Journal of Mammalogy, 100(3):1069–1086, 2019
DOI:10.1093/jmammal/gyz024

Gradients of mammalian biodiversity through space and time

Richard D. Stevens,* Rebecca J. Rowe, and Catherine Badgley

Department of Natural Resources Management and Museum of Texas Tech University, 007d Goddard Hall, Lubbock, TX 79409, USA (RDS)
Department of Natural Resources and the Environment, University of New Hampshire, James Hall, 56 College Road, Durham, NH 03824, USA (RJR)
Department of Ecology and Evolutionary Biology, University of Michigan, 830 North University, Ann Arbor, MI 48109-1048, USA (CB)

* *Correspondent: richard.stevens@ttu.edu*

Mammalian biodiversity exhibits strong geographic gradients that correspond to variation in the physical environment (habitat, area, climate, and landforms) and reflect biogeographic processes that have unfolded over millennia. Principal among these patterns are the species–area relationship, as well as latitudinal, elevational, and topographic gradients. We review these gradients for mammalian assemblages of today and over geologic time. Contemporary gradients are for the most part general. Nonetheless, variation across different phylogenetic and ecological subsets of continental mammalian faunas illuminates the multifactorial, historical nature of biodiversity gradients in terms of the diversification history of clades, variation in resources that support species with different ecological traits, and changes in landscapes over time. Accordingly, future work should integrate modern and historical patterns of taxonomic richness with phylogenetic and functional diversity of different clades and ecological subsets of continental faunas. Changes in global climate and land use are disrupting the integrity of biogeographic patterns. Insights from the study of gradients of mammalian biodiversity should address the challenges of conservation in a rapidly changing world.

La biodiversidad de mamíferos exhibe un marcado gradiente geográfico que corresponde con variaciones del ambiente físico (hábitat, área, clima y relieve) y refleja los procesos biogeográficos desarrollados durante milenios. La relación especie-área es uno de los patrones principales de biodiversidad de mamíferos, al igual que los gradientes de latitud, de elevación y de topografía. En este estudio se analizan dichos gradientes en ensamblajes de mamíferos contemporáneos y de diversos tiempos geológicos. Los gradientes de biodiversidad contemporáneos son en su mayoría, generales. A pesar de éstas generalidades entre gradientes, la variación a través de varios subgrupos filogenéticos y ecológicos de mamíferos continentales demuestra la naturaleza multifactorial e histórica de los gradientes de biodiversidad con relación a la diversificación histórica de los linajes, la variación en los recursos que sustentan a las especies con diferentes rasgos ecológicos, y los cambios en el paisaje a través del tiempo. Por lo tanto, subsiguientes estudios deben integrar patrones modernos e históricos de riqueza taxonómica con los patrones de diversidad filogenéticos y funcionales de los diferentes linajes y subgrupos ecológicos de fauna continental. Los cambios climáticos globales y el uso de la tierra interrumpen la integridad de estos patrones biogeográficos. El entendimiento que proviene de estudios de gradientes de biodiversidad de mamíferos, deben dirigir las estrategias de conservación en un ambiente de cambios rápidos.

Key words: biogeography, elevational gradient, fossil record, functional diversity, latitudinal gradient, phylogenetic diversity, species–area relationship, species richness gradient, topography

Biodiversity gradients along spatial and temporal dimensions have fascinated mammalian ecologists, biogeographers, and evolutionary biologists for more than a century. Indeed, such patterns are some of the most conspicuous on earth and attempts to understand the mechanistic basis of such variation underlie some of the most general questions in biology. Moreover, understanding mechanisms that drive biodiversity gradients is an urgent societal need, given realized and anticipated global climate change and increased human impacts on the biota. Mammals are an ideal group for gaining insights into mechanisms that shape biodiversity gradients. While less diverse than many arthropod clades, or even other vertebrate groups, mammals inhabit a wide range of habitats and latitudes, are well studied taxonomically and ecologically, and exhibit substantial variation in species richness worldwide. Living mammals include 6,495 species classified into 27 orders, 167 families, and 1,314 genera (Burgin et al. 2018). Mammals exhibit strong geographic gradients of biodiversity, including taxonomic, functional, and phylogenetic dimensions (e.g., Badgley and Fox 2000; Stevens et al. 2003, 2013; Cisneros et al. 2014), which often are complementary to gradients in species richness.

Variation in biodiversity among areas and over spatial and environmental gradients is the outcome of several interacting evolutionary and ecological processes, predominantly speciation, extinction, dispersal, and habitat filtering. Speciation and extinction are the fundamental evolutionary processes influencing number of species. Because of niche conservatism (Wiens et al. 2010), processes such as adaptation, diversification-extinction dynamics, and differential speciation create variation along multiple dimensions of biodiversity through both space and time. Dispersal similarly has multiple effects on patterns of biodiversity. Relatively high dispersal rates facilitate considerable interchange among regions and effectively homogenize spatial variation in species composition. In contrast, low dispersal rates reduce species richness and prevent species with particular attributes from colonizing distant areas, thereby affecting variation in other dimensions of biodiversity. Ecological specialization determines the breadth of species distributions over environmental gradients. If all species are extreme generalists, then, in the absence of dispersal limitation, they should all occur everywhere, thereby diminishing geographic gradients in biodiversity. Since most mammals are not generalists, specialization determines where along a gradient a species occurs and how patterns of co-occurrence ultimately emerge. Indeed, gradients of biodiversity are the result of differences in the relative contributions of these evolutionary and ecological processes and these effects give rise to the complex mosaic of patterns through space and time.

Characterizing patterns of mammalian biodiversity has been a productive exercise and sufficient information has accumulated to allow synthesis of their mechanistic bases. Herein, we review the current understanding of patterns and theory of mammalian biodiversity gradients. We summarize evidence for four ubiquitous gradients of mammal biodiversity and the principal ideas about their causes: 1) species–area relationships, 2) latitudinal gradients, 3) elevational gradients, and 4) geohistorical gradients. We then review methodological challenges to the study of biodiversity gradients. We close with ideas for future research that build on current findings, pose new questions, and utilize new methods.

Four Kinds of Biodiversity Gradients

Species–area relationships.—The species–area relationship was first described by H. C. Watson in 1835 (Williams 1964) based on plants in Great Britain. It is the oldest known empirically described macroecological pattern (Rosenzweig 1995), is ubiquitous, and has a temporal analog in the species–time relationship (White et al. 2006). The relationship, whereby species richness increases with area sampled, typically fits a "power law", $S = cA^z$, in which S is the number of species, c is a constant, A is the area sampled, and z is the slope of the relationship between S and A (Rosenzweig 1995). Based on 42 studies that documented 73 species–area curves, the average z, or rate of increase of species richness with increase in area, was 0.27 (range −0.24 to 0.93—Drakare et al. 2006). All but two of these relationships had a positive z-value, indicating the generality of the positive relationship between area and species richness. Although many studies conform to a power law, species–area relationships can also assume other relational forms. Indeed, no model fits all empirical richness–area data and uncritical acceptance of a single model is not justified (Mazel et al. 2014).

Classical studies of mammalian species–area relationships have illuminated numerous biogeographic patterns and conservation implications. For example, for many oceanic archipelagos, the number of mammal species increases with increasing island size (Dueser and Brown 1980; Bowers 1982; Lomolino 1982; Lawlor 1983; Heaney 1984, 1986; Presley and Willig 2010). Species–area relationships also have been studied in other insular systems. For example, mammals on mountaintops show strong relationships between habitat area and species richness, often exhibiting nested patterns of taxonomic composition (Brown 1971; Patterson and Atmar 1986; Lomolino et al. 1989) that reflect the colonization-extinction dynamics of montane systems. Habitat fragments exhibit the same kind of pattern (Rosenblatt et al. 1999; Kelt 2001; Lomolino and Perault 2001; Harcourt and Doherty 2005; Santos-Filho et al. 2012; Benchimol and Peres 2013; Muylaert et al. 2016) that results from the increase in population extinction rates when entire landscapes are reduced to a number of smaller fragments. In some situations, however, fragment size can be a poor predictor of species occupancy, as edge and matrix effects covary with species-specific traits and tolerances (Laurance 2008; Prugh et al. 2008).

Two complementary biological factors contribute to species–area relationships (Connor and McCoy 1979). The first involves dynamics of populations. In particular, dispersal and colonization increase and extinction decreases in areas of larger size (Preston 1962; MacArthur and Wilson 1967; Lomolino 1990). The second factor is habitat heterogeneity: new resources and substrates become available as area increases, thereby allowing coexistence of more species (Williams 1964; Simberloff

1976). For many studies of mammalian species–area relationships, habitat heterogeneity has received more empirical evaluation than population dynamics. For example, for non-volant mammals distributed over 29 national parks in western North America, both area and elevation range (a measure of climatic and habitat heterogeneity) exhibited significant partial correlations of similar magnitude with species richness, suggesting comparable influence of these two factors (Newmark 1986). In two archipelagos in the Gulf of California, Frick et al. (2008) demonstrated significant species–area relationships of equal slope for bats. A higher intercept for the archipelago with more vegetation suggested that both area and habitat heterogeneity contribute to species richness. Ricklefs and Lovette (1999), however, tested the effects of area and habitat heterogeneity on species richness of bats for a suite of islands in the Caribbean. In a multiple regression analysis, area was a significant unique predictor, whereas habitat diversity was not. Although each factor had significant simple correlation with species richness, the effect of area was distinct from that of habitat heterogeneity. Willig et al. (2009) corroborated this finding based on further analyses using updated and more comprehensive data on the distribution of bats across Caribbean islands. Overall, the relationship between habitat heterogeneity and mammalian species richness has been variable and may reflect the scale dependence of habitat as a driver (Rosenzweig 1995; Williams et al. 2002), differences in the metric used to quantify heterogeneity, or the manner in which habitat data are compiled from either remotely sensed or on-the-ground surveys (Southwood 1996; Williams et al. 2002; Kerr and Ostrovsky 2003; Vierling et al. 2008).

Although species richness is conceptually tangible and readily measured, it represents only one dimension of biodiversity. Recent comparisons of patterns measured across multiple dimensions of biodiversity, including taxonomic, functional, phylogenetic, and morphological diversity, have demonstrated the complementary nature of these different properties. As species richness increases, so does the magnitude of many indices estimated for other dimensions of biodiversity (Stevens et al. 2013). Differences between species richness and other dimensions, such as functional or phylogenetic diversity, in relation to area may provide insight regarding the processes that structure variation at numerous spatial scales. Moreover, relationships between these other dimensions of biodiversity and area are more likely reflective of scaling of environmental heterogeneity with area than variation in species richness (Mazel et al. 2014, 2015). For example, phylogenetic and functional diversity of terrestrial mammals increase with area more rapidly than does species richness. One implication is that decrease in habitat size in large areas has a small effect on non-taxonomic dimensions of biodiversity (i.e., those not involving species richness). In contrast, decreases in habitat size have a greater effect in small areas where decreases in richness are more precipitous (Mazel et al. 2014, 2015). Indeed, multidimensional diversity–area relationships deserve more investigation in order to better understand how changes in biodiversity scale with area.

