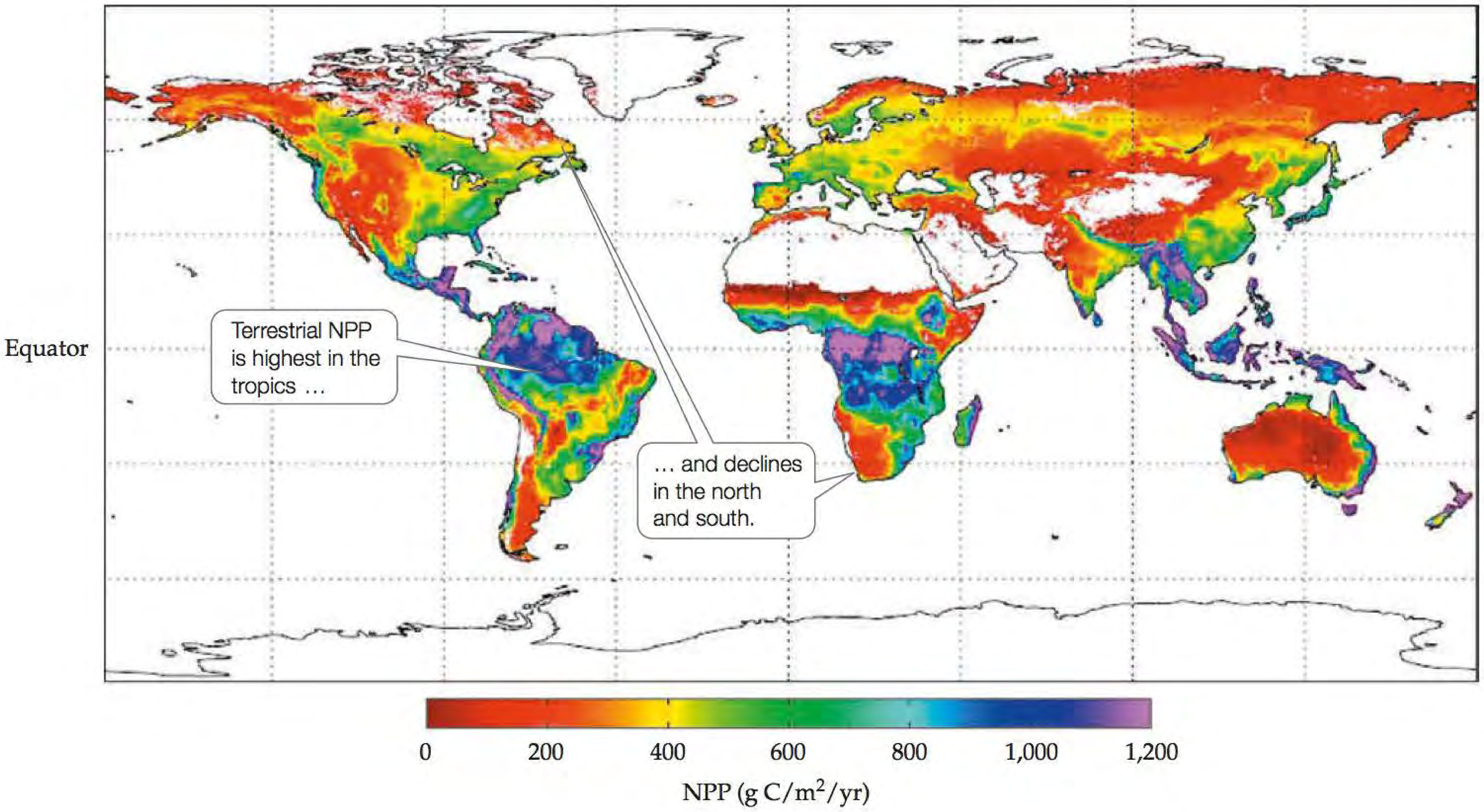


Figure 20.6 A Tool for Viewing Belowground Dynamics (A) Minirhizotrons allow researchers to observe the dynamics of root growth and death belowground. (B) A view of roots from a minirhizotron tube installed in a bog ecosystem in Northern Minnesota (www.mnspruce.ornl.gov). Small-diameter roots from ericaceous shrubs can be seen in the foreground against a background of decomposing *Sphagnum* mosses and peat. (B courtesy of Joanne Childs and Colleen Iversen, Oak Ridge National Laboratory.)

concentration in a closed system, which can be created by placing a chamber around stems and leaves, whole plants, or whole stands of plants. For example, Howard Odum estimated NPP for a tropical forest in Puerto Rico by enclosing a stand of trees inside a 200 m^2 × 20 m tall clear plastic "tent" (Odum and Jordan 1970). The emissions of CO_2 to the atmosphere in such a closed system are from respiration by the plants and heterotrophs, including microorganisms in the soil and animals in the forest. Uptake of CO_2 from the atmosphere results from photosynthesis. Thus, the net change in CO_2 inside the system results from the balance between GPP and total respiratory release by the plants and the heterotrophs. This net

Figure 20.7 Remote Sensing of Terrestrial NPP Global terrestrial NPP for the period 2000–2005, estimated using a satellite-based sensor [Moderate Resolution Imaging Spectroradiometer (MODIS)]. Note the latitudinal patterns in NPP corresponding to climate zones. (From Zhao et al. 2006.)



ECOLOGICAL TOOLKIT 20.1 Remote Sensing

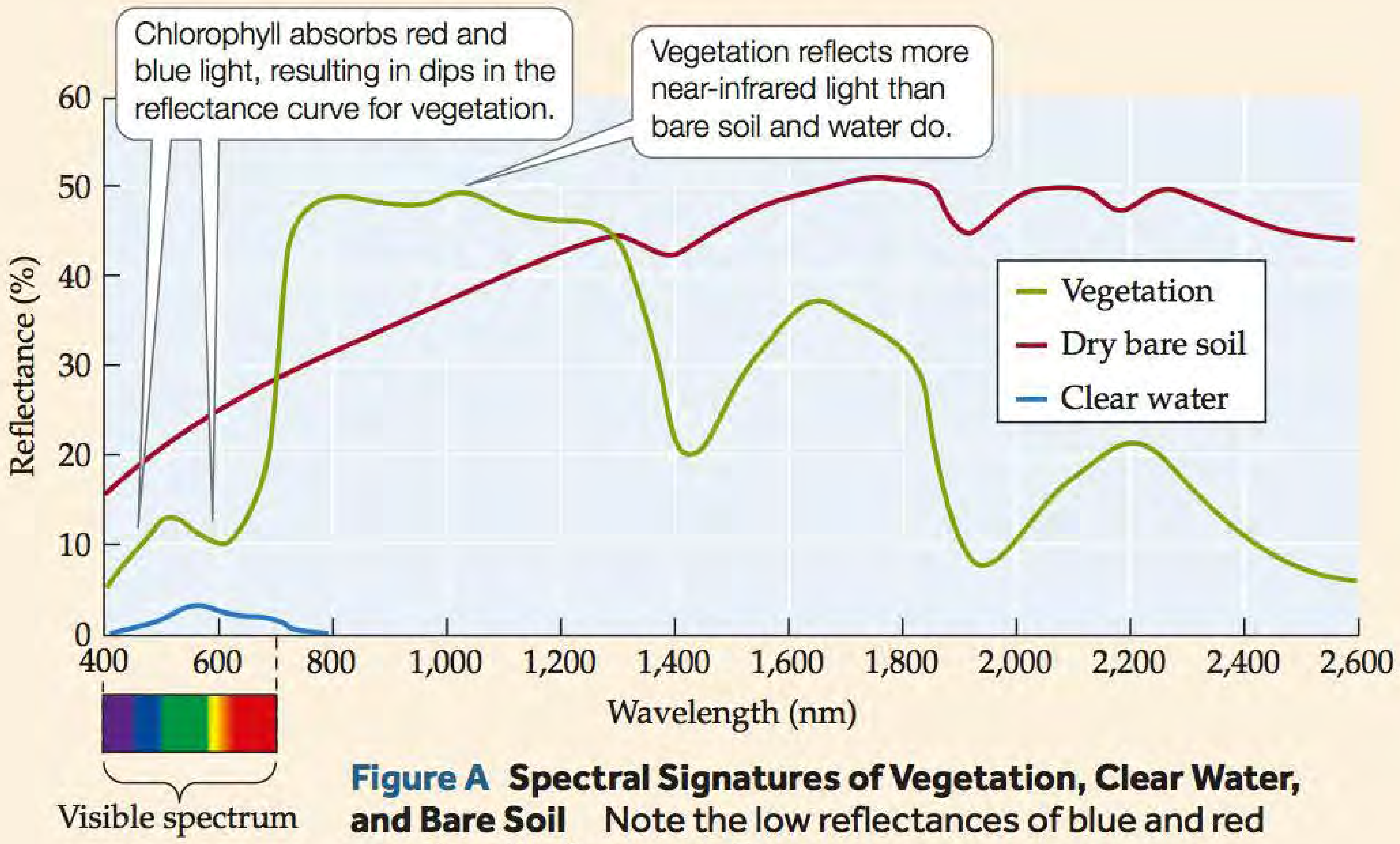


Figure A Spectral Signatures of Vegetation, Clear Water, and Bare Soil Note the low reflectances of blue and red wavelengths for vegetation.

When sunlight strikes an object, it is absorbed or scattered in such a way that the amount and quality of the light that reflects off of the object is changed. For example, when sunlight strikes a clear lake, about 5% of the visible light is reflected, while a light-colored sandy soil, such as might be found in a desert, reflects back as much as 40%. The amount of light reflected depends on the wavelengths of the light: different kinds of objects absorb or reflect some wavelengths more than others. The atmosphere scatters more blue wavelengths than red or green, and therefore the sky appears blue to our eyes. The lake, however, appears blue because most of the red and green light is absorbed by the water before it can be scattered back to our eyes. Lakes with high concentrations of phytoplankton appear green because much of the blue light is absorbed by the phytoplankton, leaving only the green light to be scattered back to our eyes.

Remote sensing is a technique that takes advantage of light reflection and absorption to estimate the density and composition of objects on Earth's surface, in its waters, and in its atmosphere. Ecologists use remote sensing to estimate NPP by taking advantage of the unique reflectance pattern of chlorophyll-containing plants, algae, and bacteria (**Figure A**). Because chlorophyll absorbs visible solar radiation in blue and red wavelengths, it has a characteristic *spectral signature* with greater reflection of green wavelengths. In addition, vegetation absorbs more light of red wavelengths than do bare soil or water.

Ecologists can measure the reflection of specific wavelengths from a land or water surface and estimate NPP using several indices that have been developed. One of the most commonly used indices is the *normalized difference vegetation index*, or NDVI, which uses differences between visible-light and near-infrared reflectance to estimate the density of chlorophyll:

$$\text{NDVI} = \frac{(\text{NIR} - \text{red})}{(\text{NIR} + \text{red})}$$

where NIR is the near-infrared wavelength band (700–1,000 nm) and red is the red wavelength band (600–700 nm). Note that the spectral signature of vegetation in Figure A shows a large difference between reflectance of red and near-infrared wavelengths relative to the spectral signatures of water and soil, which gives vegetation a high NDVI value and water and soil low NDVI values. The NDVI is coupled with estimates of the efficiency of light absorption to estimate photosynthetic CO_2 uptake.

Remote sensing of light reflectance from Earth's surface and atmosphere can be done at large spatial scales using satellites (**Figure B**), which transmit their measurements to receiving stations. Depending on the spatial resolution of the surface measurement and the number of wavelengths measured, satellite remote sensing can generate massive amounts of data that need to be processed. Advances in computing power have enhanced the spatial and temporal capabilities of remote sensing, making it a powerful tool for measuring NPP as well as deforestation, desertification, atmospheric pollution, and many other phenomena of interest to ecologists.

Figure B Remote Sensing by Satellite Remote sensing instruments mounted on satellites can measure the reflectance of solar radiation from Earth to provide ecologists with large-scale measurements of NPP and other phenomena.

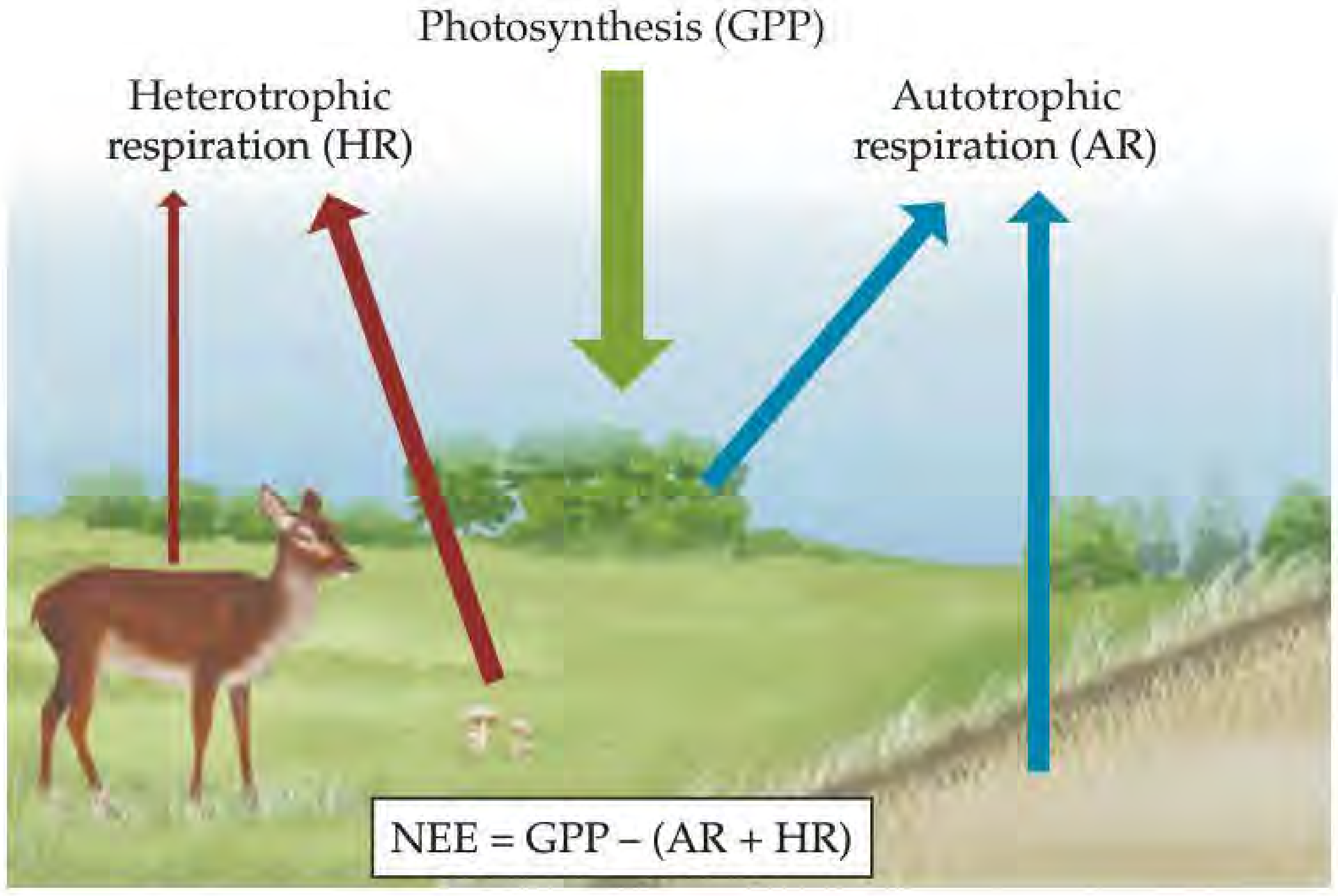


Figure 20.8 Components of Net Ecosystem Exchange (NEE) Net ecosystem exchange includes all of the components of an ecosystem that either take up CO_2 (autotrophs, through photosynthesis) or release CO_2 (both autotrophs and heterotrophs).

exchange of CO_2 is called **net ecosystem exchange** (**NEE**) (**Figure 20.8**). Heterotrophic respiration must be subtracted from NEE to obtain NPP; as a result, NEE provides a more refined estimate of ecosystem carbon storage than NPP. Carbon movement into and out of ecosystems, such as carbon lost through leaching from the soil or through disturbances (e.g., fire or deforestation; **Analyzing Data 20.1**) can influence estimates of NEE and NPP.

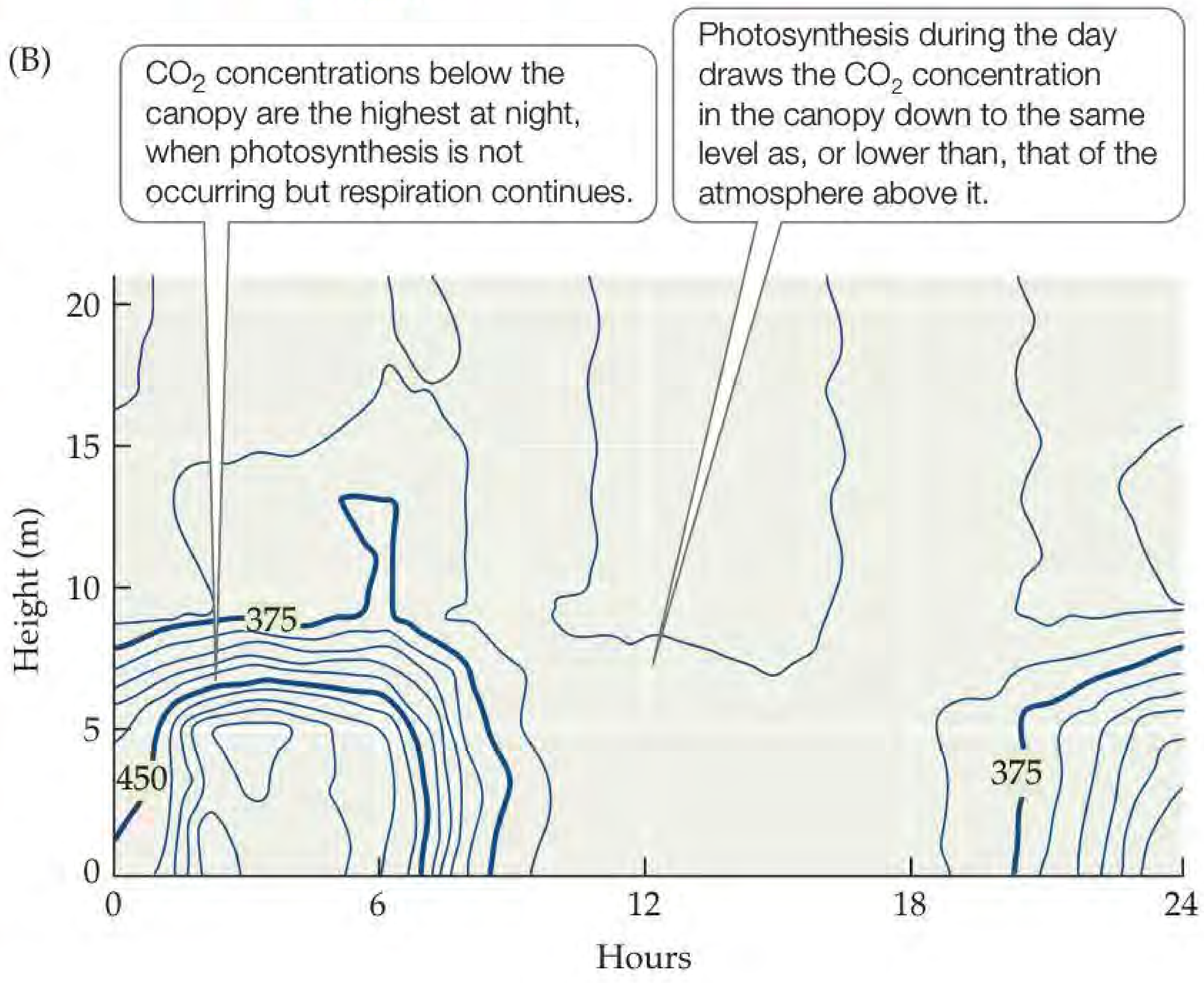
Another noninvasive approach to estimating NEE uses frequent measurements of CO_2 and microclimate at various heights throughout a plant canopy and into the open air above the canopy. This technique, known as *eddy covariance* or *eddy correlation*, takes advantage of the gradient in CO_2 concentration between the plant canopy and the atmosphere that develops because of photosynthesis and respiration. During the day, when plants are photosynthetically active, the concentration of CO_2 is lower in the plant canopy than in the air above the plant canopy. At night, when photosynthesis shuts down but respiration continues, the CO_2 concentration in the canopy is higher than that in the atmosphere. Instrument-bearing towers established in forest, shrubland, and grassland canopies have been used to measure the NEE of CO_2 over long periods (**Figure 20.9**). Depending on the tower height, eddy covariance can provide an integrated NEE for up to several square kilometers of the surrounding area. A network of eddy covariance sites in the Americas (Ameriflux: www.ameriflux.lbl.gov) has been established to help researchers better understand the uptake and fate of carbon in terrestrial ecosystems and how carbon uptake is influenced by climate.

Figure 20.9 Eddy Covariance Estimates of NEE (A) A tower projecting above a subalpine forest on Niwot Ridge, Colorado. Instruments attached to the tower measure the microclimate (temperature, wind speed, radiation) and atmospheric CO_2 concentrations at frequent intervals. These measurements are used to estimate net ecosystem exchange of CO_2. (B) Concentrations of CO_2 (in parts per million) from the ground surface to above the canopy in a boreal forest in Siberia, measured over the course of a 24-hour period in the summer. Average canopy height was 16 m. (B after Hollinger et al. 1998.)

? What would the daily pattern of CO_2 concentrations look like during the summer in a community made up primarily of cacti?

(A)

(B)



CO_2 concentrations below the canopy are the highest at night, when photosynthesis is not occurring but respiration continues.

Photosynthesis during the day draws the CO_2 concentration in the canopy down to the same level as, or lower than, that of the atmosphere above it.

ANALYZING DATA 20.1 Does Deforestation Influence Atmospheric CO_2 Concentrations?

We know that on a yearly basis trees take up large amounts of CO_2 from the atmosphere, converting it through photosynthesis to fixed carbon. We also know that occasionally large numbers of trees succumb to fire, insect predation, diseases, and human activities. What effect, if any, might this deforestation have on atmospheric concentrations of CO_2? Two studies shed light on this question.

Over the past decade, mountain pine beetles (*Dendroctonus ponderosae*) killed millions of trees throughout western North America. Kurz et al. (2008)* studied the effects of a massive beetle infestation in British Columbia, Canada. The team measured and estimated NPP and heterotrophic respiration before and after the outbreak. Use their data (below) to answer Questions 1 and 2.

	NPP[a]	HETEROTROPHIC RESPIRATION[a]
Before outbreak	440	408
After outbreak	400	424

[a] In g C/m^2/yr

1. Prior to the mountain pine beetle outbreak, was the forest taking up more CO_2 than it was releasing? In other words, was the forest a sink or a source of CO_2 for the atmosphere?
2. Was the forest a sink or a source of atmospheric CO_2 following the outbreak? Would you expect this trend in net carbon exchange with the atmosphere to change over the next 100 years?

Trees are also being lost at a high rate from the tropical rainforest biome, in this case because of land use change (see Concept 3.1). The ongoing conversion of tropical rainforest to pasture by humans is altering the NEE of this biome. In a study that compared the NEE of a tropical pasture with that of second-growth tropical rainforest in Panama, Wolf et al. (2011)† obtained the following data, which you can use to answer Questions 3 and 4.

	GPP[a]	TOTAL RESPIRATION[a] (AUTOTROPHIC + HETEROTROPHIC)
Pasture	2,345	2,606
Second-growth forest	2,082	1,640

[a] In g C/m^2/yr

3. What is the NEE for the tropical pasture? For the second-growth forest?
4. As noted in Table 20.1, today the tropical forest biome accounts for 35% of terrestrial NPP. The NEE of Earth's total land surface accounts for a net uptake of 3 petagrams (3×10^{15} grams) of carbon each year. Given these considerations, use the NEE figures you obtained for Question 3 to determine how much less annual global carbon uptake there would be if half of the existing tropical forest were converted to pasture. (Assume that the numbers from the Wolf et al. study represent the average conditions for undisturbed tropical forest and tropical pasture.)

---

*Kurz, W. A. and 7 others. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452: 987–990.

†Wolf, S., W. Eugster, C. Potvin, B. L. Turner and N. Buchmann. 2011. Carbon sequestration potential of tropical pasture compared with afforestation in Panama. *Global Change Biology* 17: 2763–2780.

See the companion website for a similar ANALYZING DATA exercise.

AQUATIC ECOSYSTEMS The dominant autotrophs in both freshwater and marine ecosystems are phytoplankton, including algae and cyanobacteria. These organisms have much shorter life spans than terrestrial plants, so the biomass present at any given time is very low compared with NPP; therefore, harvest techniques are not used to estimate NPP for phytoplankton, although they can be used for seagrasses and macroalgae. Instead, rates of photosynthesis and respiration are measured in water samples collected in bottles and incubated at the collection site with light (for photosynthesis) and without light (for respiration). The difference between the two rates is equal to GPP. Although there are errors associated with the artificial environment of the bottles, as well as the inclusion of respiration by heterotrophic bacteria and zooplankton in the bottles, this technique is used widely in freshwater and marine ecosystems.

Remote sensing of chlorophyll concentrations in the oceans using satellite-based instruments provides good estimates of marine NPP (**Figure 20.10**). As described for terrestrial remote sensing, indices based on absorption and reflection of light of different wavelengths are used to indicate how much light is being absorbed by chlorophyll, which is then related to NPP by using a light utilization coefficient, a term that incorporates the efficiency of light absorption into photosynthetic CO_2 uptake.

As Figure 20.7 shows, there can be as much as a 50-fold difference in NPP between Arctic and tropical ecosystems. In the following section we will investigate the role of abiotic and biotic factors that influence differences in NPP among ecosystems.

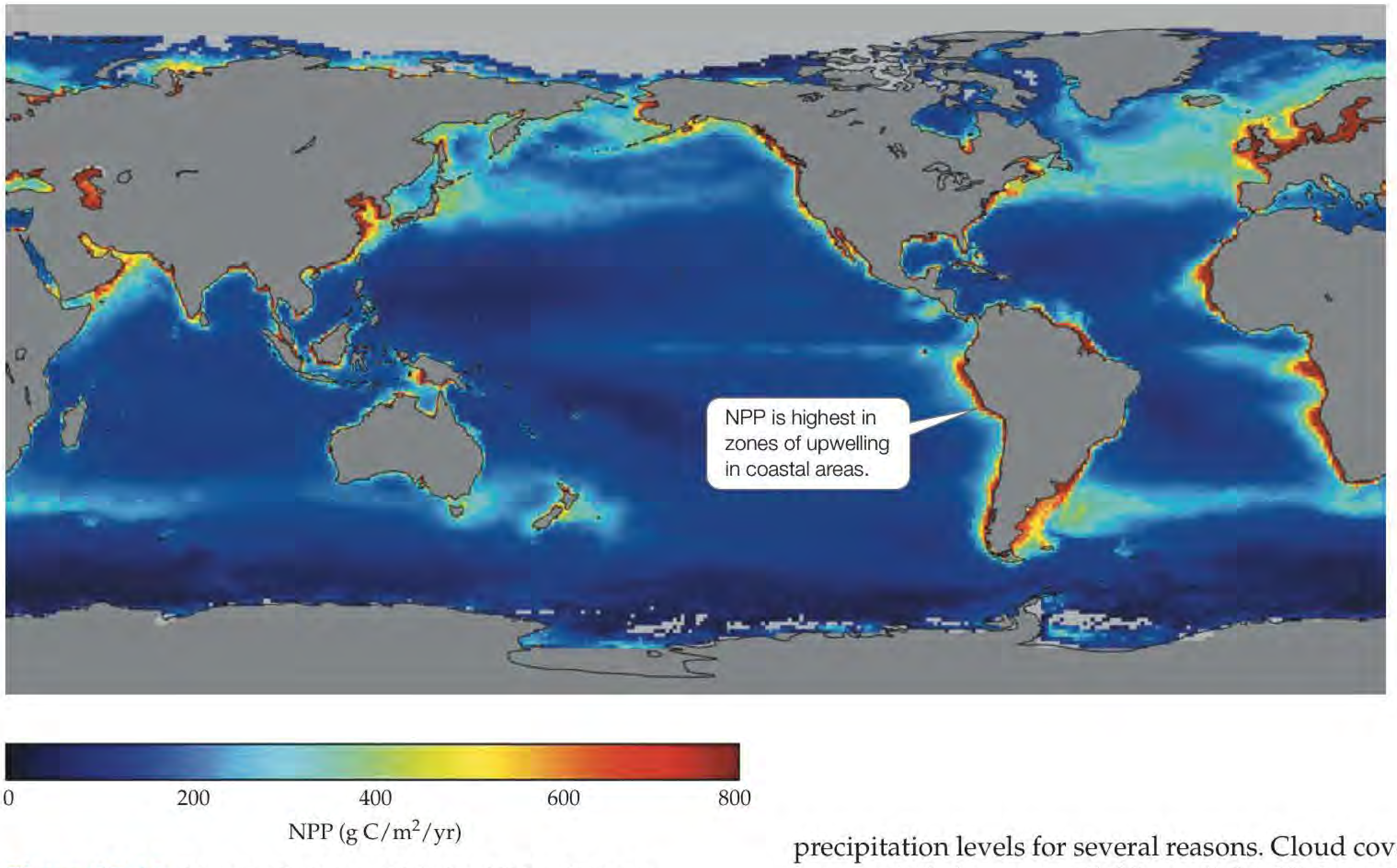


Figure 20.10 Remote Sensing of Marine NPP Primary production in the oceans, estimated using a satellite-based sensor [Sea-viewing Wide Field-of-view Sensor (SeaWiFS)].

? In addition to zones of upwelling, what other kinds of coastal areas with high rates of NPP might be visible in this image?

CONCEPT 20.2

Net primary production is constrained by both physical and biotic environmental factors.

Environmental Controls on NPP

As we have seen, NPP varies substantially over space and time. Much of this variation is associated with differences in climate, such as the latitudinal gradients in temperature and precipitation discussed in Concept 2.3. In this section, we explore the factors that constrain rates of NPP.

NPP in terrestrial ecosystems is controlled by climate

Variation in terrestrial NPP at the continental to global scales correlates with variation in temperature and precipitation. NPP increases as average annual precipitation increases up to a maximum of about 2,400 mm per year, after which it decreases in some ecosystems (e.g., highland tropical forests), but not in others (e.g., lowland tropical forests) (**Figure 20.11A**). NPP may decrease at very high precipitation levels for several reasons. Cloud cover over long periods lowers available sunlight. High amounts of precipitation leach nutrients from soils, and high soil water content results in hypoxic conditions that cause stress for both plants and decomposers.

NPP increases with average annual temperature (**Figure 20.11B**). This does not mean, however, that ecosystem carbon storage (NEE, discussed earlier) does the same. The loss of carbon from ecosystems due to respiration of heterotrophic organisms also increases at warmer temperatures, so NEE may potentially decrease. Several lines of evidence suggest that climate change over the past decades has changed NEE in some ecosystems. For example, tundra sites that were once carbon *sinks* (with GPP greater than carbon loss due to respiration) are now carbon *sources* (with respiratory carbon loss greater than GPP). These changes are increasing CO_2 losses to the atmosphere, as **Online Climate Change Connection 20.1** explains.

These correlations of NPP with climate suggest that NPP is directly linked to water availability and temperature. Such links make sense when we consider the direct influence of water availability on photosynthesis via the opening and closing of stomates and the influence of temperature on the enzymes that facilitate photosynthesis (see Concept 5.2). In deserts and in some grassland ecosystems, water availability has a clear, direct influence on NPP. In other ecosystems where water limitation is not as severe, the causal connection between precipitation and NPP is less clear.

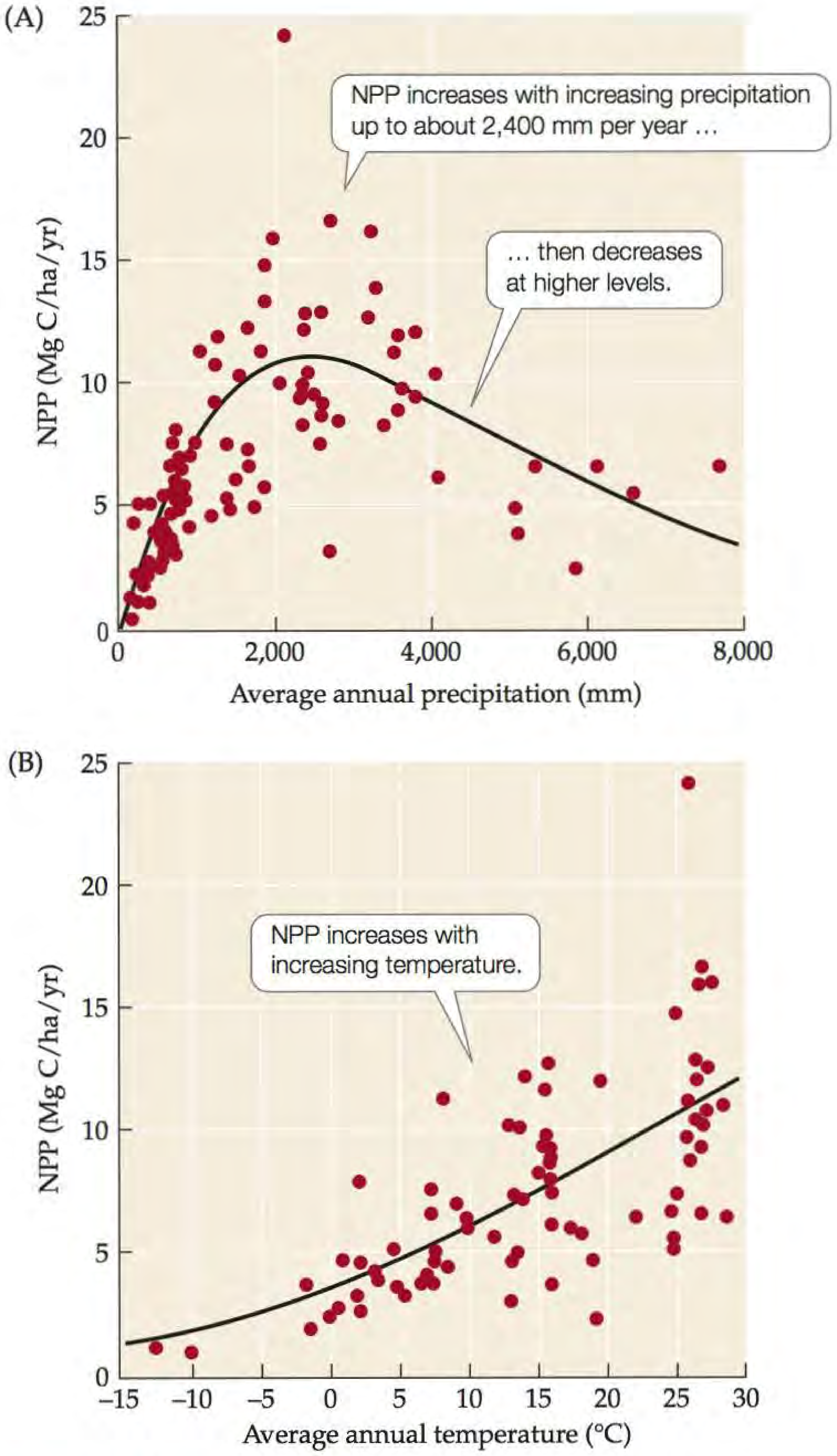


Figure 20.11 Global Patterns of Terrestrial NPP Are Correlated with Climate The graphs show the relationships between NPP and (A) precipitation and (B) temperature in terrestrial ecosystems worldwide. (Mg = 10^6 g.) (After Schuur 2003.)

The links between climate and NPP may also be indirect, mediated by factors such as nutrient availability or the particular plant species found within an ecosystem. How can we detect whether the influence of climate on NPP is direct or indirect? Several approaches, both observational and experimental, have been used. William Lauenroth and Osvaldo Sala examined how NPP in a short-grass steppe ecosystem responded to year-to-year variation in precipitation (Lauenroth and Sala 1992). They also examined the average annual NPP and precipitation across several grassland ecosystems at different locations in the central United States. When they compared the correlations between NPP and precipitation in their two analyses, they found that NPP increased more as precipitation increased for the site-to-site comparison than for the comparison among years in the short-grass steppe (**Figure 20.12**). They attributed the difference in the response of NPP to precipitation to variation in plant species composition among the grasslands. Some grass species have a greater inherent capacity than others to respond to enhanced water availability with growth, associated with greater ability to produce new shoots and flowers. Lauenroth and Sala also suggested that there was a time lag in the response to increased precipitation in the short-grass steppe ecosystem; that is, the increase in NPP in response to an increase in precipitation did not occur in the same year, but was delayed one to several years. Within the grassland biome, differences in the abilities of species to respond to climate variation can contribute to site-to-site variation in NPP, influencing the correlation between climate and NPP among sites.

Experimental manipulations of water, nutrients, carbon dioxide, and plant species composition have been used to examine the direct influence of those factors on NPP. The results of numerous experiments indicate that nutrients, particularly nitrogen, control NPP in terrestrial ecosystems. For example, William Bowman, Terry Theodose, and their colleagues used a fertilization experiment in alpine communities of the southern Rocky Mountains to determine whether the supply of nutrients limits NPP (Bowman et al. 1993). They knew that spatial differences in NPP among alpine communities were correlated with differences in soil water availability, as in the grassland ecosystems described

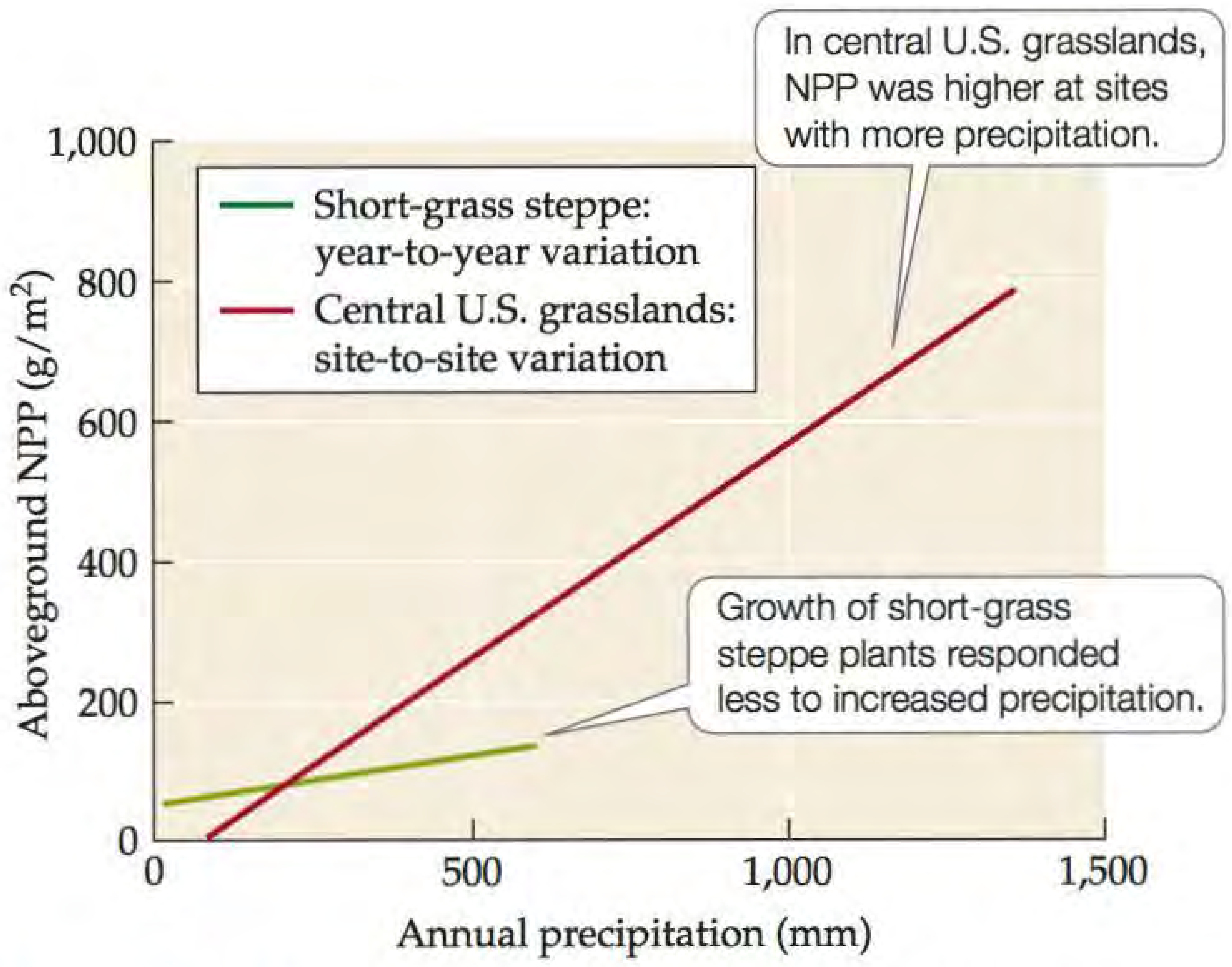
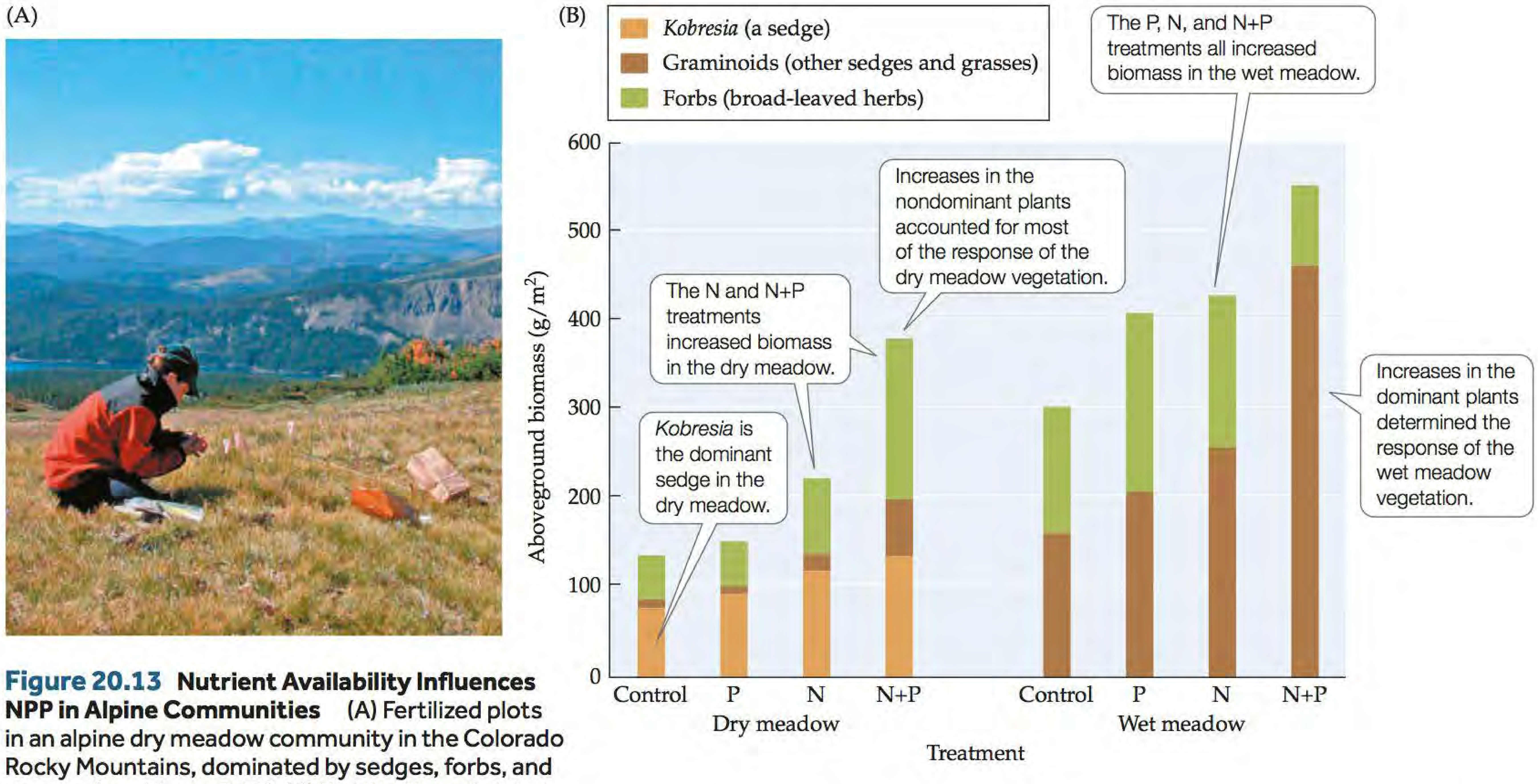


Figure 20.12 The Sensitivity of NPP to Changes in Precipitation Varies among Grassland Ecosystems The relationship between aboveground NPP and precipitation is shown for a short-grass steppe ecosystem and for several grassland ecosystems of different types at different sites in the central United States. (After Lauenroth and Sala 1992.)



The P, N, and N+P treatments all increased biomass in the wet meadow.

Increases in the nondominant plants accounted for most of the response of the dry meadow vegetation.

The N and N+P treatments increased biomass in the dry meadow.

Kobresia is the dominant sedge in the dry meadow.

Increases in the dominant plants determined the response of the wet meadow vegetation.

Figure 20.13 Nutrient Availability Influences NPP in Alpine Communities (A) Fertilized plots in an alpine dry meadow community in the Colorado Rocky Mountains, dominated by sedges, forbs, and grasses (see Figure 3.11). (B) Fertilization of plots in a resource-poor dry meadow and a resource-rich wet meadow with nitrogen (N), phosphorus (P), and both N and P showed that nutrient availability limits NPP. (B after Bowman et al. 1993.)

? In which community would you expect a higher proportion of belowground NPP? Would the allocation to belowground NPP change in response to fertilization?

above. Bowman and colleagues' fertilization experiment was performed in two communities, a nutrient-poor dry meadow and a more nutrient-rich wet meadow. They sought to determine whether the supply of nutrients influenced NPP and, if so, whether the response differed between the two communities. They added nitrogen or phosphorus or both nitrogen and phosphorus to different plots in both communities, and they maintained plots with no nutrient additions as controls. Their results indicated that the supply of nitrogen limited NPP in the dry meadow, while nitrogen and phosphorus both limited NPP in the wet meadow (**Figure 20.13**). An additional experiment indicated that the addition of water to the dry meadow did not increase NPP, despite the positive relationship between NPP and soil moisture across the communities. These results suggest that the correlation between soil moisture and NPP in these alpine communities does not indicate a direct causal relationship, but rather is determined by the effect of soil moisture on nutrient supply through its effects on decomposition and movement of nutrients in the soil (described in Concept 22.2).

Closer examination of Figure 20.13B shows that the increase in NPP was not uniform across all plant species groups. The dominant plant type of the alpine dry meadow (*Kobresia* spp.) did not increase its biomass as much as the less common sedge and grass species. The change in NPP in the dry meadow occurred largely as a result of a change in plant species composition within the experimental plots. This was not the case in the wet meadows, where the dominant sedges increased their growth more than the subdominant forb species. These results are consistent with the general trend of results from many fertilization experiments, which indicate that plant species from resource-poor communities have lower growth responses to fertilization than species from resource-rich communities. This apparent contradiction is the result of differences in the capacity of plant species to respond to fertilization. Plants of resource-poor communities tend to have low intrinsic growth rates, a characteristic that lowers their resource requirements. Plants of resource-rich communities tend to have higher growth rates, which make them better able to compete for resources, particularly light. Although NPP increases in nutrient-poor communities when they are fertilized, the change in plant species composition that occurs in many such experiments indicates that plant species composition can determine the intrinsic capacity of an ecosystem to increase its NPP when resources are increased (**Figure 20.14**). This study provides an example of the important roles that community dynamics can play in ecosystem function.

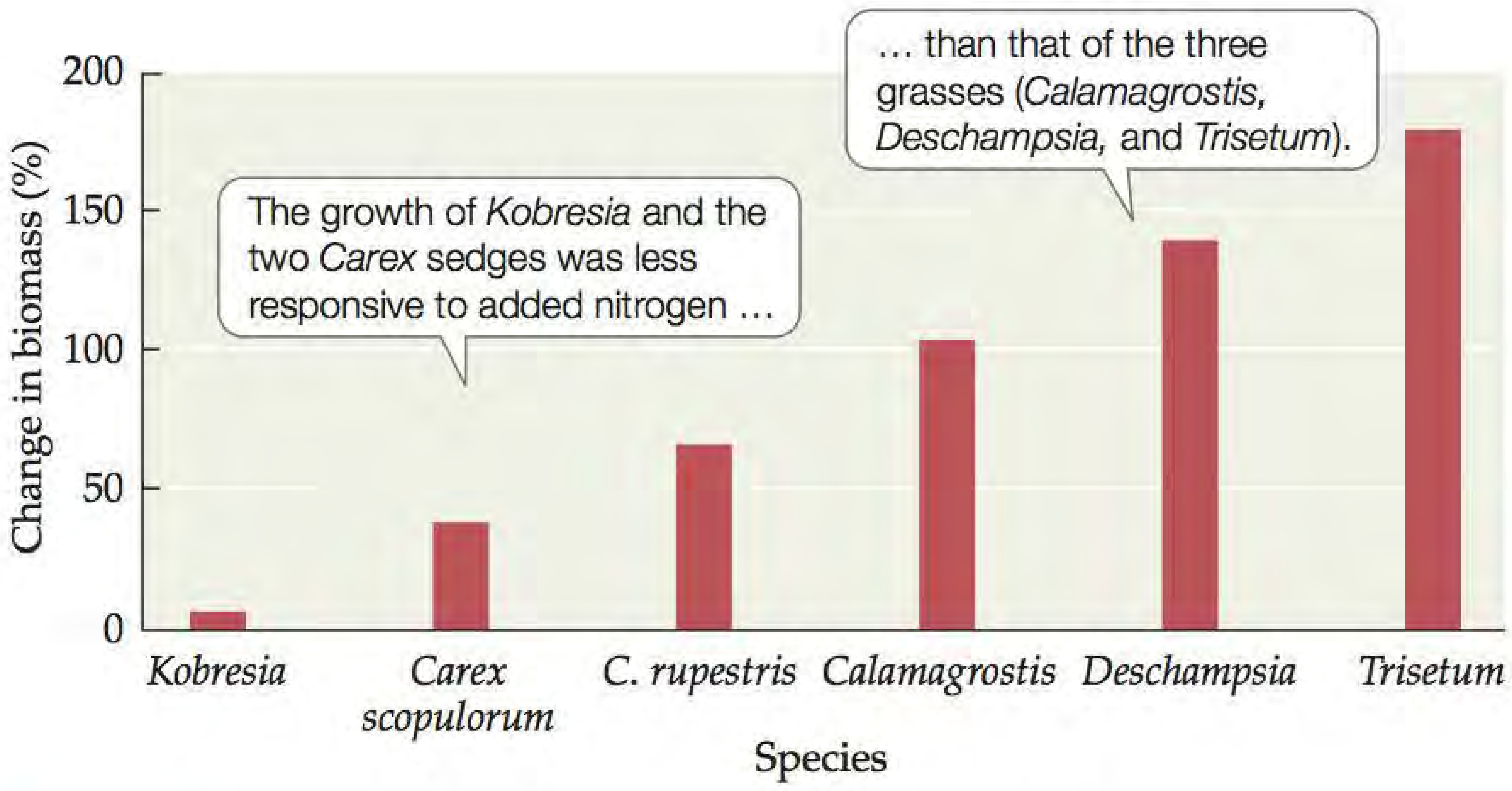


Figure 20.14 Growth Responses of Alpine Plants to Added Nitrogen The effect on plant growth of low to high nitrogen levels (with all other nutrients maintained at optimal concentrations) indicated that alpine plant species vary substantially in their ability to increase growth in response to an increase in nitrogen availability. (After Bowman and Bilbrough 2001.)

NPP is often limited by nutrients in nondesert terrestrial ecosystems. Some general differences among terrestrial ecosystem types have emerged from resource manipulation experiments and measurements of plant and soil chemistry. In lowland tropical rainforests, NPP is often limited by the supply of phosphorus, since the relatively old, leached tropical soils in which they grow are low in available phosphorus relative to other nutrients. Other nutrients, such as calcium and potassium, can also limit production in lowland tropical ecosystems. Montane tropical ecosystems, and most temperate and Arctic ecosystems, are limited by the supply of nitrogen, and occasionally by phosphorus. Even in some desert ecosystems, NPP is co-limited by water and nitrogen.

NPP in aquatic ecosystems is controlled by nutrient availability

The primary producers in lake ecosystems are phytoplankton and rooted macrophytes. NPP in lake ecosystems is often limited by the supply of both phosphorus and nitrogen, as we know not only from the results of experimental manipulations, but also from unintentional "experiments" set in motion by wastewater discharges into lakes (see Figure 22.18). A common approach to determining the response of NPP in lakes to changes in nutrient supply is to incubate translucent or open-top containers, sometimes referred to as "limnocorrals," of lake water, amended with one or more nutrients, in the lake (**Figure 20.15**). The NPP response is measured by changes in chlorophyll concentrations or numbers of phytoplankton cells.

One of the most convincing studies of the effect of nutrients on NPP in lakes was a series of whole-lake fertilization experiments by David Schindler (Schindler 1974). The experiments were initiated in 1969 in the Experimental Lakes Area in Ontario, a series of 58 small lakes set aside for experimental manipulations. Concern over declining water quality in the lakes of North America and Europe motivated Schindler and his colleagues to establish several experiments to determine whether inputs of nutrients in wastewater were involved in the dramatic increases in the growth of phytoplankton that had been observed. They added nitrogen, carbon, and phosphorus to all or half of several individual lakes. The results of these experiments provided strong evidence for phosphorus limitation of NPP (**Figure 20.16**). Massive increases in the abundances of cyanobacteria were responsible for the increase in NPP in response to phosphorus addition. Evidence for nitrogen limitation of NPP in high-elevation lakes, based on small-scale fertilization experiments and measurements of the ratio of nitrogen to phosphorus in the water, also exists (Elser et al. 2007).

NPP in streams and rivers is often low, and the majority of the energy in those ecosystems is derived from terrestrial organic matter (see Concept 21.1). Water movement limits the abundance of phytoplankton, except where the water velocity is relatively low. In Concept 3.2, we introduced the *river continuum concept*, which describes the increasing importance of in-stream NPP as the river flows downstream. Most of the NPP in streams and rivers comes from photosynthesis by macrophytes and algae attached to the bottom in shallow areas where there is enough light for photosynthesis. Suspended sediment in rivers can limit light penetration; thus, turbidity often controls NPP. Nutrients, particularly nitrogen and phosphorus, can also limit NPP in streams and rivers.

Marine NPP is usually limited by nutrient supply, but the specific limiting nutrients vary among marine

Figure 20.15 Limnocorral Fertilization Studies Student assistants add nutrients to an experimental enclosure in Redfish Lake, Idaho. The experiment tested whether nutrients stimulate NPP in the lake, in the hope of assisting the recovery of the endangered Snake River sockeye salmon (*Oncorhynchus nerka*).

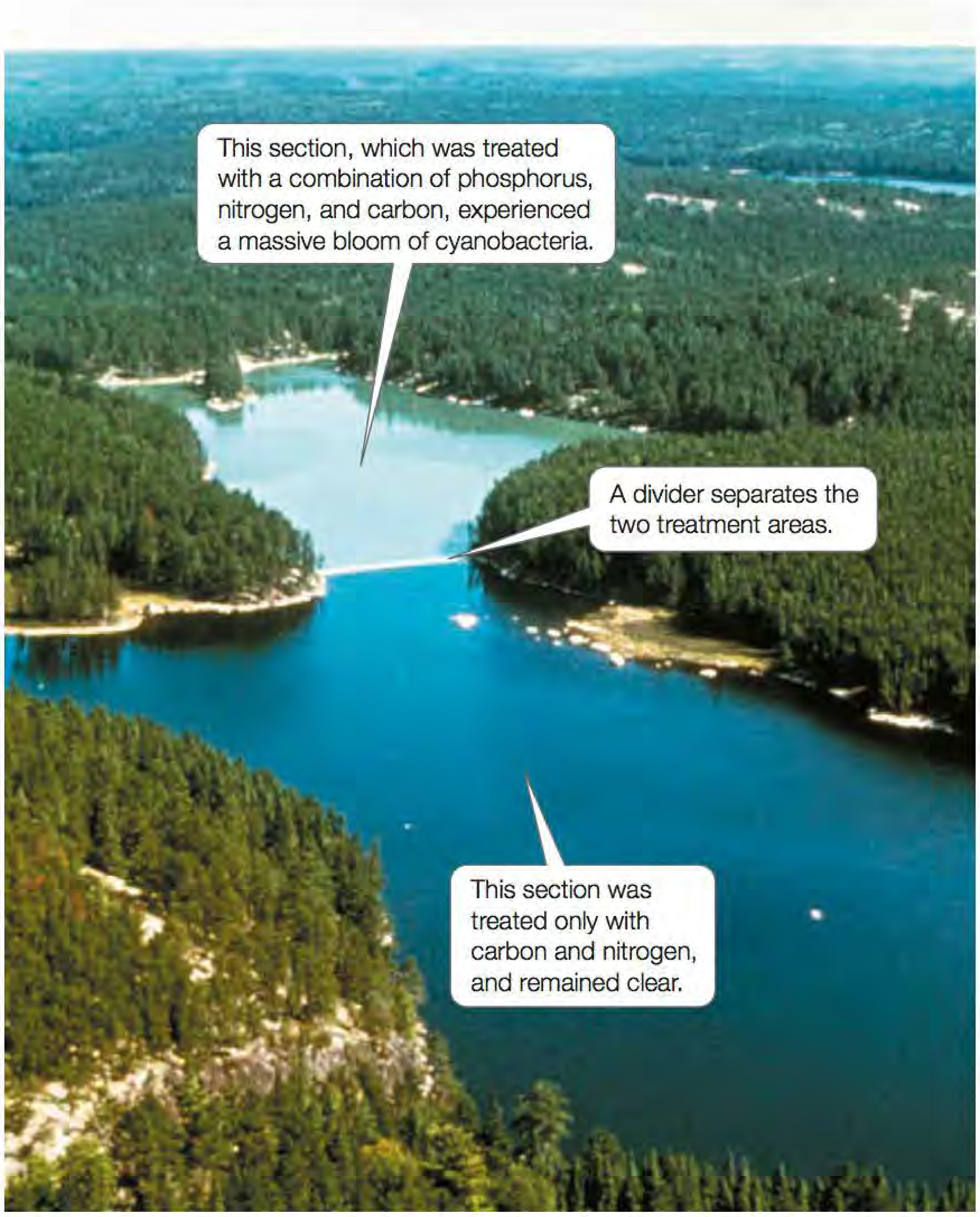


Figure 20.16 Response of a Lake to Phosphorus Fertilization Experimental Lake 226 was divided into two sections as part of David Schindler's experiments on the effects of nutrient availability on NPP.

ecosystem types. Estuaries, the zones where rivers empty into the ocean (see Concept 3.3), are rich in nutrients relative to other marine ecosystems. Variation in NPP among estuaries is correlated with variation in nitrogen inputs from rivers. Agricultural and industrial activities have increased riverine inputs of nitrogen into estuaries, which have caused periodic "blooms" of algae. These blooms have been implicated in the development of "dead zones"—areas of high fish and zooplankton mortality—in over 400 nearshore ecosystems worldwide.

NPP in the open ocean is derived primarily from phytoplankton, including a group referred to as the *picoplankton*, consisting of cells smaller than 1 μm. Picoplankton contribute as much as 50% of the total marine NPP. Smaller contributions come from floating mats of seaweeds such as *Sargassum*. Near the coast, kelp forests may have leaf area indices and rates of NPP as high as those of tropical forests. "Meadows" of seagrasses such as eelgrass (*Zostera* spp.) are also important contributors to NPP in shallow nearshore zones.

In much of the open ocean, NPP is limited by nitrogen. In the equatorial Pacific Ocean, however, detectable concentrations of nitrogen can be found in the water even when peak NPP occurs, suggesting that some other factor limits NPP. John Martin and colleagues measured the concentrations of nutrients in the open waters of the Pacific and performed bottle incubation experiments with added nutrients. They found that adding iron to the bottles increased NPP (Martin et al. 1994). Based on this evidence that iron limits NPP in some ocean regions, Martin suggested that aeolian (windblown) dust from Asia, a source of iron for the open ocean, could play an important role in the global climate system through its influence on marine NPP, and thus on atmospheric CO_2 concentrations. During glacial periods, large areas of the continents lacking vegetative cover could have contributed aeolian dust that would have fertilized the ocean. As NPP in marine ecosystems increased, those ecosystems might have taken up more CO_2 from the atmosphere, reducing its atmospheric concentration and serving as a positive feedback to cool the climate further. Martin suggested that these findings might be applied to address global warming, saying at the time, "Give me half a tankerload of iron, and I'll give you an Ice Age." He recommended the use of large-scale experiments to investigate the influence of iron on ocean NPP. Unfortunately, Martin died in 1993, before his ambitious experiments could be carried out.

Martin's colleagues subsequently performed the first of several experiments in 1993, adding iron sulfate to surface waters of the equatorial Pacific west of the Galápagos archipelago. This experiment was alternatively referred to as IronEx I or the "Geritol solution"[1] to global climate change. During IronEx I, a 64 km^2 area was fertilized with 445 kg of iron, which resulted in a doubling of phytoplankton biomass and a fourfold increase in NPP (**Figure 20.17**). Three other iron fertilization experiments were subsequently performed, one in 1995 (IronEx II), which produced a tenfold increase in phytoplankton biomass; a second in 1999 in the Southern Ocean; and the last in 2002, also in the Southern Ocean. While the iron limitation hypothesis has been strongly supported by these experiments, fertilizing large areas of the ocean is unlikely to provide a solution to increasing atmospheric CO_2 concentrations and global climate change. Some of the CO_2 taken up by phytoplankton is eventually reemitted to the atmosphere via respiration by zooplankton and bacteria that consume the phytoplankton. In addition, the iron is lost

---

[1] Geritol is a dietary supplement once widely believed to help cure "iron-poor, tired blood."

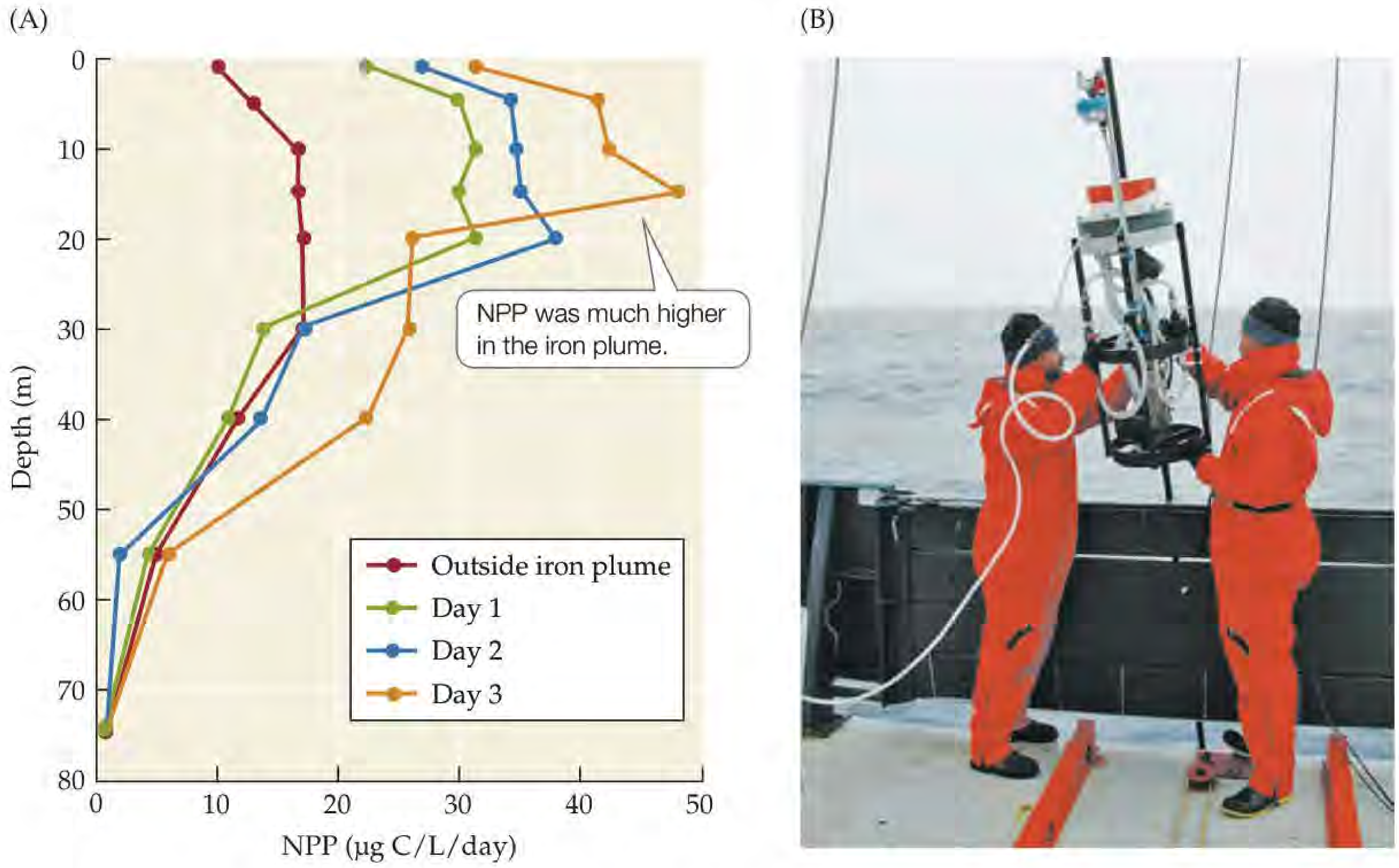


Figure 20.17 Effect of Iron Fertilization on Marine NPP IronEx I released a plume of iron into the equatorial Pacific Ocean to study the effects of iron fertilization on NPP. (A) This vertical profile shows primary production at various depths outside and inside the iron plume on three specific days: 1, 2, and 3 days following the release of the iron. (B) Researchers deploy a pump to add iron to the ocean. (A after Martin et al. 1994.)

relatively quickly from the surface photic zone, sinking to deeper layers where it is unavailable to support phytoplankton photosynthesis and growth. Iron fertilization on a large scale could also have detrimental effects on ocean biodiversity and could create large dead zones similar to those generated by nitrogen inputs into estuaries.

The development of remote sensing and eddy covariance techniques has improved our ability to discern global patterns of NPP. We'll examine those patterns in the next section.

CONCEPT 20.3

Global patterns of net primary production reflect climate constraints and biome types.

Global Patterns of NPP

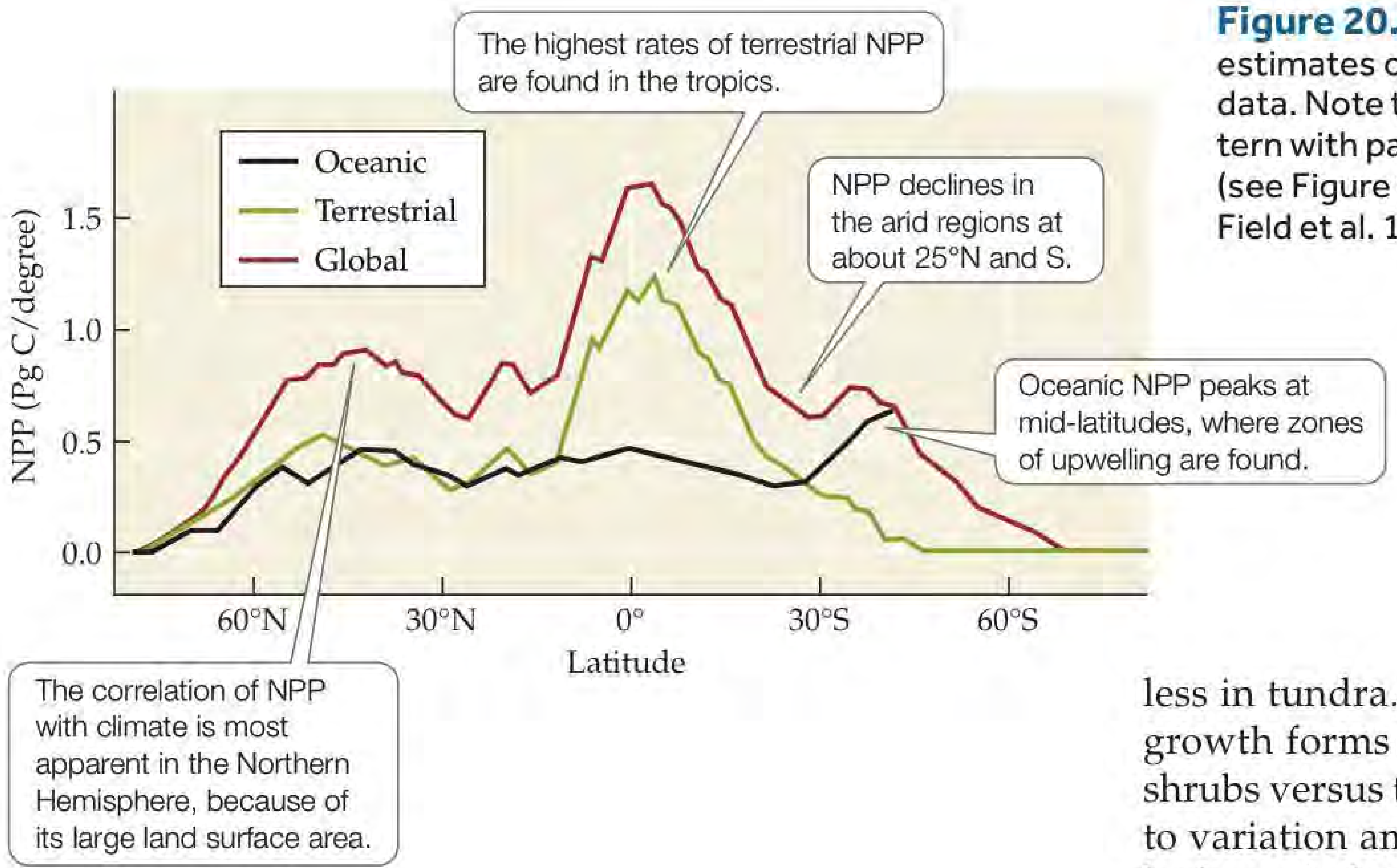
Which biomes and marine biological zones have the highest NPP and, as a consequence, the greatest effect on atmospheric CO_2 dynamics? Knowing how NPP varies at a global scale is key to understanding how biotic factors affect the global carbon cycle and how future changes in biomes could affect climate change (see Concept 25.1).

Initial estimates of global NPP were based on compilations of plot-level measurements from different biomes, scaled up using estimates of the spatial distributions of those biomes. These estimates were subject to error associated with the uncertainty of the actual area covered by each biome type, as well as with the potential for overestimating NPP if undisturbed, old-growth study plots were selected to represent a biome. Remote sensing data now give us rapid direct measurements of NPP, providing an estimate of Earth's capacity to take up CO_2 and its response to climate variation and climate change.

Terrestrial and oceanic NPP are nearly equal

Chris Field and colleagues estimated total planetary NPP to be 105 petagrams (1 Pg = 10^{15} g) of carbon per year, based on remote sensing data collected over multiple years (Field et al. 1998). They determined that 54% of this carbon is taken up by terrestrial ecosystems, while the remaining 46% is taken up by primary producers in the oceans. Their estimate of oceanic NPP (which comes to 48 Pg C/year) was considerably higher than previous estimates. Despite the similar contributions of land and oceans to total global NPP, the average rate of NPP on the land surface (426 g C/m^2/year) is higher than that in the oceans (140 g C/m^2/year). The lower rate in the oceans is compensated for by the greater percentage (70%) of Earth's surface they cover.

Most of the surface of both oceans and land is dominated by areas with relatively low NPP (see Figures 20.7 and 20.10). The highest rates of NPP on land are found in the tropics (**Figure 20.18**). This pattern results from latitudinal variation in climate and in the length of the growing season. Higher latitudes have shorter growing seasons, and low temperatures constrain nutrient supply by lowering decomposition rates, which in turn limits NPP. Tropical zones have long growing seasons and high rates of precipitation, promoting high rates of NPP. NPP declines to the north and south of the tropics at about 25°, reflecting the increasing aridity associated with the high-pressure zones generated by the descending air of the Hadley cells (see Concept 2.2). Another peak in terrestrial NPP



The highest rates of terrestrial NPP are found in the tropics.

NPP declines in the arid regions at about 25°N and S.

Oceanic NPP peaks at mid-latitudes, where zones of upwelling are found.

The correlation of NPP with climate is most apparent in the Northern Hemisphere, because of its large land surface area.

Figure 20.18 Latitudinal Variation in NPP These estimates of NPP are based on satellite remote sensing data. Note the strong correlation of the terrestrial pattern with patterns in global average annual temperature (see Figure 2.14) and precipitation (see Figure 2.16). (After Field et al. 1998.)

occurs at the northern mid-latitudes, where the temperate forest biome is found. NPP in the mid- to high latitudes shows strong seasonal trends, with peaks in summer and declines in winter. In contrast, seasonal trends in the tropics are often slight and are associated with wet–dry cycles.

Oceanic NPP peaks at the mid-latitudes between 40° and 60° (see Figure 20.18). These peaks are associated with zones of upwelling, areas where ocean currents bring nutrient-rich deep water to the surface (see Concept 2.2). High NPP is also associated with estuaries at these latitudes. Seasonal trends in NPP occur in the oceans, but their magnitude is less than on the land surface.

Differences among biomes in NPP reflect climate and biotic variation

It is not surprising that NPP varies among biomes, since biomes are associated with latitudinal climate variation. For example, the high NPP in the tropics is associated with tropical ecosystems, including forests, grasslands, and savannas. The low NPP at high latitudes is associated with boreal forests and tundra. Tropical forests and savannas contribute approximately 60% of terrestrial NPP (**Table 20.1**), or about 30% of total global NPP. In the oceans, zones of upwelling have high rates of NPP, but they cover less than 5% of the ocean surface. Coastal zones, including estuaries, account for approximately 20% of oceanic NPP, or about 10% of total global NPP. Despite its low rate of NPP, the vast area of the open ocean accounts for the majority of oceanic NPP and approximately 40% of total global NPP.

As noted in Concept 20.1, much of the variation in NPP among terrestrial biomes is associated with differences in leaf area index. In addition, the length of the growing season varies markedly among biomes, from year-round in some tropical ecosystems to 100 days or less in tundra. Variation associated with different plant growth forms (e.g., C_3 versus C_4 plants; grasses versus shrubs versus trees) is also important but contributes less to variation among biomes than do growing season and leaf area index. Variation in NPP among aquatic ecosystems, as we saw in Concept 20.2, is primarily related to variation in inputs of nutrients.

What happens to all of this NPP? In the next section, we will introduce some of the concepts associated with secondary production. We will cover energy flow among organisms and its consequences for population growth, community dynamics, and ecosystem function in Chapter 21.

CONCEPT 20.4

Secondary production is generated through the consumption of organic matter by heterotrophs.

Secondary Production

Energy that is derived from the consumption of organic compounds produced by other organisms is known as **secondary production**. Organisms that obtain their energy

TABLE 20.1 Variation in NPP among Terrestrial Biomes

BIOME	NPP (G C/M^2/YR)	TOTAL NPP (PG C/YR)	PERCENTAGE OF TERRESTRIAL NPP
Tropical forest	2,500	21.9	35
Tropical savanna	1,080	14.9	24
Temperate forest	1,550	8.1	13
Temperate grassland	750	5.6	9
Boreal forest	390	2.6	4
Temperate shrubland	500	1.4	2
Tundra	180	0.5	1
Desert	250	3.5	5
Crops	610	4.1	6

Source: Saugier et al. 2001.

in this manner are known as *heterotrophs*, and they include archaea, bacteria, fungi, animals, and even a few plants (see the Case Study in Chapter 14).

Heterotrophs are classified according to the type of food they consume. The most general categories, introduced in Concept 5.4, are **herbivores**, which consume plants and algae; **carnivores**, which consume live animals; and **detritivores**, which consume dead organic matter (*detritus*). Organisms that consume live organic matter from both plants and animals are called **omnivores**. Further refinement of feeding preferences is sometimes incorporated into the terminology used to describe heterotrophs; insect eaters, for example, are referred to as *insectivores*.

Heterotroph diets can be determined from the isotopic composition of food sources

Determining what heterotrophs eat may be as simple as watching them feed. Such observations, however, may be a time-consuming and imprecise exercise. Another option is examining their fecal material (scat), which can also be imprecise and not a pleasant task. An alternative method of determining a heterotroph's diet involves measuring stable isotopes (see Ecological Toolkit 5.1). The ratios of naturally occurring stable isotopes of carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$), and sulfur ($^{34}S/^{32}S$) differ among potential food items. Measurements of the isotopic composition of a heterotroph and its potential food sources can identify the food sources that make up its diet (Peterson and Fry 1987).

