A HEMISPHERIC ASSESSMENT OF SCALE DEPENDENCE IN LATITUDINAL GRADIENTS OF SPECIES RICHNESS

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Abstract. Considerable controversy surrounds the importance of historical, evolutionary, and ecological factors affecting continental patterns in species richness. Although the importance of area and latitude are both well documented, few attempts have been made to integrate their effects in a single model. Most studies have been conducted by superimposing grids on equal-area projection maps and counting the number of species occurring within grid cells (i.e., quadrats). Unfortunately, different grid-based studies use different quadrat sizes, making comparisons tenuous. We developed a hierarchical model to evaluate the degree to which area (based on a nested series of quadrats of five sizes, 1000–25 000 km^2) affects the latitudinal gradient in species richness. The model allows the relationship between latitude and area to be nonlinear and, in its simple form, evaluates how well species richness can be predicted by the additive influences of latitude and area. The complex model evaluates whether an area $\times$ latitude interaction accounts for significant additional variation in species richness above that in the simple model (i.e., assesses the scale dependence of the latitudinal gradient). For bats and marsupials, the simple model included only latitudinal effects and accounted for over half of the variation in species richness of each of the two taxa. The interactive effect was nonsignificant for each taxon, accounting for <0.1% of additional variation in species richness in each case. If other taxa or land masses produce similar relationships, then the form of the latitudinal gradient is relatively invariant with respect to area at 1000–25 000 km^2 scales, and comparisons among studies at this spatial scale are straightforward.

Key words: areography; bats; biodiversity; geographical ecology; macroecology; marsupials; scale dependence.

INTRODUCTION

The recent works of Brown (1995), Gaston (1996), and Rosenzweig (1995) bring into clear focus the importance of quantifying patterns of species diversity and understanding the mechanisms responsible for their existence. Nonetheless, uncertainty in the shape of the patterns has been eclipsed by disagreement, sometimes quite vehemently, surrounding the causes of those patterns (e.g., Rosenzweig 1995, Rosenzweig and Sandlin 1997, Rohde 1997, 1998). Indeed, the controversy surrounding mechanism may be an artifact, at least in part, of differences in the scale of experiments, natural or manipulative. Different mechanisms likely operate at different spatial and temporal scales, and it is within this context (Pickett et al. 1994) that we must understand the interrelationships between pattern and process in ecology.

Two environmental factors, latitude and area, long have been integral to theories concerning spatial vari-ation in species richness. Historically, area has been of prime importance in considerations of patterns of richness in island systems (MacArthur and Wilson 1967, Gilbert 1980, Coleman et al. 1982), whereas latitude has dominated the literature concerning mainland patterns (e.g., Simpson 1964, Wilson 1974). In fact, fascination with the pattern between species richness and latitude has engendered no less than 21 phenomenological or mechanistic explanations (Rohde 1992, Rosenzweig 1995, Willig and Lyons 1998), with interest waxing and waning for particular explanations over time. Nonetheless, productivity, because of its direct linkage to the currency upon which ecosystems are based, has received increasing attention as a prime factor affecting global patterns of species richness at a variety of spatial scales (Waide et al. 1999; G. G. Mittelbach, C. Steiner, K. L. Gross, H. Reynolds, S. M. Scheiner, R. B. Waide, M. R. Willig, and S. I. Dodson, *unpublished manuscript*). Alternatively, the larger areal extent of the tropics has been championed as the factor affecting high tropical diversity at continental scales (Rosenzweig 1995, Rosenzweig and Sandlin 1997). A more inclusive view, simultaneously assessing the cumulative effects of area and latitude on species richness, should lend considerable insight into patterns and mechanisms.

Scale

Scale is the unit of space or time over which signals are integrated to convey a message (Allen and Starr 1982). The importance of scale in ecological research is reflected in the growing body of literature devoted to the subject (Levin 1992). In general, systems are organized into a hierarchy of spatial and temporal scales, and theory predicts that the dynamics of a system at a lower scale affects the dynamics of systems at higher levels and vice versa (Allen and Starr 1982, O'Neill 1989). A few ecological studies have found scale to be relatively unimportant (Stiling et al. 1991, Aronson 1992), but it is increasingly apparent that results at one spatial or temporal scale may not necessarily be recapitulated at larger or smaller scales (Kerfoot and DeAngelis 1989, Rose and Leggett 1990, Hanski 1991, Camus and Ojeda 1992, Gascon and Travis 1992, Levin 1992; K. L. Gross, M. R. Willig, L. Gough, R. Inouye, and S. B. Cox, *unpublished manuscript,* S. M. Scheiner, S. B. Cox, M. R. Willig, G. G. Mittelbach, C. Osenberg, and M. Kaspari, *unpublished manuscript*).

