

Latitudinal patterns of mammalian species richness in the New World: the effects of sampling method and faunal group

DAWN M. KAUFMAN* and MICHAEL R. WILLIG *Ecology Program, Department of Biological Sciences and The Museum, Texas Tech University, Lubbock, Texas 79409-3131, U.S.A.*

Abstract. Although the latitudinal gradient of species richness for mammals in North America is well documented, few investigators have quantified the relationship in South America. We examined the pattern in North and South America, at two spatial scales (2.5° and 5°) for each of two sampling methods (quadrats and latitudinal bands). A scale effect was evident for quadrats but not for bands. Significant linear relationships between species richness and latitude were found for three faunal groups: all mammals, nonvolant species, and bats. Effects of area confound the latitudinal relationship. By statistically removing such effects, we found that the latitudinal gradient is not an artifact of the species-area relationship, and that the latitudinal gradients for

North and South America were statistically indistinguishable. Our data suggest that both faunal subgroups, nonvolant species and bats, contributed substantially to the overall mammalian pattern. Further, multiple regression analyses showed that only latitude is a necessary variable to explain bat richness; for nonvolant species, in addition to latitude, area and longitude may be important.

Key words. Latitudinal gradient, species diversity, macroecology, area, mammals, bats, North and South America.

INTRODUCTION

Biogeography is the study of the distribution of organisms in space and time (Cox, Healey & Moore, 1976). Much research has focused on patterns of organismal distribution, including work on the pattern of species distribution on island systems (island biogeography), species distribution within continents (those dealing with latitude, longitude, and elevation), and other aspects of areography or macroecology. The ubiquity of the latitudinal gradient of species richness (an inverse relationship) has led ecologists to attempt to identify the features or properties of the tropics that cause high species richness. Clearly, a plethora of taxonomic groups exhibit a latitudinal pattern (Fischer, 1960; Cook, 1969; Kiester, 1971; Rabinovich & Rapoport, 1975; Schall & Pianka, 1978). Mammals are no exception. Simpson (1964) quantitatively documented the latitudinal gradient for North American mammals, and was among the first, along with MacArthur (1965), to demonstrate that species diversity is greatest in the tropics. Although species richness of various mammalian groups repeatedly has been shown to vary inversely with latitude, the form of the relationship has not been consistent (Simpson, 1964; Wilson, 1974; McCoy & Connor, 1980; Mares & Ojeda, 1982; Willig & Selcer, 1989; Arita, Robinson & Redford, 1990; Currie, 1991; Meserve, Kelt & Martinez, 1991; Pagel, May & Collie,

1991; Willig & Sandlin, 1991; Mares, 1992; Kaufman, 1995; Willig & Gannon, 1997).

Several theories have been developed to explain the latitudinal gradient, including the different ages of systems, spatial heterogeneity, competition, predation, climatic stability, and productivity (see Pianka, 1966; Rohde, 1992; Rosenzweig, 1992, 1995). More recently, Rosenzweig & Abramsky (1993) suggested that the relationship of diversity to productivity must be considered in the evaluation of the latitudinal gradient; they contended that competition for resources or environmental heterogeneity most likely produces the latitudinal gradient. Kaufman (1995) suggested that the pattern is due to a trade-off between the effects of abiotic factors and biotic interactions. Rosenzweig has championed area as the driving factor that affects latitudinal gradients (Rosenzweig, 1992, 1995; Rosenzweig & Sandlin, 1997). At the same time, Colwell & Hurtt (1994), as well as Willig & Lyons (1998), have claimed that stochastic processes can generate gradients of richness with maxima in the tropics. Consensus is elusive concerning the driving factor or factors that cause the latitudinal gradient in diversity.

A number of sampling strategies can be used to quantify latitudinal gradients. We have taken an approach that makes our results comparable to those of other studies and that makes biological sense. First, we examined mammals not only as a single taxon, but in two faunal subgroups, bats and nonvolant species. In part, this was done to determine if bats contribute disproportionately to the overall

*Present address. Department of Biology, 167 Castetter Hall, University of New Mexico, Albuquerque, New Mexico 87131-1091, U.S.A.

mammalian pattern, as has been suggested previously (Fleming, 1973; Wilson, 1974; McCoy & Connor, 1980). Second, we examined North and South America, whereas most studies in the New World have been confined to North America. It is counterproductive to question why the tropics is the richest region, while limiting analyses to North America, which does not encompass the main breadth of the tropics. Moreover, two continents provide replication. Finally, researchers (e.g. McCoy & Connor, 1980; Willig & Selcer, 1989) have debated which sampling methodology, quadrats or bands, are better units with which to measure species density or species richness. We have utilized both methods, as suggested by Willig & Sandlin (1991), in an attempt to measure different aspects of diversity.

Although species richness is negatively correlated with latitude, latitude is not directly the cause of the pattern. Latitude likely is a surrogate for another factor or set of factors (e.g. the input of solar radiation). The effects of other, possibly confounding, aspects (e.g. area) of the physical template must be controlled to isolate the effects of latitude on species richness. Species-area relationships are well-documented (MacArthur & Wilson, 1967; Gilbert, 1980; Coleman *et al.*, 1982; Rosenzweig, 1992) and may confound latitudinal patterns. For North America, Pagel *et al.* (1991) attempted to minimize this effect by dividing the number of taxa at a particular latitude by the length of that latitude to produce a taxon per space metric. The inherent problem with this approach is that area and species richness are assumed to have a one-to-one relationship. Previous work on the species-area relationship has shown that species richness scales to area at a rate of less than one (e.g. Rosenzweig, 1995). In other words, if a sampling area is increased ten-fold in size, it is likely that the number of species present will increase, but at a rate less than ten-fold. Thus, Pagel *et al.* (1991) overcompensated for the lack of species in bands of small area and underestimated richness in bands of large area. A two-fold procedure can overcome this problem. First, by examining South America as well as North America, as suggested by Willig and colleagues (Willig & Selcer, 1989; Willig & Sandlin, 1991; Willig & Gannon, 1997), the effect of the continental shape with respect to the equator is balanced, because the majority of area in North America is in the temperate zone (high latitudes) and the majority of area in South America is within the tropics (low latitudes). Second, use of an appropriate statistical approach, such as an analysis of covariance, controls for the linear effect of area in latitudinal analyses of richness.

For conceptual and empirical reasons, we restricted our analyses to the linear effects of area on richness. The positive association between species richness and area is almost universally recognized. Nonetheless, considerable controversy has surrounded the form of the relationship (Connor & McCoy, 1979; Gilbert, 1980; Coleman *et al.*, 1982; Willig & Selcer, 1989; Willig & Sandlin, 1991; Rosenzweig, 1992; Gotelli & Graves, 1996). Indeed, linear and higher order equations, as well as semi-logarithmic and log-log plots (Connor & McCoy, 1979), have been used to characterize the relationship between species richness and area. The form of the relation may be taxon-specific and scale-dependent, and differ between island and continental

systems. However, in quadrat and band analyses at the continental or hemispheric level, area has been shown to have linear (Mares & Ojeda, 1982) or nonsignificant (Willig & Selcer, 1989) effects on species richness. As a consequence, we considered linear controls for areal effects to be simple first approximations in the absence of strong and consistent conceptual or empirical data to the contrary.