Latitudinal gradients.—Attempts to characterize and understand gradients of biodiversity that extend from the poles to the equator have been a major focus of mammalian biogeography for decades. Initial investigations were descriptive, primarily characterizing the relationship between number of species and latitude (Simpson 1964; Wilson 1974; McCoy and Connor 1980). Species richness of continental mammals covaries strongly with latitude (Fig. 1), irrespective of the size of the sampling unit or whether data are based on overlapping geographic range maps or on-the-ground sampling of actual communities (Willig and Selcer 1989; Willig and Sandlin 1991; Kaufman and Willig 1998; Lyons and Willig 1999, 2002; Stevens and Willig 2002). Nonetheless, strength and form of relationships vary depending on mammalian group (i.e., order

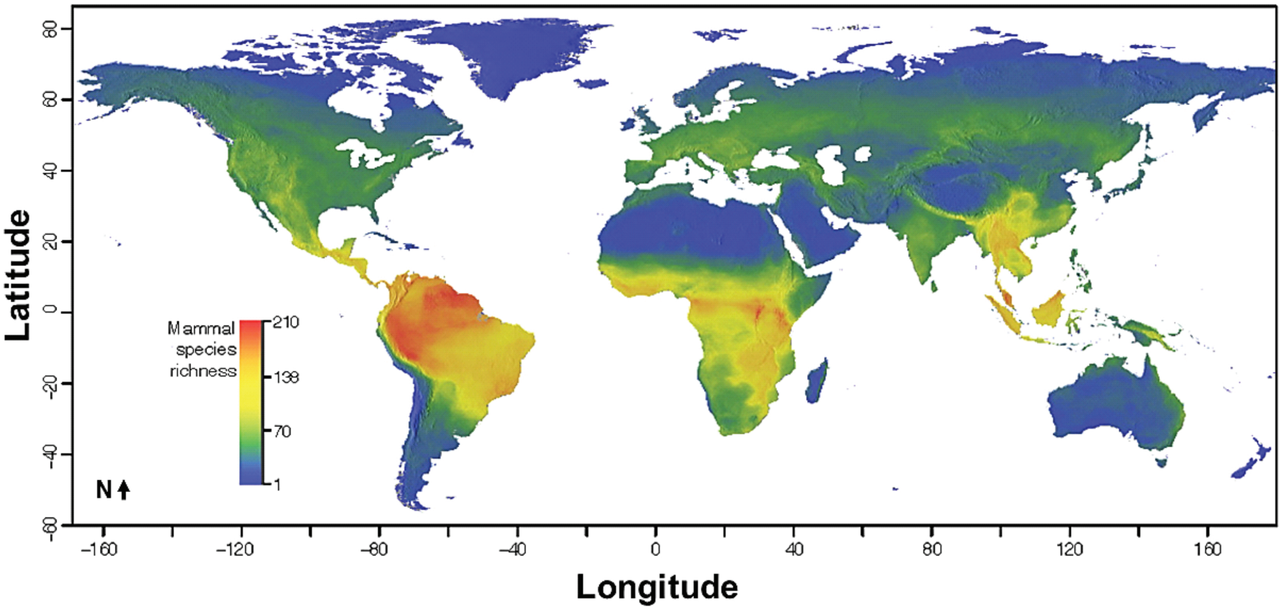

Fig. 1.—Map of global patterns of mammalian species richness. From Jenkins et al. (2013).

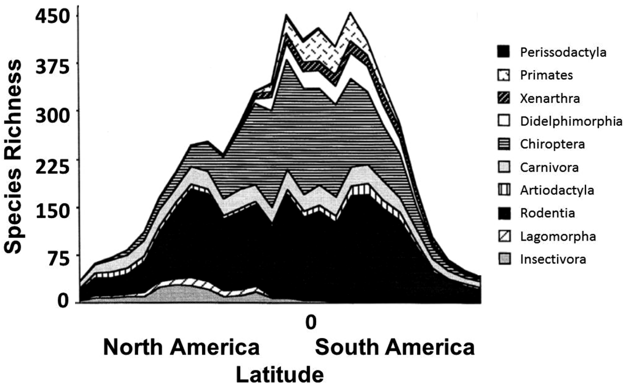

Fig. 2.—Latitudinal gradients of diversity of different families of mammals in the New World. Redrawn from Kaufman (1995).

or family [Fig. 2]; Wilson 1974; Mares and Ojeda 1982; Willig and Selcer 1989; Pagel et al. 1991; Kaufman 1995; Kaufman and Willig 1998; Badgley and Fox 2000; Stevens 2004). For example, in North America, different clades dominate low-latitude (Chiroptera) versus high-latitude (Carnivora) portions of the latitudinal richness gradient (Simpson 1964). Bats show a strong latitudinal gradient in richness, whereas rodents show a strong longitudinal gradient that follows topographic complexity (Badgley and Fox 2000). In contrast, carnivores show no clear gradient. In South America, the highest species richness of caviomorph rodents occurs along the eastern slopes of the Andes, in Amazonia, and in Atlantic Forest (Ojeda et al. 2015). In contrast, the highest richness of sigmodontine (cricetid) rodents occurs in the Andes and Atlantic Forest, with low richness throughout Amazonia (Maestri and Patterson 2016). In terms of ecological diversity, North American mammals exhibit several geographic trends. Species richness of frugivores and invertivores decreases strongly with increasing latitude, whereas richness of herbivores peaks in topographically complex regions at mid-latitudes (Badgley and Fox 2000).

Latitude covaries with a number of attributes including surface area, primary productivity, climate, solar radiation, and mean elevation. Attempts to understand the mechanistic basis of latitudinal gradients of mammals have primarily focused on environmental factors, such as area and biome characteristics (Willig and Selcer 1989; Willig and Bloch 2006) or climatic and physiographic variables (Badgley and Fox 2000; Currie et al. 2004). When the magnitude and variability of productivity, temperature, precipitation, and habitat heterogeneity are considered jointly, temperature and its seasonality are among the variables most strongly correlated with variation in species richness for many mammalian clades (Badgley and Fox 2000; Tello and Stevens 2010; Stevens 2013). However, since many environmental variables associated with latitude strongly covary, insights from correlative approaches can be difficult to interpret.

Many biotic and abiotic properties peak near the equator. Moreover, distributions of many terrestrial species are bounded by continental borders where they meet the ocean. Many properties that vary geographically, such as the number of overlapping geographic ranges, peak in the middle of bounded domains when stochastically distributed, a pattern known as the mid-domain effect (Colwell and Hurt 1994; Willig and Lyons 1998). If species geographic ranges differ in latitudinal extent and these ranges are randomly shuffled in a bounded latitudinal domain, then a peak in species richness often occurs somewhere in the middle of the domain, with a decrease toward continental termini. The mid-domain effect produces latitudinal gradients in species richness that are qualitatively similar to many patterns of mammalian richness and has provided a useful null model for analyzing empirical latitudinal richness gradients (Willig and Lyons 1998). Nonetheless, assumptions of random placement of geographic ranges are unrealistic (Hawkins et al. 2005) and empirical gradients often systematically deviate from null expectations, even when different ways of formulating the null model are utilized (Willig and Lyons 1998; Zapata et al. 2003). While the mid-domain effect can generate simulated peaks of species richness at middle latitudes, it does not replicate geographic patterns in functional, phylogenetic, or phenetic dimensions of biodiversity (Stevens et al. 2013). Although the mid-domain effect represents an informed null hypothesis for assessing geographic gradients of biodiversity, the random placement of species within a geographic domain likely is not the primary mechanism that generates the empirical latitudinal gradient.

The development of comprehensive molecular phylogenies has provided opportunities to test hypotheses about the contribution of historical processes to spatial patterns of biodiversity. Ancestral geographic distribution and diversification from a common ancestor can give rise to strong latitudinal gradients. Most mammalian higher taxa originated in the late Cretaceous to early Cenozoic, when tropical (megathermal) climates covered most of the world (Janis and Damuth 1990; Meredith et al. 2011). During Cenozoic cooling, megathermal environments and species retreated toward the equator into the tropics of today. Thus, tropical environments have had more time and area over the Cenozoic for diversification and accumulation of taxa than temperate or boreal biomes (Wiens and Donoghue 2004; Fine and Ree 2006). Indeed, time for speciation (Stephens and Wiens 2003) and tropical niche conservatism (Wiens 2004) likely have allowed differential accumulation of tropical taxa at low latitudes, and slowed their expansion into temperate environments, thereby contributing to the tropical–temperate disparity in biodiversity (Jablonski et al. 2006; Stevens 2006, 2011; Buckley et al. 2010; Villalobos et al. 2013). Only some lineages within most major clades have expanded into temperate environments, thereby contributing to the tropical–temperate disparity in biodiversity (Stevens 2006, 2011; Buckley et al. 2010; Villalobos et al. 2013).

Although historical processes are important spatially biased generators of mammalian biodiversity (Cardillo 1999; Stevens 2011; Villalobos et al. 2013), not all clades exhibit the classical latitudinal gradient (Willig et al. 2003) and not all are of tropical origin, such as many marine taxa (Proches 2001). Unique insights will come from analyses of groups, such as pinnipeds and vespertilionid bats, which do not follow the general latitudinal pattern. Because environmental, biodiversity, and historical gradients characterizing such groups likely vary more independently than groups with peaks in diversity in the tropics, they may be well suited for decoupling effects of contemporary and historical processes on biodiversity gradients.

Latitudinal gradients also manifest across multiple dimensions of biodiversity. For example, noctilionoid bats exhibit strong latitudinal gradients of phylogenetic, functional, and phenetic diversity (Fig. 3; Stevens et al. 2013). Moreover, these latitudinal patterns are stronger than expected from the mid-domain effect on species distributions and from the underlying gradient in species richness, at least for functional and morphological dimensions of biodiversity (Stevens et al. 2013). Different aspects of biodiversity provide complementary insights because they covary to different degrees depending on which dimensions are under consideration (Stevens et al. 2013; Cisneros et al. 2014). For example, phylogenetic diversity is more strongly related to environmental gradients than either functional or phenetic diversity (Stevens and Gavilanez 2015; Cisneros et al. 2016), even when shared variation with other dimensions of biodiversity is controlled for using multivariate regression. Indeed, variation in different dimensions of biodiversity provides an ideal context from which to evaluate different mechanisms that structure latitudinal gradients of biodiversity. If a particular mechanism is important, then it should generate gradients in species richness but also gradients across the multiple dimensions that characterize biodiversity.

Elevational gradients.—The study of elevational gradients of biodiversity complements that of latitudinal gradients. As with latitude, temperature decreases with increasing elevation (Barry 2008), which structures the distribution of biomes through

