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The status of competition theory in ecology

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Current ecological theory on present effects of interspecific competition, as summarized by Roughgarden (1979), has not helped us to understand how nature works. It has generated predictions that are either practically untestable, by virtue of unmeasurable parameters or unrealizable assumptions, or trivially true. Whether or not it has influenced a productive set of investigators of natural systems is debatable, but such influences are not explicit in the writings of most such investigators. On the other hand, the theory has caused a generation of ecologists to waste a monumental amount of time. However, specific investigations, usually experimental, of well-defined field systems have in a gradual and hierarchical way told us quite a bit about how nature works and about the role of interspecific competition among plant and animal populations. These investigations are strongly in the hypothesis-testing tradition, but rather than testing general theory they test specific predictions about specific systems, and they seem to arise as much out of intense curiosity about these systems as out of a desire to find general laws or patterns of nature.

As a group, these investigations suggest that competitive exclusion of one species by another is exceptional and that more frequently species sharing resources either do not affect one another or contrive to coexist with changes less drastic than local extinction. When species do compete with one another, effects are usually moderated by other factors (*e.g.*, weather, predators, pathogens) that keep populations below levels at which exclusion would occur, or else each competitor is favored in a different set of times and/or places and this fact combined with normal individual movements keep all species in the system. Interspecific competition is as likely to be by interference as by exploitation, and is frequently affected by biological idiosyncrasies of the individual species. Chance plays a major role in many potentially competitive interactions, and there is good evidence that many species that do compete with one another do so rarely or intermittently, and at most times their population dynamics are governed by other forces.

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1. Introduction

MacArthur (1972), citing Eddington, accorded theory at least an equal role with fact in helping us to understand ecological populations and communities: "Scientists are perennially aware that it is best not to trust theory until it is confirmed by evidence. It is equally true. . .that it is best not to put too much faith in facts until they have been confirmed by theory." Less contentiously, Haila & Järvinen (1982) similarly suggest that the significance of ecological and other scientific facts is unlikely to be appreciated unless they are gathered in the framework of general theories. I will examine this view with respect to the contention that presently occurring competition is frequently an important force in day-to-day regulation of species' abundances and distributions, but it is important at the outset to dispel the notion that any scientist gathers facts in the absence of theory, or that any philosopher or scientist has advocated that this is how facts should be gathered.

Perhaps the foremost symbol to many persons of rampant, theory-free fact-gathering is Francis Bacon, and the most denigrating epithet that can be hurled at a naturalist is "Baconian." It seems to connote, according to Cannon (1978), "something like the collection of facts, lots of facts, in all sorts of places, and on queer applied subjects; the absence of an analytic theory or of sophisticated mathematical tools; the belief that a hypothesis will emerge somehow from the accumulation of factors; and so forth, and so on." That such an activity is even possible, except perhaps in clinical pathologies, should be cast into doubt by the realization that Bacon himself advocated no such method, but rather something almost diametrically opposite: deduction, generalization, and explicit tests to choose among alternative hypotheses (Platt 1964, Eiseley 1973, Cannon 1978). Gregory (1973) and Gombrich (1973) go so far as to suggest that hypothesis-formation is adaptive and that the human mind has evolved to form perceptual hypotheses from sensory data as a way to deal with the welter of conflicting stimuli that continually besiege us. Although such perceptual hypotheses are usually subconscious, Gregory (1973) shows that they are formally completely analogous to scientific hypotheses. So even if scientists attempted to gather data without any preconceived model of how nature is structured, it is unlikely that they could succeed.

However, I doubt if ecologists, even the most unrepentant field naturalists, ever even attempt to proceed this way. Instead, it seems that they undertake what Pielou (1981) has termed "investigating," as distinct from "modelling." By "investigating," Pielou means direct search for empirical answers to single, clearcut questions about single local populations or communities. Investigating frequently uses experiment and/or statistical tests, and seems to have as a distinctive trait the absence of a general or global model about the importance of various forces that could conceivably structure nature. Pielou (1981) cites a number of examples to contrast "investigating" with "modelling," and I will give a number of others below in discussing their accomplishments.

I will not address the question of how much coevolutionary theory has contributed to an understanding of whether interspecific competition has occurred in the past. Nor will I treat theoretical contributions to understanding whether interspecific competition has constituted a major selective force in the evolutionarily generated patterns of morphology, habitat use, geographic distribution, etc. that we see today. These "ghosts of competition past" (Connell 1980) are exceedingly difficult to exorcise, and in principle it may be that many of them can never be falsified. It is this lack of falsifiability that led Popper (1972, 1976) to suggest that the status of selection-powered evolution as a scientific field is problematic. Whether one demands, with Popper (1963), immediate falsifiability or, with Lakatos (1970), allows a liberal but not indefinite grace period, it is clear that theoretical attempts to demonstrate effects of past interspecific competition have so far yielded very little. A recent review (Arthur 1982) concludes, "Yet in very few instances have such studies been able to conclusively demonstrate that variation observed in a character was a direct consequence of selection resulting from the competitive process." Rosenzweig's theoretical demonstration (1981) that competition-induced patterns of habitat selection may produce a situation in which no competition now occurs only exacerbates an already difficult situation. A related problem for coevolutionary scenarios is that the only data, as opposed to theory, that can support them often, when analyzed statistically, support completely different causal hypotheses as well as they support the coevolutionary scenario (Strong et al. 1979, Pielou 1981, Simberloff 1982a).

