4

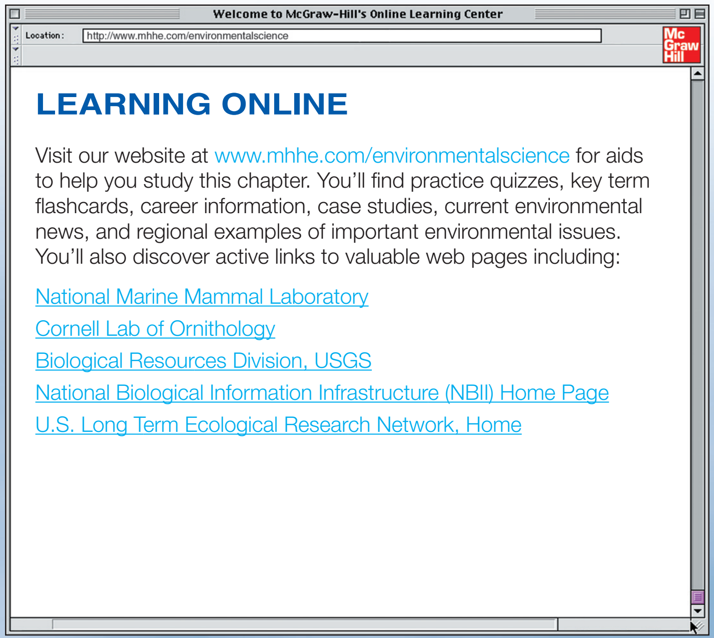
Biological Communities and Species Interactions

> *Any species of bug is an irreplaceable marvel, equal to the works of art which we religiously preserve in our museums.*
>
> Claude Levi-Strauss

OBJECTIVES

After studying this chapter, you should be able to:

- describe how environmental factors determine which species live in a given ecosystem and where or how they live.
- understand how random genetic variation and natural selection lead to evolution, adaptation, niche specialization, and partitioning of resources in biological communities.
- compare and contrast interspecific predation, competition, symbiosis, commensalism, mutualism, and coevolution.
- discuss productivity, diversity, complexity, and structure of biological communities and how these characteristics might be connected to resilience and stability.
- explain how ecological succession results in ecosystem development and allows one species to replace another.
- give some examples of exotic species introduced into biological communities and describe the effects such introductions can have on indigenous species.



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The bears, birds, and fish of the McNeil River, Alaska, form an interconnected biological community together with terrestrial and aquatic plants and invertebrates. © John Warden/Stone.

Why Trees Need Salmon

Ecologists have long known that salmon in the Pacific Northwest need clear streams to breed, and that clear streams need healthy forests. Surprising new evidence now indicates that forests themselves need salmon to remain healthy.

Pacific salmon (*Onchorhyncus spp.*) are anadromous: they hatch in freshwater lakes and streams, spend much of their lives at sea, then return to the stream where they were born to breed and die. To reproduce successfully, these fish require clear, cold, shaded streams and a clean gravel riverbed. When forests are cut, sediment washes down hillsides and into streams, clogging gravel streambeds and suffocating eggs. Sediment also absorbs sunlight, warming water and reducing oxygen saturation in the water. Lower oxygen level reduces survival rates of eggs and young fish.

Every year, as millions of fish return to spawn and die, they provide a banquet for bears, eagles, and other species that gorge themselves on the fat-rich fish. Ecologist Thomas Riemchen has found that bears fishing in British Columbia's rivers can catch 500 fish in a six-week salmon migration season (about 12 fish per bear per day). He also estimates that a bear gets 70 percent of its annual protein intake from fish. But bears also drag tons of fish up on shore and leave half-eaten carcasses strewn about the forest floor. Riemchen calculates that these scattered fish fertilize the forest at a rate of about 120 kg of nitrogen per acre. British Columbia's rainforests, with at least 30,000 fishing bears, may receive 60 million kg of salmon each year. Nitrogen is often a limiting nutrient for rainforest vegetation. Between one-quarter and one-half of the nitrogen in a towering Sitka Spruce or Douglas Fir may derive from salmon carcasses.

In addition to fertilizing trees, salmon carcasses provide food for insects and other scavengers. Birds and other predators consume these insects, and nutrients from salmon thus work through the entire forest ecosystem.

In a separate study, ecologists Robert Naiman and James Helfield found that trees along salmon-rich rivers can grow up to three times as fast as trees along streams without salmon. This is important, they point out, because salmon stocks are dwindling throughout the Pacific Northwest. In Washington, Oregon, and California, salmon populations have fallen by 90 percent from their historic numbers. Because of this close relationship, they argue, forest management and fish management need to be integrated. Each population—rainforest trees and ocean-going fish—affects the stability of the other.

Apparently, salmon need healthy forests, and forests need healthy salmon populations. Stream ecosystems need standing trees to retain soil and provide shade. So healthy streams depend on fish, just as the fish depend on the streams. As this case shows, links among organisms in an ecosystem are intricate, often subtle, and essential for ecological stability. Relationships between apparently separate environments, such as rivers and forests, can be equally important. In this chapter we'll explore some of these relationships among organisms and between organisms and their environment.

To read more:

Reimchen, T. E., D. Mathewson, M. D. Hocking, J. Moran, and D. Harris. 2003. Isotopic evidence for enrichment of salmon-derived nutrients in vegetation, soil and insects in riparian zones in coastal British Columbia. *American Fisheries Society Symposium* 34:59–69.

Helfield J. M., and R. J. Naiman. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. *Ecology* 82(9):2403–09.

WHO LIVES WHERE, AND WHY?

"Why" questions often are the stimulus for scientific research, but the research itself centers on "how" questions. Why, we wonder, does a particular species live where it does? More to the point, how is it *able* to live there? How does it deal with the physical resources of its environment and are some of its techniques unique? How does it interact with the other species present? And what gives one species an edge over another species in a particular habitat?

In this section we will examine some specific ways organisms are limited by the physical aspects of their environment. We then will discuss how members of a biological community interact, pointing out a few of the difficulties ecologists encounter when they attempt to discern patterns and make generalizations about community interactions and organization.

Critical Factors and Tolerance Limits

Every living organism has limits to the environmental conditions it can endure. Temperatures, moisture levels, nutrient supply, soil and water chemistry, living space, and other environmental factors must be within appropriate levels for life to persist. In 1840, Justus von Liebig proposed that the single factor in shortest supply relative to demand is the critical determinant in the distribution of that species. Ecologist Victor Shelford later expanded this principle of limiting factors by stating that each environmental factor has both minimum and maximum levels, called **tolerance limits,** beyond which a particular species cannot survive (fig. 4.1) or is unable to reproduce. The single factor closest to these survival limits, he postulated, is the critical limiting factor that determines where a particular organism can live.

At one time, ecologists accepted this concept so completely that they called it Liebig's or Shelford's law and tried to identify unique factors limiting the growth of every population of plants and animals. For many species, however, we find that the interaction of several factors working together, rather than a single limiting factor, determines biogeographical distribution. If you have ever explored the rocky coasts of New England or the Pacific Northwest, for instance, you probably have noticed that mussels and barnacles endure extremely harsh conditions but generally are sharply limited to an intertidal zone where they grow so thickly that they often completely cover the substrate. No single factor determines this distribution. Instead, a combination of temperature extremes, drying time between tides, salt concentrations, competitors, and food availability limits the number and location of these animals.

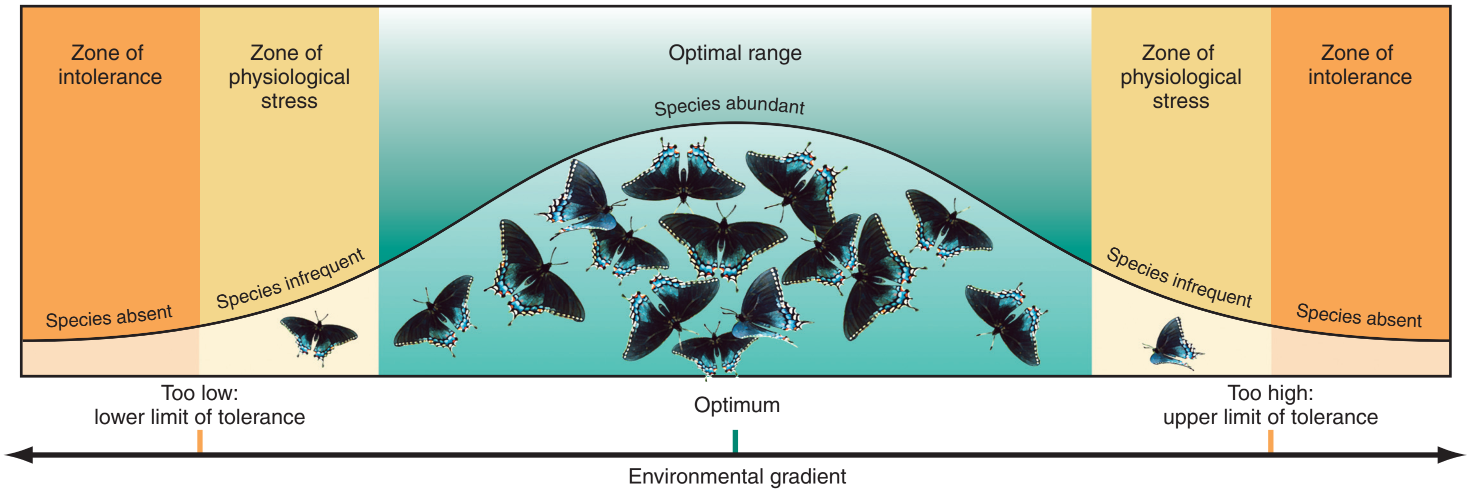


FIGURE 4.1 The principle of tolerance limits states that for every environmental factor, an organism has both maximum and minimum levels beyond which it cannot survive. The greatest abundance of any species along an environmental gradient is around the optimum level of the critical factor most important for that species. Near the tolerance limits, abundance decreases because fewer individuals are able to survive the stresses imposed by limiting factors.

For other organisms, there may be a specific *critical factor* that, more than any other, determines the abundance and distribution of that species in a given area. A striking example of cold intolerance as a critical factor is found in the giant saguaro cactus (*Carnegiea gigantea*), which grows in the dry, hot Sonoran desert of southern Arizona and northern Mexico (fig. 4.2). Saguaros are extremely sensitive to low temperatures. A single exceptionally cold winter night with temperatures below freezing for 12 hours or more will kill growing tips on the branches. Young saguaros are more susceptible to frost damage than adults, but seedlings typically become established under the canopy of small desert trees such as mesquite that shield the young cacti from the cold night sky. Unfortunately, the popularity of grilling with mesquite wood has caused extensive harvesting of the nurse trees that once sheltered small saguaros, adversely affecting reproduction of this charismatic species.

Animal species, too, exhibit tolerance limits that often are more critical for the young than for the adults. The desert pupfish (*Cyprinodon*), for instance, occurs in small isolated populations in warm springs in the northern Sonoran desert. Adult pupfish can survive temperatures between 0°C and 42°C (a remarkably high temperature for a fish) and are tolerant to an equally wide range of salt concentrations. Eggs and juvenile fish, however, can only live between 20°C and 36°C and are killed by high salt levels. Reproduction, therefore, is limited to a small part of the range of adult fish, which is often restricted anyway by the size of the small springs and desert seeps in which the species lives.

Sometimes the requirements and tolerances of species are useful indicators of specific environmental characteristics. The presence or absence of such species can tell us something about the community and the ecosystem as a whole. Locoweeds, for example, are small legumes that grow where soil concentrations of selenium are high. Because selenium is often found with uranium deposits, locoweeds have an applied economic value as **environmental indicators.** Such indicator species also may demonstrate the effects of human activities. Lichens and eastern white pine are less restricted in habitat than locoweeds, but are indicators of air pollution because they are extremely sensitive to sulfur dioxide and acid precipitation. Bull thistle is a weed that grows on disturbed soil but is not eaten by cattle; therefore, an abundant population of bull thistle in a pasture is a good indicator of overgrazing. Similarly, anglers know that trout species require clean, well-oxygenated water, so the presence or absence of trout can be an indicator of water quality.

