

GEOGRAPHICAL ECOLOGY AT THE COMMUNITY LEVEL: PERSPECTIVES ON THE DIVERSITY OF NEW WORLD BATS

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Abstract. The ubiquity of the latitudinal gradient of species richness is well documented at coarse scales of resolution, but the extent to which the pattern is recapitulated at the level of local communities for any aspect of biodiversity (i.e., richness, evenness, or diversity) is unclear. We examined how attributes of New World bat diversity vary with each other and with latitude at two scales of resolution: local communities and regional species pools. We calculated 14 indices of diversity (species richness [three], evenness [four], dominance [three], and diversity [four]) from species abundance distributions for 32 intensively sampled local sites between 42.25° N and 24.12° S latitude. The species richness of each corresponding regional pool was estimated from published range maps. In general, the gradient of local species richness was less steep than the corresponding gradient of regional species richness; beta diversity in the tropics is greater than that for temperate communities. All aspects of diversity at the local scale did not vary with latitude in the same manner. The latitudinal gradient in species diversity of local communities was primarily a consequence of the corresponding gradient in species richness. Local richness increased and became more variable with decreasing latitude. In contrast, species evenness did not vary in a systematic fashion with latitude. Although the absolute number of rare species in communities increased faster with latitude than did that of common species, both abundance classes proportionately increased with latitude in equivalent ways throughout the New World. In general, latitudinal variation at the community level was detected in diversity indices that were insensitive to the abundance of species. The dramatic increase in species richness at broad scales of resolution toward the tropics (gamma diversity) was as much a consequence of increased richness at the local level (alpha diversity) as it was a consequence of the latitudinal increase in species turnover among communities (beta diversity). Future theoretical research should examine the correlates of latitude that enhance differentiation among communities at low latitudes (i.e., those which enjoy high productivities). Conservation strategies based on assessments of diversity at coarse levels of resolution (gamma diversity) should be implemented with caution because beta diversity inflates regional estimates of diversity.

Key words: *beta diversity; community structure; geographical ecology; latitudinal gradient; macroecology; New World bats; rarity; scale dependence; species diversity; species evenness; species richness; species turnover.*

INTRODUCTION

Quantifying broadscale spatial patterns in the distribution and abundance of organisms (Fischer 1960, Pianka 1966, MacArthur 1972), and postulating causative mechanisms (MacArthur 1972, Colwell and Hurtt 1994, Rosenzweig 1995, Rohde 1997), have dominated much of contemporary ecological research over the last two decades (Gaston and Blackburn 1999). Studies of latitudinal gradients have contributed greatly to our understanding of the geographic distribution of diversity (Willig 2000). These studies primarily have examined patterns of species richness at or above the regional scale (sampling units ≥ 25 km²), and typically are based on data garnered from distribution maps, field guides, atlases, or checklists that characterize the dis-

tribution of taxa across broad geographic areas at coarse scales of resolution (e.g., Fischer 1960, Cook 1969, Kiester 1971, Willig and Selcer 1989, Rohde 1992, Rex et al. 1993). This approach has documented one of the most pervasive patterns characterizing the spatial distribution of organisms. Systematic increases in the number of species with decreases in latitude have been demonstrated for plants and animals, in terrestrial and aquatic environments, and during contemporary and past times (see Gaston 1994, Brown 1995, Rosenzweig 1995, Willig 2000). Moreover, this pattern is robust with respect to systematic hierarchy and can be demonstrated at specific, generic, familial, and ordinal levels (e.g., Fischer 1960, Kaufmann 1995). Ecologists, however, have become bogged down in a quagmire of contention concerning the mechanisms that produce the gradient (see Rohde 1997, Rosenzweig and Sandlin 1997). Moreover, distinguishing the process or subset of mechanisms that are responsible for latitudinal pat-

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terns will be a daunting task because most mechanisms only lead to qualitative predictions that are not mutually exclusive, and because null models can give rise to latitudinal gradients in the absence of underlying environmental heterogeneity (Colwell and Hurtt 1994, Willig and Lyons 1998, Colwell and Lees 2000).

Many factors limit the development of theory. For example, much of what has been learned regarding spatial variation in diversity comes from two distinct approaches. The first uses species richness as a surrogate of diversity and then evaluates patterns at large spatial scales. Because differences in relative abundances of species are ignored, such an approach provides limited understanding of the ways in which diversity per se responds to environmental variation. The second evaluates simultaneous changes in richness and evenness along environmental gradients (e.g., productivity), but this typically is done at relatively small spatial scales in terms of both focus or extent (Rotenberry 1978, Wilson and Gitay 1995, Drobner et al. 1998, Weiher and Keddy 1999, Wilsey and Potvin 2000). The way in which species richness and evenness interact and give rise to empirical patterns of diversity at large scales, especially along extensive environmental gradients, remains poorly understood. The marriage of these two approaches likely will hasten a unified understanding of patterns of diversity.

Advancement of theory also has been stymied by the scale-dependent nature of patterns of diversity. Studies of the productivity–diversity relationship offer a good example (Pastor et al. 1996, Waide et al. 1999, Gross et al. 2000, Mittlebach et al. 2001). The consensus is that productivity affects species diversity; however, little agreement exists regarding the form of this relationship from either theoretical or empirical perspectives. Productivity increases diversity at some of spatial scales, whereas at others it can decrease diversity. Along extensive gradients the relationship between diversity and productivity can be unimodal or linear. The generalization of patterns of species diversity across spatial scales, and hence the production of unified theories, depends on understanding scale dependence from both qualitative and quantitative perspectives (Scheiner et al. 2000). Scale dependence should be expected as long as richness increases with area in a nonlinear way (Lyons and Willig 1999, 2002).

The greatest obstacles that impede the description of broadscale patterns of diversity are practical. Detailed information from intensive sampling of numerous local sites across a variety of latitudes must be accurate and comparable. Because ecological communities generally comprise more relatively rare species than common ones (Gaston 1994), especially in tropical environments, intensive efforts are necessary to estimate confidently the right-hand tail of species abundance distributions. Moreover, the collection of such information across a number of sites is too prodigious a task for any one investigator, and the only practical way to

amass such data is to wait patiently for a number of investigators to independently collect detailed data on species composition at a variety of sites. Only recently has such information become available for even common taxa. Fortunately, studies quantifying bat species composition at a number of New World locales have accumulated over the last 25 yr and make such broad analyses a feasible endeavor (Table 1).

New World bats

Bats are exceptional in that they generally have broad geographic distributions and exhibit high degrees of taxonomic and functional diversity (Stevens and Willig 2000, Patterson et al. 2001). They exhibit pronounced latitudinal gradients of species richness at the regional scale (Willig and Selcer 1989, Willig and Sandlin 1991, Kaufman and Willig 1998) that are not solely a consequence of stochastic processes (Willig and Lyons 1998). Moreover, bats are often the most abundant vertebrates at the level of local communities and often the most species-rich mammalian taxon in the tropics (Patterson et al. 2001). Functionally, compositionally, and structurally, New World bat communities are highly variable (Findley 1993, Stevens and Willig 1999, 2000). Communities comprise species from a single feeding guild at high latitudes, and exhibit an increase in the number of functional groups to at least seven (aerial insectivores, frugivores, gleaning animalivores, high-flying insectivores in the family Molossididae, nectarivores, sanguinivores, and piscivores) at the equator (Stevens and Willig 2000). Moreover, communities vary considerably in morphological and numerical patterns related to size assortment and density compensation (Stevens and Willig 1999, 2000). Nonetheless, it is unclear if such community characteristics, or even more basic attributes like species diversity, are related to latitude and its primary correlates of temperature, seasonality, or energy.