The challenge to contemporary ecology and biogeography is to document scale dependence or independence in different systems, facilitating comparisons among scales or among systems. For example, the possible scale dependence of the relationship between productivity (or any environmental variable) and species richness has been explored in a quantitative fashion by S. M. Scheiner, S. B. Cox, M. R. Willig, G. G. Mittelbach, C. Osenberg, and M. Kaspari, (*unpublished manuscript*). Similarly, K. L. Gross, M. R. Willig, L. Gough, R. Inouye, and S. B. Cox, (*unpublished manuscript*) provided an empirical evaluation of the effect of scale on patterns between productivity and diversity for low-stature vascular plants. Clearly, patterns of diversity can be scale dependent, and often are (Pastor et al. 1996, Waide et al. 1999; K. L. Gross, M. R. Willig, L. Gough, R. Inouye, and S. B. Cox, *unpublished manuscript,* G. G. Mittelbach, C. Steiner, K. L. Gross, H. Reynolds, S. M. Scheiner, R. B. Waide, M. R. Willig, and S. I. Dodson, *unpublished manuscript*). An analogous evaluation of scale dependence in the relationship between species richness and latitude is the focus of this paper.

Area

Areography is the study of geographical ranges of taxa (Rapoport 1982), but with the exception of Anderson and Marcus (1993), areographic studies that focus on gradients of species richness have not addressed the problem of spatial scale in a comprehensive fashion. Most areographic studies have been conducted by superimposing grids on equal-area projection maps, and counting the number of species that occur within grid-cells (i.e., quadrats). Quadrat sizes have been based on linear scales ranging from 62.5 km to 500 km, and meridial scales ranging from 1° to 10° (An-

derson and Marcus 1993). Because the linear distance encompassed by one degree longitude depends upon latitudinal position, quadrat sizes of degree-based grids even differ within a study. Similarly, quadrats based on a linear distance often include different sampling areas because coastal grid cells are not full of land. As a consequence, it is difficult to discern scale-based effects from other biogeographic, ecological, or evolutionary phenomena. For example, Wilson (1974) used quadrats that were 240 km (originally published as 150 mi.) on a side and found that the relationship between species richness of North American mammals and latitude was best described by a fifth-order polynomial. In contrast, Willig and Selcer (1989) used quadrats that were 500 km on a side and found that the relationship for New World bats and latitude was a second-order polynomial. Meaningful comparisons cannot be made unless the effect of area (quadrat size) on patterns of species richness is quantified and understood.

The power function of Arrhenius (1921, 1923*a, b*) commonly is used to model the way in which species richness increases with area in both ecological (Coleman et al. 1982, Lyons 1994, 1995, Rosenzweig 1995) and biogeographic contexts (MacArthur and Wilson 1967, Gilbert 1980). Hence, it is reasonable to apportion the variation due to area in studies of latitudinal gradients in species richness using a power function. However, adjusting for area is complex when degree-based grids are employed, because area is not the same for quadrats spanning equal degrees; it is confounded, decreasing with increasing latitude (i.e., longitudinal meridia converge toward the poles). As a result, any statistical attempt to remove variation due to area will have the effect of removing variation that correctly should be attributed to latitude. Moreover, the way in which area affects latitudinal gradients of species richness may not be consistent. At the level of the landscape, size of the sampling unit has been shown to have a considerable effect on patterns of vertebrate species richness (Storms 1994).

