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Diversity and the coevolution of competitors, or the ghost of competition past

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That niches of competitors in ecological communities are shaped by mutual coevolution, which thus allows many species to coexist, is a commonly-held view. Two species must live together consistently to coevolve, so since predators (or parasites) are dependent upon their prey, they will necessarily co-occur with them and so should coevolve. In contrast, competing species, which are not dependent on each other, need not consistently co-occur or coevolve. Increased diversity, by reducing the consistency of co-occurrence, also reduces the chance of coevolution.

To demonstrate coevolutionary divergence of competitors one must show: 1) that divergence has actually occurred: this has been done for some fossil sequences but not for any extant competitors; 2) that competition, rather than some other mechanism, is responsible; and 3) that it has a genetic basis. To demonstrate 2) and 3) for natural populations requires appropriate field experiments, which are suggested in the paper. This has been done, in part, in only one case.

Thus the notion of coevolutionary shaping of competitors' niches has little support at present. Theory and evidence suggest that it is probable only in low diversity communities.

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То, что ниши конкурентов в экологических сообществах оформились в процессе коэволюции, позволяющей т.о. сосуществовать многим видам, общепринятая точка зрения. Два вида должны сосуществовать, последовательно коэволюционируя, так что, по-скольку хищники (или паразиты) зависят от своих жертв, они должны непременно встречаться вместе и т.о. могут коэволюционировать. В противоположность этому, конкурирующие виды, независимые друг от друга, наобязательно должны встречаться вместе и коэволюционировать. Повышение разнообразия при снижении постоянства совместной встречаемости также снижает возможность коэволюции.

Для демонстрации коэволюционной дивергенции конкурентных видов следует показать: 1. что дивергенция реально существует; это было сделано для некоторых ископаемых рядов, но не для современных конкурирующих форм. 2. что конкуренция более реактивна, чем любой другой механизм; 3. и что она имеет генетическую основу. Чтобы доказать второй и третий пункты для естественных популяций, необходимо проведение полевых экспериментов, которые предложены в статье. Это было частично проделано лишь в одном случае. Таким образом, представление о формах коэволюции ниш конкурирующих видов плохо обосновано. Теория и имеющиеся факты говорят о том, что это возможно лишь для сообществ с низким разнообразием.

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1. Introduction

A very general definition of an ecological community is that it is an assemblage of organisms living together. Interactions of various sorts confer structure on the community: energy flowing from plants to animals and microbes, matter cycling from one to another, animals pollinating flowers, etc. Whereas some of these interactions are positive for both members (mutualistic) or positive for one with no apparent harm to the other (commensals), those that are negative for one or both species (predation, parasitism, competition) present a problem, namely how do such antagonistic pairs of species persist together without one driving the other extinct? What mechanisms stabilize these negative interactions, allowing persistence? In the following I will concentrate on the problem of the persistence of coexisting competitors.

In species that compete for space, such as attached plants and sedentary aquatic animals, the possibilities for niche differentiation are limited, and will generally be constrained to occurring in different habitats, i.e. parts of the space that have different characteristics, e.g. soil type, soil water content, slope, soil depth that roots occupy, light levels, water depth, abundance of grazers, predators, pathogens, etc. If each species is a superior competitor on a different range of such environmental conditions, several competing species will be able to coexist at equilibrium. Each will tend to occupy that part of a local site where it is the superior competitor.

There are two general ways in which this situation may have come about. First, the species may have evolved separately and become adapted to different sets of environmental conditions; when they later come together each becomes established in that part of the site in which it is pre-adapted to do best, excluding inferior competitors from its habitat. Second, the two species may have coevolved under pressure of competition, diverging from each other so that each then occupied a different part of the site (MacArthur 1972, May 1974). This is usually termed "habitat shift" (Schoener 1974).

In species that compete for a resource other than space, the divergence is usually visualized as taking place along one or more resource axes. Each species has a resource utilization curve along this axis; one common example is an axis of particle size of food, e.g. seed size in granivores. The above remarks about habitat shift among competitors for space should also apply to shifts in resource utilization curves among species that compete for food, etc.

