

Biodiversity and metacommunity structure of animals along altitudinal gradients in tropical montane forests

Michael R. Willig¹ and Steven J. Presley

Center for Environmental Sciences and Engineering and Department of Ecology and Evolutionary Biology, University of Connecticut, 3107 Horsebarn Hill Road, Storrs, Connecticut 06269-4210, USA

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Abstract: The study of altitudinal gradients has made enduring contributions to the theoretical and empirical bases of modern biology. Unfortunately, the persistence of these systems and the species that compose them is threatened by land-use change at lower altitudes and by climate change throughout the gradients, but especially at higher altitudes. In this review, we focus on two broad themes that are inspired by altitudinal variation in tropical montane regions: (1) dimensions of biodiversity and (2) metacommunity structure. Species richness generally decreased with increasing altitude, although not always in a linear fashion. Mid-altitudinal peaks in richness were less common than monotonic declines, and altitudinal increases in richness were restricted to amphibian faunas. Moreover, gradients of biodiversity differed among dimensions (taxonomic, phylogenetic and functional) as well as among faunas (bats, rodents, birds) in the tropical Andes, suggesting that species richness is not a good surrogate for dimensions that reflect differences in the function or evolutionary history of species. Tropical montane metacommunities evinced a variety of structures, including nested (bats), Clementsian (rodents, bats, gastropods), quasi-Clementsian (reptiles, amphibians, passerines) and quasi-Gleasonian (gastropods) patterns. Nonetheless, compositional changes were always associated with the ecotones between rain forest and cloud forest, regardless of fauna.

Key Words: Clementsian structure, conservation biology, ecotones, functional biodiversity, island biogeography, metacommunity structure, nestedness, phylogenetic biodiversity, taxonomic biodiversity, tropical animal ecology

INTRODUCTION

Understanding how species distributions and emergent patterns of biodiversity respond to spatial variation in the environment is a dominant theme in ecology and biogeography (Lomolino *et al.* 2010, Rosenzweig 1995). Indeed, some of the most important concepts and notable controversies in environmental biology have emerged from studying gradients associated with latitude (Hillebrand 2004, Willig *et al.* 2003), depth (Hernandez-Alcantara *et al.* 2014, Rex 1981), area (Coleman *et al.* 1982, MacArthur & Wilson 1963, Rosenzweig & Sandlin 1997, Scheiner *et al.* 2011), productivity (Mittelbach *et al.* 2001, Waide *et al.* 1999) or landscape structure (Fahrig 2003, Turner 1989, Turner *et al.* 2001). Similarly, the study of altitudinal gradients (McCain 2005, 2009,

Rahbek 1995, Terborgh 1971, Whittaker 1960) has made enduring contributions to the theoretical and empirical bases of modern biology.

Scientific studies of montane systems are critical from numerous perspectives. Montane systems comprise approximately 25% of the area of all terrestrial ecosystems (Miller & Spoolman 2011), and are inhabited by an equivalent fraction of the world's human population (Meybeck *et al.* 2001). Mountainous environs harbour high biodiversity – over a third of terrestrial plant species (Barthlott *et al.* 1996) – and are hot spots of endemism, especially in tropical regions (Andelman & Willig 2003, Gradstein *et al.* 2008). Finally, tropical mountains harbour some of the most anthropogenically threatened environments in the world. Dependent on cloud formation and cloud height, the biodiversity as well as ecosystem structure and function of tropical montane systems are being significantly altered by land-use change at low altitudes (Becker *et al.* 2007) and imperilled by climate change throughout, but especially at high altitudes (McCain & Colwell 2011).

¹ Corresponding author. Email: michael.willig@uconn.edu

Montane regions are model systems (Garten *et al.* 1999) in which to conduct ecological research (Körner 2003). Because of their global distribution, recurrent broad-scale ecological patterns can be detected with reasonable power, and contrasts between tropical and temperate or humid and arid contexts are possible (Grytnes & McCain 2007, McCain & Grytnes 2010). The rapid rate of environmental change within relatively short geographic distances facilitates identification of mechanisms that mould species distributions and community assembly (Terborgh 1971, Whittaker 1960), which can be contrasted among taxa (Presley *et al.* 2012), through space (McCain 2005, 2009) or over time (Rowe 2007, Moritz *et al.* 2008). More specifically, altitudinal gradients reflect substantial changes in temperature, rainfall, cloud interception, soil and wind exposure, with environmental conditions at the extremes that strongly challenge species tolerances in both evolutionary and physiological contexts (Cavaler 1986, Grubb 1977). Moreover, altitudinal variation in plant communities often manifests as vegetative zones with discrete altitudinal boundaries (Lieberman *et al.* 1996). Such zones (e.g. forest types, biomes) represent distinct habitats and resource bases on which consumer populations rely. Tropical organisms should respond more strongly to environmental changes associated with altitudinal gradients than do their temperate counterparts because, from an evolutionary perspective, tropical organisms face little intra-annual variation in climate and, therefore, are more sensitive to other forms of environmental variability (Janzen 1967). To the extent that this is true, environmental responses to global change drivers on tropical mountains may provide an early indication of the future for many of the world's ecosystems. Indeed, the interaction between global-change drivers and altitudinal gradients of ecological characteristics has stimulated considerable long-term ecological research (Brokaw *et al.* 2012, González *et al.* 2013).

A comprehensive or integrative overview of the rich body of ecological research addressing faunal responses to altitudinal gradients in environmental characteristics is beyond the scope of a single contribution. Rather, we consider the dynamics of terrestrial animal biodiversity along montane tropical gradients, with a focus on emerging themes associated with multiple dimensions of biodiversity and metacommunity structure.

DIMENSIONS OF BIODIVERSITY

Conceptual framework

Quantifying spatial patterns of biodiversity and uncovering the mechanisms that mould them are fundamental goals of environmental biology that

critically inform conservation, management and policy. Nonetheless, spatial dynamics have been primarily documented only for the taxonomic dimension of biodiversity (TD), generally considering only species richness, although some research has incorporated information on species abundances into metrics (e.g. species evenness, species diversity, dominance and rarity) of taxonomic biodiversity as well (Gaston 1998, Schluter & Ricklefs 1993, Wilsey *et al.* 2005). Such approaches consider all species to be equally distinct (notwithstanding differences in abundance), and are insensitive to interspecific variation in ecological or evolutionary characteristics, therefore representing an incomplete or potentially biased view of biodiversity dynamics (Stevens *et al.* 2003).

