

Gradients of Species Density and Species Turnover in New World Bats: A Comparison of Quadrat and Band Methodologies

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Patterns in the distribution of species have long been of interest to evolutionary biologists (see references in Brown and Maurer, 1989; Brown and Gibson, 1983; MacArthur, 1972; and Rapoport, 1982) from both an ecological and biogeographic perspective. Like many other taxa, mammals exhibit increases in species density as one proceeds from high to low latitudes in North America (Simpson, 1964). However, this increase in mammalian species density is attributable, for the most part, to the Chiroptera rather than to quadrupedal terrestrial mammals (Wilson, 1974). Willig and Selcer (1989) have shown that bat species density responds to latitude, longitude, area, and biome richness in a similar fashion in both North and South America. Bat species density is primarily a product of latitude, and is otherwise little affected by any of the other factors that they measured. They thereby concluded that latitudinal patterns in bat species density in North America are not a product of the peculiarities of geography, evolutionary history, or biogeography of that continent, but are more directly associated with latitude per se or its direct correlates (e.g., incident solar energy) because a similar pattern of species density was observed in South America.

Despite the consensus regarding the patterns of mammalian species density, differences exist concerning methodological approaches. With the exception of McCoy and Connor (1980), who used band methods, most previous studies have used quadrat methods to evaluate patterns in species density. Moreover, McCoy and Connor (1980) argued that band methods were superior to quadrat methods. Willig and Selcer (1989) contended that both methods could reveal unique information concerning density gradients, but restricted their attention to quadrat methods. Herein, we employ both band and quadrat methods in an attempt to evaluate their utility and degree of congruence. Moreover, we statistically examine the effect of species turnover among quadrats within bands, and evaluate its relevance to species density gradients.

MATERIALS AND METHODS

Quadrat Method

An equal area projection map for North and South America was superimposed with a grid system created by the intersection of 5° lines of longitude or latitude (Fig. 1). A total of 238 quadrats contained at least some portion of the continental land masses; however, some quadrats contained land areas too small to measure with precision, and were excluded from further consideration. Four independent descriptors were used to characterize each quadrat. The area of the continental land mass within each quadrat was estimated using a compensating polar planimeter. Mid-latitude and mid-longitude were obtained directly from equal area projection maps. The number of biomes within each quadrat was obtained from the world vegetation map in *The Times Atlas of the World* (1983). The number of bat species per quadrat (bat species density) was obtained from species distribution maps in Koopman (1982) for South America and in Hall (1981) for North and Central America.

Multiple regression analyses were performed using SPSS program REGRESSION (Nie et al., 1975) in order to identify the contribution of independent descriptors in accounting for variation in bat species density. First (X), second (X^2), and third (X^3) powers of the value of each independent descriptor were calculated, and together constituted twelve independent variables for each quadrat. Because different taxa could respond to these factors in different ways, sepa-

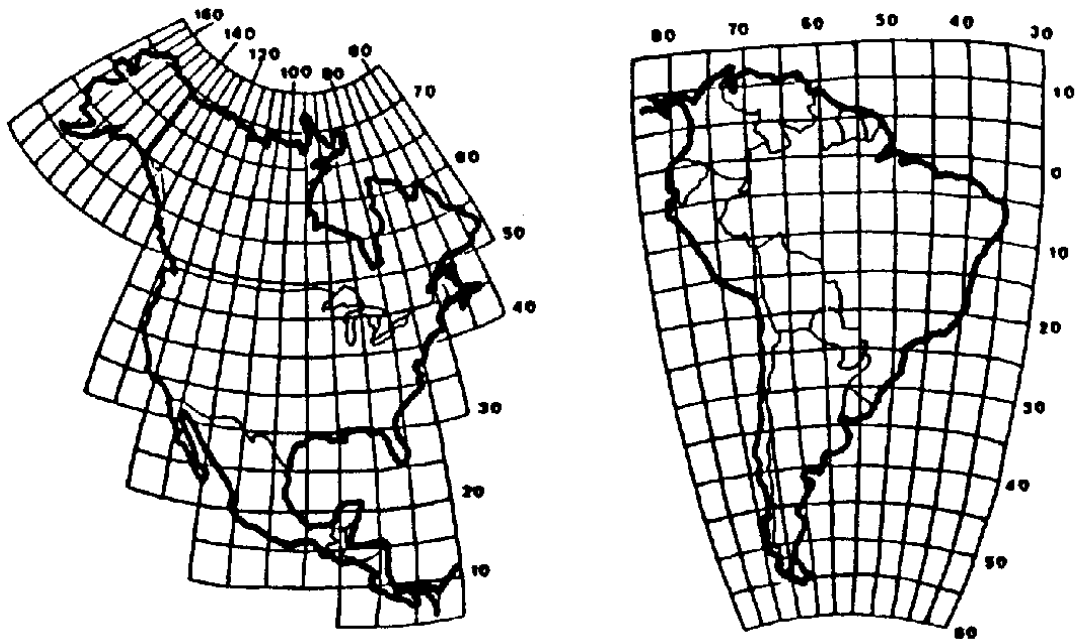


FIG. 1.—Maps of North and South America showing the location and size of the quadrats and bands that were used in analyses of bat species density.