2. Coevolution: what circumstances promote it?

In this paper I will evaluate the idea that niche differentiation of competitors has come about by coevolutionary processes. This idea is a popular one: "The notion that species niches within a biological community are shaped by mutual coevolution is nearly axiomatic in the ecological literature" (Case 1979). It has also been the subject of extensive mathematical modelling (Roughgarden 1979). Despite all the theoretical attention it has received, there remains a real question as to how much this notion applies to real communities, and what sorts of circumstances would promote coevolutionary partitioning of resources between competing species.

To answer these questions we must first consider the general case, coevolution between species in all types of interactions, e.g. predator-prey, parasite-host, etc., as well as competition. It seems clear that coevolution between a pair of species is more likely to happen, or happens more rapidly, in some sorts of interactions than in others because the species are more likely to co-occur in some interactions than in others. Co-occurrence is the first requirement for coevolution. Obviously coevolution also depends upon the degree of selective pressure, i.e. the amount that each species affects the other's reproduction and mortality. For simplicity I will assume that selective pressures are equal in all of the different types of interactions I will discuss here.

Given this assumption, the more interdependent two species are, the more likely it is that they will co-occur and so coevolve. For example, specialist predators or parasites, being completely dependent upon their prey or hosts for survival, search assiduously for them or disperse vast numbers of spores, etc. Such behavior ensures co-occurrence between pairs of species on different trophic levels.

In contrast are interacting species in which neither seeks out the other, but the two co-occur because both share a common resource, e.g. competitors. The likelihood of coevolution between two competing species depends upon how similar their resource requirements are and how often they meet. For simplicity, let us assume that the resource shared is identical, for example space, which is an essential resource for plants, sessile aquatic animals, etc. For such competitors, if space is in short supply (i.e. if the populations are not kept below carrying capacity by predators, catastrophes, etc.), the essential variables determining the likelihood of coevolution then become the frequency and duration of co-occurrence.

The likelihood that two species of competitors with very similar resource requirements will co-occur will be low under the following circumstances: if they have very different tolerances to the physical environment, and if that environment, both physically and biologically, has high variability in space and time. Different tolerances will mean that the different species will probably not live in the same sorts of habitats. High environmental variability will reduce the frequency of co-occurrence in several ways: if suitable habitat occurs in small patches, this will reduce the chance that the species will co-occur. High temporal variability will reduce the time of effective coexistence, e.g. periods of winter inactivity.

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Biological variability is another form of environmental variation. A higher species diversity of guild members, both more species and more equal relative abundances, will mean that a species will tend to co-occur less often with a particular other species than if diversity were lower. High species diversity is often associated with changing species composition, as during the intermediate stages of a succession after a disturbance (Connell 1978). The combination of changing species composition and high diversity further reduces the probability of consistent co-occurrence of a particular pair of competing species.

The upshot of this discussion is that coevolution is more likely to happen (a) in pairs of species on different trophic levels than in pairs competing on the same trophic level, (b) in communities with low species diversity in which there are low rates of change of species composition. The first prediction, that coevolution between competitors is unlikely, conforms with the views of others that competition may not be of primary importance in community structure, e.g. Ramensky (1924) and Gleason (1926) in plant communities, and Andrewartha and Birch (1954) and Wiens (1977) in animal communities. These views contrast with those of Clements (1916) on plants, and Nicholson (1954), MacArthur (1972), Cody (1974) and Diamond (1978) on animals, and prompt the following general questions: What is the evidence for coevolution between competitors and what factors affect it?

3. On the measurement of coevolution between competitors

To measure the degree of coevolution within a guild of competing species is very difficult. Ideally, three things need to be demonstrated: (1) that divergence between the species in use of resources has occurred, (2) that it was caused by competition rather than by some other mechanism, and (3) that the divergence has a genetic, not simply a phenotypic, basis. While it should be possible to demonstrate all three in laboratory populations, it is perhaps of more general interest to be able to do so under conditions closer to nature. As we will see, this has been accomplished to varying degrees with populations of parasites and hosts, rather than with competitors, but the principles are the same. The first step, to establish the fact of divergence, requires observations before and after contact between the species. This has been done directly with the pests of certain crop plants (Bush 1975) and with fossil sequences (Eldridge 1974). The problem with fossils is that the second and third steps can seldom, if ever, be demonstrated. In most extant species there is usually no direct evidence of the process of divergence, so that we can only observe the species in allopatry and sympatry and assume that the latter followed the former, and that the present condition in allopatry truly represents the pre-contact condition. In some instances this assumption seems justified (Grant 1972, Husar 1976).