Roughgarden (ms. and Roughgarden, Heckel & Fuentes, ms.) and Grant & Schluter (1982) believe that one can gradually construct a coevolutionary case that is so convincing, by virtue of fitting so many facts, that it sweeps away opposing views even if it is not falsifiable. We are here dealing more with a psychological than a logical matter, and there is no doubt that there are certain explanations that virtually all scientists in some fields view as correct even though there is currently no way to attempt to falsify them. Natural selection is such an explanation; though its falsification has not been rigorously attempted (Brady 1979), it seems to provide such a reasonable explanation of such a diversity of patterns that, in the absence of a strong alternative hypothesis, we are very inclined to assume it is the correct explanation. To me, competitively-driven coevolution scenarios do not seem nearly so cogent as natural selection does. I find too many pieces that do not fit and too many assumptions. Most of all, I see a strong, though not necessarily mutually exclusive, competing hypothesis: individual species' adaptations to their physical environment. This competitor seems to me so well-established in so many more instances than coevolution is that I assume it always must be at least partially correct. Since this is a psychological matter I will not argue here in favor of my view on coevolution. Suffice it to say that even when I am less than enthralled by a coevolutionary scenario, I can still find myself very informed by direct investigation adduced in support of it (*e.g.*, Roughgarden et al. 1982, Schluter 1982).

2. The accomplishments of theory

What, then, does current theory predict about the presently occurring effects of interspecific competition? This is difficult to assess. If we were to define "current" as "within the last two decades," my guess is that for virtually every interspecific competitive effect predicted by a theoretician, the opposite effect has been predicted, at least in principle, by some other theoretician (or even the same theoretician). Part of the difficulty, of course, is that models usually contain parameters whose values are to be determined directly for any particular system, and the structure of many models is such that different sets of parameter values lead to qualitatively different predictions. The Lotka-Volterra two-species competition equations, for example, predict survival by species 1 or species 2 or coexistence depending on the values of the competition coefficients and carrying capacities. Another part of the difficulty, apparently, is that there is good theory and bad theory (Levin 1975, Slobodkin 1975, Pielou 1981). According to Roughgarden (ms.) the major problem that ecological theory faces in achieving wider acceptance as a fruitful endeavor is "the set of popular impressions about 'what theory says.' These impressions are always naive and usually incorrect." Presumably, then, to discuss what theory says about present day effects of interspecific competition, my first task is to make sure I am talking about the fair dinkum article — good theory — and my second is to make sure I understand it. A good way to avoid being misled on either account is to use Roughgarden's authoritative textbook (1979).

Roughgarden's treatment of competition theory begins by elucidating the Lotka-Volterra two-species competition equations and concludes that they predict either coexistence or exclusion of one species by another. This prediction seems unexceptionable. As stated above, the prediction depends on parameter values. Roughgarden discusses three applications of these results that he views as successes: laboratory microcosm experiments, studies of resource partitioning and limiting similarity, and studies on zonation.

The laboratory studies of two-species competition by Gause (1934) and Vandermeer (1969), which Roughgarden describes, are so well known that they need not be summarized here. Suffice it to say that the results are in general agreement with the predictions of the Lotka-Volterra model. The values of r_i and K_i ($i = 1, 2$) derived in single-species cultures can be used along with two-species cultures to estimate α_{12} and α_{21}, and both the trajectories of population growth of the two species in culture and the ultimate outcome (who wins) are in reasonable agreement with the model's predictions (although, to my knowledge, there has not been a statistical treatment of how close the agreement is). A common complaint (e.g. Pielou 1981) about such microcosmic research is that there is an unwarranted tendency, if a model is not rejected, to extrapolate it to much larger systems to which it is surely ill-suited, with at best a perfunctory admonition that it provides only a "crude caricature" (May et al. 1979). If such extrapolation is thus used to justify a specific recommendation in some area of applied ecology (e.g. pest control), this tendency is ominous indeed. But the microcosms themselves are not without interest (they are, after all, ecological systems), and I agree with Mertz & McCauley (1980) that such simple laboratory experiments cannot help but provide insight into at least some of the forces acting in larger systems.

An interesting point about Roughgarden's treatment of laboratory tests of the Lotka-Volterra two-species model is the complete omission of equally famous microcosms whose results are sufficiently anomalous with respect to this model as to render it a crude caricature of even two-species competition. Perhaps best known is the research on *Tribolium castaneum* and *T. confusum* by Park and his co-workers (Park 1962, Mertz 1972, Mertz & McCauley 1980), in which in certain environmental conditions no deterministic prediction was possible. This failure of prediction did not result because $\alpha_{21} < K_2/K_1$, and $\alpha_{12} < K_1/K_2$, the only circumstance under which the Lotka-Volterra equations predict this outcome, and in fact a host of elaborations making the model more and more realistic (and complicated: e.g. Taylor 1968) still did not produce reliable deterministic predictions. One effect of this research was to spawn a widespread effort to show that aspects of the competing cultures were really uncontrolled, and thus to salvage a deterministic model, however far removed it is from the original Lotka-Volterra model (Simberloff 1980). The key observation here, it seems to me, is that the forces that have so far prevented a deterministic *Tribolium* model from succeeding are not unique to *Tribolium.* They include genetic heterogeneity and change, parasite and disease organisms, environmental heterogeneity, different relationships between the species in different life history stages, etc. All two-species systems in nature must have at least a subset of these forces operating, so it is hard to see how the Lotka-Volterra two-species model, even modestly sophisticated, could have even moderately general application.

