

Niche Overlap as a Function of Environmental Variability

(food size/birds/ecology/exclusion/model)

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ABSTRACT The relationship between environmental variability and niche overlap is studied for a class of model biological communities in which several species compete on a one-dimensional continuum of resources, e.g., food size. In a strictly unvarying (deterministic) environment, there is in general no limit to the degree of overlap, short of complete congruence. However, in a fluctuating (stochastic) environment, the average food sizes for species adjacent on the resource spectrum must differ by an amount roughly equal to the standard deviation in the food size taken by either individual species. This mathematical result emerges in a nonobvious yet robust way for environmental fluctuations whose variance relative to their mean ranges from around 0.01% to around 30%. In short, there is an effective limit to niche overlap in the real world, and this limit is insensitive to the degree of environmental fluctuation, unless it be very severe. Recent field work, particularly on bird guilds, seems in harmony with the model's conclusion.

One of the central concepts in ecology is the competitive exclusion principle, which forbids the coexistence of two or more species making their livings in identical ways. Recently, an increasing amount of attention has been paid to the questions: How similar can competing species be if they are to remain in an equilibrium community? How identical is "identical"? How close can species be packed in a natural environment?

An answer to these questions may begin by noticing that in laboratory experiments, where the environment can be carefully kept unvarying, species whose ecology is well-nigh identical have coexisted for long periods (1). A conjecture (2, 3) is that in the real world, environmental fluctuations will put a limit to the closeness of species packing compatible with an enduring community, and that species will be packed closer or wider as the environmental variations are smaller or larger.

Motivated by these ideas, we consider a one-dimensional resource spectrum, sustaining a series of species, each of which has a preferred position in the spectrum, and a characteristic variance about this mean position, as given by some "utilization function" (see Fig. 1). For example, the resource spectrum may be food size, and the consumers may be bird species each having a utilization function that describes their mean food size and its variance. The dynamics of this situation may be plausibly modeled by a system of first-order differential equations, with competition coefficients that depend on how closely species are packed; that is, on the degree of niche overlap (on the ratio of d to w in Fig. 1).

In the stability analysis of such models, two qualitatively different circumstances need be distinguished. In the un-

realistic case when all the environmental parameters are strictly constant (deterministic), then in general the system remains stable even if an arbitrarily large number of species are packed in, arbitrarily close. On the other hand, when the relevant environmental parameters fluctuate (stochastic environment), there is a limit to the niche overlap consistent with long-term stability.

However, this limit to species packing depends on the environmental variance in a far-from-obvious and extremely interesting way (Fig. 3). If the fluctuations in the resource spectrum are severe, having variances comparable in magnitude with their mean values, the species packing is indeed roughly proportional to the environmental variance, as one would expect intuitively. But for fluctuations ranging from moderate to exceedingly small, the species packing attains an effective limiting value roughly equal to the width of the utilization functions. Thus, as the ratio between the variance and mean value in the resource spectrum, or other pertinent environmental parameter, falls from 0.3 to 0.0001, the closest species packing consistent with stability falls only from 2 to 1 times the utilization function variance. Moreover, our general result is a robust one, being rather insensitive to the details of the mathematical model.

Collecting these statements, we observe that the species packing parameter d indeed goes to zero when the environmental variance becomes strictly zero, but that for any finite environmental variance, d remains roughly equal to the utilization function width, w . This result, which at first glance seems odd, reflects the technical fact that the mathematics contains an essential singularity around $d = 0$ (Eq. [6] and Fig. 2), so that there is a qualitative difference between an environmental variance that is small but finite, and one that is zero.

Following Hutchinson's (4) initial observations, Mac Arthur (3) has recently reviewed a body of semiquantitative work

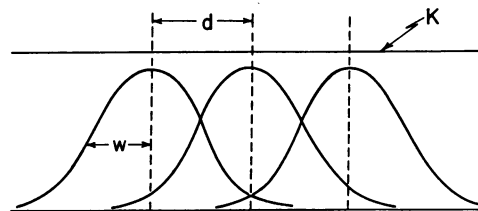


FIG. 1. The curve labeled K represents some resource continuum, say amount of food as a function of food size, that sustains various species whose utilization functions (characterized by a standard deviation w and a separation d) are as shown.

