CHAPTER

41 Species Interactions

KEY CONCEPTS

- 41.1 Interactions within a community may help, harm, or have no effect on the species involved
- 41.2 Diversity and trophic structure characterize biological communities
- 41.3 Disturbance influences species diversity and composition
- 41.4 Biogeographic factors affect community diversity
- 41.5 Pathogens alter community structure locally and globally

AP® **BIG IDEAS:** Interactions between populations affect the distribution and reproductive success of populations **(Big Ideas 1 & 4)** by limiting or providing free energy and matter **(Big Idea 2)**.

▲ **Figure 41.1** Which species benefits from this interaction?

Communities in Motion

Deep in the Lembeh Strait of Indonesia, a carrier crab scuttles across the ocean floor using its modified rear legs to hold a large sea urchin on its back (**Figure 41.1**). When a predatory fish arrives, the crab quickly settles 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. Carrier crabs use many organisms to protect themselves, including jellies (see the small photo).

The crab in Figure 41.1 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. For example, the sea urchin may be harmed if the crab sets it down in an unsuitable habitat or in a place where it is vulnerable to predators. On the other hand, the crab may also protect the sea urchin from predators while carrying it. Additional observations or experiments would be needed before ecologists could answer this question.

In Chapter 40, 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 Sequoia National Park in California.

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 41.1. 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'll apply some of the principles of community ecology to the study of human disease.

CONCEPT 41.1

Interactions within a community may 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, parasitism, mutualism, and commensalism. In this section, we'll define and describe each of these interactions, grouping them according to whether they have positive (+) or negative (–) effects on 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. We'll consider three broad categories of ecological interactions: competition (–/–), exploitation (+/–), and positive interactions (+/+ or +/0).

Competition

Interspecific competition is a –/– interaction that occurs when individuals of different species compete for a resource that limits the survival and reproduction of each species. Weeds growing in a garden compete with garden plants for nutrients and water. 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, at least on land; most terrestrial species use this resource, but they do not usually compete for it.

Competitive Exclusion

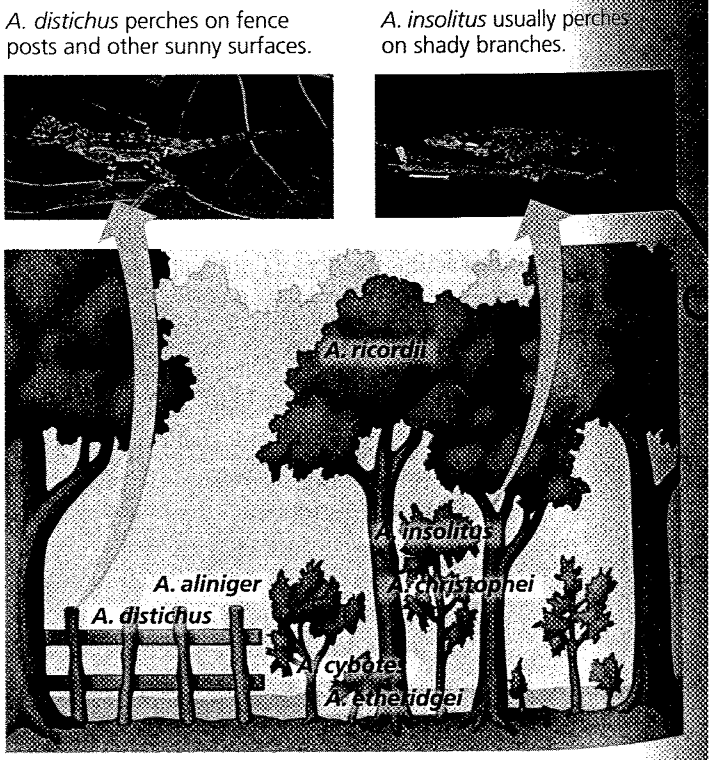
What happens in a community when two species compete for limited resources? In 1934, Russian ecologist G. F. Gause studied this question using laboratory experiments with two closely related protist species, *Paramecium aurelia* and *Paramecium caudatum*. He cultured the species under stable conditions, adding a constant amount of food each day. When Gause grew the two species separately, each population increased rapidly in number and then leveled off at the apparent carrying capacity of the culture (see Figure 40.20a for an illustration of the logistic growth of a *Paramecium* population). But when Gause grew the two species together, *P. caudatum* became extinct. Gause inferred that *P. aurelia* had a competitive edge in obtaining food. More generally, 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 th rior competitor, an outcome called **competitive exclusi**

Ecological Niches and Natural Selection

EVOLUTION The specific set of biotic and abiotic resources that an organism uses in its environment is called **ecological niche**. American ecologist Eugene Odum us following analogy to explain the niche concept: If an orga habitat is its "address," the niche is the organism's "profes The niche of a tropical tree lizard, for instance, includes th temperature range it tolerates, the size of branches on whi it perches, the time of day when it is active, and the sizes a kinds of insects it eats. Such factors define the lizard's nich 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 on 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 or similar resources different times of the day or year. The differentiation of niches that enables similar species to coexist in a community is calle **resource partitioning (Figure 41.2)**.

As a result of competition, a species' *fundamental niche*, which is the niche potentially occupied by that species, is often



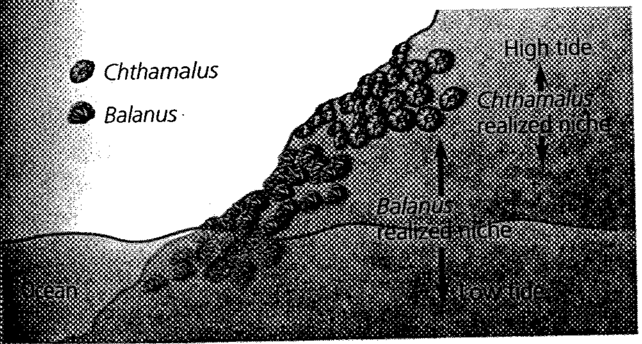
▲ Figure 41.2 Resource partitioning among Dominican Republic lizards. Seven species of *Anolis* lizards live in close proximity, and all feed on insects and other small arthropods. However, competition for food is reduced because each lizard species has a different preferred perch, thus occupying a distinct niche.

ent from its *realized niche*, the portion of its fundamental
e that it actually occupies. Ecologists can identify the fun-
ental niche of a species by testing the range of conditions
hich it grows and reproduces in the absence of competi-
They can also test whether a potential competitor limits a
ies' realized niche by removing the competitor and seeing
e first species expands into the newly available space. The
sic experiment depicted in **Figure 41.3** clearly showed that
petition between two barnacle species kept one species
m occupying part of its fundamental niche.

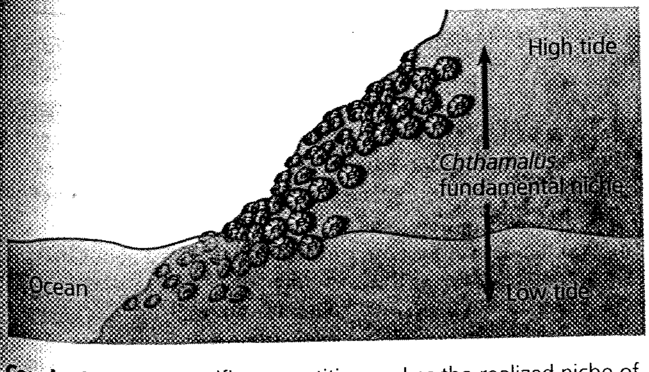
Figure 41.3 Inquiry

n a species' niche be influenced by terspecific competition?

periment Ecologist Joseph Connell studied two barnacle
ecies—*Chthamalus stellatus* and *Balanus balanoides*—that
ve a stratified distribution on rocks along the coast of Scotland.
thamalus is usually found higher on the rocks than *Balanus*. To
termine whether the distribution of *Chthamalus* is the result of
terspecific competition with *Balanus*, Connell removed *Balanus*
om 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.

Data from 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.

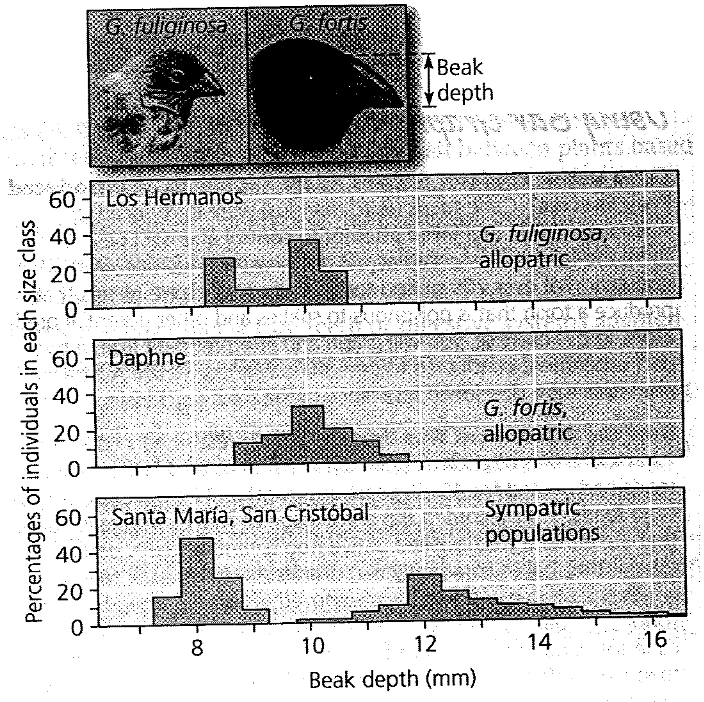
WHAT IF? Other observations showed that *Balanus* cannot survive high on the rocks because it dries out during low tides. How would *Balanus*'s realized niche compare with its fundamental niche?