Crombie (1947) cites a number of other refractory two-species microcosms and concludes that, although the Lotka-Volterra two-species theory does not seem to predict these outcomes, one can still say that two species cannot coexist if their niches are identical, or even very similar, though the degree of permissible similarity can only be determined empirically. The first part of this statement is "Gause's Law" — no two species can exist if they have identical requirements — and it is a commonplace that Gause's Law is untestable and trivially true, since no two species have completely identical requirements (e.g.

Slobodkin 1961). The second part of the statement announces the concept of "limiting similarity," which recrudesces frequently in the ecological literature. This is the second of Roughgarden's "successful" applications of the two-species Lotka-Volterra model.

Roughgarden begins by assuming exploitation competition, a unidimensional niche space (indexed by an animal's jaw or bill size or other phenotypic trait), and equality of α_{12} and α_{21} and concludes that the limiting similarity (in terms of α_{21}) is K_2/K_1 (where $K_2 \leq K_1$). Although realism *per se* is not a hallmark of good models (Pielou 1981, Simberloff 1982b), it is difficult to see what new hypotheses or perceptions this one could lead to or to believe that with these assumptions plus others implicit in the Lotka-Volterra model (Heck 1976) any prediction of value in a specific system could be generated. Roughgarden provides no biological data to test the conclusion.

The model is subsequently sophisticated, with the additional general assumption that the Lotka-Volterra competition coefficient between two species, α_{ij}, is wholly a function of overlap in their resource utilization curves:

$$\alpha_{ij} = \frac{\int u_i(x)u_j(x)dx}{\int u_i^2(x)dx}$$

That competition is exploitative is still assumed, but Roughgarden suggests that the niche need not be one-dimensional for this formulation of α_{ij} since the integral can be viewed as a volume of any number of dimensions. How to determine the degree of independence of these dimensions, and thus actually to do the integration, is not discussed; there are an infinity of possibilities (May 1973). However, assuming the correspondences of overlap with competitive effect and phenotype with resource use, Roughgarden summarizes two elaborations of the theory. First is its extension to more than two species, which I will discuss below. Second is the development of models for resource partitioning within species, ultimately expanded to yield predictions about limiting similarity between two competing species.

In the latter expansion, resource utilization curves are assumed log-normal, and with this assumption plus the earlier ones, one predicts that the competition coefficient between two individuals depends only on the difference of the logs of their phenotypic values, z_i, however computed. Roughgarden next assumes that an animal's total resource consumption is $A_o e^K \ln z$, where z is its phenotypic value, A_o is a constant, and K is a constant usually approximately equal to 9/4. Roughgarden concedes that we are unlikely in the near future to have good data on the carrying capacity for any phenotype, but his models assume this capacity to be either a log-normal function of the log of the phenotypic value or else constant and independent of niche (phenotype) position. Roughgarden then assumes that the resource utilization curves of two competing species have equal variance (w). If their carrying capacities are fixed, he finally concludes that, for two species whose mean phenotypic difference is d,

$$\alpha = e^{w^2 K^2} \exp\left(\frac{-s(d + 2w^2K^2)^2}{2w^2}\right)$$

If $z_1 \leq z_2$, one sets $wK = C$, and defines

$$d_1/w = 2\ [C + \sqrt{C^2 + \ln\ (K_2/K_1)}\ ]$$

$$d_2/w = 2[-C + \sqrt{C^2 - \ln\ (K_2/K_1)}]$$

Roughgarden contends that the limiting similarity is then max (d_1, d_2). Again no biological data are presented to test this conclusion. In fact, until carrying capacity is measurable for two species, no data can test this conclusion. Further, as with the simple treatment of limiting similarity, this model has not produced new insights into the behavior of any biological system, as opposed to the behavior of models.

For carrying capacities not fixed, but rather a log-normal function of niche position, assuming $K = 0$, Roughgarden finds the limiting similarity between two species to be expressed by $\sigma_K^2 > 2w^2$. That is, if the variance of the carrying capacity function exceeds twice the phenotypic variance (assumed equal for the two species), there is *no* limiting similarity. Two species can be infinitely similar. Characteristically, no biological data are provided to test this conclusion, and though "interesting" elaborations are suggested in which the K's and α's have different functional forms and/or are not symmetric, no reason is given why they are interesting. My guess is that they are biologically uninteresting, but perhaps further work will show I am wrong.

Finally, Roughgarden summarizes the literature, beginning with May & MacArthur (1972), on limiting similarity between two species when the environment varies stochastically. One assumes that for each species i,

$$r_{i_t} = r_{i_o} + \sigma z_{i_t} \text{ and } K_{i_t} = K_{i_o} + \sigma(K_{i_o}/r_{i_o})z_{i_t},$$

where z_{i_t} is a "white noise" random variable with standard deviation σ. One then constructs the matrix

$$\left[\begin{array}{cc} \frac{\partial(dN_1/dt)}{\partial N_1} & \frac{\partial(dN_1/dt)}{\partial N_2} \\ \frac{\partial(dN_2/dt)}{\partial N_1} & \frac{\partial(dN_2/dt)}{\partial N_2} \end{array}\right]_{N_i = \hat{N}_i}$$

and, assuming there is a positive equilibrium, calculates the eigenvalues, λ_j. The limiting similarity between the two species is expressed by $\sigma^2 << |\lambda_{min}|$. Turelli (1978) criticizes this model on mathematical grounds, and Roughgarden observes that the condition $\sigma^2 << |\lambda_{min}|$ is strongly model-dependent. Again, no biological data are related to this inequality, and several "important" and "interesting" observations on this approach seem to me irrelevant from a biological, as opposed to mathematical, standpoint.

