Chapter 54

Community Ecology

Lecture Outline

Overview: A Sense of Community

- A biological **community** is defined as a group of different species living close enough together for potential interaction.
- Ecologists define the boundaries of a particular community to fit their research questions.
    - An ecologist might study the community of decomposers living on a rotting log, the benthic community in Lake Superior, or the community of trees and shrubs in Shenandoah National Park.

Concept 54.1 Community interactions are classified by whether they help, harm, or have no effect on the species involved.

- **Interspecific interactions** that link the species of a community include competition, predation, herbivory, and symbiosis (including parasitism, mutualism, and commensalism).
- Interspecific interactions can be symbolized by the positive (+) or negative (−) effects they have on the survival and reproduction of the two species engaged in the interaction.
    - 0 indicates that a population is not affected by the interaction in any known way.

Interspecific competition can occur when species compete for a resource that limits their growth and survival.

- When two species engage in **interspecific competition** for a limiting resource, the result is detrimental to one or both species (−/−).
    - For example, grasshoppers and bison in the Great Plains compete for grass.
    - In contrast, oxygen is rarely in short supply. Although most species use oxygen, they rarely compete for it.
- Strong competition between two species can lead to the local elimination of one of the two competing species, a process called **competitive exclusion**.
    - When Russian ecologist G. F. Gause cultured two species of *Paramecium* together, one species was driven to extinction in the culture.
    - Gause concluded that two species competing for the same limiting resources cannot coexist in the same place.
    - One species will always use the resources more efficiently, gaining a reproductive advantage that will eventually lead to local elimination of the inferior competitor.
- A species' **ecological niche** is the sum total of its use of abiotic and biotic resources in its environment.

- In the analogy stated by ecologist Eugene Odum, an organism's habitat is its "address," and the niche is the organism's "profession."
- The niche is an organism's ecological role—how it "fits into" an ecosystem.
- For example, the niche of a tropical tree lizard includes the temperature range it tolerates, the size of the branches it perches on, the time of day when it is active, and the sizes and kinds of insects it eats.

- The competitive exclusion principle can be restated to say that two species cannot coexist permanently in a community if their niches are identical.
  - However, ecologically similar species *can* coexist in a community if their niches differ in one or more significant ways.
- When competition between two species with identical niches does not lead to the local extinction of either species, it is generally because evolution by natural selection has resulted in the modification of the resources used by one of the species.
- **Resource partitioning** is the differentiation of niches that enables two similar species to coexist in a community.
- As a result of competition, a species' *fundamental niche*, the niche potentially occupied by that species, may differ from its *realized niche,* the niche a species actually occupies in a particular environment.
- Ecologists can identify a species' fundamental niche by testing the range of conditions in which it grows and reproduces in the absence of competition.
- Ecologists can test whether a potential competitor limits a species' realized niche by removing the competitor and seeing whether the first species expands into the newly available space.
  - A classic experiment of this type, performed in the rocky intertidal zone of Scotland, showed that competition from one barnacle species kept a second barnacle species from occupying part of its fundamental niche.
- **Character displacement** is the tendency for characteristics to be more divergent in sympatric populations of two species than in allopatric populations of the same two species.
  - An example of character displacement is the variation in beak size between different populations of the Galápagos finches *Geospiza fuliginosa* and *Geospiza fortis*.

In predation, the predator kills and eats the prey.

- **Predation** is a +/− interaction between species in which one species, the predator, kills and eats the other, the prey.
  - The term *predation* elicits images such as a lion attacking and eating an antelope.
  - An animal that kills and eats a plant may also be considered a predator.
- Natural selection favors adaptations of predators and prey.
- Predators have many feeding adaptations, including acute senses and weaponry, such as claws, teeth, fangs, stingers, or poison to help them catch and subdue prey.
- Predators that pursue prey are generally fast and agile; those that lie in ambush are often camouflaged.
- Prey animals have evolved adaptations that help them avoid being eaten.
- The behavioral defenses of prey animals include fleeing, hiding, and forming herds and schools.
  - Active self-defense is less common, although large grazing mammals may vigorously defend their young from predators.
  - Alarm calls may summon many individuals of the prey species to mob the predator.