Character Displacement

Closely related species whose populations are sometimes allopatric (geographically separate; see Concept 22.2) 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 41.4**.

Exploitation

All nonphotosynthetic organisms must eat, and all organisms are at risk of being eaten. Thus, much of the drama in nature involves **exploitation**, a term for any type of +/− interaction in which one species benefits by feeding on the other species, which in turn is harmed by the interaction. Exploitative interactions include predation, herbivory, and parasitism.



▲ **Figure 41.4 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.

INTERPRET THE DATA *If the beak length of* G. fortis *is typically 12% longer than the beak depth, what is the predicted beak length of* G. fortis *individuals with the smallest beak depths observed on Santa María and San Cristóbal Islands?*

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. A rotifer (a tiny aquatic animal that is smaller than many protists) that kills a unicellular alga by eating it can also be considered a predator. Because eating and avoiding being eaten are prerequisites to reproductive success, the adaptations of both predators and prey tend to be refined through natural selection. In the **Scientific Skills Exercise**, you can interpret data from an experiment investigating a specific predator-prey interaction.

Many important feeding adaptations of predators are obvious and familiar. Most predators have acute senses that enable them to find and identify potential prey. 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 38.17b). Many predators also have adaptations such as claws, fangs, or poison that help them catch and subdue their food. Predators that pursue their prey are generally fast and agile, whereas those that lie in ambush are often in their environments.

Just as predators possess adaptations for capturing potential prey animals have adaptations that help them being eaten. Some common behavioral defenses are fleeing, and forming herds or schools. Active self-defe less common, though some large grazing mammals vi defend their young from predators such as lions.

Animals also display a variety of morphological and ological defensive adaptations. **Cryptic coloration**, or ouflage, makes prey difficult to see **(Figure 41.5a)**. Mech or chemical defenses protect species such as porcupine skunks. Some animals, such as the European fire salama can synthesize toxins; others accumulate toxins passively the plants they eat. Animals with effective chemical defe often exhibit bright **aposematic coloration**, or warning oration, such as that of poison dart frogs **(Figure 41.5b)** coloration seems to be adaptive because predators often brightly colored prey.

Some prey species are protected by their resemblance other species. For example, in **Batesian mimicry**, a palata

Scientific Skills Exercise

AP® **SPs 1.1, 1.4, 5.1, 5.3, 6.2**

Using Bar Graphs and Scatter Plots to Present and Interpret Data

Can a Native Predator Species Adapt Rapidly to an Introduced Prey Species? Cane toads (*Bufo marinus*) were introduced to Australia in 1935 in a failed attempt to control an insect pest. Since then, the toads have spread across northeastern Australia, with a population of over 200 million today. Cane toads have glands that produce a toxin that is poisonous to snakes and other potential predators. In this exercise, you will graph and interpret data from a two-part experiment conducted to determine whether native Australian predators have developed resistance to the cane toad toxin.

How the Experiment Was Done In part 1, researchers collected 12 black snakes (*Pseudechis porphyriacus*) from areas where cane toads had existed for 40–60 years and another 12 from areas free of cane toads. They recorded the percentage of snakes from each area that ate either a freshly killed native frog (*Limnodynastes peronii*, a species the snakes commonly eat) or a freshly killed cane toad from which the toxin gland had been removed (making the toad nonpoisonous). In part 2, researchers collected snakes from areas where cane toads had been present for 5–60 years. To assess how cane toad toxin affected the physiological activity of these snakes, they injected small amounts of the toxin into the snakes' stomachs and measured the snakes' swimming speed in a small pool.

Data from the Experiment, Part 1

	Percentage of Snakes from Each Area That Ate the Native Frog vs. Cane Toad	
Type of Prey Offered	Area with Cane Toads Present for 40–60 Years	Area with No Cane Toads
Native frog	100	100
Cane toad	0	50

Data from the Experiment, Part 2

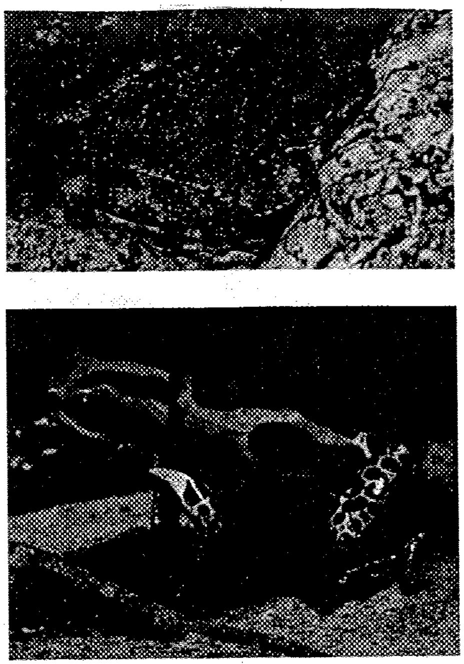
Number of Years Cane Toads Were Present in the Area	5	10	10	20	50	60	60	60	60	6
Percent Reduction in Snake Swimming Speed	52	19	30	30	5	5	9	11	12	2

Data from B. L. Phillips and R. Shine, An invasive species induces rapid adaptive change in a native predator: cane toads and black snakes in Australia, *Proceedings of the Royal Society B* 273:1545–1550 (2006).

INTERPRET THE DATA

1. Make a bar graph of the data in part 1. (For additional information about graphs, see the Scientific Skills Review in Appendix F and in the Study Area in MasteringBiology.)
2. What do the data represented in the graph suggest about the effects of cane toads on the predatory behavior of black snakes in areas where the toads are and are not currently found?
3. Suppose a novel enzyme that deactivates the cane toad toxin evolved in a black snake population exposed to cane toads. If the researchers repeated part 1 of this study, predict how the results would change.
4. Identify the dependent and independent variables in part 2 and make a scatter plot. What conclusion would you draw about whether exposure to cane toads is having a selective effect on black snakes? Explain.
5. Explain why a bar graph is appropriate for presenting the data in part 1 and a scatter plot is appropriate for the data in part 2.

(MB) A version of this Scientific Skills Exercise can be assigned in MasteringBiology.



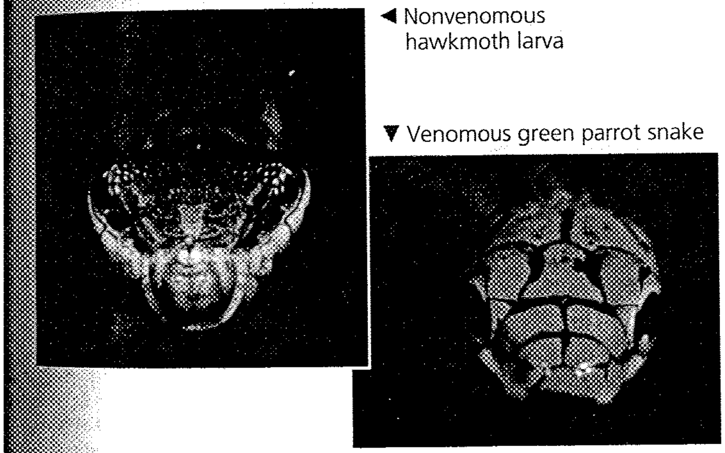
(a) Cryptic coloration

▶ Canyon tree frog

(b) Aposematic coloration

▶ Poison dart frog

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



◀ Nonvenomous hawkmoth larva

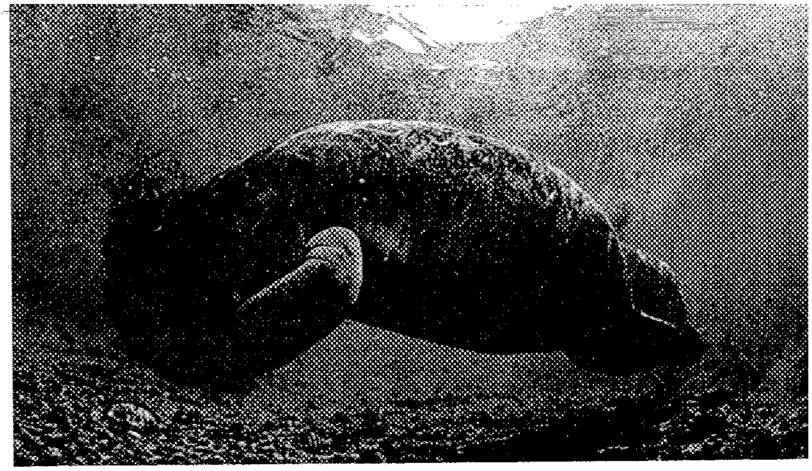
▼ Venomous green parrot snake

▲ **Figure 41.5 Examples of defensive adaptations in animals.**

MAKE CONNECTIONS *Explain how natural selection could increase the resemblance of a harmless species to a distantly related harmful species. Along with selection, what else could account for a harmless species resembling a closely related harmful species? (See Concept 19.2.)*

or harmless species mimics an unpalatable or harmful species to which it is not closely related. The larva of the hawkmoth *Hemeroplanes ornatus* puffs up its head and thorax when disturbed, looking like the head of a small venomous snake **(Figure 41.5c)**. In this case, the mimicry even involves behavior; the larva weaves its head back and forth and hisses like a snake. In Batesian mimicry, the resemblance of a prey species to a distantly related unpalatable or harmful species is thought to have resulted from natural selection.

