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THE LIMITING SIMILARITY, CONVERGENCE, AND DIVERGENCE OF COEXISTING SPECIES

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INTRODUCTION

The diversity of coexisting species can be limited in at least three ways depending upon the circumstances. First, there is a lower limit to the abundance of each species which sets an upper limit to the number of species (Schoener, 1965). Second, there may be an upper limit to the abundance of each species, set by the danger from predators and disease, which increases the possibilities for more species (Paine, 1966). Finally, environmental instability sets a limit to the degree of specialization and, for a given degree of specialization, competition may, but does not always, set a limit to the similarity of coexisting species. We investigated this limit in the particular case of discrete, renewable resources (MacArthur and Levins, 1964); and here we extend the analysis to include continuous, and non-renewable resources in uniform and patchy environments, and we consider the effects of evolution. In particular, we predict situations under which character divergence and character convergence should occur.

1. *Competitive limits to similarity*

Consider a community of n species obeying the Volterra (1926) equations

$$\frac{dX_i}{dt} = r_i X_i \frac{\left(K_i - X_i - \sum_j \alpha_{ij} X_j \right)}{K_i} \quad (1)$$

Such a community can retain all n species if any one of them can increase when rare, i.e. when X_i is near zero and all the others are at the equilibrium values which they would reach in the absence of X_i . Therefore we want to determine conditions for which

$$K_i > \sum_j \alpha_{ij} X_j^* \quad \text{for all } i,$$

where X_j^* are the equilibrium values which satisfy

$$K_j = X_j^* + \sum_k \alpha_{jk} X_k^*; \quad j, k \neq i.$$

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In other words, X_j^* are equilibrium values in the absence of X_i . These conditions will, of course, depend on how the α 's are specified, which in turn will reflect the structure of the niche.

We will begin with the familiar two species system in which equation (1) takes the form

$$\begin{aligned}\frac{dx_1}{dt} &= r_1 X_1 \frac{(K_1 - X_1 - \beta X_2)}{K_1} \\ \frac{dx_2}{dt} &= r_2 X_2 \frac{(K_2 - X_2 - \beta X_1)}{K_2}\end{aligned}\quad (2)$$

When X_1 is rare, X_2 comes to equilibrium near K_2 , which we call X_2^* , and conversely. Then X_1 will increase when rare provided

$$K_1 > \beta X_2^* = \beta K_2$$

Similarly X_2 will increase when rare provided

$$K_2 > \beta X_1^* = \beta K_1$$

These are the well-known Volterra conditions for coexistence for two species systems. Note that for $K_1 = K_2$, $\beta < 1$ allows for stable coexistence. This case will turn out to be the most favorable for invasion. But when we reach three species, new conditions must be imposed.

First, we must specify whether the niche is one-dimensional, in which case there is a middle one which competes intensively with two neighbors, or two-dimensional, in which case each may overlap the other two equally.

We now examine three species in a linear array, the middle one competing heavily (we will use α) with both outer ones but these interacting more weakly (we will use β) with each other. This case will turn out to be the most unfavorable for invasion. This is the most unstable situation. We assume $K_1 = K_3$ and $\alpha_{12} = \alpha_{32} = \alpha'$. The equations now are

$$\begin{aligned}\frac{dX_1}{dt} &= r_1 X_1 (K - X_1 - \alpha' X_2 - \beta X_3) / K \\ \frac{dX_2}{dt} &= r_2 X_2 (K_2 - X_2 - \alpha X_1 - \alpha X_3) / K_2 \\ \frac{dX_3}{dt} &= r_3 X_3 (K - X_3 - \beta X_1 - \alpha' X_2) / K\end{aligned}$$

Since the middle species is the most precarious, the community can be stable only if the middle one can increase when rare. This requires that

$$K_2 > \alpha X_1^* + \alpha X_3^*$$

where X_1^* and X_3^* are, from 2, $K/(1 + \beta)$, and $K/(1 + \beta)$, respectively. Hence the condition for coexistence becomes

$$\frac{K_2}{K} > \frac{2\alpha}{1 + \beta}$$

Conversely, species 1 and 3 can keep species 2 out, provided

$$\frac{K_2}{K} < \frac{2\alpha}{1+\beta} \quad (3)$$

Clearly when K is greater than K_2 , this latter condition is easy to achieve; but even when they are equal species, 2 may be unable to invade. For when $1 + \beta < 2\alpha$, then $K < \frac{2\alpha K}{1 + \beta}$ and invasion is impossible. Biologically

we interpret this result as follows, using equation (3). If species 1 and 3 do not compete with each other, X_1^* and X_3^* can reach level K , and α must be less than $1/2$ for successful invasion. However, if species 1 and 3 do compete, so that $\beta > 0$, X_1^* and X_3^* will be somewhat below K , and a somewhat higher α will permit coexistence. We now investigate under what conditions of niche overlap $1 + \beta$ will be less than 2α . From resource utilization efficiencies and habitat preferences α and β can be calculated.