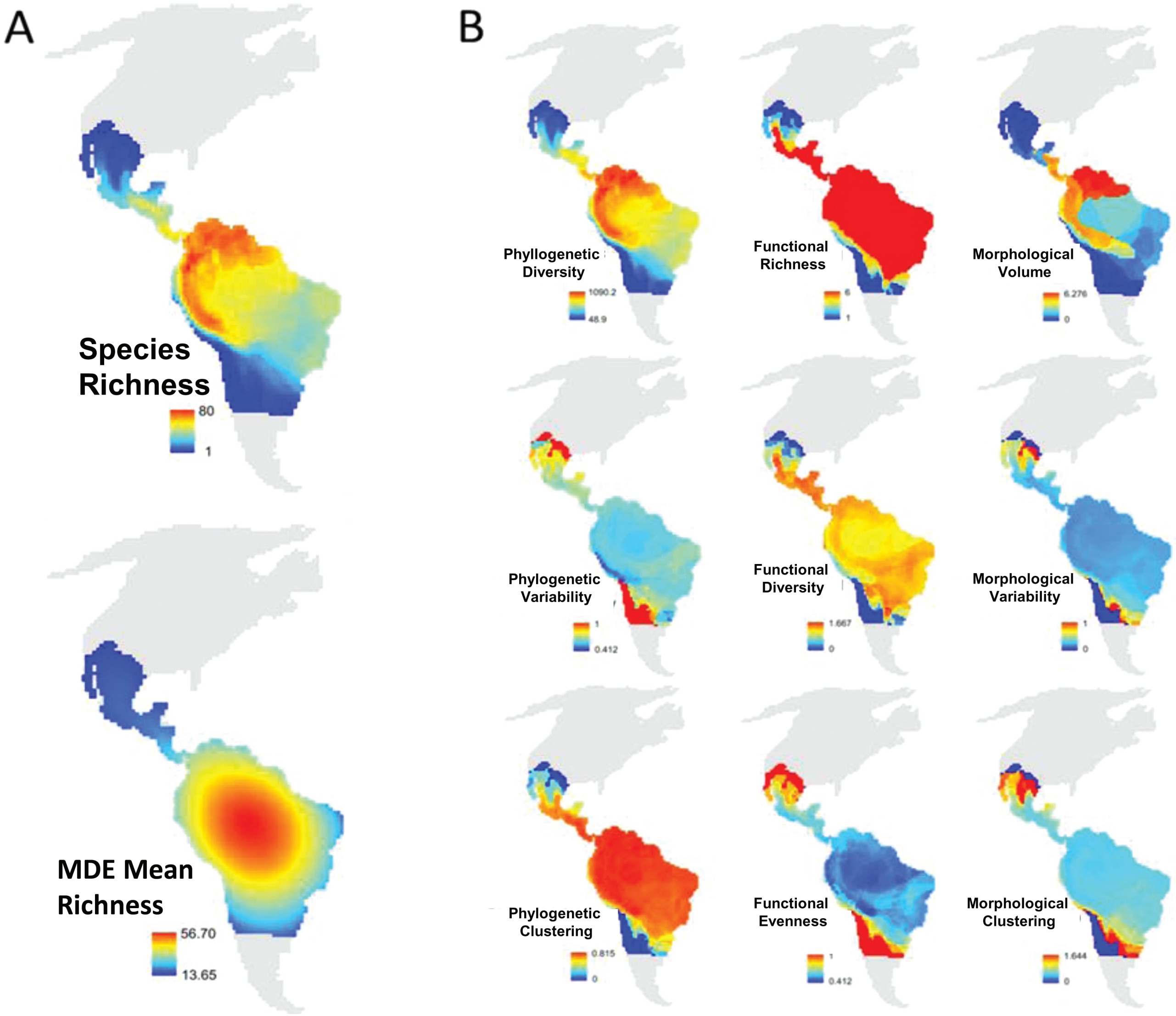

Fig. 3.—Spatial variation across multiple dimensions of biodiversity of noctilionoid bats in the New World. Four dimensions of biodiversity are represented: Panel A, Taxonomic Diversity (Species Richness, MDE [Mid-Domain Effect] Mean Richness); Panel B, Phylogenetic (Phylogenetic Diversity, Phylogenetic Variability, Phylogenetic Clustering), Functional (Functional Richness, Functional Diversity, Functional Evenness), and Phenetic (Morphological Volume, Morphological Variability [Standard Deviation of Minimum Spanning Tree Distances], Morphological Clustering [Mean Nearest-Neighbor Distance]) Diversities. Phylogenetic Diversity measures are based on the Mammal Supertree (Bininda-Emonds et al. 2008), Functional Diversity measures are based on the distribution of species to functional groups, and Phenetic Diversity is based on variation of species regarding six cranial and one body size measure. Figures redrawn from Stevens et al. (2013).

space. Area also generally declines with increasing elevation (Rahbek 1995; Körner 2007; but see Elsen and Tingley 2015), and both the mountain peak and the sea (or softer boundaries at the base of a mountain) can impose geometric constraints (Colwell and Hurt 1994; McCain 2005). Analogous to latitude, elevation therefore represents a surrogate for geophysical, environmental, and physiographic factors that can influence fundamental processes and ultimately the location and overlap of species ranges, resulting in geographic variation in biodiversity.

Unlike the single latitudinal gradient present in the northern and southern hemispheres, the abundance of mountain systems worldwide and their small spatial extent provide advantages over latitudinal gradients for the study of biodiversity (Sanders and Rahbek 2011; Szewczyk and McCain 2016). Replicates within and among ecological regions offer opportunities to test for generality of pattern and process, while accounting for confounding issues of unique histories and differences in climate or area. Moreover, sampling also can be standardized along an elevation gradient and experiments can be more readily integrated into these traditionally observational studies. Thus, elevational gradients are well suited for linking local processes to landscape-scale patterns in space and time to better understand biodiversity dynamics.

Elevational gradients in biodiversity have been documented extensively. Most have focused on the species richness–elevation relationship. Two common patterns have emerged: 1) a unimodal (or hump-shaped) relationship with richness that is greatest at mid-elevation (Fig. 4), and 2) a decrease (often monotonic) in richness with increasing elevation (Rahbek 1995; Willig and Presley 2016). Mammals exhibit both patterns. Non-flying small mammal assemblages (rodents, shrews, marsupial mice) exhibit great generality in a mid-elevation peak in richness (Brown 2001; Li et al. 2003; McCain 2005; Rowe and Lidgard 2009). For bats, equal support has been found for mid-elevation peaks and decreasing species richness with elevation (McCain 2007; Peters et al. 2016). Most studies of mammalian elevational diversity are of bats and non-flying small mammals (rodents, shrews, marsupial mice) because these groups are species-rich and locally abundant, and therefore well suited to the scale of a mountain range. Where evident, variation among case studies in the form of the richness–elevation relationship is often attributed to differences in scale, in terms of both the extent of the gradient and the grain size at which biodiversity is measured or aggregated (e.g., local sites versus interpolated ranges, elevational bins, or bands—Heaney 2001; Rahbek 1995; Rowe and Lidgard 2009; Willig and Presley 2016). Different patterns may also reflect unique biogeographic or evolutionary histories of biotas (Heaney 2001; Sanders and Rahbek 2011) and ecological differences among taxa or guilds. For example, species richness patterns for the small mammal fauna along an elevational gradient in subtropical China differed in form for endemic versus non-endemic species, and in the location of peak richness between rodents versus insectivores (Wu et al. 2013). Similarly, a study in the Sonoran Desert in southern California included the full suite of mammals known to occur

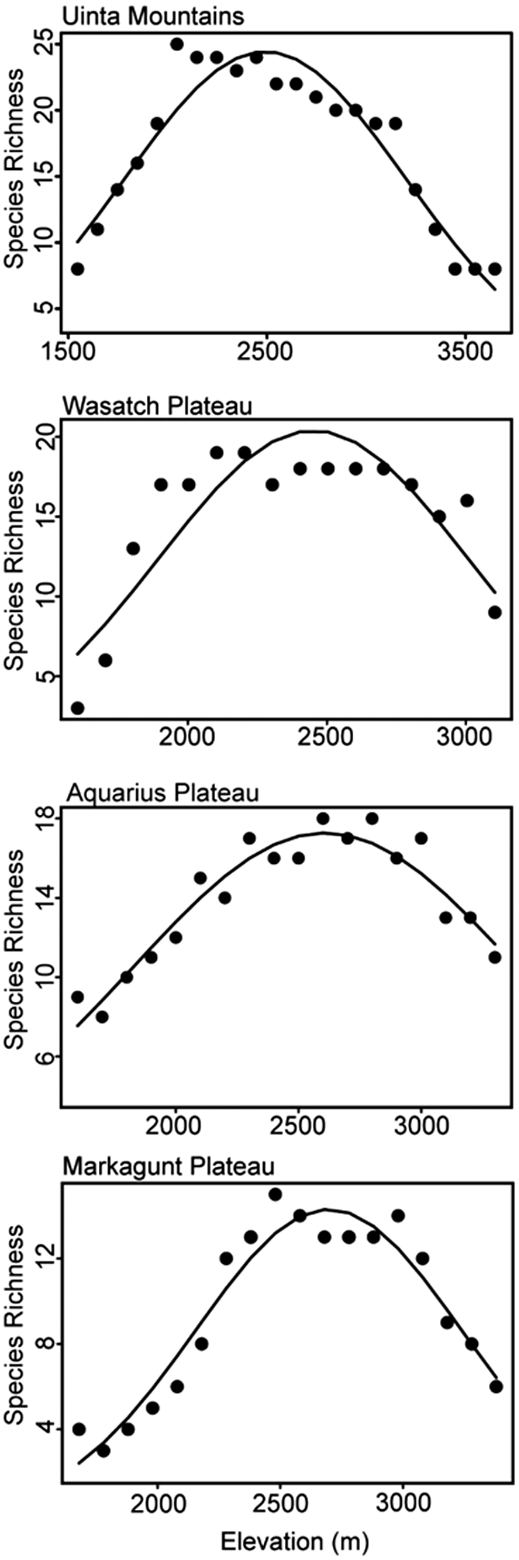

Fig. 4.—Representative unimodal species richness–elevation relationships for non-volant small mammals on four independent mountain ranges in central Utah. Richness values are based on species ranges, where presences are inferred in all bins between the highest and lowest recorded localities. Solid lines represent fit under a generalized linear model. From Rowe (2009).

in the region and found a mid-elevation peak in richness for the entire terrestrial assemblage, as well as for rodents and carnivores. However, each order reached peak numbers in different habitat types that abutted one another along the elevation gradient (Shepherd and Kelt 1999). The perception of richness patterns can therefore be sensitive to the subset of species examined, and comparisons among groups may enrich our understanding.

Despite the generality of patterns, much debate surrounds the underlying cause(s) of elevational gradients in richness. Correlative studies suggest strong support for climatic factors for both non-flying small mammals and bats (McCain 2004, 2005, 2007; Rowe 2009). Yet, dissimilarity is evident among the climatic variables identified as drivers of richness, even among neighboring mountain ranges with similar richness patterns (Rowe 2009), and for subsets of species within a single gradient (Wu et al. 2013; Hu et al. 2017). Moreover, model fit is sensitive to the grain size at which climatic variables are measured (Rowe et al. 2015). Climate may structure patterns of richness directly through variation in temperature tolerances or indirectly through the establishment of variable resource conditions (habitat and food availability) along which generalist and specialist species are distributed. The combination of temperature and water availability is often proposed as a driver of richness because it approximates productivity (or energy availability), which generally affects rates of critical biological processes (Allen et al. 2002; Hawkins et al. 2003; Currie et al. 2004). It is often presumed that productivity is greatest in regions of high temperature and high water availability, and that those areas correspond to peaks in mammalian richness along elevational gradients (e.g., Heaney 2001; McCain 2007). Hu et al. (2017) recently tested the water–energy dynamics model (O'Brien 1998) and found that it explained a high proportion of variation in overall species richness of small mammals (66%), as well as among species groups (53–88%). In contrast, studies using remotely sensed vegetation indices (i.e., normalized difference vegetation index or enhanced vegetation index) as proxies for productivity have found variable and relatively weak support for productivity in structuring richness of non-volant small mammals and bats along elevational gradients (Rowe 2009; Peters et al. 2016; Hu et al. 2017). More work is needed to ascertain variation in the productivity–elevation relationship among mountains as well as to quantify the relative contribution of productivity to larger-scale patterns of mammalian biodiversity. Inclusion of other environmental factors, such as habitat heterogeneity or other local resources, in elevational gradient studies has been infrequent and has yielded variable results (e.g., Rickart et al. 1991; Md. Nor 2001; Rowe 2009; Hu et al. 2017). Non-environmental factors have provided limited evidence for structuring elevational gradients of biodiversity of mammals. While area effects have been variable, the mid-domain effect has demonstrated low predictability for non-flying small mammals and bats alike (McCain 2005, 2007; Rowe 2009; Peters et al. 2016), with the exception of analyses restricted to species with large ranges (Wu et al. 2013; Hu et al. 2017).

Evaluation of biodiversity–elevation relationships beyond species richness is more limited than those along latitudinal gradients. Some case studies of mammals do consider richness patterns among species groups or guilds (e.g., Patterson et al. 1998; Md. Nor 2001; Wu et al. 2013; Xu et al. 2015), but only a few studies have evaluated elevational gradients in multiple dimensions of biodiversity (Cisneros et al. 2014; Dreiss et al. 2015). These studies suggest that species richness is not always a good surrogate for phylogenetic or functional diversity. Although bats (Cisneros et al. 2014) and rodents (Dreiss et al. 2015) show a similar species richness–elevation relationship in the Andes, clade-specific patterns emerged for phylogenetic and functional diversity. For example, phylogenetic diversity of rodents was congruent with that of taxonomic diversity, decreasing non-linearly with elevation, whereas elevation explained little variation in the phylogenetic diversity of bats. The birds along this elevation gradient show a similar species richness–elevation relationship, which also parallels trends in their functional diversity but not phylogenetic diversity (Willig and Presley 2016). Different dimensions of biodiversity may respond to different environmental drivers along elevation gradients, and this underscores the need to consider phylogenetic and functional measures of biodiversity further in order to develop a better understanding of the mechanisms underlying spatial patterns of biodiversity.

