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Challenges to community theory

Introduction

Community ecology is a subject in ferment. After a decade or more of virtually universal acceptance, community theory based on interspecific competition and niche partitioning is under challenge from several directions. The so-called null models have received the most attention and have drawn the most vigorous responses from proponents of the conventional theories of community evolution and their biogeographic corollaries. Null models are not the oldest challenge to community theory. All forms of community theory depend on the importance of interspecific interactions, and these in turn cannot be important without a negative relationship between the density of a population and the rate of increase in its numbers. Now, whereas the promulgators of null models argue that interspecific interactions, especially the kind used commonly in community theory, remain to be demonstrated, their arguments are quite different from those of the proponents of density-independent factors as the dominant determinants of the abundance of organisms. One could say that those who argue in favor of density-independent factors would automatically support null models, but that proponents of null models do not necessarily agree with the density-independent school, because they do not deny the importance of interspecific interactions.

In this chapter, I describe a number of models in community ecology, with some of their evolutionary correlates. Mathematical models have been used extensively in ecology. They have the great merit of requiring both the creator and the user to think clearly and to be precise as to the meaning of the implications of the terms used. It is important to understand the assumptions that were made in constructing the models. The challenges in the title of the chapter come from pointing out unsatisfactory assumptions, from field experiments, the results of which refute the validity of one or more models, and from arguments that confirmation of their validity is based on poor application of the scientific method. The criticisms are offered in a constructive spirit and in the hope that theoretical community ecology of the future will take into

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account the results of the large number of experiments and will be such that specific experimental tests of the principles can be devised.

It is beyond the scope of this book to cover the field completely, and attention is centered on those aspects of community theory that lend themselves to testing experimentally. Salamander communities have been shown to provide excellent material for these tests, and experiments involving them will be described in detail in later chapters. More complete mathematical statements of community theory can be found in Roughgarden (1979), May (1981a), Vandermeer (1981a), and Pimm (1982).

Descriptive models

The first quantitative models of natural communities were mathematical descriptions of the relative abundances of species (Fisher, Corbet, & Williams 1943; Preston 1948, 1962a,b). These models proposed no mechanisms to account for the observed frequency distributions, and for some communities it was shown that the constants varied with the inclusiveness of a sample from the community (Hairston & Byers 1954). These patterns continue to attract some attention (Sugihara 1980; May 1981b), but since the appearance of truly mechanistic models, most ecologists have ignored them.

MacArthur (1957, 1960) proposed the first models that started from biological premises. In his "broken-stick" models of animal communities, he suggested that a limiting resource could be thought of as being divided up among species in several different ways, and he proposed that a choice among the models could be made by comparing them with observed species abundance distributions. The approach attracted much attention (e.g., King 1964), but some predictions were found not to be upheld (Hairston 1959), and the mathematical development of one of the models was incorrect (Pielou & Arnason 1966; Vandermeer & MacArthur 1966). This caused MacArthur (1966) to abandon the whole approach, although it continues to appeal to some ecologists (e.g., Bush & Holmes 1983).

The niche-preemption model, analogous to the broken-stick models (Whittaker 1965), involves similar biological premises, but different mathematical relationships.

Mechanistic models

The development of current theories of community composition began with the papers of MacArthur and Levins (1964, 1967). The approach was through the familiar Lotka–Volterra equations describing competition between two species. The equations are themselves extensions of the logistic equation for population growth. As with any mathematical model of a biological process, the equations contain certain assumptions. Some of the assumptions are biological; others are within the mathematics. If the mathematical manipulations involved in the construction of a model have been properly carried out, the conclusions reached from the application of the model are dependent on the assumptions. It is therefore essential that the assumptions be identified, and evidence of their validity be produced, before the conclusions can be accepted.

I show in later chapters that salamanders meet some of the important assumptions better than most other kinds of organisms, and then I describe the use of these animals in testing models of community organization, including well-known null models.

