



Taxonomic, functional, and phylogenetic dimensions of rodent biodiversity along an extensive tropical elevational gradient

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Relationships among taxonomic, functional, and phylogenetic dimensions of biodiversity provide insight about the relative contributions of ecological and evolutionary processes in structuring local assemblages. We used data for rodent species distributions from an extensive tropical elevational gradient to 1) describe elevational gradients for each of three dimensions of biodiversity, 2) evaluate the sufficiency of species richness as a surrogate for other dimensions, and 3) quantify the relative support for mechanisms that increase or decrease phylogenetic or functional dispersion. Taxonomic biodiversity was quantified by species richness, as well as by richness, evenness, diversity, dominance, and rarity at generic and familial levels. Morphological and categorical traits were used to estimate functional biodiversity, and an ultrametric mammalian supertree was used as the basis for estimating phylogenetic biodiversity. Elevational gradients of each dimension of biodiversity were strong, with significant linear and non-linear components based on orthogonal polynomial regression. Empirical linear and non-linear regression components were consistently different than those expected based on species richness for generic, familial, and phylogenetic biodiversity, but not for functional biodiversity. Nevertheless, the congruence of dimensions of biodiversity based on correlation analyses indicated that any one dimension is a useful surrogate for the other dimensions for rodents at Manu. Given variation in species richness, assemblages from lowland rainforests comprised more biodiversity than expected, whereas assemblages from cloud and elfin forests represented less biodiversity than expected. Warm temperatures, vertical complexity of the vegetation, and high productivity likely facilitate niche differentiation in rainforests, whereas cricetid rodents are competitively superior to other clades in the less structurally complex, less productive, and colder, high elevation habitats.

Maintaining essential ecosystem services and the genetic bases for future adaptation in a changing environment are among the primary goals of sustaining biodiversity (Naeem and Li 1997, Cardinale et al. 2012). Nonetheless, management efforts and conservation policies do not always reflect these goals, as they are often based on approaches that deem all species to be equally distinct and equally important to ecosystem functioning (May 1988, Humphries et al. 1995). More specifically, species richness (i.e. the number of species) is generally used to characterize patterns of biodiversity among sites and along gradients, and often is the primary basis for conservation decisions (Beier et al. 2002, Schipper et al. 2008, Ahumada et al. 2013). Although it is relatively easy to quantify, richness alone is an incomplete and potentially misleading surrogate for biodiversity as functional, phylogenetic, and genetic aspects may respond to different factors (i.e. have different mechanistic bases) or may have different kinds of responses to the same factors. As such, species richness may fail to reflect dynamics of communities or

ecosystems that are important from theoretical and applied perspectives (Gotelli and Colwell 2001, Orme et al. 2005).

For the taxonomic dimension to be an effective surrogate for biodiversity in general, the form and predictability of its relationship with other dimensions of biodiversity must hold for a variety of taxa and systems. In addition, the degree of congruence between dimensions of biodiversity provides insights into the relative importance of different processes that structure local assemblages. A more comprehensive approach for understanding spatial and temporal variation in biodiversity can better advance theory and can enhance efficacy of ecosystem management and the preservation of services they provide to humans.

Patterns of taxonomic biodiversity are well-documented along elevational gradients, as these gradients are proxies for variation in environmental characteristics (i.e. temperature, solar irradiation, precipitation, productivity, habitat type) that affect the distribution and abundance of species (Körner 2007). Although relationships between species richness and

elevation are often quantified, variation exists in their form or parameterization. Biogeographic or macroecological studies demonstrate that species richness may decrease with increasing elevation (Terborgh 1977, Graham 1990, Patterson et al. 1998) or may evince a mid-elevational peak (Rahbek 1995, McCain 2005), and in a few cases richness peaks on mountain summits (Bobretsov et al. 2005). Critically, relationships between biodiversity and elevation may be more complex than suggested by previous studies because differences among species with regard to function or evolutionary history have been ignored or minimized. If patterns in other dimensions of biodiversity are not well represented by patterns in species richness, then scientific understanding of community assembly and structure along gradients based on taxonomic data may be misleading or simplistic.

Functional biodiversity reflects variability in ecological attributes among species or individuals. Traits that quantify the functional diversity of an assemblage provide insight about functional uniqueness, redundancy, and complementarity, and offer clues to the resistance or resilience of ecosystems (Walker 1992, Vandewalle et al. 2010). Functional traits must be selected with care to ensure that they measure functional aspects of interest and to ensure that results are interpretable and ecologically meaningful (Petchey and Gaston 2006). Phylogenetic biodiversity represents variation in evolutionary history among species, and is based on the evolutionary distance between species in a phylogeny (i.e. time since divergence from a common ancestor; Vellend et al. 2010). An assemblage with greater phylogenetic biodiversity may be buffered from long-term environmental change because species are less likely to share evolutionary constraints. Phylogenetic and functional biodiversity may be related because evolutionary diversification generates trait diversification (Faith 1992). A comparison of spatial patterns of functional and phylogenetic biodiversity provides insight as to whether trait convergence or trait conservatism has been important in shaping the composition of ecological assemblages. The extent to which the variation in dimensions of biodiversity is congruent with variation in species richness may help to identify mechanisms that structure communities along gradients (Cisneros et al. 2014, Fig. 1). However, few studies have concurrently quantified all three dimensions to assess spatial patterns of biodiversity (Devictor et al. 2010, Flynn et al. 2011, Safi et al. 2011, Cisneros et al. 2014).

In general, phylogenetic or functional biodiversity is expected to increase in a saturating fashion with increasing taxonomic biodiversity (Fig. 1) because the probability of adding species with new ecological attributes or evolutionary lineages to an assemblage decreases as assemblages become more species rich (Kluge and Kessler 2011). In addition, phylogenetic inertia – the idea that organisms are not designed from scratch, but evolve through modification of a template inherited from an ancestor (Shanahan 2011) – gives rise to the a priori expectation that more closely related species will be functionally more similar and that more distantly related species will be functionally less similar (Safi et al. 2011). If these general expectations are true for different taxa and ecosystems, dimensions are expected to be positively correlated and one dimension may be a useful surrogate to estimate biodiversity. In contrast, deviations from expectation may occur in relationships between dimensions

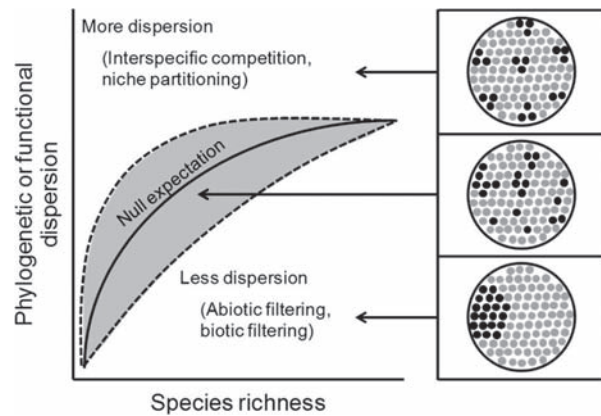


Figure 1. Framework for evaluating the relative importance of ecological processes based on the extent to which phylogenetic or functional dispersion differ from expectation given variation in species richness (i.e. shaded area, see text for reasoning of increasing asymptotic relationship). Phylogenetic 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 null expectation. 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 exhibit a phylogenetic signal (after Cisneros et al. 2014).

if community assembly is dominated by mechanisms that tend to increase (e.g. interspecific competition, niche partitioning) or decrease (e.g. abiotic or biotic filtering) functional or phylogenetic dispersion (Fig. 1).