For two species the growth equations, (1), have the form

$$\begin{aligned} \frac{dX_1}{dt} &= r_1 X_1 \frac{(K_1 - X_1 - \alpha_{12} X_2)}{K_1} \\ \frac{dX_2}{dt} &= r_2 X_2 \frac{(K_2 - X_2 - \alpha_{21} X_1)}{K_2} \end{aligned}$$

α_{12} , therefore, measures the relative depression in r_1 , caused by an individual of species 2 compared to another of species 1. $U_1(R)$ of Fig. 1 measures the probability that an item of resource R is consumed in a unit of time by an individual of species 1. Here the R continuum may be one of resource quality or location. Hence, the probability of species 1 and 2 simultaneously trying for the same resource, R , is $U_1(R)U_2(R)$. In terms of this result, we now give a heuristic justification of the α formula used in

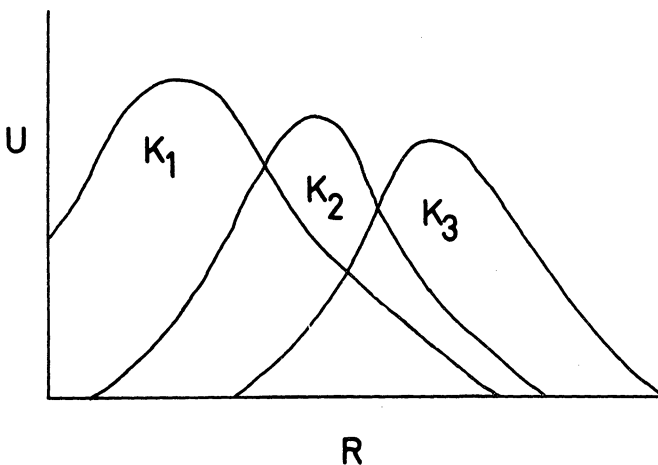


FIG. 1. The form of the niche. For each resource r , U is the probability of its utilization in a unit time by an individual. The area under each curve, therefore, is the total resource utilization K_i for species i .

the text. Basically, to compete for space individuals of species 1 and 2 must confront one another and hence be present simultaneously. Similarly, when resources are rapidly renewed, individuals only compete if they are present within a short time of each other. In either case $\frac{\int U_1(R) U_2(R) dR}{\int [U_1(R)]^2 dR}$ measures the relative probability of the simultaneous presence of species 1 and species 2 compared to species 1 and species 1. Hence it measures α . If the resources are discrete, the integrals are replaced by sums:

$$\alpha = \frac{\sum_i U_1(R_i) U_2(R_i)}{\sum_i [U_1(R_i)]^2}$$

In case the resources are not rapidly renewed, the precise formula for α is more complicated. However, it will not be needed in our discussion.

Clearly if the U -curves differ only in location, being otherwise congruent, then α and β decrease as the separation increases. The relation between α and β depends upon the shape of the curves. In fact, if the tails are truncated so that U_1 and U_3 do not overlap, β will be zero. To make the relation between α and β more precise, we investigate several shapes of U curves. For instance, if $U_1(R)$, $U_2(R)$ and $U_3(R)$ are rectangles, then α is the proportion of the total area under the U curve which is overlap between $U_1(R)$ and $U_2(R)$. Similarly β is the proportion of area under U_1 which is U_1 , U_3 overlap. But since these are rectangles, β is 0 for $\alpha \leq 1/2$ and equals $2\alpha - 1$ for $\alpha \geq 1/2$ which was precisely the value which prevents invasion. Hence, $\alpha = 1/2$ is the limiting similarity between species 1 and 2, or in other words, invasion is only possible between species whose U curves do not overlap. Hence, for rectangular U curves, this result applies to a linear packing of any number of species. We now turn our attention to a normal-shaped U curve. Here

$$U_1(R) = e^{-\frac{X^2}{H^2}}, \quad U_2(R) = e^{-\frac{(X-D)^2}{H^2}}, \quad U_3(R) = e^{-\frac{(X-2D)^2}{H^2}},$$

$$\text{whence } \alpha = \frac{\int e^{-\frac{X^2}{H^2}} e^{-\frac{(X-D)^2}{H^2}} dX}{\int \left[e^{-\frac{X^2}{H^2}} \right]^2 dX} = \frac{e^{-D^2} \int e^{-\frac{2(X-D/2)^2}{H^2}} dX}{\int e^{-\frac{2X^2}{H^2}} dX} = e^{-\frac{D^2}{2H^2}}$$

