Vertebrate metacommunity structure along an extensive elevational gradient in the tropics: a comparison of bats, rodents and birds

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ABSTRACT

Aim We evaluated the structure of metacommunities for each of three vertebrate orders (Chiroptera, Rodentia and Passeriformes) along an extensive elevational gradient. Using elevation as a proxy for variation in abiotic characteristics and the known elevational distributions of habitat types, we assessed the extent to which variation in those factors may structure each metacommunity based on taxon-specific characteristics.

Location Manu Biosphere Reserve in the Peruvian Andes.

Methods Metacommunity structure is an emergent property of a set of species distributions across geographic or environmental gradients. We analysed elements of metacommunity structure (coherence, range turnover and range boundary clumping) to determine the best-fit structure for each metacommunity along an elevational gradient comprising 13 250-m elevational intervals and 58 species of rodent, 92 species of bat or 586 species of passerine.

Results For each taxon, the environmental gradient along which the metacommunity was structured was highly correlated with elevation. Clementsian structure (i.e. groups of species replacing other such groups along the gradient) characterized rodents, with a group of species that was characteristic of rain forests and a group of species that was characteristic of higher elevation habitats (i.e. above 1500 m). Distributions of bats were strongly nested, with more montane communities comprising subsets of species at lower elevations. The structure of the passerine metacommunity was complex and most consistent with a quasi-Clementsian structure.

Main conclusions Each metacommunity exhibited a different structure along the same elevational gradient, and each structure can be accounted for by taxon-specific responses to local environmental factors that vary predictably with elevation. The structures of rodent and bird metacommunities suggest species sorting associated with habitat specializations, whereas structure of the bat metacommunity is probably moulded by a combination of species-specific tolerances to increasingly cold, low-productivity environs of higher elevations and the diversity and abundance of food resources associated with particular habitat types.

Keywords
Chiroptera, Clementsian structure, elevation, Manu, Neotropics, nestedness, Passeriformes, Peruvian Andes, Rodentia, species sorting.

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INTRODUCTION

The composition of communities is a combined result of local and regional processes (Ricklefs, 1987; Holt, 1993). A greater understanding of local community assembly and species coexistence can be realized by complementing experiment-based studies of local communities with studies that focus on the distribution of species along gradients or throughout a region (Ricklefs, 2008), thereby placing local processes within a regional ecological context. The metacommunity concept (Leibold et al., 2004) considers both local and regional processes to evaluate the organization of biotas along environmental gradients that span large spatial scales (landscape, regional or continental). In general, two interrelated and complementary approaches have been followed to evaluate patterns of spatial variation in a metacommunity framework: one approach focuses on mechanistic models (Cottenie, 2005) and the other focuses on patterns of species distribution along environmental gradients (Leibold & Mikkelson, 2002). The mechanistic approach for understanding variation in site composition considers the possible roles of patch dynamics, species sorting, mass effects and neutrality (Leibold et al., 2004; Holyoak et al., 2005). In contrast, the pattern-based approach evaluates characteristics of species distributions along latent environmental gradients that emerge as a result of combinations of mechanisms and that manifest as particular metacommunity structures (random, checkerboard, nested, evenly spaced, Gleasonian or Clementsian structures sensu Leibold & Mikkelson, 2002).

Metacommunity structure is evaluated with respect to a multidimensional continuum of possible structures. Several idealized structures have been identified by ecologists, with idealizations differing in the amount of turnover and patterns of range boundary distribution. Clements (1916) regarded communities to be discrete entities; a concept that evolved into the community unit hypothesis (Whittaker, 1975). Despite the abandonment of Clements' idea that species function in concert as a 'superorganism', the pattern that he recognized in species distributions continues to be used as a working hypothesis of structure (Terborgh, 1971; Whittaker, 1975; Collins et al., 1993; Leibold & Mikkelson, 2002). Gleason (1926) described a pattern of continual change in species composition along environmental gradients without the formation of discrete assemblages, which result from idiosyncratic, species-specific responses to the environment. In situations where strong inter-specific competition exists, trade-offs in competitive ability may manifest as distributions that are more evenly spaced along environmental gradients than expected by chance (Tilman, 1982). Alternatively, strong competition may result in checkerboards produced by pairs of species with mutually exclusive ranges (Diamond, 1975). For checkerboards to characterize an entire metacommunity, and not just pairs of species, the environmental distributions of mutually exclusive species pairs must be independent of other such pairs, resulting in a concept that is reminiscent of, but not identical to, that first proposed by Diamond (1975). Finally, nested subsets form if the environmental ranges of species with more narrow distributions are contained within the ranges of species with more broad distributions (Patterson & Atmar, 1986), with predicable patterns of environmental range breadth associated with variation in species-specific characteristics (dispersal ability, habitat specialization, extinction risk).