We quantitatively describe diversity in 32 bat communities from throughout the New World. We also evaluate 14 popular indices of diversity based on how they reflect species richness, evenness, or dominance, and evaluate the sensitivity of these measures to detect a gradient when data are based on successively less effort at each site. We then quantify latitudinal gradients in diversity at the community level and evaluate scale dependence in latitudinal gradients of species richness by determining the linkage between the latitudinal gradient of species richness at regional and local scales.

MATERIALS AND METHODS

Available data

Data on species composition and abundance of 32 bat communities were obtained from the literature (Table 1, Fig. 1). Although data based on samples from local communities provide finer grain resolution than

TABLE 1. Geographic and environmental characteristics of each of 32 bat communities used to evaluate patterns of diversity in the New World.

Community	Country	Latitude (degrees)	Longitude (degrees)	Habitat	Source
Iowa	USA	42.3	93.0	riparian	Kunz (1973)
California	USA	36.5	117.3	desert	Suprenant (1977)
Nevada	USA	36.2	115.2	desert	O'Farrell and Bradley (1970)
New Mexico	USA	33.9	107.4	desert	Black (1974)
Big Bend Ranch	USA	29.8	103.8	desert	Yancey (1996)
Queretaro	Mexico	21.1	99.3	montane tropical forest	Navarro and Leon-Paniagua (1995)
Manantlan	Mexico	19.3	104.0	montane tropical forest	Iniguez Davalos (1993)
Ixtapan del Oro	Mexico	19.3	100.2	montane tropical forest	Alvarez and Alvarez-Castaneda (1996)
Los Tuxtlas	Mexico	18.4	95.0	wet tropical forest	Estrada et al. (1993)
Chiapas	Mexico	16.1	91.0	wet tropical forest	Medellin (1993)
Guanacaste-1	Costa Rica	9.5	85.2	wet tropical forest	LaVal and Fitch (1977)
Guanacaste-2	Costa Rica	9.5	85.2	wet tropical forest	Fleming et al. (1972)
Puntarenas	Costa Rica	10.0	84.8	montane tropical forest	LaVal and Fitch (1977)
Heredia	Costa Rica	10.5	83.8	wet tropical forest	LaVal and Fitch (1977)
Sherman	Panama	9.3	80.0	wet tropical forest	Fleming et al. (1972)
Rodman	Panama	9.0	79.6	dry tropical forest	Fleming et al. (1972)
BCI	Panama	9.2	79.8	wet tropical forest	Handley et al. (1991)
Paroucou	French Guiana	5.3	52.9	wet tropical forest	Simmons and Voss (1998)
Zabelitas	Colombia	4.0	76.5	wet tropical forest	Thomas (1972)
Marcarena	Colombia	3.3	73.9	wet tropical forest	Sanchez-Palomino et al. (1993)
Pance	Colombia	3.0	76.0	montane tropical forest	Thomas (1972)
Hormiguero	Colombia	3.0	76.0	montane tropical forest	Thomas (1972)
Manaus	Brazil	3.0	60.0	wet tropical forest	Dos Reis (1984)
Edaphic Cerrado	Brazil	7.2	39.4	tropical woodland-savannah	Willig (1982)
Caatinga	Brazil	7.6	39.7	dry tropical forest	Willig (1982)
Linhares	Brazil	19.0	40.3	wet semi-tropical forest	Peracchi and Albuquerque (1993)
Panga	Brazil	19.3	48.4	wet semi-tropical forest	Pedro and Taddei (1997)
Minas Gerais	Brazil	19.8	41.8	wet semi-tropical forest	Moura de Souza Aguiar (1994)
Jenaro Herrera	Peru	4.9	73.8	wet tropical forest	D. Gorchov and C. F. Ascorra (<i>personal communication</i>)
Manu	Peru	11.9	71.3	wet tropical forest	Ascorra et al. (1996)
Mbaracayu	Paraguay	24.1	55.5	wet semi-tropical forest	(<i>unpublished data</i>)
Rio Verde	Paraguay	23.5	56.1	dry semi-tropical forest	(<i>unpublished data</i>)

do studies based solely on distribution maps, they suffer from a suite of unique limitations. For example, a number of different investigators collected data across a number of different years; inter-investigator differences in sampling protocol and inter-year environmental differences may affect the number of individuals obtained at a site. These communities span environmental gradients that we did not attempt to control, such as elevation and precipitation, and these gradients often may be influenced by edaphic characteristics. These environmental factors may not vary with latitude in simple ways and may obscure relationships between diversity and latitude. Nonetheless, data from these sites represent taxonomic and functional subsets of real communities (i.e., groups of species, which as a consequence of spatial and temporal constraints, have the potential to interact and affect local demographics), and if broadscale geographic patterns are the result of strong structuring mechanisms operating at the community level, then such uncontrolled factors should cause only minor departures from true relationships and not affect a bias.

We used several criteria to select sites for inclusion in analyses. Data must have been based on collections

from more than one location in a community, but the area of sampling must have been constrained spatially so that information likely was from a single community. This criterion was somewhat subjective. Many facets of bat community ecology remain enigmatic (Findley 1993). For example, no estimates currently exist as to the aerial extent of bat communities. It is unknown whether the boundaries of bat communities are sharp and correspond to boundaries elicited by the environment, such as those between habitats or between life zones, or whether boundaries are spatially broad and represent gradual transitions whereby communities progressively intergrade into each other along environmental gradients. In general, we incorporated studies that sampled bats within an area of ~ 1000 km² (~ 32 by 32 km). Although some studies included data from more than one habitat in heterogeneous environments or from more than one life zone in montane environments, the data characterizing each study always came from a single biome and were bounded spatially so that it would not be unreasonable to encounter the same individuals across the entire suite of habitats encompassed in the study. Additionally, sampling must have been conducted on a regular basis, in

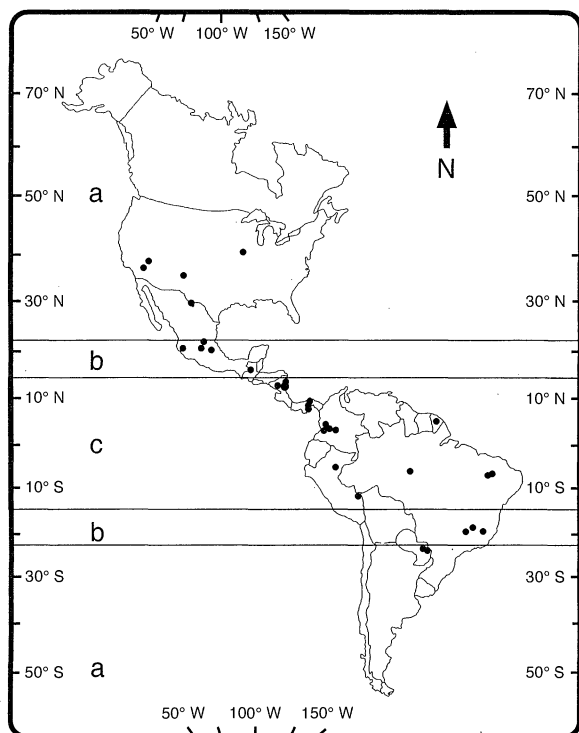


FIG. 1. Location of 32 New World bat communities (solid dots) used to evaluate geographic patterns of diversity. The letters a, b, and c denote temperate, subtropical, and tropical latitudinal regions, respectively.

all seasons during which bats were active, for at least one but not exceeding five years. Clearly, the most effective means to increase the probability of encountering rare species is to increase sampling effort. Nonetheless, if the time period over which sampling is conducted is too long, samples may include species that do not coexist in time and may be biased in the alternate direction of overestimating the richness of a community and underestimating its evenness or dominance. A 1-to 5-yr time span is a trade-off that minimizes the possibility of missing rare species and increases the accuracy of relative abundances while minimizing the possibility of including species that, due to temporal changes in community structure, may not coexist in time. As a final safeguard, we constructed collectors curves for all communities, and included only those communities whose diversity was at the asymptote of a collectors curve representing diversity as a function of numbers of captured individuals. Two of the 32 communities did not meet all criteria. The Nevada community did not meet spatial sampling criteria and the Linhares community did not meet temporal sampling criteria. Neither of these sites greatly influenced statistical results nor did they represent outliers in any analysis. Because these sites enhance our ability to describe the great variety of bat communities found in the New World and increase our ability to obtain suf-

ficiently large sample sizes to resolve patterns in diversity, we included them in analyses.

