46

COMMUNITY STRUCTURE AND BIODIVERSITY

Fire Ants in the Pants

Solenopsis richteri and *S. invicta* entered the United States in the 1930s, probably as stowaways on cargo ships. These two species of Argentine fire ants infiltrated communities throughout the Northern Hemisphere, starting with the southeastern states. *S. invicta*, the imported red fire ant, recently colonized Southern California and New Mexico.

Disturb a fire ant that crawled onto your skin and it will bite down even as it pumps venom into you through a stinger. Searing pain follows, then a pus-filled bump forms where you were bitten (Figure 46.1). At one time or another, about half of all the Americans who live where fire ants are common have been stung. More than eighty people have died from the attacks.

Imported fire ants menace more than people. These insects attack just about anything that disturbs them, including livestock, pets, and wildlife. They also are more competitive than native ant species and other animals that feed on insects. The imports may be contributing to the declines of some native wildlife species.

To give an example, the Texas horned lizard (*Phrynosoma cornutum*) vanished from most of its home range when red fire ants moved in and displaced the native ants. To the Texas horned lizard, native ants are the food of choice, and it cannot tolerate eating the invaders.

The young of other lizard species are worse off. So are the hatchlings of quail and other ground-nesting birds. Fire ants swarm all over them and kill them directly.

Invicta means "invincible" in Latin. So far, *S. invicta* is living up to its species name. Pesticides have not slowed its invasions of new habitats. To the contrary, they might even be facilitating the invasions by wiping out most of the native ant populations.

Ecologists are enlisting biological controls. Two phorid fly species attack *S. invicta* in its native habitat. Both are parasitoids, a specialized type of parasite that kills its host in a rather gruesome way. A female fly pierces the cuticle of an adult ant, then lays an egg in the ant's soft tissues. The egg hatches into a larva, which grows and then eats

Figure 46.1 Fire ant mounds in west Texas, and agitated fire ants swarming over a leather boot. *Facing page*, skin eruptions that typically follow a concerted attack by these exotic imports.

IMPACTS, ISSUES

Watch the video online!

its way through tissues to the ant's head. After it gets big enough, the larva secretes an enzyme that makes the head fall off. The larva, sheltered inside the detached, cuticle-covered head, undergoes metamorphosis into an adult.

The flies are choosy about where they lay their eggs. Native ants are not candidates. Knowing this, ecologists released one of the parasitic fly species in Florida in 1997. They released a second species in other southern states in 2001. It is too soon to know whether these biological controls are working.

As ecologists wait for results, they are exploring other options. One idea is to use imported, pathogenic fungi or protists that will infect *S. invicta* but not the native ants. Another idea is to introduce a parasitic ant species that invades *S. invicta* colonies and decapitates the queens.

This example invites you into the sometimes rough-and-tumble aspects of **community structure**, or patterns in the number of species and their relative abundances. As you will see, species interactions and disturbances to the habitat shift community structure in small and large ways—some predictable, others unexpected.

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? See BiologyNow for details, then vote online.

Key Concepts

COMMUNITY CHARACTERISTICS

A community consists of all species in a habitat. Each species has a niche—the sum of activities and relationships in which its individuals take part as they secure and use vital resources. The habitat's history and characteristics, resource availability over time, and the history, adaptations, and interactions of its array of species shape community structure. Section 46.1

FORMS OF SPECIES INTERACTIONS

Commensalism, mutualism, competition, predation, and parasitism are forms of symbiotic interactions that directly involve two or more species. Sections 46.2–46.7

COMMUNITY STABILITY AND CHANGE

By an older model, a predictable succession of species in a habitat stabilizes as a climax community, which thereafter does not change much. It now appears that abiotic and human-created disturbances are more significant factors in shaping community structure. Sections 46.8–46.10

GLOBAL PATTERNS IN COMMUNITY STRUCTURE

Biogeographers identify patterns in species richness of mainland and island communities around the world. Two of the most striking patterns correlate with distance from the equator and from colonizing sources. Section 46.11

Links to Earlier Concepts

In this chapter, you will see how studies from diverse fields of inquiry often converge to explain big patterns in life. You will draw on the Unit IV survey of biodiversity. You will deepen your sense of the challenges facing conservation biology, as by species introductions (Chapter 27). You will revisit biogeography and take a closer look at global patterns in species richness (Sections 17.1, 17.3). You also will see how microevolutionary processes and population dynamics can influence community structure (18.4,18.7, 45.1, 45.5). You will come across modern expressions of evolutionary arms races that started in the Cambrian seas (26.2).

COMMUNITY CHARACTERISTICS

46.1 Which Factors Shape Community Structure?

The type of place where each organism normally lives is its ***habitat****. All species that directly or indirectly associate with one another in a habitat represent a* ***community****.*

Each community has a characteristic structure, which we define by **species richness**—the number of species—and their relative abundances. That structure arises largely in response to these abiotic and biotic factors:

1. The physical and chemical conditions that prevail in the habitat, such as temperature, rainfall, soil type, size, and annual incoming solar radiation.
2. The type, amount, and seasonal availability of food and other resources, as in Figure 46.2.
3. The evolutionary history of the habitat and of each resident species.
4. The morphological, physiological, and behavioral traits that help species survive in the habitat.
5. Interactions among species.
6. Natural and human-induced physical disturbances that vary unpredictably in magnitude and frequency.

It will take more than one chapter to survey these factors. Chapter 47, for example, focuses on energy flow and nutrient cycling among species. Here we start with the niche of each species in the community.

THE NICHE

All species of a community share the same habitat—the same "address"—but each has a "profession" that sets it apart. It has a distinct **niche**, the sum of its activities and interactions as it goes about acquiring and using the resources it must have to survive and reproduce. Its *fundamental* niche would prevail even in the absence of competition or any other factors that might limit how individuals get and use resources. However, constraining factors come into play, and they tend to bring about a more limited, *realized* niche. The realized niche is dynamic. It shifts over time, in small or large ways, in response to a mosaic of changes.

CATEGORIES OF SPECIES INTERACTIONS

Even in the simplest communities, dozens to hundreds of species interact. Interactions between two species may have indirect effects on others, but focus now on five forms of *symbiosis*, or close associations between two or more species during part or all of the life cycle. Each can promote or suppress population growth of a participating species. Let's simplify things by casting the definitions in terms of two-species interactions.

Commensalism directly helps one species but affects the other little, if at all. A bird may get a roosting site from a tree, which gets no benefit but is not harmed. In **mutualism**, both species benefit. Don't think of this as cozy cooperation; the benefits flow from a two-way exploitation. In **interspecific competition**, one species wins or loses with respect to access to some resource. **Predation** and **parasitism** directly benefit one species. Predators typically kill and eat prey. Parasites live in or on hosts and weaken but rarely kill them outright.

A habitat is the type of place where individuals of a species normally live. All of its species form a community. The community's structure arises from a habitat's physical and chemical features, resource availability over time, adaptive traits of its species, how its species interact, and the history of the habitat and its occupants.

A niche is the sum of all activities and relationships in which individuals of a species engage as they secure and use the resources necessary to survive and reproduce.

Commensalism, mutualism, competition, predation, and parasitism are all forms of symbiotic interactions.

Figure 46.2 Three of twelve fruit-eating pigeon species in Papua New Guinea's tropical rain forests. *Left to right*, the tiny pied imperial pigeon, the superb crowned fruit pigeon, and the turkey-sized Victoria crowned pigeon. The forest's trees differ in the size of fruit and fruit-bearing branches. The big pigeons eat big fruit. Smaller ones, with smaller bills, cannot peck open big, thick-skinned fruit. They eat small, soft fruit on branches too spindly to hold big pigeons.

Trees feed the birds, which help the trees. Seeds in fruit resist digestion in the bird gut. Flying pigeons disperse seed-rich droppings, often some distance from tall, mature trees that are established competitors for water, minerals, and sunlight. With dispersal, some seedlings have a better chance to take hold.

46.2 Mutualism

In a mutualistic interaction, two species take advantage of their partner in ways that benefit both, as when one withdraws nutrients from the other while sheltering it.

LINKS TO SECTIONS 20.4, 24.6, 28.5, 31.2

Interactions in which positive benefits flow both ways abound in nature. Remember Section 31.2? Flowering plants and the insects, birds, bats, and other animals that pollinate them are vivid examples. Similarly, rain forest trees give pigeons food, and pigeons disperse seeds from the trees to new sites (Figure 46.2).

In *facultative* mutualism, the interaction is helpful but not vital. Ants and aphids get along well without each other, but ants do protect aphids as they feed on sugar droplets exuding from aphids (Figure 31.14).

With *obligatory* mutualism, each species must have access to the other in order to complete its life cycle and reproduce. Yucca plants and the yucca moths that pollinate them are obligatory mutualists (Figure 46.3). So are fungi that interact with a photobiont in lichens or with plant roots in mycorrhizae (Section 24.6). In a mycorrhiza, fungal hyphae penetrate root cells or form a dense, velvety mat around them. The plant pilfers mineral ions from the fungus, which absorbs far more ions than the plant could do on its own. The fungus pilfers a few photosynthetic products—sugars—from the plant. The fungus depends on the plant mutualist for its reproductive success. It will stop making spores if the plant stops photosynthesizing.

Anemone fishes can hide out among the tentacles of one or more species of sea anemones; a thick coat of mucus makes them impervious to nematocysts. In one mutualistic interaction, the sea anemone benefits, too. An aggressive anemone fish chases off another kind of fish that likes to eat the tentacles (Figure 46.4).

Or reflect on the apparent endosymbiotic origin of eukaryotes (Section 20.4). Long ago, phagocytes were engulfing aerobic bacterial cells—but some resisted digestion, tapped into host nutrients, and then kept reproducing independently of the host cell body. In time, the hosts came to depend on the ATP produced by the guests—which evolved into mitochondria and chloroplasts. If those ancient prokaryotic cells had not coevolved as mutualists, you and all other eukaryotic species would not be around today.

Mutualism is a common form of symbiosis. Each species benefits as it exploits a partner in some way that helps assure its own reproductive success. In cases of obligatory mutualism, one or both partners cannot complete its life cycle in the absence of the interaction.

Figure 46.3 Mutualism on a rocky slope of the high desert in Colorado.

