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Spatial Methods for the Macroecological Study of Bats

MICHAEL R. WILLIG
S. KATHLEEN LYONS
RICHARD D. STEVENS

THE DISCIPLINES OF ECOLOGY, biogeography, and conservation are inherently rooted in considerations of geographic variation among individuals, populations, or communities. Indeed, geographic variability or heterogeneity in the distribution of ecologically relevant characteristics (e.g., body mass, density, and species richness) at any of these levels in the biological hierarchy can arise because of underlying spatial or environmental gradients. Importantly, geographic space (e.g., latitudinal or elevational gradients) and environmental space (e.g., temperature or precipitation gradients) frequently are not linked in a simple manner because of the complex correspondence between spatial proximity and environmental similarity (Fig. 11.1), as well as the multidimensional nature of organismal niches (Hall et al., 1992). Consequently, much of contemporary ecology focuses on documenting geographic patterns from micro- to mega-scales, and on understanding the underlying mechanistic bases for the pattern by considering environmentally relevant characteristics that vary in geographic space.

Purely spatial models are those in which linear distances (e.g., latitudinal, elevational, or bathymetric) in geographic space (i.e., geometry) are considered to be the primary drivers of variation or heterogeneity. In contrast, environmental models are those in which biologically relevant characteristics (e.g., temperature, precipitation, N concentration, productivity) effect variation or heterogeneity in geographic space. In this chapter, we consider a selection of methods that are useful for defining patterns as well as understanding spatial or environmental factors as causes of geographic patterns. For the most part, we restrict our attention to methods that are pertinent to the macroecological study of bats, and illustrate them with examples that have used bats as the focal organism of study. By necessity, this approach is not comprehensive and does not produce an exhaustive list of methodological or analytical tools for studying the macroecology of bats. Rather, we focus on a number of

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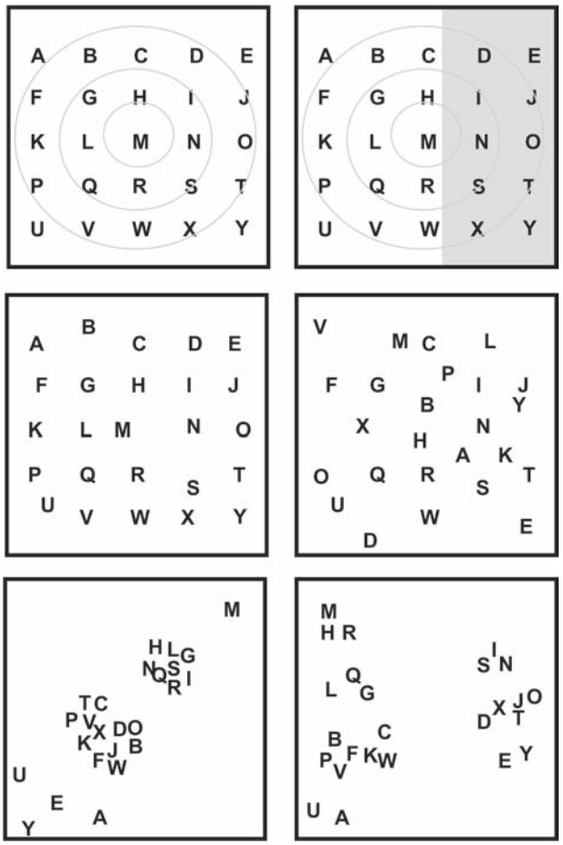

Figure 11.1. Diagrammatic representation of possible relationships between geographic space and environmental space (top row), and their consequences to biotic space (bottom two rows). In all panels, letters A through Y represent sites. An elevational gradient is superimposed on geographic space, as illustrated by the concentric ellipses (contours) in panels of the top row. A rain shadow (gray shading) is superimposed on the upper right panel. For the sake of illustration, the relationship of sites based on species composition is illustrated via a data reduction method such as factor analysis or multidimensional scaling (i.e., biotic space) in the bottom four panels (see Species Composition). If geographic distance is the primary determinant of a species' composition, then the juxtaposition of sites in biotic space will reflect that in geographic space (middle left panel). If spatial proximity or associated environmental gradients (e.g., temperature, precipitation) have no effect of species composition, then the juxtaposition of sites in biotic space should bear no resemblance to the distribution of sites in geographic or environmental space (middle right panel). If all species primarily responded to environmental parameters determined by elevation, then species that share a similar position with respect to elevational contours should be more similar to each other than to those at sites of disparate elevation (lower left panel). If the determinants of species composition were related to elevation as well as position with respect to a rain shadow, then an alternate juxtaposition of sites might occur in biotic space reflecting gradients associated with elevation and those associated with the rain shadow (lower right panel).

methods that show considerable promise, discuss them in modest detail, and provide sufficient reference to the primary literature for the interested reader to obtain a depth and breadth of understanding to use such tools with agility. Because the conceptual underpinnings and methodological approaches associated with the various topical sections are not equally pervasive in the common ecological literature, our treatment of topics differs in both depth and scope. As such, the conceptual context and interpretation of results associated with more recently developed methods (e.g., gradients of range size, body size, and abundance) are considered in greater detail than are those associated with more established areas of research (e.g., latitudinal gradients).

Macroecology is the study of empirical patterns of ecological relevance with respect to broad spatial extents or long temporal scales (Brown, 1995; Brown and Maurer, 1989). Although macroecology is still a relatively young field, many macroecological patterns are predictable and repeatable across geographic space and taxonomic group, suggesting predictable and repeatable underlying processes (Brown, 1999; Gaston and Blackburn, 1999). Indeed, understanding the processes that give rise to macroecological patterns provides insight into mechanisms operating on ecological and evolutionary time scales. Macroecological patterns have been studied extensively for bats, including geographic variation in range size (e.g., Arita, 2005; Arita and Rodriguez, 2004; Arita et al., 1997; Lyons and Willig, 1997; Rodriguez and Arita, 2004), body size (e.g., Pagel et al., 1991; Jones and Purvis, 1997; Arita and Figueroa, 1999; Aava, 2001; Jones and MacLarnon, 2001; Storz et al., 2001; Willig et al., 2003b; Maurer et al., 2004; Isaac et al., 2005; Proches, 2005), morphology (e.g., Stevens, 2005; Stevens et al., 2006), and species diversity (e.g., Willig and Selcer, 1989; Willig and Sandlin, 1991; Kaufman and Willig, 1998; Willig and Lyons, 1998; Lyons and Willig, 1999, 2002; Stevens, 2002; Stevens and Willig, 2002; Stevens et al., 2003; Willig et al., 2003a ; Patten, 2004; Willig and Bloch, 2006), including landscape (e.g., Gorresen and Willig, 2004; Gorresen et al., 2005) and conservation (e.g., Andelman and Willig, 2002, 2003) perspectives. Nonetheless, the methods for obtaining macroecological data or analyzing it in a quantitative manner are evolving at a rapid rate. For those interested in the study of bats, we consider a spectrum of approaches that relate to spatial dynamics, but acknowledge that our coverage is both incomplete and biased. Advanced search engines on the world wide web provide a rapid means to identify and explore both novel and conventional methods for quantifying spatial patterns.

GEOGRAPHIC RANGE SIZE

Ecology typically is defined as the study of the abundance and distribution of organisms (e.g., Begon et al., 1990). As such, a species geographic range is a fundamental unit of study for which continuous variation in abundance is visualized in a binary fashion (i.e., presence versus absence). Understanding the processes that give rise to and limit a species geographic range can yield insights about many ecological phenomena, including species traits (e.g., life history characteristics, body size, and population size) that are correlated with range size.

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Geographic range size can be measured in several ways depending on the underlying data (Fig. 11.2). If equal area projection range maps are used, area can be measured by using a planimeter (e.g., Willig and Selcer, 1989; Willig and Sandlin, 1991; Willig and Gannon, 1997). Range maps also can be digitized and area calculated using various GIS programs (e.g., Andelman and Willig, 2003; Patterson et al., 2003). If the underlying data are collection localities, geographic range area can be estimated by calculating the area within a convex hull enclosing all the localities (e.g., Lyons, 2003). If accurate or area-based measures of geographic range size are not possible or necessary, range size can be estimated as latitudinal range (e.g., Lyons and Willig, 1997) or as measures of occupancy (for a review, see

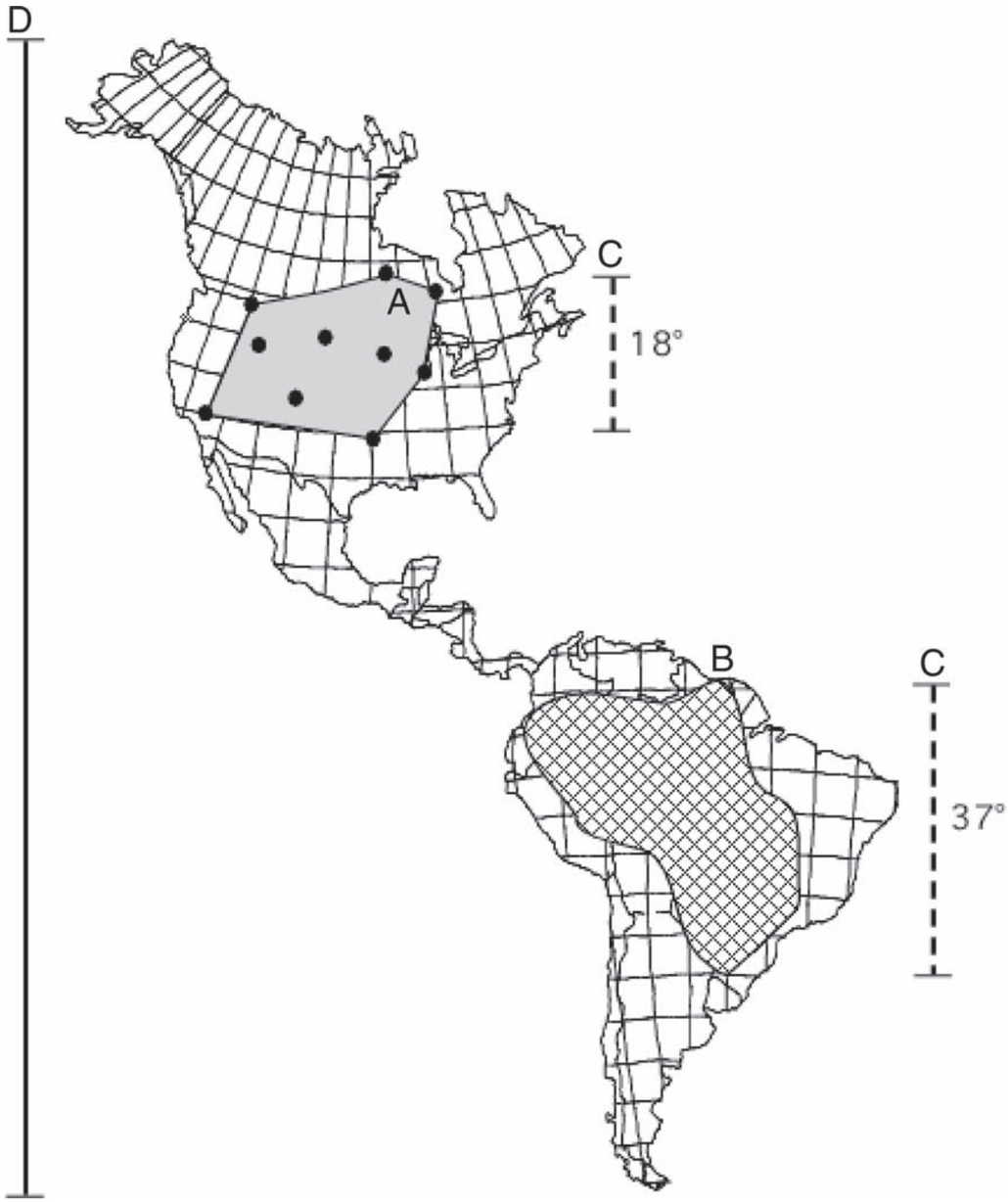

Figure 11.2. Diagrammatic representation of a domain of interest and three different methods for estimating geographic range size. Black circles (A) represent sampling localities for a species, and the gray shaded area delimits the minimum convex polygon enclosing the sampling localities. The hatched area (B) represents a species geographic range map. Because the map of North and South America is an equal area projection, area could be estimated using a planimeter or GIS techniques. Each of two dashed vertical lines (C) delimits the latitudinal ranges of two species whose range size was measured by a minimum convex polygon (A) and the standard range map (B). The solid line (D) represents the domain of the study area, the continental extent of North and South America.

Gaston, 2003). Latitudinal range is the number of degrees of latitude between minimum and maximum latitudinal extents. Occupancy is the ratio of occupied to unoccupied sites. Decisions about the total number of sampled sites are somewhat arbitrary and often are determined by data availability. Moreover, the effect of sample size on the efficacy of occupancy measures as surrogates of geographic range size has not been quantified in a rigorous manner. Latitudinal range and occupancy are correlated positively with geographic range size (e.g., Gaston, 2003; Lyons, 1994); however, occupancy is not used widely as a measure of range area (Rodriguez and Arita, 2004).

Patterns of range size most commonly are evaluated along a latitudinal gradient (Stevens, 1989; Pagel et al., 1991; Rohde et al., 1993; Roy et al., 1994; Ruggiero, 1994; Brown et al., 1996; Rohde, 1996; Lyons and Willig, 1997; Gaston et al., 1998; Johnson, 1998; Arita and Figueroa, 1999; Gaston and Chown, 1999; Lees et al., 1999; Whittaker et al., 2001; Cardillo, 2002b; McCain, 2003; Reed, 2003; Diniz-Filho, 2004a; Rodriguez and Arita, 2004; Arita et al., 2005). They have been evaluated with respect to body size (Brown et al., 1996; Arita and Figueroa, 1999; Kelt and Van Vuren, 1999; Rosenfield, 2002; Gaston, 2003; Reed, 2003; Diniz-Filho, 2004a; Lyons, 2005) and population density or abundance (Brown et al., 1996; Gaston et al., 1997a; Johnson, 1998; Blackburn and Gaston, 2001; Willig et al., 2003b; Diniz-Filho, 2004a). The shape of frequency distributions of range size are of interest (Gaston et al., 1997a; Gaston, 1998, 2003; Reed, 2003; Webb and Gaston, 2003; Willig et al., 2003b) as well.

