4
NICHE OVERLAP

NICHE OVERLAP AND LIMITING SIMILARITY

Historically, analyses of niche overlap were based on the theory of limiting similarity (MacArthur and Levins 1967). This model predicts the coexistence of species and the overlap in their utilization of resources along a single, ordered resource dimension. The overlap of species 2 on species 1 in resource use is calculated as

$$\alpha = \frac{\int U_1(R)U_2(R)dR}{\int [U_1(R)]^2 dR} \qquad (4.1)$$

where $U_1(R)$ and $U_2(R)$ are the utilization functions for species 1 and 2, respectively. Overlaps calculated this way have been equated with the competition coefficients of the Lotka-Volterra equations (Levins 1968). In other words, the amount of overlap in resource utilization is assumed to be proportional to the intensity of competition between two species (Schoener 1974b).

Community change in the limiting similarity model comes about through repeated colonization and extinction of species with different utilization curves. If adjacent species are "too close" together, one of the pair will go extinct, depending on the overlap and the carrying capacity of the environment, as dictated by the Lotka-Volterra equations (Schoener 1986a). On the other hand, if two species are widely separated on the resource axis, a third species can be sandwiched between them. After repeated colonizations and extinctions, an equilibrium will be established, with a maximum number of coexisting species separated by a critical minimum spacing (Figure 4.1).

The prediction of a limit to similarity is sensitive to a number of assumptions, including: (1) the normality of the resource utilization curves (Rough-garden 1974); (2) the measurement of overlap by Equation 4.1 (Abrams 1975); (3) the linearity of the zero isoclines assumed by the Lotka-Volterra model
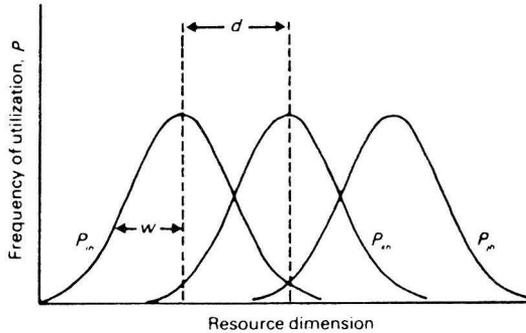
Figure 4.1. Resource utilization and limiting similarity in the MacArthur and Levins (1967) model. The model predicts a limit (d/w) to the similarity of competing species. This theory motivated a vast amount of ecological research into patterns of niche overlap, but relatively few studies have compared overlap patterns to an appropriate null model. From Schoener (1986a), with permission.

(Schoener 1976a); (4) the presence or absence of environmental stochasticity (May and MacArthur 1972; Turelli 1978a,b).

NICHE OVERLAP AND EVOLUTIONARY DISPLACEMENT

Limiting similarity models predict a reduction in niche overlap of competitors through ecological assortment of colonization and extinction. A second set of models also predicts a reduction in niche overlap through genetic change in competing populations that causes evolutionary shifts in niche position and/or niche width (Bulmer 1974). These models were inspired by the pattern of character displacement in allopatric versus sympatric populations (Brown and Wilson 1956) and by Hutchinson's (1959) suggestion that competing species might differ in body size by a constant ratio (see Chapter 6). These models are sensitive to the amount of within- and between-phenotype variance (Taper and Case 1992), whether or not resources are completely utilized (Milligan 1985), and the symmetry of resource use between species (Slatkin 1980). Depending on the underlying assumptions, some of these models predict a substantial displacement of competitors (Gotelli and Bossert 1991; Taper and Case 1992); others predict little displacement, or even convergence of utilization phenotypes (Slatkin 1980; Abrams 1986).

TESTING NICHE OVERLAP PATTERNS

The central prediction of both ecological and evolutionary models of displacement is that species should overlap less in resource use than they would in the absence of competition (Schoener 1974a). How has this body of ecological theory been treated in empirical analyses? First, empiricists have largely abandoned the idea of discovering a "magic number" for limiting similarity or body size differences (see Chapter 6). Instead, the qualitative prediction that competition should lead to reduced overlap has been investigated. Early analyses focused on the description and quantification of resource use (Schoener 1986a). If one had faith in the underlying theory of limiting similarity and character displacement, then utilization differences between species would reflect resource partitioning.

But this approach now seems naive. Even in the absence of competition, different species will utilize resources in different ways (Sale 1974). The mere demonstration of utilization differences is no longer accepted as sufficient evidence for competition (Connell 1980). Null models have been used to ask what niche overlap patterns would be expected in the absence of competition (Silvertown 1983). If competition influences resource utilization at the community level, niche overlap in nature should be significantly less than in an idealized competition-free community (Schoener 1974a).

Few studies of niche overlap are based on the direct measurement of resource utilization curves along an ordered niche axis, as diagrammed in Figure 4.1. Studies of dietary and habitat niches usually rely on discrete, unordered resource states, and studies of character displacement rely on measurements of body size or morphology, which are assumed to reflect resource utilization. Schluter and Grant's (1984) study of Galápagos finches is a notable exception, and their finding that utilization and availability curves are asymmetrical and polymodal contradicts one of the important underlying assumptions of niche theory (see Chapter 6).

Although null models can be used to establish whether observed niche overlap is more or less than expected by chance, it is still difficult to infer the mechanisms responsible for such patterns. For example, most null models do not distinguish between ecological niche shifts and evolutionary character displacement (Case and Sidell 1983). Interpreting patterns of high niche overlap can be equally problematic. High niche overlap may reflect intense competition for shared resources or, alternatively, a surplus of resources and the absence of competition (Glasser and Price 1988). Both scenarios have been revealed in experimental field studies of competition (Schoener 1983).

Interestingly, null model studies of niche overlap have not addressed these alternatives, and interpretations have been remarkably consistent: those authors who detected unusually low overlap have concluded that competition has been an important force, either currently or in the past (e.g., Pianka et al. 1979), whereas those who found unusually large niche overlap have concluded that competition is not currently important (e.g., Tokeshi 1986; Griffiths 1987). For any particular pair of species, the finding that niche overlap is statistically lower than expected is difficult to evaluate. Phylogenetic and historical effects may result in different utilization patterns for this pair that have nothing to do with competitive interactions. However, it is more difficult to explain strong low-overlap patterns for an assemblage of several coexisting species.

The Utilization Matrix

Construction of a utilization matrix is the starting point for a null model analysis of niche overlap. An investigator first defines a set of resource states, and then measures the utilization of these resources by each species in the assemblage. For example, if the states are microhabitats, then the number of individual occurrences of each species in the different microhabitats is recorded. Likewise, if dietary categories are of interest, the number or volume of prey items in each category is measured.

Utilization data often summarize extensive collecting efforts and natural history observations on undisturbed communities. Pianka's (1986) long-term studies are noteworthy in this regard. Twelve person-years of field work in Australia, North America, and South Africa yielded collections representing over 90 species and 15,000 individuals of desert lizards, with detailed observations on their microhabitat utilization and stomach contents. Table 4.1 illus-

Table 4.1

Frequency of microhabitat utilization by five species of North American lizards

| Species | Microhabitat | | | | |
	Open	Grass	Bush	Tree	Other
Cnemidophorus tigris	0.475	0.025	0.424	0.025	0.051
Uta stansburiana	0.279	0.046	0.473	0.046	0.156
Phrynosoma platyrhinos	0.950	0.000	0.050	0.000	0.000
Crotaphytus wislizeni	0.613	0.007	0.321	0.007	0.052

Adapted and simplified from Appendix C of Pianka (1986).

trates a utilization matrix with a small subset of Pianka's (1986) data. Species and resource states are represented by rows and columns, respectively. The entries in the matrix p_{ij} represent the fraction of total utilization by species i of resource state j. The matrix summarizes resource utilization along a single resource axis, which may be either ordered or unordered.

