

# Latitudinal gradients in the phenetic diversity of New World bat communities

Richard D. Stevens, Michael R. Willig and Richard E. Strauss

Stevens, R. D., Willig, M. R. and Strauss, R. E. 2006. Latitudinal gradients in the phenetic diversity of New World bat communities. – *Oikos* 112: 41–50.

Although the examination of latitudinal gradients of species richness is common, little attention has been devoted to other components of biodiversity such as phenetic diversity. Because the phenotype reflects aspects of an organism's environment, ecological relationships and evolutionary history, measures of phenetic diversity likely provide complimentary information to that of species richness, and may provide unique insights for understanding the mechanistic basis to patterns of biodiversity. Herein, we evaluate latitudinal gradients in the phenetic diversity of 32 New World bat communities. Seven morphological characters were used to estimate phenotypic variation among bat species within local communities. Principal components analysis decomposed this variation into axes of size and shape. Three measures of phenetic diversity were calculated separately for size and for shape axes. The range of species scores on a particular axis described the amount of phenetic variation encompassed by species in a community. The standard deviation of minimum spanning-tree segment lengths described uniformity of species. Average nearest-neighbor distances described local packing. We separately regressed these six measures on local species richness and latitude separately. Variation in species richness accounted for a significant amount of variation in each measure of phenetic diversity. Latitude also accounted for significant variation in phenetic diversity except for the standard deviation of minimum-spanning tree segment lengths and the average nearest-neighbor distance on the shape axis. More importantly, gradients in phenetic diversity were significantly different than would be expected as a consequence of latitudinal gradients in species richness. Nonetheless, when variation among communities regarding the richness and composition of their regional faunas was taken into consideration, differences between empirical and simulated gradients were nonsignificant. Thus, factors that determine the composition of regional faunas have a great impact on the phenetic diversity of communities and ultimately the latitudinal gradient in biodiversity.

*R. D. Stevens, M. R. Willig and R. E. Strauss, Dept of Biological Sciences and The Museum, Texas Tech University, Lubbock, TX 79409-3131, USA. Present address for RDS: Dept of Biological Sciences, Louisiana State Univ., Baton Rouge, LA 70803, USA (rstevens@lsu.edu).*

The latitudinal gradient in species diversity is one of the earliest and most frequently described biogeographic patterns characterizing the distribution of taxa across space and time (Willig et al. 2003). Latitudinal effects on mammalian species diversity manifest at a number of levels in the taxonomic hierarchy (Kaufman 1995), at multiple spatial extents (Lyons and Willig 1999, 2001),

and at different ecological scales (Stevens and Willig 2002). Although latitudinal gradients in diversity have represented important foci in the development of ecological theory, the empirical characterization of variation among communities has been limited primarily to the richness and to a lesser extent relative abundances of co-existing species (Roy et al. 2001, Stevens and Willig

Accepted 10 June 2005

Copyright © OIKOS 2006  
ISSN 0030-1299

2002). Nonetheless, taxonomic diversity is not the only aspect of biodiversity that may be affected by latitude and its correlates. Different components of biodiversity (e.g. functional, genetic, or interaction diversity) may or may not exhibit similar geographic variation. Moreover, it is uncertain whether these basic constituents of biodiversity respond in an independent fashion along environmental gradients, or whether they co-vary spatially.

Phenotypic attributes of species have a profound impact on their ecology and provide an integrated view of ecological relationships over space and time (Wainright and Reilly 1994). For example, to the degree that morphology determines the ecological characteristics of a species, it may limit distribution by affecting the coexistence of populations in local communities (Ricklefs and Miles 1994). Moreover, morphology, especially body size, is a useful predictor of species-specific characteristics such as metabolic rate, energy use, home range-size, population density, population growth rate, and food particle size (Brown 1995). Morphology has been used extensively to inform rules that govern the assembly of ecological communities (Ricklefs and Travis 1980, Bowers and Brown 1982, Moulton and Pimm 1987, Stevens and Willig 2000). Lastly, morphological measures prove to be excellent descriptors of the trophic position of bat species in the New World and may reflect the outcome of ecological interactions among sympatric species (Stevens and Willig 1999).

To be useful as a descriptor of biodiversity, phenotypic variation should describe the ecological relationships among species that characterize their organization within communities. Measures of phenetic diversity reflect the variety of phenotypes inhabiting a particular community, and describe the distribution of species within phenotypic space (Fenton 1972, Findley 1973, Foote 1992, Roy and Foote 1997, Fenton and Bogdanowicz 2002). More specifically, the size of the phenetic volume and the distribution of species within that volume are analogous to richness (i.e. magnitude) and evenness (i.e. dispersion) components of species diversity, respectively. Communities can have high phenetic diversity relative to other communities if they occupy a larger phenetic volume due to the presence of species that are phenotypically novel. Similarly, communities can have relatively high phenetic diversity if they possess species that are more evenly distributed within a particular phenotypic volume. Because phenetic and taxonomic diversity measure different aspects of the structure of communities, geographic patterns in phenetic diversity provide alternative perspectives regarding patterns of biodiversity that may not be obtainable by examination of taxonomic diversity alone (Findley 1973, Foote 1993, Aguirre et al. 2003). Herein, we describe the phenetic diversity of 32 New World bat communities and evaluate latitudinal gradients regarding this component

of biodiversity. We evaluate the strength of the association between phenetic diversity and species richness, and determine the degree to which latitudinal gradients in phenetic diversity can be explained solely by latitudinal changes in the number of species or the composition of regional species pools.

