54

Community Ecology

▲ **Figure 54.1 Which species benefits from this interaction?**

KEY CONCEPTS

54.1 Community interactions are classified by whether they help, harm, or have no effect on the species involved

54.2 Diversity and trophic structure characterize biological communities

54.3 Disturbance influences species diversity and composition

54.4 Biogeographic factors affect community diversity

54.5 Pathogens alter community structure locally and globally

OVERVIEW

Communities in Motion

Deep in the Lembeh Strait of Indonesia, a crab in the family Homolidae scuttles across the ocean floor holding a large sea urchin on its back **(Figure 54.1)**. When a predatory fish arrives, the crab settles quickly into the sediments and puts its living shield to use. The fish darts in and tries to bite the crab. In response, the crab tilts the spiny sea urchin toward whichever side the fish attacks. The fish eventually gives up and swims away.

The "carrier crab" in Figure 54.1 clearly benefits from having the sea urchin on its back. But how does the sea urchin fare in this relationship? Its association with the crab might harm it, help it, or have no effect on its survival and reproduction. Additional observations or experiments would be needed before ecologists could answer this question.

In Chapter 53, you learned how individuals within a population can affect other individuals of the same species. This chapter will examine ecological interactions between populations of different species. A group of populations of different species living close enough to interact is called a biological **community**. Ecologists define the boundaries of a particular community to fit their research questions: They might study the community of decomposers and other organisms living on a rotting log, the benthic community in Lake Superior, or the community of trees and shrubs in Banff National Park in Alberta.

We begin this chapter by exploring the kinds of interactions that occur between species in a community, such as the crab and sea urchin in Figure 54.1. We'll then consider several of the factors that are most significant in structuring a community—in determining how many species there are, which particular species are present, and the relative abundance of these species. Finally, we will apply some of the principles of community ecology to the study of human disease.

CONCEPT **54.1**

Community interactions are classified by whether they help, harm, or have no effect on the species involved

Some key relationships in the life of an organism are its interactions with individuals of other species in the community. These **interspecific interactions** include competition, predation, herbivory, symbiosis (including parasitism, mutualism, and commensalism), and facilitation. In this section, we will define and describe each of these interactions, recognizing that ecologists do not always agree on the precise boundaries of each type of interaction.

We will use the symbols + and − to indicate how each interspecific interaction affects the survival and reproduction of the two species engaged in the interaction. For example, predation is a +/− interaction, with a positive effect on the survival and reproduction of the predator population and a negative effect on that of the prey population. Mutualism is a +/+ interaction because the survival and reproduction of both species are increased in the presence of the other. A 0 indicates that a population is not affected by the interaction in any known way.

Historically, most ecological research has focused on interactions that have a negative effect on at least one species, such as competition and predation. However, positive interactions are ubiquitous, and their contributions to community structure are the subject of considerable study today.

Competition

Interspecific competition is a −/− interaction that occurs when individuals of different species compete for a resource that limits their growth and survival. Weeds growing in a garden compete with garden plants for soil nutrients and water. Grasshoppers and bison in the Great Plains compete for the grass they both eat. Lynx and foxes in the northern forests of Alaska and Canada compete for prey such as snowshoe hares. In contrast, some resources, such as oxygen, are rarely in short supply; thus, although most species use this resource, they do not usually compete for it.

Competitive Exclusion

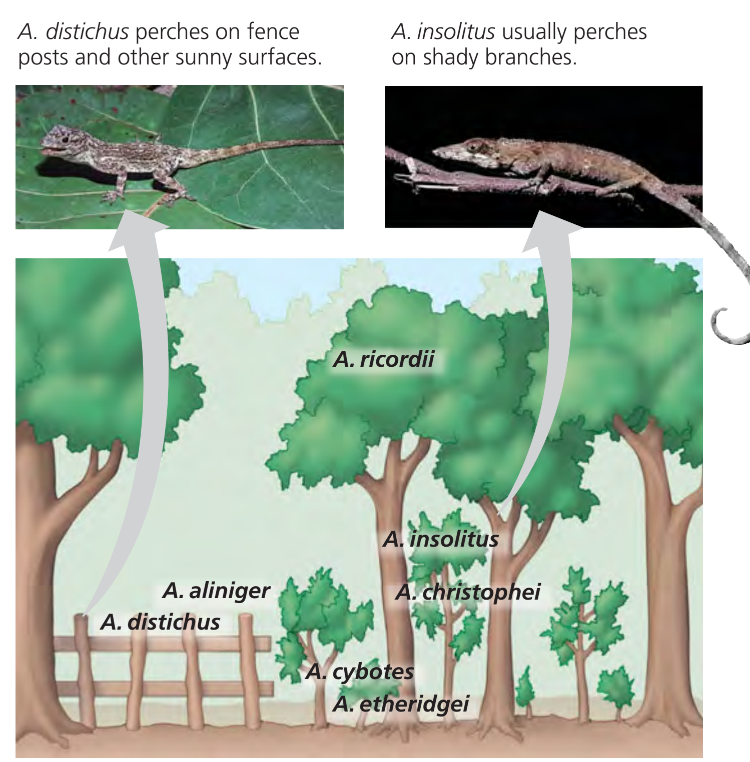
What happens in a community when two species compete for limited resources? In 1934, Russian ecologist G. F. Gause studied this question using laboratory experiments with two closely related species of ciliated protists, *Paramecium aurelia* and *Paramecium caudatum*. He cultured the species under stable conditions, adding a constant amount of food each day. When Gause grew the two species separately, each population grew rapidly and then leveled off at the apparent carrying capacity of the culture (see Figure 53.10a for an illustration of the logistic growth of *P. aurelia*). But when Gause grew the two species together, *P. caudatum* became extinct in the culture. Gause inferred that *P. aurelia* had a competitive edge in obtaining food. He concluded that two species competing for the same limiting resources cannot coexist permanently in the same place. In the absence of disturbance, one species will use the resources more efficiently and reproduce more rapidly than the other. Even a slight reproductive advantage will eventually lead to local elimination of the inferior competitor, an outcome called **competitive exclusion**.

Ecological Niches and Natural Selection

EVOLUTION The sum of a species' use of the biotic and abiotic resources in its environment is called its **ecological niche**. American ecologist Eugene Odum used the following analogy to explain the niche concept: If an organism's habitat is its "address," the niche is the organism's "profession." The niche of a tropical tree lizard, for instance, includes the temperature range it tolerates, the size of branches on which it perches, the time of day when it is active, and the sizes and kinds of insects it eats. Such factors define the lizard's niche, or ecological role—how it fits into an ecosystem.

We can use the niche concept to restate the principle of competitive exclusion: Two species cannot coexist permanently in a community if their niches are identical. However, ecologically similar species *can* coexist in a community if one or more significant differences in their niches arise through time. Evolution by natural selection can result in one of the species using a different set of resources. The differentiation of niches that enables similar species to coexist in a community is called **resource partitioning** **(Figure 54.2)**. You can think of resource partitioning in a community as "the ghost of competition past"—the indirect evidence of earlier interspecific competition resolved by the evolution of niche differentiation.

As a result of competition, a species' *fundamental niche*, which is the niche potentially occupied by that species, is often different from its *realized niche*, the portion of its fundamental niche that it actually occupies in a particular environment. Ecologists can identify the fundamental niche of a species by testing the range of conditions in which it grows and reproduces in the absence of competitors. They can also test whether a potential competitor limits a species' realized niche by removing the competitor and seeing if the first species expands into the newly available space. The classic experiment depicted in **Figure 54.3**, on the next page, clearly showed that competition between two barnacle species kept one species from occupying part of its fundamental niche.

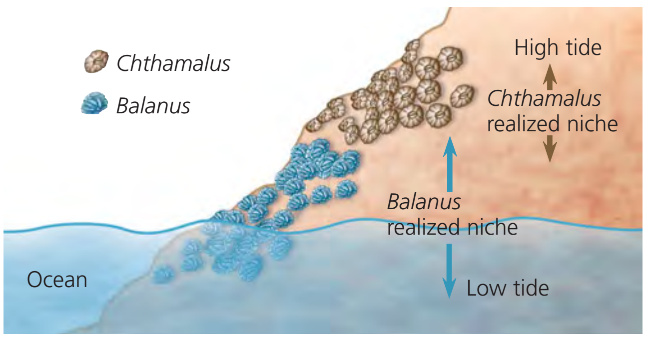


▲ **Figure 54.2 Resource partitioning among Dominican Republic lizards.** Seven species of *Anolis* lizards live in close proximity, and all feed on insects and other small arthropods. However, competition for food is reduced because each lizard species has a different preferred perch, thus occupying a distinct niche.

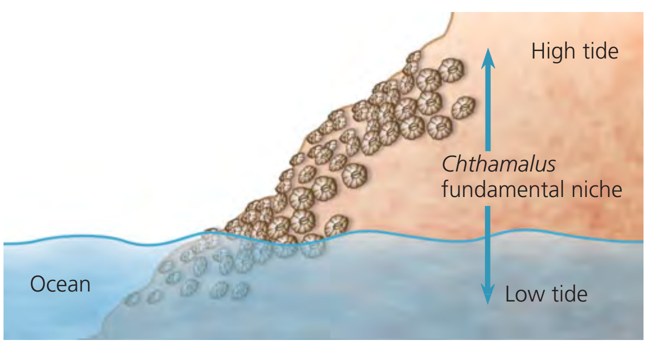
▼ **Figure 54.3** **INQUIRY**

Can a species' niche be influenced by interspecific competition?

EXPERIMENT Ecologist Joseph Connell studied two barnacle species—*Chthamalus stellatus* and *Balanus balanoides*—that have a stratified distribution on rocks along the coast of Scotland. *Chthamalus* is usually found higher on the rocks than *Balanus*. To determine whether the distribution of *Chthamalus* is the result of interspecific competition with *Balanus*, Connell removed *Balanus* from the rocks at several sites.



RESULTS *Chthamalus* spread into the region formerly occupied by *Balanus*.



CONCLUSION Interspecific competition makes the realized niche of *Chthamalus* much smaller than its fundamental niche.

SOURCE J. H. Connell, The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*, *Ecology* 42:710–723 (1961).

MB See the related Experimental Inquiry Tutorial in MasteringBiology.

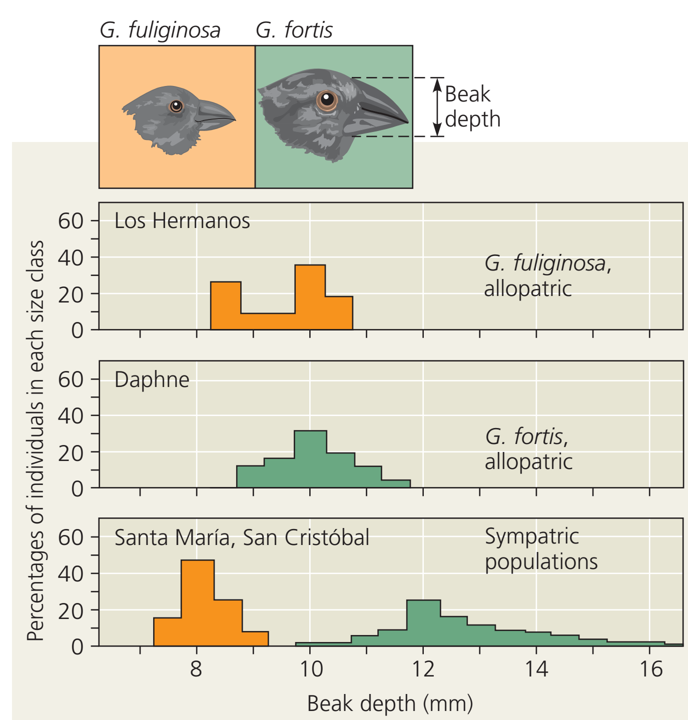
WHAT IF? Other observations showed that *Balanus* cannot survive high on the rocks because it dries out during low tides. How would *Balanus*'s realized niche compare with its fundamental niche?

Species can partition their niches not just in space, as lizards and barnacles do, but in time as well. The common spiny mouse (*Acomys cahirinus*) and the golden spiny mouse (*A. russatus*) live in rocky habitats of the Middle East and Africa, sharing similar microhabitats and food sources. Where they coexist, *A. cahirinus* is nocturnal (active at night), while *A. russatus* is diurnal (active during the day). Surprisingly, laboratory research showed that *A. russatus* is naturally nocturnal. To be active during the day, it must override its biological clock in the presence of *A. cahirinus*. When researchers in Israel removed all *A. cahirinus* individuals from a site in the species' natural habitat, *A. russatus* individuals at that site became nocturnal, consistent with the laboratory results. This change in behavior suggests that competition exists between the species and that partitioning of their active time helps them coexist.

▲ **The golden spiny mouse (*Acomys russatus*)**

Character Displacement

Closely related species whose populations are sometimes allopatric (geographically separate; see Chapter 24) and sometimes sympatric (geographically overlapping) provide more evidence for the importance of competition in structuring communities. In some cases, the allopatric populations of such species are morphologically similar and use similar resources. By contrast, sympatric populations, which would potentially compete for resources, show differences in body structures and in the resources they use. This tendency for characteristics to diverge more in sympatric than in allopatric populations of two species is called **character displacement**. An example of character displacement in Galápagos finches is shown in **Figure 54.4**.



▲ **Figure 54.4 Character displacement: indirect evidence of past competition.** Allopatric populations of *Geospiza fuliginosa* and *Geospiza fortis* on Los Hermanos and Daphne Islands have similar beak morphologies (top two graphs) and presumably eat similarly sized seeds. However, where the two species are sympatric on Santa María and San Cristóbal, *G. fuliginosa* has a shallower, smaller beak and *G. fortis* a deeper, larger one (bottom graph), adaptations that favor eating different-sized seeds.

Predation

Predation refers to a +/− interaction between species in which one species, the predator, kills and eats the other, the prey. Though the term *predation* generally elicits such images as a lion attacking and eating an antelope, it applies to a wide range of interactions. An animal that kills a plant by eating the plant's tissues can also be considered a predator. Because eating and avoiding being eaten are prerequisite to reproductive success, the adaptations of both predators and prey tend to be refined through natural selection.

Many important feeding adaptations of predators are obvious and familiar. Most predators have acute senses that enable them to find and identify potential prey. Many predators also have adaptations such as claws, teeth, fangs, stingers, or poison that help them catch and subdue their food. Rattlesnakes and other pit vipers, for example, find their prey with a pair of heat-sensing organs located between their eyes and nostrils (see Figure 50.7a), and they kill small birds and mammals by injecting them with toxins through their fangs. Predators that pursue their prey are generally fast and agile, whereas those that lie in ambush are often disguised in their environments.

Just as predators possess adaptations for capturing prey, prey animals have adaptations that help them avoid being eaten. Some common behavioral defenses are hiding, fleeing, and forming herds or schools. Active self-defense is less common, though some large grazing mammals vigorously defend their young from predators such as lions. Other behavioral defenses include alarm calls that summon many individuals of the prey species, which then mob the predator.

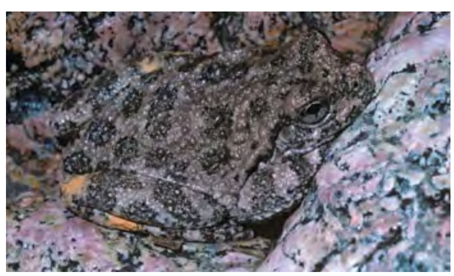
Animals also display a variety of morphological and physiological defensive adaptations. **Cryptic coloration**, or camouflage, makes prey difficult to see **(Figure 54.5a)**. Mechanical or chemical defenses protect species such as porcupines and skunks. Some animals, including the European fire salamander, can synthesize toxins, whereas others accumulate toxins passively from the plants they eat. Animals with effective chemical defenses often exhibit bright **aposematic coloration**, or warning coloration, such as that of the poison dart frog **(Figure 54.5b)**. Aposematic coloration seems to be adaptive because predators often avoid prey that have bright color patterns (see Chapter 1).

Some prey species are protected by their resemblance to other species. In **Batesian mimicry**, a palatable or harmless species mimics an unpalatable or harmful one. The larva of the hawkmoth *Hemeroplanes ornatus* puffs up its head and thorax when disturbed, looking like the head of a small poisonous snake **(Figure 54.5c)**. In this case, the mimicry even involves behavior; the larva weaves its head back and forth and hisses like a snake. In **Müllerian mimicry**, two or more unpalatable species, such as the cuckoo bee and yellow jacket, resemble each other **(Figure 54.5d)**. Presumably, the more unpalatable prey there are, the more quickly predators learn

▼ **Figure 54.5 Examples of defensive coloration in animals.**

(a) Cryptic coloration

▶ Canyon tree frog



(b) Aposematic coloration

▶ Poison dart frog

(c) Batesian mimicry: A harmless species mimics a harmful one.

◀ Hawkmoth larva

▼ Green parrot snake

(d) Müllerian mimicry: Two unpalatable species mimic each other.

◀ Cuckoo bee

▼ Yellow jacket

to avoid prey with that particular appearance. The shared appearance thus becomes a kind of aposematic coloration. In an example of convergent evolution, unpalatable animals in several different taxa have similar patterns of coloration: Black and yellow or red stripes characterize unpalatable animals as diverse as yellow jackets and coral snakes (see Figure 1.25).

Many predators also use mimicry. Alligator snapping turtles have tongues that resemble a wriggling worm, thus luring small fish. Any fish that tries to eat the "bait" is itself quickly consumed as the turtle's strong jaws snap closed. Anglerfish also lure prey with their own bait, in this case a modified bone of the dorsal fin that luminesces in some species.

Herbivory

Ecologists use the term **herbivory** to refer to a +/− interaction in which an organism eats parts of a plant or alga. While large mammalian herbivores such as cattle, sheep, and water buffalo may be most familiar, most herbivores are actually invertebrates, such as grasshoppers and beetles. In the ocean, herbivores include snails, sea urchins, some tropical fishes, and certain mammals, including the manatee **(Figure 54.6)**.

Like predators, herbivores have many specialized adaptations. Many herbivorous insects have chemical sensors on their feet that enable them to distinguish between toxic and nontoxic plants as well as between more nutritious and less nutritious plants. Some mammalian herbivores, such as goats, use their sense of smell to examine plants, rejecting some and eating others. They may also eat just a specific part of a plant, such as the flowers. Many herbivores also have specialized teeth or digestive systems adapted for processing vegetation (see Chapter 41).

Unlike prey animals, plants cannot run away to avoid being eaten. Instead, a plant's arsenal against herbivores may feature chemical toxins or structures such as spines and thorns. Among the plant compounds that serve as chemical weapons are the poison strychnine, produced by the tropical vine *Strychnos toxifera*; nicotine, from the tobacco plant; and tannins, from a variety of plant species. Plants in the genus *Astragalus* accumulate selenium; they are known as "locoweeds" because the cattle and sheep that eat them wander aimlessly in circles and may even die. Compounds that are not toxic to humans but may be distasteful to many herbivores are responsible for the familiar flavors of cinnamon, cloves, and peppermint. Certain plants produce chemicals that cause abnormal development in some insects that eat them.

▲ **Figure 54.6 A West Indies manatee (*Trichechus manatus*) in Florida.** The animal in this photo is feeding on hydrilla, an introduced species.

Symbiosis

When individuals of two or more species live in direct and intimate contact with one another, their relationship is called **symbiosis**. In this book, we adopt a general definition of symbiosis that includes all such interactions, whether they are harmful, helpful, or neutral. Some biologists define symbiosis more narrowly as a synonym for mutualism, an interaction in which both species benefit.

Parasitism

Parasitism is a +/− symbiotic interaction in which one organism, the **parasite**, derives its nourishment from another organism, its **host**, which is harmed in the process. Parasites that live within the body of their host, such as tapeworms, are called **endoparasites**; parasites that feed on the external surface of a host, such as ticks and lice, are called **ectoparasites**. In one particular type of parasitism, parasitoid insects—usually small wasps—lay eggs on or in living hosts. The larvae then feed on the body of the host, eventually killing it. Some ecologists have estimated that at least one-third of all species on Earth are parasites.

Many parasites have complex life cycles involving multiple hosts. The blood fluke, which currently infects approximately 200 million people around the world, requires two hosts at different times in its development: humans and freshwater snails (see Figure 33.11). Some parasites change the behavior of their hosts in a way that increases the probability of the parasite being transferred from one host to another. For instance, the presence of parasitic acanthocephalan (spiny-headed) worms leads their crustacean hosts to engage in a variety of atypical behaviors, including leaving protective cover and moving into the open. As a result of their modified behavior, the crustaceans have a greater chance of being eaten by the birds that are the second host in the parasitic worm's life cycle.

Parasites can significantly affect the survival, reproduction, and density of their host population, either directly or indirectly. For example, ticks that live as ectoparasites on moose weaken their hosts by withdrawing blood and causing hair breakage and loss. In their weakened condition, the moose have a greater chance of dying from cold stress or predation by wolves (see Figure 53.18).

Mutualism

Mutualistic symbiosis, or **mutualism**, is an interspecific interaction that benefits both species (+/+). We have described many examples of mutualism in previous chapters: nitrogen fixation by bacteria in the root nodules of legumes; the digestion of cellulose by microorganisms in the digestive systems of termites and ruminant mammals; the exchange of nutrients in mycorrhizae, associations of fungi and the roots of plants; and photosynthesis by unicellular algae in corals. The interaction between termites and the microorganisms in their digestive system is an example of *obligate mutualism*, in which at least one species has lost the ability to survive without its partner. In *facultative mutualism*, as in the acacia-ant example shown in **Figure 54.7**, both species can survive alone.

Mutualistic relationships sometimes involve the coevolution of related adaptations in both species, with changes in either species likely to affect the survival and reproduction of the other. For example, most flowering plants have adaptations such as nectar or fruit that attract animals that function in pollination or seed dispersal (see Chapter 38). In turn, many animals have adaptations that help them find and consume nectar.

(a) Certain species of acacia trees in Central and South America have hollow thorns that house stinging ants of the genus *Pseudomyrmex*. The ants feed on nectar produced by the tree and on protein-rich swellings (orange in the photograph) at the tips of leaflets.

(b) The acacia benefits because the pugnacious ants, which attack anything that touches the tree, remove fungal spores, small herbivores, and debris. They also clip vegetation that grows close to the acacia.

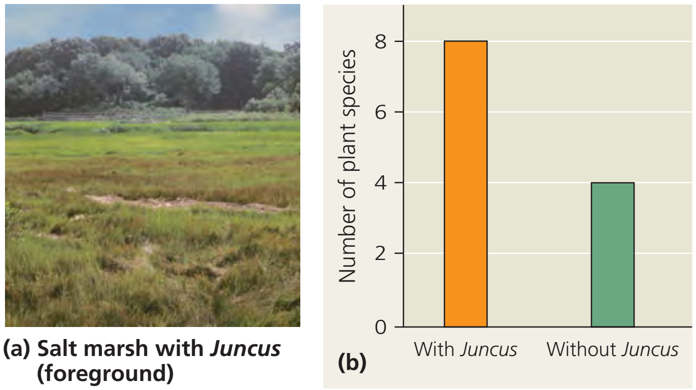
▲ **Figure 54.7 Mutualism between acacia trees and ants.**

Commensalism

An interaction between species that benefits one of the species but neither harms nor helps the other (+/0) is called **commensalism**. Commensal interactions are difficult to document in nature because any close association between species likely affects both species, even if only slightly. For instance, "hitchhiking" species, such as algae that live on the shells of aquatic turtles or barnacles that attach to whales, are sometimes considered commensal. The hitchhikers gain a place to grow while having seemingly little effect on their ride. However, the hitchhikers may in fact slightly decrease the reproductive success of their hosts by reducing the hosts' efficiency of movement in searching for food or escaping from predators. Conversely, the hitchhikers may provide a benefit in the form of camouflage.

Some associations that are possibly commensal involve one species obtaining food that is inadvertently exposed by another. Cowbirds and cattle egrets feed on insects flushed out of the grass by grazing bison, cattle, horses, and other herbivores. Because the birds increase their feeding rates when following the herbivores, they clearly benefit from the association. Much of the time, the herbivores may be unaffected by the relationship **(Figure 54.8)**. However, they, too, may sometimes derive some benefit; the birds tend to be opportunistic feeders that occasionally remove and eat ticks and other ectoparasites from the herbivores. They may also warn the herbivores of a predator's approach.

▲ **Figure 54.8 A possible example of commensalism between cattle egrets and water buffalo.**



(a) Salt marsh with *Juncus* (foreground)

(b)

▲ **Figure 54.9 Facilitation by black rush (*Juncus gerardi*) in New England salt marshes.** Black rush increases the number of plant species that can live in the upper middle zone of the marsh.

Facilitation

Species can have positive effects (+/+ or 0/+) on the survival and reproduction of other species without necessarily living in the direct and intimate contact of a symbiosis. This type of interaction, called **facilitation**, is particularly common in plant ecology. For instance, the black rush *Juncus gerardi* makes the soil more hospitable for other plant species in some zones of New England salt marshes **(Figure 54.9a)**. *Juncus* helps prevent salt buildup in the soil by shading the soil surface, which reduces evaporation. *Juncus* also prevents the salt marsh soils from becoming oxygen depleted as it transports oxygen to its belowground tissues. In one study, when *Juncus* was removed from areas in the upper middle intertidal zone, those areas supported 50% fewer plant species **(Figure 54.9b)**.

All five types of interactions that we have discussed so far—competition, predation, herbivory, symbiosis, and facilitation—strongly influence the structure of communities. You will see other examples of these interactions throughout this chapter.

CONCEPT CHECK 54.1

1. Explain how interspecific competition, predation, and mutualism differ in their effects on the interacting populations of two species.
2. According to the principle of competitive exclusion, what outcome is expected when two species with identical niches compete for a resource? Why?
3. MAKE CONNECTIONS Figure 24.14 (p. 499) illustrates the formation of and possible outcomes for a hybrid zone over time. Imagine that two finch species colonize a new island and are capable of hybridizing. The island contains two plant species, one with large seeds and one with small, growing in isolated habitats. If the two finch species specialize in eating different plant species, would reproductive barriers be reinforced, weakened, or unchanged in this hybrid zone? Explain.

For suggested answers, see Appendix A.

CONCEPT **54.2**

Diversity and trophic structure characterize biological communities

Along with the specific interactions described in the previous section, communities are also characterized by more general attributes, including how diverse they are and the feeding relationships of their species. In this section, you will read why such ecological attributes are important. You will also learn how a few species sometimes exert strong control on a community's structure, particularly on the composition, relative abundance, and diversity of its species.

Species Diversity

The **species diversity** of a community—the variety of different kinds of organisms that make up the community—has two components. One is **species richness**, the number of different species in the community. The other is the **relative abundance** of the different species, the proportion each species represents of all individuals in the community.

Imagine two small forest communities, each with 100 individuals distributed among four tree species (A, B, C, and D) as follows:

Community 1: 25A, 25B, 25C, 25D

Community 2: 80A, 5B, 5C, 10D

The species richness is the same for both communities because they both contain four species of trees, but the relative abundance is very different **(Figure 54.10)**. You would easily notice the four types of trees in community 1, but without looking carefully, you might see only the abundant species A in the second forest. Most observers would intuitively describe community 1 as the more diverse of the two communities.

Ecologists use many tools to quantitatively compare the diversity of different communities across time and space. They often calculate indexes of diversity based on species richness and relative abundance. One widely used index is **Shannon diversity** (H):

$$H = -(p_A \ln p_A + p_B \ln p_B + p_C \ln p_C + \ldots)$$

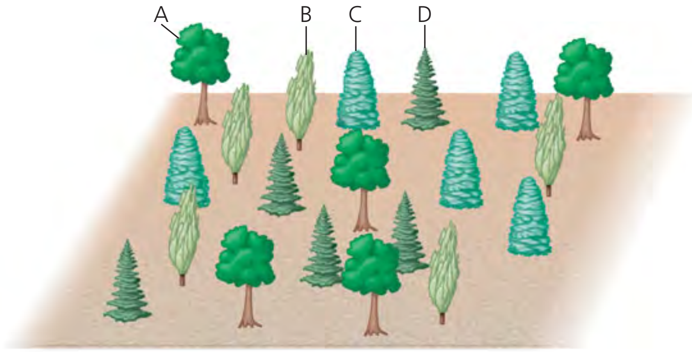
where A, B, C . . . are the species in the community, p is the relative abundance of each species, and ln is the natural logarithm. A higher value of H indicates a more diverse community. Let's use this equation to calculate the Shannon diversity index of the two communities in Figure 54.10. For community 1, $p = 0.25$ for each species, so

$$H = -4(0.25 \ln 0.25) = 1.39.$$

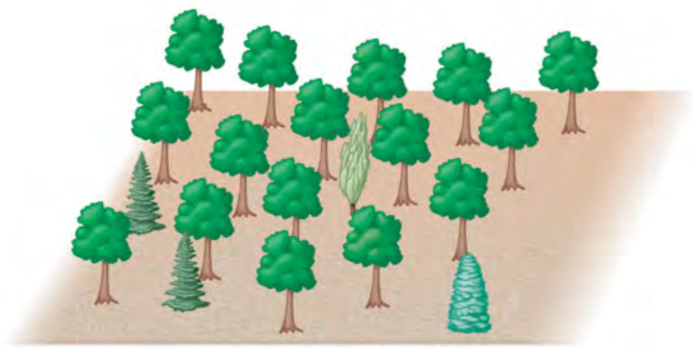
For community 2,

$$H = -[0.8 \ln 0.8 + 2(0.05 \ln 0.05) + 0.1 \ln 0.1] = 0.71.$$

These calculations confirm our intuitive description of community 1 as more diverse.



Community 1
A: 25% B: 25% C: 25% D: 25%



Community 2
A: 80% B: 5% C: 5% D: 10%

▲ **Figure 54.10 Which forest is more diverse?** Ecologists would say that community 1 has greater species diversity, a measure that includes both species richness and relative abundance.

Determining the number and relative abundance of species in a community is easier said than done. Many sampling techniques can be used, but since most species in a community are relatively rare, it may be hard to obtain a sample size large enough to be representative. It is also difficult to census the highly mobile or less visible or accessible members of communities, such as microorganisms, nematodes, deep-sea creatures, and nocturnal species. The small size of microorganisms makes them particularly difficult to sample, so ecologists now use molecular tools to help determine microbial diversity **(Figure 54.11)**. Measuring species diversity is often challenging but is essential for understanding community structure and for conserving diversity, as you will read in Chapter 56.

Diversity and Community Stability

In addition to measuring species diversity, ecologists manipulate diversity in experimental communities in nature and in the laboratory. They do this to examine the potential benefits of diversity, including increased productivity and stability of biological communities.

Researchers at the Cedar Creek Natural History Area, in Minnesota, have been manipulating plant diversity in

▼ **Figure 54.11** **RESEARCH METHOD**

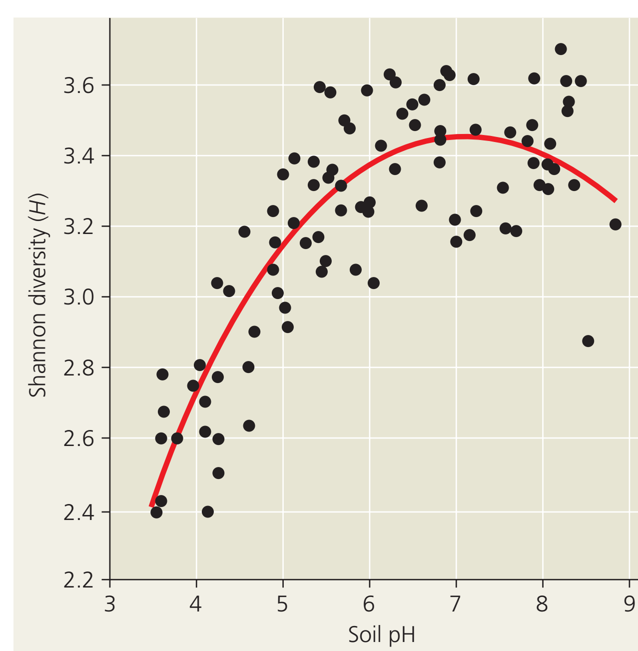
Determining Microbial Diversity Using Molecular Tools

APPLICATION Ecologists are increasingly using molecular techniques, such as the analysis of restriction fragment length polymorphisms (RFLPs), to determine microbial diversity and richness in environmental samples. As used in this application, RFLP analysis produces a DNA profile for microbial taxa based on sequence variations in the DNA that encodes the small subunit of ribosomal RNA. Noah Fierer and Rob Jackson, of Duke University, used this method to compare the diversity of soil bacteria in 98 habitats across North and South America to help identify environmental variables associated with high bacterial diversity.

TECHNIQUE Researchers first extract and purify DNA from the microbial community in each sample. They use the polymerase chain reaction (PCR) to amplify the ribosomal DNA and label the DNA with a fluorescent dye (see Chapter 20). Restriction enzymes then cut the amplified, labeled DNA into fragments of different lengths, which are separated by gel electrophoresis. The number and abundance of these fragments characterize the DNA profile of the sample.

Based on their RFLP analysis, Fierer and Jackson calculated the Shannon diversity (H) of each sample. They then looked for a correlation between H and several environmental variables, including vegetation type, mean annual temperature and rainfall, and acidity and quality of the soil at each site.

RESULTS The diversity of bacterial communities in soils across North and South America was related almost exclusively to soil pH, with the Shannon diversity being highest in neutral soils and lowest in acidic soils. Amazonian rain forests, which have extremely high plant and animal diversity, had the most acidic soils and the lowest bacterial diversity of the samples tested.



SOURCE N. Fierer and R. B. Jackson, The diversity and biogeography of soil bacterial communities, *Proceedings of the National Academy of Sciences USA* 103:626–631 (2006).

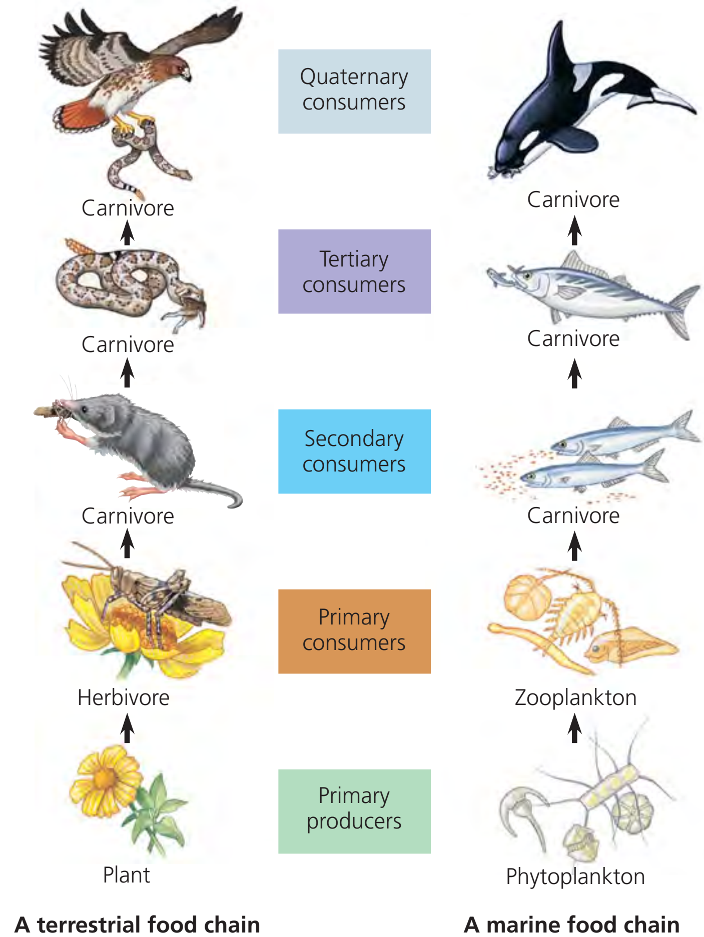
▲ **Figure 54.12 Study plots at the Cedar Creek Natural History Area, site of long-term experiments on manipulating plant diversity.**

experimental communities for two decades **(Figure 54.12)**. Higher-diversity communities generally are more productive and are better able to withstand and recover from environmental stresses, such as droughts. More diverse communities are also more stable year to year in their productivity. In one decade-long experiment, for instance, researchers at Cedar Creek created 168 plots, each containing 1, 2, 4, 8, or 16 perennial grassland species. The most diverse plots were 70% more stable than the single-species plots in the amount of plant mass produced each year.

Higher-diversity communities are often more resistant to **invasive species**, which are organisms that become established outside their native range. Scientists working in Long Island Sound, off the coast of Connecticut, created communities of different diversity consisting of sessile marine invertebrates, including tunicates (see Figure 34.5). They then examined how vulnerable these experimental communities were to invasion by an exotic tunicate. They found that the exotic tunicate was four times more likely to survive in lower-diversity communities than in higher-diversity ones. The researchers concluded that relatively diverse communities captured more of the resources available in the system, leaving fewer resources for the invader and decreasing its survival.

Trophic Structure

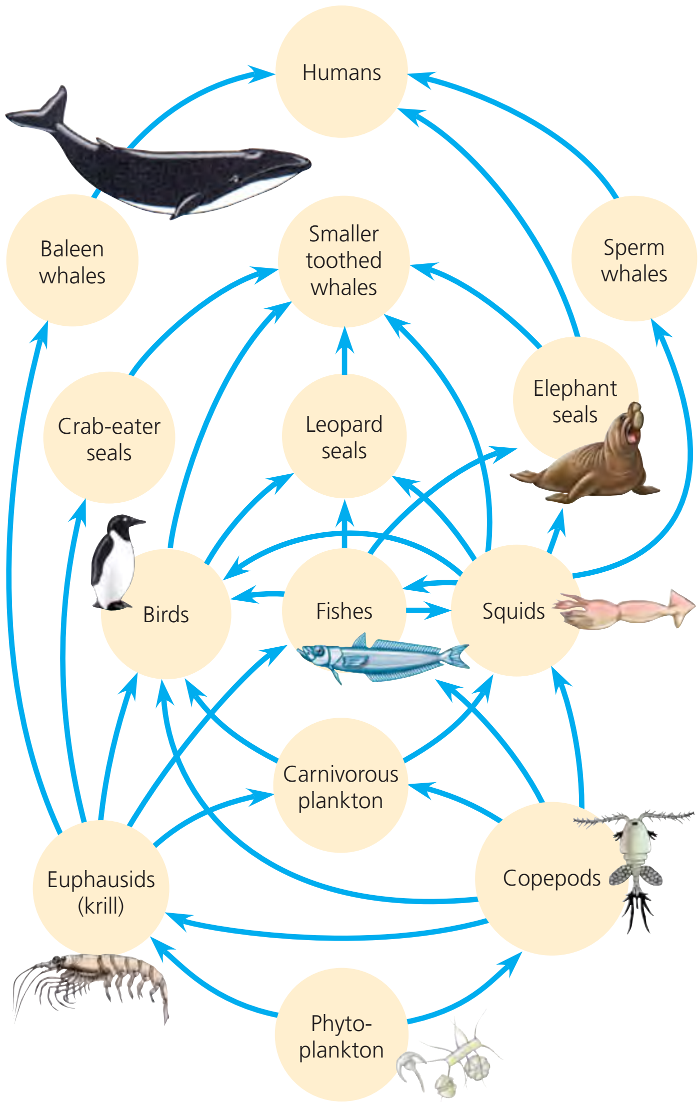
Experiments like the ones just described often examine the importance of diversity within one trophic level. The structure and dynamics of a community also depend on the feeding relationships between organisms—the **trophic structure** of the community. The transfer of food energy up the trophic levels from its source in plants and other autotrophic organisms (primary producers) through herbivores (primary consumers) to carnivores (secondary, tertiary, and quaternary consumers) and eventually to decomposers is referred to as a **food chain (Figure 54.13)**.