Rodents are species rich, often comprising taxa that are locally abundant and responsive to environmental variation (Kattan et al. 2004, McCain 2004, 2005), making them particularly useful for understanding effects of environmental variation on species distributions and community structure. Topography has played a key role in the arrival, radiation, and diversification of Andean rodents, making them a particularly suitable taxon for exploring questions in large-scale ecology. To date, most studies that have examined rodent communities along elevational gradients have focused on the taxonomic dimension, and almost exclusively on species richness (Patterson et al. 1989, Sánchez-Cordero 2001, Kryštufek and Griffiths 2002, McCain 2004, Caceres et al. 2011). Studies that have incorporated functional or phylogenetic biodiversity have shown inconsistent relationships between those dimensions and species richness. More specifically, foraging guild (Sánchez-Cordero 2001) and morphological diversity (Shepherd and Kelt 1999) may have positive associations with species richness along elevational gradients, whereas phylogenetic diversity may increase, decrease, or have no relationship with species richness (Moritz et al. 2000, Cardillo et al. 2008).

We quantified elevational gradients in taxonomic, functional, and phylogenetic biodiversity of the rodent fauna in the Peruvian Andes. We assessed the congruence of

elevational gradients of the three dimensions, and the extent to which variation in species richness accounted for variation in taxonomic biodiversity at the generic and familial levels as well as for variation in functional and phylogenetic biodiversity. The main objectives of this study were three-fold: 1) to describe elevational gradients for each of the three dimensions of biodiversity, 2) to evaluate the utility of species richness as a surrogate for other dimensions, and 3) to quantify the relative support for mechanisms that increase or decrease phylogenetic or functional dispersion.

Methods

Study area and dataset

Manu Biosphere Reserve is in southeastern Peru and covers 1 881 200 ha. It harbors high levels of endemism and species richness, much of which is associated with topographic relief and numerous habitats that occur between the mouth of the Río Manu at 340 m and the peak at 3450 m elevation (Patterson et al. 1998). Lowland rainforest occurs below 500 m, where canopy trees reach 50–60 m in height. As the Andes rise above the basin floor, lowland rainforest is replaced by montane rainforest that is similar in species composition, but lacks emergent trees. Around 1400 m, clouds form daily, resulting in a moist, humid environment. In this cloud forest, epiphytes, dense thickets of climbing bamboo, and moss occur throughout the understory. Above 2800 m, cloud forest transitions to elfin forest, characterized by low canopies and abundant microphyllous vegetation. Open grasslands intermixed with elfin forest occur at elevations above 3200 m.

Extensive and intensive vertebrate surveys have been conducted in Manu Biosphere Reserve since its creation in 1973, producing a well-documented rodent fauna of 56 species along the entire elevational gradient (Solari et al. 2006). We use nomenclature and taxonomy that follow Wilson and Reeder (2005), except for recognizing *Dasyprocta variegata* as distinct from *D. punctata* (cf. Emmons and Freer 1997), *Nectomys apicalis* as distinct from *N. squamipes* (Pacheco et al. 2009), *Pattonomys occasius* as the appropriate name for *Makalata occasius* (Emmons 2005), *Nephelomys*, *Euryoryzomy*, and *Hylaeamys* species as separate from *Oryzomys* (Weksler et al. 2006), and a newly described species, *Isothrix barbarabrownae* (Patterson and Velazco 2006). We also recognize two undescribed taxa: a species of *Neacomys* and a species of *Oligoryzomys* (Patterson et al. 2006). Because these records were assembled in a general survey, reliable estimates of abundance are not available; therefore, we use only incidence data for all analyses. Species records were pooled into 13 strata, each spanning 250 m of elevation. 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. Intervals that are too small may create gaps in distributions that are not real, but that represent sampling deficiencies. Consequently, smaller elevational intervals offer greater statistical power, but reduced confidence in the completeness of data for each stratum.

The functional dimension was evaluated based on attributes derived from the literature or from museum specimens, and was restricted to records from South American records when possible. Categorical data were associated with aspects of resource use including the type of resources (e.g. insects, seeds) as well as the location and time of resource acquisition (e.g. foraging location, habitat, and time of activity; Table 1). For categorical functional attributes, each species was assigned a '1' for each attribute that it exhibited and a '0' for each attribute that it lacked. Gaps in categorical data following literature review (7.8% of data) were filled based on expert opinion (B. Patterson). Mensural values were averaged estimates of size (i.e. mass, hind foot length, tail length, and total length) based on multiple adult individuals for each species. A single missing mensural value for *Pattonomys occasius* was estimated via linear regression of that trait with a second mensural attribute (head and body length) with which it is highly correlated. This regression was based on data from species of Echimyinae.

The phylogenetic dimension was evaluated based on branch lengths from a species-level supertree for mammals (Bininda-Emonds et al. 2007). Ten species (*Dasyprocta variegata*, *Isothrix barbarabrownae*, *Myoprocta pratti*, *Neacomys musseri*, *Nectomys apicalis*, *Hylaeamys perenensis*, *Pattonomys occasius*, *Proechimys pattoni*, *Rhagomys longilingua*, *Rhipidomys gardneri*) from Manu were not present in the supertree and their positions were substituted by the most closely related congener in the tree. 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 general, analyses of phylogenetic biodiversity are robust with respect to variation in resolution of more recent phylogenetic relationships (Webb 2000); therefore, replacement of taxa missing from the tree with sister taxa should not greatly affect the results.

Metrics of biodiversity

Taxonomic richness was calculated at the specific, generic, and familial levels. In addition, Shannon's diversity (Pielou

Table 1. Functional attributes that reflect niche axes (functional components) were used to estimate functional biodiversity of rodent assemblages from Manu.