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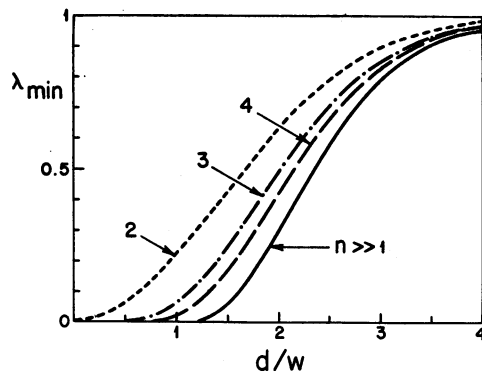


Fig. 2. The minimum eigenvalue of the stability matrix (Eq. [4]) as a function of niche overlap, d/w , for an n -species guild, where $n = 2, 3, 4$ and $n \gg 1$.

bearing on species packing and character displacement among competing species. These empirical data, which are discussed more fully in section IV, match the conclusions drawn from our model.

Two corollaries are worth mentioning.

First, most of the ideas advanced to account for the gradient in species diversity as one goes from the tropics to the poles may be summarized under three headings (1, 5): (i) as a matter of history, there has been more time for speciation in the tropics than most other places; (ii) total niche "volume" is greater in the tropics, which tend to be more productive, less seasonal, and more floristically complex, both in stratification and diversity; (iii) more niche overlap is permitted in the tropics by the unvarying environment. The potential number of species is the total volume [i.e., (ii)] divided by the effective niche volume per species [i.e., (iii)], and this potential will be realized if enough time is available [i.e., (i)]. The intuitive basis for the argument (iii) was set out in the second paragraph of this introduction, but the quantitative conclusion that niche overlap is only weakly dependent on the degree of environmental fluctuation (unless very severe) suggests that (iii) is a relatively unimportant factor in explaining the species diversity gradient, at least until one gets to extreme latitudes. It should be emphasized that our conclusion that species packing, d , is roughly proportional to utilization function width, w , implies only that niche overlap is largely independent of the environmental variance, σ^2 . It remains true that the total number of species packed into an interval on the resource spectrum is greater if they are specialists (small w) than if they are generalists (large w); the question as to what ultimately determines w remains open.

Second, in this model, which explicitly treats only one trophic level, it is obvious that greater complexity (in the form of more species, more closely packed) makes for lesser stability. In a perfectly stable deterministic environment, arbitrarily close packing and rich speciation is possible, and to a certain limited extent the greater the environmental steadiness, the closer the packing, and the richer the consequent assembly of species. Insofar as this example adds a piece to the complexity-stability jigsaw puzzle, it is that complexity is a fragile thing, permitted in this instance by environmental steadiness: this is quite the opposite of the conventional "complexity begets stability" wisdom (6).

The details of the model are outlined in section I, and the results derived in section II. Section III contains a short account of work bearing on the insensitivity of the main results to the details of the model.

I. THE MODEL DEFINED

Suppose one has a one-dimensional continuum of resources, such as food size, or vertical habitat, or horizontal habitat, that may be schematically depicted as in Fig. 1, where the curve labeled K shows amount of food as a function of food size, or amount of habitat as a function of height, and, in general, amount of resource as a function of x . Suppose further that this resource sustains various species, each of which has a utilization function $f(x)$ as depicted in Fig. 1, which characterizes the species' use of the resource spectrum. In particular, we note the mean position and the standard deviation, w , about this mean for the various species; i.e., the mean and the variance of the food size, or of the habitat height, etc. The separation, d , between the mean positions of species that are adjacent on the resource continuum will clearly be a measure of how densely the species are packed.

Mac Arthur (3, 7) has established a criterion that ensures that the actual community utilization of the resource will provide the best least-squares fit to the available resource spectrum. This requires the populations of the n species, $N_i(t)$ [labeled sequentially $i = 1, 2, \dots, n$], to obey

$$\frac{dN_i(t)}{dt} = N_i(t) \left[k_i - \sum_{j=1}^n \alpha_{ij} N_j(t) \right] \quad [1]$$

where the k_i are integrals with respect to x over the product of the resource spectrum and the utilization function of the i th species, and the competition coefficients α_{ij} are convolution integrals between the utilization functions of the i th and j th species. With this, we are assured both that the equilibrium populations (obtained by setting all $d/dt = 0$) minimize the squared difference between available and actual "production," and also that nonequilibrium initial populations will move in time towards this minimum configuration.