Latitudinal Gradients in Range Size

The appropriate method for evaluating the relationship between geographic range size and latitude is controversial. Rapoport's rule, or the observation that mean geographic range size decreases towards the tropics, was first quantified based on mean range size of all species whose ranges crossed a 5-degree latitudinal band (Stevens, 1989). This method was criticized because many species are counted more than once (Rohde et al., 1993; Roy et al., 1994; Rohde, 1996), violating the assumption of independence that underlies many regression techniques. Critics of Stevens' method evaluated the relationship between geographic range size and the midpoint of each species range (Rohde et al., 1993; Roy et al., 1994 ; Rohde, 1996). Unfortunately, the midpoint method is biased mathematically (Lyons and Willig, 1997). Because a midpoint must be in the center of a species geographic range and because the tropics cross the equator, species with tropical midpoints can have larger ranges than do species with extratropical midpoints. Consequently, species with tropical midpoints will have larger ranges on average than will species with extratropical midpoints (Fig. 11.3).

In one of the few papers to analyze data by both methods, Lyons and Willig (1997) showed that New World bats and marsupials evince a Rapoport effect when analyzed using Stevens' method, but greater mean geographic range size in the Tropics, or a reverse Rapoport effect, when analyzed using the midpoint method. They advocate using simulation analyses to determine the relationship between

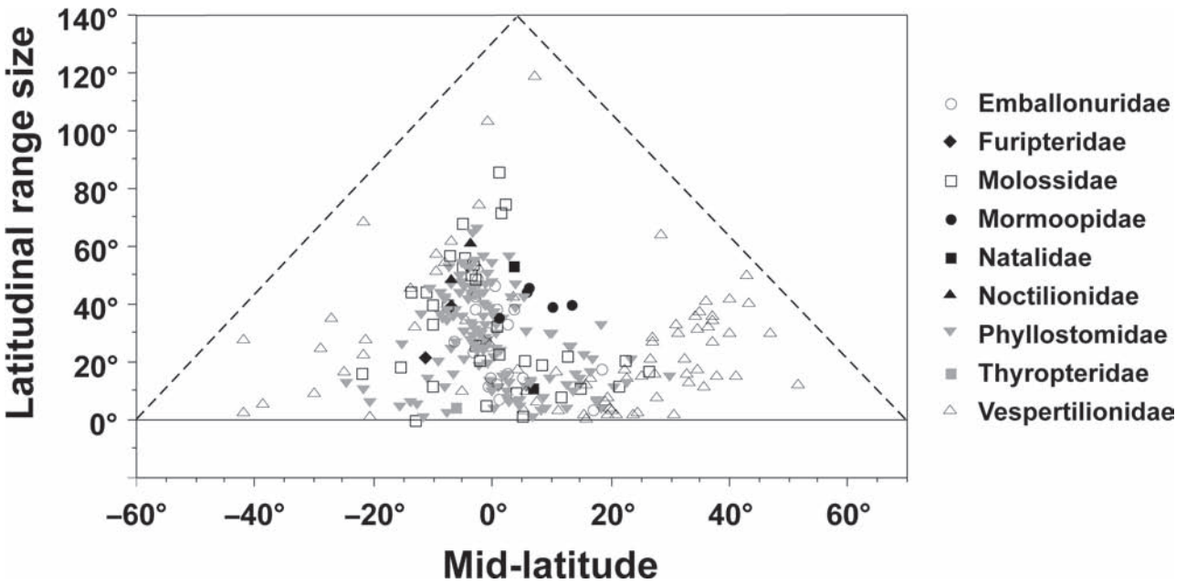

Figure 11.3. Relationship between latitudinal range size and midpoint for New World bat families. Latitudinal range is calculated as the number of degrees between the minimum and maximum extent of a geographic range. Dashed lines delimit the maximum possible range size for each midpoint. Negative values for mid-latitude represent southern latitudes, whereas positive values represent northern latitudes.
Ranges obtained from distribution maps of Patterson et al., 2003.

midpoint and geographic range size. Simulations were produced using two different rule sets. In the first, species ranges were simulated by randomly choosing upper and lower latitudinal limits, with the only spatial constraint being that latitudinal range must be within the New World. In the second, randomly generated ranges had to have a distribution of midpoints or most-distal points (i.e., the latitudinal extent farthest from the equator) that corresponded exactly to the distribution for the taxon of interest. The latitudinal extents were then randomized within those constraints. A number of species ranges equal to the number of species in the domain of interest were randomly chosen in each iteration of the simulations, and a correlation coefficient was calculated between latitudinal range size and midpoint or most distal point. This process was repeated 1000 times to generate a distribution of correlation coefficients expected under different spatial constraints, and the actual correlation coefficients for bats and marsupials were compared to corresponding simulated distributions. Lyons and Willig (1997) concluded that bats evinced a Rapoport effect in that ranges in the tropics were smaller and ranges in the temperate zones were larger than expected by chance. The simulation methods employed by Lyons and Willig (1997) are equivalent to applying different mid-domain models, but evaluating the relationship between range size and latitude, rather than between species richness and latitude.

Arita et al. (2005) used fully stochastic mid-domain models to explore geographic patterns of range size. When range size is of interest, these models can be developed in one of two ways. Endpoints can be generated by randomly sampling from a uniform distribution, or by sampling from available pairs of range size and midpoint locations (Colwell and Hurtt, 1994; Colwell and Lees, 2000; Arita et al., 2005). Arita et al. (2005) performed numerical simulations using these methods, and showed that fully stochastic models predict no gradient in average continental range size of species (i.e., no Rapoport's rule). They compared this prediction to the pattern obtained from data for North American mammals (176 bat species and 537 nonvolant species). They found significant deviations from null model predictions in the direction of Rapoport's rule. However, they did not limit analyses to species endemic to North America (an assumption of the model is that only species that are endemic to the domain may be included in analyses), and they truncated the ranges of species that extended into South America. Consequently, the southern portion of their domain was not a hard boundary. As a result, the proportion of truncated ranges included in the calculation of mean range size increased as latitude decreased. These truncated ranges would bias findings to correspond to a pattern consistent with Rapoport's rule (Weiser, unpublished).

A potentially more useful way to evaluate the relationship between range size and latitude involves use of a new metric, distance to range boundary (Weiser et al., unpublished). The distance to a range boundary (DTRB) is greatest at the midpoint of a range and smallest at the edges of a range. For any latitudinal band, the mean and variance of DTRBs can be calculated for a higher taxon of interest. This provides a visualization of the pattern of range midpoints and endpoints across a latitudinal domain. Moreover, it provides a way to evaluate deviations from mid-domain expectations with respect to latitudinal variation in midpoints and range size. As such, the method identifies potential geographic barriers (or geometric constraints) that may not be obvious, *a priori*. For example, when applying DTRB analysis to New World bats, Weiser et al. (unpublished) identified three peaks and two troughs in mean and median DTRB when plotted as a function of latitudinal band. This suggests that the latitudinal gradient in range size for bats is formed by three broadly overlapping domains.

Studies of elevational gradients in range size suffer from the same problems as do studies of latitudinal gradients in range size. Estimates of variation in elevational range size with elevation will be biased toward having large ranges in the center of an elevational domain if each species range is characterized by the midpoint of its elevational distribution. Moreover, studies of elevational variants of Rapoport's rule suffer from additional problems (C. McCain, pers. com) because geographic variation in mountain height will affect variation in elevational range distributions.

Studies of gradients in range size are fraught with statistical and mathematical biases. Most straightforward methods (e.g., Steven's method; midpoint method) will produce unreliable and biased results. For significance testing of patterns in range size, we recommend a simulation approach using mid-domain models (e.g., Lyons and Willig, 1997; Arita, 2005). An alternative method that seems promising and allows for visualization of the pattern is the distance to range boundary method (Weiser et al., unpublished).

Body Size, Population Abundance, and Range Size

Many physical and ecological traits of species scale with geographic range size. Documenting and understanding the relationship between such traits and range size provides insight into the factors that limit a species distribution. The two traits we consider are body size and population abundance. Generally, the relationship between body size and range size is evaluated by plotting the log of geographic or latitudinal range size as a function of the log of body size (Fig. 11.4). However, quantitative methods for dealing with messy relationships that arise because of various constraints are in desperate need of development (Brown, 1995). In addition, caution must be used when defining the geographic domain of study (i.e.,

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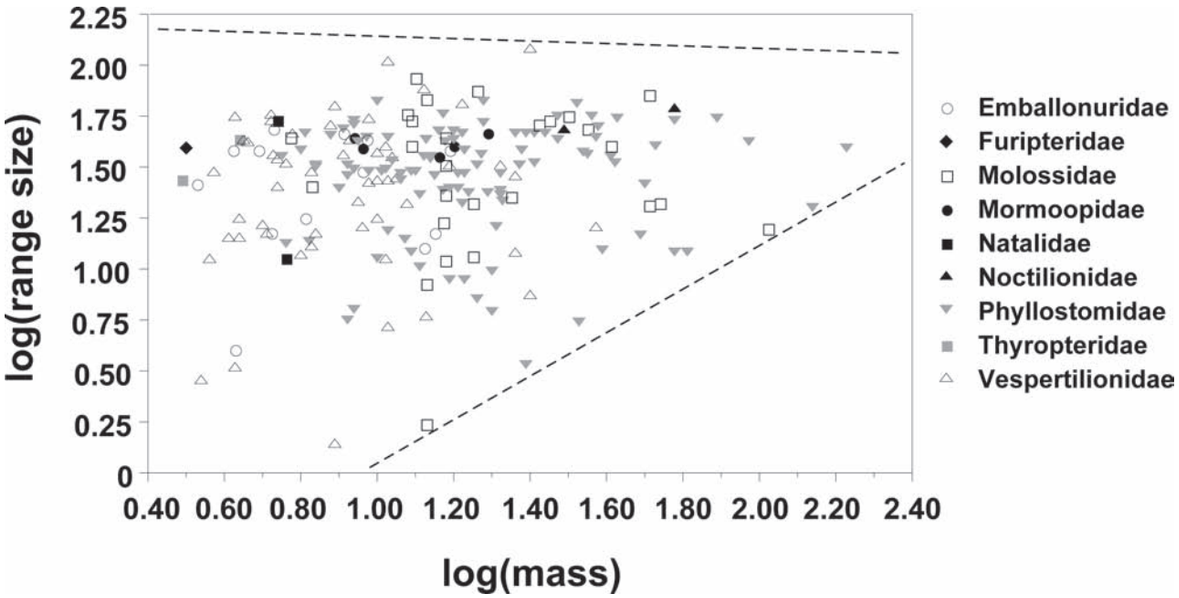

Figure 11.4. Relationship between latitudinal range size and body size for New World bat families. Latitudinal range is calculated as the number of degrees between the minimum and maximum extent of a geographic range. All data were log-transformed. The dashed lines identify the typical triangular boundaries of the relationship. Small-bodied bats have greater variation in latitudinal range size than do large-bodied bats, which generally have large ranges [log(range size) = 1.309 + 0.103 · log(mass); $R^2 = 0.012$]. Examination of each of the three most species-rich families (i.e., Molossidae, Phyllostomidae, and Vespertilionidae) indicates a similar pattern. *Ranges were obtained from distribution maps of Patterson et al., 2003. Body sizes were taken from Jones et al., 2003, as updated by Smith et al., 2003.*

area within which geographic ranges are studied; Gaston and Blackburn, 1996). Modeling approaches show that if the domain is smaller than the geographic ranges of the focal taxa, the estimated relationship between body size and range size may not represent the true underlying relationship (Madin and Lyons, 2005). The relationship between body size and range size typically is triangular, such that small-bodied species show greater variation in geographic range sizes than do large-bodied species, which characteristically have large geographic range sizes (Brown, 1995; Willig, 2003b).

The relationship between range size and abundance is evaluated in the same manner as is the relationship between body size and range size. Local population abundance or density is plotted as a function of range size, resulting in a positive correlation (Brown, 1995; Brown et al., 1996; Gaston et al., 1997a, 1997b; Holt et al., 1997; Blackburn and Gaston, 2001; Gaston, 2003). However, range size occasionally is plotted as a function of population size (Gaston, 2003). In both approaches, variables should be log transformed before analysis. Generally, the relationship between range size and abundance is triangular, with wide-ranging species evincing great variation in local population size and narrow-ranging species possessing smaller population sizes (e.g., Brown, 1995; Gaston, 2003).

Currently, a standard method for estimating population abundance for use in macroecological studies does not exist. Authors typically use whatever data are available and assume that variation in data quality likely adds noise but will not systematically bias results. In particular, few studies have evaluated range size–abundance relationships for bats (but see Blackburn et al., 1997). Occupancy is correlated with population abundance and has been used as an estimate for population size (Gaston, 2003); however, the absence of studies evaluating the effects of sampling on measures of occupancy make such measures difficult to interpret.

