

Multiple dimensions of bat biodiversity along an extensive tropical elevational gradient

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Summary

1. Research concerning spatial dynamics of biodiversity generally has been limited to considerations of the taxonomic dimension, which is insensitive to interspecific variation in ecological or evolutionary characteristics that play important roles in species assembly and provide linkages to ecosystem services. Consequently, the assumption that the taxonomic dimension is a good surrogate for other dimensions remains unconfirmed.

2. We assessed variation in taxonomic (species richness) as well as phylogenetic and functional (Rao's quadratic entropy, a measurement of dispersion) dimensions of bat biodiversity along an elevational gradient in the Manu Biosphere Reserve of Peru. Phylogenetic dispersion was based on relatedness of species derived from a mammalian supertree. Functional dispersion was estimated separately for each of six functional components that reflect particular niche axes (e.g. diet, foraging strategy, body size) and for all functional components combined.

3. Species richness declined nonlinearly with elevation, whereas phylogenetic dispersion and functional dispersion based on all functional components were not significantly associated with elevation (orthogonal polynomial regression). Moreover, considerable heterogeneity in the form of elevational relationships existed among functional components. After accounting for variation in species richness, dispersion of phylogenetic, diet and foraging strategy attributes were significantly greater than expected at high elevations, whereas dispersion of body size was significantly less than expected at high elevations.

4. Species richness was a poor surrogate for phylogenetic or functional dispersion. Functional dispersion based on multiple components obscured patterns detected by particular components and hindered identification of mechanistic explanations for elevational variation in biodiversity.

5. Variation in phylogenetic dispersion effectively captured the composite variation represented by all functional components, suggesting a phylogenetic signal in functional attributes.

6. Mechanisms that give rise to variation in richness do not fully account for variation in phylogenetic or functional characteristics of assemblages. Greater than expected phylogenetic, diet and foraging strategy dispersion at high elevations were associated with the loss of phylogenetically or functionally redundant species, suggesting that increasing interspecific competition with decreasing productivity resulted in competitive exclusion. In contrast, low dispersion of size attributes at high elevations suggests the importance of abiotic filtering that favours small-sized species that can more easily enter torpor.

Key-words: Andes, competition, filtering, functional, Manu, neotropics, niche partitioning, phylogenetic, surrogacy, taxonomic

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Introduction

Understanding spatial patterns of biodiversity and the mechanisms that mould them is vital to accurately forecast the effects of global climate change on populations and communities, as well as to inform conservation policy. The factors that underlie spatial dynamics of biodiversity have been primarily explored based on the taxonomic dimension. Most often, species richness has been used as a surrogate for biodiversity, although some research has incorporated information on species abundances as well (Gaston 1998; Wilsey *et al.* 2005). These approaches consider all species to be equally distinct and are insensitive to ecological and evolutionary variation among species. Consequently, analyses based on taxonomic considerations alone produce an incomplete and potentially biased view of biodiversity dynamics (Stevens *et al.* 2003). For the taxonomic dimension to be used as an effective surrogate, the form and predictability of its relationship with other dimensions of biodiversity must be evaluated for a variety of taxa and systems.

Recent efforts expanded the conceptual framework of biodiversity and developed analytical approaches to estimate biodiversity based on the evolutionary histories or ecological functions of species (e.g. Webb *et al.* 2002; Pavoine & Bonsall 2011). The phylogenetic dimension of biodiversity reflects evolutionary differences among species based on times since divergence from a common ancestor (Faith 1992) and represents a comprehensive estimate of phylogenetically conserved ecological and phenotypic differences among species (Cavender-Bares *et al.* 2009). The functional dimension of biodiversity reflects variability in ecological attributes among species and provides a mechanistic link to ecosystem resistance, resilience and functioning (Petchey & Gaston 2006). The simultaneous assessment of variation in taxonomic, phylogenetic and functional dimensions of biodiversity along environmental gradients provides insights into the relative importance of ecological and evolutionary mechanisms that structure different components of assemblages.

The extent to which variation in the phylogenetic or functional dimension of biodiversity is a consequence of variation in species richness provides insight into the relative importance of various processes (e.g. abiotic or biotic filtering, niche partitioning, interspecific competition) along gradients. Phylogenetic or functional dimensions can be measured by the dispersion of species in evolutionary or ecological space defined by phylogenetic relatedness or functional attributes, respectively. Phylogenetic or functional dispersion should increase with species richness if species are randomly drawn from a regional species pool with a finite number of attributes. However, this increase should be asymptotic because the probability of adding species to an assemblage with new ecological or evolutionary attributes decreases as the assemblage becomes more species rich (i.e. null expectation indicated by the shaded area of Fig. 1; Kluge & Kessler 2011). The

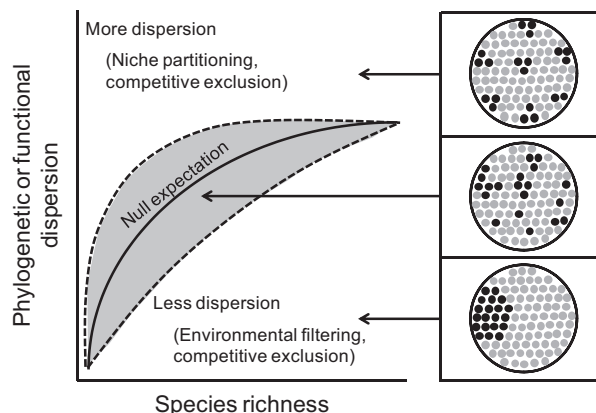


Fig. 1. Framework for evaluating the relative importance of ecological processes based on the extent to which phylogenetic or functional dispersion differs from the null expectation given variation in species richness (i.e. shaded area; see text for reasoning of increasing asymptotic relationship). Phylogenetic or functional dispersion that is significantly more or less dispersed than expected given variation in species richness (i.e. non-shaded area) suggests the operation of different processes. Boxes to the right illustrate an assemblage with more dispersion (top), expected dispersion (middle) and less dispersion (bottom) of attributes given random species assembly. Large circles represent functional or phylogenetic space of the regional species pool. Species locations within this space are represented by dots. Black dots signify species present in a particular assemblage, whereas grey dots signify the remaining species of the regional species pool that are not present in a particular assemblage. Interpretations of phylogenetic patterns are based on the assumption that critical ecological characteristics of species are phylogenetically conserved. Competitive exclusion can result in more dispersion than expected if it operates primarily between phylogenetically or functionally similar species, or it can result in less dispersion than expected if one clade or functional group is competitively superior to other clades or groups.

form of the relationship predicted by the null model can be altered if strong ecological or evolutionary processes are in operation, leading to more or less dispersion than expected (i.e. non-shaded area of Fig. 1).

