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AREA AND MAMMALIAN ELEVATIONAL DIVERSITY

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Abstract. Elevational gradients hold enormous potential for understanding general properties of biodiversity. Like latitudinal gradients, the hypotheses for diversity patterns can be grouped into historical explanations, climatic drivers, and spatial hypotheses. The spatial hypotheses include the species–area effect and spatial constraint (mid-domain effect null models). I test these two spatial hypotheses using regional diversity patterns for mammals (non-volant small mammals and bats) along 34 elevational gradients spanning 24.4° S–40.4° N latitude. There was high variability in the fit to the species–area hypothesis and the mid-domain effect. Both hypotheses can be eliminated as primary drivers of elevational diversity. Area and spatial constraint both represent sources of error rather than mechanisms underlying these mammalian diversity patterns. Similar results are expected for other vertebrate taxa, plants, and invertebrates since they show comparable distributions of elevational diversity patterns to mammalian patterns.

Key words: altitude; area; diversity gradient; mammals; mid-domain effect; space; species–area relationships; species richness.

INTRODUCTION

More than 30 hypotheses exist in the literature to explain gradients in species richness (e.g., Pianka 1966, Rohde 1992, Heaney 2001, Rahbek and Graves 2001). These can be grouped into three categories: historical hypotheses invoking processes occurring across evolutionary time scales, climatic hypotheses based on current abiotic conditions, and spatial hypotheses of area and spatial constraint. Most examinations of these hypotheses were conducted along the latitudinal diversity gradient, but because historical, climatic, and spatial factors are correlated and confounded latitudinally, it is difficult to distinguish the influence of each. The existence of only two independent latitudinal gradients worldwide further inhibits our ability to discriminate between hypotheses.

In contrast, there are thousands of independent elevational gradients that occur across mountain ranges at smaller spatial scales allowing for field studies and replication. Additionally, because elevational diversity patterns occur on a mountain within a single region, this eliminates the confounding processes of latitudinal trends in speciation rates, extinction rates, and clade age. Elevational gradients have predictable changes in abiotic factors altitudinally on a single mountain, but also have predictable variability between wet and dry slopes and among mountains occurring in various biomes (e.g., tropical, temperate, desert mountains). These characteristics allow globally distributed elevational gradients to be used as natural experiments, thus making them invaluable for discerning between diversity hypotheses.

In this paper I examine the two spatial hypotheses to which elevational diversity may be responding, (1) area and (2) spatial constraint (i.e., mid-domain effect), and their combined effect. I focus on elevational gradients for mammals, including non-volant small mammals (NVSM) and bats, which are the two most diverse groups of mammals and have well-known taxonomy at a global level. Additionally, elevational diversity has been well-documented along multiple mountains across the world ranging from 24.4° S to 40.4° N latitude (McCain 2005, 2006*b*), and the distribution of elevational diversity patterns (mid-elevation peaks, decreasing diversity, low-elevation plateaus) mirrors that estimated for all taxonomic groups including vertebrates, invertebrates, and plants (Rahbek 1995, 2005).

The area hypothesis proposes that regions with the largest area will have more species (Terborgh 1973, Rosenzweig 1992, 1995). At the regional and global scales, Rosenzweig (1992, 1995) argued that extinction rates should decrease and speciation rates should increase with area due to the increased likelihood of barrier formation and increased population densities. At small spatial scales, Rosenzweig (1995) argued that habitat diversity and the strong ties of particular species to habitat drive the local species–area relationship. Area–diversity patterns on mountains may fall somewhere on the continuum between these two scales and processes. The tests of the area hypothesis on elevational gradients will determine whether the amount of area for each elevational band on a mountain (e.g., 0–100 m, 100–200 m, etc.) will be positively related to diversity in that band.

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The heated debate and most tests of the area hypothesis have been along the latitudinal gradient (e.g., Rosenzweig 1992, 1995, Blackburn and Gaston 1997, Rohde 1997, 1998, Rosenzweig and Sandlin 1997, Lyons and Willig 1999, Ruggiero 1999, Hawkins and Porter 2001, Romdal et al. 2004, Willig and Bloch 2006). The recent tests for birds (Hawkins and Porter 2001) and bats (Willig and Bloch 2006) have both questioned the viability of the area hypothesis at the latitudinal scale. The area hypothesis has received less scrutiny along elevational gradients, although a few studies have attempted to assess area's influence on diversity (Rahbek 1997, Odland and Birks 1999, Sanders 2002, Vetaas and Grytnes 2002, Jones et al. 2003, Sanders et al. 2003, Bachman et al. 2004, Bhattarai et al. 2004, Fu et al. 2004, Kattan and Franco 2004, Oommen and Shanker 2005). Based on these studies there is no general consensus on how area varies with elevation or how strongly elevational diversity is related to trends in area.

Spatial constraints on species' ranges have been proposed to account for peaks in diversity at the middle of geographic regions in the absence of clines in climate or history, and this null model has been termed the mid-domain effect (MDE; Colwell et al. 2004 and references therein). The basic premise of the mid-domain effect is that spatial boundaries (e.g., base and top of mountain) cause more overlap of species' ranges toward the center of an area where many large- to medium-sized ranges must overlap but are less likely to abut an edge of the area (Colwell et al. 2004 and references therein). This hypothesis also has generated considerable controversy and debate (e.g., Diniz-Filho et al. 2002, Laurie and Silander 2002, Colwell et al. 2004, 2005, Hawkins et al. 2005, Zapata et al. 2005), although some support for MDE has been found along elevational gradients (e.g., Fleishman et al. 1998, Kessler 2001, Grytnes and Vetaas 2002, Sanders 2002, McCain 2004, Cardelús et al. 2006) and latitudinal gradients (e.g., Jetz and Rahbek 2001, 2002, Connolly et al. 2003, McCain 2003).

The most comprehensive test of the spatial hypotheses—area and spatial constraint (MDE)—will come from comparative analyses among different types of mountains and montane regions across a broad scale of climates and latitudes. I use 34 elevational gradients in regional diversity of mammals (NVSM = 26; bats = 8) to quantitatively test the strength of each spatial hypothesis and their combined influence.

Methods

Diversity data

The 34 elevational diversity data sets for non-volant small mammals (rodents, insectivores, and marsupial mice) and bats were taken from my studies in Costa Rica (McCain 2004, 2006*a*) or reanalyzed from the literature (Grinnell and Storer 1924, Linzey 1995, McCain 2005, 2006*b*). Of these, 27 have mid-elevation diversity peaks, five decrease in diversity with increasing elevation, and two have high diversity across the lower elevations and then decrease at the highest elevations (low plateaus) in diversity. This distribution of diversity patterns mirrors that estimated for all taxonomic groups: 65% mid-elevation peaks, 20% decreasing, and 7% low-elevation plateaus (Rahbek 2005). Details of each mammalian data set, including location, diversity, and area analyses, are listed in Appendix A. Data sets were included only if sampling covered most ($\geq$70%) of the elevational gradient and if sampling did not exhibit substantial elevational biases. The diversity pattern for each elevational gradient was examined in 100-m elevational bands.