METHODS

Our study was based on distributional data in the literature (see Kaufman, 1994) for all known mammals (1418 total species) found in contiguous North and South America, including peninsulas, but excluding offshore islands (Fig. 1). Distribution maps of mammals were plotted manually on gridded projections of North and South America. Because bats may be responsible for the mammalian latitudinal gradient in the New World (Fleming, 1973; Wilson, 1974; McCoy & Connor, 1980), we categorized species richness of all mammals into two faunal subgroups: bats (255 species) and nonvolant mammals (1163 species). We followed the mammalian classification of Wilson & Reeder (1993). Species richness was analysed for sampling units consisting of both bands or quadrats to determine if each type of data was consistent or provided unique insight. Simple regression analyses quantified the effect of latitude on absolute and area-controlled richness. Multiple regression techniques allowed an assessment of the possible importance of other physical factors besides latitude (i.e., area and longitude). In all cases, absolute values of latitude were analysed (e.g. $10^\circ = 10^\circ\text{N} = 10^\circ\text{S}$).

Quadrats

Species richness, area, mid-latitude, and mid-longitude were measured for quadrats of two sizes (Fig. 1), with four small quadrats ($2.5^\circ \times 2.5^\circ$) nested within large quadrats ($5^\circ \times 5^\circ$). There were 220 large quadrats and 738 small quadrats. Land area was estimated with a compensating polar planimeter from an equal area projection. Quadrats that contained too little land area to be estimated precisely using a planimeter were not used in analyses; consequently, the smallest quadrats used in analyses were 65 km² and 72 km², respectively, for analyses of 2.5° and 5° quadrats. Quadrats north and west of the isthmus of Panama were considered to be part of North America, whereas quadrats south and east were considered to be part of South America (Fig. 1).

Latitudinal bands

Species richness, area, and mid-latitude were measured for latitudinal bands of both 5° and 2.5° widths, with 2.5° bands nested within 5° bands (Fig. 1). There were twenty-six 5° -bands and fifty-one 2.5° -bands. Area was assessed in the same manner for bands as for quadrats. Bands south of 10°N were considered part of South America, whereas bands north of 10°N were considered part of North America (Fig. 1).

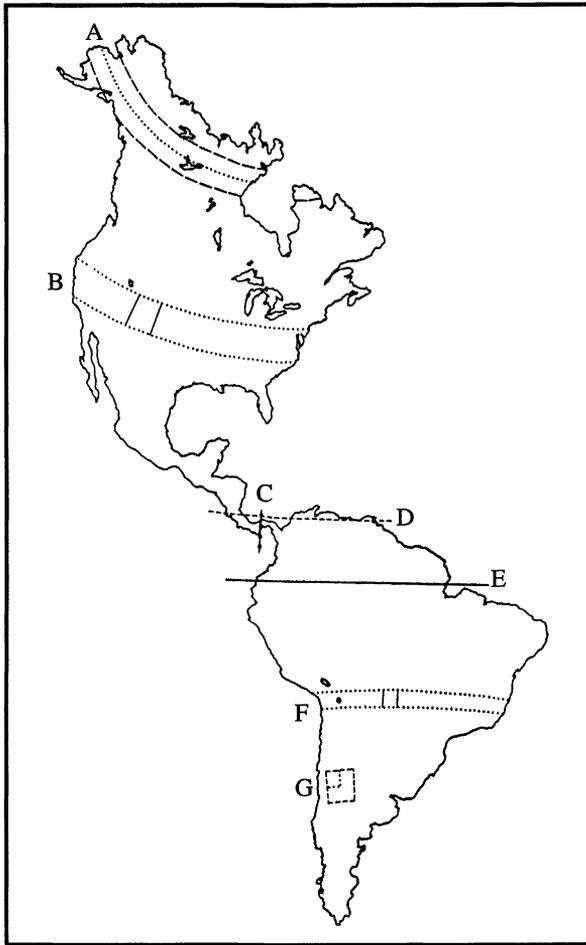


FIG. 1. Equal area projection of the Americas. The equator is a solid line in northern South America (E). The vertical line with dots (C) across the isthmus of Panama delineates the division of North and South America for quadrats. For bands, the horizontal dashed line (D) crossing southernmost North America and northernmost South America divides the continents. The equal area projection shows examples of the nested relationship of sampling methods (quadrats and bands) and scales (2.5° and 5°). In northern North America, a 5° band (bordered by dashed lines) is divided into two 2.5° bands (with a dotted line, A). In central North America, a 5° quadrat (solid vertical lines) is shown within a 5° band (dotted lines, B). In central South America, a 2.5° quadrat (solid vertical lines) is shown within a 2.5° band (dotted lines, F). Finally, in southern South America, a 2.5° quadrat (dotted lines), of which there would be four, is delineated inside a 5° quadrat (bordered by dashed lines, G).

Statistical analyses

All statistical analyses were conducted using SPSSX (SPSS, 1988). Simple linear regression analyses (procedure REGRESSION) between species richness and latitude were conducted separately for all combinations of sampling method and scale (2.5° bands, 5° bands, 2.5° quadrats, and 5° quadrats) and continent (North and South America). Each faunal group (bats, nonvolant species, and all mammals) was analyzed individually. Relationships were considered significant if $P \leq 0.05$; marginal significance ($0.10 \geq P > 0.05$) was not used in any of the regression

analyses because we only wanted to consider strong relationships, especially in light of the nature of our multiple comparisons. If relationships were not significantly different for North and South America based on tests of equality of slope and intercept, data were pooled and analyses performed for the entire New World.

Simple linear regression analyses of species richness as a function of latitude were performed after controlling for the linear influence of area. Analyses paralleled those for absolute species richness. Specifically, simple linear regression analyses were performed between species richness and area (for North and South America together), and residuals saved. Residuals were analyzed for a relationship with latitude (separately for North and South America). This procedure removed the linear effects of area on species richness, and thus allowed evaluation of a latitudinal pattern that was not confounded by the linear effects of area. If the area-controlled relationships (regression slope and intercept) were not significantly different between the two continents, data were combined and analyses were performed for the pooled area-controlled data.

In the case of absolute or area-controlled analyses of species richness, and for quadrats and bands separately, a series of continental, faunal, and scale comparisons were conducted. First, comparisons of simple linear regression parameters (intercepts or slopes) between continents (North America and South America) were done separately for each combination of faunal group and scale. Similarly, comparisons of regression parameters between faunal subgroups (nonvolant species and bats) were done separately for each combination of continent and scale. Finally, comparisons of regression parameters between scales (2.5° and 5°) were done separately for each combination of continent and faunal group. In all three cases, we considered parameters to be significantly different if their 95% confidence intervals did not overlap. As a consequence, experiment-wise error was greater than 0.05: each parameter pertaining to all mammals was involved in two pairwise comparisons (EWER = 0.10), and each parameter pertaining to nonvolant species and bats was involved in three pairwise comparisons (EWER = 0.14). For heuristic purposes, this allowed us to detect potentially important factors which might affect latitudinal gradients. Moreover, type II errors are reduced; we are more confident that the failure to detect significance in our analyses is not a consequence of low power. In other words, if we failed to find differences, we are confident that gradients were consistent.