Latitude

Studies detailing latitudinal trends in mammalian richness have focused on North American mammals (Hagmeier and Stults 1964, Simpson 1964, Hagmeier 1966, Wilson 1974, McCoy and Connor 1980, Pagel et al. 1991). Regardless of taxon, few studies of New World patterns (e.g., Pielou 1977, Mares and Ojeda 1982, Willig and Selcer 1989, Willig and Sandlin 1991, Kaufman 1995, Blackburn and Gaston 1996, Willig and Gannon 1997, Kaufman and Willig 1998) have included South America and North America. Without corroborative evidence for latitudinal trends in South America, caution must be used in extrapolating latitudinal trends in North America to other continents. If similar patterns are not found on both continents, then observed latitudinal trends may be caused by unique attributes of North America (e.g., geography, physi-
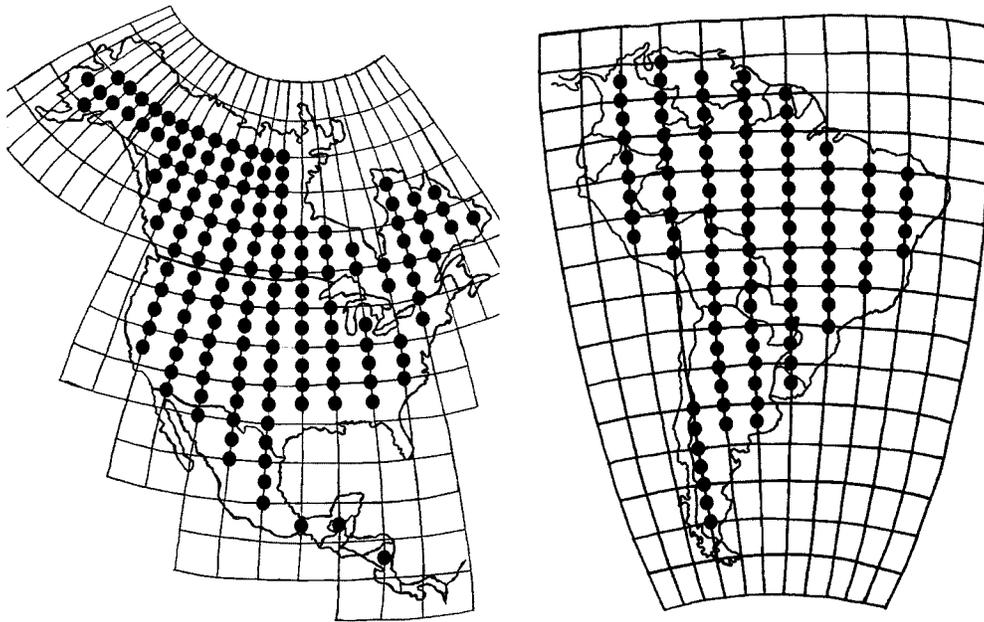
Fig. 1. Equal-area projection maps of North and South America with solid circles placed every 5° longitude and 2.5° latitude to indicate position of the nested sets of quadrats used in this study of relationships between species richness, area, and latitude. All quadrats are fully contained within the land mass.

ography, evolutionary history) rather than by latitudinal correlates, per se (Rapoport 1982, Willig and Selcer 1989).

Bats and marsupials exhibit disparate attributes, making them ideal for comparative purposes. Bats (~244 New World species) occur throughout most of North and South America (Willig and Selcer 1989, Willig and Sandlin 1991, Lyons and Willig 1997, Willig and Lyons 1998), with many species having extensive ranges that encompass a large portion of both continents (Lyons and Willig 1997). Moreover, bat species richness peaks above the equator at about 10° N (Willig and Lyons 1998). In contrast, the majority of marsupials (~82 New World species) are limited to Central and South America, with only one species (*Didelphis virginiana*) penetrating very far into North America (Gardner 1973, Lyons and Willig 1997, Willig and Gannon 1997). Current ecological diversity of New World marsupials is much less than that prior to the Great American Interchange (Simpson 1980). Moreover, most marsupials have relatively restricted ranges, probably due to their relatively small size, lack of vagility, and poor dispersal abilities (Lyons and Willig 1997). These factors combine to produce a platykurtic distribution with maximum richness at ~20° S (Willig and Gannon 1997, Willig and Lyons 1998).

The biological and historical differences between these two taxa makes them ideal for examining the possible effects of scale on gradients of species richness. Similarities and differences in the effect of area on latitudinal patterns of species richness between these two taxa should provide additional insight into

the effects of scale. Once the effect of quadrat size on richness patterns is understood, differences in observed patterns may be attributed more correctly to differences in ecological, evolutionary, or biogeographical characteristics of biotas or regions.

METHODS AND MATERIALS

Distribution maps for bats were constructed using Hall (1981) for North and Central America, and Koopman (1982) for South America. Distribution maps for marsupials were prepared using Hall (1981) for North and Central America, and Streilein (1982) for South America. Eisenberg (1989) and Redford and Eisenberg (1992) were referenced to update distributions of both taxa in South America. A detailed rationale for inclusion of taxa based on systematic considerations appears in Lyons (1994).

