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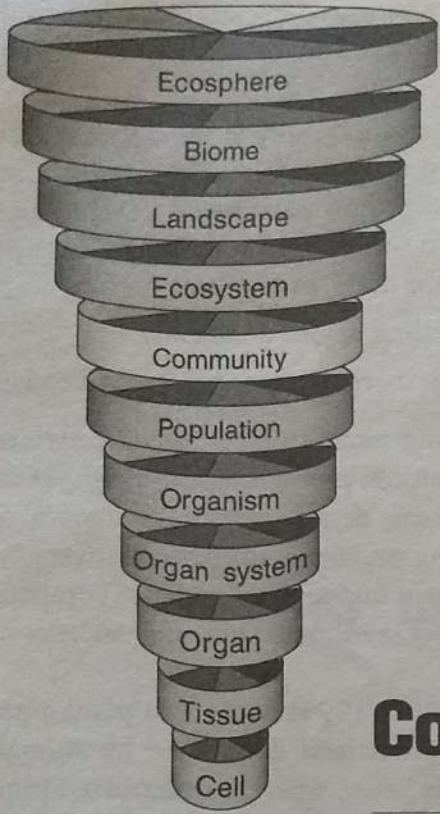

Community Ecology

1 Types of Interaction Between Two Species

Statement

Theoretically, populations of two species may interact in basic ways that correspond to combinations of neutral, positive, and negative (0, +, and −) as follows: 0 0, − −, + +, + 0, − 0, and + −. Three of these combinations (+ +, − −, and + −) are commonly subdivided, resulting in nine important interactions and relationships. The terms applied to these relationships in the ecological literature are as follows (see Table 7-1 and Fig. 7-1):

1. **neutralism**, in which neither population is affected by association with the other;
2. **competition, direct interference type**, in which both populations actively inhibit each other;
3. **competition, resource use type**, in which each population adversely affects the other indirectly in the struggle for resources in short supply;
4. **amensalism**, in which one population is inhibited and the other not affected;
5. **commensalism**, in which one population is benefited, but the other is not affected;
6. **parasitism**; and
7. **predation**, in which one population adversely affects the other by direct attack but nevertheless depends on the other;
8. **protocooperation** (also frequently referred to as *facultative cooperation*), in which both populations benefit by the association but their relations are not obligatory; and
9. **mutualism**, in which the growth and survival of both populations is benefited, and neither can survive under natural conditions without the other.

Three trends in the occurrence of these relationships are especially worthy of emphasis:

- Negative interactions tend to predominate in pioneer communities or in disturbed conditions where *r*-selection counteracts high mortality.
- In the evolution and development of ecosystems (succession), negative interactions tend to be minimized in favor of positive interactions that enhance the survival of the interacting species in mature or crowded communities.
- Recent or new associations are more likely to develop severe negative interactions than are older associations.

Explanation

The nine interactions listed in the Statement are analyzed in terms of a two-species relationship at the community level in Table 7-1, and a coordinate model of these interactions is displayed in Figure 7-1. All these population interactions are likely to occur in any large-scale biotic community, such as a large tract of forest, wetland, or grassland. For a given species pair, the type of interaction may change under different conditions or during successive stages in their life histories. Thus, two species might exhibit parasitism at one time, exhibit commensalism at another, and be completely neutral at still another time. Simplified communities (such as mesocosms) and

Table 7-1

Analysis of two-species population interactions

Type of interaction	*Species 1*	*Species 2*	*General nature of interaction*
Neutralism	0	0	Neither population affects the other
Competition, direct interference type	–	–	Direct inhibition of each species by the other
Competition, resource use type	–	–	Indirect inhibition when common resource is in short supply
Amensalism	–	0	Population 1 inhibited, 2 not affected
Commensalism	+	0	Population 1, the *commensal*, benefits, while 2, the *host*, is not affected
Parasitism	+	–	Population 1, the *parasite*, generally smaller than 2, the *host*
Predation (including herbivory)	+	–	Population 1, the *predator*, generally larger than 2, the *prey*
Protocooperation	+	+	Interaction favorable to both but not obligatory
Mutualism	+	+	Interaction favorable to both and obligatory

Note: 0 indicates no significant interaction; + indicates growth, survival, or other population attribute benefited (positive term added to growth equation); – indicates population growth or other attribute inhibited (negative term added to growth equation).

laboratory experiments allow ecologists to single out and quantitatively study the various interactions. Also, deductive mathematical models derived from such studies permit ecologists to analyze factors not ordinarily separable from the others.

Growth equation models make definitions more precise, clarify thinking, and allow a determination of how factors operate in complex natural situations. If the growth of one population can be described by an equation, such as the logistic equation, the influence of another population may be expressed by a term that modifies the growth of the first population. Various terms can be substituted according to the type of interaction. For example, in the case of competition, the growth rate of each population is equal to the unlimited rate minus its own self-crowding effects (which increase as its population increases) minus the detrimental effects of the competing species, N_2 (which also increase as the numbers of both species, N and N_2, increase), or

$$\frac{dN}{dt} = rN - \left(\frac{r}{K}\right)N^2 - CN_2N \quad \text{or}$$

$$\text{Growth rate} = \text{Unlimited rate} - \text{Self-crowding effects} - \begin{array}{c}\text{Detrimental effects}\\ \text{of the other species,}\end{array}$$

C being a constant reflecting the efficiency of the other species.