To determine the regional richness of a site, we counted the number of bat species whose geographic distributions overlapped that site. Distribution maps for each species were prepared using Hall (1981), Eisenberg (1989), Koopman (1982), and Redford and Eisenberg (1992). Following Kaufman (1998), we used the equation $(1 - \text{local species richness}/\text{regional species richness})$ as an estimate of species turnover or beta diversity for each of the 32 communities. Based on latitude, communities were classified into one of three geographic zones: tropical (12° N to 12° S), subtropical (13° N to 23.45° N and 13° S to 23.45° S), or temperate ($>23.45^\circ \text{ N}$ or 23.45° S).

Characterization of diversity

The multifaceted nature of diversity presents a number of methodological complications. Changes in diversity can result from changes in species richness, changes in equability, or both. Accordingly, attempts to differentially weight richness and evenness have resulted in more than 20 measures of diversity. Many are mathematically complex and disguise the relative degree to which evenness and richness are weighted in a composite index. Indeed, no one measure has achieved hegemony.

Fourteen measures of diversity (Table 2) were calculated using a program written in Matlab for the Macintosh (Math Works 1995). These measures differentially reflect species richness, evenness, dominance, or diversity. Species richness (R_c) was estimated as the number of species sampled from the community. In addition, Margalef's index (MAR, Margalef 1957) and Menhinick's index (MER, Menhinick 1964) were used because they take into account the increases in species richness with increases in effort. The equability of species abundances (evenness) was estimated using an index reflecting the probability of an interspecific encounter (PIE, Hurlbert 1971), Schoener's index (O, Schoener 1970, Camargo 1995), Shannon's index (SHE, Pielou 1975), and Camargo's index (CE, Camargo 1993). Diversity measures that capture simultaneous variation in richness and evenness were estimated by log-series alpha (A, Fisher et al. 1943), Shannon's index (SHD, Pielou 1975), Brillouin's index (B, Pielou 1969, 1975), and Camargo's index (CD, Camargo 1993). Finally, the degree to which community composition is dominated by one or a few abundant species (dominance) was estimated using Simpson's index (SI, Simpson 1949), Berger-Parker index (BP, Berger and Parker 1970), and McIntosh D-index (McIntosh 1967). Following Magurran (1988), BP and SI were scaled so that a large index represents low dominance. All indices are well described in the literature (e.g., Peet 1974, Magurran 1988, Camargo 1995, Biesel et al. 1996, Smith and Wilson 1996, Camargo 1997) and will not be defined in additional detail here. This

TABLE 2. Fourteen measures of diversity used to characterize New World bat communities.

Measure	Source	Code	Aspect
Species richness		R_c	richness (Magurran 1988)
Margalef index	Clifford and Stephenson (1975)	MAR	richness (Magurran 1988)
Menhinick index	Whittaker (1977)	MER	richness (Magurran 1988)
Shannon diversity	Pielou (1975)	SHD	diversity (Magurran 1988)
Shannon evenness	Pielou (1975)	SHE	evenness (Magurran 1988)
Simpson index	Simpson (1949)	SI	dominance (Magurran 1988)
Berger-Parker index	Berger and Parker (1970)	BP	dominance (Magurran 1988)
McIntosh D-index	McIntosh (1967)	MD	dominance (McIntosh 1967)
Log series alpha	Fisher et al. (1943)	A	diversity (Magurran 1988)
Brillouin index	Pielou (1975), (1969)	B	diversity (Magurran 1988)
PIE index	Hurlbert (1971)	PIE	evenness (Hurlbert 1971)
Camargo diversity	Camargo (1993)	CD	diversity (Camargo 1993)
Camargo evenness	Camargo (1993)	CE	evenness (Smith and Wilson 1996)
Schoener's index	Schoener (1970)	O	evenness (Smith and Wilson 1996)

is not an exhaustive survey of diversity measures. Rather, we selected measures that were easy to calculate, commonly used, or proposed to be improvements over previously described and commonly used indices. Taken together, we expect this suite of measures to reveal variation in the complexion of diversity throughout the range of sites from which we have data.

We conducted a factor analysis (Procedure FACTOR, SPSS 1990) to construct derived measures of diversity based on the original 14 indices. Factor analysis derives variables that are linear combinations of the original ones. Our analysis constrained factors to be orthogonal. Thus, because original indices were correlated, fewer than 14 factors were necessary to represent the structure of the original data (i.e., accurately reflect intersite differences in empirical diversity). Analysis began with a principal components analysis (PCA) of the correlation matrix. PCA extracts derived orthogonal variables such that each subsequent axis accounts for a maximal amount of residual variation. Thus, the first few principal components characterize the main axes of variation in diversity embodied in the 32 communities. Only those principal components with eigenvalues greater than unity (i.e., accounted for more variation on average than one of the original indices) were included in inferential analyses and subsequent aspects of the factor analysis. These principal components were rotated via a varimax procedure to produce factors. Rotation causes variation in each of the original indices to be maximal on one factor and minimal on all others, predisposing correlated variables to have maximal loadings on the same factor, and equalizing variation among factors. The varimax rotation facilitated the decomposition of variation in diversity into constituents of evenness and richness.

Inferential analyses

We used linear regression analyses (Procedure REGRESSION, SPSS 1990) to determine if latitude accounted for a significant proportion of the variation among sites in each of the original diversity measures separately, as well as for each of the orthogonal axes

derived from factor analyses. We maintained experiment-wise error rate at 5% by conducting separate sequential Bonferroni adjustments (Rice 1989) for the set of 14 indices, as well as for each set of derived variables. Linear regression may lack power to detect latitudinal effects related to differences among broad climatological regions. Thus, we used MANOVA (Procedure MANOVA, SPSS 1990) to evaluate differences regarding diversity among temperate, subtropical, and tropical communities. Subsequently, we used Student-Newman-Keuls tests (Sokal and Rohlf 1995) to further resolve mean differences with respect to each of the derived variables provided that their associated ANOVAs were significant. To evaluate differences between local and regional richness regarding their relationship with latitude, we compared the 95% confidence intervals of both the slopes and intercepts generated from least squares linear regressions.

In addition, we categorized species as common or rare based on four considerations of abundance (i.e., rare species are those with $<1/R_c$, 5%, 2%, or 1% of all individuals in the community). To evaluate if the absolute rate of increase in species richness with decreasing latitude is the same for rare and common taxa, we compared slopes from least squares regressions of the number of rare and common taxa and latitude. To evaluate if the proportional rate of increase in species richness with decreases in latitude is the same for rare and common species, we compared slopes from least squares regressions of the log of the numbers of rare and common taxa and latitude.

Finally, we conducted a sensitivity analysis to explore the effect of sampling intensity on latitudinal gradients of diversity. We randomly sampled individuals from each community until their number in a subsample equaled a particular percentage of the total number of individuals in the entire sample. Diversity measures for each community were recalculated, and the correlation was determined between diversity and latitude. We then used the mean and two standard deviations of 100 iterations of this process for each subsample (defined by

TABLE 3. Empirical estimates of diversity and factor scores characterizing structure of 32 bat communities from the New World.