Type of data	Functional component	Attribute	Trait values
Categorical	Location	Terrestrial	0, 1
		Semiaquatic	0, 1
		Arboreal	0, 1
	Habitat	Grassland	0, 1
		Marsh	0, 1
		Forest	0, 1
		Vegetation	0, 1
	Diet	Insects	0, 1
		Activity	Diurnal
	Mensural	Size	Nocturnal
Mass			Mean (g)
Hind foot length			Mean (mm)
Tail length			Mean (mm)
		Total length	Mean (mm)

1966), Camargo's evenness (Camargo 1993), Berger–Parker dominance (Berger and Parker 1970) and rarity were estimated at the generic and familial levels by using proportional richness of a genus or family rather than proportional abundance (Stevens et al. 2003). Rarity at the generic level was estimated as the number of genera in a stratum with less than the average species richness for genera in that stratum (i.e. S/G where S is the species richness of the stratum and G is the generic richness of the stratum). Rarity at the familial level was calculated as the number of families in a stratum with less than the average species richness for the families in that stratum (i.e. S/F where F is the familial richness of the stratum). To promote meaningful comparisons among dimensions, each metric was transformed into its effective number of species or numbers equivalent. The numbers equivalent of an index is the number of maximally-dissimilar, equally-abundant taxa required to produce the observed value of a metric (Jost 2006). This transformation facilitates intuitive interpretation of differences among assemblages because metrics are expressed in the same units (Jost 2006). Entropy values for diversity, evenness, and dominance were transformed into number equivalents via algorithms written in Matlab 7.5.0.342. Species richness and rarity are already expressed as numbers equivalents.

We estimated functional and phylogenetic biodiversity based on Rao's quadratic entropy (Rao's Q , Botta-Dukat 2005). When abundances are unavailable, as in the case for rodents 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 among species and reflects multivariate dispersion. Gower's distances estimated pairwise functional differences between species in each stratum, and were calculated using the cluster and ade4 packages for R (Chessel et al. 2004, Maechler et al. 2005). Functional components were weighted equally despite variation in the number of attributes associated with them. Functional biodiversity was calculated separately for categorical attributes (Table 1, top) and for mensural attributes (Table 1, bottom), as well as for all functional attributes (i.e. combining categorical and mensural attributes). The use of Rao's Q for functional biodiversity requires fewer assumptions than do measures that include hierarchical clustering (Petchey and Gaston 2006), but regardless of the method, all measures of functional biodiversity suffer limitations. Most notably, the number and type of functional traits together with their correlations might alter the level of redundancy that assemblages appear to exhibit. We selected traits to balance having a comprehensive set of functional traits with concerns for multicollinearity. Pairwise phylogenetic distance matrices were calculated via the 'cophenetic' function of the ape package in R (Paradis et al. 2004). For functional and phylogenetic biodiversity, the numbers equivalent for Rao's Q was quantified using R functions developed by de Bello et al. (2010).

Statistical analyses

We employed a statistical framework that facilitates the detection of multiple elevational relationships (e.g.

random, linear, and non-linear relationships such as saturating, modal, or u-shaped) based on the significance of parameters in a second-order orthogonal polynomial (Dutka and Ewens 1971). Because no a priori evidence was available to justify exploration of higher-order polynomials, we used second-order polynomials to capture linear and non-linear responses of each dimension of biodiversity to variation in elevation. Orthogonal regression (Dutka and Ewens 1971) allows for the evaluation of independent estimates of the importance of 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 a biodiversity metric that is related to variation in elevation; however, the identification of the contributions of linear and non-linear components can be obscured because parameter estimates (e.g. b_1 and b_2) are not independent. Orthogonal polynomial regression decomposes the general relationship from ordinary polynomial regression into a suite of additive polynomials (0th, 1st, and 2nd order relationships) whose coefficients (b^*_0 , b^*_1 , and b^*_2) are weightings representing independent and unbiased contributions of elevation to variation in biodiversity among strata. Relationships among the three dimensions of biodiversity were evaluated via Spearman rank correlations.

To evaluate the extent to which the elevational relationship of taxonomic biodiversity at the generic and familial levels, functional biodiversity, and phylogenetic biodiversity arose as a consequence of variation in species richness (i.e. the species selection effect sensu Huston 1997), site-by-species presence–absence matrices were randomized 1000 times using the trial-swap method (Miklós and Podani 2004). This method maintains the empirical richness of the stratum as well as the empirical frequency of the species in the fauna to equal observed values, with only the identities of the species determined by chance (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 that of the simulated gradient if the empirical coefficient was greater than or less than 97.5% of the values defined from randomly generated matrices (i.e. a two-tailed test with $\alpha = 0.05$). Deviations of empirical gradients from simulated gradients (i.e. empirical b^*_1 or b^*_2 that are significantly different from mean simulated b^*_1 or b^*_2 , respectively) suggest the relative importance of environmental processes that appreciably enhance or reduce attribute dispersion.

Results

Elevational gradients for each dimension of biodiversity were strong: taxonomic, functional, and phylogenetic dimensions each decreased non-linearly with increasing elevation (Fig. 2, $R^2_{TD} = 0.91$, $R^2_{FD} = 0.78$, $R^2_{PD} = 0.91$). For taxonomic biodiversity, this decline occurred regardless of level in the taxonomic hierarchy or metric (Fig. 3). Both linear and quadratic components from orthogonal polynomial regression were significant for all taxonomic metrics, for each approach to functional biodiversity, and for phylogenetic biodiversity (Fig. 2–4, Table 2).