rate analyses were performed on each of ten taxonomic groups: all bats, phyllostomids, phyllostomines, glossophagines, stenodermatines, non-phyllostomids, emballonurids, mormoopids, vespertilionids, and molossids. Only quadrats with non-zero species densities for the taxon under consideration were used in analyses. The importance of each descriptor, X , (e.g., latitude, biome richness, area, or longitude), was assessed by adding the ΔR^2 associated with each of the three powers of that descriptor (i.e., X^1 , X^2 , X^3) that were incorporated into the multiple regression equation. In this way, factors associated with species density in a nonlinear fashion would not be excluded from detection by our analyses.

Simple polynomial regression analyses were performed using BMDP program PSR (Dixon and Brown, 1979) in order to identify the best relation between bat species density and the most important descriptor (latitude) from the multiple regression analyses. Two a priori criteria were established to determine the polynomial of choice (see Willig and Selcer, 1989). The chosen polynomial must be a statistical improvement over lower polynomials, and the next higher polynomial, even if significant, must increase R^2 by less than 0.05. These two criteria designate the simple polynomial that accounts for significant and appreciable variation in species densities. Separate analyses were performed for each of the 10 previously mentioned taxonomic groups.

Band Method

An equal area projection map for North and South America was superimposed with a series of 5° latitudinal lines (Fig. 1) that corresponded exactly with the latitudinal divisions from the quadrat method. This resulted in 27 bands, each encompassing 5° latitude. Three independent descriptors were used to characterize each band. The area of continental land mass within each band was estimated using a compensating polar planimeter. Mid-latitude was calculated as the mean of the latitudinal lines defining the extent of each band. The number of biomes per band was obtained from the world vegetation map in *The Times Atlas of the World* (1983). Bat species densities were obtained from the species distribution maps of Koopman (1982) and Hall (1981). Multiple regression analyses paralleled those for quadrats, except that a mid-longitude descriptor was not included, resulting in only nine independent variables (three for each descriptor). As before, the importance of each descriptor was assessed as the cumulative contribution to R^2 from each power of that descriptor that was incorporated into the multiple regression analysis. Polynomial regression analyses for bands were identical to those used for quadrats.

Within Latitude Diversity Trends

Beta diversity, or the extent of species replacement along a gradient (Whittaker, 1972), was estimated using the beta turnover index (β_1) of Wilson and Shmida (1984). In this context, it measures species replacement among quadrats within latitudinal bands. This index was employed because it has been shown to be su-

terior to other commonly used measures of beta diversity such as the indices of Cody (1975) or Routledge (1977). The beta turnover index exhibits a number of important attributes; it is additive, independent of alpha diversity (and thereby can be used to compare species rich and species poor systems), and is independent of sample size. Moreover, the calculation of β , is straightforward, given by

$$\beta_i = [G(H) + L(H)] / 2A,$$

where $G(H)$ represents the cumulative gain in species along the gradient, $L(H)$ represents the cumulative loss of species along the gradient, and A is the average species density of quadrats within a latitudinal band. Cumulative gains or losses are based upon comparisons of all $n - 1$ pairs of adjacent quadrats within a band containing n quadrats. For example, if a band contains three quadrats (in order: a , b , and c), and quadrat b contains two species that quadrat a does not, and quadrat c contains four species that quadrat b does not, then the cumulative gain, $G(H)$, for the band equals six. Similarly, if quadrat b does not contain one species that exists in quadrat a , and quadrat c does not contain two species that occur in quadrat b , then the cumulative loss, $L(H)$, for the band equals three. Thus, if a species is lost in one quadrat-to-quadrat comparison but later is regained, that species contributes two units to the numerator of β . Values of β , were calculated for each latitudinal band for each of 10 taxonomic groups considered in the previous analyses. We evaluated the hypothesis that beta diversity is independent of latitude by conducting regression analyses between β , and mid-latitude for each taxon. A significant regression with negative slope would indicate that increased diversity in tropical areas (if detected by band methods) could, at least in part, be accounted for by higher species turnover among quadrats in tropical bands.