The second step, to establish that the divergence was due to interspecific competition rather than to some other mechanism, is very difficult. The surest method is a field experiment in which the distribution and abundance of one or both species is manipulated (Connell 1974, 1975, Colwell and Fuentes 1975). This method is not without problems. Controls are often difficult to arrange, and certain sorts of organisms cannot be manipulated as easily as others, e.g. open-ocean plankton, long-lived trees, etc. However if carefully controlled and replicated, field experiments offer perhaps the strongest evidence for the existence of competition in natural populations.

Non-experimental methods of demonstrating competition suffer from several difficulties. For example, if one compares the populations in allopatry and sympatry, one must establish (or assume) that the only relevant difference between the environments in the two situations is the absence of one species in allopatry. All other ecological conditions (physical environment, history, predators, parasites, etc.) must be similar, or else there must be evidence that they could not have produced the divergence.

If the only populations observed are in sympatry, more difficulties arise. For example, one standard method is to construct resource utilization curves along some resource dimension and to calculate the degree of niche overlap between species along the resource axis. If the overlap is less than some theoretical threshold (Hutchinson 1959, MacArthur 1969, 1972), the species can supposedly coexist. There are several problems with this method. First, it contains a convenient loophole: if the reduced overlap of the resource utilization curves is not found, the objection can be raised that the resource dimension chosen was not the one along which competition is occurring. Second, niche space is probably multidimensional, yet it is impossible to obtain data on all relevant dimensions (Pianka 1975). Third, the thresholds chosen for overlap, i.e. the limiting similarity, are theoretical but have no proven biological basis. Fourth, even if the species overlap in resources they may not compete (Menge 1979). Last but not least is the problem of deciding how available the resources or habitats to be partitioned are to the organisms. The usual assumption is that they are equally available over the entire existing range of resources or habitats. However, this assumption will seldom apply to real communities. Petraitis (1979) points out that this error makes many previously published estimates of niche breadth and overlap invalid. He proposes a new method but also points out that this whole approach hinges upon how well we can discover the proportions in which the resources are actually available to the organisms. This is the Achilles Heel of the whole notion: *can ecologists judge availability as the organisms do?*

To see whether the niches have diverged sufficiently,

Tab. 1. To demonstrate that coevolution between competitors has occurred, two propositions must be demonstrated: I, that competition is the underlying mechanism, and II, that the divergence has a genetic basis. The following field experiments will test these propositions. Only if the answers to all the questions posed under treatments 1, 2, 5 and 6 are affirmative, are the propositions acceptable. (The allopatric populations of species X are referred to as X_a, the sympatric populations as X_s. The other species, Y, is the presumed competitor.)

| | Species Y present naturally (sympatric locality) | | Species Y absent naturally (allopatric locality) |
	Species Y not removed	Species Y removed	
Proposition I is tested by observing changes in the breadth of the niche of X_a:	Treatment 1. (X_a transplanted, X_s removed) Is X_a niche compressed so that it is significantly narrower than X_a niche in treatment 2?	Treatment 2. (X_a transplanted, X_s removed) Does X_a niche remain broader than in treatments 1 and 5?	Treatment 3. (X_a left in place as a control)
Proposition II is tested by observing changes in the breadth of the niche of X_s: (It need not change for Proposition II to be acceptable.)	Treatment 4. (X_s left in place as a control)	Treatment 5. (X_s left in place) If X_s niche expands, is it always narrower than X_a niche in treatment 2?	Treatment 6. (X_s transplanted, X_a removed) If X_s niche expands, is it always narrower than X_a niche in treatment 3?

one must compare the observed with a random assemblage. To do this, one randomly chooses a set of potentially competing species or randomly places a set of curves on a resources axis, then compares its structure to that of the real one to test the hypothesis that the divergence is significant (Sale 1974, Leviten 1978, Simberloff 1978, Strong et al. 1979). For this method to be useful, the source from which the random set of species or utilization curves are drawn should be identical with that from which the actual community was assembled. This identity may be very difficult to ensure.