▲ **Figure 54.13 Examples of terrestrial and marine food chains.** The arrows trace energy and nutrients that pass through the trophic levels of a community when organisms feed on one another. Decomposers, which "feed" on organisms from all trophic levels, are not shown here.

Food Webs

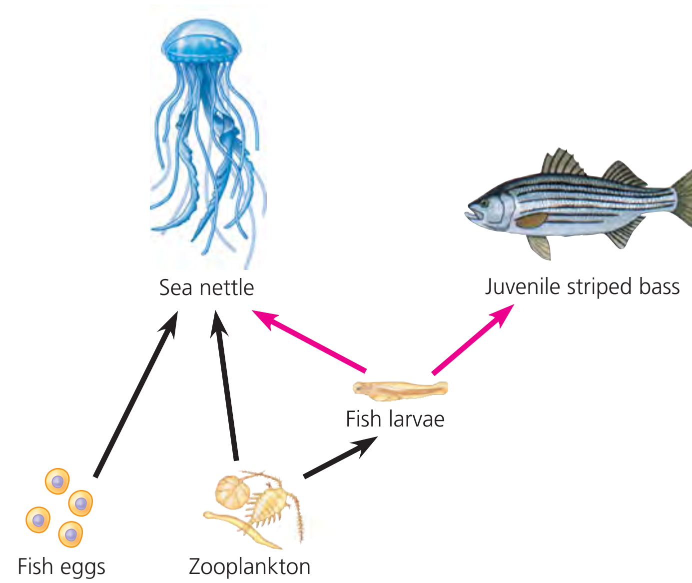
In the 1920s, Oxford University biologist Charles Elton recognized that food chains are not isolated units but are linked together in **food webs**. Ecologists summarize the trophic relationships of a community by diagramming a food web with arrows linking species according to who eats whom. In an Antarctic pelagic community, for example, the primary producers are phytoplankton, which serve as food for the dominant grazing zooplankton, especially euphausids (krill) and copepods, both of which are crustaceans **(Figure 54.14)**. These zooplankton species are in turn eaten by various carnivores, including other plankton, penguins, seals, fishes, and baleen whales. Squids, which are carnivores that feed on fish and zooplankton, are another important link in these food webs, as they are in turn eaten by seals and toothed whales. During the time when whales were commonly hunted for food, humans became the top predator in this food web. Having hunted many whale species to low numbers, humans are now harvesting at lower trophic levels, catching krill as well as fishes for food.



▲ **Figure 54.14 An Antarctic marine food web.** Arrows follow the transfer of food from the producers (phytoplankton) up through the trophic levels. For simplicity, this diagram omits decomposers.

How are food chains linked into food webs? A given species may weave into the web at more than one trophic level. In the food web shown in Figure 54.14, euphausids feed on phytoplankton as well as on other grazing zooplankton, such as copepods. Such "nonexclusive" consumers are also found in terrestrial communities. For instance, foxes are omnivores whose diet includes berries and other plant materials, herbivores such as mice, and other predators, such as weasels. Humans are among the most versatile of omnivores.

Complicated food webs can be simplified in two ways for easier study. First, species with similar trophic relationships in a given community can be grouped into broad functional groups. In Figure 54.14, more than 100 phytoplankton species are grouped as the primary producers in the food web. A second way to simplify a food web for closer study is to isolate a portion of the web that interacts very little with



▲ **Figure 54.15 Partial food web for the Chesapeake Bay estuary on the U.S. Atlantic coast.** The sea nettle (*Chrysaora quinquecirrha*) and juvenile striped bass (*Morone saxatilis*) are the main predators of fish larvae (bay anchovy and several other species). Note that sea nettles are secondary consumers (black arrows) when they eat zooplankton, but tertiary consumers (red arrows) when they eat fish larvae, which are themselves secondary consumers of zooplankton.

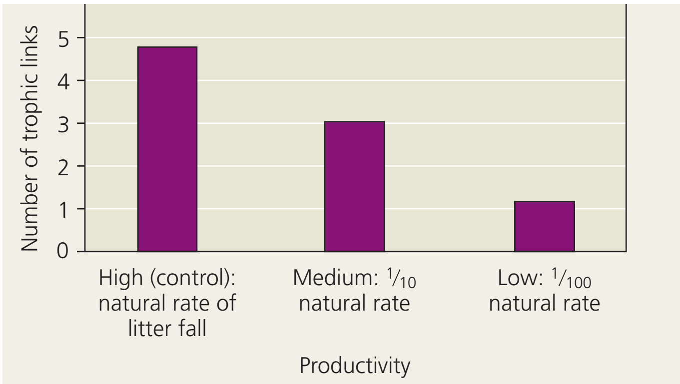
the rest of the community. **Figure 54.15** illustrates a partial food web for sea nettles (a type of cnidarian) and juvenile striped bass in Chesapeake Bay.

Limits on Food Chain Length

Each food chain within a food web is usually only a few links long. In the Antarctic web of Figure 54.14, there are rarely more than seven links from the producers to any top-level predator, and most chains in this web have fewer links. In fact, most food webs studied to date have chains consisting of five or fewer links.

Why are food chains relatively short? There are two main hypotheses. One, the **energetic hypothesis**, suggests that the length of a food chain is limited by the inefficiency of energy transfer along the chain. As you will read in Chapter 55, only about 10% of the energy stored in the organic matter of each trophic level is converted to organic matter at the next trophic level. Thus, a producer level consisting of 100 kg of plant material can support about 10 kg of herbivore **biomass** (the total mass of all individuals in a population) and 1 kg of carnivore biomass. The energetic hypothesis predicts that food chains should be relatively longer in habitats of higher photosynthetic production, since the starting amount of energy is greater than in habitats with lower photosynthetic production.

A second hypothesis, the **dynamic stability hypothesis**, proposes that long food chains are less stable than short chains. Population fluctuations at lower trophic levels are magnified at higher levels, potentially causing the local extinction of top



▲ **Figure 54.16 Test of the energetic hypothesis for the restriction of food chain length.** Researchers manipulated the productivity of tree-hole communities in Queensland, Australia, by providing leaf litter input at three levels. Reducing energy input reduced food chain length, a result consistent with the energetic hypothesis.

? *According to the dynamic stability hypothesis, which productivity treatment should have the most stable food chain? Explain.*

predators. In a variable environment, top predators must be able to recover from environmental shocks (such as extreme winters) that can reduce the food supply all the way up the food chain. The longer a food chain is, the more slowly top predators can recover from environmental setbacks. This hypothesis predicts that food chains should be shorter in unpredictable environments.

Most of the data available support the energetic hypothesis. For example, ecologists have used tree-hole communities in tropical forests as experimental models to test the energetic hypothesis. Many trees have small branch scars that rot, forming holes in the tree trunk. The holes hold water and provide a habitat for tiny communities consisting of microorganisms and insects that feed on leaf litter, as well as predatory insects. **Figure 54.16** shows the results of experiments in which researchers manipulated productivity by varying the amount of leaf litter in tree holes. As predicted by the energetic hypothesis, holes with the most leaf litter, and hence the greatest total food supply at the producer level, supported the longest food chains.

Another factor that may limit food chain length is that carnivores in a food chain tend to be larger at successive trophic levels. The size of a carnivore and its feeding mechanism put some upper limit on the size of food it can take into its mouth. And except in a few cases, large carnivores cannot live on very small food items because they cannot procure enough food in a given time to meet their metabolic needs. Among the exceptions are baleen whales, huge suspension feeders with adaptations that enable them to consume enormous quantities of krill and other small organisms (see Figure 41.6).

Species with a Large Impact

Certain species have an especially large impact on the structure of entire communities because they are highly abundant or play a pivotal role in community dynamics. The impact of these species occurs through trophic interactions and their influence on the physical environment.

Dominant Species

Dominant species in a community are the species that are the most abundant or that collectively have the highest biomass. As a result, dominant species exert a powerful control over the occurrence and distribution of other species. For example, the dominance of sugar maples in an eastern North American forest community has a major impact on abiotic factors such as shading and soil nutrient availability, which in turn affect which other species live there.

There is no single explanation for why a species becomes dominant in a community. One hypothesis suggests that dominant species are competitively superior in exploiting limited resources such as water or nutrients. Another explanation is that dominant species are most successful at avoiding predation or the impact of disease. This latter idea could explain the high biomass attained in some environments by invasive species. Such species may not face the natural predators and agents of disease that would otherwise hold their populations in check.

One way to discover the impact of a dominant species is to remove it from the community. The American chestnut was a dominant tree in deciduous forests of eastern North America before 1910, making up more than 40% of mature trees. Then humans accidentally introduced the fungal disease chestnut blight to New York City via nursery stock imported from Asia. Between 1910 and 1950, this fungus killed almost all of the chestnut trees in eastern North America. In this case, removing the dominant species had a relatively small impact on some species but severe effects on others. Oaks, hickories, beeches, and red maples that were already present in the forest increased in abundance and replaced the chestnuts. No mammals or birds seemed to have been harmed by the loss of the chestnut, but seven species of moths and butterflies that fed on the tree became extinct.

Keystone Species and Ecosystem Engineers

In contrast to dominant species, **keystone species** are not usually abundant in a community. They exert strong control on community structure not by numerical might but by their pivotal ecological roles, or niches. **Figure 54.17** highlights the importance of a keystone species, a sea star, in maintaining the diversity of an intertidal community.

The sea otter, a keystone predator in the North Pacific, offers another example. Sea otters feed on sea urchins, and sea urchins feed mainly on kelp. In areas where sea otters are abundant, sea urchins are rare and kelp forests are well developed. Where sea otters are rare, sea urchins are common and kelp is almost absent. Over the last 20 years, orcas have been preying on sea otters as the orcas' usual prey has

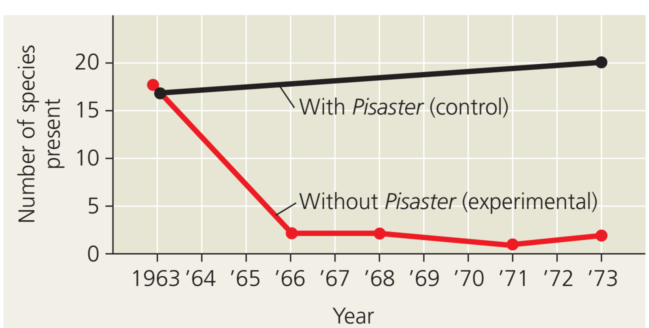
▼ Figure 54.17 INQUIRY

Is *Pisaster ochraceus* a keystone predator?

EXPERIMENT In rocky intertidal communities of western North America, the relatively uncommon sea star *Pisaster ochraceus* preys on mussels such as *Mytilus californianus*, a dominant species and strong competitor for space.

Robert Paine, of the University of Washington, removed *Pisaster* from an area in the intertidal zone and examined the effect on species richness.

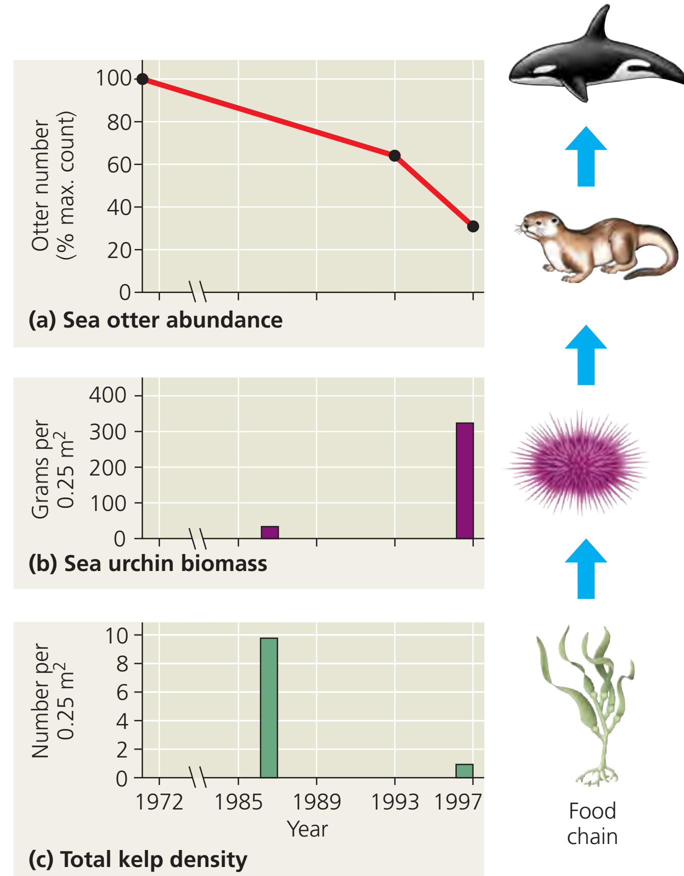
RESULTS In the absence of *Pisaster*, species richness declined as mussels monopolized the rock face and eliminated most other invertebrates and algae. In a control area where *Pisaster* was not removed, species richness changed very little.



CONCLUSION *Pisaster* acts as a keystone species, exerting an influence on the community that is not reflected in its abundance.

SOURCE R. T. Paine, Food web complexity and species diversity, *American Naturalist* 100:65–75 (1966).

WHAT IF? Suppose that an invasive fungus killed most individuals of *Mytilus* at these sites. Predict how species richness would be affected if *Pisaster* were then removed.



▲ Figure 54.18 Sea otter as a keystone predator in the North Pacific. The graphs correlate changes over time in sea otter abundance **(a)** with changes in sea urchin biomass **(b)** and changes in kelp density **(c)** in kelp forests at Adak Island (part of the Aleutian Island chain). The vertical diagram on the right represents the food chain after orcas (top) entered the chain.

▲ Figure 54.19 Beavers as ecosystem engineers. By felling trees, building dams, and creating ponds, beavers can transform large areas of forest into flooded wetlands.

declined. As a result, sea otter populations have plummeted in large areas off the coast of western Alaska, sometimes at rates as high as 25% per year. The loss of this keystone species has allowed sea urchin populations to increase, resulting in the loss of kelp forests **(Figure 54.18)**.

Other organisms exert their influence on a community not through trophic interactions but by changing their physical environment. Species that dramatically alter their environment are called **ecosystem engineers** or, to avoid implying conscious intent, "foundation species." A familiar ecosystem engineer is the beaver **(Figure 54.19)**. The effects of ecosystem engineers on other species can be positive or negative, depending on the needs of the other species.

Bottom-Up and Top-Down Controls

Simplified models based on relationships between adjacent trophic levels are useful for discussing community organization. For example, let's consider the three possible relationships between plants (V for vegetation) and herbivores (H):

$$V \rightarrow H \quad V \leftarrow H \quad V \leftrightarrow H$$

The arrows indicate that a change in the biomass of one trophic level causes a change in the other trophic level. $V \rightarrow H$ means that an increase in vegetation will increase the numbers or biomass of herbivores, but not vice versa. In this situation, herbivores are limited by vegetation, but vegetation is not limited by herbivory. In contrast, $V \leftarrow H$ means that an increase in herbivore biomass will decrease the abundance of vegetation, but not vice versa. A double-headed arrow indicates that feedback flows in both directions, with each trophic level sensitive to changes in the biomass of the other.

Two models of community organization are common: the bottom-up model and the top-down model. The $V \rightarrow H$ linkage suggests a **bottom-up model**, which postulates a unidirectional influence from lower to higher trophic levels. In this case, the presence or absence of mineral nutrients (N) controls plant (V) numbers, which control herbivore (H) numbers, which in turn control predator (P) numbers. The simplified bottom-up model is thus $N \rightarrow V \rightarrow H \rightarrow P$. To change the community structure of a bottom-up community, you need to alter biomass at the lower trophic levels, allowing those changes to propagate up through the food web. For example, if you add mineral nutrients to stimulate growth of vegetation, then the higher trophic levels should also increase in biomass. If you add predators to or remove predators from a bottom-up community, however, the effect should not extend down to the lower trophic levels.

In contrast, the **top-down model** postulates the opposite: Predation mainly controls community organization because predators limit herbivores, herbivores limit plants, and plants limit nutrient levels through nutrient uptake. The simplified top-down model, $N \leftarrow V \leftarrow H \leftarrow P$, is also called the *trophic cascade model*. In a lake community with four trophic levels, the model predicts that removing the top carnivores will increase the abundance of primary carnivores, in turn decreasing the number of herbivores, increasing phytoplankton abundance, and decreasing concentrations of mineral nutrients. If there were only three trophic levels in a lake, removing primary carnivores would increase the number of herbivores and decrease phytoplankton abundance, causing nutrient levels to increase. The effects thus move down the trophic structure as alternating +/− effects.

The top-down model has practical applications. For example, ecologists have applied the top-down model to improve water quality in polluted lakes. This approach, called **biomanipulation**, attempts to prevent algal blooms and eutrophication by altering the density of higher-level consumers in lakes instead of using chemical treatments. In lakes with three trophic levels, removing fish should improve water quality by increasing zooplankton density and thereby decreasing algal populations. In lakes with four trophic levels, adding top predators should have the same effect. We can summarize the scenario of three trophic levels with the following diagram:

	Polluted State	**Restored State**
Fish	Abundant	Rare
↓ Zooplankton	Rare	Abundant
↓ Algae	Abundant	Rare

Ecologists in Finland used biomanipulation to help purify Lake Vesijärvi, a large lake that was polluted with city sewage and industrial wastewater until 1976. After pollution controls reduced these inputs, the water quality of the lake began to improve. By 1986, however, massive blooms of cyanobacteria started to occur in the lake. These blooms coincided with an increase in the population of roach, a fish that had benefited from the mineral nutrients that the pollution provided over many years. Roach eat zooplankton, which otherwise keep the cyanobacteria and algae in check. To reverse these changes, ecologists removed nearly a million kilograms of fish from Lake Vesijärvi between 1989 and 1993, reducing roach abundance by about 80%. At the same time, they added a fourth trophic level by stocking the lake with pike perch, a predatory fish that eats roach. The water became clear, and the last cyanobacterial bloom was in 1989. The lake remains clear even though roach removal ended in 1993.

As these examples show, communities vary in their degree of bottom-up and top-down control. To manage agricultural landscapes, parks, reservoirs, and fisheries, we need to understand each particular community's dynamics.

CONCEPT CHECK 54.2

1. What two components contribute to species diversity? Explain how two communities that contain the same number of species can differ in species diversity.
2. Describe two hypotheses that explain why food chains are usually short, and state a key prediction of each hypothesis.
3. **WHAT IF?** Consider a grassland with five trophic levels: plants, grasshoppers, snakes, raccoons, and bobcats. If you released additional bobcats into the grassland, how would plant biomass change if the bottom-up model applied? If the top-down model applied?

For suggested answers, see Appendix A.

CONCEPT 54.3

Disturbance influences species diversity and composition

Decades ago, most ecologists favored the traditional view that biological communities are at equilibrium, a more or less stable balance, unless seriously disturbed by human activities. The "balance of nature" view focused on interspecific competition as a key factor determining community composition and maintaining stability in communities. *Stability* in this context refers to a community's tendency to reach and maintain a relatively constant composition of species.

One of the earliest proponents of this view, F. E. Clements, of the Carnegie Institution of Washington, argued in the early 1900s that the community of plants at a site had only one state of equilibrium, controlled solely by climate. According to Clements, biotic interactions caused the species in this *climax community* to function as an integrated unit—in effect, as a superorganism. His argument was based on the observation that certain species of plants are consistently found together, such as the oaks, maples, birches, and beeches in deciduous forests of the northeastern United States.

Other ecologists questioned whether most communities were at equilibrium or functioned as integrated units. A. G. Tansley, of Oxford University, challenged the concept of a climax community, arguing that differences in soils, topography, and other factors created many potential communities that were stable within a region. H. A. Gleason, of the University of Chicago, saw communities not as superorganisms but more as chance assemblages of species found together because they happen to have similar abiotic requirements—for example, for temperature, rainfall, and soil type. Gleason and other ecologists also realized that disturbance keeps many communities from reaching a state of equilibrium in species diversity or composition. A **disturbance** is an event, such as a storm, fire, flood, drought, overgrazing, or human activity, that changes a community by removing organisms from it or altering resource availability.

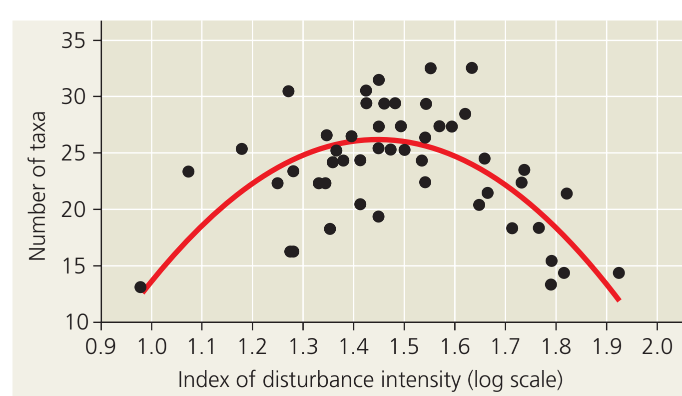
This recent emphasis on change has produced the **nonequilibrium model**, which describes most communities as constantly changing after being affected by disturbances. Even where relatively stable communities do exist, they can be rapidly transformed into nonequilibrium communities. Let's now take a look at the ways disturbances influence community structure and composition.

Characterizing Disturbance

The types of disturbances and their frequency and severity vary among communities. Storms disturb almost all communities, even those in the oceans, through the action of waves. Fire is a significant disturbance in most terrestrial communities; in fact, chaparral and some grassland biomes require regular burning to maintain their structure and species composition. Freezing is a frequent occurrence in many rivers, lakes, and ponds, and many streams and ponds are disturbed by spring flooding and seasonal drying. A high level of disturbance is generally the result of a high intensity *and* high frequency of disturbance, while low disturbance levels can result from either a low intensity or low frequency of disturbance.

The **intermediate disturbance hypothesis** states that moderate levels of disturbance foster greater species diversity than do low or high levels of disturbance. High levels of disturbance reduce diversity by creating environmental stresses that exceed the tolerances of many species or by disturbing the community so often that slow-growing or slow-colonizing species are excluded. At the other extreme, low levels of disturbance can reduce species diversity by allowing competitively dominant species to exclude less competitive ones. Meanwhile, intermediate levels of disturbance can foster greater species diversity by opening up habitats for occupation by less competitive species. Such intermediate disturbance levels rarely create conditions so severe that they exceed the environmental tolerances or recovery rates of potential community members.

The intermediate disturbance hypothesis is supported by many terrestrial and aquatic studies. In one such study, ecologists in New Zealand compared the richness of invertebrate taxa living in the beds of streams exposed to different frequencies and intensities of flooding **(Figure 54.20)**. When floods occurred either very frequently or rarely, invertebrate richness was low. Frequent floods made it difficult for some species to become established in the streambed, while rare floods resulted in species being displaced by superior competitors. Invertebrate richness peaked in streams that had an intermediate frequency or intensity of flooding, as predicted by the hypothesis.



▲ **Figure 54.20 Testing the intermediate disturbance hypothesis.** Researchers identified the taxa (species or genera) of invertebrates at two locations in each of 27 New Zealand streams. They assessed the intensity of flooding at each location using an index of streambed disturbance. The number of invertebrate taxa peaked where the intensity of flooding was at intermediate levels.

Although moderate levels of disturbance appear to maximize species diversity, small and large disturbances often have important effects on community structure. Small-scale disturbances can create patches of different habitats across a landscape, which help maintain diversity in a community. Large-scale disturbances are also a natural part of many communities. Much of Yellowstone National Park, for example, is dominated by lodgepole pine, a tree that requires the rejuvenating influence of periodic fires. Lodgepole cones remain closed until exposed to intense heat. When a forest fire burns the trees, the cones open and the seeds are released. The new generation of lodgepole pines can then thrive on nutrients released from the burned trees and in the sunlight that is no longer blocked by taller trees.

In the summer of 1988, extensive areas of Yellowstone burned during a severe drought. By 1989, burned areas in the park were largely covered with new vegetation, suggesting that the species in this community are adapted to rapid recovery after fire **(Figure 54.21)**. In fact, large-scale fires have periodically swept through the lodgepole pine forests of Yellowstone and other northern areas for thousands of years. In contrast, more southerly pine forests were historically affected by frequent but low-intensity fires. In these forests, a century of human intervention to suppress small fires has allowed an unnatural buildup of fuels in some places and elevated the risk of large, severe fires to which the species are not adapted.

Studies of the Yellowstone forest community and many others indicate that they are nonequilibrium communities, changing continually because of natural disturbances and the internal processes of growth and reproduction. Mounting evidence suggests that nonequilibrium conditions resulting from disturbance are in fact the norm for most communities.

Ecological Succession

Changes in the composition and structure of terrestrial communities are most apparent after some severe disturbance, such as a volcanic eruption or a glacier, strips away all the existing vegetation. The disturbed area may be colonized by a variety of species, which are gradually replaced by other species, which are in turn replaced by still other species—a process called **ecological succession**.

When this process begins in a virtually lifeless area where soil has not yet formed, such as on a new volcanic island or on the rubble (moraine) left by a retreating glacier, it is called **primary succession**. Often the only life-forms initially present are autotrophic prokaryotes and heterotrophic prokaryotes and protists. Lichens and mosses, which grow from windblown spores, are commonly the first macroscopic photosynthesizers to colonize such areas. Soil develops gradually as rocks weather and organic matter accumulates from the decomposed remains of the early colonizers. Once soil is present, the lichens and mosses are usually overgrown by grasses, shrubs, and trees that sprout from seeds blown in from nearby areas or carried in by animals. Eventually, an area is colonized by plants that become the community's prevalent form of vegetation. Producing such a community through primary succession may take hundreds or thousands of years.

Secondary succession occurs when an existing community has been cleared by some disturbance that leaves the soil intact, as in Yellowstone following the 1988 fires (see Figure 54.21). Sometimes the area begins to return to something like its original state. For instance, in a forested area that has been cleared for farming and later abandoned, the earliest plants to recolonize are often herbaceous species that

(a) Soon after fire. The fire has left a patchy landscape. Note the unburned trees in the far distance.

(b) One year after fire. The community has begun to recover. A variety of herbaceous plants, different from those in the former forest, cover the ground.

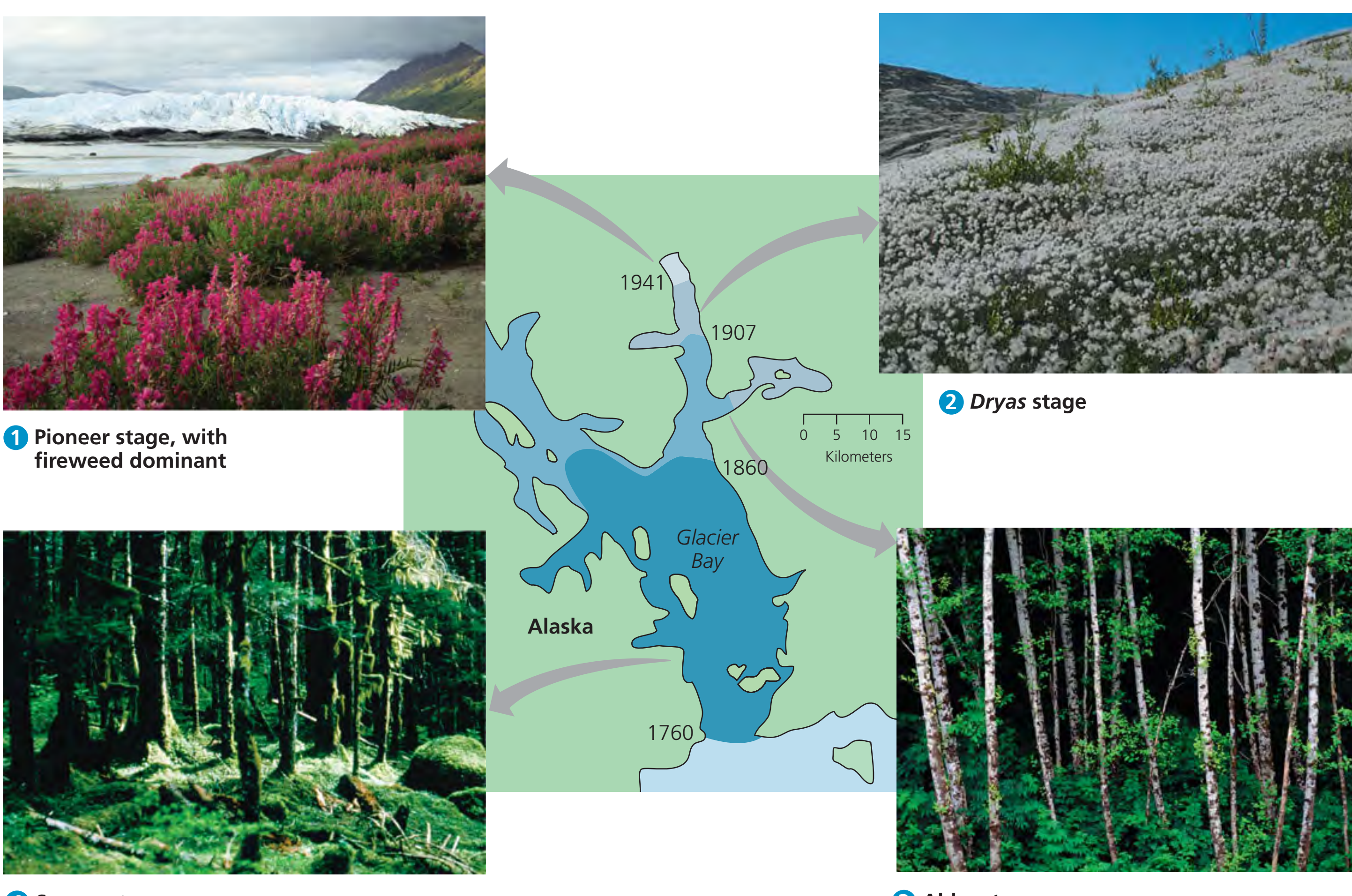
▲ **Figure 54.21 Recovery following a large-scale disturbance.** The 1988 Yellowstone National Park fires burned large areas of forests dominated by lodgepole pines.

grow from windblown or animal-borne seeds. If the area has not been burned or heavily grazed, woody shrubs may in time replace most of the herbaceous species, and forest trees may eventually replace most of the shrubs.

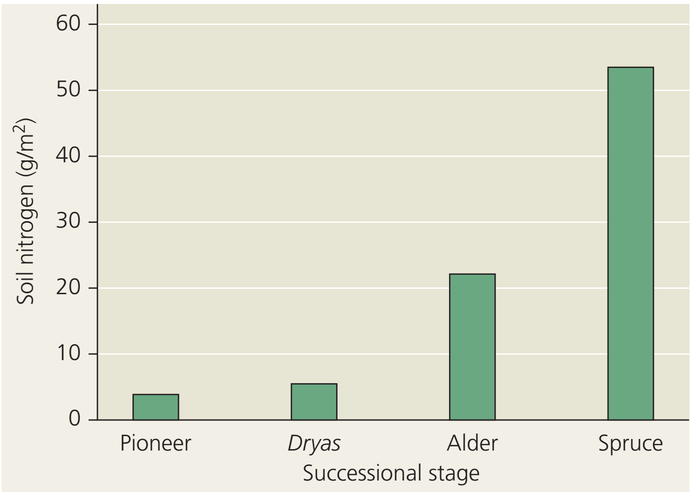
Early arrivals and later-arriving species may be linked in one of three key processes. The early arrivals may *facilitate* the appearance of the later species by making the environment more favorable—for example, by increasing the fertility of the soil. Alternatively, the early species may *inhibit* establishment of the later species, so that successful colonization by later species occurs in spite of, rather than because of, the activities of the early species. Finally, the early species may be completely independent of the later species, which *tolerate* conditions created early in succession but are neither helped nor hindered by early species.

Let's look at how these various processes contribute to primary succession on glacial moraines. Ecologists have conducted the most extensive research on moraine succession at Glacier Bay in southeastern Alaska, where glaciers have retreated more than 100 km since 1760 (**Figure 54.22**). By studying the communities on moraines at different distances from the mouth of the bay, ecologists can examine different stages in succession. ❶ The exposed moraine is colonized first by pioneering species that include liverworts, mosses, fireweed, scattered *Dryas* (a mat-forming shrub), willows, and cottonwood. ❷ After about three decades, *Dryas* dominates the plant community. ❸ A few decades later, the area is invaded by alder, which forms dense thickets up to 9 m tall. ❹ In the next two centuries, these alder stands are overgrown first by Sitka spruce and later by a combination of western hemlock and mountain hemlock. In areas of poor drainage, the forest floor of this spruce-hemlock forest is invaded by sphagnum moss, which holds large amounts of water and acidifies the soil, eventually killing the trees. Thus, by about 300 years after glacial retreat, the vegetation consists of sphagnum bogs on the poorly drained flat areas and spruce-hemlock forest on the well-drained slopes.

How is succession on glacial moraines related to the environmental changes caused by transitions in the vegetation? The bare soil exposed as the glacier retreats is quite basic, with a pH of 8.0–8.4 due to the carbonate compounds in the parent rocks. The soil pH falls rapidly as vegetation develops.

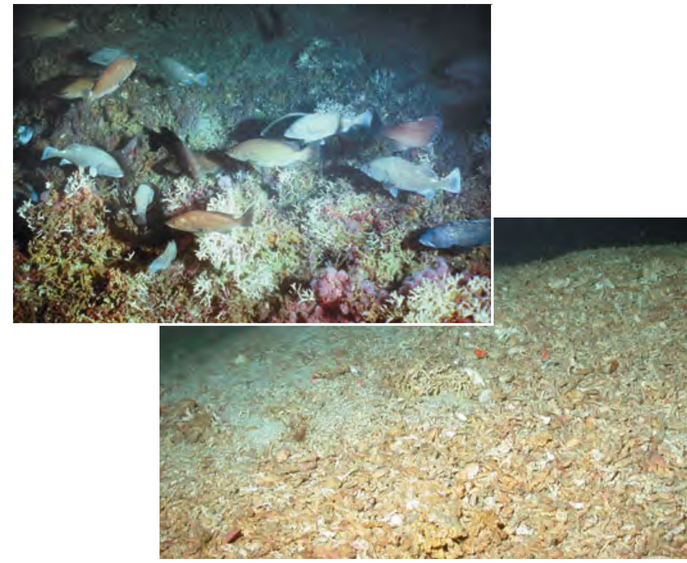


▲ **Figure 54.22 Glacial retreat and primary succession at Glacier Bay, Alaska.** The different shades of blue on the map show retreat of the glacier since 1760, based on historical descriptions.



▲ **Figure 54.23 Changes in soil nitrogen content during succession at Glacier Bay.**

MAKE CONNECTIONS *Figures 37.10 and 37.11 illustrate two types of atmospheric nitrogen fixation by prokaryotes. At the earliest stages of primary succession, before any plants are present at a site, which type of nitrogen fixation would occur, and why?*



▲ **Figure 54.24 Disturbance of the ocean floor by trawling.** These photos show the seafloor off northwestern Australia before (top) and after (bottom) deep-sea trawlers have passed.

Decomposition of acidic spruce needles in particular reduces the pH of the soil from 7.0 to approximately 4.0. The soil concentrations of mineral nutrients also change with time. Because the bare soil after glacial retreat is low in nitrogen content, almost all the pioneer plant species begin succession with poor growth and yellow leaves due to inadequate nitrogen supply. The exceptions are *Dryas* and, particularly, alder; these species have symbiotic bacteria that fix atmospheric nitrogen (see Chapter 37). Soil nitrogen content increases rapidly during the alder stage of succession and continues to increase during the spruce stage **(Figure 54.23)**. By altering soil properties, pioneer plant species permit new plant species to grow, and the new plants in turn alter the environment in different ways, contributing to succession.

Human Disturbance

Ecological succession is a response to disturbance of the environment, and the strongest agent of disturbance today is human activity. Agricultural development has disrupted what were once the vast grasslands of the North American prairie. Logging and clearing for urban development, mining, and farming have reduced large tracts of forests to small patches of disconnected woodlots in many parts of the United States and throughout Europe. After forests are clear-cut, weedy and shrubby vegetation often colonizes the area and dominates it for many years. This type of vegetation is also found in agricultural fields that are no longer under cultivation and in vacant lots and construction sites.

Human disturbance of communities is not limited to the United States and Europe, nor is it a recent problem. Tropical rain forests are quickly disappearing as a result of clear-cutting for lumber, cattle grazing, and farmland. Centuries of overgrazing and agricultural disturbance have contributed to famine in parts of Africa by turning seasonal grasslands into vast barren areas.

Humans disturb marine ecosystems as well as terrestrial ones. The effects of ocean trawling, where boats drag weighted nets across the seafloor, are similar to those of clear-cutting a forest or plowing a field **(Figure 54.24)**. The trawls scrape and scour corals and other life on the seafloor and in its sediments. In a typical year, ships trawl 15 million km^2 of ocean floor, an area about the size of South America and 150 times larger than the area of forests that are clear-cut annually.

Because disturbance by human activities is often severe, it reduces species diversity in many communities. In Chapter 56, we will take a closer look at how human-caused disturbance is affecting the diversity of life.

CONCEPT CHECK 54.3

1. Why do high and low levels of disturbance usually reduce species diversity? Why does an intermediate level of disturbance promote species diversity?
2. During succession, how might the early species facilitate the arrival of other species?
3. **WHAT IF?** Most prairies experience regular fires, typically every few years. If these disturbances were relatively modest, how would the species diversity of a prairie likely be affected if no burning occurred for 100 years? Explain your answer.

For suggested answers, see Appendix A.