Species rarely respond identically to the same suite of environmental characteristics. Consequently, empirical structures typically only approximate particular idealizations, and identification of best-fit structures is often difficult in the absence of objective criteria (Shipley & Keddy, 1987). Leibold & Mikkelson (2002) developed a set of objective criteria and a rigorous quantitative approach to simultaneously test the correspondence of an empirical structure to each of six idealized structures of species distribution. This approach combined evaluations of three elements of metacommunity structure (coherence, range turnover and range boundary clumping) to identify which idealized metacommunity structure is the best fit for an empirical structure. Each non-random structure assumes that species distributions are moulded by a combination of biotic and abiotic factors that differ among sites and constitute an environmental gradient. This allows for the testing of multiple hypotheses of structure, as well as for the generation of hypotheses related to structuring mechanisms.

Elevational gradients have tractable qualities that make them useful for studying the responses of species to variation along environmental gradients. Although elevational changes in abiotic characteristics and associated vegetation are predictable, they differ in the form of their variation. Abiotic characteristics generally change gradually with elevation (Whiteman, 2000), allowing elevation to serve as an effective proxy for variation in abiotic factors. For example, there is a 6.5 °C decrease for temperatures above freezing for every 1 km increase in elevation (i.e. wet adiabatic lapse rate; Jacobson, 2005). In contrast, floral associations often have more-or-less discrete boundaries along elevational gradients that are recognized as distinct habitat types (Terborgh, 1971; Kessler, 2000; Hemp, 2006). Because habitat specializations and responses to abiotic characteristics are important in defining the distributions of animals, elevation-induced environmental variation provides a useful system for exploring metacommunity structure. Many recent studies have evaluated metacommunity structure along environmental gradients (e.g. Burns, 2007; Presley et al., 2009, 2011; Presley & Willig, 2010; Keith et al., 2011; Willig et al., 2011); however, no comparative evaluation of multiple taxa along the same gradient has been conducted. We address this deficiency by evaluating the metacommunity structure of three vertebrate orders that have been well sampled along an extensive elevational gradient in Peru (Patterson et al., 1996, 1998, 2006). Using the comprehensive data set on vertebrate distributions in the Manu Biosphere Reserve (hereafter Manu), as well as the analytical tools of Leibold & Mikkelson (2002), we evaluated metacommunity structure for the Rodentia, Chiroptera and Passeriformes. We chose rodents, bats and passerines because each is species rich and represents an order that should have comparable levels of phylogenetic constraints. Each order has unique characteristics (e.g. only passerines are predominantly diurnal, only rodents are cursorial, only bats have thermoregulatory constraints associ-

ated with energy loss via naked membranes), as well as shared characteristics (e.g. bats and rodents are predominantly nocturnal, bats and passerines fly, rodents and birds build nests), enhancing the likelihood that comparisons among taxa would yield insights into local and regional processes that structure metacommunities along extensive elevational gradients.

Our goals are: (1) to identify the best fit metacommunity structure for each taxon; (2) to determine if the latent environmental gradient associated with each metacommunity is correlated with elevation; and (3) to propose hypotheses that specify structuring mechanisms for bat, rodent or passerine metacommunities based on shared and unique characteristics of the orders.

METHODS

Study area and organisms

Manu covers 1,881,200 ha, includes Manu National Park, and is located in the drainage basin of the Río Alto Madre de Dios along the eastern slopes of the Andes of south-eastern Peru (MacQuarrie, 1992). Manu ranges in elevation from 365 to 3500 m above sea level, and comprises lowlands and highlands from the Departments of Madre de Dios and Cuzco. This biodiverse region is an IUCN World Heritage site and a UNESCO Biosphere Reserve. More species of mammal (222) and bird (1005) are recorded along the elevational gradient of Manu (Patterson *et al.*, 2006) than are recorded from any other protected area in the world.