To return to direct methods, the surest way to demonstrate that competition, rather than some other mechanism, caused the divergence, is to do the following field experiments (see Tab. 1, Proposition I, for an outline of the experiments). In these experiments the breadth of the niche of a species is measured. Actual niche dimensions such as range of habitat occupied or diet are more useful than indirect indicators such as morphological differences, body size, etc. The former will also be expected to respond to the experimental treatments more quickly than the latter.

The experimental treatments to test Proposition I constitute the first set of experiments in Tab. 1, as follows. Individuals from the allopatric population, X_a, are transplanted to the sympatric locality, and then observed where the other species, the presumed competitor Y, is present (treatment 1) vs. where it is experimentally removed (treatment 2). In treatment 3, individuals are not transplanted, but are handled and observed in the same manner as those transplanted, to serve as controls for the experimental results. This control treatment 3 is crucial because the weather or some other factor extraneous to the experiment might change during the experiment, causing a change in the niche breadth unrelated to the experimental treatments.

We conclude that competition is the likely mechanism if: the niche of the transplants in the presence of the competitor (treatment 1) is compressed to be significantly narrower than the niche of the transplants without the competitor (treatment 2). This tests for competition operating in the present. However if the niches of the transplants either do not change or change equally in both treatments 1 and 2, then some mechanism other than competition from species Y caused the narrowing of the niche of the sympatric population. Thus if the answers to either of the questions under treatments 1 and 2 in Tab. 1 are negative, then competition by Y must be rejected as the mechanism underlying the differences in niche breadth observed between the natural populations in sympatry and allopatry.

For the third and last step, it must be shown that evolution has actually occurred, i.e. that the divergence has a genetic basis. Various methods exist for doing this in the laboratory: breeding experiments, electrophoretic techniques, etc. As an alternative to these laboratory methods, certain field experiments can demonstrate a genetic basis (see Proposition II in Tab. 1). This part of the experiment is designed as follows. In the region of sympatry, one set of replicate populations, X_s, is left in place, in the presence of the competitor, Y. This serves as a control (treatment 4); like treatment 3, this is needed to control for extraneously caused changes in niche breadth. In treatment 5, X_s populations are left in place, but the competitor is removed. In treatment 6, X_s populations are transplanted to the allopatric area where Y is absent naturally.

We conclude that the observed natural differences in niche breadths between the sympatric and allopatric populations have a genetic basis if two conditions are met: (a) In treatment 5 (Y removed), the niche of X_s either does not expand or, if it does, it does not become

as wide as the niche of population X_a in the *same* situation (treatment 2); and (b) In treatment 6, where Y is naturally absent, the niche of the transplanted X_s again does not change or, if it does, must be narrower than the niche of X_a in treatment 3 (the natural allopatric population). Thus if the answers to either of the questions under treatments 5 and 6 in Tab. 1 are negative, this indicates that a genetic change has not occurred. The experimental manipulations in Tab. 1 are, it seems to me, both necessary and sufficient to satisfy the latter two of the three steps posed as being essential in demonstrating coevolution between competitors.

4. The evidence for coevolution within guilds

4.1. Increased diversity reduces the probability of coevolution

The best evidence concerning the factors affecting the rate of coevolution comes not from guilds of competitors, but from the evolution of resistance by plants to parasites or pathogens. For example, the counter-adaptation of pathogens to overcome the resistance of certain strains of wheat has been reviewed by Van der Plank (1968). He describes how certain races of the pathogenic stem rust *Puccinia graminis* have evolved that can overcome the resistance of spring wheat with the SR_6 genetic strain, if this variety of wheat is exposed to the rust for long periods in monoculture. However, if the rust moves from the SR_6 spring wheat to another variety (winter wheat) that lacks the SR_6 gene, the rust loses its ability to attack the spring wheat. This loss of fitness by pathogens that have such "unnecessary virulence" is well documented (Van der Plank 1968). Thus alternation between different kinds of hosts, by reducing the probability of consistent co-occurrence between pathogens and a particular host, slows or prevents the coevolution between them.

Another example has been documented for scale insects on pine trees (Edmunds and Alstad 1978). They found that individual trees differed in defensive chemicals and that the pests were adapted to attack individual trees. But success on one tree was maladaptive for colonization of another tree. Thus, like the different strains of wheat, intrapopulation diversity of trees prevented the pest species from evolving consistently effective methods of attack. In both of these examples diversity refers to the genetic variation within species. However the principle should also apply to variation between species. The examples involve coevolution between consumers and their hosts; I am not aware of any similar evidence concerning the effect of diversity on the rate of coevolution between competing species within a guild, but there seems to be no reason to believe that increased diversity would not also reduce the rate of coevolution between competitors.

