

REPORT

Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal trends

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Abstract

Over the last two decades, although much has been learned regarding the multifaceted nature of biodiversity, relatively little is known regarding spatial variation in constituents other than species richness. This is particularly true along extensive environmental gradients such as latitude. Herein, we describe latitudinal gradients in the functional diversity of New World bat communities. Bat species from each of 32 communities were assigned to one of seven functional groups. Latitudinal gradients existed for the richness, diversity and scaled-dominance of functional groups. No significant patterns were observed for evenness of functional groups. Measures of functional diversity were different in magnitude and increased towards the equator at a faster rate than expected given the underlying spatial variation in species richness. Thus, latitudinal gradient in species richness alone do not cause the latitudinal gradient in functional diversity. When variation in species composition of the regional fauna of each community was incorporated into analyses, many differences between observed and simulated patterns of functional diversity were not significant. This suggests that those processes that determine the composition of regional faunas strongly influence the latitudinal gradient in functional diversity at the local level. Nonetheless, functional diversity was lower than expected across observed sites. Community-wide responses to variation in the quantity and quality of resources at the local level probably contribute to differences in functional diversity at local and regional scales and enhance beta diversity.

Keywords

Bats, beta diversity, biodiversity, dominance, evenness, functional diversity, latitudinal gradient, macroecology, richness, selection probability effect.

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INTRODUCTION

The term 'biodiversity' has developed into a concept that embraces multiple forms of biological variation including taxonomic, genetic and phenetic diversity within communities, the resultant complexity of biotic interactions, and the associated production, nutrient cycling, decomposition and energy flow within ecosystems (Tilman 2001). While the term biodiversity provides a comprehensive conceptual framework from which to investigate patterns of variation, such a broad definition compromises the tangibility of the concept and makes its very measurement problematic. Moreover, failure to achieve empirical and conceptual integration of the multifaceted nature of biodiversity has limited progress in understanding the mechanistic basis of its spatial and

temporal dynamics. Indeed, little is known regarding broad-scale variation in many forms of biodiversity, even those that are relatively easy to quantify such as functional (Tilman 2001), phenetic (Findley 1973), genetic, or phylogenetic (Faith 1996) diversity. In the few cases that have been examined (e.g. functional, phenetic and character diversity), the form of the relationship between species richness and other forms of biodiversity is asymptotic (Schum 1984; Williams & Humphries 1996; Naeem 2002). Nonetheless, the extent to which non-taxonomic components of biodiversity exhibit latitudinal gradients similar to those of species richness remains unclear (however see Willig 2001). Herein, we focus on functional diversity and explore how its examination can enhance our understanding of the effects of the environmental correlates of latitude on biodiversity.

Functional significance of New World bats

From a functional perspective, bats play important roles in terrestrial ecosystems (Findley 1993; Patterson *et al.* 2003). As consumers, bats are involved in the transfer of energy and cycling of nutrients via secondary production, immobilization and mineralization. Moreover, because of their high mobility, bats can have great impacts on the redistribution of nutrients and energy across a landscape. Because of their high density [some colonies of bats can range from several thousands to tens of millions (Davis *et al.* 1962, Findley 1993)], bats may be considered keystone species in many ecosystems (Fleming 1988; Willig & Gannon 1996). This, coupled with their large metabolic demand [many bats eat from between 50 and 120% of their own body weight nightly (Fenton 1992)], probably contributes to spatial dynamics in pathways of energy flow and nutrient cycling, enhances spatial heterogeneity of nutrients, and may contribute substantially to the spatial distribution and genetic structure of plant populations, particularly in the tropics (Fleming 1988; Fujita & Tuttle 1991; Ascorra & Wilson 1992; Gorchoff *et al.* 1993). Bats perform a number of ecosystem functions and services associated with various aspects of their niches. Nonetheless, perhaps the best information regarding the functional consequences of their niche characteristics comes from dietary affinities. Considerations of the different ways that bats are involved in resource exploitation can be used to define functional groups. Moreover, the number of functional groups and the distribution of species among groups can be used to form measures of functional diversity. As with most taxa, bats exhibit strong latitudinal gradients in species richness (Stevens & Willig 2002). The extent to which functional diversity exhibits a latitudinal gradient is unknown. Indeed, the examination of variation in functional diversity along extensive environmental gradients may provide complementary insights to those gained from examination of species richness, and identify general phenomena regarding variation in biodiversity.