More phylogenetic or functional dispersion than expected based on species richness arises when coexistence is caused by increasing niche dissimilarity among species. Multiple processes may simultaneously operate to increase such dissimilarities, including interspecific competition and niche partitioning (Fig. 1). As resources become limiting, interspecific competition increases among phylogenetically (if attributes have a strong phylogenetic signal) or functionally similar species, increasing dispersion for these dimensions of biodiversity (MacArthur & Levins 1967; Mayfield & Levine 2010). In contrast, partitioning of niche space allows for more efficient use of resources, while minimizing interspecific competition (MacArthur & Levins 1967). Resources are less limiting when productivity is high and predictable, which may increase niche partitioning as smaller niches can support viable populations.

Less phylogenetic or functional dispersion than expected based on species richness can occur when abiotic

or biotic filtering acts on particular attributes that are obligatory for persistence (Fig. 1). Factors that constrain species distributions may include abiotic conditions (e.g. temperature, humidity), resource diversity and abundance, or the presence of superior competitors. In such scenarios, assemblages will comprise species that share similar functional characteristics (and phylogenetic histories if functional characteristics have a strong phylogenetic signal), as these attributes make them more adapted to local abiotic or biotic conditions, which may represent environmental filtering or competitive superiority of a particular clade over other clades (Weiher & Keddy 1995; Mayfield & Levine 2010).

Three limitations must be considered when developing hypotheses about ecological processes based on comparisons of empirical phylogenetic or functional dispersion to null model expectations. First, interpretations of phylogenetic patterns are based on the assumption that critical ecological characteristics of species are phylogenetically conserved (Cavender-Bares *et al.* 2009; Losos 2011), such that closely related species exhibit ecological similarity inherited from a common ancestor. Caution must be used when interpreting phylogenetic patterns if the strength of phylogenetic signals is not evaluated explicitly and inferences about ecological mechanisms should rely on patterns of dispersion of functional attributes. Secondly, lack of deviation from the null expectation does not necessarily indicate the absence of deterministic structuring mechanisms. Multiple processes may simultaneously affect dispersion, but may do so in opposing directions (HilleRisLambers *et al.* 2012). Finally, inferring process from pattern does not unequivocally identify particular structuring mechanisms. Such inferences require assumptions about the way in which attributes play pivotal roles in the assembly process.

Although many studies have explored multiple dimensions of biodiversity in plants (e.g. Tilman *et al.* 1997; Webb 2000; Díaz & Cabido 2001; Cadotte *et al.* 2009; Swenson & Enquist 2009; Spasojevic & Suding 2012), only a few recent studies have carried out so for vertebrates (e.g. Stevens *et al.* 2003, 2012; Stevens, Willig & Strauss 2006; Mason *et al.* 2007; Petchey *et al.* 2007; Weins *et al.* 2007; Devictor *et al.* 2010; Safi *et al.* 2011). From a number of perspectives, bats are a useful taxon for assessing the way in which multiple dimensions of biodiversity respond to environmental change. It is a diverse mammalian order from taxonomic and functional perspectives (Patterson, Willig & Stevens 2003). In the tropics, bats are generally the most species rich and locally abundant mammalian group, and provide important ecological services, such as seed dispersal and pollination (Kunz *et al.* 2011).

Elevational gradients are particularly useful for exploring patterns of biodiversity and their underlying structuring mechanisms because they represent considerable environmental change over relatively short geographical distances (Körner 2007). For the most part, descriptive

and mechanistic studies of bat biodiversity along elevational gradients have been restricted to the taxonomic dimension (Graham 1990; Patterson *et al.* 1998; McCain 2007). A global meta-analysis of elevational gradients in bat species richness suggested that maximum richness occurs where temperature and water availability are greatest (McCain 2007). Nonetheless, it is unclear whether the relative importance of temperature and water availability is associated with thermoregulatory constraints (i.e. abiotic filtering) or is mediated through the distribution of resources (e.g. interspecific competition and niche partitioning).

We quantified taxonomic, phylogenetic and functional dimensions of biodiversity along an extensive elevational gradient using comprehensive presence–absence data from the Manu Biosphere Reserve (hereafter Manu; Patterson, Stotz & Solari 2006). Moreover, we compared empirical elevational gradients in phylogenetic and functional dispersion to expected gradients given variation in species richness. The main objectives of this study were threefold: (i) to describe elevational gradients for each of the three dimensions of biodiversity, (ii) to evaluate the utility of species richness as a surrogate for other dimensions and (iii) to quantify the relative support for mechanisms that increase or decrease phylogenetic or functional dispersion.

Materials and methods

STUDY AREA AND ORGANISMS

Manu is located in the watersheds of the Río Alto Madre de Dios, along the eastern slopes of the Andes of southeastern Peru (MacQuarrie 1992). This 1881 200 ha reserve comprises lowlands and highlands that range from 340 to 3625 m above sea level, and supports diverse faunal and floral assemblages (Patterson, Stotz & Solari 2006). Structurally distinct vegetation types replace one another along the elevational gradient of Manu (Terborgh 1971; Patterson *et al.* 1998). Lowland rain forest has 50–60 m canopies and occurs below 500 m of elevation. Montane rain forest is shorter (*c.* 35 m tall), less vertically complex, and occurs from 500 to 1400 m. A persistent cloud layer defines the presence of cloud forest from 1400 to 2800 m. Elfin forest (2800–3200 m) supports a low canopy (*c.* 15 m) and dense vegetation. Above 3200 m, patches of elfin forest are intermixed with tall grasslands.

Comprehensive data on the elevational distributions of 92 species of bat from Manu were compiled from museum specimens, published literature and recent surveys (Patterson, Stotz & Solari 2006). Data on species incidence were organized into thirteen 250 m elevational strata, with the lowest stratum at 500 m (elevational range from 251 to 500 m) and the highest stratum at 3500 m (from 3251 to 3500 m). We selected 250 m intervals to balance the resolution of empirical records, amount of collection effort in each interval, power of statistical analyses and the need for a scale of analysis that is ecologically meaningful. Smaller intervals, such as 100 m, may not be ecologically meaningful because of the high vagility of bats. Moreover, intervals that are too small may create gaps in distributions that are not real, but that represent sampling deficiencies. Consequently, smaller

elevational intervals may provide greater statistical power, but reduced confidence in the completeness of data for each stratum.