To sum up, a sequence of models purporting to characterize limiting similarity for two species in terms of measurements on the phenotypes, their resource use, and the environment have generated supposed criteria for coexistence. None of them have been tested and all have parameters that are as yet unmeasurable. That they are very unrealistic would not necessarily negate their usefulness in allowing new biological insights, but not one such insight has yet been forthcoming.

The third success that Roughgarden perceives for the Lotka-Volterra two-species equations is in elucidating intertidal zonation. Here he suggests that the carrying capacities and competition coefficients are functions of height in the intertidal and considers plots of K_1/K_2, α_{12}, K_2/K_1, and α_{21} vs. height. From a consideration of possible relationships of the abscissas of the intersections of the first pair of curves and the second, he concluded that there will always be a region below which one species wins, another region above which the other species wins, and usually an intermediate region of coexistence, which will consist of either a smooth transition or a set of patches depending on whether the abscissa of the first intersection is left or right of the second intersection. No data are cited that support the model, and since the situation that exemplifies the model — *Chthamalus-Balanus* competition — has been so thoroughly and satisfactorily explored in one locale by Connell (1961a, b) without recourse to the Lotka-Volterra model it is far from clear that this application of the model promises novel biological insights.

Expansion to three species of the version of the Lotka-Volterra competition model where the α_{ij} are symmetric and vary with position and the K's are fixed has generated a model that Roughgarden finds "surprisingly rich." MacArthur & Levins (1967) used this model first, to ask under what circumstances a "middle species," 2 (again one assumes a unidimensional niche), can invade a community consisting of two other species, 1 and 3, with equal carrying capacities, k. They found that if α is the competition coefficient between 1 and 2 or 3 and 2, and β the competition coefficient between 1 and 3, the limit to similarity for 2 to invade is $K_2/k < 2\alpha/(1+\beta)$. If this inequality does not hold, 2 is excluded, or else converges evolutionarily to one of the exterior species and ultimately replaces it. Assuming $\beta = \alpha^4$, they suggested that invasion requires $\alpha < 0.544$. The debilitating assumptions of the model are apparent (Heck 1976), and only one direct test has been performed, to my knowledge. In that test Dayton (1973) found that the forces acting on three intertidal invertebrates are not treated by the model.

Roughgarden (1974, 1979), extended MacArthur & Levins' model by considering an entire family of utilization curves and their corresponding competition functions, plus various relationships among the carrying capacities. Several new predictions are forthcoming, but, as with the basic model, since the parameters to generate specific predictions are not available for any group of species, and in most instances it is very likely that one or more key assumptions will be violated (Heck 1976), it is hard to tell whether these extensions constitute progress. What is "surprisingly rich" to me is the number of published variations of a basic theme that have still failed to demonstrate any predictions about or insights into nature. "Data have not been obtained from natural populations to allow a detailed test of the preceding theory" (Roughgarden 1974). Until they have there is no particular benefit to be gained from further elaboration.

Other results for three-species Lotka-Volterra competition systems include Strobeck's demonstration (1973) that there are sets of α_{ij}, K_i, and r_i for which there is no equilibrium point, so that the three population sizes may fluctuate eternally and irregularly, and May's extension (1973) of the limiting similarity model to three or more species with even spacings and equal carrying capacities. As with the other three-species results, no biological data have yet been brought to bear on these propositions.

Finally, there is the generalization of the two-species Lotka-Volterra competition (and predation) models to n species:

$$dN_i/dt = r_iN_i(K_i - \sum_j(\alpha_{ij}N_j/K_j))$$

Aside from the potential limitations of the two-species Lotka-Volterra model already discussed, the *n*-species version is valid only to the extent that higher-order interactions are nil. That is, the interaction between species i and j must be unaffected by the presence of other species, so that terms β_{ijk}, γ_{ijkl}, etc. need not be added to the α_{ij}. Whether it is or not in nature has been hotly debated; of course higher-order interactions could be important in some systems but not in others. Data are scarce. Vandermeer's protozoan microcosm (1969) seems not much affected by higher-order interactions, in that the above equation with α_{ij} estimated from the single and pairwise cultures seemed to yield predictions that were quite close to the observed performance of three of the four species in a four-way culture and not very far afield for the fourth species. Brenchley (1979) has criticized Vandermeer's conclusion and feels his results are consistent with either the presence of higher-order interactions, or the existence of interference competition, or both. Wilbur (1972) and Neill (1974) studied other artificial communities and concluded that higher-order interactions were occurring. On the other hand, Pomerantz (1981), Thomas & Pomerantz (1981), and Case & Bender (1981) contend that neither of these investigators nor Brenchley has conclusively demonstrated higher-order interactions. However, Pomerantz (1981) concedes that if higher-order interactions did not arise in Neill's study, there were nonlinearities in the growth of at least some populations that would demand modification of at least some species' growth equations from the original Lotka-Volterra form. Such nonlinearities are well known from a number of other tests of the Lotka-Volterra equations (references in Pomerantz 1981). Fowler (1981) has recently reported nonlinearities in plant competition that she interprets as higher-order interactions.