Recent efforts have expanded the conceptual framework of biodiversity beyond TD, by incorporating analytical approaches that estimate biodiversity based on the evolutionary histories or ecological functions of species (Pavoine & Bonsall 2011, Webb *et al.* 2002). The phylogenetic dimension of biodiversity (PD) 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 within assemblages (Cavender-Bares *et al.* 2009). The functional dimension of biodiversity (FD) 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 TD, PD and FD along environmental gradients provides insights into the relative importance of ecological and evolutionary mechanisms (e.g. abiotic or biotic filtering, niche partitioning, interspecific competition) that structure different components of assemblages.

In the sections that follow, we highlight and integrate the literature on tropical altitudinal gradients as it relates to (1) species richness, (2) abundance-weighted measures of taxonomic biodiversity, and (3) multiple dimensions of biodiversity. We restrict our attention to montane tropical systems.

Empirical patterns in species richness

The generalization that species richness declines with increasing altitude enjoyed popular (Begon *et al.* 1990, Brown & Gibson 1983) and somewhat uncritical support because it mirrored the latitudinal gradient of species richness and because it was promulgated in foundational publications from both empirical (Kikkawa & Williams 1971, Terborgh 1971, 1977) and theoretical (MacArthur 1972) perspectives. More recent studies, especially those

that are synthetic, control for area and sampling biases, or are based on meta-analyses, suggest that a monotonic decrease in richness with altitude is far from universal and for some taxa may be rare (McCain 2005, Rahbek 1995). Moreover, this body of literature suggests that empirical patterns are likely driven by a suite of factors, rather than by a single overarching mechanism.

In general, the most pervasive altitudinal gradient in montane tropical systems is clearly one in which species richness decreases with increasing altitude. Linear decreases in richness with increasing altitude have been documented for mammals (Graham 1983, 1990), birds (Blake & Loiselle 2000, Kattan & Franco 2004, Terborgh 1977) and invertebrates (Fernandes & Lara 1993, Fisher 1996, Liew *et al.* 2010, Wolda 1987). Non-linear declines in richness with increasing altitude (i.e. saturating relationships) are common as well, occurring in mammals (Patterson *et al.* 1998, Sánchez-Cordero 2001), birds (Fauth *et al.* 1989, Graham 1990) and insects (Brühl *et al.* 1999). Mid-altitudinal peaks in richness are less common than monotonic declines but are not rare, having been documented for mammals (Heaney 2001, Nor 2001), frogs (Smith *et al.* 2007) and invertebrates (Liew *et al.* 2010, Olson 1994). After controlling for confounding montane characteristics (area generally decreases with increasing altitude), altitudinal patterns of species density may be modal (Rahbek 1997). The only well-documented cases of increases in richness with increasing altitude in tropical montane systems are for frogs in Brazil (Giaretta *et al.* 1999) or in India (Naniwadekar & Vasudevan 2007), perhaps because of strong physiological constraints associated with a need for standing water or high humidity, especially during reproduction. Rarely is there no relationship between altitude and species richness, but a lack of association has been found for tropical rodents (Sánchez-Cordero 2001) and for moths (Brehm *et al.* 2003).

Altitudinal variation in species richness has been explored for a number of biotas in the Luquillo Mountains of north-eastern Puerto Rico (Brokaw *et al.* 2012, González *et al.* 2013). The essentially synoptic characterization of gradients for multiple taxa at a single site eliminates the influence of differences in geography, historical legacies or environmental variability among mountainous regions on the interpretation of factors affecting differences among taxa. Nonetheless, caution must be used in extrapolating patterns or mechanisms from the Luquillo Mountains to other tropical montane settings.

Altitudinal patterns of species richness are taxon-specific in the Luquillo Mountains, and include monotonic decreases, monotonic increases, modal relationships and random patterns. Species richness declines with altitude for tree species (Waide *et al.* 1999), litter invertebrates along a mixed-forest transect (Richardson *et al.* 2005)

and gastropods along both mixed-forest and palm-forest transects (Willig *et al.* 2013). In contrast, species richness increases with altitude for earthworms (González *et al.* 2007) and attains mid-altitudinal peaks for invertebrates that inhabit bromeliads (Richardson & Richardson 2013) and for vascular epiphytes and climbers (Brown *et al.* 1983). Finally, altitudinal variation in species richness is essentially flat for litter invertebrates along a palm-forest transect (Richardson *et al.* 2005). This diversity of patterns could emerge as a consequence of a variety of factors, including considerations of the correspondence between the grain of perception of taxa and the spatial scale (focus and extent) of sampling, experimental design (analyses of forest types rather than altitudes, *per se*), analytical approaches and the niche characteristics of biotas as well as the salient environmental characteristics to which they respond.

Empirical patterns in abundance-weighted measures of taxonomic biodiversity

Recent research on aspects of biodiversity that weight richness by measures of importance (e.g. abundance, biomass, frequency of occurrence), such as species evenness, dominance, diversity and rarity, have documented considerable variability among aspects in responses to gradients of latitude (Stevens & Willig 2002, Willig *et al.* 2003) and productivity (Vance-Chalcraft *et al.* 2010, Wilsey *et al.* 2005). The theory of such gradients is at an early stage of maturation (*sensu* Pickett *et al.* 1994) and ripe for development based on the detection of recurrent patterns or linkages to established mechanisms.

Using a non-manipulative experimental approach, Willig *et al.* (2013) quantified altitudinal gradients in species richness, evenness (Camargo's index), diversity (Shannon's index), dominance (Berger-Parker Index) and rarity (the number of species whose proportional abundance in the assemblage was $< 1/S$, where S equals species richness) along each of two parallel transects. One transect (mixed-forest transect) passed through each of three forest types (tabonuco forest, palo colorado forest and elfin forest), whereas the second transect passed through only a single forest type (palm forest dominated by *Prestoea acuminata*). Altitudinal variation in each aspect of taxonomic biodiversity was significant and independent of transect. More specifically, gastropod richness, diversity and evenness decreased with increasing altitude along each transect, and were consistently higher along the palm-forest transect than their altitudinally paired mixed-forest counterparts. This may arise because nutrients critical for gastropod metabolism and shell growth, such as nitrogen, phosphorus, calcium, potassium and magnesium, are generally higher in litter from

palm-dominated areas compared with litter from non-palm-dominated areas at the same altitude, and because these same nutrients generally decrease with increasing altitude from tabonuco to palo colorado to elfin forest (Richardson *et al.* 2005). Because these factors contribute to higher abundances in palm versus mixed forest for the majority of gastropod species, and to higher snail abundance in lower versus higher altitudes (Willig *et al.* 2011, 2013), the more individuals hypothesis or passive sampling (Coleman *et al.* 1982, Scheiner & Willig 2005, Srivastava & Lawton 1998) may account for higher biodiversity in aspects that are sensitive to variation in species number.

