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IMPLICATIONS OF DIFFERENT SORTS OF EVIDENCE FOR COMPETITION

The pitfalls of inferring competition from resource use patterns are well known (Colwell and Futuyma 1971; Colwell and Fuentes 1975; May 1975; Connell 1975; Wiens 1977), and there seems to be increasing agreement that manipulative experiments and, to a lesser degree "natural experiments," yield less equivocal evidence for the action of competition (Connell 1975; Pianka 1976). A manipulative experiment here conforms to one of the following models: (1) a population is studied in isolation, a potential competitor is introduced, and the original population is studied again; or (2) one of two coexisting populations is studied, the second removed, and the first population restudied. Two sorts of changes are usually considered sufficient evidence for competition (Pianka 1976): changes in numbers (decreases in model 1, increases in model 2); and changes in resource use (divergence in model 1, convergence in model 2). I will refer to the first of these changes as the numerical response to competition. The second sort of change, in resource use, is usually called a niche shift. Because there is some ambiguity in the literature, I will break niche shifts into two subclasses. I will call nonevolutionary shifts of behavior (or morphological changes of plastic individuals) functional responses to competition and evolved shifts such as character displacements, evolutionary responses. This terminology is from Moermond (1978), following Holling (1965). I will continue to use niche shift as a general term including both functional and evolutionary responses.

Early considerations of competition concerned the numerical response (e.g., Gause 1934; Park 1948), and led attention directly to the questions of coexistence. This viewpoint was crystalized and perpetuated by the Lotka-Volterra equations which are still used, occasionally with disclaimers, in almost all introductory treatments of the subject. Lack (1945, 1947) pioneered investigation of resource utilization. With the added impetus of magnetic papers by MacArthur (e.g., 1968), Levins (1968), and others, competition theory has become increasingly concerned with resource use, in turn aiming attention at the functional and evolutionary responses. I will take Pianka's (1976) treatment of competition and niche theory as an authoritative precis of the recent state of this school of thought. He begins,

> By definition, competition occurs when two or more organisms, or other organismic units such as populations, interfere with or inhibit one another. Organisms concerned typically use some common resource which is in short supply. Moreover, the presence of each organismic unit reduces the fitness and/or equilibrium population size of the other. . . . Because it is always advantageous for either party in a competitive interaction to avoid the other whenever possible, competition presumably promotes the use of different resources and hence generates ecological diversity. The mechanisms by which members of a community of organisms partition resources among themselves and reduce interspecific competition shapes community structure and may often influence species diversity profoundly.

This definition clearly includes the three sorts of response. I contend, however, that there is a general idea in the literature—which Pianka accurately reflects—

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that when competition provokes a numerical response or a niche shift, both processes have equivalent end results, i.e., both affect community structure, species diversity, etc. However, these processes and results are not necessarily equivalent, and the fallacy that they are has produced other fallacies in turn, especially regarding coexistence of competitors.

The following arguments are based on the most familiar representation of resource sharing between two species populations: two partially overlapping normal curves on a horizontal axis which represents a gradient of resource types (e.g., a particle size gradient). The vertical axis represents resource use by the populations. Resource availability need not be uniform along this gradient. The arguments to follow rest first on assumptions related to this availability, second on assumptions regarding the abilities of the organisms to use the resources.

Assumption 1.—The resources of the resource gradient limit the population sizes.

Assumption 2.—Within each species-population, niches are uniform, i.e., the individuals are identical in their abilities to use these resources.