Geohistorical gradients.—The geohistorical record (fossils in their spatial, temporal, and paleoenvironmental contexts) provides opportunities to evaluate the dynamics of mammalian biodiversity gradients over evolutionary time scales in relation to cyclical and directional environmental changes. The ideal information needed for such analyses includes species occurrences for estimates of geographic distribution, ecological traits (such as feeding habit or body size, inferred from morphology), paleoenvironment (vegetation, climate, general landscape setting), and a phylogeny that encompasses extant and extinct species within the focal clade.

Such information enables testing of hypotheses about drivers of diversification and biodiversity gradients over time (Fritz et al. 2013). For example, the Neogene (23.0–2.6 million years ago [Ma]) fossil record for mammals in the northern hemisphere coupled with fossil data on regional plant communities demonstrated a 20-million-year biodiversity–productivity relationship for terrestrial large mammals (Fritz et al. 2016). Such information is available globally for much of the Quaternary (2.6 Ma to present) but becomes more geographically and temporally discontinuous and restricted for older records of mammalian history. Nonetheless, major insights about geographic gradients have emerged from studies of the geohistorical record, and we summarize three.

First, the Quaternary record demonstrates that geographic ranges of mammals can shift substantially in location and size over a few thousand years. The compilation of fossil occurrences and associated geochronology and paleoenvironments for North American mammals, first in FAUNMAP and now in its successor, NEOTOMA (www.neotomadb.org), provides a dynamic view of mammalian responses to glacial–interglacial cycles (FAUNMAP Working Group 1996). In North America, species ranges shifted south, east, or west during the last glacial advance. Geographic ranges shifted idiosyncratically rather than as coordinated associations. Consequently, some local faunal assemblages during glacial maxima exhibited co-occurrences that have no modern counterparts. A similar pattern occurred for North American plant associations (Williams et al. 2004). For mammals of the conterminous United States, the center of the geographic range shifted by an average of 1,200–1,400 km from pre-glacial to glacial and from glacial to post-glacial intervals, respectively (Lyons 2003). Range shifts during glacial advances would have maintained but compressed latitudinal richness gradients. In contrast, elevational richness gradients may have disappeared (or become extremely weak), as species ranges in montane regions shifted to lower elevations (e.g., Grayson 1987; Barnosky et al. 2004).

Second, the latitudinal gradient of biodiversity has waxed and waned over earth history for several groups that have good fossil records (Mannion et al. 2014). For example, during the warm greenhouse climate of the Cretaceous (145–66 Ma), dinosaur diversity was greatest at middle to high latitudes in both the northern and southern hemispheres (Mannion et al. 2012). Taxonomic diversity tracked continental land area, and shallow seas covered vast areas of continental interiors, resulting in much greater fragmentation of continental regions than what exists today. Although the record for Mesozoic mammals is too sparse to evaluate geographic gradients, a Paleocene (66–56 Ma) record of North American mammal assemblages extending from 35° to 63° N latitude shows a flat richness gradient in contrast to the familiar latitudinal gradient over the same region today (Rose et al. 2011). Stable isotopes of oxygen from mammal teeth followed the modern oxygen isotope gradient, even during Paleocene greenhouse conditions, indicating that climatic temperature and hydrology expressed a latitudinal gradient but were not determinants of the latitudinal richness patterns then. A recent study of the mammalian fossil record over the entire Cenozoic (last 66 Ma) of North America assessed the latitudinal gradient with sample-standardized data (Marcot et al. 2016) and demonstrated either a flat richness gradient or a reverse latitudinal gradient for most Paleocene, Eocene, and Miocene time intervals. The modern gradient emerged during the Pliocene (5.3–2.6 Ma). Thus, the latitudinal richness gradient for mammals may not have persisted through deep time, and continental-scale biodiversity patterns have tracked gradients in environmental conditions, especially temperature and temperature seasonality. In addition, the latitudinal gradient in beta diversity (spatial turnover in species composition and richness) of North American mammals has varied over the Cenozoic, being weaker in the early Cenozoic and peaking during the late Miocene, around 10 Ma (Fraser et al. 2014). Mean beta diversity among faunas was inversely correlated with mean annual precipitation, a pattern similar to geographic variation in beta diversity among present-day mammalian faunas of North America.

The third insight relates to a spatial contrast, the topographic richness "gradient," which is present for living mammals on all of the ice-free continents today (Badgley et al. 2017). The topographic richness gradient refers to the increase in species richness with increased elevation and relief, in contrast to adjacent lowlands. In North America, for example, the number of present-day mammal species per unit area (for areas of ~50,000 km^2) is nearly twice as high in the intermontane west as on the Great Plains (Fig. 1; Badgley and Fox 2000). Since the topographic complexity of montane regions is millions of years old, one might expect that this contrast should be a long-term feature of the Cenozoic fossil record. The North American record, which is dense and well sampled from both the Great Plains and the intermontane west, shows otherwise. For both large and small mammals, species richness on the Great Plains was higher than or similar to species richness of the intermontane west over millions of years (Kohn and Fremd 2008; Finarelli and Badgley 2010; Badgley et al. 2014). Over the last 20 Ma, the topographic richness gradient was strongest during the middle Miocene from 17 to 14 Ma, during a period of global warming and intensified tectonic activity in the Great Basin. Both diversification and dispersal dynamics have likely influenced the middle Miocene contrast in topographic richness in mammals (Badgley and Finarelli 2013).

Most studies of spatial gradients have focused on continental lineages and faunas. Marine mammals, including pinnipeds, sirenians, and cetaceans, exhibit several fascinating trends over their Cenozoic history, including periods of accelerated evolution of feeding adaptations, origination, increase in body size, and increase in gigantism (Uhen 2010; Pyenson and Vermeij 2016; Slater et al. 2017). In present-day oceans, species richness of marine mammals peaks in temperate latitudes in regions where marine productivity is high, with pinnipeds showing richness peaks at higher latitudes than cetaceans (Kaschner et al. 2011). Historical changes in spatial gradients are difficult to ascertain because of poor or variable preservation of wide-ranging species. A recent analysis of fossil marine mammals of northern hemisphere Atlantic and Pacific records (Peredo and Uhen 2018) documents moderate faunal similarity between the Atlantic and the Mediterranean for faunas of middle Eocene to middle Miocene age (ca. 42–15 Ma). All other regions of the northern hemisphere show low similarity that declined further through the Miocene. Modern marine mammal faunas have much greater similarity, dating only to the Quaternary, when many species dispersed through the Arctic Ocean during interglacial intervals.

These insights from the fossil record imply that broad-scale tectonic and climatic history, including changes in topographic complexity, climatic gradients, and habitat area, have strongly influenced the rate and timing of diversification, the environmental filtering of species, and the composition of regional assemblages over deep time. For example, in South America, topographic relief is the best predictor of rodent species richness and turnover, in particular for sigmodontine rodents (Novilla and Ojeda 2014; Maestri and Patterson 2016). The geologically young age (late Neogene) of major sigmodontine clades coincides with late stages of Andean uplift, supporting the hypothesis that strong environmental gradients and high-elevation peaks and plateaus stimulated diversification of sigmodontines over the last 6 Ma. Another example involves the influence of climatic conditions on current community composition of mammalian faunas distributed throughout Africa. Rowan et al. (2016) analyzed modern and paleoclimatic data from the last 20 thousand years as predictors of phylogenetic structure and functional trait structure of modern assemblages of primates, ungulates, and carnivores. Climatic data from the Mid-Holocene and the Last-Glacial Maximum were strong or stronger predictors of community structure than were modern climatic data for each group and for all of these mammals together. This result suggests that faunal composition can reflect prior environmental conditions for millennia even after those conditions have changed dramatically. Further work is needed to evaluate the influence of tectonic and climatic history on the biogeographic processes that shape the temporal dynamics of mammalian biodiversity.

Biodiversity Gradients Under Future Climate and Land-Use Change

Our current understanding of biodiversity gradients and their underlying mechanisms is being tested by ongoing and future challenges posed by anthropogenic changes to the biosphere. In particular, two types of anthropogenic change are restructuring the physical template and will likely have associated effects on biodiversity gradients. Structural changes, especially habitat conversion and fragmentation, have resulted in the emergence of anthropogenic biomes such as agricultural monocultures and rangelands dominated by exotic species (Haberl et al. 2007). Already, land use at the global scale is at a tipping point whereby anthropogenic modifications are so extensive that they represent the spatial norm, and the distribution and biodiversity of species are losing their tight association with climatic gradients.

The influence of land conversion on mammal distributions and biodiversity is already evident. A global assessment of 177 terrestrial mammal species found that 56% have lost more than 60% of their historic range, with the greatest range reductions occurring in Africa, Asia, and Australia (Ceballos et al. 2017). In North America, range collapse of many large carnivores and ungulates is associated with areas of high human influence (e.g., population density and land-use—Laliberte and Ripple 2004). In West African reserves, the extinction rates of carnivores, ungulates, and primates are tied to increased hunting pressure in areas of increasing human population density (Brashares et al. 2001). Collectively, these range collapses have diminished regional species richness and shifted areas of peak richness over time (Laliberte and Ripple 2004). A number of studies on geographic patterns of range collapse have distinguished between modern-day populations located in the range core or the periphery. Indeed, in many cases of range contraction, species persist at the periphery of their historical range (Channell and Lomolino 2000). Such perspectives may illuminate drivers of extinction (natural versus anthropogenic processes), the conservation status, or extinction risk of populations, and identify areas suitable for protection, translocation, and reintroduction (Channell and Lomolino 2000; Eckert et al. 2008; Boakes et al. 2018).

Human land use can also modify spatial patterns of community composition and turnover. For example, urbanization causes extensive homogenization of the physical environment. Subsequently, only urban-adapted species persist and a homogenized biota results (McKinney 2006). In addition, species for which urban and agricultural conditions provide plentiful resources (e.g., raccoons [*Procyon lotor*] and coyotes [*Canis latrans*]) will continue to experience range expansions (Laliberte and Ripple 2004; DeVault et al. 2011). In fragmented landscapes, habitat specialists tend to exhibit responses of greater magnitude than those of habitat generalists, and homogenization proceeds by local extinction of specialists until fragments contain only generalists (Swihart et al. 2003).

Little is known regarding how land-use change may modulate changes in biodiversity over extensive environmental gradients of climatic or other factors that are not related to disturbance. Already, species geographic distributions have been shifting as they track ongoing changes in climate (e.g., Scheel et al. 1996; Moritz et al. 2008; Sherwin et al. 2012), with species of different biogeographic affinities changing in different ways (Rebelo et al. 2009). Of great concern are the regions where specific climatic conditions are disappearing, both at high elevations and at high latitudes, as well as the appearance and expansion of novel climatic conditions without analogs during the Holocene (Williams et al. 2007). For regions with disappearing climates, for example on mountain tops and at the poles, populations and species are destined for local and eventually global extinction. Forecasts of novel climates are most prevalent at low latitudes, as familiar thermal zones shift poleward and new, warmer thermal zones expand in the tropics. As a result, substantial changes in geographic distribution of subtropical species are expected, along with concomitant changes in biodiversity gradients. Since most ecological niche models (Peterson et al. 2011) are based on bioclimatic conditions of the last 100 years, extrapolations based on familiar climatic conditions may provide only limited insights (Faurby and Araujo 2018). In many cases, no overlap exists between present and predicted future geographic distributions of species, and given the rate of change in climate, it is doubtful that all species can change their distributions fast enough to track future climate over the next century (Rebelo et al. 2009). In the extreme case, a number of species are likely to undergo global extinction (Burns et al. 2003; Thomas et al. 2004). We can also expect novel species associations, in which species that did not coexist and potentially interact in the recent past do so under altered and non-analog climatic conditions.