The depressing effect of high diversity on coevolution applies only if all the species being considered actually interact. However if the interactions occur mainly within sets of a few species each, with the different sets loosely coupled to each other, the depressing effect may not apply. The idea that communities are organized into such small "components" has been proposed by Root (1973), May (1977), and Gilbert (1979). However, Murdoch (1979) has pointed out that even in the temperate zone where diversity is low, those natural communities which have been intensively studied are composed of many, not few, strongly interacting species. In diverse tropical communities, competitive interactions also appear to involve many, not few, species. Corals on even small plots on reef crests at Heron Island, Great Barrier Reef, interact strongly with many other species (Connell 1976). Likewise, in rain forests the tree species are intermingled so that each species interacts with many others. For example, in a rain forest in south Queensland, Australia, the mean number of tree species (all stems $\geq$ 0.5 m height) per 10 × 10 m plot varied from 12 to 34 on 8 different sites (Hopkins 1975). In a north Queensland rain forest the species were also highly intermingled. This is shown in a tally of the species of nearest neighbor of each tree $\geq$ 10 cm diameter. The commonest species, with 119 trees, had 57 other species amongst its nearest neighbors; in some of the less common species, all of the nearest neighbors were different species (Connell et al. unpubl.). Although these data do not prove that small "component communities" of competitors do not occur in diverse tropical assemblages, they render it unlikely. Therefore I conclude that coevolution of competitors is also unlikely in communities of high diversity.

4.2. The evidence for coevolution between competitors

Evidence that divergence has occurred between competitors comes from the fossil record (Eldridge 1974, Kellogg 1975, Schindel and Gould 1977). While these examples are interesting, they provide no evidence that competition was necessarily the mechanism, nor that the divergence had a genetic basis. Evidence from extant species is, in the main, even less complete than these fossil studies, since there is neither direct evidence for the divergence nor for the other two aspects referred to above. Most studies simply compare sympatric and allopatric populations, which is equivalent to single observations of treatments 3 and 4 of Tab. 1. The variables compared are usually morphological characters, since shifts in these are assumed to be likely to have a genetic basis. Unfortunately, there is little evidence that the character displacements observed are due to competition. Grant (1972, 1975) came to this conclusion after a thorough review of all instances published up to that time.

Studies of character displacement published since Grant's 1972 review do not, in my view, change his original conclusions. For example, in three recent studies the environment in sympatry was very different

from that in allopatry. In studies of a Danish mud snail (Fenchel 1975a,b), salinity, degree of water turbulence and substrate particle size all were different between the localities. In studies of African burrowing desert lizards (Huey et al. 1974), the topography and soil were strikingly different in the two situations. Since both sets of species (mud snails and burrowing lizards) would be expected to be strongly influenced by substrate conditions, and since no field evidence for competition was produced, it is impossible to conclude that competition was more important than adaptation to the physical environment in producing the observed divergence. Likewise in a study of lizards in sympatry on the mainland vs. allopatry on islands in Mexico (Case 1979), there is no direct evidence of competition, and the environments are acknowledged to be different in the two situations. However Case (1979) did address the alternative mechanisms and gave some evidence indicating that they are not likely to be relevant in this situation. Another problem is that the distribution of the competitors may be quite variable. In the case of the mud snails (Fenchel 1975a: Fig. 9), the co-occurrence at four localities varied drastically; at one locality it changed from allopatry to sympatry whereas at another it changed from sympatry to allopatry, both within a month. Such variability suggests that there may not be sufficiently consistent co-occurrence for coevolution to occur between these species which disperse so actively.