Many predators also use mimicry. The alligator snapping turtle has a tongue that resembles a wriggling worm, which is used to lure small fish. Any fish that tries to eat the "bait" is itself quickly consumed as the turtle's strong jaws snap closed.



▲ **Figure 41.6 A marine herbivore.** This West Indian manatee (*Trichechus manatus*) in Florida is grazing on *Hydrilla*, an introduced plant.

Herbivory

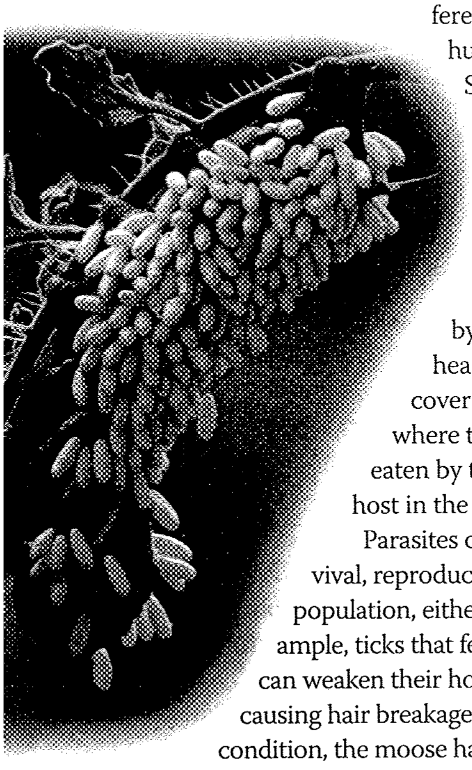
Ecologists use the term **herbivory** to refer to a +/− interaction in which an organism—an herbivore—eats parts of a plant or alga, thereby harming it. While large mammalian herbivores such as cattle, sheep, and water buffalo may be most familiar, most herbivores are actually invertebrates, such as grasshoppers, caterpillars, and beetles. In the ocean, herbivores include sea urchins, some tropical fishes, and certain mammals, including the manatee **(Figure 41.6)**.

Like predators, herbivores have many specialized adaptations. Many herbivorous insects have chemical sensors on their feet that enable them to distinguish between plants based on their toxicity or their nutritional value. 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 Concept 33.4).

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 defenses are the poison strychnine, produced by the tropical vine *Strychnos toxifera*, and nicotine, from the tobacco plant. 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.

Parasitism

Parasitism is a +/− exploitative 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**. Some ecologists have estimated that at least one-third of all species on Earth are parasites. In one particular type of parasitism, parasitoid insects—usually small wasps—lay eggs on or in living hosts, such as the braconid wasp parasitizing a tobacco hornworm (*Manduca sexta*) in the photo.



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. Some parasites change the behavior of their current host in ways that increase the likelihood that the parasite will reach its next host. For instance, crustaceans that are parasitized by acanthocephalan (spiny-headed) worms leave protective cover and move into the open, where they are more likely to be eaten by the birds that are the second host in the worm's life cycle.

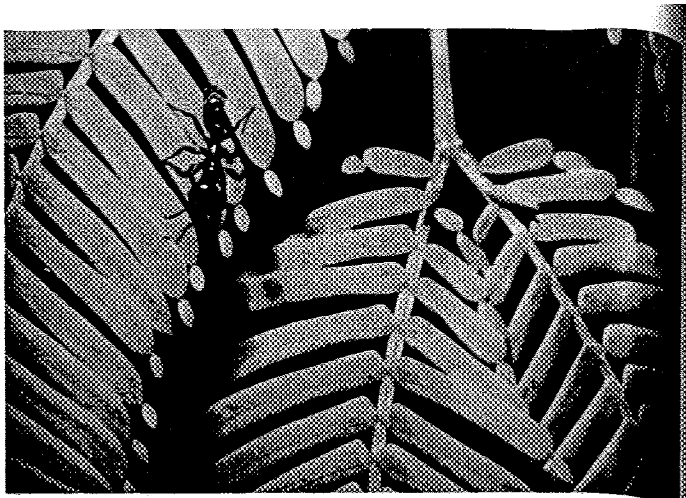
Parasites can significantly affect the survival, reproduction, and density of their host population, either directly or indirectly. For example, ticks that feed as ectoparasites on moose can weaken their hosts by withdrawing blood and causing hair breakage and loss. In their weakened condition, the moose have a greater chance of dying from cold stress or predation by wolves (see Figure 40.24).

Positive Interactions

While nature abounds with dramatic and gory examples of exploitive interactions, ecological communities are also heavily influenced by **positive interactions**, a term that refers to a +/+ or +/0 interaction in which at least one species benefits and neither is harmed. Positive interactions include mutualism and commensalism. As we'll see, they can affect the diversity of species found in ecological communities.

Mutualism

Mutualism is an interspecific interaction that benefits both species (+/+). Mutualisms are common in nature, as illustrated by examples seen in previous chapters, including cellulose digestion by microorganisms in the digestive systems of termites and ruminant mammals, animals that pollinate flowers or disperse seeds, nutrient exchange between fungi and plant roots in mycorrhizae, and photosynthesis by unicellular algae in corals. In the acacia-ant example shown in **Figure 41.7**, each species depends on the other for their survival and reproduction. However, in other mutualisms—including some other acacia-ant interactions—both species can survive on their own.



(a) Certain species of acacia trees in Central and South America have hollow thorns (not shown) that house stinging ants of the genus *Pseudomyrmex*. The ants feed on nectar produced by the tree and on protein-rich swellings (yellow 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 41.7 Mutualism between acacia trees and ants.**

Typically, both partners in a mutualism incur costs as well as benefits. In mycorrhizae, for example, the plant often transfers carbohydrates to the fungus, while the fungus transfers limiting nutrients, such as phosphorus. Each partner benefits, but each partner also experiences a cost: It transfers materials that it could have used to support its own growth and metabolism. The key point is that for an interaction to be a mutualism, the benefits to each partner must exceed the costs.

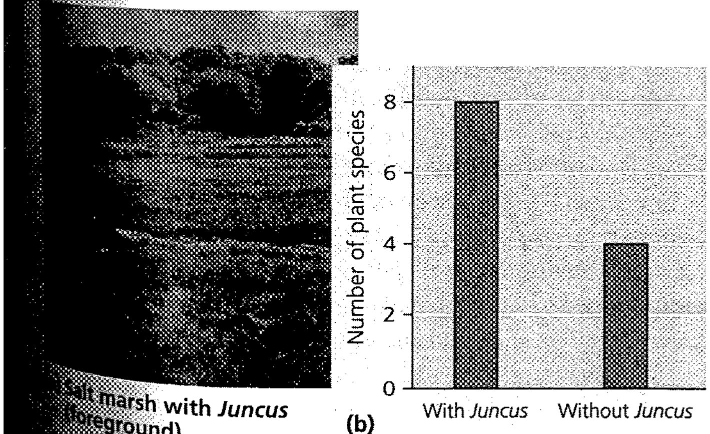
Commensalism

An interaction between species that benefits one of the species but neither harms nor helps the other (+/0) is called **commensalism**. Like mutualism, commensal interactions are common in nature. For instance, many wildflowers that live on the forest floor depend entirely on the trees that tower above them—the trees provide the habitat in which they live. Yet the survival and reproduction of the trees are not affected by these wildflowers. Thus, these species are involved in a +/0 interaction in which the wildflowers benefit and the trees are not affected.

Figure 41.8 Commensalism between cattle egrets and an African buffalo.

In another example of a commensal association, cattle egrets feed on insects flushed out of the grass by grazing bison, cattle, and other herbivores **(Figure 41.8)**. Because the birds typically find more prey when they follow herbivores, they clearly benefit from the association. Much of the time, the herbivores are not affected by the birds. At times, however, they, too, may derive some benefit; the birds occasionally remove and eat ticks and other ectoparasites from the herbivores or may warn the herbivores of a predator's approach. This example illustrates another key point about ecological interactions: Their effects can change. In this case, an interaction whose effects are typically +/0 (commensalism) may at times become +/+ (mutualism).