There are two general sampling scales in studies of elevational diversity: local and regional analyses. Local studies detail alpha diversity from standardized samples taken along field transects of a single elevational gradient; regional data sets assess gamma diversity compiled from trapping records, specimen records, and field notes for an entire mountain or mountainous region. Because of the large spatial scale of regional diversity data these elevational gradients may be highly influenced by area (Rahbek 1997, Brown 2001, Lomolino 2001, Willig et al. 2003, McCain 2005), whereas area should have less influence on standardized sampling of local sites (Lomolino 2001, McCain 2005). Local diversity analyses could be influenced by higher immigration from a larger regional community (i.e., mass effect), but is thought to be less pervasive (Lomolino 2001). Additionally, McCain (2005) found that the potential influence of area was markedly lower in local elevational gradients than regional for NVSM, and Sanders et al. (2003) found that area was negatively correlated with alpha diversity along three elevational gradients. For these reasons, only regional data sets are considered.

Area data

Area measurements for each mountain were calculated from digital elevation models (DEMs) using ArcGIS version 9 (Environmental Systems Research Institute, Redlands, California, USA). All raw DEM data were downloaded from the U.S. Geological Survey web site for mountains of the United States using 100-m resolution in 1° DEMs (*available online*)[2] and for international mountain regions using 90-m resolution in 1° × 1° data (*available online*).[3] All GIS maps were then converted into equal area maps with Albers Equal Area Conic projections and classified into standardized 100-m elevational zones (i.e., 0–100 m, 101–200 m, etc). Each mountain region was delimitated by the scale and/or geopolitical boundaries used in the original study. The lower boundaries of stand-alone mountains were delineated by a 50-km radius from the mountain top, and those mountains surrounded by other mountains were delineated by the 50 km radius in the lowlands and

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[2] ⟨http://edc.usgs.gov/products/elevation/dem.html⟩

[3] ⟨http://edcftp.cr.usgs.gov/pub/data/srtm/⟩

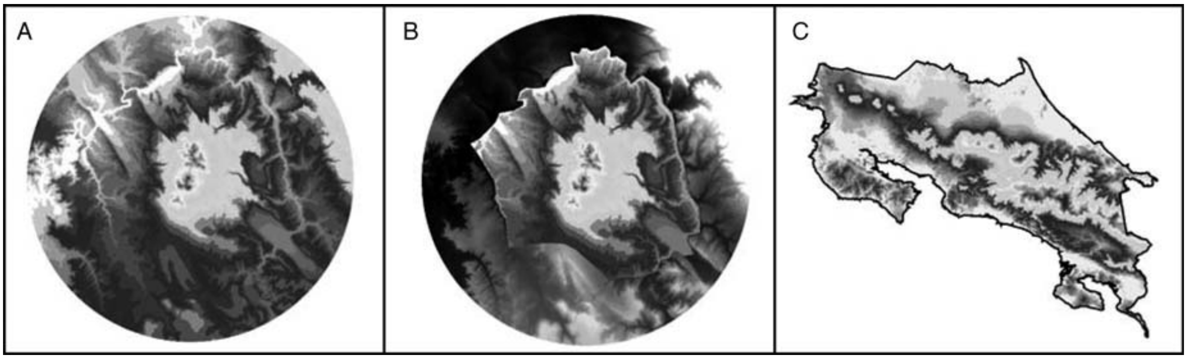

FIG. 1. Two examples of montane delineation using ArcGIS version 9 (Environmental Systems Research Institute, Redlands, California, USA). (A) The topography of La Sal Mountain, Utah, USA, delineated by a 50 km radius from the mountain peak. (B) La Sal Mountain is then separated from surrounding mountains through watersheds and montane saddles. (C) The political delineation of an elevational gradient for Costa Rica, Central America. See Appendix B for a color version of this figure.

through watersheds and saddles separating the different mountains (e.g., Fig. 1A, B; for a version in color, see Appendix B). Geopolitical boundaries are not ideal montane delimitations, although the influence is minimal in area estimation at this scale. Country area curves are dominated by the extensive low-elevation area (see Costa Rica, Fig. 1C, Appendix B), and the addition of excluded area in neighboring countries, also mostly low elevation, simply reinforces this pattern. (For elevational profiles see Supplement.) The area of each 100-m elevational band was then calculated using an area calculation utility written in Visual Basic for use in ArcGIS 9.

Tests of area and MDE hypotheses

The species–area relationship follows a curvilinear relationship in arithmetic space: diversity increases rapidly over small areas but once successively large areas are examined diversity plateaus (Arrhenius 1921, Preston 1962, Conner and McCoy 1979, McGuinness 1984, Williamson 1988, Rosenzweig 1995, Lomolino 2000). Due to this curvilinearity, log–log linear regressions are used to test for a significant relationship between area and diversity (e.g., Hawkins and Porter 2001, Sanders 2002, Jones et al. 2003, Willig and Bloch 2006). Conner and McCoy (1979) found that some species–area relationships were better characterized by linear or semi-logarithmic relationships, thus for all the current analyses linear, semi-logarithmic, and log–log-transformed regressions will be calculated to test the area hypothesis.

To test the spatial constraint hypothesis, species richness patterns were compared to mid-domain null model predictions with a Monte Carlo simulation procedure. This procedure simulates species richness curves using empirical range sizes within the bounded domain of mountain summit and lowest elevation for the mountain range (Colwell and Hurtt 1994, Colwell et al. 2004, McCain 2004, 2005, 2006*b*). Richness data were examined in 100-m increments. Regressions of the empirical values on predicted values, based on the mean of the 50 000 simulations, gave r^2 estimates of the fit to MDE.

Previous analyses suggested that MDE was modified by the species–area relationship (McCain 2005; R. K. Colwell, *personal communication*), meaning that error around MDE fits was caused by differences in area. To assess if fits to MDE are improved once the area effect is accounted for, I calculated area-corrected diversity patterns. Several procedures exist for producing area-corrected diversity curves on elevational gradients. Rahbek (1997) used a method based on the well-known power function model for species–area curves: $S = cA^z$ (Arrhenius 1921, Rosenzweig 1995 and references therein), which is inherently curvilinear. Here the z parameter needs to be estimated, which can prove difficult (see Appendix C). Vetaas and Grytnes (2002) simply divided species richness in each elevational band by log(area) of that elevational band, which assumes a semi-logarithmic area function. Bachman et al. (2004) used a GIS to delineate bands of elevation with equal area. In this case, the bands differ in elevational extent (in some cases <1 m) but are equal in area. Lastly, linear correction methods could be employed by adjusting the diversity of each elevational band by a correction factor equal to the difference in area (e.g., Fu et al. 2004).