Range Size Distributions

Frequency distributions of range size long have been of interest to ecologists (e.g., Willis, 1922). Although multiple factors can limit the distributions of particular species, the characteristic shape of range size distributions suggests that processes acting on evolutionary time scales may have predictable effects. Range size distributions are constructed by allocating species into range size categories and producing a histogram of the number of species in each category (Fig. 11.5, top). Regardless of taxon, frequency distributions of range size generally exhibit a similar pattern when plotted on an arithmetic scale (e.g., Brown, 1995; Gaston, 2003). The majority of species have small ranges with a minority having large ranges. The resulting distributions typically are unimodal and right-skewed, and were termed "hollow curves" by Willis (1922). Hollow curve

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distributions characterize the range sizes of plants, invertebrates, fish, amphibians, reptiles, birds and mammals (see Gaston, 2003). Log transformation of range size does not produce a normal distribution (Fig. 11.5, bottom). Rather, frequency distributions of log-transformed range size generally are unimodal and somewhat left skewed (Willig et al., 2003b).

Mid-domain models enhance understanding of geographic variation in the frequency distribution of range size (Arita, 2005). Building on the one-dimensional analytical model of Willig and Lyons (1998), Arita (2005) derived the expected mean and variance in range size for species whose ranges intersect a particular point along a domain or latitudinal extent of interest. He extended this model to the two-dimensional case using the equations of Bokma et al. (2001). Although fully stochastic mid-domain models predict a flat relationship between mean range size and latitude, they predict variation in range size frequency distributions depending on position along a domain (Arita, 2005). For example, the one-dimensional model predicts that the frequency distribution of range sizes should be almost uniform near the edges of a domain (i.e., the same percentage of narrow-ranging versus wide-ranging species). However, in the middle of the domain most species should have ranges of intermediate size, with narrow- and wide-ranging species being relatively rare (Arita, 2005).

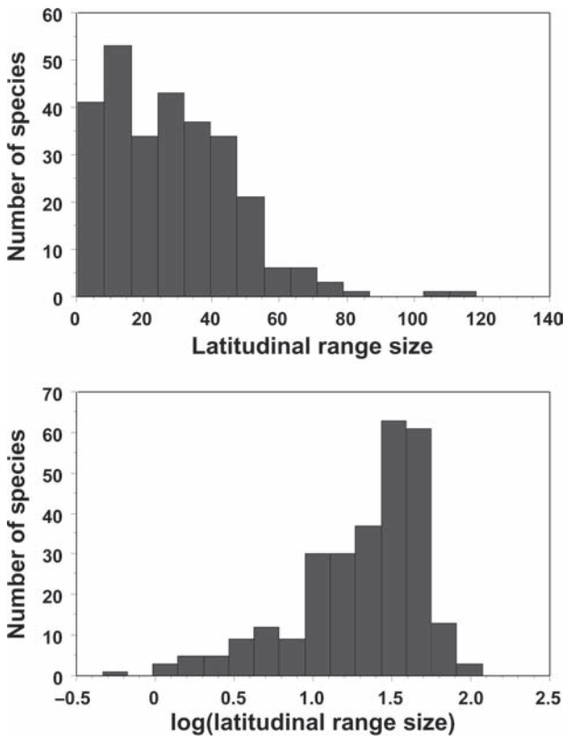

Figure 11.5. Frequency distributions of range size for New World bats plotted on an arithmetic scale (top) and a log scale (bottom). Latitudinal range is calculated as the number of degrees between the minimum and maximum extent of a geographic range. Ranges were obtained from distribution maps (Patterson et al., 2003). Although bats show the predicted hollow curve pattern (top), the decline in numbers of species within latitudinal range size categories is not as precipitous as in other taxa.

BODY SIZE

Macroecological studies involving body size usually employ a single estimate to represent the body size of a species. Ideally, this value should be a measure of central tendency incorporating any geographic variation or sexual dimorphism inherent in the species (e.g., Smith et al., 2003). In practice, body sizes for rare species can be sufficiently hard to find that investigators will use an estimate representing a single population or even a single individual. Depending on the group of interest, surrogates of body size include body length, mass, or for bats, forearm length (e.g., Stevens and Willig, 1999; Storz et al., 2001). The best measures are those that are correlated strongly with body mass. For many mammalian groups, standard regression equations have been formulated to estimate body mass from other morphological characteristics (e.g., Damuth and MacFadden, 1990; Silva and Downing, 1995).

Latitudinal Gradients in Body Size

Geographic variation in body size of particular species is embodied in Bergmann's rule: body size increases with increasing latitude or decreasing temperature (e.g., Smith et al., 1995; Storz et al., 2001; Freckleton et al., 2003; Katti and Price, 2003; Ochocinska and Taylor, 2003). It also has been explored among groups of species along latitudinal or elevational gradients (Arita and Figueroa, 1999; Blackburn et al., 1999; Blackburn and Ruggiero, 2001; Roy and Martien, 2001; Cardillo, 2002a; Katti and Price, 2003). Much of the work on Bergmann's rule has been done in the temperate zones. However, Storz et al. (2001) showed a pattern consistent with Bergmann's rule in the tropical fruit bat, *Cynopterus sphinx*.

When considering a single species, Bergmann's rule is evaluated by calculating the mean and variance for body size of a series of populations, and by plotting body size as a function of temperature or latitude (e.g., Smith et al., 1995). Because of the constraints associated with flight, bats may respond to variation in temperature by varying body shape and aspects of wing morphology. In such cases, multivariate ordination can be used to describe variation in body shape. For example, Storz et al. (2001) sampled bats at 12 localities along a 1,200-km transect, and used eight log-transformed external characters to represent overall body shape, body size, and wing area. Morphological differences related to geographic location or sex were evaluated using multivariate analysis of variance (a significant sex by location interaction occurred). Next,

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morphometric data were subjected to principle components (PC) analysis, and canonical discriminant analysis was used to evaluate the contributions of each PC axis to the pattern of multivariate differences between sexes. Ultimately, correlations were calculated between ecogeographic characteristics, including latitude, and principle component scores. Storz et al (2001) found a significant, positive correlation between latitude and size (i.e., first PC axis).

Although the most widely used definition of Bergmann's rule applies to intraspecific variation in body size, the original definition by Bergmann applied to interspecific variation in body size among closely related species (see Blackburn et al., 1999). Studies of interspecific variation in body size often examine latitudinal gradients in mean body size of a taxon or biota (Arita and Figueroa, 1999; Blackburn and Ruggiero, 2001; Roy and Martien, 2001; Cardillo, 2002a; Katti and Price, 2003). These studies either examine mean body size of all species in a latitudinal band (Roy and Martien, 2001), the relationship between a species' body size and the midpoint of its latitudinal range (Blackburn and Ruggiero, 2001; Katti and Price, 2003), or variation in the body size distribution of all species at different latitudes (Roy and Martien, 2001; Cardillo, 2002a) or at a regional spatial scale (Arita and Figueroa, 1999; Roy et al., 2000). Often these studies use independent contrasts to account for shared phylogenetic history of related species (e.g., Blackburn and Ruggiero, 2001; Cardillo, 2002b; Katti and Price, 2003).

The methods employed by most studies of Bergmann's rule that consider multiple species are problematic (see Roy and Martien, 2001). Evaluating the relationship between mean body size of all species in a latitudinal band and latitude is problematic because the replicated observations of the dependent variable are not independent as many species are included in more than one latitudinal band. Alternatively, using mid-latitude to characterize a species' latitudinal position assumes that species range endpoints are distributed evenly in space. Because the distributions of most groups of organisms are concentrated within biogeographic provinces, most groups likely violate this assumption. Randomization methods avoid these problems and have the added advantage of accounting for empirical spatial autocorrelation. For example, Roy and Martien (2001) evaluated the relationship between latitude and body size in marine bivalves by randomly assigning observed body sizes of species to observed latitudinal ranges, and calculating the mean and variance of body size for 2-degree latitudinal bins. This preserved the spatial autocorrelation and patterns of species richness along the gradient, but randomized body size with respect to latitude. Regressions for the relationship between the mean or variance of body size and latitude were calculated for each randomization, and the process was repeated 100 times for means or 500 times for variances. The regression coefficients for empirical data were compared to the distributions of regression coefficients created by the randomizations. Roy and Martien (2001) did not find a significant relationship between body size and latitude for Pacific bivalves.

Studies of Bergmann's rule within a higher taxon (i.e., interspecific variation in body size) can be problematic for a number of reasons. In particular, it is undesirable to use a single estimate of body size at all latitudes for a species that has a broad spatial distribution and for which geographic variation in body size is significant. Such approaches may be inaccurate and violate assumptions of independence or replicated observations of the dependent variables. Simulation analyses and randomization tests are the best methods to employ in such scenarios, because they avoid issues of nonindependence and simultaneously account for autocorrelation.

Body Size Distributions from Local to Continental Scales

Differences in the shapes of body size distributions provide insight into ecological and evolutionary processes. For example, continent-wide body size distributions for North American mammals were bimodal (i.e., one mode corresponding to small bodied mammals and one mode for large bodied mammals) for the last 40 million years (Alroy, 1998). The present day unimodal pattern (i.e., most species are small with a few large species, resulting in a long tail) documented by Brown and Nicoletto (1991) likely is a result of the end-Pleistocene extinction of large bodied mammals (Lyons et al., 2004). Similarities in the shapes of continental distributions of body size on different land masses prior to the end-Pleistocene extinction (Lyons et al., 2004) despite disparate evolutionary histories, suggest strong constraints on the evolution of body size in mammals.

Frequency distributions of body size are constructed using the same methodology as employed for frequency distributions of range size (Brown and Nicoletto, 1991; Maurer et al., 1992, 2004; Arita and Figueroa, 1999; Marquet and Cofre, 1999; Bakker and Kelt, 2000; Willig et al., 2003b; Lyons et al., 2004; Rodriguez et al., 2004; Smith et al., 2004; Stevens, 2005; Stevens et al., 2006). Species are allocated to size categories based on log-transformed body size. The number of species that occurs in each category is the basis for a histogram. Generally, the shapes of body size distributions change with spatial scale. For example, body size distributions of mammals flatten (i.e., become platykurtic with fewer species in the modal size classes) and become more uniform as spatial scale decreases from the continental to the community level (Brown and Nicoletto, 1991). At a global scale, the body size distribution for bats is unimodal and right skewed (Fig. 11.6, top; Maurer et al., 2004), however, the body size distribution for New World bats is more flat and less skewed (i.e., fewer species

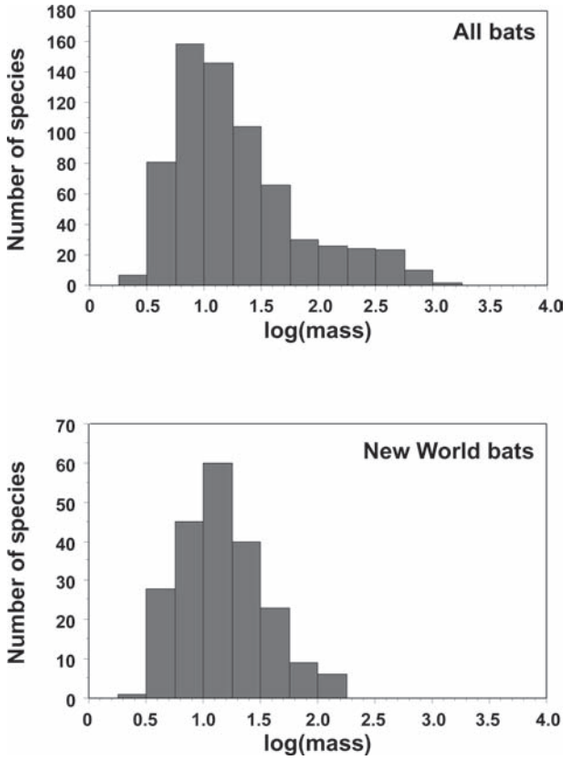

Figure 11.6. Frequency distributions of body size for bats on earth (top) and for New World bats (bottom). As in other groups, the shape of the distribution for bats on a global scale is right-skewed with a long tail. However, the shape of the distribution for New World bats is much flatter and more log-normal, as noted by Willig et al. (2003b). Body sizes from Jones et al., 2003, as updated by Smith et al., 2003.

in the modal size classes and the tail is truncated; Fig. 11.6, bottom; Willig et al., 2003b; Stevens, 2005). Moreover, body size distributions for New World bat communities (Fig. 11.7) do not become uniform at local scales (Arita and Figueroa, 1999).

Two general approaches are useful in comparing body size distributions. Nonparametric techniques, such as the Mann-Whitney U or Kolmogorov-Smirnov tests (Sokal and Rohlf, 1981), represent the classic approach to evaluate if two independent samples have been drawn from the same population. The former is based on the distribution of body sizes from a combined pool in which body size has been replaced by rank order. The latter is based on the maximum difference between the distribution functions (cumulative frequency distributions) for the two samples. These nonparametric tests are sensitive to differences with respect to any aspect of a frequency distribution, such as central tendency, dispersion, skewness, or kurtosis (i.e., moment statistics).

Randomization tests based on simulation analysis have become especially popular to compare body size distributions between geographic localities or to assess if a distribution of body sizes at a smaller scale arise as a consequence of random sampling of body sizes at a larger scale (e.g., Brown and Nicoletto, 1991; Marquet and Cofre, 1999; Bakker and Kelt, 2000; Smith et al., 2004). Critically, the use of nonparametric tests for comparisons involving scale may be inappropriate, as the targeted samples are not independent. The sample for the smaller scale is, by definition, contained within the sample for the larger scale. Moreover, simulation analyses can be used to compare any aspect of a distribution by use of a corresponding metric related to the statistical moment of interest (e.g., G_4 for kurtosis). Nonetheless, care should be used to do so, especially when distributions of body size at the larger scale are multimodal.

