

# 25

## Community Ecology

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### Concept Outline

#### 25.1 Interactions among competing species shape ecological niches.

**The Realized Niche.** Interspecific interactions often limit the portion of their niche that they can actually use.

**Gause and the Principle of Competitive Exclusion.** No two species can occupy the same niche indefinitely without competition driving one to extinction.

**Resource Partitioning.** Species that live together partition the available resources, reducing competition.

**Detecting Interspecific Competition.** Experiments are often the best way to detect competition, but they have their limitations.

#### 25.2 Predators and their prey coevolve.

**Predation and Prey Populations.** Predators can limit the size of populations and sometimes even eliminate a species from a community.

**Plant Defenses against Herbivores.** Plants use chemicals to defend themselves against animals trying to eat them.

**Animal Defenses against Predators.** Animals defend themselves with camouflage, chemicals, and stings.

**Mimicry.** Sometimes a species copies the appearance of another protected one.

#### 25.3 Evolution sometimes fosters cooperation.

**Coevolution and Symbiosis.** Organisms have evolved many adjustments and accommodations to living together.

**Commensalism.** Some organisms use others, neither hurting or helping their benefactors.

**Mutualism.** Often species interact in ways that benefit both.

**Parasitism.** Sometimes one organism serves as the food supply of another much smaller one.

**Interactions among Ecological Processes.** Multiple processes may occur simultaneously within a community.

#### 25.4 Ecological succession may increase species richness.

**Succession.** Communities change through time.

**The Role of Disturbance.** Disturbances can disrupt successional change. In some cases, moderate amounts of disturbance increase species diversity.



FIGURE 25.1

**Communities involve interactions between disparate groups.**

This clownfish is one of the few species that can nestle safely among the stinging tentacles of the sea anemone—a classic example of a symbiotic relationship.

All the organisms that live together in a place are called a community. The myriad species that inhabit a tropical rain forest are a community. Indeed, every inhabited place on earth supports its own particular array of organisms. Over time, the different species have made many complex adjustments to community living (figure 25.1), evolving together and forging relationships that give the community its character and stability. Both competition and cooperation have played key roles; in this chapter, we will look at these and other factors in community ecology.

## 25.1 Interactions among competing species shape ecological niches.

### The Realized Niche

Each organism in an ecosystem confronts the challenge of survival in a different way. The **niche** an organism occupies is the sum total of all the ways it utilizes the resources of its environment. A niche may be described in terms of space utilization, food consumption, temperature range, appropriate conditions for mating, requirements for moisture, and other factors. *Niche* is not synonymous with **habitat**, the place where an organism lives. *Habitat* is a place, *niche* a pattern of living.

Sometimes species are not able to occupy their entire niche because of the presence or absence of other species. Species can interact with each other in a number of ways, and these interactions can either have positive or negative effects. One type of interaction is **interspecific competition**, which occurs when two species attempt to utilize the same resource when there is not enough of the resource to satisfy both. Fighting over resources is referred to as **interference competition**; consuming shared resources is called **exploitative competition**.

The entire niche that a species is capable of using, based on its physiological requirements and resource needs, is called the **fundamental niche**. The actual niche the species occupies is called its **realized niche**. Because of interspecific interactions, the realized niche of a species may be considerably smaller than its fundamental niche.

In a classic study, J. H. Connell of the University of California, Santa Barbara investigated competitive interactions between two species of barnacles that grow together on rocks along the coast of Scotland. Of the two species Connell studied, *Chthamalus stellatus* lives in shallower water, where tidal action often exposed it to air, and *Semibalanus balanoides* (called *Balanus balanoides* prior to 1995) lives lower down, where it is rarely exposed to the atmosphere (figure 25.2). In the deeper zone, *Semibalanus* could always outcompete *Chthamalus* by crowding it off the rocks, undercutting it, and replacing it even where it had begun to grow, an example of interference competition. When Connell removed *Semibalanus* from the area, however, *Chthamalus* was easily able to occupy the deeper zone, indicating that no physiological or other general obstacles prevented it from becoming established there. In contrast, *Semibalanus* could not survive in the shallow-water habitats where *Chthamalus* normally occurs; it evidently does not have the special adaptations that allow *Chthamalus* to occupy this zone. Thus, the fundamental niche of the barnacle *Chthamalus* included both shallow and deeper zones, but its realized niche was much narrower because *Chthamalus* was outcompeted by *Semibalanus* in parts of its fundamental niche. By contrast, the realized and fundamental niches of *Semibalanus* appear to be identical.

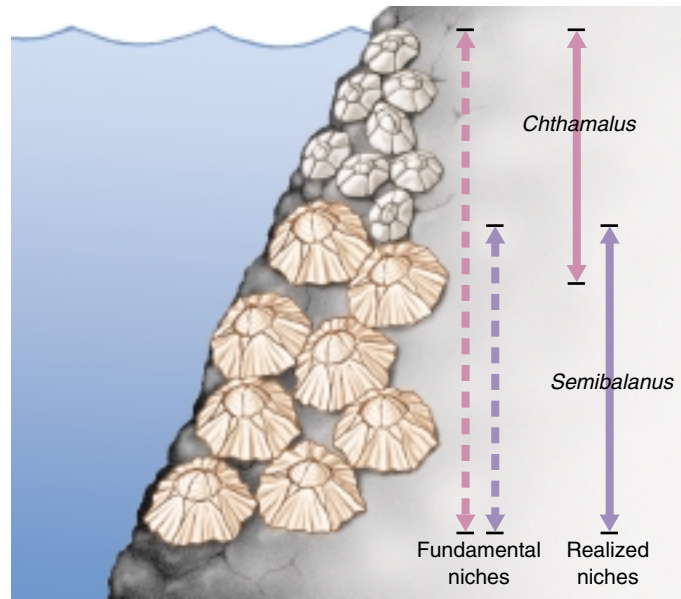


FIGURE 25.2

#### Competition among two species of barnacles limits niche use.

*Chthamalus* can live in both deep and shallow zones (its fundamental niche), but *Semibalanus* forces *Chthamalus* out of the part of its fundamental niche that overlaps the realized niche of *Semibalanus*.

Processes other than competition can also restrict the realized niche of a species. For example, a plant, the St. John's-wort, was introduced and became widespread in open rangeland habitats in California until a specialized beetle was introduced to control it. Populations of the plant quickly decreased and it is now only found in shady sites where the beetle cannot thrive. In this case, the presence of a predator limits the realized niche of a plant.

In some cases, the absence of another species leads to a smaller realized niche. For example, many North American plants depend on the American honeybee for pollination. The honeybee's population is currently declining for a variety of reasons. Conservationists are concerned that if the honeybee disappears from some habitats, the niche of these plant species will decrease or even disappear entirely. In this case, then, the absence—rather than the presence—of another species will be cause of a relatively small realized niche.

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A niche may be defined as the way in which an organism utilizes its environment. Interspecific interactions may cause a species' realized niche to be smaller than its fundamental niche. If resources are limiting, two species normally cannot occupy the same niche indefinitely.

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## Gause and the Principle of Competitive Exclusion

In classic experiments carried out in 1934 and 1935, Russian ecologist G. F. Gause studied competition among three species of *Paramecium*, a tiny protist. All three species grew well alone in culture tubes, preying on bacteria and yeasts that fed on oatmeal suspended in the culture fluid (figure 25.3a). However, when Gause grew *P. aurelia* together with *P. caudatum* in the same culture tube, the numbers of *P. caudatum* always declined to extinction, leaving *P. aurelia* the only survivor (figure 25.3b). Why? Gause found *P. aurelia* was able to grow six times faster than its competitor *P. caudatum* because it was able to better utilize the limited available resources, an example of exploitative competition.

From experiments such as this, Gause formulated what is now called the **principle of competitive exclusion**. This principle states that if two species are competing for a limited resource, the species that uses the resource more efficiently will eventually eliminate the other locally—no two species with the same niche can coexist when resources are limiting.

### Niche Overlap

In a revealing experiment, Gause challenged *Paramecium caudatum*—the defeated species in his earlier experiments—with a third species, *P. bursaria*. Because he expected these two species to also compete for the limited bacterial food supply, Gause thought one would win out, as had happened in his previous experiments. But that's not what happened. Instead, both species survived in the culture tubes; the

paramecia found a way to divide the food resources. How did they do it? In the upper part of the culture tubes, where the oxygen concentration and bacterial density were high, *P. caudatum* dominated because it was better able to feed on bacteria. However, in the lower part of the tubes, the lower oxygen concentration favored the growth of a different potential food, yeast, and *P. bursaria* was better able to eat this food. The fundamental niche of each species was the whole culture tube, but the realized niche of each species was only a portion of the tube. Because the niches of the two species did not overlap too much, both species were able to survive. However, competition did have a negative effect on the participants (figure 25.3c). When grown without a competitor, both species reached densities three times greater than when they were grown with a competitor.

