9
BIOGEOGRAPHY

Chapters 7 and 8 emphasized assemblage patterns on islands or in discrete habitat patches. This chapter considers community patterns measured against a more continuous spatial background. For this problem, we need to consider not only the occurrence of a species, but its spatial distribution. The spatial distribution of individuals or populations can be mapped as a line segment in one dimension or as a polygon in two dimensions. Null models have been applied to the pattern of species occurrences in one and two dimensions across a spectrum of spatial scales. At small scales, one-dimensional analyses are appropriate for species occurrences along environmental gradients such as mountainsides (McCoy 1990) or intertidal transects (Colman 1933). At large scales, one-dimensional patterns include geographic gradients, such as the distributional ranges of species along coastlines (Pielou 1977) or narrow peninsulas (Brown and Opler 1990). Two-dimensional patterns include the small-scale occurrence of species in quadrats of fixed size (Hurlbert 1990) or the large-scale spatial overlap of the geographic ranges of species (Lynch 1989).

ASSUMPTIONS

The occurrence of a species or a set of populations can be represented as a line segment in one dimension, or as a closed polygon in two dimensions. This representation requires the following two assumptions:

1. Spatial patterns do not change through time. As in analyses of island assemblages, the mapped distribution of a species is treated as a static "snapshot" (Diamond 1986). It is difficult to evaluate patterns in the distributional maps of species if their ranges are constantly changing size and shape. If we wait long enough, all distributional maps will change, if only because all species have finite lifetimes. However, spatial patterns may be stable on time scales that are relevant to ecological or evolutionary mechanisms. In general,

the smaller the spatial scale, the shorter the time until the distribution pattern changes. For example, the vertical distribution of an intertidal barnacle may change on a seasonal basis (Wethey 1983), whereas its geographic range may remain stable for decades or centuries (Wethey 1985).

2. Distributions of species are continuous throughout their mapped ranges. In other words, we assume there are no "gaps" in the spatial occurrence of a species. Null model analyses become exceedingly complex if rules must be specified for the origin and placement of disjunct populations or individuals. In the extreme, if there are many gaps and relatively few areas of continuous distribution, it may be more appropriate to represent the occupied sites as insular populations in an archipelago of habitat patches.

If gaps are present, they may represent true biological disjunctions or gaps in sampling of sparsely inhabited areas (Lawton and Woodroffe 1991). No species has a truly continuous distribution. Representing spatial pattern as a line segment or a closed polygon is a simplification, but this in itself does not invalidate the analysis. For example, occupied sites within the geographic range of a species may be organized as a metapopulation (Levins 1969), in which local extinctions and recolonizations are common. Nevertheless, drawing a closed polygon around the metapopulation delineates a somewhat arbitrary "area of occurrence" (Gaston 1991), which may reflect important climatic boundaries that limit distribution (Brown 1988).

The danger arises when we attempt to make inferences between different spatial scales. For example, patterns of co-occurrence of Australian reef fishes in small coral heads are highly unpredictable in time and space (Sale 1979; Sale and Steel 1989). Persistent species combinations and strong local organization seem absent (Sale 1984), suggesting a lottery for species coexistence (Sale 1982). In contrast, species combinations at the regional or biogeographic scale exhibit apparent stability and consistency. Competitive interactions have been invoked to explain community organization at this level (Anderson et al. 1981), but similar patterns can be generated with null models that do not incorporate competition (Sale and Williams 1982). Long-term studies of shrubsteppe bird assemblages (Wiens and Rotenberry 1980, 1981b) have also shown that community patterns depend on the spatial scale of sampling (Wiens et al. 1987) and that a hierarchical analysis may be necessary (Kotliar and Wiens 1990). Unfortunately, most ecological data sets do not offer the luxury of exploring assemblage patterns at different hierarchical scales, making it especially important to restrict the analysis and interpretation of mechanisms to an appropriate spatial scale.

Range gaps may represent sampling error and bias. At regional geographic scales, in particular, it may be difficult to obtain an accurate spatial map of

species occurrence. For example, in elevational surveys of bird communities in the Andes (Terborgh 1971, 1977), species sightings can be influenced by topography, habitat patchiness, trail location, weather, observer experience, and sampling intensity (Graves 1985). Even intensive field efforts may sample only a small fraction of available sites during a limited time of year. In many cases, distributional maps derived from such surveys are crude approximations, at best.

Sampling at small spatial scales also presents challenges. Although small quadrats may be thoroughly searched, many life history stages, such as eggs, seeds, or larvae, cannot be accurately censused. As Hurlbert (1990) has demonstrated in a simulation study of the "montane unicorn" (*Monoceros montanus della Roba*), statistical analyses of quadrat data are sensitive to both the spatial distribution of organisms and the size, number, and placement of quadrats (Williams 1964; Anderson and Marcus 1993). No two species will have identical spatial patterns, but if quadrats are too large or too widely separated, many species may show concordant distributions. These apparent "ties" will affect the power of null model tests of spatial pattern. Quadrat sampling is dealt with in many ecological texts (Greig-Smith 1964; Pielou 1974) and will not be discussed extensively here.

In spite of these limitations, distribution maps at all spatial scales can be studied profitably with null models. In this chapter, we discuss the analysis of both one- and two-dimensional spatial maps. Such maps are relevant to problems of ecological zonation along small-scale environmental gradients, as well as the origin and maintenance of range boundaries on large-scale geographic gradients. Next, we consider the relationship between regional distribution and local abundance. Finally, we discuss correlations at large biogeographic scales among population size, body size, and geographic range, including recent studies of "macroecology" (Brown and Maurer 1989), plus older analyses of the "taxon cycle" (Wilson 1961; Ricklefs and Cox 1972).

PATTERNS IN ONE DIMENSION

The distribution of organisms along one-dimensional environmental gradients provides some of the best examples of the organization of natural communities. The striking patterns of zonation of plants and animals in the rocky intertidal (Colman 1933; Paine and Levin 1981) and the orderly appearance of vegetation associations along altitudinal gradients (Whittaker 1967) suggest that strong nonrandom forces determine the position of each species within the gradient. These forces include (1) biotic interactions, such as competition (MacArthur 1972), predation (Paine 1966), or mutualism (Bertness and Hacker 1994) with
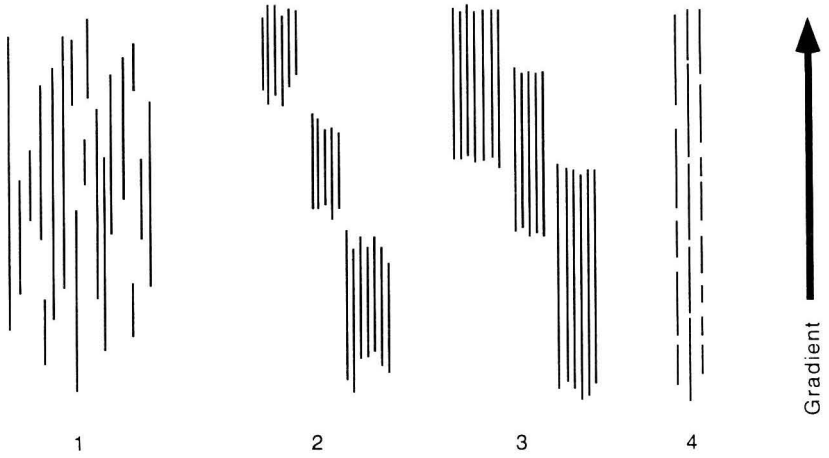
Figure 9.1. Four models of community organization in gradients. Each vertical line represents the range of a different species. Model 1: Random arrangements of range boundaries and species overlap. Species distributions are completely independent of one another. Model 2: Abutting range boundaries and high overlap. The species are organized into well-defined communities, with sharp ecotonal boundaries between communities. Model 3: Nonabutting range boundaries and high overlap. The species are still organized into well-defined communities, but there is more overlap between assemblages and a lack of sharp ecotonal boundaries. Model 4: Abutting range boundaries and low overlap. The species are organized into several guilds, with abutting ranges within a guild but no pattern of overlap between guilds. Adapted from Dale (1986).

syntopic species; (2) abiotic limits, which represent physiological tolerance boundaries (Connell 1961); (3) ecotones, or sharp discontinuities in habitat or vegetation (Terborgh 1977); (4) dispersal constraints, which prevent species from colonizing some habitable regions of the gradient (Rabinowitz 1978; Grosberg 1982).

At the community level, Whittaker (1967) described four models of organization that provide a useful framework for understanding assemblage patterns along gradients. The four models are distinguished on the basis of whether species form discernable groupings and the extent to which boundaries between species are exclusive (Figure 9.1). At one extreme, ranges of species might occur independently of one another along the gradient. The resulting assemblage would show no natural groupings and no unusual exclusions, although the ranges of some species might abut by chance. This assemblage could be taken as a reasonable null model for community organization on an

environmental gradient. At the other extreme, species might co-occur in well-defined exclusive groups, with nonoverlapping sets of species replacing one another along the gradient. This pattern reflects Clements's (1904) "super-organism" view of tightly integrated communities separated by sharp ecotonal boundaries. A third model also results in species groups, but with a good deal of overlap in ranges, so there are not well-defined boundaries between communities. In such an assemblage, apparent community structure arises because species share similar preferences along the gradient, as envisioned by Gleason (1926). Some might argue that Model 1 also describes a Gleasonian community, because species are distributed independently of one another. A final model is that the assemblage is organized into guilds of competing species (Root 1967), and that species within a guild replace one another sequentially along the gradient. If the guild structure is ignored, the entire assemblage might fit the pattern of Models 1 or 3. As we will explain, null models developed by Pielou (1977, 1978) and Dale (1984, 1986, 1988) allow one to distinguish among the spatial patterns predicted by these four models.