QUANTIFICATION OF DIMENSIONS OF BIODIVERSITY

Data

To evaluate the taxonomic dimension, we determined species richness of bat assemblages for each elevational stratum. We followed the nomenclature and taxonomy of Simmons (2005), except for recognizing newly described species *Carollia manu* (Pacheco, Solari & Velazco 2004), *Platyrrhinus albericoi* and *P. masu* (Velazco 2005), and an undescribed species in the genus *Anoura*.

We evaluated the phylogenetic dimension based on branch lengths from a species-level supertree for bats (Jones, Bininda-Emonds & Gittleman 2005). Ten of 92 species from Manu were not present in this supertree, four of which were the newly described species. The closest congener present in the supertree that was not from Manu was substituted for each missing species. The effects of these substitutions on phylogenetic characteristics of strata likely are small because the lengths of terminal branches for congeners are often the same or very similar within the context of tree height (distance from root to tips) in the supertree. In addition, these substitutions likely did not disproportionately affect particular elevational strata because missing species were relatively evenly distributed along the gradient. Multiple phylogenetic trees are available for bats; however, the supertree developed by Jones, Bininda-Emonds & Gittleman (2005) is the most complete and accurate and contains the greatest representation of species that are present in Manu. Moreover, assessment of phylogenetic dispersion is robust with respect to variation in the resolution of nodes near terminal branches of phylogenies (Webb 2000).

The functional dimension was estimated using two types of data: categorical and mensural attributes (Table 1). Each functional attribute was assigned to a group that reflects a particular niche axis and defines a functional component of biodiversity. Categorical components were associated with (i) diet, (ii) foraging location and (iii) foraging strategy. Mensural components were associated with (i) body size, (ii) masticatory mode (i.e. skull characteristics) and (iii) aerodynamic mode (i.e. wing characteristics). These functional components reflect physiological constraints, diet and foraging behaviour, respectively. For each categorical attribute, a species received a '1' if it exhibited the characteristic or a '0' if it did not exhibit the characteristic. For each mensural attribute, an average value was obtained for each species based on measurements of multiple male and female adults.

Information for all attributes was derived from the literature and museum specimens, and was restricted to records from South America when possible (Table S1, Supporting Information). Missing mensural values were estimated using linear regression with mass or forearm length as the independent variable. Selection of mass or forearm length as the independent variable was based on the R^2 for linear or quadratic models using attribute values of other species from the same subfamily. Missing categorical data were replaced by values from congeners. Only 9.1% of species traits were estimated or replaced (i.e. 218 of 2392 traits). Because environmental gradients may affect particular functional components differently, integration of ecological attributes into a

Table 1. Functional attributes that reflect niche axes (functional components) were used to estimate functional dispersion of bat assemblages from Manu. Mensural attributes were measured as described in sources (see Table S1, Supporting Information)

Type of data	Functional component	Attribute	Trait value	
Categorical	Diet	Fruit or plant	0, 1	
		Nectar or pollen	0, 1	
		Invertebrates	0, 1	
		Vertebrates	0, 1	
		Fish	0, 1	
		Blood	0, 1	
	Foraging location	Open area	0, 1	
		Over water	0, 1	
		Above canopy	0, 1	
		Canopy	0, 1	
		Subcanopy	0, 1	
		Understorey	0, 1	
	Foraging strategy	Aerial	0, 1	
		Gleaning	0, 1	
		Hover	0, 1	
Mensural	Size	Mass	Mean value (g)	
		Forearm length	Mean value (mm)	
	Skull	Greatest length of skull	Mean value (mm)	
		Condylbasal length	Mean value (mm)	
		Length of maxillary toothrow	Mean value (mm)	
		Breadth across upper molars	Mean value (mm)	
		Width across post-orbital constriction	Mean value (mm)	
		Breadth of braincase	Mean value (mm)	
		Wing	Wing loading	Mean value (mm)
			Aspect ratio	Mean value (mm)

single multivariate measure may obscure important patterns (Spasojevic & Suding 2012). Accordingly, mean functional differences between species were estimated for each functional component separately (Table 1), as well as for all functional components combined (each component was weighted equally despite having unequal number of attributes).

Biodiversity indices

The taxonomic dimension of biodiversity was estimated by species richness, whereas phylogenetic and functional dimensions were estimated by Rao's quadratic entropy (Rao's Q ; Botta-Dukát 2005). When abundances are unavailable, as in the case for bats at Manu, Rao's Q is the sum of the distances (phylogenetic or functional) between all possible pairs of species, divided by the square of the number of species in the assemblage (Weiher 2011). In general, Rao's Q measures the average difference between species and reflects multivariate dispersion. Hereafter, dispersion and Rao's Q will be used interchangeably when referring to phylogenetic or functional dimensions. Average

phylogenetic or functional distances among species were obtained from pairwise dissimilarity matrices for the phylogenetic approach, for each functional component and for all functional components combined. The phylogenetic pairwise dissimilarity matrix was calculated via the 'cophenetic' function of the R package 'APE' (Paradis, Claude & Strimmer 2004). Functional pairwise dissimilarity matrices were calculated using the Gower metric from the R package 'CLUSTER' (Maechler *et al.* 2012). The Gower metric can quantify dissimilarities based on categorical and mensural attributes at the same time (Botta-Dukat 2005).

To facilitate comparisons among dimensions, each metric was transformed into its effective number of species or Hill numbers (hereafter numbers equivalent). The numbers equivalent is the number of maximally dissimilar species with equal abundances that is required to produce the empirical value of a metric (Jost 2006; Villéger *et al.* 2012). This transformation facilitates intuitive interpretation of differences between assemblages or dimensions because indices are expressed in the same units (Jost 2006). Species richness is its own numbers equivalent. Quantification of Rao's Q as numbers equivalent was conducted using R functions developed by de Bello *et al.* (2010).

QUANTITATIVE ANALYSES

We employed a statistical framework that facilitates the detection of multiple elevational relationships (e.g. random, linear and nonlinear relationships) based on the significance of parameters in a second-order orthogonal polynomial (Dutka & Ewens 1971). We have no *a priori* empirical evidence or theoretical argument on which to base the exploration of higher-order polynomials and used second-order polynomials to capture linear and nonlinear responses of different dimensions of biodiversity to environmental variation associated with elevation. We used orthogonal regression (see Dutka & Ewens 1971) because it decomposes relationships into components that represent independent estimates of the importance of magnitude (b_0^*), a constant rate of change (b_1^*) and a varying rate of change (b_2^*). Conceptually, the best-fit curve from ordinary polynomial regression accurately estimates the amount of variation (R^2) in the dependent variable (i.e. biodiversity metric) that is associated with variation in the independent variable (i.e. elevation); however, the identification of the contributions of linear and nonlinear components can be obscured because parameter estimates (i.e. b_1 and b_2) are confounded. Orthogonal polynomial regression decomposes the general relationship from ordinary polynomial regression into a suite of additive independent polynomials (zeroth, first- and second-order relationships) whose coefficients (b_0^* , b_1^* and b_2^*) represent their independent contributions, and whose statistical significance can then be evaluated in an unbiased fashion. Relationships between the three dimensions of biodiversity were evaluated using Spearman rank correlations.