RESULTS

Multiple Regression Analyses

A comparison of the results from multiple regression analyses for each of the 10 taxonomic groups is presented in Table 1. In general, latitude is the most important predictor of bat species densities for each taxon using band (cumulative R^2 for latitude varies from 0.59 for the Vespertilionidae to 0.98 for the Emballonuridae) or quadrat (cumulative R^2 for latitude varies from 0.85 for all bats to 0.23 for the Mormoopidae) methodologies. The only exception occurs when using the quadrat method for mormoopids, in which longitude accounts for 1% more of the variation in bat species density than does latitude (24% versus 23%, respectively). In all cases, the variation accounted for by latitude was greater when using the band method than when using the quadrat method. The absence of longitude as a potential descriptor in the band method, and the presence of intra-band variation in the quadrat method, biases the results in the observed direction. With two exceptions (area for mormoopids when using the band method, and longitude for stenodermatines when using the quadrat method), only latitude ac-

TABLE 1.—Results of multiple regression analyses of bat species density as a function of latitude, biome richness, area, and for quadrat method, longitude, for a variety of taxonomic groupings using quadrat (Q) and band (B) methodologies. Cumulative contributions to R^2 of each independent variable indicate the importance of that variable in accounting for the variation in bat species density. See text for a detailed presentation of methodologies.

Group	Method	Independent variable			
		Latitude	Biome	Area	Longitude
All Bats	B	0.97	<0.01	0.03	—
All Bats	Q	0.85	0.01	<0.01	<0.01
Phyllostomidae	B	0.97	<0.01	0.01	—
Phyllostomidae	Q	0.73	0.04	0.02	0.03
Phyllostominae	B	0.96	0.02	<0.01	—
Phyllostominae	Q	0.66	0.01	0.01	0.06
Glossophaginae	B	0.91	0.05	0.05	—
Glossophaginae	Q	0.37	0.10	0.01	0.21
Stenodermatinae	B	0.94	0.04	0.02	—
Stenodermatinae	Q	0.66	0.06	0.02	0.16
Non-Phyllostomidae	B	0.94	<0.01	<0.01	—
Non-Phyllostomidae	Q	0.84	0.02	0.01	0.01
Emballonuridae	B	0.98	<0.01	<0.01	—
Emballonuridae	Q	0.60	0.02	0.03	0.02
Mormoopidae	B	0.72	0.02	0.18	—
Mormoopidae	Q	0.23	0.05	<0.01	0.24
Vespertilionidae	B	0.59	0.04	0.05	—
Vespertilionidae	Q	0.52	0.04	0.03	0.16
Molossidæ	B	0.93	0.02	0.01	—
Molossidæ	Q	0.75	0.03	0.07	<0.01

counts for more than 10% of the variation in species densities in multiple regression analyses.

Polynomial Regression Analyses

Because latitude was identified in multiple regression analyses as the descriptor that consistently satisfied our a priori selection criteria, we chose to evaluate the form of the relation between species density and latitude that best accounted for variation among sampling units from each method separately. Again, band and quadrat methods yielded the same degree equations for polynomial regressions for each particular taxonomic group (Table 2). A second degree polynomial with a strong linear component best described species density trends with latitude for all New World bats (Figs. 2 and 3). In general, the best relation for other taxonomic groups, when using band or quadrat methods, was a first degree polynomial (with the exception of vespertilionids that exhibited a second degree equation).

TABLE 2.—Results of polynomial regression analyses of bat species density as a function of latitude using quadratic (Q) and binal (B) methodologies for a variety of taxonomic groupings. An asterisk (*) indicates the polynomial degree which satisfies our acceptance criteria. See text for a detailed description of methodologies.

Group	Method	Polynomial degree											
		1	2	3	4	5	R^2	ΔR^2	R^2	ΔR^2	R^2	ΔR^2	
All Bats	B	0.89	0.89	0.96	0.07*	0.97	0.01	0.99	0.02	0.99	0.02	0.99	0.02
All Bats	Q	0.77	0.77	0.85	0.08*	0.85	0.00	0.87	0.02	0.87	0.02	0.88	0.01
Phyllostomidae	B	0.95	0.95*	0.69	0.01	0.72	0.03						
Phyllostomidae	Q	0.68	0.68*										
Phyllostominae	B	0.92	0.92*	0.64	0.01	0.68	0.04						
Phyllostominae	Q	0.63	0.63*										
Glossophaginae	B	0.86	0.86*										
Glossophaginae	Q	0.31	0.31*										
Stenodermatinae	B	0.93	0.93*										
Stenodermatinae	Q	0.45	0.45*										
Non-Phyllostomidae	B	0.91	0.91*										
Non-Phyllostomidae	Q	0.82	0.82*	0.84	0.02	0.85	0.01						
Emballonuridae	B	0.96	0.96*										
Emballonuridae	Q	0.57	0.57*										
Mormoopidae	B	0.53	0.53*										
Mormoopidae	Q	—	—										
Vespertilionidae	B	—	—	0.55	0.22*								
Vespertilionidae	Q	0.33	0.33										
Molossidae	B	0.91	0.91*										
Molossidae	Q	0.71	0.71*	0.72	0.01	0.75	0.03						