Isotopic measurements of preserved bone specimens have been used to study the diets of extinct animals as well as modern ones. One mystery in feeding ecology that was solved using isotopic measurements was the diet of European cave bears (*Ursus spelaeus*). Cave bears went extinct about 25,000 years ago, during the height of the last Ice Age. Cave bears were much larger than the temperate-zone bears of today, as much as triple the size of the modern grizzly bear (*Ursus arctos horribilis*) of North America. Examination of the teeth and the jaw structure of cave bears led some mammalogists to hypothesize that they were primarily herbivores. However, the fact that plants afford such a poor diet quality, as noted in Concept 5.4, led to skepticism about an herbivorous diet adequately sustaining such a massive bear. G. V. Hilderbrand and colleagues measured the C and N isotope composition of bone samples provided by museums from across the world (Hilderbrand et al. 1996). The samples included cave bears and the herbivores that occurred alongside them (woolly rhinoceros, woolly mammoth, horse, and aurochs, an ancestor of modern cattle). Hilderbrand and colleagues found that bones of cave bears had an isotopic composition different from that of Pleistocene herbivores (**Figure 20.19**). Using information about the isotopic composition of food sources, the researchers estimated that the average diet of cave bears consisted of 58% meat (range from 41% to 78%). This finding refuted the hypothesis that cave bears were primarily herbivores, indicating that the bulk of their diet was meat. In this and other studies, isotopic measurements have provided a useful tool for determining the diets of animals that is more accurate and integrative, and less time-consuming, than other techniques.

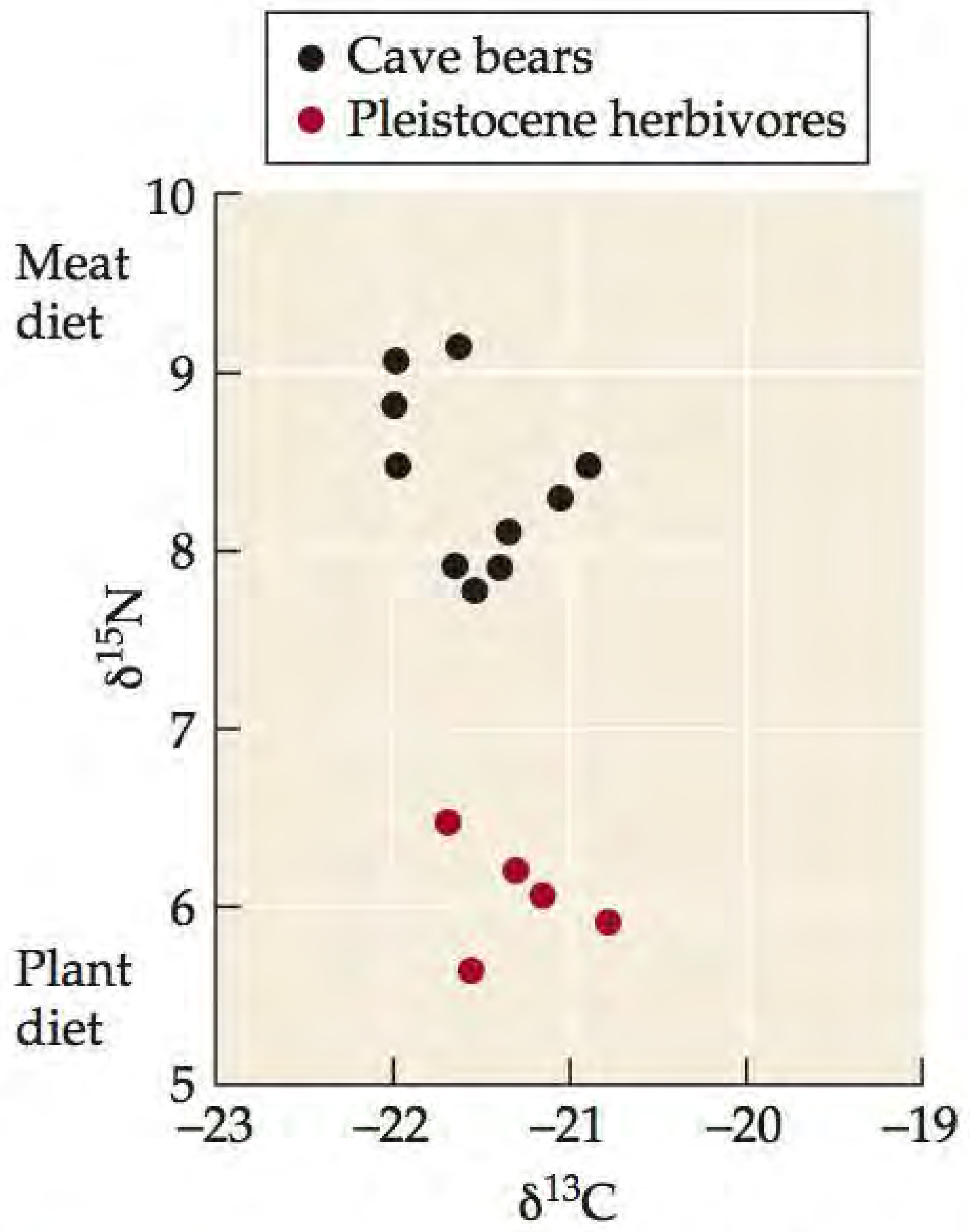


Figure 20.19 Isotopic Composition and Diet Carbon and nitrogen isotope composition of bones of museum specimens of cave bears and herbivores from about 20,000 years ago. The isotopic compositions are expressed as ratios of heavier to lighter isotopes compared with a standard. Higher numbers mean more of the heavier isotope. (After Hilderbrand et al. 1996.)

Net secondary production is equal to heterotroph growth

Not all of the organic matter consumed by heterotrophs is incorporated into heterotroph biomass. Some is used in respiration, and some is egested (lost in urine and feces). **Net secondary production** is therefore the balance between ingestion, respiratory loss, and egestion:

$$\text{net secondary production} = \text{ingestion} - \text{respiration} - \text{egestion}$$

Net secondary production by a heterotroph depends on the quality of its food, related to its digestibility and nutrient content. In addition, the physiology of the heterotroph influences how effectively its food intake is channeled into growth. Animals with high respiration rates (e.g., endotherms) have less energy left over to allocate to growth.

Net secondary production in most terrestrial ecosystems is a small fraction of NPP, because of predation on herbivores, plant defenses, and the low nutrient content of many plants, as we'll see in Chapter 21. Net secondary production represents a greater fraction of NPP in aquatic ecosystems than it does in terrestrial ecosystems. The majority of net secondary production in most ecosystems is associated with detritivores, primarily bacteria and fungi.

A CASE STUDY REVISITED

Life in the Deep Blue Sea, How Can It Be?

In this chapter, we have emphasized the importance of photosynthetic autotrophs as the source of energy for ecosystems, since the vast majority of the energy that enters ecosystems is derived from visible solar radiation. Here and in Chapter 5, however, we have alluded to another source of energy for ecosystems: chemosynthesis. Some bacteria can use chemicals such as hydrogen sulfide (H_2S and related chemical forms, HS^- and S^{2-}) as electron donors to take up carbon dioxide and convert it into carbohydrates:

$$S^{2-} + CO_2 + O_2 + H_2O \rightarrow SO_4^{2-} + (CH_2O)_n$$

Bacteria that provide energy for ecosystems via chemosynthesis are known as *chemoautotrophs*. The existence of chemoautotrophic bacteria was known for at least a century before the discovery of hydrothermal vents, but their role in providing energy for the vent communities was uncertain.

Initially, hypotheses suggested that the high velocity of water flow around the hydrothermal vents helped direct organic matter from the photic zone toward the filter-feeding invertebrates. However, several lines of evidence suggested that chemoautotrophs were the major source of energy for these ecosystems. First, the carbon isotopic ratios ($^{13}C/^{12}C$) in the bodies of the vent invertebrates were different from those of phytoplankton in the photic zone (see Ecological Toolkit 5.1). Second, the tube worms collected from the vents (*Riftia* spp.) lacked mouths and digestive systems. These gutless tube worms also had structures called trophosomes, made up of highly vascularized tissues with specialized cells containing large amounts of bacteria (**Figure 20.20**). Elemental sulfur was found in the trophosomes, suggesting that sulfides were being chemically transformed in the tube worms' bodies. Enzymes associated with the Calvin cycle, the biochemical pathway used by autotrophs to synthesize carbohydrates (see Concept 5.2), as well as enzymes involved in sulfur metabolism were found in the trophosomes. Furthermore, the clams and other mollusks collected from the vent communities lacked some of the critical tissues for filter feeding, and they also had large amounts of bacteria in specialized tissues, as well as enzymes associated with the Calvin cycle.

All of this evidence pointed to the conclusion that deep-sea hydrothermal vent communities derive their energy from chemoautotrophic bacteria. These bacteria also aid in detoxifying the sulfides in the water, which would normally inhibit aerobic respiration. Many of the abundant organisms have symbiotic relationships with the bacteria—that is, they house the chemoautotrophs in their bodies, often in specialized structures. Is this interaction a mutualistic symbiosis of the kind described in Chapter 15? The tube worms and clams housing the bacteria benefit by obtaining carbohydrates to fuel their metabolic processes, growth, and reproduction, as well as from detoxification of the sulfides. Do the bacteria derive any benefit from the invertebrates? The answer is yes: the invertebrates provide them with a chemical environment unlike that found in the surrounding water, supplying them with more carbon dioxide, oxygen, and sulfides than they could obtain if they were free-living in the water or the sediments surrounding the vent. The symbiosis between the bacteria and the invertebrates is therefore mutualistic, resulting in higher productivity than if the organisms lived separately.

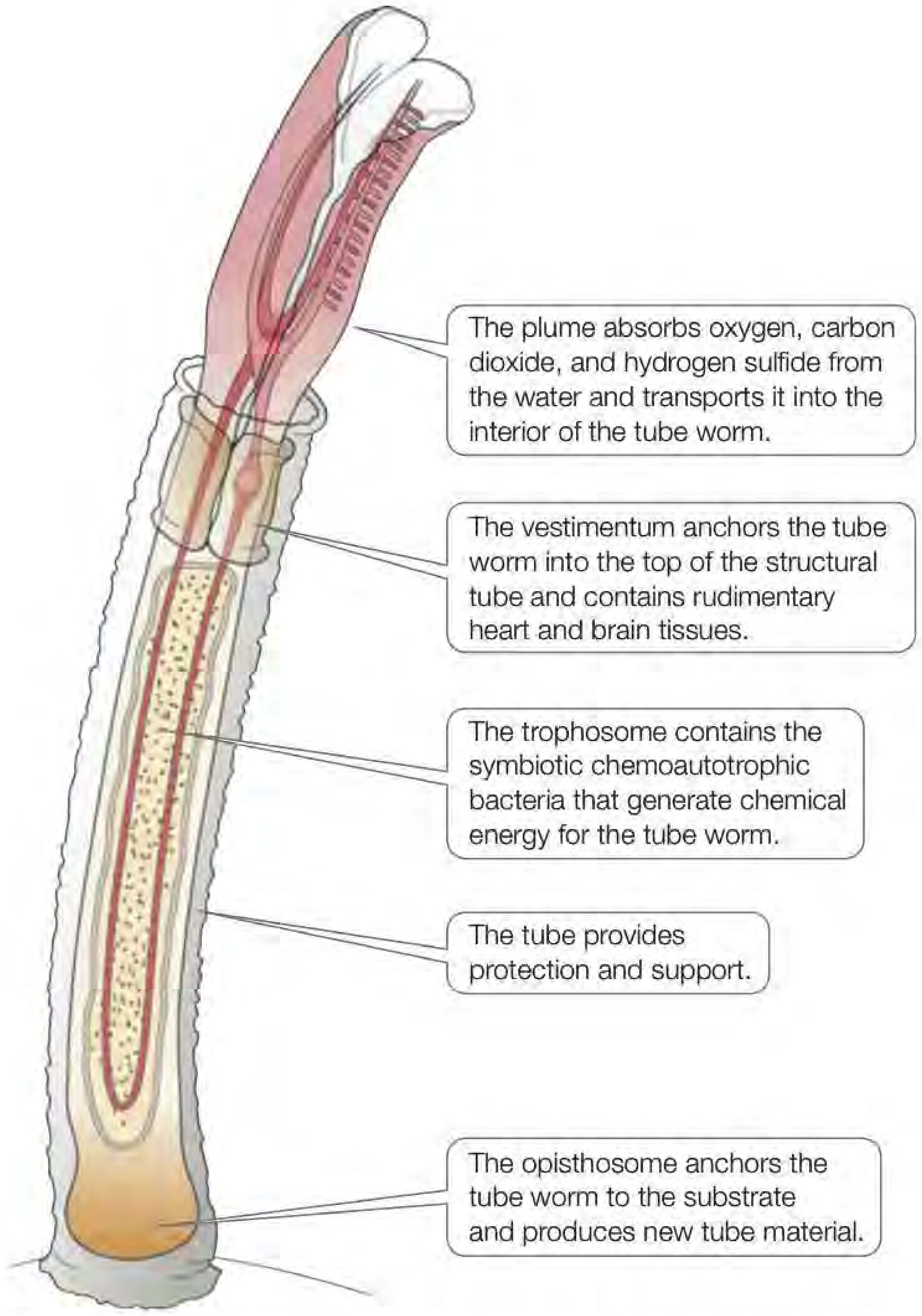


Figure 20.20 ***Riftia* Anatomy** *Riftia* tube worms have a number of specialized structures that make them well adapted to their hydrothermal vent environment.

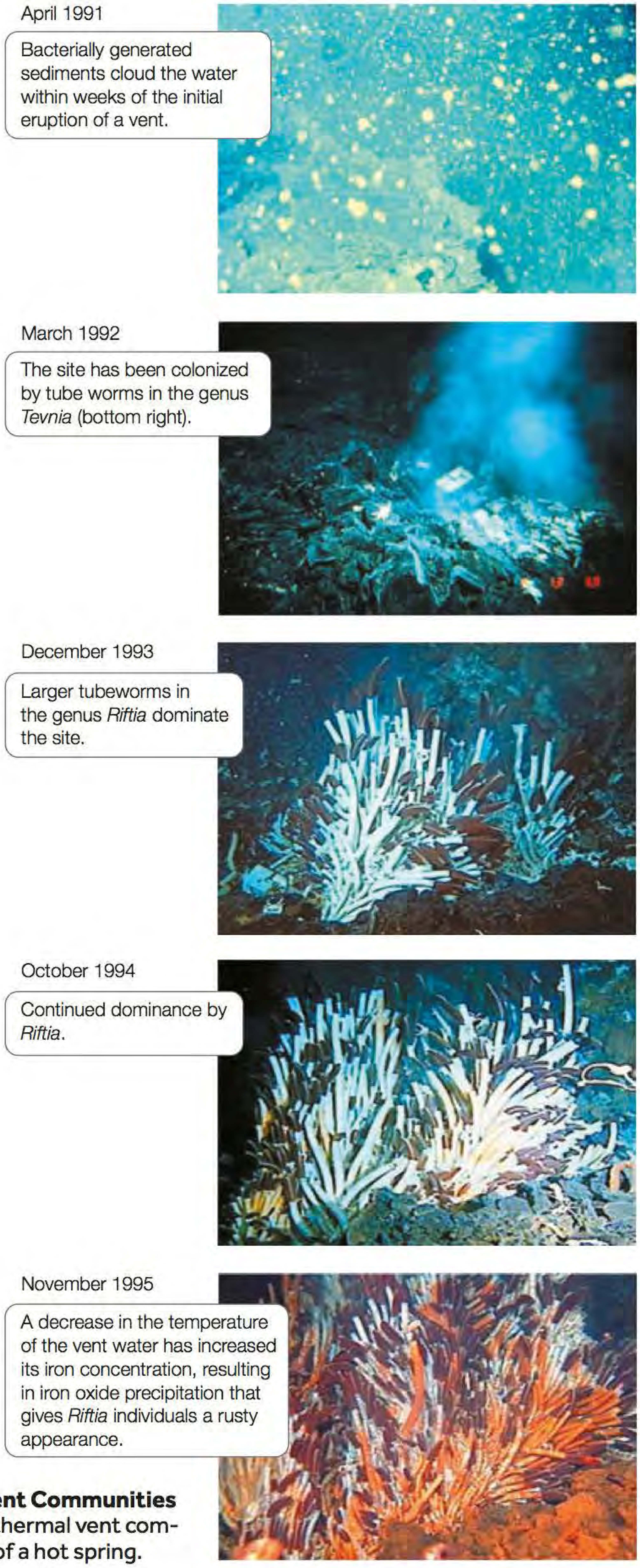
CONNECTIONS IN NATURE

Energy-Driven Succession and Evolution in Hydrothermal Vent Communities

Hydrothermal vent environments are dynamic, born with the eruption of new hot springs, which eventually cease to emit sulfide-laden water as the subsurface water channels are altered and the underlying magma cools (Van Dover 2000). When the hot springs no longer emit water, and the sulfide in the seawater has been consumed, the communities surrounding the vents collapse as their energy source disappears and the physical substrate falls apart. The life span of vent communities varies from approximately 20 to 200 years. Studies of colonization and development in these communities over the past 3 decades have provided insights into succession in marine communities in general (see Chapter 17 for a general discussion of succession).

Succession in hydrothermal vent communities is relatively rapid and can be observed by periodically revisiting specific vents (**Figure 20.21**). Although the logistic difficulty and expense of such investigations has limited the number of observations, some general trends have emerged. The rates of colonization and development of hydrothermal vent communities are higher when they are closer to other existing vent communities, as we might predict based on the theory of island biogeography (see Concept 18.3). Because the community's energy is derived from chemosynthesis, colonization begins with chemoautotrophic bacteria, sometimes in numbers large enough to cloud the water. Tube worms are often the first invertebrates to arrive. Clams and other mollusks are thought to be stronger competitors for sites with optimal temperatures and water chemistry, and over time they increase in abundance at the expense of the tube worms. A few scavengers and carnivores, such as crabs and lobsters, are found in the developing community, although at low abundances. As the tube worm and bivalve populations decline with the drop in sulfide input when water flow from the vent decreases, the abundance of scavenger organisms increases until the energy available in the form of detritus is gone.

The pattern of succession in hydrothermal vent communities is subject to the same random factors that influence succession in other habitats: the order of arrival of organisms at a site can influence the long-term dynamics of the community (see Concept 17.4). Neighboring vent communities found in the same area of a mid-ocean ridge may show different stages of succession, associated with



April 1991

Bacterially generated sediments cloud the water within weeks of the initial eruption of a vent.

March 1992

The site has been colonized by tube worms in the genus *Tevnia* (bottom right).

December 1993

Larger tubeworms in the genus *Riftia* dominate the site.

October 1994

Continued dominance by *Riftia*.

November 1995

A decrease in the temperature of the vent water has increased its iron concentration, resulting in iron oxide precipitation that gives *Riftia* individuals a rusty appearance.

Figure 20.21 Succession in Hydrothermal Vent Communities Species composition and abundances in a hydrothermal vent community change over time following the eruption of a hot spring.

the stages of hot spring development, as well as different trajectories of succession due to differences in the organisms present. Thus, collections of hydrothermal vents within the same general area are a mosaic of communities at different successional stages, similar to those in terrestrial forest patches, albeit separated by greater distances than the patches within a forest.

The unique nature of the energy supply in hydrothermal vent communities would suggest strong evolutionary divergence between the organisms that inhabit the vents and their nearest non-vent relatives (see Concept 6.4). Where phylogenetic relationships between the vent organisms and their non-vent relatives have been worked out, the divergence is indeed deep, usually at the level of genus, family, or order. Since the discovery of hydrothermal vents, approximately 500 new vent species have been described; of these species, about 90% are endemic to hydrothermal vents. However, large areas of mid-ocean ridges potentially containing hydrothermal vents have yet to be explored.

The close association between the chemoautotrophic bacteria and their invertebrate hosts suggests the potential for a coevolutionary relationship of the type described in Concept 15.1. Have the invertebrates and their chemosynthetic bacterial symbionts evolved in concert? To address this question, Andrew Peek and colleagues compared the evolutionary relationships (phylogenetic trees; see Figure 6.16) of vent-dwelling clams in the family Vesicomyidae with those of their symbiotic bacteria (Peek et al. 1998). Clams in this family transfer bacteria to their offspring in the cytoplasm of their eggs. Peek and colleagues collected eight species of clams in three genera from hydrothermal vent communities at latitudes ranging from 18°N to 47°N and at depths ranging from 500 to 6,370 m. Ribosomal DNA taken from the clams and the bacteria was used to construct the phylogenetic trees. The two trees showed remarkable congruence (**Figure 20.22**), providing strong evidence that speciation in the clams and in their bacterial symbionts has occurred synchronously. Other vent groups lack this apparent coevolutionary relationship, however. For example, three different species of tube worms found in different geographic locations have been found to contain the same species of sulfur-oxidizing bacteria.

Recently, it has been suggested that hydrothermal vents are a potential site for the origin of life on Earth. The reducing (i.e., electron-donating) geochemical environment of hydrothermal vents is conducive to the abiotic synthesis of amino acids, which would have been required for the development of living systems. Although amino acids are not stable in ocean water under the high pressures and temperatures found at some deep-sea hydrothermal vents, there are vents with lower temperatures at shallower depths where amino acid genesis could (and does) occur. As Cyndy Lee Van Dover (2000) so eloquently stated, "Vent water may be the ultimate soup in the sorcerer's kettle."

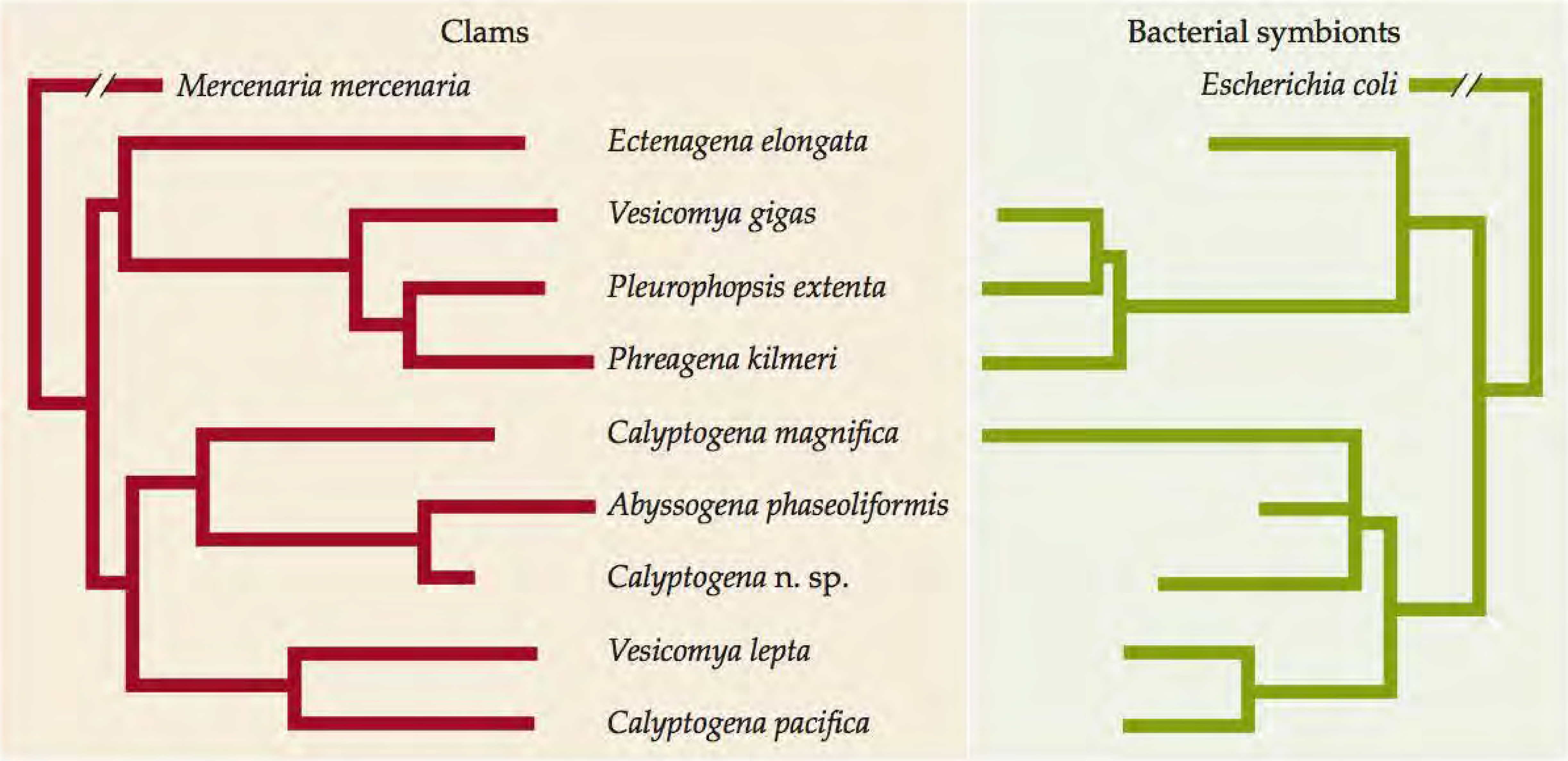


Figure 20.22 Coevolution of Vent Clams and Their Symbiotic Bacteria The phylogenetic trees of vesicomyid clams collected from hydrothermal vents and their accompanying chemoautotrophic bacterial symbionts show remarkable parallels, suggesting that these species have coevolved. (After Peek et al. 1998.)

Summary

CONCEPT 20.1 Energy in ecosystems originates with primary production by autotrophs.

- Gross primary production (GPP) is the total amount of carbon fixed by the autotrophs in an ecosystem.
- The GPP of a terrestrial ecosystem is determined by the rate of photosynthesis and the leaf area index.
- Net primary production (NPP) is equal to GPP minus autotrophic respiration.
- NPP changes during succession because of changes in leaf area index and in the proportions of photosynthetic and nonphotosynthetic plant tissues.
- Researchers have developed diverse approaches to measuring NPP at different spatial and temporal scales.

CONCEPT 20.2 Net primary production is constrained by both physical and biotic environmental factors.

- Variation in terrestrial NPP is associated with variation in temperature and precipitation, both of which affect resource availability and the types and abundances of plants.
- The intrinsic growth rates of different plant species influence spatial variation in NPP and its response to variation in resource availability.
- NPP in aquatic ecosystems is controlled by the supply of nutrients, particularly phosphorus and nitrogen.

CONCEPT 20.3 Global patterns of net primary production reflect climate constraints and biome types.

- Terrestrial and oceanic NPP contribute nearly equal proportions of global NPP.
- The majority of terrestrial NPP occurs in the tropics.
- Although zones of upwelling and coastal zones have the highest rates of NPP, the open ocean accounts for the majority of oceanic NPP because of its larger area.
- Differences in NPP among terrestrial biomes reflect differences in leaf area index and in the length of the growing season.

CONCEPT 20.4 Secondary production is generated through the consumption of organic matter by heterotrophs.

- Heterotrophs derive energy from the consumption of live or dead organic matter.
- Heterotroph diets can be determined by measuring and comparing the ratios of stable isotopes in the tissues of the feeding organism and in those of its potential food sources.
- Net secondary production is the energy ingested by heterotrophs minus the energy used in respiration and egested in feces and urine.

Review Questions

1. Why is it important to know how much primary production occurs in ecosystems?
2. Plants allocate the energy they acquire through photosynthesis to different functions, including growth and metabolism. The allocation to growth can go preferentially to particular organs, such as leaves, stems, roots, or flowers. How would you expect the allocation of energy among plant organs to change as the amount of terrestrial ecosystem NPP increased? Explain why you would expect the allocation pattern you describe.
3. Some ecologists interested in the underlying factors that control variation in NPP in tundra measured the growth of plants at several locations over multiple years. They also measured air and soil temperatures, wind speed, solar radiation, and soil moisture. When they analyzed all of their data, they found that the best correlation between NPP and any of the physical environmental factors they had measured was with soil temperature. The researchers concluded that NPP in tundra is controlled by the effect of soil temperature on root growth. Is this conclusion correct?
4. What are some of the benefits and drawbacks associated with measuring NPP using (a) harvest techniques and (b) remote sensing?

Hone Your Problem-Solving Skills

In addition to examining the cave bear food preferences described in this chapter, Hilderbrand and colleagues wanted to see whether grizzly bears living near coastal areas relied more heavily on fish in their diet than bears from inland areas that did not have access to salmon (Hilderbrand et al. 1996). They measured the isotopic composition of bone and hair samples from grizzly bears from the western United States killed before 1931, prior to the construction of dams that restricted salmon runs up the Columbia River basin. Meat is more enriched in ^{15}N than plants, so bears with a carnivorous diet have higher ratios of ^{15}N/^{14}N, expressed as a higher δ ^{15}N, than bears with a diet of plant tissues. Meat food sources have δ ^{15}N values of 12 to 15, while δ ^{15}N values of plant food sources are between 7 and 8. Marine sources of meat (e.g., fish) have a higher proportion of ^{13}C (higher ^{13}C/^{12}C ratio expressed as a higher δ ^{13}C) than terrestrial food sources (e.g., small mammals). Marine food sources have δ ^{13}C values of −17.5 to −18.5, while terrestrial food sources have a δ ^{13}C of between −20 and −22.

1. Using the data in the table, construct a graph that tests the hypothesis that grizzly bears of coastal areas consume more fish than bears from inland areas. Use δ ^{13}C on the *x* axis (going from more negative to less negative) and δ ^{15}N on the *y* axis.
2. The availability of salmon for consumption by bears has declined since 1931 because of lower numbers of fish spawning in rivers.
   - **a.** What changes isotopic composition would you expect if the bears compensated for the lower salmon availability by consuming a higher proportion of terrestrial plant material in their diet?
   - **b.** What changes would you expect in the isotopic composition if they compensated by eating more terrestrial mammals?

INDIVIDUAL	δ ^{13}C	δ ^{15}N
Coastal population		
1	−17.9	12.6
2	−18.2	13.0
3	−18.6	12.2
4	−19.1	11.5
5	−19.0	11.5
River basin population		
1	−18.9	11.3
2	−19.1	10.8
3	−19.5	10.5
4	−19.6	10.0
5	−20.0	10.0
Inland population		
1	−20.0	8.9
2	−20.1	8.2
3	−20.6	8.9
4	−20.8	8.2
5	−21.2	7.8

ON THE COMPANION WEBSITE
ecology4e.sinauer.com

The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

20.1 The Long Hot Summer: Ecosystem Effects of the Drought of 2003 in Europe

20.2 The Cost of Staying Alive: Nitrogen and Energy in Subalpine Plants

Online Climate Change Connection

20.1 The Transformation of Arctic Ecosystems from Carbon Sinks to Carbon Sources

21 Energy Flow and Food Webs

KEY CONCEPTS

CONCEPT 21.1 Trophic levels describe the feeding positions of groups of organisms in ecosystems.

CONCEPT 21.2 The amount of energy transferred from one trophic level to the next depends on food quality and on consumer abundance and physiology.

CONCEPT 21.3 Changes in the abundances of organisms at one trophic level can influence energy flow at multiple trophic levels.

CONCEPT 21.4 Food webs are conceptual models of the trophic interactions of organisms in an ecosystem.

Toxins in Remote Places: A Case Study

The Arctic is considered one of most pristine regions on Earth. Human effects on its environment are thought to be slight relative to those in the temperate and tropical zones, where the vast majority of humans live. Thus, the Arctic is one of the last places one would expect to find high levels of pollutants in living organisms.

In the mid-1980s, Eric Dewailly, a toxicologist, was studying concentrations of polychlorinated biphenyls (PCBs) in the breast milk of mothers in southern Quebec. PCBs belong to a group of chemical compounds called persistent organic pollutants (POPs) because they remain in the environment for a long time. POPs originate from industrial and agricultural activities and from the burning of industrial, medical, or municipal wastes. Exposure to PCBs has been linked to increased incidence of cancer, impaired ability to fight infections, decreased learning ability in children, and lower birth weights in newborns.

Dewailly was seeking a human population from a pristine area that could be used as a control in his study. He enlisted the help of some Inuit mothers from Arctic Canada. The Inuit are primarily subsistence hunters, and they have no developed industry or agriculture that would provide direct exposure to POPs (**Figure 21.1**). Dewailly therefore assumed that Inuit mothers would have few or no PCBs in their breast milk, providing a benchmark against which to compare populations in more industrialized areas.

What Dewailly found was startling: the Inuit women had concentrations of PCBs in their breast milk that were seven times higher than those in women of southern Quebec (**Figure 21.2**) (Dewailly et al. 1993). These alarming findings were reinforced by the work of Harriet Kuhnlein, who at the same time found that approximately two-thirds of the children from an Inuit community in northeastern Canada had PCB levels in their blood that exceeded Canadian health guidelines (Kuhnlein et al. 1995). More extensive surveys found that POPs were widespread in Inuit populations. As many as 95% of the people in Inuit communities of Greenland had blood levels of PCBs that exceeded health standards (Pearce 1997).

Figure 21.1 Subsistence Hunting Inuit hunters peel layers of skin and fat from a slaughtered bowhead whale in a remote, very sparsely populated Arctic region.

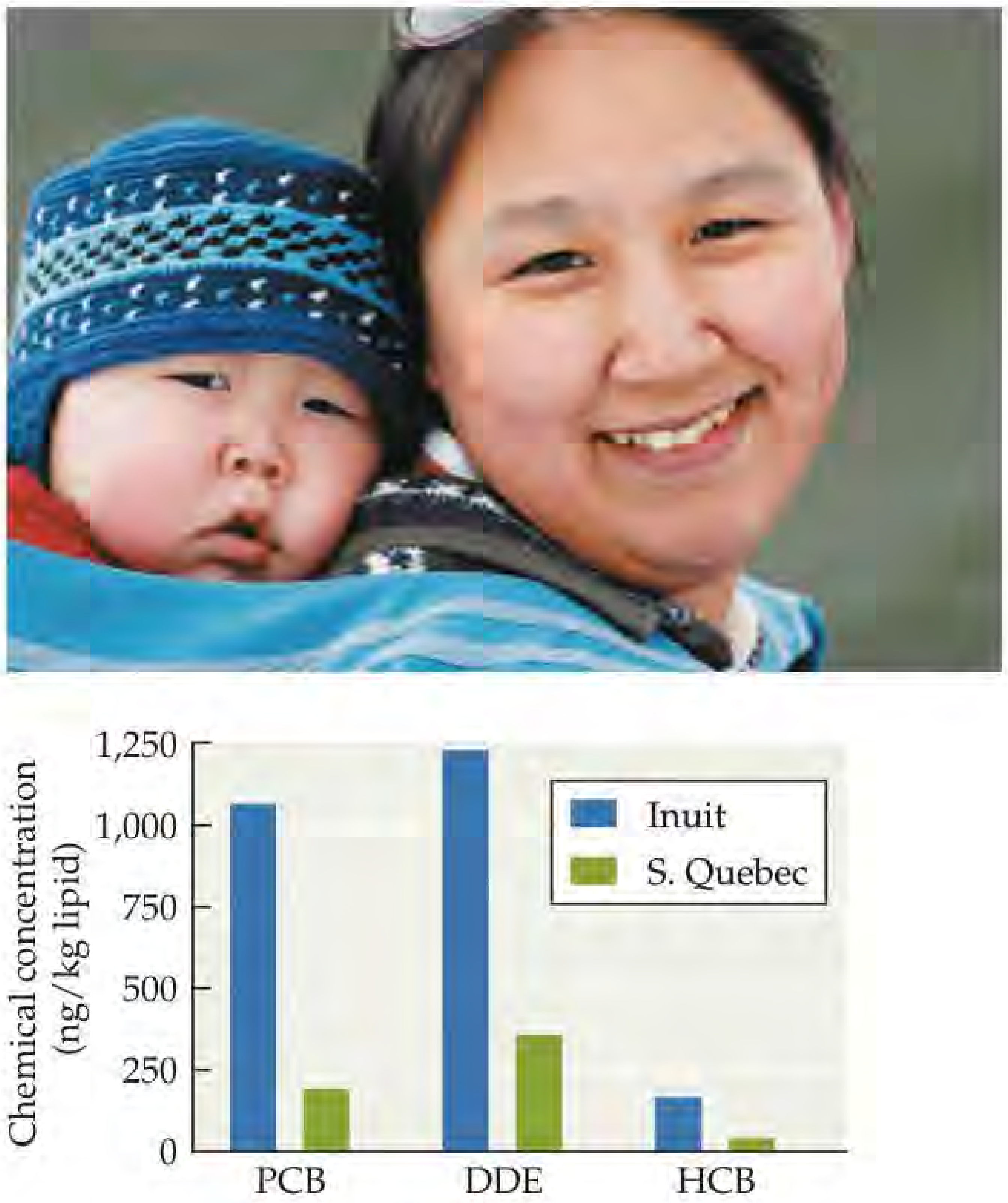


Figure 21.2 Persistent Organic Pollutants in Canadian Women The breast milk of Inuit mothers from Arctic Canada was found to contain substantially higher concentrations of polychlorinated biphenyls (PCBs) and two other POPs—dichlorodiphenyldichloroethylene (DDE, a pesticide similar to DDT) and hexachlorobenzene (HCB, an agricultural fungicide)—than that of mothers from southern Quebec. (After Dewailly et al. 1993.)

How were these toxins finding their way into the Arctic environments where the Inuit live? The POPs that were found in the tissues of Inuit populations occur in gaseous form at most environmental temperatures. Produced in lower-latitude industrial areas, these compounds enter the atmosphere under warm temperatures, but when carried by atmospheric circulation patterns into the colder atmosphere of the Arctic, they condense into liquid forms and fall from the atmosphere, sometimes in snowflakes. The manufacture and use of most POPs has been banned in North America since the 1970s. Some developing countries continue to produce POPs, however, and they are important sources of the compounds found in Arctic regions. Although emissions of POPs have decreased, these compounds may remain in Arctic snow and ice for many decades, being released slowly during snowmelt every spring and summer.

While the source of the POPs was known, the high concentrations of these compounds in the Inuit were a mystery. The concentrations of POPs in their drinking water were not high enough to explain this phenomenon. One hint came from the correlation between the levels of the toxins in people and their preferred diets. Communities that had traditionally relied on marine mammals for their food tended to have the highest levels of POPs, while communities that consumed herbivorous caribou had lower levels. We will discover the ecological basis for this difference as we trace the flow of energy and materials through ecosystems in this chapter.

Introduction

To begin our discussion of energy flow in ecosystems, let's move from the Arctic to a much warmer place: a North American desert. Despite their aridity, deserts contain diverse assemblages of plants, animals, and microorganisms. This diversity is reflected in the variation in the sizes, shapes, and physiology of the animals making up the desert fauna, from nematodes in the soil to grasshoppers in the plant canopy to hawks in the sky. What links these animals together in the context of ecological functioning isn't necessarily their physical appearances or their evolutionary relationships. Rather, their ecological roles are determined by what they eat and by what eats them—that is, by their feeding, or *trophic*, interactions. In other words, the influence an organism has on the movement of energy and nutrients through an ecosystem is determined by the type of food it consumes as well as by what consumes it. For example, grasshoppers and scorpions are both arthropods, with similar morphology and physiology, yet their ecological effects on energy flow through the desert ecosystem are quite different. In the context of energy flow, grasshoppers are more similar to mule deer than to scorpions. Grasshoppers and mule deer are both generalist herbivores that consume a variety of desert plant species. The scorpion, by contrast, is a carnivorous arthropod feeding primarily on insects and thus has an ecological role more similar to that of a kestrel than to that of a grasshopper.

In this chapter, we continue the discussion of energy that we began in Chapter 20, describing its flow through ecosystems and the factors that control its movement through different trophic levels. We will also look at the feeding relationships in an ecosystem as an intricate web of interactions among species, a view that has important implications for energy flow and ecosystem function as well as for species interactions and community dynamics (topics that were covered in Units 4 and 5).

CONCEPT 21.1

Trophic levels describe the feeding positions of groups of organisms in ecosystems.

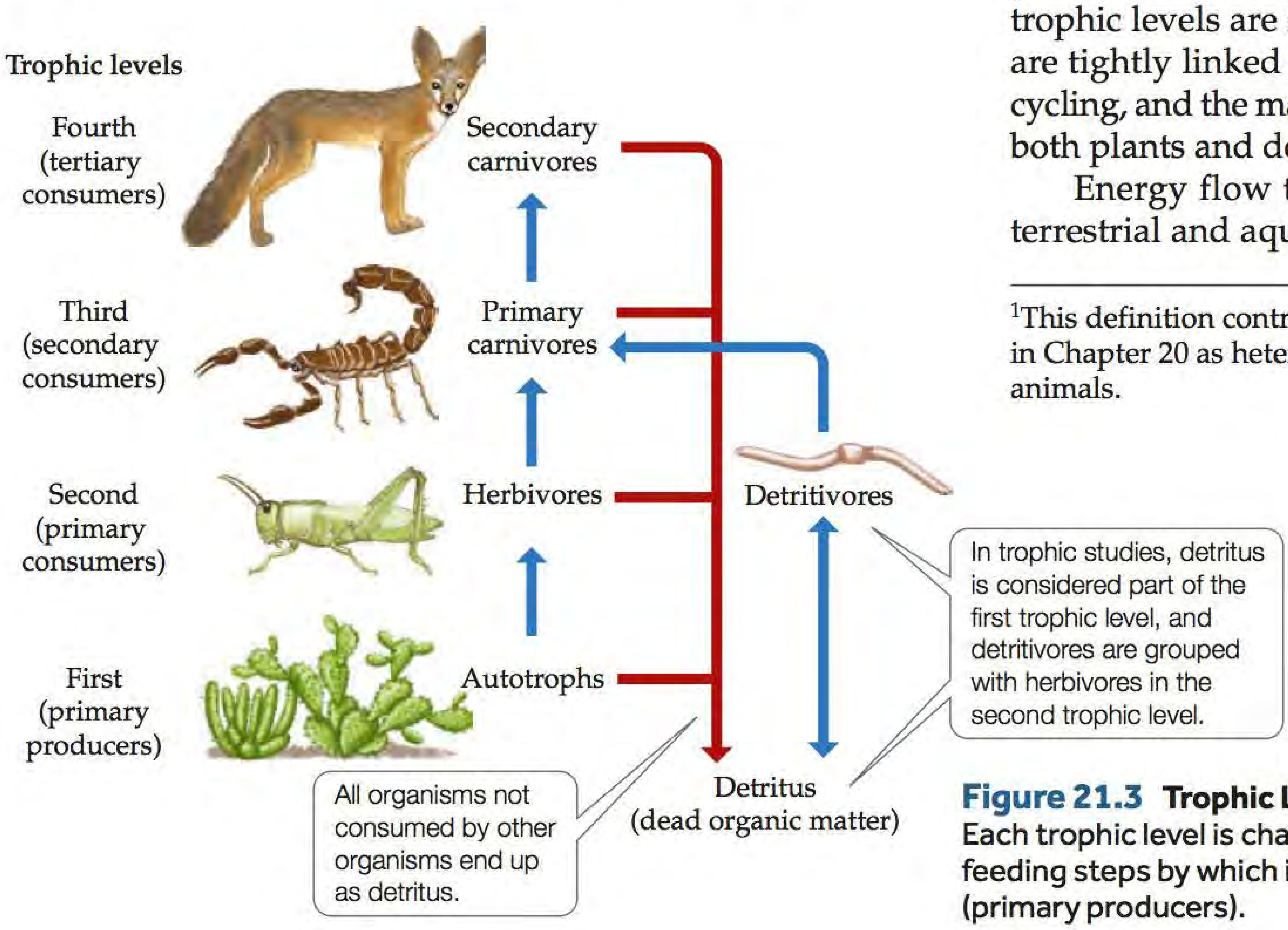
Feeding Relationships

In Chapter 20, we introduced Ray Lindeman's simplified approach to categorizing groups of organisms in an ecosystem according to how they obtain energy (see Figure 20.3). Rather than grouping them by their taxonomic identity, he grouped them into categories based on how they obtained energy in the ecosystem. In this section, we'll take a closer look at these feeding categories.

Organisms can be grouped into trophic levels

Each feeding category, or **trophic level**, is based on the number of feeding steps by which it is separated from autotrophs (**Figure 21.3**). The first trophic level consists of the autotrophs, the primary producers that generate chemical energy from sunlight or inorganic chemical compounds. The first trophic level also generates most of the dead organic matter in an ecosystem. In our desert ecosystem, the first trophic level includes all of the plants, which we lump together to form a single group, regardless of their taxonomic identity. In Lindeman's lake ecosystem (see Figure 20.3), the first trophic level was composed primarily of dead organic matter, which Lindeman poetically referred to as "ooze," as well as autotrophs such as phytoplankton and pondweeds. The second trophic level consisted of the herbivores that consume autotroph biomass—which in our desert ecosystem would include grasshoppers and mule deer—as well as the detritivores that consume dead organic matter. The remaining trophic levels (third and up) contain the carnivores that consume animals at the trophic level below them. The primary carnivores constituting the third trophic level in our desert ecosystem would include small birds and scorpions, while examples of the secondary carnivores making up the fourth trophic level would be foxes and birds of prey. Most ecosystems have four or fewer trophic levels.

Some organisms do not fit conveniently into the trophic levels defined here. Coyotes, for example, are opportunistic feeders, consuming vegetation, mice, other carnivores, and old leather boots. In trophic studies, heterotrophs that feed at multiple trophic levels are called **omnivores**.[1] Such heterotrophs defy our attempt to group organisms into simple feeding categories. However, their diets can be partitioned to reflect how much energy they consume within each trophic level (Pimm 2002). This partitioning is facilitated by the use of stable isotopes to trace food sources (Post 2002a) (see Ecological Toolkit 5.1 and Concept 20.4). Thus, omnivores occupy intermediate trophic levels as determined by the proportions of the foods they consume. Omnivory is common in many ecosystems.



In trophic studies, detritus is considered part of the first trophic level, and detritivores are grouped with herbivores in the second trophic level.

All organisms not consumed by other organisms end up as detritus.

Figure 21.3 Trophic Levels in a Desert Ecosystem Each trophic level is characterized by the number of feeding steps by which it is removed from autotrophs (primary producers).

All organisms are either consumed or end up as detritus

All organisms in an ecosystem are either consumed by other organisms at higher trophic levels or enter the pool of dead organic matter, or *detritus* (Lindeman's "ooze" in Figure 20.3, or as Tom Waits put it, "We're all gonna be just dirt in the ground"). In most terrestrial ecosystems, a relatively small proportion of the biomass is consumed, and most of the energy flow passes through detritus (**Figure 21.4**). Because most of this energy flow occurs in the soil, we are not always aware of its magnitude and importance. Dead plant, microbial, and animal matter, as well as feces, are consumed by a multitude of organisms, known as *detritivores* (primarily bacteria, archaea, and fungi), in a process known as *decomposition*. We will describe decomposition in more detail in Chapter 22 in the context of nutrient cycling. Detritus is part of the first trophic level, and detritivores are placed with herbivores in the second trophic level. Although autotroph-based and detritus-based trophic levels are sometimes considered separately, they are tightly linked through primary production, nutrient cycling, and the many organisms that acquire energy from both plants and detritus.

Energy flow through detritus is important in both terrestrial and aquatic ecosystems. Detritus in terrestrial

---

[1] This definition contrasts with our earlier definition of omnivores in Chapter 20 as heterotrophs that consume both plants and animals.

Hypholoma fasciculare

Polydesmus sp.

Figure 21.4 Ecosystem Energy Flow through Detritus Detritus is consumed by a multitude of organisms, including fungi (these are the fruiting bodies of sulfur tuft fungi) and arthropods (such as millipedes).

ecosystems comes primarily from plants within the ecosystem. On the other hand, a large proportion of the input of detritus into stream, lake, and estuarine ecosystems is derived from terrestrial organic matter, which is considered external to the aquatic ecosystem. External energy inputs are referred to as **allochthonous inputs**, while energy produced by autotrophs within the system is known as **autochthonous energy**. Allochthonous inputs into aquatic ecosystems include plant leaves, stems, wood, and dissolved organic matter. These inputs fall into the water from adjacent terrestrial ecosystems or flow in via groundwater. Allochthonous inputs tend to be more important in stream and river ecosystems than in lake and marine ecosystems. For example, Bear Brook, a headwater stream in New Hampshire, receives 99.8% of its energy as allochthonous inputs; the rest is net primary production (NPP) derived from benthic algae and mosses in the stream (Fisher and Likens 1973). In contrast, autochthonous energy accounts for almost 80% of the energy in nearby Mirror Lake (Jordan and Likens 1975). Allochthonous energy is often of lower quality, however, because of the chemical composition of the carbon compounds that enter the system. As a result, the fraction of allochthonous energy that is actually used is lower than the inputs indicate (Pace et al. 2004). The importance of autochthonous energy inputs usually increases from the headwaters toward the middle reaches of a river, in concert with decreases in water velocity and increases in nutrient concentrations, as suggested by the river continuum concept (described in Concept 3.2).

As this aquatic example shows, grouping organisms into trophic levels makes it easier to trace the flow of energy through an ecosystem. That flow is the topic to which we'll turn next.

CONCEPT 21.2

The amount of energy transferred from one trophic level to the next depends on food quality and on consumer abundance and physiology.

Energy Flow between Trophic Levels

The second law of thermodynamics states that during any transfer of energy, some energy is dispersed as unusable energy because of the tendency toward an increase in disorder (entropy). Thus, we can expect that available energy will decrease with each trophic level as we move from the first trophic level upward. We know from our discussion of primary production in Chapters 5 and 20 that autotrophs lose chemical energy through cellular respiration, lowering the amount of energy available to heterotrophs. In this section, we will examine more closely the factors influencing energy movement between trophic levels.

Energy flow between trophic levels can be depicted using energy or biomass pyramids

A common approach to conceptualizing trophic relationships in an ecosystem is to construct a stack of rectangles, each of which represents the amount of energy or biomass within one trophic level. When assembled from lower to higher trophic levels, these rectangles form a **trophic pyramid**. By portraying the relative amounts of energy or biomass at each trophic level, these pyramids show us how energy flows through the ecosystem.

As we have noted, some of the biomass at each trophic level is not consumed, and a proportion of the energy at each trophic level is lost in the transfer to the next trophic level. Therefore, the rectangles in a trophic energy pyramid always decrease in size as we move from one trophic level to the one above it. In terrestrial ecosystems, energy and biomass pyramids are usually similar because biomass is typically a good proxy for energy (**Figure 21.5A**). In aquatic ecosystems, however, the high consumption rates and the relatively short life spans of

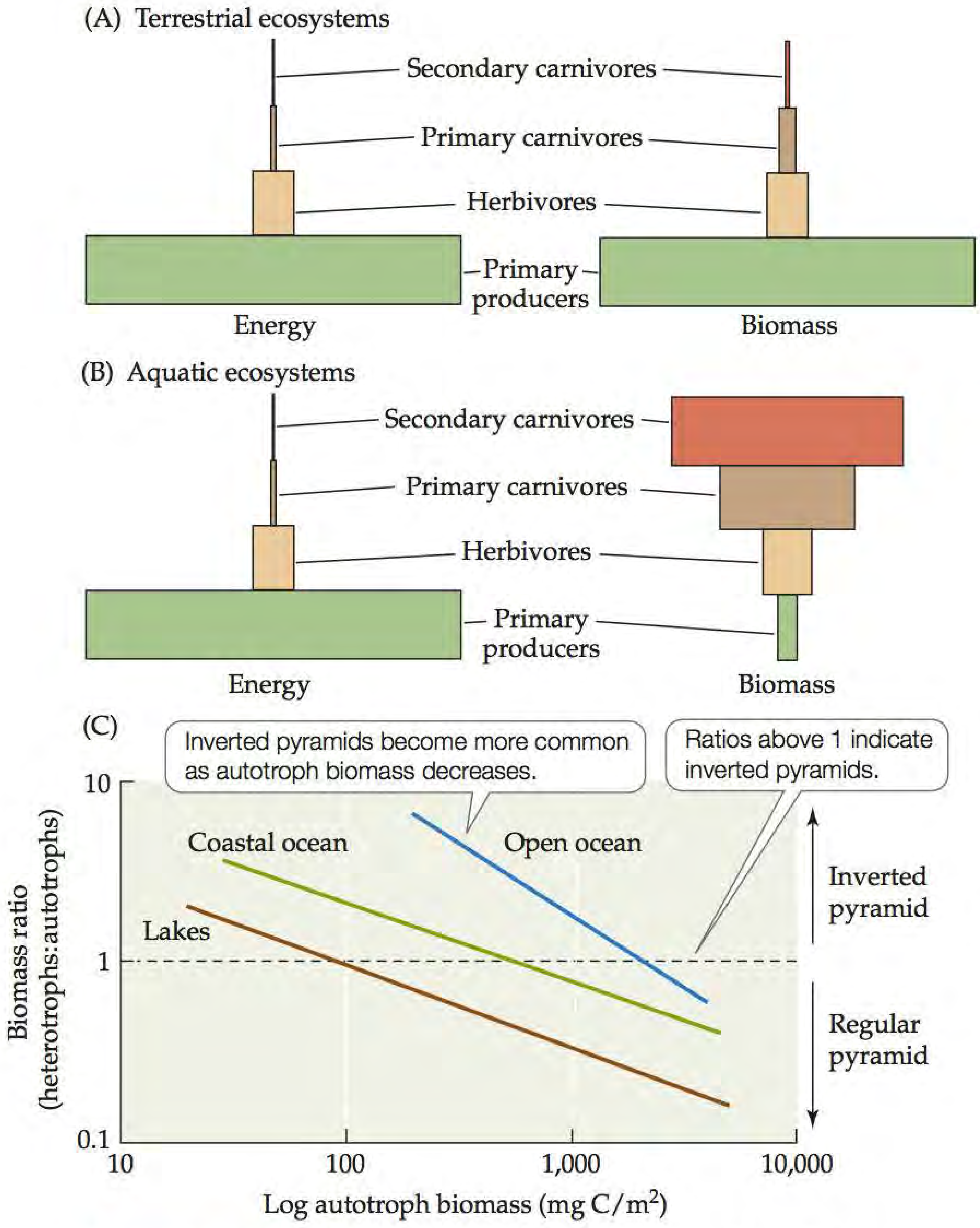


Figure 21.5 **Trophic Pyramid Schemes** (A) In terrestrial ecosystems, energy and biomass pyramids are usually similar. (B) In many aquatic ecosystems, the biomass pyramid is inverted relative to the energy pyramid. (C) Inverted biomass pyramids in aquatic ecosystems are most common in nutrient-poor waters with low autotroph biomass. (C after Gasol et al. 1997.)

the primary producers (mainly phytoplankton) result in a biomass pyramid that is inverted relative to the energy pyramid (**Figure 21.5B**). In other words, the biomass of heterotrophs may be greater at any given time than the biomass of autotrophs. However, the *energy* produced by the autotrophs is still greater than that produced by the heterotrophs.

This tendency toward inverted biomass pyramids is greatest where productivity is lowest, such as in nutrient-poor regions of the open ocean (**Figure 21.5C**). The higher proportion of primary consumer biomass relative to producer biomass in these nutrient-poor regions results from a more rapid turnover of phytoplankton, which have higher growth rates and shorter life spans than the phytoplankton of more nutrient-rich waters. Phytoplankton in nutrient-poor regions thus provide a greater energy supply per unit of time (Gasol et al. 1997). In addition, detritus makes a higher proportional contribution to energy flow in these nutrient-poor waters than in nutrient-rich waters.

Energy flow between trophic levels differs among ecosystem types

What factors determine the amount of energy that flows from one trophic level to the next? In Concept 20.2, we evaluated the factors that influence NPP in terrestrial and aquatic ecosystems, emphasizing abiotic factors such as climate and nutrient availability as well as differences in the inherent ability of autotroph species to produce biomass. It would be reasonable to assume that the flow of energy to higher trophic levels is associated with the amount of NPP at the base of the food web. As we will see, however, the situation is not quite so simple. The proportion of each trophic level consumed by the one above it; the nutritional content of autotrophs, detritus, and prey; and the efficiency of energy transfers also play roles in determining the flow of energy between trophic levels.

A comparison of the proportions of autotroph biomass consumed in terrestrial and in aquatic ecosystems provides some insight into the factors that influence energy flow between trophic levels. When viewed from space, some parts of Earth's terrestrial surface appear green, while the ocean appears blue. Why is the land surface green and the ocean blue? Furthermore, in Concept 20.2, we saw that very productive lakes (e.g., those that are experimentally fertilized; see Figure 20.16) can appear green. What these green areas have in common is primary productivity that far exceeds rates of herbivory. Herbivores on land consume a much lower proportion of autotroph biomass than do herbivores in most aquatic ecosystems. On average, about 13% of terrestrial NPP is consumed (range 0.1%–75%), while in aquatic ecosystems, an average of 35% of NPP is consumed (range 0.3%–100%) (Cebrian and Lartigue 2004).

There is a positive relationship between NPP and the *amount* of biomass consumed by herbivores (**Figure 21.6**). This relationship, which holds within most ecosystem types, would seem to suggest that herbivore production is limited by the amount of food available. Why, then, is the *proportion* of autotroph biomass consumed in terrestrial ecosystems relatively low? If herbivore production is limited by the supply of energy and nutrients from plants, why don't terrestrial herbivores consume a greater proportion of the biomass that is available?

Several hypotheses have been proposed to explain the lower proportion of autotroph biomass consumed in terrestrial ecosystems. First, Hairston and Hairston (1993) have argued that the population growth of herbivores is more constrained by predation in aquatic ecosystems than in terrestrial ecosystems because of the better-developed higher trophic levels in aquatic ecosystems. Predator removal experiments such as those described in Concept

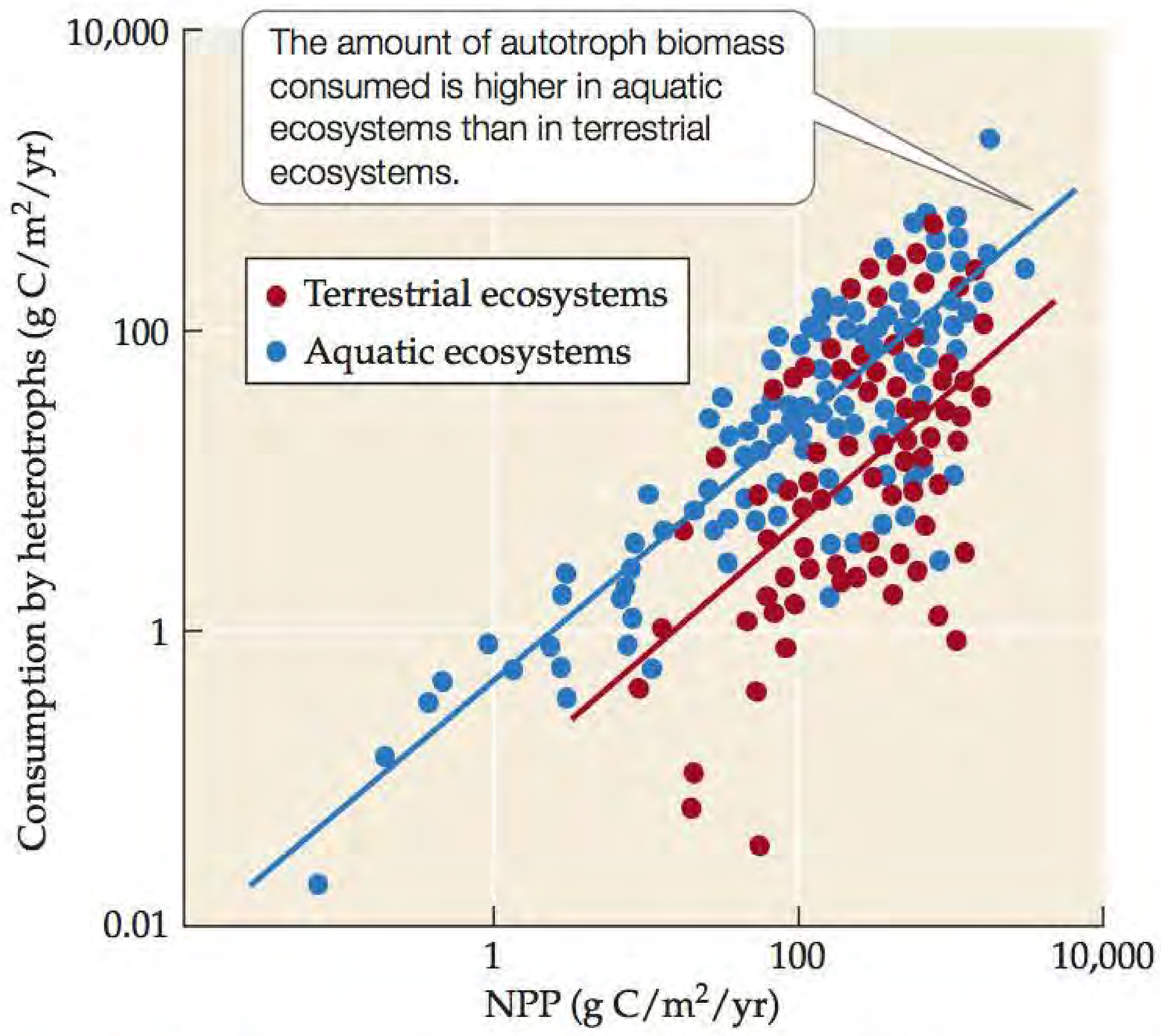


Figure 21.6 Consumption of Autotroph Biomass Is Correlated with NPP The amount of autotroph biomass consumed increases with increasing available NPP in both terrestrial and aquatic ecosystems. (After Cebrian and Lartigue 2004.)

12.4 and Concept 21.4 demonstrate that predators can effectively influence autotroph biomass through their influence on the abundance of herbivores.

Second, defenses against herbivory, such as the secondary compounds and structural defenses described in Concept 13.2, lower the amount of autotroph biomass that is consumed. Plants of resource-poor environments, such as desert and tundra, tend to be more strongly defended against herbivory than plants from resource-rich environments. This greater allocation to defense may explain why the proportion of plant biomass consumed is lower in resource-poor terrestrial environments. Unicellular algae make up the bulk of autotroph biomass in aquatic ecosystems, and they generally lack the chemical and structural defenses of their multicellular terrestrial counterparts.

Third, the chemical composition of phytoplankton makes them more nutritious for herbivores than terrestrial plants are. Terrestrial plants contain nutrient-poor structural materials such as stems and wood, which are typically absent in aquatic autotrophs. Herbivores typically require large amounts of nutrients such as nitrogen and phosphorus to meet their demands for structural growth, metabolism, and protein synthesis. The ratio of nutrients to carbon (with carbon representing energy) is thus an important measure of food quality. Carbon:nutrient ratios differ markedly between autotrophs in terrestrial and in freshwater ecosystems. Freshwater phytoplankton have carbon:nutrient ratios closer to those of herbivores than terrestrial plants do (Elser et al. 2000) and thus better meet the nutritional needs of the herbivores that eat them. Each of these factors—predation, plant defenses, and food quality—contributes to differences in the proportion of NPP consumed among ecosystems and, in particular, the greater consumption of autotroph biomass in aquatic ecosystems (Shurin et al. 2006).

The efficiency of energy transfer varies among consumers

Not all of the food energy consumed by a heterotroph gets incorporated into heterotroph biomass. Some is lost to respiration and excretion. We can use the concept of *energy efficiency*, defined as the output of energy per unit of energy input, to characterize the transfer of energy between trophic levels. In studies of energy transfer in trophic systems, the concept of **trophic efficiency** is used, defined as the amount of energy at one trophic level divided by the amount of energy at the trophic level immediately below it. Trophic efficiency incorporates the proportion of available energy that is consumed (consumption efficiency), the proportion of ingested food that is assimilated by the consumer (assimilation efficiency), and the proportion of assimilated food that goes into producing new consumer biomass (production efficiency) (**Figure 21.7**).

As we saw above, not all of the biomass available at one trophic level is consumed by the next trophic level. The proportion of the available biomass that is ingested is the **consumption efficiency**. Consumption efficiency is

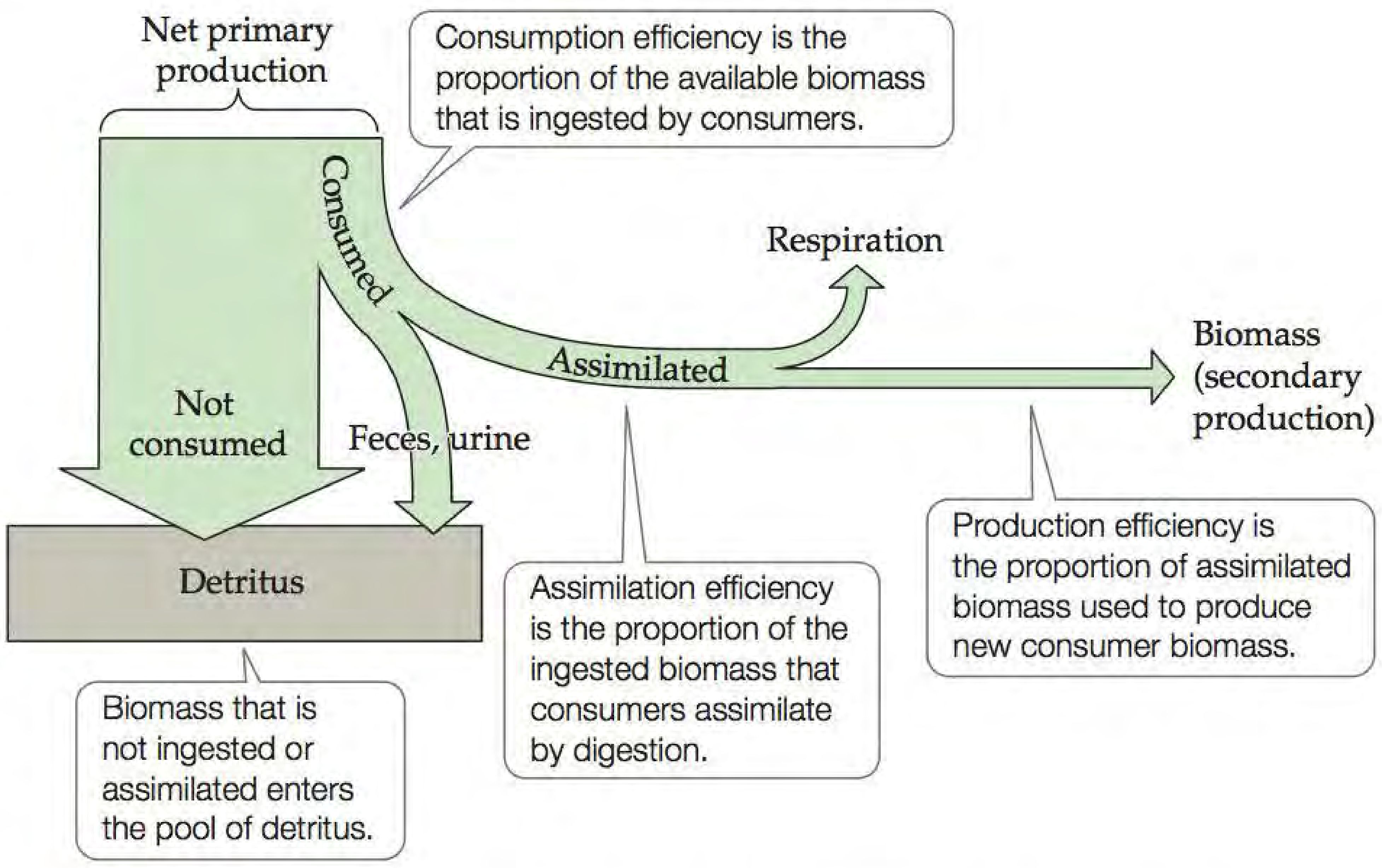


Figure 21.7 Energy Flow and Trophic Efficiency The proportion of energy transferred between trophic levels depends on efficiencies of consumption, assimilation, and production.

? How do the trends in consumption efficiency vary in Figure 21.6? What does this variation suggest about differences in consumption efficiency in aquatic versus terrestrial ecosystems?

typically higher in aquatic ecosystems than in terrestrial ecosystems (see Figure 21.6). Consumption efficiencies also tend to be higher for carnivores than for herbivores, although a systematic survey comparing the two groups has not been done.

Once biomass is ingested by the consumer, it must be assimilated by the digestive system before the energy it contains can be used to produce new biomass. The proportion of the ingested food that is assimilated is the **assimilation efficiency**. Food that is ingested but not assimilated is lost to the environment as feces, entering the pool of detritus, or as urine. Assimilation efficiency is determined by the quality of the food (its chemical composition) and the physiology of the consumer.

The quality of the food available to herbivores and detritivores is generally lower than that of the food available to carnivores. Plants and detritus are composed of relatively complex carbon compounds, such as cellulose, lignins, and humic acids, that are not easily digested. In addition, plants and detritus have low concentrations of nutrients. Animal bodies, on the other hand, have carbon:nutrient ratios that are usually very similar to those of the animals consuming them and so are assimilated more readily. Assimilation efficiencies of herbivores and detritivores vary between 20% and 50%, while those of carnivores are about 80%.

How thoroughly food is digested is influenced by the consumer's thermal physiology. Endotherms tend to digest food more completely than ectotherms and therefore have higher assimilation efficiencies. Additionally, some herbivores have mutualistic symbionts that help them digest cellulose. For example, as described in Concept 5.4, ruminants have a modified stomach chamber that contains bacteria and protists that increase the breakdown of cellulose-rich foods. This mutualistic symbiosis, coupled with a longer period of digestion, gives ruminants higher assimilation efficiencies than nonruminant herbivores.

Assimilated food can be used to produce new biomass in the form of consumer growth and production of new consumer individuals (reproduction). However, a portion of the assimilated food must be used for respiration associated with maintenance of existing molecules and tissues as well as with construction of new biomass (see Concept 5.4). The proportion of the assimilated food that is used to produce new consumer biomass is **production efficiency**.

Production efficiency is strongly related to the thermal physiology and size of the consumer. Endotherms allocate much of their assimilated food to metabolic production of heat and therefore have less energy left over to allocate to growth and reproduction than ectotherms do (**Table 21.1**). Thus, ectotherms have considerably higher production efficiencies than endotherms. Body size in endotherms is an important determinant of heat loss and thus of production efficiency. If body shape and insulation (fat, feathers, and fur) are held constant, then, as animal body size increases, the surface area-to-volume ratio decreases. Thus, a small endotherm, such as a shrew, will lose a greater proportion of its internally generated heat across its body surface than a large endotherm, such as a grizzly bear, and thus a small endotherm will tend to have a lower production efficiency.

TABLE 21.1 Production Efficiencies of Consumers

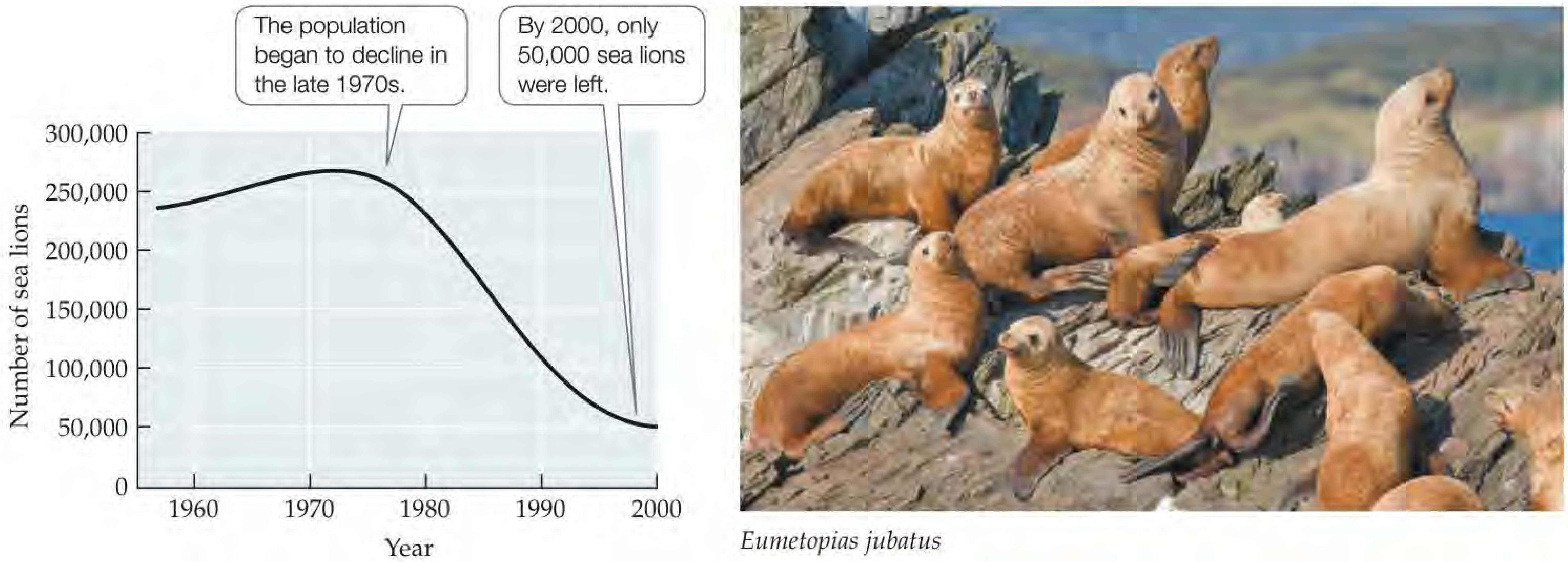
CONSUMER GROUP	PRODUCTION EFFICIENCY (%)
Endotherms	
Birds	1.3
Small mammals	1.5
Large mammals	3.1
Ectotherms	
Fishes and social insects	9.8
Nonsocial insects	40.7
Herbivores	38.8
Detritivores	47.0
Carnivores	55.6
Non-insect invertebrates	25.0
Herbivores	20.9
Detritivores	36.2
Carnivores	27.6

Sources: Chapin et al. 2002; Humphreys 1979.

Trophic efficiencies can influence population dynamics

Changes in food quantity and quality, and the resulting changes in trophic efficiency, can determine the consumer population sizes that can be sustained, as well as the health of the individuals in consumer populations. Here we'll examine the potential contribution of changes in food quality to the decline in numbers of Steller sea lions (*Eumetopias jubatus*) in Alaska.

From the late 1970s into the 1990s, the total population of Steller sea lions in the Gulf of Alaska and the Aleutian Islands decreased by about 80%, from approximately 250,000 sea lions in 1975 to 50,000 in 2000 (**Figure 21.8**). The population in the eastern part of the range has recovered some since that time and was taken off the endangered species list in 2013. However, the population in the western part of its range, along the southern coast of Alaska, has continued to decline. Andrew Trites and C. P. Donnelly reviewed the available information to try to determine possible causes for this decline (Trites and Donnelly 2003). They found that individual sea lions collected during the period of decline were smaller than individuals within the same age classes collected before the start of the decline. There was also a reduction in the number of



Eumetopias jubatus

Figure 21.8 Steller Sea Lion Population Decline in Alaska The population of sea lions in the Gulf of Alaska and the Aleutian Islands decreased by about 80% over 25 years. (After Trites and Donnelly 2003.)

pups born per female during this period, which resulted in a shift in the age structure toward older individuals. No evidence was found for outbreaks of disease or parasites. The smaller body sizes and declining birth rates suggested that there were fewer prey available, or that the available prey were not providing sufficient nourishment to sustain the sea lions—in other words, that trophic efficiency had declined. Additional data indicated that the sea lions were obtaining prey—primarily fish—as regularly as they had before the decline. Nursing females in the declining population were actually spending less time hunting for the same amount of fish as nursing females in other populations that were not declining. Therefore, the availability of prey, or the sea lions' ability to capture it, did not appear to be limiting their growth and reproduction.

Trites and Donnelly considered the possibility that changes in the species of prey fish available had contributed to the decline of the Steller sea lions. They and others suggested that the decline might be related to declining prey quality, an idea they referred to as the "junk food hypothesis." Prior to the decline, the diet of the sea lions had been primarily herring, a fish that is relatively rich in fats, along with small amounts of pollock, cod, salmon, and squid. During the period of the population decline, the sea lion diet shifted away from herring toward a greater proportion of pollock and cod (**Table 21.2**). This change in diet reflected a shift toward cod dominance of the fish community from the 1970s through the 1990s. The causes of the change in fish community composition are uncertain but may be associated with long-term climate change. The proportions of fat and energy per mass of pollock and cod are approximately half those of herring. Captive Steller sea lions raised on a diet of herring and then switched to a diet of pollock lose body mass and fat, even with an unlimited supply of pollock.

Based on their review of the available information, Trites and Donnelly concluded that nutritional stress was the most likely cause of the decline in the Steller sea lion population. The amount of prey available to the sea lions did not appear to have changed, but changes in the quality of that prey, and associated changes in trophic efficiency, contributed to the decline in the population through their effects on individual growth rates and birth rates. Others have suggested that the decline in Steller sea lion numbers may also be linked to changes in the trophic structure of the North Pacific (Springer et al. 2003). As described in the Case Study Revisited in Chapter 9, massive harvesting of great whales by humans in the mid-twentieth century may have forced their predators, killer

TABLE 21.2 Proportion of Steller Sea Lion Scats and Stomachs Containing Five Prey Categories

YEARS	GADIDS (COD, POLLOCK, HAKE)	SALMON	SMALL SCHOOLING FISH (HERRING, CAPELIN, EULACHON, SAND LANCE)	CEPHALOPODS (SQUID)	FLATFISH (FLOUNDER, SOLE)
1990–1993	85.2	18.5	18.5	11.1	13.0
1985–1986	60.0	20.0	20.0	20.0	5.0
1976–1978	32.1	17.9	60.7	0.0	0.0

Sources: Trites and Donnelly 2003; Merrick et al. 1987.

whales, to hunt other prey, including Steller sea lions. As we describe in the next section, such "top-down" effects of predators on prey can have important consequences for energy flow in ecosystems.