Only one yucca moth species pollinates plants of each *Yucca* species; it cannot complete its life cycle with any other plant. The moth matures when yucca flowers blossom. The female has specialized mouthparts that collect and roll sticky pollen into a ball. She flies to another flower and pierces its ovary, where seeds will form and develop, and lays eggs inside. As she crawls out, she pushes a ball of pollen onto the flower's pollen-receiving platform.

After pollen grains germinate, they give rise to pollen tubes, which grow through the ovary tissues and deliver sperm to the plant's eggs. Seeds develop after fertilization.

Meanwhile, moth eggs develop into larvae that eat a few seeds, then gnaw their way out of the ovary. Seeds that larvae do not eat give rise to new yucca plants.

Figure 46.4 The sea anemone *Heteractis magnifica*, which shelters about a dozen fish species. It has a mutualistic association with the pink anemone fish (*Amphiprion perideraion*). This tiny but aggressive fish chases away predatory butterfly fishes that bite off the tips of its partner's tentacles. In return, the fish and its eggs get protection and shelter—scarce commodities on tropical reefs (Section 27.5).

46.3 Competitive Interactions

LINKS TO SECTIONS 29.5, 45.4

Where you come across limited supplies of energy, nutrients, living space, and other natural resources, there you are likely to find organisms competing for a share of them.

Competition for resources is typically intense between individuals of the same species (Chapters 45 and 49). At the community level, competition between species usually is not as intense. Why not? *The requirements of two species may be similar but are never as close as they are among individuals of the same species*. Let's consider two forms of interspecific competition.

In **interference competition**, one species controls or blocks access of another species to some resource, regardless of its abundance. The leaves of some plant species exude aromatic compounds that taint soil and prevent potential competitors from taking root. A few aggressive chipmunk species keep others out of their habitats (Figure 46.5). In spring and early summer, a male broadtailed hummingbird evicts birds of its own species from its richly flowered territory in the Rocky Mountains. In August, however, *rufous* hummingbirds migrate through the Rockies on their way to Mexico. Until they fly on, the stronger, more aggressive rufous males force the male broadtails to give up territory.

In **exploitative competition**, different species have equal access to a resource, but one is better at using it. In one experiment, a large and a small species of water flea (*Daphnia*) that feed on the same alga were grown together in an alga-enriched culture flask. The larger species increased in body mass. Also, its population expanded. The smaller species lost body mass, and its population shrank—which leads us to a theory.

THEORY OF COMPETITIVE EXCLUSION

Any two species differ to a greater or lesser extent in their capacity to secure and use resources. The more they overlap in these respects, the less likely they are to coexist in the same habitat.

Years ago, G. Gause found evidence of this when he grew two species of *Paramecium* separately and then together (Figure 46.6). Both of these ciliated protozoans hunt the same prey—bacteria—and compete intensely for it. Gause's species, which use identical resources, could not coexist indefinitely. Later experiments with water fleas and many other species yielded the same results, in support of what ecologists now call the theory of **competitive exclusion**.

Gause also studied two other *Paramecium* species that did not overlap much in requirements. He grew them together. One species tended to feed on bacteria suspended in culture tube liquid. The other ate yeast cells near the bottom of the tube. Population growth rates slowed for both species—but the overlap in use

Figure 46.5 Example of interspecific competition in nature. On the slopes of the Sierra Nevada, competition helps keep nine species of chipmunks (*Tamias*) in different habitats.

The alpine chipmunk (**a**) lives in the alpine zone, the highest elevation. Below it are the lodgepole pine, piñon pine, and then sagebrush habitat zones. Lodgepole pine chipmunks (**b**), least chipmunks (**c**), and other species live in the forest zones. Merriam's chipmunk (**d**) lives at the base of the mountains, in sagebrush. Its traits would allow it to move up into the pines, but the aggressively competitive behavior of forest-dwelling chipmunks won't let it. Food preferences keep the pine forest chipmunks out of the sagebrush habitat.

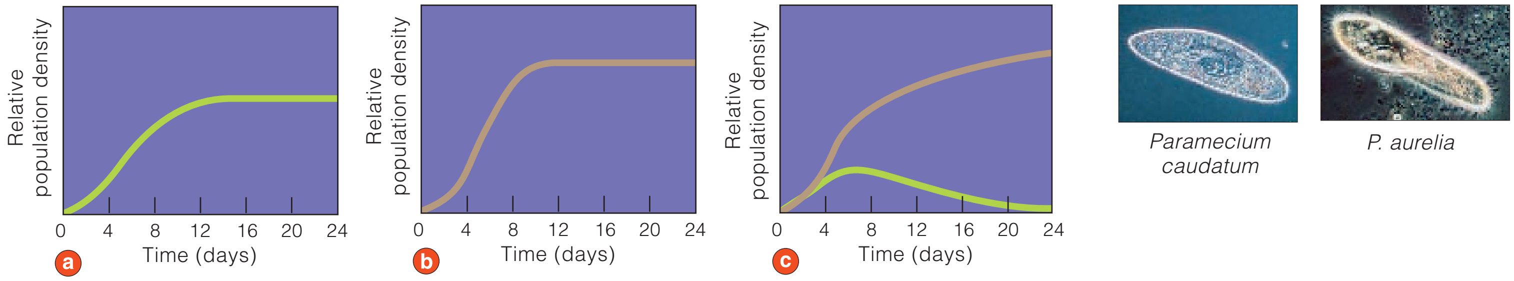


Figure 46.6 ***Animated!*** Results of competitive exclusion between two protozoan species that compete for the same food. (**a**) *Paramecium caudatum* and (**b**) *P. aurelia* were grown in separate culture flasks and established stable populations. The S-shaped graph curves indicate logistic growth and stability.

(**c**) Then the two species were grown together. *P. aurelia* (*brown* curve) drove *P. caudatum* toward extinction (*green* curve in **c**). This experiment and others suggest that two species cannot coexist indefinitely in the same habitat *when they require identical resources*. If their requirements do not overlap much, one might influence the population growth rate of the other, but they may still coexist.

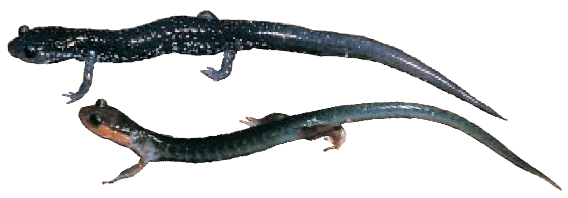


Figure 46.7 Two coexisting species of salamanders: (**a**) *Plethodon glutinosus* complex and (**b**) *P. jordani.*

of resources was not enough for one species to fully exclude the other. The two continued to coexist.

Field experiments also reveal effects of competition. For instance, N. Hairston studied salamanders in the Balsam Mountains and Great Smoky Mountains. One species, *Plethodon glutinosus,* lives at lower elevations than its relative *P. jordani,* but the home ranges overlap in some areas (Figure 46.7). Hairston removed one or the other species from test plots in the overlap areas. He left some plots untouched as controls. Five years later, nothing had changed in those control plots; the species were coexisting. Population sizes in test plots were growing. Plots cleared of *P. jordani* had a greater proportion of *P. glutinosus*. In addition, plots cleared of *P. glutinosus* had a greater proportion of *P. jordani*.

Hairston concluded that, where populations of the two salamander species coexist in nature, competitive interactions suppress the growth rate of both.

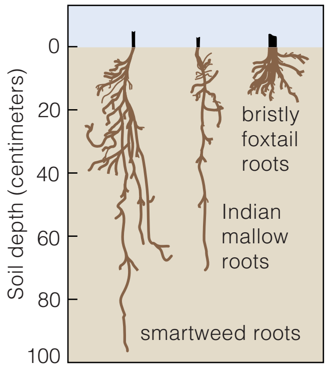


Figure 46.8 Resource partitioning among three annual plant species in an abandoned field. The plants differ in how they are adapted to secure soil water and mineral ions. The roots of each species tap into different depths of soil.

RESOURCE PARTITIONING

Think back on those fruit-eating pigeon species. They all use the same resource: fruit. Yet they overlap only a bit in their use of it, because each prefers fruits of a certain size. They are a case of **resource partitioning**—a *subdividing* of some category of similar resources, which allows competing species to coexist.

Similarly, three annual plant species live in the same plowed, abandoned field. All require sunlight, water, and minerals. Each exploits a slightly different part of the habitat (Figure 46.8). Bristly foxtail grasses have a shallow, fibrous root system that absorbs water fast during rains. They grow where moisture shifts daily, and are drought-tolerant. Indian mallow has a taproot system in deeper soil that is moist early in spring and drier later. The taproot system of smartweed branches in topsoil and soil below the roots of other species. It grows where soil is perpetually moist (Section 29.5).

In some competitive interactions, one species controls or blocks access to a resource, regardless of whether it is scarce or abundant. In other interactions, one is better than another at exploiting a shared resource.

When two species overlap too much in their requirements, they cannot coexist in the same habitat unless they share required resources in different ways or at different times.

46.4 Predator–Prey Interactions

LINKS TO SECTIONS 1.5, 1.6, 26.2

***Predators** are consumers that obtain energy and nutrients from living organisms—their prey—which they generally capture and kill. The quantity and types of prey species affect predator diversity and abundances, and the types of predators and their numbers do the same for prey.*

COEVOLUTION OF PREDATORS AND PREY

Coevolution influences predator and prey interactions. The term refers to species that evolve jointly as their close ecological interaction exerts selection pressure on each other over the generations. If a gene mutation in a prey organism leads to a more effective defense against predators, the mutant allele will increase in frequency in the prey population. Its bearers and their offspring will tend to survive in greater numbers. If a gene mutation in a predator leads to a better way to overcome the novel prey defense, its bearers and their offspring will eat better; they will tend to survive and leave more descendants in the predator population.

Thus, over time, the predators are selective agents that favor improved prey defenses in prey. The prey with better defenses are selective agents that favor more effective predators. This type of coevolutionary arms race started among vertebrate predators and their prey when jawed fishes emerged (Section 26.2).

MODELS FOR PREDATOR–PREY INTERACTIONS

The extent to which predators limit numbers of prey depends on several factors. A key factor is the response of individual predators to increases or decreases in prey density. Figure 46.9*a* is an overview of the three general patterns of functional responses.