Multiple regression analyses were performed to determine which physical factors best explained species richness. Possible factors included latitude, area, and longitude for quadrats, and latitude and area for bands. Two techniques were employed. The first was a stepwise procedure (SPSS, 1988), in which variables were assessed for inclusion or exclusion at each step of the algorithm. For the second procedure, area initially was forced into the equation and then the analyses proceeded in a stepwise fashion, as before. These analyses were completed for both scales of quadrats and bands, for all faunal groups, and for North and South America individually and for the pooled New World. Because we were interested in significant relationships that

TABLE 1. Descriptive statistics (mean, maximum, and minimum) are presented for species richness of each faunal group, corresponding to each sampling method and scale, for each continent. For mean values (\pm SE) of the number of species, the number of quadrats or bands is given in parentheses for each continent. For maximum and minimum values, the coordinates are given in parentheses (mid-latitude and mid-longitude for quadrats and mid-latitude for bands). The maxima and minima are selected for all mammals and decomposed into number of nonvolant species and bats. If there was a more extreme value for either nonvolant species or bats elsewhere, that has been indicated in the table by a superscript, with the more extreme values (and coordinates of the quadrat or band) reported below the table.

	North America			South America		
	Mean \pm SE	Maximum	Minimum	Mean \pm SE	Maximum	Minimum
2.5° Quadrats	(<i>n</i> = 468)	(18.75°N \times 98.75°W)	(61.25°N \times 76.25°W)	(<i>n</i> = 270)	(1.25°N \times 76.25°W)	(48.75°S \times 66.25°W)
All Mammals	62.6 \pm 1.7	218	15	146.9 \pm 3.7	283	26
Nonvolants	50.6 \pm 0.9	130	15	81.8 \pm 1.6	159	24
Bats	12.0 \pm 0.9	88 ^a	0	65.1 \pm 2.3	124 ^b	2 ^c
5° Quadrats	(<i>n</i> = 140)	(17.5°N \times 97.5°W)	(62.5°N \times 77.5°W)	(<i>n</i> = 80)	(2.5°S \times 77.5°W)	(52.5°S \times 67.5°W)
All Mammals	74.1 \pm 4.1	259	15	170.8 \pm 8.1	319	28
Nonvolants	58.7 \pm 2.4	150	15	99.2 \pm 4.1	189	26
Bats	15.5 \pm 2.1	109	0	71.6 \pm 4.6	130 ^d	2
2.5° Bands	(<i>n</i> = 25)	(11.25°N)	(71.25°N)	(<i>n</i> = 26)	(13.75°S)	(53.75°S)
All Mammals	164.9 \pm 16.2	312	34	253.9 \pm 29.2	416	29
Nonvolants	123.7 \pm 9.9	168 ^e	34	172.8 \pm 17.7	284	28
Bats	42.2 \pm 8.5	144	0	81.1 \pm 12.3	132 ^f	1
5° Bands	(<i>n</i> = 13)	(12.5°N)	(72.5°N)	(<i>n</i> = 13)	(2.5°S)	(52.5°S)
All Mammals	185.6 \pm 29.3	344	34	280.9 \pm 46.3	457	42
Nonvolants	140.8 \pm 18.0	193 ^g	34	194.8 \pm 28.9	317	38
Bats	44.8 \pm 13.9	151	0	86.1 \pm 18.3	140 ^h	4

^aMaximum richness of bats for 2.5° quadrats in North America was 103 at 11.25°N \times 83.75°W.

^bMaximum richness of bats for 2.5° quadrats in South America was 130 at 8.75°N \times 68.75°W.

^cMinimum richness of bats for 2.5° quadrats in South America was 1 at 53.75°S \times 71.25°W.

^dMaximum richness of bats for 5° quadrats in South America was 138 at 7.5°N \times 72.5°W and 7.5°N \times 67.5°W.

^eMaximum richness of nonvolant species for 2.5° bands in North America was 195 at 36.25°N.

^fMaximum richness of bats for 2.5° bands in South America was 165 at 1.25°N.

^gMaximum richness of nonvolant species for 5° bands in North America was 214 at 37.5°N.

^hMaximum richness of bats for 5° bands in South America was 171 at 7.5°N.

accounted for appreciable variation in species richness, we further limited the multiple regression procedures so that selected variables had a unique contribution to R^2 of at least 5% (Willig & Selcer, 1989; Willig & Sandlin, 1991).

RESULTS

Comparison of descriptive statistics (mean, maximum, and minimum) showed that species richness for North America was less than that for South America (Table 1). Richness ranged from 15 to 218 (2.5° quadrats) and from 34 to 344 mammalian species (5° bands) for North America, whereas the ranges were 26 to 283 and 42 to 457 mammalian species, respectively, for 2.5° quadrats and 5° bands for South America. Richness increased as sample area increased (2.5° quadrats < 5° quadrats < 2.5° bands < 5° bands). Richness of nonvolant mammals was greater than that of bats, and often did not reach maximum richness at the same latitude. The latitude at which richness peaked for all mammals corresponded to that of at least one the faunal subgroups (Table 1).

Regression analyses revealed highly significant relationships (i.e., slopes \neq 0) between species richness and

latitude for absolute (Tables 2–3) and area-controlled data (Tables 2–4). This was true for data collected in quadrats or in bands (for either scale) across either continent, regardless of faunal group. In addition, all multiple regression analyses resulted in significant equations between species richness and one or more physical variables, which always included latitude (Tables 5–6).

Linear regression analyses of absolute richness

Quadrats

When continental comparisons of the species-latitude relationship were made, differences between North and South America occurred in all cases except for species richness of nonvolants in 5° quadrats (Table 2). Continental differences were found with regard to slope and intercept for all mammals and bats, at both scales of quadrat, whereas only a difference in slope was found for nonvolant species in 2.5° quadrats. The amount of variation in species richness in each of the faunal groups explained by the variation in latitude (R^2) was similar in North America and South America.

TABLE 2. Estimates of parameters (\pm SE) from simple regression analyses of absolute species richness and latitude, and area-controlled species richness and latitude, for 2.5° and 5° quadrats. All regressions were significant ($P \leq 0.001$). Intercepts and slopes were tested for differences between continents, holding faunal group and scale constant; therein, parameters sharing the same alphabetic superscript are statistically indistinguishable ($P \leq 0.05$). Pairwise comparisons of faunal subgroup and scale are not shown.

