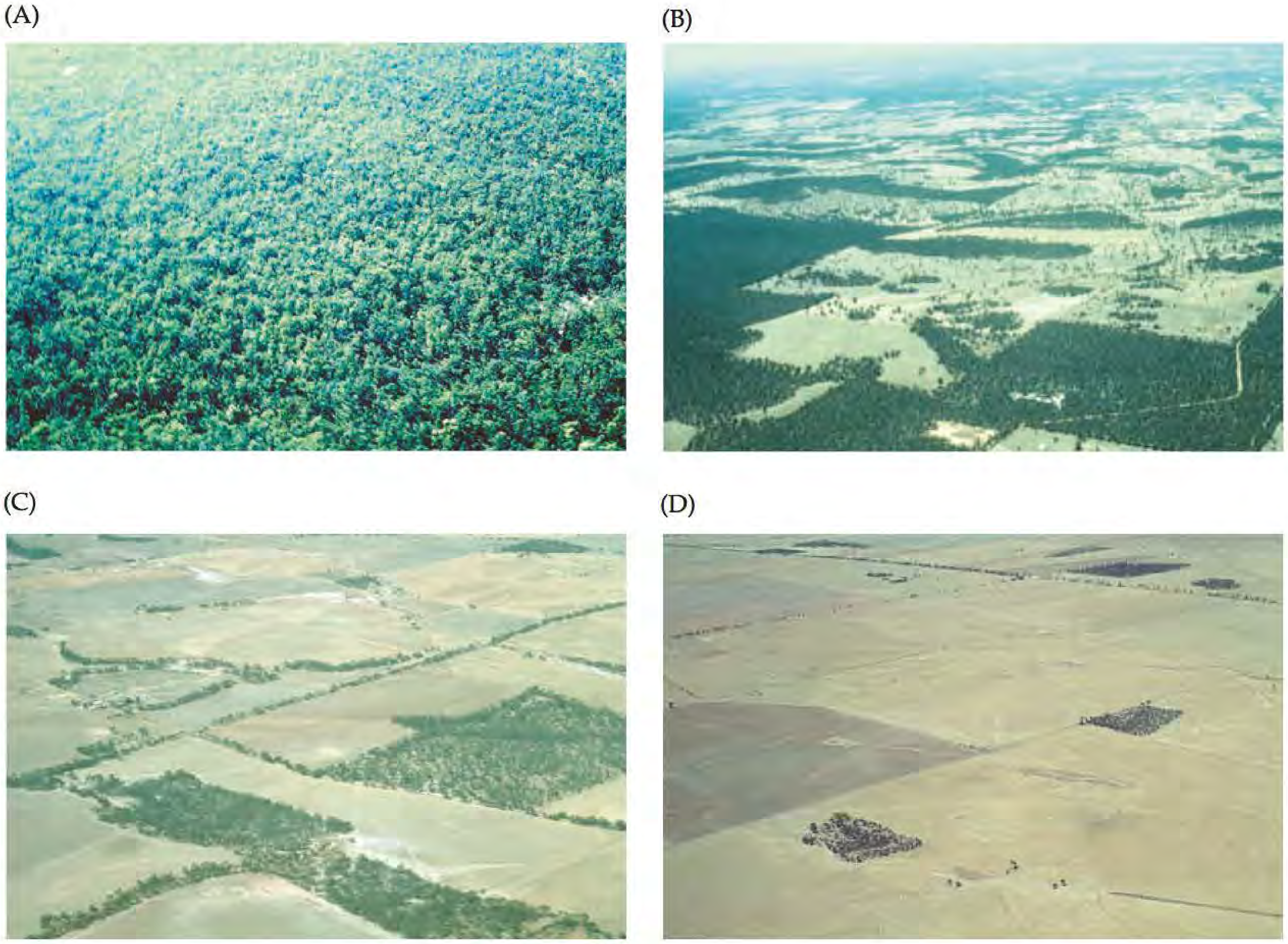


Figure 24.13 The Process of Habitat Loss and Fragmentation Historically intact habitats are gradually reduced with increased human presence. These contemporaneous photographs (taken from different locations) illustrate a process that typically takes decades to complete. (A) An intact eucalyptus forest in Western Australia. (B) Areas within the forest have been cleared for grazing. (C) The forest has become further fragmented over time. (D) Only a few remnants of forest remain. (From McIntyre and Hobbs 1999.)

Fragmentation often leads to losses of top predators, giving rise to cascading effects, sometimes with large consequences for the remaining community as we saw with the Lago Guri example. Another example of such a cascade that has implications for human health is the growing risk of Lyme disease as a result of forest fragmentation in the northeastern United States. Brian Allan and colleagues found that forest fragments of less than 2 ha (5 acres) were very densely populated white-footed mice (*Peromyscus leucopus*). Fragments of that size did not support substantial predator populations, and the mice had few competitors there. White-footed mice are the most important reservoir of *Borrelia burgdorferi*, the spirochete bacterium that causes Lyme disease. Ticks are the vector of this disease. Tick nymphs collected in these small fragments were significantly more likely to carry the disease, and occurred at higher densities, than nymphs in larger fragments (**Figure 24.14**). The outcome—an increased risk of human infection with Lyme disease—is ultimately a result of the biological impoverishment of habitat fragments (Allan et al. 2003).

The matrix between habitat fragments varies in permeability

Models of fragmented landscapes, which were initially derived from the equilibrium theory of island biogeography (see Concept 18.3), depict habitat fragments as islands isolated in a "sea" of unsuitable matrix, just as the islands of Lago Guri literally are. But do those models truly fit? For some species, such as the eastern wallaroo (*Macropus robustus robustus*) of Australia, it appears that habitat fragments function as islands surrounded by a

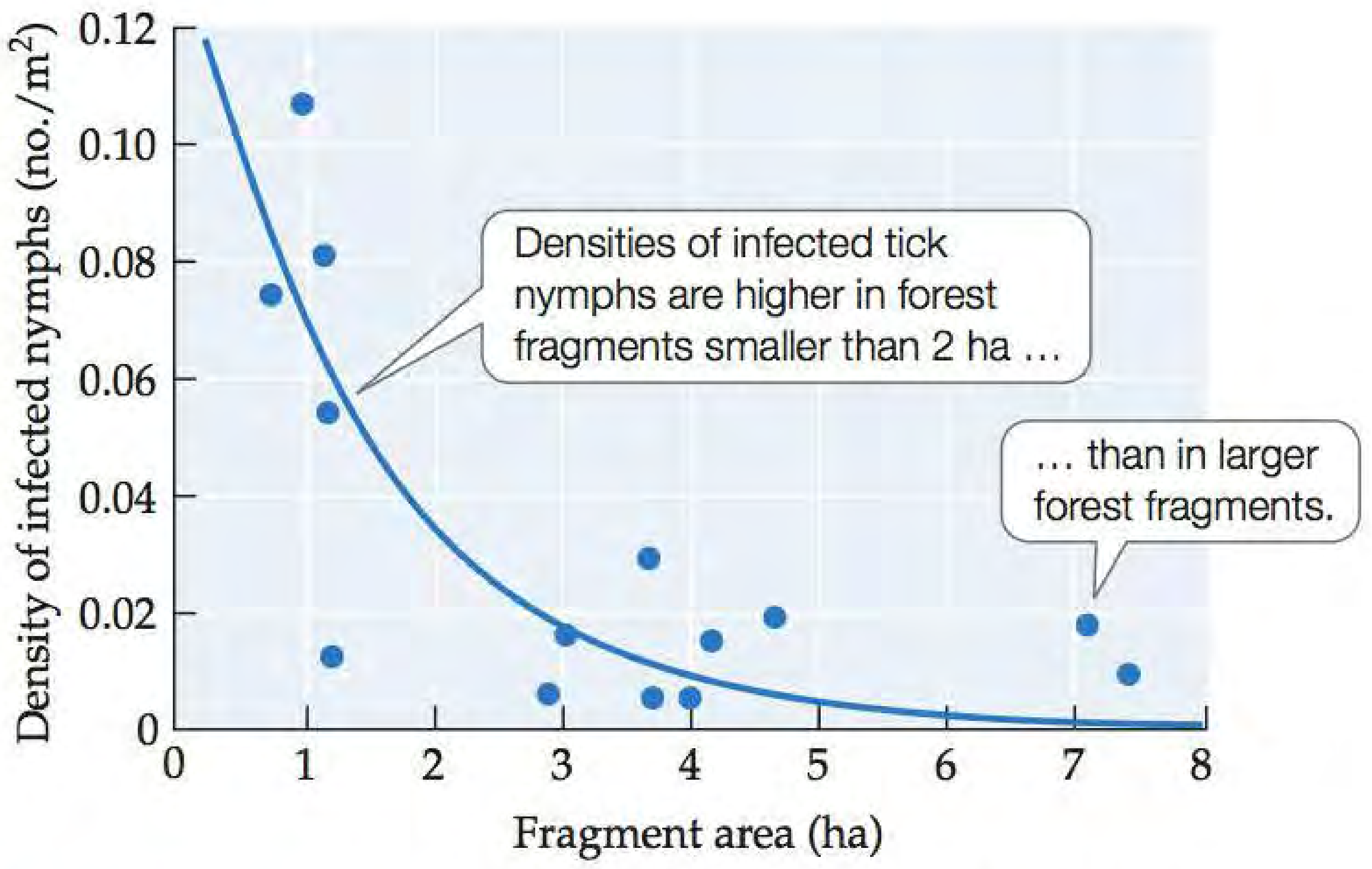


Figure 24.14 Habitat Fragmentation Can Have Consequences for Human Health The loss of predators from small forest fragments in New York State has led to elevated populations of white-footed mice in those fragments. As a result, densities of tick nymphs infected with the spirochete bacterium that causes Lyme disease are higher than in larger forest areas. (After Allan et al. 2003.)

matrix that individuals occasionally cross, as described in Web Extension 24.1. In other cases, however, fragmented landscapes have proved to be more complex than island models would suggest. The matrix may be *permeable* to some extent, and it may consist of a mosaic of different patch types, of which some are more permeable than others.

In an example from South America, Traci Castellón and Kathryn Sieving studied the dispersal of a small insectivorous understory bird, the chucao tapaculo (*Scelorchilus rubecula*). They moved individual birds to habitat fragments located in different landscape contexts and followed their subsequent movements. They found that birds translocated to fragments surrounded by pasture were much more reluctant to leave the fragments to get to larger forest blocks than were birds that either had a shrubby habitat to cross or were in fragments connected to larger forest blocks by a forested corridor (Castellón and Sieving 2006). Similar observations were made in a study of rodents in the Atlantic forest of Brazil, in which some species moved readily through the matrix, while other species were hesitant to cross into unfamiliar patch types (Pardini 2004). As this study showed, the permeability of the matrix is species-dependent.

Edge effects change abiotic conditions and species abundances in fragments

As intact habitat is fragmented, an abrupt boundary between two dissimilar patch types is created. The total length of habitat boundary, or *edge*, increases as fragmentation increases. **Edge effects** are the diverse abiotic and biotic changes that are associated with habitat boundaries (**Figure 24.15**). The effect of edge formation is a change in the physical environment over a certain distance into the remaining fragment. As a result, biological interactions and ecological processes can change as well, as you can explore in **Analyzing Data 24.1**. The course of such changes plays out over time, so we can separate the immediate responses to fragmentation and edge formation from the responses that develop later (see Figure 18.24).

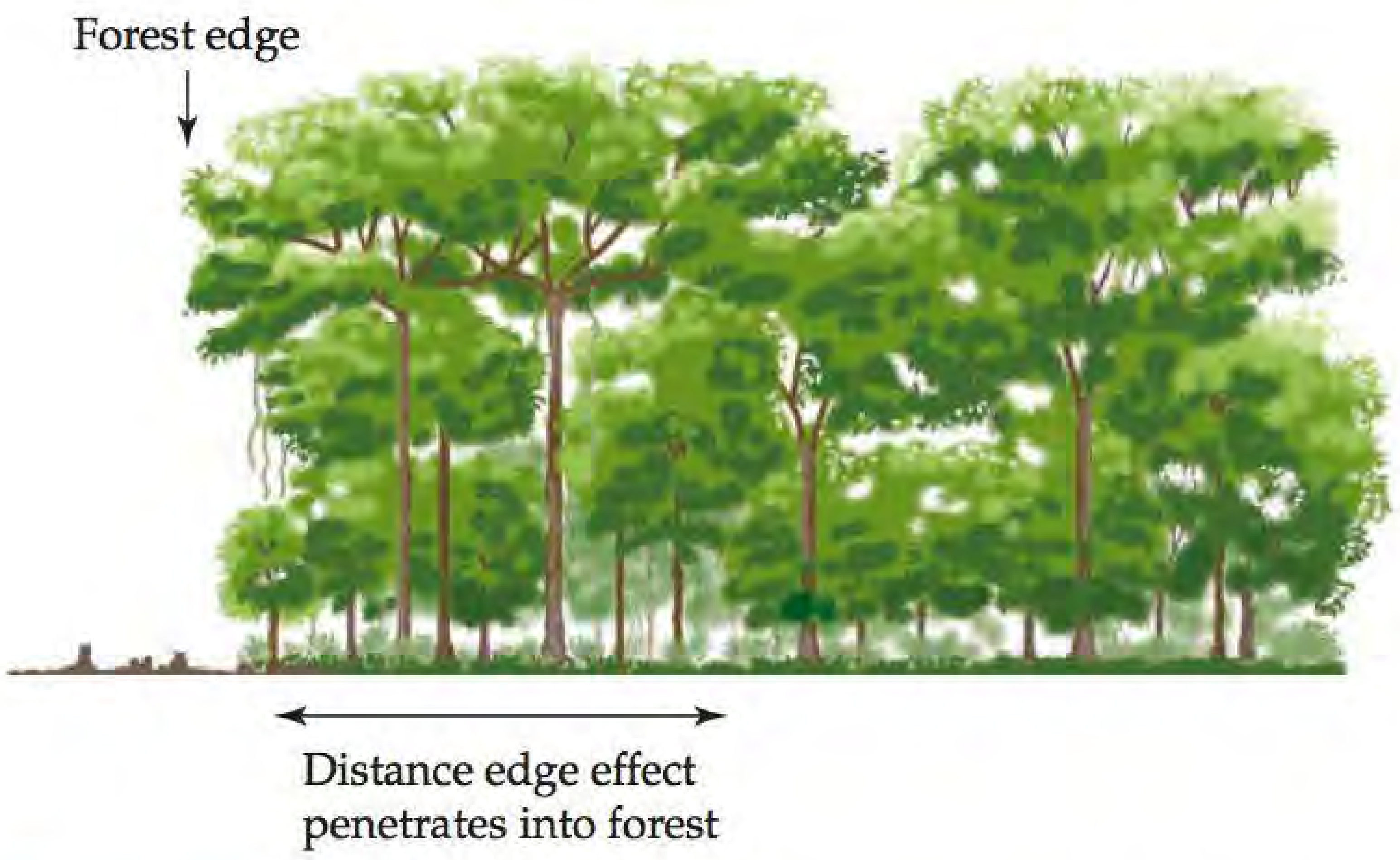


Figure 24.15 Edge Effects Deforestation creates new forest edges, exposing trees that once were surrounded by forest to edge effects such as increased light levels, higher temperatures, greater wind speeds, decreased soil moisture, and invasion of disturbance-adapted plants and animals. Some edge effects penetrate a few tens of meters into the forest fragment, while others penetrate hundreds of meters (see Analyzing Data 24.1).

Analyzing Data 24.1 and the Case Study Revisited in Chapter 18 describe edge effects seen in large-scale experiments in Brazil. The effects of abiotic changes at a forest edge were also illustrated by a study of microclimates 10–15 years after the clear-cutting of an old-growth Douglas fir forest in the Pacific Northwest (Chen et al. 1995). Edges were generally characterized by higher temperatures, higher wind speeds, and more light penetration. Daily temperature extremes were also greater at the edges because more heat was lost from the forest edge at night than in the interior forest. The biotic consequences of these abiotic changes included higher rates of decomposition, more windthrown trees and thus more woody debris on the forest floor, and greater seedling survival of some tree species (Pacific fir) over others (Douglas fir and western hemlock).

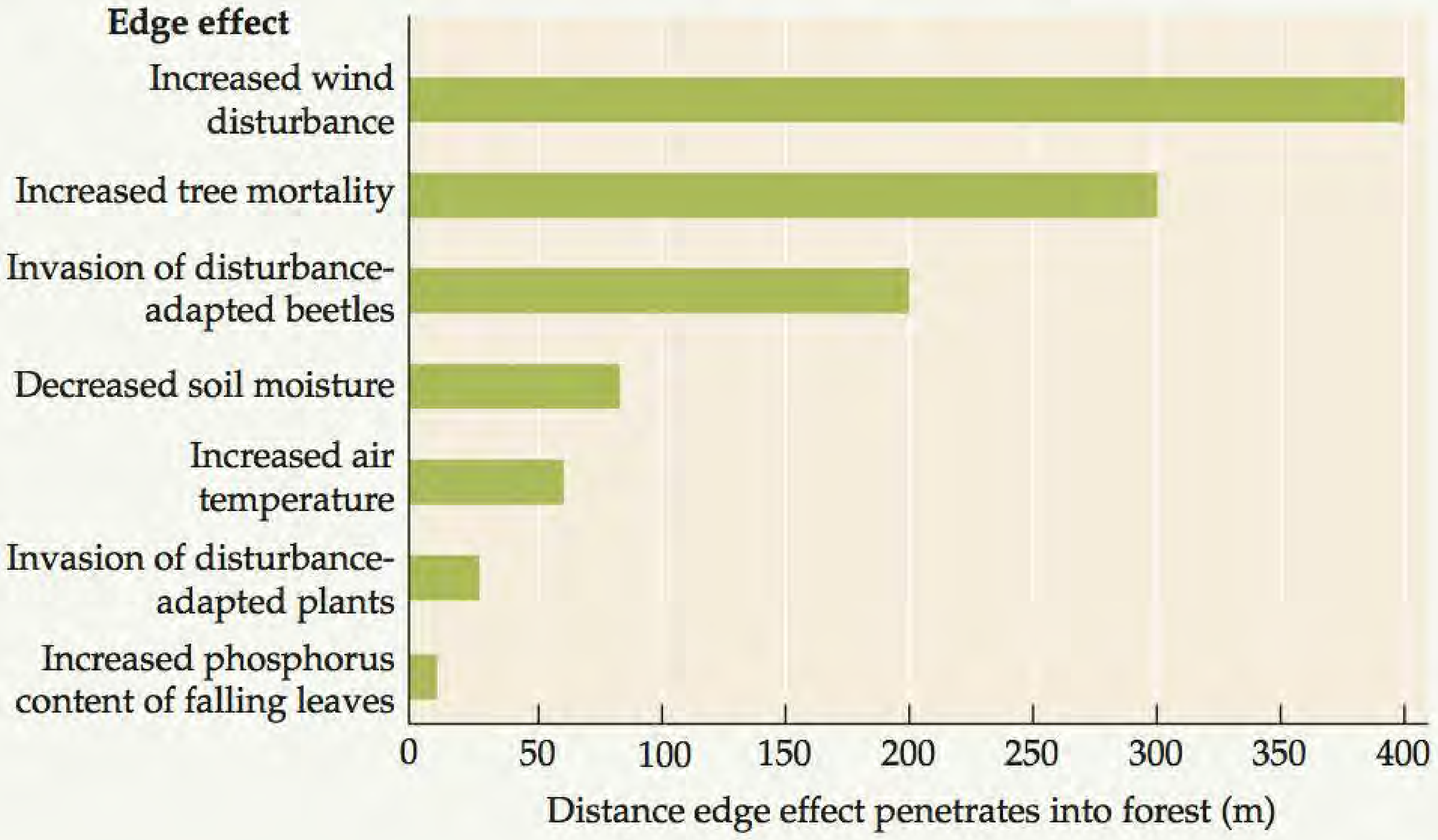
Habitat edges can either enhance or inhibit dispersal of organisms. Novel species interactions may take place at the junctions of two ecosystems. Some species may benefit from foraging in one habitat and reproducing in another. Invasive species are commonly more abundant in habitat edges, influencing the population dynamics for native species (Fagan et al. 1999). For example, birds adapted to the forest interior often have lower breeding success when their nests are close to habitat edges; this can result from higher rates of egg predation by raccoons, crows, and other predators as well as higher rates of nest parasitism, especially by cowbirds. In the tallgrass prairie of Wisconsin, Johnson and Temple (1990) studied the reproductive success of five species of ground-nesting birds. They found that the closer nests were to a wooded edge of the prairie habitat, the greater the probability of nest predation by medium-sized predators and of nest parasitism by cowbirds, and the lower the rate of reproductive success. Similar patterns have been observed in other prairies, in Scandinavian forests, in eastern deciduous forests, and in the tropics (Paton 1994). Some biologists have characterized edges as "biological traps" as a result of the increased risks that some species face there (Battin 2004).

Fragmentation alters evolutionary processes

In the time since G. Evelyn Hutchinson's 1965 depiction of "the ecological theatre and the evolutionary play," the

ANALYZING DATA 24.1 How Far Do Edge Effects Penetrate into Forest Fragments?

When an intact forest is first fragmented, abiotic conditions change near the edge of the patch of forest that remains, giving rise to biotic changes (see Figure 24.15). In a landmark study on edge effects, William Laurance and his colleagues (2002)* synthesized 22 years of data from the Biological Dynamics of Forest Fragments Project, the world's largest ecological experiment (see the Case Study in Chapter 18). The graph shows some of the changes they measured in Amazon rainforest fragments.



1. According to the graph, how far from the edge must a tree be located if it is not to experience an increase in wind disturbance?
2. If the tree mortality effect penetrated 300 m on each side of an 800 m × 800 m forest fragment, tree mortality would increase in what percentage of the fragment's area?
3. Are edge effects such as those shown here likely to cause other changes (not shown) in species interactions, community structure, or ecosystem processes? Explain.

See the companion website for a similar ANALYZING DATA exercise.

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*Laurance, W. F. and 10 others. 2002. Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology* 16: 605–618.

stage set has been substantially rearranged by human actions. The "evolutionary play" will indeed go on, but in altered ways that we are only now trying to understand. What are the evolutionary consequences when populations of all species are split into smaller and more isolated populations and thrown together in new communities that lack historical precedent?

You have already read in Chapters 11 and 23 about the genetic and demographic problems of small, isolated populations. Marcel Goverde and his colleagues studied the evolutionary consequences of fragmentation by watching bumblebee behavior in the Jura Mountains of Switzerland (Goverde et al. 2002). Their experimental plots included meadow fragments of different sizes (created by mowing) and control plots in unfragmented meadow habitat. The researchers studied the foraging behavior of bumblebees as they visited the flowers of wood betony (*Stachys officinalis*), which were common in both experimental fragments and control plots. The bees visited fragments less frequently than they visited control plots, and once there, they tended to stay longer in the fragments. Ultimately, these two changes in bumblebee behavior resulted in a lower probability of pollination and an increased likelihood of inbreeding for the wood betony in the fragments, resulting in an altered evolutionary trajectory for those plants.

In many other cases, habitat fragmentation has been shown to increase rates of inbreeding and genetic drift for those species confined to fragments. For example, Keller and Largiadèr (2003) found significant genetic divergence between populations of the flightless ground beetle *Carabus violaceus* that had been isolated by roads. Habitat fragmentation can also alter selection pressures on organisms. Where plant populations become small and isolated, their chances of encountering their pollinators, their pathogens, their herbivores, their dispersers, and their competitors may all be reduced, with subsequent evolutionary consequences. Similar effects have been observed in animals, whose breeding systems and survival patterns can be altered in small fragments (Barbour and Litvaitis 1993).

We have only begun to study the evolutionary implications of habitat fragmentation, and we still have much to learn. As we'll see in the next section, however, such evolutionary information is only one part of what must be considered in designing nature reserves that will work well to maintain biodiversity in landscapes increasingly modified by humans.

CONCEPT 24.3

Biodiversity can best be sustained by large reserves connected across the landscape and buffered from areas of intense human use.

Designing Nature Reserves

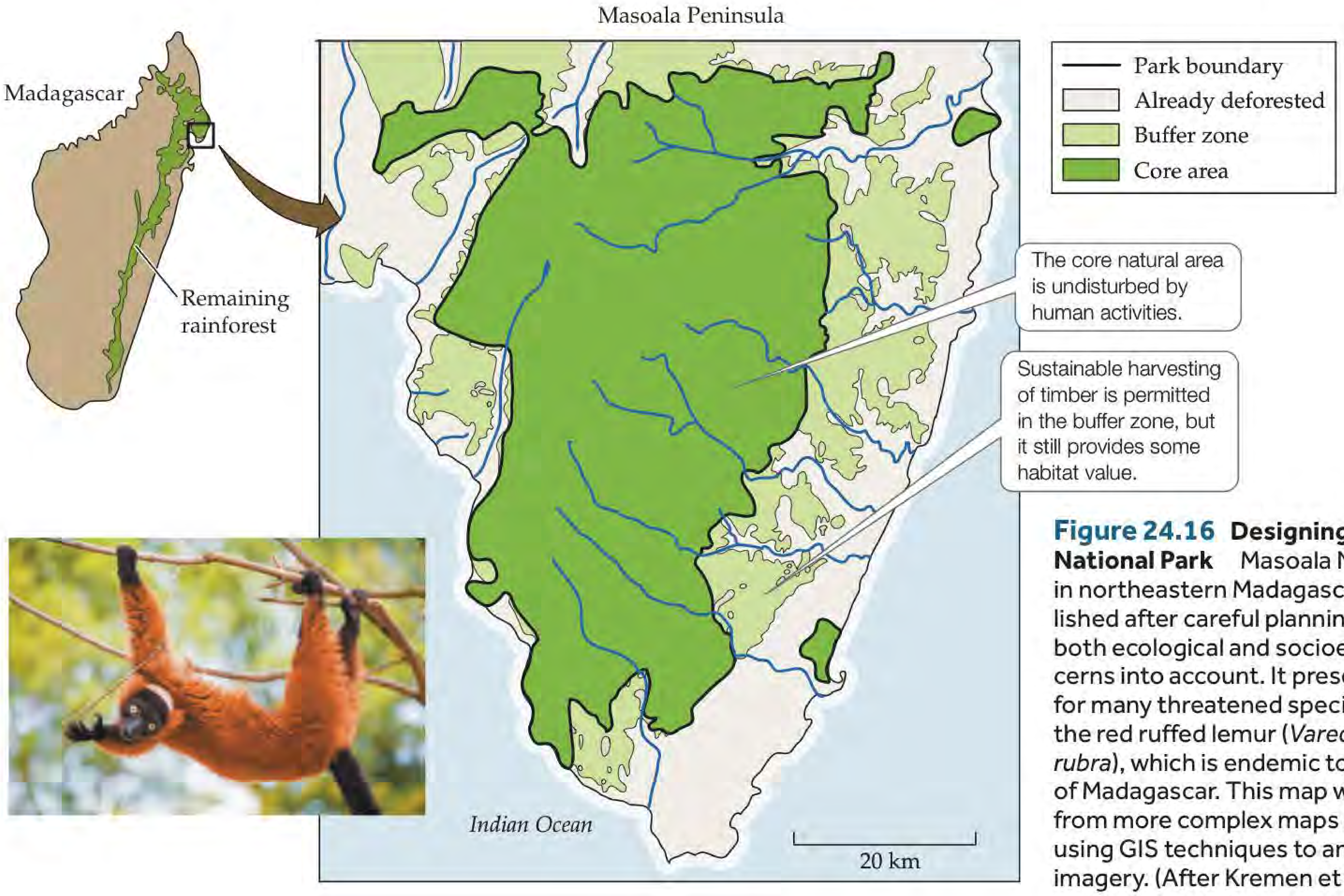
You may have a favorite national park, such as Everglades in Florida, Grand Canyon in Arizona, Bialowieski in Poland, or Torres del Paine in Chile. How did these places get to be national parks? What were they before they were parks? Are they the best possible sites for maintaining biodiversity in their regions? Now consider how well the land around you is functioning to sustain native species. Your view is undoubtedly shaped by where you are right now, by what the human history of your area is, and by how effective past conservation work there has been. We turn now to an examination of the ways in which people can work to improve the likelihood of the persistence of species native to their region.

To counteract habitat loss, conservation planners worldwide are working to locate and design protected areas where species can persist. The identification and preservation of core natural areas, buffer zones surrounding them, and habitat corridors connecting them is key to maintaining and allowing the growth of populations. In some cases, as we'll see, degraded ecosystems can be restored as viable habitat for wild species.

Core natural areas should be large and compact

The principles of landscape ecology and conservation biology have come together to guide biologists in selecting the most vital lands for conservation. The design of new nature reserves focuses on **core natural areas**, where the conservation of biodiversity and ecological integrity take precedence over other values or uses, and "where nature can operate in its own way in its own time" (Noss et al. 1999). Populations that are able to maintain themselves in core areas may serve as sources of individuals for populations outside the protected areas. Ideally, core areas also provide enough land to meet the large habitat area requirements of top predators.

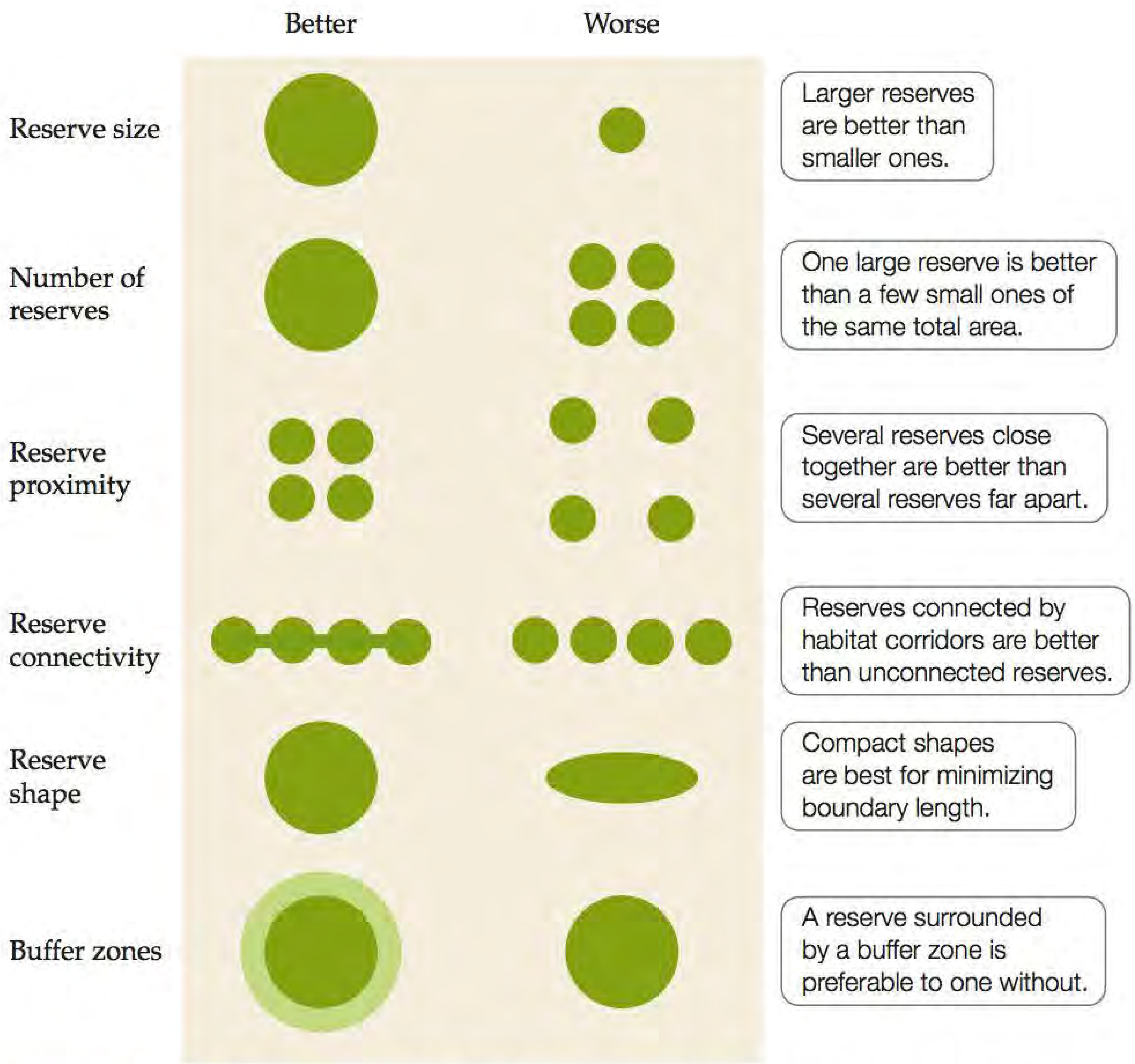
Madagascar is a large island that is a global priority for conservation. It has a rich biota and many endemic species, including more than 70 species of lemurs, a group of primates found only on Madagascar. The biota of Madagascar is seriously imperiled, as only 15% of the island's original forest remains. Efforts are under way to put more of its land into conservation. In designing a new national park in northeastern Madagascar, Claire Kremen and her colleagues examined both the biological and the socioeconomic circumstances of the region. Their design (**Figure 24.16**) was based on a core natural area



The core natural area is undisturbed by human activities.

Sustainable harvesting of timber is permitted in the buffer zone, but it still provides some habitat value.

Figure 24.16 Designing Masoala National Park Masoala National Park, in northeastern Madagascar, was established after careful planning that took both ecological and socioeconomic concerns into account. It preserves habitat for many threatened species, including the red ruffed lemur (*Varecia variegata rubra*), which is endemic to this region of Madagascar. This map was simplified from more complex maps generated by using GIS techniques to analyze satellite imagery. (After Kremen et al. 1999.)



Larger reserves are better than smaller ones.

One large reserve is better than a few small ones of the same total area.

Several reserves close together are better than several reserves far apart.

Reserves connected by habitat corridors are better than unconnected reserves.

Compact shapes are best for minimizing boundary length.

A reserve surrounded by a buffer zone is preferable to one without.

Figure 24.17 The Best Spatial Configurations for a Core Natural Area Some spatial configurations are usually better than others for fostering biodiversity. (After Diamond 1975; Williams et al. 2005.)

? For the first five characteristics (reserve size, number of reserves, reserve proximity, reserve connectivity, reserve shape), explain the underlying reasons why the design on the left is better than the one on the right.

that extended across several elevational and precipitation zones, encompassing a range of vegetation types. The proposed core area encompassed habitat for all of the region's rare species of butterflies, birds, and primates, and it had as yet been little affected by deforestation. The researchers excluded areas close to villages that had already been fragmented and where hunting had negatively affected animal populations (Kremen et al. 1999). The Masoala National Park, which opened in 1997, is now the largest national park in Madagascar at 211,230 ha (over 521,000 acres). With proper management, the park will give the unique biodiversity of this region an improved chance of being maintained in perpetuity.

Ideally, core natural areas must be large and uncut by roads or even by trails. Thus, not all protected areas qualify as core natural areas. Many do not fully serve the purpose of protecting the whole biota from human interference. Most national parks in the United States were not established with the conservation of biodiversity as their primary mission, but rather to preserve scenery, often on land that was not useful for anything else. Conservation planners recognize that many countries do not have the luxury of carving out large areas of land to be solely dedicated to biodiversity conservation. Therefore, the cores of many reserves do not meet all the criteria for core natural areas.

In the design of nature reserves, some spatial configurations are better than others for fostering the persistence of biodiversity (**Figure 24.17**). Overall, large, compact, and connected reserves are ideal, but there may be times when smaller or disconnected reserves may be more desirable. For example, diseases may spread less easily between isolated smaller reserves than within a large reserve. The primary biological objectives of reserve configuration are the maintenance of the largest possible populations of organisms, the provision of habitat for species throughout their area of distribution, and the provision of adequate area for maintenance of natural disturbance regimes.

In many settings where conservation is being accomplished, either the landscape or the social context may not realistically permit adhering to these principles (Williams et al. 2005). There are many smaller reserves that have been established with the conservation of a single species or ecological community as their main objective. Such **biological reserves**, even if they are small, are nevertheless an important part of our conservation efforts. Critically situated smaller reserves may be the best available option, particularly where human population density is high and large reserves are unfeasible.

Core natural areas should be buffered by compatible land uses

Due to many constraints, relatively small areas of land are most commonly designated as core natural areas. If we are to conserve the majority of the world's species, however, areas outside of the core areas will have to be able to provide adequate habitat for biodiversity persistence (Soulé and Sanjayan 1998). We can augment the effectiveness of protected areas by surrounding them with **buffer zones** (see Figure 24.17), large areas with less stringent controls on land use, yet which are at least partially compatible with the resource requirements of many species. Such lands can be managed in ways that permit the production of needed human resources, such as timber, fiber, wild fruits, nuts, and medicines, but still maintain some habitat value. Activities that may be compatible with the conservation function of buffer zones include selective logging, grazing, agriculture, tourism, and limited residential development (Groom et al. 1999).

In the plan for Masoala National Park, Kremen and her colleagues included a buffer zone on the eastern side of the park, which consisted of more than 71,000 ha of forest land designated for sustainable timber harvesting (see Figure 24.16). The researchers first identified areas that were at high risk of deforestation due to their proximity to villages. They then established how much wood each family, and thereby each village, consumed, and calculated how much area would be required to meet this need on a sustainable basis. The buffer zone augments the effective area of the park for many lowland species, even though they may be subjected to some level of hunting or collection.

On a cautionary note, buffer zones may serve as *population sinks* (areas where death rates are higher than birth rates) for some species, as animals that stray out of core areas and into buffer zones become vulnerable to hunting, vehicle collisions, or other sources of mortality. In Peru, where slash-and-burn agriculture is commonly practiced just outside nature reserves, wild animals such as agoutis, armadillos, and tapirs often damage farmers' crops. As a result, these animals are targeted by hunters, and such hunting has altered the relative abundances of mammals in the forest (Naughton-Treves et al. 2003). In other cases, however, buffer zones do not appear to act as population sinks. An analysis of data from 785 animal species found that buffer zones can allow populations to persist in habitat fragments that might otherwise be too small or too isolated to support viable populations (Prugh et al. 2008). The key to success boils down to simple demography: if a buffer zone provides a threatened species with habitat in which birth rates are higher than death rates, it can aid conservation goals.

If we can succeed in establishing core areas for protection surrounded by sparsely inhabited buffer zones, have we done all that is necessary for conservation? Recall that landscape connectivity is another important consideration in reserve design.

Corridors can help maintain biodiversity in a fragmented landscape

Habitat corridors—linear patches that connect blocks of habitat—have become a staple of urban, suburban, and rural planning (**Figure 24.18**). Connectivity among habitat patches might lessen the impact of fragmentation on small populations by helping to ensure that there are corridors of habitat that link them together. This solution made intuitive sense.

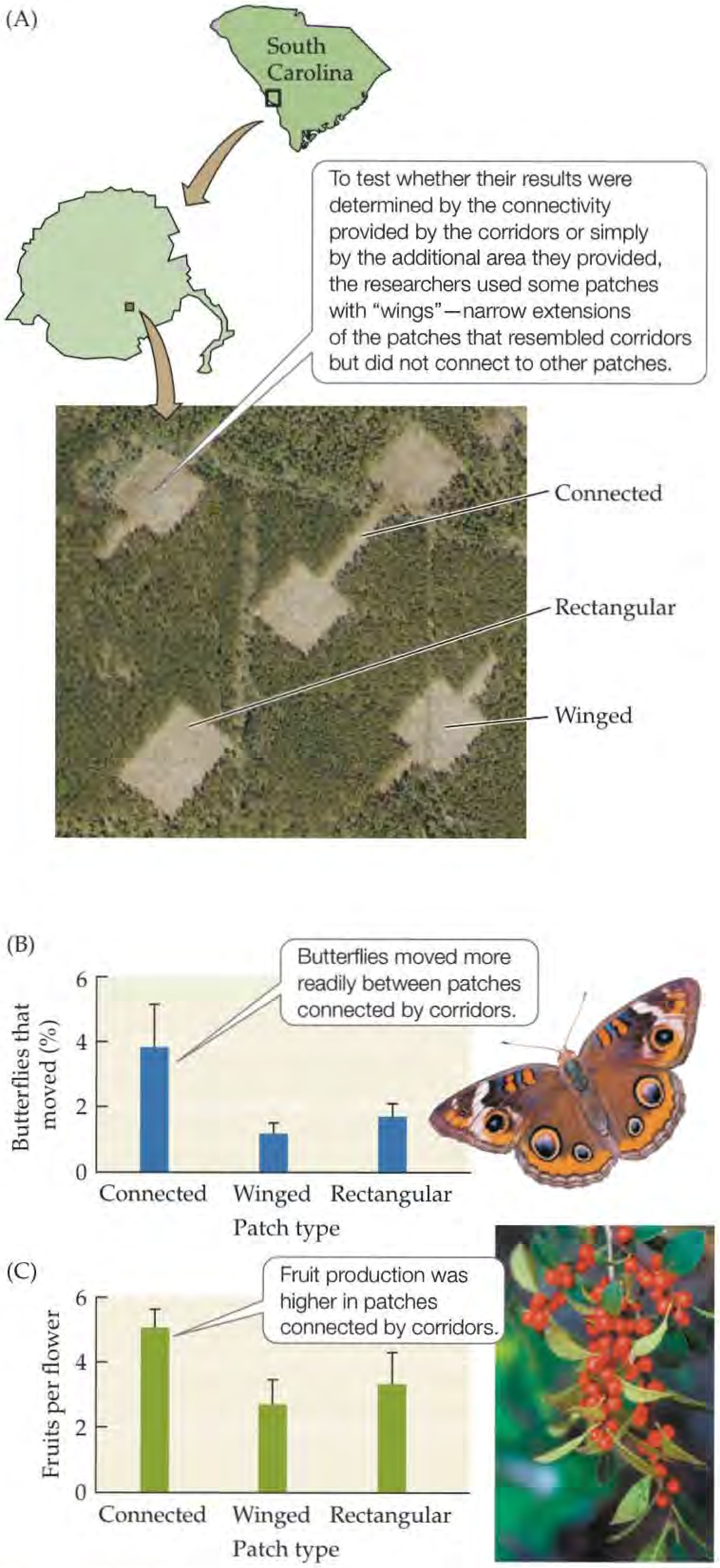
When designing Masoala National Park, Kremen and her colleagues looked at the larger landscape and anticipated connections that would be important in the future. Many of Masoala's target species are found in areas northwest of the park that lie between Masoala and two important protected areas to the north. The park plan included three narrow corridors to provide connections to those protected areas. The researchers developed this part of the plan by examining maps, but out of expediency, they did not actually do studies of animal movements (Kremen et al. 1999).

The intended function of habitat corridors is to prevent the isolation of populations in fragments. But do we know that corridors actually help to overcome this isolation? And do corridors work for beetles as well as for wolves? Is a stream corridor in the suburbs providing necessary landscape connectivity for some species? At the continental scale, could we link the Greater Yellowstone Ecosystem to the Yukon through habitat corridors, as some have proposed? Experimental and observational studies of corridors' utility have shown mixed results.

Nick Haddad and his colleagues established a test of the utility of corridors at the Savannah River Ecology Laboratory in South Carolina. They set up patches of early successional habitat in a matrix of pine forest, some of them connected by corridors, and observed the

Figure 24.18 A Habitat Corridor Grizzlies and other wildlife can cross this highway overpass in Banff National Park, Canada.

movements of organisms between patches (**Figure 24.19**). Their results showed that the corridors did indeed serve to facilitate the movement of butterflies, pollen, and bird-dispersed fruits (Tewksbury et al. 2002).



To test whether their results were determined by the connectivity provided by the corridors or simply by the additional area they provided, the researchers used some patches with "wings"—narrow extensions of the patches that resembled corridors but did not connect to other patches.

Butterflies moved more readily between patches connected by corridors.

Fruit production was higher in patches connected by corridors.

Figure 24.19 How Effective Are Habitat Corridors? (A) Nick Haddad and his colleagues tested the effectiveness of habitat corridors by creating experimental patches of early successional habitat within a pine forest and creating corridors between some of the patches. They then observed (B) movements of the common buckeye butterfly (*Junonia coenia*) between patches and (C) fruit production (which provides evidence of pollination) in winterberry (*Ilex verticillata*) in patches. Error bars in (B) and (C) show one SE of the mean. (After Tewksbury et al. 2002.)

Other studies, however, have found no benefits of corridors, and still others have found negative effects. For example, in the same experimental system at the Savannah River Ecology Laboratory, predation on indigo bunting (*Passerina cyanea*) nests was higher in patches connected by corridors (Weldon 2006). There are also concerns that corridors could facilitate the movement of pathogens (Hess 1994) or invasive species (Simberloff and Cox 1987).

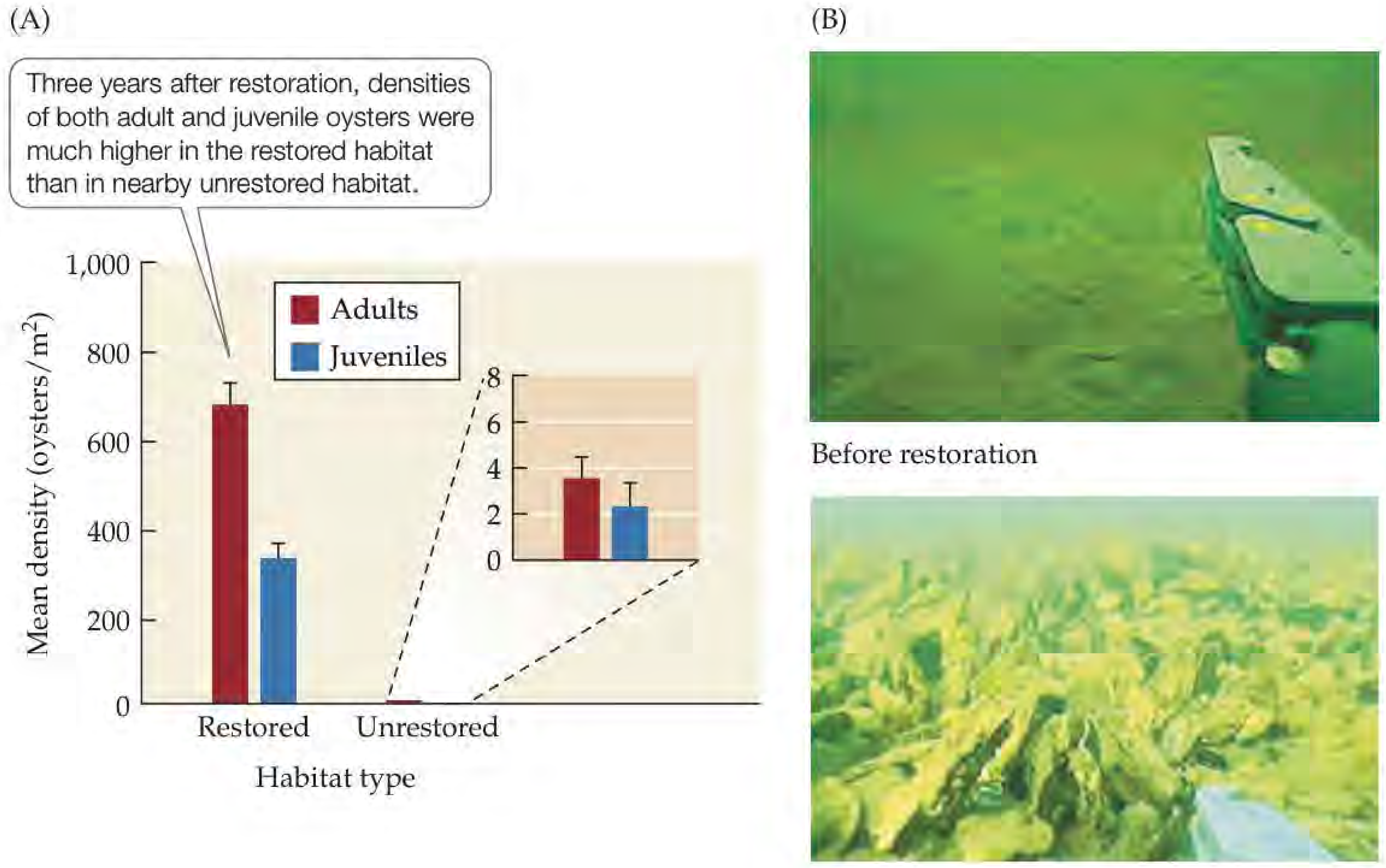
Ecological restoration can increase biodiversity in degraded landscapes

What if habitat corridors are lacking and organisms' ability to move is impaired by an unsuitable matrix of degraded habitat? This was the case in Guanacaste Province on the Pacific coast of Costa Rica, where Santa Rosa National Park, in a lowland area of tropical dry forest, was largely separated by 35 km of cattle pasture and forest fragments from the upland forest habitat of the nearby mountains.

Tropical ecologist Dan Janzen knew that many insects, birds, and mammals needed to migrate between these lowland and upland forests. He also saw that the tropical dry forest that he had spent his career studying was fast disappearing. Janzen's effort to reverse this trend became one of the largest and most ambitious ecological restoration projects ever undertaken in the Neotropics. Now covering some 120,000 ha of land and 70,000 acres of marine reserve, the Area de Conservación Guanacaste (ACG) includes three national parks, a protected corridor linking them, and the surrounding agricultural areas. The ACG is home to some 230,000 species, or 65% of the species in Costa Rica (Daily and Ellison 2002).

Within the ACG, cattle ranches have occupied much of the land between the three parks for decades. Janzen has launched an effort to restore 75,000 ha of these pasturelands to the original forest types. His strategies include planting trees, suppressing fires, and limiting hunting (to maintain mammalian and avian seed dispersers). Fire suppression is necessary to halt fires that burn readily in pastures covered in jaragua grass (*Hyparremia rufa*), an invasive plant introduced from Africa. Grazing will be maintained for some time in some areas to suppress the jaragua grass; cows and horses have also been found to help in tree seed dispersal.

Ecological restoration is being applied in many other ecosystems, with varying degrees of success. To be successful, restoration ecologists must correctly diagnose the ecological state of an area, decide what the goals of the restoration should be, and then apply their understanding of ecological processes to re-create the desired type of ecosystem. Anthony Bradshaw, a founder of restoration



Before restoration

After restoration

Figure 24.20 Dramatic Effects of an Ecological Restoration Project Native oyster populations have collapsed worldwide as a result of habitat loss and overharvesting. (A) In an ecological restoration experiment that began in 2004, oyster reefs were constructed in nine protected areas along the Great Wicomico River in Virginia. Three years later, native oyster populations had recovered dramatically across the 35 ha restoration project. Error bars show one SE of the mean. (B) Oyster habitat before and after restoration. The object on the right in each photograph is a robotic arm that can be used to pick up an individual oyster. Videos of restored and unrestored habitat can be found in **Web Extension 24.2**. (A after Schulte et al. 2009; B from Schulte et al. 2009.)

ecology, referred to this process as the "acid test" of ecology: "Each time we undertake restoration we are seeing whether, in the light of our knowledge, we can recreate ecosystems that function, and function properly" (Bradshaw 1987).

In some cases, such as the recovery of native oyster populations highlighted in **Figure 24.20**, results quickly suggest that we've passed this acid test. But in others, such as Janzen's efforts to restore tropical dry forests in Guanacaste, the process is likely to be a long and slow one. That is not surprising, since large-scale changes in ecological communities can take many decades, and it can also take a long time for people to change the ways in which we relate to and manage nature. In the next section, we will look more closely at how ecological principles are applied in making decisions about how to manage natural resources sustainably.

CONCEPT 24.4

Ecosystem management is a collaborative process with the maintenance of long-term ecological integrity as its core value.

Ecosystem Management

In 1989, a convoy of logging trucks and about 300 loggers made the journey to a packed public hearing in Olympia, Washington, to defend their jobs. There was talk that the northern spotted owl (*Strix occidentalis caurina*; see Figure 11.18) could be listed as a threatened species under the U.S. Endangered Species Act, which would place its old-growth forest habitat off-limits to logging. Tempers were flaring among loggers and others supported by the timber industry. "When it comes to choosing between owls and the welfare of families, the hell with the owl as far as I'm concerned," said a state politician. At times, some of the testimony was drowned out by the honking of truck horns. The contentious debate about the logging of forests in the Pacific Northwest was reduced to "owls versus jobs" and resulted in bumper sticker and T-shirt slogans, vandalism by both sides, and the exchange of many angry words.

Some people recognized that there might be a better way to make decisions about the use of natural resources. The conflict in the Pacific Northwest was in part the outcome of a long history of top-down management of natural resources with a focus on resource production and extraction. In 1995, a federal Interagency Ecosystem Management Task Force was formed to develop alternatives to this approach (DellaSala and Williams 2006).

Approaches to managing natural resources have become more collaborative over time

Through most of the twentieth century, management of natural resources on U.S. public lands was focused on maintaining individual resources of economic value, whether timber, deer or ducks for hunting, or scenery for visitors. This focus remained at the core of many land management policies until Congress passed the Multiple-Use Sustained-Yield Act of 1960. By the late 1980s, natural resource agencies had gradually expanded their missions to include "multiple use," in recognition that different people had different interests and that it was possible to manage public lands to meet diverse, and at times competing, demands. This was frequently done through spatial compartmentalization of uses, as when different blocks of land were designated as timber extraction zones, recreation zones, or wilderness areas.

Since the 1980s, with our greater awareness of the necessity of preserving biodiversity, our goals for land management have shifted again. The **ecosystem management** approach has emerged as a way to expand the scope of management to include protection of all native species and ecosystems while focusing on the sustainability of the whole system, not just the sustainability of resources of interest.

What is ecosystem management? Most simply stated, it is "managing ecosystems so as to assure their sustainability" (Franklin 1996). A committee of the Ecological Society of America arrived at a less simple but more comprehensive consensus definition in 1996: "Ecosystem management is management driven by explicit goals, executed by policies, protocols, and practices, and made adaptable by monitoring and research based on our best understanding of the ecological interactions and processes necessary to sustain ecosystem structure and function" (Christensen et al. 1996). This definition emphasizes sustainability but also recognizes the need for setting goals and using science to evaluate and adjust management practices over time.

The conflict in the late 1980s over old-growth forests in the Pacific Northwest was a stimulus to ecologists, government land managers, industry, and citizens to seek a less confrontational way to make decisions. Since that time, more collaborative decision making has been combined with better incorporation of science to arrive at management plans that not only attempt to sustain both biodiversity and people's livelihoods, but also are responsive to changing conditions. In ecosystem management, the focus is on a particular biophysical ecosystem, or *ecoregion,* delineated by natural boundaries rather than political boundaries: a watershed, a mountain range, a stretch of coastline. The full range of *stakeholders*—people with some interest in the project—becomes involved in decision making for the ecoregion, joined together by the common goal of maintaining its ecological integrity and economic viability.

Ecosystem management sets sustainable goals, implements policies, monitors effectiveness, and adjusts as necessary

Ecosystem management is a process, one that may be implemented in different ways for different projects. Most ecosystem management projects begin with the gathering of scientific data to define the nature of the problems in the ecosystem. That information is then used to set sustainable goals. To meet those goals, a set of actions is needed, many of which may require adapting new policies. Once a new policy is implemented, the ecosystem is monitored to gauge whether that action brings about the desired result. Adjustments to the policies are then made as needed. In this iterative process, known as **adaptive management** (**Figure 24.21**), management actions are seen as experiments, and future management decisions are determined by the outcome of present decisions.

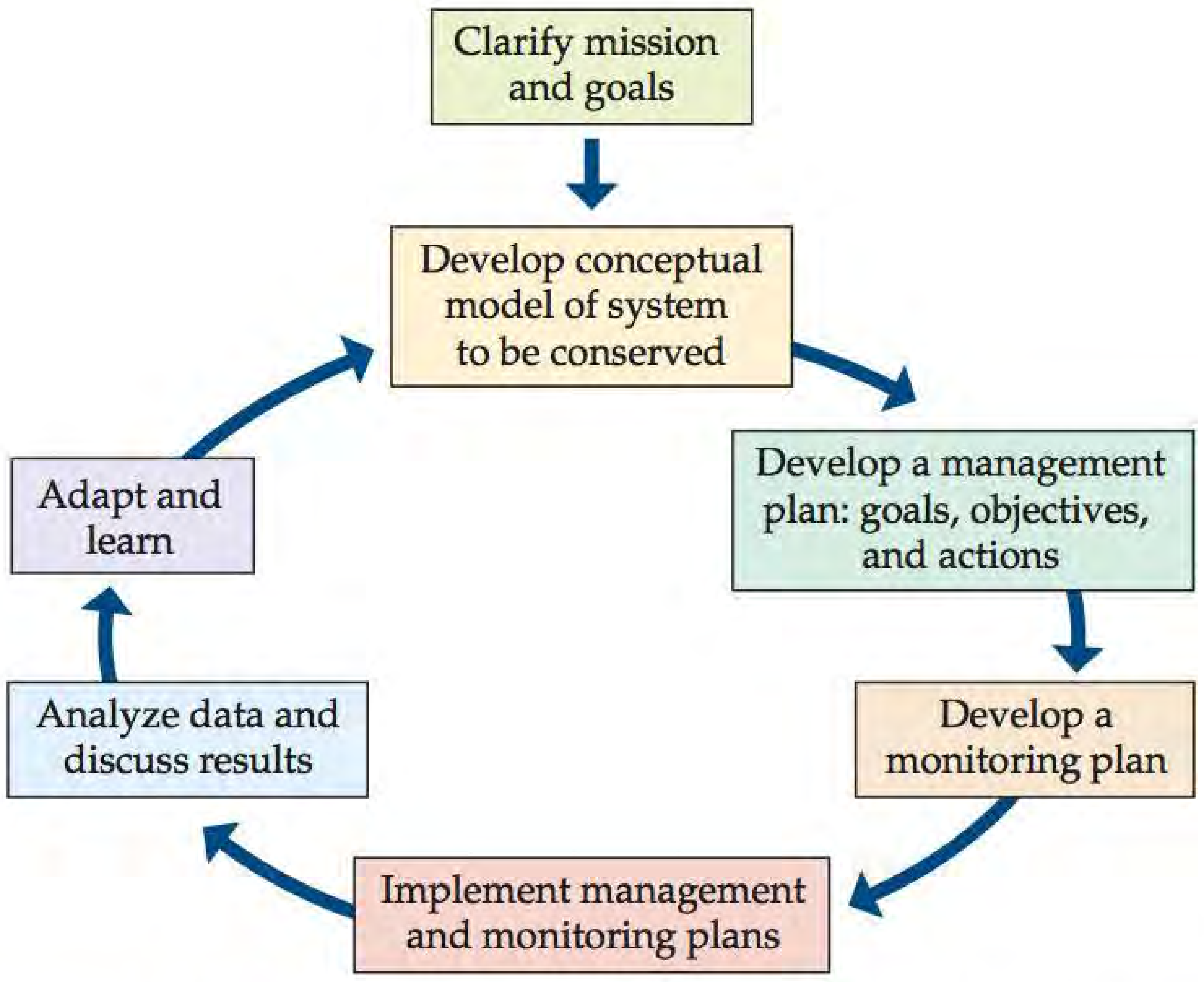


Figure 24.21 Adaptive Management Is a Vital Component of Ecosystem Management Adaptive management is a systematic way of learning from past management actions and adjusting future decisions accordingly. (After Margoluis and Salafsky 1998.)

Monitoring is a vital component of adaptive management. For example, Mark Boyce developed a model predicting elk and wolf population dynamics in Yellowstone National Park following the reintroduction of wolves described in this chapter's Case Study. He and his colleague Nathan Varley have taken an adaptive management approach by adjusting this model based on demographic data from the first 10 years of wolf presence. Since their original model estimated elk numbers well, but underestimated wolf numbers, they knew that some of the model's assumptions needed adjustment (Varley and Boyce 2006). This approach will be important for determining acceptable hunting levels for elk and for future adjustments in response to changing circumstances.

Although it is extremely useful, ecosystem management has limitations and drawbacks. One drawback is that it may take a long time to reach a consensus decision—yet averting an environmental crisis may require that preventative actions be taken immediately. There is also potential for continued conflict generated by those who simply want to disrupt the process, even when extensive efforts at stakeholder involvement have been made. In some instances, a lack of unbiased information, a struggle for power among different government agencies, the presence of corruption, or the unmet needs of the people

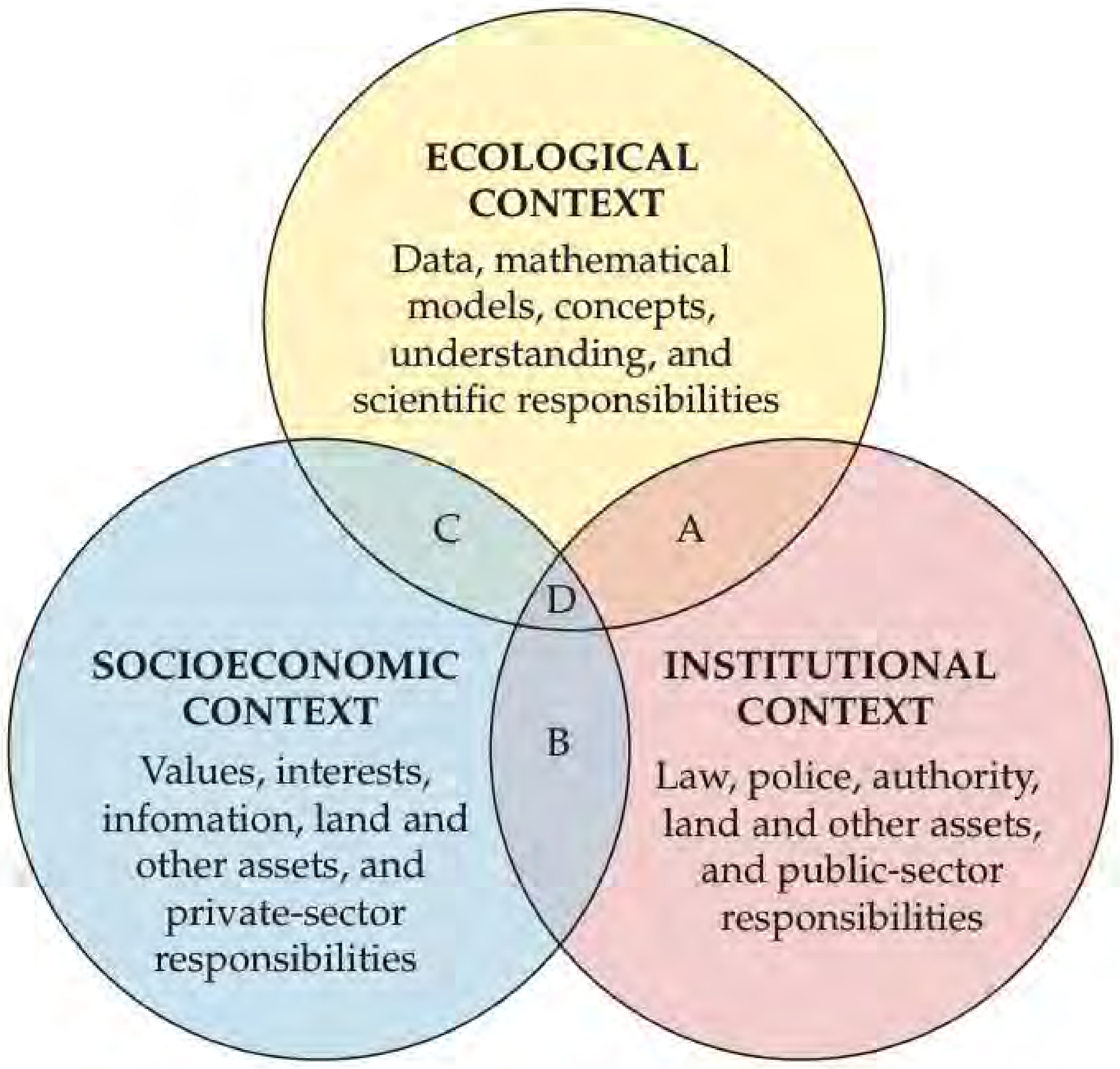


Figure 24.22 Humans Are an Integral Part of Ecosystem Management Ecosystem management integrates interests derived from ecological, institutional, and socioeconomic contexts. The letters represent the overlap of the three contexts: A, zone of regulatory or management authority; B, zone of social obligations; C, zone of informal decisions (as opposed to legal requirements); D, zone of win–win–win partnerships.

in local communities can produce situations that may not lend themselves to participatory governance.

Humans are an integral part of ecosystems

Human actions affect natural ecosystems, and human economies are affected by supplies of natural resources. Ecosystem managers must not only manage natural resources and biodiversity across large landscapes, but also devise plans that protect both natural ecosystems and human economies. Ecosystem management incorporates human social and economic factors as fundamental parts of the decision-making process, along with legal requirements and, of course, ecological integrity (**Figure 24.22**). The integration of these different components is seen as necessary to achieve a successful management outcome.

As we have seen, people need natural ecosystems for many reasons, ranging from the economic to the spiritual. Ecosystem management incorporates education of the public about their reliance on ecosystem services as part of its mission. It also engages the public in helping to solve those problems that degrade the ecosystem services that they rely on.

Any conservation plan that excludes the human component will not be accepted, ultimately, by the stakeholders. The plan for Masoala National Park took the needs of the people living around the park into consideration. Conservation planners not only calculated their wood needs and provided for them in a buffer zone designated for managed forestry, but also surveyed the region for tree species that would have value in an export market and included them in an economic plan for future use. The idea was to remove economic pressure from park resources by identifying ways that people could support themselves and increase their incomes using resources outside the park. In addition, Kremen's team worked in conjunction with local people and with the Malagasy government to develop the plan, recognizing the importance of local acceptance of any proposal they made. In the end, the park plan provided for the economic needs of the people, by identifying forest resources that could be used to enrich the region, as well as for the habitat requirements of all the taxa included in the planners' analysis. While some problems have arisen with time, such as illegal hunting and logging within the park, the original conservation goals have generally been achieved (Kremen 2014).

A CASE STUDY REVISITED

Wolves in the Yellowstone Landscape

The reintroduction of wolves into the Greater Yellowstone Ecosystem in 1995 reflected a shift to an ecosystem management approach to decision making. It was a bold step that followed years of study and preparation. That it happened at all reflects a quantum shift in human attitudes toward nature over the last century. In the late 1800s and early 1900s, wolves were feared and reviled. They were perceived as a threat to people and livestock—an accurate perception as far as livestock were concerned. Wolves were hunted to extinction in the area of Yellowstone National Park by the late 1930s and throughout virtually all of the conterminous United States not long thereafter.

The removal of a top predator can alter the landscape substantially, in part because herbivores whose populations were once controlled by the predator may increase in number and negatively affect vegetation dynamics. In Yellowstone, the growth and reproduction of riparian tree species, such as cottonwoods, aspens, and willows, declined after wolves were removed (Ripple and Beschta 2007). A possible reason was that the trees experienced heavy browsing by herbivores such as elk, which roamed freely along rivers and streams once the wolves were gone. How strong is the support for this explanation?

Many observations are consistent with this idea. The reintroduction of wolves began in the winter of 1995–1996, when 31 wolves captured in Canada were released into the park. Their numbers increased rapidly; by 2004, there were about 250 wolves in the park. Following the reintroduction, populations of elk, the wolves' principal prey, have declined by 50%. Elk were initially naive and very vulnerable to wolf predation, but they have since modified their behavior, showing a preference for foraging in places that provide high visibility (see Figure 8.10). Furthermore, cottonwoods, aspens, and willows have begun

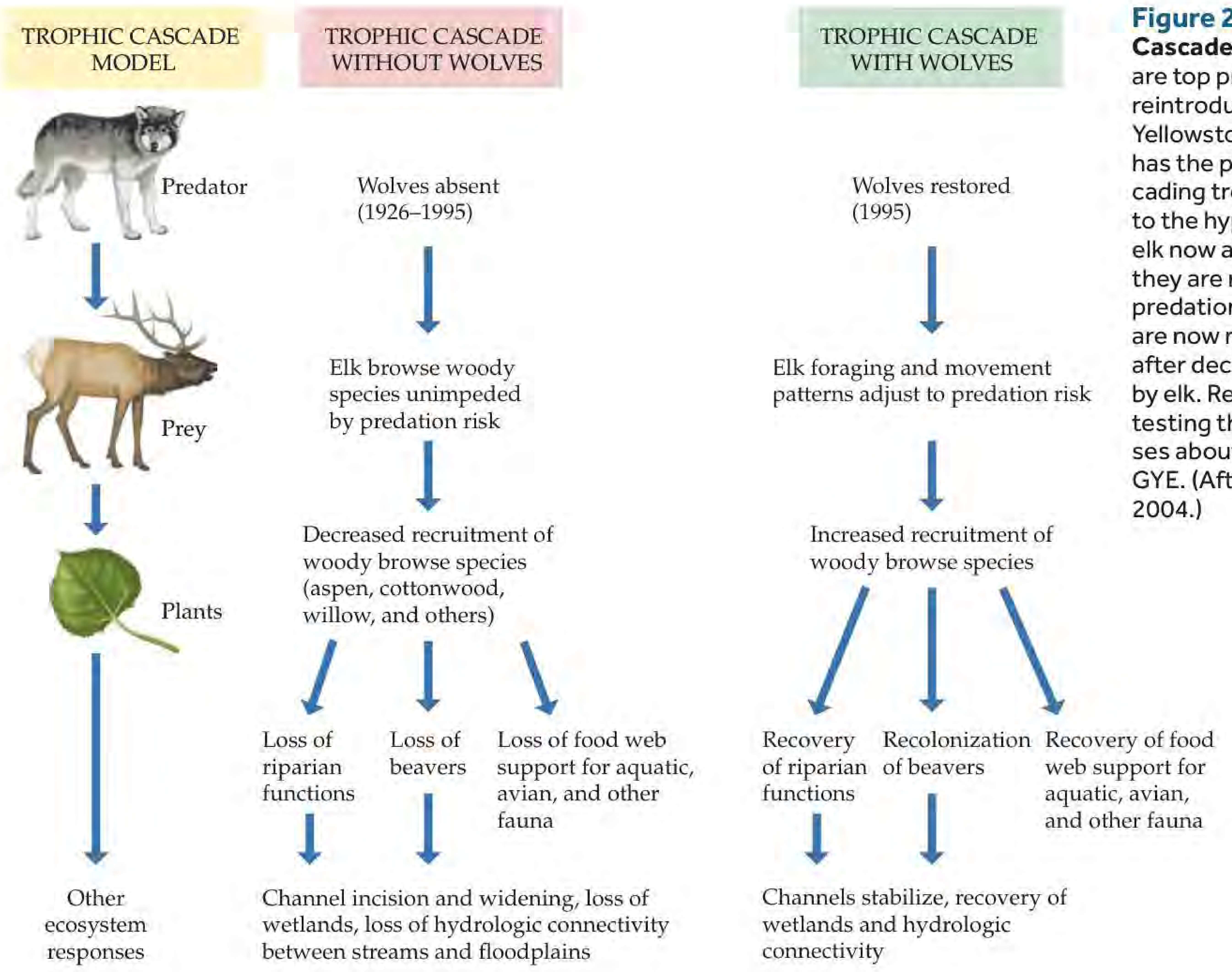


Figure 24.23 A Trophic Cascade Hypothesis Wolves are top predators, and their reintroduction to the Greater Yellowstone Ecosystem (GYE) has the potential to cause cascading trophic effects. According to the hypothesis shown here, elk now avoid those sites where they are most vulnerable to predation, and trees and shrubs are now returning to those sites after decades of suppression by elk. Researchers are actively testing this and other hypotheses about effects of wolves in the GYE. (After Ripple and Beschta 2004.)

to recover in some areas. In some cases, the early signs of recovery appeared to be concentrated in areas where elk face a high risk of predation, such as locations where visibility is poor, escape routes are lacking, or ambush sites are common. Thus, elk may be avoiding areas where they are most vulnerable to attack by wolves, allowing trees in those areas to recover—and possibly leading to a series of other, cascading effects (**Figure 24.23**).

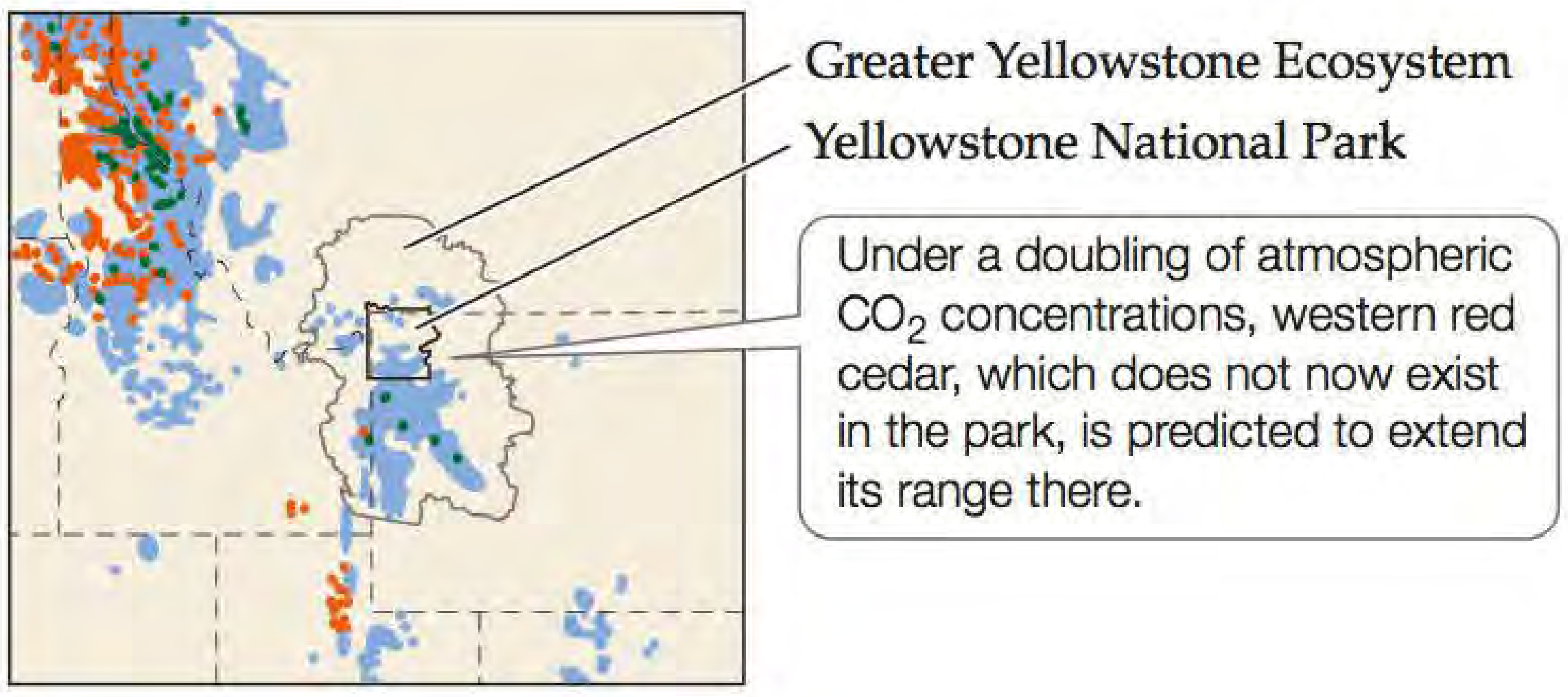
However, some studies have questioned whether a trophic cascade like that diagrammed in Figure 24.23 is occurring. In an experimental test of the hypothesis that elk forage less in areas with wolves, leading to the recovery of woody species in those areas, Kauffman et al. (2010) found that aspen survival was not affected by the presence of wolves. Similarly, Creel and Christianson (2009) found that willow consumption by elk was more strongly affected by snow conditions than by the presence of wolves. Contrary to expectation, willow consumption actually increased when wolves were present. While the reintroduction of wolves may have affected willow and aspen abundance, it may be because predation by wolves has decreased the size of the elk population, not because fear of predation has led to changes in elk foraging behavior. Whatever the outcome of this debate, the reintroduction of wolves provides a wonderful opportunity to test hypotheses about how heterogeneity of a large landscape can be influenced by its component organisms.

CONNECTIONS IN NATURE

Future Changes in the Yellowstone Landscape

If riparian trees continue to increase in abundance in the GYE, a series of cascading effects (like those described in Concepts 16.3 and 21.3) may ensue. In some locations, increased numbers of willows have slowed stream flow and increased sedimentation rates (Beschta and Ripple 2006). The increased growth of riparian tree species is also expected to provide shade and habitat for migratory birds and for trout, which prefer shade-cooled waters. More riparian bird species have been observed in a similarly recuperating ecosystem in Alberta (Hebblewhite et al. 2005). As populations of willows, a preferred food for beavers, have increased, new beaver colonies have appeared. In turn, the dams built by the beavers have changed patterns

(A) Western red cedar (*Thuja plicata*)



(B) Whitebark pine (*Pinus albicaulis*)

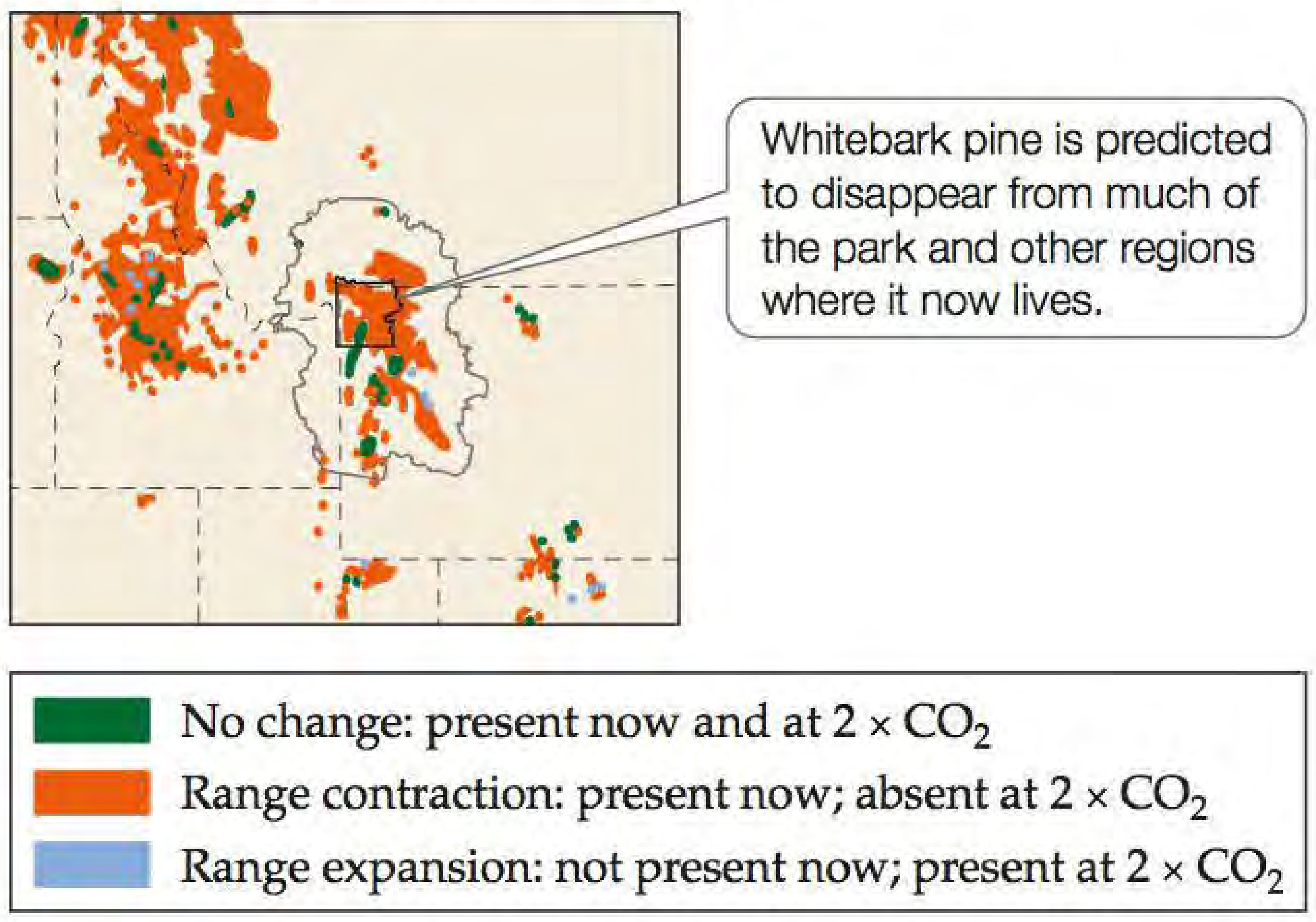


Figure 24.24 Projected Effects of Climate Change in the Northern Rockies Shifts in the distributions of some principal tree species in the northern Rocky Mountains are projected by a model of a future climate driven by twice the current atmospheric CO_2 concentrations. These shifts include (A) the increased distribution of western red cedar, which is currently uncommon in the region, and (B) the near disappearance of whitebark pine. (After Bartlein et al. 1997.)

Figure 24.25 Warm Winters Have Promoted a Devastating Insect Outbreak Once excluded from whitebark pine forests by cold winter temperatures, the mountain pine beetle has expanded its range as temperatures have warmed in recent decades. These beetles have contributed to the death of millions of whitebark pines, which turn red and subsequently grey when they die (as in this forest in Wyoming, USA). In July 2011, the U.S. Fish and Wildlife Service announced that it will list whitebark pine as a candidate species under the Endangered Species Act.

of water flow, creating marshlands that may favor the return of otters, ducks, muskrats, and mink.

Other even more fundamental changes may be taking place in the Yellowstone ecosystem. Recall from Chapters 2–4 that climate is the single most important determinant of where species live. With rising concentrations of greenhouse gases in the atmosphere, climate warming is occurring and will continue in the coming century (see Chapter 25). Will Yellowstone be able to maintain its current biological diversity in the face of global climate change?

A modeling study shows what the vegetation of the region surrounding Yellowstone National Park may look like under a doubling of current atmospheric CO_2 concentrations, which may happen within a century (**Figure 24.24**). Generally, the projections are for higher temperatures, no increase in precipitation, and more frequent fires. Based on these projected changes in the physical environment, the model predicts upslope and northward migrations of many species. These migrations will cause shifts in forest communities, with some species declining within the park and others increasing their range to include the park. Species currently rare in or absent from the GYE that may increase substantially there include gambel oak, western red cedar, and ponderosa pine. A near elimination of whitebark pine is predicted to occur as suitable habitat for that species shifts to the north (Bartlein et al. 1997).

The loss of whitebark pine would have a number of other ecological impacts. This tree is a keystone species that produces large, fatty, and nutritious nuts, an important food source for Clark's nutcracker, as well as for black and grizzly bears. Clark's nutcracker, in turn, is the primary disperser of the whitebark pine's seeds (Tomback 1982). One consequence of warmer winters during the past few decades has been an expansion of the range of the mountain pine beetle (*Dendroctonus ponderosae*) to high-elevation pine forests, including those where whitebark pine grows (Logan and Powell 2001). This beetle has devastating effects on whitebark pine (**Figure 24.25**). Whitebark pine is also being attacked throughout much of its North American range by the fungus *Cronartium ribicola*, an introduced pathogen that causes white pine blister rust (Tomback and Achuff 2010). The combined effects of the mountain pine beetle and blister rust have caused an extensive die-off of whitebark pine, and this die-off has potentially reduced the occurrence of Clark's nutcracker in some areas (McKinney et al. 2009). Loss of whitebark pine also means loss of a food source for grizzly bears. Thus, it appears that climate change and introduced disease are having a major influence on whitebark pine populations, and that these effects have the potential to be transferred to wildlife, such as grizzly bears. (See **Online Climate Change Connection 24.1** for more information on how climate change is affecting biodiversity in forests and other ecosystems.)

As we've seen in this chapter, landscape ecology and the use of tools such as remote sensing and GIS can elucidate current patterns of biodiversity and help us to predict future ones. Over the past 30 years, we have put much effort into selecting, establishing, and undertaking management of new protected areas, but now we need to ask how well those areas will maintain their species in a warmer world. If biodiversity losses are projected under climate change, are there steps we can take now that can improve habitat connectivity, create or improve buffer zones around core natural areas, or restore degraded areas to greater ecological integrity? Or will we need to move species to new areas of suitable habitat, especially if they cannot migrate quickly enough to keep up with climate change?

With a growing human population and growing demands on ecosystems, these challenges will be considerable. Ecologists will have the critical role of providing the scientific information needed to make decisions about how we proceed as a society. The future of untold numbers of species relies on how effective we can be at this task.

Summary

CONCEPT 24.1 Landscape ecology examines spatial patterns and their relationship to ecological processes.

- A landscape is a heterogeneous area made up of a dynamic mosaic of different components that interact through the exchange of materials, energy, and organisms.
- Landscapes are characterized by their composition—the elements that constitute them—as well as by their structure—how those elements are arranged on the landscape.
- Landscape patterns influence ecological processes by determining how easily organisms can move among elements as well as by influencing ecosystem properties such as rates of biogeochemical cycling.
- Landscape patterns both shape and are shaped by disturbances.

CONCEPT 24.2 Habitat loss and fragmentation decrease habitat area, isolate populations, and alter conditions at habitat edges.

- Habitat fragments are biologically impoverished compared with the intact habitat from which they were derived.
- Once a patch of habitat is isolated by fragmentation, organisms reliant on that habitat may be isolated or may be able to cross the intervening matrix to some extent.
- The edges of habitat fragments have different abiotic conditions, and thus have different population dynamics, than interior habitats.
- The isolation of populations and the shifts in ecological communities that result from habitat fragmentation alter the evolutionary process.

CONCEPT 24.3 Biodiversity can best be sustained by large reserves connected across the landscape and buffered from areas of intense human use.

- The ideal spatial configuration for a core natural area is large, compact, and connected to or close to other protected natural areas.
- Core natural areas should be surrounded by buffer zones where human economic uses that are compatible with biodiversity conservation are allowed.
- Habitat corridors are instrumental in facilitating the movements of organisms between natural areas.
- Ecological restoration allows areas that have been degraded to support native species and ecosystem processes once again.

CONCEPT 24.4 Ecosystem management is a collaborative process with the maintenance of long-term ecological integrity as its core value.

- Collaboration among all stakeholders is key to arriving at effective management plans.
- Ecosystem management is a process of setting sustainable goals, developing and implementing land use management policies, monitoring the effectiveness of prior decisions, and adapting plans accordingly.
- Humans are an integral part of ecosystems. Conservation plans that include the economic and social well-being of local human populations are more likely to succeed over the long term.

Review Questions

1. How are islands of terrestrial habitat that result from habitat fragmentation like actual islands surrounded by water? How are they different? How do the principles of island biogeography apply to habitat islands in a fragmented landscape?
2. Are habitat corridors just long, skinny habitat patches? Describe how a corridor is like the habitat blocks it is meant to join and how it is different from them, and outline the implications for organisms using the corridor. Do you think corridors are beneficial? Do you think they are necessary? Why?
3. The western boundary of Yellowstone National Park, where it borders a national forest, is visible from space (check it out with Google Earth at 44°21′45″ N, 111°05′50″ W). Explain this observation in terms of the contrasting missions of a national park and a national forest. What are the ecological implications of these contrasting institutional functions for biodiversity? For ecosystem management?

Hone Your Problem-Solving Skills

One of the criteria used in determining the design of nature reserves is the shape of the habitat patch, which gives an indication of the amount of edge versus area of core habitat. Some species have greater needs for edge habitat, while others are negatively impacted by edges. Consider **Figure A**, indicating the sensitivity of three bird species to the shape of a habitat patch, estimated as the ratio of perimeter (length) to area.

Figure A

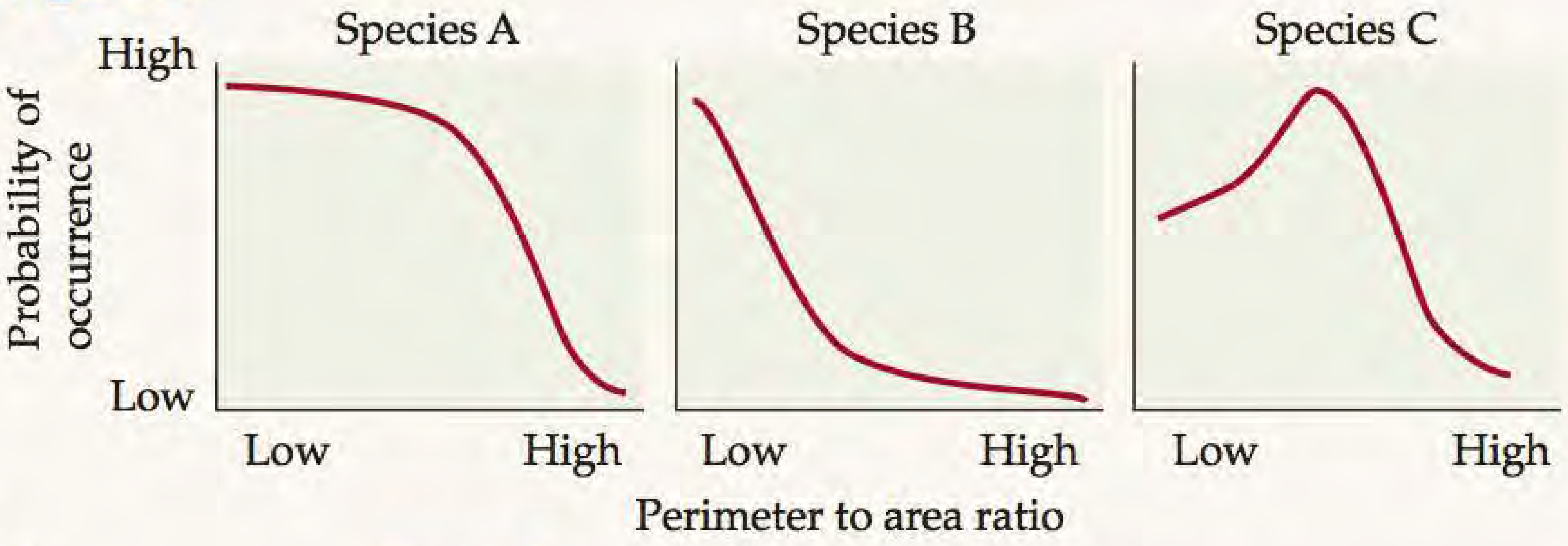


Figure B

1. Each of the three bird species is likely to do better in either design 1 or design 2 shown in the maps of habitat patches (**Figure B**). What is your prediction?
2. Describe some of the ecological considerations that might positively or negatively impact the response of a species to a habitat edge. Consider factors such as food preference, predation risk, physical environment, and reproduction.

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

24.1 You Can't Get There from Here: Movement in Heterogeneous Landscapes

Web Extensions

24.1 Habitat Islands and the Eastern Wallaroo

24.2 Effects of an Ecological Restoration Experiment

Online Climate Change Connection

24.1 Effects of Climate Change on Biodiversity

25 Global Ecology

KEY CONCEPTS

CONCEPT 25.1 Elements move among geologic, atmospheric, oceanic, and biological pools at a global scale.

CONCEPT 25.2 Earth is warming because of anthropogenic emissions of greenhouse gases.

CONCEPT 25.3 Anthropogenic emissions of sulfur and nitrogen cause acid deposition, alter soil chemistry, and affect the health of ecosystems.

CONCEPT 25.4 Losses of ozone in the stratosphere and increases in ozone in the troposphere both pose risks to organisms.

Dust Storms of Epic Proportions: A Case Study

Dust is usually a subtle nuisance for most city dwellers, a reminder of neglect and lax housekeeping. Living in islands of asphalt and concrete, most urbanites see little bare soil, let alone clouds of blowing dust in the sky. Yet in late spring of 1934, a massive dust storm shrouded the U.S. cities of Chicago and New York in a dark haze never seen before by their residents. People choked on the dust, and it burned their eyes. Twelve million tons of dust fell on Chicago—4 pounds for each resident—and an estimated 350 million tons of dust were carried by the storm to the Atlantic Ocean. As frightening as this event was to city dwellers, farmers in the southern Great Plains had suffered through multiple years of frequent severe dust storms throughout the 1930s (**Figure 25.1**). During this period, many people in that region, known as the Dust Bowl, suffered from an often fatal dust-induced pneumonia similar to the black lung disease that was killing coal miners.

Beijing, China, has experienced comparable dust storms since the mid-1990s, associated with widespread storms that affect China, South Korea, and Japan. An April 2006 storm dropped more than 300,000 tons of dust on Beijing. Residents were encouraged to stay indoors to avoid inhaling the dust and getting it in their eyes. Many of those brave enough to venture out wore surgical face masks to protect their lungs. Some residents lined their windows and doors with rags in an attempt to keep the dust out of their houses and apartments. More intense and frequent dust storms have occurred in the Middle East in the past decade. One storm in August 2015 was so bad that ports and airports throughout the region had to close. Several deaths and thousands of injuries were attributed to the dust.