The assumptions of the logistic model of population growth have been discussed in detail by Smith (1952), Slobodkin (1953, 1962), and Andrewartha and Birch (1954). They are carried over into the Lotka–Volterra equations for interspecific competition and into the community models, except where the latter have been explicitly modified to alter particular assumptions. It is well to recall them. The equation is

$$dN/dt = rN(K - N)/K \qquad (1.1)$$

where r is the intrinsic rate of natural increase, N is the number of individuals present, and K is the maximum number that can be supported by the specified environment. The model assumes that all individuals have the same impact on the population growth rate per individual, $dN/N\,dt$, regardless of age, sex, or population density. The growth rate per individual declines in linear manner from rate r when N approaches zero to a rate of zero when N reaches K. The equation is valid only when the population starts at the stable age distribution: that condition in which all age classes are increasing at the same rate, and in which each age class is represented in the same proportion at successive times. If K is determined by a consumable, renewable resource, that resource is assumed to be renewed at a constant rate. If it is set by some fixed resource, such as space, the assumption of equality of effects by different individuals is unlikely to be correct for different densities.

Every ecologist can provide objections to each of the assumptions, but the equation and the models using it as a starting point continue to be used, sometimes with claims of validation in various observational and experimental situations. A widely quoted example is the yeast culture to which Pearl (1925, p. 10) applied the logistic equation, despite Smith's analysis (1952) showing that several of the assumptions were not met in the culture. In the general enthusiasm for elegant mathematical models – called "physics envy" by Cohen (1971) – these important and largely unrealistic assumptions have been overlooked, ignored, or glossed over by a large number of ecologists.

The Lotka–Volterra model of interspecific competition considers two or more species by modifying the logistic equation with terms that allow individuals of all other species to have effects on the population growth rate for each species in the competing group:

$$dN_i/dt = r_iN_i(K_i - N_i - \sum\alpha_{ij}N_j)/K_i \qquad (1.2)$$

where α_{ij} (the competition coefficient) is the effect of an individual of species j on the population growth rate of species i, relative to the effect of an individual of species i on its own population growth rate, and the other terms are as in the logistic equation. The competition coefficient is constant for all densities of all species, and the effect of adding an individual of any of the species is instantaneous; that is, time lags are assumed to be negligible. The analyses begin with the further assumption that the populations are in equilibrium, and therefore dN_i/dt is zero. This assumption collapses the equation to

$$K_i = N_i + \sum\alpha_{ij}N_j \qquad (1.3)$$

and r_i does not need to be estimated in order to specify the relationships numerically. If either K_i or α_{ij} can be estimated, the other can be found.

Plainly, the most direct method would be to remove members of species j and observe an increase in the number of species i. The ratio of the number of i added to the number of j removed is α_{ij}. This approach measures the effect of one species on the other. It does not detect the nature of the interaction, whether it be competition for some consumable resource, competition for a fixed resource, or interference with the ability of species i to obtain a critical resource, or, in some cases, whether the interaction is competition or predation (Hairston 1980a, 1986). Moreover, it is "labor-intensive, time-consuming and expensive" (Rosenzweig et al. 1985, p. 194).

Not surprisingly, many ecologists have turned to indirect methods to estimate the coefficients (MacArthur & Levins 1967; Schoener 1974b; Hallett & Pimm 1979). MacArthur and Levins showed mathematically the conditions necessary for a third species to invade a habitat occupied by two species, when all three are dependent on overlapping parts of a single resource. The conditions concern the amount by which the demands of each species overlap the demands of its competitor(s), taking into consideration the variance in use of a range of the resource by each. This "limiting similarity," then, will determine the number of species that can coexist and hence will determine the

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structure of the community. It depends heavily on the assumption that overlap is *the* measure of interspecific competition, and hence represents α_{ij}. The original MacArthur–Levins approach was to estimate the overlapping proportion of use of the assumed limiting resource by each of two species. The product of the overlapping proportions, divided by the square of the proportion of the first species' use of the resource, was equated with the competition coefficient:

$$\alpha_{ij} = \sum p_{ih} p_{jh} / \sum p_{ih^2} \tag{1.4}$$

Schoener (1974b) considered the necessity of taking into account the renewable nature of many resources and the fact that their equilibrium densities in the environment may be different. He modified the original appealingly simple formula accordingly:

$$\alpha_{ij} = \left(\frac{T_j}{T_i}\right) \left[\frac{\sum_{k=1}^{m} (d_{ik}/f_k)\,(d_{jk}/f_k)\,(b_{ik}K_k/r_k)}{\sum_{k=1}^{m} (d_{ik}/f_k)^2\,(b_{ik}K_k/r_k)} \right] \tag{1.5}$$