Overlap Indices

How can overlap between species be quantified with a utilization matrix? Many different indices have been proposed to measure the overlap between individual species pairs, and to quantify the overall "niche breadth" or degree of specialization of each species. Because these indices were first derived from the theory of limiting similarity, they emphasize pairwise comparisons of overlap along ordered resource axes, although the calculations work equally well with unordered resource states. For a pair of species, the overlap in resource use of species 2 on species 1 can be measured in terms of the frequency of utilization (p) of n different resource states. Some commonly used indices include

$$O_{21} = \frac{\sum_{i=1}^{n} p_{2i} p_{1i}}{\sum_{i=1}^{n} (p_{1i})^2} \tag{4.2}$$

where p_{xi} is the frequency of utilization of resource state i by species x. This familiar index by MacArthur and Levins (1967) is the discrete version of Equation 4.1. Early studies equated this overlap with the Lotka-Volterra competition coefficient (Levins 1968), although this equivalence cannot be readily justified (Lawlor 1980a). Equation 4.2 is asymmetrical, in that the overlap of species 2 on species 1 does not equal the overlap of species 1 on species 2. Pianka (1973) proposed a modified symmetrical index:

$$O_{21} = O_{12} = \frac{\sum_{i=1}^{n} p_{2i} p_{1i}}{\sqrt{\sum_{i=1}^{n} p_{2i} \sum_{i=1}^{n} p_{1i}}} \tag{4.3}$$

In this index, the denominator has been normalized, but the stability properties are the same as those of Equation 4.2 (May 1975b). The Czekanowski

Index (Feinsinger et al. 1981) has also been used as a simple measure of the area of intersection of two utilization histograms:

$$O_{12} = O_{21} = 1 - 0.5 \sum_{i=1}^{n} |p_{i1} - p_{i2}| \tag{4.4}$$

Finally, Colwell and Futuyma (1971) proposed an information theory index that quantifies the "uncertainty" in a utilization matrix. Similar equations have been used to quantify the niche breadth of a species, that is, the extent to which a species is specialized or generalized in its utilization of resources (Feinsinger et al. 1981).

As in the study of species diversity, there is a large, unsatisfying literature, mostly from the 1970s, that explores different algebraic measures of niche overlap (e.g., Colwell and Futuyma 1971; Pielou 1972b; Hurlbert 1978; Petraitis 1979). Niche overlap indices are invariably correlated with one another, sample-size dependent (Hanski 1978), and only tenuously linked to theories of competition (Lawlor 1980a). In the absence of an appropriate null model, it is impossible to evaluate or compare these indices, either among species or among communities. For example, under some circumstances, average overlap, as measured by Equation 4.4, can actually increase following species deletion from a community (Thomson and Rusterholz 1982). Even with an appropriate null model, different indices can generate different results. In a study of niche shifts in Greater Antillean *Anolis* communities, observed overlaps were usually less than expected, but the null hypothesis was rejected more often using Equation 4.2 than Equation 4.3 (Haefner 1988a).

Weighted versus Unweighted Indices

The most important assumption implicit in the use of overlap indices is that all resource states are equally available to all species. If resource states are not equally abundant, observed overlaps in utilization may not accurately reflect similarity in resource use. In particular, if some resource states are extremely common and others are extremely rare, species may appear very similar in their resource utilization (Lawlor 1980a).

How can resource indices be modified to account for resource availability? Colwell and Futuyma (1971) suggested expansion of the resource utilization matrix in proportion to the total utilization of each category. The resource categories in the expanded matrix are assumed to be equiprobable and thus to provide a better measure of species electivities. The Colwell and Futuyma (1971) technique has been applied to associations of drosophilid flies on

different plant types (Sabath and Jones 1973) and anuran larvae in tropical ponds (Heyer 1974). However, the Colwell and Futuyma (1971) expansion is somewhat arbitrary and sample-size dependent (Hanski 1978) and still requires comparison with an appropriate null model (e.g., Sale 1974; Inger and Colwell 1977).

Schoener (1974b) and Lawlor (1980a) both suggested modifications of existing indices to account for the "electivity," the relative ability (or preference) of a consumer to catch and consume a particular prey type. In the simplest case, consumers will use resources in the proportions in which they are available in the environment (Holling Type I functional response). Thus

$$p_{ij} = a_{ij} R_j \tag{4.5}$$

where R_j is the relative density of resource j and a_{ij} is the electivity of species i for resource j. Thus, the utilization (p_{ij}) of resource state j can be high either because the electivity for that resource is large, or because the resource is very common. Lawlor (1980a) argued that electivities are more relevant to theories of limiting similarity than direct utilizations, in part because electivities are a better measure of a consumer's phenotype. Incorporating resource availability may have a major effect on measures of overlap. Table 4.2 illustrates sample calculations for some of Pianka's (1986) data on microhabitat utilization by North American lizards. Calculated overlaps vary, depending on the availability of different resource states.

In theory, independent resource measurements could be incorporated with measures of utilization to estimate electivities, but in practice these data are rarely available. In addition, it may be impossible to realistically compare the densities of different resource categories. Consequently, the relative consump-

Table 4.2

Pairwise niche overlap of North American lizards

	Cnemidophorus *tigris*	*Uta* *stansburiana*	*Phrynosoma* *platyrhinos*	*Crotaphytus* *wislizeni*
Cnemidophorus tigris	—	0.934	0.776	0.969
Uta stansburiana	0.806	—	0.528	0.831
Phrynosoma platyrhinos	0.967	0.636	—	0.906
Crotaphytus wislizeni	0.991	0.751	0.986	—

Each entry is the overlap in utilization, calculated with Equation 4.3. Above the diagonal: overlap calculated assuming resource states are equally available. Below the diagonal: overlap calculated assuming that 95% of the available microhabitats are bushes. Based on the utilization data in Table 4.1.

tion of different prey items may serve as the most relevant "bioassay" of availability (Colwell and Futuyma 1971; but see Hanski 1978). If species are using resources randomly, then the summed resource use across species will reflect the relative availability of different resource states. Lawlor (1980a) advocated this approach for estimating electivities, and the Colwell and Futuyma (1971) matrix expansion produced a similar weighting.

If resource states are not equally abundant, observed utilizations will tend to overestimate the amount of ecological overlap. Electivities based on marginal resource totals remove some of this bias, and may be a more reliable measure of ecological overlap. For example, only two of 10 mean utilization overlaps for Pianka's (1967) North American lizard communities differed from null model expectations, whereas all 10 mean electivities differed significantly (Lawlor 1980b). For Greater Antillean *Anolis* communities, significant results were somewhat more common when comparing electivities versus utilization overlaps (Haefner 1988a). Some critics object to the use of marginal constraints in null model simulations (Case 1983a), on the grounds that these marginals may themselves be influenced by competition (Colwell and Winkler 1984). Analyses of niche overlap can be greatly affected by the methods used to estimate electivities (Lawlor 1980a; Haefner 1988a), but marginal constraints do not automatically bias the test towards accepting the null hypothesis.

We see two potential problems with electivity calculations. The first is that the electivities that are estimated from summed resource use will be influenced not only by the relative availability of different resource states, but also by overall productivity (Haefner 1988a). Second, Equation 4.5 may adequately describe the utilization of different microhabitats, but more complex functions may be necessary to characterize prey utilization, which can be affected by search images, handling times, and satiation levels.

Moreover, electivities may give large, counterintuitive weight to trace components in pooled diets (Winemiller and Pianka 1990). This will be especially true when electivities are estimated without reference to an appropriate sampling model (Ricklefs and Lau 1980). On the other hand, observed utilizations are biased towards the finding of large overlap when certain resource states are very common. To overcome these problems, Winemiller and Pianka (1990) proposed a hybrid index, the geometric mean of utilization and electivity:

$$g_{ij} = \sqrt{a_{ij}\, p_{ij}} \qquad\qquad (4.6)$$

They suggested that g_{ij} should reduce the positive correlation of p_{ij} with resource availability and the negative correlation of a_{ij} with resource availability without entirely eliminating available resources from the analysis. However, electivity and utilization measure two different things, and it may not be

wise to combine them in an aggregate index. One advantage of using observed utilizations (p_{ij}) to test niche overlap is that the tests will be conservative with respect to competition hypotheses. Because unequal resource availability will lead to large overlap, we can be sure that the reduction in overlap is strong when the null hypothesis is rejected. At least in comparison to idealized communities of known structure, results were quite similar for p_{ij}, a_{ij}, and g_{ij} (Winemiller and Pianka 1990).