I discuss and compare these correction methods in Appendix C including the curvilinear method ($S = cA^z$), the semi-logarithmic method, and a linear area correction method. I evaluated five z values for the curvilinear method: (1) mountain-specific z value, (2, 3, 4) taxon-specific z values (the mean and the lower and upper 95% confidence limits, respectively) and (5) the canonical value of Preston (0.25; Preston 1962). All methods show highly correlated area-corrected diversity curves. For simplicity, I contrast two methods: (1) the best-fit model for each data set (see Table 1; mountain z value used for power function best fits) and (2) the power function model that is most supported among the included data sets and generally in the literature. In this case, I use the most inclusive method for determining the z value with a taxon-specific, global z value. This procedure covers the widest available set of area values and includes hundreds of data points in the regressions (NVSM, 399; bats, 140). Such a composite z value also eliminates the influence of extreme values resulting in a more conservative estimate than other potential estimators (see Appendix C).

RESULTS

Area does not always decrease with increasing elevation. Of the 34 elevational profiles of area, 21 had monotonically decreasing area with a strongly recurved slope (Fig. 2A, B), five had a generally decreasing slope (Fig. 2C), and eight had a mid-elevational peak in area (Fig. 2D). Most of the mid-elevational area peaks occur in highly mountainous regions (western North America, western Mexico, and northwestern China) where the lowest elevations are within valleys or ravines thus covering less area. The two area profiles on the eastern slope of Peru (southeast Peru and the Manu National Park region) had the strongly recurved, decreasing slope with a small secondary peak in area coinciding with the high-elevation plateau of the Andes in this region (Fig. 2A).

Significant log–log species–area effects were detected in 59% of the elevational gradients (Table 1; e.g., Fig. 3). Similarly, 59% had significant relationships in species richness and log(area), although including some different data sets than the log–log relationships (Table 1). Only 32% showed a significant species–area relationship in non-log-transformed linear regressions. Besides the two Peruvian bat gradients, the curvilinear and semi-logarithmic species–area regressions had higher r^2 values than the linear regressions. In comparing the curvilinear (log–log) and with the semi-logarithmic method (log(area)), 13 curvilinear had higher r^2 values and 10 semi-logarithmic had higher r^2 values. On average, area r^2 values were low for all area relationships: curvilinear (NVSM, $r^2 = 0.33$; bats, $r^2 = 0.33$), linear (NVSM, $r^2 = 0.09$; bats, $r^2 = 0.24$), and semi-logarithmic (NVSM, $r^2 = 0.31$; bats, $r^2 = 0.41$). Of the 11 data sets with no significant, positive relationship between diversity and area, most (10) actually had diversity negatively related to area (Table 1; e.g., Fig. 3B).

The fit to spatial constraints (mid-domain null model = MDE) was highly variable (Table 1). Non-volant small mammals' fits ranged from nearly zero to 78%; on average the fits were low ($r^2 = 0.31 \pm 0.052$, mean ± SE). The bats either had fits near zero or ~45%; again on average fits were low ($r^2 = 0.11 \pm 0.075$). Fig. 2 shows examples of how MDE predictions relate to empirical diversity patterns. To eliminate the possibility that deviations in MDE fits are due to area (see McCain 2005), I calculated area-corrected diversity curves using curvilinear (power model with various ways of estimating the z), semi-logarithmic, and linear methods for those gradients with significant species–area effects (Appendix C). There was little difference in the area-corrected diversity curves among the various correction methods (Fig. 4; Appendix D), resulting in highly correlated diversity curves (Appendix E; mean r = 0.836–0.994). For simplicity, I contrast (1) the best fit correction and (2) the power model corrections ($S = cA^z$) with the z calculated from a global, taxon-specific species–area relationship. The taxon-specific z value for NVSM was 0.22 with 95% confidence limits of 0.19–

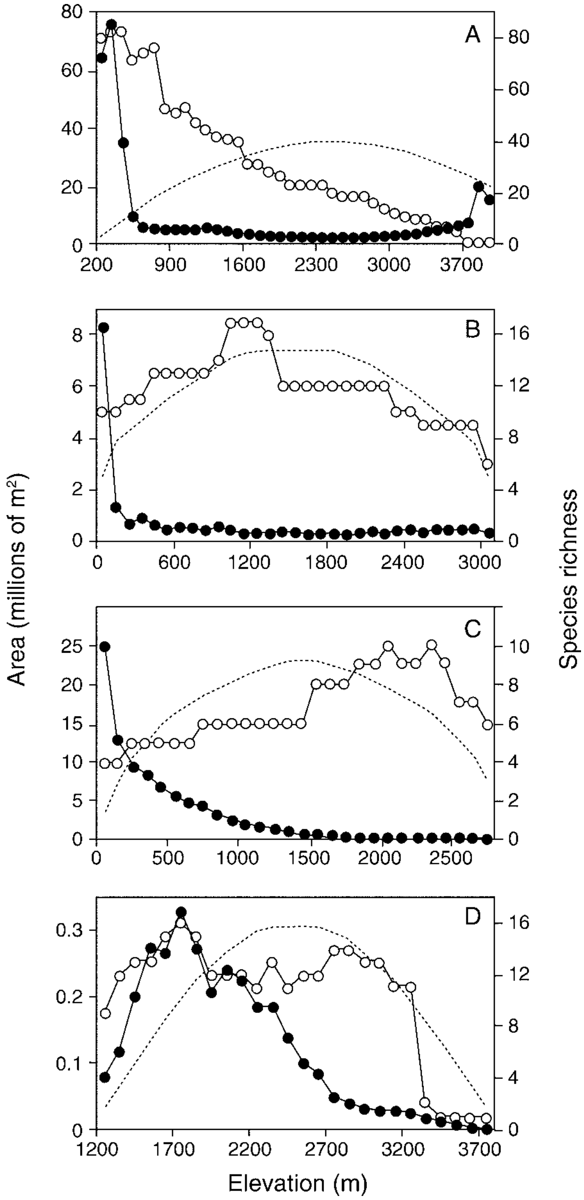

FIG. 2. Examples of area (solid circles), mid-domain effect (MDE, dotted lines), and diversity (open circles) along four elevational gradients: (A) bats of southeastern Peru; (B) bats of Yosemite National Park, California, USA; (C) non-volant small mammals of Mindanao, Philippines; (D) non-volant small mammals of La Sal Mountain, Utah, USA. Both (A) and (B) show the strongly recurved, decreasing area pattern; (C) shows the generally decreasing area pattern, and (D) shows the mid-elevation area peak.

Table 1. Linear regressions statistics for all elevational diversity data sets to detect species–area relationships and spatial constraint effects (mid-domain effect, MDE).

