

Community Ecology

I. Species Interactions

A. Commensalism

1. Definition: Competition is a +/0 interaction.
2. Example: Some birds follow moving army ants on the forest floor. As the ants march along the forest floor, hunting insects and small vertebrates, the birds follow and pick off individuals that fly or jump out of the way of the ants. (Fig. 53.1)

B. Competition

1. Definition: Competition is a -/- interaction that occurs when individuals use the same resources and when those resources are limited.
2. Example: G. Evelyn Hutchinson proposed that a species' niche could be envisioned by plotting habitat requirements along a series of axes. (Fig. 53.2)
3. The consequences of competition—theory
 - a. The principle of competitive exclusion states that it is not possible for species within the same niche to coexist. But, if the niches do not overlap completely, then the weaker species should be able to retreat into an area of non-overlap, a mechanism called niche differentiation. (Fig. 53.3)
 - b. The fundamental niche is the combination of conditions that the species will occupy in the absence of competitors; its realized niche is that portion of resources used when competition occurs. (Fig. 53.4)
 - c. Mechanisms of competitive exclusion are explained. (Fig. 53.5)
4. The consequences of competition—experimental studies
 - a. Example: Joseph Connell noticed two species of barnacles with interesting distributions on an intertidal rocky shore of Scotland.
 - b. This is one of the first experimental examples of how competition can modify a distribution of a species. In this case, the poorer competitor (*Chthamalus*) is restricted to the upper intertidal zone, which is a more severe habitat. (Fig. 53.6)

C. Consumption

1. Definition: Consumption occurs when one organism eats another.
 - a. Herbivory—when herbivores consume plant tissues.
 - b. Parasitism—when parasite consumes small amounts of tissues from another organism, or host.
 - c. Predation—when a predator kills and consumes most or all of another individual
2. How do prey defend themselves?
 - a. Some species run or hide in response to predators; others sequester or spray toxins or employ weaponry for defense. (Fig. 53.7a)
 - b. Mimicry occurs when one species closely resemble another species. (Fig. 53.7b)
 - c. Müllerian mimicry occurs when harmful species resemble each other. For example, brightly colored wasps resemble each other and by this, predators tend to avoid these colors.
 - d. Batesian mimicry occurs when a harmless species resembles a harmful one.
 - e. Researchers hypothesized that if blue mussels possess inducible defenses against crabs, they should occur in the low-flow area where predation pressure is higher. They found that mussels in the high-predation area had thicker shells. (Fig. 53.8)
3. Are animal predators efficient enough to reduce prey populations?
 - a. Species interactions have a strong impact on the evolution of predator and prey populations.
 - b. A wolf control program in Alaska during the 1970s decreased predator abundance to 55-80% below pre-control density. Concurrently, the population of moose tripled. This observation

suggests that predators reduced this moose population far below the maximum number that the habitat can support.

- c. Hypotheses: A classic case of population cycling—Hares use up all their food when their populations reach high density, starve, and thus induce starvation by lynx—or, lynx populations reach high density in response to increases in hare density. (Fig. 53.10)
 - d. Experiment: Researchers set up a series of 1 km² plots in boreal forest habitats one treatment excluded lynx. (Fig. 53.11)
 - e. In the arctic, tests have shown that hare population is limited by the availability of food as well as by predation, and that food availability and predation intensity interact; thus the combined effect of food and predation is much larger than their impact in isolation.
4. Why don't herbivores eat everything—why is the world green?
- a. Top-down control over herbivores occurs when predation or disease limits herbivore populations.
 - b. Example: After twelve pairs of European rabbits were introduced to Australia in 1859, the population exploded. Similar results have occurred when goats and pigs have escaped from captivity and established large, wild populations in areas that lack their natural predators or diseases.
 - c. In the poor-nutrition hypothesis, the quality of the resources available at the base of the food chain limits herbivore density. More specifically, growth and reproduction of herbivores could be limited by the availability of nitrogen.
 - d. A recent meta-analysis examined 185 studies of how insect herbivores had responded to plant fertilization. In over half of the cases, herbivores showed a significant increase in growth rate or reproduction when the plants that they feed on were fertilized. Based on this result, the researchers concluded that nitrogen limitation is an important factor in a large fraction of plant-herbivore interactions.
 - e. In the plant defense hypothesis, plants produce toxins to repel herbivores.
 - f. Researchers studied interactions between cottonwood trees, beavers, and a leaf beetle called *Chrysomela confluens* in northern Utah. They found that individual cottonwood trees that had resprouted in response to browsing by beavers contained significantly higher concentrations of several defense compounds when compared to individuals of similar size and age that had never been browsed. (Fig. 53.12)
5. Adaptation and arms races
- a. A coevolutionary arms race between parasites and hosts begins when a parasitic species develops a trait that allows it to survive and reproduce in a host. In response, natural selection favors host individuals that are able to defend themselves against the parasite.
 - b. *Plasmodia* are unicellular protists that cause malaria. They have a complex life cycle that includes the mosquito as the main vector.
 - c. Researchers have found a strong association between a certain allele in the major histocompatibility complex (MHC) and protection against malaria. HLA-B53 proteins bind to a particular protein found in sporozoites.
 - d. Researchers have also shown that *Plasmodium* populations in West Africa now have a variety of alleles for the protein recognized by HLA-B53. This suggests that natural selection has favored the evolution of *Plasmodium* strains with weapons to counter HLA-B53. (Fig. 53.13)
6. Can parasites manipulate their hosts?
- a. Example: Snails infected with flukes become attracted to light.
 - b. They are therefore more easily eaten by birds, thus continuing the life cycle of the fluke. (Fig. 53.14)