## **Material and methods**

### **Structure of communities and measurement of phenetic diversity**

Species composition of 32 New World bat communities (Appendix 1) was derived from the literature. These studies were distinguished from a large number available based on criteria that spatially and temporally bounded sites so as to enhance the likelihood that they addressed the structure of a single community. Bats were primarily censused by mist netting and effort in all seasons during which bats were active needed to be employed so as to enhance the detection of rare or hard to capture species. Details regarding these criteria can be found in Stevens (2002) and Stevens and Willig (2002).

For each species, we obtained measurements of seven morphological characters. These characters reflect variation in body-size (i.e. forearm length and greatest length of skull), as well as cranial geometry and associated trophic structures (i.e. greatest length of skull, condylobasal length, length of maxillary toothrow, breadth across upper molars, width across post-orbital constriction, breadth of braincase). In most cases, means were determined from a sample of at least four males and four females of each species. Measurements came from Swanepoel and Genoways (1979), the description of the actual community, other literature sources, or museum specimens. Morphological variables were log-transformed prior to analyses to enhance the likelihood of fulfilling assumptions of the multivariate approach and to enhance the interpretation of axes (Marcus 1990).

We used principal components (PCA) derived from a covariance matrix to create composite morphological axes that reflect the salient features of body-size and shape variation expressed by continental New World bats. Correlation analyses were used to interpret principal components (PCs). Principal components based on morphological data with loadings that are all positive and relatively uniform in magnitude represent variation in body size, whereas PCs with loadings that are variable in magnitude and sign represent shape variation (Marcus 1990, Klingenberg 1996). Only the first two PCs were retained for further analyses. In this particular analysis, these two components characterized the major axes of variation in size and shape.

The phenetic diversity of species within communities was estimated in three ways on size and shape axes (Fig. 1). To estimate the extent and uniformity of the distribution of species on a particular axis, we calculated the range of PC scores and the standard deviation of minimum spanning-tree segment lengths that connected all species in the community on that PC axis (Ricklefs and Travis 1980). The average euclidean distance between species and their nearest morphological neighbor estimated local species packing or the degree of crowding in morphological space (Findley 1976, Ricklefs and Travis 1980, Schum 1984, Shepherd 1998).

### Inferential analyses

We used orthogonal polynomial regression analysis to determine the relationship between each measure of phenetic diversity and species richness or latitude. The advantage of orthogonal polynomial regression analysis is that the intercept, linear, quadratic, and higher order regression coefficients are independent of each other, thereby allowing the decomposition of relationships into general components of magnitude as well as into linear and nonlinear rates of change (Sokal and Rohlf 1995). We used a function written in Matlab (Math Works 1995) to conduct the procedure described in Dutka and

Ewens (1971) for executing orthogonal polynomial regressions when values of the independent variable are not evenly spaced. Experiment-wise error rate was held at 5 percent for each morphological component (i.e. size or shape) by application of a Bonferroni sequential adjustment (Rice 1989).

Latitudinal gradients in phenetic diversity could result primarily from latitudinal gradients in species richness Huston 1997 because the morphological volume of a community is likely to increase by chance alone as the number of species increases toward the equator. Thus, we conducted simulation analyses to evaluate if observed gradients in phenetic diversity are due to the underlying gradient in species richness. Phenetic diversity gradients that are significantly different than those simulated from the underlying latitudinal gradient in species richness offer unique insights into the complexity of biodiversity gradients. In these analyses, species were drawn randomly from a pool comprising all continental New World bat species. For each community, a simulated community was assembled by randomly selecting from the pool the same number of species as occurred in an actual community. Measures of phenetic diversity were calculated for each simulated community and then regressed on latitude using orthogonal polynomial regression analysis. This process was then iterated 1000 times to create a distribution of gradients in phenetic diversity that could be produced by the empirical latitudinal gradient in species richness. Parameter estimates ( $b_0$ ,  $b_1$ ,  $b_2$ ) characterizing the latitudinal gradient in phenetic diversity from actual communities were then compared with the distribution of like values from the simulated gradients to determine significance. The position of the observed parameter estimate relative to the distribution of simulated values describes the probability that the observed value was randomly obtained from the simulated distribution. Parameter estimates were deemed significantly different when they were among the rarest of values in either tail of the simulated distribution. Alpha levels for each morphological component (i.e. size or shape) were determined by a Bonferroni sequential adjustment (Rice 1989).

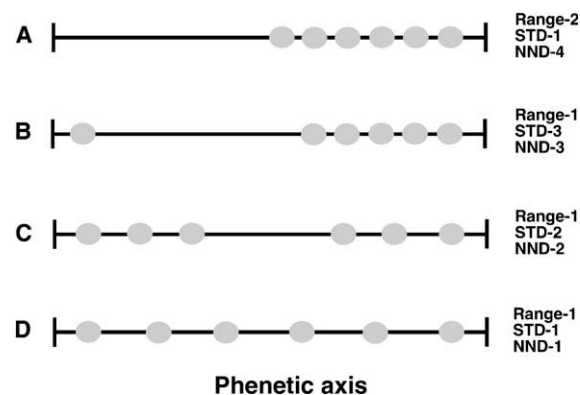


Fig. 1. Diagrammatic representation of variation in phenetic diversity and the differential sensitivity of indices of diversity to this variation. A through D represent the dispersion of species (grey dots) in four different communities on a hypothetical phenetic axis. Range refers to the amount of space on a phenetic axis that is represented by all species in a local community. STD represents the standard deviation of segment lengths of a minimum spanning-tree connecting all species in a community. NND represents the average nearest-neighbor distance and is a measure of the degree of species packing or crowding in phenetic space. Numbers next to Range, STD or NND correspond to their rank value for the four communities. Low values represent high phenetic diversity. When species occupy a relatively small space (A) or are unevenly distributed in phenetic space (B) they exhibit low phenetic diversity. When species are more evenly distributed within a large space (C and D), they exhibit high phenetic diversity.