Large dust storms in urban areas are perceived as rare events, potentially linked to unsustainable land use practices such as overgrazing or farming on marginal lands. In the examples mentioned above, farming and grazing in arid areas had increased prior to the dust storms. There is evidence, however, that massive dust storms occur at regular, but infrequent, intervals irrespective of human activities, moving large amounts of soil across whole continents. Over the past century, these events have been associated with prolonged droughts. The urban dust storms in the United States during the 1930s were associated with a decade-long drought in the Dust Bowl (**Figure 25.2**). Similarly, the Beijing dust storms of the past two decades have been associated with drought in Mongolia. The increase in the Middle

Figure 25.1 **A Massive Dust Storm** A wall of dust approaches the town of Rolla, Kansas, May 6, 1935, in this photograph taken from a 100-foot high water tower. This storm was one of several "black dusters" that swept through the Dust Bowl during the 1930s.

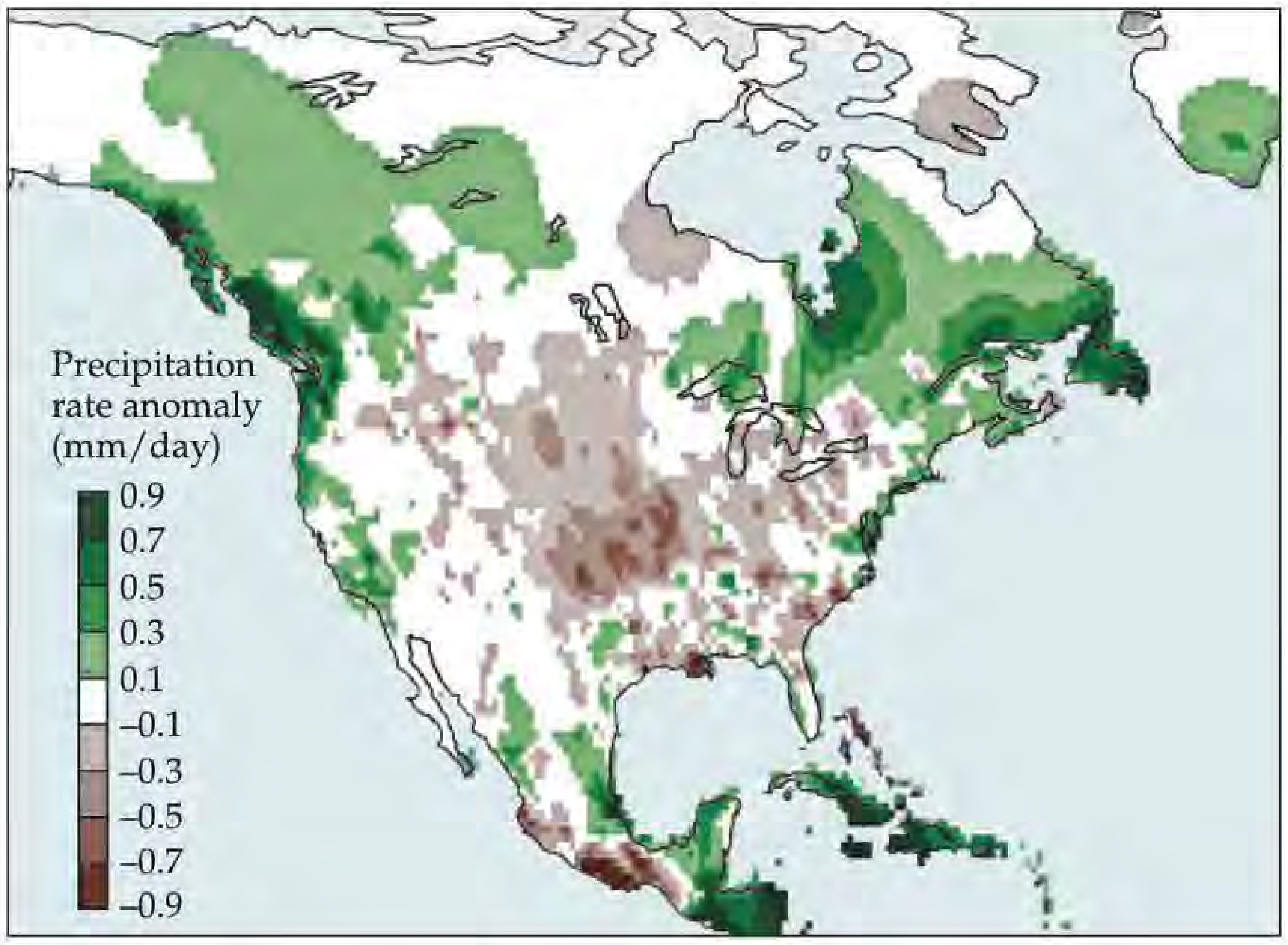


Figure 25.2 Drought in the Southern Plains During the 1930s, the southern Great Plains of the United States experienced the driest weather on record. The drought, in combination with loss of vegetation cover, created conditions conducive to dust input into the atmosphere. The values shown are anomalies (differences between averages for the period 1932–1939 and long-term averages). (After Cook et al. 2009.)

East dust storm frequency has been attributed to climate change and diversion of rivers for agriculture.

Dust in the atmosphere is made up of soil particles blown from regions that lack vegetative cover to protect their soils from the wind. As discussed in Chapters 4 and 22, soils are important as sources of nutrients, determinants of terrestrial moisture availability, and habitat for organisms. Therefore, the redistribution of soils from one area to another has the potential to cause ecological change. How widespread are these ecological effects? What role have humans played in the dust storms of the past century? As we will see in this chapter, the movement of dust is an important component in the movement of elements at the global scale.

Introduction

In Chapter 22, we reviewed the cycling of nutrients within ecosystems associated with biological uptake and decomposition. The movements of these biologically important elements are linked at a global scale that transcends ecological boundaries at the ecosystem and biome scales. Ecological processes at the ecosystem scale (e.g., net primary production, decomposition) influence global phenomena (e.g., greenhouse gas emissions and uptake). In addition, the realization that humans are increasingly changing the physical and chemical environment at a global scale has fostered a greater awareness of ecology at these larger spatial scales. Emissions of pollutants, dust, and greenhouse gases into the atmosphere have caused widespread environmental problems, including climate change, acid precipitation, eutrophication, and loss of stratospheric ozone. A major focus of global ecology is therefore the study of the extensive environmental effects of human activities.

The first part of this chapter will cover the global-scale cycles of chemical elements, which are related to, but distinct from, the ecosystem-scale cycles covered in Chapter 22. Knowledge of these cycles is important for understanding global environmental change. Humans have had profound effects on these element cycles, and the environmental changes associated with these effects will be discussed in the remaining sections.

CONCEPT 25.1

Elements move among geologic, atmospheric, oceanic, and biological pools at a global scale.

Global Biogeochemical Cycles

In this section, we will follow the biogeochemical cycling of carbon, nitrogen, phosphorus, and sulfur at the global scale. These particular elements are emphasized both because of their importance to biological activity and because of their roles as pollutants. The cycles are discussed in terms of *pools*, or reservoirs—the amounts of elements within components of the biosphere—and *fluxes*, or rates of movement, between pools. For example, terrestrial plants constitute a pool of carbon, while photosynthesis represents a flux—in this case, the movement of carbon from the atmospheric pool to the terrestrial plant pool.

Carbon cycles dynamically at the global scale

Carbon (C) is critically important for life because of its role in energy transfer and the construction of biomass. At a global scale, C that is actively cycling is relatively dynamic, moving between atmospheric, terrestrial, and oceanic pools relatively quickly (over weeks to decades). It is important that we understand the global C cycle because changes in the fluxes of C among these pools are influencing Earth's climate system. Carbon in the atmosphere occurs primarily as carbon dioxide (CO_2) and methane (CH_4). As we saw in Chapter 2, both of these greenhouse gases influence atmospheric absorption of infrared radiation and its reradiation from Earth's surface. Thus, any changes in the atmospheric concentrations of these gases can have profound effects on the global climate, as we will see later in this chapter.

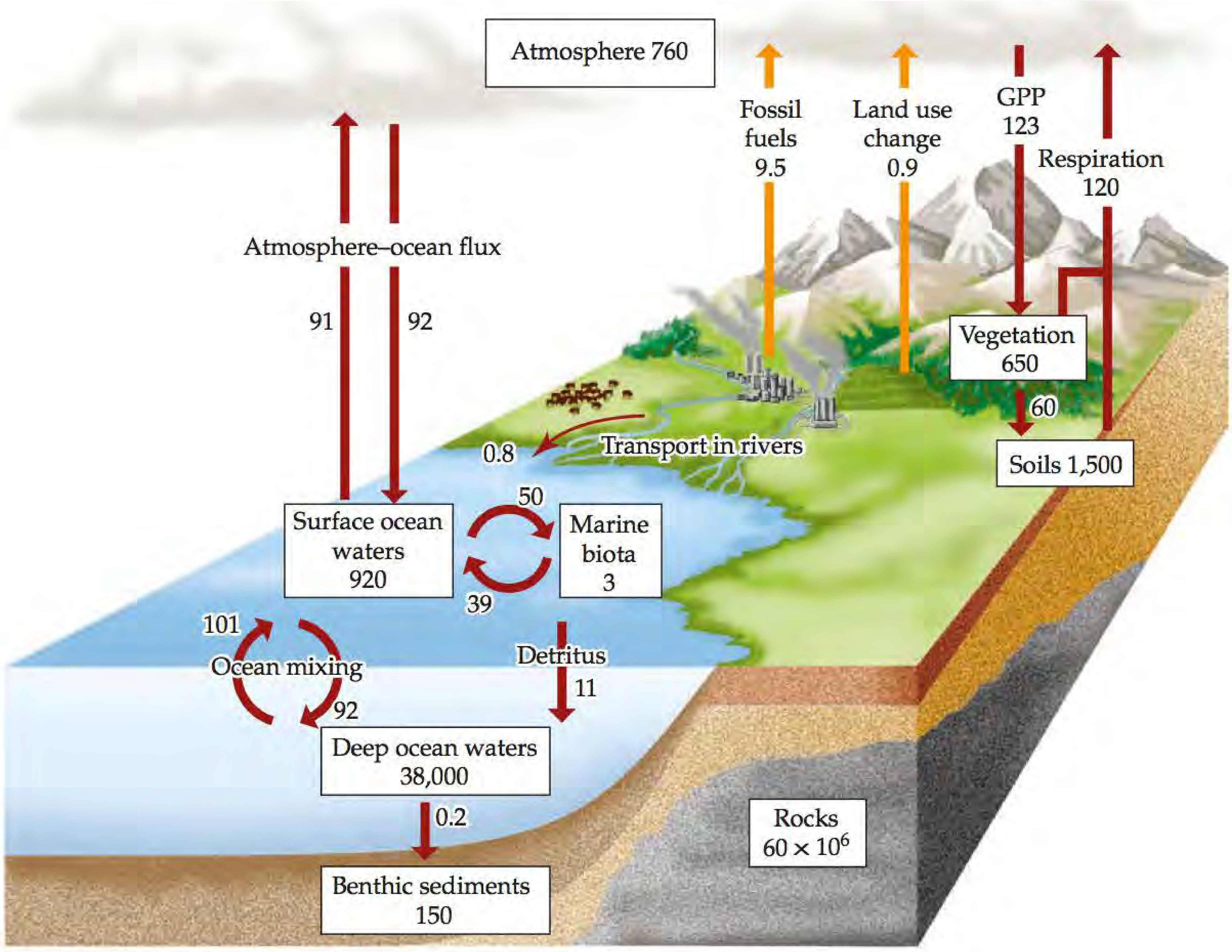


Figure 25.3 The Global Carbon Cycle Boxes represent major pools of C, measured in petagrams (1 Pg = 10^{15} g). Arrows represent major fluxes of C, measured in petagrams per year; anthropogenic fluxes are shown in orange. Note that the largest fluxes are terrestrial gross primary production (GPP) and respiration. (Additional data from IPCC 2013.)

? How would deforestation influence the magnitude of carbon fluxes?

There are four major global pools of C: atmosphere, oceans, land surface (including soils and vegetation), and sediments and rock (**Figure 25.3**) (Schlesinger and Bernhart 2013). The largest of these pools is the combination of sediments and rock, which contain 99% of global C. The C in this pool is found primarily in the form of carbonate minerals and organic compounds. It is the most stable of the major pools, taking up and releasing C on geologic time scales.

The oceanic pool consists of two main components: surface waters (to depths of 75–200 m), where most marine biological activity occurs, and deeper, colder waters. Carbon dioxide dissolves in ocean water because of the concentration gradient between the atmosphere (which has a higher concentration) and the ocean (which has a lower concentration). There is relatively little mixing between ocean surface waters and deeper waters, although C is transferred between them by the sinking of detritus and carbonate shells of marine organisms and by the downwelling of polar ocean currents described in Concept 2.2. Most of the C in the oceans (>90%) is in the deeper waters. Some flux from this deep ocean pool occurs when upwelling brings carbon-rich water to the surface, releasing CO_2 into the atmosphere.

The terrestrial pool, which includes vegetated and nonvegetated land surfaces and their associated soils, is the largest pool of biologically active C. The soil pool contains approximately twice as much C as the vegetation pool. The terrestrial pool exchanges C with the atmospheric pool primarily through photosynthetic uptake of CO_2 by plants and respiratory CO_2 release by plants and heterotrophs. Prior to the Industrial Revolution that began in the early nineteenth century, the exchanges between these two pools were roughly equal, with no net change in atmospheric CO_2.

As a result of the rapid growth of the human population over the past 160 years and associated industrial and agricultural development, there has been an increase in the release of C to the atmosphere from the terrestrial pool. This **anthropogenic** (human-associated) release of C is the result of land use change—mainly in the form of forest clearing for agricultural development—and the burning of fossil fuels. Prior to the mid-nineteenth century, deforestation was the largest contributor to anthropogenic C release to the atmosphere. Removing the forest canopy warms the soil surface, increasing rates of decomposition and heterotrophic respiration. Burning of the trees also releases CO_2, as well as small amounts of carbon monoxide (CO) and CH_4, into the atmosphere. During the last half of the twentieth century, deforestation for agricultural development shifted from the mid-latitudes of the Northern Hemisphere to the tropics.

The rate of anthropogenic emission of C into the atmosphere has continued to increase in recent decades. In 1970, anthropogenic CO_2 emissions added C to the atmosphere at a rate of 4.1 petagrams (1 Pg = 10^{15} g) per year; by 2011, this rate had more than doubled to 10.4 Pg C per year (IPCC 2013). Today, burning of fossil fuels accounts for approximately 90% of the anthropogenic C flux to the atmosphere; the remaining 10% is associated with deforestation. Approximately half of these anthropogenic CO_2 emissions are taken up by the oceans and terrestrial biota. This proportion will decrease with time, however, as the uptake of CO_2 by terrestrial and marine ecosystems will not keep pace with the rate of emissions to the atmosphere (IPCC 2013).

Emissions of CH_4 to the atmosphere from the terrestrial pool have also increased as a result of human activities. Although atmospheric concentrations of CH_4 are much lower than those of CO_2, even small increases in CH_4 could influence the global climate because it is 25 times more effective as a greenhouse gas per molecule than CO_2. Methane is emitted naturally by anaerobic methanogenic archaea that live in wetlands and shallow marine sediments. Methanogenic archaea in the rumens of ruminant animals are also a source of atmospheric CH_4. Anthropogenic emissions of CH_4 have doubled since the early nineteenth century as a result of the processing and burning of fossil fuels, agricultural development (primarily that of rice, which is grown in flooded fields), burning of forests and crops, and livestock production (IPCC 2013). As a result, atmospheric CH_4 concentrations have more than doubled over the past 2 centuries.

The process of photosynthesis is sensitive to the concentration of CO_2 in the atmosphere. As a result, we might expect increases in rates of photosynthesis as anthropogenic CO_2 emissions increase, primarily in plants with the C_3 photosynthetic pathway (see Concept 5.3). Experiments have shown, however, that for some herbaceous plants, these increases may be short-term because the plants may become acclimatized to elevated CO_2 concentrations. For other plants, such as forest trees, increases in photosynthetic rates may be more sustained.

It is extremely important that we understand the response of forest ecosystems to elevated CO_2 concentrations. Because much of terrestrial net primary production (NPP), and thus C uptake, occurs in these ecosystems, their response will have a profound effect on the fate of anthropogenic CO_2 emissions. However, it is difficult to manipulate atmospheric CO_2 concentrations experimentally in an intact forest. In one successful approach, called free-air CO_2 enrichment, or FACE, researchers inject CO_2 into the air through vertical pipes surrounding stands of trees while monitoring the atmospheric concentration of CO_2 within the experimental stands. The rate of CO_2 injection is controlled to maintain a relatively constant elevated level.

Figure 25.4 A FACE Experiment The circles visible in this aerial photo are free-air CO_2 enrichment (FACE) treatment rings in a loblolly pine (*Pinus taeda*) forest in the Duke Forest in North Carolina. Carbon dioxide is released from plastic pipes surrounding treatment plots at a rate calculated to raise the CO_2 concentration to 200 ppm above ambient atmospheric CO_2 concentrations. (Courtesy of Evan DeLucia.)

A FACE experiment was used by Evan DeLucia and his colleagues to investigate the ecosystem effects of elevated CO_2 concentrations in a young loblolly pine (*Pinus taeda*) forest in North Carolina (DeLucia et al. 1999) (**Figure 25.4**). The experiment was initiated in 1997, when three plots exposed to elevated CO_2 concentrations and three control plots exposed to ambient CO_2 concentrations were established. The researchers used measurements of tree basal area to estimate aboveground NPP and repeated collections of soil cores to estimate fine root growth and belowground NPP. DeLucia and his colleagues found that the elevated CO_2 concentrations increased the overall NPP of the forest by 25%. Input of C into the soil, from both aboveground litter and belowground fine root turnover, also increased. The results of this experiment indicated that forests may be an important sink for anthropogenic CO_2. However, DeLucia et al. suggested that their young forest stand represents the upper limit of potential CO_2 uptake and that older forests, and forests with lower water and nutrient supplies, may not have as great a capacity to take up CO_2. Results from other FACE experiments in forest ecosystems have found similar responses to elevated CO_2 concentrations (an average increase in NPP of 23%; Norby et al. 2005). The greater productivity observed in forests in the Northern Hemisphere over the past 5 decades may be related in part to elevated atmospheric CO_2 concentrations (Graven et al. 2013), verifying the predictions of the FACE experiments.

Changing atmospheric CO_2 concentrations directly alter the acidity (pH) of the oceans by affecting the rate

ANALYZING DATA 25.1

How Much Will Ocean pH Drop in the Twenty-First Century?

Ocean acidification is one of the consequences of increased anthropogenic CO_2 emissions. There is already substantial evidence that the pH of ocean waters is declining (**Figure A**). Using information about the chemistry of seawater and diffusion of CO_2 from the atmosphere, marine geochemists have projected that the pH of the ocean will have decreased to 7.9 by the year 2050, and by 2100 it will be 7.75, assuming "business as usual" CO_2 emissions (a continued increase in the rate of emissions growth) during the twenty-first century (IPCC 2013).*

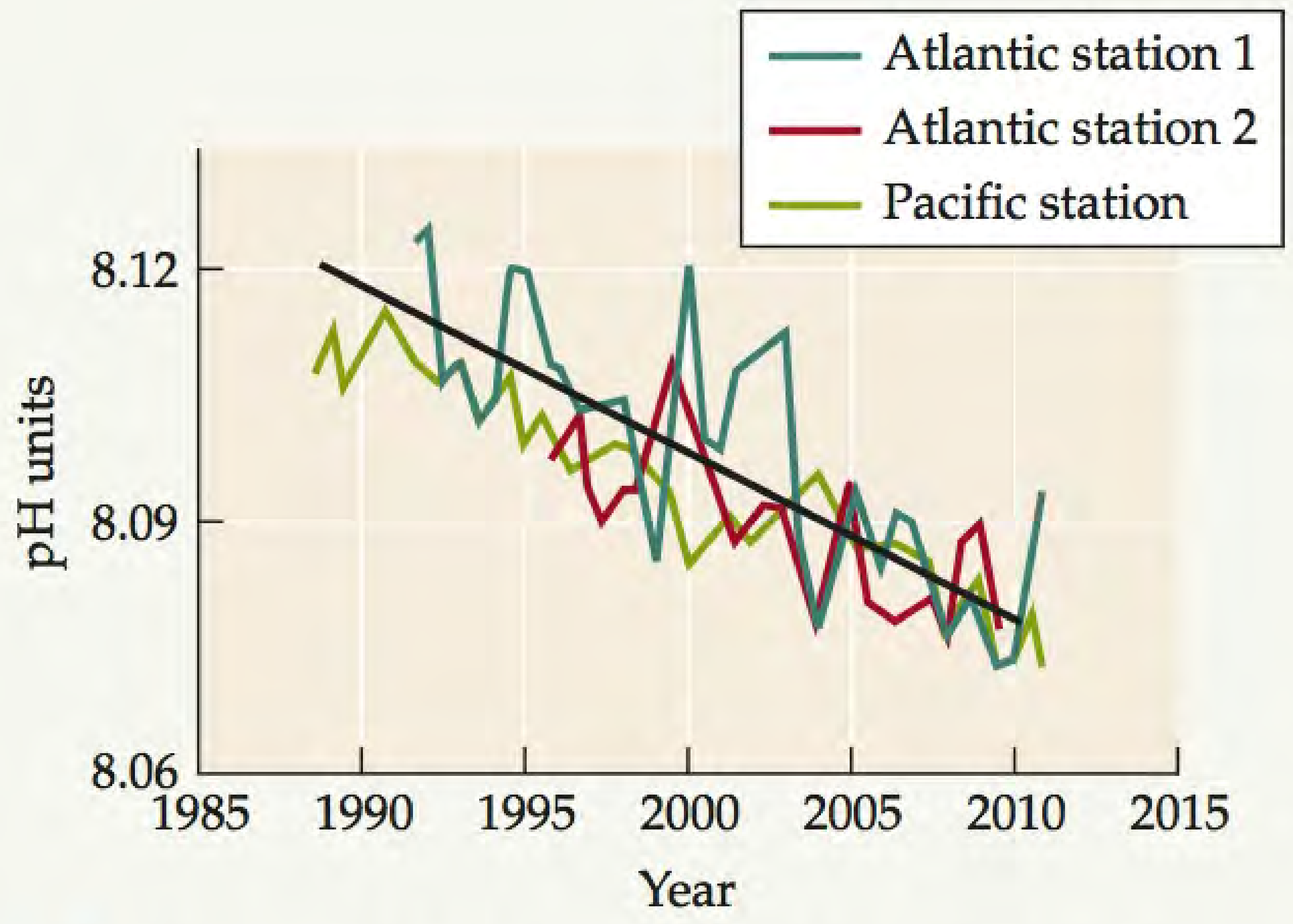


Figure A **Measured Trend in Ocean pH for Two Stations in the Atlantic Ocean and One in the Pacific Ocean**
(After IPCC 2013.)

1. Using the data in Figure A, derive a simple linear mathematical relationship or draw a graph to come up with your own prediction of the ocean pH in the years 2050 and 2100. How well do your predictions match up with the IPCC's predictions based on seawater chemistry and continued increases in atmospheric CO_2? Your answer should give you a higher estimated ocean pH than the one predicted in the IPCC report. What might account for this discrepancy?
2. The decrease in ocean pH is already affecting the calcification rates of marine organisms, as indicated for corals in Figure 25.5. To get a view of what may occur with an even more CO_2-rich future, Uthicke et al. (2013)† studied the abundance and diversity of foraminiferans (zooplankton that form carbonate shells) in sediments around natural CO_2 seeps in the ocean (**Figure B**). Using your own and the IPCC's prediction of change in ocean pH from Question 1 and the relationships shown in Figure B, estimate the percentage decrease in abundance (density) and species richness of foraminiferans from 2000 (pH = 8.10) to 2050 and from 2000 to 2100.

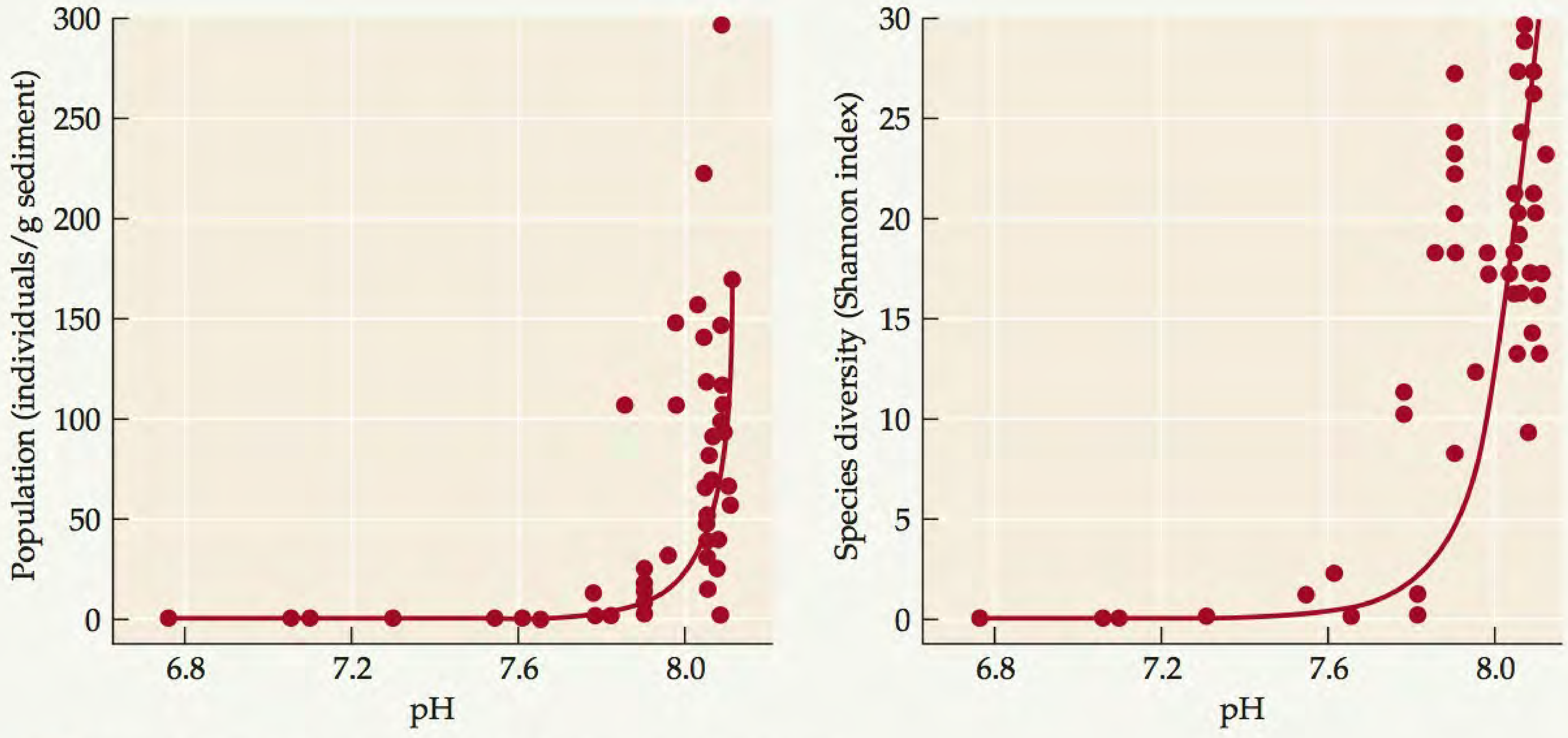


Figure B **Influence of Ocean pH on the Density and Species Richness of Foraminiferans near Natural CO_2 Seeps**
(After Uthicke et al. 2013.)

See the companion website for a similar ANALYZING DATA exercise.

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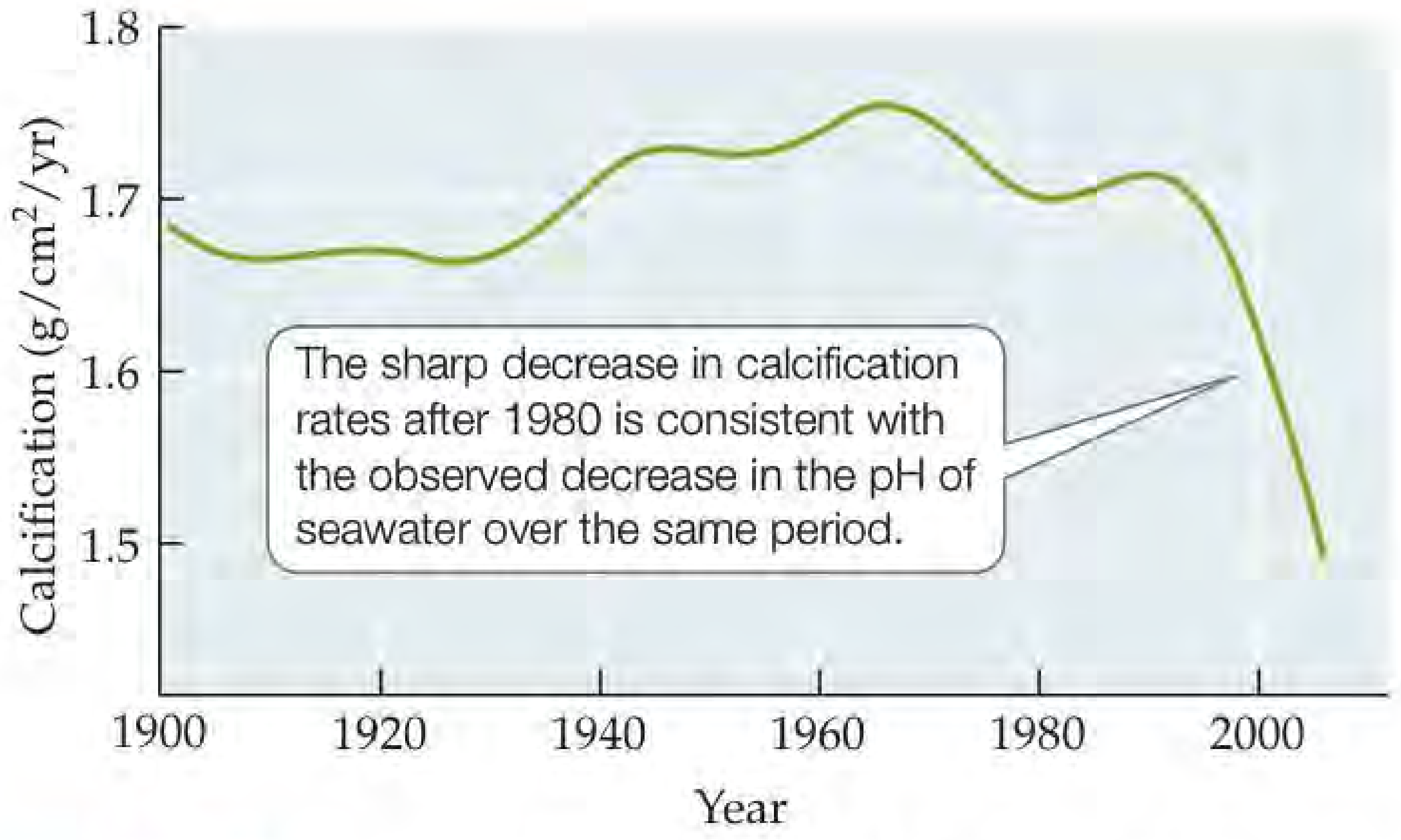
*IPCC. 2013. *Climate Change 2013: The Physical Science Basis.* Available at the IPPC website: www.ipcc.ch/report/ar5/wg1.

†Uthicke, S., P. Momigliano and K. E. Fabricius. 2013. High risk of extinction of benthic foraminifera in this century due to ocean acidification. *Scientific Reports* 3: 1–5.



The sharp decrease in calcification rates after 1980 is consistent with the observed decrease in the pH of seawater over the same period.

Figure 25.5 Rates of Calcification of Corals on Australia's Great Barrier Reef, 1900–2005 The sharp decline in calcification rates after 1980 is associated with the combined effects of decreasing pH and increasing ocean water temperature. (After De'ath et al. 2009.)

at which CO_2 diffuses into seawater. Greater diffusion of CO_2 into seawater enhances the formation of carbonic acid, which lowers the pH of the seawater:

$$CO_2 + H_2O \rightleftharpoons H_2CO_3 \text{ (carbonic acid)} \rightleftharpoons H^+ + HCO_3^- \text{ (bicarbonate)} \rightleftharpoons 2\ H^+ + CO_3^{2-} \text{ (carbonate)}$$

During the past century, ocean acidity has increased by about 30%. Further increases have been forecast using model simulations incorporating the expected increases in anthropogenic CO_2 emissions over the twenty-first century (Caleira and Wickett 2003). The predicted increases will have two negative effects on marine organisms that form their protective external shells from calcium carbonate, including corals, mollusks, and many plankton. First, the increase in acidity will dissolve the existing shells of the organisms. Second, lower concentrations of carbonate in seawater will decrease the organisms' ability to synthesize shells (Feely et al. 2004; Orr et al. 2005). Between 1990 and 2009, the rate of formation of calcium carbonate by corals on Australia's Great Barrier Reef declined by 14%, an amount consistent with observed decreases in the pH of seawater (**Figure 25.5**) (De'ath et al. 2009). Both effects will increase mortality and lower the abundances of marine organisms that rely on calcium carbonate, altering the diversity and function of marine ecosystems. (Make your own prediction of the future of ocean pH and its effect in **Analyzing Data 25.1**.)

Atmospheric concentrations of C have changed dynamically throughout Earth's history in association with geologic and climate changes. Concentrations of CO_2 have ranged from greater than 3,000 parts per million (ppm) 60 million years ago to less than 200 ppm 140,000 years ago. Over the past 400,000 years, variations in the concentrations of CO_2 and CH_4, as measured in tiny bubbles preserved in polar ice, have followed glacial–interglacial cycles (see Concept 2.5). The lowest CO_2 concentrations during this time were associated with glacial periods (**Figure 25.6**). Over most of the past 12,000 years, atmospheric CO_2 concentrations remained relatively stable, varying between 260 and 280 ppm. Since the mid-nineteenth century, however, CO_2 concentrations have increased at a rate faster than at any other time over the past 400,000 years (IPCC 2013), reaching values of 404 ppm in 2016. Even if we dramatically decreased our CO_2 emissions starting today, atmospheric CO_2 concentrations would remain elevated for a long time to come because of a time lag (decades to centuries) in oceanic uptake. The influence of CO_2 and CH_4 on climate change will be discussed later in this chapter.

Biological fluxes dominate the global nitrogen cycle

Nitrogen (N) plays a key role in biological processes as a constituent of proteins and enzymes, and it is one of the resources that most commonly limits primary production, as we saw in Concept 20.2. Thus, cycles of N and C are tightly coupled through the processes of photosynthesis and decomposition.

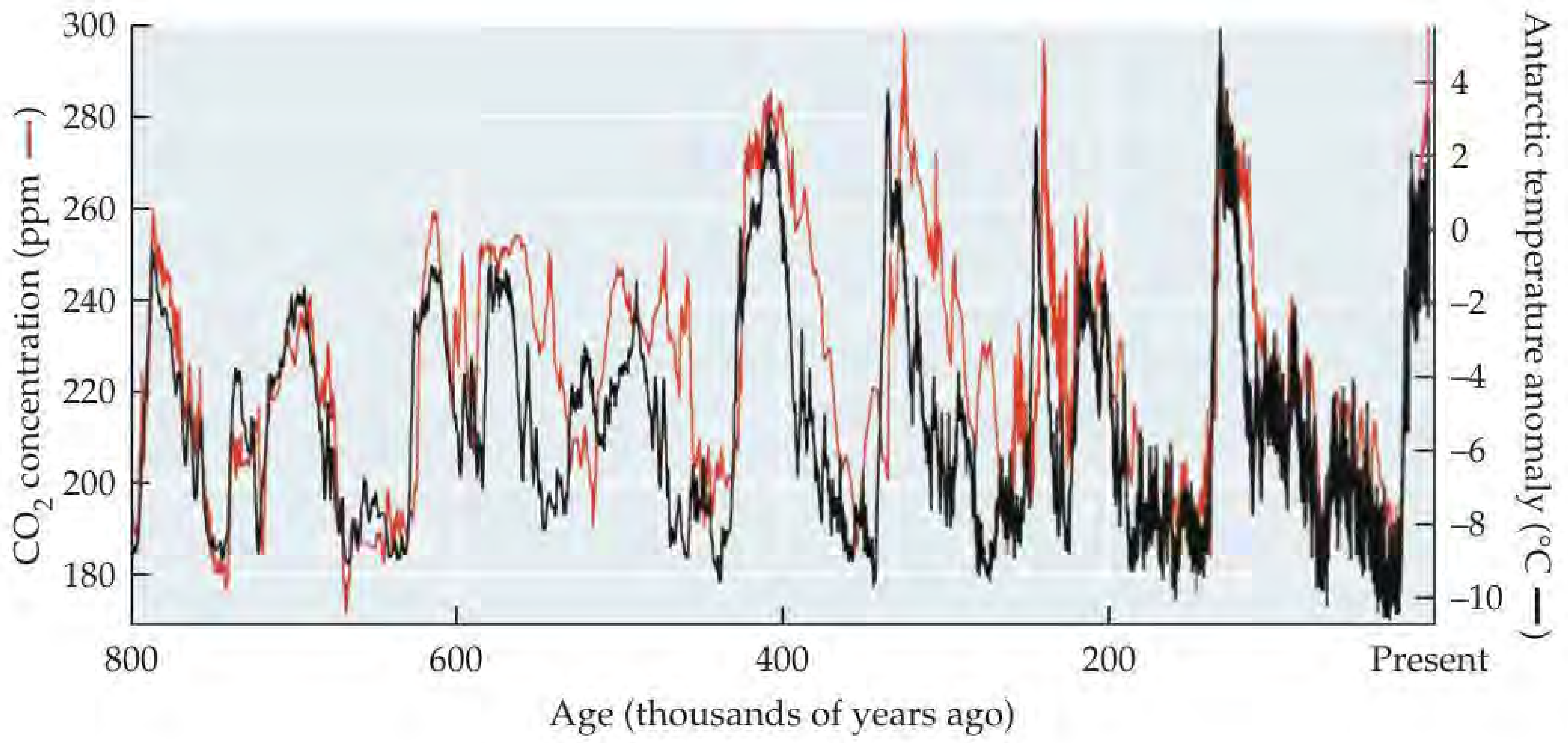


Figure 25.6 Changes in Atmospheric CO_2 Concentrations over Time Atmospheric CO_2 concentrations have varied with temperature over the past 800,000 years. These gas concentrations were measured in bubbles trapped in Antarctic ice; temperatures were estimated using oxygen isotopic analyses (see Ecological Toolkit 5.1). (After Lüthi et al. 2008.)

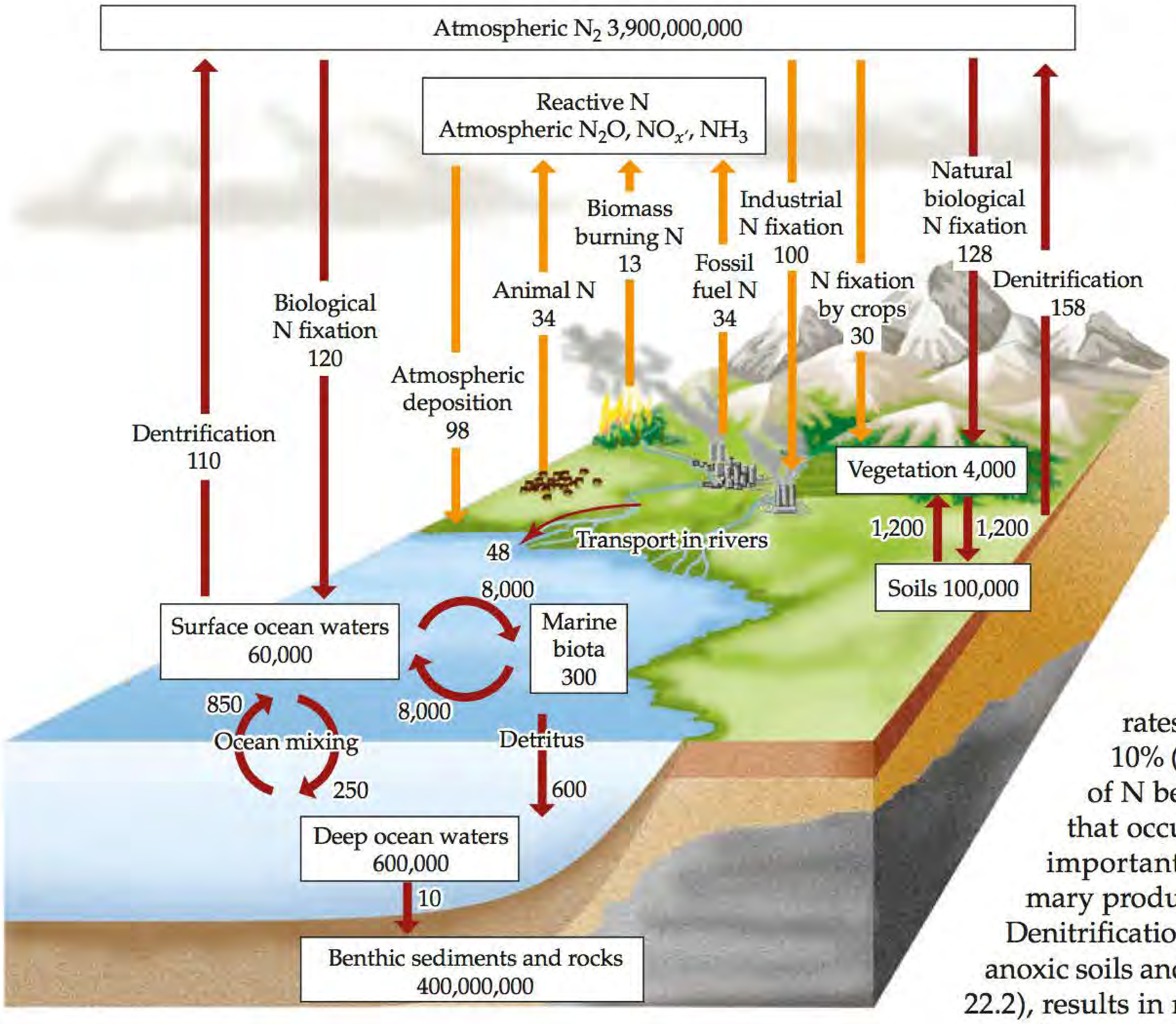


Figure 25.7 The Global Nitrogen Cycle Boxes represent major pools of N, measured in teragrams (1 Tg = 10^{12} g). Arrows represent major fluxes of N, measured in teragrams per year; anthropogenic fluxes are shown in orange. The percentage of the total atmospheric N pool made up of reactive N is minuscule (it is also difficult to quantify because it is very dynamic). (After Cleveland et al. 1999; Galloway et al. 2004.)

? Given its small size, why is the reactive pool of N of such great interest?

The largest pool of N (>90%) is atmospheric dinitrogen gas (N_2) (**Figure 25.7**). This form of N is very stable chemically and cannot be used by most organisms, with the important exception of nitrogen-fixing bacteria, which are able to convert it to more chemically usable forms, as described in Concept 22.1. These fixed chemical compounds are referred to as *reactive* N because, unlike N_2, they can participate in chemical reactions in the atmosphere, soils, and water. Terrestrial N_2 fixation by bacteria provides approximately 128 teragrams (1 Tg = 10^{12} g) of reactive N per year (Cleveland et al. 1999; Galloway et al. 2004) and supplies 12% of the annual biological demand (Schlesinger and Bernhart 2013). The remaining 88% is met by uptake of N from the soil in forms released by decomposition. Oceanic N_2 fixation contributes another 120 Tg to the biosphere annually. Geologic pools associated with sediments containing organic matter represent a much smaller fraction of global N than of global C, but some N-rich sedimentary sources may be important sources in some sites (Morford et al. 2016).

Although the pools of N at land and ocean surfaces are relatively small, they are very active biologically, and they are held tightly by internal ecosystem cycling processes. Fluxes from these pools are small relative to the rates of internal cycling, usually less than 10% (Chapin et al. 2002). The natural flux of N between terrestrial and oceanic pools that occurs via rivers is tiny, but it plays an important biological role by enhancing primary production in estuaries and salt marshes. Denitrification, a microbial process that occurs in anoxic soils and in the ocean (described in Concept 22.2), results in movement of N (as N_2 and as N_2O, a greenhouse gas, also known as laughing gas) from terrestrial and marine ecosystems into the atmosphere. These ecosystems also lose N through burial of organic matter in sediments and through burning of biomass.

Human activities have altered the global N cycle tremendously—even more than they have altered the global C cycle. Anthropogenic fluxes are now the dominant components of the N cycle (Galloway et al. 2004; Canfield et al. 2010) (**Figure 25.8**). The rate of fixation of atmospheric N_2 by humans now exceeds the rate of natural terrestrial biological fixation. Emissions of N associated with industrial and agricultural activities are causing widespread environmental changes, including acid precipitation, as we'll see in Concept 25.3. Three major processes account for these anthropogenic effects. The first is the manufacture of agricultural fertilizers by the Haber–Bosch process, described in Concept 22.1. Second, growing N-fixing crops such as soybeans, alfalfa, and peas has increased biological N_2 fixation. Flooding of agricultural fields for other crops, such as rice, has increased N_2 fixation by cyanobacteria. Finally, anthropogenic emissions of certain gaseous forms of nitrogen have greatly increased the concentrations of these compounds in the atmosphere. Unlike N_2, these compounds, which include oxygenated nitrogen compounds (NO, NO_2, HNO_3, and NO_3^-, collectively referred to as NO_x, and N_2O), ammonia (NH_3),

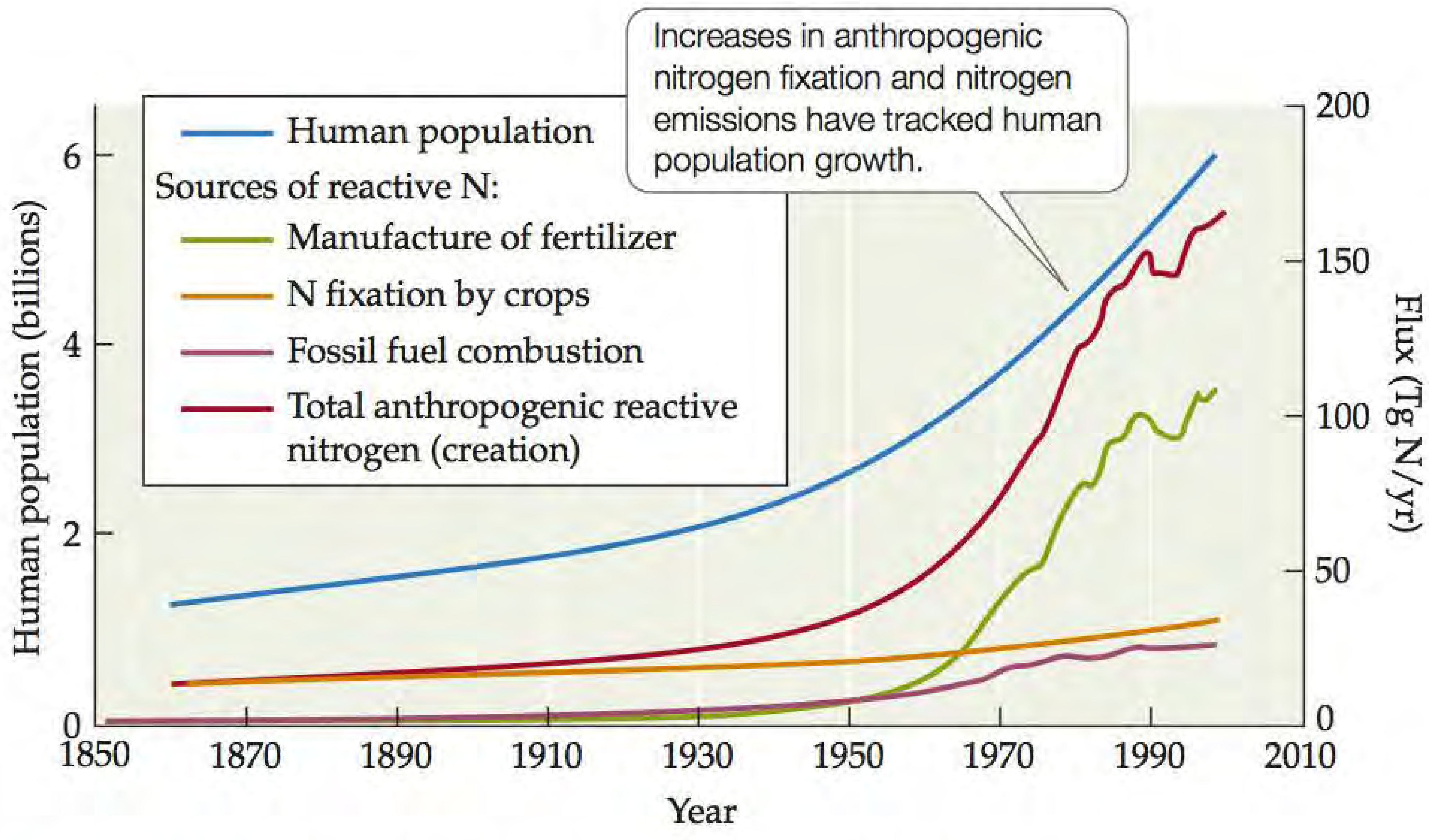


Figure 25.8 Changes in Anthropogenic Fluxes in the Global Nitrogen Cycle Increases in fertilizer production through the Haber–Bosch process, the growing of nitrogen-fixing crops, and combustion of fossil fuels have all contributed to the tremendous increase in biologically available (reactive) N. (After Galloway et al. 2004.)

and peroxyacetyl nitrate (PAN), can undergo chemical reactions in the atmosphere and are potentially available for biological uptake. Fossil fuel combustion is the primary source of these nitrogenous gas emissions. Other contributors include biomass burning associated with deforestation, denitrification and volatilization (conversion to gaseous form) of fertilizers, and emissions from livestock feedlots and human sewage treatment plants. All of these reactive forms of N are returned to terrestrial and marine ecosystems through the process of atmospheric deposition (described in Concept 22.1).

The global phosphorus cycle is dominated by geochemical fluxes

Phosphorus (P) limits primary production in some terrestrial ecosystems—particularly those with old, well-weathered soils, such as tropical lowland forests—and in many freshwater and some marine ecosystems. Phosphorus is added to crops as a fertilizer globally. Phosphorus availability can also control the rate of biological N_2 fixation because that process has a high metabolic demand for P. Consequently, the C, N, and P cycles are linked to one another through photosynthesis and NPP, decomposition, and N_2 fixation.

Unlike C and N, P has essentially no atmospheric pool, with the exception of dust (**Figure 25.9**). Gaseous forms of P are extremely rare. The largest pools of P are in terrestrial soils and marine sediments. Phosphorus is released from sedimentary rocks in biologically available forms by weathering. The largest fluxes of P occur in internal ecosystem cycles, which form a tight recycling loop between biological uptake by plants and microorganisms and release by decomposition. Typically, very little of the P cycling through terrestrial and aquatic ecosystems is lost. In terrestrial ecosystems, most P loss is associated with the process

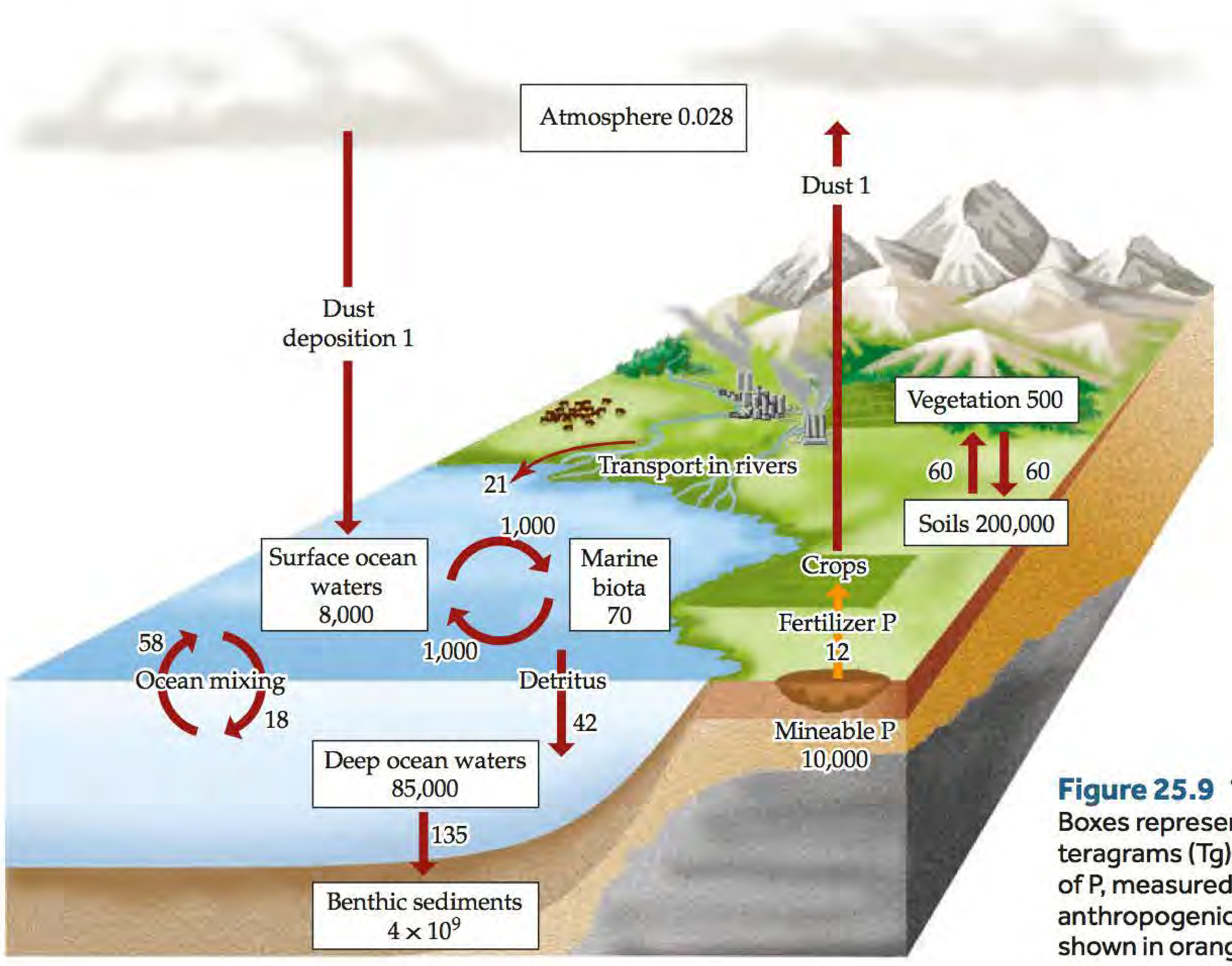


Figure 25.9 The Global Phosphorus Cycle Boxes represent major pools of P, measured in teragrams (Tg); arrows represent major fluxes of P, measured in teragrams per year. The major anthropogenic flux (P fertilization of crops) is shown in orange.

of occlusion (described in Concept 22.3). Movement of P from terrestrial to aquatic ecosystems occurs primarily through erosion and movement of particulate organic matter—mainly from plants—into streams. Much of the P transported from terrestrial to marine ecosystems (about 90%) is lost when it is deposited in deep ocean sediments. Ultimately, P in sediments in both marine and terrestrial ecosystems is cycled again in association with tectonic uplift and weathering of rocks, which occurs on a scale of hundreds of millions of years.

Anthropogenic effects on the global P cycle are associated with use of agricultural fertilizers, discharges of sewage and industrial wastes, and increases in terrestrial surface erosion. Phosphorus fertilizers are usually derived from the mining of uplifted ancient marine sediments. Phosphorus from soils and marine sediments is a nonrenewable resource, subject to depletion. Mining releases four times more P annually than is liberated through natural weathering of rock. Globally, P is applied as fertilizer in an amount equivalent to approximately 20% of the P that cycles naturally through terrestrial ecosystems (Schlesinger and Bernhart 2013). While occlusion of P in the soil minimizes the flux of anthropogenic P from terrestrial to aquatic ecosystems, that flux still has great potential for negative environmental effects. One such effect is eutrophication in lakes, as described in Concept 22.4.

Biological and geochemical fluxes both determine the global sulfur cycle

Sulfur (S) is a constituent of some amino acids, but it is rarely, if ever, in short supply for organismal growth. Sulfur plays important roles in atmospheric chemistry. As with the C, N, and P cycles, anthropogenic changes to the global S cycle have important negative environmental consequences, primarily through the generation of acid precipitation.

The major global pools of S are in rocks, sediments, and the ocean, which contains a large pool of dissolved sulfate (SO_4^{2-}) (**Figure 25.10**). Fluxes of S among these global pools can occur in gaseous, dissolved, or solid forms. Weathering of S-containing minerals, mainly sedimentary pyrite, releases soluble forms of S that may enter the atmosphere or oceans. There is a net movement of S from the terrestrial pool to the oceanic pool, associated with transport in rivers and in atmospheric dust. Volcanic eruptions emit substantial amounts of sulfur dioxide (SO_2) into the atmosphere. Because they are episodic events, however, the amount of S emitted to the atmosphere by volcanic eruptions, on a time scale of centuries, is approximately the same as the amount blown into the atmosphere as dust from bare soils. Oceans release S to the atmosphere as small particles of windborne ocean spray and as gaseous emissions associated with microbial activity. Bacteria and archaea in anaerobic soils also

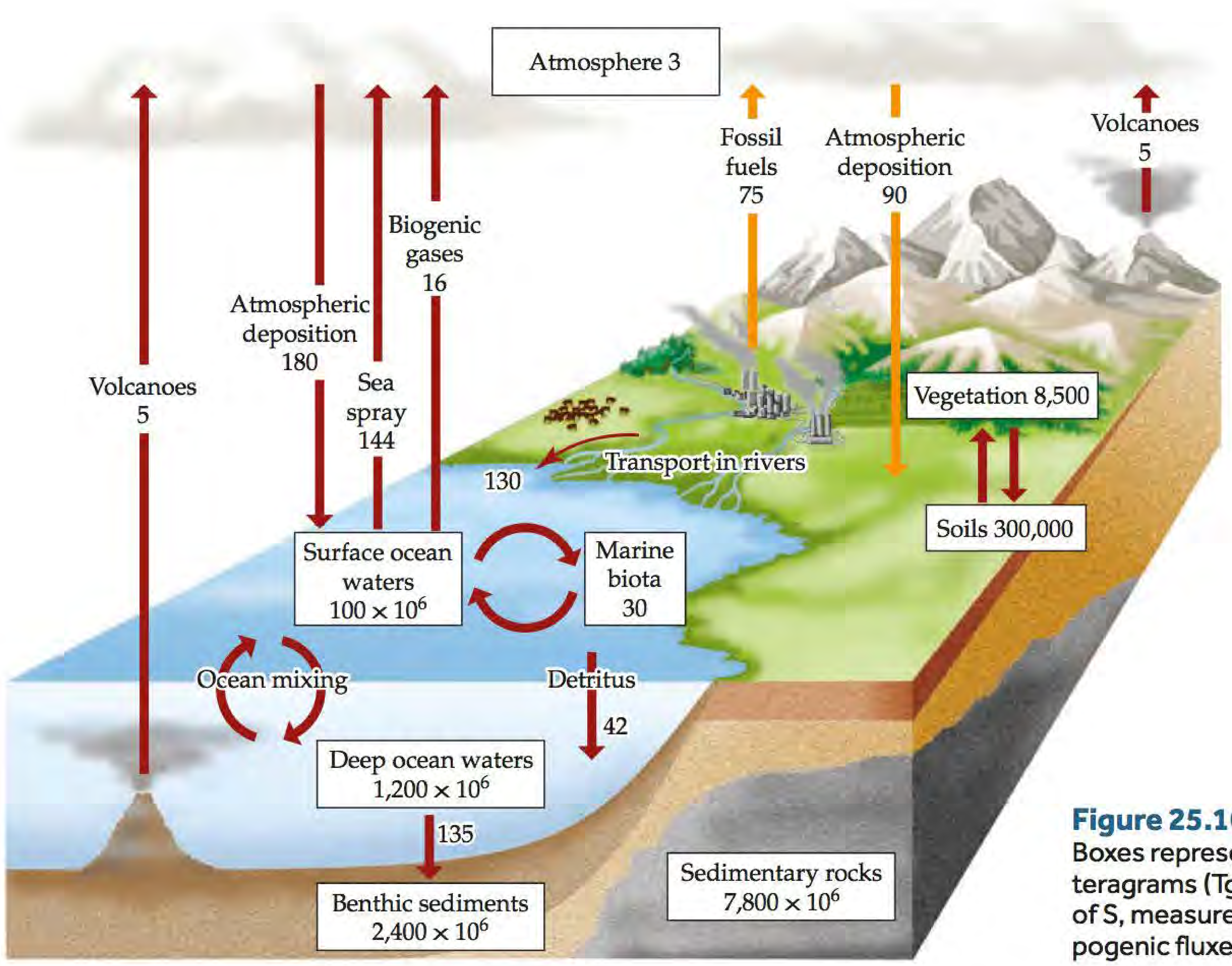


Figure 25.10 The Global Sulfur Cycle Boxes represent major pools of S, measured in teragrams (Tg). Arrows represent major fluxes of S, measured in teragrams per year; anthropogenic fluxes are shown in orange.

emit S-containing gases such as hydrogen sulfide (H_2S). Most gaseous S compounds in the atmosphere undergo oxidation to SO_4^{2-} and H_2SO_4 (sulfuric acid), which are removed relatively quickly by precipitation.

Anthropogenic emissions of S to the atmosphere, which include gaseous and particulate forms (e.g., dust, aerosols), have quadrupled since the Industrial Revolution. Most of these emissions are associated with the burning of S-containing coal and oil and the smelting of metal-containing ores. What goes up must come down in the form of atmospheric deposition, usually within the same region from which it was emitted, but not always. Long-distance transport of fine dust occurs episodically in association with droughts and major wind events, as described in this chapter's Case Study. Increases in erosion associated with clearing of vegetation and overgrazing have contributed to anthropogenic input of S into the atmosphere as dust. Transport of S in rivers has doubled over the past 200 years (Schlesinger and Bernhart 2013).

Human activities have resulted in changes in all four of the global biogeochemical cycles we have just described, and as we have noted, some of those changes have had important environmental effects. Let's turn our attention to those effects next.

CONCEPT 25.2

Earth is warming because of anthropogenic emissions of greenhouse gases.

Global Climate Change

Throughout this book, we have emphasized the role that climate plays in ecological processes, including the distributions and physiological performance of organisms, the rates of resource supply, and the outcomes of biological interactions such as competition. Thus, changes in climate—particularly changes in the frequency of extreme events such as extensive droughts, violent storms, or extreme high and low temperatures—have profound effects on ecological patterns and processes. Because they are disturbances that result in significant mortality within populations, these extreme events are often critical in determining the geographic ranges of species.

As we learned in Concept 2.1, *weather* is the current state of the atmosphere around us at any given time. *Climate* is the long-term description of weather, including both average conditions and the full range of variation. Climate *variation* occurs at a multitude of time scales, from the daily changes associated with daytime solar heating and nighttime cooling, to seasonal changes associated with the tilt of Earth's axis, to decadal changes associated with interactions between ocean currents and the atmosphere (such as the Pacific Decadal Oscillation, described in Case Study Revisited in Chapter 2). Climate change, on the other hand, refers to *directional* change in climate

Evidence of climate change is substantial

Climate change is distinguished from climate variation by the presence of significant directional trends lasting at least 3 decades. Based on analyses of records from numerous climate-monitoring stations, atmospheric scientists have determined that Earth is currently experiencing significant climate change (IPCC 2013) (**Figure 25.11A**). Between 1880 and 2012, the average annual global surface temperature increased 0.8°C ± 0.2°C (1.1°F ± 0.4°F), with the greatest change occurring in the past 50 years. This rapid rise in global temperature is unprecedented in the past 10,000 years, although temperature changes at similar rates may have occurred at the onset and end of some glacial cycles (see Figure 25.6). The first decade of the twenty-first century was the warmest decade of the previous 1,000 years, and 2016 was the warmest year since record keeping started. In association with this warming trend, there has been a widespread retreat of mountain glaciers, thinning of the polar ice caps and thawing of permafrost, and a rate of sea level rise that is greater than any estimated from the past 3,000 years (Kopp et al. 2016), posing a serious threat to coastal communities.

This warming trend has been heterogeneous across the globe, with most regions warming, others not changing significantly, and some even cooling (**Figure 25.11B**). The warming trend has been greatest in the mid- to high latitudes of the Northern Hemisphere. Changes in terrestrial precipitation have also occurred, with more precipitation in portions of the high latitudes of the Northern Hemisphere and drier weather in the subtropics and tropics (**Figure 25.11C**). There has also been a tendency toward greater frequencies of some extreme weather events, such as hurricanes (including massive storms such as Hurricane Katrina in 2005 and Hurricane Sandy in 2012), droughts, and heat waves (IPCC 2013).

What are the causes of the observed climate change?

As we saw in Chapter 2, climate change may result from changes in the amount of solar radiation absorbed by Earth's surface or in the amount of absorption and reradiation of infrared radiation by gases in the atmosphere. Changes in absorption of solar radiation may be associated with variation in the amount of radiation emitted by the sun, in Earth's position relative to the sun, or in the reflection of solar radiation by clouds or surfaces with high reflectivity (albedo), such as snow and ice.

The warming of Earth by atmospheric absorption and reradiation of infrared radiation emitted by Earth's surface is known as the **greenhouse effect** (see Figure 2.4). This phenomenon is associated with radiatively active **greenhouse gases** in the atmosphere, primarily water vapor, CO_2, CH_4, and N_2O. The effectiveness of these gases in absorbing radiation depends on their concentrations in the atmosphere as well as their chemical properties. Water vapor contributes the most to the greenhouse effect, but its atmospheric concentration varies greatly from region to region, and changes in its average concentration have been small. Of the remaining greenhouse gases, which tend to be more evenly distributed in the atmosphere, CO_2 contributes the most to greenhouse warming, followed by CH_4 (which has about 30% of the effect of atmospheric CO_2) and N_2O (with about 10% of the effect of CO_2).

As we saw in our discussion of the global biogeochemical cycles of C and N, atmospheric concentrations of CO_2, CH_4, and N_2O are increasing substantially, primarily as a result of fossil fuel combustion and land use change (**Figure 25.12**). Are increases in anthropogenic emissions of these greenhouse gases responsible for global climate change? To evaluate the underlying causes of climate change, its potential effect on ecological and socioeconomic systems, and our options for limiting climate change associated with human activities, the World Meteorological Organization and the United Nations Environment Programme established the Intergovernmental Panel on Climate Change (IPCC) in 1988. The IPCC convenes panels of experts in atmospheric and climate science to evaluate trends in climate and the probable causes for any changes observed. These experts use a combination of sophisticated modeling and analysis of data from the scientific literature to evaluate potential underlying causes of observed climate change, as well as to predict future climate change scenarios. The IPCC releases assessment reports periodically to enhance the understanding of climate change among scientists, policymakers, and the general public. In recognition of their efforts to spread

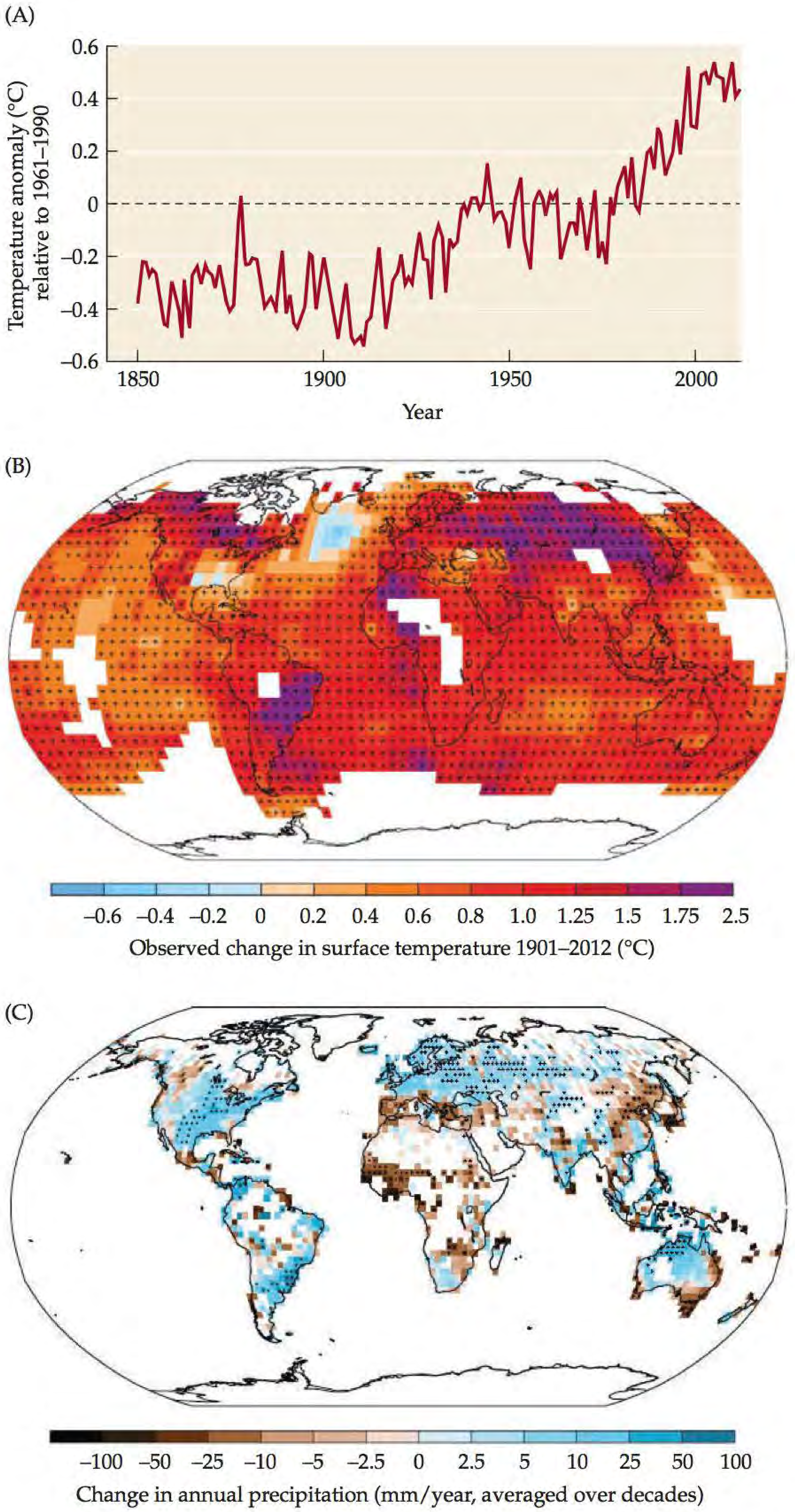
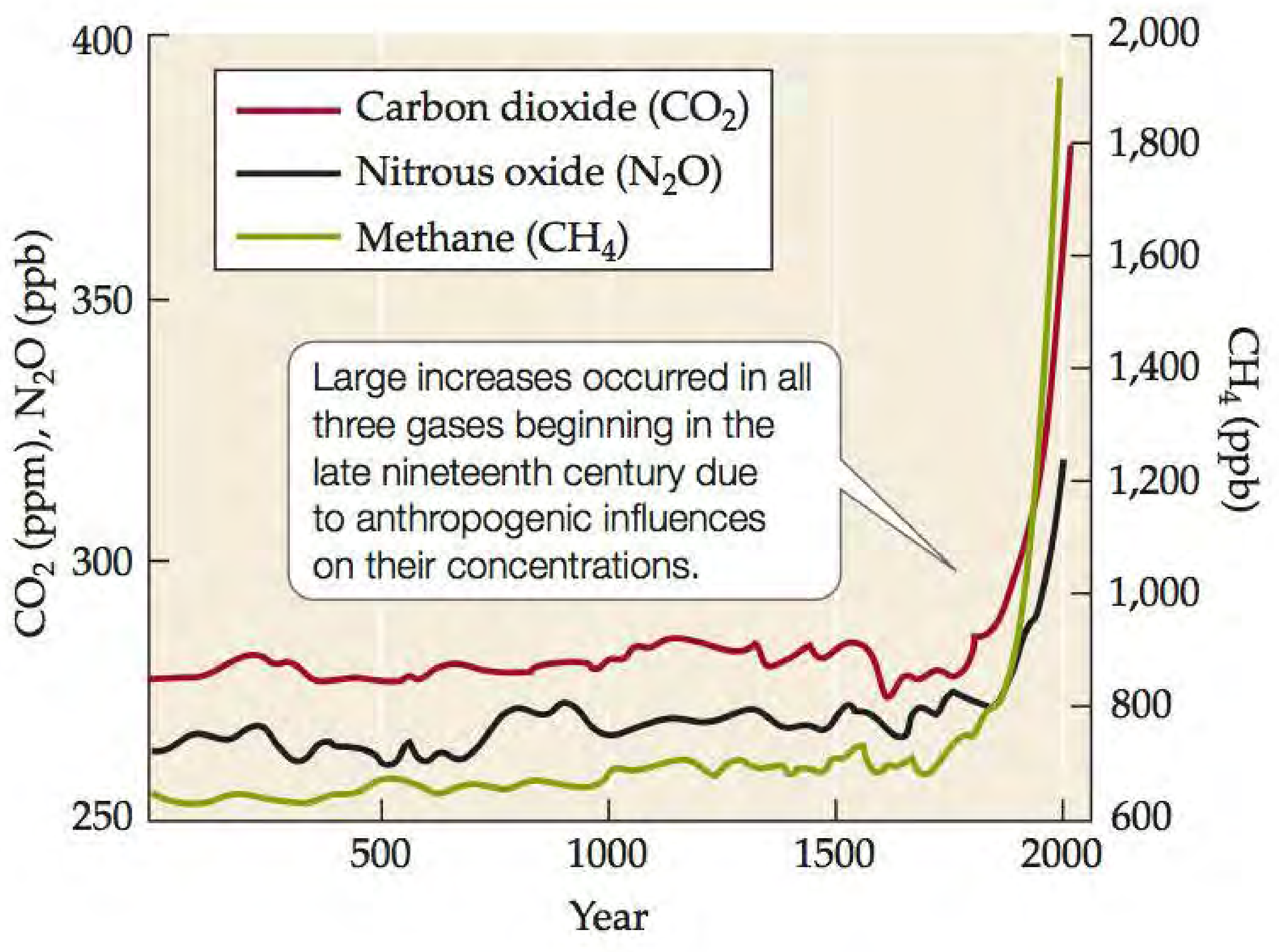


Figure 25.11 Changes in Global Temperature and Precipitation (A) Average annual global temperature anomalies (relative to the average global temperature for 1961–1990) between 1850 and 2005, averaged from numerous air and sea surface temperature records and normalized to sea level. (B) Regional trends in average annual temperatures for 1901–2012. (C) Trends in global precipitation from 1951 to 2010. (A after IPCC 2013; B,C from IPCC 2013.)



Large increases occurred in all three gases beginning in the late nineteenth century due to anthropogenic influences on their concentrations.

Figure 25.12 Atmospheric Concentrations of Greenhouse Gases Concentrations prior to 1958 were determined from ice cores; concentrations since 1958 have been measured directly. (After Hartmann et al. 2013.)

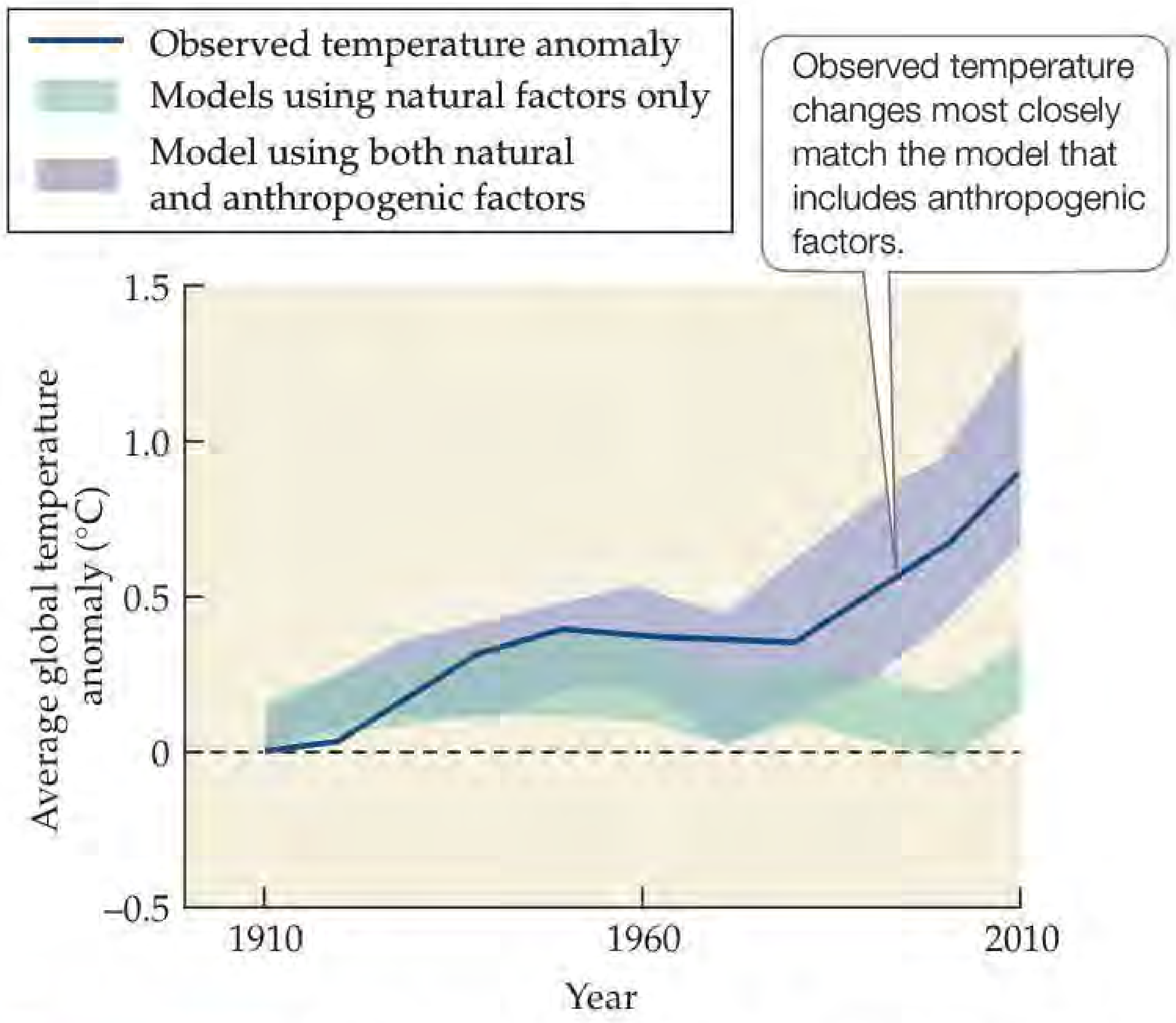


Figure 25.13 Contributors to Global Temperature Change IPCC scientists compared observed global temperature changes between 1910 and 2010 with the results of computer models. The models predicted the temperature changes that would have been expected in that period due to natural climatological factors only, including variation in solar radiation and in atmospheric concentrations of aerosols from volcanic eruptions, and due to both natural and anthropogenic factors, including emissions of greenhouse gases and sulfate aerosols. These comparisons suggest that anthropogenic factors have played a large role in the observed warming. (After IPCC 2013.)

"knowledge about man-made climate change," the IPCC was awarded the Nobel Peace Prize in 2007.

In its third assessment report, released in 2001, the IPCC concluded that the majority of the observed global warming is attributable to human activities (**Figure 25.13**). While this conclusion is still occasionally debated in the political arena, it is backed by the majority of the world's leading atmospheric scientists. The certainty of an anthropogenic cause of climate change has increased with each new IPCC report, with the 2013 report stating, "It is extremely likely (95%–100% probability) that human influence has been the dominant cause of the observed warming since the mid-20th century." Paul Crutzen, who was awarded the Nobel Prize in Chemistry for his work on stratospheric ozone loss, has suggested that we have entered a new geologic period, which he calls the *Anthropocene epoch* (*anthropo*, "human"; *cene*, "recent"; *epoch*, "geologic age") to indicate the extensive impact of humans on our environment, particularly the climate system (Crutzen and Stoermer 2000).

Will the climate continue to grow warmer? The IPCC's models project an additional increase in average global temperature of 1.1°C–4.8°C over the twenty-first century (IPCC 2013). The range of variation in this estimate is associated with uncertainties about future rates of anthropogenic greenhouse gas emissions and about the behavior of the terrestrial–atmospheric–oceanic system. Model simulations incorporating different economic development scenarios have predicted vastly different future rates of emissions. Aerosols in the atmosphere represent another source of uncertainty in the models' predictions. Aerosols, which reflect solar radiation, have a cooling effect on global temperatures; for example, emissions of large amounts of aerosols associated with major volcanic eruptions have had notable cooling effects at a global scale, as described in **Web Extension 25.1**. While some aerosols have been increasing in the atmosphere (e.g., dust, in association with land use change and desertification), others have been decreasing (e.g., SO_4^{2-}, due to decreasing anthropogenic SO_2 emissions). Water in the atmosphere may play contradictory roles: clouds may have a cooling effect, while water vapor, which may increase because of greater evapotranspiration, may increase greenhouse warming. Despite these uncertainties in predicting the magnitude of future climate warming, there is a high probability that global temperatures will continue to rise. Even if anthropogenic CO_2 emissions were halted completely, global temperatures would likely continue to rise for decades or even centuries due to the reduced capacity of the ocean to absorb heat (Frölicher et al. 2014).

Climate change will have ecological consequences

What does a 1.1°C–4.8°C change in average global temperature mean for biological communities? We can get a sense of what such a temperature change might mean by comparing it with the climate variation associated with elevation in mountains. A median value for the projected temperature change (2.9°C) would correspond to a 500 m (1,600-foot) shift in elevation. In the Rocky Mountains, this change in climate would correspond approximately to a full change in vegetation zone, from subalpine forest (dominated by spruce and fir) to montane forest (dominated by ponderosa pine) (see Figure 3.11). Thus, if we assume perfect tracking of climate change by the current vegetation, climate change during the twenty-first century would result in an elevational shift in vegetation zones of 200–860 m. Similar predictions for latitudinal climate shifts suggest movement of biological communities 500–1,000 km toward the poles.

Climate–biome correlations, such as those described in Concepts 3.1 and 4.1, are useful as a demonstration of what could happen with climate change, but it would be naive to use them to predict what will actually happen to biological communities. We know that biological composition is influenced by a multitude of factors, including climate—particularly climate extremes—as well as species interactions, the dynamics of succession, dispersal ability, and barriers to dispersal (as described in Unit 5). Because the ongoing climate change will continue to be rapid relative to the climate changes that have shaped current biological communities, it is unlikely that the same assemblages of organisms will form the communities of the future.

Paleoecological records reinforce the suggestion that novel communities may emerge with climate change by showing that some plant communities of the past were quite different from modern plant communities. Jonathan Overpeck and colleagues used pollen records to reconstruct large-scale vegetation changes since the most recent glacial maximum in eastern North America (18,000 years ago) (Overpeck et al. 1992). They found not only that community types had made latitudinal shifts as the climate warmed, but also that community types without modern analogs existed under climate regimes that were unique and no longer present (**Figure 25.14**). Overpeck and his colleagues concluded that future vegetation assemblages would follow similar trends, given the predicted rapid rate of global warming and the potential for the emergence of unique climate patterns with no current analogs.

The rate of climate change will require rapid evolutionary change or the ability to disperse to new environments. The Climate Change Connection for Chapter 6 and Web Extension 6.2 present evidence that organisms with rapid life cycles have undergone evolutionary change in response to climate change. For more long-lived species, evolutionary responses are less likely, and thus for those species dispersal may be the only way to avoid extinction. Organisms' dispersal abilities, and barriers to their dispersal associated with anthropogenic habitat fragmentation, will be important constraints on their responses to climate change. Plant dispersal rates are, on average, much slower than the predicted rate of climate change. In order to track the projected change in climate over the twenty-first century, plant species populations will need to move 5–10 km per year. Plant species that have animal-dispersed seeds, and which can establish viable populations and grow to reproductive maturity in a relatively short time, may be able to disperse rapidly enough to keep pace with climate change. However, this kind of dispersal strategy is common mainly in ruderal (weedy) herbaceous plants. Shrubs and trees have much slower rates of dispersal; as a result, there may be significant time lags in their response to climate change.

For most animals, mobility is not a problem, but their habitat and food requirements are intimately associated with the presence of specific vegetation types. In addition, barriers to dispersal may prevent organisms of all kinds from migrating in response to climate change. Dams, for example, may prevent fish from moving to water with more suitable temperatures. Fragmentation of habitat by human development may pose significant barriers to dispersal for some species (see Concept 24.2). Without habitat

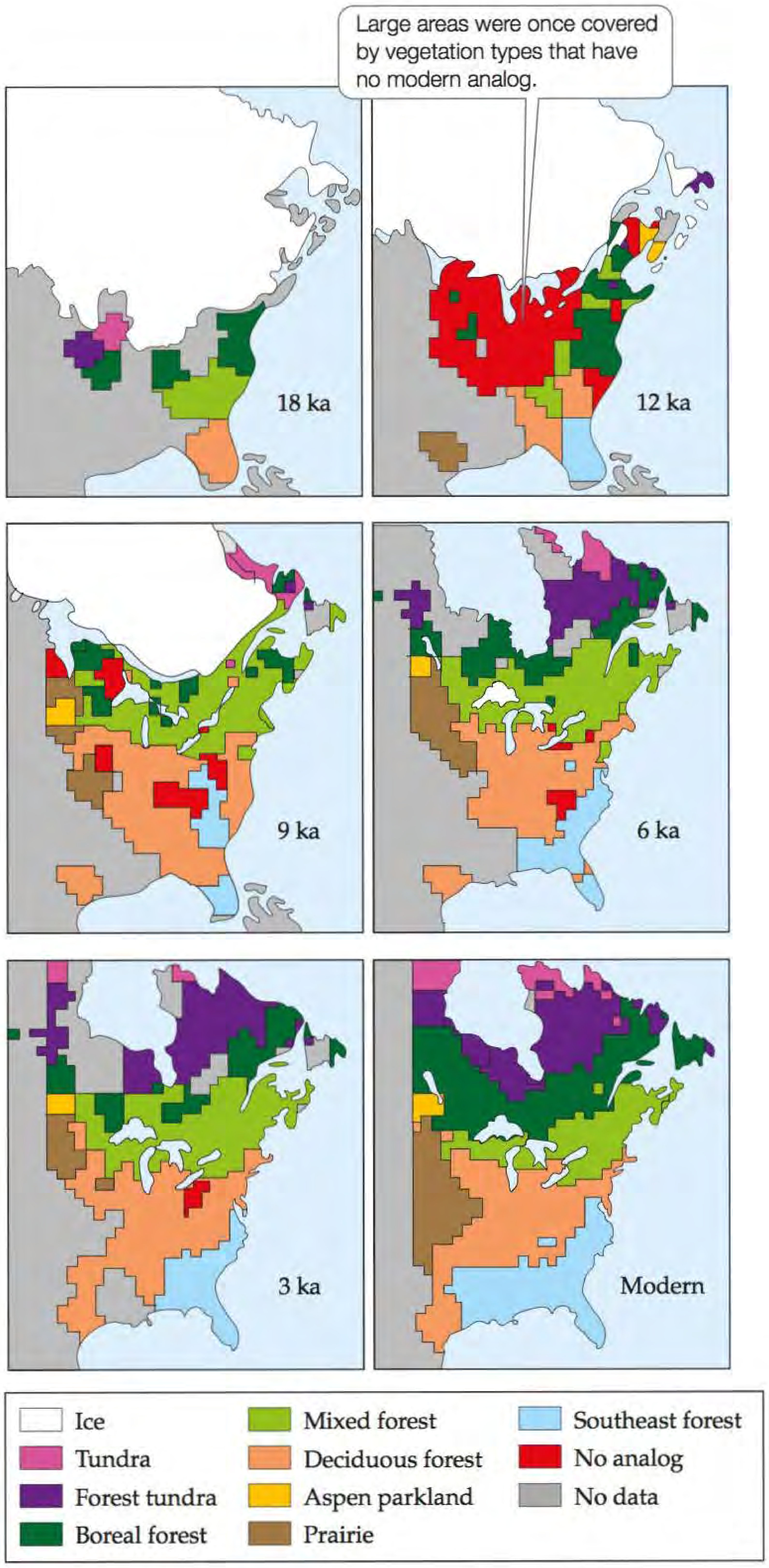

Large areas were once covered by vegetation types that have no modern analog.

Figure 25.14 Past Changes in Plant Communities
Vegetation types in eastern North America have changed since the last glacial maximum, 18,000 years ago (ka = thousand years ago). Vegetation composition was determined from pollen preserved in sediments. (From Overpeck et al. 1992.)

? What factors may have led to the development of vegetation types different from those found in North America today following retreat of the continental glacier?

corridors through which they can disperse, species face a greater probability of local extinction in the face of climate change.

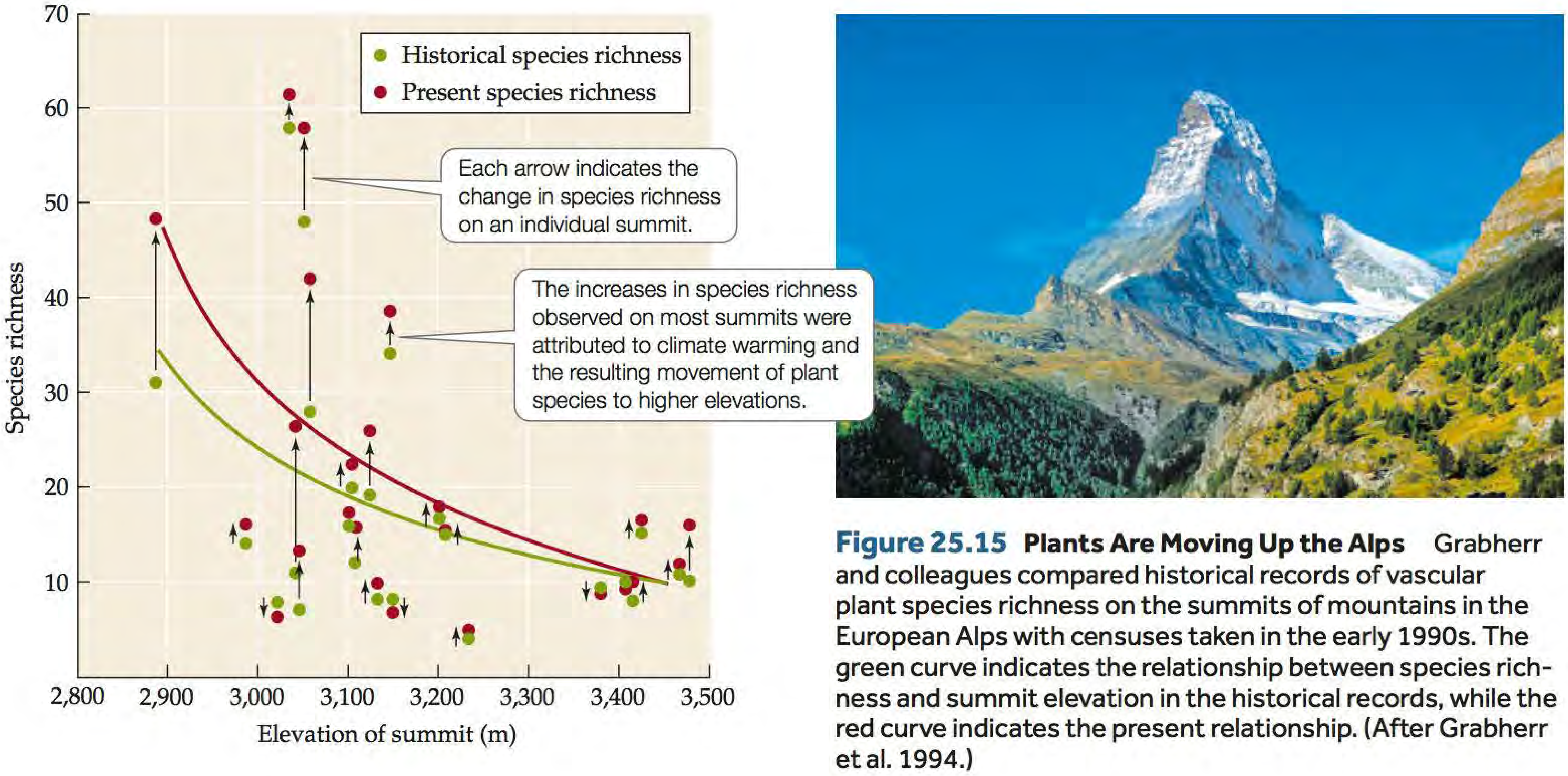
In addition to affecting the geographic ranges of species, climate change will affect ecosystem processes, such as NPP, decomposition, and nutrient cycling and retention. Both photosynthesis and respiration are sensitive to temperature, and because their balance determines NPP, the direct effects of climate warming on NPP may be relatively minor. As indicated in Concept 20.2, however, variation in NPP is related to water and nutrient availability and vegetation type, all of which may be affected by climate change. Changes in precipitation patterns and evapotranspiration rates resulting from climate change may strongly influence both water and nutrient availability. Because of the heterogeneity of climate change, and of the resulting changes in vegetation types, both increases and decreases in NPP may occur. Thus, the effect of climate change on NPP will probably not be uniform. The effect of warming on nutrient supplies will be most pronounced in mid- to high-latitude terrestrial ecosystems, where low temperatures constrain rates of nutrient cycling and soils have large pools of nutrients. As a result, climate change may lead to increases in NPP in some temperate and boreal forest ecosystems.