Geographic region	Linear area effect		Curvilinear area effect	
	r^2	P	r^2	P
Non-volant small-mammal transects				
Madagascar	0.047	0.298	**0.240**	**0.013**
New Guinea	0.028	0.269	**0.804**	**<0.001**
Rwenzori Mountains, Uganda	0.108	0.076	**0.513**	**<0.001**
Mt. Kinabalu, Sabah, Borneo	**0.151**	**0.018**	**0.603**	**<0.001**
Mindanao, Philippines	<0.001	0.001	<0.001	<0.001
Costa Rica	0.079	0.088	**0.832**	**<0.001**
Tiliran Mountains (eastern slope), Costa Rica	<0.001	0.045	<0.001	0.431
Oaxaca, Mexico	<0.001	0.039	<0.001	0.684
Ba Vi Highlands, Vietnam	<0.001	0.137	<0.001	0.046
Taiwan	<0.001	0.018	<0.001	0.196
Central Nepal	<0.001	0.465	<0.001	0.102
Great Smokies, Tennessee and North Carolina, USA	0.001	0.880	**0.251**	**0.029**
Abajo Mountains, Utah, USA‡	0.075	0.271	**0.420**	**0.004**
Yosemite (western slope), California, USA	<0.001	0.524	**0.592**	**<0.001**
Mt. Qilian Region, China	<0.001	0.604	<0.001	0.252
Aquarius Mountains, Utah, USA	<0.001	0.183	<0.001	0.461
Henry Mountains, Utah, USA‡	**0.248**	**0.042**	**0.538**	**0.001**
Tushar Mountains, Utah, USA	0.020	0.585	**0.337**	**0.015**
LaSal Mountains, Utah and Colorado, USA	**0.395**	**0.001**	**0.677**	**<0.001**
Pavant Mountains, Utah, USA	0.031	0.548	**0.297**	**0.002**
Wasatch Plateau, Utah, USA	0.041	0.408	**0.630**	**<0.001**
Deep Creek Mountains, Nevada and Utah, USA	0.001	0.943	0.132	0.127
Oquirrh Mountains, Utah, USA	<0.001	0.093	<0.001	0.421
Ruby Mountains, Nevada, USA†	**0.320**	**0.035**	**0.480**	**0.006**
Wasatch Range, Utah, USA	0.001	0.968	**0.358**	**0.007**
Uinta Mountains, Utah, USA	**0.670**	**<0.001**	**0.798**	**<0.001**
Bat transects				
Southeast Peru (eastern slope)†	**0.280**	**0.001**	0.004	0.704
Manu National Park Region, Peru†	**0.189**	**0.007**	0.001	0.910
New Guinea†	**0.250**	**0.001**	**0.667**	**<0.001**
Ecuador (eastern slope)	0.040	0.349	0.027	0.443
Venezuela†	**0.531**	**<0.001**	**0.812**	**<0.001**
Sierra de Manantlan, Jalisco, Mexico	**0.214**	**0.030**	**0.383**	**0.002**
White-Inyo Mountains, California and Nevada, USA	**0.430**	**<0.001**	**0.708**	**<0.001**
Yosemite (western slope), California, USA	<0.001	0.394	<0.001	0.029

Notes: Species area was examined with non-log-transformed area and diversity (linear species–area effect), log-transformed variables (curvilinear species–area effect), and log-transformed area (semi-logarithmic species–area effect). Significant area effects are shown in boldface type. Mid-domain effect (MDE) was examined alone and with the area effect removed for taxon z value (Area MDE$^{\text{t}}$) and best-fit z value (Area MDE$^{\text{b}}$). All negative linear relationships have $r^2 < 0.001$. Mountains are ordered by latitude from south to north.

† Decreasing diversity.

‡ Low-elevation plateau.

0.25 (Fig. 5A; log(species) = −0.7152 + (0.2223) log(area)) and 0.38 for bats with 95% confidence limits of 0.32–0.44 (Fig. 5B; log(species) = −2.3803 + (0.3767) log(area)).

The regressions of area-corrected diversity curves with MDE predictions resulted in increased fits for 39% (best fit) and 48% (taxon z) of the data sets with a mean increase in r^2 value of 0.18 for both methods (Table 1). In contrast, 35% and 26% decreased their fit to MDE by an average of 0.15 and 0.19 for best-fit model and taxon z, respectively. Finally, 26% had r^2 values that did not change for both methods. Thus, accounting for the area effect in regional data sets did little to improve the overall fit to spatial constraints for either NVSM (best fit, mean $r^2 = 0.33$; taxon z, mean $r^2 = 0.34$) or bats (best fit, mean $r^2 = 0.09$; taxon z, mean $r^2 = 0.12$). These results were consistent across all area corrections methods and z values (Appendix C).

After correcting for area effects, all diversity curves showed mid-elevational peaks in diversity regardless of whether the empirical diversity pattern was mid-elevational, decreasing, or low-elevation plateau (Appendix D). Most ($n = 13$) diversity patterns had their diversity peak shift to higher elevations to some degree (mean shift, NVSM, ~670 m; bats, ~500 m; Fig. 4C, G), while eight gradients showed little to no change in the peak location but in some cases a secondary peak became prominent (Fig. 4A, E).

Discussion

The earliest biologists, Darwin, Wallace, and von Humboldt, determined that diversity varies spatially.

TABLE 1. Extended.

Semi-log area effect		MDE,	Area	Area
r^2	P	r^2	MDE^t, r^2	MDE^b, r^2
0.149	0.057	0.721	0.631	0.784
0.676	<**0.001**	0.261	0.613	0.898
0.434	**0.001**	<0.001	<0.001	<0.001
0.690	<**0.001**	<0.001	0.202	0.002
<0.001	<0.001	0.170		
0.787	<**0.001**	0.117	0.480	0.499
<0.001	0.585	0.475		
<0.001	0.740	0.430		
<0.001	0.095	0.727		
<0.001	0.442	0.312		
<0.001	0.034	0.444		
0.277	**0.021**	0.554	<0.001	0.308
0.338	**0.011**	0.317	0.121	0.268
0.431	<**0.001**	0.586	0.568	0.582
<0.001	0.144	0.002		
<0.001	0.680	0.782		
0.560	**0.001**	0.026	0.237	0.001
0.211	0.063	0.326	0.426	0.357
0.659	<**0.001**	0.313	0.327	0.119
0.193	0.116	0.451	0.560	0.476
0.403	**0.003**	0.733	0.491	0.245
0.250	**0.029**	0.012	0.114	0.025
<0.001	0.581	0.200		
0.733	**0.001**	0.001	0.176	0.014
0.330	**0.010**	0.055	0.372	0.505
0.888	<**0.001**	0.017	<0.001	<0.001
0.265	**0.001**	<0.001	<0.001	<0.001
0.242	**0.002**	<0.001	0.001	<0.001
0.851	<**0.001**	<0.001	<0.001	<0.001
0.050	0.295	<0.001		
0.968	<**0.001**	<0.001	<0.001	<0.001
0.273	**0.013**	<0.001	<0.001	<0.001
0.641	<**0.001**	0.435	0.447	0.220
<0.001	0.230	0.483		

However, uncovering the mechanisms that shape diversity gradients in space and time has proven elusive because multiple factors act together to affect diversity. Of the three groups of proposed drivers (historical, climatic, and spatial), I found that spatial factors (area and spatial constraint) influence elevational diversity but clearly they cannot be the main drivers of elevational richness.