Previous studies rightly have been criticized because richness data for quadrats not wholly contained on land were included in statistical analyses (Rosenzweig 1995). To avoid this problem, nested sets of quadrats (25 000, 20 000, 15 000, 10 000, and 1000 km²) were superimposed in a systematic fashion on an equal-area projection map of the New World. Centers of the nested quadrats were located along each five degree meridian of longitude at 2.5° latitudinal intervals, with the constraint that all quadrats centered at a location must be full of land (Fig. 1). To avoid sampling bias, we limited the set to 252 locations, governed by the size of the largest quadrat in the nested series that would not overlap adjacent quadrats of the same size. Species richness of a quadrat was considered to be the number of species

whose geographic range overlapped a quadrat. Because the number of quadrats situated at a given latitude differed depending on width of the continent, only the mean number of species found in quadrats at each latitude were used in analyses. As a consequence, each latitude had equal weighting in affecting the form of diversity gradients.

Data analysis

A nonlinear statistical model was developed to evaluate simultaneously the effects of latitude, area, and their interaction on species richness. In general,

$$S = A + L* + AL* + e \qquad (1)$$

where S is the number of species in a quadrat, A is the areal effect, $L*$ is the latitudinal effect, $AL*$ is the interaction term, and e represents random error. Neither areal nor latitudinal effects need manifest in a linear manner (Rosenzweig 1995). In fact, when species pools are much larger than the size of the fauna occupying quadrats or quadrats that are positioned in a nested fashion, area (A) should affect richness (S) in an exponential fashion (i.e., power function of Arrhenius 1923a, b):

$$S = CA^Z \qquad (2)$$

where C and Z are constants determined by best-fit least-squares methods (MacArthur and Wilson 1967).

Latitudinal effects likely are nonlinear as well. For example, the relationships between bat species richness and latitude for North America (Simpson 1964, Wilson 1974) as well as for the entire New World (Willig and Selcer 1989, Willig and Sandlin 1991, Willig and Lyons 1998) were described better by polynomial relationships than linear relationships. The same was true for New World marsupials (Willig and Gannon 1997, Willig and Lyons 1998). However, polynomial models may force unrealistic equations to fit data when asymptotic relationships are likely. Negative exponential equations allow species richness to gradually decrease towards a minimum value (Fig. 2). Hence, latitudinal effects were modeled by

$$S = Fe^{G(L*+1)} \qquad (3)$$

where F is a constant, and G is a value that determines the rate of decrease of the negative exponential curve. A constant (1) was added to latitude to prevent mathematical complications that occur when latitude equals zero (i.e., log 0 is undefined). In its simple form, the negative exponential requires richness to peak at the equator. Because empirical data (Willig and Lyons 1998) reveal that richness of bats and marsupials attain maximal richness at 10° N and 20° S, respectively, we rescaled the algorithm so that richness declined in an exponential fashion from the latitude that corresponds to the midpoint of the latitudinal range of each higher taxon (i.e., 0° for marsupials and 7.5° N for bats). As
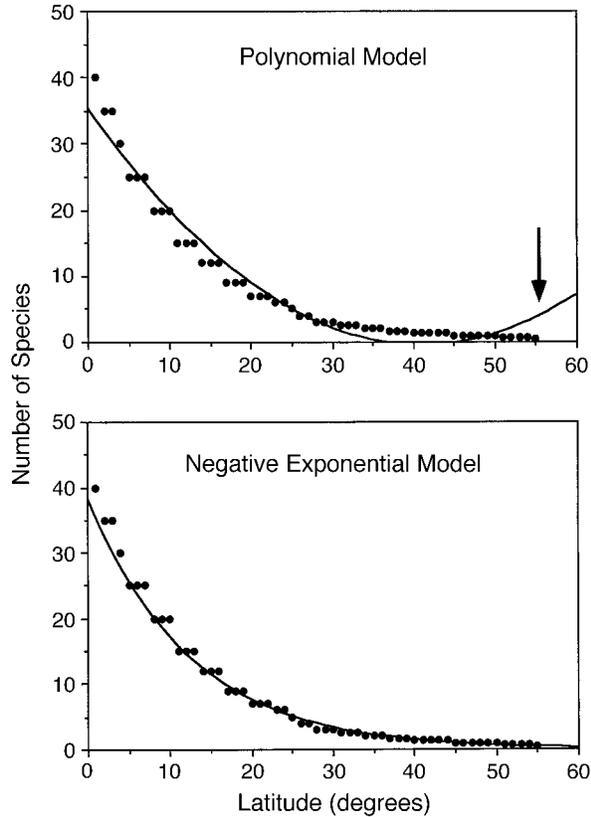