Eq. [1] is, of course, the Lotka-Volterra competition equation, but tied to the underlying model illustrated by Fig. 1, so that we have explicit recipes for the k_i and α_{ij} in terms of direct biological assumptions. Specifically, if we assume that all the species' utilization functions are the usual bell-shaped gaussian curves, with common width w , and that they are uniformly spaced along the resource continuum (common d), the competition coefficients are

$$\alpha_{ij} = (w^2\pi)^{-1/2} \int_{-\infty}^{\infty} dx \exp \left[-\frac{x^2}{2w^2} - \frac{(x - (i-j)d)^2}{2w^2} \right] = [\alpha]^{(i-j)^2}, \quad [2]$$

where we have for notational convenience defined

$$\alpha = \exp(-d^2/4w^2). \quad [3]$$

Quite apart from the teleology implicit in the assumption that communities minimize anything, a choice of fit other than least-squares will lead to equations superficially different from [1]: however, their competition matrix characterizing small displacements from equilibrium will end up similar to that given below. As Lotka (8), and others since, have emphasized, Eq. [1] represents the first term in a Taylor expansion of a much wider class of equations, and thus should be useful in discussing the stability of potential equilibria.

In the stability analysis of equations such as [1], we first find the equilibrium populations, N_i^* , and then study small-amplitude perturbations by linearizing about this equilibrium. As a further simplification in our model, we rather arbitrarily choose the resource spectrum to be such that the community best-fit to it (i.e., the equilibrium community) has equal populations for all species; for a large number of species, $n \gg 1$; this means a flat resource spectrum. The conventional analysis then shows the stability of the system to be given simply by the eigenvalues of the $n \times n$ competition matrix A , which from [2] has the form

$$A = \begin{bmatrix} 1 & \alpha & \alpha^4 & \alpha^9 & \dots & \alpha^{n^2} \\ \alpha & 1 & \alpha & \alpha^4 & \dots & \dots \\ \alpha^4 & \alpha & 1 & \alpha & \dots & \dots \\ \alpha^9 & \alpha^4 & \alpha & 1 & \dots & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \\ \alpha^{n^2} & \dots & \dots & \dots & \dots & 1 \end{bmatrix} \quad [4]$$

In short, in this section we have made several particular assumptions, which have given a specific form for the competition matrix, namely [4]. Indeed, this is a form that can be plausibly justified from quite *ad hoc* considerations. In general, the system stability, and hence the permissible degree of niche overlap, hinges upon some such competition matrix. Other assumptions could give other (but similar) matrices, and the extent to which our conclusions are or are not tied up with the specific model outlined here is discussed in section III.

II. THE MODEL ANALYZED

Deterministic environment

As just described, all the parameters in our model system are unvarying constants. Consequently the equilibrium configuration is stable, with perturbations damping out, so long as all the eigenvalues, λ , of A are positive (notice that a minus sign was absorbed in the definition of the competition matrix). But A is a positive definite form for all $0 \leq \alpha < 1$ (i.e., for all d , see Eq. [3]), with the consequence that stability sets no limit to the species packing in a strictly deterministic environment. Moreover, in general the more species packed in, the better the least-squares fit to the resource spectrum.

Nevertheless it is interesting to see how the *smallest* eigenvalue of A , which sets the stability character, varies with niche overlap, as measured by d/w . For $n \gg 1$, we have (see Appendix)

$$\lambda_{\min} = 1 - 2\alpha + 2\alpha^4 - 2\alpha^9 + 2\alpha^{16} - \dots \quad [5]$$

This series may be summed, by an elegant method, to get an approximation that is very accurate unless $d \gg w$ (see Appendix):

$$\lambda_{\min} = 4\pi^{1/2}(w/d) \exp[-\pi^2 w^2/d^2]. \quad [6]$$

This is a remarkable result. For substantial niche overlap, i.e., d/w small, λ_{\min} tends to zero faster than any finite power of d/w : there is an essential singularity at $d/w = 0$. Thus, although λ_{\min} is indeed necessarily positive even for small d/w , it becomes exceedingly tiny, corresponding to extremely long damping times. This result foreshadows the results below.