- Adaptive coloration has evolved repeatedly in prey animals.
    - Camouflage or **cryptic coloration** makes prey difficult to spot against the background.
- Some prey animals have mechanical or chemical defenses.
    - Chemical defenses include odors and toxins, synthesized by the prey species or passively acquired from the food the prey eats.
    - Prey animals with effective chemical defenses often exhibit bright warning **aposematic coloration**.
        - Predators are cautious in approaching potential prey with bright coloration.
- One prey species may gain protection by mimicking the appearance of another prey species.
    - In **Batesian mimicry**, a harmless or palatable species mimics a harmful or unpalatable model.
    - In **Müllerian mimicry**, two or more unpalatable species resemble each other.
        - Each species gains an additional advantage because predators are more likely to encounter an unpalatable prey and learn to avoid prey with that appearance.
        - The shared appearance thus becomes a kind of aposematic coloration.
- Predators may also use mimicry.
    - Some snapping turtles have tongues resembling wiggling worms to lure small fish.

Herbivores eat parts of a plant or alga.

- **Herbivory** is a +/− interaction in which an herbivore eats parts of a plant or alga.
- Terrestrial herbivores include large mammals, such as cattle and water buffalo, and small invertebrates, such as grasshoppers. Aquatic herbivores include snails, sea urchins, and some tropical fishes.
- Herbivores have many specialized adaptations.
    - Many herbivorous insects have chemical sensors on their feet to recognize appropriate food plants that are nutritious and nontoxic.
    - Mammalian herbivores have specialized dentition and digestive systems to process vegetation.
- Plants may produce chemical toxins, which may act in combination with spines and thorns to prevent herbivory.
    - Plants' chemical weapons include strychnine, nicotine, and tannins.
    - The familiar flavors of cinnamon, cloves, and peppermint are distasteful to many herbivores.
    - Some plants produce chemicals that cause abnormal development in insect herbivores.

When individuals of two or more species live in direct and intimate contact with one another, they have a symbiotic relationship.

- **Symbiosis** includes all direct and intimate relationships between species, whether harmful, helpful, or neutral.
- **Parasitism** is a +/− symbiotic interaction in which a **parasite** derives its nourishment from a **host,** which is harmed in the process.
- **Endoparasites** live within the body of the host; **ectoparasites** live and feed on the external surface of the host.
- Parasitoid insects (usually small wasps) are a special type of parasites that lay eggs on or in living hosts.

- The larvae feed on the body of the host, eventually killing it.

- Some ecologists believe that at least one-third of all species on Earth may be parasites.
- Many parasites have complex life cycles involving a number of hosts.
  - For example, the life cycle of the blood fluke, which infects approximately 200 million people around the world, involves two hosts: humans and freshwater snails.
- Some parasites change the behavior of their hosts in ways that increase the probability of the parasite being transferred from one host to another.
  - For instance, the presence of parasitic acanthocephalan (spiny-headed) worms leads their crustacean hosts to move into the open, where they have a greater chance of being eaten by the birds that are the second host in the parasitic worm's life cycle.
- Parasites can have significant direct and indirect effects on the survival, reproduction, and density of their host populations.
  - For example, ticks that live as ectoparasites on moose weaken their hosts by withdrawing blood and causing hair breakage and loss, thus increasing the chance that the moose will die from cold, stress, or predation by wolves.
  - Some of the declines of the moose population on Isle Royale, Michigan, have been attributed to tick outbreaks.
- **Mutualism** is an interspecific symbiosis in which two species benefit from their interaction (+/+).
  - Examples of mutualism include nitrogen fixation by bacteria in the root nodules of legumes; digestion of cellulose by microorganisms in the guts of ruminant mammals; and the exchange of nutrients in mycorrhizae, the association of fungi and plant roots.
- The interaction between termites and the microorganisms that live in their digestive system is an example of an *obligate mutualism,* in which at least one species has lost the ability to survive without its partner.
- In a *facultative mutualism*, both species can survive alone.
- Mutualistic interactions may result in the evolution of related adaptations in both species.
  - For example, most flowering plants have adaptations such as nectar or fruit to attract pollinators.
  - In turn, many pollinators have adaptations to help them find or consume nectar or fruit.
- **Commensalism** is an interaction that benefits one species but neither harms nor helps the other (+/0).
- Commensal interactions are difficult to document in nature because any close association between species likely affects both species, if only slightly.
  - For example, "hitchhiking" species, such as the barnacles that attach to whales, are sometimes considered commensal.
  - The hitchhiking barnacles gain access to a substrate and seem to have little effect on the whale.
  - The barnacles may slightly reduce the host's efficiency of movement or may provide some camouflage.
- Some commensal associations involve one species obtaining food that is inadvertently exposed by another.
  - For instance, cowbirds and cattle egrets feed on insects flushed out of the grass by grazing bison, cattle, horses, and other herbivores.

- The birds benefit, increasing their feeding rates when they follow the herbivores.
- The herbivores may derive some benefit because the birds are opportunistic feeders that occasionally remove and eat ticks and other ectoparasites from the herbivores. The birds may also warn the herbivores of a predator's approach.