At the outset, we note that any null model for community structure in one dimension will involve the random placement of species ranges or their range limits within a bounded number line. For this reason, some of the statistical tests and biological interpretations are identical to those used to recognize niche segregation (Chapters 4 and 5), nonrandom dispersion patterns of body sizes in a community (Chapter 6), or the distribution of relative abundances from the broken-stick model (MacArthur 1957) or some of its variants (Chapter 3).

The Statistics of Overlapping Sheaves

Suppose that an assemblage of species occurs along a well-defined spatial gradient in one dimension, such as an intertidal transect. The gradient can be represented as a number line of length one, and the species distributions can be portrayed as line segments that occur within this number line. The species distributions are analogous to a sheaf of overlapping line segments (Pielou 1977). Qualitative patterns of co-occurrence (segregated, overlapping, or nested occurrences) and quantitative patterns, (the degree of overlap and the size of the gaps in species distributions) can be analyzed with null models.

Pielou (1977, 1978) developed the first models for analyzing the overlap of species ranges. For a set of n species, there are $n(n-1)/2$ pairwise overlaps that can be measured. For each pair of species, she assigned a score of 0, 1, or 2, depending on whether the ranges are nonoverlapping, partially overlapping, or nested (Figure 9.2). This index, summed over all species pairs, characterizes

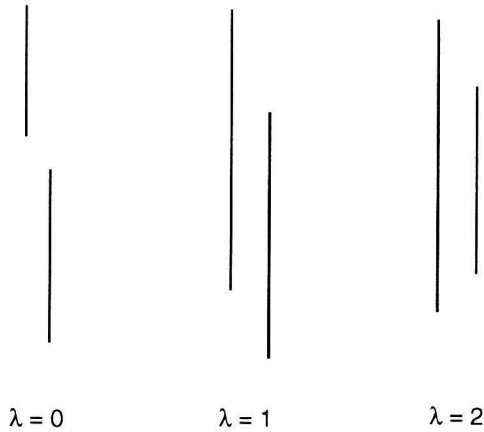$\lambda = 0$ $\lambda = 1$ $\lambda = 2$

Figure 9.2. A qualitative index of range overlap in one dimension. For each species pair, $\lambda = 0$, no overlap; $\lambda = 1$, partial overlap; $\lambda = 2$, complete overlap. Adapted from Pielou (1977).

the average amount of overlap between any randomly chosen pair of species in the assemblage. Because it relies on the qualitative pattern of overlap, the index is insensitive to minor sampling errors in range estimates.

If the species are distributed independently of one another, how much overlap is expected? Pielou (1977, 1978) suggested two null hypotheses. The first was that the upper and lower range boundaries for each species were randomly placed on the gradient. The only restriction on randomization was that the lower bound of a species fell below its upper bound. Under this model, the expectation for the index is

$$E(\text{overlap}) = n(n-1)/2 \qquad\qquad (9.1)$$

which is simply the number of unique species pairs. The distribution is symmetric with variance

$$\sigma^2 = n(n^2 - 1)/9 \qquad\qquad (9.2)$$

One can compute from this expectation and variance whether a single set of species is unusually nested or nonoverlapping. Alternatively, if many sets of species are available, one can tally the number of sets for which the observed overlap is above or below the expectation. For 684 species of benthic marine algae on the western shores of the Atlantic, latitudinal ranges within a genus overlapped significantly more often than expected by chance (Pielou 1977).

Table 9.1

The observed fraction of Atlantic algal genera for which observed overlaps exceeded null expectations

	Rhodophyta	Chlorophyta	Phaeophyta
Null Hypothesis 1	51/69	22/26	17/23
Null Hypothesis 2	29/63	13/27	8/21

Null Hypothesis 1 is that the north and south range boundaries are located randomly and independently. Null Hypothesis 2 is that species ranges are placed randomly, but observed range lengths are retained. For Null Hypothesis 1, there were too many genera with high overlap, whereas approximately half of the genera had high overlaps under Null Hypothesis 2. Adapted from Pielou (1977).

The overlap statistic can be divided into components due to overlapping and nested ranges. Atlantic coast algae were more often nested than overlapping, and the overlap within a genus was consistently higher than the overlap between genera (Pielou 1978). This result parallels studies of the species/genus (S/G) ratio (Chapter 1), which have often revealed that insular coexistence of congeners is greater than expected (Simberloff 1970). Based on the high frequency of nested congeners, Pielou (1978) suggested that Atlantic coast algae may frequently undergo "quasi-sympatric" speciation, in which sister species diverge and become isolated within a single geographic region.

In contrast, the latitudinal spans of Pacific coast algae overlapped one another significantly less than those of Atlantic seaweeds. Because the location of range boundaries was randomized, this null hypothesis did not take into account the length of the range of each species. Thus, part of the difference between Atlantic and Pacific algal distributions could be attributed to the fact that geographic ranges were much smaller on the Pacific coast than on the Atlantic coast. However, because Pielou (1978) compared each species with its congeners, differences in range size cannot entirely explain different overlap patterns on the two coasts.

A second, more realistic null hypothesis retained the range lengths for each species but randomized their position within the range. For a pair of species with range lengths x and y ($x \geq y$) and a total space of length W, the expected overlap between any pair of species is

$$E(\text{overlap}) = \frac{2x(W-x) - y^2}{(W-x)(W-y)} \quad \text{if } W \geq x+y \tag{9.3}$$

$$E(\text{overlap}) = \frac{W + x - 2y}{W - y} \quad \text{if } W < x + y \tag{9.4}$$

Summing these terms over all possible species pairs gives the expected overlap for the entire assemblage; the variance does not have a simple derivation. For the Atlantic coast genera of algae, overlaps were greater than expected for about half of the species pairs. Thus, at least some of the nonrandomness in range distributions of Atlantic coast algae could be attributed to the length of the geographic spans of the species (Table 9.1).

Null Models for Quadrat Data

Pielou's (1977, 1978) null hypotheses are appropriate if the species ranges have been estimated on a continuous scale. If the data have been collected in discrete quadrats sampled along a transect, other methods of analysis are required. Pielou and Routledge (1976) used Bose-Einstein statistics to distinguish between random, clustered, and regular boundaries of species. This test considers the distribution of upper (or lower) boundaries of k species among a set of Q quadrats. Let U equal the number of quadrats cut by at least one upper boundary. If the boundaries are assigned randomly to quadrats, the probability that U is unusually large or small can be calculated. If U is large, the range boundaries are regularly dispersed, whereas if U is small, range boundaries are clustered.

Using these methods, Pielou and Routledge (1976) showed that the landward boundaries of marsh plant species tended to be more clustered than the seaward boundaries, which, in some cases, were distributed more evenly than expected. The tendency toward clustering of both landward and seaward boundaries was more pronounced at high latitudes.

The use of Bose-Einstein statistics implies that each species combination is equiprobable (Feller 1968). The Pielou and Routledge (1976) method is valid for the null hypothesis that species boundaries and quadrat boundaries are randomly interspersed (Pielou 1979b). However, these two kinds of boundaries have completely different meanings and should probably not be equated in the same test. It is more appropriate to treat the quadrats as fixed "boxes" and the assignment of each species boundary to a quadrat as an independent event. For this model, Maxwell-Boltzman statistics should be used to calculate the probability of observed arrangements (Underwood 1978a).

Unfortunately, the exact calculation of these probabilities is difficult. Gardiner and Haedrich (1978) used a Poisson approximation and detected a clustering of species boundaries for deep megafauna living between 200 and 3,000 m
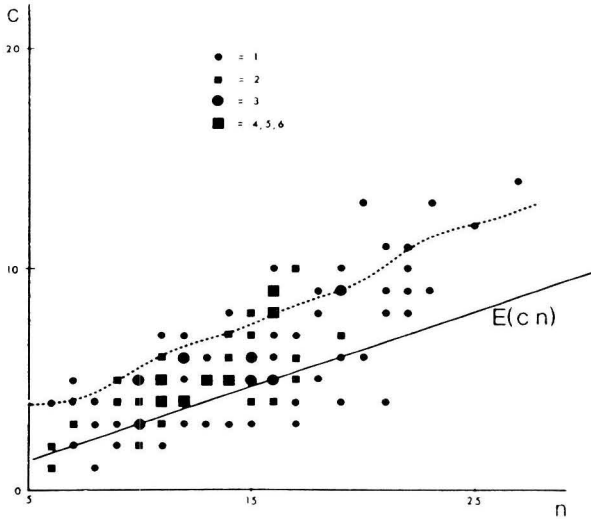
Figure 9.3. Observed and expected number of range contiguities of marine intertidal algae. The *x* axis is the number of species (*n*) in the transect, and the *y* axis is the number of range contiguities (*c*) for that transect. Each point is a transect, and the different symbols represent different numbers of observations. The solid line is the null expectation, and the dotted line is the 5% significance level. Note that most transects contained more range contiguities than expected. From Dale (1984), with permission.

depth. Underwood (1978a) used a similar binomial approximation and found no evidence for a clustering of vertical boundaries of intertidal organisms in Britain. Null model analyses of these and other data (Underwood 1978b) do not support the hypothesis that intertidal distributions are clustered at certain critical tidal levels (Doty 1946; Doty and Archer 1950).

The preceding tests treat upper and lower boundaries in separate analyses. However, competitively structured communities are best identified by the intermingling of upper and lower boundaries. Specifically, the "contiguity hypothesis" predicts that the upper boundary of one species tends to be followed by the lower boundary of a second species (Chapman 1973). If the boundaries are placed randomly with respect to one another, the expected number of contiguities for *n* species boundaries is

$$E(\text{contiguities}) = (n - 1) / 3 \tag{9.5}$$

Dale (1984) applied the test to zoned communities of marine algae in transects and found that, in the majority of transects, the number of contiguities was greater than expected (Figure 9.3).

Null Models for Quantitative Overlap Patterns

One drawback of the previous null models is that they only consider the qualitative pattern of overlap. They do not test for the degree of overlap in species ranges or the size of gaps between nonoverlapping spans. For example, Dale's (1984) contiguity test considered only the sequence of upper and lower boundaries, and not the spacing between them. A pattern in which ranges of species abut closely suggests strong species interactions at the boundary. In contrast, a pattern in which ranges of species are separated by wide gaps (with no intervening range boundaries) suggests ecotonal boundaries, habitat patchiness, or sampling error.