Multidimensional Niche Metrics

Once an appropriate utilization measure and resource weighting have been selected, there is still the problem that the niche of a species is rarely represented along a single resource axis. Most authors have appreciated the multidimensional nature of the niche and have measured utilization along several resource axes. Most of these are subdivisions of the major niche axes of time, space, and food (Schoener 1974a). Multivariate approaches can be useful for reducing the number of correlated variables to a handful of independent resource axes (Green 1971). But even if individual utilization curves are properly evaluated, comparisons in multidimensional niche space are problematic. Specifically, the overlap among species in multidimensional space could be higher or lower than overlap along individual niche dimensions (Figure 4.2).
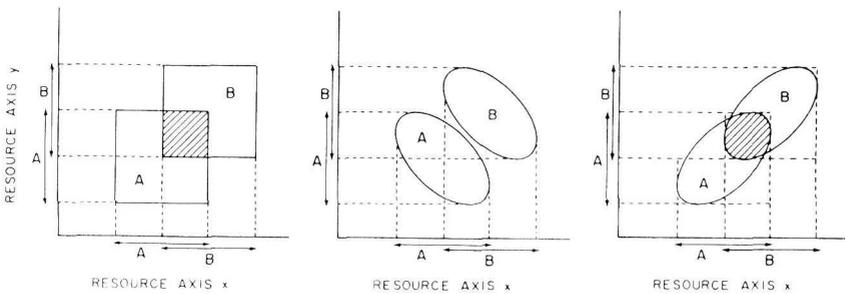
Figure 4.2. Multidimensional niche overlap is not always reflected in overlap along individual dimensions. In the left-hand plot, niche overlap of species A and B along two resource axes is independent, and the product accurately reflects total overlap. In the middle and right-hand plots, resource use is not independent, and the total overlap cannot be readily predicted from utilization of individual resources. From E. R. Pianka, R. B. Huey, and L. R. Lawlor. Niche segregation in desert lizards. In *Analysis of Ecological Systems.* D. J. Horn, R. D. Mitchell, and G. R. Stairs (eds). Copyright © 1979 by the Ohio State University Press. Reprinted by permission. All rights reserved.

There are two extreme cases. First, suppose that uniform resource utilization for a species is entirely independent along two orthogonal resource axes (x and y). Utilization of this rectangular niche space can be estimated as the simple product of overlap (xy). At the other extreme, utilization along two niche axes may be entirely correlated, so that knowing the utilization along one axis allows you to predict the other. In this case, the arithmetic average of the two axes ($(x + y)/2$) is the best estimate of multidimensional utilization. This "summation overlap" represents a maximum upper bound for overlap in a multidimensional niche space (May 1975b). Between these extremes, there is no way to predict from the unidimensional overlaps whether true overlap is large or small. The geometric mean overlap ($\sqrt{xy}$) may serve as a useful approximation of multidimensional overlap (Case 1983a), because it will always lie above the arithmetic mean and below the product mean.

Aggregate Statistics for Pairwise Overlaps

Even in proper multidimensional form, the overlaps calculated for each species pair do not convey a full picture of niche overlap at the community level. Several different statistics have been proposed for summarizing overlap for an entire assemblage. One obvious measure is the mean or median of all $\binom{n}{2}$ pairwise overlaps. The median may be preferable, because it will reflect the nonnormal distribution of pairwise overlaps. However, the expected median overlap quickly converges on the mean as species number increases (Case 1983a).

Mean or median overlap is a useful summary statistic for niche analyses, but, as a single number, it hides a good deal of pattern at the community level (Pianka 1980). Inger and Colwell (1977) recommended a more subtle measure. For each of the n species, order the remaining $n - 1$ neighbors on the basis of their overlap. If a single utilization measure is used, the ordering is based on the pairwise overlaps. If multiple niche axes are retained, the $n - 1$ neighbors can be ranked according to Euclidian distances. These orderings are then averaged to give the mean overlap of the first, second, ... $n - 1$ neighbors in niche space. By definition, overlap is highest with the closest neighbor, then drops off as more dissimilar neighbors are compared (Figure 4.3). The plot of average overlap versus ranked neighbor distance can then be compared to the predictions of null models. Comparisons with all neighbors in niche space are of interest, because the hypothesis of diffuse competition predicts that utilization will be affected by many competing species (MacArthur 1972; Pianka 1974).

Figure 4.3. Nearest-neighbor plots in niche space for three assemblages of amphibians and reptiles in Thailand. Each point represents the average niche overlap of each species with its *n*th nearest neighbor. These curves can be compared with the predictions of null models and are more sensitive indicators of community structure than a simple median or mean of pairwise niche overlap. From Inger and Colwell (1977), with permission.
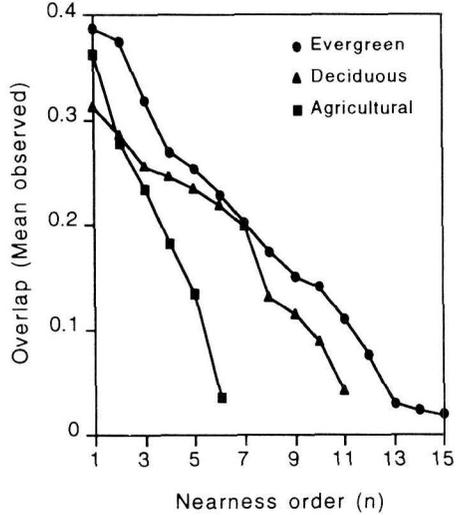
Still another approach is to compute the mean overlap for each species pair and compare it to the expected overlap for that pair in a null community. Particular pairs of species may exhibit nonrandom patterns of overlap that may not be apparent from the mean or median overlap of all possible pairs. However, assessing the statistical significance of many nonindependent pairs may be problematic (see Chapter 7). Haefner (1988a) compared all three measures with the same data set. He detected significant overlap more frequently with nearest neighbor and individual pairwise overlaps than with the mean overlap for an entire assemblage.

A NULL MODEL FOR THE HUTCHINSONIAN NICHE

How would niche overlap patterns appear in the complete absence of competition? If we could answer this question, we would have a reference for comparison with observed patterns of overlap. Innis and Haefner (1980) addressed the question with a detailed simulation of the Hutchinsonian niche that excluded competitive processes. The Innis and Haefner (1980) model began with random placement of rectangular niches of species in a two-dimensional niche space (Figure 4.4). Populations of each species were uniformly distributed throughout the niche space and were changed by two processes: (1) a random, uniform deviate was added at each time step, which could either increase or decrease population size; (2) populations were reduced in size through "perfect preda-
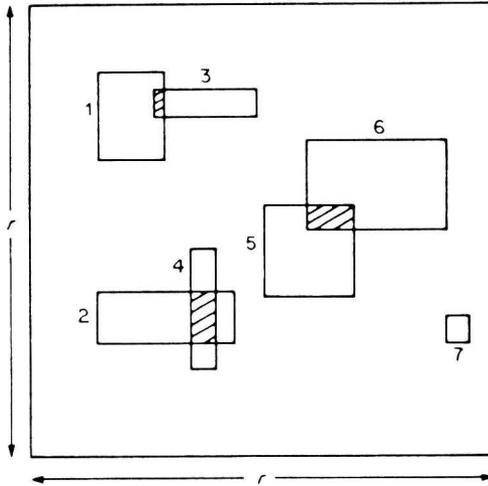
Figure 4.4. A null model of niche overlap. Seven hypothetical species are randomly placed in niche space, and niche overlap is calculated from the area of overlap. Niches change in size from stochastic growth and reduction from randomly occurring predators. From Innis and Haefner (1980), with permission.

tors." A predator niche was superimposed on the populations, and all individuals within that niche were removed. Niches of populations that declined to zero were removed from the simulation.

At each time step, the model generated the average niche size, average overlap between niches, species diversity, number of niches, average population size, and average number of neighbors. The model predicted that in the absence of competition, niche overlap would range from 25 to 100% for a community of specialists or generalists, respectively. The lower bound compared favorably with some estimates of minimal overlap from mammal (Brown 1975) and lizard (Pianka 1974) communities. The model also provided a baseline for comparisons with Pianka's (1972) niche overlap hypothesis: if competition were important, the number of species in a community would be negatively correlated with average niche overlap. However, if the niche breadth of colonizing species was variable, rather than constant, the Innis and Haefner (1980) model also predicted a negative correlation, even in the absence of competition.

The Innis and Haefner (1980) model is an important first step toward understanding niche dynamics in the absence of competition. However, it is a complex model, and much of the output is cast in terms of dimensionless parameters that are difficult to interpret. Most empirical null model studies have opted for a simpler approach through the randomization of utilization or species occurrence matrices. We outline these methods in the following sections.