FIGURE 4.2 Saguaro cacti, symbolic of the Sonoran desert, are an excellent example of distribution controlled by a critical environmental factor. Extremely sensitive to low temperatures, saguaros are found only where minimum temperatures never dip below freezing for more than a few hours at a time. © William P. Cunningham.

Natural Selection, Adaptation, and Evolution

How is it that mussels have developed the ability to endure pounding waves, daily exposure to drying sun and wind, and seasonal threats of extreme cold or hot temperatures? What enables desert pupfish to tolerate hot, mineral-laden springs? How does the saguaro survive in the harsh temperatures and extreme dryness of the desert? We commonly say that each of these species is "adapted" to its special set of conditions, but what does that mean? In this section, we will examine one of the most important concepts in biology: how species acquire traits that allow them to live in unique ways in particular environments.

In common use, to *adapt* means to modify slightly, usually temporarily. We use the term *adapt* in two ways. One is a limited range of *physiological modifications* (called acclimation) available to individual organisms. If you keep house plants inside all winter, for example, and then put them out in full sunlight in the spring, they get sunburned. If the damage isn't too severe, your plants will probably grow new leaves with a thicker cuticle and denser pigments that protect them from the sun. But this change isn't permanent. Another winter inside will make them just as sensitive to the sun as before. Furthermore, the changes they acquire are not passed on to their offspring.

In biological terms, adaptation refers specifically to inherited traits that gradually change a *population* or a species, not an individual. These inherited traits allow a species to live in a particular environment. This process is explained by the theory of **evolution,** developed by Charles Darwin and Alfred Wallace. According to this theory, species change gradually through competition for scarce resources and **natural selection,** a process in which those members of a population that are best suited for a particular set of environmental conditions will survive and produce offspring more successfully than their ill-suited competitors.

Natural selection acts on preexisting genetic diversity created by a series of small, random mutations (changes in genetic material) that occur spontaneously in every population. These mutations produce a variety of traits, some of which are more advantageous than others in a given situation. Where resources are limited or environmental conditions place some selective pressure on a population, individuals with those advantageous traits become more abundant in the population, and the species gradually evolves or becomes better suited to that particular environment. Although each change may be very slight, many mutations over a very long time have produced the incredible variety of different life-forms that we observe in nature (fig. 4.3).

The variety of finches observed by Charles Darwin on the Galápagos Islands is a classic example of speciation driven by availability of different environmental opportunities (fig. 4.4). Originally derived from a single seed-eating species that somehow crossed the thousands of kilometers from the mainland, the finches have evolved into a dozen or more distinct species that differ markedly in appearance, food preferences, and habitats they occupy. Fruit eaters have thick parrot-like bills; seed eaters have heavy, crushing bills; insect eaters have thin probing beaks to catch their prey. One of the most unusual species is the woodpecker finch, which pecks at tree bark for hidden insects. Lacking the woodpecker's long tongue, however, the finch uses a cactus spine as a tool to extract bugs.

FIGURE 4.3 Giraffes don't have long necks because they stretch to reach tree-top leaves, but those giraffes that happened to have longer necks got more food and had more offspring, so the trait became fixed in the population. © Corbis/Volume 6.

The amazing variety of colors, shapes, and sizes of dogs, cats, rabbits, fish, flowers, vegetables, and other domestic species is evidence of deliberate selective breeding. The various characteristics of these organisms arose through mutations. We simply kept the ones we liked. Note that sexual reproduction helps to redistribute genetic material in new and novel combinations that greatly increase the variation and diversity we see in both wild and domestic species. Organisms that reproduce asexually can evolve, but often do so very slowly.

What environmental factors cause selective pressure and influence fertility or survivorship in nature? They include (1) physiological stress due to inappropriate levels of some critical environmental factor, such as moisture, light, temperature, pH, or specific nutrients; (2) predation, including parasitism and disease; (3) competition; and (4) chance. In some cases the organisms that survive environmental catastrophes or find their way to a new habitat where they start a new population may simply be lucky rather than more fit or better suited to subsequent environmental conditions than their less fortunate contemporaries.

Be sure you understand that while selection affects individuals, evolution and adaptation work at the population level. Individuals don't evolve; species do. Each individual is locked in by genetics to a particular way of life. Most plants, animals, or microbes have relatively limited ability to modify their physical makeup or behavior to better suit a particular environment. Over time, however, random genetic changes and natural selection can change an entire population.

Given enough geographical isolation or selective pressure, the members of a population become so different from their ancestors that they may be considered an entirely new species that has

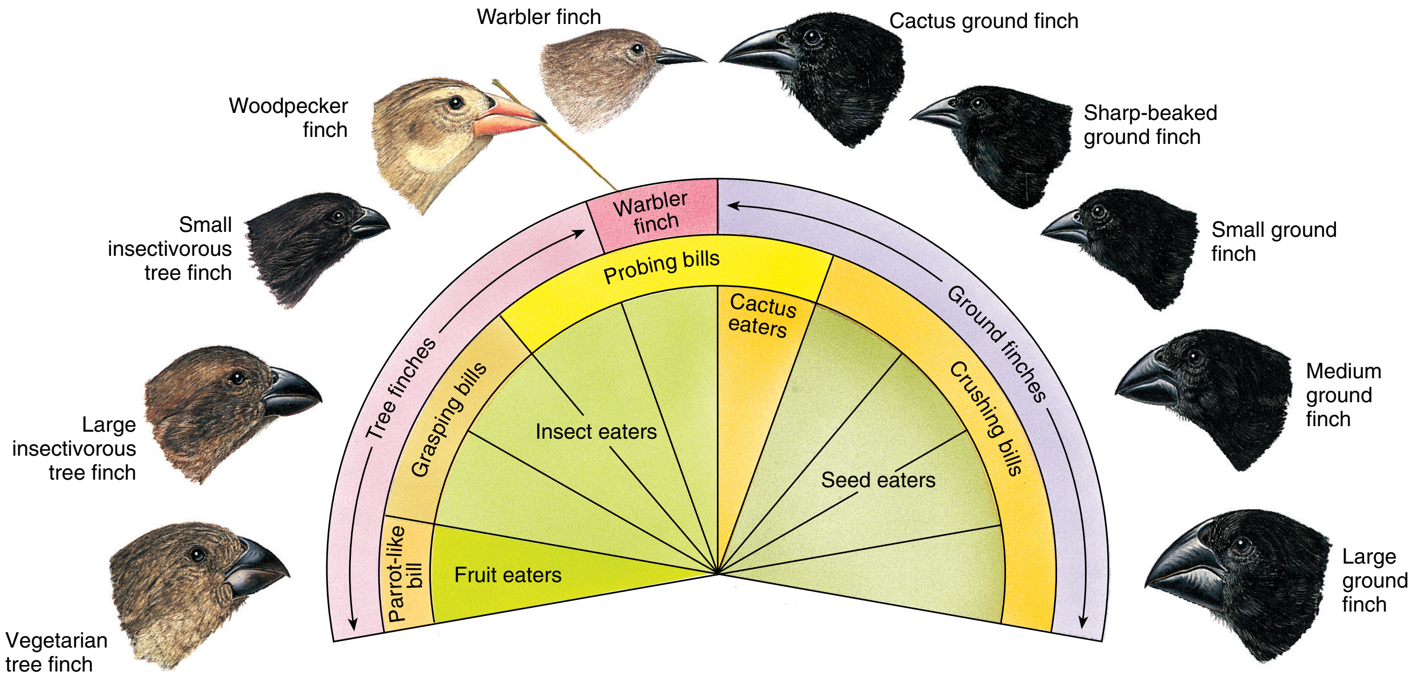


FIGURE 4.4 Some species of Galápagos Island finches. Although all are descendents of a common ancestor, they now differ markedly in appearance, habitat, and feeding behavior. Ground finches (*lower right*) eat cactus leaves; warbler finches (*upper left*) eat insects; others eat seeds or have mixed diets. The woodpecker finch (*upper left*) pecks tree bark as do woodpeckers, but lacks a long tongue. Instead, it uses cactus spines as tools to extract insects. *Source:* From Peter H. Raven and George B. Johnson, *Biology,* 4th edition. Copyright © 1996 McGraw Hill Company, Inc. All rights reserved. Reprinted by permission.

replaced the original one. Alternatively, isolation of population subsets by geographical or behavioral factors that prevent exchange of genetic material can result in branching off of new species that coexist with their parental line. Suppose that two populations of the same species become separated by a body of water, a desert, or a mountain range that they cannot cross. Over a very long time—often millions of years—random mutations and different environmental pressures may cause the populations to evolve along such dissimilar paths that they can no longer interbreed successfully even if the opportunity to do so arises. They have now become separate species as in the case of the Galápagos finches. The barriers that divide subpopulations are not always physical. In some cases, behaviors such as when and where members of a population feed, sleep, or mate—or how they communicate—may separate them sufficiently for divergent evolution and speciation to occur even though they occupy the same territory.

Natural selection and adaptation can cause organisms with a similar origin to become very different in appearance and develop different habits over time, but they can also result in unrelated organisms coming to look and act very much alike. We call this latter process *convergent* evolution. The cactus-eating Galápagos finches (fig. 4.4), for example, look and act very much like parrots even though they are genetically very dissimilar. The features that enable parrots to eat fruit successfully work well for these finches also.

A common mistake is to believe that organisms develop certain characteristics because they want or need them. This is incorrect. A duck doesn't have webbed feet because it wants to swim or needs to swim in order to eat; it has webbed feet because some ancestor happened to have a gene for webbed feet that gave it some advantage over other ducks in its particular pond and because those genes were passed on successfully to its offspring. A variety of different genetic types are always present in any population, and natural selection simply favors those best suited for particular conditions. Whether there is a purpose or direction to this process is a theological question rather than a scientific one and is beyond the scope of this book.

The Ecological Niche

Habitat describes the place or set of environmental conditions in which a particular organism lives. A more functional term, the **ecological niche,** is a description of either the role played by a species in a biological community or the total set of environmental factors that determine species distribution. Niches as community roles—describing how a species obtains food, what relationships it has with other species, and the services it provides its community, for example—were first described by the British ecologist, Charles Elton in 1927. Thirty years later, the American limnologist G. E. Hutchinson proposed a more biophysical definition of this concept. Every species, he pointed out, has a range of physical and chemical conditions (temperature, light levels, acidity, humidity, salinity, etc.) as well as biological interactions (predators and prey present, defenses, nutritional resources available, etc.) within which it can exist. Figure 4.1, for example, shows the abundance of a hypothetical species along a single factor gradient. If it were possible to

FIGURE 4.5 The giant panda feeds exclusively on bamboo. Although its teeth and digestive system are those of a carnivore, it is not a good hunter, and has adapted to a vegetarian diet. In the 1970s, huge acreages of bamboo flowered and died, and many pandas starved.
© William P. Cunningham.

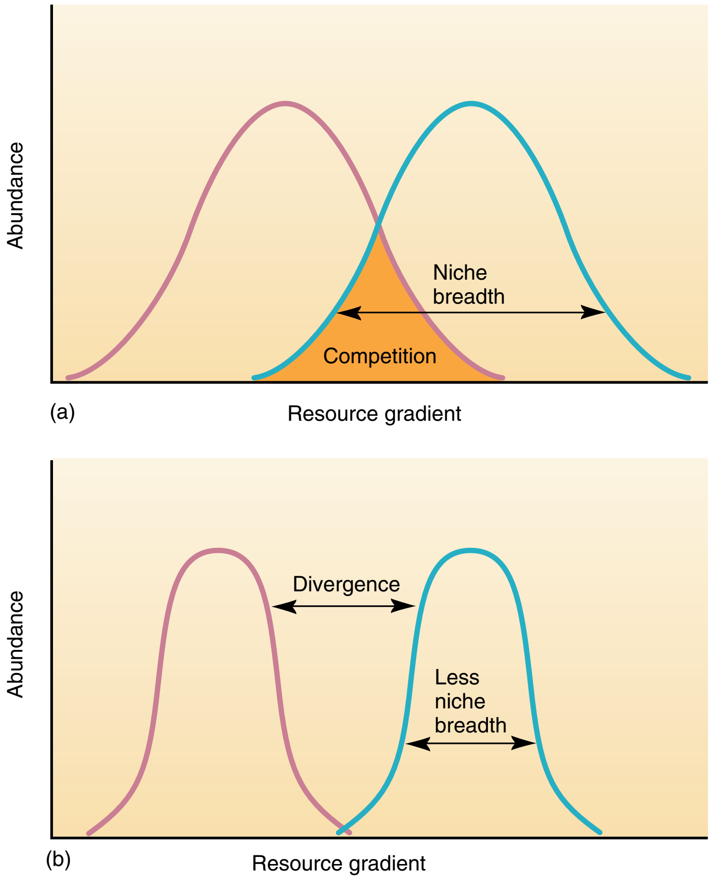


FIGURE 4.6 Resource partitioning and niche specialization caused by competition. Where niches of two species overlap along a resource gradient, competition occurs (shaded area in (*a*)). Individuals occupying this part of the niche are less successful in reproduction so that characteristics of the population diverge to produce more specialization, narrower niche breadth, and less competition between species (*b*).

graph simultaneously all of the factors that affect a particular species, a multidimensional space would result that describes the ecological niche available to that species.