If the assumptions apply, interaction should have numerical consequences, and if the area of overlap is so great that the few uncontested resources (i.e., those outside the overlap zone) cannot support any individuals (MacArthur and Levins 1967; May 1974; Roughgarden 1972), the less able competitor may decline to extinction. Whether a functional response, moving the curves apart, would also occur depends upon: a sufficient plasticity of behavior of the contestants; their accurate perception (in some sense) of the problem and its solution; and the presence of available resources, not monopolized by other species, to which they could shift. If these conditions were met, however, a resource-limited population such as this should already have spread outward as far as possible as a result of intraspecific competition. Thus assumption 1 may also be taken to imply that useful resource availability tapers off at either end of the gradient, in step with the tails of the two resource use functions. (Individuals might still show some shifting since they can choose between trying to subsist on resources that are not as conducive for growth and survival as those within the overlap zone, or trying to subsist on the contested resources within the overlap zone.) Because of the complicated balancing required to predict which of these two alternatives an organism should choose, even assuming a highly perceptive organism, I will concentrate on evolutionary responses hereafter. In this case, successful spreading of curves in response to interspecific competition would only be possible through a directional evolutionary change in the organisms' innate abilities (see Roughgarden 1972). Such an evolutionary response could not proceed by natural selection in a genetically uniform population. Since assumptions 1 and 2 are implied in the Lotka-Volterra equations, data from competition experiments based on these equations would show numerical changes but little niche shifting.

If assumption 2 is relaxed, allowing a substantial amount of heritable between-individual variation in resource use efficiency at points along the gradient, i.e., allowing nonzero between-phenotype niche width, the end product of natural selection is a divergent evolutionary response. Since assumption 1 still holds, it is still unlikely that individuals engaging in functional response niche shifting would discover any free resources that they were capable of using, unless they had undergone evolutionary change rendering them better able to use previously marginal resources. In this case, the competition experiment would probably produce a numerical response, but it is unlikely that extinction would ensue, for two reasons. First, if between-phenotype niche width is substantial, there may be individuals near the outer tails of the resource-gradient curve that are virtually unaffected by the competition. Second, since selection would be brought to bear, after a period of time one would see an evolutionary response that might reduce the intensity of competition, and hence densities of both species to nonexclusion levels before exclusion could occur (Pimentel et al. 1965; Seaton and Antonovics 1967). Again, in this instance behavioral niche shifts might occur, but would provide little solid advantage to the shifters unless they stumbled upon previously unexploited resources. The existence of such resources violates assumption 1, although something like it may occur in nature.

For a third case, remove both assumptions 1 and 2. The population sizes are now not limited by the resources of the gradient in question. One may imagine the main effect on numbers to be disease, weather, predation, etc., or competition for other resources than those being examined. There is also heritable variation (see above). It is often suggested that competition for a resource only occurs when that resource is limiting or "in short supply," but selection for individual efficiency will still operate in this instance as long as the resource has an abundance less than infinity and as long as it costs something to obtain. Removal of some resource by a "competitor" will still depress the efficiency of one individual relative to another individual whose resources are not shared by the "competitor." Relative efficiency differences are likely to translate to fitness differences. Fitness is inherently a relative measure; therefore intrapopulation evolution can occur whether the population as a whole is increasing, decreasing, or stable. Conducting a competition experiment when these relationships obtain will produce evolved divergence of resource use. Behavioral shifting is also likely, since assumption 1 is relaxed and shifters thus have a fair chance of finding surplus resources. Numerical changes may or may not be seen. If numbers do change in a way consistent with competition, it need not indicate that the resource on which the functional response was noted is the resource whose shortage is reducing numbers; that may be a different, uninvestigated resource. So niche shifts may be expected from efficiency considerations without the resources in question limiting population size.

The idea that niche shifts should occur for nonlimiting resources is hardly new. Hespenheide (1973) and Taylor (1978) are two authors who make this argument explicitly, and various others, including Pianka (1976; see fig. 7.1) seem at times to agree implicitly. However, this recognition has not been followed to its logical consequence, that competition, if it can be shown by niche or numerical changes, is not a unitary concept, but has different properties depending on the definition chosen for it and on the evidence used to demonstrate it. Some "thought experiments" will demonstrate this.