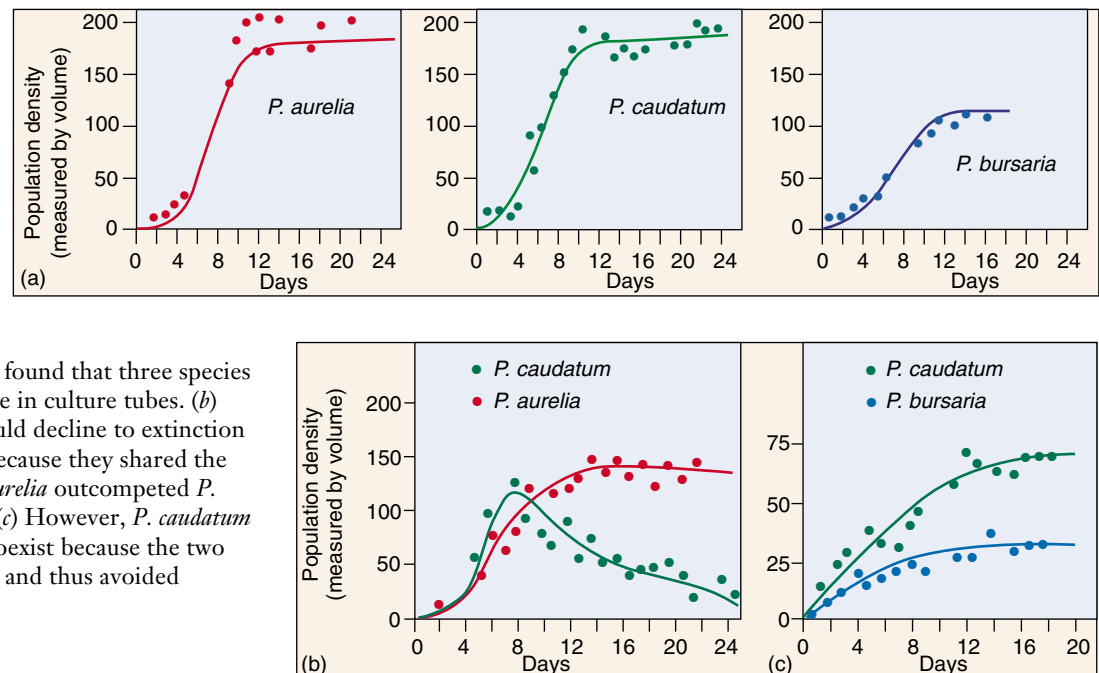
### Competitive Exclusion

Gause's principle of competitive exclusion can be restated to say that *no two species can occupy the same niche indefinitely when resources are limiting*. Certainly species can and do coexist while competing for some of the same resources. Nevertheless, Gause's theory predicts that when two species coexist on a long-term basis, either resources must not be limited or their niches will always differ in one or more features; otherwise, one species will outcompete the other and the extinction of the second species will inevitably result, a process referred to as **competitive exclusion**.

**If resources are limiting, no two species can occupy the same niche indefinitely without competition driving one to extinction.**

**FIGURE 25.3**  
**Competitive exclusion among three species of *Paramecium*.** In the microscopic world, *Paramecium* is a ferocious predator. Paramecia eat by ingesting their prey; their cell membranes surround bacterial or yeast cells, forming a food vacuole containing the prey cell.

(a) In his experiments, Gause found that three species of *Paramecium* grew well alone in culture tubes. (b) But *Paramecium caudatum* would decline to extinction when grown with *P. aurelia* because they shared the same realized niche, and *P. aurelia* outcompeted *P. caudatum* for food resources. (c) However, *P. caudatum* and *P. bursaria* were able to coexist because the two have different realized niches and thus avoided competition.



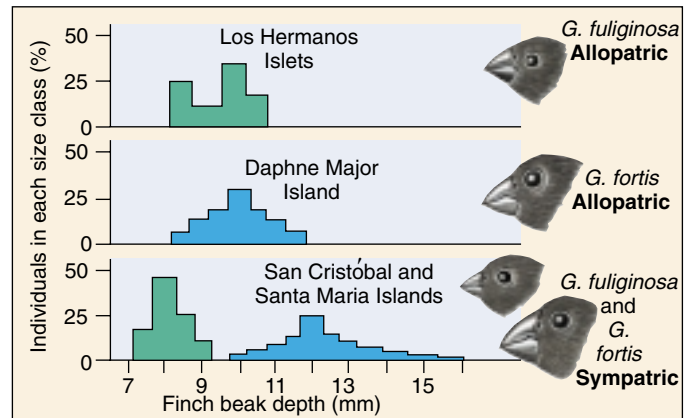


## Resource Partitioning

Gause's exclusion principle has a very important consequence: persistent competition between two species is rare in natural communities. Either one species drives the other to extinction, or natural selection reduces the competition between them. When the late Princeton ecologist Robert MacArthur studied five species of warblers, small insect-eating forest songbirds, he found that they all appeared to be competing for the same resources. However, when he studied them more carefully, he found that each species actually fed in a different part of spruce trees and so ate different subsets of insects. One species fed on insects near the tips of branches, a second within the dense foliage, a third on the lower branches, a fourth high on the trees and a fifth at the very apex of the trees. Thus, each species of warbler had evolved so as to utilize a different portion of the spruce tree resource. They *subdivided the niche*, partitioning the available resource so as to avoid direct competition with one another.

Resource partitioning is often seen in similar species that occupy the same geographical area. Such **sympatric species** often avoid competition by living in different portions of the habitat or by utilizing different food or other resources (figure 25.4). This pattern of resource partitioning is thought to result from the process of natural selection causing initially similar species to diverge in resource use in order to reduce competitive pressures.

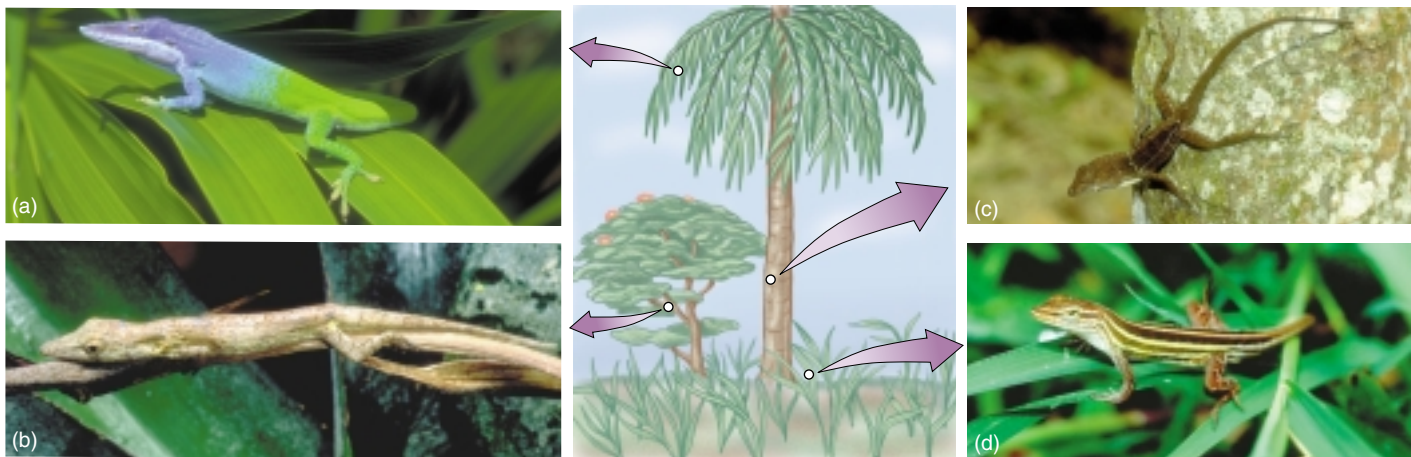
Evidence for the role of evolution comes from comparison of species whose ranges are only partially overlapping. Where the two species co-occur, they tend to exhibit greater differences in **morphology** (the form and structure of an organism) and resource use than do their allopatric



**FIGURE 25.5**  
**Character displacement in Darwin's finches.** These two species of finches (genus *Geospiza*) have bills of similar size when allopatric, but different size when sympatric.

populations. Called **character displacement**, the differences evident between sympatric species are thought to have been favored by natural selection as a mechanism to facilitate habitat partitioning and thus reduce competition. Thus, the two Darwin's finches in figure 25.5 have bills of similar size where the finches are allopatric, each living on an island where the other does not occur. On islands where they are sympatric, the two species have evolved beaks of different sizes, one adapted to larger seeds, the other to smaller ones.