CONCEPT 21.3

Changes in the abundances of organisms at one trophic level can influence energy flow at multiple trophic levels.

Trophic Cascades

There are two possible ways to look at the control of energy flow through ecosystems. First, the amount of energy that flows through trophic levels may be determined by how much energy enters an ecosystem via NPP, which in turn is related to the supply of resources (as we saw in Concept 20.2). The greater the NPP entering the ecosystem, the more energy can be passed on to higher trophic levels. This view, which is often referred to as "bottom-up" control of energy flow, holds that the resources that limit NPP determine energy flow through an ecosystem (**Figure 21.9A**). Alternatively, energy flow may be governed by rates of consumption (as well as other, nonconsumptive interactions such as competition and facilitation, as discussed in Concept 16.3) at the highest trophic levels, which influence abundances and species composition at multiple trophic levels below them. This view is often referred to as "top-down" control of energy flow (**Figure 21.9B**). In reality, both bottom-up and top-down controls are operating simultaneously in ecosystems, but the top-down view has important implications for the effects of trophic interactions on energy flow in ecosystems.

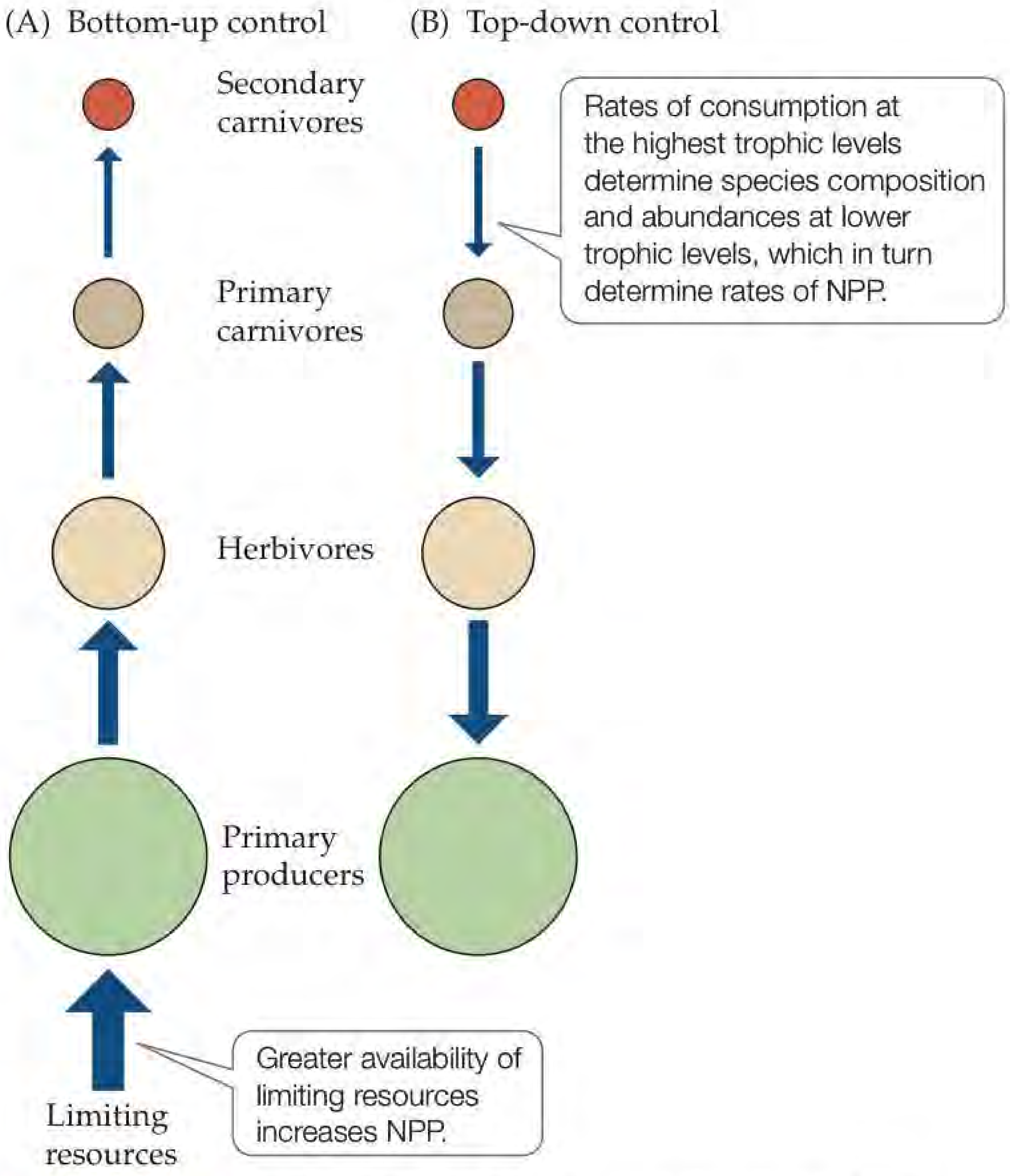


Figure 21.9 Bottom-Up and Top-Down Control of NPP Production in an ecosystem can be viewed as being controlled (A) by limiting resources or (B) by controls exerted on the species composition and abundances of autotrophs by consumption at higher trophic levels.

Trophic interactions can trickle down through multiple trophic levels

Changes in abundance or species composition at one trophic level can lead to important changes in abundance and species composition at other trophic levels. For example, an increase in the rate of predation by a carnivore at the fourth trophic level on carnivores at the third trophic level would lead to a lower rate of consumption of herbivores at the second trophic level. More herbivory would decrease the abundance of autotrophs and would therefore lower rates of NPP. Nonconsumptive species interactions, such as competition, can have similar top-down effects on abundance and species composition at lower trophic levels, as we'll see shortly. Such a series of changes in abundance and species composition is referred to as a **trophic cascade**.

Our understanding of trophic cascades comes primarily from aquatic ecosystems, although there are examples from terrestrial ecosystems as well. Several generalizations have been drawn from studies of these interactions. First, trophic cascades are most often associated with changes in the abundance of top specialist predators. Second, omnivory may act to buffer the effects of trophic cascades through the consumption of prey at multiple trophic levels. Finally, trophic cascades have been hypothesized to be most important in relatively simple, species-poor ecosystems. However, several recent experiments have demonstrated trophic cascades in ecosystems with relatively high species diversity.

AN AQUATIC TROPHIC CASCADE Many examples of trophic cascades come from unintended experiments associated with introductions of non-native species or near extinctions of native species. A classic example of the latter type is the interaction among sea otters (*Enhydra lutris*), sea urchins, and killer whales on the west coast of North America, which was discussed in the Case Study Revisited in Chapter 9. Unfortunately, there is no shortage of examples of trophic cascades associated with the intentional or unintentional introduction of non-native species. One such example resulted from the release of brown trout (*Salmo trutta*), a popular sport fish, into streams and lakes of New Zealand. The stocking of Kiwi waters by European settlers began in the 1860s, and by 1920 an estimated 60 million fish had been released throughout

New Zealand. Native fish populations have declined as a result, and some species have disappeared from streams now dominated by trout.

Alexander Flecker and Colin Townsend (1994) investigated the influence of the brown trout on the species composition of its prey (primarily stream insects) and associated effects on primary production in the Shag River. Brown trout were originally released into the Shag River in 1869 by the "Otago Acclimatisation Society" to make settlers feel more at home. The Shag River is one of a small number of streams in New Zealand that still holds both native fish and trout in the same sections. Native fish species include the common river galaxias (*Galaxias vulgaris*). The morphology and feeding behavior of galaxias are similar to those of trout, as indicated by the common name for the galaxias, Maori trout.

Flecker and Townsend compared the effects of brown trout and galaxias on stream invertebrate species composition and abundance as well as on primary production by algae. To manipulate fish presence and absence, they constructed artificial stream channels adjacent to the natural channel, made of 5 m lengths of half cylinders of PVC pipe. The PVC channels had mesh on the ends that kept fish in or out but allowed free movement of stream invertebrates and algae. The researchers placed clean gravel and stone cobbles in the bottoms of the channels to provide a substrate for the invertebrates and algae. The channels were allowed to accumulate algae and invertebrates for 10 days before the fish were added. Three treatments were initiated: channels with introduced brown trout, channels with galaxias, and channels with no fish (controls). Eight fish of similar size and mass were used for each fish species addition. The experiment was run for 10 days, after which samples were collected to determine invertebrate species composition and abundance and algal biomass.

Flecker and Townsend had expected brown trout to decrease invertebrate diversity more than the native galaxias, but the effect of fish on invertebrate diversity was relatively small and did not differ between the two fish species. The brown trout, however, reduced total invertebrate density by approximately 40% relative to the control channels, while galaxias resulted in a smaller reduction (**Figure 21.10A**). The abundance of algae increased with both fish, but the effect was greater in the channels with trout (**Figure 21.10B**). Flecker and Townsend suggested that the effect on algal biomass was the result of a trophic cascade in which fish predation not only reduced the density of stream invertebrates, but also caused them to spend more time in refugia on the stream bottom rather than feeding on algae. The trout had a much greater effect on invertebrate density, and thus on primary production, than the native galaxias. These results suggested that trophic cascades associated with the stocking of non-native fish for sport may have consequences not just for native biodiversity, but for the functioning of stream ecosystems as well.

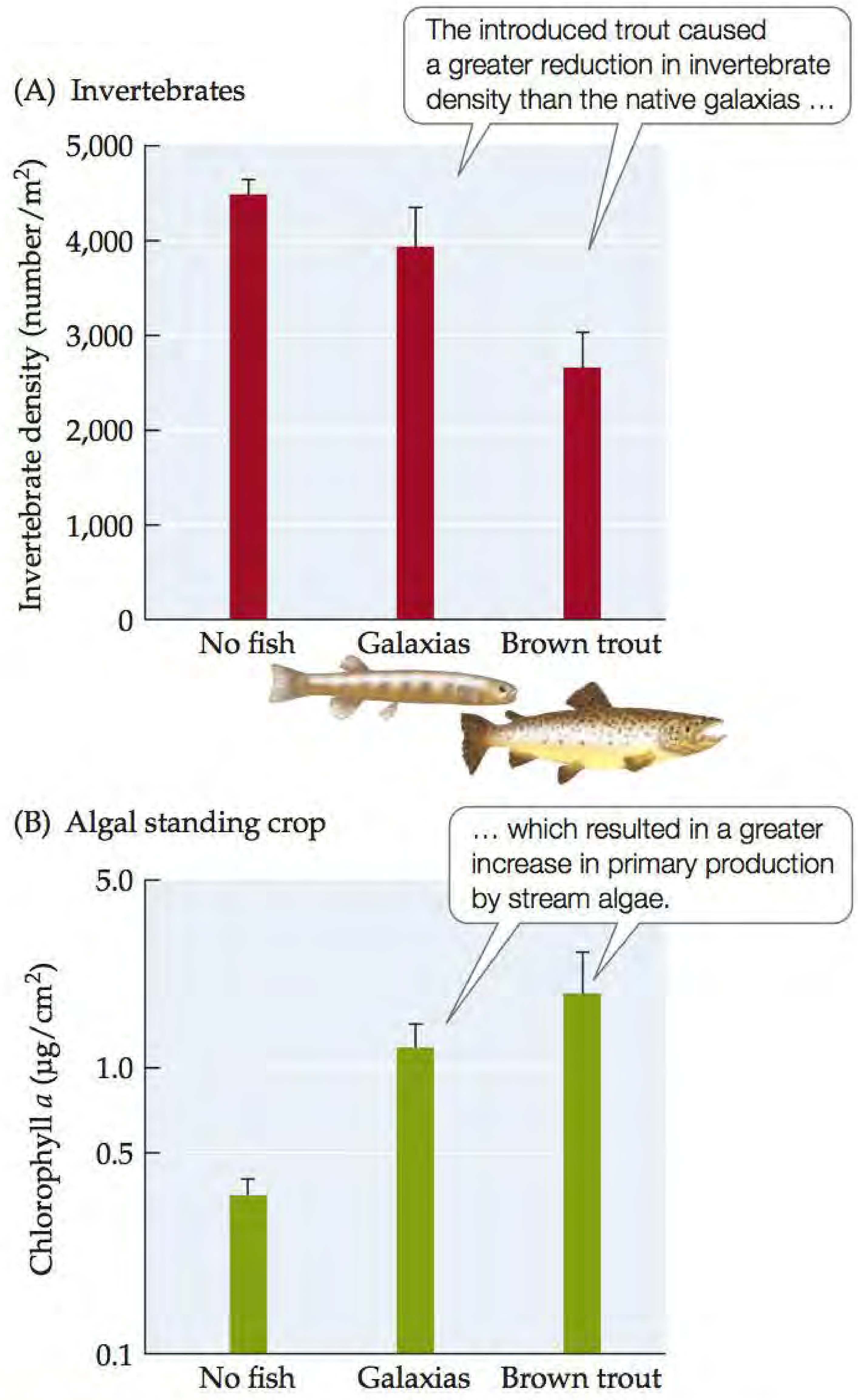


Figure 21.10 An Aquatic Trophic Cascade Flecker and Townsend used artificial stream channels to study the effects of non-native brown trout and a native fish (galaxias) on stream invertebrates and algae in the Shag River, New Zealand. (A) Effects on invertebrate density. (B) Effects on algal biomass, as estimated using chlorophyll concentrations in stream water. Error bars show one SE of the mean. (After Flecker and Townsend 1994.)

? What factor other than overall consumption rate might explain why the presence of brown trout results in a larger increase in primary production than the presence of native galaxias?

A TERRESTRIAL TROPHIC CASCADE As mentioned earlier, trophic cascades have been most commonly observed in aquatic ecosystems, where they are more frequent and their effects are stronger than in terrestrial ecosystems (Shurin et al. 2002). Terrestrial ecosystems are generally thought to be more complex than aquatic ecosystems. In addition, it was believed that a decrease in the abundance of one species in a terrestrial ecosystem was more likely to be compensated for by an increase in the abundances of similar species that were not being consumed as heavily.

Thus, trophic cascades were considered unlikely in diverse terrestrial ecosystems such as tropical forests.

Lee Dyer and Deborah Letourneau (1999a) tested the effects of a potential trophic cascade on the production of *Piper cenocladum* trees in the understory of a lowland tropical rainforest in Costa Rica. *Piper cenocladum* is a relatively common component of the understory in these forests and is eaten by dozens of different herbivore species. Ants of the genus *Pheidole* live in chambers in the petioles of the leaves of the *Piper* trees. The ants eat food bodies provided by the trees, and they also consume herbivores that attack the trees. These ants, in turn, are eaten by beetles of the genus *Tarsobaenus*. Thus, four distinct trophic levels exist in this system (**Figure 21.11**). Dyer and Letourneau had previously noted that plant biomass was lower, and rates of herbivory were higher, when densities of *Tarsobaenus* beetles were high. They performed experiments to test whether a trophic cascade involving the beetles, ants, and herbivores influenced the production of the *Piper* trees and how strong that influence was, compared with that of bottom-up factors such as light and soil fertility.

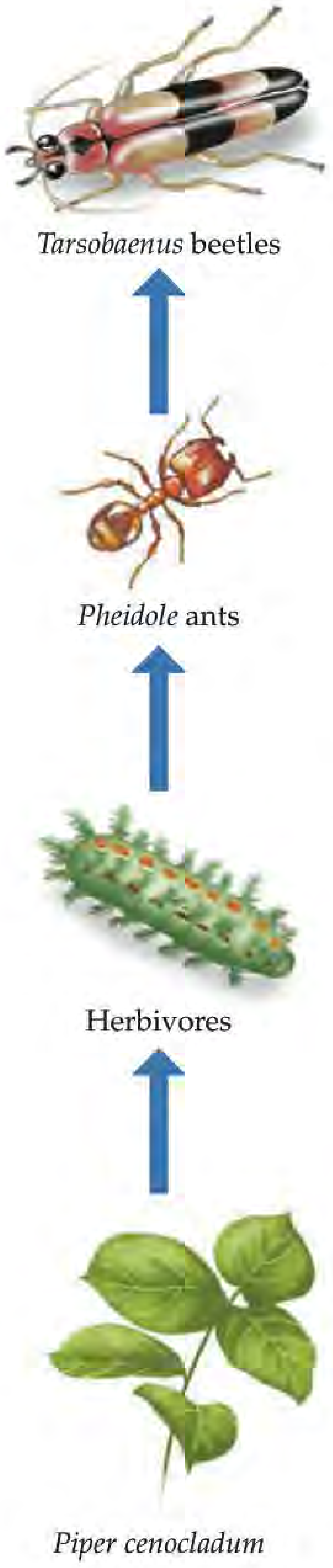
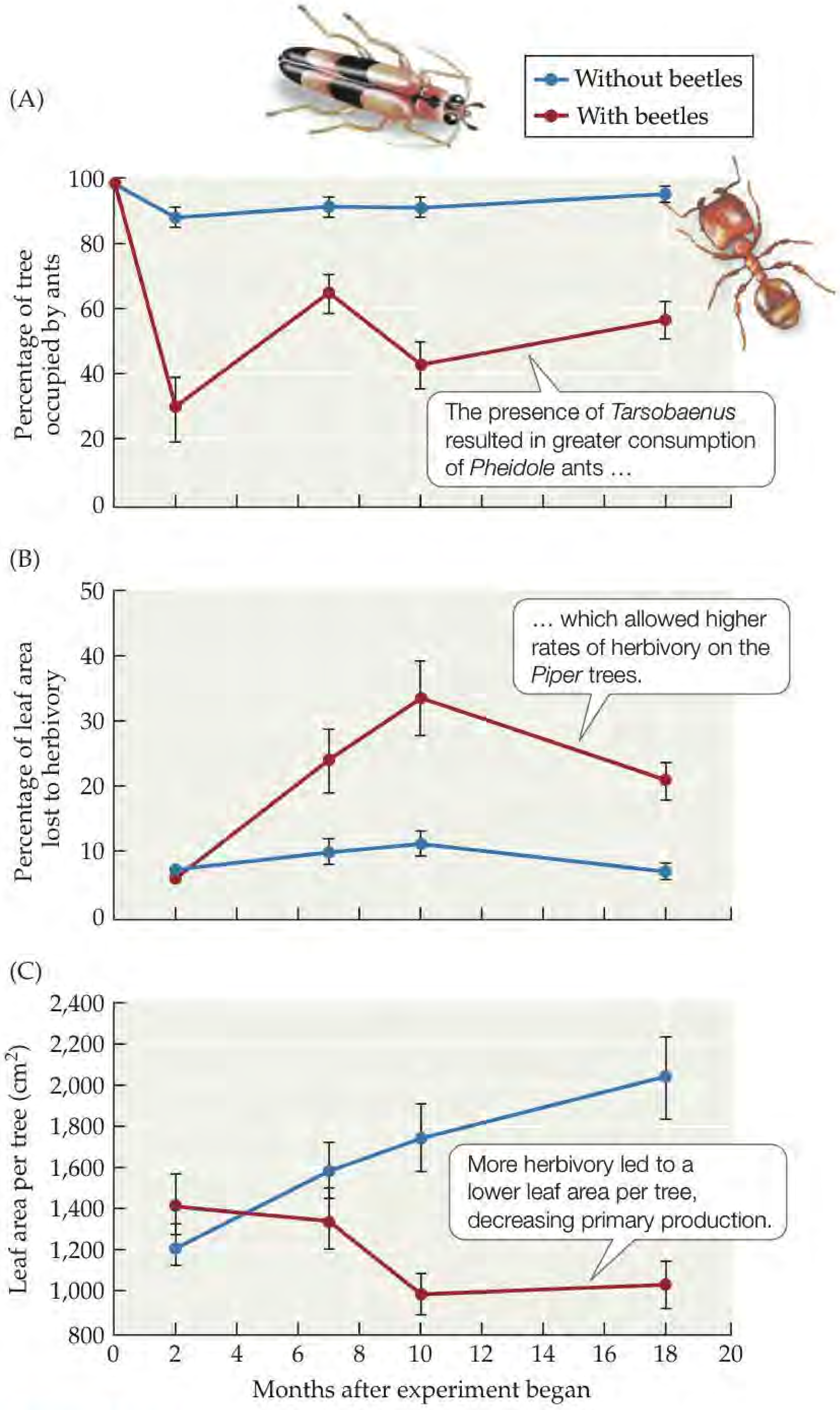


Figure 21.11 A Terrestrial Trophic Cascade Trophic interactions in the understory ecosystem of a lowland tropical rainforest in Costa Rica. *Piper cenocladum* trees are consumed by herbivores but provide shelter for *Pheidole* ants, which consume herbivores attacking the trees. *Pheidole* ants are consumed by *Tarsobaenus* beetles. Both ants and beetles also consume food bodies produced by the trees. (After Dyer and Letourneau 1999a.)



The presence of *Tarsobaenus* resulted in greater consumption of *Pheidole* ants …

… which allowed higher rates of herbivory on the *Piper* trees.

More herbivory led to a lower leaf area per tree, decreasing primary production.

Figure 21.12 Effects of a Trophic Cascade on Production A trophic cascade in a tropical rainforest understory ecosystem (see Figure 21.11) was shown to have important effects on (A) predation, (B) herbivory, and (C) production. Error bars show ± one SE of the mean. (After Dyer and Letourneau 1999a.)

Dyer and Letourneau established experimental plots in the understory by planting uniform-sized cuttings of *Piper* trees. They treated two groups of plots with an insecticide to kill any ants present, then added *Tarsobaenus* beetle larvae to one of those groups of plots. This procedure established three groups of treatment plots: one group of insecticide-treated plots with beetles, one control group of insecticide-treated plots without beetles, and one control group of untreated plots. In the plots with beetles, the insecticide treatment facilitated the establishment of the beetles by preventing ant attacks on the beetle larvae. In addition, half of the plots were on a relatively fertile soil type, and the other half were on a relatively infertile soil type. Natural light levels in the plots were also varied such that half of the plots were assigned to a high-light treatment and half to a low-light treatment. Dyer and Letourneau maintained these treatments for 18 months and measured herbivory and leaf production within each of the plots.

If the production of the *Piper* trees was limited primarily by resource supply (bottom-up control), then the addition of the *Tarsobaenus* beetles would be expected to have little effect on *Piper* leaf production. Soil fertility and light levels would be expected to have greater effects on leaf production if these effects were more important than the influence of the trophic cascade associated with beetles, ants, and herbivores (top-down control). Dyer and Letourneau found, however, that the trophic cascade was the only significant influence on leaf production. The addition of the predatory beetles decreased ant abundance fivefold, increased rates of herbivory threefold, and decreased leaf area per tree to half that in the control plots (**Figure 21.12**). This experiment provided convincing evidence of a trophic cascade affecting the production of the *Piper* trees. It should be noted, however, that the lack of an effect of soil fertility and light in the control treatments, which had low rates of herbivory, indicates that the resource(s) that actually limit production may not have been manipulated in this experiment. An additional experiment that used more controlled manipulation of light levels and soil nutrients, rather than relying on variation in natural levels, found significant effects of these resources on *Piper* production, but it also found a continued strong effect of herbivory (Dyer and Letourneau 1999b). Thus, it is clear that trophic cascades do occur in diverse terrestrial ecosystems, although they may require strong interactions between specialist predators and their prey.

What determines the number of trophic levels?

What determines the variation among ecosystems in their numbers of trophic levels, and why do so few ecosystems have five or more trophic levels? This question is not simply an academic one. Through trophic cascades, the number of trophic levels in an ecosystem can influence movements of energy and nutrients as well as the potential for toxins in the environment to become concentrated at higher trophic levels, as we will see in this chapter's Case Study Revisited. Change in the number of trophic levels may be due to the addition or loss of a predator at the top of the food web, the insertion or loss of a predator in the middle of the food web, or changes in omnivore feeding preference for foods at different trophic levels (**Figure 21.13**).

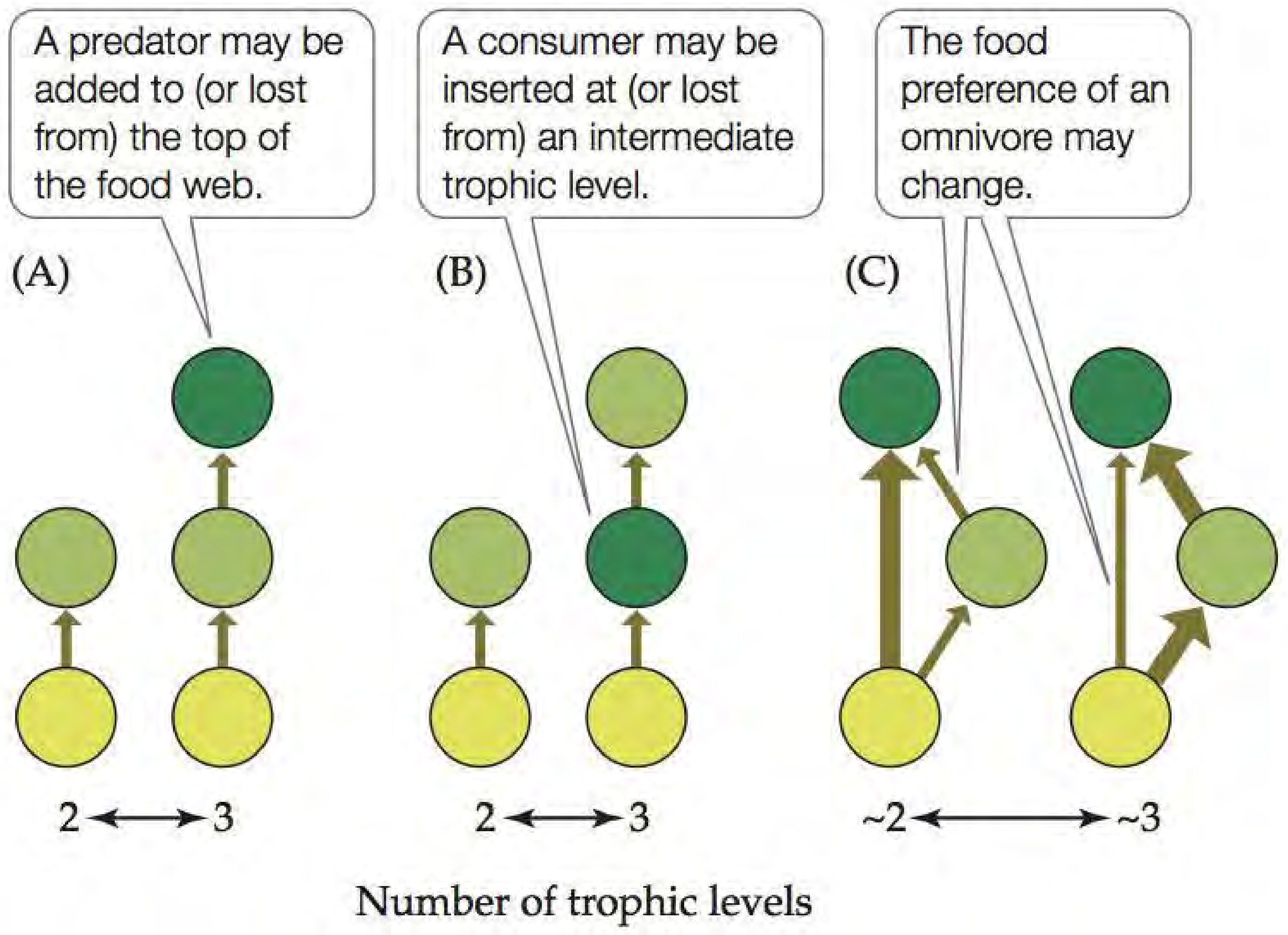


Figure 21.13 Changes in the Number of Trophic Levels Circles represent species at different trophic levels, and the thickness of the arrows represents the amount of energy flowing between species pairs. Differences among ecosystems in the number of trophic levels may occur because of (A) the addition or loss of a consumer at the top level, (B) the insertion or loss of a consumer at an intermediate level, or (C) a change in the preferred feeding level of an omnivore. (After Post and Takimoto 2007.)

Several interacting ecological factors can control the number of trophic levels in ecosystems (Post 2002b). First, the amount of energy entering an ecosystem through primary production has been proposed as a determinant of the number of trophic levels. Because a relatively large amount of energy is lost in the transfer from one trophic level to the next, the more energy there is entering a system, the more is potentially available to support viable populations of higher-level predators (see **Analyzing Data 21.1**). However, this explanation appears to be important primarily in ecosystems with low resource availability. Second, the frequency of disturbances or other agents of change, such as disease outbreaks, can determine whether populations of higher-level predators can be sustained. Because lower trophic levels are required to sustain higher trophic levels, there is a longer time lag for the reestablishment of the higher trophic levels following a disturbance. If disturbances occur frequently, then higher trophic levels may never become established, no matter how much energy is entering the system (Pimm and Lawton 1977). While some support for this hypothesis exists, the ability of some organisms to adapt to frequent disturbances and the potential for rapid colonization of disturbed sites (see Concept 17.1) result in a smaller effect of disturbance on trophic level number than expected. Finally, the area of an ecosystem can influence the number of trophic levels. Larger ecosystems support larger population sizes, which are less prone to local extinction (see Concept 11.3). Larger ecosystems also have more habitat heterogeneity and thus tend to have higher species diversity.

Support for the effect of ecosystem size on the number of trophic levels is derived primarily from studies of lakes and oceanic islands, ecosystems with discrete boundaries. For example, Gaku Takimoto and colleagues (2008) tested the relative effects of disturbance and island size on the number of trophic levels on 36 islands in the Bahamas. The effect of disturbance was tested by examining 33 of the smaller islands that were either exposed to (19 islands) or protected from (14 islands) storm surges. The number of trophic levels was estimated using isotopic ratios of carbon and nitrogen (as described in Concept 20.4) in tissues from the top predators, spiders and lizards. Takimoto and colleagues found that exposure to storm surges had no effect on the number of trophic levels. However, disturbance did influence the identity of the top predators: orb spiders were more frequently the top predators on exposed islands, and *Anolis* lizards were at the apex of the food web on protected islands. Island size, however, was strongly correlated with the number

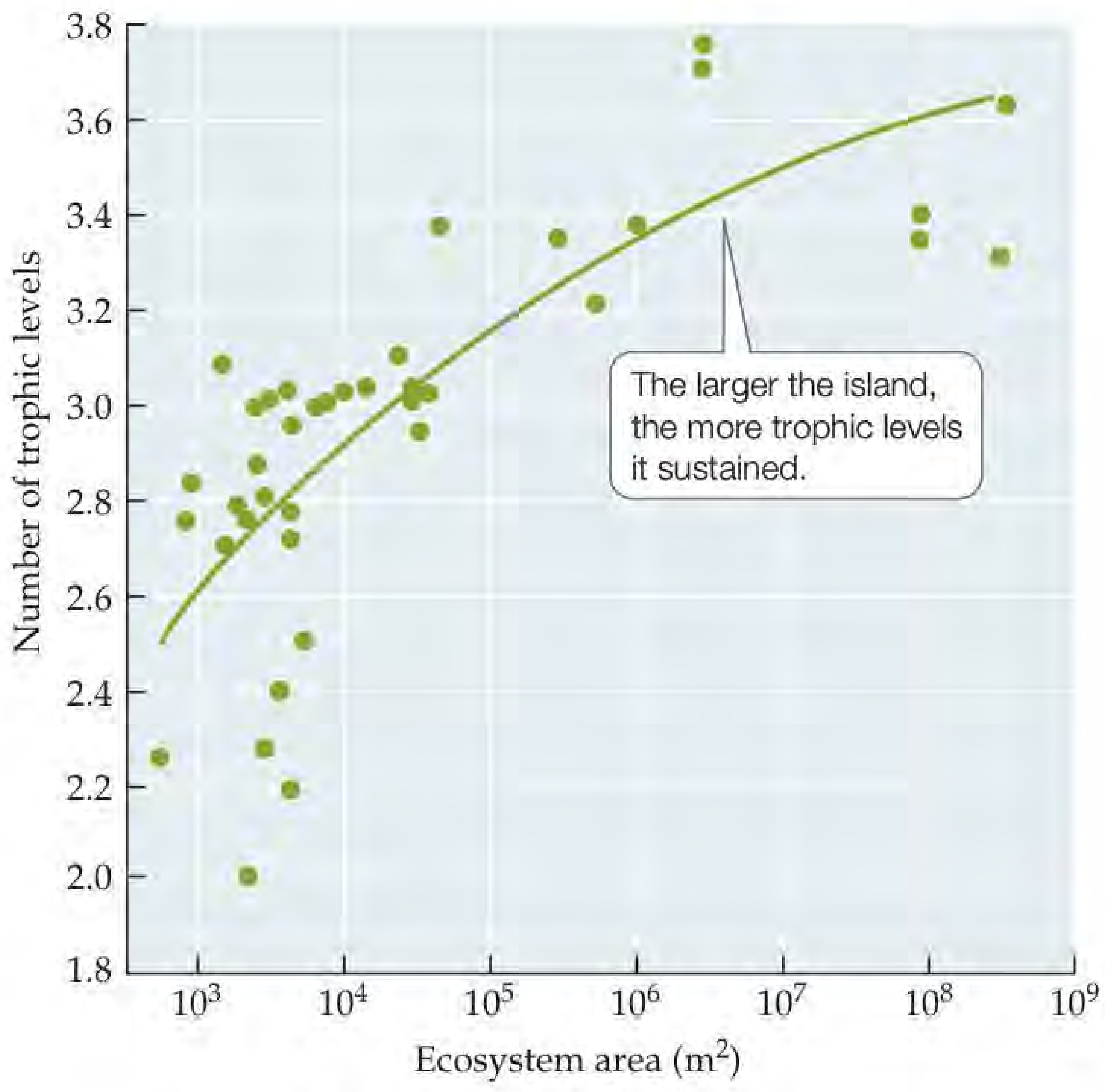
ANALYZING DATA 21.1 Does the Identity of Organisms Influence Energy Flow between Trophic Levels?

Ecologists have noted that individuals and populations of some species (known as keystone species; see Concept 16.3) influence energy flow between trophic levels more than others. In particular, we've seen several examples in which invasive species have greatly altered energy transfers as well as diversity within communities. Attention has largely been focused on the behavioral characteristics of a species, such as how effective individuals of a species are at hunting or grazing, or its population dynamics (e.g., whether a population exhibits exponential growth; see Concept 10.3). Additionally, the thermal physiology and sizes of the species making up a trophic level can influence how much energy makes it from one trophic level to the next.

Using information from the text and Table 21.1, provide a rough estimate of how much energy would make it to the second, third, and fourth trophic levels in the following simplified food chains. Start with 100 units of energy in the autotrophic base of each of these food chains (i.e., plants or algae). Assume the production efficiencies for endotherms do not vary according to diet.

1. plants → non-insect invertebrate herbivores → small mammals → large mammals
2. algae → aquatic non-insect invertebrate herbivores → insect predators → fish
3. plants → large mammal herbivores → large mammal predators → large mammal predators
4. plants → insect herbivores → insect predators → insect predators
5. Remembering that the transfer of energy between trophic levels can influence the number of trophic levels an ecosystem can sustain, and that greater energy transfer usually enhances the establishment of higher tropic levels, which of the hypothetical food chains in Questions 1–4 would be *most* likely, and which *least* likely, to sustain the highest trophic level?

See the companion website for a similar ANALYZING DATA exercise.



The larger the island, the more trophic levels it sustained.

Figure 21.14 Ecosystem Size Is Correlated with the Number of Trophic Levels On islands in the Bahamas, Takimoto and colleagues found that as island size increased, the number of trophic levels also increased. (After Takimoto et al. 2008.)

of trophic levels (**Figure 21.14**), providing evidence that ecosystem size can influence the number of trophic levels in a terrestrial ecosystem.

We turn our attention next to a more detailed investigation of trophic relationships in ecosystems as we cross the disciplinary boundaries of ecosystem ecology and community ecology (the topic of Unit 5) to examine how energy flow can influence the diversity and stability of communities and ecosystems.

CONCEPT 21.4

Food webs are conceptual models of the trophic interactions of organisms in an ecosystem.

Food Webs

Ever since Charles Darwin, in *The Origin of Species* (1859), described "a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, … dependent upon each other in so complex a manner," the interdependence of species has been a central concept in ecology. When we examine these links among species with a focus on feeding relations, they can be described by a **food web**, a diagram showing the connections among organisms and the food they consume. For the desert ecosystem we considered at the start of this chapter, we can construct a simplified food web showing that plants are consumed by insects and ground squirrels and that these herbivores are food for scorpions, eagles, and foxes (**Figure 21.15A**). In this way, we can begin to understand qualitatively how energy flows from one component of this ecosystem to another, and how that energy flow may influence changes in population sizes and the species composition of communities.

Food webs are complex

The desert food web in Figure 21.15A is far from complete. Depending on our purposes, we may wish to add other organisms and links to the food web, providing additional complexity. For example, the scorpion consumes insects such as the grasshopper, but like the grasshopper, it may be food for birds such as shrikes and owls (**Figure 21.15B**). As we continue to add more and more organisms to the food web, we add complexity, such that the food web may take on the appearance of a "spaghetti diagram" (**Figure 21.16**). In order to add greater realism, it is important to recognize that the feeding relationships of animals can span multiple trophic levels (omnivory) and may even include cannibalism (half-circle arrows in Figure 21.16) (Polis 1991).

Although food webs are useful conceptual tools, even a simplified food web is a static description of energy flow and trophic interactions in a temporally dynamic ecosystem. Actual trophic interactions can change over time (Wilbur 1997). Some organisms alter their feeding patterns as they age. Maturing frogs, for example, make the transition from omnivorous aquatic tadpoles to carnivorous adults. Some animals, such as migratory birds, are relatively mobile and are thus components of multiple food webs. Furthermore, most food webs fail to account for additional biological interactions among organisms that influence population and community dynamics, such as pollination mutualisms. (In community studies, this problem may be addressed by the use of interaction webs, as described in Figure 16.5.) The critically important roles of microorganisms are often ignored as well, despite their processing of a substantial amount of the energy moving through ecosystems. What are food webs good for, then? Despite these apparent shortcomings, food webs are important conceptual tools for understanding the dynamics of species interactions and energy flow in ecosystems and hence the community and population dynamics of their component organisms.

The strengths of trophic interactions are variable

As indicated in the quote from Darwin above and in earlier chapters, a core concept of ecological thought is that "everything is connected to everything else." However,

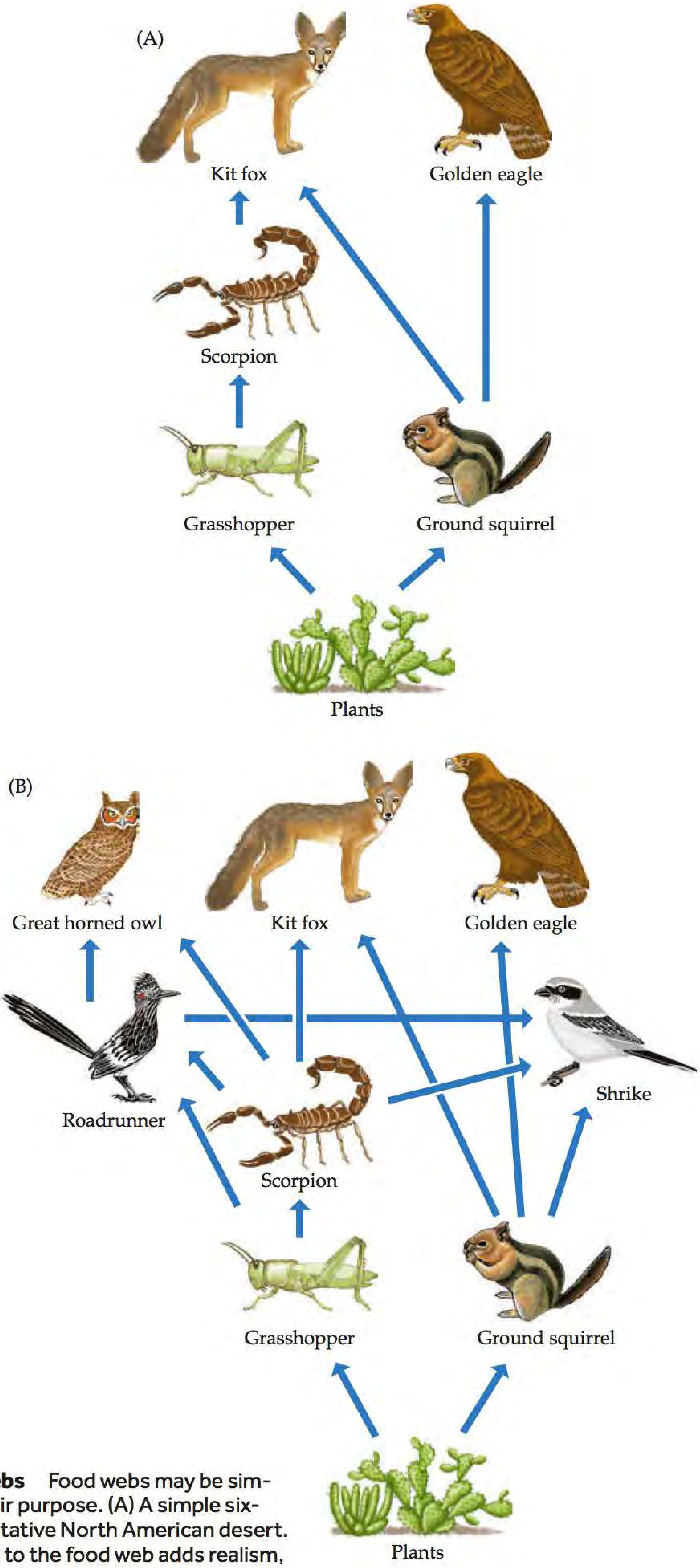


Figure 21.15 Desert Food Webs Food webs may be simple or complex depending on their purpose. (A) A simple six-member food web for a representative North American desert. (B) Addition of more participants to the food web adds realism, but the inclusion of additional species adds complexity.

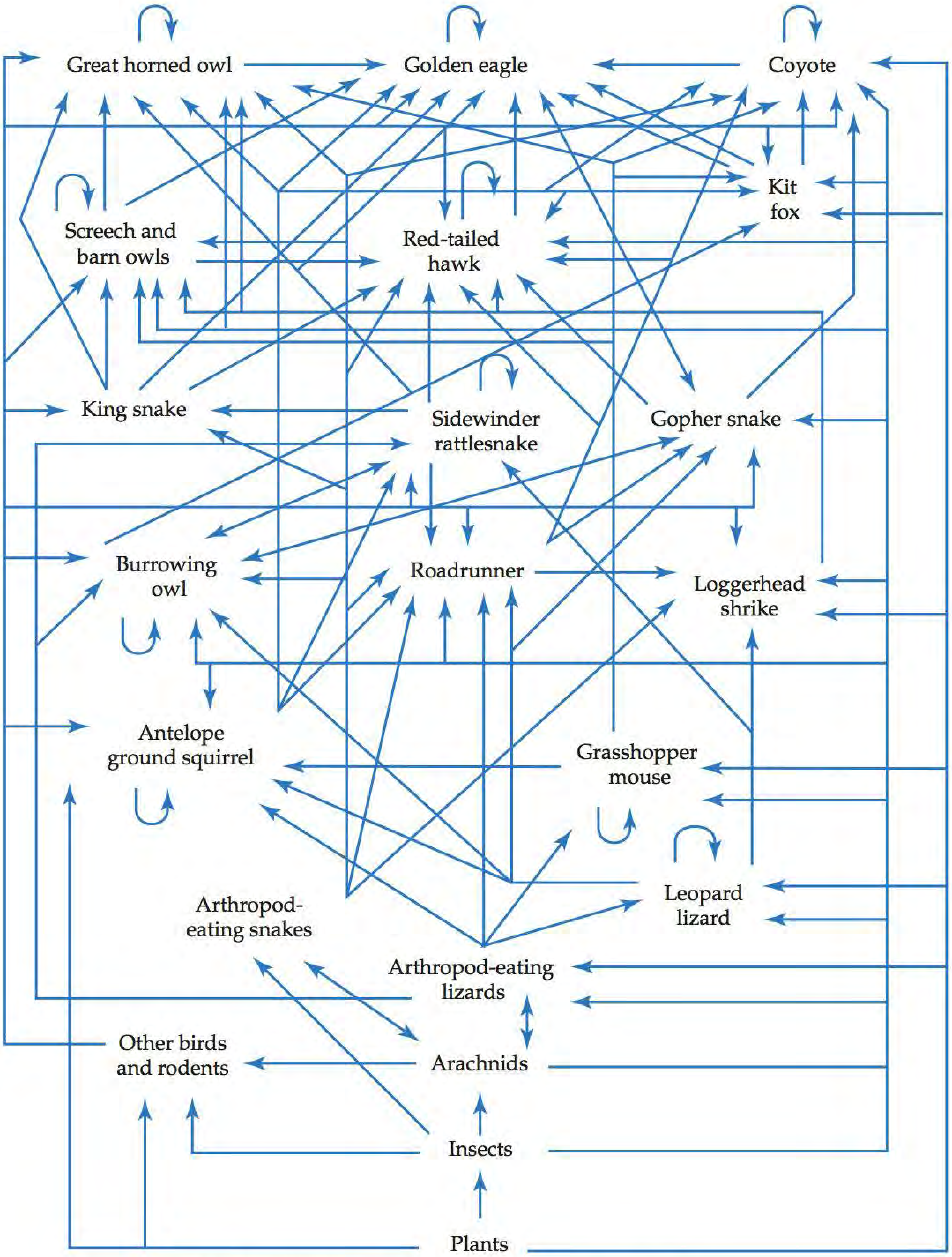


Figure 21.16 Food Webs Can Be Complex In this North American desert food web, complexity overwhelms any interpretation of interactions among the members. Even this food web, however, lacks the majority of the trophic interactions in the ecosystem. (From Polis 1991.)

? How many of the organisms or feeding groups depicted in this food web consume both plants and animals as food sources? What does this suggest about the frequency of omnivory in this food web?

the links among the species in an ecosystem vary in their importance to energy flow and species population dynamics; in other words, not all connections are equally important. Some trophic relationships play larger roles than others in dictating how energy flows through the ecosystem. *Interaction strength* is a measure of the effect of the population of one species on the population size of another species (see Ecological Toolkit 16.1). Determining interaction strengths is an important goal of ecologists because it helps us simplify the "spaghetti" in a complex food web by focusing attention on those links that are most important for basic research and conservation.

How are interaction strengths determined? Several approaches have been used. Removal experiments, like those described in Concept 16.3 to determine competition or facilitation, can be employed, but performing such experimental removals to quantify every link in a food web would be logistically overwhelming. Therefore, much current ecological research is devoted to discovering simpler, less direct measures that can still give us a reliable estimate of the relative importance of different links. For example, simple food webs can be coupled with observations of the feeding preferences of predators and of changes in the population sizes of predators and prey over time to provide an estimate of which interactions are the strongest. Similarly, comparisons of two or more food webs in which a predator or prey species is present in some but absent in others may provide evidence for the relative importance of links. Predator and prey body sizes have been used to predict the strengths of predator–prey interactions because feeding rate is known to be related to metabolic rate, which in turn is governed by body size. The best estimates of interaction strengths in food webs often come from a combination of these approaches.

A series of classic studies examining interaction strengths in food webs was performed in rocky intertidal zones of the Pacific Northwest by Robert Paine. Paine (1966) had observed that the diversity of organisms in rocky intertidal zones declined as the density of predators decreased. He reasoned that some of those predators might be playing a greater role than others in controlling the diversity of these communities. One of Paine's critical observations was that one mussel species (*Mytilus californianus*) had the ability to overgrow and smother many of the other sessile invertebrate species that compete with it for space. Paine hypothesized that predators might play a key role in maintaining diversity in this community by consuming these mussels and preventing them from competitively excluding other species.

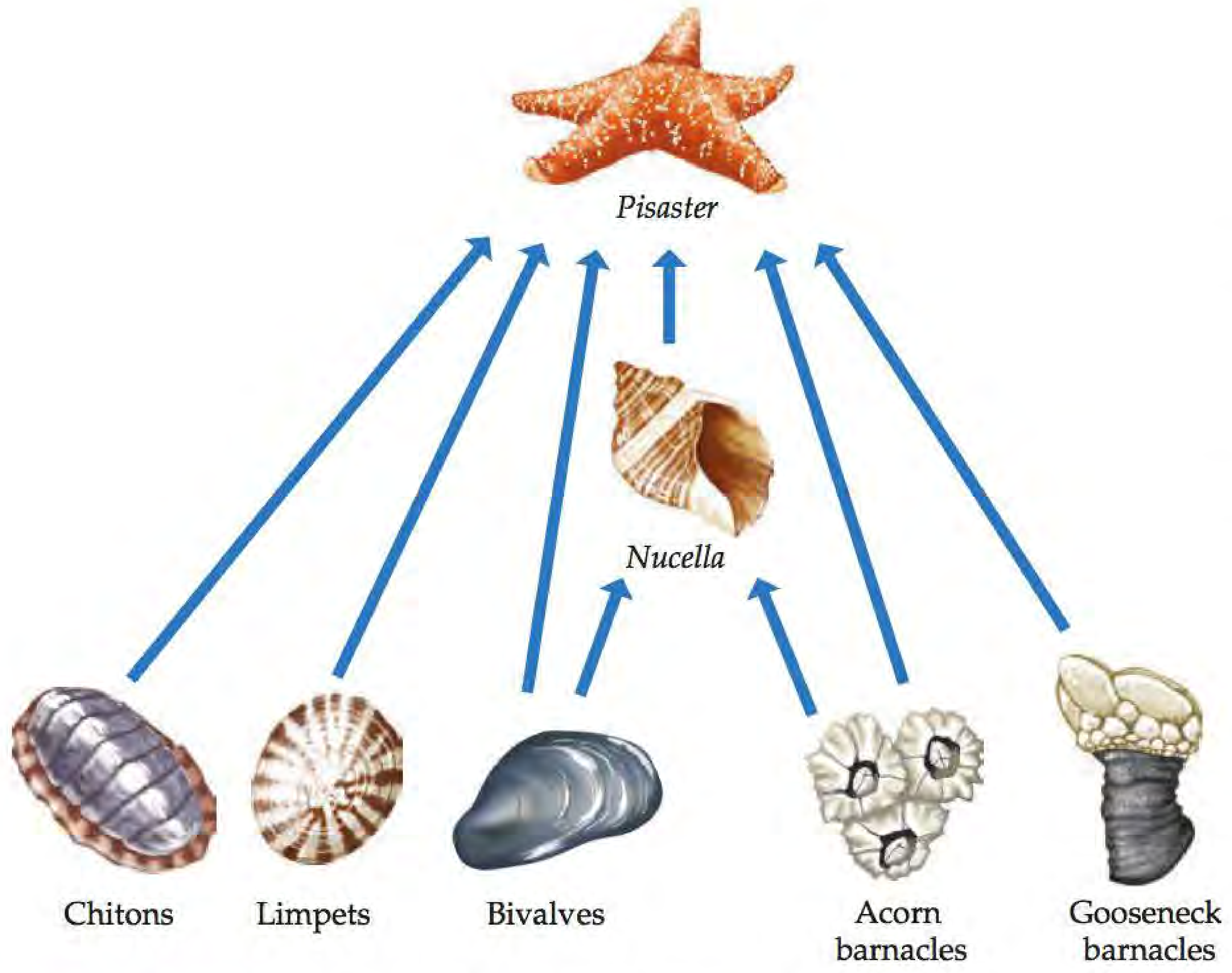


Figure 21.17 An Intertidal Food Web This food web from the rocky intertidal zone of Mukkaw Bay, Washington State, was used by Robert Paine to investigate the strength of the interaction between the sea star *Pisaster ochraceus* and its prey.

To test these hypotheses, Paine conducted an experiment in Washington State, in which he removed the top predator in the system, the sea star *Pisaster ochraceus*, from experimental plots. *Pisaster* feeds primarily on bivalves and barnacles and to a lesser extent on other mollusks, including chitons, limpets, and a predatory whelk (*Nucella* sp.) (**Figure 21.17**). Following the continuous manual removal of *Pisaster* from 16 m^2 plots, acorn barnacles (*Balanus glandula*) became more abundant, but with time, they were crowded out by mussels (*Mytilus*) and gooseneck barnacles (*Pollicipes* spp.). After 2½ years, the number of species in the community had decreased from 15 to 8. Even 5 years after the experiment began, when sea stars were no longer being removed, dominance by the mussels continued, as individual mussels had grown to sizes that prevented predation by sea stars, and diversity remained lower in the experimental plots than in adjacent control plots (Paine et al. 1985). Experimental removals of higher-level predators in other intertidal zones, including one in New Zealand, which shares no species with the intertidal zone of the Pacific Northwest, resulted in similar reductions in diversity. Predators in these intertidal ecosystems are thus key to maintaining species diversity by preventing competitive exclusion. Such species are more important in food webs than their numbers would indicate.

The experimental research of Paine and others was an encouraging advance in ecology because it demonstrated that, despite the potential complexity of trophic interactions among species, patterns of energy flow and community structure might be governed by a small subset of those species. Paine called animals like it *Pisaster keystone species*, defining them as species that have a greater influence on energy flow and community composition than their abundance or biomass would predict (see Figure 16.16). The keystone species concept has become an important focus in ecology and conservation biology because it implies that protecting such species may be critical for protection of the many other species that depend on them (as we'll see in Concept 23.5). Many keystone species are predators at higher trophic levels, which tend to have large effects on prey populations relative to their own abundance.

Some species act as keystone species in only part of their geographic range, suggesting that interaction strengths are dependent on the environmental context. Several studies, including those described in Figure 16.19 and Ecological Toolkit 16.1, have found context-dependent variation in the degree to which species behave as keystone species. Thus, while the keystone species concept is intuitively simple, predicting when and where a particular species will behave as a keystone species remains a challenge.

Direct and indirect effects determine net interaction strength

One reason it remains difficult to predict the strength of trophic interactions is that the ecological importance of a keystone predator such as *Pisaster* manifests itself not only through one strong link, such as that between *Pisaster* and mussels, but also through strong indirect effects (see Figure 16.11), such as the effects *Pisaster* has on other species by reducing the abundance of mussels. If *Pisaster* consumed only the species that are inferior competitors for space (such as barnacles), it would not play a keystone role in the rocky intertidal community. Thus, predicting the effects of species losses on the remaining community requires an understanding of not only the strengths of individual links, but also the strengths of chains of indirect effects.

Removal experiments can provide estimates of the *net* effect of an interactor species on a target species (see Ecological Toolkit 16.1). This net effect includes the sum of the interactor's direct effect and all of its possible indirect effects mediated through the other species present in the community (**Figure 21.18**). The net effect of a predator on its prey, for example, includes not only the direct effect of prey consumption, but also the effects the predator has on other species that compete with, facilitate, or modify the environment of the target prey species. For example, *Pisaster* has a negative direct effect on barnacles by consuming them. However, the positive indirect effect *Pisaster* has on barnacles by consuming mussels (and thus freeing the barnacles from competition for space) is much stronger;

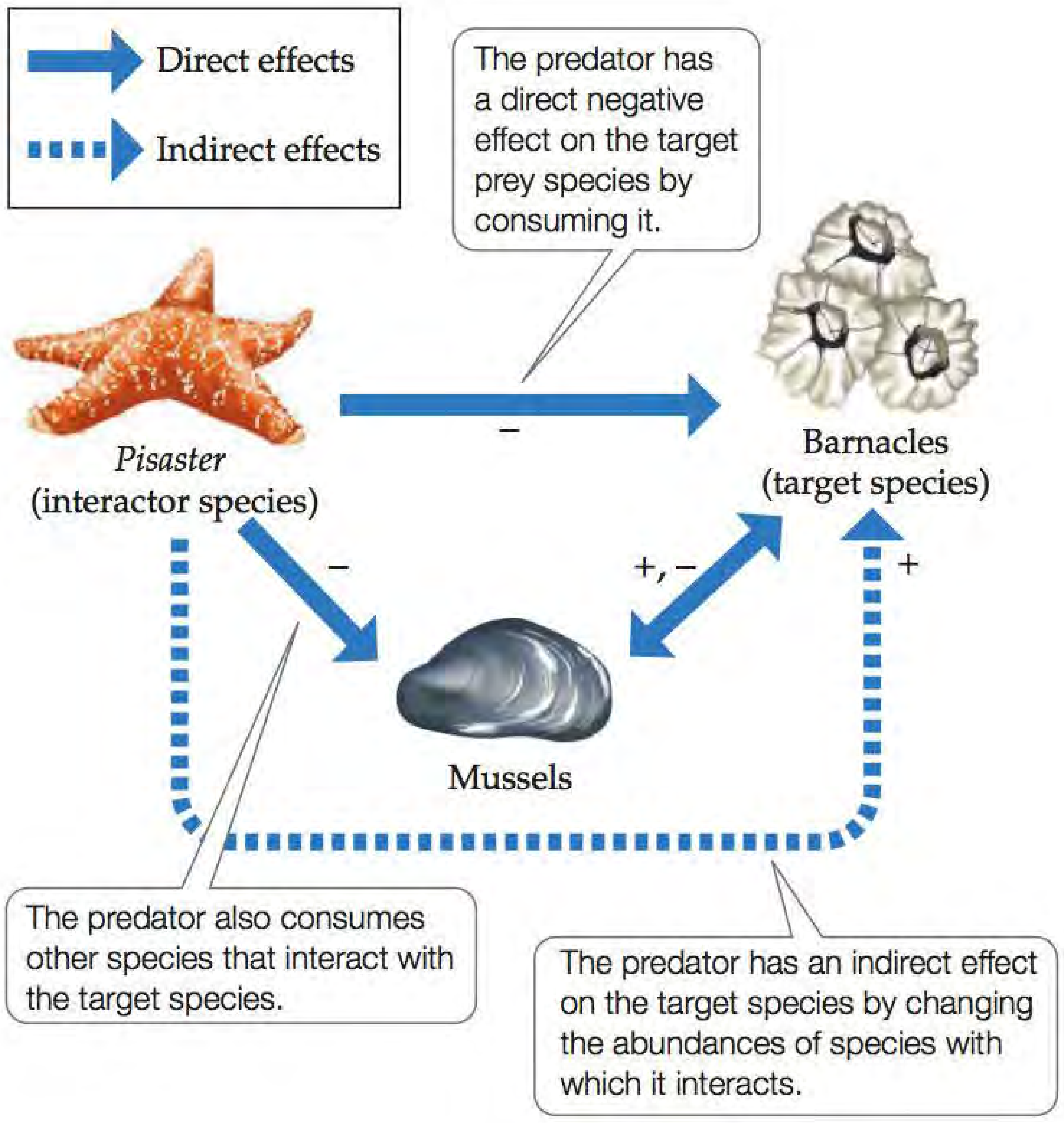


Figure 21.18 Direct and Indirect Effects of Trophic Interactions The net effect of a predator on a target prey species includes all possible indirect effects of the predator on other species in the community that interact with the target prey species as well as the direct effect of consumption.

thus, *Pisaster* has a net positive effect on this inferior competitor. If the negative direct effect of a predator on the abundance of a target prey species is offset by its positive indirect effects on that species, the net effect may appear weak. Alternatively, the net effect of a predator on a target prey species may appear very strong if both the direct and indirect effects are in the same direction.

Eric Berlow (1999) hypothesized that the potential for indirect effects to offset or reinforce the direct effect of a predator should be greatest when the direct effect is weak. Berlow tested his hypothesis by manipulating the direct and indirect effects of predatory whelks (snails of the genus *Nucella*) on a target prey species, the mussel *Mytilus trossulus*. The whelks also prey on acorn barnacles (*Balanus glandula*), which compete with the mussels for space. While whelks have a negative direct effect on mussels (by eating them), they can have either a positive or a negative indirect effect on mussels by eating barnacles. Barnacles generally facilitate mussels by providing safe "nooks and crannies" for mussel larvae to settle in. If barnacles settle on a rock in very dense clusters, however, they grow thin and are not well attached to the rock. When that happens, the barnacles, and any mussels that have settled on them, are more easily knocked off the rocks by waves. Therefore, when barnacles are at low densities, whelk predation on barnacles has a negative indirect effect on mussels by removing the mussels' preferred settlement substrate. However, when barnacles are at high densities, some thinning of the barnacles by whelks has a positive indirect effect on mussels by providing them with a more stable settlement substrate (**Figure 21.19A**).

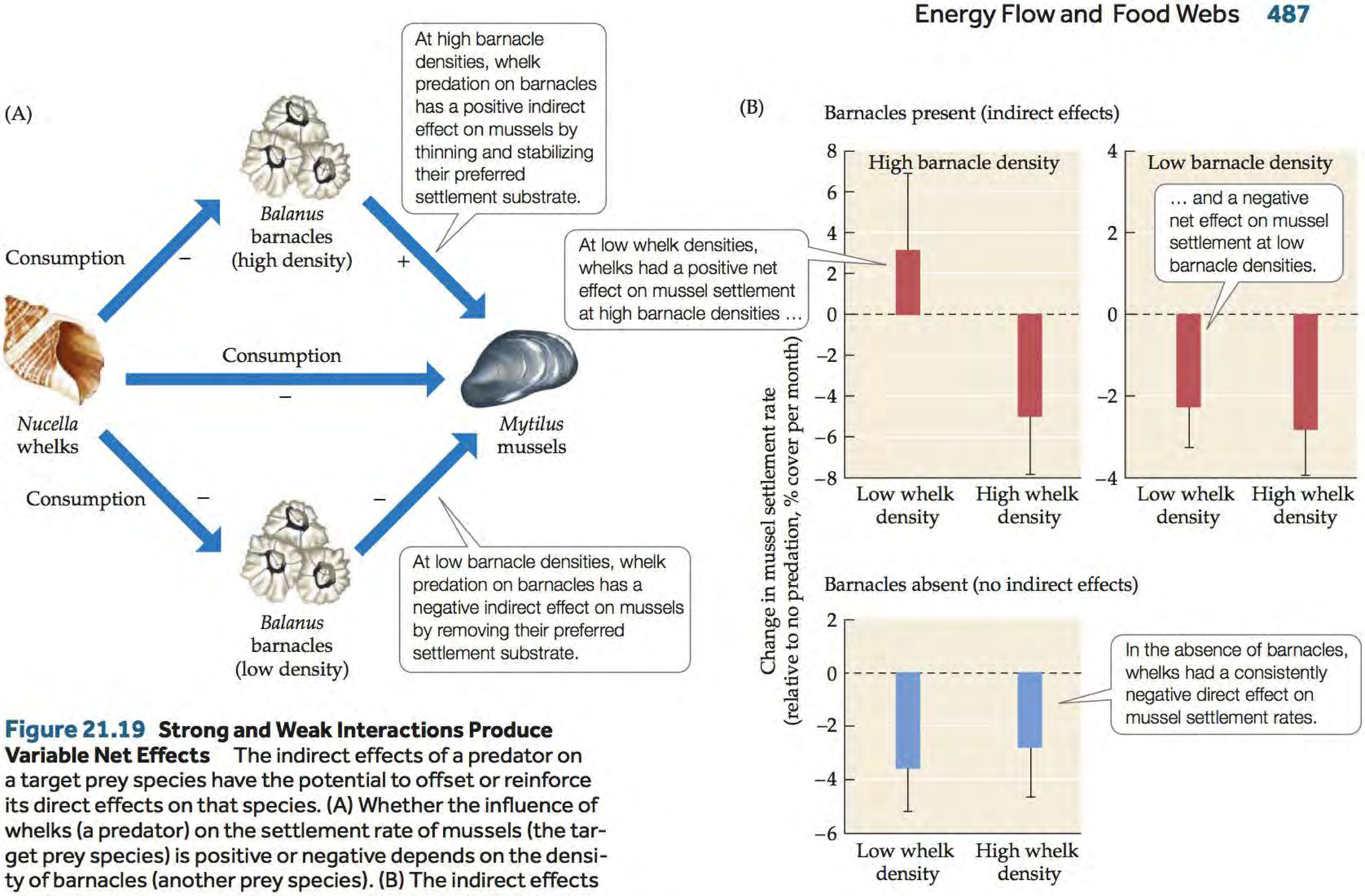
Berlow manipulated the strength of the direct effect of whelk predation by using high and low densities of whelks. He then measured the effect of whelks on mussel settlement rates in the presence (with indirect effects) and absence (no indirect effects) of barnacles. Whelk predation, without the indirect effects mediated by barnacles, had a consistent negative direct effect on the settlement rate of mussels, regardless of whelk density (**Figure 21.19B**). In the presence of barnacles, however, the effect of whelk density on mussel settlement rates changed. At high whelk densities (i.e., when the direct effect of whelks was strong), the whelks had a consistently negative net effect on mussel settlement, regardless of the densities of barnacles. When whelks were at low densities, however (i.e., when their direct effect was weak), the net effect on mussel settlement was either positive or negative depending on the density of the barnacles, as described above.

The results of Berlow's experiment supported his hypothesis, showing that the outcome of weak direct effects varied as a result of indirect effects. This mix of positive and negative indirect effects contributes to variation in the outcomes of species removal experiments when the direct effect is too weak to overcome the indirect effects. Why is this variation important? If a predator has varying (positive or negative) effects on a target prey species depending on the presence or absence of another species, the potential for the predator to eliminate that prey species throughout its range is lower. The variation associated with weak interactions may therefore promote coexistence of multiple prey species because different prey are facilitated in different places.

Does complexity enhance stability in food webs?

Ecologists have pondered whether more complex food webs—those with more species and more links among them—are more stable than simpler food webs with lower diversity and fewer links. Stability, in this context, is usually evaluated by the magnitude of changes in the population sizes of the organisms in the food web over time. As we saw in Chapter 11, large oscillations in population size over time increase the susceptibility of species to local extinction. Thus, a less stable food web means a greater potential for extinction of its component species. The question of stability is taking on ever greater importance with increasing rates of biodiversity loss and nonnative species invasions worldwide. How an ecosystem responds to species loss or gain is strongly related to the stability of its food webs.

Early proponents of the idea that food web complexity increases stability based their arguments on observations of real trophic interactions as well as on intuition.



At high barnacle densities, whelk predation on barnacles has a positive indirect effect on mussels by thinning and stabilizing their preferred settlement substrate.

At low barnacle densities, whelk predation on barnacles has a negative indirect effect on mussels by removing their preferred settlement substrate.

At low whelk densities, whelks had a positive net effect on mussel settlement at high barnacle densities ...

... and a negative net effect on mussel settlement at low barnacle densities.

In the absence of barnacles, whelks had a consistently negative direct effect on mussel settlement rates.

Figure 21.19 Strong and Weak Interactions Produce Variable Net Effects The indirect effects of a predator on a target prey species have the potential to offset or reinforce its direct effects on that species. (A) Whether the influence of whelks (a predator) on the settlement rate of mussels (the target prey species) is positive or negative depends on the density of barnacles (another prey species). (B) The indirect effects of whelks were apparent, however, only at low whelk densities (when the direct effect of whelks was weak). Error bars show one SE of the mean. (After Berlow 1999.)

Ecologists such as Charles Elton and Eugene Odum argued that simpler, less diverse food webs should be more easily perturbed, experience larger changes in species population densities, and experience greater species losses as a result. More rigorous mathematical analyses of food webs, however, provided a contrary view. Robert May (1973) used food webs made up of random assemblages of organisms to demonstrate that food webs with higher diversity are less stable than those with lower diversity. The instability in May's models resulted from accentuation of population fluctuations by strong trophic interactions: the more interacting species there were, the more likely that their population fluctuations would reinforce one another, leading to the extinction of one or more of the species.

May's work overturned the notion that more complex systems are inherently more stable than simpler ones. Yet anyone visiting a tropical rainforest or a coral reef can attest to the fact that highly diverse and complex communities do persist in nature. Therefore, much ecological research has been devoted to discovering the factors that allow naturally complex food webs to be stable. More recent models, for example, have incorporated distributions of interaction strengths more closely resembling those observed in nature. In addition, there is a greater realization that weak interactions can stabilize trophic relationships, as demonstrated by the results of Eric Berlow's work described above. These models and experiments suggest that, while more complex systems are not necessarily more stable, some natural food webs may have a particular structure or organization that allows increased species diversity to have a stabilizing effect. Other studies suggest that the buffering influence of weak interactions (McCann et al. 1998; Neutel et al. 2002) and of behavioral or evolutionary changes in prey choice (Kondoh 2003) can help to reduce the population fluctuations associated with complex food webs. Additionally, the identity of the species in a food web is important to its behavior, with some species exerting a disproportionally greater influence on stability, and others being more likely to go extinct (Lawler 1993).

How diversity at one trophic level affects the stability of populations at other trophic levels has also been of interest to ecologists, particularly in the context of biodiversity loss (as we will see in Concept 23.3). Elton (1958) proposed that plant diversity influences diversity at higher trophic levels, with greater plant diversity stabilizing animal populations. We saw in Concept 19.4 that plant production is often higher in more diverse communities and that more diverse plant communities are better able

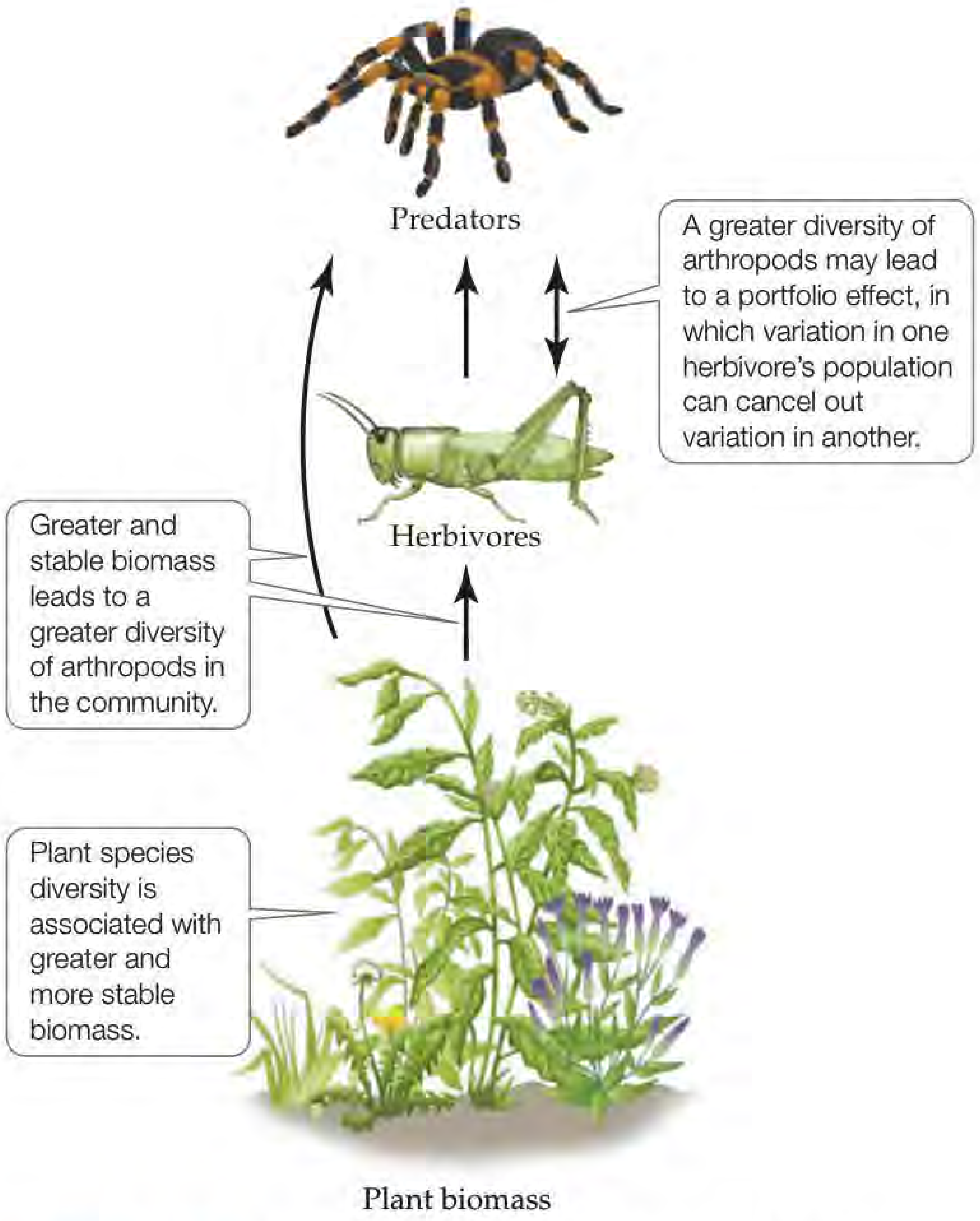


Figure 21.20 Plant Diversity and Stability in Food Webs Greater plant diversity enhanced the stability of arthropod communities in experimental plots. The potential mechanisms of this effect include greater and more stable plant biomass. Plant diversity, which is associated with greater habitat complexity, may be associated with greater abundance and diversity of predators, which may lead to greater top-down influences on herbivores and plants (trophic cascades). In addition, plant diversity enhances the diversity of the arthropod community as a whole, enhancing portfolio effects, which keep overall abundance stable. (After Haddad et al. 2011.)

to recover from disturbances. Do these properties convey greater stability to higher trophic levels? Nick Haddad and colleagues set out to test this hypothesis, using experimental prairie plots established by David Tilman at the Cedar Creek Ecosystem Science Reserve in Minnesota (Haddad et al. 2011). They studied the abundance and species composition of arthropod (primarily insect and spider) communities in plots with 1, 2, 4, 8, or 16 plant species over an 11-year period. A total of 733 different arthropod species were sampled during this period. These arthropods were divided into communities by their feeding preferences, which included detritivores, herbivores, predators, and parasitoids. Stability was evaluated by the amount of change in the abundances of individuals within populations and communities.

Haddad et al. found that in general, the arthropod communities were more stable in the plots with higher plant diversity. However, not all arthropod communities exhibited the same relationship between plant diversity and stability. Populations of specialist herbivores (those that eat one or a few species of plants) had lower stability with increases in plant diversity. In contrast, the community of all herbivores showed greater stability with increasing plant diversity. The researchers suggested that the underlying mechanisms by which plant diversity influences arthropod community stability include greater and more stable plant biomass and increased diversity in the arthropod communities (**Figure 21.20**). Higher plant diversity was linked to greater predator abundance and diversity through its influence on habitat diversity. These predators may exert top-down effects on herbivore and plant abundances (trophic cascades). Haddad et al. also suggested that community stability is enhanced by a *portfolio effect*, in which variation in the population of one species cancels out variation in another such that overall abundance in the community remains the same. Greater diversity among the arthropods would lead to a greater probability of the portfolio effect. The researchers concluded that plant diversity in the prairie ecosystem provides services to humans not only in the form of potential biofuels, but also by keeping arthropod communities more stable and preventing outbreaks of insects that can be problematic for crops and forests.

A CASE STUDY REVISITED
Toxins in Remote Places

Knowledge of how energy flows through the trophic levels of ecosystems is key to understanding the environmental effects of persistent organic pollutants like those described in this chapter's Case Study. Some chemical compounds taken up by organisms, either directly from the environment or by consumption with their food, can become concentrated in their tissues. For a variety of reasons, these compounds are not metabolized or excreted, so they become progressively more concentrated in the body over the organism's lifetime, a process known as **bioaccumulation**. Bioaccumulation can lead to increasing tissue concentrations of these compounds in animals at successively higher trophic levels as animals at each trophic level consume prey with higher concentrations of the compounds. This process is known as **biomagnification** (**Figure 21.21**). The POPs we discussed at the beginning of this chapter are particularly susceptible to these processes.