Concept 54.2 Dominant and keystone species exert strong controls on community structure.

Species diversity is a fundamental aspect of community structure.

- The **species diversity** of a community is the variety of different kinds of organisms that make up the community.
- Species diversity has two components.
  1. **Species richness** is the total number of different species in the community.
  2. **Relative abundance** is the proportion each species represents of the total individuals in the community.
- Species diversity is dependent on *both* species richness and relative abundance.
- Measuring species diversity may be difficult, but it is essential for understanding community structure and for conserving biodiversity.
- Ecologists calculate indexes of diversity based on species richness and relative abundance so they can quantitatively compare the diversities of different communities across time and space.
  - One widely used index is Shannon diversity (H):

$$H = -\sum_{i=1}^{S} p_i \ln p_i$$

    where S is species richness and p_i is the proportion of each species in the community.
- Determining the number and relative abundance of species in a community can be difficult.
  - Because most species in a community are relatively rare, it may be hard to obtain a sample size large enough to be representative.
  - It is difficult to census highly motile or less visible members of communities, such as mites, nematodes, and microorganisms.
  - The small size of microorganisms makes them particularly difficult to sample, so ecologists now use molecular tools to help determine microbial diversity.

Trophic structure is a key factor in community dynamics.

- The **trophic structure** of a community is determined by the feeding relationships between organisms.
- The transfer of food energy up the trophic levels from its source in plants and other autotrophs (primary producers) through herbivores (primary consumers) to carnivores (secondary and tertiary consumers) and eventually to decomposers is called a **food chain**.
- In the 1920s, Oxford University biologist Charles Elton recognized that food chains are not isolated units but are linked together into **food webs**.
  - A food web uses arrows to link species according to who eats whom in a community.
- A given species may weave into the web at more than one trophic level.

- For example, foxes are omnivores whose diets include berries and other plant materials, herbivores such as mice, and other predators such as weasels.

- Food webs can be simplified in two ways.
  1. The species in a given community can be grouped into broad functional groups.
     - For example, phytoplankton can be grouped as primary producers in an aquatic food web.
  2. A portion of the web that interacts little with the rest of the community can be isolated.

Why are food chains relatively short?

- The length of most food chains in a food web is only four or five links.
- The **energetic hypothesis** suggests that the length of a food chain is limited by the inefficiency of energy transfer along the chain.
  - Only about 10% of the energy stored in the organic matter of each trophic level is converted to organic matter at the next higher trophic level.
  - Thus, a producer level consisting of 100 kg of plant material can support only about 10 kg of herbivore **biomass** (the sum weight of all individuals in a population) and 1 kg of carnivore biomass.
  - The energetic hypothesis predicts that food chains should be relatively longer in habitats that have higher photosynthetic productivity.
- The **dynamic stability hypothesis** suggests that long food chains are less stable than short chains.
  - Population fluctuations at lower trophic levels are magnified at higher levels, making top predators vulnerable to extinction.
  - In a variable environment, top predators must be able to recover from environmental shocks that can reduce the food supply all the way up the food chain.
  - The dynamic stability hypothesis predicts that food chains should be shorter in unpredictable environments.
- Most of the available data support the energetic hypothesis.
  - For example, ecologists have used tree-hole communities in tropical forests as experimental models to test the energetic hypothesis.
  - Many trees have small branch scars that rot, forming small holes in the tree trunk.
  - The tree holes hold water and provide a habitat for tiny communities consisting of decomposer microorganisms and insects that feed on leaf litter as well as predatory insects.
  - Researchers manipulated productivity (leaf litter falling into the tree holes).
  - As predicted by the energetic hypothesis, holes with the most leaf litter, and hence the greatest total food supply at the producer level, supported the longest food chains.
- Another factor that may limit the length of food chains is that animals tend to be larger at successively higher trophic levels.
  - The size of a carnivore places an upper limit on the size of the food it can take into its mouth.
  - Most large carnivores cannot live on very small food items because they cannot procure enough food in a given time to meet their metabolic needs.
  - An exception is the baleen whales, huge suspension feeders with adaptations that enable them to consume enormous quantities of krill and other small organisms.

Certain species have an especially large impact on community structure.