A second suite of analyses addressed whether gradients in phenetic diversity are different from those generated by drawing species at random from the regional pool of species surrounding each community. In these analyses, simulated communities were assembled as before, except that species were drawn from a taxonomically restricted pool (i.e. regional fauna) comprising only those species whose geographic distributions encompassed the location of a particular community. This provided a more restrictive constraint in that only those species with the dispersal potential to be part of a particular community were included in analyses. Distribution maps for each species were modified from

Willig and Selcer (1989) and Willig and Sandlin (1991) using information in Hall (1981) and Koopman (1982), and updated by Lyons and Willig (1999) based on Eisenberg (1989) and Redford and Eisenberg (1992). All simulation analyses were performed using Matlab (Math Works 1995).

## Results

### Characterization of phenetic diversity

The first two principal components accounted for approximately 87% of the variation among continental New World bat species regarding the seven morphological characters. The first PC was correlated positively and significantly ( $P < 0.05$ ) with each morphological character and represents the principal axis of size variation among species (Fig. 2). Correlations of the second PC with the seven morphological characters were variable in magnitude, positive for measures of width, and negative for measures of length. All cranial measures were significantly ( $P < 0.05$ ) correlated with the second PC, whereas forearm length was not correlated significantly with this axis. Consequently, this axis reflects the degree of cranial roundness (Fig. 3). Large, positive values on the second PC indicate species with a

short and round cranium (i.e. frugivores), whereas large negative values indicate species with a long and narrow cranium (i.e. nectarivores). In addition, characters that reflect variation in tooth area (i.e. breadth across the upper molar and length of maxillary toothrow) were correlated more strongly with the second PC than were characters that reflect cranial features that facilitate muscle attachment (i.e. breadth of braincase and width of the post-orbital constriction).

### Empirical patterns

Phenetic diversity varied with changes in species richness (Fig. 3A). Statistically significant coefficients of determination ranged from 0.79 (range of species scores on size axis versus species richness) to 0.14 (standard deviation of minimum spanning tree segment lengths on the size axis versus species richness). In all significant cases, the range of phenotypes was related positively to species richness, whereas variability of minimum-spanning tree segment lengths and averages of nearest-neighbor distances was related negatively to species richness.

Significant latitudinal gradients in phenetic diversity existed on size and shape axes (Fig. 3B). Statistically significant coefficients of determination ranged from 0.67 (between latitude and the range of species scores on the size axis) to 0.14 (between latitude and the average nearest-neighbor distance among species on the size axis). In all significant cases, increases in the range of species scores were associated with decreases in latitude, whereas the increase in phenetic diversity involving nearest-neighbors was associated with an increase in latitude.

### Differences between empirical and simulated gradients

Latitudinal gradients in phenetic diversity were not solely a consequence of variation in species richness (Appendix 2). For all three measures of phenetic diversity measured on the size axis, linear coefficients were smaller than expected given changes in species richness. On the shape axis, the magnitude of phenetic diversity was lower for all three measures and the linear slope of the relationship between latitude and average nearest-neighbor distance was smaller than expected given empirical gradients in richness. Significant differences existed even after a Bonferroni sequential adjustment. On the size axis, the linear slope for the range of species phenotypes was much smaller than expected given observed changes in species richness. On average, the range of species was smaller in empirical communities than in those created by simulation.

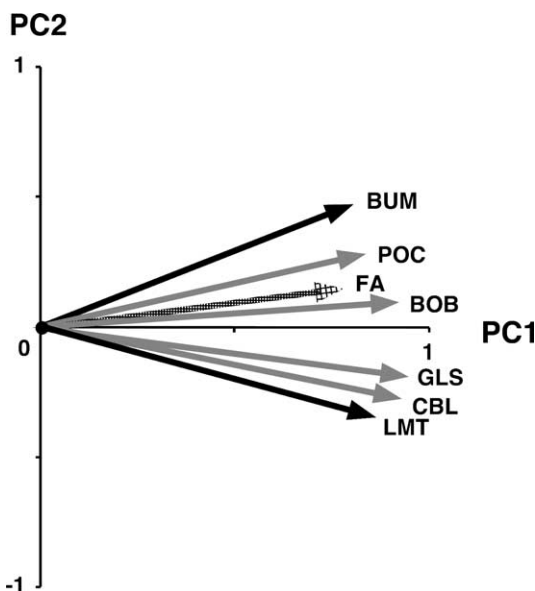
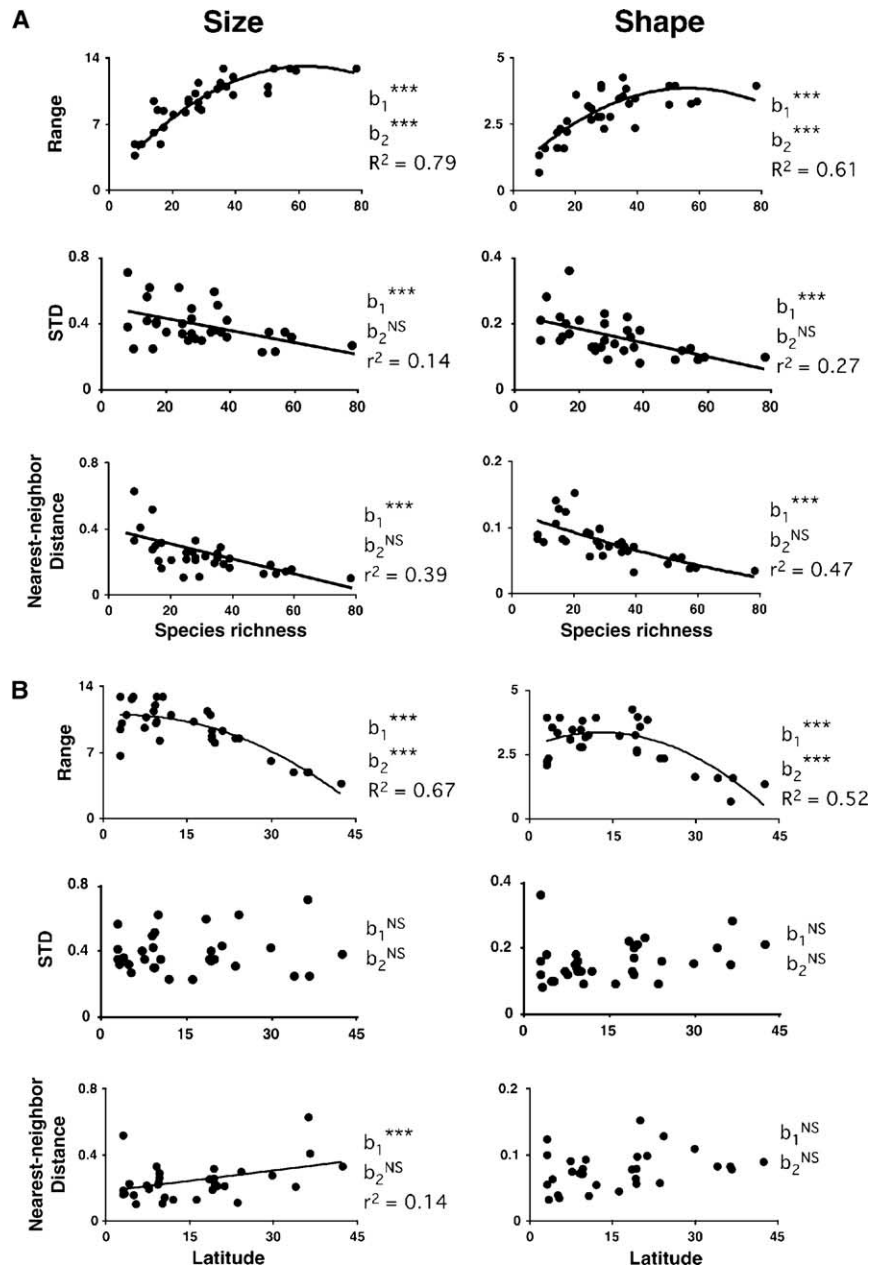