Site	Latitude (degrees)	Richness			Diversity			
		R_c	MAR	MER	A	B	SHD	CD
Iowa	42.25	8	1.11	0.34	1.33	1.48	1.51	3.49
California	36.50	10	1.10	0.17	1.26	0.57	0.57	1.53
Nevada	36.20	8	1.04	0.27	1.22	0.68	0.69	1.61
New Mexico	33.87	16	2.22	0.55	2.79	1.66	1.70	4.44
Big Bend Ranch	29.75	14	2.07	0.60	2.62	1.78	1.83	4.65
Queretaro	21.12	28	4.48	1.38	6.79	2.29	2.40	8.72
Manantlan	19.33	28	4.20	1.12	6.02	2.12	2.20	7.47
Ixtapan del Oro	19.25	25	3.85	1.11	5.12	2.27	2.36	8.86
Los Tuxtlas	18.42	35	4.33	0.69	5.72	2.50	2.53	9.36
Chiapas	16.10	50	7.12	1.60	11.15	2.80	2.89	14.29
Guanacaste-1	9.47	36	5.33	1.35	8.00	2.34	2.43	9.71
Guanacaste-2	9.47	27	3.73	0.83	5.04	2.01	2.06	6.01
Puntarenas	10.00	24	3.38	0.80	4.52	1.93	1.98	5.61
Heredia	10.50	57	7.44	1.32	11.11	2.79	2.85	14.12
Sherman	9.33	31	4.20	0.87	5.75	1.93	1.98	5.87
Rodman	8.95	28	3.88	0.87	5.29	1.85	1.89	5.30
BCI	9.17	39	4.17	0.41	5.22	1.74	1.76	5.94
Paracou	5.27	78	9.58	1.40	14.54	2.87	2.92	19.08
Zabelitas	4.00	35	4.52	0.81	6.13	2.41	2.44	8.69
Marcarena	3.25	39	5.57	1.29	8.26	1.90	1.97	7.84
Pance	3.00	17	2.42	0.62	3.10	2.24	2.29	7.59
Hormiguero	3.00	14	1.87	0.44	2.29	0.96	0.98	2.18
Manaus	3.00	52	7.22	1.52	11.14	2.42	2.50	11.79
Edaphic Cerrado	7.23	25	3.18	0.57	4.07	2.28	2.31	7.81
Caatinga	7.58	34	4.50	0.87	6.15	2.43	2.47	9.07
Linhares	19.01	37	5.73	1.60	9.03	2.84	2.96	14.48
Panga	19.25	17	2.94	1.11	4.22	1.99	2.11	6.31
Minas Gerais	19.83	20	3.26	1.09	4.65	1.84	1.94	6.02
Jenaro Herrera	4.92	59	7.52	1.25	11.11	2.61	2.66	12.02
Manu	11.93	50	7.63	2.02	12.86	3.00	3.14	17.62
Mbaracayu	24.12	15	1.66	0.22	1.93	1.23	1.24	2.62
Rio Verde	23.49	29	3.54	0.55	4.52	1.48	1.50	3.82
Mean		30.78	4.21	0.93	6.03	2.04	2.10	7.93
Variance		267.72	4.63	0.21	12.51	0.37	0.40	19.76
cv		53.16	51.06	49.98	58.65	29.94	30.24	56.02

Note: Sites are described in Table 1. Diversity acronyms correspond to those in Table 2. cv refers to coefficient of variation. R_c refers to regional species richness.

a percentage of total sampling effort) as measures of the average latitudinal gradient and its variability.

RESULTS

Measures of diversity

All measures of diversity were quite variable among the 32 bat communities (Table 3). In general, indices of richness and dominance were most variable and indices of evenness were least variable among sites based on relative measures of dispersion (coefficient of variation, cv). More specifically, PIE (cv = 21.20) and O (cv = 21.74) exhibited the least relative variation among sites whereas A (cv = 58.65) and SI (cv = 57.31) exhibited the most relative variation among sites. The degree of association between pairs of measures of diversity was generally high but variable. Correlations ranged from -0.01 between CE and MAR to ~ 1.00 between SHD and B.

Factor analysis reduced the 14 measures of diversity to two major axes (Fig. 2a). Eigenvalues for the first

two principal components were 9.88 and 2.72, and together accounted for 90.0% of the variation among communities regarding all measures of diversity. All variables were significantly ($P < 0.05$) correlated with PC1, and correlations were positive (Fig. 2b). Thus, PC1 reflects a general component of variation in the magnitude of diversity among sites. PC2 was correlated most highly with indices of species richness and evenness (Fig. 2b). Indices of species richness were correlated negatively and indices of evenness were correlated positively with this component. PC2 reflected the trade-offs between richness and evenness that integrate empirically to constitute local diversity.

The varimax procedure decomposed variation in diversity into aspects of species richness and evenness (Fig. 2c). The first rotated factor was significantly ($P < 0.05$) and most highly correlated with measures of species richness (Fig. 2d). The second factor was correlated significantly and most highly with measures of evenness (Fig. 2d).

TABLE 3. Extended.

Evenness				Dominance			Principal factors		Rotated factors		R_c
SHE	PIE	CE	O	SI	BP	MD	PC1	PC2	Factor 1	Factor 2	
0.73	0.72	0.44	0.57	3.53	2.22	0.49	-0.59	2.29	-1.95	1.33	9
0.25	0.24	0.15	0.23	1.32	1.15	0.13	-2.29	-0.73	-1.24	-2.06	18
0.33	0.39	0.20	0.28	1.64	1.33	0.23	-1.96	-0.16	-1.37	-1.41	19
0.61	0.71	0.28	0.40	3.42	2.10	0.48	-0.68	0.67	-0.95	0.05	21
0.69	0.79	0.33	0.46	4.80	3.01	0.57	-0.34	1.31	-1.12	0.76	26
0.72	0.85	0.31	0.47	6.69	3.44	0.64	0.47	0.46	0.05	0.66	41
0.66	0.81	0.27	0.41	5.17	2.70	0.58	0.07	0.11	-0.02	0.13	69
0.73	0.83	0.35	0.52	5.79	2.70	0.61	0.32	0.93	-0.37	0.91	52
0.71	0.89	0.27	0.39	9.09	5.54	0.68	0.52	0.34	0.16	0.60	85
0.74	0.91	0.29	0.44	10.97	5.95	0.72	1.37	-0.44	1.32	0.57	96
0.68	0.83	0.27	0.41	5.71	2.65	0.60	0.41	-0.29	0.50	0.05	101
0.62	0.82	0.22	0.33	5.53	3.24	0.59	-0.17	-0.08	-0.07	-0.18	101
0.62	0.80	0.23	0.36	4.93	3.15	0.57	-0.27	0.13	-0.29	-0.07	107
0.70	0.89	0.25	0.40	9.28	4.05	0.69	1.11	-0.98	1.49	0.00	106
0.58	0.77	0.19	0.33	4.43	2.61	0.54	-0.30	-0.49	0.10	-0.56	107
0.57	0.77	0.19	0.31	4.34	2.94	0.54	-0.38	-0.42	-0.01	-0.57	106
0.48	0.62	0.15	0.30	2.65	1.66	0.39	-0.80	-1.06	0.10	-1.33	107
0.67	0.85	0.24	0.42	6.52	2.70	0.62	1.31	-2.03	2.32	-0.66	112
0.69	0.89	0.25	0.36	8.87	5.42	0.68	0.46	0.11	0.27	0.38	111
0.54	0.67	0.20	0.34	3.03	1.79	0.44	-0.24	-1.17	0.59	-1.04	119
0.81	0.88	0.45	0.53	8.15	5.97	0.67	0.44	2.20	-1.12	1.94	114
0.37	0.45	0.16	0.28	1.80	1.37	0.26	-1.68	-0.50	-0.94	-1.49	114
0.63	0.80	0.23	0.36	5.08	2.39	0.57	0.57	-1.39	1.34	-0.67	95
0.72	0.88	0.31	0.41	8.06	4.27	0.66	0.22	0.89	-0.42	0.81	78
0.70	0.89	0.27	0.36	9.02	6.22	0.68	0.54	0.23	0.25	0.53	78
0.82	0.93	0.39	0.50	14.48	7.85	0.77	1.60	0.83	0.66	1.68	75
0.74	0.84	0.37	0.47	6.12	4.24	0.64	0.17	1.32	-0.74	1.11	73
0.65	0.73	0.30	0.45	3.67	2.02	0.51	-0.27	0.54	-0.56	0.22	72
0.65	0.87	0.21	0.34	7.76	3.66	0.65	0.82	-1.40	1.54	-0.51	101
0.80	0.94	0.35	0.48	15.60	8.20	0.78	2.03	-0.11	1.60	1.25	110
0.46	0.60	0.17	0.29	2.51	1.75	0.37	-1.38	-0.12	-0.96	-1.00	49
0.45	0.62	0.13	0.26	2.66	1.74	0.39	-1.05	-0.99	-0.13	-1.43	49
0.63	0.77	0.26	0.39	6.02	3.44	0.55					78.78
0.02	0.03	0.01	0.01	11.90	3.49	0.02					1146.31
21.89	21.20	31.16	21.74	57.31	54.32	27.81					42.98