Assuming that the literal Lotka-Volterra equation (above) holds for all species, Roughgarden finds two main results for the multi-species system. First, so long as there is an equilibrium point where all species' populations exceed zero, there is only one such point and the system will always converge to it. Second, provided the determinant of the matrix of interaction coefficients α_{ij} is positive, and the determinants of all the principal minors of that matrix are positive as well, any species in the system will increase when it is rare. There are no data to test these two conclusions. Except for the microcosms above, the α_{ij} have not been calculated for any set of species, so that the second result will be very hard to test. Both results seem to rest on a conception of a community as a closed entity with well-defined boundaries and little or no immigration, a concept that usually accords poorly with nature (Simberloff 1980). This lack of realism would not necessarily render the model useless, but any observed falsification of the two results could probably be attributed to immigration. Finally, the model seems to assume habitat homogeneity, a patently poor depiction of most communities and one that would surely affect predictions of coexistence, stability, and invasibility. To me it seems as if the multispecies model, like the two-species and three-species models, has told us little or nothing about the operation of specific systems and has provided few or no insights to help us to understand the nature and effects of competition.

3. The accomplishments of "investigations"

Against the meager accomplishments of competition theory in ecology one can set the considerable progress that has been made in understanding the causes and consequences of competitive relationships in many systems by the "investigations" defined above — specific questions about specific systems, often using no more than a verbal model and never motivated by a general model. Experimental perturbation is a common but by no means universal feature of such investigations. Birch (1979) summarizes many of these studies.

I have already mentioned Connell's research (1961a, b) on barnacles of the genera *Chthamalus* and *Balanus* in Scotland. By removing *Balanus* from selected plots, he demonstrated that *Balanus* exclude *Chthamalus* from part of the intertidal by overgrowing, undercutting, or surrounding them. *Chthamalus* can survive, however, in part of the high intertidal from which *Balanus* are excluded by desiccation. Dayton (1971) and Connell (1972) demonstrated by similar experiments that species of *Balanus* and *Chthamalus* in the U.S. Pacific northwest interact in much the same way, with the same result: exclusion of *Chthamalus* from the lower intertidal. Branch (1976) experimentally demonstrated a similar interaction between two intertidal South African limpets. *Patella longicosta* specialize in feeding on algae of the genus *Ralfsia* and by stylized pushing exclude *P. oculus* from patches of *Ralfsia*. However, *P. oculus* can survive on a number of substrates other than *Ralfsia*. That *P. oculus* flourish on *Ralfsia* Branch showed by removing *P. longicosta*. Stimson (1970, 1973) demonstrated that the intertidal California limpet *Lottia gigantia* excludes limpets of the genus *Acmaea* (and other animals such as snails, anemones, and barnacles) by simply shoving them off the substrate so that they are washed away. By removing *Lottia,* he showed that *Acmaea* would increase in their absence, while adding *Lottia* causes *Acmaea* density to decrease. Creese (1978) showed that the intertidal Australian limpet *Cellana tramoserica* excludes two limpets of the genus *Siphonaria* from a dry mid-level zone, not by pushing but by grazing the rock surface so thoroughly that no algal turf grows, and *Siphonaria,* which must feed on such a turf, either starve or move to a zone where *Cellana* are absent. Connell (1961b), Dayton (1971), and Branch (1976) have by similar removals and detailed observation demonstrated space competition between limpet species and barnacle species, though in no such contest is the effect as severe as in the limpet-limpet or barnacle-barnacle studies sketched above. Dayton (1971) experimentally demonstrated space competition between the intertidal anemone *Anthopleura elegantissima* and barnacles. Here again, the mechanism is not pushing, but rather prevention, by virtue of prior occupancy, of settling by propagules of competitors. Underwood & Jernakoff (1981) showed that large algae in lower zones prevent *Cellana tramoserica* from colonizing simply by occupying space and thus preventing the limpet from grazing.

Underwood (1978) showed experimentally that the Australian intertidal nerite *Nerita atramentosa* reduces populations of *Cellana tramoserica,* probably by inducing a food shortage, but that *Cellana* are not thereby excluded since *Cellana* propagules continually immigrate from subtidal populations. Branch's research (1976) on South African barnacles and limpets similarly shows the limpets to be outcompeted in the mid-levels, but not eliminated because they continually immigrate from lower zones where barnacles are few or absent.

One may have the impression from this incomplete survey of rocky intertidal investigations that interspecific competition between species that use similar space is the dominant force affecting abundance if not distribution, but this is almost certainly not so (Dayton 1973, Connell 1975, Birch 1979). It is likely that physical factors and predation are far more important in most instances.

Terrestrial plant communities are often felt to resemble the rocky intertidal in being dominated by space competition. As just stated, the rocky intertidal is *not* dominated by space competition, and a scan of the literature suggests that plant communities are also affected by many other forces. But just as local field investigations have established mechanisms and consequences of certain instances of interspecific competition in the intertidal, so have they provided much insight into plant interactions. McIntosh (1970) discusses many early studies. Here I give a sample of later efforts.

One excellent example is Rabinowitz's research (1978a, b, c) on mangrove zonation in Panama. The classical explanation (e.g. Lind & Morrison 1974) has been that each species has somewhat different physical requirements and so outcompetes the others, primarily during the seedling stage, in the intertidal zone with physical habitat closest to its optimum. By simply observing the "behavior" of floating mangrove propagules (mangroves produce "viviparous seedlings") and by transplanting seedlings of each of four genera into solid stands of each of the other genera, Rabinowitz was able to reject this hypothesis and replace it with an alternative. The length of its propagule determines how high in the intertidal a particular species will tend to settle. As the tide comes in, longer propagules stick in the substrate at greater depths, and subsequent seedling competition has little or no effect.