A general simulation approach for comparing distributions from two independent samples follows a number of steps, illustrated by the following consideration of a continental comparison of body size distributions. A pool of body sizes is constructed by combining data for continents. Then species are allocated randomly from the pool to each of two samples, with the constraint that the species richness of each sample is equal to the empirical species richness of the continent that it represents. A metric is then used to reflect the distributional difference between the two random samples. This randomization is repeated a large number of times, to create a distribution of metrics. If the difference metric for the two empirical samples occurs in the tails of the distribution of like metrics generated stochastically, the contrast between continents is considered to be significant. In analyses by Smith et al. (2004), the metric of distributional difference was *D* from the Kolmogorov-Smirnov test. Consequently, it was sensitive to distributional differences with regard to all moment statistics. All pairwise comparisons of continental body size distributions for mammals were significant, suggesting to Smith et al. (2004) that evolutionary, historical, or ecological differences between continents have molded unique body size distributions despite similarity in general shape.

Randomization tests based on simulation analyses also can be used to assess the effects of spatial scale on body size distributions (Brown and Nicoletto, 1991; Marquet and Cofre, 1999; Bakker and Kelt, 2000). This is straightforward for measures of central tendency and dispersion, as well as for overall differences based on metrics such as *U* from the Mann-Whitney test or *D* from the Kolmogorov-Smirnov test (Sokal and Rohlf, 1981). Assessments for skewness (G_3) are difficult when one is interested in evaluating differences between scales. The shapes of the distributions at smaller scales generally are predicted to be symmetrical (e.g., uniform), resulting in values of skewness close to zero. A straightforward randomization using skewness as the metric is problematic because a distribution of skewness values determined from a series of ran-

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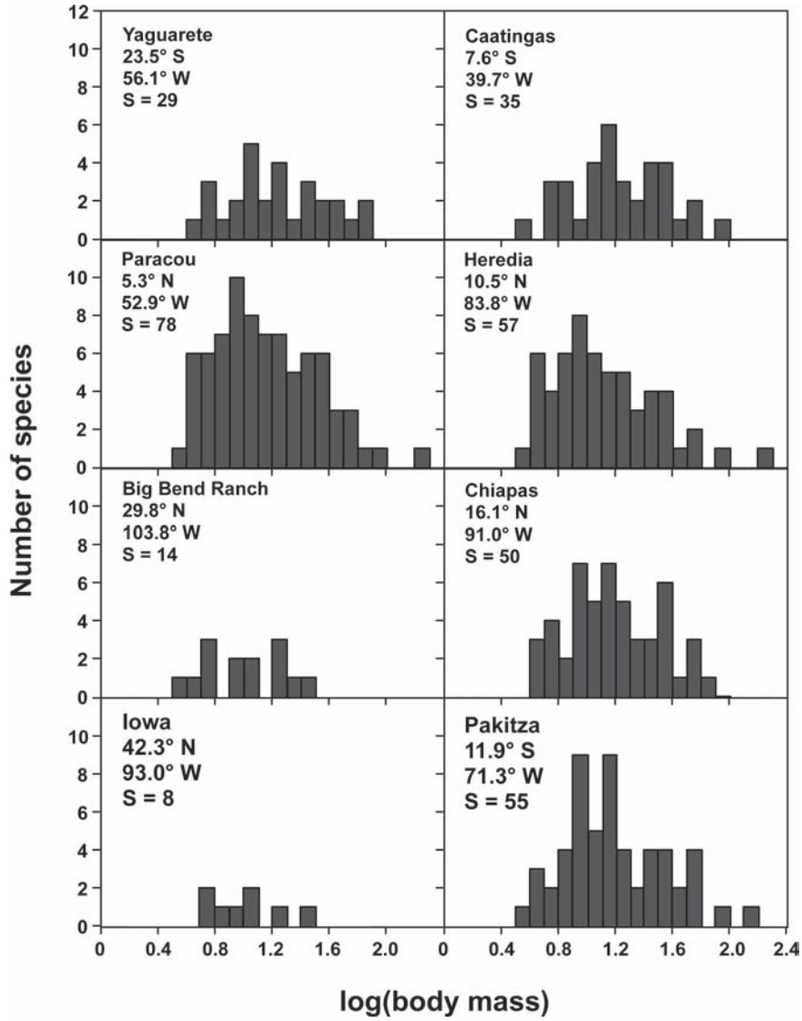

Figure 11.7. Frequency distributions of body size for eight New World bat communities. Unlike other groups, body size distributions for bat communities do not flatten with decreasing focal scale, except in northern temperate communities (e.g., Big Bend Ranch and Iowa). *Body sizes from Jones et al., 2003, as updated by Smith et al., 2003. Species lists for communities from Stevens et al., 2006.*

dom draws from the larger pool would run the gamut from highly left-skewed to highly right-skewed, and the value for the uniform distribution would occur in the middle of such a distribution. Assessments of kurtosis (G_4) are problematic because three general conditions are possible based on the sign and magnitude of G_4: positive values indicate a peaked distribution, negative values greater than −1 indicate a flat distribution, and values less than −1 indicate multimodality. Thus to evaluate skewness and kurtosis, an alternative to the usual simulation approach is necessary.

Quantitative approaches for examining kurtosis are particularly important, because macroecological predictions are that local-scale distributions of body size are more flat than associated continental-scale distributions. If this is true, then the median of a local body size distribution should be among the largest medians derived by sampling the same number of species at random from the continental pool, but such is true if and only if the continental pool is modal and right skewed (Brown and Nicoletto, 1991). If the continental pool is modal and left skewed, then the empirical median should be among the smallest medians derived by random sampling from the continental pool. In either case, a randomization test using simulation would provide insight to the hypothesis of interest. If the continental pool is multimodal (e.g., Africa), the empirical median should be intermediate compared to medians derived by random sampling from the continental pool. In this case, a simple randomization test will be of no use.

The body size distribution index (BSDI) also can be used to evaluate the shape of a distribution (Bakker and Kelt, 2000). BSDI is calculated as:

$$BSDI = \frac{I_{site}}{I_{uniform}}$$

where

$$I_{site} = \sum (SC_i (n_i/N))$$

and n_i is the number of species in size class i, and N is the total number of species at a particular site. SC is the size class number (using $\log_2$ of body mass, measured in grams). The sum in the numerator for the empirical distribution, is standardized by dividing by the equivalent sum ($I_{uniform}$) for a uniform distribution (i.e., one in which each size class has the same number of species, totaling N as at the site). Consequently, a perfectly uniform distribution at a site would have a BSDI of one. Higher and lower values indicate greater numbers of large- or small-bodied species, respectively. To evaluate whether body-size distributions of communities of mammals from South America were significantly different from a random selection from a species pool, Bakker and Kelt (2000) created a simulation using BSDI. First, they sampled randomly with replacement from an appropriate species pool up to the number of species in each community and calculated BSDI. This process was repeated, 2000 times to create a distribution of BSDIs expected by chance. Because they expected an increase in BSDI with decreasing spatial scale, Bakker and Kelt (2000) used a one-tailed t-test to compare actual values of BSDI to their simulated distributions.

In addition, randomization tests may be used to evaluate the effects of phylogenetic or other constraints. For example, Maurer et al. (2004) were interested in determining whether constraints associated with flight influence the evolution of body size distributions. First, they calculated moments of body size distributions (i.e., mean, variance, skewness, and kurtosis) for several small-bodied vertebrate clades and determined the likelihood that these moments could come from a random sample of the sister clade. Comparisons were conducted by drawing bootstrap samples from each pair of clades and testing the hypothesis that the difference between clades for each of the first four moments of the distributions was zero. Ten thousand bootstrap samples were drawn and the four moments were calculated to obtain a frequency distribution of each moment. Actual moments were compared to these randomly generated distributions using likelihood ratio statistics. The body mass distributions of small-bodied flying vertebrates (i.e., Passeriformes, Apodiformes, and Trochiliformes as a group, and Chiroptera) showed significant differences from the distributions for small-bodied nonvolant vertebrates (i.e., Insectivora and Rodentia). Next, they evaluated the degree to which body mass similarity was due to functional symmetry versus phylogenetic symmetry using independent contrasts. The hypothesis of phylogenetic symmetry was tested by conducting 100 randomizations for which species within the three mammalian taxa were assigned randomly to a mammal clade, and species within the two avian taxa were assigned randomly to an avian clade. The probability of being assigned to a taxon was constrained by sample size. For each randomization, a dendrogram was constructed, and cophenetic similarities were correlated with the cophenetic similarities from the empirical data. Congruence was determined between the empirical dendrogram and the population of dendrograms resulting from the hypothesis of phylogenetic similarity. A similar process was used to evaluate the hypothesis of functional symmetry, except that species were assigned randomly to volant or nonvolant clades depending on their original membership. The empirical data were consistent with the hypothesis of functional symmetry, but not with phylogenetic similarity (Maurer et al, 2004).

BIODIVERSITY

Understanding the mechanisms that enhance and sustain biodiversity—including its spatial and temporal dynamics—is a grand challenge of critical importance. Several mechanisms have been postulated to effect environmental gradients of biodiversity, and recent synthesis suggests that a unified theory of such gradients is in sight (Scheiner and Willig, 2005).

Species Composition

Species identities and their relative abundances—species composition—represent a fundamental community characteristic. Spatial analyses involving species composition typically are conducted on a species by site matrix in which the value of a cell is the abundance of a species at a particular site. Such spatial analyses are inherently multivariate and most commonly involve either cluster or ordination analyses. Cluster analysis classifies sites, species, or variables into groups (van Tongren, 1995), whereas ordination distributes samples along putatively biologically important environmental gradients (Gotelli and Ellison, 2004). Each provides insight regarding the nature of spatial patterns.

When analyzing spatial variation, cluster analysis classifies sites into groups and illustrates their relationships with a dendrogram based on similarity in species composition. Although commonly populated by absolute or relative abundances, the species by site matrix can be populated by ranks or even by the presences and absences of species (Sneath and Sokal, 1973; Gauch, 1982; Digby and Kempton, 1987; Gotelli and Ellison, 2004). Before executing a cluster analysis, the typically asymmetrical species by site matrix must be transformed into a symmetrical

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distance or similarity matrix. A fundamental decision when conducting cluster analysis involves the choice of a distance or similarity measure for use in characterizing relationships among sites. Valuable discussions of such considerations, as well as methods to calculate similarity and distance measures, appear in Sneath and Sokal, 1973; Digby and Kempton, 1987; Legendre and Legendre, 1998; and Gotelli and Ellison, 2004.

Two additional decisions are necessary to conduct a cluster analysis: use of hierarchical versus nonhierarchical methods, and use of agglomerative versus divisive clustering algorithms (Gotelli and Ellison, 2004). Agglomerative algorithms group observations into successively larger clusters until one cluster is formed, whereas divisive algorithms arrange all observations into a single group and then divide them into successively smaller groups until each site is a single cluster. Typically, divisive methods produce fewer clusters, each comprising more sites, whereas agglomerative methods produce more clusters, each comprising fewer sites (Gotelli and Ellison, 2004). Agglomerative hierarchical methods generally have been used to explore relationships among bat assemblages.

The most widely used method of clustering bat assemblages is the unweighted pair group method with arithmetic averaging (UPGMA). Analyses begin with a comprehensive account of community composition complemented by an understanding of underlying biogeographic affinities of bat species (Simmons and Voss, 1998; Bernard and Fenton, 2002). Such an approach appears in a number of studies focusing on spatial variation in species composition in Amazonia (Simmons and Voss, 1998; Simmons et al., 2000; Bernard and Fenton, 2002). Interactions among three large assemblages of bats (i.e., northern Guiana subregion, eastern Amazonia, and western Amazonia) contribute to spatial variation among local assemblages in the Amazon as a whole; nevertheless, much of the variation is related to geographic proximity. This suggests that spatial autocorrelation is an important contributor to spatial dynamics in the area. Similar analyses for Paraguayan bat assemblages (Willig et al., 2000; Lopez-Gonzalez, 2004) have demonstrated that geographic proximity can account for much of the compositional similarity among sites. Nonetheless, geographic sites in Paraguay can be classified into groups that roughly correspond to phytogeographic regions. Bat species composition does not always conform to phytogeographic boundaries. A cluster analysis of 14 different phytogeographic zones in Venezuela revealed little correspondence between a hierarchical arrangement of phyogeographic zones and dendrograms based on species composition of bat assemblages (Willig and Mares, 1989). Gallery-forest bat assemblages inlay many phytogeographic zones, thereby homogenizing species composition among otherwise different assemblages. Moreover, bats may not respond to underlying environmental gradients in the same way that floral elements respond.

Species composition of sites (site by species matrix) can be ordered along putatively important environmental gradients with ordination analyses. When no information regarding other environmental characteristics is available, indirect gradient analysis orders sites based solely on species composition. Potentially important environmental gradients can then be inferred from the proximity of sites based on species composition. When environmental characteristics are known for each site, compositional similarity can be assessed with respect to environmental gradients.

A wide variety of ordination techniques are available (e.g., polar ordination, principal coordinates analysis, multidimensional scaling, principal components analysis, correspondence analysis, detrended correspondence analysis, redundancy analysis, canonical correspondence analysis, and detrended canonical correspondence analysis). As with cluster analysis, polar ordination, principal coordinates analysis, and multidimensional scaling are distance-based indirect ordinations in which a distance matrix is decomposed into important vectors of variation among sites. Polar ordination (i.e., Bray-Curtis ordination) arranges sites between endpoints of an axis, referred to as poles. Poles are defined by the two sites with the greatest distance between them. The axis is interpreted as a putatively important biological gradient. Although the determination of poles on the first axis is fairly straightforward, selection on subsequent axes is more complicated. Often, the first and subsequent axes are correlated, indicating that axes higher than the first offer limited unique insights. A number of modifications have been developed to minimize such correlation (Beals, 1985). Principal coordinates analysis is an eigen analysis conducted on a distance matrix, thus it selects orthogonal axes that account for a maximal amount of variation in the distance matrix. This analysis is similar to principal components analysis. In fact, when distances among sites in the species by site matrix are measured by Euclidean distance, results of principal coordinates analysis are identical to those from principal components analysis on the original data matrix (Digby and Kempton, 1987). One of the drawbacks of principal coordinates analysis is that it maximizes linear correlations among distances. When gradients are long, distances may be nonlinear because species exhibit modal distributions along such an extensive gradient. In such a case, linear methods are not the most appropriate. Nonmetric multidimensional scaling maximizes the rank order correlations between the distances and overcomes the limitations imposed by the linearity assumption. Such an approach applied to data for bat species composition in 16 South American communities (Fig. 11.8) illustrates the distinctiveness of tropical sites from those in savanna-grassland and Atlantic rainforest, as well the similarity of sites from savanna-grassland and Atlantic rainforest (Stevens et al., 2004).