Five distinct habitat types occur along the elevational gradient of Manu (Terborgh, 1971; Patterson *et al.*, 1998). Lowland rain forest typifies areas below 500 m elevation, has a high canopy (50–60 m) with scattered emergent trees, and supports lianas and epiphytes. Montane rain forest occurs between 500 and 1400 m, and is distinguished by a uniform canopy of *c.* 35 m, with abundant tree ferns and grasses in the understorey. Cloud forest harbours moss- and epiphyte-laden trees and occurs between 1400 and 2800 m, where a cloud layer persists within the forest canopy. Elfin forest occurs between 2800 and 3200 m, has a canopy that reaches only 15 m and is characterized by dense vegetation, microphyllous foliage and epiphytic plants on the forest floor. A habitat characterized by inter-digitating areas of elfin forest and tall grassland, locally known as *pajonal*, occurs above 3200 m.

Comprehensive distributional data for mammals and birds from Manu were compiled from museum specimens, published literature and recent surveys (Patterson *et al.*, 2006). To address uneven sampling effort along the gradient, several expeditions conducted from 1997–2001 focused on mid and high elevations and comprised six person-years of effort (Patterson *et al.*, 2006). Recent expeditions to Manu resulted in the addition of 11 species of bat, 12 species of rodent and 44 species of passerine, many of which are mid- or high-elevation specialists, resulting in a total of 58 rodent species, 92 bat species and 586 passerine species.

Occurrences of species were pooled into 13 intervals (hereafter sites) along the elevational gradient, each of which spanned

250 m of elevation. For example, the 1000-m site included all records from 751 to 1000 m of elevation. We selected 250-m intervals to balance the resolution of empirical records, the amount of collection effort in each interval and the need for a scale of analysis that is ecologically meaningful. For example, a 100-m difference in the location of an elevational boundary for two species may not represent an ecologically meaningful difference or may be a grain size that is too fine to confidently detect presences with available data. For analyses to have sufficient statistical power, at least 10 sites are needed. For analyses of coherence (see below), which evaluates the pervasiveness of gaps in species distributions, intervals that are too small may create gaps in distributions that are not real, but that represent sampling deficiencies. Consequently, smaller elevational intervals would provide greater statistical power, but reduced confidence in the completeness of data for each interval.

Quantitative methods

We used the analytical methods of Leibold & Mikkelson (2002) and the conceptual framework of Presley *et al.* (2010) to identify the best fit metacommunity structure for rodents, bats and passerines along an extensive elevational gradient (from 365 to 3500 m) at Manu. For each order, structure was evaluated using three characteristics of species distributions (coherence, species range turnover and boundary clumping) in an ordinated site-by-species incidence matrix (Fig. 1). Prior to analysis, matrices were ordered using the primary axis extracted via reciprocal averaging, which optimizes the proximity of species with similar distributions and the proximity of sites with similar species compositions. Reciprocal averaging is appropriate for identifying patterns in response to latent gradients because similarities in species occurrences determine the positions of sites along the axis of correspondence without a priori knowledge of or assumptions about the particular factors that govern species responses (Gauch, 1982; Leibold & Mikkelson, 2002).

For analyses of coherence, a null model with fixed column totals (site richness) that equalled observed totals and with row probabilities (species occurrences) that were equiprobable was chosen a priori. For many statistics, this level of constraint has a more desirable combination of Type I and Type II error properties than do alternative models. In addition, this null model creates a biologically realistic null space for analyses of coherence in which the number of species at sites is fixed, but the number of sites at which a species occurs is random (for more detailed explanations of null model selection see Presley *et al.*, 2009, 2010; Presley & Willig, 2010). For each metacommunity, 1000 randomly generated matrices were created using the chosen null model, and the number of empirical embedded absences was compared with the null distribution of embedded absences to determine significance. A metacommunity was considered significantly and positively coherent if the likelihood of having fewer embedded absences than observed was $\leq \alpha/2$, and a metacommunity was considered significantly and negatively coherent if the likelihood of having more embedded absences than observed was $\leq \alpha/2$. Positive coherence indicates that the
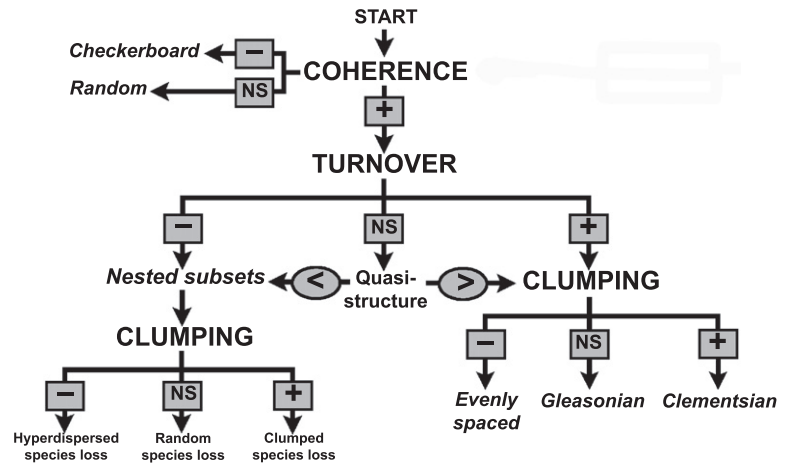
Figure 1 Flow chart depicting the progression of analyses to distinguish among six idealized structures, namely checkerboard, evenly spaced, Gleasonian, Clementsian, nested and random distributions (Leibold & Mikkelson, 2002), three patterns of species loss for nested structures, and six quasi-structures (Presley *et al.*, 2010). Boxes designate statistical results; ovals indicate direction with respect to the mean for non-significant species turnover (modified from Presley *et al.*, 2010).

