

Three interacting populations. Ladybird beetles (*Coccinella septempunctata*) feed on aphids (order Hemiptera), which consume the sap of plants.

## STUDY PLAN

### 50.1 Population Interactions

Coevolution produces reciprocal adaptations in species that interact ecologically

Predation and herbivory define many relationships in ecological communities

Interspecific competition occurs when different species depend on the same limiting resources

In symbiotic associations, the lives of two or more species are closely intertwined

### 50.2 The Nature of Ecological Communities

Most ecological communities blend into neighboring communities

### 50.3 Community Characteristics

The growth forms of plants establish a community's overall appearance

Communities differ in species richness and the relative abundance of species they contain

Feeding relationships within a community determine its trophic structure

### 50.4 Effects of Population Interactions on Community Characteristics

Interspecific competition can reduce species richness within communities

Predators can boost species richness by stabilizing competitive interactions among their prey

Herbivores may counteract or reinforce competition among their food plants

### 50.5 Effects of Disturbance on Community Characteristics

Frequent disturbances keep some communities in a constant state of flux

Moderate levels of disturbance may foster high species richness

### 50.6 Ecological Succession: Responses to Disturbance

Succession begins after disturbance alters a landscape or changes the species composition of an existing community

Community characteristics change during succession

Several hypotheses help to explain the processes underlying succession

### 50.7 Variations in Species Richness among Communities

Many types of organisms exhibit latitudinal gradients in species richness

The theory of island biogeography explains variations in species richness

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# 50 Population Interactions and Community Ecology

## WHY IT MATTERS

In some open woodlands in Central America, flocks of chestnut-headed oropendolas (*Zarhynchus wagleri*), members of the blackbird family, build hanging nests in isolated trees (**Figure 50.1**). Female giant cowbirds (*Scaphidura oryzivora*) often bully their way into a colony, laying an egg or two in each oropendola nest. Cowbirds are *brood parasites* on oropendolas, tricking them into caring for cowbird young. The cowbird chicks grow faster than oropendola chicks, and they consume much of the food that the oropendolas bring to their own offspring. Because cowbird chicks take food away from their oropendola nest mates, we might expect adult oropendolas to eject cowbird eggs and chicks from their nests—but often they don't.

Why do some oropendolas care for offspring that are not their own? In an ingenious study conducted in the 1960s, Neal Smith of the Smithsonian Tropical Research Institute determined that cowbird chicks could actually increase the number of offspring that some oropendolas raise. Oropendola chicks are frequently parasitized by botfly larvae, which feed on their flesh. The aggressive cowbird chicks snap at adult botflies and pick fly larvae off their nest mates. Although cowbird chicks eat food meant for oropendola chicks, they also protect



Cortez, C. Austin

**Figure 50.1**  
Potential victims of brood parasitism. Chestnut-headed oropendolas (*Zarhynchus wagleri*) rear their young in elaborate hanging nests. Some populations of oropendolas are subject to brood parasitism by giant cowbirds (*Scaphi-dura oryzivora*).

them from potentially lethal parasites; twice as many young oropendolas survive in nests with cowbird chicks as in nests without them.

In other areas of Central America, oropendolas build nests near the hives of bees or wasps. These oropendolas chase cowbirds from their colonies, and when a cowbird does manage to sneak an egg into one of their nests, the oropendolas frequently eject it. Why do oropendolas in these colonies reject cowbird eggs when others do not? Smith determined that the swarms of bees and wasps keep botflies away from the oropendola colonies. At these sites, twice as many oropendola chicks survive in nests without cowbirds as in those that include them. Thus the oropendolas derive no benefit from having cowbird chicks in their nests, and natural selection has favored discriminating behavior in oropendolas that nest near bees and wasps.

The story of the oropendolas, cowbirds, botflies, bees, and wasps provides an example of the population interactions that characterize life in an **ecological community**, an assemblage of species living in the same place. And as this story reveals, the presence or absence of certain species may alter the effects of such interactions in almost unimaginably complex ways. We begin this chapter with a description of some of the many ways that populations in a community interact. We then examine how population interactions and other factors, such as the kinds of species present and

the relative numbers of each species, influence a community's characteristics.

## 50.1 Population Interactions

Population interactions usually provide benefits or cause harm to the organisms engaged in the interaction (**Table 50.1**). And because interactions with other species often affect the survival and reproduction of individuals, many of the relationships that we witness today are the products of long-term evolutionary modification. Before examining several general types of population interactions, we briefly consider how natural selection has shaped the relationships between interacting species.

### Coevolution Produces Reciprocal Adaptations in Species That Interact Ecologically

Population interactions change constantly. New adaptations that evolve in one species exert selection pressure on another, which then evolves adaptations that exert selection pressure on the first. The evolution of genetically based, reciprocal adaptations in two or more interacting species is described as **coevolution**.

Some coevolutionary relationships are straightforward. For example, ecologists describe the coevolutionary interactions between some predators and their prey as a race in which each species evolves adaptations that temporarily allow it to outpace the other. When antelope populations suffer predation by cheetahs, natural selection fosters the evolution of faster speed in the antelopes. Cheetahs then experience selection for increased speed so that they can overtake and capture antelopes. Other coevolved interactions provide bene-

**Table 50.1** Population Interactions and Their Effects

Interaction	Effects on Interacting Populations
Predation	+/- Predators gain nutrients and energy; prey are killed or injured.
Herbivory	+/- Herbivores gain nutrients and energy; plants are killed or injured.
Competition	-/- Both competing populations lose access to some resources.
Commensalism	+/0 One population benefits; the other population is unaffected.
Mutualism	+/+ Both populations benefit.
Parasitism	+/- Parasites gain nutrients and energy; hosts are injured or killed.

fits to both partners. For example, the flower structures of different monkey-flower species have evolved characteristics that allow them to be visited by either bees or hummingbirds (see Figure 21.7).

Although one can hypothesize a coevolutionary relationship between any two interacting species, documenting the evolution of reciprocal adaptations is difficult. As our introductory story about oropendolas and their parasites illustrated, coevolutionary interactions often involve more than two species. Indeed, most organisms experience complex interactions with numerous other species in their communities, and the simple portrayal of coevolution as taking place between two species rarely does justice to the complexity of these relationships.

### Predation and Herbivory Define Many Relationships in Ecological Communities

Because animals acquire nutrients and energy by consuming other organisms, **predation** (the interaction between predatory animals and the animal prey they consume) and **herbivory** (the interaction between herbivorous animals and the plants they eat) are often the most conspicuous relationships in ecological communities.

**Adaptations for Feeding.** Both predators and herbivores have evolved remarkable characteristics that allow them to feed effectively. Carnivores use sensory systems to locate animal prey and specialized behaviors and anatomical structures to capture and consume it. For example, a rattlesnake (genus *Crotalus*) uses heat sensors on its head (see Figure 39.22) and chemical sensors in the roof of its mouth to find rats or other endothermic prey. Its hollow fangs inject toxins that kill the prey and begin to digest its tissues even before the snake consumes it. And elastic ligaments connecting the bones of its jaws and skull allow a snake to swallow prey that is larger than its head. Herbivores have comparable adaptations for locating and processing their food plants. Insects use chemical sensors on their legs and heads to identify edible plants and sharp mandibles or sucking mouthparts to consume plant tissues or sap. Herbivorous mammals have specialized teeth to harvest and grind tough vegetation (see Section 45.5).

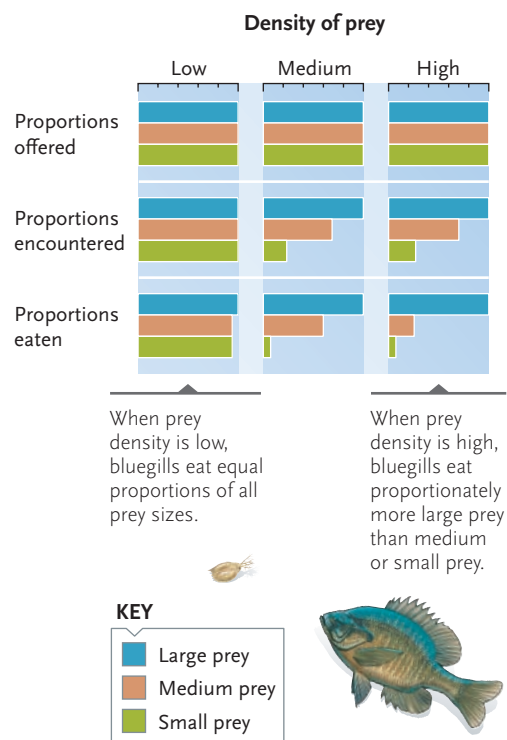
All animals must select their diets from a variety of potential food items. Some species, described as *specialists*, feed on one or just a few types of food. Among birds, for example, the Everglades kite (*Rostrhamus sociabilis*) consumes just one prey species, the apple snail (*Pomacea paludosa*). Other species, described as *generalists*, have broader tastes. Crows (genus *Corvus*) consume food ranging from grain to insects to carrion.

How does an animal select what type of food to eat? Some mathematical models, collectively described as **optimal foraging theory**, predict that an animal's diet is a compromise between the costs and benefits associ-

ated with different types of food. Assuming that animals try to maximize their energy intake in a given feeding time, their diets should be determined by the time and energy it takes to pursue, capture, and consume a particular kind of food compared with the energy that food provides. For example, a cougar (*Puma concolor*) will invest more time and energy hunting a mountain goat (*Oreamnos americanus*) than a jackrabbit (*Lepus townsendii*), but the payoff for the cougar is a bigger meal.

Food abundance also affects food choice. When prey are scarce, animals often take what they can get, settling for food that has a low benefit-to-cost ratio. But when food is abundant, they may specialize, selecting types that provide the largest energetic return. Bluegill sunfish (*Lepomis macrochirus*), for example, feed on *Daphnia* and other small crustaceans. When crustacean density is high, the fish hunt mostly large *Daphnia*, which provide more energy for their effort; but when prey density is low, bluegills feed on *Daphnia* of all sizes (**Figure 50.2**).

**Defenses against Herbivory and Predation.** Because herbivory and predation have a negative impact on the organisms being consumed, plants and animals have evolved mechanisms to avoid being eaten. Some plants



**Figure 50.2**

An experiment demonstrating that prey density affects predator food choice. Researchers tested the food size preferences of captive bluegill sunfish (*Lepomis macrochirus*) by offering them equal numbers of small, medium, and large-sized prey (*Daphnia magna*) at three different prey densities. Because large prey are the easiest to find, bluegills encountered them more frequently than small or medium-sized prey, especially at the highest prey density. The bluegills' selection of prey varied with prey density; they strongly preferred large prey when prey of all sizes were abundant.

**Figure 50.3**

**Hiding in plain sight.** Some animals, such as **(a)** giant swallowtail butterfly (*Papilio cresphontes*) larvae that resemble bird droppings and **(b)** some katydids (*Mimetica* species) that resemble insect-damaged leaves, do not attract the attention of predators.

**a. Bird dropping mimic**



**b. Damaged leaf mimic**



use spines, thorns, and irritating hairs to protect themselves from herbivores. Many plant tissues also contain poisonous chemicals that deter herbivores from feeding. For example, plants in the milkweed family (Asclepiadeceae) exude a milky, irritating sap that contains cardiac glycosides, even small amounts of which are toxic to vertebrate heart muscle. Other compounds mimic the structure of insect hormones, disrupting the development of insects that consume them. Most of these poisonous compounds are volatile, giving plants their typical aromas; some herbivores have co-evolved the ability to recognize these odors and avoid the toxic plants. Recent research indicates that some plants increase their production of toxic compounds in response to herbivore feeding. For example, potato and tomato plants that have been damaged by herbivores produce higher levels of protease-inhibiting chemicals; these compounds prevent herbivores from digesting proteins they have just consumed, reducing the food value of these plant tissues.

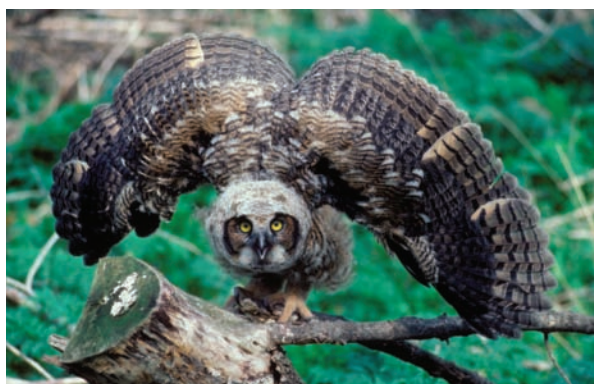
Many animals have evolved an appearance that provides a passive defense against predation (**Figure 50.3**). Caterpillars that look like bird droppings, for example, may not attract much attention from a hungry predator. And as you learned in Chapter 1 (see Figure 1.9), **cryptic coloration** helps some prey (as well as some predators) to blend in with their surroundings.

Once discovered by a predator, many animals first try to run away. When cornered, they may try to startle

or intimidate the predator with a display that increases their apparent size or ferocity (**Figure 50.4**). Such a display might confuse the predator just long enough to allow the potential victim to escape. Other species seek shelter in protected sites. For example, flexible-shelled African pancake tortoises (*Malacochersus tornieri*) retreat into rocky crevices and puff themselves up with air, becoming so tightly wedged between rocks that predators cannot extract them.

Other animals defend themselves actively. North American porcupines (genus *Erethizon*) release hairs modified into sharp, barbed quills that stick in a predator's mouth, causing severe pain and swelling. Other species fight back by biting, charging, or kicking an attacking predator. Chemical defenses also provide effective protection. Skunks release a noxious spray when threatened, and some frogs and toads produce neurotoxic skin secretions that paralyze and kill mammals. Some insects even protect themselves with poisons acquired from plants. The caterpillars of monarch butterflies (*Danaus plexippus*) are immune to the cardiac glycosides in the milkweed leaves they eat. They store these chemicals at high concentration, even through metamorphosis, making adult monarchs poisonous to vertebrate predators.

Poisonous or repellant species often advertise their unpalatability with bright, contrasting patterns, called **aposematic coloration** (**Figure 50.5**). Although a predator might attack a black-and-white skunk, a



**Figure 50.4**

**Startle defenses.** A short-eared owl (*Asio flammeus*) increases its apparent size when threatened by a predator.



**Figure 50.5**

**Aposematic coloration.** Poisonous animals, like the harlequin toad (*Atelopus varius*) from Central America often have bright warning coloration.

yellow-banded wasp, or an orange monarch butterfly once, it quickly learns to associate the gaudy color pattern with pain, illness, or severe indigestion—and rarely attacks these easily recognized animals again.

**Mimicry**, in which one species evolves an appearance resembling that of another (Figure 50.6), is also a form of defense. In **Batesian mimicry**, named for English naturalist Henry W. Bates, a palatable or harmless species, the **mimic**, resembles an unpalatable or poisonous one, the **model**. Any predator that eats the poisonous model will subsequently avoid other organisms that resemble it. In **Müllerian mimicry**, named for German zoologist Fritz Müller, two or more unpalatable species share a similar appearance, which reinforces the lesson learned by a predator that attacks any species in the mimicry complex.

Despite the effectiveness of many antipredator defenses, coevolution has often molded the responses of predators to overcome them. For example, when threatened by a predator, the beetle *Eleodes longicollis* raises its rear end and sprays a noxious chemical from a gland at the tip of its abdomen. Although this behavior deters many would-be predators, grasshopper mice (genus *Onychomys*) of the American southwest circumvent this defense: they grab the beetles and shove their abdomens into the ground, rendering the beetle's spray ineffective (Figure 50.7).

### Interspecific Competition Occurs When Different Species Depend on the Same Limiting Resources

Populations of different species often use the same limiting resources, causing **interspecific competition** (competition between species). The competing populations may experience increased mortality and decreased reproduction, responses that are similar to the effects of intraspecific competition (see Section 49.5). Interspecific competition reduces the size and population growth rate of one or more of the competing populations.

