

## Niche Overlap and Diffuse Competition

(desert lizards/resource partitioning/community structure/species diversity)

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Communicated by Edward O. Wilson, March 11, 1974

**ABSTRACT** Current theory predicts a distinct upper limit on the permissible degree of niche overlap; moreover, theory suggests that maximal tolerable overlap should be relatively insensitive to environmental variability. Data presented here demonstrate that, within the lizard subset of natural desert communities, niche overlap decreases both with increasing environmental variability and with increasing numbers of lizard species. The latter two factors are themselves positively correlated. A partial correlation analysis is interpreted as indicating that the extent of tolerable niche overlap does not necessarily decrease due to environmental variability, but rather that overlap is probably more closely related to the number of potential interspecific competitors in a community, or what has been termed "diffuse competition." This result lends support to the "niche overlap hypothesis," which asserts that maximal tolerable overlap should vary inversely with the intensity of competition. Moreover, this empirical discovery indicates that niche overlap theory could be profitably expanded to incorporate the number of competing species. Although the average amount of overlap between pairs of species decreases with the intensity of diffuse competition, the overall degree of competitive inhibition tolerated by individuals comprising an average species could nevertheless remain relatively constant, provided that extensive niche overlap with a few competitors is roughly equivalent to lower average overlap with a greater number of competitors.

### NICHE OVERLAP THEORY

The ways in which species within ecological communities partition available resources among themselves is a major determinant of the diversity of coexisting species. All else being equal, a community with more resource sharing, or greater niche overlap, will clearly support more species than one with less niche overlap. In attempts to understand competition and determinants of species diversity, population biologists have reasoned that coexisting species must differ in their ecological requirements by at least some minimal amount to avoid competitive exclusion. Such thinking has led to the related concepts of "character displacement" (1), "limiting similarity" (2), "species packing" (3, 4), and "maximum tolerable niche overlap," which is simply the notion that there must be an upper limit on the permissible degree of niche overlap (5-8).

May and MacArthur (5) recently developed an elegant analytic model of niche overlap as a function of environmental variability. Their theory predicts an upper limit on the degree of tolerable overlap; moreover, the derivation suggests that maximal permissible overlap should be relatively insensitive to both number of species and environmental variability. The May-MacArthur niche overlap model assumes an equilibrium

community in a fully saturated environment with all resources being used fully; as such, variation in the intensity of competition is not modelled (see also next paragraph). The model assumes a one-dimensional resource spectrum, but May (7) recently indicated that the argument can be expanded without qualitative change to a multidimensional niche space. In development of this theory, May and MacArthur express the inverse of niche overlap as a ratio of the distance between the centers of two "utilization curves" (niche separation) over the standard deviation in utilization (niche breadth), with the latter assumed to be constant and identical for all species. Their model thus somewhat confounds niche overlap and niche breadth.

Estimates of overlap in resource utilization have often been equated with the "competition coefficients" or "alphas" of the much overworked Lotka-Volterra competition equations:

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

where  $i$  and  $j$  subscript each of the  $n$  different species,  $N_i$  is the abundance of the  $i$ th species,  $r_i$  is its maximal intrinsic rate of increase per capita,  $K_i$  is the "carrying capacity" of species  $i$ , and  $\alpha_{ij}$  represents the per capita competitive inhibition of species  $j$  on the population growth rate of species  $i$ . Alphas are extremely difficult to estimate directly except by population removal experiments, and ecologists have often equated estimates of overlap with competition coefficients (9). However, tempting though it may be, equating overlap with competition is an extremely dubious and misleading procedure (10, 11). Clearly niche overlap, in itself, need not necessitate competition; in fact, there may often be an inverse relationship between overlap and competition. If resources are not in short supply, two organisms can share them without detriment to one another. Thus, extensive niche overlap may actually be correlated with *reduced* competition. Similarly, disjunct niches may often indicate avoidance of competition in situations where it could potentially be severe. Such reasoning led me to propose that maximal tolerable niche overlap should be lower in intensely competitive situations than in environments with lower demand/supply ratios; I termed this the "niche overlap hypothesis" (8).