By the type I model, a predator removes a constant proportion of prey over time, regardless of levels of prey abundance. The number of prey killed in a given interval depends only on the prey density. This model applies to passive predators, such as web spiders. The more flies there are, the more get caught in webs.

By the type II model, the capacity of predators to consume and digest prey determines how many prey they capture. When prey density rises, the proportion captured rises steeply at first, then slows as predators are exposed to more prey than they can deal with at one time. Figure 46.9*b* offers an example. A wolf that just killed a caribou will not hunt another until it has eaten and digested the first one.

By the type III model, predator response is lowest when prey density is low. It is highest at intermediate prey densities, then levels off. This type of response is observed for predators that can switch to other prey when individuals of a prey species are scarce and hard to find. Predators that can make the type I and type II responses can limit prey at a stable equilibrium point.

Other factors besides individual predator response to prey density are at work. For example, predator and prey reproductive rates affect the interaction. So do hiding places for prey, the presence of other prey or predator species, and carrying capacities.

THE CANADIAN LYNX AND SNOWSHOE HARE

In some cases, shifts in environmental conditions can cause predator and prey densities to oscillate. At the lowest level, predation will strongly depress the prey density. At the highest level, predation is absent and the prey population nears the carrying capacity.

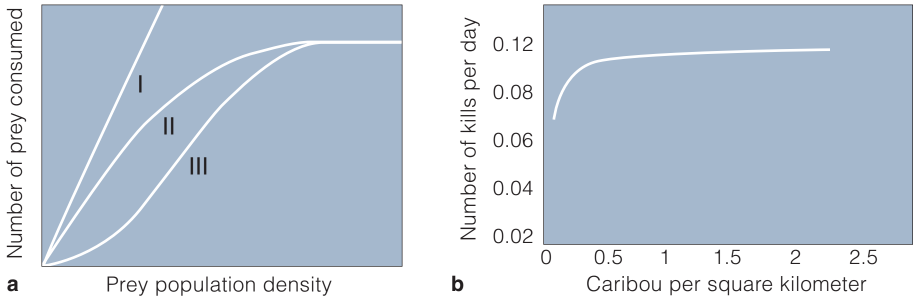


Figure 46.9 ***Animated!*** (**a**) Three models for responses of predators to prey density. Type I: Prey consumption rises linearly as prey density rises. Type II: Prey consumption is high at first, then levels off as predator bellies stay full. Type III: When prey density is low, it takes longer to hunt prey, so the predator response is low. (**b**) A type II response in nature. For one winter month in Alaska, B. W. Dale and his coworkers observed four wolf packs (*Canis lupus*) feeding on caribou (*Rangifer tarandus*). The interaction fit the type II model for the functional response of predators to the prey density.

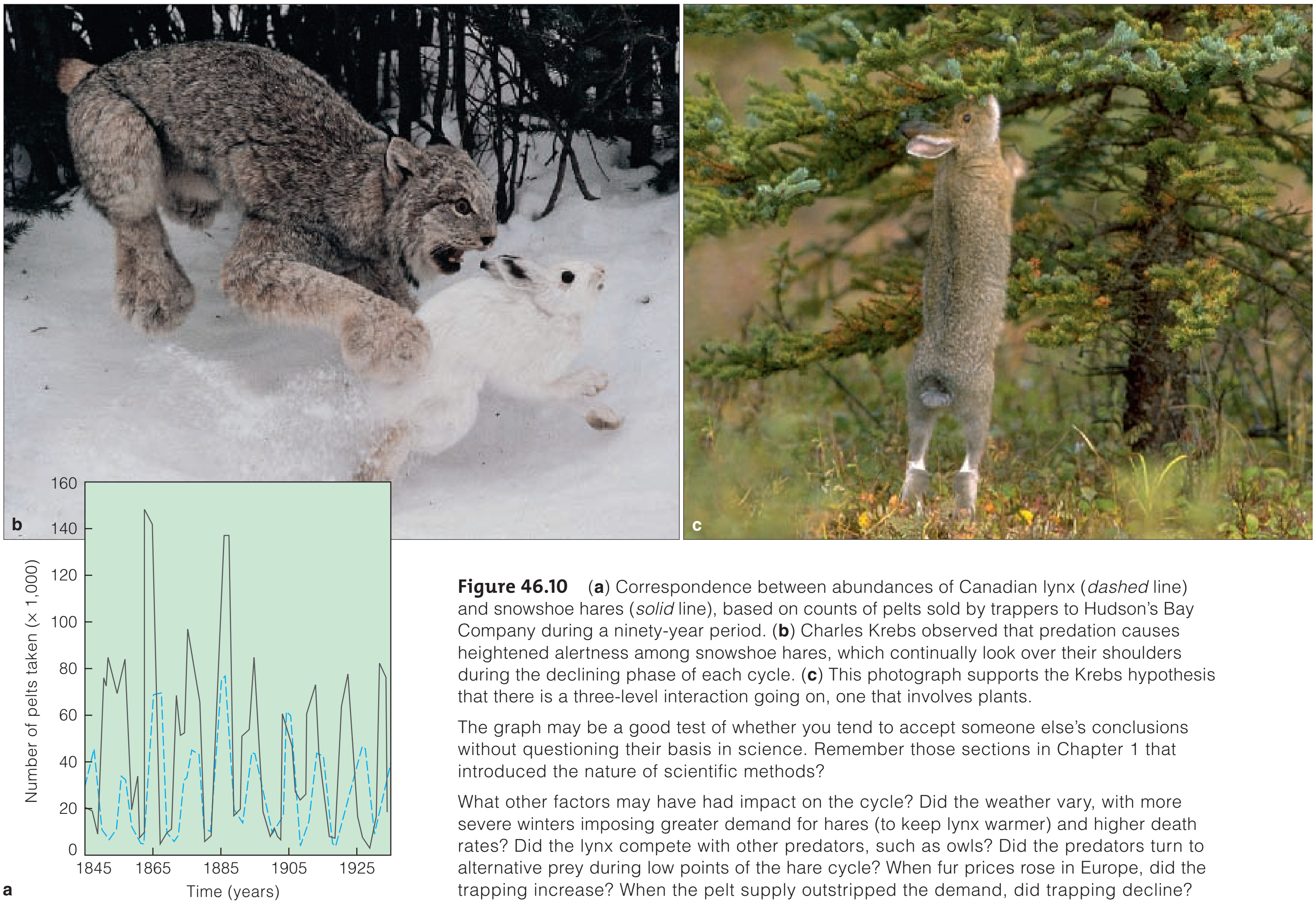


Figure 46.10 (**a**) Correspondence between abundances of Canadian lynx (*dashed* line) and snowshoe hares (*solid* line), based on counts of pelts sold by trappers to Hudson's Bay Company during a ninety-year period. (**b**) Charles Krebs observed that predation causes heightened alertness among snowshoe hares, which continually look over their shoulders during the declining phase of each cycle. (**c**) This photograph supports the Krebs hypothesis that there is a three-level interaction going on, one that involves plants.

The graph may be a good test of whether you tend to accept someone else's conclusions without questioning their basis in science. Remember those sections in Chapter 1 that introduced the nature of scientific methods?

What other factors may have had impact on the cycle? Did the weather vary, with more severe winters imposing greater demand for hares (to keep lynx warmer) and higher death rates? Did the lynx compete with other predators, such as owls? Did the predators turn to alternative prey during low points of the hare cycle? When fur prices rose in Europe, did the trapping increase? When the pelt supply outstripped the demand, did trapping decline?

Consider a ten-year oscillation in populations of a predator, the Canadian lynx, and the snowshoe hare that is its main prey (Figure 46.10). To identify the causes of this pattern, the ecologist Charles Krebs and his coworkers tracked hare population densities for ten years in Alaska, in the Yukon River Valley. They set up 1-square-kilometer control plots and experimental plots. Electric fences kept predatory mammals out of some plots. Extra food or fertilizers that fanned plant growth were placed in other plots. The team captured and released more than a thousand snowshoe hares, lynx, and other animals, giving each a radio collar.

In predator-free plots, the hare density doubled. In plots with extra food, it tripled. In plots having extra food and fewer predators, it increased elevenfold.

The experimental manipulations delayed the cyclic declines in population density but did not stop them. Why not? Owls and other raptors flew over the fences. Only 9 percent of the collared hares starved to death; predators devoured most of the rest. Krebs concluded that a simple predator–prey or plant–herbivore model cannot fully explain his Yukon River Valley results. For the Canadian lynx and snowshoe hare cycle, other variables are at work, during multilevel interactions.

Predator and prey populations tend to exert coevolutionary pressures on one another.

Predators may affect prey density. There are three general patterns of response to changes in prey density. Population levels of prey may also show periodic oscillations.

Predator and prey numbers often vary in complex ways that reflect the multiple levels of interaction in a community.

46.5 An Evolutionary Arms Race

LINKS TO
SECTIONS 1.6,
18.4, 26.8, 33.1

As explained in the preceding section, predators and prey exert selective pressure on one another. One defends itself and the other must overcome defenses. Such interactions are often evidence of a coevolutionary arms race.

PREY DEFENSES

Camouflage Many heritable traits help an organism hide in the open; they function in **camouflaging**. Body form, patterning, color, behavior, or some combination of these blend with the surroundings and help the organism avoid detection. Consider Figure 46.11. Some nesting birds thrust their beak upward and sway slightly, like the plants around them. A caterpillar with special color patterns passes itself off as a bird dropping. When a certain desert plant (*Lithops*) is not flowering, it looks like a rock. It flowers only during a brief rainy season, when herbivores are more likely to be distracted by the profuse growth of other plants. Section 18.4 explains the genetic basis for camouflage among rock pocket mice as part of an example of natural selection.

Mimicry Many prey species closely resemble a hard-to-catch, dangerous, or unpalatable species. **Mimicry** is the name for an ecological association between one species that is a *model* for deception and a different species—a *mimic*, which very closely resembles it in form, behavior, or both. Predators often avoid a model species because of a repellent taste, toxic secretion, or painful bite or sting, and so they tend also to avoid the mimic. Section 1.6 offers an experimental test of mimicry. Here, Figure 46.12 shows the deceptive look of three tasty but weaponless mimics. All strongly resemble a very aggressive wasp that can sting repeatedly, with painful results.