Ecological responses to climate change are occurring

As noted earlier, global warming of 0.8°C has occurred since 1880. Several physical environmental changes have occurred over the same period, including the retreat of glaciers, increased melting of sea ice, and a rise in sea level. Have biological systems also responded to this warming? Numerous reports of biological changes are consistent with recent global warming (Parmesan 2006; Walther 2010). These changes include earlier migration of birds, local extinction of amphibian and reptile populations, and earlier spring greening of vegetation.

Although they are more difficult to link directly to climate change, there have been changes in the geographic ranges of species that are consistent with warming. For example, Georg Grabherr and colleagues studied the vascular plant communities found on summits of mountains in the European Alps. They compared the current species richnesses of those communities with records dating back to the eighteenth and early nineteenth centuries (Grabherr et al. 1994). They found a consistent trend of increasing species richness resulting from the upward movement of species from lower elevations onto the summits (**Figure 25.15**). Similarly, Camille Parmesan and colleagues recorded a northward shift in the ranges of European nonmigratory butterfly species (Parmesan et al. 1999). Of the 35 species examined, 63% had shifted their ranges northward, while only 3% had shifted their ranges southward. More than half of the plant and animal species that have been investigated have shown geographic range shifts that are consistent with recent climate changes (Parmesan and Yohe 2003).

Climate change may be causing populations of some species to go extinct. Barry Sinervo and colleagues (2010) found that 12% of Mexico's *Sceloporus* lizard populations had gone extinct between 1975 and 2009. Recall from Concept 23.2 that population extinctions are potentially the



Each arrow indicates the change in species richness on an individual summit.

The increases in species richness observed on most summits were attributed to climate warming and the resulting movement of plant species to higher elevations.

Figure 25.15 Plants Are Moving Up the Alps Grabherr and colleagues compared historical records of vascular plant species richness on the summits of mountains in the European Alps with censuses taken in the early 1990s. The green curve indicates the relationship between species richness and summit elevation in the historical records, while the red curve indicates the present relationship. (After Grabherr et al. 1994.)

initial steps toward the extinction of a species. The extinctions of the lizard populations corresponded more closely to increases in temperature than to losses of habitat. Surprisingly, warming in the spring was better correlated with the extinctions than extreme temperatures during the summer. Sinervo and colleagues concluded that the warmer spring temperatures limited the lizards' foraging time during the breeding season. Ectothermic lizards must move into the shade and remain there to avoid overheating when temperatures become too warm (see Concept 4.2), and during that time they cannot seek out food. The observation that the probability of extinction was greatest at low-elevation and low-latitude sites, where the animals were most likely to be at the limits of their thermal tolerance, was consistent with this explanation.

Sinervo and colleagues also used a model of lizard thermal physiology to evaluate current and future worldwide effects of climate change on lizard populations. They estimated that climate change has already resulted in extinction of 4% of lizard populations worldwide. Using projections of future climate change, they suggested that 39% of the world's lizard populations, and 20% of its lizard species, may go extinct by 2050.

Migratory animals may also be adversely affected by climate change (Root et al. 2003). For example, migrating marine species, including whales and fish, may need to make longer journeys because of substantial changes in the distributions of their prey species as ocean temperatures warm. Some migratory bird species that breed in England and North America have been arriving at nest sites as much as 3 weeks earlier than they did 30 years ago because of warmer spring temperatures and faster snowmelt. However, plants and invertebrate prey species have responded faster to climate change than the migrating birds, resulting in a mismatch between bird arrival and prey availability. On the other hand, longer breeding seasons may increase the number of offspring produced by some bird species, particularly in high-latitude ecosystems.

Changes in community composition may also be indicators of climate change. These effects may be particularly apparent in some sessile marine species. Concepts 3.3 and 17.1 have described the effects of rising water temperatures on corals and the resulting changes in coral reef communities. Changes in the abundances of marine foraminiferans—a type of zooplankton—also reflect global climate trends during the past century (Field et al. 2006). Foraminiferan species have characteristic shells that allow them to be identified in marine sediments. Cores collected from benthic sediments can be examined to determine changes in the species composition of foraminiferans over time. Because the environmental tolerances of different species are known, these changes provide a means of reconstructing marine environments of the past. Following the mid-1970s, an increase in tropical and subtropical foraminiferan species, and a decrease in temperate and polar species, occurred in the eastern North Pacific Ocean, indicating a warming of ocean waters there.

Climate change is impacting forest composition in western North America through changes in the frequency and intensity of bark beetle attacks (Anderegg et al. 2015) and forest fires. Longer frost-free seasons are allowing mountain pine beetles (*Dendroctonus ponderosae*) in some regions to transition from completing one life cycle per year to two, greatly enhancing their population growth and potential outbreaks (Mitton and Ferrenberg 2012). In addition, the beetles are found at higher altitudes and latitudes than in the past, where they are attacking trees lacking defenses to the beetles. As a result of climate change effects on weather and fuel moisture content, forest fires have doubled since 1984 (Abatzoglou and Williams 2016). Climate change will continue to enhance forest fires until fuels become the limiting factor for their occurrence.

Changes in global NPP also indicate biological responses to climate change. Ramakrishna Nemani and colleagues used remote sensing data to examine global patterns of NPP over an 18-year period (1982–1999) (Nemani et al. 2003). They found that global NPP increased 6% during the study period, or 0.3% per year (**Figure 25.16**). Tropical ecosystems exhibited the largest increase in NPP, which was associated with increases in solar radiation due to less cloud cover in the tropics during the study period. During the first decade of the twenty-first century, however, the trend toward increasing NPP was reversed. The decrease in global NPP during this decade was attributed to major droughts, particularly in the Southern Hemisphere (Zhao and Running 2010).

There has been a notable decrease in net ecosystem exchange (NEE) at high northern latitudes during the past 30 years, which has coincided with some areas of the Arctic switching from a net uptake of CO_2 from the atmosphere (acting as a *sink*) to a net export of CO_2 (acting as a *source*) (Oechel et al. 1993). Large amounts of C are stored in the soils of boreal and tundra ecosystems as a result of low-temperature constraints on decomposition and the long-term buildup of carbon since the last glacial maximum. Warming during the twentieth century, however, increased the rate of CO_2 export from Arctic soils, such that losses now exceed gains from NPP. Warming of these high-latitude terrestrial ecosystems could provide a positive feedback to climate change by enhancing their emissions of CO_2 and CH_4. However, the rates of CO_2 loss from Arctic ecosystems have decreased since the early 1990s, possibly due to changes in rates of nutrient cycling and physiological and compositional changes in the plants (Oechel et al. 2000).

Biological indicators of global climate change are diverse, and they are increasing over time. Experiments, modeling, and comparisons with historical and paleoecological records provide clues to how Earth's biota will

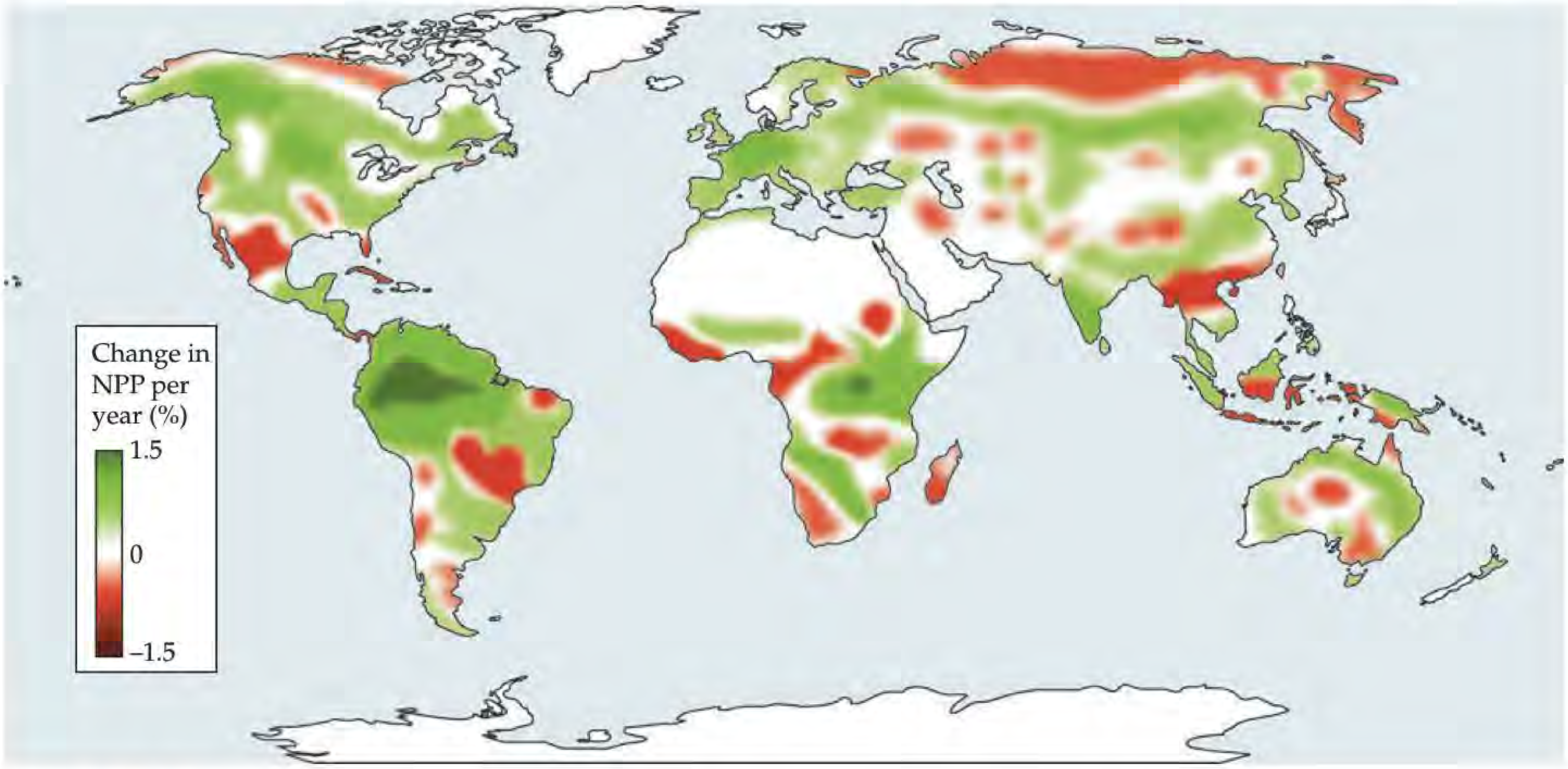


Figure 25.16 Changes in Terrestrial NPP Nemani and colleagues calculated changes in net primary production (NPP) between 1982 and 1999, expressed here as percentage change per year. The trend toward increased NPP in tropical regions of South America shown here was reversed in the first decade of the twenty-first century due to prolonged drought. (From Nemani et al. 2003.)

respond to climate change. Substantial uncertainties in predicting the effects of climate change still exist, however, many of which are associated with other environmental changes that are occurring at the same time. In the next section, we'll look at two such anthropogenic changes that are having profound effects on ecosystems: emissions of sulfur and nitrogen into the atmosphere.

CONCEPT 25.3
Anthropogenic emissions of sulfur and nitrogen cause acid deposition, alter soil chemistry, and affect the health of ecosystems.

Acid and Nitrogen Deposition

The negative effects of air pollution have been known since at least the time of the ancient Greeks, when laws protected the quality of air, as indicated by its odor (Jacobson 2002). Since the Industrial Revolution, air pollution has mainly been associated with urban industrial centers, power plants, and oil and gas refineries. These stationary sources of atmospheric pollutants mainly affect the areas immediately adjacent to them and are usually considered regional rather than global problems. During the twentieth century, however, effective emissions dispersal strategies (e.g., tall smokestacks), widespread industrial development, and greater emissions of pollutants from mobile sources, such as automobiles, have increased the spatial extent of air pollution tremendously.

Fossil fuel combustion, agriculture, and urban and suburban development have influenced fluxes of N and S to an even greater degree than fluxes of C. Emissions of N and S into the atmosphere have resulted in two related environmental issues: acid precipitation and N deposition. Emissions of N and S are only a subset of the multiple types of air pollution, but they are among the most far-reaching. Sites affected by acid precipitation and N deposition now include national parks and wilderness areas (**Figure 25.17**).

Acid precipitation causes nutrient imbalances and aluminum toxicity

The detrimental effects of acidic air pollution on nearby vegetation, buildings, and human health have been known for several centuries, although their mechanisms were not well understood. In England during the mid-nineteenth century, industrial processes that released acidic compounds into the atmosphere, primarily hydrochloric acid, were implicated as a major source of harmful pollution (Jacobson 2002). Legislation was enacted in 1863 to reduce these acidic emissions. Despite such legislation, acid precipitation continued to be a problem throughout the nineteenth and twentieth centuries in large industrialized urban centers. During the 1960s, awareness of the widespread effects of acid precipitation, including its effects on nearby "pristine" ecosystems and agriculture, increased. In particular, damage to forests and mortality among aquatic organisms in northern

Figure 25.17 Air Quality Monitoring in Grand Canyon National Park Visibility, which serves as an index of air quality, is evaluated by the visual range: the maximum distance this Web camera can resolve (up to 225 miles). Air quality in national parks and wilderness areas, such as the Grand Canyon, has been compromised by emissions of pollutants, including sulfate aerosols. These pollutants not only lower visibility, but also pose a health hazard to the organisms that come into contact with them, including humans.

Europe, parts of Asia, and northeastern North America prompted greater attention to acid precipitation.

Sulfuric acid (H_2SO_4) and nitric acid (HNO_3) are the main acidic compounds found in the atmosphere. As we saw in Concept 25.1, sulfuric acid forms in the atmosphere from the oxidation of gaseous sulfur compounds. Likewise, nitric acid originates from the oxidation of other NO_x compounds. Sulfuric and nitric acids can dissolve in water vapor and fall to the ground with precipitation (*wet deposition*). Naturally occurring precipitation has a slightly acidic pH of 5.0 to 5.6 due to the natural dissolution of CO_2 and formation of carbonic acid. Acid precipitation has a pH range from 5.0 to 2.0. Acidic compounds may also be deposited on Earth's surface when they form aerosols too large to be suspended or when they attach to the surfaces of dust particles (*dry deposition*).

Research has focused on determining the causes of the environmental degradation associated with acid precipitation, including increased mortality of plants and amphibians and decreased diversity. Initially, the acidity was considered the main culprit. In most cases, however, rainfall and surface waters did not have a low enough pH to cause the observed biological responses. An exception is found in regions at high latitudes or high elevations that develop a seasonal snowpack. During winter, acidic compounds accumulate in the snow. When temperatures increase in spring, water percolates through the snowpack, leaching out all the accumulated soluble compounds. The first meltwater of spring is therefore more acidic than the precipitation that fell during winter. This *acid pulse* has the potential to be toxic to sensitive organisms in soils and streams, including microorganisms, invertebrates, amphibians, and fish.

The vulnerability of organisms in soils, streams, and lakes to inputs of acid precipitation is determined by the ability of their chemical environment to counteract the acidity, known as its **acid neutralizing capacity**. The acid neutralizing capacity of soils and water is usually associated with their concentrations of base cations, including Ca^{2+}, Mg^{2+}, and K^+. Soils derived from parent material with high concentrations of these cations, such as limestone, are better able to neutralize acid precipitation than those derived from more acidic parent material, such as granite.

The detrimental effects of acid precipitation on plants and aquatic organisms are associated with biogeochemical reactions in the soil that decrease nutrient supplies and increase concentrations of toxic metals. As H^+ percolates through the soil, it replaces Ca^{2+}, Mg^{2+}, and K^+ at cation exchange sites on the surfaces of clay particles (see the description of cation exchange in Concept 22.1). These

Figure 25.18 Air Pollution Has Damaged European Forests The high tree mortality seen in this spruce forest in southeastern Germany is associated with acid precipitation and the resulting nutrient imbalance, particularly losses of base cations. Extensive forest decline occurred in Germany and northern Czechoslovakia (now part of the Czech Republic) in the 1970s and 1980s.

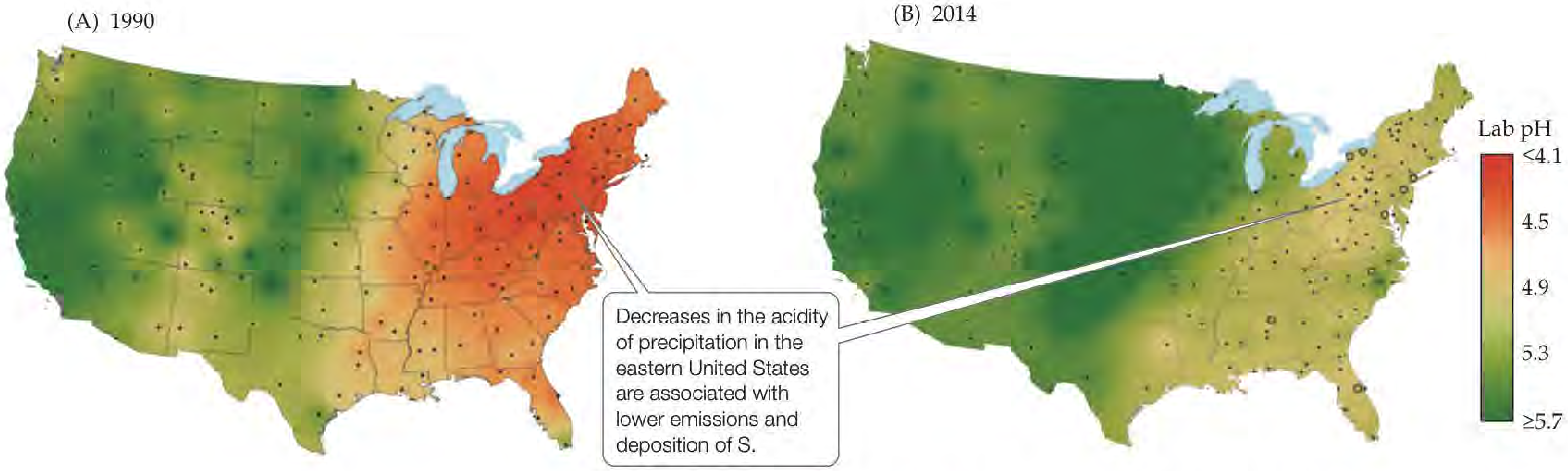


Figure 25.19 Decreases in Acid Precipitation The pH of precipitation in different parts of the United States as measured in (A) 1990 and (B) 2014, estimated based on measurements made at sampling points indicated by the dots. (From National Atmospheric Deposition Program/National Trends Network.)

cations are released into the soil solution and can then leach out of the rooting zone of plants. The loss of these base cations leads to a decrease in soil pH, or *soil acidification*. Deficiencies in Ca and Mg, sometimes in combination with other stresses, were associated with large-scale mortality of trees in European forests during the 1970s and 1980s (**Figure 25.18**). In advanced stages of soil acidification, aluminum (Al^{3+}) is released into the soil from cation exchange sites. Aluminum is toxic to plant roots, soil invertebrates, and aquatic organisms, including fish. The combination of increasing acidity in precipitation and increasing aluminum concentrations in terrestrial runoff has been linked to fish die-offs in lakes and streams in northern Europe and eastern North America.

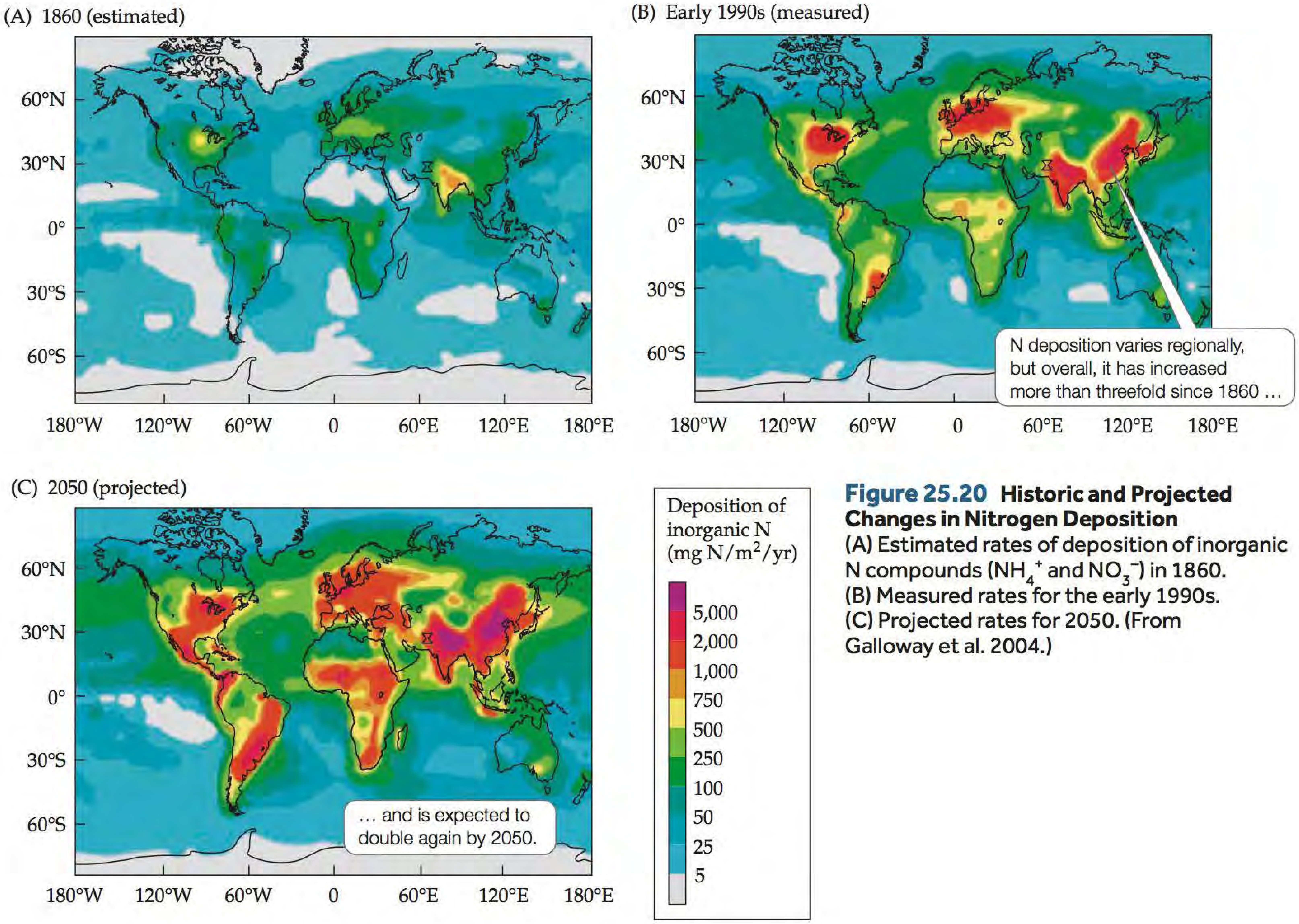
The realization that acid precipitation was negatively affecting the biota of forest and lake ecosystems prompted enhanced monitoring of atmospheric deposition and, eventually, laws to limit acidic emissions. Restrictions on emissions of S in North America and Europe have resulted in significant reductions in the acidity of precipitation (**Figure 25.19**). Forests are recovering from the effects of acid precipitation in central Europe, thanks to legislation limiting S emissions as well as decreased industrial activity in the former Soviet Union. Stream chemistry measurements also reflect the reduced acidity of precipitation and the recovery of aquatic ecosystems. Acid precipitation remains a problem, however, in some countries that have experienced rapid industrial development, such as China and India.

Nitrogen deposition: Too much of a good thing can be bad

As we have seen, anthropogenic emissions of reactive nitrogen into the atmosphere have greatly altered global N cycles. Reactive N can fall back to Earth (via dry and wet deposition) after being transported away from the emission source in the atmosphere. Globally, anthropogenic emissions and deposition of reactive N compounds are more than three times greater now than they were in 1860 (Galloway et al. 2004, 2008) (**Figure 25.20**). Emissions and deposition of reactive N are expected to double between 2000 and 2050 as industrial development increases to keep pace with the human population. Greater deposition of N will increase the supply of N for biological activity, but this abundance will come with an environmental cost.

The role of N as a determinant of rates of primary production was described in Concept 20.2. Nitrogen plays an important role in photosynthesis, which forms the base of the food webs that provide energy to all other organisms. Considerable benefit to humanity has accrued from the manufacture of N fertilizers and their widespread application to crops since the early twentieth century. We might expect, therefore, that an increased supply of N would facilitate plant growth and greater overall production in a N-limited ecosystem. Primary production has indeed increased in some ecosystems as a result of increased N deposition (e.g., forests in Scandinavia; Binkley and Högberg 1997). Nitrogen deposition may be partly responsible for the greater uptake of atmospheric CO_2 by terrestrial ecosystems observed in the Northern Hemisphere (Thomas et al. 2010).

Although primary production is increasing in some ecosystems because of N deposition, there is also strong evidence that N deposition is associated with environmental degradation, loss of biodiversity, and acidification. While N limits primary production in many terrestrial ecosystems, the capacity of vegetation, soils, and soil microbes to take up greater N inputs can be exceeded.



N deposition varies regionally, but overall, it has increased more than threefold since 1860 …

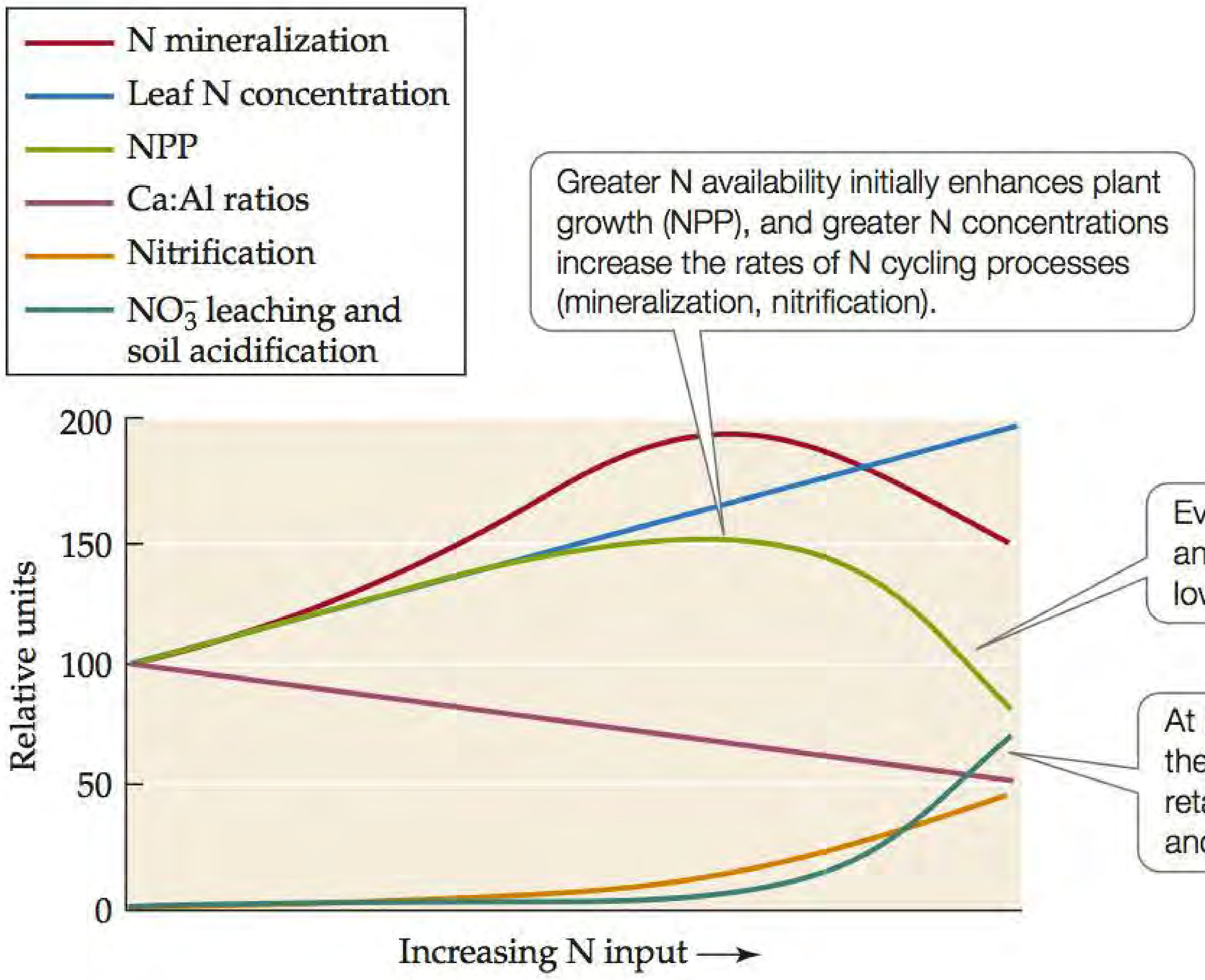
… and is expected to double again by 2050.

Figure 25.20 Historic and Projected Changes in Nitrogen Deposition (A) Estimated rates of deposition of inorganic N compounds (NH_4^+ and NO_3^-) in 1860. (B) Measured rates for the early 1990s. (C) Projected rates for 2050. (From Galloway et al. 2004.)

This condition, known as *nitrogen saturation*, has a number of effects on ecosystems (Aber et al. 1998) (**Figure 25.21**). Greater concentrations of inorganic N compounds (NH_4^+ and NO_3^-) in the soil lead to enhanced rates of microbial processes (nitrification and denitrification) that release N_2O, a potent greenhouse gas. Nitrate (NO_3^-) is easily leached from soils and can move into groundwater, eventually entering aquatic ecosystems. When NO_3^- moves through the soil, it carries cations, including K^+, Ca^{2+}, and Mg^{2+}, in solution to maintain a charge balance. As in the case of acid precipitation, losses of these cations can lead to nutrient deficiencies and eventually to acidification of soils.

Most aquatic ecosystems are limited by P, so the biological uptake of anthropogenic NO_3^- that enters them from terrestrial ecosystems may be relatively small (although there is greater biological processing of N than expected; see Figure 22.15). Riverine transport of N to nearshore marine ecosystems has increased as inputs of N fertilizer have increased (Howarth et al. 1996). Primary production in estuarine and marsh communities is often limited by N, and thus the influx of N from terrestrial sources into these ecosystems has resulted in eutrophication (described in Concept 22.4). Eutrophication results in heavy algal growth, which can create hypoxic conditions in the bottom waters of nearshore ecosystems. The resulting high inputs of organic matter lead to high rates of decomposition by microorganisms, which consume most of the available oxygen. The resulting hypoxic conditions are lethal for most marine life, including fish. Hypoxic conditions may occur over large areas, creating "dead zones." Dead zones of up to 18,000 km^2 form annually in the Gulf of Mexico, and over 400 dead zones form in locations around the world, including the Baltic Sea, the Black Sea, and Chesapeake Bay.

In nutrient-poor ecosystems, many plants have adaptations that lower their nutrient requirements, which also lower their capacity to take up additional inputs of N. As a result, N inputs may cause faster-growing species to outcompete the species adapted to low-nutrient conditions. Acidification and increases in soluble aluminum may lead to declines in intolerant species. Eventually, this increased competition and toxicity can lead to lower diversity and alteration of community composition. In the



Greater N availability initially enhances plant growth (NPP), and greater N concentrations increase the rates of N cycling processes (mineralization, nitrification).

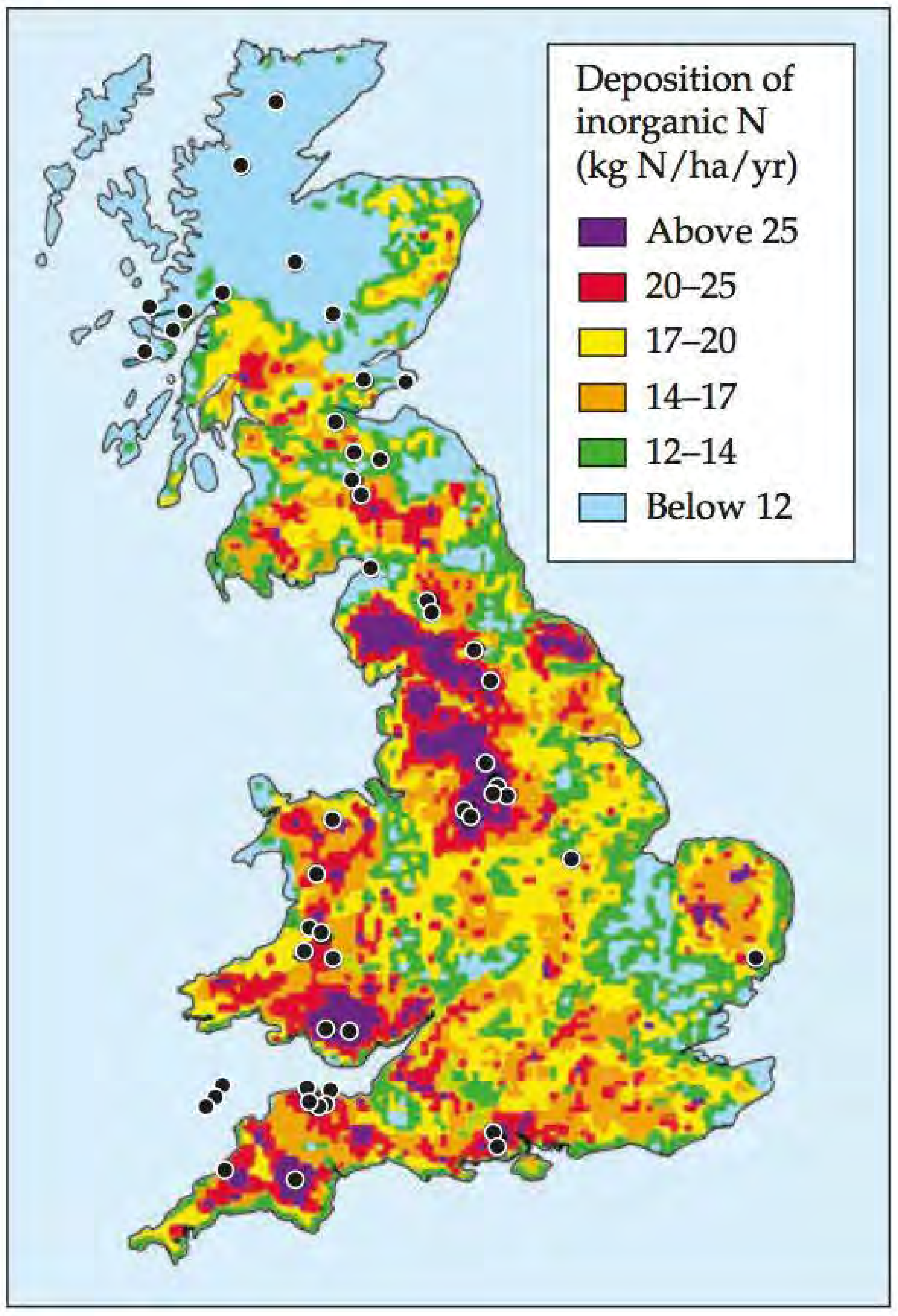
Eventually, losses of calcium and magnesium and greater aluminum concentrations lead to lower plant growth and a decrease in NPP.

At high rates of N input, the ecosystem reaches the final stage of N saturation: the system cannot retain N from both inputs and mineralization, and leaching of N into groundwater occurs.

Figure 25.21 Effects of Nitrogen Saturation Aber and colleagues devised a conceptual model of the response of forest ecosystems to increasing inputs of inorganic N resulting in nitrogen saturation. (After Aber et al. 1998.)

Netherlands, species-rich heath communities adapted to low-nutrient conditions have been replaced by species-poor grassland communities as a result of very high rates of N deposition (Berendse et al. 1993). In Great Britain, Carly Stevens and colleagues surveyed grassland communities across the country with a range of N deposition rates (**Figure 25.22A**). At 68 sites, they measured the mean plant species richness in multiple study plots, along with several environmental variables, to try to explain the variation in plant diversity among the sites. The environmental variables included nine soil chemical factors, nine physical environmental variables, grazing intensity, and the presence or absence of grazing enclosures (Stevens et al. 2004). Of the 20 possible factors that may have influenced differences in species richness among the study sites, the amount of N deposition explained the greatest amount of variation (55%): higher inputs of N were associated with lower species richness (**Figure 25.22B**). The results of this study are supported by a similar large-scale study in the United States that found at least 25% of the sites surveyed had reduced species richness in association with greater N deposition (Simkin et al. 2016). In general, rare species appear to be most at risk for loss from plant communities (Suding et al. 2005). High rates of N

(A)



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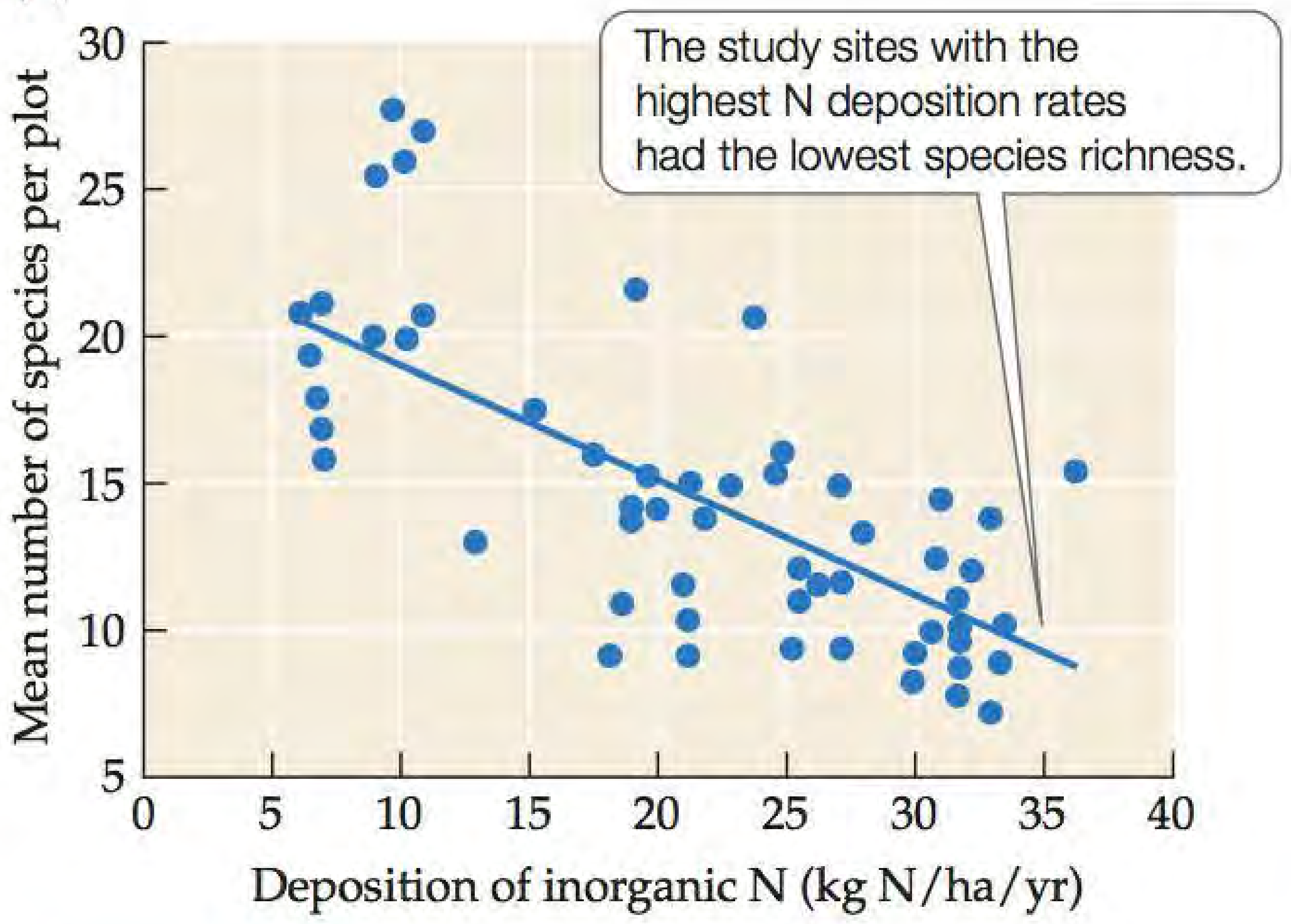


The study sites with the highest N deposition rates had the lowest species richness.

Figure 25.22 Nitrogen Deposition Lowers Species Diversity (A) Inorganic N deposition in Great Britain. Dots on the map indicate the study sites where plant species richness in grassland ecosystems was measured. (B) Correlation between rates of inorganic N deposition and plant species richness. (A from Stevens et al. 2004; B after Stevens et al. 2004.)

deposition also facilitate the successful spread of some invasive plant species at the expense of native species (Dukes and Mooney 1999).

The ecological effects of S and N result when atmospheric deposition returns anthropogenic emissions to Earth's surface. In the next section, we'll describe some anthropogenic compounds that exert negative effects while remaining in the atmosphere.

CONCEPT 25.4

Losses of ozone in the stratosphere and increases in ozone in the troposphere both pose risks to organisms.

Atmospheric Ozone

Ozone is good for biological systems, but only when it is not in close contact with them. In the upper atmosphere (the *stratosphere*), ozone provides a shield that protects Earth from harmful ultraviolet radiation. When in contact with organisms in the lower atmosphere (the *troposphere*), however, ozone can harm them. Detrimental changes in ozone concentrations have occurred in both the stratosphere and the troposphere as a result of anthropogenic emissions of air pollutants.

Loss of stratospheric ozone increases transmission of harmful radiation

About 2.3 billion years ago, when prokaryotes first evolved the capacity to carry out photosynthesis, oxygen began to accumulate in Earth's atmosphere, leading to a series of changes that facilitated the evolution of greater physiological and biological diversity. The increase in atmospheric oxygen (in the form of O_2) also led to the formation of a layer of ozone (O_3) in the stratosphere (at 10–50 km altitude). This ozone layer acts as a shield protecting Earth's surface from high-energy ultraviolet-B (UVB) radiation (0.25–0.32 μm). UVB radiation is harmful to all organisms, causing damage to DNA and photosynthetic pigments in plants and bacteria, impairment of immune responses, and cancerous skin tumors in animals, including humans.

Stratospheric ozone concentrations change seasonally as a result of changes in atmospheric circulation patterns, particularly in the polar zones, where they decline in spring. British scientists measuring ozone concentrations in the Antarctic were the first to record an unusually large decrease in springtime stratospheric ozone concentrations starting in 1980. Springtime minimum ozone concentrations decreased by as much as 70% between 1980 and 1995 (**Figure 25.23**). There was also a concomitant increase in the area of the Antarctic region experiencing a decrease in ozone, called the ozone hole. An **ozone hole** is defined as an area with an ozone concentration of less than 220 Dobson units (= 2.7 × 10^{16} molecules of ozone) per square centimeter; prior to 1979, average annual ozone concentrations had never been recorded below this level. Ozone decreases have been recorded between 25°S and the South Pole. Similar reductions in ozone have been recorded in the Arctic (from 50°N to the North Pole), although the magnitude of the decrease has not been as great (thus conferring the name **Arctic ozone dent**, since ozone concentrations have not dropped below 220 Dobson units).

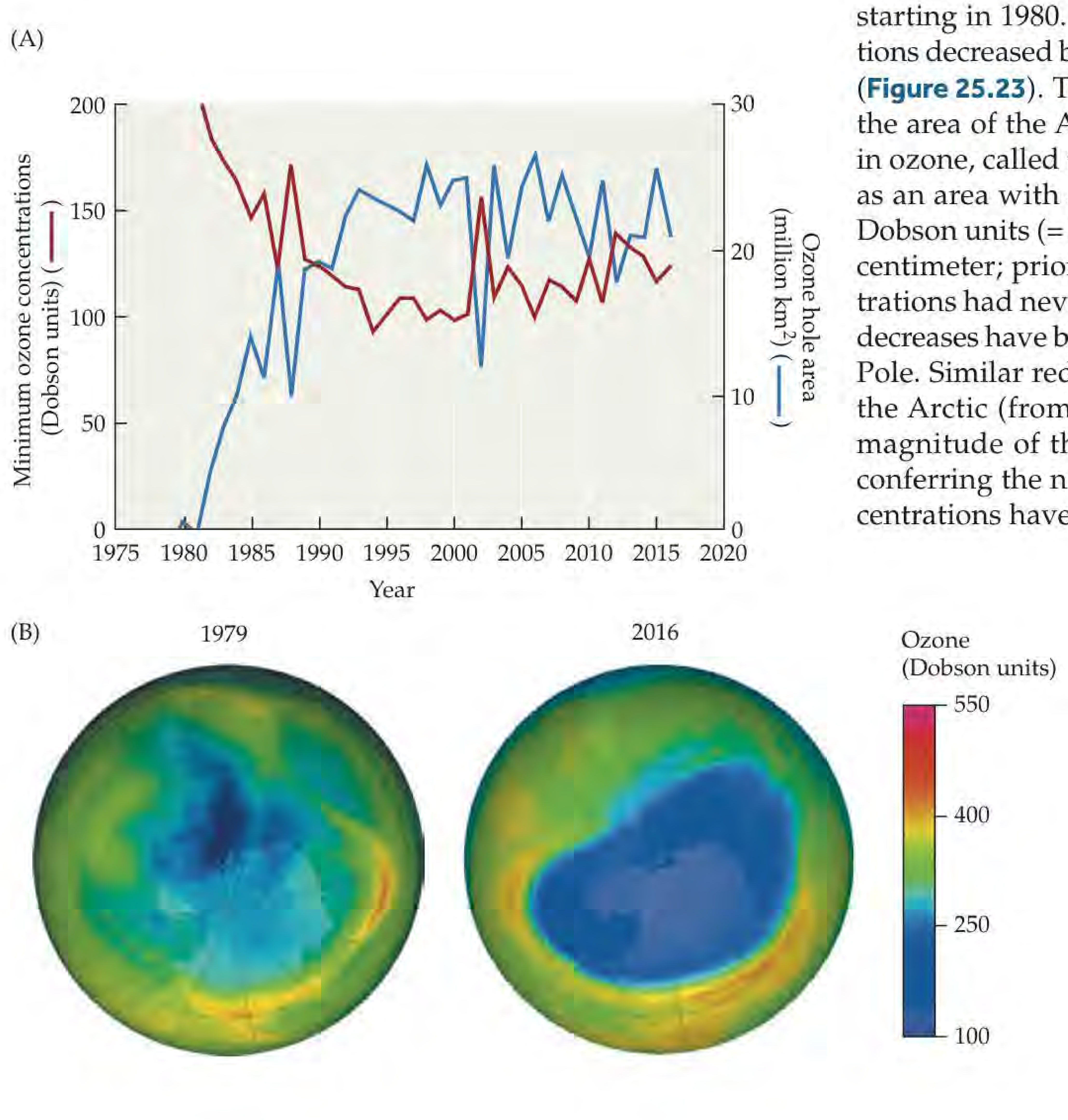


Figure 25.23 The Antarctic Ozone Hole (A) Since 1980, there has been a dramatic decrease in springtime ozone concentrations over the Antarctic region, with concentrations dropping below the threshold for ozone hole status (220 Dobson units) for a large proportion of the region after 1984. (B) Average ozone concentrations over Antarctica for the month of September in 1979 and 2016 demonstrate the dramatic decrease that occurred during this period. The lowest ozone concentrations are shown in dark blue. (A data from ozonewatch.gsfc.nasa.gov.)
]

The decrease in stratospheric ozone was predicted in the mid-1970s by Mario Molina and Sherwood Rowland, who discovered that certain chlorinated compounds, particularly chlorofluorocarbons (CFCs), could destroy ozone molecules. CFCs were developed in the 1930s for use as refrigerants and were later found to be useful as propellants in spray cans dispensing hair spray, paint, deodorants, and many other products. By the 1970s, as much as a million metric tons of CFCs were being produced every year. Molina and Rowland (1974) found that CFCs did not degrade in the troposphere and could remain there for a very long time. From the troposphere, CFCs can move slowly into the stratosphere, where they react with other compounds, particularly in the polar regions during winter, to produce reactive chlorine molecules that destroy ozone. Other anthropogenic compounds with the same effect include carbon tetrachloride, used as a solvent and to fumigate grain, and methyl chloroform, used as an industrial solvent and degreaser. A single reactive chlorine atom has the potential to destroy 100,000 ozone molecules. Thus, the danger posed by chlorinated compounds to the stratospheric ozone layer was clear to Molina and Rowland.

The amount of UVB radiation at Earth's surface increased as concentrations of stratospheric ozone decreased (Madronich et al. 1998). These increases in UVB have been most striking in the Antarctic region, which has experienced an increase in UVB radiation of as much as 130% during spring. Increases have also been recorded in the Northern Hemisphere, including a 22% increase at mid-latitudes during spring.

These increases in UVB radiation at Earth's surface have coincided with an increasing incidence of skin cancer in humans, which is now approximately ten times more common than it was in the 1950s. UVB radiation had an important role in the evolution of pigmentation in humans (Jablonski 2004). The production of melanin, a protective skin pigment, was selected for in humans living at low latitudes, where ozone levels are naturally lowest and the highest levels of UVB radiation reach Earth's surface. As humans migrated away from equatorial Africa into colder climates with less sunlight, however, high amounts of melanin in the skin limited production of vitamin D, resulting in selection for lower melanin production in peoples of higher latitudes. As these lighter-skinned humans have subsequently migrated into environments with higher UVB radiation, to which their complexions are not adapted, they have increased their risk of skin cancers. This has become particularly true for populations at high latitudes in the Southern Hemisphere, including Australia, New Zealand, Chile, Argentina, and South Africa, where exposure to UVB is enhanced by stratospheric ozone loss. Concern is particularly great in Australia, where nearly 30% of the population has been diagnosed with some form of skin cancer.

Substantial evidence exists to indicate that increasing UVB radiation has important ecological effects (Caldwell et al. 1998; Paul and Gwynn-Jones 2003). Sensitivity to UVB radiation varies among the species within a community, and as a result, changes in community composition are likely to result from increased UVB radiation. The potential for detrimental UVB effects due to stratospheric ozone loss is greatest at high latitudes and at high elevations (>3,000 m, or 9,800 feet) because of lower atmospheric filtering of UV radiation.

The realization of the rapid decreases in stratospheric ozone concentrations, and of their probable anthropogenic cause, resulted in several international conferences on ozone destruction in the 1980s. At these conferences, the Montreal Protocol, an international agreement calling for the reduction and eventual end of production and use of CFCs and other ozone-degrading chemicals, was developed. The Montreal Protocol has been signed by more than 150 countries. Atmospheric concentrations of CFCs have remained the same or, in most cases, declined since the Montreal Protocol went into effect in 1989 (**Figure 25.24**). A progressive recovery of the ozone layer is expected to occur over several decades, since the slow mixing of the troposphere, with the long-lived CFCs it still contains, and the stratosphere will result in a time lag before stratospheric ozone concentrations rise. The trends in stratospheric ozone concentrations shown in Figure 25.23 indicate ozone destruction is declining in response to lower emissions of CFCs, but a full recovery of the ozone layer is not expected until 2050.

Tropospheric ozone is harmful to organisms

Ninety percent of Earth's ozone is found in the stratosphere. The remaining 10% occurs in the troposphere. Tropospheric (including ground level) ozone is generated by a series of reactions involving sunlight, NO_x, and volatile organic compounds such as hydrocarbons, carbon monoxide, and methane. In some regions, natural vegetation can be an important source of volatile organic compounds, which include terpenes (which give pines their characteristic odor) and isoprene. Under natural atmospheric conditions, the amount of ozone produced in the troposphere is very small, but anthropogenic emissions of ozone precursor molecules have greatly increased its production. Air pollutants that produce ozone can travel long distances, and thus tropospheric ozone production is a widespread concern.

Tropospheric ozone is environmentally damaging for two main reasons. First, ozone is a strong oxidant; that is, the oxygen in it reacts easily with other compounds. Ozone causes respiratory damage and is an eye irritant in humans and other animals. An increase in the incidence of childhood asthma has been linked to exposure to ozone. Ozone damages the membranes of plants and can decrease their photosynthetic rates and growth. Ozone also

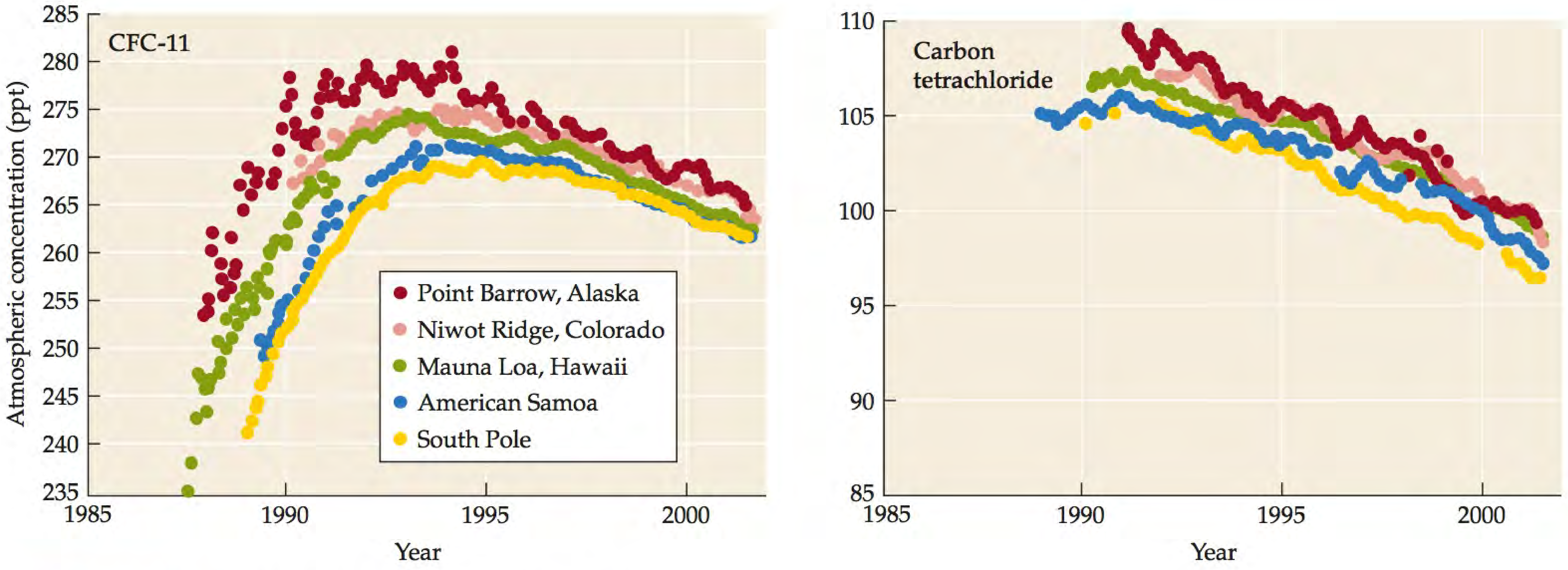


Figure 25.24 Progress against the Ozone Killers Measurements of atmospheric concentrations of ozone-destroying chlorinated compounds, in parts per trillion (ppt), at five monitoring locations across the globe show that several of them have declined since the signing of the Montreal Protocol in 1989.

increases the susceptibility of plants to other stresses, such as low water availability. Decreases in crop yields have been associated with exposure to ozone. Characteristic symptoms of ozone pollution have been found in plants near urban areas since the 1940s and 1950s (e.g., in the San Gabriel Mountains near Los Angeles and in the northern Alps in Italy), but more recently, symptoms have been noted in national parks and wilderness areas farther from sources of pollution. For example, plants in the Sierra Nevada of California are negatively affected by ozone generated in the Central Valley and the San Francisco and Los Angeles urban areas (Bytnerowicz et al. 2003). Growth rates of trees in forests of the eastern United States are as much as 10% lower than they would be in the absence of ozone (Chappelka and Samuelson 1998).

Second, ozone is a greenhouse gas that can contribute to global climate change. Ozone has a short life span in the atmosphere relative to other greenhouse gases, however, and its concentration can vary greatly from place to place. Thus, the effect of anthropogenic ozone on climate change is difficult to estimate.

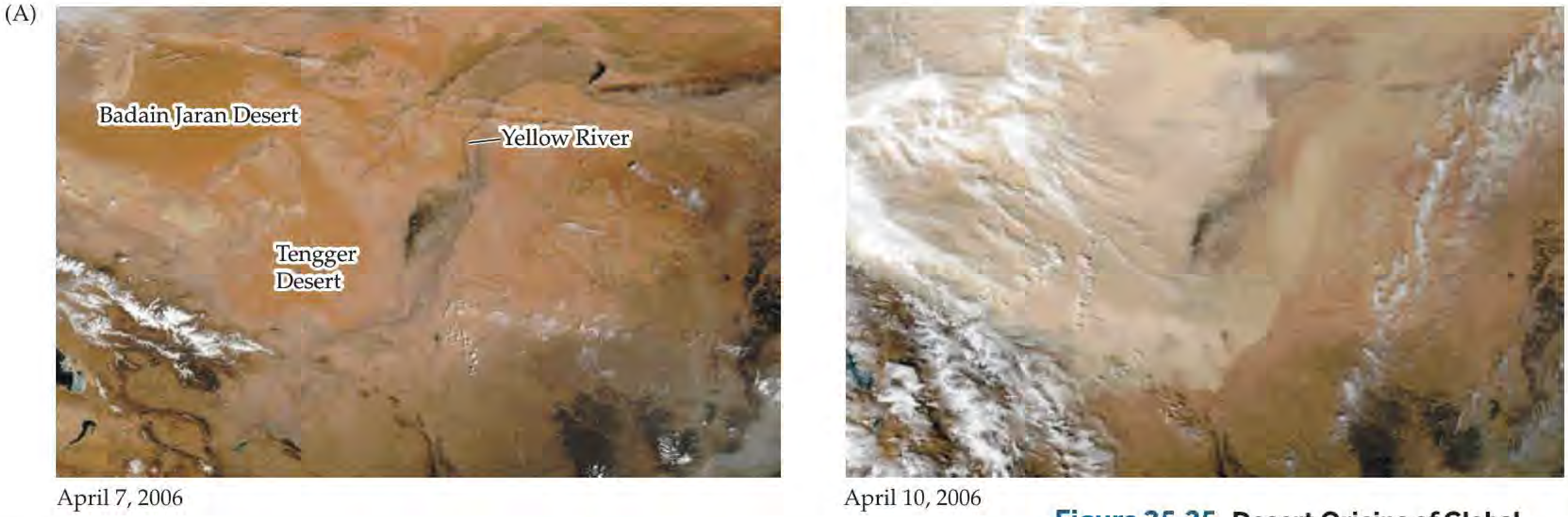
Strategies to limit tropospheric ozone production have focused on lowering anthropogenic emissions of NO_x and volatile organic compounds. In most developed countries, efforts to lower emissions of ozone-producing compounds have met with success. In the United States, for example, emissions of volatile organic compounds dropped by 50% between 1970 and 2004, emissions of NO_x dropped by more than 30% (U.S. EPA 2005), and tropospheric ozone concentrations are decreasing near large urban areas (Cooper et al. 2014). Regulation of emissions of ozone-producing compounds has not been as strict in some developing countries, however. Ozone is a serious air pollutant in urban and agricultural regions of China and India, but stricter environmental regulations are now being put in place.

A CASE STUDY REVISITED

Dust Storms of Epic Proportions

We've seen throughout this chapter that many aspects of global ecology—such as greenhouse gases and climate change, emissions and deposition of N and S, and stratospheric destruction and tropospheric production of ozone—involve transport and chemical processes in the atmosphere. The movements of dust described in this chapter's Case Study are also influenced by atmospheric processes, including rainfall patterns and wind. We've also seen that humans change the environment at a global scale through emissions of greenhouse gases and pollutants into the atmosphere. Land use change, which alters the amount and type of vegetation cover, generally influences the environment at a more local scale. However, land use change in arid zones that are subject to periodic severe droughts can have global-scale effects by enhancing the amount and spread of dust into the atmosphere.

During the early part of the twentieth century, the southwestern Great Plains was opened up for agricultural development. The natural vegetation of the region consisted of drought- and grazing-tolerant grasses. Bison, which had grazed the land for centuries, were replaced by cattle in the late nineteenth century. Economic demand for wheat, due to losses of agricultural lands in Europe during World War I, and the recent population expansion



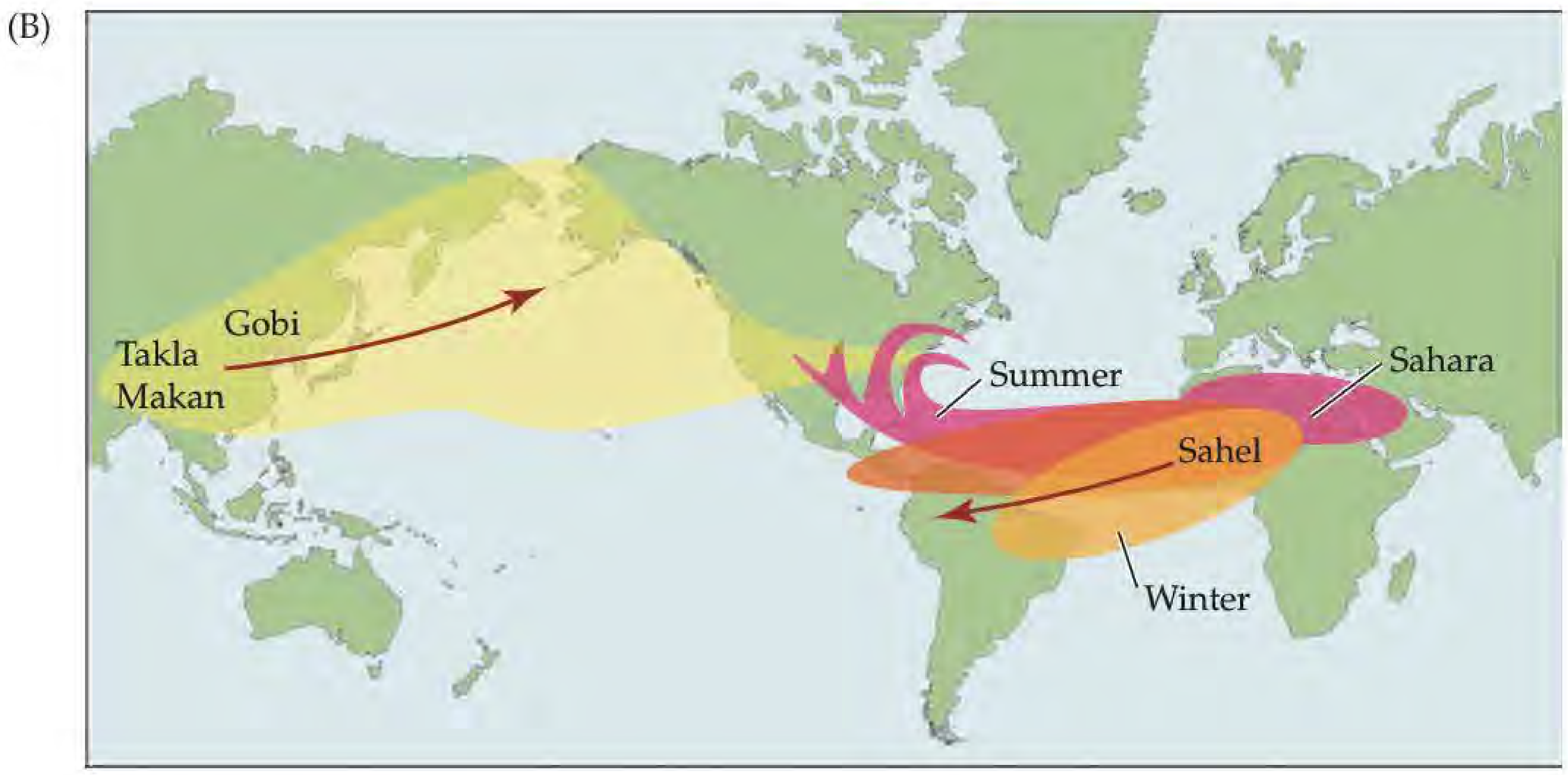


Figure 25.25 Desert Origins of Global Dust Storms Deserts are sources of dust that may travel large distances and have important ecological impacts in distant regions. (A) The photo on the left is a satellite image of the Gobi desert in early April 2006. The photo on the right shows the same region 3 days later, obscured by a massive dust storm. (B) Sources of the dust deposited in the Caribbean region include the deserts of North America and Asia. The main directions of dust flow are indicated by arrows. (B after Garrison et al. 2003, courtesy of Betsy Boynton.)

into the southern Great Plains encouraged the development of agriculture. Although this area was known to experience periodic droughts, farmers, encouraged by the notion that "rain follows the plow" and by recent technological developments in farming, cultivated large areas of land, plowing under the native prairie grasses and replacing them with wheat. For a while, the weather was conducive to agriculture, and the farmers prospered. However, the 1930s brought prolonged severe drought. Fields dried up, and with no protective network of roots to hold it together, the soil began to blow away. Major dust storms carried the soil across the North American continent and all the way to the Atlantic Ocean. The Dust Bowl event is still considered the worst environmental disaster the United States has ever experienced (Egan 2006). Similar circumstances in Asia enhanced the severity of dust storms there. Deforestation, the development of agriculture in marginal zones, overgrazing, and the drainage of the Aral Sea for irrigation have all been implicated in the increased severity of dust storms following the mid-1990s (Wang et al. 2004).

While dust storms in urban areas are a rarity, large-scale dust storms regularly occur in desert regions (**Figure 25.25**). However, both the American Dust Bowl and Asian examples suggest that while dust storms are a natural phenomenon, a combination of agricultural development of marginal lands and severe drought exacerbates these events (Cook et al. 2009). At a global scale, extreme droughts and land use change contribute one-third to one-half of the inputs of dust into the atmosphere (Tegen and Fung 1995). Desert regions, such as the Gobi and Sahara–Sahel regions, have expanded at their margins because of land use change since the 1970s, increasing the global impact of dust storms. For example, Asian dust has been detected in the European Alps, traveling two-thirds of the way around the globe in approximately a week (Grousset et al. 2003). On a geologic time scale, major periods of dust redistribution occur in association with the recession of large ice sheets during interglacial periods (see the discussion of glacial cycles in Concept 2.5), as evidenced by the distribution of loess soils, some hundreds of meters thick, across North America and Europe (**Figure 25.26**).

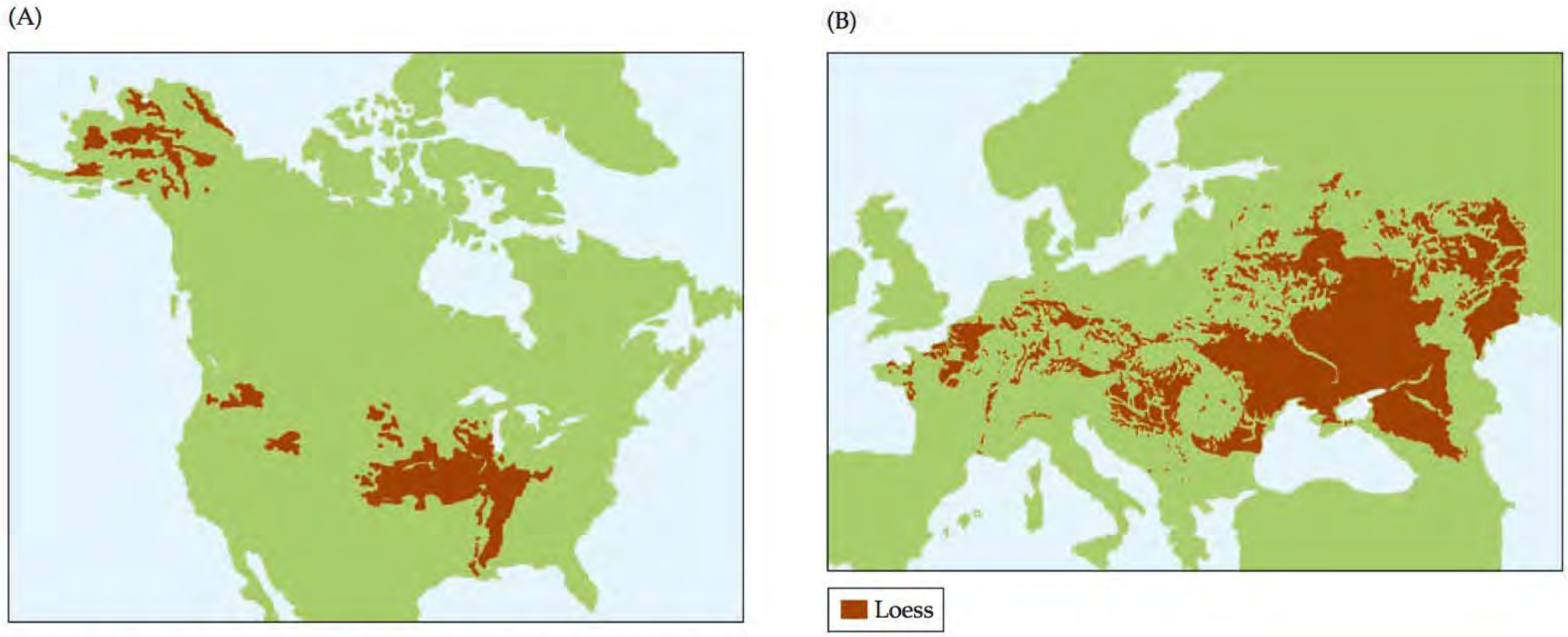


Figure 25.26 Distribution of Loess Soils As continental glaciers receded following the most recent glacial maximum, wind carried substantial amounts of loose soil from the exposed areas. Large areas of (A) North America and (B) Europe were covered with deep layers of this material, which developed into loess soils.

CONNECTIONS IN NATURE

Dust as a Vector of Ecological Impacts

The ecological effects of dust removal and deposition are not fully understood, but one of the best-studied effects is the movement of nutrients (as described in Chapter 22) at spatial scales ranging from a few meters to continents and oceans (Field et al. 2010). Dust deposition of nutrients can have important consequences for primary production and the global carbon cycle. The supply of iron (Fe) from dust deposition is important for oceanic primary production (Mahowald et al. 2005), as we saw in Concept 20.2. Dust from the Asian storms described earlier has been associated with algal blooms in the Pacific, and inputs of cations from African dust are important to primary production in tropical forests in the Amazon (Okin et al. 2004). In contrast, the removal of surface soils by wind can lead to lower production due to losses of organic matter and fine mineral particles, which are important for nutrient supply and retention. Dust may also be important in long-distance transport of pathogens (Garrison et al. 2003) and pollutants (Jaffe et al. 2003) and may influence disease dynamics (as described in Concept 13.5).

The ecological effects of dust movement can be both direct and indirect. Nutrient input and loss are examples of its direct effects. An example of an indirect effect occurs in the southwestern United States when dust transported from the Colorado Plateau falls in the Rocky Mountains and alters the timing of snowmelt. As noted in the Case

Figure 25.27 Dusty Snow in the Rockies Dust from the Colorado Plateau is carried by spring storms to the Rocky Mountains, where it increases absorption of sunlight by snow and accelerates its melting. Earlier snowmelt has important implications for mountain ecosystems and regional hydrology.

Study in Chapter 22, grazing and recreational vehicle use have disturbed biological soil crusts in arid lands of the Colorado Plateau, increasing their erodibility and dust input into the atmosphere. Most of the dust is swept away in spring storms, and some ends up deposited in snow on the Rockies (**Figure 25.27**). The dust increases the amount of sunlight absorbed by the land surface, warming the snow and causing accelerated melting. Earlier snowmelt has the potential to increase the length of the growing season for plants growing in areas with deep snow cover. However, rather than stimulating earlier growth of plants in areas that melt sooner, accelerated snowmelt delays the initiation of growth and flowering of alpine plants, which wait to grow when air temperatures are suitable. This delay results in greater synchrony of greening up of alpine plants, possibly leading to greater competition (Steltzer et al. 2009). In contrast, earlier snowmelt in lower-elevation subalpine meadows triggers some plants to initiate growth immediately, exposing them to potentially killing frosts (Inouye 2008). The surrounding subalpine forests may experience water shortages when snowmelt occurs earlier, which may lower their NPP (Hu et al. 2010). The ecological impacts of dust, both direct and indirect, remind us that ecological phenomena occur at a global scale, have widespread importance, and testify to the role of humans in intensifying their effects.

Summary

CONCEPT 25.1 Elements move among geologic, atmospheric, oceanic, and biological pools at a global scale.

- The global carbon cycle includes large fluxes of CO_2 between the atmosphere and Earth's land surface associated with photosynthesis and respiration and, within the last 160 years, anthropogenic emissions of CO_2 and CH_4.
- Atmospheric concentrations of CO_2 and CH_4 are increasing because of burning of fossil fuels, deforestation, and agricultural development.
- Elevated atmospheric CO_2 concentrations may increase terrestrial plant growth and the acidity of the oceans, causing ecological changes.
- Global fluxes of nitrogen are associated with biological uptake and chemical transformations. Anthropogenic nitrogen fixation and emissions now dominate the global nitrogen cycle.
- The global cycles of phosphorus and sulfur include both geochemical and biological fluxes.
- Anthropogenic fluxes of phosphorus associated with mining and industrial emissions of sulfur far exceed natural fluxes associated with weathering.

CONCEPT 25.2 Earth is warming because of anthropogenic emissions of greenhouse gases.

- Elevated levels of CO_2, CH_4, N_2O, and other greenhouse gases in the atmosphere have warmed Earth, particularly since the 1950s. This warming trend is expected to continue throughout the twenty-first century.
- Large changes in species distributions, community composition, and ecosystem processes are expected as a result of global climate change.
- Recent changes in the geographic ranges of species and in carbon source–sink relationships have been attributed to climate change.

CONCEPT 25.3 Anthropogenic emissions of sulfur and nitrogen cause acid deposition, alter soil chemistry, and affect the health of ecosystems.

- Sulfuric and nitric acids form in the atmosphere from compounds emitted by human activities. These compounds are subsequently deposited on Earth's surface as acid precipitation.
- Acid precipitation causes nutrient imbalances and aluminum toxicity in soils.
- Atmospheric deposition of reactive nitrogen compounds can increase productivity in some ecosystems, but it may also lead to soil acidification, eutrophication and dead zones in nearshore aquatic ecosystems, losses of species diversity, and increases in invasive species.

CONCEPT 25.4 Losses of ozone in the stratosphere and increases in ozone in the troposphere both pose risks to organisms.

- Anthropogenic emissions of chlorinated compounds have led to a loss of stratospheric ozone since the 1980s, particularly at high latitudes, and thus to an increase in the levels of harmful ultraviolet-B radiation reaching Earth's surface.
- Reactions involving volatile organic compounds, many of which are of anthropogenic origin, generate ozone in the troposphere, where it can harm organisms.

Review Questions

1. What are the major biological influences on the global carbon cycle? How have human influences during the past two centuries affected the fluxes of CO_2 associated with these biological influences (i.e., other than by fossil fuel burning) and, subsequently, atmospheric CO_2 concentrations?
2. Terrestrial animals are capable of migrating to regions where the climate is optimal for their function. Despite animals' mobility, ecologists are still predicting that as the climate changes, many animal species will experience local extinctions. Explain why animal responses to climate change will depend on factors other than physiological tolerances and dispersal rates.
3. How can ozone in the atmosphere be both good and bad for organisms?

Hone Your Problem-Solving Skills

Forests are important to the global carbon cycle, taking up a substantial amount of CO_2 from the atmosphere via photosynthesis. As we discussed in Concept 20.2, the production of forests is often limited by the supply of N, and thus greater C uptake may occur with elevated N deposition.

1. How much additional C has been taken up and stored as wood if N deposition has added an average of 15 kg N per hectare per year to temperate deciduous forests for 20 years? Assume that 10% of the N deposition has been taken up and used for increased plant growth, that the C:N ratio in wood is 500:1, and that the temperate deciduous biome makes up 13 million km^2 [1 hectare (ha) = 0.01 km^2].
2. Make the same calculation for the boreal forest biome, with a N deposition rate of 5 kg N per hectare per year for 20 years, the same N uptake amount and C:N ratio of the wood, and an areal coverage of 19 million km^2 for this biome.
3. Calculate the annual sum of the C taken up and stored as wood from your answers to Questions 1 and 2, and compare that to the amount of anthropogenic C emitted in Figure 25.3.

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

25.1 Too Much of a Good Thing: Anthropogenic Effects on the Global Nitrogen Cycle

Web Extensions

25.1 Climate Models, Volcanoes, and Climate Change

Appendix

Some Metric Measurements Used in Ecology

MEASURES OF	UNIT	EQUIVALENTS	METRIC → ENGLISH CONVERSION
Length	meter (m)	base unit	1 m = 39.37 inches = 3.28 feet
	kilometer (km)	1 km = 1000 (10^3) m	1 km = 0.62 miles
	centimeter (cm)	1 cm = 0.01 (10^{-2}) m	1 cm = 0.39 inches
	millimeter (mm)	1 mm = 0.1 cm = 10^{-3} m	1 mm = 0.039 inches
	micrometer (μm)	1 μm = 0.001 mm = 10^{-6} m	
	nanometer (nm)	1 nm = 0.001 μm = 10^{-9} m	
Area	square meter (m^2)	base unit	1 m^2 = 1.196 square yards
	hectare (ha)	1 ha = 10,000 m^2	1 ha = 2.47 acres
Volume	liter (L)	base unit	1 L = 1.06 quarts
	milliliter (ml)	1 ml = 0.001 L = 10^{-3} L	1 ml = 0.034 fluid ounces
	microliter (μl)	1 μl = 0.001 ml = 10^{-6} L	
Mass	gram (g)	base unit	1 g = 0.035 ounces
	kilogram (kg)	1 kg = 10^3 g	1 kg = 2.20 pounds
	teragram (Tg)	1 Tg = 10^{12} g	
	petagram (Pg)	1 Pg = 10^{15} g	
	milligram (mg)	1 mg = 10^{-3} g	
	microgram (μg)	1 μg = 10^{-6} g	
	picogram (pg)	1 pg = 10^{-12} g	
Temperature	degree Celsius (°C)	base unit	°C = $\frac{5}{9}$(°F – 32) 0°C = 32°F (water freezes) 100°C = 212°F (water boils) 20°C = 68°F (“room temperature”)
Pressure	Megapascal (MPa)		1 MPa = 145 psi (pounds per square inch)
Energy	joule (J)		1 J ≈ 0.24 calorie = 0.00024 kilocalorie*

*A calorie is the amount of heat necessary to raise the temperature of 1 gram of water 1°C. The kilocalorie, or nutritionist’s calorie, is what we commonly think of as a calorie in terms of food.

Answers

CHAPTER 1

Answers to Figure Legend Questions

Figure 1.4 Estimating from the graph, about 88% of tadpoles in the control group survived, and 0% of them had deformities. Since there were 35 tadpoles in the control group, this indicates that 31 (0.88 × 35) of the tadpoles in the control group survived, and none had deformities.

Figure 1.5 The results for cages from which *Ribeiroia* was excluded show that pesticides acting alone do not cause frog deformities. The results for cages exposed to *Ribeiroia* show that pesticides do affect frogs, since the percentage of frogs with deformities was higher in ponds where pesticides were present. However, the results do not indicate how pesticides caused that effect.

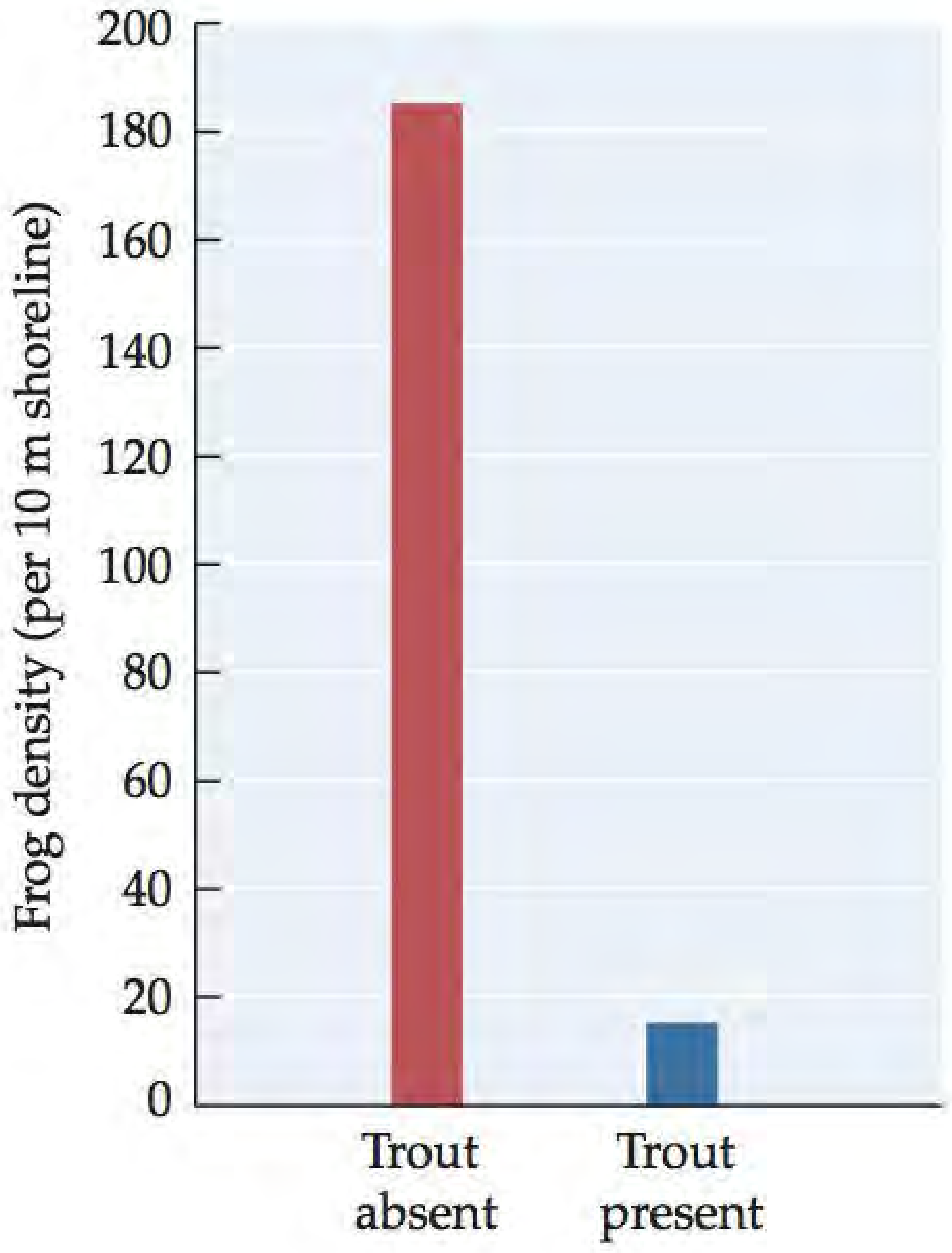
Figure 1.6 By comparing results from the controls with results from treatments in which pesticides were added, the investigator could test whether addition of a pesticide affected either the immune system response (number of eosinophils) of the tadpoles or the number of *Ribeiroia* cysts per tadpole. The intent of the "solvent control" was to check for possible effects of the solvent in which the pesticide was dissolved.

Figure 1.7 By 2006, the disease had spread to all of the lower 48 states except Maine. The disease reached two states in 2006, Oregon and Washington.

Figure 1.11 Producers absorb nutrients such as nitrogen from the environment and use them for growth (step 1). The nitrogen in the producer's body may then be transferred to a series of consumers: to an herbivore that eats the plant, a carnivore that eats the herbivore, a second carnivore that eats the first, and so on (step 2). Eventually, however, the nitrogen is returned to the physical environment when the dead body of the organism containing it is broken down by decomposers (step 3).

Answers to Analyzing Data 1.1 Questions

1. Lakes with trout have lower densities of frogs than do lakes without trout, suggesting that the introduction of trout may have reduced frog density. However, while data from this study show that frog densities are correlated to the presence or absence of trout, they do not show that the trout *caused* frog densities to decline. To test whether the introduction of trout caused frog densities to decline, the researchers would need to perform a controlled experiment.



2. Results from control lakes that contain trout can be compared to results from trout-removal lakes: If the introduction of trout caused frog densities to decline, frog densities should increase in trout-removal lakes, whereas they should not change in the control lakes that still contain trout. Additionally, if the introduction of trout is the primary factor causing a decline in frog densities, frog densities also should not change very much in control lakes that never contained trout. Thus, if frog densities do not change very much in control lakes that never contained trout, such a result would strengthen the argument that changes in frog density observed in trout-removal lakes was due to the removal of trout, not to other unmeasured variables.
3. a. For the 1-year period that ends just prior to when trout began to be removed from Lakes 1, 2, and 3, frog densities were close to zero per 10 m of shoreline in each of these lakes.
   b. For the 1-year period that started one year after the removal of trout began, average frog densities were: 1.5 (Lake 1), 0.9 (Lake 2), and 0.9 (Lake 3) frogs per 10 m of shoreline. These data indicate that the removal of trout caused frog densities to increase within one year of beginning to remove trout from these lakes.
4. a. The experimental results suggest that introduced trout caused frog densities to decline.

b. The experimental results suggest that frog populations can recover once trout are removed.

Answers to Review Questions

1. The phrase "connections in nature" is meant to evoke the fact that interactions among organisms and between organisms and their environment cause events in nature to be interconnected. As a result of such connections, an action that directly affects one part of an ecological community may cause unanticipated side effects in another part of the community. Various examples related to amphibian deformities and population declines illustrate such connections and their side effects. For example, it appears that the addition of fertilizers to ponds has led to the following chain of events: the fertilizer stimulates increased algal growth, which then leads to increased snail abundance, increased *Ribeiroia* abundance, and hence more frequent amphibian deformities.
2. Ecology is the scientific study of interactions between organisms and their environment. The scope of ecology is broad, and it may address virtually any level of biological organization (from molecules to the biosphere). Most ecological studies, however, emphasize on one or more of the following levels: individuals, populations, communities, or ecosystems. Thus, if ecologists studied the effects of a particular gene, they probably would emphasize how the gene affected interactions in nature—they might, for example, study how a gene affected the ability of an organism to cope with its environment, or how a gene affected interactions among species. Compared with a geneticist or cell biologist, an ecologist would be less likely to emphasize either the gene itself or its effects on the workings of a cell, and more likely to study how the gene affected interactions in nature that occur at the individual, population, community, or ecosystem levels.
3. The scientific method summarizes the process of scientific inquiry. The four key steps in this inquiry process are: (1) observe nature and ask a question about those observations; (2) use previous knowledge or intuition to develop hypotheses (possible answers) to those questions; (3) evaluate different hypotheses by performing experiments, collecting new observations, or analyzing results from quantitative models; and (4) use the results from the approaches taken in (3) to modify the hypotheses, pose new questions, or draw conclusions about the natural world. An essential feature of many scientific investigations is a controlled experiment in which results from an experimental group (that has the factor being tested) are compared with results from a control group (that lacks the factor being tested).

Answers to Hone Your Problem-Solving Skills Questions

1. The five tanks with no atrazine serve as the control. By comparing results from control tanks to results from tanks with atrazine, an investigator could test whether the presence of atrazine affected one or more of the six variables measured in the experiment (phytoplankton abundance, attached algae abundance, water clarity, eosinophil number, tadpole survival, and number of *Ribeiroia* cysts).
2. Compared to the controls, when atrazine is added phytoplankton abundance decreases more than three-fold, the abundance of attached algae increases, and water clarity increases. To interpret these results, note that atrazine may have caused phytoplankton abundance to drop, which would cause water clarity to increase (because fewer phytoplankton were suspended in water), and that, in turn, would cause more sunlight to reach the algae attached to rocks, causing their abundance to increase.
3. Compared to the controls, when atrazine is added the number of eosinophils decreases more than two-fold, tadpole survival drops from 72% to 45%, and the number of *Ribeiroia* cysts increases more than four-fold. Atrazine may have impaired the tadpole's immune response, thereby causing the number of *Ribeiroia* cysts to increase, which would harm the tadpoles and cause their survival to drop.
4. The addition of atrazine to a pond could cause phytoplankton abundance to drop, thereby increasing the sunlight available to attached algae, hence increasing the growth of attached algae. Snails eat attached algae, so an increase in the abundance of those algae could cause snail abundance to increase, and that, in turn, could cause *Ribeiroia* abundance to increase (because *Ribeiroia* depends on snails to complete its life cycle). Atrazine also impairs the tadpole's immune response. Overall, since atrazine increases *Ribeiroia* abundance and impairs the tadpole's immune response, that could cause the number of *Ribeiroia* cysts to increase and tadpole survival to decrease.

CHAPTER 2

Answers to Figure Legend Questions

Figure 2.4 An increase in atmospheric greenhouse gases would increase the flux of infrared radiation back to Earth's surface and would have a warming effect on Earth's climate. Atmospheric aerosols reflect incoming solar radiation, so an increase in these particles would have a cooling effect on Earth's climate.

Figure 2.15 The larger a continent, the greater the seasonal temperature changes there. Because water has a higher heat capacity than land, seasonal temperature changes increase with distance from the ocean. Higher latitudes experience greater seasonal changes in radiation, for reasons we will explore in Concept 2.5.

Figure 2.18 Winds in the tropics blow from east to west, so the east-facing aspect would have the highest precipitation, and the west-facing slope would be in the rain shadow.

Figure 2.22 Seasonal changes in lake stratification would be unlikely in tropical lakes because seasonal changes in air temperature, and therefore water temperature, would be small.

Figure 2.26 Glacial periods would be promoted by (1) an elliptical orbit, taking Earth farther from the sun during the aphelion; (2) a maximum tilt in Earth's axis, lowering the amount of solar radiation received during winter, and (3) having Earth's axis tilted such that winter in the Northern Hemisphere, where the majority of the land mass is found, occurs during the aphelion, when Earth is farthest from the sun.

Figure 2.29 In 11 out of 19 (58%) cases the cool phase of PDO corresponds with a higher-than-average catch. In 15 out of 22 cases (68%) the warm phase of PDO corresponds to a lower-than-average catch of salmon.