preponderance of species in a metacommunity respond to the same latent environmental gradient, whereas negative coherence is characteristic of checkerboards (Fig. 1). Non-significant coherence is consistent with random structure and indicates that occurrences of species are not determined by the same environmental gradient. Manifestation of checkerboard distributions at the metacommunity level may be unlikely (Presley *et al.*, 2009). Nonetheless, we include this possibility for completeness of the framework, as well as to ensure that our selected null model was not overly liberal.

Species range turnover was evaluated via the number of replacements of one species by another along the gradient. To determine significance, the empirical number of replacements was compared to a null distribution of replacement values created from 1000 matrices that contained randomly shifted species ranges (Leibold & Mikkelson, 2002). A metacommunity exhibited positive species turnover (more turnover than expected by chance) if the likelihood of randomly generating more replacements than expected by chance was $\leq \alpha/2$; positive turnover is a trait of Clementsian, Gleasonian and evenly spaced distributions (Fig. 1). A metacommunity exhibited negative species turnover (less turnover than expected by chance) if the likelihood of randomly generating fewer replacements than expected by chance was $\leq \alpha/2$; negative turnover is indicative of nested distributions. Metacommunities with non-significant turnover have a quasi-structure (Presley *et al.*, 2010). Each quasi-structure is consistent with the conceptual underpinning of Clementsian, evenly spaced, Gleasonian or nested distributions. The level of significance associated with turnover may indicate the strength of structuring mechanisms, with quasi-structures resulting from weaker structuring forces than in those structures for which turnover is significant (Presley *et al.*, 2010).

Range boundary clumping was evaluated via Morisita's index (I), which estimates the clumping of species distributional boundaries (Hurlbert, 1990). The significance of boundary clumping was determined via a χ^2 test that compared an empirical distribution of boundaries with an expected uniform distribution. Range boundaries that are distributed at random have $I \sim 1$ and are consistent with Gleasonian or quasi-Gleasonian structures, as well as with randomly distributed range boundaries

in nested or in quasi-nested structures (Fig. 1). Range boundaries that are more clumped than expected by chance have a significant χ^2 test with $I > 1$, indicating positive boundary clumping that is characteristic of Clementsian or quasi-Clementsian structures, as well as with clumped range boundaries in nested or in quasi-nested structures. Range boundaries that are more evenly distributed than expected by chance have a significant χ^2 test with $I < 1$, indicating negative boundary clumping that is characteristic of evenly spaced or quasi-evenly spaced structures, as well as with hyperdispersed range boundaries in nested or in quasi-nested structures. More detailed descriptions of the analytical and conceptual approaches appear elsewhere (Leibold & Mikkelson, 2002; Presley *et al.*, 2009, 2010; Presley & Willig, 2010).

We used a *z*-transformation to standardize metrics for coherence and species turnover to facilitate inter-taxon comparisons (Keith *et al.*, 2011). The *z*-score is the number of standard deviations (SD) from the mean. For normal distributions, *z*-scores that differ by > 3.92 (2×1.96 SD) are significantly different values. We used this standard to quantify significant differences in coherence or turnover between pairs of taxa.

To determine if elevation was associated with the latent environmental gradient for each taxon, Spearman rank correlations were conducted between site scores from the primary axis of correspondence and elevation. To determine if sites were ordered similarly along the latent environmental gradient for each order, Spearman rank correlations of site scores for primary axes were performed for all possible pairs of orders.