### Diffuse competition

MacArthur (4) coined the term "diffuse competition" to describe the total competitive effects of a number of interspecific competitors. To illustrate the concept, consider Eq.

1. At equilibrium, all  $dN_i/dt$  must equal zero; that is

$$N_i^* = K_i - \sum_{j \neq i}^n \alpha_{ij} N_j \quad [2]$$

where  $N_i^*$  is the equilibrium abundance of species  $i$ . Eq. 2 must be true for all  $i$  at equilibrium. Note that the term,  $-\sum_{j \neq i}^n \alpha_{ij} N_j$ , increases with the number of competing species,  $n$ , and that the equilibrium abundance of species  $i$ ,  $N_i^*$ , decreases as one sums over a greater number of competitors. Further, note that a little bit of competitive inhibition by a lot of other species (diffuse competition) can be equivalent to strong competitive inhibition by fewer competing species.

#### DESERT LIZARD COMMUNITIES

A series of 28 study areas at similar latitudes on three continents support from 4 to 40 sympatric species of desert lizards (12–14). Estimated species densities and lizard species diversities for these sites have been given elsewhere (14). My assistants and I recorded data on microhabitat, time of activity, and stomach contents of over 15,000 lizards of some 91 species on these desert study areas, which I use for the following analysis of niche overlap. Results presented rather briefly here are documented more fully elsewhere (14).

#### Environmental variability

In deserts, water is a master limiting factor, and long-term mean annual precipitation is very strongly correlated with average annual productivity. Moreover, standard deviation in annual precipitation can be considered an indicator of environmental variability since year-to-year variation in annual precipitation should generate temporal variability in food availability. I estimated both the long-term mean and standard deviation in annual precipitation from nearby weather stations for most study areas. Both precipitation statistics are significantly correlated with lizard species densities and diversities ( $r_s > 0.41$ ,  $P_s < 0.05$  to  $0.001$ ).

#### Niche dimensionality

Although some pairs of sympatric competitors avoid competition primarily through differences in the use of a single resource gradient or niche dimension, it is far more prevalent for coexisting species to differ in their use of two or more niche dimensions simultaneously. Pairs with high overlap along one dimension often overlap relatively little along another, reducing overall effective niche overlap [see figure 6.7, page 198 in Pianka (11) and/or figure 1 in May (16)].

Like most animals, desert lizards subdivide resources in three major ways: they differ in what they eat, where they forage, and when they are active. Ecological differences in each of these three niche dimensions should reduce competition and thus facilitate coexistence of a variety of species. It is difficult or impossible to evaluate the degree of interdependence of these three niche dimensions for most lizard species because the animals move and are active over a period of time. However, the degree to which foods eaten depend upon microhabitat can be assessed in some relatively sedentary subterranean skinks (15); in these lizards, diet and microhabitat appear to be largely independent. Clear interactions among niche dimensions are apparent in other cases (13, 14). The vast majority of interspecific pairs of sympatric lizard species have substantial niche separation along one or more of

these three niche dimensions (trophic, spatial, and/or temporal), making it unnecessary to subdivide the three basic dimensions any further to analyze resource partitioning in these lizard communities.

Niche dimensionality has another important aspect: the number of potential neighbors in niche space increases more or less geometrically with the number of niche dimensions actually subdivided (4, 14). Hence a greater number of effective niche dimensions provides a greater potential for diffuse competition.

#### Niche overlap

Overlap has been quantified in numerous ways (2, 9, 10, 13). The particular overlap index used is somewhat arbitrary since similar qualitative results are obtained with a wide variety of indices. Here I use the following modification (13) of the equation first proposed by MacArthur and Levins (2) and Levins (12) for estimating competition coefficients, or alphas, from field data on resource utilization:

$$O_{jk} = O_{kj} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where  $p_{ij}$  and  $p_{ik}$  represent the proportions of the  $i$ th resource used by the  $j$ th and  $k$ th species. May (16) discusses a mathematical rationale for the convenience of this symmetric measure over the original asymmetric form. I do not consider values obtained from this equation "competition coefficients," but rather merely measures of niche overlap (see above and refs. 10 and 11 for further discussion of the distinction between overlap and competition).