Cable (1969) removed different combinations of annual grasses, perenial grasses, and burroweed (*Aplopappus tenuisectus*) in Arizona to produce all seven possible combinations of these plants and then observed production. He found that each type of plant reduced production of the others, but that the major effects were of perennial grasses on burroweed in all years and on annual grasses in wet years. The competitive mechanism appeared to be water reduction, which in turn was a function of growing season and root system geometry and depth; perennial grass roots exhaust the soil moisture before burroweed starts to grow and prevent summer moisture from reaching burroweed's deeper roots. McCown & Williams (1968) studied the California annuals *Bromus mollis* and *Erodium botrys* and found competition for sulfur and light. Superior root extension allowed *Erodium* to dominate at low sulfur levels, while at high sulfur levels *Bromus* shaded out *Erodium.* Fowler (1981) studied 20 species in a grassy field in North Carolina by removing, in separate treatments, each of seven species and also all grasses in one treatment and all dicots in another. In all instances cover returned to its original value, but species composition remained altered. Of 72 pairwise effects, 14 were significant, and on average the effect of removing one species on the abundance of another species was non-reciprocal and small, constituting but 7 % of the variance. Sharitz & McCormick (1973) investigated competition between *Sedum smallii* and *Minuartia uniflora* on granite outcrops in Georgia. Initial field observations plus laboratory studies suggested that the two species are strictly zoned because 1) in shallow soils *Sedum* can tolerate low moisture levels, 2) in soils from 4 to 10 cm deep *Minuartia* outcompetes *Sedum* if moisture levels are not low, and 3) in deeper moist soils both species are outcompeted by larger species. Field experiments generally confirmed this explanation, and the authors contend that key traits that generate these patterns include *Minuartia*'s extensive root system (which precludes it from very shallow soil but confers an advantage over *Sedum* in deeper soil) and various morphological and life historical traits of *Sedum* that vitiate the effects of drought.

Clatworthy & Harper (1962) performed laboratory experiments on competition among four aquatic higher plants, *Lemna polyrrhiza, L. gibba, L. minor,* and *Salvinia natans*. *Lemna minor* was slowly eliminated by *L. polyrrhiza,* while *L. gibba* and *S. natans* each quickly excluded *L. polyrrhiza.* Harper (1977) feels that these results are completely unpredicted by any available one-species or multispecies theoretical model but at least some can be readily explained by natural history. *Salvinia* replaces *L. polyrrhiza* because *Salvinia* fronds are produced in the air and lowered onto the water, where they overtop *Lemna*. *Lemna gibba* develops aerenchymous fronds when crowded, and these remain high in the frond mat and overtop *L. polyrrhiza.*

A plethora of greenhouse and field experiments have been performed in which greenhouse or field plots are sown with various mixtures of seeds (de Wit 1961, Harper 1977). For example, Obeid (1965) showed by such plots that *Linum usitatissimum, Camelina alyssum,* and *C. sativa* affect one another. For each species, increasing the density of surrounding individuals comprising the other two species lowered mean weight. The interspecific effects were non-reciprocal, and though the exact biological reasons for the effects are not known (as is often true of such greenhouse or field studies), it is undeniable that, at least at some densities, competition is occurring. It has been suggested that *Camelina*'s effect on *Linum* is an interference one — liberation of toxic chemicals — but since the effect is frequency-independent, this explanation is doubtful (Harper 1977). Rabinowitz (1982) studied two common and three sparse grasses in Missouri by planting different proportions of seed of eight two-species pairs. She was able to show interspecific effects on weights for most pairs, although the mechanisms are unknown. In all cases of competition between a common and a rare species, the rare species is competitively superior. There was no evidence that this result was frequency-dependent, and it is obvious that the competition in this case is not leading to the local extinction of the poorer competitors!

Although it is doubtless true that sessile or very slowly moving organisms like plants and marine invertebrates suggest straightforward investigations more readily than do highly mobile animals, there are still many elegant studies of competition among the latter. I will focus on three such groups: salamanders, ants, and rodents.

Hairston (1980, 1981) has embarked on an ambitious study of the interactions among *Plethodon jordani, Plethodon glutinosus,* and several less abundant salamanders on the forest floor of the southern Appalachian Mountains. Removal of *P. jordani* resulted in increased abundance of *P. glutinosus,* while removal of *P. glutinosus* did not affect *P. jordani* densities, but did increase the fraction of young among *P. jordani.* Neither species' removal affected remaining species, including a congener. Detailed natural historical information rules out food as the limiting resource for the two abundant species, and Hairston feels that nest sites may be limited but that an enormous amount of field work will be required to demonstrate this. Fraser (1976a) studied *Plethodon hoffmani* and *P. punctulatus* in Virginia by exhaustively analyzing food availability and intake and by laboratory cage experiments. Although food may periodically be unavailable, he concluded that neither species was likely to affect the other by reducing food density, but that it was possible that nest sites were limiting and the object of competition. Fraser (1976b) also felt that space competition might occur between adult *P. hoffmani* and juvenile *P. punctatus,* but was unable to demostrate any effect of one species on the other. Jaeger (1970, 1971) studied survivorship in cages containing populations of *Plethodon richmondi,* of *P. shenandoah,* and of both species together. Although results were inconclusive (Birch 1979), there was some indication that *P. cinereus* lowers survival of *P. shenandoah* in deep soil; in nature *P. shenandoah* is found only on talus, while *P. cinereus* is never found on talus.