Similarly, $\beta = e^{-\frac{2D^2}{H^2}} = \alpha^4$. Hence, invasion is impossible if $\alpha^4 < 2\alpha - 1$ which reduces to $\alpha > .544$. This α corresponds roughly to a separation, D , between U curves of $1.1H$ units. Other shapes for the U curves also give α values slightly above $1/2$ at the limiting similarity. Notice that in the above examples, the limiting α was independent of niche breadth (i.e. H)

but the limiting distance was measured in terms of H . Thus, the total number of species which can persist in a unidimensional array is the total environmental range divided by the niche breadth. This result assumes a uniform distribution of resources.

The foregoing results maximize the difficulty of invasion in that by placing the invader precisely between species 1 and 3 we built in a large α , relative to β . If we increase the subdivided niche space to two dimensions, then the three species could lie at the vertices of an equilateral triangle, and all ordering relations between them disappear. That is, $\alpha = \beta$. Hence, $2\alpha < 1 + \beta$ since $\alpha < 1$, and the three species can always coexist. This result extends readily to the coexistence of n species in an $n - 1$ dimensional niche-space. In other words, packing can be closer when niche dimensionality increases.

The case we have dealt with (equal K 's) is the most favorable to close packing of species. If we allow the K 's to vary, we can use equations (2) or (3) to distinguish successful invaders. For instance, if α, β are those for normal shaped U curves $\left(\alpha = e^{-\frac{D^2}{2H^2}}; \beta = e^{-\frac{2D^2}{H^2}} \right)$, then in the two species case, equation (2) shows that the species with smaller K (suppose it

to be species 1) can invade if $\frac{K_1}{K_2} > \alpha = e^{-\frac{D^2}{2H^2}}$. (Here, since we are using α as the competition between neighboring species, we substitute it for the β of equation [2].) Fig. (2) shows minimum D/H values for each $\frac{K_1}{K_2}$. Notice

that a small departure from equality of the K 's rapidly produces a positive minimum distance. As the figure shows, the effect of varying K on the success of a third species attempting to invade between two established ones is more complicated. If $K_1 = K_2 = K_3$ the invader (species 2) can insert itself between 1 and 3 provided $D/H > 1.1$. If $K_2 < K_1 = K_3 = \bar{K}$, then a greater separation is necessary as shown in the figure. On the other hand, if K_2 is much greater than \bar{K} , then species 2 can invade no matter how close 1 and 3 are, while if K_2 is barely greater than \bar{K} , it can invade if either 1 and 3 are exceedingly close or if they are rather different. If, for instance, $K_2 = 1.06\bar{K}$ then species 2 can invade if the distance between it and 1 or 3 is either greater than H or less than $.4H$. This startling invasibility between closely packed species can be explained by noticing that the combined equilibrium populations of species 1 and 3 are, when closely packed, virtually those of a single species. Species 2, with larger K can always invade such an assemblage. We shall refer to this figure again when we discuss evolutionary convergence.

In summary, we see that species packing can be close if the K 's are uniform, if the niche dimension is high, or if niche-breadth, H , is small. H tends to increase when the environment is uncertain and when food density is low, so that, in turn, packing can be tighter in a predictable or productive environment. These conclusions are qualitatively the same as those