Chemical Defenses The leaves, flowers, and seeds of many plants contain bitter, hard-to-digest, or dangerous repellents. Peach, apricot, and rose seeds are loaded with cyanide. Remember the Chapter 14 introduction? The castor bean plant did not develop its capacity to make the lethal chemical ricin in an evolutionary vacuum. Ricin protects this plant from herbivores that would otherwise eat it.

Many prey species that taste bad or that make toxins announce their unpalatability with **warning coloration**. They have conspicuous patterns and colors that predators learn to recognize as avoidance signals. For instance, a young, inexperienced bird might eat an orange-and-black patterned monarch butterfly once. It quickly learns to associate the butterfly's coloration and patterning with "Eat me and you will vomit foul-tasting toxins."

Figure 46.11 Prey camouflage. (**a**) What bird??? When a predator approaches its nest, the least bittern stretches its neck (which is colored like the surrounding withered reeds), points its bill upward, and sways like reeds in the wind. (**b**) An inedible bird dropping? No. This caterpillar's body coloration and its capacity to hold its body in a rigid position help camouflage it from predatory birds. (**c**) Find the plants (*Lithops*) hiding in the open from herbivores with the help of their stonelike form, pattern, and coloration.

a A dangerous model **b** One of its edible mimics **c** Another edible mimic **d** And another edible mimic

Figure 46.12 An example of mimicry. Edible insect species often resemble toxic or unpalatable species that are not at all closely related. (**a**) A yellowjacket can deliver a painful sting. It might be the model for nonstinging wasps (**b**), beetles (**c**), and flies (**d**) of strikingly similar appearance.

Truly dangerous or repugnant species often make little or no attempt to conceal themselves. Remember the vividly colored and poisonous frogs (Section 33.1)? Or think about skunks, which spray one of the most odious repellents.

Moment-of-Truth Defenses When luck runs out and an animal is cornered or under attack, survival may turn on a last-chance trick. Many animals try to startle predators. For instance, some hiss, puff up, flash big eye-shaped spots on their body, bare sharp teeth, or flare neck ruffs (Figure 26.17*d*). Opossum and hognose snakes make a big show of pretending to be dead. Many cornered animals, including hognose snakes and certain beetles, secrete or squirt out irritating chemical repellents or toxins (Figure 46.13*a*).

ADAPTIVE RESPONSES OF PREDATORS

Again, predators tend to counter prey defenses with their own adaptations. Stealth, camouflage, and ingenious ways of avoiding repellents are some countermeasures. Consider the edible beetles that direct sprays of noxious chemicals at attackers. A grasshopper mouse grabs the beetle and plunges the sprayer end into the ground, and then chews on the tasty, unprotected head (Figure 46.13*a*,*b*).

Some prey can outrun even cheetahs when they get a head start. But the cheetah is the world's fastest land animal. One was clocked at 114 kilometers (70 miles) per hour. Compared to other big cats, the cheetah has longer legs relative to its body size and nonretractable claws that act like cleats to increase traction. Thomson's gazelle, its main prey, can run longer but not as fast (80 kilometers per hour). Without a head start, it is toast, so to speak.

Camouflaging helps predators as well as prey. Think of white polar bears stalking seals over ice, striped tigers crouched in tall-stalked, golden grasses, and scorpionfish hidden on the seafloor (Figure 46.13*c*). Camouflage is often stunning among predatory insects (Figure 46.13*d*). With camouflaging, predators select for enhanced sensory systems in prey. By one theory, primate color vision may have evolved in part to enhance detection of predators.

Figure 46.13 Predator responses to prey defenses. (**a**) Some beetles spray noxious chemicals at attackers, which deters them some of the time. (**b**) At other times, grasshopper mice plunge the chemical-spraying tail end of their beetle prey into the ground and feast on the head end. (**c**) Find the scorpionfish, a venomous predator with camouflaging fleshy flaps, multiple colors, and profuse spines. (**d**) Where do the pink flowers end and the pink praying mantis begin?

46.6 Parasite–Host Interactions

LINKS TO SECTIONS 21.8, 25.5, 25.10, 25.16

***Parasites** spend all or part of their life cycle in or on other living organisms, from which they draw nutrients. They weaken a host but usually do not kill it outright. Different kinds complete their life cycle in one or more host species.*

PARASITES AND PARASITOIDS

Parasites have pervasive impacts on populations. By draining nutrients from hosts, they alter the amount of energy and nutrients the host population demands from a habitat. Also, weakened hosts are usually more vulnerable to predation and less attractive to potential mates. Some parasite infections cause sterility. Others shift the ratio of host males to females. In such ways, parasitic infections lower birth rates, raise death rates, and affect intraspecific and interspecific competition.

Sometimes the gradual drain of nutrients during a parasitic infection indirectly leads to death. The host becomes so weakened that it can't fight off secondary infections. Nevertheless, in evolutionary terms, killing a host too quickly is bad for a parasite's reproductive success. A parasitic infection must last long enough to give the parasite time to produce some offspring. The longer it lives in the host, the more offspring. We may therefore expect selective agents to favor parasites that have less-than-fatal effects on hosts (Section 21.8).

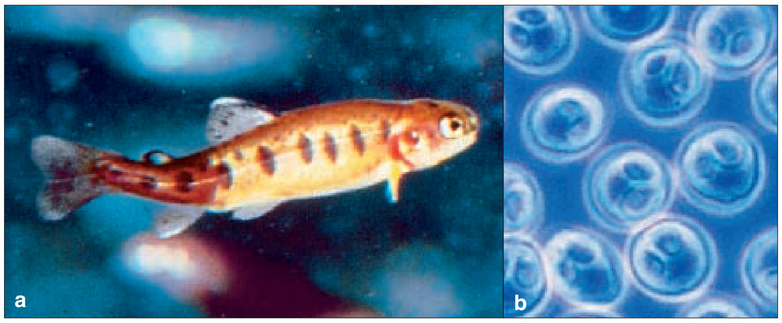


Figure 46.14 (**a**) A young trout with a twisted spine and darkened tail caused by whirling disease, which damages cartilage and nerves. Jaw deformities and whirling movements are other symptoms. (**b**) Spores of *Myxobolus cerebralis*, the introduced protist that causes the disease. It is now in many lakes and streams in Western and Northeastern states.

Usually, death occurs only when a parasite attacks a novel host—one with no coevolved defenses against it—or when too many parasitic individuals attack at the same time and collectively overwhelm the body.

You looked at many parasites in the diversity unit, especially in Chapters 21, 24, and 25. You saw how some species require a single host and how others are free-living some of the time or residents of different hosts at different times. Many types ride inside insects and other arthropods, which are vectors between one host organism and the next (Section 25.16).

All viruses and some bacteria, protists, and fungi are parasites. Figure 46.14 shows a young trout that was parasitized by *Myxobolus cerebralis*, a protist.

Even a few plants are parasitic. Nonphotosynthetic types, such as dodders, obtain energy and nutrients from other plants (Figure 46.15). Other types carry out photosynthesis but still tap into the nutrients and water in tissues of a host plant. Mistletoe is like this; its modified roots invade the sapwood of host trees.

Many tapeworms, flukes, and certain roundworms are well-known invertebrate parasites (Figure 46.16). So are ticks, many insects, and many crustaceans.

You already read about **parasitoids**. An immature stage of these insects matures in a different insect's body, which they devour from the inside out. Unlike parasites, parasitoids always kill their hosts directly. About 15 percent of all insects may be parasitoids.

Social parasites are animals that take advantage of the social behavior of a host as a way to complete the life cycle. The cuckoos and North American cowbirds, described shortly, are like this.

Figure 46.15 Dodder (*Cuscuta*), also known as strangleweed or devil's hair. This parasitic flowering plant's sporophytes have no chlorophylls. They wind around a host plant during growth. Modified roots penetrate the host's vascular tissues and absorb water and nutrients from them.

Figure 46.16 Adult roundworms (*Ascaris*), an endoparasite, packed inside the small intestine from a host pig. Sections 25.5 and 25.10 give more examples of parasitic worms.

Figure 46.17 Biological control agent: a commercially raised parasitoid wasp about to deposit an egg in an aphid. This wasp reduces aphid populations. It stops the aphid from laying eggs even before the wasp egg develops into a larva that will eat it.

USES AS BIOLOGICAL CONTROLS

Parasites and parasitoids are commercially raised and released in target areas as *biological controls*. They are promoted as a workable alternative to pesticides. The chapter introduction and Figure 46.17 give examples.

Effective biological controls display five attributes. The agents are adapted to a specific host species and to its habitat; they are good at locating hosts; their population growth rate is high compared to the host's; their offspring are good at dispersing; and they make a type III functional response to prey, without much lag time after shifts occur in the host population size.

Biological control is not without risks of its own. Releasing more than one kind of biological control agent in an area may invite competition among them, which can lower their effectiveness against an intended target. In addition, an introduced parasite sometimes parasitizes nontargeted species as well as—or instead of—the species they were expected to control.

In Hawaii, the introduction of several parasitoids to control an imported stink bug resulted in the decline of the koa bug, the state's largest native bug. Few koa bugs have been collected since 1978. Apparently the koa bugs, which congregate in big groups, were more tempting to parasitoids. Also, introduced parasitoids have been implicated in the ongoing decline of many native Hawaiian butterflies and moths.

Natural selection favors parasitic species that temper their attacks in ways that ensure an adequate supply of hosts.

Parasitic species belong to many groups, including bacteria, protists, invertebrates, and plants. Parasitoids are insects that feed on and kill other insects. Social parasites use the social behavior of another species to their own benefit.

46.7 Cowbird Chutzpah

FOCUS ON EVOLUTION

The brown-headed cowbird's genus name (Molothrus) *means "intruder" in Latin. This bird intrudes, sneakily, into the life cycle of other species. Let us ask: Why?*

Brown-headed cowbirds (*Molothrus ater*) evolved in the Great Plains of North America. They lived as commensalists with bison. Great herds of these hefty ungulates stirred up plenty of insects as they migrated through the grasslands, and, being insect-eaters, the cowbirds wandered around with them (Figure 46.18*a*).