- Certain species strongly affect community structure because they are highly abundant or because they play a pivotal role in community dynamics.
- The exaggerated impact of these species may occur through their trophic interactions or through their influences on the physical environment.
- **Dominant species** are those species in a community that are most abundant or have the highest biomass.
- There is no single explanation for why a species becomes dominant in a community.
- One hypothesis suggests that dominant species are competitively successful at exploiting limiting resources.
- Another hypothesis suggests that dominant species are most successful at avoiding predation or disease.
    - This hypothesis could explain why **invasive species** can achieve such high biomass in their new environments, in the absence of their natural predators and agents of disease.
- One way to investigate the impact of a dominant species is to remove it from the community.
- This type of experiment has been carried out many times by accident.
- The American chestnut was a dominant tree in deciduous forests of eastern North America before 1910, making up more than 40% of mature trees.
- The fungal disease chestnut blight killed all the chestnut trees in eastern North America between 1910 and 1950.
- The removal of American chestnut trees had a relatively small impact on some species but severe effects on others.
    - Oaks, hickories, beeches, and red maples increased in abundance and replaced the chestnuts.
    - No mammals or birds were harmed by the loss of the chestnut, but seven species of moths and butterflies that fed on the tree became extinct.
- **Keystone species** are not necessarily abundant in a community, but they influence community structure by their key ecological niches.
- If keystone species are removed, community structure is greatly affected.
- Ecologist Robert Paine of the University of Washington first developed the concept of keystone species when he removed the sea star *Pisaster ochraceous* from rocky intertidal communities.
    - *Pisaster* is a predator on mussels such as *Mytilus californianus*, a superior competitor for space in the intertidal areas.
    - After Paine removed *Pisaster*, the mussels were able to monopolize space and exclude other invertebrates and algae from attachment sites.
    - When sea stars were present, 15 to 20 species of invertebrates and algae lived in the intertidal zone.
    - After the experimental removal of *Pisaster*, species diversity declined to fewer than 5 species.
    - *Pisaster* thus acts as a keystone species, exerting an influence on community structure that is disproportionate to its abundance.
- The sea otter, a keystone predator in the North Pacific, provides another example.
    - Sea otters feed on sea urchins, and sea urchins feed mainly on kelp.
    - In areas where sea otters are abundant, sea urchins are rare and kelp forests are well developed. Where sea otters are rare, sea urchins are common and kelp is almost absent.

- Over the last 20 years, orcas have been preying on sea otters as the whales' usual prey has declined.
- As a result, sea otter populations have declined precipitously in large areas off the coast of western Alaska.
- The loss of this keystone species has allowed sea urchin populations to increase, resulting in the loss of kelp forests.

- Some organisms, called ecosystem "engineers" or "foundation species," exert their influence by causing physical changes in the environment that affect community structure.
  - An example of such a species is the beaver, which transforms landscapes by felling trees and building dams.
- By altering the structure or dynamics of the environment, foundation species act as **facilitators**, having positive effects on the survival and reproduction of other species.
  - By modifying soils, the black rush *Juncus gerardi* increases the species richness in New England salt marshes.
  - *Juncus* helps prevent salt buildup in the soil by shading the soil surface, which reduces evaporation and also prevents the salt marsh soils from becoming oxygen-depleted as it transports oxygen to its below-ground tissues.
  - Sally Hacker and Mark Bertness removed *Juncus* from study plots and the result was that the upper middle intertidal zone supported 50% fewer plant species.

The structure of a community may be controlled from the bottom up by nutrients or from the top down by predators.

- Simplified models based on relationships between adjacent trophic levels are useful for discussing how communities might be organized.
- Consider three possible relationships between plants (V for vegetation) and herbivores (H):

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

  - Arrows indicate that a change in biomass at one trophic level causes a change in biomass at the other trophic level.
- We can define two models of community organization: bottom-up and top-down.
- The **bottom-up model** postulates $V \rightarrow H$ linkages, in which the presence or absence of mineral nutrients (N) controls plant (V) numbers, which control herbivore (H) numbers, which control predator (P) numbers.
  - A simplified bottom-up model is $N \rightarrow V \rightarrow H \rightarrow P$.
  - Alterations in biomass at the lower trophic levels of a bottom-up community propagate up through the food web.
  - For example, if mineral nutrients are added to stimulate the growth of vegetation, then the biomass of the higher trophic levels should also increase.
  - If predators are added to or removed from a bottom-up community, the effect should not extend down to the lower trophic levels.
- The **top-down model** postulates that predation is the primary factor that controls community organization.
  - Predators limit herbivores, which limit plants, which limit nutrient levels through the uptake of nutrients during growth and reproduction.
  - A simplified top-down model is thus $N \leftarrow V \leftarrow H \leftarrow P$, also called the *trophic cascade model.*

- For example, in a lake community with four trophic levels, the top-down model predicts that removing the top carnivores will increase the abundance of primary carnivores, in turn decreasing the number of herbivores, increasing phytoplankton abundance, and decreasing concentrations of mineral nutrients.
- The effect of any manipulation thus moves down the trophic structure as a series of +/− effects.