Community ecologists identify two main forms of interspecific competition. In **interference competition**, individuals of one species harm individuals of another species directly. Animals may fight for access to resources, as when lions chase smaller scavengers like hyenas and jackals from their kills. Similarly, many plant species, including creosote bushes (see Figure 49.4), release toxic chemicals, which prevent other plants from growing nearby. In **exploitative competition**, two or more populations use (“exploit”) the same limiting resource; the presence of one species reduces resource availability for the others, even in the absence of snout-to-snout or root-to-root confrontations. For example, in the deserts of the American Southwest, many bird and ant species feed largely on seeds. Thus, each seed-eating species may deplete the food supply available to others.

#### a. Batesian mimicry

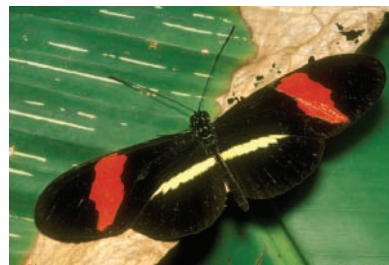


Drone fly (*Eristalis tenax*), the mimic

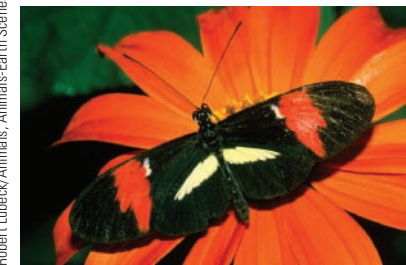


Honeybee (*Apis mellifera*), the model

#### b. Müllerian mimicry



*Heliconius erato*



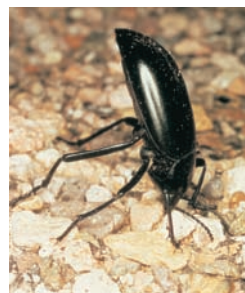
*Heliconius melpone*

#### Figure 50.6

**Mimicry.** (a) Batesian mimics are harmless animals that mimic a dangerous one. The harmless drone fly (*Eristalis tenax*) is a Batesian mimic of the stinging honeybee (*Apis mellifera*). (b) Müllerian mimics are poisonous species that share a similar appearance. Two distantly related species of butterfly, *Heliconius erato* and *Heliconius melpone*, have nearly identical patterns on their wings.

**Competitive Exclusion and the Niche Concept.** In the 1920s, the Russian mathematician Alfred J. Lotka and the Italian biologist Vito Volterra independently proposed a model of interspecific competition, modifying the logistic equation (see Section 49.5) to describe the effects of competition between two species. In their model, an increase in the size of one population reduces the population growth rate of the other.

#### a. *Eleodes* beetle



#### b. Grasshopper mouse



#### Figure 50.7

**Coevolution of predators and prey.** (a) When disturbed by a predator, the beetle *Eleodes longicollis* sprays a noxious chemical from its posterior end. (b) Grasshopper mice (genus *Onychomys*) overcome this defense by shoving a beetle's rear end into the soil and dining on it headfirst.

## Figure 50.8 Experimental Research

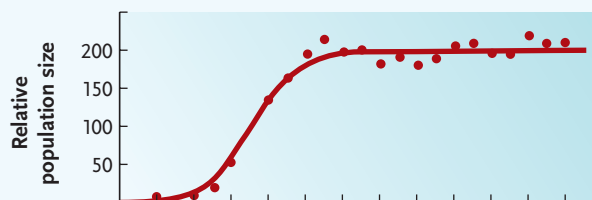
### Gause's Experiments on Interspecific Competition in Paramecium

**RESULTS:** When grown separately, *P. caudatum* (a) and *P. aurelia* (b) each exhibited logistic population growth. But when the two species were grown together in a mixed culture (c), *P. aurelia* persisted and *P. caudatum* was nearly eliminated from the culture.

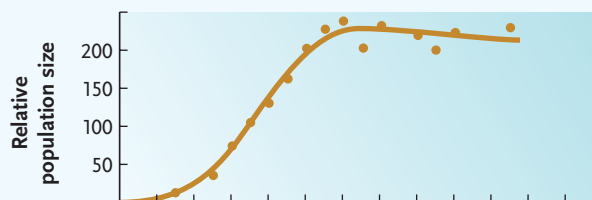
**QUESTION:** Can two species of *Paramecium* coexist in a simple laboratory environment?

**EXPERIMENT:** Gause grew populations of two *Paramecium* species, *Paramecium aurelia* and *Paramecium caudatum*, alone (single species cultures) or together (mixed culture) in small bottles in his laboratory. To determine whether the growth of these populations followed the predictions of the logistic equation, Gause had to maintain a reasonably constant carrying capacity in each culture. Thus, he fed the cultures a broth of bacteria, and he eliminated their waste products (by centrifuging the cultures and removing some of the culture medium) on a regular schedule. He then monitored their population sizes through time.

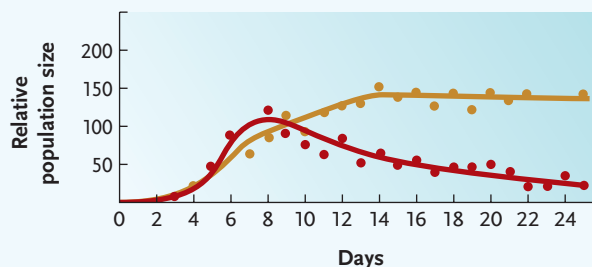
a. *P. caudatum* alone



b. *P. aurelia* alone



c. Mixed culture



*Paramecium caudatum*



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*Paramecium aurelia*



© Eric V. Grave/Photo Researchers, Inc.

**CONCLUSION:** Because one species was almost always eliminated from mixed species cultures, Gause formulated the competitive exclusion principle: populations of two or more species cannot coexist indefinitely if they rely on the same limiting resources and exploit them in the same way.

A Russian biologist, G. F. Gause, tested the model experimentally in the 1930s. He grew cultures of two *Paramecium* species (ciliate protozoans) under constant laboratory conditions, regularly renewing food and removing wastes. Both species feed on bacteria suspended in the culture medium. When grown alone, each species exhibited logistic growth; but when grown together in the same dish, *Paramecium aurelia* persisted at high density, but *Paramecium caudatum* was nearly eliminated (Figure 50.8). These results inspired Gause to define the **competitive exclusion principle**: populations of two or more species cannot coexist indefinitely if they rely on the same limiting resources and exploit them in the same way. One species inevi-

tably harvests resources more efficiently and produces more offspring than the other.

Ecologists developed the concept of the **ecological niche** as a tool for visualizing resource use and the potential for interspecific competition in nature. We define a population's niche by the resources it uses and the environmental conditions it requires over its lifetime. In this context, the niche includes food, shelter, and nutrients as well as abiotic conditions, such as light intensity and temperature, which cannot be depleted. In theory, one could identify an almost infinite variety of conditions and resources that contribute to a population's niche. In practice, ecologists usually analyze a few critical resources for which

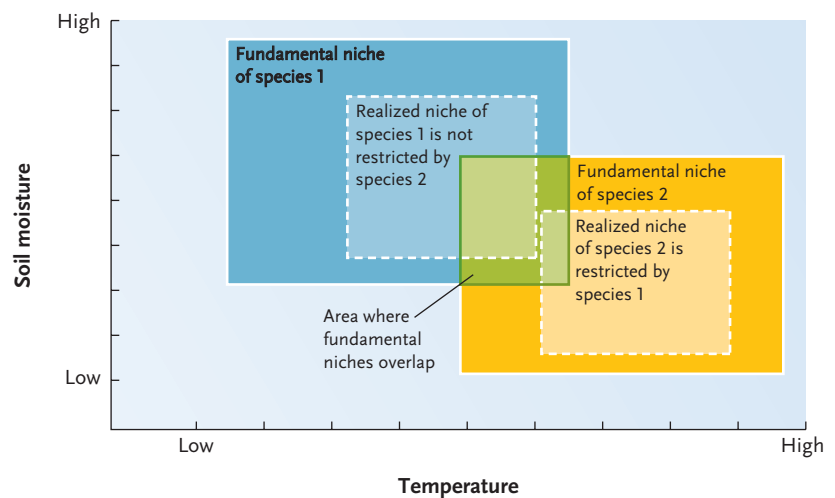
populations might compete. Sunlight, soil moisture, and inorganic nutrients are important resources for plants. Food type, food size, and nesting sites are important for animals.

Ecologists distinguish the **fundamental niche** of a population, the range of conditions and resources that it can possibly tolerate and use, from its **realized niche**, the range of conditions and resources that it actually uses in nature. Realized niches are smaller than fundamental niches, partly because all tolerable conditions are not always present in a habitat, and partly because some resources are used by other species. We can visualize competition between two populations by plotting their fundamental and realized niches with respect to one or more resources (**Figure 50.9**). If the fundamental niches of two populations overlap, they *might* compete in nature.

**Evaluating Competition in Nature.** The observation that several populations use the same resource does not demonstrate that competition occurs. For example, all terrestrial animals consume oxygen, but they don't compete for oxygen because it is usually plentiful. Nevertheless, two general observations provide *indirect* evidence that interspecific competition may have important effects. The first is the extremely common observation of **resource partitioning**, the use of different resources or the use of resources in different ways, by species living in the same place. For example, weedy plants might compete for water and dissolved nutrients in abandoned fields. But they avoid competition by partitioning these resources, collecting them from different depths in the soil (**Figure 50.10**).

A second phenomenon that suggests the importance of competition is observed in comparisons of species that are sometimes sympatric (that is, living in the same place) and sometimes allopatric (that is, living in different places). In several studies of animals, researchers have documented **character displacement**: allopatric populations are morphologically similar and use similar resources, but sympatric populations are morphologically different and use different resources. The differences between the sympatric populations allow them to coexist without competing. Differences in bill size among sympatric finch species on the Galápagos Islands (see Sections 19.2 and 20.3) may be the product of character displacement (**Figure 50.11**).

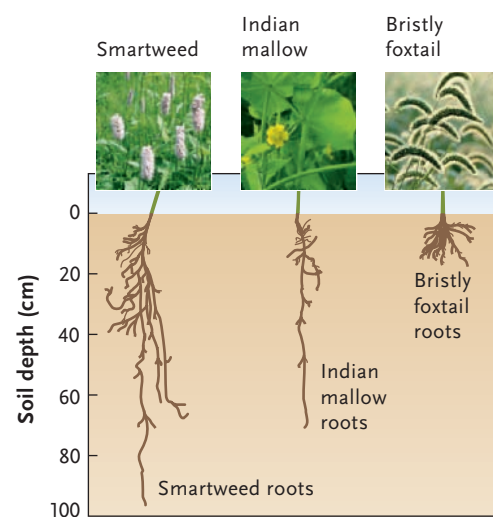
Data on resource partitioning and character displacement merely suggest the possible importance of interspecific competition in nature. To demonstrate *conclusively* that interspecific competition limits natural populations, one must show that the presence of one population reduces the population size or distribution of its presumed competitor. In a classic field experiment, Joseph Connell of the University of California, Santa Barbara, determined that competition between two barnacle species caused the realized niche of one species to be smaller than its fundamental niche



**Figure 50.9** Fundamental versus realized niches. In this hypothetical example, both species 1 and species 2 can survive intermediate temperature and soil moisture conditions, as indicated by the shading where their fundamental niches overlap. Because species 1 actually occupies most of this overlap zone, its realized niche is not much affected by the presence of species 2. By contrast, the realized niche of species 2 is restricted by the presence of species 1, and species 2 occupies warmer and dryer parts of the habitat.

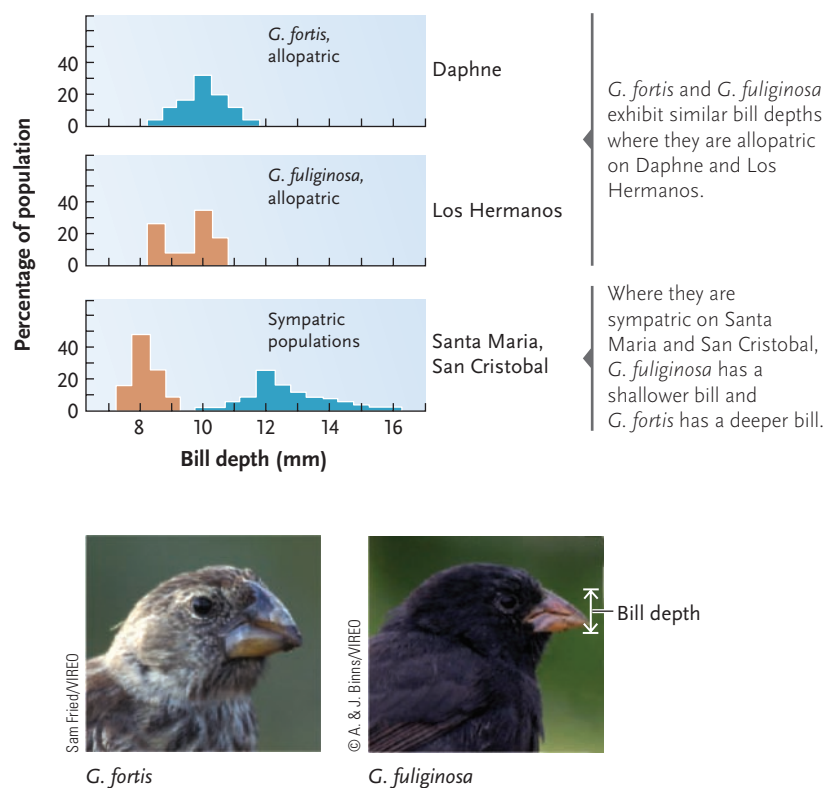
(**Figure 50.12**). Connell first observed the distributions of barnacles in undisturbed habitats. *Chthamalus stellatus* is generally found in shallow water on rocky coasts, where it is periodically exposed to air. *Balanus balanoides* typically lives in deeper water, where it is usually submerged.

Connell determined the fundamental niche of each species by removing either *Chthamalus* or *Balanus* from rocks and monitoring the distribution of each



**Figure 50.10** Resource partitioning. The root systems of three plant species that grow in abandoned fields partition water and nutrient resources in soil. Bristly foxtail grass (*Setaria faberii*) has a shallow root system; Indian mallow (*Abutilon theophraste*) has a moderately deep taproot; and smartweed (*Polygonum pensylvanicum*) has a deep taproot that branches at many depths.

(Photos: left, © Tony Wharton, Frank Lane Picture Agency/Corbis; middle, © Hal Horwitz/Corbis; right, © Joe McDonald/Corbis.)



**Figure 50.11**  
Character displacement. *Geospiza fortis* and *Geospiza fuliginosa* exhibit character displacement in the depth of their bills, a trait that is correlated with the sizes of seeds they eat.

species in the absence of the other. When Connell removed *Balanus* from rocks in deep water, larval *Chthamalus* colonized the area and produced a flourishing population of adults. Connell observed that *Balanus* physically displaced *Chthamalus* from these rocks. Thus, interference competition from *Balanus* prevents *Chthamalus* from occupying areas where it would otherwise live. By contrast, the removal of *Chthamalus* from rocks in shallow water did not result in colonization by *Balanus*. *Balanus* is apparently unable to live in habitats that are frequently exposed to air. Connell therefore concluded that competition from *Chthamalus* does not affect the distribution of *Balanus*. Thus, the competitive interaction between these two species is asymmetrical: *Balanus* has a substantial effect on *Chthamalus*, but *Chthamalus* has virtually no effect on *Balanus*.

### In Symbiotic Associations, the Lives of Two or More Species Are Closely Intertwined

Some species have a physically close ecological association called **symbiosis** (*sym* = together; *bio* = life; *sis* = process). Biologists define three types of symbiotic interactions—*commensalism*, *mutualism*, and *parasitism*—that differ in their effects.