Fig. 2. Correlogram depicting the magnitude and direction of correlations of the original morphological characteristics with the first two axes from principal components analysis. Black arrows represent dental attributes (breadth across upper molars (BUM) and length of maxillary toothrow (LMT)). Grey arrows represent cranial attributes (width of post-orbital constriction (POC), breadth of braincase (BOB), greatest length of skull (GLS) and condylobasal length (CBL)). The hatched arrow represents forearm length (FA).

Fig. 3. Relationships of phenetic diversity with species richness (A) and latitude (B) on size (left column) and shape (right column) axes. Range refers to the range of phenetic values among species. STD refers to the standard deviation of minimum spanning-tree segment lengths.  $b_1$  refers to the linear slope,  $b_2$  refers to the quadratic slope,  $r^2$  refers to the coefficient of determination associated with the linear model,  $R^2$  refers to the coefficient of determination associated with the quadratic model. NS refers to a nonsignificant regression whereas asterices refer to significance. Solid lines indicate situations in which variation in the independent variable accounted for a significant amount of the variation in a measure of phenetic diversity (determined by orthogonal polynomial regression analysis). Experiment-wise error rate was held constant at five percent for measures of size separately from measures of shape by imposing two different Bonferroni sequential adjustments (Rice 1989).



Regionally constrained models further illustrate how biogeographic processes determining the composition of regional faunal pools in conjunction with local processes affecting species richness influence local gradients in phenetic diversity (Appendix 2). Only two analyses exhibited differences between simulated and empirical communities when decisions were based on the traditional level of alpha ( $P < 0.05$ ). Although all three p-values were close to traditional levels of significance, no significant differences between observed and simulated latitudinal gradients existed after a Bonferroni sequential adjustment. In all cases, variation in the composition

of regional faunas was sufficient to account for latitudinal gradients in the phenetic diversity of bat communities.

## Discussion

The spatial variation in phenetic diversity of bat communities is considerable throughout the New World. As with other measures of biodiversity (Stevens 2002, Stevens and Willig 2002, Stevens et al. 2003, Willig et al. 2003), phenetic diversity is greatest toward the

equator and least toward the poles. Although latitudinal gradients in phenetic and taxonomic diversity are inter-related, some lack direct correspondence. Indeed, the range of phenotypes on both the size and shape axes exhibits rapid increase at low to moderate species richness, with changes becoming asymptotic with further increase in the number of species. To this end, morphological volume and species richness provide two unique estimates of variation in the magnitude of biodiversity and how it varies spatially. This is further exemplified by differences in latitudinal gradients between empirical communities and communities generated from the New World pool; the underlying gradient in species richness cannot account for gradients in phenetic diversity measured on the size axis.

Those processes that determine the composition of regional faunas have important influences on the phenetic variation of species within local communities. Indeed, as determined by simulation analyses using species drawn from regional faunas, both local and regional processes influence the types of species from which communities are assembled and thus determine much of the variation among sites regarding phenetic diversity. Differences in results generated from the two simulation analyses likely reflect differential spatial diversification of particular bat families in the New World. Indeed, different families have different latitudinal termini to their geographic distribution (Findlay 1993, Stevens 2004). Accounting for these differences by using regional species pools eliminates much of the difference between simulated and empirical gradients. Considerations of the interplay between local and regional processes, and how this interplay translates biogeographically will enhance an understanding of the community ecology of New World bats, as well as the multifaceted gradients of biodiversity.