Altitudinal variation in gastropod species evenness and dominance in the Luquillo Mountains was not so simply associated with the variation in the number of individuals from a mechanistic perspective, although the correlative associations are clearly strong. As altitude increases, species richness decreases, in part because of the loss of rare species. This is consistent with the hypothesis that increasing productivity from elfin to palo colorado to tabonuco forest (Weaver 1994, Weaver & Murphy 1990) should support more populations at higher densities, such that taxa are less likely to suffer local extinction, especially as a consequence of environmental stochasticity. In a straightforward manner, greater productivity supports more species and more rare species, resulting in communities with lower evenness. At the same time, the loss of species from low productivity sites (i.e. higher altitudes) should allow the relative abundances of the remaining taxa to increase, effecting an increase in dominance, as was observed as well.

In an insightful assessment of altitudinal variation in aspects of abundance-sensitive metrics of bird biodiversity, Jankowski *et al.* (2009) explored environmental gradients in the Tilaran Mountains of Costa Rica. The Pacific slope study area (36 km²) comprised six altitudinal zones, each spanning 100 m of altitude and comprising 12–17 census points. Estimates of species richness and diversity were lowest at high-altitude zones, with a suggestion of mid-altitudinal peaks reported between 1200 and 1300 m asl. The richness of species endemic to Costa Rica and Panama, as well as their proportional representation in the biota of altitudinal zones, increased with increasing altitude. Similar patterns were not apparent when considering species endemic to Central America: their richness and proportional representation in the biota of altitudinal zones was greater at lower altitudes (<1500 m asl) than at higher altitudes (>1500 m asl). Moreover, compositional variation among points within zones, pattern diversity, was higher at lower altitudes, and beta diversity (estimated by the inverse of Sørensen's similarity index with respect to the plots in the highest altitudinal zone), generally increased with increasing altitudinal distance from the highest zone.

We used summary data from Jankowski *et al.* (2009) for a number of metrics of taxonomic biodiversity, to more quantitatively explore altitudinal gradients (based on mid-altitude of each zone) using orthogonal polynomial regression, as done in studies of biodiversity in the Peruvian Andes (Cisneros *et al.* 2014, Dreiss *et al.* 2015). Because of the small number of zones (N = 6), we used 0.10 as the Type I error rate for identifying the form and significance of altitudinal trends. Metrics sensitive to the total number of species (i.e. species richness, and the incidence-based cover estimator (ICE)), evinced significant non-linear relationships with altitude, attaining maxima near 1300–1400 m asl (Figure 1a, b), with altitude accounting for between 77% and 96% of the variation in richness. Altitudinal patterns of endemic species richness depended on definition of endemic (Figure 1c, d). Richness of species endemic to Panama and Costa Rica increased with increasing altitude ($R^2 = 0.87$) with only a significant linear component, whereas richness of species endemic to Central America increased with decreasing altitude in a saturating fashion (significant linear and quadratic components), essentially remaining constant below 1500 m asl. Simpson's reciprocal diversity decreased with increasing altitude ($R^2 = 0.92$) with only a significant linear component (Figure 1e). Finally, compositional similarity among census points within zones (Sørensen's index) increased with increasing altitude ($R^2 = 0.81$) with only a significant linear component (Figure 1f), indicating that β diversity within zones decreases with increasing altitude.

Empirical patterns in multiple dimensions of biodiversity

Although many studies have explored multiple dimensions of biodiversity in plants (Cadotte *et al.* 2009, Díaz & Cabido 2001, Spasojevic & Suding 2012, Swenson & Enquist 2009, Tilman *et al.* 1997, Webb 2000), only a few recent studies have done so for animals, mostly for vertebrates (Devictor *et al.* 2010, Mason *et al.* 2007, Petchey *et al.* 2007, Safi *et al.* 2011, Stevens *et al.* 2003, 2006, 2012, Weins *et al.* 2007). With few exceptions, such research has not been undertaken within the context of tropical montane systems.

A recent suite of contributions focusing on bats (Cisneros *et al.* 2014), rodents (Dreiss *et al.* 2015) and birds along an extensive (500–3500 m asl) tropical gradient in the Andes (Manu Biosphere Reserve, Peru) quantified the form and parameterization of altitudinal gradients in TD (species richness), PD (Rao's Q) and FD (Rao's Q). All three studies used identical statistical methodologies to characterize independent linear and non-linear components of altitudinal change (orthogonal polynomial regression), and the extent to which such