Many investigations of insects have provided insight into competition or lack thereof between pairs of species. Birch (1979) summarizes some of these. Interference competition between ant species is particularly well known (Wilson 1971). For example, Brian (1956) has shown that habitat separation between Scottish *Myrmica rubra* and *M. scabrinodis* is effected by aggregation of *M. scabrinodis* workers on *M. rubra* workers and males. *Myrmica rubra* would likely be eliminated but for a series of adaptations that render it superior in cooler, moister sites. Brown (1959) describes similar interference competition among ants of the genera *Pheidole, Anoplolepis, Oecophylla,* and *Iridomyrmex* in Solomon Islands coconut groves. Each genus has a stylized fighting behavior, often involving coordination among many workers. Although interspecific battles may last weeks, eventually one colony is destroyed. In the Solomons this process has not yet led to any species' geographic replacement or even exclusion from a particular habitat, but Wilson (1971) observes that a number of introduced ants have actually extinguished native ants (or earlier introductions) on islands around the world, probably primarily by such aggression.

Davidson (1977a, b, 1978) contends that seed-eating ants of south-western U.S. deserts compete interspecifically for seeds. Interspecific donnybrooks of the sort described above are not routinely observed, and though occasional sparring is seen between individual workers, only one pair of some 14 species has spacing between colonies greater than random. Davidson performed no food augmentation or individual species removal experiments to demonstrate competition directly, but supports her contention with several observations of passive patterns that she feels are consistent with competitive structuring of the ant community. Although microhabitat partitioning does not appear very pronounced, size of seeds eaten correlates well with ant body size. Since the ant species in any local community are of different sizes (or, if similar in size, forage differently — singly or in groups), Davidson feels that competition prevents other species combinations from arising. However, Simberloff (1983) has shown by simulation that, compared to a null hypothesis that each local community draws its harvester ant species randomly from the available pool, there is no remarkable tendency for similar-sized species of similar foraging behavior to be exclusively distributed among Davidson's ten local communities. Thus, the co-occurrence pattern, though it could be construed as consistent with an hypothesis of interspecific competition, is equally consistent with the hypothesis that the set of sites any particular species occupies is independent of which other species occupy the sites. This result is similar to those arising from a number of other studies that my colleagues and I have conducted of claims that patterns of which species are found together implicate interspecific competition (references in Simberloff 1983).

Several investigations provide evidence of competition between rodent species. Grant (1969) and Morris & Grant (1972) maintained species of *Clethrionomys* and *Microtus* alone and together is enclosures and found that *Microtus* tend to exclude *Clethrionomys* from grassland enclosures while *Clethrionomys* tend to exclude *Microtus* from woodland ones. How such exclusion occurs is unknown, but habitat use on mainland and habitat expansion by species of either genus on islands where the other is absent suggest that whatever processes are occurring in the cages may also occur in nature. Redfield et al. (1977) studied the interaction of *Microtus townsendii* and *Peromyscus maniculatus* by continually removing *Microtus* for three years from sites where *Peromyscus* had previously been scarce. *Peromyscus* density increased, relative to both a control plot and original numbers. When *Microtus* were permitted to recolonize a site from which they had been removed, *Peromyscus* density decreased. In natural grasslands *Peromyscus* are less frequent when *Microtus* are present, so the effects demonstrated by the above experiment may well occur in nature. The exact means by which *Microtus* affect *Peromyscus* is unknown, but somehow the vole prevents recruitment by new deer mice and increases dispersal and/or mortality of resident adults.

Munger & Brown (1981) investigated communities of ten desert rodents in Arizona by fencing plots and excluding or permitting entry of the three largest species of granivores (all of the genus *Dipodomys*) with holes cut in the fence. Densities of the four smaller granivore species (summed) increased when *Dipodomys* were excluded, while densities of three omnivores (summed) were unaffected. Although Munger and Brown infer from these results that *Dipodomys* compete for food with the smaller granivores, they caution that the increased density and biomass of the latter compensated for only 26.5 % and 6.2 %, respectively, of the *Dipodomys* density and biomass that were excluded.

One possible reason for the relatively small effect on small rodents of excluding *Dipodomys* is that other animals, especially harvester ants, may compete for the same seeds (Brown & Davidson 1977, Davidson et al. 1980). The strongest evidence for this effect is from a removal experiment in which rodents were excluded from several plots by fencing and trapping while ants were removed from others by insecticide. Ant populations increased in the absence of rodents and rodent populations increased in the absence of ants.

4. Conclusions

The preceding examples are but a sample of those I could have chosen to show what investigations have told us about interspecific competition. Birch (1979) documents many equally impressive studies, while more recent research, mostly experimental (e.g. Wise 1979, 1981; Strong 1982), both carries on this investigative tradition and confirms the patterns manifested by Birch's summary. Before listing these patterns, I should indicate Birch's general conclusion that competitive exclusion of one species by another is unusual and that more often species that share resources have no effect on one another (Connell 1975) or have much less drastic effects and manage to coexist. When species do compete with one another, the effects are usually moderated by one of three factors: 1) Other components of the environment (weather, predators, pathogens) may combine to keep potential competitors usually below the levels at which they would exclude one another; 2) The species that would otherwise be outcompeted may be favored in some other habitat or region and thus continually replenish the populations being outcompeted; 3) One species may be favored at one time or place, and the other species at another time or place, with the advantages effectively cancelling one another. When major competitive effects do occur between species, they are as likely to be interference phenomena like aggression or allelopathy as they are to be exploitation competition for some limiting resource.