- Diana Wall-Freckman and her colleague, Ross Virginia, found that top-down factors control the organization of a simple community of soil nematodes in the deserts of Antarctica.
  - They chose this extreme environment because its nematode community contains only two or three species and is therefore easier to manipulate and study than the more species-rich communities found elsewhere.
- Because many freshwater lakes seem to be structured according to the top-down model, ecologists have a potential means of improving water quality in polluted lakes.
- This strategy, called **biomanipulation**, attempts to prevent algal blooms and eutrophication by altering the density of higher-level consumers in lakes instead of using chemical treatments.
  - In lakes with three trophic levels, removing fish may improve water quality by increasing zooplankton and thus decreasing algal populations.
  - In lakes with four trophic levels, adding top predators has the same effect.
- Ecologists used biomanipulation on a large scale in Lake Vesijärvi, a large, shallow lake in southern Finland.
- Lake Vesijärvi was polluted with city sewage and industrial wastewater until 1976, when pollution controls were put in place.
- By 1986, massive blooms of cyanobacteria started to appear in the lake.
- These blooms coincided with an increase in the population size of roach, a fish that eats the zooplankton that keep cyanobacteria and algae in check.
- To reverse these changes, ecologists removed nearly a million kilograms of fish from Lake Vesijärvi between 1989 and 1993, reducing roach to about 20% of their former abundance.
- At the same time, ecologists added a fourth trophic level to the lake by stocking it with pike perch, a predatory fish that eats roach.
- Biomanipulation was a success in Lake Vesijärvi.
  - The water became clear, and cyanobacterial blooms disappeared in 1989.
  - The lake remains clear even though roach removal ended in 1993.

Concept 54.3 Disturbance influences species diversity and composition.

- In the traditional view, biological communities are in a state of equilibrium, a more or less stable balance, unless seriously disturbed by human activities.
- This "balance of nature" view focused on interspecific competition as a key factor determining community composition and maintaining stability in communities.
- *Stability* is the tendency of a community to reach and maintain a relatively constant composition of species despite disturbance.
- Early ecologists thought that the community of plants at a site had only one state of equilibrium that was controlled solely by climate.

- F. E. Clements, of the Carnegie Institution, argued that mandatory biotic interactions caused the species in this *climax community* to function as an integrated unit—in effect, as a superorganism.
- His argument was based on the observation that certain species of plants are consistently found together, such as the oaks, maples, birches, and beeches in deciduous forests of the northeastern United States.

- Other ecologists questioned whether most communities were at equilibrium or functioned as integrated units.
  - A. G. Tansley, of Oxford University, challenged the concept of a climax community, arguing that differences in soils, topography, and other factors created many potential communities that were stable within a region.
  - H. A. Gleason, of the University of Chicago, saw communities as chance assemblages of species found in the same area simply because they happen to have similar abiotic requirements—for example, for temperature, rainfall, and soil type.
  - Gleason and other ecologists also realized that disturbance keeps many communities from reaching a state of equilibrium in species diversity or composition.

Many communities seem to be characterized by change rather than stability.

- A **disturbance** is an event that changes a community by removing organisms or altering resource availability.
  - Storms, fires, floods, droughts, frosts, human activities, and overgrazing can all be disturbances.
- The **nonequilibrium model** proposes that communities constantly change following a disturbance.
- The types of disturbances and their frequency and severity vary from community to community.
- Storms disturb almost all communities, even those in the oceans.
- Fire is a significant disturbance in most terrestrial communities.
  - Chaparral and some grassland biomes require regular burning to maintain their structure and species composition.
- Freezing is a frequent occurrence in many rivers, lakes, and ponds, and many streams and ponds are disturbed by spring flooding and seasonal drying.
- A high level of disturbance is generally the result of a high intensity *and* high frequency of disturbance, whereas a low level of disturbance can result from either a low intensity or a low frequency of disturbance.

Moderate levels of disturbance may foster greater species diversity.

- The **intermediate disturbance hypothesis** suggests that moderate levels of disturbance create conditions that foster greater species diversity than a low or high level of disturbance.
- The stresses associated with high levels of disturbance may exceed the tolerances of many species, thus reducing species diversity.
  - At a high frequency of disturbance, slowly colonizing or slowly growing species may be excluded.
- At the other extreme, low levels of disturbance allow competitively dominant species to exclude less competitive species.