**Commensalism**, in which one species benefits and the other is unaffected, is rare in nature, because

few species are unaffected by their interactions with another. One possible example is the relationship between cattle egrets (*Bubulcus ibis*), birds in the heron family, and the large grazing mammals with which they associate (**Figure 50.13**). Cattle egrets feed on insects and other small animals that their commensal partners flush from grass. Feeding rates of egrets are higher when they associate with large grazers than when they do not. The birds clearly benefit from this interaction, but the presence of birds has no apparent positive or negative impact on the mammals.

**Mutualism**, in which both partners benefit, is extremely common. The coevolved relationships between flowering plants and animal pollinators are largely mutualistic. Animals that feed on a plant's nectar or pollen carry its gametes from one flower to another (**Figure 50.14**). Similarly, animals that eat the fruits of flowering plants disperse the seeds, "planting" them in a pile of nutrient-rich feces. These mutualistic relationships between plants and animals do not require active cooperation. Each species simply exploits the other for its own benefit.

Some associations between bacteria and plants are also mutualistic. One of the most important of these associations is between *Rhizobium* and leguminous plants, such as peas, beans, and clover (see Section 33.3). *Insights from the Molecular Revolution* describes how the genes responsible for the association were identified and their possible evolutionary origin.

Mutualistic relationships between animal species are also common. For example, some small marine fishes feed on parasites that attach to the mouths and gills of large predatory fishes (**Figure 50.15**). Parasitized fishes hover motionless while the "cleaners" scour their tissues. The relationship is mutualistic because the cleaner fishes get a meal, and the larger fishes are relieved of parasites.

The relationship between the bull's horn acacia tree (*Acacia cornigera*) of Central America and a small ant species (*Pseudomyrmex ferruginea*) is one of the most highly coevolved mutualisms known (**Figure 50.16**). Each acacia is inhabited by an ant colony that lives in the tree's swollen thorns. The ants swarm out of the thorns to sting—and sometimes kill—herbivores that touch the tree. The ants also clip any vegetation that grows nearby. Thus, acacia trees that are colonized by ants grow in a space free of herbivores and competitors, and occupied trees grow faster and produce more seeds than unoccupied trees. In return, the plants produce sugar-rich nectar consumed by adult ants and protein-rich structures that the ants feed to their larvae. Ecologists describe the coevolved mutualism between these species as *obligatory*, at least for the ants; they cannot subsist on any other food sources.



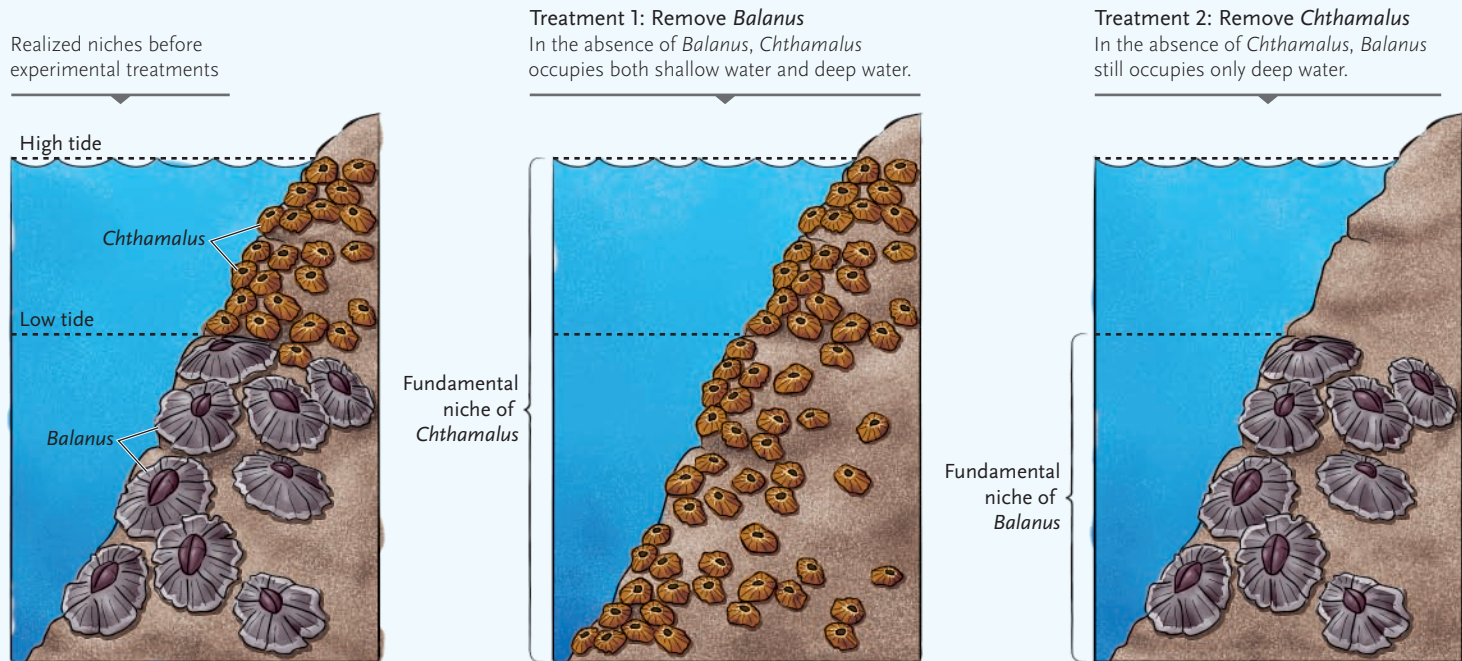
## Figure 50.12 Experimental Research

### Demonstration of Competition between Two Species of Barnacles

**QUESTION:** Do two barnacle species limit one another's realized niche in habitats where they coexist?

**EXPERIMENT:** Connell observed a difference in the distributions of two barnacle species on a rocky coast: *Chthamalus stellatus* occupies shallow water, and *Balanus balanoides* lives in deeper water. He then determined the fundamental niche of each species by removing either *Chthamalus* or *Balanus* from rocks and monitoring the distribution of each species in the absence of the other.

**RESULTS:** When Connell removed *Balanus* from rocks in deep water, larval *Chthamalus* colonized the area and produced a flourishing population of adults. By contrast, the removal of *Chthamalus* from rocks in shallow water did not result in colonization by *Balanus*.



**CONCLUSION:** In habitats where *Balanus* and *Chthamalus* coexist, the realized niche of *Chthamalus* is smaller than its fundamental niche because of competition from *Balanus*. The realized niche of *Balanus* is similar to its fundamental niche because it is not affected by the competitive interaction.

**Parasitism** is a type of interaction in which one species, the **parasite**, uses another, the **host**, in a way that is harmful to the host. Parasite–host relationships are like predator–prey relationships: one population of organisms feeds on another. But parasites rarely kill their hosts quickly because a dead host is useless as a continuing source of nourishment.

Tapeworms and other parasites that live *within* a host are **endoparasites**. Many endoparasites acquire their hosts passively, when a host accidentally ingests the parasite's eggs or larvae (see *Focus on Research*, Chapter 29). Endoparasites generally complete their



Fritz Polking/Frank Lane Picture Agency

**Figure 50.13**  
**Commensalism.** Cattle egrets (*Bubulcus ibis*) feed on insects and other small animals flushed by the movements of large grazing mammals, like this African buffalo (*Syncerus coffer*).

**Figure 50.14**

**Mutualism between plants and animals.** Several species of yucca plants (*Yucca* species) are each pollinated exclusively by one species of yucca moth (*Tegeticula* species). The adult stage of each moth appears at the time of year when its yucca plant flowers. These species are so mutually interdependent that the larvae of each moth species can feed on only one type of yucca, and the flowers of each yucca can be fertilized by only one species of moth. Most plant-pollinator mutualisms are much less specific.

**a. Flowering yucca plant**



Harlow H. Harlow

**b. Female yucca moth**



Bob and Miriam Francis/Tom Stack & Associates

A female yucca moth uses highly modified mouthparts to gather the sticky pollen and roll it into a ball. She carries the pollen to another flower, and after piercing its ovary wall, she lays her eggs. She then places the pollen ball into the opening of the stigma.

**c. Yucca moth larva**



Harlow H. Harlow

When moth larvae hatch from the eggs, they eat some of the yucca seeds and gnaw their way out of the ovary to complete their life cycle. Enough seeds remain undamaged to produce a new generation of yuccas.

life cycle in one or two host individuals. By contrast, leeches, aphids, mosquitoes, and other parasites that feed on the *exterior* of a host are **ectoparasites**. Most animal ectoparasites have elaborate sensory and behavioral mechanisms that allow them to locate specific hosts, and they feed on numerous host individuals during their lifetimes. Some plants, such as mistletoes (genus *Phoradendron*), live as ectoparasites on the trunks and branches of trees; their roots penetrate the host's xylem and extract water and nutrients.

Not all parasites feed directly on a host's tissues. The giant cowbirds described earlier are brood parasites, as are other species of cowbirds and cuckoos. Although oropendolas sometimes benefit from the presence of cowbirds, most brood parasites have negative effects on their hosts. For example, brood parasitism by the brown-headed cowbird (*Molothrus ater*) has

played a large role in the near-extinction of Kirtland's warbler (*Dendroica kirtlandii*).

The feeding habits of some insects, called **parasitoids**, fall somewhere between true parasitism and predation. A female parasitoid lays eggs in the larva or pupa of another insect species, and her young consume the tissues of the living host. Because the hosts chosen by most parasitoids are highly specific, agricultural ecologists often release parasitoids to control populations of insect pests.

## STUDY BREAK

1. Why are some carnivores willing to spend more time and energy capturing large prey than small prey?
2. What are the differences between cryptic coloration, aposematic coloration, and mimicry? Can a mimic ever have aposematic coloration?
3. How can field experiments demonstrate conclusively that two species compete for limiting resources?



Cleaner wrasse

© Erik Schiøgl

**Figure 50.15**

**Mutualism between animal species.** A large potato cod (*Epinephelus tukula*) from the Great Barrier Reef in Australia remains nearly motionless in the water while a striped cleaner wrasse (*Labroides dimidiatus*) carefully removes and eats ectoparasites attached to its lip. The potato cod is a predator, and the striped cleaner wrasse is a potential prey—but their mutualistic interaction supersedes a possible predator-prey interaction.

## 50.2 The Nature of Ecological Communities

Ecologists have often debated the nature of ecological communities, asking if they have emergent properties that transcend the interactions among the populations they contain.

### Most Ecological Communities Blend into Neighboring Communities

How do complex population interactions affect the organization and functioning of ecological communities? In the 1920s, ecologists in the United States de-

## INSIGHTS FROM THE MOLECULAR REVOLUTION

### Finding a Molecular Passport to Mutualism

The mutualistic association between *Rhizobium* bacteria and leguminous plants is established through a complex signaling process. When roots of one of these plants are invaded by *Rhizobium*, the plants respond by developing *root nodules* that house the bacteria and supply them with carbohydrates. In return, the bacteria fix atmospheric nitrogen into ammonia, which the plants use as a nitrogen source. This mutualistic association fixes about 120 million metric tons of nitrogen annually into ammonia, and greatly reduces farmers' need to use nitrogen-containing chemical fertilizers.

Proteins encoded in several sets of *Rhizobium* genes (called *nod*, *nif*, and *fix*) promote the mutualistic association with legumes. Enzymes encoded in the *nod* genes catalyze the synthesis of polysaccharides stimulating growth of a tubelike *infection thread*, which admits the bacteria to the root tissue. Once inside, the same polysaccharides promote development of the root nodule. The *nif* and *fix* genes encode enzymes involved in nitrogen fixation.

Most of these genes are carried on a single plasmid in *Rhizobium*. (Plasmids are small circles of DNA located outside the main bacterial chromosome.) The DNA sequence of the plasmid carrying the *nod*, *nif*, and *fix* genes was revealed by Cristoph Freiberg and his colleagues at the Institute for Molecular Biotechnology in Jena, Germany, and the University of Geneva in Switzerland.

The investigators studied the large plasmid of the *Rhizobium* species designated NGR234, which can invade an unusually large selection of legumes—more than 110 genera—and even one nonleguminous plant. They isolated the bacterium from root nodules and extracted the plasmid DNA. Sequencing showed that the plasmid contains an astounding 416 coding sequences. A computer search identified 277 sequences as relatives of known genes with established functions, including relatives of *nod*, *nif*, and *fix*. The remaining 139 genes have no known counterparts in any other living organism.

Among the known genes, close similarities were found to genes of a plas-

mid in *Rhizobium radiobacter*, another bacterium able to invade plant hosts. *Rhizobium radiobacter* invades various deciduous plants and promotes growth of large masses of tissue called *crown gall tumors* (see Figure 18.14). The similarities between the *Rhizobium* NGR234 and *Rhizobium radiobacter* plasmids suggest that the mechanisms by which they invade their host plants may have originated in a common evolutionary ancestor.

This research sequencing the *Rhizobium* NGR234 plasmid may help to reveal the molecular and biochemical basis of the mutualistic relationship between nodule-inducing *Rhizobium* and legumes. As a practical matter, the plasmid and its genes may provide a “genetic passport” that could be adapted to allow nodule-inducing *Rhizobium* to invade nonleguminous plants. If successful, this adaptation might allow the equivalent of nitrogen-fixing root nodules to be developed in many nonleguminous crops, eliminating their need for nitrogenous fertilizers and reducing both the cost of growing food crops and pollution by fertilizer runoff.

veloped two extreme hypotheses about the nature of ecological communities. Frederic Clements of the University of Minnesota championed an *interactive* view of communities. He described communities as “superorganisms,” assemblages of species bound together by complex population interactions. According to this view, each species in a community requires interactions with a set of ecologically different species, just as every cell in an organism requires services that other types of cells provide. Clements believed that once a mature community was established, its **species composition**—the particular combination of species that occupy the site—was at *equilibrium*. If a fire or some other environmental factor disturbed the community, it would return to its predisturbance state.

Henry A. Gleason of the University of Michigan proposed an alternative, *individualistic* view of ecological communities. He believed that population interactions do not always determine species composition. Instead, a community is just an assemblage of species that are individually adapted to similar environmental conditions. According to Gleason's hy-

pothesis, communities do not achieve equilibrium; rather, they constantly change in response to disturbance and environmental variation.