T_i is the total number of resource items utilized per unit time by competitor i; d_{ik} is the frequency of resource k in the diet of i; f_k is the frequency of resource k in the environment; b_k is the net energy per item of resource k extractable by an individual of competitor i; r_k is the intrinsic rate of increase of resource k; K_k is the carrying capacity of the environment for resource k in the absence of predation; and m is the total number of different resources. Schoener suggested some simplifying reductions, but admitted the formidable practical problems. Indeed, one could characterize any attempt to compute the competition coefficients as labor-intensive, time-consuming, and expensive. A notable example is that of Spiller (1986), who obtained values for all of the terms except for the carrying capacities and intrinsic rates of increase of the resource items. His calculated values of the competition coefficients were "qualitatively consistent" with experimentally determined effects of competition on spider food-consumption rates.

Hallett and Pimm (1979), following Schoener (1974c), proposed to estimate the coefficients of competition between two species by comparing their respective densities in a large number of habitats. The data would then be used by assuming the equilibrium condition for the two-species Lotka–Volterra equation

$$N_{1h} = K_1 - \alpha_{12} N_{2h} \tag{1.6}$$

as a regression equation with N_{1h} as the dependent variable, and K and α as the regression coefficients. In order to allow for differential habitat selection by the two species, they proposed a more elaborate regression using the components of the different habitats as additional partial regression coefficients. This method obviously carries all of the assumptions in the Lotka–Volterra equations. Moreover, as Schoener recognized, it is assumed that the competition coefficients are constant over all of the habitats. There is also the practical problem of making a sufficient number of density estimates in different habitats, and assessing independently the effect of each habitat on the selection by each species.

There have been at least two tests of the validity of the Hallett–Pimm method of estimating competition coefficients. The first can be described as inadvertent. Hallett (1982) used the method on guilds of desert rodents. He found statistically significant negative coefficients within the *Perognathus–Peromyscus* guild, but not within the *Dipodomys* guild, and he also found no significant negative coefficients between these two guilds. Meanwhile, a different approach to competition in this community had recently been undertaken by Munger and Brown (1981), apparently too late to be included in Hallett's discussion. They constructed fences around four plots each 50 × 50 m. In these fences, they made holes 1.9 cm in diameter – large enough to allow passage of small granivorous and small omnivorous rodents. The granivores present included two species that were investigated by Hallett (*Perognathus penicillatus* and *Peromyscus maniculatus*), plus an additional species of *Perognathus* and *Peromyscus eremicus* (which they classified as an omnivore, though it had been placed in the same guild as the others by Hallett). The fence excluded the three species of *Dipodomys*, which were removed by trapping. Two of the species of *Dipodomys* were the ones investigated by Hallett. Control plots were also fenced, but the holes were 6.5 cm in diameter – large enough to allow passage of *Dipodomys*. The results were unequivocal. Exclusion of *Dipodomys* led to a statistically significant increase in the abundance of the small granivores, but not of the omnivores. Thus, the results of the direct experiment contradicted the indirect regression method.

The second test of the Hallett–Pimm method was intentional. Rosenzweig and associates (1985) trapped desert rodents in seven sites in arid parts of Israel. After exhaustive statistical analysis of their data, they concluded that the results were too inconsistent to be relied on for estimation of coefficients of competition. The paper has aroused a controversy, with Pimm (1985) and Schoener (1985a) arguing that the consistency among methods is better than admitted by Rosenzweig and associates. It seems unlikely that the matter will be settled without satisfactory simultaneous experiments and regression analyses on the same species in the same areas.