SAMPLING ERROR IN NICHE INDICES

Two basic approaches have been used in null models of niche overlap: (1) randomization of utilization functions for dietary or activity data, and (2) randomization of species occurrences. Both approaches assume that utilization frequencies have been estimated accurately, which is probably true if many individuals or dietary items have been sampled. But at small sample sizes, estimates of utilization frequency may be biased and give inaccurate estimates of niche overlap. In the extreme case, if only one individual of a species is sampled, it will appear to be a "specialist" on whatever microhabitat it happens to be found in. These same problems arise in the study of diversity indices (Chapter 2) and relative abundance patterns (Chapter 3).

Ricklefs and Lau (1980) used Monte Carlo simulations to explore bias in several common niche overlap indices. Estimates of overlap were systematically biased downward when sample size was small and when expected overlap was high. Even with samples as large as 25 or 50, bias in some indices was substantial (Figure 4.5). To date, most null model analyses of niche overlap have not incorporated this sampling variability. Randomizing the raw utilization data (counts of individuals or dietary items) rather than the utilization frequencies would control for this source of bias.

Figure 4.5. Bias in niche overlap indices as a function of the true overlap value and the number of individuals sampled. The "coefficient of community" (S_{ij}) is equivalent to O_{12} in Equation 4.4. From Ricklefs and Lau (1980), with permission.
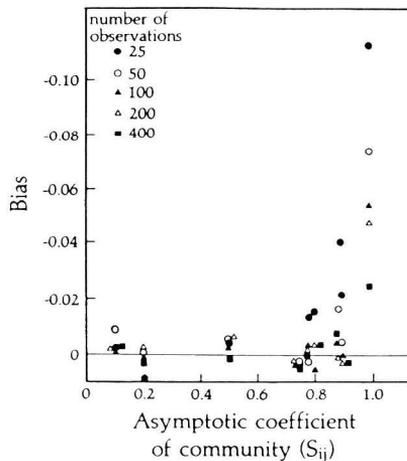
RANDOMIZATION OF SPECIES OCCURRENCES

Imagine a source pool of species, each with its own utilization function, that colonizes a small island. If competition limits niche overlap, then the particular combination of species that coexist on the island should have lower overlap than a randomly assembled set of species from the same source pool. A simulation of this scenario treats the utilization functions for each species (or population) as constants and randomizes the combination of species that co-occur. This analysis will be sensitive to the composition of the source pool fauna and whether species are sampled equiprobably.

Case (1983a) used this approach in a study of niche overlap of 18 species of lizards on 37 islands in the Sea of Cortez. Utilization along four niche axes (time of day, microhabitat, food size, and food type) was summarized as the product, summation, and geometric mean of overlap between each species pair. Using realistic criteria, Case (1983a) delineated a source pool of 18 mainland species that could potentially colonize each island. Observed island communities were a subset of these 18 species, and island species richness ranged from 1 to 13. For each island with i species, Case (1983a) enumerated all the unique combinations $\binom{18}{i}$ of exactly i species as null communities. For 30 of the 37 islands, the observed overlap was less than the median overlap for null communities of the same size (Figure 4.6). This result suggests that species combina-
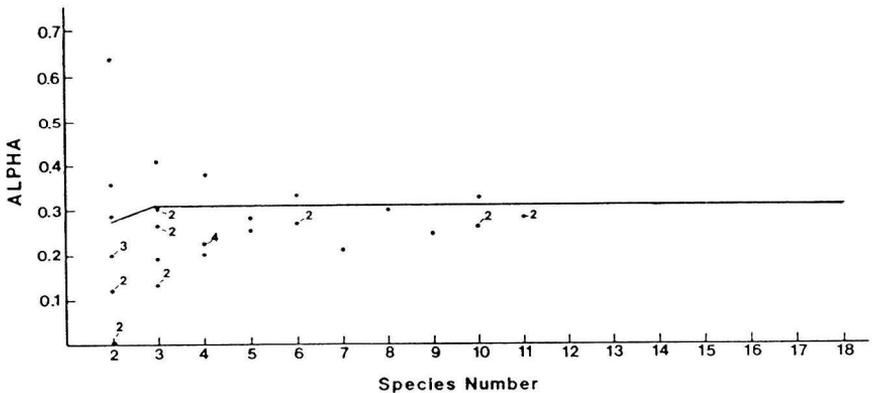
Figure 4.6. Niche overlap of insular lizard communities in the Sea of Cortez. The solid line is the median overlap for all possible combinations of a given number of species, assuming species colonize islands equiprobably. Most observed island assemblages fell below this expectation, suggesting that niche overlap was less than would be expected with random colonization. From Case (1983a), with permission.

tions that coexisted on islands had lower niche overlap than would be expected in the absence of competition.

An alternative to the competition hypothesis is that low overlap reflected nonrandom patterns of resource availability on islands. If the same nonoverlapping sets of resources were present on several islands, the same combinations of low-overlap species would tend to be found. For most island size classes, an improbably small number of species combinations was represented (Case 1983a), suggesting that the same low-overlap configurations tended to recur. This result argues against the competition hypothesis and in favor of the idea of nonrandom resource distributions.

Both of the preceding tests assumed that species colonized islands equiprobably. Case (1983a) relaxed this assumption with a simulation in which the probability of placement of each species in a random community was proportional to the number of island occurrences (Connor and Simberloff 1979). Compared to this model, only 23 of the 37 islands fell below the median, which is marginally nonsignificant ($0.05 < p < 0.10$), but still indicative of low niche overlap. Thus, differential dispersal ability of species may have contributed to the pattern of reduced niche overlap of insular lizards in the Gulf of Cortez. However, it is difficult to know whether the low overlap is a cause or a consequence of differential success of species on islands.

Schoener (1988a) also examined niche overlap of island lizard species sampled from a larger source pool. He analyzed utilization of seven microhabitat categories on satellite islands of the Greater Antilles, and found that coexisting species usually differed in the structural habitats they occupied. On two-species islands, each species occupied a different structural category. Coexistence in the same habitat was only found once on three-species islands, and never on four-species islands.

How likely were these patterns to have arisen by chance? Schoener (1988a) compared these habitat occupancy patterns to a null model based on four different source pool definitions: (1) all species from the appropriate "mainland" (one of the four Greater Antilles source islands); (2) the subset of mainland species whose structural-habitat categories were found on small islands; (3) only species present on two-, three-, or four-species islands (i.e., the archipelago method of using only species present on the islands); and (4) those species found on islands with equal or lesser species richness.

For each source pool, Schoener (1988a) assumed that all microhabitats were equally available and used a binomial expansion to calculate the tail probability of observing a given number of co-occurring species. About 15% of the tests were significant at the 0.05 level, and significant results were consistently obtained only for source pool (2), which Schoener (1988a) considered to be the

most realistic of the four. Among the island sets, four-species islands and satellite islands of Cuba frequently showed nonrandom patterns.

These studies by Schoener (1988a) and Case (1983a) suggest that comparing overlap values of observed communities with those of null communities drawn from a larger source pool is an effective method for evaluating niche overlap. However, the results will be sensitive to sample size, methods used for designating source pools, and assumptions about the colonization potential of species.

RANDOMIZATION OF UTILIZATION MATRICES

Although comparisons of niche overlap in real communities with overlap in null communities derived from an appropriate source are worthwhile, no such "external reference" is available in many cases. Instead, the observed utilization matrix must be used to estimate overlap values in the absence of competition. The randomization algorithms (RAs) described below assume that interspecific variation in resource utilization provides information about expected niche overlap in the absence of competition. Lawlor (1980b) developed four algorithms that are listed in increasing order according to the amount of original utilization data retained in the null community:

1. RA1. For each species, utilization of each dietary category is replaced by a random uniform number [0,1]. After randomization, entries in the matrix are scaled so that the row sums for each species sum to 1.0.
2. RA2. Resource utilization is again replaced by a random uniform number [0,1], but only for those resource states in which utilization is greater than zero. Those resource states that were not used in nature by a species are left in the zero state. As in RA1, row sums are rescaled after randomization.
3. RA3. Resource utilization for each species is not replaced by a random number. Instead, the observed utilizations are randomly reassigned to different resource categories ("scrambled zeros"; Winemiller and Pianka 1990). Because the rows of the utilization matrix are simply reshuffled (Inger and Colwell 1977), RA3 effectively retains observed niche breadths for each species (Sale 1974).
4. RA4. Only the nonzero resource states in each row are reshuffled ("conserved zeros"; Winemiller and Pianka 1990). As in RA2,

the placement of the zeros is retained. Of the four algorithms, RA4 produces synthetic communities in which utilizations are most similar to the original communities.