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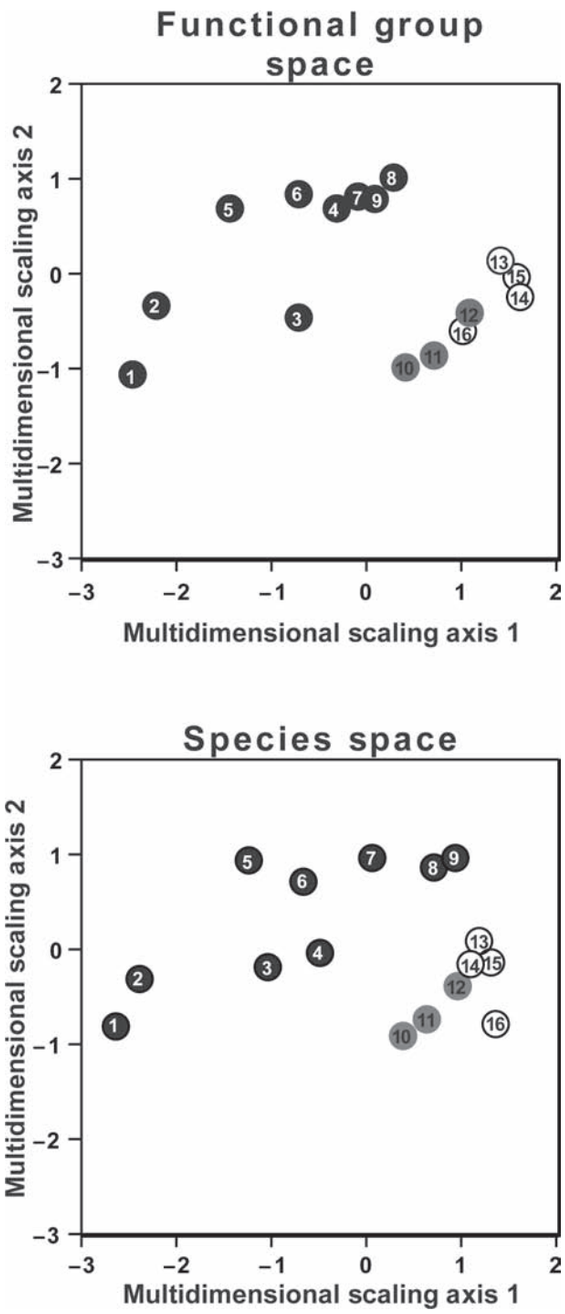

Figure 11.8. Relationships among 16 South American bat communities based on the first two axes from multidimensional scaling, in which species composition (taxonomic identity and relative abundance) forms the basis of the analysis. Numbers in circles refer to community sites: 1, Paracou, French Guiana; 2, Iwokrama Forest, Guyana; 3, Manaus, Brazil; 4, Duida-Marahuaka National Park, Venezuela; 5, Jenaro Herrera, Perú; 6, Pakitza, Perú; 7, Marcarena, Colombia; 8, Zabelitas, Colombia; 9, Cordillera Central, Colombia; 10, Espíritu, Bolivia; 11, Caatinga, Brazil; 12, Edaphic Cerrado, Brazil; 13, Minas Gerais, Brazil; 14, Panga, Brazil; 15, Mbaracayu, Paraguay; 16, Yaguarete, Paraguay. Sites in black are communities in tropical forest, sites in gray are communities in savannah-grassland, and sites in white are communities in Atlantic rainforest. *Modified from Stevens et al., 2004.*

Three other forms of indirect gradient analysis order sites with respect to putatively important biological gradients but do so using the original data as opposed to a distance matrix. Principal components analysis creates gradients that reflect linear combinations of the original variables, such that each accounts for a maximal amount of residual variation in the original data. Gradients are independent and account for unique variation in the original data. As with principal coordinates analysis, a limitation of principal components analysis is that it maximizes linear associations among variables and may not be suitable when gradients are long and species exhibit modal patterns of abundance along the gradients. Correspondence analysis relies on reciprocal averaging to maximize the correspondence between site scores and species scores. Species abundance distributions are assumed to be unimodal and approximately normal across the putative gradient. Correspondence analysis attempts to maximize the differences in peak abundance along the formulated gradient (Gotelli and Ellison, 2004). A disadvantage of principal components analysis and correspondence analysis is that the distances among sites on a derived axis can become distorted relative to actual positions in nature (i.e., the arch, or horseshoe, effect; Gotelli and Ellison, 2004). In particular, these analyses often compress distances on the ends and enhance distances in the middle of the gradient; detrended correspondence analysis provides a solution to such distortion (Gauch, 1982). In such analyses, simple trends in the second and subsequent axes are removed to eliminate compression of sites at either end of derived gradients. Nonetheless, detrending may not be the best solution (Gotelli and Ellison, 2004), because the arch effect may be a general artifact of applying distance measures to species that have unimodal responses along environmental gradients (Podani and Miklos, 2002). Moreover, use of any of a wide variety of alternate distance measures may be a better solution than detrending (Gotelli and Ellison, 2004).

In direct gradient analysis, sites are ordered along known and measured environmental gradients. The three types of direct gradient analysis correspond to variants of indirect gradient analysis. Accordingly, limitations and solutions are similar for direct and indirect counterparts. Redundancy analysis is a counterpart to principal components analysis. In such an analysis, sets of orthogonal linear combinations of environmental variables are selected to maximally account for variation in species composition. Each set of linear combinations characterizes a multivariate environmental gradient. Canonical correspondence analysis is the counterpart to canonical analysis, and is similar to redundancy analysis except that it assumes that the abundances of species evince unimodal responses to environmental gradients.

Despite their utility, indirect and direct gradient analyses have rarely been applied to quantify spatial variation

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in bat species composition. Bernard et al. (2001) used multidimensional scaling based on a Bray-Curtis index of association to order sites based on species composition. They were interested in whether undisturbed forests would constitute a cluster based on species composition that was distinct from a cluster comprising fragmented counterparts, and they concluded that fragmented sites differed greatly from undisturbed forest based on relative abundances, but not based on binary data (i.e., presence versus absence). Finally, Lopez-Gonzalez (2004) used detrended canonical correspondence analysis to examine the distribution of Paraguayan bat assemblages along vegetation gradients. Historically, Paraguay was considered to possess two distinct bat faunas, each residing on a different side of the Paraguay River. Phyllostomids dominated communities in eastern Paraguay, whereas molossids and vespertilionids dominated western Paraguay. Lopez-Gonzalez (2004) demonstrated the existence of three faunas: eastern Paraguay, western Paraguay, and floodable lands that serve as a transition zone between the two.

Indices of Biodiversity

Since its inception, the concept of biodiversity has grown to represent multiple forms of complexity. Although the term biodiversity often is used as a synonym of species richness, it more generally refers to the totality of variation in living things (Wilson, 1994). Indeed, biodiversity is multifaceted and represents a latent variable that integrates various components including, but not limited to, taxonomic, genetic, functional, phenetic, and phylogenetic diversity, as well as the concept of complexity. Although each of these components represents aspects of biodiversity, none constitutes a complete or comprehensive descriptor (Fig. 11.9).

Taxonomic diversity is a product of the number of species and the equability of their importances, which can be estimated based on relative abundance, relative biomass, or relative frequency. More than 20 measures of taxonomic diversity exist, in part, because of the variety of ways to balance considerations of species richness and evenness. Alternative approaches focus on construction of an evenness index that is orthogonal to species richness. Several reviews provide guidelines in the use of indices of taxonomic diversity (Peet, 1974; Magurran, 1988; Camargo, 1995; Biesel et al., 1996; Smith and Wilson, 1996; Hubalek, 2000; Stevens and Willig, 2002).

Functional diversity represents those aspects of biodiversity that influence how an ecosystem operates or functions (Tilman, 2001). The functional diversity of a community can be determined by enumerating the number of species or individuals that occur in each of a number of functional groups, and calculating an index (e.g., richness, evenness, diversity, or dominance) that differentially weights the various groups (e.g., Naeem and Li, 1997; Hooper, 1998; Fonseca and Ganade, 2001; Tilman et al., 2001; Stevens et al., 2003; Micheli and Halpern, 2005). Promising alternative approaches utilize the total branch length of a functional dendrogram (Petchey and Gaston, 2002) or the sum of species distances in trait space (Walker et al., 1999).

Measures of phylogenetic diversity are based on the branching pattern in a phylogeny and reflect the phylogenetic variation among species that constitute a community (Barker, 2002). Phylogenetic diversity originally was proposed by Vane-Wright et al. (1991) and developed by Faith (1992) as a measure in which the identity of species and their proximity to each other on a phylogenetic tree are used to represent biodiversity. Such measures quantify the phylogenetic variability among species within a community, as well as the relative degree to which constituent species are related (or derived) on average (e.g., Webb, 2000; Sechrest et al., 2002; Diniz-Filho, 2004b; Rodrigues et al., 2005). Elements of magnitude (i.e., richness) and equability (i.e., evenness) that constitute measures of species diversity have analogous elements in terms of phylogenetic diversity. For example, the average distance between all pairs of species within a community on a phylogenetic tree characterizes the magnitude of phylogenetic diversity, whereas mean nearest-neighbor distances characterize the evenness of species within a tree (Webb, 2000). Although the use of phylogenetic diversity measures has gained acceptance as a useful conservation tool (Barker, 2002), they have been used less often to characterize spatial variation in biodiversity.

Measures of phenetic diversity are integrative measures of biodiversity. Indeed, morphology is a reflection of the ecology and evolutionary history of organisms. It integrates both functional and phylogenetic components of biodiversity, and it is correlated with species richness. Although direct morphological distances can be calculated from raw or log-transformed characters (Findley, 1973, 1976), indices of diversity often are derived from the position of species on principal components based on morphological attributes that reflect ecological characteristics (Schum, 1984; Stevens et al., 2006). For example, the variance of species scores on principal components provides a good estimate of the morphological volume occupied by species in a community. Such variances are ideal because PC axes are dimensionless, and axes conserve the distances among species in morphological space. Consequently, the variance of PC scores is independent of sample size and the means of the morphological characters on which they are based (Ricklefs, 2004). Other measures include the variance of distance among species and the average nearest-neighbor distance. These distances provide information regarding the evenness of species in morphological space and the degree of clumping, respectively.

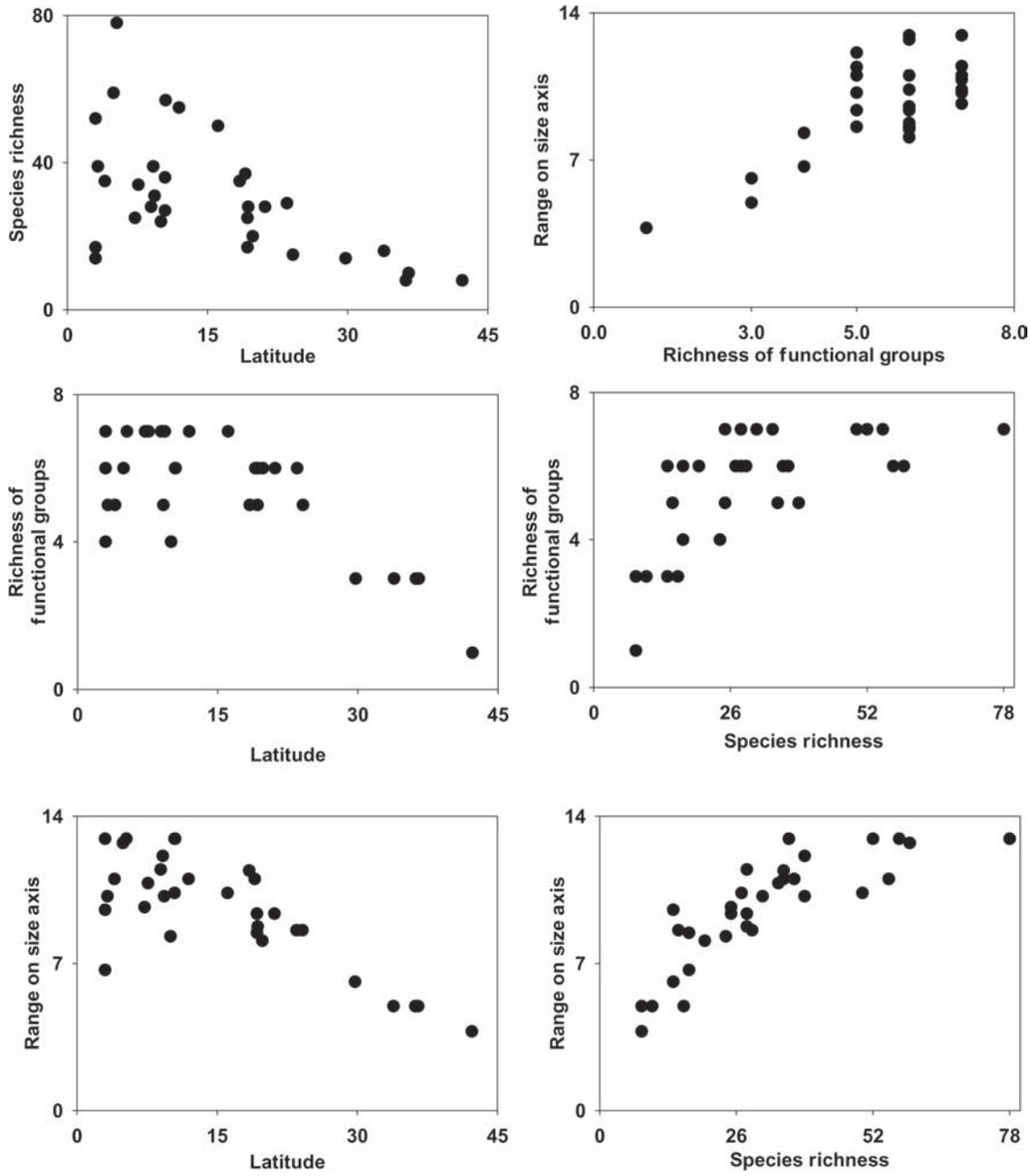

Figure 11.9. Latitudinal gradient (left column) for each of three components of biodiversity (taxonomic, functional, and phenetic) based on 32 bat communities from the New World. Scatter plots (right column) of all possible pairwise combinations of the three measures of biodiversity for the 32 sites indicate the spatial nature of correlation. *Species richness* refers to the number of species in each community; *richness of functional groups* is the number of functional groups in each community; *range on size axis* refers to the phenetic displacement of species within a community based on morphological surrogates of size. *Data from Stevens and Willig, 2002, and Stevens et al., 2003, 2006.*

