Chapter 53

Community Ecology

Lecture Outline

Overview: What Is a Community?

- A **community** is defined as an assemblage of species living close enough together for potential interaction.
- Communities differ in their species richness, the number of species they contain, and the relative abundance of different species.

Concept 53.1 A community's interactions include competition, predation, herbivory, symbiosis, and disease

- There are a number of possible **interspecific interactions** that link the species of a community.
- Interspecific interactions can be symbolized by the positive (+) or negative (−) effects of the interaction on the individual populations.
  - 0 indicates that a population is not affected by the interaction.
  - The effect of an interaction between two species may change as circumstances change.
- **Interspecific competition** can occur when species compete for a specific limiting resource.
  - When two species compete for a resource, the result is detrimental to one or both species (−/−)
- Strong competition can lead to the local elimination of one of the two competing species, a process called **competitive exclusion.**
  - The *competitive exclusion principle* states that two species with similar needs for the same limiting resources cannot coexist in the same place.
- The **ecological niche** is the sum total of a species' use of abiotic and biotic resources in the environment.
  - In the analogy stated by ecologist Eugene Odum, an organism's habitat is its "address," and the niche is the organism's "profession."
  - For example, the niche of a tropical tree lizard includes the temperature range it tolerates, the size of branches it perches on, the time of day when it is active, and the kind of insects it eats.
  - The competitive exclusion principle can be restated to say that two species cannot coexist 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.

- A species' *fundamental niche* is the niche potentially occupied by that species.
  - The fundamental niche may differ from the *realized niche,* the niche a species actually occupies in a particular environment.
- 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 results in 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.
  - **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.
- **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.
  - This interaction also includes interactions such as *seed predation,* in which seed-eating weevils eat plant seeds.
- Natural selection favors adaptations of predators and prey.
  - Predators have many feeding adaptations, including acute senses and weaponry such as claws, fangs, stingers, or poison to help catch and subdue prey.
  - Predators that pursue prey are generally fast and agile; those who lie in ambush are often camouflaged.
- Prey animals have evolved adaptations that help them avoid being eaten.
  - Behavioral defenses include fleeing, hiding, and self-defense.
  - Alarm calls may summon many individuals of the prey species to mob the predator.
  - Adaptive coloration has evolved repeatedly in animals.
    - Camouflage or **cryptic coloration** makes prey difficult to spot against the background.
  - Some animals have mechanical or chemical defenses.
    - Chemical defenses include odors and toxins.
    - Animals with effecting 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, palatable species mimics a harmful, 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.
- Predators may also use mimicry.
  - Some snapping turtles have tongues resembling wiggling worms to lure small fish.
- **Herbivory** is a +/− interaction in which an herbivore eats parts of a plant or alga.
  - Herbivores include large mammals and small invertebrates.
  - Herbivores have specialized adaptations.

        - Many herbivorous insects have chemical sensors on their feet to recognize appropriate food plants.
        - 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.
- **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.
    - **Parasitoidism** is a special type of parasitism in which an insect (usually a wasp) lays eggs on or in living hosts.
        - The larvae feed on the body of the host, eventually killing it.
    - Many parasites have complex life cycles involving a number of hosts.
    - Some parasites change the behavior of their hosts in ways that increase the probability of the parasite being transferred from one host to another.
    - Parasites can have significant direct and indirect effects on the survival, reproduction, and density of their host populations.
- **Pathogens** are disease-causing agents that have deleterious effects on their hosts (+/−)
    - Pathogens are typically bacteria, viruses, or protists.
    - Fungi and prions can also be pathogenic.
- Parasites are generally large, multicellular organisms, while most pathogens are microscopic.
    - Many pathogens are lethal.
- **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.
- Mutualistic interactions may result in the evolution of related adaptations in both species.
- **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.
        - However, the barnacles may slightly reduce the host’s efficiency of movement.
        - Conversely, they may provide some camouflage.
- **Coevolution** refers to reciprocal evolutionary adaptations of two interacting species.
    - A change in one species acts as a selective force on another species, whose adaptation in turn acts as a selective force on the first species.
    - The linkage of adaptations requires that genetic change in one of the interacting populations of the two species be tied to genetic change in the other population.