The four randomization algorithms differ in whether utilizations are re-shuffled or replaced by a random number, and in whether the zeros in the matrix are retained or not (Table 4.3). Both decisions have implications for the structure of the null community, and affect the power of the test.

By replacing the observed utilizations with a uniform random variate (RA1), we assume that utilization of any resource state is possible and equiprobable. At the other extreme, reshuffling of nonzero utilizations (RA4) assumes that only permutations of nonzero utilizations are permissible. All these algorithms are reasonable methods for constructing random communities, although we still do not have a clear expectation of how utilization spectra should look in communities that are unstructured by competition (Bradley and Bradley 1985).

This problem is highlighted in the treatment of the "zero" states. Assuming that sampling effort has been sufficient to ensure that the zeros are not due to inadequate censusing of individuals or dietary items, there are two principal interpretations of a zero in a utilization matrix. The first is that the observed utilization values are determined primarily by competition. In this case, competition is so severe that some species are completely denied the use of certain resources by the presence of competitors. RA1 is consistent with this interpretation, because it allows a species in the null community to use a resource that it does not exploit in nature.

The other interpretation of zeros in the utilization matrix is that species are not able to use all resource states in a community because of constraints related to behavior, morphology, physiology, or phylogeny. These restrictions have

Table 4.3
Four null model randomization algorithms (RA)

	Zero states randomized	Zero states retained
Observed utilizations drawn from a uniform distribution	RA1	RA2
Observed utilizations reshuffled	RA3	RA4

The algorithms differ in whether unused resource states (zeros) are retained or randomized and in whether observed utilizations are reshuffled or replaced with a value drawn randomly from a uniform distribution. Adapted from Pianka (1986).

nothing to do with present or past competition, and should not be obscured in a null model test. Following this logic, RA2 and RA4 ensure that species which do not use certain resource states in nature never do so in a null community either. RA3 is a compromise. It retains the same *number* of zero states in the simulation, but does not constrain those zeros to their original placement.

PERFORMANCE OF RANDOMIZATION ALGORITHMS

What patterns result from these different simulations? RA1 destroys all structure in the matrix and usually results in null communities that exhibit a high mean and small variance in overlap. Figure 4.7 compares pairwise overlaps in microhabitat use of ground beetles collected in pitfall traps with simulated overlaps based on RA1 (Kobayashi 1991). Observed overlaps were much more variable than those predicted by RA1, and followed a nearly uniform distribution, compared to a peaked distribution of overlap values for the null commu-
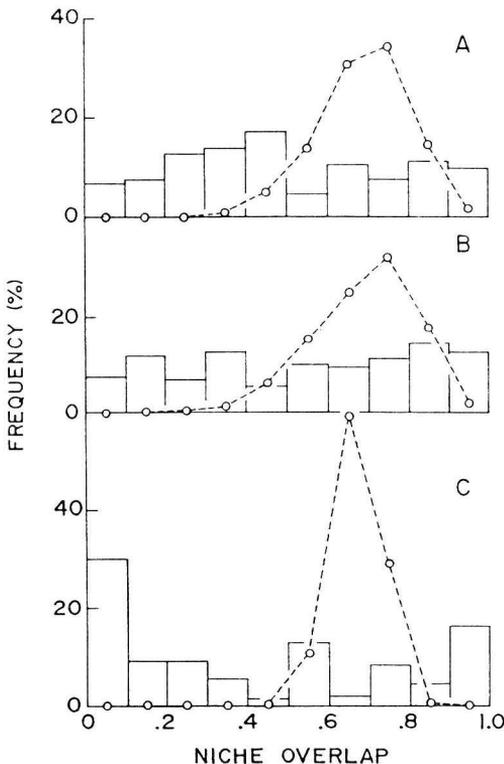
Figure 4.7. Observed and expected niche overlap of ground beetles collected from pitfall traps in Towada-Hachimantai National Park, Japan. Each histogram shows the distribution of species pairs with niche overlap calculated according to methods in Colwell and Futuyma (1971). The dashed line is the expected value generated by RA1. RA1 creates null assemblages with a high mean and low variance in niche overlap. From S. Kobayashi. 1991. Interspecific relations in forest floor coleopteran assemblages: niche overlap and guild structure. *Researches on Population Ecology* 33:345–360, Figure 2, page 352.
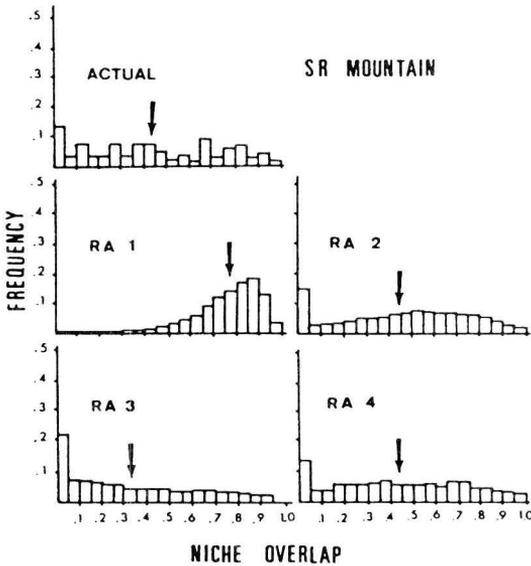
Figure 4.8. Observed niche overlap for a Texas grasshopper assemblage. Comparisons are shown with simulated data using RA1–RA4. Arrows indicate mean overlap. Note the low overlap of the observed data compared to RA1, and the similarity of the distributions for the more restrictive algorithms (RA2–RA4). From Joern and Lawlor (1981), with permission.

nities. High-overlap and low-overlap species pairs were more frequent than predicted by RA1, although there were more pairs below the expectation than above it. RA2 generated similar results, although simulated overlaps were more similar to observed overlaps because the zero structure of the utilization matrix was retained (Figure 4.8).

Winemiller and Pianka (1990) explored the performance of RA3 and RA4 in a series of detailed benchmark simulations that compared 100 randomized communities to idealized communities of known structure. Idealized communities consisted of 10 species with either "high," "medium," or "low" average overlap in their use of 10 resource states. Within each of these categories, four variants of assembly structure were established for a total of 12 trials: (1)–(3) "equal-sized guilds"—assemblages with two internal guilds of five species each (overlap in resource use occurred only among guild members); (4)–(6) "unequal-sized guilds" —assemblages with two internal guilds of three and seven species each; (7)–(9) "no guilds"—overlaps in resource use among all 10 species of the assemblage; (10)–(12) "core resources"—the 10 species shared four core resources with high (trial 10) or medium (trial 11) overlap, and did not overlap in use of the
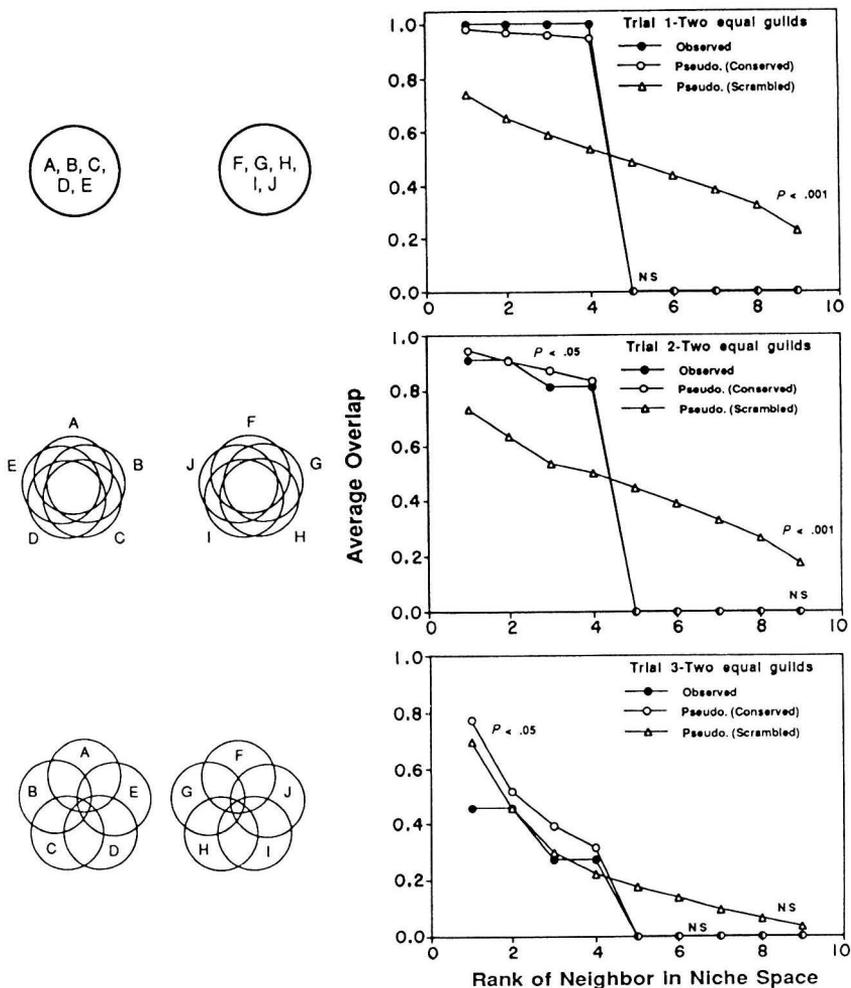
Figure 4.9. Benchmark performance of RA3 and RA4 compared to idealized communities. The three graphs correspond to patterns of high, medium, and low niche overlap of species organized into two internal guilds of five species each (A–E, F–J). For each assemblage, the observed average overlap is plotted as a function of the nth nearest neighbor. This curve drops off sharply beyond four nearest neighbors, which is the boundary for the internal guilds. Note that RA4 [Pseudo (Conserved)] closely mimics the observed overlap patterns, whereas RA3 [Pseudo (Scrambled)] produces a distinctive nearest-neighbor curve that reveals internal guild structure in the high- and medium-overlap trials. From Winemiller and Pianka (1990), with permission.