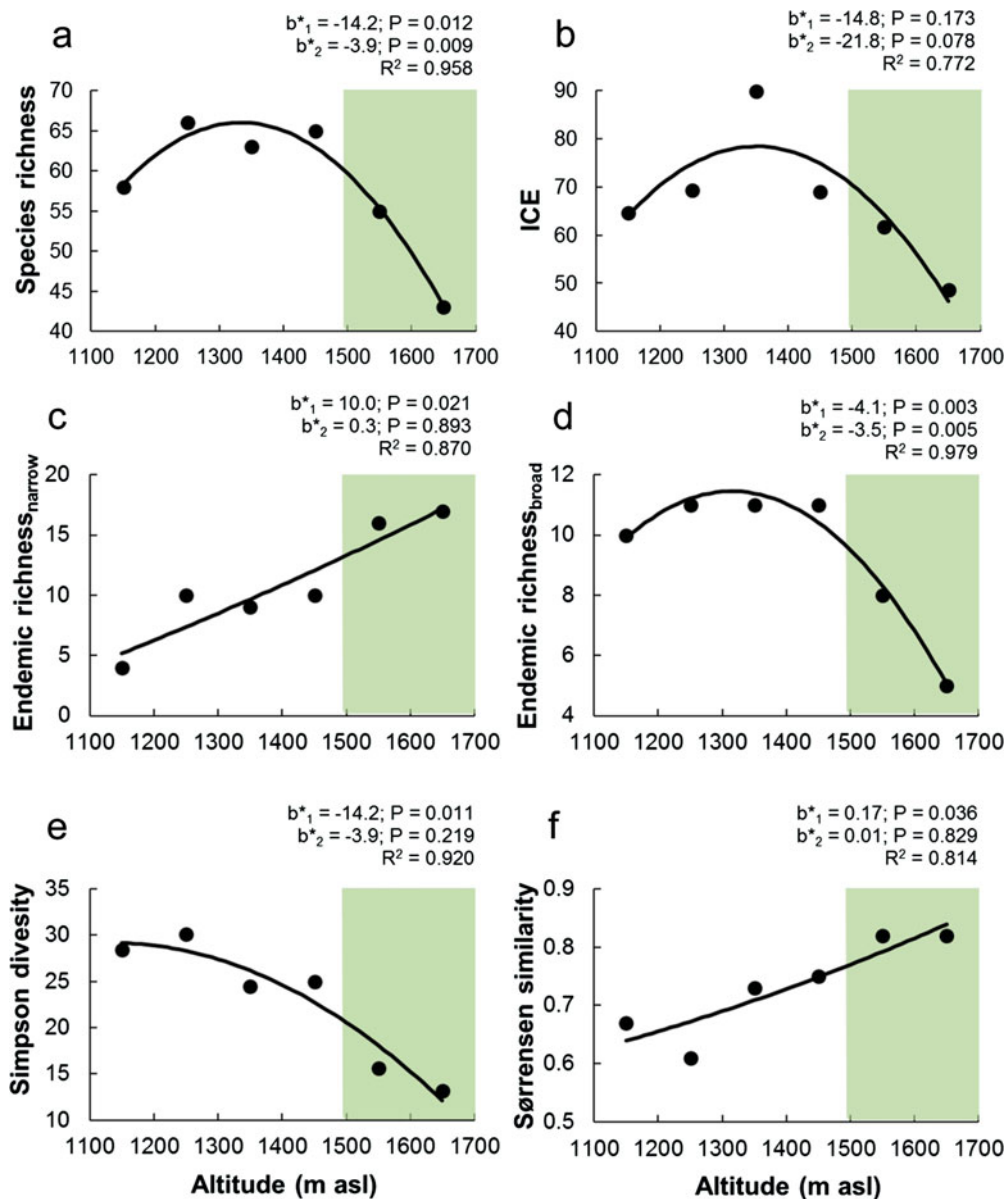


Figure 1. Altitudinal variation in metrics of taxonomic biodiversity: species richness (a); incidence-based coverage estimator, ICE (b); richness of endemic species restricted to Costa Rica and Panama (c); richness of endemic species restricted to Central America (d); Simpson's reciprocal index of diversity (e); and Sørensen's similarity index (f) of birds along the Pacific versant of the Tilaran Mountains in Costa Rica. Empirical values of each metric are represented by black dots; a solid line represents an empirical second-order polynomial relationship. Coefficients from orthogonal polynomial regression analyses are indicated by b^*_1 and b^*_2 for linear and quadratic components, respectively. Plotted values for the zones on the x-axis are altitudinal mid-points. Green and white regions of the altitudinal gradient correspond to areas of cloud forest and rain-shadow forest, respectively, and are reflected in differences in bird species composition as well (Jankowski *et al.* 2009).

variation could arise from random assembly of species from the species pool for each fauna (via simulation analyses). For all three taxa, much of the variation in richness was related to altitude ($R^2 > 0.90$), and the decrease in richness with increasing altitude had strong linear and non-linear components (Figure 2), but with no evidence of mid-altitudinal peaks.

Altitudinal gradients in FD and PD were taxon-specific (Figure 2). A large amount of variation in PD was

associated with altitude for rodents ($R^2 = 0.91$), with the gradient evincing significant linear and non-linear components (i.e. decreasing quickly from low to middle altitudes (500–1750 m asl), and essentially remaining low at high altitudes (1750–3500 m asl)). Much of the variation in PD of birds was related to altitude ($R^2 = 0.90$), with evidence for only a significant linear decline with increasing altitude. In contrast, very little of the variation in PD of bats was related to altitude ($R^2 = 0.02$), with