The potential dangers associated with bioaccumulation and biomagnification of POPs were well publicized by Rachel Carson's book *Silent Spring*, published in 1962, in which she described the devastating effects that pesticides, particularly DDT, were having on nontarget bird and mammal populations. DDT was thought of as a "miracle" insecticide during the 1940s and 1950s, when it was widely used to control a variety of crop and garden pests

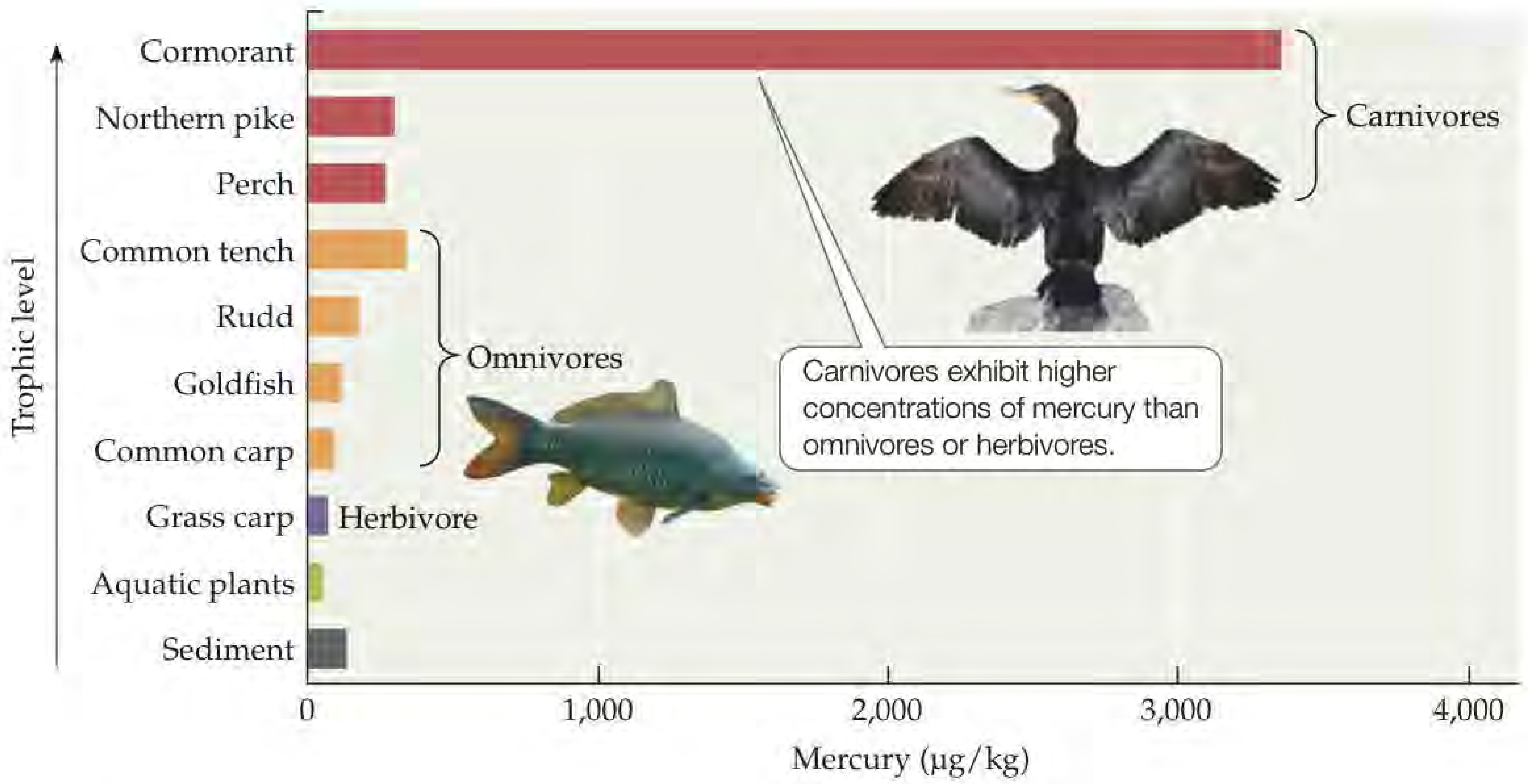


Figure 21.21 Bioaccumulation and Biomagnification Levels of mercury (a toxic heavy metal) show bioaccumulation and biomagnification in a Czech pond ecosystem. (After Houserová et al. 2007.)

and disease vectors. However, DDT was also accumulating in higher-level predators as a result of biomagnification, and it contributed to the near extinction of some birds of prey, including the peregrine falcon and the bald eagle. In *Silent Spring*, Carson described the persistence of DDT in the environment, its accumulation in the tissues of consumers, including humans, and its health hazards. Because of Carson's careful documentation and her ability to convey her message in a well-crafted manner that could be appreciated by the general public, *Silent Spring* led to increased scrutiny of the use of chemical pesticides, which eventually resulted in a ban on the manufacture and use of DDT in the United States.

The concept of biomagnification led researchers to suspect that the high concentrations of POPs found in the Inuit resulted from their position at the highest trophic levels of the Arctic ecosystem. This suspicion was reinforced by comparisons of the concentrations of toxins among different Inuit communities. The highest concentrations of toxins were found in communities that consumed marine mammals such as whales, seals, and walruses—animals that occupy the third, fourth, or fifth trophic levels. Inhabitants of communities where herbivorous caribou (at the second trophic level) were a more important part of the diet had lower concentrations of toxins. The Inuit preference for foods rich in fatty tissues, such as whale blubber (muktuk), poses a problem as well because many POPs are preferentially stored in the fatty tissues of animals.

Although emissions of some POPs and other pollutants are declining globally as awareness of their effects increases and regulations are put in place, the potential for long-term storage of these compounds in the Arctic environment means that their effects may not disappear any time soon (Pearce 1997). While the cold temperatures and relatively low light levels in the Arctic limit the chemical breakdown of POPs, their concentrations have gradually decreased in lake sediments. There has also been a gradual decline in the concentrations of some POPs and heavy metals in the blood of Inuit individuals, but new emerging POPs and mercury continue to be a concern for public heath. While switching to alternative food sources might seem to be a potential solution to the problem, the cultural identity of the Inuit is strongly associated with their hunting traditions and their diet, and they would be unlikely to make such a switch easily.

CONNECTIONS IN NATURE
Biological Transport of Pollutants

Pollutants have been reported in almost all environments on Earth—even Antarctic ice holds trace amounts of DDT and lead emitted from the burning of leaded gasoline. Animals in many remote areas have high concentrations of industrial and agricultural toxins in their tissues. Fish in isolated alpine lakes of the Canadian Rockies, for example, contain high concentrations of POPs, which have been associated with condensation of these compounds in snowfields and glaciers above the lakes (Blais et al. 1998). As suggested in the Case Study Revisited, the concentrations of these pollutants are related to the trophic positions of the animals: consumers at the highest trophic levels, such as polar bears, seals, and birds of prey, contain the highest concentrations. The widespread nature of this problem underscores the notion that ecosystems are connected by the movements of energy and materials among them. Ecological processes in one ecosystem can have effects on other ecosystems through these movements (Polis et al. 2004).

The movement of POPs and other human-made toxins is usually associated with atmospheric transport from low to high latitudes. However, the behaviors of animals can also influence the movement of POPs. Salmon, for example, have been shown to transport nutrients from marine to freshwater and terrestrial ecosystems during

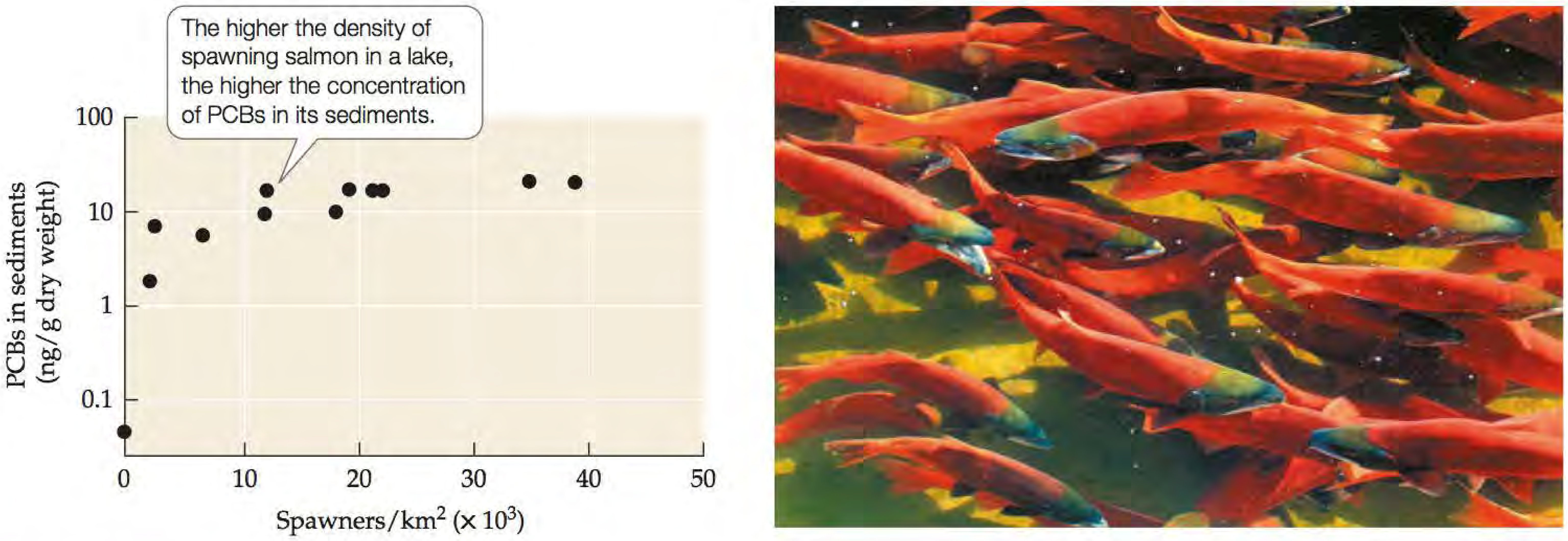


Figure 21.22 Biological Pumping of Pollutants Spawning salmon act as biological pumps, concentrating toxins from the oceans in their bodies and transporting them en masse to freshwater ecosystems. (After Krümmel et al. 2003.)

their spawning runs. At reproductive maturity, salmon leave the ocean and move up rivers in large numbers, as described in the Case Study in Chapter 2. From the rivers, they move into freshwater lakes and streams, where they spawn and then die. The potential exists for salmon to move toxins, as well as nutrients, from the oceans to freshwater ecosystems via this spawning behavior.

E. M. Krümmel and colleagues studied the potential for spawning sockeye salmon (*Oncorhynchus nerka*) to act as a "fish pump" for pollutants by moving PCBs from the ocean to remote lakes in Alaska (Krümmel et al. 2003). Salmon occupy the fourth trophic level, and thus, through bioaccumulation and biomagnification, they accumulate PCBs in their body fat at concentrations more than 2,500 times higher than those found in seawater. Krümmel and colleagues collected sediment cores from eight lakes in Southwest Alaska that had different densities of spawning salmon (ranging from 0 to 40,000 spawners/km^2) and measured PCBs in the sediments. They found that the concentrations of PCBs were strongly correlated with the density of spawners (**Figure 21.22**). Lakes that did not have visits from spawning fish had concentrations of PCBs similar to expectations based on atmospheric transport alone. The lake with the highest density of spawning fish (40,000 per km^2) had PCB concentrations that were six times higher than the levels associated with atmospheric transport. A similar study found that DDT, other POPs, and mercury are transported by northern fulmars (*Fulmarus glacialis*, pelagic fish-eating seabirds) from the ocean to small ponds near their nesting colonies (Blais et al. 2005). These examples demonstrate how the behaviors of some species (spawning in fish, colonial nesting in birds) can exacerbate problems of pollution associated with biomagnification in ecosystems.

Summary

CONCEPT 21.1 Trophic levels describe the feeding positions of groups of organisms in ecosystems.

- An organism's trophic level is determined by the number of feeding steps by which it is removed from the first trophic level, which contains autotrophs and detritus.
- Omnivores feed at multiple trophic levels, although their diets can be partitioned to reflect their consumption at each level.
- All organisms eventually end up as food for other organisms or as detritus.

CONCEPT 21.2 The amount of energy transferred from one trophic level to the next depends on food quality and on consumer abundance and physiology.

- Trophic energy and biomass pyramids portray the relative amounts of energy and biomass at different trophic levels.
- The high turnover of autotroph biomass in aquatic ecosystems can result in biomass pyramids that are inverted relative to energy pyramids.
- The proportion of autotroph biomass consumed in terrestrial ecosystems tends to be lower than that in aquatic ecosystems.
- The efficiency of energy transfer from one trophic level to the next is determined by food quality and the physiology of consumers.

CONCEPT 21.3 Changes in the abundances of organisms at one trophic level can influence energy flow at multiple trophic levels.

- Changes in the numbers and types of consumers at higher trophic levels can influence primary production through influences on the consumption of herbivores.
- Trophic cascades tend to be more apparent in aquatic ecosystems than in terrestrial ecosystems, but they have been demonstrated in complex terrestrial ecosystems as well.
- The number of trophic levels that can be sustained in an ecosystem is determined by the size of the ecosystem, the amount of energy entering the ecosystem through primary production, and the frequency of disturbances.

CONCEPT 21.4 Food webs are conceptual models of the trophic interactions of organisms in an ecosystem.

- Food webs are diagrams that portray the diverse trophic interactions among species in an ecosystem.
- Although trophic interactions are extremely complex, food webs can be simplified by focusing on the strongest interactions among the component organisms.
- Keystone species have greater effects on energy flow and community composition than their abundance or biomass would predict.
- Indirect effects of a predator on a target prey species, including its effects on other species that compete with, facilitate, or modify the environment of the target species, can offset or reinforce the direct effects of predation on the target species. These indirect effects may have stabilizing effects on inherently unstable food webs.

Review Questions

1. Suppose one population of coyotes (population A) demonstrates a greater degree of omnivory than another population (population B). Population A relies on a diet that includes road-killed animal carcasses, plants, and rotten food from dumpsters, while population B has a steady diet of small rodents. Which population should have a higher assimilation efficiency, and why?
2. Mammals in temperate terrestrial and temperate marine ecosystems occupying similar trophic levels may have different production efficiencies. Assuming similar food quality, food abundance, and food capture rates, explain why the production efficiencies of these mammals would differ between a marine ecosystem and a terrestrial ecosystem. (Hint: Consider how the mammals maintain their body heat, as well as the temperature variation of their environments as described in Chapter 2.)
3. Which ecosystem would you expect to have a greater total amount of energy passing through its trophic levels: a lake or a forest adjacent to the lake? Which of these ecosystems would have a higher *proportion* of NPP moving through all of its trophic levels, the forest or the lake?

Hone Your Problem-Solving Skills

Generalist herbivores, which are often insects, consume a greater number of plant species than specialist herbivores do. Specialist herbivores are often protected against predation by acquiring protective chemicals from their plant food sources. Thus dietary specialization may have consequences for the impact of herbivory on the flow of energy and nutrients in ecosystems.

1. Would you expect that a trophic cascade would have a greater or lesser effect on herbivory and NPP if only specialist herbivores were present? Assume a high diversity of plant species. Provide your answer in the form of a prediction, and describe an experiment in which you could test this hypothesis.
2. Michael Singer and colleagues investigated the influence of predatory birds on caterpillars and the subsequent effect on plant damage through herbivory in a deciduous forest ecosystem (Singer et al. 2014). They manipulated the presence and absence of birds (third trophic level) using exclosures, manipulated the proportion of specialist and generalist caterpillars (second trophic level), and measured abundances of the caterpillars and levels of damage to trees. **Figure A** shows the impact of bird predation on damage to the trees, expressed as relative to controls with no bird predation (zero point). Negative values indicate less herbivore damage to trees as a result of the bird predation; positive values indicate more herbivore damage to trees as a result of bird predation. **Figure B** shows the effect of predation on abundance of herbivores according to whether they are generalists (G) or specialists (S). Error bars in Figure B show ± one SE of the mean.
   a. How do these results support or refute the hypothesis you derived in Question 1?
   b. What factors would have contributed to the observed result?

Figure A

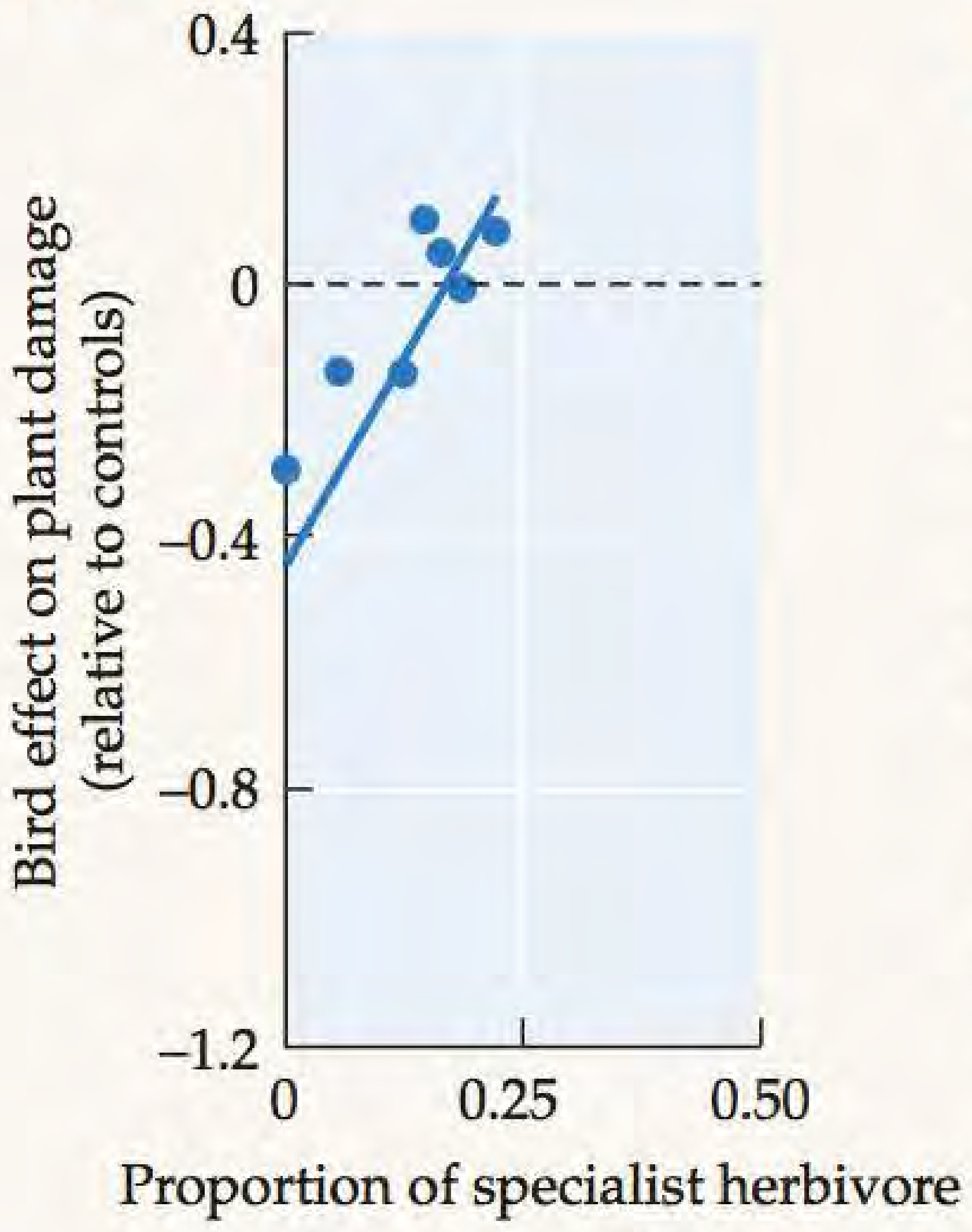
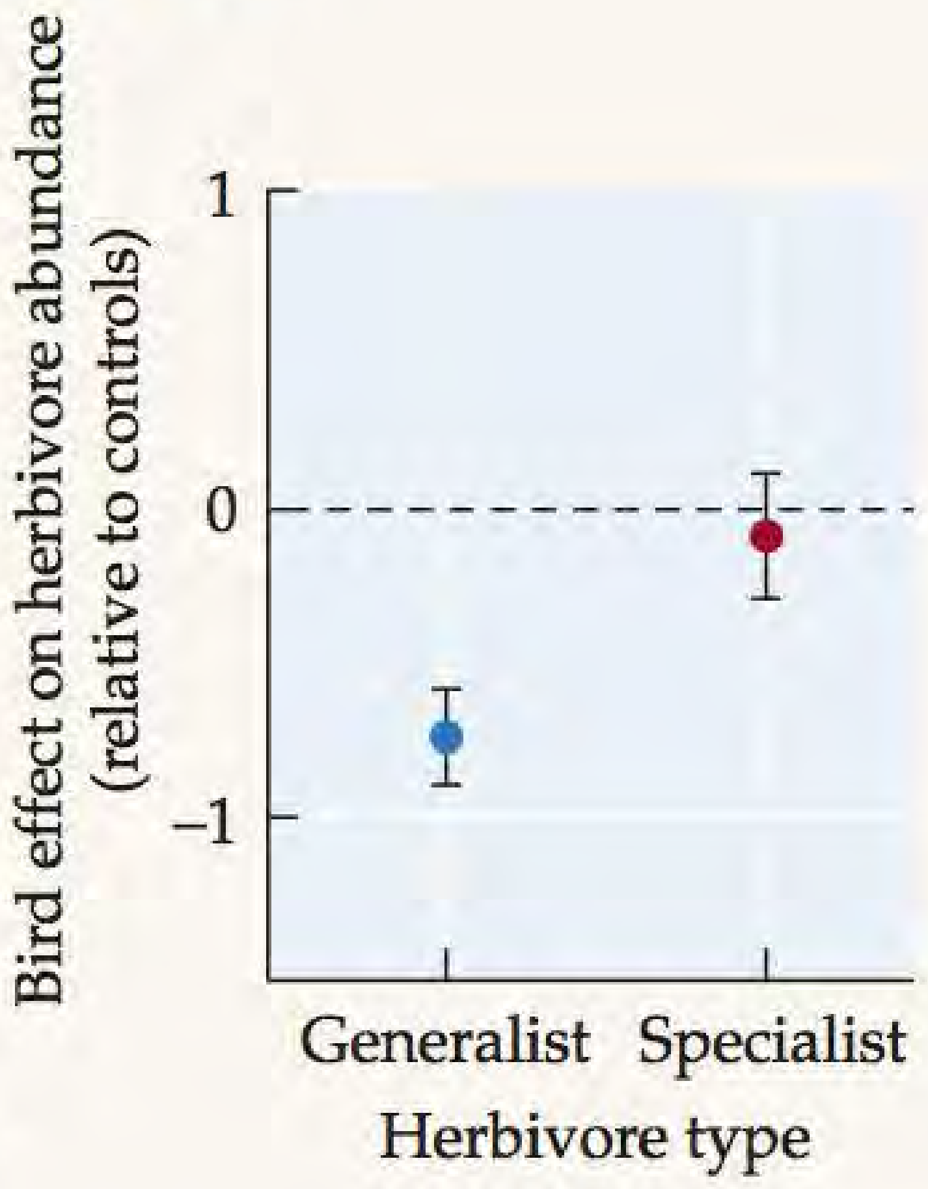


Figure B



ON THE COMPANION WEBSITE

ecology4e.sinauer.com

The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

21.1 A Pound of Flesh: Trophic Efficiency in a Coral Reef

21.2 A Safe Place for My Children: Trophic Cascades and Neighborhood Effects

Online Climate Change Connection

21.1 Polar Bears, Climate Change, and Biomagnification

Nutrient Supply and Cycling

22

A Fragile Crust: A Case Study

The Colorado Plateau in western North America includes vast expanses of isolated mountains, intricately folded sandstone formations, and deeply cut, multicolored canyons. One of the most unusual features found in this rugged and beautiful region, however, occurs at a very small scale: its patchy cover of dark, convoluted soil (**Figure 22.1**). On closer examination, the soil looks like a miniature landscape of hills and valleys, covered with black, dark green, and white splotches resembling lichens. The comparison is apt, because this crust on the soil surface, known simply as a **biological soil crust** (or **biocrust**), is composed of a mix of hundreds of species of cyanobacteria, lichens, and mosses (Belnap 2003). Approximately 70% of the soils on the Colorado Plateau, which covers parts of Utah, Arizona, Colorado, and New Mexico, have some biocrust development. Similar crusts, containing a surprisingly similar suite of species, are found in many other arid and semiarid regions throughout the world. The crusty nature of the soil is largely the work of filamentous cyanobacteria, which create a sheath of mucilaginous material as they move through the soil after a rain. When the soil dries out, the cyanobacteria withdraw to deeper soil layers, leaving behind the sheathing material, which helps bind the coarse soil particles together (**Figure 22.2**).

The soils of the Colorado Plateau are exposed to tremendous climate variation and strong erosive forces (Belnap 2003). Surface temperatures can range from –20°C (–4°F) in winter to 70°C (158°F) in summer. High evapotranspiration rates often dry out the soils, and the sparseness of the vegetation allows the strong surface winds to carry away fine soil particles. Precipitation in spring and summer often occurs as brief, intense thunderstorms. Biocrusts are critical for anchoring the soil in place in the face of high winds and torrential rains.

Although the Colorado Plateau is sparsely populated, humans have had a large and lasting effect on its landscape. Livestock grazing has been an important use of public lands in the region since cattle were introduced there in the 1880s. Most of the land has been affected to some degree by grazing, which has resulted in the trampling of biocrusts and overgrazing of vegetation. Until recently, grazing was the most important human-associated disturbance in the region. Recently, however, a proliferation of off-road vehicles has invaded the region. During the 2005 Moab Jeep Safari, for example, an estimated 30,000–40,000 participants descended on a town with a year-round population of 5,000. All-terrain vehicle use is also increasing dramatically, joining the motorcycle, mountain bike, and hiking traffic in the wilds. The majority of these users of the desert

KEY CONCEPTS

CONCEPT 22.1 Nutrients enter ecosystems through the chemical breakdown of minerals in rocks or through fixation of atmospheric gases.

CONCEPT 22.2 Chemical and biological transformations in ecosystems alter the chemical form and supply of nutrients.

CONCEPT 22.3 Nutrients cycle repeatedly through the components of ecosystems.

CONCEPT 22.4 Freshwater and marine nutrient cycles occur in a moving medium and are linked to terrestrial ecosystems.

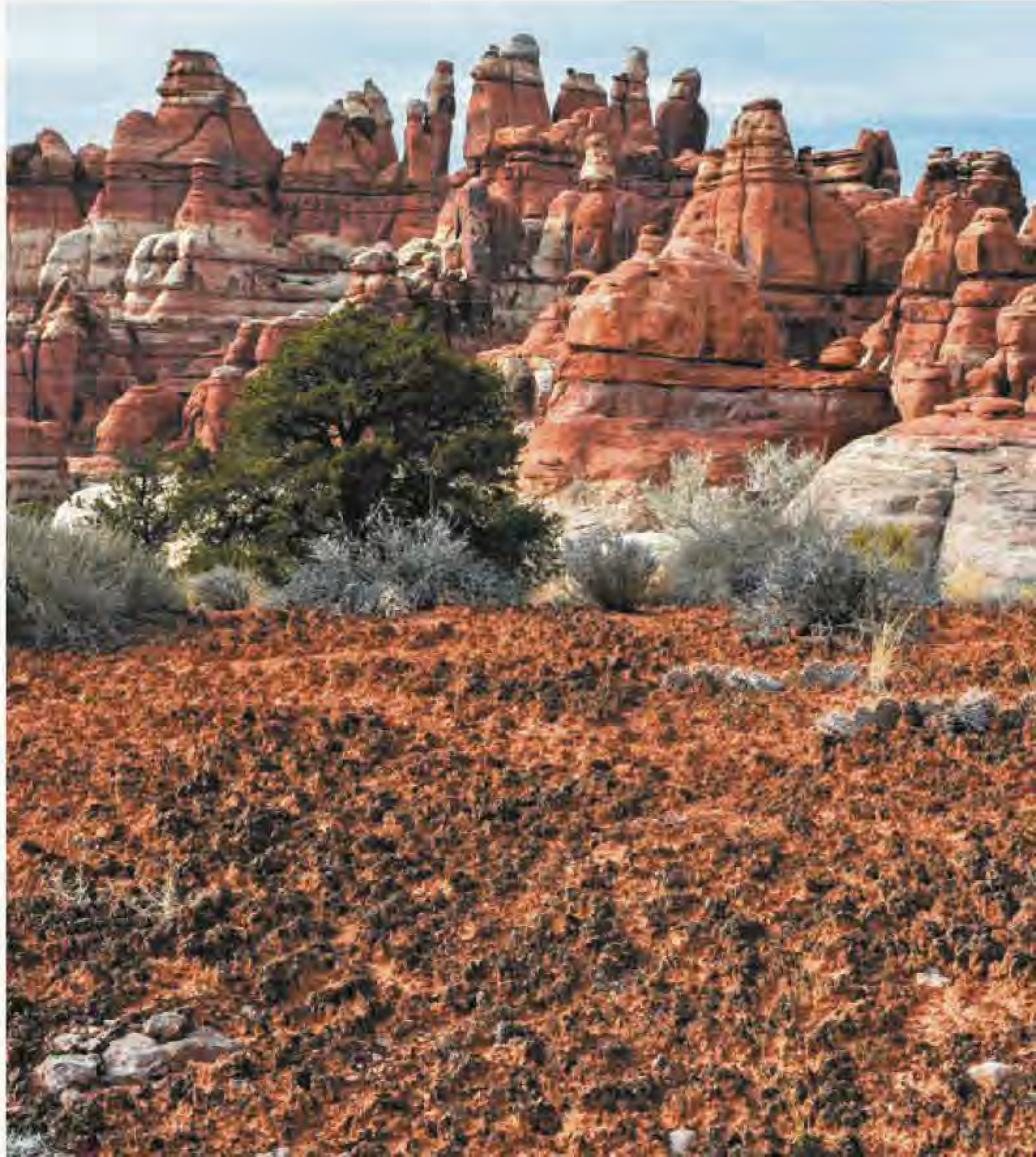


Figure 22.1 Biological Soil Crust on the Colorado Plateau Biological soil crusts are a common feature in the deserts of the Colorado Plateau. The surface topography and coloration of the crust are clearly visible in this photo.

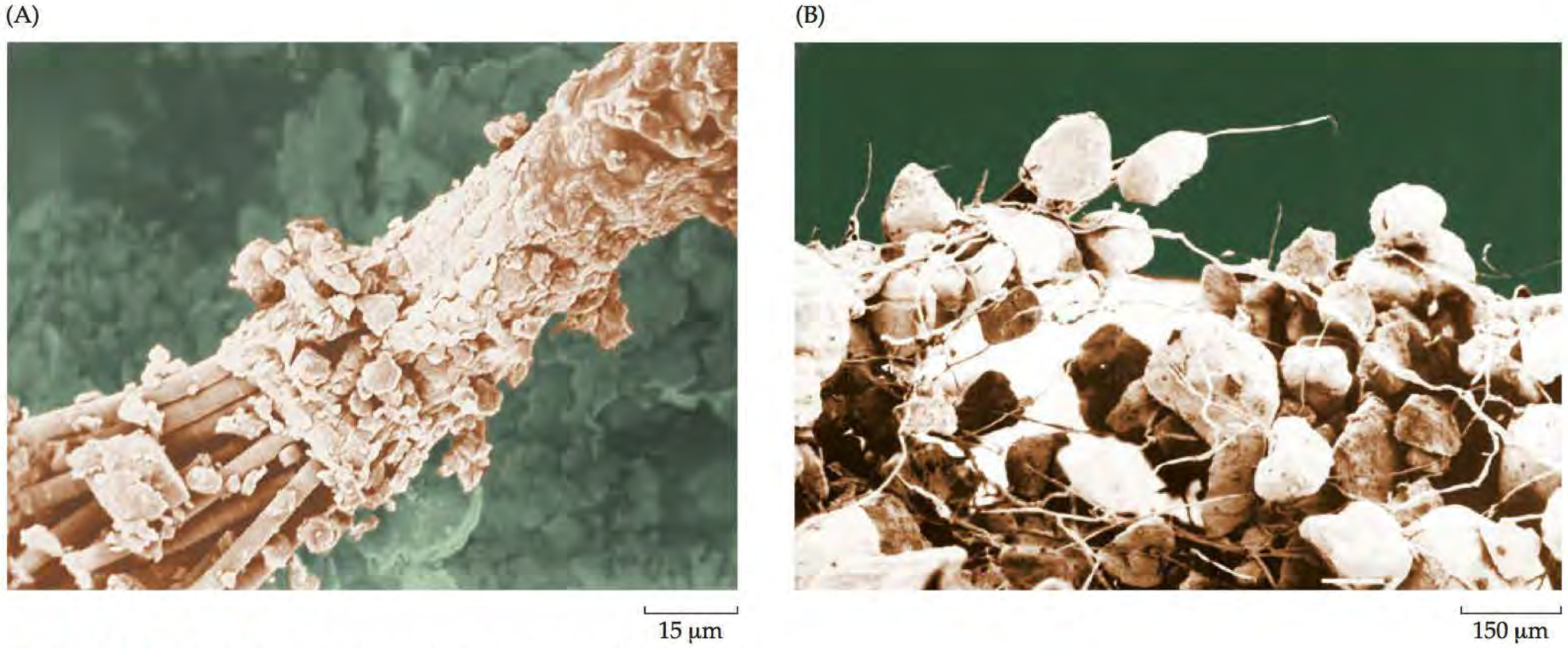


Figure 22.2 **Cyanobacterial Sheaths Bind Soil into Crusts** (A) Cyanobacterial strands surround themselves with a sheath of mucilaginous material as they move through the soil. (B) The sheaths left behind by the cyanobacteria help to bind soil particles together and protect soils from erosional loss.

backcountry obey federal and local laws, staying on designated trails and roads. However, a minority of users drive their vehicles off designated roads and across soils covered with biocrusts.

While the spatial extent of soil surface disturbance associated with off-road vehicle use and livestock grazing has not been well quantified, it is clear that a large part of the landscape has been disturbed to some degree during the past 150 years, and that the rate of disturbance is increasing. The recovery of biocrusts following disturbance is extremely slow in arid environments: decades are required for the reestablishment of the cyanobacteria and up to centuries for recolonization by lichens and mosses (Belnap and Eldridge 2001).

What are the implications of the loss of biocrusts for the functioning of desert ecosystems? How important are they to the supply of nutrients in those ecosystems? Given the long-term nature of disturbances associated with livestock grazing across the Colorado Plateau, can we still find areas that can serve as controls for studies of the disturbance that has already occurred?

Introduction

In addition to energy, all organisms require specific chemical elements to function and grow. Organisms get these elements by absorbing them from the environment or by consuming other organisms, living or dead. Iron, for example, is needed by all organisms for several important metabolic functions, but how those organisms get their iron and where it comes from vary substantially. Phytoplankton in the Atlantic Ocean may take up iron that came from dust that blew in from the Sahara. Lions on an African savanna get their iron from the prey they kill and consume. Aphids get their iron in the sap they suck from a plant, whereas the plant takes up water containing dissolved iron from the soil. The ultimate source of all of this iron, however, is solid minerals in Earth's crust, which are subjected to chemical transformations as they move through the different physical and biological components of ecosystems.

The study of the physical, chemical, and biological factors that influence the movements and transformations of elements is known as **biogeochemistry**. An understanding of biogeochemistry is important for determining the availability of **nutrients**, which are defined as the chemical elements an organism requires for its metabolism and growth. Nutrients must be present in certain chemical forms to be available for uptake by organisms. The rate at which physical and chemical transformations occur determines the supply of nutrients. Biogeochemistry also encompasses the study of non-nutrient elements that can serve as tracers in ecosystems and of pollutant compounds, such as persistent organic pollutants and heavy metals, that cause environmental damage. Biogeochemistry is a discipline that integrates contributions from soil science, hydrology, and atmospheric science as well as ecology.

In this chapter, we will consider the biological, chemical, and physical factors that control the supply and availability of nutrients in ecosystems. We will emphasize nutrient requirements and acquisition by autotrophs because they in turn are the principal source of nutrients for heterotrophs. We will describe what nutrients are most important, their sources, and how they enter ecosystems, and review some of the important chemical and biological transformations that constitute the cycling of nutrients in ecosystems. In Concept 25.1, we will consider the global-scale cycling of some of these elements.

CONCEPT 22.1

Nutrients enter ecosystems through the chemical breakdown of minerals in rocks or through fixation of atmospheric gases.

Nutrient Requirements and Sources

All organisms, from bacteria to blue whales, share similar nutrient requirements. How those nutrients are obtained, the chemical forms of those nutrients that are taken up, and the relative amounts of those nutrients that are required vary greatly among organisms. All of these nutrients, however, come from a common source: inorganic mineral forms that are present in Earth's crust or as gases in the atmosphere.

Organisms have specific nutrient requirements

An organism's nutrient requirements are related to its physiology. The amounts and specific nutrients needed therefore vary according to the organism's mode of energy acquisition (autotrophs vs. heterotrophs), mobility, and thermal physiology (ectotherms vs. endotherms). Mobile animals, for example, generally have higher rates of metabolic activity than plants or bacteria, and they therefore have higher requirements for nutrients such as nitrogen (N) and phosphorus (P) to support the biochemical reactions associated with movement. Differences in nutrient requirements are reflected in the chemical composition of organisms (**Table 22.1**). Carbon is often associated with structural compounds in plant cells and tissues, while nitrogen is largely found in enzymes. Accordingly, the ratios of carbon to nitrogen (C:N) in organisms can indicate the relative concentrations of biochemical machinery in cells. Animals and microorganisms typically have lower C:N ratios than plants: for example, humans and bacteria have C:N ratios of 6.0 and 3.0, respectively, whereas those of plants range from 10 to 40. This difference is one reason why herbivores must consume more food than carnivores to acquire enough nutrients to meet their nutritional demands.

The nutrients essential for all plants, and the functions associated with them, are presented in **Table 22.2**. Some plant species have specific requirements for other nutrients not found in Table 22.2. For example, many, but not all, C_4 and CAM plants (see Concept 5.3 for discussion of these photosynthetic pathways) require sodium, while most plants do not. In contrast, sodium is an essential nutrient for all animals, critical for maintaining pH and osmotic balances. Cobalt is required by some plants that host nitrogen-fixing symbionts (discussed later in this section). Selenium is toxic to most plants, but a small number of plants growing on soils rich in selenium may require it (in contrast, selenium is an essential nutrient for animals and bacteria).

Plants and microorganisms usually take up nutrients from their environment in relatively simple, soluble chemical forms, from which they synthesize the larger molecules needed for their metabolism and growth. Animals, on the other hand, typically take up their nutrients through the consumption of living organisms or detritus, obtaining their nutrients in larger, more complex chemical compounds. Animals break down some of these compounds and resynthesize new molecules; others are absorbed intact and used directly in biosynthesis. For example, 9 of the 20 amino acids that are essential for metabolism in humans and other mammals must be absorbed intact, since we cannot synthesize them ourselves.

Minerals and atmospheric gases are the ultimate sources of nutrients

All nutrients are ultimately derived from two abiotic sources: minerals in rocks and gases in the atmosphere. Over time, as nutrients are taken up and incorporated by organisms, they accumulate in ecosystems in organic forms (i.e., in association with carbon and hydrogen molecules). Nutrients may be cycled within an ecosystem,

TABLE 22.1 Elemental Composition of Organisms (as Percentage of Dry Mass)

ELEMENT (SYMBOL)	BACTERIA (IN GENERAL)	PLANT (CORN, *ZEA MAYS*)	ANIMAL (HUMAN, *HOMO SAPIENS*)
Oxygen (O)	20	44.43	14.62
Carbon (C)	50	43.57	55.99
Hydrogen (H)	8	6.24	7.46
Nitrogen (N)	10	1.46	9.33
Silicon (Si)		1.17	0.005
Potassium (K)	1–4.5	0.92	1.09
Calcium (Ca)	0.01–1.1	0.23	4.67
Phosphorus (P)	2.0–3.0	0.20	3.11
Magnesium (Mg)	0.1–0.5	0.18	0.16
Sulfur (S)	0.2–1.0	0.17	0.78
Chlorine (Cl)		0.14	0.47
Iron (Fe)	0.02–0.2	0.08	0.012
Manganese (Mn)	0.001–0.01	0.04	—
Sodium (Na)	1.3	—	0.47
Zinc (Zn)		—	0.01
Rubidium (Rb)		—	0.005

Sources: Aiba et al. 1973; Epstein and Bloom 2005.

Note: Dashes indicate a negligible amount of an element; blank spaces indicate that the element has not been measured.

TABLE 22.2 Plant Nutrients and Their Principal Functions

NUTRIENTS	PRINCIPAL FUNCTIONS
Carbon, hydrogen, oxygen	Components of organic molecules
Nitrogen	Component of amino acids, proteins, chlorophyll, nucleic acids
Phosphorus	Component of ATP, NADP, nucleic acids, phospholipids
Potassium	Ionic/osmotic balance, pH regulation, regulation of guard cell turgor
Calcium	Cell wall strengthening and functioning, ionic balance, membrane permeability
Magnesium	Component of chlorophyll, enzyme activation
Sulfur	Component of amino acids, proteins
Iron	Component of proteins (e.g., heme groups), oxidation–reduction reactions
Copper	Component of enzymes
Manganese	Component of enzymes, activation of enzymes
Zinc	Component of enzymes, activation of enzymes, component of ribosomes, maintenance of membrane integrity
Nickel	Component of enzymes
Molybdenum	Component of enzymes
Boron	Cell wall synthesis, membrane function
Chlorine	Photosynthesis (water splitting), ionic and electrochemical balance

Sources: Salisbury and Ross 1992; Marschner 1995.

repeatedly passing through organisms and the soil or water in which the organisms live. They may even be cycled internally within an organism, stored or mobilized for use as its needs for specific nutrients change. Here we describe the inputs of nutrients into ecosystems from minerals and the atmosphere. In the following sections, we will complete the steps that constitute nutrient cycling within an ecosystem.

MINERAL SOURCES OF NUTRIENTS The breakdown of minerals in rock supplies ecosystems with nutrients such as potassium, calcium, magnesium, and phosphorus. *Minerals* are solid substances with characteristic chemical properties, derived from a multitude of geologic processes. *Rocks* are collections of different minerals. Nutrients and other elements are released from minerals in a two-step process known as **weathering**. The first step, **mechanical weathering**, is the physical breakdown of rocks. Expansion and contraction processes, such as freeze–thaw and drying–rewetting cycles, act to break rocks into progressively smaller particles. Gravitational mechanisms (such as landslides) and the growth of plant roots also contribute to mechanical weathering. Mechanical weathering exposes greater amounts of surface area of mineral particles to **chemical weathering**, in which the minerals are subjected to chemical reactions that release soluble forms of nutrients.

Weathering is one of the processes involved in soil development. **Soil** is formally defined as a mix of mineral particles; solid organic matter (detritus, primarily decomposing plant matter); water containing dissolved organic matter, minerals, and gases (the *soil solution*); and organisms. Soils have several important properties that influence the delivery of nutrients to plants and microorganisms. One property is their texture, which is defined by the sizes of the particles that make up the soil. The coarsest soil particles (0.05–2 mm) are referred to as **sand**. Intermediate-sized particles (0.002 to 0.05 mm) are called **silt**. Fine soil particles (<0.002 mm), known as **clays**, have weak negative charges on their surfaces that can hold onto cations and exchange them with the soil solution. As a result, clay particles serve as a reservoir of nutrient cations such as Ca^{2+}, K^+, and Mg^{2+}. A soil's ability to hold these cations and exchange them with the soil solution, referred to as its **cation exchange capacity**, is determined by the amounts and types of clay the soil contains. Soil texture also influences the soil's water-holding capacity and thus the movement of nutrients in the soil solution. Soils with a high proportion of sand have a large volume of spaces between particles. These spaces (called *macropores*) allow water to drain through the soil and limit the amount of water it can hold.

Another important property of a soil is its **parent material**, the rock or mineral material that was broken down by weathering to form that soil. Parent material for soil is usually the underlying bedrock but may also include thick layers of sediment deposited by glaciers (known as **till**), by wind (**loess**), or by water. The chemistry and structure of the parent material are important determinants of the rate of weathering and the amount and types of nutrients released, and they thus influence the fertility of the soil. Limestone, for example, is high in the nutrient cations Ca^{2+} and Mg^{2+}. Soils derived from more acidic parent material, such as granite, have lower concentrations of these elements. In addition, the higher acidity (lower pH) of soils derived from granite lowers the availability of nitrogen and phosphorus to plants.

The chemistry and pH of the parent material exert an important influence on the abundance, growth, and diversity of plants in ecosystems. For example, Laura Gough and colleagues (2000) demonstrated that variation in the acidity of the parent material is associated with differences in plant species richness among Arctic ecosystems in Alaska. They surveyed Arctic vegetation across natural gradients in soil acidity associated with the differential distribution of calcium-rich loess, which has lower

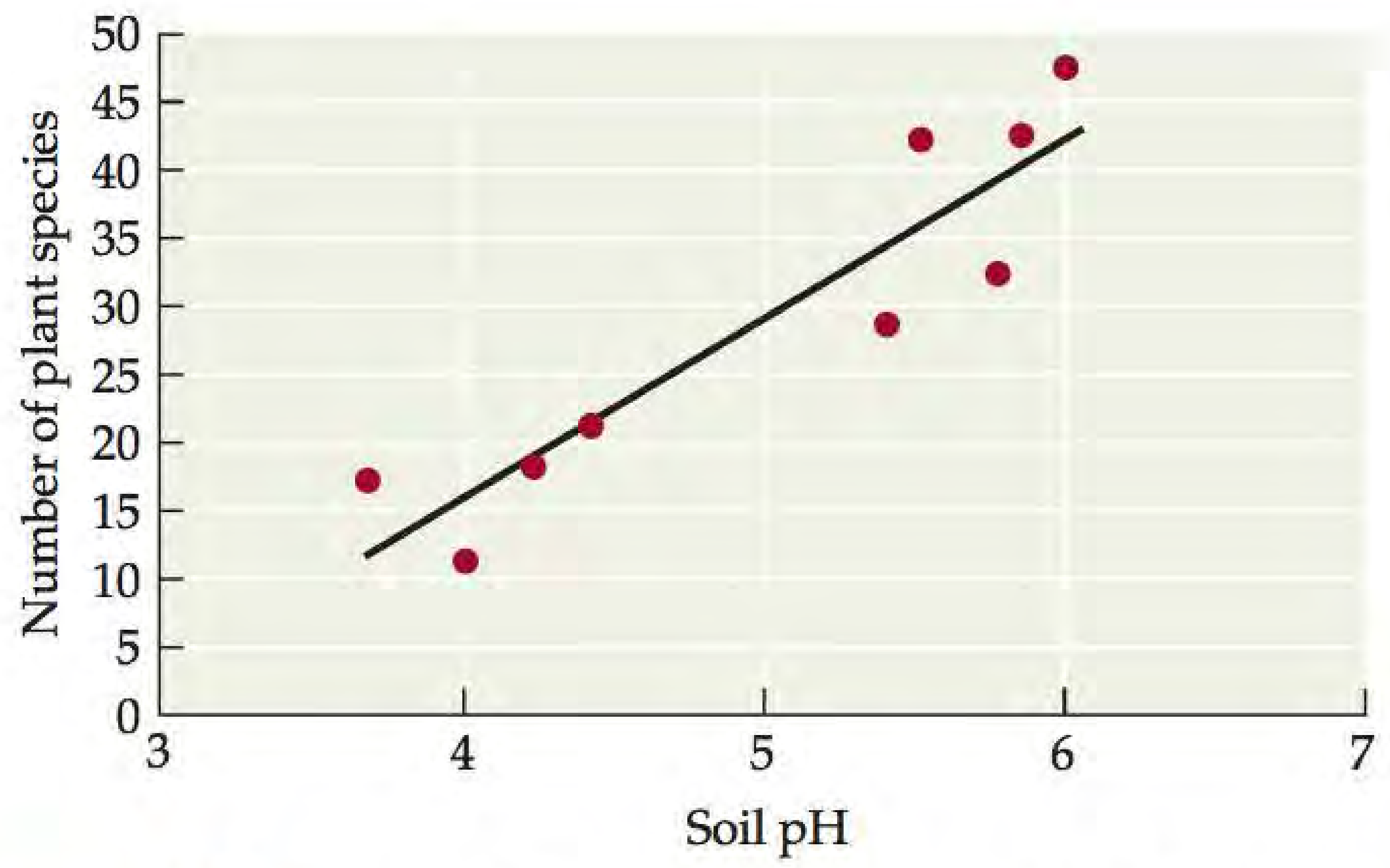


Figure 22.3 Species Richness Increases with Decreasing Soil Acidity Vascular plant species richness in the Alaskan Arctic tundra varies with soil acidity. The gradient in soil acidity is primarily due to differences in parent material: less acidic soils (with higher pH) are associated with greater loess deposits. (After Gough et al. 2000.)

acidity than other parent materials. They found that the number of plant species increased as acidity decreased (**Figure 22.3**). This variation in diversity was attributed to the negative effects of soil acidity on nutrient availability as well as its inhibitory effects on plant establishment.

Over time, soils undergo changes associated with weathering, accumulation and chemical alteration of organic matter, and **leaching**: the movement of dissolved organic matter and fine mineral particles from upper to lower layers. These processes form **horizons**, layers of soil distinguished by their color, texture, and permeability (**Figure 22.4**). Variations in soil horizons are used by soil scientists to characterize different soil types.

Climate influences the rates of many of the processes associated with soil development, including weathering, biological activity (such as the input of organic matter and its decomposition in the soil), and leaching. In general, these processes occur most rapidly under warm, wet conditions. Thus, the soils of lowland tropical forest ecosystems, which have experienced high rates of weathering and leaching for a long time, are poor in mineral-derived nutrients such as calcium and magnesium. A high proportion of the nutrients in lowland tropical forest ecosystems are found in the living biomass of trees, in contrast to most other terrestrial ecosystems, in which these nutrients are mostly found in the soil. When lowland tropical forests are cleared and burned to make way for pastures or cropland, most of the nutrients are lost in smoke and ash and through soil erosion following the fires. As a result, these ecosystems may become severely nutrient-impoverished, and it may take them centuries to return to their previous state. Soils in higher-latitude ecosystems have lower leaching rates and are usually richer in mineral-derived nutrients.

Organisms—primarily plants, bacteria, and fungi—influence soil development by contributing organic matter, which is an important reservoir of nutrients such as nitrogen and phosphorus. Organisms also increase rates of chemical weathering through the release of organic acids (from plants and detritus) and CO$_2$ (from metabolic respiration). Thus, rates of biological activity have a strong influence on the development of soils.

ATMOSPHERIC SOURCES OF NUTRIENTS The atmosphere is composed of 78% nitrogen (as dinitrogen gas, N$_2$), 21% oxygen, 0.9% argon, increasing amounts of carbon dioxide (0.040%, or 404 parts per million, in 2016), and other trace gases—some natural, others pollutants derived from human activities. The atmosphere is the ultimate source of

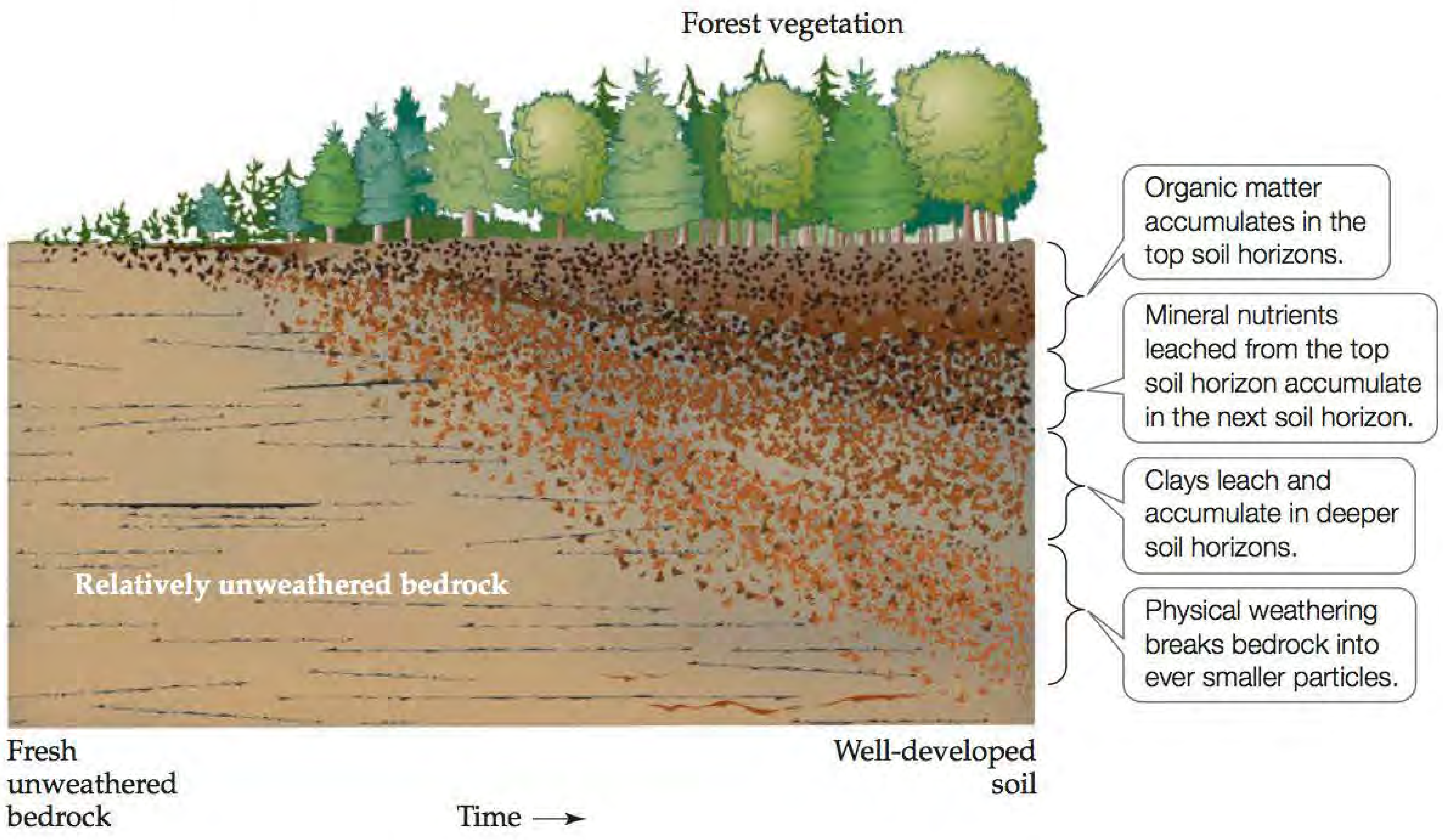


Figure 22.4 Development of Soil Horizons Soils develop over time as parent material is weathered and broken up into ever finer soil particles, increasing amounts of organic matter accumulate in the soil, and materials are leached and deposited in deeper soil layers. The rate of soil development is dependent on the climate, the parent material, and the organisms associated with the soil.

? Given what you've learned about primary production in Chapter 20 and about the climate factors that determine weathering and soil development in this chapter, what do you think the horizons of a desert soil would look like?

carbon and nitrogen for ecosystems. These nutrients become biologically available when they are taken up from the atmosphere and chemically transformed, or *fixed*, by organisms. They may then be transferred from organism to organism before returning to the atmosphere.

Carbon is taken up by autotrophs as CO_2 through photosynthesis. (The process of photosynthesis was described in Concept 5.2, and the global cycling of carbon is discussed in Concept 25.1.) Carbon compounds store energy in their chemical bonds, and they are important structural components of autotrophs (e.g., cellulose) as well.

Although the atmosphere is a huge reservoir of nitrogen, it is in a chemically inert form (N_2) that cannot be used by most organisms because of the high energy required to break the triple bond between the two atoms. The process of taking up N_2 and converting it into chemically available forms is known as **nitrogen fixation** (see Connections in Nature in Chapter 17). Biological nitrogen fixation is accomplished with the aid of the enzyme *nitrogenase*, which is synthesized by only certain bacteria. Some of these nitrogen-fixing bacteria are free-living; others are partners in mutualistic symbiotic relationships (see Figure 15.21). Nitrogen-fixing symbioses include associations between plant roots and soil bacteria, most notably between legumes and bacteria in the family Rhizobiaceae. Legumes "host" rhizobia in special root structures called nodules and supply them with carbon compounds as an energy source to meet the high energy demands of nitrogen fixation (**Figure 22.5**; see also Figure 17.21). In return for supplying the rhizobia with room and board, the plant gets nitrogen fixed by the bacteria. Other examples of nitrogen-fixing symbioses include associations between woody plants such as alders and bacteria in the genus *Frankia* (called actinorhizal associations), associations between *Azolla* ferns and cyanobacteria, lichens that include fungal and nitrogen-fixing symbionts, and termites with nitrogen-fixing bacteria in their guts. Humans also fix atmospheric nitrogen when they manufacture synthetic fertilizers using the Haber–Bosch process, in which ammonia is produced from atmospheric nitrogen and hydrogen under high pressures and temperatures using an iron catalyst. The Haber–Bosch process requires substantial energy input in the form of fossil fuels.

Natural nitrogen fixation also requires a large amount of energy. It consumes as much as 25% of the photosynthetic energy obtained by plants with nitrogen-fixing symbiotic partners. Thus, nitrogen fixation provides these plants with a source of nitrogen, but it represents a trade-off with other energy-demanding processes such as growth and reproduction. Allocation of energy to nitrogen fixation rather than to growth lowers the ability of nitrogen-fixing plants to compete for resources other than nitrogen. Nitrogen fixation is particularly important during the early stages of primary succession, as we saw in Chapter 17.

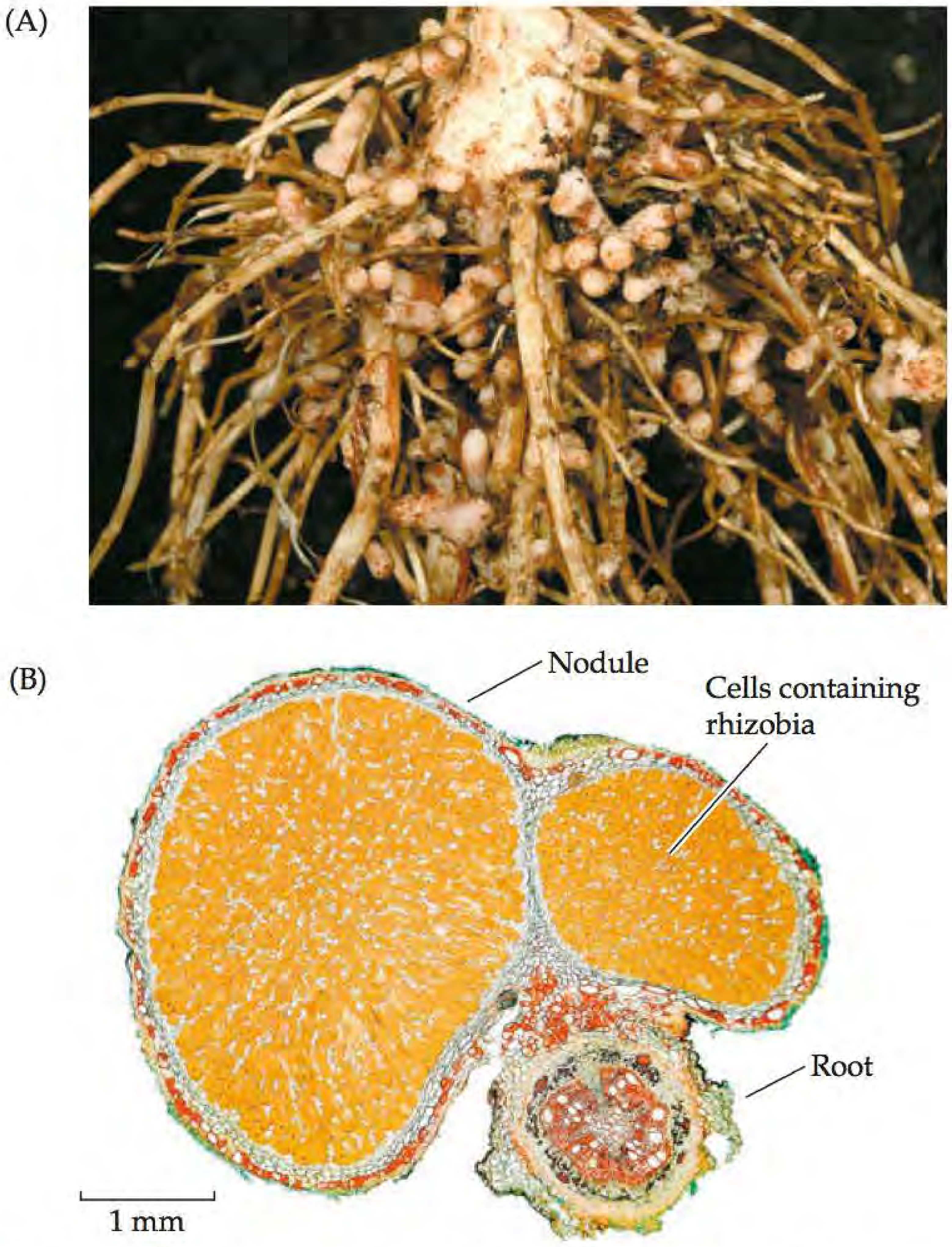


Figure 22.5 Legumes Form Nitrogen-Fixing Nodules (A) These swollen nodules on the roots of a red clover (*Trifolium pratense*) plant contain nitrogen-fixing bacteria. (B) Cells inside this soybean root nodule (yellow in this micrograph) are filled with rhizobia.

In addition to carbon and nitrogen, the atmosphere contains fine soil particles (dust) and a collection of suspended solid, liquid, and gaseous particles known as **aerosols**. Some of this particulate matter enters ecosystems when it falls from the atmosphere because of gravity or in precipitation, a process known as **atmospheric deposition**. Atmospheric deposition represents an important natural source of nutrients for some ecosystems. Aerosols containing cations derived from sea spray, for example, may be an important source of nutrients in coastal areas. Atmospheric deposition of dust originating in the Sahara is an important input of iron into the Atlantic Ocean and of phosphorus into the Amazon Basin. On the other hand, some ecosystems have been negatively affected by atmospheric deposition associated with human industrial and agricultural activities. Acid rain, for example, is an atmospheric deposition process that has been associated with declines in forest ecosystems in the eastern United States and Europe (as we will see in Concept 25.3).

Now that we've seen how nutrients enter ecosystems, let's follow their movements within ecosystems as they are taken up and transformed. The next two sections will focus on terrestrial ecosystems; we will take a closer look at nutrient cycling in aquatic ecosystems in the final section.

CONCEPT 22.2

Chemical and biological transformations in ecosystems alter the chemical form and supply of nutrients.

Nutrient Transformations

Once they have entered an ecosystem, nutrients are subjected to further modifications as a result of uptake by organisms and other chemical reactions that alter their form and influence their movement and retention within the ecosystem. Foremost among these transformations is the decomposition of organic matter, which releases nutrients back into the ecosystem.

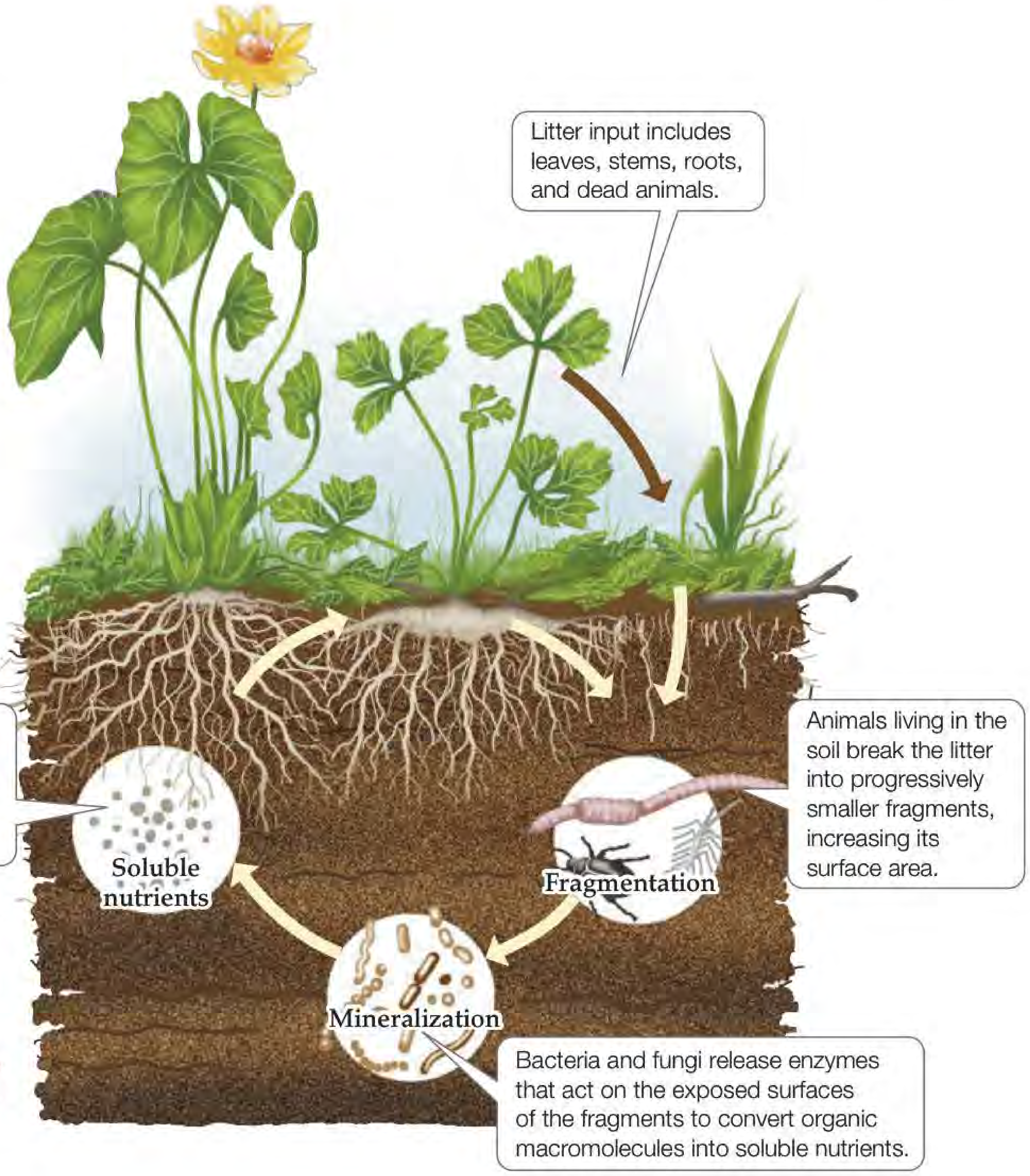
Decomposition is a key nutrient recycling process

As detritus (dead plants, animals, and microorganisms and egested waste products) builds up in an ecosystem, it becomes an increasingly important source of nutrients, particularly nitrogen and phosphorus. Those nutrients are made available by **decomposition**, the process by which detritivores break down detritus to obtain energy and nutrients (**Figure 22.6**). Decomposition releases nutrients as soluble organic and inorganic compounds that can be taken up by other organisms.

Organic matter in soil is derived primarily from plant matter, which comes from above and below the soil surface. Fresh, undecomposed organic matter on the soil surface is known as **litter** and is typically the most abundant substrate for decomposition. The litter is used by animals, protists, bacteria, and fungi as a source of energy and nutrients. As animals such as earthworms, termites, and nematodes consume the litter, they break it up into progressively finer particles. This physical fragmentation enhances the chemical breakdown of the litter by increasing its surface area.

An important final step in decomposition is the chemical conversion of organic matter into inorganic nutrients (i.e., nutrients that are not associated with carbon molecules), which is known as **mineralization**. It is the result of the breakdown of organic macromolecules in the soil by enzymes released by heterotrophic microorganisms. Because plants often rely on inorganic nutrients, ecologists use measurements of mineralization to estimate rates of nutrient supply. An understanding of the abiotic and biotic controls on decomposition and mineralization is key to understanding nutrient availability to autotrophs.

Rates of decomposition are greatly influenced by climate. Decomposition, like other biologically mediated processes, proceeds most rapidly at warm temperatures. Soil moisture also controls rates of decomposition by influencing the availability of water and oxygen to detritivores. Dry soils may not provide enough water for these organisms, and wet soils have low oxygen concentrations, which lower aerobic respiration and the rate of biological



Litter input includes leaves, stems, roots, and dead animals.

Animals living in the soil break the litter into progressively smaller fragments, increasing its surface area.

Bacteria and fungi release enzymes that act on the exposed surfaces of the fragments to convert organic macromolecules into soluble nutrients.

Small organic compounds and inorganic nutrients are released into the soil solution, from which they can be taken up by plants and microorganisms.

Figure 22.6 **Decomposition** Decomposition of organic matter in the soil provides an important input of nutrients into terrestrial ecosystems. Similar steps occur in freshwater and marine ecosystems.

? How would the use of a nonselective pesticide (i.e., one that does not target any specific animals) to control insect herbivores affect the rate of decomposition in a lawn ecosystem?

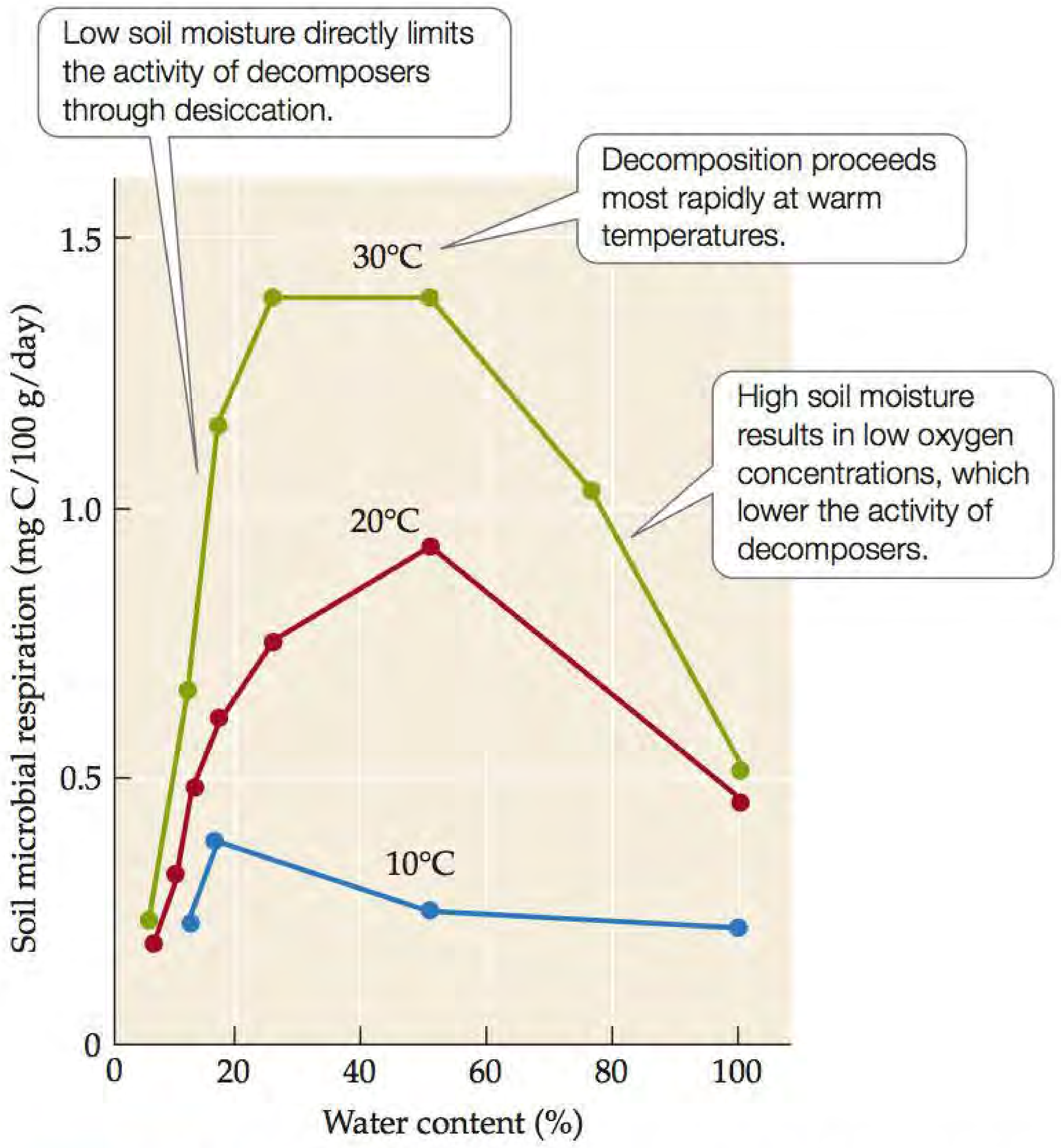


Figure 22.7 Climate Controls the Activity of Decomposers Changes in soil microbial respiration, used as an estimate of decomposition, are plotted as a function of soil moisture at different temperatures. (After Paul and Clark 1996.)

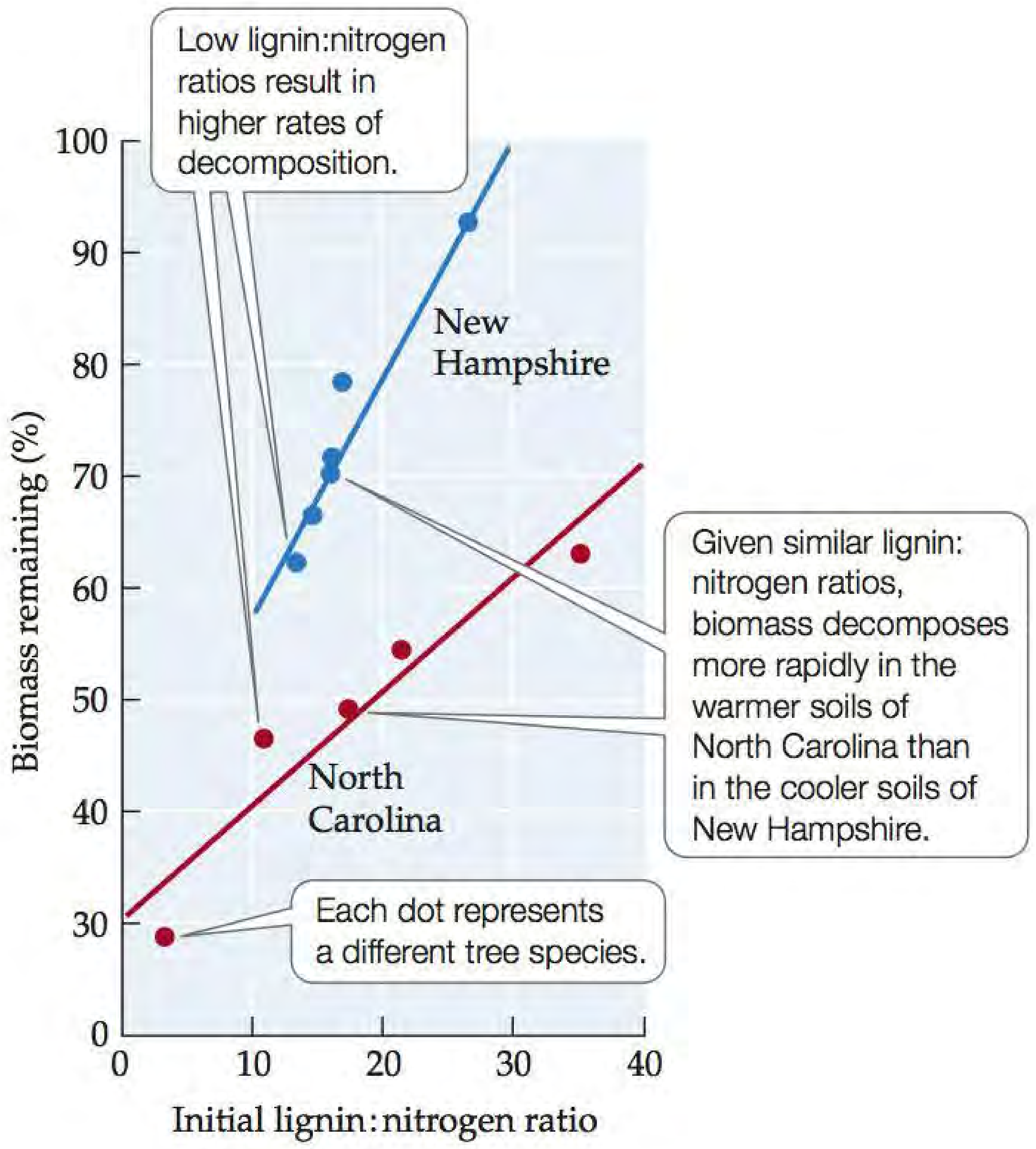


Figure 22.8 Lignin Decreases the Rate of Decomposition The rate of decomposition of leaf litter, expressed as the percent of biomass remaining, decreases as the ratio of lignin to nitrogen in the litter increases. This ratio varies among forest tree species. Note, however, that climate also has an important influence on decomposition rates. (After Melillo et al. 1982.)

activity. Therefore, the activity of detritivores is highest at intermediate soil moistures and warm temperatures (**Figure 22.7**).

Some nutrients are consumed by detritivores during decomposition, so not all of the nutrients released during mineralization become available for uptake by autotrophs. The amounts of nutrients that are released from organic matter during decomposition depend on the nutrient requirements of the decomposers and the amount of energy the organic matter contains. These factors can be approximated by the ratio of carbon (representing energy) to nitrogen (since nitrogen is the nutrient most often in short supply for detritivores) in the organic matter. A high C:N ratio in organic matter will result in a low net release of nutrients during decomposition, since heterotrophic microbial growth is more limited by nitrogen supply than by energy. For example, most heterotrophic microorganisms require approximately 10 molecules of carbon for every molecule of nitrogen they take up. About 60% of the carbon they take up is lost through respiration. Therefore, the optimal C:N ratio of organic matter for microbial growth is about 25:1. Organic matter with a C:N ratio greater than 25:1 would result in all of the nitrogen being taken up by the microbes during decomposition. Decomposition of organic matter with a C:N ratio of less than 25:1 would result in some nitrogen being released into the soil and made available for plants.

Not all of the carbon in litter is equally available as an energy source for decomposers: the chemistry of that carbon determines how rapidly the material can be decomposed. **Lignin**, a structural carbon compound that strengthens plant cell walls, is difficult for soil microorganisms to break down and thus decomposes very slowly (**Figure 22.8** and **Analyzing Data 22.1**). The rate of nutrient release from plant material containing high lignin concentrations, such as oak or pine leaves, is lower than that from material with low lignin concentrations, such as maple and aspen leaves. In addition, plant litter may contain secondary compounds, chemical compounds not used directly for growth (examples include those described in Concepts 5.4 and 12.2 associated with defense against herbivores and excess light), that can lower nutrient release during decomposition. Secondary compounds slow decomposition by inhibiting the activity of heterotrophic microorganisms and the enzymes they release into the soil or, in some cases, by stimulating their growth, leading to greater microbial uptake of nutrients.

By varying the chemistry of their litter, as well as the amount of litter they produce, plants can influence decomposition rates in the soil. Lowering decomposition rates lowers the fertility of the soil. What is the consequence for

ANALYZING DATA 22.1 Does Lignin Always Inhibit Decomposition?