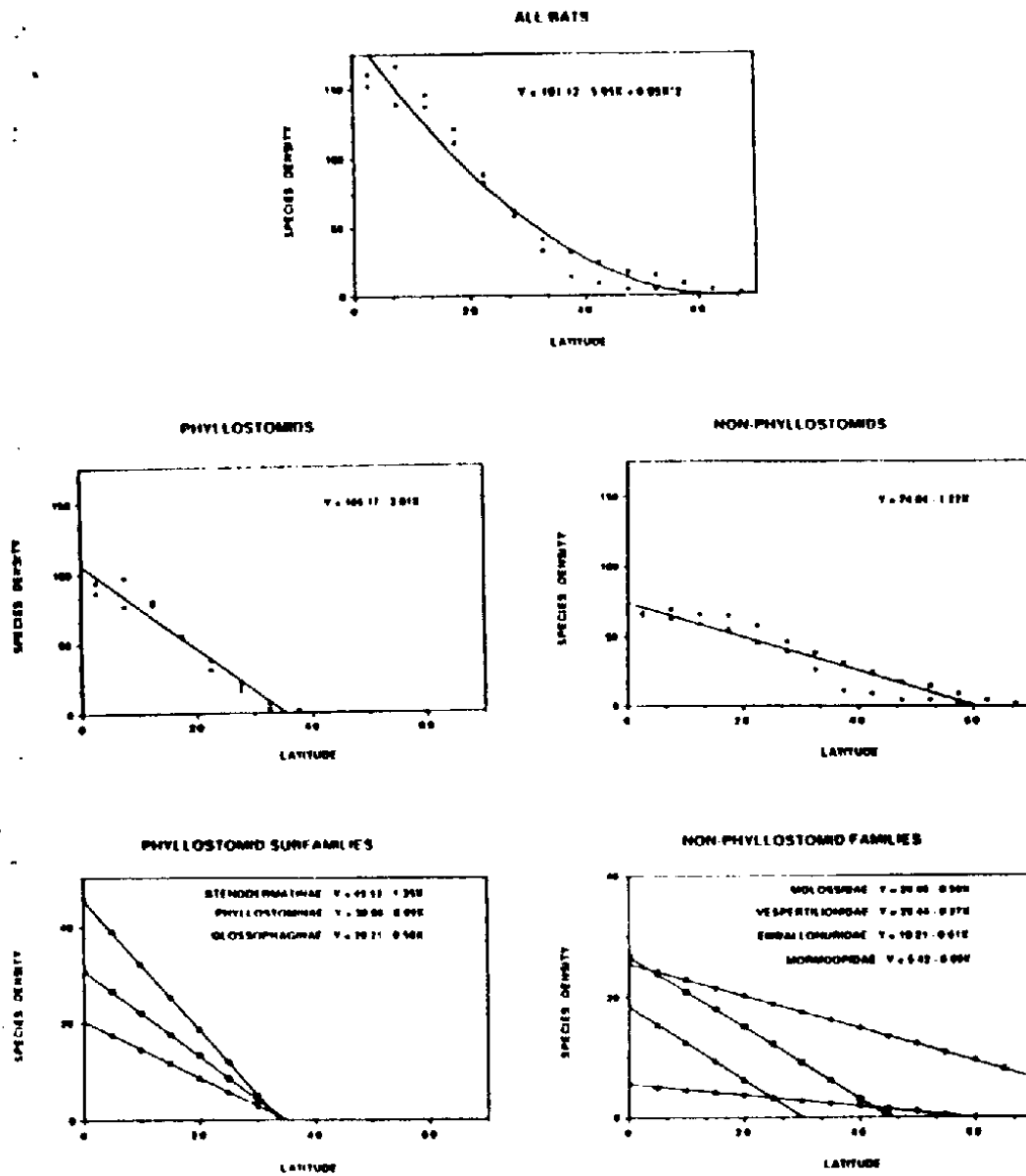


FIG. 2.—Graphic representation based upon band methods of the relationship between bat species density and latitude for all bats, phyllostomids, the phyllostomid subfamilies (Stenodermatinae, solid circles; Phyllostominae, open squares; and Glossophaginae, solid triangles), non-phyllostomids, and the non-phyllostomid families (Molossidae, solid squares; Vespertilionidae, solid diamonds; Emballonuridae, open triangles; and Mormoopidae, open diamonds) from polynomial regression analyses. See text and Table 2 for additional details.