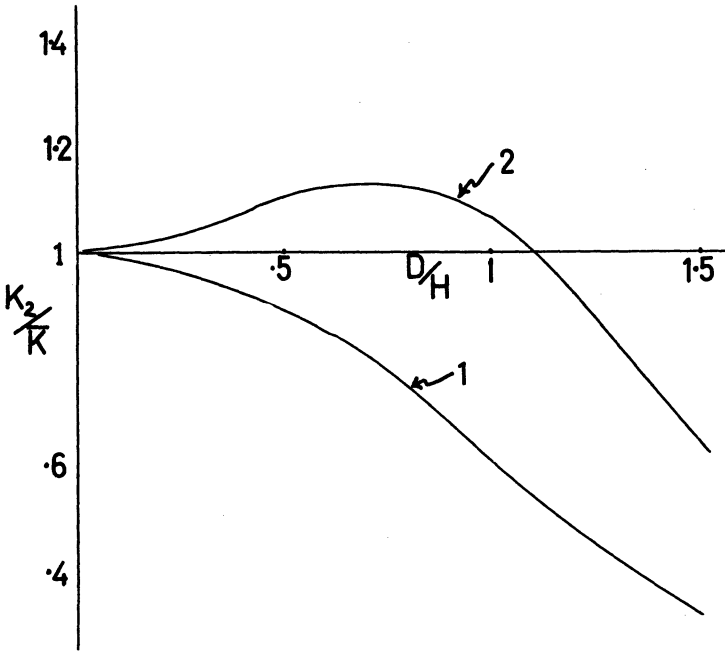


FIG. 2. The relation between minimum interspecies distance and the ratio of the species K values, for normal shaped U curves. K_2 is taken to be the K of the invader and \bar{K} the common K of the established species. The distance is measured by D/H where D is the intermodal distance and H is the standard deviation. The curve marked 1 represents distances when the invader finds a species present only on one side, while the curve marked 2 represents distances when the invader is sandwiched in line between two previous species. These represent the one dimensional situations in which invasion is (respectively) easiest and hardest.

which we reached from considering discrete renewable resources (MacArthur and Levins, 1964) suggesting that they apply more widely than the details of the model.

2. The evolution of limiting similarity

In the foregoing we have assumed the position and breadth of the species' niches are fixed, and have inquired whether they could persist. Here we ask how the position and breadth might be expected to change under the action of natural selection. We begin with changes in position only. For this purpose, we resort to the graphical analysis of Fig. 3 and 4 using the method of fitness sets. If the competing species are sufficiently different as in Fig. 3, the entering one should settle in between at phenotype Q . On the other hand, if the competing species are similar as in Fig. 4, the entering species should actually converge toward one of the competitors. In the figure, it should approach P or Q , provided there is a large linear array of competing species. Both the demographic and evolutionary arguments provide a limiting similarity, but these will not in general coincide. For instance, it may be that a species which would settle in an intermediate

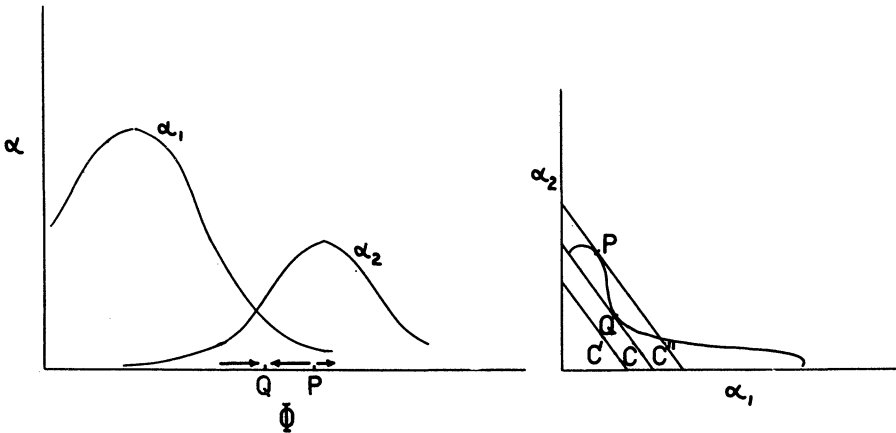


FIG. 3. In the left graph Φ represents phenotype, defined as the midpoint of the niche along some environmental axis. α_1 and α_2 are then the values of the competition coefficients due to the two competing species. The right hand graph shows which value of Φ results in the largest population for an intermediate species. Here the axes are α_1 and α_2 and the curve corresponds to the α_1 and α_2 curves in the left hand graph. It, therefore, represents all values of α_1 and α_2 open to the invading species. The straight lines C'' , C , C' satisfy the equations $K - \alpha_1 X_1 - \alpha_2 X_2 = C''$, C , C' , respectively (where X_1 and X_2 are treated as constants). Hence, lines nearer the origin represent decreasing competitive inhibition. Line C , tangent to the curve on the inside at Q , corresponds to the minimum possible competition. Conversely, point P represents a local maximum. Hence, to avoid competition, the species niche should move toward Q and away from P as shown in the left figure.