To address this problem, Dale (1986) expanded Pielou's (1978) analyses of the expected number of species pairs that were nonoverlapping, lapped, and nested. He derived expressions for the expected gap length (g) and the expected overlap length (y) for any pair of species given their observed range lengths. The derivation is similar to Cole's (1981) calculation of phenological overlap for a pair of plant species with fixed flowering times (see Chapter 5).

Using the idealized communities in Figure 9.1, Dale (1986) showed that it is possible to distinguish among the four models of community organization. For intertidal algae, the patterns were consistent with the guild model of organization (Model 4): there was little evidence of natural groupings of species, but pairwise overlaps with narrow zones of intermingling were common.

Finally, Dale (1988) derived tests for the clustering of range boundaries at particular locations in the gradient, again retaining the observed range lengths as a constraint and randomly placing species ranges within the gradient. The test statistic is the sum of the product of pairwise distances between adjacent boundaries. This number should be unusually small if boundaries are clustered and unusually large if boundaries are evenly spaced throughout the gradient. Using this test, Dale (1988) detected only weak evidence for a critical clustering of species boundaries, a result that was consistent with Underwood's (1978b) tests of the critical tidal-level hypothesis.

In summary, the null model machinery for analyzing community patterns of overlap in one dimension is well-developed. We now need tests of communities other than intertidal algae to gain an understanding of community structure in gradients. Reanalysis of disputed avian distributions on elevational gradients (Terborgh 1971, 1977; Graves 1985) might be especially informative.

PATTERNS IN TWO DIMENSIONS

Once the analysis is expanded to two dimensions, simple statistical tests are no longer practical. Instead, the placement and possibly the size of each species range must be determined by simulation. We begin by considering null models that have been applied to the general problem of global diversity gradients. Next, we discuss relatively simple examples, in which investigators have considered only the placement of one range boundary, before turning to studies of the placement of entire geographic ranges.

Global Diversity Gradients

On a global scale, three major diversity gradients have been described: latitudinal gradients in species richness, which usually increases at low latitudes (Dobzhansky 1950; Pianka 1966); (2) elevational gradients in species richness, which often peaks at mid-elevation (Terborgh 1971; Olson 1994); and (3) gradients in the latitudinal spans of geographic ranges, which sometimes decrease at low latitudes (Stevens 1989). Stevens (1989) designated this third pattern Rapoport's rule (Rapoport 1982), and it seems to hold for many, but not all (Rohde et al. 1993), taxa. Stevens (1989) suggested that Rapoport's rule might be the cause of latitudinal gradients in species richness. If low-latitude species have low tolerance for environmental variability, then most of the populations at any particular site in the tropics might be "marginal populations" that are poorly adapted for the site but maintained by immigration.

A great deal of effort has gone into understanding the causes of diversity gradients, but few studies have asked what diversity gradients would arise with minimal biological assumptions. Osman and Whitlach (1978) warned that diversity gradients can be artifacts of open and dynamic systems. They suggested that an equilibrium patch model (Terborgh 1973b) might account for diversity gradients without invoking factors such as global environmental gradients, niche characteristics, trophic complexity, or temporal stability. However, because their null model invokes dynamic turnover, there must ultimately be spatial gradients in the frequency of disturbance or the probability of local colonization and extinction to produce observed species richness gradients.

More recently, Colwell and Hurtt (1994) developed a much simpler null model to account for global diversity patterns that does not invoke dynamic turnover. The model begins with a globe that is covered with randomly located circles, which represent the geographic ranges of species. A point is randomly chosen to represent the "pole," and diversity gradients and species ranges are mapped from pole to equator. The poles represent a "soft boundary," because
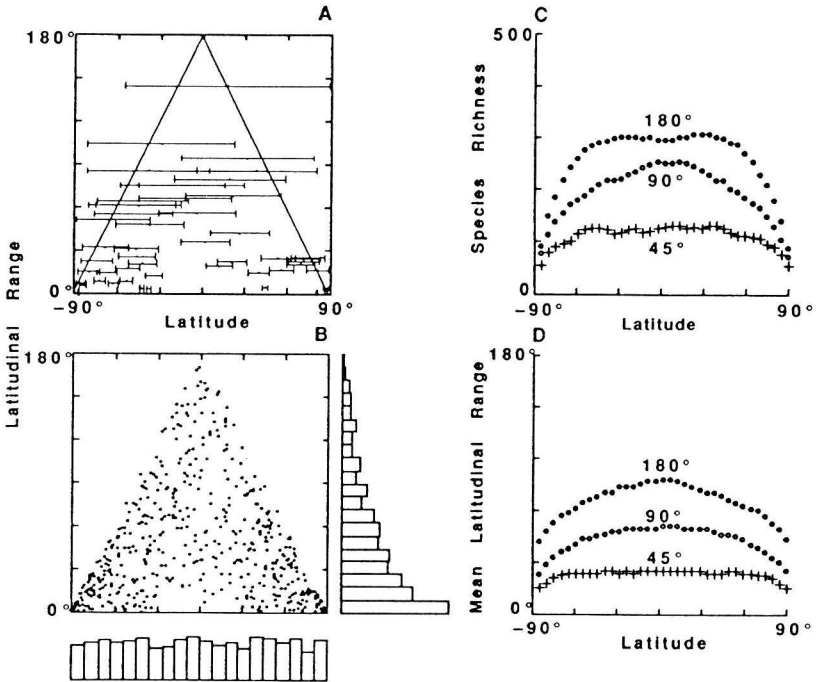
Figure 9.4. Latitudinal gradients in species richness and range distributions from a simple null model. (**A**) A latitudinal range midpoint is randomly chosen from a uniform distribution for each species, and then a permissible latitudinal range is chosen. (**B**) The resulting distribution of ranges and midpoints falls within the triangle of acceptable values. Ranges are limited above and below the equator by a "hard boundary" at a specified latitude. (**C**) The null model generates a latitudinal gradient of species richness and a "reverse Rapoport effect," in which the latitudinal span of species near the hard boundary is less than the span of species near the equator (**D**). Reprinted by permission of the publisher from Colwell, R. K., and G. C. Hurtt. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. *American Naturalist* 144:570–595. Copyright © 1994 by The University of Chicago.

ranges that cross over one of the poles are measured only in one focal hemisphere. This baseline model shows no latitudinal gradient in species richness.

Next, Colwell and Hurtt (1994) imposed a symmetric "hard boundary" in both hemispheres, beyond which no species range could extend. Such a boundary might represent a major barrier or climatic limit, or a continental boundary for all species in the assemblage. For each species, a midpoint was randomly selected within the hard boundary limits, and then a feasible latitudinal range

was chosen. The simulation results (Figure 9.4) show that species richness decreases as a hard boundary is approached, even though there is no biological or physical gradient between the boundaries. Thus, the model might account for both latitudinal gradients and mid-elevational peaks in species richness. However, the model did not produce a Rapoport effect. In fact, species ranges actually decreased in size as the hard boundary was approached. Thus, a Rapoport effect need not be the cause of species richness gradients, as Stevens (1989) suggested.

These results are based on perfect knowledge of range distributions. Colwell and Hurtt (1994) next used a sampling model to understand the effects of sampling biases on diversity gradients. They began by imposing a species richness gradient above and beyond that produced by the null model. Next, they assumed that within a species, the distribution of individuals across its geographic range was either uniform or normal. Finally, they sampled a finite number of individuals at each point in a latitudinal transect. The model mimics diversity gradients that would be expected when sampling is less than complete.

The estimated geographic ranges for this model often led to a Rapoport effect. The problem was that individual species in the diverse tropics were often poorly sampled compared to species at high latitudes. Consequently, the geographic ranges of tropical species were underestimated, leading to a spurious Rapoport effect. This sampling bias arises from equal sampling effort at all locations, because fewer individuals per species are collected at species-rich sites. For well-studied North American taxa, there is no question that diversity gradients are real and do not represent sampling artifacts. But the distributions of many tropical taxa are poorly known, and this form of sampling bias may be important. Colwell and Hurtt's (1994) study suggests that even "obvious" diversity patterns may have a sampling component to them that reflects the geometry of the continents rather than underlying biological or physical gradients.

The Location of Range Boundaries

Just as the range limit of a species can be represented as a point on a one-dimensional number line, the range boundary can be represented as a line segment on a two-dimensional map. One of the simplest cases for analysis is the placement of range boundaries along a large-scale geographic gradient. For example, species richness often decreases from the base to the tip of geographic peninsulas (Simpson 1964). This "peninsular effect" can be investigated by examining the placement of the range boundaries of species that drop out along a peninsula. Three hypotheses have been proposed for the peninsular effect:

1. An equilibrium hypothesis, which posits that immigration rates decrease and extinction rates increase from the base to the tip of a peninsula (MacArthur and Wilson 1967).
2. A time hypothesis, which posits that peninsulas are geologically young and have not had enough time for recolonization, or are historically depauperate because of small source pools (Orr 1960).
3. A habitat diversity hypothesis, which posits that low habitat diversity in peninsulas is responsible for the progressive dropout of species (Taylor and Regal 1978).

Means and Simberloff (1987) tested the habitat diversity hypothesis in an analysis of range boundaries along the Florida peninsula for 48 species of amphibians and reptiles. As a null model, they generated species range distributions that were independent of one another and independent of habitat features of the peninsula. The simulation retained the size and general range features for each species but allowed the position of the range boundary to vary randomly.

Compared to this simulation, herpetofauna range boundaries were highly clustered in a few counties along the mid-peninsular axis of Florida (Figure 9.5). These counties have the highest elevations and greatest habitat diversity in the state, both of which decline rapidly to the south. Historical and island biogeographic explanations seem relatively unimportant in this case, and the results suggest that habitat reduction alone could account for the peninsular effect in Florida herpetofauna.