remaining six resources. Species in trial 12 had medium overlap for a core group of 40 shared resources and 60 nonoverlapping resources. All simulations were compared to observed communities using Inger and Colwell's (1977) nearest-neighbor distance. Statistical significance was assessed by the percentage of randomized mean overlaps that exceeded mean observed overlap.

These benchmark tests revealed that RA3 was superior to RA4 in detecting nonrandom overlap. For example, in trials (1)–(3) (two equal-sized guilds), the null hypothesis was never rejected for RA4 but was significant for RA3 under conditions of low and medium overlap. RA3 always generated a decreasing curve of average nearest-neighbor distances that did not change much as a function of resource overlap (Figure 4.9). In trials (1)–(6), RA3 accurately revealed the internal guild structure of the assemblages: overlap in RA3 correctly fell below the observed curve for the first four (or seven) nearest neighbors, which were in the same guild, and above the observed curve for the more distant neighbors, which were in different guilds. When no guild structure was present, simulated overlaps did not differ significantly from observed values. Thus, differences between observed overlaps and null communities can depend on internal guild structure as well as average overlap. For these reasons, nearest-neighbor plots may be superior to mean or average overlap values (Haefner 1988a). Finally, for shared resource scenarios, significant guild structure for RA3 was detected only when observed overlap was high. RA3, the original matrix shuffling used by Sale (1974) and by Inger and Colwell (1977), may be the best existing algorithm to use in resource overlap null models.

VARIANCE IN NICHE OVERLAP

Simulations can be used to study the variance as well as the mean of resource overlap. With RA3, variance in randomized communities generally decreased as neighbor distance increased (Winemiller and Pianka 1990). In contrast, observed variances in amphibian (Inger and Colwell 1977), lizard (Pianka 1986), and fish (Winemiller and Pianka 1990) communities exhibited a sharp peak at an intermediate neighbor distance (Figure 4.10). Both Inger and Colwell (1977) and Pianka (1986) interpreted this peak as evidence for the existence of internal guild structure. At low nearest-neighbor distances, variance in overlap is small, because all the species belong to the same guild. As nearest-neighbor distance increases, variance in overlap increases as some neighbors are sampled from other guilds. Finally, variance decreases at large neighbor distances because distant neighbors belong to different guilds. Null model comparisons with hypothetical communities that exhibit internal guild struc-
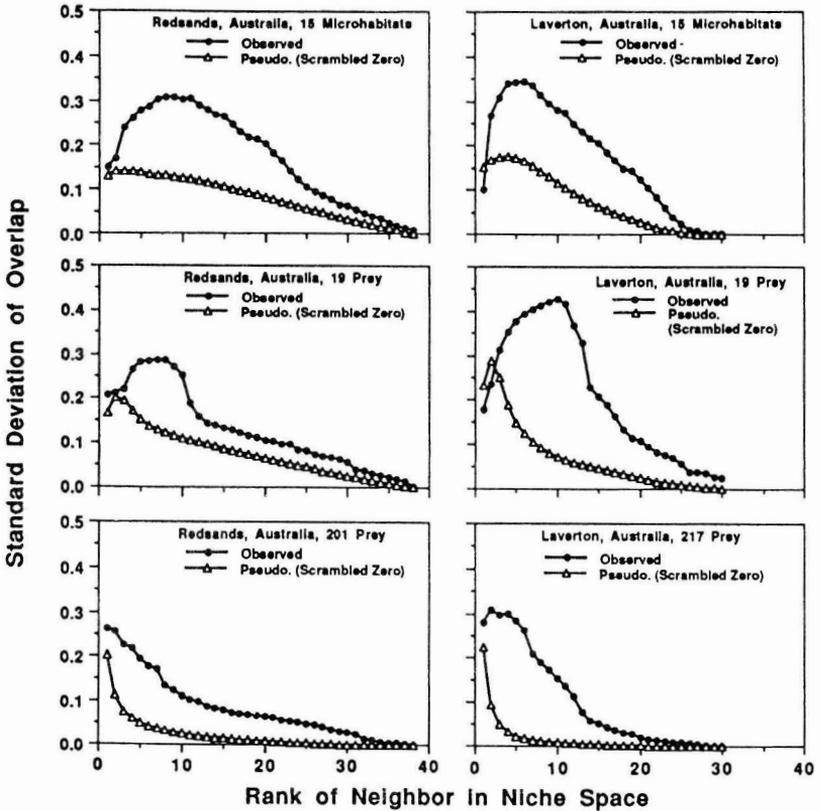
Figure 4.10. Comparisons of standard deviations of dietary and microhabitat niche overlap of Australian lizards with the predictions of RA3. Most assemblages exhibited a peak in variance at intermediate neighbor distance that was not present in the randomized communities. From Winemiller and Pianka (1990), with permission.

ture confirm this interpretation of the variance peak (Eric R. Pianka, personal communication). Whether cogent alternative explanations for the variance peak can be constructed remains to be seen.

Bradley and Bradley (1985) argued that nonrandom overlap patterns as revealed by RA1–RA4 need not imply competitive interactions. They pointed out that RA1–RA4 not only eliminate relationships among consumers, but also obscure the tendency for consumers to specialize on related types of resources. In RA1–RA4, the transition from one resource state to another is equiprobable ("random environment" model), whereas in nature, species will tend to forage on similar resources ("structured environment" model). Bradley and Bradley
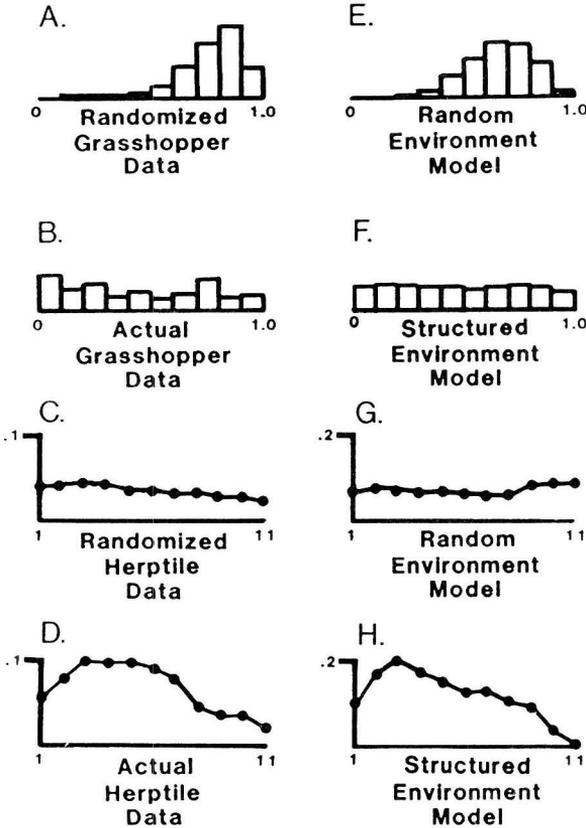
Figure 4.11. Alternative randomizations of niche overlap data. **A** and **B** show observed and randomized (RA1) niche overlap data of Joern and Lawlor (1981; see Figure 4.8). **C** and **D** show the standard deviation of niche overlap for the nth nearest neighbor from Inger and Colwell (1977; see Figure 4.3). **E–H** show two alternative null models that use Markov transitions to specify consumers that move randomly between different resource states ("random environment model") or that preferentially choose "similar" resources ("structured environment model"). Note the similarity of the observed data to the structured environment model. From Bradley and Bradley (1985), with permission.