A tight linear correspondence between species richness and phenotypic volume would indicate that as species richness increases, species are added preferentially to the periphery of a morphological volume (Roy et al. 2001). While this has been reported for a wide variety of organisms (summarized in Ricklefs and Miles 1994) including birds (Ricklefs and Travis 1980), fish (Strauss 1987, Winemiller 1991) and gastropods (Roy et al. 2001), this is not so for entire communities of bats. Latitudinal gradients in phenetic diversity were consistently asymptotic for indices measuring the range of species in morphological space. The asymptotic relationship suggests that at intermediate and high levels of species richness, taxa are differentially added to the center of the morphological space and relatively fewer forms are added at the periphery. Indeed, different families and functional groups of bats, and their associated morphological differences, do not gradually increase from the poles to the equator. The biogeographic radiation of these groups in the New World likely contributes to the

form of the relationship between phenotypic range and species richness. In a narrow zone within the subtropics, the number of families increases to eight of the nine found in the New World (Stevens, 2004). Moreover, the largest and smallest New World taxa, such as phyllostomines and myotines, respectively, while not always abundant, are widely distributed and commonly occurring throughout the tropics and subtropics. Thus much of the range on the size axis is well represented in the subtropics with a decelerating decrease toward the equator.

A similar biogeographic pattern occurs with respect to the shape axis. The shape axis is represented by frugivorous bats on one end and by nectarivorous bats on the other. Moreover, frugivores and nectarivores are pervasive components of tropical and subtropical communities. Once in the subtropic, much of the range of phenotypes on the shape axis has been established by species from these two functional groups. Further latitudinal changes in community composition lead to only dampening increases in the range of phenotypes on this axis. Moreover, this pattern combined with latitudinal variation in nearest-neighbor distances suggests that spatial variation on the shape axis reflects resource expansion of taxa that occurs towards the equator. An increase in phenotypic volume in the absence of increases in nearest-neighbor distances is indicative of niche diversification due to resource expansion (Winemiller 1991). Nonetheless, the asymptotic increase in the range of phenotypes on the shape axis suggests that the rate of resource expansion declines towards the equator.

Whereas niche expansion characterizes the latitudinal increase in phenetic diversity on the shape axis, species packing characterizes the increase on the size axis. This is indicated by diminishing increases in the ranges of sizes and simultaneous decreases in nearest-neighbor distances. As the range of sizes expands within a community, constituent species also become more tightly packed within this space. Within communities, numbers of species from all bat families increase towards the equator (Stevens 2004). This results in a tropical increase in the range of sizes found in communities. As latitude decreases in the temperate zone, niche expansion likely contributes to increases in phenetic diversity on the size axis. Nonetheless, once in the subtropics, most families of bats are represented in communities, and niche expansion diminishes towards the equator. Once this has transpired, latitudinal increases in species richness are facilitated by adding species within the same range of body sizes as opposed to adding markedly larger or smaller sizes, and increasing the range by decreasing nearest-neighbor distances.

Differences in the degree of species packing on size and shape axes are tightly coupled with patterns of functional diversity. Ecological groups of bats (e.g. frugivores, nectarivores, aerial insectivores) partition

the shape axis more than the size axis. Indeed, only two of the five feeding guilds examined by Stevens and Willig (1999) overlapped on the shape axis whereas four of the five guilds overlapped on the size axis. Thus, when focusing on entire communities of bats, nearest-neighbors are likely to be species from the same ecological group on the shape axis, but could be from a different ecological group on the size axis. Because latitudinal gradients characterize the species richness within functional groups of bats, and because these functional groups reside on different portions of the shape axis, species are added relatively more uniformly to the shape axis. The overlap among functional groups regarding size suggests that species are not added uniformly across this axis. At the community level, this results in complementarity whereby taxa are more tightly packed on the size axis because of differences on the shape axis. Such niche complementarity likely causes "apparent species-packing" on the size axis.

## Overview

Latitudinal gradients in the phenetic diversity of New World bats provide perspectives on patterns of biodiversity that compliment taxonomic or functional characteristics. Tropical increases in the biodiversity of local communities are a consequence of increases in the number of species (Stevens and Willig 2002), increases in the number of functional groups (Stevens et al. 2003), and by a nonrandom assembly of species into communities based on morphology (this study). Phenetic diversity gradients primarily reflect variation in the range of morphologies that New World bats assume at a particular place in time. The nonrandom geographic distribution of families and subfamilies of bats in the New World (Willig and Sandlin 1989, Willig and Selcer 1989, Stevens 2004) contributes to patterns of morphological diversity of local communities. Future research should decouple the influences of ecology and phylogeny on patterns of phenetic diversity, as well as address the extent to which historical phylogenetic radiation has molded contemporary patterns of biodiversity at multiple spatial scales.

**Acknowledgements** – This research was supported by the American Society of Mammalogists, Grants in Aid of Research, as well as by the office of the Vice-President for Research and Graduate Studies, the office of Research Services, the Graduate School, Dept of Biological Sciences, and the Association of Biologists at Texas Tech Univ. to RDS. In part, research was supported by grants (DEB-9400926, DEB 9741543, DEB 9741134) from the National Science Foundation to R. D. Owen and MRW. This work was partially conducted while RDS was a postdoctoral fellow at the National Center for Ecological Analysis and Synthesis, a center funded by NSF (Grant #DEB-0072909) and the Univ. of California. We would like to thank D. Gorchov and C. Ascorra for providing unpublished data for the bat community at Jenaro Herrera. C. Bloch, M. McGinley, R. Owen, S. Presley, D.

Schmidly, and E. Sobek, provided important insights either through discussions or comments on previous versions of the manuscript. This manuscript was greatly improved by critical reviews by C. Rahbek and R. Ricklefs.