To evaluate the extent to which the elevational relationship of phylogenetic or functional dispersion arose as a consequence of variation in species richness (i.e. species selection effect *sensu* Huston 1997), we conducted a suite of randomizations, each comprising 1000 iterations. We used the trial-swap method (Miklós & Podani 2004) on a species pool defined as the bat fauna from Manu. This method shuffles the phylogenetic or functional identities of species at elevational strata while constraining species richness of elevational strata to equal empirical values and constraining the frequency of occurrence for species to equal

empirical frequencies along the gradient (The R package 'PICANTE'; Kembel *et al.* 2010). For each iteration, we calculated b_1^* and b_2^* using orthogonal polynomial regression, thereby creating a distribution of 1000 values for each coefficient. We considered an empirical coefficient to be different from those of gradients based on null expectations (hereafter, null gradients) if the empirical coefficient was greater than or <97.5% of the values defined from randomly generated matrices (two-tailed test). Deviations of empirical gradients from null gradients suggest the relative importance of environmental processes that enhance or reduce attribute dispersion depending on the direction of the deviation (Fig. 1).

Results

Relationships among the three dimensions were complex. Species richness was significantly correlated with only half of the phylogenetic or functional approaches (Fig. 2). Of the significant correlations with species richness, half were negative associations (foraging location, foraging strategy) and half were positive associations (size, skull). Relationships between phylogenetic and functional Rao's Q were also complex. Phylogenetic Rao's Q was positively correlated with Rao's Q based on all functional components ($\rho = 0.70$, $P = 0.007$); however, only two of the six functional components were positively correlated with phylogenetic Rao's Q (foraging strategy: $\rho = 0.73$, $P = 0.005$; wing: $\rho = 0.57$, $P = 0.041$), and the other four had non-significant relationships with phylogenetic Rao's Q (diet: $\rho = 0.24$, $P = 0.437$; foraging location: $\rho = 0.39$, $P = 0.188$; size: $\rho = -0.21$, $P = 0.494$; skull: $\rho = 0.20$, $P = 0.517$).

Elevational gradients of biodiversity differed among dimensions (Fig. 3; Table S2, Supporting Information). Most of the variation in species richness among strata ($R^2 = 0.98$) was accounted for by variation in elevation (a proxy for environmental variation along the gradient). Moreover, the elevational decline in richness was steep and nonlinear. In contrast, variation in phylogenetic Rao's Q was not associated with elevation ($R^2 = 0.02$), with non-significant linear and quadratic components from the orthogonal polynomial regression. Similarly, linear and quadratic components were non-significant for functional Rao's Q based on all functional components, with the overall model accounting for only 30% of variation between strata. Importantly, considerable heterogeneity existed among the elevational relationships of functional components (Fig. 4), with functional components exhibiting U-shaped, linearly decreasing, linearly increasing or stochastic relationships.

The extent to which empirical variation in phylogenetic or functional dispersion arose as a consequence of elevational variation in species richness was quantified by a randomization approach (Figs 3 and 4; Table S3, Supporting Information). For phylogenetic dispersion, the empirical linear coefficient (b_1^*) was greater than expected after accounting for variation in species richness (arrow in Fig. 3b). In contrast, empirical linear and quadratic

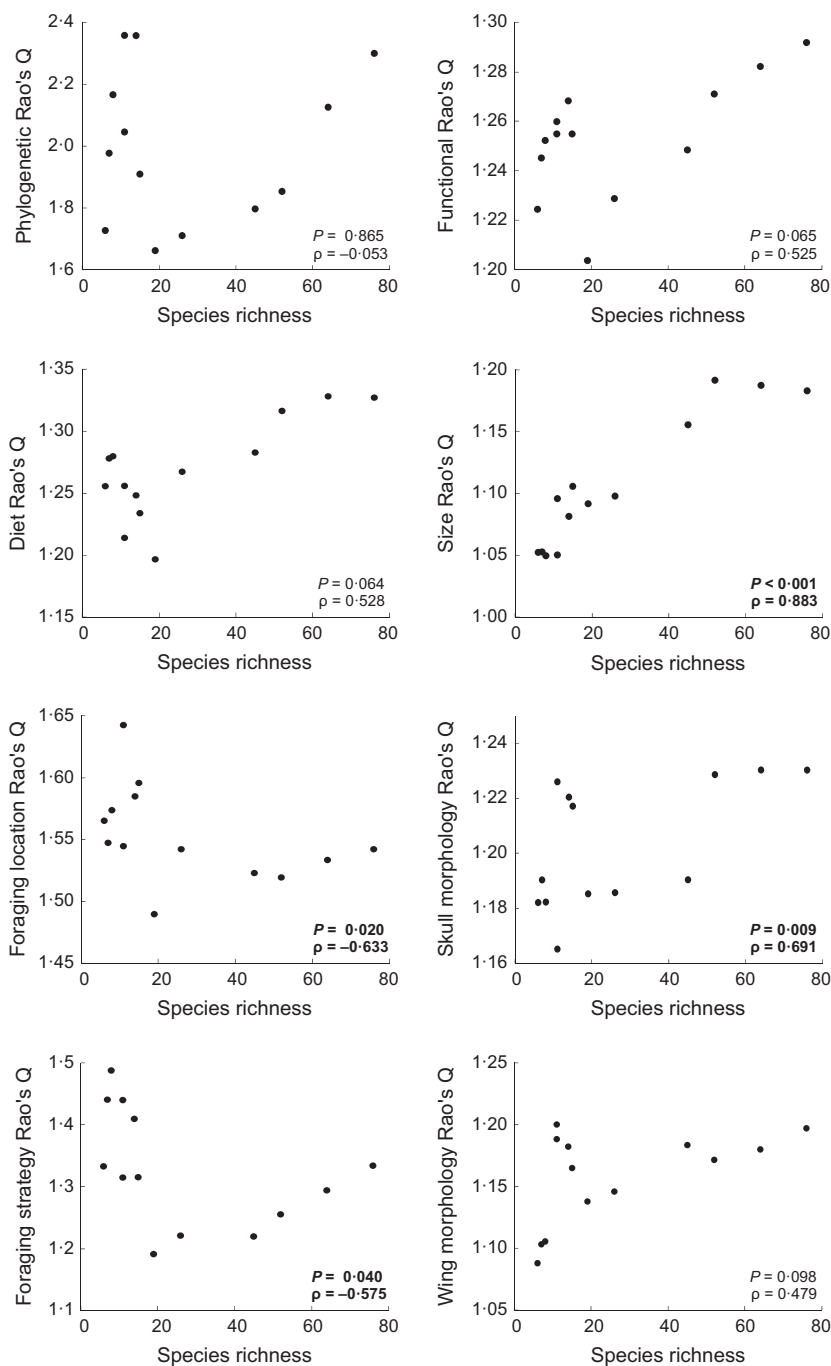


Fig. 2. Variation in phylogenetic and functional Rao's Q as well as in six functional components with respect to species richness. Spearman rank correlation coefficients (ρ) and associated significance are reported for each relationship. Significant correlations are in boldface ($P \leq 0.05$).

