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

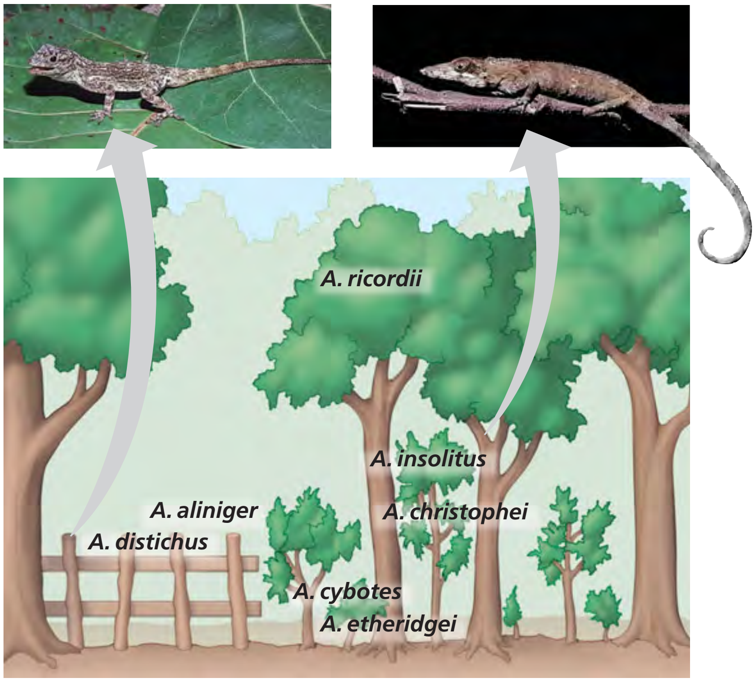
EVOLUTION The sum of a species' use of the biotic and abiotic resources in its environment is called its **ecological niche**. American ecologist Eugene Odum used the following analogy to explain the niche concept: If an organism's habitat is its "address," the niche is the organism's "profession." The 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.

A. distichus perches on fence posts and other sunny surfaces.

A. insolitus usually perches on shady branches.

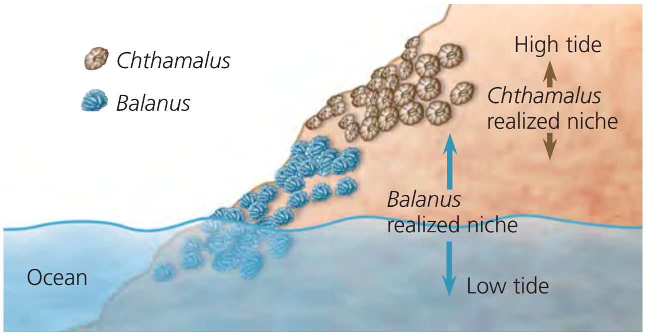


▲ **Figure 54.2 Resource partitioning among Dominican Republic lizards.** Seven species of *Anolis* lizards live in close proximity, and all feed on insects and other small arthropods. However, competition for food is reduced because each lizard species has a different preferred perch, thus occupying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

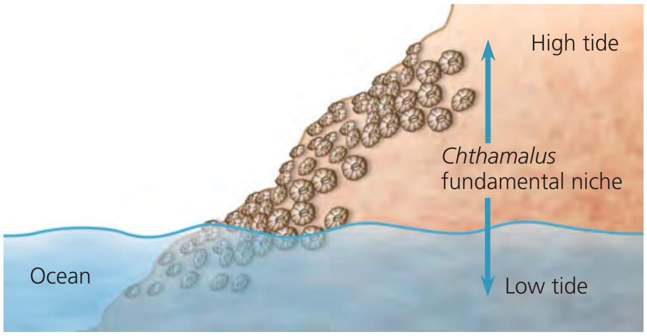
▼ Figure 54.3 INQUIRY

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.

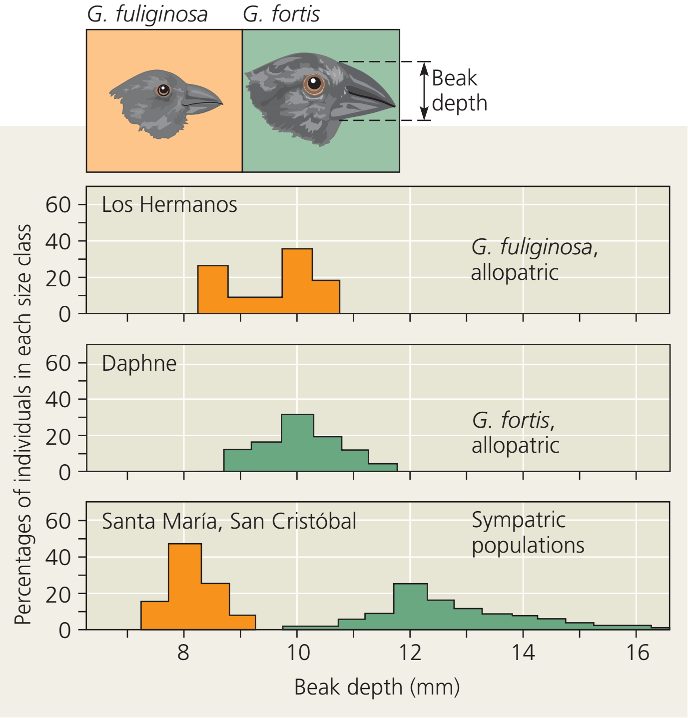
WHAT IF? Other observations showed that *Balanus* cannot survive high on the rocks because it dries out during low tides. How would *Balanus*'s realized niche compare with its fundamental niche?