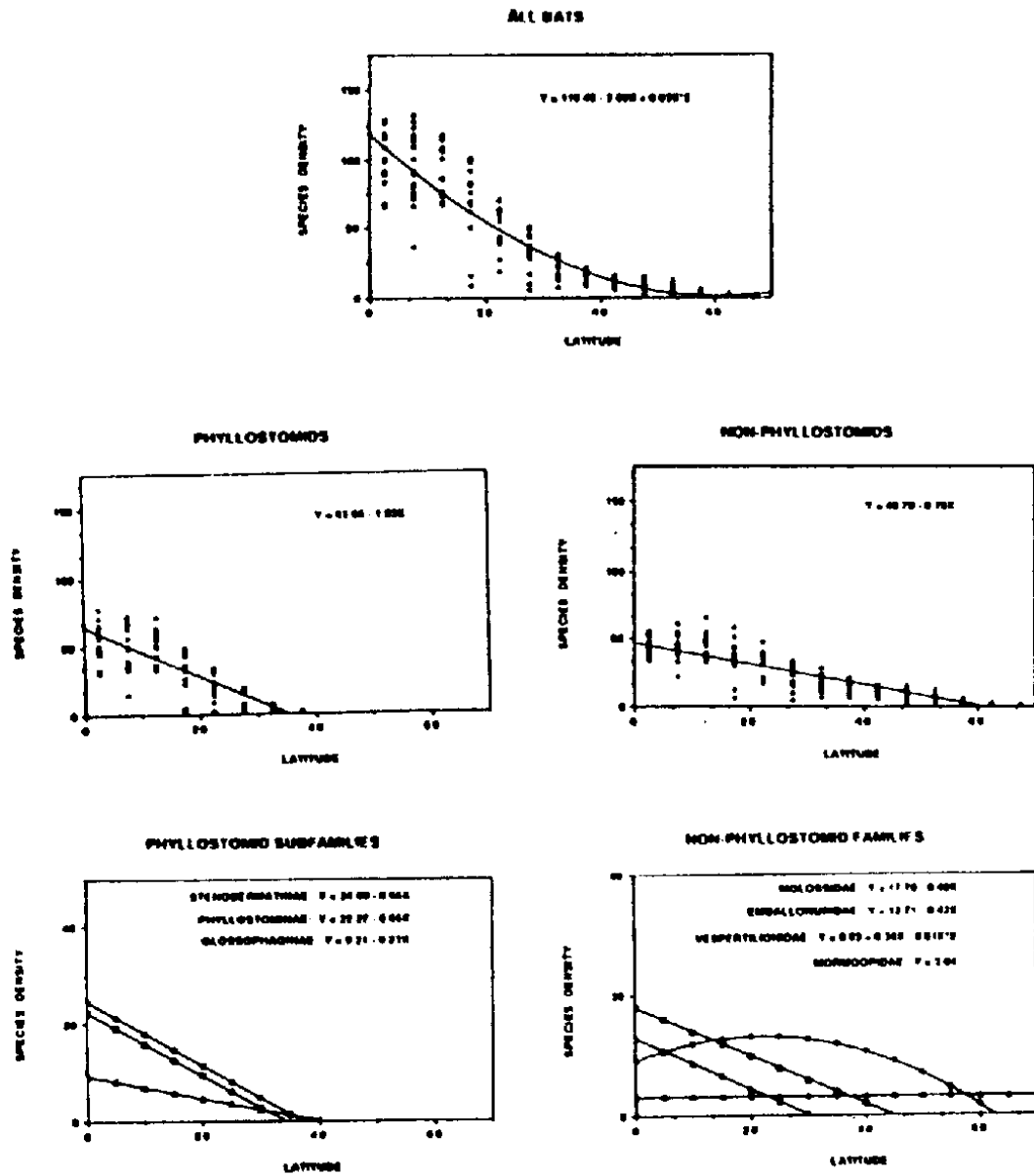


FIG. 3.—Graphic representation based upon quadrat methods of the relationship between bat species density and latitude for all bats, phyllostomids, the phyllostomid subfamilies (Stenodermatinae, solid circles; Phyllostominae, open squares; and Glossophaginae, solid triangles), non-phyllostomids, and the non-phyllostomid families (Molossidac, solid squares; Vespertilionidac, solid diamonds; Emballonuridac, open triangles; and Mormoopidac, open diamonds) from polynomial regression analyses. See text and Table 2 for additional details.

Within Latitude Diversity Trends

Species turnover among quadrats within latitudinal bands for all New World bats is not independent of latitude (Table 3, Fig. 4); however, it decreases toward tropical latitudes. The significant positive slope indicates that tropical latitudes actually exhibit less species turnover than more temperate latitudes. Significance for the analysis involving non-phyllostomids, and nonsignificance for the analysis involving phyllostomids, suggest that the overall lack of independence for all bats is primarily a result of trends within non-phyllostomids, especially the emballonurids, molossids, and vespertilionids, which each exhibited significant decreases in species turnover at tropical latitudes. No taxonomic grouping evidenced a negative slope between β , and latitude; and all significant regressions had small positive slopes with low R^2 , never exceeding 0.36.