Some possible results of competition experiments are shown in table 1, and I have attempted to classify the kind of interaction (competition, neutralism, etc.)

TABLE 1

Possible Outcomes of Competition Experiments

Change in numbers	Niche Shift (Functional or evolutionary response)		
	Convergence	No Change	Divergence
+	1. mutualism	2. mutualism	3. competition??
0	4. mutualism?	5. neutralism	6. competition?
−	7. competition?	8. competition	9. competition

from the experimental outcomes. For simplicity, I will assume that both species react similarly, so that any negative effects are reciprocal and thus imply proper competition rather than amensalism, for instance. Outcomes 1, 5, and 9 are easy to categorize because we expect positive correlation between two indicators of a phenomenon. The point of the preceding argument, however, is that some off-diagonal elements are also possible, since these two indicators indicate somewhat different phenomena. Outcome 7 could occur only if the species' responses to competition were wholly inappropriate, and may be discounted, but reasonable scenarios can be produced for the other possibilities. Most ecologists would consider outcome 8 to imply a competitive interaction, but some might resist such classification for case 6 even though it meets Pianka's (1976) criterion of a niche shift. Case 3 meets the niche shift criterion as well, but it defies intuition—and other definitions—to describe as competitive a situation in which both participant species increase numerically.

I know of no well-documented example of case 3 from the literature, but very few studies have considered numerical and functional responses simultaneously. If more research addresses this question, examples may emerge. While waiting, we can construct some reasonable, hypothetical, composite examples by patching together bits and pieces of demonstrated interactions. In general, case 3 interactions can result when two species are basically mutualistic but share resources.

Consider two obligatory outcrossing annual plants whose numbers in a habitat are determined by pollination rates; pollination is the limiting resource for each population; the plants bloom simultaneously and share the same pollinators. Where they grow together, pollination rates for both are higher than when they grow alone because the more spatially concentrated bloom attracts more visitors, a result which I have found in several pairs of entomophilous plants (Thomson 1978, in prep.). However, the plants show only a small diel overlap in reward presentation. Species 1, say, is visited early in the day, species 2 late. Because the plants share pollinators around midday, per flower visitation rates on each decrease, and the number of useful cross-pollinations is likely to decrease even more as the result of delivery of improper pollen by inconstant pollinators (Waser 1977). The logical consequence is selection against blooming in the midday overlap period, which should directly effect a diel partitioning of pollinators. Such patterns are also known from nature (e.g., Pleasants 1977; Thomson, in prep.). In this hypothetical case, a study of the population dynamics discovers a mutualism; a study of resource use (timing of bloom) implicates competition. Only a combination study reveals the real interaction, which combines competitive and cooperative elements, and becomes harder to pigeonhole as it becomes more fully understood.

Another possible interaction might be competition combined with mutual predator defense. Baboons and vervets, for instance, "compete" in some areas for several major foods and for roosting trees, but respond to each other's alarm calls (Stuart Altmann, personal communication). It is conceivable that populations of this sort could increase when sympatric because of more successful predator avoidance, even while selection acts to reduce their feeding overlap.

If one considers nonreciprocal interactions (allowing amensalism instead of true competition, for example) more complicated patterns can be cited. The division of African vultures into hide rippers, soft tissue tearers, bone pickers, etc., suggests food competition (Kruuk 1967; Cody 1974). However, it seems plausible that viscera-eating vultures which are not adapted for hide ripping might do better, and maintain larger populations, when they coexist with a hide ripper than when they occur alone. How should this interaction be characterized?