FIG. 2. Panels show graphical representations of the way in which a polynomial model as opposed to an exponential model describes latitudinal gradients in species richness (data points are positioned for illustrative purposes and are not indicative of a pattern for bats or marsupials). The polynomial model fails to predict the correct relationship between species richness and latitude at high and low latitudes, whereas the negative exponential model is a much better predictor at all latitudes. Moreover, the polynomial model forces unrealistic forms (bold vertical arrow) to fit the data.

such, $L*$ was set to L for marsupials, and to $L - 7.5°$ for bats.

Areal relations (Eq. 2) and latitudinal relations (Eq. 3) were substituted in Eq. 1, yielding

$$S = CA^Z + Fe^{G(L*+1)} + B\{e^{G(L*+1)}\}(A^Z) + e. \qquad (4)$$

B is a coefficient for the interaction term, which embodies scale dependence in the latitudinal gradient of species richness. This composite model was evaluated using iterative nonlinear regression techniques in SPSS Program CNLR (SPSS 1990).

Hierarchical analyses were conducted with and without the interaction term to determine its significance and contribution to the relationship between S and both independent variables (A and $L*$). If the interactive model (including $AL*$) was significant and accounted for at least 5% more variation than did the simple model (not including the interaction term), then the interaction was considered important. More specifically, estimates

TABLE 1. Results of nonlinear regression analysis (SPSS Program CNLR [SPSS 1990]) of the relationship in which species richness is a function of area and latitude.

| | Simple model | | | | | Interactive model | |
| | Area | | Latitude | | | | |
Taxon	C	Z	F	G	R^2	B	ΔR^2
Marsupials	1.000^{ns}	0.061^{ns}	14.116	-0.046^*	0.596	0.071^{ns}	0.000
Bats	1.000^{ns}	0.000^{ns}	133.752^*	-0.053^*	0.866	0.000^{ns}	0.000

Notes: The simple model is additive, with area affecting species richness via a power function and latitude affecting species richness via an exponential function (see *Methods and materials: Data analysis* for details and definitions of parameters). In the interactive model, a multiplicative term (latitude × area) is added to the simple model to assess the scale dependence of the relationship. Analyses were conducted separately for bats and marsupials in the New World.

$* P < 0.05.$

of $C, Z, F,$ and G (only B was allowed to vary) from the simple model were substituted into the interactive model for two reasons: (1) to ensure that the degree of significance for the interaction term was independent of pure areal and latitudinal effects and (2) to constrain the additive contributions of area and latitude to be the same in both models. In this way, the interactive model accounted for variation in the residuals of S from the simple model via a multiplicative term.

An iterative solution to Eq. 4, in program CNLR, requires initial estimates of parameters. Consequently, initial values for $F, B, C, Z,$ and G were estimated using Program REGRESSION (SPSS 1990) or taken from values in the literature. To determine an initial estimate for $C,$ species richness from the data was used as $S,$ and the equation $S = CA^z$ was solved for C for each latitudinal band. The average of these estimates of C determined the initial value. Simple linear regressions were conducted between number of species and latitude for each quadrat size. Values of F for each area were averaged to obtain the initial value. B was arbitrarily set at 1.0; if an interaction between latitude and area existed, B would be statistically distinguishable from zero. The initial value for Z ($Z = 0.18$) was taken from the literature for mainland species–area curves (Rosenzweig 1995) and G was set arbitrarily to 0.99. G is a scalar for the way in which latitude affects species richness. If G equaled 1.0, the way in which latitude affected species richness could be directly accounted for by the negative exponential model. Therefore, G was set close to, but not equal to, 1.

RESULTS

We successfully designed a sampling protocol and analytical model to assess the joint effects of area, latitude, and their interaction on species richness. Despite systematic, ecological, and historical differences between bats and marsupials, we have shown that latitude is the dominant factor affecting spatial variation in species richness, and this relationship is independent of area.

Marsupials

The simple model accounted for 59.6% of the variation in species richness, with only latitudinal parameters being significant (Table 1, Fig. 3). The way in which latitude affected the number of species is consistent with a negative exponential relation. In contrast, marsupials did not show a significant areal effect. Moreover, the interactive model was nonsignificant (Table 1, Fig. 3), and it accounted for <0.1% of the additional variation beyond that of the simple model. Hence, the way in which area affected species richness is independent of latitudinal position, and the way in which latitude accounted for variation in species richness is also independent of the size of sampling units.