(1985) used a Markovian model to simulate a consumer's transition between resource states under these two scenarios. The random environment model matched the predictions of Lawlor's (1980b) RA3 for pairwise overlaps and variances of overlap. In contrast, the structured environment model provided a good match with the observed data, including the variance peak at intermediate neighbor distances (Figure 4.11).

One could argue that Bradley and Bradley's (1985) model is too restrictive to test patterns of evolutionary divergence, because species would have more opportunity to specialize on different resources in the face of persistent competition. In any case, their results suggest that competitive interactions and internal guild structure are not the only possible explanations for nonrandom patterns of niche overlap.

RANDOMIZATION OF RESOURCE UTILIZATION PEAKS

Rather than analyze niche overlap per se, some authors have examined the spacing of utilization peaks on a single resource dimension. If species are competing for this resource, utilization peaks should be evenly spaced. The rationale and statistical analyses are identical to studies of flowering phenology of competing plants (Chapter 5) and body sizes of competing consumers (Chapter 6).

The null model in this case is MacArthur's (1957, 1960) broken stick—a number line is broken into random segments, and the length of each segment represents the spacing of resource peaks between two adjacent species (see Chapter 3). De Vita (1979) used the broken-stick model to compare measures of resource utilization peaks within assemblages of tropical hummingbirds (Snow and Snow 1972), herbivorous stem-boring insects (Rathcke 1976), and tropical intertidal snails (Kohn 1959). For each assemblage, De Vita (1979) compared segment lengths of individual species pairs with those predicted by the broken-stick model. The observed points all fell within two standard deviations of the predicted values, and De Vita (1979) concluded that the null hypothesis could not be rejected.

Three criticisms apply to De Vita's (1979) analysis. First, the distances between resource peaks are not independent points, so they should not be compared simultaneously to the null predictions (Pielou 1981). Second, De Vita (1979) did not provide an explicit test for evaluating the fit of the null model. The fact that all the points fell within two standard deviations was not a valid test (Shelly and Christensen 1982). Finally, distances measured for the "terminal" species are arbitrary and not equivalent to distances between adjacent species (De Vita 1979; Cole 1981).

Bush and Holmes (1983) offered a biological system and a new analysis that addressed all three criticisms. The spacing of helminth parasites along the small intestine of Lesser Scaup ducks (*Aythya affinis*) is well suited for tests of niche displacement. The vertebrate intestine is a complex linear gradient for parasites with biologically defined end points, the position of individuals
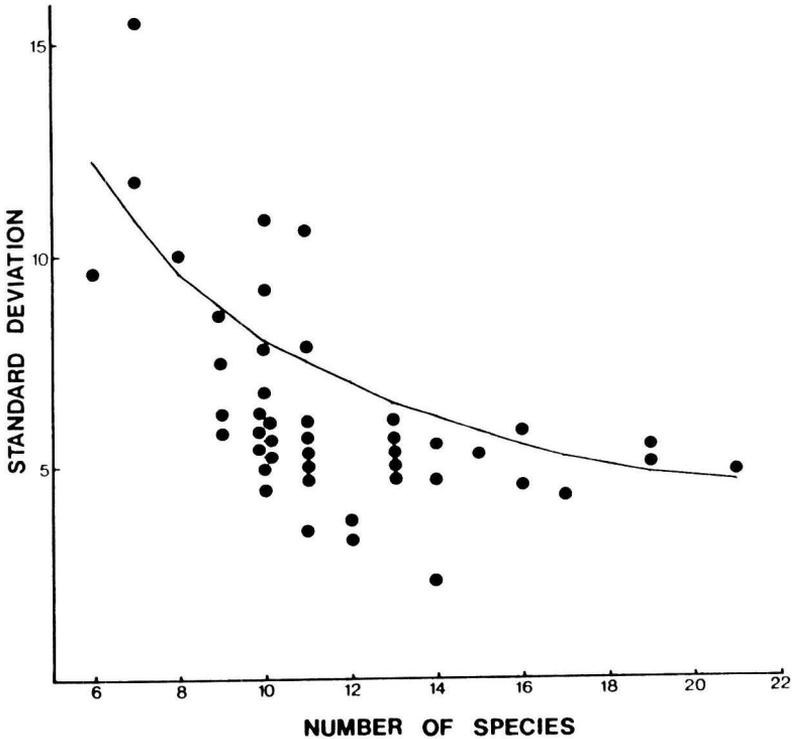
Figure 4.12. Variation of niche distances between adjacent helminth species co-occurring in the small intestine of lesser scaup (*Aythya affinis*). The solid line is the predicted value from the broken-stick model. Each point represents an independent assemblage. The results suggest that the spacing of the median individual of each parasite species is more regular than expected. From Bush, A. O., and J. C. Holmes. 1983. Niche separation and the broken stick model: use with multiple assemblages. *American Naturalist* 122:849–859. Copyright © 1983 by The University of Chicago. Reprinted by permission of the publisher.

within the gradient can be determined accurately, and many replicate communities can be sampled.

Bush and Holmes (1983) measured "location" as the placement of the median individual of a species. They summarized community dispersion patterns as a single number, the variance of segment lengths. This is the same approach used by Poole and Rathcke (1979) in their analyses of phenological overlap (Chapter 5). Whereas Poole and Rathcke (1979) derived the expected variance analytically, Bush and Holmes (1983) estimated it with a simulation of the broken stick. The observed variance was less than expected for most assemblages (Figure 4.12), suggesting that the spatial occurrence of species

Table 4.4

Summary of null model studies of resource utilization

Citation	Taxon	Samples	Overlap measurement	Resources	Multidimensional niche	Randomization	Overlap
Schoener (1988)	West Indian *Anolis* lizards (37)	24 island communities, compared to source pools from 4 Greater Antillean islands	Number of co-occurring species in each microhabitat	Structural microhabitat (8)	No	Binomial exact tests, assuming equi-probable species placement and equivalent resource availability	$O < E$, but only for appropriate source pools with habitat specialists eliminated.
Griffiths (1987)	Smooth and palmate newts (*Triturus*) (2)	Funnel-trap samples from a single pond in mid-Wales	Eq. 4.4	Pond location microhabitat (7) Time of year (22)	Product, average, individual	RA3	Microhabitat: $O > E$ Time: $O > E$
Case 1983	Sea of Cortez lizards (18)	37 island communities	Eq. 4.3	Food type (24) Food size (18) Microhabitat (16) Time of day–temperature (24)	Geometric mean	Utilization fixed; Species sampled equiprobably (or weighted by occurrence) from archipelago source pool	$O < E$
Pianka et al (1979)	Kalahari lacertid lizards (7)	Long-term censuses, diet analysis 10 sites	Eq. 4.3	Microhabitat (15) Time of day (24) Prey volume (19)	Multiplicative Summation means	RA2	Microhabitat: $O = E$ Food: $O < E$ Time: $O = E$
	Australian *Ctenotus* (7)	Long-term censuses, diet analysis 10 sites	Eq. 4.3	Microhabitat (15) Time of day (24) Prey volume (19)	Multiplicative Summation means	RA2	Microhabitat: $O = E$ Food: $O = E$ Time: $O = E$
	Australian geckos (9)	Long-term censuses, diet analysis 10 sites	Eq. 4.3	Microhabitat (15) Time of day (24) Prey volume (19)	Multiplicative Summation means	RA2	Microhabitat: $O < E$ Food: $O < E$ Time: $O > E$
	Australian *Varanus* (5)	Long-term censuses, diet analysis 10 sites	Eq. 4.3	Microhabitat (15) Time of day (24) Prey volume (19)	Multiplicative Summation means	RA2	Microhabitat: $O < E$ Food: $O = E$ Time: $O = E$