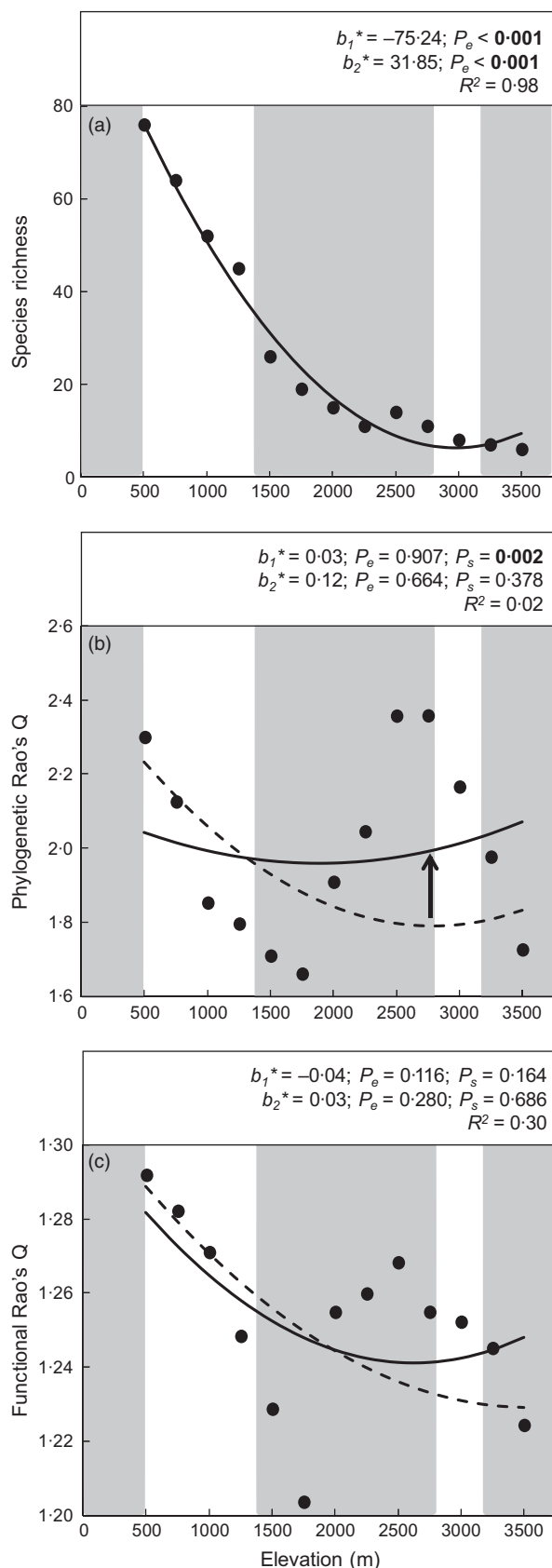
components of the elevational gradient in functional dispersion based on all functional components were not significantly different than the null expectation. For particular functional components, considerable heterogeneity existed in the ability of variation in species richness to account for variation in functional dispersion. Gradients in functional attributes associated with diet, foraging strategy and size were each different than the null expectation (Fig. 4; directions of deviations indicated by arrows), whereas gradients associated with foraging location, skull attributes and wing characteristics were not significantly different than expected. Results from

stratum-level randomization analyses were consistent with results from gradient-level randomization analyses (Fig. S1, Supporting Information).

Discussion

SURROGACY OF DIMENSIONS

Recent analytical and technological advances allow for a more complete characterization of biodiversity by including taxonomic, phylogenetic and functional dimensions. Nonetheless, if the relationships between dimensions are



strong and predictable, one dimension may serve as an effective surrogate for other dimensions. To justify the use of surrogates to estimate biodiversity, two general

Fig. 3. Elevational variation in (a) taxonomic, (b) phylogenetic and (c) functional dimensions of biodiversity of bats at Manu. Empirical values of the taxonomic dimension (i.e. species richness) and of the phylogenetic and functional dimensions (i.e. Rao's Q transformed as numbers equivalents) are represented by black dots. Phylogenetic Rao's Q is based on a supertree (Jones, Bininda-Emonds & Gittleman 2005). Functional Rao's Q is based on all attributes, with each functional component weighted equally. A solid line represents an empirical polynomial relationship, and R^2 is the fit of the model. Significant ($P_e \leq 0.05$) orthogonal regression coefficients (b_1^* and b_2^*) are indicated by boldface. Dashed lines represent mean polynomial relationships derived from randomizations. Orthogonal regression coefficients of empirical gradients that are significantly different ($P_s \leq 0.05$) from those of null gradients are indicated by boldface. An arrow between empirical and null gradients illustrates direction of significant deviations. Alternating shaded regions of the graphic correspond to elevationally defined forest types (see text for details).

expectations should be true. First, for species richness to be a useful surrogate, phylogenetic or functional dispersion, as measured by Rao's Q , should increase in a saturating fashion with increasing species richness (see Introduction for reasoning of null expectation; Fig. 1). Deviations from this null expectation indicate the presence of strong ecological processes that structure functional or phylogenetic aspects of assemblages (Fig. 1); consequently, species richness will not accurately portray variation in other dimensions of biodiversity. Secondly, for phylogenetic and functional dimensions to be effective surrogates of each other, functional components need to be phylogenetically conserved, resulting in a strong correlation between phylogenetic and functional dispersion.

For bats at Manu, species richness was not an effective surrogate for phylogenetic or functional dispersion. In general, the expected form of the relationship between phylogenetic dispersion and richness or between functional dispersion and richness (i.e. an increasing and saturating curve) was not evident, and correlations were not significant (Fig. 2). Nonetheless, richness was a reasonable surrogate for functional components based on size and skull attributes. Bat richness decreased quickly until 2000 m, but exhibited much less variation at higher elevations (Fig. 3a). Despite species richness varying only between six and 11 species above 2000 m, variation in phylogenetic dispersion (Fig. 3b) and in most functional components (e.g. diet, foraging location, foraging strategy, skull, wing; Fig. 4) above 2000 m was equal to or greater than the variation at lower elevations at which richness decreased from 76 to 15 species.