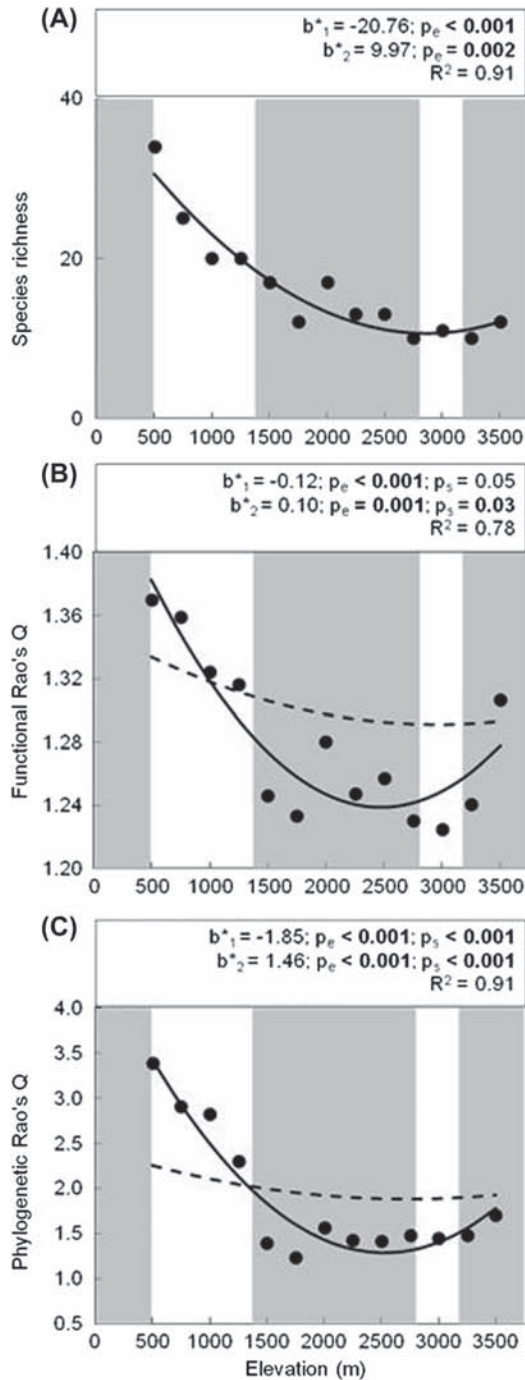


Figure 2. Elevational variation in taxonomic (species richness), functional and phylogenetic dimensions of biodiversity among rodents at Manu. Empirical values are represented by black dots. Phylogenetic diversity (i.e. Rao's Q, transformed as numbers equivalents) is based on a supertree (Jones et al. 2005). Functional biodiversity (i.e. Rao's Q, transformed as numbers equivalents) is based on all attributes (Table 1), with each functional component weight equally. A solid line represents an empirical quadratic relationship and R^2 is the fit of the model. Significant ($p_e < 0.05$) orthogonal regression coefficients (b^*_1 and b^*_2) are indicated by bold p-values. Dashed lines represent mean quadratic relationships derived from simulations. Orthogonal regression coefficients of empirical gradients that are significantly different ($p_s < 0.05$) from those produced by simulations are indicated by bold p-values. Alternating shaded regions correspond to elevationally define forest types (see text for details).

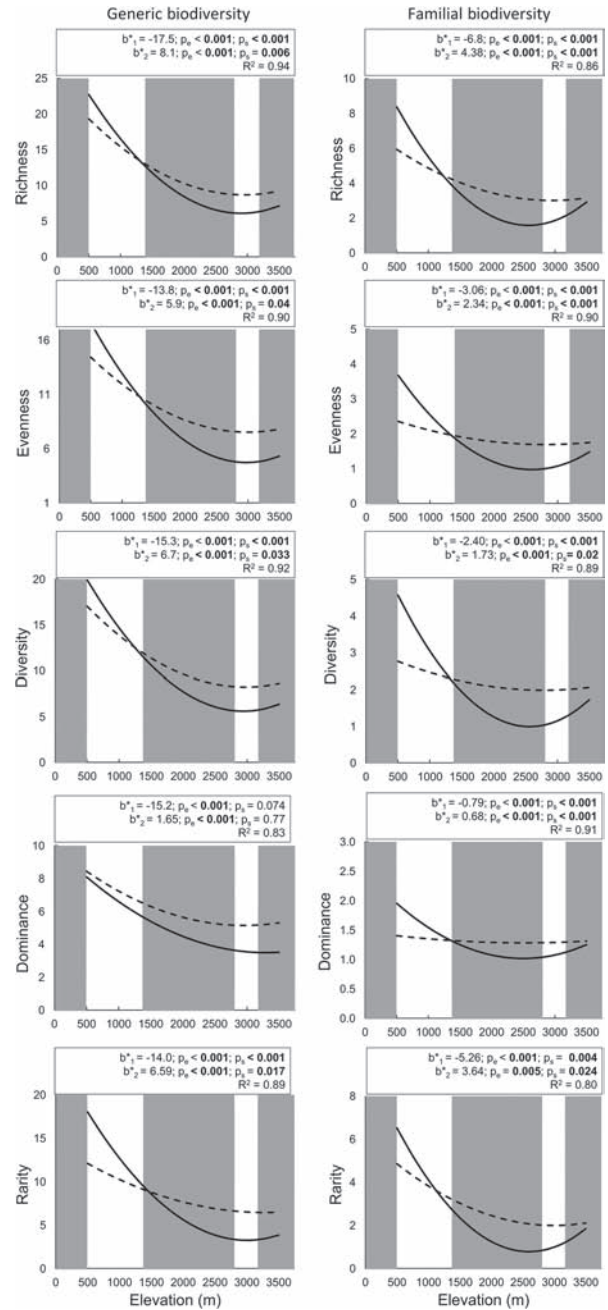


Figure 3. Elevational gradients of rodent taxonomic biodiversity based on consideration of generic and familial richness, evenness, diversity, dominance, and rarity. A solid line represents an empirical quadratic relationship and R^2 is the fit of the model. Significant ($p_e < 0.05$) orthogonal regression coefficients (b^*_1 and b^*_2) are indicated by bold p-values. Dashed lines represent mean quadratic relationships derived from simulations. Orthogonal regression coefficients of empirical gradients that are significantly different ($p_s < 0.05$) from those produced by simulations are indicated by bold p-values. Alternating shaded regions correspond to elevationally define forest types (see text for details).

The extent to which empirical variation in taxonomic biodiversity at the generic and familial levels, functional biodiversity, or phylogenetic biodiversity arose as a consequence of elevational variation in species richness was quantified by simulation analyses (Fig. 2–4, Table 3). For taxonomic