A vagabond way of life did not lend itself to nesting in any one place. However it happened, cowbirds learned to lay eggs in nests constructed by other species, then leave them and move on with the herds. Many species became "hosts"; they did not have the neural wiring to recognize the differences between cowbird eggs and their own eggs. Concurrently, cowbird hatchlings became innately wired for hostile takeovers. Even before hatchlings open their eyes, they shove the owner's eggs out of the nest and demand to be fed as rightful occupants (Figure 46.18*b*). Thus, for thousands of years, cowbirds have perpetuated their genes by way of parasitic chutzpah.

When American pioneers moved west, many cleared swaths of woodlands for pastures. Cowbirds now moved in the other direction. They adapted easily to a life with new ungulates—cattle—in the manmade grasslands; hence their name. They started to penetrate adjacent woodlands and exploit novel species. Today, brown-headed cowbirds parasitize at least fifteen species of native North American birds. Some of those birds are threatened or endangered.

Besides being successful opportunists, cowbirds are big-time reproducers. A female can lay an egg a day for ten days, give her ovaries a rest, do the same again, and then again in one season. As many as thirty eggs in thirty nests—that is a lot of cowbirds.

Figure 46.18 Oh give me a home, where the buffalo roam—brown-headed cowbirds (*Molothrus ater*) originally evolved as commensalists with bison and as social parasites of other bird species of the North American Great Plains. When conditions changed, they expanded their range. They became nest usurpers in woodlands as well as grasslands in much of the United States.

46.8 Ecological Succession

LINKS TO SECTIONS 17.4, 23.11

*By an older model for **ecological succession**, a community comes into being through competition and other species interactions and in time stabilizes into a predictable array of species. However, abiotic forces, including fire, storms, and human-created disturbances, may be more important in shaping community structure.*

Figure 46.19 In Alaska's Glacier Bay region, one pathway of primary succession. (**a**) As a glacier retreats from the sea, meltwater leaches minerals from the glacial till. (**b**) Lichens, horsetails, mosses, fireweed, and mountain avens are pioneer species; some are mutualists with nitrogen-fixing microbes. Within twenty years, alder, cottonwood, and willow seedlings take hold. Alders have nitrogen-fixing symbionts. (**c**) Within fifty years, they form dense, mature thickets in which cottonwood, hemlock, and a few evergreen spruce grow fast. (**d**) After eighty years, western hemlock and spruce crowd out mature alders. (**e**) In areas deglaciated for more than a century, forests of Sitka spruce dominate.

SUCCESSIONAL CHANGE

A concept of "nature in balance" once guided studies in community ecology. Researchers knew that **pioneer species** are the start of community structure. These are opportunistic colonizers of new or newly vacated habitats. They have high dispersal rates, they grow and mature quickly, and they produce many offspring. In time, more competitive species replace them. Then the replacements are replaced.

Primary succession is a process that begins when pioneer species colonize a barren habitat, such as a new volcanic island and land exposed when a glacier retreats (Figure 46.19). Pioneers include lichens and plants, such as club mosses, that are small, have short life cycles, and can survive intense sunlight, extreme temperature changes, and nutrient-poor soil. Early on, hardy annual flowering plants put out many small seeds, which are quickly dispersed.

Established pioneers often improve soil and other conditions. In doing so, they typically set the stage for their own replacement. Many of the new arrivals are mutualists with nitrogen-fixing bacteria, so they can grow in nitrogen-poor habitats. Seeds of later species find shelter inside mats of the pioneers, which do not grow high enough to shade out the new seedlings.

Organic wastes and remains accumulate over time, which add volume and nutrients to soil, which favors invasions by other species. Later successional species crowd out earlier ones, whose spores and seeds travel as fugitives on wind and water—destined, perhaps, for another new but temporary habitat.

In **secondary succession**, a disturbed area within a community recovers. If improved soil is still present, secondary succession can be fast. It commonly occurs in abandoned fields, burned forests, and tracts of land cleared by volcanic eruptions.

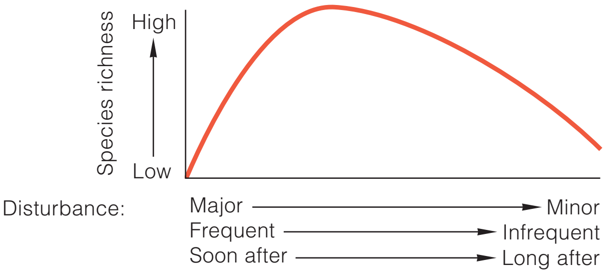
INTERMEDIATE DISTURBANCE HYPOTHESIS

In a traditional view, a predictable array of species in the habitat stabilizes as the *climax* community, after which not much changes. The community is adapted to many factors, such as topography, climate, soil, and species interactions, and it may show some variation

Figure 46.20 A natural laboratory for succession after the 1980 Mount Saint Helens eruption (**a**). The community at the base of this Cascade volcano was destroyed. (**b**) In less than a decade, pioneer species took hold. (**c**) Twelve years later, seedlings of the dominant species, Douglas firs, were taking hold.

along gradients of environmental conditions. In this view, even after a disturbance, the community reverts to a climax state. Later, Henry Gleason proposed that most communities are *not* stable, that unpredictable disturbances can alter the direction of succession.

It turned out that the magnitude and frequency of disturbances may be more important than interactions among species in defining the community. According to the **intermediate disturbance hypothesis**, species richness of a community becomes greatest in between disturbances of moderate intensity or frequency. There is enough time for many colonizing species to enter the habitat but not enough time for many species to be competitively excluded from it:



Tolerance, inhibition, and facilitation may be three successional mechanisms. In cases of *tolerance*, an early colonizer has no effect on which species will colonize the habitat after it. In *inhibition*, the early colonizer changes conditions of the habitat in specific ways that bar colonization by later species. In *facilitation*, early colonizers improve conditions for later ones.

Ecologists documented inhibition and facilitation in intertidal zone succession. After Wayne Sousa cleared algae from an intertidal zone in Southern California, different algae moved in. After Teresa Turner removed attached algae from plots in an Oregon intertidal zone, surf grass could not move in, because they use algae as anchoring sites. Experimental studies in old fields, temperate forests, and other land regions where major disturbances have occurred also give evidence of these three mechanisms of succession.

For instance, after Washington state's Mount Saint Helens erupted in 1980, the blast wave, superheated mudslides, and floods obliterated approximately 600 square kilometers of forests (Figure 46.20). Afterward, ecologists moved in to monitor succession first-hand. They observed and recorded in detail natural patterns of colonization. They also manipulated plots inside the blast zone. William Morris and David Wood showed that facilitation and inhibition were factors in plant succession. By adding seeds of certain plant species to some plots and keeping some other plots barren, they demonstrated that early colonizers helped several other species of colonizing plants move in. They also found that earlier colonizers kept some plant species out.

A community develops through a succession of stages, starting with pioneer species that are replaced by others. Biotic (biological) and abiotic (physical and chemical) factors affect community structure.

Disturbances are unpredictable and vary in magnitude and frequency. By an intermediate disturbance hypothesis, species richness is greatest between moderate disturbances.

46.9 Species Interactions and Community Instability

LINKS TO SECTIONS 17.4, 23.11

The loss or addition of even one species may destabilize the number and relative abundances of species in a community.

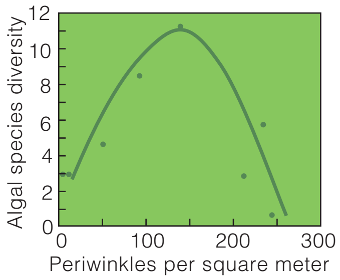
As you read earlier, short-term physical disturbances can knock a community out of equilibrium. Long-term changes in climate or another environmental variable also have destabilizing effects. Besides this, a shift in species interactions also can tip a community out of its uneasy balance. Remember, resources are sustained as long as populations do not flirt dangerously with the carrying capacity. Predators and their prey coexist as long as neither wins. Competitors have no sense of fair play. Mutualists are stingy, as when plants make as little nectar as necessary to attract pollinators and the pollinators take as much nectar as they can for the least possible effort.

Whether biotic or abiotic, a disturbance sometimes causes the number and relative abundances of species to shift irrevocably. For instance, if some occupants of the habitat happen to be rare or do not compete well with the others, they might be driven to extinction.

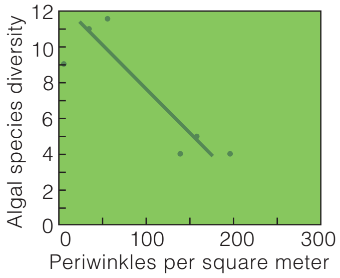
THE ROLE OF KEYSTONE SPECIES

The uneasy balancing of forces in a community comes into focus when we observe the effects of a **keystone species**. Such a species has a disproportionately large effect on a community relative to its abundance. Robert Paine was the first to describe the role of a keystone species after his experiments on the rocky shores of California's coast. Species in this rocky intertidal zone survive by clinging to rocks, and access to spaces to cling to is a limiting factor. Paine set up control plots with the sea star *Pisaster ochraceus* and its main prey—chitons, limpets, barnacles, and mussels. He removed all sea stars from his experimental plots.

Mussels (*Mytilus*) happen to be the prey of choice for sea stars. In the absence of sea stars, they took over Paine's experimental plots; they became the strongest competitors and crowded out seven other species of invertebrates. In this intertidal zone, predation by sea stars normally keeps the number of prey species high because it restricts competitive exclusion by mussels.



d Algal diversity in tidepools



e Algal diversity on rocks that become exposed at high tide

Figure 46.21 Effect of competition and predation in an intertidal zone. (**a**) Grazing periwinkles (*Littorina littorea*) affect the number of algal species in different ways in different marine habitats. (**b**) *Chondrus* and (**c**) *Enteromorpha*, two kinds of algae in their natural habitats. (**d**) By grazing on the dominant alga in tidepools (*Enteromorpha*), the periwinkles promote the survival of less competitive algal species that would otherwise be overgrown. (**e**) *Enteromorpha* doesn't grow on rocks. Here, *Chondrus* is dominant. Periwinkles find *Chondrus* tough and dine instead on less competitive algal species. By doing so, periwinkles decrease the algal diversity on the rocks.