In conclusion, I wish to comment very generally on community studies. It is the avowed goal of many such studies to discover the factors "allowing coexistence," and these "coexistence mechanisms" (Cody 1968, 1974) are usually sought in resource use patterns. Certainly cases exist, perhaps commonly, where exploitation of a shared resource does determine population dynamics. In such cases, this standard procedure is acceptable, if resource limitation can be shown. However, since divergence in resource use should cause displacement patterns ("overdispersion of niches," Schoener 1974) even for resources that do not limit population size, resource limitation must be determined by some other criterion than the existence of "competitive" resource use patterns. This may be taken as an "awful warning" in the spirit of May's (1975) criticism of other conceptual shortcuts common to community studies. It would certainly be a travesty of science, for example, if a program to save an endangered species by "competitor control" succeeded in demonstrating a case 3 interaction. There are powerful analogies in predator control programs that became fiascos because the real numerical response of the prey depended on subtle factors opposing the more attention-commanding predation itself.

Although this paper argues for tightened restrictions on coexistence studies, its premises can also be viewed as liberating for competition studies in general. Specifically, the validity of a resource-partitioning study is not dependent on demonstration of resource limitation of numbers, if the author is willing to relinquish the contention that the patterns he demonstrates determine coexistence. Numerous studies (e.g., Waser 1977; Thomson 1975, in prep.; Pleasants 1977), have found pollinator partitioning by plants, although the connections between pollination rate and plant population size are incredibly obscure in real communities. Some of these authors (Waser, Pleasants) have phrased their arguments for partitioning in terms of coexistence and competitive exclusion and have therefore been required to propose, without particularly strong evidence, that pollination is the determinant of plant numbers. Such arguments, which are abundant in all sections of the literature, seem overextended and unnecessary to explain the observed patterns.

I have suggested that the literature is confused regarding evolutionary and numerical responses. This is true in the context of my discussion, but it must be recognized that several authors (e.g., Leon 1974; Lawler and Maynard Smith 1976; Roughgarden 1976, 1979) have discussed evolution within competing species, explicitly and without confusion. However, their models continue to specify deterministic (Lotka-Volterra) growth models, and, as Roughgarden (1976) says, are attempts to couple the evolutionary and dynamic parameters. In contrast, I have tried to consider the consequences when these responses are uncoupled.

Wiens (1977) quite properly points out that when any of a number of factors keep systems from reaching ''resource-defined equilibrium,'' it is incorrect to call species differences in resource use ''coexistence mechanisms''. His further contention that competition theory is inapplicable in such situations is only partly right, or refers only to part of the theory. In his view, those who believe competition is important (e.g., Diamond 1978) also believe that resource-defined equilibrium is a common state of nature. Wiens believes the opposite, and would set up ''equilibrium'' versus ''nonequilibrium'' as a basic bone of contention between two thoroughly opposed camps. This is partly a false issue since, as shown above, evolutionary responses to competition can determine a species' attributes while its numbers respond to other pressures, perhaps predation. What is important in the coevolution of attributes is not how closely the system approaches numerical equilibrium, but how predictable is the species makeup of the community; how reliably, over evolutionary time, does a particular species have to contend with a particular competitor.

The recognition that niche shifts do not require equilibrial conditions should provide some grounds for accommodation between the competitive and noncompetitive factions, but this seems not to have happened, because such recognition is lacking. Pianka (1976): ''. . . . with a surplus of resources available, niches could presumably overlap completely without detriment to the organisms concerned.'' Wiens (1977, p. 595): ''At such times, resources may be superabundant and ecological overlap carries no selective penalties.'' Or MacArthur (1972): ''If abundant predators prevent any species from becoming common, the entire picture changes. Resources are no longer of any concern and our Eqs. 1 and 2 are irrelevant. More correctly, resources are still a concern, but their manner of subdivision is irrelevant.''

MacArthur's equations concern numbers, of course, and then resource subdivision is indeed irrelevant to numerical changes. It is hardly irrelevant if one is interested not only in numbers but in the general biology of resource sharing. Parsimony will often be better served by interpreting resource use patterns as determining, through functional and evolutionary responses, the style of coexistence rather than the fact. Comfort may be found in reflection that, in Schoener's (1974) phrase, one is still comprehending much of the natural control of organic diversity.

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