The idea of niches can be further defined in terms of *fundamental niche* and *realized niche.* A species' fundamental niche is the full range of resources or habitat it *could* exploit if there were no competition with other species. A species' realized niche, the resources or habitat it actually uses, may be much less than its fundamental niche.

Some species, like raccoons or coyotes, are generalists that eat a wide variety of food and live in a broad range of habitats (including urban areas). Others, such as the panda (fig. 4.5), are specialists that occupy a very narrow niche. Specialists often tend to be rarer than generalists and less resilient to disturbance or change.

A few species such as elephants, chimpanzees, and baboons learn how to behave from their social group and can invent new ways of doing things when presented with new opportunities or challenges. Most organisms, however, are limited by genetically determined physical structure and instinctive behavior to established niches.

Over time, though, niches can evolve, just as physical characteristics do. The law of competitive exclusion states that no two species will occupy the same niche and compete for exactly the same resources in the same habitat for very long. Eventually, one group will gain a larger share of resources while the other will either migrate to a new area, become extinct, or change its behavior or physiology in ways that minimize competition. We call this latter process of niche evolution **resource partitioning** (fig. 4.6). It can produce high levels of specialization that allow several species to utilize different parts of the same resource and coexist within a single habitat (fig. 4.7).

Niche specialization also can create behavioral separation that allows subpopulations of a single species to diverge into separate species. Why doesn't this process continue until there is an infinite number of species? The answer is that a given resource can be partitioned only so far. Populations must be maintained at a minimum size to avoid genetic problems and to survive bad times. This puts an upper limit on the number of different niches—and therefore the number of species—that a given community can support.

Perhaps you haven't thought of time as an ecological factor, but niche specialization in a community is a 24-hour phenomenon. Swallows and insectivorous bats both catch insects, but some insect species are active during the day and others at night, providing noncompetitive feeding opportunities for day-active swallows and night-active bats.

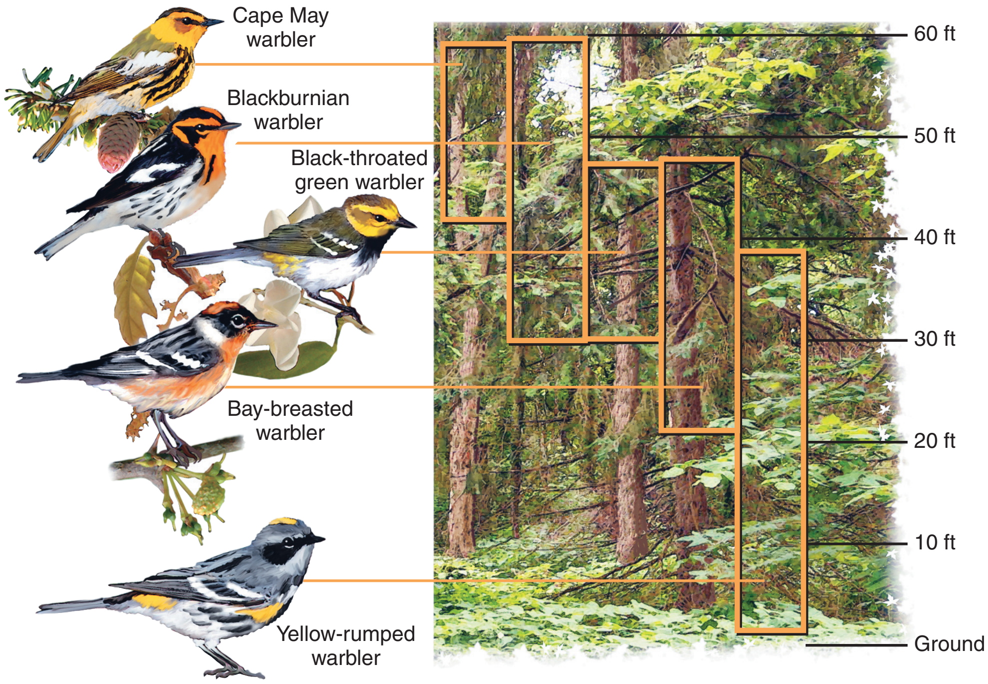


FIGURE 4.7 Resource partitioning and the concept of the ecological niche are demonstrated by several species of wood warblers that use different strata of the same forest. This is a classic example of the principle of competitive exclusion.
Source: Original observation by R. H. MacArthur.

SPECIES INTERACTIONS

Predation and competition for scarce resources are major factors in evolution and adaptation. Not all biological interactions are competitive, however. Organisms also cooperate with, or at least tolerate, members of their own species as well as individuals of other species in order to survive and reproduce. In this section, we will look more closely at the different interactions within and between species that shape biological communities.

Exploitation Predation and Parasitism

All organisms need food to live. Producers make their own food, and consumers eat organic matter created by other organisms. In most communities, as we saw in chapter 3, photosynthetic organisms are the producers. Consumers include herbivores, carnivores, omnivores, scavengers, and decomposers. With which of these categories do you associate the term *predator?* Ecologically, the term has a much broader meaning than you might expect. A **predator** in an ecological sense, is an organism that feeds directly upon another living organism, whether or not it kills the prey to do so (fig. 4.8). By this definition herbivores, carnivores, and omnivores that feed on live prey are predators, but scavengers, detritivores, and decomposers that feed on dead things are not.

FIGURE 4.8 Insect herbivores are predators as much as are lions and tigers. In fact, insects consume the vast majority of biomass in the world. Complex patterns of predation and defense have often evolved between insect predators and their plant prey. © Ray Coleman/Photo Researchers, Inc.

Predatory relationships can be complex, as in the case of marine shellfish. Many crustaceans, mollusks, and worms release eggs directly into the water, and the eggs and free-living larval and juvenile stages are part of the floating community, or **plankton** (fig. 4.9). Planktonic animals feed upon each other and are food for successively larger carnivores, including small fish. As prey species mature, their predators change. Barnacle larvae are planktonic and are eaten by fish. Adult barnacles, on the other hand, build hard shells that protect them from fish but can be crushed by limpets and other mollusks. Predators also may change their feeding targets. Adult frogs, for instance, are carnivores, but the tadpoles of most species are grazing herbivores. Sorting out the trophic levels in these communities can be very difficult.

Predation is an important factor in evolution. Predators prey most successfully on the slowest, weakest, least fit members of their target population, thus reducing competition, preventing excess population growth, allowing successful traits to become dominant in the prey population, and making the prey population stronger and healthier. As the poet Robinson Jeffers said, “What but the wolf’s tooth whittled so fine/The fleet limbs of the antelope?”.

FIGURE 4.9 Microscopic plants and animals form the basic levels of many aquatic food chains and account for a large percentage of total world biomass. Many oceanic plankton are larval forms that have habitats and feeding relationships very different from their adult forms. © D. P. Wilson/Photo Researchers, Inc.

Prey species have evolved many protective or defensive adaptations to avoid predation. In plants, for instance, this often takes the form of thick bark, spines, thorns, or chemical defenses. Animal prey may become very adept at hiding, fleeing, or fighting back against predators. Predators, in turn, evolve mechanisms to overcome the defenses of their prey. This process in which species exert selective pressure on each other is called **coevolution.**

Parasites are organisms that feed on a host, or take resources from it, without killing the host. Some parasites do little damage: a mosquito takes blood but usually causes little damage. Others cause significant harm and may eventually kill a host. **Pathogens** (disease-causing organisms) are often considered parasites. Your immune system is an evolved defense against pathogens in our environment.

Keystone Species

A **keystone species** is a species or group of species whose feeding activity has an inordinate influence on the structure of its community. Originally, keystone species were thought to be top predators, such as wolves, whose presence limits the abundance of herbivores and thereby reduces their grazing or browsing on plants. Recently, it has been recognized that less conspicuous species also play essential community roles. Certain tropical figs, for example, bear during seasons when no other fruit is available for frugivores (fruit-eating animals). If these figs were removed, many animals would starve to death during periods of fruit scarcity. With those animals gone, many other plant species that depend on them at other times of the year for pollination and seed-dispersal would disappear as well.

Even microorganisms can play vital roles. In some forest ecosystems, mycorrhizae (fungi associated with tree roots) are essential for mineral mobilization and absorption. If the fungi die, so do the trees and many other species that depend on a healthy forest community. Rather than being a single species, mycorrhizae are actually a group of species that together fulfill a keystone function.

Often a number of species are intricately interconnected in biological communities so that it is difficult to tell which is the essential key. A classic example is in the Pacific kelp forests, where towering columns of kelp (algae) shelter myriad fish, shellfish, and mammals (fig. 4.10). The sheltering kelp could be regarded as the key to community structure. Sea urchins, however, feed on the kelp and determine their number and distribution while sea otters regulate urchins and kelp provides a resting place for dozing otters. Which of these species is the most important? Each depends on and affects the others. Perhaps we should think in terms of a "keystone set" of organisms in some ecosystems. (See "Oreas, Otters, Urchins, and Kelp: Disrupting a Marine Food Web," on the Online Learning Center in the chapter 4 Case Studies.)

FIGURE 4.10 Giant kelp is a massive alga that forms dense "forests" off the Pacific coast of California. It is a keystone species in that it provides food, shelter, and structure essential for a whole community. Removal of sea otters allows sea urchin populations to explode. When the urchins destroy the kelp, many other species suffer as well. © Randy Morse/Tom Stack & Associates.

Competition

Competition is another kind of antagonistic relationship within a community. For what do organisms compete? To answer this question, think again about what all organisms need to survive: energy and matter in usable forms, space, and specific sites for life activities (What Do You Think? p. 80). Plants compete for growing space for root and shoot systems so they can absorb and process sunlight, water, and nutrients. Animals compete for living, nesting, and feeding sites, as well as for food, water, and mates. Competition among members of the same species is called **intraspecific competition,** whereas competition between members of different species is called **interspecific competition.**

You can observe interspecific competition if you look closely at a patch of weeds growing on good soil early in the summer. First of all, many weedy species attempt to crowd out their rivals by producing prodigious numbers of seeds. After the seeds germinate, the plants race to grow the tallest, cover the most ground, and get the most sun. You may observe several strategies to do this. For example, vines don't build heavy stems of their own; they simply climb up over their neighbors to get to the light.

Species also race to new territory. Plants with highly mobile seeds can reach and colonize open ground ahead of other species (fig. 4.11). Some plants secrete substances that inhibit the growth of seedlings near them, including their own and those of other species. This strategy is particularly significant in deserts where water is a limiting factor.

We often think of competition among animals as a bloody battle for resources. A famous Victorian description of the struggle for survival was "nature red in tooth and claw." In fact, a better metaphor is a race. Have you ever noticed that birds always eat fruits and berries just before they are ripe enough for us to pick? Having a tolerance for bitter, unripe fruit gives them an advantage in the race for these food resources. Many animals tend to avoid fighting if possible. It's not worth getting injured. Most confrontations are more noise and show than actual fighting.

FIGURE 4.11 Dandelions and other opportunistic species generally produce many highly mobile offspring. © William P. Cunningham.