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.

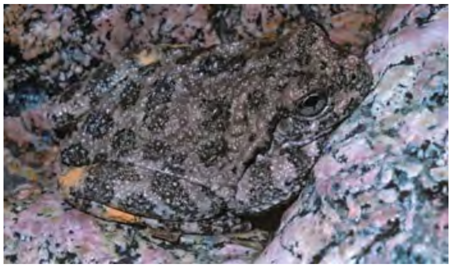
Animals also display a variety of morphological and physiological defensive adaptations. **Cryptic coloration**, or camouflage, makes prey difficult to see **(Figure 54.5a)**. Mechanical or chemical defenses protect species such as porcupines and skunks. Some animals, including the European fire salamander, 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

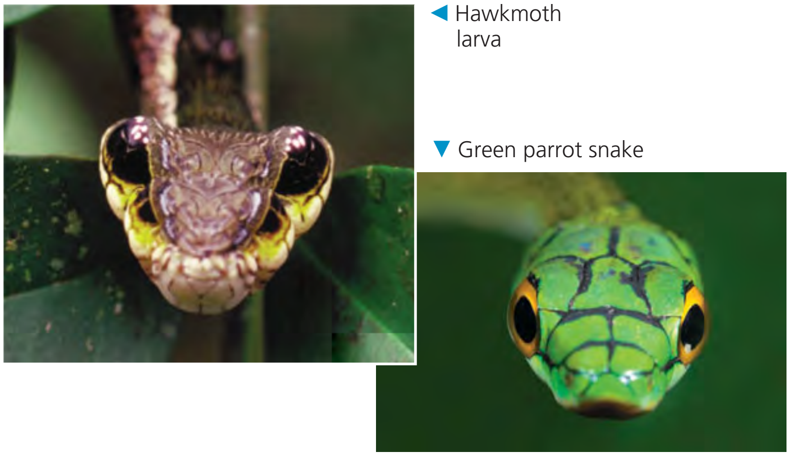
▶ Canyon tree frog



(b) Aposematic coloration

▶ Poison dart frog

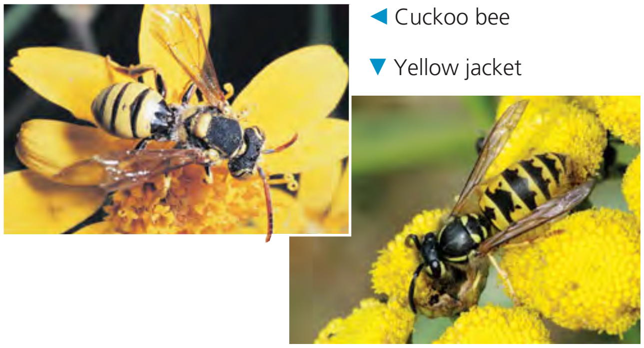
(c) Batesian mimicry: A harmless species mimics a harmful one.



◀ 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.

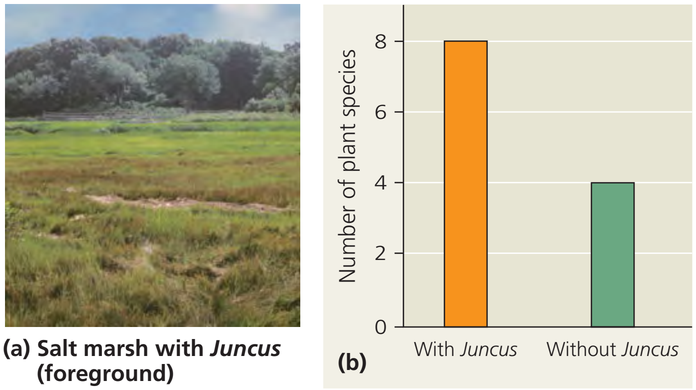
▲ **Figure 54.7 Mutualism between acacia trees and ants.**

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):

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

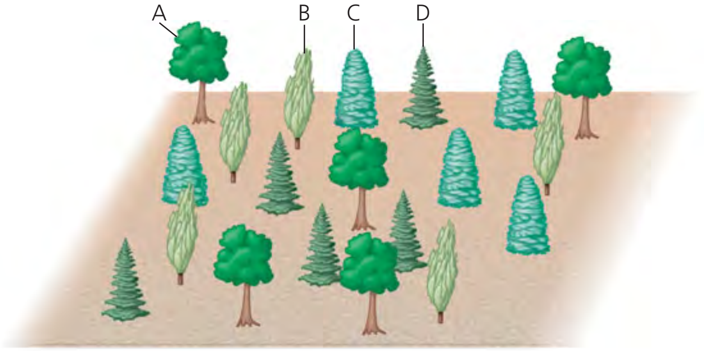
where A, B, C . . . are the species in the community, p is the relative abundance of each species, and ln is the natural logarithm. A higher value of H indicates a more diverse community. Let's use this equation to calculate the Shannon diversity index of the two communities in Figure 54.10. For community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