Diversity differed among communities based on latitudinal affiliation (Fig. 2a; MANOVA, $F_{28,32} = 2.25$, $P = 0.014$). Regarding PC1 (Table 4), temperate communities were significantly less diverse than were tropical or subtropical communities whereas tropical and subtropical communities were indistinguishable. No significant differences among regions existed on PC2 (Table 4). Differences in diversity among sites also can be distinguished by examination of derived factors of evenness and richness (Fig. 2d). Temperate communities were different from both tropical and subtropical communities on the richness factor (Factor 1), whereas differences between tropical and subtropical communities were detectable on Factor 2. Temperate communities evinced relatively low species richness and low evenness. Tropical and subtropical communities evinced similar levels of diversity. Tropical communities attained high diversity primarily as a consequence of species richness, whereas subtropical communities attained higher diversity as a consequence of more even abundances.

Latitudinal gradients

Differences among regions reflected a continuous latitudinal gradient in Factor 1 and the two principal components (Fig. 3). Two of the three measures of species richness and two of the four measures of diversity also were significant linear functions of latitude (Table 5). The amount of variation in an index that was related significantly to latitude ranged from 0.27 for SHD to 0.35 for R_c . In general, evenness and dominance did not exhibit latitudinal gradients.

Because results were qualitatively the same regardless of the criterion for rarity, we only present those based on $1/R_c$. Latitudinal gradients exist regarding the number of both common and rare taxa; however, latitude had a stronger effect on the number of rare species. Compared to common species (95% CI for b_1 : -0.30 to -0.07), rare species (95% CI for b_1 : -1.05 to -0.34) increased more rapidly in richness toward the tropics (Fig. 4). Nonetheless, the proportional rate of increase in species richness toward the tropics was indistinguishable for common species (95% CI for b_1 : -0.02

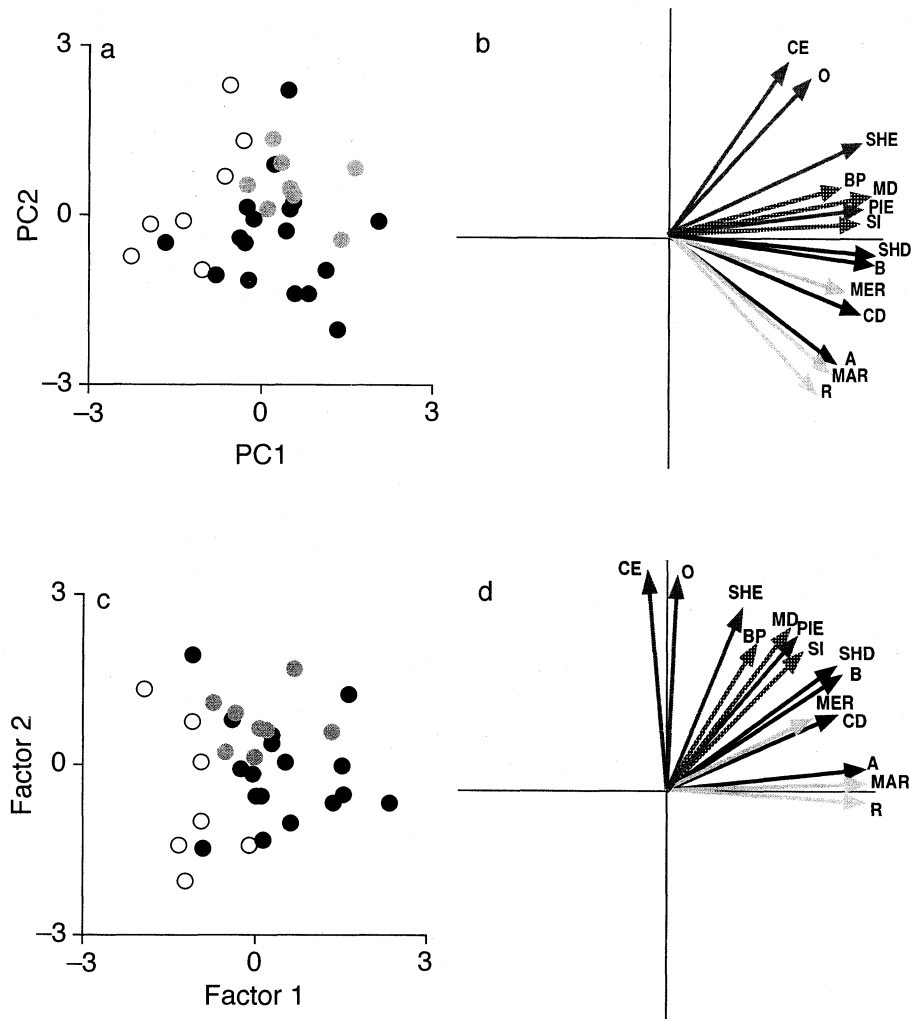


FIG. 2. The projection of each of 32 communities in two-dimensional diversity space (left panels) defined by (a) principal components and (c) rotated factors. Principal components correspond to the two main axes of variation in diversity among the 32 sites; Factor 1 corresponds to species richness and Factor 2 corresponds to species evenness. Temperate, subtropical, and tropical communities are indicated by white, gray, and black circles, respectively. The relationships of each measure of diversity with (b) principal components and (d) factors are depicted in right panels. The length and direction of each arrow indicate the magnitude and sign of correlation of each index with the corresponding derived axis, respectively. The black, light gray, dark gray, and hatched arrows correspond to indices of diversity, richness, evenness, and dominance, respectively. Acronyms for each measure of diversity appear in Table 2.

TABLE 4. Comparisons of aspects of diversity among tropical, subtropical, and temperate communities based on principal components as well as factors.

Dependent variable	ANOVA		Means		
	F_{\dagger}	P	Tropical	Subtropical	Temperate
Principal components					
PC1	10.54	<0.001	0.24 ^a	0.53 ^a	-1.18 ^b
PC2	2.93	0.069	-0.37 ^a	0.51 ^a	0.33 ^a
Factors					
Factor 1	8.72	0.001	0.43 ^a	0.06 ^a	-1.10 ^b
Factor 2	3.94	0.031	-0.12 ^a	0.74 ^b	-0.54 ^a

Note: Means for latitudinal regions that share an alphabetic superscript are statistically indistinguishable (Student-Newman-Keuls tests, comparison-wise error rate held constant at 5%).

† With $df = 2, 29$.