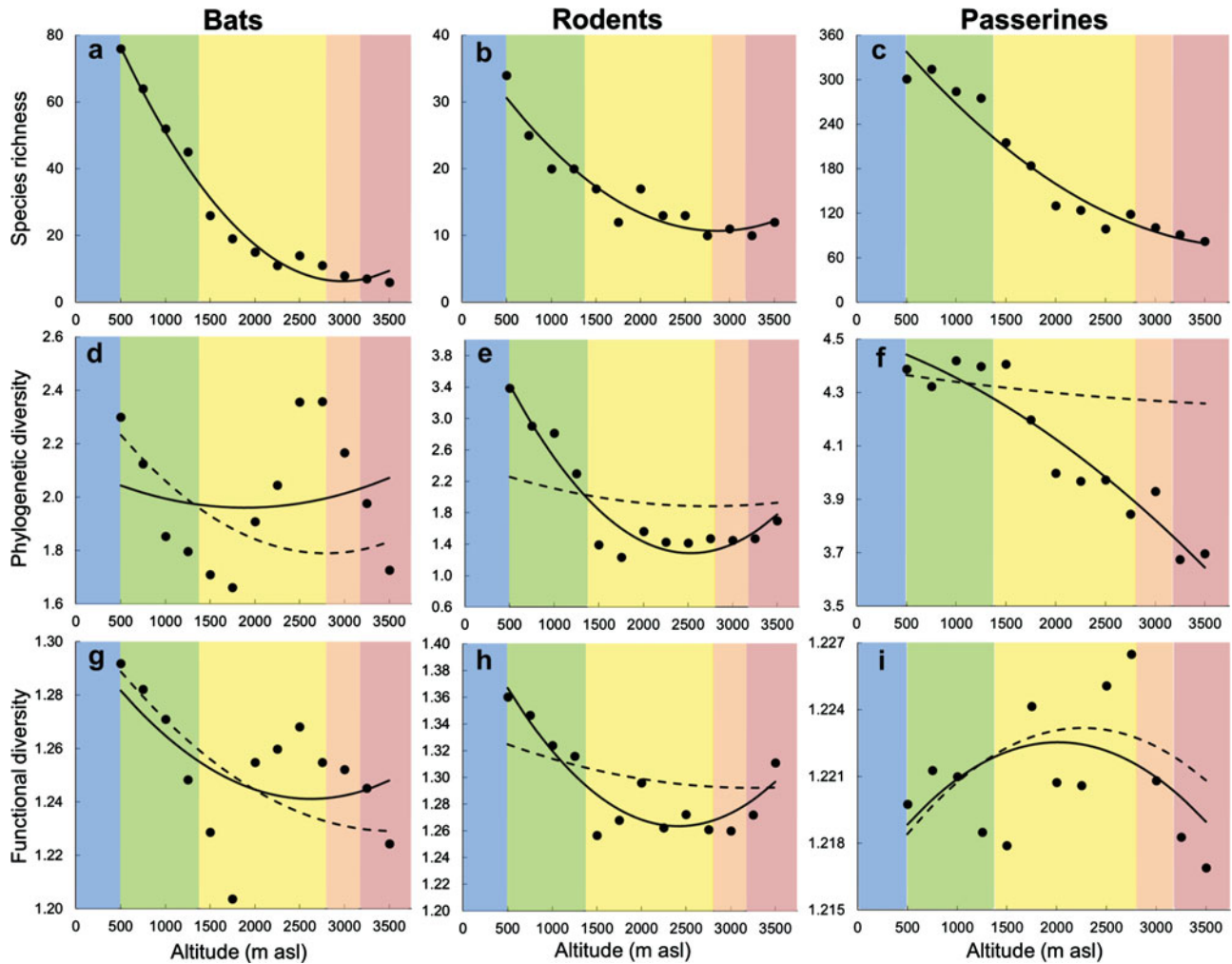


Figure 2. Altitudinal variation in taxonomic biodiversity for bats (a), rodents (b) and passerines (c); phylogenetic biodiversity for bats (d), rodents (e) and passerines (f); and functional biodiversity for bats (g), rodents (h) and passerines (i) at Manu. Empirical values are represented by black dots. A solid line represents an empirical polynomial relationship. Dashed lines represent mean polynomial relationships derived from randomly drawn assemblages holding species richness equal to empirical values. Shaded regions correspond to altitudinally defined forest types: lowland rain forest (blue), montane rain forest (green), cloud forest (yellow), elfin forest (orange), and mixed grassland and elfin forest (red). Graphics modified from Cisneros *et al.* (2014) and Dreiss *et al.* (2015).

non-significant linear and non-linear components. Much of the empirical variation in FD of rodents was related to altitude ($R^2 = 0.78$), and the variation evinced strong linear and non-linear components, with the suggestion of a mid-altitudinal minimum (n.b. not maximum). In contrast, variation in FD associated with altitude was small for bats ($R^2 = 0.30$) and birds ($R^2 = 0.21$), with no evidence of significant linear or non-linear components.

Regardless of the significance of linear or non-linear trends in FD or PD, their empirical patterns may arise as a consequence of variation in species richness (i.e. selection effect; Huston 1997). The extent to which that is true differed among taxa, depending on dimension of biodiversity. For PD, gradients exhibited by rodents were no different than those that would arise from a

random selection of taxa from the species pool. In contrast, gradients of PD for bats (linear component only) and birds (both linear and non-linear components) were different than those arising as a consequence of variation in species richness. Empirical PD of bats was generally higher than expected at upper altitudes (>2000 m asl), whereas empirical PD of birds was generally lower than expected at upper altitudes (>2000 m asl).

For FD, gradients exhibited by bats and birds were no different from those that would arise from a random selection of taxa from the species pool while maintaining altitude-specific richness. In contrast, gradients of FD for rodents differed from those produced by random selection of taxa from the species pool in terms of both linear and non-linear components: empirical FD was higher than

expected at low altitudes (< 1000 m asl) but was lower than expected at middle to high altitudes (>1250 m asl).

These results demonstrate similarities in the form of altitudinal gradients of species richness for bats, rodents and birds. Nonetheless, TD was not an effective surrogate for either FD or PD, and the extent to which variation in richness accounted for variation in FD or PD was taxon-specific. The unique biogeographic histories of these vertebrate groups, their different physiological constraints and variation among them in habitat specificity combine to produce complex altitudinal relationships. Moreover, differences among vertebrate groups in the magnitude or pervasiveness of interspecific interactions, including competition, could also contribute to these complexities. Insufficient autecological or synecological understanding of most of the species within these faunas prevents incontrovertible resolution of competing hypotheses concerning the mechanistic bases for differences.

METACOMMUNITY STRUCTURE

Conceptual framework

The metacommunity concept (Leibold *et al.* 2004) provides a framework with which to evaluate the organization of biotas along environmental gradients. A metacommunity is a set of ecological communities that occur at sites that are effectively connected by dispersal, with each community being a group of species at a particular site (Leibold & Mikkelsen 2002). Metacommunity structure is an emergent property of a set of species distributions across a geographic or environmental gradient. Several conceptual models of spatial structure describe patterns of species distribution. Clements (1916) described an idealized metacommunity structure comprising communities with distinctive species compositions based on shared evolutionary history and inter-dependent ecological relationships, resulting in coincident range boundaries and compositional unity along different portions of the environmental gradient. In contrast, Gleason (1926) described a structure based on idiosyncratic species-specific responses to the environment, with coexistence resulting from chance similarities in requirements or tolerances. In situations where interspecific competition exists, trade-offs in competitive ability may result in distributions that are more evenly spaced along environmental gradients than expected by chance (Tilman 1982). Alternatively, strong competition may result in checkerboard patterns produced by pairs of species with mutually exclusive ranges (Diamond 1975). If mutually exclusive pairs occur at random with respect to other such pairs, checkerboards will manifest at the

metacommunity level. Finally, species-poor communities may form nested subsets of increasingly species-rich communities (Patterson & Atmar 1986), with predictable patterns of species gain associated with variation in species-specific characteristics (e.g. dispersal ability, degree of habitat specialization, tolerance to abiotic conditions).

Three attributes of species distributions (i.e. coherence, species turnover and range-boundary clumping) can discriminate among metacommunity structures (Leibold & Mikkelsen 2002, Presley *et al.* 2010). Analyses of metacommunity structure are based on reciprocal averaging or correspondence analysis, which allows the entire suite of species under consideration to define response gradients and facilitates the quantification of structure along multiple environmental gradients (Presley *et al.* 2009). If a preponderance of species in a metacommunity does not respond to the same environmental gradient, non-coherence and random structure arise. Importantly, random structure does not indicate that species occur at random, only that they occur at random with respect to each other (i.e. that their distributions are not defined by the same environmental gradient). In contrast, each coherent structure is characterized by species distributions that are moulded by a common environmental gradient defined by variation among sites in biotic and abiotic factors. Nested structures are defined by negative turnover (i.e. less turnover than expected by chance) along the environmental gradient, whereas Clementsian, Gleasonian and evenly spaced structures are defined by positive turnover (i.e. more turnover than expected by chance). Quasi-structures have turnover that is indistinguishable from that expected by chance, but have structures consistent with the conceptual underpinning of Clementsian, evenly spaced, Gleasonian, or nested distributions (Presley *et al.* 2010). Range boundary clumping distinguishes among the types of nestedness or among structures with positive turnover. In the case of significantly nested metacommunities, clumped boundaries suggest that species are being added or lost along a gradient in groups (i.e. not randomly with respect to each other). For metacommunities with significant turnover along gradients, positive clumping corresponds to the existence of compartments (Clementsian structure), negative clumping corresponds to evenly spaced structures and randomness with respect to clumping suggests Gleasonian structure (species distributions are unrelated to each other along the gradient).