Recent Advances

Data availability.—Documenting patterns of biodiversity requires data on species geographic distributions or occurrences. In the era of "big data," online biological databases have facilitated biodiversity research, especially for well-known groups such as mammals. Broad-scale patterns, including the latitudinal gradient of biodiversity, are typically generated from the overlap of species range maps. Through the International Union for the Conservation of Nature (IUCN) Global Mammal Assessment, range maps are now available for most mammal species (5,487 species in Schipper et al. 2008, see also Ceballos et al. 2005), and regional databases of range maps are becoming more common (Boitani et al. 2011). Advances in biodiversity informatics have also improved the accessibility of occurrence records associated with museum specimens (e.g., Arctos, GBIF, VertNet). Despite greatly facilitating biodiversity research, taxonomic and geographic biases of these data abound (e.g., Boitani et al. 2011) and serve as an important reminder that our knowledge of the distribution of even modern mammals is heterogeneous and sparse. New field studies and the continued growth of museum collections are necessary to fill these knowledge gaps and contribute to comparative datasets needed to further understanding of how variation in species groups and site characteristics contribute to patterns of biodiversity (Lacey et al. 2017). Databases of fossil occurrence records (e.g., Paleobiology Database) that are similarly limited in temporal and spatial extent will also benefit from new field collections and more extensive identification of material in museum collections. Independent of data availability, all studies of mammalian biodiversity would benefit from greater discussion of the appropriate resolution of range map data and the spatial accuracy of occurrence records (Rowe 2005; Boitani et al. 2011; Jenkins et al. 2013).

Examining biodiversity gradients across multiple dimensions requires data on phylogenetic relationships and species morphological or functional traits. The Bininda-Emonds et al. (2008) supertree contains most extant mammal species and represents a robust hypothesis of evolutionary relationships from which distance matrices can be generated, although the analysis of Meredith et al. (2011) provides more reliable divergence estimates. In contrast, trait data for mammalian species are far less complete. Although existing databases provide nearly comprehensive data on a suite of measured or modeled traits including body size, generation time, and activity period, data deficiencies remain for many basic physiological and ecological attributes (Ernest et al. 2003; Smith et al. 2003; Jones et al. 2009; Pacifica et al. 2013; Wilman et al. 2014; Gonçalves et al. 2018). Additional work is needed to populate data on key attributes and to identify redundancy among traits and trait combinations to facilitate the development of more mechanistic hypotheses that may better predict mammalian biodiversity, especially at finer taxonomic and spatial scales.

Niche models as improvements over polygon range maps.—Most studies of continental spatial patterns of mammalian biodiversity have utilized range maps based on polygons drawn from the marginal records of species distributions. Such data are inherently biased in a number of ways. First, the depiction of a range map based on drawing a polygon around marginal records, often collected over more than a 100-year span, presents a static view of the distribution of populations. However, distributions are dynamic and expand, contract, and shift based on short-term and long-term climate change, as well as interannual variability in weather or changes in biotic interactions. Polygons likely overestimate the edges of species distributions. Moreover, they typically depict distribution as continuous across the entire polygon and tell nothing about spatial dynamics of abundance within the geographic range of a species.

Recently, coarse-scale habitat suitability models have been developed for most (5,027) mammal species within their IUCN range boundaries, and comparisons have confirmed substantial discrepancies in richness estimates when occurrences based on habitat suitability models are compared to range map data, with the greatest discrepancies in subtropical and tropical regions (Rondinini et al. 2011). In contrast to habitat suitability models, species distribution models (Peterson et al. 2011) couple known occurrence records with environmental conditions at those same locations to provide more informed insights about species distribution, especially within the region that falls inside marginal records. Species distribution models have the advantage that they can be used to model presence and absence (based on a minimal suitability cutoff) across the geographic range. Moreover, these models estimate suitability of each pixel within the range of a species and suitability values are often positively correlated with actual abundance (Weber et al. 2017). Combining multiple distribution models for a number of species in order to estimate patterns of mammalian biodiversity and evaluate underlying mechanisms is a growing field (Herkt et al. 2017). Such approaches can provide more finely resolved biodiversity patterns based on modeled estimates of presence and absence of species and to characterize properties such as evenness that entail species abundance. This approach may be further amplified by data from the Quaternary and older records of mammal distributions and climatic conditions. Inclusion of paleontological and paleoclimatic data into species distribution models will provide a more complete view of species climatic niches (Davis et al. 2014; Fraser et al. 2014; Faurby and Araujo 2018).

Diversity and dispersion fields.—Patterns of biodiversity are usually analyzed by characterizing geographic variation in species richness or derived indices based on attributes of species, such as their abundance, phylogenetic affinity, functional traits, or morphology. An alternative approach is to examine characteristics of the presence–absence matrix of sites within the geographic distribution of a focal taxon. Variables derived from these matrices are: 1) sums of the rows to examine differences in species richness among sites within the geographic range of a species, or 2) sums of the columns to examine differences among species in terms of their geographic range size that occurs within the geographic range of a focal species. These are referred to as Q- and R-mode analyses, respectively (Legendre and Legendre 1998). A more informative approach is to analyze distribution and diversity simultaneously in Rq-mode (dispersion fields) or Qr-mode (diversity fields - Arita et al. 2008). A dispersion field estimates characteristics of the geographic ranges of species occurring at a particular site, whereas a diversity field characterizes diversity and patterns of coexistence within the geographic range of a focal taxon. Across sites, dispersion fields systematically covary with species richness, such that sites with greater species richness have dispersion fields that are more leptokurtic, left-skewed, variable, and possess species with larger range sizes (Graves and Rahbek 2005). The statistical properties (i.e., mean, variance, skew, kurtosis) of dispersion fields exhibit considerable geographic variation that follows biome boundaries and environmental conditions in which particular sites are embedded. For diversity fields of New World bats, the frequency distributions of species richness are multimodal, whereas distributions generated from null models are unimodal (Fig. 5; Villalobos and Arita 2010). Because species co-occur more often than expected by chance at high-diversity sites, a higher variance in species richness among sites as well as a wider frequency distribution of species richness than expected is generated. Diversity fields also have been applied to other dimensions of biodiversity. For example, phyllostomid bats tend to coexist with more closely related species (Villalobos et al. 2013), and gradients in phylogenetic diversity fields involve changes from phylogenetically overdispersed to underdispersed assemblages along a latitudinal gradient. Although complex, dispersion and diversity fields promise much in terms of site-based and species-based perspectives on patterns of biodiversity.

Pattern-oriented and general simulation modeling.—Since biodiversity gradients span domains that are often too spatially or temporally extensive for use of manipulative experiments to evaluate causal factors, the search for mechanisms must rely on analyses of observational data and comparisons among natural experiments. Correlative models typically relate variation in biodiversity to environmental conditions (especially climate) from local to global scales. A common approach to assessing the mechanistic basis of biodiversity gradients has been to collect data throughout the distribution of a group of species and to use regression analysis to evaluate the degree to which an empirical biodiversity pattern is predicted by particular environmental characteristics. Spatially explicit, correlative approaches suffer from a range of limitations (Willig et al. 2003) and alone are considered by some to be poor indicators of causation. One limitation is the high covariation (collinearity) among environmental variables that are selected to evaluate patterns. For example, at broad scales, topography and land cover track climatic gradients of temperature and precipitation which themselves are, in places, highly correlated. A second limitation is that many mechanistic explanations for biodiversity gradients only make qualitative predictions (e.g., species richness increases with productivity), and many putative mechanisms make the same qualitative prediction (e.g., species richness increases with productivity, temperature, ambient energy, and habitat heterogeneity). In the absence of quantitative predictions, it is often difficult to distinguish among mechanisms (Willig et al. 2003).

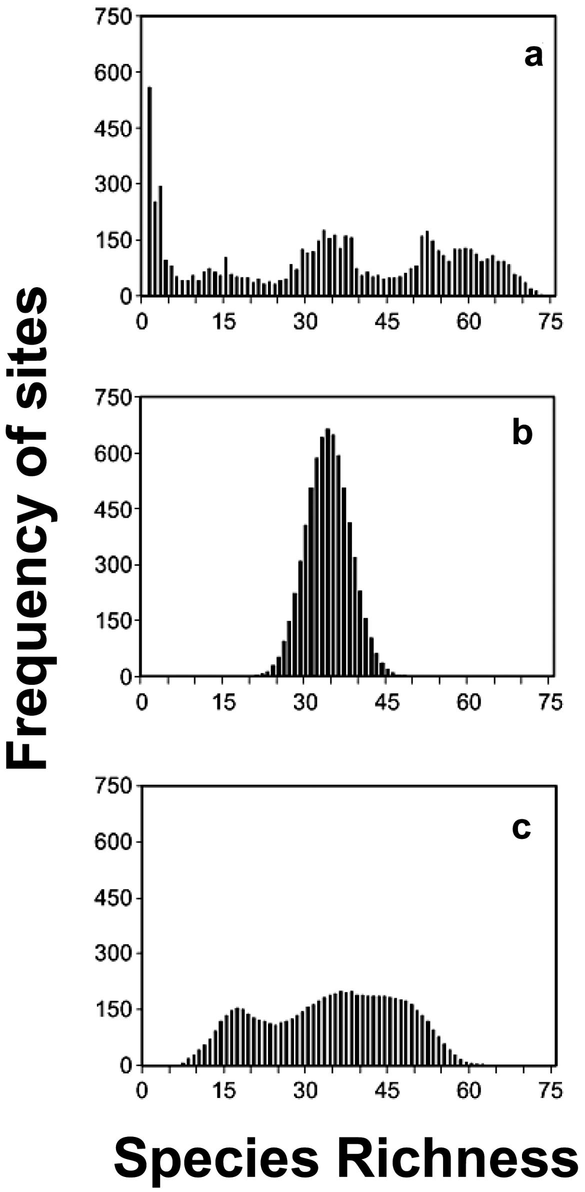

Fig. 5.—Diversity fields of New World phyllostomid bats. Species richness frequency distributions of 143 phyllostomid bat species in 6,794 quadrats that were 2,500 km^2 in size. Each bar in each histogram represents the number of quadrats within a species geographic range that possessed that number of species that co-occurred. A) Data for the 143 real species geographic ranges. B) Result of simulations using scattered (non-cohesive) random geographic ranges. C) Result of simulations using cohesive random ranges, applying a spreading-dye algorithm. To allow comparisons with (A), histograms in (B) and (C) represent the cumulative frequency of 100 simulations, adjusting the x-axis to correspond to a single assemblage. Figure and legend modified from Villalobos and Arita (2010).

Recent alternative approaches involve agent-based, pattern-oriented modeling to assess the fit of model outcomes to empirical patterns (Grimm et al. 2005; Rangel et al. 2007; Gotelli et al. 2009; Stevens et al. 2013). Species and their geographic distributions are considered "agents" that are free to respond uniquely and independently to a set of environmental stimuli.

The joint yet independent responses of all species in a domain produce a spatial pattern, and the goodness-of-fit of a pattern-oriented model to the empirical pattern can be used to assess how a particular response variable contributes to a biodiversity gradient. Also, pattern-oriented models can be used to generate secondary patterns that can be used as another measure of goodness-of-fit of the model to data.

Rangel et al. (2007) constructed a pattern-oriented model for South American birds to generate geographic ranges of species and thereby gradients in species richness. Ranges were simulated based on the starting position of the center of the geographic range, niche breadth, conservatism of the geographic or climatic center of the niche, conservatism of niche breadth, extinction probability, and six environmental niche axes. Simulated species ranges were initiated and their geographic distributions grew to equilibrium within a domain via modeling. Overlapping geographic distributions generated gradients of species richness. This model produced results that accounted for approximately 80% of the variation in empirical species richness and the observed slope of the relationship between observed and expected values was 0.97 (relative to 1.0 if the model exactly predicted observed species richness). This pattern-oriented model also produced realistic variation in other characteristics, such as the frequency distribution of geographic range sizes that matched the empirical right-skewed, range-size distribution of South American birds. Moreover, incorporating simple evolutionary processes of niche conservatism and expansion into a pattern-oriented model provided substantive predictive ability of contemporary gradients. Application of pattern oriented modeling would provide many insights into mammalian biogeography.