Analyses of coherence, species range turnover and range boundary clumping were conducted with algorithms written in Matlab 7.5.0.342 (script files available at http://www.tarleton.edu/~higgins/EMS.htm). Site scores for primary axes were derived from reciprocal averaging using the simple correspondence analysis option in Mini-Tab 15.1.20.0. The R programming environment was used to conduct Spearman rank correlations (R Development Core Team, 2009).

RESULTS

Along the primary axis of correspondence, each metacommunity exhibited positive coherence. Positive coherence indicates

Table 1 Analyses of metacommunity structure based on distributional characteristics (i.e. coherence, species turnover, and boundary clumping) of rodents, bats and passerines of Manu Biosphere Reserve, Peru. Significant results ($P \leq 0.05$) are bold. z-scores (number of standard deviations from the mean) are presented for inter-taxon comparisons, with differences > 3.96 representing significant inter-taxon differences in coherence or turnover.

Taxon	Coherence					Species turnover					Boundary clumping		Metacommunity structure
	Abs	P	Mean	SD	z	Rep	P	Mean	SD	z	I	P	
Rodents	20	**< 0.001**	339	20.3	−15.7	10,556	**< 0.001**	8162	657	3.6	1.529	**< 0.001**	Clementsian
Bats	40	**< 0.001**	507	42.7	−10.9	11,657	**< 0.001**	19,625	952	−8.4	1.799	**< 0.001**	Nested, clumped range boundaries
Passerines	503	**< 0.001**	4386	161.1	−24.1	1,102,942	0.362	1,081,600	23,418	0.9	1.347	**< 0.001**	Quasi-Clementsian

Abs, number of embedded absences; Rep, number of replacements; SD, standard deviation; *I*, Morisita's index.

that the distributions of the preponderance of species within each metacommunity were moulded by the same latent environmental gradient. Site scores of each primary axis were correlated strongly with elevation (rodents, $\rho = 1.00$, $P < 0.001$; bats, $\rho = 0.94$, $P < 0.001$; passerines, $\rho = 1.00$, $P < 0.001$). The quality of the distributional data for these faunas along the elevational gradient at Manu is particularly high, with species averaging less than one embedded absence per species (0.35, 0.43 and 0.86 embedded absence per species of rodent, bat and passerine, respectively; Table 1). Manu has been surveyed extensively and intensively during the past 40 years, with recent surveys (Patterson *et al.*, 2006) designed to address elevational gaps previously identified in the data (Patterson *et al.*, 1998). As evidenced by the low number of embedded absences in species distributions, these expeditions have substantially addressed those data concerns (Patterson *et al.*, 1998).

Site scores for primary axes were significantly correlated for each possible pair of taxonomic groups (rodents and bats, $\rho = 0.94$, $P < 0.001$; rodents and passerines, $\rho = 1.00$, $P < 0.001$; bats and passerines, $\rho = 0.94$, $P < 0.001$). Nonetheless, metacommunity structure along that gradient was distinct for each taxon (Table 1). Rodents evinced Clementsian structure, bats exhibited nested structure with clumped range boundaries and passerines evinced quasi-Clementsian structure.

The rodent metacommunity was characterized by a group of species associated with low-elevation rain forests and a group of species associated with upland habitats, with a transition zone between groups occurring from 1500 to 1750 m (Fig. 2a). Bats were highly nested, with most species occurring at lower elevations, a predictable pattern of decreasing richness with increasing elevation, and clumped range boundaries (Fig. 2b). The quasi-Clementsian structure for passerines exhibited a less distinct transition zone between low-elevation and high-elevation species than did rodents. The clumped boundary aspect of this structure may result from a large proportion of species whose ranges are truncated at the lower end of the gradient (Fig. 2c). Passerines exhibited the least amount of boundary clumping of the three taxa (Table 1).

DISCUSSION

Although each metacommunity exhibited significant coherence, orders differed in the degree of coherence (Table 1). Passerines exhibited the highest degree of coherence ($z = -24.1$), indicating that the distributions of a greater proportion of passerines was moulded by a common environmental gradient compared to the situation for bats ($z = -10.9$) or rodents ($z = -15.7$). Alternatively, the data for passerines may be more complete than those for rodents or bats, leading to fewer embedded absences as a result of sampling omissions. This is a distinct possibility, because records of occurrence for birds are more easily obtained than for rodents or bats. Bats exhibited significantly less turnover than did passerines or rodents; turnover for passerines and rodents was not significantly different (difference in z-score of 2.7; Table 1). This indicates that, within the constraints of each metacommunity structure (e.g. distribution of elevational range sizes compared with the length of the gradient), birds and rodents exhibited similar non-random rates of turnover in response to environmental variation associated with elevation.