## References

- Aguirre, L. F., Herrel, A., Can Damme, R. et al. 2003. The implications of food hardness for diet in bats. – *Funct. Ecol.* 17: 201–212.
- Alvarez, T. and Alvarez-Castaneda, S. T. 1996. Aspectos biológicos y ecológicos de los murciélagos de Ixtapan del Oro, Estado de Mexico, Mexico. – In: Genoways, H. H. and Baker, R. J. (eds), *Contributions in mammalogy: a memorial volume honoring J. Knox Jones, Jr.* The Museum, Texas Tech Univ, pp. 169–182.
- Ascorra, C. F., Solari-T., S. and Wilson, D. E. 1996. Diversidad y ecología de los quiropteros en Pakitzta. – In: Wilson, D. E. and Sandoval, A. (eds), *Manu: the biodiversity of southwestern Peru*. Smithsonian Inst. Press, pp. 593–612.
- Black, H. L. 1974. A north temperate bat community: structure and prey populations. – *J. Mammal.* 55: 138–157.
- Bowers, M. A. and Brown, J. H. 1982. Body size and coexistence in desert rodents: chance or community structure. – *Ecology* 63: 391–400.
- Brown, J. H. 1995. *Macroecology*. – Univ. of Chicago Press.
- dos Reis, N. R. 1984. Estrutura de comunidade de morcegos na região de Manaus, Amazonas. – *Rev. Bras. Biol.* 44: 247–254.
- Dutka, A. F. and Ewens, F. J. 1971. A method for improving the accuracy of polynomial regression analysis. – *J. Qual. Tech.* 3: 149–155.
- Eisenberg, J. F. 1989. *Mammals of the Neotropics*. Vol. 1. – The northern Neotropics, Univ. of Chicago Press.
- Estrada, A., Coates-Estrada, R. and D. Meritt, Jr. 1993. Bat species richness and abundance in tropical rain forest fragments in agricultural habitats at Los Tuxtlas, Mexico. – *Ecography* 16: 309–318.
- Fenton, M. B. 1972. Structure of aerial-feeding bat faunas as indicated by ears and wing elements. – *Can. J. Zool.* 50: 287–296.
- Fenton, M. B. and Bogdanowicz, W. 2002. Relationships between external morphology and foraging behavior: bats in the genus *Myotis*. *Can. J. Zool.* 80: 1004–1013.
- Findley, J. S. 1973. Phenetic packing as a measure of faunal diversity. – *Am. Nat.* 107: 580–584.
- Findley, J. S. 1976. The structure of bat communities. – *Am. Nat.* 110: 129–139.
- Findley, J. S. 1993. *Bats: a community perspective*. – Cambridge Univ. Press.
- Fleming, T. H., Hooper, E. T. and Wilson, D. E. 1972. Three Central American bat communities: structure, reproductive cycles, and movement patterns. – *Ecology* 53: 555–569.
- Foote, M. 1992. Rarefaction analysis of morphological and taxonomic diversity. – *Paleobiology* 18: 1–16.
- Foote, M. 1993. Discordance and concordance between morphological and taxonomic diversity. – *Paleobiology* 19: 185–204.
- Hall, E. R. 1981. *The mammals of North America*, (2nd ed.). – John Wiley and Sons.
- Handley, C. O., Jr., Wilson, D. E. and Gardner, A. L. 1991. Demography and natural history of the common fruit bat *Artibeus jamaicensis* on Barro Colorado Island, Panama. – Smithsonian Inst. Press.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. – *Oecologia* 110: 449–460.
- Iniguez Davalos, L. I. 1993. Patrones ecológicos en la comunidad de murciélagos de la Sierra de Manantlan. – In: Medellín, R. A. and Ceballos, G. (eds), *Avances en el*