In the 1960s, Robert Whittaker of Cornell University suggested that ecologists could determine which

a. Ants patrolling an acacia



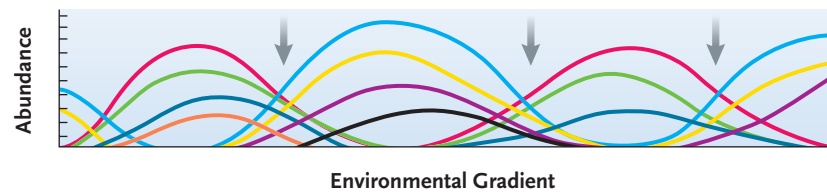
b. Cleared area around an acacia



**Figure 50.16**

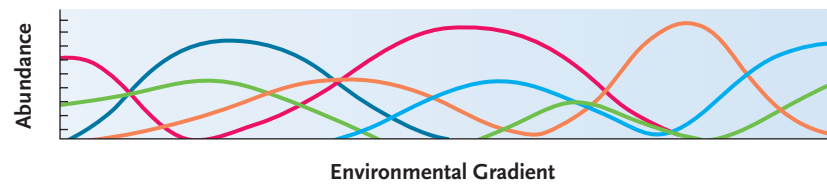
A highly coevolved mutualism. (a) Bull's horn acacia trees (*Acacia cornigera*) provide colonies of small ants (*Pseudomyrmex ferruginea*) with homes in hollow enlarged thorns as well as other resources. Although individual ants are small, they are numerous and aggressive. (b) Because the ants attack herbivores and remove vegetation near their tree, acacias occupied by ants grow in a space that is free of herbivores and competitors.

a. Interactive hypothesis



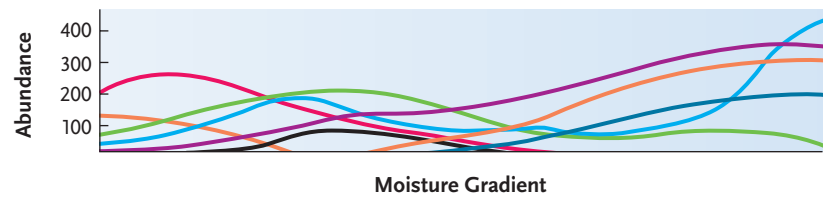
The interactive hypothesis predicts that species within communities exhibit similar distributions along environmental gradients (indicated by the close alignment of several curves over each section of the gradient) and that boundaries between communities (indicated by arrows) are sharp.

b. Individualistic hypothesis



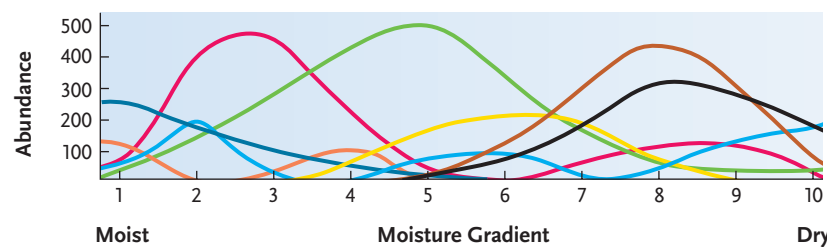
The individualistic hypothesis predicts that species distributions along the gradient are independent (indicated by the lack of alignment of the curves) and that sharp boundaries do not separate communities.

c. Siskiyou Mountains



Most gradient analyses support the individualistic hypothesis, as illustrated by distributions of tree species along moisture gradients in Oregon's Siskiyou Mountains and Arizona's Santa Catalina Mountains.

d. Santa Catalina Mountains



**Figure 50.17**

Two views of ecological communities.



**Figure 50.18**

Sharp community boundaries. Soils derived from serpentine rock have high magnesium and heavy metal content, which many plants cannot tolerate. Although native California wildflowers (bright yellow in this photograph) thrive on serpentine soil at the Jasper Ridge Preserve of Stanford University, introduced European grasses (green in this photograph) competitively exclude them from adjacent soils derived from sandstone.

hypothesis was correct by analyzing communities along environmental gradients, such as temperature or moisture (**Figure 50.17**). According to Clements' interactive hypothesis, species that typically occupy the same communities should always occur together. Thus, their distributions along the gradient would be clustered in discrete groups with sharp boundaries between groups (see **Figure 50.17a**). According to Gleason's individualistic hypothesis, each species is distributed over the section of an environmental gradient to which it is adapted. Different species would have unique distributions, and species composition would change continuously along the gradient. In other words, communities would not be separated by sharp boundaries (see **Figure 50.17b**).

Most gradient analyses support Gleason's individualistic view of ecological communities. Environmental conditions vary continuously in space, and most plant distributions match these patterns (see **Figure 50.17c, d**). Species occur together in assemblages because they are adapted to similar conditions, and the

species compositions of the assemblages change gradually across environmental gradients.

Nevertheless, the individualistic view does not fully explain all patterns observed in nature. Ecologists recognize certain assemblages of species as distinctive communities and name them accordingly—redwood forests and coral reefs are good examples. But the borders between adjacent communities are often wide transition zones, called **ecotones**. Ecotones are generally rich with species because they include plants and animals from both neighboring communities as well as some species that thrive only under transitional conditions. In some places, however, a discontinuity in a critical resource or some important abiotic factor produces a sharp community boundary. For example, chemical differences between soils derived from serpentine rock and sandstone establish sharp boundaries between communities of native California wildflowers and introduced European grasses (Figure 50.18).

### STUDY BREAK

1. Which view of communities suggests that they are just chance assemblages of species that happen to be adapted to similar abiotic environmental conditions?
2. Why would you often find more species living in an ecotone than you would in the communities on either side of it?

## 50.3 Community Characteristics

Although the species composition of an ecological community may vary somewhat over geographical gradients, every community has certain characteristics that define its overall appearance and structure.

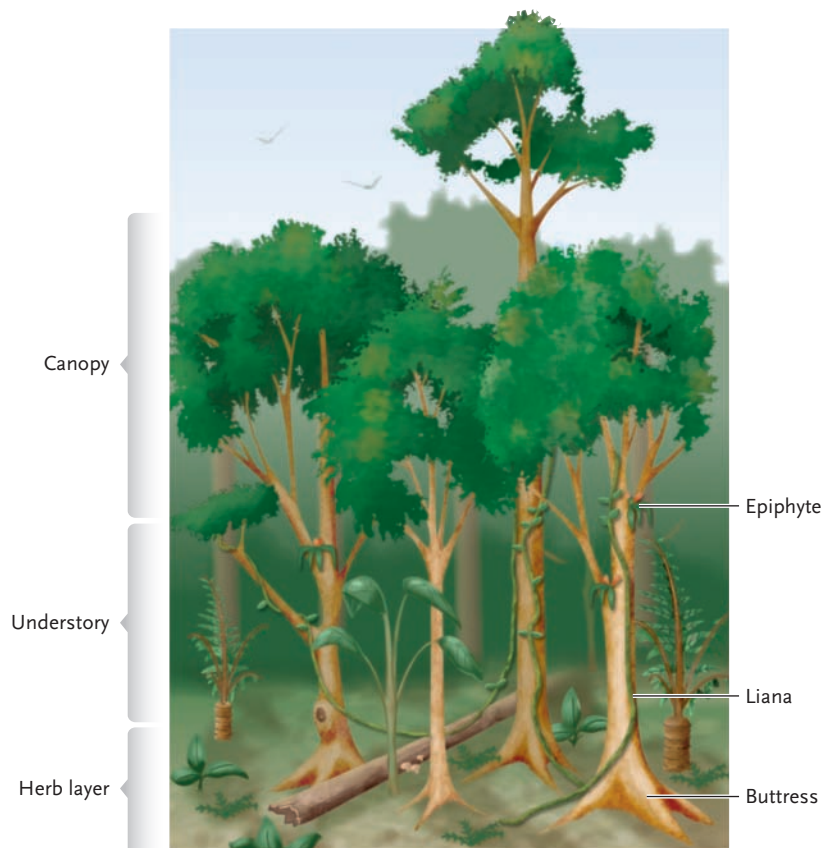
### The Growth Forms of Plants Establish a Community's Overall Appearance

The growth forms—sizes and shapes—of plants vary markedly in different environments. Warm, moist environments support complex vegetation with multiple vertical layers. For example, tropical forests include a canopy, formed by the tallest trees; an understory of shorter trees and shrubs; an herb layer under openings in the canopy; vinelike lianas; and epiphytes, which grow on the trunks and branches of trees (Figure 50.19). By contrast, physically harsh environments are occupied by low vegetation with simple structure. For example, trees on mountaintops buffeted by cold winds are short, and the plants below them cling to rocks and soil. Other environments support growth forms between these extremes (see Chapter 52).

### Communities Differ in Species Richness and the Relative Abundance of Species They Contain

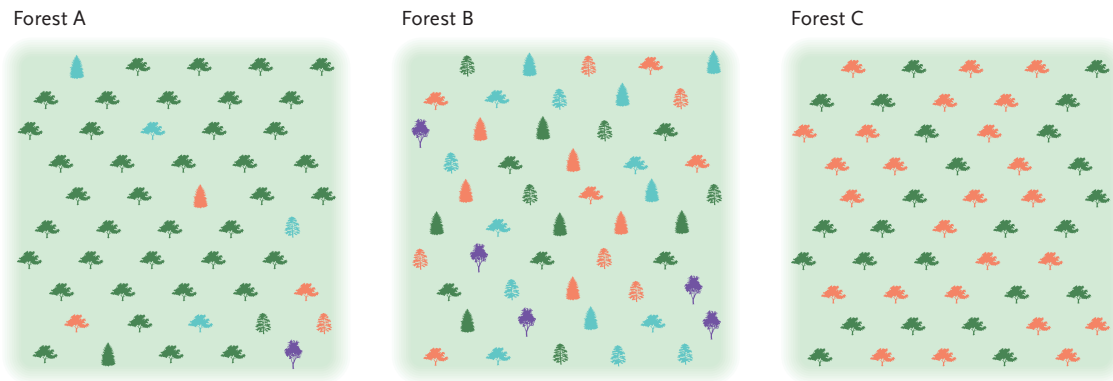
Communities differ greatly in their **species richness**, the number of species that live within them. For example, the harsh environment on a low desert island may support just a few species of microorganisms, fungi, algae, plants, and arthropods. By contrast, tropical forests, which grow under milder physical conditions, include many thousands of species. Ecologists have studied global patterns of species richness (described below in Section 50.7) for decades. Today, as human disturbance of natural communities has reached a crisis point, conservation biologists focus on such studies to determine which regions of Earth are most in need of preservation (see Chapter 53).

Within every community, populations differ in their commonness or the **relative abundance** of individuals. Some communities have just one or two abundant species and a number of rare species; in other communities, species are represented by more equal numbers of individuals. For example, in a temperate deciduous forest in West Virginia, tulip poplar (*Liriodendron tulipifera*) and sassafras (*Sassafras albidum*)



**Figure 50.19**

**Layered forests.** Tropical forests include a canopy of tall trees and an understory of short trees and shrubs. Huge vines (lianas) climb through the trees, eventually reaching sunlight in the canopy; and epiphytic plants grow on trunks and branches, increasing the structural complexity of the habitat.



**Figure 50.20**

**Species diversity.** In this hypothetical example, each of three forests contains 50 trees. Forest A and forest B each include 10 tree species, but forest C includes only two tree species. Because forest A is dominated by one tree species, but forest B is not, ecologists would say that forest B is more diverse. Forest C, with only two tree species, is less diverse than the others.

might together account for nearly 85% of the trees. By contrast, a tropical forest in Costa Rica may include more than 200 tree species, each making up only a small percentage of the total.

Species richness and relative abundance together contribute to a community characteristic that ecologists call **species diversity**. To demonstrate species diversity, we will compare two hypothetical forest communities, each with 50 trees distributed among 10 species (**Figure 50.20**). In Forest A, the dominant species is represented by 39 individuals, two species by two individuals each, and seven species by one individual each. In Forest B, each of the 10 species is represented by five individuals. Although both communities have the same species richness (10 species), Forest A is less diverse than Forest B, because most of its trees are of the same species. A forest with only two tree species (Forest C in **Figure 50.20**) would be less diverse than either of the others.

### Feeding Relationships within a Community Determine Its Trophic Structure

All ecological communities, regardless of their species richness, also have a trophic structure (*troph* = nourishment) that comprises all of the plant–herbivore, predator–prey, host–parasite, and potential competitive interactions (**Figure 50.21**).

**Trophic Levels.** We can visualize the trophic structure of a community as a hierarchy of **trophic levels**, defined by the feeding relationships among its species (see **Figure 50.21a**). Photosynthetic organisms are the **primary producers**, the first trophic level. Primary producers are often described as **autotrophs** (*auto* = self) because they capture sunlight and convert it into chemical energy, using simple inorganic molecules acquired from the environment to build larger organic molecules that

other organisms can use. Plants are the dominant primary producers in terrestrial communities. Multicellular algae and plants are the major primary producers in shallow freshwater and marine environments, but photosynthetic protists and cyanobacteria play that role in deep, open water.

Animals, by contrast, are **consumers**. Herbivores, which feed directly on plants, form the second trophic level, the **primary consumers**. Carnivores that feed on herbivores are the third trophic level, or **secondary consumers**; and carnivores that feed on other carnivores form the fourth trophic level, the **tertiary consumers**. For example, songbirds feeding on herbivorous insects are secondary consumers, and falcons feeding on songbirds are tertiary consumers. Some organisms, like humans and some bears, are **omnivores**, feeding at several trophic levels simultaneously.

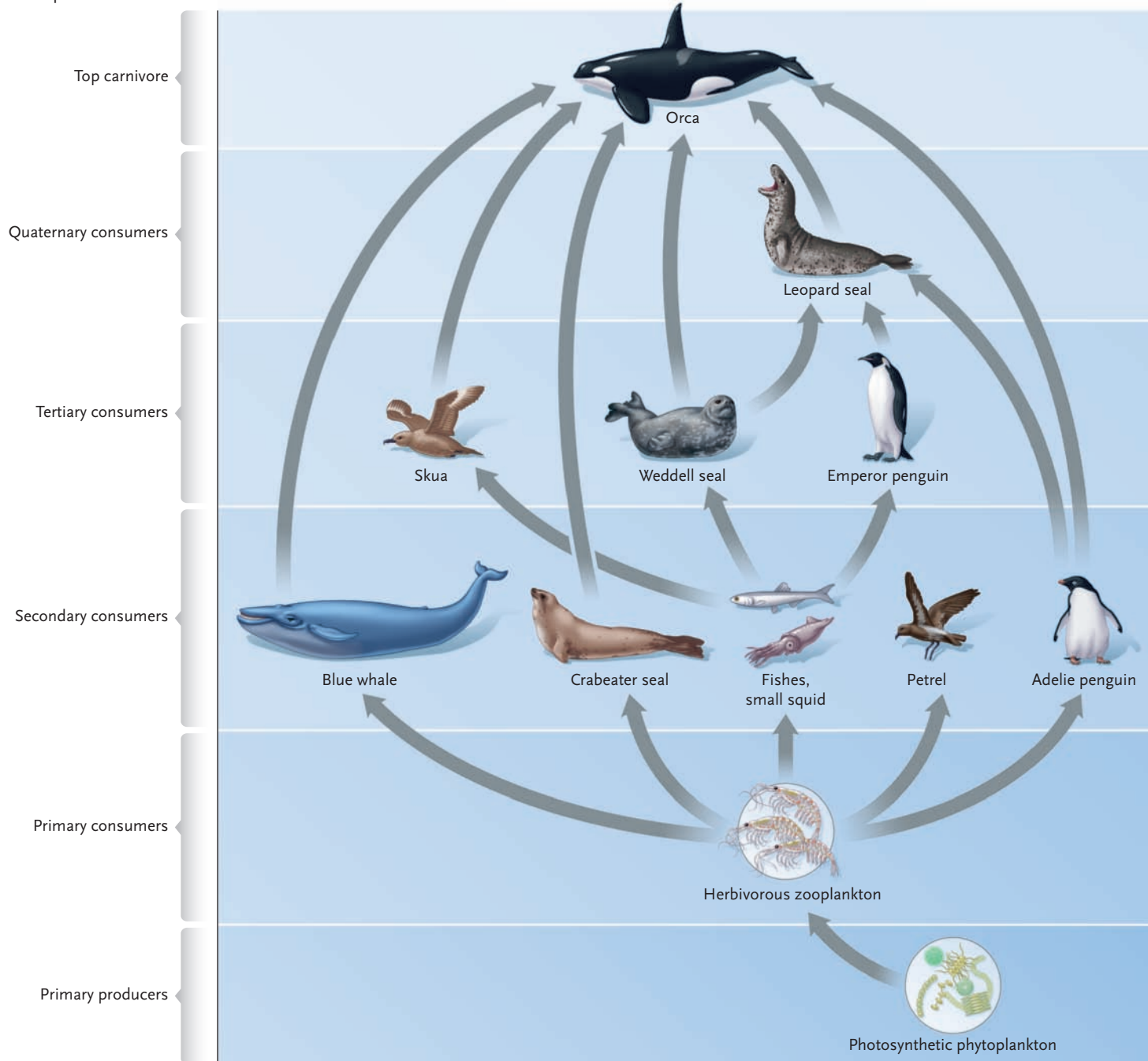
A separate and distinct trophic level includes organisms that extract energy from the organic detritus (refuse) produced at other trophic levels. Scavengers, or **detritivores**, are animals such as earthworms and vultures that ingest dead organisms, digestive wastes, and cast-off body parts such as leaves and exoskeletons. **Decomposers** are small organisms, such as bacteria and fungi, that feed on dead or dying organic material. As described in Chapter 51, detritivores and decomposers serve a critical ecological function because their activity reduces organic material to small inorganic molecules that producers can assimilate.