MATERIALS AND METHODS

Available data and definition of functional groups

Data on the species composition of 32 New World bat communities (Fig. 1) came from the literature. These data were distinguished from a large number of potential sources based on criteria that spatially and temporally bounded studies so as to enhance the likelihood that they addressed the structure of a single community (i.e. groups of taxa with the potential to interact through space and time). Moreover, sufficient effort in all seasons that bats were active needed to be employed so as to enhance the detection of rare species.

Details regarding these communities, criteria for selection and aspects of taxonomic diversity, including estimates of local and regional species richness, appear in Stevens (2002) and Stevens & Willig (2002). Incomplete knowledge of the species composition of particular communities could cause variation in estimates of functional diversity. Nonetheless, only if a systematic bias was associated with either species richness or latitude could a dubious latitudinal gradient in functional diversity result. Although samples may underestimate the true species composition of communities, there is no evidence to suggest that changes in species richness or latitude involve a systematic bias in estimates of functional diversity. Because of an *a priori* requirement of intensive sampling and the observation that taxonomic measures of diversity attained asymptotic values within the sampling domain of each site (Stevens & Willig 2002), we are confident in the ability of these data to detect meaningful gradients in functional diversity.

We categorized species of bats to one of seven functional groups based on dietary affinities (*sensu* Stevens & Willig 1999, 2001). Two groups of insectivores forage in different areas and thus exploit two distinct resource bases. Aerial insectivores primarily consume insects obtained while in flight yet fairly close to the ground, or within forest canopies or surrounding edges. High-flying insectivores consume insects while foraging above forest canopies, or in more open areas and at higher altitudes than those used by aerial insectivores. Frugivores, nectarivores, piscivores and sanguivores primarily consume fruit, nectar, fish and the blood of vertebrates, respectively. Finally, gleaning animalivores primarily consume vertebrates and invertebrates that are gleaned from surfaces such as leaves, the trunks of trees or the ground. Grouping species into one of seven functional categories is a human abstraction. The assignment of species along some functional continuum might present a more accurate representation of the functional characteristics of species and ultimately communities. Unfortunately, our understanding of the dietary affinities of bats, especially those with extensive geographical distributions, precludes such an assignment. Moreover, as long as the category in which a species is placed reflects the typical diet of members of that species, this categorization probably will not create a bias.

Quantification of functional diversity

We use functional diversity as an inclusive term to describe aspects of the distribution of species among functional groups within communities. We use other terms to refer to the operational measures of aspects of functional diversity. For example, the richness of functional groups represents the number of functional groups inhabiting a local community. The diversity of functional groups reflects the