Bats

Similar results were obtained for bats. The simple model accounted for almost 87% of the variation in species richness. All latitudinal parameters were significant, but areal parameters were not (Table 1, Fig. 3). Again, the interactive model accounted for <0.1% of additional variation in species richness, and the interaction term was nonsignificant (Table 1, Fig. 3).

DISCUSSION

The effect of scale and its consequences for comparisons among studies is an important question in contemporary ecology (Levin 1992, Anderson and Marcus 1993; K. L. Gross, M. R. Willig, L. Gough, R. Inouye, and S. B. Cox, *unpublished manuscript,* S. M. Scheiner, S. B. Cox, M. R. Willig, G. G. Mittelbach, C. Osenberg, and M. Kaspari, *unpublished manuscript*). It is becoming increasingly clear that the pattern observed may be a function of the scale at which we are working (S. M. Scheiner, S. B. Cox, M. R. Willig, G. G. Mittelbach, C. Osenberg, and M. Kaspari, *unpublished manuscript*). Given that the controversy (Rohde 1992, 1997, 1998, Rosenzweig 1995, Rosenzweig and Sandlin 1997) surrounding mechanisms to explain the latitudinal gradient in species richness may be a by-product of this scale dependence, it is necessary to understand the ef-
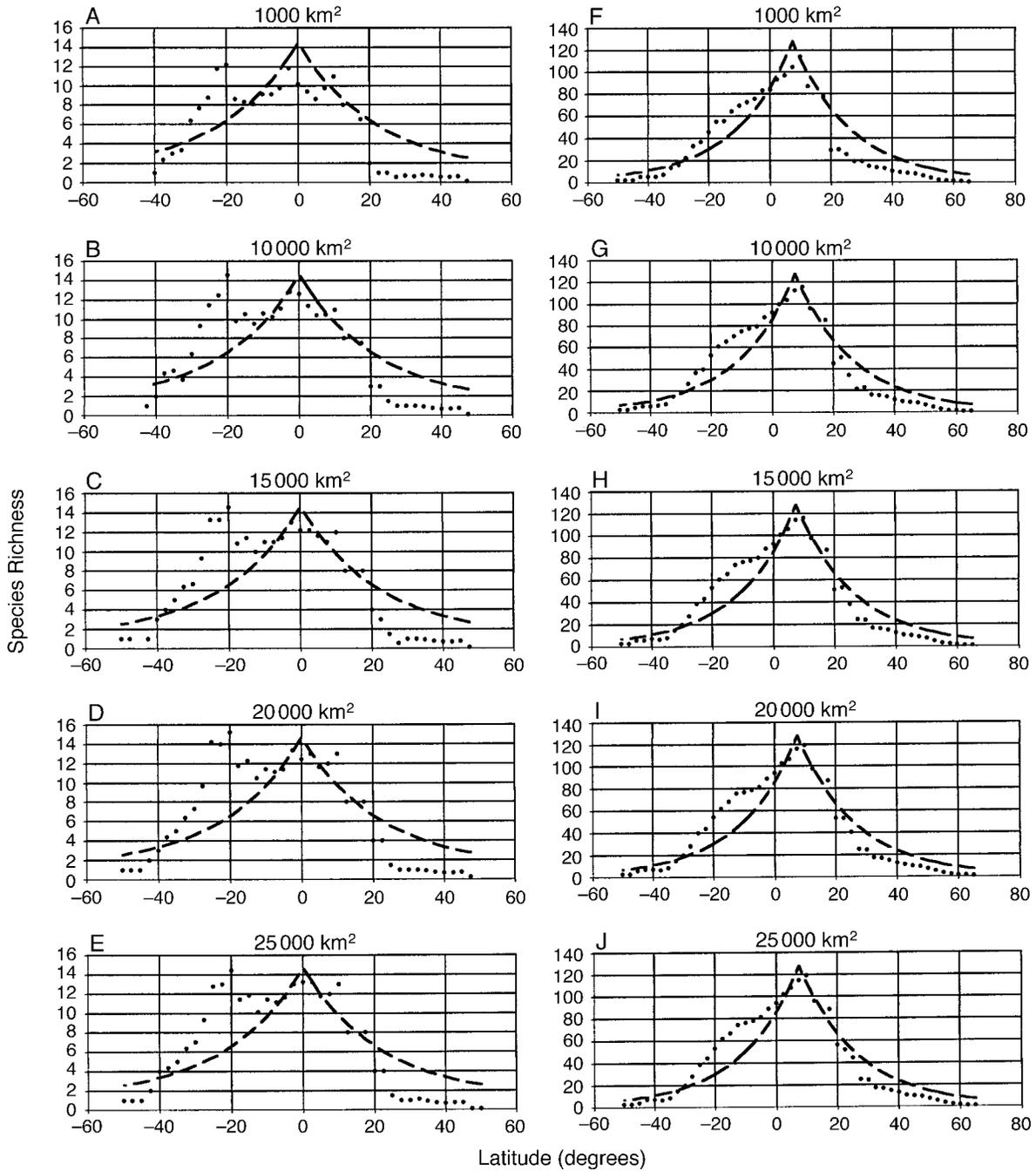
FIG. 3. Empirical (plotted points [dots]) and predicted (dashed line) relationships between species richness (*S*) and latitude (*L*) based on the simple additive model (see *Methods and materials: Data analysis* for details). Panels A–E and F–J represent the relationships at different spatial scales for marsupials and bats, respectively.