In terms of spatial analyses, all measures of biodiversity generally can be analyzed in the same fashion. Care must be taken when using nontaxonomic measures, though, because they inherently reflect variation in species richness to some extent. For example, while relationships are noisy and not always linear, the magnitudes of functional and phenetic diversity are dependent on the number of species in a community (Stevens et al., 2003; Stevens et al., 2006); consequently, biodiversity gradients other than those of taxonomic diversity may be confounded by spatial variation in species richness. Nevertheless, such an effect can be disentangled using simulation approaches. For example, empirical latitudinal gradients in functional diversity of New World bats were compared to simulated gradients caused by random selection of species to demonstrate that the underlying gradient in species richness

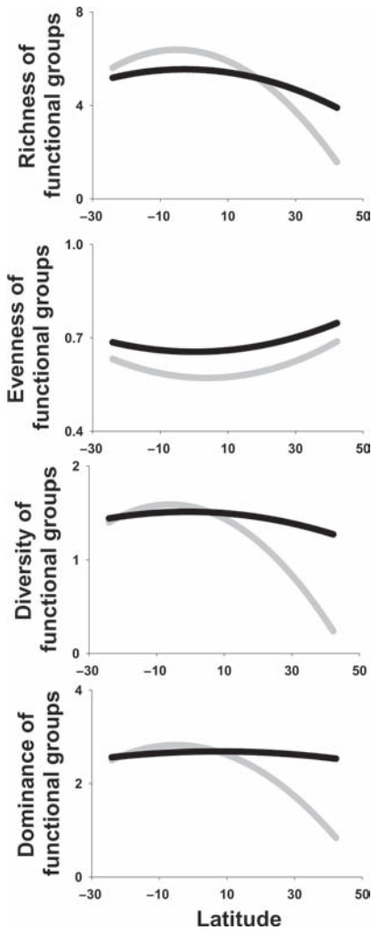

Figure 11.10. Based on 32 New World bat communities, a comparison of empirical latitudinal gradients in different aspects of functional biodiversity (gray lines) with those produced via simulations (black lines) accounting for the latitudinal gradient in species richness. Empirical gradients are based on orthogonal polynomial regression analyses of richness, evenness, diversity, and dominance of functional groups. In each case, the simulated gradient was produced by (1) selecting randomly (without replacement) from the continental New World pool of bats, the same number of species as found in each of the empirical communities; (2) repeating the process 1,000 times; (3) calculating means for simulated values at each site; and (4) conducting orthogonal polynomial regression analysis based on those means. The distinctive nature of empirical and simulated gradients (i.e., absence of coincidence) indicates that variation among sites regarding species richness does not drive latitudinal gradients in functional diversity. Negative values for latitude indicate southern hemisphere locations. Modified from Stevens et al., 2003.

was not the primary driver of the functional diversity gradient (Stevens et al., 2003; Fig. 11.10). This was done for each community, and functional diversity subsequently was regressed against the latitude of the simulated communities. This process was repeated 1,000 times to generate a distribution of gradients in functional diversity that result from a latitudinal gradient in species richness. Quantitative characteristics of empirical gradients (i.e., slopes, coefficients of determination, and F-statistics) were compared to simulated distributions of like characteristics to evaluate the extent to which the empirical gradient arose as a consequence of the stochastic assembly of communities with constrained richnesses. Significant differences, in which characteristics of the empirical community occur in the tails of the distribution of characteristics for the simulated communities, suggest that species richness alone cannot account for empirical patterns of functional diversity.

Differences between Two Sites

Perhaps the most basic spatial contrast involves the difference between two sites. Numerous rarefaction techniques have been developed to evaluate such differences and have been discussed elsewhere (see Kingston, this volume). Another approach, developed by Solow (1993), simulates random differences between communities and then compares the observed difference to random differences. More specifically, all individuals from both samples are combined into a pool; then, individuals (and their species identities) are randomly allocated from the pool to communities. Individuals are allocated until their number equals that in the original sample, a diversity index is calculated for each sample, and the difference between these two diversity measures is retained. This process is iterated many times to create a distribution of random differences. The empirical difference is then compared to the distribution of simulated differences. If the empirical difference occurs within the tails of the random distribution, a significant difference in diversity exists between the two communities. Such an approach has been used to evaluate differences in diversity between two bat communities in eastern Paraguay (Stevens et al., 2004).

Differences among Three or More Sites

If replicated sites within communities are sampled and diversity measures are calculated for these sites, then traditional statistical analyses can be performed to identify differences. For example, if a number of sites within two or more communities are sampled, then a t-test or one-way analysis of variance (ANOVA) can be performed. If numerous communities are examined, a one-way ANOVA can be performed, followed by a posteriori, mean-separation tests to determine the existence of pairwise site differences (Day and Quinn, 1989).

An even more powerful approach requires calculation of a number of indices reflecting aspects of richness, evenness, diversity, and dominance for each community. This suite of indexes is then subjected to a multivariate analysis of variance (MANOVA). Such an approach was used by Stevens and Willig (2002) to determine differences among temperate, subtropical, and tropical zones with respect to taxonomic aspects of biodiversity. The temperate zone differed from the other two zones in terms of species richness, whereas the richness of the tropics was less even than that in the subtropics. Characteristics of associated

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species pools in these three areas likely contributed to these differences. Similar analyses for functional and phenetic diversity are presented in Stevens (2002).

Gradients of Biodiversity

At large spatial extents ranging from regional to hemispheric to global, variation in aspects of biodiversity is often associated with latitude or elevation. Latitude and elevation represent geographic gradients that are considered to be surrogates for some underlying environmental gradient such as energy, temperature, seasonality, or productivity. Because the underlying mechanistic bases for the two gradients may be the same, and because biodiversity data that are used to explore latitudinal and elevational gradients are inferred from comparable kinds of survey approaches, similar approaches and methods have been used to understand such spatial variation.

LATITUDINAL GRADIENTS

The latitudinal gradient of species richness is one of the most fundamental macroecological patterns characterizing life on earth (Rosenzweig, 1995; Brown and Lomolino, 1998; Willig, 2001; Willig et al., 2003a; Hillebrand, 2004). Studies of variation in bat species richness have contributed greatly to this field, despite early controversy concerning methodological approaches, such as the use of bands versus quadrats as focal units or the use of equal area sampling units versus controlling for variation in area when sampling units are of different size (see Simpson, 1964; McCoy and Connor, 1980; Willig and Selcer, 1989; Kaufman and Willig, 1998; Willig and Sandlin, 1991; Romdal et al., 2004). Although a variety of patterns have been documented during the past half-century, at broad spatial extents (i.e., those spanning at least, 20 degrees of latitude), species richness generally increases from polar to tropical latitudes (Willig et al., 2003a), with bats contributing greatly to the mammalian pattern, at least in the New World.

Most work on gradients of richness that span broad latitudinal gradients involves the extrapolation of species distributions for the constituents of a taxonomic clade or biologically relevant group, rather than an accumulation of intensive presence and absence data for each sampling unit in the domain of interest. This can be methodologically challenging, as sampling generally is not extensive, uniform, or random throughout that domain for the vast majority of species. Moreover, data on species occurrences that support a particular range distribution usually were collected by numerous scientists over scores of years, and summarized as a single range map based on expert opinion rather than a formal algorithm based on available data. Moreover, a latitudinal bias may exist—the geographic ranges of tropical species are underestimated because of less intensive and extensive sampling in the tropics compared with that in temperate zones.

In general, synthetic maps of species richness can be constructed from a set of range maps that delineate the geographic distributions or latitudinal ranges of species within a group of interest (e.g., Koopman, 1982; Patterson et al., 2003). The data for quantifying gradients of richness are obtained by superimposing a framework (e.g., a rectilinear grid or set of contiguous bands) on synthetic maps, and estimating richness within each of a number of sampling units (e.g., constituent quadrats in the grid or bands in the set) that differ in latitude. If sampling units are all equal in amount of contained land, then the application of ordinary least squares (OLS) techniques (e.g., linear regression and polynomial regression) to estimate the form and parameterization of the gradient are possible. Nonetheless, the significance of such approaches can be compromised because of spatial autocorrelation or the lack of independence between estimates of richness for sampling units that are spatially proximate (Legendre, 1993; Legendre et al., 2002). In essence, if OLS models are applied to data for which spatial autocorrelation is significant, degrees of freedom are essentially overestimated, thereby resulting in unrealistic test statistics and significance levels as well as underestimated error terms for model parameters. Awareness of this problem has increased in biogeography and ecology, and a variety of statistical approaches such as conditional autoregressive and simultaneous autoregressive (Haining, 1990; Cressie, 1993) models can be used in concert with ordinary least squares models to obviate such shortcomings and guide interpretation of results (e.g., Tognelli and Kelt, 2004).

Although the latitudinal gradient of species richness is well documented and increasingly quantified from rigorous analytical perspectives, resolution of the identity of its underlying mechanistic bases remains elusive, in part because so many of the hypotheses are circular or untestable (Gaston and Blackburn, 2000; Rahbek and Graves, 2001; Willig et al., 2003a). Most of the hypotheses about the latitudinal gradient assume that variation in underlying environmental characteristics effect the pattern. These ideas often are tested using multiple regression models, in which the identity of contributory mechanisms is determined by consideration of a correlation matrix between all possible pairs of independent and dependent variables, and the identity of independent variables (i.e., environmental characteristics) that are included in the final regression model (e.g., Currie, 1991; Kerr and Packer, 1997; Rahbek and Graves, 2001; Tognelli and Kelt, 2004).

Alternative approaches to understanding latitudinal patterns of species richness involve both simulation and analytical models that are geometric in nature, independent of environmental variation, and based on the bounded nature of domains in which species exist (e.g., Colwell and Hurtt, 1994; Willig and Lyons, 1998; Veech, 2000; Colwell and Lees, 2000; Colwell et al., 2004; Connolly, 2005). In addition to these one-dimensional models, two-dimensional

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models have been developed (e.g., Jetz and Rahbek, 2001, 2002; Rangel and Diniz-Filho, 2005) and applied to understanding the role of stochastic processes in effecting spatial variation in general. Still, considerable controversy surrounds the use and interpretation of geometric constraints models to understand spatial variation in general and latitudinal gradients in particular (Hawkins and Diniz-Filho, 2002; Laurie and Silander, 2002; Davies et al., 2005; Hawkins et al., 2005).

The sizes of species ranges and the geographic locations of their midpoints are the proximate determinants of any gradient of species richness. Consequently, a number of simulation (Colwell and Hurtt, 1994; Colwell and Lees, 2000) and analytical models (Willig and Lyons, 1998; Lees et al., 1999) have been developed that incorporate considerations of geometric constraints on the placement of species ranges within a bounded domain (e.g., land for terrestrial mammals, oceans for marine fish). Three kinds of null models—unconstrained, constrained by the location of range midpoints, and constrained by distribution of range sizes—have been developed, applied to a diversity of organisms in a variety of environmental settings, and are available as freeware (Colwell, 2005) on the world wide web (http://viceroy.eeb.uconn.edu/RangeModel). For each species in a bounded domain, the basic input data for analyses of the effects of geometric constraints on gradients of richness include the northern and southern latitudinal termini, or midpoint and latitudinal range size. Because all models generally predict a peak in species richness in the middle of the domain, they are often referred to as mid-domain models. Unlike most other models that have been applied to latitudinal gradients, geometric constraints models make quantitative predictions in terms of the latitudinal location of the peak in richness, the form of the relationship between richness and latitude, and the number of species expected at each latitudinal location. For methodological purposes, only taxa endemic to the domain of interest should be considered in analyses.

ELEVATIONAL GRADIENTS

Changes in species composition and richness with elevation is a ubiquitous pattern in ecology and biogeography that has been recognized for over a 150 years (Darwin, 1839; von Humboldt, 1849; Wallace, 1876; Merriam, 1890). It has been explored from both empirical and theoretical perspectives, and recently, it has been reviewed and synthesized by Rahbek (1995) and by contributors to a dedicated issue of *Global Ecology and Biogeography* (see Heaney and Lomolino, 2001). The lowest elevations generally support higher richness than do the highest elevations, but mid-elevational peaks in species richness are both common and ubiquitous. Elevational gradients are less well documented and understood for bats than for nonvolant mammals or birds (Willig et al., 2003a), with a few notable exceptions. In the Peruvian Andes, bat species richness increases with decreasing elevation, from almost 100 species in the lowlands to about 10 species at elevations over 3,000 m (Patterson et al., 1998). In contrast, in the Mexican Sierra Madre del Sur, species richness is relatively constant (11–12 species) from 500 to 1500 m, sharply rises to a peak of about 20 species at mid-elevation (approximately 2,000 m), and then exhibits a precipitous decline to fewer than 5 species at the summit (2,500 m).