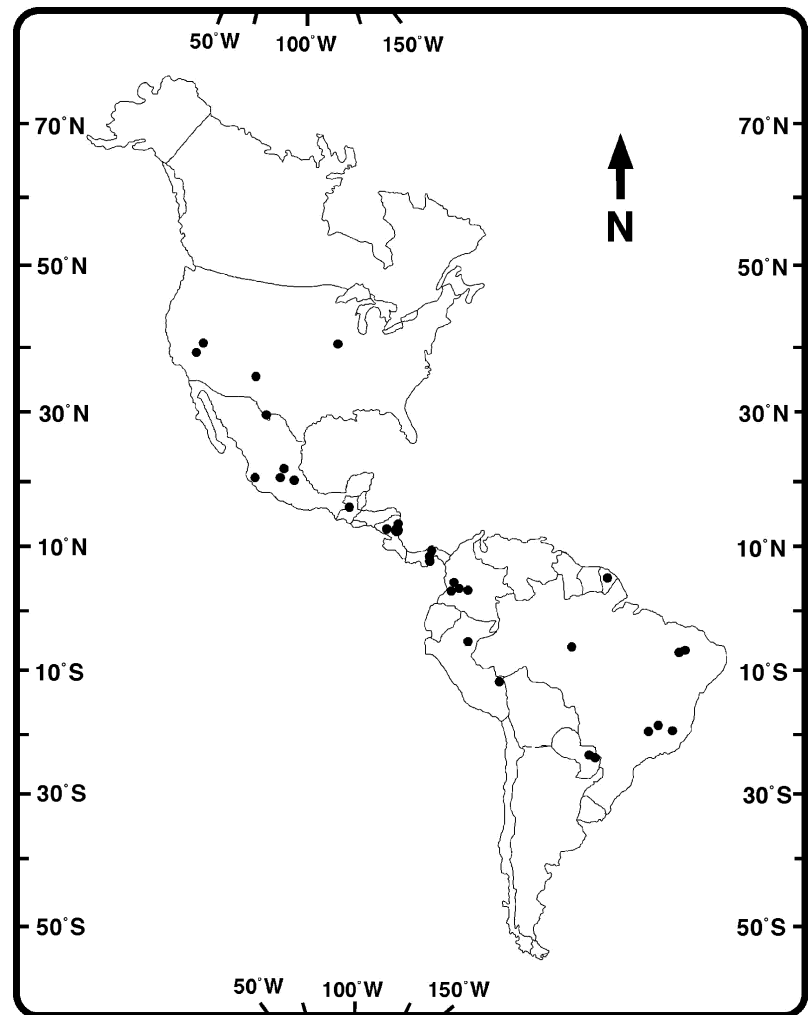


Figure 1 Locations of 32 New World bat communities (solid dots) used to evaluate geographical patterns of functional diversity (modified from Stevens 2002 and Stevens & Willig 2002).

number of groups and equability of species richness among them, and was estimated based on the Shannon index (Pielou 1975). The evenness of functional groups reflects equability in the distribution of species among functional groups and was estimated using the Camargo evenness index (Camargo 1993). The dominance of functional groups describes the degree to which the number of species in the most species-rich functional group dominates the community in terms of species richness, and was estimated by the Berger–Parker index (Berger & Parker 1970). Following Magurran (1988), the dominance index was scaled so that a large index represents low dominance and high diversity (hereafter termed scaled dominance). With the exception of the relationship among some measures of evenness and species richness, diversity measures are correlated. Nonetheless, these four measures are conceptually different and characterize four unique aspects of spatial variation in diversity (Stevens & Willig 2002). Richness and evenness are independent measures of the number of species and the

equability of abundances, whereas the Shannon index combines these two attributes, but is more sensitive to variation in species richness than evenness. Dominance measures are influenced by both richness and evenness, but are more sensitive to variation in evenness.

Quantitative analyses

We used orthogonal polynomial regression analysis (Dutka & Ewens 1971) to model the relationship of each measure of functional diversity with species richness and with latitude. In addition to fit (R^2) of the relationship between latitude and functional diversity, we compared empirical parameter estimates (e.g. b_0 , b_1 and b_2) to simulated parameter estimates as a way to evaluate the selection probability effect (Huston 1997, see below). In particular, we assessed if the magnitude of empirical parameter estimates was different from simulated estimates. Parameter estimates generated from traditional polynomial regression

analysis are not statistically independent. For example, the interpretation of the magnitude of the linear slope is contingent on the magnitude of both the intercept and the quadratic term. However, orthogonal polynomial regression analysis allows the decomposition of relationships into components of magnitude (b_0), linear (b_1) and nonlinear rates (b_2 , a measure of saturation) of change, each of which is independent of the other coefficients in the model (Sokal & Rohlf 1995). We used a function written in Matlab (Math Works 1995) to conduct the procedure described in Dutka & Ewens (1971) for determining orthogonal polynomials when values of the independent variable are not evenly spaced. Experiment-wise error rate was held at 5% within each of the two suites of regression analyses (i.e. those involving richness vs. those involving latitude) by application of a Bonferroni sequential adjustment (Rice 1989). We conducted analyses using both the absolute value of latitude and signed latitude (i.e. the same latitude north and south of the equator have a different sign). Results were qualitatively similar; we report only those involving signed latitude.

Accounting for hidden treatments

Because of the general positive relationship between species richness and functional diversity, the empirical gradient in functional diversity could result from underlying variation among communities regarding species richness (selection probability effect, Huston 1997). Thus, to be considered non-trivial, the parameterization of the empirical gradient in functional diversity must be significantly different from a gradient that could result from spatial variation among sites in species richness. To address this, we could randomly assign each species within a community to a functional group and then re-examine the latitudinal gradient in functional diversity. However, not all functional groups are represented by the same number of bat species in the New World, and thus they are not equiprobable. To impose the more realistic constraint that the probability of selection of a particular functional group was proportional to its frequency in the New World, we conducted simulation analyses in which species were drawn randomly from a pool comprising all continental New World bat species. More specifically, for each real community, a simulated community was assembled by randomly selecting without replacement the same number of species as occurred in the actual community. Sampling without replacement ensures that a particular species occurs in a random community only once, consistent with the assembly of real communities. Measures of functional diversity were calculated and then each measure was regressed separately on latitude using orthogonal polynomial regression. This process was iterated to produce 1000 gradients in functional diversity resulting from the latitudinal gradient in species richness. Parameter