All of the consumers in a community—the animals, fungi, and diverse microorganisms—are described as **heterotrophs** (*hetero* = other) because they acquire energy and nutrients by eating other organisms or their remains.

**Food Chains and Webs.** Ecologists depict the trophic structure of a community in a **food chain**, a portrait

a. Trophic levels

b. Marine food web



**Figure 50.21**  
The marine food web off the coast of Antarctica.

of who eats whom. Each link in a food chain is represented by an arrow pointing from the food to the consumer. Simple, straight-line food chains are rare in nature because most consumers feed on more than one type of food, and because most organisms are eaten by more than one type of consumer. These complex relationships are portrayed as a **food web**, a set of interconnected food chains with multiple links.

In the food web for the waters off the coast of Antarctica (see Figure 50.21b), the primary producers and primary consumers are small organisms that occur in

vast numbers. Microscopic diatoms (phytoplankton) are responsible for most photosynthesis, and small shrimplike krill (zooplankton) are the major primary consumers. These tiny organisms are eaten by larger species, such as fishes, seabirds, and suspension-feeding baleen whales. Some of the secondary consumers are themselves eaten by birds and mammals at higher trophic levels. The top carnivore in this ecosystem, the orca (*Orcinus orca*), feeds on carnivorous birds and mammals.

Ideally, depictions of food webs would include all species in a community, from microorganisms to

the top consumer. But most ecologists simply cannot collect data on every species, particularly those that are rare or very small. Instead, they study the links between the most important species and simplify the analysis by grouping together trophically similar species. For example, Figure 50.21b categorizes the many different species of primary producers and primary consumers as phytoplankton and zooplankton, respectively.

**Food-Web Analysis.** In the late 1950s, Robert MacArthur of Princeton University pioneered the analysis of food webs to determine how the many links between trophic levels may contribute to a community's **stability**—its ability to maintain its species composition and relative abundances when environmental disturbances eliminate some species from the community. MacArthur hypothesized that in species-rich communities, where animals feed on many food sources, the absence of one or two species would have only minor effects on the structure and stability of the community as a whole. He therefore proposed a connection between species diversity, food-web complexity, and community stability.

Recent research has confirmed MacArthur's reasoning. For example, the average number of links per species generally increases with increasing species richness. Comparative food-web analysis also reveals that the relative proportions of species at the highest, middle, and lowest trophic levels are reasonably constant across communities. When researchers compared the number of prey species to the number of predator species in food webs from 92 communities of freshwater invertebrates, they discovered that, regardless of species richness, a community includes between two and three prey species for every predator species.

Interactions among species in a food web are often complex, indirect, and hard to unravel. In desert communities of the American Southwest, for example, rodents and ants potentially compete for seeds, their main food source. And the plants that produce the seeds compete for water, nutrients, and space. Rodents generally prefer to eat large seeds, but ants prefer small seeds. Thus, feeding by rodents reduces the potential population sizes of plants that produce large seeds. As a result, the population sizes of plants that produce small seeds may increase, ultimately providing more food for ants.

Some analyses of food webs focus on interactions in which predators or prey have significant influence on the growth rates and sizes of other populations in the community; these *strong interactions* can affect overall community structure. In the next section we provide examples of strong interactions when we describe how consumers influence the competitive interactions among populations of their prey.

## STUDY BREAK

1. What plant growth forms are common in tropical forests?
2. What is the difference between species richness and relative abundance?
3. Peregrine falcons are predatory birds that have been introduced into many North American cities, where they feed primarily on pigeons. The pigeons eat mostly vegetable matter. To what trophic level do pigeons and peregrine falcons belong?

## 50.4 Effects of Population Interactions on Community Characteristics

Numerous studies have shown that interspecific competition and predation can influence a community's species composition.

### Interspecific Competition Can Reduce Species Richness within Communities

Interspecific competition can cause the local extinction of species or prevent new species from becoming established in a community, thus reducing its species richness. During the 1960s and early 1970s, ecologists emphasized competition as the primary factor structuring communities. Observations of resource partitioning and character displacement suggested that some process had fostered differences in resource use among coexisting species, and competition provided the most straightforward explanation of these patterns.

Seeking to uncover direct evidence of competition, ecologists undertook many field experiments on competition in natural populations. The experiment on barnacles depicted in Figure 50.12 is typical of this approach, in which researchers determine whether adding or removing a species changes the distribution or population size of its presumed competitors. In the early 1980s, two independent reviews of the literature on these field experiments, one by Joseph Connell and the other by Thomas W. Schoener of the University of California at Davis, suggested that competition is sometimes a potent force. Connell's survey, which included 527 published experiments on 215 species, identified competition in roughly 40% of the experiments and more than 50% of the species. Schoener's review, which used different criteria to evaluate 164 experiments on approximately 400 species, found that competition affected more than 75% of the species.

Although these reviews confirm the importance of competition, the ecological literature upon which they



were based probably contains several significant biases. First, ecologists who set out to study competition are more likely to study interactions in which they think competition occurs, and they are more likely to publish research that documents its importance. Thus, the literature includes more studies of competition in *K*-selected species than in *r*-selected species. Recall that populations of *r*-selected species, such as herbivorous insects, rarely reach carrying capacity, and competition may not limit their population sizes (review Section 49.6). Thus, the Connell and Schoener surveys may *overestimate* the importance of competition. (Nevertheless, a more recent survey suggests that interspecific competition may be common even among populations of herbivorous insects.) Another bias, which Connell called “the ghost of competition past,” *underestimates* the importance of competition. If, as many ecologists believe, resource partitioning and character displacement are the results of past competition, we are unlikely to witness much competition today, even though it was once important in structuring those population interactions.

Ecologists have not yet reached consensus about whether interspecific competition strongly influences the species composition and structure of most communities. Plant ecologists and vertebrate ecologists, who often study *K*-selected species, generally believe that competition has a profound effect on species distributions and resource use. Insect ecologists and marine ecologists, who often study *r*-selected species, argue that competition is not the major force governing community structure, pointing instead to predation or parasitism and physical disturbance.

### Predators Can Boost Species Richness by Stabilizing Competitive Interactions among Their Prey

Predators can influence the species richness and structure of communities by reducing the population sizes of their prey. On the rocky coast of the American Northwest, for example, algae and sessile invertebrates compete for attachment sites on rocks, a requirement for life on a wave-swept shore. Mussels (*Mytilus californianus*) are the strongest competitors for space, eliminating other species from the community. But at some sites, predatory sea stars (*Pisaster ochraceus*) preferentially feed on mussels, reducing their numbers and creating space for other species to grow. Because the interaction between *Pisaster* and *Mytilus* affects other species as well, it qualifies as a strong interaction.

In the 1960s, Robert Paine of the University of Washington conducted removal experiments to evaluate the effects of *Pisaster* predation (Figure 50.22). In predator-free experimental plots, mussels outcompeted barnacles, chitons, limpets, and other invertebrate herbivores, reducing species richness from 18 species to 2 or 3. In control plots that contained preda-

tors, however, all 18 species persisted. Ecologists describe predators like *Pisaster* as **keystone species**, species that have a greater effect on community structure than their numbers might suggest.

### Herbivores May Counteract or Reinforce Competition among Their Food Plants

Herbivores also exert complex effects on communities. In the 1970s, Jane Lubchenco, then of Harvard University, studied herbivory in a periwinkle snail (*Littorina littorea*), a keystone species on rocky shores in Massachusetts (Figure 50.23). Periwinkles preferentially graze on the tender green alga *Enteromorpha*. In tidepools, which are usually submerged, *Enteromorpha* outcompetes other algae. Moderate feeding by periwinkles, however, eliminates some *Enteromorpha*, allowing less competitive algal species to grow. Moderate herbivory by periwinkles therefore increases algal species richness in tidepools. But on high rocks, which are exposed to air during low tide, the dehydration-resistant red alga *Chondrus* is competitively dominant. Periwinkles don't eat the tough *Chondrus*, however, feeding instead on the less abundant and competitively inferior *Enteromorpha*. Thus, on exposed rocks, feeding by the snails reduces algal species richness.

### STUDY BREAK

1. How is the scientific literature on interspecific competition biased?
2. What are keystone species, and how do they influence species richness in communities?

## 50.5 Effects of Disturbance on Community Characteristics

Recent research tends to support the individualistic view that many communities are not in equilibrium and that their species composition changes frequently. Environmental disturbances—storms, landslides, fires, floods, and cold spells—often eliminate some species, providing opportunities for others to become established.

### Frequent Disturbances Keep Some Communities in a Constant State of Flux

Physical disturbances are common in some environments. For example, lightning-induced fires commonly sweep through grasslands, powerful hurricanes routinely demolish patches of forest, and waves wash over communities that live at the edge of the sea.

Joseph Connell and his colleagues conducted an ambitious long-term study of the effects of disturbance

## Figure 50.22 Experimental Research

### Effect of a Predator on the Species Richness of Its Prey

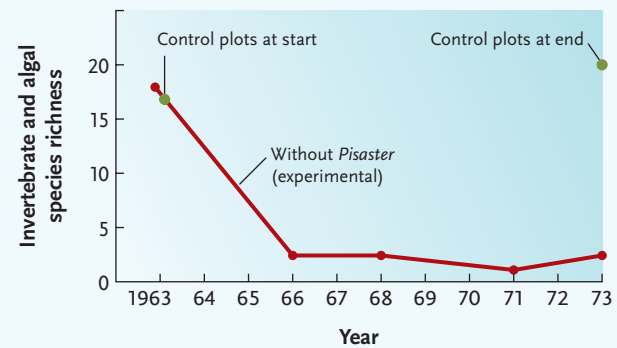
**QUESTION:** Does feeding by a predator influence the species richness and relative abundances of the species on which it feeds?

**EXPERIMENT:** The predatory sea star *Pisaster ochraceus* preferentially feeds on mussels (*Mytilus californianus*), which is the strongest competitor for space in rocky intertidal habitats in Washington State. Paine removed *Pisaster* from caged experimental study plots, but left control study plots undisturbed. He then monitored the species richness of *Pisaster*'s invertebrate prey over many years.

**RESULTS:** Paine documented an increase in mussel populations in the experimental plots as well as complex changes in the feeding relationships among species in the intertidal food web. The overall effect of removing *Pisaster*, the top predator in this food web, was a rapid decrease in the species richness of invertebrates and algae. By contrast, control plots maintained their species richness over the course of the experiment.



Nancy Rotenberg/Animals, Animals-Earth Scenes



**CONCLUSION:** Predation by the sea star *Pisaster ochraceus* maintains the species richness of its prey by preventing mussels from outcompeting other invertebrates and algae on rocky shores.

on coral reefs, shallow tropical marine habitats that are among the most species-rich communities on Earth. In some parts of the world, reefs are routinely battered by violent storms, which wash corals off the substrate, creating bare patches in the reef. The scouring action of storms creates opportunities for coral larvae to settle on bare substrates and start a new colony; ecologists use the word *recruitment* to describe the process in which young individuals join a population.

From 1963 to 1992, Connell and his colleagues tracked the fate of the Heron Island Reef at the south end of Australia's Great Barrier Reef (Figure 50.24). The inner flat and protected crests of the reef are sheltered from severe wave action during storms, whereas some pools and crests are routinely exposed to physical disturbance. Because corals live in colonies of variable size, the researchers monitored coral abundance by measuring the percentage of the substrate (that is, the seafloor) that colonies covered. They revisited marked study plots at intervals, photographing and identifying individual coral colonies.

Five major cyclones crossed the reef during the 30-year study period. Coral communities in the exposed areas of the reef were in a nearly continual state of flux. In exposed pools, four of the five cyclones re-

duced the percentage of cover, often drastically. On exposed crests, the cyclone of 1972 eliminated virtually all of the corals, and subsequent storms slowed the recovery of these areas for more than 20 years. By contrast, corals in sheltered areas suffered much less storm damage. Nevertheless, their coverage also declined steadily during the study as a natural consequence of the corals' growth. As colonies grew taller and closer to the ocean's surface, their increased exposure to air resulted in substantial mortality.

Connell and his colleagues also documented recruitment, the growth of new colonies from settling larvae, in their study plots. They discovered that the rate at which new colonies developed was almost always higher in sheltered areas than in exposed areas. However, recruitment rates were extremely variable, depending in part on the amount of space that storms or coral growth had made available.

This long-term study of coral reefs illustrates that frequent disturbances prevent some communities from reaching an equilibrium determined by interspecific interactions. Changes in the coral reef community at Heron Island result from the combined effects of external disturbances that remove coral colonies from the reef and internal processes (growth and recruit-

## Figure 50.23 Experimental Research

### The Complex Effects of an Herbivorous Snail on Algal Species Richness

**QUESTION:** How does feeding by periwinkle snails (*Littorina littorea*) influence the species richness of algae in intertidal communities?

**EXPERIMENT:** Lubchenco manipulated the densities of periwinkle snails in tidepools and on exposed rocks in a rocky intertidal habitat by creating enclosures that prevented snails from either entering or leaving her study plots. She then monitored the species composition of algae in the study plots and examined those data by plotting them against periwinkle density.

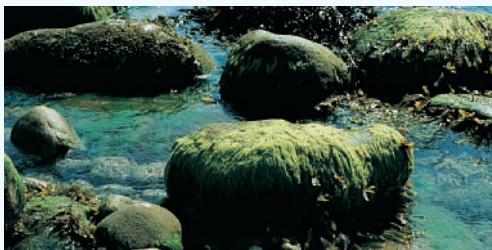
**RESULTS:** The effects of periwinkle density on algal species richness varied dramatically between study plots in tidepools and on exposed rocks.

Periwinkle snails (*Littorina littorea*)



© Jane Burton/BruceColman, Ltd.

*Enteromorpha* growing in tidepools



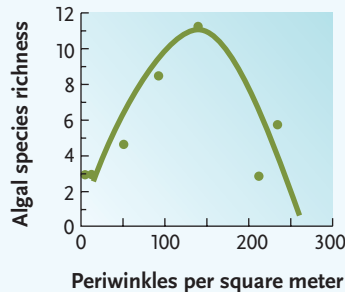
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*Chondrus* growing on exposed rocks



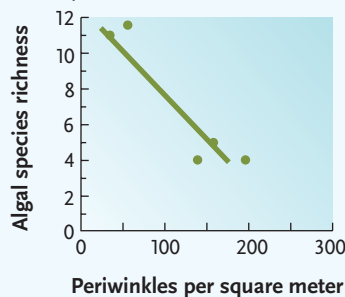
Heather Angel/Natural Visions

In tidepools



In tidepools, snails at low densities eat little algae and *Enteromorpha* competitively excludes other algal species, reducing species richness. At high snail densities, heavy feeding on all species reduces algal species richness. At intermediate snail densities, grazing eliminates some *Enteromorpha*, allowing other species to grow.

On exposed rocks



On exposed rocks, periwinkles never eat much *Chondrus*, but they consume the tender, less successful competitors. Thus, feeding by periwinkles reinforces the competitive superiority of *Chondrus*: as periwinkle density increases, algal species richness declines.