CONCEPT 54.4

Biogeographic factors affect community diversity

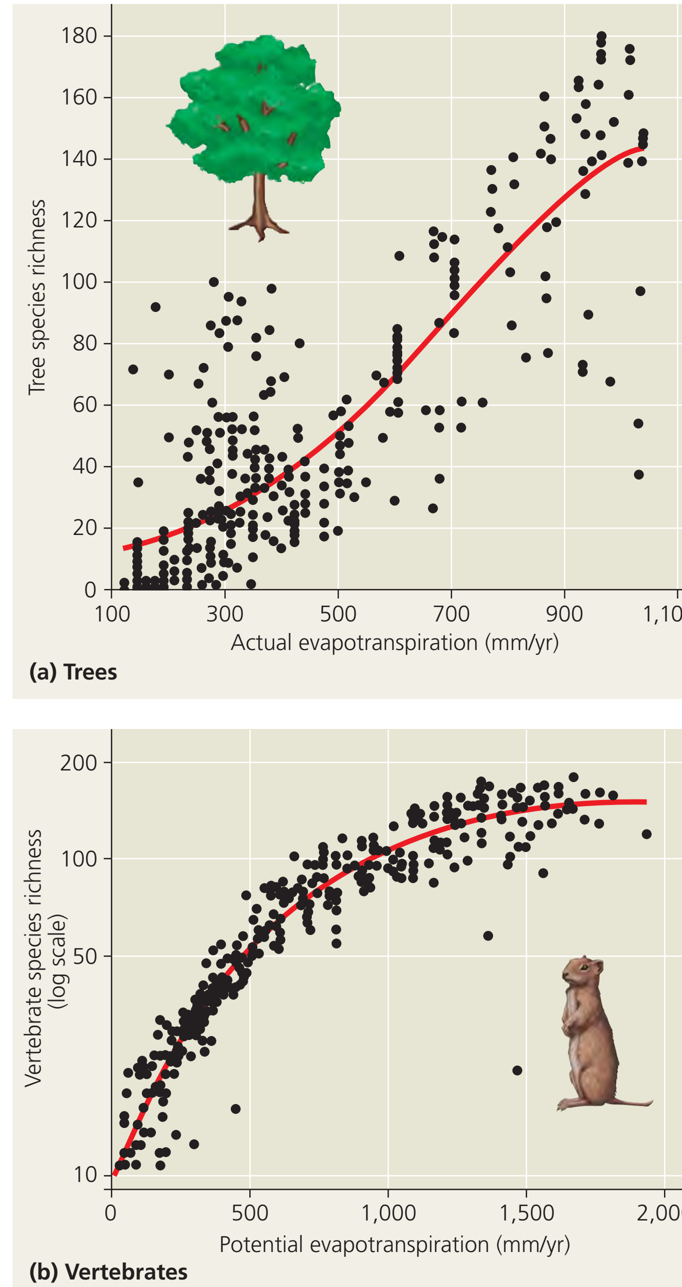
So far, we have examined relatively small-scale or local factors that influence the diversity of communities, including the effects of species interactions, dominant species, and many types of disturbances. Ecologists also recognize that large-scale biogeographic factors contribute to the tremendous range of diversity observed in biological communities. The contributions of two biogeographic factors in particular—the latitude of a community and the area it occupies—have been investigated for more than a century.

Latitudinal Gradients

In the 1850s, both Charles Darwin and Alfred Wallace pointed out that plant and animal life was generally more abundant and diverse in the tropics than in other parts of the globe. Since that time, many researchers have confirmed this observation. One study found that a 6.6-hectare (1 ha = 10,000 m^2) plot in tropical Malaysia contained 711 tree species, while a 2-ha plot of deciduous forest in Michigan typically contained just 10 to 15 tree species. Moreover, there are only 50 tree species in all of western Europe north of the Alps. Many groups of animals show similar latitudinal gradients. There are more than 200 species of ants in Brazil but only 7 in Alaska, for instance.

The two key factors in latitudinal gradients of species richness are probably evolutionary history and climate. Over the course of evolutionary time, species richness may increase in a community as more speciation events occur (see Chapter 24). Tropical communities are generally older than temperate or polar communities because temperate and polar communities have repeatedly "started over" after major disturbances from glaciations. Another factor is that the growing season in tropical forests is about five times as long as in the tundra communities of high latitudes. In effect, biological time runs about five times as fast in the tropics as near the poles, so intervals between speciation events are shorter in the tropics.

Climate is likely the primary cause of the latitudinal gradient in richness and diversity. In terrestrial communities, the two main climatic factors correlated with diversity are solar energy input and water availability, both of which are relatively high in the tropics. These factors can be considered together by measuring a community's rate of **evapotranspiration**, the evaporation of water from soil plus the transpiration of water from plants. Evapotranspiration, a function of solar radiation, temperature, and water availability, is much higher in hot areas with abundant rainfall than in areas with low temperatures or low precipitation. *Potential evapotranspiration*, a measure of potential water loss that assumes that water is readily available, is determined by the amount of solar radiation

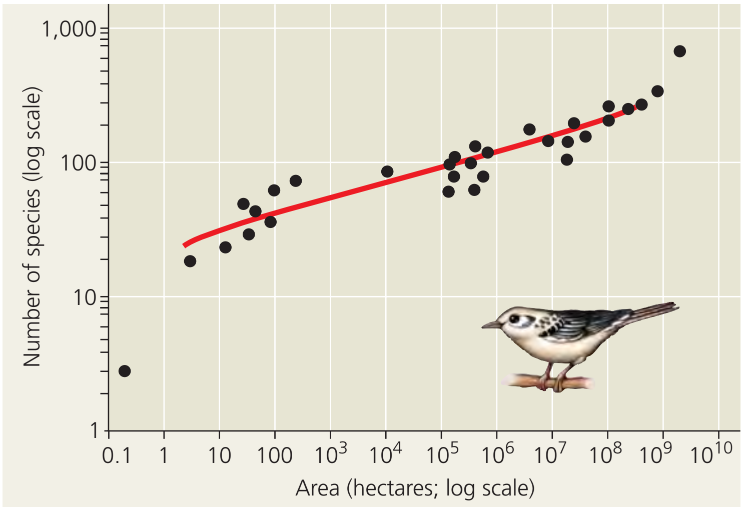


▲ **Figure 54.25 Energy, water, and species richness. (a)** Species richness of North American trees increases most predictably with actual evapotranspiration, while **(b)** vertebrate species richness in North America increases most predictably with potential evapotranspiration. Evapotranspiration values are expressed as rainfall equivalents.

and temperature and is highest in regions where both are plentiful. The species richness of plants and animals correlates with both measures of evapotranspiration **(Figure 54.25)**.

Area Effects

In 1807, naturalist and explorer Alexander von Humboldt described one of the first patterns of species richness to be recognized, the **species-area curve**: All other factors being equal, the larger the geographic area of a community, the



▲ **Figure 54.26 Species-area curve for North American breeding birds.** Both area and number of species are plotted on a logarithmic scale. The data points range from a 0.2-ha plot with 3 species in Pennsylvania to the whole United States and Canada (1.9 billion ha) with 625 species.

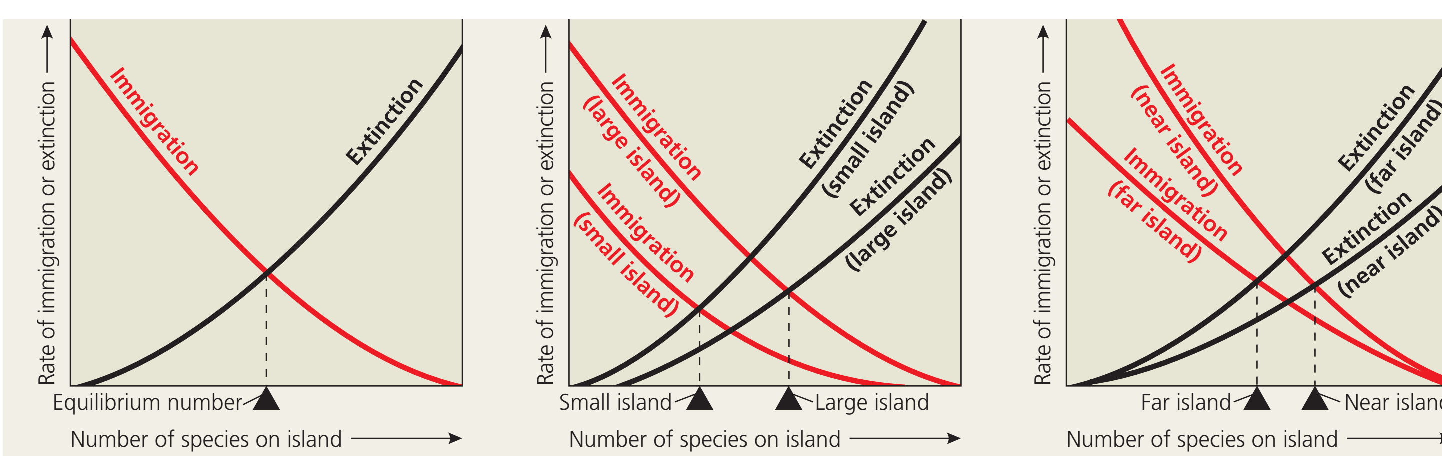
more species it has. The likely explanation for this pattern is that larger areas offer a greater diversity of habitats and microhabitats than smaller areas. In conservation biology, developing species-area curves for the key taxa in a community helps ecologists predict how the potential loss of a certain area of habitat is likely to affect the community's diversity.

Figure 54.26 is a species-area curve for North American breeding birds (birds with breeding populations in the mapped area, as opposed to migrant populations). The slope indicates the extent to which species richness increases with community area. While the slopes of different species-area curves vary, the basic concept of diversity increasing with increasing area applies in a variety of situations, from surveys of ant diversity in New Guinea to the number of plant species on islands of different sizes. In fact, island biogeography provides some of the best examples of species-area curves, as we will discuss next.

Island Equilibrium Model

Because of their isolation and limited size, islands provide excellent opportunities for studying the biogeographic factors that affect the species diversity of communities. By "islands," we mean not only oceanic islands, but also habitat islands on land, such as lakes, mountain peaks separated by lowlands, or natural woodland fragments surrounded by areas disturbed by humans—in other words, any patch surrounded by an environment not suitable for the "island" species. In the 1960s, American ecologists Robert MacArthur and E. O. Wilson developed a general model of island biogeography, identifying the key determinants of species diversity on an island with a given set of physical characteristics **(Figure 54.27)**.

Consider a newly formed oceanic island that receives colonizing species from a distant mainland. Two factors that determine the number of species on the island are the rate at which new species immigrate to the island and the rate at which species become extinct on the island. At any given time, an island's immigration and extinction rates are affected by the number of species already present. As the number of species on the island increases, the immigration rate of new species decreases, because any individual reaching the island is less likely to represent a species that is not already present. At the same time, as more species inhabit an island, extinction rates on the island increase because of the greater likelihood of competitive exclusion.



(a) Immigration and extinction rates. The equilibrium number of species on an island represents a balance between the immigration of new species and the extinction of species already there.

(b) Effect of island size. Large islands may ultimately have a larger equilibrium number of species than small islands because immigration rates tend to be higher and extinction rates lower on large islands.

(c) Effect of distance from mainland. Near islands tend to have larger equilibrium numbers of species than far islands because immigration rates to near islands are higher and extinction rates lower.

▲ **Figure 54.27 The equilibrium model of island biogeography.** Black triangles represent equilibrium numbers of species.

Two physical features of the island further affect immigration and extinction rates: its size and its distance from the mainland. Small islands generally have lower immigration rates because potential colonizers are less likely to reach a small island. For instance, birds blown out to sea by a storm are more likely to land by chance on a large island than on a small one. Small islands also have higher extinction rates because they generally contain fewer resources, have less diverse habitats, and have smaller population sizes. Distance from the mainland is also important; for two islands of equal size, a closer island generally has a higher immigration rate than one farther away. Because of their higher immigration rates, closer islands tend to have lower extinction rates, as arriving colonists help sustain the presence of a species on a near island and prevent its extinction.

MacArthur and Wilson's model is called the *island equilibrium model* because an equilibrium will eventually be reached where the rate of species immigration equals the rate of species extinction. The number of species at this equilibrium point is correlated with the island's size and distance from the mainland. Like any ecological equilibrium, this species equilibrium is dynamic; immigration and extinction continue, and the exact species composition may change over time.

MacArthur and Wilson's studies of the diversity of plants and animals on many island chains support the prediction that species richness increases with island size, in keeping with the island equilibrium model (**Figure 54.28**). Species counts also fit the prediction that the number of species decreases with increasing remoteness of the island.

Predictions of species composition based on the island equilibrium model may apply in only a limited number of cases and over relatively short periods, where colonization is the main process affecting species composition. Over longer periods, abiotic disturbances such as storms, adaptive evolutionary changes, and speciation generally alter the species composition and community structure on islands. Nonetheless, the model is widely applied in conservation biology, particularly for the design of habitat reserves and for providing a starting point for predicting the effects of habitat loss on species diversity.

CONCEPT CHECK 54.4

1. Describe two hypotheses that explain why species diversity is greater in tropical regions than in temperate and polar regions.
2. Describe how an island's size and distance from the mainland affect the island's species richness.
3. **WHAT IF?** Based on MacArthur and Wilson's model of island biogeography, how would you expect the richness of birds on islands to compare with the richness of snakes and lizards? Explain.

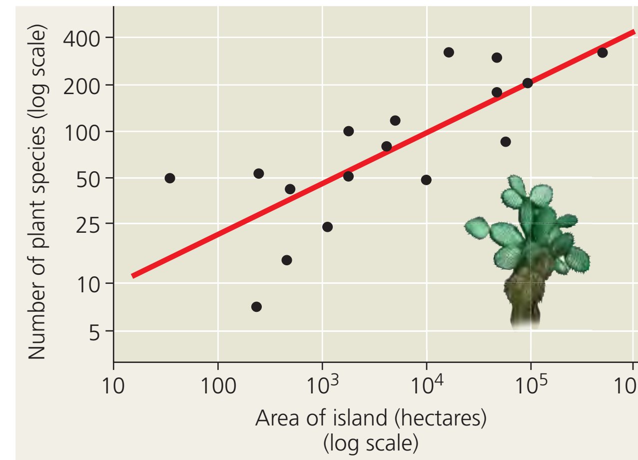
For suggested answers, see Appendix A.

▼ **Figure 54.28** **INQUIRY**

How does species richness relate to area?

FIELD STUDY Ecologists Robert MacArthur and E. O. Wilson studied the number of plant species on the Galápagos Islands in relation to the area of the different islands.

RESULTS



CONCLUSION Plant species richness increases with island size, supporting the island equilibrium model.

SOURCE R. H. MacArthur and E. O. Wilson, *The Theory of Island Biogeography*, Princeton University Press, Princeton, NJ (1967).

WHAT IF? Four islands in this study ranging in area from about 40 to 10,000 ha each contained about 50 plant species. What does such variation tell you about the simple assumptions of the island equilibrium model?

CONCEPT **54.5**

Pathogens alter community structure locally and globally

Now that we have examined several important factors that structure biological communities, we will finish the chapter by examining community interactions involving **pathogens**—disease-causing microorganisms, viruses, viroids, or prions. (Viroids and prions are infectious RNA molecules and proteins, respectively; see Chapter 19.) Scientists have only recently come to appreciate how universal the effects of pathogens are in communities.

As you will read, pathogens can alter community structure quickly and extensively. They produce especially clear effects when they are introduced into new habitats, as in the case of chestnut blight and the fungus that causes it (see Concept 54.2). A pathogen can be particularly virulent in a new habitat because new hosts have not had a chance to become resistant to the pathogen through natural selection. The invasive chestnut blight fungus had far stronger effects on the American chestnut, for instance, than it had on Asian chestnut species in the fungus's native habitat. Humans are similarly vulnerable to the effects of emerging diseases spread by our increasingly global economy. Ecologists are applying ecological knowledge to help track and control the pathogens that cause such diseases.

Pathogens and Community Structure

In spite of the potential of pathogens to limit populations, pathogens have until recently been the subject of relatively few ecological studies. This imbalance is now being addressed as events highlight the ecological importance of disease.

Coral reef communities are increasingly susceptible to the influence of newly discovered pathogens. White-band disease, caused by an unknown pathogen, has resulted in dramatic changes in the structure and composition of Caribbean reefs. The disease kills corals by causing their tissue to slough off in a band from the base to the tip of the branches. Because of the disease, staghorn coral (*Acropora cervicornis*) has virtually disappeared from the Caribbean since the 1980s. In the same region, populations of elkhorn coral (*Acropora palmata*) have also been decimated. Such corals provide key habitat for lobsters as well as snappers and other fish species. When the corals die, they are quickly overgrown by algae. Surgeonfish and other herbivores that feed on algae come to dominate the fish community. Eventually, the corals topple because of damage from storms and other disturbances. The complex, three-dimensional structure of the reef disappears, and diversity plummets.

Pathogens also influence community structure in terrestrial ecosystems. In the forests and savannas of California, trees of several species are dying from sudden oak death (SOD). This recently discovered disease is caused by the fungus-like protist *Phytophthora ramorum* (see Chapter 28). SOD was first described in California in 1995, when hikers noticed trees dying around San Francisco Bay. By 2010, it had spread more than 800 km. During that time, it killed more than a million oaks and other trees from the central California coast to southern Oregon. The loss of these oaks has led to the decreased abundance of at least five bird species, including the acorn woodpecker and the oak titmouse, that rely on the oaks for food and habitat. Although there is currently no cure for SOD, scientists recently sequenced the genome of *P. ramorum* in hopes of finding a way to fight the pathogen.

Human activities are transporting pathogens around the world at unprecedented rates. Genetic analyses using simple sequence DNA (see Chapter 21) suggest that *P. ramorum* likely came to North America from Europe through the horticulture trade. Similarly, the pathogens that cause human diseases are spread by our global economy. H1N1, the virus that causes "swine flu" in humans, was first detected in Veracruz, Mexico, in early 2009. It quickly spread around the world when infected individuals flew on airplanes to other countries. By mid-2010, the world's first flu pandemic in 40 years had killed more than 17,000 people.

▼ **Figure 54.29**

IMPACT

Identifying Lyme Disease Host Species

A student researcher collects ticks from a white-footed mouse.

For years, scientists thought that the white-footed mouse was the primary host for the Lyme pathogen because mice are heavily parasitized by young ticks. When researchers vaccinated mice against Lyme disease and released them into the wild, however, the number of infected ticks hardly changed. That result prompted biologists in New York to look for other hosts for the Lyme pathogen. They first trapped individuals of 11 potential host species in the field and measured the density of larval ticks on the animals. They showed that each host species transmitted to the ticks a unique set of alleles of a gene that encodes a protein on the pathogen's outer surface. The researchers then collected ticks in the field that were no longer attached to any host and used the genetic database to identify their former hosts. They were surprised to learn that two inconspicuous shrew species had been the hosts of more than half the ticks examined.

WHY IT MATTERS By identifying the species that host a pathogen and determining their abundance and distribution, community ecologists obtain information that can be used to control the hosts most responsible for spreading diseases.

FURTHER READING D. Brisson et al., Conspicuous impacts of inconspicuous hosts on the Lyme disease epidemic, *Proceedings of the Royal Society B* 275:227–235 (2008).

MAKE CONNECTIONS Concept 23.1 (p. 470) describes genetic variation between populations. How might genetic variation between shrew populations in different locations affect the results of this study?

Community Ecology and Zoonotic Diseases

Three-quarters of emerging human diseases and many of the most devastating diseases are caused by **zoonotic pathogens**. Zoonotic pathogens are defined as those that are transferred to humans from other animals, either through direct contact with an infected animal or by means of an intermediate species, called a **vector**. The vectors that spread zoonotic diseases are often parasites, including ticks, lice, and mosquitoes. Identifying the community of hosts and vectors for a pathogen can help prevent disease **(Figure 54.29)**.

Ecologists also use their knowledge of community interactions to track the spread of zoonotic diseases. One example, avian flu, is caused by highly contagious viruses transmitted through the saliva and feces of birds (see Chapter 19). Most of these viruses affect wild birds mildly, but they often cause stronger symptoms in domesticated birds, the most common source of human infections. Since 2003, one particular viral strain, called H5N1, has killed hundreds of millions of poultry and more than 250 people. Millions more people are at risk of infection.

Control programs that quarantine domestic birds or monitor their transport may be ineffective if avian flu spreads naturally through the movements of wild birds. From 2003 to 2006, the H5N1 strain spread rapidly from southeast Asia into Europe and Africa, but by mid-2010, it had not appeared in Australia or the Americas. The most likely place for infected wild birds to enter the Americas is Alaska, the entry point for ducks, geese, and shorebirds that migrate across the Bering Sea from Asia every year. Ecologists are studying the spread of the virus by trapping and testing migrating and resident birds in Alaska **(Figure 54.30)**. These ecological detectives are trying to catch the first wave of the disease entering North America.

Community ecology provides the foundation for understanding the life cycles of pathogens and their interactions with hosts. Pathogen interactions are also greatly influenced by changes in the physical environment. To control pathogens and the diseases they cause, scientists need an ecosystem perspective—an intimate knowledge of how the pathogens interact with other species and with all aspects of their environment. Ecosystems are the subject of Chapter 55.

▲ **Figure 54.30 Tracking avian flu.** Graduate student Travis Booms, of Boise State University, bands a young gyrfalcon as part of a project to monitor the spread of the disease.

CONCEPT CHECK 54.5

1. What are pathogens?
2. **WHAT IF?** Rabies, a viral disease in mammals, is not currently found in the British Isles. If you were in charge of disease control there, what practical approaches might you employ to keep the rabies virus from reaching these islands?

For suggested answers, see Appendix A.

54 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

CONCEPT 54.1

Community interactions are classified by whether they help, harm, or have no effect on the species involved (pp. 1194–1200)

- A variety of **interspecific interactions** affect the survival and reproduction of the species that engage in them. These interactions include **interspecific competition**, **predation**, **herbivory**, **symbiosis**, and **facilitation**. **Parasitism**, **mutualism**, and **commensalism** are types of symbiotic interactions.
- **Competitive exclusion** states that two species competing for the same resource cannot coexist permanently in the same place. **Resource partitioning** is the differentiation of species **niches** that enables species to coexist in a community.

? *Give an example of a pair of species that exhibit each interaction listed in the table at right.*

Interspecific Interaction	Description
Competition (−/−)	Two or more species compete for a resource that is in short supply.
Predation (+/−)	One species, the predator, kills and eats the other, the prey. Predation has led to diverse adaptations, including mimicry.
Herbivory (+/−)	An herbivore eats part of a plant or alga. Plants have various chemical and mechanical defenses against herbivory, and herbivores have specialized adaptations for feeding.
Symbiosis	Individuals of two or more species live in close contact with one another. Symbiosis includes parasitism, mutualism, and commensalism.
Parasitism (+/−)	The **parasite** derives its nourishment from a second organism, its **host**, which is harmed.
Mutualism (+/+)	Both species benefit from the interaction.
Commensalism (+/0)	One species benefits from the interaction, while the other is unaffected by it.
Facilitation (+/+ or 0/+)	Species have positive effects on the survival and reproduction of other species without the intimate contact of a symbiosis.

CONCEPT 54.2

Diversity and trophic structure characterize biological communities (pp. 1200–1206)

- **Species diversity** measures the number of species in a community—its **species richness**—and their **relative abundance**. A community with similar abundances of species is more diverse than one in which one or two species are abundant and the remainder are rare.
- More diverse communities typically produce more **biomass** and show less year-to-year variation in growth than less diverse communities and are more resistant to invasion by exotic species.
- **Trophic structure** is a key factor in community dynamics. **Food chains** link the trophic levels from producers to top carnivores. Branching food chains and complex trophic interactions form **food webs**. The **energetic hypothesis** suggests that the length of a food chain is limited by the inefficiency of energy transfer along the chain.
- **Dominant species** are the most abundant species in a community and possess high competitive abilities. **Keystone species** are usually less abundant species that exert a disproportionate influence on community structure because of their ecological niche. **Ecosystem engineers** influence community structure through their effects on the physical environment.
- The **bottom-up model** proposes a unidirectional influence from lower to higher trophic levels, in which nutrients and other abiotic factors primarily determine community structure, including the abundance of primary producers. **The top-down model** proposes that control of each trophic level comes from the trophic level above, with the result that predators control herbivores, which in turn control primary producers.

? *Based on indexes such as Shannon diversity, is a community of higher species richness always more diverse than a community of lower species richness? Explain.*

CONCEPT 54.3

Disturbance influences species diversity and composition (pp. 1207–1210)

- Increasing evidence suggests that **disturbance** and lack of equilibrium, rather than stability and equilibrium, are the norm for most communities. According to the **intermediate disturbance hypothesis**, moderate levels of disturbance can foster higher species diversity than can low or high levels of disturbance.
- **Ecological succession** is the sequence of community and ecosystem changes after a disturbance. **Primary succession** occurs where no soil exists when succession begins; **secondary succession** begins in an area where soil remains after a disturbance. Mechanisms that produce community change during succession include facilitation and inhibition.
- Humans are the most widespread agents of disturbance, and their effects on communities often reduce species diversity. Humans also prevent some naturally occurring disturbances, such as fire, which can be important to community structure.

? *Is the disturbance pictured in Figure 54.24 more likely to initiate primary or secondary succession? Explain.*

CONCEPT 54.4

Biogeographic factors affect community diversity (pp. 1211–1213)

- Species richness generally declines along a latitudinal gradient from the tropics to the poles. The greater age of tropical environments may account for the greater species richness of the tropics. Climate also influences the diversity gradient through energy (heat and light) and water.
- Species richness is directly related to a community's geographic size, a principle formalized in the **species-area curve**.
- Species richness on islands depends on island size and distance from the mainland. The island equilibrium model maintains that species richness on an ecological island reaches an equilibrium where new immigrations are balanced by extinctions. This model may not apply over long periods, during which abiotic disturbances, evolutionary changes, and speciation may alter community structure.

? *How have periods of glaciation influenced latitudinal patterns of diversity?*

CONCEPT 54.5

Pathogens alter community structure locally and globally (pp. 1213–1215)

- Recent work has highlighted the role that **pathogens** play in structuring terrestrial and marine communities.
- **Zoonotic pathogens** are transferred from other animals to humans and cause the largest class of emerging human diseases. Community ecology provides the framework for identifying key species interactions associated with such pathogens and for helping us track and control their spread.

? *In what way can a vector of a zoonotic pathogen differ from a host of the pathogen?*

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

1. The feeding relationships among the species in a community determine the community's
   a. secondary succession.
   b. ecological niche.
   c. species richness.
   d. species-area curve.
   e. trophic structure.

2. The principle of competitive exclusion states that
   a. two species cannot coexist in the same habitat.
   b. competition between two species always causes extinction or emigration of one species.
   c. competition in a population promotes survival of the best-adapted individuals.
   d. two species that have exactly the same niche cannot coexist in a community.
   e. two species will stop reproducing until one species leaves the habitat.

3. Based on the intermediate disturbance hypothesis, a community's species diversity is increased by
   a. frequent massive disturbance.
   b. stable conditions with no disturbance.
   c. moderate levels of disturbance.
   d. human intervention to eliminate disturbance.
   e. intensive disturbance by humans.

4. According to the equilibrium model of island biogeography, species richness would be greatest on an island that is
   a. large and close to a mainland.
   b. large and remote.
   c. small and remote.
   d. small and close to a mainland.
   e. environmentally homogeneous.

LEVEL 2: APPLICATION/ANALYSIS

5. Keystone predators can maintain species diversity in a community if they
   a. competitively exclude other predators.
   b. prey on the community's dominant species.
   c. allow immigration of other predators.
   d. reduce the number of disruptions in the community.
   e. prey only on the least abundant species in the community.

6. Food chains are sometimes short because
   a. only a single species of herbivore feeds on each plant species.
   b. local extinction of a species causes extinction of the other species in its food chain.
   c. most of the energy in a trophic level is lost as it passes to the next higher level.
   d. predator species tend to be less diverse and less abundant than prey species.
   e. most producers are inedible.

7. Which of the following could qualify as a top-down control on a grassland community?
   a. limitation of plant biomass by rainfall amount
   b. influence of temperature on competition among plants
   c. influence of soil nutrients on the abundance of grasses versus wildflowers
   d. effect of grazing intensity by bison on plant species diversity
   e. effect of humidity on plant growth rates

8. The most plausible hypothesis to explain why species richness is higher in tropical than in temperate regions is that
   a. tropical communities are younger.
   b. tropical regions generally have more available water and higher levels of solar radiation.
   c. higher temperatures cause more rapid speciation.
   d. diversity increases as evapotranspiration decreases.
   e. tropical regions have very high rates of immigration and very low rates of extinction.

9. Community 1 contains 100 individuals distributed among four species (A, B, C, and D). Community 2 contains 100 individuals distributed among three species (A, B, and C).

   Community 1: 5A, 5B, 85C, 5D
   Community 2: 30A, 40B, 30C

   Calculate the Shannon diversity (*H*) for each community. Which community is more diverse?

LEVEL 3: SYNTHESIS/EVALUATION

10. **DRAW IT** Another important species in the Chesapeake Bay estuary (see Figure 54.15) is the blue crab (*Callinectes sapidus*). It is an omnivore, eating eelgrass and other primary producers as well as clams. It is also a cannibal. In turn, the crabs are eaten by humans and by the endangered Kemp's Ridley sea turtle. Based on this information, draw a food web that includes the blue crab. Assuming that the top-down model holds for this system, what would happen to the abundance of eelgrass if humans stopped eating blue crabs?

11. **EVOLUTION CONNECTION**
    Explain why adaptations of particular organisms to interspecific competition may not necessarily represent instances of character displacement. What would a researcher have to demonstrate about two competing species to make a convincing case for character displacement?

12. **SCIENTIFIC INQUIRY**
    An ecologist studying plants in the desert performed the following experiment. She staked out two identical plots, each of which included a few sagebrush plants and numerous small annual wildflowers. She found the same five wildflower species in roughly equal numbers on both plots. She then enclosed one of the plots with a fence to keep out kangaroo rats, the most common grain-eaters of the area. After two years, four of the wildflower species were no longer present in the fenced plot, but one species had increased drastically. The control plot had not changed in species diversity. Using the principles of community ecology, propose a hypothesis to explain her results. What additional evidence would support your hypothesis?

13. **SCIENCE, TECHNOLOGY, AND SOCIETY**
    By 1935, hunting and trapping had eliminated wolves from the United States except for Alaska. Wolves have since been protected as an endangered species, and they have moved south from Canada and become reestablished in the Rocky Mountains and northern Great Lakes region. Conservationists who would like to speed up wolf recovery have reintroduced wolves into Yellowstone National Park. Local ranchers are opposed to bringing back the wolves because they fear predation on their cattle and sheep. What are some reasons for reestablishing wolves in Yellowstone National Park? What effects might the reintroduction of wolves have on the biological communities in the region? What might be done to mitigate the conflict between ranchers and wolves?

14. **WRITE ABOUT A THEME**
    Genetic Basis of Life In Batesian mimicry, a palatable species gains protection by mimicking an unpalatable one. Imagine that several individuals of a palatable, brightly colored fly species are carried by the wind to three remote islands. The first island has no predators of that species; the second has predators but no similarly colored, unpalatable species; and the third has both predators and a similarly colored, unpalatable species. In a short essay (100–150 words), predict what might happen to the coloration of the palatable species on each of the islands through evolutionary time if coloration is a genetically controlled trait. Explain your predictions.

For selected answers, see Appendix A.

55

Ecosystems and Restoration Ecology

▲ **Figure 55.1 Why is this Antarctic ice blood red?**

KEY CONCEPTS

55.1 **Physical laws govern energy flow and chemical cycling in ecosystems**
55.2 **Energy and other limiting factors control primary production in ecosystems**
55.3 **Energy transfer between trophic levels is typically only 10% efficient**
55.4 **Biological and geochemical processes cycle nutrients and water in ecosystems**
55.5 **Restoration ecologists help return degraded ecosystems to a more natural state**

OVERVIEW

Cool Ecosystem

Three hundred meters below Taylor Glacier, in Antarctica, an unusual community of bacteria lives on sulfur- and iron-containing ions. These organisms thrive in harsh conditions, without light or oxygen and at a temperature of −10°C, so low that the water would freeze if it weren't three times as salty as the ocean. How has this community survived, isolated from Earth's surface for at least 1.5 million years? The bacteria are chemoautotrophs, which obtain energy by oxidizing sulfur taken up from their sulfate-rich environment (see Chapter 27). They use iron as a final electron acceptor in their reactions. When the water flows from the base of the glacier and comes into contact with air, the reduced iron in the water is oxidized and turns red before the water freezes. The distinctive color gives this area of the glacier its name—Blood Falls **(Figure 55.1)**.

Together, the bacterial community and surrounding environment make up an **ecosystem**, the sum of all the organisms living in a given area and the abiotic factors with which they interact. An ecosystem can encompass a vast area, such as a lake or forest, or a microcosm, such as the space under a fallen log or a desert spring **(Figure 55.2)**. As with populations and communities, the boundaries of ecosystems are not always discrete. Many ecologists view the entire biosphere as a global ecosystem, a composite of all the local ecosystems on Earth.

Regardless of an ecosystem's size, its dynamics involve two processes that cannot be fully described by population or community phenomena: energy flow and chemical cycling. Energy enters most ecosystems as sunlight. It is converted to chemical energy by autotrophs, passed to heterotrophs in the organic compounds of food, and dissipated as heat. Chemical elements, such as carbon and nitrogen, are cycled among abiotic and biotic components of the ecosystem. Photosynthetic and chemosynthetic organisms assimilate these elements in inorganic form from the air, soil, and water and incorporate them into their biomass, some of which is consumed by animals. The elements are returned in inorganic form to the environment by the metabolism of plants and animals and by organisms such as bacteria and fungi that break down organic wastes and dead organisms.

Both energy and matter are transformed in ecosystems through photosynthesis and feeding relationships. But unlike matter, energy cannot be recycled. An ecosystem must be powered by a continuous influx of energy from an external source—in most cases, the sun. Energy flows through ecosystems, whereas matter cycles within and through them.

Resources critical to human survival and welfare, ranging from the food we eat to the oxygen we breathe, are products of ecosystem processes. In this chapter, we will explore the dynamics of energy flow and chemical cycling, emphasizing the results of ecosystem experiments. One way to study ecosystem processes is to alter environmental factors, such as temperature or the abundance of nutrients, and study how ecosystems respond. We will also consider some of the impacts of human activities on energy flow and chemical cycling. Finally, we will explore the growing science of restoration ecology, which focuses on returning degraded ecosystems to a more natural state.

▲ **Figure 55.2 A desert spring ecosystem.**

CONCEPT **55.1**

Physical laws govern energy flow and chemical cycling in ecosystems

In Unit Two, you learned how cells transform energy and matter, subject to the laws of thermodynamics. Like cell biologists, ecosystem ecologists study the transformations of energy and matter within a system and measure the amounts of both that cross the system's boundaries. By grouping the species in a community into trophic levels of feeding relationships (see Chapter 54), we can follow the transformations of energy in an ecosystem and map the movements of chemical elements.

Conservation of Energy

Because ecosystem ecologists study the interactions of organisms with the physical environment, many ecosystem approaches are based on laws of physics and chemistry. The first law of thermodynamics, which we discussed in Chapter 8, states that energy cannot be created or destroyed but only transferred or transformed. Thus, we can potentially account for the transfer of energy through an ecosystem from its input as solar radiation to its release as heat from organisms. Plants and other photosynthetic organisms convert solar energy to chemical energy, but the total amount of energy does not change: The amount of energy stored in organic molecules must equal the total solar energy intercepted by the plant, minus the amounts reflected and dissipated as heat. One area of ecosystem ecology involves computing energy budgets and tracing energy flow through ecosystems in order to understand the factors that control these energy transfers. Such transfers help determine how many organisms a habitat can support and the amount of food humans can harvest from a site.

One implication of the second law of thermodynamics, which states that every exchange of energy increases the entropy of the universe, is that energy conversions are inefficient; some energy is always lost as heat (see Chapter 8). We can measure the efficiency of ecological energy conversions just as we measure the efficiency of light bulbs and car engines. Energy flowing through ecosystems is ultimately dissipated into space as heat, so if the sun were not continuously providing energy to Earth, most ecosystems would vanish.

Conservation of Mass

Matter, like energy, cannot be created or destroyed. This **law of conservation of mass** is as important for ecosystems as the laws of thermodynamics are. Because mass is conserved, we can determine how much of a chemical element cycles within an ecosystem or is gained or lost by that ecosystem over time.

Unlike energy, chemical elements are continually recycled within ecosystems. A carbon atom in CO_2 is released from the soil by a decomposer, taken up by a grass through photosynthesis, consumed by a bison or other grazer, and returned to the soil in the bison's waste. The measurement and analysis of chemical cycling within ecosystems and in the biosphere as a whole are an important aspect of ecosystem ecology.

Although elements are not significantly gained or lost on a global scale, they can be gained by or lost from a particular ecosystem. In a forest ecosystem, most mineral nutrients—the essential elements that plants obtain from soil—enter as dust or as solutes dissolved in rainwater or leached from rocks in the ground. Nitrogen is also supplied through the biological process of nitrogen fixation (see Figure 37.10). In terms of losses, some elements return to the atmosphere as gases, and others are carried out of the ecosystem by moving water. Like organisms, ecosystems are open systems, absorbing energy and mass and releasing heat and waste products.

In nature, most gains and losses to ecosystems are small compared to the amounts recycled within them. Still, the balance between inputs and outputs determines whether an ecosystem is a source or a sink for a given element. If a mineral nutrient's outputs exceed its inputs, it will eventually limit production in that system. Human activities often change the balance of inputs and outputs considerably, as we will see later in this chapter and in Chapter 56.

Energy, Mass, and Trophic Levels

As you read in Chapter 54, ecologists assign species to trophic levels based on their main source of nutrition and energy. The trophic level that ultimately supports all others consists of autotrophs, also called the **primary producers** of the ecosystem. Most autotrophs are photosynthetic organisms that use light energy to synthesize sugars and other organic compounds, which they then use as fuel for cellular respiration and as building material for growth. Plants, algae, and photosynthetic prokaryotes are the biosphere's main autotrophs, although chemosynthetic prokaryotes are the primary producers in ecosystems such as deep-sea hydrothermal vents (see Figure 52.16) and places deep under the ground or ice (see Figure 55.1).

Organisms in trophic levels above the primary producers are heterotrophs, which depend directly or indirectly on the outputs of primary producers for their source of energy. Herbivores, which eat plants and other primary producers, are **primary consumers**. Carnivores that eat herbivores are **secondary consumers**, and carnivores that eat other carnivores are **tertiary consumers**.

Another group of heterotrophs is the **detritivores,** or **decomposers**, terms we use synonymously in this text to refer to consumers that get their energy from detritus. **Detritus** is nonliving organic material, such as the remains of dead organisms, feces, fallen leaves, and wood. Many detritivores are in turn eaten by secondary and tertiary consumers. Two important groups of detritivores are prokaryotes and fungi **(Figure 55.3)**. These organisms secrete enzymes that digest organic material; they then absorb the breakdown products, linking the consumers and primary producers in an ecosystem. In a forest, for instance, birds eat earthworms that have been feeding on leaf litter and its associated prokaryotes and fungi.

▲ **Figure 55.3 Fungi decomposing a dead tree.**

Detritivores also play a critical role in recycling chemical elements back to primary producers. Detritivores convert organic matter from all trophic levels to inorganic compounds usable by primary producers, closing the loop of an ecosystem's chemical cycling. Producers can then recycle these elements into organic compounds. If decomposition stopped, life would cease as detritus piled up and the supply of ingredients needed to synthesize new organic matter was exhausted. **Figure 55.4** summarizes the trophic relationships in an ecosystem.