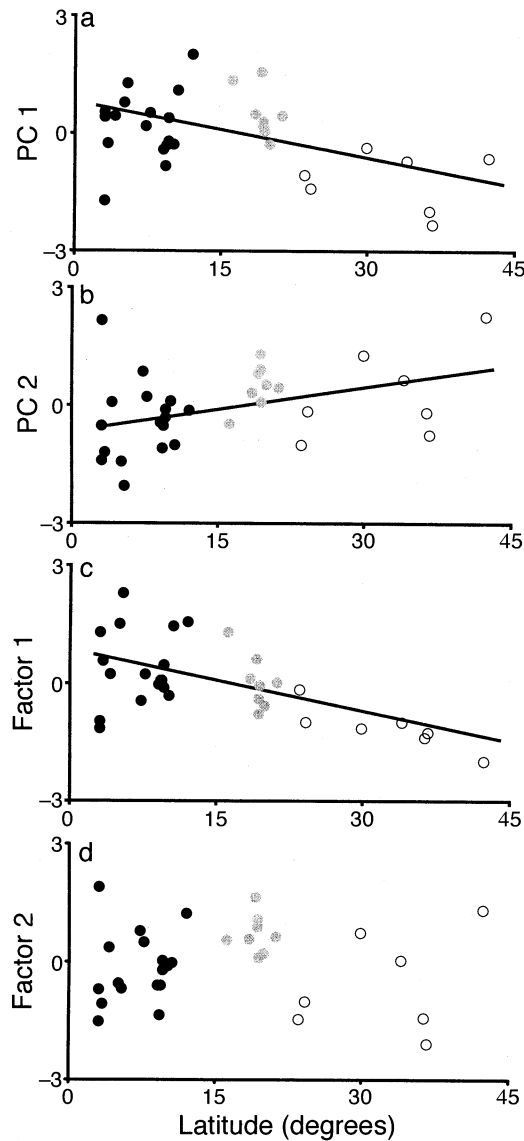


FIG. 3. Relationships of principal components and rotated factors with latitude for New World bats. Latitude accounted for a significant amount of the variation in both principal components (a and b) as well as the first rotated factor (c). In contrast, the regression of the rotated factor of evenness (Factor 2) on latitude was not significant (d).

to -0.01) and rare species (95% CI for b_1 : -0.02 to -0.01). For sites that differ by 1° latitude, the richness at the higher latitude will be $\sim 96\%$ of the richness at the lower latitude.

Sensitivity analyses indicated that measures of diversity for subsamples, on average, recapitulated the latitudinal gradient to the same degree as did the complete samples, even when subsamples constituted a small percentage of the original data (Fig. 5). Results within index classes based on richness, diversity, evenness, and dominance were always similar. Consequently, we illustrate results for only two of the available

indices for each of the four diversity classes. The environmental pattern among sites embodied by latitude is strong, and not extremely sensitive to the number of individuals sampled from each of the communities. Although mean characteristics of diversity were stable, variability increased with decreases in the size of subsamples. Nonetheless, even very small samples, on average, evinced the observed significant latitudinal gradient in species diversity.

Scale dependence of latitudinal richness gradients

Latitude accounted for much more of the variation in regional richness ($r^2 = 0.88$) than in local richness ($r^2 = 0.35$). Nonetheless, both relationships were significant (Fig. 6a). More specifically, almost three times as many species of bats are predicted to occur at the equator in regional faunas ($b_0 \pm 1$ SE; 124 ± 4 species) than in local communities ($b_0 \pm 1$ SE; 44 ± 4 species), and this difference was significant. Nonetheless, the rate of decrease of the number of species with increasing latitude was significantly higher for regions ($b_1 \pm 1$ SE; -2.89 ± 0.20 species) than for local communities ($b_1 \pm 1$ SE; -0.88 ± 0.22 species), suggesting that environmental filters (the proportion of the regional fauna occupying a local community) are most selective in tropical areas.

Local and regional richness

Species richness at the regional level accounted for a significant amount of the variation in species richness at the local level (Fig. 6b, $b_1 = 0.30$, $F_{1,30} = 17.91$, $r^2 = 0.37$, $P \ll 0.001$) and no evidence exists for a qua-

TABLE 5. Results of simple linear regression analyses between latitude and each of the measures of diversity (Table 1).

Measure	Intercept	Slope	r^2	Significance
PC1	0.649	-0.042	0.209	0.009†
PC2	-0.571	0.037	0.162	0.022†
Factor 1	0.864	-0.055	0.371	<0.001†
Factor 2	~ -0.001	~ 0.001	0.000	0.999
R_c	44.438	-0.877	0.346	<0.001†
MAR	5.982	-0.114	0.337	<0.001†
A	8.740	-0.174	0.292	0.001†
B	2.498	-0.030	0.282	0.002†
SHD	2.564	-0.030	0.271	0.002†
CD	10.874	-0.189	0.217	0.007
PIE	0.868	-0.007	0.199	0.010
MER	1.206	-0.018	0.181	0.015
MD	0.645	-0.006	0.170	0.019
SI	7.548	-0.098	0.098	0.082
BP	4.191	-0.048	0.081	0.115
SHE	0.677	-0.003	0.060	0.177
CE	0.244	0.001	0.027	0.373
O	0.376	0.001	0.012	0.545
R_r	123.729	-2.885	0.876	<0.001†

Notes: A dagger indicates significant regressions between latitude and a particular measure of diversity. Experiment-wise error rate was held constant of 5% by application of a Bonferonni's sequential adjustment within each of three separate analyses (principal components, derived factors, and the entire suite of diversity measures).

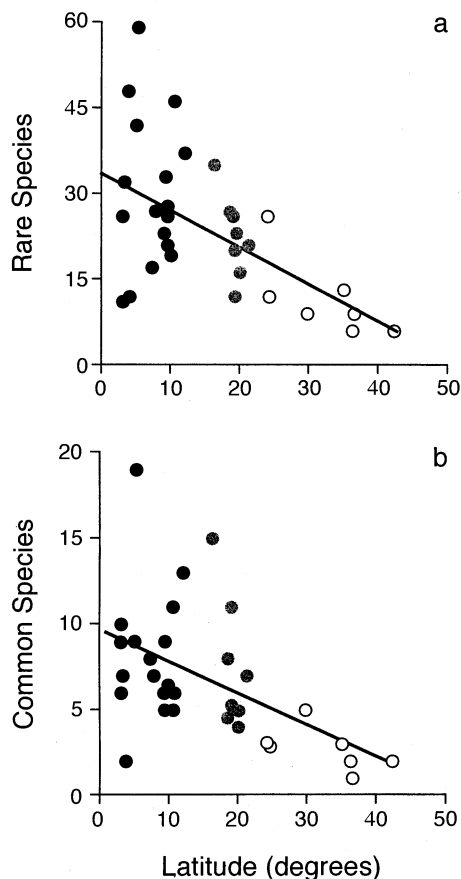


FIG. 4. Relationships between the number of (a) rare and (b) common species and latitude. Rare species were those with an abundance $< 1/R_c$ of the total number of individuals from a community. Latitude accounted for a significant amount of the variation in both abundance classes. White, gray, and black dots correspond to temperate, subtropical, and tropical communities, respectively.

dratic component (i.e., a nonsignificant [$P = 0.509$] quadratic coefficient in the second degree polynomial with a ΔR^2 of only 0.01) in the relationship. As the number of species increased in regional faunas, so did the number of species in local communities. Although this relationship was linear, it was more variable when the richness of regional pools was higher. Beta diversity, measured as species turnover between faunal pools and local communities, increased significantly with decreases in latitude (Fig. 6c, $b_1 = -0.009$, $F_{1,30} = 11.72$, $r^2 = 0.28$, $P = 0.002$) for the entire New World.