Positive interactions can have large effects on ecological communities. For instance, the black rush *Juncus gerardii* makes the soil more hospitable for other plant species in some zones of New England salt marshes **(Figure 41.9a)**. *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 41.9b)**.



Salt marsh with *Juncus* (foreground)

(b)

Figure 41.9 Facilitation by black rush (*Juncus gerardii*) in New England salt marshes. Black rush increases the number of species that can live in the upper middle zone of the marsh.

In fact, as is true for positive interactions, competition and exploitation (predation, herbivory, and parasitism) also can have large effects on ecological communities. You'll see examples of how this can occur throughout this chapter.

CONCEPT CHECK 41.1

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 22.13 illustrates how a hybrid zone can change over time. Imagine that two finch species colonize a new island and are capable of hybridizing (mating and producing viable offspring). The island contains two plant species, one with large seeds and one with small seeds, 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 41.2

Diversity and trophic structure characterize biological communities

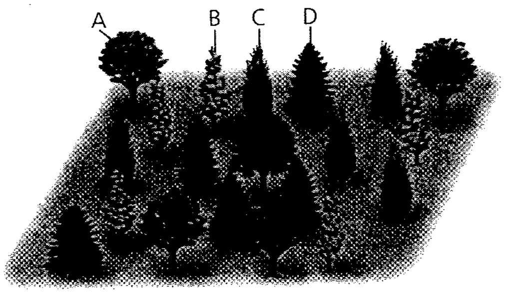
Along with the specific interactions described in the previous section, communities are also characterized by more general attributes, including how diverse they are and the feeding relationships of their species. In this section, you'll see why such ecological attributes are important. You'll also learn 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



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

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

▲ **Figure 41.10 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.

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 41.10)**. 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 compare the diversity of communities across time and space. They often calculate indexes of diversity based on species richness and relative abundance. One widely used index is the **Shannon diversity index** (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; the ln of each value of p can be determined using the "ln" key on a calculator. 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 41.10. 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.

Determining the number and relative abundance of species in a community can be challenging. Because most species in a community are relatively rare, it may be hard to obtain a sample size large enough to be representative. It can also be difficult to census highly mobile or less visible members of communities, such as microorganisms, insects, 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 41.11)**.

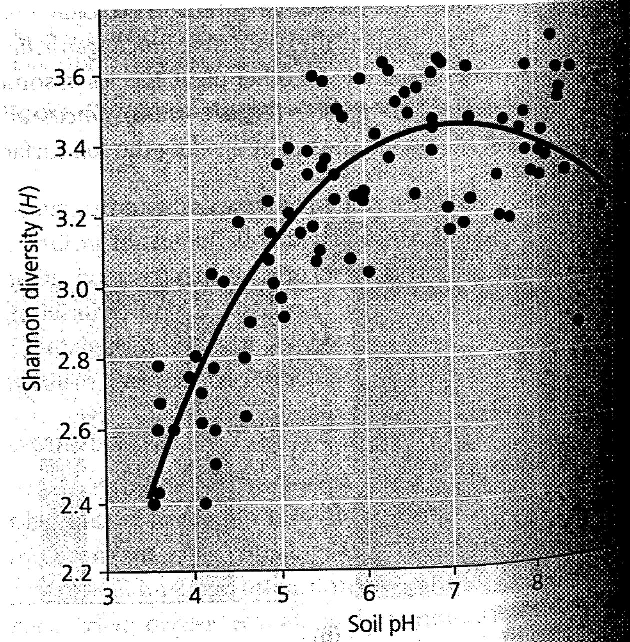
▼ **Figure 41.11 Research Method**

Determining Microbial Diversity Using Molecular Tools

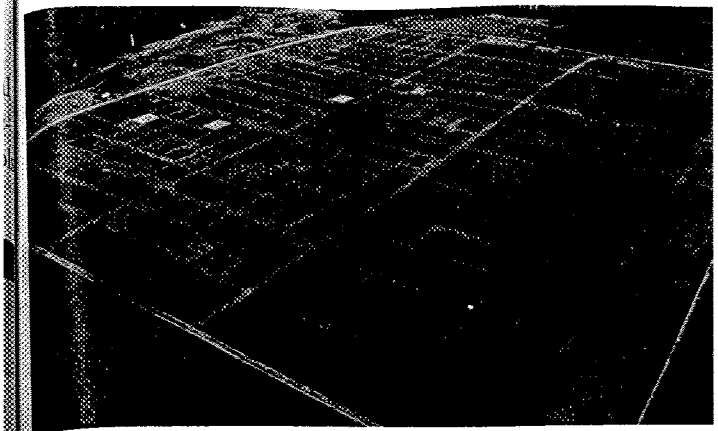
Application Ecologists are increasingly using molecular techniques to determine microbial diversity and richness in environmental samples. One such technique produces a DNA profile for microbial taxa based on sequence variations in the DNA that encodes the small subunit of ribosomal RNA. Noah Fierer 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; see Figure 13.27) to amplify the ribosomal DNA and label it with a fluorescent dye. 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 analysis, Fierer and Jackson calculated the Shannon diversity index (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 soil acidity.

Results The diversity of the sampled bacteria was related almost exclusively to soil pH, with the Shannon diversity index 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.



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



▲ Figure 41.12 Study plots at the Cedar Creek Ecosystem Science Reserve, site of long-term experiments in which researchers have manipulated plant diversity.

Diversity and Community Stability

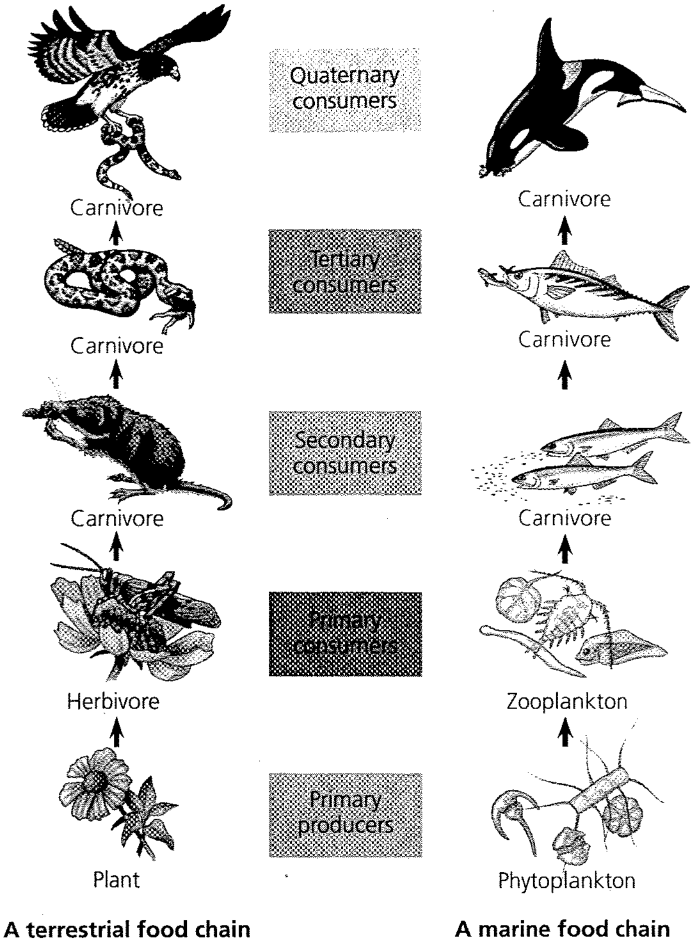
In addition to measuring species diversity, ecologists manipulate diversity in experimental communities in nature and in the laboratory. They do this to examine the potential benefits of diversity, including increased productivity and stability of biological communities.

Researchers at the Cedar Creek Ecosystem Science Reserve, in Minnesota, have been manipulating plant diversity in experimental communities for more than two decades **(Figure 41.12)**. 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 consistently produced more **biomass** (the total mass of all organisms in a habitat) than the single-species plots 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 with different levels of diversity consisting of sessile marine invertebrates, including tunicates (see Figure 27.15b). 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 autotrophs (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 41.13)**.