This equation will be recognized as the logistic equation (see Chapter 6), except for the addition of the last term, "minus detrimental effects of the other species." There are several possible results for this kind of interaction. If the competitive efficiency, C, is small for both species, so that the interspecific depressing effects are less than the intraspecific (self-limiting) effects, the growth rate and perhaps the final density of both species will be depressed slightly; but both species will probably be able to live together, because the depressing interspecific effects will be less important than the competition within the species. Also, if the species exhibit exponential growth (with self-limiting factors absent from the equation), interspecific competition might provide the leveling-off function missing from the species' own growth form. However, if C is large, the species exerting the largest effect will eliminate its competitor or force it into another habitat. Thus, theoretically, species having similar requirements cannot live together because strong competition will likely develop, causing one of them to be eliminated. These models suggest some of the possibilities; how these possibilities actually work out will be discussed later in this chapter.

When both species of interacting populations have beneficial effects on each other instead of detrimental ones, a *positive* term is added to the growth equations. In such cases, both populations grow and prosper, reaching equilibrium levels that are mutually beneficial. If the beneficial effects of the other population (the positive term in the equation) are necessary for the growth and survival of both populations, the relation is known as *mutualism*. If, on the other hand, the beneficial effects only increase the size or growth rate of the population but are not necessary for growth or survival, the relationship comes under the heading of *protocooperation*. In both protocooperation and mutualism, the outcome is similar; the growth of either population is less or zero without the presence of the other population. When a balance is reached, the two populations pulse together, usually in a definite proportion.

Consideration of population interactions, as shown in Table 7-1 and Figure 7-1, or in terms of the growth equations, avoids the confusion that often results when terms and definitions alone are considered. Thus, the term *symbiosis* is sometimes used in the same sense as *mutualism*. Because **symbiosis** literally means "living together," the word is used in this book in its broad sense, without regard to the exact nature of the relationship. The term *parasitism* and the science of **parasitology** are generally con-

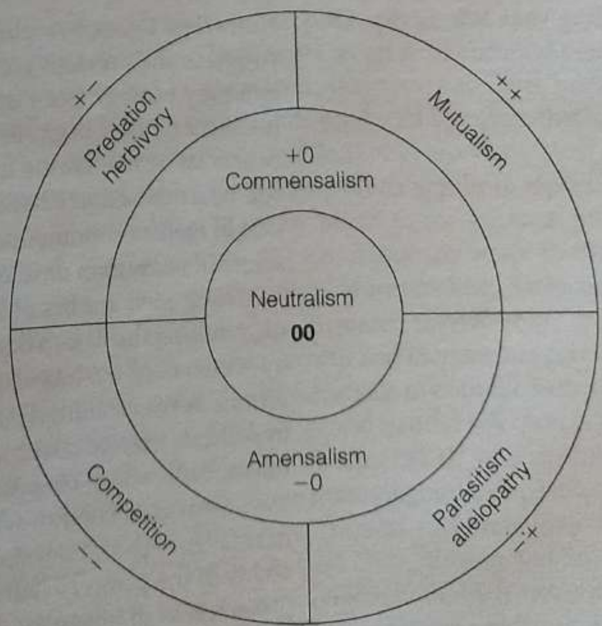

Figure 7-1. Coordinate model of two-species interactions.

sidered to deal with any small organism that lives on or in another organism, regardless of whether its effect is negative, positive, or neutral. Various nouns have been proposed for the same type of interaction, adding to the confusion. When relations are diagrammed, however, there is little doubt about the type of interaction being considered; the word or label then becomes secondary to the mechanism and its result.

Note that the word "harmful" was not used in describing negative interactions. Competition and predation decrease the growth rate of affected populations, but this does not necessarily mean that the interaction is harmful either to long-term survival or by evolutionary considerations. In fact, negative interactions can increase the rate of natural selection, resulting in new adaptations. Predators and parasites often benefit populations that lack self-regulation, because they prevent overpopulation that otherwise might result in self-destruction.

2 Coevolution

Statement

Coevolution is a type of community evolution (an evolutionary interaction among organisms in which the exchange of genetic information among the kinds is minimal or absent). **Coevolution** is the joint evolution of two or more noninterbreeding species that have a close ecological relationship, such as plants and herbivores, large organisms and their microorganism symbionts, or parasites and their hosts. Through reciprocal selective pressures, the evolution of one species in the relationship depends in part on the evolution of the other.

Explanation

Numerous interactive phenomena occur among sets of interacting species as discussed in the previous section. Indeed, these interactions dominate the field of evolutionary ecology (see Pianka 2000 for a detailed description of this field of study). Interactions that begin as a competitive interaction between species may become beneficial or mutualistic interactions for both species through evolutionary time. As will be discussed in Chapter 8, species interactions appear to become more mutualistic in mature communities and ecosystems compared to young systems in the early stages of ecosystem development.

Using their studies of butterflies and plants as a basis, Ehrlich and Raven (1964) were among the first to outline the theory of coevolution as it is now widely accepted by students of evolutionary biology. This early seminal research focused on interactions between butterflies and the plants on which they feed. Ehrlich and Raven's hypothesis may be stated as follows: plants, through occasional mutations or recombinations, produce chemical compounds not directly related to basic metabolic pathways (that is, related to what is termed *secondary chemistry*) that are not inimical to normal growth and development. Some of these compounds either reduce the palatability of the plants to herbivores or are toxic to herbivores on ingestion. A plant thus protected from phytophagous insects would, in a sense, have entered a new adaptive zone. Evolutionary radiation of these plants might follow, and what began as a chance