D. Mutualisms

1. Mutualisms are +/- interactions that involve a wide variety of organisms and rewards. For example, bees visit flowers to harvest nectar and pollen, and the flowers benefit by being fertilized.

2. Examples are the association between fungi and roots, bacteria and certain species of plants, and rancher ants that protect aphids in exchange for sugar. (**Fig. 53.15**)
3. Hypothesis: Ants protect treehoppers.
4. Experiment: Biologists compared growth and survival of treehoppers on plants with and without ants. (**Fig. 53.16**)

II. Community Structure

A. Two Views of Community Dynamics—Clements vs. Gleason

1. Frederick Clements promoted the idea that communities are stable, integrated, and orderly entities.
 - a. Biologically they have a highly predictable composition.
 - b. The diversity and abundance of a species in a particular community will be the same before and after a disturbance.
 - c. Communities develop by passing through a series of predictable stages, culminating in a stable climax community.
 - (1) The nature of any climax community is determined by the area's climate and does not change over time.
 - (2) If some disturbance destroys a climax community, it will reform through repetition of the developmental stages.
2. Henry Gleason contended that communities found in a particular area are neither stable nor predictable.
 - a. Plant and animal communities are ephemeral associations of species that just happen to share similar climatic requirements.
 - b. It is largely a matter of chance whether a similar community develops in the same area after a disturbance occurs.
3. Keystone species: Robert Paine conducted a series of classic experiments on the intertidal Pacific Northwest. (**Fig. 53.17**)
4. Historical data on community structure
 - a. Studies of fossils confirmed that the distribution of species and communities in North America has changed radically since the end of the last Ice Age.
 - b. Groups of species did not change their distributions in close associations.
 - (1) Species tended to change their ranges independently of one another.
 - (2) The composition of plant communities has been dynamic and unpredictable over time rather than static.
 - c. All data supports Gleason's view of communities, contradicting Clements.
5. Experimental tests on community structure
 - a. Researchers studied whether similar communities of animals develop in the plankton of similar ponds. (**Fig. 53.18**)
 - (1) Experiment
 - (a) The researchers constructed 12 identical ponds.
 - (b) Each pond was filled at the same time with water that contained enough chlorine to kill any preexisting organisms.
 - (c) Water was sampled from the ponds repeatedly for one year.
 - (d) Temperature, chemical makeup, and other physical characteristics of the water were measured.
 - (e) The diversity and abundance of animals was determined by examining samples under a microscope.
 - (2) Results
 - (a) A total of 61 species were found in all of the ponds, but individual ponds contained only 31 to 39 species each.

(b) Each pond in the study developed a different assemblage of species, even though they were all identical at the outset.

(3) Conclusions

- (a) Some species are good at dispersing and are likely to colonize most of the habitat (ponds).
- (b) The arrival of competitors and/or predators early in the colonization process greatly affects which species are able to successfully invade later.
- (c) The specific details of community assembly and composition are contingent on many factors and are thus unpredictable.
- (d) These results support Gleason's view that communities are a product of chance and history.