		Absolute richness			Area-controlled richness		
		R^2	Intercept	Slope	R^2	Intercept	Slope
All mammals							
2.5°	North America	0.70	165.0 \pm 3.3 ^a	-2.10 \pm 0.07 ^c	0.26	46.5 \pm 4.7 ^a	-1.16 \pm 0.09 ^c
	South America	0.72	210.9 \pm 3.1 ^b	-3.80 \pm 0.15 ^d	0.38	59.3 \pm 4.2 ^a	-2.49 \pm 0.20 ^d
5°	North America	0.69	198.0 \pm 7.5 ^a	-2.56 \pm 0.15 ^c	0.49	80.8 \pm 9.2 ^a	-2.05 \pm 0.18 ^c
	South America	0.62	243.0 \pm 8.1 ^b	-4.16 \pm 0.37 ^d	0.38	83.2 \pm 9.3 ^a	-2.93 \pm 0.42 ^c
Nonvolant species							
2.5°	North America	0.51	99.4 \pm 2.3 ^a	-1.00 \pm 0.05 ^c	0.28	26.0 \pm 2.2 ^a	-0.57 \pm 0.04 ^c
	South America	0.44	103.8 \pm 1.9 ^a	-1.31 \pm 0.09 ^d	0.17	15.4 \pm 2.1 ^b	-0.71 \pm 0.10 ^c
5°	North America	0.50	120.2 \pm 5.5 ^a	-1.27 \pm 0.11 ^c	0.45	42.3 \pm 4.7 ^a	-0.99 \pm 0.09 ^c
	South America	0.35	126.5 \pm 5.4 ^a	-1.57 \pm 0.25 ^c	0.16	24.7 \pm 5.1 ^a	-0.89 \pm 0.23 ^c
Bats							
2.5°	North America	0.65	65.6 \pm 1.9 ^a	-1.10 \pm 0.04 ^c	0.16	20.5 \pm 3.2 ^a	-0.59 \pm 0.06 ^c
	South America	0.79	107.1 \pm 1.7 ^b	-2.49 \pm 0.08 ^d	0.45	43.9 \pm 2.6 ^b	-1.78 \pm 0.12 ^d
5°	North America	0.68	77.9 \pm 3.9 ^a	-1.29 \pm 0.08 ^c	0.39	38.5 \pm 5.8 ^a	-1.07 \pm 0.11 ^c
	South America	0.76	116.5 \pm 3.7 ^b	-2.58 \pm 0.17 ^d	0.51	58.5 \pm 5.1 ^a	-2.05 \pm 0.23 ^d

TABLE 3. Estimates of parameters (\pm SE) from simple regression analyses of absolute species richness and latitude, and area-controlled species richness and latitude, for 2.5° and 5° bands. All regressions were significant ($P \leq 0.001$). Intercepts and slopes were tested for differences between continents, holding faunal group and scale constant; therein, parameters sharing the same alphabetic superscript are statistically indistinguishable ($P \leq 0.05$). Pairwise comparisons of faunal subgroup and scale are not shown.

		Absolute richness			Area-controlled richness		
		R^2	Intercept	Slope	R^2	Intercept	Slope
All mammals							
2.5°	North America	0.91	338.3 \pm 12.2 ^a	-4.02 \pm 0.27 ^c	0.86	190.0 \pm 21.7 ^a	-5.72 \pm 0.48 ^c
	South America	0.93	456.4 \pm 13.9 ^b	-8.43 \pm 0.47 ^d	0.85	170.6 \pm 13.3 ^a	-5.26 \pm 0.45 ^c
5°	North America	0.97	412.2 \pm 13.7 ^a	-5.33 \pm 0.30 ^c	0.82	225.6 \pm 41.4 ^a	-6.39 \pm 0.89 ^c
	South America	0.92	502.4 \pm 23.9 ^b	-9.21 \pm 0.82 ^d	0.83	186.7 \pm 23.3 ^a	-5.85 \pm 0.80 ^c
Nonvolant species							
2.5°	North America	0.58	208.9 \pm 16.3 ^a	-2.06 \pm 0.36 ^c	0.83	106.7 \pm 13.6 ^a	-3.20 \pm 0.30 ^c
	South America	0.84	289.0 \pm 12.6 ^b	-4.84 \pm 0.43 ^d	0.65	83.5 \pm 10.7 ^a	-2.46 \pm 0.37 ^c
5°	North America	0.80	267.5 \pm 20.8 ^a	-2.98 \pm 0.45 ^c	0.83	135.3 \pm 24.3 ^a	-3.79 \pm 0.52 ^c
	South America	0.84	327.1 \pm 21.2 ^a	-5.50 \pm 0.73 ^d	0.66	96.2 \pm 18.6 ^a	-2.93 \pm 0.63 ^c
Bats							
2.5°	North America	0.85	129.4 \pm 8.4 ^a	-2.14 \pm 0.19 ^c	0.76	83.3 \pm 13.3 ^a	-2.52 \pm 0.30 ^c
	South America	0.96	167.4 \pm 4.6 ^b	-3.59 \pm 0.16 ^d	0.90	87.1 \pm 5.6 ^a	-2.80 \pm 0.19 ^c
5°	North America	0.84	144.7 \pm 14.7 ^a	-2.35 \pm 0.32 ^c	0.72	90.3 \pm 23.0 ^a	-2.60 \pm 0.49 ^c
	South America	0.96	175.3 \pm 6.9 ^a	-3.71 \pm 0.24 ^d	0.90	90.4 \pm 8.5 ^a	-2.92 \pm 0.29 ^c

TABLE 4. Estimates of parameters (\pm SE) from simple regression analyses of area-controlled species richness and latitude, with data pooled for North and South America, for 2.5° and 5° bands. All regressions were significant ($P \leq 0.001$).

	2.5° bands			5° bands		
	R^2	Intercept	Slope	R^2	Intercept	Slope
All mammals	0.88	176.9 \pm 11.1	-5.45 \pm 0.29	0.84	196.4 \pm 20.3	-5.90 \pm 0.52
Nonvolant species	0.79	92.8 \pm 8.1	-2.86 \pm 0.21	0.78	109.1 \pm 13.9	-3.28 \pm 0.36
Bats	0.85	84.1 \pm 6.0	-2.59 \pm 0.16	0.81	87.4 \pm 9.9	-2.63 \pm 0.26

TABLE 5. Significant parameters (indicated by 'X'), and total R^2 , from multiple regression analyses completed between species richness and latitude (LA), area (A), and longitude (LO), for 2.5° and 5° quadrats. Analyses were completed in a completely stepwise fashion (Stepwise) or with area initially forced into the equation and subsequent stepwise method (Area-forced). All regressions were significant ($P \leq 0.001$).

	North America								South America								New World							
	Stepwise				Area-forced				Stepwise				Area-forced				Stepwise				Area-forced			
	LA	A	LO	R^2	LA	A	LO	R^2	LA	A	LO	R^2	LA	A	LO	R^2	LA	A	LO	R^2	LA	A	LO	R^2
All mammals																								
2.5°	X		X	0.76	X	X	X	0.77	X			0.72	X	X		0.73	X			0.80	X	X		0.81
5°	X		X	0.74	X	X	X	0.78	X			0.68	X	X		0.68	X			0.77	X	X		0.80
Nonvolant species																								
2.5°	X	X	X	0.71	X	X	X	0.71	X	X		0.51	X	X		0.51	X	X	X	0.74	X	X	X	0.74
5°	X	X	X	0.75	X	X	X	0.75	X	X	X	0.58	X	X	X	0.58	X	X	X	0.75	X	X	X	0.75
Bats																								
2.5°	X			0.65	X	X		0.67	X			0.78	X			0.78	X			0.80	X			0.80
5°	X			0.68	X			0.68	X			0.75	X			0.75	X			0.80	X			0.80

TABLE 6. Significant parameters (indicated by 'X'), and total R^2 , from multiple regression analyses completed between species richness and latitude (LA) and area (A), for 2.5° and 5° bands. Analyses were completed in a completely stepwise fashion (Stepwise) or with area initially forced into the equation and subsequent stepwise method (Area-forced). All regressions were significant ($P \leq 0.001$).