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The use of any of these indirect methods requires acceptance of the assumption that competition is taking place with no more evidence than common occurrence and the use of some resource in common. Because the resource can be habitat, common occurrence plus the suspicion that the species might be competing are the only requirements. The methods are popular for the very reason that the assumption gives the appearance of relieving the investigator of the necessity of demonstrating that the species are competing. Attempts to validate the assumption are not always successful, especially when done in a noncircular way, as by a field experiment. The most convincing experiments on niche partitioning as a result of competition have been those of Werner (1977) and Werner and Hall (1976, 1977, 1979). In a series of experiments with three species of sunfish, they showed that interspecific crowding resulted in a shift of *Lepomis macrochirus* from feeding in the pond-edge vegetation to feeding in open water, and of *L. gibbosus* from feeding in the vegetation to feeding on bottom-living prey. *Lepomis cyanellus* continued to feed in the vegetation. It was shown to be a better competitor there than *L. macrochirus*. Despite a lack of replication and problems of different densities in one experiment, this work represents the best experimental evidence for an effect of interspecific competition in causing niche partitioning.

Competition within guilds

The foregoing comments do not relate to experiments in which interspecific competition has been found. They have been the subjects of two recent reviews (Connell 1983; Schoener 1983). There is little doubt that interspecific competition is widespread in nature. The question being addressed here is the extent to which niche partitioning has been demonstrated experimentally.

Several ecological systems have been subjects of less successful experiments. It happens that five such attempts were published within less than two years; none reported confirmation of guildwide competition, and two failed to detect any competition in guilds where it had been expected.

Dunham (1980) carried out experimental removals of two species of lizards in Big Bend National Park, Texas. He obtained positive responses of each to the removal of the other, but only during the two dry years (out of four) of the experiment. He informed me that he observed no response by the other ten species of lizards in the area (Dunham, pers. commun.). Smith (1981) obtained similar results in an experiment on two species of lizards in Arizona. During the first year, which was unusually dry, he observed positive results of removing each of the species, but only on growth and survival of immature animals. There was no effect during the normal second year, nor did two rare

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species respond to the experimental removals. The experiment of Tinkle (1982) gave completely negative results. After nearly four years of close observation of the population histories of three species of lizards in central Arizona, he removed the most abundant and one other for a period of two more years. Based on its natural history in other areas, he expected a specific shift in habitat as a result of the removals. No shift occurred, and there were no other kinds of responses, although abundance, survival, and growth were followed closely. As in the other two experiments, the remaining species in the community showed no effect of the removal of the numerically dominant species.

Wise (1981) carried out removal experiments on darkling beetles (Tenebrionidae) over a period of three years in New Mexico. Five species were "common" in the community. One of them, *Eleodes obscurus*, accounted for more than 50 percent of the adult tenebrionid biomass in the community. Wise removed these adults from three fenced 0.1-ha plots and kept three other plots as controls. There was no increase in the abundance of adults of the other four species of Tenebrionidae during the three years, nor was there any increase in the mean sizes of those adults. He concluded that despite similar omnivorous food habits by the beetles, competition was unimportant in this community.

My test of the assumption of competition between related species was of a guild of seven species of terrestrial salamanders (Hairston 1981, 1984). I selected two areas in the southern Appalachian Mountains for the experiments. The original purpose (Hairston 1973) was to test for competition between the two most abundant species in that habitat (*Plethodon jordani* and *P. glutinosus*). Removal of either of them resulted in a positive response by the other, demonstrating that they were in competition, which was much stronger in the Great Smoky Mountains than in the Balsam Mountains (Hairston 1980a; see Chapter 5).