We've learned that lignin, a structural compound found in leaves and stems, can lower rates of decomposition because it is a poorer carbon substrate for microorganisms. However, not all organic matter degradation is biotic. In arid ecosystems, for example, sunlight can break down organic matter on the surface of soils, and it can be more important than biological decomposition (Austin and Vivanco 2006; see also Hands-On Problem Solving 22.1). How does lignin influence the abiotic decomposition associated with photodegradation? Lignin absorbs more solar radiation than cellulose, and thus it might potentially *increase* abiotic decomposition. To test this hypothesis, Amy Austin and Carlos Ballaré (2010)* did a field experiment examining how the concentration of lignin influenced decomposition via both abiotic photodegradation and biotic activity. They used uniform cellulose sheets (filter paper) with a dilute solution of nutrients added to mimic leaf litter substrate. They added varying amounts of lignin to the sheets and then subjected them to conditions of mainly abiotic or biotic decomposition, by filtering light (biotic) or keeping the substrates isolated from the soil (abiotic). The mass loss from each sheet was measured to estimate the rate of decomposition. The results of Austin and Ballaré's experiment are presented in the table.

BIOTIC DECOMPOSITION		ABIOTIC DECOMPOSITION	
LIGNIN CONCENTRATION (%)	MASS LOSS (%/DAY)	LIGNIN CONCENTRATION (%)	MASS LOSS (%/DAY)
0	0.29	0	0.01
5	0.15	5	0.07
8	0.13	9	0.10
13	0.11	14	0.13
17	0.10		

1. Use the data in the table to plot the relationship between lignin concentration and mass loss for both biotic and abiotic decomposition.
2. What can you conclude about the influence of lignin on abiotic versus biotic decomposition? How does your conclusion support the general hypothesis that plant tissues high in lignin decompose more slowly than plant tissues low in lignin?
3. Under what kinds of environmental conditions and in what types of biomes would you expect the assumption that lignin will lower decomposition *not* to hold true?

See the companion website for a similar ANALYZING DATA exercise.

---

*Austin, A. T. and C. L. Ballaré. 2010. Dual role of lignin in plant litter decomposition in terrestrial ecosystems. *Proceedings of the National Academy of Sciences USA* 107: 4618–4622.

a plant of decreasing its own nutrient supply? For plants that have inherently slow growth rates, lowering soil fertility may protect them from competitive exclusion by neighbors with higher growth and resource uptake rates. Low soil nutrient concentrations can therefore be perpetuated through plant chemistry in a way that benefits the plants themselves (Van Breemen and Finzi 1998).

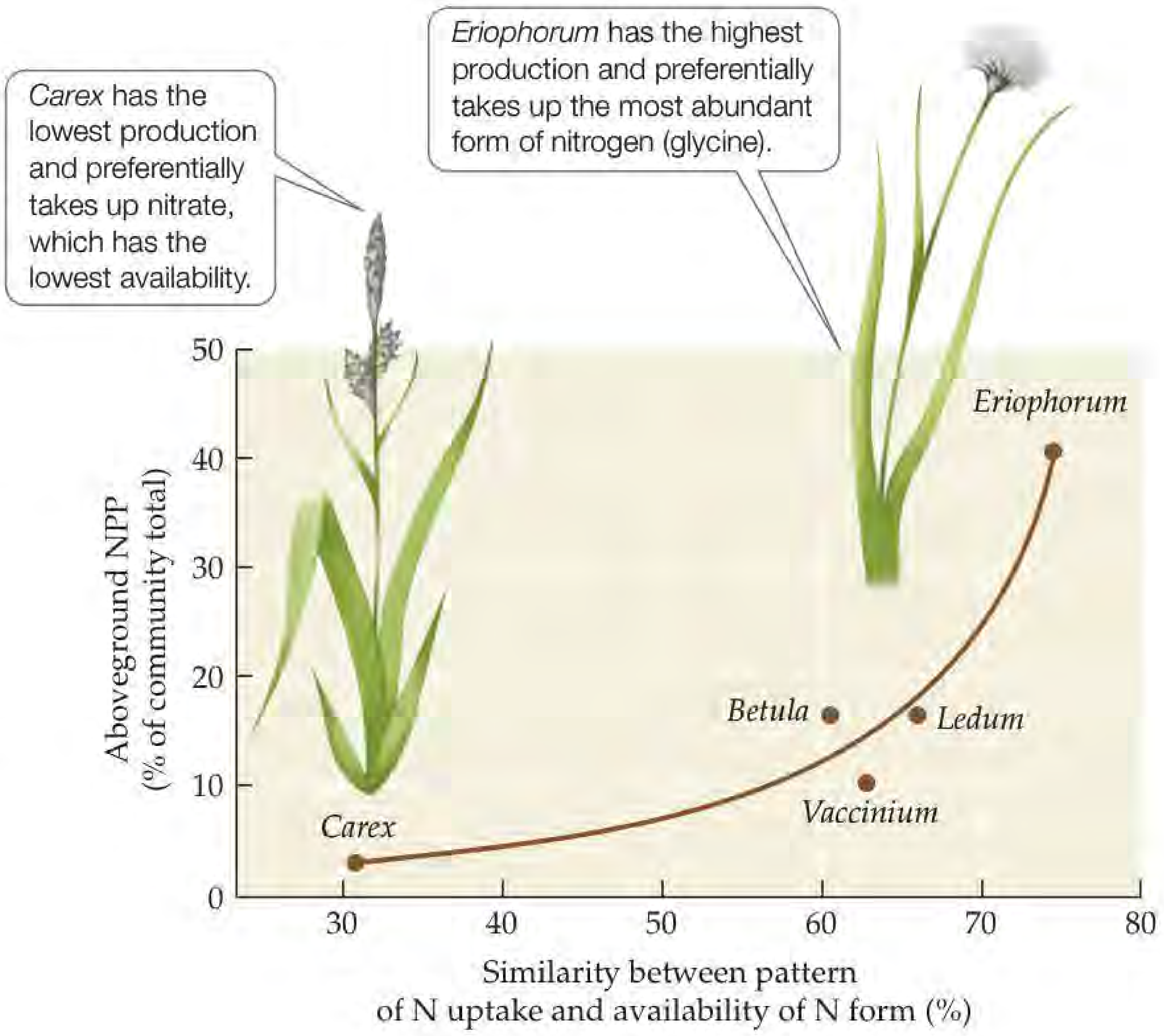
Microorganisms modify the chemical form of nutrients

Microorganisms in soil and freshwater and marine ecosystems transform some of the inorganic nutrients released during the process of mineralization. These transformations are particularly important in the case of nitrogen, since they can determine its availability to plants and the rate at which it is lost from the ecosystem (see Figure 22.11 below). Certain chemoautotrophic bacteria, known as *nitrifying bacteria*, convert ammonia (NH_3) and ammonium (NH_4^+) released by mineralization into nitrate (NO_3^-) by a process called **nitrification**. Nitrification occurs under aerobic conditions, so it is limited primarily to terrestrial environments. Under hypoxic conditions, some bacteria use nitrate as an electron acceptor, converting it into N_2 and nitrous oxide (N_2O, a potent greenhouse gas) by a process known as **denitrification**. These gaseous forms of nitrogen are lost to the atmosphere and thus represent a loss of nitrogen from ecosystems.

Plant ecologists and physiologists once believed that nitrogen availability to plants was dependent solely on the supply of inorganic nitrogen—nitrate and ammonium. Therefore, soil fertility has traditionally been estimated using measurements of these inorganic forms of nitrogen.

During the 1990s, much effort was invested in understanding what controls nitrogen mineralization rates, particularly in ecosystems where fertilization experiments had indicated that nitrogen availability limits primary production and influences community diversity. Measurements of inorganic nitrogen production in forest and grassland soils generally came close to estimates of the amount taken up by plants. However, rates of inorganic nitrogen supply in Arctic and alpine ecosystems were substantially lower than what plants were actually taking up. These apparent shortfalls in nitrogen supply led to the realization that some plants were using organic forms of nitrogen to meet their nutritional requirements. Earlier work in marine ecosystems had shown that phytoplankton could take up amino acids directly from water, and mycorrhizae had been shown to take up organic nitrogen from the soil and supply it to plants. However, Terry Chapin and colleagues (1993) and Ted Raab and colleagues (1996) demonstrated that some plant species, primarily sedges, take up organic forms of nitrogen without mycorrhizae. Arctic sedges may take up as much as 60% of their nitrogen in organic form. Organic nitrogen uptake has been observed in plants in other ecosystems as well, including boreal forests, salt marshes, savannas, grasslands, deserts, and rainforests. Thus, the mineralization step in decomposition may not be as important for plant nutrition as has been commonly thought (Schimel and Bennett 2004).

The use of soluble organic nitrogen by plants has important implications for competition among plants and between plants and soil microorganisms. There is evidence to support the hypothesis that plants in some Arctic and alpine communities avoid competition through the preferential uptake of specific forms of nitrogen—an example of resource partitioning (described in Concept 14.2). Robert McKane and colleagues (2002) examined the forms of nitrogen taken up by several plant species growing together in the Arctic tundra of northern Alaska. For each species, they measured uptake of inorganic and organic forms of nitrogen, as well as the depth in the soil at which nitrogen was taken up and the time of year when it was taken up. They found that all three factors (form of nitrogen, depth of uptake, and timing of uptake) differed among species. Furthermore, the researchers found that the dominant plants in the community tended to be the species that used the form of nitrogen that was most abundant in the soil (**Figure 22.9**). Thus, ability of a species to dominate a community where nitrogen limits growth may be determined in part by its ability to take up a specific form of nitrogen.



Carex has the lowest production and preferentially takes up nitrate, which has the lowest availability.

Eriophorum has the highest production and preferentially takes up the most abundant form of nitrogen (glycine).

Figure 22.9 Community Dominance and Nitrogen Uptake Dominance of a species in a plant community in the Alaskan Arctic tundra (measured by proportional contribution to the community's total net primary production, NPP) is related to the similarity between the plant's preferred form of nitrogen (ammonium, nitrate, or glycine, a small amino acid) and the availability of that form in the soil. (After McKane et al. 2002.)

Plants can recycle nutrients internally

Leaves, fine roots, and flowers, which are the metabolic powerhouses of plants, contain the highest nutrient concentrations of any plant organ. During seasonal leaf senescence, nutrients and nonstructural carbon compounds (such as starch and carbohydrates) in perennial plants are broken down into simpler, more soluble chemical forms and moved into stems and roots, where they are stored. This phenomenon is most obvious in mid- to high-latitude ecosystems as chlorophyll molecules in the leaves of deciduous species are broken down to recover their nitrogen and other nutrients, while other pigments, such as carotenoids, xanthophylls, and anthocyanins, remain, providing the autumnal splendor we humans enjoy. Some of the fall coloration is due to an increase in pigment production, possibly to protect the leaves from high light levels or from herbivores. When growth resumes in spring, the nutrients are transported to growing tissues for use in biosynthesis. Plants may resorb as much as 60%–70% of the nitrogen and 40%–50% of the phosphorus in their leaves before they fall. This recycling reduces their need to take up "new" nutrients in the following growing season.

As we've traced the chemical transformations of nutrients in terrestrial ecosystems, we've seen that they move through various components of those ecosystems as they are transformed. In the next section, we'll look at those movements in more detail and trace the fates of the nutrients as they move through an ecosystem.

CONCEPT 22.3

Nutrients cycle repeatedly through the components of ecosystems.

Nutrient Cycles and Losses

In the previous section, we saw how nutrients undergo biological, chemical, and physical transformations as they are taken up by organisms and released through decomposition, ultimately returning to their original forms (or

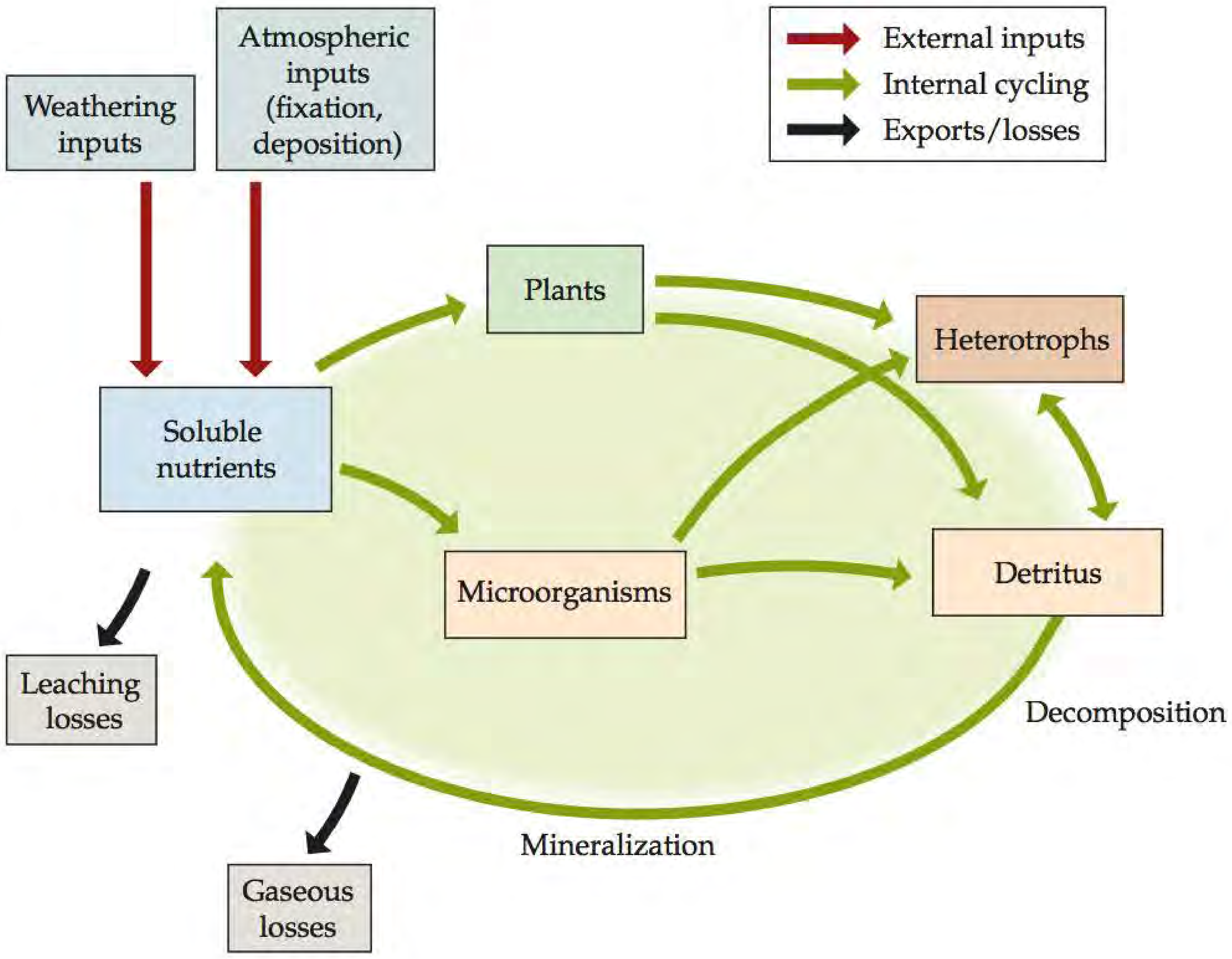


Figure 22.10 Nutrient Cycles A generalized nutrient cycle, showing the movements of a nutrient among the components of an ecosystem and the potential pathways for inputs and losses.

similar ones). This movement of nutrients within ecosystems is known as **nutrient cycling** (**Figure 22.10**). For example, we've traced the path of nitrogen into and through an ecosystem, starting with nitrogen-fixing microorganisms, as it is converted into chemical forms that can be used by plants. The plants incorporate the nitrogen into organic compounds (e.g., proteins and enzymes), which may end up being consumed by heterotrophs. Eventually plants, heterotrophs, and microorganisms all end up as detritus. Inorganic and organic nitrogen released from the detritus by decomposition is taken up again by plants and microorganisms, thereby completing the nitrogen cycle (**Figure 22.11**).

Nutrients cycle at different rates according to element identity and ecosystem type

The time it takes a nutrient molecule to cycle through an ecosystem, from uptake by organisms to release to subsequent uptake, can vary substantially depending on the element in question and the ecosystem where the cycle is occurring. In general, nutrients that limit primary production are cycled more rapidly than nonlimiting nutrients. For example, nitrogen and phosphorus may cycle through the photic zone of the open ocean over a period of hours or days, while zinc may cycle over geologic time scales associated with sedimentation, mountain building, and erosional processes. Nutrient cycling rates also vary with climate because of the effects of temperature and moisture on the metabolic rates of the organisms associated with production, decomposition, and chemical transformations of nutrients.

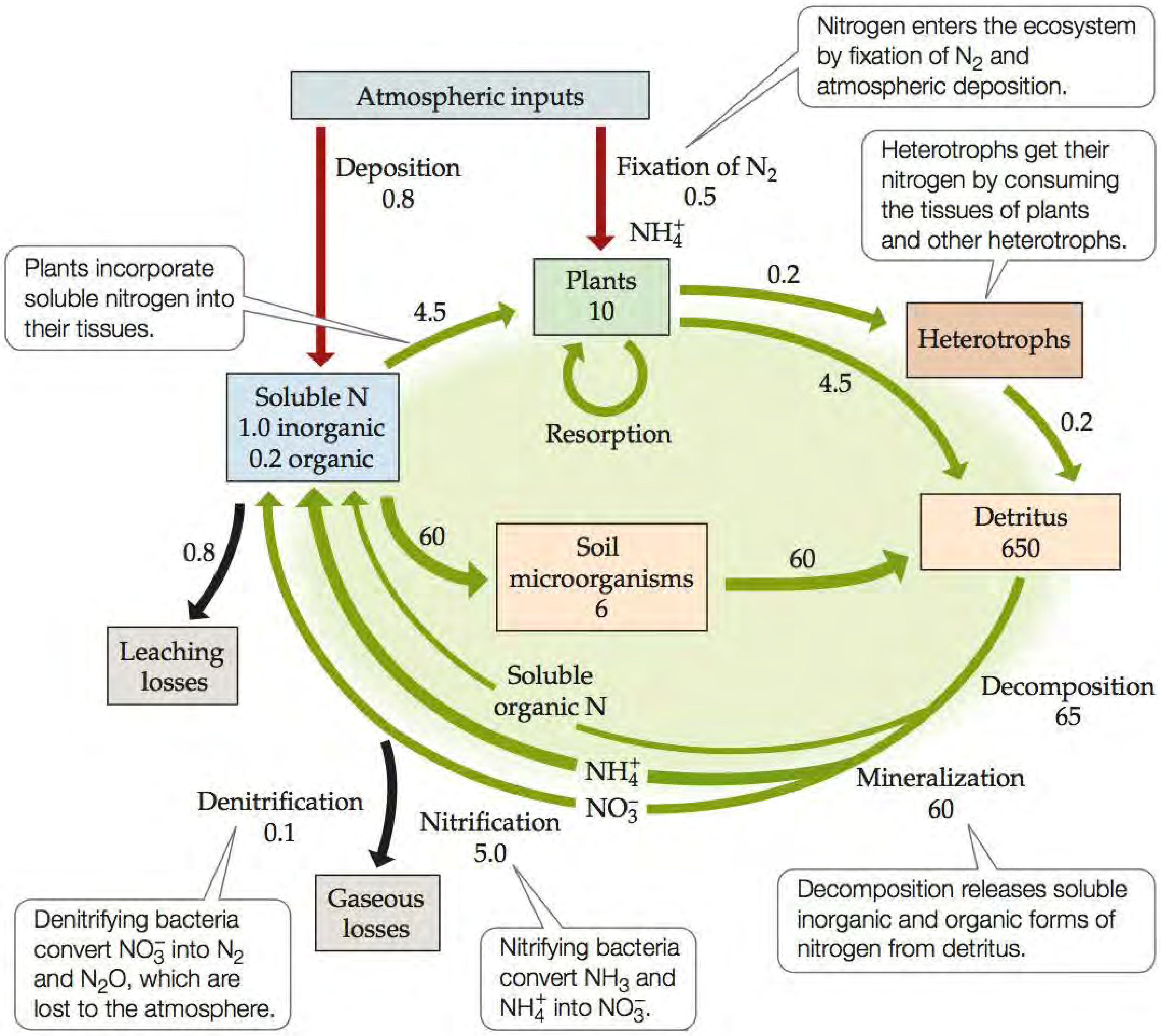


Figure 22.11 Nitrogen Cycle for an Alpine Ecosystem, Niwot Ridge, Colorado Boxes represent pools of nitrogen, measured in grams per square meter; arrows represent flows of nitrogen, measured in grams per square meter per year. Note the large amount of nitrogen passing through soil microorganisms, which indicates a high turnover rate for nitrogen in this relatively small pool. (After Bowman and Seastedt 2001.)

Nitrogen enters the ecosystem by fixation of N_2 and atmospheric deposition.

Heterotrophs get their nitrogen by consuming the tissues of plants and other heterotrophs.

Plants incorporate soluble nitrogen into their tissues.

Denitrifying bacteria convert NO_3^- into N_2 and N_2O, which are lost to the atmosphere.

Nitrifying bacteria convert NH_3 and NH_4^+ into NO_3^-.

Decomposition releases soluble inorganic and organic forms of nitrogen from detritus.

Biogeochemists measure rates of nutrient cycling by estimating the **mean residence times** of elements in some component of an ecosystem:

$$\text{mean residence time} = \frac{\text{total pool of element}}{\text{rate of input}}$$

The mean residence time is the amount of time an average molecule of an element spends in a pool before leaving it. The **pool** of an element is the total amount found within a physical or biological component of the ecosystem, such as soil or biomass. The inputs include all possible sources of the element for that ecosystem component. This approach to estimating mean residence time assumes that pools of nutrients do not change over time and that the mean residence time reflects the overall rate of nutrient cycling. It is most commonly used for estimating rates of nutrient turnover in soil organic matter, which reflect rates of nutrient input and subsequent decomposition. Decomposition rates, as we have seen, are related to climate and the chemistry of plant litter.

Given that both inputs of plant litter and decomposition rates control the mean residence times of nutrients in soil, and that both are subject to climatic control, what differences would we expect to see among ecosystems with similar plant growth forms (e.g., forests) in different climates? Relative to boreal and temperate forests, tropical forests have higher net primary productivity, and therefore higher litter input rates. Does this difference result in differences in the mean residence times of nutrients? A comparison of mean residence times for organic matter and for several nutrients indicates that nutrient pools in the soils of tropical forests are much smaller than those in boreal forests (**Table 22.3**). The turnover rates of nitrogen and phosphorus are more than 100 times faster in tropical forest soils than in boreal forest soils. Temperate forests and chaparral have turnover rates that fall in between but are closer to those in the tropics.

The main reason for this trend in mean residence times is that the influence of climate on rates of decomposition is greater than its influence on primary productivity. Boreal forest soils often have permafrost layers, which cool the soils and lower rates of biological activity. The permafrost also blocks the percolation of water through the soil, creating wet, anoxic soil conditions. Furthermore, the litter produced by boreal forest trees is rich in secondary compounds that slow rates of decomposition in the soil.

The variation in mean residence times among specific nutrients is related to their chemical properties (e.g., solubility). Some nutrients, such as potassium, occur in more soluble forms, and thus are lost from soil organic matter more quickly, than others, such as nitrogen, some of which is found as insoluble organic compounds.

In Chapter 25, we will return to nutrient cycling at a much larger spatial scale as we consider global cycles of carbon, nitrogen, phosphorus, and sulfur in the context of human alterations of these cycles.

Catchment studies measure losses of nutrients from ecosystems

What determines how long nutrients remain in an ecosystem? The retention of nutrients within an ecosystem is related to their uptake into its biological and physical pools and to the stability of their forms. Nitrogen, for example, is more stable as part of an insoluble organic molecule, such as a protein, than as nitrate, which is more easily leached from the soil. Nutrients are lost from an ecosystem when they move below the rooting zone by leaching, and from there into groundwater and streams. Nutrients are also lost to the atmosphere as gases or small particles and by conversion into chemical forms that cannot be used by organisms.

In our consideration of nutrient inputs into and losses from ecosystems, we have been referring to ecosystems as if they had definitive spatial units, but what defines the boundaries of an ecosystem? Ecologists studying terrestrial ecosystems commonly focus on a single drainage basin. This unit of study, which is called a **catchment** or **watershed**, includes the terrestrial area that is drained by a single stream (**Figure 22.12**). By measuring the inputs and outputs of elements in a catchment and calculating the balance between them, ecologists can make inferences about the use of nutrients in the ecosystem and their importance to ecosystem processes such as primary production.

Figure 22.13 presents a conceptual model of a catchment. Nutrient inputs into the catchment include atmospheric deposition and fixation. Nutrients that enter the catchment may be stored in the soil (on cation exchange sites or in the soil solution) or taken up by organisms. They are transferred within and between these ecosystem components by consumption, decomposition, and weathering

TABLE 22.3 Mean Residence Times of Soil Organic Matter and Nutrients in Forest and Shrubland Ecosystems

	MEAN RESIDENCE TIME (YR)					
ECOSYSTEM TYPE	SOIL ORGANIC MATTER	N	P	K	CA	MG
Boreal forest	353	230	324	94	149	455
Temperate coniferous forest	17	18	15	2	6	13
Temperate deciduous forest	4	5	6	1	3	3
Chaparral	4	4	4	1	5	3
Tropical rainforest	0.4	2	2	1	1.5	1

Source: Schlesinger 1997.

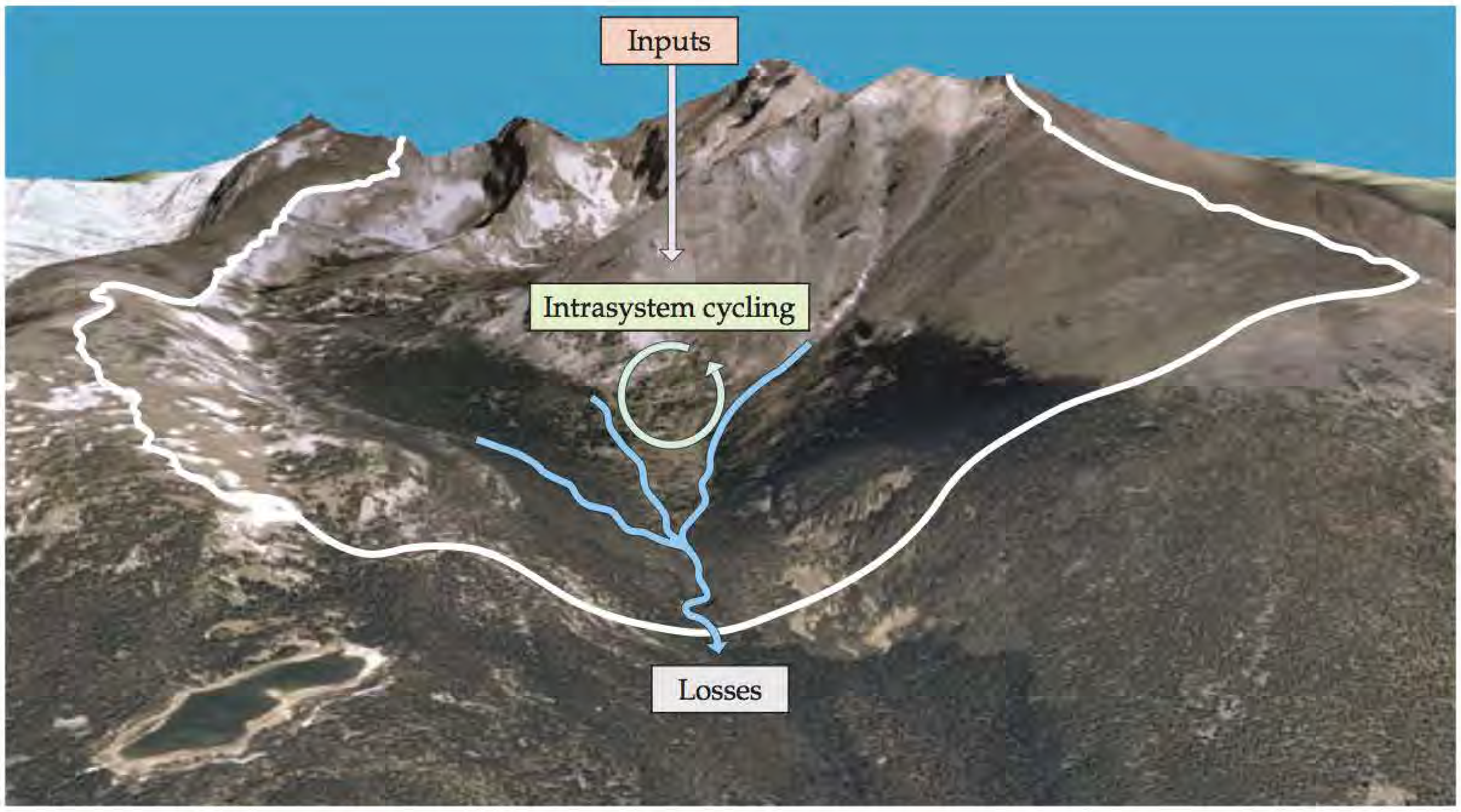


Figure 22.12 Catchments Are Common Units of Ecosystem Study A drainage basin (known as a catchment or watershed) associated with a single stream system (blue lines), with boundaries determined by topographic divides (outlined in white), is a unit commonly used in terrestrial ecosystem studies to measure inputs and outputs of nutrients. This catchment is the upper Hunters Creek basin, draining the south side of Longs Peak in Rocky Mountain National Park.

? What assumptions are made in this simple input–output model of a catchment that may not be realistic? (Hint: Compare this figure with Figure 22.13.)

processes. Nutrients are assumed to be lost from the catchment primarily in stream water, so measurements of dissolved and particulate matter in streams draining the catchment are often used to quantify these losses. In reality, the situation is often more complicated, as nutrients are also lost to the atmosphere in gaseous forms (e.g., N_2 and N_2O from denitrification) and as coarse particulate matter, usually fragmented litter (e.g., bits of leaves), and organisms moving out of the ecosystem. However, measurement of the input–output balance of different nutrients, using methods such as those described in **Ecological Toolkit 22.1**, is instructive for determining their biological importance.

The best-known catchment studies have been performed at the Hubbard Brook Experimental Forest in New Hampshire (Likens and Bormann 1995), which is considered to be representative of the northern deciduous forests of the United States. Continuous monitoring of the Hubbard Brook catchment began in 1963 under the direction of Herb Bormann and Gene Likens, whose studies have served as models for a number of other catchment-level studies. These studies are providing information about the roles of organisms and soils in nutrient retention, how ecosystems respond to disturbances such as logging and fire, and long-term trends in nutrient flows associated with acid rain and climate change.

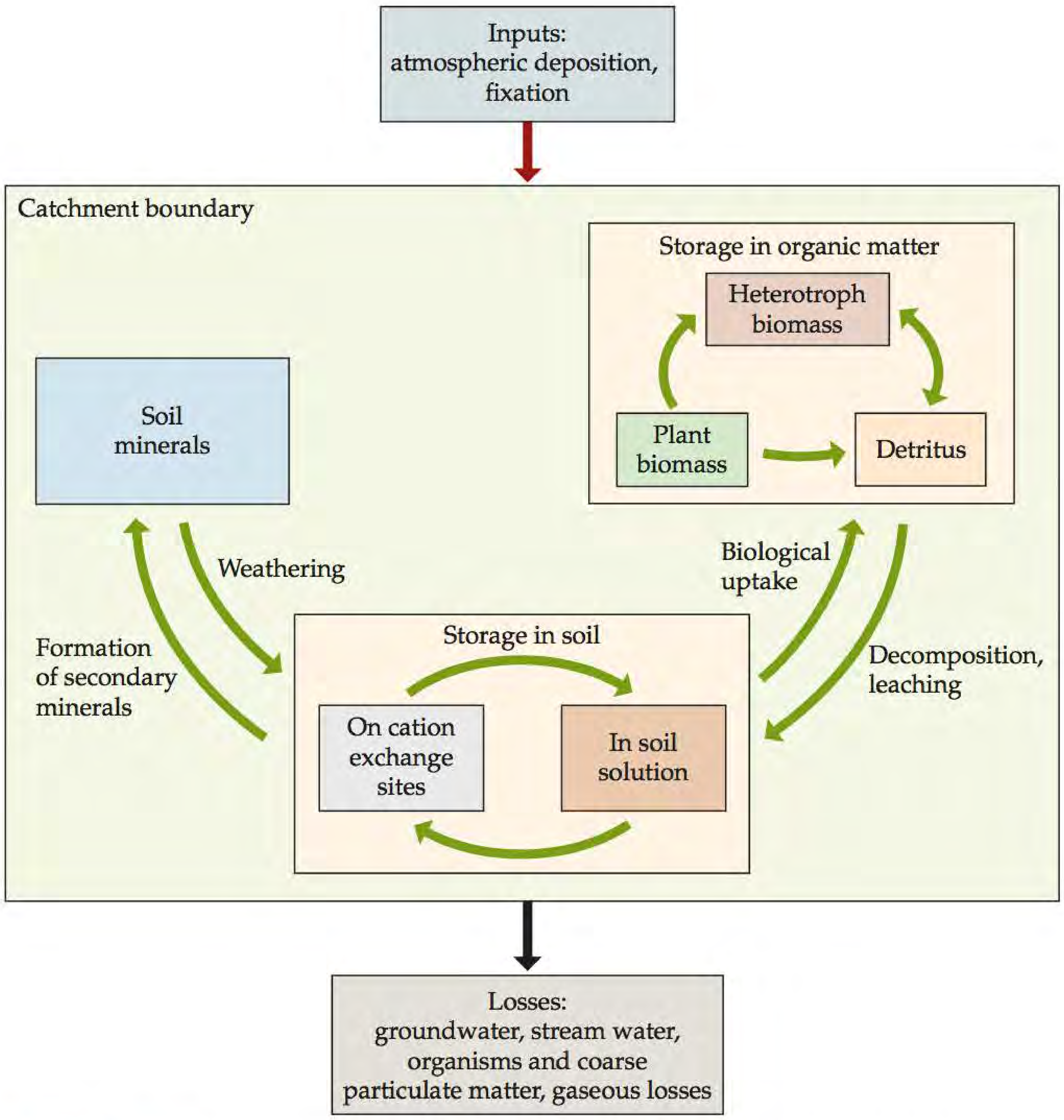


Figure 22.13 Biogeochemistry of a Catchment This conceptual model depicts the major pathways of nutrient movement into, through, and out of a catchment. (After Likens and Bormann 1995.)

ECOLOGICAL TOOLKIT 22.1 Instrumenting Catchments

Measuring the inputs of nutrients into catchments via atmospheric deposition, as well as their losses in stream water, requires knowing the concentrations of the elements in water as well as the volume of water entering and leaving the catchment (i.e., the amount of precipitation and stream flow). The product of the two, concentration times volume, gives the total amount of the element entering or leaving the catchment. These values are usually averaged over periods ranging from a week to a year to provide input–output balances of specific elements.

Atmospheric deposition includes (1) elements captured in precipitation when it falls to the surface (wet deposition) and (2) particles, including aerosols and fine dust, that are transferred to the surface by gravitational fallout or air movement (dry deposition). Total atmospheric deposition can be sampled by placing buckets above the surrounding vegetation to collect the deposited material. However, buckets make good perches for birds, which may deposit their own contribution to ecosystem nutrient input inside the bucket, albeit at much higher concentrations than those found in most other parts of the catchment. This problem can be avoided by placing spiky projections around the edge of the bucket to prevent birds from landing on it. Another problem is that open buckets lose water to evaporation, increasing the concentration of the elements inside. Furthermore, in windy, cold climates, buckets are not good collectors or holders of snow because of their aerodynamics.

Wet deposition collectors have been developed that open to the atmosphere only during precipitation events and then close to prevent evaporation (**Figure A**). A moisture-sensitive surface controls a switch that opens and closes the collector. Where snow and wind occur together, windscreens help to prevent loss of snow from the bucket and enhance the capture of the deposition. Separate precipitation gauges may also be used to more accurately estimate the volume of precipitation entering the ecosystem. At regular intervals, the precipitation in the bucket or collector is analyzed for the elements of interest using chemical analyses that typically meet some government standard (e.g., in the United States, the Environmental Protection Agency provides these standards). In many developed nations, networks of wet deposition samplers have been established to provide spatial estimates of atmospheric deposition (e.g., the National Atmospheric Deposition Program in the United States: nadp.sws.uiuc.edu; see Figure 25.19).

Figure A Measuring Deposition A wet deposition collector is serviced on Niwot Ridge, Colorado. The bucket on the right is covered except during precipitation events. (Courtesy of Mark Losleben.)

Dry deposition measurements are more complex, usually involving collection of atmospheric samples to measure the sizes of atmospheric particles and their chemical composition. These measurements are combined with wind speed and direction measurements to estimate movements of elements to the surface. Because of the greater difficulty of the sampling and the larger uncertainties, dry deposition is measured less frequently than wet or bulk (total) deposition. In some areas, however, such as deserts or Mediterranean-type ecosystems, dry deposition is the largest component of total deposition.

Measuring nutrient losses in stream flow is straightforward. The chemical composition of stream water leaving the catchment is measured by periodically collecting water samples and analyzing their chemistry. The volume of stream water is often estimated by constructing a *weir*, a small, usually V-shaped overflow dam made of concrete or wood and metal to control the size of the channel, and placing a depth gauge to calculate the volume of water passing through it (**Figure B**). The depth of the water can be measured with an automated system to give continuous volume estimates.

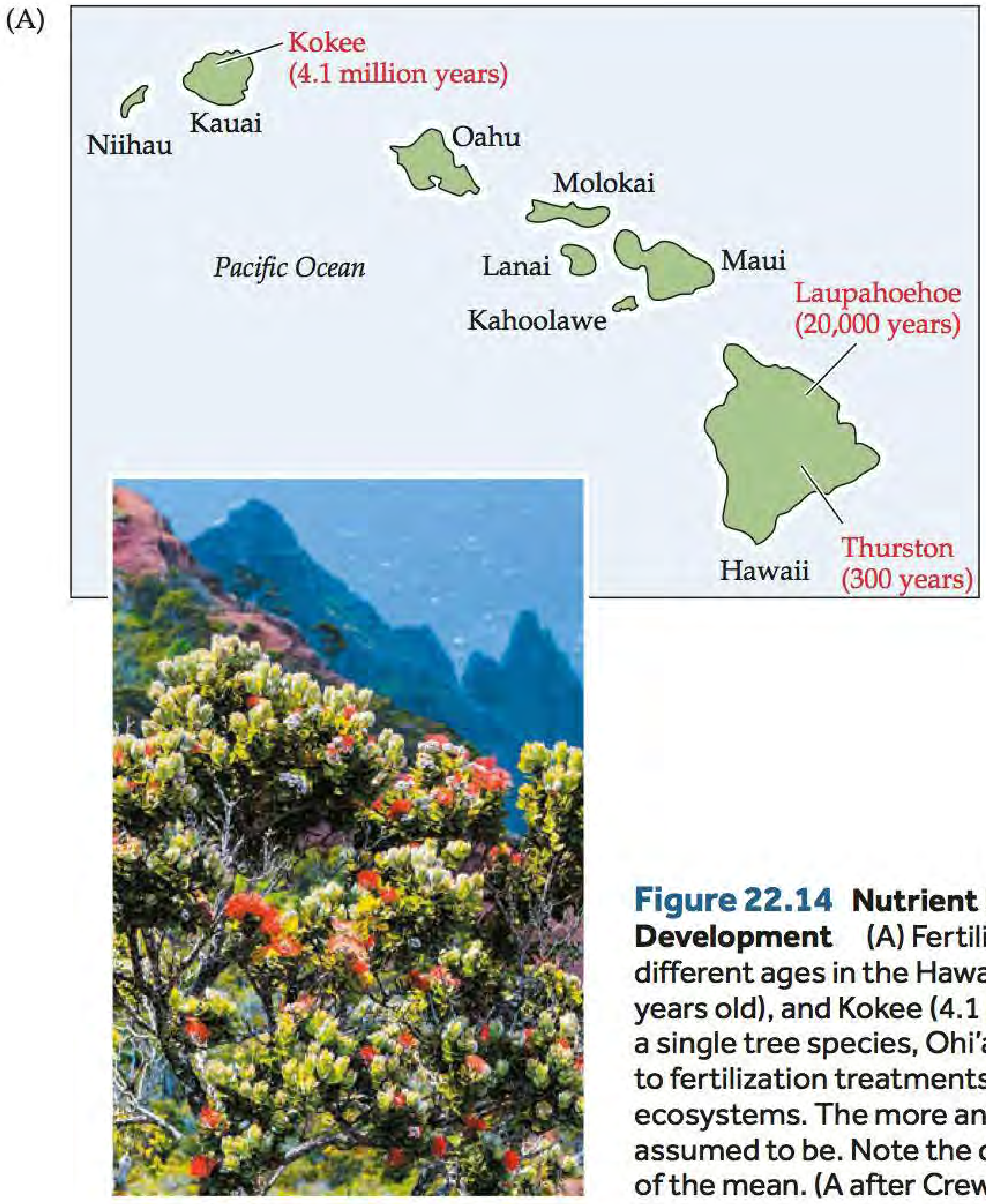
Figure B Measuring Water Flow A weir on Fool Creek in the Fraser Experimental Forest, Colorado.

Long-term ecosystem development affects nutrient cycling and constraints on primary production

As terrestrial ecosystems develop on new substrates (e.g., in primary succession on new volcanic flows), soil weathering, nitrogen fixation, and the buildup of organic matter in the soil determine the supply of nutrients available to plants. Early in ecosystem development, there is little organic matter in the soil, so supplies of nitrogen derived from decomposition are low. Supplies of mineral nutrients derived from weathering are also low, but higher relative to the supply of nitrogen. Accordingly, nitrogen availability should be an important constraint on primary production and plant community composition early in primary succession (see Chapter 17). As the pool of nitrogen in soil organic matter increases, its limitation of primary production should decrease.

Phosphorus enters ecosystems through the weathering of a single rock mineral (apatite), and its supply is high relative to that of nitrogen early in succession. As the supply of phosphorus from weathering is exhausted over time, however, decomposition becomes increasingly important as a source of phosphorus for plants. In addition, soluble phosphorus may combine with iron, calcium, or aluminum to form secondary minerals that are unavailable as nutrients, a process known as **occlusion**. The amount of phosphorus in occluded forms increases over time, further reducing its availability. As a result, phosphorus should become more limiting to primary production during later stages of succession (Walker and Syers 1976).

These observations of changes in nutrient cycling during ecosystem development provide a hypothetical framework for considering how those changes should influence the specific nutrients that limit primary production. Nitrogen should be most important in determining rates of primary production early in succession, nitrogen and phosphorus should both be important at intermediate stages of succession, and phosphorus should be most important late in succession. This hypothesis was tested in the Hawaiian Islands by Peter Vitousek and his colleagues. The movement of the Pacific tectonic plate over millions of years has given rise to the chain of volcanoes that form these islands. The oldest islands are in the northwestern part of the chain, the youngest in the southeast (**Figure 22.14A**). Vitousek's group studied Hawaiian ecosystems on soils with ages ranging from 300 years to over 4 million years to determine which nutrients were most limiting to primary production. Their study was aided by the similarity of the vegetation and climate at each of



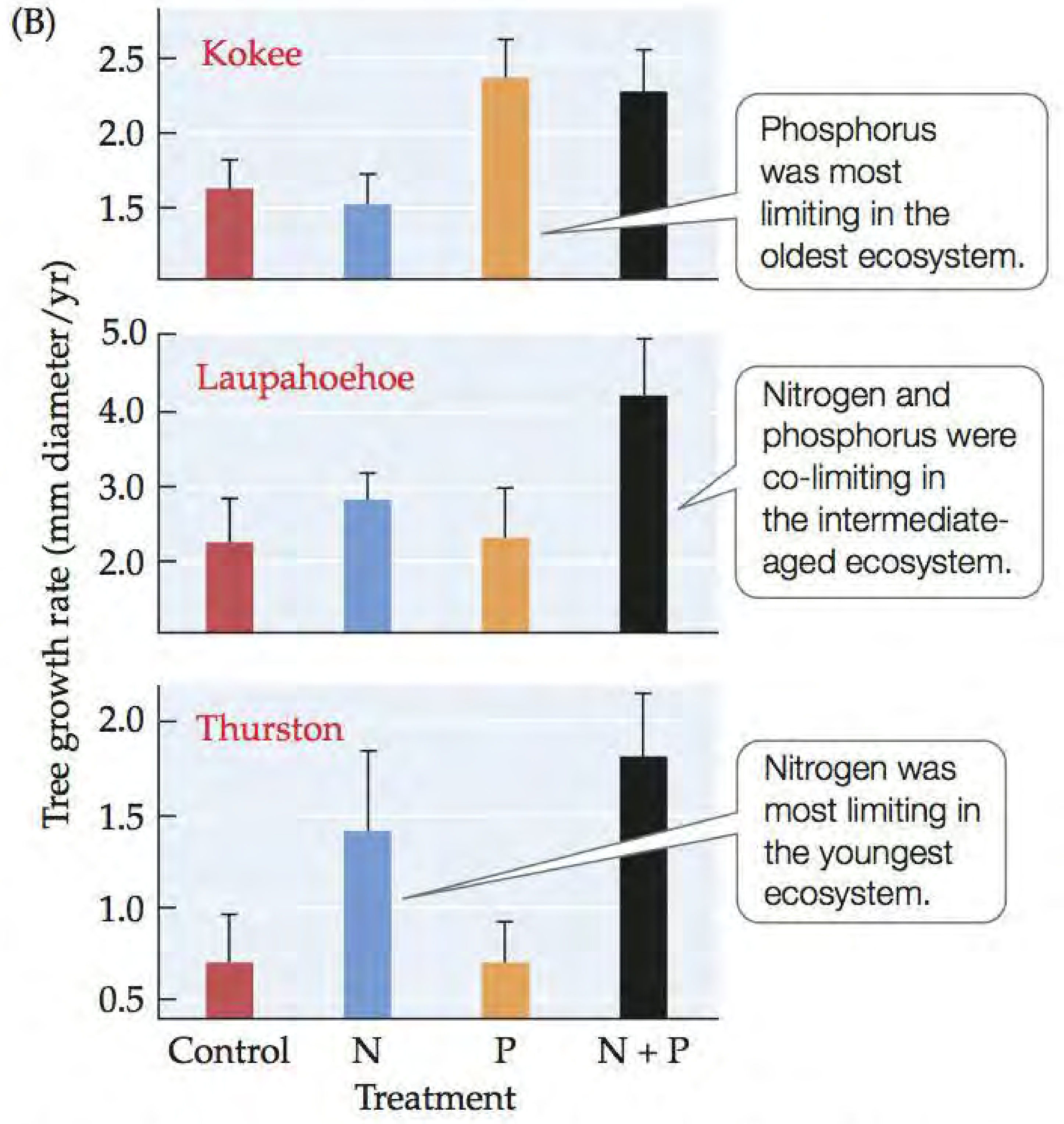


Figure 22.14 Nutrient Limitation of Primary Production Changes with Ecosystem Development (A) Fertilization experiments were conducted in three ecosystems of different ages in the Hawaiian Islands: Thurston (300 years old), Laupahoehoe (20,000 years old), and Kokee (4.1 million years old). Vegetation at all three sites is dominated by a single tree species, Ohi'a (*Metrosideros polymorpha*). (B) Ohi'a growth rates in response to fertilization treatments with nitrogen (N), phosphorus (P), and both (N + P) in the three ecosystems. The more an added nutrient increased tree growth, the more limiting it was assumed to be. Note the differences in the ranges of the *y* axes. Error bars show one SE of the mean. (A after Crews et al. 1995; B after Vitousek and Farrington 1997.)

the study sites. Vitousek and colleagues added nitrogen, phosphorus, or both nitrogen and phosphorus to plots in three ecosystems of different ages and measured the effects of these treatments on the growth of the dominant tree, Ohi'a (*Metrosideros polymorpha*). Consistent with their hypothesis, nitrogen was most limiting to tree growth in the youngest ecosystem, while phosphorus was most important in the oldest ecosystem (Vitousek and Farrington 1997) (**Figure 22.14B**). Nitrogen and phosphorus added in combination increased tree growth in the intermediate-aged ecosystem. In contrast to these tropical soils, the soils of ecosystems in temperate, high-latitude, and high-elevation zones are often subjected to major disturbances (e.g., large-scale glaciation, landslides) and are less likely to reach ages at which phosphorus becomes limiting.

Nutrients lost from terrestrial ecosystems often end up in streams, lakes, and oceans. They are a critical source of nutrients for those aquatic ecosystems, but they can have negative effects as well, as we'll see in the next section.

CONCEPT 22.4

Freshwater and marine nutrient cycles occur in a moving medium and are linked to terrestrial ecosystems.

Nutrients in Aquatic Ecosystems

In freshwater and marine ecosystems, nutrient transformations and transfers have the added complexity of occurring in a moving aqueous medium. Inputs of nutrients from outside the ecosystem are much more important than in terrestrial ecosystems. Furthermore, oxygen concentrations are often lower than in terrestrial ecosystems, constraining biological activity and the biogeochemical processes associated with it.

Nutrients in streams and rivers cycle while moving downstream

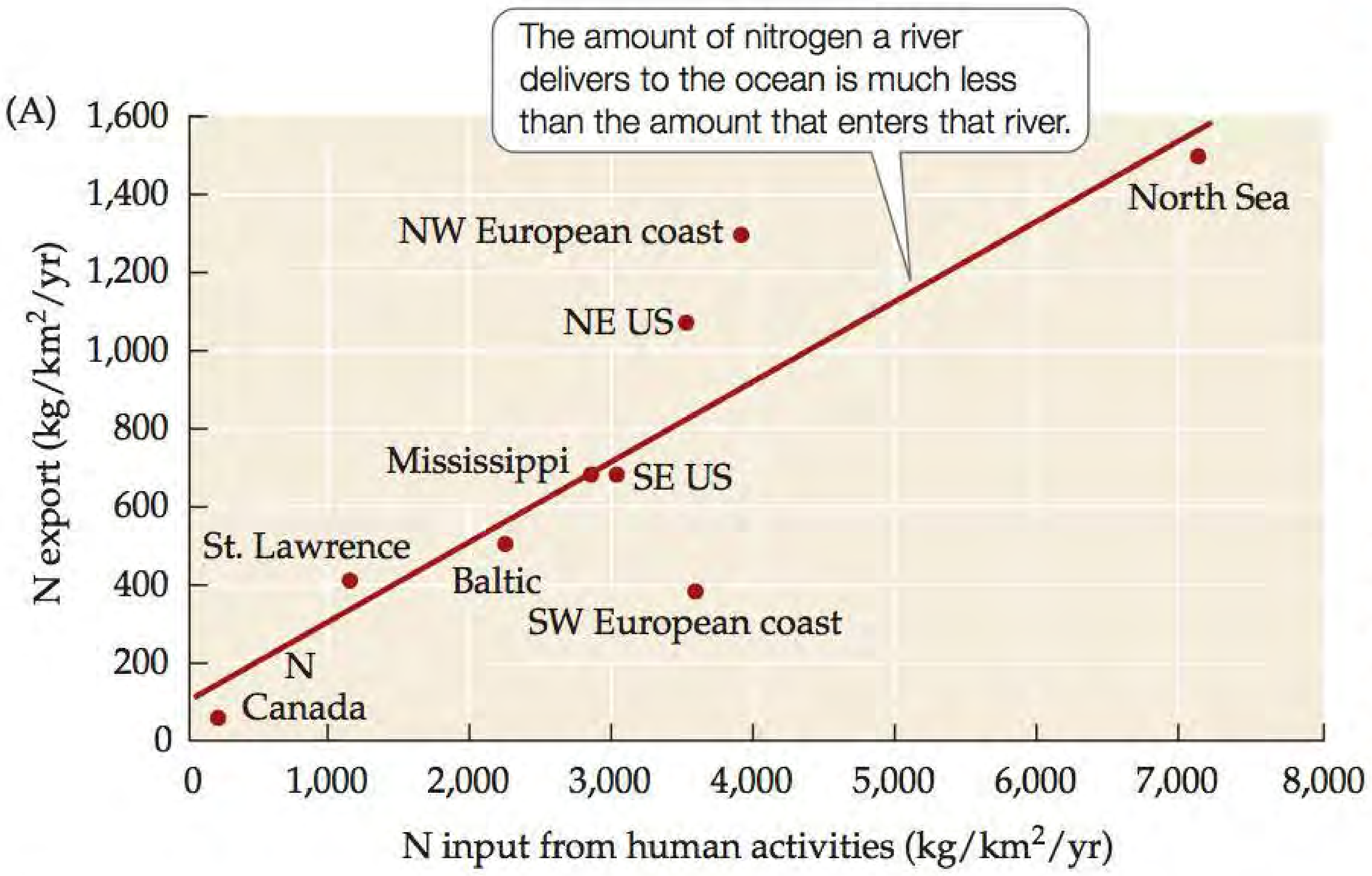
Nutrient supplies in streams and rivers are highly dependent on external inputs from terrestrial ecosystems. Terrestrial inputs of organic matter, dissolved nutrients derived from chemical weathering and decomposition in surrounding soils, and particulate minerals are the primary sources of nutrients for riverine organisms. Rivers and streams carry these materials to the ocean, but they are not just conduits for the movement of material between terrestrial and marine ecosystems. Biogeochemical processing in moving stream water can change the forms and concentrations of the elements it contains. For example, denitrification and biological uptake in streams and rivers may result in significant losses of nitrogen during transport in stream water. These processes may explain why rivers export less nitrate from regions receiving high amounts of nitrogen pollution than would be expected (**Figure 22.15A**). Both processes are enhanced when detritus is abundant on the stream bottom (**Figure 22.15B**).

Nutrients in rivers and streams are cycled repeatedly as the water flows downstream. Dissolved inorganic forms of nutrients are taken up by organisms, including fungi, bacteria, and phytoplankton, which incorporate them into organic molecules. These organisms may be consumed by others and pass through a food web, eventually entering the pool of stream detritus. Following decomposition of the detritus, the mineralized nutrients are released back into the water in dissolved inorganic forms. This repeated uptake and release in association with the movement of water can be thought of as nutrient "spiraling" (Newbold et al. 1983) (**Figure 22.16**). The time it takes for a full nutrient spiral to occur (i.e., from uptake and incorporation into organic forms to release in inorganic forms) is related to the amount of biological activity in the stream, the water velocity, and the chemical form of the nutrient. Retention of nitrate and phosphate in rivers increases downstream because of increasing spiral lengths; thus, higher-order streams (see Figure 3.13) are particularly important in buffering the effects of nutrient pollutants on estuarine and marine ecosystems (Ensign and Doyle 2006).

Nutrients in lakes cycle efficiently in the water column

Lake ecosystems receive inputs of nutrients from streams, by atmospheric deposition and nitrogen fixation, and as litter falling from adjacent terrestrial ecosystems. Biological demand for nutrients is highest in the photic zone, where phytoplankton are suspended in the water column, and in the shallow zones at the margins of the lake, where rooted aquatic plants are found. Phosphorus commonly limits primary production in lakes, although nitrogen may also be limiting in some lakes. Nutrient transfers between trophic levels, like energy transfers (see Figure 21.5C), are very efficient in lakes. Some detritus is decomposed and mineralized in the water column and in sediments in the shallow zones, providing an internal input of nutrients. Nitrogen fixation by cyanobacteria occurs in the photic zone, particularly when demand for nitrogen by organisms is greater than for phosphorus. Rates of nitrogen fixation in lake ecosystems are similar to those in terrestrial ecosystems.

Over time, nutrients are progressively lost from the photic zone of a lake. Dead organisms sink through the water column and are deposited in the sediments of the benthic zone. These sediments are characterized by hypoxic conditions that limit biological activity, including decomposition, and by a reducing chemical environment that may change the chemical form of some nutrients. Iron, for example, is often reduced from Fe^{3+} to Fe^{2+}, contributing to the dark color of lake sediments. Denitrification is also promoted by the low oxygen concentrations in the sediments, and bacteria may reduce sulfate (SO_4^{2-}) to hydrogen sulfide (H_2S).



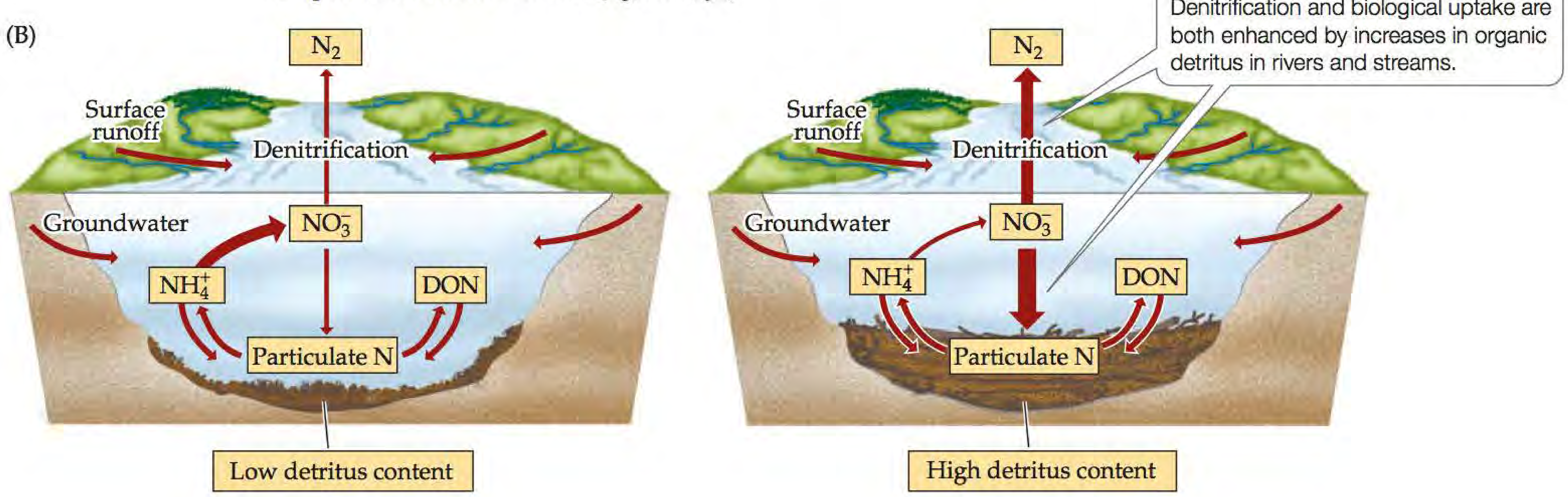


Figure 22.15 Rivers Are Important Modifiers of Nitrogen Exports Nitrogen that enters rivers from terrestrial ecosystems is not simply carried to the ocean. (A) The rates of nitrogen exports to the North Atlantic Ocean from major drainage basins are correlated with rates of nitrogen inputs into rivers by human activities. The export rates, however, are substantially lower than the input rates because of biogeochemical processing of the nitrogen in the rivers (notice the difference between the scales in the *x* and *y* axes). (B) Denitrification and biological uptake are two of the main processes that lower the export of nitrogen from drainage basins. Both processes are enhanced when benthic detritus is high. DON, dissolved organic nitrogen. (A after Howarth et al. 1996; B after Bernhardt et al. 2005.)

Decomposition in the benthic sediments cannot provide nutrients to the photic zone unless there is mixing of the water column. In stratified temperate-zone lakes, as we saw in Concept 2.5, this mixing occurs in fall and spring, when the lake's water from top to bottom becomes isothermal and wind facilitates its turnover. This seasonal turnover brings dissolved nutrients from the bottom water to the surface layers, along with detritus that may be subsequently decomposed by bacteria. Mixing of water layers is less common in tropical lakes, so external inputs of nutrients may be more important for maintaining production in those lakes.

Lake ecosystems are often classified according to their nutrient status. Nutrient-poor waters with low primary productivity are referred to as **oligotrophic**, while nutrient-rich waters with high primary productivity are referred to as **eutrophic**. **Mesotrophic** waters are intermediate in nutrient status between oligotrophic and eutrophic waters. The nutrient status of a lake is the result of natural processes associated with climate and with lake size and shape. For example, lakes in high mountain areas are typically oligotrophic because of their short growing season, low temperatures, and tendency to be deep with a low surface area-to-volume ratio, which constrains the rate of nutrient input by atmospheric deposition. In contrast, shallow lakes at lower elevations or in the tropics tend to be

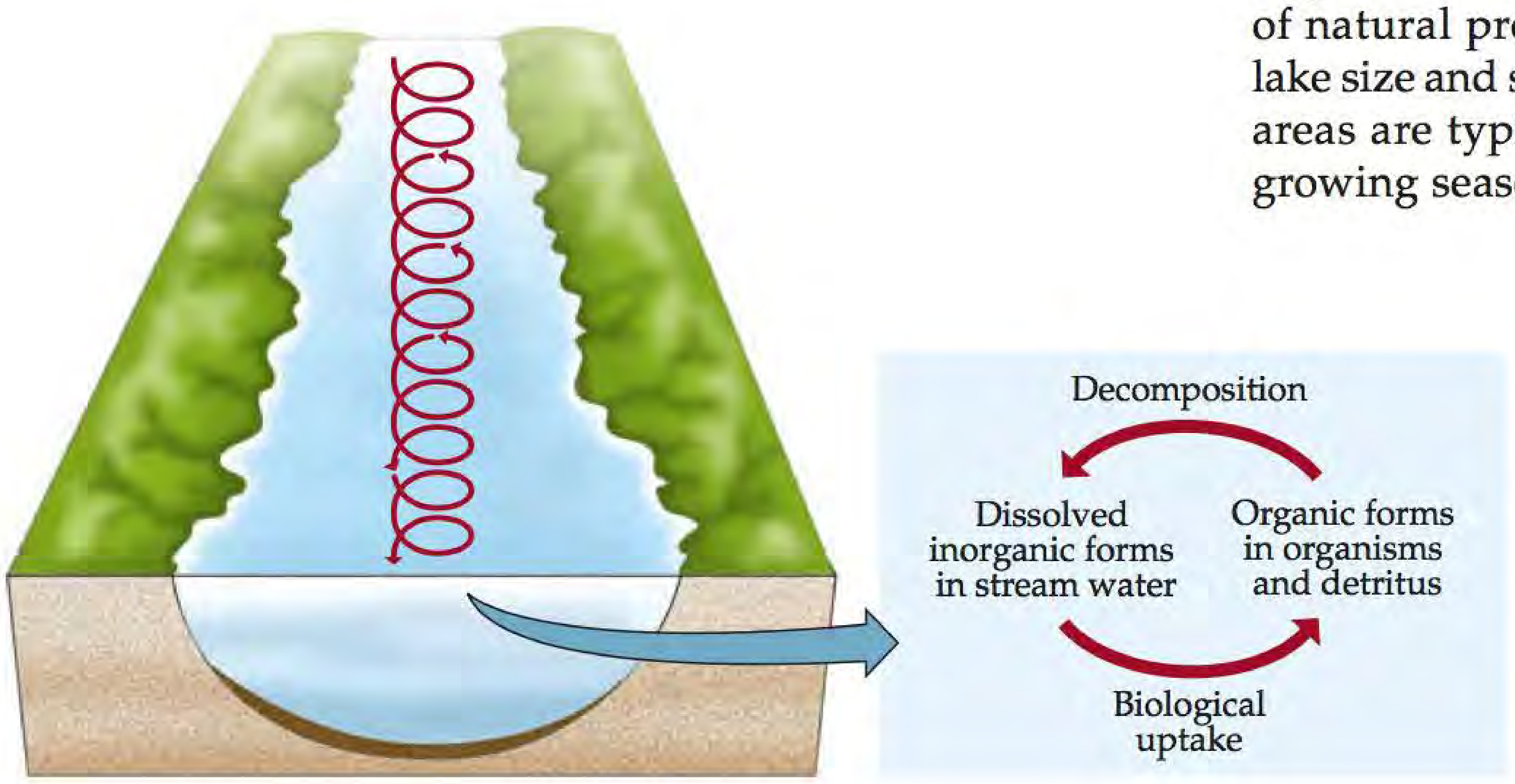


Figure 22.16 Nutrient Spiraling in Stream and River Ecosystems Cycling of nutrients as the water moves downstream results in repeated spirals of nutrient uptake and release.

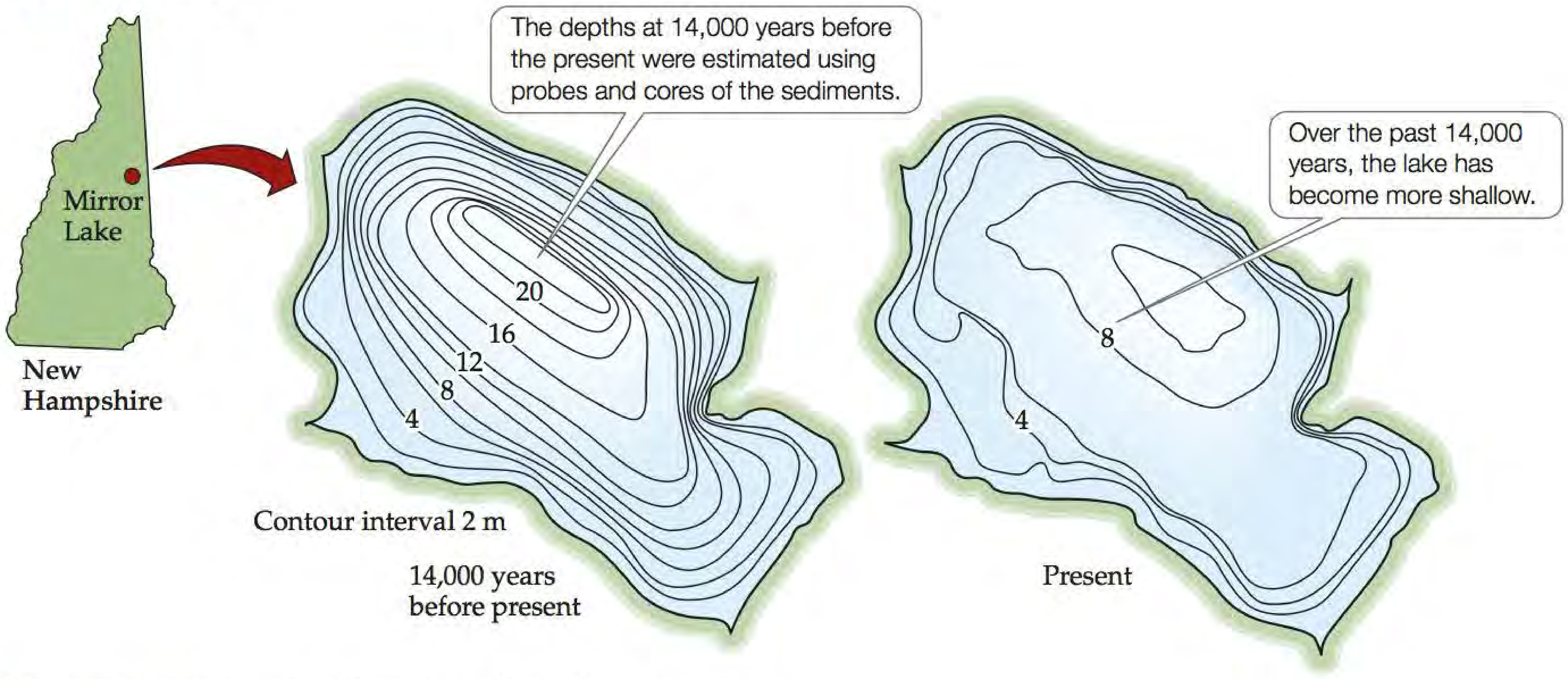


Figure 22.17 Lake Sediments and Depth Sediments accumulate at the bottom of a lake over time, making it progressively shallower and leading to eutrophication. Changes in the depth contours of Mirror Lake in New Hampshire show the accumulation of sediments there over the past 14,000 years. (After Davis et al. 1985.)

eutrophic because of their warmer temperatures and higher nutrient availability.

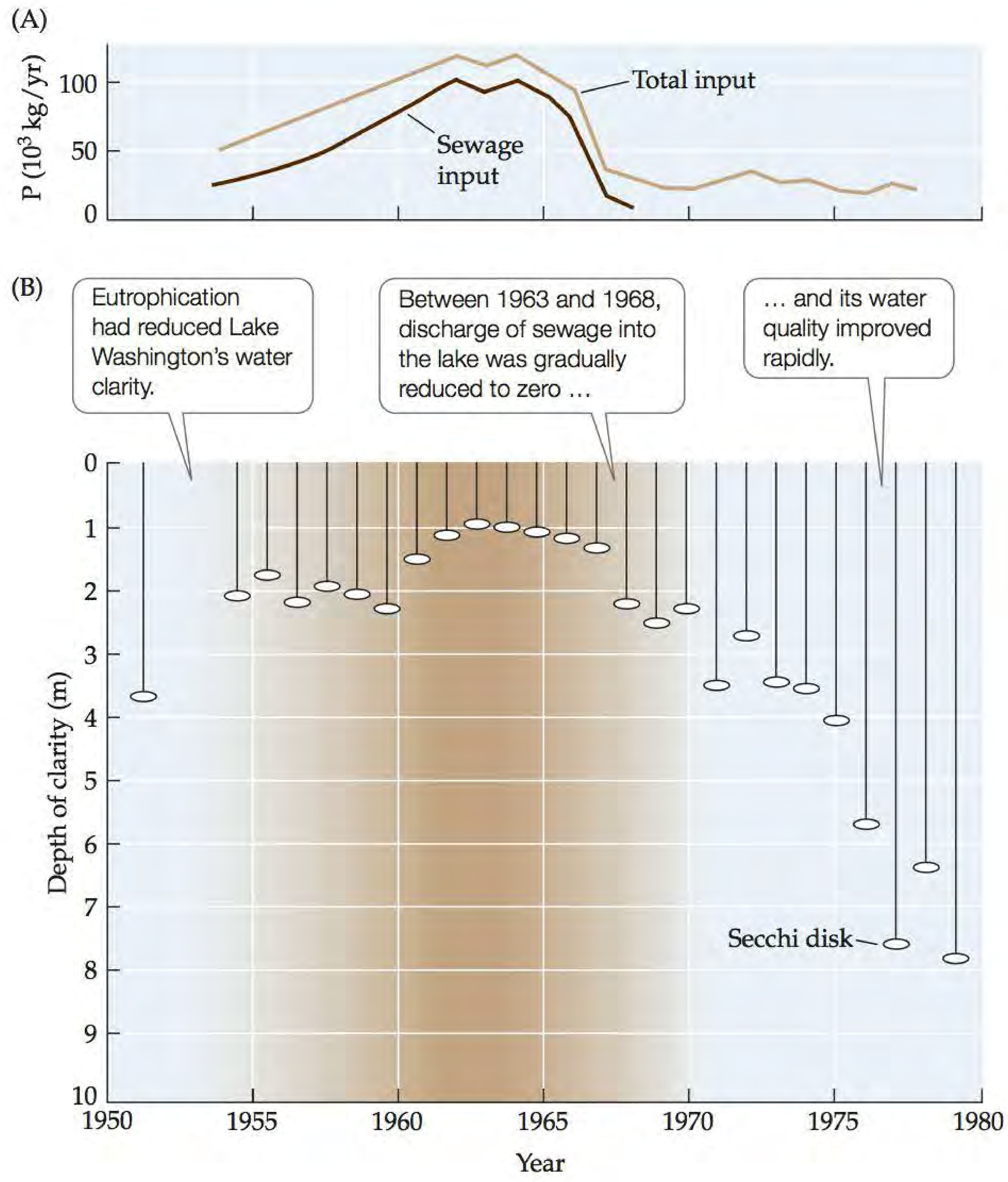
The nutrient status of a lake tends to shift naturally from oligotrophic to eutrophic over time. This process, known as **eutrophication,** occurs as sediments accumulate on the lake bottom (**Figure 22.17**). As the lake becomes shallower, its summer temperatures become warmer, more decomposition occurs, nutrient pools and the amount of mixing increase, and the lake becomes more productive. Human activities have accelerated the process of eutrophication in many lakes through discharges of sewage, agricultural fertilizers, and industrial wastes containing high concentrations of nitrogen and phosphorus. For example, the water of Lake Tahoe, on the border between Nevada and California, has lost much of its clarity because of increased inputs of phosphorus and nitrogen from streams, groundwater, and surface runoff from neighboring communities. Water clarity, which is used as an indicator of a lake's nutrient status, is primarily determined by the density of plankton in the water column. It can be measured using a Secchi disk, a black-and-white circular plate that is lowered gradually into the water; the maximum depth at which the disk can be seen is referred to as the *depth of clarity*. Over the past 3 decades, the average depth of clarity in Lake Tahoe has risen by 10 m (Murphy and Knopp 2000). The rate at which water clarity has been decreasing has declined since 2000, partly because of lower amounts of precipitation.

Anthropogenic eutrophication can be reversed if the discharge of wastes into surface waters is decreased. A classic example of such a reversal occurred in the 1960s and 1970s in Lake Washington, near Seattle. Treated sewage, containing high concentrations of phosphorus, was released into Lake Washington beginning in the late 1940s as neighborhoods and accompanying sewage treatment plants were built near the shore of the lake. Decreases in water clarity were noted during the 1950s, corresponding to increases in phytoplankton densities and blooms of cyanobacteria. Public concern grew, and local governments debated what action to take. A prominent local limnologist, W. T. Edmondson, believed that the problem was associated with phosphorus inputs from the treated sewage, which included wastewater from washing machines containing phosphorus-laden detergents. Based on Edmondson's advice, Seattle stopped its sewage input into Lake Washington completely by 1968. Increases in water clarity were soon noted, and by 1975, the lake was considered recovered from eutrophication (**Figure 22.18**). Edmondson's recommendation was crucial to the lake's recovery, and the case contributed to the current U.S. restrictions on the use of phosphates in detergents.

Imports and upwelling are important sources of nutrients in marine ecosystems

Rivers join marine ecosystems in estuaries (described in Concept 3.3). In these zones where fresh water meets seawater, salinity—and thus water density—is variable. This variation influences the mixing of waters and the chemical forms of some nutrients. For example, phosphorus bound to soil particles may be released in a form more easily available to phytoplankton as a result of changes in pH and water chemistry when river water mixes with seawater.

As the velocity of water flow decreases toward the mouth of a river, suspended sediments begin to settle out of the water. These sediments are resuspended by the influx of saltier, denser seawater into the fresher, less dense river water, providing detritus for detritivores and nutrients for phytoplankton in the estuary. Estuaries are often associated with salt marshes, which are rich in nutrients because they trap both riverine and ocean sediments. Like benthic sediments in lakes, estuarine and salt



Eutrophication had reduced Lake Washington's water clarity.

Between 1963 and 1968, discharge of sewage into the lake was gradually reduced to zero …

… and its water quality improved rapidly.

Figure 22.18 Lake Washington: Reversal of Fortune Inputs of treated sewage between the 1940s and the 1960s caused eutrophication in Lake Washington; cessation of sewage inputs between 1963 and 1968 increased lake clarity. (A) Phosphorus inputs. (B) Measurements of water clarity made with a Secchi disk. (After Edmondson and Litt 1982.)

? While the story of Lake Washington seems to be a clear "experimental" demonstration of pollution influencing the nutrient status of a lake, what would make it an even more convincing example?

marsh sediments have low oxygen concentrations that limit decomposition.

As described in Concept 20.2, primary production in the open ocean is limited by several nutrients, including nitrogen, phosphorus, and in some areas, iron and silica. Seawater has relatively high concentrations of magnesium, calcium, potassium, chloride, and sulfur. Sources of nitrogen in marine ecosystems include inputs from rivers and atmospheric deposition as well as tight internal cycling through decomposition. Rates of nitrogen fixation by cyanobacteria in the oceans are lower than those in freshwater lakes, possibly because these organisms are limited by molybdenum, which is a component of the nitrogenase enzyme. Phosphorus, iron, and silica enter the marine ecosystem primarily in dissolved and particulate form in rivers; a smaller but important contribution comes from atmospheric deposition of dust. Inputs from both of these terrestrial sources are increasing as a result of human activities, including large-scale desertification and deforestation.

Deep deposits of sediments (up to 10 km, or 6 miles thick!) have accumulated in the benthic zones of the open ocean. These deposits, which consist of a mix of ocean-derived detritus and terrestrial erosional sediments, are important potential sources of nutrients. Sulfate reduction and denitrification occur in these anoxic sediments, and some decomposition and mineralization of organic matter also occur there. Bacteria have been found as deep as 500 m in these sediments. Mixing of deep, nutrient-rich waters with nutrient-poor surface waters occurs in zones of upwelling, where ocean currents bring deep waters to the surface (**Figure 22.19**). These zones of upwelling are highly productive and thus are important areas for commercial fisheries.

Figure 22.19 Zones of Upwelling Enhance Nutrient Supply for Marine Ecosystems Phytoplankton blooms (green areas), fed by upwelling of nutrient-rich deep ocean water, can be seen off the coast of the Pribilof Islands in this satellite image.

A CASE STUDY REVISITED
A Fragile Crust

We've seen that nutrient supplies for plants in terrestrial ecosystems are dependent on the weathering of rock minerals and the decomposition of detritus in the soil, as well as on the fixation of atmospheric nitrogen. How might the loss of biocrusts from desert soils influence these processes? As this chapter's Case Study explained, the crusts prevent erosional losses of soil by helping to bind soil particles together. The activity of the organisms that make up the crusts may also influence nutrient inputs and, in turn, the productivity of the desert ecosystem, as well as its capacity to withstand the desert climate.