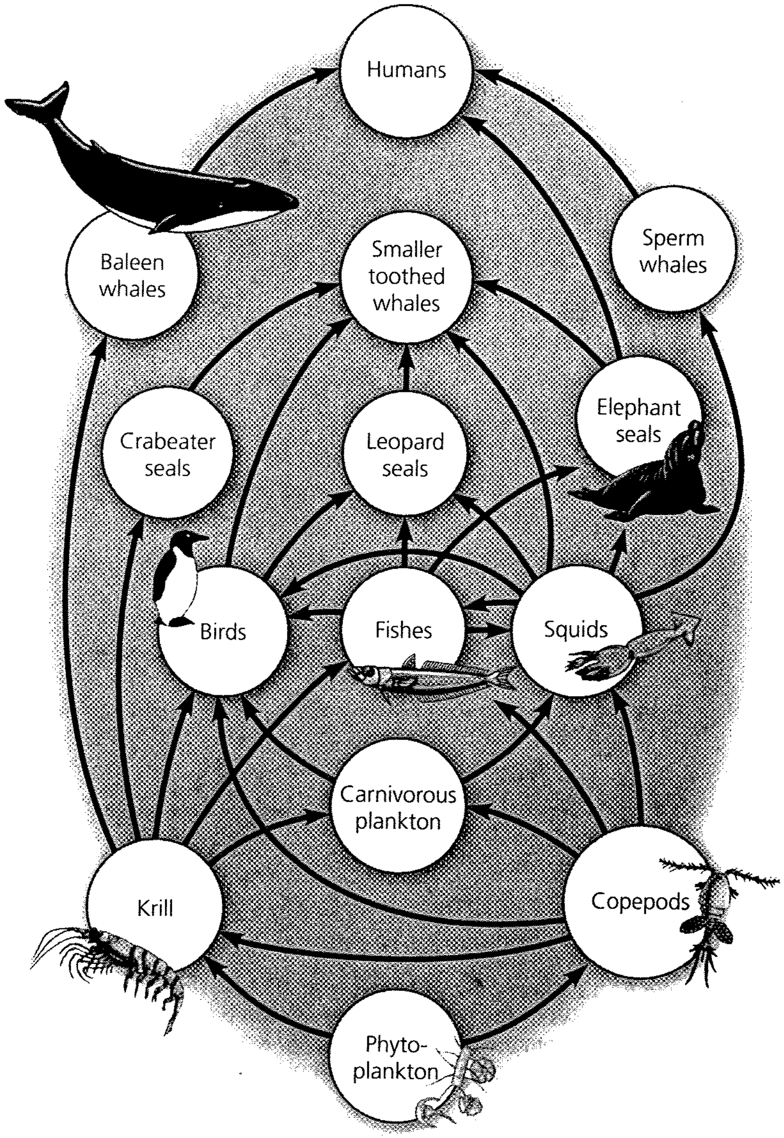


A terrestrial food chain **A marine food chain**

▲ Figure 41.13 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 the remains of organisms from all trophic levels, are not shown here.

? *Suppose the abundance of carnivores that eat zooplankton increased greatly. How might that affect phytoplankton abundance?*

In the 1920s, Oxford University biologist Charles Elton recognized that food chains are not isolated units but are linked together in **food webs**. Ecologists diagram the trophic relationships of a community using arrows that link 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 krill and copepods, both of which are crustaceans. 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,



▲ **Figure 41.14 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.

? *In the food web shown here, indicate the number of organism types that each group eats. Which two groups are both predator and prey for each other?*

are another important link in these food webs, as they are in turn eaten by seals and toothed whales **(Figure 41.14)**.

Note that a given species may weave into the web at more than one trophic level. For example, in the food web shown in Figure 41.14, krill feed on phytoplankton as well as on other grazing zooplankton, such as copepods.

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 in a community are the species that are the most abundant or that collectively have the highest biomass. There can be different explanations for why different species become dominant. One hypothesis suggests that dominant species are competitively superior in exploiting limited resources such as water or nutrients. Another hypothesis is that dominant species are most successful at avoiding predation or the impact of disease. The latter idea could explain the high biomass attained in some environments by invasive species. Such species may not face the natural predators or parasites that would otherwise hold their populations in check.

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 41.15** highlights the importance of a keystone species, a sea star, in maintaining the diversity of an intertidal community.

Still 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

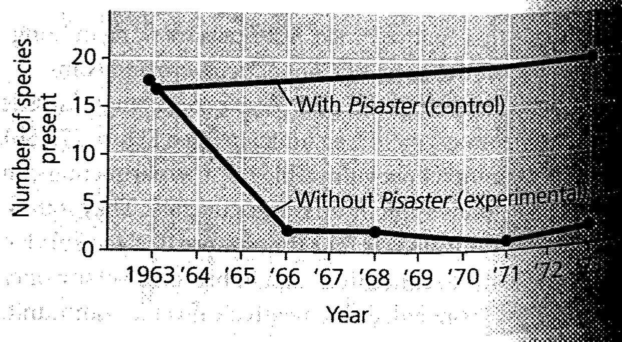
▼ Figure 41.15 Inquiry

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.

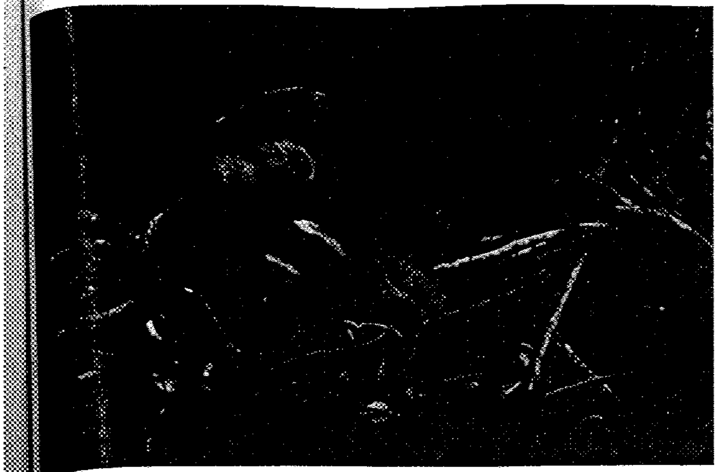
Results In the absence of *Pisaster*, species richness declined as mussels monopolized the rock face and eliminated most other invertebrates and algae. In a control area where *Pisaster* was not removed, species richness changed very little.



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

Data from 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 affected if *Pisaster* were then removed.



▲ **Figure 41.16 Beavers as ecosystem engineers.** By felling trees, building dams, and creating ponds, beavers can transform large areas of forest into flooded wetlands.

conscious intent, "foundation species." A familiar ecosystem engineer is the beaver **(Figure 41.16)**. 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 describing community organization. Let's consider the three possible relationships between plants (V for vegetation) and herbivores (H):

$$V \rightarrow H \qquad V \leftarrow H \qquad V \leftrightarrow H$$

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 each trophic level is sensitive to changes in the biomass of the other.

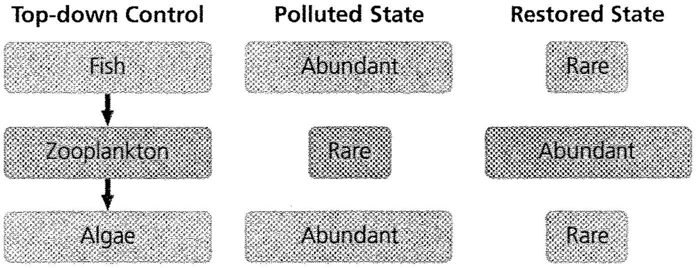
Two models of community organization are common: the bottom-up model and the top-down model. The $V \rightarrow H$ linkage suggests a **bottom-up model**, which postulates a unidirectional influence from lower to higher trophic levels. In this case, the presence or absence of mineral nutrients (N) controls 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. If you add mineral nutrients to stimulate plant growth, then the higher trophic levels should also increase in biomass. If you change predator abundance, 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. The effects thus move down the trophic structure as alternating +/− effects.

Ecologists have applied the top-down model to improve water quality in lakes with high abundances of algae. This approach, called **biomanipulation**, attempts to prevent algal blooms by altering the density of higher-level consumers. In lakes with three trophic levels, removing fish should improve water quality by increasing zooplankton density, thereby decreasing algal populations. In lakes with four trophic levels, adding top predators should have the same effect **(Figure 41.17)**.

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 species that eats zooplankton, which otherwise keep the cyanobacteria and algae in check. To reverse these changes, ecologists removed nearly a million kilograms of fish from the lake 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. Ecologists continue to monitor the lake for evidence of cyanobacterial blooms and low oxygen availability, but the lake has remained 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.



▲ **Figure 41.17 Results of biomanipulation in a lake with top-down control of community organization.** Decreasing the abundance of fish that ate zooplankton results in a decrease in the biomass of algae, improving water quality.

CONCEPT CHECK 41.2

1. What two components contribute to species diversity? Explain how two communities with the same number of species can differ in species diversity.
2. How is a food chain different from a food web?
3. **WHAT IF?** Consider a grassland with five trophic levels: grasses, mice, snakes, raccoons, and bobcats. If you released additional bobcats into the grassland, how would grass biomass change if the bottom-up model applied? If the top-down model applied? Explain.
4. **MAKE CONNECTIONS** Rising atmospheric CO_2 levels lead to ocean acidification (see Figure 2.24) and global warming, both of which can reduce krill abundance. Predict how a drop in krill abundance might affect other organisms in the food web shown in Figure 41.14. Which organisms are particularly at risk? Explain.

For suggested answers, see Appendix A.