On the experimental plots there were five other species of Plethodontidae in the Great Smoky Mountains, and four other species in the Balsam Mountains. All of them spend most or all of their adult lives on the forest floor with the two competing species, eat the same kinds of food (insects and other small invertebrates), and use the same kinds of burrows as refuges. Thus, from the standpoint of theoretical community ecology, they qualify as members of the same guild as the competing species. The names and abundances on the control plots are shown in Table 1.1. Removal of either *P. jordani* or *P. glutinosus* had no statistically significant effect (Table 1.2). One of sixteen tests was "significant" at the 5 percent level – close to the proportion expected by random chance. It should be noted that one of these five species

Table 1.1. *Mean number of individuals per plot search*

	Great Smoky Mtns.		Balsam Mtns.	
	Control plots	All plots	Control plots	All plots
Plethodon jordani	27.48		35.36	
P. glutinosus	5.00		4.36	
P. serratus	0.69	0.54	1.12	1.05
Eurycea bislineata	0.80	1.09	0.20	0.18
Desmognathus ochrophaeus	3.19	3.25	0.17	0.25
D. wrighti	0.08	0.08	0.28	0.38

Note: Plethodon jordani and *P. glutinosus* were affected by the manipulations, and their numbers were not comparable to those of the other species, except for the control plots. "*Desmognathus ochrophaeus*" includes *D. imitator* in the Great Smoky Mountains.
Source: Hairston (1981).

Table 1.2. *Mean number seen per plot search*

	P. serratus	*D. wrighti*	*D. ochrophaeus*	*E. bislineata*
Great Smoky Mountains				
Controls	0.69	0.08	3.19	0.80
P. jordani out	0.67	0.07	4.75	1.27
P. glutinosus out	0.65	0.10	3.25	0.90
Balsam Mountains				
Controls	1.12	0.28	0.17	0.20
P. jordani out	1.48	0.40	0.05	0.32
P. glutinosus out	0.97	0.30	0.50[a]	0.08

Note: D. ochrophaeus includes *D. imitator* in the Great Smoky Mountains.
[a] Significantly greater than control ($p < .05$).
Source: Hairston (1981).

(*Plethodon serratus*) is congeneric with the two competing species, and reducing the "guild" to congeners would not solve the problem. It has been suggested (Schoener 1983) that the experiment was not conclusive, because competition between the less abundant species and the others could be of a kind that gave curved zero isoclines (described in a later section), which would require a greater reduction in numbers of *P. jordani* or *P. glutinosus* than was achieved (about 60 percent of the mean of controls). I showed (Hairston 1985) that in the case of *P. serratus*, it would require an extreme curvature of the zero isocline. Such an effect could be obtained only from a

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virtual threshold – a few individuals having the same practical effect as the total. The mechanism of competition of that kind is not easy to visualize, and the evidence is strongly against detectable interspecific competition between the two species that compete with each other and the remaining five species of Plethodontidae.

These examples of tests of the assumption of universality of competition, plus another to be described in detail in Chapter 6, show that ecological differences among coexisting species are insufficient evidence on which to base any broad conclusions. It should be noted that in all five of these studies, there was a priori reason to expect to find competition, and, if anything, there was bias in favor of a positive result. This effect has been discussed by Connell (1983). We need many more experiments, specifically with the designs published in advance, before we can make generalizations about the extent and the nature of interspecific interactions.

The community matrix

As an extension of the ideas about limiting similarity formulated by MacArthur and Levins (1967), Levins (1968) proposed that the competition coefficients among a number of species could be used as the elements of a matrix. This community matrix could be used to make several interesting predictions about the composition of communities, such as the number of species that a particular set of competition coefficients would permit to coexist, and the importance of relative niche breadths.

One study was specifically designed to test an implied prediction of the community matrix. This was Vandermeer's experiment on ciliate protozoans (Vandermeer 1969). He grew each pair of four species together in the laboratory and used the dynamic form of the Lotka–Volterra equations to calculate the competition coefficients. These were in turn used to predict the course of population histories of the four species when they were grown together. Specifically, Vandermeer assumed correctness of the model as far as the two-species systems were concerned. The question to be answered from the four species together was whether or not there were interactions among the species that were not accounted for by the observed competition coefficients. He called these "higher order interactions." They can be thought of as representing either coalitions of two species increasing the effect on a third species or some form of beneficial effect between two species reducing the negative effect of a third. Vandermeer's results were that the two-species competition coefficients, used in the community matrix, gave predictions that were satisfying in correctly representing the trends of the separate populations, but that