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

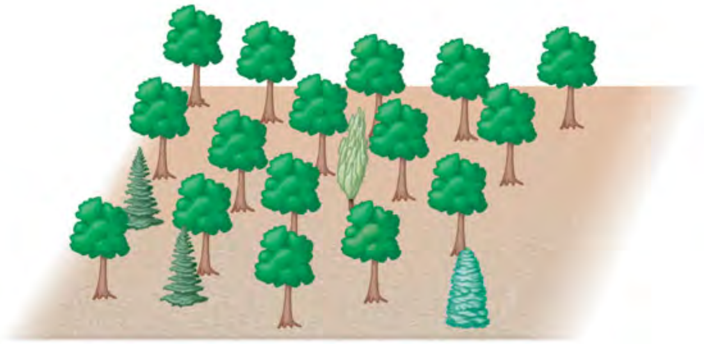
For community 2,

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

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**

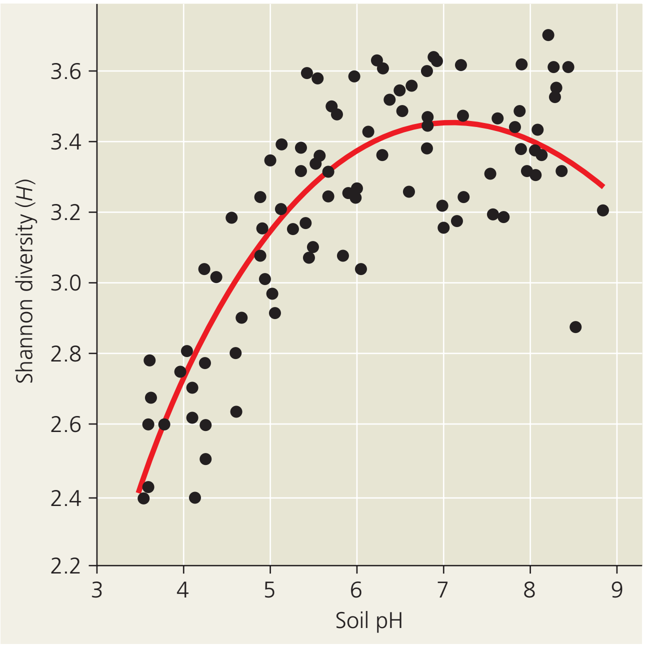
Determining Microbial Diversity Using Molecular Tools

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).

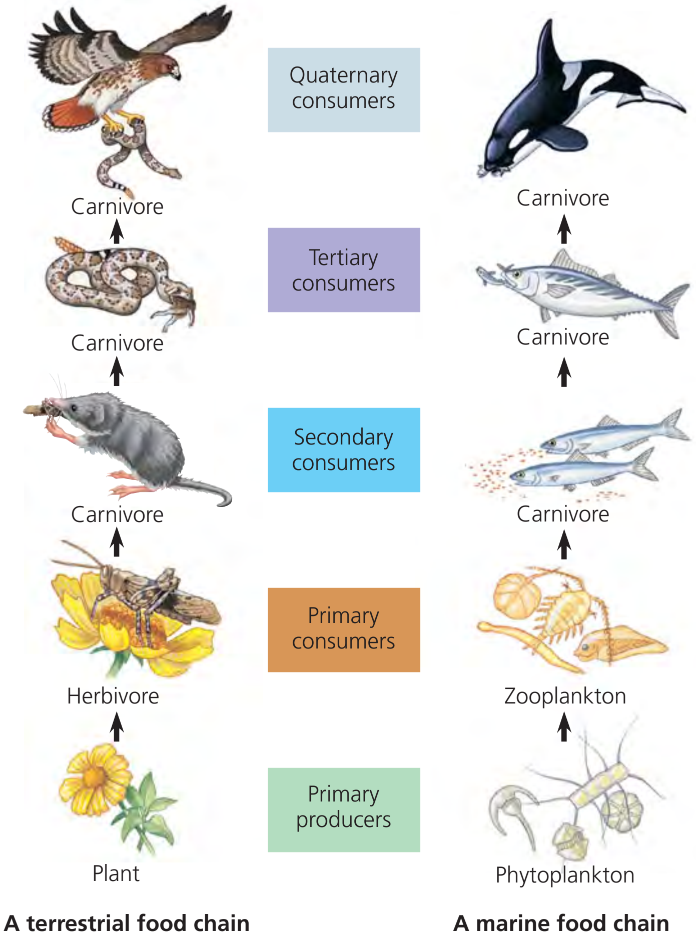
▲ **Figure 54.12 Study plots at the Cedar Creek Natural History Area, site of long-term experiments on manipulating plant diversity.**

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)**.