CONCEPT 41.3

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 stable equilibrium, a *climax community* controlled solely by climate. According to Clements, biotic interactions caused the species in the 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 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, or human activity—that changes a community by removing organisms from it or altering resource availability.

This emphasis on change has led to the formulation of the **nonequilibrium model**, which describes most communities as constantly changing after disturbance. Even relatively stable communities can be rapidly transformed into nonequilibrium communities. Let's examine some of the ways that disturbances influence community structure and composition.

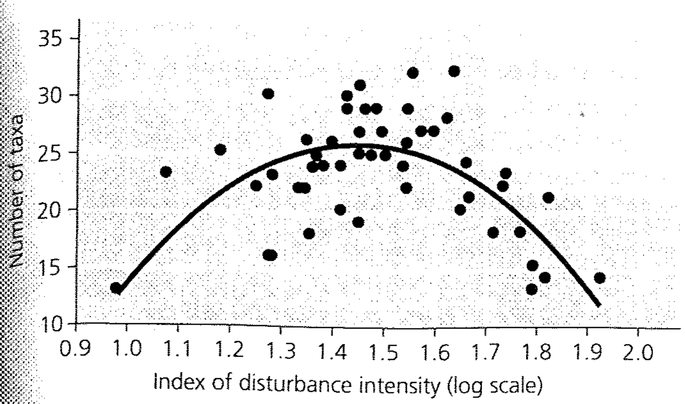
Characterizing Disturbance

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 fact, chaparral and some grassland biomes require regular burning to maintain their structure and species composition. Many streams and ponds are disturbed by spring flooding and seasonal drying. A high level of disturbance is generally the result of frequent *and* intense disturbance, while low disturbance levels can result from either a low frequency or low intensity of disturbance.

The **intermediate disturbance hypothesis** states that moderate levels of disturbance foster greater species diversity than do high or low 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 study, ecologists in New Zealand compared the richness of invertebrates living in the beds of streams exposed to different frequencies and intensities of flooding **(Figure 41.18)**. 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.

Although moderate levels of disturbance appear to maximize species diversity in some cases, small and large disturbances also can 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



▲ **Figure 41.18 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.

Park, for example, is dominated by lodgepole pine, a tree species that requires the rejuvenating influence of periodic fires. Lodgepole pine 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.

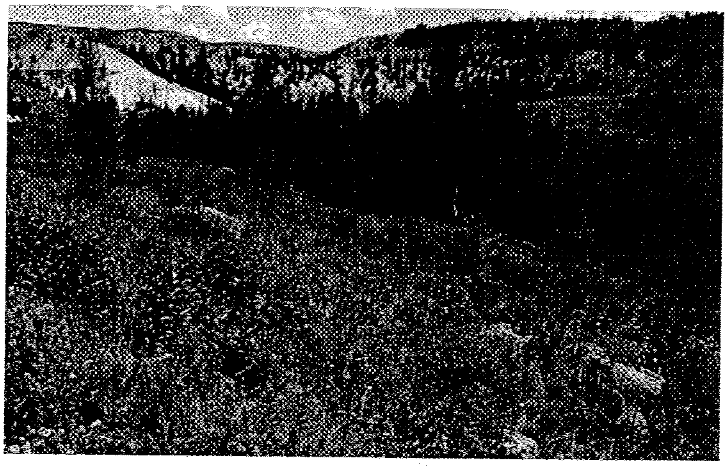
In the summer of 1988, extensive areas of Yellowstone burned during a severe drought. By 1989, burned areas in the park were largely covered with new vegetation, suggesting that the species in this community are adapted to rapid recovery after fire **(Figure 41.19)**. In fact, large-scale fires have periodically swept through the lodgepole pine forests of Yellowstone and other northern areas for thousands of years.

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 are in fact the norm for most communities.

Ecological Succession

Changes in the composition and structure of terrestrial communities are most apparent after a 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**. Another type of succession, **secondary succession**, occurs when an existing community has been cleared by a disturbance that leaves the soil intact, as in Yellowstone following the 1988 fires (see Figure 41.19).

(a) Soon after fire. While all trees in the foreground of this photograph were killed by the fire, unburned trees can be seen in other locations.



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

▲ **Figure 41.19 Recovery following a large-scale disturbance.** The 1988 Yellowstone National Park fires burned large areas of forests dominated by lodgepole pines.

During primary succession, the only life-forms initially present are often 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 dominant form of vegetation. Producing such a community through primary succession may take hundreds or thousands of years.

Early-arriving species and later-arriving ones may be linked by 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.

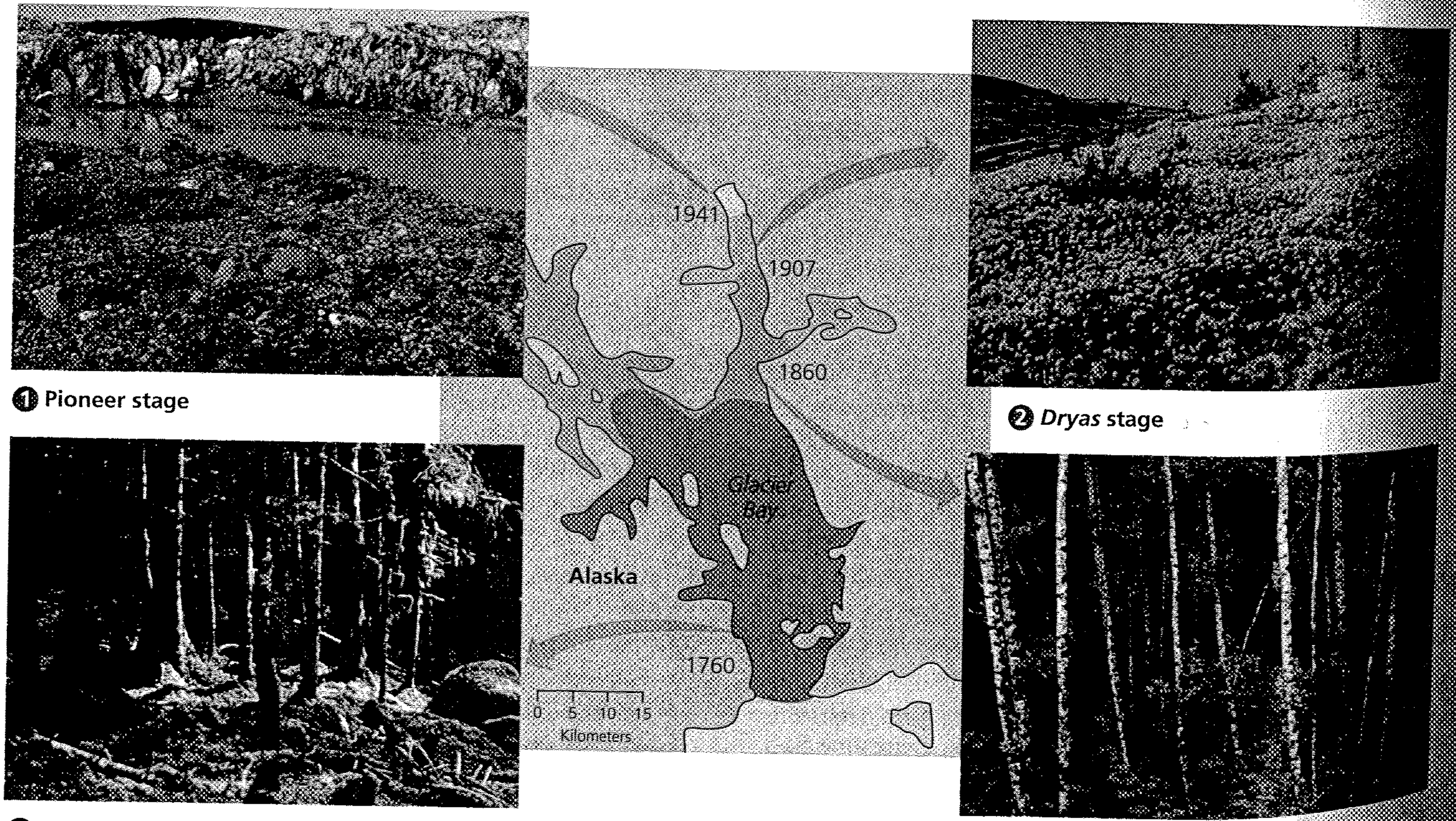
Ecologists have conducted some of the most extensive research on primary succession at Glacier Bay in southeastern Alaska, where glaciers have retreated more than 100 km since 1760 **(Figure 41.20)**. By studying the communities at different distances from the mouth of the bay, ecologists can examine different stages in succession. ❶ The exposed glacial moraine is colonized first by pioneering species that include liverworts, mosses, fireweed, scattered *Dryas* (a mat-forming shrub), and willows. ❷ After about three decades, *Dryas* dominates the plant community. ❸ A few decades later, the area is invaded by alder, which forms dense thickets up to 9 m tall. ❹ In the next two centuries, these alder stands are overgrown first by Sitka spruce and later by 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 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.