The degree to which phylogenetic or functional dispersion is an effective surrogate of the other was dependent on the functional component. Nonetheless, phylogenetic dispersion was correlated with functional dispersion based on all functional components. Thus, combining many functional components into a single measurement of functional diversity captured similar variation to that associated with evolutionary history. Nonetheless, only two of the six functional components were positively correlated

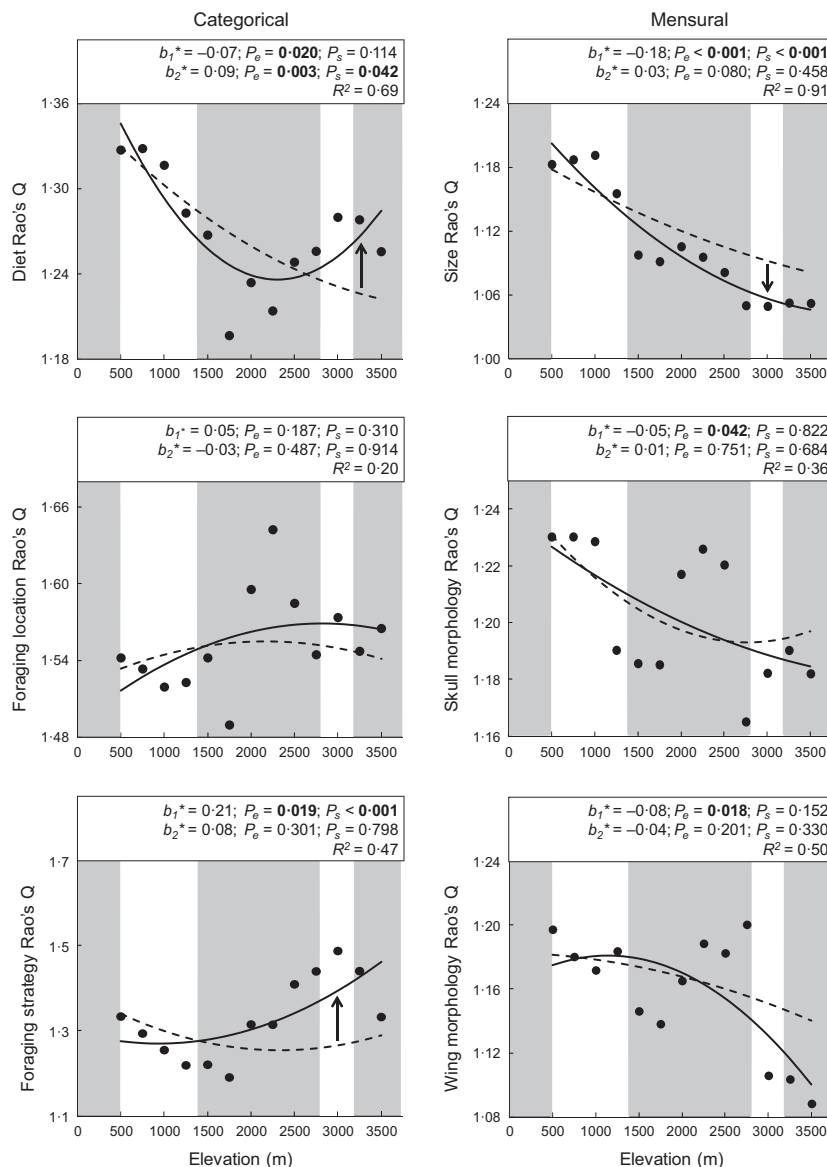


Fig. 4. Elevational gradients of functional Rao's Q based on consideration of each functional component separately. Empirical values of Rao's Q (transformed as numbers equivalents) are represented by black dots. A solid line represents the empirical polynomial relationship, and R^2 is the fit of the model. Significant ($P_e \leq 0.05$) orthogonal regression coefficients (b_1^* and b_2^*) are indicated by boldface. Dashed lines represent mean polynomial relationships derived from randomizations. Orthogonal regression coefficients of empirical gradients that are significantly different ($P_s \leq 0.05$) from those of null gradients are indicated by boldface. An arrow between empirical and null gradients illustrates direction of significant deviations. Alternating shaded regions of the graphic correspond to elevationally defined forest types (see text for details).

with phylogenetic dispersion, which may reflect different strengths of the phylogenetic signal exhibited by particular functional components.

STRUCTURING MECHANISMS

Because species richness is a poor surrogate for other dimensions of biodiversity, structuring mechanisms that mould elevational gradients in species richness of bats likely do not account for much of the variation in ecological or evolutionary attributes of bat assemblages in Manu. Moreover, the identification of mechanisms that structure phylogenetic or functional dispersion may enhance understanding about the relative contribution of mechanisms that affect spatial patterns of species richness. For bats, abiotic factors, habitat characteristics and resource availability are important determinants of species richness along elevational gradients (Graham 1990; Patterson, Pacheco & Solari 1996; Willig, Patterson & Stevens 2003;

McCain 2007). However, the relative importance of abiotic and biotic processes in structuring bat biodiversity remains poorly understood (McCain 2007). Deviations of phylogenetic or functional dispersion from those predicted based on variation in species richness may help identify abiotic or biotic processes that influence community assembly.

Phylogenetic dispersion

Assessment of the relative importance of niche-based processes is dependent on the assumption that critical ecological attributes are conserved phylogenetically. In Manu, attributes from all functional components exhibit strong phylogenetic signals (unpublished data). Consequently, elevational patterns of phylogenetic dispersion may integrate results of multiple processes associated with different ecological attributes, including attributes with a phylogenetic signal that were not included in the functional data.

The elevational gradient of phylogenetic dispersion was different from that expected based on variation in species richness, especially at high elevations where empirical phylogenetic dispersion deviated the most from the null expectation (arrow in Figs 3b and S1, Supporting Information). This result is inconsistent with the general expectation that attributes of assemblages should be more similar when environmental conditions are stressful to a majority of species in an assemblage (Weiher & Keddy 1995). For tropical bats, environmental conditions become more physiologically stressful with increasing elevation as temperature, area, productivity per unit area and resource diversity decrease (Terborgh 1977; Gentry 1988; Graham 1990; Körner 2007). However, phylogenetic dispersion was greatest at high elevations, suggesting the greater importance of interspecific competition (possibly due to reduction in resource availability) as opposed to abiotic or biotic filtering in structuring assemblages when resources are limiting and productivity is low.