In a literature survey involving 27 elevational gradients from Old and New World spanning 12.5°S to 38°N latitude, McCain (2007) found the number of gradients with mid-elevational peaks to be equal to the number of gradients in which richness declined with elevation. Climatic conditions associated with mountains consistently predicted the type of richness gradient. More specifically, richness decreased with decreasing elevation in mountains whose lowlands were warm and wet, whereas mid-elevational peaks in richness typified mountains whose lowlands were dry. The interaction between water availability and temperature may be the critical driving factor that determines the form of elevational gradients of richness for bats.

Like the situation for the latitudinal gradient in species richness, numerous hypotheses have been proposed to account for elevational patterns, but the hypotheses are not independent or mutually exclusive. Elevational gradients in richness have been attributed to environmental variation in competition, disturbance, habitat complexity and diversity, productivity, resource diversity, and stress as well as to historical factors related to speciation, immigration, and extinction dynamics (see Brown, 2001; Heaney, 2001; Lomolino, 2001). More recently, geometric constraints models have shown promise in contributing to a deeper understanding of elevational gradients by providing an explicit null hypothesis with which to compare empirical patterns. Such analyses have indicated that the mid-domain mechanism, climatic attributes, and other environmental factors likely interact to produce elevational gradients of richness in nature (McCain, 2004, 2005).

Methodological approaches for the study of elevational gradients parallel those used to study latitudinal gradients, and may be categorized into those focusing on alpha versus gamma diversity (see Lomolino, 2001; McCain, 2004, 2005). Studies of alpha diversity focus on local richness and estimate species density. They are based on data derived from intensive sampling within well-defined plots that are dispersed at multiple locations along a transect that comprises an extensive elevational gradient. In contrast, information for studies of gamma diversity generally derives from multiple investigators, including information that appears in scientific publications, field guides, museum collections, and field notes. These studies construct the elevational distributions for species based on such records and consider the elevational range of each

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species to span its highest and lowest elevational records. The species richness of each particular elevational zone is then determined by tallying the number of species whose distributions overlap that zone. Because estimates of gamma diversity that are derived in this fashion reflect sampling biases and differences in area among elevational zones (i.e., the area of zones of equal elevational breadth decrease with increasing elevation), caution should be deployed in the interpretation of analyses based on these data (Rahbek, 1997; Lomolino, 2001; Rickart, 2001).

Area and Scale

The effect of area on species richness is perhaps the most universal law in ecology: as area increases, so too does species richness. Two ecological factors contribute to the pattern (Rosenzweig, 1995). As area increases, the number of individuals increases (more individuals hypothesis; Srivastava and Lawton, 1988). As a consequence, even in a homogeneous domain, large areas with high abundance should contain more species than do small areas with low abundance: the likelihood of obtaining rare species increases as the number of sampled individuals increases. Of course, the earth is heterogeneous at most spatial extents, so that the number of habitats included in a contiguous sample increases as the area of the sample increases. If species exhibit habitat specificity, then larger areas should support more distinct habitats and thereby have more species than would smaller areas (habitat heterogeneity hypothesis). To the extent that the areas are island-like in character, evolutionary mechanisms reinforce this pattern. Species in larger areas with higher abundance enjoy lower extinction rates because of buffering from stochastic or density-independent phenomena, such as disasters. At the same time, speciation rates in larger areas may be higher than in small areas because of greater opportunities for populations to accumulate mutations or be dissected by barriers.

Because of the way in which area affects species richness, care must be taken to ensure that variation in area among sampling units does not confound spatial analyses with respect to other environmental characteristics. Because longitudinal meridians converge toward the poles, quadrats defined by latitude and longitude (e.g., 1-×1-degree quadrats), as well as bands defined by latitude (e.g., 5-degree bands), systematically decrease in area from tropical to polar regions, creating a bias in patterns of species richness. A similar consideration relates to the fill of the quadrats used to estimate species richness. If some quadrats are not filled by land (e.g., coastal quadrats), then two things are possible. First, variation in area can give rise to variation in richness that is unrelated to a particular environmental mechanism, leading to decreased power to detect trends. Second, partially filled quadrats that vary in a systematic way with respect to geography could enhance or diminish the effects of an environmental gradient that vary with space.

A similar area effect causes scale dependence. Scale dependence occurs when patterns measured at one focal scale are not recapitulated at another. Scheiner et al. (2000) illustrated how productivity-diversity gradients can be positive, negative, nonsignificant, or unimodal depending on the focal scale or the spatial extent of an analysis. As such, scale dependence is a critical consideration when comparing studies that were conducted at different focal scales. This is particularly true if the form of the species-area relationship changes in a consistent fashion among sites or along environmental and spatial gradients. The form of the species-area relationship (e.g., log-log or semi-log relationships between richness and area) is a consequence of the extent to which different ecological and evolutionary mechanisms operate within the areas of interest. Species richness can increase with area in markedly different ways in different geographic areas, confounding attempts at standardization (Lyons and Willig, 2002). This problem enhances the likelihood of scale-dependence in gradients of richness, such as those involving latitude (Lyons and Willig, 1999, 2002), productivity (Gross et al., 2000; Scheiner et al., 2000; Scheiner and Jones, 2002), or elevation (Rahbek, 2005). Indeed, the form or parameterization of any gradient involving species richness likely will change as focal scale changes.

LANDSCAPE APPROACHES

Human activities are reducing the extent and increasing the fragmentation of native habitats by converting areas to land uses that are dominated by agricultural and industrial activities (Walker, 1999; Walker and Willig, 1999; Willig and Walker, 1999). Landscape ecology involves the study of the effects of simple (e.g., areal extent of habitat) and complex (e.g., perimeter to area ratio; patch density) features of the landscape on populations and communities, thereby providing critical insight to guide conservation and restoration strategies. Landscape ecology is based on the premise that spatial characteristics of patches as well as spatial attributes of surrounding habitats interact to determine the biotic properties of those patches. A recent special feature in *Ecology* (Volume 86, Number 8, August, 2005) provides a rapid introduction to the history of the field (Turner, 2005), approaches for measuring, modeling, and analyzing landscapes (Belisle, 2005; Urban, 2005; Wagner and Fortin, 2005), and the role of uncertainty in managing landscapes for conservation (Burgman et al., 2005).

From the perspective of bats and many other taxa, landscape effects manifest at the levels of population abundance and community structure (for methods of estimating such attributes for bats, see chapters from Kunz, Betke, and Hristov, and Vonhof; O'Donnell; and Kingston, in this volume). Importantly, the scales at which landscape

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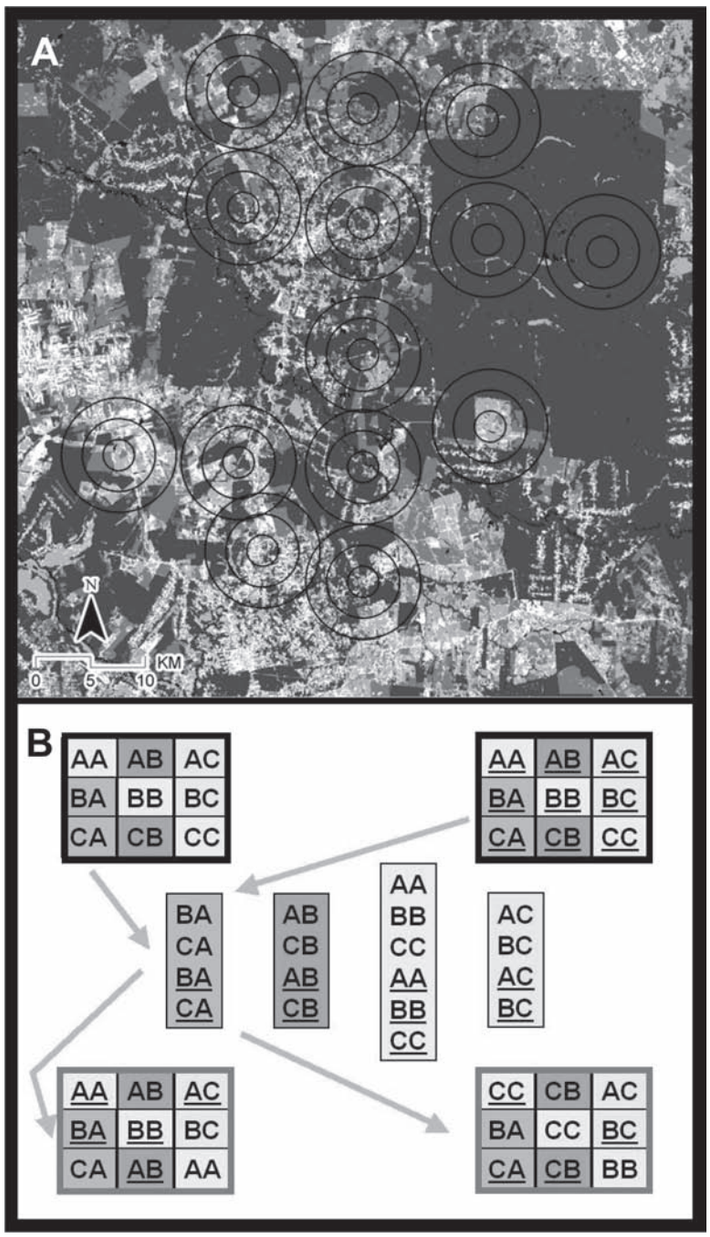

Figure 11.11. Landscape structure can be quantified at a number of scales. A, land cover types, classified from Landsat Thematic Mapper imagery of eastern Paraguay in the vicinity of the Reserva Natural del Bosque Mbaracayu, Departamento de Canindeyu (upper left corner and lower right corners of panel are located at 23°55'22" S, 55°54'40" W and 24°30'6" S, 55°16'43" W, respectively). Landscape structure was measured in each of a sequence of concentric circles (1-, 3-, and 5-km radii); species abundances of phyllostomid bats and community composition were estimated at sites located at the center of each nested set of circles. Land cover types were classified as water (black), forest (dark gray), regrowth (mid-tone gray), pasture or grassland (light gray), and bare soil (white), with forest habitat as the focal landscape type in all quantitative analyses. B, illustrative example of the random permutation method used to develop a null model for two matrices. Elements for each empirical matrix (thick black border surrounds each empirical matrix) are differentiated with underlining (non-underlined and underlined), and letter combinations indicate row and column position within the matrix. Diagonal matrix elements correspond to simple correlation coefficients, and off-diagonal elements comprise partial correlation coefficients. Matrix elements from diagonal (yellow) and each of five off-diagonal columns (purple, red, and blue) from the empirical matrices are pooled separately (thin black borders), and the locations of elements in each pool are permuted. Arrows from the empirical matrices portray an example of the pooling of off-diagonal elements from paired columns. Subsequently, elements from each pool are randomly reassigned a new position in one of two simulated matrices (thick gray border surrounds each simulated matrix), but the affiliation of an element with its original pool (i.e., column location) is retained. Arrows to simulated matrices illustrate an example of the reallocation of off-diagonal elements into original column locations. *Image A, after Gorresen and Willig, 2004, and Gorresen et al., 2005; B, modified from Gorresen et al., 2005*

—-1
—0
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features affect the dynamics of populations and communities are understood poorly. Nonetheless, growing evidence suggests that populations and communities respond to landscape characteristics at a variety of spatial scales. As a result, considerations of scale are integral to understanding biotic responses to characteristics of the landscape.

Aerial photography or satellite imagery often provides the raw data that document spatial heterogeneity in studies of landscape ecology. Such images are then processed with any of a number of programs such as ERDAS (ERDAS, 1997) or ARC-INFO (Environmental Systems Research Institute, 1997) to produce classified scenes (i.e., vegetative or land-use classes are assigned to different components of the remote images) of the landscape (Fig. 11.11A). Thereafter, quantification of landscape attributes is conducted with additional software such as LEAP II (Perera et al., 1997). In general, quantification can occur for the entire domain or extent of the study, or it can occur within focal units to illustrate how variation in landscape characteristics affects population (density of each of a number of species) or community (e.g., richness, evenness, dominance, rarity, or diversity) attributes. Because of uncertainty about the appropriate size of focal units, use of nested areas in which to measure landscape features facilitates assessment of biotic responses in a scale-sensitive manner. Because proximity itself can affect similarity in biotic response variables, procedures to adjust for spatial autocorrelation should be considered early in the design of research or in the analysis of data. Regardless of autocorrelation, two general approaches, regression and simulation analyses, have been used to determine biotic responses to a suite of intercorrelated landscape characteristics. Species presence and abundance are often related to the amount of preferred habitat in a landscape (McGarigal and McComb, 1995; Villard et al., 1999). Moreover, complex landscape characteristics can be correlated with the area of preferred habitat in a focal unit, confounding associations. Consequently, residuals from linear regressions between particular landscape characteristics and area of preferred habitat are useful input for identifying the role of those more complex landscape characteristics in affecting spatial dynamics at the population and community level.

Multiple regression analyses quantify the influence of landscape attributes on each of a number of biotic response variables. These analyses generally assume that landscape characteristics have a linear effect on biotic response variables, although more complex relationships based on any of a number of transformations of landscape characteristics (e.g., quadratic, cubic, or logarithmic transformations) can be executed to capture nonlinear responses. Each of three basic algorithmic approaches (i.e., step-up, step-down, or step-wise analyses) provides parsimonious combinations of landscape characteristics that reflect spatial variation in biotic response variables. Indeed, the different approaches sometimes yield distinctly different results. In all cases, statistical results should be interpreted with reference to a correlation matrix that describes the association among all possible pairwise combinations of landscape characteristics.

