

### THE IMPORTANCE OF THE MECHANISMS OF INTERSPECIFIC COMPETITION

Schoener (1983, 1985) and Connell (1983*a*) summarized more than 150 field experiments designed to test for the existence of interspecific competition in natural communities. Although there are differences between their reviews (Schoener 1985), both concluded that interspecific competition was detectable in more than half of the species studied. That more than 150 such field experiments were available for review is a testimonial to the dissatisfaction with which ecologists have viewed traditional studies that attempted to infer the presence of competition using correlational or distributional data.

The design of the experiments, though, is a memorial to the extent to which the often-criticized Lotka-Volterra competition equations still pervade ecological thought. The experiments used a nonmechanistic, Lotka-Volterra-based, phenomenological definition of competition: two species compete when an increase in the density of one species leads to a decrease in the density of the other, and vice versa. Schoener stated, "I consider an interspecific competition experiment to be a manipulation of the abundances of one or more hypothetically competing species" (1983, p. 241). I question whether such experiments actually measure the "importance" of interspecific competition in nature and whether the Lotka-Volterra definition of competition, which is based on the interactions of a single pair of species, applies to species living in multispecies communities. I raise these questions and direct the comments that follow not as criticisms of Schoener's or Connell's reviews, but from concern about the pattern of thought in ecology that generated the more than 150 papers available for review.

In a natural community, one species may influence a second species both directly and indirectly (Levine 1976; Lawlor 1979; Vandermeer 1980). For instance, Lawlor (1979) considered a theoretical case of four warbler species whose only direct interactions were competitive. Lawlor used MacArthur's (1968) field data on competition coefficients for these four species and had the warblers compete according to the Lotka-Volterra equations. In the four-species community, however, one of the species pairs behaved, in total, as if they were mutualists, and two other pairs behaved, in total, as if they barely interacted, even though they were strong direct competitors. This marked difference between the direct process of pairwise interspecific competition and the total effect that one species has on another in a multispecies community is caused by indirect effects. As soon as there are more than two interacting species, one species can potentially influence a second species both directly and indirectly through another species.

Bender et al. (1984) defined a *press* experiment as one in which the density of one species is changed to and held at a new level (often zero) and the resulting equilibrium densities of all other species are measured. They showed, for the idealized case of Lotka-Volterra competition, that the density of every species must be manipulated in separate, replicated experiments, in order to use press experiments to determine the actual direct effect of one species on another. Thus, for a community with 40 species, 40 different press experiments, each of them replicated well enough to allow statistically valid detection of the changes in densities of all other species, would be required just to describe the direct effects of species on each other. They stated that "In practice, no community ecologist can measure the density of every potentially interacting species in a community, yet once some species are neglected and others lumped into composite categories, there is a real danger that indirect effects can confuse and confound the interpretation of the results" (Bender et al. 1984, p. 11). They discussed a second type of density-manipulation experiment, a *pulse* experiment, in which the immediate effect of a transient change in the density of one species on the population densities and growth rates of all other species is determined. Assuming that species follow the Lotka-Volterra equations, only two replicated pulse experiments are required to determine whether two species are competing. Bender et al. (1984) stressed, however, that the apparent ease with which pulse experiments can demonstrate competition hinges on the assumption that the interactions are actually governed by direct density effects with no time lags, as assumed in the Lotka-Volterra model. For instance, pulse experiments would indicate that there was no interaction between two species that competed for the same limiting resources if resource availabilities changed slowly in response to density manipulation. Pulse experiments thus would be an unacceptable way to study resource competition.

As they have been performed and interpreted to date, field manipulations of population densities are not capable of indicating what the actual process of interspecific interaction might be. The density-based, phenomenological definition of pairwise competition applies to interactions between two species in the absence of any other species. It is logically incorrect to use this definition in multispecies communities. The existence of indirect effects means that there need be no simple relation between the actual mechanism of pairwise interspecific interaction and the total effect that one species has on another. Recognizing this problem, Connell (1983a,b) suggested that we need to manipulate simultaneously the densities of many different species. However, the work of Bender et al. (1984) demonstrated that any attempt to simplify—to ignore just a single species—can cause press experiments to give results that are not indicative of the actual direct interactions among species. Pulse experiments can, in theory, overcome this problem, but may not be capable of detecting many cases of exploitative competition (Bender et al. 1984). Does this mean that we must manipulate the density of every species in a community in order to learn what the direct effects of one species are on another? Must plant ecologists manipulate the densities of every species of plant, every soil bacterium, every fungus, every nematode, every herbivore, etc., and establish the effects of each manipulation on the population densities and/or growth rates of all

other species, just to determine whether plants are actually competing with each other? Such an approach is so complex as to be ridiculous; yet that is the approach that a purely phenomenological perspective seems to require.