	North America						South America						New World											
	Stepwise			Area-forced			Stepwise			Area-forced			Stepwise			Area-forced								
	LA	A	R^2	LA	A	R^2	LA	A	R^2	LA	A	R^2	LA	A	R^2	LA	A	R^2						
All mammals																								
2.5°	X		0.91	X	X	0.93	X		0.93	X	X	0.94	X	X	0.93	X	X	0.93	X	X	0.93	X	X	0.93
5°	X		0.97	X	X	0.97	X		0.92	X		0.92	X		0.87	X	X	0.87	X	X	0.87	X	X	0.91
Nonvolant species																								
2.5°	X	X	0.78	X	X	0.78	X		0.84	X	X	0.89	X	X	0.87	X	X	0.87	X	X	0.87	X	X	0.87
5°	X	X	0.88	X	X	0.88	X		0.84	X		0.84	X	X	0.88	X	X	0.88	X	X	0.88	X	X	0.88
Bats																								
2.5°	X	X	0.93	X	X	0.93	X		0.96	X		0.96	X		0.88	X			0.88	X				0.88
5°	X	X	0.93	X	X	0.93	X		0.96	X		0.96	X		0.87	X			0.87	X				0.87

Scale differences were found in all but one case (bats in South America). Scale effects were due to intercept differences only for all mammals in South America, for nonvolant species for both continents, and for bats in North America. Slope and intercept differences were found for all mammals in North America. Magnitudes of R^2 were similar at either scale (Table 2).

Differences between nonvolant species and bats occurred in all cases. In North America, faunal differences in the species-latitude relationship were due only to intercept, whereas faunal differences were due only to slope in South America. A tighter-fitting relationship between richness and latitude was found for bats than for nonvolant species, with values for all mammals being intermediate (Table 2).

Latitudinal bands

Species-latitude relationships for each faunal group differed between North and South America at each spatial scale (Table 3). Differences in slope and intercept were found for

all mammals at both scales (but see Fig. 2A and 2C) and for nonvolant species and bats in 2.5° bands. Only differences in slope occurred for nonvolant species and bats in 5° bands. Within each faunal group, R^2 -values were similar for North America and South America.

Scale differences were evident in only one case, for all mammals in North America. Generally, similar amounts of variation in species richness were explained by latitude at both scales (Table 3).

Differences in species-latitude relationships between nonvolant species and bats occurred at both scales and for both continents. Faunal differences between nonvolant species and bats were due to intercept for both scales of band in North and South America; in addition, differences in intercept were found for 2.5° bands in South America (but see Fig. 2B and 2D for pooled data from the New World). The fit of species richness data to latitudinal relationships was better for bats than for nonvolant species, and best overall for all mammals (Table 3).

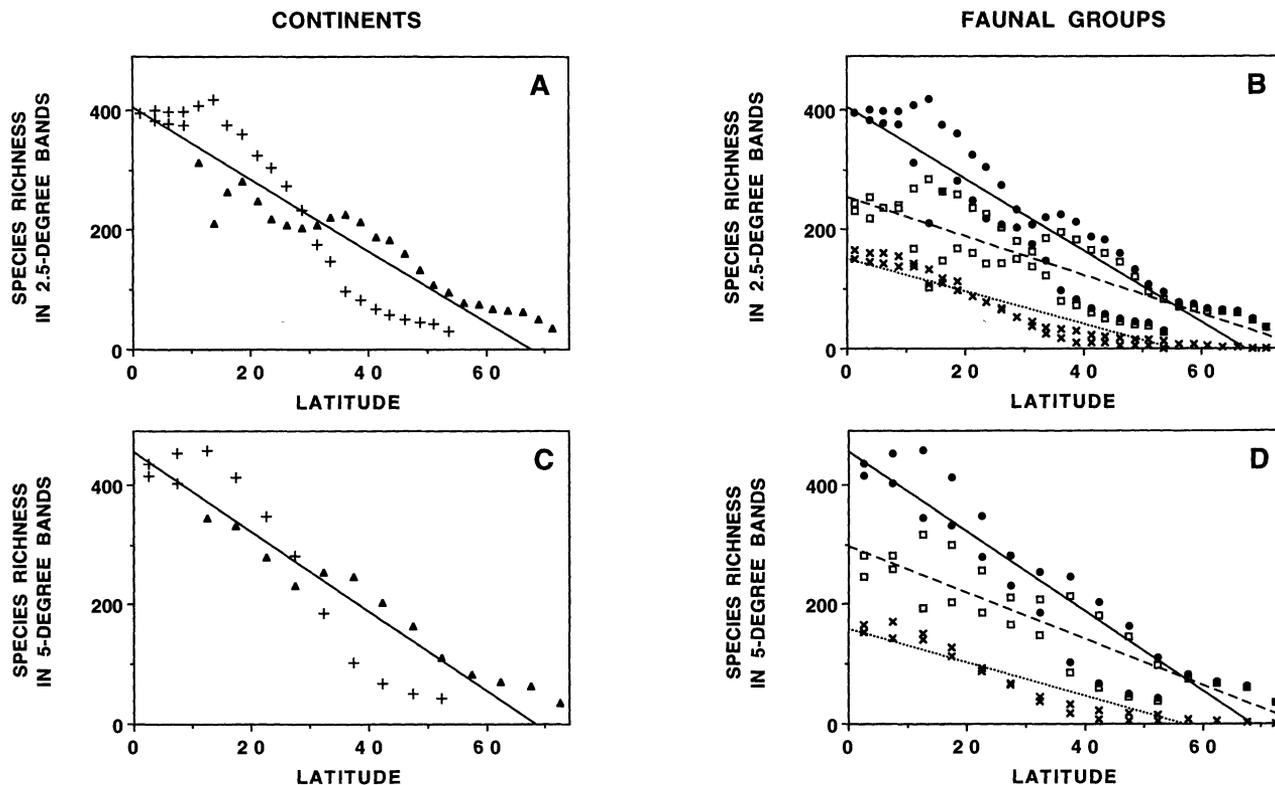


FIG. 2. Absolute species richness for bands. The upper graphs (A and B) represent species richness in 2.5° bands, whereas the lower graphs (C and D) represent species richness in 5° bands. Graphs on the left (A and C) show species richness by continent; filled triangles represent bands in North America and pluses represent bands in South America. Graphs on the right (B and D) show species richness by faunal group; filled circles represent all mammals (regression, a solid line), open squares are nonvolant species (regression, a dashed line), and Xs are bats (regression, a dotted line).