Pattern-oriented modeling provides two distinct advantages. First, the models are mechanistic and employ realistic biological processes to generate simulated outcomes that can be directly compared to empirical patterns. Second, these models generate secondary patterns that can be used to further assess efficacy of the model via strong inference (Platt 1964). Since biodiversity is multidimensional, one strong test of a pattern-oriented model is good fit of simulated values across several dimensions (e.g., Stevens et al. 2013). Nonetheless, pattern-oriented modeling does have limitations. First, decisions about model complexity have critical impact on whether a sufficient number of mechanisms have been employed in model development. With too few mechanisms, the model does not produce repeatable expected values. With too many mechanisms, the analysis may be cumbersome and interactions among mechanisms may limit inference as to their relative importance. Second, repeatable quantitative assessments of how particular factors affect species and their geographic distributions are not yet available for many biological processes. The use of patterned-oriented modeling to address biogeographic questions is in its infancy, but has great promise to test alternative hypotheses about processes that shape gradients of mammalian biodiversity.

New Conceptual Horizons

Building on prior findings, future research on gradients of mammalian biodiversity faces opportunities in data integration and new analytical methods. We see four themes that point to advances in biological understanding.

1) Future research should build on the substantive foundation of information regarding mammalian biodiversity gradients to better understand their mechanistic bases. Much research over the last 100 years has quantified patterns of mammalian biodiversity, often accompanied by statistical measures between biodiversity and environmental characteristics. Most research to this point has focused heavily on climatic drivers. Nonetheless, to better understand processes that underpin geographic variation in biodiversity, it is necessary to evaluate the fundamental processes of diversification, particularly speciation, extinction, and dispersal, within a hypothesis-testing or modeling context (e.g., Silvestro et al. 2014). Evolutionary processes that generate or diminish biodiversity should be distinguished from processes that rearrange species distributions over the landscape. Since both kinds of processes unfold over millions of years and are only partially captured by present-day species distributions, the fossil record has an important role for testing hypotheses about biogeographic processes when historical records are sufficiently rich to provide robust estimates of pattern.
2) Engagement of the fossil record may enhance our understanding of processes that cause biodiversity gradients to become stronger or weaker over time. Despite its limitations, the fossil record provides a dynamic view of biodiversity gradients with respect to changing climates, landscapes, barriers, and intercontinental connections. In combination with hypotheses and models of biotic and abiotic drivers of biogeographic processes, the fossil record offers a history of natural experiments in mammalian biodiversity in relation to environmental history, from local to continental scales. Potential insights include the ecological and evolutionary responses of mammal populations, species, and assemblages to sustained climatic and ecosystem change (e.g., Lyons 2003; Badgley et al. 2008; Eronen et al. 2015), including trends that are coupled to unique periods in earth history (e.g., Slater et al. 2017).
3) Insights from foundational research on biodiversity gradients should be used to address urgent challenges in conservation planning at regional to global scales. Integration of field studies of extant species with phylogenetic and historical data can increase understanding of the resilience and vulnerability of species and biotic associations to environmental change (Lawing and Matzke 2014; McGuire and Davis 2014; Terry and Rowe 2015). Responses of species to changes in climate and vegetation during glacial–interglacial cycles present a wealth of information about rates and magnitudes of geographic range shifts and changing faunal associations across landscapes and seascapes (Blois et al. 2010; Terry et al. 2011). Over deeper time, the fossil record can illuminate selectivity of range shifts and extinction of lineages in terms of ecological traits or lineage age (Finarelli and Goswami 2013; Domingo et al. 2014).

4) Studies of biodiversity gradients differ in spatial scales. Comparisons within and among biomes may enable researchers to tease apart climate or land-use drivers of species distributions and patterns of biodiversity. This refinement will allow better understanding of relationships between biodiversity and ecosystem services. This approach lends itself to the evaluation of the scale dependence of fundamental biogeographic relationships (e.g., the species–area relationship—Harte et al. 2009).

Over the last century, mammalogists have gone from documenting basic taxonomy, natural history, and geographic ranges of species to synthesizing this information to explore patterns and underlying mechanisms of mammalian biodiversity across various dimensions, as well as over different scales of space and time. Although geographic patterns are well described, much remains to be learned about underlying mechanisms. Despite the global challenges of human land use and climate change, the next century promises much in terms of advancing our understanding of biodiversity gradients. Massive amounts of data have become widely available. Analyses continue to become more sophisticated and better suited for complex questions. The most urgent need is to integrate past and ongoing insights to develop effective conservation strategies so as to mitigate the intensifying impacts of human activities on species and habitats.

Acknowledgments

We thank Heidi Amarila-Stevens and Sergio Solari for help in preparing the Spanish summary.

Literature Cited

Allen, A. P., J. H. Brown, and J. F. Gillooly. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. Science 297:1545–1548.

Arita, H. T., J. A. Christen, P. Rodríguez, and J. Soberón. 2008. Species diversity and distribution in presence-absence matrices: mathematical relationships and biological implications. The American Naturalist 172:519–532.

Badgley, C., and J. A. Finarelli. 2013. Diversity dynamics of mammals in relation to tectonic and climatic history: comparison of three Neogene records from North America. Paleobiology 39:373–399.

Badgley, C., and D. L. Fox. 2000. Ecological biogeography of North American mammals: species density, and ecological structure in relation to environmental gradients. Journal of Biogeography 27:1437–1467.

Badgley, C., T. M. Smiley, and J. A. Finarelli. 2014. Great Basin mammal diversity in relation to landscape history. Journal of Mammalogy 95:1090–1106.

Badgley, C., et al. 2008. Ecological changes in Miocene mammalian record show impact of prolonged climatic forcing. Proceedings of the National Academy of Science USA 105:12145–12149.

Badgley, C., et al. 2017. Biodiversity and topographic complexity: modern and geohistorical perspectives. Trends in Ecology & Evolution 32:211–226.

Barnosky, A. D., P. L. Koch, R. S. Feranec, S. L. Wing, and A. B. Shabel. 2004. Assessing the causes of late Pleistocene extinctions on the continents. Science 306:70–75.

Barry, R. G. 2008. Mountain weather and climate. 3rd ed. Cambridge University Press, New York.

Benchimol, M., and C. A. Peres. 2013. Anthropogenic modulators of species-area relationships in Neotropical primates: a continental-scale analysis of fragmented forest landscapes. Diversity and Distributions 11:1339–1352.

Bininda-Emonds, O. R. P., et al. 2008. The delayed rise of present-day mammals. Nature 446:507–512.

Blois, J. L., J. L. McGuire, and E. A. Hadly. 2010. Small mammal diversity loss in response to late-Pleistocene climatic change. Nature 465:771–774.

Boakes, E. H., N. J. B. Isaac, R. A. Fuller, G. M. Mace, and P. J. K. McGowan. 2018. Examining the relationship between local extinction risk and position in range. Conservation Biology 32:229–239.

Boitani, L., L. Maiorano, D. Baisero, A. Falcucci, P. Visconti, and C. Rondinini. 2011. What spatial data do we need to develop global mammal conservation strategies? Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences 366:2623–2632.

Bowers, M. A. 1982. Insular biogeography of mammals in the Great Salt Lake. Great Basin Naturalist 42:589–896.

Brashares, J. S., P. Arcese, and M. K. Sam. 2001. Human demography and reserve size predict wildlife extinction in West Africa. Proceedings of the Royal Society of London, Series B: Biological Sciences 268:2473–2478.

Brown, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. American Naturalist 105:467–478.

Brown, J. H. 2001. Mammals on mountainsides: elevational patterns of diversity. Global Ecology and Biogeography 10:101–109.

Buckley, L. B., et al. 2010. Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. Proceedings of the Royal Society of London B: Biological Sciences 277:2131–2138.

Burgin, C. J., J. P. Colella, P. L. Kahn, and N. S. Upham. 2018. How many species of mammals are there? Journal of Mammalogy 99:1–14.

Burns, C. E., K. M. Johnston, and O. J. Schmitz. 2003. Global climate change and mammalian species diversity in US national parks. Proceedings of the National Academy of Sciences of the USA 100:11474–11477.

Cardillo, M. 1999. Latitude and rates of diversification in birds and butterflies. Proceedings of the Royal Society B 266:1221–1225.

Ceballos, G., P. R. Ehrlich, and R. Dirzo. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proceedings of the National Academy of Sciences of the USA 114: E6089–E6096.

Ceballos, G., P. R. Ehrlich, J. Soberón, I. Salazar, and J. P. Fay. 2005. Global mammal conservation: what must we manage? Science 309:603–607.

Channel, R., and M. V. Lomolino. 2000. Dynamic biogeography and conservation of endangered species. Nature 403:84–86.

Cisneros, L. M., et al. 2014. Multiple dimensions of bat biodiversity along an extensive tropical elevational gradient. The Journal of Animal Ecology 83:1124–1136.

Cisneros, L. M., M. E. Fagan, and M. R. Willig. 2016. Environmental and spatial drivers of taxonomic, functional, and phylogenetic characteristics of bat communities in human-modified landscapes. PeerJ 4:e2551.

Colwell, R. K., and G. C. Hurt. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. American Naturalist 144:570–595.

Connor, E. F., and E. D. McCoy. 1979. The statistics and biology of the species-area relationship. American Naturalist 113:791–833.

Currie, D. J., et al. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters 7:1121–1134.

Davis, E. B., J. L. McGuire, and J. D. Orcutt. 2014. Ecological niche models of mammalian glacial refugia show consistent bias. Ecography 37:1133–1138.

DeVault, T. L., Z. H. Olson, J. C. Beasley, and O. E. Rhodes, Jr. 2011. Mesopredators dominate competition for carrion in an agricultural landscape. Basic and Applied Ecology 12:268–274.

Domingo, M. S., C. Badgley, B. Azanza, D. DeMiguel, and M. T. Alberdi. 2014. Diversification of mammals from the Miocene of Spain. Paleobiology 40:196–220.

Drakare, S., J. J. Lennon, and H. Hillebrand. 2006. The imprint of the geographical, evolutionary and ecological context on species-area relationships. Ecology Letters 9:215–227.

Dreiss, L. M., et al. 2015. Taxonomic, functional, and phylogenetic dimensions of rodent biodiversity along an extensive tropical elevational gradient. Ecography 38:876–888.

Dueser, R. D., and W. C. Brown. 1980. Ecological correlates of insular rodent diversity. Ecology 61:50–56.

Eckert, C. G., K. E. Samis, and S. C. Lougheed. 2008. Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. Molecular Ecology 17:1170–1188.

Elsen, P. R., and M. W. Tingley. 2015. Global mountain topography and the fate of montane species under climate change. Nature Climate Change 5:772–776.

Ernest, S. M., et al. 2003. Life history characteristics of placental nonvolant mammals: ecological archives E084-093. Ecology 84:3402–3402.

Eronen, J. T., C. M. Janis, C. P. Chamberlain, and A. Mulch. 2015. Mountain uplift explains differences in Palaeogene patterns of mammalian evolution and extinction between North America and Europe. Proceedings of the Royal Society B 282: 20150136.

FAUNMAP Working Group. 1996. Spatial response of mammals to late Quaternary environmental fluctuations. Science 272:1601–1606.

Faurby, S., and M. B. Araujo. 2018. Anthropogenic range contractions bias species climate change forecasts. Nature Climate Change 8:252–256.

Finarelli, J. A., and C. Badgley. 2010. Diversity dynamics of Miocene mammals in relation to the history of tectonism and climate. Proceedings of the Royal Society B 277:2721–2726.