fects of scale on observed patterns before trying to quantify causal relationships.

Some studies have addressed the effect of quadrat size on species richness patterns by assuming an arithmetic relation between area and richness, and have concluded that differences did not affect broad patterns (Schall and Pianka 1978, Willig and Sandlin 1991,

Kaufman 1994, Kaufman and Willig 1998). However, all of these studies controlled for area either by dividing by area or by regression techniques. If the relationship with area is nonlinear (as it is in almost all ecological and biogeographic models of the way in which *S* increases with *A*), if the relation is at the asymptotic portion of the logistic relation discussed by S. M.

Scheiner, S. B. Cox, M. R. Willig, G. G. Mittelbach, C. Osenberg, and M. Kaspari, (*unpublished manuscript*), or if the rate of change of the relationship between area and species richness is changing, arithmetic methods are inadequate.

In an attempt to understand the effect of different quadrat sizes on richness patterns, Anderson and Marcus (1993) controlled for area by using species density (number of species per unit area) and found that density of Australian mammals increased with increasing quadrat size. They noted that species in areas of low density have large ranges, and that species with small ranges are aggregated. As a consequence, small changes in quadrat size can strongly affect areas of low density because the addition of one species can substantially change density, but will only weakly affect areas of high density. Although they attempted to determine the effect of quadrat size on gradients of species richness by systematically increasing quadrat size (Anderson and Marcus 1993), only the fact that richness increased in a nonlinear manner with increasing quadrat size was documented. Moreover, they controlled for area by dividing by a variable, quadrat area. Again, this assumes an arithmetic relationship between area and richness. No attempt was made to predict the way in which species richness patterns changed with quadrat size. Knowing that the value obtained for richness differs among quadrat sizes is not sufficient. Comparisons among studies are invalid if the effect of area is not consistent at all latitudes. Our study is the first attempt to model the effects of quadrat size on hemispheric patterns of species richness with the aim of quantifiable comparisons among studies.

Why are areal effects of minor importance?

For both bats and marsupials, neither C nor Z was significant in the simple model. Variation in area has an effect on richness no greater than that of chance alone. This appears contrary to the conventional wisdom concerning the importance of area in biogeographic studies of both terrestrial and insular biotas (for a summary, see Rosenzweig [1995]). A number of factors may conspire to produce this result. First, if biotas develop in such a manner as to produce groups of species with broadly coincident ranges (i.e., tropical faunas vs. temperate faunas), then quadrats centered in space should be more similar than expected by their different areas. Second, the smallest quadrat in our series may have been sufficiently large to have sampled most taxa in its regional species pool, but not large enough to sample multiple species pools. Essentially, if the relationship between S and A is a logistic function rather than a power function, then S is expected to attain an asymptotic value at some value of A. If the smallest quadrat in the series is close in size to this asymptotic value, then subsequent variation in S as a consequence of increasing A would be indistinguishable from chance. Third, published range maps are imperfect es-

timates of the actual ranges of species. Indeed, the accuracy of placement of the boundaries of species distributions is likely less than the linear dimensions of the largest quadrat (158 km on a side) in our series. For example, examination of distribution maps in Hall (1981) reveals considerable discrepancy between the actual localities at which specimens were found and the distribution drawn to encompass those ranges. In fact, the edges of species boundaries often are extrapolated to parallel political boundaries (for convenience) or those of published vegetation maps (for ecological reasons). As a consequence, the distributions of species may appear more coincident than is the case in reality. This would bias published range maps to minimize the variation in apparent species richness at some spatial scales, such as those used in this study.