In none of the studies discussed so far have any of the field experiments been done that are necessary to establish either that competition is the relevant mechanism or that the divergence has a genetic basis, as summarized in Tab. 1. The only instance I am aware of in which some of these experiments have been done is the work of J. R. E. Harger on intertidal mussels (*Mytilus* spp.) that occur commonly on temperate rocky shores. *M. edulis* L. occurs allopatrically in the Atlantic and sympatrically with *M. californianus* Conrad in the north Pacific. In sympatry the two do not usually coexist on a small scale; *edulis* is most commonly found on sheltered shores whereas *californianus* is commoner on more wave-beaten ones. In allopatry, *edulis* occurs in both sorts of habitats (Kitching et al. 1959, Lewis 1964, Seed 1969, Menge 1976, Peterson 1979). In an elegant series of field and laboratory experiments, Harger showed that the two compete in sympatry; young *edulis* invade wavebeaten locations but are torn off by surf when they grow large (Harger 1970c). In some wave-beaten locations they may persist as very small individuals high on the shore or as short-lived invaders of openings in *californianus* beds or in refuges in crevices in algal clumps (Suchanek 1978). *M. californianus* thrives in wave-beaten places, has thicker shells and a stronger attachment to the rocks than does *edulis* (Harger 1970a). As the mussels grow on wavebeaten shores, *californianus* grows around any surviving *edulis* and crushes them (Harger 1970b). In shelter, *edulis* crawls above *californianus* which then become

smothered in the silt that collects within the clumps of mussels in quiet water (Harger 1968). The difference between the distribution of *edulis* in allopatry and sympatry may be an instance of "habitat shift", and the difference may have a genetic basis. Harger (1970c, 1972b,c) found that if *californianus* were removed, *edulis* could not expand its niche to occupy the wave-beaten places (treatments 4 and 5, Tab. 1). A comparison between the sympatric and allopatric populations indicated that there were genetic differences; shell shape remained different even when the two were reared together in the field (Harger 1972a). As to the question of whether competition, rather than some other mechanism, is responsible for the narrower habitat niche of *edulis* in sympatry, the relevant experiments have not yet been performed. Although allopatric *edulis* individuals were transplanted to a sympatric location, the critical field experiments to see whether they could shift their habitat to occupy a greater range of wave exposures in the absence of *californianus* (treatments 1 and 2, Tab. 1), were not done. However, Harger has demonstrated the feasibility of transplants from allopatry to sympatry and has shown that competition is important in sympatry. The hypothesis that these species of mussels have coevolved seems clearly to be testable in this instance.

5. Diversity, coevolution and community organization

I have proposed (Connell 1975) that interspecific competition is more likely to happen in moderately harsh physical environments than either in very harsh or in benign conditions. This is because at one extreme, populations may be reduced by the direct action of very harsh conditions below the densities at which they would compete. Harshness here does not connote reduction in resources; what is meant is that the extreme physical conditions directly reduce populations below the carrying capacity of the resources. In contrast, under benign conditions, natural enemies (predators, parasites, herbivores) tend to be more effective (Connell 1971) so they also keep the populations below the level at which they compete. In environments intermediate between these, the effectiveness of natural enemies is less, as is the mortality from direct physical stresses. Therefore, the populations are more likely to reach high densities and competition is likely. Examples supporting this idea are presented in Connell (1975) with a model of how weather, competition and natural enemies affect the process of recolonization after a community is perturbed.

If competition is reduced in more benign environments, there will be reduced selection pressure for guild members to coevolve and diverge from each other. If at the same time diversity is high, as it often tends to be in more benign environments, this will further reduce the likelihood of coevolution of competitors. In contrast, in

moderately harsh environments, where species diversity tends to be lower, competition should be more intense and coevolution more likely. Coevolution between pairs of species on different trophic levels (e.g. predator-prey, parasite-host) is more likely, even in high diversity communities, since the species are more often in contact, the predator assiduously searching for the prey.

In summary, if the mechanism of niche differentiation contributes at all to coexistence in many-species guilds, it seems unlikely to have commonly arisen by species having diverged by coevolution. Instead, it is more likely that they diverged as they evolved separately so that, when they later came together, they coexisted because they had already become adapted to different resources or parts of the habitat. Thereafter competition may keep them apart, as has been demonstrated in several instances. This is also the view of Grant (1975): "adaptations already possessed by the species at the time of meeting are the principal determinants of coexistence". In any case, other mechanisms such as those described in Connell (1978, 1979) could also operate, separately or together, to maintain the coexistence of competitors.