Answers to Analyzing Data 2.1 Questions

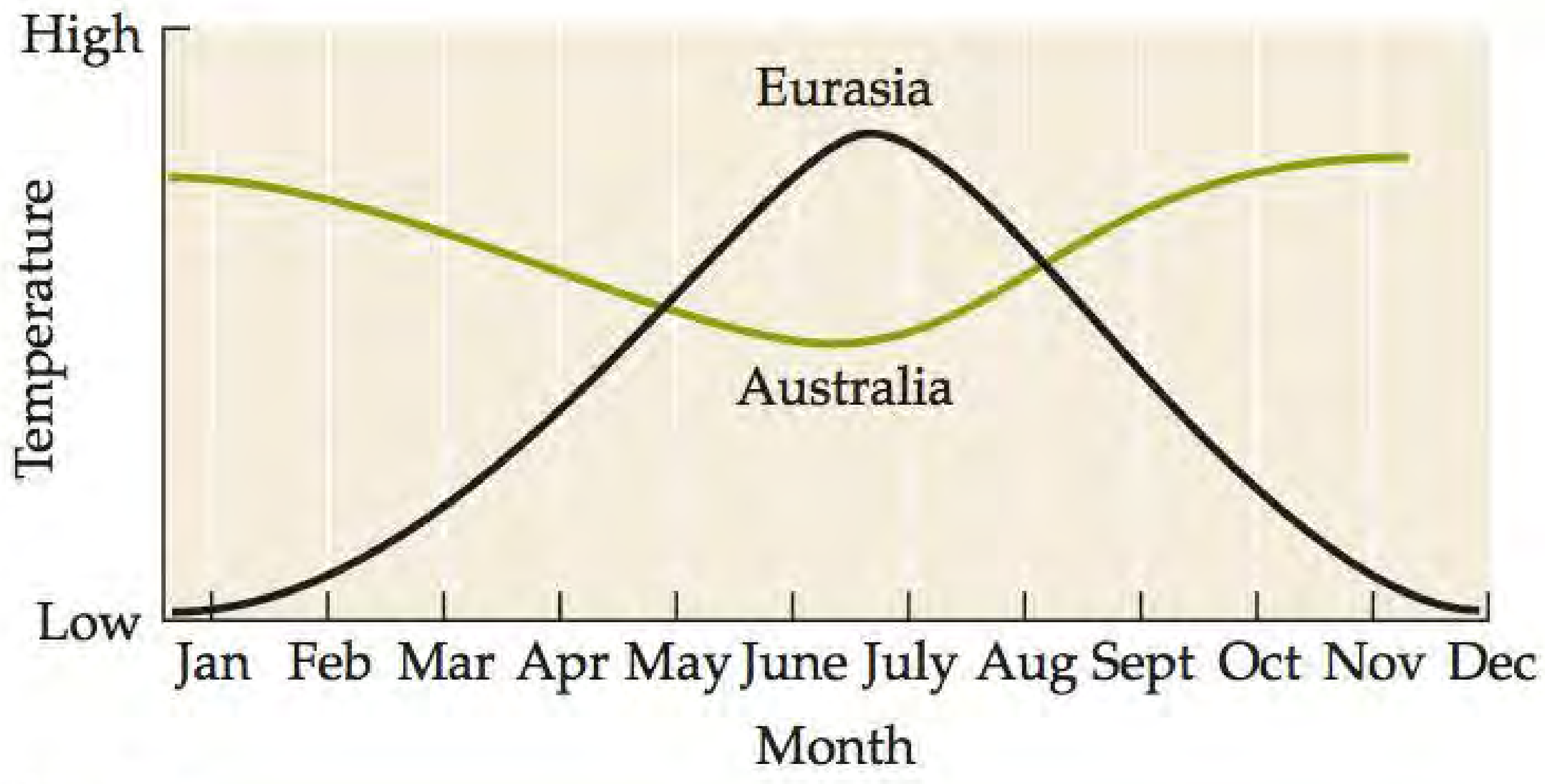
1. Greater solar radiation would be absorbed by the dark green crops. Given incoming radiation of 470 W/m^2, light-colored grasses reflect 122 W/m^2 (26% of 470), and absorb 345 W/m^2. With irrigated crops, 85 W/m^2 (18% of 470) is reflected and 385 W/m^2 is absorbed. Thus, with approximately 40 W/m^2 greater heat absorption, the change in albedo alone would result in warming.
2. The greater surface roughness of the crop plants would cause greater heat loss (approximately 40 W/m^2) due to convective transport of pockets of warm air from the surface to the upper atmosphere.
3. Higher leaf area coupled with greater soil moisture in the irrigated crop system would result in higher evapotranspiration. As a result more heat is lost from the surface to the atmosphere via latent heat flux by the irrigated cropland relative to the short-grass steppe.
4. The total difference in heat lost associated with the land use change from grassland to irrigated crop is 60 W/m^2 – 40 W/m^2 = 20 W/m^2. The greater total heat loss by the irrigated crop relative to the short-grass steppe would result in cooler temperatures.

Answers to Review Questions

1. Extreme environmental conditions, such as high and low temperatures or droughts, are important determinants of mortality in organisms. As a result, species' distributions often reflect extreme environmental conditions more than average conditions. The timing of changes in the physical environment is also important, as exemplified by the response of vegetation to the timing of precipitation, which is not reflected in average annual conditions.
2. Differences in the intensity of solar radiation across Earth's surface establish latitudinal gradients of surface heating. Greater heating in the tropics results in rising air currents, which establish large-scale atmospheric circulation cells, called Hadley cells. The warm rising air also promotes high amounts of precipitation on the tropics. Polar cells form where cold, dense air descends at the poles. Between the Hadley and polar cells are the Ferrell cells, driven by the movement of the Hadley and polar cells and the exchange of energy between equatorial and polar air masses. The temperate zone is found at mid-latitudes in association with the Ferrell cells.
3. Salinization is a progressive increase in soil salinity due to surface evapotranspiration of water. Desert areas have high rates of evapotranspiration and little precipitation to leach salts to deeper soil layers. Some desert soils also have impervious soil layers underlying the surface layer that impede leaching, increasing the potential for salinization.

Answers to Hone Your Problem-Solving Skills Questions

1.



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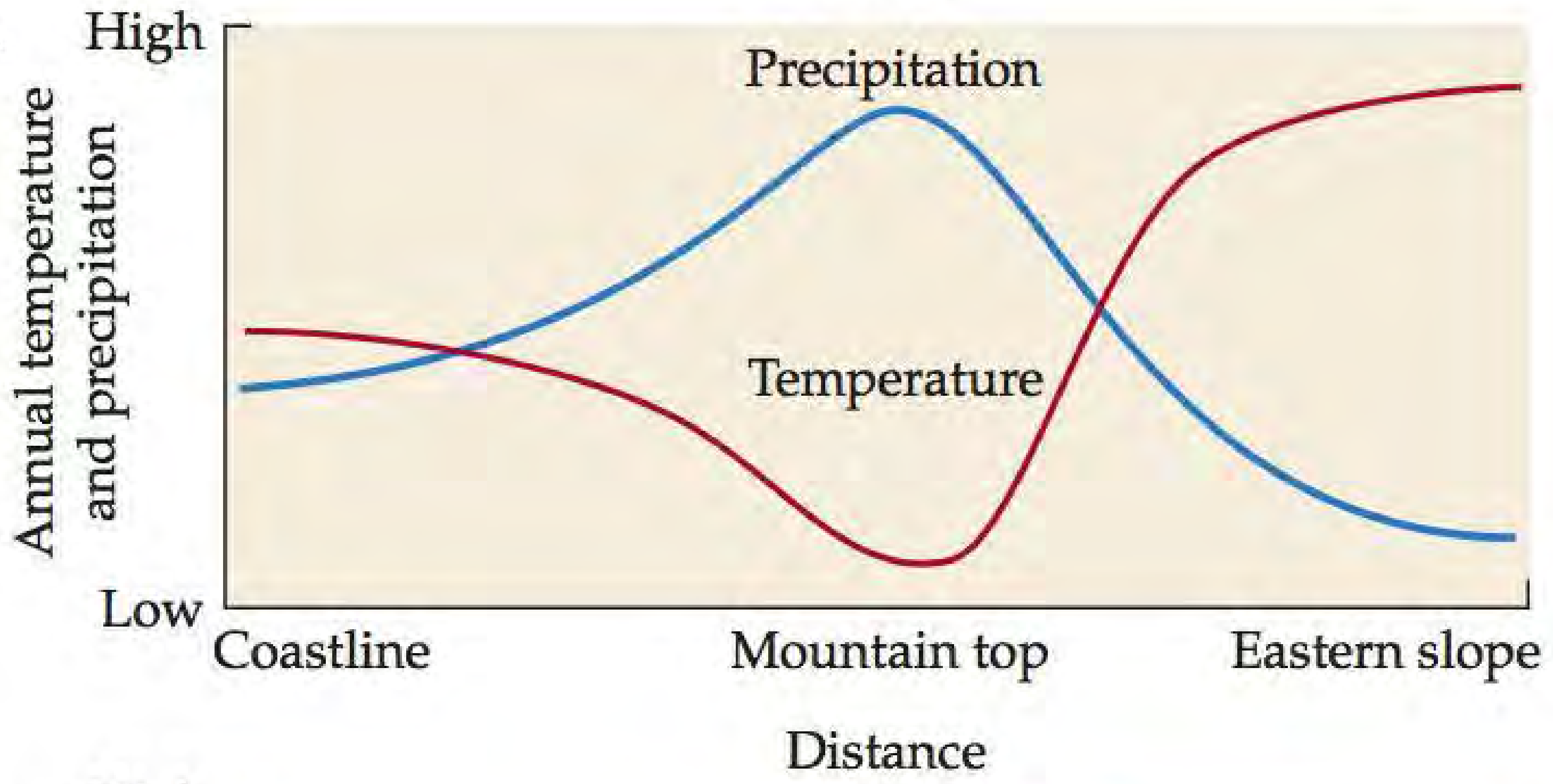

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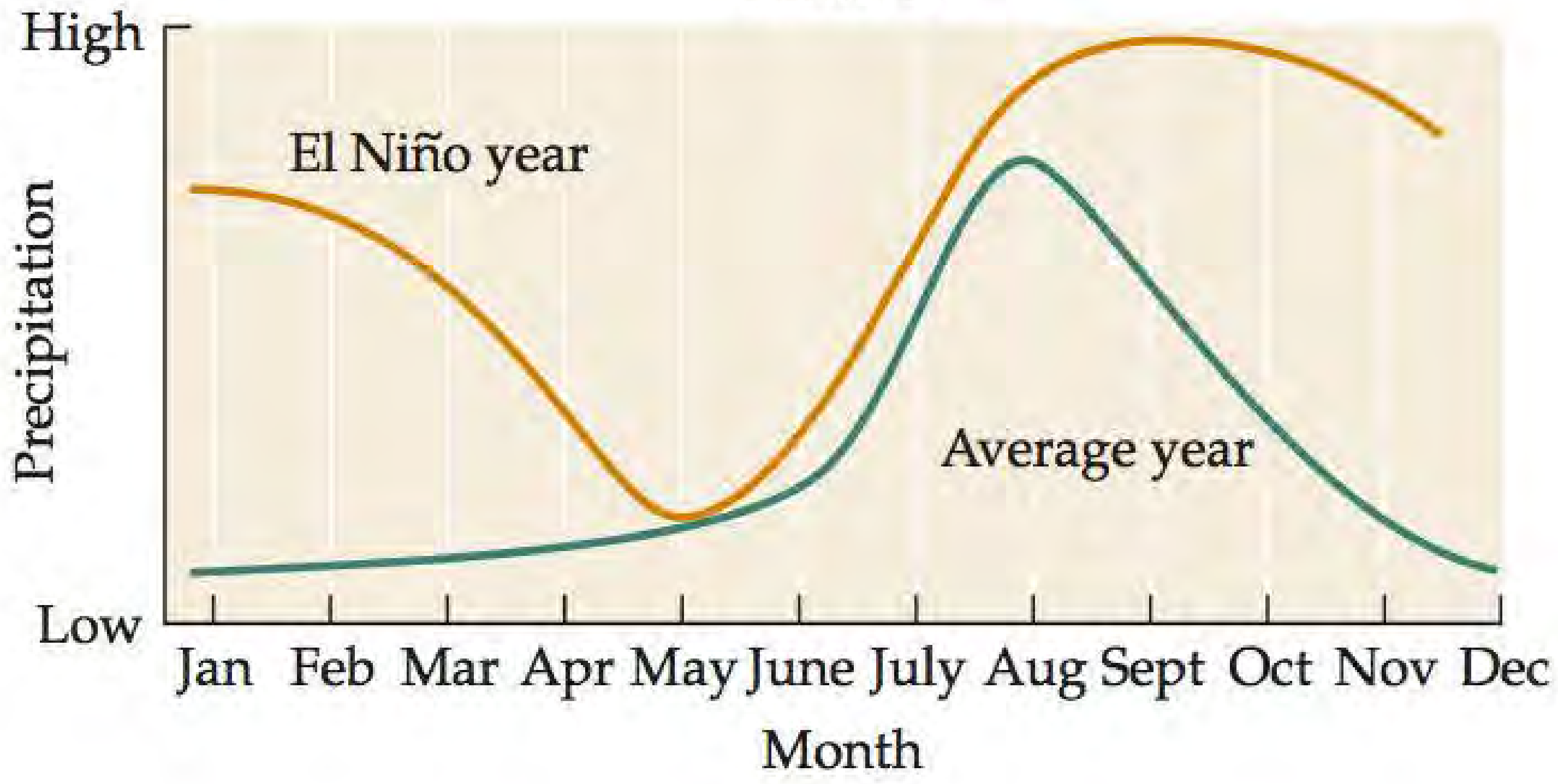


CHAPTER 3

Answers to Figure Legend Questions

Figure 3.4 Grasslands and shrublands might occur in areas with combinations of precipitation and temperature usually associated with forests or savannas due to disturbances such as fire or deforestation by humans or an outbreak of herbivory. These factors would limit successful establishment of trees, which would normally crowd out grasses and shrubs.

Figure 3.5 A comparison of Figures 3.5A and B shows that the greatest human impacts have occurred in grassland and deciduous forest biomes of North America and Eurasia (principally due to cropland development). Note that in the Indian subcontinent and in South America, human impacts have occurred primarily in the tropical seasonal forest biome.

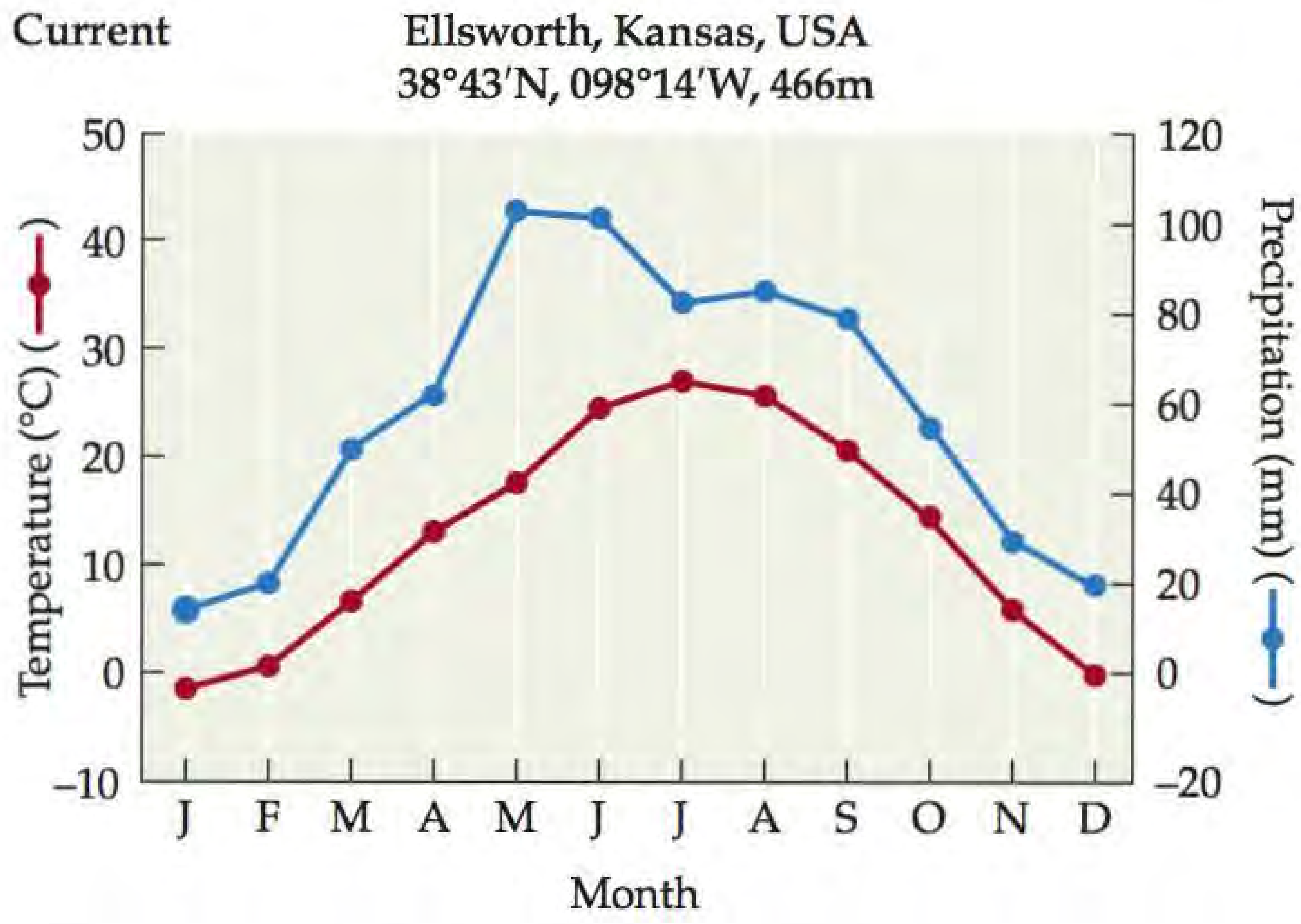
Figure 3.11 Both east- and west-facing slopes would have distinct biological zonation associated with gradients of temperature and precipitation, but precipitation would be lower on the east-facing slope due to the rain-shadow effect. As a result, a forest community on the west-facing slope might be replaced by a shrub or grassland community at the same elevation on the east-facing slope.

Figure 3.14 Oxygen levels would be highest where the stream velocity is the fastest, in the main channel. This is where organisms with the highest oxygen demands, typically fish, are found. The lowest oxygen levels are found in the benthic and hyporheic zones, where organisms must be able to tolerate hypoxic conditions.

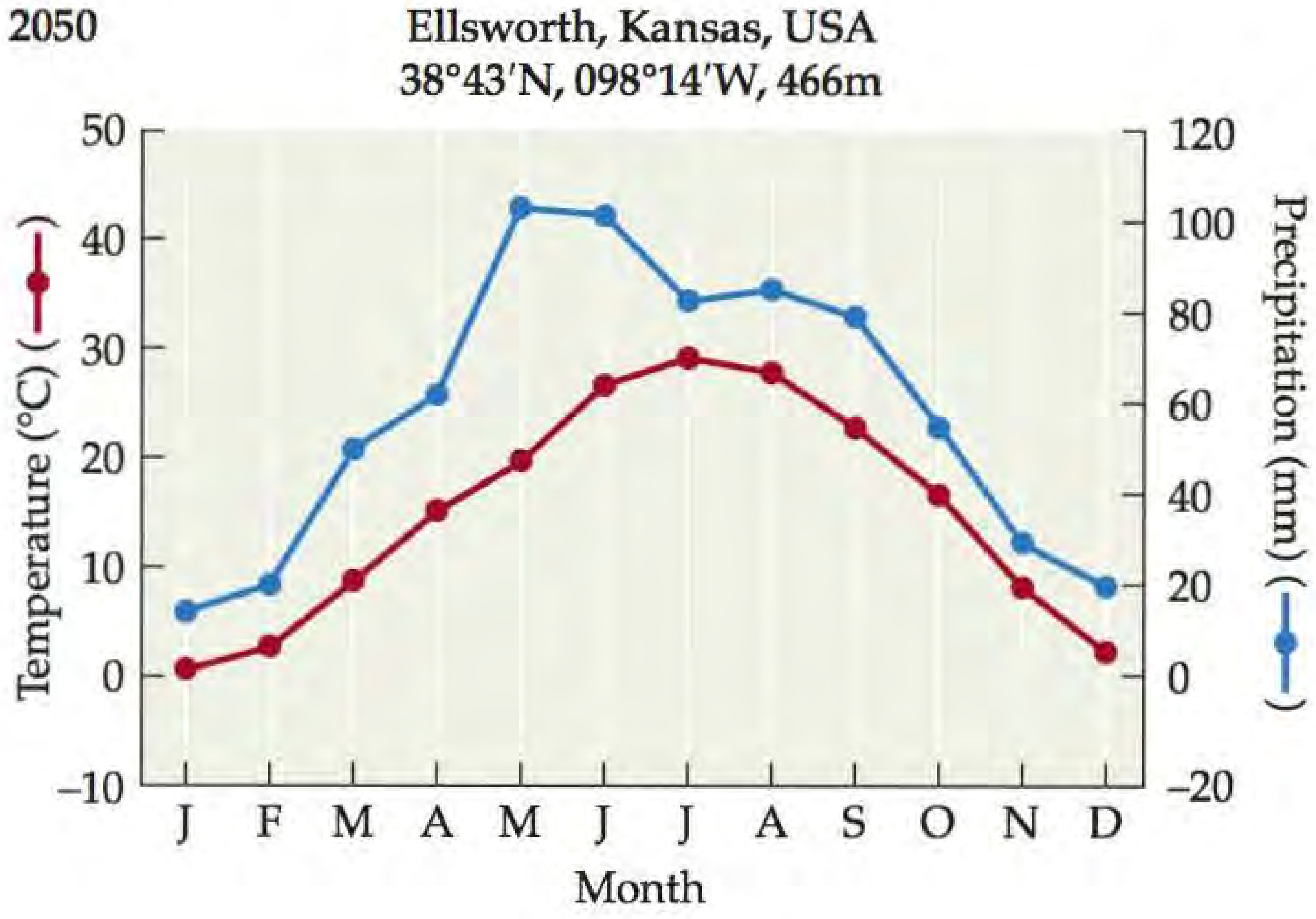
Answers to Analyzing Data 3.1 Questions

1.

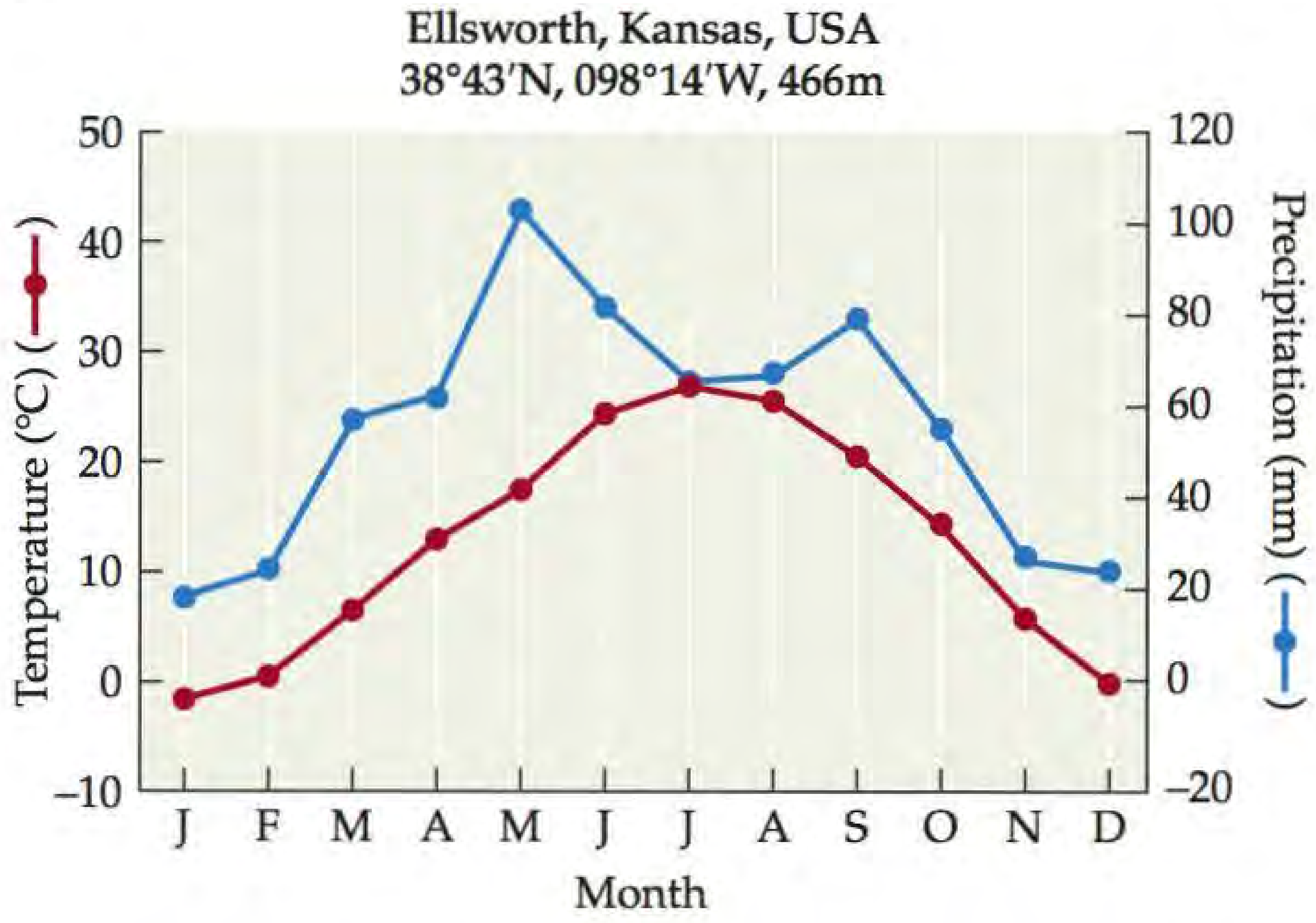
Current



2050



2.



3. A decrease in precipitation during the summer growing season, coupled with warmer temperatures, results in a period of water stress in July, as indicated by the crossing of the temperature and precipitation lines. The occurrence of water stress in the summer along with higher winter precipitation are more characteristic of the temperate shrubland biome, as shown in the exemplary climate diagram. With an increase in average annual temperature the climate averages for Ellsworth cross the boundary between temperate grasslands and temperate shrublands.
4. Grazing and fire frequency also play roles in determining the occurrence of the grassland and shrubland biomes. If fires continue to be a part of the landscape, greater frequency due to warmer, drier conditions may allow grasslands to persist, as frequent fires promote grasses more than shrubs. Grazing may also help promote the persistence of grasslands rather than shrublands, as grasses are more tolerant of grazing.

Answers to Review Questions

1. Plant growth forms are good indicators of the physical environment, particularly climatic and soil conditions. Because plants are immobile as adults (seeds can move), they have evolved morphological features that allow them to cope with their physical environment, including its extremes. Leaf life span (evergreen versus deciduous leaves), for example, reflects the fertility of the soil. Some biomes, such as grasslands, can also be indicators of disturbances such as grazing or fire. Animals can be important features of and controls on biome distribution, but their mobility renders them less useful as indicators of biomes.
2. Biomes are associated with the major climatic zones described in Chapter 2. Tropical rain forests are associated with a tropical climate characterized by high annual precipitation with only slight seasonal variations in the amount of precipitation. As the seasonality of rainfall becomes more pronounced further north and south from the tropics, regular dry periods occur, giving rise to the seasonal tropical forest biome. High pressure zones associated

with Hadley cells create extremely dry zones that promote the desert biome. Seasonality of both temperature (cool winters, warm summers) and precipitation in the temperate climatic zone give rise to grassland (wet summers, dry winters) and shrubland (wet winters, dry summers) biomes. Temperate deciduous forests occur where seasonal temperature changes are moderate, and both summer and winter are moist. Moving toward the polar climatic zone, winter temperatures and precipitation decrease, the period of subfreezing winter temperature increases, marking the transition to the Boreal and tundra biomes.

3. According to the river continuum concept, water velocity, stream bed particle size, and input of detritus from riparian vegetation all decrease as rivers move downstream. As a result, the importance of the surrounding terrestrial ecosystems as sources of energy for stream organisms tends to decrease downstream. Stream insects include more shredders near the source of a stream and more collectors in the lower portions. Attached plants and free-floating algae become more abundant downstream.
4. Light penetration varies according to the depth and clarity of the water. Where there is enough light for photosynthesis (the photic zone), photosynthetic organisms provide food for consumers, increasing the abundance of those organisms. The stability of the substrate determines whether organisms can anchor themselves or bury themselves in sand. Nearshore zones with rocky substrata tend to have the most abundant organisms and the most diverse communities. Photosynthetic organisms are more sparse in nearshore zones with sandy bottoms and below the photic zone in the open ocean.

Answers to Hone Your Problem-Solving Skills Questions

1. At the base of the mountains on the western slope, the biome type would be temperate evergreen forest (using the 12°C annual average temperature and 120 cm annual average precipitation). Using the environmental lapse rate of 4.5°C per 1,000 m, the annual average temperature will drop to –1.5°C by the summit ridges and peaks. With an annual average precipitation of 180 cm, this puts the trajectory of biome (vegetation) change through temperate deciduous forest, boreal forest, tundra, and finally into a gray area of ice and snow year-round. In fact, several coniferous forest bands are encountered, but the deciduous forest biome analog is generally missing.

   Descending on the east slope, the temperature warms more quickly. Using an environmental lapse rate of 6.5°C per 1,000 m, the average annual temperature at the base of the mountains (2,700 m lower) would be 16°C. With an annual average precipitation of 50 cm, shrubland vegetation would occur at the base of the mountains. Between the alpine ridges and the shrubland at the base, vegetation zones of tundra, boreal forest (subalpine forest), deciduous forest, grassland, and shrubland would be encountered.
2. The starting point on the western slope would have average annual temperature and precipitation of 16°C and 84 cm, respectively, with future climate change projections. The summit ridges would have annual average temperature and precipitation of 2.5°C and 126 cm with climate change projections. The vegetation transition from the base of the western slope to the summits would include grassland, deciduous forest, and boreal (subalpine) forest.

   With projected climate change, annual average temperature and precipitation at the base of the western slopes of the Cascades would be 20°C and 35 cm. Descending the eastern slopes, the transect would encounter boreal (subalpine) forest, deciduous forest, grassland, shrubland, and finally desert.

CHAPTER 4

Answers to Figure Legend Questions

Figure 4.4 The southern limit of aspen's range tends to be associated with survival of drought conditions, which are becoming more frequent in the center of the continent. As a result, the southern range limit of aspen may move to the north. At the northern limit of aspen, the effects of low temperatures on its survival and reproduction tend to limit its distribution. Climate warming may offset this effect, and aspen may move northward in the future.

Figure 4.9 Cooling is important in any biome where leaf temperatures may rise to levels that are stressful, including many temperate and tropical biomes. However, a steady supply of water is needed to support transpirational cooling, which would be the case in tropical biomes and subtropical biomes during the rainy season.

Figure 4.10 Cooling mechanisms that do not use water, such as leaf pubescence or increasing convective heat loss, may be more important to cooling in deserts than in moister habitats such as the tropics, where the water supply is sufficient water for transpirational cooling.

Figure 4.15 Moving between sun and shade influences the energy balance of the lizard. The lizard gains energy, particularly by solar radiation, when it moves to a sunny location. Moving into the shade results in net energy loss to the surrounding environment (losses > gains). If the rock on which the lizard basks is warmer than its body, then the lizard gains heat energy from the rock via conduction. A cooler rock in the shade will receive heat energy by conduction from the lizard's body.

Figure 4.21 Closing stomates during midday lowers transpiration by increasing the resistance to water loss. Opening the stomates later in the afternoon when the air is cooler exposes the leaf to a concentration gradient of water from the plant to the air that is lower than at midday. As a result, transpirational water loss is less than it would be during the hotter part of the day.

Figure 4.25 The rate of water loss for each animal is given by slope of the line. If the external environment (light, temperature, humidity) is kept relatively constant, then the gradient of water potential from the animal to the air is the same, and the resistance modifies the actual water loss. Differences in the slopes therefore reflect differences in resistance to water loss.

Answers to Analyzing Data 4.1 Questions

1. Red represents the red squirrel, and blue represents the wolf. The larger animal (wolf) would have thicker fur with a greater insulative value than the red squirrel would. Longer fur in smaller mammals inhibits their mobility.
2. The circles represent the summer values for fur, and the triangles represent the winter values. Because the wolf is larger, its fur length varies more to adjust for seasonal changes in air temperature. The red squirrel may rely on torpor to survive the cold winter.

Answers to Review Questions

1. Plants as a group exhibit slightly greater tolerances of temperature extremes than ectotherms (see Figure 4.7), and both of these groups have tolerances much greater than those of endothermic animals. Plants and ectotherms, most of which do not generate heat internally, are more reliant on tolerance as a strategy for adapting to tissue temperature variation, while endotherms rely on avoidance of temperature extremes through internal heat generation and behavior, such as migration. Plants can exhibit avoidance of temperature extremes through leaf deciduousness.
2. a. Transpiration is an evaporative cooling mechanism that allows the plant to lower its leaf temperature below the air temperature. However, transpiration also results in water loss from the plant. If the water is not replaced, because the soil is too dry or the water loss is too rapid, the plant will experience water stress, and the rates of its physiological processes, such as photosynthesis, will decrease.

   b. Dark-colored animals may be able to warm themselves more effectively, but they may also be more visible to their predators or prey. In many cases, it appears that camouflage is more important than the ability to absorb sunlight effectively.
3. The principal ways in which plants determine their resistance to water loss are by adjusting the degree of opening of their stomates and by the thickness of the outer cuticle. Arthropods have cuticles that are extremely resistant to water loss. Similarly, skin thickness in amphibians, birds, and mammals affects their resistance to water loss. Reptiles have particularly thick skin, often overlain by scales, that provides a very effective barrier to water movement into the atmosphere. Note, however that increasing the resistance of a barrier to water loss requires trade-offs with evaporative cooling as well as gas exchange.

Answers to Hone Your Problem-Solving Skills Questions

1. The most leaf pubescence would be expected for the population from the driest site (Death Valley), the least pubescence for the wettest site (Superior), with the amount for Oatman intermediate but probably closer to that for Death Valley, based on the magnitude of annual average rainfall. The same order would be expected for seasonal changes in pubescence (acclimatization): Death Valley > Oatman > Superior.
2. A quantitative expression of the answers from question 1 should show highest absorption in the plants from the Superior population, lowest absorption in the Death Valley population, and intermediate absorption in the Oatman population. If seasonal acclimatization is occurring, this will be reflected in lower absorption of radiation during the driest part of the year.
3. The results generally support the hypothesis that the Death Valley population has the most pubescence and lowest absorption of solar radiation, the Superior population has the least pubescence and highest absorption of solar radiation, and the Oatman population is intermediate for pubescence and absorption of solar radiation. While acclimatization occurs in all three populations during the drying cycle, the magnitude of the change in leaf absorption of solar radiation is roughly the same for each population.

CHAPTER 5

Answers to Figure Legend Questions

Figure 5.7 The light saturation level would be lower than the maximum light level the plant experiences because the energy invested in achieving a higher light saturation level might not pay off. The plant experiences the maximum light level for only short periods of time, and the increase in CO_2 taken up during those short periods might not pay for the additional machinery (e.g., chlorophyll, enzymes) needed to increase the light saturation level.

Figure 5.10 At low carbon dioxide and high oxygen concentrations, the photorespiratory carbon dioxide loss can exceed photosynthetic carbon dioxide gain. This is because oxygen is taken up to a greater extent than carbon dioxide by rubisco when the ratios of oxygen to carbon dioxide increase.

Figure 5.14 Extrapolation of the line used to fit the data to the x axis indicates that the proportion of the grass flora that is C_4 drops to zero when the growing season minimum temperature is around 4°C–5°C. This would correspond to an average growing season temperature of 9°C–10°C, which is at or above the growing season temperatures for boreal forests and tundra shown in the climate diagrams. This result agrees well with the observed lack of C_4 plants in these biomes.

Ecological Toolkit 5.1 CAM plants exhibit a wider range of δ ^{13}C values because some are facultative CAM plants. At some times they use C_3 photosynthesis, but during drier periods they use CAM photosynthesis. The δ ^{13}C of their tissues would reflect a mixing of C taken up using both of these photosynthetic pathways.

Answers to Analyzing Data 5.1 Questions

Note: Numerical answers may vary slightly due to differences in interpolation from the graph.

1. a. *High-light grown plant*

   Gains: (2.5 μmol/m^2/s × 7200 s) + (32 μmol/m^2/s × 36,000 s) + (2.5 μmol/m^2/s × 7200 seconds) = 1,188,000 μmols CO_2/m^2 or 1.188 mols CO_2/m^2

   Losses: 3 μmol/m^2/s × 36,000 s = 108,000 μmols CO_2/m^2 or 0.108 mols CO_2/m^2

   Total daily balance for the high-light grown plant: +1.08 mols CO_2/m^2

   Low-light grown plant

   Gains: (2.5 μmol/m^2/s × 7200 s) + (5 μmol/m^2/s × 36,000 s) + (2.5 μmol/m^2/s × 7200 seconds) = 216,000 μmols CO_2/m^2 or 0.216 mols CO_2/m^2

   Losses: 2 μmol/m^2/s × 36,000 s = 72,000 μmols CO_2/m^2 or 0.072 mols CO_2/m^2

   Total daily balance for the high-light grown plant: +0.144 mols CO_2/m^2

   b. *High-light grown plant*

   Gains: (–2 μmol/m^2/s × 7200 s) + (2.5 μmol/m^2/s × 36,000 s) + (–2 μmol/m^2/s × 7200 seconds) = 61,200 μmols CO_2/m^2 or 0.0612 mols CO_2/m^2

   Losses: 3 μmol/m^2/s × 36,000 s = 108,000 μmols CO_2/m^2 or 0.108 mols CO_2/m^2

   Total daily balance for the high-light grown plant: –0.047 mols CO_2/m^2

   Low-light grown plant

   Gains: (0 μmol/m^2/s × 7200 s) + (2.5 μmol/m^2/s × 36,000 s) + (0 μmol/m^2/s × 7200 seconds) = 90,000 μmols CO_2/m^2 or 0.090 mols CO_2/m^2

   Losses: 2 μmol/m^2/s × 36,000 s = 72,000 μmols CO_2/m^2 or 0.072 mols CO_2/m^2

   Total daily balance for the high-light grown plant: +0.018 mols CO_2/m^2

2. The higher light saturation point in the high-light grown plants contributed significantly to the more positive carbon balance relative to the low-light grown plants when exposed to high-light conditions. Gains in carbon uptake were substantially higher in the high-light grown plants than in the low-light grown plants at high-light conditions. However, in low-light conditions, the lower light compensation point and nighttime respiration rates allowed the low-light grown plant to maintain a positive carbon balance, whereas the high-light grown plant had a negative carbon balance.

3. Low-light grown plants have lower concentrations of enzymes to support photosynthesis, and thus will have lower respiratory rates and lower carbon loss at night.

Answers to Review Questions

1. Autotrophy is the use of sunlight (photosynthesis) or inorganic chemicals (chemosynthesis) to fix CO_2 and synthesize energy storage compounds containing carbon–carbon bonds. Photosynthesis occurs in archaea, bacteria, protists, algae, and plants. Heterotrophy is the consumption of organic matter to obtain energy. The organic matter includes both living and dead organisms. Living organisms vary in their mobility, and their consumers (predators) have adapted ways to improve their efficiency in capturing their food (prey). Dead organic matter can be eaten and digested internally by multicellular heterotrophs or externally broken down by enzymes excreted into the environment and then absorbed by archaea, bacteria, and fungi.
2. CAM plants open their stomates to take up CO_2 at night, when the humidity of the air is higher than it is during the day. They store CO_2 in the form of a four-carbon organic acid, then release it to the Calvin cycle during the day. The storage of CO_2 allows the stomates to be closed during the day, when the potential for transpirational water loss is greater.
3. Live animals are a higher-quality food source, but they are rarer and thus harder to find, and they may have defense mechanisms that require expenditure of energy to overcome. Plant detritus is abundant in many ecosystems, so little energy needs to be expended in locating it, but its food quality is low.

Answers to Hone Your Problem-Solving Skills Questions

1. The photosynthesis rate for the C_3 plant increases from 32 to 39 μmol/m^2/s, or an increase of 22%. The photosynthesis rate for the C_4 plant does not increase at all—the photosynthesis rate is CO_2 saturated above an atmospheric concentration of about 200 ppm. If the increase in photosynthesis results in greater growth of the C_3 plants but not the C_4 plants, the abundances of the C_3 plants may increase at the expense of the C_4 plants, which would decrease in abundance.
2. The observed increase in photosynthesis is greater than expected for plants of both photosynthetic pathways but unexpectedly so for the C_4 plants, for which no increase was expected based on the modeled response. Reasons may be related to benefits to all plants in water savings, due to lower transpiration rates from stomatal closure, and thus less water stress lowering photosynthesis rates. Additionally, plants may be able to acclimatize to the elevated CO_2 and more effectively invest in enzymes to increase photosynthesis rates as CO_2 concentrations increase. Finally, the photosynthetic CO_2 response shown in the model may not be representative for all species. Some

C_4 plants may have higher CO_2 saturation points than what is shown in the figure.

CHAPTER 6

Answers to Figure Legend Questions

Figure 6.6 The "Before selection" and "After selection" data show that nearly all fly larvae in galls less than 17 mm in diameter were killed by wasps. A much greater proportion of larvae in the largest galls survived, suggesting that wasps provide a stronger source of selection than do birds.

Figure 6.7 When the simulation began, each population had 9 *A* alleles and 9 *a* alleles. At generation 20, 8 populations still had both alleles. Eventually, it is likely that the *A* allele would either reach fixation (a frequency of 100%) or be lost from each of those 8 populations.

Figure 6.13 No. The added risk of mortality due to reproduction is represented by the difference between the blue curve (females that reproduced) and the red curve (females that did not reproduce). That added risk decreases for females 3–7 years old, then rises for females 8–13 years old (and remains roughly constant thereafter).

Figure 6.23 If evolutionary changes in plant genotype did not affect moth abundance, we would expect that predicted and observed moth abundance would not be correlated to one another. If that were the case, the graph should look like this:

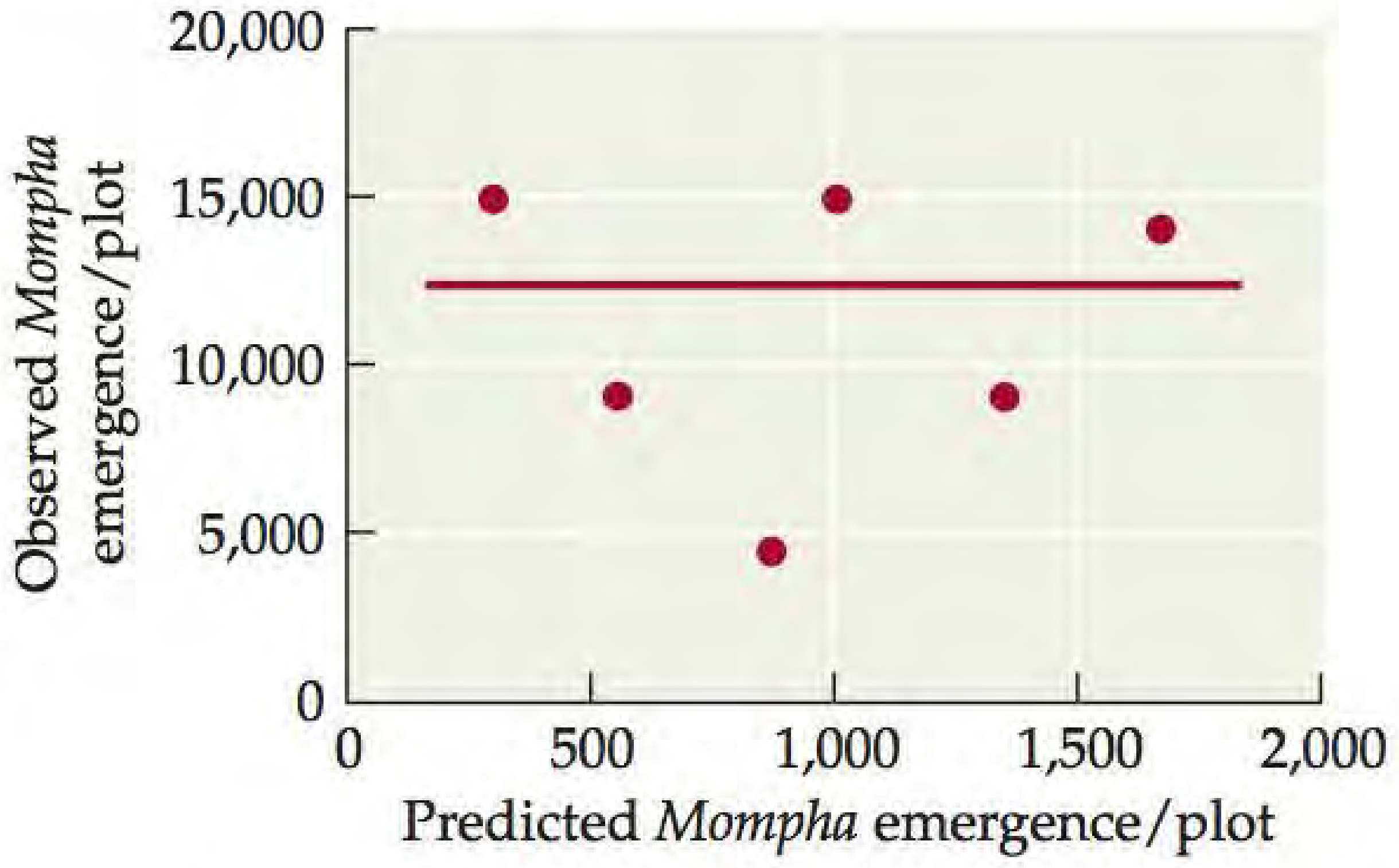
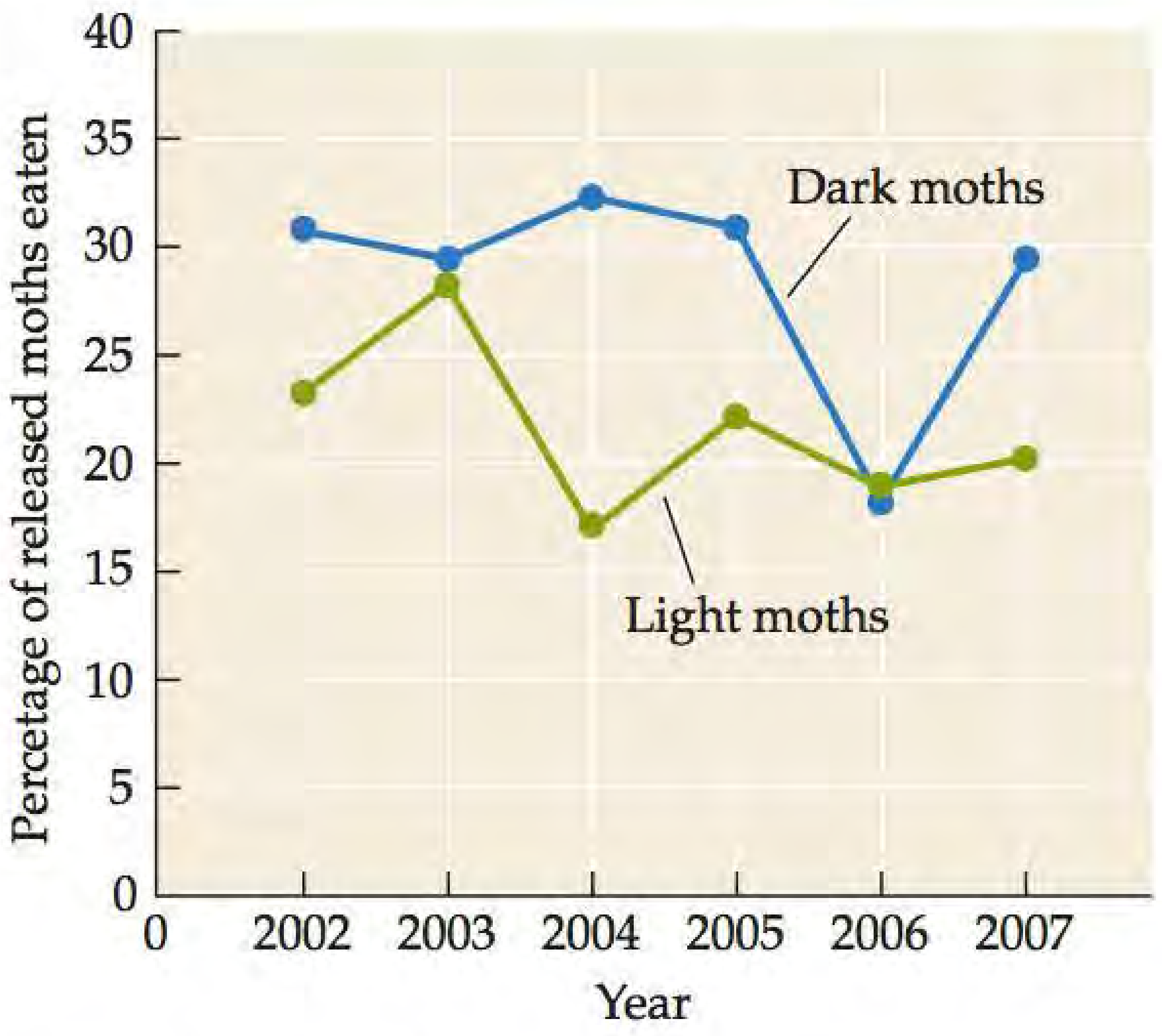


Figure 6.24 From the graph we can estimate that in 1832, the initial frequencies were 0.52 for genotype *AA*, 0.31 for genotype *Aa*, and 0.17 for genotype *aa*. Likewise, we can estimate that in 1923, the final frequencies were 0.73 for genotype *AA*, 0.22 for genotype *Aa*, and 0.05 for genotype *aa*. Using the approach for genotype frequencies described in the footnote in Concept 6.1, we can calculate that the frequency of the *a* allele was about 0.33 in 1832 and about 0.16 in 1923. Thus, the frequency of the *a* allele declined by more than 50% in about 100 years.

Answers to Analyzing Data 6.1 Questions

1. Releasing moths at densities and proportions similar to those observed in the field helped to remove potential complicating factors; this makes the experiment more realistic and the results easier to interpret. For example, some predators prefer to attack abundant prey, so if moths had been released at unusually high densities, predators might have devoted more effort to catching the moths than they typically do, thus making the results of the experiment more difficult to interpret.
2. We can see from the table from the analyzing data exercise for this chapter, that in 2002 about 13% (101/807) of the moths that Majerus released were dark in color. Over time, that percentage dropped—from 13% in 2002 to 10% in 2003, 7% in 2004, 7% in 2005, 4% in 2006, and 2% in 2007. Because the proportions of dark moths that Majerus released were similar to those he observed in the field, this indicates that dark-colored moths were declining in frequency in the area where he conducted his experiment.
3. In every year but one (2006), the percentage of released dark-colored moths that were eaten was higher than the percentage of released light-colored moths that were eaten. Since the trees in the region in which the experiment was conducted were light in color, this result supports the hypothesis that natural selection caused the frequency of dark-colored moths to decline over time.



Answers to Review Questions

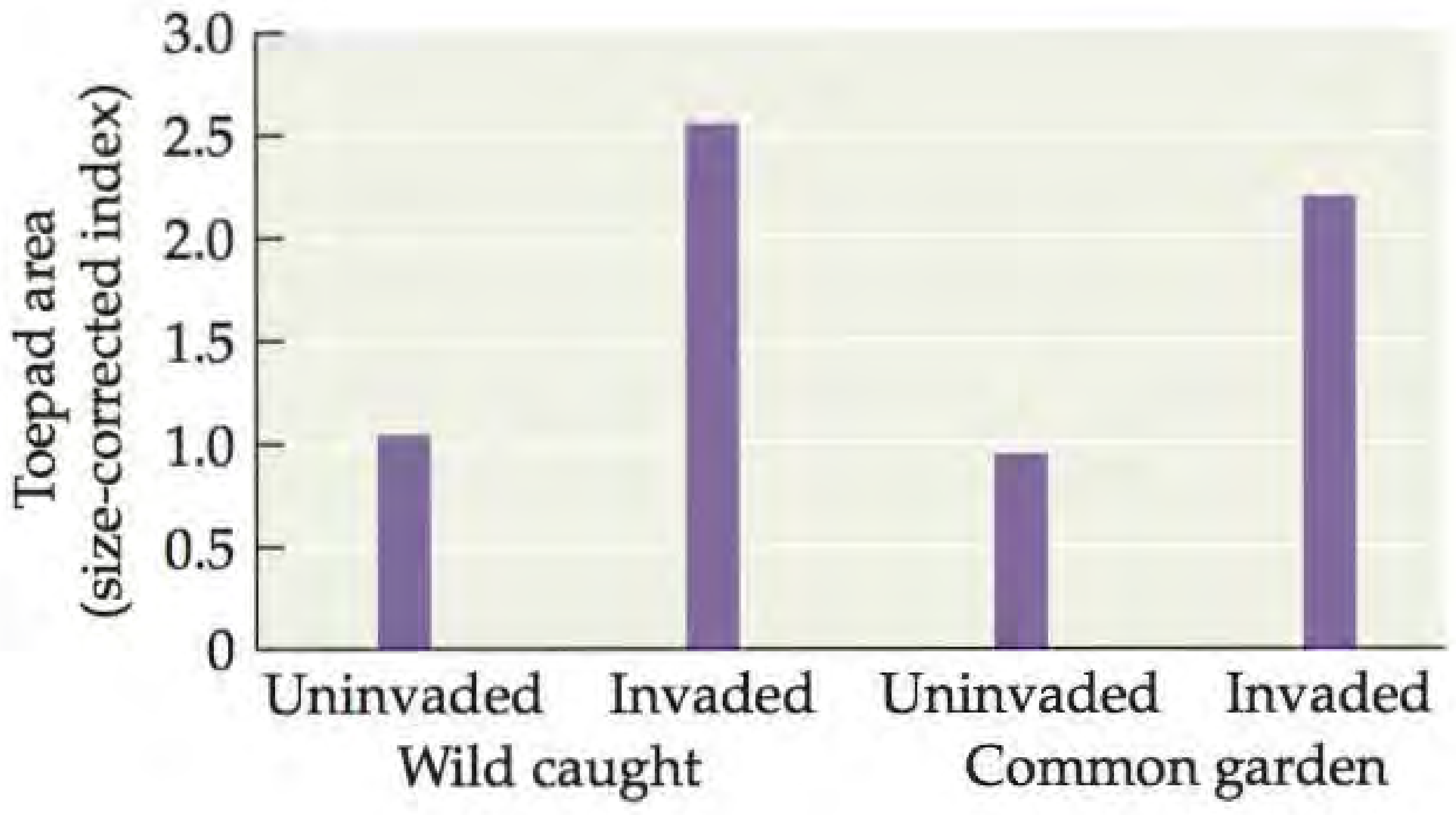
1. Natural selection acts as a sorting process, favoring individuals with some heritable traits over individuals with other heritable traits. As a result, the frequency of the favored traits in a population may increase over time. When this occurs, the frequencies of alleles that determine the favored traits also increase over time, and hence the population has evolved. But the individuals in the population do not evolve—each individual either has the trait favored by selection or it does not.
2. By consistently favoring individuals with one heritable trait over individuals with other heritable traits, natural selection can lead to a steady increase in the frequency of alleles that determine the favored trait. Although gene flow and genetic drift can also cause the frequency of alleles that determine an advantageous trait to increase over time, each of these processes can also do the reverse—that is, they can promote an increase in the

frequency of disadvantageous alleles. Gene flow, for example, can transfer disadvantageous alleles to a population, thereby impeding adaptive evolution. Similarly, the random fluctuations in allele frequencies that result from genetic drift can promote an increase in the frequency of a disadvantageous allele. Hence, natural selection is the only evolutionary mechanism that consistently causes adaptive evolution.

3. Patterns of evolution over long time scales result from large-scale processes such as speciation, mass extinction, and adaptive radiation. The fossil record shows us that life on Earth has changed greatly over time, as seen in the rise and fall of different groups of organisms (for example, the rise of the amphibians and their later fall as reptiles became the dominant group of terrestrial vertebrates). Such changes in the diversity of life are due in part to speciation, the process by which one species splits to form two or more species. The rise and fall of different groups of organisms is also determined by mass extinctions and adaptive radiations. By removing large proportions of the species on Earth and hence altering the patterns of evolution observed after the extinction event, a mass extinction forever changes the evolutionary history of life. Similarly, by promoting an increase in the number of species in a group of organisms, an adaptive radiation shapes the patterns of evolution observed over long time scales.
4. Evolution occurs as organisms interact with one another and with their environment. Hence, evolution occurs partly in response to ecological interactions, and those interactions help to determine the course of evolution. The reverse is also true: as the species in a biological community evolve, the ecological interactions among those species change. Thus, ecology and evolution have joint effects because they both depend on how organisms interact with one another and their environments.
5. Rutter was concerned that by focusing harvesting efforts on the largest fish (because those fish are worth the most money), people would alter the fish population in ways that harm its future viability. In particular, by comparison to cattle, he is pointing out that it is a mistake to keep only the "runts" to breed. From an evolutionary perspective, Rutter was warning that fishing practices would cause the frequency of alleles favoring large size in fish to decrease over time, thus causing inadvertent and undesirable evolutionary change. Indeed, as we saw in the Case Study, harvesting-induced evolution is affecting fish populations today in ways that match his concerns.

Answers to Hone Your Problem-Solving Skills Questions

1. For *A. carolinensis* lizards that were either caught in the wild or reared in a common garden, the average toepad area of lizards from un-invaded islands was lower than the average toepad area of lizards from invaded islands.



2. If toepad area differences resulted from evolution, individuals caught in the wild on un-invaded islands would differ genetically from individuals caught on invaded islands—and the same would be true for individuals reared from eggs collected on un-invaded vs. invaded islands. Hence, if changes in *A. carolinensis* toepad area were caused by evolution, wild-caught results and common garden results should be similar.
3. If phenotypic plasticity was the primary cause of differences in toepad area, genes that affect toepad area would not differ between individuals living on un-invaded islands vs. invaded islands. Thus, individuals reared from eggs collected on un-invaded vs. invaded islands would also be similar genetically. In a common garden in which those (genetically similar) eggs were reared under identical conditions, toepad area should not change depending on whether the eggs were collected on un-invaded vs. invaded islands. Hence, if changes in *A. carolinensis* toepad area were caused by phenotypic plasticity, wild-caught results and common garden results should differ from one another.
4. Since wild-caught results and common garden results were similar, this suggests that changes in toepad area resulted primarily from evolution, not phenotypic plasticity. Because an ecological event (invasion by a competitor species, *A. sagrei*) drove these evolutionary changes, this indicates that the invasion did lead to eco-evolutionary effects.

CHAPTER 7

Answers to Figure Legend Questions

Figure 7.2 Starting with the fish on the top left and proceeding clockwise, the genders are male, smallest nonbreeder, female, and largest nonbreeder. We can be confident of these predictions because the largest fish is female, the next largest a male, and the rest are sexually immature nonbreeders.

Figure 7.4 A 5 m tall tree growing in a cool, moist climate is estimated to have a trunk diameter between 10 and 20 cm (the log scale makes it difficult to provide a precise estimate, but it is probably close to 15 cm), while a 5 m tall tree growing in a desert climate is estimated to have a trunk diameter between 20 and 30 cm (probably close to 22 cm). To illustrate how these estimates are obtained: if you follow the line that moves horizontally to the right from the 5 m mark on the *y* axis, that line intersects the blue curve (the regression line for a cool, moist climate) at a point whose trunk diameter is about 15 cm.

Figure 7.7 The larva would be genetically identical to the polyp because both result from the same zygote (which in turn was produced when a sperm cell fertilized an egg cell). Two different larvae, however, would not be genetically identical because each resulted from a different fertilization event.

Figure 7.9 In Generation 3 there are 8 sexual and 16 asexual individuals, while in Generation 4 there will be 16 sexual and 64 asexual individuals. Note that the number of sexual individuals is increasing half as rapidly as the number of asexual individuals. This occurs because half of the offspring produced by sexual females are males (and males do not give birth to offspring). As a result, from one generation to the next, the number of sexual individuals doubles whereas the number of asexual individuals quadruples.

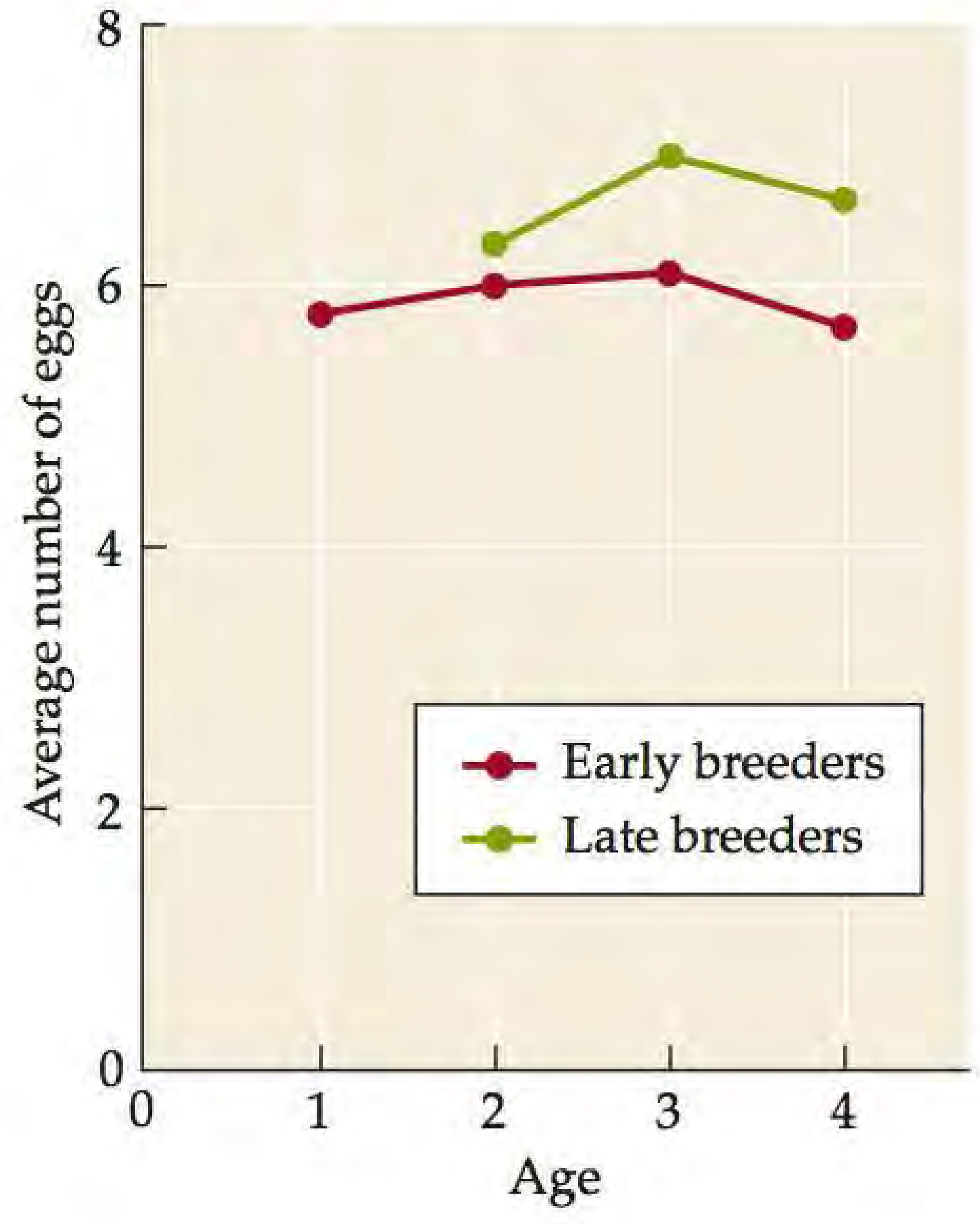
Figure 7.10 The green line shows the results for the control populations. In this study, the experimental populations were exposed to a bacterial pathogen while the control populations were not. The results show that the outcrossing rate remained roughly constant in the control populations whereas it increased dramatically in the experimental populations, indicating that increased levels of outcrossing are favored by selection in populations exposed to pathogens.

Figure 7.15 No. When $c > 1$, the average age of sexual maturity is greater than the average life span. For this occur, the majority of individuals must die before they are old enough to reproduce.

Figure 7.19 For males with a thorax length of 0.8 mm, those kept with virgin females had an average life span of about 40 days while those kept with previously-mated females had an average life span of about 63 days.

Answers to Analyzing Data 7.1 Questions

1.



2. No. To see why, we can calculate how many eggs (on average) birds produced over the four years. Birds that reproduced in their first year had laid an average total of 23.6 eggs by the end of the fourth year, whereas birds that delayed reproduction until their second year had laid only 19.9 eggs in the same amount of time.
3. Yes. On a year-to-year basis, early breeders produced fewer eggs each year in years 2, 3, and 4 than did late breeders. This suggests that allocating resources to reproducing in their first year can reduce an individual's potential for reproducing in years 2–4.
4. Factors other than whether a bird reproduced in its first year may influence its reproductive success in years 2–4. An experimental approach to control for such factors would assign birds at random to the different treatments used in the experiment. There are several ways to test whether females experience a cost to reproduction that reduces their potential for future reproduction. For example, females could be assigned at random to one of the following three treatments: a control in which the number of eggs they laid was not altered; an experimental treatment in which extra eggs were added to their nest (increasing the female's costs of caring for eggs laid); and a second experimental treatment in which eggs were removed from the nest (reducing the female's costs).

Answers to Review Questions

1. In many plants and marine invertebrate animals, dispersal is negatively correlated with propagule size: smaller propagules can disperse farther than larger ones. In invertebrate animals, smaller egg size is also correlated with longer development times and increased reliance on food (rather than yolk provided in the egg) to complete development. However, in some vertebrates (for example, Sinervo's fence lizards), smaller egg sizes actually lead to more rapid development to hatching. In both cases, the correlation between egg size and development time is striking, and the pattern that is favored varies with environmental conditions (e.g., temperature, rates of predation on larvae, etc.). An important reason why species that live in the same habitats may still exhibit different reproductive patterns is that different strategies may be favored in different years, depending on the particular environmental conditions. For example, in years with abundant food availability, a small-egg strategy may be favored, as offspring can acquire resources readily from the environment. However, in years when food is limited, a large-egg strategy may be advantageous due to its decreased reliance on external energy sources.
2. Asexual reproduction allows even a single individual to quickly increase the population size and allows a single highly successful genotype to dominate the population. The primary benefit of sex is the recombination of genetic material through the merging of unique genotypes, allowing potentially beneficial new combinations of genes to be introduced. The maintenance of both sexual and asexual

reproduction allows rotifers to quickly increase the size of the reproductive population under beneficial environmental conditions while maintaining sufficient genetic variation to evolve in response to new environmental challenges.

3. Removal of small to medium-sized fish might produce selection for rapid growth through the size ranges that are favored by the fishery. This might lead to reproduction at older ages and larger sizes if there is a trade-off between growth and reproduction. Fish that are selected to grow quickly would allocate fewer resources to reproduction at smaller sizes so that they could allocate more resources to growth. Unfortunately, this is not the only effect of the Nassau grouper fishery. Because of heavy overfishing for both small and large fish and methods that target fish when they come together in large groups to spawn, Nassau grouper populations have declined precipitously.

Answers to Hone Your Problem-Solving Skills Questions

1. Intensive fishing began at Catalina and San Nicolas islands in the early 1980s. At Catalina island, where fishing pressure continued from the 1980s through 2007, the size at which sheephead became sexually mature decreased from 213 mm in 1980 to 178 in 2007; the size at which sheephead changed sex decreased from 350 mm to 225 mm during the same time period. At San Nicolas island, fishing also appears to have affected size at maturation and size at sex change from 1980 to 1998, the time period during which intensive fishing occurred.
2. We can answer this question using data at San Nicolas island because the sheephead population at that location was subjected intensive fishing from the 1980s through 1998, but then (starting in 1999) the population was protected from fishing. At that island, size at maturation and size at sex change declined from 1980 to 1998. However, by 2007 (8 years after protection from fishing began), both the size at maturation and the size at sex change had increased substantially—indicating that size at maturation and size at sex change can recover once fishing pressure is reduced.
3. Protection from fishing should have an immediate effect of increasing population abundance (since fewer fish are being killed by humans). In addition, protection from fishing causes the size at maturation and the size at sex change to increase in size. As a result, the size of fertile females will increase over time, causing the number of offspring produced per female to increase over time (since larger individuals are assumed to produce more offspring). This change in the number of offspring produced per female should cause population abundance to increase more rapidly than it otherwise would.

CHAPTER 8

Answers to Figure Legend Questions

Figure 8.3 A proximate explanation for glucose aversion could describe how in cockroaches that exhibit this behavior, glucose activates taste neurons that in other individuals are activated only by bitter substances. An ultimate explanation for glucose aversion would be based on the fact that cockroaches exhibiting this behavior are more likely to survive than are other individuals (when exposed to baits containing glucose and insecticides).

Figure 8.5 Yes. The pie charts for the deer mouse and oldfield mouse each have a solid color (red for the deer mouse, blue for the oldfield mouse), indicating that 100% of the genome of each mouse is composed of markers specific to its species. For the F_1 hybrids, 50% of the genome is from deer mice (as indicated by the red half of the pie chart) and 50% of the genome is from oldfield mice (as indicated by the blue half of the pie chart). Backcross individuals represent offspring between F_1 hybrids (50% deer mouse genome and 50% oldfield mouse genome) and deer mice (100% deer mouse genome). Thus, we would expect that on average, 75% of their genome would be from deer mice and 25% of their genome would be from oldfield mice—and, as expected, the pie chart for backcross individuals is 75% red in color and 25% blue in color.

Figure 8.6 Under conditions like those in which the relationship between net energy gained and foraging effort was estimated, you could test whether the effort lizards invested in acquiring food was similar to that which would maximize their net energy gained.

Figure 8.8 The rate of energy gain with both long and short distances between patches declines if the quality or abundance of the prey is low. As a result, the giving up times come sooner.

Figure 8.11 When wolves arrive, the probability that a female is found in grassland decreases whereas the probability a female is found in conifer forest increases; when wolves depart, the reverse is true. Similar patterns are observed for males, but males are less likely to change their behavior in response to the arrival of wolves than are females. For example, males are more likely to remain in grassland when wolves are present than are females.

Figure 8.16 In the first control, the tails of birds were not altered; results from this control can be compared to results from experimental treatments in which the tail lengths of birds were either shortened or lengthened. The second control (in which a portion of the tail was removed and then glued back on) was included so that Andersson could determine whether cutting a bird's tail had unintended effects.

Figure 8.20 This benefit cannot be compared directly to the cost shown in the figure because the benefit is in terms of food intake per hour, while the cost is in terms of increased flying times. To make this comparison you would need to use a common currency, such as the amount of energy gained from the increased food intake vs. the amount of energy used during the increased flying times.

Figure 8.23 In the absence of wasps, laying eggs on food containing 6% alcohol causes larval survival to drop by about 18% (from 90% in food without alcohol to 72% in food with 6% alcohol). In the presence of wasps, larval survival increases by about 40% (from 10% in food without alcohol to 50% in food with 6% alcohol).

Figure 8.24 About 2.9 offspring per nest survived to young adulthood in nests that were not exposed to predator playbacks, whereas about 1.9 offspring per nest survived to young adulthood in nests exposed to predator playbacks. These results indicate that the "cost of fear" was a reduction of 1 offspring per nest.

Answers to Analyzing Data 8.1 Questions

1. The average number of attacks (per five minutes) is 10.3 for a single individual (a group of size 1); 12 for a group of 4; 9.3 for a group of 6; 8.5 for a group of 15; 13 for a group of 50; and 10.5 for a group of 70. These results indicate that the predator does not have a strong preference for attacking either small or large groups—the risk of attack is similar for groups of all sizes.

NUMBER OF INSECTS IN GROUP	NUMBER OF ATTACKS (PER 5 MINUTES)
1	10.3
4	12.0
6	9.3
15	8.5
50	13.0
70	10.5

2. To determine the average number of attacks per individual (per 5 minutes), we must divide the results we found in Question 1 by the number of individuals in the different groups. Thus we have:

NUMBER OF INSECTS IN GROUP	NUMBER OF ATTACKS PER INDIVIDUAL (PER 5 MINUTES)
1	10.3
4	3.0
6	1.6
15	.56
50	0.26
70	0.15

These results show that the average number of attacks per individual (per 5 minutes) declines dramatically with group size.

3. Yes, these results are consistent with the dilution effect: as the size of a group increases, an individual's chance of being eaten decreases.

Answers to Review Questions

1. A proximate explanation of a behavior would look within the organism to explain *how* the behavior occurs, focusing on events that serve as the immediate causes of the behavior. In contrast, an ultimate explanation of a behavior would seek to explain *why* the behavior occurs by examining the evolutionary and historical reasons for the behavior.
2. Natural selection is a process in which individuals with certain traits consistently survive and reproduce at higher rates than do individuals with other traits. An animal's behaviors can affect its ability to survive and reproduce. Therefore, natural selection should favor individuals whose behaviors make them efficient at performing such activities as foraging, obtaining mates, and avoiding predators. If the behaviors that confer advantage are heritable, then an animal will pass its advantageous behaviors to its offspring. When this is so, adaptive evolution can occur, in which the frequency of the advantageous behavior in a population increases over time. In cases where we demonstrate that natural selection has favored (or continues to favor) a particular heritable behavior, we can provide an ultimate explanation of the behavior by focusing on the evolutionary and historical reasons for why the behavior occurs.
3. A foraging animal often faces tradeoffs in which its ability to obtain food comes at the expense of other important activities, such as avoiding predators. When this occurs, individuals often alter their foraging decisions; they may, for example, choose to forage in areas that provide less food but greater protective cover from predators. Fear of predators can have similar effects. For example, song sparrows exposed to playbacks of sounds made by predators (but no actual predators) fed their young less often, built their nests in denser, thornier vegetation, and spent less time incubating their eggs than did sparrows exposed to playbacks of nonpredators.
4. Sexual selection is a process in which individuals with certain characteristics have a consistent advantage over other members of their sex solely with respect to mating success. Charles Darwin pointed out that when sexual selection occurs, individuals typically use force or charm to gain access to mates. Often, the males compete with one another for the right to mate with females, while the females choose among the competing males; in some cases, the reverse occurs, and females compete for the right to mate with choosy males. Observational, genetic, and experimental evidence indicate that the large size, strength, or special weaponry of the males of many species result from sexual selection; such evidence also indicates that extravagant traits used to charm members of the opposite sex can result from sexual selection. Specific examples mentioned in the chapter include genetic evidence that the large body size and full curl of horns of male bighorn sheep result from sexual selection, along with Malte Andersson's classic experiments showing that sexual selection can explain the extremely long tails of male widowbirds.
5. In one example of how group living has both benefits and costs, goldfinches in a flock consumed more seeds per unit of time than did solitary birds. However, as the size of the flock increased, food supplies were depleted more rapidly, causing the birds to spend more time flying between feeding sites; traveling between feeding sites is

energetically expensive and can lead to an increased risk of predation.

6. The greater expenditure of energy required by species B to fly between patches would dictate that it needs to spend longer in each patch in order to meet the assumptions of the marginal value theorem. Because its overall rate of energy gain in the habitat is lower, due to greater amount of energy it expends in traveling between patches, species B should deplete each patch to a greater degree before leaving it than species A.

Answers to Hone Your Problem-Solving Skills Questions

1. Perch larvae exposed to high concentrations of microplastics moved 80% of the total distance moved by perch larvae in the control treatment (0 microplastic particles/m^3). This suggests that consumption of microplastics may reduce the activity level of perch larvae; in the wild, a decrease in overall activity could reduce the effectiveness with which an individual searches for food.
2. The second experiment included a control (0 particles/m^3) for the concentration of microplastics to which fish were exposed. By comparing results for individuals in this control group to results for individuals exposed to average or high levels of microplastics, this control allowed researchers to distinguish effects due to microplastics from effects due to the other treatment being tested (presence of a chemical alarm cue). The second experiment also included a seawater control: seawater lacking the alarm cue was added to the tanks of some perch larvae, whereas a mixture of seawater and the chemical alarm cue was added to the tanks of other perch larvae. This control allows effects of the chemical alarm cue to be determined for each concentration of microplastics.
3. In the "freezing behavior" experiment (experiment 2), individuals that had not been exposed to microplastics exhibited a 3.5-fold increase in the performance of the freezing behavior when they sensed the chemical alarm cue. Individuals exposed to average levels of microplastics only exhibited a 1.4-fold increase in performance of the freezing behavior when they sensed the alarm cue. Individuals exposed to high concentrations of microplastics did not respond at all to the chemical alarm cue. These results are consistent with the results from experiment 3 (survival after exposure to predator). A perch larva with a reduced response to the alarm cue (or one lacking a response altogether) might be more likely to be eaten than would a larva with a strong response to the alarm cue. Thus, based on the results from experiment 2, we might predict that perch larvae exposed to average or high concentrations of microplastics would survive more poorly when faced with a predator than would perch in the control group (0 microplastic particles/m^3)—exactly the results that were observed in experiment 3.

CHAPTER 9

Answers to Figure Legend Questions

Figure 9.3 There was considerable variation in abundance from one field site to another in many of the years. In 1984 and 1989, for example, abundance was high at Hector but low at the other two locations.

Figure 9.4 There were 7 habitat patches in 1759 and about 86 patches in 1978. Thus, in 1759, the average patch size was $400 \text{ km}^2/7 = 57.1 \text{ km}^2$. Patch sizes were much smaller in 1978: the average at that time was $60 \text{ km}^2/86 = 0.7 \text{ km}^2$.

Figure 9.6 In clones that form by budding or apomixis, identification of groups of genetically identical individuals may require the use of genetic analyses. In clones that form by horizontal spread, groups of individuals that are still connected to one another could be marked; however, to tell whether members of two such groups were in fact genetically identical would again require genetic analyses.

Figure 9.9 Because it competes poorly with other barnacle species in relatively warm waters, *S. balanoides* is currently excluded from the region shaded purple on the map. Thus, by warming northern waters, global warming will probably decrease the geographic range of *S. balanoides*.

Figure 9.11 Both. Each curve increases as the density of offspring increases, indicating that wing production increases as offspring density increases. In addition, at all but the lowest offspring densities, the percentage of aphids that develop wings is higher for offspring whose mothers were reared at high densities than it is for offspring whose mothers were reared at low densities. This observation shows that the density experienced by the mother also influences whether offspring develop wings.

Figure 9.19 Urchin biomass declined at Sites 1, 2, 3, 4, 5, and 9; kelp density increased at Sites 1 and 5.

Answers to Analyzing Data 9.1 Questions

1. During the 41 year period before introduced grasses had invaded the park, the fire frequency was 0.22 fires per year with an average burn size of 0.26 ha per fire. In the 20 year period after introduced grasses had invaded the park, the fire frequency was 1.6 fires per year with an average burn size of 243.8 ha per fire. These data suggest that the introduction of non-native grasses has resulted in a sevenfold increase in the frequency and a nearly 1000-fold increase in the scope of fires on Hawaii.
2. The data in Table B indicate that fire reduces the abundance of native trees and shrubs, while it increases the abundance of introduced grasses.
3. If a fire occurs in a Hawaiian dry forest after introduced grasses are present, the introduced grasses should recover quickly and provide fuel for later fires. We would predict that this fuel would make it more likely that a second fire would occur; in addition, should a second fire occur, the increased fuel levels would probably cause it to burn with greater intensity than the first fire. Thus there is the

potential for a "fire cycle" in which a fire causes the abundance of introduced grasses to increase, and also makes future fires both more likely and more intense, leading to further increases in introduced grasses and further declines in native trees and shrubs. Such a fire cycle is consistent with data in Table A: after introduced grasses arrived, fires occurred more often and covered larger areas. A fire cycle is also consistent with data in Table B: introduced grasses were least abundant in unburned areas and most abundant in areas burned twice.

Answers to Review Questions

1. Complicating factors discussed in the text include (1) limited knowledge about the dispersal capabilities of the organism under study, (2) the fact that populations may have a patchy structure, and (3) the fact that individuals may be hard to define. The first two factors—limited information about dispersal and patchy populations—can make it difficult to determine the area within which individuals interact, and hence what constitutes a population. The third factor—difficulty in defining individuals—applies to the many organisms that reproduce asexually to form clones. In such organisms, it can be hard to determine what an individual is, thus making it difficult to estimate abundance.
2. The simplest reason that no species is found everywhere is that much of Earth does not provide suitable habitat. There can, in turn, be many reasons why portions of Earth are not suitable for a particular species. For example, the abiotic or biotic conditions of an environment may limit the growth, survival, or reproduction of the species, as may disturbance or the interaction between abiotic and biotic conditions. Furthermore, a species may be absent from environments where we would expect it to thrive because of dispersal limitation or historical factors (including evolutionary history and continental drift).
3. A niche model is a tool that predicts the environmental conditions occupied by a species based on the conditions at where the species has been found. Niche models can be used to predict the future distribution of an introduced species by collecting as much information as possible about environments where the species currently is found. Those data are then used to construct a niche model, which in turn is used to identify currently unoccupied locations that are likely to provide suitable habitat for the species. For such predictions to accurately reflect the future spread of the organism, information also must be gathered about its dispersal capabilities.
4. For a conservative estimate, assume there are 20 otters per square kilometer, each of which eats 20% of its body weight in food each day. Since urchins, on average, weigh 0.55 kg each, a kilogram of urchins consists of roughly 1/0.55 = 1.82 urchins. Thus, the number of urchins per square kilometer that an otter population would be expected to eat each year is:

   $(20 \text{ otters/km}^2) \times (0.2 \times 23 \text{ kg/otter/day}) \times (365 \text{ days/year}) \times (1.82 \text{ urchins/kg}) = 61{,}116 \text{ urchins/km}^2\text{/year}$

Answers to Hone Your Problem-Solving Skills Questions

1. Four quadrats were used in each patch. Each treatment had 3 patches, so there was a total of 12 quadrats used in each treatment. The mean values for each treatment are:

TREATMENT	TOTAL NO. TAXA	TOTAL NO. INDIVIDUALS
Intact kelp beds	68.1	434.4
Recovered kelp beds	73.8	580.8
Urchins present	12.1	63.5

2. In the recovered kelp beds, there was an average of 580.8 individuals per quadrat or 580.8 individuals per 0.25 m^2. In the entire patch (which had an area of 40 m^2), this suggests that we would have a total of

   $$\frac{580.8 \text{ individuals}}{0.25 \text{ m}^2} \times 40 \text{ m}^2 = 92{,}928 \text{ individuals}$$

   in the patch.

   Likewise, in areas where urchins were present, there was an average of 63.5 individuals per quadrat or 63.5 individuals per 0.25 m^2. In the entire patch (which had an area of 40 m^2), this suggests that we would have a total of

   $$\frac{63.5 \text{ individuals}}{0.25 \text{ m}^2} \times 40 \text{ m}^2 = 10{,}160 \text{ individuals}$$

   in the patch.
3. Urchins had large impacts on species diversity and overall abundance. Compared to intact or recovered kelp beds, the presence of urchins had very large effects, reducing the total number of taxa by 6-7 fold and the total number of individuals in the patch by about 8 fold. The total number of taxa and the total number of individuals in recovered kelp beds were similar to the total number of taxa and the total number of individuals in intact kelp beds; this indicates that when protected from urchins, previously-degraded patches can recover.

CHAPTER 10

Answers to Figure Legend Questions

Figure 10.4 About 47% of Gambians born in the hungry season live to age 45; a similar percentage (48.5%) of U.S. females live to be 85 years old.

Figure 10.6 100 sheep survive to age 11; thus 10% (100/1,000) of sheep survive from birth to age 11.

Figure 10.8 The year-to-year population growth rate (λ) from year 4 to year 5 for age class 2 is the number of individuals in age class 2 at year 5 divided by the number in age class 2 at year 4. Filling in those numbers from (A), we find that $\lambda = 38/19 = 2$.

Figure 10.16 Since there were about 35 breeding females in 1975, results from previous years suggest that roughly 4 young per female should have been reared to independence. In fact, less than 1.5 young per female were reared to independence, suggesting that conditions on the island were different in 1975 than in other years (there could have been a drought or a disease outbreak, among many other possibilities).

Figure 10.17 High density populations are increasing in density in (A) because λ is greater than 1 in those populations. In contrast, in (B) the high density populations are decreasing in size because *r* is less than zero in those populations.

Figure 10.19 As *N* becomes increasingly close to *K*, the term $(1 - N/K)$ becomes increasingly close to zero; this causes the population growth rate, dN/dt, to become increasingly close to zero. A population with a growth rate of zero does not increase in size; hence, as *N* approaches *K*, the population stops increasing in size.

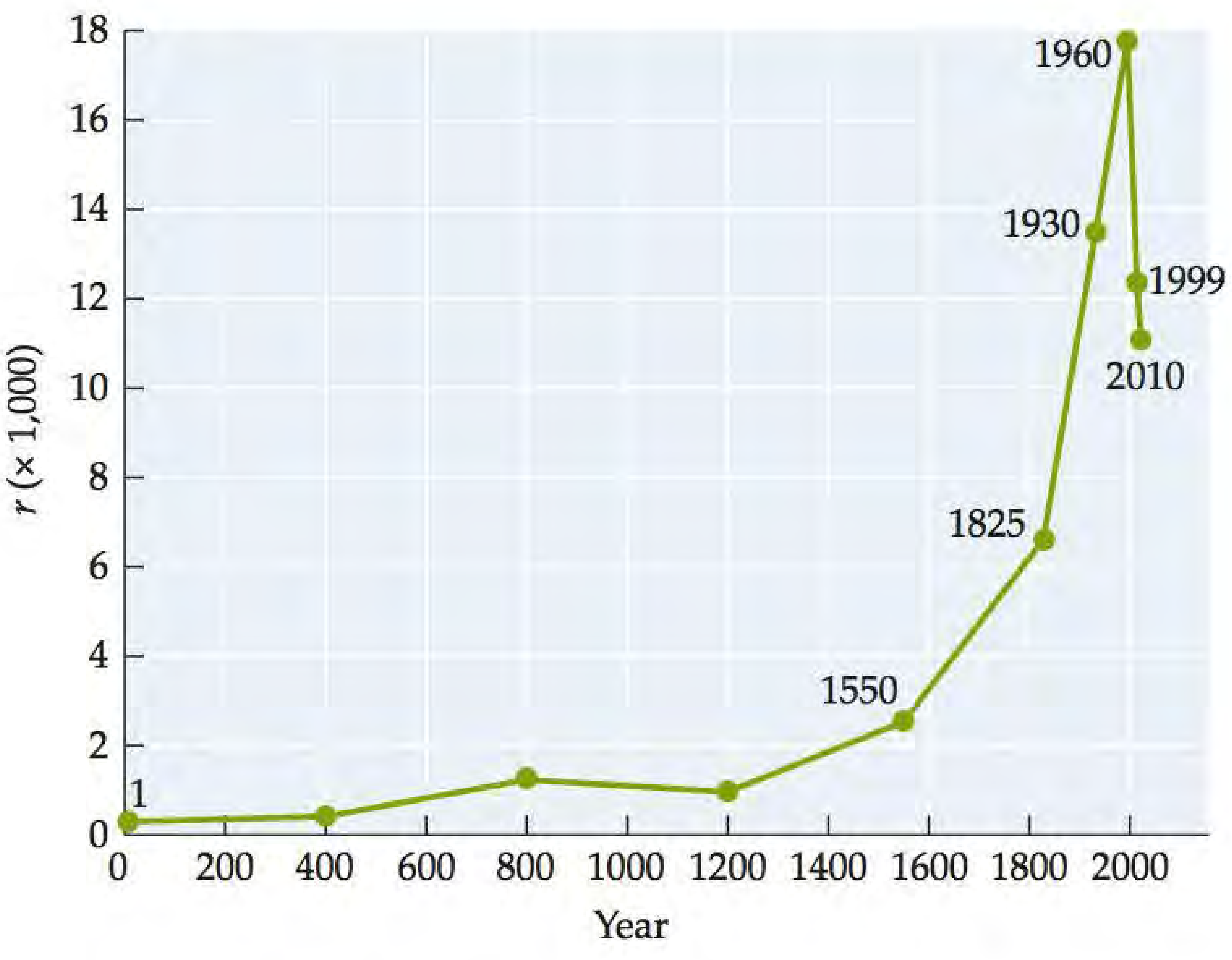
Figure 10.22 The graph shows that the human population is projected to have an annual growth rate of 0.5% in 2050. This rate is greater than zero, so the human population will still be increasing in size in 2050.

Figure 10.23 The best-estimate curve indicates there will be 9.6 billion people in 2050, and Figure 10.22 indicates that our annual growth rate will be 0.5% at that time. Hence, from 2050 to 2051, we would expect to add about 48 million (9,600,000,000 × 0.005) to our population. Thus, the human population size in 2051 would be about 9,048,000,000.

Answers to Analyzing Data 10.1 Questions

1.

YEAR	R
1	0.00028
400	0.00037
800	0.00123
1200	0.00094
1550	0.00252
1825	0.00660
1930	0.0135
1960	0.0178
1999	0.0123
2010	0.0110
2013	(NA)



2. Based on a value of $r = 0.011$ and a population size of 6.87 billion in 2010, we can use Equation 10.4 to estimate the population size in 2060:

   $N(2060) = N(2010) \times e^{rt} = 6.87 \times e^{(0.011 \times 50)} = 11.9$ billion people

3. The calculations in Question 2 assume that the human population is growing exponentially and that the exponential growth rate, *r*, remains constant and equal to 0.011 from 2010 to 2060. However, the answer to Question 1 indicates that *r* reached a maximum value (0.0178) in 1960 and has declined since that time. If *r* continues to decline, it is unlikely that the human population will reach 11.9 billion in 2060.

Answers to Review Questions

1. a.

AGE (x)	N_x	S_x	l_x
0	100	0.4	1.0
1	40	0.375	0.4
2	15	0.333	0.15
3	5	0	0.05
4	0		0

   b. In a cohort life table, the fate of a group of individuals born during the same time period (a cohort) is followed from birth to death. This type of life table is often used for sessile or relatively immobile organisms that do not have long life spans, but is less useful for organisms that are highly mobile or long-lived. For those organisms, a static life table may be used, in which the survival and fecundity of individuals of different ages are observed during a single time period.

2. a. 3,240.

   b. Substituting the values $N_0 = 40$, $\lambda = 3$, and $t = 27$, we have

   $N_t = N_0 \lambda^t = 40 \times 3^{27}$

   c. In this case, we have the values $N_0 = 100$, $\lambda = 0.75$, and $t = 3$, which we plug into the relation

   $N_t = N_0 \lambda^t = 100 \times (0.75)^3 = 42.19$

3. Factors that regulate population size are density-dependent: when *N* (the number of individuals in a population) is below some level, they cause the population size to increase, whereas when *N* goes above some level, they cause the population size to decrease. Even if density-independent factors, such as year-to-year variations in temperature or rainfall, are the primary cause of year-to-year changes in abundance, those factors do not regulate population size.

4. Each student will calculate their own answer.

Answers to Hone Your Problem-Solving Skills Questions

1.

YEAR	N_0	N_1	N_2
0	50	50	50
1	100	16.7	25
2	116.7	33.3	8.3
3	150	38.9	16.7
4	188.9	50	19.4
5	238.9	63	25
6	301.9	79.6	31.5

From these results we estimate:

$\lambda = 31.5/25 = 1.26$

The stable age distribution is 73% N_0; 19% N_1; 8% N_2.

2.

YEAR	N_0	N_1	N_2
0	80	50	20
1	130	26.7	25
2	156.7	43.3	13.3
3	200	52.2	21.7
4	252.2	66.7	26.1
5	318.9	84.1	33.3
6	403	106.3	42

From these results we estimate:

$\lambda = 42/33.3 = 1.26$

The stable age distribution is 73% N_0; 19% N_1; 8% N_2.

3. Based on the results in parts (a) and (b), we estimate:

$\lambda = 1.26$

The stable age distribution is 73% N_0; 19% N_1; 8% N_2.

CHAPTER 11

Answers to Figure Legend Questions

Figure 11.5 The carrying capacity that results from the second death rate curve, labeled K_2 in the drawing, is lower than the original carrying capacity, K.

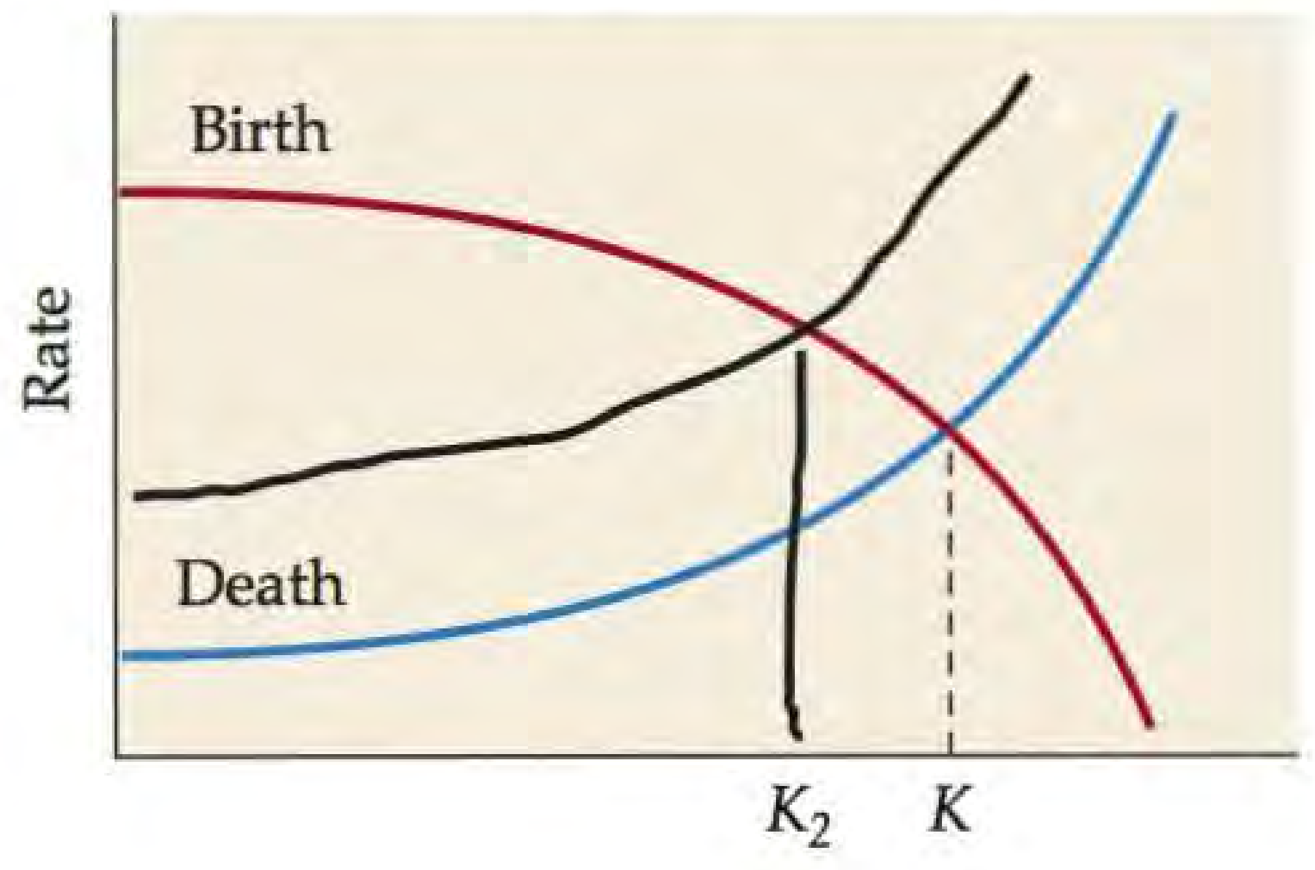


Figure 11.9 From 1988 to 2000, the collared lemming population exhibited regular cycles, reaching peak abundance every 4 years. Because abundances peaked at about 10 lemmings per hectare in 1990, 1994, and 1998, we would have expected the next peak to occur in 2002, again at about 10 lemmings per hectare. However, the actual abundance in 2002 was less than 1 lemming per hectare.