When expanded to a continental scale, the analysis of range boundaries is often more challenging. Root (1988a) analyzed distributional boundaries of 148 wintering land bird species in North America. She compared range boundaries to gradient maps of six environmental factors: average minimum January temperature, mean length of frost-free period, potential vegetation, mean annual precipitation, average general humidity, and elevation. The first three factors were frequently associated with northern range boundaries (60%, 50%, 64%), whereas vegetation (63%) and precipitation (40%) were most frequently associated with eastern boundaries. Associations with western boundaries were less clear-cut, and southern boundaries were not studied because most species occurred throughout the southern United States.

With six intercorrelated environmental variables and 148 species, some associations are expected to occur by chance alone. Root (1988a) used a simple null model to place species range boundaries and evaluate this effect. She first selected 51 species randomly from the list of 148. For each species, she used a
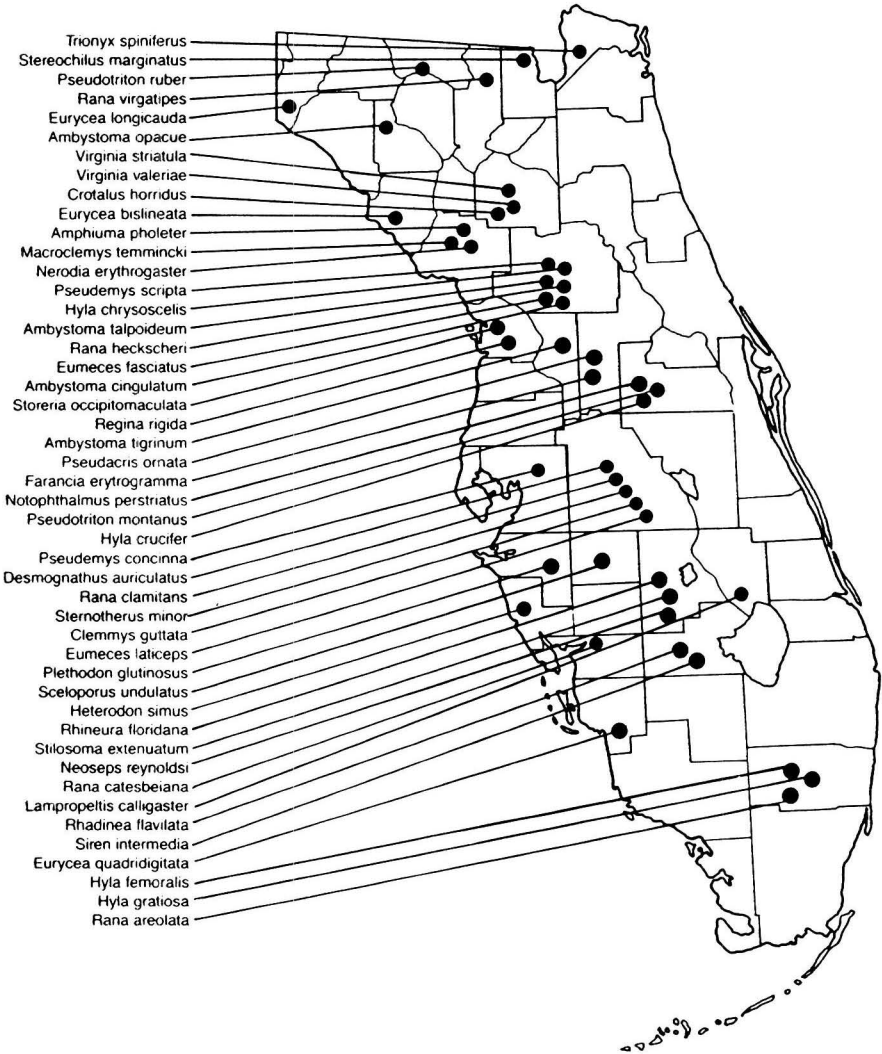
Figure 9.5. Distribution of tipward range termini of amphibians and reptiles in the Florida peninsula. Compared to null model simulations, these range boundaries are clustered in counties with the highest elevations and greatest habitat diversity in the state. From Means and Simberloff (1987), with permission.
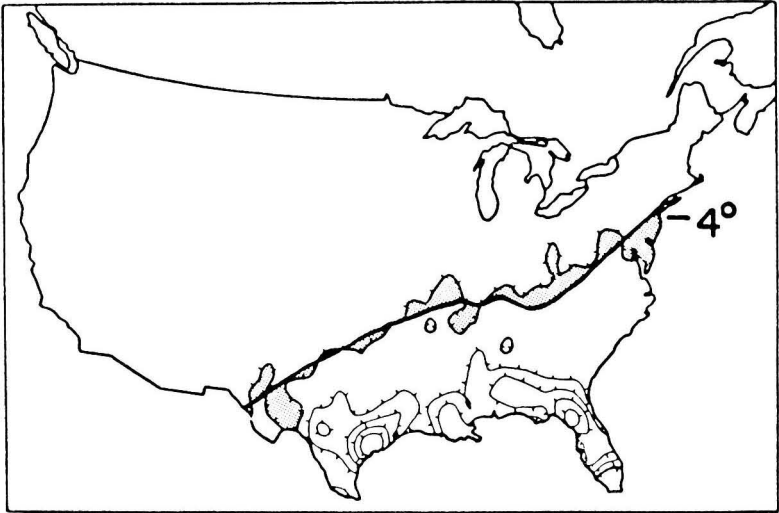
Figure 9.6. Distribution and abundance of the Eastern Phoebe (*Sayornis phoebe*) with respect to winter isotherms. The tick-marked lines represent four contour intervals of 20%, 40%, 60%, and 80% of maximum abundance, which is highest in the southern United States. The thick black line is the –4° C average minimum January temperature isotherm. The stippled area highlights the difference between this isotherm and the northern range limit. Compared to randomly placed range boundaries, most species range boundaries showed unusual concordance with temperature isotherms or other environmental measures. From Root (1988b), with permission.

random number table to move the distribution *x* degrees latitude north or south, and *y* degrees longitude east or west, and to rotate it *z* number of octants clockwise or counterclockwise. Thus, the simulation retained the shape of each range boundary but randomized its location and orientation (Figure 9.6). In these simulated ranges, only two of the 51 species range boundaries coincided with environmental factors, compared to over 50% of the real boundaries. Range boundaries of wintering birds coincided with environmental factors more often than expected, and the patterns may reflect energetic constraints associated with cold temperatures (Root 1988b). However, the strong intercorrelation among the variables makes it difficult to pin down the mechanisms (Castro 1989; Root 1989).

The Size of the Geographic Range

A primary question in any simulation of geographic ranges is whether the size of the range ought to be strictly retained or possibly allowed to vary. Indeed,
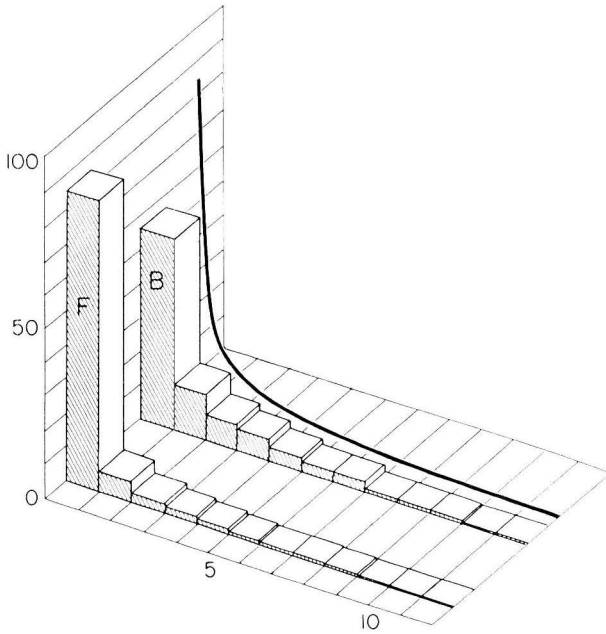
Figure 9.7. Range size distributions of North American fishes (F) and birds (B). The x axis is the area of the geographic range (1×10^6 km^2), and the y axis is the percentage of species. These distributions contain more species with intermediate-sized ranges than predicted by a logarithmic series (solid line), which results from a simple Markovian model of range expansion and contraction. From Anderson (1985), courtesy of the American Museum of Natural History.

before considering the placement of geographic ranges, it is worthwhile to ask what factors determine range size.

The frequency distributions of range sizes of related species tend to follow a log normal distribution (Anderson 1984), with most species having relatively small geographic ranges. Anderson (1985) constructed a number of Markovian null models in which transition probabilities between cells in a gridded map dictated random increases or decreases in range size. The equilibrium distribution of range sizes in this model qualitatively fit the observed range sizes for North American vertebrate taxa, although there were usually more intermediate-sized ranges than predicted (Figure 9.7).

An important consideration in the analysis of geographic ranges is the extent to which historical versus ecological mechanisms are invoked (Endler 1982). Anderson's (1985) null models did not specify the biological factors that influenced range size. However, the mechanisms are clearly ecological and

operate on relatively short time scales, because the model predicts that ranges are continuously expanding and contracting in size. Carter and Prince (1981) used epidemic models of invasion that also invoke short-term changes in site occupancy to explain biogeographic range limits.

An alternative perspective is that range limits are relatively static and largely reflect the historical legacy of speciation (Lynch 1989). This perspective can also be incorporated into simple null models. For example, Rapoport (1982) showed that the distribution of range sizes of mammalian subspecies (and the relative areas of land held by rich and poor landowners) could be approximated by taking random partitions of *x* and *y* coordinates in a square. If these random partitions represented the emergence of dispersal barriers, and each isolated taxon speciated allopatrically, the resulting range areas would reflect historical speciation events with no current change in range size. Similarly, the species composition in local assemblages may be a reflection of biogeographic constraints on source pools rather than ecologically driven assembly rules (Cornell and Lawton 1992).