Although altitudinal changes in abiotic characteristics (e.g. temperature, precipitation) and associated vegetation (composition and physiognomy) are predictable, they typically differ in the form of their variation. Abiotic characteristics generally change gradually with altitude, but not necessarily in a linear fashion (Barry 2008,

Table 1. Summary of empirical analyses of metacommunity structure or nested subsets along tropical altitudinal gradients. *, significant ($P \leq 0.05$); NS, non-significant; NA, not applicable. The direction of deviations from random expectation are indicated by a + or –.

Source	Taxon	Location	Altitude (m asl)	Coherence	Turnover	Boundary clumping	Structure
Metacommunity structure							
Hofer <i>et al.</i> 1999	Amphibians	Cameroon	900–2000	+, *	+, NS	+, *	Quasi-Clementsian
Hofer <i>et al.</i> 1999	Reptiles	Cameroon	900–2000	+, *	+, NS	+, *	Quasi-Clementsian
Presley <i>et al.</i> 2011	Gastropods	Puerto Rico	300–1000	+, *	+, *	+, *	Clementsian
Willig <i>et al.</i> 2011	Gastropods	Puerto Rico	300–1000	+, *	+, NS	NS	Quasi-Gleasonian
López-González <i>et al.</i> 2012	Bats	Mexico	0–3500	+, *	+, *	+, *	Clementsian
Presley <i>et al.</i> 2012	Bats	Peru	340–3500	+, *	–, *	+, *	Nested
Presley <i>et al.</i> 2012	Rodents	Peru	340–3500	+, *	+, *	+, *	Clementsian
Presley <i>et al.</i> 2012	Passerines	Peru	340–3500	+, *	+, NS	+, *	Quasi-Clementsian
Nested subsets							
Patterson <i>et al.</i> 1998	Bats	Peru	340–3500	NA	NA	NA	Nested
Patterson <i>et al.</i> 1998	Mice	Peru	340–3500	NA	NA	NA	Non-nested
Patterson <i>et al.</i> 1998	Birds	Peru	340–3500	NA	NA	NA	Nested
Wilson <i>et al.</i> 2007	Schizophoran flies	Australia	100–1200	NA	NA	NA	Non-nested
Palin <i>et al.</i> 2011	Termites	Peru	190–3025	NA	NA	NA	Non-nested

Whiteman 2000), whereas floral associations often have more-or-less discrete boundaries recognized as habitat types, forest types or life zones (Barone *et al.* 2008, Hemp 2006, Kessler 2000, Kitayama 1992, Martin *et al.* 2007, Woldu *et al.* 1989). Because habitat specialization and responses to abiotic characteristics are important in defining faunal ranges, the structure of a metacommunity is contingent on the dominant mechanism that moulds animal species distributions. If habitat boundaries are more-or-less discrete, metacommunities along altitudinal gradients that are moulded by habitat preferences or specializations should include multiple species with range boundaries that are coincident with ecotones (i.e. range boundary clumping), evincing Clementsian structure. Alternatively, if abiotic characteristics change gradually with altitude and species-specific tolerances are idiosyncratic, then metacommunities moulded by responses to abiotic characteristics should have Gleasonian structure. Finally, altitudinal variation in temperature and resource abundance may create physiological constraints associated with energy budgets (Speakman & Thomas 2003), resulting in nested altitudinal distributions. Distributions of species that are highly constrained by environmental conditions will be nested within those of species that can maintain populations along a larger portion of the gradient (Presley *et al.* 2012).

Interspecific interactions (e.g. competition, predation) may affect metacommunity structure; however, these effects are an aspect of species sorting processes as other species represent part of the environment to which species respond (Holyoak *et al.* 2005). Species sorting requires taxa to perform (i.e. survive and reproduce) differently under different conditions. Within the context of altitudinal gradients, different habitat types along gradients represent the environmental setting and often

contribute to the outcome of interspecific interactions such as competition (e.g. species A excludes species B from montane rain forest, but species B excludes species A from cloud forest). Such mutual exclusion may be actively maintained via competitive interactions or may represent habitat associations due to the legacy of historical competition (i.e. the ‘ghost of competition past’; Connell 1980). To influence metacommunity structure, the strength of such interactions would have to completely exclude individuals, because the elements of metacommunity structure evaluate patterns of the spatial distributions of species and are not sensitive to changes in abundance that do not reduce populations to zero. In most studies of metacommunity structure, including those reviewed here, insufficient knowledge of the autecology or synecology of species is available within the context of local communities to assess the relative importance of antagonistic interspecific interactions versus abiotic filtering or habitat associations.

Empirical structures

Metacommunity structure along extensive tropical altitudinal gradients has been evaluated for gastropods in Puerto Rico (Presley *et al.* 2011, Willig *et al.* 2011), for reptiles and amphibians in Cameroon (Hofer *et al.* 1999, 2000), for bats in Mexico (López-González *et al.* 2012) and for bats, rodents and passerines in Peru (Patterson *et al.* 1998, Presley *et al.* 2012). These metacommunities (Table 1) manifest a number of structures, including nested (Peruvian bats), Clementsian (Peruvian rodents, Mexican bats and Puerto Rican gastropods), quasi-Clementsian (Cameroon herpetofauna and Peruvian passerines) and quasi-Gleasonian (Puerto Rican gastropods) patterns.

Nonetheless, transitions between habitat types (i.e. ecotones) along altitudinal gradients are generally important for defining the altitudinal range boundaries of many species. Most of these metacommunities have distinctive lowland and upland faunal compartments, with the transition between rain forest and cloud forest often being the ecotone that defines the altitudinal boundaries between compositionally distinct communities (Patterson *et al.* 1998, Presley *et al.* 2012, Terborgh 1985). Because altitude gives rise to considerable environmental variation and because changes in assemblage composition occur in response to such gradients, the latent environmental gradients for these metacommunity structures were strongly associated with altitude.