Figure 11.11 In (A), abundance rises and falls in a regular manner, reaching a peak about every 40 days; thus, this curve shows regular population cycles. In (B), to the left of the dotted vertical line, the results are again consistent with a regular population cycle that reaches peak abundance every 40 days. After food for adults is limited, however, the regular population cycle no longer occurs. Instead, abundance rises and then fluctuates around a roughly stable population size. This pattern that can be viewed as illustrating either population fluctuations or logistic growth (with fluctuations).

Figure 11.13 About 100 breeding pairs would be needed for the risk of extinction to drop to 5%.

Figure 11.19 The chance of colonization is between 50% and 90%.

Figure 11.21 From 1952 to 1957, the abundance of predatory fish increased while the abundance of planktivorous fish showed little change. In the 1970s, predatory fish abundance dropped, planktivorous fish abundance increased, zooplankton abundance dropped, and phytoplankton abundance increased. Overall, the chain of feeding relationships for the Black Sea in the 1970s is more similar to that in Alaska pre-1990 than to that in Alaska in the late 1990s. In both cases, the organisms at the base of the food chain (phytoplankton in the Black Sea, kelp in Alaska) were only weakly controlled by their grazers (zooplankton in the Black Sea, urchins in Alaska), which in turn were strongly controlled by the organisms that ate them (planktivorous fish in the Black Sea, otters in Alaska).

Answers to Analyzing Data 11.1 Questions

For years 2–6 (respectively), the five missing values for the Table are: 1.22, 0.87, 1.17, 1.02, and 1.13.

1. If λ remained constant and equal to 1.02, when $N_0 = 1{,}000$ the population size at year 7 would be: $N_7 = N_0\,(1.02)^7 =$

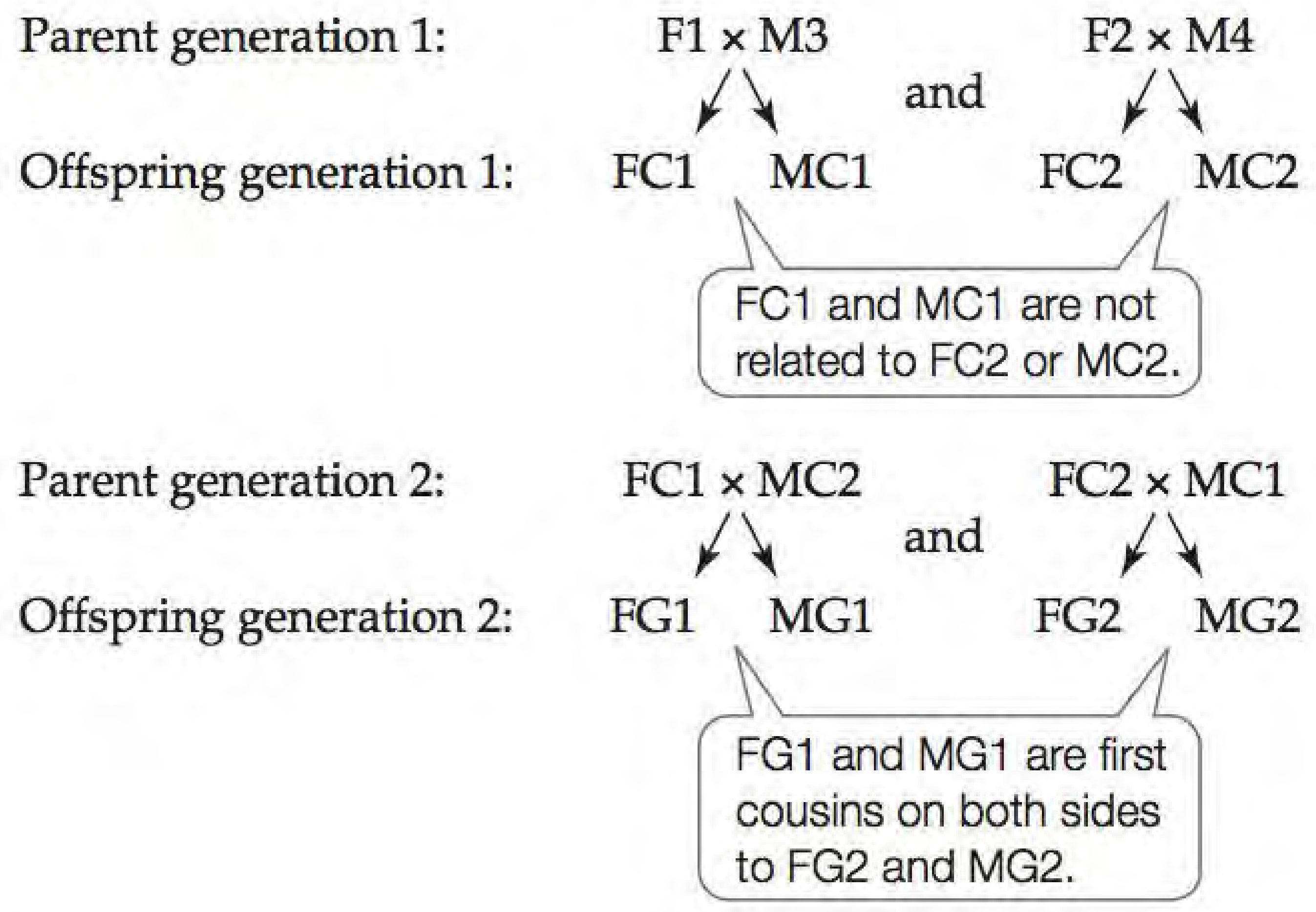
1,149. This predicted value is higher than the observed value of 1,069, suggesting that the observed variation in λ decreased the growth of the population.

2. The geometric mean of the yearly population growth rates equals 1.00945.
3. Using the geometric mean calculated in Question 2 as our estimate of λ, we have: $N_7 = N_0\ (1.000945)^7 = 1{,}068$. This value is lower than that calculated in Question 1 (1,149) and almost identical to the value in the Table (1,069).
4. When environmental conditions vary, it is likely that the growth rate of a population will also vary over time. The results in Questions 1–3 suggest that using the arithmetic mean of such variable population growth rates will overestimate the population size, whereas using the geometric mean would be more accurate. Because the arithmetic mean is known to overestimate actual population sizes, in that sense it would be wrong to use the arithmetic mean to describe the growth of a population in a variable environment.

Answers to Review Questions

1. There are many built-in time lags in the responses of populations to changes in density. For example, the amount of available food may increase or decrease between the time the parent generation feeds and the time its offspring are born. In such a situation, the number of offspring produced may be more closely related to the previous conditions than to the conditions at the time of their birth. As a result of such time lags, the population may experience delayed density dependence, which may cause it to fluctuate in abundance over time.
2. Small populations can be threatened by chance events associated with genetic factors, demographic stochasticity, environmental stochasticity, and natural catastrophes. Genetic factors that increase the risk of extinction in small populations include genetic drift and inbreeding, both of which can increase the frequencies of harmful alleles. Demographic stochasticity results from chance events related to the reproduction and survival of individuals; such events can cause population growth rates to drop, as might occur if considerably more females than males happened to die in a small population, leaving few females to produce the next generation of offspring. Environmental stochasticity refers to unpredictable variation in environmental conditions; such variation can cause population growth rates to vary dramatically from year to year, increasing the chance of extinction in small populations. Finally, natural catastrophes can cause sudden reductions in population size, subjecting a population to increased risks from genetic factors, demographic stochasticity, and environmental stochasticity.
3. a. Yes, as illustrated by the two generations of parents and offspring in the diagram.

   KEY: FC = female child; MC = male child; FG = female grandchild, MG = male grandchild



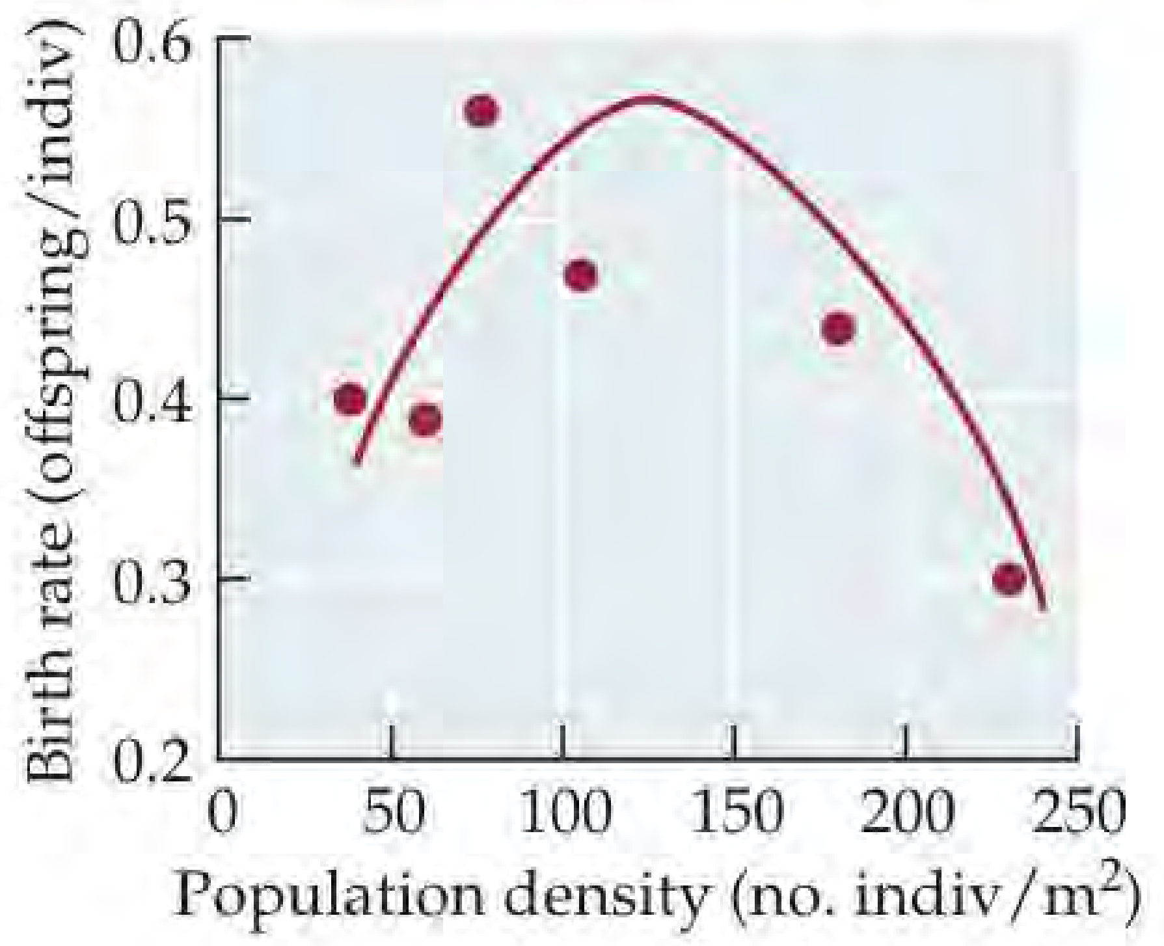
   b. No, all of the individuals in the second generation of offspring are related to one another. As illustrated by this example, inbreeding is likely to be common in small populations.
4. a. As the proportion of the habitat that is suitable for the species drops, the colonization rate may decrease (because the distance between remaining populations increases) and the extinction rate may increase (because the loss of habitat may cause the remaining populations to become smaller, making them more prone to extinction). Once the extinction rate exceeds the colonization rate, the metapopulation will decline to extinction because existing populations will become extinct more rapidly than new populations are established.

   b. A large habitat patch is likely to have a larger population than a small habitat patch. As a result, the populations in the two large habitat patches are less likely to go extinct than the others. Thus, the large habitat patches could serve as source populations from which individuals disperse to small patches, thereby reducing the extinction rate of the small populations (the rescue effect). Positioning the large habitat patches far from each other and far from any of the small habitat patches would make it less likely that they could have a rescue effect, thus making it more likely that the metapopulation would not persist.

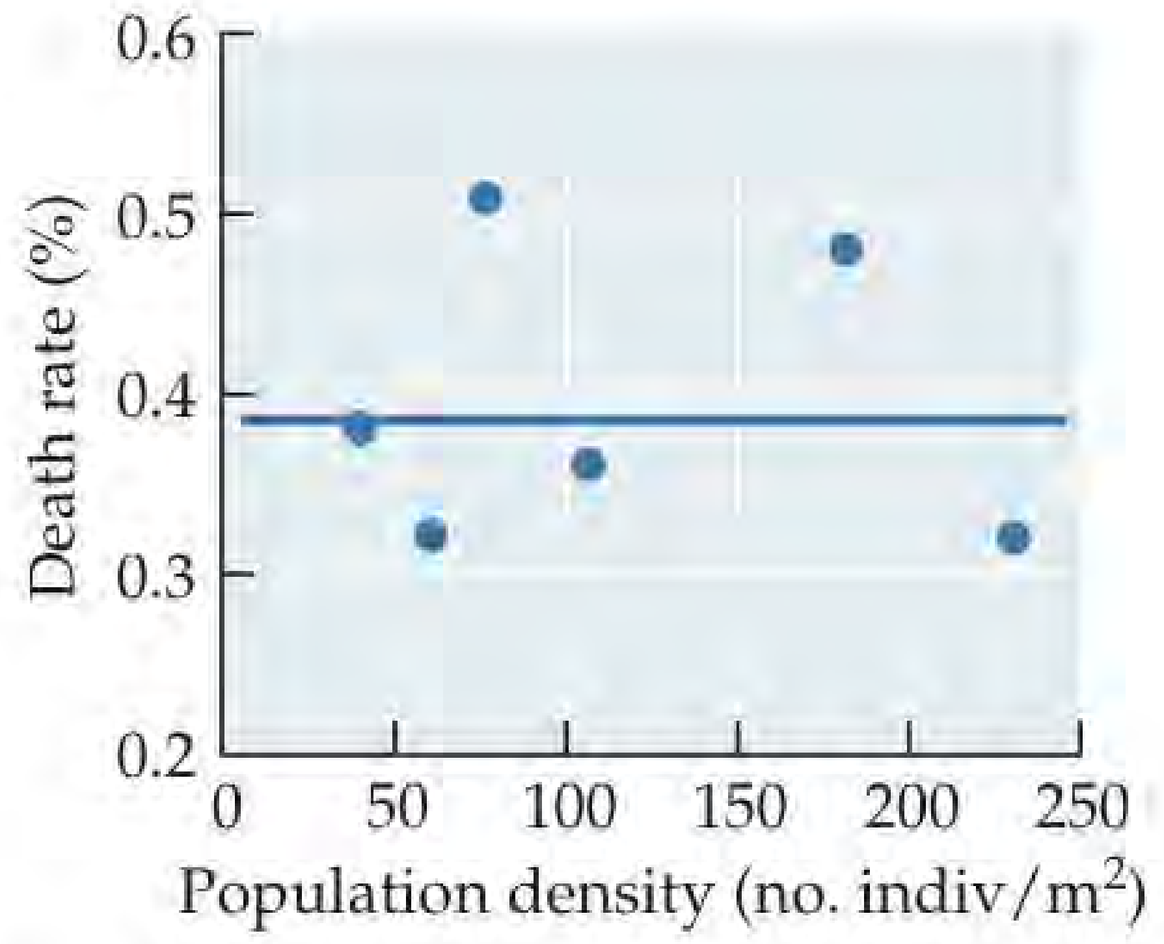
Answers to Hone Your Problem-Solving Skills Questions

1. Densities in this population ranged from a minimum of fewer than 2 individual/m^2 to a maximum of nearly 300 individuals/m^2. Since the densities of this population show considerable variation over time (and do not cycle in a regular manner), the growth of this population is best described by the third pattern described in Concept 11.1, population fluctuations.

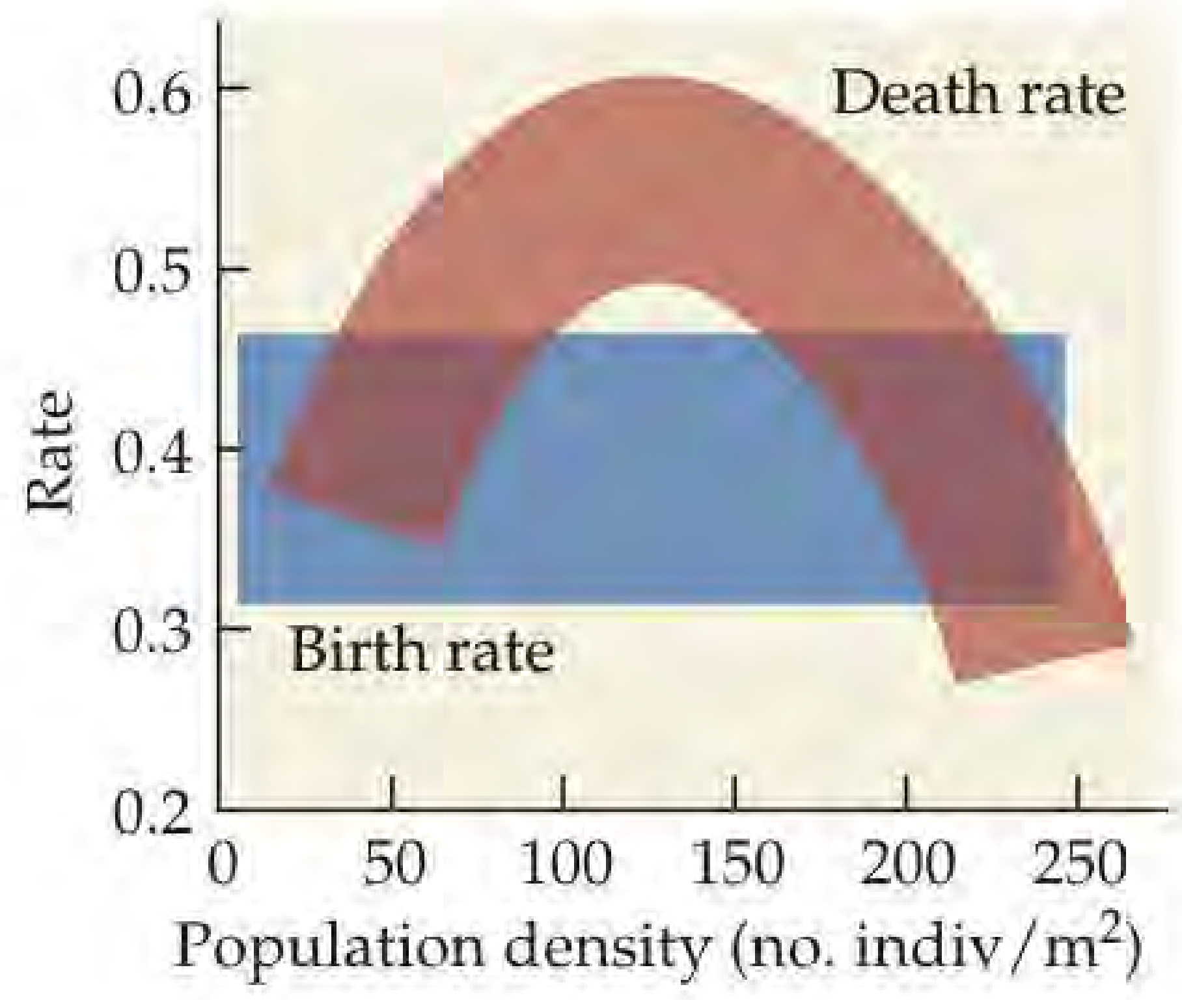
2. The graph shows that birth rates initially increase with density, indicating that Allee effects may occur in the study populations; for population densities greater than 100 individuals/m^2, birth rates decrease as density increases. Since birth rates change as a function of population density, birth rates are density dependent.



3. The graph shows that death rates do not change as a function of population density; thus, death rates are density independent.



4. Since the bands surrounding the birth rate and death rates curves overlap across a broad range of population densities, the graph indicates that the sea squirt population should not reach a steady carrying capacity (K). Instead, we would expect to see population densities fluctuate over time.



CHAPTER 12

Answers to Figure Legend Questions

Figure 12.2 The peak abundance of lynx usually occurs after the peak abundance of hares. One reason this might occur is that as hare abundance rises, the increased availability of food enables the lynx to produce more offspring; however, these offspring are not born immediately, so the rise in lynx abundance lags behind the rise in hare abundance.

Figure 12.7 To answer this question, we must use the data in the graph to determine the total number of agromyzid fly species and the number of agromyzid fly species that feed on fewer than five host plant species. We can do this using the scale on the *y* axis, which indicates that a bar that is 2.15 cm in height represents 50 fly species. Measuring all 13 bars on the graph, we find that their heights sum to 12.05 cm; this indicates that in total, there are about 280 fly species (280 = 12.05 cm/2.15 cm × 50). Similarly, the heights of the four bars representing fly species that feed on fewer than five host plant species sum to 10.4 cm, indicating that about 242 fly species feed on fewer than five host plant species. Thus, about 86% of agromyzid fly species feed on fewer than five host plant species.

Figure 12.11 On average (based on the height of the bar graph), the control plants produced about 11–12 fruits per plant. This indicates that a plant that compensated fully for clipping would also produce 11–12 fruits.

Figure 12.18 The density of other plants in the community would probably increase after herbivory by *C. quadrigemina* reduced the density of Klamath weed. Because Klamath weed was originally a dominant member of the community, it is likely that the community would change considerably after introduction of the beetle.

Figure 12.22 In the absence of snails, wetlands had phosphorus concentrations of less than 100 µg/L. When snails were present, phosphorus concentrations were usually much greater than 100 µg/L; for example, in the seven wetlands with snail densities greater than 10 snails per square meter, the average phosphorus concentration was close to 1,000 µg/L. Thus, the presence of snails is associated with an increase in the phosphorus concentration of these wetlands.

Answers to Analyzing Data 12.1 Questions

1. A total of 18 plant populations were established in this experiment. In each of these populations, the initial frequency of each plant genotype was 1/27 = 0.037 or 3.7%.
2. If evolution had not occurred in the control populations, we would have expected all 27 plant genotypes to survive and their frequencies to change little from their initial values of 3.7% for each genotype. This was not the case: Many genotypes did not survive (and hence had a final frequency of 0%), while others increased dramatically in frequency. Genotype 6, for example, reached a frequency of 42.3% when grown in the control environment. Genotype 6 may have been particularly well suited to the growing conditions experienced in the control populations, where plant genotypes were grown at high densities and in soil that may have differed from the soil of

their home environments. Such changes in environmental conditions could have caused natural selection to occur in the control populations.

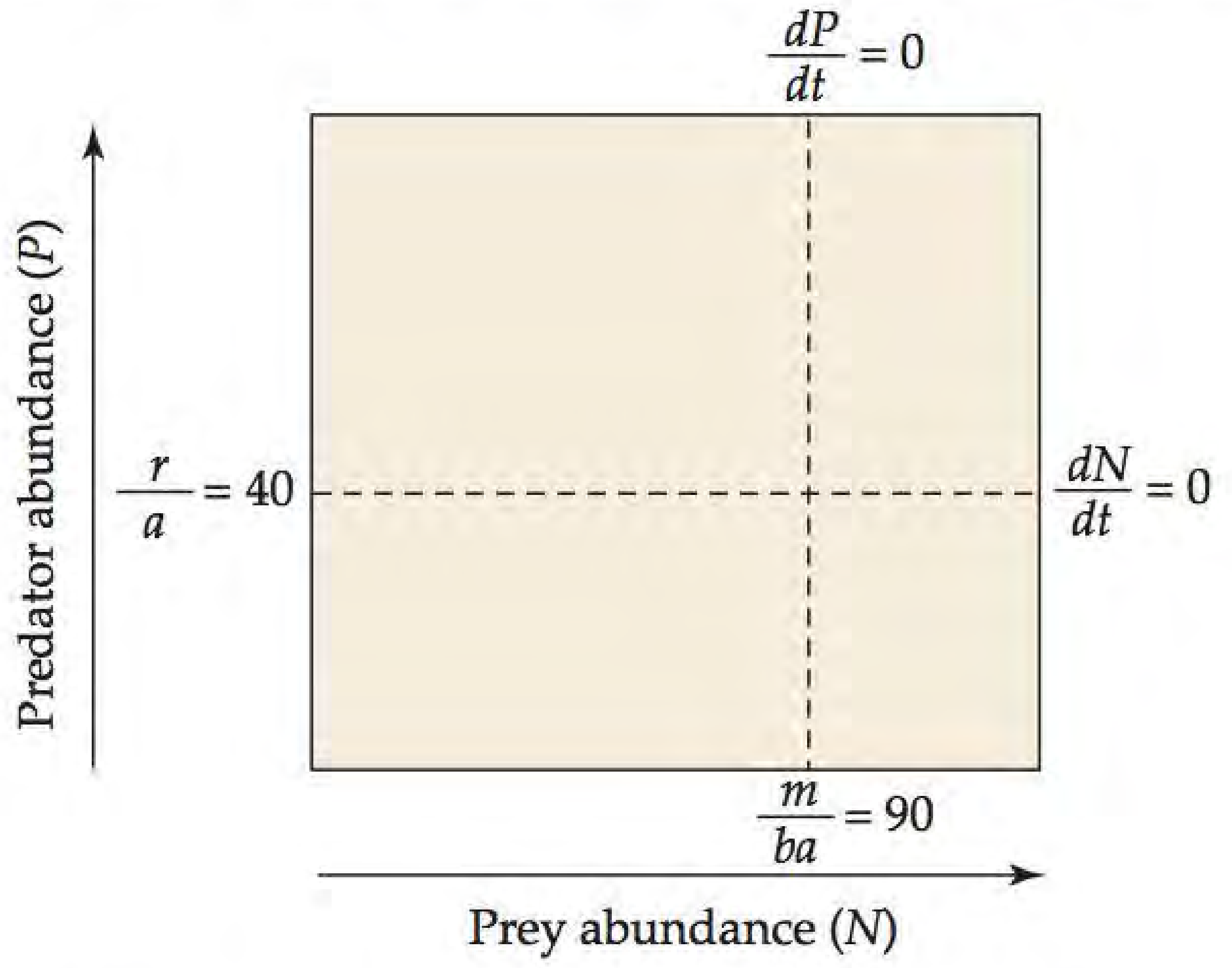
3. Plant genotype frequencies also changed in populations exposed to aphid herbivores, with many genotypes being driven to extinction while others increased dramatically in frequency. Hence, evolution occurred in these populations as well. Plant populations exposed to aphid herbivores could have experienced multiple sources of selection, such as novel environmental conditions (e.g., high plant densities and different soil from those found in their home environments) as well as the consequences of feeding by aphid herbivores.
4. In the *B. brassicae* treatment, 75% of the surviving plants encoded 4C defensive compounds; one of these, genotype 25, was the most common surviving genotype (67.4% of the surviving plants had this genotype). In contrast, in the *L. erysimi* treatment, 83% of the surviving plants had 3C genotypes, the most common of which was genotype 9, at 63.2%. Although a few genotypes performed reasonably well in both treatments (e.g., genotypes 9 and 25), overall, the outcome of selection differed considerably between treatments. These results suggest that natural selection by different herbivore species can favor different plant genotypes.

Answers to Review Questions

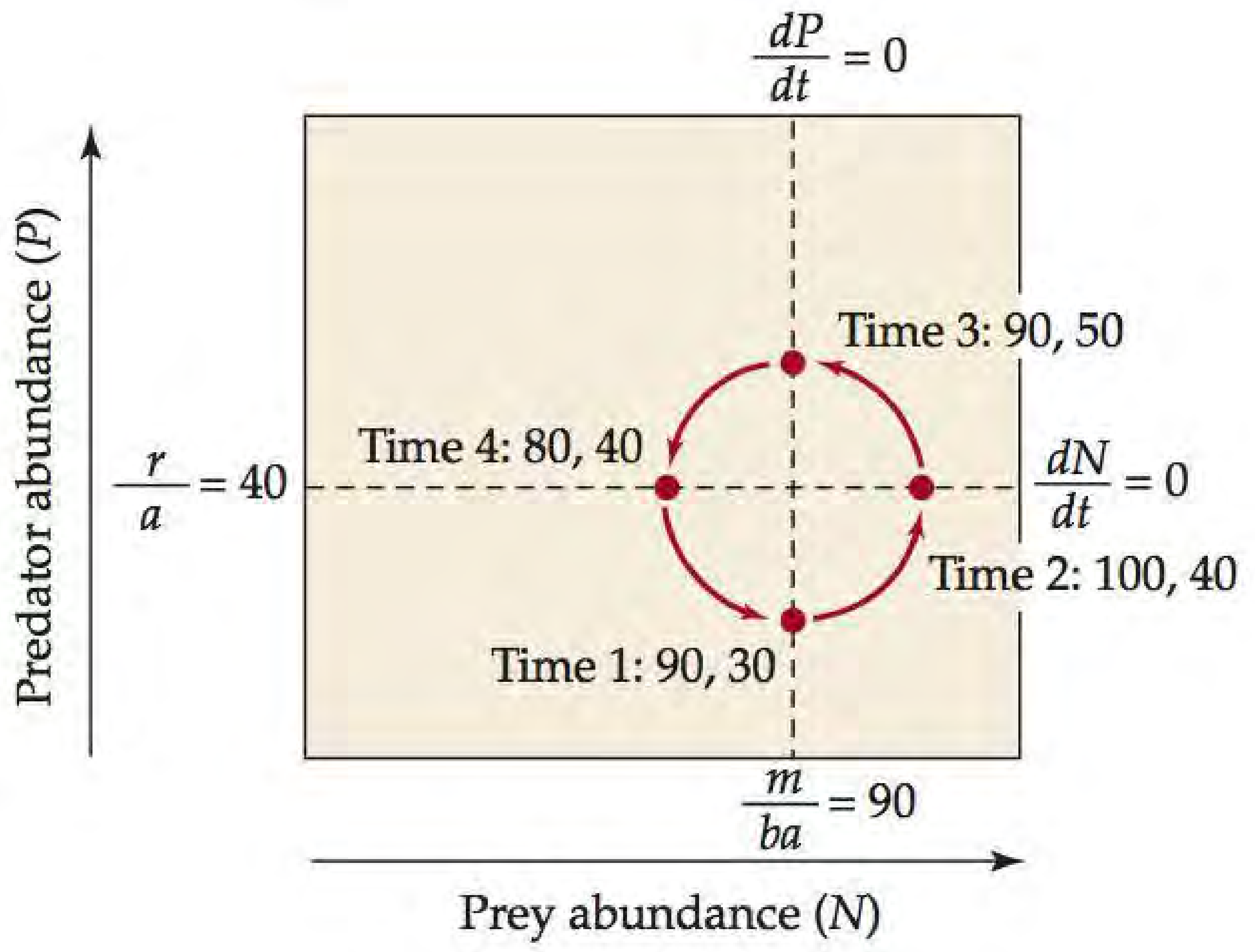
1. Most carnivores have a broad diet in that they eat a wide range of prey species. Although a substantial number of herbivores can eat many different plant species, the majority of herbivores are insects, most of which feed on just one or a few plant species. This difference is hypothesized to be due to the differences carnivores and herbivores experience related to encountering and handling their food. Carnivores are mostly generalists because their encounter rates are low for mobile prey, and thus they should not be too narrow in their prey choices. Herbivores are specialists because they have relatively high encounter rates with their immobile prey, but their handling times are longer because plants are less nutritious food.
2. A prey individual that cannot evade a carnivore is killed and eaten. While herbivores do not typically kill their food plants, they do have powerful negative effects on the plants on which they feed. As a result of this strong selection pressure that carnivores and herbivores exert on their food organisms, prey species have evolved a wide range of defensive mechanisms that increase the chance that they will not be eaten. Animals must eat if they are to survive, so there is also strong selection pressure on them to overcome the defenses of their prey. These effects are pervasive because all organisms must obtain food—setting in motion the conflicts just described. The effects are pronounced because there is such strong selection for both defensive and counterdefensive mechanisms.
3. a. Evidence described in this and preceding chapters indicates that predation can have a powerful effect on the abundance and distribution of prey species and this can affect communities in dramatic ways.
   b. The scientific evidence strongly supports this claim. As described in this chapter, in many cases the effects of carnivory and herbivory have been so pronounced that they have altered ecological communities greatly, in some cases causing a shift from one community type to another. For example, arctic foxes feeding on seabirds, lesser snow geese feeding on marsh grasses, and aquatic snails feeding on large aquatic plants had such effects.

Answers to Hone Your Problem-Solving Skills Questions

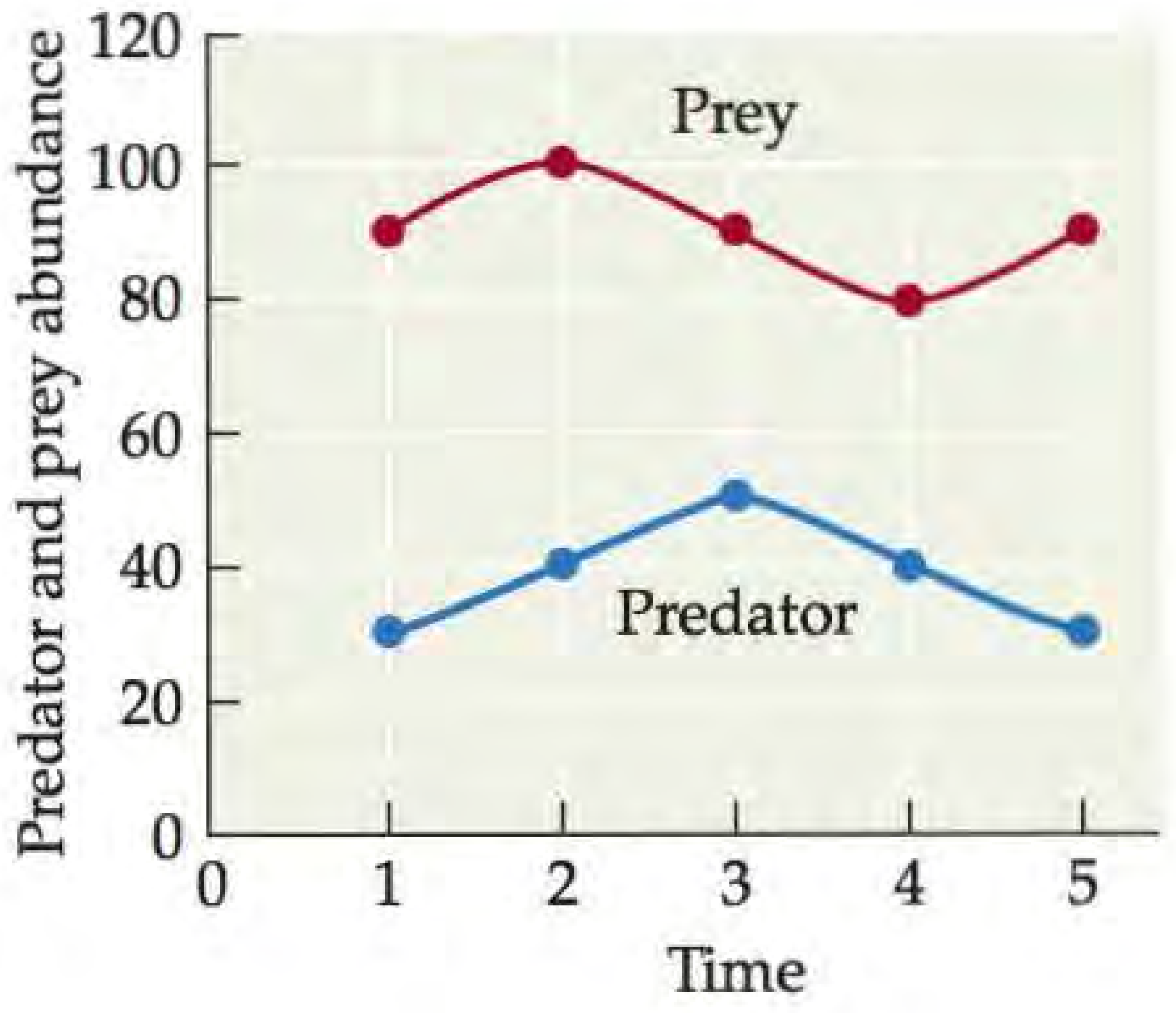
1. $dP/dt = 0$, $N = m/ba$, which is $N = 0.90/0.01 = 90$ prey
   $dN/dt = 0$, $P = r/a$, which is $P = 0.40/0.01 = 40$ predators



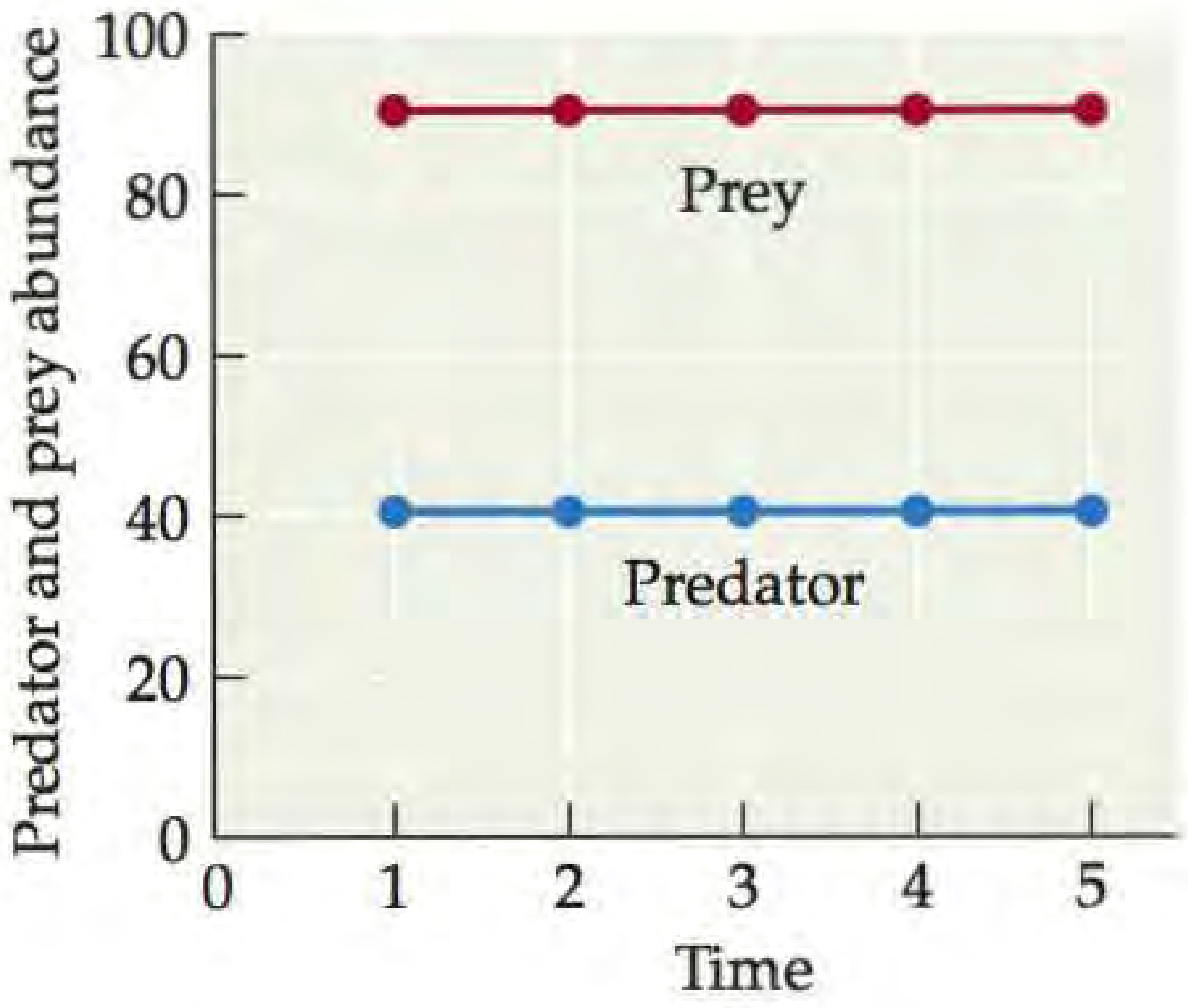
2. Given Lotka–Volterra model assumptions, the two populations will cycle with no change in the amplitude of the cycle. Thus, the values for Time 3 will be 90 prey and 50 predators and for Time 4 will be 80 prey and 40 predators.



3.



4. The populations will not cycle but will remain at equilibrium over time.



CHAPTER 13

Answers to Figure Legend Questions

Figure 13.4 Averaging across the six groups, there are about 21 parasite species per host. This average would probably not be close to the number of parasite species found in a previously unstudied host from one of the six groups of organisms. A reason for this is that in five of the groups (all but the trees), the average number of parasites per host is less than 12, while in the trees, the average is 95. Thus, we might expect that 95 parasite species would be found in another tree, 7 parasite species would be found in another wasp, etc.—but we would not expect to find 21 parasite species in a host from any of the six groups.

Figure 13.9 The gamete-producing cells enable the parasite to disperse from a human host to a mosquito.

Figure 13.11 No. For example, with an infection rate of 70%, the Lake Wahapo snails are very poorly defended against parasites from their own lake, but they are reasonably well defended against parasites from both other lakes. Similarly, Lake Paringa snails are poorly defended against parasites from their own lake (infection rate = 51%), but they are well defended against parasites from Lake Mapourika (infection rate = 11%).

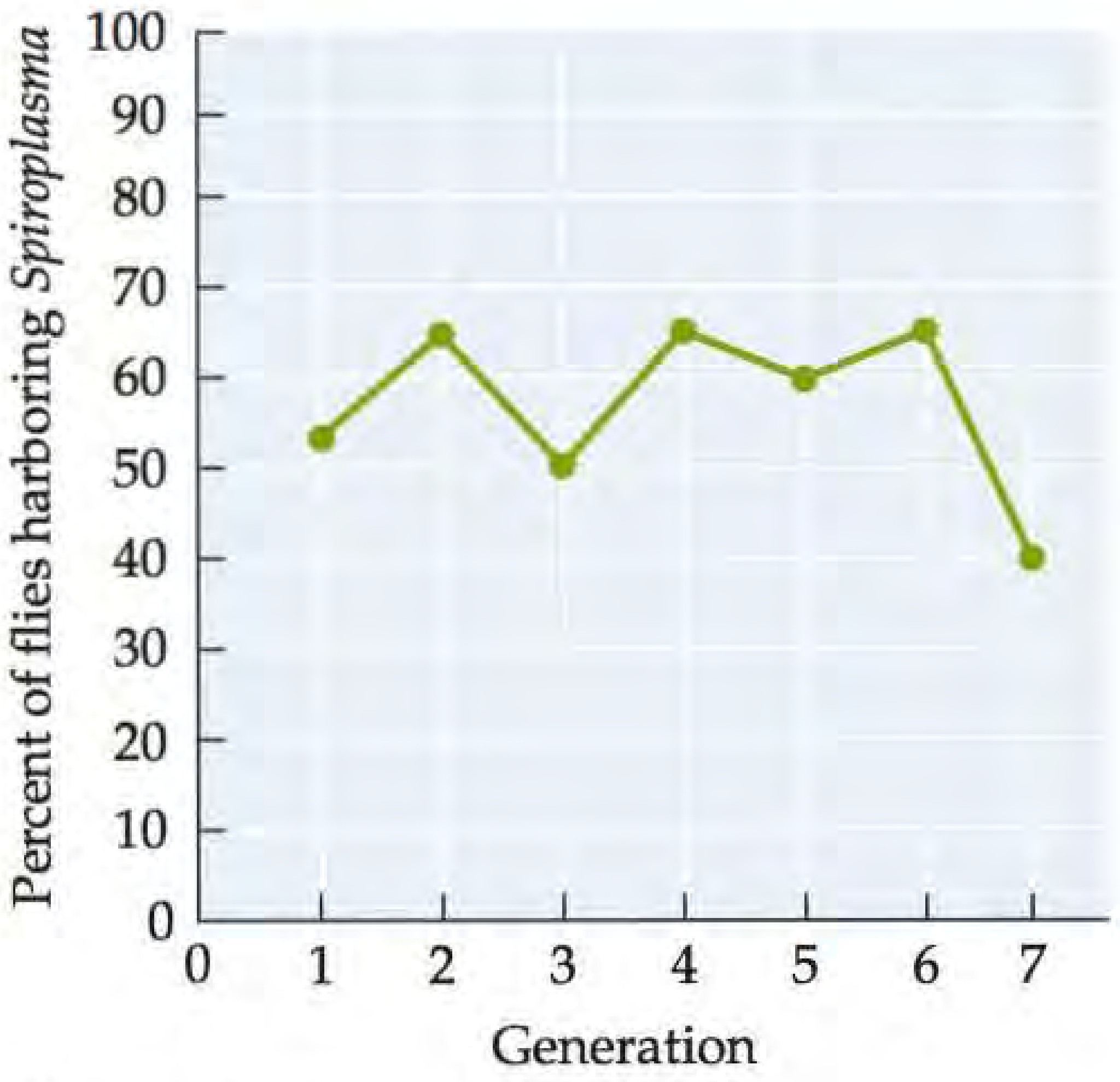
Figure 13.15 If the cycles stopped completely, we would not expect the numbers in both of the treated populations to drop in 1989 and again in 1993—the same years that the control populations were predicted to drop based on long-term data on population cycles in red grouse.

Figure 13.23 The WT and EGT+ treatments represent two types of controls. The WT treatments are unmanipulated controls; results from these controls can be compared with results from the EGT– experimental treatments. The EGT+ controls can be used to check whether the procedures used to remove (and insert) the *egt* gene have inadvertent effects. Hence, in the EGT+ controls, the gene is removed and then reinserted—if these experimental procedures do not have inadvertent effects, results from these controls should be similar to results from the WT controls. In fact, this is what was found.

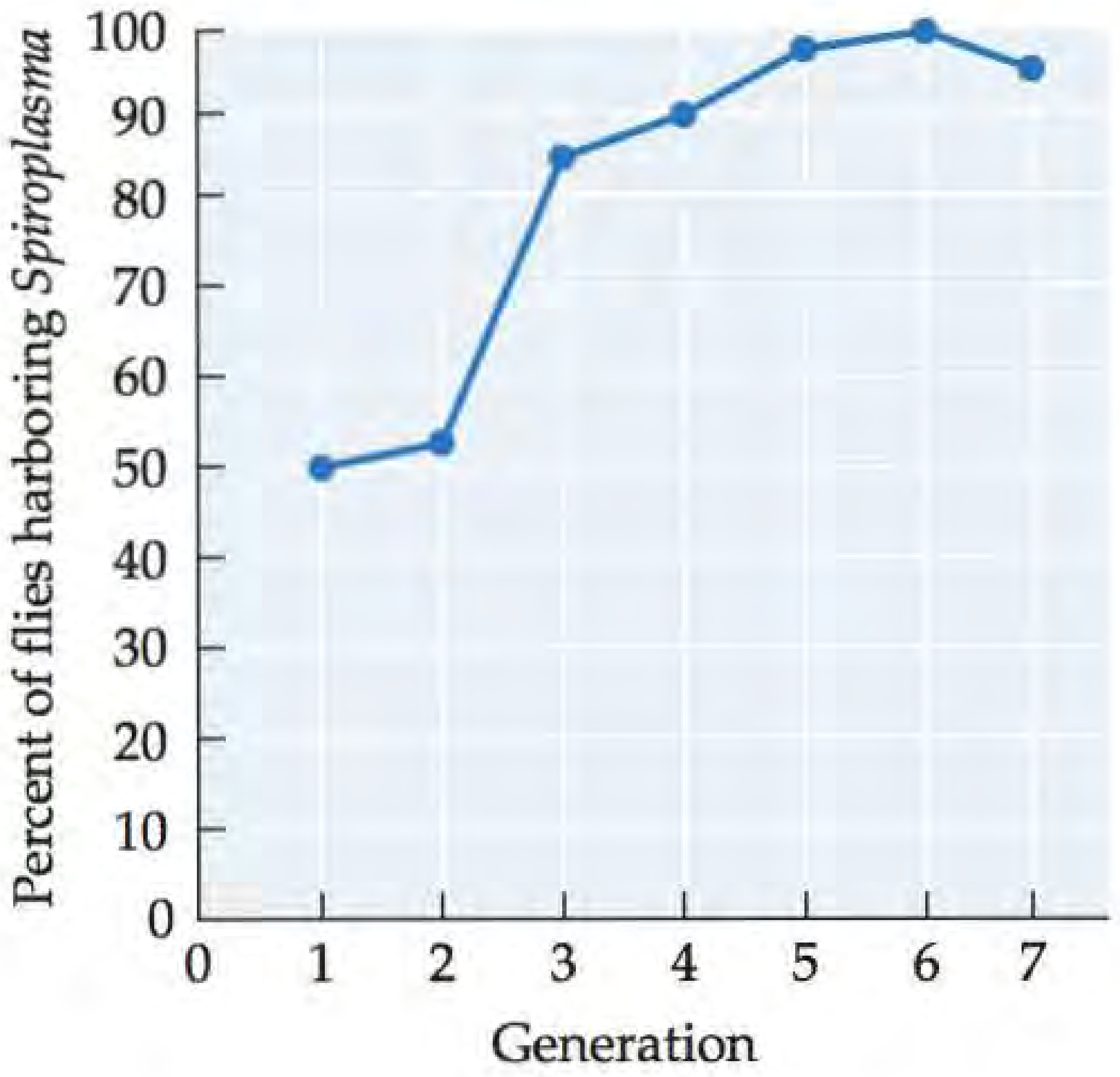
Answers to Analyzing Data 13.1 Questions

1. This experiment tests the hypothesis that the symbiont *Spiroplasma* is more common in fruit flies harboring the nematode parasite *Howardula*. The "*Howardula* absent" treatment serves as the control. The frequency of *Spiroplasma* fluctuated in the control but did not rise or fall consistently over time. In contrast, the frequency of *Spiroplasma* in the "*Howardula* present" treatment rose from its initial value of 50% to more than 95% by generation 5, supporting the hypothesis.

Howardula absent

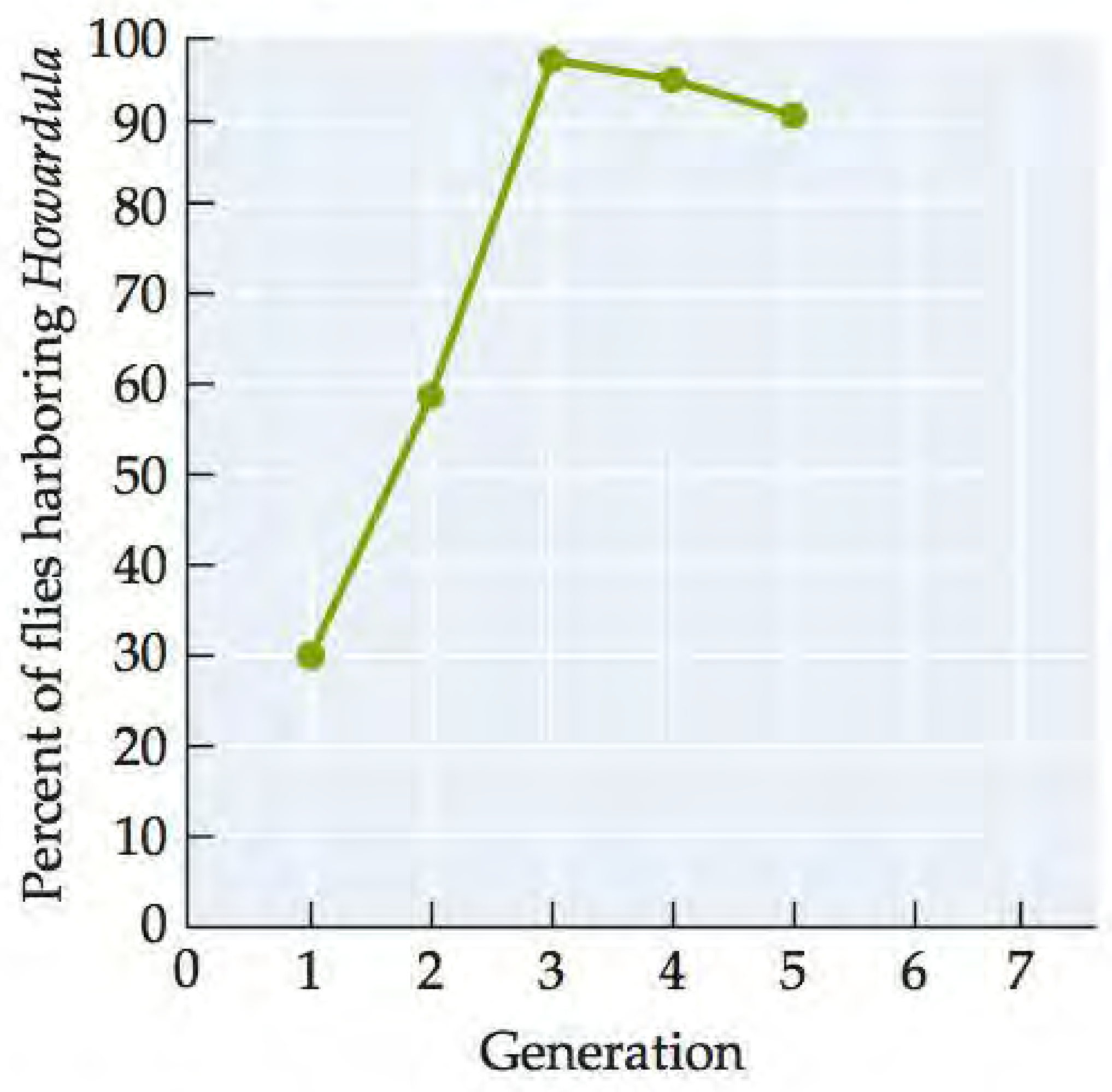


Howardula present

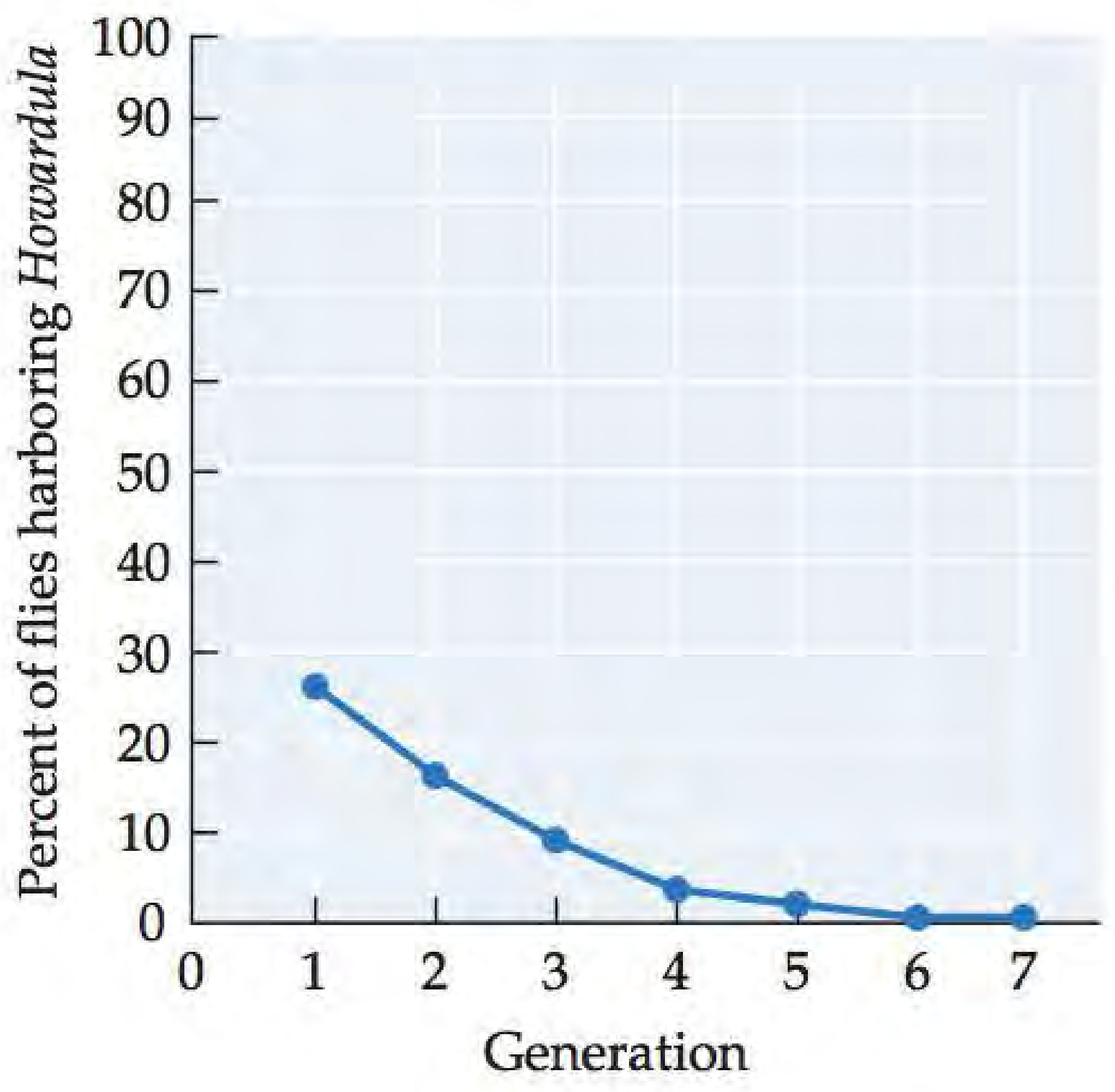


2. This experiment tests the hypothesis that the presence of the symbiont *Spiroplasma* protects fruit flies from the nematode parasite, *Howardula*. The "*Spiroplasma* absent" treatment serves as the control. In control populations, by generation 3, 95% of fruit flies were infected by the nematode parasite; all control populations declined to extinction by generation 6 (because, without the symbiont, the parasite sterilizes flies that it infects). In contrast, the frequency of *Howardula* dropped steadily in the "*Spiroplasma* present" treatment, reaching 0% by generation 6. These results support the hypothesis that the symbiont can protect fruit flies from attack by *Howardula*.

Spiroplasma absent



Spiroplasma present



3. We would predict that if there was a large cost for harboring the symbiont, the frequency of flies harboring the symbiont would decline in the absence of the parasite. This did not occur (see the graph in Question 1 for the "*Howardula* absent" treatment), suggesting that the flies experience few costs for harboring the symbiont.

Answers to Review Questions

1. Ectoparasites live on the surface of their host, whereas endoparasites live inside the body of their host. Examples of ectoparasites include plants such as dodder and fungi such as rusts and smuts; examples of endoparasites include tapeworms and bacterial pathogens such as *Mycobacterium tuberculosis*. Ectoparasites can disperse more easily from one host individual to the next than can endoparasites; however, ectoparasites are at greater risk from natural enemies than are endoparasites.
2. Parasites can greatly reduce the growth, reproduction, or survival of host individuals, thereby reducing the growth rate of host populations. As a result, we would expect that parasites could also alter both the outcomes of species interactions and the composition of ecological communities. For example, if two plant species compete for resources and one typically outcompetes the other, a parasite that reduces the performance of the superior competitor may cause a competitive reversal in which the inferior competitor becomes the superior competitor. Such changes in the outcome of species interactions can cause changes in the relative abundances of the interacting species, thus altering the ecological community.
3. a. Host organisms have a wide range of defensive mechanisms that include a protective outer covering, an immune system that kills or limits the effectiveness of the parasite, and biochemical conditions inside the host's body that reduce the ability of the parasite to grow or reproduce.

   b. The statement could be true if the plant populations in Australia possessed specific defensive features that limited the ability of the parasite to grow or reproduce, yet the populations in Europe lacked such adaptations. Among many other possible examples, plants in the Australian populations might possess a specific allele that enabled them to kill or disable the parasite—hence causing the parasite to have mild effects there—whereas plants in the European populations might lack this allele, making them more vulnerable to parasite attack.

Answers to Hone Your Problem-Solving Skills Questions

1. The rodents serve as an alternative, or reservoir, host for the disease. Thus, if leishmaniasis infection can be reduced within rodents, fewer sand flies will carry the disease and fewer humans will be infected.
2. A given disease will become established and spread in a given host population only if the density of susceptible hosts exceeds a critical threshold density (S_T). The concept of a threshold density has considerable medical and ecological importance because it indicates that a disease will *not* spread if the density of susceptible hosts can be held below the threshold density.
3. The following populations will need to be reduced to S_T, which is 5,000 individuals: Population 1 (decrease by 4,000 individuals), population 3 (decrease by 500 individuals), population 5 (decrease by 3,000 individuals), and population 8 (decrease by 5,000 individuals).
4. 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 $S_T = m/\beta$). This can be accomplished by early

3. a. Possible reasons why these meadows harbor one or the other (or both) of these two plant species include the following: (1) both species could persist at all locations, but one species (or the other) has yet to disperse to some meadows; (2) the physical conditions of the meadows differ such that in some meadows species 1 is favored, while in others species 2 is favored, and in still others, the species can partition resources such that both persist; (3) the abundances of herbivores or pathogens that feed on species 1 or 2 may vary between the meadows, causing the outcome of competition to differ from meadow to meadow; (4) the rates of a periodic disturbance such as fire may differ among meadows (if one of the species is an inferior competitor but is more tolerant of fire).

   b. Addition and removal experiments would help to evaluate these possible explanations for the observed distributions of the species. For example, in meadows where only species 1 is found, individuals of species 2 could be planted next to some individuals of species 1, but not others. Similarly, in meadows where both species are found, removal experiments could be performed in which individuals of species 1 were be removed from the vicinity of some species 2 individuals, but not others (and vice versa).

Answers to Hone Your Problem-Solving Skills Questions

1. Results from laboratory experiments, field observations, and mathematical models all suggest that competing species are more likely to coexist when they use resources in different ways. For example, in Gause's experiments with *Paramecium*, *P. caudatum* coexisted with *P. bursaria*, most likely because one species fed primarily on bacteria, the other on yeast. Likewise, in the case of four species of *Anolis* lizards that lived together on Jamaica and ate similar food, Schoener's field observations indicated that these species used space in different ways (an example of resource partitioning). Finally, graphical analysis of the Lotka–Volterra competition model indicates that competing species can coexist when the inequality shown in Equation 14.4 holds. That inequality is more likely to hold when competing species use resources in very different ways (e.g., when α and β are not close to 1).
2. Because $\beta = 1.6$ and there are 140 individuals of species 1, it would take $1.6 \times 140 = 224$ individuals of species 2 to reduce its own growth rate by the same amount that the 140 individuals of species 1 do. Therefore, because there are 230 individuals of species 2 present, species 2 is having a slightly greater effect on its own growth rate than is species 1.
3. The statement is not correct. For example, if $\alpha = 0.5$ and $\beta = 1$, Equation 14.4 predicts that both species will persist when $0.5 < K_1/K_2 < 1$. Thus, for example, if $K_1 = 100$ and $K_2 = 150$, both species should persist when $\alpha = 0.5$ and $\beta = 1$. (The statement can be shown to be false in many other ways; for example, in Figure 14.14B, values for α, β, K_1, and K_2 can be selected such that species 2 always drives species 1 to extinction, even though $\alpha < \beta$.)

CHAPTER 15

Answers to Figure Legend Questions

Figure 15.3 The regions colored light green are similar to the regions in which tropical rainforests are found. Thus, the plants in this mycorrhizal association are likely to be tropical rainforest trees and other plants found in the rainforest biome.

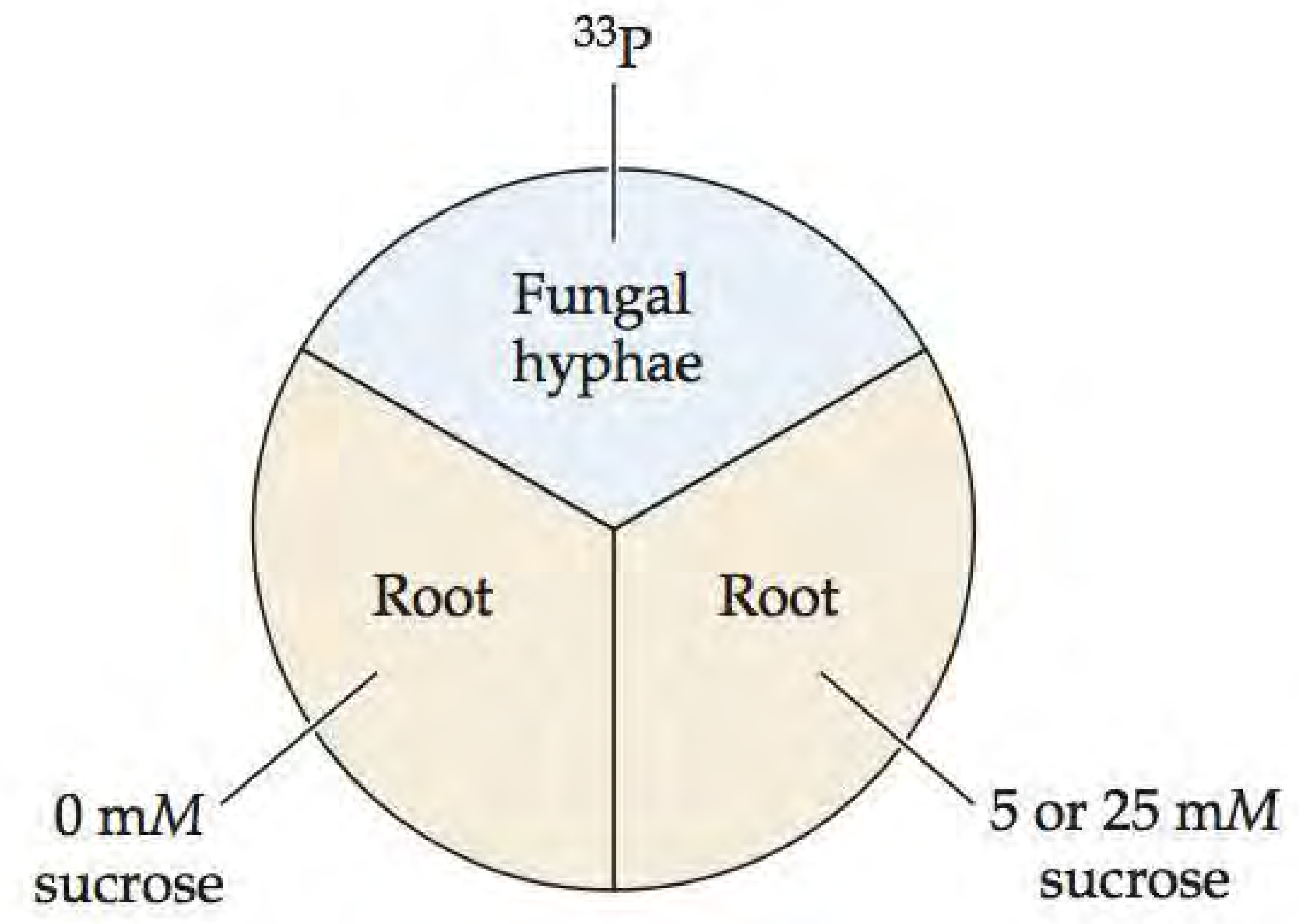
Figure 15.4 Ectomycorrhizae form a mantle around the root, while arbuscular mycorrhizae can penetrate the cell wall of a root cell and form an arbuscule (a branching network of hyphae).

Figure 15.8 *Myosotis laxa* grows best under colder conditions of 11°C–12°C with cattail neighbors present.

Figure 15.20 These results would suggest that although ants increase their frequency of weeding when parasites are present, they do not discriminate among parasites.

Answers to Analyzing Data 15.1 Questions

1.



2. The results in the figure show that the fungus transferred more phosphorus to plant roots that had greater access to sucrose.
3. Both partners play a role. As shown in Figure 15.13, the plant transfers more carbohydrates to fungi that have access to phosphorus. Similarly, as shown in the figure here, the fungus transfers more phosphorus to plants that have greater access to carbohydrates.

Answers to Review Questions

1. Commensalism and mutualism share a number of characteristics: they are both very common, they can evolve in many ways, and they can cease to be beneficial if conditions change such that the costs of the interaction exceed its benefits. In addition, some evidence indicates that positive interactions may be particularly common in stressful environments. Positive interactions can also differ from one another in that they can range from obligate and coevolved to facultative and not coevolved relationships.
2. When a species in a mutualistic interaction provides its partner with a benefit, that action comes at a cost to the

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CHAPTER 15

Answers to Figure Legend Questions

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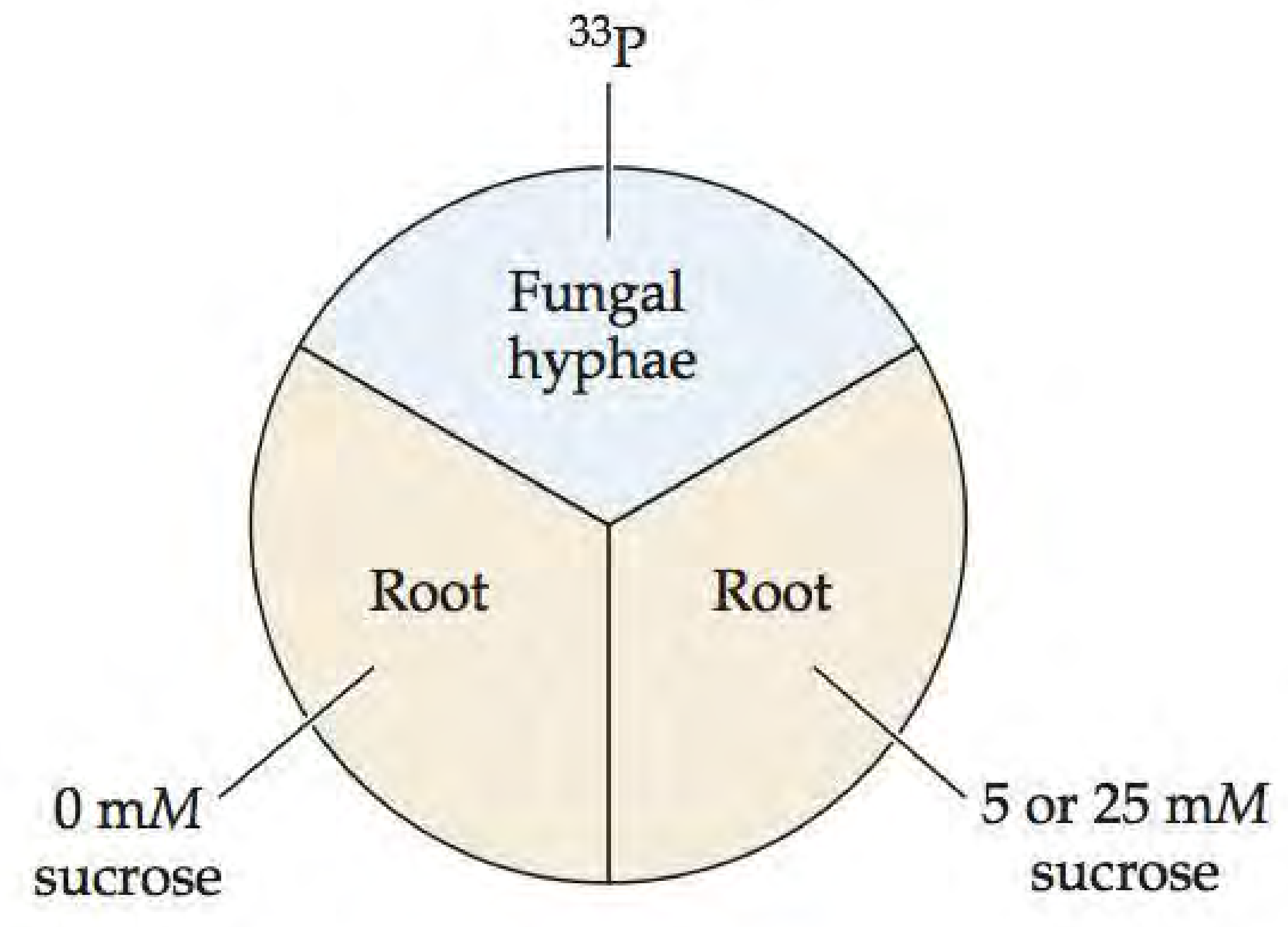
Answers to Analyzing Data 15.1 Questions

1.



2. The results in the figure show that the fungus transferred more phosphorus to plant roots that had greater access to sucrose.
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Answers to Review Questions

1. Commensalism and mutualism share a number of characteristics: they are both very common, they can evolve in many ways, and they can cease to be beneficial if conditions change such that the costs of the interaction exceed its benefits. In addition, some evidence indicates that positive interactions may be particularly common in stressful environments. Positive interactions can also differ from one another in that they can range from obligate and coevolved to facultative and not coevolved relationships.
2. When a species in a mutualistic interaction provides its partner with a benefit, that action comes at a cost to the

species providing the benefit. If circumstances change such that the costs of the interaction are greater than the benefits to one of the species, that species may cease to provide benefits to its partner, or it may penalize its partner. The fact that mutualists may stop providing benefits to their partners when it is not advantageous for them to do so has convinced researchers that mutualism is not an altruistic interaction.

3. Initially, we could expect a decrease in the growth or reproduction of the coral species that are most sensitive to high water temperatures. If high temperatures continued long enough to cause repeated bleaching, it is likely that these more sensitive species would begin to suffer heavy mortality. As a result of the decreased growth, reproduction, and survival of the these sensitive species, the species composition of the reef would change: those coral species that were better able to tolerate high water temperatures would constitute an increasingly high percentage of the corals found in the reef. Such changes in the composition of the coral reef community might also affect other species; for example, a fish that depended on an increasingly rare coral for shelter or food might also decline in abundance. As water temperatures continued to rise, other, less sensitive corals might also experience negative effects. Eventually, if temperatures continued to rise, the abundance of all corals in the reef might decline, as would the abundance of the many species that depend on the reef.

Answers to Hone Your Problem-Solving Skills Questions

1. Scotch pine tree seedlings survive at much higher rates when growing under *Salvia* shrubs than when growing in open areas; thus, *Salvia* appear to serve as nurse plants for Scotch pine tree seedlings.
2. Scotch pine seedlings growing under *Salvia* shrubs experience lower light levels, lower soil temperatures, and higher soil moisture content than do Scotch pine seedlings growing in open areas. Any of these three (correlated) factors could contribute to the increased survival of pine seedlings that grow beneath *Salvia*; controlled experiments would be needed to separate their effects.
3. As a Scotch pine tree increased in size, it could begin to compete with (and hence harm) the *Salvia* shrub that once served as its nurse plant.

CHAPTER 16

Answers to Figure Legend Questions

Figure 16.2 Based on the dates of *Caulerpa* sightings, it is likely the seaweed spread from Monaco west to Spain and east to Sicily, Italy, at about the same time (1992, 1993). It was restricted to these locations for 2 years, but then traveled to the eastern coast of Italy, and from there to the island of Hvar (1995), from which it spread to the northern islands of Croatia (1996). Finally, it was sighted much later in Tunisia (2000), even though Tunisia is closer to Sicily than is Croatia. This may have been because there was less boat traffic to Tunisia than to Croatia, thus lowering the chance of invasion, or it may have been due to a lack of recognition until 2000 that the seaweed was present.

Figure 16.3 The desert and hot springs communities are defined by physical attributes of their environment, whereas the tropical rainforest and coral reef communities are defined by biological attributes of their environment, particularly by the presence and importance of abundant species (i.e., trees and corals, respectively).

Figure 16.10 The tropical soil bacterial community requires much more sampling because each sample contains new species, thus producing a linear species accumulation curve. The sampling in the temperate forest plant and tropical bird communities was sufficient to identify a large majority of the species in these communities, and thus more sampling would not be needed. This is clear from the leveling off of the species accumulation curves once all the samples were analyzed. Finally, although the human oral bacterial and tropical moth communities showed some leveling off of their species accumulation curves, new species were being found even once all the samples were analyzed. Thus, they also need more sampling to adequately capture their species richness.

Figure 16.18 Beavers act as ecosystem engineers by damming streams with cut trees and woody debris. This behavior creates a flooded area, which accumulates sediment and eventually becomes dominated by marsh vegetation. At a landscape scale, by creating a mosaic of wetlands within a larger forest community, the beavers' actions enhance regional species diversity. Thus, beavers can also be classified as keystone species because they have such a large effect on diversity relative to their size and abundance.

Answers to Analyzing Data 16.1 Questions

1. The number of invasive species that likely caused negative effects on species richness is 11. The number of invasive species that likely caused positive effects on species richness is 1. The number of invasive species that likely had no effect is also 1.
2. The percentage change in species richness suggests that most invasive species had strong to intermediate negative effects on species richness. Only two invasive plants had neutral or positive effects, and these effects were weak.
3. The order of the magnitude of the change in species diversity (*H*) did differ between the two measures, with some species having higher species richness but lower species diversity than other species. This suggests that the proportional abundance of the species within the plots (evenness), which is used along with species richness to calculate species diversity, also changed with the invasion. In some cases, evenness increased, and in others, it decreased.

Answers to Review Questions

1. A community is a group of interacting species that exist together at the same place and time. Interactions among multiple species and their physical environment give communities their character and function.
2. Species richness is the number of species in a community, but that measure tells us nothing about the relative abundances of those species. If two communities had a similar number of species, but great differences in species evenness (as in Figure 16.6), species richness would not reflect this difference, but species diversity indices would. Rank abundance curves (as in Figure 16.8) allow hypotheses to be generated about how those species may be interacting in the community based on their abundances.
3. Foundation species have a large effect on other species due to their large size and high abundance. For example, kelp and trees have a large influence on species diversity by virtue of providing their communities with habitat, food, and other services that are directly related to their size. Keystone species have a large effect despite their small size and low abundance, because of the important role they play in their communities. For example, sea otters have large effects on their communities by preying on herbivores (sea urchins), which, in turn, eat primary producers (kelp). This indirect interaction can allow primary producers to have higher abundances. Finally, ecosystem engineers are able to create, modify, or maintain physical habitat for themselves and other species. Trees and kelp are examples of ecosystem engineers that are foundation species, and beavers are an example of a keystone species that is also an ecosystem engineer.

Answers to Hone Your Problem-Solving Skills Questions

1. The per capita interaction strength (IS) values between seagulls and the species listed in the table are the following: ribbed limpet IS = $\ln (10/100)/10 = -0.23$, gooseneck barnacle IS = $\ln (500/3{,}000)/10 = -0.18$, checkered limpet IS = $\ln (100/50)/10 = 0.07$, mussel IS = $\ln (3{,}000/2{,}500)/10 = 0.02$, microalgae IS = $\ln (500/100)/10 = 0.16$.
2. Of the prey species, ribbed limpet experience the greatest negative affect of seagull predation. Of the nonprey species, microalgae have the greatest positive interaction with seagulls because they indirectly benefit from the fact that their herbivore, the ribbed limpet, is eaten by the birds.
3. *Indirect effect 1*: Removing seagulls decreases the abundance of mussels because of increased competition with the gooseneck barnacle. *Indirect effect 2*: Removing seagulls decreases the abundance of the checkered limpet because of increased competition with the ribbed limpet. *Indirect effect 3*: Removing seagulls decreases the abundance of microalgae because of increased herbivory by the ribbed limpet. *Indirect effect 4*: Although the experiment cannot test for the effect on phytoplankton, it is likely that removing seagulls decreases the abundance of phytoplankton because of increased herbivory by the gooseneck barnacle.
4. The effect of seagulls would be even more positive. That's because seagulls, by eating the ribbed limpet and gooseneck barnacle, reduce the competition for the mussel and checkered limpet (the interaction strength measurements for those species indicated that they indirectly benefited from their interaction with seagulls). By reducing competition, excluding the mussel and checkered limpet allows those nonprey species to increase in abundance and prey more heavily on microalgae and phytoplankton.

CHAPTER 17

Answers to Figure Legend Questions

Figure 17.2 The most destruction occurred immediately below the mountain, where a huge magma-filled bulge exploded and released rock and mud down the north side of the mountain. An area later known as the Pumice Plain, formed by the hot, pelting pumice rock, experienced the most destruction. The massive wave of debris from the explosion was funneled down the North Fork Toutle River, removing most life along the way. Spirit Lake was also completely destroyed because of its location within the path of the avalanche. Other areas, such as the south side of the mountain and the locations farther from the explosion (mudflow zone and blowdown zone), experienced blowdown of all trees, but some life remained, especially underground. Finally, the least destruction occurred in the scorch zone, where trees were denuded but remained standing.

Figure 17.4 Whether a disturbance is intense or frequent will depend on the susceptibility of the organisms involved and their ability to respond to the disturbance. The intensity and frequency of disturbance for an insect population will be quantitatively different from that for an elephant population. The same disturbance—let's say, a tree falling in a forest—could cause major destruction for the insect population living on that tree while having little effect on the elephant population, even if an elephant were struck by the tree. Of course, the insect population would recover much faster than an elephant population might.

Figure 17.9 The oldest communities are located in the areas that have been exposed the longest since glacial retreat, such as the mouth of the bay. Here, succession has been able to proceed for over 200 years and has allowed the formation of mature spruce forests. As the glacial retreat becomes more recent, the communities become younger, such that the youngest, pioneer community is located closest to the glacier.

Figure 17.17 The fish preferred to eat the tunicate *Styela*, because when the tiles were protected from fish predation, it was the species that dominated. When fish predation was allowed, the bryozoan *Schizoporella* dominated, suggesting that it was unpalatable to the fish. This experiment suggests that *Styela* is the dominant competitor over *Schizoporella* in the absence of predation.

Answers to Analyzing Data 17.1 Questions

1. Aspen suckers colonize all the successional stages but are most abundant in aspen stands and least abundant in meadow and fir stands. In contrast, subalpine fir seedlings are most abundant in the mixed aspen–fir and fir stands and least abundant in the meadow and aspen stands. The data show that aspen are the first to colonize meadows, establishing aspen stands that are then colonized by firs. As firs increase and form mixed and fir-dominated stands, aspen decline and fir seedlings increase. This pattern supports the successional sequence described in the introductory paragraph of this Analyzing Data exercise.
2. The most consistent hypothesis is that fir seedlings are facilitated by aspen, because their densities are highest in aspen stands but lowest in meadows. However, competition seems to drive aspen out in later stages, because they decline in mixed aspen–fir and fir-dominated stages.
3. Fir trees have lower mortality when they live close to aspen than when they live farther away, suggesting that they are facilitated by aspen. However, aspen trees show greater mortality close to firs than farther away, suggesting that they compete with firs and are eventually excluded from the community. These results support the previous hypotheses from Question 2.
4. This study best fits the facilitation model inspired by Frederick Clements and later described by Connell and Slatyer. In this model, only certain species, such as aspen, can establish themselves in early successional habitats. This might be a consequence of clonal growth. In time, species such as aspen modify the habitat in such a way that they facilitate later successional species such as firs, which may be intolerant of full sun. As firs grow and mature, they continue to be facilitated by aspen but eventually displace them through competition for resources. In this system, firs are expected to dominate and exclude aspen until they are disturbed by fire or humans, resetting the system back to meadow.

Answers to Review Questions

1. Abiotic and biotic agents of change include those listed in Table 17.1. Intense disturbances such as hurricanes, tsunamis, fires, and volcanic eruptions can cause major damage but are relatively infrequent. Other agents of change, such as sea level rise, competition, or parasitism, may not cause major damage initially but may be frequent or constant and have dramatic effects over time. Still others, such as predation, may be relatively frequent but not very intensive, thus forming patches of available resources.
2. Primary succession involves the colonization of habitats devoid of life. Species colonizing these habitats must deal with stressful conditions and transform their habitats to create soils, nutrients, and food. Secondary succession involves the reestablishment of a community in which most, but not all, of the organisms have been destroyed. Under these conditions, colonizing species benefit from the biological legacy of the preexisting species, but they are likely to face more competition for resources than the species involved in primary succession.
3. A hypothetical community might be a newly cleared vacant lot in an unnamed city. The facilitation model would be supported if the first species to arrive were stress-tolerant and had the ability to modify their habitat in positive ways. In this case, those early species would facilitate the growth of later species, which would be better competitors but less stress-tolerant. Over time, these later species would dominate as they outcompeted the facilitating species. The tolerance model assumes that the earliest species modify the environment, but in ways that neither help nor hinder later species. Later species are merely those that live longer and tolerate stressful conditions longer than early species. Finally, the inhibition model would be supported if the early species created conditions that benefited themselves but inhibited later species. Only through the removal of those inhibitory early species—for example, via disturbance or stress—would later species be able to displace them.
4. It is hard to know whether a community is stable because stability depends on the spatial and temporal scale at which the community is observed. All communities fluctuate and change over time, but how long must we wait for a community to return to some original state before we assume it is stable? There is no single answer. Although Sutherland did observe the formation of alternative communities on his tiles when predators were manipulated, did he follow the communities long enough, and at a large enough spatial scale, to show stability? Again, it depends on how you define "stability," leaving us with an unresolved question.

Answers to Hone Your Problem-Solving Skills Questions

1. In 1982, the Pumice Plain had no surviving species, while the reference area had the highest species richness (five species). The blowdown and scorch zones both had intermediate species richness (three species). Species richness generally increased over time, even in the reference area. By 2000, the Pumice Plain had one species, the blowdown zone had seven species, and the scorch zone and reference area had six species each.
2. Small mammals recovered in the two least disturbed successional habitats (blowdown and scorch zones) but not in the Pumice Plain. The pattern of species richness seen in the blowdown and scorch zones was likely due to their being secondary successional communities and thus having more resources available to them after the eruption. In the primary successional community of the Pumice Plain, the habitats and resources were nonexistent and had to be reestablished over time. Thus, it makes sense that this

community could not support more than one small mammal species.

3. This suggests that the deer mouse has a life history that allows it to live in primary, secondary, and climax successional communities. It is likely able to disperse widely, grow quickly, and reproduce often—all characteristics of an early successional, pioneer species. The deer mouse is also likely to be an opportunistic and generalist species, living in a variety of habitats and feeding on a variety of food items.
4. It may be that some small mammal species were affected by the eruption, even though the trapping site was 21 km away from the mountain. Over time, these species recovered and were present in the reference community. In addition, it may be that the researchers did not trap individuals of a particular species some of the years, thus underestimating species richness. Alternatively, it may be that the animals became habituated to the traps because they contained bait. This could have resulted in individuals of rare species being caught more often over time.

CHAPTER 18

Answers to Figure Legend Questions

Figure 18.2 The goal of the study was to look at the effect of fragmentation on species diversity in the *remaining* forest fragments rather than considering the direct effects of deforestation itself.

Figure 18.6 No, there could never be more local species than would be contained within a region, because the spatial scale of the region is larger than that of the local community.

Figure 18.9 Holt et al. (2013) used phylogenetic information acquired from DNA analysis and more recent global species distribution patterns to test whether Wallace's original biogeographic regions were supported by modern data collection.

Figure 18.11 One would expect speciation to increase as land masses separate because species would become reproductively isolated from one another, thus increasing the chance that they would follow different evolutionary trajectories. The separation of species in this way is known as vicariance.

Figure 18.16 The idea that the tropics serve as a cradle is meant to suggest that it is a place in which species arise or "are born." The reference to the tropics as a museum is meant to suggest that it is a place in which species are protected from extinction and thus are "on display" for a long time.

Answers to Analyzing Data 18.1 Questions

1. There was a steeper slope (z) and lower y intercept (c) for the species–area relationship of invaded communities compared with uninvaded communities. These results suggest that invaders have strong negative effects on species richness at the smallest spatial scales and little or no effect at large spatial scales.
2. To convert log x values to x values, solve for 10^x. The approximate range of area values is from (at the smallest scale) 1 m^2 to (at the largest scale) 500 m^2. The approximate range in species richness for invaded plots is 0.6 (smallest scale) to 16 species (largest scale). For uninvaded plots, it is 3 (smallest scale) to 20 species (largest scale).
3. One hypothesis is that the invaded areas turn into island-like habitat where native species occur within a sea of invaders. As we saw in the example in Ecological Toolkit 18.1, island-like systems tend to have steeper slopes and lower y intercepts than mainland-like habitats. The equilibrium theory of island biogeography posits that smaller areas and those more distantly connected to the sources of species will have higher extinction rates and lower immigration rates and thus fewer species per given area. At the largest spatial scale, however, even though invasions may have negative effects on native species, the area may be large enough that immigration of species from uninvaded areas may rescue species from extinction. At some point, though, if large enough areas are invaded and/or immigration from uninvaded areas ceases, one could see a decline in species richness.

Answers to Review Questions

1. The largest spatial scale is the global scale, which covers the entire world, over which there are major differences in species diversity and composition with latitude and longitude. These patterns are controlled by speciation, extinction, and dispersal. The next scale down is the regional scale, defined by areas of uniform climate and by species that are bound by dispersal limitation to the region. Within a region, species diversity and composition depend on dispersal and extinction rates across the landscape. The regional species pool (also called gamma diversity) has an important influence on the species present at the next scale down, the local scale (also called alpha diversity). The relationship between regional and local species richness can help us to determine the extent to which the regional species pool or the local effects of species interactions and physical conditions determine local species richness.
2. Wallace identified six terrestrial biogeographic regions, which represent distinct biotas that vary in species diversity and composition. Wallace believed that these biogeographic regions reflect the evolutionary isolation of species due to the movements of the continents. Thus, the ancestors of many modern species may have occurred together in the evolutionary past, but since Pangaea began breaking up into the continents we know today, they have evolved separately. Recent research suggests that the biogeographic regions are more subdivided than previously thought, suggesting more isolation than simply the movements of the continents. There are also impediments to dispersal within oceans, such as currents, thermal

gradients, differences in water depth, and the continents themselves, so it is assumed that the oceans could be divided into biogeographic regions, but that effort has received considerably less attention.

