needed to sustain the exploited species. Top predators such as humans (or major grazers such as cattle) can easily tip the balance of a competitive equilibrium so that the exploited species is replaced by another species that the predator or grazer may not be prepared to use. In the real world, examples of such shifts are being documented ever more often as human beings strive to become more "efficient" at fishing, hunting, and harvesting plants. This situation poses both a challenge and a danger: *one-species harvest systems and monocultural systems* (such as one-crop agriculture) *are inherently unstable* because, when stressed, they are vulnerable to competition, disease, parasitism, predation, and other negative interactions. Some examples of this general principle are to be found in the fishing industry.

Myers and Worm (2003) evaluated the effects of industrial fishing on fish community biomass and composition for large predatory fishes in four continental-shelf and nine oceanic systems. They estimated that large predatory fish biomass is only about 10 percent of pre-industrial levels. They concluded that the decline of large predators in coastal regions has extended throughout the global ocean, resulting in serious consequences, such as relatively low economic yields. Thus, the reduction of fish biomass to low levels may compromise the sustainability of the fishing industry and will require a global management approach to address its consequences.

The stress of predation or harvest often affects the size of individuals in the exploited populations. Thus, harvesting at the maximum sustained yield level usually reduces the average size of fish, just as maximizing timber yields for volume of wood reduces the size of trees and the quality of the wood. As reiterated many times in this book, a system cannot maximize quality and quantity at the same time. In a classic study, Brooks and Dodson (1965) described how large species of zooplankton are replaced by smaller species when zooplankton-feeding fish are introduced into lakes that formerly lacked such direct predators. In this case, in which the ecosystem is relatively small, both the size and species composition of a whole trophic level may be controlled by one or a few species of predators. The contrast between predator-driven and resource-driven food webs was detailed in Chapter 6.

Amensalism is where one species has a marked negative effect on the other, but there is no detectable reciprocal effect (− 0). Lawton and Hassell (1981) refer to this interaction as *asymmetrical competition*. Amensalism is just one evolutionary step from interactions such as allelopathy (− +).

Classic examples of allelopathy can be cited from the work of C. H. Muller, who studied inhibitors produced by shrubs in the vegetation of the California Chaparral. These investigators have not only examined the chemical nature and physiological action of the inhibitory substances but have also shown that they are important in regulating the composition and dynamics of the community (C. H. Muller et al. 1964, 1968; C. H. Muller 1966, 1969). Figure 7-10 shows how volatile terpenes produced by two species of aromatic shrubs inhibit the growth of herbaceous plants. The volatile toxins (notably cineole and camphor) are produced in the leaves and accumulate in the soil during the dry season to such an extent that when the rainy season comes, the germination and subsequent growth of seedlings is inhibited in a wide belt around each shrub group. Other shrubs produce water-soluble antibiotics of a different chemical nature (such as phenols and alkaloids), which also favor shrub dominance. However, periodic fires, which are an integral part of the ecosystem of the Chaparral, effectively remove the source of the toxins, denaturing those accumulated in the soil and triggering the germination of fire-adapted seeds. Accordingly, fire is followed in the next rainy season by a conspicuous blooming of annuals, which continue to appear each spring until the shrubs grow back and the toxins again be-

Table 7-2 Comparison of apparent and cryptic plants

Apparent plants	*Cryptic plants*
Common	Rare
Woody perennials	Herbaceous annuals
Slow growing (competitive)	Fast growing (fugitive)
Late seral stages	Early seral stages
Certain to be found by herbivores	Protected from herbivores in time and space
Produce expensive antiherbivore defenses (such as tannins)	Produce inexpensive chemical defenses (such as poisons or toxins)
Quantitative defenses constitute effective ecological barriers to herbivores	Qualitative defenses may be broken down by detoxification mechanisms

Source: After Pianka 2000.

Attempts have been made to generalize about the coevolution of herbivores and plant antiherbivore tactics. Feeny (1975), for example, argued that rare or ephemeral plant species are difficult to find and, hence, are protected in time and space. Moreover, he asserted that such *cryptic* plants have evolved a diversity of **qualitative defenses,** such as chemically inexpensive poisons and toxins, that constitute effective evolutionary barriers to herbivory by the herbivores most likely to find cryptic plants. In contrast, Feeny reasoned, abundant or persistent plant species (*apparent* plants) cannot prevent herbivores from finding them either in ecological or evolutionary time. Such apparent species appear to have evolved more expensive **quantitative defenses,** such as leaves high in tannins and antiherbivore defense chemicals, and adaptations such as tough leaves and thorns.

Table 7-2 summarizes the coevolutionary differences between plants with high and low apparency and quantitative versus qualitative defenses. Readings on this topic include D. F. Rhoades and Cates (1976); Futuyma (1976); Futuyma and Slatkin (1983); Palo and Robbins (1991); Gershenzon (1994); and Hunter (2000).

6 Positive Interactions: Commensalism, Cooperation, and Mutualism

Statement

Associations between two populations of species that result in positive effects are exceedingly widespread and probably as important as competition, parasitism, and other negative interactions in determining the function and structure of populations and communities. Positive interactions may be conveniently considered in an evolutionary series as follows:

- *commensalism*—one population benefits;
- *protocooperation*—both populations benefit; and
- *mutualism*—both populations benefit and become completely dependent on each other.