- In contrast, intermediate levels of disturbance result in greater species diversity by opening up habitats for occupation by less competitive species yet not creating conditions so severe that they exceed the environmental tolerances or rates of recovery by potential community members.
- The intermediate disturbance hypothesis is supported by many terrestrial and aquatic studies.
  - Ecologists in New Zealand compared the richness of invertebrate taxa living in the beds of 27 streams exposed to different frequencies and intensities of flooding.
  - When floods occurred either very frequently or rarely, invertebrate richness was low.
  - Frequent floods made it difficult for some species to become established in the streambed, and rare floods resulted in some species being displaced by superior competitors.
  - Invertebrate richness peaked in streams that had an intermediate frequency or intensity of flooding, as predicted by the intermediate disturbance hypothesis.
- Small and large disturbances can also have important effects on community structure.
  - Small-scale disturbances can create patches of different habitats across a landscape, which can be a key to maintaining diversity in a community.
  - Large disturbances, such as large-scale fires, can affect community structure.
- Yellowstone National Park is dominated by lodgepole pines, a tree whose cones remain closed until exposed to intense heat.
- When a forest fire burns the trees, the cones open and the seeds are released, allowing a new generation of lodgepole pines to thrive on nutrients released from the burned trees, in sunlight no longer blocked by taller trees.
  - In the summer of 1988, extensive areas of Yellowstone burned during a severe drought.
  - By 1989, the burned areas in the park were largely covered with new vegetation, suggesting that the species in this community are adapted to rapid recovery after fire.
- Large-scale fires have swept through the lodgepole pine forests of Yellowstone and other northern areas for thousands of years, while more southerly pine forests were historically affected by frequent but low-intensity fires.
- Human fire suppression has allowed an unnatural buildup of fuels and elevated the risk of large, severe fires to which the species are not adapted.
- The Yellowstone forest community is a nonequilibrium community, continually changing because of natural disturbances.
- Nonequilibrium conditions resulting from disturbance appear to be the norm for most communities.

Ecological succession is the sequence of community changes after a disturbance.

- **Ecological succession** is the transition in species composition in disturbed areas over ecological time.
- **Primary succession** begins in a lifeless area where soil has not yet formed, such as a volcanic island or the moraine left behind as a glacier retreats.
  - Initially, only autotrophic prokaryotes and heterotrophic bacteria and protists may be present.
  - Next, mosses and lichens colonize by windblown spores and cause the development of soil.
  - Once soil is present, grasses, shrubs, and trees sprout from seeds blown or carried in from nearby areas.
- **Secondary succession** occurs where an existing community has been removed by a disturbance, such as a clear-cut or fire, but the soil is left intact.

- Herbaceous species grow first, from windblown or animal-borne seeds.
- Woody shrubs replace the herbaceous species, and they in turn are replaced by forest trees.

- Early arrivals and later-arriving species are linked in one of three key processes.
  1. Early arrivals may *facilitate* the appearance of later species by changing the environment.
     - For example, early herbaceous species may increase soil fertility.
  2. Early species may *inhibit* the establishment of later species.
  3. Early species may *tolerate* later species but neither hinder nor help their colonization.
- Ecologists have conducted extensive research on primary succession on glacial moraines at Glacier Bay in southeastern Alaska, where glaciers have retreated more than 100 km since 1760.
- By studying the communities on moraines at different distances from the mouth of the bay, ecologists can examine different stages in succession.
  - The exposed moraine is colonized first by pioneering species, including liverworts, mosses, fireweed, and scattered *Dryas* (a mat-forming shrub), willows, and cottonwood.
  - After about three decades, *Dryas* dominates the plant community.
  - A few decades later, the area is invaded by alder, which forms dense, tall thickets.
  - During the next two centuries, these alder stands are overgrown first by Sitka spruce and then by a combination of western hemlock and mountain hemlock.
  - In poorly drained areas, the forest floor of this spruce-hemlock forest is invaded by sphagnum mosses, which increases soil moisture and acidifies the soil, killing the trees.
  - Later, 300 years after glacial retreat, the vegetation consists of sphagnum bogs on the poorly drained flat areas and spruce-hemlock forest on the well-drained slopes.
- How is succession on glacial moraines related to environmental changes caused by transitions in the vegetation?
- The bare soil exposed as the glacier retreats is quite basic, with a pH of 8.0–8.4 due to the carbonate compounds in the parent rocks.
- The soil pH falls rapidly as vegetation becomes established.
  - Decomposition of acidic spruce needles in particular reduces the pH of the soil from 7.0 to approximately 4.0.
- The soil concentrations of mineral nutrients also change with time.
- The bare soil after glacial retreat is low in nitrogen content.
  - Most pioneer plant species begin succession with poor growth and yellow leaves due to an inadequate nitrogen supply. However, *Dryas* and alder have symbiotic bacteria that fix atmospheric nitrogen.
- The soil nitrogen content increases rapidly during succession.
- By altering soil properties, pioneer plant species permit new plant species to grow, and the new plants in turn alter the environment in different ways, thus contributing to succession.