Quadrats versus latitudinal bands

Latitude significantly affected species richness in all analyses (Tables 2–3). Continental comparisons for quadrats and bands produced qualitatively similar results for all mammals and for bats. For nonvolants, there were fewer differences in continental comparisons of regressions for quadrats (slope differences only for 2.5° quadrats and no differences for 5° quadrats) than for bands (intercept and slope differences for 2.5° bands and slope differences only for 5° bands).

Scale comparisons for quadrats and bands generally produced qualitatively different results. The only exceptions were for all mammals within North America (scale differences were found in both intercept and slope for both quadrats and bands) and for bats within South America (no differences were found for either quadrats or bands). Otherwise, only intercept differences in regression equations between scales were found for quadrats, and no differences were found for different scales of bands.

Faunal differences were qualitatively similar for quadrats and bands within North America. When regression equations of richness and latitude were compared between nonvolant species and bats for both scales of quadrats and bands, only differences in intercept were found. Conversely, faunal differences were different for quadrats and bands within South America. Both scales of quadrats revealed significant differences in slope for faunal comparisons of

regressions, whereas both scales of bands revealed intercept differences, and 5° bands had slope differences as well.

Linear regression analyses of area-controlled richness

Our latitudinal analyses controlled for the linear effects of area on species richness. Nonetheless, R^2 -values based on semi-logarithmic relations between species and area were at best only slightly better ($\Delta R^2 = 0.03$) than those based on arithmetic relationships. More importantly, the arithmetic relation was superior to the semi-logarithmic relation for most analyses and was sometimes much better ($\Delta R^2 = 0.19$).

Quadrats

Continental comparisons of regression equations of species-area residuals and latitude revealed differences between North and South America in four of six cases; no differences were found in 5° quadrats for all mammals or nonvolant species (Table 2). Significant differences were found for all continental comparisons of 2.5° quadrats (differences in slope for all mammals, intercept for nonvolant species, and both intercept and slope for bats) and for continental comparisons of bats in 5° quadrats (differences in slope). Although R^2 -values for relationships between area-controlled richness and latitude were similar for North and

South America, they were low overall for area-controlled richness as compared to absolute richness (Table 2).

Scale differences were found in intercept and slope for all mammals, nonvolant species, and bats in North America. In contrast, no scale differences were revealed for any faunal group in South America. There were scale differences in the tightness of fit for relationships in North America; R^2 -values were consistent between scales of quadrats for each faunal group in South America (Table 2).

No faunal differences in regression equations were revealed between nonvolant species and bats for North America, whereas intercept and slope differences were found for both 2.5° and 5° quadrats in South America. For North America, regressions of nonvolant richness had higher R^2 -values than did those for bats; the reverse occurred in South America (Table 2).

Latitudinal bands

Analyses of species-latitude relationships revealed no differences between North and South America for any faunal group or any scale (Table 3). Therefore, relationships between area-controlled richness and latitude were pooled across continents (Table 4). When pooled data were examined, no scale differences were found for any faunal group, and no faunal differences were found between nonvolant species and bats when examined at either scale. (This also was true of unpooled continental data.) R^2 -values for species-latitude relationships were universally high for area-controlled richness data from bands (from 0.78 to 0.88; Table 4).

Quadrats versus latitudinal bands

In all area-controlled analyses, richness increased significantly with latitude (Tables 2–4). Generally, results from continental comparisons based on quadrats and bands were qualitatively dissimilar. Most continental comparisons for quadrats revealed differences between North and South America. In contrast, no statistically distinguishable differences existed between continents after controlling for area.

The effects of scale on area-controlled species-latitude relationships differed between quadrats and bands. For quadrats, scale differences always were found in regression equations (both intercept and slope) for North America, whereas no significant scale differences existed in equations for South America. However, for bands, there were no scale differences in species-latitude relationships for either continent.

Faunal comparisons of area-controlled data differed between quadrats and bands. For quadrats in North America, no significant faunal differences existed. In contrast, for quadrats in South America, faunal differences occurred between nonvolant species and bats (in both intercept and slope of regression equations). Again, for bands, there were no faunal differences in species-latitude relationships between nonvolant species and bats for either continent.

Multiple regression analyses

Quadrats

Generally, there were no scale differences in the variables included in final multiple regression equations (Table 5). For the New World, only latitude was important for explaining bat richness, whereas inclusion of latitude, area, and longitude was necessary for nonvolant species richness (some variation occurred for North or South America individually). For either of these faunal subgroups, it did not matter whether analyses proceeded in an entirely stepwise manner, or if area initially was forced into the equation, with a subsequent stepwise procedure; the final equation was the same. For all mammals in the New World, the stepwise technique included only latitude, whereas the area-forced technique included latitude and area (Table 5).

Latitudinal bands

Tightly-fit multiple regression equations were obtained in all cases (R^2 ranged from 0.78 to 0.96; Table 6). Scale effects were rare. For the New World, only latitude was important for explaining bat richness; in equations for nonvolant species richness, area was often necessary in addition to latitude. Results were the same for nonvolant species and bats, regardless of whether analyses were performed in a stepwise or area-forced manner. For all mammals in the New World, the stepwise technique included only latitude for 5° bands (with the addition of area for 2.5° bands) in the multiple regression equation, whereas the area-forced technique included latitude and area (Table 6).

Quadrats versus latitudinal bands

Multiple regression analyses of data from quadrats and bands produced similar results. (Of course, longitude was a possible variable for quadrats and not bands.) Scale effects for either quadrats or bands were infrequent. All variables were important in explaining nonvolant species richness (latitude, area, and longitude for quadrats and latitude and area for bands), whereas only latitude was needed to account for variation in bat species richness for either quadrats or bands. For all mammals, the area-forced procedure included area in final equations in addition to latitude; however, the stepwise procedure always included latitude, and almost always excluded area, in final equations.

DISCUSSION

The latitudinal gradient

Analyses of geographic patterns of mammalian species richness in North and South America have demonstrated repeatedly that richness decreases with increasing latitude (Simpson, 1964; Wilson, 1974; McCoy & Connor, 1980; Mares & Ojeda, 1982; Willig & Selcer, 1989; Pagel *et al.*, 1991; Willig & Sandlin, 1991; Mares, 1992; Willig & Gannon, 1997). Not unexpectedly, our analyses clearly corroborated that pattern; the negative relationship between richness and latitude was evident for all mammals, nonvolant species, and bats, regardless of scale or sampling method. Although the relationship between species richness and latitude was

highly significant and negative for all analyses (three taxonomic groups by four sampling types) in both continents, mathematical relationships of richness and latitude differed between North and South America in eleven of twelve comparisons. Differences for each continent are partly due to disparity in the shapes, areas, and faunas of the continents. Of the eleven comparisons that differed, all involved slope (and eight involved intercepts as well), suggesting that taxa are being added or removed at different rates, depending on histories and physical characteristics of the two continents.