Geographic ranges reflect both ecological and historical processes, so neither scenario is entirely correct (Taylor and Gotelli 1994). Historical processes are difficult to incorporate into null models, so most analyses have either taken the range sizes as a constraint (Beven et al. 1984) or constructed them with simple accretion algorithms (Means and Simberloff 1987) that do not resemble explicit speciation or dispersal processes.

Randomization of Geographic Ranges

The random placement of geographic ranges can be simulated in two ways. First, the map of the range can be randomly relocated on the continental map. Alternatively, an algorithm can be used to specify the "growth" of the range in a grid of cells superimposed on the map. Problems arise at the edge of maps with either approach. If the species range maps were distributed at random across a map surface, one could discard those placements that spilled over the map boundary. However, as Ashton et al. (1988) showed for one-dimensional simulations of flowering phenology (Chapter 5), this procedure inevitably biases the model toward "interior" distributions with high overlap among species.

If the ranges are created by filling a grid, growth rules must be specified at boundaries. Haefner et al. (1991) examined the performance of several edge algorithms used in simulation models of spatial competition.The best procedure was to simply embed the grid in a larger area, but this does not solve the problem for continental maps with natural coastal boundaries. Mapping the

area onto a torus is also inappropriate for geographic maps, because it would introduce extreme range disjunctions. We think the best solution for geographic range maps is to choose the starting cell randomly and then use an algorithm to accumulate contiguous cells until the desired area is filled.

Pleistocene Forest Refugia

The analysis of gridded maps is well illustrated by a study of Pleistocene refugia (Beven et al. 1984). The "biological model for diversification in the tropics" proposes that range fragmentation during Pleistocene glaciations led to increased rates of allopatric speciation and high species richness (Haffer 1969; Simpson and Haffer 1978; Haffer 1982). Several authors have used biogeographic data to delineate the locations of hypothesized Pleistocene refugia. If the refugia hypothesis is correct, then the occurrence of species distributional boundaries should be concentrated between refugia, with few or no boundaries occurring within refugia. Similarly, refugia should correspond to centers of high endemism for particular taxa. Finally, there should be an unusual concordance between refugia delineated for different taxa if they were influenced by the same vicariant events.

Beven et al. (1984) used null models to test for these patterns in proposed refugia and centers of endemism for Amazonian birds (Haffer 1978). Distributional maps for Amazonian birds were digitized and converted to a 100 × 77 rectangular grid covering Amazonia. Next, centers of endemism and Haffer's (1969) refugia were superimposed on the maps (Figure 9.8). Finally, the number of species boundary segments in each square was tabulated and compared to those generated by a null model.

Rather than randomize species ranges, Beven et al. (1984) randomized the position of the proposed refugia while maintaining their observed areas. Two randomization algorithms were used. In the first, grid squares were chosen completely at random. In the second, grid squares were chosen randomly but constrained so that the refugia remained contiguous. The analyses were repeated excluding squares that had major rivers, which might act as current ecological barriers to dispersal (Salo et al. 1986). Finally, they measured the overlap between sets of refugia proposed independently for plants (Prance 1973), birds (Haffer 1969), and lizards (Vanzolini and Williams 1973). To test whether such refugia were unusually concordant, Beven et al. (1984) cast scale cutouts of the proposed refugia by hand onto a map of South America and then measured the overlap between refugia proposed for different taxa. The only restriction was that the randomly thrown refugia lie entirely on land and not overlap within a given set of proposed refugia.
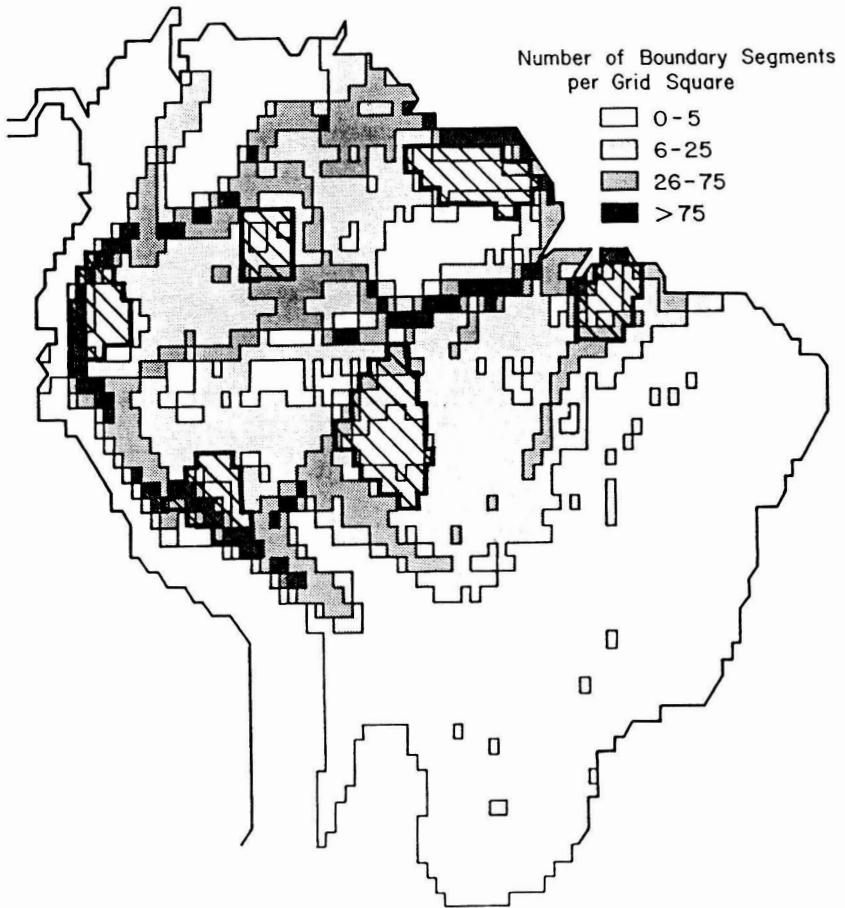
Figure 9.8. Digitized map illustrating the density of species range boundaries and the centers of endemism proposed by Haffer (1978) for birds of Amazonia. Centers of endemism are indicated by thick boundaries and diagonal hatching. From Beven et al. (1984), with permission.

The results of these analyses were mixed. Some refugia and centers of endemism included substantially fewer range boundaries than expected, as predicted by the refugia hypothesis. Others did not differ from the simulation results, and in a few cases, refugia had significantly more distributional boundaries than expected by chance. Most proposed refugia had fewer boundaries than expected, although the pattern was not striking (Figure 9.9; 14 of 21 refugia; $p = 0.094$, rivers excluded). Overlap among refugia proposed for different taxa also was not significantly large. However, the simulation was
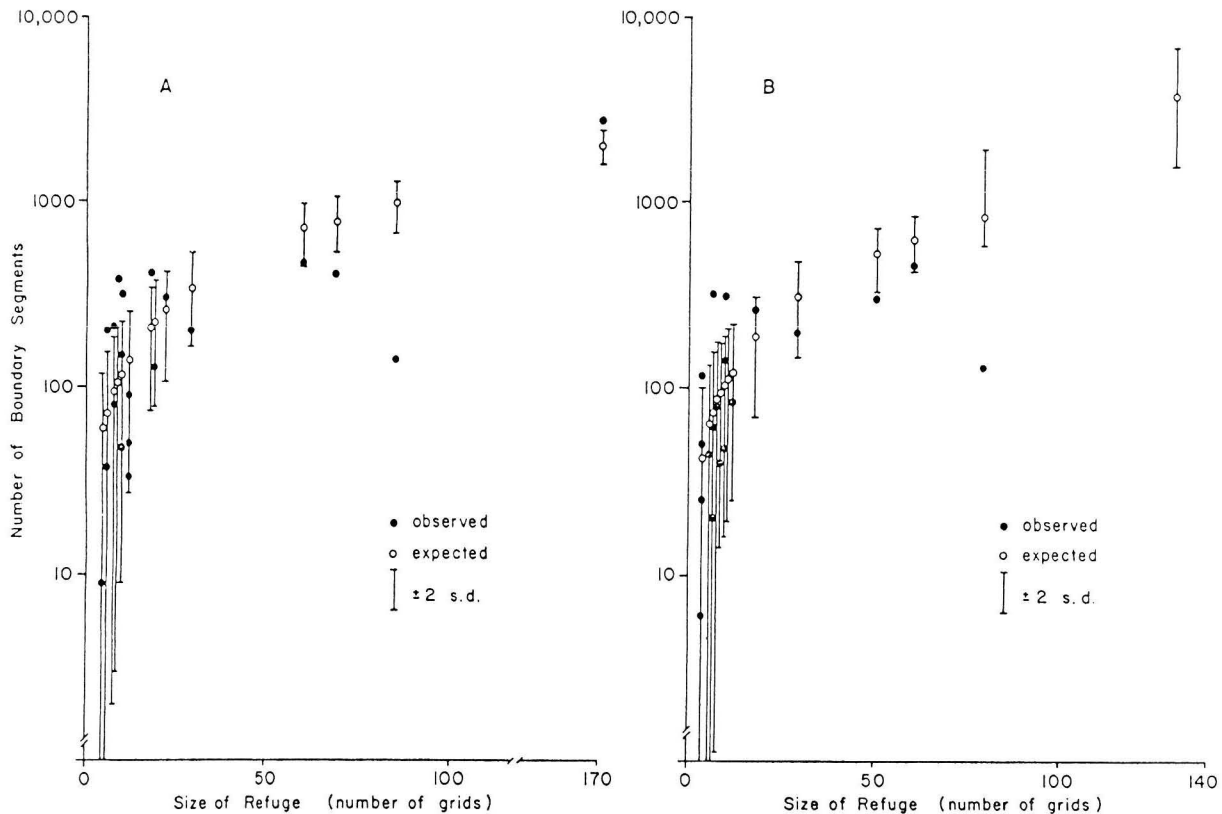
Figure 9.9. Observed and expected number of species boundary segments in proposed refugia. Distributions are shown for simulations with (**A**) and without (**B**) river squares excluded. If the refugium hypothesis were correct, the proposed refuges would have significantly fewer range boundaries than predicted by the simulations. Note that most proposed refuges have about the number of range boundaries predicted by the null model. From Beven et al. (1984), with permission.

biased toward finding this result, because the hand-thrown ranges were restricted by map edges (Ashton et al. 1988). Given that the refugia and centers of endemism were delineated primarily on the basis of the range maps themselves (Nelson et al. 1990), the evidence in support of such refugia is hardly overwhelming. These null model results seem to confirm detailed geological (Räsänen et al. 1987) and palynological studies (Salo 1987; Bush et al. 1990) that also find little evidence for the refugia hypothesis.