Explanation

Several decades after Darwin, the Russian Prince Pëtr Alekseevich Kropotkin published a book entitled *Mutual Aid: A Factor of Evolution* (Kropotkin 1902). Kropotkin chided Darwin for his overemphasis on natural selection as a bloody battle (Tennyson's "red in tooth and claw" metaphor). He outlined in considerable detail how survival was often enhanced by—or even dependent on—one individual helping another or one species aiding another for mutual benefit.

Kropotkin's writings were influenced by his personal philosophy of peaceful coexistence. Like Mahatma Gandhi and Martin Luther King, Jr., who made their contributions later, he was a firm believer in nonviolent solutions to human conflict. At the time he wrote *Mutual Aid*, he was a political refugee living in England. A large portion of his book is devoted to documenting the importance of cooperation in primitive human societies, rural villages, and labor union guilds as well as among animals (for more information on Kropotkin, see S. J. Gould 1988; Todes 1989).

Lynn Margulis convinced biologists after a long battle that eucaryotes originated through fusion of an archaebacterium with some eubacteria. It is now understood that mitochondria in all eucaryotes and chloroplasts in plants were once independently living procaryotes. They are examples, much like corals and lichens, of how integrating symbionts evolved into mutualistic entities.

In their book *Acquiring Genomes*, Margulis and Sagan (2002) advanced a theory that speciation is not due to random events and neo-Darwinian processes, such as mutation and natural selection acting through competition; rather, they argued, speciation events are caused by interacting symbionts, cooperation, and reticulation of genomes. Their theory questions some of the central tenets of Darwinism. They speculated that Darwin was wrong to emphasize competition and natural selection as the sole forces shaping speciation and evolution; instead, they postulated that cooperation and mutualism drive evolution. This theory promises to become a fertile area of research during the twenty-first century.

Until recently, positive interactions were not subjected to as much quantitative study as negative interactions. One might reasonably assume that negative and positive relations between populations eventually tend to balance one another, and that both are equally important in the evolution of species and in the stabilization of the ecosystem.

Commensalism is a simple type of positive interaction and perhaps represents the first step toward the development of beneficial relations (see Table 7-1). It is especially common between sessile plants and animals on the one hand and mobile organisms on the other. Practically every worm burrow, shellfish, or sponge contains various "uninvited guest" organisms that require the shelter of the host but do neither harm nor good in return. Oysters, for example, sometimes have a small, delicate crab in the mantle cavity. These crabs are usually commensal, although sometimes they overdo their guest status by partaking of the host's tissues. Dales (1957), in his early review of marine commensalism, listed 13 species that live as guests in the burrows of large sea worms (*Erechis*) and burrowing shrimp (*Callianassa* and *Upogebia*). This array of commensal fish, clams, polychaete worms, and crabs lives by snatching surplus or rejected food or waste materials from the host. Many commensals are not host specific, but some apparently are found associated with only one species of host.

It is but a short step from commensalism to a situation in which both organisms gain by an association or interaction of some kind; this relationship is termed **protocooperation.** W. C. Allee (1951) studied and wrote extensively about this subject. He stressed the importance of cooperation and aggregation among species—a principle frequently termed the *Allee principle of aggregation* (discussed in Chapter 6). He believed that cooperation between species is to be found throughout nature. Returning to the sea for an example, crabs and coelenterates often associate with mutual benefit. The coelenterates grow on the backs of the crabs (and are sometimes "planted" there by the crabs), providing camouflage and protection (as coelenterates have stinging cells). In turn, the coelenterates are transported about and obtain particles of food when the crab captures and eats another animal.

In the preceding example, the crab does not absolutely depend on the coelenterate, nor vice versa. A further step in cooperation results when each population becomes completely dependent on the other. Such cases have been termed **mutualism** or **obligate symbiosis.** Often quite diverse kinds of organisms are associated. In fact, instances of mutualism are most likely to develop between organisms with widely different requirements (organisms with similar requirements are more likely to get involved in competition). The most important examples of mutualism develop between autotrophs and heterotrophs, which is not surprising, as these two components of the ecosystem must ultimately achieve some kind of balanced symbiosis. Examples that would be labeled as mutualistic go beyond general community interdependence to the extent that one particular kind of heterotroph becomes completely dependent on a particular kind of autotroph for food, and the latter becomes dependent on the protection, mineral cycling, or other vital functions provided by the heterotroph. The different kinds of partnerships between nitrogen-fixing microorganisms and higher plants were discussed in Chapter 4. Mutualism is also common between microorganisms that can digest cellulose (and other resistant plant residues) and animals that do not have the necessary enzyme systems for this purpose. As previously suggested, mutualism seems to replace parasitism as ecosystems evolve toward maturity, and it seems to be especially important when some aspect of the environment is limiting (such as water or infertile soil).

Examples

Obligate symbiosis between ungulates (such as cattle) and rumen bacteria is a well-studied example of mutualism. The anaerobic nature of the rumen system is inefficient for bacterial growth (only 10 percent of the energy in grass or hay eaten by the cow is assimilated by the bacteria), but the very nature of this inefficiency constitutes the reason that the ruminant can subsist at all on such a substrate as cellulose. The major portion of the residual energy of microbial action consists of fatty acids that are converted from cellulose but are not further degraded. These end products, however, are directly available for assimilation by the ruminant. Accordingly, the partnership is very efficient for the ruminant, because it gets most of the energy in the cellulose, which it could not obtain without the help of the bacteria. In return, of course, the bacteria get a temperature-controlled culture medium.