DISCUSSION

Latitudinal gradients in species density have been analyzed for a number of taxa from a variety of geographic perspectives (Cook, 1969—North American birds; Kiestler, 1971—North American reptiles and amphibians; Mares and Ojeda, 1982—South American hystricognath rodents; Rabinovich and Rapoport, 1975—Argentine birds; Schall and Pianka, 1978—Australian and American (U.S.) reptiles; Wilson, 1974—North American mammals) using quadrat methodologies similar to those employed by Simpson (1964) in his classic quantification of mammalian species density gradients in North America. McCoy and Connor (1980) criticized the quadrat methodology and reanalyzed data on North

TABLE 3.—Results of regression analyses between β , and latitude for each taxonomic group of bats. Analyses of variance (ANOVAs) evaluate if the slope differs significantly from zero. The proportion of variation in β , among bands accounted for by latitude is measured by R^2 , the coefficient of variation.

Taxon	df	ANOVA			Slope	R^2
		F ₁	Significance			
All Bats	1,23	10.46	0.004 **	0.029	0.283	
Phyllostomidae	1,13	2.06	0.145 NS	0.036	0.070	
Phyllotominae	1,13	3.36	0.084 NS	0.050	0.205	
Glossophaginae	1,12	6.70	0.024 *	0.056	0.358	
Stenodermatinae	1,11	2.06	0.152 NS	0.060	0.158	
Non-Phyllostomidae	1,23	12.65	0.002 **	0.031	0.327	
Emballonuridae	1,10	4.10	0.072 NS	0.126	0.291	
Mormoopidae	1,9	0.24	0.633 NS	0.023	0.026	
Vespertilionidae	1,23	11.61	0.002 **	0.030	0.335	
Molossidae	1,16	4.44	0.053 NS	0.024	0.217	

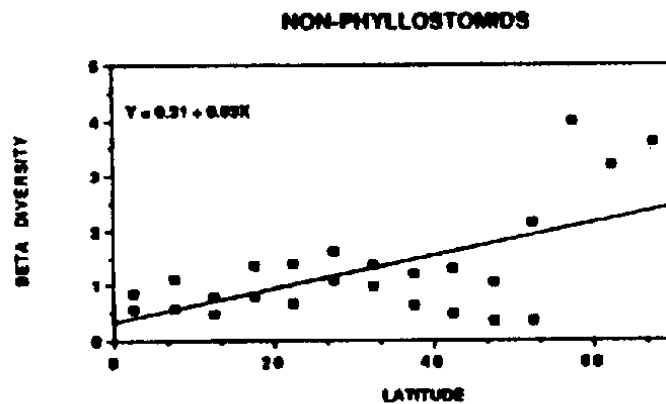
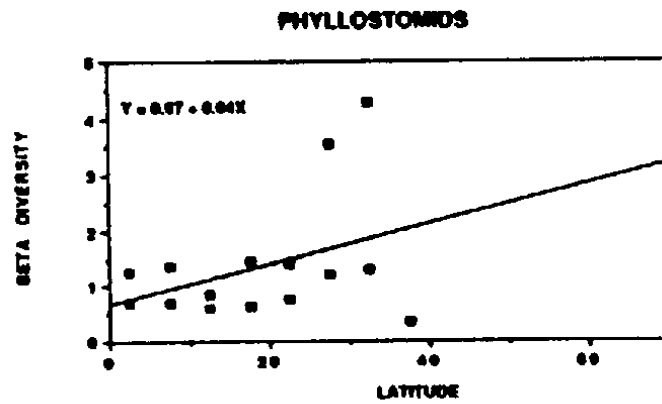
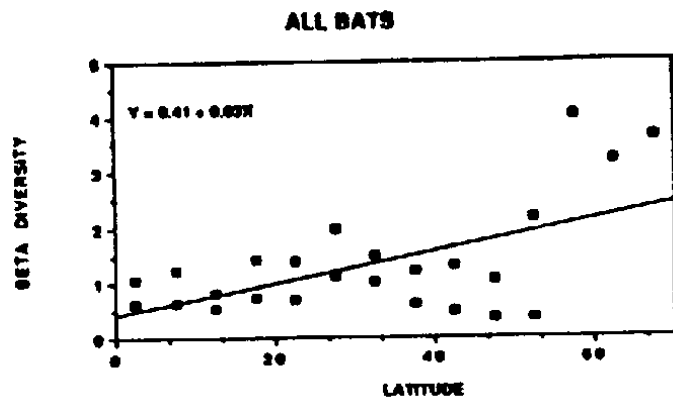


FIG. 4.—Graphic representation of the linear relation between species turnover (β) within latitudinal bands and latitude for all bats, phyllostomids, and non-phyllostomids. See text and Table 3 for additional details.