estimates (b_0 , b_1 and b_2) characterizing the empirical latitudinal gradient in functional diversity were then compared with the distributions of parameter estimates from the simulated gradients to determine P values. The position of the parameter estimate for real communities relative to the distribution of simulated values describes the probability that the observed value is a random variate from the simulated distribution, and that the observed latitudinal gradient in functional diversity is a product of spatial variation in species richness. Parameter estimates for the empirical relationship were deemed to be significantly different from simulated parameter estimates when they were not encompassed by the middle $(1-\alpha) \times 100\%$ of the simulated distribution. The levels of α were determined by a Bonferroni sequential adjustment in which experiment-wise error rate was equal to 5% (Rice 1989).

Although the above simulation analyses are not realistic (all species have the potential to assemble random communities whereas the biogeography of New World bats prevents many species from assembling many empirical communities), they are necessary to address the selection probability effect (could the latitudinal gradient in functional diversity result from variation among sites regarding their species richness?). Moreover, deviations of empirical gradients from simulated gradients suggest that latitudinal gradients in functional diversity result from phenomena other than spatial variation in species richness (e.g. biogeographical processes).

A second suite of analyses examined the extent to which variation in the species richness and composition (i.e. functional identity of species) of regional faunas associated with the geographical location of a community affected latitudinal gradients in functional diversity at the local level. Simulations such as these control for variation among sites regarding species richness, as well as the evolutionary history and biogeographical processes (e.g. extinction and dispersal) that operate at larger regional scales. As with species richness, the taxonomic and functional characteristics of bat species are not distributed homogeneously throughout the New World. At both local and regional scales, all New World bat families and functional groups occur at the equator (Willig & Selcer 1989; Stevens *in press*). The number of families and functional groups diminishes with increases in latitude, with each group exhibiting a unique biogeographical terminus. In this set of analyses, only those species with the dispersal potential to be part of a particular community were included in the randomization process for that site. As such, species were drawn randomly from a regional bat fauna that represents a reasonable pool from which each community potentially was assembled (Stevens & Willig 1999). The regional fauna for a site was considered to be those species whose geographical distributions included the particular community. To define regional

species pools, distribution maps for each species were modified from Willig & Selcer (1989) and Willig & Sandlin (1991) using information in Hall (1981) and Koopman (1982), and updated by Lyons & Willig (1999, 2002 based on Eisenberg (1989) and Redford & Eisenberg (1992). Simulation analyses were performed using functions written in Matlab (Math Works 1995) that are available from the authors.

RESULTS

Empirical patterns

Richness, diversity and scaled dominance of functional groups varied consistently with species richness (Fig. 2). This was not true for the evenness of functional groups. Moreover, significant latitudinal gradients existed with

respect to all aspects of functional diversity except the evenness of functional groups (Fig. 2). In all significant cases, increases in functional diversity were associated with decreases in the magnitude of latitude, and linear and nonlinear rates of change were significantly different than zero. Although linear and quadratic slopes are mathematically orthogonal, the way that they vary with latitude is correlated. This indicates separate linear and nonlinear components to spatial variation in functional diversity.

Simulation analyses

The selection probability effect cannot explain latitudinal gradients in functional diversity. Significant differences between simulated and empirical latitudinal gradients existed for the richness, diversity and dominance, but not