B. Disturbance and Change in Ecological Communities

- 1. Research in community ecology has shifted dramatically over the past 50 years.
 - a. Orderly development of stable climax communities is not studied as much.
 - b. Biologists are interested in documenting how communities change through time and how they respond to disturbance.
 - c. Communities are dynamic entities, not static.
- 2. Disturbance is any event that removes some individuals or biomass from a community.
 - a. It alters light levels, nutrients, unoccupied space, or some other aspect of resource availability.
 - b. Examples: Fires, windstorms, floods, the fall of large-canopy trees, disease, herbivore outbreaks

C. How Often and How Severe Are Disturbances?

- 1. Each community type experiences a characteristic type, frequency, and severity of disturbance.
 - a. This is known as a community's disturbance regime.
 - b. Examples: Fires in boreal forests and tree falls in temperate and tropical forests
- 2. Disturbance patterns profoundly affect the composition of communities.
- 3. Land managers are actively trying to duplicate natural disturbance regimes in many reserves.
- 4. How do researchers determine and document a community's disturbance regime?
 - a. Long-term patterns of disturbance can be inferred from data obtained in a short-term analysis.
 - (1) This extrapolation approach is straightforward to implement.
 - (2) Its major drawback is that disturbances do not occur randomly in either space or time, so it is difficult to avoid errors unless sampling is extensive.
 - b. Reconstructing the history of a particular site
 - (1) Histories of floods, windfalls, and fires were reconstructed by this method.
 - (2) Fire history can be determined using radiocarbon dating, determining the date of death for trees killed by fire, and examining scars left by fire on trees that are still alive.
- 5. Why is it important to understand disturbance regimes?
 - a. Swetnam studied the fire history of giant sequoia groves in California. (Figs. 53.19a, b, and c)
 - (1) Experiment: He obtained samples of cross sections through the bases of trees from different groves.
 - (2) Results
 - (a) He found that 10-15 fires had occurred each century for the past 1500 to 2000 years.
 - (b) Each tree had been burned an average of 64 times.
 - (3) Conclusion: Fires are extremely frequent and of low severity in this community.
 - b. Biologists now set controlled fires or let low-intensity natural fires burn instead of suppressing them immediately.

- c. Studies of disturbance regimes in the Colorado River and in southwestern North America:
 - (1) Inspired land managers to release a huge pulse of water from reservoirs behind dams on the waterway.
 - (2) The flood that resulted was designed to mimic a natural disturbance event because it appears to have beneficially affected the plant and animal communities downstream.
- D. Succession—Development of Communities after Disturbance
1. The recovery and development of communities after a disturbance is known as succession.
 - a. Primary succession occurs when a disturbance removes the soil and its organisms, as well as organisms living above the surface. Examples: *Glaciers, floods, volcanoes, and landslides*
 - b. Secondary succession occurs when a disturbance removes some or all of the organisms from an area, but leaves the soil intact. Examples: *Fire and logging*
 2. A distinct sequence of communities develops as succession proceeds. (**Fig. 53.20**)
 - a. Early successional communities are dominated by species that disperse their seeds long distances, are short lived, and are small.
 - b. Late successional communities are dominated by species that tend to be long lived, large, and good competitors for resources.
 - c. The specific sequence that appears over time in a specific area is called a successional pathway.
 3. Theoretical considerations
 - a. Biologists focus on three factors to predict the outcome of succession in a community:
 - (1) The particular traits of the species involved
 - (2) How species interact
 - (3) Environmental circumstances, such as the size of the area involved and short-term weather conditions
 - b. Species traits are important early in succession.
 - (1) Recently disturbed sites are colonized by plants and animals with good dispersal ability.
 - (2) These pioneering species must be able to withstand harsh environmental conditions.
 - c. Once colonization is under way, the course of succession depends less on how species cope with the abiotic environment and more on how they interact with other species.
 - (1) Different species interactions influence successional pathways in different ways.
 - (2) The presence of one species can inhibit the establishment of another.
 - (3) An early-arriving species might facilitate the arrival of certain later species.
 - d. The pattern and rate of succession depends on the environmental context in which it occurs.
 - (1) Example: Communities that develop after a fire depend on the size of the burned patch and how hot the fire was.
 - (2) Succession is also affected by the particular weather or climate conditions that occur during the process.
 - (3) Variation in weather and climate causes different successional pathways to occur in the same place at different times.
 4. A case history of primary succession—*Glacier Bay, Alaska*
 - a. Extensive glacial regression has provided a great site for studying succession. (**Fig. 53.21a**)
 - b. Fastie found that three distinct successional pathways have occurred here: (**Fig. 53.21b**)
 - (1) Species traits are important in explaining certain details about each pathway.
 - (2) Species interactions are important in all three pathways.
 - (a) One species may facilitate the growth of another.
 - (b) Competition is another important interaction that is involved.
 - (3) Environmental context influenced the succession at all levels and helped determine exactly how the community developed.
 5. Because of all these interrelating factors, the outcome of succession is not entirely predictable.