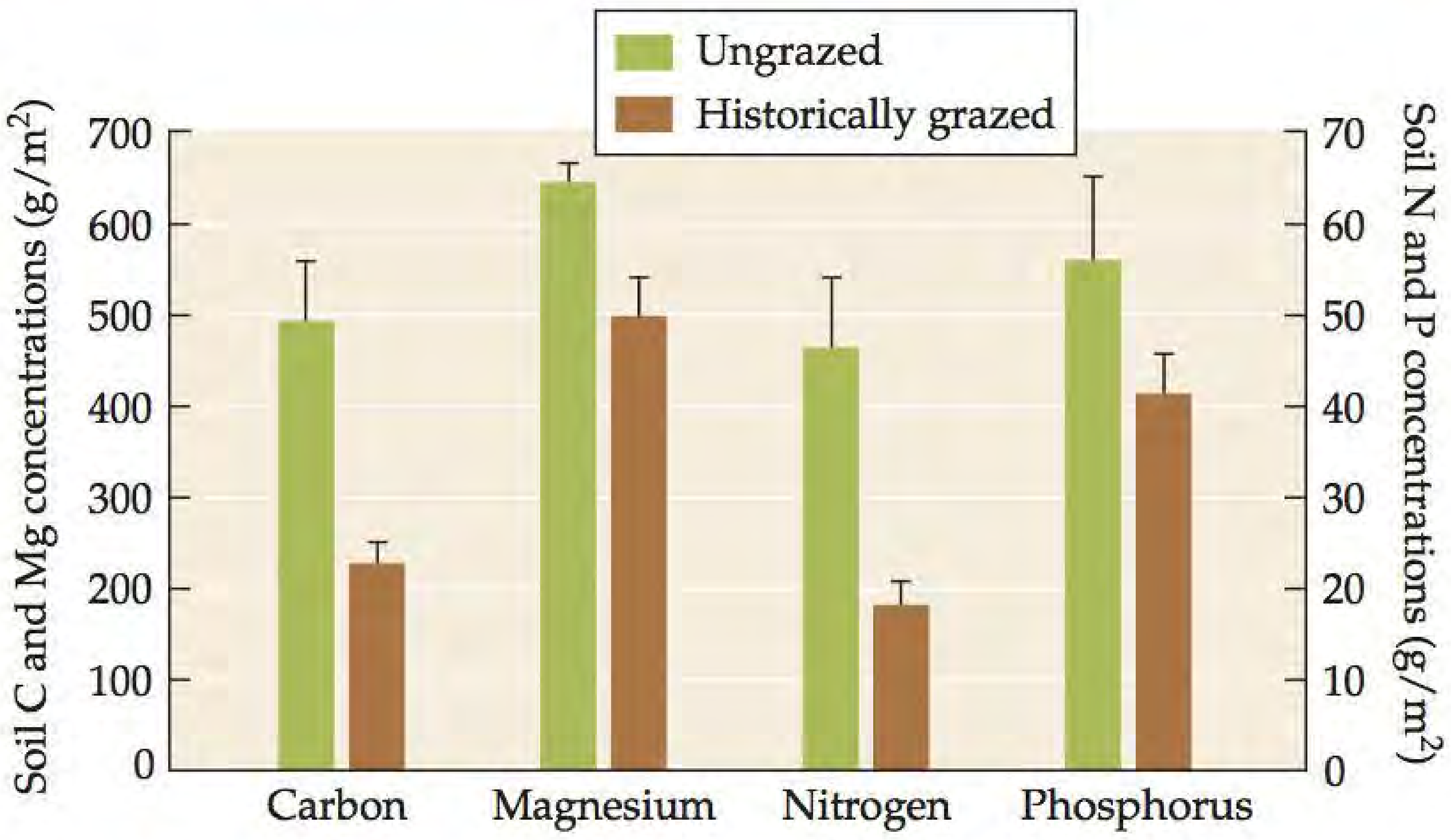


Figure 22.20 Loss of Biocrusts Results in Smaller Nutrient Supplies Historically grazed soils in Canyonlands National Park contained less carbon, magnesium, nitrogen, and phosphorus than soils that had never been grazed. Error bars show one SE of the mean. (Graph after Neff et al. 2005.)

Jason Neff and colleagues conducted a study to evaluate the effects of cattle grazing on soil erosion and nutrient availability on the Colorado Plateau (Neff et al. 2005). They selected three study sites in Canyonlands National Park: one that had never been grazed and two that had been grazed historically but were closed to grazing after 1974 (30 years of recovery). Cattle grazing in the park first occurred in the 1880s, and most of its soil surface has been affected. The ungrazed study site was surrounded by rock formations that prevented the movement of cattle into the area. The study sites all had the same parent material and similar plant communities and were located within 10 km of one another. Biocrusts were present at all three sites, although those at the historically grazed sites had clearly been damaged, as they appeared less well developed than those at the site that had never been grazed.

Samples of soil and bedrock were collected from each of the sites, and the textures and nutrient contents of the soils were compared. In addition, the retention of fine dust from the atmosphere was estimated by measuring the magnetic properties of the soil. Dust blown in from distant areas contains higher amounts of iron oxides than the native soil, so the more dust present, the stronger the magnetic signal. Retention of this dust is important because it is a source of mineral nutrients; in addition, loss of this dust indicates the potential for erosional loss of the native soil as well.

Neff and colleagues found that the historically grazed soils had less fine-textured soil, and substantially less magnesium and phosphorus, than the ungrazed soils (**Figure 22.20**). They attributed these differences to greater retention of dust and lower rates of erosion in the soils with better-developed biocrusts. The crusts may also enhance rates of weathering by altering pH, by increasing the rates of chemical reactions that release mineral nutrients, and by increasing water retention in the soil. Soils in the historically grazed sites also contained 60%–70% less carbon (from organic matter) and nitrogen than those in the ungrazed sites. These differences were also related to biocrusts. Although a crust had begun to recover at the historically grazed sites, comparison with the ungrazed site showed that the cumulative loss of carbon and nitrogen from the soils during the period of grazing was high. The cyanobacteria in biocrusts fix atmospheric N_2 (Belnap 2003), which represents an important input of a nutrient that may limit plant growth in the absence of water limitation during the spring growing season. In addition, crust-covered soils absorb more solar radiation and retain more water than soils without crusts, creating conditions more conducive to decomposition and mineralization.

Figure 22.21 Scourge of the Intermountain West Large areas of the intermountain West of North America are now dominated by cheatgrass (*Bromus tectorum*), an invasive species that increases fire frequencies, outcompetes native plants for resources, and spreads rapidly across the landscape.

CONNECTIONS IN NATURE

Nutrients, Disturbance, and Invasive Species

By increasing nutrient supplies and stabilizing soils, biocrusts enhance primary production. Plants growing in association with the crusts have higher growth rates, and contain more nutrients, than plants growing in soils without crusts. Plant cover also increases in the presence of biocrusts. Furthermore, biocrusts have been shown to lower the germination and survival rates of invasive plants (Mack and Thompson 1982) (see Chapter 23). Thus, the destruction of crusts by cattle grazing has had multiple ecological effects.

Are the negative effects of cattle grazing on soil stability and nutrient availability that Neff and colleagues observed in Canyonlands National Park common in other areas? The answer lies in part with the long-term history of grazing and climate in North America. Prior to Euro-American settlement, soils in much of the intermountain West did not experience the amount of grazing by native animals that occurred in other areas, such as the Great Plains, where large herds of bison roamed (see the Case Study in Chapter 3 and the discussion in Concept 3.2). A combination of aridity and long-term development of biocrusts may have given the soils of the Colorado Plateau an especially low tolerance for heavy grazing.

In the grasslands of the intermountain West, the combination of soil disturbance and loss of biocrust has created a situation conducive to the spread of non-native species—most notably cheatgrass (*Bromus tectorum*; **Figure 22.21**), a native of Eurasia. Cheatgrass has had profound effects on the ecology of much of western North America. Cheatgrass is a spring annual that sets seed, dies, and dries out by early summer. This life history increases the amount of dry, combustible vegetation that is present during the summer. As a result, cheatgrass has increased the frequency of fires, which now occur about every 3–5 years, compared with more natural fire frequencies of 60–100 years. Native grasses and shrubs cannot recover from such frequent fires, so cheatgrass increases its dominance under these conditions. Cheatgrass is an effective competitor for soil resources, and it also lowers rates of nitrogen cycling by producing litter with a C:N ratio higher than those of native species (Evans et al. 2001). This combination of increasing fire frequency, increasing competition, and changes in nutrient cycling has led to decreases in native species richness in many parts of the intermountain grasslands.

Summary

CONCEPT 22.1 Nutrients enter ecosystems through the chemical breakdown of minerals in rocks or through fixation of atmospheric gases.

- The nutrient requirements of organisms are specific to their physiology and thus differ between autotrophs and heterotrophs.
- Autotrophs absorb nutrients in simple, soluble forms from their environment, while heterotrophs obtain them in more complex forms by consuming prey or detritus.
- The physical and chemical breakdown of minerals (weathering) releases soluble nutrients.
- Soils are made up of mineral particles, detritus, dissolved organic matter, water containing dissolved minerals and gases, and organisms.
- Carbon and nitrogen enter ecosystems through fixation of atmospheric gases by autotrophs and by bacteria, respectively.

CONCEPT 22.2 Chemical and biological transformations in ecosystems alter the chemical form and supply of nutrients.

- Decomposition of organic matter releases the nutrients it contains in soluble forms that can be reused by plants and microorganisms.
- Modification of the chemical forms of nutrients, particularly nitrogen, by microorganisms influences the nutrients' availability to organisms or loss from the ecosystem.
- Plants recycle nutrients by reabsorbing them from senescing tissues and remobilizing them when growth commences again.

CONCEPT 22.3 Nutrients cycle repeatedly through the components of ecosystems.

- Nutrient cycling rates are controlled primarily by the rate of decomposition, which in turn is controlled by climate and the chemistry of plant litter.
- Losses of nutrients from terrestrial ecosystems can be estimated by measuring nutrient outputs in stream water.
- Changes in the relative amounts of nutrients supplied by weathering and decomposition determine the specific nutrients that limit primary production at different stages of ecosystem development.

CONCEPT 22.4 Freshwater and marine nutrient cycles occur in a moving medium and are linked to terrestrial ecosystems.

- The cycling of nutrients in streams and rivers can be thought of as a spiral of repeated biological uptake and incorporation into organic forms followed by release in inorganic forms.
- In lakes, nutrients are cycled between the water column and the benthic sediments.
- Imports of nutrients from rivers and terrestrial ecosystems support production in marine ecosystems.

Review Questions

1. Describe the processes involved in the transformation of solid minerals in rock into soluble nutrients in soil. What biological factors can influence the rate of this transformation?
2. Why is nitrogen often in short supply relative to other nutrients required by plants, despite being the most abundant element in the atmosphere? How does the supply of nitrogen change during terrestrial ecosystem development?
3. Which factor is more important in controlling the mean residence times and pools of nutrients in soil organic matter in terrestrial ecosystems: the rate of input (i.e., primary productivity) or the rate of decomposition? Would you expect to find larger nutrient pools in the soils of a tropical forest than in those of a boreal forest, given that primary productivity is higher in the tropics?
4. Why might you expect nutrient input from terrestrial and stream ecosystems to be more important in tropical lakes than in temperate-zone lakes?

Hone Your Problem-Solving Skills

How would disturbances and subsequent succession (see Chapter 17) influence nutrient cycling and nutrient losses in an ecosystem? As discussed above, nutrient losses are in part related to uptake by plants (see Figure 22.13). Uptake in turn is related to the rates of plant growth (net primary production, or NPP). As a result the losses of nutrients during succession are related to patterns of plant growth. The lowest nutrient losses should correspond to the highest growth rates.

1. Based on patterns of community replacement during succession discussed in Chapter 17, what pattern of nutrient loss from a catchment would you hypothesize following a disturbance in a forest? Consider how nutrient loss would change just after the disturbance, into the intermediate stages of succession, and finally into an old-growth community made up of long-lived mature trees.
2. Would the patterns of nutrient loss that you hypothesized in Question 1 be the same for all nutrients? Would nutrients that limit NPP show the same patterns as nutrients that are not limiting to growth?
3. Peter Vitousek (1977) used a catchment approach to study nutrient retention by spruce–fir forests in the White Mountains of New Hampshire at different stages of secondary succession following logging. He measured nutrient loss in streams draining catchments of different successional stages. In order to evaluate the hypothesis that late successional communities would be more "leaky" than intermediate stage communities, he examined the ratio of old-growth losses to losses during intermediate successional stages. He did this for several elements, some potentially more limiting to NPP than others. His results are shown in the table (μeq/L, microequivalents/liter). Do the data support Vitousek's hypothesis regarding changes in nutrient losses between intermediate and late successional forest communities? Do all of the elements show the same patterns of loss for intermediate and late successional communities? How do the differences in the patterns of element losses relate to their importance to plant growth?

	MEAN GROWING-SEASON STREAM WATER CONCENTRATIONS (μeq/L) ± SE		
	LATE SUCCESSIONAL	INTERMEDIATE SUCCESSIONAL	RATIO LATE:INTERMEDIATE
NO_3^-	53 ± 5	8 ± 1.3	6.52
K^+	13 ± 1	7 ± 0.5	1.81
Mg^{2+}	40 ± 4.9	24 ± 1.6	1.66
Ca^{2+}	56 ± 4.5	36 ± 2.5	1.56
Cl^-	15 ± 0.3	13 ± 0.3	1.16
Na^+	29 ± 2.6	28 ± 0.9	1.03

ON THE COMPANION WEBSITE

ecology4e.sinauer.com

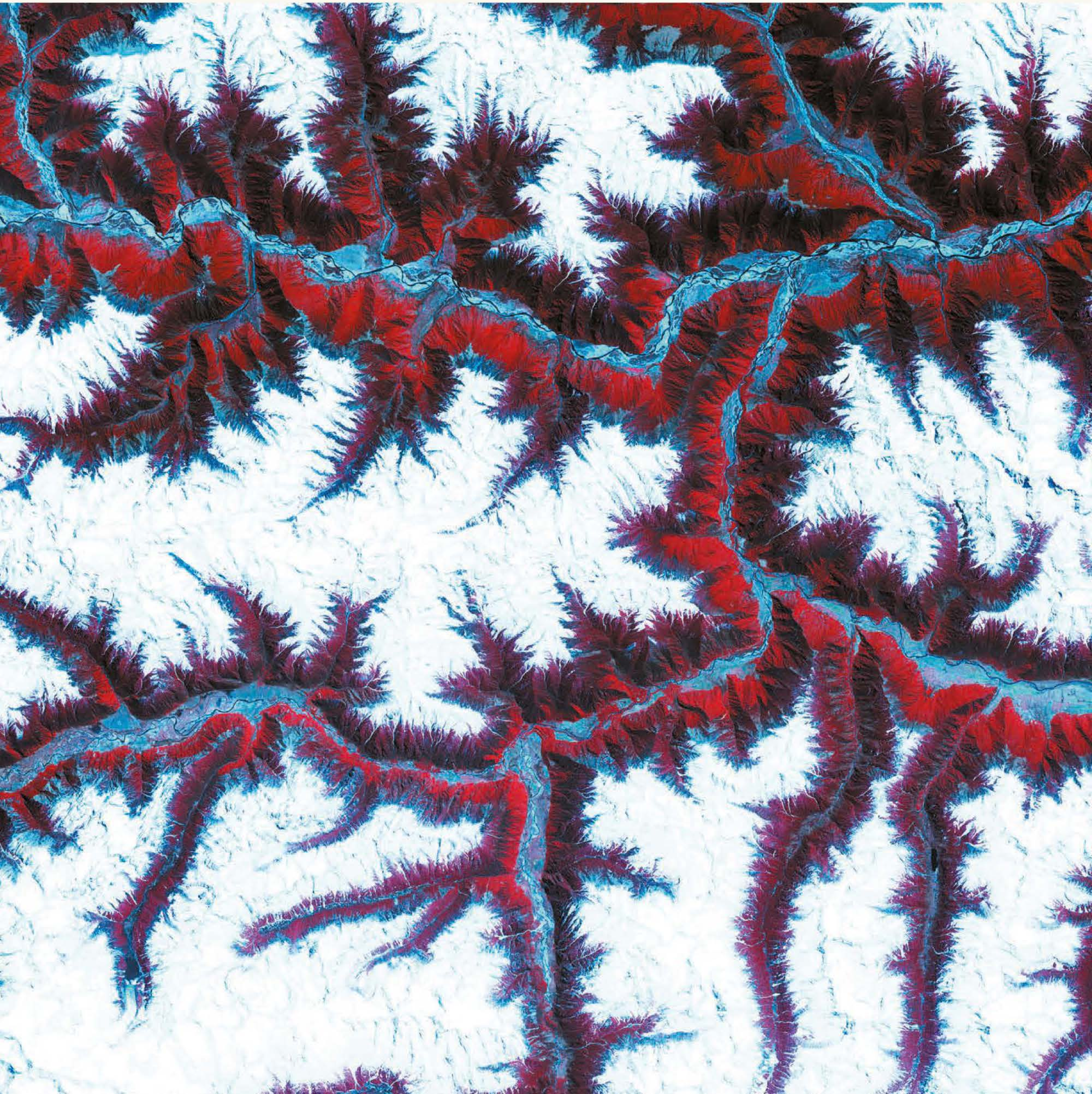
The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

22.1 Breaking It Down: Decomposition in Dry Environments

Unit 7

Applied and Large-Scale Ecology



23 Conservation Biology

KEY CONCEPTS

CONCEPT 23.1
Conservation biology is an integrative discipline that applies the principles of ecology to the protection of biodiversity.

CONCEPT 23.2 Biodiversity is declining globally.

CONCEPT 23.3 Primary threats to biodiversity include habitat loss, invasive species, overexploitation, pollution, disease, and climate change.

CONCEPT 23.4
Conservation biologists use many tools and work at multiple scales to manage declining populations.

CONCEPT 23.5 Prioritizing species helps maximize the biodiversity that can be protected with limited resources.

Can Birds and Bombs Coexist? A Case Study

How could the chaos and destruction of preparing for battle be beneficial for conservation efforts? Although it may seem strange, bombing for decades on the Fort Bragg military base in the North Carolina Sandhills has inadvertently protected thousands of acres of longleaf pine savanna, aiding efforts to save the endangered red-cockaded woodpecker (**Figure 23.1**).

For 90 years, the forests of Fort Bragg have been used for military training exercises, degraded by off-road vehicles and earth-moving equipment, and set on fire by explosives. These destructive activities take place in the midst of a vibrant but now uncommon ecosystem—one that, ironically, survives in large part as a result of the military presence. How can this be? First, pine savanna depends on fire for its persistence, so the fires that result from explosions benefit rather than harm the ecosystem. Second, the designation of large blocks of forest land for military use has kept them from being converted to farmland, forest plantations, and residential uses.

While some longleaf pine savanna has been preserved at Fort Bragg and other military bases, overall, this ecosystem has been reduced to only 3% of the more than 35 million hectares (>86 million acres) it once covered (**Figure 23.2**). Various factors have contributed to its decline, including rapid growth of the human population; the clearing of land for large plantations where other tree species, such as loblolly pine, are grown; and fire suppression. With the decline of the longleaf pine savanna ecosystem, several plant, insect, and vertebrate species that depend on it have also undergone substantial declines.

One of these species is the red-cockaded woodpecker (*Picoides borealis*), a small insectivorous bird that requires large tracts of open pine savanna. Once far more abundant, the species currently stands at about 6,100 breeding pairs and their associated helpers. Whereas other woodpeckers nest in dead snags, red-cockaded woodpeckers require mature, living pine trees, especially the longleaf pine (*Pinus palustris*), for their nesting cavities.

Periodic fires historically helped to maintain longleaf pine savanna. Without those fires, the longleaf pine community soon undergoes succession. As an understory of young oaks and other hardwoods grows up, red-cockaded woodpeckers abandon their nesting cavities, apparently because of a decrease in food resources. In the past, the birds would move to parts of the forest that

Figure 23.1 The Red-Cockaded Woodpecker: An Endangered Species A female red-cockaded woodpecker (*Picoides borealis*) approaches her nest cavity. This species was once abundant throughout the pine savannas (communities dominated by grasses intermixed with pine trees) of the United States but has been severely reduced in numbers by the loss of its required habitat.

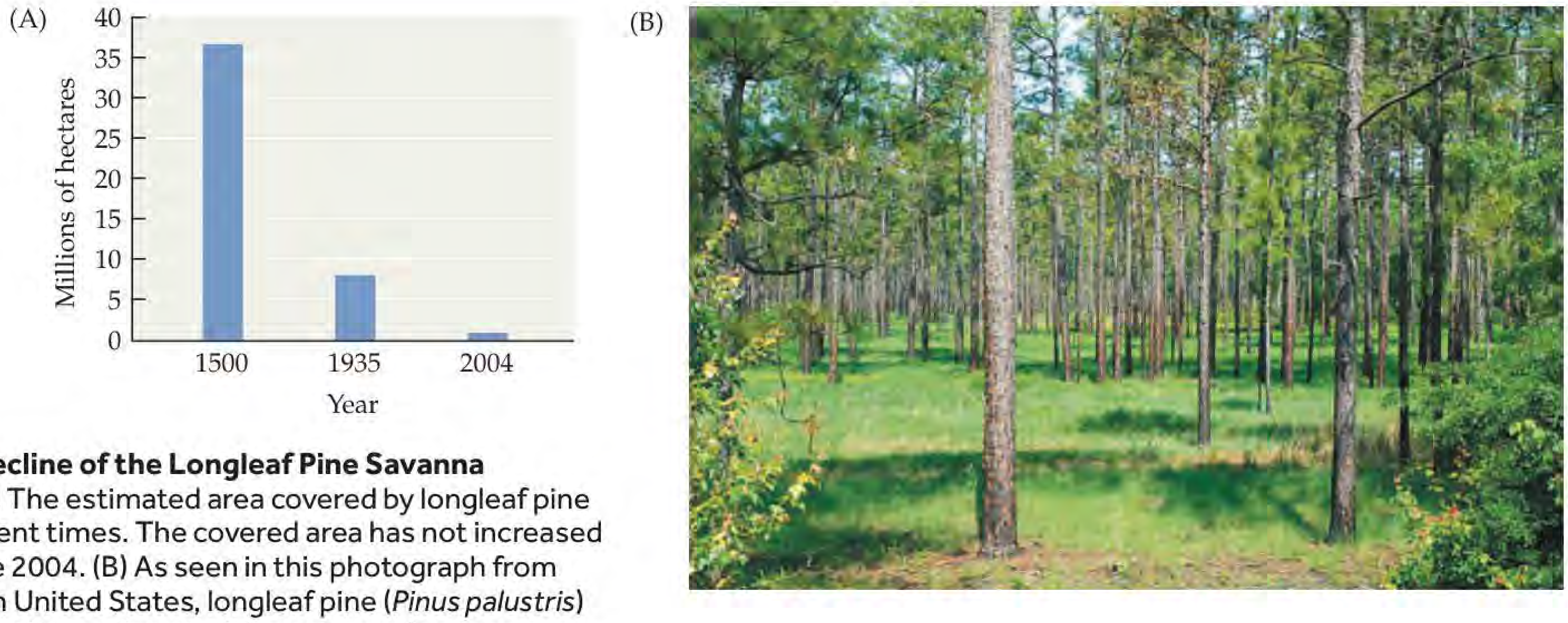


Figure 23.2 Decline of the Longleaf Pine Savanna Ecosystem (A) The estimated area covered by longleaf pine savanna at different times. The covered area has not increased appreciably since 2004. (B) As seen in this photograph from the southeastern United States, longleaf pine (*Pinus palustris*) savanna consists of open forest with a grass understory. (A after Van Lear et al. 2005.)

? Estimate the hectares of longleaf pine savanna that existed in 1500, 1935, and 2004. Was the annual loss of longleaf pine savanna greater from 1500 to 1935, or from 1935 to 2004?

had been more recently burned, but as the area of suitably mature longleaf pines declines, there are fewer and fewer places for the birds to go. This loss of habitat has reduced the woodpecker's populations, making them vulnerable to the problems associated with small, isolated populations that we discussed in Concept 11.3. There is evidence of genetic inbreeding among the birds, and in 1989, Hurricane Hugo killed 70% of the birds in one population.

The recent history of the red-cockaded woodpecker reflects that of thousands of other imperiled species around the world that have experienced gradual population declines with extensive loss of habitat, to critically low numbers. Species that require a specific habitat that is degraded by human activities will experience reductions in populations until, in some cases, they vanish. What can be done to protect species such as the red-cockaded woodpecker? Do we have a responsibility to protect existing biodiversity and to restore some of what has been lost? If so, how can we best allocate our limited resources to be most effective in our conservation efforts?

Introduction

Over the last few centuries, as the human population has grown and increased its use of resources, many species have lost their habitats through direct destruction or through changes in their biological or physical properties. These changes have precipitated a major increase in the rate of species extinctions and loss of diversity. The 2015 analysis of the Red List of Threatened Species, compiled by the International Union for Conservation of Nature and Natural Resources (IUCN), lists 23,250 species as threatened with extinction—about 1% of all described species worldwide (**Table 23.1**). This number is certainly an underestimate, as only 5% of the species that have been described have been evaluated, and many species have yet to be taxonomically described.

Ecologists play an important role in measuring the losses of species and their underlying causes. As we'll see in this chapter and the next, ecologists are also one part of a diverse team working to find ways to slow the decline of species and their habitats. We'll begin by introducing you to the field of biology dedicated to reversing those declines: conservation biology.

CONCEPT 23.1
Conservation biology is an integrative discipline that applies the principles of ecology to the protection of biodiversity.

Conservation Biology

The preservation of longleaf pine savanna at the Fort Bragg military base (described in the Case Study) and on other federal and state lands, coupled with legal protection and extraordinary human effort, has led to stabilization and slow recovery of the numbers of red-cockaded woodpeckers (U.S. Fish and Wildlife Service 2003). As we'll see in the Case Study Revisited, this slow recovery has required expertise from biological disciplines such as population biology, genetics, and pathology as well as contributions from disciplines outside biology, including law, economics, political science, communications, and sociology. It has also required working with farmers, landowners, the U.S. military, and the business community. Arriving at a successful management approach required not only data collection and analysis, but also creativity and the ability to work with a wide variety of people with interests and concerns (stakeholders) in the

TABLE 23.1 Global Summary of the Number of Documented Imperiled Species

GROUP	ESTIMATED NUMBER OF DESCRIBED SPECIES	NUMBER OF SPECIES EVALUATED BY 2015	NUMBER OF THREATENED SPECIES BY 2015	ESTIMATED PERCENTAGE OF SPECIES THREATENED
VERTEBRATES				
Mammals	5,515	5,502	1,197	22
Birds	10,424	10,424	1,375	13.37
Reptiles	10,272	4,669	944	*
Amphibians	7,448	6,460	1,994	31
Fishes	33,200	14,462	2,271	*
Subtotal	66,859	41,517	7,781	
INVERTEBRATES				
Insects	1,000,000	5,573	1,046	*
Mollusks	85,000	7,216	1,950	*
Crustaceans	47,000	3,168	728	*
Corals	2,175	862	237	*
Arachnids	102,248	210	164	*
Others	68,827	487	76	*
Subtotal	1,305,250	17,516	4,201	
PLANTS				
Mosses	16,236	102	76	*
Ferns and allies	12,000	365	197	*
Gymnosperms	1,052	1,011	400	40
Angiosperms	268,000	19,206	10,551	*
Green algae	6,050	13	0	*
Red algae	7,104	58	9	*
Subtotal	310,442	20,755	11,233	
FUNGI & PROTISTS				
Lichens	17,000	9	7	*
Mushrooms	31,496	25	22	*
Brown algae	3,784	15	6	*
Subtotal	52,280	49	35	
TOTAL	1,734,831	79,837	23,250	

Source: Data from the 2015 IUCN Red List of Threatened Species, www.iucnredlist.org

Note: "Imperiled" includes the IUCN Red List categories "critically endangered," "endangered," and "vulnerable." Some groups have been more thoroughly evaluated (mammals, birds) for conservation status than other groups, for which only a small percentage of described species have been evaluated. For those groups, there may be a bias toward completing assessments of imperiled species and making assessments of more common species a lower priority, and thus the estimate of the percent of species is not included. That only 1% of described species are shown as imperiled is an artifact of incomplete evaluation, as the percentage is believed to be much higher. An asterisk (*) indicates insufficient coverage for accurate estimate.

longleaf pine savanna ecosystem. Such an integrative approach is characteristic of conservation biology.

Conservation biology is the scientific study of the amount of biodiversity, how human activities are impacting it, and how best to maintain it and prevent its loss. **Biodiversity** includes genetic diversity within a species, the diversity of species, and the diversity of communities across landscapes (see Figure 16.7). Conservation biology applies many of the ecological principles and tools that you have studied in this book to the halting or reversal of biodiversity declines. Later in this chapter, we will look at the reasons why biodiversity is declining and at the tools conservation biologists use to address conservation problems. But first let's consider why it is so important to prevent and reverse declines in biodiversity.

Protecting biodiversity is important for both practical and moral reasons

People rely on nature's diversity. In addition to the hundreds of domesticated species that sustain us, we make abundant use of wild species for food, fuel, and fiber. We harvest wild species for medicines, building materials, spices, and decorative items. Many people rely on these natural resources for their livelihoods. As discussed in Concept 19.4, the natural functioning of biological communities provides valuable services to humans. All of us are dependent on a wide range of these **ecosystem services**, such as water purification, generation and maintenance of soils, pollination of crops, climate regulation, and flood control (Ehrlich and Wilson 1991). These life-sustaining functions are themselves dependent on the integrity of natural communities and ecosystems. Furthermore, for our emotional health, many people require time spent surrounded by nature's beauty and complexity. Spiritually, we go to natural ecosystems for solace, wonder, and insight.

But beyond our physical dependence on biodiversity, do we have some moral obligation to the other species that inhabit Earth? For many people, biodiversity has inherent value and warrants protection simply for that reason. For others, religious or spiritual beliefs lead to a sense of stewardship, or to the view that other species have a right to exist just as we do. Still others, however, do not share these views and see natural resources primarily as commodities that benefit human society.

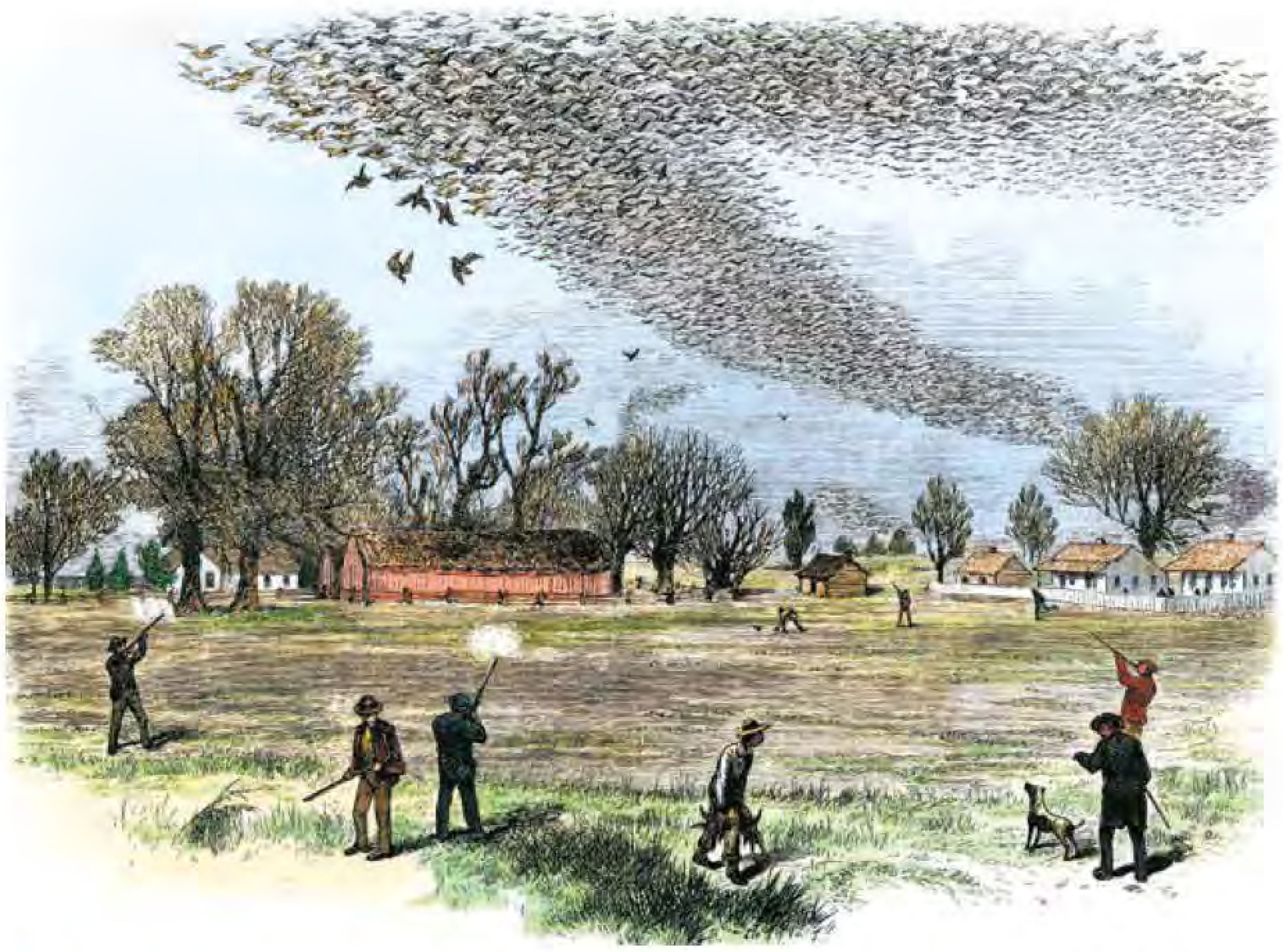


Figure 23.3 The Passenger Pigeon: From Great Abundance to Extinction The passenger pigeon (*Ectopistes migratorius*), once one of the most abundant birds in North America, was hunted extensively in the nineteenth century. The last passenger pigeon died in the Cincinnati Zoo in 1914. The ecological effects of its extinction on the eastern deciduous forest, coincident with the loss of the American chestnut (see Concept 13.4), are difficult to estimate but are presumed to be considerable.

The field of conservation biology arose in response to global biodiversity losses

Scientists have long been aware that human activity affects the abundances and distributions of organisms. In the nineteenth century, Alfred Russel Wallace, the "father of biogeography" whose work we described in Concept 18.2, foresaw the current biodiversity crisis, warning in 1869 that humanity was at risk of obscuring the record of past evolution by bringing about extinctions. In the United States, there was a rising public outcry over the rapid decline of bison in the West, the stunning harvest to extinction of the passenger pigeon (**Figure 23.3**), the extensive use of bird feathers in ladies' hats, and other assaults on animal populations.

Ecologists in the United States in the first half of the twentieth century were divided over how strongly they could advocate for the preservation of nature while still maintaining scientific objectivity (Kinchy 2006). Before 1945, the Ecological Society of America frequently lobbied Congress for the establishment of national parks or for better management of existing parks. In 1948, however, the society decided to separate "pure" science from advocacy, and the Ecologists' Union branched off as an independent entity focused on the preservation of nature. In 1950, this offshoot organization changed its name to The Nature Conservancy, rising in prominence as a nonprofit organization that integrates science with advocacy and on-the-ground conservation work (Burgess 1977).

Conservation biology emerged as a scientific discipline in the early 1980s as ecologists and other scientists saw the need to apply their knowledge to the preservation of species and ecosystems. The Society for Conservation Biology, founded in 1985, arose in response to the biodiversity crisis. The emergence of professional journals dedicated to conservation biology during the 1980s and 1990s, and an ongoing increase in the number of academic programs for the training of graduate students and professionals, demonstrate the growing acceptance of and need for this specialized discipline.

Conservation biology is a value-based discipline

The methods of science call for objectivity—an assurance that the collection and interpretation of data are unbiased by preconceived ideas. Yet science is not free of human values, and it inevitably takes place within a larger social context. Conservation biologists have had to come to terms with the implicit and explicit values that are part of their work. From the founding of the Society for Conservation Biology, the designation of the discipline as "mission-driven" (Soulé and Wilcox 1980; Meine et al. 2006) and "crisis-oriented" (Soulé 1985) explicitly revealed the values behind the science.

Many ecologists have chosen to speak up or refocus their research programs as they have come to understand the biological consequences of the changes taking place on the planet. For example, in 1986, Dan Janzen, a tropical biologist who had largely committed himself until then to studying tropical plant–insect interactions, wrote that "if biologists want a tropics in which to biologize, they are going to have to buy it with care, energy, effort, strategy, tactics, time, and cash." Such motivation does not necessarily detract from the objectivity of the scientific studies done by conservation biologists, as they understand that conserving biodiversity will require decisions based on sound and credible analyses. Furthermore, those analyses are subjected to rigorous scientific review by other scientists, who may challenge or even refute their conclusions.

In the next section, we'll meet one ecologist who put the values of conservation biology into practice. Then we'll examine the extent and causes of the current declines in biodiversity.

CONCEPT 23.2

Biodiversity is declining globally.

Declining Biodiversity

The tropical botanist Alwyn Gentry devoted his life to identifying, classifying, and mapping the immense diversity of plants found in Central and South America. He also became an eyewitness to plant species extinctions as the region underwent rapid deforestation. It was not uncommon for him to identify a new *endemic* plant species (i.e., a species that occurs in a particular geographic region and nowhere else) during an expedition to Ecuador or Peru, only to return to the same spot a few years later to find the forest cleared and the species gone (Dodson and Gentry 1991) (**Figure 23.4**). Gentry worked with a growing sense of urgency to identify rare species in order to protect them from this fate. His death in a plane crash in the Ecuadorian forest in 1993, while doing an aerial survey of land proposed for conservation, cut this work short and was an enormous loss to conservation biology.

Gentry was just one of many taxonomists who have been finding and describing species while witnessing their rapid disappearance due to habitat destruction. Extinctions of barely known tropical plant species (and most likely of other species that we have yet to discover) continue throughout the tropics despite our decades-long recognition of the problem. Through greater efforts to explore Earth's ecosystems, ecologists are gaining knowledge of the world's biota and tabulating new species at a faster rate, but threats to those species are keeping pace with such gains in our knowledge about them.

The rate at which Earth is losing species is accelerating

How rapidly are species being lost? That is a difficult question to answer, in part because we do not know how many species exist that remain unknown to us. Most studies have estimated that there are about 5–10 million eukaryotic species on Earth, but there may be as few as 3 million or as many as 50 million (Scheffers et al. 2012) or even more, particularly with greater consideration of microbial diversity (Locey and Lennon 2016).

Despite this uncertainty, extinction rates can be estimated using several indirect measures (May et al. 1995; May 2011). For example, estimates of extinction rates from

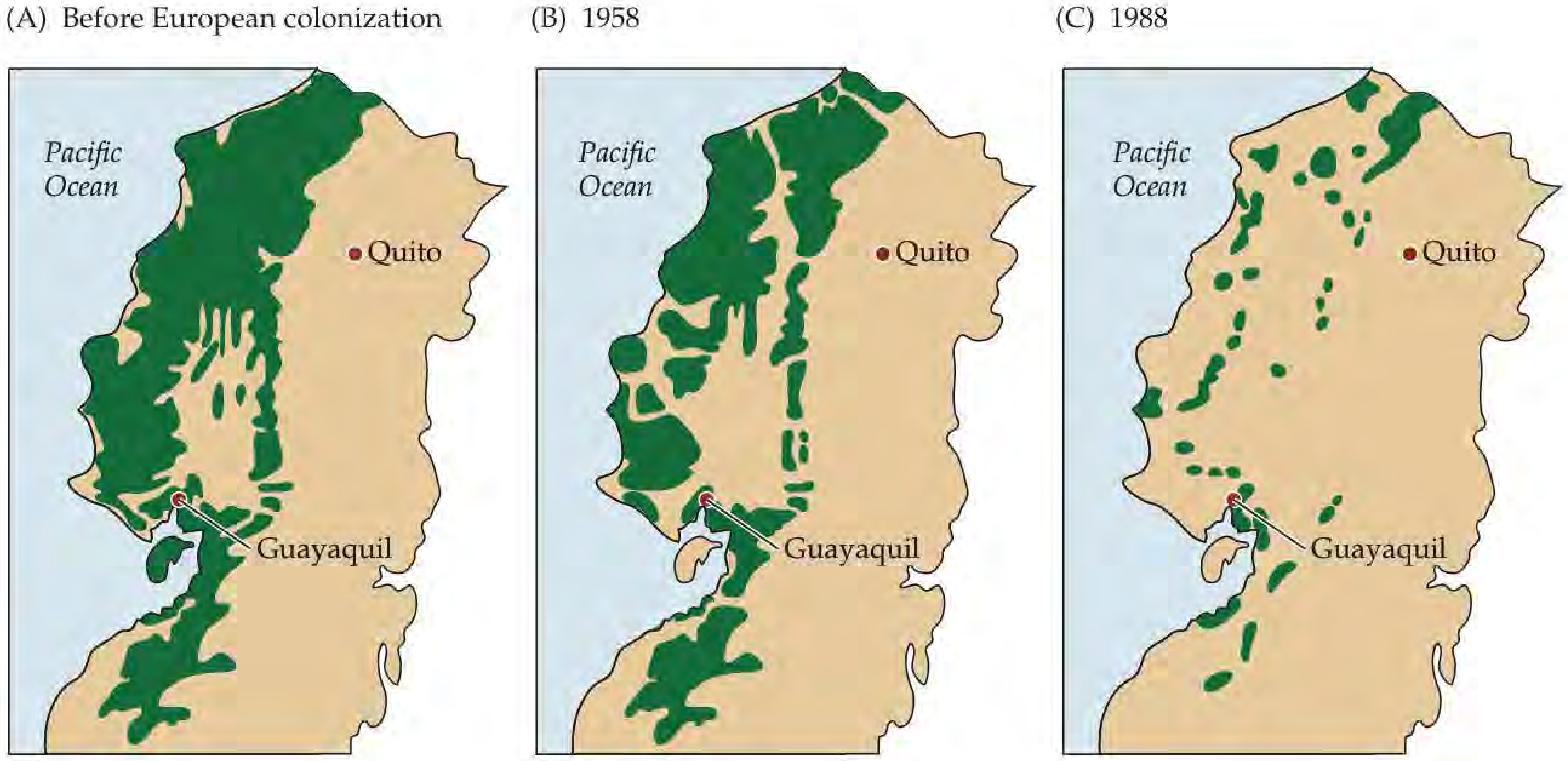


Figure 23.4 Loss of Forest Cover in Western Ecuador Between 1958 and 1988, a growing human population and government policies intended to stimulate rapid economic development led to rapid deforestation in western Ecuador. Green indicates forest cover. The extensive loss of forest habitat in this region is estimated to have resulted in the loss of more than 1,000 endemic species. (After Brooks et al. 2002.)

the fossil record can be used to establish a "background" extinction rate with which current rates can be compared. For the best-known taxonomic groups, the mammals and birds, paleontologists have estimated that the background extinction rate is on the order of one extinction every 200 years, which is equivalent to an average species life span of 1 million to 10 million years. By contrast, there was about one extinction per year among the mammals and birds over the twentieth century, which is equivalent to an average species life span of only 10,000 years. Thus, overall, the rate of extinction in the twentieth century was 100 to 1,000 times higher than the background rate estimated from the fossil record (Jablonski 2005).

A second method for estimating extinction rates uses the species–area relationship discussed in Concept 18.3. In particular, the relationship between number of endemic species and area is used to estimate the number of species that would be driven to extinction by a given amount of habitat loss (Kinzig and Harte 2000). In a third approach, biologists have used changes over time in the assessed conservation statuses of species (e.g., a shift from endangered to critically endangered) to forecast rates of extinction (Smith et al. 1993). Finally, a fourth approach is based on the rates of population decline or range contraction of common species (Balmford et al. 2003). All of these methods are fraught with uncertainty, yet they are the best ways we have devised to document losses of biodiversity.

It can also be difficult to ascertain when a species is definitely extinct. Many species are known from a single specimen or location, and the logistics of relocating them can be daunting. Even an exhaustive hunt for a very rare species can fail to detect some remnant populations. Declaring a species extinct, however, has been known to stimulate biologists' search efforts. Since the publication of a flora of Hawaiian plants in 1990, for example, 35 species listed there as extinct have been rediscovered, though only a few individuals have been found. The joy of their rediscovery is compromised by the realization that these extremely small populations cannot serve the same ecological functions as more substantial populations, and that 8% of Hawaii's native flora of 1,342 species is now considered extinct (Wagner et al. 1999).

Although humanity's growing ecological footprint (see Connections in Nature in Chapter 10) has accelerated the rates of biodiversity loss over the last century, people have had substantial effects on Earth's biota for millennia (see the Case Study in Chapter 3). David Steadman (1995) described how bones found on Pacific islands revealed the prehistoric extinction of up to 8,000 species of birds (of which perhaps 2,000 species were endemic flightless rails) after these islands were colonized by Polynesians. Most of these species were island endemics, and in some cases the extinctions encompassed entire ecological guilds (**Figure 23.5**). Ecologists can only speculate about the roles the lost frugivores and nectarivores played in maintaining endemic tree populations. Steadman's findings remind us that extinctions do not only eliminate individual species, but can also cause large changes in ecological communities.

Extinction is the end point of incremental biological decline

In 1954, Andrewartha and Birch wrote that "there is no fundamental distinction to be made between the extinction of a local population and the extinction of a species other than this: that the species becomes extinct with the extinction of the last local population." Sometimes the populations of a species gradually erode away, and

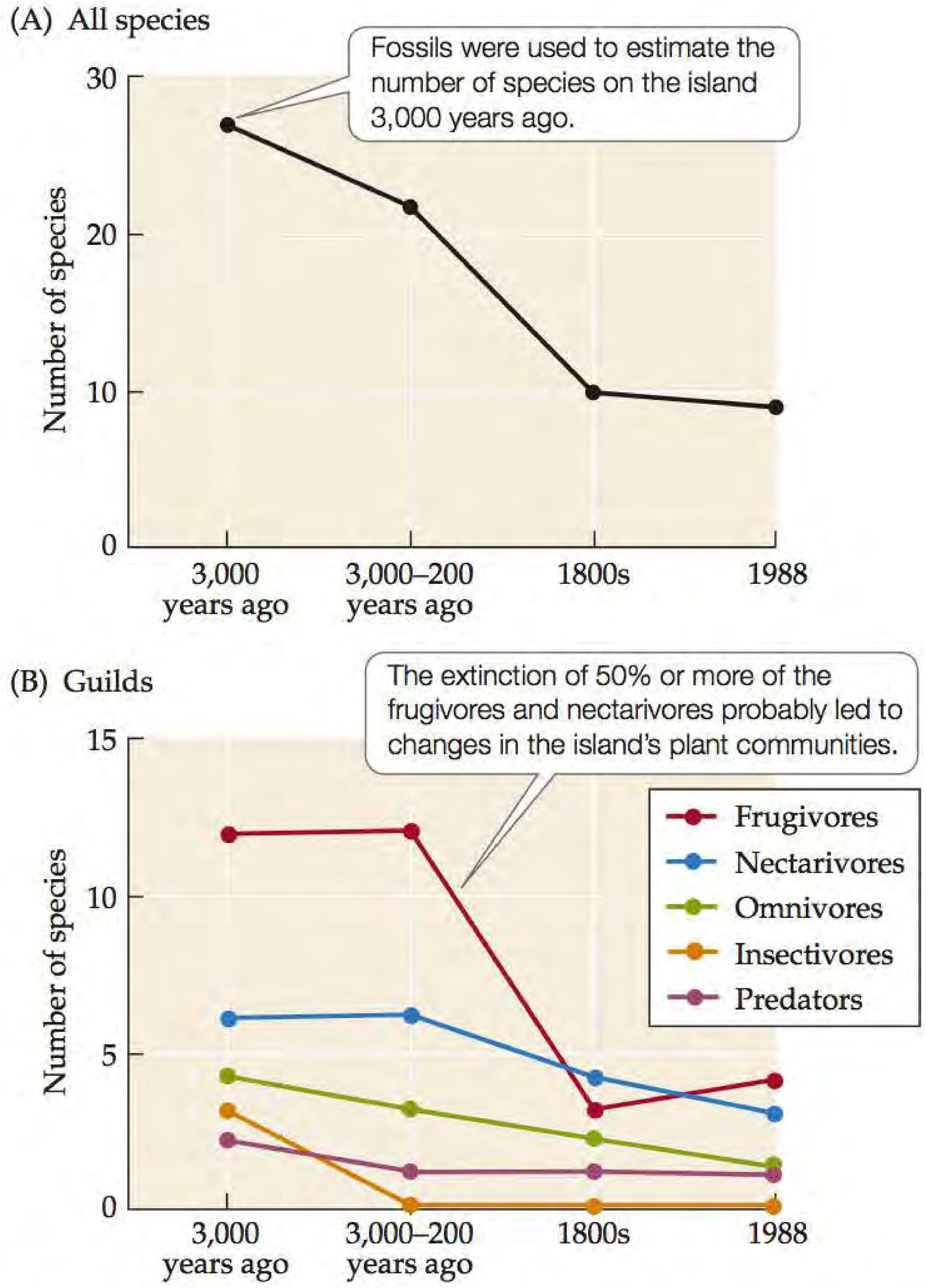


Figure 23.5 Humans Have Been Causing Extinctions for Millennia Trends over time in (A) the total number of bird species and (B) the number of species classified by feeding guild found in the Pacific island 'Eua in the nation of Tonga. Prehistoric extinctions (3,000–200 years ago) occurred on many Pacific islands as a result of hunting and the introduction of rats, dogs, and pigs. (After Steadman 1995.)

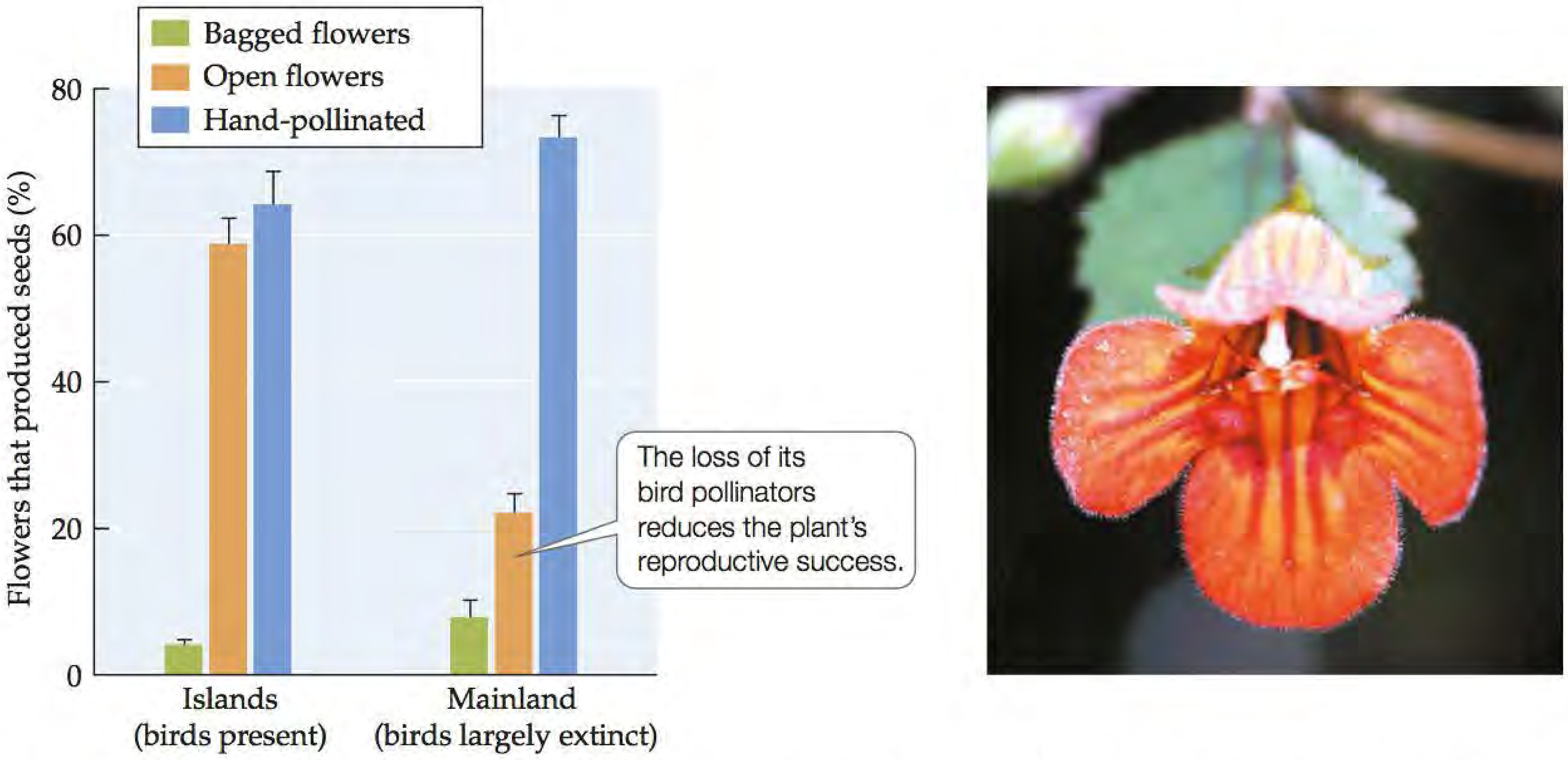
? Speculate on reasons why losses of birds that feed on fruit (frugivores) or nectar (nectarivores) may have affected the island's plant communities. (Hint: See the discussion of mutualism in Concepts 15.1 and 15.2.)

sometimes they vanish in a spectacular collapse, as in the case of the passenger pigeon.

Conservation biologists have approached the process of biological decline and extinction in numerous ways. For example, as we saw in Concept 11.3, small populations are particularly vulnerable to genetic, demographic, and environmental stochasticity, each of which can reduce the population growth rate and increase the risk of extinction. As a result, a cyclic chain of events may ensue in which an already small population drops even further in size, thereby becoming even more vulnerable to genetic, demographic, and environmental stochasticity. Known as an **extinction vortex**, this pattern can doom a population to eventual extinction once its size drops below a certain point. With this in mind, Caughley (1994) argued that it is important to determine the causes of population declines in particular species, with the aim of identifying actions that could counteract these declines before the extinction vortex takes hold.

Ecologists can also take a spatial approach to the declines of species by tracking changes in their ranges. Ceballos and Ehrlich (2002) examined patterns of range contraction in 173 declining mammal species worldwide. They found that, collectively, these species had lost 68% of their range area over the past 100–200 years, with the greatest losses in Asia (83%). In a similar study, Channell and Lomolino (2000) examined patterns of range contraction in 309 declining species. They found that a decline often moves through the historic range of a species like a wave, from one end to the other; this could occur, for example, if an invasive species entered the range at one edge and then spread through the range, eliminating the declining species population by population. Such a pattern contrasts with a retreat from all edges of the range into its center, which would probably occur if effects of small population size were prevailing.

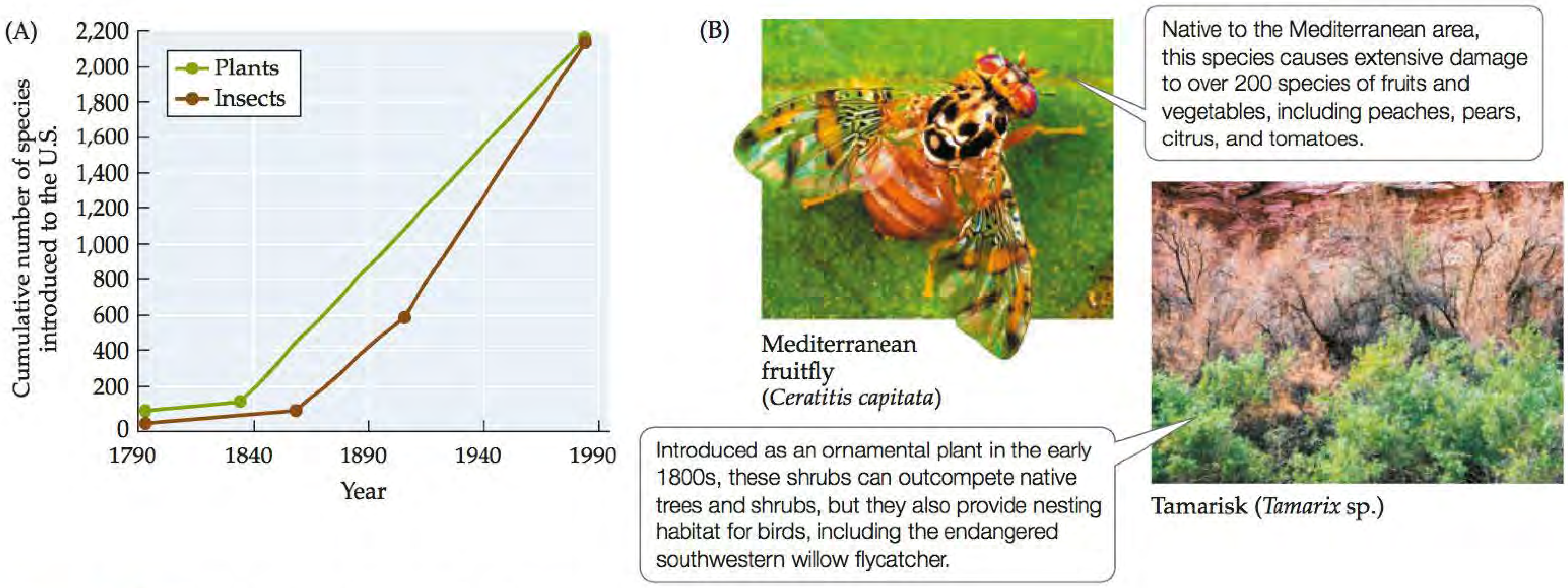
Whatever its cause, the decline of a species does not take place in a vacuum. When populations are lost from an ecological community, there are consequences not only for the declining species, but also for its predators, prey, and mutualistic partners. The loss of bird pollinators, for example, can reduce the reproductive success of plants that depend on those pollinators (**Figure 23.6**), causing plant densities to drop as well (Anderson et al. 2011; Galetti et al. 2013). The resulting changes at the community level may bring about secondary extinctions and ultimately affect ecosystem processes. Examples from earlier chapters include the local extinctions and other changes caused by the loss or removal of such species as the invertebrate *Corophium volutator* (see Concept 13.4), the marsh plant *Juncus gerardii* (see Concept 16.3), and the sea star *Pisaster ochraceus* (see Concept 21.4). Modeling results also suggest that while food webs can be resilient to species removal, the loss of certain species can trigger a cascade of secondary extinctions. As might be expected, the stronger the interactions of a species in the food web, the greater the effect of its removal (Solé and Montoya 2001). Overall, both empirical and modeling results demonstrate that incremental species loss can have broad ecological consequences.



The loss of its bird pollinators reduces the plant's reproductive success.

Figure 23.6 Loss of Bird Pollinators Reduces Reproductive Success in a New Zealand Shrub Birds that pollinate the shrub *Rhabdothamnus solandri* are nearly extinct on the New Zealand mainland, but densities of these birds remain high on nearby islands. Researchers recorded the percentage of *R. solandri* flowers that reproduced successfully (produced seeds) on island and mainland sites for each of three treatments: bagged flowers (which allowed only self-pollination), open flowers (which allowed bird pollination), and open flowers that were hand-pollinated. Error bars show one SE of the mean. (After Anderson et al. 2011.)

? Identify the control and experimental treatments in this study, and explain what can be learned from each of the three treatments.



Native to the Mediterranean area, this species causes extensive damage to over 200 species of fruits and vegetables, including peaches, pears, citrus, and tomatoes.

Mediterranean fruitfly (*Ceratitis capitata*)

Introduced as an ornamental plant in the early 1800s, these shrubs can outcompete native trees and shrubs, but they also provide nesting habitat for birds, including the endangered southwestern willow flycatcher.

Tamarisk (*Tamarix* sp.)

Figure 23.7 Species Introductions Are Increasing Globally The number of non-native species that have become established in the United States has increased about fivefold over the past century for various organisms, including molluscs, fishes, terrestrial vertebrates, and (A) plants and insects. Similar patterns are seen in many other countries. Photographs in (B) show two examples of introduced species. (Data from U.S. Congress, OTA 1993.)

Earth's biota is becoming increasingly homogenized

Organisms are naturally mobile, which influences their dispersal across their geographic ranges. Over the last century, however, people have moved over Earth's surface at an unprecedented rate, carrying organisms with them and greatly enhancing rates of introductions of new species to all parts of the globe (**Figure 23.7**). These range expansions can have both positive and negative effects.

Non-natives have negative effects on biodiversity. For example, introductions of non-natives can contribute to the range contractions of native species whose numbers may already be in decline because of habitat loss and other factors. Typically, the greatest "losers" among the native species tend to be specialists—those with morphological, physiological, or behavioral adaptations to a particular habitat—while the "winners" tend to be generalists with less stringent habitat requirements. The spread of introduced species and native generalists, coupled with declining abundances and distributions of native specialists, is part of a growing **taxonomic homogenization** of Earth's biota (Olden et al. 2004). In rare circumstances, non-native species can provide conservation benefits, such as habitat or food for rare species (Schlaepfer et al. 2011). Non-native tamarisk shrubs (*Tamarix* spp.), for example, provide nesting habitat for the endangered southwestern willow flycatcher (*Empidonax traillii extimus*). Species introductions have also increased regional biodiversity in many parts of the world (**Figure 23.8**), although the value of increasing diversity through the increase in non-natives is questionable, as it typically comes at a cost to native diversity.

Island biotas are particularly vulnerable to both invasion and extinction. The decline of island endemics is often accelerated by the introduction of more cosmopolitan species. In a survey of American Samoa, Robert Cowie (2001) found just 19 of the 42 species of land snails historically known from that island group, plus 5 species

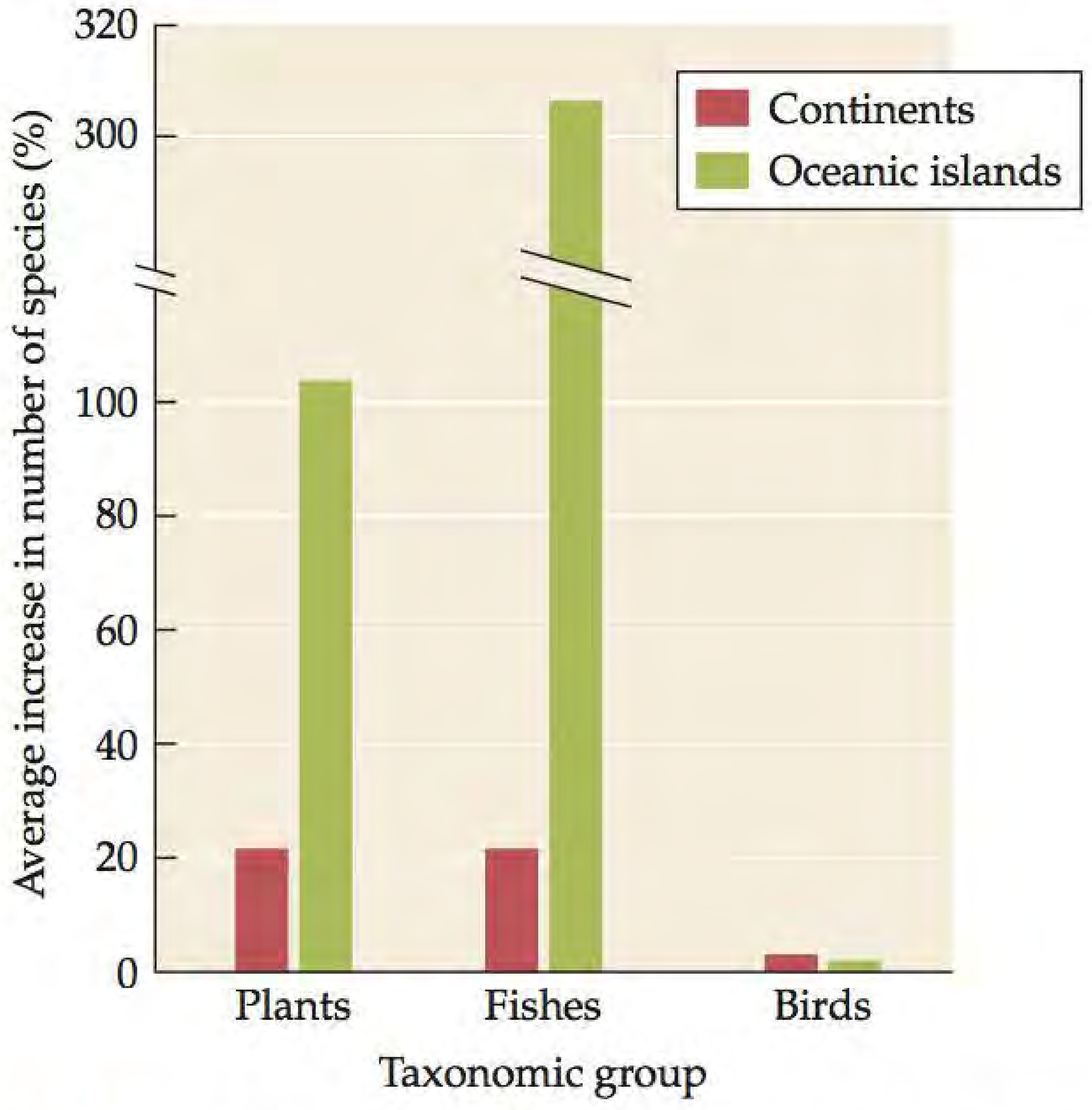


Figure 23.8 Introductions of Non-Native Species Can Increase Regional Biodiversity The introduction of non-native species to new regions has led to sizable increases in the numbers of species found on oceanic islands and within continental regions for plants and fishes, but not for birds. (After Sax and Gaines 2003.)

? The introduction of non-native plants to new regions is associated with a decrease in the global biodiversity of plants. Explain how that can be true given the results shown in this figure.

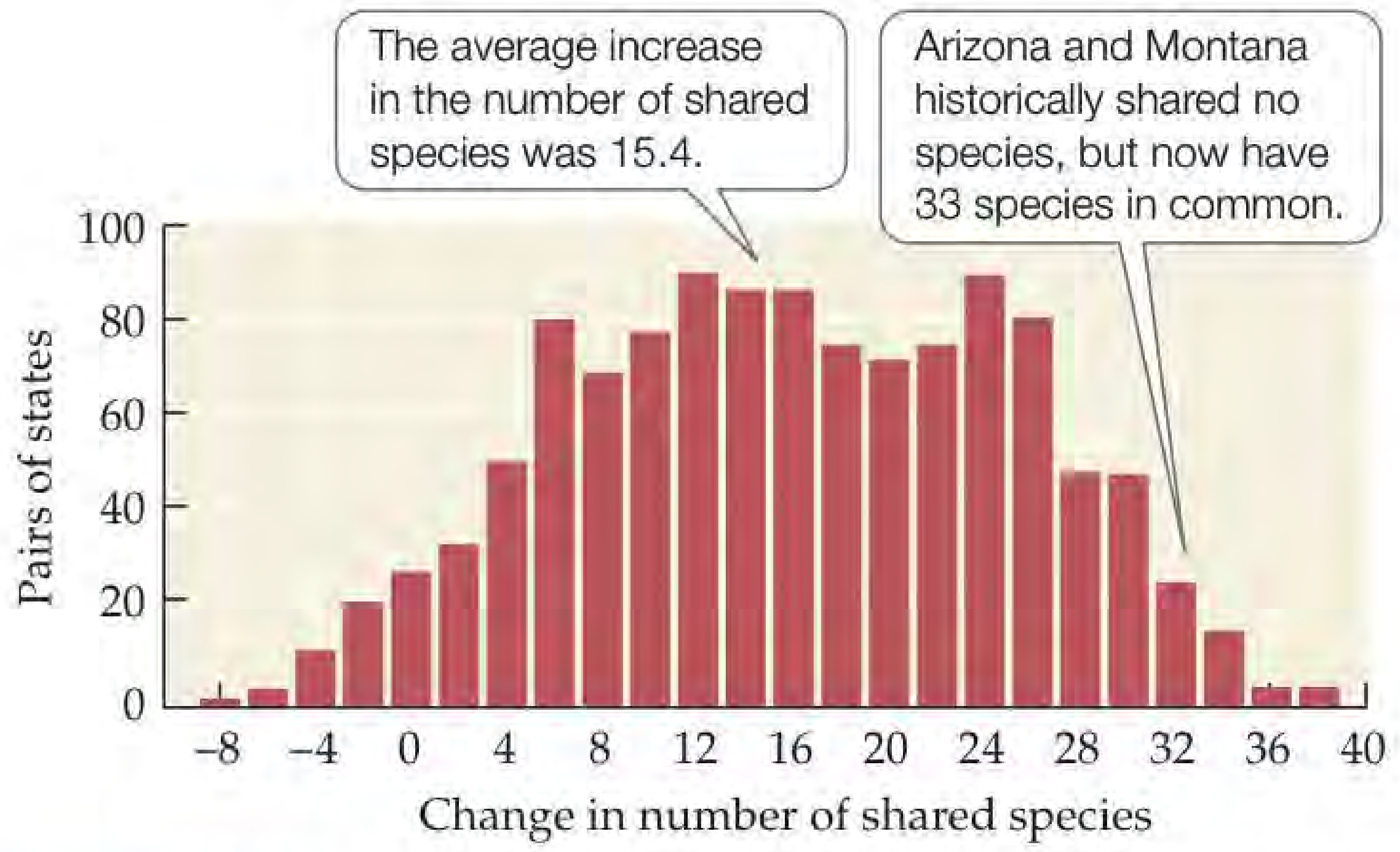


Figure 23.9 U.S. Fish Faunas Are Undergoing Taxonomic Homogenization The numbers of fish species shared by pairs of the 48 conterminous U.S. states have increased since European settlement. (After Rahel 2000.)

not previously found there but which he presumed were native. He also found that there were 12 non-native species present on the islands. These non-natives occurred in high abundances, representing about 40% of the individuals collected (there was also one abundant native species). Cowie concluded that most native species were declining in abundance, while many non-natives were increasing. Furthermore, the predators contributing to the declines of native land snail species were also non-natives, such as the predatory snail *Euglandina rosea* and the house mouse (*Mus musculus*). Cowie has found this trend toward homogenization of land snail faunas to be widespread among Pacific islands.

Homogenization has also been observed among the freshwater fishes of the United States, largely as the result of widespread introductions of game fishes. Rahel (2000) quantified the homogenization of U.S. fish faunas by examining the change in the number of species shared between all possible pairs of the 48 conterminous states. He found that, on average, pairs of states shared 15 more species than they did at the time of European colonization (**Figure 23.9**).

On a global scale, it is clear that biodiversity is being lost as a result of humanity's impact on the planet. Let's look in more detail at the reasons for these losses, and then consider what steps can be taken to counteract them.

CONCEPT 23.3
Primary threats to biodiversity include habitat loss, invasive species, overexploitation, pollution, disease, and climate change.

Threats to Biodiversity

Understanding the causes of biodiversity losses is a first step toward reversing them. Multiple factors are likely to contribute to the decline and eventual extinction of any particular species. For example, while the last Pyrenean ibex (*Capra pyrenaica pyrenaica*) was killed in 2000 by a falling tree, declines in its populations following the fourteenth century resulted from overexploitation and competition with domesticated livestock, leading to its eventual extinction (Perez et al. 2002).

Multiple causes of biodiversity loss are also apparent in higher taxonomic groups. For example, over 1,197 mammal species (22% of those for which adequate data are available) are currently threatened with extinction (see Table 23.1). Globally, the primary threats facing mammals are loss of habitat, overexploitation, accidental mortality, and pollution—but the relative importance of these factors differs between terrestrial and marine mammals (**Figure 23.10**). Some mammals are threatened by additional factors, such as disease. As we'll see, this scenario, in which multiple types of threats contribute to the decline and extinction of a taxon, is common.

Habitat loss and degradation are the most important threats to biodiversity

The next time you fly in an airplane over Earth's surface, look down and ask yourself, What species lived here before these farms and cities were here? Where do the species native to this place live now, and how do they move about?" From 30,000 feet above the landscape, you will find yourself face to face with the source of the biodiversity crisis: the scale of the human impact on the planet. Earth has been modified across 60% of its land surface (Sanderson et al. 2002), and all marine ecosystems have been affected by humans (Halpern et al. 2008). One species, *Homo sapiens*, is now appropriating about 25% of Earth's primary production (Haberl et al. 2014).

The influence of human activities on natural habitat is the most important factor contributing to global declines in biodiversity (Sax and Gaines 2003). There are areas of extreme human influence, such as agricultural regions and certain coastal waters, and areas of little human influence, such as deserts and some polar seas. Overall, however, most of the lands and waters of Earth are at least moderately affected by humans (see Figure 3.5B). It is critical that addressing the loss, fragmentation, and degradation of habitat caused by human activities is central to conservation work. **Habitat loss** refers to the outright conversion of habitat to another use, such as urban development or agriculture, while **habitat fragmentation** refers to the breaking up of once continuous habitat into a series of habitat patches amid a human-dominated landscape. **Habitat degradation** refers to changes that reduce the quality of the habitat for many, but not all, species. Concepts 24.2 and 24.3 will address habitat fragmentation and its effects in detail; in this and the following sections, we'll cover habitat loss and habitat degradation.

On a continental scale, the extent of loss of some habitats is staggering (see Figure 24.12). Similar losses can be observed on more local scales, as in the forests of western

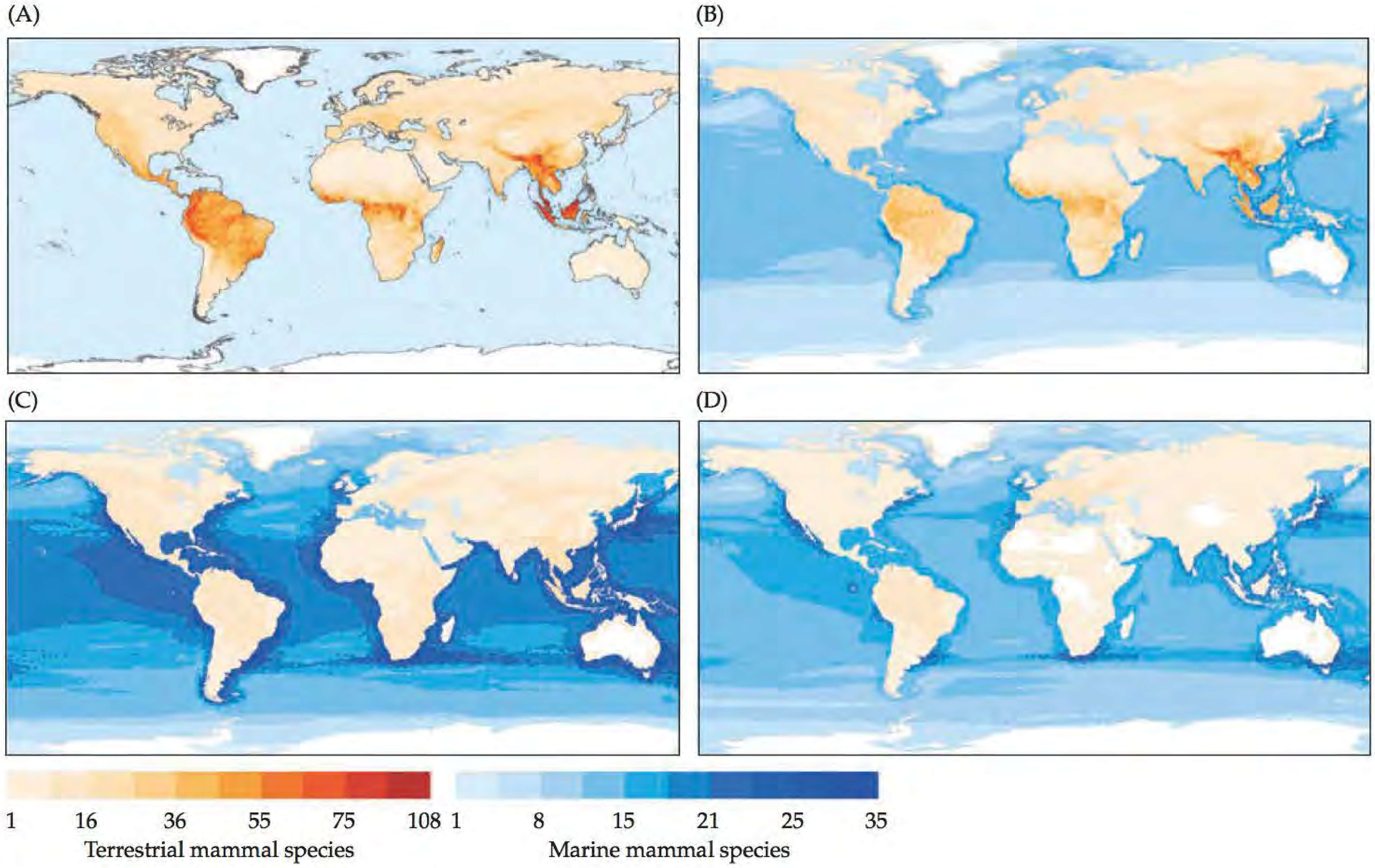


Figure 23.10 Threats to Mammal Species Globally, 22% of mammal species are threatened by extinction. These maps show the numbers of terrestrial and marine mammal species in various parts of the globe that are negatively affected by (A) habitat loss, (B) overexploitation, (C) accidental mortality, and (D) pollution. (From Schipper et al. 2008.)