CONCEPT CHECK 55.1

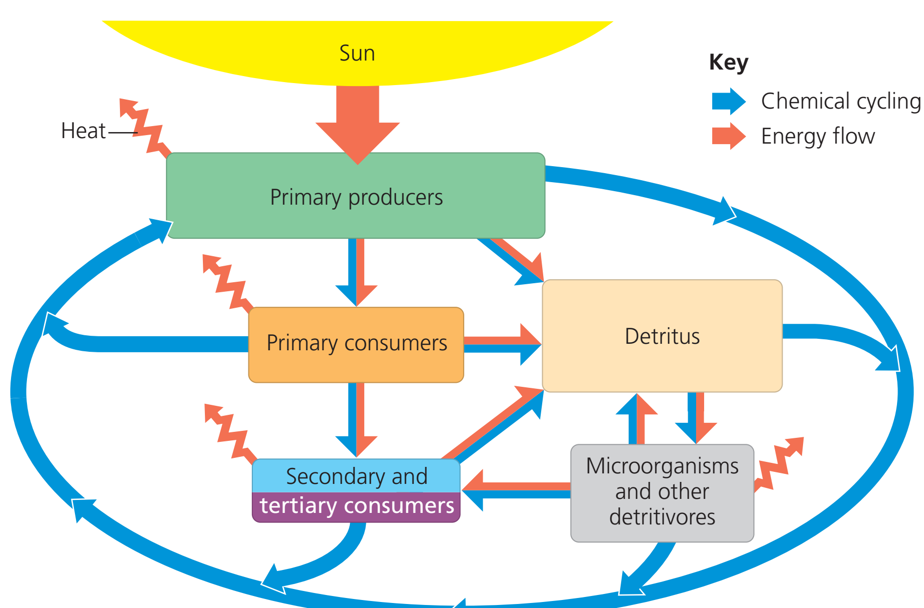
1. Why is the transfer of energy in an ecosystem referred to as energy flow, not energy cycling?
2. **WHAT IF?** You are studying nitrogen cycling on the Serengeti Plain in Africa. During your experiment, a herd of migrating wildebeests grazes through your study plot. What would you need to know to measure their effect on nitrogen balance in the plot?
3. **MAKE CONNECTIONS** Review the discussion of the second law of thermodynamics in Concept 8.1 (p. 144). How does this physical law explain why an ecosystem's energy supply must be continually replenished?

For suggested answers, see Appendix A.

CONCEPT 55.2

Energy and other limiting factors control primary production in ecosystems

As you read in Chapter 1, the theme of energy transfer underlies all biological interactions. In most ecosystems, the amount of light energy converted to chemical energy—in the form of organic compounds—by autotrophs during a given time period is the ecosystem's **primary production**. These photosynthetic products are the starting point for most studies of ecosystem metabolism and energy flow. In ecosystems where the primary producers are chemoautotrophs, as described in the Overview on page 1218, the initial energy input is chemical,



▶ **Figure 55.4 An overview of energy and nutrient dynamics in an ecosystem.** Energy enters, flows through, and exits an ecosystem, whereas chemical nutrients cycle primarily within it. In this generalized scheme, energy (dark orange arrows) enters from the sun as radiation, moves as chemical energy transfers through the food web, and exits as heat radiated into space. Most transfers of nutrients (blue arrows) through the trophic levels lead eventually to detritus; the nutrients then cycle back to the primary producers.

and the initial products are the organic compounds synthesized by the microorganisms.

Ecosystem Energy Budgets

Since most primary producers use light energy to synthesize energy-rich organic molecules, consumers acquire their organic fuels secondhand (or even third- or fourthhand) through food webs such as that in Figure 54.15. Therefore, the total amount of photosynthetic production sets the spending limit for the entire ecosystem's energy budget.

The Global Energy Budget

Each day, Earth's atmosphere is bombarded by about 10^{22} joules of solar radiation (1 J = 0.239 cal). This is enough energy to supply the demands of the entire human population for approximately 25 years at 2009 energy consumption levels. As described in Chapter 52, the intensity of the solar energy striking Earth varies with latitude, with the tropics receiving the greatest input. Most incoming solar radiation is absorbed, scattered, or reflected by clouds and dust in the atmosphere. The amount of solar radiation that ultimately reaches Earth's surface limits the possible photosynthetic output of ecosystems.

Only a small fraction of the sunlight that reaches Earth's surface is actually used in photosynthesis. Much of the radiation strikes materials that don't photosynthesize, such as ice and soil. Of the radiation that does reach photosynthetic organisms, only certain wavelengths are absorbed by photosynthetic pigments (see Figure 10.9); the rest is transmitted, reflected, or lost as heat. As a result, only about 1% of the visible light that strikes photosynthetic organisms is converted to chemical energy. Nevertheless, Earth's primary producers create about 150 billion metric tons (1.50×10^{14} kg) of organic material each year.

Gross and Net Production

Total primary production in an ecosystem is known as that ecosystem's **gross primary production (GPP)**—the amount of energy from light (or chemicals, in chemoautotrophic systems) converted to the chemical energy of organic molecules per unit time. Not all of this production is stored as organic material in the primary producers because they use some of the molecules as fuel in their own cellular respiration. **Net primary production (NPP)** is equal to gross primary production minus the energy used by the primary producers for their "autotrophic respiration" (R_a):

$$NPP = GPP - R_a$$

On average, NPP is about one-half of GPP. To ecologists, net primary production is the key measurement because it represents the storage of chemical energy that will be available to consumers in the ecosystem.

Net primary production can be expressed as energy per unit area per unit time ($J/m^2 \cdot yr$) or as biomass (mass of vegetation) added per unit area per unit time ($g/m^2 \cdot yr$). (Note that biomass is usually expressed in terms of the dry mass of organic material.) An ecosystem's NPP should not be confused with the total biomass of photosynthetic autotrophs present, a measure called the *standing crop*. Net primary production is the amount of *new* biomass added in a given period of time. Although a forest has a large standing crop, its net primary production may actually be less than that of some grasslands; grasslands do not accumulate as much biomass as forests because animals consume the plants rapidly and because grasses and herbs decompose more quickly than trees do.

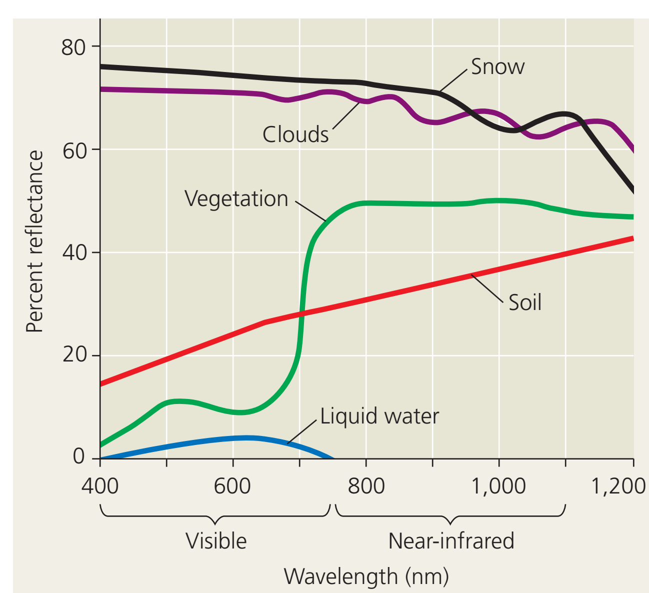
Satellites provide a powerful tool for studying global patterns of primary production **(Figure 55.5)**. Images produced from satellite data show that different ecosystems vary considerably in their net primary production. Tropical rain forests are among the most productive terrestrial ecosystems and contribute a large portion of the planet's net primary production. Estuaries and coral reefs also have very high net primary production, but their contribution to the global total is small because these ecosystems cover only about one-tenth the area covered by tropical rain forests. In contrast, while

▼ Figure 55.5 RESEARCH METHOD

Determining Primary Production with Satellites

APPLICATION Because chlorophyll captures visible light (see Figure 10.9), photosynthetic organisms absorb more light at visible wavelengths (about 380–750 nm) than at near-infrared wavelengths (750–1,100 nm). Scientists use this difference in absorption to estimate the rate of photosynthesis in different regions of the globe using satellites.

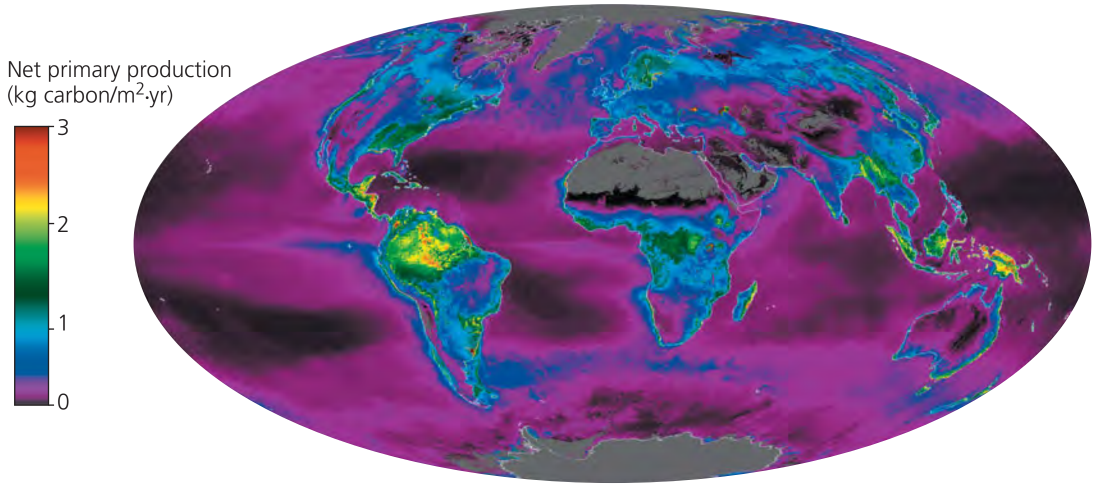
TECHNIQUE Most satellites determine what they "see" by comparing the ratios of wavelengths reflected back to them. Vegetation reflects much more near-infrared radiation than visible radiation, producing a reflectance pattern very different from that of snow, clouds, soil, and liquid water.



RESULTS Scientists use the satellite data to help produce maps of primary production like the one in Figure 55.6.

▶ **Figure 55.6 Global net primary production.** The map is based on data collected by satellites, such as amount of sunlight absorbed by vegetation. Note that tropical land areas have the highest rates of production (yellow and red on the map).

? *Does this global map accurately reflect the importance of some highly productive habitats, such as wetlands, coral reefs, and coastal zones? Explain.*



the oceans are relatively unproductive **(Figure 55.6)**, their vast size means that together they contribute as much global net primary production as terrestrial systems do.

Whereas net primary production can be stated as the amount of new biomass added in a given period of time, **net ecosystem production (NEP)** is a measure of the *total biomass accumulation* during that time. Net ecosystem production is defined as gross primary production minus the total respiration of all organisms in the system (R_T)—not just primary producers, as for the calculation of NPP, but decomposers and other heterotrophs as well:

$$\text{NEP} = \text{GPP} - R_T$$

NEP is useful to ecologists because its value determines whether an ecosystem is gaining or losing carbon over time. A forest may have a positive NPP but still lose carbon if heterotrophs release it as CO_2 more quickly than primary producers incorporate it into organic compounds.

The most common way to estimate NEP is to measure the net flux (flow) of CO_2 or O_2 entering or leaving the ecosystem. If more CO_2 enters than leaves, the system is storing carbon. Because O_2 release is directly coupled to photosynthesis and respiration (see Figure 9.2), a system that is giving off O_2 is also storing carbon. On land, ecologists typically measure only the net flux of CO_2 from ecosystems; detecting small changes in O_2 in a large atmospheric O_2 pool is difficult. In the oceans, researchers use both approaches. New marine research using O_2 measurements has revealed surprisingly high NEP in some of the nutrient-poor waters that cover much of the open ocean **(Figure 55.7)**. This result is causing biologists to reevaluate regional and global estimates of ocean productivity and to examine the constraints to marine productivity.

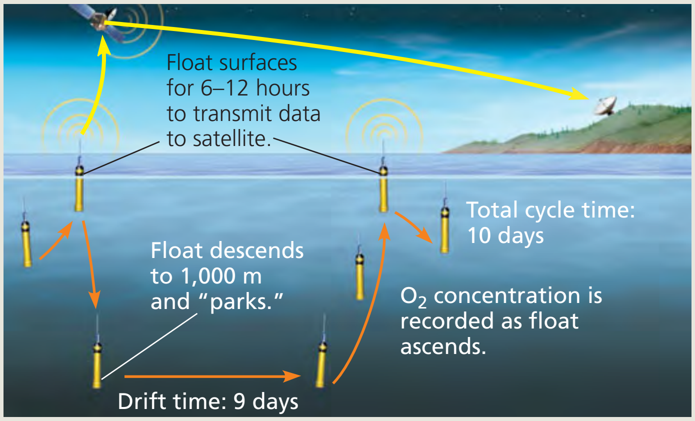
What limits production in ecosystems? To ask this question another way, what factors could we change to increase production for a given ecosystem? We'll address this question first for aquatic ecosystems.

▼ **Figure 55.7**

IMPACT

Ocean Production Revealed

Net ecosystem production (NEP) is difficult to measure in the low-nutrient regions that make up most of Earth's oceans. Rates of primary production and total respiration are low, and the difference between them—NEP—is even lower. In principle, scientists could estimate NEP by measuring the amounts of O_2 present in the water. Until recently, though, they lacked a means of obtaining the necessary data. But in 2008, researchers were able to measure NEP in parts of the Pacific Ocean using high-resolution oxygen sensors deployed on floats. The floats were "parked" about 1,000 m deep and, after drifting for 9 days, automatically rose to the surface, measuring O_2 concentrations as they went. Overall, the researchers observed an average NEP of 25 g C/m^2 over the three-year study.



WHY IT MATTERS Phytoplankton communities in extensive regions of the oceans are more productive than scientists believed even a few years ago. Biologists have a new understanding of Earth's carbon cycle and what limits marine productivity around the world.

FURTHER READING S. C. Riser and K. S. Johnson, Net production of oxygen in the subtropical ocean, *Nature* 451:323–325(2008).

MAKE CONNECTIONS Review the discussion in Concept 28.7 (p. 597) of the role of photosynthetic protists as producers in aquatic ecosystems. What factors in addition to light availability are likely to limit primary production in the oceans?

Primary Production in Aquatic Ecosystems

In aquatic (marine and freshwater) ecosystems, both light and nutrients are important in controlling primary production.

Light Limitation

Because solar radiation drives photosynthesis, you would expect light to be a key variable in controlling primary production in oceans. Indeed, the depth of light penetration affects primary production throughout the photic zone of an ocean or lake (see Figure 52.13). About half of the solar radiation is absorbed in the first 15 m of water. Even in "clear" water, only 5–10% of the radiation may reach a depth of 75 m.

If light were the main variable limiting primary production in the ocean, we would expect production to increase along a gradient from the poles toward the equator, which receives the greatest intensity of light. However, you can see in Figure 55.6 that there is no such gradient. Another factor must strongly influence primary production in the ocean.

Nutrient Limitation

More than light, nutrients limit primary production in most oceans and lakes. A **limiting nutrient** is the element that must be added for production to increase. The nutrient most often limiting marine production is either nitrogen or phosphorus. Concentrations of these nutrients are typically low in the photic zone because they are rapidly taken up by phytoplankton and because detritus tends to sink.

As detailed in **Figure 55.8**, nutrient enrichment experiments confirmed that nitrogen was limiting phytoplankton growth off the south shore of Long Island, New York. One practical application of this work is in preventing algal "blooms" caused by excess nitrogen runoff that fertilizes the phytoplankton. Prior to this research, phosphate contamination was thought to cause many such blooms in the ocean, but eliminating phosphates alone may not help unless nitrogen pollution is also controlled.

The macronutrients nitrogen and phosphorus are not the only nutrients that limit aquatic production. Several large areas of the ocean have low phytoplankton densities despite relatively high nitrogen concentrations. The Sargasso Sea, a subtropical region of the Atlantic Ocean, has some of the clearest water in the world because of its low phytoplankton density. Nutrient enrichment experiments have revealed that the availability of the micronutrient iron limits primary production there **(Table 55.1)**. Windblown dust from land supplies most of the iron to the oceans but is relatively scarce in this and certain other regions compared to the oceans as a whole.

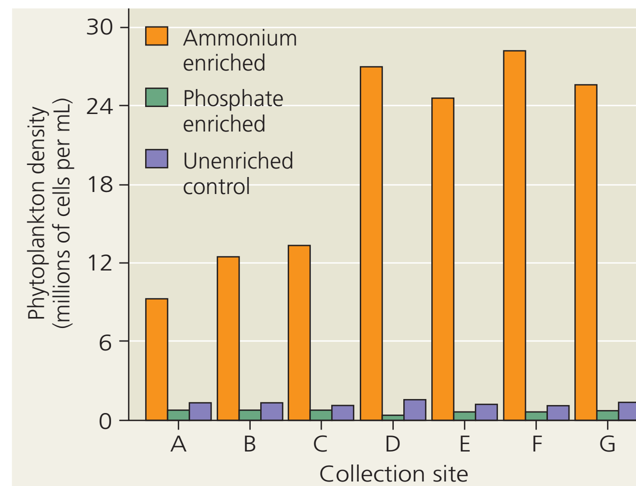
The finding that iron limits production in some oceanic ecosystems encouraged marine ecologists to carry out recent large-scale ocean fertilization experiments in the Pacific Ocean—research that might also shed light on ocean fertilization as a tool to remove the greenhouse gas carbon dioxide from the atmosphere. In one study, researchers spread low concentrations of dissolved iron over 72 km^2 of ocean and

▼ **Figure 55.8** **INQUIRY**

Which nutrient limits phytoplankton production along the coast of Long Island?

EXPERIMENT Pollution from duck farms concentrated near Moriches Bay adds both nitrogen and phosphorus to the coastal water off Long Island, New York. To determine which nutrient limits phytoplankton growth in this area, John Ryther and William Dunstan, of the Woods Hole Oceanographic Institution, cultured the phytoplankton *Nannochloris atomus* with water collected from several sites, identified as A–G. They added either ammonium (NH_4^+) or phosphate (PO_4^{3-}) to some of the cultures.

RESULTS The addition of ammonium caused heavy phytoplankton growth in the cultures, but the addition of phosphate did not.



CONCLUSION Since adding phosphorus, which was already in rich supply, did not increase *Nannochloris* growth, whereas adding nitrogen increased phytoplankton density dramatically, the researchers concluded that nitrogen is the nutrient that limits phytoplankton growth in this ecosystem.

SOURCE J. H. Ryther and W. M. Dunstan, Nitrogen, phosphorus, and eutrophication in the coastal marine environment, *Science* 171:1008–1013 (1971).

WHAT IF? How would you expect the results of this experiment to change if new duck farms substantially increased the amount of pollution in the water? Explain your reasoning.

Table 55.1 Nutrient Enrichment Experiment for Sargasso Sea Samples

Nutrients Added to Experimental Culture	Relative Uptake of ^{14}C by Cultures*
None (controls)	1.00
Nitrogen (N) + phosphorus (P) only	1.10
N + P + metals (excluding iron)	1.08
N + P + metals (including iron)	12.90
N + P + iron	12.00

*^{14}C uptake by cultures measures primary production.

Source: D. W. Menzel and J. H. Ryther, Nutrients limiting the production of phytoplankton in the Sargasso Sea, with special reference to iron, *Deep Sea Research* 7:276–281 (1961).

then measured the change in phytoplankton density over a seven-day period. A massive phytoplankton bloom occurred, as indicated by increased chlorophyll concentration in the water. Adding iron had stimulated growth of cyanobacteria that fix additional atmospheric nitrogen (see Chapter 27), and the extra nitrogen stimulated proliferation of phytoplankton.

As a tool to remove carbon dioxide from air, iron fertilization remains controversial. There is little evidence from iron fertilization experiments that organic carbon sinks into deep-ocean water and sediments. Instead, it tends to be recycled by secondary consumers and decomposers in shallow waters, returning eventually to the atmosphere. Ecologists also have concerns about the overall effects of large-scale fertilization on marine communities. Iron fertilization is therefore unlikely to be widely applied anytime soon.

Areas of upwelling, where deep, nutrient-rich waters circulate to the ocean surface, have exceptionally high primary production. This fact supports the hypothesis that nutrient availability determines marine primary production. Because upwelling stimulates growth of the phytoplankton that form the base of marine food webs, upwelling areas typically host highly productive, diverse ecosystems and are prime fishing locations. The largest areas of upwelling occur in the Southern Ocean (also called the Antarctic Ocean), along the equator, and in the coastal waters off Peru, California, and parts of western Africa.

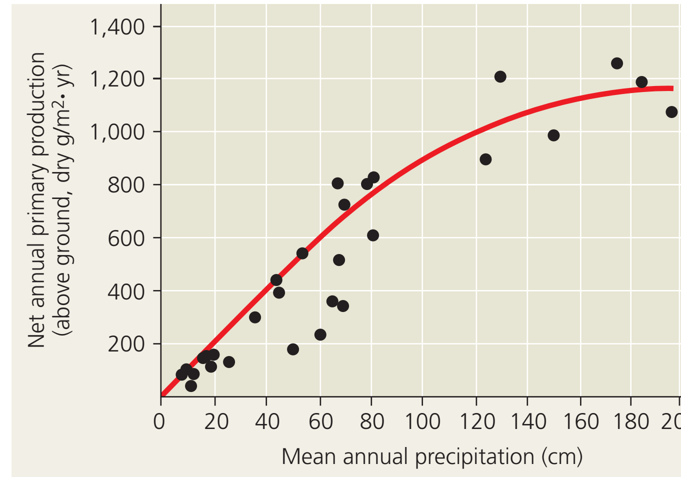
In freshwater lakes, nutrient limitation is also common. During the 1970s, scientists showed that sewage and fertilizer runoff from farms and lawns added large amounts of nutrients to lakes. Cyanobacteria and algae grow rapidly in response to these added nutrients, ultimately reducing the oxygen concentration and clarity of the water. The ecological impacts of this process, known as **eutrophication** (from the Greek *eutrophos*, well nourished), include the loss of many fish species from the lakes (see Figure 52.16).

Controlling eutrophication requires knowing which polluting nutrient is responsible. While nitrogen rarely limits primary production in lakes, a series of whole-lake experiments showed that phosphorus availability limited cyanobacterial growth. This and other ecological research led to the use of phosphate-free detergents and other important water quality reforms.

Primary Production in Terrestrial Ecosystems

At regional and global scales, temperature and moisture are the main factors controlling primary production in terrestrial ecosystems. Tropical rain forests, with their warm, wet conditions that promote plant growth, are the most productive of all terrestrial ecosystems (see Figure 55.6). In contrast, low-productivity systems are generally hot and dry, like many deserts, or cold and dry, like arctic tundra. Between these extremes lie the temperate forest and grassland ecosystems, which have moderate climates and intermediate productivity.

The climate variables of moisture and temperature are very useful for predicting NPP in terrestrial ecosystems. Primary production is greater in wetter ecosystems, as shown for the plot of NPP and annual precipitation in **Figure 55.9**. Along with mean annual precipitation, a second useful predictor is *actual evapotranspiration*, the total amount of water transpired by plants and evaporated from a landscape. Evapotranspiration increases with the temperature and amount of solar energy available to drive evaporation and transpiration.



▲ **Figure 55.9 A global relationship between net primary production and mean annual precipitation for terrestrial ecosystems.**

Nutrient Limitations and Adaptations That Reduce Them

EVOLUTION Mineral nutrients in the soil also limit primary production in terrestrial ecosystems. As in aquatic systems, nitrogen and phosphorus are the nutrients that most commonly limit terrestrial production. Globally, nitrogen limits plant growth most. Phosphorus limitations are common in older soils where phosphate molecules have been leached away by water, such as in many tropical ecosystems. Phosphorus availability is also often low in soils of deserts and other ecosystems with a basic pH, where some phosphorus precipitates and becomes unavailable to plants. Adding a nonlimiting nutrient, even one that is scarce, will not stimulate production. Conversely, adding more of the limiting nutrient will increase production until some other nutrient becomes limiting.

Various adaptations have evolved in plants that can increase their uptake of limiting nutrients. One important mutualism that you have already studied is the symbiosis between plant roots and nitrogen-fixing bacteria. Another important mutualism is mycorrhizal association between plant roots and fungi that supply phosphorus and other limiting elements to plants (see Chapters 36 and 37). Plants have root hairs and other anatomical features that increase the area of the soil that roots contact (see Chapter 35). Also, many plants release enzymes and other substances into the soil that increase the availability of limiting nutrients; examples include phosphatases, enzymes that cleave a phosphate group from larger molecules, and chelating agents that make micronutrients such as iron more soluble in the soil.

Studies relating nutrients to terrestrial primary production have practical applications in agriculture. Farmers maximize their crop yields by using fertilizers with the right balance of nutrients for the local soil and type of crop. This knowledge of limiting nutrients helps us feed billions of people on Earth today.

CONCEPT CHECK 55.2

1. Why is only a small portion of the solar energy that strikes Earth's atmosphere stored by primary producers?
2. How can ecologists experimentally determine the factor that limits primary production in an ecosystem?
3. **MAKE CONNECTIONS** Concept 10.3 (pp. 198–199) describes the Calvin cycle of photosynthesis. Explain how nitrogen and phosphorus, the nutrients that most often limit primary production, are necessary for the Calvin cycle to function.

For suggested answers, see Appendix A.

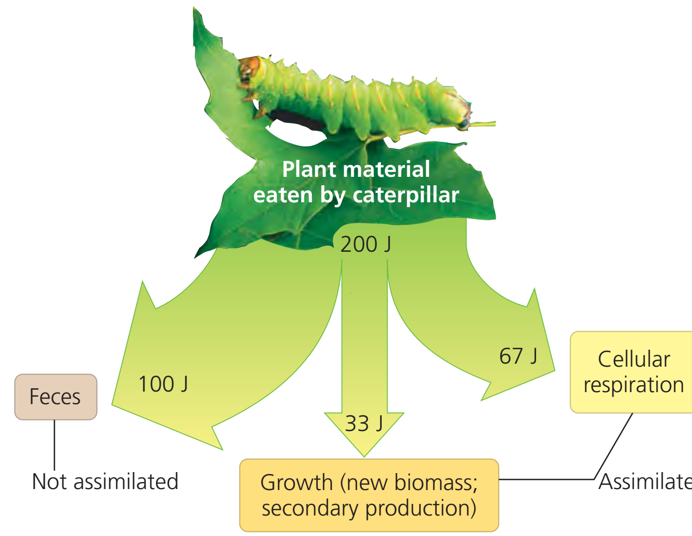
CONCEPT 55.3

Energy transfer between trophic levels is typically only 10% efficient

The amount of chemical energy in consumers' food that is converted to their own new biomass during a given period is called the **secondary production** of the ecosystem. Consider the transfer of organic matter from primary producers to herbivores, the primary consumers. In most ecosystems, herbivores eat only a small fraction of plant material produced; globally, they consume only about one-sixth of total plant production. Moreover, they cannot digest all the plant material that they *do* eat, as anyone who has walked through a dairy farm will attest. The vast majority of an ecosystem's production is eventually consumed by detritivores. Let's analyze the process of energy transfer and cycling more closely.

Production Efficiency

First we'll examine secondary production in an individual organism—a caterpillar. When a caterpillar feeds on a plant leaf, only about 33 J out of 200 J (48 cal), or one-sixth of the potential energy in the leaf, is used for secondary production, or growth **(Figure 55.10)**. The caterpillar uses some of the remaining energy (stored in organic compounds) for cellular respiration and passes the rest in its feces. The energy contained in the feces remains in the ecosystem temporarily, but most of it is lost as heat after the feces are consumed by detritivores. The energy used for the caterpillar's respiration is also eventually lost from the



▲ **Figure 55.10 Energy partitioning within a link of the food chain.** Less than 17% of the caterpillar's food is actually used for secondary production (growth).

ecosystem as heat. This is why energy is said to flow through, not cycle within, ecosystems. Only the chemical energy stored by herbivores as biomass, through growth or the production of offspring, is available as food to secondary consumers.

We can measure the efficiency of animals as energy transformers using the following equation:

$$\text{Production efficiency} = \frac{\text{Net secondary production} \times 100\%}{\text{Assimilation of primary production}}$$

Net secondary production is the energy stored in biomass represented by growth and reproduction. Assimilation consists of the total energy taken in, not including losses in feces, used for growth, reproduction, and respiration. **Production efficiency**, therefore, is the percentage of energy stored in assimilated food that is *not* used for respiration. For the caterpillar in Figure 55.10, production efficiency is 33%; 67 J of the 100 J of assimilated energy is used for respiration. (The 100 J of energy lost as undigested material in feces does not count toward assimilation.) Birds and mammals typically have low production efficiencies, in the range of 1–3%, because they use so much energy in maintaining a constant, high body temperature. Fishes, which are ectotherms (see Chapter 40), have production efficiencies around 10%. Insects and microorganisms are even more efficient, with production efficiencies averaging 40% or more.

Trophic Efficiency and Ecological Pyramids

Let's scale up now from the production efficiencies of individual consumers to the flow of energy through trophic levels.

Trophic efficiency is the percentage of production transferred from one trophic level to the next. Trophic efficiencies must always be less than production efficiencies because they take into account not only the energy lost through respiration and contained in feces, but also the energy in organic material in a lower trophic level that is not consumed by the next trophic level. Trophic efficiencies are generally only about 10% and range from approximately 5% to 20%, depending on the type of ecosystem. In other words, 90% of the energy available at one trophic level typically is *not* transferred to the next. This loss is multiplied over the length of a food chain. For example, if 10% of available energy is transferred from primary producers to primary consumers, such as caterpillars, and 10% of that energy is transferred to secondary consumers, called carnivores, then only 1% of net primary production is available to secondary consumers (10% of 10%).

The progressive loss of energy along a food chain severely limits the abundance of top-level carnivores that an ecosystem can support. Only about 0.1% of the chemical energy fixed by photosynthesis can flow all the way through a food web to a tertiary consumer, such as a snake or a shark. This explains why most food webs include only about four or five trophic levels (see Chapter 54).

The loss of energy with each transfer in a food chain can be represented by a *pyramid of net production*, in which the trophic levels are arranged in tiers **(Figure 55.11)**. The width of each tier is proportional to the net production, expressed in joules, of each trophic level. The highest level, which represents top-level predators, contains relatively few individuals. The small population size typical of top predator species is one reason they tend to be vulnerable to extinction (as well as to the evolutionary consequences of small population size, discussed in Chapter 23).

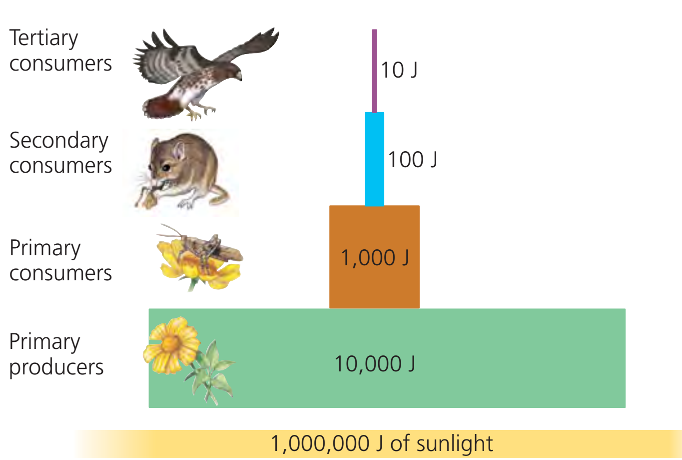
One important ecological consequence of low trophic efficiencies is represented in a *biomass pyramid*, in which each tier represents the standing crop (the total dry mass of all organisms) in one trophic level. Most biomass pyramids narrow sharply from primary producers at the base to top-level carnivores at the apex because energy transfers between trophic levels are so inefficient **(Figure 55.12a)**. Certain aquatic ecosystems, however, have inverted biomass pyramids: Primary consumers outweigh the producers **(Figure 55.12b)**. Such inverted biomass pyramids occur because the producers—phytoplankton—grow, reproduce, and are consumed so quickly by the zooplankton that they never develop a large population size, or standing crop. In other words, the phytoplankton have a short **turnover time**, which means they have a small standing crop compared to their production:

$$\text{Turnover time} = \frac{\text{Standing crop (g/m}^2\text{)}}{\text{Production (g/m}^2\cdot\text{day)}}$$

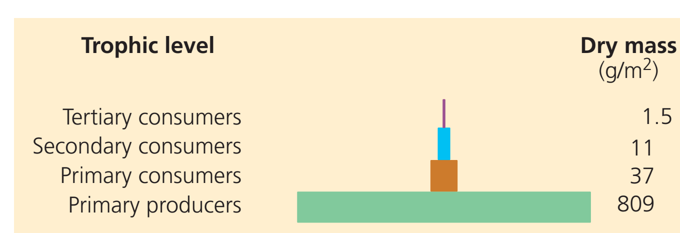
Because the phytoplankton continually replace their biomass at such a rapid rate, they can support a biomass of zooplankton bigger than their own biomass. Nevertheless, because phytoplankton have much higher production than zooplankton, the pyramid of *production* for this ecosystem is still bottom-heavy, like the one in Figure 55.11.

The dynamics of energy flow through ecosystems have important implications for humans. Eating meat is a relatively inefficient way of tapping photosynthetic production. The same pound of soybeans that a person could eat for protein produces only a fifth of a pound of beef or less when fed to a cow. Worldwide agriculture could, in fact, successfully feed many more people and require less cultivated land if humans all fed more efficiently—as primary consumers, eating plant material. Consequently, estimates of Earth's human carrying capacity (see Chapter 53) depend greatly on our diet and on the amount of resources each of us consumes.

In the next section, we will look at how the transfer of nutrients and energy through food webs is part of a larger picture of chemical cycling in ecosystems.



▲ **Figure 55.11 An idealized pyramid of net production.** This example assumes a trophic efficiency of 10% for each link in the food chain. Notice that primary producers convert only about 1% of the energy available to them to net primary production.



(a) Most biomass pyramids show a sharp decrease in biomass at successively higher trophic levels, as illustrated by data from a Florida bog.

(b) In some aquatic ecosystems, such as the English Channel, a small standing crop of primary producers (phytoplankton) supports a larger standing crop of primary consumers (zooplankton).

▲ **Figure 55.12 Pyramids of biomass (standing crop).** Numbers denote the dry mass of all organisms at each trophic level.

CONCEPT CHECK 55.3

1. If an insect that eats plant seeds containing 100 J of energy uses 30 J of that energy for respiration and excretes 50 J in its feces, what is the insect's net secondary production? What is its production efficiency?
2. Tobacco leaves contain nicotine, a poisonous compound that is energetically expensive for the plant to make. What advantage might the plant gain by using some of its resources to produce nicotine?
3. **MAKE CONNECTIONS** Figure 40.20 describes relative energy budgets for four animals. What are some ways in which the energy expenditures of the caterpillar described in Figure 55.10 would differ from the woman pictured in Figure 40.20?

For suggested answers, see Appendix A.

CONCEPT 55.4

Biological and geochemical processes cycle nutrients and water in ecosystems

Although most ecosystems receive an abundant supply of solar energy, chemical elements are available only in limited amounts. Life on Earth therefore depends on the recycling of essential chemical elements. Much of an organism's chemical stock is replaced continuously as nutrients are assimilated and waste products released. When the organism dies, the atoms in its complex molecules are returned in simpler compounds to the atmosphere, water, or soil by the action of decomposers. Decomposition replenishes the pools of inorganic nutrients that plants and other autotrophs use to build new organic matter. Because nutrient cycles involve both biotic and abiotic components, they are called **biogeochemical cycles**.

Biogeochemical Cycles

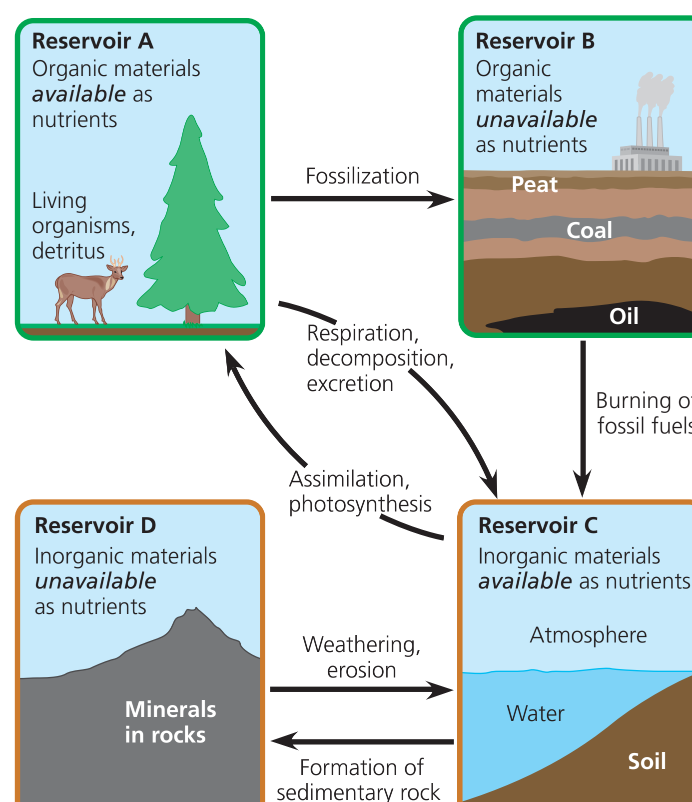
An element's specific route through a biogeochemical cycle depends on the element and the trophic structure of the ecosystem. For convenience, however, we can recognize two general categories of biogeochemical cycles: global and local. Gaseous forms of carbon, oxygen, sulfur, and nitrogen occur in the atmosphere, and cycles of these elements are essentially global. For example, some of the carbon and oxygen atoms a plant acquires from the air as CO_2 may have been released into the atmosphere by the respiration of an organism in a distant locale. Other elements, including phosphorus, potassium, and calcium, are too heavy to occur as gases at Earth's surface, although they are transported in dust. In terrestrial ecosystems, these elements cycle more locally, absorbed from the soil by plant roots and eventually returned to the soil by decomposers. In aquatic systems, however, they cycle more broadly as dissolved forms carried in currents.

Let's first look at a general model of nutrient cycling that includes the main reservoirs of elements and the processes that transfer elements between reservoirs (**Figure 55.13**). Each reservoir is defined by two characteristics: whether it contains organic or inorganic materials and whether or not the materials are directly available for use by organisms.

The nutrients in living organisms and in detritus (reservoir A in Figure 55.13) are available to other organisms when consumers feed and when detritivores consume nonliving organic matter. Some living organic material moved to the fossilized organic reservoir (reservoir B) long ago, when dead organisms were converted to coal, oil, or peat (fossil fuels). Nutrients in these deposits generally cannot be assimilated directly.

Inorganic materials (elements and compounds) that are dissolved in water or present in soil or air (reservoir C) are available for use. Organisms assimilate materials from this reservoir directly and return chemicals to it through the relatively rapid processes of cellular respiration, excretion, and decomposition. Although most organisms cannot directly tap into the inorganic elements tied up in rocks (reservoir D), these nutrients may slowly become available through weathering and erosion. Similarly, unavailable organic materials move into the available reservoir of inorganic nutrients when fossil fuels are burned, releasing exhaust into the atmosphere.