Finarelli, J. A., and A. Goswami. 2013. Potential pitfalls of reconstructing deep time evolutionary history with only extant data, a case study using the Canidae (Mammalia, Carnivora). Evolution 67:3678–3685.

Fine, P. V., and R. H. Ree. 2006. Evidence for a time-integrated species-area effect on the latitudinal gradient in tree diversity. The American Naturalist 168:796–804.

Fraser, D., C. Hassall, R. Gorelick, and N. Rybczynski. 2014. Mean annual precipitation explains spatiotemporal patterns of Cenozoic mammal beta diversity and latitudinal diversity gradients in North America. PLoS ONE 9:e106499.

Frick, W. F., J. P. Hayes and P. A. Heady III. 2008. Island biogeography of bats in Baja California: patterns of bat species richness in a near shore archipelago. Journal of Biogeography 35: 353–364.

Fritz, S. A., J. Schnitzler, J. T. Eronen, C. Hof, K. Böhning-Gaese, and C. H. Graham. 2013. Diversity in time and space: wanted dead and alive. Trends in Ecology & Evolution 28:509–516.

Fritz, S. A., et al. 2016. Twenty-million-year relationship between mammalian diversity and primary productivity. Proceedings of the National Academy of Science of the USA 113:10908–10913.

Gonçalves, F., et al. 2018. Atlantic mammal traits: a data set of morphological traits of mammals in the Atlantic Forest of South America. Ecology 99:498.

Gotelli, N. J., et al. 2009. Patterns and causes of species richness: a general simulation model for macroecology. Ecology Letters 12:873–886.

Graves, G. R., and C. Rahbek. 2005. Source pool geometry and the assembly of continental avifaunas. Proceedings of the National Academy of Sciences of the USA 162:7871–7876.

Grayson, D. K. 1987. The biogeographic history of small mammals in the Great Basin: observations on the last 20,000 years. Journal of Mammalogy 68:359–375.

Grim, V., et al. 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310:987–991.

Haberl, H., et al. 2007. Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. Proceedings of the National Academy of Sciences of the USA 104:12942–12947.

Harcourt, A. H., and D. A. Doherty. 2005. Species-area relationships in tropical forest fragments: a global analysis. Journal of Applied Ecology 42:630–637.

Harte, J., A. B. Smith, and D. Storch. 2009. Biodiversity scales from plots to biomes with a universal species-area curve. Ecology Letters 12:789–797.

Hawkins, B. A., J. A. Diniz-Filho, and A. E. Weis. 2005. The mid-domain effect and diversity gradients: is there anything to learn? The American Naturalist 166:E140–E143.

Hawkins, B. A., et al. 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84:3105–3117.

Heaney, L. R. 1984. Mammalian species richness on islands on the Sunda Shelf, Southeast Asia. Oecologia 61:11–17.

Heaney, L. R. 1986. Biogeography of mammals in SE Asia: estimates of rates of colonization, extinction and speciation. Biological Journal of the Linnean Society 28:127–165.

Heaney, L. R. 2001. Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. Global Ecology and Biogeography 10:15–39.

Herkt, K. M. B., A. K. Skidmore, and J. Fahr. 2017. Macroecological conclusions based on IUCN expert maps: a call for caution. Global Ecology and Biogeography. 26:930–941.

Hu, Y., et al. 2017. Elevational patterns of non-volant small mammal species richness in Gyirong Valley, Central Himalaya: evaluating multiple spatial and environmental drivers. Journal of Biogeography 44:2764–2777.

Jablonski, D., K. Roy, and J. W. Valentine. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. Science (New York, N.Y.) 314:102–106.

Janis, C. M., and J. Damuth. 1990. Mammals. Pp. 301–345 in Evolutionary trends (K. J. McNamara, ed.). Belhaven Press, London, United Kingdom.

Jenkins, C. N., S. L. Pimm, and L. N. Joppa. 2013. Global patterns of terrestrial vertebrate diversity and conservation. Proceedings of the National Academy of Science of the USA 110:E2602–2610.

Jones, K. E., et al. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90:2648–2648.

Kaschner, K., D. P. Tittensor, J. Ready, T. Gerrodettte, and B. Worm. 2011. Current and future patterns of global marine mammal biodiversity. PLoS One 6:e19653.

Kaufman, D. M. 1995. Diversity of New World mammals: universality of the latitudinal gradients of species and bauplans. Journal of Mammalogy 76:322–334.

Kaufman, D. M., and M. R. Willig. 1998. Latitudinal patterns of mammalian species richness in the New World: the effects of sampling method and faunal group. Journal of Biogeography 25:795–805.

Kelt, D. A. 2001. Differential effects of habitat fragmentation on birds and mammals in Valdivian temperate forests. Revista Chilena de Historia Natural 74:769–777.

Kerr, J. T., and M. Ostrovsky. 2003. From space to species: ecological applications for remote sensing. Trends in Ecology and Evolution 18:299–305.

Kohn, M. J., and T. J. Fremd. 2008. Miocene tectonics and climate forcing of biodiversity, western United States. Geology 36:783–786.

Körner, C. 2007. The use of 'altitude' in ecological research. Trends in Ecology and Evolution 212:569–574.

Lacey, E. A., et al. 2017. Climate change, collections and the classroom: using big data to tackle big problems. Evolution Education and Outreach 10:2.

Laliberte, A. S., and W. J. Ripple. 2004. Range contractions of North American carnivores and ungulates. BioScience 54:123–138.

Laurance, W. F. 2008. Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. Biological Conservation 141:1731–1744.

Lawing, A. M., and N. J. Matzke. 2014. Conservation paleobiology needs phylogenetic methods. Ecography 37:1109–1122.

Lawlor, T. E. 1983. The mammals. Pp. 265–289 in Island biogeography in the Sea of Cortez (T. J. Case, M. L. Cody, and E. Ezcurra, eds.), University of California Press, Berkeley.

Legendre, P., and L. Legendre. 1998. Numerical ecology. 2nd ed. Elsevier Press, Boston, Massachusetts.

Li, Y-M., L. Xu, Y. Ma, J.-Y. Yang, and Y.-H. Yang. 2003. The species richness of nonvolant mammals in Shennongjia Nature Reserve, Hubei Province, China: distribution patterns along elevational gradient. Biodiversity Science 11:1–9.

Lomolino, M. V. 1982. Species-area and species-distance relationships of terrestrial mammals in the thousand island region. Oecologia 54:72–75.

Lomolino, M. V. 1990. The target area hypothesis: the influence of island area on immigration rates of non-volant mammals. Oikos 57:297–300.

Lomolino, M. V., J. H. Brown, and R. Davis. 1989. Island biogeography of montane forest mammals in the American southwest. Ecology 70:180–194.

Lomolino, M. V., and D. R. Perault. 2001. Island biogeography and landscape ecology of mammals inhabiting fragmented, temperate rain forests. Global Ecology and Biogeography 10:113–132.

Lyons, S. K. 2003. A quantitative assessment of the range shifts of Pleistocene mammals. Journal of Mammalogy 84:385–402.

Lyons, S. K., and M. R. Willig. 1999. A hemispheric assessment of scale dependence in latitudinal gradients of species richness. Ecology 80:2483–2491.

Lyons, S. K., and M. R. Willig. 2002. Species richness, latitude and scale-sensitivity. Ecology 83:47–58.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Monographs on population biology, no. 1. Princeton University Press, Princeton, New Jersey.

Maestri, R., and B. D. Patterson. 2016. Patterns of species richness and turnover for the South American rodent fauna. PLoS ONE 11:e0151895.

Mannion, P. D., R. B. J. Benson, P. Upchurch, R. J. Butler, M. T. Carrano, and P. M. Barrett. 2012. A temperate palaeodiversity peak in Mesozoic dinosaurs and evidence for late Cretaceous geographical partitioning. Global Ecology and Biogeography 21:898–908.

Mannion, P. D., P. Upchurch, R. B. Benson, and A. Goswami. 2014. The latitudinal biodiversity gradient through deep time. Trends in Ecology & Evolution 29:42–50.

Marcot, J. D., D. L. Fox, and S. R. Niebuhr. 2016. Late Cenozoic onset of the latitudinal diversity gradient of North American mammals. Proceedings of the National Academy of Sciences of the USA 113:7189–7194.

Mares, M. A., and R. A. Ojeda. 1982. Patterns of diversity and adaptation in South American hystricognath rodents. Pp. 393–432 in Latin American mammalogy: history, biodiversity, and conservation (M. A. Mares and D. J. Schimdly, eds.). University of Oklahoma Press, Norman.

Marshall, C. R. 2017. Five palaeobiological laws needed to understand the evolution of the living biota. Nature Ecology & Evolution 1:165.

Mazel, F., et al. 2014. Multifaceted diversity-area relationships reveal global hotspots of mammalian species, trait and lineage diversity. Global Ecology and Biogeography 23:836–847.

Mazel, F., J. Renaud, F. Guilhaumon, D. Mouillot, D. Gravel, and W. Thuiller. 2015. Mammalian phylogenetic diversity-area relationships at a continental scale. Ecology 96:2814–2822.

McCain, C. M. 2004. The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. Journal of Biogeography 31:19–31.

McCain, C. M. 2005. Elevational gradients in diversity of small mammals. Ecology 86:366–372.

McCain, C. M. 2007. Area and mammalian elevational diversity. Ecology 88:76–86.

McCoy, E. D., and E. F. Connor. 1980. Latitudinal gradients in the species diversity of North American mammals. Evolution 34:193–203.

McGuire, J. L., and E. B. Davis. 2014. Conservation paleobiogeography: the past, present and future of species distributions. Ecography 37:1092–1094.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation 127:247–260.

Md. Nor, S. 2001. Elevational patterns of diversity on Mount Kinabalu, Sabah, Malaysia. Global Ecology and Biogeography 10:41–62.

Meredith, R. W., et al. 2011. Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. Science 334:521–524.

Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science 322:261–264.

Muylaert, R. L., R. D. Stevens, and M. C. Ribeiro. 2016. Threshold effect of habitat loss on bat richness in cerrado-forest landscapes. Ecological Applications 26:1854–1867.

Newmark, W. D. 1986. Species-area relationships and its determinants for mammals in western North American national parks. Biological Journal of the Linnean Society 28:83–98.

Novilla, A., and R. A. Ojeda. 2014. Elevation patterns in rodent diversity in the dry Andes: disentangling the role of environmental factors. Journal of Mammalogy 95:99–107.

O'Brien, E. 1998. Winter-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. Journal of Biogeography 25:379–398.

Ojeda, R. A., A. Novillo, and A. A. Ojeda. 2015. Large-scale richness patterns, biogeography and ecological diversification in caviomorph rodents. Pp. 121–138 in Biology of caviomorph rodents (A. Vasallo and D. Antenucci, eds.). Sociedad Argentina para el Estudio de los Mamíferos, Mendoza, Argentina.

Pacifica, M., et al. 2013. Generation length for mammals. Nature Conservation 5:89–94.

Pagel, M. D., R. M. May, and A. R. Collie. 1991. Ecological aspects of the geographical distribution and diversity of mammalian species. American Naturalist 137:791–815.

Patterson, B. D., and W. Atmar. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. Biological Journal of the Linnean Society 28:65–82.

Patterson, B. D., D. F. Stotz, S. Solari, J. W. Fitzpatrick, and V. Pacheco. 1998. Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. Journal of Biogeography 25:593–607.

Peredo, C. M., and M. D. Uhen. 2018. Exploration of marine mammal paleogeography in the Northern Hemisphere over the Cenozoic using beta diversity. Palaeogeography, Palaeoclimatology, Palaeoecology 449:227–235.

Peters, M. K., et al. 2016. Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. Nature Communications 7:13736.

Peterson, A. T., et al. 2011. Ecological niches and geographic distribution. Princeton Monographs in Population Biology 49:1–314.

Platt, J. R. 1964. Strong inference. Science 146:347–353.

Presley, S. J., and M. R. Willig. 2010. Bat metacommunity structure on Caribbean islands and the role of endemics. Global Ecology and Biogeography 19:185–199.