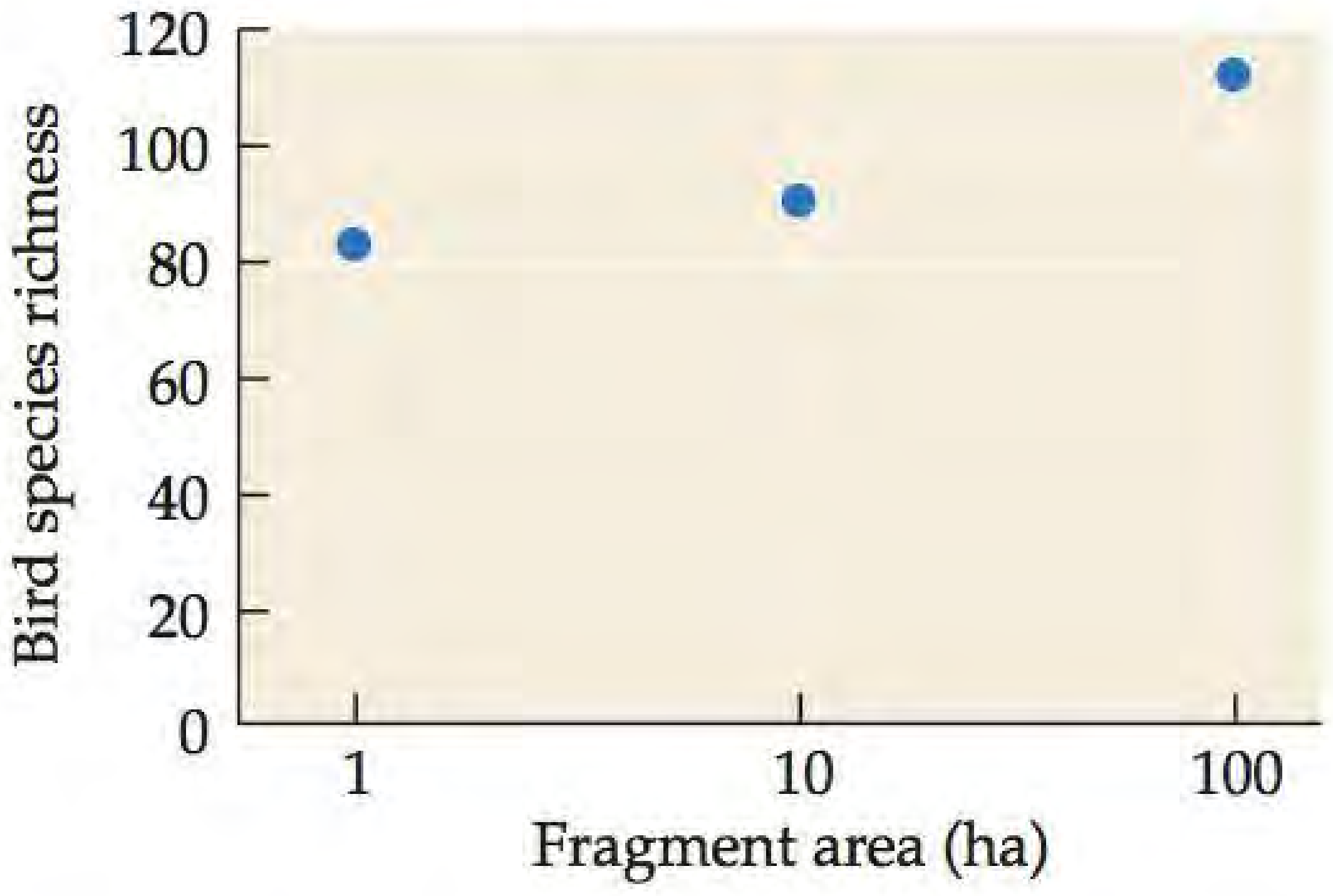
3. The three main hypotheses focus on (1) species diversification rate, (2) species diversification time, and (3) productivity. The first hypothesis proposes that both the large geographic land area and the thermal stability of the tropics might promote higher speciation rates and lower extinction rates, thereby increasing the population sizes and geographic ranges of species. Speciation rates should increase because larger geographic ranges should lead to greater reproductive isolation. Extinction rates should decrease because larger population sizes should lower the risk of extinction due to chance events while larger species ranges should spread extinction risk over a larger area.

   The second hypothesis suggests that the tropics have had a longer evolutionary history than the temperate or polar zones because of their greater climatic stability. This stability may have allowed more species to evolve without the interruption of severe climatic conditions that would have hindered speciation and increased extinctions in the temperate and polar zones.

   The third hypothesis suggests that the high productivity of the tropics increases species diversity by promoting larger population sizes, which should lead to lower extinction rates and overall higher species richness.

Answers to Hone Your Problem-Solving Skills Questions

1. Yes, the data follow the species–area relationship.



2. The percentage loss of species per year can be calculated using the t_{50} scaling factor. Divide the percentage loss (50%) by the number of years to reach that loss to get the percentage loss of species per year. Thus,

   1 hectare: 50%/5 years = 10% species loss per year

   10 ha: 50%/8 years = 6.25% species loss per year

   100 ha: 50%/12 years = 4.17% species loss per year

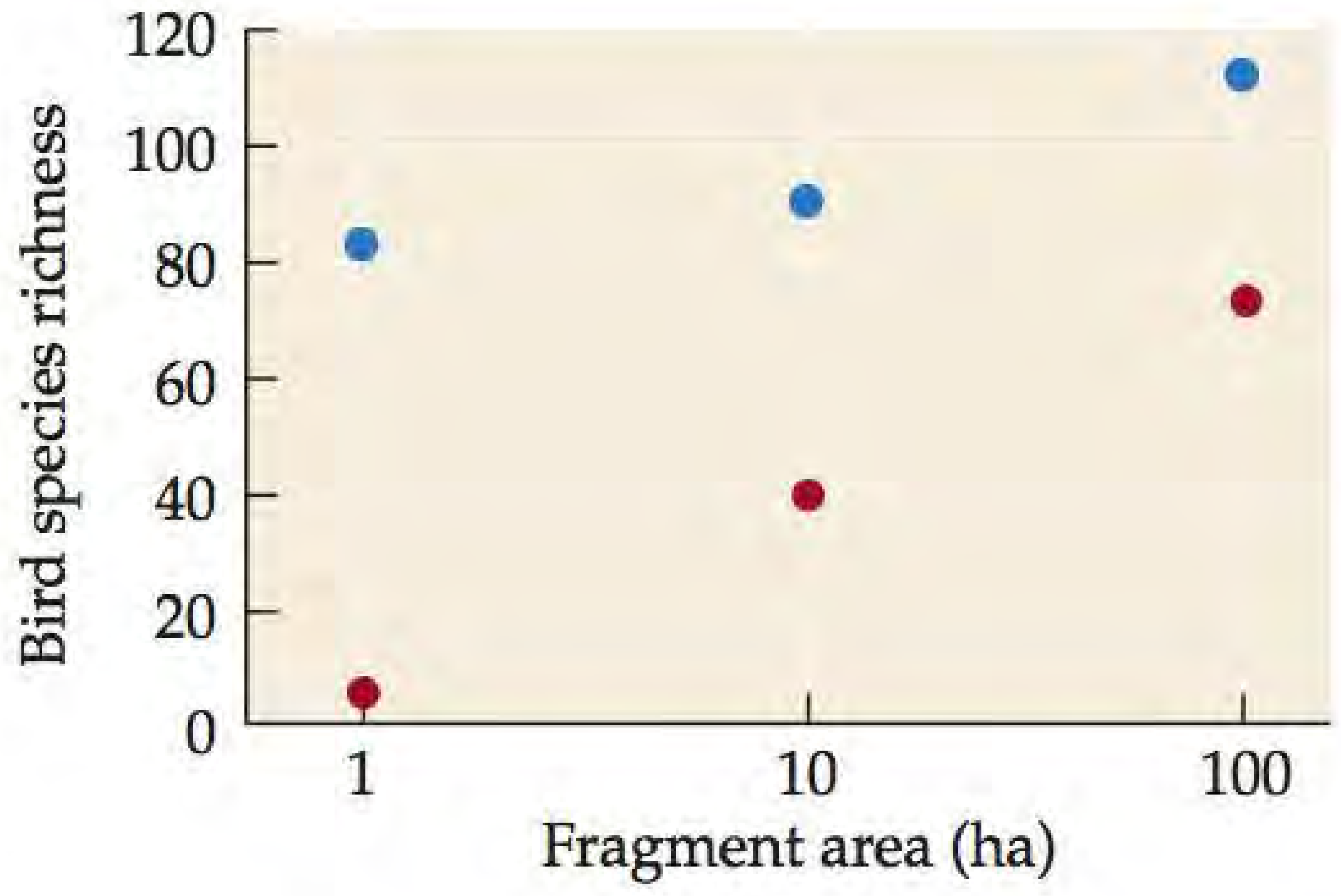
   The 1 ha fragments have the greatest species loss, and the 100 ha fragments have the least.

3. The number of species in the fragments 9 years after the start of the experiment can be calculated using the following equation: initial species number – (initial number of species × percentage species loss per year × 9 years). Thus,

   1 ha: 83 species – (83 species × 10% loss per year × 9 years) = 8 species

   10 ha: 92 species – (92 species × 6.25% loss per year × 9 years) = 40 species

   100 ha: 113 species – (113 species × 4.17% loss per year × 9 years) = 71 species



4. The fragments that had 9 years of isolation would have the steepest species–area slope. Once fragmentation occurs, the fragments act more like islands. Thus, the smallest fragments had greater species loss than the largest fragments because they had higher extinction rates and lower immigration rates. In addition, the smaller the fragment, the greater percentage of edge habitat, which is more hazardous for species, and thus extinction risk increases even more.

CHAPTER 19

Answers to Figure Legend Questions

Figure 19.4 No, it does not make sense that the fish and frog species should be present in the local community given in the figure, because that community contains terrestrial species. The abiotic filter should have excluded any aquatic species from this terrestrial community.

Figure 19.8 (B) shows the most resource partitioning (least overlap in resource use). (A) and (C) show the least resource partitioning (most overlap in resource use).

Figure 19.15 The lowest species richness occurred on the small boulders (their maximum richness was 4), which rolled over more frequently and thus experienced more disturbance compared with the other boulders.

Answers to Analyzing Data 19.1 Questions

1. The predation treatments all caused a decline in species richness compared with the control ponds without predation. Thus, it appears that predation caused the local extinction of zooplankton species. The two species of predators (fish and insect), either alone or together, did not differ in their effects on zooplankton richness.

2. Dispersal of zooplankton increased local species richness in the ponds but only if predation was present. If predators were not present, local species richness was similar

with or without dispersal. The results suggest that dispersal can have a positive effect on local species richness but presumably only if resources are freed up by predation, thus increasing species coexistence.

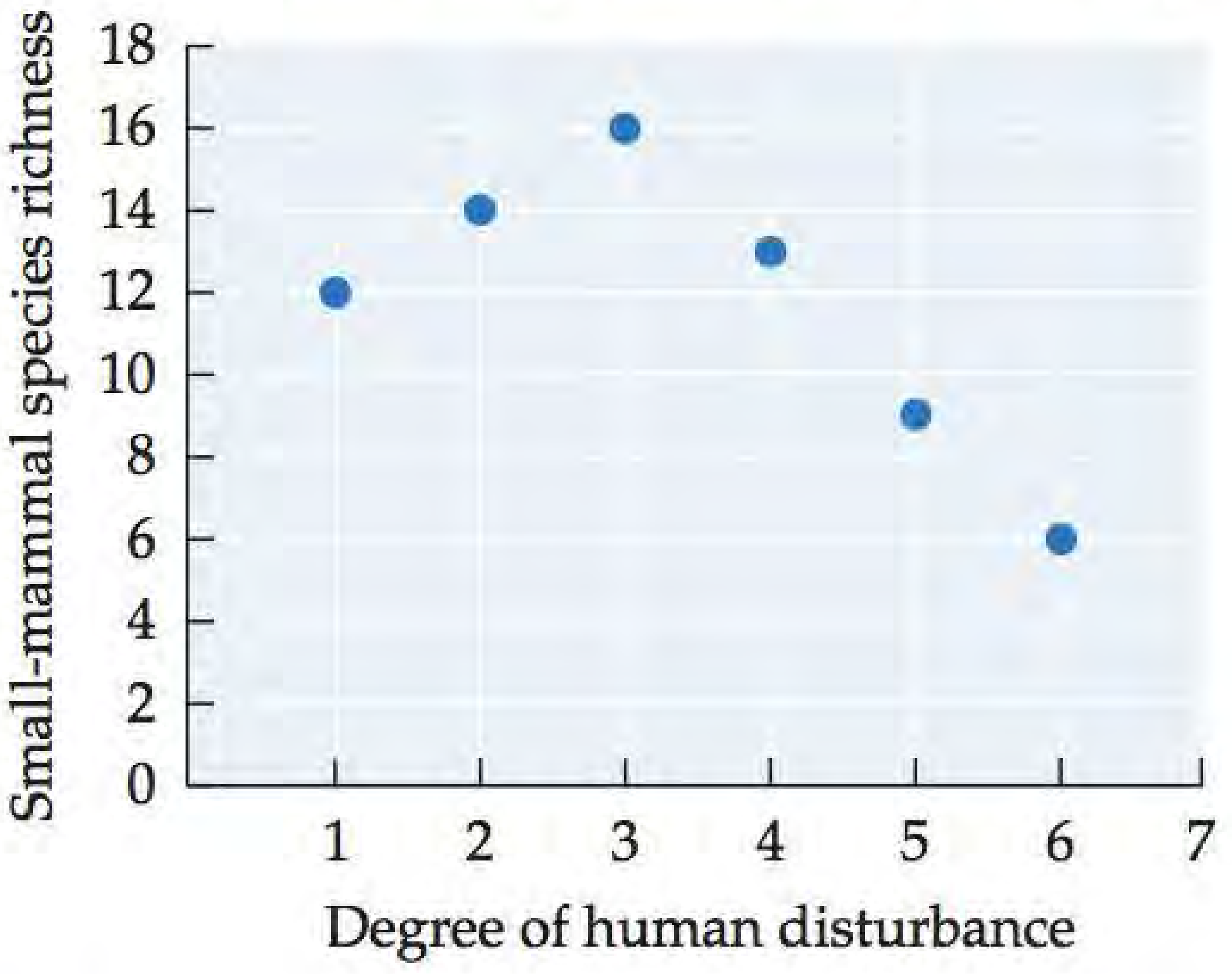
3. The results suggest that the effect of predation on local species richness can be so intense that the process of dispersal is inadequate to "rescue" the community from species loss. Yes, the results fit the intermediate disturbance hypothesis but only if dispersal is incorporated into the model.

Answers to Review Questions

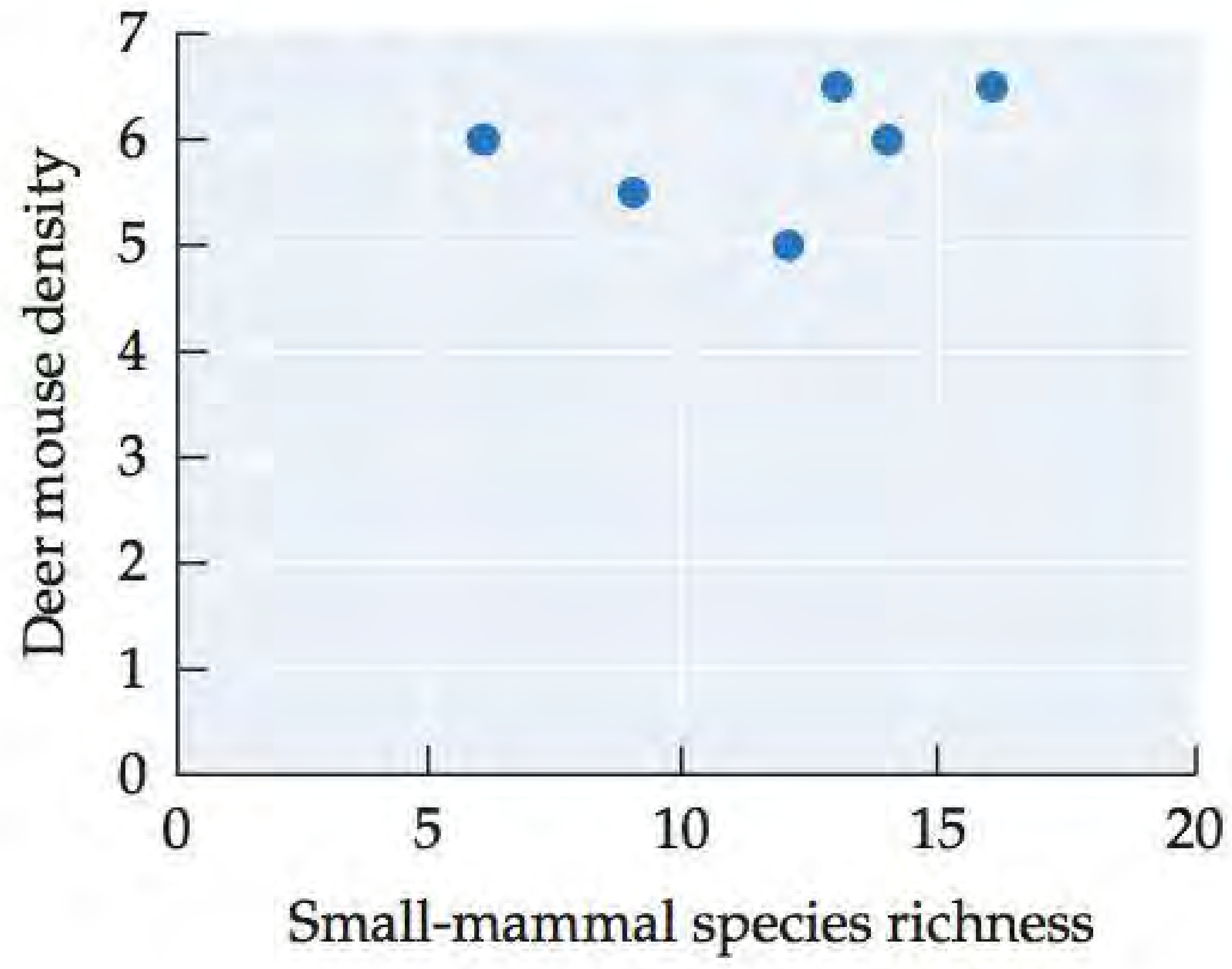
1. Yes. Community membership is dependent on dispersal, environmental factors, and biological interactions. Given all the introductions of non-native species that have occurred worldwide, it is clear that "getting there" has been an important constraint on the entrance of species into communities. In this particular case, the seeds on the ecologist's shoes are physically and biologically adapted to prairie grassland communities and are thus prime candidates for successful introduction into New Zealand grassland communities.
2. Resource partitioning is the idea that coexistence among species is possible if the species in a community use its resources in slightly different ways. Other models, such as the intermediate disturbance hypothesis, rely on population fluctuations due to disturbance, stress, or predation as the mechanism of coexistence. These models suggest that as long as populations of species never reach their carrying capacities, competitive exclusion will not occur, and coexistence will be possible. Lottery or neutral models assume that resources made available by disturbance, stress, or predation are captured at random by recruits from a larger pool of colonists, all of which have an equal chance of obtaining those resources.
3. Lottery and neutral models best support the tropical rainforest data set. These models assume that resources made available by the deaths of individuals are captured at random by recruits from a larger pool of colonists such that no one species has an advantage, and that species diversity is maintained as a result.
4. Species diversity–community function relationships can differ depending on two variables: the degree of overlap in the ecological functions of species, and variation in the strength of ecological functions of species. Graph A is best described by the complementarity hypothesis, which proposes that as species richness increases, there will be a linear increase in community function. This linear relationship occurs because each species added to the community has a unique and equally incremental effect on community function. Graph B is best described by the redundancy hypothesis, in which there is an upper limit on the effect of species richness on community function. This curvilinear relationship occurs because the unique functional contributions of species reach a threshold due to their overlap. Graph C best describes the idiosyncratic hypothesis, which suggests that the strengths of the effects of species' functions vary dramatically. Dominant species have a large effect on community function such that when they are present, they increase community function, but when they are absent, it declines. This produces a variable species richness and community function pattern.

Answers to Hone Your Problem-Solving Skills Questions

1. The model best describes the intermediate disturbance hypothesis, which shows a unimodal relationship between species richness and disturbance, stress, or predation. At low levels of disturbance, species diversity is low because dominant species are free to exclude competitively inferior species. At high levels of disturbance, species diversity declines because many species may become locally extinct as mortality increases. At intermediate levels of disturbance, species diversity is maximized simply by the balance between competition and mortality.

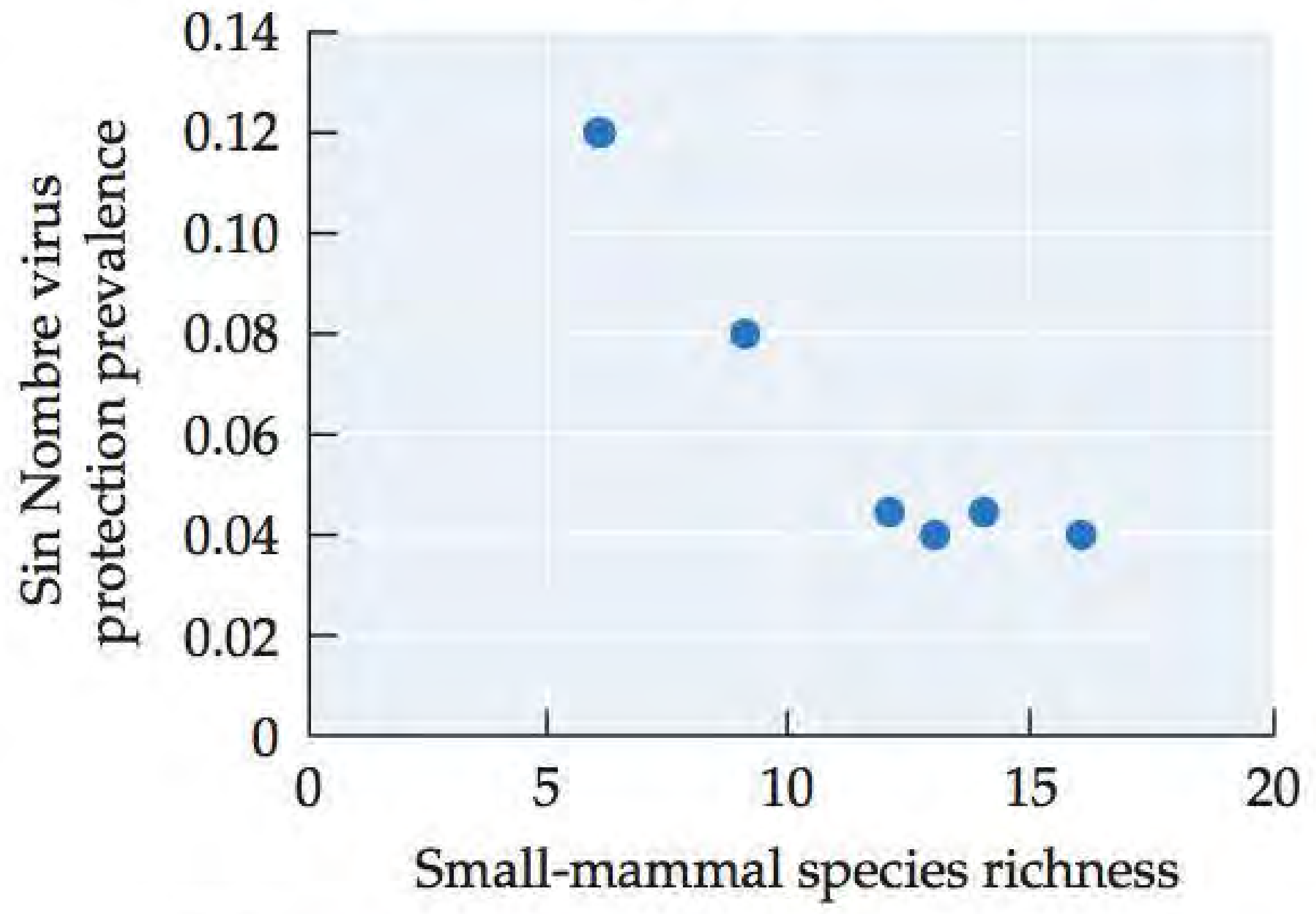


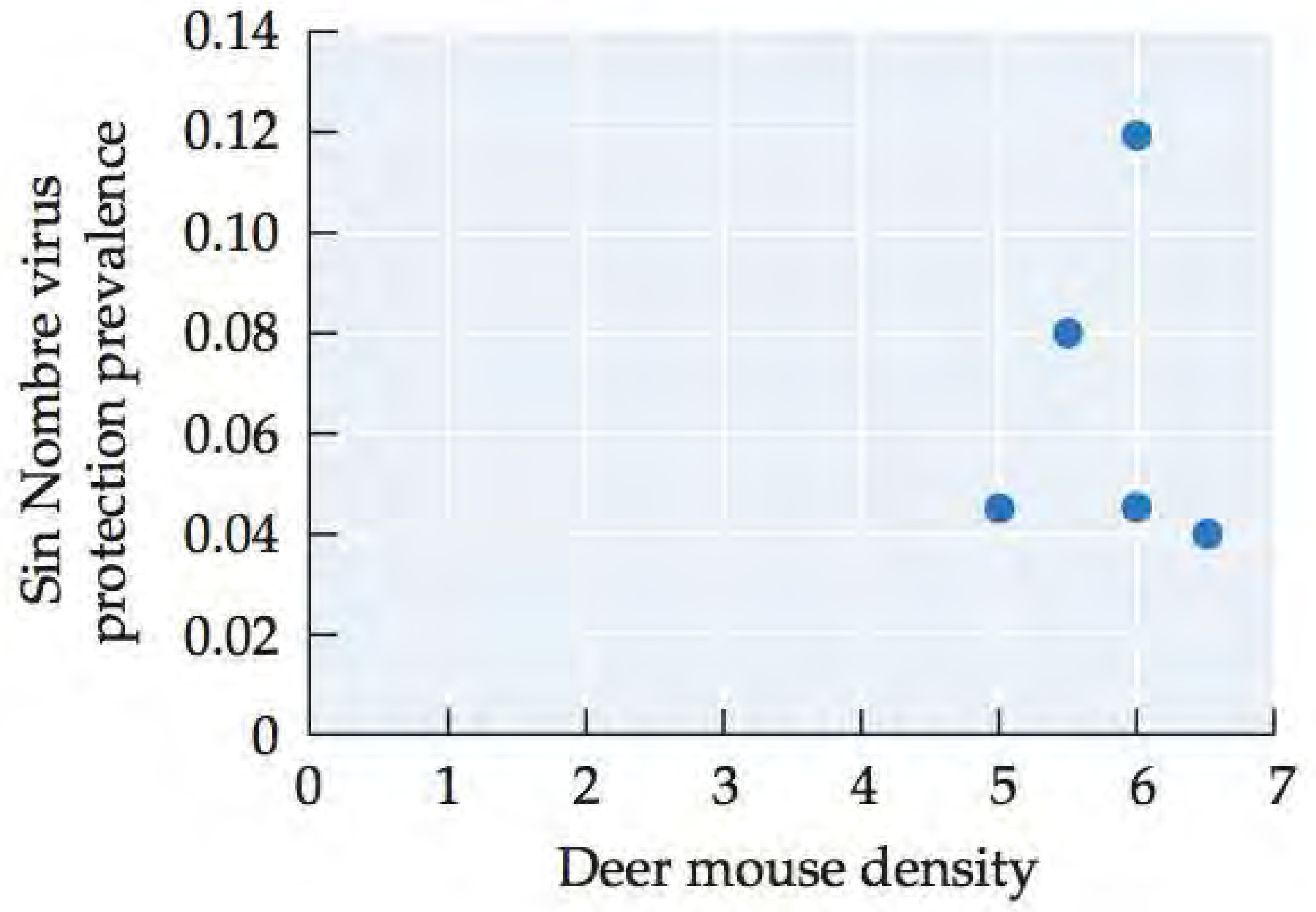
2. The graph shows that deer mouse density does not change with species richness. The data suggest that resource partitioning is not an important factor in the community. If the small-mammal species were partitioning resources, you would expect that where there is high species richness, there would also be lower densities of all species, including the deer mouse.



3. The graphs show that Sin Nombre virus infection prevalence in the deer mouse is positively related to small-mammal species richness loss. There is no clear relationship with deer mouse density. The results suggest that

when deer mouse hosts live in more species diverse communities, they are more likely to come into contact with individuals of other species than their own species (conspecifics), thus reducing the probability of transmission.





CHAPTER 20

Answers to Figure Legend Questions

Figure 20.5 Greater allocation of NPP to belowground tissues can be an adaptation to disturbances, such as fire, or to herbivory. Allocation of NPP to storage compounds allows more rapid recovery and higher survival rates following disturbance or loss of tissues to herbivory.

Figure 20.9 Cacti are CAM plants (see Chapter 5), which open their stomates and take up CO_2 during the night when air temperatures are cooler and humidities are higher. The daily pattern of atmospheric CO_2 concentrations would be reversed from what is shown for the boreal forest, with lower concentrations at night and higher concentrations during the day.

Figure 20.10 Estuaries also have high NPP due to the inputs of nutrients brought in by rivers. These nutrient subsidies include organic matter from both terrestrial and aquatic ecosystems as well as agricultural runoff.

Figure 20.13 The proportional allocation to belowground NPP would be greater in the more nutrient-poor community, the dry meadow. Greater allocation to roots enhances the uptake of the resources that most limit NPP, whereas light is more likely to be limiting in the more nutrient-rich wet meadow. Allocation to belowground NPP would decrease in response to fertilization.

Answers to Analyzing Data 20.1 Questions

1. Whether an ecosystem is a carbon sink (takes up more C than it releases) is determined by net ecosystem exchange (NEE). NEE is equal to NPP minus heterotrophic respiration. Prior to the beetle outbreak, NEE was equal to 440 g C/m^2/year – 408 g C/m^2/year = a net uptake (sink) of 32 g C/m^2/year.
2. Following the beetle outbreak, NEE was 400 g C/m^2/year – 424 g C/m^2/year = –24 g C/m^2/year, or a net source of 24 g C/m^2/year. As tree regrowth occurs during secondary succession, the forest will again revert to a net sink of C, so the trend will reverse over the next 100 years.
3. NEE is equal to GPP minus the total (autotrophic and heterotrophic) respiration. For the pasture, NEE is equal to 2,345 g C/m^2/year – 2,606 g C/m^2/year = –262 g C/m^2/year (net source), and for the second-growth forest, NEE is equal to 2,082 g C/m^2/year – 1,640 C/m^2/year = 442 C/m^2/year (net sink). Thus despite higher GPP in the pasture than in the second-growth forest, the higher respiratory losses in the pasture result in a net loss of C from the system.
4. Currently tropical rainforests account for around 3 Pg C/yr times 0.35 (35%) = 1.05 Pg C/yr. Converting half of the tropical rainforests to pasture would result in a decrease of NEE to 0.5 (–262 g C/m^2/year) + 0.5 (442 g C/m^2/year) = 90 g C/m^2/year. This is an 80% reduction in NEE by tropical rainforests, or a 28% reduction in C uptake by the terrestrial land surface. Note that this scenario is a gross oversimplification of what would actually happen, and does not take into account biotic and functional variation among tropical rainforests and pastures.

Answers to Review Questions

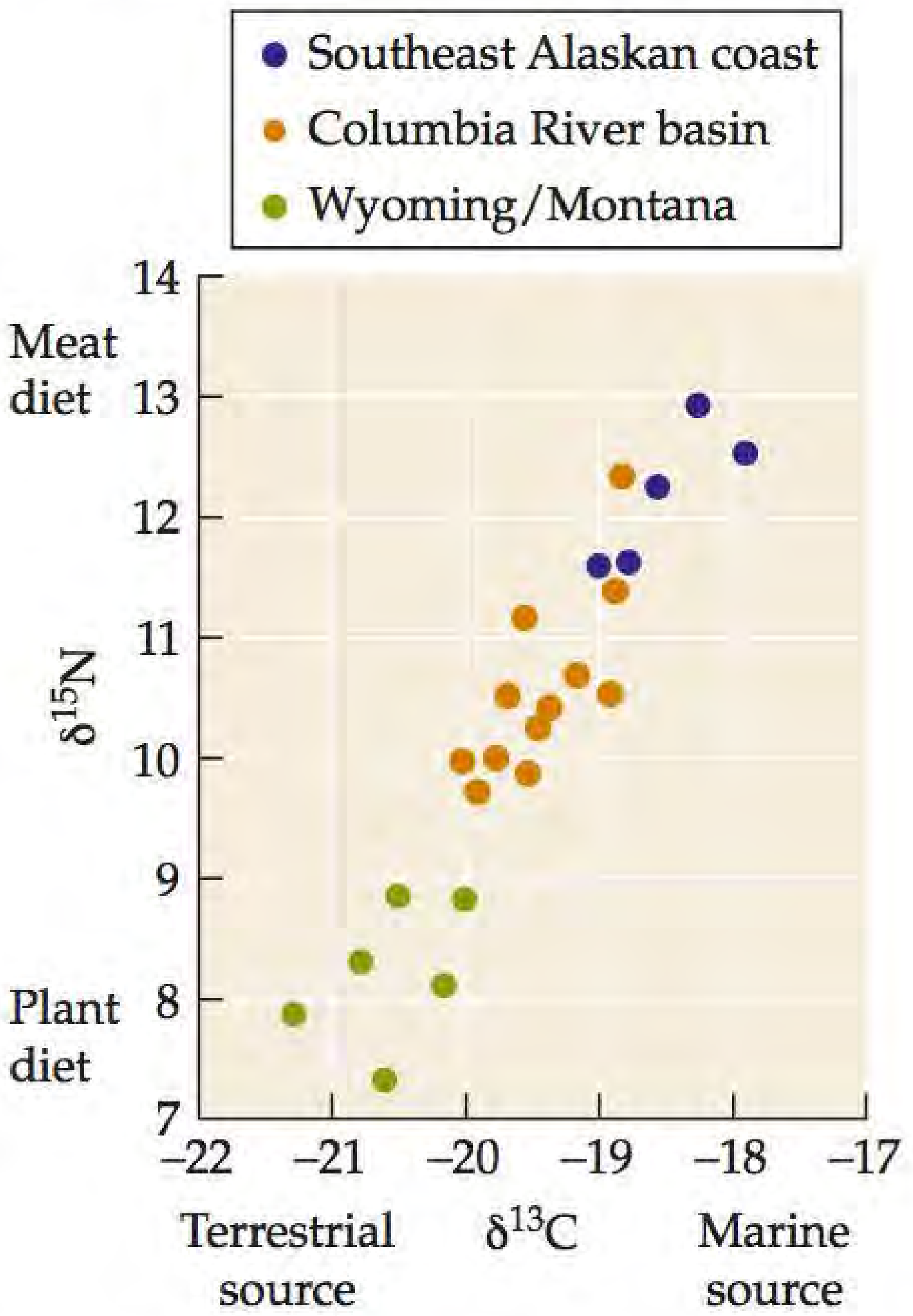
1. Primary production is the source of the energy entering an ecosystem, and it therefore determines the amount of energy available to support that ecosystem. Primary production also results in the exchange of carbon between the atmosphere and the biosphere and thus is important in determining the atmospheric concentration of CO_2, an important greenhouse gas. Finally, primary production is a measure of the functioning of an ecosystem and provides a biological indicator of the ecosystem's response to stress.
2. As NPP increased in a terrestrial ecosystem, the leaf area index would increase along with overall plant biomass. The amount of shading would increase as the leaf area index increased, and light would become increasingly limiting to growth. To compensate, plants would allocate more energy to stems and less to roots so as to increase their height and overtop neighbors in order to acquire more light.
3. The researchers found a correlation between NPP and soil temperature, and they assumed that the causal link was through the effect of soil temperature on root growth. While this assumption may be correct, the researchers failed to show the causal link conclusively, which would

require careful experimentation, or at least more thorough measurements of the effect of soil temperature on the factors that can influence plant growth. For example, soil temperature can affect the rate of decomposition of organic matter in the soil, and thus the availability of nutrients, which may influence growth rates.

4. a. Harvest techniques are simple and don't require high-tech equipment. However, harvesting can be labor-intensive, may fail to account for production that is lost to herbivores or decomposition, and is impractical at large scales.
   b. Remote sensing provides estimates of NPP at larger spatial scales and can be used at frequent intervals. However, remote sensing is expensive and requires handling of massive amounts of data. Because it is based on absorption of light by chlorophyll, remote sensing can potentially overestimate NPP if a plant canopy is physiologically inactive.

Answers to Hone Your Problem-Solving Skills Questions

1. Based on the isotopic composition of the bear tissues and of their food sources, grizzly bears living in inland areas consume less meat than coastal grizzlies, with a high proportion of their diet consisting of terrestrial plants. Grizzlies from along the coast of Southeast Alaska had the highest consumption of meat, derived primarily from marine sources, indicating fish makes up a large part of their diet. The population of grizzlies from the Columbia River drainage had an intermediate proportion of meat in their diet, with slightly less derived from marine sources.



2. a. If bears switched from a diet of primarily fish to plants, the composition of N isotopes in bone and hair samples would shift to less enriched in ^{15}N and a lower $\delta\ ^{15}N$ values. The composition of C would be less enriched in ^{13}C and a lower (more negative) $\delta\ ^{13}C$.
   b. If bears switched from consuming mostly fish to mostly terrestrial mammals the composition of C isotopes would be less enriched in ^{13}C and a lower $\delta\ ^{13}C$. N isotope composition would not change appreciably.

CHAPTER 21

Answers to Figure Legend Questions

Figure 21.7 Figure 21.6 shows that overall consumption efficiency in aquatic ecosystems is higher than in terrestrial ecosystems, as the line fitting the aquatic ecosystem data lies above the line fitting the terrestrial ecosystem data, indicating that a greater percentage of the NPP is being consumed.

Figure 21.10 Brown trout might preferentially feed on predators that are more effective in controlling insect herbivores than are the predators that galaxias feed on. As a result, the effect of the brown trout on algal abundance would be greater than the effect of the galaxias.

Figure 21.16 Eight of the 21 species or feeding groups (38%) eat both plants and animals, and most of the others eat at more than one trophic level, indicating that omnivory is very common in this desert food web.

Answers to Analyzing Data 21.1 Questions

1. Plants (100); non-insect invertebrate herbivores (100 × 0.209 = 20.9); small mammals (20.9 × 0.015 = 0.31); large mammals (0.31 × 0.031 = 0.01)
2. Algae (100); aquatic insect herbivores (100 × 0.209 = 20.9); insect predators (20.9 × 0.556 = 11.62); fish (11.62 × 0.098 = 1.14)
3. Plants (100); large mammal herbivores (100 × 0.031 = 3.1); large mammal predators (3.1 × 0.031 = 0.10); large mammal predators (0.10 × 0.031 = 0.003)
4. Plants (100); insect herbivores (100 × 0.388 = 38.8); insect predators (38.8 × 0.556 = 21.57); insect predators (21.57 × 0.556 = 11.99)
5. The trophic chains in numbers 2 and 4 have substantially greater energy available to support a fifth trophic level than do the other trophic chains, due to the higher production efficiencies of their component ectothermic consumers. In contrast, the trophic chains in numbers 1 and 3 include larger endotherms, with much lower production efficiencies, and it is unlikely that they could sustain a fifth trophic level.

Answers to Review Questions

1. Population B should have a higher assimilation efficiency due to the higher food quality of its diet. The garbage and plant component of population A's diet is higher in materials that are difficult to digest, and its C:N ratio is also lower than that of population A's rodent diet. Thus, the amount of food assimilated would be greater in population B.
2. The seasonal and diurnal temperature variations in these animals' environments are different and should result in different production efficiencies. The marine environment is more thermally stable, and thus the marine mammals

should need to invest less energy in coping with temperature changes than the mammals in the terrestrial ecosystem. As a result, the marine mammals should be able to invest more energy in growth and reproduction.

3. The forest would have a greater total amount of energy flowing through its trophic levels because a greater amount of energy would enter that ecosystem at the first trophic level. However, a larger proportion of the energy entering the lake ecosystem would pass through its higher trophic levels due to its higher consumption and production efficiencies.

Answers to Hone Your Problem-Solving Skills Questions

1. If only specialist herbivores were present, they would consume only a few or one species of plants. Furthermore, if the herbivores were chemically defended, their consumption by predators would be limited. Given a diverse plant community, we would expect a lower impact on herbivory and NPP with a trophic cascade involving specialist herbivores than if there were generalist herbivores. This prediction could be tested by varying the presence/absence, or the proportions, of specialist and generalist herbivores and the abundances of predators at the third or fourth trophic level. The response variables would include abundance of the herbivores and the amount of plant consumption.
2. a. The results support the hypothesis that a trophic cascade would influence herbivory and NPP less with specialist herbivores than with generalist herbivores. At a mix of about 25% specialist herbivores, there is little influence of a trophic cascade on herbivory in the deciduous forest ecosystem under study.

   b. This appears to be primarily due to lower consumption of herbivores rather than to less consumption of plants due to specialization.

CHAPTER 22

Answers to Figure Legend Questions

Figure 22.4 Primary production is low and plants are sparse in desert ecosystems, so the amount of soil organic matter should also be low. Wetting–drying events should enhance mechanical weathering of soils, producing a range of soil particle sizes. However, without a protective covering, winds may remove some of the finest particles, as we describe in the Case Study Revisited in Chapter 22. The low amount of precipitation and plant growth should limit the development and depth of distinct soil horizons.

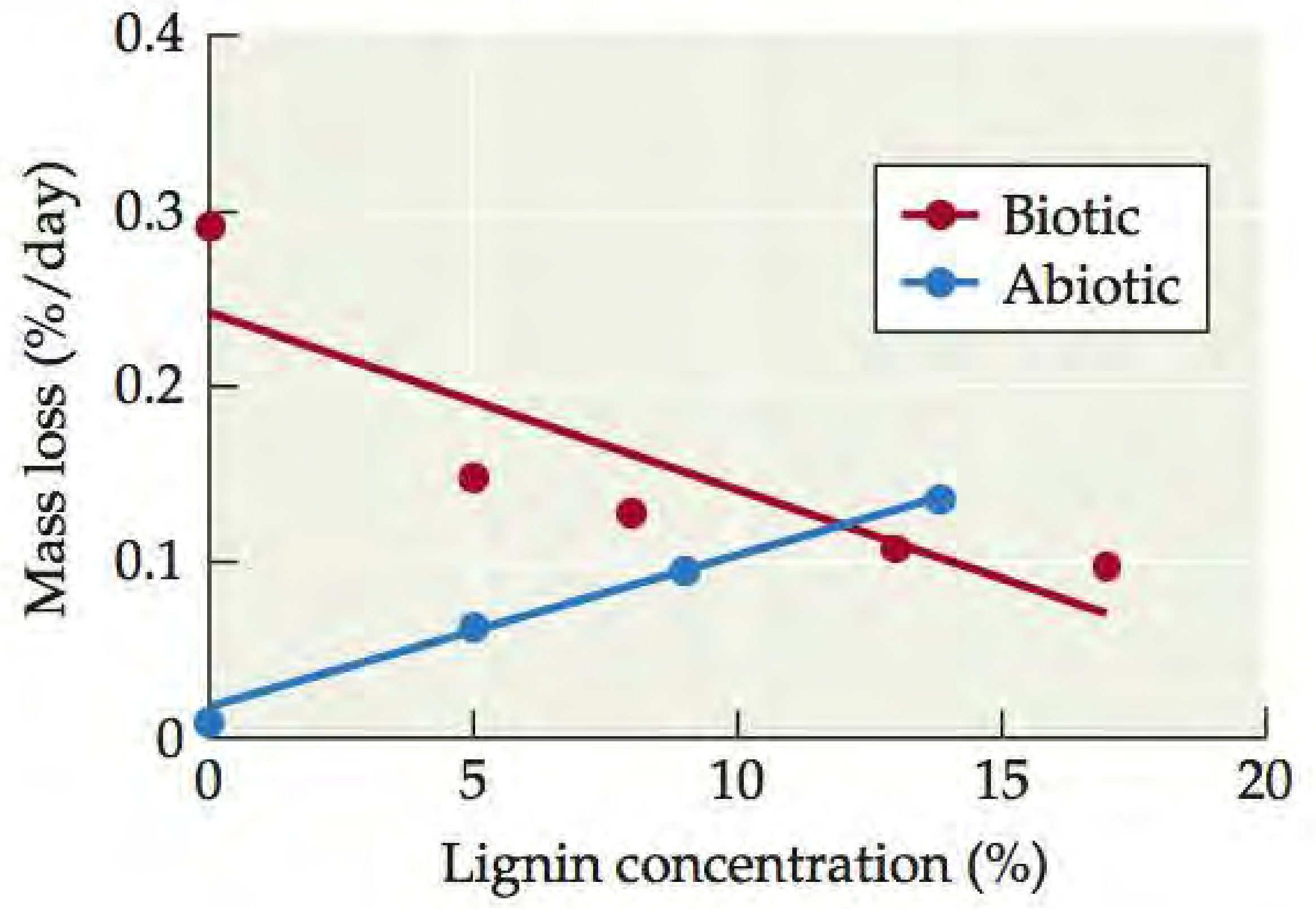
Figure 22.6 Pesticides applied to plants can wash into the organic surface layers of soils, where they can kill both herbivorous animals and soil detritivores. The loss of these animals would effectively lower the rate of decomposition and would thereby decrease soil fertility.

Figure 22.12 The simple input–output model depicted in the figure assumes that elements enter the ecosystem primarily through deposition and leave it in stream water. As noted in Figure 22.13, other modes of input and output occur, including inputs through N_2 fixation, outputs in groundwater, and gaseous losses (e.g., denitrification).

Figure 22.18 The study of eutrophication in Lake Washington is very convincing, but it lacks an appropriate control. Therefore, it is correlational; that is, it shows a quantitative link between depth of clarity and phosphorus inputs, but that link isn't necessarily causal. Appropriate controls might have included another lake that didn't have sewage inputs, or a lake that continued to have inputs of phosphorus-laden sewage during the time sewage inputs to Lake Washington were halted. (Experiments with appropriate controls have demonstrated beyond a doubt that inputs of phosphorus in sewage entering lakes do cause eutrophication.)

Answers to Analyzing Data 22.1 Questions

1.



2. The results indicate that when plant litter is exposed to light, tissues higher in lignin degrade faster than those with lower lignin concentrations. Thus the inhibitory influence of lignin on biological degradation may be at least partially offset by the stimulatory effect of photodegradation.
3. The assumption that lignin will lower decomposition rate would not be expected to hold true in environments in which the influence of photodegradation is greatest; dry, high light environments such as deserts, shrublands, grasslands, and some tundra ecosystems.

Answers to Review Questions

1. The transformation of minerals in rock involves both the physical breakdown (mechanical weathering) and chemical alteration (chemical weathering) of the minerals. Mechanical weathering occurs through expansion and contraction of solid materials due to freezing–thawing or drying–rewetting cycles, gravitational forces such as landslides, and pressure exerted by plant roots. Mechanical weathering exposes the surfaces of mineral particles to chemical weathering. Weathering is a soil-building process, leading to the development of ever finer mineral particles and greater release of the nutrients in the minerals. The release of CO_2 and organic acids into the soil from organisms and detritus enhances the rate of chemical weathering.

2. The original source of nitrogen for plants is dinitrogen gas (N_2) in the atmosphere, but they cannot use it unless it is converted to other forms by the process of nitrogen fixation. Only bacteria can carry out nitrogen fixation, which is an energetically expensive process. Some plants, such as legumes, have symbiotic relationships with nitrogen-fixing bacteria. As ecosystems develop, nitrogen builds up in the pool of detritus and is converted into soluble organic and inorganic forms through decomposition. Some of the nitrogen released by decomposition is consumed by microorganisms, lowering the supply available to plants.
3. While both primary production and decomposition influence the buildup of organic matter and associated nutrients in the soil, decomposition is more sensitive to climatic controls than is primary production. The mean residence time of nutrients is therefore more strongly controlled by decomposition. Low soil temperatures in boreal forests result in very long mean residence times. High rates of decomposition limit the buildup of soil organic matter in tropical forests, and the mean residence times of nutrients such as nitrogen and phosphorus are two orders of magnitude lower than those in boreal forests.
4. Nutrient transfers between trophic levels are efficient in both tropical and temperate-zone lakes, but organic matter is progressively lost from the surface layers in both systems, falling into the sediments in the benthic zone, where oxygen concentrations, and thus decomposition rates, are low. In the temperate zone, some of these nutrient-rich sediments are brought back to the surface layers during seasonal turnover of water, where they decompose, providing nutrients to support production. Turnover is largely absent in tropical lakes, which are therefore more dependent on external inputs of nutrients from streams and terrestrial ecosystems.

Answers to Hone Your Problem-Solving Skills Questions

1. NPP should increase following the disturbance, reaching a maximum somewhere during the intermediate stages of succession, and then decrease at late stages as the forest matures and consists of old-growth stands of trees. As a result, nutrient losses should be lowest during the intermediate stages of succession, highest just following the disturbance, and intermediate late in succession.
2. Nutrient losses should vary according to their importance to plant growth. Limiting nutrients, such as N, will be retained more with lower losses than nutrients that are not limiting growth. Elements that are not taken up by plants should be lost at the same rate throughout succession.
3. The results support Vitousek's hypothesis regarding the patterns of nutrient loss between intermediate and late stages of succession. For nutrient elements, losses are generally higher in late successional communities than in intermediate stage communities. In particular, N is retained much more than the other elements, suggesting it is probably the nutrient limiting growth of the plants. Elements such as Na and Cl, which have little or no importance to most plants, are lost at the same rates in intermediate and late stages of succession.

CHAPTER 23

Answers to Figure Legend Questions

Figure 23.2 The bar graphs indicate there were about 36 million ha in 1500, 8 million ha in 1935, and 1 million ha in 2004. The annual rate of loss appears to have been greater from 1935 to 2004 (7 million ha lost over 69 years, or approximately 100,000 ha lost per year) than from 1500 to 1935 (28 million ha lost over 435 years, or approximately 64,000 ha lost per year).

Figure 23.5 As discussed in Chapter 15, the seeds of many plant species are dispersed by animals that eat their fruit; hence the extinction of many frugivores may have reduced the ability of such plant species to disperse their seeds. Likewise, as also discussed in Chapter 15, many plants are pollinated by animals that visit flowers to collect nectar. Hence, the loss of nectarivores may have reduced the reproductive success of some plant species.

Figure 23.6 The "open flower" treatment is the control; results for this treatment indicate the percentage of flowers that currently can produce seeds on island and mainland sites. One experimental treatment was to bag flowers; results from this treatment show the percentage of flowers that produce seed in the absence of bird pollinators and all other means of pollination except self-pollination. A second experimental treatment was to hand-pollinate flowers; results from this treatment show the percentage of flowers that produce seeds when pollination is not limiting (as should be true when bird pollinators are abundant).

Figure 23.8 The difference between this statement and the results in the figure (which show that the introduction of non-native plant species can cause regional plant diversity to increase) is due to a difference in scale: When the introduction of non-native plant species causes the global extinction of one or more plant species, global plant diversity will decline even though regional plant diversity increases.

Figure 23.10 Habitat loss is the most important factor affecting terrestrial mammals; overharvesting is also an important threat to them. In contrast, accidental mortality and pollution are the most important threats affecting marine mammals.

Figure 23.12 Individual answers may vary but should include a line of reasoning similar to the following: Although there was year-to-year fluctuation in the cod harvest, overall the catch increased from roughly 100,000 tons caught in 1850 to roughly 300,000 tons caught in 1950. Because the harvest was maintained at these levels for 100 years, this suggests that at about 200,000 tons could have been caught in a sustainable manner.

Figure 23.15 Over the past decades (colored rectangles) habitat loss and pollution have been the primary causes of the loss of biodiversity from terrestrial, aquatic, and coastal habitats, while over-exploitation (hunting and harvesting) has been the largest factor influencing biodiversity in marine biological zones. Looking to the future (arrows) climate change and pollution are forecast to be the largest threats to all biological zones, with habitat loss continuing as a concern as well.

Answers to Analyzing Data 23.1 Questions

1. a. The sample size is $n = 4$ for plots with kudzu and for plots lacking kudzu.

   b. In plots with kudzu, $\bar{x}_1 = 3.68$ and $s_1 = 1.89$. In plots lacking kudzu, $\bar{x}_2 = 1.23$ and $s_2 = 0.53$.

   These results indicate that plots with kudzu have higher NO emissions than do plots lacking kudzu.

2.
$$T = \frac{3.68-1.23}{\sqrt{\frac{\left(1.89^2+0.53^2\right)}{4}}} = \frac{2.45}{\sqrt{\frac{3.853}{4}}} = 2.5$$

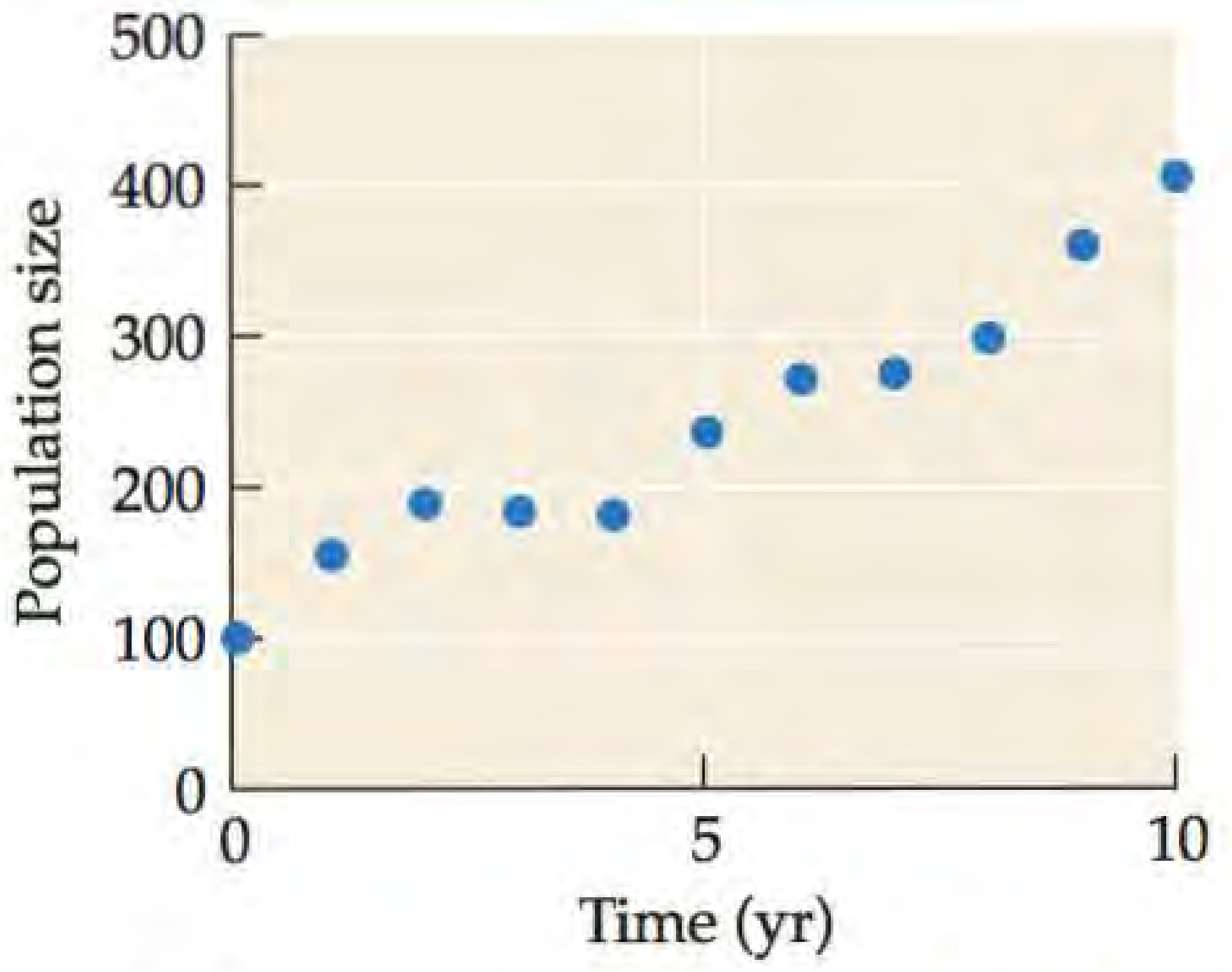
3. The degrees of freedom is df = 6, and the (two-tailed) p value of the test is $p = 0.047$. This result indicates that NO emissions in plots with kudzu differ significantly from NO emissions in plots lacking kudzu.

Answers to Review Questions

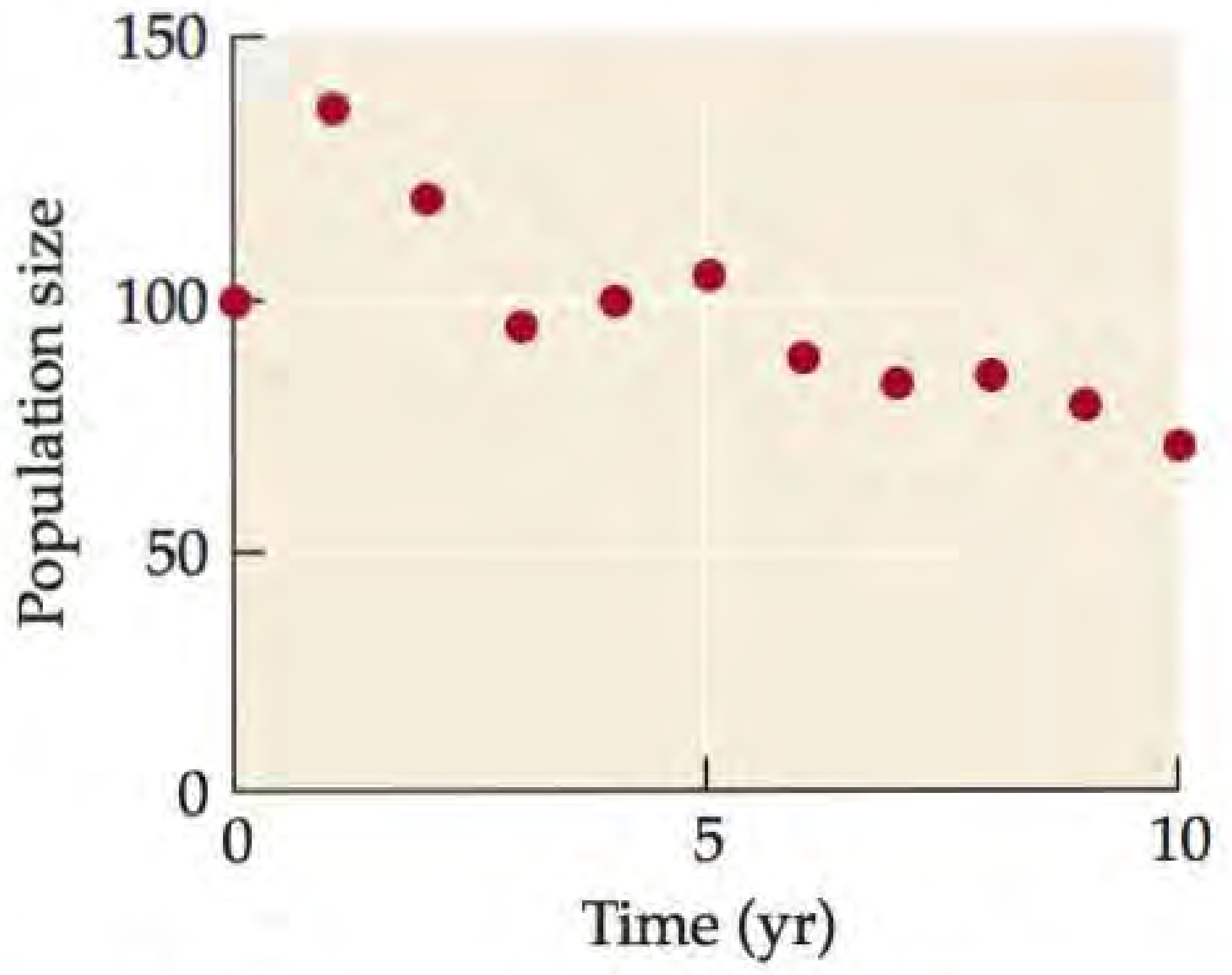
1. The principal threats to biodiversity are habitat loss, degradation, and fragmentation; the spread of invasive species; overharvesting; and climate change. For some species, disease poses a threat, and for others, particularly aquatic species, pollution is a particular threat. Many freshwater mussel species of North America are threatened both by pollution and by the invasion of the zebra mussel. The Pyrenean ibex was driven extinct by hunting, climate change, disease, and competition with domesticated species. Many other examples are possible.
2. DNA profiling (see Ecological Toolkit 23.1) and other genetic analyses are used to understand and manage genetic diversity in rare species; genetic approaches are also used in forensic studies of illegally harvested organisms. Conservation biologists use population viability analysis (PVA) models to assess extinction risk and evaluate options for managing rare species. Finally, ex-situ conservation can be used to rescue species on the brink of extinction, as illustrated by ongoing efforts to protect the California condor.
3. The classification system set up by Natural Heritage/NatureServe documents each species' conservation status from a biological perspective, while a listing under the U.S. Endangered Species Act is a legal designation. While federally endangered species would generally also be considered globally rare by Natural Heritage/NatureServe, the reverse does not necessarily hold true: many extremely rare or threatened species are not on the federal endangered species list. The Endangered Species Act (ESA) provides legal protection for listed species, and it requires the designation of critical habitat and the development and implementation of a recovery plan for those species. In contrast, Natural Heritage/NatureServe can only recommend the protection of species.
4. Answers to this question will depend on where students are located and what species they identify. The object of this question is to make students aware of species of conservation concern, threats to biodiversity, and efforts that are under way to protect species in their own region. It also invites them to identify research needs and to think about scientific approaches to conservation.

Answers to Hone Your Problem-Solving Skills Questions

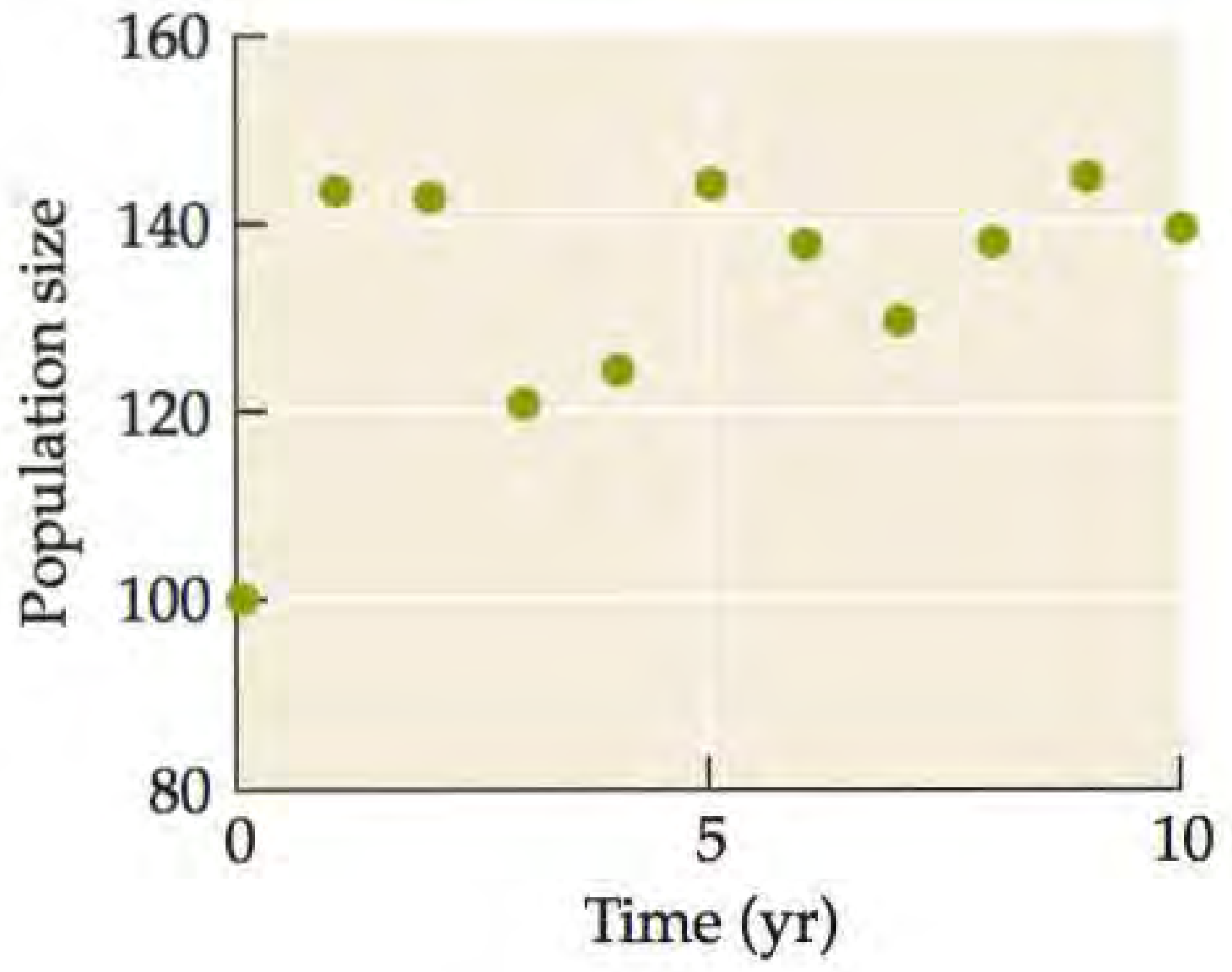
1.



2. At this level of harvesting the population would decline through time, and would not be sustainable.



3. At this level of harvest the population size remains the same, and is thus sustainable.



CHAPTER 24

Answers to Figure Legend Questions

Figure 24.3 Wet calcareous loam.

Figure 24.4 Organisms move more freely across the matrix in (B). We can infer this because exchange occurs between habitat patches separated by matrix in (B) whereas it does not occur in (A) (unless patches are connected to one another by a corridor).

Figure 24.6 It is identical to the grain in all three panels of part (B)—they each have a pixel size of 50 × 50 m.

Figure 24.17 *Reserve size*: A reserve that covers a small area typically harbors small populations—and small populations are at greater risk than larger ones from genetic factors (genetic drift and inbreeding), demographic stochasticity, environmental stochasticity, and natural catastrophes (see Chapter 11). In addition, a smaller proportion of the area is exposed to edge effects in a large reserve than in a small reserve; in a very small reserve, the entire area may be exposed to edge effects. *Number of reserves*: Although the total protected area is the same for both designs, in the design on the right each reserve is small in area and hence is likely to be at risk from problems associated with small populations. *Reserve proximity*: When several reserves are close to one another, individuals can move more freely between them. These movements help to prevent each reserve from experiencing problems associated with small population sizes. *Reserve connectivity*: Habitat corridors enable organisms to cross boundaries or landscape elements that otherwise might isolate each reserve from the other reserves (thereby exposing each reserve to problems associated with small population sizes). *Reserve shape*: When two reserves of equal area are compared, the reserve with a more compact shape (the best possible shape being a circle) will have proportionately less of its area exposed to edge effects.

Answers to Analyzing Data 24.1 Questions

1. The edge effect of increased wind disturbance penetrates 400 m into the forest; thus, for a tree not to experience increased wind disturbance it must be more than 400 m from the edge.
2. The total area of the forest is 800 m × 800 m = 640,000 m^2. Since we assume that the tree mortality effect penetrates 300 m on each side of the forest, the only region that does *not* experience a rise in tree mortality is a 200 m × 200 m section in the center of the forest. This central section has an area of 40,000 m^2. Thus, the area experiencing a rise in tree mortality is 640,000 m^2 – 40,000 m^2 = 600,000 m^2, or 93.75% of the forest's total area.
3. The edge effects shown in the graph include changes to the abiotic conditions (such as increased wind disturbance and increased air temperature) and changes to aspects of the biotic environment (such as invasion of disturbance-adapted beetles and plants). By changing both abiotic and biotic components of the environment, other aspects of the environment not shown in the graph are likely to change as well. We would expect, for example, that the changing abiotic conditions could cause the abundance of some species originally present to decline, while others might increase. As we have seen throughout the textbook, such changes in abundance could lead to further changes in species interactions, community structure, and ecosystem processes (such as nutrient cycling).

Answers to Review Questions

1. Habitat islands resemble actual islands in the way that they spatially isolate populations of some species from one another, with potential demographic and genetic consequences. They differ from islands, however, in that the matrix between habitat fragments may be more or less permeable to some species, so that movement between habitat fragments may be constrained, but may still occur with some frequency. As we saw in Chapter 18, the principles of island biogeography apply to habitat islands in that there is immigration to fragments, extinction within fragments, and some equilibrium level of species diversity. Larger habitat islands can sustain greater species diversity than smaller fragments.
2. In a sense, corridors are long, skinny habitat patches. Animals may nest in them, plants will germinate in them if conditions are right, and predation and competition occur in them. But they are likely to be biologically impoverished relative to larger habitat blocks because of the effects of their narrow dimensions on their abiotic and biotic properties. They are likely to resemble edge habitat in experiencing more light, more rapid biogeochemical cycling, and more predation than larger habitat blocks. They may be more vulnerable to invasive species, and they may permit movement of diseases between habitat blocks. Nevertheless, they are generally beneficial, at least for some species, in allowing movement of organisms across a fragmented landscape.
3. National forests and national parks have different management objectives. The difference in the resulting land uses is visible from space, in the form of a clear line separating clear-cut patches of the Targhee National Forest from the uncut forests of Yellowstone National Park. National forests permit the harvesting of timber, which is generally not permitted in national parks. Timber harvesting makes for a patchy forest of different-aged stands, which may support a different group of species than is found in a national park, and may favor early successional species over old-growth-associated species. While both national parks and national forests have a mandate to protect biodiversity, national parks must balance these aims with recreation and visitor needs, while national forests must include timber production needs in their mission as well. Under an ecosystem management approach, the emphasis would be regional, and so the national forest and national park administrations would be working together to achieve conservation goals set by consensus.

Answers to Hone Your Problem-Solving Skills Questions

1. Species A is relatively insensitive to shape until the ratio of perimeter to area is very high, and therefore species A may be found in both reserve designs. In contrast, species B is more sensitive to a large amount of edge, so it has a higher probability of occurrence in patches with lower perimeter to area ratio, and thus design 1 would be best. Species C does best with intermediate perimeter to area ratio and thus would do better with design 2, which has more edge than design 1.
2. Greater food availability at the edges, such as the occurrence and abundance of food plants or prey that thrive in edge environments, would enhance the occurrence of a species there, while lower food availability would have the opposite effect. Lower diversity of species in patches with extensive edges may decrease food availability. Edges may enhance detection of predators or prey and also provide greater habitat for escape of predation. The physical environment at edges may be more extreme than at the core habitat in the patches, excluding some species. Some species may need extensive core habitat to protect and rear their young and so avoid patches with large amounts of edge.

CHAPTER 25

Answers to Figure Legend Questions

Figure 25.3 Deforestation would immediately lower the flux of carbon from the atmosphere to the land surface due to photosynthesis, but would increase the flux from the land surface to the atmosphere due to respiration. In other words, the deforested land would change from a sink to a source of atmospheric CO_2. Cutting the trees removes the most important autotrophs in the system. It also supplies carbon (from roots and woody debris) to soil heterotrophs and warms up the soil, both of which increase respiratory C emissions to the atmosphere.

Figure 25.7 Reactive N is chemically and biologically active, as the name infers. As a result, the pool of reactive N is a potential source of nutrients for organisms. In addition, it can influence soil chemistry and the health of organisms, as we will see later in the chapter. N_2, on the other hand, is chemically inert and must be converted to other chemical forms by nitrogen fixation to be used by organisms.

Figure 25.14 In Chapters 3, 16, and 17 we discussed several factors that determine the makeup of vegetation assemblages. These factors include physiological tolerances, biotic interactions such as competition and herbivory, and dispersal ability. Following deglaciation, combinations of temperature and precipitation different from any found today occurred in parts of North America, which resulted in unique combinations of plants relative to those that occur today. In addition, by differentially consuming specific plant species, particular species of herbivores can have an effect on vegetation types. As noted in the Case Study in Chapter 3, the animals that occurred at this time were quite different from those found today, including sloths, mastodons, and camels. Finally, the rates at which different species dispersed into the newly exposed substrate would have influenced the composition of the vegetation.

Answers to Analyzing Data 25.1 Questions

1. There is around a 0.05 drop in pH over the two-decade period of observation. Thus between 2000 (pH = 8.10) and 2100, the pH should drop about 0.25 units (10 decades × 0.025 pH units/decade), for an estimated ocean pH of 7.85. The IPCC estimate is lower, due in part to the assumption of a continued increase in the rate of anthropogenic CO_2 emissions from fossil fuels.
2. Both the IPCC and empirically derived estimates for ocean pH in 2050 and 2100 are around 7.9 and 7.75, respectively. The results in Figure B indicate around a 90% decrease in abundance and a 75% decrease in species richness by 2050, and extinction of foraminiferans by 2100.

Answers to Review Questions

1. The two major biological influences on the global carbon cycle are photosynthesis, which takes up CO_2 from the atmosphere, and respiration, which releases CO_2 back to the atmosphere. Prior to the Industrial Revolution, uptake by photosynthesis and release by respiration were roughly equal at a global scale, and thus there was no net flux associated with Earth's biota. However, increasing human population growth rates resulted in increasing deforestation and agricultural development, which in turn resulted in greater decomposition and heterotrophic respiration due to warming of the soil surface. As a result, atmospheric CO_2 concentrations increased. Deforestation was the primary reason for increasing atmospheric CO_2 concentrations until the early part of the twentieth century.
2. While animals can respond to climate change by moving, their habitats cannot. Animals are dependent on plants to provide their food (or food for their prey). Climate change will be so rapid that evolutionary responses will not be possible for most species of plants, and the dispersal rates of most plant species are too slow to track the predicted climate changes. Dispersal may be inhibited by fragmentation of dispersal corridors due to land-use change. Loss of habitat will therefore result in decreased population growth for some animals. Additionally, migrating animals may respond to climate change more slowly than nonmigratory species. As a result, prey species may be less abundant or absent when these animals arrive at their destination.
3. The effect of atmospheric ozone on organisms depends on where in the atmosphere it is found. Ozone in the stratosphere acts as a shield against high-energy ultraviolet-B radiation, which is harmful to organisms. In contrast, ozone in the troposphere damages organisms that come in direct contact with it. Ozone in the troposphere also acts as a greenhouse gas, contributing to global climate change.

Answers to Hone Your Problem-Solving Skills Questions

1. 15 kg N/ha/yr for 20 years = 300 kg N/ha. Spread over 13,000,000 km^2 (1.3×10^9 ha), this is 3.9×10^{11} kg N. If 10% of this is taken up, then there is 3.9×10^{10} kg N incorporated into plant biomass. With a 500:1 ratio of C:N, that would be 7.8×10^7 kg C or 7.8×10^{10} g C.
2. 5 kg N/ha/yr for 20 years = 100 kg N/ha. Spread over 19,000,000 km^2 (1.9×10^9 ha), this is 1.9×10^{11} kg N. If 10% of this is taken up, then there is 1.9×10^{10} kg N incorporated into plant biomass. With a 500:1 ratio of C:N, that would be 3.8×10^7 kg C or 3.8×10^{10} g C.
3. On an annual basis, the greater C uptake would equal (7.8×10^{10} g C + 3.8×10^{10} g C)/ 20 years is equal to 5.8×10^9 g C/yr. Annually anthropogenic emssions are 10.4 Pg C, or 1.04×10^{16} g C, so the increased sequestration due to N deposition would be only a 0.00006 % increase in C uptake.

Glossary

Numbers in brackets refer to the chapter(s) where the term is introduced.

A

abiotic Of or referring to the physical or nonliving environment. *Compare* biotic. [1]

absolute population size The actual number of individuals in a population. *Compare* relative population size. [9]

abundance The number of individuals of a species that are found in a given area; abundance is often measured by population size or population density. [9]

acclimatization An organism's adjustment of its physiology, morphology, or behavior to lessen the effect of an environmental change and minimize the associated stress. [4]

acid neutralizing capacity The ability of the chemical environment to counteract acidity, usually associated with concentrations of base cations, including Ca^{2+}, Mg^{2+}, and K^+. [25]

acidity A measure of the ability of a solution to behave as an acid, a compound that releases protons (H^+) to the water in which it is dissolved. *Compare* alkalinity. [2]

adaptation (1) A physiological, morphological, or behavioral trait with an underlying genetic basis that enhances the survival and reproduction of its bearers in their environment. (2) *See* adaptive evolution. [1, 4]

adaptive evolution A process of evolutionary change in which traits that confer survival or reproductive advantages tend to increase in frequency in a population over time. [6, 8]

adaptive management A component of ecosystem management in which management actions are seen as experiments and future management decisions are determined by the outcome of present decisions. [24]

adaptive radiation An event in which a group of organisms gives rise to many new species that expand into new habitats or new ecological roles in a relatively short time. [6]

aerosols Solid or liquid particles suspended in the atmosphere. [22]

age structure The proportions of a population in each age class. [10]

albedo The amount of solar radiation reflected by a surface, usually expressed as a percentage of the incoming solar radiation. [2]

alkalinity A measure of the ability of a solution to behave as a base, a compound that takes up protons (H^+) or releases hydroxide ions (OH^-). *Compare* acidity. [2]

Allee effect A decrease in the population growth rate (r or λ) as the population density decreases. [11]

allele One of two or more forms of a gene that result in the production of different versions of the protein that the gene encodes. [6]

allelopathy A mechanism of competition in which individuals of one species release chemicals that harm individuals of other species. [14]

allocation The relative amounts of energy or resources that an organism devotes to different functions. [7]

allochthonous Produced outside the ecosystem. *Compare* autochthonous. [21]

alpha diversity Species diversity at the local or community scale. *Compare* beta diversity, gamma diversity. [18]

alternation of generations A complex life cycle, found in many algae and all plants, in which there is both a multicellular diploid form, the sporophyte, and a multicellular haploid form, the gametophyte. [7]

alternative stable states Different community development scenarios, or community states, that are possible at the same location under similar environmental conditions. [17]

amensalism A species interaction in which individuals of one species are harmed while individuals of the other species do not benefit and are not harmed (–/0 relationship). [14]

anisogamy Production of two types of gametes of different sizes. *Compare* isogamy. [7]

anthropogenic Of, relating to, or caused by humans or their activities. [25]

aposematic coloration *See* warning coloration.

arbuscular mycorrhizae Mycorrhizae in which the fungal partner grows into the soil, extending some distance away from the plant root, and also grows between some root cells while penetrating others. *Compare* ectomycorrhizae. [15]

Arctic ozone dent An area of the stratosphere over the Arctic region where ozone concentrations are low, but have not dropped below 220 Dobson units. [25]

assimilation efficiency The proportion of ingested food that is assimilated by an organism. [21]

atmospheric deposition The movement of particulate and dissolved matter from the atmosphere to Earth's surface by gravity or in precipitation. [22]

atmospheric pressure The pressure exerted on a surface due to the mass of the atmosphere above it. [2]

autochthonous Produced within the ecosystem. *Compare* allochthonous. [21]

autochthonous energy Energy produced within the ecosystem. [2]

autotroph An organism that converts energy from sunlight or from inorganic chemical compounds in the environment into chemical energy stored in the carbon–carbon bonds of organic compounds. *Compare* heterotroph. [5]

avoidance A response to stressful environmental conditions that lessens their effect through some behavior or physiological activity that minimizes an organism's exposure to the stress. *Compare* tolerance. [4]

B

behavioral ecology The study of the ecological and evolutionary basis of animal behavior. [8]

benthic zone The bottom of a body of water, including the surface and shallow subsurface layers of sediment. [3]

beta diversity The change in species diversity and composition, or turnover of species, from one community type to another across the landscape. *Compare* alpha diversity, gamma diversity. [18]

bioaccumulation A progressive increase in the concentration of a substance in an organism's body over its lifetime. [21]

biodiversity The diversity of important ecological entities that span multiple spatial scales, from genes to species to communities. [16, 23]

biogeochemistry The study of the physical, chemical, and biological factors that influence the movements and transformations of chemical elements. [22]

biogeographic region A portion of Earth containing a distinct biota that differs markedly from the biotas of other biogeographic regions in its species composition and diversity. [18]

biogeography The study of variation in species composition and diversity among geographic locations. [18]

biological reserve An often small nature reserve established with the conservation of a single species or ecological community as the main conservation objective. [24]

biological soil crust A crust on the soil surface composed of a mix of species of cyanobacteria, lichens, and mosses; also called a biocrust. [22]

biomagnification A progressive increase in the tissue concentrations of a substance in animals at successively higher trophic levels that results as animals at each trophic level consume prey with higher concentrations of the substance due to bioaccumulation. [21]

biomass The mass of living organisms, usually expressed per unit of area. [20]

biome A large-scale terrestrial biological community shaped by the regional climate, soil, and disturbance patterns where it is found, usually classified by the growth form of the dominant plants. [3]

biosphere The highest level of biological organization, consisting of all living organisms on Earth plus the environments in which they live; located between the lithosphere and the troposphere. [1, 3]

biotic Of or referring to the living components of an environment. *Compare* abiotic. [1]

biotic resistance Interactions of the native species in a community with non-native species that exclude or slow the growth of those non-native species. [19]

bottom-up control Limitation of the abundance of a population by nutrient supply or by the availability of food. *Compare* top-down control. [11]

boundary layer A zone close to a surface where a flow of fluid, usually air, encounters resistance and becomes turbulent. [4]

buffer zone A portion of a nature reserve surrounding a core natural area where controls on land use are less stringent than in the core natural area, yet land uses are at least partially compatible with many species' resource requirements. *Compare* core natural area. [24]

C

C_3 photosynthetic pathway A biochemical pathway involving the uptake of CO_2 by the enzyme ribulose 1,5 bisphosphate carboxylase/oxygenase (rubisco) and synthesis of sugars by the Calvin cycle. *Compare* C_4 photosynthetic pathway, crassulacean acid metabolism. [5]

C_4 photosynthetic pathway A biochemical pathway involving the daytime uptake of CO_2 by the enzyme phosphoenol pyruvate carboxylase (PEPcase) in mesophyll cells; the carbon is then transferred as a four-carbon acid to the bundle sheath cells, where CO_2 is released to the Calvin cycle for sugar synthesis. *Compare* C_3 photosynthetic pathway, crassulacean acid metabolism. [5]

Calvin cycle The biochemical pathway used by photosynthetic and chemosynthetic organisms to fix carbon and synthesize sugars. [5]

carnivore An animal predator that kills and consumes tissues or fluids of live animals. [12, 20]

carnivory A trophic species interaction in which the predator is an animal (carnivore) and the prey is an animal. [12]

carrying capacity The maximum population size that can be supported indefinitely by the environment, represented by the term *K* in the logistic equation. [10]

catchment The area in a terrestrial ecosystem that is drained by a single stream; a common unit of study in terrestrial ecosystem studies; also called a watershed. [22]

cation exchange capacity A soil's ability to hold nutrient cations such as Ca^{2+}, K^+, and Mg^{2+} and exchange them with the soil solution, determined by the clay content of the soil. [22]

character displacement A process in which competition causes the phenotypes of competing species to evolve to become more different over time, thereby easing competition. [14]

cheater In a mutualism, an individual that increases its production of offspring by overexploiting its mutualistic partner. [15]

chemical weathering The chemical breakdown of soil minerals leading to the release of soluble forms of nutrients and other elements. *Compare* mechanical weathering. [22]

chemolithotrophy *See* chemosynthesis.

chemosynthesis The use of energy from inorganic chemical compounds to fix CO_2 and produce carbohydrates using the Calvin cycle; also called chemolithotrophy. [5]

clay Fine soil particles (<2 μm) that have a semicrystalline structure and weak negative charges on their surfaces that can hold onto cations and exchange them with the soil solution. [22]

climate The long-term description of weather, based on averages and variation measured over decades. *Compare* weather. [2]

climate change Directional change in climate over a period of three decades or longer. [1, 25]

climate envelope The range of climate variables, including temperature, humidity, precipitation, and solar radiation, that are associated with a species geographic distribution. [4]

climax stage The last stage of succession that is thought to be stable until disturbances or stresses shift the community back to earlier successional stages. [17]

cline A pattern of gradual change in a characteristic of an organism over a geographic region. [6]

clone A genetically identical copy of an individual. [9]

clumped dispersion A dispersion pattern in which individuals are grouped together. *Compare* random dispersion, regular dispersion. [9]

coevolution The evolution of two interacting species, each in response to selection pressure imposed by the other. [13]

cohort life table A life table in which the fate of a group of individuals born during the same time period (a cohort) is followed from birth to death. [10]

commensalism A species interaction in which individuals of one species benefit while individuals of the other species do not benefit and are not harmed (+/0 relationship). [15]

community A group of interacting species that occur together at the same place and time. [1, 16]

community function The set of processes that shape community structure, including primary production, atmospheric gas exchange, or resistance to disturbance. [19]

community stability *See* stability.

community structure The set of characteristics that shape a community, including the number, composition, and abundance of species. [16]

compensation An adaptive growth response of plants to herbivory in which removal of plant tissues stimulates the plant to produce new tissues. [12]

competition A non-trophic interaction in which individuals of the same species (intraspecific) or different species (interspecific) are harmed by their shared use of a resource that limits their ability to grow, reproduce, or survive (–/– relationship). [14]

competition coefficient A constant used in the Lotka–Volterra competition model to describe the extent to which an individual of one competing species decreases the per capita growth rate of the other species. [14]

competitive coexistence The ability of two or more species to coexist with one another despite competing for the same limiting resources. [14]

competitive displacement A process in which the best competitor uses limiting resources that the weaker competitor requires ultimately causing a decline in the weaker competitor's population growth to the point of extinction. [19]

competitive exclusion *See* competitive displacement and competitive exclusion principle.

competitive exclusion principle The principle that two species that use a limiting resource in the same way cannot coexist indefinitely. [14]

competitive networks Sets of competitive interactions involving multiple species in which every species negatively interacts with every other species, thus promoting species coexistence. [16]

competitive plants In Grime's triangular model, plants that are superior competitors under conditions of low stress and low disturbance. *Compare* ruderals, stress-tolerant plants. [7]

complementarity hypothesis A hypothesis proposing that as the species richness of a community increases, there is a linear increase in the positive effects of those species on community function. *Compare* idiosyncratic hypothesis and redundancy hypothesis. [19]

complex life cycle A life cycle in which there are at least two distinct stages that differ in their habitat, physiology, or morphology. [7]

conduction The transfer of sensible heat through the exchange of kinetic energy between molecules due to a temperature gradient. *Compare* convection. [2]

conservation biology The scientific study of phenomena that affect the maintenance, loss, and restoration of biodiversity. [23]

consumer An organism that obtains its energy by eating other organisms or their remains. *Compare* producer. [1]

consumption efficiency The proportion of the biomass available at one trophic level that is ingested by consumers at the next trophic level. [21]

continental climate The climate typical of terrestrial areas in the middle of large continental land masses at high latitudes, characterized by high variation in seasonal temperatures. *Compare* maritime climate. [2]

continental drift The slow movement of tectonic plates (sections of Earth's crust) across Earth's surface. [18]

controlled experiment A standard scientific approach in which an experimental group (that has the factor being tested) is compared with a control group (that lacks the factor being tested). [1]

convection The transfer of sensible heat through the exchange of air and water molecules as they move from one area to another. *Compare* conduction. [2]

convergence The evolution of similar growth forms among distantly related species in response to similar selection pressures. [3]

core natural area A portion of a nature reserve where the conservation of biodiversity and ecological integrity takes precedence over other values or uses. *Compare* buffer zone. [24]

Coriolis effect The apparent deflection of air or water currents when viewed from a rotating reference point such as Earth's surface. [2]

crassulacean acid metabolism (CAM) A photosynthetic pathway in which CO$_2$ is fixed and stored as an organic acid at night, then released to the Calvin cycle during the day. *Compare* C$_3$ photosynthetic pathway, C$_4$ photosynthetic pathway. [5]

crypsis A defense against predators in which prey species have a shape or coloration that provides camouflage and allows them to avoid detection. [12]

D

damped oscillations A pattern of population fluctuations in which the extent to which the population rises and falls in abundance gradually become smaller over time. [11]

decomposition The physical and chemical breakdown of detritus by detritivores, leading to the release of nutrients as simple, soluble organic and inorganic compounds that can be taken up by other organisms. [22]

delayed density dependence Delays in the effect of population density on population size that can contribute to population fluctuations. [11]

demographic stochasticity Chance events associated with whether individuals survive or reproduce. [11]

denitrification A process by which certain bacteria convert nitrate (NO$_3^-$) into nitrogen gas (N$_2$) and nitrous oxide (N$_2$O) under hypoxic conditions. [22]

density-dependent Of or referring to a factor that causes birth rates, death rates, or dispersal rates to change as the density of a population changes. *Compare* density-independent. [10]

density-independent Of or referring to a factor whose effects on birth and death rates are independent of population density. *Compare* density-dependent. [10]

desertification Degradation of formerly productive land in arid regions resulting in loss of plant cover and acceleration of soil erosion. [3, 24]

detritivore A heterotroph that consumes detritus. [20]

detritus Freshly dead or partially decomposed remains of organisms. [3, 5]

dilution effect A phenomenon in which the chance that any particular member of a group is the one attacked (as by a predator) decreases as the number of individuals in the group increases. [8]

direct development A simple life cycle that goes directly from fertilized egg to juvenile without passing through a free-living larval stage. [7]

direct interaction An interaction that occurs between two species, such as predation, competition, or a positive interaction. *Compare* indirect interaction. [16]

directional selection Selection that favors individuals with one extreme of a heritable phenotypic trait. *Compare* disruptive selection, stabilizing selection. [6]

dispersal The movement of organisms or propagules from their birthplace. [7]

dispersal limitation A situation in which a species' limited capacity for dispersal prevents it from reaching areas of suitable habitat. [9]

dispersion The spatial arrangement of individuals within a population. [9]

disruptive selection Selection that favors individuals with a phenotype at either extreme over those with an intermediate phenotype. *Compare* directional selection, stabilizing selection. [6]

distribution The geographic area where individuals of a species are present. [9]

disturbance An abiotic event that kills or damages some individuals and thereby creates opportunities for other individuals to grow and reproduce. [9, 17]

dormancy A state in which little or no metabolic activity occurs. [4]

doubling time (t_d) The number of years it takes a population to double in size. [10]

dynamic equilibrium model An elaboration of the intermediate disturbance hypothesis proposing that species diversity is maximized when the level of disturbance and the rate of competitive displacement are roughly equivalent. [19]

E

ecological footprint The total area of productive ecosystems required to support a population. [10]

ecological niche The abiotic and biotic conditions that a species needs to grow, survive, and reproduce. [9]

ecology The scientific study of interactions between organisms and their environment. [1]

ecosystem All the organisms in a given area as well as the physical environment in which they live; an ecosystem can include one or more communities. [1, 20]

ecosystem engineer A species that influences its community by creating, modifying, or maintaining physical habitat for itself and other species. [16]

ecosystem management An approach to habitat management in which scientifically based policies and practices guide decisions on how best to meet an overarching goal of sustaining ecosystem structure and function for long periods. [24]

ecosystem services Natural processes that sustain human life and which depend on the functional integrity of natural communities and ecosystems. [18, 23]

ecotype A population with adaptations to unique local environmental conditions. [4]

ectomycorrhizae Mycorrhizae in which the fungal partner typically grows between plant root cells and forms a mantle around the exterior of the root. *Compare* arbuscular mycorrhizae. [15]

ectoparasite A parasite that lives on the surface of another organism. *Compare* endoparasite. [13]

ectotherm An animal that regulates its body temperature primarily through energy exchange with its external environment. *Compare* endotherm. [4]

edge effects Abiotic and biotic changes that are associated with an abrupt habitat boundary such as that created by habitat fragmentation. [18, 24]

El Niño Southern Oscillation (ENSO) An oscillation of pressure cells and sea surface temperatures in the equatorial Pacific Ocean that causes widespread climatic variation and changes in upwelling currents. [2]

endemic Occurring in a particular geographic location and nowhere else on Earth. [18]

endoparasite A parasite that lives inside the body of its host organism. *Compare* ectoparasite. [13]

endotherm An animal that regulates its body temperature primarily through internal metabolic heat generation. *Compare* ectotherm. [4]

environmental science An interdisciplinary field of study that incorporates concepts from the natural sciences (including ecology) and the social sciences (e.g., politics, economics, ethics), focused on how people affect the environment and how we can address environmental problems. [1]

environmental stochasticity Erratic or unpredictable changes in the environment. [11]

epilimnion The warm surface layer of water in a lake, lying above the thermocline, that forms during the summer in some lakes of temperate and polar regions. *Compare* hypolimnion. [2]

equilibrium theory of island biogeography A theory proposing that the number of species on an island or in an island-like habitat results from a dynamic balance between immigration rates and extinction rates. [18]

eutrophic Nutrient-rich; characterized by high primary productivity. *Compare* oligotrophic, mesotrophic. [22]

eutrophication A change in the nutrient status of an ecosystem from nutrient-poor to nutrient-rich; such changes occur naturally in some lakes due to the accumulation of sediments, but they may also be caused by nutrient inputs that result from human activities. [11, 22]

evapotranspiration The sum of water loss through evaporation and transpiration. [2]

evolution (1) Change in allele frequencies in a population over time. (2) Descent with modification; the process by which organisms gradually accumulate differences from their ancestors. [1, 6]

evolutionary tree A branching diagram that represents the evolutionary history of a group of organisms. [6]

exploitation competition An interaction in which species compete indirectly through their mutual effects on the availability of a shared resource. *Compare* interference competition. [14]

exponential growth Change in the size of a population of a species with continuous reproduction by a constant proportion at each instant in time. *Compare* geometric growth. [10]

exponential growth rate (r) A constant proportion by which a population of a species with continuous reproduction changes in size at each instant in time; also called the intrinsic rate of increase. *Compare* geometric population growth rate. [10]

extent In landscape ecology, the area or time period encompassed by a study; together with grain, extent characterizes the scale at which a landscape is studied. *Compare* grain. [24]

extinction vortex A pattern in which a small population that drops below a certain size becomes even more vulnerable to the problems that threaten small populations and hence may decrease even further in size, perhaps spiraling toward extinction. [23]

F

facilitation *See* positive interaction.

fecundity The average number of offspring produced by a female while she is of age *x* (denoted F_x in a life table). [10]

Ferrell cell A large-scale, three-dimensional pattern of atmospheric circulation in each hemisphere, located at mid-latitudes between the Hadley and polar cells. [2]

finite rate of increase *See* geometric population growth rate.

fitness The genetic contribution of an organism's descendants to future generations. [7]

fixation (1) The uptake of the gaseous form of a compound, including CO_2 in photosynthesis and N_2 in nitrogen fixation, by organisms for use in metabolic functions. [5] (2) With respect to the genetic composition of a population, an allele frequency of 100%. [6]

flagship species A charismatic species that may be emphasized in conservation efforts because it helps to garner public support for a conservation project. [23]

focal species One of a group of species selected as a priority for conservation efforts, chosen because its ecological requirements differ from those of other species in the group, thereby helping to ensure that as many different species as possible receive protection. [23]

food web A diagram showing the connections between organisms and the food they consume. [16, 21]

foundation species A species that has large, community-wide effects on the habitat or food of other species by virtue of its size or abundance. [16]

fugitive species A species that can persist in an area only if disturbances occur regularly, and must therefore disperse from one place to another as environmental conditions change. [14]

functional group A subset of a community that includes species that function in similar ways, but do not necessarily use the same resources. *Compare* guild. [16]

fundamental niche The full set of resources, along with other biotic and abiotic requirements, that are suitable for a species excluding the negative interactions with other species. [14]

G

gamma diversity Species diversity at the regional scale; the regional species pool. *Compare* alpha diversity, beta diversity. [18]

gene flow The transfer of alleles from one population to another via the movement of individuals or gametes. [6]

genet A genetic individual, resulting from a single fertilization event; in organisms that can reproduce asexually, a genet may consist of multiple, genetically identical parts, each of which has the potential to function as an independent physiological unit. *Compare* ramet. [9]

genetic drift A process in which chance events determine which alleles are passed from one generation to the next, thereby causing allele frequencies to fluctuate randomly over time; the effects of genetic drift are most pronounced in small populations. [6, 11]

genotype The genetic makeup of an individual. [6]

geographic range The entire geographic region over which a species is found. [9]

geometric growth Change in the size of a population of a species with discrete reproduction by a constant proportion from one discrete time period to the next. *Compare* exponential growth. [10]

geometric population growth rate (λ) A constant proportion by which a population of a species with discrete reproduction changes in size from one discrete time period to the next; also called the finite rate of increase. *Compare* exponential growth rate. [10]

grain In landscape ecology, the size of the smallest homogeneous unit of study (such as a pixel in a digital image), which determines the resolution at which a landscape is observed; together with extent, grain characterizes the scale at which a landscape is studied. *Compare* extent. [24]

gravitational potential The energy associated with gravity. [4]

greenhouse effect The warming of Earth by gases in the atmosphere that absorb and reradiate infrared energy emitted by Earth's surface. [2, 25]

greenhouse gases Atmospheric gases that absorb and reradiate the infrared radiation emitted by Earth's surface, including water vapor (H_2O), carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O). [2, 25]

gross primary production (GPP) The amount of energy that autotrophs capture by photosynthesis and chemosynthesis per unit of time. *Compare* net primary production. [20]

guild A subset of a community that includes species that use the same resources, whether or not they are taxonomically related. *Compare* functional group. [16]

H

habitat corridor A relatively narrow patch that connects blocks of habitat and often facilitates the movement of species between those blocks. [24]

habitat degradation Anthropogenic change that reduces the quality of habitat for many, but not all, species. [23]

habitat fragmentation The breaking up of once continuous habitat into a complex pattern of spatially isolated habitat patches amid a matrix of human-dominated landscape. [11, 23]

habitat loss The outright conversion of an ecosystem to another use by human activities. [23]

habitat mutualism A mutualism in which one partner provides the other with shelter, a place to live, or favorable habitat. [15]

Hadley cell A large-scale, three-dimensional pattern of atmospheric circulation in each hemisphere in which air is uplifted at the equator and subsides at about 30° N and S. [2]

heat capacity The amount of energy required to raise the temperature of a substance. [2]

herbivore An animal predator that consumes, or partially consumes, the tissues or internal fluids of living plants or algae. [12, 20]

herbivory A trophic species interaction in which the predator is an animal (herbivore) and the prey is a plant or alga. [12]

heterotroph An organism that obtains energy by consuming energy-rich organic compounds made by other organisms. *Compare* autotroph. [5]

hibernation Torpor lasting several weeks during the winter; a strategy that is possible only for animals that have access to enough food and can store enough energy reserves. [4]

horizons Layers of soil distinguished by their color, texture, and permeability. [22]

horizontal interactions Non-trophic interactions, such as competition and some positive interactions, that occur within a trophic level. [16]

host An organism on or within which an herbivore, parasite, or mutualist lives and feeds. [12, 13]

hypolimnion The densest, coldest water layer in a lake, lying below the thermocline. *Compare* epilimnion. [2]

hyporheic zone The portion of the substrate below and adjacent to a stream bed where water movement still occurs, either from the stream or from groundwater moving into the stream. [3]

hypothesis A possible answer to a question developed using previous knowledge or intuition. *See also* scientific method. [1]

hypoxic Of or relating to a condition of oxygen depletion, usually below a level that can sustain most animals. [2]

hysteresis The inability of a community that has undergone change to shift back to the original community type, even when the original conditions are restored. [17]

I

idiosyncratic hypothesis A hypothesis proposing that as the species richness of a community increases, community function will vary idiosyncratically as the result of some species having stronger effects on the community than others. *Compare* complementarity hypothesis and redundancy hypothesis. [19]

inbreeding Mating between related individuals. [11]

indirect interaction An interaction in which the relationship between two species is mediated by a third (or more) species. *Compare* direct interaction. [16]

induced defense In plant–herbivore interaction, a defense against herbivory, such as production of a secondary compound, that is stimulated by herbivore attack. [12]

interaction strength A measure of the effect of one species (the interactor) on the abundance of another species (the target species). [16]

interaction web A concept that describes both the trophic (vertical) and non-trophic (horizontal) interactions among the species in a traditional food web. [16]

interference competition An interaction in which species compete directly by performing antagonistic actions that interfere with the ability of their competitors to use a resource that both require, such as food or space. *Compare* exploitation competition. [14]

intermediate disturbance hypothesis A hypothesis proposing that species diversity in communities should be greatest at intermediate levels of disturbance (or stress or predation) because competitive exclusion at low levels of disturbance and mortality at high levels of disturbance should reduce species diversity. [19]

interspecific competition An interaction in which individuals of different species are harmed by their shared use of a resource that limits their ability to grow, reproduce, or survive (–/– relationship). *Compare* intraspecific competition. [14]

intertidal Referring to the portion of the shoreline that is affected by the rise and fall of the tides. [3]

Intertropical Convergence Zone (ITCZ) The zone of maximum solar radiation, atmospheric uplift, and precipitation within the tropical zone. [2]

intraspecific competition An interaction in which individuals of the same species are harmed by their shared use of a resource that limits their ability to grow, reproduce, or survive (–/– relationship). *Compare* interspecific competition. [14]

intrinsic rate of increase *See* exponential growth rate.

invasive species An introduced species that survives and reproduces in its new environment, sustains a growing population, and has large effects on the native community. [23]

island biogeography *See* equilibrium theory of island biogeography.

isocline The set of abundances for which the population growth rate (dN/dt) of one of the species involved in a species interaction is zero. [12, 14]

isogamy The production of equal-sized gametes. *Compare* anisogamy. [7]

isolation by distance A metapopulation pattern in which habitat patches located far from occupied patches are less likely to be colonized than are nearby patches. [11]

iteroparous Having the capacity to reproduce multiple times in a lifetime. *Compare* semelparous. [7]

J

jump dispersal A long-distance dispersal event by which a species colonizes a new geographic region. [11]

K

K *See* carrying capacity.