**Sympatric species partition available resources, reducing competition between them.**



**FIGURE 25.4**  
**Resource partitioning among sympatric lizard species.** Species of *Anolis* lizards on Caribbean islands partition their tree habitats in a variety of ways. Some species of anoles occupy the canopy of trees (a), others use twigs on the periphery (b), and still others are found at the base of the trunk (c). In addition, some use grassy areas in the open (d). When two species occupy the same part of the tree, they either utilize different-sized insects as food or partition the thermal microhabitat; for example, one might only be found in the shade, whereas the other would only bask in the sun. Most interestingly, the same pattern of resource partitioning has evolved independently on different Caribbean islands.

## Detecting Interspecific Competition

It is not simple to determine when two species are competing. The fact that two species use the same resources need not imply competition if that resource is not in limited supply. If the population sizes of two species are negatively correlated, such that where one species has a large population, the other species has a small population and vice versa, the two species need not be competing for the same limiting resource. Instead, the two species might be independently responding to the same feature of the environment—perhaps one species thrives best in warm conditions and the other in cool conditions.

### Experimental Studies of Competition

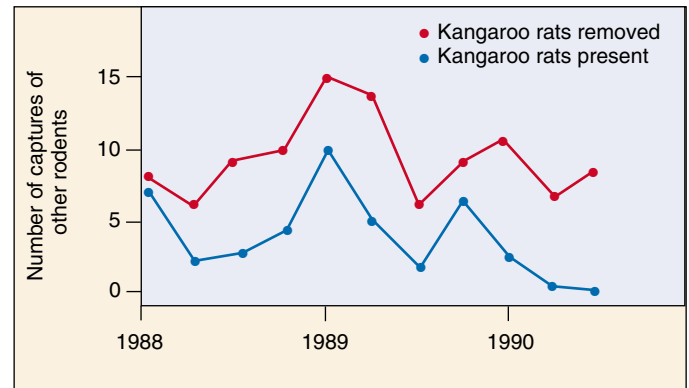
Some of the best evidence for the existence of competition comes from experimental field studies. By setting up experiments in which two species either occur alone or together, scientists can determine whether the presence of one species has a negative effect on a population of a second species. For example, a variety of seed-eating rodents occur in the Chihuahuan Desert of the southwestern part of North America. In 1988, researchers set up a series of 50 meter  $\times$  50 meter enclosures to investigate the effect of kangaroo rats on other, smaller seed-eating rodents. Kangaroo rats were removed from half of the enclosures, but not from the other enclosures. The walls of all of the enclosures had holes in them that allowed rodents to come and go, but in the kangaroo rat removal plots, the holes were too small to allow the kangaroo rats to enter. Over the course of the next three years, the researchers monitored the number of the other, smaller seed-eating rodents present in the plots. As figure 25.6 illustrates, the number of other rodents was substantially higher in the absence of kangaroo rats, indicating that kangaroo rats compete with the other rodents and limit their population sizes.

A great number of similar experiments have indicated that interspecific competition occurs between many species of plants and animals. Effects of competition can be seen in aspects of population biology other than population size, such as behavior and individual growth rates. For example, two species of *Anolis* lizards occur on the island of St. Maarten. When one of the species, *A. gingivinus*, is placed in 12 m  $\times$  12 m enclosures without the other species, individual lizards grow faster and perch lower than lizards of the same species do when placed in enclosures in which *A. pogus* is also present.

### Caution Is Necessary

Although experimental studies can be a powerful means of understanding the interactions that occur between coexisting species, they have their limitations.

First, care is necessary in interpreting the results of field experiments. Negative effects of one species on another do



**FIGURE 25.6**

**Detecting interspecific competition.** This experiment tests the effect of removal of kangaroo rats on the population size of other rodents. Immediately after kangaroo rats were removed, the number of rodents increased relative to the enclosures that still had kangaroo rats. Notice that population sizes (as estimated by number of captures) increased and decreased in synchrony in the two treatments, probably reflecting changes in the weather.

not automatically indicate the existence of competition. For example, many similar-sized fish have a negative effect on each other, but it results not from competition, but from the fact that adults of each species will prey on juveniles of the other species. In addition, the presence of one species may attract predators, which then also prey on the second species. In this case, the second species may have a lower population size in the presence of the first species due to the presence of predators, even if they are not competing at all. Thus, experimental studies are most effective when they are combined with detailed examination of the ecological mechanism causing the negative effect of one species on another species.

In addition, experimental studies are not always feasible. For example, the coyote has increased its population in the United States in recent years simultaneously with the decline of the grey wolf. Is this trend an indication that the species compete? Because of the size of the animals and the large geographic areas occupied by each individual, manipulative experiments involving fenced areas with only one or both species—with each experimental treatment replicated several times for statistical analysis—are not practical. Similarly, studies of slow-growing trees might require many centuries to detect competition between adult trees. In such cases, detailed studies of the ecological requirements of the species are our best bet to understanding interspecific interactions.

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**Experimental studies can provide strong tests of the hypothesis that interspecific competition occurs, but such studies have limitations. Detailed ecological studies are important regardless of whether experiments are conducted.**

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## 25.2 Predators and their prey coevolve.

**Predation** is the consuming of one organism by another. In this sense, predation includes everything from a leopard capturing and eating an antelope, to a deer grazing on spring grass. When experimental populations are set up under simple laboratory conditions, the predator often exterminates its prey and then becomes extinct itself, having nothing left to eat (figure 25.7). However, if refuges are provided for the prey, its population will drop to low levels but not to extinction. Low prey population levels will then provide inadequate food for the predators, causing the predator population to decrease. When this occurs, the prey population can recover.

### Predation and Prey Populations

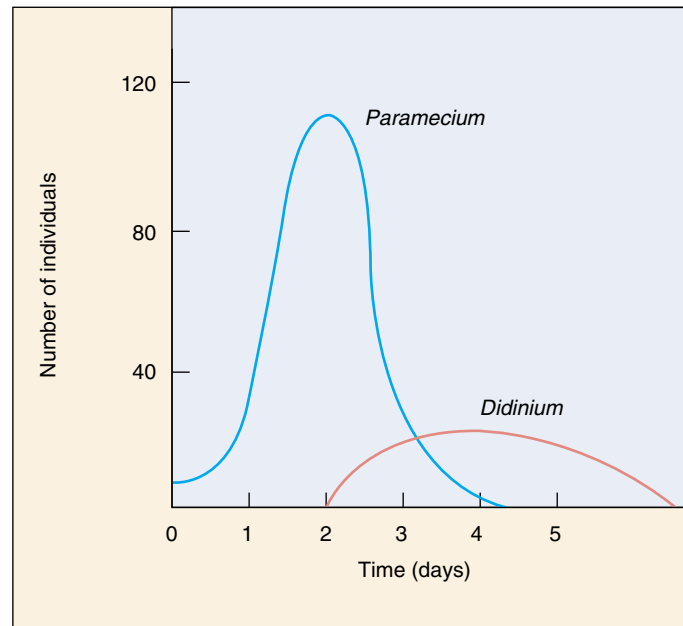
In nature, predators can often have large effects on prey populations. Some of the most dramatic examples involve situations in which humans have either added or eliminated predators from an area. For example, the elimination of large carnivores from much of the eastern United States has led to population explosions of white-tailed deer, which strip the habitat of all edible plant life. Similarly, when sea otters were hunted to near extinction on the western coast of the United States, sea urchin populations exploded.

Conversely, the introduction of rats, dogs, and cats to many islands around the world has led to the decimation of native faunas. Populations of Galápagos tortoises on several islands are endangered, for example, by introduced rats, dogs, and cats, which eat eggs and young tortoises. Similarly, several species of birds and reptiles have been eradicated by rat predation from New Zealand and now only occur on a few offshore islands that the rats have not reached. In addition, on Stephens Island, near New Zealand, every individual of the now extinct Stephen Island wren was killed by a single lighthouse keeper's cat!

A classic example of the role predation can play in a community involves the introduction of prickly pear cactus to Australia in the nineteenth century. In the absence of predators, the cactus spread rapidly, by 1925 occupying 12 million hectares of rangeland in an impenetrable morass of spines that made cattle ranching difficult. To control the cactus, a predator from its natural habitat in Argentina, the moth *Cactoblastis cactorum*, was introduced beginning in 1926. By 1940, cactus populations had been decimated, and it now generally occurs in small populations.