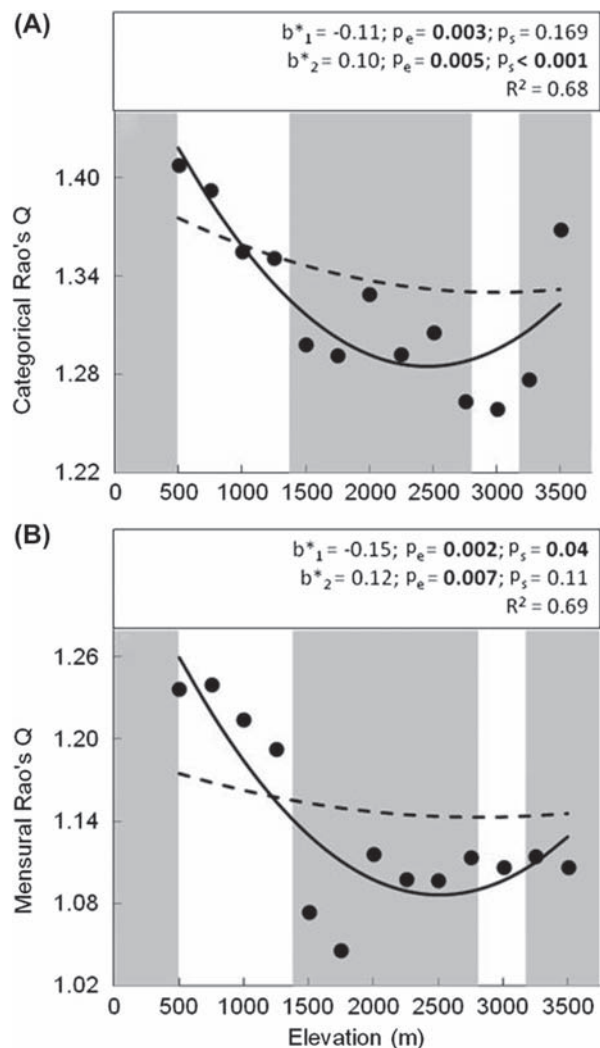


Figure 4. Elevational gradients of functional biodiversity of rodents based on (A) categorical or (B) mensural functional attributes. A solid lime represents an empirical quadratic relationship and R^2 is the fit of the model. Significant ($p_e < 0.05$) orthogonal regression coefficients (b^*_1 and b^*_2) are indicated by bold p-values. Dashed lines represent mean quadratic relationships derived from simulations. Orthogonal regression coefficients of empirical gradients that are significantly different ($p_s < 0.05$) from those produced by simulations are indicated by bold p-values. Alternating shaded regions correspond to elevationally define forest types (see text for details).

biodiversity at the generic and familial levels, the empirical linear orthogonal coefficient (b^*_1) was smaller than expected for all metrics and levels in the biological hierarchy, with the exception of generic dominance (Fig. 3, Table 3). Empirical quadratic components (b^*_2) were all significantly greater than expected given species richness, with the exception of generic dominance (Table 3). Similarly, the empirical linear component for phylogenetic biodiversity was smaller than expected, whereas the quadratic component was greater than expected based on species richness. In contrast, only quadratic components of empirical relationships were significantly different than the preponderance of simulation values for functional biodiversity based on all traits or based on categorical traits. Empirical biodiversity for taxonomic, functional, and phylogenetic dimensions was greater than expected based

on simulations in rainforest habitats (500–1400 m a.s.l.) and empirical biodiversity was less than expected in cloud (1400–2800 m a.s.l.) and elfin (2800–3500 m a.s.l.) forests (Fig. 2–4).

Of the 56 species and 30 genera of rodents, 38 species and 21 genera did not occur above 2000 m, and only 17 species and 5 genera did not occur below 1500 m (Fig. 5). Species within a broadly distributed genus were not necessarily broadly distributed along the elevational gradient; the majority of species (53%) were restricted to lowland and montane rainforests, 9% occurred only in cloud forest, and 7% occurred only in elfin forest (above 2800 m, Fig. 6).

Discussion

Surrogacy of dimensions

Historically, species richness has been the most common metric used to characterize local and regional biodiversity. However, efforts to expand understanding of functional and evolutionary dimensions of biodiversity have called into question the use of one dimension of biodiversity as a surrogate for other dimensions (Weiher and Keddy 1995, Díaz and Cabido 2001, Cadotte et al. 2013, Cisneros et al. 2014). This question of surrogacy is important from both conceptual and applied perspectives. For example, use of only taxonomic biodiversity for conservation or management could mask losses of functionality that could result in loss of ecosystem services (Díaz and Cabido 2001), trophic cascades (Finke and Denno 2005, Duffy et al. 2007), or loss of resilience to changing environmental and climatic conditions (Walker 1992, Vandewalle et al. 2010). Nonetheless, if strong and predictable relationships exist between dimensions, such as a saturating relationship between taxonomic biodiversity and functional or phylogenetic biodiversity (Fig. 1) or the positive relationship between functional and phylogenetic biodiversity (Safi et al. 2011), one dimension may sufficiently predict others. Anthropogenic pressure on natural resources throughout the world is increasing (Cardinale et al. 2012) and funding to adequately monitor biodiversity to inform conservation and management policy is limiting. Consequently, identification of useful surrogates that can reliably and efficiently estimate all dimensions of biodiversity is paramount to future conservation efforts (Rodrigues and Brooks 2007).

For the rodents of Manu, elevational gradients in biodiversity were congruent for the three dimensions (i.e. taxonomic, functional and phylogenetic, Fig. 2–4), all relationships were strong, declining, and non-linear. Species richness was an effective surrogate for, and highly correlated with, phylogenetic biodiversity (Spearman rank correlation, $\rho = 0.59$, $p = 0.034$; Supplementary material Appendix 1, Fig. A1), functional biodiversity (all traits, $\rho = 0.87$, $p = 0.001$, categorical traits, $\rho = 0.83$, $p = 0.004$; mensural traits, $\rho = 0.57$, $p = 0.041$; Supplementary material Appendix 1, Fig. A1), and multiple aspects of taxonomic biodiversity at the generic and familial levels (Supplementary material Appendix 1, Fig. A2). Phylogenetic biodiversity was also highly correlated with functional biodiversity ($\rho = 0.79$, $p = 0.001$), indicating that strong phylogenetic signals (i.e.

Table 2. Regression coefficients derived from orthogonal polynomial regressions for the relationship between various aspects of biodiversity and elevation. Orthogonal polynomial regression decomposes the relationship from ordinary polynomial regression into a suite of additive independent polynomials whose coefficients represent the independent contributions of the magnitude, linear and non-linear components (b^*_0 , b^*_1 , and b^*_2). Significant ($p \leq 0.05$) results are in boldface.

Biodiversity aspect	Orthogonal polynomial regression					Model fit	
	b^*_0	b^*_1	$p_{b^*_1}$	b^*_2	$p_{b^*_2}$	R ²	p
Taxonomic							
Species richness	16.46	-20.76	<0.001	9.97	0.002	0.91	<0.001
Generic richness	11.00	-17.49	<0.001	8.05	<0.001	0.94	<0.001
Generic evenness	8.55	-13.84	<0.001	5.88	0.002	0.90	<0.001
Generic diversity	8.84	-15.27	<0.001	6.73	<0.001	0.92	<0.001
Generic dominance	5.00	-5.15	<0.001	1.65	0.041	0.83	<0.001
Generic rarity	7.69	-15.94	<0.001	6.59	0.003	0.89	<0.001
Familial richness	3.54	-6.08	<0.001	4.38	<0.001	0.86	<0.001
Familial evenness	2.08	-3.06	<0.001	2.34	<0.001	0.90	<0.001
Familial diversity	1.77	-2.40	<0.001	1.73	<0.001	0.89	<0.001
Familial dominance	1.28	-0.79	<0.001	0.66	<0.001	0.91	<0.001
Familial rarity	2.38	-5.26	<0.001	3.64	0.005	0.80	<0.001
Phylogenetic							
Supertree	1.89	-1.85	<0.001	1.46	<0.001	0.91	<0.001
Functional							
All components	1.28	-0.12	<0.001	0.10	0.001	0.78	<0.001
Categorical	1.32	-0.11	0.003	0.10	0.005	0.68	0.001
Mensural	1.13	-0.15	0.002	0.12	0.007	0.69	0.001

ecological conservatism) may exist for functional traits of rodents. Although these results do not negate concerns of reliance on taxonomic biodiversity to inform conservation decisions, it does suggest that situations exist in which species richness can be a useful surrogate for other dimensions of biodiversity. Nonetheless, the shape of the relationships between metrics of biodiversity and species richness evinced little indication of a saturating effect. This suggests that relationships do not always conform to theory-based expectations (Fig. 1).