One last point. In the past, when I pointed out to some ecologists that competition seemed of little importance as a mechanism determining a particular species' distribution, they often gave the following answer. The reason, they said, for my inability to find evidence for competition was because it had already been eliminated by past coevolutionary divergence between those species. However, for the reasons discussed in this paper, and until some strong evidence is obtained from field experiments along the lines suggested above, I will no longer be persuaded by such invoking of "the Ghost of Competition Past".

References

Andrewartha, H. G. and Birch, L. C. 1954. The distribution and abundance of animals. – Univ. Chicago Press, Chicago, Ill.

Bush, G. L. 1975. Modes of animal speciation. – Ann. Rev. Ecol. Syst. 6: 339–364.

Case, T. J. 1979. Character displacement and coevolution in some *Cnemidophorus* lizards. – Fortschr. Zool. 25: 235–282.

Clements, F. E. 1916. Plant succession, an analysis of the development of vegetation. – Carnegie Inst. Wash. Publ. No. 242, pp. 1–512.

Cody, M. L. 1974. Competition and the structure of bird communities. – Princeton Univ. Press, Princeton, New Jersey.

Colwell, R. and Fuentes, E. 1975. Experimental studies of the niche. – Ann. Rev. Ecol. Syst. 6: 281–310.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. – In: den Boer, P. J. and Gradwell, G. R. (ed.), Dynamics of populations. PUDOC, Wageningen, pp. 298–312.

– , 1974. Field experiments in marine ecology. – In: Mariscal, R. (ed.), Experimental marine biology. Acad. Press, New York, pp. 21–54.

– , 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. – In: Cody, M. L. and Diamond, J. M. (ed.), Ecology and evolution of communities. Harvard Univ. Press, Cambridge, Mass., pp. 460–490.

– , 1976. Competitive interactions and the species diversity of corals. – In: Mackie, G. O. (ed.), Coelenterate ecology and behavior. Plenum Press, New York, pp. 51–58.

– , 1978. Diversity in tropical rain forests and coral reefs. – Science 199: 1302–1310.

– , 1979. Tropical rain forests and coral reefs as open non-equilibrium systems. – In: Anderson, R. M., Taylor, L. R. and Turner, B. (ed.), Population dynamics. Symp. British Ecol. Soc., Blackwells, Oxford, pp. 141–163.

Diamond, J. M. 1978. Niche shifts and the rediscovery of interspecific competition. – Am. Sci. 66: 322–331.

Edmunds, G. F. and Alstad, D. N. 1978. Coevolution in insect herbivores and conifers. – Science 199: 941–945.

Eldridge, N. 1974. Character displacement in evolutionary time. – Am. Zool. 14: 1083–1097.

Fenchel, T. 1975a. Factors determining the distribution patterns of mud snails (Hydrobiidae). – Oecologia (Berl.) 20: 1–17.

– , 1975b. Character displacement and coexistence in mud snails (Hydrobiidae). – Oecologia (Berl.) 20: 19–32.

Gilbert, L. E. 1979. Food web organization and the conservation of neotropical diversity. – In: Soule, M. E. and Wilcox, B. A. (ed.), Conservation biology. Sinauer Assoc. Inc., Sunderland, Mass., pp. 11–33.

Gleason, H. A. 1926. The individualistic concept of the plant association. – Bull. Torrey Bot. Club 53: 7–26.

Grant, P. 1972. Convergent and divergent character displacement. – Biol. J. Linn. Soc. 4: 39–68.

– , 1975. The classical case of character displacement. – Evol. Biol. 8: 237–337.

Harger, J. R. E. 1968. The role of behavioral traits in influencing the distribution of two species of sea mussel, *Mytilus edulis* and *Mytilus californianus*. – Veliger 11: 45–49.

– , 1970a. The effect of wave impact on some aspects of the biology of sea mussels. – Veliger 12: 401–414.

– , 1970b. Comparisons among growth characteristics of two species of sea mussel, *Mytilus edulis* and *Mytilus californianus*. – Veliger 13: 44–56.

– , 1970c. The effect of species composition on the survival of mixed populations of the sea mussels *Mytilus californianus* and *Mytilus edulis*. – Veliger 13: 147–152.

– , 1972a. Variation and relative "niche" size in the sea mussel *Mytilus edulis* in association with *Mytilus californianus*. – Veliger 14: 275–281.

– , 1972b. Competitive coexistence: maintenance of interacting associations of the sea mussels *Mytilus edulis* and *Mytilus californianus*. – Veliger 14: 387–410.