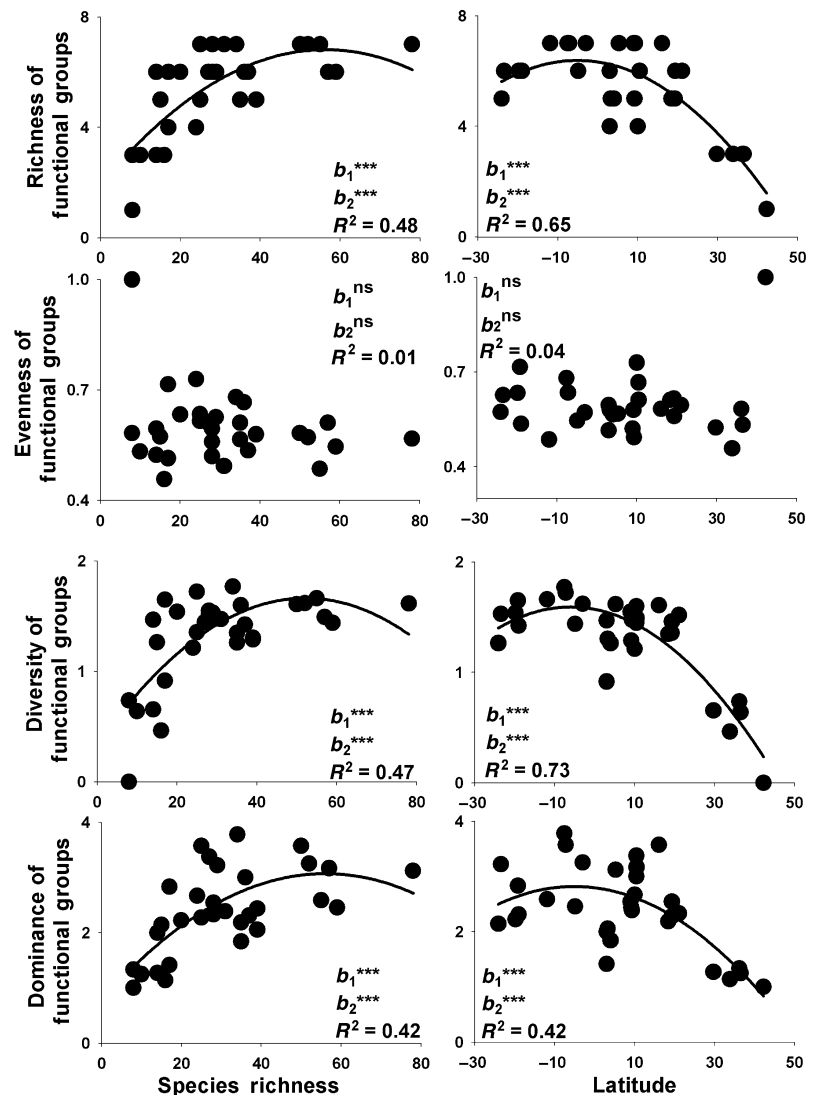


Figure 2 Gradients in four measures of functional diversity with respect to species richness (left column) or latitude (right column). Solid lines represent significant regressions; b_1 and b_2 refer to the linear and quadratic rates of change, respectively, whereas R^2 refers to the coefficient of determination describing the strength of the relationship. Asterisks indicate regression coefficients that are significantly different from zero.