The primary environmental gradients that mould species distributions of rodents, bats and passerines in Manu are correlated with elevation (Fig. 2). Environmental factors that exhibit predictable changes with elevation that commonly occur throughout the world and that are likely to determine species distributions include abiotic factors and habitat types (Terborgh, 1971; Presley *et al.*, 2011; Willig *et al.*, 2011). Importantly, each metacommunity exhibited a distinct structure along the same environmental gradient, with taxon-specific characteristics likely to determine the relative strengths of primary structuring mechanisms, as well as the form of responses associated with those mechanisms.

Species sorting and potential structuring mechanisms

In an evaluation of spatially mediated models for 158 metacommunities using a variance decomposition approach, the majority of metacommunities were consistent with expectations of species sorting rather than patch dynamics, mass effects or
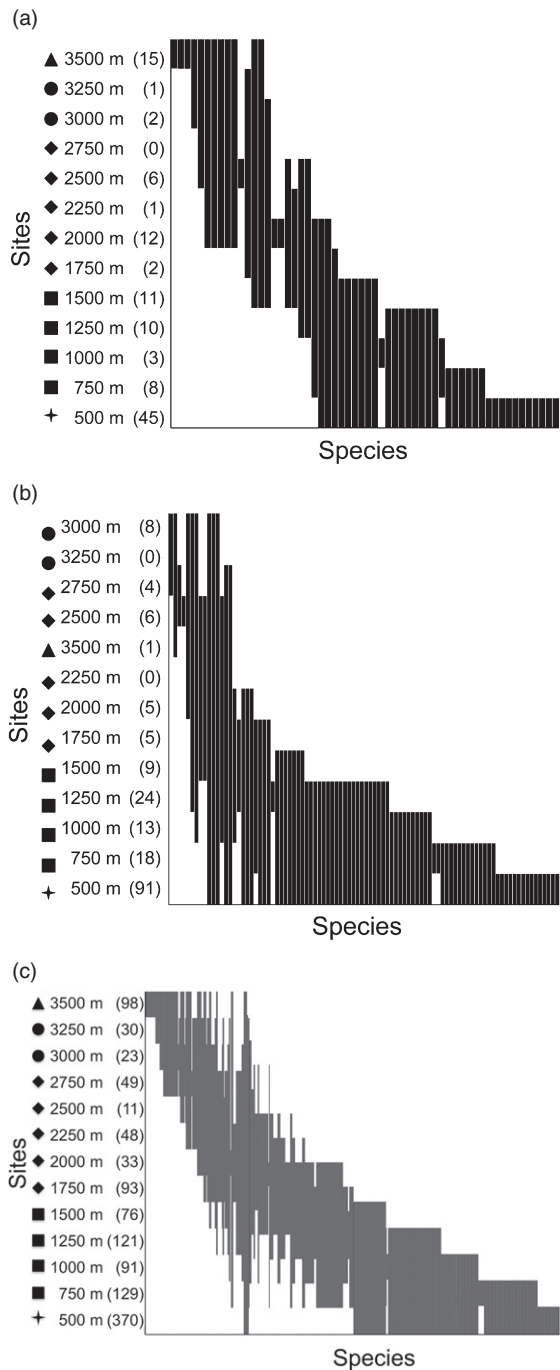
Figure 2 Distributional profiles of each species (black vertical bars) as ordered via reciprocal averaging for rodents (a), bats (b), and passerines (c). Forest classification of elevational sites is lowland rainforest, +; montane rainforest, ■; cloud forest, ◆; elfin forest, ●; and mixed *pajonal* and elfin forest, ▲. Placement of sites (identified by elevation) along the primary axis of correspondence exactly maintained elevational order after reciprocal averaging for rodents and birds and closely approximated it for bats. Numbers of distributional range boundaries at particular elevations are indicated in parentheses. Because 586 species of passerine are recorded from Manu, individual ranges for birds are not distinguishable in the figure.