Thus calculated, the average extent of overlap along various dimensions differs among the three continental desert-lizard systems (Table 1). For example, overlap in microhabitat is high in North America where many lizards frequent the open spaces between plants, whereas dietary overlap is high in the Kalahari desert of southern Africa where termites dominate the diets of many species of lizards (13). Overlap is relatively low along all three niche dimensions in the most diverse lizard communities of Australia (13, 14).

Estimating overall niche overlap along three dimensions is difficult and can be quite treacherous (16). Ideally, a proper multidimensional analysis of resource utilization and niche separation along more than a single niche dimension should proceed through estimation of the simultaneous proportional utilization of all resources along each separate niche dimension. Thus, one would like to work with the proportion of prey type  $i$  captured in microhabitat  $j$  by species  $k$ , or the true multidimensional  $p_{ijk}$ s. However, in practice it is extremely difficult or even impossible to obtain such multidimensional utilization data, because animals usually integrate over both space and time (stomachs contain prey captured over a period of time and in a variety of microhabitats). Some progress toward understanding overall niche overlap along several dimensions can, however, be made using only the proportional utilizations along each of the component niche dimensions, as follows (for greater detail, see ref. 16).

Provided that niche dimensions are truly independent (orthogonal), with for example any given prey item being equally likely to be captured in any microhabitat, overall

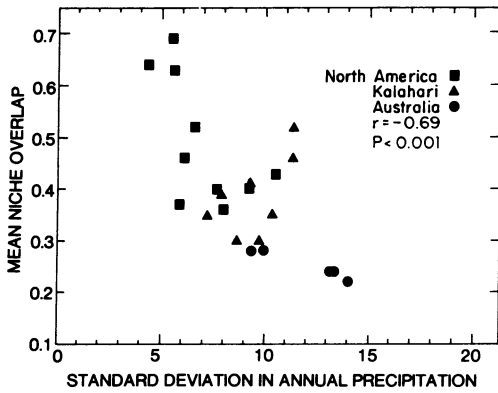


FIG. 1. Average overall summation niche overlap plotted against the standard deviation in annual precipitation. Continents coded by *shape*, as indicated. Although none of the correlations within continental desert systems is significant, the correlation coefficient for all areas is highly significant statistically. However, when the number of lizard species on various areas is held constant by partial correlation, this correlation disappears. Compare with Fig. 2.

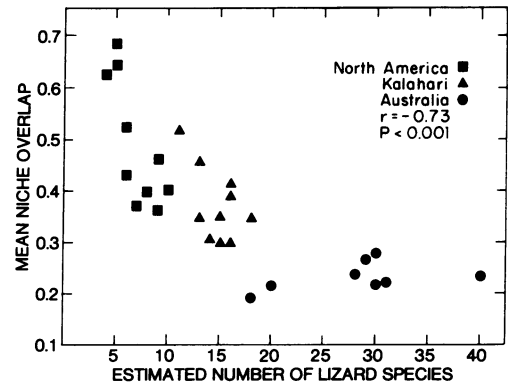


FIG. 2. Average overall summation niche overlap plotted against the estimated number of lizard species. Continents coded by *shape*, as indicated. Similar inverse correlations exist with overall multiplicative overlap values and with three different estimates of maximal tolerable niche overlap (see *text*).

multidimensional utilization is simply the product of the separate unidimensional utilizations (16); that is,  $p_{ijk} = p_{ik} \times p_{jk}$ . In this case, overlaps along component niche dimensions can simply be multiplied to estimate overall multi-

dimensional niche overlap (16). However, should niche dimensions be entirely dependent upon one another (with for example, each prey type occurring in only a particular microhabitat), there is actually only a single resource dimension. Under such complete dependency, true "multidimensional" overlap is best estimated by the arithmetic mean of the overlaps along component dimensions; such "summation over-

TABLE 1. Estimates of the number of lizard species and average niche overlap values for 28 desert study areas on three continents