DISTRIBUTION AND ABUNDANCE

Although biogeography and ecology have developed as distinct fields of study, patterns of distribution and abundance are intimately related to one another (Andrewartha and Birch 1954). *Distribution* refers to the geographic range or number of occupied sites, whereas *abundance* refers to the density of organisms within an occupied site. The two measures are closely related, because as abundance decreases across a spatial gradient, the frequency of occupied sites also tends to decrease. Finally, the edge of the range can be recognized as those sites for which abundance always equals zero (Caughley et al. 1988). Within a species, abundance usually decreases from the center to the edge of the geographic range (Hengeveld and Haeck 1981, 1982), probably because of correlated two-dimensional environmental gradients (Brown 1984). Between species, those that are widespread or have a large geographic range tend to be more locally abundant than geographically restricted species (Bock and Ricklefs 1983).

Much of the recent interest in distribution-abundance relationships can be traced to the publication of an important metapopulation model by Hanski (1982a). His model predicted the fraction of homogeneous population sites occupied by a species, following the framework established by Levins (1969, 1970). Hanski's model incorporated a "rescue effect" (Brown and Kodric-Brown 1977), because it assumed that the probability of local extinction decreased as more population sites were occupied (Gotelli 1991). It also assumed that the probabilities of local extinction and local colonization were stochastic, with large variances.

Two major predictions emerged from Hanski's (1982a) model. First, there should be a correlation between distribution and abundance. When a species occupies many population sites, its average local abundance should be high, reflecting the assumption of a rescue effect. Second, the distribution of occupied sites should be bimodal: a species will usually occupy either few or many sites, and will infrequently occupy an intermediate number of sites. Hanski (1982a) has termed this bimodal pattern "the core-satellite hypothesis."

The data needed to rigorously test this and other metapopulation models (Gyllenberg and Hanski 1992; Hanski and Gyllenberg 1993) would consist of single-species records of population occurrences among a set of patches for many different time periods. Then it should be possible to determine whether the fraction of sites occupied is correlated with local extinction or colonization, and whether the distribution of occupied sites is bimodal or not (Gotelli and Kelley 1993). Unfortunately, data of this type are very difficult to come by (Harrison et al. 1988), so that most of the "tests" of Hanski's model have been at the community level (e.g., Gotelli and Simberloff 1987; Gaston and Lawton 1989; Collins and Glenn 1990). These tests are burdened by an additional and unrealistic assumption: species in an assemblage are "similar" to one another and exhibit comparable metapopulation dynamics. If this assumption holds, then it is possible to test for bimodality and the correlation between distribution and abundance by using species as replicates and examining a snapshot of the assemblage at one time, rather than replicating through time and examining the distribution and abundance of a single species.

Although the relationship between distribution and abundance is sensitive to habitat persistence (Novotný 1991) and scale (Gaston and Lawton 1990), the pattern seems to be ubiquitous. A positive correlation is found in many assemblages that probably are not influenced by metapopulation dynamics. Brown (1984) argued that widespread species have broader niches, so that the same factors that allow a species to occur in many sites also allow it to achieve greater abundance within those sites. Nee et al. (1991) modeled species-specific carrying capacities and their effect on regional dynamics, describing Brown's (1984) idea in mathematical terms (Hanski 1991).

However, independent evidence for this niche hypothesis has not been universally established (Hanski et al. 1993). Bowers (1988) showed with computer simulation that local population size was more variable for mammalian species with small geographic ranges than for those with large, geographic ranges, which is consistent with Brown's (1984) argument. However, because Bowers's (1988) analysis appears to have included "empty" sites, local population variability was confounded with small-scale distribution patterns.

It is important to determine whether correlations between distribution and abundance are sampling artifacts or inherent properties of species (Ricklefs 1972). Bock and Ricklefs (1983) pointed out that a correlation between distribution and abundance may be an artifact of limited sampling area. That is, the abundances of species may depend upon which part of their geographic range occurs in the sample space. Species that are sampled near the edge of their range will occur with low abundance in few local sites. In contrast, species that
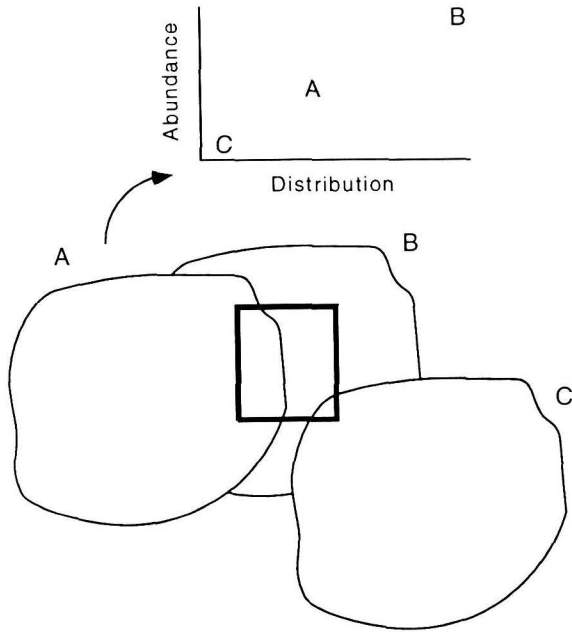
Figure 9.10. Correlations between distribution and abundance can arise from limited sampling. A, B, and C represent the geographic ranges of 3 hypothetical species, which are identical in all respects except for the placement of their ranges. The thick square represents a limited sampling area, within which distribution and abundance relationships are measured. Because the square is centered on the range of species B, this species will occur in most samples and have a high abundance. In contrast, species A and C are sampled near the edges of their ranges, so they will appear to be sparsely distributed and relatively rare in the places they do occur.

are sampled near the center of their range will appear to be more widespread and abundant (Figure 9.10). Null model analyses show that similar artifacts may confound relationships between geographic range and geologic duration of taxa in the fossil record (Russell and Lindberg 1988).

Because most species show an abundance peak at least somewhere within their biogeographic ranges (Brown 1984; Rabinowitz et al. 1986), this explanation certainly can account for some, but not all, correlations between distribution and abundance. However, the correlation between distribution and abundance holds for North American birds when abundances are measured over their entire geographic ranges (Bock and Ricklefs 1983), so this pattern cannot be attributed to a sampling artifact.

Finally, Wright (1991) argued that correlations between distribution and abundance are expected entirely by chance. If individuals are distributed by a Poisson process across a landscape, and then sampled with quadrats, rare species will be less likely to occur in samples and will have a low abundance, even in the absence of other processes controlling spatial pattern. If the Poisson null model is correct, then a plot of the natural logarithm of the frequency of absences ($\ln (1 - p)$) against the average abundance in occupied sites should have a slope of -1.0 and an intercept of 0.0. Most data sets that Wright (1991) examined did not fit the quantitative predictions of the Poisson model, in part because intraspecific clumping of individuals affected the shape of the curve.

Thus, four hypotheses have been proposed to account for the relationship between distribution and abundance: (1) metapopulation dynamics (Hanski 1982a); (2) niche relationships (Brown 1984); (3) limited sampling (Bock and Ricklefs 1983); and (4) chance correlations (Wright 1991). Because they operate at distinctly different spatial scales, the four hypotheses cannot be considered mutually exclusive or even complementary. Brown's (1984) explanation is appropriate for distribution-abundance relationships measured over the entire geographic range of a species, whereas Wright's (1991) null model operates within populations because it describes the random placement of individuals. Between these extremes, the models of Hanski (1982a) and of Bock and Ricklefs (1983) operate at an intermediate regional scale, above the level of the population but below the level of the entire biogeographic range.

The two regional-scale models make very different assumptions about population structure and patch homogeneity. In Hanski's (1982a) model, the patches are homogeneous and equivalent for the different species, and the population structure is highly dynamic. Because of stochastic variation in probabilities of extinction and colonization, there is no biological distinction between widespread "core" species and patchy "satellite" species, even though they are often discussed in this fashion. Instead, core and satellite status is expected to change unpredictably through time, so that species that are widespread and abundant at one time may be sparse and rare at another.

In Bock and Ricklefs's (1983) model, the suitability of a patch varies among species, depending on which portion of their biogeographic range has been sampled. Distribution and abundance relationships would be relatively static through time—widespread species would remain consistently abundant because the sample area occurs near the center of the biogeographic range, whereas sparse species would usually be in low abundance because they are sampled at the periphery of their ranges.

In summary, the correlation between distribution and abundance in nature is ubiquitous, and at least four hypotheses have now been proposed to account for

it. The sampling models of Wright (1991) and of Bock and Ricklefs (1983) are appropriate null hypotheses at local and regional spatial scales, respectively. We now need additional data on niche and dietary relationships, geographic ranges, metapopulation structure, and temporal constancy of community structure in order to test these hypotheses.

Bimodality

The second community-level prediction to emerge from Hanski's (1982a) metapopulation model was that the frequency distribution of site occupancy by species in a community should be bimodal, with modal peaks of widespread "core" species and sparse "satellite" species. As in the analysis of distribution and abundance, there are many alternatives to the metapopulation explanation for bimodality.