- estudio de los mamíferos de México. Publicaciones Especiales, Asociación Mexicana de Mastozoología, pp. 355–370.
- Kaufman, D. M. 1995. Diversity of New World mammals: universality of the latitudinal gradient of species and bauplans. – *J. Mammal.* 76: 322–334.
- Klingenberg, C. P. 1996. Multivariate allometry. – In: Marcus, L. S., Corti, M., Loy, A. et al. (eds), *Advances in morphometrics*. Plenum, pp. 23–52.
- Koopman, K. F. 1982. Biogeography of bats of South America. – In: Mares, M. A. and Genoways, H. H. (eds), *Mammalian biology in South America*. – Spec. Publ. Ser., Pymatuning Laboratory of Ecology. Univ. of Pittsburgh, pp. 273–302.
- Kunz, T. H. 1973. Resource utilization: temporal and spatial components of bat activity in central Iowa. – *J. Mammal.* 54: 14–32.
- LaVal, R. K. and Fitch, H. S. 1977. Structure, movements, and reproduction in three Costa Rican bat communities. – *Occas. Pap. Mus. of Nat. Hist., Univ. Kans.* 69: 1–28.
- Lyons, S. K. and Willig, M. R. 1999. A hemispheric assessment of scale-dependence in latitudinal gradients of species richness. – *Ecology* 80: 2483–2491.
- Lyons, S. K. and Willig, M. R. 2001. Species richness, latitude, and scale sensitivity. – *Ecology* 83: 47–58.
- Marcus, L. F. 1990. Traditional morphometrics. – In: Rohlf F. J. and Bookstein, F. L. (eds), *Proc. Michigan Morphometrics Workshop*. Spec. Pub. Univ. Mich. Mus. Zool, pp. 77–122.
- Math Works. 1995. Matlab reference guide. – Math Works.
- Medellín, R. A. 1993. Estructura y diversidad de una comunidad de murciélagos en el tropical húmedo Mexicano. – In: Medellín, R. A. and Ceballos, G. (eds), *Avances en el estudio de los mamíferos de México*. Publicaciones Especiales, Asociación Mexicana de Mastozoología, pp. 333–354.
- Moulton, M. P. and Pimm, S. L. 1987. Morphological assortment in introduced Hawaiian passerines. – *Evol. Ecol* 1: 41–62.
- Moura de Souza Aguiar, L. 1994. Comunidades de Chiroptera em tres áreas de Mata Atlântica em diferentes estádios de suceso-Estação Biológica de Caratinga, Minas Gerais. – Dissertation, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil.
- Navarro, L. D. and Leon-Paniagua, L. 1995. Community structure of bats along an altitudinal gradient in tropical eastern Mexico. – *Rev. Mex. de Mastoz.* 1: 9–21.
- O'Farrell, M. J. and Bradley, W. G. 1970. Activity patterns of bats over a desert spring. – *J. Mammal.* 51: 18–26.
- Pedro, W. A. and Taddei, V. A. 1997. Taxonomic assemblage of bats from Panga Reserve, southeastern Brazil: abundance patterns and trophic relations in the Phyllostomidae (Chiroptera). – *Boll. Mus. Biol. Mello Leitao* 6: 3–21.
- Peracchi, A. L. and de Albuquerque, S. T. 1993. Quirópteros do Município de Linhares, Estado do Espírito Santo, Brasil (Mammalia, Chiroptera). – *Rev. Bras. Biol.* 53: 575–581.
- Redford, K. H. and Eisenberg, J. F. 1992. *Mammals of the Neotropics*. Vol. 2. The southern cone. – Univ. of Chicago Press.
- Rice, W. R. 1989. Analyzing tables of statistical tests. – *Evolution* 43: 223–225.
- Ricklefs, R. E. and Travis, J. 1980. A morphological approach to the study of avian community organization. – *Auk* 97: 321–328.
- Ricklefs, R. E. and Miles, D. B. 1994. Ecological and evolutionary inferences from morphology: an ecological perspective. – In: Wainwright, P. C. and Reilly, S. M. (eds), *Ecological morphology: integrative organismal biology*. Univ. of Chicago Press, pp. 13–41.
- Roy, K. and Foote, M. 1997. Morphological approaches to measuring biodiversity. – *Trends Ecol. Evol.* 12: 277–281.
- Roy, K., Balch, D. P. and Hellberg, M. E. 2001. Spatial patterns of morphological diversity across the Indo-Pacific: analyses using strombid gastropods. – *Proc. R. Soc. B* 268: 2503–2508.
- Sanchez-Palomino, P., Rivas-Pava, P. and Cadena, A. 1993. Composición, abundancia, y riqueza de especies de la comunidad de murciélagos en bosques de galería en la Serranía de la Marcarena. – *Caldasia* 17: 301–312.
- Schum, M. 1984. Phenetic structure and species richness in North and Central American bat faunas. – *Ecology* 65: 1315–1324.
- Shepherd, U. L. 1998. A comparison of species diversity and morphological diversity across the North American latitudinal gradient. – *J. Biogeogr.* 25: 19–29.
- Simmons, N. B. and Voss, R. S. 1998. The mammals of Paracou, French Guiana: a neotropical lowland rainforest fauna. Part 1. Bats. – *Bull. Am. Mus. Nat. Hist.* 237: 1–219.
- Sokal, R. R. and Rohlf, F. J. 1995. *Biometry* (3rd ed.). – W. H. Freeman and Co.
- Stevens, R. D. 2002. Taxonomic, functional, and phenetic components of latitudinal gradients in biodiversity. – PhD thesis, Texas Tech Univ., Lubbock, Texas.
- Stevens, R. D. 2004. Untangling latitudinal richness gradients at higher taxonomic levels: familial perspectives on the diversity of New World bat communities. – *J. Biogeogr.* 31: 665–674.
- Stevens, R. D. and Willig, M. R. 1999. Size assortment in New World bat communities. – *J. Mammal.* 80: 644–658.
- Stevens, R. D. and Willig, M. R. 2000. Community structure, abundance, and morphology. – *Oikos* 88: 48–56.
- Stevens, R. D. and Willig, M. R. 2002. Geographical ecology at the community level: perspectives on the diversity of New World bats. – *Ecology* 83: 545–560.
- Stevens, R. D., Cox, S. B., Strauss, R. E. et al. 2003. Latitudinal gradients in the functional diversity of New World bat communities. – *Ecol. Lett.* 6: 1099–1108.
- Strauss, R. E. 1987. The importance of phylogenetic constraints in comparisons of morphological structure among fish assemblages. – In: Mathews, W. J. and Heins, D. C. (eds), *Community and evolutionary ecology of North American stream fishes*. Univ. of Oklahoma Press, pp. 136–143.
- Suprenant, H. R. 1977. Nocturnal activity patterns in a bat fauna of southern California with comments on the physiological ecology of *Pipistrellus hesperus*. – PhD thesis, California. State Univ., Fullerton, California.
- Swanepoel, P. and Genoways, H. H. 1979. Morphometrics. – In: Baker, R. J., Jones, Jr., J. K. and Carter, D. C. (eds), *Biology of bats of the New World family Phyllostomatidae*, Part III. Spec. Publ., The Museum, Texas Tech Univ, pp. 13–106.
- Thomas, M. E. 1972. Preliminary study of the annual breeding patterns and population fluctuations of bats in three ecologically distinct habitats in southwestern Colombia. – PhD thesis, Tulane Univ., New Orleans, Louisiana.
- Wainwright, P. C. and Reilly, S. M. 1994. *Ecological morphology: integrative organismal biology*. – Univ. of Chicago Press.
- Willig, M. R. 1982. A comparative ecological study of Caatingas and Cerrado chiropteran communities: composition, structure, morphometrics, and reproduction. – PhD thesis, Univ. of Pittsburgh, Pennsylvania.
- Willig, M. R. and Selcer, K. W. 1989. Bat species diversity gradients in the New World: a statistical assessment. – *J. Biogr.* 16: 189–195.
- Willig, M. R. and Sandlin, E. A. 1991. Gradients in species density and species turnover in New World bats: a comparison of quadrat and band methodologies. – In: Mares, M. A. and Schmidley, D. J. (eds), *Latin American mammals: their conservation, ecology, and evolution*. Univ. of Oklahoma Press, pp. 81–96.
- Willig, M. R., Kaufman, D. M. and Stevens, R. D. 2003. Latitudinal gradients in biodiversity: pattern, process, scale, and synthesis, *Annu. Rev. Ecol. Evol. Syst.* 34: 273–309.