Figure 55.14, on the next two pages, provides a detailed look at the cycling of water, carbon, nitrogen, and phosphorus.



▲ **Figure 55.13 A general model of nutrient cycling.** Arrows indicate the processes that move nutrients between reservoirs.

▼ **Figure 55.14**

Exploring Water and Nutrient Cycling

Examine each cycle closely, considering the major reservoirs of water, carbon, nitrogen, and phosphorus and the processes that drive each cycle. The widths of the arrows in the diagrams approximately reflect the relative contribution of each process to the movement of water or a nutrient in the biosphere.

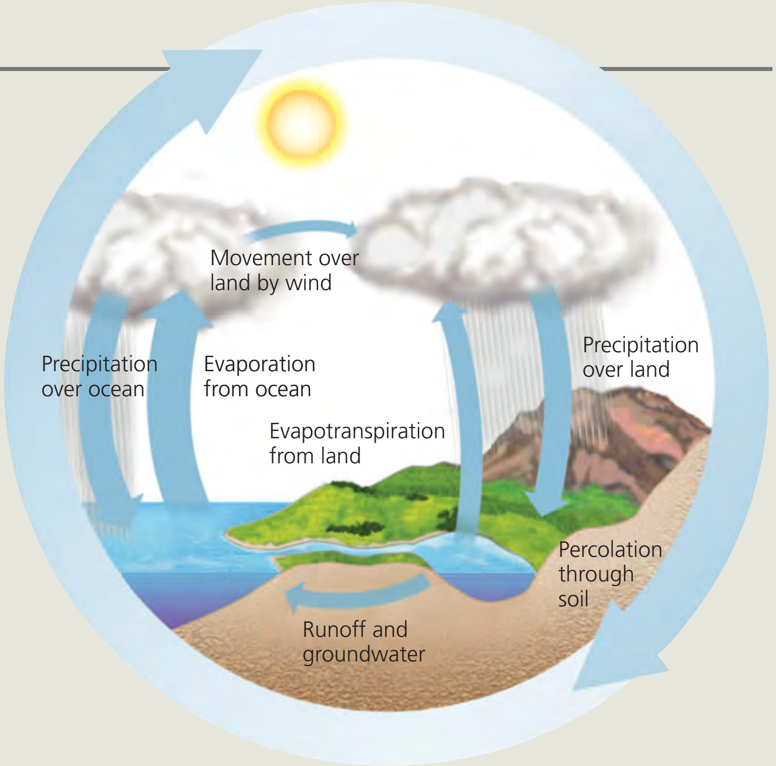
The Water Cycle

Biological importance Water is essential to all organisms (see Chapter 3), and its availability influences the rates of ecosystem processes, particularly primary production and decomposition in terrestrial ecosystems.

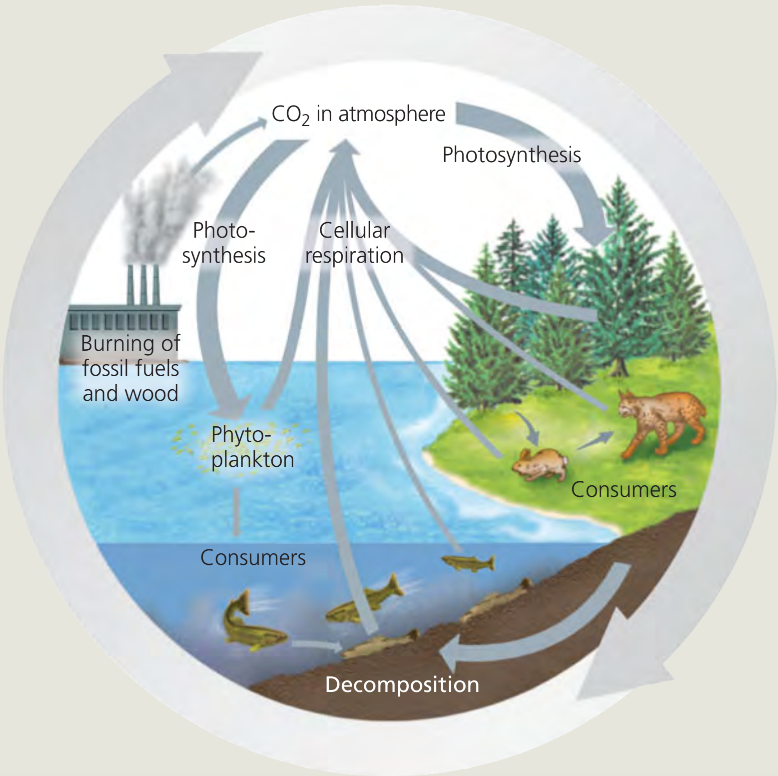
Forms available to life Liquid water is the primary physical phase in which water is used, though some organisms can harvest water vapor. Freezing of soil water can limit water availability to terrestrial plants.

Reservoirs The oceans contain 97% of the water in the biosphere. Approximately 2% is bound in glaciers and polar ice caps, and the remaining 1% is in lakes, rivers, and groundwater, with a negligible amount in the atmosphere.

Key processes The main processes driving the water cycle are evaporation of liquid water by solar energy, condensation of water vapor into clouds, and precipitation. Transpiration by terrestrial plants also moves large volumes of water into the atmosphere. Surface and groundwater flow can return water to the oceans, completing the water cycle.



The Carbon Cycle

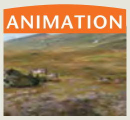


Biological importance Carbon forms the framework of the organic molecules essential to all organisms.

Forms available to life Photosynthetic organisms utilize CO_2 during photosynthesis and convert the carbon to organic forms that are used by consumers, including animals, fungi, and heterotrophic protists and prokaryotes.

Reservoirs The major reservoirs of carbon include fossil fuels, soils, the sediments of aquatic ecosystems, the oceans (dissolved carbon compounds), plant and animal biomass, and the atmosphere (CO_2). The largest reservoir is sedimentary rocks such as limestone; however, this pool turns over very slowly.

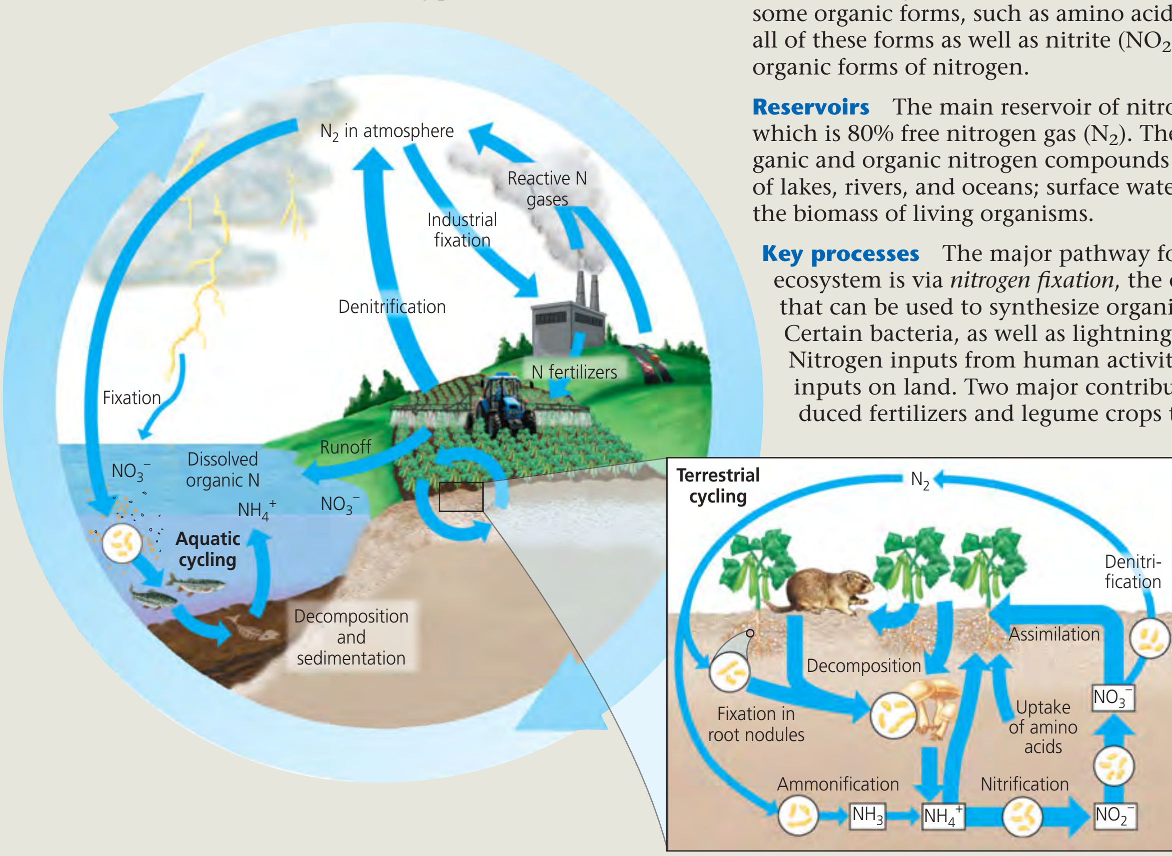
Key processes Photosynthesis by plants and phytoplankton removes substantial amounts of atmospheric CO_2 each year. This quantity is approximately equaled by CO_2 added to the atmosphere through cellular respiration by producers and consumers. The burning of fossil fuels and wood is adding significant amounts of additional CO_2 to the atmosphere. Over geologic time, volcanoes are also a substantial source of CO_2.



BioFlix® Visit the Study Area at **www.masteringbiology.com** for the BioFlix® 3-D Animation on The Carbon Cycle.

The Nitrogen Cycle

Biological importance Nitrogen is part of amino acids, proteins, and nucleic acids and is often a limiting plant nutrient.



Forms available to life Plants can assimilate (use) two inorganic forms of nitrogen—ammonium (NH_4^+) and nitrate (NO_3^-)—and some organic forms, such as amino acids. Various bacteria can use all of these forms as well as nitrite (NO_2^-). Animals can use only organic forms of nitrogen.

Reservoirs The main reservoir of nitrogen is the atmosphere, which is 80% free nitrogen gas (N_2). The other reservoirs of inorganic and organic nitrogen compounds are soils and the sediments of lakes, rivers, and oceans; surface water and groundwater; and the biomass of living organisms.

Key processes The major pathway for nitrogen to enter an ecosystem is via *nitrogen fixation*, the conversion of N_2 to forms that can be used to synthesize organic nitrogen compounds. Certain bacteria, as well as lightning, fix nitrogen naturally. Nitrogen inputs from human activities now outpace natural inputs on land. Two major contributors are industrially produced fertilizers and legume crops that fix nitrogen via bacteria in their root nodules. Other bacteria in soil convert nitrogen to different forms (see also Figure 37.9). Some bacteria carry out *denitrification*, the reduction of nitrate to nitrogen gases. Human activities also release large quantities of reactive nitrogen gases, such as nitrogen oxides, to the atmosphere.

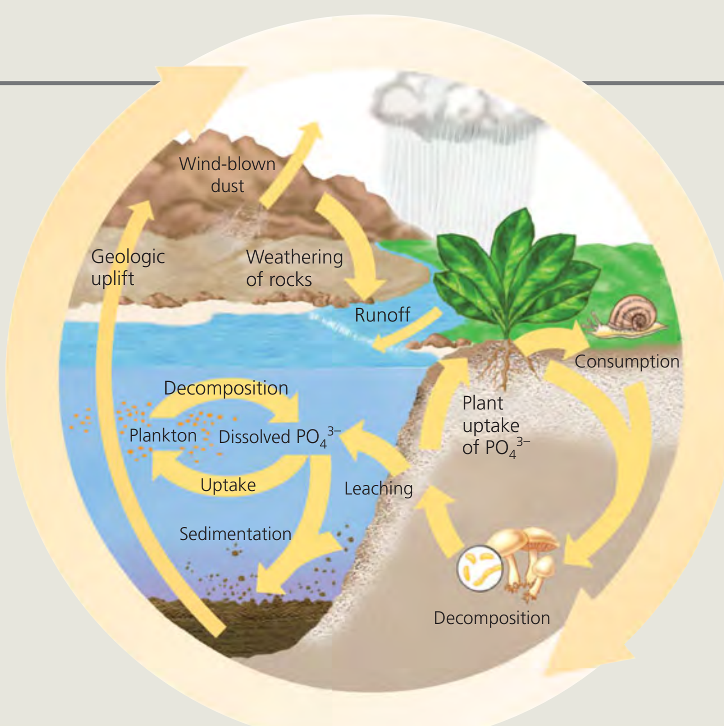
The Phosphorus Cycle

Biological importance Organisms require phosphorus as a major constituent of nucleic acids, phospholipids, and ATP and other energy-storing molecules and as a mineral constituent of bones and teeth.

Forms available to life The most biologically important inorganic form of phosphorus is phosphate (PO_4^{3-}), which plants absorb and use in the synthesis of organic compounds.

Reservoirs The largest accumulations of phosphorus are in sedimentary rocks of marine origin. There are also large quantities of phosphorus in soil, in the oceans (in dissolved form), and in organisms. Because soil particles bind PO_4^{3-}, the recycling of phosphorus tends to be quite localized in ecosystems.

Key processes Weathering of rocks gradually adds PO_4^{3-} to soil; some leaches into groundwater and surface water and may eventually reach the sea. Phosphate taken up by producers and incorporated into biological molecules may be eaten by consumers. Phosphate is returned to soil or water by either decomposition of biomass or excretion by consumers. Because there are no significant phosphorus-containing gases, only relatively small amounts of phosphorus move through the atmosphere, usually in the forms of dust and sea spray.



How have ecologists worked out the details of chemical cycling in various ecosystems? Two common methods use isotopes. One method is to follow the movement of naturally occurring, nonradioactive isotopes through the biotic and abiotic components of an ecosystem. The other method involves adding tiny amounts of radioactive isotopes of specific elements and tracing their progress. Scientists have also been able to make use of radioactive carbon (^{14}C) released into the atmosphere during atom bomb testing in the 1950s and early 1960s. Scientists use this "spike" of ^{14}C to trace where and how quickly carbon flows into ecosystem components, including plants, soils, and ocean water.

Decomposition and Nutrient Cycling Rates

The diagrams in Figure 55.14 illustrate the essential role that decomposers (detritivores) play in recycling carbon, nitrogen, and phosphorus. The rates at which these nutrients cycle in different ecosystems are extremely variable, mostly as a result of differences in rates of decomposition.

Decomposition is controlled by the same factors that limit primary production in aquatic and terrestrial ecosystems (see Concept 55.2). These factors include temperature, moisture, and nutrient availability. Decomposers usually grow faster and decompose material more quickly in warmer ecosystems **(Figure 55.15)**. In tropical rain forests, for instance, most organic material decomposes in a few months to a few years, while in temperate forests, decomposition takes four to six years, on average. The difference is largely the result of the higher temperatures and more abundant precipitation in tropical rain forests.

Because decomposition in a tropical rain forest is rapid, relatively little organic material accumulates as leaf litter on the forest floor; about 75% of the nutrients in the ecosystem is present in the woody trunks of trees, and only about 10% is contained in the soil. Thus, the relatively low concentrations of some nutrients in the soil of tropical rain forests result from a short cycling time, not from a lack of these elements in the ecosystem. In temperate forests, where decomposition is much slower, the soil may contain as much as 50% of all the organic material in the ecosystem. The nutrients that are present in temperate forest detritus and soil may remain there for fairly long periods before plants assimilate them.

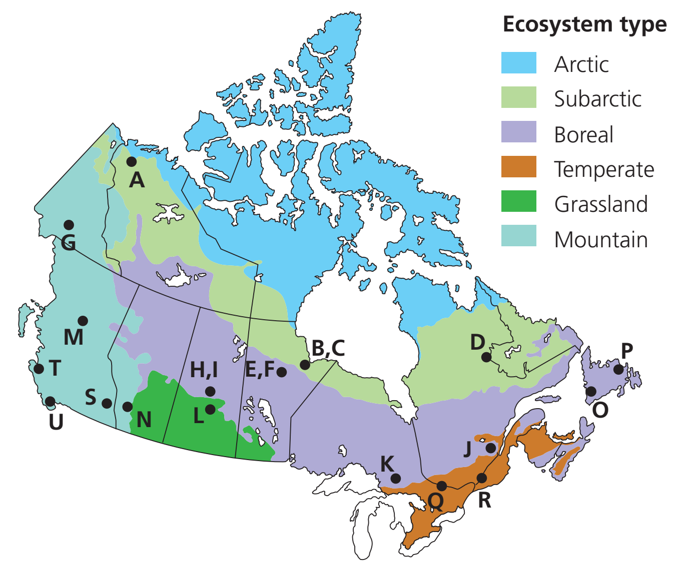
Decomposition on land is also slower when conditions are either too dry for decomposers to thrive or too wet to supply them with enough oxygen. Ecosystems that are both cold and wet, such as peatlands, store large amounts of organic matter (see Figure 29.11). Decomposers grow poorly there, and net primary production greatly exceeds decomposition.

In aquatic ecosystems, decomposition in anaerobic muds can take 50 years or longer. Bottom sediments are

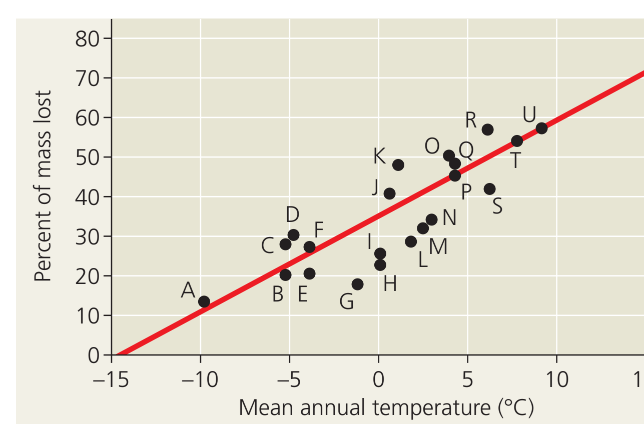
▼ **Figure 55.15** INQUIRY

How does temperature affect litter decomposition in an ecosystem?

EXPERIMENT Researchers with the Canadian Forest Service placed identical samples of organic material—litter—on the ground in 21 sites across Canada (marked by letters on the map below). Three years later, they returned to see how much of each sample had decomposed.



RESULTS The mass of litter decreased four times faster in the warmest ecosystem than in the coldest ecosystem.



CONCLUSION Decomposition rate increases with temperature across much of Canada.

SOURCE T. R. Moore et al., Litter decomposition rates in Canadian forests, *Global Change Biology* 5:75–82 (1999).

WHAT IF? What factors other than temperature might also have varied across these 21 sites? How might this variation have affected the interpretation of the results?

comparable to the detritus layer in terrestrial ecosystems; however, algae and aquatic plants usually assimilate nutrients directly from the water. Thus, the sediments often constitute a nutrient sink, and aquatic ecosystems are very productive only when there is interchange between the bottom layers of water and the water at the surface (as occurs in the upwelling regions described earlier).

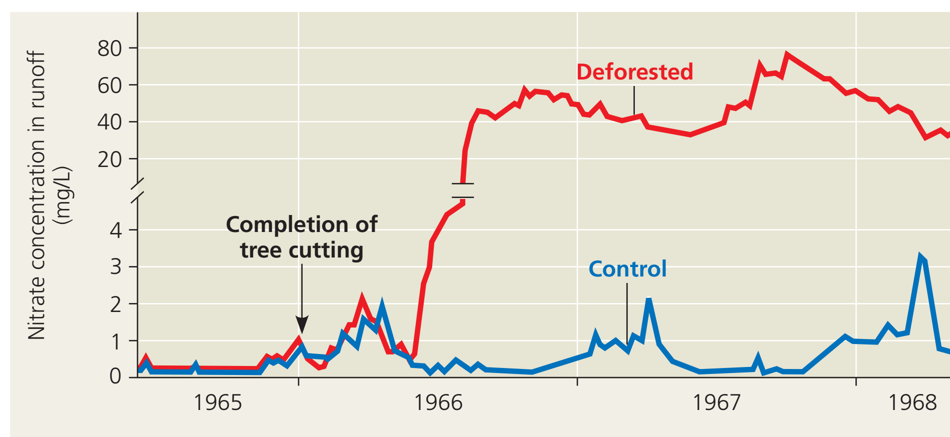
Case Study: Nutrient Cycling in the Hubbard Brook Experimental Forest

Since 1963, ecologists Herbert Bormann, Eugene Likens, and their colleagues have been studying nutrient cycling at the Hubbard Brook Experimental Forest in the White Mountains of New Hampshire. Their research site is a deciduous forest that grows in six small valleys, each drained by a single creek. Impenetrable bedrock underlies the soil of the forest.

The research team first determined the mineral budget for each of six valleys by measuring the input and outflow of several key nutrients. They collected rainfall at several sites to measure the amount of water and dissolved minerals added to the ecosystem. To monitor the loss of water and minerals, they constructed a small concrete dam with a V-shaped spillway across the creek at the bottom of each valley (**Figure 55.16a**). They found that about 60% of the water added to the ecosystem as rainfall and snow exits through the stream, and the remaining 40% is lost by evapotranspiration.

(a) Concrete dams and weirs built across streams at the bottom of watersheds enabled researchers to monitor the outflow of water and nutrients from the ecosystem.

(b) One watershed was clear-cut to study the effects of the loss of vegetation on drainage and nutrient cycling. All of the original plant material was left in place to decompose.



(c) The concentration of nitrate in runoff from the deforested watershed was 60 times greater than in a control (unlogged) watershed.

▲ **Figure 55.16 Nutrient cycling in the Hubbard Brook Experimental Forest: an example of long-term ecological research.**

MB See the related Experimental Inquiry Tutorial in MasteringBiology.

Preliminary studies confirmed that internal cycling conserved most of the mineral nutrients in the system. For example, only about 0.3% more calcium (Ca^{2+}) leaves a valley via its creek than is added by rainwater, and this small net loss is probably replaced by chemical decomposition of the bedrock. During most years, the forest even registers small net gains of a few mineral nutrients, including nitrogen.

Experimental deforestation of a watershed dramatically increased the flow of water and minerals leaving the watershed (**Figure 55.16b** and **c**). Over three years, water runoff from the newly deforested watershed was 30–40% greater than in a control watershed, apparently because there were no plants to absorb and transpire water from the soil. The concentration of Ca^{2+} in the creek increased 4-fold, and the concentration of K^{+} increased by a factor of 15. Most remarkable was the loss of nitrate, whose concentration in the creek increased 60-fold, reaching levels considered unsafe for drinking water (Figure 55.16c). The Hubbard Brook deforestation study showed that the amount of nutrients leaving an intact forest ecosystem is controlled mainly by the plants. Retaining nutrients in ecosystems helps to maintain the productivity of the systems and, in some cases, to avoid problems cause by excess nutrient runoff (see Figure 55.8).

CONCEPT CHECK 55.4

1. DRAW IT For each of the four biogeochemical cycles detailed in Figure 55.14, draw a simple diagram that shows one possible path for an atom of that chemical from abiotic to biotic reservoirs and back.
2. Why does deforestation of a watershed increase the concentration of nitrates in streams draining the watershed?
3. WHAT IF? Why is nutrient availability in a tropical rain forest particularly vulnerable to logging?

For suggested answers, see Appendix A.

CONCEPT 55.5

Restoration ecologists help return degraded ecosystems to a more natural state

Ecosystems can recover naturally from most disturbances (including the experimental deforestation at Hubbard Brook) through the stages of ecological succession that we discussed in Chapter 54. Sometimes that recovery takes centuries, though, particularly when humans have degraded the environment. Tropical areas that are cleared for farming may quickly become unproductive because of nutrient losses. Mining activities may last for several decades, and the lands are often abandoned in a degraded state. Ecosystems can also be damaged by salts that build up in soils from irrigation and by toxic chemicals or oil spills. Biologists increasingly are called on to help restore and repair ecosystem damage.

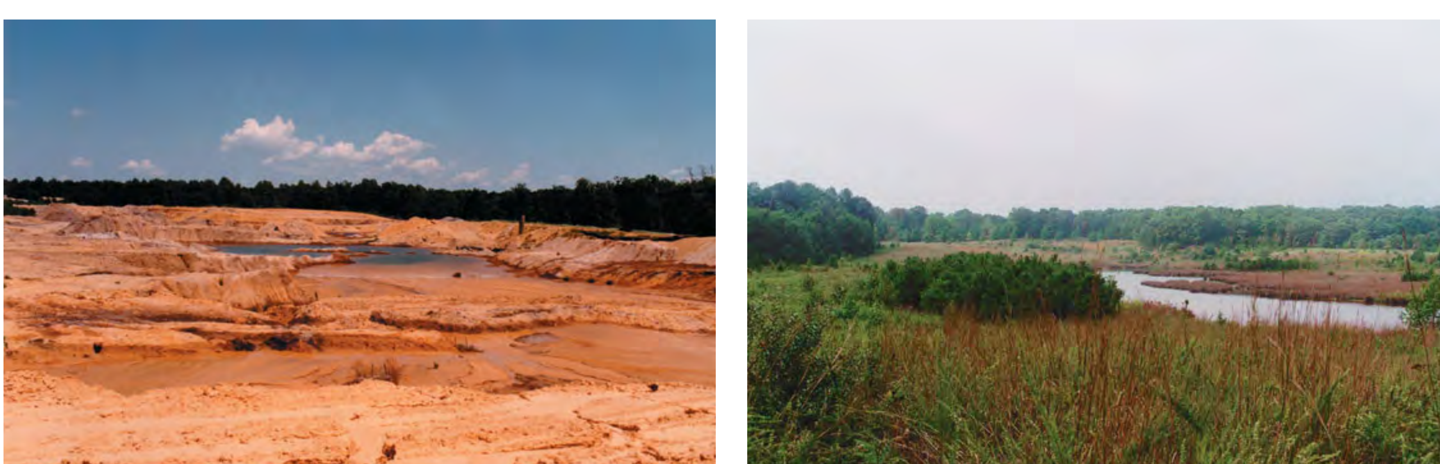
Restoration ecologists seek to initiate or speed up the recovery of degraded ecosystems. One of the basic assumptions is that environmental damage is at least partly reversible. This optimistic view must be balanced by a second assumption—that ecosystems are not infinitely resilient. Restoration ecologists therefore work to identify and manipulate the processes that most limit recovery of ecosystems from disturbances. Where disturbance is so severe that restoring all of a habitat is impractical, ecologists try to reclaim as much of a habitat or ecological process as possible, within the limits of the time and money available to them.

In extreme cases, the physical structure of an ecosystem may need to be restored before biological restoration can occur. If a stream was straightened to channel water quickly through a suburb, restoration ecologists may reconstruct a meandering channel to slow down the flow of water eroding the stream bank. To restore an open-pit mine, engineers may first grade the site with heavy equipment to reestablish a gentle slope, spreading topsoil when the slope is in place (**Figure 55.17**).

Once physical reconstruction of the ecosystem is complete—or when it is not needed—biological restoration is the next step. Two key strategies in biological restoration are bioremediation and biological augmentation.

Bioremediation

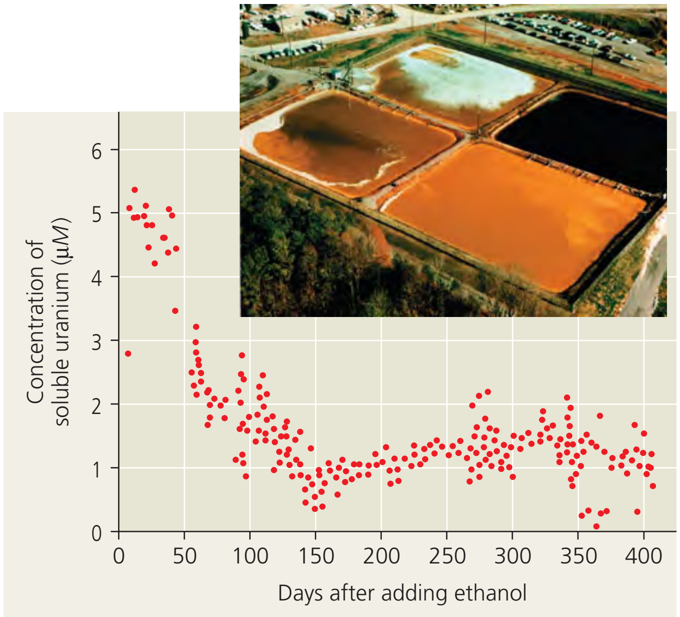
Using organisms—usually prokaryotes, fungi, or plants—to detoxify polluted ecosystems is known as **bioremediation** (see Chapter 27). Some plants and lichens adapted to soils containing heavy metals can accumulate high concentrations of potentially toxic metals such as zinc, nickel, lead, and cadmium in their tissues. Restoration ecologists can introduce such species to sites polluted by mining and other human activities and then harvest these organisms to remove the metals from the ecosystem. For instance, researchers in the United Kingdom have discovered a lichen species that grows on soil polluted with uranium dust left over from mining. The lichen concentrates uranium in a dark



(a) In 1991, before restoration

(b) In 2000, near the completion of restoration

▲ **Figure 55.17 A gravel and clay mine site in New Jersey before and after restoration.**



▲ **Figure 55.18 Bioremediation of groundwater contaminated with uranium at Oak Ridge National Laboratory, Tennessee.** Wastes containing uranium were dumped in four unlined pits (inset) for more than 30 years, contaminating soils and groundwater. After ethanol was added, microbial activity decreased the concentration of soluble uranium in groundwater near the pits.

pigment, making it useful as a biological monitor and potentially as a remediator.

Ecologists already use the abilities of many prokaryotes to carry out bioremediation of soils and water. Scientists have sequenced the genomes of at least ten prokaryotic species specifically for their bioremediation potential. One of the species, the bacterium *Shewanella oneidensis*, appears particularly promising. It can metabolize a dozen or more elements under aerobic and anaerobic conditions. In doing so, it converts soluble forms of uranium, chromium, and nitrogen to insoluble forms that are less likely to leach into streams or groundwater. Researchers at Oak Ridge National Laboratory, in Tennessee, stimulated the growth of *Shewanella* and other uranium-reducing bacteria by adding ethanol to groundwater contaminated with uranium; the bacteria can use ethanol as an energy source. In just five months, the concentration of soluble uranium in the ecosystem dropped by 80% **(Figure 55.18)**. In the future, genetic engineering could be increasingly useful as a tool for improving the performance of prokaryotes and other organisms as bioremediators.

Biological Augmentation

In contrast to bioremediation, which is a strategy for removing harmful substances from an ecosystem, **biological augmentation** uses organisms to *add* essential materials to a degraded ecosystem. To augment ecosystem processes, restoration ecologists need to determine which factors, such as chemical nutrients, have been lost from a system and are limiting its recovery.

Encouraging the growth of plants that thrive in nutrient-poor soils often speeds up succession and ecosystem recovery. In alpine ecosystems of the western United States, nitrogen-fixing plants such as lupines are often planted to raise nitrogen concentrations in soils disturbed by mining and other activities. Once these nitrogen-fixing plants become established, other native species are better able to obtain enough soil nitrogen to survive. In other systems where the soil has been severely disturbed or where topsoil is missing entirely, plant roots may lack the mycorrhizal symbionts that help them meet their nutritional needs (see Chapter 31). Ecologists restoring a tallgrass prairie in Minnesota recognized this limitation and enhanced the recovery of native species by adding mycorrhizal symbionts to the soil they seeded.

Restoring the physical structure and plant community of an ecosystem does not necessarily ensure that animal species will recolonize a site and persist there. Because animals aid critical ecosystem services, including pollination, seed dispersal, and herbivory, restoration ecologists sometimes help wildlife reach and use restored ecosystems. They might release animals at a site or establish habitat corridors that connect a restored site to other places where the animals are found. They sometimes establish artificial perches for birds or dig burrows for other animals to use at the site. These and other efforts can improve the biodiversity of restored ecosystems and help the community persist.

Restoration Projects Worldwide

Because restoration ecology is a relatively new discipline and because ecosystems are complex, restoration ecologists generally learn as they go. Many restoration ecologists advocate adaptive management: experimenting with several promising types of management to learn what works best.

The long-term objective of restoration is to return an ecosystem as much as possible to its predisturbance state. **Figure 55.19**, on the next two pages, identifies several ambitious and successful restoration projects around the world. The great number of such projects, the dedication of the people engaged in them, and the successes that have been achieved suggest that restoration ecology will continue to grow as a discipline for many years.

CONCEPT CHECK 55.5

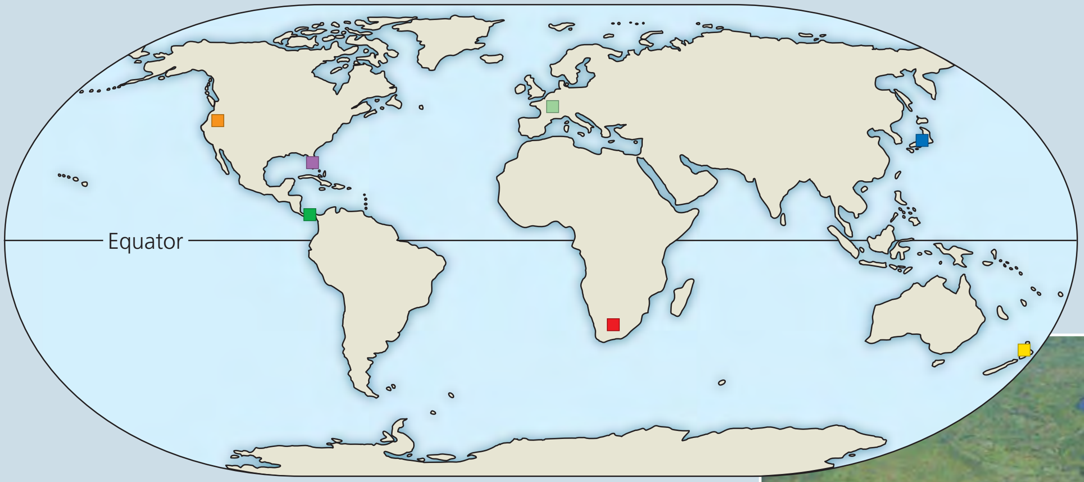
1. Identify the main goal of restoration ecology.
2. How do bioremediation and biological augmentation differ?
3. **WHAT IF?** In what way is the Kissimmee River project a more complete ecological restoration than the Maungatautari project (see Figure 55.19)?

For suggested answers, see Appendix A.

▼ Figure 55.19

Exploring Restoration Ecology Worldwide

The examples highlighted on these pages are just a few of the many restoration ecology projects taking place around the world. The color-coded dots on the map indicate the locations of the projects.



Kissimmee River, Florida

The Kissimmee River was converted from a meandering river to a 90-km canal, threatening many fish and wetland bird populations. Kissimmee River restoration has filled 12 km of drainage canal and reestablished 24 km of the original 167 km of natural river channel. Pictured here is a section of the Kissimmee canal that has been plugged (wide, light strip on the right side of the photo), diverting flow into remnant river channels (center of the photo). The project will also restore natural flow patterns, which will foster self-sustaining populations of wetland birds and fishes.

Truckee River, Nevada

Damming and water diversions during the 20th century reduced flow in the Truckee River, leading to declines in riparian (riverside) forests. Restoration ecologists worked with water managers to ensure that sufficient water would be released during the short season of seed release by the native cottonwood and willow trees for seedlings to become established. Nine years of controlled-flow release led to the result shown here: a dramatic recovery of cottonwood-willow riparian forest.

Tropical dry forest, Costa Rica

Clearing for agriculture, mainly for livestock grazing, eliminated approximately 98% of tropical dry forest in Central America and Mexico. Reversing this trend, tropical dry forest restoration in Costa Rica has used domestic livestock to disperse the seeds of native trees into open grasslands. The photo shows one of the first trees (right center), dispersed as seed by livestock, to colonize former pastureland. This project is a model for joining restoration ecology with the local economy and educational institutions.

Rhine River, Europe

Centuries of dredging and channeling for navigation (see the barges in the wide, main channel on the right side of the photo) have straightened the once-meandering Rhine River and disconnected it from its floodplain and associated wetlands. The countries along the Rhine, particularly France, Germany, Luxembourg, the Netherlands, and Switzerland, are cooperating to reconnect the river to side channels, such as the one shown on the left side of the photo. Such side channels increase the diversity of habitats available to aquatic organisms, improve water quality, and provide flood protection.

Coastal Japan

Seaweed and seagrass beds are important nursery grounds for a wide variety of fishes and shellfish. Once extensive but now reduced by development, these beds are being restored in the coastal areas of Japan. Techniques include constructing suitable seafloor habitat, transplanting from natural beds using artificial substrates, and hand seeding (shown in this photograph).

Succulent Karoo, South Africa

In this desert region of southern Africa, as in many arid regions, overgrazing by livestock has damaged vast areas. Private landowners and government agencies in South Africa are restoring large areas of this unique region, revegetating the land and employing more sustainable resource management. The photo shows a small sample of the exceptional plant diversity of the Succulent Karoo; its 5,000 plant species include the highest diversity of succulent plants in the world.

Maungatautari, New Zealand

Weasels, rats, pigs, and other introduced species pose a serious threat to New Zealand's native plants and animals, including kiwis, a group of flightless, ground-dwelling bird species. The goal of the Maungatautari restoration project is to exclude all exotic mammals from a 3,400-ha reserve located on a forested volcanic cone. A specialized fence around the reserve eliminates the need to continue setting traps and using poisons that can harm native wildlife. In 2006, a pair of critically endangered takahe (a species of flightless rail) were released into the reserve in hopes of reestablishing a breeding population of this colorful bird on New Zealand's North Island.

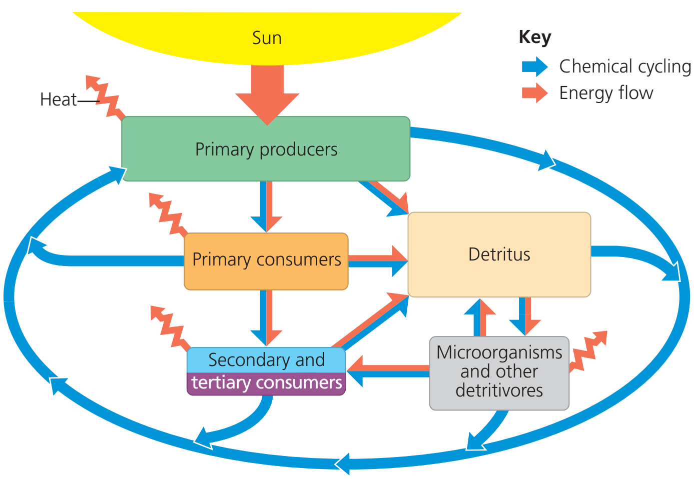
55 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

CONCEPT 55.1

Physical laws govern energy flow and chemical cycling in ecosystems (pp. 1219–1220)

- An **ecosystem** consists of all the organisms in a community and all the abiotic factors with which they interact. The laws of physics and chemistry apply to ecosystems, particularly in regard to the conservation of energy. Energy is conserved but degraded to heat during ecosystem processes.
- Based on the **law of conservation of mass**, ecologists study how much of a chemical element enters and leaves an ecosystem and cycles within it. Inputs and outputs are generally small compared to recycled amounts, but their balance determines whether the ecosystem gains or loses an element over time.