Patterns for bats and nonvolant species

McCoy & Connor (1980) reported that the effect of latitude on richness of nonvolant species was not significant for 1° bands in North America. In contrast, significant relationships existed between nonvolant richness and latitude in this study (based on analyses of 2.5° and 5° bands in North and South America individually, as well as for the entire New World). Contrasting results likely were a consequence of the smaller scale (1°) and restricted geographic focus (North America) in the earlier study. For quadrats as well as bands, species richness was significantly related to latitude for all faunal groups considered. Our data support the suggestion that bats contribute significantly to the strong latitudinal patterns observed for mammals in general (Fleming, 1973; Wilson, 1974; McCoy & Connor, 1980). However, the pattern for all mammals (bat and nonvolant faunas combined) is as strong as the bat pattern alone; this suggests that bats are not the only strong contributors to the latitudinal pattern. Slopes for relationships between species richness and latitude were not different for bats and nonvolant species. That is, bats and nonvolant species were added at statistically indistinguishable rates as latitude decreased. This suggests that nonvolant species also play a major role in creating the strong latitudinal patterns observed for mammals (in contrast to Fleming, 1973; Wilson, 1974; McCoy & Connor, 1980). Our data suggest that bat and nonvolant faunas each contribute significantly to the creation of the latitudinal gradient for all mammals.

Quadrats versus latitudinal bands

The relationships between richness and latitude differed between quadrat and band methodologies. However, results generally were consistent within either bands or quadrats. Our results agree with those of Willig & Sandlin (1991), who found consistent species-latitude relationships, regardless of the use of quadrats or bands. The two techniques measure different aspects of diversity. The quadrat methodology provides information about richness at more local scales (alpha diversity, by examining relatively homogenous quadrats). The band methodology provides information about richness of larger regions (gamma diversity, by examining richness in heterogeneous regions and biomes). Examination of variation in richness among quadrats within bands provides information about species turnover (beta diversity, by examining variation between quadrats at the same latitude). Use of each technique will make future studies more informative and comparable to previous

studies. Differences between methodologies may provide insight into the types of diversity that contribute to patterns. In this study, all latitudinal relationships were significant, regardless of whether richness data was collected with quadrats or bands. It follows then that our data suggest that more than one type of diversity contributes to the overall latitudinal pattern.

The scale effect was minor in either approach for analyses of absolute or area-controlled richness. Patterns revealed by bands and quadrats were similar when absolute richness was the dependent variable, but differed greatly when the effects of area on species richness were controlled by statistical procedures. For area-controlled richness, differences between analyses using bands and quadrats likely were due to the fundamental difference between what the removal of area controlled in the sampling methods. Statistical removal of areal effects in quadrat analyses not only controls for the decrease in quadrat size because of the convergence of longitudes at the poles (necessarily related to latitude) but also for factors (environmental heterogeneity) which affect the likelihood that species coexist. This is a consequence of the relation between habitat richness and area, as well as between species richness and area. The area of bands is dependent on the physical shape of the continent rather than latitude *per se*. When the effect of area is statistically removed from richness data for latitudinal bands, analyses of subsequent regression residuals yield species-latitude relationships that are based on a standardized continent. As McCoy & Connor (1980) suggested for absolute richness, bands are, then, useful for analyses for which area is controlled. Willig & Sandlin (1991) agreed that bands may be more sensitive to the nonindependence of longitude and latitude, but also suggested that quadrats may be more sensitive to species turnover. Consequently, they suggested the use of both techniques. However, when performing latitudinal analyses that control for area, quadrats are inferior to bands. For quadrats, area and latitude are necessarily correlated because of the convergence of longitudinal lines at the poles; this is a geographical artifact. When the effects of area on richness are removed, it cannot be discerned what portion of that variation is actually due to area *per se* and what portion is due to latitude. This would bias subsequent results to estimate poorly the importance of latitude.

The correlations between area and latitude for bands were a product of the shape of continents. Consequently, a strong negative association existed between latitude and area in South America. Only a weak positive relationship was found in North America at the 2.5° scale; small bands occurred in Central America, as well as in northern Canada. For quadrats, a negative correlation existed at both scales in both continents. This is a consequence of the convergence of longitudinal lines as they approach the poles; quadrats decrease in size as they increase in distance from the equator.

Areal effects

Relationships between species richness and latitude, after controlling for area, were highly significant in all cases (three taxonomic groups by four sampling types for each

continent). However, analyses for the two sampling methods produced different results. Part of the difference may be due to factors related to statistical power. Sample size was much greater for quadrats ($n=738$ for 2.5° quadrats and $n=220$ for 5° quadrats) than for bands ($n=51$ for 2.5° bands and $n=26$ for 5° bands), making differences in patterns more detectable for quadrats than for bands. For quadrats, area-controlled relationships differed between continents and had greatly reduced R^2 -values as compared to regressions for absolute richness data. For latitudinally-based quadrats, area and latitude are inextricably connected (because of the nature of the physical template), and attempts to remove areal effects were somewhat unsatisfactory. In contrast, area-controlled analyses for bands had high R^2 -values and were not confounded by an interaction between latitude and area. Area-controlled relationships were not significantly different between continents; this suggests a consistent effect of latitude on the mammalian faunas of two continents. In addition, this result suggests that asymmetries in patterns of diversity across the equator in our analyses based on absolute richness or in those of others (e.g. Willig & Selcer, 1989 [bats]; Blackburn & Gaston, 1996 [birds]) could be affected by differences in the area of sampling units rather than a consequence of history or other biogeographic characteristics. When we removed the linear effects of area from band data (essentially standardizing continental shape), asymmetries between North and South American diversity gradients disappeared.

Multiple regression analyses showed that area (and longitude for quadrats) in addition to latitude was important for explaining variation in nonvolant species richness, whereas only latitude was important for bats. Further, for all mammals, area was often included in equations produced by the area-forced procedure but not the stepwise technique; this indicates that latitudinal effects are more than just reflections of area. We suggest that area is often individually significant but rather a small component in the explanation for species richness given the variation in area of quadrats and bands. Certainly, area is a less important determinant for bats than for nonvolant species. Willig & Selcer (1989) found the same result for bats; namely, that the number of bat species responds primarily to latitude, not area or longitude. This result suggests that the species pattern is a common response to latitude, not a result of evolutionary history or biogeography for a particular continent.

CONCLUSIONS

Area-controlled analyses of species richness for quadrats demonstrated no consistent relationship between richness and latitude for North and South America. In contrast, the relationship between species richness and latitude in bands after controlling for area did not differ between North and South America. When the effect of continental area was statistically removed from analyses, latitude had a consistent effect on species richness in both continents. Even though North and South America have different geographies and environmental histories, and harbor mammalian faunas with unique evolutionary legacies, the effects of latitude on species richness were indistinguishable and unlikely an

artifact. In addition, comparison of the slopes of area-controlled richness-latitude relationships for bats and nonvolants showed no statistical differences; this suggests that latitude has a similar effect on each of these faunal subgroups, in terms of the manner in which species are added or removed from the species pool. Finally, latitude is the only necessary variable to explain bat species richness in multiple regression analyses, whereas the addition of area and longitude (for quadrats) to latitude was often predictive for nonvolant species.

ACKNOWLEDGMENTS

We would like to acknowledge the intellectual input of R. J. Baker, M. A. Houck, and C. Jones in initial phases of this research. Data collection was aided by N. A. Slade and R. M. Timm, who provided assistance through access to their own personal resources and references, as well as to those of the Museum of Natural History at the University of Kansas. S. B. Cox assisted in data entry. Discussions with J. H. Brown and review comments from D. W. Kaufman and two anonymous reviewers greatly strengthened the manuscript. Support was provided by the Department of Biological Sciences, Texas Tech University.