Species richness of bat assemblages at Manu also declined nonlinearly with increasing elevation (Cisneros et al. 2014). However, species richness was a poor surrogate for phylogenetic or functional biodiversity for bats. For both mammalian orders, phylogenetic and functional biodiversity were highly correlated, indicating that measurement of these dimensions may be redundant when evaluating functional diversity based on traits that represent many different functional components (e.g. diet, foraging method, foraging location, habitat preference, body size). Nonetheless, relationships among

Table 3. 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. Empirical coefficients that were significantly different from those generated by chance are in boldface ($p \leq 0.05$).

Biodiversity approach	b^*_1			b^*_2		
	Empirical value	Simulated mean	p value	Empirical value	Simulated mean	p value
Taxonomic						
Generic richness	-17.49	-11.34	<0.001	8.046	4.95	<0.001
Generic evenness	-13.84	-7.45	<0.001	5.879	3.10	0.042
Generic diversity	-15.27	-9.45	<0.001	6.729	4.01	0.033
Generic dominance	-5.15	-3.52	0.112	1.645	1.53	0.436
Generic rarity	-15.94	-6.33	<0.001	6.593	2.03	0.017
Familial richness	-6.08	-3.14	<0.001	4.381	1.36	<0.001
Familial evenness	-3.06	-0.79	<0.001	2.343	0.42	<0.001
Familial diversity	-2.40	-0.67	<0.001	1.726	0.35	0.020
Familial dominance	-0.79	-0.10	<0.001	0.657	0.08	<0.001
Familial rarity	-5.26	-3.09	0.004	3.643	1.28	0.024
Phylogenetic						
Supertree	-1.85	-0.27	<0.001	1.46	0.11	<0.0001
Functional						
All functional components	-0.12	-0.04	0.054	0.10	0.01	0.034
Categorical	-0.11	-0.05	0.169	0.10	0.01	<0.001
Mensural	-0.15	-0.03	0.040	0.12	0.02	0.108

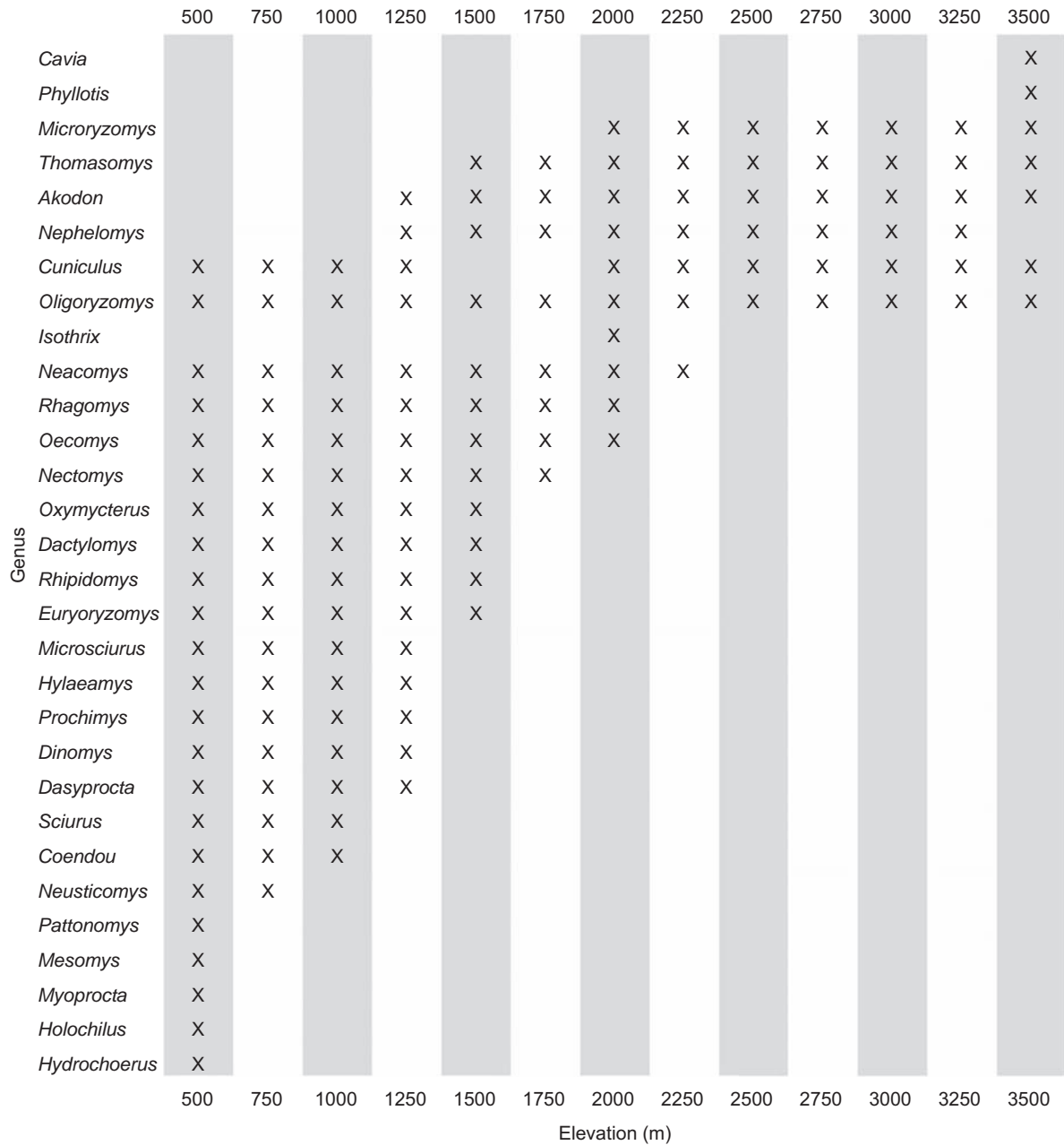


Figure 5. Distributions of rodent genera, indicated by Xs, along the elevational gradient (m a.s.l.) at Manu. Genera are ordered by elevational mid-points.

dimensions remain poorly understood as they have been studied for relatively few taxa and in relatively few settings. A lack of concordance concerning surrogacy (Cumming and Child 2009, Devictor et al. 2010, Fritz and Purvis 2010, Mayfield et al. 2010, Safi et al. 2011), including between two orders of mammals in Manu (Cisneros et al. 2014, this study), suggests that these relationships may be specific to regions and to taxa. With additional studies of surrogacy, patterns may emerge that associate particular ecological or evolutionary properties (e.g. taxon, evolutionary origin, type of ecosystem, reproductive method, dispersal ability, physiological constraints) with particular surrogacy profiles among dimensions. However, at this point, there is no a priori basis on which to predict that particular dimensions of biodiversity evince particular relationships.