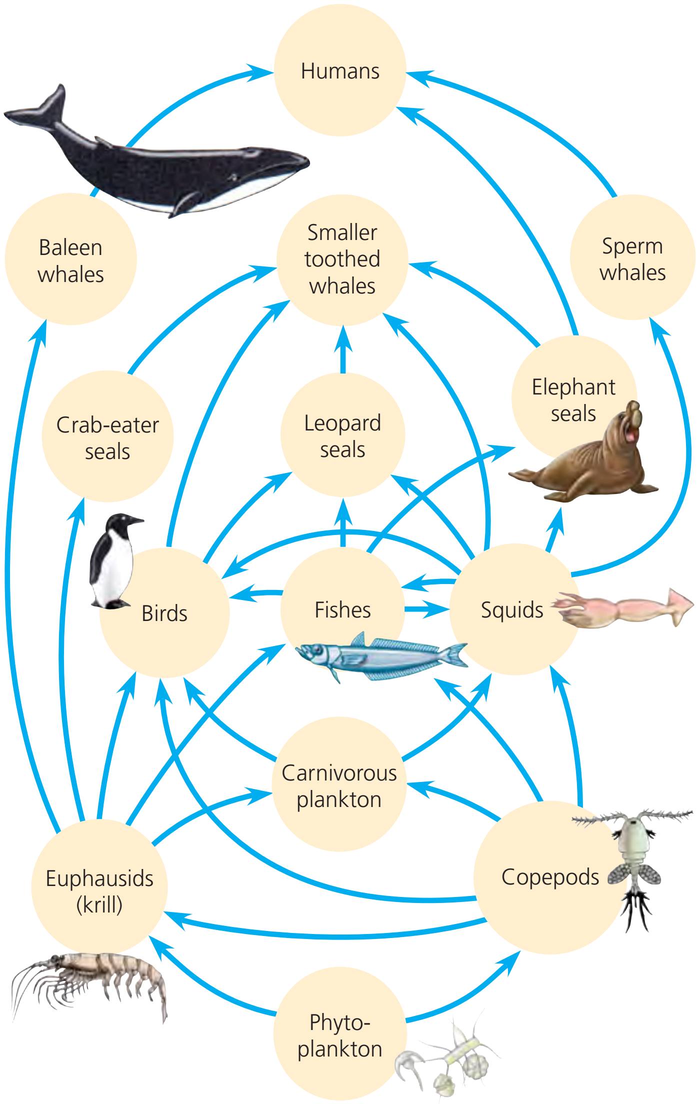
A terrestrial food chain

A marine food chain

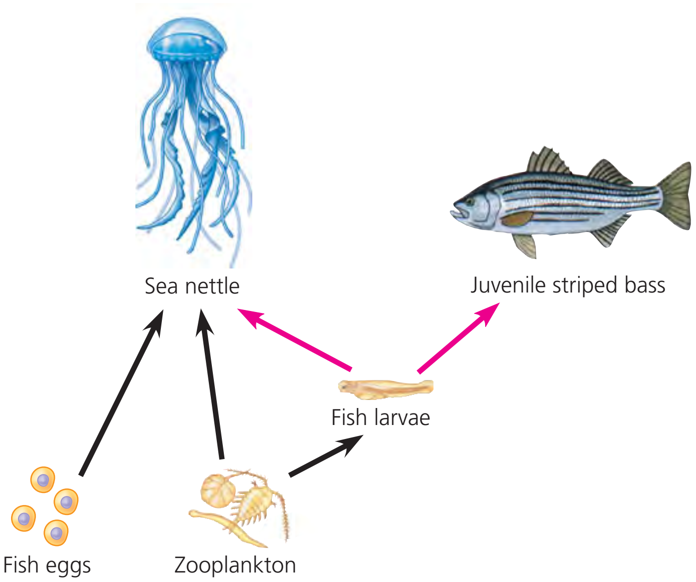
▲ **Figure 54.13 Examples of terrestrial and marine food chains.** The arrows trace energy and nutrients that pass through the trophic levels of a community when organisms feed on one another. Decomposers, which "feed" on organisms from all trophic levels, are not shown here.

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.



▲ **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.

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.

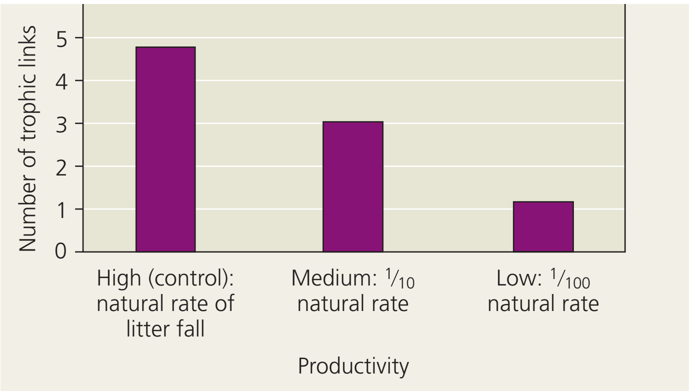
Complicated food webs can be simplified in two ways for easier study. First, species with similar trophic relationships in a given community can be grouped into broad functional groups. In Figure 54.14, more than 100 phytoplankton species are grouped as the primary producers in the food web. A second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