American mammals from Hall and Kelson (1959) using a band methodology. They contended that latitudinal distributions of species density were not independent of longitude and illustrated that point by comparing plots of species density versus latitude produced by each method. Although differences were apparent for quadrupedal mammals, bat distributional gradients appeared similar in both analyses.

More recently, Willig and Selcer (1989) argued that band and quadrat methods each could reveal unique information about latitudinal gradients. Moreover, they showed that variation in bat species density among quadrats (of equal size) was best accounted for by latitude, with area, longitude, and biome richness consistently contributing little additional information in multiple regression analyses for both North and South America. Herein, we found consistent similarities in a rigorous comparison of results from band and quadrat methods that indicate the importance of latitude in accounting for variation in species density. Even though the shape and size of the quadrats that we examined vary among themselves and are different from those considered by Willig and Selcer (1989), the conclusions are the same. To some degree, this suggests that the size of quadrats (at least within the range of scales that we and Willig and Selcer have considered) do not affect the conclusions about the factors accounting for density gradients.

MacArthur and Wilson (1967) were among the first to formalize the expected increase in species richness with increasing island area; a cogent summary of the application of their theory to mammalian biogeography is available in the contributions contained in Heaney and Patterson (1986). Beyond the domain of oceanic or insular islands, area has been documented to have a profound effect on the species richness of many organisms (see discussion and references contained in Coleman et al., 1982). Even at the scale of entire continents, area has been shown to have a significant effect on mammalian diversity (Flessa, 1975, 1981). Our results, and those of Willig and Selcer (1989), are in sharp contrast to the above, in that bat species density is not predicted by area in a significant or appreciable manner when examining area alone or after adjusting for the effects of the other variables (latitude, longitude, or biome richness).

A number of factors could account for the discrepancy between previous research and our results. Large areas are expected to be more speciose than small areas for at least two interrelated reasons. Large areas are assumed to contain higher habitat diversity, thereby supporting a larger number of species in the entire set of habitats than could have been supported in a single habitat. Moreover, each habitat would be expected to be more expansive than its equivalent within a smaller area; hence, species should avoid approaching the critical minimum population size necessary to maintain positive growth, even during periods of environmental stress. Reduced extinction or high between-habitat diversity contributes to elevated species density on large islands according to the classic paradigm.

The high mobility of bats, in conjunction with the interdigitating riverine habitats (not biomes as quantified in our analyses) that exist within quadrats, may prevent distinctive assemblages of bats from occurring in distinct habitats,

thereby reducing the between-habitat component of bat diversity. In a different context, Willig and Mares (1989) found this to be true, at the level of life zones rather than habitats, for the bat fauna of Venezuela. Unlike on true islands, local extinction of species may be countermanded by reinvasion from adjacent habitats (the rescue effect of Brown and Kodric-Brown, 1977), thereby diminishing the importance of between-habitat diversity and elevating local diversity at the community level (for a discussion of the importance of such factors to understanding bat community ecology, see Willig and Moulton, 1989). Finally, the range of land areas contained within our quadrats or bands may have been inadequate to detect an effect on bat species richness. Other factors, not assessed in this study, may confound the area effect if it is real (e.g., Mares and Ojeda, 1982).

We have shown that increased species densities in tropical latitudes are not a product of greater species turnover (beta diversity) among quadrats within latitudinal bands. In fact, tropical regions exhibit lower turnover in the bat species that occur there. If anything, trends of higher turnover among quadrats in temperate regions make it more difficult to detect latitudinal increases in species density in the tropics by band methods. These findings also corroborate the suggestion that tropical species have larger (at least latitudinally broader) distributions than temperate species (see Rapoport, 1982; and compare Mares, 1986*a*, 1986*b* with Patterson, this volume). This phenomenon is primarily attributable to the Emballonuridae, Vespertilionidae, and Molossidae. Nonetheless, the absence of a significant latitudinal response in species turnover by the Phyllostomidae