Area

Area influences montane diversity patterns but to various degrees. Thirty-two percent of the elevational gradients in NVSM and bats showed either no significant relationship or a negative association between diversity and area (Table 1; Fig. 3). Of those that had a significant relationship with area, the area relationship explained about half of the variability in diversity. For gradients with significant area effects, when the area effects were removed, 10 diversity curves changed only slightly with almost no shift in the diversity peak (Appendix D; Fig. 4). Thus, only 13 of the 34 elevational gradients showed strong diversity responses to area.

In general, the significant species–area relationships were from data sets with decreasing elevational diversity patterns or with mid-elevation peaks in diversity on the lower portion of the elevational gradient. In cases in which the area effect was negative, the peak in diversity was at a high elevation, thus occurring where area was

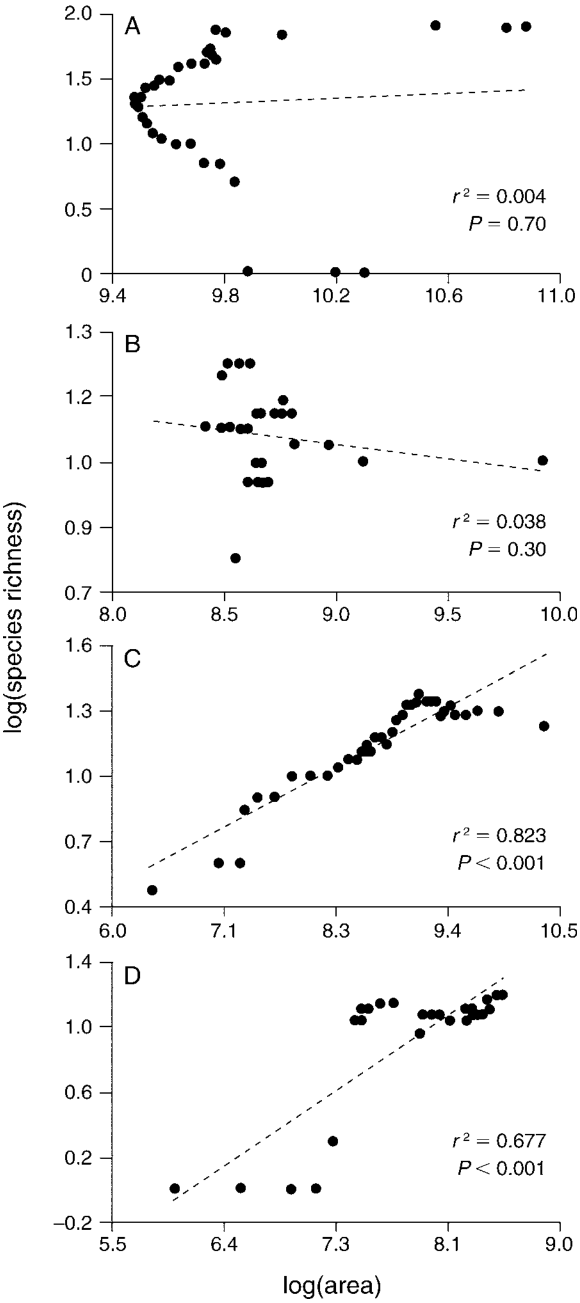

FIG. 3. Examples of the variability in log–log species–area linear regressions: (A) bats of southeastern Peru; (B) bats of Yosemite National Park, California, USA; (C) non-volant small mammals of Costa Rica; and (D) non-volant small mammals of La Sal Mountain, Utah, USA. (Compare with area and richness profiles in Fig. 2A, B, and D.)