Preston, F. W. 1962. The canonical distribution of commonness and rarity. Ecology 43:185–215.

Proches, S. 2001. Back to the sea: secondary marine organisms from a biogeographical perspective. Biological Journal of the Linnean Society 74:197–203.

Prugh, L. R., K. E. Hodges, A. R. E. Sinclair, and J. S. Brashares. 2008. Effect of habitat are and isolation on fragmented animal populations. Proceedings of the National Academy of Sciences of the USA 105:20770–20775.

Pyenson, N. D., and G. J. Vermeij. 2016. The rise of ocean giants: maximum body size in Cenozoic marine mammals as an indicator for productivity in the Pacific and Atlantic Oceans. Biology Letters 12:20160186.

Rahbek, C. 1995. The elevational gradient of species richness: uniform pattern? Ecography 18:200–205.

Rangel, T. F., J. A. Diniz-Filho, and R. K. Colwell. 2007. Species richness and evolutionary niche dynamics: a spatial pattern-oriented simulation experiment. The American Naturalist 170:602–616.

Rebelo, H., P. Tarroso, and G. Jones. 2009. Predicted impact of climate change on European bats in relation to their biogeographic patterns. Global Change Biology 16:561–576.

Rickart, E. A., L. R. Heaney, and R. C. B. Utzurrum. 1991. Distribution and ecology of small mammals along an elevational transect in southeastern Luzon, Philippines. Journal of Mammalogy 72:458–469.

Ricklefs, R. E., and I. J. Lovette. 1999. The role of island area per se and habitat diversity in the species area relationships of four Lesser Antillean faunal groups. Journal of Animal Ecology 68:1142–1160.

Rondinini, C., et al. 2011. Global habitat suitability models of terrestrial mammals. Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences 366:2633–2641.

Rose, P. J., D. L. Fox, J. Marcot, and C. Badgley. 2011. Flat latitudinal gradient in Paleocene mammal richness suggests decoupling of climate and biodiversity. Geology 39:163–166.

Rosenblatt, D. L., E. J. Heske, S. L. Nelson, D. M. Barber, M. A. Miller, and B. MacAllister. 1999. Forest fragments in east-central Illinois: islands or habitat patches for mammals? American Midland Naturalist 141:115–123.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, New York.

Rowan, J., J. M. Kamilar, L. Beaudrot, and K. E. Reed. 2016. Strong influence of palaeoclimate on the structure of modern African mammal communities. Proceedings of the Royal Society B 283:20161207.

Rowe, R. J. 2005. Elevational gradient analysis and the use of historical museum specimens: a cautionary tale. Journal of Biogeography 32:1883–1897.

Rowe, R. J. 2009. Environmental and geometric drivers of small mammal diversity along elevational gradients in Utah. Ecography 32:411–422.

Rowe, R. J., L. R. Heaney, and E. A. Rickart. 2015. Scale effects on the pattern and predictors of small mammal diversity along a local elevational gradient in the Great Basin. Journal of Biogeography 42:1964–1974.

Rowe, R. J., and S. Lidgard. 2009. Elevational gradients and species richness: do methods change pattern perception? Global Ecology and Biogeography 18:163–177.

Sanders, N. J., and C. Rahbek. 2011. The patterns and causes of elevational diversity gradients. Ecography 35:1–3.

Santos-Filho, M., C. A. Peres, D. J. Silva, and T. M. Sanaiotti. 2012. Habitat patch and matrix effects on small-mammal persistence in Amazonian forest fragments. Biodiversity and Conservation 21:1127–1147.

Scheel, D., T. L. S. Vincent, and G. N. Cameron. 1996. Global warming and the species richness of bats in Texas. Conservation Biology 10:452–464.

Schipper, J., et al. 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. Science 322: 225–230.

Shepherd, U. L., and D. A. Kelt. 1999. Mammalian species richness and morphological complexity along an elevational gradient in the arid south-west. Journal of Biogeography 26:843–855.

Sherwin, H. A., W. I. Montgomery, and M. G. Lundy. 2012. The impacts and implications of climate change for bats. Mammal Review 43:171–182.

Silvestro, D., J. Schnitzler, L. H. Liow, A. Antonelli, and N. Salamin. 2014. Bayesian estimation of speciation and extinction from incomplete fossil occurrence data. Systematic Biology 63:349–367.

Simberloff, D. S. 1976. Experimental zoogeography of islands: effects of island size. Ecology 57:629–648.

Simpson, G. G. 1964. Species density of North American recent mammals. Systematic Zoology 13:57–73.

Slater, G. J., J. A. Goldbogen, and N. D. Pyenson. 2017. Independent evolution of baleen whale gigantism linked to Plio-Pleistocene ocean dynamics. Proceedings of the Royal Society B 284:20170546.

Smith, F. A., et al. 2003. Body mass of late Quaternary mammals. Ecology 84:3403–3403.

Southwood, T. R. E. 1996. Natural communities: structure and dynamics. Philosophical Transactions: Biological Sciences 351:1113–1129.

Stephens, P. R., and J. J. Wiens. 2003. Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. The American Naturalist 161:112–128.

Stevens, R. D. 2004. Untangling latitudinal richness patterns at higher taxonomic levels: familial perspectives on the diversity of New World bat communities. Journal of Biogeography 31:665–674.

Stevens, R. D. 2006. Historical processes enhance patterns of diversity along latitudinal gradients. Proceedings of the Royal Society of London B 273:2283–2289.

Stevens, R. D. 2011. Relative effects of time for speciation and tropical niche conservatism on the latitudinal diversity gradient of phyllostomid bats. Proceedings of the Royal Society B 278:2528–2536.

Stevens, R. D. 2013. Gradients of bat diversity in Atlantic Forest of South America: environmental seasonality, sampling effort and spatial autocorrelation. Biotropica 45:764–770.

Stevens, R. D., S. B. Cox, R. E. Strauss, and M. R. Willig. 2003. Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal trends. Ecology Letters 6:1099–1108.

Stevens, R. D., and M. M. Gavilanez. 2015. Dimensionality of community structure: phylogenetic, morphological and functional perspectives along biodiversity and environmental gradients. Ecography 38:861–875.

Stevens, R. D., J. S. Tello, and M. M. Gavilanez. 2013. Stronger tests of mechanisms underlying geographic gradients of biodiversity: insights from the dimensionality of biodiversity. PLoS ONE 8:e56853.

Stevens R. D., and M. R. Willig. 2002. Geographical ecology at the community level: perspectives on the diversity of New World bats. Ecology 83:545–560.

Swihart, R. K., T. M. Gehring, M. B. Kolozsvary, and T. E. Nupp. 2003. Responses of 'resistant' vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. Diversity and Distributions 9:1–18.

Szewczyk, T., and C. M. McCain. 2016. A systematic review of global drivers of ant elevational diversity. PLoS ONE 11:e0155404.

Tello, J. S., and R. D. Stevens. 2010. Multiple environmental determinants of regional species richness and effects of geographic range size. Ecography 33:796–808.

Terry, R. C., C. Li, and E. A. Hadly. 2011. Predicting small-mammal responses to climatic warming: autecology, geographic range, and the Holocene fossil record. Global Change Biology 17:3019–3034.

Terry, R. C., and R. J. Rowe. 2015. Energy flow and functional compensation in Great Basin small mammals under natural and anthropogenic environmental change. Proceedings of the National Academy of Sciences of the USA 112:9656–9661.

Thomas, C. D., et al. 2004. Extinction risk from climate change. Nature 427:145–148.

Uhen, M. D. 2010. The origin(s) of whales. Annual Review of Earth and Planetary Sciences 38:189–219.

Vierling, K. T., L. A. Vierling, W. A. Gould, S. Martinuzzi, and R. M. Clawges. 2008. Lidar: shedding new light on habitat characterization and modeling. Frontiers in Ecology and the Environment 6:90–98.

Villalobos, F., and H. T. ARita. 2010. The diversity field or New World leaf-nosed bats (Phyllostomidae). Global Ecology and Biogeography 19:200–211.

Villalobos, F., T. F. Rangel, and J. A. F. Diniz-Filho. 2013. Phylogenetic fields of species: cross-species patterns of phylogenetic structure and geographical coexistence. Proceedings of the Royal Society B 280:20122570.

Weber, M. M., R. D. Stevens, J. A. F. Diniz-Filho, and C. E. V. Grelle. 2017. Is there correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. Ecography. 40:817–828.

White, E. A., et al. 2006. A comparison of species-time relationships across ecosystems and taxonomic groups. Oikos 112:185–195.

Wiens, J. J. 2004. Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. Evolution 58:193–197.

Wiens, J. J., and M. J. Donoghue. 2004. Historical biogeography, ecology and species richness. Trends in Ecology & Evolution 19:639–644.

Wiens, J. J., et al. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters 13:1310–1324.

Williams, C. B. 1964. Patterns in the balance of nature. Academic Press, London, United Kingdom.

Williams, J. W., S. T. Jackson, and J. E. Kutzbach. 2007. Projected distributions of novel and disappearing climates by 2100 AD. Proceedings of the National Academy of Sciences of the USA 104:5738–5742.

Williams, S. E., H. Marsh, and J. Winter. 2002. Spatial scale, species diversity, and habitat structure: small mammals in Australian tropical rain forest. Ecology 83:1317–1329.

Williams, J. W., B. N. Shuman, T. Webb III, P. J. Bartlein, and P. L. Leduc. 2004. Late-Quaternary vegetation dynamics in North America: scaling from taxa to biomes. Ecological Monographs 74:309–334.

Willig, M. R., and C. P. Bloch. 2006. Latitudinal gradients of species richness: a test of the geographic areas hypothesis at two ecological scales. Oikos 112:163–173.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. Annual Review of Ecology, Evolution and Systematics 34:273–309.

Willig, M. R., and S. K. Lyons. 1998. An analytical model of latitudinal gradients of species richness with an empirical test for marsupials and bats in the New World. Oikos 81:93–98.

Willig, M. R., and S. J. Presley. 2016. Biodiversity and metacommunity structure of animals along an altitudinal gradient in tropical montane forest. Journal of Tropical Ecology 32:421–436.

Willig, M. R., S. J. Presley, C. P. Bloch, and H. Genoways. 2009. Macroecology of Caribbean bats: effects of area, elevation, latitude and hurricane induced disturbance. Pp. 216–264 in Island bats: evolution, ecology and conservation (T. H. Fleming and P. A. Racey, eds.). University of Chicago Press, Chicago, Illinois.

Willig, M, R., and E. A. Sandlin. 1991. Gradients of species density and species turnover in New World bats: a comparison of quadrat and band methodologies. Pp. 81–96 in Latin American mammalogy: history, biodiversity, and conservation (M. A. Mares and D. J. Schimdly, eds.) University of Oklahoma Press, Norman.

Willig, M. R., and K. W. Selcer. 1989. Bat species density gradients in the New World: a statistical assessment. Journal of Biogeography 16:189–195.

Wilman, H., J. Belmaker, J. Simpson, C. de la Rosa, M. M. Rivadeneira, and W. Jetz. 2014. EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. Ecology 95:2027–2027.

Wilson, J. W., 3rd. 1974. Analytical zoogeography of North American mammals. Evolution; International Journal of Organic Evolution 28:124–140.

Wu, Y., Q. Yang, Z. Wen, L. Xia, Q. Zhang, and H. Zhou. 2013. What drives the species richness patterns of non-volant small mammals along a subtropical elevational gradient? Ecography 36: 185–196.

Xu, H., et al. 2015. Determinants of mammal and bird species richness in China based on habitat groups. PLoS ONE 10:e0143996.

Zapata, F. A., K. J. Gaston, and S. L. Chown. 2003. Mid-domain models of species richness gradients: assumptions, methods and evidence. Journal of Animal Ecology 72:677–690.

Submitted 3 January 2018. Accepted 21 March 2019.

Special Issue Editor was Michael R. Willig.