Beyond these generalities about the role of competition, one may ask what these investigations tell us about how to study nature. First, it is clear that integral to all of these systems are biological idiosyncrasies, most of which are insufficiently represented by such parameters as intrinsic rates of increase, carrying capacities, and interaction coefficients. An understanding of each system was thus accessible only to those who studied the natural history very intensively, and results from each system are not easily extrapolated to other systems. Second, at risk of flogging a dead horse, I would observe that most of these incisive investigations used experimental manipulation. This is not to say that controlled experiment is an absolute requirement if one is to present a cogent explanation, but obviously it helps a lot. The contention that different sites with different conditions (e.g., different sets of species) constitute a "natural experiment" analogous to, e.g., species removal is incorrect. Results of such uncontrolled experiments are far too ambiguous to be convincing (Abbott 1980). In particular, habitats almost always differ between sites.

Third, if we ask what role competition theory played in the knowledge accrued by the above investigations, we find a simple answer: almost none. I quote Brown (1981) at length as someone who is convinced that interspecific competition is an extremely important ecological force, who is sympathetic to the efforts of competition theorists, and who has done a fair amount of investigation (see above):

> "[Limiting similarity] has received by far the most attention from theoretical ecologists. Virtually all of their endeavors are based on the Lotka-Volterra models of interspecific competition . . . Levins (1968) extended the Lotka-Volterra model to express the pairwise interactions among all species in a community . . . Theoreticians were not alone in their enthusiasm for these models. Many more empirical ecologists spent much time studying interspecific competition and trying to measure the α_{ij}'s required to test the theories. Among both theoretical and field ecologists there was widespread belief that interspecific competition was the primary factor which limits diversity, and that working out the mechanisms of competitive interaction was the key to understanding the organization of communities. In the last few years enthusiasm has given way to disappointment as this approach has proven unproductive. It is worth inquiring into the reasons for this failure so that we may avoid making the same mistakes in the future."

I agree with this scathing assessment of the accomplishmets of competition theory. Doubtless Haila & Järvinen (1982) would claim that, had not the theory been developed, the sorts of investigations I have described would not have been undertaken or their significance appreciated. It would be difficult directly to rebut this claim or its alternative — that the existence of the theory was largely irrelevant — since it is difficult to know what influences people. I can only point out that none of the investigations I cite above except for that by Davidson seem to have been directly influenced by the theory. Most do not even cite the theory, though this need not imply absence of influence. The only such investigation that I can find that was unequivocally motivated primarily by the theory was that of Roughgarden et al. (1982) on anoles (Roughgarden, pers. comm.). On the other hand, many of these studies were conducted before the theory's heyday (say, 1965-present). Almost all seem to be motivated heavily by interest in the studied system, and they usually draw extensively for inspiration on previous work on the system. In short, this work gives every sign to me of being part of a hierarchical, progressive tradition of learning how actual systems operate. This tradition probably antedates the competition theory outlined above; certainly before the 1950's these two approaches were quite separate.

So the good news is that a lot has already been discovered about interspecific competition, by a general method that promises many further successes. The bad news is not so much that competition theory has failed to contribute to these discoveries as that, as Brown points out, much time has been wasted by ecologists as well as by theoreticians pursuing this fruitless path. It seems to me that much of this wasted effort could have been avoided; we could have known that this theory was irrelevant to nature. Brown attributes its failure to three aspects of the theory: 1) It has unrealistic assumptions, and the theoretical predictions are very sensitive to relaxation of these assumptions (e.g. Abrams 1975). 2) It is not empirically operational; one cannot measure the parameters or generate falsifiable predictions. 3) It is too reductionist; e.g., a theoretical description of how two species in isolation would interact does not allow us to extrapolate to how they would affect one another when embedded in a complex natural community. These are all sound points, and every one of them should have been realized by 1970, probably by 1960.

To these reasons for the theory's failure, I would add five suggested by the above investigations: 1) The theory assumes interspecific competition is the important force determining population sizes; in the Lotka-Volterra equations N_i is a function of all the N_j and no other variables. We know that this would be an unusual system in nature. 2) The outcome of competition when it occurs is often influenced heavily by biological idiosyncrasies that are not modelled by the theory and are probably highly nonlinear. 3) Chance is given short shrift in spite of massive evidence (e.g. Park 1962) of its importance (Birch 1979, Simberloff 1980). 4) The theory assumes closed communities and uniform habitat, whereas habitat heterogeneity and immigration are very well known and seem to play a key role in vitiating effects of competition that would otherwise be manifest. There is a growing literature on a different sort of model (e.g. Slatkin 1974) that is based on habitat patchiness and immigration. I do not believe it has yet accomplished more than Lotka-Volterra theory, but that belief is perhaps premature and in any event is more properly the subject of a separate study. 5) There is every reason to believe that, even when groups of species compete, they often do so rarely or intermittently, and their population dynamics are thus usually dominated by other forces (Wiens 1977).

As with the problems Brown sees with the theory, the above five points should all have been evident years ago. In specific studies they *were* evident years ago. If one asks why, then, has competition theory attracted the attention that it has and generated such a proliferated literature, one must look not to ecological advancement but to psychological and sociological forces. I have suggested some of these elsewhere (Simberloff 1980).

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