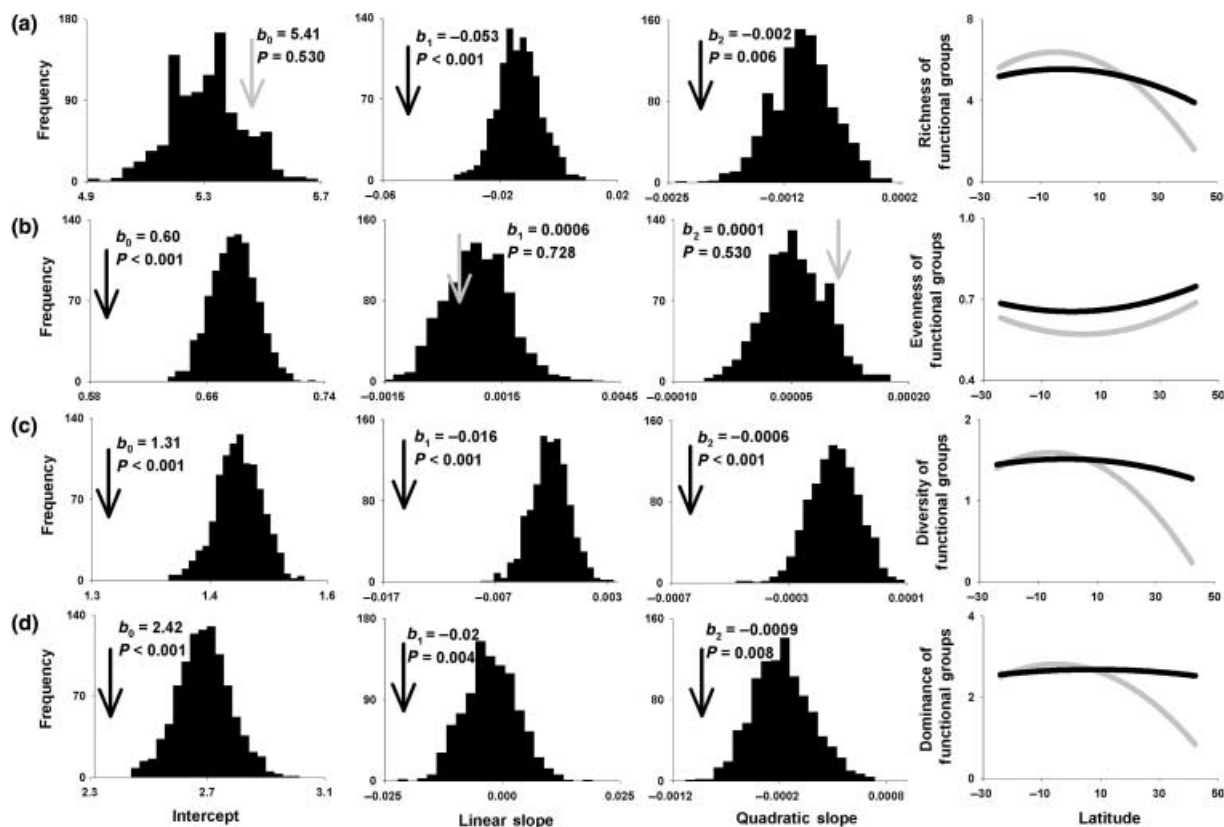


Figure 3 Results from simulation analyses evaluating the degree to which latitudinal gradients in functional diversity could result from a latitudinal gradient in species richness. (a), (b), (c) and (d) refer to analyses involving the richness, evenness, diversity and dominance of functional groups, respectively. Histograms (first three columns) refer to distributions of simulated regression coefficients. Arrows refer to the position of the empirical parameter estimates describing the relationship between a particular aspect of functional diversity and latitude across real communities relative to the distribution of simulated parameter estimates. Black arrows refer to situations in which the empirical parameter estimate is significantly different from simulated parameter estimates after a Bonferroni sequential adjustment (Rice 1989). Graphs in the right column represent expected values from the empirical (grey line) and simulated (black line) relationships between an aspect of functional diversity and latitude.

the evenness of functional groups (Fig. 3). With the exception of the evenness of functional groups, linear and quadratic coefficients were significantly more negative than expected given a selection probability effect. Functional diversity increases towards the equator at a faster rate than expected given the underlying latitudinal gradient in species richness. This suggests that the environmental gradients that are embodied in latitude affect functional diversity beyond that expected from additions of species to communities. Empirical communities also differ from simulated communities based on the magnitude of evenness, diversity and scaled dominance of functional groups. Empirical communities are less even, less diverse and more dominated than expected based on the random assembly of species from the species pool. This is particularly true at extreme extratropical latitudes, and likely results at least in part from the non-random biogeographical distribution of functional groups.

Results from simulation analyses that accounted for variation among sites regarding both species richness and the species composition of regional faunas were different from those accounting only for variation in species richness (Fig. 4). In all cases, linear and quadratic rates of change describing the empirical communities were statistically indistinguishable from those for simulated communities after a Bonferroni sequential adjustment. Thus, latitudinal variation among communities regarding functional diversity can be accounted for by latitudinal changes in species richness and composition of regional faunas. This suggests the importance of regional processes in the determination of gradients of functional diversity. As with analyses addressing the selection probability effect, empirical communities are less even, less diverse and more dominated by a single functional group than those randomly assembled from the regional fauna. This suggests that an ecological filter is in operation that predisposes communities to be represented