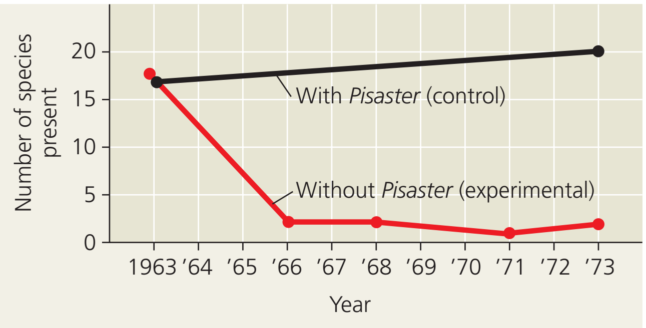
▼ Figure 54.17 **INQUIRY**

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.

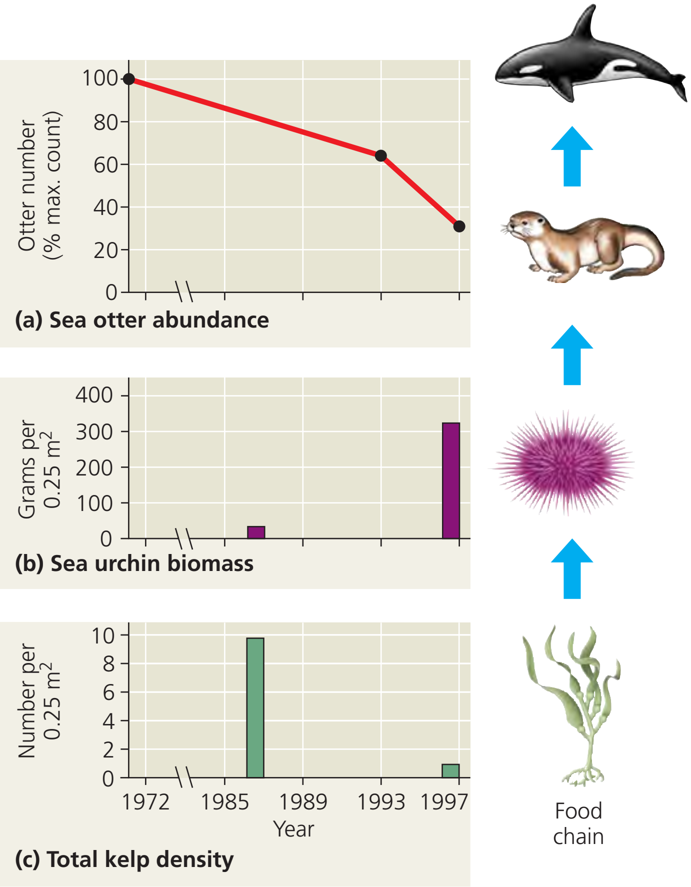
RESULTS In the absence of *Pisaster*, species richness declined as mussels monopolized the rock face and eliminated most other invertebrates and algae. In a control area where *Pisaster* was not removed, species richness changed very little.



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):

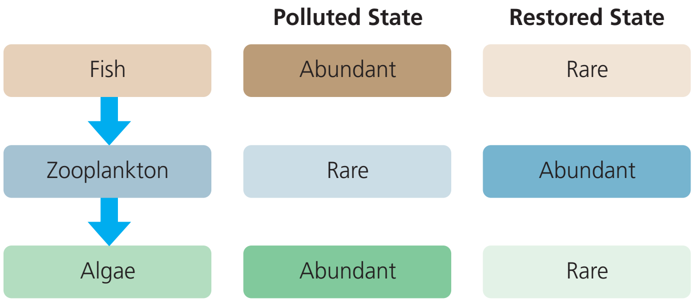
$$V \rightarrow H \quad V \leftarrow H \quad V \leftrightarrow H$$

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.

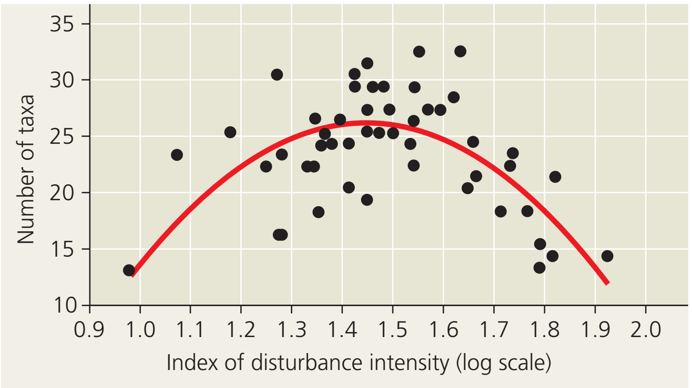
This recent emphasis on change has produced the **nonequilibrium model**, which describes most communities as constantly changing after being affected by disturbances. Even where relatively stable communities do exist, they can be rapidly transformed into nonequilibrium communities. Let's now take a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