REFERENCES

- Arita, H.T., Robinson, J.G. & Redford, K.H. (1990) Rarity in Neotropical forest mammals and its ecological correlates. *Cons. Biol.* **4**, 181–192.
- Blackburn, T.M. & Gaston, K.J. (1996) Spatial patterns in the species richness of birds in the New World. *Ecography* **19**, 369–376.
- Coleman, B.D., Mares, M.A., Willig, M.R. & Hsieh, Y. (1982) Randomness, area, and species richness. *Ecology* **63**, 1121–1133.
- Colwell, R.K. & Hurtt, G.C. (1994) Nonbiological gradients in species richness and a spurious Rapoport effect. *Am. Nat.* **144**, 570–595.
- Connor, E.F. & McCoy, E.D. (1979) The statistics and biology of the species-area relationship. *Am. Nat.* **113**, 791–833.
- Cook, R.E. (1969) Variation in species density of North American birds. *Syst. Zool.* **18**, 63–84.
- Cox, C.B., Healey, I.N. & Moore, P.D. (1976) *Biogeography. an ecological and evolutionary approach*, 2nd edn. John Wiley & Sons, New York.
- Currie, D.J. (1991) Energy and large-scale patterns of animal- and plant-species richness. *Am. Nat.* **137**, 27–49.
- Fischer, A.G. (1960) Latitudinal variations in organic diversity. *Evolution* **14**, 64–81.
- Fleming, T.H. (1973) Numbers of mammal species in North and Central American forest communities. *Ecology* **54**, 555–563.
- Gilbert, F.S. (1980) The equilibrium theory of island biogeography: fact or fiction? *J. Biogeogr.* **7**, 209–235.
- Gotelli, N.J. & Graves, G.R. (1996) *Null models in ecology*. Smithsonian Institution Press, Washington, D.C.
- Kaufman, D. M. (1994) *Patterns of mammalian diversity in the New World: the role of taxonomic hierarchy*. M.S. thesis, Texas Tech University, Lubbock.
- Kaufman, D. M. (1995) Diversity of New World mammals: universality of the latitudinal gradients of species and bauplans. *J. Mamm.* **76**, 322–334.
- Kiester, A. R. (1971) Species density of North American amphibians and reptiles. *Syst. Zool.* **20**, 127–137.

- MacArthur, R.H. (1965) Patterns of species diversity. *Biol. Rev. Camb. Phil. Soc.* **40**, 510–533.
- MacArthur, R.H. & Wilson, E.O. (1967) The theory of island biogeography. *Monogr. Pop. Biol.* **1**, 1–203.
- McCoy, E.D. & Connor, E.F. (1980) Latitudinal gradients in the species diversity of North American mammals. *Evolution* **34**, 193–203.
- Mares, M.A. (1992) Neotropical mammals and the myth of Amazonian biodiversity. *Science* **255**, 976–979.
- Mares, M.A. & Ojeda, R.A. (1982) Patterns of diversity and adaptation in South American hystricognath rodents. *Mammalian biology in South America* (ed. by M. A. Mares and H. H. Genoways), pp. 393–432. Special Publication, Series Number 6, Pymatuning Laboratory of Ecology, University of Pittsburgh, Linesville, Pennsylvania.
- Meserve, P.L., Kelt, D.A. & Martinez, D.R. (1991) Geographical ecology of small mammals in continental Chile Chico, South America. *J. Biogeogr.* **18**, 179–187.
- Pagel, M.D., May, R.M. & Collie, A.R. (1991) Ecological aspects of the geographical distribution and diversity of mammalian species. *Am. Nat.* **137**, 791–815.
- Pianka, E.R. (1966) Latitudinal gradients in species diversity: a review of concepts. *Am. Nat.* **100**, 33–46.
- Rabinovich, J.E. & Rapoport, E.H. (1975) Geographical variation in Argentine passerine birds. *J. Biogeogr.* **2**, 141–157.
- Rohde, K. (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* **65**, 514–527.
- Rosenzweig, M.L. (1992) Species diversity gradients: we know more and less than we thought. *J. Mamm.* **73**, 715–730.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Rosenzweig, M.L. & Abramsky, Z. (1993) How are diversity and productivity related? *Species diversity in ecological communities* (ed. by R. E. Ricklefs and D. Schluter), pp. 52–65. University of Chicago Press, Chicago.
- Rosenzweig, M.L. & Sandlin, E.A. (1997) Species diversity and latitudes: listening to area's signal. *Oikos* **80**, 172–176.
- Schall, J.J. & Pianka, E.R. (1978) Geographical trends in numbers of species. *Science* **201**, 679–686.
- Simpson, G.G. (1964) Species density of North American recent mammals. *Syst. Zool.* **13**, 57–73.
- SPSS, Inc. (1988) *SPSS-X User's Guide*, 3rd edn. SPSS, Inc., Chicago.
- Willig, M.R. & Gannon, M.R. (1997) Gradients of species density and turnover in marsupials: A hemispheric perspective. *J. Mamm.* **78**, 756–765.
- Willig, M.R. & Lyons, S.K. (1998) An analytical model of latitudinal gradients of species richness with empirical test for marsupials and bats in the New World. *Oikos* **81**, 93–98.
- Willig, M.R. & Sandlin, E.A. (1991) Gradients of species density and species turnover in New World bats: a comparison of quadrat and band methodologies. *Latin American mammals: their conservation, ecology, and evolution* (ed. by M.A. Mares and D.J. Schmidly), pp. 81–96. University of Oklahoma Press, Norman.
- Willig, M.R. & Selcer, K.W. (1989) Bat species gradients in the New World: a statistical assessment. *J. Biogeogr.* **16**, 189–195.
- Wilson, D.E. & Reeder, D.M. (eds.) (1993) *Mammal species of the World: a taxonomic and geographic reference*, 2nd edn. Smithsonian Institution Press, Washington, D.C.
- Wilson, J.W. (1974) Analytical zoogeography of North American mammals. *Evolution* **28**, 124–140.

BIOSKETCHES

Dawn M. Kaufman, a doctoral candidate at the University of New Mexico, recently was awarded a Postdoctoral Fellowship at the National Center for Ecological Analysis and Synthesis (NCEAS). Her research focuses on patterns and processes of the spatiotemporal distribution of species and ecological types (and characteristics thereof, such as abundance and geographic range size), especially as related to latitude. Recent publications include *Ann. Rev. Ecol. Syst.* **27**, 597–623 (1996); *J. Mammal.* **76**, 322–334 (1995); *J. Mammal.* **77**, 642–654 (1996).

Michael R. Willig is a quantitative ecologist with interests in: gradients of diversity with respect to latitude, area, and productivity; ecomorphological structure of communities; disturbance ecology; island biogeography, functional diversity of microbial communities; and phylogenetic and ontogenetic constraints on sexual dimorphism. He is currently a Sabbatical Fellow at NCEAS.