**CONCLUSION:** Grazing by periwinkle snails has complex effects on the species richness of competing algae. In tidepools, where periwinkle snails preferentially feed on *Enteromorpha*, the competitively dominant alga, snails at an intermediate density remove some *Enteromorpha*, which allows weakly competitive algae to grow, increasing species richness. Feeding by snails at either low or high densities reduces algal species richness. On exposed rocks, where periwinkle snails rarely eat the competitively dominant alga *Chondrus*, feeding by snails reduces algal species richness.

ment) that either eliminate colonies or establish new ones. In this community, growth and recruitment are slow processes, and disturbances are frequent. Thus, the community never attains equilibrium.

### Moderate Levels of Disturbance May Foster High Species Richness

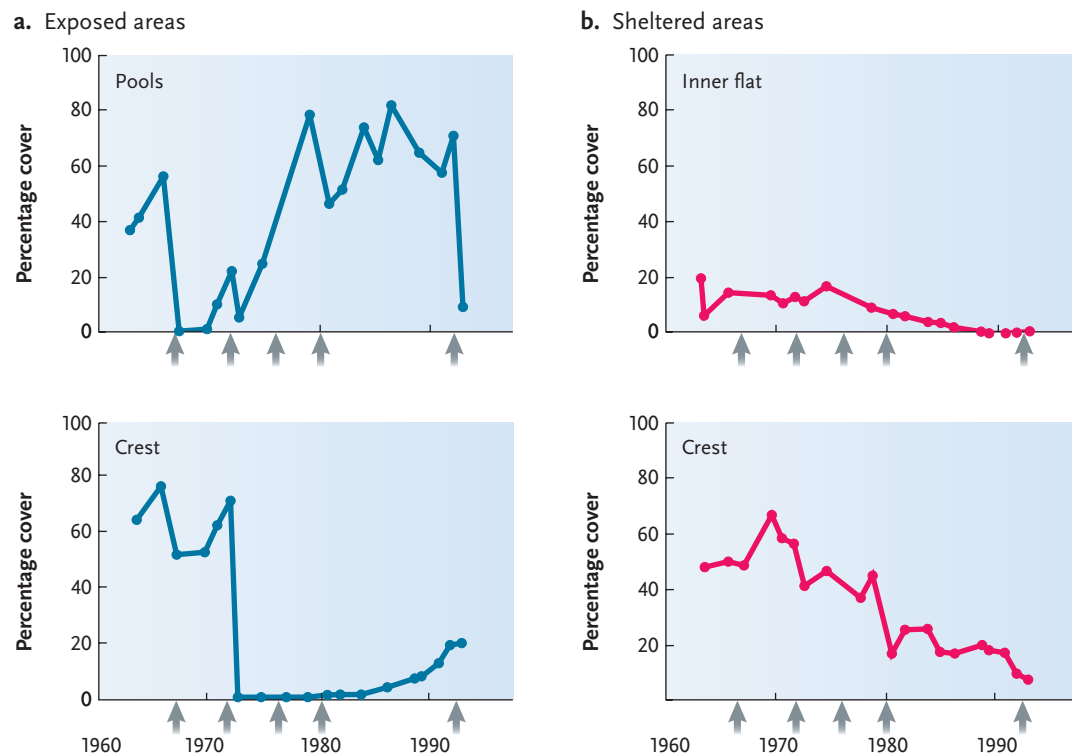
According to the **intermediate disturbance hypothesis**, proposed by Connell in 1978, species richness is greatest in communities that experience fairly frequent disturbances of moderate intensity. Moderate distur-

bances create some openings for *r*-selected species to arrive and join the community, but they allow *K*-selected species to survive. Thus, communities that experience intermediate levels of disturbance contain a rich mixture of species. Where disturbances are severe and frequent, communities include only *r*-selected species that complete their life cycles between catastrophes. Where disturbances are mild and rare, communities are dominated by long-lived *K*-selected species that competitively exclude other species from the community.

Several studies in diverse habitats have confirmed the predictions of the intermediate disturbance hy-

**Figure 50.24**

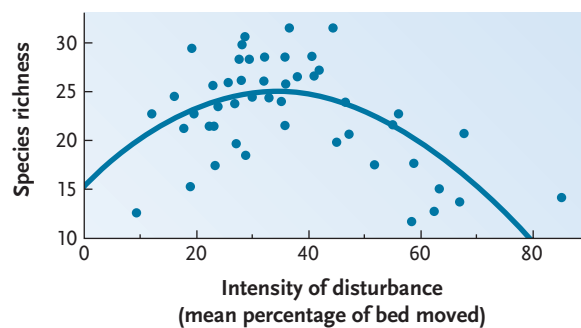
The effects of storms on corals. Five tropical cyclones (marked by gray arrows) damaged corals on the Heron Island Reef during a 30-year period. Storms reduced the percentage cover of corals in exposed parts of the reef (a) much more than in sheltered parts of the reef (b).



**Figure 50.24**

The effects of storms on corals. Five tropical cyclones (marked by gray arrows) damaged corals on the Heron Island Reef during a 30-year period. Storms reduced the percentage cover of corals in exposed parts of the reef (a) much more than in sheltered parts of the reef (b).

pothesis. For example, Colin R. Townsend and his colleagues at the University of Otago studied the effects of disturbance at 54 stream sites in the Taieri River system in New Zealand. Disturbance occurs in these communities when water flow from heavy rains moves the rocks, soil, and sand in the streambed, disrupting the habitats where animals live. Townsend and his colleagues measured how much of the substrate moved in different streambeds to index the intensity of the disturbance. Their results indicate that species richness is highest in areas that experience intermediate levels of disturbance (Figure 50.25).



**Figure 50.25**

An observational study that supports the intermediate disturbance hypothesis. In the Taieri River system in New Zealand, species richness was highest in stream communities that experienced an intermediate level of disturbance.

Some ecologists have also suggested that species-rich communities recover from disturbances more readily than do less diverse communities. For example, David Tilman and his colleagues at the University of Minnesota conducted large-scale experiments in mid-western grasslands on the relationship between species number and the ability of communities to recover from disturbance. Their results demonstrate that grassland plots with high species richness recover from drought faster than plots with fewer species.

### STUDY BREAK

1. How might disturbances from storms allow coral reefs to be rejuvenated by the recruitment of young individuals?
2. How do moderately severe and moderately frequent disturbances influence a community's species richness?

## 50.6 Ecological Succession: Responses to Disturbance

In response to disturbance, communities undergo **ecological succession**, a somewhat predictable series of changes in species composition over time.

## Succession Begins after Disturbance Alters a Landscape or Changes the Species Composition of an Existing Community

**Primary succession** begins when organisms first colonize habitats without soil, such as those created by erupting volcanoes and retreating glaciers (**Figure 50.26**). Lichens (see Section 28.3), which derive nutrients from rain and bare rock, are usually the first visible colonizers of such inhospitable habitats. They secrete mild acids that erode rock surfaces, initiating the slow development of soil, which is enriched by the organic material lichens produce. After lichens modify a site, mosses (see Section 27.2) colonize patches of soil and grow quickly.

As soil accumulates, hardy opportunistic plants—grasses, ferns, and broad-leaved herbs—colonize the site from surrounding areas. Their roots break up rock, and as they die, their decaying remains enrich the soil. Detritivores and decomposers facilitate these processes. As the soil gets deeper and richer, increased moisture and nutrients support bushes and, eventually, trees. Late successional stages are often dominated by *K*-selected species with woody trunks and branches that position leaves in sunlight and large root systems that acquire water and nutrients from soil.

In the classical view of ecological succession, long-lived species, which replace themselves over time, eventually dominate a community, and new species join it only rarely. This relatively stable, late successional stage is called a **climax community** because the dominant vegetation replaces itself and persists until an environmental disturbance eliminates it, allowing other species to invade. Local climate and soil conditions, the surrounding communities where colonizing species originate, and chance events determine the species composition of climax communities. However, recent research suggests that even “climax communities” change slowly in response to environmental fluctuations, as described below.

**Secondary succession** occurs after existing vegetation is destroyed or disrupted by an environmental disturbance, such as a fire, a storm, or human activity. The presence of soil makes the disturbed sites ripe for colonization. Moreover, the soil may contain numerous seeds that germinate after the disturbance. The early stages of secondary succession proceed rapidly, but later stages parallel those of primary succession.

Secondary succession in the North Temperate Zone is well studied in abandoned farms, called “old fields,” where forests were cleared centuries earlier. Because the transformation from old field back to forest takes at least a hundred years, ecologists use historical records to find the age of different stands of vegetation and reconstruct the successional sequence by comparing stands of different ages. In the Piedmont region of southeastern North America, an abandoned field is covered by crabgrass (genus *Digitaria*), an an-

nual plant, during the first growing season. The following year, crabgrass is replaced by horseweed (*Conyza canadensis*), which cannot persist because it secretes substances that inhibit the germination of its own seeds. Ragweed (*Ambrosia artemisiifolia*), another annual, dominates during the third year, but it is gradually replaced by perennial asters (genus *Erigeron*) and broomsedges (genus *Andropogon*), which are, in turn, replaced by shrubs. Ten to fifteen years after the field was abandoned, pine (genus *Pinus*) seedlings germinate. Growing pines cast substantial shade and their fallen needles acidify the soil, making the site unsuitable for the plants from earlier successional stages. Because pines are intolerant of shade, pine seedlings don't flourish under mature pine trees. Thus, after 50 to 100 years, pines are replaced by a taller mixed hardwood forest of oaks (genus *Quercus*) and hickories (genus *Carya*), which develops in the thick, moist soil. The hardwood forest forms the climax community after more than a century of successional change.

Similar climax communities sometimes arise from alternative successional sequences. For example, hardwood forests also develop in sites that were once ponds. During **aquatic succession**, debris from rivers and runoff accumulates in a body of water, causing it to fill in at its margins. The pond is transformed into a swamp, inhabited by plants adapted to a semisolid substrate. As larger plants get established, their high transpiration rates dry the soil, allowing other plant species to colonize. Given enough time, the site may become a meadow or forest, where an area of moist, low-lying ground is the only remnant of the original pond.

## Community Characteristics Change during Succession

Several characteristics undergo directional change as succession proceeds. First, because *r*-selected species are short-lived and *K*-selected species long-lived, species composition changes rapidly in the early stages, but slowly in the late stages of succession. Second, species richness increases rapidly during the early stages because new species join the community faster than resident species become extinct; as succession proceeds, however, species richness stabilizes or may even decline. Third, in terrestrial communities that receive sufficient rainfall, the maximum height and total mass of the vegetation increase steadily as large species replace small ones, creating the complex structure of the climax.

Because plants influence the physical environment below them, the community itself increasingly moderates the microclimate. The shade cast by a forest canopy retains soil moisture and reduces temperature fluctuations. The trunks and canopy also reduce wind speed. By contrast, the short vegetation in an early successional stage does not effectively shelter the space below it.



Roger K. Burnard

1 The glacier has retreated about 8 m per year since 1794.



Roger K. Burnard

2 This site was covered with ice less than 10 years before this photo was taken. When a glacier retreats, a constant flow of melt water leaches minerals, especially nitrogen, from the newly exposed substrate.



Roger K. Burnard

3 Once lichens and mosses have established themselves, mountain avens (genus *Dryas*) grows on the nutrient-poor soil. This pioneer species benefits from the activity of mutualistic nitrogen-fixing bacteria, spreading rapidly over glacial till.



Roger K. Burnard

4 Within 20 years, shrubby willows (genus *Salix*), cottonwoods (genus *Populus*), and alders (genus *Alnus*) take hold in drainage channels. These species are also symbiotic with nitrogen-fixing microorganisms.



Roger K. Burnard

5 In time, young conifers, mostly hemlocks (genus *Tsuga*) and spruce (genus *Picea*), join the community.



Ed Degginger

6 After 80 to 100 years, dense forests of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) have crowded out the other species.

### Figure 50.26

Primary succession following glacial retreat. The retreat of glaciers at Glacier Bay, Alaska, has allowed ecologists to document primary succession on newly exposed rocks and soil.

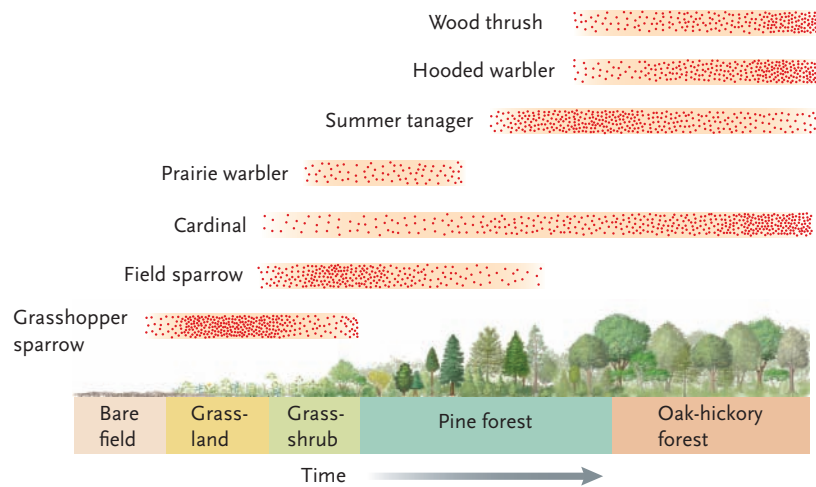
Although ecologists usually describe succession in terms of vegetation, animals undergo succession, too. As the vegetation shifts, new resources become available, and animal species replace each other over time. Herbivorous insects, which often have strict food preferences, undergo succession along with their food plants. And as the herbivores change, so do their predators, parasites, and parasitoids. In old-field succession in eastern North America, different vegetation stages harbor a changing assortment of bird species (Figure 50.27).

### Several Hypotheses Help to Explain the Processes Underlying Succession

Differences in dispersal abilities, maturation rates, and life spans among species are at least partly responsible for ecological succession. Early successional stages harbor many *r*-selected species because they produce numerous small seeds that colonize open habitats and grow quickly. Mature successional stages are dominated by *K*-selected species because they are long-lived. Nevertheless, coexisting populations inevitably affect one another. Although the role of population interactions in succession is generally acknowledged, ecologists debate the relative importance of processes that either facilitate or inhibit the turnover of species in a community.

The **facilitation hypothesis** suggests that species modify the local environment in ways that make it less suitable for themselves but more suitable for colonization by species typical of the next successional stage. For example, when lichens first colonize bare rock, they produce a small quantity of soil, which is required by mosses and grasses that grow there later. According to this hypothesis, changes in species composition are both orderly and predictable because the presence of each stage facilitates the success of the next. Facilitation is very important in primary succession, but it may not be the best model of interactions that influence secondary succession.

The **inhibition hypothesis** suggests that new species are prevented from occupying a community by whatever species are already present. According to this hypothesis, succession is neither orderly nor predictable because each stage is dominated by whichever species happen to colonize the site first. Species replacements occur only when individuals of the dominant species die of old age or when an environmental disturbance reduces their numbers. Eventually, long-lived species replace short-lived species, but the precise species composition of a mature community is up for grabs. Inhibition appears to play a role in some secondary successions. For example, the interactions among early successional species in an old field are highly competitive. Horseweed inhibits the growth of asters, which follow them in succession, by shading the aster seedlings and by releasing toxic substances from their roots. The experimental removal of horseweed enhances the growth of asters, confirming the inhibitory effect.



**Figure 50.27**

Succession in animals. Successional changes in bird species composition in an abandoned agricultural field in eastern North America parallel the changes in plant species composition. Residence times of several representative species are illustrated. The density of stippling inside each bar illustrates the density of each species through time.