DISCUSSION

The latitudinal gradient in species diversity is one of the most well recognized and frequently substantiated patterns known to biogeographers. Nonetheless, this pattern rarely is evaluated for local communities, and almost all studies, regardless of spatial scale, consider only species richness. We substantiate that, albeit weaker than at the regional scale, a latitudinal gradient

in species richness exists at the community level for bats. In addition, latitude affects other aspects of diversity. Many of the existing measures of diversity are robust and can detect latitudinal patterns even with relatively small sampling effort. We demonstrate that latitudinal gradients at local and regional levels are quantitatively different, with regional richness being more strongly influenced by latitude than is community richness. Moreover, the scale dependence of latitudinal richness gradients is further suggested by latitudinal increases in the magnitude of beta diversity.

Gradients of diversity

Classically, latitudinal gradients of diversity have been explored by evaluating the relationship between regional richness and latitude. Indeed, our results regarding latitudinal gradients in species richness at both the regional and local level corroborate previous findings. Gradients in species richness should result when environmental variation affects the number and diversity of resources (Rotenberry 1978). Latitudinal increases in the kinds of resources utilized by New World bats are implied by latitudinal increases in the number of trophic guilds (Stevens and Willig 2000, Willig 2000). The trophic diversity of bats in the New World ranges from only aerial insectivores at the highest latitudes to the full complement of trophic strategies (seven) at the equator. Thus, latitudinal gradients in species richness result at least in part because increases in the number of resource types (e.g., seeds, fruit, insects, nectar, fish) allow for increases in the number of trophic guilds. Furthermore, increases in resource abundance with latitude may also affect the number of species within trophic guilds. Thus, the latitudinal gradient in bat species richness likely results from the interaction of a number of environmental gradients that affect community composition at a number of different levels.

Few empirical investigations have explored variation in evenness along environmental gradients (Drobner et al. 1998, Weiher and Keddy 1999). Moreover, theory to explain changes in species evenness is not as well developed as that for species richness or diversity. Changes in evenness have been predicted to be associated with changes in stability (Rotenberry 1978) as well as stress and biomass (Drobner et al. 1998). Communities should be less even in situations of low stress and high biomass because these circumstances allow a few species to dominate community composition (Grime 1973a, b, Drobner et al. 1998). We find no empirical support for this prediction given the degree to which decreases in latitude can be associated with decreases in environmental variability and increases in productivity (Rosenzweig 1995). No latitudinal gradient existed with respect to the evenness axis derived from factor analysis. Moreover, the lack of a latitudinal gradient was not just a consequence of the derived evenness axis being an amalgam of all diversity indi-

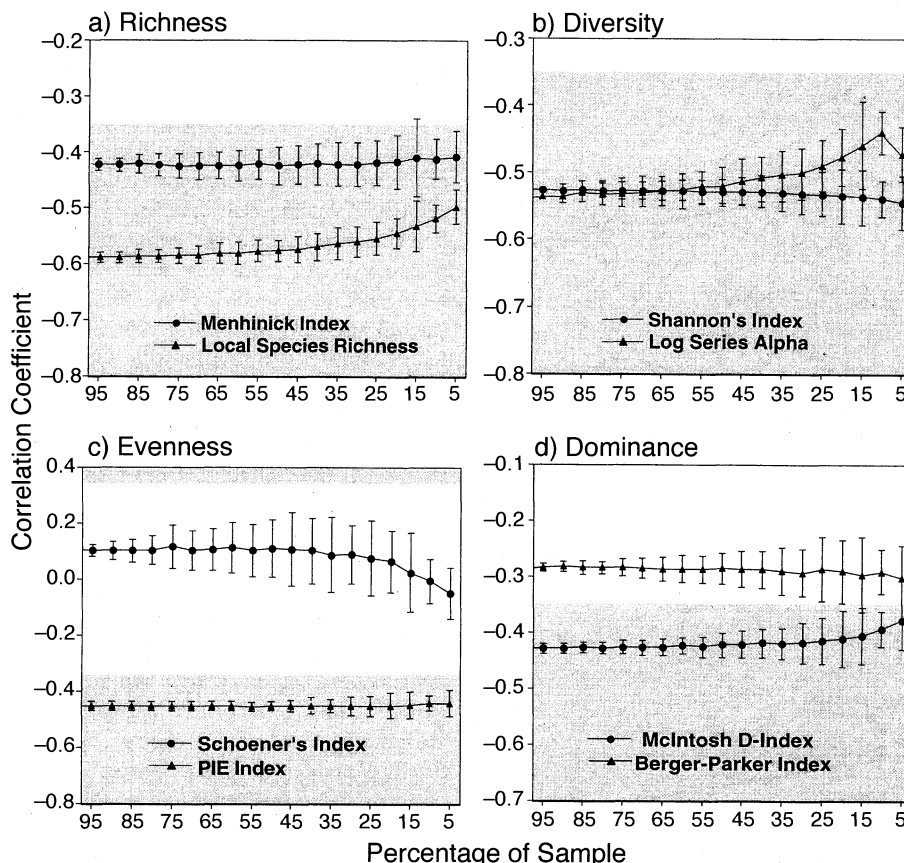


FIG. 5. The ability of diversity indices to detect a latitudinal gradient, as measured by the correlation coefficient, is not greatly affected by changes in sampling intensity. An index is insensitive when its correlation with latitude remains stable, regardless of sample size. Two representative indices for each class of measure illustrate the general trend: (a) richness, (b) diversity, (c) evenness; and (d) dominance. Because the number of communities is constant in all analyses, the correlation coefficient is significant at the 0.05 level if the absolute value of its magnitude exceeds 0.349 (gray shading). Error bars represent ± 2 SD.

ces; it was also true of those evenness indices which were orthogonal to species richness.

Although latitude likely reflects global changes in productivity, it significantly affects only the richness component of diversity. Nonetheless, changes in diversity due primarily to changes in evenness may only be detected over relatively short environmental gradients, or those that only entail changes in the amounts of common resources and not changes in the number of resources. When gradients become sufficiently extensive so as to entail variation in both the amount and kinds of resources, variation in diversity may stem primarily from changes in species richness. If changes in species richness reflect changes in available energy, and changes in evenness reflect variation in environmental stability, then the types of environmental changes associated with latitude are more linked to considerations of energy than to stability. Indeed, theoretical predictions addressing how diversity might change along environmental gradients need to be tempered to take into account that gradients reflecting qualitative environmental differences may affect patterns of di-

versity differently than do gradients that reflect only quantitative environmental differences.

From a mathematical perspective, indices of species richness and evenness should be independent components of diversity (Smith and Wilson 1996). Although this need not be true from an empirical perspective, spatial variation in the magnitude of richness and evenness are independent (two orthogonal factors distinguished by factor analysis) for New World bats. Moreover, spatial variation in two evenness indices (CE and O) was uncorrelated with species richness (R_c). Nonetheless, the independence of these two components of diversity when measured along a gradient of latitude for New World bats applies only to magnitude. These components are related by virtue of their variances. As the magnitude of richness increases, variation in evenness decreases. Similarly, as the magnitude of evenness increases, the variation in richness decreases. Although this pattern has been reported for plant communities (Weiher and Keddy 1999), this is the first report for animal communities and may suggest a general characteristic of how diversity varies in nature. Thus, to