Table 46.1 Adverse Effects of Some Species Introduced Into the United States

Species Introduced	Origin	Mode of Introduction	Outcome
Water hyacinth	South America	Intentionally introduced (1884)	Clogged waterways; other plants shaded out
Dutch elm disease:			
Ophiostoma ulmi (fungus)	Asia (by way of Europe)	Accidental; on infected elm timber (1930)	Millions of mature elms destroyed
Bark beetle (vector)		Accidental; on unbarked elm timber (1909)	
Chestnut blight fungus	Asia	Accidental; on nursery plants (1900)	Nearly all eastern American chestnuts killed
Zebra mussel	Russia	Accidental; in ballast water of ship (1985)	Clog pipes and water intake valves of power plants; displacing native Great Lake bivalves
Japanese beetle	Japan	Accidental; on irises or azaleas (1911)	Close to 300 plant species (e.g., citrus) defoliated
Sea lamprey	North Atlantic	Ship hulls, through canals (1860s, 1921)	Trout, other fish species destroyed in Great Lakes
European starling	Europe	Intentional release, New York City (1890)	Outcompete native cavity-nesting birds; crop damage; swine disease vector
Nutria	South America	Accidental release of captive animals being raised for fur (1930)	Crop damage, destruction of levees, overgrazing of marsh habitat

Remove all the sea stars, and the community shrinks from fifteen species to eight.

The impact of a keystone species can vary between habitats that differ in their species arrays. Periwinkles (*Littorina littorea*) are alga-eating snails of intertidal zones. Jane Lubchenco showed that their removal can increase *or* decrease the diversity of algal species in different habitats (Figure 46.21).

In tidepools, the periwinkles prefer to eat the alga *Enteromorpha*, which can outgrow other algal species. By keeping *Enteromorpha* in check, periwinkles help less competitive algal species survive. However, on exposed rocks in the lower intertidal zone, they avoid *Chondrus* and other tough, unpalatable red algae that persist as the dominant species. Periwinkles on these rocks graze on competitively weaker algal species. In short, they help *maintain* the number of algal species in tidepools but *reduce* it on exposed rock surfaces.

HOW SPECIES INTRODUCTIONS TIP THE BALANCE

Instabilities also are set in motion when residents of established communities move out from their home range and successfully take up residence elsewhere. This type of directional movement, called **geographic dispersal**, happens in three ways.

First, over a number of generations, a population might expand its home range by slowly moving into outlying regions that prove hospitable. Second, some individuals might be rapidly transported across great distances, an event called *jump* dispersal. This often takes individuals across regions where they could not survive on their own, as when insects travel from the mainland to Maui in a ship's cargo hold. Third, some population might be moved away from a home range by continental drift, at an almost imperceptibly slow pace over long spans of time.

Successful dispersal and colonization of a vacant adaptive zone can be remarkably rapid. Consider one of Amy Schoener's experiments in the Bahamas. She set out plastic sponges on barren sand at the bottom of Bimini Lagoon. How fast did aquatic species take up residence on or in the artificial habitats? Schoener recorded occupancy by 220 species within thirty days.

When you hear someone bubbling enthusiastically about an exotic species, you can safely bet the speaker isn't an ecologist. An **exotic species** is a resident of an established community that dispersed from its home range and became established elsewhere. Unlike most imports, which never do take hold outside the home range, an exotic species permanently insinuates itself into a new community.

Following jump dispersal, more than 4,500 exotic species have become established in the United States. We put some of the new arrivals, including soybeans, rice, wheat, corn, and potatoes, to use as food crops.

Accidental imports also alter community structure. You learned about imported fire ants in the chapter introduction. Table 46.1 lists others, and the section to follow describes the unintended impact of a few more.

A keystone species is one that has a major effect on species richness and relative abundances in particular habitats.

Species introductions and other biotic disturbances can permanently alter community structure.

46.10 Exotic Invaders

LINKS TO
SECTIONS
17.4, 23.11

Nonnative species are on the loose in communities on every continent. They can alter habitats; they often outcompete and displace native species.

THE ALGA TRIUMPHANT

They looked so perfect in saltwater aquariums, those long, green, feathery branches of *Caulerpa taxifolia*. So Stuttgart Aquarium researchers in Germany developed a hybrid, sterile strain of this green alga and magnanimously shared it with other marine institutions. Was it from Monaco's Oceanographic Museum that the hybrid strain escaped into the wild? Some say yes, Monaco says no.

The aquarium strain grows asexually by runners, just a few centimeters a day, but boat propellers and fishing nets dispersed it. Between 1984 and 2000, this alga blanketed over 30,000 hectares of seafloor near the Mediterranean coast (Figure 46.22*a*). Scuba divers found it growing off the Southern California coast. Someone might have drained water from a home aquarium into a storm drain or into the lagoon itself. Governmental and private groups sprang into action. They tarped over the area to shut out sunlight, pumped chlorine into the mud to poison the alga, and used welders to boil it. So far, eradication and surveillance programs have worked, but they have cost more than 3.4 million dollars.

It is now illegal to import the harmful strain into the United States. Interstate sale also is prohibited. Some still slip into the country because the aquarium industry has successfully lobbied against a ban on all *Caulerpa* species, and it is difficult to distinguish the invasive strain without genetic analysis.

Just how bad is it? The aquarium strain of *C. taxifolia* thrives on sandy or rocky shores and in mud. It can live ten days after being discarded in meadows. Unlike its tropical parents, it survives in cool water and polluted water. It also displaces endemic algae. Its toxin poisons invertebrates and fishes, including herbivorous types that might keep it in check. It has the potential to overgrow reefs and destroy marine food webs. Can you sense why this algal strain has been nominated as one of the 100 worst exotic invaders?

THE PLANTS THAT ATE GEORGIA

One more of the infamous 100: In 1876, kudzu (*Pueraria montana*) from Japan was introduced to the United States. In its native habitat—temperate regions of Asia—this vine is a well-behaved legume with a strong root system. It *seemed* like a good idea to use it for forage and to control erosion. But kudzu grew faster in the Southeast, where herbivores, pathogens, and less competitive plants posed no serious threat to it.

With nothing to stop it, kudzu shoots grow sixty meters per year. Its vines now blanket streambanks, trees, telephone poles, houses, and almost everything else in their path (Figure 46.22*b*). It withstands burning, and its deep roots resist being dug up. Grazing goats and herbicides help. But goats eat most other plants along with it, and herbicides taint water supplies. Kudzu invasions now stretch from Connecticut down to Florida and are reported in Arkansas. It has crossed

Figure 46.22 (**a**) Aquarium strain of *Caulerpa taxifolia* suffocating yet another richly diverse marine ecosystem.

(**b**) Kudzu (*Pueraria montana*) taking over part of Lyman, South Carolina. This vine has become invasive in many states from coast to coast. Ruth Duncan of Alabama, who makes 200 kudzu vine baskets a year, just can't keep up.

Figure 46.23 Rabbit-proof fence? Not quite. This is part of a fence built to hold back the 200 million to 300 million rabbits that are wreaking havoc with the vegetation in Australia. It didn't work.

the Mississippi River into Texas, and thanks to jump dispersal, it is now an invasive species in Oregon.

On the bright side, Asians use a starch extracted from kudzu in drinks, herbal medicines, and candy. A kudzu processing plant in Alabama may export this starch to Asia, where the demand currently exceeds the supply. Also, kudzu may help save trees; it can be an alternative source for paper. Today, about 90 percent of Asian wallpaper is kudzu-based.

THE RABBITS THAT ATE AUSTRALIA

During the 1800s, British settlers in Australia just couldn't bond with koalas and kangaroos, and so they imported familiar animals from home. In 1859, in what would be the start of a major disaster, a landowner in northern Australia imported and then released two dozen European rabbits (*Oryctolagus cuniculus*). Good food and sport hunting—that was the idea. An ideal rabbit habitat with no natural predators—that was the reality.

Six years later, the landowner had killed 20,000 rabbits and was besieged by 20,000 more. The rabbits displaced livestock and caused the decline of native wildlife. Now 200 to 300 million are hippity-hopping through the southern half of the country. They graze on grasses in good times and strip bark from shrubs and trees during droughts. Thumping hordes turn shrublands as well as grasslands into eroded deserts. Their burrows undermine the soil and set the stage for widespread erosion.

Rabbit warrens have been shot at, fumigated, plowed under, and dynamited. The first all-out assaults killed 70 percent of them, but the rabbits rebounded in less than a year. When a fence 2,000 miles long was built to protect western Australia, rabbits made it from one side to the other before workers could finish the job (Figure 46.23).

In 1951, the government introduced a myxoma virus that normally infects South American rabbits. The virus causes *myxomatosis*. This disease has mild effects on its coevolved host but nearly always kills *O. cuniculus*. Mosquitoes and fleas transmit the virus to new host. Having no coevolved defenses against the import, European rabbits died in droves. But natural selection has since favored a rise in rabbit populations resistant to the imported virus.

In 1991, on an uninhabited island in Australia's Spencer Gulf, researchers released rabbits that were injected with a calicivirus. The rabbits died from blood clots in their lungs, heart, and kidneys. The test virus escaped from the island in 1995, perhaps on insect vectors.

By 2001, the rabbit population sizes were staying 80 to 85 percent below their peak values. Grasses, nonwoody shrubs, and woody shrubs are rebounding. Different kinds of herbivores are increasing in density.

The rabbit calicivirus was discovered in China in 1984 and is now found in Europe and other countries as well. To date, tests on more than forty animal species indicate that it replicates in rabbits alone. However, other caliciviruses can and do cross species barriers. The jury is still out on the long-term impact of the viral releases.

As you might have deduced, *O. cuniculus* is another one of the 100 worst exotic invaders. Also on the list are two *Anopheles* species, the vectors for malaria. So is the cane toad (*Bufo marinus*). It was introduced as a biological control of pests in fields of sugarcane and other crops all over the world, but it eats almost everything. Despite its catchy name, the banana bunchy top virus is another one of the worst. So is the house cat (*Felis catus*) turned feral. Finally, the house mouse (*Mus musculus*) probably has a greater distribution than any other mammal except humans. Populations of this prolific breeder destroy crops and consume or contaminate much of our food supplies. They are implicated in the extinction of many species. Interested in learning more? Go to http://www.issg.org/ for some eye-openers.