***K*-selection** In the *r*–*K* continuum used for classifying life history strategies, the selection pressure for slower rates of increase faced by organisms that live in environments where population densities are high (at or near the carrying capacity, *K*). *Compare* *r*-selection. [7]

keystone species A strong interactor species that has an effect on energy flow and community structure that is disproportionate to its small size, abundance, or biomass. [16, 21]

L

land use change The alteration of terrestrial surface, including vegetation and landforms, by human activities such as agriculture, forestry, or mining. [3]

landscape An area that is spatially heterogeneous in one or more features of the environment, such as the number or arrangement of different habitat types; a landscape typically includes multiple ecosystems. [1, 24]

landscape composition In landscape ecology, the kinds of elements or patches comprised by a landscape and how much of each kind is present. *Compare* landscape structure. [24]

landscape ecology The study of landscape patterns and the effects of those patterns on ecological processes. [24]

landscape structure In landscape ecology, the physical configuration of the different compositional elements of a landscape. *Compare* landscape composition. [24]

lapse rate The rate at which atmospheric temperature decreases with increasing distance from the ground. [2]

latent heat flux Heat transfer associated with the phase change of water, such as evaporation, sublimation, or condensation. [2]

leaching The vertical movement of dissolved matter and fine mineral particles from upper to lower layers of soil. [22]

leaf area index The area of leaves per unit of ground area (a dimensionless number, since it is an area divided by an area). [20]

lentic Of or referring to still water. *Compare* lotic. [3]

life history The major events relating to an organism's growth, development, reproduction, and survival; these events include the age and size of first reproduction, the amount and timing of reproduction, and longevity. [7]

life history strategy The overall pattern in the timing and nature of life history events, averaged across all the individuals of a species. [7]

life table A summary of how survival and reproductive rates in a population vary with the age of individuals; in species for which age is not informative or is difficult to measure, life tables may be based on the size or life cycle stage of individuals. [10]

lignin A structural compound that strengthens plant tissues. [22]

line transect When estimating population abundance, a straight line from which the distance to each individual an observer can see is measured; these distances are then converted into estimates of the number of individuals per unit of area. [9]

litter Fresh, undecomposed organic matter on the soil surface. [22]

littoral zone The nearshore zone of a lake where the photic zone reaches to the bottom. [3]

local scale A spatial scale that is essentially equivalent to a community. [18]

loess Sediment deposited by wind. [22]

logistic growth Change in the size of a population that is rapid at first, then decreases as the population approaches the carrying capacity of its environment. [10]

lotic Of or relating to flowing water. *Compare* lentic. [3]

Lotka–Volterra competition model A modified form of the logistic equation used to model interspecific competition. [14]

Lotka–Volterra predator–prey model A modified form of the logistic equation used to model predator–prey interaction cycles. [12]

lottery model A hypothesis proposing that species diversity in communities is maintained by a "lottery" in which resources made available by the effects of disturbance, stress, or predation are captured at random by recruits from a larger pool of potential colonists. [19]

lower critical temperature The environmental temperature at which the heat loss of an endotherm triggers an increase in metabolic heat generation. [4]

M

macroparasites Relatively large parasite species, such as arthropods and worms. *Compare* microparasites. [13]

macrophyte A rooted or floating aquatic vascular plant. [3]

marginal value theorem A conceptual optimal foraging model proposing that an animal should stay in a food patch until the rate of energy gain in that patch has declined to the average rate for the habitat, then depart for another patch. [8]

maritime climate The climate typical of coastal terrestrial regions that are influenced by an adjacent ocean, characterized by low daily and seasonal variation in temperature. *Compare* continental climate. [2]

mass extinction An event in which a large proportion of Earth's species are driven to extinction worldwide in a relatively short time. [6]

mating system The number of mating partners that males or females have and the pattern of parental care in which they engage. [8]

matric potential The energy associated with attractive forces on the surfaces of large molecules inside cells or on the surfaces of soil particles. [4]

mean residence time The amount of time an average molecule of an element spends in a pool before leaving it. [22]

mechanical weathering The physical breakdown of rocks into progressively smaller particles without chemical change. *Compare* chemical weathering. [22]

mesotrophic Having a nutrient status that is intermediate between oligotrophic and eutrophic, usually used in reference to lakes. *Compare* eutrophic, oligotrophic. [22]

metamorphosis An abrupt transition from a larval to a juvenile life cycle stage that is sometimes accompanied by a change in habitat. [7]

metapopulation A set of spatially isolated populations linked to one another by dispersal. [11]

microparasites Parasite species too small to be seen with the naked eye, such as bacteria, protists, and fungi. *Compare* macroparasites. [13]

Milankovitch cycles Cycles of regular change over thousands of years in the shape of Earth's orbit, in the angle of tilt of its axis, and in its orientation toward other celestial bodies that change the intensity of solar radiation received by Earth. [2]

mimicry A defense against predators in which prey species resemble less palatable organisms or physical features of their environment, causing potential predators to mistake them for something less desirable to eat. [12]

mineralization The chemical conversion of organic matter into inorganic compounds. [22]

morphs Discrete phenotypes with few or no intermediate forms. [7]

mosaic The composite or pattern of the heterogeneous features of the environment in a landscape. [24]

mutation Change in the DNA of a gene. [6]

mutualism A mutually beneficial interaction between individuals of two or more species (+/+ relationship). [15]

mycorrhizae Symbiotic associations between plant roots and various types of fungi that are usually mutualistic. [15]

N

natural catastrophe An extreme environmental event such as a flood, severe windstorm, or outbreak of disease that can eliminate or drastically reduce the sizes of populations. [11]

natural selection The process by which individuals with certain heritable characteristics tend to survive and reproduce more successfully than other individuals because of those characteristics. [1, 6]

nekton Swimming organisms capable of overcoming water currents. *Compare* plankton. [3]

net ecosystem exchange (NEE) The combined fluxes of CO_2 into and out of an ecosystem principally by net primary production and autotrophic and heterotrophic respiration. [20]

net ecosystem production *See* net ecosystem exchange.

net primary production (NPP) The amount of energy per unit of time that producers capture by photosynthesis and chemosynthesis, minus the amount they use in cellular respiration. *Compare* gross primary production. [1, 20]

net reproductive rate (R_0) The mean number of offspring produced by an individual in a population during its lifetime. [10]

net secondary production The balance between heterotroph energy gains through ingestion and heterotroph energy losses by cellular respiration and egestion. [20]

neutral model *See* lottery model.

niche *See* ecological niche.

niche model A predictive tool that models the ecological niche occupied by a species based on the conditions at locations the species is known to occupy. [9]

niche partitioning *See* resource partitioning.

nitrification A process by which certain chemoautotrophic bacteria, known as nitrifying bacteria, convert ammonia (NH_3) and ammonium (NH_4^+) into nitrate (NO_3^-) under aerobic conditions. [22]

nitrogen fixation The process of taking up nitrogen gas (N_2) and converting it into chemical forms that are more chemically available to organisms. [22]

North Atlantic Oscillation An oscillation in atmospheric pressures and ocean currents in the North Atlantic Ocean that affects climatic variation in Europe, in northern Asia, and on the east coast of North America. [2]

nutrient A chemical element required by an organism for its metabolism and growth. [22]

nutrient cycle The cyclic movement of nutrients between organisms and the physical environment. [1, 22]

O

occlusion A process by which soluble phosphorus combines with iron, calcium, and aluminum to form insoluble compounds (secondary minerals) that are unavailable to organisms as nutrients. [22]

oligotrophic Nutrient-poor, characterized by low primary productivity. *Compare* eutrophic, mesotrophic. [22]

omnivore (1) An organism that feeds on both plants and animals. [20] (2) In trophic studies, an organism that feeds on more than one trophic level. [21]

optimal foraging A theory proposing that animals will maximize the amount of energy acquired per unit of feeding time. [8]

osmotic adjustment An acclimatization response to changing water availability or salinity in terrestrial and aquatic environments that involves changing the solute concentration, and thus the osmotic potential, of the cell. [4]

osmotic potential The energy associated with dissolved solutes. [4]

outbreak An extremely rapid increase in the number of individuals in a population. [11]

ozone hole An area of the stratosphere with an ozone concentration of less than 220 Dobson units (= 2.7×10^{16} molecules of ozone) per square centimeter; found primarily over the Antarctic region. [25]

P

Pacific Decadal Oscillation (PDO) A long-term oscillation in sea surface temperatures and atmospheric pressures in the North Pacific Ocean that has widespread climatic effects. [2]

paedomorphic Resulting from a delay of a developmental event relative to sexual maturation. [7]

parasite An organism that lives in or on a host organism and feeds on its tissues or body fluids. [12, 13]

parasitism A trophic species interaction in which a predator (parasite) lives and feeds on or in its prey (host) without necessarily killing it. [12]

parasitoid An insect that lays one or a few eggs on or in a host organism (itself usually an insect), which the resulting larvae remain with, eat, and almost always kill. [12]

parent material The rock or sediments that are broken down by weathering to form mineral particles in soil. [22]

pathogen A parasite that causes disease. [12, 13]

pelagic zone The open water column of a lake or ocean. [3]

permafrost A subsurface soil layer that remains frozen year-round for at least 3 years. [3]

phenotype The observable characteristics of an organism. [6]

phenotypic plasticity The ability of a single genotype to produce different phenotypes under different environmental conditions. [7]

photic zone The surface layer of a lake or ocean where enough light penetrates to allow photosynthesis. [3]

photorespiration A chemical reaction in photosynthetic organisms in which the enzyme rubisco takes up O_2, leading to the breakdown of sugars, the release of CO_2, and a net loss of energy. [5]

photosynthesis A process that uses sunlight to provide the energy needed to take up CO_2 and synthesize sugars. [5]

physiological ecology The study of the interactions between organisms and the physical environment that influence their survival and persistence. [4]

phytoplankton Photosynthetic plankton. *Compare* zooplankton. [3]

pioneer stage The first stage of primary succession. [17]

plankton Small, often microscopic organisms that live suspended in water; although many plankton are mobile, none can swim strongly enough to overcome water currents. *Compare* nekton. [3]

polar cell A large-scale, three-dimensional pattern of atmospheric circulation in which air subsides at the poles, moves toward the equator when it reaches Earth's surface, and is replaced by air moving through the upper atmosphere from lower latitudes. [2]

polar zone The major climatic zone above 60° N and S. [2]

pool The total amount of a nutrient or other element found within a component of an ecosystem. [22]

population A group of individuals of the same species that live within a particular area and interact with one another. [1, 9]

population cycles A pattern of population fluctuations in which alternating periods of high and low abundance occur after nearly constant intervals of time. [11]

population density The number of individuals per unit of area. [9]

population fluctuations The most common pattern of population growth, in which population size rises and falls over time. [11]

population regulation A pattern of population growth in which one or more density-dependent factors increase population size when numbers are low and decrease population size when numbers are high. [10]

population size The number of individuals in a population. [9]

population viability analysis (PVA) Projection of the potential future status of a population through use of demographic models; a PVA approach is often used to estimate the likelihood that a population will persist for a certain amount of time in different habitats or under different management scenarios. [23]

positive interaction A trophic or non-trophic species interaction in which one or both species benefit and neither is harmed. *See also* mutualism, commensalism. [15]

predation A trophic interaction in which an individual of one species, a predator, consumes individuals (or parts of individuals) of another species, its prey. [12]

predator An organism that consumes other organisms (or parts of organisms), referred to as its prey. [12]

prey An organism eaten by a predator. [12]

pressure potential The energy associated with the exertion of pressure; has a positive value if pressure is exerted on the system and a negative value if the system is under tension. [4]

primary producer *See* producer.

primary production The rate at which chemical energy in an ecosystem is generated by autotrophs, derived from the fixation of carbon during photosynthesis and chemosynthesis. *Compare* secondary production. *See also* gross primary production, net primary production. [20]

primary succession Succession that involves the colonization of habitats devoid of life. *Compare* secondary succession. [17]

producer An organism that can produce its own food by photosynthesis or chemosynthesis; also called a primary producer or autotroph. *Compare* consumer. [1]

production efficiency The proportion of assimilated food that is used to produce new consumer biomass. [21]

proximate cause An immediate, underlying cause that is based on internal features of an organism and can be used to explain how a behavior (or other characteristic of the organism) occurs. *Compare* ultimate cause. [8]

pubescence The presence of hairs on the surface of an organism. [4]

R

***r*-selection** In the *r–K* continuum used for classifying life history strategies, the selection pressure for high population growth rates faced by organisms that live in environments where population densities are usually low. *Compare K*-selection. [7]

radiatively active gases *See* greenhouse gases.

rain-shadow effect The effect a mountain range has on regional climate by forcing moving air upward, causing it to cool and release precipitation on the windward slopes, resulting in lower levels of precipitation and soil moisture on the leeward slope. [2]

ramet An actually or potentially physiologically independent member of a genet that may compete with other members for resources. *Compare* genet. [9]

random dispersion A dispersion pattern that is similar to what would occur if individuals were positioned at locations selected at random. *Compare* clumped dispersion, regular dispersion. [9]

rank abundance curve A graph that plots the proportional abundance of each species in a community relative to the others in rank order, from most abundant to least abundant. [16]

realized niche The part of a fundamental niche that a species occupies as a result of species interactions. *Compare* fundamental niche. [14]

recombination Rearrangements of genetic material during sexual reproduction that result in the production of offspring that have combinations of alleles that differ from those in either of their parents. [6]

redundancy hypothesis A hypothesis that assumes an upper limit on the positive effect of species richness on community function because once species richness reaches some threshold, the functions of species in the community will overlap. *Compare* complementarity hypothesis and idiosyncratic hypothesis. [19]

redundant species Having the same function in a community as other species in that community within a larger functional group. [16]

regional scale A spatial scale that encompasses a geographic area where the climate is roughly uniform and the species contained therein are often restricted to that region by dispersal limitation. [18]

regional species pool All the species contained within a region; sometimes called gamma diversity. [18]

regular dispersion A dispersion pattern in which individuals are relatively evenly spaced throughout their habitat. *Compare* clumped dispersion, random dispersion. [9]

relative population size An estimate of population size based on data that are related in an unknown way to the absolute population size, but which can be compared from one time period or place to another. *Compare* absolute population size. [9]

replication The performance of each treatment of a controlled experiment, including the control, more than once. [1]

rescue effect A tendency for high rates of immigration to protect a population from extinction. [11]

resistance Any force that impedes the movement of compounds such as water or gases such as carbon dioxide along an energy or concentration gradient; its inverse is conductance. [4]

resource A feature of the environment, such as food, water, light, and space, that is required for growth, reproduction, or survival. [14]

resource partitioning The use of limiting resources by different species in a community in different ways. [14, 19]

resource ratio hypothesis A hypothesis proposing that species can coexist in a community by using the same resources, but in differing proportions. [19]

ruderals In Grime's triangular model, plants that are adapted to environments with high levels of disturbance and low levels of stress. *Compare* competitive plants, stress-tolerant plants. [7]

S

salinity The concentration of dissolved salts in water. [2]

salinization A process by which high rates of evapotranspiration in arid regions result in a progressive buildup of salts at the soil surface. [2]

sand The coarsest soil particles (0.05–2 mm). [22]

savanna A vegetation type dominated by grasses with intermixed trees and shrubs. [3]

scale The spatial or temporal dimension at which ecological observations are collected. [1, 24]

scientific method An iterative and self-correcting process by which scientists learn about the natural world, consisting of four steps: (1) observe nature and ask a question about those observations; (2) develop possible answers to that question (hypotheses); (3) evaluate competing hypotheses with experiments, observations, or quantitative models; (4) use the results of those experiments, observations, or models to modify the hypotheses, pose new questions, or draw conclusions. [1]

secondary compound A chemical compound in plants not used directly in growth, and often used in such functions as defense against herbivores or protection from harmful radiation. [12]

secondary production Energy in an ecosystem that is derived from the consumption of organic compounds produced by other organisms. *Compare* primary production. [20]

secondary succession Succession that involves the reestablishment of a community in which some, but not all, of the organisms have been destroyed. *Compare* primary succession. [17]

semelparous Reproducing only once in a lifetime. *Compare* iteroparous. [7]

sensible heat flux The transfer of heat through the exchange of energy by conduction or convection. [2]

sequential hermaphroditism A change or changes in the sex of an organism during the course of its life cycle. [7]

sexual selection A process in which individuals with certain characteristics have an advantage over others of the same sex solely with respect to mating success. [8]

Shannon index The index most commonly used to describe species diversity quantitatively. [16]

silt Intermediate-sized soil particles, often ranging in size between 0.05 and 0.002 mm. [22]

soil A mix of mineral particles, detritus, dissolved organic matter, water containing dissolved minerals and gases (the soil solution), and organisms that develops in terrestrial ecosystems. [22]

speciation The process by which one species splits into two or more species. [6]

species accumulation curve A graph that plots species richness as a function of the total number of individuals that are present with each additional sample. [16]

species–area relationship The relationship between species richness and area sampled. [18]

species composition The identity of the species present in a community. [16]

species diversity A measure that combines the number of species (species richness) in a community and their relative abundances compared with one another (species evenness). [16]

species evenness The relative abundances of different species compared to one another in a community. [16]

species richness The number of species in a community. [16]

stability When a community retains, or returns to, its original structure and function after some perturbation. [17]

stabilizing selection Selection that favors individuals with an intermediate phenotype. *Compare* directional selection, disruptive selection. [6]

stable age distribution A population age structure that does not change from one year to the next. [10]

stable limit cycle A pattern of population fluctuations in which abundance cycles indefinitely. [11]

static life table A life table that records the survival and reproduction of individuals of different ages during a single time period. [10]

stomate A pore in plant tissues, usually leaves, surrounded by specialized guard cells that control its opening and closing. [4]

stratification The layering of water in oceans and lakes due to differences in water temperature and density with depth. [2]

stress An abiotic factor that results in a decrease in the rate of an important physiological process, thereby lowering the potential for an organism's growth, reproduction, or survival; the condition caused by such a factor. [4, 17]

stress-tolerant plants In Grime's triangular model, plants that are adapted to conditions of high stress and low disturbance. *Compare* competitive plants, ruderals. [7]

subsidence A sinking (downward) movement of air in the atmosphere, usually over a broad area, leading to the development of a high-pressure cell. *Compare* uplift. [2]

succession The process of change in the species composition of a community over time as a result of abiotic and biotic agents of change. [17]

surrogate species A species selected as a priority for conservation with the assumption that its conservation will serve to protect many other species with overlapping habitat requirements. [23]

survival rate The proportion of individuals of age x that survive to be age $x + 1$ (denoted S_x in a life table). [10]

survivorship The proportion of individuals that survive from birth (age 0) to age x (denoted l_x in a life table). [10]

survivorship curve A graph based on survivorship data (l_x) that plots the numbers of individuals from a hypothetical cohort (typically, of 1,000 individuals) that will survive to reach different ages. [10]

symbiont An organism that lives in or on an organism of another species, referred to as its host; a symbiont is the smaller member of a symbiosis. *See also* host, symbiosis. [13]

symbiosis A relationship in which two species live in close physical and/or physiological contact with each other. *See also* host, symbiont. [12, 15]

T

taxonomic homogenization The worldwide reduction of biodiversity resulting from the spread of non-native and native generalists coupled with declining abundances and distributions of native specialists and endemics. [23]

temperate zone The major climatic zone between 30° and 60° N and S. [2]

territory An area that an animal defends against intruders. [8]

thermocline The zone of rapid temperature change in a lake beneath the epilimnion and above the hypolimnion. [2]

thermoneutral zone The range of environmental temperatures over which endotherms maintain a constant basal metabolic rate. [4]

threshold density The minimum number of individuals susceptible to a disease that must be present in a population for the disease to become established and spread. [13]

tides Patterns of rising and falling of ocean water generated by the gravitational attraction between Earth and the moon and sun. [3]

till Layers of sediment deposited by glaciers. [22]

tolerance The ability to survive stressful environmental conditions. *Compare* avoidance. [4]

top-down control Limitation of the abundance of a population by consumers. *Compare* bottom-up control. [11]

torpor A state of dormancy in which endotherms drop their lower critical temperature and associated metabolic rate. [4]

trade-off An organism's allocation of its limited energy or other resources to one structure or function at the expense of another. [6]

trophic cascade A change in the rate of consumption at one trophic level that results in a series of changes in species abundance or composition at lower trophic levels. [16, 21]

trophic efficiency A measure of the transfer of energy between trophic levels, consisting of the amount of energy at one trophic level divided by the amount of energy at the trophic level immediately below it. [21]

trophic facilitation An interaction in which a consumer is indirectly facilitated by a positive interaction between its prey or food plant and another species. [16]

trophic interaction An interaction in which a predator consumes a prey. [12]

trophic level A group of species that obtain energy in similar ways, classified by the number of feeding steps by which the group is removed from primary producers, which are the first trophic level. [16, 21]

trophic mutualism A mutualism in which one or both of the mutualists receives energy or nutrients from its partner. [15]

trophic pyramid A common approach to conceptualizing trophic relationships in an ecosystem in which a stack of rectangles is constructed, each of which represents the amount of energy or biomass within one trophic level. [21]

tropical zone The major climatic zone between 25° N and S, encompassing the equator; also called the tropics. [2]

turgor pressure Pressure that develops in a plant cell when water moves into it, following a gradient in water potential. [4]

turnover (1) The mixing of the entire water column in a stratified lake when all the layers of water reach the same temperature and density. [2] (2) The change in species diversity and composition from one community type to another across the landscape; *See* beta diversity. [18]

type I survivorship curve A survivorship curve in which newborns, juveniles, and young adults all have high survival rates and death rates do not begin to increase greatly until old age. [10]

type II survivorship curve A survivorship curve in which individuals experience a constant chance of surviving from one age to the next throughout their lives. [10]

type III survivorship curve A survivorship curve in which individuals die at very high rates when they are young, but those that reach adulthood survive well later in life. [10]

U

ultimate cause The underlying evolutionary or historical reason for a particular behavior (or other characteristic of an organism). *Compare* proximate cause. [8]

umbrella species A surrogate species selected with the assumption that protection of its habitat will serve as an "umbrella" to protect many other species; often a species with large or specialized habitat requirements or one that is easy to count. [23]

uplift The rising of warm, less dense air in the atmosphere due to heating of Earth's surface. *Compare* subsidence. [2]

upwelling The rising of deep ocean waters to the surface. [2]

V

vicariance The evolutionary separation of species due to a barrier that results in the geographic isolation of species that once were connected to one another. [18]

W

warning coloration A defense against predators in which prey species that contain powerful toxins advertise those toxins with bright coloration; also called aposematic coloration. [12]

water potential The overall energy status of water in a system; the sum of osmotic potential, gravitational potential, turgor pressure, and matric potential. [4]

watershed *See* catchment.

weather The temperature, humidity, precipitation, wind, and cloud cover at a particular time and place. *Compare* climate. [2]

weathering The physical and chemical processes by which rock minerals are broken down, eventually releasing soluble nutrients and other elements. [22]

Z

zooplankton Nonphotosynthetic plankton. *Compare* phytoplankton. [3]

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Literature Cited

Numbers in brackets refer to the chapter(s) where this reference is cited.

A

Abatzoglou, J. T. and P. Williams. 2016. Impact of anthropogenic climate change across western US forests. *Proceedings of the National Academy of Sciences USA* 113: 11770–11775. [25]

Aber, J. and 9 others. 1998. Nitrogen saturation in temperate forest ecosystems: Hypotheses revisited. *BioScience* 48: 921–934. [25]

Adey, W. H. and R. S. Steneck. 2001. Thermogeography over time creates biogeographic regions: A temperature/space/time-integrated model and an abundance-weighted test for benthic marine algae. *Journal of Phycology* 37: 677–698. [18]

Agrawal, A. A. and M. Fishbein. 2006. Plant defense syndromes. *Ecology* 87: S132–S149. [12]

Agrawal, A. A., M. T. J. Johnson, A. P. Hastings and J. L. Maron. 2013. A field experiment demonstrating plant life-history evolution and its eco-evolutionary feedback to seed predator populations. *American Naturalist* 181: S35–S45. [6]

Aiba, S., A. E. Humphrey and N. F. Mills. 1973. *Biochemical Engineering*. 2nd ed. Academic Press, New York. [22]

Allan, B. F., F. Keesing and R. S. Ostfeld. 2003. Effect of forest fragmentation on Lyme disease risk. *Conservation Biology* 17: 267–272. [24]

Allan, B. F. and 15 others. 2009. Ecological correlates of risk and incidence of West Nile virus in the United States. *Oecologia* 158: 699–708. [1]

Allen, E. B., P. J. Temple, A. Bytnerowicz, M. J. Arbaugh, A. G. Sirulnik and L. E. Rao. 2007. Patterns of understory diversity in mixed coniferous forests of Southern California impacted by air pollution. *Scientific World Journal* 7: 247–263. [18]

Allstadt, A. J., K. J. Haynes, A. M. Liebhold and D. M. Johnson. 2013. Long-term shifts in the cyclicity of outbreaks of a forest-defoliating insect. *Oecologia* 172: 141–151. [11]

Alexander, S. and 10 others. 2011. Opportunities and challenges for ecological restoration within REDD+. *Restoration Ecology* 19: 683–689. [3]

Alliende, M. C. and J. L. Harper. 1989. Demographic studies of a dioecious tree. I. Colonization, sex, and age structure of a population of *Salix cinerea*. *Journal of Ecology* 77: 1029–1047. [10]

Allin, E. F. and J. A. Hopson. 1992. Evolution of the auditory system in Synapsida ("mammal-like reptiles" and primitive mammals) as seen in the fossil record. In *The Evolutionary Biology of Hearing*, D. B. Webster, R. R. Fay and A. N. Popper (eds.), 587–614. Springer, New York. [6]

Alsterberg, C., J. S. Eklof, L. Gamfeldt, J. N. Havenhand and K. Sundback. 2013. Consumers mediate the effects of experimental ocean acidification and warming on primary producers. *Proceedings of the National Academy of Sciences USA* 110: 8603–8608. [16]

Alpert, P. 2006. Constraints of tolerance: Why are desiccation tolerant organisms so small or rare? *Journal of Experimental Biology* 209: 1575–1584. [4]

Anderegg, W. R. L. and 16 others. 2015. Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytologist* 208: 674–683. [25]

Andersen, S. B. and 7 others. 2009. The life of a dead ant: The expression of an adaptive extended phenotype. *American Naturalist* 174: 424–433. [13]

Anderson, J. T., D. W. Inouye, A. M. McKinney, R. I. Colautti and T. Mitchell-Olds. 2012. Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. *Proceedings of the Royal Society of London* B 279: 3843–3852. [6]

Anderson, S. H., D. Kelly, J. J. Ladley, S. Molloy and J. Terry. 2011. Cascading effects of bird functional extinction reduce pollination and plant density. *Science* 331: 1068–1071. [23]

Andersson, M. 1982. Female choice selects for extreme tail length in a widowbird. *Nature* 299: 818–820. [8]

Andrewartha, H. G. and L. C. Birch. 1954. *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago. [23]

Arcese, P. and J. N. M. Smith. 1988. Effects of population density and supplemental food on reproduction in song sparrows. *Journal of Animal Ecology* 57: 119–136. [10]

Arias, E. 2015. *United States Life Tables, 2011*. National Vital Statistics Reports, vol. 64, no. 11. National Center for Heath Statistics, Hyattsville, MD. www.cdc.gov/nchs/data/nvsr/nvsr64/nvsr64_11.pdf. [10]

Armitage, K. B., D. T. Blumstein and B. C. Woods. 2003. Energetics in hibernating yellow belly marmots (*Marmota* *flaviventris*). *Comparative Biochemistry and Physiology* A 134: 101–114. [4]

Asner, G. P., T. K. Rudel, T. M. Aide, R. Defries and R. Emerson. 2009. A contemporary assessment of change in humid tropical forests. *Conservation Biology* 6: 1386–1395. [3]

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. [22]

Austin, A. T. and L. Vivanco. 2006. Plant litter decomposition in a semiarid ecosystem controlled by photodegradation. *Nature* 442: 555–558. [22]

B

Baker, C. S., M. L. Dalebout, G. M. Lento and N. Funahashi. 2002. Gray whale products sold in commercial markets along the Pacific coast of Japan. *Marine Mammal Science* 18: 295–300. [23]

Balanyá, J., J. M. Oller, R. B. Huey, G. W. Gilchrist and L. Serra. 2006. Global genetic change tracks global climate warming in *Drosophila subobscura*. *Science* 313: 1773–1775. [6]

Balmford, A., R. E. Green and M. Jenkins. 2003. Measuring the changing state of nature. *Trends in Ecology and Evolution* 18: 326–330. [23]

Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Koch, A. C. Stier and B. R. Silliman. 2011. The value of estuarine and coastal ecosystem services. *Ecological Monographs* 81: 169–193. [3]

Barbour, M. A. and R. W. Clark. 2012. Ground squirrel tail-flag displays alter both predatory strike and ambush site selection behaviours of rattlesnakes. *Proceedings of the Royal Society of London* B 279: 3827–3833. [8]

Barbour, M. S. and J. A. Litvaitis. 1993. Niche dimensions of New England cottontails in relation to habitat patch size. *Oecologia* 95: 321–327. [24]

Barnosky, A. D., P. L. Koch, R. S. Feranec, S. L. Wing and A. B. Shabel. 2004. Assessing the causes of Late Pleistocene extinctions on the continents. *Science* 306: 70–75. [3]

Barringer, B. C., W. D. Koenig and J. M. H. Knops. 2013. Interrelationships among life-history traits in three California oaks. *Oecologia* 171: 129–139. [7]

Bartlein, P., J. C. Whitlock and S. L. Shafer. 1997. Future climate in the Yellowstone National Park region and its potential impact on vegetation. *Conservation Biology* 11: 782–792. [24]

Battin, J. 2004. When good animals love bad habitats: Ecological traps and the conservation of animal populations. *Conservation Biology* 18: 1482–1491. [24]

Beall, C. M. 2007. Two routes to functional adaptation: Tibetan and Andean high-altitude natives. *Proceedings of the National Academy of Sciences USA* 104: 8655–8660. [4]

Becerra, J. X. 2003. Synchronous coadaptation in an ancient case of herbivory. *Proceedings of the National Academy of Sciences USA* 100: 12804–12807. [12]

Becerra, J. X. 2007. The impact of herbivore–plant coevolution on plant community structure. *Proceedings of the National Academy of Sciences USA* 104: 7483–7488. [12]

Beck, B. B. 1980. *Animal Tool Behavior: The Use and Manufacture of Tools by Animals*. Garland STPM Press, New York. [5]

Begon, M., M. Mortimer and D. J. Thompson. 1996. *Population Ecology: A Unified Study of Animals and Plants*. 3rd ed. Blackwell Science, Oxford. [10]

Behrens Yamada, S., B. R. Dumbauld, A. Kalin, C. E. Hunt, R. Figlar-Barnes and A. Randall. 2005. Growth and persistence of a recent invader *Carcinus maenas* in estuaries of the northeastern Pacific. *Biological Invasions* 7: 309–321. [19]

Beisner, B. E., D. T. Haydon and K. Cuddington. 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment* 1: 376–382. [17]

Beissinger, S. R. and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62: 821–841. [23]

Bell, M. A., M. P. Travis and D. M. Blouw. 2006. Inferring natural selection in a fossil threespine stickleback. *Paleobiology* 32: 562–577. [6]

Bellows, T. S. Jr. 1981. The descriptive properties of some models for density dependence. *Journal of Animal Ecology* 50: 139–156. [10]

Belnap, J. 2003. The world at your feet: Desert biological crusts. *Frontiers in Ecology and Environment* 1: 181–189. [22]

Belnap, J. and D. Eldridge. 2001. Disturbance and recovery of biological soil crusts. In *Biological Soil Crusts: Structure, Function, and Management*, J. Belnap and O. L. Lange (eds.), 363–383. Springer, Berlin [22]

Belt, T. 1874. *The Naturalist in Nicaragua*. Murray, London. [15]

Belz, R. G. 2007. Allelopathy in crop/weed interactions: An update. *Pest Management Science* 63: 308–326. [14]

Benkman, C. W. 1993. Adaptation to single resources and the evolution of crossbill (*Loxia*) diversity. *Ecological Monographs* 63: 305–325. [5]

Benkman, C. W. 2003. Divergent selection drives the adaptive radiation of crossbills. *Evolution* 57: 1176–1181. [5]

Benton, M. J. and B. C. Emerson. 2007. How did life become so diverse? The dynamics of diversification according to the fossil record and molecular phylogenetics. *Palaeontology* 50: 23–40. [6]

Berendse, F., R. Aerts and R. Bobbink. 1993. Atmospheric nitrogen deposition and its impact on terrestrial ecosystems. In *Landscape Ecology of a Stressed Environment*, C. C. Vos and P. Opdam (eds.), 104–121. Chapman & Hall, London. [25]

Berger, L., A. A. Roberts, J. Voyles, J. E. Loncore, K. A. Murray and L. F. Skerratt. 2016. History and recent progress on chytridioimycosis in amphibians. *Fungal Ecology* 19: 89–99. [1]

Berglund, A. and G. Rosenqvist. 1993. Selective males and ardent females in pipefishes. *Behavioral Ecology and Sociobiology* 32: 331–336. [8]

Berlow, E. L. 1997. From canalization to contingency: Historical effects in a successional rocky intertidal. *Ecological Monographs* 67: 435–460. [17]

Berlow, E. L. 1999. Strong effects of weak interactions in ecological communities. *Nature* 398: 330–334. [21]

Bernhardt, E. S. and 13 others. 2005. Can't see the forest for the stream? In-stream processing and terrestrial nitrogen exports. *BioScience* 55: 219–230. [22]

Bertness, M. D. 1989. Interspecific competition and facilitation in a northern acorn barnacle population. *Ecology* 70: 257–268. [15]

Bertness, M. D. and S. D. Hacker. 1994. Physical stress and positive associations among marsh plants. *American Naturalist* 144: 363–372. [19]

Bertness, M. D. and G. H. Leonard. 1997. The role of positive interactions in communities: Lessons from intertidal habitats. *Ecology* 78: 1976–1989. [15]

Bertness, M. D. and S. W. Shumway. 1993. Competition and facilitation in marsh plants. *American Naturalist* 142: 718–724. [17]

Beschta, R. L. and W. J. Ripple. 2006. River channel dynamics following extirpation of wolves in northwestern Yellowstone National Park, USA. *Earth Surface Processes and Landforms* 31: 1525–1539. [24]

Bierregaard, R. O. Jr., C. Gascon, T. E. Lovejoy and R. C. G. Mesquita. 2001. *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest*. Yale University Press, New Haven, CT. [18]

Bigler, C., D. G. Gavin, C. Gunning and T. T. Veblen. 2007. Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. *Oikos* 116: 1983–1994. [10]

Binkley, D. and P. Högberg. 1997. Does atmospheric deposition of acidity and nitrogen threaten Swedish forests? *Forest Ecology and Management* 92: 119–152. [25]

Birkeland, C. 1997. Symbiosis, fisheries and economic development on coral reefs. *Trends in Ecology and Evolution* 12: 364–367. [3]

Bishop, J., W. F. Fagan, J. D. Schade and C. M. Crisafulli. 2005. Causes and consequences of herbivory on prairie lupine (*Lupinus lepidus*) in early primary succession. In *Ecological Responses to the 1980 Eruption of Mount St. Helens*, V. H. Dale, F. J. Swanson and C. M. Crisafulli (eds.), 151–161. Springer, New York. [17]

Björkman, O. 1981. Responses to different quantum flux densities. In *Physiological Plant Ecology I: Encyclopedia of Plant Physiology*, O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler (eds.), 57–101. Springer, Berlin. [5]

Blais, J. M., D. W. Schindler, D. C. G. Muir, L. E. Kimpe, D. B. Donald and B. Rosenberg. 1998. Accumulation of persistent organochlorine compounds in mountains of western Canada. *Nature* 395: 585–588. [21]

Blais, J. M., L. E. Kimpe, D. McMahon, B. E. Keatley, M. L. Mattory, M. S. V. Douglas and J. P. Smol. 2005. Arctic seabirds transport marine-derived contaminants. *Science* 309: 445–445. [21]

Blaustein, A. R. and P. T. J. Johnson. 2003. Explaining frog deformities. *Scientific American* 288: 60–65. [1]

Boonstra, R., D. Hik, G. R. Singleton and A. Tinnikov. 1998. The impact of predator-induced stress on the snowshoe hare cycle. *Ecological Monographs* 79: 371–394. [12]

Booth, M. G. and J. D. Hoeksema. 2010. Mycorrhizal networks counteract competitive effects of canopy trees on seedling survival. *Ecology* 91: 2294–2302. [15]

Borland, A. M., H. Griffiths, C. Maxwell, M. S. J. Broadmeadow, N. M. Griffiths and J. D. Barnes. 1992. On the ecophysiology of the Clusiaceae in Trinidad: Expression of CAM in *Clusia minor* L. during the transition from wet to dry season and characterization of three endemic species. *New Phytologist* 122: 349–357. [5]

Borries, C., K. Launhardt, C. Epplen, J. T. Epplen and P. Winkler. 1999. DNA analyses support the hypothesis that infanticide is adaptive in langur monkeys. *Proceedings of the Royal Society of London* B 266: 901–904. [8]

Bouzat, J. L., H. A. Lewin and K. N. Paige. 1998. The ghost of genetic diversity past: Historical DNA analysis of the greater prairie chicken. *American Naturalist* 152: 1–6. [6]

Bowman, W. D. and C. J. Bilbrough. 2001. Influence of a pulsed nitrogen supply on growth and nitrogen uptake in alpine graminoids. *Plant and Soil* 233: 283–290. [20]

Bowman, W. D. and T. R. Seastedt. 2001. *Structure and Function of an Alpine Ecosystem, Niwot Ridge, Colorado.* Oxford University Press, New York. [22]

Bowman, W. D., T. A. Theodose, J. C. Schardt and R. T. Conant. 1993. Constraints of nutrient availability on primary production in two alpine communities. *Ecology* 74: 2085–2098. [20]

Braby, M. F. 2002. Life history strategies and habitat templets of tropical butterflies in north-eastern Australia. *Evolutionary Ecology* 16: 399–413. [7]

Bradshaw, A. D. 1987. Restoration: An acid test for ecology. In *Restoration Ecology: A Synthetic Approach to Ecological Restoration*, W. R. Jordan, M. E. Gilpin and J. D. Aber (eds.), 23–30. Cambridge University Press, Cambridge. [24]

Bradshaw, C. J. A. and B. W. Brook. 2007. Ecological–economic models of sustainable harvest for an endangered but exotic megaherbivore in northern Australia. *Natural Resource Modeling* 20: 129–156. [23]

Bradshaw, W. E. and C. M. Holzapfel. 2001. Genetic shift in photoperiodic response correlated with global warming. *Proceedings of the National Academy of Sciences USA* 98: 14509–14511. [6]

Breshears, D. D. and 12 others. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences USA* 10: 15144–15148. [2]

Brewer, J. S. 2003. Why don't carnivorous pitcher plants compete with non-carnivorous plants for nutrients? *Ecology* 84: 451–462. [14]

Briggs, J. C. 2006. Proximate sources of marine biodiversity. *Journal of Biogeography* 33: 1–10. [18]

Britton, R. A. and V. B. Young. 2012. Interaction between the intestinal microbiota and host in *Clostridium difficile* colonization resistance. *Trends in Microbiology* 20: 313–319. [13]

Brommer, J. E., H. Pietiainen, K. Ahola, P. Karell, T. Karstinen and H. Kolunen. 2010. The return of the vole cycle in southern Finland refutes the generality of the loss of cycles through "climatic forcing." *Global Change Biology* 16: 577–586. [11]

Bronstein, J. L. 1992. Seed predators as mutualists: Ecology and evolution of the fig/pollinator interaction. In *Insect-Plant Interactions* (vol. 4), E. A. Bernays (ed.), 1–44. CRC Press, Boca Raton, FL. [15]

Bronstein, J. L. 1994. Conditional outcomes in mutualistic interactions. *Trends in Ecology and Evolution* 9: 214–217. [15]

Brooks, T., J. Tobias and A. Balmford. 1999. Deforestation and bird extinctions in the Atlantic forest. *Animal Conservation* 2: 211–222. [23]

Brooks, T. M. and 9 others. 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* 16: 909–923. [23]

Brown, J. H. and D. W. Davidson. 1977. Competition between seed-eating rodents and ants in desert ecosystems. *Science* 196: 880–882. [14]

Brown, J. H. and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology* 58: 445–449. [11]

Bruno, J. F., J. J. Stachowicz and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18: 119–125. [19]

Bruno, J. F. and 7 others. 2007. Thermal stress and coral cover as drivers of coral disease outbreaks. *PLoS Biology* 5: 1220–1227. [13]

Bullock, S., H. Mooney and E. Medina, eds. 1995. *Seasonally Dry Tropical Forests*. Cambridge University Press, Cambridge. [3]

Bunn, R., Y. Lekberg and C. Zabinski. 2009. Arbuscular mycorrhizal fungi ameliorate temperature stress in thermophilic plants. *Ecology* 90: 1378–1388. [15]

Burgess, R. L. 1977. The Ecological Society of America: Historical data and preliminary analyses. In *History of American Ecology*, F. N. Egerton (ed.), 1–24. Arno Press, New York. [23]

Buss, L. W. and J. B. C. Jackson. 1979. Competitive networks: Nontransitive competitive relationships in cryptic coral reef environments. *American Naturalist* 113: 223–234. [16]

Buston, P. M. 2003a. Size and growth modification in clownfish. *Nature* 424: 145–146. [7]

Buston, P. M. 2003b. Forcible eviction and prevention of recruitment in the clown anemonefish. *Behavioral Ecology* 14: 576–582. [7]

Buston, P. M. 2004. Territory inheritance in clownfish. *Proceedings of the Royal Society of London* B (suppl.) 271: S252–S254. [7]

Butzer, K. W. 1992. The Americas before and after 1492: An introduction to current geographical research. *Annals of the Association of American Geographers* 82: 345–368. [24]

Bytnerowicz, A., M. J. Arbaugh and R. Alonso. 2003. *Ozone Pollution in the Sierra Nevada: Distribution and Effects on Forests*. Elsevier, Amsterdam. [25]

C

Cain, M. L., B. G. Milligan and A. E. Strand. 2000. Long-distance seed dispersal in plant populations. *American Journal of Botany* 87: 1217–1227. [9]

Calder, W. J. and S. B. St. Clair. 2012. Facilitation drives mortality patterns along successional gradients of aspen-conifer forest. *Ecosphere* 3: 1–11. [17]

Caldwell, M. M., L. O. Björn, J. F. Bornman, S. D. Flint, G. Kulandaivelu, A. H. Teramura and M. Tevini. 1998. Effects of increased solar ultraviolet radiation on terrestrial ecosystems. *Journal of Photochemistry and Photobiology* B: *Biology* 46: 40–52. [25]

Caleira, K. and M. E. Wickett. 2003. Anthropogenic carbon and ocean pH. *Nature* 425: 365. [25]

Callaway, R. M. and L. King. 1996. Temperature-driven variation in substrate oxygenation and the balance of competition and facilitation. *Ecology* 77: 1189–1195. [15]

Callaway, R. M., E. H. DeLucia and W. H. Schlesinger. 1994. Biomass allocation of montane and desert ponderosa pine: An analog for response to climate change. *Ecology* 75: 1474–1481. [7]

Callaway, R. M. and 12 others. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417: 844–848. [15]

Canfield, D. E., A. N. Glazer and P. G. Falkowski. 2010. The evolution and future of Earth's nitrogen cycle. *Science* 330: 192–196. [25]

Carlsson, J. O. L., C. Brönmark and L.-A. Hansson. 2004. Invading herbivory: The golden apple snail alters ecosystem functioning in Asian wetlands. *Ecology* 85: 1575–1580. [12]

Carlton, J. T. and J. B. Geller. 1993. Ecological roulette: The global transport and invasion of non-indigenous marine organisms. *Science* 261: 78–82. [19]

Carroll, S. P. and C. Boyd. 1992. Host race radiation in the soapberry bug: Natural history with the history. *Evolution* 46: 1052–1069. [6]

Carroll, S. P., H. Dingle and S. P. Klassen. 1997. Genetic differentiation of fitness-associated traits among rapidly evolving populations of the soapberry bug. *Evolution* 51: 1182–1188. [6]

Carson, R. 1962. *Silent Spring*. Houghton Mifflin, Boston. [21]

Carson, W. P. and R. B. Root. 2000. Herbivory and plant species coexistence: Community regulation by an outbreaking phytophagous insect. *Ecological Monographs* 70: 73–99. [1]

Cary, J. R and L. B. Keith. 1979. Reproductive change in the ten-year cycle of snowshoe hares. *Canadian Journal of Zoology* 57: 375–390. [12]

Castellón, T. D. and K. E. Sieving. 2006. An experimental test of matrix permeability and corridor use by an endemic understory bird. *Conservation Biology* 20: 135–145. [24]

Castro, J., R. Zamora, J. A. Hódar and J. M. Gómez. 2002. The use of shrubs as nurse plants: A successional-friendly technique for pine reforestation in Mediterranean mountains. *Restoration Ecology* 10: 297–305. [15]

Caswell, H. 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*. 2nd ed. Sinauer Associates, Sunderland, MA. [10]

Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63: 215–244. [23]

Caughley, G., N. Shepherd and J. Short. 1987. *Kangaroos: Their Ecology and Management in the Sheep Rangelands of Australia*. Cambridge University Press, Cambridge. [9]

Ceballos, G. and P. R. Ehrlich. 2002. Mammal population losses and the extinction crisis. *Science* 296: 904–907. [23]

Cebrian, J. and J. Lartigue. 2004. Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. *Ecological Monographs* 74: 237–259. [21]

Cerling, T. E., J. M. Harris, B. J. MacFadden, M. G. Leakey, J. Quade, V. Eisenmann and J. R. Ehleringer. 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389: 153–158. [5]

Channell, R. and M. V. Lomolino. 2000. Trajectories to extinction: Spatial dynamics of the contraction of geographical ranges. *Journal of Biogeography* 27: 169–179. [23]

Chapin, F. S. III, L. Moilanen and K. Kielland. 1993. Preferential use of organic nitrogen for growth by a non-mycorrhizal Arctic sedge. *Nature* 361: 150–153. [22]

Chapin, F. S. III, L. R. Walker, C. L. Fastie and L. C. Sharman. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs* 64: 149–175. [17]

Chapin, F. S. III, P. A. Matson and H. A. Mooney. 2002. *Principles of Terrestrial Ecosystem Ecology*. Springer, New York. [21, 25]

Chappelka, A. and L. Samuelson. 1998. Ambient ozone effects on forest trees of the eastern United States: A review. *New Phytologist* 139: 91–108. [25]

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9: 129–136. [8]

Charnov, E. L. 1993. *Life History Invariants*. Oxford University Press, Oxford. [7]

Charnov, E. L. and D. Berrigan. 1990. Dimensionless numbers and life history evolution: Age of maturity versus the adult lifespan. *Evolutionary Ecology* 4: 273–275. [7]

Chase, T. N., R. Pielke Sr., T. G. F. Kittel, J. S. Baron and T. J. Stohlgren. 1999. Impacts on Colorado Rocky Mountain weather due to land use changes on the adjacent Great Plains. *Journal of Geophysical Research—Atmospheres* 104: 16673–16690. [2]

Chen, J. Q., J. F. Franklin and T. A. Spies. 1995. Growing-season microclimatic gradients from clear-cut edges into old-growth Douglas-fir forests. *Ecological Applications* 5: 74–86. [24]

Chen, J.-Y. and 10 others. 2009. Complex embryos displaying bilaterian characters from Precambrian Doushantuo phosphate deposits, Weng'an, Guizhou, China. *Proceedings of the National Academy of Sciences USA* 106: 19056–19060. [6]

Chen, M., M. Schliep, R. D. Willows, Z. Cai, B. A. Neilan and H. Scheer. 2010. A red-shifted chlorophyll. *Science* 329: 1318–1319. [5]

Chesson, P. L. and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* 117: 923–943. [19]

Christensen, N. L. and 12 others. 1996. The report of the Ecological Society of America Committee on the Scientific Basis for Ecosystem Management. *Ecological Applications* 6: 665–691. [24]

Clay, C. A., E. M. Lehmer, S. S. Jeor and M. D. Dearing. 2009. Sin Nombre virus and rodent species diversity: A test of the dilution and amplification hypotheses. *PLoS ONE* 4: e6467. [19]

Clements, F. E. 1916. *Plant Succession: An Analysis of the Development of Vegetation*. Publication 42. Carnegie Institution of Washington, Washington, DC. [17]

Cleveland, C. C. and 10 others. 1999. Global patterns of terrestrial biological nitrogen (N_2) fixation in natural ecosystems. *Global Biogeochemical Cycles* 13: 623–645. [25]

Clutton-Brock, T. H., F. E. Guinness and S. D. Albon. 1983. The costs of reproduction to red deer hinds. *Journal of Animal Ecology* 52: 367–383. [6]

Cohen, J. E. 1995. *How Many People Can the Earth Support*? W. W. Norton, New York. [10]

Coltman, D. W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature* 426: 655–658. [6, 8]

Connell, J. H. 1961a. The effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle, *Balanus balanoides*. *Ecological Monographs* 31: 61–104. [14, 19]

Connell, J. H. 1961b. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42: 710–723. [14,19]

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310. [19]

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: Evidence from field experiments. *American Naturalist* 122: 661–696. [14]

Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111: 1119–1144. [17]

Connell, J. H. and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. *American Naturalist* 121: 789–824. [17]

Cook, B. I., R. L. Miller and R. Seager. 2009. Amplification of the North American "Dust Bowl" drought through human-induced land degradation. *Proceedings of the National Academy of Sciences USA* 106: 4997–5001. [25]

Cook, L. M., B. S. Grant, I. J. Saccheri and J. Mallet. 2012. Selective bird predation on the peppered moth: The last experiment of Michael Majerus. *Biology Letters* 8: 609–612. [6]

Cooper, O. R. and 10 others. 2014. Global distribution and trends of tropospheric ozone: An observation-based review. *Elementa* 2: 29. [25]

Cooper, W. S. 1923a. The recent ecological history of Glacier Bay, Alaska: The interglacial forests of Glacier Bay. *Ecology* 4: 93–128. [17]

Cooper, W. S. 1923b. The recent ecological history of Glacier Bay, Alaska: Permanent quadrats at Glacier Bay: An initial report upon a long-period study. *Ecology* 4: 355–365. [17]

Copeyon, C. K., J. R. Walters and J. H. Carter III. 1991. Induction of red-cockaded woodpecker group formation by artificial cavity construction. *Journal of Wildlife Management* 55: 549–556. [23]

Cornulier, T. and 20 others. 2013. Europe-wide dampening of population cycles in keystone herbivores. *Science* 340: 63–66. [11]

Costanzo, J. P., R. E. Lee Jr., A. L. DeVries, T. Wang and J. R. Layne Jr. 1995. Survival mechanisms of vertebrate ectotherms at subfreezing temperatures: Applications in cryomedicine. *FASEB Journal* 9: 351–358. [4]

Costello, A. and 28 others. 2009. Managing the health effects of climate change. *The Lancet* 373: 1693–1733. [13]

Cotton, P. A., S. D. Rundle and K. E. Smith. 2004. Trait compensation in marine gastropods: Shell shape, avoidance behavior, and susceptibility to predation. *Ecology* 85: 1581–1584. [12]

Courchamp, F., T. Clutton-Brock and B. Grenfell. 1999. Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution* 14: 405–410. [11]

Cowie, R. H. 2001. Decline and homogenization of Pacific faunas: The land snails of American Samoa. *Biological Conservation* 99: 207–222. [23]

Cowie, R. J. 1977. Optimal foraging in great tits (*Parus major*). *Nature* 268: 137–139. [8]

Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Botanical Gazette* 27: 95–117, 167–202, 281–308, 361–391. [17]

Creel, S. and D. Christianson. 2009. Wolf presence and increased willow consumption by Yellowstone elk: Implications for trophic cascades. *Ecology* 90: 2454–2466. [24]

Creel, S. and N. M. Creel. 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour* 50: 1325–1339. [8]

Creel, S., J. Winnie Jr., B. Maxwell, K. Hamlin and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86: 3387–3397. [8]

Crews, T. E., K. Kitayama, J. H. Fownes, D. A. Herbert, R. H. Riley, D. Mueller-Dombois and P. M. Vitousek. 1995. Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. *Ecology* 76: 1407–1424. [22]

Crisafulli, C. M., J. A. MacMahon and R. R. Parmenter. 2005. Small-mammal survival and colonization on the Mount St. Helens volcano: 1980–2005. In *Ecological Responses to the 1980 Eruption of Mount St. Helens*, V. H. Dale, F. J. Swanson and C. M. Crisafulli (eds.), 183–197. Springer, New York. [17]

Croll, D. A., J. L. Maron, J. A. Estes, E. M. Danner and G. V. Byrd. 2005. Introduced predators transform subarctic islands from grassland to tundra. *Science* 307: 1959–1961. [12]

Crouse, D. T., L. B. Crowder and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* 68: 1412–1423. [10]

Crowder, L. B., D. T. Crouse, S. S. Heppell and T. H. Martin. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. *Ecological Applications* 4: 437–445. [10]

Crutzen, P. J. and E. F. Stoermer. 2000. The "Anthropocene." *Global Change Newsletter* 41: 12–13. [25]

Currie, C. R. and A. E. Stuart. 2001. Weeding and grooming of pathogens in agriculture by ants. *Proceedings of the Royal Society of London* B 268: 1033–1039. [15]

Currie, C. R., U. G. Mueller and D. Malloch. 1999a. The agricultural pathology of ant fungus gardens. *Proceedings of the National Academy of Sciences USA* 96: 7998–8002. [15]

Currie, C. R., J. A. Scott, R. C. Summerbell and D. Malloch. 1999b. Fungus-growing ants use antibiotic-producing bacteria to control garden parasites. *Nature* 398: 701–704. [15]

Currie, C. R., M. Poulsen, J. Mendenhall, J. J. Boomsma and J. Billen. 2006. Coevolved crypts and exocrine glands support mutualistic bacteria in fungus-growing ants. *Science* 311: 81–83. [15]

D

Dahlgren, C. P. and D. B. Eggleston. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef. *Ecology* 81: 2227–2240. [7]

Daily, G. C. and K. Ellison. 2002. *The New Economy of Nature: The Quest to Make Conservation Profitable*. Island Press, Washington, DC. [24]

Dale, V. H., F. J. Swanson and C. M. Crisafulli, eds. 2005. *Ecological Responses to the 1980 Eruption of Mount St. Helens*. Springer, New York. [17]

Dambrine, E., J. L. Dupouey, L. Laut, L. Humbert, M. Thinon, M. T. Beaufils and H. Richard. 2007. Present forest biodiversity patterns in France related to former Roman agriculture. *Ecology* 88: 1430–1439. [24]

Damman, H. and M. L. Cain. 1998. Population growth and viability analyses of the clonal woodland herb, *Asarum canadense*. *Journal of Ecology* 86: 13–26. [10]

Darimont, C. T., S. M. Carlson, M. T. Kinnison, P. C. Paquet, T. E. Reimchen and C. C. Wilmers. 2009. Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences USA* 106: 952–954. [6]

Darwin, C. 1859. *On the Origin of Species*. J. Murray, London. [6, 8, 12, 14, 16, 18, 19, 21]

Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. John Murray, London. [8]

Darwin, C. 1875. *Insectivorous Plants*. Appleton and Company, New York. [14]

Daskalov, G. M., A. N. Grishin, S. Rodionov and V. Mihneva. 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceedings of the National Academy of Sciences USA* 104: 10518–10523. [11]

David, P., A. Hingle, D. Greig, A. Rutherford, A. Pomiankowski and K. Fowler. 1998. Male sexual ornament size but not asymmetry reflects condition in stalk-eyed flies. *Proceedings of the Royal Society of London* B 265: 2211–2216. [8]

Davidson, J. 1938. On the growth of the sheep population in Tasmania. *Transactions of the Royal Society of South Australia* 62: 342–346. [11]

Davidson, J. and H. G. Andrewartha. 1948. The influence of rainfall, evaporation and atmospheric temperature of fluctuations in the size of a natural population of *Thrips imaginis* (Thysanoptera). *Journal of Animal Ecology* 17: 200–222. [10]

Davies, N. B., J. R. Krebs and S. A. West. 2012. *An Introduction to Behavioural Ecology.* 4th ed. Wiley-Blackwell, Oxford. [8]

Davis, C. C. 1964. Evidence for the eutrophication of Lake Erie from phytoplankton records. *Limnology and Oceanography* 9: 275–283. [11]

Davis, M. B., J. Ford and R. E. Moeller. 1985. Paleolimnology. In *An Ecosystem Approach to Aquatic Ecology: Mirror Lake and Its Environment*, G. E. Likens (ed.), 345–366. Springer, New York. [22]

Dawson, J. and R. Lucas. 2000. *Nature Guide to the New Zealand Forest*. A Godwit Book. Random House New Zealand, Auckland. [18]

Dayton, P. K. 1971. Competition, disturbance and community organization: The provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41: 351–389. [16]

De'ath, G., J. M. Lough and K. E. Fabricus. 2009. Declining coral calcification in the Great Barrier Reef. *Science* 323: 116–119. [25]

Deevey, E. S. 1947. Life tables for natural populations. *Quarterly Review of Biology* 22: 283–314. [10]

Delcourt, H. R. 2002. Creating landscape pattern. In *Learning Landscape Ecology*, S. E. Gergel and M. G. Turner (eds.), 62–82. Springer, New York. [24]

Delcourt, P. A., H. R. Delcourt, C. R. Ison, W. E. Sharp and K. J. Gremillion. 1998. Prehistoric human use of fire, the eastern agricultural complex, and Appalachian oak–chestnut forests: Paleoecology of Cliff Palace Pond, Kentucky. *American Antiquity* 63: 263–278. [3]

DellaSala, D. A. and J. E. Williams. 2006. The northwest forest plan: A global model of forest management in contentious times. *Conservation Biology* 20: 274–276. [24]

Del Moral, R., D. M. Wood and J. H. Titus. 2005. Proximity, microsites, and biotic interactions during early succession. In *Ecological Responses to the 1980 Eruption of Mount St. Helens*, V. H. Dale, F. J. Swanson and C. M. Crisafulli (eds.), 93–107. Springer, New York. [17]

DeLucia, E. H. and 10 others. 1999. Net primary production of a forest ecosystem under experimental CO_2 enrichment. *Science* 284: 1177–1179. [25]

DeMaster, D. P., A. W. Trites, P. Clapham, S. Mizroch, P. Wade, R. J. Small and J. Ver Hoef. 2006. The sequential megafaunal collapse hypothesis: Testing with existing data. *Progress in Oceanography* 68: 329–342. [9]

Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* 18: 431–451. [7]

Dewailly, E., P. Ayotte, S. Bruneau, C. Laliberte, D. C. G. Muir and R. J. Norstrom. 1993. Inuit exposure to organochlorines through the aquatic food-chain in Arctic Quebec. *Environmental Health Perspectives* 101: 618–620. [21]

Diamond, J. M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation* 7: 129–146. [24]

Diamond, J. M. 1997. *Guns, Germs, and Steel: The Fates of Human Societies*. W. W. Norton, New York. [13]

Dirzo, R. and P. H. Raven. 2003. Global state of biodiversity and loss. *Annual Review of Environment and Resources* 28: 137–167. [3]

Dixon, A. F. G. 1971. The role of aphids in wood formation. II. The effect of the lime aphid, *Eucallipterus tiliae* L. (Aphididae), on the growth of lime *Tilia* × *vulgaris* Hayne. *Journal of Applied Ecology* 8: 393–399. [12]

Dixon, R. K., A. M. Solomon, S. Brown, R. A. Houghton, M. C. Trexier and J. Wisniewski. 1994. Carbon pools and flux of global forest ecosystems. *Science* 263: 185–190. [3]

Dizney, L. J. and L. A. Ruedas. 2009. Increased host species diversity and decreased prevalence of Sin Nombre virus. *Emerging Infectious Diseases* 15: 1012–1018. [19]

Dobson, A. and M. Meagher. 1996. The population dynamics of brucellosis in the Yellowstone National Park. *Ecology* 77: 1026–1036. [13]

Dodd, D. M. B. 1989. Reproductive isolation as a consequence of adaptive divergence in *Drosophila pseudoobscura*. *Evolution* 43: 1308–1311. [6]

Dodson, C. H. and A. H. Gentry. 1991. Biological extinction in western Ecuador. *Annals of the Missouri Botanical Garden* 78: 273–295. [23]

Du, M. and J. D. Kessler. 2012. Assessment of the spatial and temporal variability of bulk hydrocarbon respiration following the Deepwater Horizon oil spill. *Environmental Science & Technology* 46: 10499–10507. [5]

Dugger, K. M., R. G. Anthony and L. S. Andrews. 2011. Transient dynamics of invasive competition: Barred owls, spotted owls, habitat, and the demons of competition present. *Ecological Applications* 21: 2459–2468. [11]

Duggins, D. O. 1980. Kelp beds and sea otters: An experimental approach. *Ecology* 61: 447–453. [9]

Duggins, D. O., C. A. Simenstad and J. A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245: 170–173. [9]

Dukes, J. S. and H. A. Mooney. 1999. Does global change increase the success of biological invaders? *Trends in Ecology and Evolution* 14: 135–139. [25]

Dybdahl, M. F. and C. M. Lively. 1998. Host–parasite coevolution: Evidence for rare advantage and time-lagged selection in a natural population. *Evolution* 52: 1057–1066. [13]

Dyer, L. A. and K. K. Letourneau. 1999a. Trophic cascades in a complex terrestrial community. *Proceedings of the National Academy of Sciences USA* 96: 5072–5076. [21]

Dyer, L. A. and K. K. Letourneau. 1999b. Relative strengths of top-down and bottom-up forces in a tropical forest community. *Oecologia* 119: 265–274. [21]

E

Eberhard, W. G. 2001. Under the influence: Webs and building behavior of *Plesiometa argyra* (Araneae, Tetragnathidae) when parasitized by *Hymenoepimecis argyraphaga* (Hymenoptera, Ichneumonidae). *Journal of Arachnology* 29: 354–366. [13]

Edmondson, W. T. and A. H. Litt. 1982. *Daphnia* in Lake Washington. *Limnology and Oceanography* 27: 272–293. [22]

Egan, T. 2006. *The Worst Hard Time: The Untold Story of Those Who Survived the Great American Dust Bowl.* Houghton Mifflin, Boston. [25]

Ehleringer, J. R. and C. S. Cook. 1990. Characteristics of *Encelia* species differing in leaf reflectance and transpiration rate under common garden conditions. *Oecologia* 82: 484–489. [4]

Ehleringer, J. R., T. E. Cerling and B. R. Helliker. 1997. C_4 photosynthesis, atmospheric CO_2, and climate. *Oecologia* 112: 285–299. [5]

Ehrlich, P. R. and E. O. Wilson. 1991. Biodiversity studies: Science and policy. *Science* 253: 758–762. [23]

Eis, S., E. H. Garman and L. F. Ebell. 1965. Relation between cone production and diameter increment of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl.) Lindl.), and western white pine (*Pinus monticola* Dougl.). *Canadian Journal of Botany* 43: 1553–1559. [7]

El-Sabaawi, R. W., M. C. Marshall, R. D. Bassar, A. López-Sepulcre, E. P. Palkovacs and C. Dalton. 2015. Assessing the effects of guppy life history evolution on nutrient recycling: From experiments to the field. *Freshwater Biology* 60: 590–601. [6]

Elser, J. J. and 11 others. 2000. Nutritional constraints in terrestrial and freshwater food webs. *Nature* 408: 578–580. [21]

Elser, J. J. and 9 others. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* 10: 1135–1142. [20]

Elton, C. S. 1927. *Animal Ecology*. Sidgwick and Jackson, London. [17]

Elton, C. S. 1942. *Voles, Mice and Lemmings: Problems in Population Dynamics*. Oxford University Press, Oxford. [6]

Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. Chapman & Hall, London. [19, 21]

Emlen, S. T. and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215–223. [8]

Endler, J. A. 1986. *Natural Selection in the Wild*. Princeton University Press, Princeton, NJ. [6]

Ensign, S. H. and M. W. Doyle. 2006. Nutrient spiraling in streams and river networks. *Journal of Geophysical Research* 111: G04009, doi:10.1029/2005JG000114. [22]

Epstein, E. and A. J. Bloom. 2005. *Mineral Nutrition of Plants: Principles and Perspectives*. 2nd ed. Sinauer Associates, Sunderland, MA. [22]

Epstein, P. R. 2000. Is global warming harmful to health? *Scientific American* 283: 50–57. [13]

Erickson, R. O. 1945. The *Clematis fremontii* var. *riehlii* population in the Ozarks. *Annals of the Missouri Botanical Garden* 32: 413–460. [9]

Eskew, W. A., S. J. Worth, J. E. Foley and B. D. Todd. 2015. American bullfrogs (*Lithobates catesbeianus*) resist infection by multiple isolates of *Batrachochytrium dendrobatidis*, including one implicated in wild mass mortality. *EcoHealth* 12: 513–518. [1]

Estes, J. A. and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: Generality and variation in a community ecology paradigm. *Ecological Monographs* 65: 75–100. [9]

Estes, J. A., M. T. Tinker, T. M. Williams and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282: 473–476. [9]

Evans, R. D., R. Rimer, L. Sperry and J. Belnap. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications* 11: 1301–1310. [22]

Ewing, B., D. Moore, S. Goldfinger, A. Oursler, A. Reed, and M. Wackernagel. 2010. *The Ecological Footprint Atlas 2009*. Global Footprint Network, Oakland, CA. [10]

F

Fagan, W. F., R. S. Cantrell and C. Cosner. 1999. How habitat edges change species interactions. *American Naturalist* 153: 165–182. [24]

Faithfull, I. 1997. *Etiella behrii* (Zeller) (Lepidoptera: Pyralidae) bred from pods of gorse, *Ulex europaeus* L. (Fabaceae). *Victorian Entomologist* 27: 34. [19]

FAO. *Global Forest Resources Assessment 2005*. Food and Agriculture Organization of the United Nations. www.fao.org/forestry/site/24690/en. [24]

FAO. *Global Forest Resources Assessment 2015. How Are the World's Forests Changing?* 2nd ed. Food and Agriculture Organization of the United Nations. www.fao.org/forestry/site/24690/en. [2]

Farrell, B. D. 1998. "Inordinate fondness" explained: Why are there so many beetles? *Science* 281: 555–559. [6]

Farrell, T. M. 1991. Models and mechanisms of succession: An example from a rocky intertidal community. *Ecological Monographs* 61: 95–113. [17]

Favreau, J. M., C. A. Drew, G. R. Hess, M. J. Rubino, F. H. Koch and K. A. Eschelbach. 2006. Recommendations for assessing the effectiveness of surrogate species approaches. *Biodiversity and Conservation* 15: 3949–3969. [23]

Feder, J. L. 1998. The apple maggot fly, *Rhagoletis pomonella*: Flies in the face of conventional wisdom about speciation? In *Endless Forms: Species and Speciation*, D. J. Howard and S. H. Berlocher (eds.), 130–144. Oxford University Press, Oxford. [6]

Fedonkin, M. A., A. Simonetta and A. Y. Ivantsov. 2007. New data on *Kimberella*, the Vendian mollusc-like organism (White Sea region, Russia): Palaeoecological and evolutionary implications. *Geological Society, London, Special Publications* 286: 157–179. [6]

Feely, R. A., C. L. Sabine, K. Lee, W. Berrelson, J. Kleypas, V. J. Fabry and F. J. Millero. 2004. Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. *Science* 305: 362–366. [25]

Fenner, F. and F. N. Ratcliffe. 1965. *Myxomatosis*. Cambridge University Press, Cambridge. [13]

Fernández-Marín, H., J. K. Zimmerman, D. R. Nash, J. J. Boomsma and W. T. Wcislo. 2009. Reduced biological control and enhanced chemical pest management in the evolution of fungus farming in ants. *Proceedings of the Royal Society of London* B 276: 2263–2269. [15]

Ferraz, G., G. J. Russell, P. C. Stouffer, R. O. Bierregaard Jr., S. L. Pimm and T. E. Lovejoy. 2003. Rates of species loss from Amazonian forest fragments. *Proceedings of the National Academy of Sciences USA* 100: 14069–14073. [18]

Field, C. B., M. J. Behrenfeld, J. T. Randerson and P. Falkowski. 1998. Primary productivity of the biosphere: Integrating terrestrial and oceanic components. *Science* 281: 237–240. [20]

Field, D. B., T. R. Baumgartner, C. D. Charles, V. Ferreira-Bartrina and M. D. Ohman. 2006. Planktonic foraminifera of the California current reflect 20th-century warming. *Science* 311: 63–66. [25]

Field, J. P. and 9 others. 2010. The ecology of dust. *Frontiers in Ecology and the Environment* 8: 423–430. [25]

Findley, R. and J. P. Blair. 1990. Will we save our own? *National Geographic* 178: 106–136. [24]

Finkbeiner, E. M., B. P. Wallace, J. E. Moore, R. L. Lewison, L. B. Crowder and A. J. Read. 2011. Cumulative estimates of sea turtle bycatch and mortality in USA fisheries between 1990 and 2007. *Biological Conservation* 144: 2719–2727. [10]

Finkelstein, M. E. and 7 others. 2012. Lead poisoning and the deceptive recovery of the critically endangered California condor. *Proceedings of the National Academy of Sciences USA* 109: 11449–11454. [23]

Fisher, S. G. and G. E. Likens. 1973. Energy budget in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism. *Ecological Monographs* 43: 421–439. [21]

Fitter, A. H. 2005. Darkness visible: Reflections on underground ecology. *Journal of Ecology* 93: 231–243. [15]

Flecker, A. S. and C. R. Townsend. 1994. Community-wide consequences of trout introduction in New Zealand streams. *Ecological Applications* 4: 798–807. [21]

Fleishman, E., D. D. Murphy and P. E. Brussard. 2000. A new method for selection of umbrella species for conservation planning. *Ecological Applications* 10: 569–579. [23]

Flessa, K. W. 1975. Area, continental drift and mammalian diversity. *Paleobiology* 1: 189–194. [18]

Foley, J. A., M. H. Costa, C. Delire, N. Ramankutty and P. Snyder. 2003. Green surprise? How terrestrial ecosystems could affect Earth's climate. *Frontiers in Ecology and Environment* 1: 38–44. [2]

Food and Agriculture Organization of the United Nations. *See* FAO.

Forbes, A. A., T. H. Q. Powell, L. L. Stelinski, J. J. Smith and J. L. Feder. 2009. Sequential sympatric speciation across trophic levels. *Science* 323: 776–779. [6]

Forman, R. T. T. 1995. Some general principles of landscape and regional ecology. *Landscape Ecology* 10: 133–142. [24]

Forrester, M. L., G. Krotkov and C. D. Nelson. 1966. Effect of oxygen on photosynthesis, photorespiration and respiration in detached leaves. II. Corn and other monocotyledons. *Plant Physiology* 41: 428–431. [5]

Foster, W. A. and J. E. Treherne. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature* 293: 466–467. [8]

Frank, P. W., C. D. Boll and R. W. Kelly. 1957. Vital statistics of laboratory cultures of *Daphnia pulex* De Geer as related to density. *Physiological Zoology* 30: 287–305. [10]

Franklin, J. F. 1996. Ecosystem management: An overview. In *Ecosystem Management: Applications for Sustainable Forest and Wildlife Resources*, M. S. Boyce and A. Haney (eds.), 21–53. Yale University Press, New Haven, CT. [24]

Franklin, J. F. and C. T. Dyrness. 1988. *Natural Vegetation of Oregon and Washington*. Oregon State University Press, Corvallis. [18]

Franks, S. J., S. Sim and A. E. Weis. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences USA* 104: 1278–1282. [6]

Frölicher, T. L., M. Winton and J. L. Sarmiento. 2014. Continued global warming after CO_2 emissions stoppage. *Nature Climate Change* 4: 40–44. [25]

Fry, B. 2007. *Stable Isotope Ecology*. Springer, New York. [5]

Funk, D. J., P. Nosil and W. J. Etges. 2006. Ecological divergence exhibits consistently positive associations with reproductive isolation across disparate taxa. *Proceedings of the National Academy of Sciences USA* 103: 3209–3213. [6]

G

Galetti, M. and 14 others. 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* 340: 1086–1090. [23]

Galloway, J. N. and 14 others. 2004. Nitrogen cycles: Past, present, and future. *Biogeochemistry* 70: 153–226. [25]

Galloway, J. N. and 8 others. 2008. Transformation of the nitrogen cycle: Recent trends, questions, and potential solutions. *Science* 320: 889–892. [25]

Garrison, V. H. and 9 others. 2003. African and Asian dust: From desert soils to coral reefs. *BioScience* 53: 469–480. [25]

Gascon, C., G. B. Williamson and G. A. B. da Fonseca. 2000. Receding forest edges and vanishing reserves. *Science* 288: 1356–1358. [18]

Gasol, J. M., P. A. del Giorio and C. M. Duarte. 1997. Biomass distribution in marine planktonic communities. *Limnology and Oceanography* 42: 1353–1363. [21]

Gaston, K. J. 2003. *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, Oxford. [9]

Gaston, K. J., P. H. Williams, P. Eggleton and C. J. Humphries. 1995. Large scale patterns of biodiversity: Spatial variation in family richness. *Proceedings of the Royal Society of London* B 260: 149–154. [18]

Gause, G. F. 1934a. Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. *Science* 79: 16–17. [4, 19]

Gause, G. F. 1934b. *The Struggle for Existence*. Williams & Wilkins, Baltimore, MD. [14]

Geffeney, S. L., E. Fujimoto, E. D. Brodie III, E. D. Brodie Jr. and P. C. Ruben. 2005. Evolutionary diversification of TTX-resistant sodium channels in a predator–prey interaction. *Nature* 434: 759–763. [12]

Gilg, O., I. Hanski and B. Sittler. 2003. Cyclic dynamics in a simple vertebrate predator–prey community. *Science* 302: 866–868. [11, 12]

Gilg, O., B. Sittler and I. Hanski. 2009. Climate change and cyclic predator–prey population dynamics in the high Arctic. *Global Change Biology* 15: 2634–2652. [11]

Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist and R. D. Holt. 2010. A framework for community interactions under climate change. *Trends in Ecology and Evolution* 25: 325–331. [13]

Gleason, H. A. 1917. The structure and development of the plant association. *Bulletin of the Torrey Botanical Club* 44: 463–481. [17]

Glück, E. 1987. Benefits and costs of social foraging and optimal flock size in goldfinches (*Carduelis carduelis*). *Ethology* 74: 65–79. [8]

Godin, J. G. J. and S. E. Briggs. 1996. Female mate choice under predation risk in the guppy. *Animal Behaviour* 51: 117–130. [8]

González, C., O. Wang, S. E. Strutz, C. González-Salazar, V. Sánchez-Cordero and S. Sarkar. 2010. Climate change and risk of leishmaniasis in North America: Predictions from ecological niche models of vector and reservoir species. *PLoS Neglected Tropical Diseases* 4: 1–16. [13]

Gotelli, N. J. and A. M. Ellison. 2013. *A Primer of Ecological Statistics*. 2nd ed. Sinauer Associates, Sunderland, MA. [1]

Gough, L., G. R. Shaver, J. Carroll, D. L. Royer and J. A. Laundre. 2000. Vascular plant species richness in Alaskan arctic tundra: The importance of soil pH. *Journal of Ecology* 88: 54–66. [22]

Goverde, M., K. Schweizer, B. Baur and A. Erhardt. 2002. Small-scale habitat fragmentation effects on pollinator behaviour: Experimental evidence from the bumblebee *Bombus veteranus* on calcareous grasslands. *Biological Conservation* 104: 293–299. [24]

Grabherr, G., M. Gottfried and H. Pauli. 1994. Climate effects on mountain plants. *Nature* 369: 448. [25]

Graham, I. M. and X. Lambin. 2002. The impact of weasel predation on cyclic field-vole survival: The specialist predator hypothesis contradicted. *Journal of Animal Ecology* 71: 946–956. [11]

Grant, B. R. and P. R. Grant. 2003. What Darwin's finches can teach us about the evolutionary origin and regulation of biodiversity. *BioScience* 53: 965–975. [6]

Grant, P. R. and B. R. Grant. 2006. Evolution of character displacement in Darwin's finches. *Science* 313: 224–226. [14]

Graven, H. D. and 13 others. 2013. Enhanced seasonal exchange of CO_2 by northern ecosystems since 1960. *Science* 341: 1085–1089. [25]

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111: 1169–1194. [7]

Groom, M. J. and 7 others. 1999. Buffer zones: Benefits and dangers of compatible stewardship. In *Continental Conservation: Scientific Foundations of Regional Reserve Networks*, M. E. Soulé and J. Terborgh (eds.), 171–197. Island Press, Washington, DC. [24]

Grousset, F. E., P. Ginoux, A. Bory and P. E. Biscaye. 2003. Case study of a Chinese dust plume reaching the French Alps. *Geophysical Research Letters* 30: 1277, doi:10.1029/2002GL016833. [25]

Grutter, A. S., J. M. Murphy and J. H. Choat. 2003. Cleaner fish drives local fish diversity on coral reefs. *Current Biology* 13: 64–67. [15]

Guo, L. B. and R. M. Gifford. 2002. Soil carbon stocks and land use change: A meta analysis. *Global Change Biology* 8: 345–360. [3]

Gurevitch, J., L. L. Morrow, A. Wallace and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. *American Naturalist* 140: 539–572. [14]

Gustafsson, L. and T. Pärt. 1990. Acceleration of senescence in the collared flycatcher *Ficedula albicollis* by reproductive costs. *Nature* 347: 279–281. [7]

H

Haberl, H., K. Erb and F. Krausmann. 2014. Human appropriation of net primary production: Patterns, trends, and planetary boundaries. *Annual Review of Environment and Resources* 39: 363–391. [23]

Hacker, S. D. and M. D. Bertness. 1996. Trophic consequences of a positive plant interaction. *American Naturalist* 148: 559–575. [16]

Hacker, S. D. and M. D. Bertness. 1999. Experimental evidence for the factors maintaining plant species diversity in a New England salt marsh. *Ecology* 80: 2064–2073. [19]

Hacker, S. D. and S. D. Gaines. 1997. Some implications of direct positive interactions for community species diversity. *Ecology* 78: 1990–2003. [19]

Haddad, N. M., G. M. Crutsinger, K. Gross, J. Haarstad and D. Tilman. 2011. Plant diversity and the stability of foodwebs. *Ecology Letters* 14: 42–46. [21]

Haines, B. L. 1978. Element and energy flows through colonies of the leaf-cutting ants, *Atta colombica*, in Panama. *Biotropica* 10: 270–277. [15]

Hairston Jr, N. G. and N. G. Hairston Sr. 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *The American Naturalist* 142: 379–411. [21]

Halpern, B. S. and 18 others. 2008. A global map of human impact on marine ecosystems. *Science* 319: 948–952. [3, 23]

Hamilton, S. L. and J. E. Caselle. 2015. Exploitation and recovery of a sea urchin predator has implications for the resilience of southern California kelp forests. *Proceedings of the Royal Society of London* B 282: 20141817. [7]

Hansen, T. A. 1978. Larval dispersal and species longevity in lower Tertiary gastropods. *Science* 199: 885–887. [7]

Hanski, I. 1999. *Metapopulation Ecology*. Oxford University Press, New York. [11]

Harding, S. R. and J. R. Walters. 2002. Processes regulating the population dynamics of red-cockaded woodpecker cavities. *Journal of Wildlife Management* 66: 1083–1095. [23]

Hare, S. R. and R. C. Francis. 1994. Climate change and salmon production in the Northeast Pacific Ocean. In *Climate Change and Northern Fish Populations*, R. J. Beamish (ed.), 357–372. Canadian Special Publication of Fisheries and Aquatic Sciences, 121. [2]

Harley, C. D. G. 2011. Climate change, keystone predation, and biodiversity loss. *Science* 334: 1124–1127. [23]

Harrison, G. W. 1995. Comparing predator-prey models to Luckinbill's experiment with *Didinium* and *Paramecium*. *Ecology* 76: 357–374. [12]

Harrison, P. 1987. *A Field Guide to Seabirds of the World*. Stephen Greene Press, Lexington, MA. [18]

Harrison, P. and F. Pearce. 2001. *AAAS Atlas of Population and the Environment*. University of California Press, Berkeley. [3]

Harrison, R. G. 1980. Dispersal polymorphisms in insects. *Annual Review of Ecology and Systematics* 11: 95–118. [9]

Hart, M. W. and R. R. Strathmann. 1994. Functional consequences of phenotypic plasticity in echinoid larvae. *Biological Bulletin* 186: 291–299. [7]

Hartl, D. L. and A. G. Clark. 2007. *Principles of Population Genetics*. 4th ed. Sinauer Associates, Sunderland, MA. [6]

Hartmann, D. L. and 13 others. 2013. Observations: Atmosphere and surface. In *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, T. F. Stocker and 9 others (eds.). Cambridge University Press, Cambridge. [25]

Hartnett, D. C. and G. W. T. Wilson. 1999. Mycorrhizae influence plant community structure and diversity in tallgrass prairie. *Ecology* 80: 1187–1195. [15]

Harvell, C. D., C. E. Mitchell, J. R. Ward, S. Altizer, A. P. Dobson, R. S. Ostfeld and M. D. Samuel. 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* 296: 2158–2162. [13]

Harvell, C. D., S. Altizer, I. M. Cattadori, L. Harrington and E. Weil. 2009. Climate change and wildlife diseases: When does the host matter the most? *Ecology* 90: 912–920. [13]

Hawkins, C. E. and 11 others. 2006. Emerging disease and population decline of an island endemic, the Tasmanian devil *Sarcophilus harrisii*. *Biological Conservation* 131: 307–324. [23]

Hawlena, D., M. S. Strickland, M. A. Bradford and O. J. Schmitz. 2012. Fear of predation slows plant-litter decomposition. *Science* 336: 1434–1438. [8]

Hays, J. D., J. Imbrie and N. J. Shackleton. 1976. Variations in the Earth's orbit: Pacemaker of the ice ages. *Science* 194: 1121–1132. [2]

Hearne, S. 1911. *A Journey from Prince of Wales's Fort in Hudson's Bay to the Northern Ocean in the years 1769, 1770, 1771 and 1772*. The Champlain Society, Toronto. [4]

Hebblewhite, M. and 7 others. 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology* 86: 2135–2144. [24]

Hegazy, A. K. 1990. Population ecology and implications for conservation of *Cleome droserifolia*: A threatened xerophyte. *Journal of Arid Environments* 19: 269–282. [10]

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. [16]

Hellmann, J. J., J. E. Byers, B. G. Bierwagen and J. S. Dukes. 2008. Five potential consequences of climate change for invasive species. *Conservation Biology* 22: 534–543. [19]

Henderson, S., P. Hattersley, S. von Caemmerer and C. B. Osmond. 1995. Are C_4 pathway plants threatened by global climatic change? In *Ecophysiology of Photosynthesis*, E.-D. Schulze and M. M. Caldwell (eds.), 529–549. Springer, New York. [5]

Henry, M., J. M. Pons and J. F. Cosson. 2007. Foraging behaviour of a frugivorous bat helps bridge landscape connectivity and ecological processes in a fragmented rainforest. *Journal of Animal Ecology* 76: 801–813. [24]

Hersperger, A. M. 2006. Spatial adjacencies and interactions: Neighborhood mosaics for landscape ecological planning. *Landscape and Urban Planning* 77: 227–239. [24]

Hess, G. R. 1994. Conservation corridors and contagious disease: A cautionary note. *Conservation Biology* 8: 256–262. [24]

Hetrick, B. A. D., G. W. T. Wilson and D. C. Hartnett. 1989. Relationship between mycorrhizal dependence and competitive ability of two tallgrass prairie grasses. *Canadian Journal of Botany* 67: 2608–2615. [15]

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. [23]

Hik, D. S. and R. L. Jefferies. 1990. Increases in the net above-ground primary production of a salt-marsh forage grass: A test of the predictions of the herbivore-optimization model. *Journal of Ecology* 78: 180–195. [12]

Hilderbrand, G. V., S. D. Farley, C. T. Robbins, T. A. Hanley, K. Titus and C. Servheen. 1996. Use of stable isotopes to determine diets of living and extinct bears. *Canadian Journal of Zoology* 74: 2080–2088. [20]

Hiller, N. L., S. Bhattacharjee, C. van Ooij, K. Liolios, T. Harrison, C. Lopez-Estraño and K. Haldar. 2004. A host-targeting signal in virulence proteins reveals a secretome in malarial infection. *Science* 306: 1934–1937. [13]

Hochochka, P. W. and G. N. Somero. 2002. *Biochemical Adaptation, Mechanism and Process in Physiological Evolution*. Oxford University Press, Oxford. [4]

Hof, C., I. Levinsky, M. B. Araujo and C. Rahbek. 2011. Rethinking species' ability to cope with rapid climate change. *Global Change Biology* 17: 2987–2990. [1]

Hof, C., M. B. Araújo, W. Jetz and C. Rahbek. 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature* 480: 516–519. [1]

Hoffmann, M. and 173 others. 2010. The impact of conservation on the status of the world's vertebrates. *Science* 330: 1503–1509. [23]

Hollinger, D. Y. and 14 others. 1998. Forest–atmosphere carbon dioxide exchange in eastern Siberia. *Agricultural and Forest Meteorology* 90: 291–306. [20]