Intraspecific competition can be especially intense because members of the same species have the same space and nutritional requirements; therefore, they compete directly for these environmental resources. How do plants cope with intraspecific competition? The inability of seedlings to germinate in the shady conditions created by parent plants acts to limit intraspecific competition by favoring the mature, reproductive plants.

Symbiotic relationships often enhance the survival of one or both partners. Symbiotic relationships often entail some degree of coadaptation or coevolution of the partners, shaping—at least in part—their structural and behavioral characteristics. An interesting case of mutualistic coadaptation is seen in Central and South American swollen thorn acacias and their symbiotic ants. Acacia ant colonies live within the swollen thorns on the acacia tree branches and feed on two kinds of food provided by the trees: nectar produced in glands at the leaf bases and special protein-rich structures produced on leaflet tips. The acacias thus provide shelter and food for the ants. Although they spend energy to provide these services, the trees are not physically harmed by ant feeding.

Animals also have developed adaptive responses to intraspecific competition. Two major examples are varied life cycles and territoriality. The life cycles of many invertebrate species have juvenile stages that are very different from the adults in habitat and feeding. Compare a leaf-munching caterpillar to a nectar-sipping adult butterfly or a planktonic crab larva to its bottom-crawling adult form. In these examples, the adults and juveniles of each species do not compete because they occupy different ecological niches.

You may have observed robins chasing other robins during the mating and nesting season. Robins and many other vertebrate species demonstrate **territoriality,** an intense form of intraspecific competition in which organisms define an area surrounding their home site or nesting site and defend it, primarily against other members of their own species. Territoriality helps to allocate the resources of an area by spacing out the members of a population. It also promotes dispersal into adjacent areas by pushing grown offspring outward from the parental territory.

Territory size depends on the size of the species and the resources available. A pair of robins might make do with a suburban yard, but a large carnivore like a tiger may need thousands of square kilometers.

Symbiosis

In contrast to predation and competition, symbiotic interactions between organisms can be nonantagonistic. **Symbiosis** is the intimate living together of members of two or more species. **Commensalism** is a type of symbiosis in which one member clearly benefits and the other apparently is neither benefited nor harmed. Cattle often are accompanied by cattle egrets, small white shore birds who catch insects kicked up as the cattle graze through a field. The birds benefit while the cattle seem indifferent. Many of the mosses, bromeliads, and other plants growing on trees in the moist tropics are also considered to be commensals (fig. 4.12). These epiphytes get water from rain and nutrients from leaf litter and dust

What do you think?

Understanding Competition

Ecology is a relatively young science. Consequently, many ecological processes are incompletely understood. How a community comes to have its particular organization is one area of uncertainty. Some ecologists feel that physical factors are the most important determinants in community organization, while others feel that interspecific competition is most important.

How can we find out which view is correct? Ecologists employ the scientific method, as described in chapter 2, to better understand community dynamics. This process is mostly refined common sense and its basic elements can be useful in everyday life.

Once ecologists have decided on the concept to be investigated, they look for a specific situation that can either be observed or manipulated to provide relevant information. For example, ecologist Richard Karban was interested in how competition affected a community. He learned that larvae of two insect species, the meadow spittlebug and the calendula plume moth, both feed and develop on the seaside daisy, a common beach plant on the American west coast. The specific question to be investigated was: Does competition affect these two insect species, therefore impacting community organization?

Competition might reduce survival rate, larval growth, or both. Karban's procedure involved setting up four groups of plants at Bodega Bay, CA: one got both spittlebugs and moths, another got only spittlebugs, another only moths, and a fourth had neither. He compared survival rates of spittlebugs and moths when competitors were present and absent.

There are three important general considerations in designing scientific investigations:

1. Things need to be organized in such a way that the outcome can clearly be linked to a particular cause. In other words, differences in insect survival rates need to be clearly attributable to competition and not to other factors. Karban accomplished this by making his plant/insect groups as uniform as possible, except for the presence or absence of competitors. He eliminated genetic differences between plants by using plants from the same clone. He was careful to put the same numbers of insects on each plant to eliminate animal density as a factor, and so on.
2. The data collected must be a reliable representation of the larger situation and not simply the result of chance. This is usually accomplished by replicating the procedure many times. Instead of setting up just a few plants with one or both insects present, Karban set up 30 plants with each treatment. The procedure was repeated a second year. This gave him a cumulative total of 60 plants that had just spittlebugs, 60 plants having just moths, and 60 plants each having both or neither spittlebugs and moths. With such a large number of replications it was highly likely that differences in survival rates were, in fact, the result of competition and not simply chance occurrences.
3. Finally, conclusions must be justified by the data. Karban's statistical analysis revealed that spittlebug persistence was nearly 40 percent higher when the plume moths were absent. Plume moth persistence was not significantly affected by spittlebug presence, however.

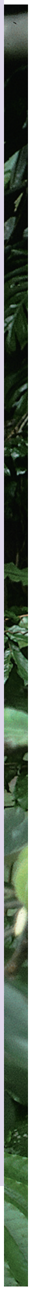
His overall conclusion was:

Evidence from this and other studies supports the contention that interspecific competition can play an important role in influencing densities of plant-feeding insects.

Spittlebugs produce mounds of foam under which they hide from predators while feeding on host plants. © Milton Tierney/Visuals Unlimited.

Notice the caution expressed in these words. He did not claim to have proven anything. Instead, his study "*supports* the contention." Second, he states competition "*can* play an important role," instead of using stronger language. And finally, he restricts these conclusions to plant-feeding insects. Karban carefully avoids drawing conclusions beyond the realm supported by his data.

Based on a healthy skepticism, clarity of language, critical evaluation of relationships and information, and caution in coming to judgment, critical thinking in science has been a very successful tool in enhancing understanding.



fall, and often neither help nor hurt the trees on which they grow. In a way, the robins and sparrows that inhabit suburban yards are commensals with humans.

Lichens are a combination of a fungus and a photosynthetic partner, either an alga or a cyanobacterium. Their association is a type of symbiosis called **mutualism,** in which both members of the partnership benefit (fig. 4.13). Some ecologists believe that cooperative, mutualistic relationships may be more important in evolution than we have commonly thought. Aggressive interactions often are dangerous and destructive, while cooperation and compromise may have advantages that we tend to overlook. Survival of the fittest often may mean survival of those organisms that can live best with one another.

What do the acacias get in return and how does the relationship relate to community dynamics? Ants tend to be aggressive defenders of their home areas, and acacia ants are no exception. They drive off herbivorous insects that attempt to feed on their home acacia, thus reducing predation. They also trim away vegetation that grows around their home tree, thereby reducing competition. This is a fascinating example of how a symbiotic relationship fits into community interactions. It is also an example of coevolution based on mutualism rather than competition or predation.

FIGURE 4.12 Plants compete for light and growing space in this Indonesian rainforest. Epiphytes, such as the ferns and bromeliads shown here, find a place to grow in the forest canopy by perching on the limbs of large trees. This may be a commensal relationship if the epiphytes don't hurt their hosts. Sometimes, however, the weight of epiphytes breaks off branches and even topples whole trees. © William P. Cunningham.

Defensive Mechanisms

Many species of plants and animals have toxic chemicals, body armor, and other ingenious defensive adaptations to protect themselves from competitors or predators. Arthropods, amphibians, snakes, and some mammals, for instance, produce noxious odors or poisonous secretions to induce other species to leave them alone. Plants also produce a variety of chemical compounds that make them unpalatable or dangerous to disturb. Perhaps you have brushed up against poison ivy or stinging nettles in the woods or you have encountered venomous insects or snakes and appreciate the wisdom of leaving them alone. Often, species possessing these chemical defenses will evolve distinctive colors or patterns to warn potential enemies (fig. 4.14).

FIGURE 4.13 Lichens, such as the various species growing on this log, are a combination of algae and fungi in a classic example of mutualistic symbiosis. © William P. Cunningham.

FIGURE 4.14 Poison arrow frogs of the family Dendrobatidae use brilliant colors to warn potential predators of the extremely toxic secretions from their skin. Native people in Latin America use the toxin on blowgun darts. © Michael Fogden/Animals Animals/Earth Scenes.

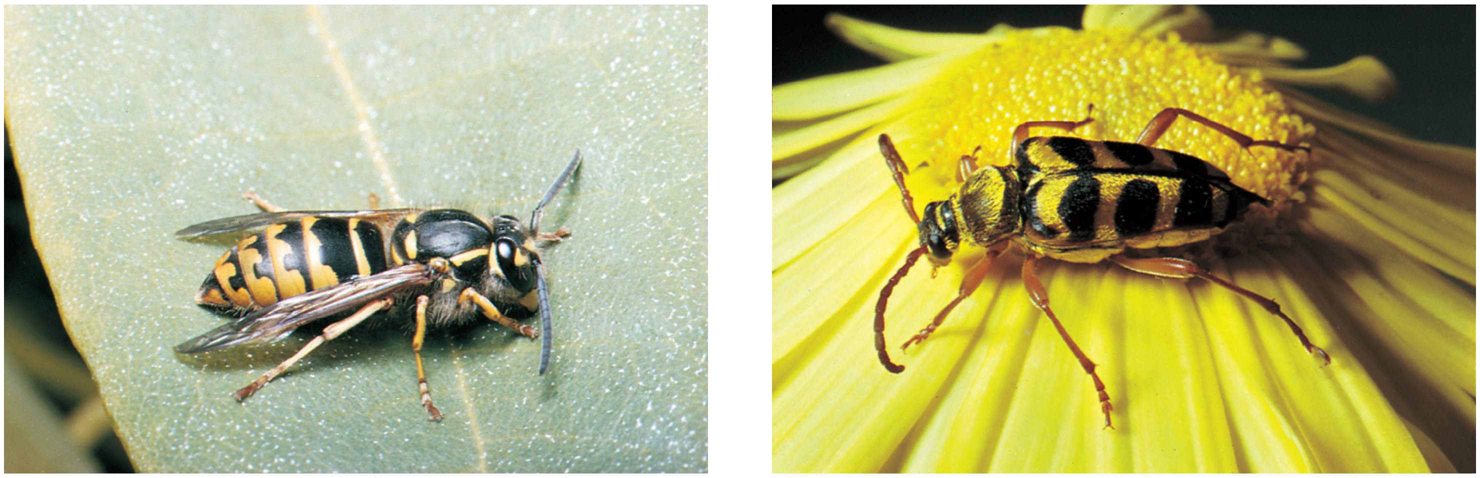


FIGURE 4.15 An example of Batesian mimicry. The dangerous wasp (*left*) has bold yellow and black bands to warn predators away. The much rarer longhorn beetle (*right*) has no poisonous stinger, but looks and acts like a wasp and thus avoids predators as well. © Edward S. Ross.

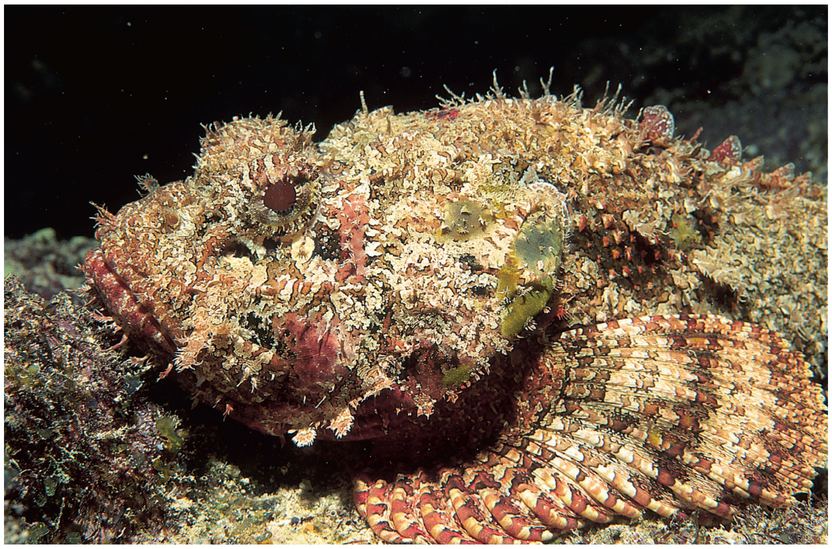


FIGURE 4.16 This highly camouflaged scorpion fish lies in wait for its unsuspecting prey. Natural selection and evolution have created the elaborate disguise seen here. © Brian Parker/Tom Stack & Associates.