Changes in the relative proportions of species from different families along the elevational gradient (Fig. 5) may be the result of niche partitioning and increased interspecific competition as resources become more limiting. Variation in Rao's Q reflects changes in the dispersion of species in multidimensional space. Consequently, Rao's Q can increase in magnitude if new evolutionary lineages or functions are added to an assemblage, thereby increasing the size of the space, or if redundant species (i.e. species that perform similar roles; Rosenfeld 2002) are removed from it, which increases the dispersion of species within the space. Although phylogenetic spaces occupied by assemblages in cloud forest were similar in size (i.e. representatives from clades 1, 2 and 3 from 1750 to 2750 m; Fig. 5), the proportional representation of each clade became more equable with increasing elevation. At the lower limit of cloud forest, phyllostomids (clade 3; Fig. 5) represented 89% of species. A decrease in phyllostomid richness, coupled with increases in the richness of vespertilionids and molossids (clades 1 and 2, respectively; Fig. 5), resulted in a more uniform representation of these families and greater phylogenetic dispersion at the upper limit of cloud forest than elsewhere. Greater phylogenetic dispersion at high elevations resulted from the loss of redundant species, rather than a gain of new evolutionary lineages. Loss of redundant phyllostomids, primarily frugivorous species that forage in highly cluttered spaces, with increasing elevation may result from increased competition within the frugivore ensemble associated with a simplification of vertical vegetative structure (Terborgh 1971) and a reduction in the abundance and diversity of fruits eaten by bats (Gentry 1988).

Functional dispersion

The identity and manner in which particular assembly mechanisms affect the structure of assemblages may depend on the nature of the functional components. One

mechanism could cause an increase in dispersion of one functional component and a decrease in dispersion of another (Figs 4 and S1, Supporting Information). Consequently, dispersion based on composite variation in multiple functional components reflects the interactions of multiple mechanisms. Indeed, bat functional dispersion based on all functional components did not vary much along the elevational gradient at Manu. Moreover, it was not significantly different from expectations associated with variation in species richness (Fig. 3c), despite elevational variation in each of three constituent components being significantly different than expected. This may be a common phenomenon, as little change in functional diversity along environmental gradients has been observed for a variety of plant assemblages when functional diversity reflected multiple functional components simultaneously (Mason *et al.* 2011; Spasojevic & Suding 2012). Because the relative importance of structuring mechanisms may vary between functional components, decomposing the functional dimension into constituent components may identify opposing effects of ecological processes on functional dispersion.

Elevational gradients in dispersion of three functional components revealed opposing influences of ecological processes on attributes associated with diet, food acquisition and body size. The greatest deviation between empirical and expected patterns for each of these three functional components occurred at high elevations; however, dispersion of diet and foraging strategy attributes was greater than expected at high elevations, whereas size dispersion was less than expected at high elevations (direction of deviations indicated by arrows in Fig. 4). All diet and foraging strategy attributes present at 1750 m were also present at the upper limit of cloud forest and in elfin forest, confirming that functional dispersion based on these functional components did not increase due to additions of new functional attributes. Similar to the situation for phylogenetic dispersion, competitive interactions and niche partitioning may play significant roles in promoting increased diet and foraging strategy dispersion at high elevations. Variation in the proportions of diet or foraging strategy attributes suggests that increased interspecific competition reduces the number of functionally redundant species (Fig. 6). Bat assemblages at the lower limit of the cloud forest (*c.* 1750 m) were dominated by frugivorous species or species that glean from surfaces and shifted to assemblages characterized by more even proportions of diet or foraging strategy attributes at the upper limit of cloud forest and in elfin forest (2750–3000 m; Fig. 6). Attributes that define these functional components exhibit strong phylogenetic signals (unpublished data) and likely represent the attributes on which mechanisms operate to determine species richness and composition of assemblages as well as variation in phylogenetic dispersion along the gradient.

At high elevations, size dispersion was less than null model expectations (Fig. 4), which suggests that the most