- An example is the gene-for-gene recognition between a plant species and a species of virulent pathogen.
- In contrast, the aposematic coloration of various tree frog species and the aversion reactions of various predators are not examples of coevolution.
  - These are adaptations to other organisms in the community rather than coupled genetic changes in two interacting species.

Concept 53.2 Dominant and keystone species exert strong controls on community structure

Species diversity is a fundamental aspect of community structure.

- A small number of species in the community exert strong control on that community's structure, especially on the composition, relative abundance, and diversity of species.
- The **species diversity** of a community is the variety of different kinds of organisms that make up the community.
- Species diversity has two components.
  - **Species richness** is the total number of different species in the community.
  - The **relative abundance** of the different species 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 is essential for understanding community structure and for conserving biodiversity.

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 autotrophs (usually photosynthetic organisms) through herbivores (primary consumers) and 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.
- How are food chains linked into food webs?
  - A given species may weave into the web at more than one trophic level.
- Food webs can be simplified in two ways.
  - We can group species in a given community into broad functional groups.
    - For example, phytoplankton can be grouped as primary producers in an aquatic food web.
  - A second way to simplify a food web is to isolate a portion of the web that interacts little with the rest of the community.
- Each food chain within a food web is usually only a few links long.
  - Charles Elton pointed out that the length of most food chains is only four or five links.
- Why are food chains relatively short?

- 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 trophic level.
    - The energetic hypothesis predicts that food chains should be relatively longer in habitats with 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 supports the energetic hypothesis.
- Another factor that may limit the length of food chains is that, with the exception of parasites, animals tend to be larger at successive trophic levels.
- Certain species have an especially large impact on 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** (the sum weight of all individuals in a population).
- 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 could explain why invasive species can achieve such high biomass in their new environments, in the absence of their natural predators and pathogens.
- One way to investigate the impact of a dominant species is to remove it from the community.
- **Keystone species** are not necessarily abundant in a community.
    - 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.
    - Paine 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 occurred in the intertidal zone.

        - After 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.
    - Some organisms 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.
    - Such species are called ecosystem "engineers" or "foundation species."
        - These influential species act as **facilitators,** with positive effects on the survival and reproduction of other 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*).
        - $V \rightarrow H$ $V \leftarrow H$ $V \leftrightarrow H$
        - Arrows indicate that a change in biomass at one trophic level causes a change in biomass at in the other trophic level.
- We can define two models of community organization.
    - 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 $N \rightarrow V \rightarrow H \rightarrow P$.
    - The **top-down model** postulates that it is mainly predation 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 $N \leftarrow V \leftarrow H \leftarrow P$.
        - The top-down control of community structure is also called the *trophic cascade model.*
        - The effect of any manipulation thus moves down the trophic structure as a series of +/− effects.
- Many intermediate models are between extreme bottom-up and top-down models.
    - For example, all interactions between trophic levels may be reciprocal ($\leftarrow \rightarrow$).
    - The direction of interaction may alternate over time.
    - Communities vary in their relative degree of bottom-up and top-down control.
- Simplified models are valuable as a starting point for the analysis of communities.
    - Pollution has degraded freshwater lakes in many countries.
    - Because many freshwater lakes seem to be structured according to the top-down model, ecologists have a potential means of improving water quality.
        - This strategy is called **biomanipulation.**

  - 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 will have the same effect.

Concept 53.3 Disturbance influences species diversity and composition

- *Stability* is the tendency of a community to reach and maintain a relatively constant composition of species despite disturbance.
  - Many communities seem to be characterized by change rather than stability.
- The **nonequilibrium model** proposes that communities constantly change following a disturbance.
- A **disturbance** is an event that changes a community by removing organisms or altering resource availability.
  - Storms, fires, floods, droughts, frosts, human activities, or overgrazing can be disturbances.
- A disturbance can have a beneficial effect on a community.
  - Disturbances can create opportunities for species that have not previously occupied habitat in a community.
  - Small-scale disturbances can enhance environmental patchiness and thus maintain species diversity in a community.
- The **intermediate disturbance hypothesis** suggest that moderate levels of disturbance can create conditions that foster greater species diversity than low or high levels of disturbance.
- Frequent small-scale disturbances may prevent a large-scale disturbance.
- Increasing evidence suggests that some amount of nonequilibrium resulting from disturbance is the norm for communities.