The **tolerance hypothesis** asserts that succession proceeds because competitively superior species replace competitively inferior ones. According to this model, early-stage species neither facilitate nor inhibit the growth of later-stage species. Instead, as more species arrive at a site and resources become limiting, competition eliminates species that cannot harvest scarce resources successfully. In the Piedmont region of North America, for example, hardwood trees are more tolerant of shade than pine trees are, and hardwoods gradually replace pines during succession. Thus, the climax community includes only strong competitors. Tolerance may explain the species composition of many transitional and mature communities.

At most sites, succession probably results from a combination of facilitation, inhibition, and tolerance, coupled with interspecific differences in dispersal, growth, and maturation rates. Moreover, within a community, the patchiness of abiotic factors also strongly influences plant distributions and species composition. In the deciduous forests of eastern North America, maples (genus *Acer*) predominate on wet, low-lying ground, but oaks (genus *Quercus*) are more abundant at higher and drier sites. Thus, a mature deciduous forest is often a mosaic of species and not a uniform stand of trees.

Disturbance and density-independent factors also play important roles, in some cases speeding successional change. In northern forests, for example, moose prefer to feed on deciduous shrubs, accelerating the rate at which conifers replace them. In other cases, disturbance inhibits successional change, establishing a *disturbance climax* or **disclimax community**. In many grassland communities, grazing by large mammals and periodic fires kill the seedlings of trees that would otherwise become established. Thus, disturbance prevents the succession from grassland to forest, and grassland persists as a disclimax community.

On a local scale, disturbances often destroy small patches of vegetation, returning them to an earlier successional stage. A hurricane may knock over trees in a forest, creating small, sunny patches of open ground. Locally occurring *r*-selected species take advantage of the resources that are suddenly available and quickly colonize the openings. These local patches then undergo succession that is out of step with the immediately surrounding forest. Thus, moderate disturbance, accompanied by succession in local patches, can increase species richness in many communities.

### STUDY BREAK

1. What is the difference between primary succession and secondary succession?
2. How does a climax community differ from early successional stages?
3. How do the three hypotheses about the causes of ecological succession view the role of population interactions in the successional process?

## 50.7 Variations in Species Richness among Communities

Species richness often varies among communities according to a recognizable pattern. Two large-scale patterns of species richness—latitudinal trends and island patterns—have captured the attention of ecologists for more than a century.

### Many Types of Organisms Exhibit Latitudinal Gradients in Species Richness

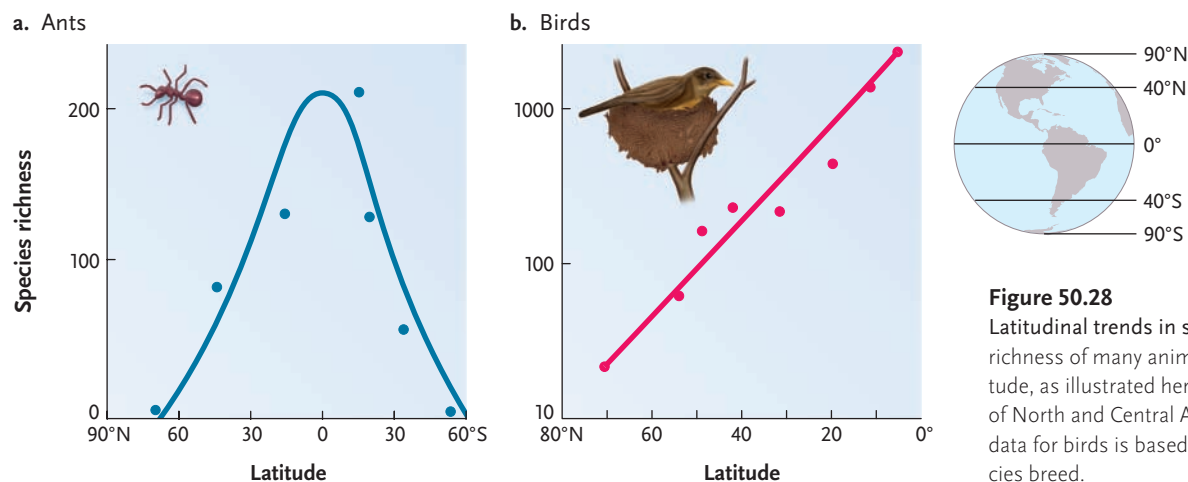
Ever since Darwin and Wallace traveled the globe (see Section 19.2), ecologists have recognized broad latitudinal trends in species richness. For many, but not all, plant and animal groups, species richness follows a

latitudinal gradient, with the most species in the tropics and a steady decline in numbers toward the poles (**Figure 50.28**). Several general hypotheses may explain these striking patterns.

Some hypotheses propose historical explanations for the *origin* of high species richness in the tropics. The benign climate in tropical regions allows some tropical organisms to have more generations per year than their temperate counterparts. And, given the small seasonal changes in temperature, tropical species may be less likely than temperate species to migrate from one habitat to another, thus reducing gene flow between geographically isolated populations (see Section 21.3). These factors may have fostered higher speciation rates in the tropics, accelerating the accumulation of species. Tropical communities may also have experienced severe disturbance less often than communities at higher latitudes, where periodic glaciations have caused repeated extinctions. Thus, new species may have accumulated in the tropics over longer periods of time.

Other hypotheses focus on ecological explanations for the *maintenance* of high species richness in the tropics. Some resources are more abundant, predictable, and diverse in tropical communities. Tropical regions experience more intense sunlight, warmer temperatures in most months, and higher annual rainfall than temperate and polar regions (see Chapter 52). These factors provide a long and predictable growing season for the lush tropical vegetation, which supports a rich assemblage of herbivores, and through them many carnivores and parasites. Furthermore, the abundance, predictability, and year-round availability of resources allow some tropical animals to have specialized diets. For example, tropical forests support many species of fruit-eating bats and birds, which could not survive in temperate forests where fruits are not available year-round.

Species richness may therefore be a self-reinforcing phenomenon in tropical communities. Complex webs of population interactions and interdependency





have coevolved in relatively stable and predictable tropical climates. Predator–prey, competitive, and symbiotic interactions may prevent individual species from dominating communities and reducing species richness.

### The Theory of Island Biogeography Explains Variations in Species Richness

Although the species richness of communities may be stable over time, species composition is often in flux as new species join a community and others drop out. In the 1960s, Robert MacArthur of Princeton University and Edward O. Wilson of Harvard University addressed the question of why communities vary in species richness, using islands as model systems. Islands provide natural laboratories for studying ecological phenomena, just as they do for evolution (see *Focus on Research* in Chapter 21). Island communities are often small, have well-defined boundaries, and are isolated from surrounding communities.

In developing the **equilibrium theory of island biogeography**, MacArthur and Wilson sought to explain variations in species richness on islands of different size and different levels of isolation from other landmasses (Figure 50.29). They hypothesized that the number of species on any island was governed by a give and take between two processes: the immigration of new species to an island and the extinction of species already there (see Figure 50.29a).

According to the MacArthur–Wilson model, the mainland harbors a *species pool* from which species immigrate to offshore islands. Seeds and small arthropods are carried by wind or floating debris; some animals, such as birds, arrive under their own power. When few species are already on an island, the rate at which new species immigrate to the island is high. But

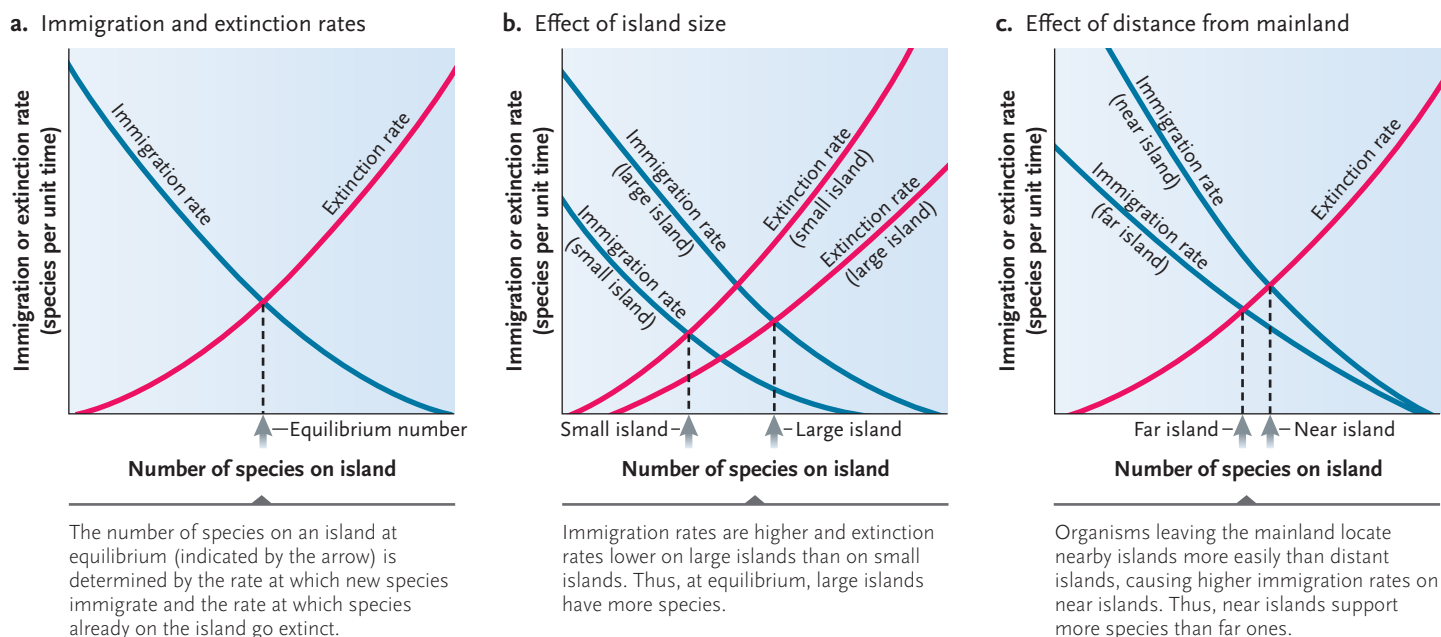
as more species inhabit the island over time, the immigration rate declines because there are fewer species left in the mainland pool that can still arrive on the island as *new colonizers*.

Once a species immigrates to an island, its population grows and persists for some time. But as the number of species on the island increases, the rate at which those species go extinct also rises. The extinction rate increases through time partly because there are more species that can go extinct there. In addition, as the number of species on the island increases, competition and predator–prey interactions can reduce the population sizes of some species and drive them to extinction.

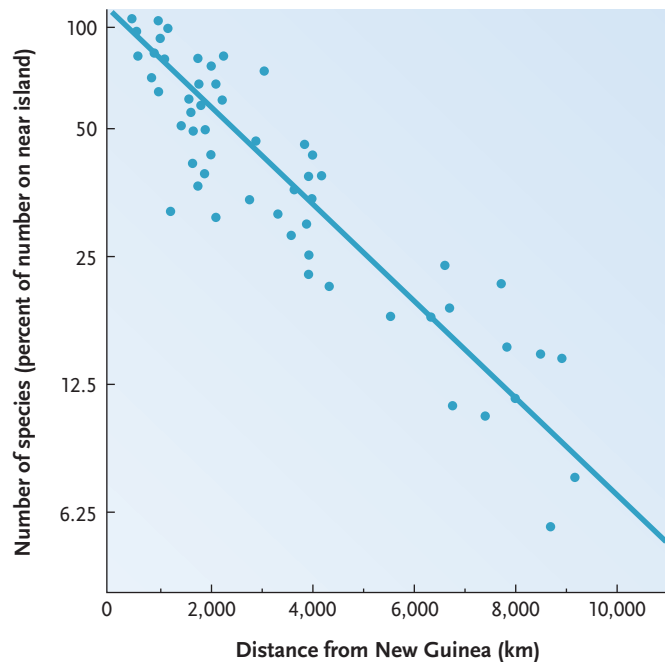
According to MacArthur and Wilson’s theory, an equilibrium between immigration and extinction determines the number of species that ultimately occupy an island. In other words, once equilibrium is reached, the number of species remains relatively constant because one species already on the island goes extinct in about the same time it takes a new species to immigrate to the island. The model does not specify which species immigrate to the island or which ones already on the island go extinct. It simply predicts that the number of species on the island is in equilibrium, although species composition is not. The ongoing processes of immigration and extinction establish a constant turnover in the roster of species that live on any island.

The MacArthur–Wilson model explains why some islands harbor more species than others. Large islands have higher immigration rates than small islands do because they present a larger target for dispersing organisms. Moreover, large islands have lower extinction rates because they can support larger populations and provide a greater range of habitats and resources. Thus, at equilibrium, large islands have more species than small islands (see Figure 50.29b). Similarly, islands

**Figure 50.29**  
Predictions of the theory of island biogeography.

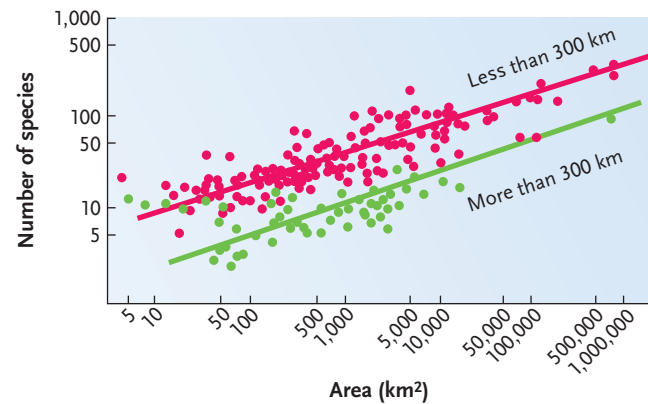


a. Distance effect



The number of lowland bird species on islands of the South Pacific declines with the islands' distance from the species source, the large island of New Guinea. Data in this graph were corrected for differences in the sizes of the islands. The number of bird species on each island is expressed as a percentage of the number of bird species on an island of equivalent size close to New Guinea.

b. Area effect



The number of bird species on tropical and subtropical islands throughout the world increases dramatically with island area. The data for islands near to a source and islands far from a mainland source are presented separately to minimize the effect of distance. Notice that the "distance effect" reduces the number of bird species on islands that are more than 300 km from a mainland source.

**Figure 50.30**

Factors that influence bird species richness on islands.

(a) Fewer bird species colonize islands that are distant from the mainland source. (b) More bird species colonize large islands than small ones.

near the mainland have higher immigration rates than distant islands do, because dispersing organisms are more likely to locate islands that are close to their point of departure. Distance does not affect extinction rates. Thus, at equilibrium, near islands have more species than far islands (see Figure 50.29c).

The equilibrium theory's predictions about the effects of area and distance are generally supported by data on plants and animals (Figure 50.30). Experimental work has also verified some of its basic assumptions. For example, Amy Schoener of the University of Washington found that, within 30 days, more than 200 species of marine organisms colonized tiny artificial "islands" (plastic kitchen scrubbers) that she placed in a Bahaman lagoon. Her research confirmed that immigration rate increases with island size. In another ambitious study, Daniel Simberloff and Edward O. Wilson exterminated insects on small islands in the Florida Keys and monitored subsequent immigration and extinction (see the *Focus on Research*). Their research also confirmed the equilibrium theory's predictions that an island's size and distance from the mainland influence how many species will occupy it.

The equilibrium view of species richness also applies to mainland communities, which exist as islands in a metaphorical sea of dissimilar habitat. Lakes are "islands"

in a "sea" of dry land, and mountaintops are habitat "islands" in a "sea" of low terrain. Species richness in these communities is partly governed by the immigration of new species from distant sources and the extinction of species already present. As human activities disrupt environments across the globe, undisturbed sites function as islandlike refuges for threatened and endangered species. Conservation biologists now apply the general lessons of MacArthur and Wilson's theory to the design of nature preserves (see Chapter 53).

In the next chapter we examine ecosystems, which include ecological communities interacting with their abiotic environments, focusing on the movements of energy and nutrients.