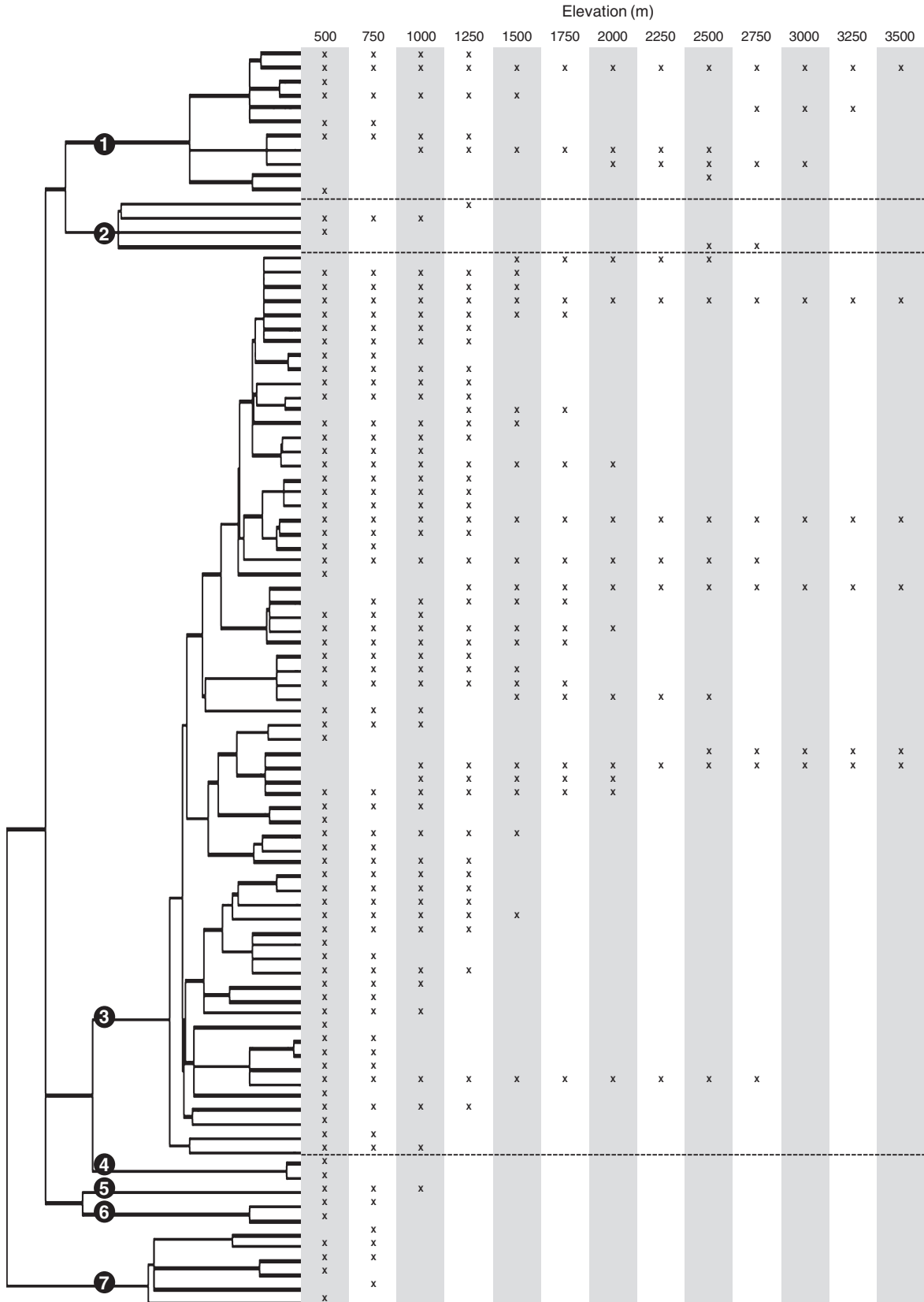


Fig. 5. Dispersion of species (represented by *x*) on the supertree for bats at each elevational stratum at Manu. Clades representing seven bat families are indicated by numbered black dots (1 = Vespertilionidae; 2 = Molossidae; 3 = Phyllostomidae; 4 = Noctilionidae; 5 = Furipteridae; 6 = Thyropteridae; and 7 = Emballonuridae). Dashed lines separate four groups of families to illustrate differences in the representation of families along the gradient.

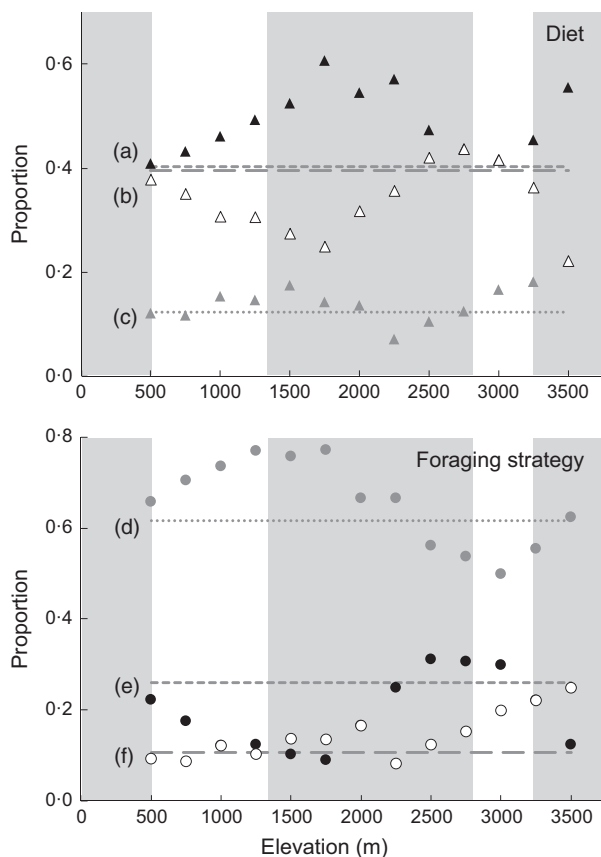


Fig. 6. Proportion of bats at each elevational stratum with a diet of fruit (\blacktriangle), invertebrates (\triangle) or nectar (\blacktriangle) and that glean (\bullet), hover (\circ) or aerially catch prey (\bullet). The proportion of each food type in the diet of the fauna is shown as a short-dashed line for fruit (a), a long-dashed line for invertebrates (b) and a dotted line for nectar (c). The proportion of each foraging strategy of the fauna is shown as a dotted line for gleaning bats (d), a short-dashed line for hovering bats (e), and a long-dashed line for aerial bats (f). Alternating shaded regions of the graphic correspond to elevationally defined forest types (see text for details).

influential mechanisms for body size dispersion are abiotic or biotic filtering (Fig. 1). Decreasing temperature and productivity per unit area with increasing elevation (Terborgh 1977; Gentry 1988; Körner 2007) may constrain variation in body size to an optimum, with constraints leading to an expectation of smaller body sizes with increasing elevation. Indeed, species at high elevations were smaller than the mean of the entire bat fauna of Manu (e.g. average mass for entire gradient = 20.6 g, range = 3.2–169.4 g; average mass above 2750 m = 12.4 g, range = 5.3–27.0 g). The absence of larger species from higher elevations likely is associated with a reduction in resource abundance and increased energy demands required to maintain viable populations (Graham 1990). In addition, smaller bats enter daily torpor more easily than do larger bats (McNab 1982), which may be a more efficient strategy for balancing energy expenditures between thermal regulation and other physiological demands (e.g. reproduction, growth).

Conclusion

Elevational gradients in taxonomic, phylogenetic and functional dimensions of bat biodiversity differed in the significance of the linear and quadratic components. Moreover, the elevation gradient in functional dispersion based on all functional components obscured heterogeneous elevational responses of constituent components. Elevational variation in phylogenetic dispersion and in dispersion of most functional components did not exhibit the expected relationship with species richness (i.e. asymptotic increase; Figs 1 and 2) that is based on theory (i.e. sampling effects and phylogenetic signals). This suggests that a single dimension may not be a good surrogate for others. Assessment of deviations of empirical elevational gradients in phylogenetic and functional dispersion to null gradients based on empirical species richness revealed that significant deviations occurred at high elevations. Greater dispersion in phylogenetic, diet and foraging strategy attributes at high elevations was due to loss of redundant species, suggesting that enhanced interspecific competition associated with lower productivity structures assemblages at higher elevations. In contrast, body size dispersion was less than expected at high elevations, suggesting the importance of abiotic filtering associated with physiological constraints.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Results from stratum-level randomization analyses evaluating the degree to which (a) phylogenetic dispersion, functional

dispersion based on all functional components and (b) dispersion of each functional component separately differ from the null expectation based on empirical species richness at each elevational stratum.

Table S1. Sources of information for functional attributes of bat species were compiled from the literature and supplemented with data obtained from museum specimens.

Table S2. Regression coefficients derived from ordinary and orthogonal polynomial regressions for the relationship between various aspects of biodiversity and elevation (m).

Table S3. Comparison of empirical orthogonal regression coefficients to mean expected orthogonal regression coefficients based on 1000 randomizations in which species richness of each stratum and frequency of occurrence of each species were maintained to equal those in the empirical data.