### Predation and Evolution

Predation provides strong selective pressures on prey populations. Any feature that would decrease the probability of



**FIGURE 25.7**

**Predator-prey in the microscopic world.** When the predatory *Didinium* is added to a *Paramecium* population, the numbers of *Didinium* initially rise, while the numbers of *Paramecium* steadily fall. When the *Paramecium* population is depleted, however, the *Didinium* individuals also die.

capture should be strongly favored. In the next three pages, we discuss a number of defense mechanisms in plants and animals. In turn, the evolution of such features will cause natural selection to favor counteradaptations in predator populations. In this way, a coevolutionary arms race may ensue in which predators and prey are constantly evolving better defenses and better means of circumventing these defenses.

One example comes from the fossil record of molluscs and gastropods and their predators. During the Mesozoic period (approximately 65 to 225 million years ago), new forms of predatory fish and crustaceans evolved that were able to crush or tear open shells. As a result, a variety of defensive measures evolved in molluscs and gastropods, including thicker shells, spines, and shells too smooth for predators to be able to grasp. In turn, these adaptations may have pressured predators to evolve ever more effective predatory adaptations and tactics.

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**Predation can have substantial effects on prey populations. As a result prey species often evolve defensive adaptations.**

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## Plant Defenses against Herbivores

Plants have evolved many mechanisms to defend themselves from herbivores. The most obvious are **morphological defenses**: thorns, spines, and prickles play an important role in discouraging browsers, and plant hairs, especially those that have a glandular, sticky tip, deter insect herbivores. Some plants, such as grasses, deposit silica in their leaves, both strengthening and protecting themselves. If enough silica is present in their cells, these plants are simply too tough to eat.

### Chemical Defenses

Significant as these morphological adaptations are, the chemical defenses that occur so widely in plants are even more crucial. Best known and perhaps most important in the defenses of plants against herbivores are **secondary chemical compounds**. These are distinguished from primary compounds, which are regular components of the major metabolic pathways, such as respiration. Many plants, and apparently many algae as well, contain very structurally diverse secondary compounds that are either toxic to most herbivores or disturb their metabolism greatly, preventing, for example, the normal development of larval insects. Consequently, most herbivores tend to avoid the plants that possess these compounds.

The mustard family (Brassicaceae) is characterized by a group of chemicals known as mustard oils. These are the substances that give the pungent aromas and tastes to such plants as mustard, cabbage, watercress, radish, and horseradish. The same tastes we enjoy signal the presence of chemicals that are toxic to many groups of insects. Similarly, plants of the milkweed family (Asclepiadaceae) and the related dogbane family (Apocynaceae) produce a milky sap that deters herbivores from eating them. In addition, these plants usually contain cardiac glycosides, molecules named for their drastic effect on heart function in vertebrates.

### The Evolutionary Response of Herbivores

Certain groups of herbivores are associated with each family or group of plants protected by a particular kind of secondary compound. These herbivores are able to feed on these plants without harm, often as their exclusive food source. For example, cabbage butterfly caterpillars (subfamily Pierinae) feed almost exclusively on plants of the mustard and caper families, as well as on a few other small families of plants that also contain mustard oils (figure



(a)



(b)

**FIGURE 25.8**

**Insect herbivores are well suited to their hosts.** (a) The green caterpillars of the cabbage butterfly, *Pieris rapae*, are camouflaged on the leaves of cabbage and other plants on which they feed. Although mustard oils protect these plants against most herbivores, the cabbage butterfly caterpillars are able to break down the mustard oil compounds. (b) An adult cabbage butterfly.

25.8). Similarly, caterpillars of monarch butterflies and their relatives (subfamily Danainae) feed on plants of the milkweed and dogbane families. How do these animals manage to avoid the chemical defenses of the plants, and what are the evolutionary precursors and ecological consequences of such patterns of specialization?

We can offer a potential explanation for the evolution of these particular patterns. Once the ability to manufacture mustard oils evolved in the ancestors of the caper and mustard families, the plants were protected for a time against most or all herbivores that were feeding on other plants in their area. At some point, certain groups of insects—for example, the cabbage butterflies—evolved the ability to break down mustard oils and thus feed on these plants without harming themselves. Having developed this ability, the butterflies were able to use a new resource without competing with other herbivores for it. Often, in groups of insects such as cabbage butterflies, sense organs have evolved that are able to detect the secondary compounds that their food plants produce. Clearly, the relationship that has formed between cabbage butterflies and the plants of the mustard and caper families is an example of **coevolution**.

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**The members of many groups of plants are protected from most herbivores by their secondary compounds. Once the members of a particular herbivore group evolve the ability to feed on them, these herbivores gain access to a new resource, which they can exploit without competition from other herbivores.**

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## Animal Defenses against Predators

Some animals that feed on plants rich in secondary compounds receive an extra benefit. When the caterpillars of monarch butterflies feed on plants of the milkweed family, they do not break down the cardiac glycosides that protect these plants from herbivores. Instead, the caterpillars concentrate and store the cardiac glycosides in fat bodies; they then pass them through the chrysalis stage to the adult and even to the eggs of the next generation. The incorporation of cardiac glycosides thus protects all stages of the monarch life cycle from predators. A bird that eats a monarch butterfly quickly regurgitates it (figure 25.9) and in the future avoids the conspicuous orange-and-black pattern that characterizes the adult monarch. Some birds, however, appear to have acquired the ability to tolerate the protective chemicals. These birds eat the monarchs.

### Defensive Coloration

Many insects that feed on milkweed plants are brightly colored; they advertise their poisonous nature using an ecological strategy known as **warning coloration**, or **aposematic coloration**. Showy coloration is characteristic of animals that use poisons and stings to repel predators, while organisms that lack specific chemical defenses are seldom brightly colored. In fact, many have **cryptic coloration**—color that blends with the surroundings and thus hides the individual from predators (figure 25.10). Camouflaged animals usually do not live together in groups because a predator that discovers one individual gains a valuable clue to the presence of others.

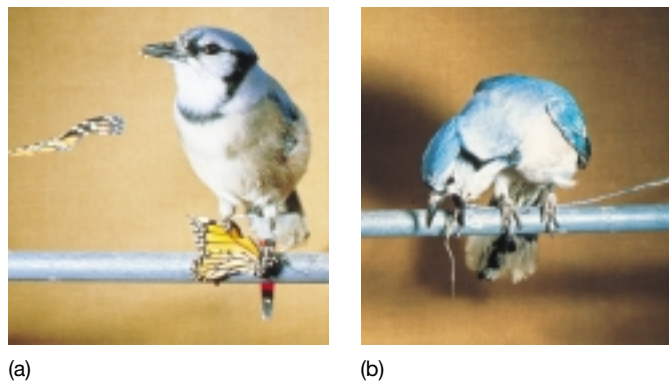
### Chemical Defenses

Animals also manufacture and use a startling array of substances to perform a variety of defensive functions. Bees, wasps, predatory bugs, scorpions, spiders, and many other arthropods use chemicals to defend themselves and to kill their prey. In addition, various chemical defenses have evolved among marine animals and the vertebrates, including venomous snakes, lizards, fishes, and some birds. The poison-dart frogs of the family Dendrobatidae produce toxic alkaloids in the mucus that covers their brightly colored skin (figure 25.11). Some of these toxins are so powerful that a few micrograms will kill a person if injected into the bloodstream. More than 200 different alkaloids have been isolated from these frogs, and some are playing important roles in neuromuscular research. There is an intensive investigation of marine animals, algae, and flowering plants for new drugs to fight cancer and other diseases, or as sources of antibiotics.

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**Animals defend themselves against predators with warning coloration, camouflage, and chemical defenses such as poisons and stings.**

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**FIGURE 25.9**

**A blue jay learns that monarch butterflies taste bad.** (a) This cage-reared jay had never seen a monarch butterfly before it tried eating one. (b) The same jay regurgitated the butterfly a few minutes later. This bird will probably avoid trying to capture all orange-and-black insects in the future.



**FIGURE 25.10**

**Cryptic coloration.** An inchworm caterpillar (*Necophora quernaria*) (hanging from the upper twig) closely resembles a twig.



**FIGURE 25.11**

**Vertebrate chemical defenses.** Frogs of the family Dendrobatidae, abundant in the forests of Latin America, are extremely poisonous to vertebrates. Dendrobatids advertise their toxicity with aposematic coloration, as shown here.



## Mimicry

During the course of their evolution, many species have come to resemble distasteful ones that exhibit aposematic coloration. The mimic gains an advantage by looking like the distasteful model. Two types of mimicry have been identified: Batesian and Müllerian mimicry.