The more than 150 density-manipulation experiments performed have determined the total effect of one species on another, not the mechanism of interaction. Perhaps the cases that Schoener and Connell listed as indicative of competition actually were. Perhaps, as the work of Lawlor suggests, a much greater proportion of species were competing directly, but the effect of their direct competition was masked by indirect effects. Perhaps many interactions were just apparent competition caused by shared predators (Holt 1977). Unfortunately, even after more than 150 field manipulations of population densities, we are still uncertain.

This uncertainty can be directly attributed to the paucity of experimental field studies of the mechanisms of competition. For over 60 years, most ecological thought about competition has been influenced by a model that summarizes the effect of competition on population densities but ignores the underlying mechanisms. Ecology textbooks present the Lotka-Volterra model, or its cousin, the deWit replacement model, as *the* models of competition. One text even claims that the Lotka-Volterra model is a model of resource competition (Krebs 1985). With a few notable exceptions (reviewed in Schoener 1986), most ecologists have studied competition by asking if an increase in the density of one species leads to a decrease in the density of another, without asking how this might occur. This preoccupation with the phenomenon of competition, rather than with the underlying mechanisms, has occurred despite the frequent recognition that direct antagonistic interactions or direct density effects are rarely the proximate, much less the ultimate, cause of competition (e.g., Connell 1983a, p. 662; Schoener 1983, 1986).

The appeal of the phenomenological approach to competition has been its apparent simplicity and generality: a single model, the Lotka-Volterra competition equations, can approximately describe the phenomenon of competition, whereas each distinct mechanism of competition requires its own model. Once applied to multispecies communities, however, the phenomenological approach becomes extremely cumbersome (Bender et al. 1984). There is an equally simple and possibly more general way to study interspecific interactions that may ultimately allow us to construct predictive models of natural communities; and that is to study the actual mechanisms of interaction. I define a study of competition as *mechanistic* if it includes both the direct process by which competition occurs and information on the physiology, morphology, and/or behavior of individual species or functional groups relevant to that direct process. Thus, if species compete for resources, resource levels would be explicitly considered, just as the levels of inhibitory chemicals would be explicitly included in an allelopathic interaction.

A major goal of the mechanistic approach is to use information on the physiology, morphology, and/or behavior of individual species to predict the outcome of pairwise or multispecies interactions. Schoener (1986) reviewed several studies that have accomplished this. The potential ability to predict the outcome of competition before ever observing the competitive interactions separates mechanistic approaches from phenomenological approaches. Although mechanistic approaches were used initially as a means for estimating competition coefficients

(MacArthur 1972), I view the mechanistic approach as an independent endeavor that loses its power as soon as its information is reduced to the level of Lotka-Volterra coefficients.

A mechanistic approach to competition is potentially powerful because of the wide variety of patterns that it can predict. Each prediction provides an opportunity to test the approach. Direct experimental tests of the mechanisms of competition can be complex, and any single field experiment can always be subject to alternative interpretations. However, knowledge of the mechanisms of competition can be used to make many separate, testable predictions about natural patterns and experimental responses in natural or artificial communities. For instance, a mechanistic approach to resource competition predicts how foraging and life history traits should change with resource availability (Rapport 1971; Covich 1972), how species should be separated along natural or experimental resource gradients, what their dynamics should be during succession or after other perturbations, the dependence of species diversity on resource availability and spatial heterogeneity, and the dynamics and outcome of competition among pairs of species competing under controlled conditions (Tilman 1977, 1982, 1985). All such predictions are interdependent. Observation of any one element can constrain patterns that can be seen in other elements and still be consistent with the hypothesized mechanisms.