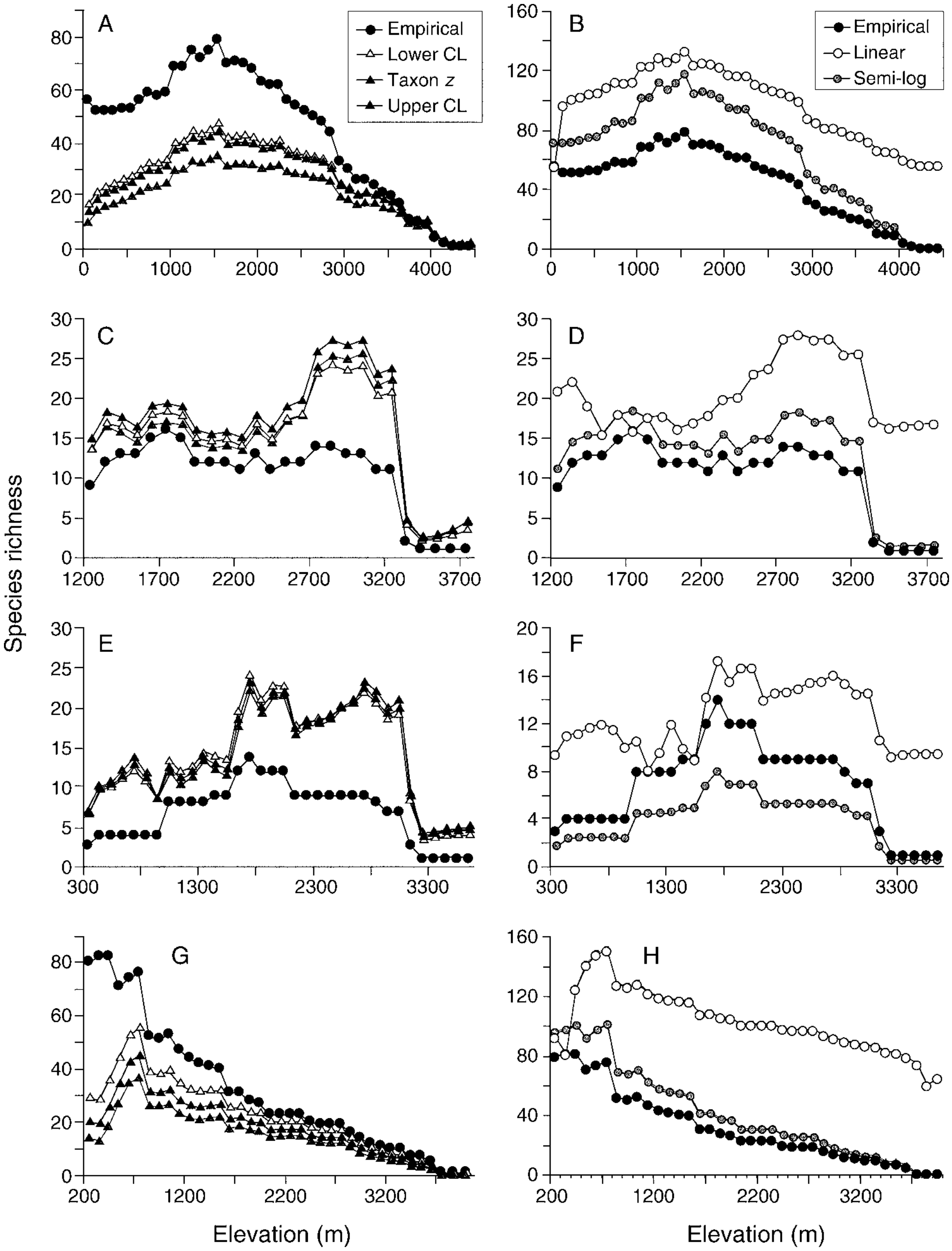

FIG. 4. Comparisons among general area effects on diversity patterns and the curvilinear (left panels) and semi-log and linear (right panels) area correction methods. Note that each correction method is on a slightly different scale; thus the important comparison is of the curve, not specific diversity values. Area effects are shown for: (A) and (B) non-volant small mammals, New Guinea, same diversity peak but a more pronounced, centered peak; (C) and (D) non-volant small mammals, La Sal Mountains, USA, diversity peak shifted to a higher elevation; (E) and (F) bats, White-Inyo Mountains, USA, same diversity peak with a stronger secondary peak; and (G) and (H) bats, southeastern Peru, eastern slope, shift from a decreasing diversity pattern to a mid-elevational peak.

consistently low. So regardless of whether area is highest at the base of the mountain or at a low mid-elevation, when diversity is highest above the midpoint of the mountain, there will be no significant species–area effect. This is the reason why local data sets for elevational diversity of NVSM (McCain 2005) and ants (Sanders et al. 2003) have a low probability of species–area effects since the diversity peaks are all significantly higher than the midpoint of the mountain.

The results of previous analyses between elevational diversity and area found similar variability in the species–area relationship. Six found significant species–area effects: ants in western North America (Sanders 2002), birds in South America (Rahbek 1997) and the

Andes (Kattan and Franco 2004), freshwater fish in China (Fu et al. 2004), aquatic plants in Norway (Jones et al. 2003), and palms in New Guinea (Bachman et al. 2004). All but one of these (Sanders 2002) showed a decreasing diversity pattern with elevation. Five found diversity not to be significantly related to area: plants in Norway (Odland and Birks 1999), vascular plants in Nepal (Vetaas and Grytnes 2002), ants in the Spring Mountains, Nevada (Sanders et al. 2003), ferns in Nepal (Bhattarai et al. 2004), and woody plants in the Himalayas (Oommen and Shanker 2005). All of these had mid-elevational diversity peaks. Thus, the variability in species–area relationships is mostly attributable to the general elevational diversity pattern; those with decreasing diversity with elevation showed strong species–area relationships. Since the distribution of mammalian diversity patterns mirrors that estimated for all taxonomic groups (Rahbek 1995, 2005), plants, all vertebrates, and invertebrates, a similar distribution of species–area effects are expected. The majority of elevational gradients (~65%) has mid-elevational peaks and thus is less likely to show strong species–area effects. The 25% with decreasing diversity patterns should show strong species–area effects. Thus, it is likely that only 25% to a generous 50% of elevational gradients in diversity across taxonomic groups will have strong species–area effects. Such percentages demonstrate area influencing diversity but not a consistent signal that pinpoints a major driver globally.

Spatial constraint

Results of spatial constraints tests (MDE) on elevational diversity were also highly variable (Table 1). On average the fits were low for both NVSM and bats as only ~30% of the variability was attributable to MDE. This is in accordance with previous results for elevational diversity across taxonomic groups (mostly vertebrates and plants), where fits are highly variable and on average low (Dunn et al., *in press*; mean $r^2 = 0.29$, SD $= 0.30$, $n = 94$). It has been suggested that variance around MDE fits may stem from the species–area relationship (McCain 2005; R. K. Colwell, *personal communication*). In fact, Sanders (2002) and Bachman et al. (2004) both found significant increases in MDE fit when area was also included in the model. The tests here found no large improvements to MDE fits as a whole when area was included. Some individual patterns improved, but others worsened or did not change (Table 1). This result should be robust across other taxonomic groups since the variability in elevational diversity patterns and MDE fits of the mammalian data used here encompasses the variability present in other taxonomic groups (Rahbek 2005; Dunn et al., *in press*; C. M. McCain, *unpublished data*). The value of the spatial constraint null model is its quantitative predictions of diversity and its simplicity. The low fits to MDE predictions along elevational gradients clearly show that diversity is responding to biological factors and not simply space.

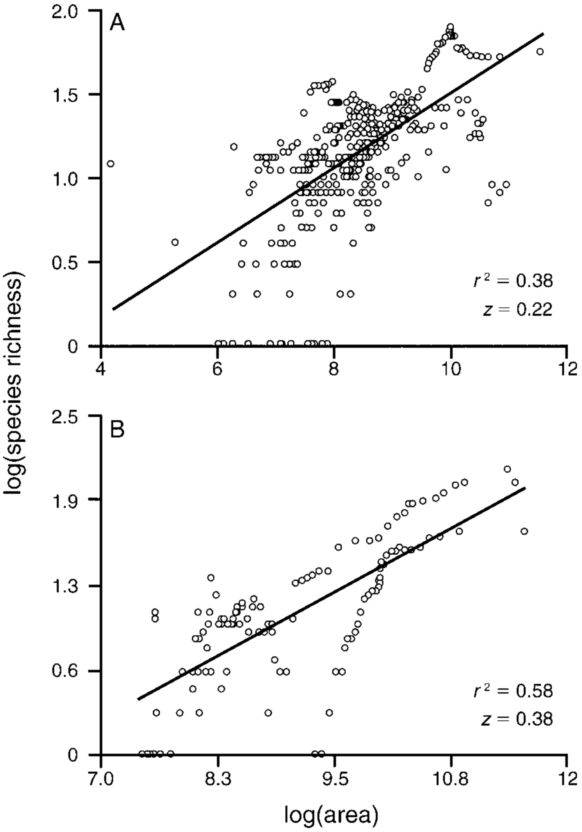

FIG. 5. Log–log species–area linear regressions to determine global, taxon-specific z values (slope of regression line) to be used in species–area corrections with the power model ($S = cA^z$) for (A) non-volant small mammals and (B) bats. Regressions were calculated using only those elevational gradients with significant log–log species–area relationships (see Table 1).

Climatic factors

The rejection of space (area and MDE) as the main driver of diversity leaves evolutionary history and climatic factors as potential main drivers. Because elevational gradients control for gradients in speciation rates, extinction rates, and clade age latitudinally, rejecting spatial hypotheses provides support for climatic drivers. Climatic drivers (e.g., temperature, precipitation, productivity, humidity, cloud cover) were not directly tested here or elsewhere (McCain 2005, 2006*b*) because these data have not been systematically collected at the small spatial scale necessary for elevational gradients. The global data sets available from remote sensing and interpolated from weather stations are too coarse (10–100 km^2 scales; e.g., United Nations Environment Programme [UNEP] climate data: Hawkins et al. 2003*a, b*). Temperature is known to decrease linearly with elevation at the environmental lapse rate of ~0.6°C/100 m (Barry 1992), so interpolated temperature data is testable. In previous meta-analyses of elevational diversity in mammals climatic proxies were used to detect broad-scale climate effects (McCain 2005, 2006*b*) beyond simple temperature effects.