Why are latitudinal effects of major importance?

The significance of latitudinal components (G and F) in the simple nonlinear model is a consequence of two empirical phenomena: a decrease in species richness away from the latitude of maximal richness, and symmetrical decreases in northern and southern directions (Fig. 3). Importantly, neither taxon attains maximal richness at the equator, but because we use L^* in our models, this does not constrain our interpretations in any manner. Nonetheless, the identity of the causal agents that are correlated with latitude (or more precisely, correlated with distance from midlatitudinal location in the domain of each taxon) remains elusive. However, the random placement of the geographic boundaries of species gives rise to symmetrical and unimodal distributions of species richness about the center of a distribution of a taxon (Colwell and Hurt 1994, Willig and Lyons 1998). Moreover, a significant proportion of the observed latitudinal variation in species richness of both marsupials and bats (based on latitudinal bands) was correlated with the predictions of a null model that was constrained only by continental boundaries rather than biological assumptions about latitudinal position (Willig and Lyons 1998). Hence, stochastic factors may play a large role in determining latitudinal patterns of species richness.

In reality, each species undoubtedly is limited by particular environmental constraints, whether they be abiotic (e.g., temperature, precipitation), biotic (e.g., competition, predation, parasitism), geographic (e.g., mountains, rivers), or historical (e.g., glacial positions during the Pleistocene). Moreover, different factors may operate in northern and southern portions of a species range (Kaufman 1995, Kaufman and Willig 1998). Within a larger taxon such as bats or marsupials, no single factor may attain hegemony in limiting the distribution of constituent species, and as a consequence, range boundaries may have a geographic distribution that is quite similar to those produced by chance, even though different deterministic factors account for the limitations of each species. In such a

chaotic scenario, unimodal distributions would be common and richness would tend to decrease in a symmetrical and monotonic fashion about a modal value (Willig and Lyons 1998).

The complex model

Inclusion of a term for scale dependence in the latitudinal gradient of species richness did not increase the coefficient of determination and indeed was nonsignificant. However, the same biases against detecting an areal effect may have reduced our power in detecting scale dependence as well. Although the interactive effect is nonsignificant, we suggest caution in interpreting-comparisons among studies without properly controlling for area, especially at scales smaller than those at which range maps are drawn. In an analogous study of the relationship between area (quadrat sizes on the order of square meters), productivity, and species diversity, Pastor et al. (1996) showed an interaction between area and productivity. Specifically, using the power function to model area, they showed that Z was negatively correlated and C was positively correlated with productivity. Moreover, they show in an elegant mathematical proof that the unimodal relationship between diversity and productivity can be derived from the interaction between area and productivity.

Future directions

Similar designs and analyses need to be conducted with other groups of organisms or at different spatial scales to asses the generality of our results. Moreover, different algorithms should be used in some circumstances to assess areal (e.g., exponential or logistic functions) or latitudinal (e.g., normal, parabolic) relationships. The composite model represented by Eq. 1 is sufficiently general to accommodate these approaches.

Comparison of the latitudinal gradient in species richness among studies that use different quadrat sizes can be meaningful and useful if the effects of area are additive and there is no interaction or scale effects. In such a scenario, area simply changes the position (elevation) of the relation between richness and latitude. Area would not affect the form of the latitudinal relation. Alternatively, if one wished to compare actual values of richness in studies of the latitudinal gradient that differ in quadrat size, then the parameters C and Z can be estimated using nonlinear regression, and be used to scale richness to equivalent areas.

The methodological approach in this paper is designed to assess the scale independence of area and latitude and has applicability to a wide variety of taxa, regardless of geographic domain. Although subsequent work needs to determine if gradients of species richness are independent of scale for groups of organisms other than New World bats and marsupials, these results indicate that differences in the quadrat sizes, at least between 1000 and 25 000 km^2, are relatively simple

and straightforward. However, because scale dependence has been found at smaller scales in an analogous study (Pastor et al. 1996), differences in area should be taken into consideration if reliable comparisons among studies at scales smaller than our smallest quadrat are to be made.

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