No. of lizard species	Average niche-overlap			Estimates of average overall niche overlap				
	Food	Microhabitat	Time	Multiplicative		Summation	Largest tenth	
				(All)	(Nonzero)		(Multiplicative)	(Summation)
<i>North America</i>								
4	0.49	0.80	0.58	0.20	0.20	0.63	0.41	0.76
5	0.75	0.78	0.53	0.33	0.36	0.69	0.73	0.90
5	0.52	0.92	0.49	0.25	0.36	0.64	0.71	0.90
6	0.55	0.55	0.47	0.22	0.37	0.52	0.61	0.86
6	0.34	0.55	0.20	0.12	0.27	0.43	0.57	0.75
7	0.39	0.42	0.31	0.11	0.39	0.37	0.52	0.82
8	0.56	0.31	0.32	0.10	0.24	0.40	0.37	0.74
9	0.28	0.52	0.58	0.11	0.23	0.46	0.50	0.82
9	0.38	0.32	0.39	0.06	0.18	0.36	0.37	0.70
10	0.37	0.33	0.50	0.08	0.25	0.40	0.20	0.76
<i>Kalahari</i>								
11	0.92	0.35	0.28	0.18	0.41	0.52	0.69	0.89
13	0.36	0.39	0.30	0.08	0.26	0.35	0.50	0.80
13	0.56	0.47	0.34	0.13	0.36	0.46	0.61	0.85
14	0.56	0.21	0.15	0.04	0.27	0.31	0.19	0.61
15	0.45	0.23	0.21	0.04	0.22	0.30	0.31	0.70
15	0.56	0.25	0.24	0.06	0.23	0.35	0.44	0.76
16	0.72	0.22	0.23	0.09	0.35	0.39	0.64	0.85
16	0.44	0.22	0.24	0.05	0.22	0.30	0.34	0.73
16	0.71	0.28	0.26	0.11	0.36	0.42	0.69	0.88
18	0.51	0.26	0.27	0.07	0.24	0.35	0.44	0.77
<i>Australia</i>								
18	0.23	0.16	0.18	0.01	0.14	0.19	0.08	0.59
20	0.18	0.36	0.13	0.01	0.02	0.22	0.10	0.54
28	0.25	0.32	0.16	0.03	0.21	0.24	0.23	0.65
29	0.27	0.30	0.27	0.04	0.23	0.28	0.29	0.69
30	0.23	0.24	0.19	0.02	0.19	0.22	0.14	0.59
30	0.37	0.24	0.27	0.03	0.18	0.28	0.26	0.66
31	0.19	0.28	0.18	0.02	0.16	0.22	0.14	0.60
40	0.23	0.25	0.22	0.02	0.15	0.24	0.19	0.61

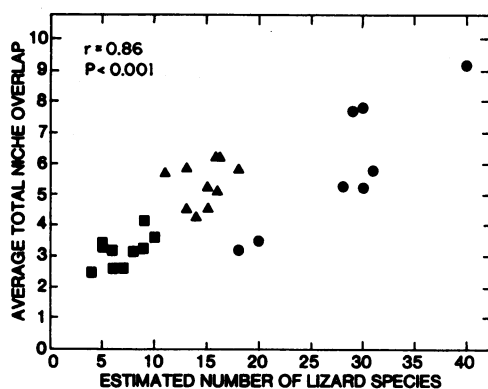


FIG. 3. Average total niche overlap (summation) plotted against the estimated number of lizard species, to show that total niche overlap increases with lizard species density even though overlap between average pairs of species decreases (compare with Fig. 2). Continents coded by shape as in previous figures.

laps" constitute upper bounds on the true multidimensional overlap (16). Since real niche dimensions are presumably seldom, if ever, either perfectly independent or perfectly dependent, neither the multiplication nor the summation technique is entirely satisfactory. Summation overlaps generally overestimate true niche overlap, whereas multiplicative overall overlaps often underestimate true multidimensional niche overlap (16).