? Contrast the threats to land mammals with those to marine mammals.

Ecuador (see Figure 23.4). Another example is provided by the Atlantic forest of Brazil (Ranta et al. 1998). This moist tropical forest has many endemic species, perhaps because it has been isolated from the Amazon rainforest for millions of years. Of South America's 904 mammal species, 73 are endemic to this forest, and 25 of those endemics are threatened with extinction. The forest's location also coincides with that of 70% of Brazil's human population. As a result, more than 92% of this habitat has been cleared to make room for agriculture and urban development, and what remains has been highly fragmented, pushing many species to endangerment.

How has the loss of Atlantic forest habitat affected biodiversity? Brooks and colleagues (1999) asked why there have been no reports of extinctions among birds of this region. They offered three possible explanations, which may apply to patterns of biological decline in other ecosystems as well. First, the birds may be adjusting to living in forest fragments. Second, the most vulnerable species might have gone extinct before they were known to biologists. Their third explanation, which they see as the most plausible, is that the time lag between deforestation and extinction has not yet played out. While there may have been no reported extinctions yet, populations have been reduced to such an extent that the birds may no longer be capable of maintaining their populations. Unless drastic measures are taken, such species are doomed to extinction. Moreover, the loss of bird species will have negative effects on other species. Already, as bird populations in the Brazilian Atlantic forest have dwindled to low numbers, reductions in seed size and seedling survival have been observed in plant populations that depend on these birds for seed dispersal (Galetti et al. 2013).

Habitat degradation is extremely widespread, and it has diverse causes, including invasive species, overexploitation, and pollution. We'll turn now to one of those causes, invasive species.

Invasive species can displace native species and alter ecosystem properties

As discussed earlier, the introduction of non-native species generally has negative effects on biodiversity. Here, we'll consider how declines in biodiversity can be caused by the arrival of these **invasive species**: non-native, introduced species that sustain growing populations and have large effects on communities. Worldwide, 20% of endangered vertebrates, especially those on islands, are imperiled as a result of invasive species (MacDonald et al. 1989).

Invasive species are of particular concern where they compete with, prey on, or change the physical environment of endangered native species. The effect of the Eurasian zebra mussel (*Dreissena polymorpha*) on the freshwater mussel species of North America is a prime example (see Figure 19.5). North America is the center of diversity for freshwater mussels (bivalves of the order Unionoida), with 297 species, a third of those in the world. Prior to the invasion of the zebra mussel in the late 1980s, North American freshwater mussels were already in trouble. Most of these species are globally imperiled, many are endemic and thus naturally rare, and all are threatened by compromised water quality and river channelization. Competition with zebra mussels has brought about steep declines in populations of native freshwater mussels (60%–90%), including some regional extinctions (Strayer and Malcom 2007).

Invasive predators can also contribute to extinctions. In Lake Victoria (one of the African Great Lakes), introduction of the Nile perch (*Lates niloticus*) has reduced the diversity and abundance of the native cichlid fishes, a group that shows *adaptive radiation* (a phenomenon discussed in Concept 6.4), with many species in specific habitats. Historically, about 600 species of cichlids had been recorded, most of which were endemic to Lake Victoria. The Nile perch is a large predator, and its introduction into the lake in the early 1960s has contributed to the extinction of roughly 200 cichlid species. Before the introduction, the cichlids made up 80% of the biomass of fish in the lake; the Nile perch now accounts for 80% of the biomass. As is often the case, more than one factor is driving the cichlids' decline: pollution and overfishing augment the negative effect of predation by the Nile perch (Seehausen et al. 1997).

In many ecosystems, habitat loss and degradation have increased vulnerability to invasion by non-native species, which in turn may lead to consequences that further degrade the ecosystem. The tropical dry forest of Hawaii, for example, harbors more than 25% of Hawaii's threatened plant species. The area of tropical dry forest has been reduced by 90% since human settlement. The arrival of invasive feral hogs, rats, and even grasses has made a bad situation worse. In addition to outcompeting and displacing local plants, these grasses are an excellent source of fuel for fires. As a result, the frequency of fires has increased (see Analyzing Data 9.1), furthering the decline of Hawaiian dry forests but favoring the spread of the fire-adapted, introduced grasses.

Ecosystem properties such as nitrogen cycling (see Figure 22.11) can be altered by some invasive species. One such species is kudzu (*Pueraria montana*), an invasive vine that covers more than 3 million ha (7.4 million acres) in the southeastern United States. This species disrupts communities by outcompeting other plants for light (see Figure 14.4). In addition, kudzu can fix up to 235 kg of nitrogen per hectare per year, an amount that far exceeds the atmospheric deposition of nitrogen in the eastern United States (7–13 kg N/ha/year).

To examine the extent to which nitrogen fixation by kudzu affects the nitrogen cycle, Hickman et al. (2010) measured the nitrogen mineralization rate in plots with and without kudzu (as discussed in Concept 22.2, the nitrogen mineralization rate provides an estimate of the rate at which nitrogen is supplied to plants). On average, nitrogen mineralization rates increased more than sevenfold in plots invaded by kudzu (**Figure 23.11**), indicating a large effect on the availability of nitrogen to plants. In addition, more than twice as much of the gas nitric oxide (NO) was released from the soil in plots invaded by kudzu as in plots lacking kudzu; see **Analyzing Data 23.1** to test whether NO emissions at one of the study sites differ statistically between plots with kudzu and plots lacking kudzu. In the atmosphere, NO participates in chemical reactions that produce ground-level ozone, a pollutant that affects human health and agricultural production (see Concept 25.4). Modeling results suggest that kudzu has the potential to increase the number of high-ozone event days by as many as 7 days per summer across broad regions of the southeastern United States (Hickman et al. 2010).

As we saw in the Case Study of the invasive alga *Caulerpa taxifolia* in Chapter 16, control or eradication of invasive species is difficult, labor-intensive, and expensive, but at times it may be warranted in the interest of protecting economically or culturally valuable native species or natural resources. The best strategy for combating invasive species is to prevent their arrival through careful screening of biological materials at international borders. But once potentially invasive species are present, control measures are best implemented immediately; constant

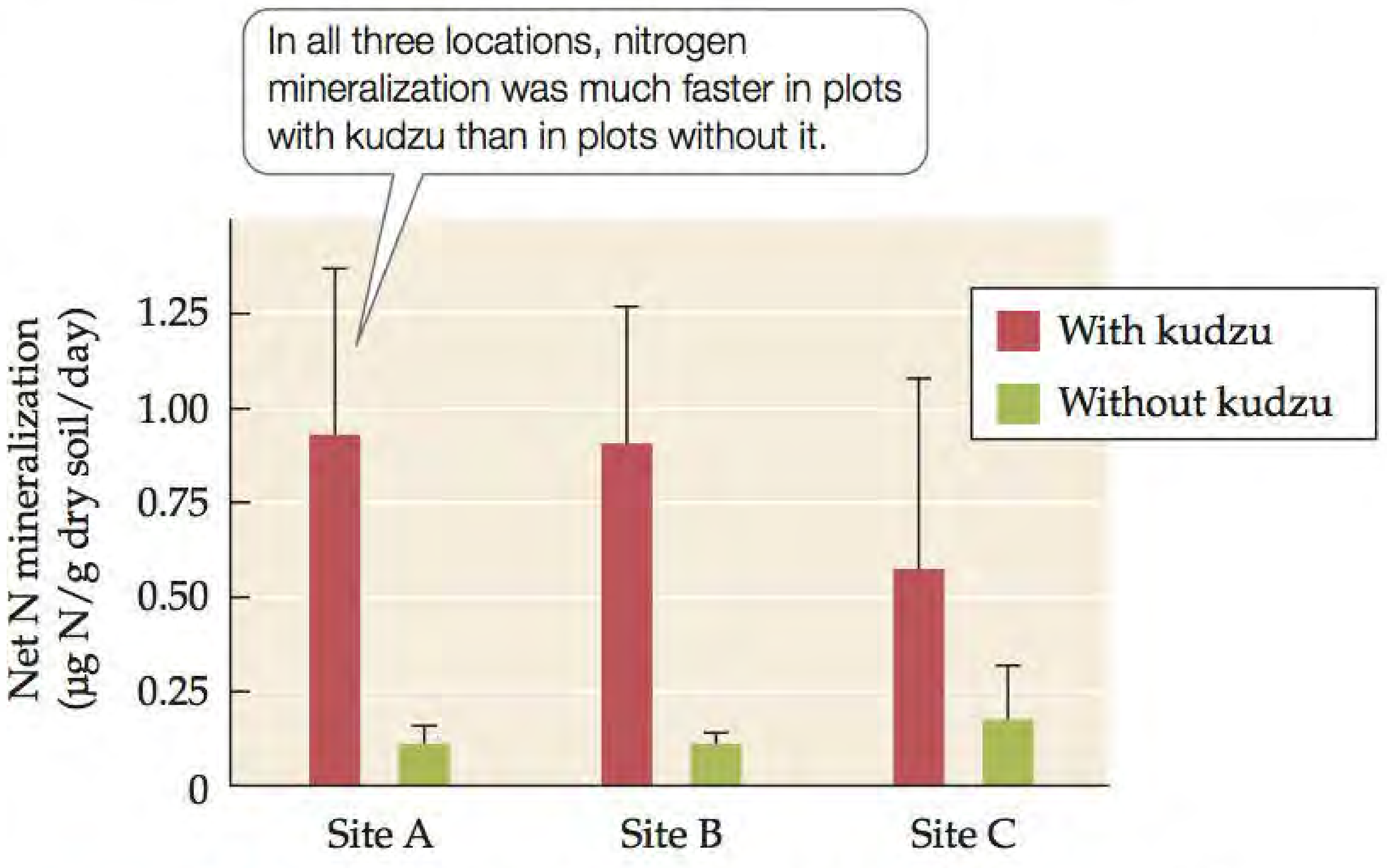


Figure 23.11 Invasive Species Can Alter the Nitrogen Cycle At three sites in Georgia, net nitrogen mineralization rates (an index of how rapidly nitrogen cycling occurs in an ecosystem) were much higher in soils supporting kudzu than in soils with native vegetation. Error bars show one SE of the mean. (After Hickman et al. 2010.)

ANALYZING DATA 23.1 Do Nitric Oxide Emissions Differ Statistically between Plots with and without Kudzu?

Hickman et al. (2010)* examined the impact of the invasive species kudzu (*Pueraria montana*) on nitric oxide (NO) emissions at three study sites in Georgia. NO is an important contributor to pollutant ozone formation. At each site, NO emissions were recorded from four plots with kudzu and four plots lacking kudzu.

Data from one study site are presented in the table. In this exercise, you will perform a statistical test (the *t*-test) to determine whether NO emissions in plots invaded by kudzu are significantly different from NO emissions in plots lacking kudzu.

NITRIC OXIDE EMISSIONS (ng N/cm^2/hr)	
PLOTS WITH KUDZU	PLOTS LACKING KUDZU
4.1	2.0
1.7	0.9
6.1	1.1
2.8	0.9

1. a. What is the sample size (*n*) for plots with kudzu and plots without kudzu?
   b. Using the definitions provided below, calculate the mean $(\bar{x})$ and standard deviation (*s*) of NO emissions for plots invaded by kudzu and for plots lacking kudzu (more information on $(\bar{x})$ and *s* can be found in **Web Stats Review 1.2**). What do your results suggest?
2. The *t*-test provides a standardized way to determine whether the means of two treatments differ enough from one another to be considered "significantly different." The *t*-test is based on calculation of the *T* statistic, defined below and described more fully in the Web Stats Review. Calculate the *T* statistic using the data provided above.
3. Based on information in the Drawing Inferences section of the Web Stats Review, determine the "degrees of freedom" and "*p* value" associated with the value you obtained for *T*. Interpret the results of your *t*-test.

DEFINITIONS

Mean: For *n* data points $x_1, x_2, x_3, \ldots, x_n$, the (arithmetic) mean $(\bar{x})$ equals

$$\bar{x} = \frac{(x_1 + x_2 + x_3 + \ldots + x_n)}{n} = \frac{1}{n}\sum_{i=1}^{n} x_i$$

Standard deviation: For *n* data points $x_1, x_2, x_3, \ldots, x_n$, the standard deviation (*s*) equals

$$s = \sqrt{s^2} = \sqrt{\frac{1}{n-1}\sum (x_i - \bar{x})^2}$$

***T* statistic:** When comparing the means of two samples, each of size *n*, the *T* statistic equals

$$T \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{\frac{1}{n}\left(s_1^2 + s_2^2\right)}}$$

See the companion website for a similar ANALYZING DATA exercise.

---

*Hickman, J. E., S. Wu, L. J. Mickley and M. T. Lerdau. 2010. Kudzu (*Pueraria montana*) invasion doubles emissions of nitric oxide and increases ozone pollution. *Proceedings of the National Academy of Sciences USA* 107: 10115–10119.

vigilance and quick action are key to minimizing their effects (Simberloff 2003).

Overexploitation of species has large effects on ecological communities

Overexploitation, the harvest of wild organisms at a rate that exceeds their replacement, can also lead to loss of biodiversity. For example, many of the world's people obtain their food, at least in part, directly from a natural ecosystem. The problem is that as the human population increases and natural habitats shrink, the harvesting of many species from the wild has become unsustainable. Globally, overexploitation is contributing to the imperilment of many species, including many fishes, mammals, birds, reptiles, and plants. Overexploitation has been the cause of the probable extinction of at least one primate, Miss Waldron's red colobus monkey (*Procolobus badius waldroni*), a subspecies endemic to Ghana and Côte d'Ivoire whose last confirmed sighting was in 1978 (Oates et al. 2000; McGraw 2005).

The effects of overexploitation on tropical forests have been substantial, resulting in what Kent Redford (1992) has called an "empty forest." This phrase refers to forests that look healthy in satellite images, but in which the abundances and diversity of large vertebrates have decreased. The increased accessibility of forests as roads are built through them facilitates this overharvesting of wildlife, as does the widespread availability of guns. The enormous quantity of "bushmeat" being taken from tropical forests is sobering. Redford has calculated that 13 million mammals are killed each year in the Amazon rainforests of Brazil by rural hunters, and it is estimated that in western and central Africa, 1 million tons of forest animals are taken annually for food (Wilkie and Carpenter 1999). Vast numbers of animals are also captured from tropical forests, coral reefs, and other ecosystems and then imported legally to other countries. For example, government records indicate that from 2000 to 2006, 1.5 billion animals, most of which were for the pet trade, were imported to the United States alone (Smith et al. 2009).

In the oceans, rapid and steep declines have taken place in both the abundances (**Figure 23.12**) and sizes (**Figure 23.13**) of top-level predators (Myers and Worm 2003). For every ton of fish caught by commercial trawlers, 1 to 4 tons of other marine life may be brought aboard. Some organisms may survive the experience and be released back into the sea; the rest comprise what is called *bycatch*. The bycatch of certain threatened species, such as marine mammals, seabirds, and marine turtles, has received attention from fisheries managers, and in some cases, losses have been reduced through changes in gear design (see Ecological Toolkit 10.1). But bycatch remains common, and concern has been raised about the ecological effects of this unnecessary mortality on marine food webs (Lewison et al. 2004). In addition, repeated trawling on the coastal sea bottom has affected benthic species such as corals and sponges and has thereby degraded benthic habitat for many other species. Studies indicate that habitat recovery following trawling is very slow (National Research Council 2002).

Whenever a species has market value, it is likely to be overharvested. And, in an unfortunate confluence between human behavior (i.e., greed) and declining animal and plant populations, when threatened species have monetary value, an "anthropogenic Allee effect" (see Figure 11.15) can occur in which their increasing economic value can lead to more aggressive search and collection missions. Many scientists and policymakers argue that the best approach to protecting overexploited species is to determine the levels of harvest that will be sustainable and to establish regulatory mechanisms to permit only those levels to be taken. In one example of how this could be done, Bradshaw and Brook (2007) describe management options that provide revenue from meat and trophy hunting of the wild banteng (*Bos javanicus*), a member of the cattle genus, yet do not jeopardize the prospects for the recovery of this rare species.

Pollution, disease, and climate change erode the viability of populations

More insidious effects of human activities, such as air and water pollution and climate change, are causing declines in populations of many species. We are also seeing the emergence of new diseases and the transmission of diseases from domesticated animals into wildlife. The effects of all these factors exacerbate declines in species already reduced by habitat loss, invasive species, or overexploitation.

Pollutants released by human activities are omnipresent in air and water—demonstrating one of the ecological maxims introduced in Table 1.1: "Everything goes somewhere." These pollutants become contributors to habitat degradation and biodiversity loss where they are present at levels that cause physiological stress. We will see in

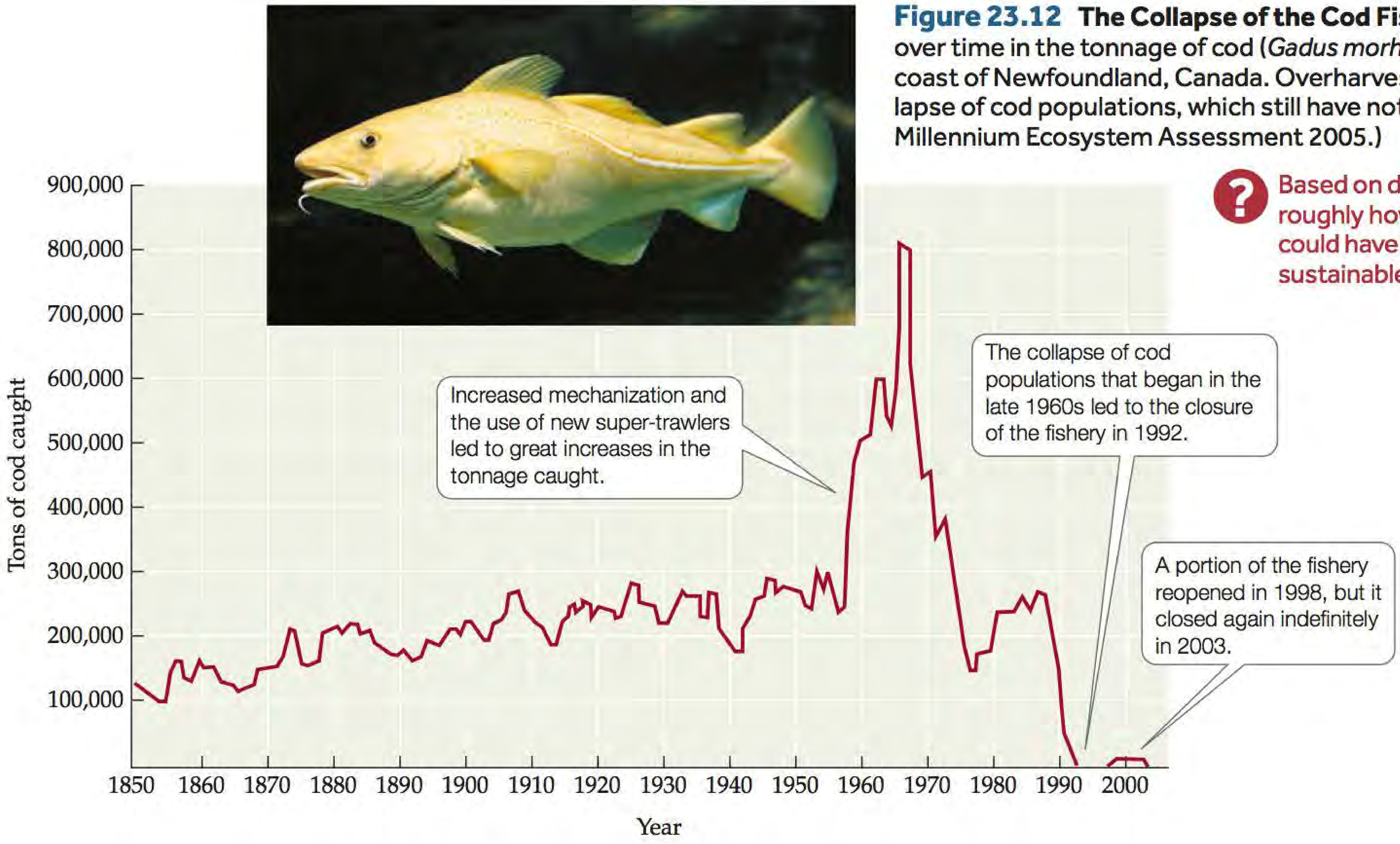


Figure 23.12 The Collapse of the Cod Fishery Changes over time in the tonnage of cod (*Gadus morhua*) caught off the coast of Newfoundland, Canada. Overharvesting led to the collapse of cod populations, which still have not recovered. (After Millennium Ecosystem Assessment 2005.)

? Based on data prior to 1950, roughly how many tons of cod could have been harvested in a sustainable manner? Explain.

Increased mechanization and the use of new super-trawlers led to great increases in the tonnage caught.

The collapse of cod populations that began in the late 1960s led to the closure of the fishery in 1992.

A portion of the fishery reopened in 1998, but it closed again indefinitely in 2003.

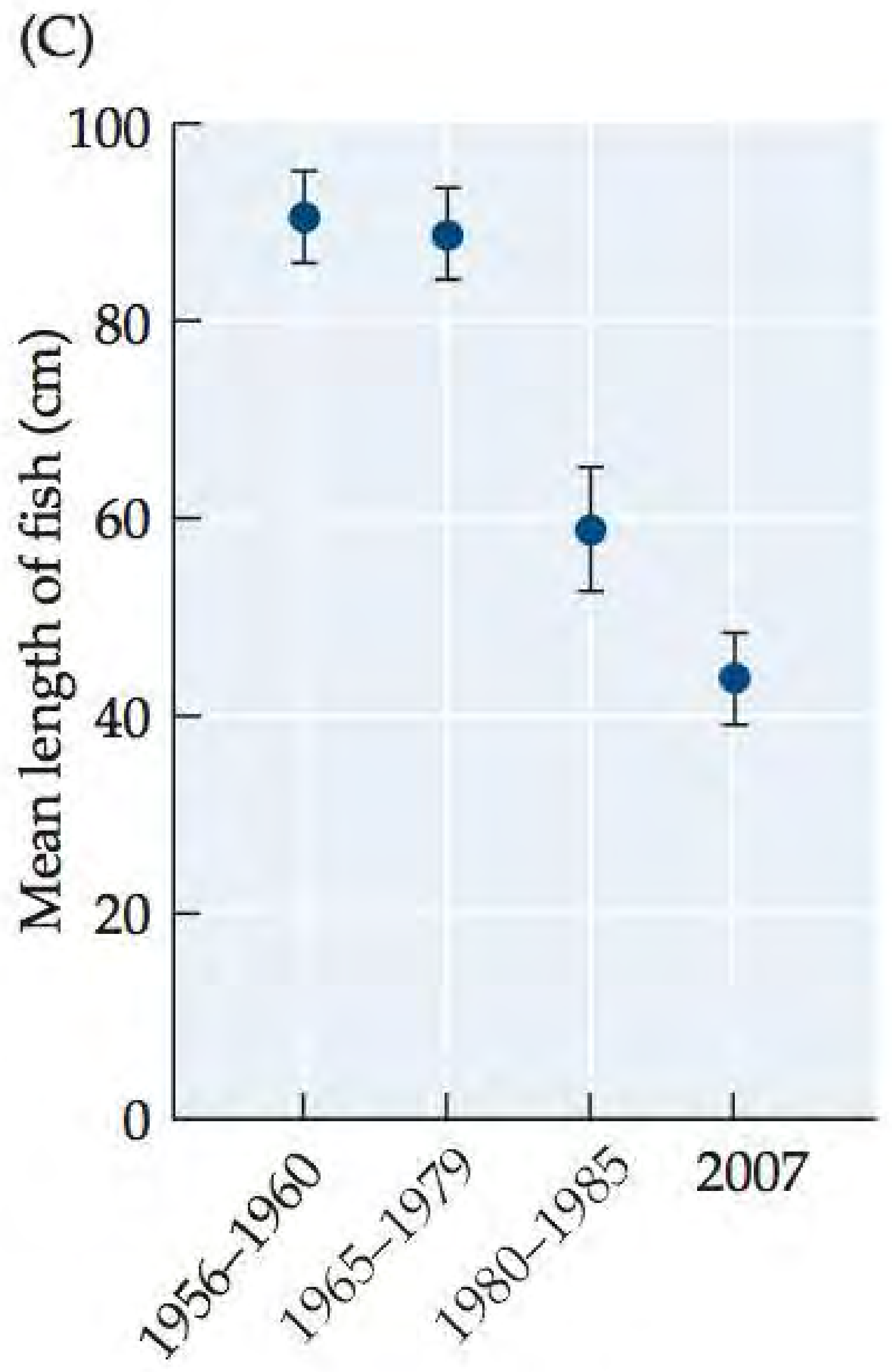


Figure 23.13 **Overharvesting Has Led to a Decline in the Sizes of Top Marine Predators** Photographs of trophy fish caught on charter fishing boats based in Key West, Florida, in (A) 1957 and (B) 2007. In commercial and recreational fisheries, the largest fish are often the preferred prey. (C) The total length of trophy fish declined more than 50% between 1960 and 2007. Error bars show ± one SE of the mean. (A,B from McClenachan 2009; C after McClenachan 2009.)

Concept 25.3 how some of these pollutants degrade habitats, reduce populations, and threaten the persistence of species.

One example of an emerging pollution threat is the growing concentration of persistent endocrine-disrupting contaminants (EDCs), particularly in the marine environment. As we saw in the Case Study Revisited in Chapter 21, persistent organic pollutants such as DDT, PCBs, flame retardants, and organophosphates from agricultural pesticides, some of which are EDCs, end up in marine food webs, where they are bioaccumulated and biomagnified, particularly in top predators. The number of chemicals found in marine mammals, the number of individuals affected, and the concentrations found have risen markedly in the last 40 years (Tanabe 2002). Peter Ross refers to the orcas of British Columbia as "fireproof killer whales" because of the extremely high levels of flame-retardant chemicals (polybrominated diphenyl ethers, or PBDEs) found in their bodies (**Figure 23.14**). These EDCs have been observed to interfere with reproduction, neurological development, and immune function in mammals (Ross 2006). EDCs have also interfered with reproduction—basically by turning males into females—in many other species as well, including a population of the endangered pallid sturgeon (*Scaphirhynchus albus*) in the Mississippi River downriver from Saint Louis. Such problems for species already at low numbers do not improve the outlook for their future.

Disease has also contributed to the decline of many endangered species. In a striking example, an emerging disease caused by the fungus *Batrachochytrium dendrobatidis* has decimated amphibian populations around the globe (Skerrat et al. 2007) (see also the Case Study Revisited in Chapter 1). In the 1930s, the final decline to extinction of the thylacine, or Tasmanian wolf (*Thylacinus cynocephalus*), was hastened by an undetermined disease, and now the

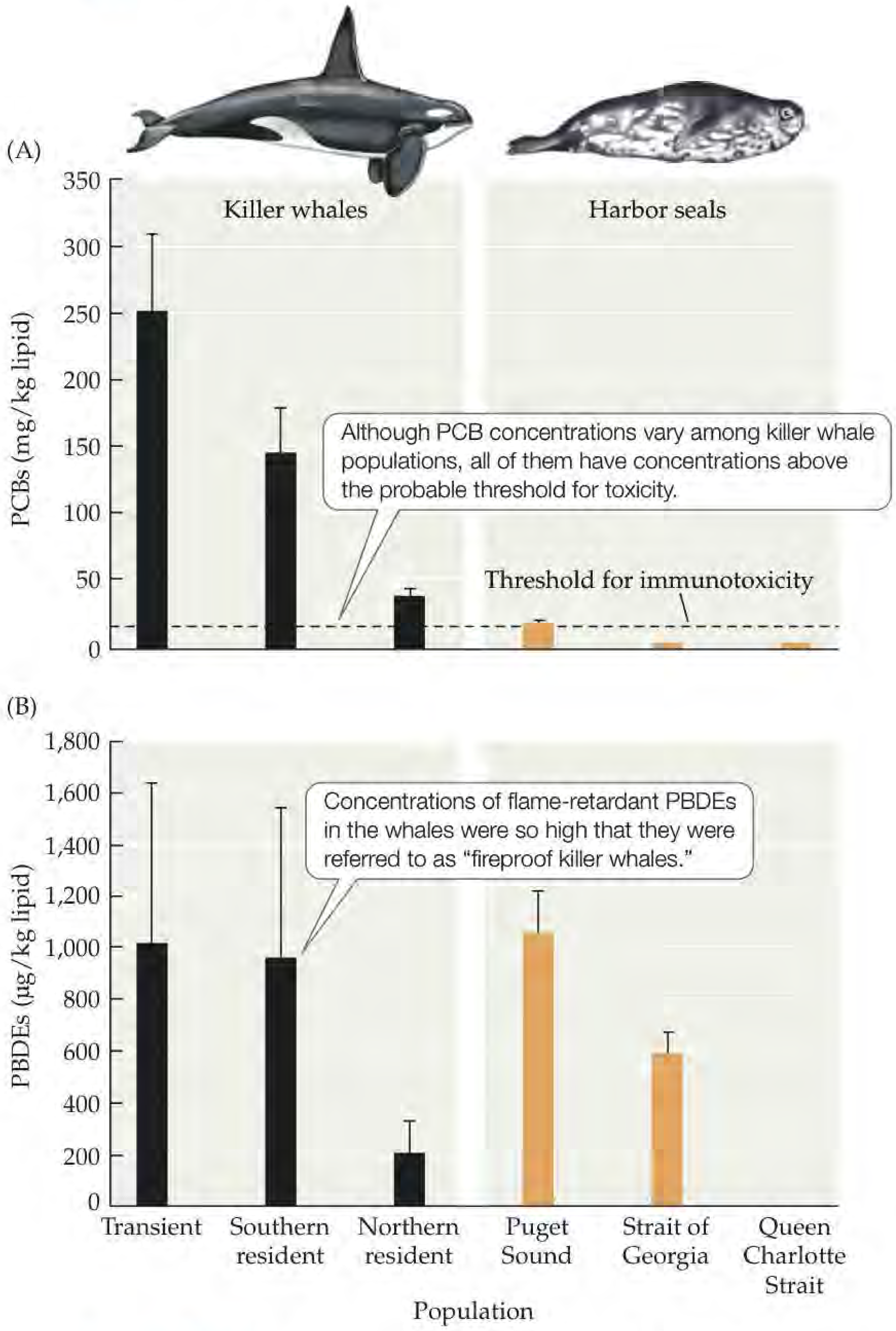


Figure 23.14 Persistent Organic Pollutants That Disrupt the Endocrine System Are a Growing Threat to Marine Mammals In British Columbia, the concentrations of PCBs (A) and PBDEs (B) found in killer whales (*Orcinus orca*) and harbor seals (*Phoca vitulina*) are very high. Error bars show one SE of the mean. (After Ross 2006.)

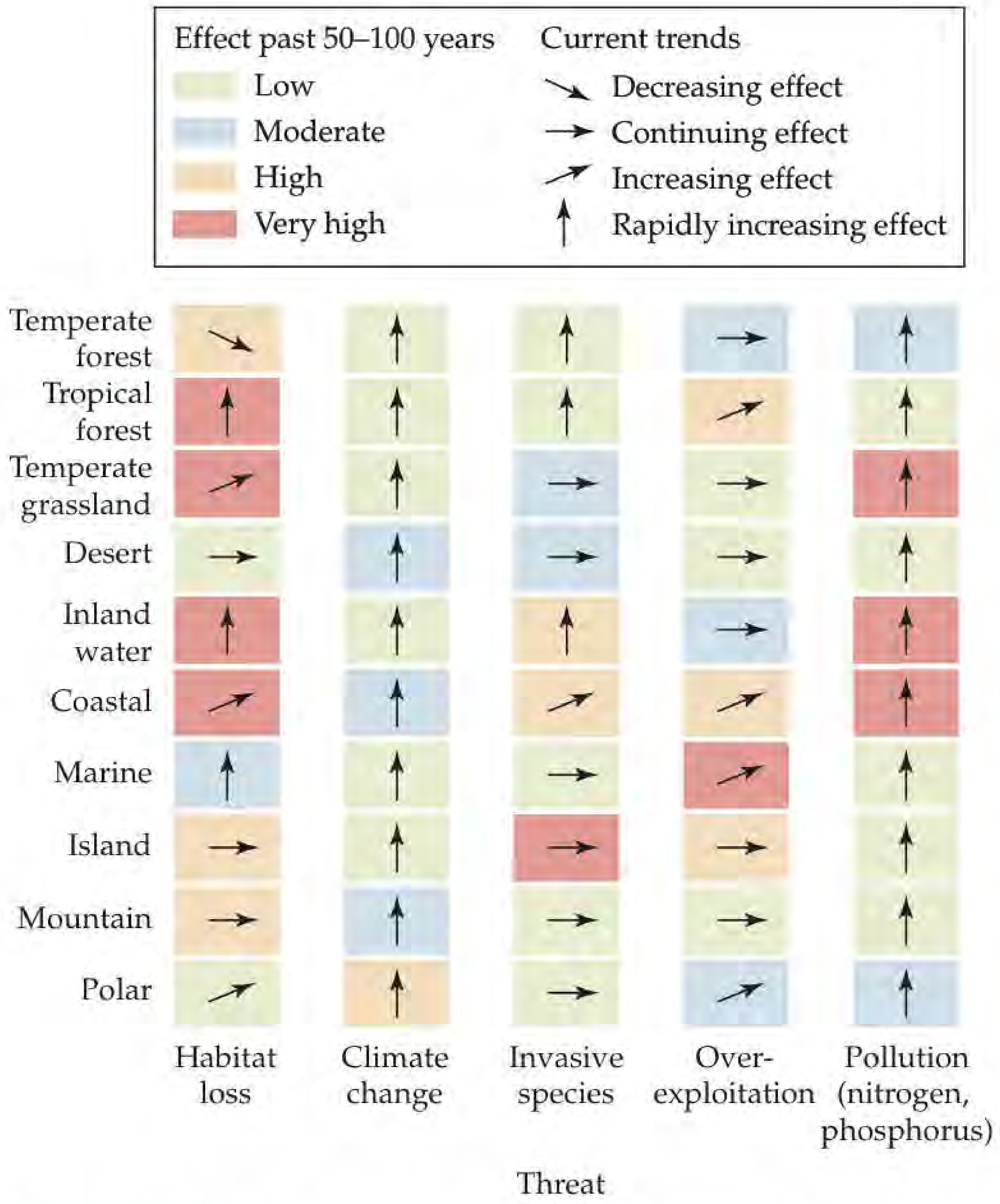
Tasmanian devil (*Sarcophilus harrisii*) appears to be similarly threatened because of the spread of a facial tumor disease (Hawkins et al. 2006). In the North American prairie, the threatened status of the black-footed ferret (*Mustela nigripes*) was exacerbated by canine distemper (Woodroffe 1999).

CLIMATE CHANGE CONNECTION

Impacts on Biodiversity Although hundreds of species have shifted their distributions to higher latitudes or elevations in response to global warming (Parmesan 2006), only a few cases are known in which species are imperiled directly by climate change. However, the number of extinctions associated with climate change is expected to increase (Thomas et al. 2004). Throughout this book and the accompanying Climate Change Connections on the website, we've emphasized that climate change has influenced and will continue to influence biodiversity in multiple ways. Warmer temperatures can directly influence physiological activity and behavior, influencing reproduction and mortality of individuals (see Online Climate Change Connection 24.1). We saw an example of this with changes in the length of time lizards can be active, alterations due to climate warming (see Online Climate Change Connection 4.1). As a consequence of climate change, the probability of population extinctions increases because of constraints on the amount of time the lizards can forage, which may explain local extinction of some lizard populations in Mexico (Sinervo et al. 2010). Climate change may affect how species interact and the intensity of those interactions, as indicated in Online Climate Change Connection 1.1, which showed that some aquatic ecosystems experience increases in food web connections in a warmer world (Woodward et al. 2010). Changes in the type (antagonistic versus facilitative) and intensity of biotic interactions make prediction of the fates of species in a warmer world challenging.

We saw in Concept 12.3 that the distribution of organisms and diversity in communities can be influenced by predation. If predators and prey respond differently to climate change, the influence of predation on diversity can be positive or negative, depending on which species is more sensitive. If prey are more sensitive to warmer temperatures than predators, then climate change will accentuate the negative impact of predation on diversity. This hypothesis was supported in the rocky intertidal zone by Christopher Harley (2011). Using a combination of experiments and observational studies employing variation in both space and time to examine variation in climate, Harley demonstrated a decrease in diversity of shellfish communities (barnacles and mussels) in the rocky intertidal zone consistent with greater predation and a restriction of habitat associated with climate change. The main predator, a sea star, was less sensitive to warming than barnacle and mussel species. The reduction in habitat increased the susceptibility of the prey species to predation, contributing to the local extinction of some species under warmer conditions. We will explore climate change in greater depth in Chapters 24 and 25.

As the human population passed the 7 billion mark, our impact on the environment had already caused all of the world's biomes to be affected by the threats we have just described. However, the importance of these threats varies among biomes (**Figure 23.15**). Habitat loss is greater in the tropics than in the polar zones, for example, but climate change is having more of an effect in the polar zones than in the tropics. What can conservation biologists offer as solutions to these threats from so many fronts?



	Habitat loss	Climate change	Invasive species	Over-exploitation	Pollution (nitrogen, phosphorus)
Temperate forest	High ↘	Low ↑	Low ↑	Moderate →	Moderate ↑
Tropical forest	Very high ↑	Low ↑	Low ↑	High ↗	Low ↑
Temperate grassland	Very high ↗	Low ↑	Moderate →	Low →	Very high ↑
Desert	Low →	Moderate ↑	Moderate →	Low →	Low ↑
Inland water	Very high ↑	Low ↑	High ↑	Moderate →	Very high ↑
Coastal	Very high ↗	Moderate ↑	High ↗	High ↗	Very high ↑
Marine	Moderate ↑	Low ↑	Low →	Very high ↗	Low ↑
Island	High →	Low ↑	Very high →	High →	Low ↑
Mountain	High →	Moderate ↑	Low →	Low →	Low ↑
Polar	Low ↗	High ↑	Low →	Moderate ↗	Moderate ↑

Figure 23.15 Different Biomes Face Different Principal Threats The effects of different types of threats on different biomes over the past 50–100 years were examined as part of the Millennium Ecosystem Assessment, an international collaboration among more than 1,000 ecologists commissioned by the United Nations. The color of each box indicates the effect of the threat to date; the direction of the arrow indicates the trend in that threat. (After Millennium Ecosystem Assessment 2005.)

? At a global scale, what factors have been the most important threats to biodiversity over the past decades, and what factors are projected to be the most important in the future? How do these current and future threats differ between terrestrial and marine biological zones?

CONCEPT 23.4
Conservation biologists use many tools and work at multiple scales to manage declining populations.

Approaches to Conservation

Where should we put our focus in preventing species loss—on the species or the habitat? Conservation biologists have debated this question and have generally concluded that protecting habitat is of primary importance but that understanding species is also important. There is no real dichotomy here, as we must understand the biology of a threatened species in order to identify and preserve its habitat. The U.S. Endangered Species Act functions through the listing of particular species threatened with extinction, but for each of those species, it mandates the identification and protection of critical habitat. Worldwide, many other laws protecting biodiversity take a similar approach.

Chapter 24 will describe how the principles of ecology are applied to protecting habitat and how conservation biologists work to manage ecosystems and landscapes. In this section, we will look at the variety of ways in which conservation biologists work to understand and protect biodiversity at the level of genes, populations, and species.

Genetic analyses are important conservation tools

As we saw in Concepts 6.2 and 11.3, small populations are particularly vulnerable to the effects of genetic drift and inbreeding, which can result in a decrease in genetic variation and an increase in the frequency of deleterious alleles. A decrease in genetic variation can limit the extent to which a population can evolve in response to environmental change, potentially placing the population at a greater risk of extinction. An increase in the frequency of deleterious alleles is also of concern because it can cause birth or survival rates to drop, thereby decreasing the population growth rate—again increasing the risk of extinction.

By increasing the risk of extinction in these ways, genetic problems resulting from small population sizes can ruin efforts to conserve a species. In some cases, conservation biologists have addressed this threat head-on by attempting the "genetic rescue" of populations that otherwise would appear doomed to extinction. Consider the Florida panther (*Puma concolor coryi*), a subspecies of puma (pumas are also called panthers, cougars, and mountain lions). By the early 1990s, the number of panthers in Florida had decreased to fewer than 25 individuals. Compared with other puma populations, the Florida panther population had low genetic diversity and a high frequency of problems such as heart defects, kinked tails, poor sperm quality, and adult males in which one or both testes failed to descend properly. Models similar to those discussed in Concept 11.3 indicated a 95% chance that the population would become extinct within 20 years.

In 1995, to rescue the Florida panther from genetic decline and likely extinction, biologists captured eight female pumas from populations in Texas and released them in southern Florida. They selected females from Texas because historically gene flow occurred between the Florida and Texas puma populations. The results were striking (Johnson et al. 2010). Panther numbers tripled, levels of genetic variation doubled, and the frequency of genetic abnormalities decreased substantially

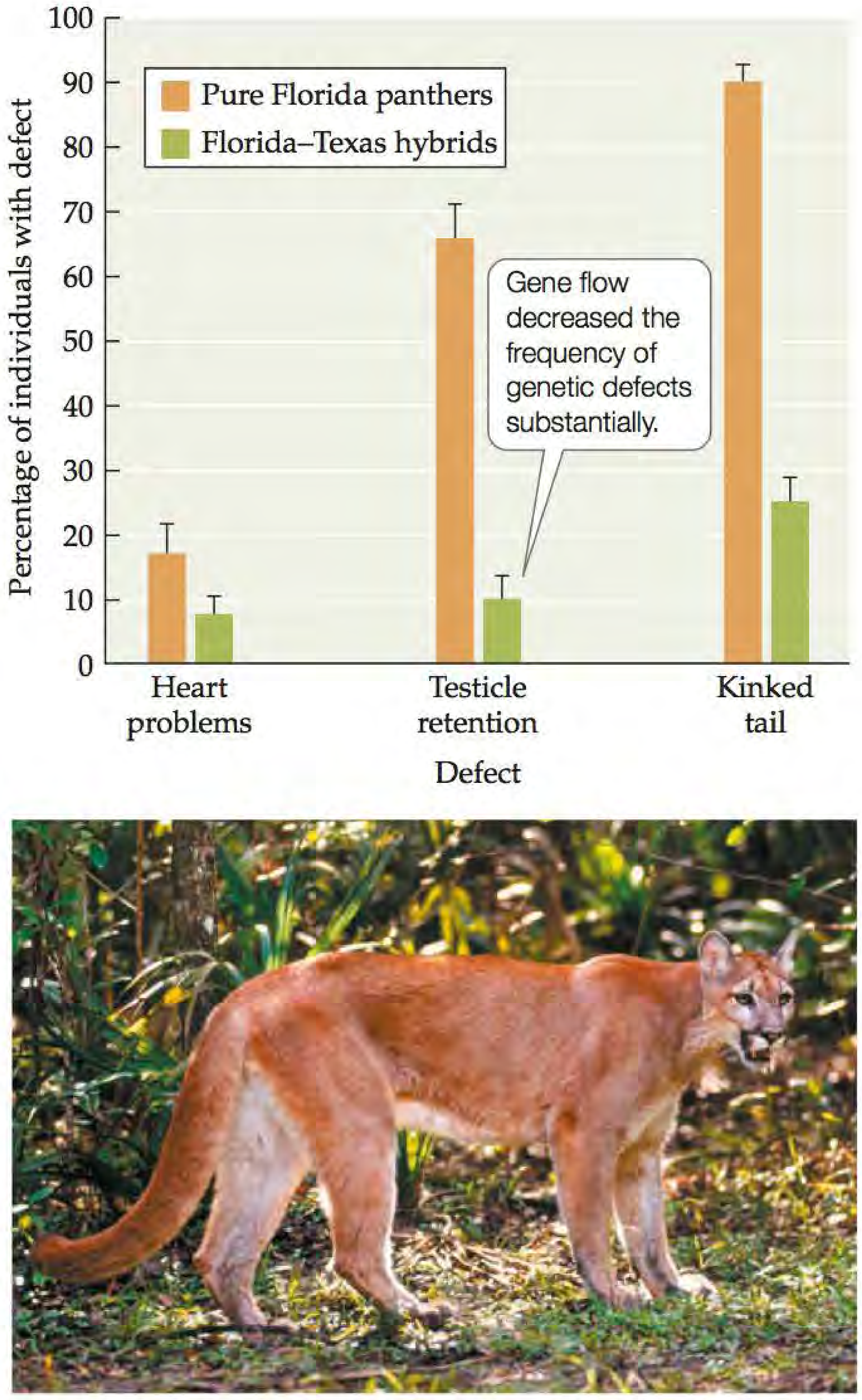


Figure 23.16 **Genetic Rescue of the Florida Panther** With depleted genetic diversity, frequent genetic defects, and a precariously small population size (fewer than 25 individuals), the Florida panther (*Puma concolor coryi*) seemed doomed to extinction in the early 1990s. The gene flow that resulted from the translocation of eight females from *P. concolor* populations in Texas helped to reverse these trends. Error bars show one SE of the mean. (After Johnson et al. 2010.)

(**Figure 23.16**). Increases in panther numbers no doubt were aided by other conservation efforts, including habitat protection and the construction of highway underpasses to reduce mortality from collisions with vehicles, but it is clear that genetic restoration has contributed to the recovery of the Florida panther. Another example of successful genetic rescue includes the case of the greater prairie chicken (see Concept 6.2).

As the Florida panther example suggests, genetic analyses can inform conservation decisions by revealing the genetic diversity present in a species and, in extreme cases, by guiding efforts to rescue a population or species from problems stemming from genetic decline. Genetic techniques can also be used in forensic applications related to conservation biology. For example, molecular genetic analyses permitted the identification of illegally harvested whale species in meat that was sold in Japan and labeled as either dolphin or (Southern Hemisphere) minke whale, both of which are legal to hunt (Baker et al. 2002). Cycads have also been genetically "fingerprinted," allowing tracking of these highly valuable and frequently poached plants (Little and Stevenson 2007). In **Ecological Toolkit 23.1**, we explore how such "forensic conservation biology" is done and how it was used to track the source of a large shipment of contraband elephant ivory.

The availability of molecular genetic tools has enhanced our ability to understand the genetic problems faced by small populations and has helped us to address some of those problems. Let's turn next to some of the ways we can approach conservation at the population level.

Demographic models can guide management decisions

Is the growth rate of the Yellowstone grizzly bear population high enough to allow it to persist? At what life stages are loggerhead sea turtles most vulnerable to predation, and what management decisions would be most expedient to ensure their continued viability? How much old-growth forest habitat must be preserved to ensure the persistence of the northern spotted owl? Such questions arise with nearly any species of conservation concern, and demographic models offer approaches to answering them.

There are hundreds of quantitative demographic models in use, tailored to the specific biological traits of particular species. The quantitative approach most widely used for projecting the potential future status of populations is referred to as **population viability analysis** (**PVA**). This approach allows ecologists to assess extinction risks and evaluate management options for populations of rare or threatened species (Morris and Doak 2002). PVA is a process by which biologists can calculate the likelihood that a population will persist for a certain amount of time under various scenarios. It encompasses a variety of models, ranging from relatively simple stage- or age-based demographic models like those described in Concept 10.2 to more complex, spatially explicit models that can take actual landscape features and dispersal of individuals from multiple populations into account.

PVA provides conservation biologists with the probabilities that certain outcomes will occur, given certain assumptions about future conditions (e.g., changes in threats or in management efforts). Thus, PVA is a tool with which ecologists can synthesize data collected in the field, assess the risk of extinction for a population or populations, identify particularly vulnerable age or stage classes, determine how many animals to release or how many plants to propagate to ensure the establishment of a new population, or determine what might be a safe number of animals to harvest (Beissinger and Westphal 1998).

PVA has been used to make a wide variety of decisions about how best to manage rare species. In Florida,

ECOLOGICAL TOOLKIT 23.1 Forensics in Conservation Biology

As we saw in Concept 23.3, overexploitation of wildlife can lead to population declines across entire continents and throughout the world's oceans. In some cases, conservation biologists or wildlife authorities may know that individuals from protected populations have been captured or killed, but without further information they cannot determine the extent or source of such illegal harvests. This lack of information can make laws that protect threatened species difficult to enforce. Fortunately, in some species, molecular genetic techniques can be used to monitor the extent of illegal harvesting or trace the source of illegally harvested wildlife products.

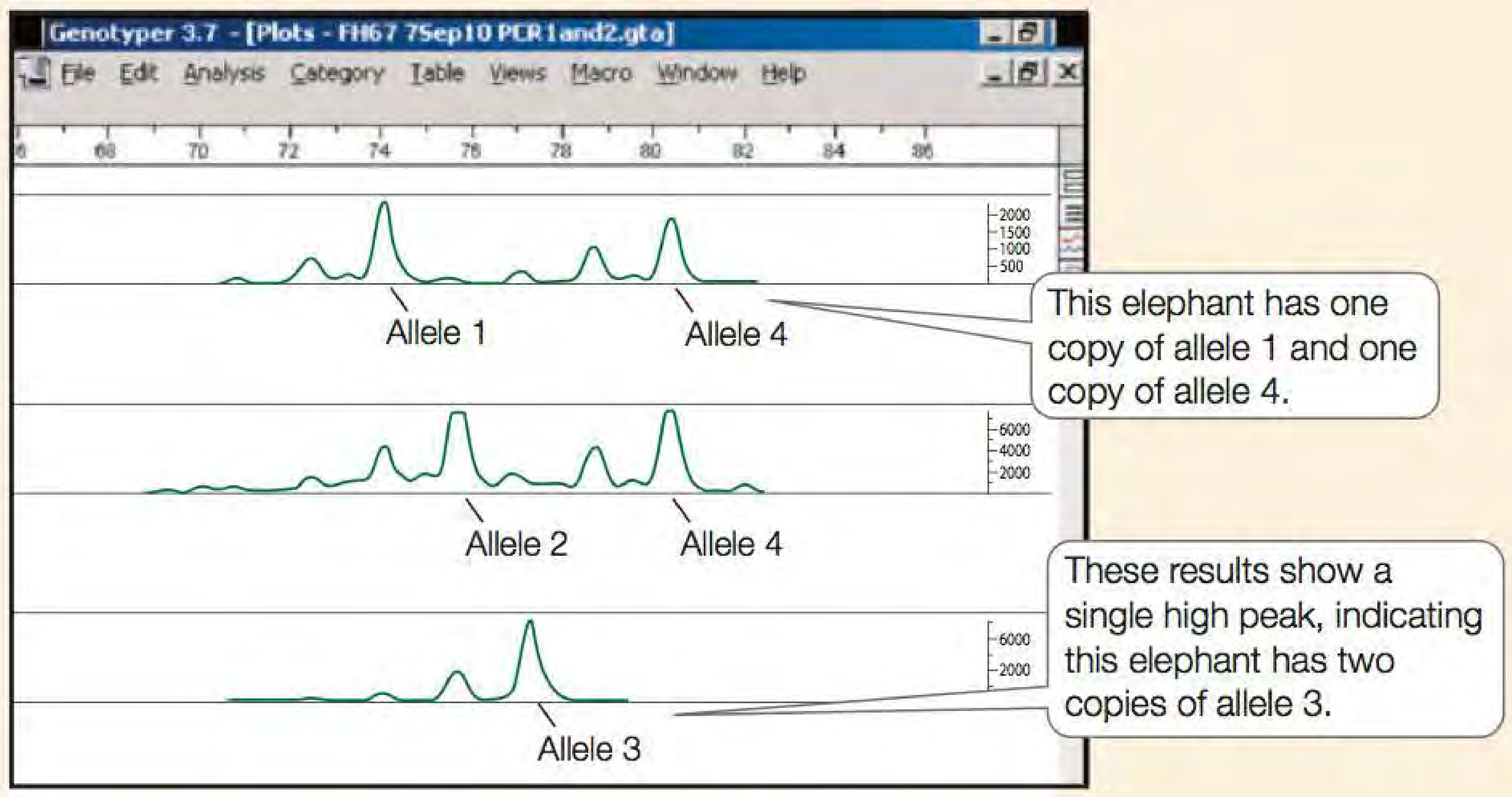
As an example, consider the trade in ivory. High demand for ivory led to the widespread slaughter of African elephants (*Loxodonta africana*), causing their numbers to drop from 1.3 million to 600,000 individuals between 1979 and 1987. As a response to this problem, an international ban on ivory trade was established in 1989. Initially the ban was successful, but soon an illegal ivory trade sprang up, leading to further declines in elephant populations.

The illegal trade in ivory proved hard to combat because even if a shipment was intercepted, it could be difficult to identify where the tusks had come from. In June 2002, more than 5,900 kg (>13,000 pounds) of ivory were confiscated in Singapore—the largest seizure of ivory since the 1989 ban (**Figure A**). Law enforcement officials suspected that these tusks came from elephants killed in multiple regions of Africa. Were they correct?

Figure A Ivory from the 2002 Seizure in Singapore

As in some human forensic cases, DNA evidence was used to answer this question. First, DNA was obtained from tusks seized in the June 2002 raid. As you may recall from your introductory biology class, the polymerase chain reaction (PCR) can be used to amplify (i.e., produce many copies of) specific regions of DNA that often differ from one individual to another. Such highly variable DNA segments can then be visualized in a computer scan, as shown in **Figure B**. By amplifying several of these highly variable segments, researchers can create a "DNA profile" that characterizes an individual's genetic makeup.

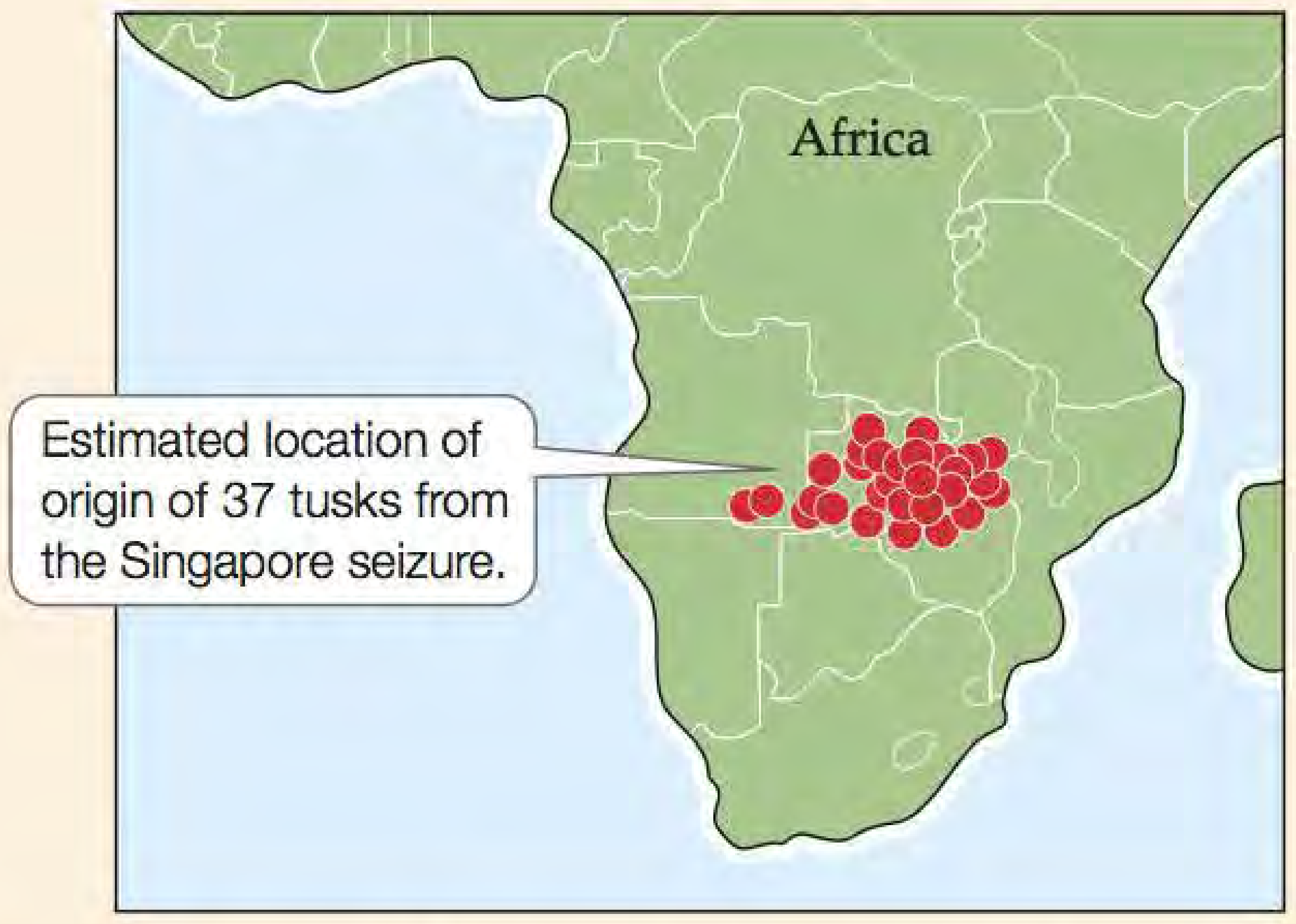
To locate the source of the confiscated ivory, Samuel Wasser and colleagues amplified seven highly variable DNA segments and used them to produce a DNA profile for each of 37 of the confiscated tusks. The place of origin of each tusk was then estimated by comparing its DNA profile with those in a reference database of elephant DNA collected from known geographic locations (Wasser et al. 2007). Contrary to what law enforcement officials had originally suspected, the results indicated that all of the tusks came from a relatively small region in southern Africa, centered on Zambia (**Figure C**). These findings enabled wildlife authorities to focus their investigation on a smaller area and fewer trade routes, and they led the Zambian government to improve its antipoaching efforts. More broadly, the approach described by Wasser and colleagues shows promise in forensic applications designed to limit illegal trade in a wide range of threatened animal and plant species.



This elephant has one copy of allele 1 and one copy of allele 4.

These results show a single high peak, indicating this elephant has two copies of allele 3.

Figure B Identifying Individual Elephants DNA from elephant tusks can be analyzed using molecular genetic techniques that detect individual-specific alleles. The graphs show results for three elephants; the highest peak(s) on each graph represent(s) specific alleles.



Estimated location of origin of 37 tusks from the Singapore seizure.

Figure C Tracking Contraband Ivory DNA methods indicated that the ivory shown in Figure A came from a relatively small geographic region—a finding that differed from what law enforcement officials had originally suspected. Each red dot shows the estimated location of origin of one individual elephant. (After Wasser et al. 2007.)

the fire regime that would best serve population growth in the rare plant *Chamaecrista keyensis* was determined through PVA simulations of burns at different times of year and at different intervals (Liu et al. 2005). In Australia, the forest-cutting practices that would best serve the persistence of two endangered arboreal marsupial species, the greater glider and Leadbeater's possum, were determined through extensive PVA modeling coupled with long-term monitoring to verify the accuracy of the data going into the model (Lindenmayer and McCarthy 2006). Such analyses have played a critical role in management decisions for a number of species.

Some conservation biologists, however, caution against excessive reliance on conclusions based on the results of PVA. They point to the high level of uncertainty in the dynamics of small populations, the paucity of demographic and environmental data for many endangered species, and the high probability that a model will leave critical factors unaccounted for. To be used effectively, PVA models need to be constantly refined and revisited by different researchers to check their validity against field observations, just as management strategies must be checked and adjusted for effectiveness (Beissinger and Westphal 1998).

Ex situ conservation is a last-resort measure to rescue species on the brink of extinction

When remaining populations of a species fall below a certain size, direct, hands-on action may be called for. Such actions can include the introduction of individuals into threatened populations (as in the Florida panther) or extensive habitat manipulations intended to improve the chance that individuals will reproduce successfully (as in the red-cockaded woodpecker, as we will see in the Case Study Revisited). In some cases, however, the only hope for preserving a species may be to take some or all of the remaining individuals out of their habitat—ex situ—and allow them to multiply in sheltered conditions under human care with the hope of later returning some individuals to the wild.

Ex situ conservation efforts have played a major role for 17 of the 68 vertebrate species whose numbers have increased in recent years, causing their threat levels to be reduced (Hoffman et al. 2010). The rescue of the California condor (*Gymnogyps californianus*) is a leading example of this strategy (**Figure 23.17**). This great bird once ranged throughout much of North America, and by the nineteenth century, it was still distributed from British Columbia to Baja California. The condor population declined steeply between the 1960s and 1980s, however, reaching a low of 22 birds by 1982. The species became extinct in the wild in 1987, when the last birds were captured and brought to an ex situ facility in California for breeding (Ralls and Ballou 2004).

There are now nearly 400 California condors, some in the wild and some remaining in captivity. Increasing the population to this point has required careful genetic analysis, hand rearing of some chicks, and wide cooperation among zoos, managers of natural areas, hunters, and ranchers. An ultimate goal is to establish self-sustaining condor populations in the wild. One of the greatest remaining threats is lead poisoning from ammunition found in the carrion condors eat, which has prevented this goal from being met (Finkelstein et al. 2012). Other barriers to the condor's recovery include the negative health effects of ingesting plastic and other trash, West Nile virus, and genetic drift. Given all these risks and costs, is the recovery of the California condor worth all the effort that has gone into it? Without that effort, the species would now be extinct.

Ex situ conservation programs are taking place in zoos, special breeding facilities, botanical gardens, and aquariums all over the world. Such programs have allowed many species at risk of extinction to increase their numbers sufficiently to permit reintroduction into the wild. While ex situ programs play important roles in keeping our most threatened species from extinction, as well as in publicizing the plight of those species, they are expensive, and they can introduce a host of problems, such as exposure to disease, genetic adaptation to captivity, and behavioral changes (Snyder et al. 1996). Furthermore, as the case of the California condor shows, it can be difficult to restore self-sustaining populations in the wild. Could the funds dedicated to ex situ efforts be better spent on managing species in the wild or on securing land for the establishment of new protected areas—that is, for in situ conservation? Sometimes the answer is no, usually when populations have been reduced to critical levels or when not enough suitable habitat is available. But the question must always be asked.

Legal and policy measures support biological methods of protecting species and habitat

Conservation biologists seek to gain the best scientific information possible to inform decisions that will benefit the welfare of species or ecosystems. The process of making many of these decisions, however, is more of a societal than a scientific one and falls into the realm of public policy and communications. The outcome of a society's collective decisions on conservation issues can be seen in national and state laws, the policies set by natural resource agencies, and the work and policies of nongovernmental organizations. At times, these decisions are guided by global processes in the form of international treaties, agreements, and conventions. At other times, they are driven by grassroots efforts. The interplay between science and this composite of human decision-making entities is complex, but it is an integral part of any successful conservation effort.

In the United States, the most prominent legislation protecting species, the Endangered Species Act (ESA),

Figure 23.17 Ex Situ Conservation Efforts Can Rescue Species from the Brink of Extinction Ex situ efforts to save the California condor (*Gymnogyps californianus*) involve multiple steps. (A) To reduce inbreeding and increase the number of eggs that hatch successfully, a U.S. Fish and Wildlife Service biologist removes eggs from the wild (to be taken to an ex situ breeding facility) and replaces them with one egg from the San Diego Zoo. (B) At the San Diego Zoo, condor chick "Hoy" is being fed by a condor-feeding puppet to avoid its becoming acclimated to humans. (C) Two condors at the time of their release (spring 2000). The instrument in the right foreground is a scale from which condor weight can be read by telescope when a bird perches on it. (D) This adult, with a wingspan of 9 feet, was bred in captivity and later released.

has played a vital role in protecting many of the country's most threatened species. It was passed by Congress in 1973 to "provide a means whereby the ecosystems on which endangered and threatened species depend may be conserved, and to provide a program for the conservation of these species." The U.S. Fish and Wildlife Service and the National Marine Fisheries Service are charged with listing federally threatened and endangered species, identifying critical habitat for each species, drafting recovery plans, and carrying out actions necessary to increase abundances to target numbers.

The ESA currently protects more than 1,300 species native to the United States and another 570 from other countries. The ESA extends its influence beyond U.S. borders by regulating trade in endangered species as a result of an international treaty called the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). This treaty, which has been in place for nearly 40 years, regulates international trade in listed organisms and their parts. It mandates a virtual prohibition on trade in some species recognized to be endangered, while others, deemed to be less threatened, must be monitored in their home countries for indications that trade should be restricted. Currently, 183 countries have agreed to adhere to CITES regulations, and about 35,000 species receive some protection. While the treaty has the potential to be a key instrument in protecting species worldwide, enforcement of CITES regulations remains a difficult task for many governments.

The Convention on Biological Diversity, which most nations have signed (the most notable exception being the United States), is the outcome of the Earth Summit held in Rio de Janeiro in 1992. This agreement acknowledges declining biodiversity as a problem shared by all the world's people and establishes goals for actions to counteract it. For example, the agreement urges nations to document the biodiversity contained within their borders, identifies the rights of nations to benefit from patents derived from their biodiversity, and calls for mechanisms to protect biodiversity from genetically modified organisms. It has provided a fruitful structure for nations developing their own conservation plans and has served as a framework for bringing nations together to address global biodiversity losses.

The protection of biodiversity is also dependent on a wide array of national, state, and local regulations and policies that set restrictions on land development, call for environmental review prior to land disturbances, and manage harvest levels. There is a limit to the percentage of the landscape we will be able to place under protected status, so much of the world's biodiversity will continue to reside on private lands and working landscapes. Therefore, it is vital that we maintain a legal framework that will serve to protect the most critical components of biodiversity in those places, and that those laws and policies be crafted with the best available science to support them.

CONCEPT 23.5

Prioritizing species helps maximize the biodiversity that can be protected with limited resources.

Ranking Species for Protection

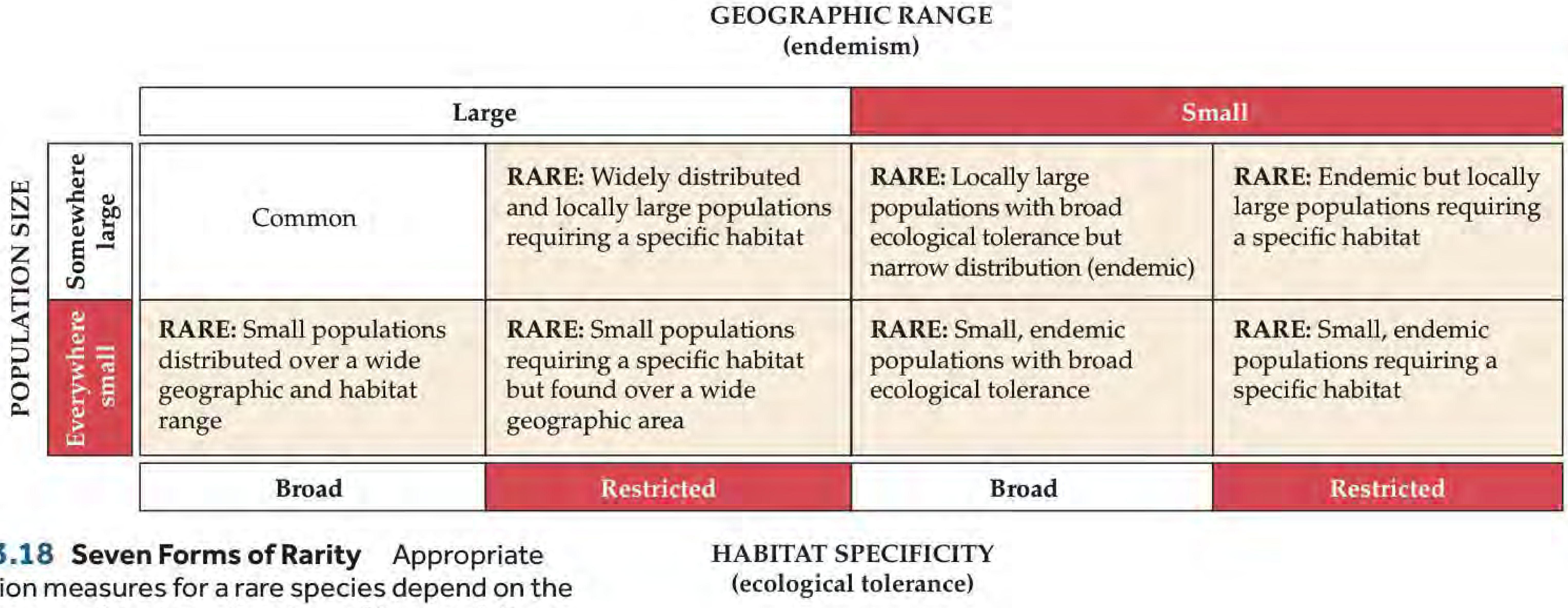
Conservation efforts can succeed. Indeed, an analysis concluded that conservation actions have reduced the rate of loss of threatened vertebrates by over 20% (Hoffman et al. 2010). But such successes are outweighed by the severity of ongoing threats. In the face of such need, how do we allocate the limited resources that are available for species conservation? Do we protect those species that are most threatened, or do we focus on those that play a substantial ecological role? And how should conservation biologists and policymakers decide which areas are the most critical to protect?

The rarest and the most rapidly declining species are priorities for protection

Many species have become rare only recently as a result of the threats we outlined earlier in this chapter. Other species may have always been rare. In either case, having a measure of how threatened a species is permits us to focus our efforts on those species that are most threatened: the rarest and the most rapidly declining. We may be able to postpone attending to species that are naturally low in abundance but not particularly threatened.

What do we mean by rarity, and how do we determine just how rare something is? To clarify the different concepts of rarity, we can use a matrix that sorts out whether a species has a wide or a narrow geographic range, whether it is broad or restricted in its habitat specificity, and whether its local populations tend to be small or large (**Figure 23.18**). There are some rare species, for example, that exist over a wide geographic area and are relatively broad in their habitat requirements, yet tend to occur in very small populations. Other rare species inhabit specific habitats within a narrow geographic range, but may have large populations in those specific locations (Rabinowitz et al. 1986). Conservation of these different types of rare species requires different approaches. Some species require small reserves to protect well-established populations; others require management practices that create habitat conditions suitable for a rare but geographically widespread species.

Objective, scientific assessment of the conservation status of species began in 1963 with the IUCN Red List (see Table 23.1). A parallel effort was developed in the United States by The Nature Conservancy, which established the Natural Heritage Program (now NatureServe)



GEOGRAPHIC RANGE (endemism)

POPULATION SIZE	Large		Small	
	Broad	**Restricted**	**Broad**	**Restricted**
Somewhere large	Common	**RARE:** Widely distributed and locally large populations requiring a specific habitat	**RARE:** Locally large populations with broad ecological tolerance but narrow distribution (endemic)	**RARE:** Endemic but locally large populations requiring a specific habitat
Everywhere small	**RARE:** Small populations distributed over a wide geographic and habitat range	**RARE:** Small populations requiring a specific habitat but found over a wide geographic area	**RARE:** Small, endemic populations with broad ecological tolerance	**RARE:** Small, endemic populations requiring a specific habitat

HABITAT SPECIFICITY (ecological tolerance)

Figure 23.18 Seven Forms of Rarity Appropriate conservation measures for a rare species depend on the size of its geographic range, the sizes of its populations, and its habitat specificity. (After Rabinowitz et al. 1986.)

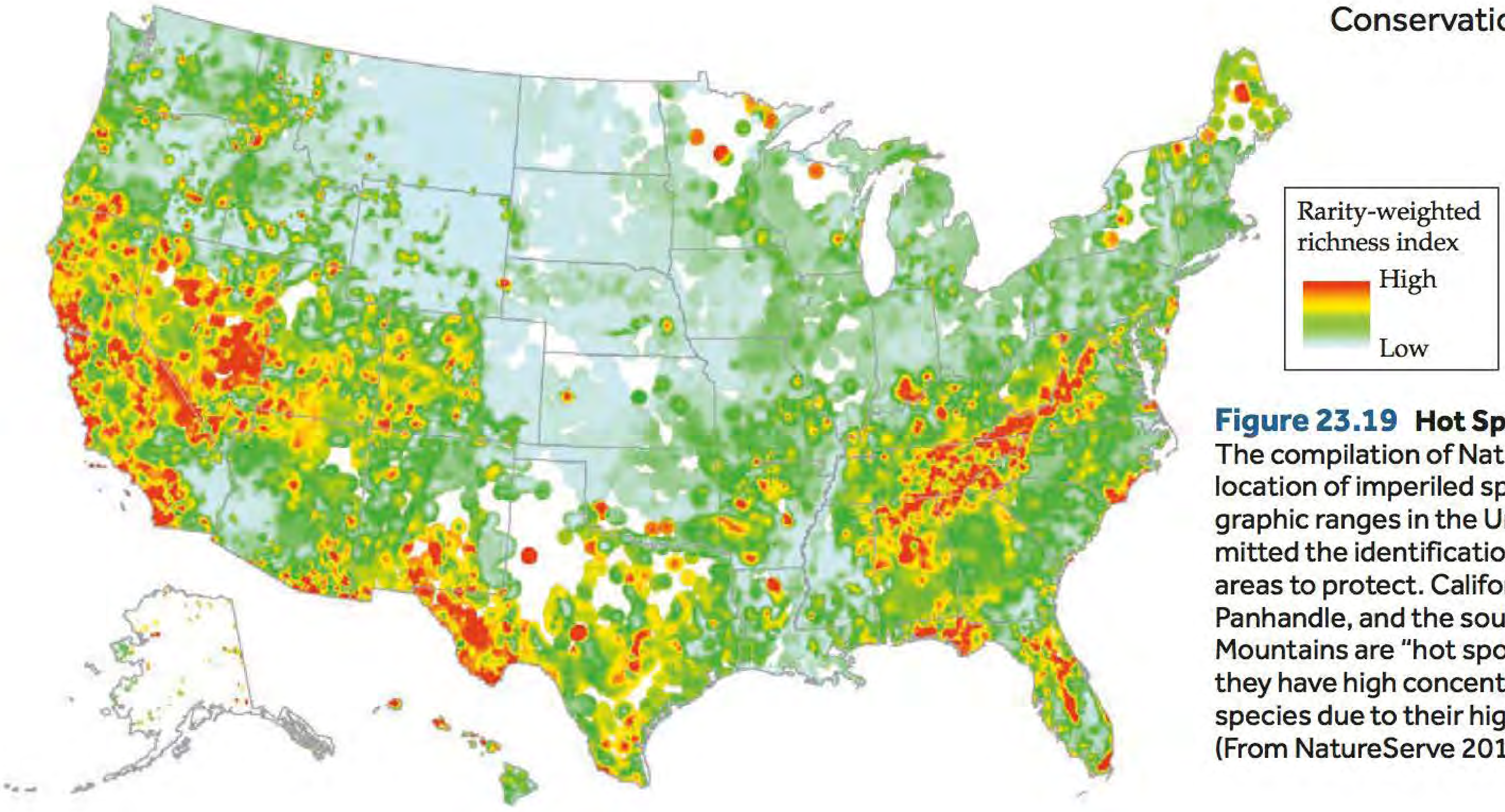


Figure 23.19 Hot Spots of Imperilment The compilation of NatureServe data on the location of imperiled species and their geographic ranges in the United States has permitted the identification of the most critical areas to protect. California, Hawaii, the Florida Panhandle, and the southern Appalachian Mountains are "hot spots" of imperilment—they have high concentrations of imperiled species due to their high rates of endemism. (From NatureServe 2013.)

in the early 1970s in order to assess the conservation status of U.S. species. Both organizations have developed a ranking structure that indicates how threatened a species is and an assessment protocol to determine its rank. The assessment protocol takes into account not only numbers of populations or individuals, but also the total geographic area the species occupies, the rate of its decline, and the threats it faces. Because of the challenge of creating a system that can be applied equally well to a skipper butterfly, a cycad, or a shark, and because the information available on rare species is often incomplete, both systems allow assessors to choose among different sets of criteria to decide whether a species is critically endangered, endangered, vulnerable, or under some lesser level of threat.

Such assessments of conservation status can be used to locate clusters of threatened species and thus identify areas that are critical to protect (**Figure 23.19**). They are frequently consulted when development projects are planned, and they are important for keeping the public aware of the degree of threat faced by Earth's biota. These databases are dynamic in that they can change as scientific information is updated: the conservation status assigned to a species can be downgraded if its numbers increase, or upgraded if its numbers decline.

Protection of surrogate species can provide protection for other species with similar habitat requirements

If we protect the habitat that is necessary for the red-cockaded woodpecker, as described in the Case Study, will we simultaneously provide protection for the gopher tortoise, Bachman's sparrow, Michaux's sumac, and other rare species that are dependent on the longleaf pine savanna ecosystem? Species may become conservation priorities not only because of their own conservation status, but also because of their capacity to serve as **surrogate species** whose conservation will serve to protect many other species with overlapping habitat requirements. Some surrogate species can help us garner public support for a conservation project; examples of such **flagship species** include charismatic animals such as the mountain gorilla (**Figure 23.20**). Other surrogate species are referred to as **umbrella species**, which we select with the assumption that protection of their habitat will serve as an "umbrella" to protect many other species with similar habitat requirements. Umbrella species are typically species with

Figure 23.20 A Flagship Species The mountain gorilla (*Gorilla beringei beringei*) is critically endangered in its highland forest habitat of central Africa. Only two populations remain in the wild, with a combined total of only 300 mature animals. Threats to their persistence include loss of habitat, hunting, and disease transmission from humans.

large area requirements, such as grizzly bears, or habitat specialists, such as the red-cockaded woodpecker. But they may also include animals that are relatively easy to count, such as butterflies (Fleishman et al. 2000). Some researchers prefer to choose not just one species, but several **focal species**, selected for their different ecological requirements or susceptibility to different threats, with the realization that by thus casting a broader net, we improve our chances of covering regional biodiversity with protection.