Humans are the most widespread agents of 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.
- Human-caused disturbances usually reduce species diversity in 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 may be present.
  - Next, mosses and lichens colonize 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, while the soil is left intact.
  - Herbaceous species grow first, from wind-blown 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* establishment of later species.
  3. Early species may *tolerate* later species but neither hinder nor help their colonization.

Concept 53.4 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 were more abundant and varied in the tropics.
  - They also noted that small or remote islands have fewer species than large islands or those near continents.
- 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 much larger numbers of species of organisms than do temperate and polar regions.
- What causes these gradients?
  - The two key factors are probably 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 plans.
    - *Actual evapotranspiration,* determined by the amount of solar radiation, temperature, and water availability, is much higher in hot areas with abundant rainfall than in areas with low temperatures or precipitation.

- *Potential evapotranspiration,* a measure of energy availability, is determined by the amount of 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 allows 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.
- Imagine a newly formed oceanic island that receives colonizing species from a distant mainland.
- Two factors will determine the number of species that eventually inhabit the island:
  1. The rate at which new species immigrate to the island.
  2. The rate at which species become extinct on the island.
- Two physical features of the island affect immigration and extinction rates:
  1. Its size.
  2. Its distance from the mainland.
- Small islands have lower immigration rates because potential colonizers are less likely to happen upon 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 will have a higher immigration rate than islands that are farther away.
- Arriving colonists of a particular species will reduce the chance that the species will go extinct.
- At any given time, an island's immigration and extinction rates are also affected by the number of species already present.
  - As the number of species increases, any individual reaching the island is less likely to represent a new species.
  - As more species are present, extinction rates increase because of the greater likelihood of competitive exclusion.

- The hypothesis 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 Galapagos, support these predictions.
- The island equilibrium model has been attacked as an oversimplification.
  - Over longer periods, abiotic disturbances such as storms, adaptive evolutionary changes, and speciation may alter species composition and community structure on islands.

Concept 53.5 Contrasting views of community structure are the subject of continuing debate

- The **integrated hypothesis** of community structure depicts a community as an assemblage of closely linked species locked into association by mandatory biotic interactions.
  - The community functions as an integrated unit, as a superorganism.
- The **individualistic hypothesis** of community structure depicts a community as a chance assemblage of species found in the same area because they happen to have similar abiotic requirements for rainfall, temperature, or soil type.
- These two very different hypotheses suggest different priorities in studying biological communities.
  - The integrated hypothesis emphasizes assemblages of species as the essential units for understanding the interactions and distributions of species.
  - The individualistic hypothesis emphasizes single species.
- The hypotheses make contrasting predictions about how plant species should be distributed along an environmental gradient.
  - The integrated hypothesis predicts that species should be clustered into discrete communities with noticeable boundaries because the presence or absence of a particular species is largely governed by the presence or absence of other species.
  - The individualistic hypothesis predicts that communities should generally lack discrete geographic boundaries because each species has an independent, individualistic, distribution along the environmental gradient.
- In most cases where there are broad regions characterized by gradients of environmental variation, the composition of plant communities does seem to change continuously, with each species more or less independently distributed.

The debate continues with the rivet and redundancy models.

- The individualistic hypothesis is generally accepted by plant ecologists.
- Further debate arises when these ideas are applied to animals.
- American ecologists Anne and Paul Ehrlich proposed the **rivet model** of communities.
- This hypothesis is a reincarnation of the interactive model and suggests that most animal species are associated with particular other species in the community.
  - Reducing or increasing the abundance of one species in a community will affect many other species.

- Australian ecologist Brian Walker's **redundancy model** proposes that most animal species in a community are not closely associated with one another.
  - Species operate independently, and an increase or decrease in one species in a community has little effect on other species.
  - In this sense, species in a community are redundant.
  - If a predator disappears, another predatory species will take its place as a consumer of specific prey.
- The rivet and redundancy models represent extremes; most communities have some features of each model.
  - We still do not have enough information to answer the fundamental questions raised by these models: Are communities loose associations of species or highly integrated units?
  - To fully assess these models, we need to study how species interact in communities and how tight these interactions are.