For species to coexist stably, there must be trade-offs in their physiological, morphological, or behavioral traits. If, during speciation, there were a few major axes along which species differentiated, then a few mechanisms could explain much of the pattern that we see in nature. For each species, knowledge of the aspects of its behavior, morphology, and/or physiology that are relevant to these mechanisms might allow prediction of its responses to a variety of other species and habitats. If this is true, mechanistic approaches may prove to be simpler, more general, and more predictive than phenomenological approaches.

Interspecific competition is often regarded as being caused by mutual exploitation of limiting resources (resource consumption, including light interception by plants and space occupancy by space-limited sessile organisms), by direct density effects (territoriality and nonterritorial fighting), by the production of toxins, and by various combinations of these mechanisms. As stressed by Roughgarden (1983), there is no single approach that can be used to detect and quantify these mechanisms, or any other mechanisms, in nature. A study of competition requires a multifaceted approach that is both observational and experimental. It should include experimental manipulations that are designed to test for the presence of specific mechanisms of competition. Experiments designed to determine which resources, if any, are limiting would be a critical part of the approach, as would density-manipulation experiments designed to test for direct density effects. Chemicals released by one species could be applied to other species to determine whether they function in an allelopathic manner. Once the mechanisms of interspecific competition have been determined, information on relevant aspects of the behavior, physiology, and/or morphology of the major species could be used to make a series of testable predictions about correlations that should be observed in nature and about the expected responses of these communities to

various manipulations. An approach that started by looking at interactions on two trophic levels (e.g., consumers and their resources) could be expanded, as needed, to include more trophic levels. Such multi-trophic-level approaches could directly include the processes that lead to the indirect effects of phenomenological approaches.

As ecology has developed as a science, it has changed from being highly descriptive to being increasingly experimental and theoretical. This transition represents a strong desire by ecologists to understand the processes that cause the patterns we see in nature. We can greatly increase the rate at which we gain this understanding if we focus on the mechanisms of interspecific interaction, and design experimental, observational, and theoretical protocols to test for the actions of these mechanisms. Experiments that concentrate on the phenomenon of interspecific interactions, but ignore the underlying mechanisms, are difficult to interpret and thus are of limited usefulness. However, studies of the mechanisms of interactions among species can be generalized to a wide variety of situations and can be easily combined with studies of other mechanisms that field studies indicate are important.

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## LITERATURE CITED

- Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* 65:1-13.
- Connell, J. H. 1983a. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* 122:661-696.
- . 1983b. Interpreting the results of field experiments: effects of indirect interactions. *Oikos* 41:290-291.
- Covich, A. 1972. Ecological economics of seed consumption by *Peromyscus*—a graphical model of resource substitution. *Trans. Conn. Acad. Arts Sci.* 44:71-93.
- Holt, R. D. 1977. Predation, apparent competition and the structure of prey communities. *Theor. Popul. Biol.* 12:197-229.
- Krebs, C. J. 1985. *Ecology: the experimental analysis of distribution and abundance*. Harper & Row, New York.
- Lawlor, L. R. 1979. Direct and indirect effects of *n*-species competition. *Oecologia (Berl.)* 43:355-364.
- Levine, S. H. 1976. Competitive interactions in ecosystems. *Am. Nat.* 110:903-910.
- MacArthur, R. H. 1968. The theory of the niche. Pages 159-176 in R. C. Lewontin, ed. *Population biology and evolution*. Syracuse University Press, Syracuse, N.Y.
- . 1972. *Geographical ecology*. Harper & Row, New York.
- Rapport, D. J. 1971. An optimization model of food selection. *Am. Nat.* 105:575-578.
- Roughgarden, J. 1983. Competition and theory in community ecology. *Am. Nat.* 122:583-601.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *Am. Nat.* 122:240-285.
- . 1985. Some comments on Connell's and my reviews of field experiments on interspecific competition. *Am. Nat.* 125:730-740, 126:300-301.
- . 1986. Mechanistic approaches to community ecology: a new reductionism? *Am. Zool.* 26:81-106.

- Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology* 58:338-348.
- . 1982. Resource competition and community structure. Princeton University Press, Princeton, N.J.
- . 1985. The resource-ratio hypothesis of plant succession. *Am. Nat.* 125:827-852.
- Vandermeer, J. H. 1980. Indirect mutualism: variations on a theme by Stephen Levine. *Am. Nat.* 116:441-448.

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