III. Species Diversity in Ecological Communities

- A. Species diversity is a key feature of biological communities.
- B. Quantifying Diversity
 - 1. It can be a simple count of species present.
 - 2. The measuring process usually involves more complex calculations that incorporate a species' abundance as well as its presence or absence. (**Box 53.1**)
- C. Research on diversity has focused on two questions:
 - 1. Why are some communities more diverse than others?
 - 2. Why is diversity important?
- D. Global Patterns of Species Diversity
 - 1. A latitudinal gradient of species diversity exists for many taxa.
 - a. Species diversity declines as latitude increases. (**Fig. 53.23**)
 - b. Examples: Birds, mammals, fish, reptiles, aquatic and terrestrial invertebrates, orchids, trees
 - c. This pattern is not universal, but is widespread.
 - (1) A few species show a positive relationship between latitude and diversity.
 - (2) Others show no relationship.
 - 2. Hypotheses offered to explain why this latitudinal gradient occurs:
 - a. High productivity in the tropics promotes high diversity.
 - (1) Increased biomass production supports more herbivores, and thus more predators, parasites, and scavengers.
 - (2) This hypothesis is supported by the global-scale correlation between productivity and diversity, but refuted by experimental studies.
 - (3) Productivity alone is not a sufficient explanation for the higher diversity in the tropics.
 - b. Habitats with complex physical structures have more niches than habitats with simple physical structures.
 - (1) This hypothesis was inspired by the impressive physical complexity of tropical forests.
 - (2) This hypothesis explains some aspects of increased species diversity, but does not explain why there are more tree species in the tropics.
 - c. Tropical regions have had more time for speciation to occur.
 - (1) Temperate and arctic latitudes were repeatedly scoured by ice over many years, while tropical forests were not.
 - (2) Tropical forests were dramatically reduced in size by widespread drying trends.
 - (3) Therefore, tropical habitats are also disturbed by climate change, though at a much smaller scale than the higher latitudes.
 - d. Tropical areas experience fewer disturbances than do temperate or subarctic regions.
 - (1) The idea is that species accumulate slowly following a disturbance, so frequent disturbances hold species numbers down.
 - (2) However, researchers proposed that species diversity should be highest at intermediate levels of disturbance.
 - (a) Such communities would contain pioneering species as well as species better adapted to late successional conditions.
 - (b) Recent studies confirm that tree falls and canopy gaps occur as regularly in tropical forests as they do in temperate forests.
 - (c) Occasional fires have been an important source of disturbance in both regions.
 - (d) Small amounts of disturbance can actually increase diversity and benefit communities.
 - 3. There is no simple answer to the question of why some communities are more diverse than others.
- E. The Role of Diversity in Ecological Communities

1. Recent research has focused on whether species diversity affects the stability and productivity of communities.
2. This research focuses on measuring the effect of diversity on two characteristics of communities:
 - a. Resistance—how much a community is affected by a disturbance.
 - b. Resilience—how quickly a community returns to its prior state following a disturbance.
3. Hypotheses offered to explain how species diversity affects resistance and resilience:
 - a. Diversity is positively correlated with stability.
 - (1) Highly diverse communities are more resistant and more resilient.
 - (2) When large numbers of species are present, some are likely to be redundant in their role in the community.
 - (3) Thus, wiping out one or a few species is unlikely to profoundly affect the community as a whole.
 - b. High diversity leads to high productivity.
 - (1) If species differ in the way they use resources, then the total resource base available in a particular habitat will be used more completely.
 - (2) In turn, this will cause productivity to be higher.
4. Researchers tested these two hypotheses in North American prairies.
 - a. Experiment 1
 - (1) Conduct a series of experiments using plants native to the prairies North America.
 - (2) The researchers grew seedlings from 24 species and established 147 study plots.
 - (3) Each plot received a similar number of individuals, but a different number of species.
 - (4) The plants were allowed to grow for one year, and the plots were weeded to remove any invading species.
 - (5) In the second year, they measured productivity by quantifying the area of the plot covered by plants.
 - b. Experiment 2
 - (1) The researchers followed up on a natural drought that hit sites in Minnesota.
 - (2) When the drought ended, they determined if resistance and resilience correlated with the number of species that existed before the disturbance.
 - c. Results
 - (1) Their plant-cover experiments confirmed that more diverse communities are more productive. **(Fig 53.24)**
 - (2) Experiments following the natural drought confirmed that communities with greater species diversity also had higher resistance and resilience. **(Fig. 53.25)**
 - d. Conclusions
 - (1) Species diversity undoubtedly affects how communities function.
 - (2) Communities that are more diverse are more productive, more resistant, and more resilient than are less diverse communities.
 - (3) Why this pattern occurs is not absolutely clear.