	Kalahari skinks (4)	Long-term censuses, diet analysis 10 sites	Eq. 4.3	Microhabitat (15) Time of day (24) Prey volume (19)	Multiplicative Summation means	RA2	Microhabitat: $O < E$ Food: $O = E$ Time: $O = E$
	Kalahari geckos (6)	Long-term censuses, diet analysis 10 sites	Eq. 4.3	Microhabitat (15) Time of day (24) Prey volume (19)	Multiplicative Summation means	RA2	Microhabitat: $O < E$ Food: $O = E$ Time: $O > E$
	Australian Amphibolurus (7)	Long-term censuses, diet analysis 10 sites	Eq. 4.3	Microhabitat (15) Time of day (24) Prey volume (19)	Multiplicative Summation means	RA2	Microhabitat: $O = E$ Food: $O < E$ Time: $O > E$
	North American saurofauna (9)	Long-term censuses, diet analysis 10 sites	Eq. 4.3	Microhabitat (15) Time of day (24) Prey volume (19)	Multiplicative Summation means	RA2	Microhabitat: $O < E$ Food: $O < E$ Time: $O = E$
	Kalahari saurofauna (17)	Long-term censuses, diet analysis 10 sites	Eq. 4.3	Microhabitat (15) Time of day (24) Prey volume (19)	Multiplicative Summation means	RA2	Microhabitat: $O < E$ Food: $O < E$ Time: $O > E$
	Australian saurofauna (40)	Long-term censuses, diet analysis 10 sites	Eq. 4.3	Microhabitat (15) Time of day (24) Prey volume (19)	Multiplicative Summation means	RA2	Microhabitat: $O < E$ Food: $O < E$ Time: $O = E$
Tokeshi (1986)	Chironomids of River Tud, eastern England (9)	Replicated vegetation samples. Gut contents of chironomids	Time: geometric mean proportion of the overlapping area under two resource utilization curves [0,1] Diet: Eq. 4.4	Time of year (365) Diet (3)	No	Time: (a) resource peaks placed randomly; (b) resource peaks limited to nonwinter months Diet: RA1	Time: $O > E$ Diet: $O >$ or $= E$ (in different months)
Sale (1974)	MacArthur's (1958) warblers of New England (4)	Foraging time in different microhabitats	Eq. 4.4	Foraging zone (16)	No	RA3	$O < E$

(Table continues on next page)

Table 4.4

Summary of null model studies of resource utilization (*Continued*)

Citation	Taxon	Samples	Overlap measurement	Resources	Multidimensional niche	Randomization	Overlap
Sale (1974)	Ueckert and Hansen's (1972) grasshoppers of Colorado (14)	Stomach contents	Eq. 4.4	Dietary category (20)	No	RA3	$O > E$
Kobayashi (1991)	Forest-floor coleopterans of Toweda-Hachimantai National Park, Japan (18)	Pitfall traps	Colwell-Futuyma index	Habitat (6) Bait types (5)	Individual	RA1	Habitat: $O < E$ Bait type: $O < E$ Habitat × Bait type: $O < E$
Field (1992)	Spider-hunting pompilid wasps at a Breckland heath (24)	Water/pitfall traps	Eq. 4.3	Microhabitat (7) Time of year (9)	No	RA1, weighted by estimated areas of microhabitats and abundance of species	Microhabitat: $O < E$ Time of year: $O < E$
Haefner (1988a)	Greater Antillean *Anolis* lizard communities of Schoener and Schoener (1971a,b) (9)	First-sighting observations	Eq. 4.2, Eq. 4.3	Perch diameter Perch height	Product Summation Individual	Random selection of individuals and placement in sites; overlaps weighted by Lawlor's (1980b) electivities to account for unequal resource availability	Mixed. Eq. 4.2 gives less significant overlap than Eq. 4.3. Use of mean, median, or geometric mean gives weak or no support for niche shifts. Rank orders give better support.
Inger and Colwell (1977)	Herpetofauna of broadleaf evergreen forest, deciduous dipterocarp forest, and agricultural land in Thailand (105)	Quadrat, transect censuses	Colwell-Futuyma index, with weighting for resource availability	Microhabitat (26)	Principal components of niche axes	RA3	O (var) $< E$ for closest neighbors

Joern and Lawlor (1981)	Grasshoppers of 3 arid grassland communities in western Texas (35)	First sightings and gut content analyses	Eq. 4.3	Plant resource (56) Microhabitat (27)	No	RA1	Inger-Colwell comparison of neighbors. $O < E$ O (var) $> E$
MacNally and Doolan (1986)	Cicadas of eastern Australia (9)	First sightings	Average group centroid distances in multivariate niche space	Habitat (16) Morphology (10) Behavior (15)	Yes, factor analysis reducing to 3 niche axes	All possible n-species combinations were compared for a particular guild	$O = E$
Winemiller and Pianka (1990)	Freshwater fish assemblages of Cano Maraca, Venezuela (wet season) (59)	Gut content analyses	Eq. 4.3 with standardized electivity coefficients	Prey (94)	No	RA3 RA4	RA3: $O > E$ RA4: $O < E$
	Freshwater fish assemblages of Cano Volcan, Venezuela (wet season) (19)	Gut content analyses	Eq. 4.3 with standardized electivity coefficients	Prey (68)	No	RA3 RA4	RA3: $O > E$ RA4: $O < E$
	Freshwater fish assemblages of Cano Agua Fria, Venezuela (wet season) (50)	Gut content analyses	Eq. 4.3 with standardized electivity coefficients	Prey (82)	No	RA3 RA4	RA3: $O > E$ RA4: $O < E$
	Freshwater fish assemblages of Quebadra, Venezuela (wet season) (23)	Gut content analyses	Eq. 4.3 with standardized electivity coefficients	Prey (67)	No	RA3 RA4	RA3: $O > E$ RA4: $O < E$

Taxon: number in parentheses is number of species compared. Resources: number in parentheses is number of resource states. Overlap: O = observed overlap, E = expected overlap based on the null model. Inequalities indicate statistically significant patterns ($p < 0.05$). O (var) = observed variances of overlap; otherwise, patterns refer to median or mean of pairwise niche overlaps.

was significantly regular. Note that a regular spacing does not preclude high overlap, because the analysis considers only the distribution of utilization peaks (Cole 1981).

SUMMARY OF FINDINGS

Table 4.4 describes some of the studies that have used null models to examine resource overlap. It is difficult to summarize the findings, because the methods vary widely from one study to the next. However, nearly all of these studies detected some nonrandomness in niche overlap, although not always in a negative direction. Most studies included more than one resource axis, summarized as a mean or aggregate overlap. Few studies explored the use of electivities versus utilizations, even though this may greatly affect the results. Finally, most studies randomized utilizations directly, even though these indices are sample-size dependent. In 1977, Inger and Colwell noted "there is no such thing as a standard protocol for community analysis." The same thing can be said with respect to overlap studies today. However, we now have a number of null models that can be used to assess the mean, variance, and nearest-neighbor distance of niche overlap in the absence of species interactions.

RECOMMENDATIONS

Several decisions need to be made in a null model analysis of niche overlap. Electivity measures are theoretically desirable, but utilization measures are usually more practical for analysis. Niche overlap analyses should ideally be based on 50 or more observations of use of food items or other resources by each species. If not, the indices may be biased, and the simulation procedures of Ricklefs and Lau (1980) should be followed. The choice of an overlap index is somewhat arbitrary; we suggest Pianka's (1973) index as symmetric measure of overlap between two species. To summarize overlap for an entire assemblage, we recommend using the median overlap and Inger and Colwell's (1977) nearest-neighbor plots of the mean and variance of overlap. If the source pool for an assemblage can be estimated independently, we recommend the procedures of Case (1983a) and Schoener (1988a) for determining whether overlap is unusually low for the particular combination of coexisting species. If there is no independent source pool, the observed utilization data will have to be randomized. Lawlor's (1980b) RA3 and RA2 seem to be the most desirable for this purpose.