Structuring mechanisms

Species richness of rodents at Manu exhibited a strong elevational gradient (Fig. 2), and this elevational pattern can result in elevational variation in generic biodiversity, familial biodiversity, functional biodiversity, or phylogenetic biodiversity. Aspects of all dimensions of biodiversity (Fig. 2–4) exhibited consistent deviations from expectations, indicating the existence of structuring mechanisms that shape elevational gradients of each dimension of biodiversity. In each case, biodiversity was greater than expected in rainforest habitats (< 1400 m a.s.l.) and less than expected in cloud and elfin forests (> 1400 m a.s.l.). These consistent patterns imply that different mechanisms structure rodent assemblages in rainforests compared to higher elevation habitats.

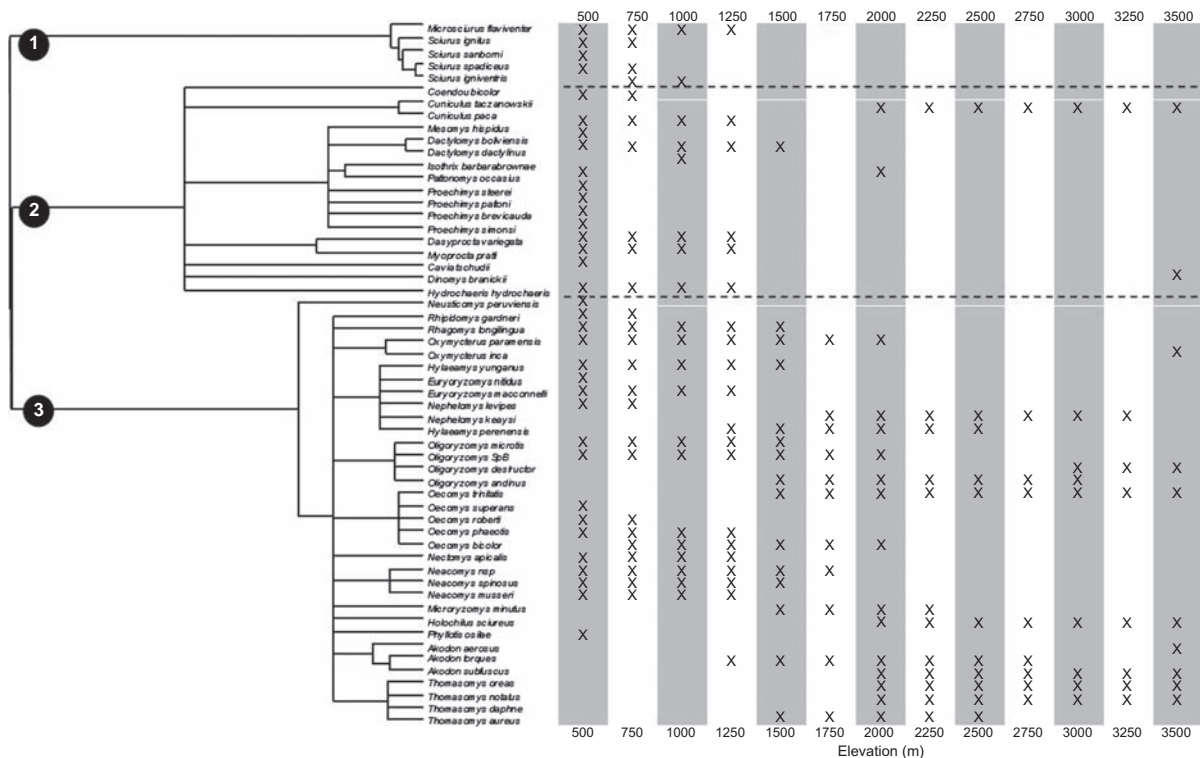


Figure 6. Phylogenetic tree of rodents from Manu and their elevational distributions (m a.s.l.) represented by Xs. Phylogenetic relationships are based on a supertree with divergence times for extant mammals (Bininda-Emonds et al. 2007). Clades representing rodent families are indicated by numbered black dots (1 = Sciuridae, 2 = Caviidae, Cuniculidae, Dasyproctidae, Dinomyidae, Echimyidae, and Erethizontidae, 3 = Cricetidae [Sigmodontinae]). Dashed lines separate groups to illustrate differences in their representation along the gradient.

Despite rainforest rodent faunas having greater richness than those at higher elevations, all dimensions of biodiversity exhibited greater dispersion than expected in rainforests. These deviations are consistent with niche differentiation or interspecific competition (Kluge and Kessler 2011) as dominant structuring forces for rainforest rodent communities in Manu. The great vertical and structural complexity of rainforests may facilitate increased niche differentiation in rodent assemblages. In contrast, species in cloud and elfin forests represented fewer genera, fewer families, fewer lineages, and fewer functional traits than expected. These deviations from expectation are consistent with abiotic or biotic filtering as dominant structuring forces in high-elevation habitats. For example, species belonging to particular genera, families, lineages, functional groups, or body sizes are better adapted to cloud or elfin forests. These adaptations could lead to competitive advantages in which an entire clade can exclude other less well-adapted clades (Mayfield and Levine 2010). These systematic deviations from expectations suggest that the relative importance of particular structuring mechanisms for rodent assemblages change along the gradient.

Taxonomic biodiversity and functional dispersion

In contrast to the rodent fauna at Manu, a mid-elevational peak in species richness is common for small mammals in montane systems regardless of global location (McCain 2005). Area and spatial constraints have been eliminated as important explanatory factors for these patterns (McCain 2007). However, many tropical studies indicate that climatic conditions are important, with optimal conditions for small

mammals typically occurring a few hundred meters below cloud condensation points (McCain 2005 and sources therein). These effects likely manifest directly via physiological constraints, and indirectly via their effect on vegetation and productivity (Sánchez-Cordero 2001, McCain 2007). In addition, locations of changes in biodiversity along elevational gradients often correspond to transition zones between habitats (Lomolino 2001); cloud condensation layers typically are the most dramatic of these transition zones in tropical montane systems. Although the transition between montane rainforest and cloud forest did not mark the location of optimal biodiversity for any dimension at Manu, it did mark the elevation at which assemblages changed from more diverse than expected to less diverse than expected (Fig. 2–4). This elevational also marked the boundary between distinct compartments in the Manu rodent metacommunity (Presley et al. 2012).