The occurrence of bimodality in quadrat data has a long history in plant ecology. In particular, Raunkiaer's (1934) "law of frequencies" described a pattern of bimodality in the fraction of quadrat occurrences of plant species. Specifically, if the occurrence of species is partitioned into five frequency classes ($A = 1–20\%, B = 21–40\%, C = 41–60\%, D = 61–80\%, E = 81–100\%$), the law states that the A ("satellite") and E ("core") classes will form peaks in the histogram. Raunkiaer's (1934) explanation for this pattern was one of habitat specificity: species constituting the core (E) mode were those best adapted to the local habitat, so they occurred in most quadrats, whereas the rare species in the (A) mode were poorly adapted and occurred infrequently. His model predicted that the occurrence of species in the A and E modes would shift in different habitats. Note that Raunkiaer's (1934) explanation accounted for the identity of species in the rare and common classes, but it did not actually explain why the distribution was bimodal.

Raunkiaer's (1934) law has been repeatedly criticized as a sampling artifact that is sensitive to the size, placement, and number of quadrats examined (Gleason 1929; Williams 1950; McIntosh 1962; Greig-Smith 1964). In his characteristic fashion, Williams (1950, 1964) developed an appropriate null model and showed that the fraction of species in the core mode was sensitive to both the number and size of quadrats sampled: the E mode decreased in size as more quadrats were sampled or as quadrat size was decreased (Figure 9.11). The reason is that many species will occur in nearly every sample if the quadrats are large or if few samples are taken. As sampling intensity increases or the size of the quadrat is reduced, species shift into less common abundance classes and the E mode shrinks in size.

However, the fact that bimodality is sensitive to sample size does not mean that all bimodal patterns are artifacts. Using Williams's (1964) approach,
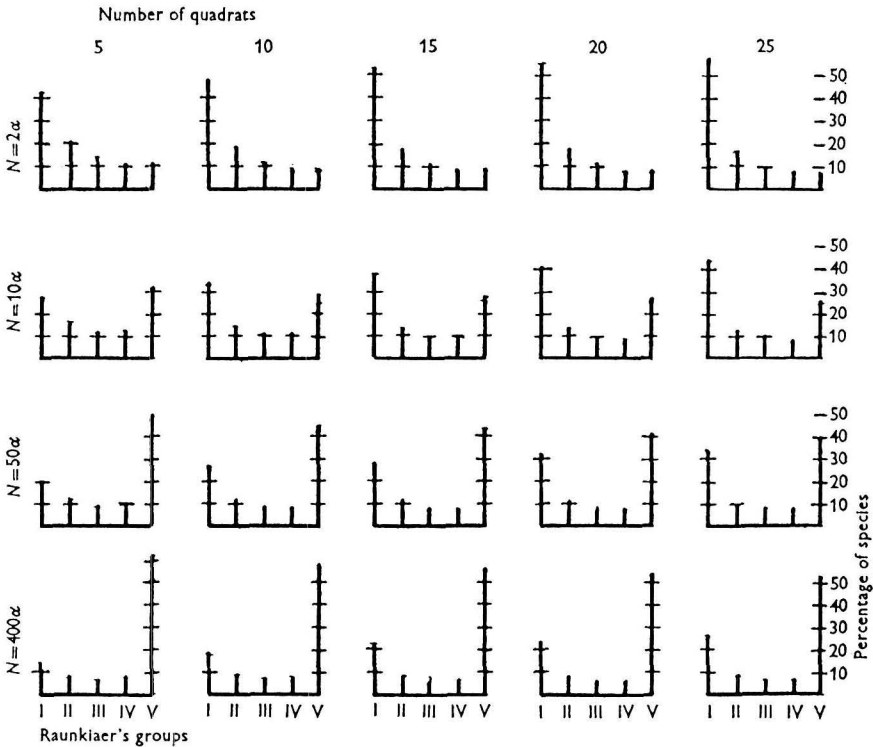
Figure 9.11. Effects of quadrat size and number on the occurrence of species. In each histogram, groups I–V represent the fraction of quadrats occupied, in 20% intervals. The *y* axis is the number of species that falls in each frequency class. The sizes of the histogram bars are based on random samples from a log series species abundance distribution. The columns are arranged in order of increasing quadrat number, and the rows are arranged in order of increasing quadrat size. Note that the fraction of species in the right-hand tail increases with quadrat size and decreases with sample size. From Williams (1964), with permission.

Gotelli and Simberloff (1987) randomized the placement of prairie plant quadrat data among different soil types and found that the size of the core mode was still greater than expected by chance (Figure 9.12). Alternatively, Collins and Glenn (1990) distributed species randomly among sites and showed that the bimodality of prairie grasses persisted at several sampling scales. However, because their null model did not control for quadrat number, it did not specifically address Williams's (1964) sampling hypothesis.

Finally, Brown (1984) argued that the bimodal patterns predicted by Hanski's (1982a) model are an artifact of sampling at a small spatial scale: when
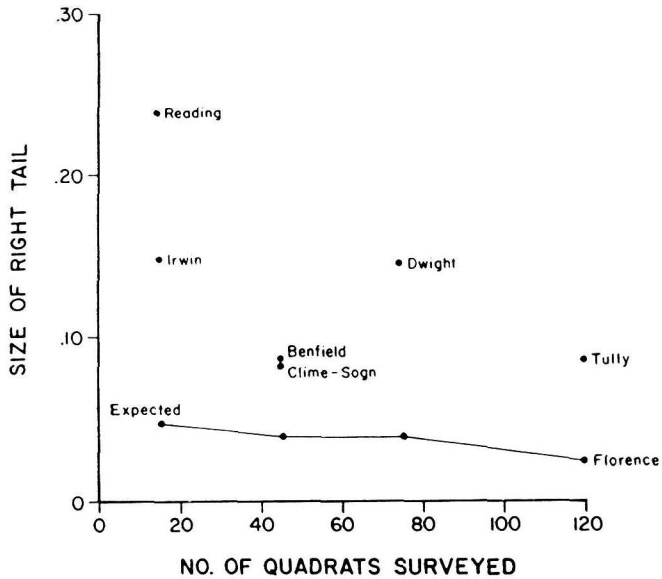
Figure 9.12. Effects of quadrat number on the fraction of widespread plant species in tallgrass prairie. Each point represents a set of quadrats sampled on a different soil series. The solid line gives the expected size of the right-hand tail of the distribution if quadrats were assigned randomly to soil series. Note that six of the seven series fall significantly above the expectation. Reprinted by permission of the publishers from Gotelli, N. J., and D. Simberloff. 1987. The distribution and abundance of tallgrass prairie plants: a test of the core-satellite hypothesis. *American Naturalist* 130:18–35. Copyright © 1987 by The University of Chicago.

species are sampled over their entire geographic ranges, bimodal distributions disappear. Brown (1984) was correct in asserting that bimodal patterns are less likely at the continental scale, but this is not a valid criticism of Hanski's (1982a) model. Hanski's (1982a) model was formulated at a regional scale, and we expect patterns to change at large spatial scales because sites are no longer homogeneous when sampling occurs across the entire geographic range of a species.

Macroecology

The field of macroecology seeks to understand the partitioning of physical space and ecological resources by species (Brown and Maurer 1989). In these analyses, individual species function as replicates and may exhibit correlated patterns of geographic range size, body size, and population density (Damuth

1981; Gaston and Lawton 1988a,b; Lawton 1990). Brown and Maurer (1989) have argued that both absolute and probabilistic boundaries determine the shape of the polygon when these variables are projected in two dimensions. These boundaries, in turn, are thought to reflect energetic constraints, and correlations with dispersal and extinction probabilities.

To explain these patterns, macroecology emphasizes ecological factors and deemphasizes historical or evolutionary mechanisms. But in many assemblages, the history of speciation affects species geographic range sizes (Taylor and Gotelli 1994), and phylogeny has an equally strong influence on body sizes (Elgar and Harvey 1987), so that ecological correlates may ultimately reflect historical or phylogenetic processes.

Even ignoring historical or evolutionary mechanisms, it is difficult to tease apart statistically the highly intercorrelated set of macroecological variables. For example, in some assemblages, body size and geographic range size are positively correlated (Brown and Maurer 1987; Gaston 1990). One interpretation of this correlation is that large-bodied species have large home range requirements and low population densities (Brown 1981). Consequently, a large-bodied species with a small geographic range would have a small total population size and a high probability of extinction (Brown and Maurer 1987). Alternatively, small-bodied species might be more vulnerable to density-independent fluctuations. In this scenario, differential extinction (or range contraction) of small-bodied species leads to the positive correlation between range size and body size (Gaston 1990).

But neither scenario takes account of latitudinal variation in body size and geographic range size. Body sizes tend to increase away from the tropics (Bergmann's rule), as does the north-south span of geographic range in many taxa (Rapoport's rule). Consequently, the correlation between body size and range size may be spurious and reflect underlying latitudinal gradients in both variables (Pagel et al. 1991b). When latitude and longitude are incorporated as covariates in macroecological analyses, correlations between body size and geographic range size may disappear (Taylor and Gotelli 1994).