Succession on glacial moraines is related to changes in soil nutrients and other environmental factors caused by transitions in the vegetation. 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 limited nitrogen supply. The exceptions are *Dryas* and alder, which have symbiotic bacteria that fix atmospheric nitrogen (see Concept 29.4). Soil nitrogen content increases quickly during the alder stage of succession and keeps increasing during the spruce stage. By altering soil properties, pioneer plant species can facilitate colonization by new plant species during succession.

Human Disturbance

Ecological succession is a response to disturbance of the environment, and the strongest disturbances are human activities. Agricultural development has disrupted what were once the vast grasslands of the North American prairie. 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, in which boats drag weighted nets across the seafloor, are similar to those of clear-cutting a forest or plowing a field **(Figure 41.21)**. The trawls scrape and scour corals and other life on the seafloor. In a typical year, ships trawl an area about the size of South America, 150 times larger than the area of forests that are clear-cut annually.



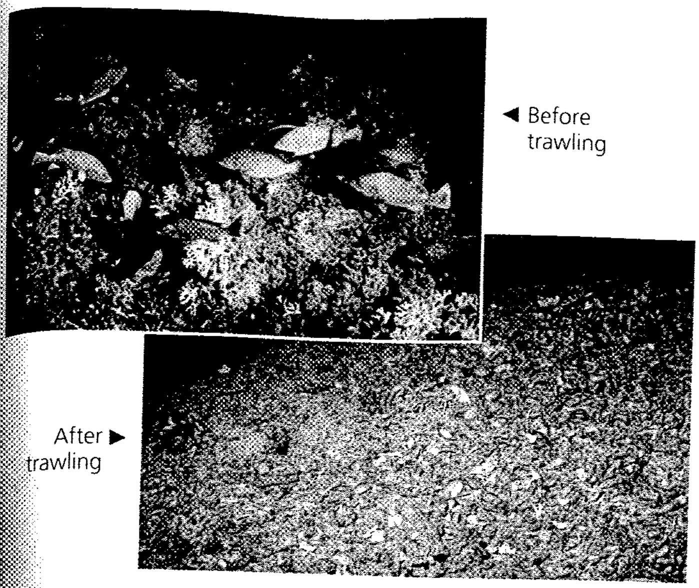
❶ Pioneer stage

❷ *Dryas* stage

❹ Spruce stage

❸ Alder stage

▲ **Figure 41.20 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 41.21 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.

Because disturbance by human activities is often severe, it reduces species diversity in many communities. In Chapter 43, we'll take a closer look at how human-caused disturbance is affecting the diversity of life.

CONCEPT CHECK 41.3

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 41.4

Biogeographic factors affect ommunity diversity

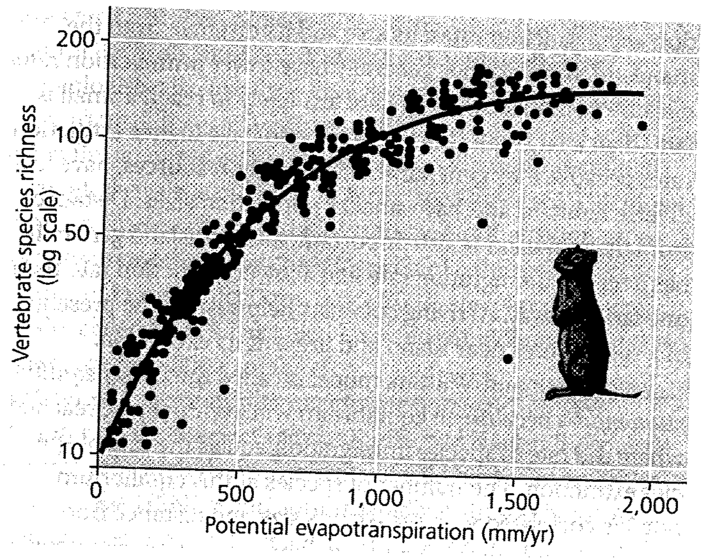
ar we have examined relatively small-scale or local factors influence the diversity of communities, including the ef- s of species interactions, dominant species, and many types isturbances. Ecologists also recognize that large-scale bio- graphic factors contribute to the tremendous range of di- ity observed in biological communities. The contributions o biogeographic factors in particular—the latitude of a munity and the area it occupies—have been investigated ore than a century.

udinal Gradients

e 1850s, both Charles Darwin and Alfred Wallace pointed at plant and animal life was generally more abundant and e 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. Many groups of animals show similar latitudinal gradients. For instance, there are more than 200 species of ants in Brazil, but only 7 in Alaska.

Two key factors that can affect latitudinal gradients of species richness are evolutionary history and climate. Over the course of evolution, species richness may increase in a community as more speciation events occur (see Concept 22.2). Tropical communities are generally older than temperate or polar communities, which have repeatedly "started over" after major disturbances such as glaciations. As a result, species diversity may be highest in the tropics simply because there has been more time for speciation to occur in tropical communities than in temperate or polar communities.

Climate is another key factor thought to affect latitudinal gradients of richness and diversity. In terrestrial communities, the two main climatic factors correlated with diversity are sunlight and precipitation, both of which occur at high levels in the tropics. These factors can be considered together by measuring a community's rate of **evapotranspiration**, the evaporation of water from soil and 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, as shown for vertebrates and potential evapotranspiration in **Figure 41.22**.



▲ **Figure 41.22 Energy, water, and species richness.** Vertebrate species richness in North America increases predictably with potential evapotranspiration, expressed as rainfall equivalents (mm/yr).

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 more species it has, in part because larger areas offer a greater diversity of habitats and microhabitats. The basic concept of diversity increasing with increasing area applies in many situations, from surveys of ant diversity in New Guinea to studies of plant species richness on islands of different sizes.

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 habitat fragments—any patch surrounded by an environment not suitable for the "island" species. 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.

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 on the island become extinct. 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.

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 than a large 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; a closer island generally has a higher immigration rate and a lower extinction rate than one farther away. Arriving colonists help sustain the presence of a species on a near island and prevent its extinction.

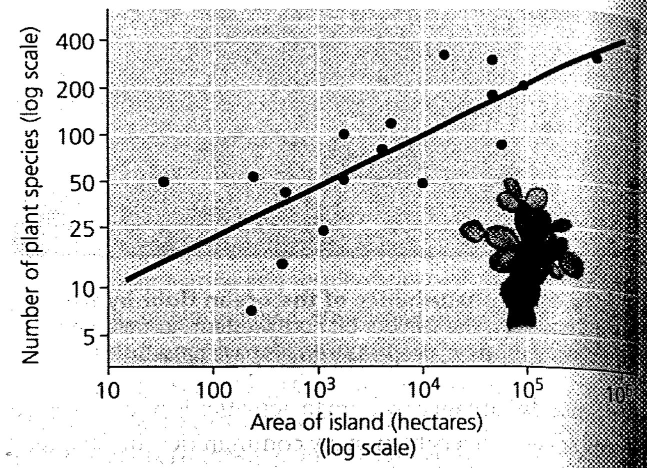
MacArthur and Wilson's model is called the *island equilibrium model* because an equilibrium will eventually be reached where the rate of species immigration equals the rate of species extinction. The number of species at this equilibrium point is correlated with the island's size and distance from the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

▼ Figure 41.23 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.

Data from R. H. MacArthur and E. O. Wilson, The theory of island biogeograp Princeton University Press, Princeton, NJ (1967).

WHAT IF? Five islands in this study ranging in area from about 40 ha 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?

MacArthur and Wilson's studies of the diversity of plants and animals on island chains support the prediction that species richness increases with island size, in keeping with the island equilibrium model **(Figure 41.23)**. Species counts als fit the prediction that the number of species decreases wit increasing remoteness of the island.

Over long periods, disturbances such as storms, adapti evolutionary changes, and speciation generally alter the sp composition and community structure on islands. Nonetheless, the island equilibrium model is widely applied in ecol Conservation biologists in particular use it when designin habitat reserves or establishing a starting point for predic the effects of habitat loss on species diversity.

CONCEPT CHECK 41.4

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

For suggested answers, see Appendix A.

CONCEPT 41.5

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 and viruses. Scientists have only recently come to appreciate how universal the effects of pathogens are in structuring ecological communities.