Sometimes species that actually are harmless will evolve colors, patterns, or body shapes that mimic species that are unpalatable or poisonous. This is called **Batesian mimicry** after the English naturalist H. W. Bates, who described it in 1857. Wasps, for example, often have bold patterns of black and yellow stripes to warn off potential predators. The rarer longhorn beetle (fig. 4.15), although it has no stinger, looks and acts much like wasps and thus avoids predators as well. Another form of mimicry, called **Müllerian mimicry,** named for the German biologist Fritz Müller, who described it in 1878, involves two species, both of which are unpalatable or dangerous and have evolved to look alike. When predators learn to avoid either species, both benefit.

Species also evolve amazing abilities to avoid being discovered. You very likely have seen examples of insects that look exactly like dead leaves or twigs to hide from predators. Predators also use camouflage to hide as they lie in wait for their prey. The scorpion fish (fig. 4.16) blends in remarkably well with its surroundings as it waits for smaller fish to come within striking distance. Not all cases of mimicry are to avoid or carry out predation, however. Some tropical orchids have evolved flower structures that look exactly like female flies. Males attempting to mate unwittingly carry away pollen.

COMMUNITY PROPERTIES

The processes and principles that we have studied thus far in this chapter—tolerance limits, species interactions, resource partitioning, evolution, and adaptation—play important roles in determining the characteristics of populations and species. In this section we will look at some fundamental properties of biological communities and ecosystems—productivity, diversity, complexity, resilience, stability, and structure—to learn how they are affected by these factors.

Productivity

A community's **primary productivity** is the rate of biomass production, an indication of the rate of solar energy conversion to chemical energy. The energy left after respiration is net primary production. Photosynthetic rates are regulated by light levels, temperature, moisture, and nutrient availability. Figure 4.17 shows approximate productivity levels for some major ecosystems. As you can see, tropical forests, coral reefs, and estuaries (bays or inundated river valleys where rivers meet the ocean) have high levels of productivity because they have abundant supplies of all these resources. In deserts, lack of water limits photosynthesis. On the arctic tundra or in high mountains, low temperatures inhibit plant growth. In the open ocean, a lack of nutrients reduces the ability of algae to make use of plentiful sunshine and water.

Some agricultural crops such as corn (maize) and sugar cane grown under ideal conditions in the tropics approach the productivity levels of tropical forests. Because shallow water ecosystems such as coral reefs, salt marshes, tidal mud flats, and other highly productive aquatic communities are relatively rare compared to the vast extent of open oceans—which are effectively biological deserts—marine ecosystems are much less productive on average than terrestrial ecosystems.

Even in the most photosynthetically active ecosystems, only a small percentage of the available sunlight is captured and used to make energy-rich compounds. Between one-quarter and three-quarters of the light reaching plants is reflected by leaf surfaces. Most of the light absorbed by leaves is converted to heat that is either radiated away or dissipated by evaporation of water. Only 0.1 to 0.2 percent of the absorbed energy is used by chloroplasts to synthesize carbohydrates.

In a temperate-climate oak forest, only about half the incident light available on a midsummer day is absorbed by the leaves. Ninety-nine percent of this energy is used to evaporate water. A large oak tree can transpire (evaporate) several thousand liters of water on a warm, dry, sunny day while it makes only a few kilograms of sugars and other energy-rich organic compounds.

Abundance and Diversity

Abundance is an expression of the total number of organisms in a biological community, while **diversity** is a measure of the number of different species, ecological niches, or genetic variation present. The abundance of a particular species often is inversely related to the total diversity of the community. That is, communities with a very large number of species often have only a few members of any given species in a particular area. As a general rule, diversity decreases but abundance within species increases as we go from the equator toward the poles. The arctic has vast numbers of insects such as mosquitoes, for example, but only a few species. The tropics, on the other hand, have vast numbers of species—some of which have incredibly bizarre forms and habits—but often only a few individuals of any particular species in a given area.

Consider bird populations. Greenland is home to 56 species of breeding birds, while Colombia, which is only one-fifth the size of Greenland, has 1,395. Why are there so many species in Colombia and so few in Greenland?

Climate and history are important factors. Greenland has such a harsh climate that the need to survive through the winter or escape to milder climates becomes the single most important critical factor that overwhelms all other considerations and severely limits the ability of species to specialize or differentiate into new forms. Furthermore, because Greenland was covered by glaciers until about 10,000 years ago, there has been little time for new species to develop.

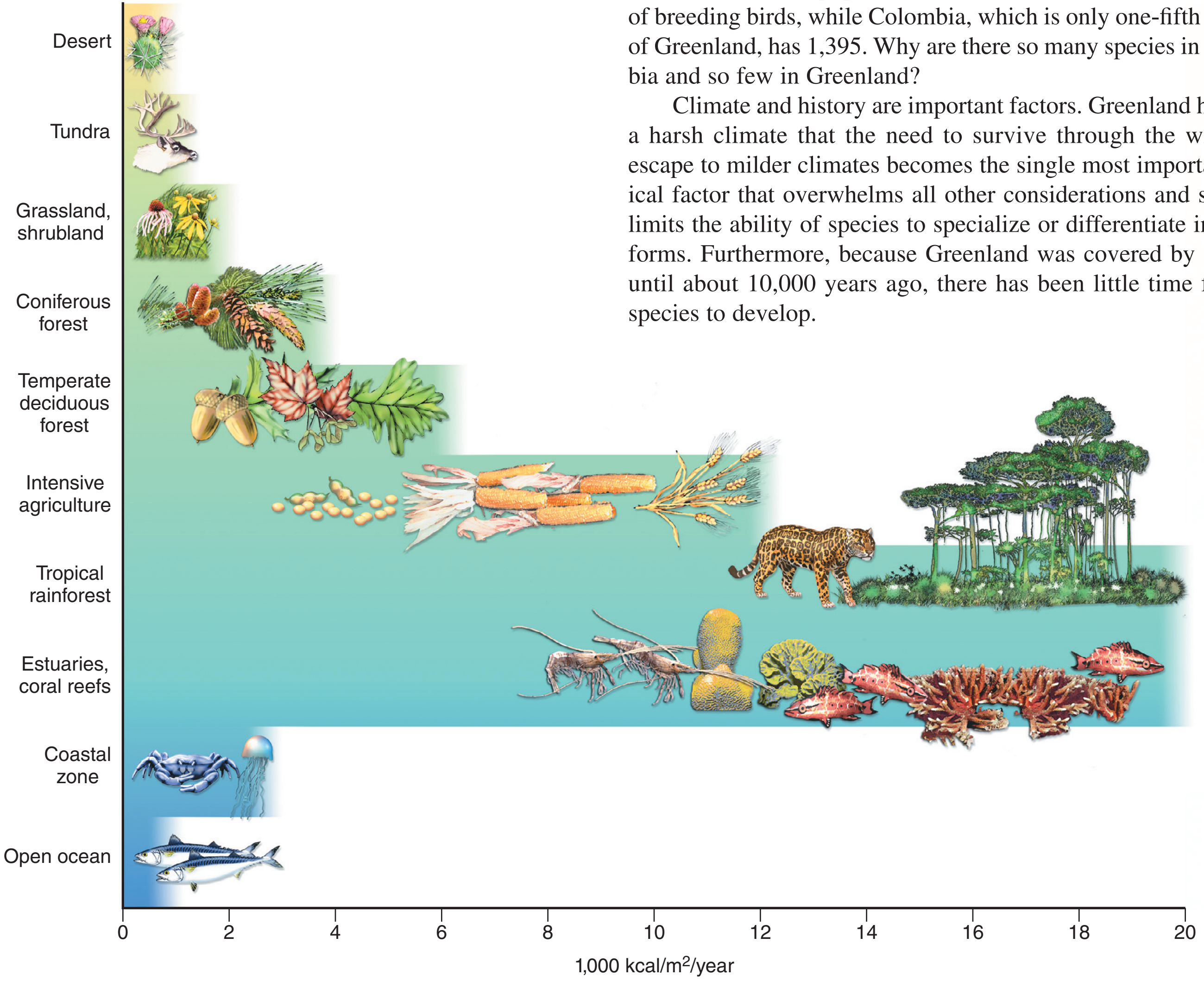


FIGURE 4.17 Relative biomass accumulation of major world ecosystems. Only plants and some bacteria capture solar energy. Animals consume biomass to build their own bodies.

Key Concepts

- Natural selection explains species change and adaptation: members of a population that are most suited to survive environmental conditions are most likely to survive and reproduce.
- Predation can lead to evolution as species develop evasive characteristics. Symbiotic relationships can enhance changes through competitive advantages of both species.
- A species' niche is its ecological role or its environmental conditions.
- Ecological communities can be compared by quantitative measures such as primary productivity, complexity, and diversity.
- Ecological succession refers to the gradual change from one set of species to another in a location.

Many areas in the tropics, by contrast, have relatively abundant rainfall and warm temperatures year-round so that ecosystems there are highly productive. The year-round dependability of food, moisture, and warmth supports a great exuberance of life and allows a high degree of specialization in physical shape and behavior. Coral reefs are similarly stable, productive, and conducive to proliferation of diverse and amazing life-forms. The enormous abundance of brightly colored and fantastically shaped fish, corals, sponges, and arthropods in the reef community is one of the best examples we have of community diversity.

Productivity is related to abundance and diversity, both of which are dependent on the total resource availability in an ecosystem as well as the reliability of resources, the adaptations of the member species, and the interactions between species. You shouldn't assume that all communities are perfectly adapted to their environment. A relatively new community that hasn't had time for niche specialization, or a disturbed one where roles such as top predators are missing, may not achieve maximum efficiency of resource use or reach its maximum level of either abundance or diversity.

Complexity and Connectedness

Community complexity and connectedness generally are related to diversity and are important because they help us visualize and understand community functions. **Complexity** in ecological terms refers to the number of species at each trophic level and the number of trophic levels in a community. A diverse community may not be very complex if all its species are clustered in only a few trophic levels and form a relatively simple food chain.

By contrast, a complex, highly interconnected community (fig. 4.18) might have many trophic levels, some of which can be compartmentalized into subdivisions. In tropical rainforests, for instance, the herbivores can be grouped into "guilds" based on the specialized ways they feed on plants. There may be fruit eaters, leaf nibblers, root borers, seed gnawers, and sap suckers, each composed of species of very different size, shape, and even biological kingdom, but that feed in related ways. A highly interconnected community such as this can form a very elaborate food web.

Resilience and Stability

Many biological communities tend to remain relatively stable and constant over time. An oak forest tends to remain an oak forest, for example, because the species that make it up have self-perpetuating mechanisms. We can identify three kinds of stability or resiliency in ecosystems: *constancy* (lack of fluctuations in composition or functions), *inertia* (resistance to perturbations), and *renewal* (ability to repair damage after disturbance).

In 1955, Robert MacArthur, who was then a graduate student at Yale, proposed that the more complex and interconnected a community is, the more stable and resilient it will be in the face of disturbance. If many different species occupy each trophic level, some can fill in if others are stressed or eliminated by external forces, making the whole community resistant to perturbations and able to recover relatively easily from disruptions. This theory has been controversial, however. Some studies support it, while others do not. For example, Minnesota ecologist David Tilman, in studies of native prairie and recovering farm fields, found that plots with high diversity were better able to withstand and recover from drought than those with only a few species.

On the other hand, in a diverse and highly specialized ecosystem, removal of a few keystone members can eliminate many other associated species. Eliminating a major tree species from a tropical forest, for example, may destroy pollinators and fruit distributors as well. We might replant the trees, but could we replace the whole web of relationships on which they depend? In this case, diversity has made the forest less resilient rather than more.

Diversity is widely considered important and has received a great deal of attention. In particular, human impacts on diversity are a primary concern of many ecologists (Case Study, p. 87).