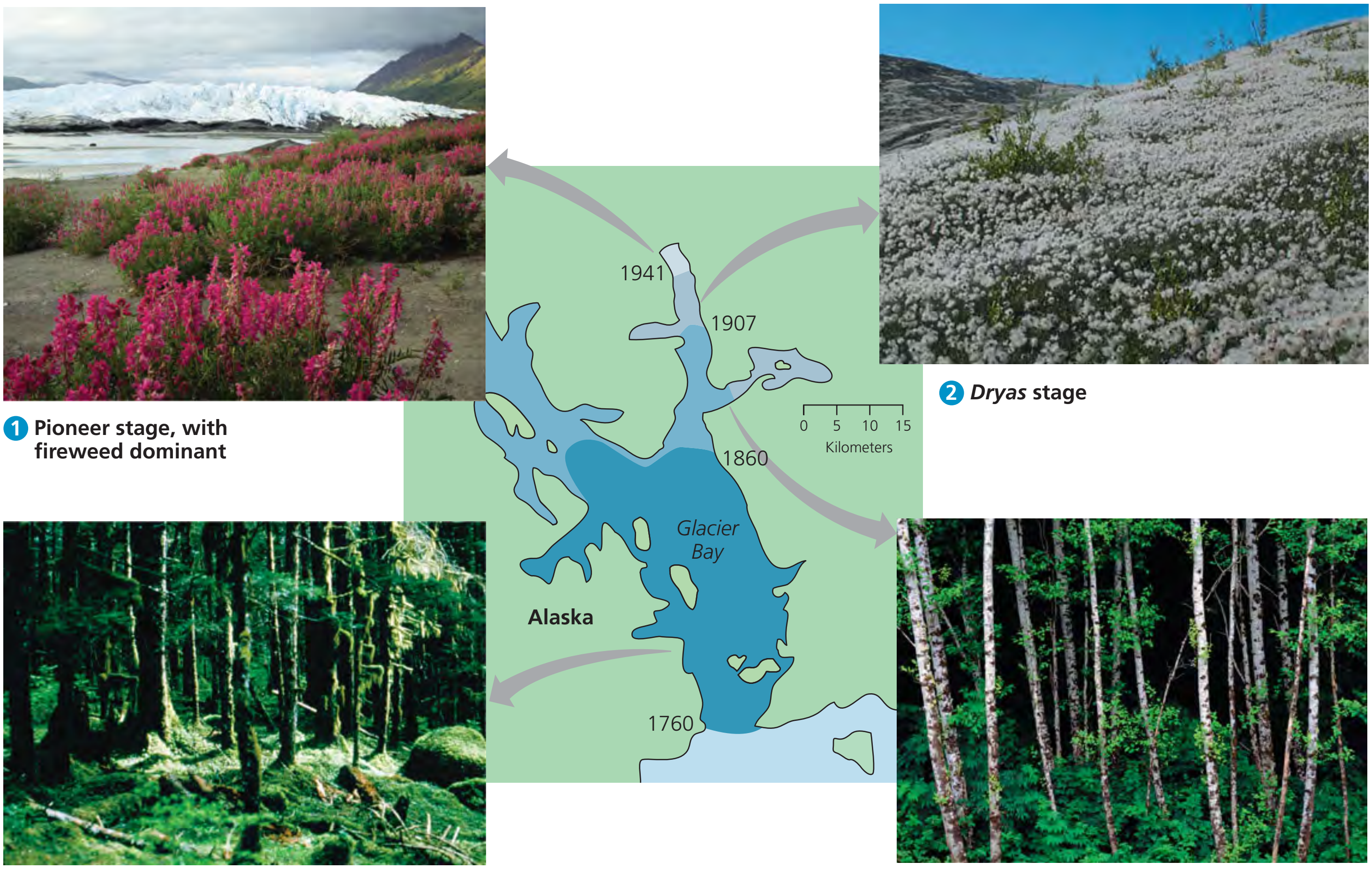
▲ **Figure 54.21 Recovery following a large-scale disturbance.** The 1988 Yellowstone National Park fires burned large areas of forests dominated by lodgepole pines.

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. ① The exposed moraine is colonized first by pioneering species that include liverworts, mosses, fireweed, scattered *Dryas* (a mat-forming shrub), willows, and cottonwood. ② After about three decades, *Dryas* dominates the plant community. ③ A few decades later, the area is invaded by alder, which forms dense thickets up to 9 m tall. ④ 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.