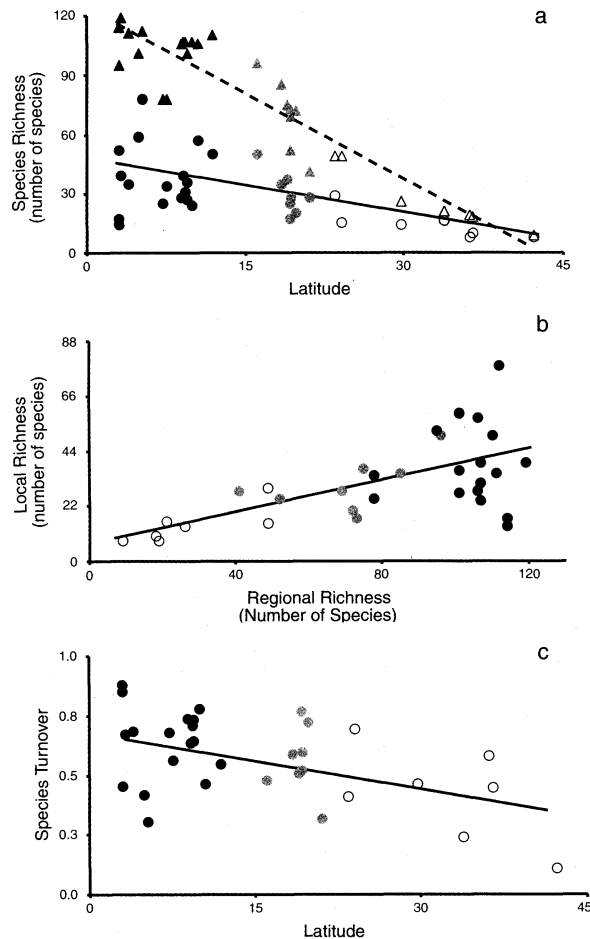


FIG. 6. Significant relationships between (a) local species richness (solid line) and regional species richness (dashed line) with latitude for New World bats. (b) Significant relationship between local and regional richness of bats in the New World. (c) Significant relationship between species turnover and latitude for New World bats. White, gray, and black dots correspond to temperate, subtropical, and tropical communities, respectively.

the degree that latitude reflects a gradient in productivity, concomitant changes in diversity and productivity are constrained. The relationship between richness and evenness may reflect the naturally constrained way in which species are added to species-rich communities. With decreases in latitude, the number of rare species increases at a faster rate than does the number of common species. Moreover, when species richness is high, the addition of rare species affects richness disproportionately more than it affects evenness; the increment in richness is relatively greater than the decrement in evenness. At high species richness, the addition of rare species has a dampened effect on evenness, giving rise to a situation where variation in evenness is low.

Scale dependence

Although latitude accounts for a significant amount of the variation in species richness at the community

level, this relationship is much weaker than at the regional level. At least two explanations may account for such scale dependence.

First, mechanisms that give rise to latitudinal gradients may be scale dependent. The weak latitudinal gradient at the community level may simply reflect effects of latitude on species richness at the regional level. Latitude, or those environmental gradients with which it is correlated, may only set the upper limit to local species richness. From this upper bound is subtracted species who cannot tolerate particular environmental regimes or competitive interactions germane to the structure of the actual community. Although regional richness sets the upper bound, local conditions determine the realized number of species in the community. If the richness of only a few communities approaches the limit set by regional species pools and there is a latitudinal gradient at the regional scale, a weaker yet significant latitudinal gradient in species richness at the community level may result.

Second, scale dependence may be a pervasive characteristic of macroecological patterns. For example, distributions of body size are right-skewed at continental scales, log-normal at regional scales, and log-uniform at local scales (Brown and Nicoletto 1991). Scale dependence in the strength of macroecological patterns could be the common result of two interacting factors. Sample sizes underlying most macroecological patterns are smaller for communities than for regions. Thus, the reason many ecological patterns are scale dependent may be because regional scales comprise more data and naturally manifest stronger patterns (Gaston and Blackburn 1999). Alternatively, larger scales likely integrate greater quantities of environmental variability than do smaller scales. If local sites are variable when combined to form regional patterns, this variability will be homogenized and likely will cause local and regional patterns to differ. The greater the variability among sites within a region, the less the regional characteristic will characterize any one of the sites. The scale dependence of macroecological patterns makes generalization tenuous, and only by improved understanding of how mechanisms and resultant patterns translate across spatial scales will macroecologists be able to attain a broader synthesis.

Beta diversity

Tropical and subtropical communities attain similar degrees of high diversity, but they do so in different ways. Tropical communities are characterized by relatively high species richness and relatively low species evenness, whereas subtropical communities are characterized by the opposite pattern. Trade-offs between increasing richness or increasing evenness that facilitate increases in diversity may be related to levels of beta diversity. In situations where beta diversity is high, relatively more species are available to colonize communities and increases in diversity may be facilitated

more easily by increases in species richness. When beta diversity is low, however, relatively fewer species are available for colonization and increases in diversity may be facilitated more easily by changes in the evenness of species already in the community. Differences in beta diversity between subtropical and tropical communities may explain how they achieve similarly high levels of species diversity while exhibiting consistent differences regarding evenness and richness.

Increases in beta diversity with decreases in latitude may be a consistent attribute of mammalian faunas. Kaufman (1998) found that terrestrial mammals in North America exhibited a similar latitudinal pattern of beta diversity to that quantified here. Although she found no significant difference in beta diversity between the temperate and tropical zones, species turnover increased significantly with decreases in latitude. The latitudinal gradient in beta diversity was stronger for terrestrial mammals than for bats (terrestrial mammals, $r^2 = 0.50$; bats, $r^2 = 0.28$). Beta diversity of terrestrial mammals was a significant function of latitude in the temperate zone and unassociated with latitude in the tropics.

The ecological interpretation of beta diversity is straightforward. Beta diversity results from species-specific responses to variation along environmental gradients (Shmida and Wilson 1985). Thus, beta diversity should increase with the magnitude of environmental heterogeneity within a region. Significant increases in beta diversity with decreases in latitude for both terrestrial and volant mammals suggests that both groups perceive the tropics as more heterogeneous than temperate areas. Variation in beta diversity also is a reflection of species- or group-specific niche breadth. Taxa with relatively high beta diversities should exhibit relatively narrow tolerances for heterogeneity (Harrison et al. 1992). Kaufman's terrestrial mammals disproportionately comprise small mammals (rodents and marsupials). Compared to bats, these small mammals were influenced more by environmental heterogeneity characterized by changes in latitude, and this may reflect differences in mobility, and hence, differences in the way these two groups deal with environmental heterogeneity.

The volant nature of bats has major implications for their foraging behavior, population dynamics, and ultimately community organization (Willig 1986, Willig and Moulton 1989, Findley 1993, Stevens and Willig 1999, 2000). Instead of specializing on particular facets of heterogeneity, the best strategy for bats may be to exploit their high mobility and integrate the environmental heterogeneity encountered over relatively larger spatial scales. Thus, patterns of beta diversity may reflect both the amount of variability along an environmental gradient and the grain at which a group of organisms perceives its environment. To this end, interpretations of differences in beta diversity should con-

sider not only environmental differences among sites but also ecological differences among organisms.

Implications for the conservation of New World bats

Bats exhibit their highest levels of alpha, gamma, and beta diversity in the tropics, intermediate levels in the subtropics, and lowest levels in the temperate zones. Coincident with the increase in beta diversity, as one moves toward the equator, gamma diversity of a region becomes less reflective of the actual number of species residing at the local level. Gamma diversity (the number of species whose geographic distributions overlap a point on a range map) has often been used to characterize biogeographic patterns in local diversity and to make decisions regarding conservation priorities (Rebelo and Siegfried 1992, Pomeroy 1993, Lombard et al. 1995, 1997, Williams et al. 1996, Kerr 1997). Ironically, tropical and subtropical areas represent the greatest conservation priorities (Myers 1980, Soule and Kohm 1989, Mares 1992), but the metric typically used to determine places of greatest importance for conservation efforts (gamma diversity) may provide only limited utility toward identifying areas of elevated local species richness. As data continue to be collected regarding the composition of local communities, dependence on surrogates such as gamma diversity will lessen. Nonetheless, latitudinal changes in beta diversity should admonish the conservation community of the potentially loose linkage between gamma and alpha diversity in tropical and subtropical systems, and emphasize the importance of continued collection of intensive inventories at the community level to accurately chart conservation priorities.

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