The ecotones between rain forest and cloud forest are important loci of compositional change for faunas along tropical altitudinal gradients. However, the ways in which metacommunities are structured around these ecotones is taxon-specific (Figure 3). For example, the rain forest–cloud forest ecotone in Manu is an important boundary for compositional change of rodents, bats and passerines, but each group had different metacommunity structure because of differences in their autecologies (Presley *et al.* 2012). Rodents have low vagility compared with their volant counterparts (birds and bats), resulting in greater habitat specialization. Rodents were specialists of lowland rain forest, montane rain forest, cloud forest or elfin forest. However, habitat generalists only spanned portions of the gradient, either above or below the cloud condensation point, defining the primary aspect of this Clementsian metacommunity (Figure 3a).

In contrast to rodents, bats in the Peruvian Andes generally do not specialize on particular forest types along the gradient. Rather, nearly all bat species occur in lowland rain forest, with species loss accompanying increasing altitude so as to produce a nested structure (Figure 3b). Importantly, range boundaries are clumped in the nested structure, with most of them occurring at ecotones. The nested structure of bats is a function of direct (colder temperatures) and indirect (reduced resource diversity and abundance) effects of altitudinal variation in climate. Bats have thermoregulatory constraints due to the combination of energy expenditures required for flight, heat loss via naked wing membranes, and nocturnal activity, making it more difficult for them to balance energy budgets in colder climates (Speakman & Thomas 2003, von Helversen & Winter 2003). In addition, loss of bat species can be partially explained by altitudinal changes in resources. All resources used by bats (i.e. fruit, nectar, arboreal insects, aerial insects) are diverse and abundant at low altitudes, but decline in these characteristics with increasing altitude. The most dramatic loss of bat species occurs at the ecotone between montane and cloud forests.

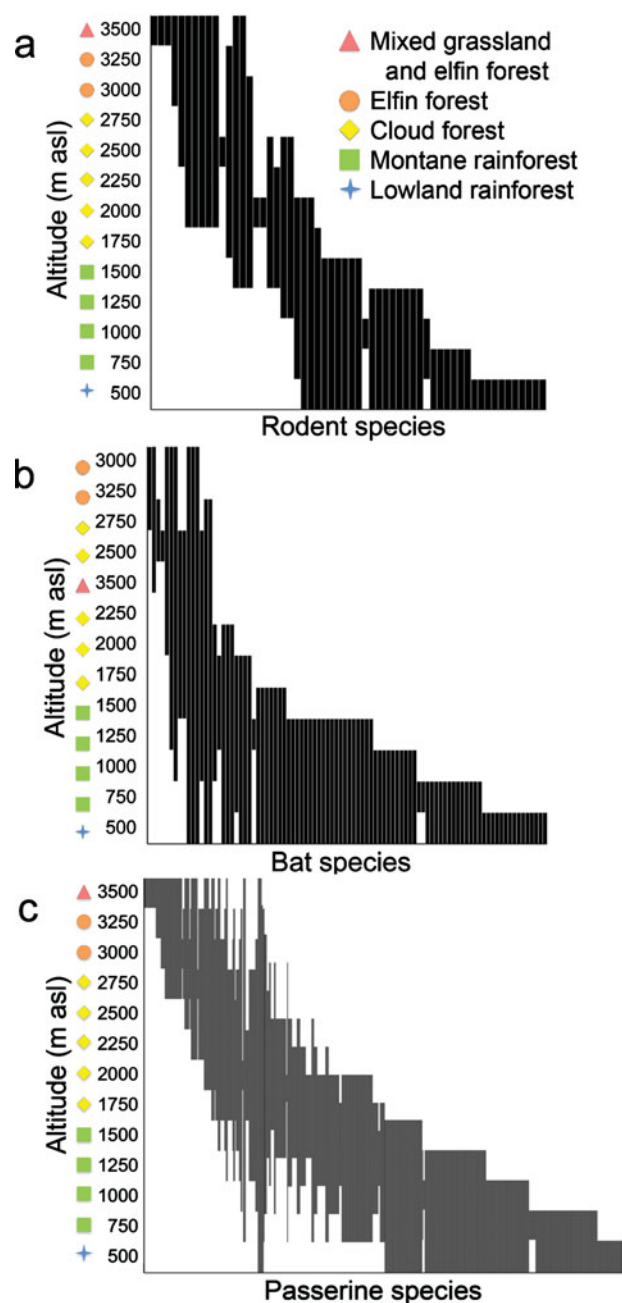


Figure 3. Distributional profiles of each species (black vertical bars) as ordered via reciprocal averaging for rodents (a), bats (b) and passerines (c). Placement of sites (identified by altitude) along the primary axis of correspondence exactly maintained altitudinal order after reciprocal averaging for rodents and birds and closely approximated it for bats (modified from Presley *et al.* 2012).

Passerines in the Peruvian Andes form two compartments, one associated with rain forests (lowland and montane) and another associated with upland forests (cloud and elfin). Few species have an appreciable portion of their altitudinal range in both rain forest and upland habitats (Patterson *et al.* 1998, Presley

et al. 2012, Terborgh 1985). The transition zone between low-altitude and high-altitude compartments is relatively broad and indistinct compared with that of rodents (Figure 3), and is centred on the ecotone between montane rain forest and cloud forest. This broad transition zone for birds may arise from the relaxation of environmental constraints during particular seasons, allowing species of this volant taxon to move up or down the gradient for short time periods, obscuring the effects of ecotones on metacommunity structure. For example, birds that reproduce at higher altitudes may move to lower altitudes during colder seasons or during times of lower resource abundance at high altitudes. This ability to move quickly in response to seasonal changes in environmental conditions may explain why the transition between upland and lowland bird faunas is broad compared with that of the less vagile rodents.

The herpetofauna comprises two compartments on Mount Kupe in Cameroon, with a faunal discontinuity at 1250 m asl, resulting in a distinct assemblage from 900 to 1200 m asl and another from 1300 to 2000 m asl. Importantly, the boundary between lowland and montane faunas was not associated with an ecotone or habitat discontinuity (Hofer *et al.* 1999). Rather, this abrupt change occurred in the midst of submontane forest, which spans altitudes from 900 to 1800 m asl. In contrast to responses of endotherms, temperature and water availability likely are of primary importance for defining altitudinal distributions of amphibians and reptiles than are changes in vegetation along the gradient. More specifically, reptile distributions were best explained by altitudinal variation (a proxy for abiotic variation, including temperature), whereas amphibian distributions were best explained by the availability of streams that serve as breeding sites (Hofer *et al.* 2000).