neutrality (Cottenie, 2005). The species-sorting model describes effects of the local environment and biotic interactions on community assembly (Chase & Leibold, 2003), and requires patchy habitats, limited inter-habitat movement and species that perform differently in different habitats. Animal species distributions can be directly affected by the discontinuities in plant associations along an environmental gradient or can indirectly respond to different abiotic characteristics that arise from those distinctive plant associations. In either case, two metacommunity structures can arise as a consequence of responses to strong habitat associations, depending on the nature of species turnover along the gradient. If distributions of species are moulded primarily by habitat specializations, including distributions determined by variation in resource availability that is associated with habitat type, metacommunities with positive turnover should exhibit clumped range boundaries that are coincident with ecotones, resulting in Clementsian structures. Alternatively, metacommunities with negative turnover should exhibit nested structures with clumped species boundaries at ecotones (Presley *et al.*, 2010). Moreover, the locations of clumped boundaries indicate ecotones that are ecologically important to particular taxa, as changes in habitat type based on plant composition do not necessarily represent important transitions for faunal groups. If species distributions are moulded by physiological constraints, metacommunities will be structured in response to factors that change gradually and predictably with elevation (temperature, atmospheric pressure, precipitation, evapotranspiration, insolation). Gleasonian or quasi-Gleasonian structures, in cases of positive turnover, and nested or quasi-nested distributions with random species loss, in cases of negative turnover, are consistent with distributions that are defined by species-specific physiological constraints.

Rodents

The Clementsian structure of the rodent metacommunity suggests the operation of a species sorting mechanism related to habitat specialization, with most ecotones representing distributional boundaries for multiple rodent species (Fig. 2a). Many rodent species were restricted to lowland rain forest (17 species), occurred throughout lowland and montane rainforest (14 species), occurred primarily in cloud forest (8 species), occurred in all non-rain forest habitats (10 species), or were restricted to the grasslands of the *pajonal* (3 species). In contrast to bats and passerines, rodents have relatively low vagility. This inability to quickly and safely move between habitats constrains the ability of rodents to respond to seasonal variation in resource abundance via habitat switching and obliges them to conduct critical biological activities (forage, nest, mate, reproduce) within a local area. This may enhance the influence of local factors in structuring rodent metacommunities compared with those of bats and passerines, and foster specialization on particular habitat types along elevational gradients, such as those observed for rodents in the mountains of Argentina (Gonnet & Ojeda, 1998) and Mexico (Sánchez-Cordero, 2001).

Bats

The nested structure of the bat metacommunity suggests that a different mechanism or combination of mechanisms moulds their distributions compared with the situation for rodents. The bat fauna has clumped range boundaries, with many in proximity to ecotones (Fig. 2), indicating shared responses by many bat species to changes in habitat type. The primary difference between the nested structure for bats and the Clementsian structure for rodents is that species sorting limits species distributions only at the high-elevation end of the gradient for bats but does so at both ends of the gradient for rodents. The upper distribution of bat species is determined by environmental tolerance, whereas the lower distributional limit of 83% of bats extends to the low-elevation end of the gradient (Fig. 2b). That is, nearly all bats occurred at the lower end of the gradient, with progressively fewer species occurring at higher elevations. Some of this pattern can probably be attributed to the distribution of food resources for bats, with all food types (e.g. fruit, nectar, arboreal insects, aerial insects) present and abundant at lower elevations and declining in diversity and abundance with increasing elevation. This pattern mirrors latitudinal variation in bat species richness throughout the New World (Stevens *et al.*, 2003), with the loss of functional guilds contributing to decreasing species richness with latitude (Stevens, 2004). Similarly, the number of functional groups of bats decreases with elevation in Manu, with all guilds present at lower elevations (Patterson *et al.*, 1996).

The distribution and abundance of food resources for bats may be associated with particular habitat types, thereby favouring habitat specializations and clumped boundaries in the nested structure. Most (78%) bat species in Manu occur only in rain forest habitats (below 1750 m), where the fruit- and nectar-bearing plants on which they rely are more species rich and abundant (Graham, 1990; Sánchez-Cordero, 2001). Similarly, abundances of nocturnal flying insects decrease with elevation, which probably decreases the number of individuals and species of insectivorous bats that can persist at higher elevations (Terborgh, 1977; Graham, 1990). In addition to resource availability, bat distributions may be constrained by thermoregulatory constraints that do not apply to passerines or rodents. Flight is an energetically expensive form of travel (von Helversen & Winter, 2003), and bats use a great deal of energy in thermoregulation because they have large naked wings that quickly lose heat, especially during cool nights at higher elevations (Speakman & Thomas, 2003). The synergism among these factors is likely to make it more difficult for many species of bat to persist in colder latitudes (Stevens *et al.*, 2003) or elevations (Graham, 1990). In addition, these factors probably constrain species of frugivore that occur in habitats above 1500 m to be among the smaller species (e.g. *Anoura* spp., *Artibeus glaucus*, *Carollia manu*, *Enchisthenes hartii*, *Sturnira erythromos*) at Manu (Patterson *et al.*, 2006). Consequently, the nested structure of the Manu bat metacommunity may arise from direct (colder temperatures) and indirect (reduced resource abundance) effects of variation in climate with elevation.