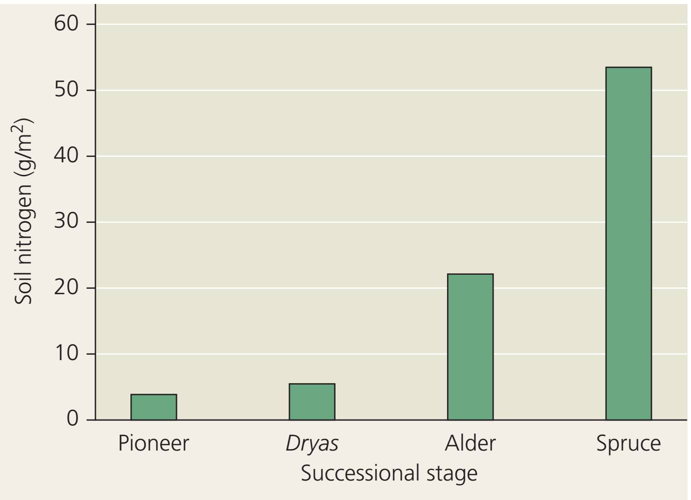
① **Pioneer stage, with fireweed dominant**

② ***Dryas* stage**

③ **Alder stage**

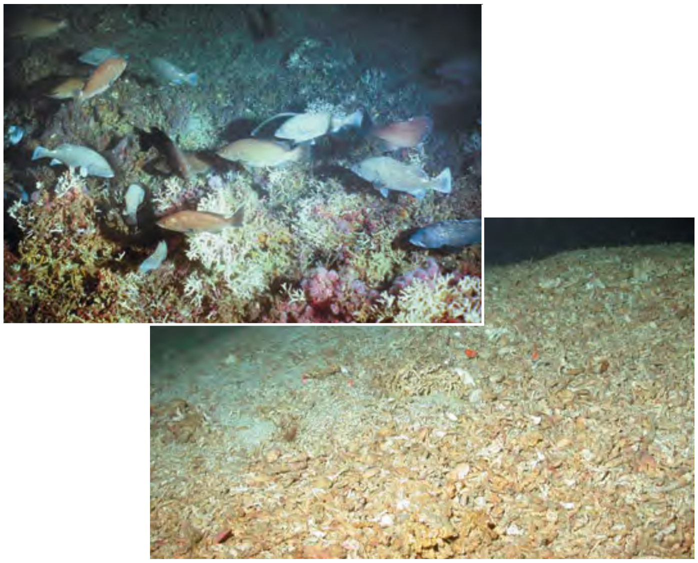
④ **Spruce stage**

▲ **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

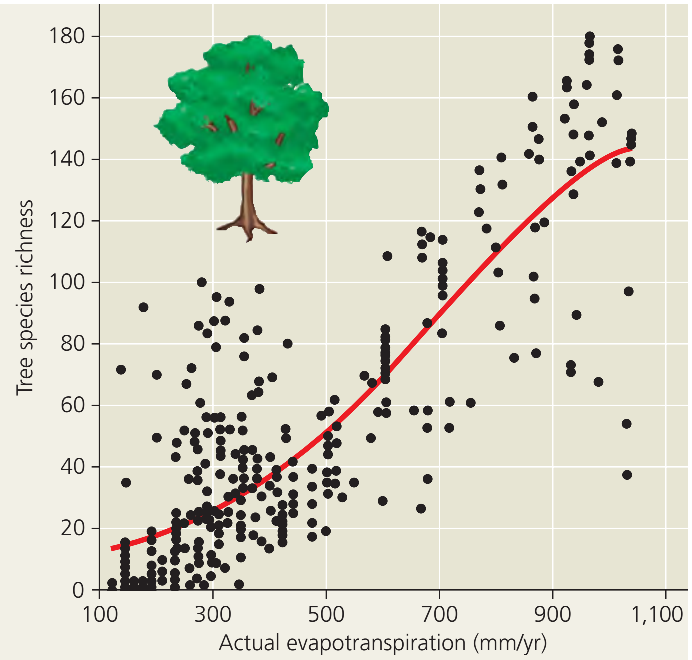
So far, we have examined relatively small-scale or local factors that influence the diversity of communities, including the effects of species interactions, dominant species, and many types of disturbances. Ecologists also recognize that large-scale biogeographic factors contribute to the tremendous 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

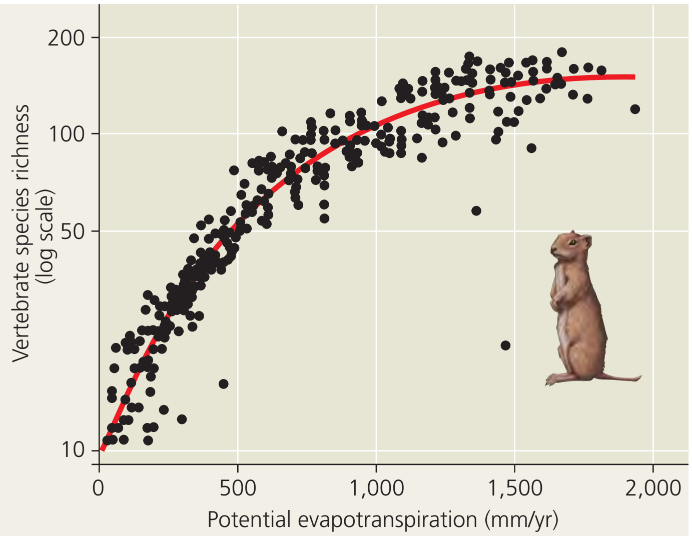
In the 1850s, both Charles Darwin and Alfred Wallace pointed out that plant and animal life was generally more abundant and diverse in the tropics than in other parts of the globe. Since that time, many researchers have confirmed this observation. One study found that a 6.6-hectare (1 ha = 10,000 m^2) 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 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)**.