Edges and Boundaries

An important aspect of community structure is the boundary between one habitat and its neighbors. We call these relationships **edge effects.** Sometimes, the edge of a patch of habitat is relatively sharp and distinct. In moving from a woodland patch into a grassland or cultivated field, you sense a dramatic change from the cool, dark, quiet forest interior to the windy, sunny, warmer, open space of the field or pasture (fig. 4.19). In other cases, one habitat type intergrades very gradually into another, so there is no distinct border.

Ecologists call the boundaries between adjacent communities **ecotones.** A community that is sharply divided from its neighbors is called a closed community. In contrast, communities with gradual or indistinct boundaries over which many species cross are called open communities. Often this distinction is a matter of degree or perception. As we saw earlier in this chapter, birds might feed in fields or grasslands but nest in the forest. As they fly back and forth, the birds interconnect the ecosystems by moving energy and material from one to the other, making both systems relatively open. Furthermore, the forest edge, while clearly different from the open field, may be sunnier and warmer than the forest interior, and may have a different

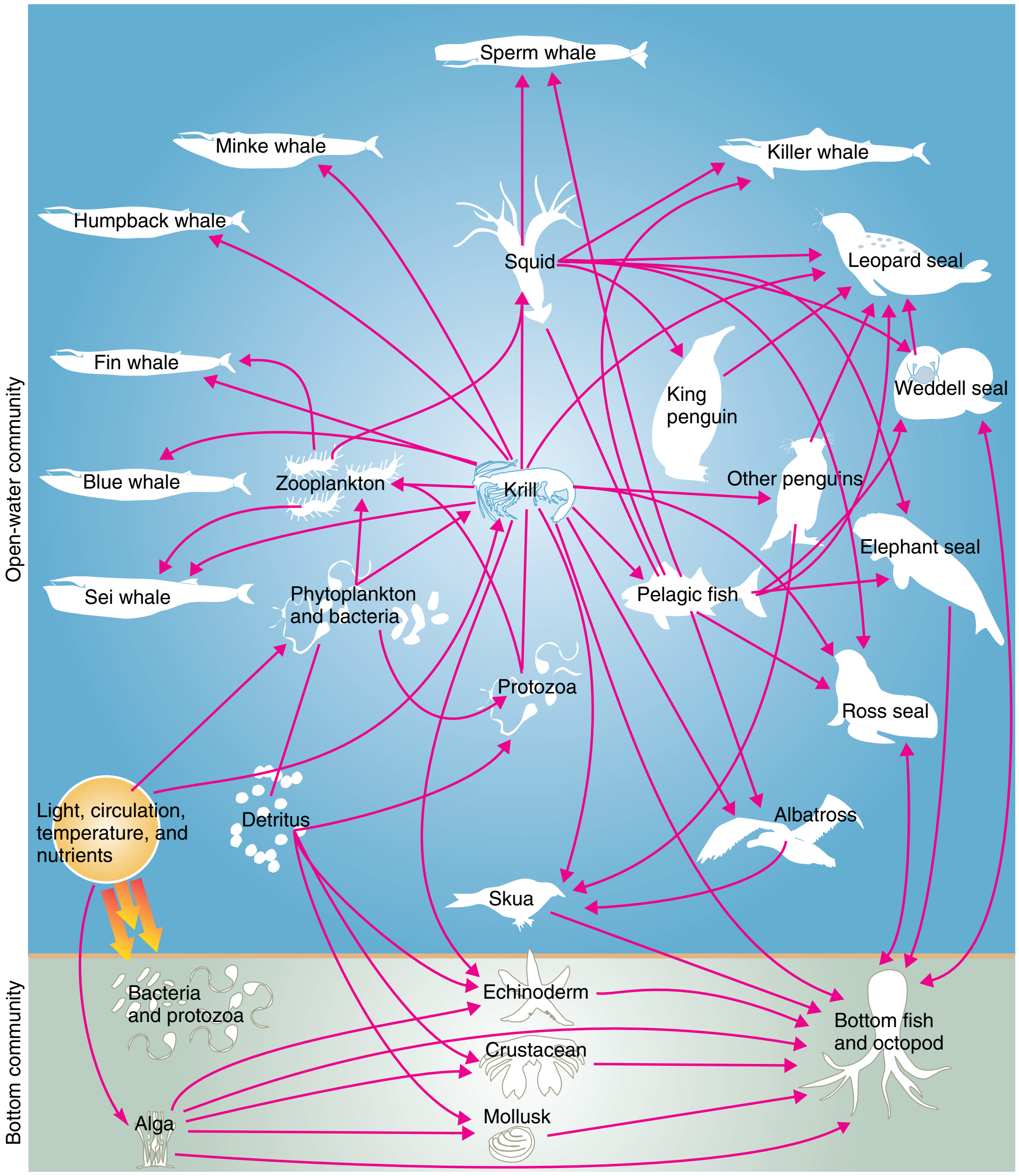


FIGURE 4.18 A complex and highly interconnected community can have many species at each trophic level and many relationships, as illustrated by this Antarctic marine food web.

combination of plant and animal species than either field or forest "core."

Depending on how far edge effects extend from the boundary, differently shaped habitat patches may have very dissimilar amounts of interior area (fig. 4.20). In Douglas fir forests of the Pacific Northwest, for example, increased rates of blowdown, decreased humidity, absence of shade-requiring ground cover, and other edge effects can extend as much as 200 m into a forest. A 40-acre block (about 400 meters square) surrounded by clear-cut would have essentially no true core habitat at all.

Many popular game animals, such as white-tailed deer and pheasants that are adapted to human disturbance, often are most plentiful in boundary zones between different types of habitat. Game managers once were urged to develop as much edge as possible to promote large game populations. Today, however, most wildlife conservationists recognize that the edge effects associated with habitat fragmentation are generally detrimental to biodiversity. Preserving large habitat blocks and linking smaller blocks with migration corridors may be the best ways to protect rare and endangered species (see chapter 13).

FIGURE 4.19 Ecological edges are known as ecotones. Temperature, wind, and humidity differ at the edges in a landscape. Edge conditions do extend into patches of habitat. Small or linear fragments may be mostly edge. © Corbis/Volume 262.

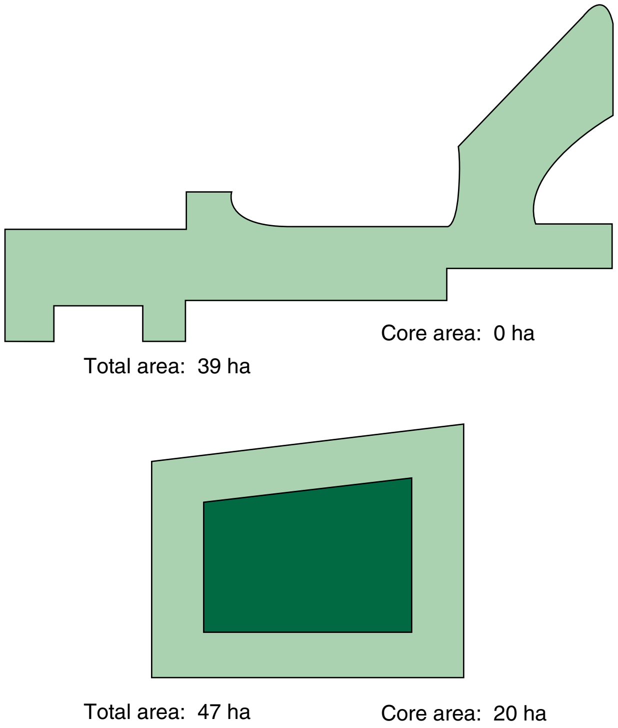


FIGURE 4.20 Shape can be as important as size in small preserves. While these areas are close to the same size, no place in the top figure is far enough from the edge to have characteristics of core habitat, while the bottom patch has a significant core.

COMMUNITIES IN TRANSITION

So far our view of communities has focused on the day-to-day interactions of organisms with their environments, set in a context of survival and selection. In this section, we'll step back to look at some transitional aspects of communities, including where communities meet and how communities change over time.

Ecological Succession

Biological communities have a history in a given landscape. The process by which organisms occupy a site and gradually change environmental conditions by creating soil, shade, shelter, or increasing humidity is called ecological succession or development. **Primary succession** occurs when a community begins to develop on a site previously unoccupied by living organisms, such as an island, a sand or silt bed, a body of water, or a new volcanic flow (fig. 4.21). **Secondary succession** occurs when an existing community is disrupted and a new one subsequently develops at the site. The disruption may be caused by some natural catastrophe, such as fire or flooding, or by a human activity, such as deforestation, plowing, or mining. Both forms of succession usually follow an orderly sequence of stages as organisms modify the environment in ways that allow one species to replace another.

In primary succession on a terrestrial site, the new site first is colonized by a few hardy **pioneer species,** often microbes, mosses, and lichens that can withstand harsh conditions and lack of resources. Their bodies create patches of organic matter in which protists and small animals can live (fig. 4.22). Organic debris accumulates in pockets and crevices, providing soil in which seeds can become lodged and grow. We call this process of environmental modification by organisms **ecological development** or facilitation. The community of organisms often becomes more diverse and increasingly competitive as development continues and new niche opportunities appear. The pioneer species gradually disappear as the environment changes and new species combinations replace the preceding community. In a global sense, the gradual changes brought about by living organisms have created many of the conditions that make life on earth possible. You could consider evolution to be a very slow, planetwide successional and developmental process.

Examples of secondary succession are easy to find. Observe an abandoned farm field or clear-cut forest (fig. 4.23) in a temperate climate. The bare soil first is colonized by rapidly growing annual plants (those that grow, flower, and die the same year) that have light, wind-blown seeds and can tolerate full sunlight and exposed soil. They are followed and replaced by perennial plants (those that live for several to many years), including grasses, various nonwoody flowering plants, shrubs, and trees. As in primary succession, plant species progressively change the environmental conditions. Biomass accumulates and the site becomes richer, better able to capture and store moisture, more sheltered from wind and climate change, and biologically more complex. Species that cannot survive in a bare, dry, sunny, open area find shelter and food as the field turns to prairie or forest.

Eventually, in either primary or secondary succession, a community often develops that resists further change. Ecologists call this a **climax community** because it appears to be the culmination of the successional process. An analogy is often made between community succession and organism maturation. Beginning with a primitive or juvenile state and going through a complex developmental process, each progresses until a complex, stable, and mature form is reached. It's dangerous to carry this analogy too far, however, because no mechanism is known to regulate communities in

Case Study

Where Have All the Songbirds Gone?

Every June, some 2,200 amateur ornithologists and bird watchers across the United States and Canada join in an annual bird count called the Breeding Bird Survey. Organized in 1966 by the U.S. Fish and Wildlife Service to follow bird population changes, this survey has discovered some shocking trends. While birds such as robins, starlings, and blackbirds that prosper around humans have increased their number and distribution over the past 30 years, many of our most colorful forest birds have declined severely. The greatest decreases have been among the true songbirds such as thrushes, orioles, tanagers, catbirds, vireos, buntings, and warblers. These long-distance migrants nest in northern forests but spend the winters in South or Central America or in the Caribbean Islands. Scientists call them neotropical migrants.

In many areas of the eastern United States and Canada, three-quarters or more of the neotropical migrants have declined significantly since the survey was started. Some that once were common have become locally extinct. Rock Creek Park in Washington, D.C., for instance, lost 75 percent of its songbird population and 90 percent of its long-distance migrant species in just 20 years. Nationwide, cerulean warblers, American redstarts, and ovenbirds declined about 50 percent in the single decade of the 1970s. Studies of radar images from National Weather Service stations in Texas and Louisiana suggest that only about half as many birds fly across the Gulf of Mexico each spring now compared to the 1960s. This could mean a loss of about half a billion birds in total.

What causes these devastating losses? Destruction of critical winter habitat is clearly a major issue. Birds often are much more densely crowded in the limited areas available to them during the winter than they are on their summer range. Unfortunately, forests throughout Latin America are being felled at an appalling rate. Central America, for instance, is losing about 1.4 million hectares (2 percent of its forests or an area about the size of Yellowstone National Park) each year. If this trend continues, there will be essentially no intact forest left in much of the region in 50 years.