### STUDY BREAK

1. What factors may foster the maintenance of high species richness in tropical communities?
2. According to the equilibrium theory of island biogeography, what are the effects of an island's size and its distance from the mainland on the number of species that can occupy it?

## FOCUS ON RESEARCH

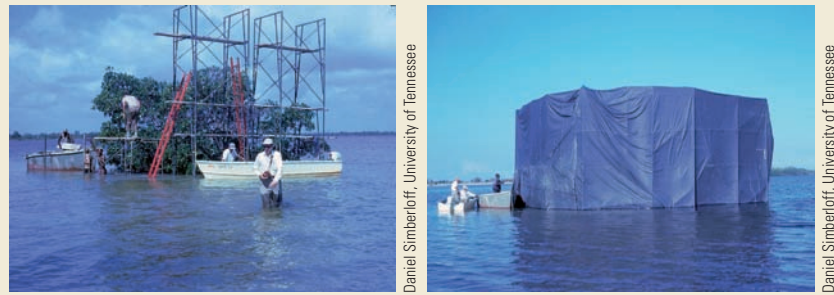
### Basic Research: Testing the Theory of Island Biogeography

Shortly after Robert MacArthur and Edward O. Wilson published the equilibrium theory of island biogeography in the 1960s, Daniel Simberloff, one of Wilson's graduate students at Harvard University, and Wilson himself undertook one of the most ambitious experiments ever attempted in community ecology. Simberloff reasoned that the best way to test the theory's predictions was to monitor immigration and extinction on barren islands.

Simberloff and Wilson devised a system for removing all the animals from individual red mangrove trees in the Florida Keys. The trees, with canopies that spread from 11 to 18 m in diameter, grow in shallow water and are isolated from their neighbors; thus, each tree is an island that harbors an arthropod community. The species pool on the Florida mainland includes about 1000 arthropod species, but each mangrove island contains no more than 40 species at one time.

After cataloging the species on each island, Simberloff and Wilson hired an extermination company to erect large tents and fumigate the islands to eliminate all arthropods on them (**Figure a**). The exterminators used methyl bromide, a pesticide that doesn't harm trees or leave any residue. Simberloff then monitored both the immigration of arthropods to the islands and the extinction of species that became established on them. He surveyed six islands regularly for 2 years and at intervals thereafter.

The results of this experiment confirm several predictions of MacArthur and Wilson's theory (**Figure b**). Arthropods recolonized the islands rapidly, and within 8 or 9 months the number of species living on each island had reached an equilibrium that was near the original species number. In addition, the island nearest to the mainland had more species than the most distant island. However, immigration

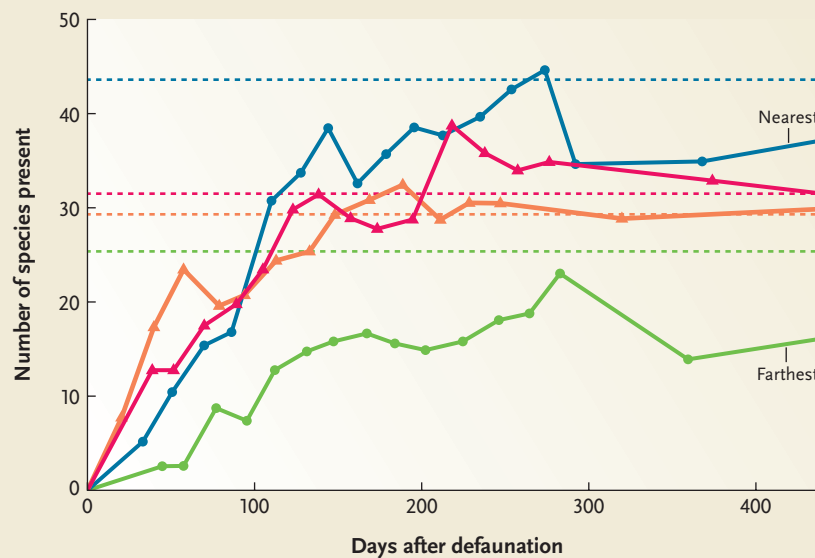


**Figure a**

After cataloguing the arthropods, Simberloff and Wilson hired an exterminating company to erect a tent over each mangrove island. Once the islands were fully covered, exterminators used methyl bromide to eliminate all living arthropods.

and extinction were incredibly rapid, and Simberloff and Wilson suspected that some species went extinct even before they had noted their presence. The researchers also discovered that 3 years after the experimental treatments, the species composition of the islands was still changing constantly and did not remotely resemble the species composition in the islands before they were defaunated.

Simberloff and Wilson's research was a landmark study in ecology because it tested the predictions of an important theory using a field experiment. Although such efforts are now almost routine in ecological studies, this project was one of the first to demonstrate that large-scale experimental manipulations of natural systems are feasible and that they often produce clear results.



**Figure b**

On three of four islands, species richness gradually returned to the predefaunation level (indicated by color-coded dashed lines on the graph). The most distant island had not reached its predefaunation species richness after 2 years.

## UNANSWERED QUESTIONS

### Do species interactions change predictably across environments?

As we learned in this chapter, the population interactions that occur between species range from mutualistic to parasitic. Some biologists have suggested that we should expect more competitive interactions between species in some kinds of environments, but more positive interactions in others. Community ecology will become a more quantitative and predictive discipline if researchers focus on how abiotic and biotic environmental factors—such as the presence of particular community members, environmental gradients, or global climate change—influence the strength of the interactions between species. For example, as physical environments become more stressful, the abundance and distribution of species should be determined less by resource limitation and more by the stress itself. Accordingly, plants tend to compete far less with each other in stressful environments than they do under ideal growing conditions. Scientists are now engaged in the intellectual feedback of theory development and experimental testing aimed at generating a predictive framework for particular types of interactions and their consequences for community structure.

### What is the relative importance of positive versus negative interactions for community structure?

It was once suggested that ecologists in capitalist societies, like the United States, tend to more often study competition and predation, but ecologists in socialist societies tend to study mutualism. Although the truth of this anecdote is unclear, it is remarkable that ecologists still do not agree on the relative importance of positive interactions (for example, mutualism or commensalism) versus negative interactions (such as predation or competition) in generating community structure. Advances in this area of study may result from “factorial” experiments, in which two or more types of interactions are manipulated. For example, one might examine the relative effects of excluding pollinators versus excluding herbivores on the success of a plant popu-

lation. In factorial experiments, the researcher can conclude that one factor has a bigger effect than the other, because all other factors were controlled. These sorts of experiments may eventually lead to an emerging picture of the relative importance of positive versus negative population interactions.

### How does the evolutionary history of a species influence its ecology today?

The great evolutionary biologist Theodosius Dobzhansky once noted that “Nothing in biology makes sense except in the light of evolution.” Although we know a great deal about both ecology and evolutionary biology, researchers are only beginning to explore the impact of an organism’s evolutionary history on its ecology. This very active area of research includes the use of phylogenetic information (see Chapter 23), selection experiments (see Chapter 21), and a knowledge of the genetic basis of particular traits (see Chapter 12). For example, are closely related species more likely to compete with each other than more distantly related species are? Do organisms that are well adapted to particular environments fare poorly in other environments? Why do some organisms specialize in their resource use? Are the population dynamics that species experience shaped by past evolutionary events? These questions are currently being addressed, and the answers uncovered by researchers may unravel many current mysteries about the ecology of populations and communities.



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## Review

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### 50.1 Population Interactions

- Coevolution is the evolution of reciprocal adaptations in species that interact ecologically (Figure 50.1).
- Predators and herbivores use diverse adaptations to select, locate, capture, and ingest an appropriate diet (Figure 50.2). Plants have both structural and chemical defenses against herbivores. Animal prey may try to hide or escape from predators, defend themselves actively, or advertise their unpalatability (Figures 50.3–50.5); some species mimic the appearance of poisonous species (Figure 50.6). Predators may evolve adaptations to counter prey defenses (Figure 50.7).
- Interspecific competition results if two or more populations use the same limiting resources; competition may lead to the extinction of one competitor (Figure 50.8). Ecologists use the ecological niche concept to visualize a population’s resource use (Figure 50.9). Observations of resource partitioning (Figure 50.10) and character displacement (Figure 50.11) suggest that competition may be important, but only field experiments can demonstrate that competition occurs (Figure 50.12).
- Symbiosis is a close ecological association between species. In commensal interactions, one species benefits and the other is unaffected (Figure 50.13). In mutualistic interactions, both partners benefit (Figures 50.14–50.16). In parasitic interactions, one species benefits and the other is harmed.

**Animation: Predator–prey interactions**

**Animation: Competitive exclusion**

**Animation: Hairston’s experiment**

**Animation: Resource partitioning**

**Animation: Wasp and mimics**

**Practice: Understanding the major types of species interactions: competition, predation, parasitism, and mutualism**

## 50.2 The Nature of Ecological Communities

- An interactive view suggests that species in a community are bound together in a complex web of necessary biotic interactions; an individualistic view recognizes communities as loose assemblages of organisms that have similar physical requirements (Figure 50.17).
- Ecotones occur where adjacent communities grade into one another; sharp boundaries occur between communities where a critical resource or an important abiotic factor is discontinuous (Figure 50.18).

## 50.3 Community Characteristics

- In benign environments, vegetation is tall and has a complex physical structure (Figure 50.19). In stressful environments, vegetation is short and has a simple physical structure.
- Communities differ in species richness and the relative abundances of species. Both characteristics contribute to a community's species diversity (Figure 50.20).
- Organisms are classified as producers, consumers, detritivores, or decomposers. Ecologists depict the trophic structure (feeding relationships) of communities in food webs (Figure 50.21). Food-web analyses seek to identify generalities about trophic structure and its relationship to community stability.

[Animation: Trophic levels in a simple food chain](#)

[Animation: Rain forest food web](#)

## 50.4 Effects of Population Interactions on Community Characteristics

- Interspecific competition often affects the species composition and structure of communities.
- Predators may increase species richness by reducing the population size of the competitively most successful prey, thus allowing other prey species to occupy the community (Figure 50.22).
- Herbivores sometimes increase species richness and sometimes decrease it (Figure 50.23).

[Animation: Effect of keystone species on diversity](#)

## 50.5 Effects of Disturbance on Community Characteristics

- Environmental disturbances may eliminate populations from a community. Some communities, such as coral reefs, experience

such frequent disturbance that their species composition is never at equilibrium (Figure 50.24).

- Disturbances of intermediate intensity and frequency allow both *r*-selected and *K*-selected species to occupy a site, increasing species richness (Figure 50.25).

## 50.6 Ecological Succession: Responses to Disturbance

- Ecological succession is a somewhat predictable change in species composition over time.
- Primary succession occurs on bare ground or rock (Figure 50.26). Secondary succession occurs where a community existed in the past (Figure 50.27).
- Species composition changes quickly and species richness rises rapidly during early successional stages. Early stages include short-lived *r*-selected species; later stages include long-lived *K*-selected species. Some communities eventually achieve a relatively stable climax state.
- Most communities include a mosaic of species that reflect patchiness in environmental conditions and the mixture of relatively undisturbed and recently disturbed sites.

[Animation: Succession](#)

## 50.7 Variations in Species Richness among Communities

- Communities near the equator have higher species richness than those near the poles (Figure 50.28). Explanations for this latitudinal gradient focus on either the origin or the maintenance of high species richness in the tropics.
- The equilibrium theory of island biogeography predicts that the number of species on an island represents a balance between the immigration of new species and the extinction of species already present (Figure 50.29). Studies show that large islands harbor more species than small islands and that islands near a mainland source have more species than distant islands (Figure 50.30).

[Animation: Species diversity by latitude](#)

[Animation: Area and distance effects](#)

## Questions

### Self-Test Questions

1. According to optimal foraging theory, predators:
  - a. always feed on the largest prey possible.
  - b. always feed on the prey that are easiest to catch.
  - c. choose prey based on the costs of capturing and consuming it compared with the energy it provides.
  - d. feed on plants when animal prey are scarce.
  - e. have coevolved mechanisms to overcome prey defenses.
2. The use of the same limiting resource by two species is called:
  - a. brood parasitism.
  - b. interference competition.
  - c. exploitative competition.
  - d. mutualism.
  - e. optimal foraging.
3. The range of resources that a population can possibly use is called:
  - a. its fundamental niche.
  - b. its realized niche.
  - c. character displacement.
  - d. resource partitioning.
  - e. its relative abundance.
4. Differences in bill size of finch species living on the same island in the Galápagos may be caused by:
  - a. predation.
  - b. character displacement.
  - c. mimicry.
  - d. interference competition.
  - e. cryptic coloration.

5. Bacteria that live in the human intestine assist digestion and feed on nutrients the human consumed. This relationship might best be described as:
- commensalism.
  - mutualism.
  - endoparasitism.
  - ectoparasitism.
  - predation.
6. The table below shows how many individuals were recorded for each of five species in five separate communities (a–e). Which community has the highest species diversity?

Community	Species 1	Species 2	Species 3	Species 4	Species 5
a.	90	10	0	0	0
b.	80	10	10	0	0
c.	25	25	25	25	0
d.	2	4	6	8	80
e.	20	20	20	20	20

7. A keystone species:
- is usually a primary producer.
  - has a critically important role in determining the species composition of its community.
  - is always a predator.
  - usually reduces the species diversity in a community.
  - usually exhibits aposematic coloration.
8. Species richness is often highest in communities where disturbances are:
- very frequent and severe.
  - very frequent and of moderate intensity.
  - very rare and severe.
  - of intermediate frequency and moderate intensity.
  - very rare and mild.
9. The change in the species composition of a community from bare and lifeless rock to climax vegetation is called:
- disturbance.
  - competition.
  - secondary succession.
  - primary succession.
  - facilitation.
10. The equilibrium theory of island biogeography predicts that the number of species found on an island:
- increases steadily until it equals the number in the mainland species pool.
  - is greater on large islands than on small ones.
  - is smaller on islands near the mainland than on distant islands.
  - can never reach an equilibrium number.
  - is greater for islands near the equator than for islands near the poles.

## Questions for Discussion

- Using the terms and concepts introduced in this chapter, describe the interactions that humans have with ten other species. Try to pick at least eight species that we do not eat.
- After reading about the two potential biases in the scientific literature on competition, describe how future studies of competition might avoid such biases.
- Humans are destroying natural communities at an ever-increasing pace. Using the predictions of the theory of island biogeography, develop hypotheses about what might happen as patches of natural habitats get smaller and smaller. How would you test these hypotheses?

## Experimental Analysis

Chaparral, a community of woody shrubs that is fairly common in California, often grows adjacent to grassland. The two communities are consistently separated by a “bare zone,” usually less than 1 m wide, where no vegetation of either type grows. Ecologists have proposed two possible explanations for this strip of bare soil: (1) that the leaves of chaparral shrubs release harmful, water-soluble chemicals that keep the grass seeds from germinating in the adjacent soil; and (2) that small mammals living in the dense cover provided by chaparral consume the grass seeds before they germinate; the animals don’t venture very far from the shrubs because they would be easy targets for predatory hawks. Design a set of field experiments to test the two hypotheses.

## Evolution Link

Five processes can foster microevolutionary change: gene flow, genetic drift, mutation, natural selection, and nonrandom mating (see Section 20.3). Which of those processes might contribute to the evolution of Batesian mimicry in two butterfly species? Would the same processes affect both the mimic and the model similarly? Which processes might have contributed to the evolution of the mutualistic relationship between ants and acacia trees, and how would their action on the two mutualists differ?

## How Would You Vote?

Currently, only a fraction of the crates being imported into the United States are inspected for the inadvertent or deliberate presence of exotic species. Would the cost of added inspections be worth it? Go to [www.thomsonedu.com/login](http://www.thomsonedu.com/login) to investigate both sides of the issue and then vote.