Humans are the agents of the most widespread disturbance.

- Human activities cause more disturbances than natural events do.
- Agricultural development has disrupted the vast grasslands of the North American prairie.
- Logging and clearing for urban development have reduced large tracts of forest to small patches of disconnected woodlots throughout North America and Europe.
- Tropical rain forests are disappearing due to clear-cutting for lumber, grazing, and farmland.

- Humans disturb marine ecosystems just as extensively as terrestrial ones.
    - The effects of ocean trawling, where boats drag weighted nets across the seafloor, are similar to the effects of clear-cutting a forest or plowing a field.
- Human-caused disturbances usually reduce species diversity in communities.

Concept 54.4 Biogeographic factors affect community biodiversity.

- Two key factors correlated with a community's **biodiversity** (species diversity) are its geographic location and its size.
- In the 1850s, both Charles Darwin and Alfred Wallace pointed out that plant and animal life was more abundant and varied in the tropics than in temperate and polar areas.
    - A recent study found that a 6.6-hectare plot in tropical Malaysia contains 711 tree species, while a 2-ha plot of deciduous forest in Michigan typically contains just 10 to 15 tree species.
    - All of Western Europe north of the Alps has only 50 tree species.
    - Many groups of animals show similar latitudinal gradients. For instance, there are more than 200 species of ants in Brazil but only 7 in Alaska.
- Such observations suggest that biogeographic patterns in biodiversity conform to a set of basic principles.

Species richness generally declines along an equatorial-polar gradient.

- Tropical habitats support many more species of organisms than do temperate and polar regions.
- Two key factors that probably cause latitudinal gradients are evolutionary history and climate.
- Over the course of evolutionary time, species diversity may increase in a community as more speciation events occur.
    - Tropical communities are generally older than temperate or polar communities.
    - The growing season in the tropics is about five times longer than that in a tundra community.
    - Biological time thus runs five times faster in the tropics.
    - Repeated glaciation events have eliminated many temperate and polar communities.
- Climate is likely the primary cause of latitudinal gradients in biodiversity.
- Solar energy input and water availability can be combined as a measure of **evapotranspiration**, the evaporation of water from soil plus the transpiration of water from plants.
    - Evapotranspiration is much higher in hot areas with abundant rainfall than in areas with low temperatures or low precipitation.
    - *Potential evapotranspiration,* a measure of potential water loss that assumes water is readily available, is determined by the amount of solar radiation and temperature and is highest in regions of high solar radiation and temperature.
- The species richness of plants and animals correlates with both measures of evapotranspiration.

Species richness is related to a community's geographic size.

- The **species-area curve** quantifies what may seem obvious: The larger the geographic area of a community, the greater the number of species.
- Larger areas offer a greater diversity of habitats and microhabitats than smaller areas.

- In conservation biology, developing species-area curves for the key taxa in a community enables ecologists to predict how loss of habitat is likely to affect biodiversity.

Species richness on islands depends on island size and distance from the mainland.

- Because of their size and isolation, islands provide excellent opportunities for studying some of the biogeographic factors that affect the species diversity of communities.
    - "Islands" include oceanic islands as well as habitat islands on land, such as lakes, mountain peaks, or natural woodland fragments.
    - An island is thus any patch surrounded by an environment unsuitable for the "island" species.
- Robert MacArthur and E. O. Wilson developed a general hypothesis of island biogeography to identify the key determinants of species diversity on an island with a given set of physical characteristics.
- Consider a newly formed oceanic island that receives colonizing species from a distant mainland.
- Two factors determine the number of species that eventually inhabit the island:
    1. The rate at which new species immigrate to the island, and
    2. The rate at which species become extinct on the island.
- As the number of species on the island increases, the immigration rate of new species decreases; any individual that reaches the island is less likely to represent a species that is not already present.
- As more species inhabit an island, extinction rates on the island increase because of the greater likelihood of competitive exclusion.
- The two physical features of the island that affect immigration and extinction rates are its size and its distance from the mainland.
    - Small islands have lower immigration rates because potential colonizers are less likely to reach them.
    - Small islands have higher extinction rates because they have fewer resources and less diverse habitats for colonizing species to partition.
    - Islands closer to the mainland have higher immigration rates than islands that are farther away.
- The arriving colonists of a particular species reduce the chance that the species goes extinct.
- MacArthur and Wilson's model of island biogeography predicts that a dynamic equilibrium will eventually be reached, where the rate of species immigration equals the rate of species extinction.
- The number of species at this equilibrium point is correlated with the island's size and distance from the mainland.
    - Studies of plants and animals on many island chains, including the Galápagos, support these predictions.
- The island equilibrium model may apply in only a limited number of cases and over relatively short periods, where colonization is the main process affecting species composition.
- Over longer periods, abiotic disturbances such as storms, adaptive evolutionary changes, and speciation may alter species composition and community structure on islands.
- Nevertheless, the model is widely applied in conservation biology for the design of habitat reserves and as a starting point for predicting the effects of habitat loss on species diversity.