Passerines

The passerine metacommunity exhibited quasi-Clementsian structure, with most species occurring primarily in rain forest habitats (< 1750 m) or primarily in upland habitats (≥ 2000 m), and few species spanning the entire elevational gradient (Fig. 2c). This distributional dichotomy between passerine species with low- or high-elevation distributions has been noted previously for the Andes (Stotz *et al.*, 1996; Patterson *et al.*, 1998); however, the transition zone between low-elevation and high-elevation species is indistinct (Fig. 2c). The lack of a single distinct transitional zone may result because passerines comprise many functional guilds (aerial insectivores, formicivores, frugivores, gleaning insectivores, granivores, nectarivores, sap suckers), and guild-specific responses to elevation characterize passerines of the Peruvian Andes (Terborgh, 1977; Graham, 1990). With increasing elevation, insectivorous passerines suffer the greatest decrease in species richness, frugivores experience a modest decrease in richness, and nectarivore richness is unaffected (Terborgh, 1977; Graham, 1990). Consequently, metacommunity structure may be distinct for each guild, but is obscured when viewed at the ordinal level. Alternatively, the use of presence–absence data combined with the high vagility of birds may account for the lack of a distinct transition zone. Constraints on elevational distributions may be relaxed during particular seasons, during which a recorded sighting of a single individual may extend the distributions of species up or down the gradient.

Metacommunity structuring processes: species sorting trumps dispersal

The metacommunity approach to evaluate variation in species distributions grew out of metapopulation theory (Hanski & Gilpin, 1997) in an attempt to integrate dispersal into approaches to understand community composition and dynamics (Holyoak *et al.*, 2005), which were previously focused on local factors. Nonetheless, attempts to understand the effects of dispersal on community or metacommunity structure have been frustrated by the lack of available data on dispersal (Jacobson & Peres-Neto, 2010). Moreover, surrogates for dispersal have been criticized (Jacobson & Peres-Neto, 2010) because they often are conflated with unmeasured, spatially structured environmental factors. More specifically, pure spatial components in a variance decomposition approach probably represent some effect of space (the surrogate for dispersal) as well as effects of spatially structured environmental characteristics that were not included in analyses. Consequently, such analyses over-estimate the importance of dispersal and under-estimate the importance of local environmental factors. As such, species sorting is likely to be even more important in structuring metacommunities than indicated in the meta-analysis of 158 metacommunities, in which 73% were considered to be structured by species sorting or a combination of species sorting and mass effects (Cottenie, 2005). Analysis of a highly connected metacommunity, in which dispersal has the capability to homogenize local communities,

found 'that local species sorting seems to be powerful in the face of very substantial dispersal rates' (Cottenie & De Meester, 2004). Similarly, mechanisms associated with species sorting structured highly connected gastropod metacommunities along an elevational gradient (Presley *et al.*, 2011; Willig *et al.*, 2011). Dispersal capabilities may be sufficient to enable colonization of suitable habitats in most cases, but dispersal is likely to play a secondary role to species sorting in structuring metacommunities because the success of dispersal events is contingent on the suitability of local environmental conditions. The focus then becomes the determination of the relative influence of local factors in the species sorting process.

For vertebrates at Manu, we generated hypotheses about the relative importance of variation in abiotic characteristics and in habitat type associated with elevation in moulding species distributions for three vertebrate taxa. More specifically, we hypothesized that habitat type is an important determinant of local community composition and of metacommunity structure; however, the importance of habitat is taxon specific. For rodents, species sorting in response to variation in habitat type is the primary mechanism that structures the metacommunity. For bats, species sorting in response to habitat type only determines the upper elevational boundaries for each species, and variation in habitat may mediate a response to food diversity and abundance, which declines with elevation (Terborgh, 1977; Graham, 1990; Sánchez-Cordero, 2001). In addition, physiological constraints associated with energy budgets, temperature, flight and naked wing membranes (Speakman & Thomas, 2003) are important to the elevational distributions of bat species. The importance of habitat type for passerines at Manu remains unclear, perhaps because this taxon is species rich, functionally diverse, highly vagile and evinces guild-specific responses to elevation at Manu (Terborgh, 1977; Graham, 1990). Consequently, guild-level analyses of passerines may provide additional insights into the relative importance of habitat to the structure of each passerine guild.

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