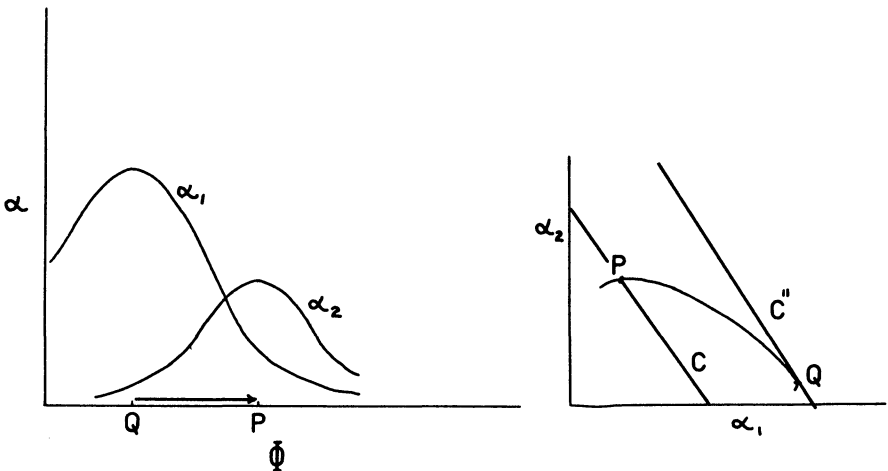


FIG. 4. Same as Fig. 3 except that now the α curves are nearer on the left hand graph causing the curve on the right hand graph to bulge outward. Although P and Q do not, in the figure, represent the best phenotypes for competing with existing species, they would be the best in an infinite linear array of competitors of which species 1 and 2 are just an adjacent pair. See text for further comments.

niche by the evolutionary argument would still be outcompeted. We can illustrate this possibility on the right hand sides of Fig. 3 and 4 by noting whether c , c' , and c'' are positive or negative constants. If c , for the point of tangency, is negative, then $K < \alpha_1 X_1 + \alpha_2 X_2$ and the invader will be outcompeted; if c is positive, the invasion will be demographically successful and therefore will have time to evolve. In the case of Fig. 3, the invader will evolve toward a phenotype intermediate between the competitors; and in the case of Fig. 4, it will converge toward one of them. This unexpected convergence would seem easily testable in laboratory experiments. For an example, if the U curves and hence the α values are normal,

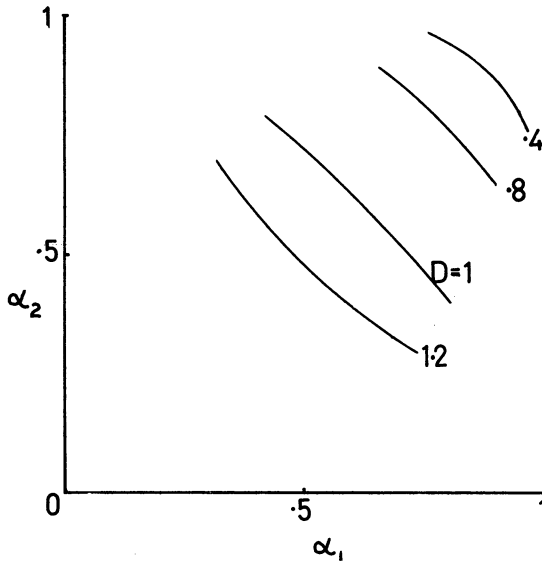


FIG. 5. Like the right hand sides of Fig. 3 and 4 but plotted from the data used in Fig. 2 for an invader sandwiched between two established species. Clearly, when $D/H < 1.1$ (which is, therefore, when $K_2 > \bar{K}$), the curve bulges inward indicating convergence. See text for further comments.

then Fig. 5 shows some α fitness sets, for varying values of D/H . Clearly, these bend inward for $D/H < 1.1$, i.e., when $\frac{K_2}{K} > 1$, as seen from Fig. 5.

Hence, in this case, only an invader with a K advantage will converge toward, and eliminate, one of the established ones.

So far our argument has been confined to the evolution of the position rather than the shape of the niche. It is clear that the shape of the niche is related to the proximity and abundance of competing species, but the precise argument is complex and we postpone its discussion to a later time.

SUMMARY

1. There is a limit to the similarity (and hence to the number) of competing species which can coexist. The total number of species is propor-

tional to the total range of the environment divided by the niche breadth of the species. The number is reduced by unequal abundance of resources but increased by adding to the dimensionality of the niche. Niche breadth is increased with increased environmental uncertainty and with decreased productivity.

2. There is a different evolutionary limit, L , to the similarity of two co-existing species such that

a) If two species are more similar than L , a third intermediate species will *converge* toward the nearer of the pair.

b) If two species are more different than L , a third intermediate species will *diverge* from either toward a phenotype intermediate between the two.

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