(a) Trees

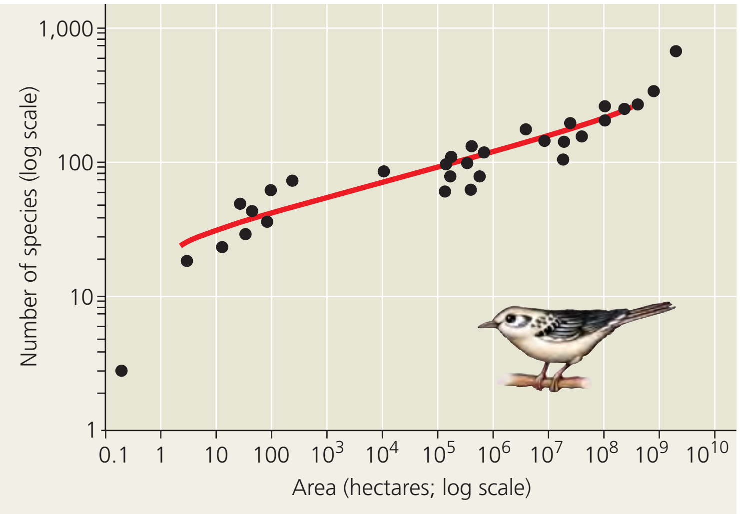


(b) Vertebrates

▲ **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.

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.

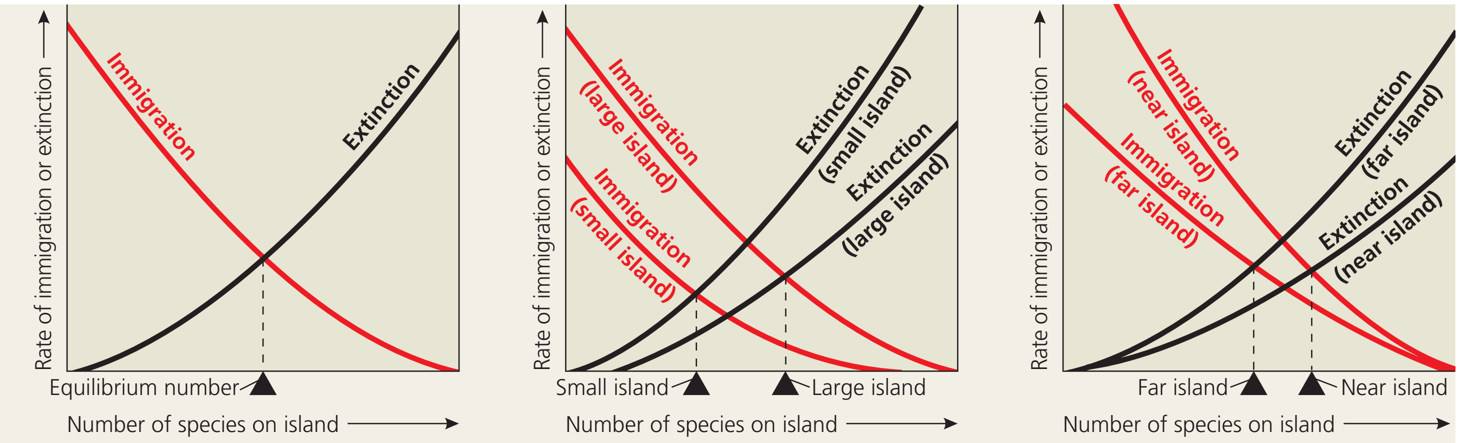
more species it has. The likely explanation for this pattern is that larger areas offer a greater diversity of habitats and microhabitats than smaller areas. In conservation biology, developing species-area curves for the key taxa in a community helps ecologists predict how the potential loss of a certain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

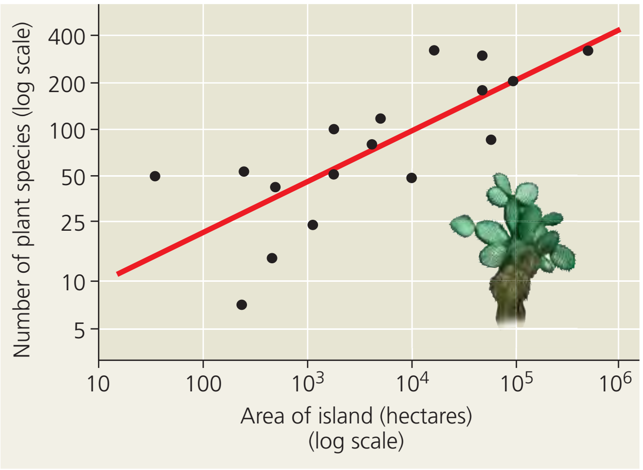
For suggested answers, see Appendix A.

▼ 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.

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