### Batesian Mimicry

**Batesian mimicry** is named for Henry Bates, the British naturalist who first brought this type of mimicry to general attention in 1857. In his journeys to the Amazon region of South America, Bates discovered many instances of palatable insects that resembled brightly colored, distasteful species. He reasoned that the mimics would be avoided by predators, who would be fooled by the disguise into thinking the mimic actually is the distasteful model.

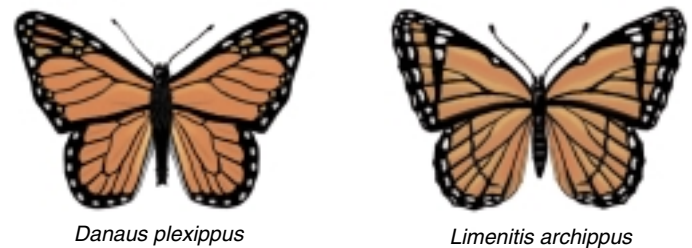
Many of the best-known examples of Batesian mimicry occur among butterflies and moths. Obviously, predators in systems of this kind must use visual cues to hunt for their prey; otherwise, similar color patterns would not matter to potential predators. There is also increasing evidence indicating that Batesian mimicry can also involve nonvisual cues, such as olfaction, although such examples are less obvious to humans.

The kinds of butterflies that provide the models in Batesian mimicry are, not surprisingly, members of groups whose caterpillars feed on only one or a few closely related plant families. The plant families on which they feed are strongly protected by toxic chemicals. The model butterflies incorporate the poisonous molecules from these plants into their bodies. The mimic butterflies, in contrast, belong to groups in which the feeding habits of the caterpillars are not so restricted. As caterpillars, these butterflies feed on a number of different plant families unprotected by toxic chemicals.

One often-studied mimic among North American butterflies is the viceroy, *Limenitis archippus* (figure 25.12a). This butterfly, which resembles the poisonous monarch, ranges from central Canada through much of the United States and into Mexico. The caterpillars feed on willows and cottonwoods, and neither caterpillars nor adults were thought to be distasteful to birds, although recent findings may dispute this. Interestingly, the Batesian mimicry seen in the adult viceroy butterfly does not extend to the caterpillars: viceroy caterpillars are camouflaged on leaves, resembling bird droppings, while the monarch's distasteful caterpillars are very conspicuous.

### Müllerian Mimicry

Another kind of mimicry, **Müllerian mimicry**, was named for German biologist Fritz Müller, who first described it in 1878. In Müllerian mimicry, several unrelated but protected animal species come to resemble one another (figure



*Danaus plexippus*

*Limenitis archippus*

(a) **Batesian mimicry:** Monarch (*Danaus*) is poisonous; viceroy (*Limenitis*) is palatable mimic



*Heliconius erato*



*Heliconius melpomene*



*Heliconius sapho*



*Heliconius cydno*

(b) **Müllerian mimicry:** two pairs of mimics; all are distasteful

### FIGURE 25.12

**Mimicry.** (a) Batesian mimicry. Monarch butterflies (*Danaus plexippus*) are protected from birds and other predators by the cardiac glycosides they incorporate from the milkweeds and dogbanes they feed on as larvae. Adult monarch butterflies advertise their poisonous nature with warning coloration. Viceroy butterflies (*Limenitis archippus*) are Batesian mimics of the poisonous monarch. (b) Pairs of Müllerian mimics. *Heliconius erato* and *H. melpomene* are sympatric, and *H. sapho* and *H. cydno* are sympatric. All of these butterflies are distasteful. They have evolved similar coloration patterns in sympatry to minimize predation; predators need only learn one pattern to avoid.

25.12b). If animals that resemble one another are all poisonous or dangerous, they gain an advantage because a predator will learn more quickly to avoid them. In some cases, predator populations even evolve an innate avoidance of species; such evolution may occur more quickly when multiple dangerous prey look alike.

In both Batesian and Müllerian mimicry, mimic and model must not only look alike but also act alike if predators are to be deceived. For example, the members of several families of insects that closely resemble wasps behave surprisingly like the wasps they mimic, flying often and actively from place to place.

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**In Batesian mimicry, unprotected species resemble others that are distasteful. Both species exhibit aposematic coloration. In Müllerian mimicry, two or more unrelated but protected species resemble one another, thus achieving a kind of group defense.**

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## 25.3 Evolution sometimes fosters cooperation.

### Coevolution and Symbiosis

The plants, animals, protists, fungi, and bacteria that live together in communities have changed and adjusted to one another continually over a period of millions of years. For example, many features of flowering plants have evolved in relation to the dispersal of the plant's gametes by animals (figure 25.13). These animals, in turn, have evolved a number of special traits that enable them to obtain food or other resources efficiently from the plants they visit, often from their flowers. While doing so, the animals pick up pollen, which they may deposit on the next plant they visit, or seeds, which may be left elsewhere in the environment, sometimes a great distance from the parental plant.

Such interactions, which involve the long-term, mutual evolutionary adjustment of the characteristics of the members of biological communities, are examples of **coevolution**, a phenomenon we have already seen in predator-prey interactions.

#### Symbiosis Is Widespread

Another type of coevolution involves **symbiotic relationships** in which two or more kinds of organisms live together in often elaborate and more-or-less permanent relationships. All symbiotic relationships carry the potential for coevolution between the organisms involved, and in many instances the results of this coevolution are fascinating. Examples of symbiosis include *lichens*, which are associations of certain fungi with green algae or cyanobacteria. Lichens are discussed in more detail in chapter 36. Another important example are *mycorrhizae*, the association between fungi and the roots of most kinds of plants. The fungi expedite the plant's absorption of certain nutrients, and the plants in turn provide the fungi with carbohydrates. Similarly, root nodules that occur in legumes and certain other kinds of plants contain bacteria that fix atmospheric nitrogen and make it available to their host plants.

In the tropics, leafcutter ants are often so abundant that they can remove a quarter or more of the total leaf surface of the plants in a given area. They do not eat these leaves directly; rather, they take them to underground nests, where they chew them up and inoculate them with the spores of particular fungi. These fungi are cultivated by the ants and brought from one specially prepared bed to another, where they grow and reproduce. In turn, the fungi constitute the primary food of the ants and their larvae. The relationship between leafcutter ants and these fungi is an excellent example of symbiosis.



**FIGURE 25.13**  
**Pollination by bat.** Many flowers have coevolved with other species to facilitate pollen transfer. Insects are widely known as pollinators, but they're not the only ones. Notice the cargo of pollen on the bat's snout.

#### Kinds of Symbiosis

The major kinds of symbiotic relationships include (1) **commensalism**, in which one species benefits while the other neither benefits nor is harmed; (2) **mutualism**, in which both participating species benefit; and (3) **parasitism**, in which one species benefits but the other is harmed. Parasitism can also be viewed as a form of predation, although the organism that is preyed upon does not necessarily die.

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**Coevolution is a term that describes the long-term evolutionary adjustments of species to one another. In symbiosis two or more species interact closely, with at least one species benefitting.**

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## Commensalism

Commensalism is a symbiotic relationship that benefits one species and neither hurts nor helps the other. In nature, individuals of one species are often physically attached to members of another. For example, epiphytes are plants that grow on the branches of other plants. In general, the host plant is unharmed, while the epiphyte that grows on it benefits. Similarly, various marine animals, such as barnacles, grow on other, often actively moving sea animals like whales and thus are carried passively from place to place. These “passengers” presumably gain more protection from predation than they would if they were fixed in one place, and they also reach new sources of food. The increased water circulation that such animals receive as their host moves around may be of great importance, particularly if the passengers are filter feeders. The gametes of the passenger are also more widely dispersed than would be the case otherwise.



**FIGURE 25.14**  
**Commensalism in the sea.** Clownfishes, such as this *Amphiprion perideraion* in Guam, often form symbiotic associations with sea anemones, gaining protection by remaining among their tentacles and gleaning scraps from their food. Different species of anemones secrete different chemical mediators; these attract particular species of fishes and may be toxic to the fish species that occur symbiotically with other species of anemones in the same habitat. There are 26 species of clownfishes, all found only in association with sea anemones; 10 species of anemones are involved in such associations, so that some of the anemone species are host to more than one species of clownfish.

### Examples of Commensalism

The best-known examples of commensalism involve the relationships between certain small tropical fishes and sea anemones, marine animals that have stinging tentacles (see chapter 44). These fish have evolved the ability to live among the tentacles of sea anemones, even though these tentacles would quickly paralyze other fishes that touched them (figure 25.14). The anemone fishes feed on the detritus left from the meals of the host anemone, remaining uninjured under remarkable circumstances.