Concept 54.5 Community ecology is useful for understanding pathogen life cycles and controlling human disease.

- **Pathogens**, which are disease-causing microorganisms, viruses, viroids, or prions, can alter community structure quickly and extensively.
- Pathogens are the subject of a number of ecological studies, as the ecological importance of disease is increasingly recognized.
- Coral reef communities are particularly susceptible to the influence of pathogens.
  - White-band disease, caused by an unknown pathogen, has caused dramatic changes in the structure and composition of Caribbean reefs.
  - The disease kills corals by causing their tissue to slough off in a band from the base to the tip of the branches.
  - The disease attacks staghorn coral (*Acropora cervicornis*) and elkhorn coral (*Acropora palmata*), key habitats for lobsters and for snappers and other fish species.
  - When the corals die, they are quickly overgrown by algae.
  - Surgeonfish and other herbivores that feed on algae come to dominate the fish community.
  - Eventually the corals topple because of damage from storms and other disturbances.
  - The complex, three-dimensional structure of the reef disappears, and diversity plummets.
- Pathogens also influence community structure in terrestrial ecosystems.
  - In the forests and savannas of California, several species of trees are dying from sudden oak death, caused by the fungus-like protist *Phytophthora ramorum*.
  - Since 1994, sudden oak death has killed more than a million oaks from the central California coast to southern Oregon.
  - The loss of these oaks decreased the abundance of at least five bird species, including the acorn woodpecker and the oak titmouse, that rely on the oaks for food and habitat.
  - Scientists recently sequenced the genome of *P. ramorum*, hoping to find a way to fight the pathogen.
- Ecologists now study pathogens because human activities are transporting pathogens around the world at unprecedented rates.
  - Genetic analyses suggest that the fungus that causes sudden oak death likely came from Europe through the horticulture trade.
- Similarly, the pathogens that cause human diseases are spread by our global economy.
  - A person traveling on a plane can quickly introduce a pathogen to a new location.
  - This may be how the West Nile virus arrived in North America in 1999.
- Three-quarters of today's emerging human diseases, including hantavirus and mad cow disease, and many historically important diseases, such as malaria, are caused by **zoonotic** pathogens.
- Zoonotic pathogens are transferred from other animals to humans, either through direct contact with an infected animal or by means of an intermediate species called a **vector**.
- The vectors that spread zoonotic diseases are often parasites, including ticks, lice, and mosquitoes.
- Understanding parasite life cycles enables scientists to devise ways to control zoonotic diseases.
  - River blindness, for instance, is caused by a nematode transmitted by black flies.
  - When the World Health Organization began a global fight against river blindness, scientists focused on controlling black flies, using airplanes to spray biodegradable insecticides.

- Black-fly control remains a key part of the river blindness program.
- The combination of vector control and new medicines has saved the sight of an estimated 300,000 people.

- Ecologists also use their knowledge of community interactions to track the spread of zoonotic diseases such as avian flu.
- Avian flu is caused by highly contagious viruses transmitted through the saliva and feces of birds.
- Most of these viruses have mild effects on wild birds but cause more severe symptoms in domesticated birds, the most common source of human infections.
    - Since 2003, one particular viral strain, called H5N1, has killed hundreds of millions of poultry and more than 150 people.
    - Millions more people are at risk of infection.
- Control programs that quarantine domestic birds or monitor their transport may be ineffective if avian flu spreads naturally through the movements of wild birds.
    - From 2003 to 2006, the H5N1 strain spread rapidly from southeast Asia into Europe and Africa, but by 2006 it had not appeared in Australia or the Americas.
    - The most likely place for infected wild birds to enter the Americas is Alaska, the entry point for ducks, geese, and shorebirds that migrate across the Bering Sea from Asia each year.
    - Ecologists are studying the potential spread of the virus by trapping and testing migrating birds in Alaska, trying to catch the first wave of the disease entering North America.
- Community ecology provides the foundation for understanding the life cycles of pathogens and their interactions with hosts.
    - Pathogen interactions are greatly influenced by changes in the environment around them.
    - To control pathogens and the diseases they cause, scientists need to have an intimate knowledge of how the pathogens interact with other species and with their environment.