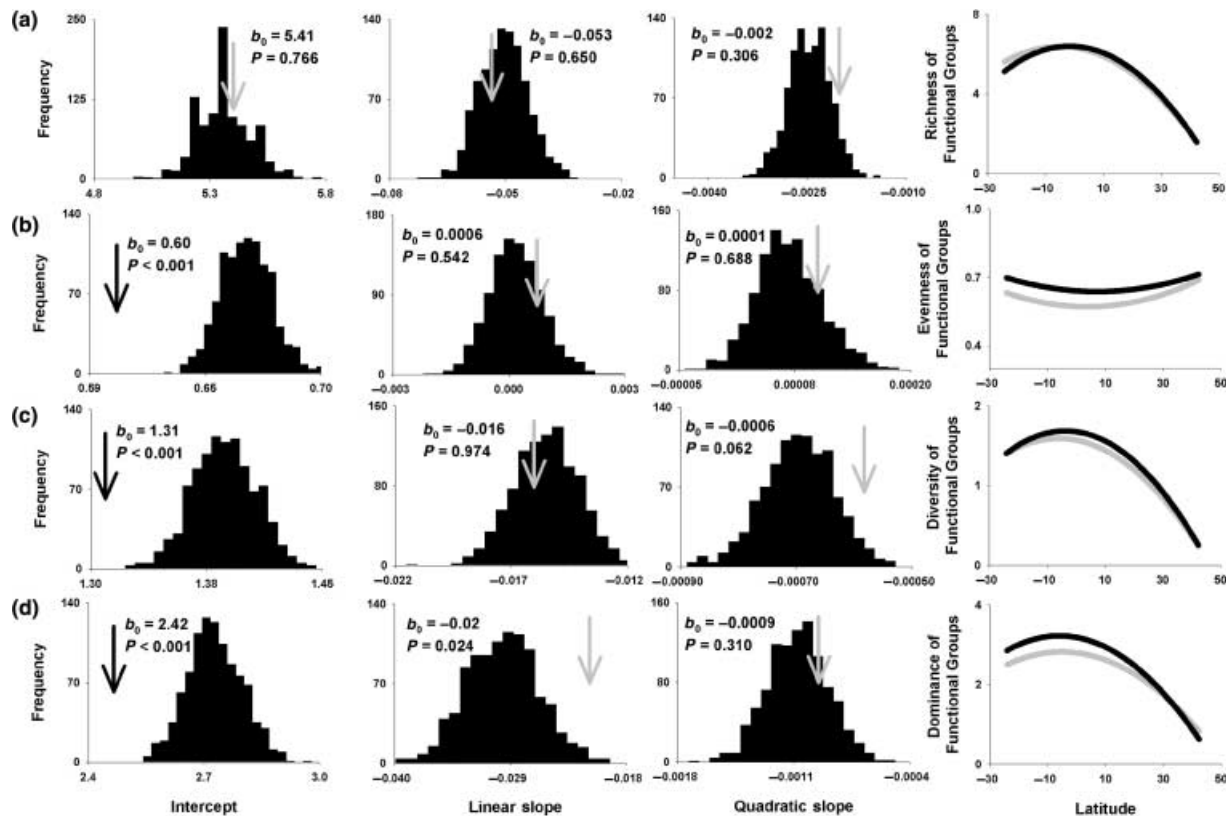


Figure 4 Results from simulation analyses evaluating the degree to which latitudinal gradients in functional diversity could result from variation among sites regarding the species richness and composition of regional faunas surrounding each community. (a), (b), (c) and (d) refer to analyses involving the richness, evenness, diversity and dominance of functional groups, respectively. Histograms (first three columns) refer to distributions of simulated regression coefficients. Arrows refer to the position of the empirical parameter estimates describing the relationship between a particular aspect of functional diversity and latitude across real communities relative to the distribution of simulated parameter estimates. Black arrows refer to situations in which the empirical parameter estimate is significantly different from simulated parameter estimates after a Bonferroni sequential adjustment (Rice 1989). Graphs in the far right column represent expected values from the empirical (grey line) and simulated (black line) relationships between an aspect of functional diversity and latitude.

by a functionally non-random subset of species from the regional fauna.

DISCUSSION

We demonstrate that strong spatial patterns in the functional diversity of bat communities exist in the New World. Moreover, latitudinal changes in biodiversity are not random with respect to the functional characteristics of species and cannot be accounted for by a selection probability effect. Independent variation in the taxonomic and functional diversity of bat communities is demonstrated by two observations. First, latitudinal variation in taxonomic diversity exhibits a constant rate (Stevens & Willig 2002), whereas latitudinal variation in functional diversity exhibits both significant linear and nonlinear components. Second, spatial variation in species richness does not produce the empirical latitudinal gradient in functional diversity. Indeed, latitudinal

variation in biodiversity is complex and involves unique variation in taxonomic and functional diversity, and possibly other components as well. Nonetheless, current general theories explaining latitudinal gradients in biodiversity only account for greater numbers of species towards the equator (Willig *et al.* 2003) and do not pertain to the enhancement of functional diversity or any other component of biodiversity as latitude decreases. For proposed mechanisms to be considered general, they should also account for multiple forms of variation that are embodied in the concept of biodiversity.

Nature of species pools

Like all models, the randomization experiments that we conducted are sensitive to the assumptions used in the formulation of simulated communities. Significant departures from patterns predicted by these simulations can be

used to invalidate assumptions and gain important insights. While models evaluating the selection probability effect are unrealistic because all species likely are not involved in the assembly of all communities, they serve the important purpose of demonstrating that variation among sites regarding species richness does not determine the way that functional diversity varies with latitude. In contrast, models using regionally constrained faunal pools do account for latitudinal variation in functional diversity. Thus, to understand how it is that functional diversity varies latitudinally, one must understand the underlying pattern of species richness and spatial variation among regional faunas regarding species composition.