46.11 Biogeographic Patterns in Community Structure

LINKS TO SECTIONS 17.1, 17.3, 18.7, 26.15, 45.3, CHAPTER 27

The richness and relative abundances of species differ from one habitat or one world province to another. Often these differences correspond to predictable patterns that have biogeographic and historical foundations.

Unit IV gave you a sense of the sweep of biodiversity, and Chapter 27 placed it in evolutionary perspective. Starting with Alfred Wallace and other naturalists of the 1800s, it became apparent that communities show *patterns* in biodiversity, as measured by the richness and relative abundances of species. Certain patterns follow environmental gradients in sunlight intensity, temperature, rainfall, and other factors that differ by latitude, elevation, and depth. Other patterns have their roots in the history of a habitat and its species, which vary in their resource requirements, physiology, capacity for dispersal, and the specific ways in which they interact with one another.

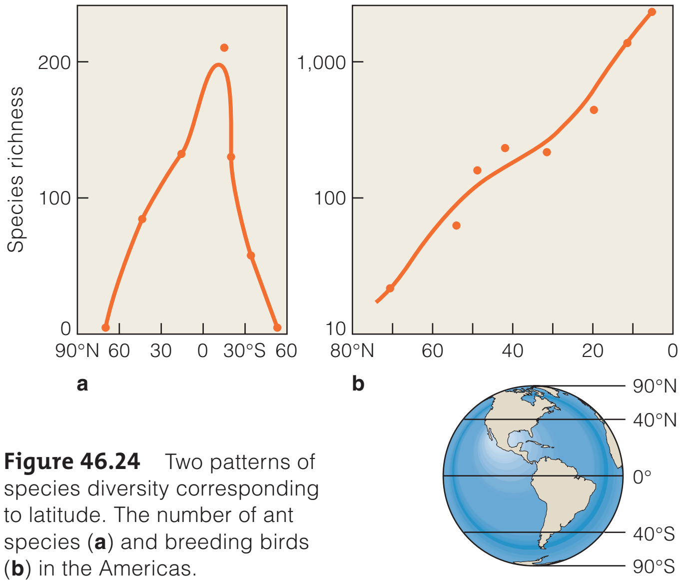


Figure 46.24 Two patterns of species diversity corresponding to latitude. The number of ant species (**a**) and breeding birds (**b**) in the Americas.

MAINLAND AND MARINE PATTERNS

Perhaps the most striking pattern of species richness corresponds with distance from the equator. *For most groups of plants and animals, the number of coexisting species on land and in the seas is greatest in the tropics, and it systematically declines from the equator to the poles.* Figure 46.24 shows two clear examples of this pattern. Consider just a few factors that help bring about such a pattern and maintain it.

First, for reasons explained in Section 46.1, tropical latitudes intercept more intense sunlight and receive more rainfall, and their growing season is longer. As one outcome, resource availability tends to be greater and more reliable in the tropics than elsewhere. This favors a degree of specialized interrelationships not possible where species are active for shorter periods.

Second, tropical communities have been evolving for a longer time than temperate ones, some of which did not start forming until the end of the last ice age.

Third, species richness may be self-reinforcing. The number of species of trees in tropical forests is much greater than in comparable forests at higher latitudes. When more plant species compete and coexist, so will more species of herbivores, partly because no single herbivore species can overcome all chemical defenses of all plants. Also, more predatory and parasitic species evolve in response to more kinds of prey and hosts. The same effect applies to the number of species on tropical reefs.

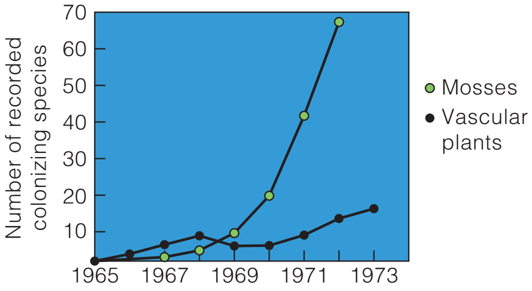


Figure 46.25 Surtsey, a volcanic island, at the time of its formation. Newly formed, isolated islands are natural laboratories for ecologists. The chart gives the number of colonizing species between 1965 and 1973.

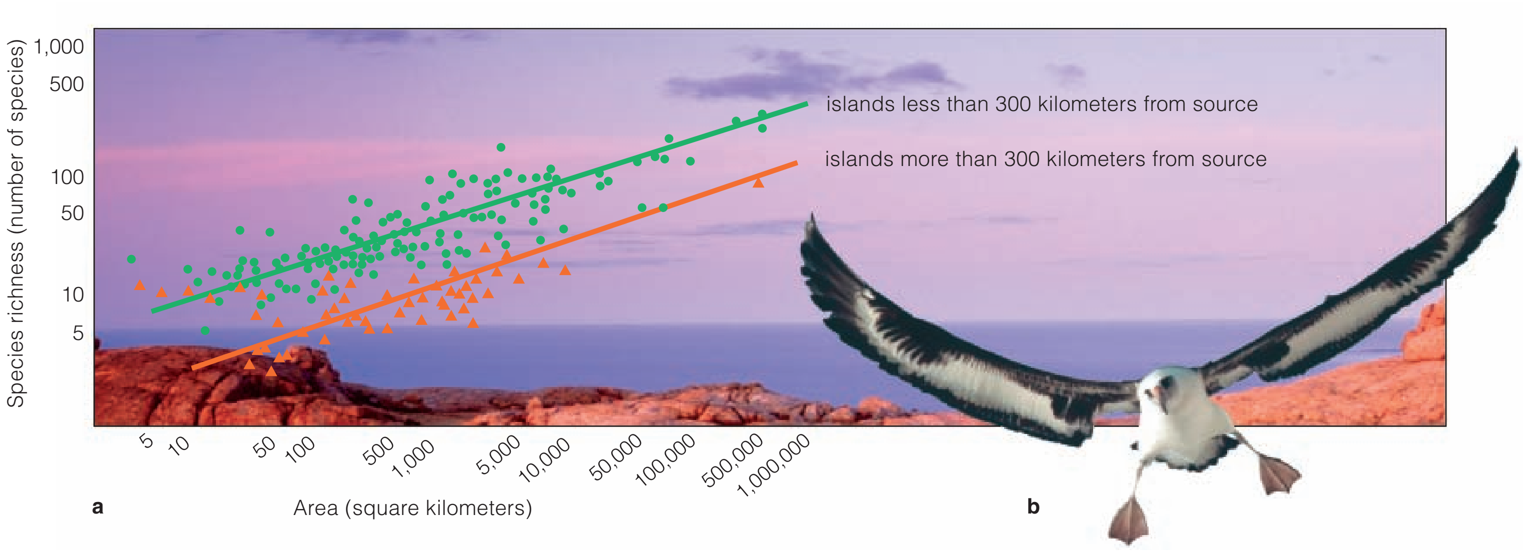


Figure 46.26 (**a**) Two island biodiversity patterns. Distance effect: Species richness on islands of a specified size declines with increasing distance from a source of colonizing species. *Green* circles signify islands less than 300 kilometers from the colonizing source. *Orange* triangles signify islands more than 300 kilometers from the source areas. Area effect: Among islands the same distance from a source of colonizing species, the larger ones support more species.

(**b**) Wandering albatross, one travel agent for jump dispersals. Seabirds that island-hop long distances often have seeds stuck to their feathers. Seeds that successfully germinate in a new island community may give rise to a population of new immigrants.

ISLAND PATTERNS

As you saw in Chapter 45, islands are laboratories for population studies. They also have been laboratories for community studies. For instance, a 1965 volcanic eruption quickly formed Surtsey, an island southwest of Iceland. Within six months, bacteria, fungi, seeds, flies, and seabirds were established on it. A vascular plant appeared two years after the island formed; the first mosses came along two years after that (Figure 46.25). As the island soil became enriched, more and more plant species began to take hold.

As is the case for other islands, the number of new species on Surtsey will not increase indefinitely. Why not? Models based on studies of island communities around the world suggest some answers.

First, larger islands tend to support more species than smaller ones the same distance from a colonizing source. This is the **area effect** (Figure 46.26*a*). Larger islands generally have more varied habitats, and more of them. Most have complex topography and higher elevations. Such variations promote species richness. Also, being bigger, the larger islands intercept more of the accidental tourists that winds and ocean currents move from the mainland but offer no way back.

Second, islands that are far away from a source of potential colonists receive fewer colonizing species. The few that do arrive naturally are adapted for long-distance dispersal (Figure 46.26*a*). This is the **distance effect**. Remember the nature of individual extinctions (Section 27.1)? Extinctions are more prevalent on the small islands. Because immigration rates are low and extinction rates are high, small islands support fewer species once the balance is struck. Island populations are far more vulnerable to famine, storms, droughts, disease and genetic drift. Remember the account of St. Matthew Island that opened Chapter 45?

One more island pattern: Remember the miniature *Homo* species that was discovered on the Indonesian island Flores (Section 26.15)? There is a trend, among new arrivals, for the big to get smaller and the small to get bigger. They adapt to fewer or different resources than in the place left behind. Biogeographers know more about patterns of diversity and the disruptions of them. If you wish to learn more, David Quammen's *Song of the Dodo* is a good place to start.

Species richness shows global patterns, as when it correlates with environmental gradients in latitude, elevation, and depth. Microenvironments along these gradients often introduce variations in the overall patterns.

Species richness in a given area also is an outcome of the evolutionary history of each species, its requirements for resources, its physiology, its capacity for dispersal, and its rates of birth, death, immigration, and emigration.

Generally, species richness is highest in the tropics and lowest at the poles. The number of species on an island also depends on its size and distance from a colonizing source.

Summary

Section 46.1 A habitat is the type of place where individuals of a species normally live. A community is an association of all populations of species that occupy a habitat. Each species in a community has a niche, the sum of all of the activities and relationships in which its individuals engage as they secure and use the resources required for their survival and reproduction.

Community structure arises from a habitat's physical and chemical features, resource availability over time, adaptive traits of its species, how its species interact, and the history of the habitat and its occupants.

Direct symbiotic interactions help shape community structure. They include commensalism, mutualism, competition, predation, and parasitism.