Holt, B. G. and 14 others. 2013. An update of Wallace's zoogeographic regions of the world. *Science* 339: 74–78. [1, 18]

Hooper, R. G., W. E. Taylor and S. C. Loeb. 2004. Long-term efficacy of artificial cavities for red-cockaded woodpeckers: Lessons learned from Hurricane Hugo. In *Red-Cockaded Woodpecker: Road to Recovery*, R. Costa and S. J. Daniels (eds.), 430–438. Hancock House, Blaine, WA. [23]

Hoover, K., M. Grove, M. Gardner, D. P. Hughes, J. McNeil and J. Slavicek. 2011. A gene for an extended phenotype. *Science* 333: 1401. [13]

Houserová, P., V. Kubáň, S. Kráčmar and J. Sitko. 2007. Total mercury and mercury species in birds and fish in an aquatic ecosystem in the Czech Republic. *Environmental Pollution* 145: 185–194. [21]

Howarth, R. W. and 14 others. 1996. Regional nitrogen budgets and riverine N & P fluxes for the drainages to the North Atlantic Ocean: Natural and human influences. *Biogeochemistry* 35: 75–139. [22, 25]

Hu, J., D. J. P. Moore, S. P. Burns and R. K. Monson. 2010. Longer growing seasons lead to less carbon sequestration by a subalpine forest. *Global Change Biology* 16: 771–783. [25]

Hubbell, S. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ. [19]

Hudson, P. J., A. P. Dobson and D. Newborn. 1998. Prevention of population cycles by parasite removal. *Science* 282: 2256–2258. [13]

Huffaker, C. B. 1958. Experimental studies on predation: Dispersion factors and predator–prey oscillations. *Hilgardia* 27: 343–383. [12]

Huffaker, C. B. and C. E. Kennett. 1957. A ten-year study of vegetational changes associated with biological control of Klamath weed. *Journal of Range Management* 12: 69–82. [12]

Huffman, M. A. 1997. Current evidence for self-medication in primates: A multidisciplinary perspective. *Yearbook of Physical Anthropology* 40: 171–200. [13]

Hughes, F., P. M. Vitousek and T. Tunison. 1991. Alien grass invasion and fire in the seasonal submontane zone of Hawai'i. *Ecology* 72: 743–746. [9]

Hughes, J. B., J. J. Hellman, T. H. Ricketts and B. J. M. Bohannan. 2001. Counting the uncountable: Statistical approaches to estimating microbial diversity. *Applied and Environmental Microbiology* 67: 4399–4406. [16]

Humphreys, W. F. 1979. Production and respiration in animal populations. *Journal of Animal Ecology* 48: 427–454. [21]

Hunt, C. E. and S. Behrens Yamada. 2003. Biotic resistance experienced by an invasive crustacean in a temperate estuary. *Biological Invasions* 5: 33–43. [19]

Hunt, G. R. 1996. Manufacture and use of hook-tools by New Caledonian crows. *Nature* 379: 249–251. [5]

Hunt, G. R. and R. D. Gray. 2003. Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proceedings of the Royal Society of London* B 270: 867–874. [5]

Hunziker, J. H., R. A. Palacios, A. G. de Valesi and L. Poggio. 1972. Species disjunctions in *Larrea*: Evidence from morphology, cytogenetics, phenolic compounds and seed albumins. *Annals of the Missouri Botanical Garden* 59: 224–233. [9]

Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* 113: 81–101. [19]

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *American Naturalist* 93: 145–159. [18]

Hutchinson, G. E. 1961. The paradox of the plankton. *American Naturalist* 95: 137–145. [19]

Hutchinson, G. E. 1965. *The Ecological Theater and the Evolutionary Play*. Yale University Press, New Haven, CT. [24]

I

Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89: 353–362. [25]

IPCC. 2013. *Climate Change 2013: The Physical Science Basis*. Available at www.ipcc.ch/report/ar5/wg1/. [25]

J

Jablonski, D. 1995. Extinctions in the fossil record. In *Extinction Rates*, J. H. Lawton and R. M. May (eds.), 25–44. Oxford University Press, Oxford. [6]

Jablonski, D. 2005. Mass extinctions and macroevolution. *Paleobiology* 31: 192–210. [23]

Jablonski, D., K. Roy and J. W. Valentine. 2006. Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. *Science* 314: 102–106. [18]

Jablonski, N. G. 2004. The evolution of human skin and skin color. *Annual Review of Anthropology* 33: 585–623. [25]

Jablonski, N. G. 2006. *Skin: A Natural History*. University of California Press, Berkeley. [4]

Jacobson, M. Z. 2002. *Atmospheric Pollution, History, Science, and Regulation*. Cambridge University Press, Cambridge. [25]

Jaenike, J. and T. D. Brekke. 2011. Defensive endosymbionts: A cryptic trophic level in community ecology. *Ecology Letters* 14: 150–155. [13]

Jaenike, J., R. Unckless, S. N. Cockburn, L. M. Boelio and S. J. Perlman. 2010. Adaptation via symbiosis: Recent spread of a *Drosophila* defensive symbiont. *Science* 329: 212–215. [15]

Jaffe, D., I. McKendry, T. Anderson and H. Price. 2003. Six "new" episodes of trans-Pacific transport of air pollutants. *Atmospheric Environment* 37: 391–404. [25]

Janzen, D. H. 1966. Coevolution of mutualism between ants and acacias in Central America. *Evolution* 20: 249–275. [15]

Janzen, D. H. 1986. The future of tropical ecology. *Annual Review of Ecology and Systematics* 17: 305–324. [23]

Jefferies, R. L., R. F. Rockwell and K. F. Abraham. 2003. The embarrassment of riches: Agricultural food subsidies, high goose numbers, and loss of Arctic wetlands—a continuing saga. *Environmental Reviews* 11: 193–232. [12]

Jentsch, A., J. Kreyling and C. Beierkuhnlein. 2007. A new generation of climate change experiments: Events, not trends. *Frontiers in Ecology and the Environment* 5: 315–324. [2]

Jeschke, J. M. 2007. When carnivores are "full and lazy." *Oecologia* 152: 357–364. [8]

Johnson, D. M. and 7 others. 2010. Climate change disrupts recurrent Alpine insect outbreaks. *Proceedings of the National Academy of Sciences USA* 107: 20576–20581. [11]

Johnson, P. T. J., K. B. Lunde, E. G. Ritchie and A. E. Launer. 1999. The effect of trematode infection on amphibian limb development and survivorship. *Science* 284: 802–804. [1]

Johnson, P. T. J. and 7 others. 2007. Aquatic eutrophication promotes pathogenic infection in amphibians. *Proceedings of the National Academy of Sciences USA* 104: 15781–15786. [1]

Johnson, P. T. J., P. Lund, R. B. Hartson and T. Yoshino. 2009. Community diversity reduces *Schistosoma mansoni* transmission and human infection risk. *Proceedings of the Royal Society of London* B 276: 1657–1663. [19]

Johnson, R. G. and S. A. Temple. 1990. Nest predation and brood parasitism of tallgrass prairie birds. *Journal of Wildlife Management* 54: 106–111. [24]

Johnson, W. E. and 15 others. 2010. Genetic restoration of the Florida panther. *Science* 329: 1641–1645. [23]

Jones, C. G., J. H. Lawton and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69: 373–386. [16]

Jones, C. G., J. H. Lawton and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78: 1946–1957. [16]

Jones, H. L. and J. M. Diamond. 1976. Short-time-base studies of turnover in breeding bird populations on the California Channel Islands. *Condor* 78: 526–549. [11]

Jones, K. E., N. G. Patel, M. A. Levy, A. Storeygard, D. Balk, J. L. Gittleman and P. Daszak. 2008. Global trends in emerging infectious diseases. *Nature* 451: 990–993. [19]

Jordan, M. J. and G. E. Likens. 1975. An organic carbon budget for an oligotrophic lake in New Hampshire. *Verhandlungen Internationale Vereinigung fur Theoretische and Angewandte Limnologie* 19: 994–1003. [21]

Jousson, O. and 8 others. 2000. Invasive alga reaches California. *Nature* 408: 157–158. [16]

K

Kacsoh, B. Z., Z. R. Lynch, N. T. Mortimer and T. A. Schlenke. 2013. Fruit flies medicate offspring after seeing parasites. *Science* 339: 947–950. [8]

Karasov, W. H. and C. Martínez del Rio. 2007. *Physiological Ecology: How Animals Process Energy, Nutrients, and Toxins*. Princeton University Press, Princeton, NJ. [5]

Karban, R. and G. English-Loeb. 1997. Tachinid parasitoids affect host plant choice by caterpillars to increase caterpillar survival. *Ecology* 78: 603–611. [13]

Karell, P., K. Ahola, T. Karstinen, J. Valkama and J. E. Brommer. 2011. Climate change drives microevolution in a wild bird. *Nature Communications* 2, doi:10.1038/ncomms1213. [6]

Kauffman, M. J., J. F. Brodie and E. S. Jules. 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology* 91: 2742–2755. [24]

Keesing, F. and 10 others. 2010. Impacts of biodiversity on the emergence and transmission of infectious diseases. *Nature* 468: 647–652. [19]

Keever, K. 1953. Present composition of some stands of the former oak–chestnut forest in the southern Blue Ridge Mountains. *Ecology* 34: 44–54. [13]

Keller, I. and C. R. Largiadèr. 2003. Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. *Proceedings of the Royal Society of London* B 270: 417–423. [24]

Kenward, B., A. A. S. Weir, C. Rutz and A. Kacelnik. 2005. Tool manufacture by naive juvenile crows. *Nature* 433: 121. [5]

Kenward, R. E. 1978. Hawks and doves: Factors affecting success and selection in goshawk attacks on woodpigeons. *Journal of Animal Ecology* 47: 449–460. [8]

Kerr, J. T. and 13 others. 2015. Climate change impacts on bumblebees converge across continents. *Science* 349: 177–180. [9]

Kerr, P. J. and S. M. Best. 1998. Myxoma virus in rabbits. *Revue scientifique et technique – Office international des epizooties* 17: 256–268. [13]

Kessler, A. and I. T. Baldwin. 2001. Defensive function of herbivore-induced plant volatile emissions in nature. *Science* 291: 2141–2144. [12]

Kettlewell, H. B. D. 1955. Selection experiments on industrial melanism in the Lepidoptera. *Heredity* 9: 323–342. [6]

Kettlewell, H. B. D. 1956. Further selection experiments on industrial melanism in the Lepidoptera. *Heredity* 10: 287–301. [6]

Kideys, A. E. 2002. Fall and rise of the Black Sea ecosystem. *Science* 297: 1482–1484. [11]

Kiehl, J. T. and K. E. Trenberth. 1997. Earth's annual global mean energy budget. *Bulletin of the American Meteorological Society* 78: 197–208. [2]

Kiers, E. T. and 14 others. 2011. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science* 333: 880–882. [15]

Kiesecker, J. M. 2002. Synergism between trematode infection and pesticide exposure: A link to amphibian limb deformities in nature? *Proceedings of the National Academy of Sciences USA* 99: 9900–9904. [1]

Kinchy, A. J. 2006. On the borders of post-war ecology: Struggles over the Ecological Society of America's preservation committee, 1917–1946. *Science as Culture* 15: 23–44. [23]

King, A. A. and W. M. Schaffer. 2001. The geometry of a population cycle: A mechanistic model of snowshoe hare demography. *Ecology* 82: 814–830. [12]

Kingsland, S. E. 1991. Defining ecology as a science. In *Foundations of Ecology: Classic Papers with Commentaries*, L. A. Real and J. H. Brown (eds.), 1–13. University of Chicago Press, Chicago. [17]

Kinnison, M. T. and A. P. Hendry. 2001. The pace of modern life II: From rates of contemporary evolution to pattern and process. *Genetica* 112–113: 145–164. [6]

Kinzig, A. P. and J. Harte. 2000. Implications of endemics–area relationships for estimates of species extinctions. *Ecology* 81: 3305–3311. [23]

Kitzes, J. and M. Wackernagel. 2009. Answers to common questions in Ecological Footprint accounting. *Ecological Indicators* 9: 812–817. [10]

Knapp, A. K. and 9 others. 2002. Rainfall variability, carbon cycling and plant species diversity in a mesic grassland. *Science* 298: 2202–2205. [3]

Kodric-Brown, A. and J. M. Brown. 1993. Highly structured fish communities in Australian desert springs. *Ecology* 74: 1847–1855. [18]

Kohler, S. L. and M. J. Wiley. 1997. Pathogen outbreaks reveal large-scale effects of competition in stream communities. *Ecology* 78: 2164–2176. [13]

Köhler, W. 1927. *The Mentality of Apes*. Routledge & Kegan Paul, London. [5]

Komdeur, J. 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* 358: 493–495. [9]

Kondoh, M. 2003. Foraging adaptation and the relationship between food-web complexity and stability. *Science* 299: 1388–1391. [21]

Kopp, R. E. and 9 others. 2016. Temperature-driven global sea-level variability in the Common Era. *Proceedings of the National Academy of Sciences USA* 113: E1434–E1441. [25]

Korpimäki, E. and K. Norrdahl. 1998. Experimental reduction of predators reverses the crash phase of small-rodent cycles. *Ecology* 79: 2448–2455. [11]

Koskela, T., S. Puustinen, V. Salonen and P. Mutikainen. 2002. Resistance and tolerance in a host plant–holoparasitic plant interaction: Genetic variation and costs. *Evolution* 56: 899–908. [5]

Kozaki, A. and G. Takeba. 1996. Photorespiration protects C_3 plants from photooxidation. *Nature* 384: 557–580. [5]

Kraaijeveld, A. R., K. A. Hutcheson, E. C. Limentani and H. C. J. Godfray. 2001. Costs of counterdefenses to host resistance in a parasitoid of *Drosophila*. *Evolution* 55: 1815–1821. [13]

Krebs, C. J. 1999. *Ecological Methodology*. Addison Wesley, Menlo Park, CA. [9]

Krebs, C. J. and 7 others. 1995. Impact of food and predation on the snowshoe hare cycle. *Science* 269: 1112–1115. [12]

Krebs, J. B., J. T. Eriksen, M. T. Webber and E. L. Charnov. 1977. Optimal prey selection in the great tit (*Parus major*). *Animal Behaviour* 25: 30–38. [8]

Kremen, C. 2014. Giving back: Nature conservation in Madagascar. *Journal of Research Practice* 10: 8. [24]

Kremen, C., V. Razafimahatratra, R. P. Guillery, J. Rakotomalala, A. Weiss and J. S. Ratsisompatrarivo. 1999. Designing the Masoala National Park in Madagascar based on biological and socioeconomic data. *Conservation Biology* 13: 1055–1068. [24]

Kricher, J. 1998. *A Field Guide to Eastern Forests*. Illustrated by G. Morrison. Houghton Mifflin, New York. [18]

Krümmel, E. M. and 7 others. 2003. Delivery of pollutants by spawning salmon. *Nature* 425: 255. [21]

Krützen, M., J. Mann, M. R. Heithaus, R. C. Connor, L. Bejder and W. B. Sherwin. 2005. Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences USA* 102: 8939–8943. [5]

Kuhnlein, H. V., O. Receveur, D. C. G. Muir, H. M. Chan and R. Soueida. 1995. Arctic indigenous women consume greater than acceptable levels of organochlorines. *Journal of Nutrition* 125: 2501–2510. [21]

Kurz, W. A. and 7 others. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452: 987–990. [11, 20]

L

Lack, D. 1947a. The significance of clutch size. *Ibis* 89: 302–352. [7]

Lack, D. 1947b. *Darwin's Finches*. Cambridge University Press, Cambridge. [14]

Lambers, H., F. S. Chapin III and T. L. Pons. 1998. *Plant Physiological Ecology*. Springer, New York. [4, 5]

Lambers, H., T. L. Pons and F. S. Chapin III. 2008. *Plant Physiological Ecology*. 2nd ed. Springer, New York. [5]

Lande, R. 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* 75: 601–607. [11]

Landesman, W. J., B. F. Allan, R. B. Langerhans, T. M. Knight and J. M. Chase. 2007. Inter-annual associations between precipitation and human incidence of West Nile virus in the United States. *Vector-Borne and Zoonotic Diseases* 7: 337–343. [1]

Langerhans, R. B., M. E. Gifford and E. O. Joseph. 2007. Ecological speciation in *Gambusia* fishes. *Evolution* 61: 2056–2074. [6]

Larcher, W. 1980. *Physiological Plant Ecology*. Springer, Berlin. [20]

Lauenroth, W. K. and O. E. Sala. 1992. Long-term forage production of North American shortgrass steppe. *Ecological Applications* 2: 397–403. [20]

Laurance, W. F. 2001. The hyper-diverse flora of the Central Amazon. In *Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest*, R. O. Bierregaard Jr., C. Gascon, T. E. Lovejoy and R. C. G. Mesquita (eds.), 47–53. Yale University Press, New Haven, CT. [18]

Laurance, W. F. and 10 others. 2002. Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology* 16: 605–618. [18, 24]

Law, R. 1975. Colonization and the evolution of life histories in *Poa annua*. Unpublished PhD thesis, University of Liverpool. [10]

Law, R., A. D. Bradshaw and P. D. Putwain. 1977. Life-history variation in *Poa annua*. *Evolution* 31: 233–246. [7]

Lawler, S. P. 1993. Species richness, species composition and population dynamics of protists in experimental microcosms. *Journal of Animal Ecology* 62: 711–719. [21]

Lawton, J. H. 2000. *Community Ecology in a Changing World*. Excellence in Ecology, O. Kinne (ed.), no. 11. Ecology Institute, Luhe, Germany. [19]

Layne, J. R. and R. E. Lee. 1995. Adaptations of frogs to survive freezing. *Climate Research* 5: 53–59. [4]

Lennartsson, T., P. Nilsson and J. Tuomi. 1998. Induction of overcompensation in the field gentian, *Gentianella campestris*. *Ecology* 79: 1061–1072. [12]

Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943–1967. [24]

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15: 237–240. [11]

Levins, R. 1970. Extinction. In *Some Mathematical Problems in Biology*, M. Gerstenhaber (ed.), 75–107. American Mathematical Society, Providence, RI. [11]

Lewison, R. L., L. B. Crowder, A. J. Read and S. A. Freeman. 2004. Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology and Evolution* 19: 598–604. [23]

Lewontin, R. C. 1969. The meaning of stability. In *Diversity and Stability in Ecological Systems*, 13–24. Brookhaven Symposia in Biology, no. 22. Brookhaven National Laboratories, Brookhaven, NY. [17]

Likens, G. E. and F. H. Bormann. 1995. *Biogeochemistry of a Forested Ecosystem*. Springer, New York. [22]

Lima, S. L. 1998. Nonlethal effects in the ecology of predator–prey interactions. *BioScience* 48: 25–34. [8]

Lindeman, R. L. 1942. The trophic–dynamic aspect of ecology. *Ecology* 23: 399–418. [20]

Lindenmayer, D. B. and M. A. McCarthy. 2006. Evaluation of PVA models of arboreal marsupials: Coupling models with long-term monitoring data. *Biodiversity and Conservation* 15: 4079–4096. [23]

Lindqvist, C. and 13 others. 2010. Complete mitochondrial genome of a Pleistocene jawbone unveils the origin of polar bear. *Proceedings of the National Academy of Sciences USA* 107: 5053–5057. [9]

Ling, S. D. 2008. Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: A new and impoverished reef state. *Oecologia* 156: 883–894. [9]

Ling, S. D., C. R. Johnson, S. D. Frusher and K. R. Ridgway. 2009. Over-fishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. *Proceedings of the National Academy of Sciences USA* 106: 22341–22345. [9]

Lippincott, C. L. 2000. Effects of *Imperata cylindrica* (L.) Beauv. (cogongrass) invasion on fire regime in Florida sandhill. *Natural Areas Journal* 20: 140–149. [23]

Little, D. P. and D. W. Stevenson. 2007. A comparison of algorithms for the identification of specimens using DNA barcodes: Examples from gymnosperms. *Cladistics* 23: 1–21. [23]

Liu, H., E. S. Menges and P. F. Quintana-Ascencio. 2005. Population viability analyses of *Chamaecrista keyensis*: Effects of fire season and frequency. *Ecological Applications* 15: 210–221. [23]

Livdahl, T. P. and M. S. Willey. 1991. Prospects for an invasion: Competition between *Aedes albopictus* and native *Aedes triseriatus*. *Science* 253: 189–191. [14]

Lively, C. M. 1989. Adaptation by a parasitic trematode to local populations of its snail host. *Evolution* 43: 1663–1671. [13]

Logan, J. A., and J. A. Powell. 2001. Ghost forest, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist* 47: 160–172. [24]

Locey, K. J. and J. T. Lennon. 2016. Scaling laws predict global microbial diversity. *Proceedings of the National Academy of Sciences USA* 113: 5970–5975. [23]

Lomolino, M. V., J. H. Brown and R. Davis. 1989. Island biogeography of montane forest mammals in the American Southwest. *Ecology* 70: 180–194. [18]

Lönnstedt, O. M. and P. Eklöv. 2016. Environmentally relevant concentrations of microplastic particles influence larval fish ecology. *Science* 352: 1213–1216. [8]

Lotka, A. J. 1932. The growth of mixed populations: Two species competing for a common food supply. *Journal of the Washington Academy of Sciences* 22: 461–469. [14]

Louda, S. M., D. Kendall, J. Conner and D. Simberloff. 1997. Ecological effects of an insect introduced for the biological control of weeds. *Science* 277: 1088–1090. [9]

Lukas, D. and T. H. Clutton-Brock. 2013. The evolution of social monogamy in mammals. *Science* 341: 526–530. [8]

Lüthi, D. and 10 others. 2008. High resolution carbon dioxide concentrations record 650,000–800,000 years before present. *Nature* 453: 379–382. [25]

M

MacArthur, R. H. 1955. Fluctuations in animal populations and a measure of community stability. *Ecology* 36: 533–536. [19]

MacArthur, R. H. 1958. Population ecology of some warblers of Northeastern coniferous forests. *Ecology* 39: 599–619. [19]

MacArthur, R. H. and J. W. MacArthur. 1961. On bird species diversity. *Ecology* 42: 594–598. [19]

MacArthur, R. H. and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17: 373–387. [18]

MacArthur, R. H. and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ. [7, 18]

MacDonald, I. A. W., L. L. Loope, M. B. Usher and O. Hamann. 1989. Wildlife conservation and the invasion of nature reserves by introduced species: A global perspective. In *Biological Invasions: A Global Perspective*, J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek and M. Williamson (eds.), 215–256. SCOPE (Scientific Committee on Problems of the Environment), 37. John Wiley & Sons, Chichester, UK. [23]

Mack, R. N. and J. N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. *American Naturalist* 119: 757–773. [22]

MacLulich, D. A. 1937. Fluctuations in the numbers of the varying hare (*Lepus americanus*). University of Toronto studies, Biological Series, no. 43. University of Toronto Press, Toronto. [12]

Macnair, M. R. and P. Christie. 1983. Reproductive isolation as a pleiotropic effect of copper tolerance in *Mimulus guttatus*. *Heredity* 50: 295–302. [6]

MacPhee, R. D. E. and P. A. Marx. 1997. Humans, hyperdisease, and first-contact extinctions. In *Natural Change and Human Impact in Madagascar*, S. M. Goodman and B. D. Patterson (eds.), 169–217. Smithsonian Institution Press, Washington, DC. [3]

Madigan, M. T. and J. M. Martinko. 2005. *Brock Biology of Microorganisms*. Prentice Hall, Upper Saddle River, NJ. [5]

Madronich, S., R. L. McKenzie, L. O. Björn and M. M. Caldwell. 1998. Changes in biologically active ultraviolet radiation reaching the Earth's surface. *Journal of Photochemistry and Photobiology* B: *Biology* 46: 5–19. [25]

Mahowald, N. and 8 others. 2005. The atmospheric global dust cycle and iron inputs to the ocean. *Global Biogeochemical Cycles* 19: GB4025 10.1029/2004GB002402. [25]

Maitland, D. P. 1994. A parasitic fungus infecting yellow dungflies manipulates host perching behaviour. *Proceedings of the Royal Society of London* B 258: 187–193. [13]

Mannion, P. D., P. Upchurch, R. B. J. Benson and A. Goswami. 2014. The latitudinal biodiversity gradient through deep time. *Trends in Ecology and Evolution* 29: 42–50. [18]

Mantua, N. J. 2001. The Pacific Decadal Oscillation. In *The Encyclopedia of Global Environmental Change*, vol. 1, *The Earth System: Physical and Chemical Dimensions of Global Environmental Change*, M. C. McCracken and J. S. Perry (eds.), 592–594. Wiley, New York. [2]

Mantua, N. J. and S. R. Hare. 2002. The Pacific Decadal Oscillation. *Journal of Oceanography* 58: 35–44. [2]

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78: 1069–1079. [2]

Margoluis, R. and N. Salafsky. 1998. *Measures of Success: Designing, Managing, and Monitoring Conservation and Development Projects*. Island Press, Washington, DC. [24]

Maron, J. L. and M. Vila. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* 95: 361–373. [19]

Marr, J. W. 1967. *Ecosystems of the East Slope of the Front Range of Colorado*. University of Colorado Studies, Series in Biology, no. 8. University of Colorado Press, Boulder. [3]

Marschner, H. 1995. *Mineral Nutrition of Higher Plants*. Academic Press, San Diego, CA. [22]

Marti, M., R. T. Good, M. Rug, E. Knuepfer and A. F. Cowman. 2004. Targeting malaria virulence and remodeling proteins to the host erythrocyte. *Science* 306: 1930–1933. [13]

Martin, J. A., B. E. Hamilton, P. D. Sutton, S. J. Ventura, F. Menacker, S. Kirmeyer and T. J. Mathews. 2009. *Births: Final data for 2006*. National Vital Statistics Reports, vol. 57, no. 7. National Center for Heath Statistics, Hyattsville, MD. www.cdc.gov/nchs/data/nvsr/nvsr57/nvsr57_07.pdf. [10]

Martin, J. H. and 43 others. 1994. Testing the iron hypothesis in ecosystems of the equatorial Pacific Ocean. *Nature* 371: 123–129. [20]

Martin, J. K. and A. A. Martin. 2007. Resource distribution influences mating system in the bobuck (*Trichosurus cunninghami*: Marsupialia). *Oecologia* 154: 227–236. [8]

Martin, P. A., A. C. Newton and J. M. Bullock. 2013. Carbon pools recover more quickly than plant diversity in tropical secondary forests. *Proceedings of the Royal Society of London* B 280: 20132236. [3]

Martin, P. S. 1984. Prehistoric overkill: The global model. In *Quaternary Extinctions: A Prehistoric Revolution*, P. S. Martin and R. G. Klein (eds.), 354–403. University of Arizona Press, Tucson. [3]

Martin, P. S. 2005. *Twilight of the Mammoths: Ice Age Extinctions and the Rewilding of America*. University of California Press, Berkeley. [3]

Maslin, M. A. and E. Thomas. 2003. Balancing the deglacial global carbon budget: The hydrate factor. *Quaternary Science Reviews* 22: 1729–1736. [5]

Mattson, W. J. Jr. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* 11: 119–161. [12]

Matsui, H. and 8 others. 2016. Adaptive bill morphology for enhanced tool manipulation in New Caledonian crows. *Scientific Reports* 6: 22776. [5]

Mauseth, J. D. 1988. *Plant Anatomy*. Benjamin Cummings, Menlo Park, CA. [15]

May, R. M. 1973. *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, NJ. [21]

May, R. M. 1976. Models for single populations. In *Theoretical Ecology: Principles and Applications*, R. M. May (ed.), 4–25. W. B. Saunders, Philadelphia. [11]

May, R. M. 2011. Why worry about how many species and their loss? *PLoS Biology* 9: e1001130. [23]

May, R. M. and R. M. Anderson. 1983. Epidemiology and genetics in the coevolution of parasites and hosts. *Proceedings of the Royal Society of London* B 219: 281–313. [13]

May, R. M. and R. M. Anderson. 1983. Parasite–host coevolution. In *Coevolution*, D. J. Futuyma and M. Slatkin (eds.), 186–206. Sinauer Associates, Sunderland, MA. [13]

May, R. M., J. H. Lawton and N. E. Stork. 1995. Assessing extinction rates. In *Extinction Rates*, J. H. Lawton and R. M. May (eds.), 1–24. Oxford University Press, Oxford. [23]

McCann, K., A. Hastings and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. *Nature* 395: 794–798. [21]

McClain, M. E. and 11 others. 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. *Ecosystems* 6: 301–312. [24]

McClenachan, L. 2009. Documenting the loss of large trophy fish from the Florida Keys with historical photographs. *Conservation Biology* 23: 636–643. [23]

McCracken, K. G. and 9 others. 2009. Parallel evolution in the major haemoglobin genes of eight species of Andean waterfowl. *Molecular Ecology* 18: 3992–4005. [6]

McDonald, M. J., D. P. Rice and M. M. Desai. 2016. Sex speeds adaptation by altering the dynamics of molecular evolution. *Nature* 531: 233–236. [7]

McEvoy, P., C. Cox and E. Coombs. 1991. Successful biological control of ragwort, *Senecio jacobaea*, by introduced insects in Oregon. *Ecological Applications* 1: 430–442. [14]

McGraw, W. S. 2005. Update on the search for Miss Waldron's red colobus monkey. *International Journal of Primatology* 26: 605–619. [23]

McIntyre, S. and R. Hobbs. 1999. A framework for conceptualizing human effects on landscapes and its relevance to management and research models. *Conservation Biology* 13: 1282. [24]

McKane, R. B. and 10 others. 2002. Resource-based niches provide a basis for plant species diversity and dominance in Arctic tundra. *Nature* 415: 68–71. [22]

McKinney, S. T., C. E. Fiedler, and D. F. Tomback. 2009. Invasive pathogen threatens bird-pine mutualism: Implications for sustaining a high-elevation ecosystem. *Ecological Applications* 19: 597–607. [24]

McMahon, T. A. and 16 others. 2014. Amphibians acquire resistance to live and dead fungus overcoming fungal immunosuppression. *Nature* 511: 224–227. [1]

McMahon, T. E. and J. C. Tash. 1988. Experimental analysis of the role of emigration in population regulation of desert pupfish. *Ecology* 69: 1871–1883. [9]

McNeill, W. H. 1976. *Plagues and Peoples*. Anchor Press/Doubleday, Garden City, NY. [13]

McNeilly, T. 1968. Evolution in closely adjacent plant populations. III. *Agrostis tenuis* on a small copper mine. *Heredity* 23: 99–108. [6]

Meine, C., M. Soulé and R. F. Noss. 2006. "A mission-driven discipline": The growth of conservation biology. *Conservation Biology* 20: 631–651. [23]

Meinesz, A. 2001. *Killer Algae*. University of Chicago Press, Chicago. [16]

Meire, P. M. and A. Ervynck. 1986. Are oystercatchers (*Haematopus ostralegus*) selecting the most profitable mussels (*Mytilus edulis*)? *Animal Behaviour* 34: 1427–1435. [8]

Melillo, J. M., J. D. Aber and J. F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63: 621–626. [22]

Mellars, P. 1989. Major issues in the emergence of modern humans. *Current Anthropology* 30: 349–385. [5]

Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: Patterns and importance. *Ecological Monographs* 65: 21–74. [16]

Menge, B. A. and J. P. Sutherland. 1987. Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* 130: 730–757. [19]

Menge, B. A., B. Daley and P. A. Wheeler. 1996. Control of interaction strength in marine benthic communities. In *Food Webs: Integration of Patterns and Dynamics*, G. A. Polis and K. O. Winemiller (eds.), 258–274. Chapman & Hall, New York. [16]

Merrick, R. L., T. R. Loughlin and D. G. Calkins. 1987. Decline in abundance of the northern sea lion, *Eumetopias jubatus*, in Alaska, 1956–86. *Fishery Bulletin* 85: 351–365. [21]

Millennium Ecosystem Assessment. 2005. *Ecosystems and Human Well-Being: Biodiversity Synthesis*. World Resources Institute, Washington, DC. [18, 19, 23]

Mills, L. S., M. Zimova, J. Oyler, S. Running, J. T. Abatzoglou and P. M. Lukacs. 2013. Camouflage mismatch in seasonal coat color due to decreased snow duration. *Proceedings of the National Academy of Sciences USA* 110: 7360–7365. [7]

Minorsky, P. V. 2002. Allelopathy and grain crop production. *Plant Physiology* 130: 1745–1746. [14]

Mittelbach, G. G. and 21 others. 2007. Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecology Letters* 10: 315–331. [18]

Mitton, J. B. and S. M. Ferrenberg. 2012. Mountain pine beetle develops an unprecedented summer generation in response to climate warming. *American Naturalist* 179: E163–E171. [25]

Mokany, K., R. J. Raison and A. S. Prokushkin. 2006. Critical analysis of root:shoot ratios in terrestrial biomes. *Global Change Biology* 12: 84–96. [4]

Molina, M. J. and F. S. Rowland. 1974. Stratospheric sink for chlorofluoromethanes: Chlorine atom-catalysed destruction of ozone. *Nature* 249: 810–812. [25]

Moore, J. A. 1957. An embryologist's view of the species concept. In *The Species Problem*, E. Mayr (ed.), 325–388. American Association for the Advancement of Science, Washington, DC. [6]

Moore, S. E., T. J. Cole, E. M. E. Poskitt, B. J. Sonko, R. G. Whitehead, I. A. McGregor and A. M. Prentice. 1997. Season of birth predicts mortality in rural Gambia. *Nature* 388: 434. [10]

Morford, S. L., B. Z. Houlton and R. A. Dahlgren. 2016. Direct quantification of long-term rock nitrogen inputs to temperate forest ecosystems. *Ecology* 97: 54–64. [25]

Morin, X., C. Augspurger and I. Chuine. 2007. Process-based modeling of species' distributions: What limits temperate tree species' range boundaries? *Ecology* 88: 2280–2291. [4]

Morran, L. T., O. G. Schmidt, I. A. Gelarden, R. C. Parrish II and C. M. Lively. 2011. Running with the Red Queen: Host–parasite coevolution selects for biparental sex. *Science* 333: 216–218. [7]

Morris, W. F. and D. F. Doak. 2002. *Quantitative Conservation Biology: Theory and Practice of Population Viability*. Sinauer Associates, Sunderland, MA. [11, 23]

Mouritsen, K. N. and R. Poulin. 2002. Parasitism, community structure and biodiversity in intertidal ecosystems. *Parasitology* 124: S101–S117. [13]

Mouritsen, K. N., L. T. Mouritsen and K. T. Jensen. 1998. Changes of topography and sediment characteristics on an intertidal mud-flat following mass-mortality of the amphipod *Corophium volutator*. *Journal of the Marine*

Biological Association of the United Kingdom 78: 1167–1180. [13]

Moutinho, P., C. D. Napstad and E. A. Davidson. 2003. Influence of leaf-cutting ant nests on secondary forest growth and soil properties in Amazonia. *Ecology* 84: 1265–1276. [15]

Muir, J. 1915. *Travels in Alaska*. Houghton Mifflin, Boston. [17]

Munger, J. 1984. Optimal foraging? Patch use by horned lizards (Iguanidae: *Phrynosoma*). *American Naturalist* 123: 654–680. [8]

Murdoch, W. W., S. Avery and M. E. B Smith. 1975. Switching in a predatory fish. *Ecology* 56: 1094–1105. [12]

Murphy, D. D. and C. M. Knopp. 2000. *Lake Tahoe Watershed Assessment.* Vol. 1. General Technical Report PSW-GTR-175. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA. [22]

Myers, J. H. and D. Bazely. 1991. Thorns, spines, prickles, and hairs: Are they stimulated by herbivory and do they deter herbivores? In *Phytochemical Induction by Herbivores*, D. W. Tallamy and M. J. Raupp (eds.), 325–344. Wiley, New York. [12]

Myers, R. A. and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423: 280–283. [23]

N

Nabhan, G. P. and A. R. Holdsworth. 1998. *State of the Sonoran Desert Biome: Uniqueness, Biodiversity, Threats and the Adequacy of Protection in the Sonoran Bioregion*. The Wildlands Project, Tucson, AZ. [3]

Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton and R. M. Woodfin. 1995. Empirical evidence that declining species diversity may alter the performance of terrestrial systems. *Philosophical Transactions of the Royal Society of London* B 347: 249–262. [19]

Nager, R. G., P. Monaghan and D. Houston. 2000. Within-clutch trade-offs between the number and quality of eggs: Experimental manipulations in gulls. *Ecology* 81: 1339–1350. [7]

Naiman, R. J., C. A. Johnston and J. C. Kelley. 1988. Alterations of North American streams by beaver. *BioScience* 38: 753–762. [16]

National Research Council. 2002. *Effects of Trawling and Dredging on Seafloor Habitat*. Committee on Ecosystem Effects of Fishing: Phase I—Effects of Bottom Trawling on Seafloor Habitats, Ocean Studies Board, Division on Earth and Life Studies, National Research Council. National Academies Press, Washington, DC. [23]

NatureServe. 2013. www.natureserve.org/conservation-tools/natureserve-hotspots-map. [23]

Naughton-Treves, L., J. L. Mena, A. Treves, N. Alvarez and V. C. Radeloff. 2003. Wildlife survival beyond park boundaries: The impact of slash-and-burn agriculture and hunting on mammals in Tambopata, Peru. *Conservation Biology* 17: 1106–1117. [24]

Nee, S., N. Colegrave, S. A. West and A. Grafen. 2005. The illusion of invariant quantities in life histories. *Nature* 309: 1236–1239. [7]

Neff, J. C., R. L. Reynolds, J. Belnap and P. Lamothe. 2005. Multi-decadal impacts of grazing on soil physical and biogeochemical properties in southeastern Utah. *Ecological Applications* 15: 87–95. [22]

Nemani, R. R. and 7 others. 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science* 300: 1560–1563. [25]

Neutel, A.-M., J. A. P. Heesterbeek and P. C. de Ruiter. 2002. Stability in real food webs: Weak links in long loops. *Science* 296: 1120–1123. [21]

Newbold, J. D., J. W. Elwood, R. V. O'Neill and A. L. Sheldon. 1983. Phosphorus dynamics in a woodland stream ecosystem: A study of nutrient spiralling. *Ecology* 64: 1249–1265. [22]

Nicholson, A. J. 1957. The self-adjustment of populations to change. *Cold Spring Harbor Symposia on Quantitative Biology* 22: 153–173. [11]

Norby, R. J. and 13 others. 2005. Forest response to elevated CO_2 is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences USA* 102: 18052–18056. [25]

Noss, R., E. Dinerstein, B. Gilbert, M. Gilpin, B. J. Miller, J. Terborgh and S. Trombulak. 1999. Core areas: Where Nature reigns. In *Continental Conservation: Scientific Foundations of Regional Reserve Networks*, M. E. Soulé and J. Terborgh (eds.), 99–128. Island Press, Washington, DC. [24]

O

Oates, J. F., M. Abedi-Lartey, W. S. McGraw, T. T. Struhsaker; and G. H. Whitesides. 2000. Extinction of a West African red colobus monkey. *Conservation Biology* 14: 1526–1532. [23]

Odum, H. T. and C. F. Jordan. 1970. Metabolism and evapotranspiration of the lower forest in a giant plastic cylinder. In *A Tropical Rain Forest*, H. T. Odum and R. F. Pigeon (eds.), 165–189. Division of Technical Information, U.S. Atomic Energy Commission. [20]

Oechel, W. C., S. J. Hastings, G. Vourlitis, M. Jenkins, G. Riechers and N. Grulke. 1993. Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature* 361: 520–523. [25]

Oechel, W. C., G. L. Vourlitis, S. J. Hastings, R. C. Zulueta, L. Hinzman and D. Kane. 2000. Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. *Nature* 406: 978–981. [25]

Ogren, W. L. 1984. Photorespiration: Pathways, regulation, and modification. *Annual Review of Plant Physiology* 35: 415–442. [5]

Okin, G. S., N. Mahowald, O. A. Chadwick and P. Artaxo. 2004. Impact of desert dust on the biogeochemistry of phosphorus in terrestrial ecosystems. *Global Biogeochemical Cycles* 18: GB2005. [25]

Olden, J. D., N. L. Poff, M. R. Douglas, M. E. Douglas and K. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution* 19: 18–24. [23]

Oliver, K. M., J. Campos, N. A. Moran and M. S. Hunter. 2008. Population dynamics of defensive symbionts in aphids. *Proceedings of the Royal Society of London* B 275: 293–299. [12]

Orr, J. C. and 26 others. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437: 681–686. [2, 3, 25]

Osborn, S. 2007. Distribution of the cattle egret (*Bubulcus ibis*) in North America. In *The Birds of North America Online*, A. Poole (ed.). Cornell Lab of Ornithology, Ithaca, NY. [11]

Osmond, C. B., K. Winter and H. Ziegler. 1982. Functional significance of different pathways of photosynthesis. In *Physiological Plant Ecology*, vol. 2, O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler (eds.), 479–547. Encyclopedia of Plant Physiology, new series, vol. 12B. Springer, New York. [5]

Ostfeld, R. S. 2009. Climate change and the distribution and intensity of infectious diseases. *Ecology* 90: 903–905. [13]

Overpeck, J. T., R. S. Webb and T. Webb. 1992. Mapping eastern North American vegetation change of the past 18,000 years: No-analogs and the future. *Geology* 20: 1071–1074. [25]

Owen-Smith, N. 1987. Pleistocene extinctions: The pivotal role of megaherbivores. *Paleobiology* 13: 351–362. [3]

P

Pace, M. L. and 8 others. 2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. *Nature* 427: 240–243. [21]

Packer, C., A. E. Pusey, H. Rowley, D. A. Gilbert, J. Martenson and S. J. O'Brien. 1991. Case study of a population bottleneck: Lions of the Ngorongoro Crater. *Conservation Biology* 5: 219–230. [11]

Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100: 65–75. [19, 21]

Paine, R. T. 1974. Intertidal community structure: Experimental studies on the relations between a dominant competitor and its principal predator. *Oecologia* 15: 93–120. [12]

Paine, R. T. 1979. Disaster, catastrophe, and local persistence of the sea palm, *Postelsia palmaeformis*. *Science* 205: 685–687. [14]

Paine, R. T., J. C. Castillo and J. Cancino. 1985. Perturbation and recovery patterns of starfish-dominated intertidal assemblages in Chile, New Zealand, and Washington State. *American Naturalist* 125: 679–691. [21]

Palumbi, S. R. 2001. Humans as the world's greatest evolutionary force. *Science* 293: 1786–1790. [6]

Pardini, R. 2004. Effects of forest fragmentation on small mammals in an Atlantic Forest landscape. *Biodiversity and Conservation* 13: 2567–2586. [24]

Park, T. 1948. Experimental studies of interspecies competition. I. Competition between populations of the flour beetles, *Tribolium confusum* Duvall and *Tribolium castaneum* Herbst. *Ecological Monographs* 18: 267–307. [13]

Parmenter, A. W. and 8 others. 2003. Land use and land cover change in the Greater Yellowstone Ecosystem: 1975–1995. *Ecological Applications* 13: 687–703. [24]

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37: 637–669. [1, 6, 23, 25]

Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42. [9, 25]

Parmesan, C. and 12 others. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399: 579–583. [25]

Partridge, L. and M. Farquhar. 1981. Sexual activity reduces lifespan of male fruitflies. *Nature* 294: 580–582. [7]

Pastor, J., R. J. Naiman, B. Dewey and P. Mcinnes. 1988. Moose, microbes, and the boreal forest. *BioScience* 38: 770–777. [24]

Paton, P. W. C. 1994. The effect of edge on avian nest success: How strong is the evidence? *Conservation Biology* 8: 17–26. [24]

Patterson, B. D. 1980. Montane mammalian biogeography in New Mexico. *Southwestern Naturalist* 25: 33–40. [14]

Patterson, B. D. 1981. Morphological shifts of some isolated populations of *Eutamias* (Rodentia: Sciuridae) in different congeneric assemblages. *Evolution* 35: 53–66. [14]

Paul, E. A. and F. E. Clark. 1996. *Soil Microbiology and Biochemistry*. Academic Press, San Diego, CA. [22]

Paul, N. D. and D. Gwynn-Jones. 2003. Ecological roles of solar UV radiation: Towards an integrated approach. *Trends in Ecology and Evolution* 18: 48–55. [25]

Paulay, G. 1997. Diversity and distribution of reef organisms. In *Life and Death of Coral Reefs*, C. Birkeland (ed.), 298–353. Chapman & Hall, New York. [3]

Paullin, C. O. 1932. *Atlas of Historical Geography of the United States*. Greenwood Press, Westport, CT. [24]

Pearce, F. 1997. Why is the apparently pristine Arctic full of toxic chemicals that started off thousands of kilometres away? *New Scientist* 154: 24–27. [21]

Pearcy, R. W. 1977. Acclimation of photosynthetic and respiratory carbon dioxide exchange to growth temperature in *Atriplex lentiformis* (Torr) Wats. *Plant Physiology* 59: 795–799. [5]

Pearl, R. and L. J. Reed. 1920. On the rate of growth of the population of the United States since 1790 and its mathematical representation. *Proceedings of the National Academy of Sciences USA* 6: 275–288. [10]

Peek, A. S., R. A. Feldman, R. A. Lutz and R. C. Vrijenhoek. 1998. Cospeciation of chemoautotrophic bacteria and deep sea clams. *Proceedings of the National Academy of Sciences USA* 95: 9962–9966. [20]

Pellmyr, O. 2003. Yuccas, yucca moths and coevolution: A review. *Annals of the Missouri Botanical Garden* 90: 35–55. [15]

Pellmyr, O. and C. J. Huth. 1994. Evolutionary stability of mutualism between yuccas and yucca moths. *Nature* 372: 257–260. [15]

Pellmyr, O., C. C. Labandeira and C. M. Herrera, eds. 2002. *Plant–Animal Interactions: An Evolutionary Approach.* Blackwell Science, Malden, MA. [12]

Perez, J. M., J. E. Granados, R. C. Soriguer, P. Fandos, F. J. Marquez and J. P. Crampe. 2002. Distribution, status and conservation problems of the Spanish Ibex, *Capra pyrenaica* (Mammalia: Artiodactyla). *Mammal Review* 32: 26–39. [23]

Peterson, B. J. and B. Fry. 1987. Stable isotopes in ecological studies. *Annual Review of Ecology and Systematics* 18: 293–320. [20]

Peterson, W. T., C. A. Morgan, J. O. Peterson, J. L. Fisher, B. J. Burke and K. Fresh. 2013. *Ocean Ecosystem Indicators of Salmon Marine Survival in the Northern California Current*. Fish Ecology Division, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northwest Fisheries Science Center. [2]

Pfennig, D. W. 1992. Proximate and functional causes of polyphenism in an anuran tadpole. *Functional Ecology* 6: 167–174. [7]

Pfennig, D. W., A. M. Rice and R. A. Martin. 2007. Field and experimental evidence for competition's role in phenotypic divergence. *Evolution* 61: 257–271. [14]

Pickett, S. T. A. 1989. Space-for-time substitution as an alternative to long-term studies. In *Long-term Studies in Ecology: Approaches and Alternatives*, G. E. Likens (ed.), 110–135. Springer, New York. [17]

Pigeon, G., M. Festa-Bianchet, D. W. Coltman, and F. Pelletier. 2016. Intense selective hunting leads to artificial evolution in horn size. *Evolutionary Applications* 9: 521–530. [6]

Pimm, S. L. 2002. *Food Webs*. University of Chicago Press, Chicago. [21]

Pimm, S. L. and J. H. Lawton. 1977. The number of trophic levels in ecological communities. *Nature* 275: 542–544. [21]

Pimm, S. L. and C. Jenkins. 2005. Sustaining the variety of life. *Scientific American* 293: 66–73. [3]

Pimm, S. L., H. L. Jones and J. Diamond. 1988. On the risk of extinction. *American Naturalist* 132: 757–785. [11]

Pinder, A. W., K. B. Storey and G. R. Ultsch. 1992. Estivation and hibernation. In *Environmental Physiology of the Amphibia*, M. E. Feder and W. W. Burggren (eds.), 250–274. University of Chicago Press, Chicago. [4]

Pinto-Tomás, A. A. and 7 others. 2009. Symbiotic nitrogen fixation in the fungus gardens of leaf-cutter ants. *Science* 326: 1120–1123. [15]

Poethke, H. J., W. W. Weisser and T. Hovestadt. 2010. Predator-induced dispersal and the evolution of conditional dispersal in correlated environments. *American Naturalist* 175: 577–586. [9]

Polis, G. A. 1991. Complex trophic interactions in deserts: An empirical critique of food web theory. *American Naturalist* 138: 123–155. [21]

Polis, G. A., M. E. Power and G. R. Huxel. 2004. *Food Webs at the Landscape Level*. University of Chicago Press, Chicago. [21]

Pollock, M. M., R. J. Naiman and T. A. Hanley. 1998. Plant species richness in riparian wetlands: A test of biodiversity theory. *Ecology* 79: 94–105. [19]

Post, D. M. 2002a. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology* 83: 703–718. [21]

Post, D. M. 2002b. The long and short of food-chain length. *Trends in Ecology and Evolution* 17: 269–277. [21]

Post, D. M. and G. Takimoto. 2007. Proximate structural mechanisms for variation in food-chain length. *Oikos* 116: 775–782. [21]

Poulin, R. and S. Morand. 2014. *Parasite Biodiversity*. Smithsonian Institution Scholarly Press. [13]

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. [18]

Power, M. E., M. S. Parker and J. T. Wootton. 1996a. Disturbance and food chain length in rivers. In *Food Webs: Integration of Patterns and Dynamics*, G. A. Polis and K. O. Winemiller (eds.), 286–297. Chapman & Hall, New York. [16]

Power, M. E. and 9 others. 1996b. Challenges in the quest for keystones. *BioScience* 46: 609–620. [16]

Power, M. E., M. S. Parker and W. E. Dietrich. 2008. Seasonal reassembly of a river food web: Floods, droughts, and impacts on fish. *Ecological Monographs* 78: 263–282. [16]

Pride, E. 2005. Optimal group size and seasonal stress in ring-tailed lemurs (Lemur catta). *Behavioral Ecology* 16: 550–560. [8]

Primack, R. B. and S. L. Miao. 1992. Dispersal can limit local plant distribution. *Conservation Biology* 6: 513–519. [9]

Prugh, L. R., K. E. Hodges, A. R. E. Sinclair and J. S. Brashares. 2008. Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences USA* 105: 20770–20775. [24]

Pyke, G. H., H. R. Pulliam and E. L. Charnov. 1977. Optimal foraging: A selective review of theory and tests. *Quarterly Review of Biology* 52: 137–154. [8]

R

Raab, T. K., D. A. Lipson and R. K. Monson. 1996. Non-mycorrhizal uptake of amino acids by roots of the alpine sedge *Kobresia myosuroides*: Implications for the alpine nitrogen cycle. *Oecologia* 108: 488–494. [22]

Rabinowitz, D., S. Cairns and T. Dillon. 1986. Seven forms of rarity and their frequency in the flora of the British Isles. In *Conservation Biology: The Science of Scarcity and Diversity*, M. E. Soulé (ed.), 182–204. Sinauer Associates, Sunderland, MA. [23]

Raffel, T. R., J. M. Romansic, N. T. Halstead, T. A. McMahon, M. D. Venesky and J. R. Rohr. 2012. Disease and thermal acclimation in a more variable and unpredictable climate. *Nature Climate Change* 3: 146–151. [1]

Rahel, F. J. 2000. Homogenization of fish faunas across the United States. *Science* 288: 854–856. [23]

Ralls, K. and J. D. Ballou. 2004. Genetic status and management of California Condors. *Condor* 106: 215–228. [23]

Ranta, P., T. Blom, J. Niemela, E. Joensuu and M. Siitonen. 1998. The fragmented Atlantic rain forest of Brazil: Size, shape and distribution of forest fragments. *Biodiversity and Conservation* 7: 385–403. [23]

Raxworthy, C. J., E. Martinez-Meyer, N. Horning, R. A. Nussbaum, G. E. Schneider, M. A. Ortega-Huerta and A. T. Peterson. 2003. Predicting distributions of known and unknown reptile species in Madagascar. *Nature* 426: 837–841. [9]

Raymond, M., C. Chevillon, T. Guillemaud, T. Lenormand and N. Pasteur. 1998. An overview of the evolution of overproduced esterases in the mosquito *Culex pipiens*. *Philosophical Transactions of the Royal Society of London* B 353: 1707–1711. [6]

Réale, D., A. G. McAdam, S. Boutin and D. Berteaux. 2003. Genetic and plastic responses of a northern mammal to climate change. *Proceedings of the Royal Society of London* B 270: 591–596. [6]

Redford, K. H. 1992. The empty forest. *BioScience* 42: 412–422. [23]

Redman, R. S., K. B. Sheehan, R. G. Stout, R. J. Rodriguez and J. M. Henson. 2002. Thermotolerance generated by plant/fungal symbiosis. *Science* 298: 1581. [15]

Rees, W. E. 1992. Ecological footprints and appropriated carrying capacity: What urban economics leaves out. *Environment and Urbanization* 4: 121–130. [10]

Reiners, W. A., I. A. Worley and D. B. Lawrence. 1971. Plant diversity in a chronosequence at Glacier Bay, Alaska. *Ecology* 52: 55–69. [17]

Reisen, W. K., Y. Fang and V. M. Martinez. 2006. Effects of temperature on the transmission of West Nile virus by *Culex tarsalis* (Diptera; Culicidae). *Journal of Medical Entomology* 43: 309–317. [1]

Relyea, R. A. 2003. Predator cues and pesticides: A double dose of danger for amphibians. *Ecological Applications* 13: 1515–1521. [1]

Ricklefs, R. E. 1977. On the evolution of reproductive strategies in birds: Reproductive effort. *The American Naturalist* 111: 453–478. [7]

Rieseberg, L. H. and 9 others. 2003. Major ecological transitions in wild sunflowers facilitated by hybridization. *Science* 301: 1211–1216. [6]

Ripple, W. J. and R. L. Beschta. 2004. Wolves and the ecology of fear: Can predation risk structure ecosystems? *BioScience* 54: 755–766. [24]

Ripple, W. J. and R. L. Beschta. 2007. Restoring Yellowstone's aspen with wolves. *Biological Conservation* 138: 514–519. [24]

Rizki, R. M. and T. M. Rizki. 1990. Parasitoid virus-like particles destroy *Drosophila* cellular immunity. *Proceedings of the National Academy of Sciences USA* 87: 8388–8392. [13]

Roberts, L. 2011. 9 billion? *Science* 333: 540–543. [10]

Robertson, G. P., M. A. Huston, F. C. Evans and J. M. Tiedje. 1988. Spatial variability in a successional plant community: Patterns of nitrogen availability. *Ecology* 69: 1517–1524. [19]

Rodriguez, R. J., J. F. White Jr., A. E. Arnold and R. S. Redman. 2009. Fungal endophytes: Diversity and functional roles. *New Phytologist* 182: 314–330. [15]

Rohr, J. R. and T. R. Raffel. 2010. Linking global climate and temperature variability to widespread amphibian declines putatively caused by disease. *Proceedings of the National Academy of Sciences USA* 107: 8269–8274. [1]

Rohr, J. R. and 11 others. 2008. Agrochemicals increase trematode infections in a declining amphibian species. *Nature* 455: 1235–1239. [1]

Root, R. B. and N. Cappuccino. 1992. Patterns in population change and the organization of the insect community associated with goldenrod. *Ecological Monographs* 62: 393–420. [9]

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421: 57–60. [25]

Rosenzweig, M. L. 1992. Species diversity gradients: We know more and less than we thought. *Journal of Mammology* 73: 715–730. [18]

Ross, P. S. 2006. Fireproof killer whales (*Orcinus orca*): Flame-retardant chemicals and the conservation imperative in the charismatic icon of British Columbia, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 224–234. [23]

Rovira, A. D., C. D. Bowen and R. C. Foster. 1983. The significance of rhizosphere microflora and mycorrhizas in plant nutrition. In *Inorganic Plant Nutrition* (*Encyclopedia of Plant Physiology*, new series, vol. 15B), A. Läuchli and R. L. Bieleski (eds.), 61–93. Springer, Berlin. [15]

Rutter, C. 1902. Natural history of the quinnat salmon. A report of investigations in the Sacramento River, 1896–1901. *Bulletin of the United States Fish Commission* 22: 65–141. [6]

Rutz, C. and 7 others. 2010. The ecological significance of tool use in New Caledonian crows. *Science* 329: 1523–1526. [5]

Rybczynski, N., M. R. Dawson and R. H. Tedford. 2009. A semi-aquatic Arctic mammalian carnivore from the Miocene epoch and origin of Pinnipedia. *Nature* 458: 1021–1024. [6]

S

Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. *American Naturalist* 111: 337–359. [19]

Sale, P. F. 1979. Recruitment, loss and coexistence in a guild of territorial coral reef fishes. *Oecologia* 42: 159–177. [19]

Salisbury, F. B. and C. Ross. 1992. *Plant Physiology*. 4th ed. Wadsworth, Belmont, CA. [22]

Sanderson, E. W., M. Jaiteh, M. A. Levy, K. H. Redford, A. V. Wannebo and G. Woolmer. 2002. The human footprint and the last of the wild. *BioScience* 52: 891–904. [3, 23]

Sandquist, D. R. and J. R. Ehleringer. 2003. Population- and family-level variation of brittlebush (*Encelia farinosa*, Asteraceae) pubescence: Its relation to drought and implications for selection in variable environments. *American Journal of Botany* 90: 1481–1486. [4]

Saugier, B., J. Roy and H. A. Mooney. 2001. Estimations of global terrestrial productivity: Converging toward a single number? In *Terrestrial Global Productivity*, J. Roy, B. Saugier and H. A. Mooney (eds.), 543–557. Academic Press, San Diego, CA. [20]

Sax, D. F. and S. D. Gaines. 2003. Species diversity: From global decreases to local increases. *Trends in Ecology and Evolution* 18: 561–566. [23]

Scarborough, C. L., J. Ferrari and H. C. J. Godfray. 2005. Aphid protected from pathogen by endosymbiont. *Science* 310: 1781. [13]

Schall, J. J. 1992. Parasite-mediated competition in *Anolis* lizards. *Oecologia* 92: 58–64. [13]

Scheffers, B. R., L. N. Joppa, S. L. Pimm and W. F. Laurance. 2012. What we know and don't know about Earth's missing biodiversity. *Trends in Ecology and Evolution* 27: 501–510. [23]

Schimel, J. P. and J. Bennett. 2004. Nitrogen mineralization: Challenges of a changing paradigm. *Ecology* 85: 591–602. [22]

Schindler, D. W. 1974. Eutrophication and recovery in experimental lakes: Implications for lake management. *Science* 184: 897–899. [20]

Schipper, J. and 132 others. 2008. The status of the world's land and marine mammals: Diversity, threats, and knowledge. *Science* 322: 225–230. [23]

Schlaepfer, M. A., D. F. Sax and J. D. Olden. 2011. The potential conservation value of non-native species. *Conservation Biology* 25: 428–437. [23]

Schlesinger, W. H. 1997. *Biogeochemistry: An Analysis of Global Change*. 2nd ed. Academic Press, San Diego, CA. [22]

Schlesinger, W. H. and E. S. Bernhart. 2013. *Biogeochemistry: An Analysis of Global Change*. Elsevier, Waltham, MA. [25]

Schluter, D. 1994. Experimental evidence that competition promotes divergence in adaptive radiation. *Science* 266: 798–801. [14]

Schluter, D. 1998. Ecological causes of speciation. In *Endless Forms: Species and Speciation*, D. J. Howard and S. H. Berlocher (eds.), 114–129. Oxford University Press, Oxford. [6]

Schluter, D., T. D. Price and P. R. Grant. 1985. Ecological character displacement in Darwin's finches. *Science* 227: 1056–1059. [14]

Schmidt-Nielsen, B. and K. Schmidt-Nielsen. 1951. A complete account of the water metabolism in kangaroo rats and an experimental verification. *Journal of Cellular and Comparative Physiology* 38: 165–182. [4]

Schmidt-Nielsen, K. 1964. *Desert Animals: Physiological Problems of Heat and Water*. Clarendon Press, Oxford. [4]

Schmidt-Nielsen, K. 1997. *Animal Physiology, Adaptation and Environment*. Cambridge University Press, Cambridge. [4]

Schnee, C., T. G. Kollner, M. Held, T. C. J. Turlings, J. Gershenzon and J. Degenhardt. 2006. The products of a single maize sesquiterpene synthase form a volatile defense signal that attracts natural enemies of maize herbivores. *Proceedings of the National Academy of Sciences USA* 103: 1129–1134. [12]

Schoener, T. W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2: 370–404. [8]

Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* 185: 27–39. [14]

Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* 122: 240–285. [14]

Schoener, T. W. and D. A. Spiller. 1996. Devastation of prey diversity by experimentally introduced predators in the field. *Nature* 381: 691–694. [12]

Scholander, P. F., V. Walters, R. Hock and L. Irving. 1950. Body insulation of some arctic and tropical mammals and birds. *Biological Bulletin* 99: 225–236. [4]

Schtickzelle, N. and M. Baguette. 2003. Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration–patch area relationships in fragmented landscapes. *Journal of Animal Ecology* 72: 533–545. [24]

Schulte, D. M., R. P. Burke and R. N. Lipcius. 2009. Unprecedented restoration of a native oyster metapopulation. *Science* 325: 1124–1128. [24]

Schuur, E. A. G. 2003. Productivity and global climate revisited: The sensitivity of tropical forest growth to precipitation. *Ecology* 84: 1165–1170. [20]

Schwarz, C. J. and G. A. F. Seber. 1999. Estimating animal abundance: Review III. *Statistical Science* 14: 427–456. [9]

Seehausen, O., J. J. M. van Alphen and F. Witte. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* 277: 1808–1811. [23]

Selosse, M.-A. and F. Le Tacon. 1998. The land flora: A phototroph–fungus partnership? *Trends in Ecology and Evolution* 13: 15–20. [15]

Sessions, S. K. and S. B. Ruth. 1990. Explanation for naturally occurring supernumerary limbs in amphibians. *Journal of Experimental Zoology* 254: 38–47. [1]

Shaw, M. J. P. 1970. Effects of population density on alienicolae of *Aphis fabae* Scop. I. The effect of crowding on the production of alatae in the laboratory. *Annals of Applied Biology* 65: 191–196. [9]

Sheriff, M. J., C. J. Krebs and R. Boonstra. 2009. The sensitive hare: Sublethal effects of predator stress on reproduction in snowshoe hares. *Journal of Animal Ecology* 78: 1249–1258. [12]

Sheriff, M. J., C. J. Krebs and R. Boonstra. 2010. The ghosts of predators past: Population cycles and the role of maternal programming under fluctuating predation risk. *Ecology* 91: 2983–2994. [12]

Shmida, A. and M. V. Wilson. 1985. Biological determinants of species diversity. *Journal of Biogeography* 12: 1–20. [18]

Shurin, J. B. 2001. Interactive effects of predation and dispersal of zooplankton communities. *Ecology* 82: 3404–3416. [19]

Shurin, J. B. and 7 others. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters* 5: 785–791. [21]

Shurin, J. B., D. S. Gruner and H. Hillebrand. 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proceedings of the Royal Society of London* B 273: 1–9. [21]

Sidor, C. A. 2003. Evolutionary trends and the origin of the mammalian lower jaw. *Paleobiology* 29: 605–640. [6]

Sih, A. and B. Christensen. 2001. Optimal diet theory: When does it work, and when and why does it fail? *Animal Behavior* 61: 379–390. [8]

Silverman, J. and D. N. Bieman. 1993. Glucose aversion in the German cockroach, *Blattella germanica*. *Journal of Insect Physiology* 39: 925–933. [8]

Simberloff, D. 2003. Eradication: Preventing invasions at the outset. *Weed Science* 51: 247–253. [23]

Simberloff, D. and J. Cox. 1987. Consequences and costs of conservation corridors. *Conservation Biology* 1: 63–71. [24]

Simberloff, D. S. and E. O. Wilson. 1969. Experimental zoogeography of islands: The colonization of empty islands. *Ecology* 50: 278–296. [18]

Simkin, S. M. and 16 others. 2016. Conditional vulnerability of plant diversity to atmospheric nitrogen deposition across the United States. *Proceedings of the National Academy of Sciences USA* 113: 4086–4091. [25]

Simenstad, C. A., J. A. Estes and K. W. Kenyon. 1978. Aleuts, sea otters, and alternative communities. *Science* 200: 403–411. [16]

Sinervo, B. 1990. The evolution of maternal investment in lizards: An experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution* 44: 279–294. [7]

Sinervo, B. and 25 others. 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328: 894–899. [23, 25]

Singer, M. S., I. H. Lichter-Marck, T. E. Farkas, E. Aaron, K. D. Whitney and K. A. Mooney. 2014. Herbivore diet breadth mediates the cascading effects of carnivores in food webs. *Proceedings of the National Academy of Sciences USA* 111: 9521–9526. [21]

Skerratt, L. F. and 7 others. 2007. Spread of chytridiomycosis has caused the rapid global decline and extinction of frogs. *EcoHealth* 4: 125–134. [1, 23]

Smith, F. D. M., R. M. May, R. Pellew, T. H. Johnson and K. R. Walter. 1993. How much do we know about the current extinction rate? *Trends in Ecology and Evolution* 8: 375–378. [23]

Smith, F. E. 1961. Density-dependence in the Australian thrips. *Ecology* 42: 403–407. [10]

Smith, K. F., M. Behrens, L. M. Schloegel, N. Marano, S. Burgiel and P. Daszak. 2009. Reducing the risks of the wildlife trade. *Science* 324: 594–595. [23]

Smith, S. E. and D. J. Read. 2008. *Mycorrhizal Symbiosis*. 3rd ed. Academic Press, San Diego, CA. [15]

Smith, T. B. 1993. Disruptive selection and the genetic basis of bill size polymorphism in the African finch *Pyrenestes*. *Nature* 363: 618–620. [6]

Snyder, N. F. R., S. R. Derrickson, S. R. Beissinger, J. W. Wiley, T. B. Smith, W. D. Toone and B. Miller. 1996. Limitations of captive breeding in endangered species recovery. *Conservation Biology* 10: 338–348. [23]

Sokal, R. R. and F. J. Rohlf. 2011. *Biometry*. 4th ed. W. H. Freeman, New York. [1]

Solé, R. V. and J. Montoya. 2001. Complexity and fragility in ecological networks. *Proceedings of the Royal Society of London* B 268: 2039–2045. [23]

Soulé, M. E. 1985. What is conservation biology? *BioScience* 35: 727–734. [23]

Soulé, M. E. and M. A. Sanjayan. 1998. Conservation targets: Do they help? *Science* 279: 2060–2061. [24]

Soulé, M. E. and B. A. Wilcox, eds. 1980. *Conservation Biology: An Evolutionary–Ecological Perspective*. Sinauer Associates, Sunderland, MA. [23]

Sousa, W. P. 1979a. Disturbance in marine intertidal boulder fields: The non-equilibrium maintenance of species diversity. *Ecology* 60: 1225–1239. [19]

Sousa, W. P. 1979b. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* 49: 227–254. [17]

Sousa, W. P. 2001. Natural disturbance and the dynamics of marine benthic communities. In *Marine Community Ecology*, M. D. Bertness, S. D. Gaines and M. E. Hay (eds.), 85–130. Sinauer Associates, Sunderland, MA. [17]

Spencer, K. A. 1972. Handbooks for the identification of British insects, *Diptera, Agromyzidae* (vol. X, part 5g). Royal Entomological Society, London. [12]

Springer, A. M. and 7 others. 2003. Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences USA* 100: 12223–12228. [9, 21]

Stachowicz, J. J. and M. E. Hay. 1999. Reducing predation through chemically mediated camouflage: Indirect effects of plant defenses on herbivores. *Ecology* 80: 495–509. [8]

Steadman, D. W. 1995. Prehistoric extinctions of Pacific island birds: Biodiversity meets zooarchaeology. *Science* 267: 1123–1131. [23]

Stebbins, G. L. 1974. *Flowering Plants: Evolution above the Species Level*. Belknap, Cambridge, MA. [18]

Stein, B. A., L. S. Kutner and J. S. Adams. 2000. *Precious Heritage*. Oxford University Press, Oxford. [23]

Steltzer, H., C. Landry, T. H. Painter, J. Anderson and E. Ayers. 2009. Biological consequences of earlier snowmelt from desert dust deposition in alpine landscapes. *Proceedings of the National Academy of Sciences USA* 106: 11629–11634. [25]

Steneck, R. S., S. D. Hacker and M. N. Dethier. 1991. Mechanisms of competitive dominance between crustose coralline algae: An herbivore-mediated competitive reversal. *Ecology* 72: 938–950. [14]

Stevens, C. J., N. B. Dise, J. O. Mountford and D. J. Gowling. 2004. Impact of nitrogen deposition on the species richness of grasslands. *Science* 303: 1876–1879. [25]

Stevens, O. A. 1932. The number and weight of seeds produced by weeds. *American Journal of Botany* 19: 784–794. [7]

Stinner, J. N. and V. H. Shoemaker. 1987. Cutaneous gas exchange and low evaporative water loss in the frogs *Phyllomedusa sauvagei* and *Chiromantis xerampelina*. *Journal of Comparative Physiology* 157: 423–427. [4]

Stomp, M. and 8 others. 2004. Adaptive divergence in pigment composition promotes phytoplankton biodiversity. *Nature* 432: 104–107. [14]

Stomp, M., J. Huisman, L. Vörös, F. R. Pick, M. Laamanen, T. Haverkamp and L. J. Stal. 2007. Colourful coexistence of red and green picocyanobacteria in lakes and seas. *Ecology Letters* 10: 290–298. [14]

Storey, K. B. 1990. Life in a frozen state: Adaptive strategies for natural freeze tolerance in amphibians and reptiles. *American Journal of Physiology* 258: R559–R568. [4]

Strayer, D. L. and H. M. Malcom. 2007. Effects of zebra mussels (*Dreissena polymorpha*) on native bivalves: The beginning of the end or the end of the beginning? *Journal of the North American Benthological Society* 26: 111–122. [23]

Strebel, P. M. and S. L. Cochi. 2001. Waving goodbye to measles. *Nature* 414: 695–696. [13]

Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306: 1783–1786. [1]

Stuart, Y. E., T. S. Campbell, P. A. Hohenlohe, R. G. Reynolds, L. J. Revell and J. B. Losos. 2014. Rapid invasion of a native species following invasion by a congener. *Science* 346: 463–466. [6]

Suding, K. and 7 others. 2005. Functional and abundance-based mechanisms explain diversity loss due to nitrogen fertilization. *Proceedings of the National Academy of Sciences USA* 102: 4387–4392. [25]

Sultan, S. E., T. Horgan-Kobelski, L. M. Nichols, C. E. Riggs and R. K. Waples. 2013. A resurrection study reveals rapid adaptive evolution within populations of an invasive plant. *Evolutionary Applications* 6: 266–278. [6]

Sunday, J. M., A. E. Bates and N. K. Dulvy. 2012. Thermal tolerance and the global redistribution of animals. *Nature Climate Change* 2: 686–690. [9]

Sutherland, J. P. 1974. Multiple stable points in natural communities. *American Naturalist* 108: 859–873. [17]

Suzán, G. and 8 others. 2009. Experimental evidence for reduced rodent diversity causing increased hantavirus prevalence. *PLoS ONE* 4: e5461. [19]

Svane, I. B. 1984. Observations on the long-term population dynamics of the perennial ascidian, *Ascidia mentula* O. F. Müller, on the Swedish west coast. *Biological Bulletin* 167: 630–646. [11]

T

Takimoto, G., D. A. Spiller and D. M. Post. 2008. Ecosystem size, but not disturbance, determines food chain length on islands of the Bahamas. *Ecology* 89: 3001–3007. [21]

Tanabe, S. 2002. Contamination and toxic effects of persistent endocrine disrupters in marine mammals and birds. *Marine Pollution Bulletin* 45: 69–77. [23]

Tansley, A. G. 1917. On competition between *Galium saxatile* L. (*G. hercynicum* Weig.) and *Galium sylvestre* Poll. (*G. asperum* Schreb.) on different types of soil. *Journal of Ecology* 5: 173–179. [14]

Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. *Ecology* 16: 284–307. [20]

Tebbich, S., M. Taborsky, B. Fessl and D. Blomqvist. 2001. Do woodpecker finches acquire tool-use by social learning? *Proceedings of the Royal Society of London* B 268: 2189–2193. [5]

Tegen, I. and I. Fung. 1995. Contribution to the atmospheric mineral aerosol load from land surface modification. *Journal of Geophysical Research–Atmosphere* 100: 18707–18726. [25]

Terborgh, J. 1973. On the notion of favorableness in plant ecology. *American Naturalist* 107: 481–501. [18]

Terborgh, J., K. Feeley, M. Silman, P. Nunez and B. Balukjian. 2006. Vegetation dynamics of predator-free land-bridge islands. *Journal of Ecology* 94: 253–263. [24]

Tewksbury, J. J. and 9 others. 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences USA* 99: 12923–12926. [24]

Thomas, C. D. and T. M. Jones. 1993. Partial recovery of a skipper butterfly (*Hesperia comma*) from population refuges: Lessons for conservation in a fragmented landscape. *Journal of Animal Ecology* 62: 472–481. [11]

Thomas, C. D. and 10 others. 2004. Extinction risk from climate change. *Nature* 427: 145–148. [23]

Thomas, F., A. Schmidt-Rhaesa, G. Martin, C. Manu, P. Durand and F. Renaud. 2002. Do hairworms (Nematomorpha) manipulate the water seeking behaviour of their terrestrial hosts? *Journal of Evolutionary Biology* 15: 356–361. [13]

Thomas, F. and 7 others. 2003. Biochemical and histological changes in the brain of the cricket *Nemobius sylvestris* infected by the manipulative parasite *Paragordius tricuspidatus* (Nematomorpha). *International Journal for Parasitology* 33: 435–443. [13]

Thomas, R. Q., C. D. Canham, K. C. Weathers and C. L. Goodale. 2010. Increased tree carbon storage in response to nitrogen deposition in the U.S. *Nature Geoscience* 3: 13–17. [25]

Thompson, J. N. 1998. Rapid evolution as an ecological process. *Trends in Ecology and Evolution* 13: 329–332. [6]

Tilman, D. 1977. Resource competition between plankton algae: An experimental and theoretical approach. *Ecology* 58: 338–348. [19]

Tilman, D. and J. A. Downing. 1994. Biodiversity and stability in grasslands. *Nature* 367: 363–365. [19]

Tilman, D., M. Mattson and S. Langer. 1981. Competition and nutrient kinetics along a temperature gradient: An experimental test of a mechanistic approach to niche theory. *Limnology and Oceanography* 26: 1020–1033. [14, 19]

Tilman, D., D. Wedin and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379: 718–720. [19]

Tinker, D. B., W. H. Romme and D. G. Despain. 2003. Historic range of variability in landscape structure in subalpine forests of the Greater Yellowstone Area, USA. *Landscape Ecology* 18: 427–439. [24]

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: A mutualism hypothesis. *Journal of Animal Ecology* 51: 451–467. [24]

Tomback, D. F. and P. Achuff. 2010. Blister rust and western forest biodiversity: Ecology, values and outlook for white pines. *Forest Pathology* 40: 186–225. [24]

Tracy, R. L. and G. E. Walsberg. 2002. Kangaroo rats revisited: Re-evaluating a classic case of desert survival. *Oecologia* 133: 449–457. [4]

Trites, A. W. and C. P. Donnelly. 2003. The decline of Steller sea lions *Eumetopias jubatus* in Alaska: A review of the nutritional stress hypothesis. *Mammal Review* 33: 3–28. [21]

Trivers, R. L. 1972. Parental investment and sexual selection. In *Sexual Selection and the Descent of Man 1871–1971*, B. Campbell (ed.), 136–179. Aldine, Chicago. [8]

Tsukaya, H., K. Fujikawa and S. Wu. 2002. Thermal insulation and accumulation of heat in the downy inflorescences of *Saussurea medusa* (Asteraceae) at high elevation in Yunnan, China. *Journal of Plant Research* 115: 263–268. [4]

Turchin, P. 2003. *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton University Press, Princeton, NJ. [12]

Turner, M. G., R. H. Gardner and R. V. O'Neill. 2001. *Landscape Ecology in Theory and Practice: Pattern and Process*. Springer, New York. [24]

Turner, M. G., W. H. Romme and D. B. Tinker. 2003. Surprises and lessons from the 1988 Yellowstone fires. *Frontiers in Ecology and the Environment* 1: 351–358. [24]

Tyerman, J. G., M. Bertrand, C. C. Spencer and M. Doebeli. 2008. Experimental demonstration of ecological character displacement. *BMC Evolutionary Biology* 8: 34. [14]

Tylianakis, J. M., R. K. Didham, J. Bascompte and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11: 1351–1363. [13]

U

Uddenberg, N., T. Fagerström and A. Jeffner. 1995. Kontakten med urkällan: Naturen, människan och religionen. In *Det Stora Sammanhanget*, N. Uddenberg (ed.), 141–186. Doxa, Nora, Sweden. [1]

Umina, P. A., A. R. Weeks, M. R. Kearney, S. W. McKechnie and A. A. Hoffmann. 2005. A rapid shift in a classic clinal pattern in *Drosophila* reflecting climate change. *Science* 308: 691–693. [6]

United Nations, Department of Economic and Social Affairs, Population Division. 2013. *World Population Prospects: The 2012 Revision, Highlights*. Working Paper no. ESA/P/WP.228. https://esa.un.org/unpd/wpp/publications/Files/WPP2012_HIGHLIGHTS.pdf. [10]

U.S. Congress, Office of Technology Assessment. 1993. *Harmful Non-Indigenous Species in the United States*. OTA-F-565. U.S. Government Printing Office, Washington, DC. [23]

U.S. Environmental Protection Agency. 2005. *Evaluating Ozone Control Programs in the Eastern United States: Focus on the NO_x Budget Trading Program, 2004*. EPA454-K-05-001. www.epa.gov/airtrends/2005/ozonenbp.pdf. [25]

U.S. Fish and Wildlife Service. 2003. *Recovery Plan for the Red-Cockaded Woodpecker* (*Picoides borealis*): Second revision. U.S. Fish and Wildlife Service, Atlanta, GA. [23]

U.S. Fish and Wildlife Service. 2008. *Birds of Conservation Concern 2008*. U.S. Fish and Wildlife Service, Division of Migratory Bird Management, Arlington, VA. [24]

Uthicke, S., P. Momigliano and K. E. Fabricius. 2013. High risk of extinction of benthic foraminifera in this century due to ocean acidification. *Scientific Reports* 3: 1–5. [25]

V

Valentine, D. L. and 12 others. 2010. Propane respiration jump-starts microbial response to a deep oil spill. *Science* 330: 208–211. [5]

Valverde, T. and J. Silvertown. 1997. A metapopulation model for *Primula vulgaris*, a temperate forest understorey herb. *Journal of Ecology* 85: 193–210. [11]

Van Breemen, N. and A. C. Finzi. 1998. Plant-soil interactions: Ecological aspects and evolutionary implications. *Biogeochemistry* 42: 1–19. [22]

Van den Bosch, F., R. Hengeveld and J. A. J. Metz. 1992. Analysing the velocity of animal range expansion. *Journal of Biogeography* 19: 135–150. [11]

Van der Heijden, M. G. A. and 7 others. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396: 69–72. [15]

Van der Veken, S., J. Rogister, K. Verheyen, M. Hermy and R. Nathan. 2007. Over the (range) edge: A 45-year transplant experiment with the perennial forest herb *Hyacinthoides non-scripta*. *Journal of Ecology* 95: 343–351. [9]

Van Dover, C. L. 2000. *The Ecology of Deep-Sea Hydrothermal Vents*. Princeton University Press, Princeton, NJ. [20]

Van Lear, D. H., W. D. Carroll, P. R. Kapeluck and R. Johnson. 2005. History and restoration of the longleaf pine–grassland ecosystem: Implications for species at risk. *Forest Ecology and Management* 211: 150–165. [23]

Van Mantgem, P. J. and 10 others. 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323: 521–524. [10]

van Wijk, S. J. and 7 others. 2013. Experimental harvesting of fish populations drives genetically based shifts in body size and maturation. *Frontiers in Ecology and the Environment* 11: 181–187. [6]

Vannote, R. L., G. W. Minshall, K. W. Cummins, K. R. Sedell and C. E. Cushing. 1980. The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130–137. [3]

Van Oers, K. and D. L. Sinn. 2013. Quantitative and molecular genetics of animal personality. In *Animal Personalities: Behavior, Physiology, and Evolution*, C. Carere and D. Maestripieri (eds.), 149–200. University of Chicago Press, Chicago. [8]

Varley, N. and M. S. Boyce. 2006. Adaptive management for reintroductions: Updating a wolf recovery model for Yellowstone National Park. *Ecological Modelling* 193: 315–339. [24]

Veblen, T. T., T. Kitzberger and J. Donnegan. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecological Applications* 10: 1178–1195. [2]

Vellend, M., J. A. Myers, S. Gardescu and P. L. Marks. 2003. Dispersal of *Trillium* seeds by deer: Implications for long-distance migration of forest herbs. *Ecology* 84: 1067–1072. [15]

Verdolin, J. L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behavioral Ecology and Sociobiology* 60: 457–464. [8]

Vié, J.-C., C. Hilton-Taylor and S. N. Stuart, eds. 2009. *Wildlife in a Changing World: An Analysis of the 2008 IUCN Red List of Threatened Species*. IUCN, Gland, Switzerland. [1]

Vitousek, P. M. 1977. The regulation of element concentrations in mountain streams in the northeastern United States. *Ecological Monographs* 47: 65–87. [22]

Vitousek, P. M. and H. Farrington. 1997. Nutrient limitation and soil development: Experimental test of a biogeochemical theory. *Biogeochemistry* 37: 63–75. [22]

Volterra, V. 1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Memorie della R. Accademia dei Lincei* 2: 31–113. Reprinted 1931 as "Variations and fluctuations of the number of individuals in animal species living together," in R. N. Chapman, *Animal Ecology*, McGraw-Hill, New York. [14]

Vonlanthen, P. and 9 others. 2012. Eutrophication causes speciation reversal in whitefish adaptive radiations. *Nature* 482: 357–362. [6]

Voyles, J. and 10 others. 2009. Pathogenesis of chytridiomycosis, a cause of catastrophic amphibian declines. *Science* 326: 582–585. [1]

Vredenburg, V. T. 2004. Reversing introduced species effects: Experimental removal of introduced fish leads to rapid recovery of a declining frog. *Proceedings of the National Academy of Sciences USA* 101: 7646–7650. [1]

W

Wackernagel, M. and 7 others. 1999. National natural capital accounting with the ecological footprint concept. *Ecological Economics* 29: 375–390. [10]

Wada-Katsumata, A., J. Silverman and C. Schal. 2013. Changes in taste neurons support the emergence of an adaptive behavior in cockroaches. *Science* 340: 972–975. [8]

Wagner, W. L., M. M. Bruegmann, D. R. Herbst and J. Q. C. Lau. 1999. Hawaiian vascular plants at risk: 1999. *Bishop Museum Occasional Papers* 60: 1–58. [23]

Walker, T. W. and J. K. Syers. 1976. The fate of phosphorus during pedogenesis. *Geoderma* 15: 1–19. [22]

Wallace, A. R. 1855. On the law which has regulated the introduction of new species. *Annals and Magazine of Natural History* 16. [18]

Wallace, A. R. 1858. On the tendency of varieties to depart indefinitely from the original type. *Journal of the Proceedings of the Linnean Society, Zoology* 3: 53–62. [18]

Wallace, A. R. 1860. On the zoological geography of the Malay Archipelago. *Journal of the Linnean Society of London* 4: 172–184. [9]

Wallace, A. R. 1869. *The Malay Archipelago, the Land of the Orangutan and the Bird of Paradise: A Narrative of Travel with Studies of Man and Nature*. Macmillan, London. [18, 23]

Wallace, A. R. 1876. *The Geographic Distribution of Animals*. 2 vols. Harper and Brothers, New York. [18]

Wallace, A. R. 1878. *Tropical Nature and Other Essays*. Macmillan, London. [18]

Walter, H. and H. Lieth. 1967. *Klimadiagram-Weltatlas*. VEB Gustav Fischer Verlag, Jena. [3]

Walters, C. 1995. *Fish on the Line: The Future of Pacific Fisheries*. A report to the David Suzuki Foundation, Fisheries Project Phase I, 219–2211 West Fourth Avenue, Vancouver, BC, V6K 4S2, Canada. [2]

Walters, J. R., C. K. Copeyon and J. H. Carter. 1992. Test of the ecological basis of cooperative breeding in red-cockaded woodpeckers. *Auk* 109: 90–97. [23]

Walther, G. 2010. Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society of London* B 365: 2019–2025. [25]

Wand, S. J. E., G. F. Midgley, M. H. Jones and P. S. Curtis. 1999. Responses of wild C4 and C3 grass (Poaceae) species to elevated atmospheric CO_2 concentration: A meta-analytic test of current theories and perceptions. *Global Change Biology* 5: 723–741. [5]

Wang, X., Z. Dong, J. Zhang and L. Liu. 2004. Modern dust storms in China: An overview. *Journal of Arid Environments* 58: 559–574. [25]

Ward, M. P., J. S. Milledge and J. B. West. 1995. *High Altitude Medicine and Physiology*. Chapman & Hall, London. [4]

Wasser, S. K., C. Mailand, R. Booth, B. Mutayoba, E. Kisamo, B. Clark and M. Stephens. 2007. Using DNA to track the origin of the largest ivory seizure since the 1989 trade ban. *Proceedings of the National Academy of Sciences USA* 104: 4228–4233. [23]

Weathers, K. C., M. L. Cadenasso and S. T. A. Pickett. 2001. Forest edges as nutrient and pollutant concentrators. *Conservation Biology* 15: 1506–1514. [24]

Webb, N. R. and L. E. Haskins. 1980. An ecological survey of heathlands in the Poole Basin, Dorset, England, in 1978. *Biological Conservation* 17: 281–296. [9]

Webberley, K. M. and 8 others. 2004. Host reproduction and a sexually transmitted disease: Causes and consequences of *Coccipolipus hippodamiae* distribution on coccinellid beetles. *Journal of Animal Ecology* 73: 1–10. [13]

Weber, J. N., B. K. Peterson and H. E. Hoekstra. 2013. Discrete genetic modules are responsible for complex burrow evolution in *Peromyscus* mice. *Nature* 493: 402–405. [8]

Weber, N. A. 1966. Fungus-growing ants. *Science* 153: 587–604. [15]

Weber, R. E. 2007. High-altitude adaptations in vertebrate hemoglobins. *Respiratory Physiology and Neurobiology* 158: 132–142. [6]

Weir, A. A. S., J. Chappell and A. Kacelnik. 2002. Shaping of hooks in New Caledonian crows. *Science* 297: 981. [5]

Weis, A. E. and W. G. Abrahamson. 1986. Evolution of host-plant manipulation by gall makers: Ecology and genetic factors in the *Solidago–Eurosta* system. *American Naturalist* 127: 681–695. [6]

Weiss, R. A. and A. J. McMichael. 2004. Social and environmental risk factors in the emergence of infectious disease. *Nature Medicine* 10: S70–S76. [1]

Weldon, A. J. 2006. How corridors reduce Indigo Bunting nest success. *Conservation Biology* 20: 1300–1305. [24]

Wernberg, T. and 21 others. 2016. Climate-driven regime shift of a temperate marine ecosystem. *Science* 353: 169–172. [9]

Werner, E. E. 1988. Size scaling and the evolution of complex life cycles. In *Size-Structured Populations*, B. Ebenman and L. Persson (eds.), 61–81. Springer, Berlin. [7]

Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64: 1540–1548. [8]

Westemeier, R. L. and 8 others. 1998. Tracking the long-term decline and recovery of an isolated population. *Science* 282: 1695–1698. [6]

Westoby, M. 1997. What does "ecology" mean? *Trends in Ecology and Evolution* 12: 166. [1]

White, J., J. Wilson and K. Horskins. 1997. The role of adjacent habitats in rodent damage levels in Australian macadamia orchard systems. *Crop Protection* 16: 727–732. [24]

Whittaker, R. H., K. J. Willis and R. Field. 2001. Towards a general, hierarchical theory of species diversity. *Journal of Biogeography* 28: 453–470. [18]

Wilbur, H. M. 1997. Experimental ecology of food webs: Complex systems in temporary ponds. The Robert H. MacArthur Award Lecture. *Ecology* 78: 2279–2302. [21]

Wilkie, D. S. and J. F. Carpenter. 1999. Bushmeat hunting in the Congo Basin: An assessment of impacts and options for mitigation. *Biodiversity and Conservation* 8: 927–955. [23]

Wilkinson, G. S. and P. R. Reillo. 1994. Female choice response to artificial selection on an exaggerated male trait in a stalk-eyed fly. *Proceedings of the Royal Society of London* B 255: 1–6. [8]

Williams, A. P. and 14 others. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change* 3: 292–297. [10]

Williams, B. K., J. D. Nichols and M. J. Conroy. 2002. *Analysis and Management of Animal Populations*. Academic Press, San Diego, CA. [9]

Williams, C. B. 1943. Area and number of species. *Nature* 152: 264–267. [18]

Williams, C. B. 1964. *Patterns in the Balance of Nature*. Academic Press, London. [18]

Williams, J. C., C. S. ReVelle and S. A. Levin. 2005. Spatial attributes and reserve design models: A review. *Environmental Modeling and Assessment* 10: 163–181. [24]

Willig, M. R., D. M. Kaufman and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology and Systematics* 34: 273–309. [18]

Willmer, P., G. Stone and I. Johnston. 2005. *Environmental Physiology of Animals*. Blackwell, Malden, MA. [4]

Wilson, E. O. 1994. *Naturalist*. Island Press, Washington, DC. [18]

Wilson, E. O. and D. S. Simberloff. 1969. Experimental zoogeography of islands: Defaunation and monitoring techniques. *Ecology* 50: 267–278. [18]

Wilson, S. D. and D. Tilman. 1993. Plant competition and resource availability in response to disturbance and fertilization. *Ecology* 74: 599–611. [14]

Windsor, D. A. 1998. Most of the species on Earth are parasites. *International Journal for Parasitology* 28: 1939–1941. [13]

Winterhalder, B. P. 1980. Canadian fur bearer cycles and Cree-Ojibwa hunting and trapping practices. *American Naturalist* 115: 870–879. [12]

Witman, J. D., R. J. Etter and F. Smith. 2004. The relationship between regional and local species diversity in marine benthic communities: A global perspective. *Proceedings of the National Academy of Sciences USA* 101: 15664–15669. [18]

Wittemyer, G., J. M. Northrup, J. Blanc, I. Douglas-Hamilton, P. Omondi and K. P. Burnham. 2014. Illegal killing for ivory drives global decline in African elephants. *Proceedings of the National Academy of Sciences USA* 111: 13117–13121. [10]

Woodward, G., D. M. Perkins and L. E. Brown. 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society* B 365: 2093–2106. [23]

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. [20]

Woodroffe, R. 1999. Managing disease threats to wild mammals. *Animal Conservation* 2: 185–193. [23]

Wright, S. J. 1981. Intra-archipelago vertebrate distributions: The slope of the species–area relation. *American Naturalist* 118: 726–748. [18]

Wright, S. J. 2005. Tropical forests in a changing environment. *Trends in Ecology and Evolution* 10: 553–560. [3]

Wrong, O. M., C. J. Edmonds and V. S. Chadwick. 1981. *The Large Intestine: Its Role in Mammalian Nutrition and Homeostasis*. Halsted, New York. [5]

Y

Yates, T. L. and 15 others. 2002. The ecology and evolutionary history of an emergent disease: Hantavirus pulmonary syndrome. *BioScience* 52: 989–998. [9]

Yoda, J. A., T. Kira, H. Ogawa and K. Hozumi. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology, Osaka City University* 14: 107–120. [10]

Yoshida, T., L. E. Jones, S. P. Ellner, G. F. Fussmann and N. G. Hairston Jr. 2003. Rapid evolution drives ecological dynamics in a predator–prey system. *Nature* 424: 303–306. [12]

Z

Zanette, L. Y., A. F. White, M. C. Allen and M. Clinchy. 2011. Perceived predation risk reduces the number of offspring songbirds produce per year. *Science* 334: 1398–1401. [8]

Zar, J. H. 2009. *Biostatistical Analysis*. 5th ed. Pearson, New York. [1]

Zhao, M. and S. W. Running. 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science* 329: 940–943. [25]

Zhao, M., S. W. Running and R. R. Nemani. 2006. Sensitivity of Moderate Resolution Imaging Spectroradiometer (MODIS) terrestrial primary production to the accuracy of meteorological reanalyses. *Journal of Geophysical Research–Biogeosciences* 111: G01002. [20]

Zimova, M., L. S. Mills and J. J. Nowak. 2016. High fitness costs of climate-change induced camouflage mismatch. *Ecology Letters* 19: 299–307. [7]

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. [12]

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