But loss of tropical forests is not the only threat. Recent studies show that fragmentation of breeding habitat and nesting failures in the United States and Canada may be just as big a problem for woodland songbirds. Many of the most threatened species are adapted to deep woods and need an area of 10 hectares (25 acres) or more per pair to breed and raise their young. As our woodlands are broken up by roads, housing developments, and shopping centers, it becomes more and more difficult for these highly specialized birds to find enough contiguous woods to nest successfully.

Predation and nest parasitism also present a growing threat to many bird species. In human-dominated landscapes, raccoons, opossums, crows, bluejays, squirrels, and house cats thrive. They are protected from larger predators like wolves or owls and find abundant supplies of food and places to hide. Cats are a particular problem. By some estimates, there are 100 million feral cats in the United States, and 73 million pet cats. A comparison of predation rates in the Great Smoky Mountain National Park and in small rural and suburban woodlands shows how devastating predators can be. In a 1,000-hectare study area of mature, unbroken forest in the national park, only one songbird nest in fifty was raided by predators. By contrast, in plots of 10 hectares or less near cities, up to 90 percent of the nests were raided.

Nest parasitism by brown-headed cowbirds is one of the worst threats for woodland songbirds. Rather than raise their young themselves, cowbirds lay their eggs in the nests of other species. The larger and more aggressive cowbird young either kick their foster siblings out of the nest, or claim so much food that the others starve. Well adapted to live around humans, there are now about 150 million cowbirds in the United States.

This thrush has been equipped with a lightweight radio transmitter and antenna so that its movements can be followed by researchers. Courtesy Dr. David Mech.

A study in southern Wisconsin found that 80 percent of the nests of woodland species were raided by predators and that three-quarters of those that survived were invaded by cowbirds. Another study in the Shawnee National Forest in southern Illinois found that 80 percent of the scarlet tanager nests contained cowbird eggs and that 90 percent of the wood thrush nests were taken over by these parasites. The sobering conclusion of this latter study is that there probably is no longer any place in Illinois where scarlet tanagers and wood thrushes can breed successfully.

What can we do about this situation? Elsewhere in this book, we discuss sustainable forestry and economic development projects that could preserve forests at home and abroad. Preserving corridors that tie together important areas also will help. In areas where people already live, clustering of houses protects remaining woods. Discouraging the clearing of underbrush and trees from yards and parks leaves shelter for the birds.

Could we reduce the number of predators or limit their access to critical breeding areas? Would you accept fencing or trapping of small predators in wildlife preserves? How would you feel about a campaign to keep house cats inside during the breeding season?

Ethical Considerations

Some wildlife managers are already trapping cowbirds. The Kirtland's warbler is one of the rarest songbirds in the United States. It nests only in young, fire-maintained jackpine forests in Michigan. Controlled burning to maintain habitat for this endangered species was started in the 1960s, but the population continued to decline. Studies showed that 90 percent of the nests were being parasitized by cowbirds. Since 1972, refuge managers have trapped and killed some 7,000 cowbirds each year to protect the warblers. In the past two decades, the number of breeding pairs of warblers has risen from about 150 to nearly 400. Would it be possible to do something similar on a nationwide scale? Could we trap and kill 150 million cowbirds? How much should we reduce one species to save another? What do you think?

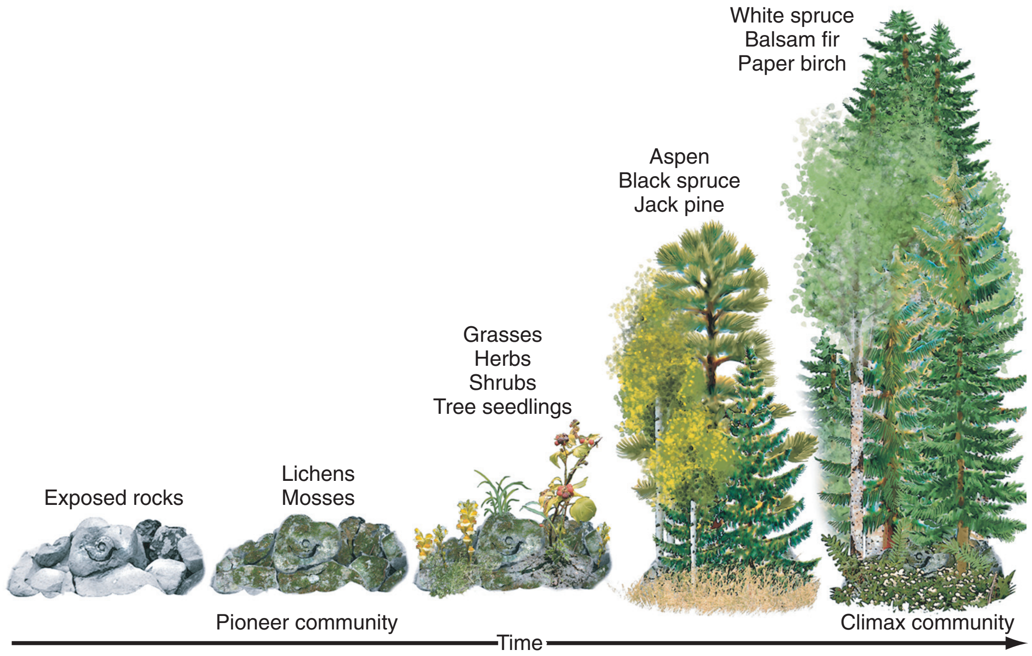


FIGURE 4.21 One example of primary succession, shown in five stages (*left to right*). Here, bare rocks are colonized by lichens and mosses, which trap moisture and build soil for grasses, shrubs, and eventually trees.

FIGURE 4.22 Primary succession occurs where there had been no living things, as on this lava in Hawaii. Fungi, algae, and bacteria grew here first, providing rooting material for these ferns. © William P. Cunningham.

the same way that genetics and physiology regulate development of the body.

The concept of succession to a climax community was first championed by the pioneer biogeographer F. E. Clements. He viewed this process as being like a parade or relay, in which species replace each other in predictable groups and in a fixed, regular order, and as being driven almost entirely by climate. This community-unit theory was opposed by Clements's contemporary, H. A. Gleason, who saw community history as a much more individualistic and random process driven by many environmental factors. He argued that temporary associations are formed according to the conditions prevailing at a particular time and the species available to colonize a given area. You might think of the Gleasonian model as a time-lapse movie of a busy railroad station. Passengers come and go; groups form and then dissipate. Patterns and assemblages that seem significant to us may not mean much in the long run.

The process of succession may not be as deterministic as we once thought, yet mature or highly developed ecological communities may tend to be resilient and stable over long periods of time because they can resist or recover from external disturbances. Many are characterized by high species diversity, narrow niche specialization, well-organized community structure, good nutrient conservation and recycling, and a large amount of total organic matter. Community functions, such as productivity and nutrient cycling, tend to be self-stabilizing or self-perpetuating. What once were regarded as "final" climax communities, however, may still be changing. It's probably more accurate to say that the rate of succession is so slow in a climax community that, from the perspective of a single human lifetime, it appears to be stable.

Some landscapes never reach a stable climax in the traditional sense because they are characterized by, and adapted to, periodic disruption. They are called **equilibrium communities** or **disclimax communities.** Grasslands, the chaparral shrubland of California, and some kinds of coniferous forests, for instance, are shaped and maintained by periodic fires that have long been a part of their history. They are, therefore, often referred to as **fire-climax communities** (fig. 4.24). Plants in these communities are adapted to resist fires,

FIGURE 4.23 This area was once a cool, shady black spruce stand. The forest floor was covered by a deep, moist layer of sphagnum moss. Clear-cutting and burning have turned it into a dry, sunny, barren ground on which few of the former residents can survive. Secondary succession will probably restore previous conditions if the climate doesn't change and further disturbance is prevented. © William P. Cunningham.

FIGURE 4.24 This lodgepole pine forest in Yellowstone National Park was once thought to be a climax forest, but we now know that this forest must be constantly renewed by periodic fire. It is an example of an equilibrium, or disclimax, community. © William P. Cunningham.

What can you do?

Working Locally for Ecological Diversity

You might think that diversity and complexity of ecological systems are too large or too abstract for you to have any influence. But you can contribute to a complex, resilient, and interesting ecosystem, whether you live in the inner city, a suburb, or a rural area.

- Keep your cat indoors. As discussed in the Case Study (p. 00), our lovable domestic cats are also very successful predators. Migratory birds, especially those nesting on the ground, have not evolved defenses against these predators.
- Plant a butterfly garden. Use native plants that support a diverse insect population. Native trees with berries or fruit also support birds. (Be sure to avoid non-native invasive species: see chapter 11). Allow structural diversity (open areas, shrubs, and trees) to support a range of species.
- Join a local environmental organization. Often, the best way to be effective is to concentrate your efforts close to home. City parks and neighborhoods support ecological communities, as do farming and rural areas. Join an organization working to maintain ecosystem health: start by looking for environmental clubs at your school, parks organizations, a local Audubon chapter, or a local Nature Conservancy branch.
- Take walks. The best way to learn about ecological systems in your area is to take walks and practice observing your environment. Go with friends and try to identify some of the species and trophic relationships in your area.
- Live in town. Suburban sprawl consumes wildlife habitat and reduces ecosystem complexity by removing many specialized plants and animals. Replacing forests and grasslands with lawns and streets is the surest way to simplify, or eliminate, ecosystems.

reseed quickly after fires, or both. In fact, many of the plant species we recognize as dominants in these communities require fire to eliminate competition, to prepare seedbeds for germination of seedlings, or to open cones or thick seed coats. Without fire, community structure may be quite different.

Introduced Species and Community Change

Succession requires the continual introduction of new community members and the disappearance of previously existing species. New species move in as conditions become suitable; others die or move out as the community changes. New species also can be introduced after a stable community already has become established. Some cannot compete with existing species and fail to become established. Others are able to fit into and become part of the community, defining new ecological niches. If, however, an introduced species preys upon or competes more successfully with one or more populations that are native to the community, the entire nature of the community can be altered.

Human introductions of Eurasian plants and animals to non-Eurasian communities often have been disastrous to native species because of competition or overpredation. Oceanic islands offer classic examples of devastation caused by rats, goats, cats, and pigs liberated from sailing ships. All these animals are prolific, quickly developing large populations. Goats are efficient, nonspecific herbivores; they eat nearly everything vegetational, from grasses and herbs to seedlings and shrubs. In addition, their sharp hooves are hard on plants rooted in thin island soils. Rats and pigs are opportunistic omnivores, eating the eggs and nestlings of seabirds that tend to nest in large, densely packed colonies, and digging up sea turtle eggs. Cats prey upon nestlings of both ground- and tree-nesting birds. Native island species are particularly vulnerable because they have not evolved under circumstances that required them to have defensive adaptations to these predators (What Can You Do? p. 89).

Sometimes we introduce new species in an attempt to solve problems created by previous introductions but end up making the situation worse. In Hawaii and on several Caribbean Islands, for instance, mongooses were imported to help control rats that had escaped from ships and were destroying indigenous birds and devastating plantations (fig. 4.25). Since the mongooses were diurnal (active in the day), however, and rats are nocturnal, they tended to ignore each other. Instead, the mongooses also killed native birds and further threatened endangered species. Our lessons from this and similar introductions have a new technological twist. Some of the ethical questions currently surrounding the release of genetically engineered organisms are based on concerns that they are novel organisms, and we might not be able to predict how they will interact with other species in natural ecosystems—let alone how they might respond to natural selective forces. It is argued that we can't predict either their behavior or their evolution.

FIGURE 4.25 Mongooses were released in Hawaii in an effort to control rats. The mongooses are active during the day, however, while the rats are night creatures, so they ignored each other. Instead, the mongooses attacked defenseless native birds and became as great a problem as the rats. © Gerard Lacz/Peter Arnold, Inc.