Section 46.2 Mutualism is a species interaction that benefits both participants. Some mutualists cannot complete their life cycle without the interaction.

Section 46.3 By the competitive exclusion theory, when two (or more) species require identical resources, they cannot coexist indefinitely. Species may coexist when they differ in their use of a resource, share it in different ways, or share it at different times.

Biology Now

Learn about competitive interactions with the animation on BiologyNow.

Sections 46.4, 46.5 Predators and prey exert selection pressure on each other. Densities of predator and prey populations often oscillate. The carrying capacity, density dependencies, refuges, predator efficiency, and often alternative prey sources affect the cycles. Threat displays, chemical weapons, camouflage, stealth, and mimicry may be outcomes of coevolution between predators and their prey.

Biology Now

Compare the three alternative models for predator responses to prey density with the animation on BiologyNow.

Read the InfoTrac article "How the Pufferfish Got Its Puff," Carl Zimmer, Discover, *September 1997.*

Sections 46.6, 46.7 Parasites live in or on other living hosts and withdraw nutrients from host tissues for part of their life cycle. Hosts may or may not die as a result. Parasitoids kill their hosts, and social parasites take over some aspect of a host's life cycle.

Section 46.8 By a model for ecological succession, a community develops in predictable sequence, from its pioneer species to a climax community—a stable, self-perpetuating array of species that are in equilibrium with one another and the environment. However, abiotic and biotic disturbances have destabilizing effects. They are unpredictable and vary in magnitude and frequency. By an intermediate disturbance hypothesis, species richness is greatest between moderate disturbances.

Sections 46.9, 46.10 Community structure reflects an uneasy balance between biotic as well as abiotic forces, including predation and competition, that can shift over time. Species introductions can change the structure.

Section 46.11 Many studies of mainland and island communities reveal global patterns in species richness.

Biology Now

Learn about the area effect and distance effect with the interaction on BiologyNow.

Read the InfoTrac article "Island Biogeography's Lasting Impact," Fred Powledge, Bioscience, *November 2003.*

Self-Quiz

Answers in Appendix II

1. A habitat ______ .
   a. has distinguishing physical and chemical features
   b. is where individuals of a species normally live
   c. is occupied by various species
   d. all of the above

2. A niche is ______ .
   a. the sum of activities and relationships by which individuals of a species secure and use resources
   b. unvarying for a given species
   c. something that shifts in large and small ways
   d. both a and c

3. Two species may coexist indefinitely in some habitat when they ______ .
   a. differ in their use of resources
   b. share the same resource in different ways
   c. use the same resource at different times
   d. all of the above

4. A predator population and prey population ______ .
   a. always coexist at relatively stable levels
   b. may undergo cyclic or irregular changes in density
   c. cannot coexist indefinitely in the same habitat
   d. both b and c

5. Parasites ______ .
   a. weaken their hosts
   b. can kill novel hosts
   c. feed on host tissues
   d. all of the above

6. By a currently favored hypothesis, species richness of a community is greatest between physical disturbances of ______ intensity or frequency.
   a. low b. intermediate c. high d. variable

7. Match the terms with the most suitable descriptions.
   ____ geographic dispersal
   ____ area effect
   ____ pioneer species
   ____ climax community
   ____ keystone species
   ____ exotic species
   ____ resource partitioning

   a. opportunistic colonizer of barren or disturbed habitat
   b. greatly affects other species
   c. individuals leave home range, become established elsewhere
   d. more species on large islands than small ones at same distance from the source of colonists
   e. array of species at the end of successional stages in a habitat
   f. allows competitors to coexist
   g. often outcompete, displace native species of established community

Additional questions are available on **Biology Now™**

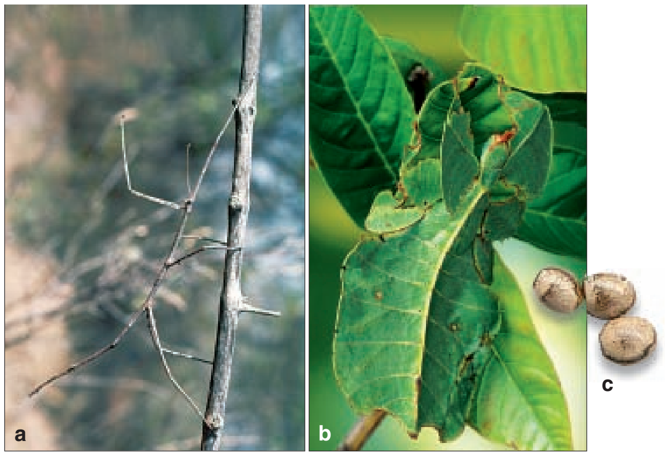


Figure 46.27 Phasmids. (**a**) South African stick insect. (**b**) Leaf insect from Java. (**c**) Phasmid eggs often look like seeds.

Figure 46.28 One of the nominations for the worst 100 invaders: water hyacinths (*Eichhornia crassipes*) choking a Florida waterway.

Critical Thinking

1. With antibiotic resistance rising, researchers are looking for ways to reduce use of antibiotics. Cattle were once fed antibiotic-laced food but now get *probiotic feeds* that contain cultured bacteria that can establish or bolster populations of helpful bacteria in the animal's gut. The idea is that if a large population of beneficial bacteria is in place, then the harmful bacteria cannot become established or thrive. Which ecological theory is guiding this research?

2. Most phasmids resemble sticks or leaves (Figure 46.27). All are herbivorous insects. Most are motionless in the day, and move and feed only at night. If disturbed, a phasmid will fall to the ground, as if dead. Speculate on the selective pressures that may have shaped phasmid morphology and behavior. Suggest an experiment with one species to test whether its appearance and behavior may be adaptive.

3. The water hyacinth (*Eichhornia crassipes*) is an aquatic plant native to South America. Today, this plant lives in nutrient-rich waters from Florida to San Francisco. It has displaced many native species, and choked rivers and canals (Figure 46.28). Research and write a brief account of how it got from one continent to another.

4. Answering this question well should earn you big points. Long ago, Alfred Wallace puzzled over an odd pattern in the distribution of organisms in the islands of Indonesia. Deep water separates Bali and Lombok and, farther north, the larger islands of Borneo and Sulawesi (Figure 46.29). Most major groups on the Asian mainland had representative species on Borneo and Bali—but few or none on Lombok and Sulawesi. The boundary he had identified came to be called *Wallace's Line*, and his explanation for it is still valid.

In Wallace's time, geologists had already discovered evidence of past ice ages, when much of the ocean's waters became locked up in vast ice sheets. Wallace's line marks the boundary of the Asian continent when the sea level fell 75 fathoms (450 feet). All of the shallow seas and straits from the Asian mainland to Borneo and Bali became dry land. Wallace inferred that many species dispersed to the east. When the sea level rose again, they became cut off from the mainland. Some survived; others vanished.

Even during the ice ages, Lombok and Sulawesi never were connected to the Asian mainland. If a plant or animal could not fly, swim, or be blown or rafted across an expanse of deep water, then they never got across Wallace's line. An expanse of deep water also separates Lombok and Sulawesi from Australia and Papua New Guinea.

Sulawesi is famous for its remarkably high percentage of endemic bird species. About one-third are endemic or close to it. By comparison, Borneo is home to relatively few endemic species of birds. Section 19.2 presents a model for speciation on island archipelagos. Review this section, and then formulate a hypothesis to explain why there are more endemic bird species on Sulawesi than on Borneo.

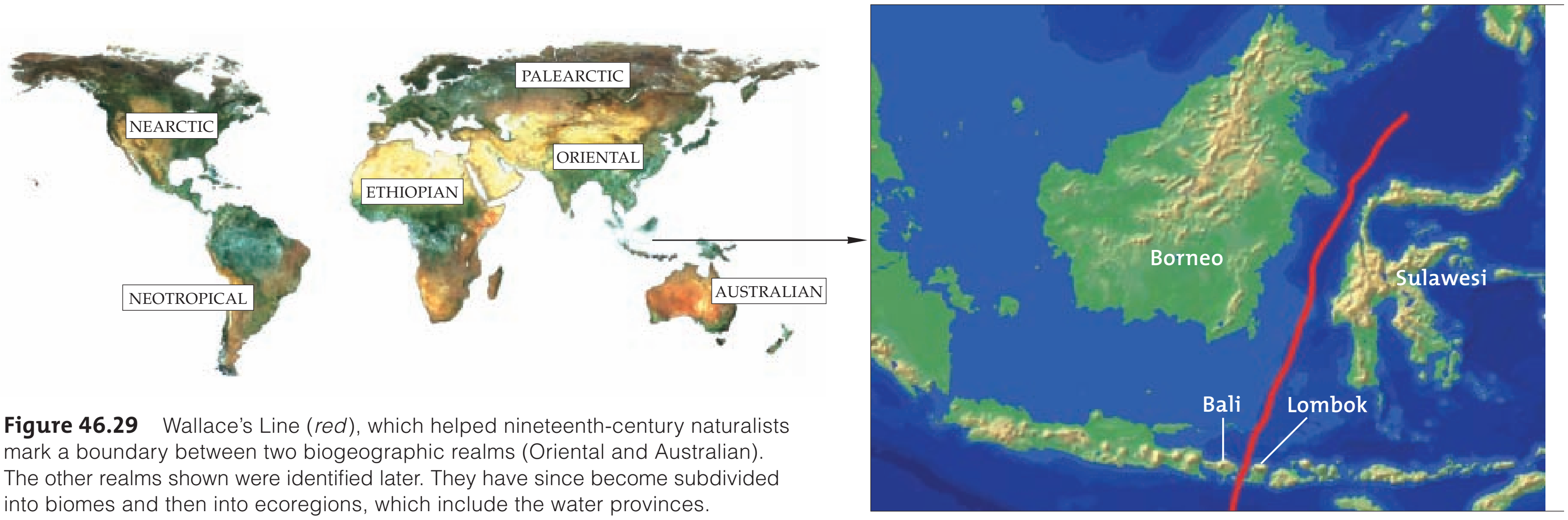


Figure 46.29 Wallace's Line (*red*), which helped nineteenth-century naturalists mark a boundary between two biogeographic realms (Oriental and Australian). The other realms shown were identified later. They have since become subdivided into biomes and then into ecoregions, which include the water provinces.