Based on the second law of thermodynamics, would you expect the typical biomass of primary producers in an ecosystem to be greater than or less than the biomass of secondary producers in the same ecosystem? Explain your reasoning.

CONCEPT 55.2

Energy and other limiting factors control primary production in ecosystems (pp. 1220–1225)

- **Primary production** sets the spending limit for the global energy budget. **Gross primary production** is the total energy assimilated by an ecosystem in a given period. **Net primary production**, the energy accumulated in autotroph biomass, equals gross primary production minus the energy used by the primary producers for respiration. **Net ecosystem production** is the total biomass accumulation of an ecosystem, defined as the difference between gross primary production and total ecosystem respiration.
- In aquatic ecosystems, light and nutrients limit primary production.
- In terrestrial ecosystems, climatic factors such as temperature and moisture affect primary production on a large geographic scale. More locally, a soil nutrient is often the limiting factor in primary production.

What additional variable do you need to know the value of in order to estimate NEP from NPP? Why might measuring this variable be difficult, for instance, in a sample of ocean water?

CONCEPT 55.3

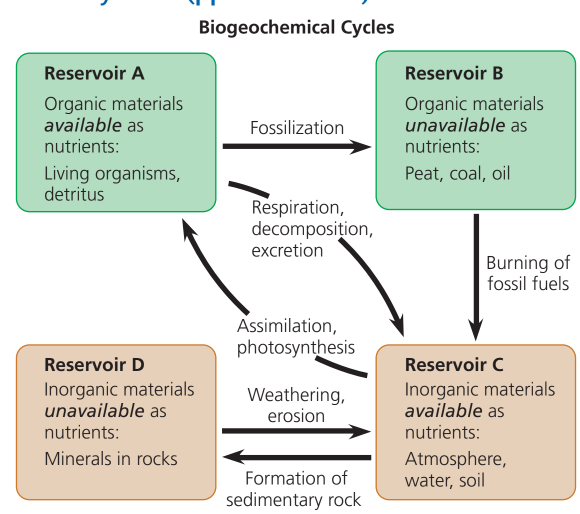
Energy transfer between trophic levels is typically only 10% efficient (pp. 1225–1227)

- The amount of energy available to each trophic level is determined by the net primary production and the **production efficiency**, the efficiency with which food energy is converted to biomass at each link in the food chain.
- The percentage of energy transferred from one trophic level to the next, called **trophic efficiency**, is generally 5–20%, with 10% being the typical value. Pyramids of net production and biomass reflect low trophic efficiency.

Why would a long-distance runner typically have a lower production efficiency than a more sedentary person?

CONCEPT 55.4

Biological and geochemical processes cycle nutrients and water in ecosystems (pp. 1227–1232)



- Water moves in a global cycle driven by solar energy. The carbon cycle primarily reflects the reciprocal processes of photosynthesis and cellular respiration. Nitrogen enters ecosystems through atmospheric deposition and nitrogen fixation by prokaryotes, but most of the nitrogen cycling in natural ecosystems involves local cycles between organisms and soil or water. The phosphorus cycle is relatively localized.
- The proportion of a nutrient in a particular form and its cycling in that form vary among ecosystems, largely because of differences in the rate of decomposition.
- Nutrient cycling is strongly regulated by vegetation. The Hubbard Brook case study showed that logging increases water runoff and can cause large losses of minerals. It also demonstrated the importance of long-term ecological measurements in documenting the occurrence of and recovery from environmental problems.

If decomposers usually grow faster and decompose material more quickly in warmer ecosystems, why is decomposition in hot deserts so slow?

CONCEPT 55.5

Restoration ecologists help return degraded ecosystems to a more natural state (pp. 1232–1235)

- Restoration ecologists harness organisms to detoxify polluted ecosystems through the process of **bioremediation**.

- In **biological augmentation**, ecologists use organisms to add essential materials to ecosystems.

? *In preparing a site for surface mining and later restoration, what would be the advantage of removing the shallow topsoil first and setting it aside separately from the deeper soil, rather than removing all soil at once and mixing it in a single pile?*

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

1. Which of the following organisms is *incorrectly* paired with its trophic level?
a. cyanobacterium—primary producer
b. grasshopper—primary consumer
c. zooplankton—primary producer
d. eagle—tertiary consumer
e. fungus—detritivore

2. Which of these ecosystems has the *lowest* net primary production per square meter?
a. a salt marsh
b. an open ocean
c. a coral reef
d. a grassland
e. a tropical rain forest

3. The discipline that applies ecological principles to returning degraded ecosystems to a more natural state is known as
a. population viability analysis.
b. landscape ecology.
c. conservation ecology.
d. restoration ecology.
e. resource conservation.

LEVEL 2: APPLICATION/ANALYSIS

4. Nitrifying bacteria participate in the nitrogen cycle mainly by
a. converting nitrogen gas to ammonia.
b. releasing ammonium from organic compounds, thus returning it to the soil.
c. converting ammonia to nitrogen gas, which returns to the atmosphere.
d. converting ammonium to nitrate, which plants absorb.
e. incorporating nitrogen into amino acids and organic compounds.

5. Which of the following has the greatest effect on the rate of chemical cycling in an ecosystem?
a. the ecosystem's rate of primary production
b. the production efficiency of the ecosystem's consumers
c. the rate of decomposition in the ecosystem
d. the trophic efficiency of the ecosystem
e. the location of the nutrient reservoirs in the ecosystem

6. The Hubbard Brook watershed deforestation experiment yielded all of the following results *except*:
a. Most minerals were recycled within a forest ecosystem.
b. The flow of minerals out of a natural watershed was offset by minerals flowing in.
c. Deforestation increased water runoff.
d. The nitrate concentration in waters draining the deforested area became dangerously high.
e. Calcium levels remained high in the soil of deforested areas.

7. Which of the following would be considered an example of bioremediation?
a. adding nitrogen-fixing microorganisms to a degraded ecosystem to increase nitrogen availability
b. using a bulldozer to regrade a strip mine
c. dredging a river bottom to remove contaminated sediments
d. reconfiguring the channel of a river
e. adding seeds of a chromium-accumulating plant to soil contaminated by chromium

8. If you applied a fungicide to a cornfield, what would you expect to happen to the rate of decomposition and net ecosystem production (NEP)?
a. Both decomposition rate and NEP would decrease.
b. Both decomposition rate and NEP would increase.
c. Neither would change.
d. Decomposition rate would increase and NEP would decrease.
e. Decomposition rate would decrease and NEP would increase.

LEVEL 3: SYNTHESIS/EVALUATION

9. **DRAW IT** Draw a simplified global water cycle showing ocean, land, atmosphere, and runoff from the land to the ocean. Add these annual water fluxes to the figure: ocean evaporation, 425 km^3; ocean evaporation that returns to the ocean as precipitation, 385 km^3; ocean evaporation that falls as precipitation on land, 40 km^3; evapotranspiration from plants and soil that falls as precipitation on land, 70 km^3; runoff to the oceans, 40 km^3. Based on these global numbers, how much precipitation falls on land in a typical year?

10. **EVOLUTION CONNECTION**
Some biologists have suggested that ecosystems are emergent, "living" systems capable of evolving. One manifestation of this idea is environmentalist James Lovelock's Gaia hypothesis, which views Earth itself as a living, homeostatic entity—a kind of superorganism. If ecosystems are capable of evolving, would this be a form of Darwinian evolution? Why or why not?

11. **SCIENTIFIC INQUIRY**
Using two neighboring ponds in a forest as your study site, design a controlled experiment to measure the effect of falling leaves on net primary production in a pond.

12. **WRITE ABOUT A THEME**
Energy Transfer As described in Concept 55.4, decomposition typically occurs quickly in moist tropical forests. However, waterlogging in the soil of some moist tropical forests results in a buildup of organic matter ("peat"; see Figure 29.11) over time. In a short essay (100–150 words), discuss the relationship of net primary production, net ecosystem production, and decomposition for such an ecosystem. Are NPP and NEP likely to be positive? What do you think would happen to NEP if a landowner drained the water from a tropical peatland, exposing the organic matter to air?

For selected answers, see Appendix A.

56

Conservation Biology and Global Change

▲ **Figure 56.1 What will be the fate of this newly described bird species?**

KEY CONCEPTS

56.1 Human activities threaten Earth's biodiversity
56.2 Population conservation focuses on population size, genetic diversity, and critical habitat
56.3 Landscape and regional conservation help sustain biodiversity
56.4 Earth is changing rapidly as a result of human actions
56.5 Sustainable development can improve human lives while conserving biodiversity

OVERVIEW

Striking Gold

Tucking its wings, a bird lands on a branch deep inside a tropical jungle. Sensing the motion, a conservation biologist scans the branch through binoculars, a glimpse of golden orange stopping her short. Staring back is a wattled smoky honeyeater (*Melipotes carolae*), a species that had never been described before **(Figure 56.1)**. In 2005, a team of American, Indonesian, and Australian biologists experienced many moments like this as they spent a month cataloging the living riches hidden in a remote mountain range in Indonesia. In addition to the honeyeater, they discovered dozens of new frog, butterfly, and plant species, including five new palms.

To date, scientists have described and formally named about 1.8 million species of organisms. Some biologists think that about 10 million more species currently exist; others estimate the number to be as high as 100 million. Some of the greatest concentrations of species are found in the tropics. Unfortunately, tropical forests are being cleared at an alarming rate to make room for and support a burgeoning human population. Rates of deforestation in Indonesia are among the highest in the world **(Figure 56.2)**. What will become of the smoky honeyeater and other newly discovered species in Indonesia if such deforestation continues unchecked?

Throughout the biosphere, human activities are altering trophic structures, energy flow, chemical cycling, and natural disturbance—ecosystem processes on which we and all other species depend (see Chapter 55). We have physically altered nearly half of Earth's land surface, and we use over half of all accessible surface fresh water. In the oceans, stocks of most major fisheries are shrinking because of overharvesting. By some estimates, we may be pushing more species toward extinction than the large asteroid that triggered the mass extinctions at the close of the Cretaceous period 65.5 million years ago (see Figure 25.16).

Biology is the science of life. Thus, it is fitting that our final chapter focuses on a discipline that seeks to preserve life. **Conservation biology** integrates ecology, physiology, molecular biology, genetics, and evolutionary biology to conserve

▲ **Figure 56.2 Tropical deforestation in West Kalimantan, an Indonesian province.**

biological diversity at all levels. Efforts to sustain ecosystem processes and stem the loss of biodiversity also connect the life sciences with the social sciences, economics, and humanities.

In this chapter, we will take a closer look at the biodiversity crisis and examine some of the conservation strategies being adopted to slow the rate of species loss. We will also examine how human activities are altering the environment through climate change, ozone depletion, and other global processes, and we will consider how these alterations could affect life on Earth.

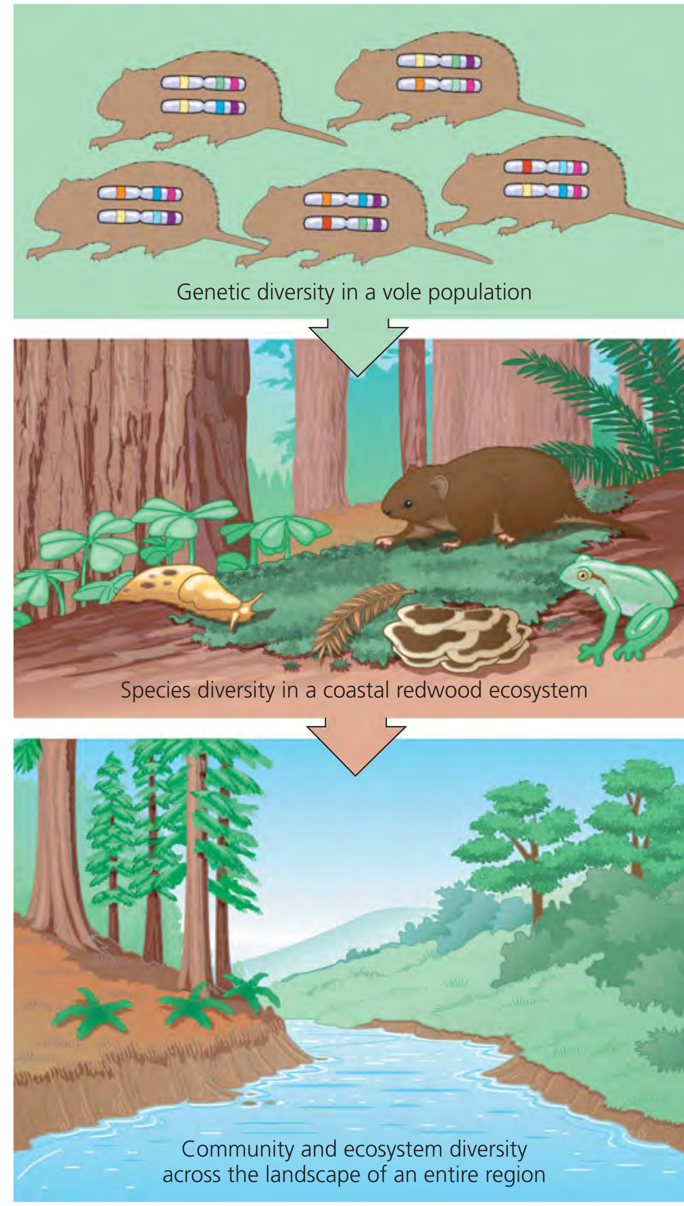
CONCEPT **56.1**

Human activities threaten Earth's biodiversity

Extinction is a natural phenomenon that has been occurring since life first evolved; it is the high *rate* of extinction that is responsible for today's biodiversity crisis (see Chapter 25). Because we can only estimate the number of species currently existing, we cannot determine the exact rate of species loss. However, we do know that the extinction rate is high and that human activities threaten Earth's biodiversity at all levels.

Three Levels of Biodiversity

Biodiversity—short for biological diversity—can be considered at three main levels: genetic diversity, species diversity, and ecosystem diversity **(Figure 56.3)**.



▲ **Figure 56.3 Three levels of biodiversity.** The oversized chromosomes in the top diagram symbolize the genetic variation within the population.

Genetic Diversity

Genetic diversity comprises not only the individual genetic variation *within* a population, but also the genetic variation *between* populations that is often associated with adaptations to local conditions (see Chapter 23). If one population becomes extinct, then a species may have lost some of the genetic diversity that makes microevolution possible. This erosion of genetic diversity in turn reduces the adaptive potential of the species.

Species Diversity

Public awareness of the biodiversity crisis centers on species diversity—the variety of species in an ecosystem or across the biosphere (see Chapter 54). As more species are lost to extinction, species diversity decreases. The U.S. Endangered Species Act (ESA) defines an **endangered species** as one that is "in danger of extinction throughout all or a significant portion of its range." **Threatened species** are those that are considered likely to become endangered in the near future. The following are just a few statistics that illustrate the problem of species loss:

- According to the International Union for Conservation of Nature and Natural Resources (IUCN), 12% of the 10,000 known species of birds and 21% of the 5,500 known species of mammals are threatened.
- A survey by the Center for Plant Conservation showed that of the nearly 20,000 known plant species in the United States, 200 have become extinct since such records have been kept, and 730 are endangered or threatened.
- More than 30% of the known species of fishes in the world either have become extinct during historical times or are seriously threatened.
- In North America, at least 123 freshwater animal species have become extinct since 1900, and hundreds more species are threatened. The extinction rate for North American freshwater fauna is about five times as high as that for terrestrial animals.
- According to a 2004 report in the journal *Science* that was based on a global assessment of amphibians by more than

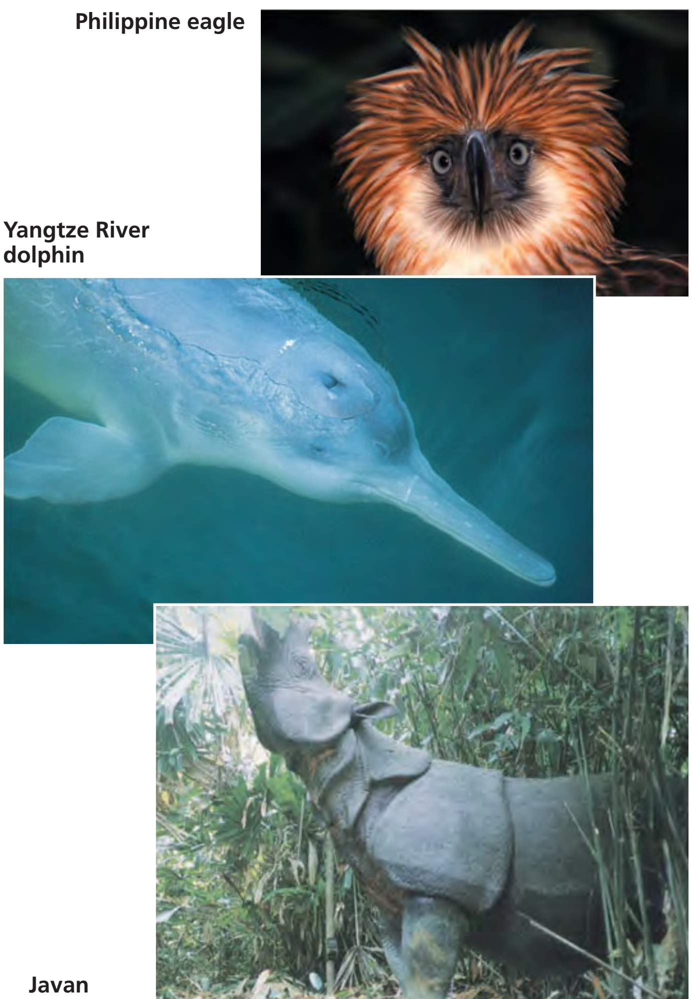
500 scientists, 32% of all known amphibian species are endangered, with many species very near extinction.

Extinction of species may also be local; for example, a species may be lost in one river system but survive in an adjacent one. Global extinction of a species means that it is lost from *all* the ecosystems in which it lived, leaving them permanently impoverished **(Figure 56.4)**.

Ecosystem Diversity

The variety of the biosphere's ecosystems is a third level of biological diversity. Because of the many interactions between populations of different species in an ecosystem, the local extinction of one species can have a negative impact on other species in the ecosystem (see Figure 54.17). For instance, bats called "flying foxes" are important pollinators and seed dispersers in the Pacific Islands, where they are increasingly hunted as a luxury food **(Figure 56.5)**. Conservation biologists fear that the extinction of flying foxes would also harm the native plants of the Samoan Islands, where four-fifths of the tree species depend on flying foxes for pollination or seed dispersal.

Some ecosystems have already been heavily affected by humans, and others are being altered at a rapid pace. Since European colonization, more than half of the wetlands in the contiguous United States have been drained and converted to agricultural and other uses. In California, Arizona, and New Mexico, roughly 90% of native riparian (streamside) communities have been affected by overgrazing, flood control, water diversions, lowering of water tables, and invasion by non-native plants.



▲ **Figure 56.4 A hundred heartbeats from extinction.** These are just three members of what E. O. Wilson calls the Hundred Heartbeat Club, species with fewer than 100 individuals remaining on Earth. The Yangtze River dolphin was even thought to be extinct, but a few individuals were reportedly sighted in 2007.

? *To document that a species has actually become extinct, what spatial and temporal factors would you need to consider?*

Biodiversity and Human Welfare

Why should we care about the loss of biodiversity? One reason is what the Harvard biologist E. O. Wilson calls *biophilia*, our sense of connection to nature and all life. The belief that other species are entitled to life is a pervasive theme of many religions and the basis of a moral argument that we should protect biodiversity. There is also a concern for future human generations. Paraphrasing an old proverb, G. H. Brundtland, a former prime minister of Norway, said: "We must consider our planet to be on loan from our children, rather than being a gift from our ancestors." In addition to such philosophical and moral justifications, species and genetic diversity bring us many practical benefits.

Benefits of Species and Genetic Diversity

Many species that are threatened could potentially provide food, fibers, and medicines for human use, making biodiversity a crucial natural resource. If we lose wild populations of plants closely related to agricultural species, we lose genetic resources

▲ **Figure 56.5 The endangered Marianas "flying fox" bat (*Pteropus mariannus*), an important pollinator.**

that could be used to improve crop qualities, such as disease resistance. For instance, plant breeders responded to devastating outbreaks of the grassy stunt virus in rice (*Oryza sativa*) by screening 7,000 populations of this species and its close relatives for resistance to the virus. One population of a single relative, Indian rice (*Oryza nivara*), was found to be resistant to the virus, and scientists succeeded in breeding the resistance trait into commercial rice varieties. Today, the original disease-resistant population has apparently become extinct in the wild.

In the United States, about 25% of the prescriptions dispensed from pharmacies contain substances originally derived from plants. In the 1970s, researchers discovered that the rosy periwinkle, which grows on the island of Madagascar, off the coast of Africa, contains alkaloids that inhibit cancer cell growth **(Figure 56.6)**. This discovery led to treatments for two deadly forms of cancer, Hodgkin's lymphoma and childhood leukemia, resulting in remission in most cases. Madagascar is also home to five other species of periwinkles, one of which is approaching extinction. The loss of these species would mean the loss of any possible medicinal benefits they might offer.

Each loss of a species means the loss of unique genes, some of which may code for enormously useful proteins. The enzyme Taq polymerase was first extracted from a bacterium, *Thermus aquaticus*, found in hot springs at Yellowstone National Park. This enzyme is essential for the polymerase chain reaction (PCR) because it is stable at the high temperatures required for automated PCR (see Figure 20.8). DNA from many other species of prokaryotes, living in a variety of environments, is used in the mass production of proteins for new medicines, foods, petroleum substitutes, other industrial chemicals, and other products. However, because millions of species may become extinct before we discover them, we stand to lose the valuable genetic potential held in their unique libraries of genes.

Ecosystem Services

The benefits that individual species provide to humans are substantial, but saving individual species is only part of the reason for preserving ecosystems. Humans evolved in Earth's ecosystems, and we rely on these systems and their inhabitants for our survival. **Ecosystem services** encompass all the processes through which natural ecosystems help sustain human life. Ecosystems purify our air and water. They detoxify and decompose our wastes and reduce the impacts of extreme weather and flooding. The organisms in ecosystems pollinate our crops, control pests, and create and preserve our soils. Moreover, these diverse services are provided for free.

◀ Figure 56.6 The rosy periwinkle (*Catharanthus roseus*), a plant that saves lives.

Perhaps because we don't attach a monetary value to the services of natural ecosystems, we generally undervalue them. In 1997, ecologist Robert Costanza and his colleagues estimated the value of Earth's ecosystem services at $33 trillion per year, nearly twice the gross national product of all the countries on Earth at the time ($18 trillion). It may be more realistic to do the accounting on a smaller scale. In 1996, New York City invested more than $1 billion to buy land and restore habitat in the Catskill Mountains, the source of much of the city's fresh water. This investment was spurred by increasing pollution of the water by sewage, pesticides, and fertilizers. By harnessing ecosystem services to purify its water naturally, the city saved $8 billion it would have otherwise spent to build a new water-treatment plant and $300 million a year to run the plant.

There is growing evidence that the functioning of ecosystems, and hence their capacity to perform services, is linked to biodiversity. As human activities reduce biodiversity, we are reducing the capacity of the planet's ecosystems to perform processes critical to our own survival.

Threats to Biodiversity

Many different human activities threaten biodiversity on local, regional, and global scales. The threats posed by these activities are of four major types: habitat loss, introduced species, overharvesting, and global change.

Habitat Loss

Human alteration of habitat is the single greatest threat to biodiversity throughout the biosphere. Habitat loss has been brought about by agriculture, urban development, forestry, mining, and pollution. Global climate change is already altering habitats today and will have an even larger effect later this century (discussed shortly). When no alternative habitat is available or a species is unable to move, habitat loss may mean extinction. The IUCN implicates destruction of physical habitat for 73% of the species that have become extinct, endangered, vulnerable, or rare in the last few hundred years.

Habitat loss and fragmentation may occur over immense regions. Approximately 98% of the tropical dry forests of Central America and Mexico have been cleared (cut down). Clearing of tropical rain forest in the state of Veracruz, Mexico,

▲ **Figure 56.7 Habitat fragmentation in the foothills of Los Angeles.** Development in the valleys may confine the organisms that inhabit the narrow strips of hillside.

mostly for cattle ranching, has resulted in the loss of more than 90% of the original forest, leaving relatively small, isolated patches of forest. Other natural habitats have also been fragmented by human activities **(Figure 56.7)**.

In almost all cases, habitat fragmentation leads to species loss because the smaller populations in habitat fragments have a higher probability of local extinction. Prairie covered about 800,000 hectares of southern Wisconsin when Europeans first arrived in North America but now occupies less than 0.1% of its original area. Plant diversity surveys of 54 Wisconsin prairie remnants conducted in 1948–1954 and repeated in 1987–1988 showed that the remnants lost between 8% and 60% of their plant species in the time between the two surveys.

Habitat loss is also a major threat to aquatic biodiversity. About 93% of coral reefs, among Earth's most species-rich aquatic communities, have been damaged by human activities. At the current rate of destruction, 40–50% of the reefs, home to one-third of marine fish species, could disappear in the next 30 to 40 years. Freshwater habitats are also being lost, often as a result of the dams, reservoirs, channel modification, and flow regulation now affecting most of the world's rivers. For example, the more than 30 dams and locks built along the Mobile River basin in the southeastern United States changed river depth and flow and helped drive more than 40 species of mussels and snails to extinction.

Introduced Species

Introduced species, also called non-native or exotic species, are those that humans move intentionally or accidentally from the species' native locations to new geographic regions. Human travel by ship and airplane has accelerated the transplant of species. Free from the predators, parasites, and pathogens that limit their populations in their native habitats, such transplanted species may spread rapidly through a new region.

Some introduced species disrupt their new community, often by preying on native organisms or outcompeting them for resources. The brown tree snake was accidentally introduced to the island of Guam from other parts of the South Pacific after World War II: It was a "stowaway" in military cargo **(Figure 56.8a)**. Since then, 12 species of birds and 6 species of lizards that the snakes ate have become extinct on Guam, which had no native snakes. The devastating zebra mussel, a filter-feeding mollusc, was introduced into the Great Lakes of North America in 1988, most likely in the ballast water of ships arriving from Europe. Zebra mussels form dense colonies and have disrupted freshwater ecosystems, threatening native aquatic species. They have also clogged water intake structures, causing billions of dollars in damage to domestic and industrial water supplies.

Humans have deliberately introduced many species with good intentions but disastrous effects. An Asian plant called kudzu, which the U.S. Department of Agriculture once introduced in the southern United States to help control erosion, has taken over large areas of the landscape there

(a) Brown tree snake, introduced to Guam in cargo

(b) Introduced kudzu thriving in South Carolina

▲ **Figure 56.8 Two introduced species.**

(**Figure 56.8b**). The European starling was brought intentionally into New York's Central Park in 1890 by a citizens' group intent on introducing all the plants and animals mentioned in Shakespeare's plays. It quickly spread across North America, where its population now exceeds 100 million, displacing many native songbirds.

Introduced species are a worldwide problem, contributing to approximately 40% of the extinctions recorded since 1750 and costing billions of dollars each year in damage and control efforts. There are more than 50,000 introduced species in the United States alone.

Overharvesting

The term *overharvesting* refers generally to the human harvesting of wild organisms at rates exceeding the ability of populations of those species to rebound. Species with restricted habitats, such as small islands, are particularly vulnerable to overharvesting. One such species was the great auk, a large, flightless seabird found on islands in the North Atlantic Ocean. By the 1840s, humans had hunted the great auk to extinction to satisfy demand for its feathers, eggs, and meat.

Also susceptible to overharvesting are large organisms with low reproductive rates, such as elephants, whales, and rhinoceroses. The decline of Earth's largest terrestrial animals, the African elephants, is a classic example of the impact of overhunting. Largely because of the trade in ivory, elephant populations have been declining in most of Africa for the last 50 years. An international ban on the sale of new ivory resulted in increased poaching (illegal hunting), so the ban had little effect in much of central and eastern Africa. Only in South Africa, where once-decimated herds have been well protected for nearly a century, have elephant populations been stable or increasing (see Figure 53.8).

Conservation biologists increasingly use the tools of molecular genetics to track the origins of tissues harvested from endangered species. Researchers at the University of Washington have constructed a DNA reference map for the African elephant using DNA isolated from elephant dung. By comparing this reference map with DNA isolated from samples of ivory harvested either legally or by poachers, they can determine to within a few hundred kilometers where the elephants were killed (**Figure 56.9**). Similarly, biologists using phylogenetic analyses of mitochondrial DNA (mtDNA) showed that some whale meat sold in Japanese fish markets came from illegally harvested species, including fin and humpback whales, which are endangered (see Figure 26.6).

Many commercially important fish populations, once thought to be inexhaustible, have been decimated by overfishing. Demands for protein-rich food from an increasing human population, coupled with new harvesting technologies, such as long-line fishing and modern trawlers, have reduced these fish populations to levels that cannot sustain further exploitation. Until the past few decades, the North Atlantic bluefin tuna was considered a sport fish of little commercial value—just a few cents per pound for use in cat food. In the 1980s, however, wholesalers began airfreighting fresh, iced bluefin to Japan for sushi and sashimi. In that market, the fish

▼ **Figure 56.9**

IMPACT

Forensic Ecology and Elephant Poaching

This array of severed tusks is part of an illegal shipment of 6,000 kg of ivory intercepted on its way from Africa to Singapore in 2002. Investigators wondered whether the elephants slaughtered for the ivory—perhaps as many as 6,500—were killed in the area where the shipment originated, primarily Zambia, or instead were killed across Africa, indicating a broader smuggling ring. Samuel Wasser, of the University of Washington, and colleagues amplified specific segments of DNA from the tusks using the polymerase chain reaction (PCR). These segments included stretches of DNA containing short tandem repeats (STRs; see Concept 20.4, pp. 420–421), the number of which varies among different elephant populations. The researchers then compared alleles at seven or more loci with a reference DNA database they had generated for elephants of known geographic origin. Their results showed conclusively that the elephants came from a narrow east-west band centered on Zambia rather than from across Africa.

WHY IT MATTERS The DNA analyses suggested that poaching rates were 30 times higher in Zambia than previously estimated. This news led to improved antipoaching efforts by the Zambian government. Techniques like those used in this study are being employed by conservation biologists to track the harvesting of many endangered species, including whales, sharks, and orchids.

FURTHER READING S. K. Wasser et al., Forensic tools battle ivory poachers, *Scientific American* 399:68–76 (2009); S. K. Wasser et al., 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 (2007).

MAKE CONNECTIONS Figure 26.6 (p. 539) describes another example in which conservation biologists used DNA analyses to compare harvested samples with a reference DNA database. How are these examples similar, and how are they different? What limitations might there be to using such forensic methods in other suspected cases of poaching?

▲ **Figure 56.10 Overharvesting.** North Atlantic bluefin tuna are auctioned in a Japanese fish market.

now brings up to $100 per pound **(Figure 56.10)**. With increased harvesting spurred by such high prices, it took just ten years to reduce the western North Atlantic bluefin population to less than 20% of its 1980 size. The collapse of the northern cod fishery off Newfoundland in the 1990s is another example of the overharvesting of a once-common species.

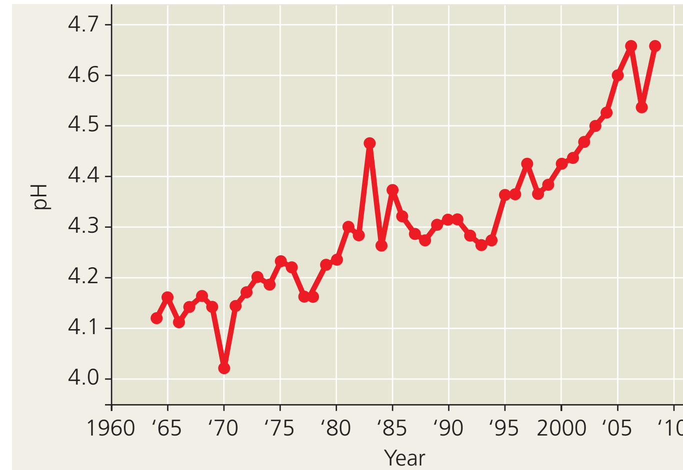
Global Change

The fourth threat to biodiversity, global change, alters the fabric of Earth's ecosystems at regional to global scales. Global change includes alterations in climate, atmospheric chemistry, and broad ecological systems that reduce the capacity of Earth to sustain life.

One of the first types of global change to cause concern was *acid precipitation*, which is rain, snow, sleet, or fog with a pH less than 5.2. The burning of wood and fossil fuels releases oxides of sulfur and nitrogen that react with water in air, forming sulfuric and nitric acids. The acids eventually fall to Earth's surface, harming some aquatic and terrestrial organisms.

In the 1960s, ecologists determined that lake-dwelling organisms in eastern Canada were dying because of air pollution from factories in the midwestern United States. Newly hatched lake trout, for instance, die when the pH drops below 5.4. Lakes and streams in southern Norway and Sweden were losing fish because of pollution generated in Great Britain and central Europe. By 1980, the pH of precipitation in large areas of North America and Europe averaged 4.0–4.5 and sometimes dropped as low as 3.0. (To review pH, see Concept 3.3.)

Environmental regulations and new technologies have enabled many countries to reduce sulfur dioxide emissions in recent decades. In the United States, sulfur dioxide emissions decreased more than 40% between 1993 and 2008, gradually reducing the acidity of precipitation **(Figure 56.11)**. However, ecologists estimate that it will take decades for aquatic



▲ **Figure 56.11 Changes in the pH of precipitation at Hubbard Brook, New Hampshire.** Although still very acidic, the precipitation in this northeastern U.S. forest has been increasing in pH for more than three decades.

ecosystems to recover. Meanwhile, emissions of nitrogen oxides are increasing in the United States, and emissions of sulfur dioxide and acid precipitation continue to damage forests in central and eastern Europe.

We will explore the importance of global change for Earth's biodiversity in more detail in Concept 56.4, where we examine such factors as global climate change and ozone depletion.

CONCEPT CHECK 56.1

1. Explain why it is too narrow to define the biodiversity crisis as simply a loss of species.
2. Identify the four main threats to biodiversity and explain how each damages diversity.
3. **WHAT IF?** Imagine two populations of a fish species, one in the Mediterranean Sea and one in the Caribbean Sea. Now imagine two scenarios: (1) The populations breed separately, and (2) adults of both populations migrate yearly to the North Atlantic to interbreed. Which scenario would result in a greater loss of genetic diversity if the Mediterranean population were harvested to extinction? Explain your answer.

For suggested answers, see Appendix A.

CONCEPT 56.2

Population conservation focuses on population size, genetic diversity, and critical habitat

Biologists who work on conservation at the population and species levels use two main approaches: the small-population approach and the declining-population approach.

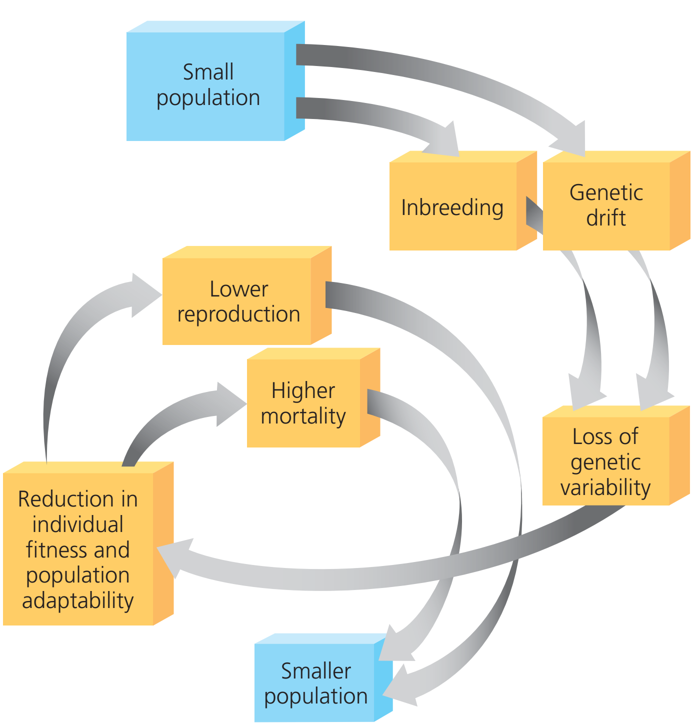
Small-Population Approach

Small populations are particularly vulnerable to overharvesting, habitat loss, and the other threats to biodiversity that you read about in Concept 56.1. After such factors have reduced a population's size, the small size itself can push the population to extinction. Conservation biologists who adopt the small-population approach study the processes that cause extinctions once population sizes have been severely reduced.

The Extinction Vortex: Evolutionary Implications of Small Population Size

EVOLUTION A small population is vulnerable to inbreeding and genetic drift, which draw the population down an **extinction vortex** toward smaller and smaller population size until no individuals survive (**Figure 56.12**). A key factor driving the extinction vortex is the loss of the genetic variation that enables evolutionary responses to environmental change, such as the appearance of new strains of pathogens. Both inbreeding and genetic drift can cause a loss of genetic variation (see Chapter 23), and their effects become more harmful as a population shrinks. Inbreeding often reduces fitness because offspring are more likely to be homozygous for harmful recessive traits.

Not all small populations are doomed by low genetic diversity, and low genetic variability does not automatically lead to permanently small populations. For instance, overhunting of northern elephant seals in the 1890s reduced the species to only 20 individuals—clearly a bottleneck with reduced genetic variation. Since that time, however, the northern elephant seal populations have rebounded to about 150,000 individuals today, though their genetic variation remains relatively low. A number of plant species also seem to have inherently low genetic variability. Many populations of cordgrass (*Spartina anglica*), which thrives in salt marshes, are genetically uniform at many loci. *Spartina anglica* arose from a few parent plants only about a century ago by hybridization and allopolyploidy (see Figure 24.11). Having spread by natural cloning, this species now dominates large areas of tidal mudflats in Europe and Asia. Thus, low genetic diversity does not always impede population growth.



▲ **Figure 56.12 Processes driving an extinction vortex.**

Case Study: *The Greater Prairie Chicken and the Extinction Vortex*

When Europeans arrived in North America, the greater prairie chicken (*Tympanuchus cupido*) was common from New England to Virginia and across the western prairies of the continent. As you read in Chapter 23, land cultivation for agriculture fragmented the populations of this species, and its abundance decreased rapidly. Illinois had millions of greater prairie chickens in the 19th century but fewer than 50 by 1993. Researchers found that the decline in the Illinois population was associated with a decrease in fertility. As a test of the extinction vortex hypothesis, scientists increased genetic variation by importing 271 birds from larger populations elsewhere (**Figure 56.13**, on the next page). The Illinois population rebounded, confirming that it had been on its way to extinction until rescued by the transfusion of genetic variation.

Minimum Viable Population Size

How small does a population have to be before it starts down an extinction vortex? The answer depends on the type of organism and other factors. Large predators that feed high on the food chain usually require extensive individual ranges, resulting in low population densities. Therefore, not all rare species concern conservation biologists. All populations, however, require some minimum size to remain viable.