Fig. 2 illustrates Eq. [6], along with numerical results for $n = 2, 3, 4$. Notice that for practical purposes, $n = 4$ is hard to distinguish from " $n = \infty$ ".

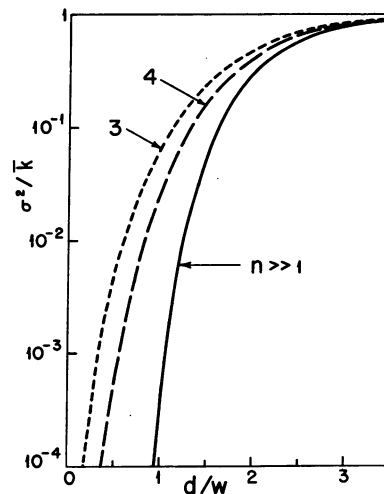


FIG. 3. The closest niche overlap, d/w , consistent with community stability in a randomly varying environment, whose fluctuations are characterized by a variance (relative to the mean) of σ^2/\bar{k} . The variance is plotted on a logarithmic scale to emphasize that, over a wide range, it has little influence on the species packing distance for $n > 2$.

Stochastic environment

More realistically, there will be random environmental fluctuations, so that the resource continuum will be noisy. This means the quantities k_i in Eq. [1] will not be constants, but rather will be random variables. We assume

$$k_i = \bar{k}_i + \gamma_i(t) \quad [7]$$

where \bar{k}_i is the constant mean value (having the common value \bar{k} for large n), and $\gamma_i(t)$ is gaussian "white noise", with variance measured by σ^2 .

In this stochastic problem, we may no longer talk of the species populations, but only of their joint probability distribution. To a good approximation, this is a multivariate normal distribution in the fluctuations about the means, and the probability of any species becoming extinct will be small (corresponding to the mechanical "stability" of the deterministic case) if the smallest eigenvalue of the competition matrix A roughly obeys

$$\lambda_{\min} > \sigma^2/\bar{k} \quad [8]$$

This result (9) is commonsensical. In a randomly fluctuating environment, it is not enough that all the eigenvalues be positive, but rather they should be bounded away from zero by an amount roughly proportional to the environmental noise level.

Combining the qualitative equation, [8], with Fig. 2, we arrive at an estimate of the closest species packing, d/w , consistent with stability for a given environmental noise level, σ^2/\bar{k} . These results, illustrated in Fig. 3, are as discussed in the Introduction.

In particular, we see explicitly from Eq. [6] that for large n this closest degree of niche overlap depends on the environmental fluctuations only as $\sqrt{\ln \sigma^2}$, a very weak dependence. The results for $n = 3, 4$, although allowing a slightly closer limiting packing distance, display a similar insensitivity to the degree of random fluctuation, so long as it is not severe.

III. HOW ROBUST ARE THESE RESULTS?

The question arises, to what extent are these results peculiar to our particular model? We catalogue some answers.

(i) We chose gaussian utilization functions. Alternative $f(x)$ ranging from the opposite extremes of rectangles through to back-to-back exponentials or Lorentz lineshapes lead to \mathbf{A} matrices different from [4], but the plot of λ_{\min} as a function of d/w retains the essential features of Fig. 2 in all cases.

(ii) We chose the width and separation of the utilization functions to be constant. If the width w changes in some systematic way along the resource continuum, our results are preserved, as long as the separation d changes in the same proportion, keeping d/w roughly constant.

(iii) The resource spectrum of Fig. 1 was assumed to be such that, at equilibrium, all populations are equal. Extensive investigation of various resource spectrum shapes for $n = 2, 3,$ and 4 suggests that our results are not dependent on this feature, so long as all species are present in significant numbers in the equilibrium community.

(iv) The implications of use of Eq. [1] were discussed in section I.

(v) The stochasticity of the environment was taken to be gaussian "white noise," i.e., no correlation between the fluctuations at successive instants. In practice, this means only that fluctuations be correlated over times short compared to all other relevant time scales in the system (9).