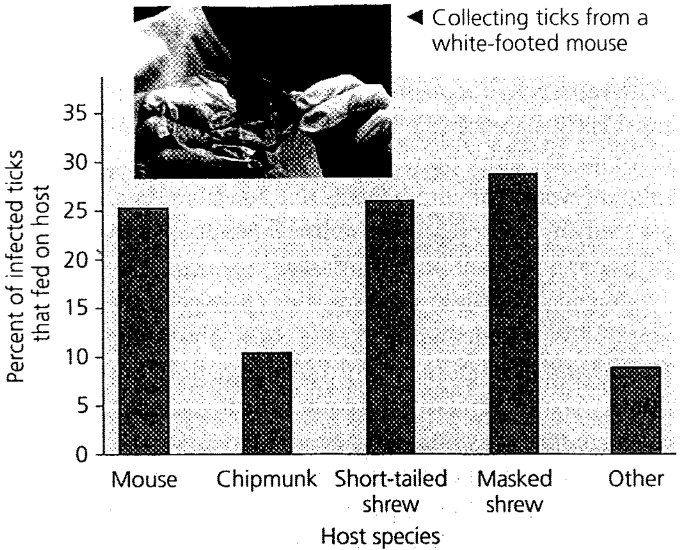
Effects on Community Structure

Pathogens produce especially clear effects on community structure when they are introduced into new habitats. Coral reef communities, for example, are increasingly susceptible 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 the disease, staghorn coral (*Acropora cervicornis*) has virtually disappeared from the Caribbean since the 1980s. Populations of elkhorn coral (*Acropora palmata*) have also been decimated. Such corals provide key habitat for lobsters as well snappers and other fish species. When the corals die, they 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 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 several species are dying from sudden oak death (SOD). This recently discovered disease is caused by the protist *Phytophthora ramorum* (see Concept 25.4). SOD was first described in California in 1995, when hikers noticed trees dying around San Francisco Bay. By 2014, it had spread more 1,000 km, from the central California coast to southern Oregon, and it had killed more than a million oaks and other The loss of the oaks has led to the decreased abundance least five bird species, including the acorn woodpecker the oak titmouse, that rely on the oaks for food and habi- 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.

Community Ecology and Zoonotic Diseases

quarters of emerging human diseases and many most devastating diseases are caused by **zoonotic pathogens**—those that are transferred to humans from other either through direct contact with an infected animal means of an intermediate species, called a **vector**. The vectors that spread zoonotic diseases are often parasites, including ticks, lice, and mosquitoes.



▲ **Figure 41.24 Unexpected hosts of the Lyme disease pathogen.** A combination of ecological data and genetic analyses enabled scientists to show that more than half of ticks carrying the Lyme pathogen became infected by feeding on the short-tailed shrew (*Blarina brevicauda*) or the masked shrew (*Sorex cinereus*).

MAKE CONNECTIONS *Concept 21.1 describes genetic variation between populations. How might genetic variation between shrew populations in different locations affect the number of infected ticks?*

Identifying the community of hosts and vectors for a pathogen can help prevent illnesses such as Lyme disease, which is spread by ticks. For years, scientists thought that the primary host for the Lyme pathogen was the white-footed mouse 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. Further investigation in New York revealed that two inconspicuous shrew species were the hosts of more than half the infected ticks collected in the field **(Figure 41.24)**. Identifying the dominant hosts for a pathogen provides information that may be used to control the hosts most responsible for spreading diseases.

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 Concept 17.3). 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 300 people.

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. By 2015, the virus had not appeared in Australia or South America, but one human case had occurred in North America; this took place in Canada when a person returning from China became ill with the virus and later died. With respect to the possible spread of H5N1 by birds, the most likely place for infected wild birds to enter the Americas is Alaska, the entry point for ducks, geese, and shorebirds that migrate every year across the Bering Sea from Asia. Ecologists are studying the spread of the virus by trapping and testing migrating and resident birds in Alaska.

Human activities are transporting pathogens around the world at unprecedented rates. Genetic analyses suggest that *P. ramorum* likely came to North America from Europe in nursery plants. 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 2010, this flu outbreak had a confirmed death toll of more than 18,000 people. The actual number may have been significantly higher since many people who died with flu-like symptoms were not tested for H1N1.

While our emphasis here has been on community ecology, pathogens 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 42.

CONCEPT CHECK 41.5

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.

41 Chapter Review

AP® Are there ecological communities in which humans could be considered a keystone species? Could they be considered an invasive species in others? What evidence do you need to evaluate the question? **(Big Idea 4)**

SUMMARY OF KEY CONCEPTS

VOCAB SELF-QUIZ
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CONCEPT 41.1

Interactions within a community may help, harm, or have no effect on the species involved (pp. 868–873)

- As shown in the table, ecological interactions can be grouped into three broad categories: competition, exploitation, and positive interactions.

Interaction	Description
Competition (−/−)	Two or more species compete for a resource that is in short supply.
Exploitation (+/−)	One species benefits by feeding upon the other species, which is harmed. Exploitation includes:
Predation	One species, the predator, kills and eats the other, the prey.
Herbivory	An herbivore eats part of a plant or alga.
Parasitism	The **parasite** derives its nourishment from a second organism, its **host**, which is harmed.
Positive interactions (+/+ or +/0)	One species benefits, while the other species benefits or is not harmed. Positive interactions include:
Mutualism (+/+)	Both species benefit from the interaction.
Commensalism (+/0)	One species benefits, while the other is not affected.

- **Competitive exclusion** states that two species competing for the same resource cannot coexist permanently in the same place. **Resource partitioning** is the differentiation of **ecological niches** that enables species to coexist in a community.

? *For each interaction listed in the table above, give an example of a pair of species that exhibit the interaction.*

CONCEPT 41.2

Diversity and trophic structure characterize biological communities (pp. 873–878)

- **Species diversity** is affected by both 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.
- **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**.
- **Dominant species** are the most abundant species in a community. **Keystone species** are usually less abundant species that exert a disproportionate influence on community structure. **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. 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 41.3

Disturbance influences species diversity and composition (pp. 878–881)

- 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.
- Humans are the most widespread agents of disturbance, and their effects on communities often reduce species diversity.

Is the disturbance pictured in Figure 41.21 more likely to initiate primary or secondary succession? Explain.

CONCEPT 41.4

Biogeographic factors affect community diversity (pp. 881–882)

- Species richness generally declines along a latitudinal gradient from the tropics to the poles. Climate influences the diversity gradient through energy (heat and light) and water. The greater age of tropical environments also may contribute to their greater species richness.
- Species richness is directly related to a community's geographic size, a principle formalized in the **species-area curve**. The island equilibrium model maintains that species richness on an ecological island reaches an equilibrium where new immigrations are balanced by extinctions.

How have periods of glaciation influenced latitudinal patterns of diversity?

CONCEPT 41.5

Pathogens alter community structure locally and globally (pp. 883–884)

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

Suppose a pathogen attacks a keystone species. Explain how this could alter the structure of the community.

TEST YOUR UNDERSTANDING

PRACTICE TEST

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Level 1: Knowledge/Comprehension

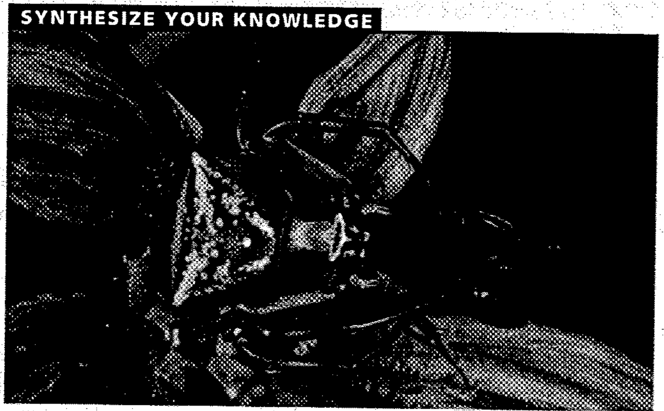
1. The feeding relationships among the species in a community determine the community's
   (A) secondary succession.
   (B) ecological niche.
   (C) species richness.
   (D) trophic structure.
2. Based on the intermediate disturbance hypothesis, a community's species diversity is increased by
   (A) frequent massive disturbance.
   (B) stable conditions with no disturbance.
   (C) moderate levels of disturbance.
   (D) human intervention to eliminate disturbance.

Level 2: Application/Analysis

3. 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
4. Community 1 contains 100 individuals distributed among four species: 5A, 5B, 85C, and 5D. Community 2 contains 100 individuals distributed among three species: 30A, 40B, and 30C. **Calculate** the Shannon diversity index (H) for each community. **Identify** which community is more diverse.

Level 3: Synthesis/Evaluation AP®

5. **SCIENTIFIC INQUIRY/Science Practice 1**
   DRAW IT In the Chesapeake Bay, the blue crab 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, **describe** what would happen to the abundance of eelgrass if humans stopped eating blue crabs.
6. **SCIENTIFIC INQUIRY/Science Practice 3**
   An ecologist studying plants in the desert performed the following experiment. She staked out two identical plots, containing sagebrush plants and 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?
7. **CONNECT TO BIG IDEA 1**
   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?
8. **CONNECT TO BIG IDEA 4**
   In Batesian mimicry, a palatable species gains protection by mimicking an unpalatable one. Imagine that individuals of a palatable, brightly colored fly species are blown 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 island over time if coloration is a genetically controlled trait. **Explain** your predictions.
9. **SYNTHESIZE YOUR KNOWLEDGE**



SCIENTIFIC INQUIRY/Science Practice 7
Describe two types of interspecific interactions that appear to be occurring between the three species shown in this photo. **Identify** the morphological adaptation that can be seen in the species that is at the highest trophic level in this scene.

For selected answers, see Appendix A.