On land, an analogous relationship exists between birds called oxpeckers and grazing animals such as cattle or rhinoceros. The birds spend most of their time clinging to the animals, picking off parasites and other insects, carrying out their entire life cycles in close association with the host animals.

### When Is Commensalism Commensalism?

In each of these instances, it is difficult to be certain whether the second partner receives a benefit or not; there is no clear-cut boundary between commensalism

and mutualism. For instance, it may be advantageous to the sea anemone to have particles of food removed from its tentacles; it may then be better able to catch other prey. Similarly, while often thought of as commensalism, the association of grazing mammals and gleaning birds is actually an example of mutualism. The mammal benefits by having parasites and other insects removed from its body, but the birds also benefit by gaining a dependable source of food.

On the other hand, commensalism can easily transform itself into parasitism. For example, oxpeckers are also known to pick not only parasites, but also scabs off their grazing hosts. Once the scab is picked, the birds drink the blood that flows from the wound. Occasionally, the cumulative effect of persistent attacks can greatly weaken the herbivore, particularly when conditions are not favorable, such as during droughts.

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**Commensalism is the benign use of one organism by another.**

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## Mutualism

Mutualism is a symbiotic relationship among organisms in which both species benefit. Examples of mutualism are of fundamental importance in determining the structure of biological communities. Some of the most spectacular examples of mutualism occur among flowering plants and their animal visitors, including insects, birds, and bats. As we will see in chapter 37, during the course of their evolution, the characteristics of flowers have evolved in large part in relation to the characteristics of the animals that visit them for food and, in doing so, spread their pollen from individual to individual. At the same time, characteristics of the animals have changed, increasing their specialization for obtaining food or other substances from particular kinds of flowers.

Another example of mutualism involves ants and aphids. Aphids, also called greenflies, are small insects that suck fluids from the phloem of living plants with their piercing mouthparts. They extract a certain amount of the sucrose and other nutrients from this fluid, but they excrete much of it in an altered form through their anus. Certain ants have taken advantage of this—in effect, domesticating the aphids. The ants carry the aphids to new plants, where they come into contact with new sources of food, and then consume as food the “honeydew” that the aphids excrete.

### Ants and Acacias

A particularly striking example of mutualism involves ants and certain Latin American species of the plant genus *Acacia*. In these species, certain leaf parts, called stipules, are modified as paired, hollow thorns. The thorns are inhabited by stinging ants of the genus *Pseudomyrmex*, which do not nest anywhere else (figure 25.15). Like all thorns that occur on plants, the acacia horns serve to deter herbivores.

At the tip of the leaflets of these acacias are unique, protein-rich bodies called Beltian bodies, named after the nineteenth-century British naturalist Thomas Belt. Beltian bodies do not occur in species of *Acacia* that are not inhabited by ants, and their role is clear: they serve as a primary food for the ants. In addition, the plants secrete nectar from glands near the bases of their leaves. The ants consume this nectar as well, feeding it and the Beltian bodies to their larvae.

Obviously, this association is beneficial to the ants, and one can readily see why they inhabit acacias of this group. The ants and their larvae are protected within the swollen thorns, and the trees provide a balanced diet, including the sugar-rich nectar and the protein-rich Beltian bodies. What, if anything, do the ants do for the plants?

Whenever any herbivore lands on the branches or leaves of an acacia inhabited by ants, the ants, which continually patrol the acacia’s branches, immediately attack and devour the herbivore. The ants that live in the acacias also help their hosts to compete with other plants. The ants cut away



**FIGURE 25.15**

**Mutualism: ants and acacias.** Ants of the genus *Pseudomyrmex* live within the hollow thorns of certain species of acacia trees in Latin America. The nectaries at the bases of the leaves and the Beltian bodies at the ends of the leaflets provide food for the ants. The ants, in turn, supply the acacias with organic nutrients and protect the acacia from herbivores.

any branches of other plants that touch the acacia in which they are living. They create, in effect, a tunnel of light through which the acacia can grow, even in the lush deciduous forests of lowland Central America. In fact, when an ant colony is experimentally removed from a tree, the acacia is unable to compete successfully in this habitat. Finally, the ants bring organic material into their nests. The parts they do not consume, together with their excretions, provide the acacias with an abundant source of nitrogen.

As with commensalism, however, things are not always as they seem. Ant-acacia mutualisms also occur in Africa. In Kenya, several species of acacia ants occur, but only one species occurs on any tree. One species, *Crematogaster nigriceps*, is competitively inferior to two of the other species. To prevent invasion by other ant species, *C. nigriceps* prunes the branches of the acacia, preventing it from coming into contact with branches of other trees, which would serve as a bridge for invaders. Although this behavior is beneficial to the ant, it is detrimental to the tree, as it destroys the tissue from which flowers are produced, essentially sterilizing the tree. In this case, what has initially evolved as a mutualistic interaction has instead become a parasitic one.

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**Mutualism involves cooperation between species, to the mutual benefit of both.**

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## Parasitism

Parasitism may be regarded as a special form of symbiosis in which the predator, or parasite, is much smaller than the prey and remains closely associated with it. Parasitism is harmful to the prey organism and beneficial to the parasite. The concept of parasitism seems obvious, but individual instances are often surprisingly difficult to distinguish from predation and from other kinds of symbiosis.

### External Parasites

Parasites that feed on the exterior surface of an organism are external parasites, or **ectoparasites**. Many instances of external parasitism are known (figure 25.16). Lice, which live on the bodies of vertebrates—mainly birds and mammals—are normally considered parasites. Mosquitoes are not considered parasites, even though they draw food from birds and mammals in a similar manner to lice, because their interaction with their host is so brief.

**Parasitoids** are insects that lay eggs on living hosts. This behavior is common among wasps, whose larvae feed on the body of the unfortunate host, often killing it.

### Internal Parasites

Vertebrates are parasitized internally by **endoparasites**, members of many different phyla of animals and protists. Invertebrates also have many kinds of parasites that live within their bodies. Bacteria and viruses are not usually considered parasites, even though they fit our definition precisely.

Internal parasitism is generally marked by much more extreme specialization than external parasitism, as shown by the many protist and invertebrate parasites that infect humans. The more closely the life of the parasite is linked with that of its host, the more its morphology and behavior are likely to have been modified during the course of its evolution. The same is true of symbiotic relationships of all sorts. Conditions within the body of an organism are different from those encountered outside and are apt to be much more constant. Consequently, the structure of an internal parasite is often simplified, and unnecessary armaments and structures are lost as it evolves.

### Brood Parasitism

Not all parasites consume the body of their host. In brood parasitism, birds like cowbirds and European cuckoos lay their eggs in the nests of other species. The host parents raise the brood parasite as if it were one of their own clutch, in many cases investing more in feeding the imposter than in feeding their own offspring (figure 25.17). The brood parasite reduces the reproductive success of the foster parent hosts, so it is not surprising that in some cases natural selection has fostered the hosts' ability to detect



**FIGURE 25.16**

**An external parasite.** The flowering plant dodder (*Cuscuta*) is a parasite and has lost its chlorophyll and its leaves in the course of its evolution. Because it is heterotrophic, unable to manufacture its own food, dodder obtains its food from the host plants it grows on.



**FIGURE 25.17**

**Brood parasitism.** This bird is feeding a cuckoo chick in its nest. The cuckoo chick is larger than the adult bird, but the bird does not recognize that the cuckoo is not its own offspring. Cuckoo mothers sneak into the nests of other birds and lay an egg, entrusting the care of their offspring to an unwitting bird of another species.

parasite eggs and reject them. What is more surprising is that in many other species, the ability to detect parasite eggs has not evolved.

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**In parasitism, one organism serves as a host to another organism, usually to the host's disadvantage.**

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## Interactions among Ecological Processes

We have seen the different ways in which species within a community can interact with each other. In nature, however, more than one type of interaction usually occurs at the same time. In many cases, the outcome of one type of interaction is modified or even reversed when another type of interaction is also occurring.

### Predation Reduces Competition

When resources are limiting, a superior competitor can eliminate other species from a community. However, predators can prevent or greatly reduce competitive exclusion by reducing the numbers of individuals of competing species. A given predator may often feed on two, three, or more kinds of plants or animals in a given community. The predator's choice depends partly on the relative abundance of the prey options. In other words, a predator may feed on species *A* when it is abundant and then switch to species *B* when *A* is rare. Similarly, a given prey species may be a primary source of food for increasing numbers of species as it becomes more abundant. In this way, superior competitors may be prevented from outcompeting other species.