– , 1972c. Competitive coexistence among intertidal invertebrates. – Am. Sci. 60: 600–607.

Hopkins, M. S. 1975. Species patterns and diversity in the subtropical rain forest. – Ph. D. thesis, Univ. of Queensland, Brisbane.

Huey, R. B., Pianka, E., Egan, M. and Coons, L. 1974. Ecological shifts in sympatry: Kalahari fossorial lizards. – Ecology 55: 304–316.

Husar, S. 1976. Behavioral character displacement: evidence of food partitioning in insectivorous bats. – J. Mamm. 57: 331–338.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? – Am. Nat. 93: 145–159.

Kellogg, D. E. 1975. Character displacement in the Radiolarian genus, *Eucyrtidium*. – Evolution 29: 736–749.

Kitching, J. A., Sloane, J. F., and Ebling, F. J. 1959. The ecology of Lough Ine. VIII, Mussels and their predators. – J. Anim. Ecol. 28: 331–341.

Leviten, P. J. 1978. Resource partitioning by predatory gastropods of the genus *Conus* on subtidal Indo-Pacific coral reefs: the significance of prey size. – Ecology 59: 619–631.

Lewis, J. R. 1964. The ecology of rocky shores. – English Univ. Press, London.

MacArthur, R. H. 1969. Species packing, or what competition minimizes. – Proc. Nat. Acad. Sci. 64: 1369–1375.

– , 1972. Geographical ecology. – Harper and Row, New York.

May, R. M. 1974. On the theory of niche overlap. – Theoret. Pop. Biol. 5: 297–332.

– , 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. – Nature, Lond. 269: 471–477.

Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. – Ecol. Monogr. 46: 355–393.

– , 1979. Coexistence between the seastars *Asterias vulgaris* and *A. forbesi* in a heterogeneous environment: a non-equilibrium explanation. – Oecologia (Berl.) 41: 245–272.

Murdoch, W. W. 1979. Predation and the dynamics of prey populations. – Fortschr. Zool. 25: 295–310.

Nicholson, A. J. 1954. An outline of the dynamics of animal populations. – Australian J. Zool. 2: 9–65.

Peterson, C. H. 1979. The importance of predation and competition in organizing the intertidal epifaunal communities of Barnegat Inlet, New Jersey. – Oecologia (Berl.) 39: 1–24.

Petraitis, P. S. 1979. Likelihood measures of niche breadth and overlap. – Ecology 60: 703–710.

Pianka, E. R. 1975. Niche relations of desert lizards. – In: Cody, M. L. and Diamond, J. M. (ed.), Ecology and evolution of communities. Harvard University Press, Cambridge, Mass., pp. 292–314.

Ramensky, L. G. 1924. The basic lawfulness in the structure of the vegetation cover. – In Russian, Vestnik opytnogo dela Sredne – Chernoz. Obl. Voronezh. 37–73; German abstract in Botanisches Centralblatt 7: 453–455.

Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). – Ecol. Monogr. 43: 95–124.

Roughgarden, J. 1979. Theory of population genetics and evolutionary ecology: an introduction. – Macmillan, New York.

Sale, P. F. 1974. Overlap in resource use, and interspecific competition. – Oecologia (Berl.) 17: 245–256.

Seed, R. 1969. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores I. Breeding and settlement. II. Growth and mortality. – Oecologia (Berl.) 3: 277–350.

Schindel, D. E. and Gould, S. J. 1977. Biological interaction between fossil species: character displacement in Bermudian land snails. – Paleobiology 3: 259–269.

Schoener, T. W. 1974. Competition and the form of habitat shift. – Theoret. Pop. Biol. 6: 265–307.

Simberloff, D. S. 1978. Using island biogeographic distributions to determine if colonization is stochastic. – Am. Nat. 112: 713–726.

Strong, D. R., Szyska, L. A., and Simberloff, D. S. 1979. Tests of community-wide character displacement against null hypotheses. – Evolution 33: 897–913.

Suchanek, T. H. 1978. The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. – J. exp. mar. Biol. Ecol. 31: 105–120.

Van der Plank, J. E. 1968. Disease resistance in plants. – Academic Press, New York.

Wiens, J. A. 1977. On competition and variable environments. – Am. Sci. 65: 590–597.