The relationship between body size and population density may be more complex and nonlinear (Lawton 1989). For North American bird species, Brown and Maurer (1987) showed that maximum population density peaked at an intermediate body size (Figure 9.13). Morse et al. (1988) reported a similar result for rain forest coleoptera. These results contrast with broad taxonomic comparisons, which have shown that population density increases as body weight decreases (Peters and Wasenberg 1983; Damuth 1987). However, in both the bird and the beetle data sets, there were more intermediate-sized species than large- or small-bodied species. Therefore, it is not surprising that
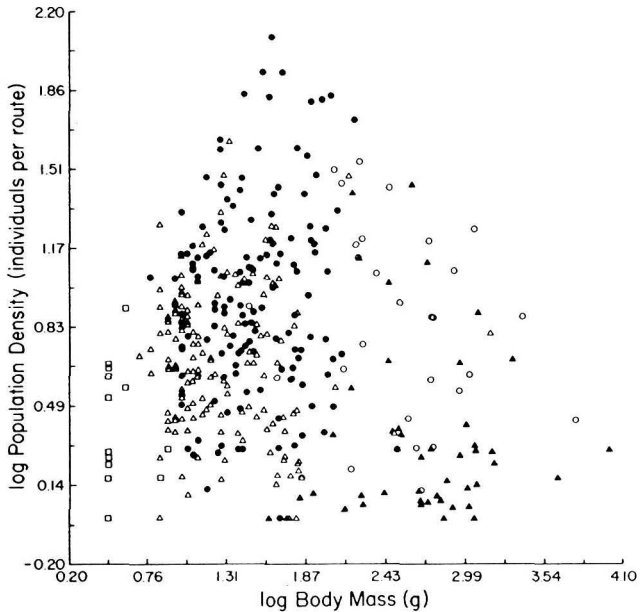
Figure 9.13. Relationship between the logarithm of body mass and the logarithm of average population density for North American terrestrial bird species. Each point in the graph represents a different species. □ = nectarivores; Δ = insectivores; ○ = herbivores; ● = omnivores-insectivores; ▲ = carnivores. Note the peak in population density for intermediate-sized species. Reprinted by permission of the publisher from Brown, J. H., and B. A. Maurer. 1987. Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. *American Naturalist* 130:1–17. Copyright © 1987 by The University of Chicago.

the *maximum* population densities were greater for intermediate body size—the more species "sampled," the more likely it is that an extreme value for population density will be found.

Blackburn et al. (1990) explored this idea in a null model reanalysis of these data sets. By fitting a second-order polynomial to the data, they tested the hypothesis that the average population density peaked at an intermediate body size. Of the four beetle and two bird guilds, only one second-order regression was significant. In fact, the remaining guilds did not even show a significant first-order term, suggesting that population density within a guild was essentially constant across the observed range of body sizes.

Next, Blackburn et al. (1990) randomly reallocated species within guilds to break up any association between body size and population density. The
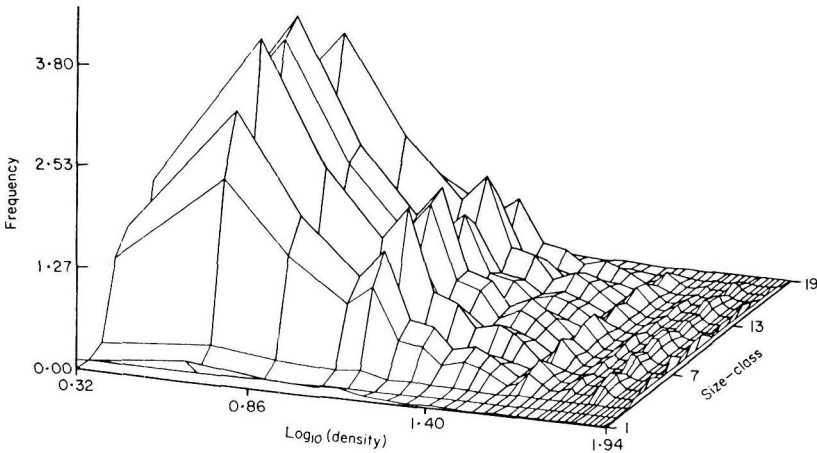
Figure 9.14. Relationship between distribution and abundance for a simulated avian guild of omnivores-insectivores. Sampling effects can lead to a peak of population abundances at intermediate body sizes. Compare with Figure 9.13, although note that the *y* axis is not log transformed. From Blackburn et al. (1990), with permission.

simulated "null guilds" also showed a pronounced peak in population density at intermediate sizes, and provided an independent check on the polynomial regressions (Figure 9.14). In sum, there seems to be little evidence that either the average or the maximum population density peaks at intermediate body size within guilds of related species. Of course, it is still interesting to consider why there are more intermediate-sized species than very large species within a guild (Van Valen 1973), but this pattern by itself seems sufficient to account for observed relationships between population density and body size.

Taxon Cycles

The taxon cycle (Wilson 1961) and taxon pulse (Erwin 1981) hypotheses predict cycles of expansion and contraction in the geographic distribution of species (Darlington 1957). The cycles are thought to be driven by community-wide competition. In the early stages of the cycle, a species is widespread and undifferentiated. As the cycle progresses, populations becomes more genetically differentiated and ecologically specialized, and the range of the species (or, more commonly, its occurrence on islands) become more fragmented.

The evidence for the taxon cycle is equivocal. On the positive side, the taxon cycle has been a useful framework for interpreting geographic distributions of Melanesian ants (Wilson 1959, 1961), insects (Greenslade 1968a, 1969), and

birds (Greenslade 1968b). Narrative accounts of habitat affinities of selected taxa conform to a taxon cycle. For example, Ricklefs (1970) and Ricklefs and Cox (1972, 1978) looked for ecological correlates with stage of the taxon cycle for West Indian birds. On Jamaica, Stage IV species (single-island endemics) occurred in fewer localities and were less widespread than Stage I species (widespread and undifferentiated; Ricklefs 1970). Across the entire archipelago, Stage I species were more likely to flock and migrate than were species in other stages (Ricklefs and Cox 1972).

However, most analyses of habitat affinity and abundance have not revealed statistically significant differences between early and late stage species (Ricklefs and Cox 1978). Pregill and Olson (1981) argued that there is no evidence that West Indian bird species actually passed through the cycle in a temporal sequence. Instead, they suggested that apparent species replacement on islands could be attributed to extensive Pleistocene climatic change in the West Indies. Studies of the Cayman Island avifauna (Johnston 1975) and the birds and butterflies of Madeira and La Gomera (Jones et al. 1987) also failed to provide evidence for progressive shifts in habitat preference and abundance that are related to geographic distribution.

One element that has been lacking in most discussions of the taxon cycle is the phylogenetic pattern of habitat association that is predicted by the hypothesis. If the taxon cycle is real, there should be an orderly progression of habitat shifts that can be superimposed on the cladogram of a monophyletic group. Liebherr and Hajek (1990) took exactly this approach in a test of the taxon cycle and taxon pulse hypotheses for eight clades of tropical carabids. In this case, the null hypothesis was that the number of evolutionary habitat shifts necessary to account for habitat distributions of extant taxa was no more than expected by chance. If the taxon cycle hypothesis is correct, then an unusually small number of such habitat shifts should occur, because these shifts will be concordant with cladogenic divergence.

To test this hypothesis, Liebherr and Hajek (1990) treated habitat affinity as a cladistic character. They randomized observed habitat affinities among taxa and counted the number of evolutionary steps necessary to fit the habitat data to the observed species cladogram. Two different scenarios of habitat change were used. One scenario implicitly assumed that the progress of a species through habitats from the presumed primitive state was linear and irreversible (Camin-Sokal coding). In a less stringent model, the primitive habitat state was inferred by parsimony and evolutionary reversals in habitat affinity were permitted (Farris optimization).

Only one of the eight carabid clades showed a significant pattern consistent with the Camin-Sokal coding and the taxon cycle hypothesis (Figure 9.15).
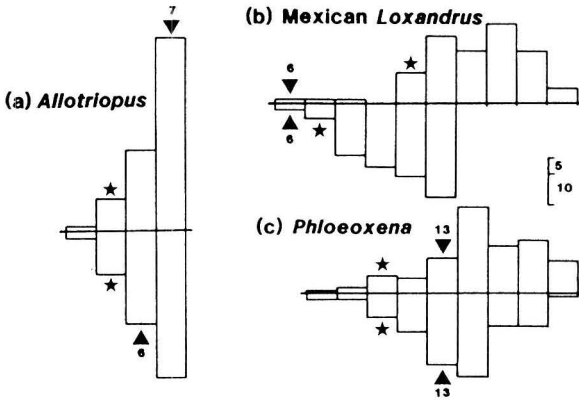
Figure 9.15. Distribution of transformation series lengths based on 100 randomizations of habitat affinity data for three groups of carabid beetles. Above the axis is the distribution of simulated series lengths using Camin-Sokal coding, and below the axis using Farris optimization. The triangle gives the observed transformation series length, and the star is the 5% tail of the distribution. If habitat affinities matched the predictions of the taxon cycle hypothesis, transformation series should be unusually short, a pattern realized only for the Mexican *Loxandrus* clade. From Liebherr and Hajek (1990), with permission.

Two clades were significant under the Farris optimization, suggesting that vicariant splitting of areas of similar habitat may have been responsible for speciation within these groups. Although habitat affinities undoubtedly change during evolution and biogeographic radiation, there do not appear to be simplified "rules" for predicting these changes, and there is little evidence (at this time) for the historical sequence of habitat shifts predicted by the taxon cycle and taxon pulse models.

RECOMMENDATIONS

For the analysis of qualitative overlap patterns in one-dimensional gradients, we recommend Pielou's (1977, 1978) tests for overlapping distributions. For tests of quantitative overlap, boundary contiguities, and simple models of community organization, we recommend Dale's (1984, 1986, 1988) tests. The location of range boundaries can be tested by the methods of Means and Simberloff (1987) or Root (1988a), depending on the type of data available. Analyses of two-dimensional patterns are more challenging. Although entire geographic ranges can be placed randomly on maps (Beven et al. 1984), we

recommend simulation algorithms that maintain the size, though not necessarily the shape, of geographic ranges. A realistic algorithm for the placement of geographic ranges would have to take account of the short-term ecological changes (Anderson 1985), long-term evolutionary processes (Lynch 1989), and limits at continental or climatic boundaries (Haefner et al. 1991). A modification of Colwell and Hurtt's (1994) null models might also be used to study diversity gradients within continents. For studies of macroecology and distribution-abundance relationships, we recommend simple sampling models by Blackburn et al. (1990), Williams (1964), Bock and Ricklefs (1983), and Wright (1991) to account for apparent patterns. For studies of the taxon cycle, Liebherr and Hajek's (1990) "phylogenetic null hypothesis" is promising.