(vi) Our model is for competition in one resource dimension. Cody's (10) classification of partitioning in the three-resource dimensions of horizontal habitat, vertical habitat, and food for 10 grassland bird communities around the world shows eight of them to be organized largely in one dimension (food selection), so that our model is not wholly unreasonable. Moreover, the model is directly relevant to niche overlap in two or more orthogonal resource dimensions, and may even be useful as a metaphor for more complicated circumstances.

IV. COMPARISON WITH REAL ECOSYSTEMS

In a classic paper, Hutchinson (4) observed that in various circumstances, including both vertebrate and invertebrate forms, character displacement among sympatric species leads to sequences in which each species is roughly twice as massive as the next; i.e., linear dimensions as measured by bills or mandibles in the ratio 1.2–1.4. Mac Arthur's more recent and quantitative reviews (3) of such data point to there being a limiting value to niche overlap in the natural world, corresponding to d/w in the range 1–2. Also pertinent is Simpson's (11) review of the factors making for latitudinal and altitudinal species diversity gradients among North American mammals; it concludes that degree of niche overlap is not an important contributing factor.

The work that seems to come closest to our one-dimensional model is that of Terborgh, Diamond, and Beaver on various guilds of birds in an assortment of habitats that have various degrees of environmental stability. Even so, such comparisons with the theory are necessarily approximate, partly because our α (Eq. [3]) comes from utilization functions that are not just percentage of time or of diet, but rather have weighting terms for resource renewal (3, 7): all available information from nature contains unweighted utilizations.

Terborgh (12) has shown five species of tropical antbird, segregating by foraging height, have mean heights separated

by one standard deviation; i.e., $d/w \simeq 1$. Mac Arthur's analysis (3) of Storer's data (13) on the food weight distribution for three congeneric species of hawks also leads to $d/w \simeq 1$. Diamond's (14) extensive data on weights of tropical bird congeners that sort out largely (but not wholly, so that d/w should be smaller than our one-dimensional theory predicts) by size differences leads to weight ratios around 1.6–2.3; when Hespeneide's analysis (15) of the relation between weight ratio and α is used, Diamond's results become $\alpha \simeq 0.8-0.9$, i.e., $d/w \simeq 0.6-1.0$. In the Sierra Nevada, Beaver (personal communication) has shown that species packing in a brushland bird community appears equal to that in a forest foliage gleaning guild, although the microenvironment is thought to be significantly more unvarying in the forest.

In brief, the basic conclusion that emerges in a nonobvious but robust way from our mathematical model, namely that there is a limit to niche overlap in the natural world and that this limit is not significantly dependent on the degree of environmental fluctuation (unless it be severe, as in the arctic), seems to be in harmony with such facts as are known about real ecosystems.

APPENDIX

For large n , where "end effects" at the extremes of the resource spectrum are unimportant, we may pretend that the resource continuum is cyclic (so that the species labeled 1 adjoins that labeled n), whereupon the competition matrix \mathbf{A} of Eq. [4] is slightly modified to become related to a class of matrices discussed by Berlin and Kac (16). Using their approach, one can obtain Eq. [5]. That this trick of imposing artificial cyclic boundary conditions does not alter the eigenvalues for $n \gg 1$ is a point made clear in the literature on the physicists' Ising model, from which comes Berlin and Kac's paper.

The series in Eq. [6] is identically equal to the contour integral

$$\frac{1}{2i} \oint_C \frac{\exp(z^2 \ln \alpha) dz}{\sin(\pi z)}$$

Here the contour C encloses all poles of the integrand up to $z = \pm n$, where the series has n terms. An $n \rightarrow \infty$, C is the circle at infinity in the complex plane. Using the standard Jordan contour, and ignoring correction terms of relative order $\exp(-4\pi^2 w^2/d^2)$, which are thoroughly negligible for $d/w < 3$ or so, we arrive neatly at Eq. [6].

At the other extreme, for $n = 2$ the eigenvalues of \mathbf{A} are easily found directly. For other finite values, such as $n = 3, 4$, we take a meat axe and display λ_{\min} as a numerical function of d/w .

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