For non-volant small mammals, the climatic proxy used was mountain mass effect: physiognomically similar vegetation types are found at higher elevations on taller mountains due to upward shifts in a combination of climatic factors with mountain mass (van Steenis 1972, Cavelier et al. 2000). The elevational diversity patterns of NVSM follow this mountain mass effect with maximum diversity shifts toward higher elevations on taller mountains appearing to follow a climatic optimum (McCain 2005). This mid-elevation climatic optimum appears to be a combination of intermediate temperatures, precipitation, and cloud cover (McCain 2004, 2005). Interpolated temperature alone is not strongly related to NVSM elevational diversity (mean $r^2 = 0.199$, gradients = 44). But until small-scale climatic data are collected, the precision of these drivers and the relative strength of each factor cannot be assessed.

Elevational diversity patterns of bats were related to two local climate trends: temperature and water availability (McCain 2006*b*). Bat diversity showed decreasing diversity with elevation on wet-based mountains (e.g., eastern versant of the Andes, New Guinea), where both temperature and water availability were high at lower elevations and decreased with increasing elevation. In these cases, temperature was strongly linked to bat elevational diversity (mean $r^2 = 0.812$, gradients = 7), whereas bat diversity on mountains with arid conditions at the base (e.g., Great Basin Mountains, USA, and western Peruvian Andes) show highest diversity at intermediate elevations where high water availability was paired with warm temperatures. In these arid environments, the temperature effect was weaker (mean $r^2 = 0.298$, gradients = 6). Again, pinpointing effect magnitudes of temperature and water availability relative to other climatic drivers awaits the appropriate data.

Conclusions

Both area and spatial constraints can influence diversity patterns, but the high variability and low explanatory power in spatial trends across multiple gradients demonstrate that neither alone nor both in combination can be the main driving force. This is consistent with the tests of the area hypotheses for birds (Hawkins and Porter 2001, Rahbek and Graves 2001) and bats (Willig and Bloch 2006) at continental scales, where again little support was found for area as the main driver underlying diversity patterns. Therefore, elevational and continental/latitudinal tests of spatial hypotheses reject area as a main driver but depict it as a factor that needs to be considered in decomposing sources of error from underlying mechanisms in multivariate analyses. Overall, elevational diversity of NVSM and bats appear to respond strongly to climate, including both temperature and water variables specific to the ecology of each taxon. Similar support for combined temperature and water diversity drivers exists globally for most plant and animal groups (Hawkins et al. 2003*a*), latitudinally for birds (Hawkins et al. 2003*b*), regionally for woody plants across southern Africa (O'Brien 1993), and elevationally for various plant groups (e.g., Bhattarai et al. 2004, Carpenter 2005, Krömer et al. 2005). Thus, most direct and indirect evidence currently supports a climatic driver underlying diversity patterns with space and evolutionary history playing less-pronounced roles, although fine-scaled climatic data for elevational gradients worldwide is urgently needed to assess the relative strength of each climatic factor with the spatial factors tested here.

Further evidence of the relative strength of climatic vs. spatial drivers will come from meta-analyses of other vertebrate, invertebrate, and plant taxa along global elevational gradients. A global climatic driver would garner additional support if the climatic factors associated with each taxonomic group were consistent with their ecological affinities. For instance, those with poor thermoregulatory abilities (e.g., bats or reptiles) should show strong trends with temperature particularly on wet mountains, whereas those taxa with life history characteristics highly associated with water and humidity (e.g., salamanders, ferns, or epiphytes) should show strong correlations with water variables.

Historical trends cannot be dismissed wholly on montane gradients because trends in climate change determining repeated habitat expansion and shrinkage may influence speciation and extinction rates elevationally, particularly on large mountain ranges (e.g., Andes, Himalayas). There also may be differential colonization probabilities at lower vs. higher elevations leading to different patterns in diversity. Niche conservatism across evolutionary time may also link contemporary climatic drivers to past evolutionary forces (e.g., Wiens and Donoghue 2004, Wiens and Graham 2005). These historical processes and the resulting diversity predictions have yet to be clearly defined elevationally and are a fruitful direction for future tests and theory.

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APPENDIX A

All mammalian elevational data sets, including diversity curve shape, mountain type, total diversity, latitude, area profile, and total mountain area (*Ecological Archives* E088-005-A1).

APPENDIX B

A color version of Fig. 1 (*Ecological Archives*: E088-005-A2).

APPENDIX C

Comparison and discussion of species–area correction techniques, including examples of methodologies (*Ecological Archives* E088-005-A3).

APPENDIX D

Comparisons of diversity peaks for the empirical diversity curve with area-corrected diversity curves of the various corrections methods (*Ecological Archives* E088-005-A4).

APPENDIX E

Correlations between the area-corrected diversity curves of various correction methods (*Ecological Archives* E088-005-A5).

SUPPLEMENT

Area estimates for each 100-m elevational band on each of the 32 mountains used in statistical analyses of species–area relationships along elevational gradients of mammals (*Ecological Archives* E088-005-S1).

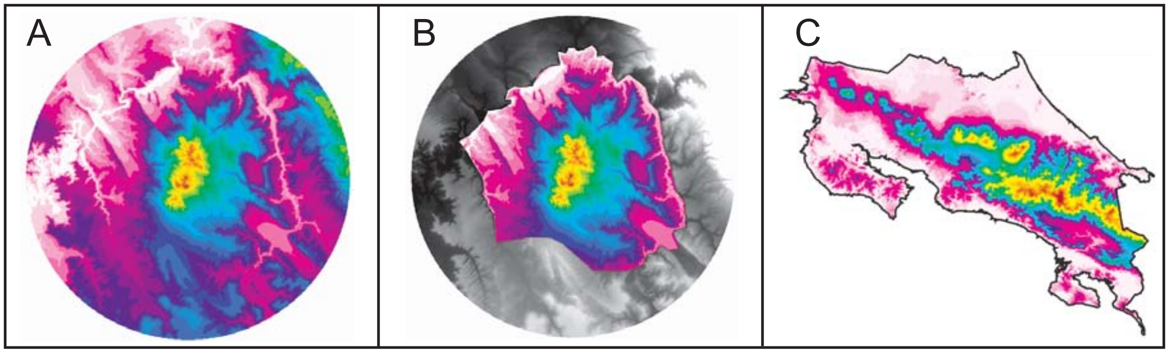

Figure 1 (Online in color)