Such patterns are often characteristic of biological communities in marine intertidal habitats. For example, in preying selectively on bivalves, sea stars prevent bivalves from monopolizing such habitats, opening up space for many other organisms (figure 25.18). When sea stars are removed from a habitat, species diversity falls precipitously, the seafloor community coming to be dominated by a few species of bivalves. Because predation tends to reduce competition in natural communities, it is usually a mistake to attempt to eliminate a major predator such as wolves or mountain lions from a community. The result is to decrease rather than increase the biological diversity of the community, the opposite of what is intended.

### Parasitism May Counter Competition

Parasites may effect sympatric species differently and thus influence the outcome of interspecific interactions. In a classic experiment, Thomas Park of the University of Chicago investigated interactions between two flour beetles, *Tribolium castaneum* and *T. confusum* with a parasite, *Adelina*. In the absence of the parasite, *T. castaneum* is dominant and *T. confusum* normally goes extinct. When the parasite is present, however, the outcome is reversed and *T. castaneum* perishes. Similar effects of parasites in natural systems have been observed in many species. For example, in the *Anolis* lizards of St. Maarten mentioned previously, the competitively inferior species is resistant to malaria, whereas the other species is highly susceptible. Only in



(a)



(b)

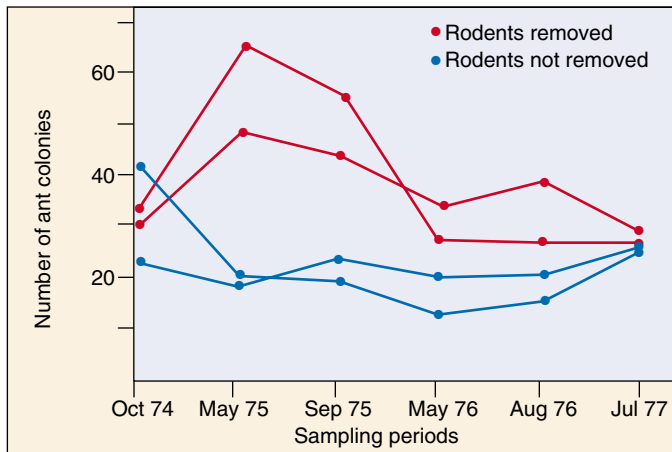
**FIGURE 25.18**  
**Predation reduces competition.** (a) In a controlled experiment in a coastal ecosystem, an investigator removed a key predator (*Pisaster*). (b) In response, fiercely competitive mussels exploded in growth, effectively crowding out seven other indigenous species.

areas in which the malaria parasite occurs are the two species capable of coexisting.

### Indirect Effects

In some cases, species may not directly interact, yet the presence of one species may effect a second species by way of interactions with a third species. Such effects are termed **indirect effects**. For example, in the Chihuahuan Desert, rodents and ants both eat seeds. Thus, one might expect them to compete with each other. However, when all rodents were completely removed from large enclosures (unlike the experiment discussed above, there were no holes in





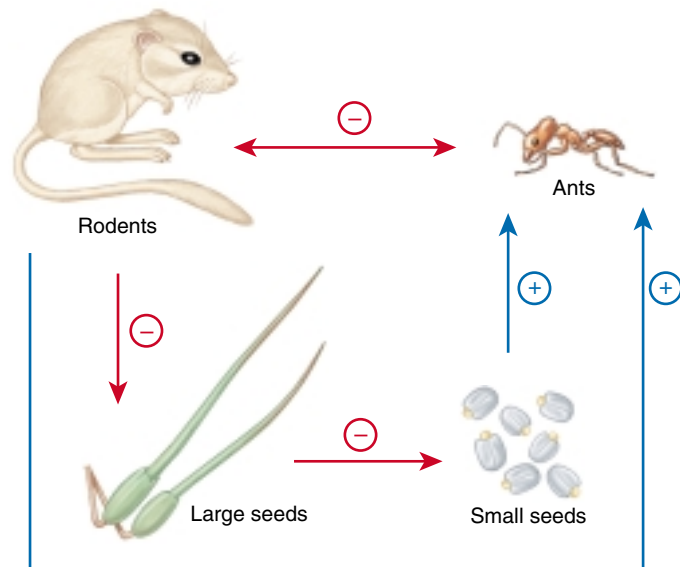
**FIGURE 25.19**  
**Change in ant population size after the removal of rodents.** Ants initially increased in population size relative to ants in the enclosures from which rodents weren't removed, but then these ant populations declined.

the enclosure walls, so once removed, rodents couldn't get back in), ant populations first increased, but then declined (figure 25.19). The initial increase was the expected result of removing a competitor; why did it reverse? The answer reveals the intricacies of natural ecosystems (figure 25.20). Rodents prefer large seeds, whereas ants prefer smaller seeds. Further, in this system plants with large seeds are competitively superior to plants with small seeds. Thus, the removal of rodents leads to an increase in the number of plants with large seeds, which reduces the number of small seeds available to ants, which thus leads to a decline in ant populations. Thus, the effect of rodents on ants is complicated: a direct negative effect of resource competition and an indirect, positive effect mediated by plant competition.

### Keystone Species

Species that have particularly strong effects on the composition of communities are termed **keystone species**. Predators, such as the starfish, can often serve as keystone species by preventing one species from outcompeting others, thus maintaining high levels of species richness in a community.

There are, however, a wide variety of other types of keystone species. Some species manipulate the environment in ways that create new habitats for other species. Beavers, for example, change running streams into small impoundments, changing the flow of water and flooding areas (figure 25.21). Similarly, alligators excavate deep holes at the bottoms of lakes. In times of drought, these holes are the only areas in which water remains, thus allowing aquatic species that otherwise would perish to persist until the drought ends and the lake refills.



**FIGURE 25.20**  
**Rodent-ant interactions.** Rodents and ants both eat seeds, so the presence of rodents has a negative effect on ants and vice versa. However, the presence of rodents has a negative effect on large seeds. In turn, the number of plants with large seeds has a negative effect on plants that produce small seeds. Hence, the presence of rodents should increase the number of small seeds. In turn, the number of small seeds has a positive effect on ant populations. Thus, indirectly, the presence of rodents has a positive effect on ant population size.



**FIGURE 25.21**  
**Example of a keystone species.** Beavers, by constructing dams and transforming flowing streams into ponds, create new habitats for many plant and animal species.

Many different processes are likely to be occurring simultaneously within communities. Only by understanding how these processes interact will we be able to understand how communities function.

## 25.4 Ecological succession may increase species richness.

Even when the climate of an area remains stable year after year, ecosystems have a tendency to change from simple to complex in a process known as **succession**. This process is familiar to anyone who has seen a vacant lot or cleared woods slowly become occupied by an increasing number of plants, or a pond become dry land as it is filled with vegetation encroaching from the sides.

### Succession

If a wooded area is cleared and left alone, plants will slowly reclaim the area. Eventually, traces of the clearing will disappear and the area will again be woods. This kind of succession, which occurs in areas where an existing community has been disturbed, is called **secondary succession**.

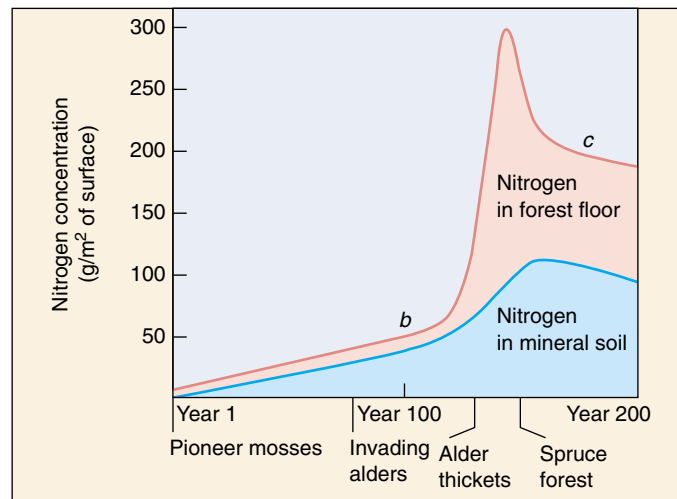
In contrast, **primary succession** occurs on bare, lifeless substrate, such as rocks, or in open water, where organisms gradually move into an area and change its nature. Primary succession occurs in lakes left behind after the retreat of glaciers, on volcanic islands that rise above the sea, and on land exposed by retreating glaciers (figure 25.22). Primary succession on glacial moraines provides an example (figure 25.23). On bare, mineral-poor soil, lichens grow first, forming small pockets of soil. Acidic secretions from the lichens help to break down the substrate and add to the accumulation of soil. Mosses then colonize these pockets of soil, eventually building up enough nutrients in the soil for alder shrubs to take hold. Over a hundred years, the alders build up the soil nitrogen levels until spruce are able to thrive, eventually crowding out the alder and forming a dense spruce forest.