Methods have been devised and criteria established to allow for strategic selection of the one or several surrogate species that will best serve conservation aims (Favreau et al. 2006). Conservation biologists recognize, however, that surrogate species approaches are not without problems, and that the distribution or habitat requirements of any one species cannot capture all the conservation targets we may have.

A CASE STUDY REVISITED

Can Birds and Bombs Coexist?

As the longleaf pine ecosystem lost 97% of its area over the last several hundred years, the biological traits of the red-cockaded woodpecker that had worked well in the extensive pine savannas of the past turned out to be detrimental in its changing environment. Prime woodpecker habitat became fragmented, consisting of islands of usable habitat in an unsuitable landscape. As a result, the woodpecker's unusual habit of excavating cavities in living trees—a process that usually takes a year or more to complete—made the availability of cavities a limiting factor for woodpecker populations.

Jeff Walters and his colleagues tested the hypothesis that a lack of high-quality habitat was limiting the woodpecker's population growth, by constructing artificial nest cavities, placing them in clusters, and observing woodpecker behavior. They tried this strategy for two reasons. First, they clustered cavities together because red-cockaded woodpeckers are *cooperative breeders* (males born in previous years help their parents raise young) and each bird in a cooperative breeding group must have its own cavity. Second, the birds typically abandon cavity clusters after several years' use, primarily because of cavity entrance enlargement by other species or mortality of cavity trees, so there is a continual demand for cavity clusters (Harding and Walters 2002). The artificial cavity clusters constructed by the researchers were rapidly colonized, mostly by helper birds from the vicinity and young dispersing birds (Copeyon et al. 1991; Walters et al. 1992).

These results suggested that people could help the red-cockaded woodpecker increase its numbers by going out with drill, wood, wire, and glue and installing clusters of cavities within living longleaf pines (**Figure 23.21**). Indeed, these activities have proved a boon to woodpecker recovery. Aided by the construction of artificial cavities, the population of red-cockaded woodpeckers at Fort Bragg increased from 238 breeding groups in 1992 to 368 breeding groups in 2006. Cavity construction has also contributed to increased abundances of red-cockaded woodpeckers at other military bases, including Eglin Air Force Base (Florida), Fort Benning (Georgia), Fort Polk (Louisiana), Fort Stewart (Georgia), and Marine Corps Base Camp Lejeune (North Carolina). Similar successes have

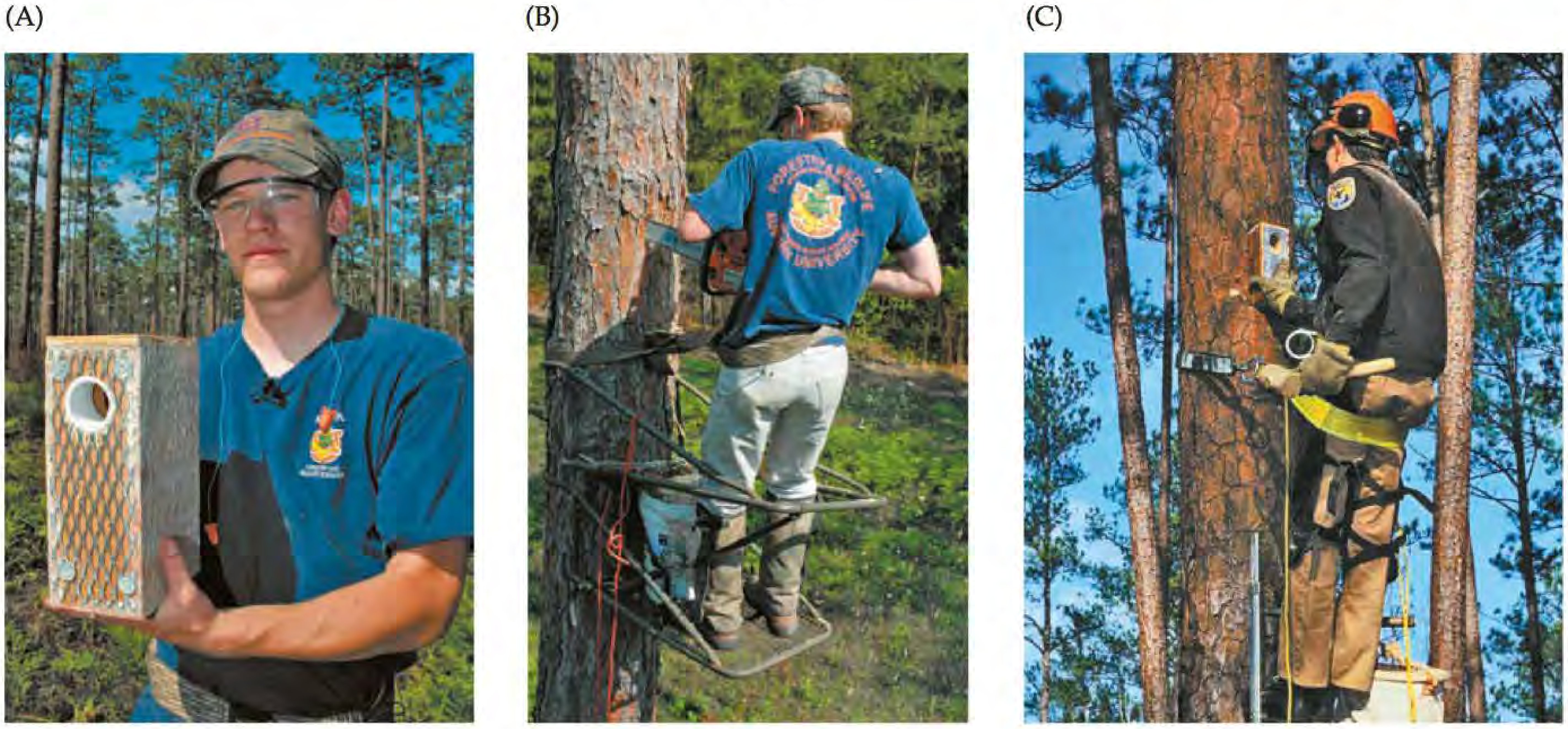

(A) (B) (C)

Figure 23.21 Construction and Installation of Artificial Nest Cavities Has Allowed Populations of Red-Cockaded Woodpeckers to Increase (A) An artificial nest cavity built for a red-cockaded woodpecker. (B) Cutting a hole in a living pine for the artificial nest cavity. (C) Installing the artificial nest cavity.

occurred at sites other than military bases. For example, when Hurricane Hugo hit the South Carolina coast in 1989, the population of red-cockaded woodpeckers in Francis Marion National Forest, previously home to 344 breeding groups, was severely reduced. The hurricane killed 63% of the birds, and another 18% died the following winter (Hooper et al. 2004). Within 2 years of the storm, however, national forest workers had installed 443 artificial cavities. This strategy averted a severe population decline; by 1992, the population had recovered to 332 breeding groups.

Now that managers have identified cavity construction and maintenance as a critical factor for the recovery of red-cockaded woodpeckers, they are obliged by the Endangered Species Act to continue doing it. This strategy is labor-intensive and expensive, but for now it is necessary for the red-cockaded woodpecker's continued existence. How long can we sustain this effort? Will we reach a point at which there is enough longleaf pine savanna that the woodpeckers will be able to maintain their own numbers without human assistance? We do not know the answers to these questions.

In the decades during which Walters and others have been researching the red-cockaded woodpecker, they have used many of the tools described in this chapter. Models of population dynamics have facilitated the identification of vulnerable stages in the woodpecker's life cycle. Genetic studies and modeling have focused attention on the threat of inbreeding. Field studies have demonstrated the need for prescribed burning to maintain the community structure required by the woodpeckers. Economic and sociological analyses have led to the development of a "safe harbor" program that makes endangered species management more acceptable to private landowners.

CONNECTIONS IN NATURE
Some Burning Questions

As we saw in Chapter 3, recurrent fires promote the establishment of savanna. Hence, to maintain red-cockaded woodpecker populations and the longleaf pine savannas on which they depend, fire is key—whether it is ignited naturally, accidentally by military training exercises, or intentionally under controlled conditions. Fire affects ecosystems at multiple scales, from the cellular and biochemical to the atmospheric. As with other regular forms of disturbance (see Concept 9.2), differences in the frequency of fires can affect the distributions and abundances of species, and those changes, in turn, along with changes in the physical environment, can affect the cycling of nutrients and water. Because fire affects communities at so many levels, prescribed burning is used as a management tool for conserving species in numerous ecosystems where fire has been a regular natural disturbance (**Figure 23.22**).

Figure 23.22 Prescribed Burning Is a Vital Management Tool in Some Ecosystems In the southeastern United States, regular burning is used to maintain the high plant biodiversity characteristic of the understory in pine savanna ecosystems. Many threatened species, including the red-cockaded woodpecker, rely on regular burning for their persistence. Here, US Fish and Wildlife Service firefighters monitor a prescribed burn intended to preserve habitat for the endangered Florida panther.

But the use of fire as a management tool can have unintended and undesirable ecological outcomes where nonnative invasive species are present. In some longleaf pine savannas in Florida, openings resulting from burning have provided favorable habitat for the establishment of cogongrass (*Imperata cylindrica*), an invasive plant from Asia. The presence of this grass, in turn, causes fires to burn hotter and more extensively. The consequences of these hotter fires are increased mortality of longleaf pine seedlings and native wiregrass, favorable conditions for further infiltration of cogongrass, and a resulting threat to the high levels of native plant diversity found in the understory of the longleaf pine savanna (Lippincott 2000). Land managers are faced with a dilemma: to burn or not to burn? The right question is more likely to be when to burn, and how often.

Adding people to the burning landscape further complicates matters. Throughout the southeastern United States, prescribed burns are taking place in a complex landscape where patches of forest are adjacent to peoples' homes and businesses. Convincing the public that these fires are necessary has required considerable outreach and public education. In the North Carolina Sandhills, the days for prescribed burns are chosen not only for safe conditions, but also with regard to wind direction so as to minimize the amount of smoke in population centers.

Here, as elsewhere, recognition of people as an integral component of the landscapes that must harbor all of nature's diversity has been a vital piece of the conservation picture. Establishing protected natural areas as sanctuaries for wildlife is an important part of the solution to the biodiversity crisis, but we must also do what we can to ensure that the vast majority of Earth's surface outside of protected areas is able to sustain both people's livelihoods and habitat for other species. This is a difficult challenge that will involve education, negotiation, legislation, and many creative approaches.

Summary

CONCEPT 23.1 Conservation biology is an integrative discipline that applies the principles of ecology to the protection of biodiversity.

- Conservation biology is the scientific study of phenomena that affect the maintenance, loss, and restoration of biodiversity.
- Biodiversity is important to human society because of our reliance on natural resources and ecosystem services that depend on the integrity of natural communities and ecosystems.
- With the growing awareness of accelerating losses of global biodiversity, ecologists saw a need for a separate discipline that would apply the principles of ecology to the preservation of species and ecosystems.
- Conservation biology is a scientific discipline instilled with the value of biodiversity.

CONCEPT 23.2 Biodiversity is declining globally.

- Earth is losing species at an accelerating rate, largely because of humanity's growing footprint on the planet.
- Extinction is the end point of incremental biological decline as species lose individuals and populations and become increasingly vulnerable to the problems of small populations.
- Earth's biota is becoming increasingly homogenized because of a rise in generalist species and a decline in specialist species.

CONCEPT 23.3 Primary threats to biodiversity include habitat loss, invasive species, overexploitation, pollution, disease, and climate change.

- Habitat degradation, fragmentation, and loss are the most important threats to biodiversity.
- Invasive species degrade local habitats by preying on or competing with native species and by altering ecosystem properties.
- Overexploitation of selected species has large effects on communities and ecosystems.
- Other factors that erode the viability of populations and contribute to losses of biodiversity include air and water pollution, diseases, and global climate change.

CONCEPT 23.4 Conservation biologists use many tools and work at multiple scales to manage declining populations.

- Genetic analyses have been used to understand and manage genetic diversity within rare species, as well as in forensic analyses of illegally harvested organisms.
- Population viability analysis (PVA) is an approach that uses demographic models to assess extinction risks and evaluate proposed management actions.
- Ex situ conservation, which involves taking organisms from the wild into human care, is a last-resort measure to rescue species on the brink of extinction.
- Laws, policies, and international treaties are vital supplements to biological methods of protecting species and habitat.

CONCEPT 23.5 Prioritizing species helps maximize the biodiversity that can be protected with limited resources.

- Conservation biologists identify those species of the highest priority for protection—the rarest and the most rapidly declining species—by assessing numbers of individuals and populations, total geographic area occupied, rates of decline, and the degree of threat faced.
- Identification of surrogate species can provide protection for other species with similar habitat requirements.

Review Questions

1. What are the principal threats to biodiversity? Describe some examples in which multiple threats have contributed to decline of a species.
2. Describe tools that conservation biologists use to protect biodiversity at the level of genes and populations.
3. What is the difference between a species determined to be endangered by the Natural Heritage/NatureServe program and one that is listed as endangered under the U.S. Endangered Species Act? What are the consequences for management of each?
4. Identify five imperiled species that live in your region, including a plant, a mammal, a bird, a fish, and an invertebrate. Are any of these species endemic to your region? For each species you have identified, try to find out whether it was rare prior to human settlement of the region. What threats does this species face today? What is being done to protect this species? Based on the ecological knowledge you have gained, what questions do you think should be researched to aid in the recovery of the species? (Much of this information is available at www.natureserve.org.)

Hone Your Problem-Solving Skills

With the realization of declining abundances of fish, greater attention has been given to demographic approaches to sustainable harvests. Here we present a hypothetical example of such an approach. A species of commercial fish lives for 4 years, with harvestable fish occurring only in the 2- and 3-year-old age classes. The growth rate of the population can be modeled using a life table approach such as the one found in Tables 10.3 and 10.4. In the absence of harvest, the fish exhibits the following demographic properties:

AGE (x)	SURVIVAL RATE (S_x)	SURVIVORSHIP (l_x)	FECUNDITY (F_x)
0	0.40	1.00	0
1	0.60	0.40	0
2	0.80	0.24	2
3	0.70	0.19	4
4	0	0.13	2

1. Starting with the following distribution of individuals in age cohorts, plot or tabulate the population growth for a population of this fish species for 10 years: $n_0 = 30$, $n_1 = 30$, $n_2 = 20$, $n_3 = 10$, $n_4 = 10$ (initial total of 100 individuals).
2. Project the same population growth if 60% of the 2- and 3-year-old cohorts are harvested for commercial use, by adjusting the survival rates. Is this level of harvest sustainable, that is, will the population be able to maintain a relatively stable size under these conditions indefinitely?
3. Now project the population growth if 40% of the 2- and 3-year-old cohorts are harvested for commercial use, and estimate whether this rate of harvest is sustainable. Try different combinations of fecundity and survival within the different age cohorts to consider how these factors influence the sustainability of populations under pressure from commercial harvest.

ON THE COMPANION WEBSITE

ecology4e.sinauer.com

The website includes companions to all of the Analyzing Data exercises, Online Quizzes, Flashcards, Suggested Readings, and more. In addition, the following resources are available for this chapter:

Hands-On Problem Solving

23.1 Not Dead Yet: Recovery of Endangered Species

24 Landscape Ecology and Ecosystem Management

KEY CONCEPTS

CONCEPT 24.1 Landscape ecology examines spatial patterns and their relationship to ecological processes.

CONCEPT 24.2 Habitat loss and fragmentation decrease habitat area, isolate populations, and alter conditions at habitat edges.

CONCEPT 24.3 Biodiversity can best be sustained by large reserves connected across the landscape and buffered from areas of intense human use.

CONCEPT 24.4 Ecosystem management is a collaborative process with the maintenance of long-term ecological integrity as its core value.

Wolves in the Yellowstone Landscape: A Case Study

The Greater Yellowstone Ecosystem (GYE) both symbolizes the soul of the American wilderness and encapsulates the challenges of managing public lands. The landscape is shaped by a complex of natural elements unique to this region: volcanic eruptions, geothermal activity, glaciers, and repeated fires, sometimes on a massive scale. In addition, the interplay between herbivorous ungulates and their predators has the potential to impact the landscape, including the vegetation and landforms. All of these factors have contributed to the mosaic of forests, meadows, grasslands, lakes, and rivers that characterize the GYE.

Prior to the early twentieth century, wolves were important predators in the GYE, but extermination programs lead to their local extinction. After 70 years of absence, wolves were reintroduced into the GYE between 1995 and 1997 from populations in Canada and northwestern Montana. Wolves hunt among a smorgasbord of ungulates and other prey (**Figure 24.1**). The reintroduction of wolves was the culmination of years of research effort and hotly contested policy debate, with vociferous objection from some residents of the region. Twenty years later, its ecological consequences have proved to be multifaceted and profound, and public opinion has become generally more favorable. Wolf reintroduction is perceived as restoring an important natural element to the GYE.

But how "wild" and natural is it? Larger in area than the state of West Virginia, the GYE includes two national parks and seven national forests as well as other public and private lands (**Figure 24.2**). The region is actively managed by more than 25 different state and federal agencies as well as private corporations, nongovernmental organizations, and private landowners. Decisions about the use of its land and natural resources are complex and often uncoordinated, yet when considered together, these decisions determine which species will or will not be sustained by the ecosystem (Parmenter et al. 2003).

Despite its fragmented management, the GYE is often perceived as one of the most biologically intact regions in North America. It sustains seven species of native

Figure 24.1 A Top Predator Returns A showdown between a pack of wolves (*Canis lupus*) and a cow moose and calf (*Alces alces*). After nearly 70 years of absence, wolves were reintroduced in 1995 to Yellowstone National Park, where they are now the main predators of moose.

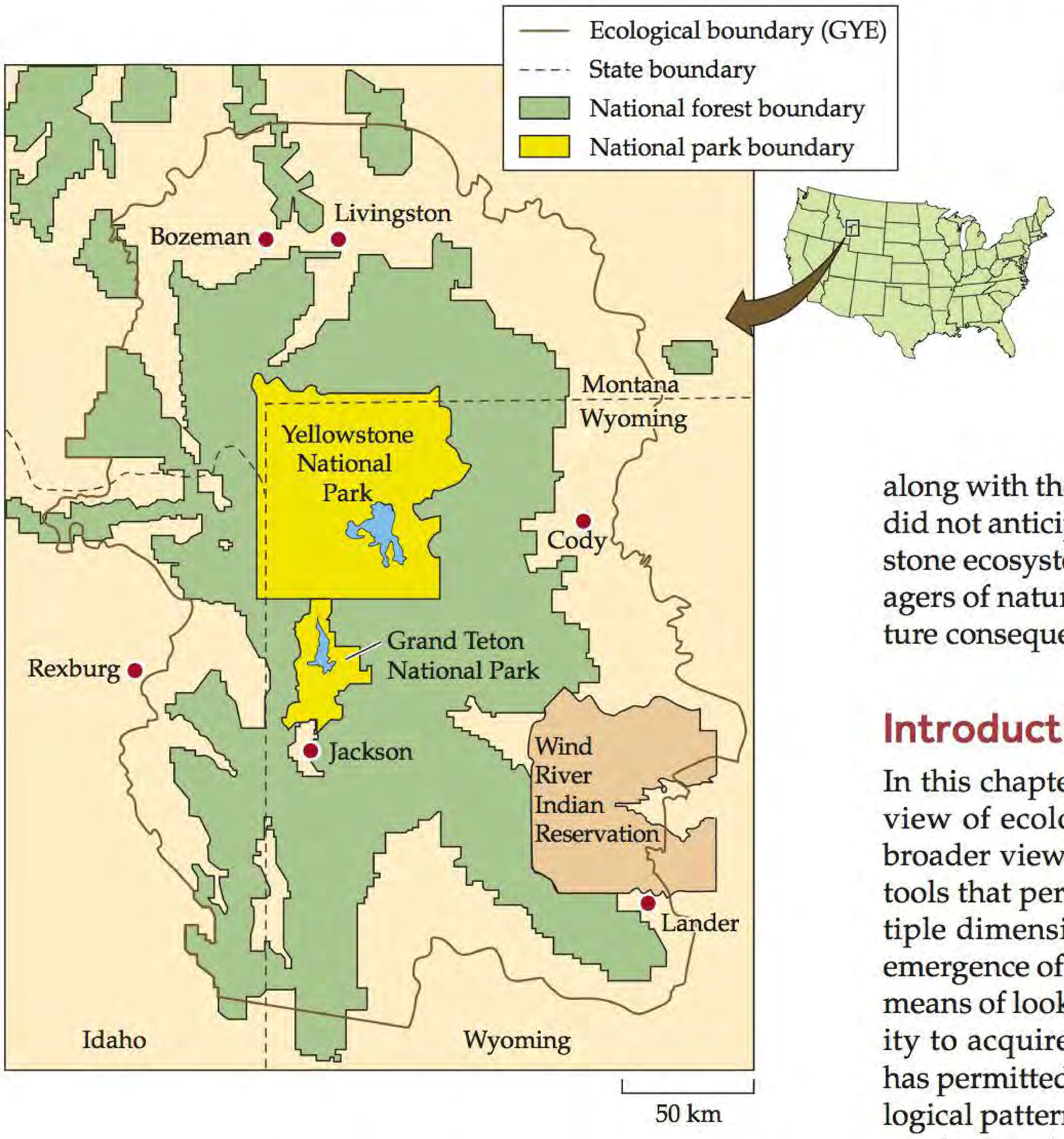


Figure 24.2 The Greater Yellowstone Ecosystem The Greater Yellowstone Ecosystem contains Yellowstone and Grand Teton National Parks, seven different national forests, and land managed by the Bureau of Land Management, as well as private lands. (After Parmenter et al. 2003.)

ungulates and five large carnivore species. Understanding how these predator and prey populations interact, and how their abundances affect the whole ecosystem, has been a persistent challenge to ecologists who study the GYE, particularly in light of a century of management of wildlife populations. After wolves were eradicated in the mid-1920s, there were concerns that elk were overgrazing meadows in the northern part of the park. The elk population was regulated from the 1920s to the late 1960s by exporting animals to elk farms and by culling. In 1968, a new policy of "natural regulation" was implemented. The elk population nearly quadrupled over a 30-year period and suppressed the plants they fed on. The reintroduction of wolves has not only reduced the elk population, but has also affected the populations of many other species. How?

To start to answer that question, let's go back to the 1950s, when ecologists noticed that beavers had become scarce in Yellowstone National Park. Gradually, it became clear that the cause was increased elk herbivory on the beavers' preferred food plants, willow and aspen. But a whole suite of other species depend on beaver ponds for their own persistence, and their abundances had declined along with the beavers'. The decision to eradicate wolves did not anticipate these ecological changes to the Yellowstone ecosystem. How can ecologists of today help managers of nature reserves make decisions that will take future consequences into account?

Introduction

In this chapter we will broaden the spatial scope of our view of ecology to take a landscape perspective. This broader view is facilitated by a powerful assemblage of tools that permit us to monitor the environment in multiple dimensions and at many scales. For example, the emergence of aerial photography gave ecologists a ready means of looking at "the big picture." Similarly, our ability to acquire images of Earth through remote sensing has permitted the interpretation of many large-scale ecological patterns, including global patterns of net primary production (see Ecological Toolkit 20.1). The use of geographic information systems (GIS), methods used to visualize and analyze spatial data, has become standard in landscape planning efforts, whether for urban development or for conservation (**Ecological Toolkit 24.1**). In the field, handheld global positioning systems (GPS) have permitted ecologists to document precise locations and integrate them with other landscape variables through GIS. Radiotelemetry has greatly enhanced our ability to follow animal movements and migration patterns, again with the help of GIS. And our ability to analyze all this information is constantly growing, thanks to better computers and new statistical methods of spatial analysis.

We saw in Concept 23.3 that habitat loss, fragmentation, and degradation are primary causes of the current declines in biodiversity. In this chapter, we'll see how the tools and methods of landscape ecology are used to address biodiversity declines at the landscape and ecosystem scales. Because protected natural areas are at the heart of conservation strategies, we will also consider how conservation biologists identify and design them to maximize their effectiveness. Finally, we'll examine how ecosystem management integrates ecological principles with social and economic information to help guide decisions about land and water use.

ECOLOGICAL TOOLKIT 24.1

Geographic Information Systems (GIS)

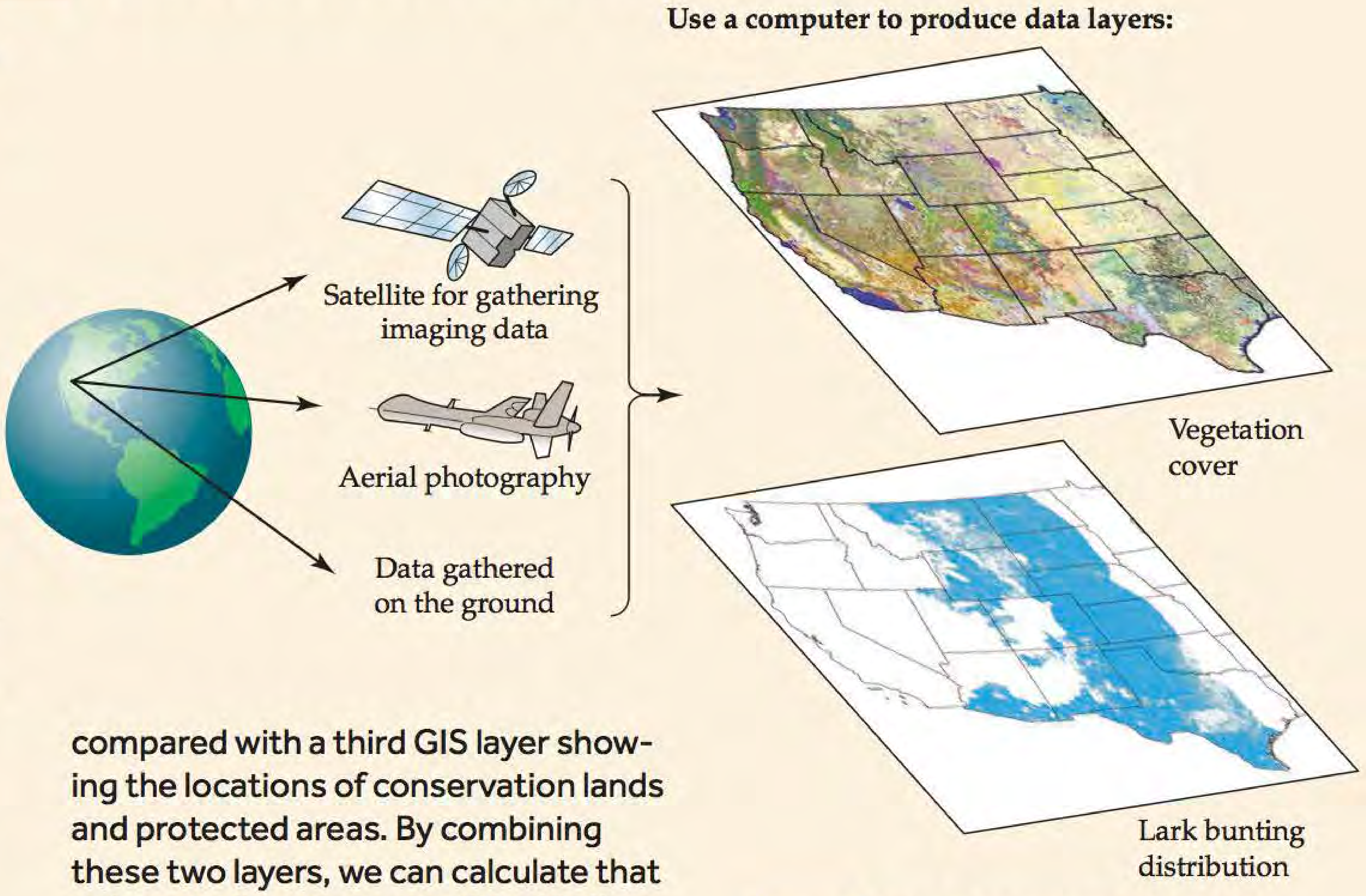


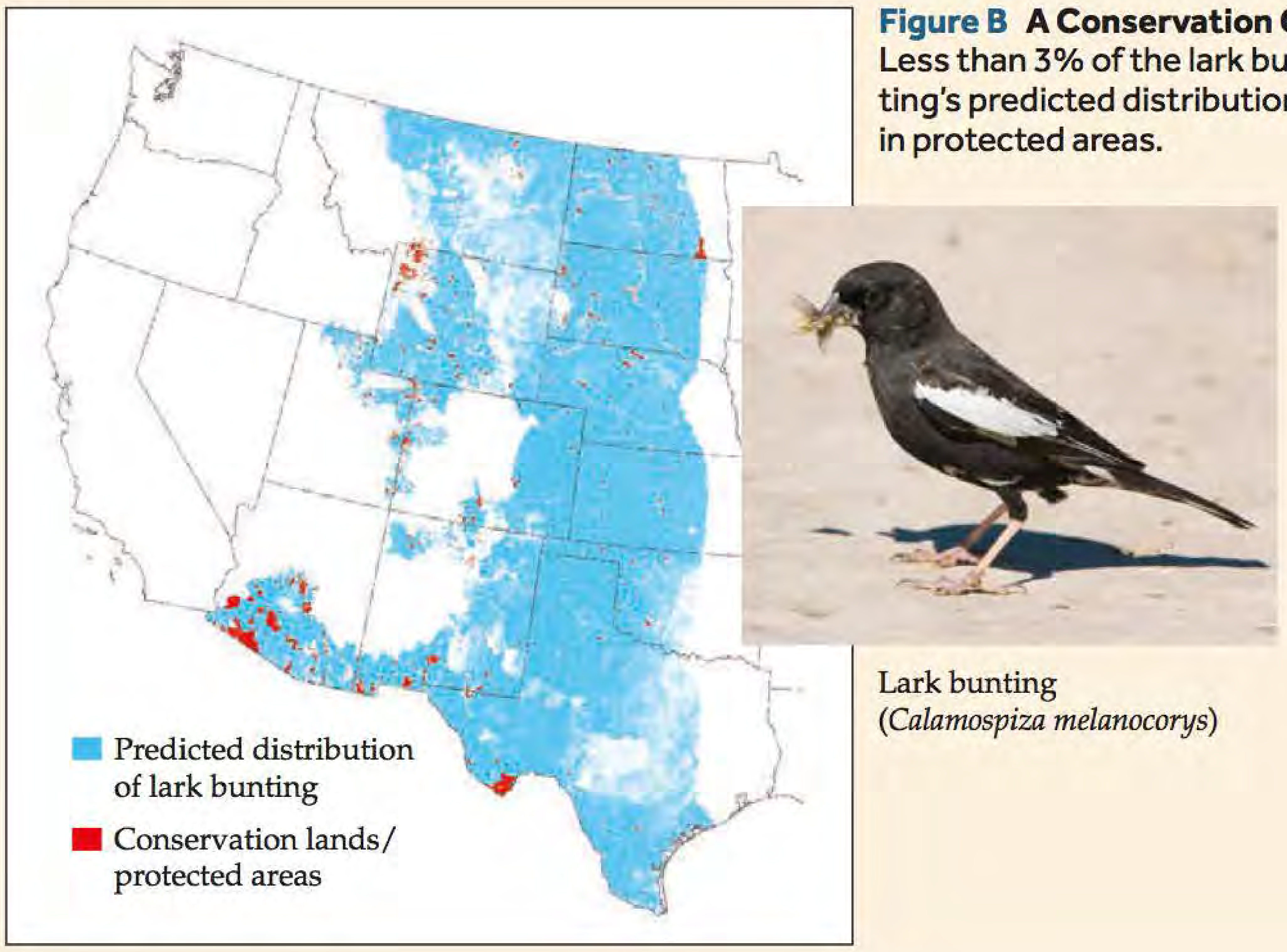
Figure A **GIS Integrates Spatial Data from Multiple Sources**

Geographic information systems (GIS) are computer-based systems that allow the storage, analysis, and display of data pertaining to specific geographic areas. The data used in GIS are derived from multiple sources, including aerial photographs, satellite imagery, and ground-based field studies (**Figure A**). Examples of such data include rainfall, elevation, and vegetation cover at specific locations. Each of these and many other variables may be used in a particular application of GIS—but whatever variables are used, the data are keyed to or referenced by spatial or geographic coordinates so that they can be assembled into a multilayered map.

Layers of mapped data can be put together in ways that help to address particular questions. We'll illustrate this process with an approach often used in conservation biology, called *gap analysis*. The acronym GAP refers to the Gap Analysis Program, a U.S. Geological Survey program whose mission is to help prevent biodiversity decline by identifying species and communities that are not adequately represented on existing conservation lands.

The lark bunting (*Calamospiza melanocorys*) is one such species. It depends on prairie habitat for its breeding grounds, but much of this habitat has been destroyed by conversion to agriculture. As a result, populations of the lark bunting have been declining by an average of 1.6% per year over the past 40 years, making it a species of conservation concern (U.S. Fish and Wildlife Service 2008).

For the lark bunting, or any other species, gap analysis is a two-step process. First, data on vegetation cover (see the top GIS layer in Figure A) and on other environmental conditions required or preferred by the lark bunting are used to predict its geographic distribution (the second GIS layer in Figure A). Next, that predicted distribution is compared with a third GIS layer showing the locations of conservation lands and protected areas. By combining these two layers, we can calculate that only a small percentage of the bird's distribution is protected (**Figure B**). Such information is critical to decisions about what lands should be protected to prevent future losses of biodiversity. (See **Web Extension 24.1** for a second example of GIS use in conservation biology.)



Lark bunting (*Calamospiza melanocorys*)

Figure B **A Conservation Gap** Less than 3% of the lark bunting's predicted distribution is in protected areas.

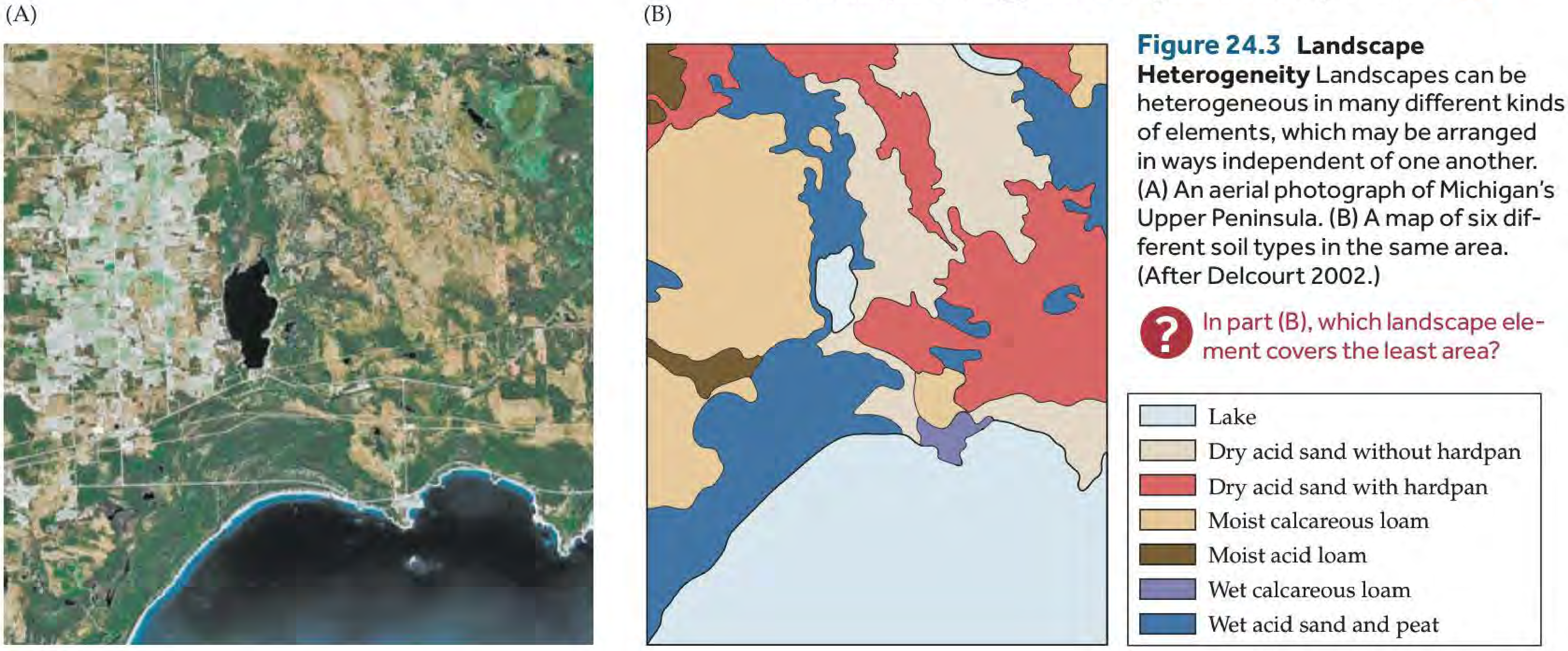


Figure 24.3 Landscape Heterogeneity Landscapes can be heterogeneous in many different kinds of elements, which may be arranged in ways independent of one another. (A) An aerial photograph of Michigan's Upper Peninsula. (B) A map of six different soil types in the same area. (After Delcourt 2002.)

? In part (B), which landscape element covers the least area?

CONCEPT 24.1
Landscape ecology examines spatial patterns and their relationship to ecological processes.

Landscape Ecology

Landscape ecology is a subdiscipline of ecology that emphasizes the causes and consequences of spatial variation across a range of scales. As such, landscape ecologists document observed spatial patterns—including those that occur across broad geographic regions—and study how those patterns affect and are affected by ecological processes. They are interested in the spatial arrangement of different *landscape elements* across Earth's surface. Examples of landscape elements include patches of forest surrounded by pasture, or lakes scattered across a large region of forest. At smaller spatial scales, individual creosote bushes in a desert, or areas of a certain soil type, could be considered landscape elements. These elements are arranged certain ways in space. As we will see, the spatial pattern of landscape elements can influence what species live in an area, as well as the dynamics of ecological processes such as disturbance and dispersal.

A landscape is a heterogeneous area composed of a dynamic mosaic of interacting ecosystems

A **landscape** is an area in which at least one element is spatially heterogeneous (varies from one place to another) (**Figure 24.3**). Landscapes can be heterogeneous either in what they are composed of—for example, twelve different vegetative cover types versus only three—or in the way their elements are arranged—such as many small patches arranged regularly over the landscape versus a few large patches. Ecologists often refer to this composite (or pattern) of heterogeneous elements that make up a landscape as a **mosaic**.

Landscapes often include multiple ecosystems. The different ecosystems that make up a landscape are dynamic and continually interacting with one another. These interactions may occur through the flow of water, energy, nutrients, or pollutants between ecosystems.

There is also biotic flow between habitat patches in the mosaic as individuals or their gametes (e.g., pollen) move between them (Forman 1995). For such movement to occur, patches of the same habitat type must be connected to one another, or the surrounding habitat (the *matrix*) must be of a type through which dispersal is possible (**Figure 24.4**). In Australia, for example, rats regularly

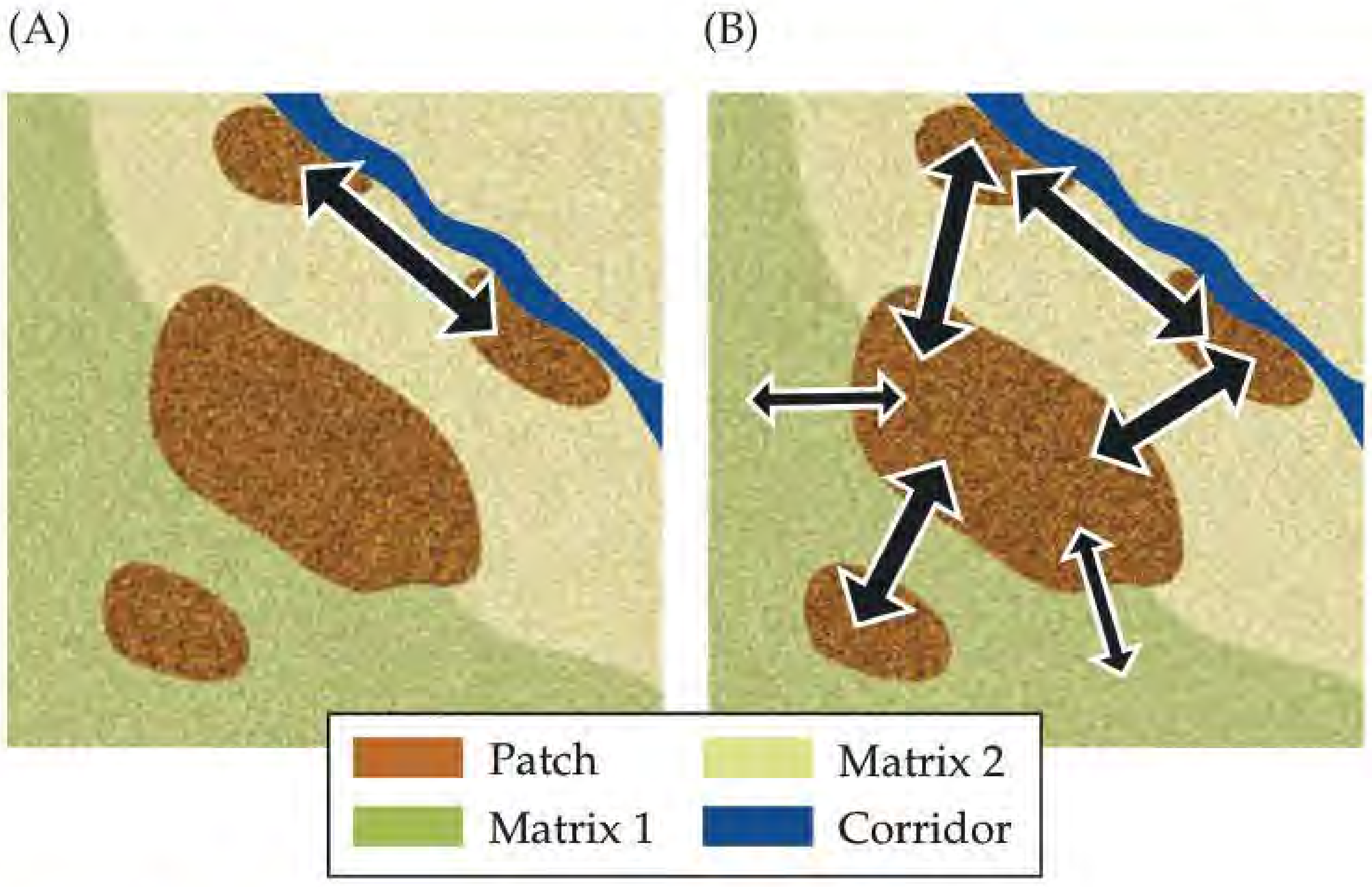


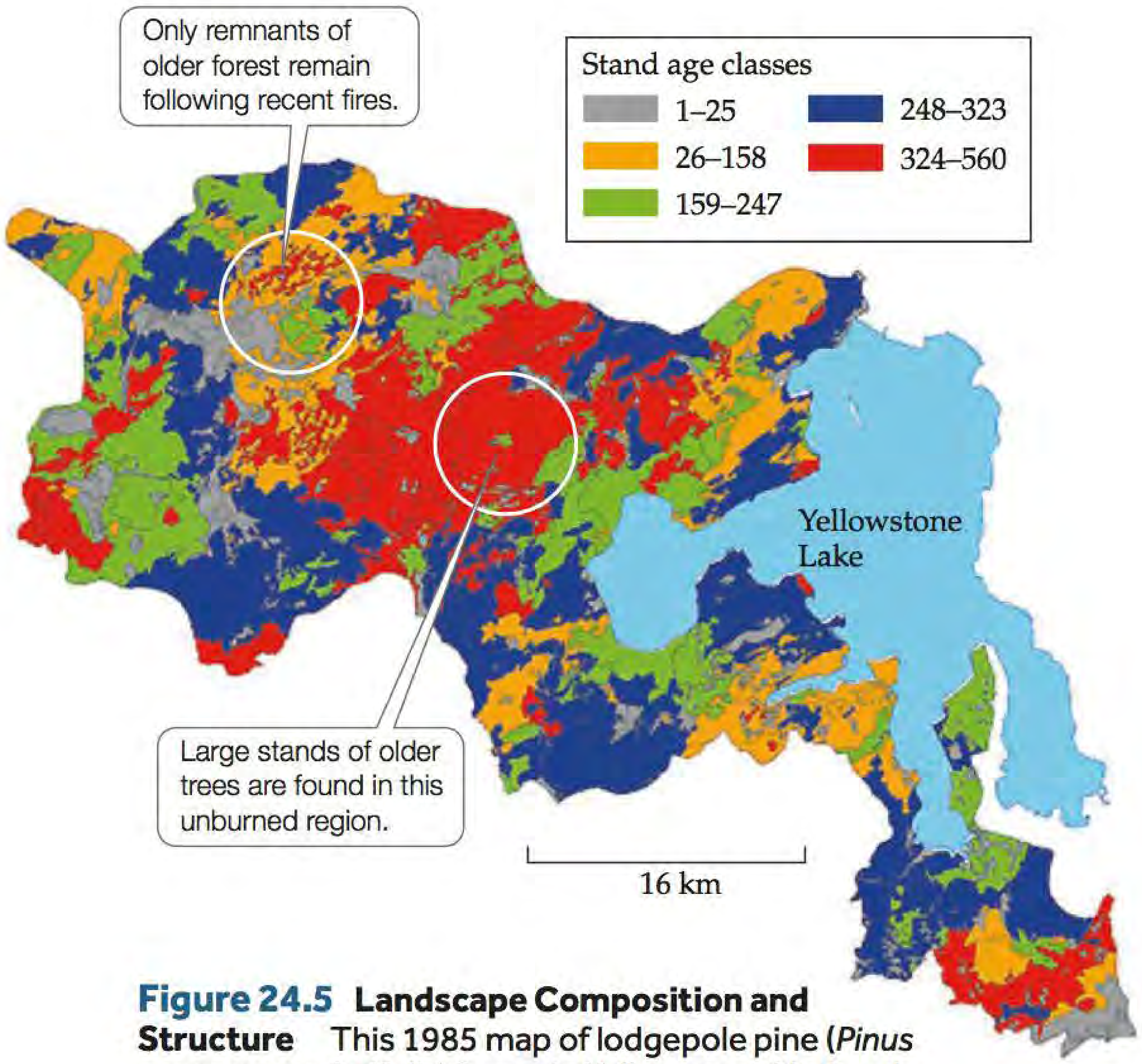
Figure 24.4 Movements Across the Landscape Movements between adjacent landscape elements may occur frequently (thicker arrows) or rarely (thinner arrows). (A) Exchange between patches of the same type occurs frequently if a corridor that allows movement connects the patches. (B) Exchange between patches of the same type occurs frequently, but exchange with the matrix occurs only rarely. (After Hersperger 2006.)

? Do organisms move more freely across the matrix in (A) or in (B)? Explain.

leave patches of forest habitat to forage in adjacent macadamia nut plantations (a part of the surrounding matrix). As a result, nut losses along plantation edges adjacent to forests are greater than along edges adjacent to grasslands or agricultural fields (White et al. 1997).

Next, let's focus in more detail on two aspects of landscape heterogeneity: how it is described, and the scale at which it is studied.

DESCRIBING LANDSCAPE HETEROGENEITY The heterogeneity that we see in landscapes can be described in terms of composition and structure. **Landscape composition** refers to the kinds of elements or patches in a landscape, as well as to how much of each kind is present. These elements are defined by the investigator and are influenced by the source of data used. In an example from Yellowstone National Park, researchers designated five different age classes of lodgepole pine forest using ground-based fieldwork, aerial photographs, and GIS (Tinker et al. 2003). The composition of the landscape in **Figure 24.5** can thus be quantified by counting the kinds of elements in the mapped area (five in this case), by calculating the proportion of the mapped area covered by each kind of element, or by measuring the diversity and dominance of the different landscape elements much as one does for species, using a measure such as the Shannon index (described in Concept 16.2).



Only remnants of older forest remain following recent fires.

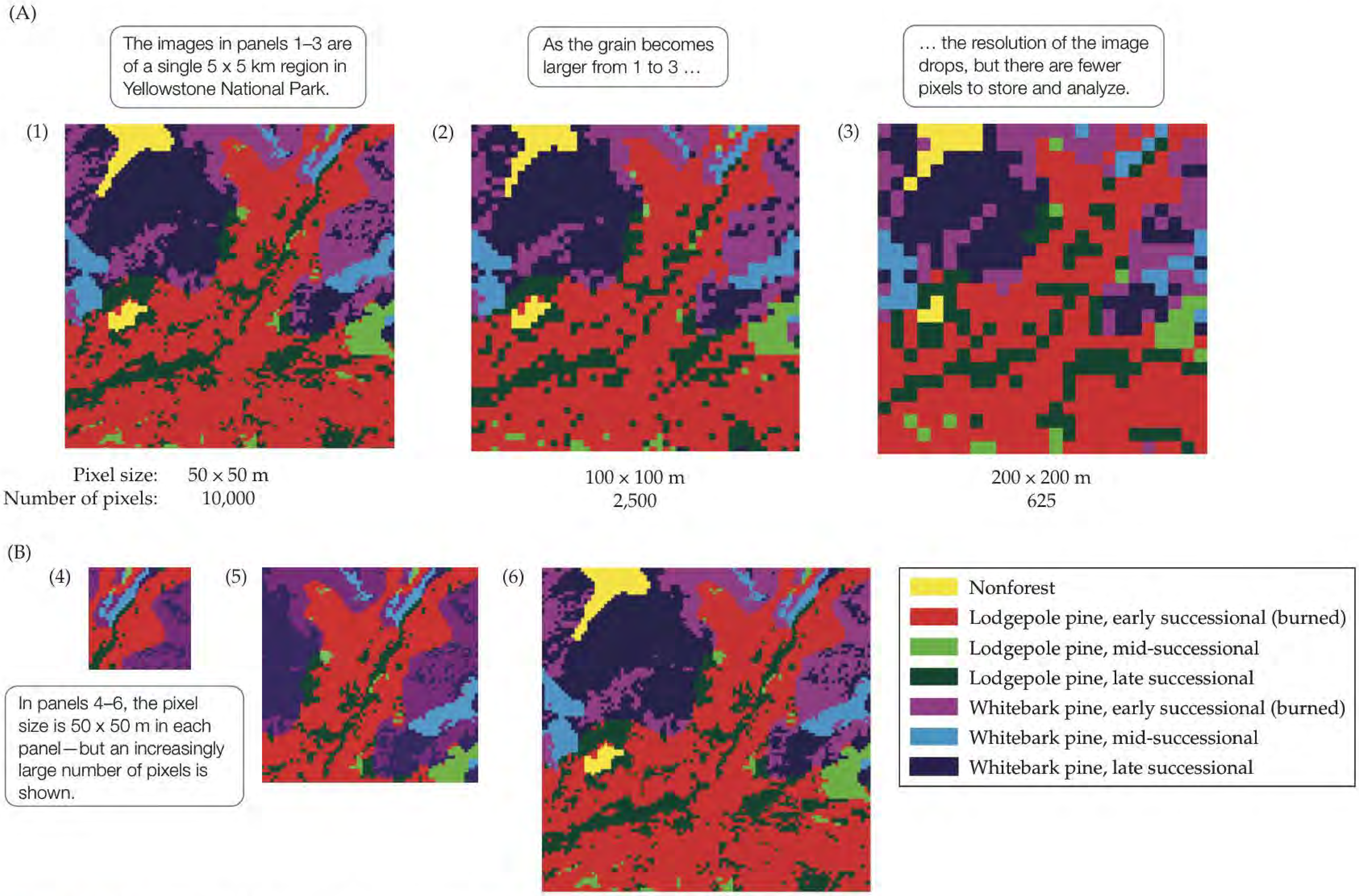
Large stands of older trees are found in this unburned region.

Figure 24.5 Landscape Composition and Structure This 1985 map of lodgepole pine (*Pinus contorta* var. *latifolia*) forest in Yellowstone National Park shows five different age classes of forest. Structural complexity varies across the landscape, as seen in the varying degree of natural fragmentation. (From Tinker et al. 2003.)

If we note that one portion of a landscape is more *fragmented* than another (i.e., broken up into distinct compositional units), we are comparing **landscape structure**: the physical configuration of the different elements that compose the landscape. In Figure 24.5, we can see that some parts of the landscape contain large contiguous blocks of older forest, while other parts are more fragmented and contain smaller patches of forest with a variety of different ages. Landscape ecologists quantify landscape structure primarily by addressing whether the landscape is characterized by large or small patches, how aggregated or dispersed the patches are, whether the patches are simple or complicated in their shape, and how fragmented the landscape is (Turner et al. 2001). Quantitative analyses of landscape structure allow us to compare one landscape with another and to relate landscape patterns to ecological processes and to the dynamics of landscape change. For example, Tinker and colleagues (2003) were able to use the measures of landscape structure that they derived for Yellowstone to compare the natural, fire-caused fragmentation within the park with fragmentation caused by clear-cutting in adjacent national forests. Logging created greater heterogeneity relative to the landscape primarily impacted by fire, with important implications for differences in population and community processes between the two landscape management types.

THE IMPORTANCE OF SCALE Considerations of scale cannot be ignored in landscape ecology. A landscape may be heterogeneous at a scale important to a tiger beetle, but homogeneous to a warbler or moose. The scale at which we choose to study a landscape determines the results we will obtain. Part of landscape ecology, therefore, is dedicated to understanding the implications of scale.

Scale, the spatial or temporal dimension of an object or process, is characterized by both grain and extent. **Grain**, which is the size of the smallest homogeneous unit of study (such as a pixel in a digital image), determines the resolution at which we view the landscape (**Figure 24.6A**). The selection of grain will affect the quantity of data that must be manipulated in analysis: using a large-grained approach may be appropriate when one is looking at patterns at a regional to continental scale. **Extent** refers to the area or time period encompassed by a study. Consider how differently we might describe the composition of a landscape depending on how we define its spatial extent. Panel 4 of **Figure 24.6B**, for example, shows little late successional whitebark pine, while panel 6 contains a considerable area



The images in panels 1–3 are of a single 5 x 5 km region in Yellowstone National Park.

As the grain becomes larger from 1 to 3 …

… the resolution of the image drops, but there are fewer pixels to store and analyze.

In panels 4–6, the pixel size is 50 x 50 m in each panel—but an increasingly large number of pixels is shown.

Figure 24.6 Effects of Grain and Extent (A) Panels 1–3 show the effect of increasing grain, measured here as pixel size. (B) Panels 4–6 show the effect of increasing extent. (After Turner et al. 2001.)

? The grain in panel 1 of part (A) is identical to the grain in which of the panels of part (B)?

of it (Turner et al. 2001). There may be natural or human-created boundaries that determine the extent of a study, or they may be defined by the researcher.

Ecosystem and landscape studies considering questions impacted by scale must also determine how processes scale up or down. For example, a researcher studying carbon exchange at the landscape level needs to know how leaf-based measurements of CO_2 exchange scale up to the whole plant, the ecosystem, and ultimately the mosaic of ecosystems that make up the landscape. This example shows the importance of connecting processes across different scales. Ecologists have developed methods to analyze how patterns and phenomena at one scale affect those occurring at either larger or smaller scales (see Levin 1992).

Landscape patterns affect ecological processes

Landscape structure plays an important role in ecological dynamics. For example, it can affect whether and how animals move and can therefore influence rates of pollination, dispersal, or consumption. Mickaël Henry and his associates studied the movements of the fruit-eating bat *Rhinophylla pumilio* in a tropical forest in French Guiana that had been fragmented by the construction of a reservoir. Using landscape metrics that quantified the degree of patch connectivity at their sampling sites, they found that more isolated forest fragments were less likely to be visited by bats, even if they contained abundant food resources (Henry et al. 2007). Thus, the landscape structure affected bat foraging behavior. Furthermore, because frugivorous bats disperse plant seeds, it is also likely that landscape structure affected the dispersal of the plants that the bats fed on.

Landscape structure also influences biogeochemical cycling. Ecosystem ecologists have identified biogeochemical "hot spots" where chemical reaction rates are higher than in the surrounding landscape. Many such hot

Figure 24.7 The Bog Fritillary Butterfly The travel patterns of these butterflies (*Proclossiana eunomia*) are influenced by features of the surrounding landscape. Butterflies will hesitate to leave the patches they inhabit if there is not another suitable habitat patch nearby, but they will traverse a matrix of unsuitable habitat when the next patch is close.

spots are found at the interfaces between terrestrial and aquatic ecosystems (McClain et al. 2003), but other factors may also play a part. For example, Kathleen Weathers and her colleagues found that inputs of sulfur, calcium, and nitrogen from atmospheric deposition were higher at forest edges than in forest interiors, primarily as a result of greater interception of airborne particles by the denser and more complex vegetation typically found at a forest edge. The fragmented forests that typically surround urban areas may therefore be substantially influenced by atmospheric inputs of pollutants and nutrients. This finding has implications for soil microbial dynamics, plant growth, and animal communities in the edges of these fragments (Weathers et al. 2001). We will discuss other such "edge effects" in Concept 24.2.

Habitat patches typically vary in both quality and resource availability. This variation can affect the diversity and population densities of the species inhabiting each patch, the time animals spend foraging in a patch, and the movement of organisms between patches. Patch boundaries, connections between patches, and the matrix between patches can also affect population dynamics, both within and among patches. For example, Schtickzelle and Baguette studied the movement patterns of the bog fritillary butterfly (*Proclossiana eunomia*) across fragmented landscapes in Belgium (**Figure 24.7**). Where patches of suitable butterfly habitat were aggregated, female butterflies crossed readily from patch to patch. However, where the habitat was more fragmented and there was a wider distance of matrix to cross, the butterflies were less likely to leave a patch (Schtickzelle and Baguette 2003).

While ecological processes are influenced by landscape patterns, landscape patterns are in turn influenced by ecological processes. Large grazing mammals, for example, often shape the landscapes they inhabit. The effects of moose (*Alces alces*) on Isle Royale in Lake Superior have been studied through the use of exclosures since the 1940s. These studies have shown that high rates of browsing by moose depress net primary production, not just directly through the removal of biomass, but also indirectly by decreasing nitrogen mineralization rates and litter decomposition rates. Moose browsing also shifts the tree species composition toward spruce, which in turn influences rates of biogeochemical processes (Pastor et al. 1988). The moose are thus both responding to and shaping the landscape. At a broader scale, landscape patterns interact with larger-scale disturbances, as we will see next.

Disturbance both creates and is influenced by landscape heterogeneity

Landscapes are dynamic. Change sometimes comes to landscapes suddenly in the form of large disturbances—forests and prairies burn over large areas, or floods bring sudden inputs of sediment into river ecosystems. Changes can also come more slowly, as a result of shifting climates and moving continents, but those changes are not our focus here. We saw in Chapter 17 that disturbances can influence community composition. Landscape ecologists have asked, in turn, whether particular landscape patterns slow or accelerate the spread of disturbances or increase or decrease an ecosystem's vulnerability to disturbances.

Consider, for example, the 1988 forest fires that burned nearly one-third of the 898,000 hectares (ha), or 2.2 million acres, of Yellowstone National Park. These fires occurred in a summer of extreme drought and high winds. Similarly extensive fires are thought to have occurred in the northern Rockies at 100- to 500-year intervals over the past 10,000 years. The 1988 fires burned through forest stands of different ages and species compositions, leaving a complex mosaic of patches that were burned at different intensities (**Figure 24.8**). The type and arrangement of these patches will probably dictate the landscape composition for decades, if not centuries, to come (Turner et al. 2003). Here, a disturbance—fire—was a primary force shaping the landscape pattern of the future. At the same time, the fire was also responding to the existing landscape structure through its influence on burn probability. This reciprocal interaction between landscape pattern and disturbance is a common one.

Human actions have greatly altered the nature and extent of landscape-level disturbance. Some places have been more subject to human disturbance than others. People first settled and cleared the areas with the most fertile

Figure 24.8 Disturbances Can Shape Landscape Patterns The fires that burned through nearly one-third of Yellowstone National Park in the summer of 1988 resulted in a complex mosaic of burned and unburned patches. Areas that appear black in this aerial view of Madison Canyon were burned by intense crown fires, and brown patches were burned by severe ground fires, both of which killed most or all of the vegetation.

soils, subjecting these ecosystems to the earliest human disturbance. Areas close to human settlements were converted to agriculture or subjected to logging and hunting earlier than outlying areas. These disturbance patterns can be detected in ecological communities even centuries after people have left the land and it has reverted to forest (Butzer 1992).

Such *landscape legacies* shape communities in ways that are just starting to be understood. In central France, Etienne Dambrine and his colleagues (2007) found that forest plant communities on the sites of recently uncovered Roman farming settlements still bore the mark of those disturbances 1,600 years later (**Figure 24.9**). These researchers studied plant diversity in the forest at various distances from the Roman ruins. The forest area they studied had not changed substantially since 1665, and it was probably maintained as forest for centuries before that. Dambrine and colleagues found that plant species richness increased in the vicinity of the ruins. An examination of soil properties revealed that this increase was primarily a consequence of higher soil pH and soil phosphorus, associated with the remnants of the lime mortar used in Roman buildings and from Roman agricultural practices. How many other ecosystems on Earth might display the signatures of human activities long since abandoned in their current community structure?

Disturbance, whether natural or human-caused, is an important factor shaping the landscape. Some current human activities are creating disturbances with far-reaching ecological effects, as we'll see in the next section.

Roman ruins in France

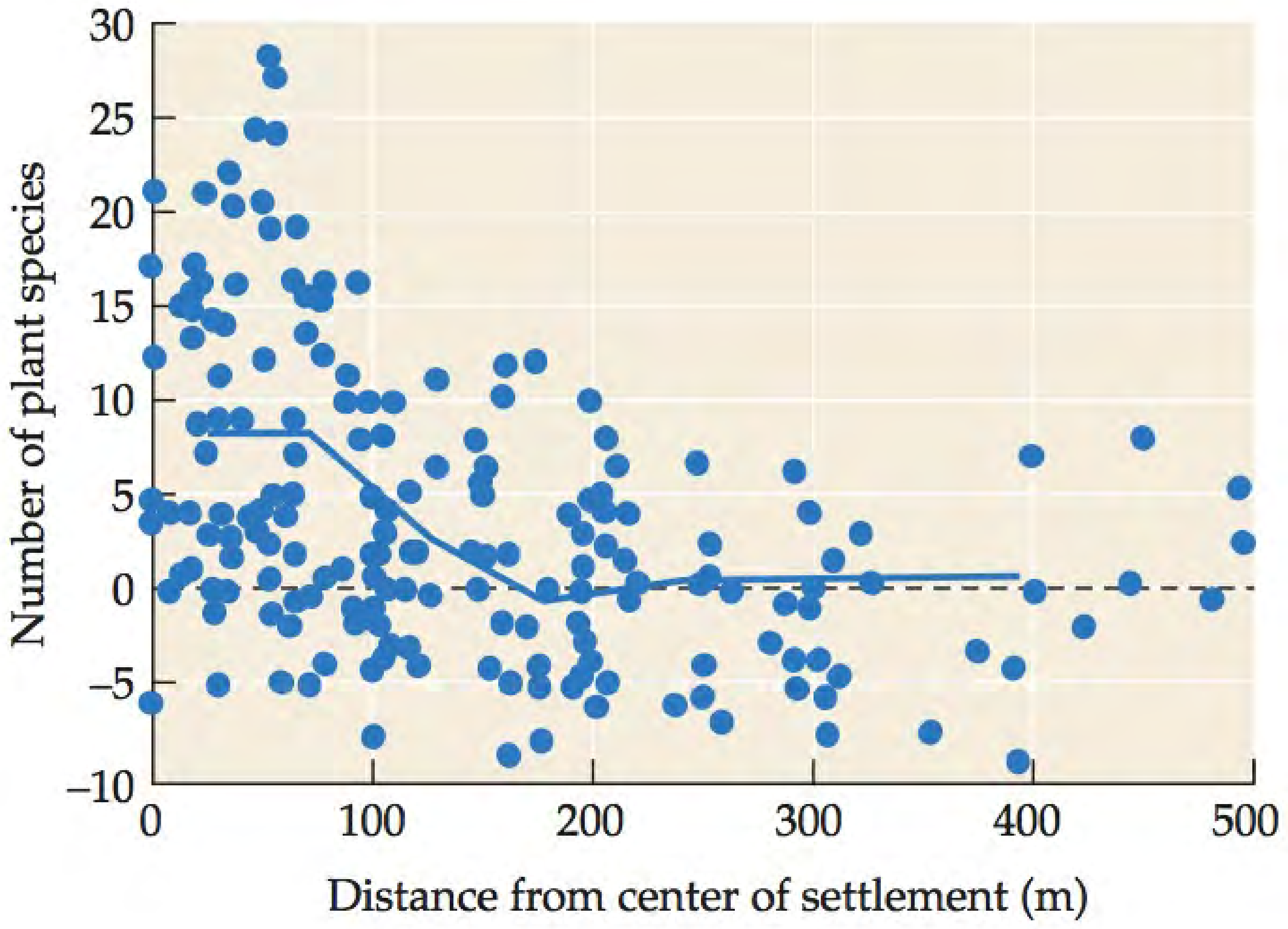


Figure 24.9 Landscape Legacies In central France, the legacy of Roman farming settlements, abandoned for nearly two millennia, is still reflected by higher plant species richness in the forest that replaced them. More plant species were found closer to the center of settlement sites, including more species that prefer a higher soil pH. The *y* axis represents departure from the mean calculated for plots 100–500 m from the settlement. (After Dambrine et al. 2007.)

CONCEPT 24.2

Habitat loss and fragmentation decrease habitat area, isolate populations, and alter conditions at habitat edges.

Habitat Loss and Fragmentation

In 1986, a massive hydroelectric project in the Caroni River valley of Venezuela inundated a large area of uneven terrain to create a reservoir known as Lago Guri (**Figure 24.10**). The result was the formation of scores of islands of tropical dry forest surrounded by water. This change in the landscape presented an opportunity for John Terborgh and his students and colleagues to study the effects of fragmentation in a tropical dry forest ecosystem. They found that small and medium-sized islands were lacking the top predators found on the mainland, primarily wild cats (ocelots, jaguars, and pumas), raptors, and large snakes (Terborgh et al. 2006). As a result, generalist herbivores, seed predators, and predators of invertebrates were 10 to 100 times more abundant on the islands than in the remaining intact forest. Species that increased in abundance included leaf-cutter ants, birds, rodents, frogs, spiders, howler monkeys, porcupines, tortoises, and lizards. The increased abundances of these species had a dramatic effect on the vegetation of these islands: tree recruitment decreased and tree mortality increased because of high rates of herbivory, primarily by leaf-cutter ants (**Figure 24.11**). What lessons can we take from this "experiment" that apply to other fragmented ecosystems?

Figure 24.10 The Islands of Lago Guri An aerial view of Lago Guri, Venezuela. This lake was formed when 4,300 km^2 (1.1 million acres) of forested land were inundated by a hydroelectric dam, leaving isolated islands of tropical forest.

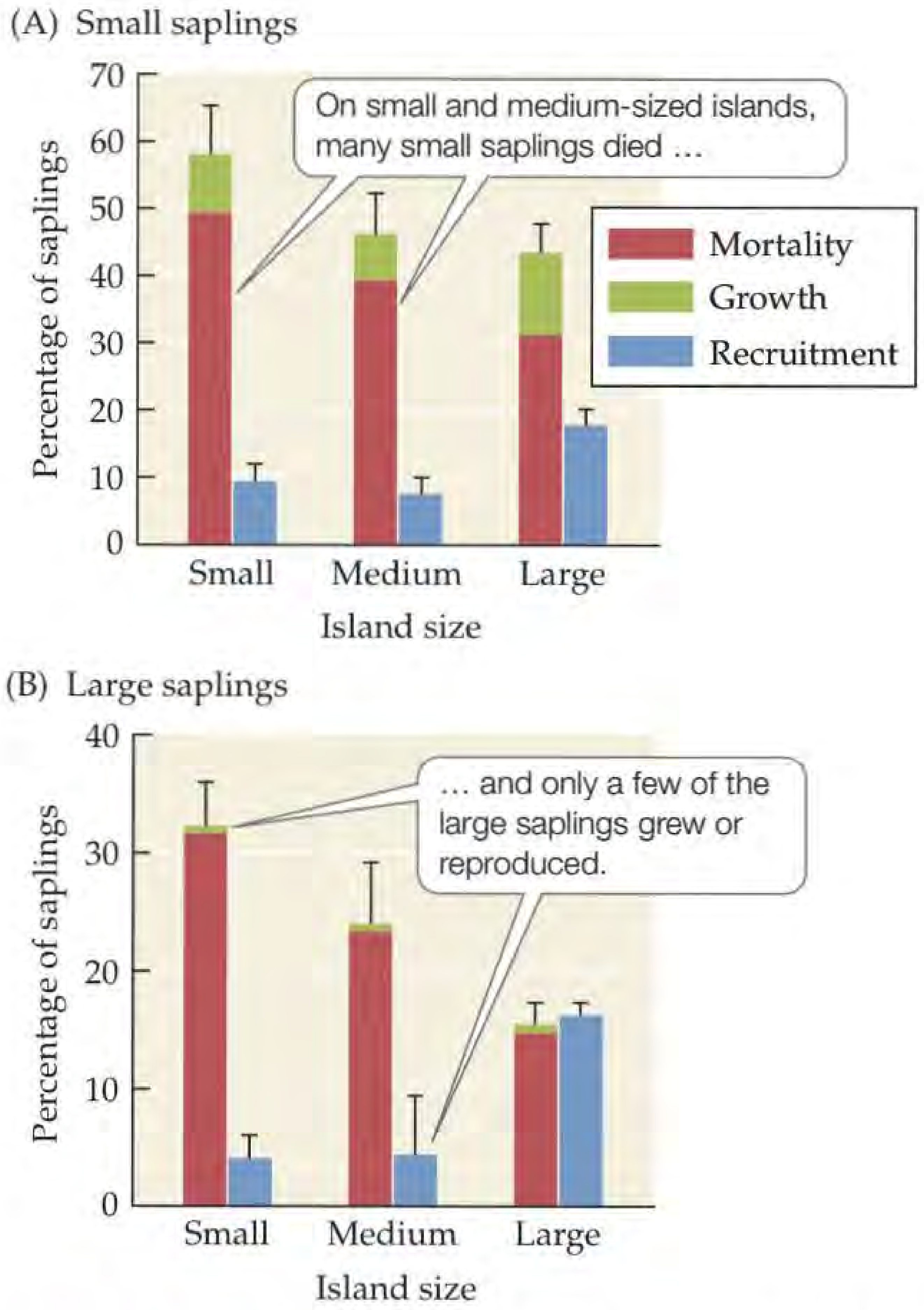
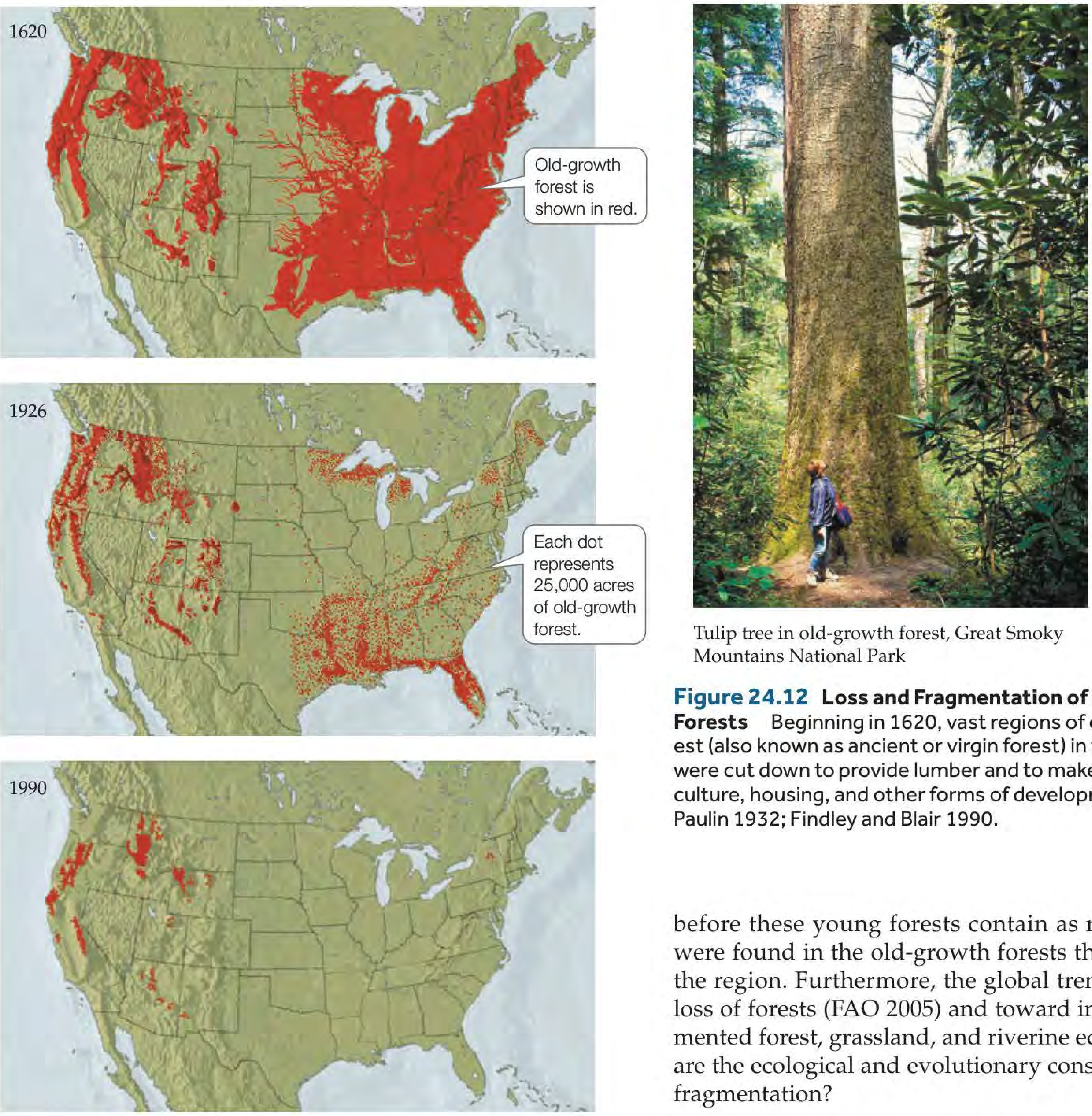


Figure 24.11 Effects of Habitat Fragmentation by Lago Guri The high abundances of herbivores on small and medium-sized islands in Lago Guri caused a dramatic decline in sapling establishment and survival. The bars show the percentages of (A) small saplings and (B) large saplings in study plots that left their size class through either mortality or growth to a larger size, as well as the number of saplings recruited to each size class, over a 5-year period. Error bars show one SE of the mean. (After Terborgh et al. 2006.)

Habitat loss and fragmentation are among the most prevalent and important human-caused changes occurring in Earth's landscapes (**Figure 24.12**). When large blocks of habitat are cleared of forests, flooded by dam construction, divided by roads, or converted to human land uses, there are several consequences for the landscape and the species living there. The first is the simple loss of habitat area. Reductions in the amount of suitable habitat available have contributed to the declines of thousands of species, including the red-cockaded woodpecker (see the Case Study in Chapter 23). Second, as the remaining habitat becomes divided into smaller and smaller patches, it is increasingly degraded and influenced by edge effects, as the Biological Dynamics of Forest Fragments Project showed (see the Case Study in Chapter 18). Third, fragmentation results in the spatial isolation of populations, making them vulnerable to the problems of small populations described in Concept 11.3.



Tulip tree in old-growth forest, Great Smoky Mountains National Park

Figure 24.12 Loss and Fragmentation of U.S. Old-Growth Forests Beginning in 1620, vast regions of old-growth forest (also known as ancient or virgin forest) in the United States were cut down to provide lumber and to make room for agriculture, housing, and other forms of development. (Maps after Paulin 1932; Findley and Blair 1990.

The process of habitat loss and fragmentation may take place over many decades. A typical pattern begins with a clearing in a forest, which is then widened bit by bit until only isolated habitat fragments remain (**Figure 24.13**). Roads are often catalysts of habitat conversion, though human access along rivers can also serve to accelerate deforestation. The principal drivers of habitat fragmentation are conversion of land for agriculture and urban expansion.

Habitat fragmentation is a reversible process. The northeastern United States, for example, has more forest cover than it did a century ago—but it will take centuries before these young forests contain as many species as were found in the old-growth forests that once covered the region. Furthermore, the global trend is toward net loss of forests (FAO 2005) and toward increasingly fragmented forest, grassland, and riverine ecosystems. What are the ecological and evolutionary consequences of this fragmentation?

Fragmented habitats are biologically impoverished relative to intact habitats

When habitat is fragmented, some species go locally extinct within many of the fragments. There are a host of reasons why this occurs. There may be inadequate food resources, shelter, or nesting sites in the fragments. Animals may need to forage over larger areas than their conspecifics in intact habitat, using multiple fragments. Mutualisms may be disrupted if pollinators are missing or as mycorrhizal fungi fail to persist in a particular fragment. Some fragments may lack the microenvironments needed for seed germination. Local extinction or decline is not inevitable; indeed, some species flourish under the changed conditions that follow fragmentation.