Metacommunity structure of terrestrial gastropods was evaluated along two altitudinal gradients in the same watershed in the Luquillo Mountains of Puerto Rico. One transect included montane rain forest, cloud forest and elfin forest, whereas the other transect was restricted to forest dominated by sierra palm (Willig *et al.* 2011, 2013). The metacommunity from the palm forest transect was quasi-Gleasonian, with structure determined by species-specific responses to altitudinal variation in abiotic factors (Willig *et al.* 2011). However, when altitudinal variation in forest type was superimposed on the gradient in abiotic variation in the mixed-forest transect, gastropods exhibited a Clementsian structure with compartmentalization associated with changes in forest type (Barone *et al.* 2008, Willig *et al.* 2013). In concert, these analyses suggest that the distribution of gastropods in the Luquillo Mountains is affected by two broad correlates of altitudinal variation: forest type and abiotic factors.

Analysis of nested subsets

A few tropical montane studies have focused on assessing the existence of nested subsets along altitudinal gradients in species richness. These studies have two potential shortcomings compared with a more comprehensive evaluation of metacommunity structure as defined by Leibold & Mikkelsen (2002). First, analyses cannot distinguish between different types of non-nested structures. This results in the grouping of non-nested structures, including chequerboard, Gleasonian and Clementsian structures, into a single category of random. Second, analyses of nestedness are conducted along gradients of richness rather than gradients defined by species distributions along environmental gradients. Consequently, environmental or ecological factors that produce nested structures can only be understood if richness gradients are correlated with environmental gradients.

Studies that evaluate nestedness of assemblages along tropical altitudinal gradients have been conducted for bats, birds, mice and termites in Peru (Palin *et al.* 2011, Patterson *et al.* 1998) as well as for schizophoran flies in Australia (Wilson *et al.* 2007). Bat and bird assemblages in Peru were highly nested and moderately nested, respectively, whereas mice, termites and schizophoran flies were not nested. Predictably, richness gradients were only associated with altitude for the nested metacommunities. Non-nested metacommunities – Peruvian birds (Patterson *et al.* 1998) and Australian schizophoran flies (Wilson *et al.* 2007) – exhibited compositional turnover with compositional changes linked to ecotones. Importantly, the ecotone between rain forest and cloud forest is an ecological barrier for termites as well; however, rather than species turnover occurring at the ecotone, termites are unable to cope with the humidity of cloud forests and do not occur at or above those altitudes (Palin *et al.* 2011).

BIOGEOGRAPHY OF TROPICAL MONTANE FORESTS

Montane biotas often are insular, with communities on each mountaintop separated from others in a mountain range by lowland environs that are distinctive in terms of climate and vegetation (Brown 1971, Patterson 1982). In general, naturally fragmented tropical montane habitats have been isolated from one another since the late Pleistocene in the Neotropics as well as in Africa, making them useful insular systems that comprise habitat islands for biogeographic study (Diamond & Hamilton 1980, Simpson 1974, Watson & Peterson 1999). Immigration among these high-altitude habitat islands may be achieved more easily than for oceanic islands, as montane islands are surrounded by other terrestrial habitats rather

than by water as in classic studies in island biogeography. Throughout the world, the isolation of montane habitats from one another has increased and their areal extents have decreased due to recent anthropogenic activities in lowlands and at lower altitudes on mountains (Cordeiro 1998, Pineda & Halffter 2004).

Biogeographic studies of insular montane faunas have generally used two approaches: (1) application of classical island biogeography theory (MacArthur & Wilson 1963) to evaluate the effects of forest area and isolation on species richness and (2) evaluation of nested subsets to determine if predictable patterns of extinction or immigration determine species composition of isolated faunas. Although there are many biogeographical studies of insular montane biotas, few have been conducted in tropical settings. These studies have focused on frogs (Cordeiro 1998), birds (Martínez-Morales 2005, Pineda & Halffter 2004, Watson 2003, Watson & Peterson 1999), or non-volant small mammals (Anderson *et al.* 2012). Although these studies represent three classes of vertebrates and three distinct biogeographic regions (Nearctic, Neotropical and Ethiopian), there is general concordance in results. Mountaintop communities formed nested subsets, with larger montane forest patches harbouring more species than smaller patches. Nonetheless, aspects of historical biogeography from each region influenced variation in biodiversity and community composition. For example, Central American birds were most species rich on mountains that were near centres of endemism and that were covered by large areas of cloud forest (Watson & Peterson 1999). In addition, species traits were associated with patterns of nestedness for Mexican birds. Species with larger altitudinal ranges, that are more vagile, or that are more abundant, occurred on more mountain-top islands (Watson 2003). In the Eastern Arc Mountains of Tanzania, rare birds occurred only in larger montane forest patches on expansive mountains, whereas common species occurred on both large and small mountains (Cordeiro 1998). Species richness of frogs from Neotropical montane cloud forests was associated with canopy cover and cloud-forest area (Pineda & Halffter 2004). Importantly, many of these frog species also use shade coffee, suggesting that some types of disturbed habitats may have conservation value and may serve as conduits of dispersal to connect isolated fragments of cloud forest.

CONCLUDING COMMENTS

Although much ecological and biodiversity research on animals occurs in tropical montane habitats, most studies focus on one or a few sites, rather than on a sufficient number of sites with a spatial distribution appropriate for characterizing altitudinal gradients. Consequently, a

concerted effort to collect synoptic environmental data along altitudinal gradients, in addition to data on the distributions of plant and animal species, would enhance the mechanistic understanding of variation in biodiversity and metacommunity structure. Similarly, understanding the extent to which variation in habitat heterogeneity, as well as in the α - and β -diversity of sites within strata along gradients, contribute to altitudinal patterns and overall γ -diversity of montane systems remains a fruitful area for future research (Jankowski *et al.* 2009). Such approaches require replicated sites within altitudinal strata for which comparable effort has been expended in estimating the abundances or incidences of species. Finally, execution of parallel projects in a variety of settings across the tropics would facilitate the ability to distinguish general patterns from those that are site- or region-specific.

Conservation action in mountainous tropical regions is a daunting challenge given their high diversity, high proportion of endemic species, high species-turnover along altitudinal gradients and the nested nature of species composition for upper-altitude habitat patches. Complicating matters further, the associations between taxonomic, functional and phylogenetic biodiversity along altitudinal gradients are complex, and species richness may not be an effective surrogate for all or most aspects of biodiversity. Because the effects of global climate change may be particularly stressful for biota that occupy high-altitude forests in the tropics (McCain & Colwell 2011), the need for increased ecological research and targeted conservation action are more urgent than ever. At the same time, changing climates will initiate a non-manipulative experiment in which the mapping of environmental conditions onto geographic space is in flux, especially along altitudinal gradients, creating increased stimulus to study mountainous tropical regions and the underlying mechanisms that give rise to their biodiversity.

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