The likelihood of committing a type I error may be enhanced in landscape studies because of two situations. The more typical situation occurs when a number of biotic response variables are examined simultaneously in the context of the same experimental design. In these circumstances, the likelihood of detecting spurious associations between landscape variables and response variables increases as the number of response variables increases. Moreover, if landscape characteristics are assessed at multiple spatial scales even for a single response variable, the likelihood of detecting spurious associations increases as the number of focal scales increases. To guard against inflated type I error rates, various corrections, such as the Bonferonni sequential adjustment, have been promoted in the literature (Rice, 1989). In effect, these corrections increase *p*-values for particular regression results by a quantity that reflects the number of response variables considered in the overall analysis. Nonetheless, uncritical application of these kinds of corrections may enhance type II error rates, leading some to suggest avoidance of such adjustments, especially in heuristic or exploratory analyses (Hurlbert, 2003; Moran, 2003), or to apply alternative approaches that control for the proportion of significant results that are type I errors (false discovery rate control methods; Verhoeven et al., 2005).

Scale sensitivity or scale dependency occurs when the relationship between a biotic response variable and landscape characteristics differs depending on the focal scale of analysis (e.g., Lyons and Willig, 1999, 2002; Scheiner et al., 2000). Relationships can differ with respect to the magnitude or direction of association between biotic response variables and landscape characteristics (i.e., the value of regression coefficients). A matrix of full and partial correlations can be used to characterize the multifaceted association between landscape attributes and any particular biotic response variable at each focal scale of interest (Fig. 11.11B). Importantly, a matrix based on one focal scale can differ from a matrix based on a different focal scale due to considerations of the magnitude or direction of association. Simulation analyses can be used to assess each kind of correspondence separately (Fig. 11.11B). Moreover, results can be combined in a meta-analysis to determine the overall significance of scale sensitivity. Such an approach was developed recently by Gorresen et al. (2005) and applied to population- and community-level characteristics of bats in Interior Atlantic Rainforest of Paraguay. Replication of three focal scales at 14 sites was sufficient to detect scale dependent responses of populations and communities to seven landscape characteristics.

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CONSERVATION APPROACHES

A cornerstone of contemporary conservation involves the creation of reserve networks to preserve and protect aspects of biodiversity at regional, national, and global scales. Particular strategies for doing so involve a number of operational goals that generally require the solution of an optimization problem: What is the suite of sites that protects the most species for the least cost? The solution to the problem is thorny and not possible using analytical approaches. Consequently, a number of simulation algorithms have been developed to provide a mechanism for designing such reserve networks. Simulated annealing algorithms provide an increasingly popular method for identifying representative and efficient reserve-system configurations. The data required for such analyses inherently are spatial, comprising information about the species composition of sites (Fig. 11.12A–B) as well as the economic value of sites.

The species composition of sites can be obtained based on historical records, intensive sampling, inferred distribution maps, or a combination of data. The sites can be dispersed or contiguous and may be equal or unequal in size. In essence, the best available data should be used to construct a species list for each site that is being considered in the creation of a reserve network. The cost of establishing the network ultimately is based on a perceived economic value of the land that constitutes each site in the pool of candidate reserves. Naïve models sometimes assume that all sites are of equal value. Others assume that value is proportional to area. Still others estimate value based on economic indicators (e.g., acquisition costs, management costs, and opportunity costs). Regardless of mechanism, most approaches assume that all sites are equally available for inclusion in a reserve system. Finally, different representational goals for biodiversity can be incorporated into an algorithm. For example, a goal might be that each species is represented in at least three sites so as to buffer the reserve system from stochastic events, local extinction dynamics, or catastrophes.

Simulated annealing algorithms (for details see Andelman et al., 1999; Ball, 2000; and Possingham et al., 2000) begin by generating a reserve system that comprises a random number of sites from the candidate pool. This initial system is compared to others based on the random addition of a site to the network or the random deletion of a site from the network. At each step or iteration, the new system is compared to the previous system. If

$$e^{(-\text{change}/\text{acceptance level})} < \text{random number},$$

the change is accepted; otherwise it is rejected. Clearly, the acceptance level affects whether a site is added or deleted from the solution. Every 1,000 iterations, the acceptance level is decreased by an increment. When the acceptance level approaches zero, alterations in the system only occur when the change enhances the solution. Incorporation of an exponential term in the algorithm enhances efficiency: little time is allocated to accepting undesirable changes and much more time is allocated to resolving small positive differences in the solution. The simulation terminates after a specified number of iterations. This algorithm is included in the software package SITES (Andelman et al., 1999; Ball, 2000) and has been used in a variety of reserve system scenarios by public and nongovernmental agencies (Groves et al., 2000; Beck and Odaya, 2001; Leslie et al., 2003). The entire simulation process is repeated de novo some predetermined number of times (e.g., 200 simulations). The percentage of times that a site was selected, known as irreplaceability (Ferrier et al., 2000), estimates the conservation value of the site or the extent to which it is required to achieve the specified conservation goal (Fig. 11.12 C–F).

Simulated annealing approaches for designing reserves for the conservation of bat biodiversity have been done at two spatial scales: (1) a national scale within Paraguay (Andelman and Willig, 2002), and (2) a hemispheric scale in the continental New World (Andelman and Willig, 2003). In the Paraguayan example, solutions based on predicted occurrence of species as suggested by range maps can be quite different from solutions based on presences confirmed by intensive site surveys. Regardless of approach, the current reserve system in Paraguay was inadequate for protection of the bat fauna. In the New World example, future reserve placement should be targeted to ten areas, five in regions that are highly threatened by anthropogenic activity (subtropical Mexico, Meso-America, Tropical Andes, Choco-Darien Region, and Brazilian Cerrado), three in moderately threatened areas (i.e., Baja California, Venezuelan Llanos, and southern Andes of Argentina and Chile), and two in relatively secure areas (Amazon Basin and Guiana Shield). Differences in the status of current reserves with respect to the algorithmic approach or differences in the conservation goal (preserves each species at least one time versus at least three times) had little effect in the identification of these targeted areas for investment (compare Fig. 11.12C–F). A growing consensus is that simulated annealing provides a viable alternative for identifying habitat for conservation, and is superior to approaches based on single species (e.g., Cook and Auster, 2005).

SUMMARY

The study of macroecology is complex and inherently quantitative. The discipline is evolving rapidly from both conceptual and analytical perspectives. In the bulleted list that follows, we identify major points that were considered in detail concerning the spatial analysis of macroecological characteristics.

- Macroecology is the study of relationships between ecological characteristics at broad spatial or temporal

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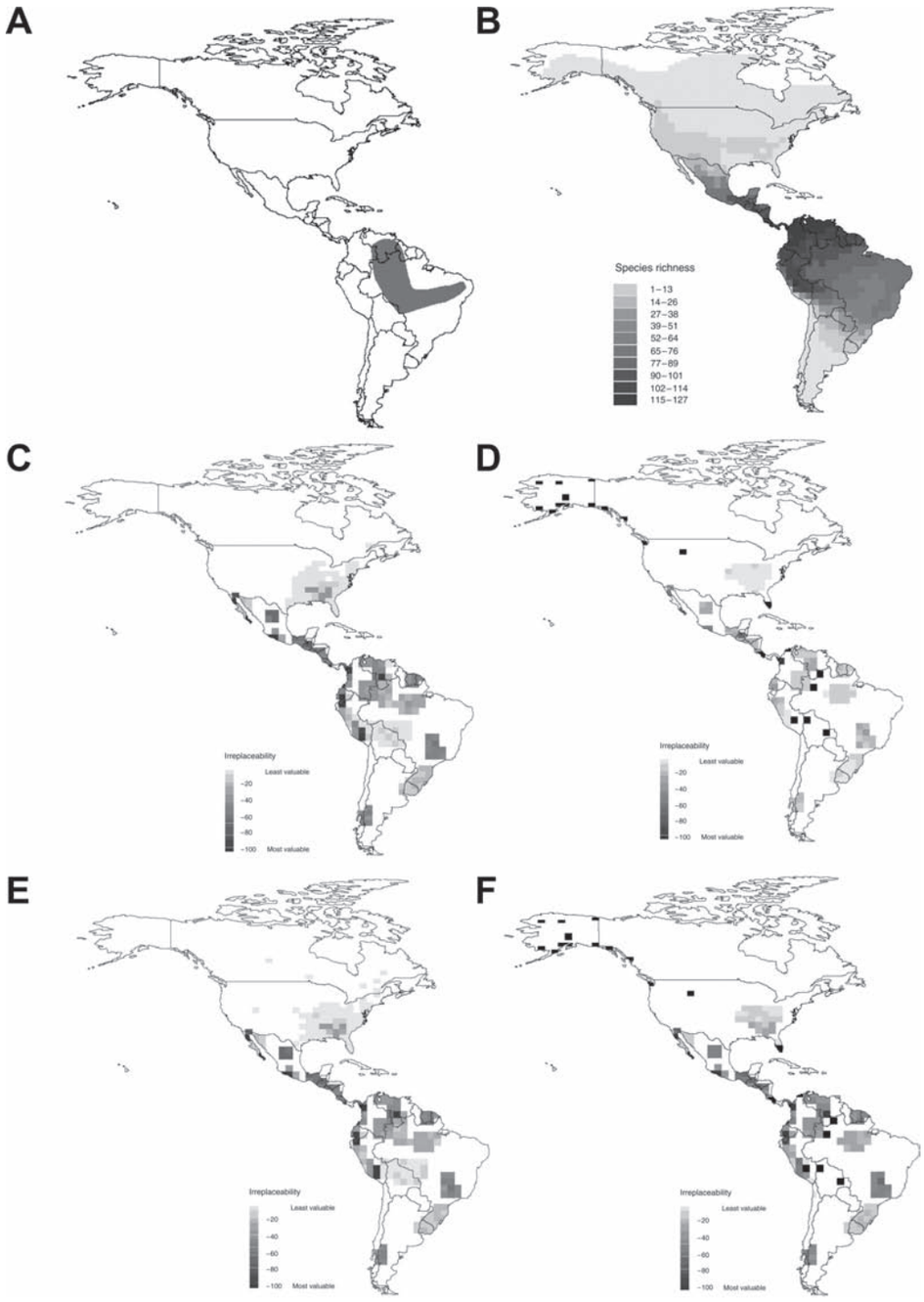

Figure 11.12. Distributional data for any single species of bat can be represented in a GIS database. A, distributional data for *Molossops mattogrossensis*. B, synthetic map of species richness in 250 250 km quadrats produced using software such as ArcGIS by superimposing ranges of all continental New World bats. C–F, irreplaceability surfaces were derived from 200 executions of simulated annealing algorithms for each of four scenarios defined by combinations of current reserve status and protection goal: C, irreplaceability surfaces in which the goal is to protect each species at least once, ignoring reserve status in the solution; D, forcing reserves into the solution; E, protecting each species at least three times; E, ignoring reserve status in the solution; F, forcing reserves into the solution. *Ferrier et al., 2000. Modified from Andelman and Willig, 2003.*

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extents. Nonetheless, macroecological patterns often are studied at restricted geographic or temporal extents, and extrapolated to larger domains. Comprehensive research should focus on the effects of restricted sampling on the form and parameterization of macroecological relationships, as well as associated biases.

- The primary data at the species level that liberate macroecological studies are often difficult to obtain from the literature. Although body size is a fundamental attribute of species that integrates much biological information, *Mammalian Species* (published by the American Society of Mammalogists), for example, does not consistently contain information on the central tendency or dispersion of body size in each published account. The study of macroecology would be served if such publishing venues included more comprehensive or detailed information on attributes of geographic range, metabolic rate, and life history.
- Macroecological patterns generally are messy and not easily evaluated using traditional statistical methods. In particular, triangular patterns that imply constraints and complex (nonlinear) relationships between variables are common. Better methods are needed to evaluate the importance of these constraints from a statistical perspective and to understand them from a biological perspective.
- Because macroecological patterns are messy, various simulation methods are an effective means to evaluate them. Consequently, students of macroecology should develop strong quantitative modeling skills, including the ability to program in a flexible computer language (e.g., C or C++) or facility with programs that execute powerful simulation analyses (e.g., Matlab or R Package).
- Although cluster analysis can be used to associate sites based on similarities in species composition, indirect and direct gradient analyses provide powerful alternatives for understanding how communities and assemblages are organized along putatively important (indirect) or empirically measured (direct) environmental gradients. These approaches represent powerful tools for exploring environmental gradients that mold geographic patterns.
- Biodiversity is a multifaceted latent variable that embodies various forms of biological complexity. In addition to its taxonomic components–which are relatively better studied at all spatial scales—functional, phylogenetic, phenetic, and interaction components provide unique perspectives of biodiversity that may vary in time and space, and do so in unique ways. The foundations of macroecology would become fortified by a broader consideration of variation in these aspects of biodiversity at all temporal and spatial scales.
- Because variation in most components of biodiversity are correlated with variation in species richness, environmental or spatial relationships involving these other components should be quantified and interpreted in a simulation context that allows their unique variation to be exposed and understood independent of variation in species richness.
- Variation in aspects of biodiversity along gradients is sensitive to the focal scale at which parameters are estimated as well as the extent of the domain over which patterns are being quantified in analyses. Extreme caution should be employed in statistical analyses in which sample units are not of the same size, and patterns of biodiversity should be interpreted within the context of the scale of analyses.
- Analyses of gradients in any aspect of biodiversity should consider the effects of spatial autocorrelation, otherwise estimates of parameters and statistical conclusions can be biased.
- Landscape approaches for exploring the effects of habitat structure on components of biodiversity are promising but need to consider fully the various ways in which scale can influence patterns as well as the biological mechanisms that give rise to scale dependence.
- The design and configuration of conservation reserve networks to protect biodiversity at regional, national, or global scales would benefit from optimization approaches such as simulated annealing. This approach can balance the cost of establishing networks with attainment of specified conservation goals.

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