In an attempt to overcome these very considerable difficulties, I computed estimates of overall overlap by both multiplication and summation of the overlaps along the three component niche dimensions (Table 1). When overlaps along the three dimensions are multiplied, the vast majority of interspecific pairs overlap very little or not at all (13, 14). The possible number of such nonoverlapping pairs increases markedly with the size of overall niche space, which is greater in more diverse saurofaunas (13, 14). Overlap between those pairs with some overlap is of greatest interest as it should reflect limiting similarity and/or maximal tolerable overlap. Average overlap values for each niche dimension in the various desert systems are listed in Table 1, along with means of all multiplicative overlaps and all summation overlaps (recall that the latter represent upper bounds on the true multidimensional overlap). Means of all nonzero multiplicative overlap pairs and the averages of the largest tenth of all multiplicative and summation overlaps are also given, as these are more likely to reflect maximal tolerable overlap. All five methods of estimating overall overlap produce strongly correlated values ( $r_s = 0.67$  to  $0.97$ ,  $P_s < 0.01$  to  $0.001$ ). Estimates of overall niche overlap are strongly correlated with both the standard deviation in precipitation (Fig. 1) and with the number of lizard species (Fig. 2). At first glance, Fig. 1 seems somewhat at odds with May and MacArthur's prediction that maximal overlap should be insensitive to environmental variability. However, the overlap values used here are not entirely appropriate for testing the May-MacArthur theory, since this model is expressed in terms of the ratio of niche separation over niche breadth, effectively the inverse of niche overlap scaled by niche breadth. To approximate conditions of their model more closely, I estimated niche separation as one minus overlap for all interspecific pairs in each continental desert-lizard system, and expressed these values as ratios of separation over standardized niche breadths (Table

TABLE 2. Means and 95% confidence limits on ratios of niche separation over niche breadth

Niche dimension	North America	Kalahari	Australia
Food	3.73(2.87-4.59)	2.51(2.21-2.81)	5.18(5.0-5.36)
Micro-habitat	5.79(4.83-6.74)	4.23(3.85-4.61)	4.60(4.48-4.72)
Time	2.78(2.0-3.56)	5.08(4.48-5.68)	5.11(4.93-5.29)
Overall	0.50(0.38-0.62)	1.54(1.16-1.92)	1.03(1.0-1.06)

2). Such an analysis modified results presented in Figs. 1 and 2 only slightly. Distinct differences among the three continents are still apparent. Moreover, an area-by-area analysis also shows that niche separation over niche breadth ratios tend to increase with lizard species density. Clearly niche separation over niche breadth ratios are not constant between the three desert systems.

I used partial correlation analysis in an attempt to interpret factors influencing niche overlap. When the effects of lizard species density are held constant by partial correlation, average overall summation overlap and mean nonzero multiplicative overlap do not remain significantly correlated with the standard deviation in precipitation. However, the inverse correlations between lizard species density and both measures of overall niche overlap remain significant at the 0.01 level when standard deviation in precipitation is held constant by partial correlation. These results suggest that, as predicted, the extent of tolerable niche overlap is not necessarily a function of the degree of environmental variability, but rather that maximal overlap is more closely related to the number of competing species and the intensity of diffuse competition.

Evidently, stronger diffuse competition requires greater average niche separation among coexisting lizard species. Low overlap with lots of competitors may be similar to high overlap with fewer interspecific competitors. Rather than remaining constant, niche overlap seems to be adjusted to the number of competing species, perhaps resulting in a relatively constant level of interspecific competitive inhibition for an average species even in communities that differ widely in diversity. A first hypothesis might be that total overlap with sympatric species remains constant; Fig. 3 shows that total overlap actually increases with lizard species density, even though the average amount of overlap between pairs decreases.

In conclusion, empirical results presented here support the niche overlap hypothesis, which predicts that maximal tolerable niche overlap should decrease with increasing intensity of competition. Moreover, these data indicate that niche overlap theory needs to be modified to incorporate more fully the phenomenon of diffuse competition.

This research was supported by grants from the National Science Foundation (GB-5216, GB-8727, and GB-31006).

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