In a similar example, an **oligotrophic** lake—one poor in nutrients—may gradually, by the accumulation of organic matter, become **eutrophic**—rich in nutrients. As this occurs, the composition of communities will change, first increasing in species richness and then declining.

Primary succession in different habitats often eventually arrives at the same kinds of vegetation—vegetation characteristic of the region as a whole. This relationship led American ecologist F. E. Clements, at about the turn of the century, to propose the concept of a final **climax community**. With an increasing realization that (1) the climate keeps changing, (2) the process of succession is often very slow, and (3) the nature of a region's vegetation is being determined to an increasing extent by human activities, ecologists do not consider the concept of "climax community" to be as useful as they once did.

### Why Succession Happens

Succession happens because species alter the habitat and the resources available in it in ways that favor other species.



**FIGURE 25.22**

#### Plant succession produces progressive changes in the soil.

Initially, the glacial moraine at Glacier Bay, Alaska, portrayed in figure 25.23, had little soil nitrogen, but nitrogen-fixing alders led to a buildup of nitrogen in the soil, encouraging the subsequent growth of the conifer forest. Letters in the graph correspond to photographs in parts *b* and *c* of figure 25.23.

Three dynamic concepts are of critical importance in the process: tolerance, inhibition, and facilitation.

- 1. Tolerance.** Early successional stages are characterized by weedy *r*-selected species that are tolerant of the harsh, abiotic conditions in barren areas.
- 2. Facilitation.** The weedy early successional stages introduce local changes in the habitat that favor other, less weedy species. Thus, the mosses in the Glacier Bay succession convert nitrogen to a form that allows alders to invade. The alders in turn lower soil pH as their fallen leaves decompose, and spruce and hemlock, which require acidic soil, are able to invade.
- 3. Inhibition.** Sometimes the changes in the habitat caused by one species, while favoring other species, inhibit the growth of the species that caused them. Alders, for example, do not grow as well in acidic soil as the spruce and hemlock that replace them.

Over the course of succession, the number of species typically increases as the environment becomes more hospitable. In some cases, however, as ecosystems mature, more *K*-selected species replace *r*-selected ones, and superior competitors force out other species, leading ultimately to a decline in species richness.

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**Communities evolve to have greater total biomass and species richness in a process called succession.**

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FIGURE 25.23

**Primary succession at Alaska's Glacier Bay.** (a) The sides of the glacier have been retreating at a rate of some 8 meters a year, leaving behind exposed soil from which nitrogen and other minerals have been leached out. The first invaders of these exposed sites are pioneer moss species with nitrogen-fixing mutualistic microbes. Within 20 years, young alder shrubs take hold. (b) Rapidly fixing nitrogen, they soon form dense thickets. As soil nitrogen levels rise, (c) spruce crowd out the mature alders, forming a forest.

## The Role of Disturbance

Disturbances often interrupt the succession of plant communities. Depending on the magnitude of the disturbance, communities may revert to earlier stages of succession or even, in extreme cases, begin at the earliest stages of primary succession. Disturbances severe enough to disrupt succession include calamities such as forest fires, drought, and floods. Animals may also cause severe disruptions. Gypsy moths can devastate a forest by consuming its trees. Unregulated deer populations may grow explosively, the deer overgrazing and so destroying the forest they live in, in the same way too many cattle overgraze a pasture by eating all available grass down to the ground.

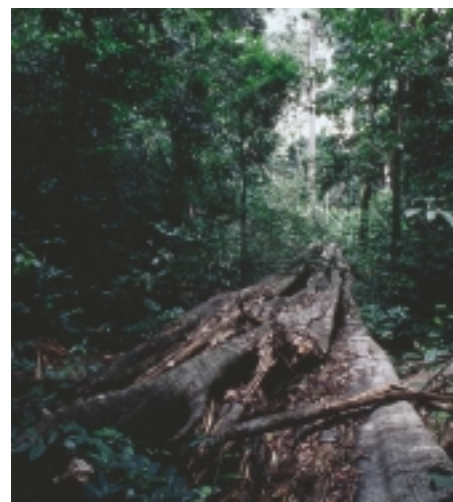
### Intermediate Disturbance Hypothesis

In some cases, disturbance may act to increase the species richness of an area. According to the intermediate disturbance hypothesis, communities experiencing moderate amounts of disturbance will have higher levels of species richness than communities experiencing either little or great amounts of disturbance. Two factors could account for this pattern. First, in communities in which moderate amounts of disturbance occur, patches of habitat will exist at different successional stages. Thus, within the area as a whole, species diversity will be greatest because the full range of species—those characteristic of all stages of succession—will be present. For example, a pattern of intermittent episodic disturbance that produces gaps in the rain forest (like when a tree falls) allows invasion of the gap by other species (figure 25.24). Eventually, the species inhabiting the gap will go through a successional sequence, one tree replacing another, until a canopy tree species comes again to occupy the gap. But if there are lots of gaps of different ages in the forest, many different species will coexist, some in young gaps, others in older ones.

Second, moderate levels of disturbance may prevent communities from reaching the final stages of succession,

FIGURE 25.24

**Intermediate disturbance.** A single fallen tree creates a small light gap in the tropical rain forest of Panama. Such gaps play a key role in maintaining the high species diversity of the rain forest.



in which a few dominant competitors eliminate most of the other species. On the other hand, too much disturbance might leave the community continually in the earliest stages of succession, when species richness is relatively low.

Ecologists are increasingly realizing that disturbance is the norm, rather than the exception, in many communities. As a result, the idea that communities inexorably move along a successional trajectory culminating in the development of a climax community is no longer widely accepted. Rather, predicting the state of a community in the future may be difficult because the unpredictable occurrence of disturbances will often counter successional changes. Understanding the role that disturbances play in structuring communities is currently an important area of investigation in ecology.

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**Succession is often disrupted by natural or human causes. In some cases, intermediate levels of disturbance may maximize the species richness of a community.**

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**Summary****Questions****Media Resources****25.1 Interactions among competing species shape ecological niches.**

- Each species plays a specific role in its ecosystem; this role is called its niche.
- An organism's fundamental niche is the total niche that the organism would occupy in the absence of competition. Its realized niche is the actual niche it occupies in nature.
- Two species cannot occupy the same niche for long if resources are limiting; one will outcompete the other, driving it to extinction.
- Species can coexist by partitioning resources to minimize competition.

1. What is the difference between interspecific competition and intraspecific competition? What is Gause's principle of competitive exclusion?
2. Is the term niche synonymous with the term *habitat*? Why or why not? How does an organism's fundamental niche differ from its realized niche?



- Introduction to Communities
- Community Organization



- On Science Article: Killer Bees

**25.2 Predators and their prey coevolve.**

- Plants are often protected from herbivores by chemicals they manufacture.
- Warning, or aposematic, coloration is characteristic of organisms that are poisonous, sting, or are otherwise harmful. In contrast, cryptic coloration, or camouflage, is characteristic of nonpoisonous organisms.
- Predator-prey relationships are of crucial importance in limiting population sizes in nature.

3. What morphological defenses do plants use to defend themselves against herbivores?
4. Consider aposematic coloration, cryptic coloration, and Batesian mimicry. Which would be associated with an adult viceroy butterfly? Which would be associated with a larval monarch butterfly? Which would be associated with a larval viceroy butterfly?

**25.3 Evolution sometimes fosters cooperation.**

- Coevolution occurs when different kinds of organisms evolve adjustments to one another over long periods of time.
- Many organisms have coevolved to a point of dependence. In mutualism the relationship is mutually beneficial; in commensalism, only one organism benefits while the other is unharmed; and in parasitism one organism serves as a host to another, usually to the host's disadvantage.

5. Why is eliminating predators a bad idea for species richness?
6. How can predation and competition interact in regulating species diversity of a community?



- Student Research: Hermit Crab—Sea Anemone Associations

**25.4 Ecological succession may increase species richness.**

- Primary succession takes place in barren areas, like rocks or open water. Secondary succession takes place in areas where the original communities of organisms have been disturbed.
- Succession occurs because of tolerance, facilitation, and inhibition.
- Disturbance can disrupt successional changes. In some cases, disturbance can increase species richness of a community.

7. Why have scientists altered the concept of a final, climax vegetation in a given ecosystem? What types of organisms are often associated with early stages of succession? What is the role of disturbance in succession?



- Succession



- Book Review: *Guns, Germs, and Steel* by Diamond