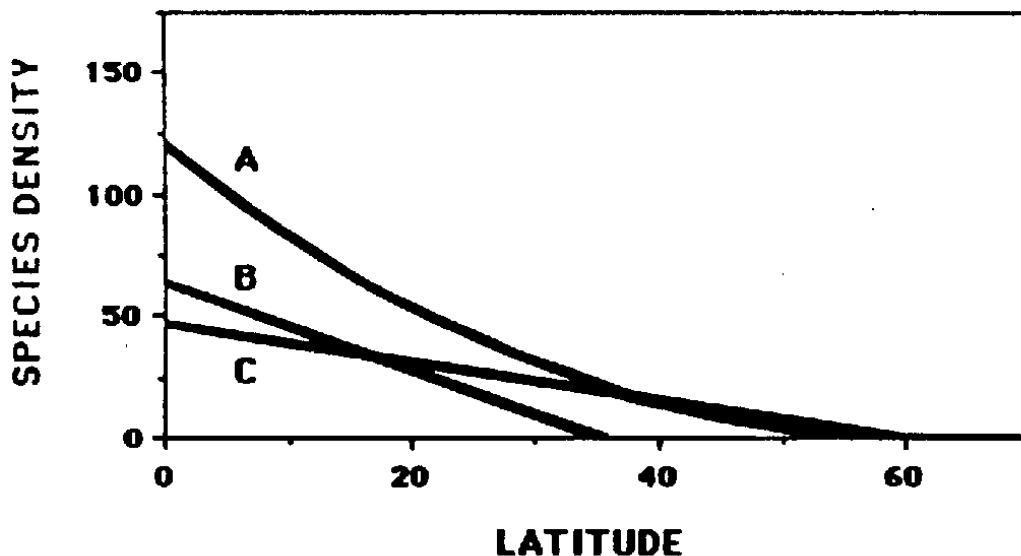


FIG. 5.—Graphic illustration of the composite nature of the quadratic response of species density to latitude by all bats (A). The steeper, low latitude portion of the curve for all bats is an approximate additive function of the response by phyllostomids and non-phyllostomids (B). The less steep, high latitude portion of the curve for all bats is almost exclusively a function of the non-phyllostomids (C).

(Table 3) is probably affected, at least in part, by the smaller number and restricted range of latitudes at which phyllostomids occur. This supposition is further supported by the similar values of the slopes for phyllostomids and non-phyllostomids (0.04 and 0.03, respectively; see Fig. 4). Considerably more variation about the curve for phyllostomids ($R^2 = 0.07$) compared to that for non-phyllostomids ($R^2 = 0.33$) also contributes to this phenomenon.

Although the species density of most taxa responded linearly to changes in latitude, all bats exhibited a quadratic response to latitude (Table 2, Figs. 2 and 3) as assessed by either method. This apparent paradox is easily resolved by referring to Figure 5. The latitudinal response in species density of all bats can be viewed as a composite of the separate responses exhibited by phyllostomids and non-phyllostomids. At low latitudes, where species densities of both phyllostomids and non-phyllostomids are high, species densities of all bats are viewed as an approximate additive function of phyllostomid and non-phyllostomid responses. This results in a steeper slope (the tangent to the second degree curve) at latitudes less than 35° for all bats than for either phyllostomids or non-phyllostomids considered separately. The smaller slope above 35° for all bats is exclusively a property of the contribution of the non-phyllostomids (in general, phyllostomids do not occur at latitudes greater than 35° in either North or South America).

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SUMMARY

Band or quadrat methodologies have been used to examine latitudinal trends in species density for a variety of taxa. We show that the results of multiple regression analyses based upon either method are equivalent for New World bats. Latitude, rather than area, biome richness, or longitude (in the case of the quadrat method), accounts for significant and appreciable quantities of the variation in

species densities for a variety of taxonomic groupings (all bats, phyllostomids, phyllostomines, glossophagines, stenodermatines, non-phyllostomids, emballonurids, mormoopids, vespertilionids, and molossids). For each method, polynomial regression analyses defined the form of the relation between species density and latitude. Again, band and quadrat methods consistently agreed upon the polynomial of choice. In all instances, either a linear relationship, or a quadratic relationship with a strong linear component in the case of all bats, best described the manner in which species density increased toward tropical latitudes. Species turnover between quadrats within a band (beta diversity) significantly increased with increasing latitude; hence, high species densities occur in the tropics despite, not because of, trends in species turnover.

RESUMEN

Metodologías de banda o cuadrante han sido utilizadas para examinar las tendencias latitudinales en la densidad de especies para una variedad de taxa. Nosotros mostramos que los resultados de análisis de regresión múltiple basados en cualquiera de los dos métodos son equivalentes para los murciélagos del nuevo mundo. La latitud, más que el área, riqueza del bioma, o la longitud (en el caso del método de cuadrante) son responsables por cantidades significativas y apreciables en la variación de las densidades de especies para una variedad de agrupaciones taxonómicas (todos los murciélagos, filostómidos, filostóminos, stenodermátinos, glosófáginos, no-filostómidos, embalanúridos, mormópodos, vespertiliónidos, y molósidos). Para cada metodología, análisis de regresión polinomial definieron la forma de la relación entre densidad de especies y latitud. Una vez más, los métodos de banda y de cuadrante consistentemente concordaron sobre la fórmula polinomial del gusto. En todos los ejemplos, ya sea una relación linear, o una relación cuadrática con un fuerte componente linear en el caso de todos los murciélagos, mejor describieron la manera en que la densidad de especies se incrementó hacia las latitudes tropicales. Reemplazo de especies entre cuadrantes dentro de una banda (diversidad beta) se incrementó significativamente con incrementos en latitud; por lo tanto, una alta densidad de especies ocurre en los trópicos a pesar de, y no como resultado de, tendencias en el reemplazo de especies.

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