Tropical montane cloud forests have less structural complexity, are less productive and produce resources that are lower in nutritional content in comparison to tropical rainforests (Terborgh 1977, Graham 1990, Bruijnzeel and Veneklaas 1998, Sánchez-Cordero 2001, McCain 2007, Hillyer and Silman 2010). This combination of factors reduces niche volume available to rodents, as well as the ability to partition that niche space in a way that supports many viable populations. Almost fifty percent of the rodent species at Manu have primarily herbivorous diets; the reduction in the quality of forage in cloud forests may explain why 64% of those species are restricted to rainforest environments. In addition, omnivorous species have larger elevational ranges

(mean of 4.6 strata) than do herbivorous species (3.0 strata). Cooler temperatures, reduced solar radiation, and continuously wet substrates in cloud forests provide inhospitable or stressful conditions for metabolic processes of insects, leading to a dramatic decrease in invertebrate richness and abundance above 1500 m in Peru (Terborgh 1977, Graham 1990). Consequently, habitat and diet options for rodents decline sharply in the transition between rainforest and cloud forest. In addition, elevational gradients in temperature and humidity make meeting energetic demands more challenging as elevation increases, especially for larger species, which require greater absolute quantities of energy (Brown and Maurer 1987). Only 6 of the 28 genera of rodents at Manu occur between 2250 and 3500 m, resulting in less overall biodiversity than expected at high elevations. This paucity of diversity could represent environmental filtering associated with few available niches and physiological constraints, or could represent competitive exclusion in which entire clades out compete other clades for limited resources at these elevations (Mayfield and Levine 2010).

Phylogenetic dispersion

Though analyses did not explicitly test for phylogenetic signals, strong correlations between phylogenetic and functional biodiversity ($\rho = 0.79$, $p < 0.001$) suggest that strong signals (Losos 2008, Pavoine and Bonsall 2011) may exist for these some of these functional attributes (Table 1). Paralleling patterns for generic, familial, and functional dimensions, elevational variation in phylogenetic biodiversity was not purely a consequence of variation in species richness, with greater than expected phylogenetic biodiversity in rainforests and less than expected phylogenetic biodiversity in cloud and elfin forests (Fig. 2). These patterns are consistent with hypothesized evolutionary history and movement of rodents: hystricognaths (Fig. 5, clade 2) arrived during the Eocene from Africa and radiated in the lowlands, where their diversity remains highest. In contrast, cricetids (Fig. 5, clade 3) arrived during the Miocene, dispersed throughout lowlands, and into montane habitats (Pascual 2006, Schenk et al. 2013).

The structure of the Neotropical rodent radiations is only now coming into focus (Lessa et al. 2014). Nearly 95% of the 642 species of rodents in South America belong to two independent radiations: the caviomorphs (guinea pigs, porcupines, and their relatives) and the sigmodontines (native rats and mice; Patton et al. in press). The caviomorphs comprise 46 genera in 10 families, whose radiation has unfolded since the late Eocene, during South America's extended Cenozoic isolation (Upham and Patterson in press). They present an exceptional range of body sizes, diets, habitat uses, and life modes. On the other hand, the sigmodontines invaded South America during the initial stages of the Great American Biotic Interchange (from the late Miocene forwards) and radiated to include at least 85 genera and more than 400 species (Leite et al. 2014). The nine tribes of sigmodontines are spatially segregated so that the lower elevations of the Manu Biosphere Reserve are dominated by oryzomyine rodents while the upper elevations are inhabited by phyllotines and akodontines (Patterson 1999).

The biodiversity represented by these radiations of rodents underscores the complex interactions of ecological

and evolutionary mechanisms in assembling communities along the elevational gradient at Manu. Body size affects not only thermoregulation and homeostasis, but also generation times (the pacarana *Dinomys* gives birth to a single offspring after a 9-month gestation period; White and Alberico 1992), space-use (Damuth 1987), and, for herbivores, diet and gut-retention times (McNab 1973). Rodents at high elevations in the Andes are even known to become more diurnal in apparent response to cold night time temperatures (Herskovitz 1962). The variable roles of body size on rodent ecology make body-size variation far more complex than is the case for bats, whose small size, short gut retention times, and thermoregulatory exposure (via wing membranes and obligate nocturnal activity) represent critical ecological constraints (Cisneros et al. 2014).

A suite of mechanisms may act in concert to facilitate diversification and to reduce extinction rates, resulting in greater phylogenetic diversity than expected in rainforests at Manu (Pavoine and Bonsall 2011). First, lowland habitats are vertically complex and highly productive, conditions that can facilitate the diversification of lineages. Second, lowland habitats in South America are extensive even during epochs that have seen contraction of rainforests in the Amazon Basin, reducing the likelihood of stochastic extinction due to small and isolated populations, and facilitating the persistence of lineages that evolved in the relatively climatically stable, productive, and diverse habitat. In contrast, phylogenetic biodiversity was less than expected throughout cloud and elfin forests (1500–3500 m; Fig. 2), habitats that are vertically less complex and less productive, and that exhibit more climatic variation annually and through evolutionary time. The result is that many diverse lineages found in lowland habitats are absent from cloud and elfin forests (Fig. 6). In addition to a diverse assemblage of cricetids and sciurids, rainforest habitats harbor echimyids, agoutis, pacas, pacaranas, porcupines, and capybaras, which are mostly absent from cloud and elfin forests. Above the cloud condensation layer (1500 m), 87% of all rodent species are cricetids, resulting in lower phylogenetic biodiversity than expected (Fig. 5–6). Despite cricetids arriving in South America after hystricognaths, they dominate rodent assemblages in montane environments, suggesting that this clade is competitively superior to other rodent clades in these environs. Importantly, the dominant clades of rodents (akodontines and phyllotines) at higher elevations are highly derived groups (Patterson 1999).

Conclusions

Regardless of dimension, biodiversity declined non-linearly with elevation. In contrast to most studies, species richness was an effective surrogate for other dimensions for rodents at Manu. Elevational patterns of biodiversity exhibited consistent deviations that suggest the existence of structuring mechanisms, with biodiversity being greater than expected in rainforests and less than expected in cloud and elfin forests. Great vertical complexity and productivity of rainforests may create more expansive niche space that can support viable populations and may allow for greater niche differentiation in those habitats. In contrast, montane cloud and elfin forests have less structural complexity, are less productive, and

represent inhospitable and stress conditions, which could result in physiological constraints and leading to competitive exclusion in which better adapted clades out compete other clades for limited resources. Importantly, evidence suggests that the relative importance of structuring mechanisms with opposing effects on functional or phylogenetic diversity can change dramatically along a single elevational gradient.

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Supplementary material (Appendix ECOG-00971 at <www.ecography.org/readers/appendix>). Appendix 1.