Winemiller, K. O. 1991. Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. – *Ecol. Monogr.* 61: 343–365.

Yancey, F. D. 1996. The mammals of Big Bend Ranch State Park. – PhD thesis, Texas Tech Univ., Lubbock, Texas.

*Subject Editor: Per Lundberg*

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

Community	Country	Latitude	Habitat	Reference
Iowa	USA	42.3°N	Riparian	Kunz 1973
California	USA	36.5°N	Desert	Suprenant 1977
Nevada	USA	36.2°N	Desert	O'Farrell and Bradley 1970
New Mexico	USA	33.9°N	Desert	Black 1974
Big Bend Ranch	USA	29.8°N	Desert	Yancey 1996
Queretaro	Mexico	21.1°N	Montane tropical forest	Navarro L. and Leon-Paniagua 1995
Manantlan	Mexico	19.3°N	Montane tropical forest	Iniguez Davalos 1993
Ixtapan del Oro	Mexico	19.3°N	Montane tropical forest	Alvarez and Alvarez-Castaneda 1996
Los Tuxtlas	Mexico	18.4°N	Wet tropical forest	Estrada et al. 1993
Chiapas	Mexico	16.1°N	Wet tropical forest	Medellin 1993
Guanacaste-1	Costa Rica	10.5°N	Wet tropical forest	LaVal and Fitch 1977
Guanacaste-2	Costa Rica	10.5°N	Wet tropical forest	Fleming et al. 1972
Puntarenas	Costa Rica	10.0°N	Montane tropical forest	LaVal and Fitch 1977
Heredia	Costa Rica	10.5°N	Wet tropical forest	LaVal and Fitch 1977
Sherman	Panama	9.3°N	Wet tropical forest	Fleming et al. 1972
Rodman	Panama	9.0°N	Dry tropical forest	Fleming et al. 1972
BCI	Panama	9.2°N	Wet tropical forest	Handley et al. 1991
Paracou	French Guiana	5.3°N	Wet tropical forest	Simmons and Voss 1998
Zabelitas	Colombia	4.0°N	Wet tropical forest	Thomas 1972
Marcarena	Colombia	3.3°N	Wet tropical forest	Sanchez-Palomino et al. 1993
Pance	Colombia	3.0°N	Montane tropical forest	Thomas 1972
Hormiguero	Colombia	3.0°N	Montane tropical forest	Thomas 1972
Manaus	Brazil	3.0°S	Wet tropical forest	Dos Reis 1984
Edaphic Cerrado	Brazil	7.2°S	Tropical woodland-savannah	Willig 1982
Caatinga	Brazil	7.6°S	Dry tropical forest	Willig 1982
Linhares	Brazil	19.0°S	Wet semi-tropical forest	Peracchi and Albuquerque 1993
Panga	Brazil	19.3°S	Wet semi-tropical forest	Pedro and Taddei 1997
Minas Gerais	Brazil	19.8°S	Wet semi-tropical forest	Moura de Souza Aguiar 1994
Jenaro Herrera	Peru	4.9°S	Wet tropical forest	Gorchov and Ascorra
Manu	Peru	11.9°S	Wet tropical forest	Ascorra et al. 1996
Mbaracayu	Paraguay	24.1°S	Wet semi-tropical forest	Stevens and Willig
Rio Verde	Paraguay	23.5°S	Dry semi-tropical forest	Stevens and Willig

**Appendix 2.** Results from simulation analyses determining whether latitudinal gradients in phenetic diversity could be produced by a latitudinal gradient in species richness. Pools for the entire New World (A) involved simulations in which all continental New World bats formed the group of species from which to assemble each local community. In regionally constrained simulations (B), only those species whose range included each community formed the species pool. Magnitude, linear decrease, quadratic decrease, and  $R^2$  refer to the four components of the relationship examined. Difference refers to the way in which the actual communities were different from those simulated. P indicates the probability that a particular component of the relationship came from the random distribution of like components generated from simulation. Bold components represent those that were significant after a Bonferonni sequential adjustment, unbolded component followed by an asterice indicate traditional significance.

Pool	Measure	Magnitude		Linear decrease		Quadratic decrease	
		Difference	P	Difference	P	Difference	P
A	Size range	None	0.376	<b>Greater</b>	<b>&lt;0.001</b>	None	0.260
	Size STD	None	0.198	Greater	0.014*	None	0.160
	Size NND	Lesser	0.040*	Greater	0.032*	None	0.316
	Shape range	<b>Lesser</b>	<b>&lt;0.001</b>	None	<0.354	None	0.084
	Shape STD	Lesser	<b>&lt;0.001</b>	None	0.458	None	0.708
	Shape NND	Lesser	0.010*	Greater	0.034*	None	0.050
B	Size range	None	0.692	Greater	0.024*	None	0.614
	Size STD	None	0.080	None	0.174	None	0.116
	Size NND	None	0.410	None	0.298	None	0.984
	Shape range	None	0.380	None	0.396	Greater	0.019*
	Shape STD	None	0.184	None	0.232	None	0.892
	Shape NND	None	0.350	None	0.158	None	0.296