The minimal population size at which a species is able to sustain its numbers is known as the **minimum viable population (MVP)**. MVP is usually estimated for a given species using computer models that integrate many factors. The calculation may include, for instance, an estimate of how many individuals in a small population are likely to be killed by a natural catastrophe such as a storm. Once in the extinction vortex, two or three consecutive years of bad weather could finish off a population that is already below its MVP.

Effective Population Size

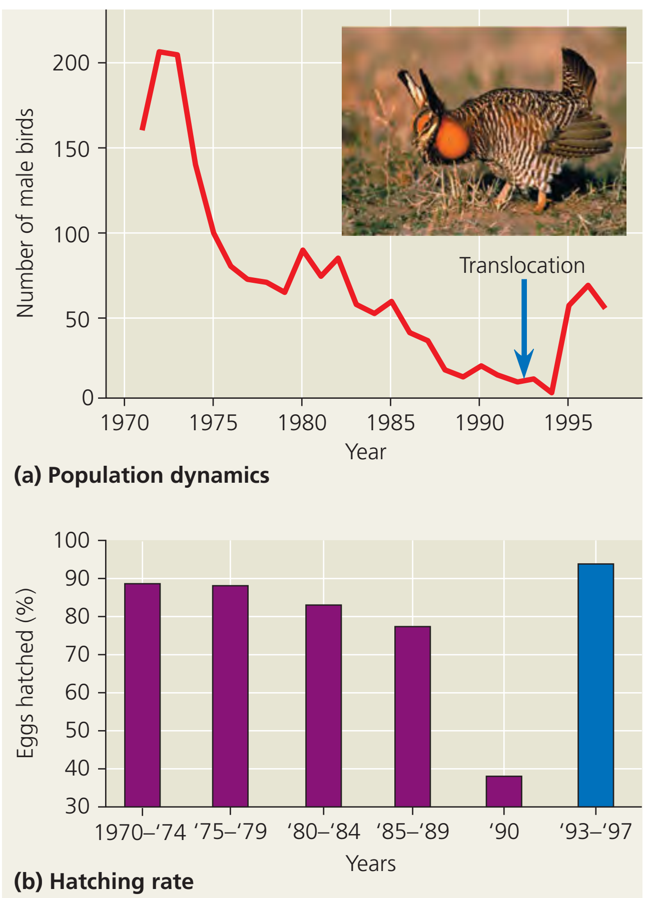
Genetic variation is the key issue in the small-population approach. The *total* size of a population may be misleading

▼ Figure 56.13 **INQUIRY**

What caused the drastic decline of the Illinois greater prairie chicken population?

EXPERIMENT Researchers had observed that the population collapse of the greater prairie chicken was mirrored in a reduction in fertility, as measured by the hatching rate of eggs. Comparison of DNA samples from the Jasper County, Illinois, population with DNA from feathers in museum specimens showed that genetic variation had declined in the study population (see Figure 23.11). In 1992, Ronald Westemeier, Jeffrey Brawn, and colleagues began translocating prairie chickens from Minnesota, Kansas, and Nebraska in an attempt to increase genetic variation.

RESULTS After translocation (blue arrow), the viability of eggs rapidly increased, and the population rebounded.



CONCLUSION Reduced genetic variation had started the Jasper County population of prairie chickens down the extinction vortex.

SOURCE R. L. Westemeier et al., Tracking the long-term decline and recovery of an isolated population, *Science* 282:1695–1698 (1998).

INQUIRY IN ACTION Read and analyze the original paper in *Inquiry in Action: Interpreting Scientific Papers.*

WHAT IF? Given the success of using transplanted birds as a tool for increasing the percentage of hatched eggs in Illinois, why wouldn't you transplant *additional* birds immediately to Illinois?

because only certain members of the population breed successfully and pass their alleles on to offspring. Therefore, a meaningful estimate of MVP requires the researcher to determine the **effective population size**, which is based on the breeding potential of the population.

The following formula incorporates the sex ratio of breeding individuals into the estimate of effective population size, abbreviated N_e:

$$N_e = \frac{4N_f N_m}{N_f + N_m}$$

where N_f and N_m are, respectively, the number of females and the number of males that successfully breed. If we apply this formula to an idealized population whose total size is 1,000 individuals, N_e will also be 1,000 if every individual breeds and the sex ratio is 500 females to 500 males. In this case, $N_e = (4 \times 500 \times 500)/(500 + 500) = 1{,}000$. Any deviation from these conditions (not all individuals breed or there is not a 1:1 sex ratio) reduces N_e. For instance, if the total population size is 1,000 but only 400 females and 400 males breed, then $N_e = (4 \times 400 \times 400)/(400 + 400) = 800$, or 80% of the total population size. Numerous life history traits can influence N_e, and alternative formulas for estimating N_e take into account factors such as family size, age at maturation, genetic relatedness among population members, the effects of gene flow between geographically separated populations, and population fluctuations.

In actual study populations, N_e is always some fraction of the total population. Thus, simply determining the total number of individuals in a small population does not provide a good measure of whether the population is large enough to avoid extinction. Whenever possible, conservation programs attempt to sustain total population sizes that include at least the minimum viable number of *reproductively active* individuals. The conservation goal of sustaining effective population size (N_e) above MVP stems from the concern that populations retain enough genetic diversity to adapt as their environment changes.

The MVP of a population is often used in population viability analysis. The objective of this analysis is to predict a population's chances for survival, usually expressed as a specific probability of survival, such as a 95% chance, over a particular time interval, perhaps 100 years. Such modeling approaches allow conservation biologists to explore the potential consequences of alternative management plans. Because modeling depends on accurate information for the populations under study, conservation biology is most effective when theoretical modeling is combined with field studies of the managed populations.

Case Study: *Analysis of Grizzly Bear Populations*

One of the first population viability analyses was conducted in 1978 by Mark Shaffer, of Duke University, as part of a long-term study of grizzly bears in Yellowstone National Park and

▲ **Figure 56.14 Long-term monitoring of a grizzly bear population.** The ecologist is fitting this tranquilized bear with a radio collar so that the bear's movements can be compared with those of other grizzlies in the Yellowstone National Park population.

its surrounding areas **(Figure 56.14)**. A threatened species in the United States, the grizzly bear (*Ursus arctos horribilis*) is currently found in only 4 of the 48 contiguous states. Its populations in those states have been drastically reduced and fragmented. In 1800, an estimated 100,000 grizzlies ranged over about 500 million hectares of habitat, while today only about 1,000 individuals in six relatively isolated populations range over less than 5 million hectares.

Shaffer attempted to determine viable sizes for the Yellowstone grizzly population. Using life history data obtained for individual Yellowstone bears over a 12-year period, he simulated the effects of environmental factors on survival and reproduction. His models predicted that, given a suitable habitat, a Yellowstone grizzly bear population of 70–90 individuals would have about a 95% chance of surviving for 100 years. A slightly larger population of only 100 bears would have a 95% chance of surviving for twice as long, about 200 years.

How does the actual size of the Yellowstone grizzly population compare with Shaffer's predicted MVP? A current estimate puts the total grizzly bear population in the greater Yellowstone ecosystem at about 400 individuals. The relationship of this estimate to the effective population size, N_e, depends on several factors. Usually, only a few dominant males breed, and it may be difficult for them to locate females, since individuals inhabit such large areas. Moreover, females may reproduce only when there is abundant food. As a result, N_e is only about 25% of the total population size, or about 100 bears.

Because small populations tend to lose genetic variation over time, a number of research teams have analyzed proteins, mtDNA, and short tandem repeats (see Chapter 21) to assess genetic variability in the Yellowstone grizzly bear population. All results to date indicate that the Yellowstone population has less genetic variability than other grizzly bear populations in North America. However, the isolation and decline in genetic variability in the Yellowstone grizzly bear population were gradual during the 20th century and not as severe as feared: Museum specimens collected in the early 1900s demonstrate that genetic variability among the Yellowstone grizzly bears was low even then.

How might conservation biologists increase the effective size and genetic variation of the Yellowstone grizzly bear population? Migration between isolated populations of grizzlies could increase both effective and total population sizes. Computer models predict that introducing only two unrelated bears each decade into a population of 100 individuals would reduce the loss of genetic variation by about half. For the grizzly bear, and probably for many other species with small populations, finding ways to promote dispersal among populations may be one of the most urgent conservation needs.

This case study and that of the greater prairie chicken bridge small-population models and practical applications in conservation. Next, we look at an alternative approach to understanding the biology of extinction.

Declining-Population Approach

The declining-population approach focuses on threatened and endangered populations that show a downward trend, even if the population is far above its minimum viable population. The distinction between a declining population (which is not always small) and a small population (which is not always declining) is less important than the different priorities of the two approaches. The small-population approach emphasizes smallness itself as an ultimate cause of a population's extinction, especially through the loss of genetic diversity. In contrast, the declining-population approach emphasizes the environmental factors that caused a population decline in the first place. If, for instance, an area is deforested, then species that depend on trees will decline in abundance and become locally extinct, whether or not they retain genetic variation.

Steps for Analysis and Intervention

The declining-population approach requires that population declines be evaluated on a case-by-case basis, with researchers carefully dissecting the causes of a decline before taking steps to correct it. If an invasive species such as the brown tree snake in Guam (see Figure 56.8a) is harming a native bird species, then managers need to reduce or eliminate the invader to restore vulnerable populations of the bird. Although most situations are more complex, we can use the following steps for analyzing declining populations:

1. Confirm, using population data, that the species was more widely distributed or abundant in the past.
2. Study the natural history of this and related species, including reviewing the research literature, to determine the species' environmental needs.

3. Develop hypotheses for all possible causes of the decline, including human activities and natural events, and list the predictions of each hypothesis.
4. Because many factors may be correlated with the decline, test the most likely hypothesis first. For example, remove the suspected agent of decline to see if the experimental population rebounds compared to a control population.
5. Apply the results of the diagnosis to manage the threatened species and monitor its recovery.

The following case study is one example of how the declining-population approach has been applied to the conservation of an endangered species.

Case Study: *Decline of the Red-Cockaded Woodpecker*

The red-cockaded woodpecker (*Picoides borealis*) is found only in the southeastern United States. It requires mature pine forests, preferably ones dominated by the longleaf pine, for its habitat. Most woodpeckers nest in dead trees, but the red-cockaded woodpecker drills its nest holes in mature, living pine trees. It also drills small holes around the entrance to its nest cavity, which causes resin from the tree to ooze down the trunk. The resin seems to repel predators, such as corn snakes, that eat bird eggs and nestlings.

Another critical habitat factor for the red-cockaded woodpecker is that the undergrowth of plants around the pine trunks must be low **(Figure 56.15a)**. Breeding birds tend to abandon nests when vegetation among the pines is thick and higher than about 4.5 m **(Figure 56.15b)**. Apparently, the birds need a clear flight path between their home trees and the neighboring feeding grounds. Periodic fires have historically swept through longleaf pine forests, keeping the undergrowth low.

One factor leading to decline of the red-cockaded woodpecker has been the destruction or fragmentation of suitable habitats by logging and agriculture. By recognizing key habitat factors, protecting some longleaf pine forests, and using controlled fires to reduce forest undergrowth, conservation managers have helped restore habitat that can support viable populations.

A successful recovery program for red-cockaded woodpeckers was hindered, however, by the birds' social organization. Red-cockaded woodpeckers live in groups of one breeding pair and up to four "helpers," mostly males (an example of altruism; see Chapter 51). Helpers are offspring that do not disperse to breed but remain behind to help incubate eggs and feed nestlings of the breeding pair. Helpers may eventually attain breeding status within the flock when older birds die, but the wait may take years, and helpers must still compete to breed. Young birds that do disperse as members of new groups also have a tough path to reproductive success. New groups usually occupy abandoned territories or start at a new site, where they must excavate nesting cavities, which can take months. Individuals generally have a better chance of reproducing by remaining behind than by dispersing and excavating cavities in new territories.

To test the hypothesis that this social behavior was contributing to the decline of the red-cockaded woodpecker, researchers constructed cavities in pine trees at 20 sites. The

(a) Forests that can sustain red-cockaded woodpeckers have low undergrowth.

(b) Forests that cannot sustain red-cockaded woodpeckers have high, dense undergrowth that interferes with the woodpeckers' access to feeding grounds.

▲ **Figure 56.15 A habitat requirement of the red-cockaded woodpecker.**

? *How is habitat disturbance absolutely necessary for the long-term survival of the woodpecker?*

results were dramatic. Cavities in 18 of the 20 sites were colonized by red-cockaded woodpeckers, and new breeding groups formed only in these sites. The experiment supported the hypothesis that this woodpecker species had been avoiding suitable habitat because of a lack of breeding cavities. Based on this experiment, conservationists initiated a habitat maintenance program that included controlled burning and excavation of new breeding cavities, enabling this endangered species to begin to recover.

Weighing Conflicting Demands

Determining population numbers and habitat needs is only part of a strategy to save species. Scientists also need to weigh a species' needs against other conflicting demands. Conservation biology often highlights the relationship between science, technology, and society. For example, an ongoing, sometimes bitter debate in the western United States pits habitat preservation for wolf, grizzly bear, and bull trout populations against job opportunities in the grazing and resource extraction industries. Programs to restock wolves in Yellowstone National Park were opposed by some recreationists concerned for human safety and by many ranchers concerned with potential loss of livestock outside the park.

Large, high-profile vertebrates are not always the focal point in such conflicts, but habitat use is almost always the issue. Should work proceed on a new highway bridge if it destroys the only remaining habitat of a species of freshwater mussel? If you were the owner of a coffee plantation growing varieties that thrive in bright sunlight, would you be willing to change to shade-tolerant varieties that produce less coffee per hectare but can grow beneath trees that support large numbers of songbirds?

Another important consideration is the ecological role of a species. Because we cannot save every endangered species, we must determine which species are most important for conserving biodiversity as a whole. Identifying keystone species and finding ways to sustain their populations can be central to maintaining communities and ecosystems.

Management aimed at conserving a single species carries with it the possibility of harming populations of other species. For example, management of open pine forests for the red-cockaded woodpecker might impact migratory birds that use later-successional broadleaf forests. To test this idea, ecologists compared bird communities near clusters of nest cavities in managed pine forests with communities in forests not managed for the woodpeckers. Contrary to expectations, the managed sites supported higher numbers and a higher diversity of other birds than the control forests did. In this case, managing for one bird species increased the diversity of an entire bird community. In most situations, conservation must look beyond single species and consider the whole community and ecosystem as an important unit of biodiversity.

CONCEPT CHECK 56.2

1. How does the reduced genetic diversity of small populations make them more vulnerable to extinction?
2. If there was a total of 50 individuals in the two Illinois populations of greater prairie chickens in 1993, what was the effective population size if 15 females and 5 males bred?
3. **WHAT IF?** In 2005, at least ten grizzly bears in the greater Yellowstone ecosystem were killed through contact with people. Three things caused most of these deaths: collisions with automobiles, hunters (of other animals) shooting when charged by a female grizzly bear with cubs nearby, and conservation managers killing bears that attacked livestock repeatedly. If you were a conservation manager, what steps might you take to minimize such encounters in Yellowstone?

For suggested answers, Appendix A.

CONCEPT 56.3

Landscape and regional conservation help sustain biodiversity

Although conservation efforts historically focused on saving individual species, efforts today often seek to sustain the biodiversity of entire communities, ecosystems, and landscapes. Such a broad view requires applying not just the principles of community, ecosystem, and landscape ecology but aspects of human population dynamics and economics as well. The goals of landscape ecology (see Chapter 52) include projecting future patterns of landscape use and making biodiversity conservation part of land-use planning.

Landscape Structure and Biodiversity

The biodiversity of a given landscape is in large part a function of the structure of the landscape. Understanding landscape structure is critically important in conservation because many species use more than one kind of ecosystem, and many live on the borders between ecosystems.

Fragmentation and Edges

The boundaries, or *edges*, between ecosystems—such as between a lake and the surrounding forest or between cropland and suburban housing tracts—are defining features of

(a) Natural edges. Grasslands give way to forest ecosystems in Yellowstone National Park.

(b) Edges created by human activity. Pronounced edges (roads) surround clear-cut areas in this photograph of a heavily logged rain forest in Malaysia.

▲ **Figure 56.16 Edges between ecosystems.**

landscapes **(Figure 56.16)**. An edge has its own set of physical conditions, which differ from those on either side of it. The soil surface of an edge between a forest patch and a burned area receives more sunlight and is usually hotter and drier than the forest interior, but it is cooler and wetter than the soil surface in the burned area.

Some organisms thrive in edge communities because they gain resources from both adjacent areas. The ruffed grouse (*Bonasa umbellus*) is a bird that needs forest habitat for nesting, winter food, and shelter, but it also needs forest openings with dense shrubs and herbs for summer food. White-tailed deer also thrive in edge habitats, where they can browse on woody shrubs; deer populations often expand when forests are logged and more edges are generated.

▲ **Figure 56.17 Amazon rain forest fragments created as part of the Biological Dynamics of Forest Fragments Project.**

The proliferation of edge species can have positive or negative effects on biodiversity. A 1997 study in Cameroon comparing edge and interior populations of the little greenbul (a tropical rain forest bird) suggested that forest edges may be important sites of speciation. On the other hand, ecosystems in which edges arise from human alterations often have reduced biodiversity and a preponderance of edge-adapted species. For example, the brown-headed cowbird (*Molothrus ater*) is an edge-adapted species that lays its eggs in the nests of other birds, often migratory songbirds. Cowbirds need forests, where they can parasitize the nests of other birds, and open fields, where they forage on insects. Thus, their populations are growing where forests are being cut and fragmented, creating more edge habitat and open land. Increasing cowbird parasitism and habitat loss are correlated with declining populations of several of the cowbird's host species.

The influence of fragmentation on the structure of communities has been explored since 1979 in the long-term Biological Dynamics of Forest Fragments Project. Located in the heart of the Amazon River basin, the study area consists of isolated fragments of tropical rain forest separated from surrounding continuous forest by distances of 80–1,000 m **(Figure 56.17)**. Numerous researchers working on this project have clearly documented the effects of this fragmentation on organisms ranging from bryophytes to beetles to birds. They have consistently found that species adapted to forest interiors show the greatest declines when patches are the smallest, suggesting that landscapes dominated by small fragments will support fewer species.

Corridors That Connect Habitat Fragments

In fragmented habitats, the presence of a **movement corridor**, a narrow strip or series of small clumps of habitat

▲ **Figure 56.18 An artificial corridor.** This bridge in Banff National Park, Canada, helps animals cross a human-created barrier.

connecting otherwise isolated patches, can be extremely important for conserving biodiversity. Riparian habitats often serve as corridors, and in some nations, government policy prohibits altering these habitats. In areas of heavy human use, artificial corridors are sometimes constructed. Bridges or tunnels, for instance, can reduce the number of animals killed trying to cross highways **(Figure 56.18)**.

Movement corridors can also promote dispersal and reduce inbreeding in declining populations. Corridors have been shown to increase the exchange of individuals among populations of many organisms, including butterflies, voles, and aquatic plants. Corridors are especially important to species that migrate between different habitats seasonally. However, a corridor can also be harmful—for example, by allowing the spread of disease. In a 2003 study, a scientist at the University of Zaragoza, Spain, showed that habitat corridors facilitate the movement of disease-carrying ticks among forest patches in northern Spain. All the effects of corridors are not yet understood, and their impact is an area of active research in conservation biology.

Establishing Protected Areas

Conservation biologists are applying their understanding of landscape dynamics in establishing protected areas to slow biodiversity loss. Currently, governments have set aside about 7% of the world's land in various forms of reserves. Choosing where to place nature reserves and how to design them poses many challenges. Should the reserve be managed to minimize the risks of fire and predation to a threatened species? Or should the reserve be left as natural as possible, with such processes as fires ignited by lightning allowed to play out on their own? This is just one of the debates that arise among people who share an interest in the health of national parks and other protected areas.

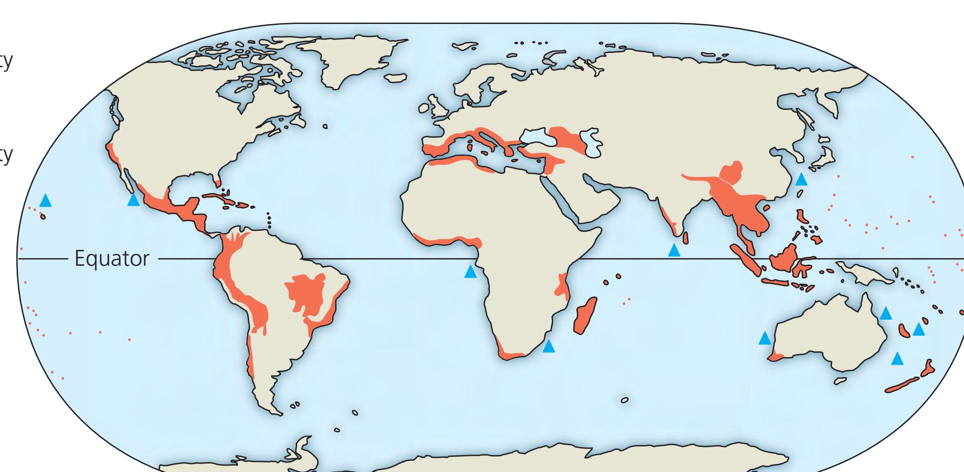
Preserving Biodiversity Hot Spots

In deciding which areas are of highest conservation priority, biologists often focus on hot spots of biodiversity. A **biodiversity hot spot** is a relatively small area with numerous endemic species (species found nowhere else in the world) and a large number of endangered and threatened species **(Figure 56.19)**. Nearly 30% of all bird species can be found in hot spots that make up only about 2% of Earth's land area. Approximately 50,000 plant species, or about one-sixth of all known plant species, inhabit just 18 hot spots covering 0.5% of the global land surface. Together, the "hottest" of the terrestrial biodiversity hot spots total less than 1.5% of Earth's land but are home to more than a third of all species of plants, amphibians, reptiles (including birds), and mammals. Aquatic ecosystems also have hot spots, such as coral reefs and certain river systems.

Biodiversity hot spots are good choices for nature reserves, but identifying them is not always simple. One problem is that a hot spot for one taxonomic group, such as butterflies, may not be a hot spot for some other taxonomic group, such as birds. Designating an area as a biodiversity hot spot is often biased toward saving vertebrates and plants, with less attention paid to invertebrates and microorganisms. Some biologists are

Terrestrial biodiversity hot spots

▲ Marine biodiversity hot spots



◀ **Figure 56.19 Earth's terrestrial and marine biodiversity hot spots.**

also concerned that the hot-spot strategy places too much emphasis on such a small fraction of Earth's surface.

Global change makes the task of preserving hot spots even more challenging because the conditions that favor a particular community may not be found in the same location in the future. The biodiversity hot spot in the southwest corner of Australia (see Figure 56.19) holds thousands of species of endemic plants and numerous endemic vertebrates. Researchers recently concluded that between 5% and 25% of the plant species they examined may become extinct by 2080 because the plants will be unable to tolerate the increased dryness predicted for this region.

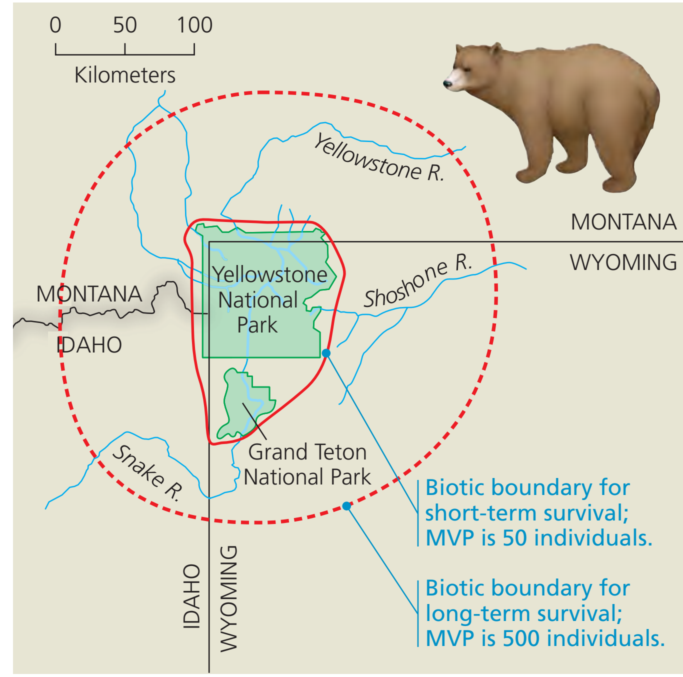
Philosophy of Nature Reserves

Nature reserves are biodiversity islands in a sea of habitat degraded by human activity. Protected "islands" are not isolated from their surroundings, however, and the nonequilibrium model we described in Chapter 54 applies to nature reserves as well as to the larger landscapes around them.

An earlier policy—that protected areas should be set aside to remain unchanged forever—was based on the concept that ecosystems are balanced, self-regulating units. As we saw in Chapter 54, however, disturbance is common in all ecosystems, and management policies that ignore natural disturbances or attempt to prevent them have generally failed. For instance, setting aside an area of a fire-dependent community, such as a portion of a tallgrass prairie, chaparral, or dry pine forest, with the intention of saving it is unrealistic if periodic burning is excluded. Without the dominant disturbance, the fire-adapted species are usually outcompeted and biodiversity is reduced.

Because human disturbance and fragmentation are increasingly common, understanding the dynamics of disturbances, populations, edges, and corridors is essential for designing and managing protected areas. An important conservation question is whether to create fewer large reserves or more numerous small reserves. One argument for large reserves is that large, far-ranging animals with low-density populations, such as the grizzly bear, require extensive habitats. Large reserves also have proportionately smaller perimeters than small reserves and are therefore less affected by edges.

As conservation biologists have learned more about the requirements for achieving minimum viable populations for endangered species, they have realized that most national parks and other reserves are far too small. The area needed for the long-term survival of the Yellowstone grizzly bear population is more than ten times the combined area of Yellowstone and Grand Teton National Parks **(Figure 56.20)**. Given political and economic realities, many existing parks will not be enlarged, and most newly created reserves will also be too small. Areas of private and public land surrounding reserves will likely have to contribute to biodiversity conservation. On the other side of the argument, smaller, unconnected reserves may slow the spread of disease between populations.



▲ **Figure 56.20 Biotic boundaries for grizzly bears in Yellowstone and Grand Teton National Parks.** The biotic boundaries (solid and dashed red lines) surround the areas needed to support minimum viable populations of 50 and 500 bears. Even the smaller of these areas is larger than the two parks.

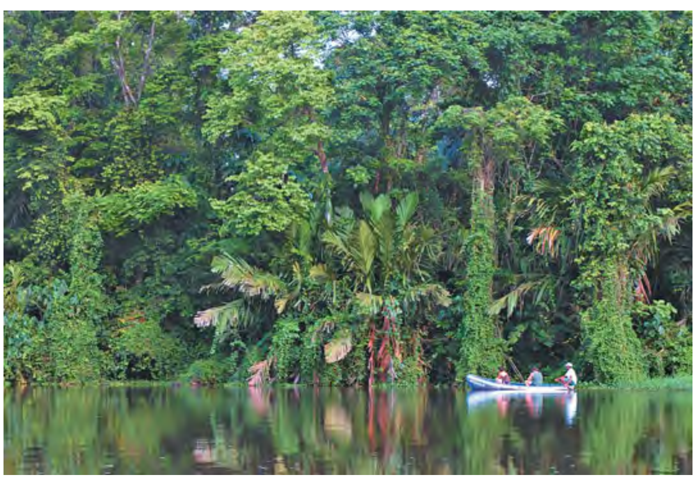
In practical terms, land use by humans may outweigh all other considerations and ultimately dictate the size and shape of protected areas. Much of the land left for conservation efforts is useless for exploitation by agriculture or forestry. But in some cases, as when reserve land is surrounded by commercially valuable property, the use of land for agriculture or forestry must be integrated into conservation strategies.

Zoned Reserves

Several nations have adopted a zoned reserve approach to landscape management. A **zoned reserve** is an extensive region that includes areas relatively undisturbed by humans surrounded by areas that have been changed by human activity and are used for economic gain. The key challenge of the zoned reserve approach is to develop a social and economic climate in the surrounding lands that is compatible with the long-term viability of the protected core. These surrounding areas continue to support human activities, but regulations prevent the types of extensive alterations likely to harm the protected area. As a result, the surrounding habitats serve as buffer zones against further intrusion into the undisturbed area.

The small Central American nation of Costa Rica has become a world leader in establishing zoned reserves **(Figure 56.21)**. An agreement initiated in 1987 reduced Costa Rica's international debt in return for land preservation there. The agreement resulted in eight zoned reserves, called "conservation areas," that contain designated national park land. Costa Rica is making progress toward managing its zoned reserves, and the buffer

(a) Boundaries of the zoned reserves are indicated by black outlines.



(b) Tourists marvel at the diversity of life in one of Costa Rica's zoned reserves.

▲ **Figure 56.21 Zoned reserves in Costa Rica.**

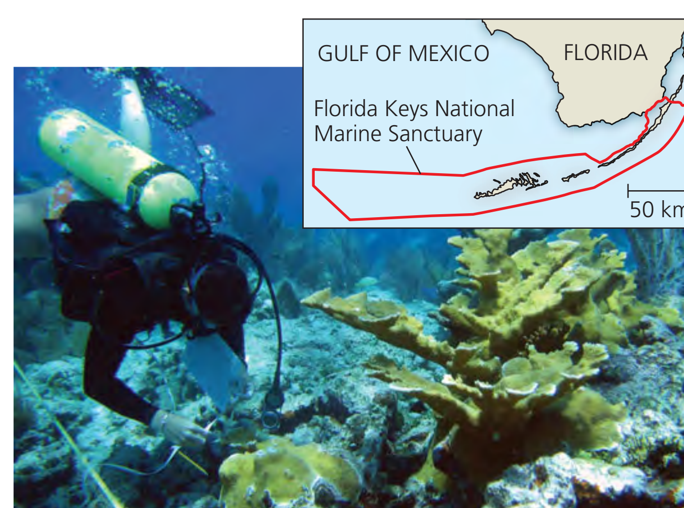
zones provide a steady, lasting supply of forest products, water, and hydroelectric power while also supporting sustainable agriculture and tourism.

An important goal of zoned reserves is to provide a stable economic base for people living there. As University of Pennsylvania ecologist Daniel Janzen, a leader in tropical conservation, has said, "The likelihood of long-term survival of a conserved wildland area is directly proportional to the economic health and stability of the society in which that wildland is embedded." Destructive practices that are not compatible with long-term ecosystem conservation and from which there is often little local profit, such as massive logging, large-scale single-crop agriculture, and extensive mining, are ideally confined to the outermost fringes of the buffer zones in Costa Rica and are gradually being discouraged.

Costa Rica relies on its zoned reserve system to maintain at least 80% of its native species, but the system is not without problems. A 2003 analysis of land cover change between 1960 and 1997 showed negligible deforestation within Costa Rica's national parks and a gain in forest cover in the 1-km buffer around the parks. However, significant losses in forest cover were discovered in the 10-km buffer zones around all national parks, threatening to turn the parks into isolated habitat islands.

Although marine ecosystems have also been heavily affected by human exploitation, reserves in the ocean are far less common than reserves on land. Many fish populations around the world have collapsed as increasingly sophisticated equipment puts nearly all potential fishing grounds within human reach. In response, scientists at the University of York, England, have proposed establishing marine reserves around the world that would be off limits to fishing. They present strong evidence that a patchwork of marine reserves can serve as a means of both increasing fish populations within the reserves and improving fishing success in nearby areas. Their proposed system is a modern application of a centuries-old practice in the Fiji Islands in which some areas have historically remained closed to fishing—a traditional example of the zoned reserve concept.

The United States adopted such a system in creating a set of 13 national marine sanctuaries, including the Florida Keys National Marine Sanctuary, which was established in 1990 **(Figure 56.22)**. Populations of marine organisms, including fishes and lobsters, recovered quickly after harvests were banned in the 9,500-km^2 reserve. Larger and more abundant fish now produce larvae that help repopulate reefs and improve fishing outside the sanctuary. The increased marine life within the sanctuary also makes it a favorite for recreational divers, increasing the economic value of this zoned reserve.



▲ **Figure 56.22 A diver measuring coral in the Florida Keys National Marine Sanctuary.**

CONCEPT CHECK 56.3

1. What is a biodiversity hot spot?
2. How do zoned reserves provide economic incentives for long-term conservation of protected areas?
3. **WHAT IF?** Suppose a developer proposes to clear-cut a forest that serves as a corridor between two parks. To compensate, the developer also proposes to add the same area of forest to one of the parks. As a professional ecologist, how might you argue for retaining the corridor?

For suggested answers, see Appendix A.

CONCEPT 56.4

Earth is changing rapidly as a result of human actions

As we've discussed, landscape and regional conservation help protect habitats and preserve species. However, environmental changes that result from human activities are creating new challenges. As a consequence of human-caused climate change, for example, the place where a vulnerable species is found today may not be the same as the one needed for preservation in the future. What would happen if *many* habitats on Earth changed so quickly that the locations of preserves today were unsuitable for their species in 10, 50, or 100 years? Such a scenario is increasingly possible.

The rest of this section describes four types of environmental change that humans are bringing about: nutrient enrichment, toxin accumulation, climate change, and ozone depletion. The impacts of these and other changes are evident not just in human-dominated ecosystems, such as cities and farms, but also in the most remote ecosystems on Earth.

Nutrient Enrichment

Human activity often removes nutrients from one part of the biosphere and adds them to another. On the simplest level, someone eating a piece of broccoli in Washington, DC, consumes nutrients that only days before were in the soil in California; a short time later, some of these nutrients will be in the Potomac River, having passed through the person's digestive system and a local sewage treatment facility. On a larger scale, nutrients in farm soil may run off into streams and lakes, depleting nutrients in one area, increasing them in another, and altering chemical cycles in both. Furthermore, humans have added entirely novel materials—some of them toxic—to ecosystems.

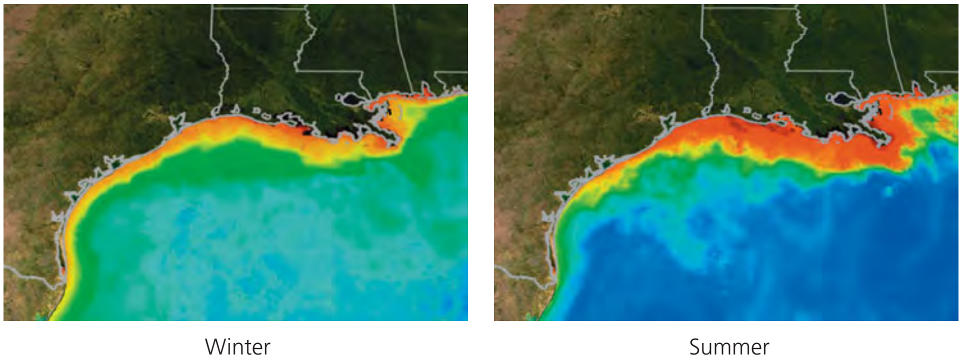
Farming is an example of how, even with the best of intentions, human activities are altering the environment through the enrichment of nutrients, particularly ones containing nitrogen. After natural vegetation is cleared from an area, the existing reserve of nutrients in the soil is sufficient to grow crops for some time. In agricultural ecosystems, however, a substantial fraction of these nutrients is exported from the area in crop biomass. The "free" period for crop production—when there is no need to add nutrients to the soil—varies greatly. When some of the early North American prairie lands were first tilled, good crops could be produced for decades because the large store of organic materials in the soil continued to decompose and provide nutrients. By contrast, some cleared land in the tropics can be farmed for only one or two years because so little of the ecosystems' nutrient load is contained in the soil. Despite such variations, in any area under intensive agriculture, the natural store of nutrients eventually becomes exhausted.

Nitrogen is the main nutrient element lost through agriculture (see Figure 55.14). Plowing mixes the soil and speeds up decomposition of organic matter, releasing nitrogen that is then removed when crops are harvested. Applied fertilizers make up for the loss of usable nitrogen from agricultural ecosystems **(Figure 56.23)**. In addition, as we saw in the case of Hubbard Brook (see Figure 55.16), without plants to take up nitrates from the soil, the nitrates are likely to be leached from the ecosystem.

Recent studies indicate that human activities have more than doubled Earth's supply of fixed nitrogen available to primary producers. Industrial fertilizers provide the largest additional nitrogen source. Fossil fuel combustion also releases nitrogen oxides, which enter the atmosphere and dissolve in rainwater; the nitrogen ultimately enters ecosystems as nitrate. Increased cultivation of legumes, with their nitrogen-fixing symbionts, is a third way in which humans increase the amount of fixed nitrogen in the soil.

A problem arises when the nutrient level in an ecosystem exceeds the **critical load**, the amount of added nutrient, usually nitrogen or phosphorus, that can be absorbed by plants without damaging ecosystem integrity. For example, nitrogenous minerals in the soil that exceed the critical load

▲ **Figure 56.23 Fertilization of a corn (maize) crop.** To replace the nutrients removed in crops, farmers must apply fertilizers—either organic, such as manure or mulch, or synthetic, as shown here.



▲ **Figure 56.24 A phytoplankton bloom arising from nitrogen pollution in the Mississippi basin that leads to a dead zone.** In these satellite images from 2004, red and orange represent high concentrations of phytoplankton in the Gulf of Mexico. This dead zone extends much farther from land in summer than in winter.

eventually leach into groundwater or run off into freshwater and marine ecosystems, contaminating water supplies and killing fish. Nitrate concentrations in groundwater are increasing in most agricultural regions, sometimes reaching levels that are unsafe for drinking.

Many rivers contaminated with nitrates and ammonium from agricultural runoff and sewage drain into the Atlantic Ocean, with the highest inputs coming from northern Europe and the central United States. The Mississippi River carries nitrogen pollution to the Gulf of Mexico, fueling a phytoplankton bloom each summer. When the phytoplankton die, their decomposition by oxygen-using organisms creates an extensive "dead zone" of low oxygen levels along the coast **(Figure 56.24)**. Fish and other marine animals disappear from some of the most economically important waters in the United States. To reduce the size of the dead zone, farmers have begun using fertilizers more efficiently, and managers are restoring wetlands in the Mississippi watershed, two changes stimulated by the results of ecosystem experiments.