Summary

- Organisms are adapted to live within certain ranges of environmental conditions. Tolerance limits are the maximum or minimum conditions, such as temperature or moisture, that an organism can survive. Since many environmental factors affect survival, it is useful to consider critical factors that limit a species' growth or expansion.
- Evolution is gradual change of organisms by *natural selection.* Natural selection refers to a higher rate of survival and reproduction among individuals that happen to have advantageous traits. Environmental conditions can exert *selective pressure* by making some traits more advantageous than others.
- An ecological niche is usually described as its ecological role in a community; a niche can also be the place or set of environmental conditions in which an organism lives. Generalist species can occupy a range of habitats and ecological roles or environmental conditions. Highly specialized species occupy narrower niches.
- Resource partitioning occurs when species adapt to use a single resource differently.
- Species interact in many ways. Some general classes of interaction include predation, parasitism, symbiosis, and competition. All of these interactions can exert selective pressure, as organisms develop defenses against predators or parasites, as they develop traits that improve competitiveness, or as they develop mutually beneficial interactions. Both interspecific (between species) and intraspecific (within a species) competition can lead to changes in traits or behavior.
- Defensive mechanisms can include Batesian mimicry, in which a harmless species looks like a dangerous one, and Müllerian mimicry, in which two dangerous species look like each other, and thus both discourage predation.
- Primary productivity, or the rate of biomass accumulation, is a basic characteristic of communities. Abundance and species diversity are also important characteristics.

- Complexity refers to the number of species at each trophic level and the number of trophic levels in a community. Many ecologists believe that complexity contributes to stability in an ecosystem, or resilience to abrupt change such as fire, flood, or drought. Others believe that complex communities can be less resilient than simple ones.
- Edges, where contrasting conditions meet, are important features in biological communities. Ecotones, or zones of transition, have great diversity. Edges also reduce habitat quality for interior species.
- Primary succession occurs when pioneer species occupy areas previously lacking living things. Secondary succession occurs when an existing community is disrupted and a new, different community develops.
- The idea of a climax community is a stable community that appears to be the culmination of successional processes. A contrasting idea is that species occur individualistically, each according to its ability to colonize an area.
- Introduced species are one of the greatest modern threats to biological diversity and ecosystem complexity. When introduced species are free of predators, they can become abundant and cause significant damage to ecosystems.

Questions for Review

1. Explain how tolerance limits (fig. 4.2) to environmental factors determine distribution of a highly specialized species such as the saguaro cactus. Compare this to the distribution of a generalist species such as cowbirds or starlings. What would the curve in fig. 4.1 look like for one of these species?
2. Productivity, diversity, complexity, resilience, and structure are exhibited to some extent by all communities and ecosystems. Describe how these characteristics apply to the ecosystem in which you live.
3. Resource partitioning (figs. 4.6, 4.7) is an important adaptive strategy. Explain resource partitioning, and think of an example in your local area.
4. Define keystone species and explain their importance in community structure and function.
5. All organisms within a biological community interact with each other. The most intense interactions often occur between individuals of the same species. What concept discussed in this chapter can be used to explain this phenomenon?
6. Relationships between predators and prey play an important role in the energy transfers that occur in ecosystems. They also influence the process of natural selection. Explain how predators affect the adaptations of their prey. This relationship also works in reverse. How do prey species affect the adaptations of their predators?
7. Competition for a limited quantity of resources occurs in all ecosystems. This competition can be interspecific or intraspecific. Explain some of the ways an organism might deal with these different types of competition.
8. Each year fires burn large tracts of forestland. Describe the process of succession that occurs after a forest fire destroys an existing biological community. Is the composition of the final successional community likely to be the same as that which existed before the fire? What factors might alter the final outcome of the successional process? Why may periodic fire be beneficial to a community?
9. Which world ecosystems are most productive in terms of biomass (fig. 4.17)? Which are least productive? What units are used in this figure to quantify biomass accumulation?
10. Discuss the dangers posed to existing community members when new species are introduced into ecosystems. What type of organism would be most likely to survive and cause problems in a new habitat?

Questions for Critical Thinking

1. Ecologists debate whether biological communities have self-sustaining, self-regulating characteristics or are highly variable, accidental assemblages of individually acting species. What outlook or worldview might lead scientists to favor one or the other of these theories?
2. The concepts of natural selection and evolution are central to how most biologists understand and interpret the world, and yet the theory of evolution is contrary to the beliefs of many religious groups. Why do you think this theory is so important to science and so strongly opposed by others? What evidence would be required to convince opponents of evolution?
3. What is the difference between saying that a duck has webbed feet because it needs them to swim and saying that a duck is able to swim because it has webbed feet?
4. The concept of keystone species is controversial among ecologists because most organisms are highly interdependent. If each of the trophic levels is dependent on all the others, how can we say one is most important? Choose an ecosystem with which you are familiar and decide whether it has a keystone species or keystone set.
5. Some scientists look at the boundary between two biological communities and see a sharp dividing line. Others looking at the same boundary see a gradual transition with much intermixing of species and many interactions between communities. Why are there such different interpretations of the same landscape?

6. The absence of certain lichens is used as an indicator of air pollution in remote areas such as national parks. How can we be sure that air pollution is really responsible? What evidence would be convincing?
7. We tend to regard generalists or "weedy" species as less interesting and less valuable than rare and highly specialized endemic species. What values or assumptions underlie this attitude?
8. What part of this chapter do you think is most likely to be challenged or modified in the future by new evidence or new interpretations?

Key Terms

abundance	83
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climax community	86
coevolution	78
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complexity	84
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Müllerian mimicry	82
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predator	77
primary productivity	82
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symbiosis	79
territoriality	79
tolerance limits	72

Further Readings

Botkin, Daniel B. 1989. *Discordant Harmonies: A New Ecology for the Twenty-First Century.* Oxford University Press.

Ehrlich, Paul R., and Peter H. Raven. 1967. Butterflies and plants: A study in coevolution. *Evolution* 18:586–608.

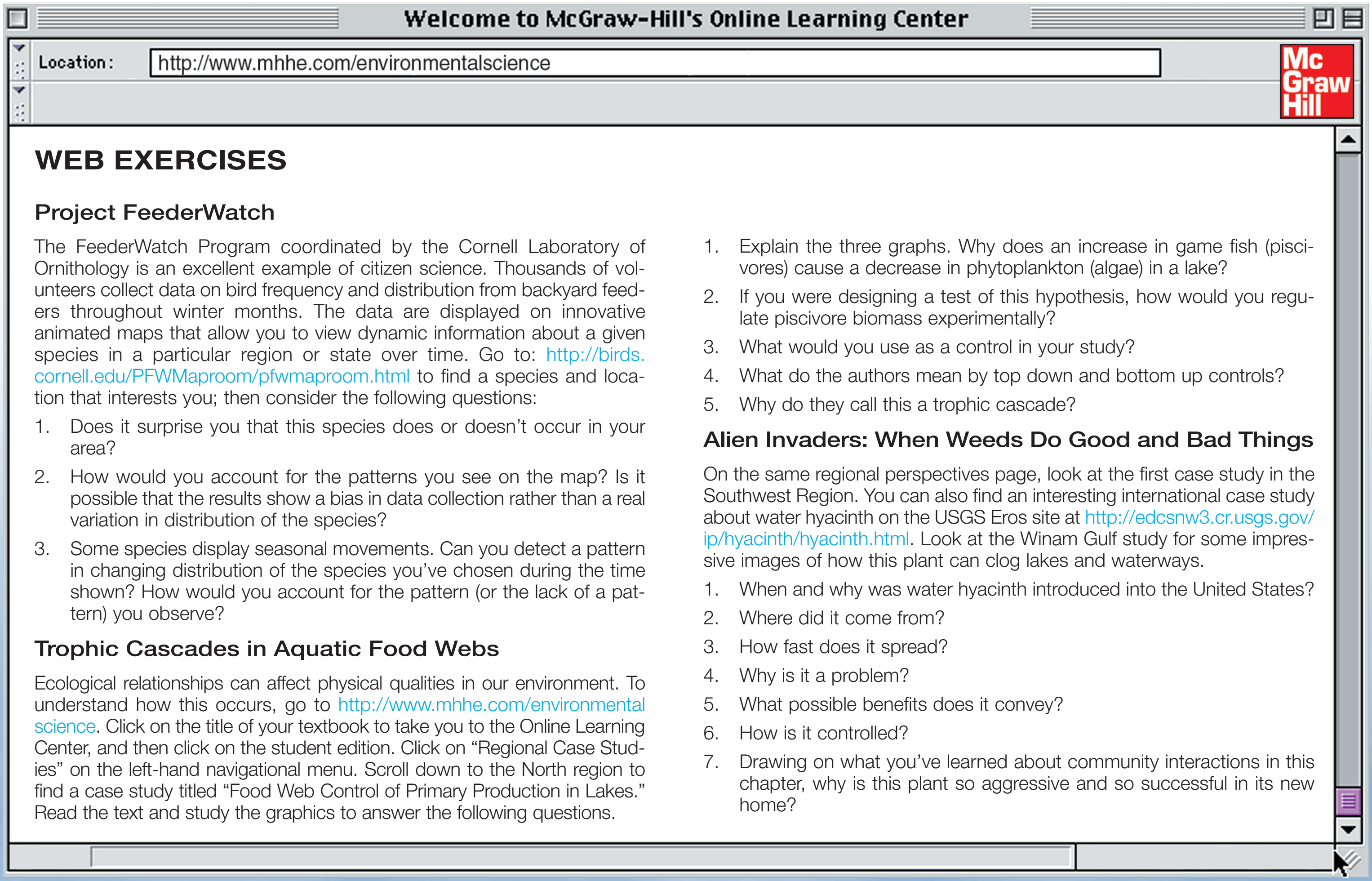
Gleason, Henry A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53:7–26.

MacArthur, R. H. 1958. Population ecology of some warblers of Northeastern coniferous forests. *Ecology* 39:599–619.

Paracer, S., and V. Ahmadjian. 2000. *Symbiosis: An Introduction to Biological Associations.* Oxford University Press.

Simberloff, D. 1997. Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? *Biological Conservation* 83:247–57.

Tilman, David, et al. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277(5330): 1300–02.



Location: http://www.mhhe.com/environmentalscience

WEB EXERCISES

Project FeederWatch

The FeederWatch Program coordinated by the Cornell Laboratory of Ornithology is an excellent example of citizen science. Thousands of volunteers collect data on bird frequency and distribution from backyard feeders throughout winter months. The data are displayed on innovative animated maps that allow you to view dynamic information about a given species in a particular region or state over time. Go to: http://birds.cornell.edu/PFWMaproom/pfwmaproom.html to find a species and location that interests you; then consider the following questions:

1. Does it surprise you that this species does or doesn't occur in your area?
2. How would you account for the patterns you see on the map? Is it possible that the results show a bias in data collection rather than a real variation in distribution of the species?
3. Some species display seasonal movements. Can you detect a pattern in changing distribution of the species you've chosen during the time shown? How would you account for the pattern (or the lack of a pattern) you observe?

Trophic Cascades in Aquatic Food Webs

Ecological relationships can affect physical qualities in our environment. To understand how this occurs, go to http://www.mhhe.com/environmentalscience. Click on the title of your textbook to take you to the Online Learning Center, and then click on the student edition. Click on "Regional Case Studies" on the left-hand navigational menu. Scroll down to the North region to find a case study titled "Food Web Control of Primary Production in Lakes." Read the text and study the graphics to answer the following questions.

1. Explain the three graphs. Why does an increase in game fish (piscivores) cause a decrease in phytoplankton (algae) in a lake?
2. If you were designing a test of this hypothesis, how would you regulate piscivore biomass experimentally?
3. What would you use as a control in your study?
4. What do the authors mean by top down and bottom up controls?
5. Why do they call this a trophic cascade?

Alien Invaders: When Weeds Do Good and Bad Things

On the same regional perspectives page, look at the first case study in the Southwest Region. You can also find an interesting international case study about water hyacinth on the USGS Eros site at http://edcsnw3.cr.usgs.gov/ip/hyacinth/hyacinth.html. Look at the Winam Gulf study for some impressive images of how this plant can clog lakes and waterways.

1. When and why was water hyacinth introduced into the United States?
2. Where did it come from?
3. How fast does it spread?
4. Why is it a problem?
5. What possible benefits does it convey?
6. How is it controlled?
7. Drawing on what you've learned about community interactions in this chapter, why is this plant so aggressive and so successful in its new home?