Regionally constrained models suggest that understanding ecological and evolutionary mechanisms that operate at larger spatial scales will enhance understanding of global patterns of functional diversity. For example, because species composition changes rapidly in areas of biogeographical intersection (Spector 2002), rapid changes in functional diversity are likely to be greatest within such areas of transition (i.e. between temperate and subtropical zones). This is true for the functional diversity of New World bats. From the perspective of favourableness (i.e. temperature and solar insolation), the tropics can be considered homogeneous, exhibiting no latitudinal gradient (Terborgh 1973). The same is true for functional diversity. Effectively no latitudinal gradient in functional diversity exists within tropical and subtropical zones (Fig. 2). Functional diversity is most dynamic in the temperate zone where a number of families reach the latitudinal terminus of their geographical distribution. Moreover, empirical latitudinal gradients in functional diversity primarily may be a consequence of decreases in the number of species in the New World bat family Phyllostomidae. Of the nine families of bats found in the New World, the Phyllostomidae is by far the most diverse from a functional perspective (Nowak 1999), comprising four (e.g. frugivores, gleaning animalivores, nectarivores, sanguinivores) of the seven functional groups found in New World bats. Although changes in the taxonomic diversity of other families of bats in the New World may be important, they involve fewer species and contribute to changes in fewer functional groups. Phyllostomid taxa are limited primarily to tropical and subtropical portions of the New World, where they exhibit strong latitudinal gradients in species richness, with the greatest number of species at lower latitudes (Willig & Selcer 1989). Moreover, phyllostomid taxa often dominate local communities in the tropics and subtropics (Voss & Emmons 1996; Stevens *in press*). Thus, latitudinal changes in the taxonomic diversity of the Phyllostomidae, in particular the decrease in species richness away from the equator greatly influences latitudinal changes in functional diversity. This suggests that the selection probability effect within particular families may

possibly contribute to latitudinal gradients in functional diversity.

Functionally dominated communities and beta diversity

Although regionally constrained models can account for the way that functional diversity changes with latitude, they cannot account for the decrease in evenness and diversity, and the increase in dominance that accompanies a change in spatial scale from the regional to the local level. This suggests that assembly of communities is influenced by local processes that favour species that are more ecologically similar, and hence dominated by a particular functional group. It has often been found that species within communities represent non-random subsets of regional faunas from phylogenetic or taxonomic perspectives (Williams 1964; Simberloff 1970; Webb 2000; Enquist *et al.* 2002). In particular, communities contain fewer higher taxa than would be expected by chance. The explanation of this for mainland communities has been that monotypic genera have restricted ecological affinities (Hairston 1964) and more generally, congeneric species are more ecologically similar to each other than more distantly related taxa and as a result tend to co-occur (Williams 1947). Moreover, the shared response of similar species to habitat heterogeneity translates into the coordinated distribution of closely related taxa across a landscape. While reflecting a broader taxonomic scale, this is also revealed in functional diversity. This is most notable through the prevalence of particular functional groups within communities and this causes lower evenness and diversity and higher dominance at the local level than expected. The fact that sites are differentially assembled by ecologically similar species could be a general characteristic that is reflected by the taxonomic, phylogenetic and functional diversity of communities.

If particular sets of species dominate communities possessing particular resources, and there is spatial heterogeneity of resources within a region, beta diversity will be enhanced. Bat communities exhibit considerable beta diversity in the New World, increasing towards the equator (Stevens & Willig 2002). The disparity in dominance of functional groups between empirical and simulated communities increases towards the equator as well, with empirical communities becoming increasingly more dominated than simulated communities (indicated by a marginally significant difference in linear slope when simulated communities are drawn from regional faunal pools, Fig. 4). This observation is consistent with an increase in beta diversity of communities towards the equator. Indeed, beta diversity may at least in part have a functional component that is related to the resource utilization of taxa and how they respond to heterogeneity of those resources. Few mechanisms attempting to explain latitudinal gradients

of diversity involve variation in either the functional characteristics of species or beta diversity measured at any level of biological organization (Willig *et al.* 2003). Nonetheless, these two components of biodiversity should be linked explicitly to mechanisms used to explain latitudinal gradients.

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