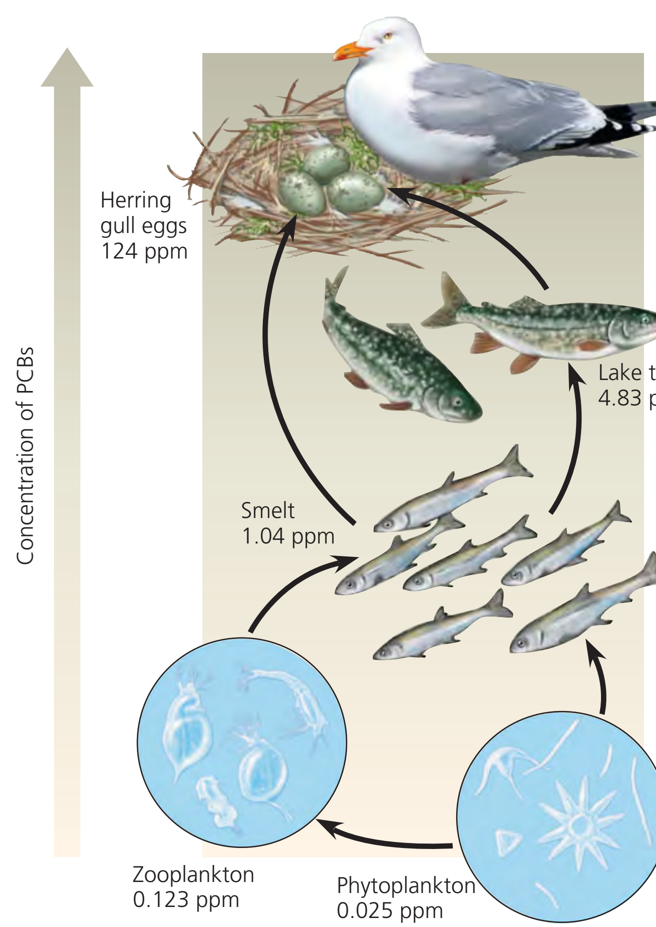
Nutrient runoff can also lead to the eutrophication of lakes, as you learned in Concept 55.2. The bloom and subsequent die-off of algae and cyanobacteria and the ensuing depletion of oxygen are similar to what occurs in a marine dead zone. Such conditions threaten the survival of organisms. For example, eutrophication of Lake Erie coupled with overfishing wiped out commercially important fishes such as blue pike, whitefish, and lake trout by the 1960s. Since then, tighter regulations on waste dumping into the lake have enabled some fish populations to rebound, but many native species of fish and invertebrates have not recovered.

Toxins in the Environment

Humans release an immense variety of toxic chemicals, including thousands of synthetic compounds previously unknown in nature, with little regard for the ecological consequences. Organisms acquire toxic substances from the environment along with nutrients and water. Some of the poisons are metabolized or excreted, but others accumulate in specific tissues, often fat.

One of the reasons accumulated toxins are particularly harmful is that they become more concentrated in successive trophic levels of a food web. This phenomenon, called **biological magnification**, occurs because the biomass at any given trophic level is produced from a much larger biomass ingested from the level below (see Concept 55.3). Thus, top-level carnivores tend to be most severely affected by toxic compounds in the environment.

One class of industrially synthesized compounds that have demonstrated biological magnification are the chlorinated hydrocarbons, which include the industrial chemicals called PCBs (polychlorinated biphenyls) and many pesticides, such as DDT. Current research implicates many of these compounds in endocrine system disruption in a large number of animal species, including humans (see pp. 992–993). Biological magnification of PCBs has been found in the food web of the Great Lakes, where the concentration of PCBs in herring gull eggs, at the top of the food web, is nearly 5,000 times that in phytoplankton, at the base of the food web **(Figure 56.25)**.



▲ **Figure 56.25 Biological magnification of PCBs in a Great Lakes food web.**

An infamous case of biological magnification that harmed top-level carnivores involved DDT, a chemical used to control insects such as mosquitoes and agricultural pests. In the decade after World War II, the use of DDT grew rapidly; its ecological consequences were not yet fully understood. By the 1950s, scientists were learning that DDT persists in the environment and is transported by water to areas far from where it is applied. One of the first signs that DDT was a serious environmental problem was a decline in the populations of pelicans, ospreys, and eagles, birds that feed at the top of food webs. The accumulation of DDT (and DDE, a product of its breakdown) in the tissues of these birds interfered with the deposition of calcium in their eggshells. When the birds tried to incubate their eggs, the weight of the parents broke the shells of affected eggs, resulting in catastrophic declines in the birds' reproduction rates. Rachel Carson's book *Silent Spring* helped bring the problem to public attention in the 1960s **(Figure 56.26)**, and DDT was banned in the United States in 1971. A dramatic recovery in populations of the affected bird species followed.

In much of the tropics, DDT is still used to control the mosquitoes that spread malaria and other diseases. Societies there face a trade-off between saving human lives and protecting other species. The best approach seems to be to apply DDT sparingly and to couple its use with mosquito netting and other low-technology solutions. The complicated history of DDT illustrates the importance of understanding the ecological connections between diseases and communities (see Concept 54.5).

Many toxins cannot be degraded by microorganisms and persist in the environment for years or even decades. In other cases, chemicals released into the environment may be relatively harmless but are converted to more toxic products by reaction with other substances, by exposure to light, or by the metabolism of microorganisms. Mercury, a by-product of plastic production and coal-fired power generation, has been routinely expelled into rivers and the sea in an insoluble form. Bacteria in the bottom mud convert the waste to methylmercury (CH_3Hg^+), an extremely toxic water-soluble compound that accumulates in the tissues of organisms, including humans, who consume fish from the contaminated waters.

▶ Figure 56.26 Rachel Carson. Through her writing and her testimony before the U.S. Congress, biologist and author Carson helped promote a new environmental ethic. Her efforts led to a ban on DDT use in the United States and stronger controls on the use of other chemicals.

Greenhouse Gases and Global Warming

Human activities release a variety of gaseous waste products. People once thought that the vast atmosphere could absorb these materials indefinitely, but we now know that such additions can cause fundamental changes to the atmosphere and to its interactions with the rest of the biosphere. In this section, we will examine how increasing atmospheric carbon dioxide concentration and global warming affect species and ecosystems.

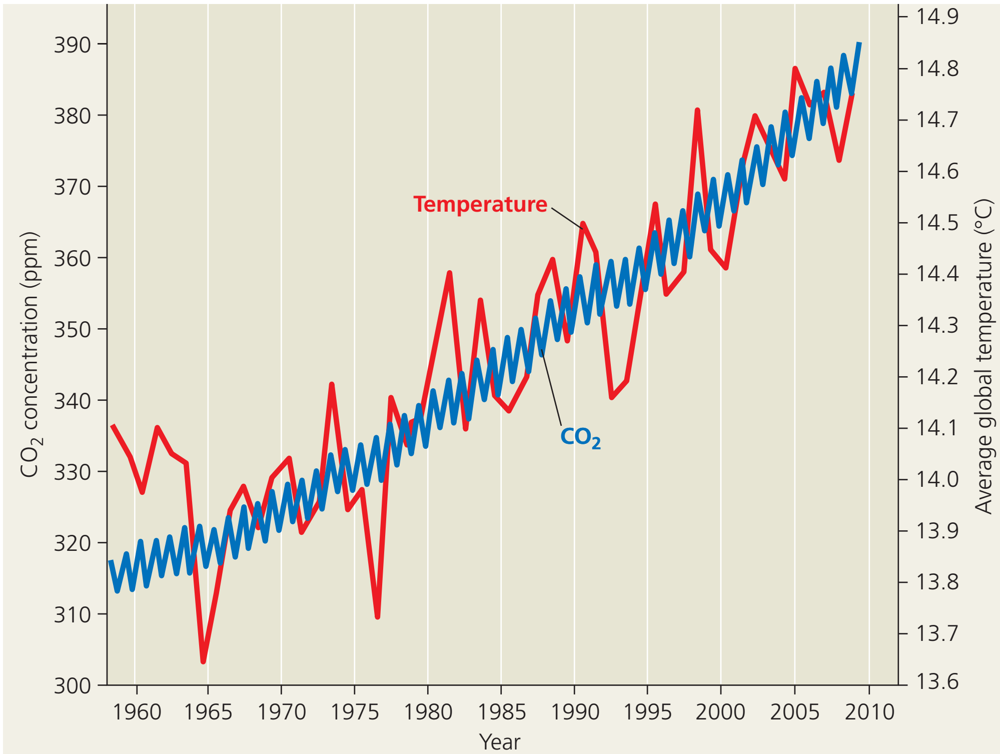
Rising Atmospheric CO_2 Levels

Since the Industrial Revolution, the concentration of CO_2 in the atmosphere has been increasing as a result of the burning of fossil fuels and deforestation. Scientists estimate that the average CO_2 concentration in the atmosphere before 1850 was about 274 ppm. In 1958, a monitoring station began taking very accurate measurements on Hawaii's Mauna Loa peak, a location far from cities and high enough for the atmosphere to be well mixed. At that time, the CO_2 concentration was 316 ppm **(Figure 56.27)**. Today, it exceeds 385 ppm, an increase of more than 40% since the mid-19th century. If CO_2 emissions continue to increase at the present rate, by the year 2075 the atmospheric concentration of this gas will be more than double what it was in 1850.

Increased productivity by plants is one predictable consequence of increasing CO_2 levels. In fact, when CO_2 concentrations are raised in experimental chambers such as greenhouses, most plants grow faster. Because C_3 plants are more limited than C_4 plants by CO_2 availability (see Concept 10.4), one effect of increasing global CO_2 concentration may be the spread of C_3 species into terrestrial habitats that currently favor C_4 plants. Such changes could influence whether corn (maize), a C_4 plant and the most important grain crop in the United States, will be replaced by wheat and soybeans, C_3 crops that could outproduce corn in a CO_2-enriched environment. To predict the gradual and complex effects of rising CO_2 levels on productivity and species composition, scientists are turning to long-term field experiments.

How Elevated CO_2 Levels Affect Forest Ecology: The FACTS-I Experiment

To assess how the increasing atmospheric concentration of CO_2 might affect temperate forests, scientists at Duke University began the Forest-Atmosphere Carbon Transfer and Storage (FACTS-I) experiment in 1995. The researchers are manipulating the concentration of CO_2 to which trees are exposed. The FACTS-I experiment includes six plots in an 80-hectare (200-acre) tract of loblolly pine within the university's experimental forest. Each plot consists of a circular area, approximately 30 m in diameter, ringed by 16 towers



◄ **Figure 56.27 Increase in atmospheric carbon dioxide concentration at Mauna Loa, Hawaii, and average global temperatures.** Aside from normal seasonal fluctuations, the CO_2 concentration (blue curve) has increased steadily from 1958 to 2009. Though average global temperatures (red curve) fluctuated a great deal over the same period, there is a clear warming trend.

(Figure 56.28). In three of the six plots, the towers produce air containing about 1½ times present-day CO_2 concentrations. Instruments on a tall tower in the center of each plot measure the direction and speed of the wind, adjusting the distribution of CO_2 to maintain a stable CO_2 concentration. All other factors, such as temperature, precipitation, and wind speed and direction, vary normally for both experimental plots and adjacent control plots exposed to atmospheric CO_2.

The FACTS-I study is testing how elevated CO_2 levels influence tree growth, carbon concentration in soils, insect populations, soil moisture, the growth of plants in the forest understory, and other factors. After 12 years, trees in the experimental plots produced about 15% more wood each year than those in the control plots. This increased growth is important for timber production and carbon storage but is far lower than predicted from the results of greenhouse experiments. The availability of nitrogen and other nutrients apparently limits the ability of the trees to use the extra CO_2. Researchers at FACTS-I began removing this limitation in 2005 by fertilizing half of each plot with ammonium nitrate.

In most of the world's ecosystems, nutrients limit ecosystem productivity and fertilizers are unavailable. The results of FACTS-I and other experiments suggest that increased atmospheric CO_2 levels will increase plant production somewhat, but far less than scientists predicted even a decade ago.

▲ **Figure 56.28 Large-scale experiment on the effects of elevated CO_2 concentration.** Rings of towers in the Duke University Experimental Forest emit enough carbon dioxide to raise and maintain CO_2 levels 200 ppm above present-day concentrations in half of the experimental plots.

The Greenhouse Effect and Climate

Rising concentrations of long-lived greenhouse gases such as CO_2 are also changing Earth's heat budget. Much of the solar radiation that strikes the planet is reflected back into space. Although CO_2, water vapor, and other greenhouse gases in the atmosphere are transparent to visible light, they intercept and absorb much of the infrared radiation Earth emits, re-reflecting some of it back toward Earth. This process retains some of the solar heat. If it were not for this **greenhouse effect**, the average air temperature at Earth's surface would be a frigid −18°C (−0.4°F), and most life as we know it could not exist.

The marked increase in the concentration of atmospheric CO_2 over the last 150 years concerns scientists because of its link to increased global temperature. For more than a century, scientists have studied how greenhouse gases warm Earth and how fossil fuel burning could contribute to the warming. Most scientists are convinced that such warming is already occurring and will increase rapidly this century (see Figure 56.27).

Global models predict that by the end of the 21st century, the atmospheric CO_2 concentration will more than double, increasing average global temperature by about 3°C (5°F). Supporting these models is a correlation between CO_2 levels and temperatures in prehistoric times. One way climatologists estimate past CO_2 concentrations is to measure CO_2 levels in bubbles trapped in glacial ice, some of which are 700,000 years old. Prehistoric temperatures are inferred by several methods, including analysis of past vegetation based on fossils and the chemical isotopes in sediments and corals. An increase of only 1.3°C would make the world warmer than at any time in the past 100,000 years. A warming trend would also alter the geographic distribution of precipitation, likely making agricultural areas of the central United States much drier, for example.

The ecosystems where the largest warming has *already* occurred are those in the far north, particularly northern coniferous forests and tundra. As snow and ice melt and uncover darker, more absorptive surfaces, these systems reflect less radiation back to the atmosphere and warm further. Arctic sea ice in the summer of 2007 covered the smallest area on record. Climate models suggest that there may be no summer ice there within a few decades, decreasing habitat for polar bears, seals, and seabirds. Higher temperatures also increase the likelihood of fires. In boreal forests of western North America and Russia, fires have burned twice the usual area in recent decades.

By studying how past periods of global warming and cooling affected plant communities, ecologists are trying to predict the consequences of future changes in temperature and precipitation. Analysis of fossilized pollen indicates that plant communities change dramatically with changes in temperature. Past climate changes occurred gradually, though, and most plant and animal populations had time to migrate into areas where abiotic conditions allowed them to survive.

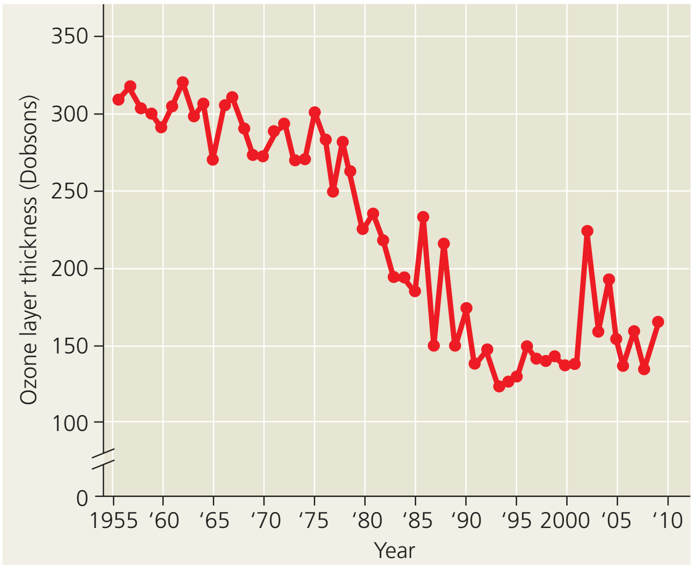
Many organisms, especially plants that cannot disperse rapidly over long distances, may not be able to survive the rapid climate change projected to result from global warming. Furthermore, many habitats today are more fragmented than ever (see Concept 56.3), further limiting the ability of many organisms to migrate. For these reasons, ecologists are debating **assisted migration**, the translocation of a species to a favorable habitat beyond its native range to protect the species from human-caused threats. Most ecologists consider such an approach only as a last resort, in part because of the dangers of introducing potentially invasive species to new regions. Although scientists have yet to perform assisted migration, activists in 2008 transplanted seedlings of the endangered tree *Torreya taxifolia* hundreds of kilometers north from its native range in Florida to western North Carolina in anticipation of climate change. This "rewilding," as it is sometimes called, appeared to be driven in part by a desire for publicity; no ecological framework yet exists for deciding if, when, and where assisted migration is desirable.

We will need many approaches to slow global warming. Quick progress can be made by using energy more efficiently and by replacing fossil fuels with renewable solar and wind power and, more controversially, with nuclear power. Today, coal, gasoline, wood, and other organic fuels remain central to industrialized societies and cannot be burned without releasing CO_2. Stabilizing CO_2 emissions will require concerted international effort and changes in both personal lifestyles and industrial processes. Many ecologists think that effort suffered a major setback in 2001, when the United States pulled out of the Kyoto Protocol, a 1997 pledge by industrialized nations to reduce their CO_2 output by about 5%. Such a reduction would be a first step in the journey to stabilize atmospheric CO_2 concentrations. Recent international negotiations, including a 2009 meeting in Copenhagen, Denmark, have yet to reach a global consensus on how to reduce greenhouse gas emissions.

Another important approach to slowing global warming is to reduce deforestation around the world, particularly in the tropics. Deforestation currently accounts for about 12% of greenhouse gas emissions. Recent research shows that paying countries *not* to cut forests could decrease the rate of deforestation by half within 10 to 20 years. Reduced deforestation would not only slow the buildup of greenhouse gases in our atmosphere, but would sustain native forests and preserve biodiversity, a positive outcome for all.

Depletion of Atmospheric Ozone

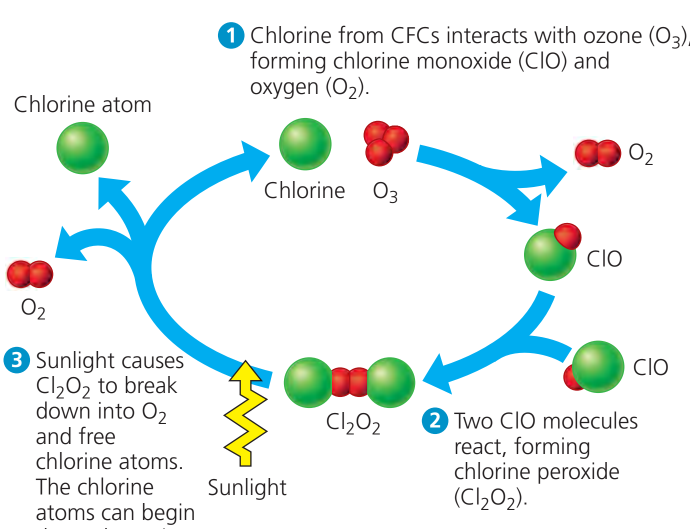
Like carbon dioxide and other greenhouse gases, atmospheric ozone (O_3) has also changed in concentration because of human activities. Life on Earth is protected from the damaging effects of ultraviolet (UV) radiation by a layer of ozone located in the stratosphere 17–25 km above Earth's surface. However, satellite studies of the atmosphere show that the springtime ozone layer over Antarctica has thinned substantially since the mid-1970s **(Figure 56.29)**. As Susan Solomon discussed in the interview opening Unit 1, the destruction of atmospheric ozone results primarily from the



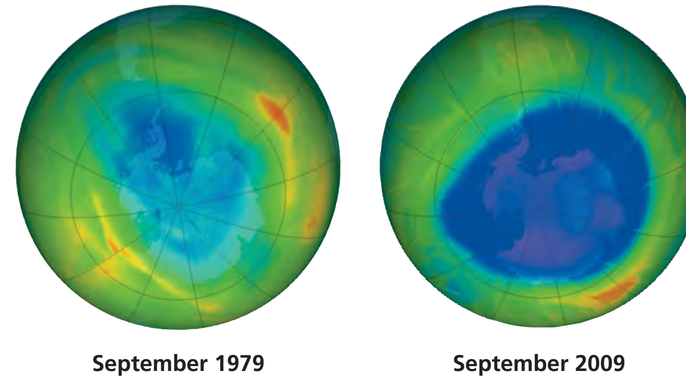
▲ **Figure 56.29 Thickness of the October ozone layer over Antarctica in units called Dobsons.**

accumulation of chlorofluorocarbons (CFCs), chemicals once widely used in refrigeration and manufacturing. In the stratosphere, chlorine atoms released from CFCs react with ozone, reducing it to molecular O_2 **(Figure 56.30)**. Subsequent chemical reactions liberate the chlorine, allowing it to react with other ozone molecules in a catalytic chain reaction.

The thinning of the ozone layer is most apparent over Antarctica in spring, where cold, stable air allows the chain reaction to continue. The magnitude of ozone depletion and the size of the ozone hole have generally increased in recent years, and the hole sometimes extends as far as the southernmost portions of Australia, New Zealand, and South America **(Figure 56.31)**. At the more heavily populated



▲ **Figure 56.30 How free chlorine in the atmosphere destroys ozone.**



▲ **Figure 56.31 Erosion of Earth's ozone shield.** The ozone hole over Antarctica is visible as the dark blue patch in these images based on atmospheric data.

middle latitudes, ozone levels have decreased 2–10% during the past 20 years.

Decreased ozone levels in the stratosphere increase the intensity of UV rays reaching Earth's surface. The consequences of ozone depletion for life on Earth may be severe for plants, animals, and microorganisms. Some scientists expect increases in both lethal and nonlethal forms of skin cancer and in cataracts among humans, as well as unpredictable effects on crops and natural communities, especially the phytoplankton that are responsible for a large proportion of Earth's primary production.

To study the consequences of ozone depletion, ecologists have conducted field experiments in which they use filters to decrease or block the UV radiation in sunlight. One such experiment, performed on a scrub ecosystem near the tip of South America, showed that when the ozone hole passed over the area, the amount of UV radiation reaching the ground increased sharply, causing more DNA damage in plants that were not protected by filters. Scientists have shown similar DNA damage and a reduction in phytoplankton growth when the ozone hole opens over the Southern Ocean each year.

The good news about the ozone hole is how quickly many countries have responded to it. Since 1987, more than 190 nations, including the United States, have signed the Montreal Protocol, a treaty that regulates the use of ozone-depleting chemicals. Most nations, again including the United States, have ended the production of CFCs. As a consequence of these actions, chlorine concentrations in the stratosphere have stabilized and ozone depletion is slowing. Even though CFC emissions are close to zero today, however, chlorine molecules already in the atmosphere will continue to influence stratospheric ozone levels for at least 50 years.

The partial destruction of Earth's ozone shield is one more example of how much humans have been able to disrupt the dynamics of ecosystems and the biosphere. It also highlights our ability to solve environmental problems when we set our minds to it.

CONCEPT CHECK 56.4

1. How can the addition of excess mineral nutrients to a lake threaten its fish population?
2. **MAKE CONNECTIONS** There are vast stores of organic matter in the soils of northern coniferous forests and tundra around the world. Based on what you learned about decomposition from Figure 55.15 (p. 1230), suggest an explanation for why scientists who study global warming are closely monitoring these stores.
3. **MAKE CONNECTIONS** Concept 17.5 (p. 346) describes the action of mutagens, chemical and physical agents that induce mutations in DNA. How does reduced ozone concentration in the atmosphere increase the likelihood of mutations in various organisms?

For suggested answers, see Appendix A.

CONCEPT 56.5

Sustainable development can improve human lives while conserving biodiversity

With the increasing loss and fragmentation of habitats and changes in Earth's climate and physical environment, we face difficult trade-offs in managing the world's resources. Preserving all habitat patches isn't feasible, so biologists must help societies set conservation priorities by identifying which habitat patches are most crucial. Ideally, implementing these priorities should also improve the quality of life for local people. Ecologists use the concept of *sustainability* as a tool to establish long-term conservation priorities.

Sustainable Biosphere Initiative

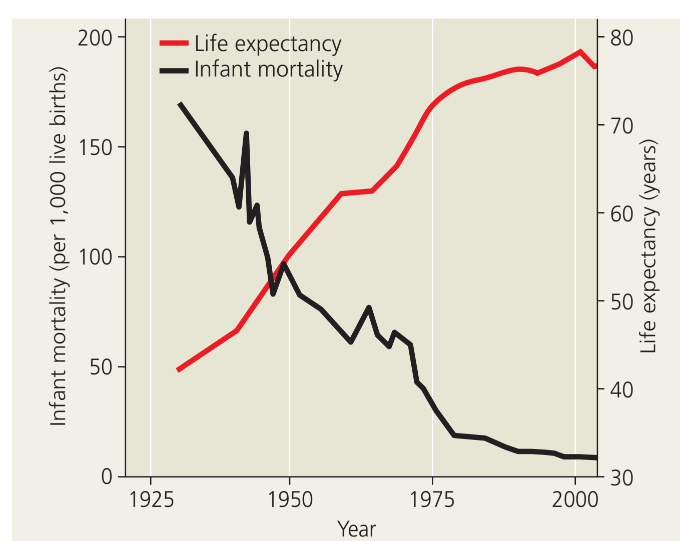
We need to understand the interconnections of the biosphere if we are to protect species from extinction and improve the quality of human life. To this end, many nations, scientific societies, and other groups have embraced the concept of **sustainable development**, economic development that meets the needs of people today without limiting the ability of future generations to meet their needs. The forward-looking Ecological Society of America, the world's largest organization of professional ecologists, endorses a research agenda called the Sustainable Biosphere Initiative. The goal of this initiative is to define and acquire the basic ecological information needed to develop, manage, and conserve Earth's resources as responsibly as possible. The research agenda includes studies of global change, including interactions between climate and ecological processes; biological diversity and its role in maintaining ecological processes; and the ways in which the productivity of natural and artificial ecosystems can be sustained. This initiative requires a strong commitment of human and economic resources.

Achieving sustainable development is an ambitious goal. To sustain ecosystem processes and stem the loss of biodiversity, we must connect life science with the social sciences, economics, and the humanities. We must also reassess our personal values. Those of us living in wealthier nations have a larger ecological footprint than do people living in developing nations (see Chapter 53). By reducing our orientation toward short-term gain, we can learn to value the natural processes that sustain us. The following case study illustrates how the combination of scientific and personal efforts can make a significant difference in creating a truly sustainable world.

Case Study: *Sustainable Development in Costa Rica*

The success of conservation in Costa Rica that we discussed in Concept 56.3 has required a partnership between the national government, nongovernment organizations (NGOs), and private citizens. Many nature reserves established by individuals have been recognized by the government as national wildlife reserves and given significant tax benefits. However, conservation and restoration of biodiversity make up only one facet of sustainable development; the other key facet is improving the human condition.

How have the living conditions of the Costa Rican people changed as the country has pursued its conservation goals? As we discussed in Chapter 53, two of the most fundamental indicators of living conditions are infant mortality rate and life expectancy. From 1930 to 2009, the infant mortality rate in Costa Rica declined from 170 to 9 per 1,000 live births; over the same period, life expectancy increased from about 43 years to 78 years **(Figure 56.32)**. Another indicator of living conditions is the literacy rate. The 2004 literacy rate in Costa Rica was 96%, compared to 97% in the United States. Such statistics show that living conditions in Costa Rica have



▲ **Figure 56.32 Infant mortality and life expectancy at birth in Costa Rica.**

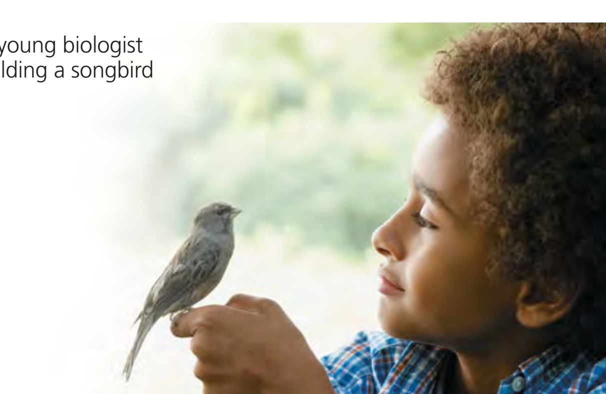
improved greatly over the period in which the country has dedicated itself to conservation and restoration. While this result does not prove that conservation *causes* an improvement in human welfare, we can say with certainty that development in Costa Rica has attended to both nature *and* people.

Despite the successes in Costa Rica, many problems remain. One of the challenges that Costa Rica faces is maintaining its commitment to conservation while its population grows. Costa Rica is in the middle of a rapid demographic transition (see Chapter 53), and even though birth rates are dropping rapidly, its population is growing at about 1.5% annually. The population, which is currently about 4 million, is predicted to continue to grow until the middle of this century, when it is projected to level off at approximately 6 million. If recent success is any guide, the people of Costa Rica will overcome the challenge of population growth in their quest for sustainable development.


(a) Detail of animals in a 36,000-year-old cave painting, Lascaux, France


(b) A 30,000-year-old ivory carving of a water bird, found in Germany

(c) Nature lovers on a wildlife-watching expedition


(d) A young biologist holding a songbird

▲ **Figure 56.33 Biophilia, past and present.**

The Future of the Biosphere

Our modern lives are very different from those of early humans, who hunted and gathered to survive. Their reverence for the natural world is evident in the early murals of wildlife they painted on cave walls **(Figure 56.33a)** and in the stylized visions of life they sculpted from bone and ivory **(Figure 56.33b)**.

Our lives reflect remnants of our ancestral attachment to nature and the diversity of life—the concept of *biophilia* that was introduced early in this chapter. We evolved in natural environments rich in biodiversity, and we still have an affinity for such settings **(Figure 56.33c, d)**. E. O. Wilson makes the case that our biophilia is innate, an evolutionary product of natural selection acting on a brainy species whose survival depended on a close connection to the environment and a practical appreciation of plants and animals.

Our appreciation of life guides the field of biology today. We celebrate life by deciphering the genetic code that makes each species unique. We embrace life by using fossils and DNA to chronicle evolution through time. We preserve life through our efforts to classify and protect the millions of species on Earth. We respect life by using nature responsibly and reverently to improve human welfare.

Biology is the scientific expression of our desire to know nature. We are most likely to protect what we appreciate, and we are most likely to appreciate what we understand. By learning about the processes and diversity of life, we also become more aware of ourselves and our place in the biosphere. We hope this book has served you well in this lifelong adventure.

CONCEPT CHECK 56.5

1. What is meant by the term *sustainable development*?
2. How might biophilia influence us to conserve species and restore ecosystems?
3. **WHAT IF?** Suppose a new fishery is discovered, and you are put in charge of developing it sustainably. What ecological data might you want on the fish population? What criteria would you apply for the fishery's development?

For suggested answers, see Appendix A.

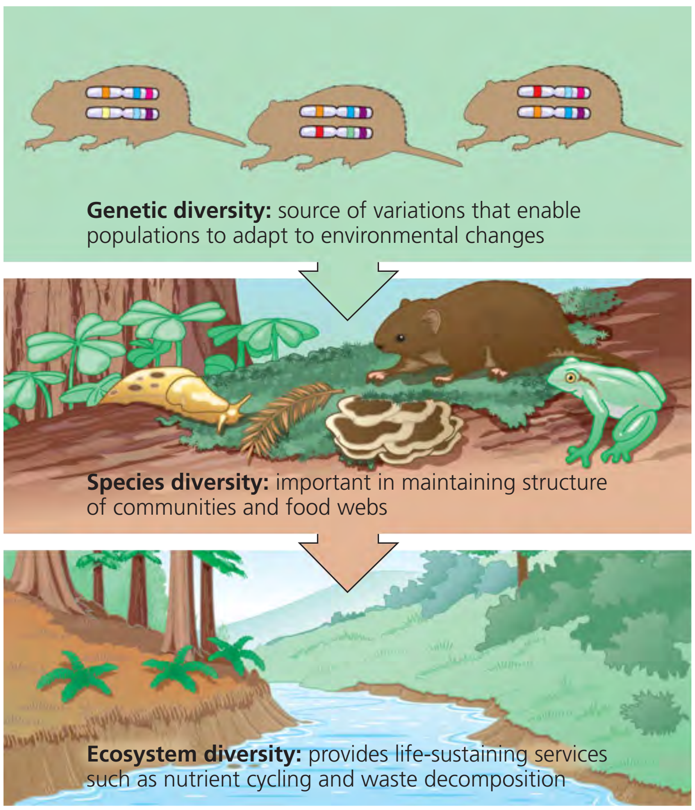
56 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

CONCEPT 56.1

Human activities threaten Earth's biodiversity (pp. 1239–1244)

- Biodiversity can be considered at three main levels:



- Our biophilia enables us to recognize the value of biodiversity for its own sake. Other species also provide humans with food, fiber, medicines, and **ecosystem services**.
- Four major threats to biodiversity are habitat loss, **introduced species**, overharvesting, and global change.

? *Give at least three examples of key ecosystem services that nature provides for people.*

CONCEPT 56.2

Population conservation focuses on population size, genetic diversity, and critical habitat (pp. 1244–1249)

- When a population drops below a **minimum viable population (MVP)** size, its loss of genetic variation due to nonrandom mating and genetic drift can trap it in an **extinction vortex**.
- The declining-population approach focuses on the environmental factors that cause decline, regardless of absolute population size. It follows a step-by-step conservation strategy.
- Conserving species often requires resolving conflicts between the habitat needs of **endangered species** and human demands.

? *Why is the minimum viable population size smaller for a population that is more genetically diverse than it is for a less genetically diverse population?*

CONCEPT 56.3

Landscape and regional conservation help sustain biodiversity (pp. 1249–1254)

- The structure of a landscape can strongly influence biodiversity. As habitat fragmentation increases and edges become more extensive, biodiversity tends to decrease. **Movement corridors** can promote dispersal and help sustain populations.
- **Biodiversity hot spots** are also hot spots of extinction and thus prime candidates for protection. Sustaining biodiversity in parks and reserves requires management to ensure that human activities in the surrounding landscape do not harm the protected habitats. The **zoned reserve** model recognizes that conservation efforts often involve working in landscapes that are greatly affected by human activity.

? *Give two examples that show how habitat fragmentation can harm species in the long term.*

CONCEPT 56.4

Earth is changing rapidly as a result of human actions (pp. 1254–1260)

- Agriculture removes plant nutrients from ecosystems, so large supplements are usually required. The nutrients in fertilizer can pollute groundwater and surface-water aquatic ecosystems, where they can stimulate excess algal growth (eutrophication).
- The release of toxic wastes has polluted the environment with harmful substances that often persist for long periods and become increasingly concentrated in successively higher trophic levels of food webs (**biological magnification**).
- Because of the burning of wood and fossil fuels and other human activities, the atmospheric concentration of CO_2 and other greenhouse gases has been steadily increasing. The ultimate effects include significant global warming and other changes in climate.
- The ozone layer reduces the penetration of UV radiation through the atmosphere. Human activities, notably the release of chlorine-containing pollutants, have eroded the ozone layer, but government policies are helping to solve the problem.

? *In the face of biological magnification of toxins, is it healthier to feed at a lower or higher trophic level? Explain.*

CONCEPT 56.5

Sustainable development can improve human lives while conserving biodiversity (pp. 1260–1261)

- The goal of the Sustainable Biosphere Initiative is to acquire the ecological information needed for the development, management, and conservation of Earth's resources.
- Costa Rica's success in conserving tropical biodiversity has involved a partnership among the government, other organizations, and private citizens. Human living conditions in Costa Rica have improved along with ecological conservation.
- By learning about biological processes and the diversity of life, we become more aware of our close connection to the environment and the value of other organisms that share it.

? *Why is sustainability such an important goal for conservation biologists?*

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

1. One characteristic that distinguishes a population in an extinction vortex from most other populations is that
   a. its habitat is fragmented.
   b. it is a rare, top-level predator.
   c. its effective population size is much lower than its total population size.
   d. its genetic diversity is very low.
   e. it is not well adapted to edge conditions.

2. The main cause of the increase in the amount of CO_2 in Earth's atmosphere over the past 150 years is
   a. increased worldwide primary production.
   b. increased worldwide standing crop.
   c. an increase in the amount of infrared radiation absorbed by the atmosphere.
   d. the burning of larger amounts of wood and fossil fuels.
   e. additional respiration by the rapidly growing human population.

3. What is the single greatest threat to biodiversity?
   a. overharvesting of commercially important species
   b. introduced species that compete with native species
   c. pollution of Earth's air, water, and soil
   d. disruption of trophic relationships as more and more prey species become extinct
   e. habitat alteration, fragmentation, and destruction

LEVEL 2: APPLICATION/ANALYSIS

4. Which of the following is a consequence of biological magnification?
   a. Toxic chemicals in the environment pose greater risk to top-level predators than to primary consumers.
   b. Populations of top-level predators are generally smaller than populations of primary consumers.
   c. The biomass of producers in an ecosystem is generally higher than the biomass of primary consumers.
   d. Only a small portion of the energy captured by producers is transferred to consumers.
   e. The amount of biomass in the producer level of an ecosystem decreases if the producer turnover time increases.

5. Which of the following strategies would most rapidly increase the genetic diversity of a population in an extinction vortex?
   a. Capture all remaining individuals in the population for captive breeding followed by reintroduction to the wild.
   b. Establish a reserve that protects the population's habitat.
   c. Introduce new individuals transported from other populations of the same species.
   d. Sterilize the least fit individuals in the population.
   e. Control populations of the endangered population's predators and competitors.

6. Of the following statements about protected areas that have been established to preserve biodiversity, which one is *not* correct?
   a. About 25% of Earth's land area is now protected.
   b. National parks are one of many types of protected areas.
   c. Most protected areas are too small to protect species.
   d. Management of a protected area should be coordinated with management of the land surrounding the area.
   e. It is especially important to protect biodiversity hot spots.

LEVEL 3: SYNTHESIS/EVALUATION

7. **DRAW IT** Using Figure 56.27 as a starting point, extend the *x*-axis to the year 2100. Then extend the CO_2 curve, assuming that the CO_2 concentration continues to rise as fast as it did from 1974 to 2009. What will be the approximate CO_2 concentration in 2100? What ecological factors and human decisions will influence the actual rise in CO_2 concentration? How might additional scientific data help societies predict this value?

8. **EVOLUTION CONNECTION**
   Concept 25.4 (pp. 521–523) described five mass extinction events in Earth's history. Many ecologists think we are currently entering a sixth mass extinction event because of the threats to biodiversity described in this chapter. Briefly discuss the history of mass extinctions and the length of time it typically takes for species diversity to recover through the process of evolution. Explain why this should motivate us to slow the loss of biodiversity today.

9. **SCIENTIFIC INQUIRY**
   DRAW IT Suppose that you are managing a forest reserve, and one of your goals is to protect local populations of woodland birds from parasitism by the brown-headed cowbird. You know that female cowbirds usually do not venture more than about 100 m into a forest and that nest parasitism is reduced when woodland birds nest away from forest edges. The reserve you manage extends about 6,000 m from east to west and 1,000 m from north to south. It is surrounded by a deforested pasture on the west, an agricultural field for 500 m in the southwest corner, and intact forest everywhere else. You must build a road, 10 m by 1,000 m, from the north to the south side of the reserve and construct a maintenance building that will take up 100 m^2 in the reserve. Draw a map of the reserve, showing where you would put the road and the building to minimize cowbird intrusion along edges. Explain your reasoning.

10. **WRITE ABOUT A THEME**
    Feedback Regulation One factor favoring rapid population growth by an introduced species is the absence of the predators, parasites, and pathogens that controlled its population in the region where it evolved. In a short essay (100–150 words), explain how evolution by natural selection would influence the rate at which native predators, parasites, and pathogens in a region of introduction attack an introduced species.

For selected answers, see Appendix A.