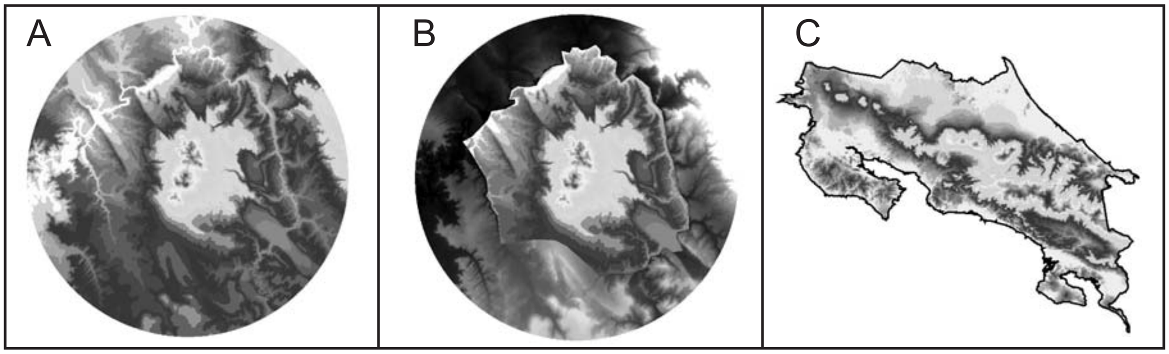

Figure 1.

Appendix B. The elevational diversity data sets included in species-area analyses: 25 regional non-volant small mammal (NVSM) data sets and 8 regional bat data sets ordered by latitude south to north. All the citations for the studies can be found in McCain (2005) for NVSM and McCain (in press) for bats except those noted otherwise. Significant species-area effects are denoted with a star on the area profile. Mountain area units are in million m^2.

NVSM	Diversity Curve	Mtn Type	Total Diversity	Latitude	Area Profile	Mtn Area
Madagascar	mid-elev.	GP	39	-19.2	DEC*	546.52
New Guinea	mid-elev.	GP	136	-5.5	SRD*	769.86
Rwenzori Mtns, Uganda	mid-elev.	Range	34	0.1	SRD*	2.73
Mt. Kinabalu, Sabah, Borneo	mid-elev.	Cone	54	6.1	SRD*	3.58
Mindanao, Philippines	mid-elev.	GP	14	7.8	SRD	92.79
Costa Rica[1]	mid-elev.	GP	35	9.7	SRD*	64.22
E Tiliran Mtns, Costa Rica	mid-elev.	Range	18	10.2	SRD	1.84
Oaxaca, Mexico	mid-elev.	GP	26	18	SRD	89.53
Ba Vi Highlands, Vietnam	mid-elev.	Cone	28	22	SRD	0.92
Taiwan	mid-elev.	GP	11	23.8	SRD	35.87
Central Nepal	mid-elev.	GP, Range	43	28	SRD	66.41
Great Smokey Mtns, USA[2]	mid-elev.	Range	34	35.7	DEC*	17.89
Abajo Mtns, UT, USA	low plateau	Cone	21	37.9	MID*	2.92
Yosemite (W Slope), CA, USA[3]	mid-elev.	GP, Range	49	38	SRD*	23.18
Mt. Qilian Region, China	mid-elev.	Range	18	38.3	MID	283.28
Aquarius Mtns, UT, USA	mid-elev.	Range	33	38.4	DEC	12.95
Henry Mtns, UT, USA	low plateau	Range	18	38.4	SRD*	2.59
Tushar Mtns, UT, USA	mid-elev.	Range	29	38.5	DEC*	2.58
La Sal Mtns UT & CO, USA	mid-elev.	Cone	25	38.7	MID*	3.16
Pavant Mtns, UT, USA	mid-elev.	Range	25	39.1	DEC*	2.74
Wasatch Plateau, UT, USA	mid-elev.	Range	36	39.4	MID*	8.27
Deep Creek Mtns, USA	mid-elev.	Range	29	40	SRD*	9.37
Oquirrh Mtns, UT, USA	mid-elev.	Range	24	40.2	SRD	3.85
Ruby Mtns, NV, USA	decreasing	Range	27	40.3	SRD*	3.52
Wasatch Range, UT, USA	mid-elev.	Range	34	40.3	SRD*	5.48
Uinta Mtns, UT, USA	mid-elev.	Range	46	40.4	MID*	24.38
Bats						
SE Peru (E Slope)	decreasing	GP	101	-12.5	SRD*	366.95
Manu NP Region, Peru	decreasing	GP	129	-12.5	SRD*	146.16
New Guinea	decreasing	GP	69	-5.5	SRD*	769.86
Ecuador (E Slope)	mid-elev.	GP	67	-2	MID	50.10
Venezuela	decreasing	GP	147	7	SRD*	900.99
Sierra de Manantlan, Mexico	mid-elev.	GP, Range	25	19	MID*	4.11
White & Inyo Mtns, USA	mid-elev.	Range	14	37.5	MID*	8.73
W Yosemite NP, CA, USA	mid-elev.	GP, Range	17	38	SRD	22.40

GP = geopolitical, Range = mountain range, Cone = cone shaped mountain, SRD = strongly recurved decreasing, DEC = generally decreasing, MID = mid-elevation peak.

1. McCain in press; 2. Linzey 1995; 3. Grinnell and Storer 1924.

Ecological Archives A/E/M000-000-A#

Christy M. McCain. Year. Area and mammalian elevational diversity. *Ecology* VOL: pp-pp.

Appendix C. Comparison and discussion of species-area correction techniques, including examples of methodologies.

The aim of this supplement is to compare area-correction methods for elevational diversity and delineate the most rigorous methods to apply. Several methods for producing area-corrected diversity curves on elevational gradients are published. Rahbek (1997) used the power function model for species-area curves: $S = c A^{z}$, which is inherently curvilinear. Vetaas and Grytnes (2002) simply divided species richness in each elevational band by log area of that elevational band, which assumes a semi-logarithmic area function ($S = \log A$). Bachman et al. (2004) used a GIS to delineate bands of elevation with equal area. In this case, the bands differ in elevational extent (in some cases <1 m) but are equal in area. Lastly, linear correction methods could be employed by adjusting the diversity of each elevational band by a correction factor equal to the difference in area (e.g. Fu et al. 2004).

Each method has its drawbacks. Methodologically the fine delineation of area into equal area bands in a GIS (Bachman et al. 2004) assumes the diversity data are as accurately measured. For instance, three equal area bands had elevational extents of less that 1m, 10 less than 50 m, and 16 less than 100 m whereas most elevational diversity data would be measured at 100m bands at the minimum and very rarely at 50m or below. The main drawback with the linear method is the assumption that the species-area relationship is linear, which is often not the case (Table 1; Preston 1962, Conner and McCoy 1979). The species-area relationship tends to be curvilinear (Preston 1962, Connor and McCoy 1979, Rosenzweig 1995). Therefore, the power function model or the semi-logarithmic area function offer more promise for accurately assessing the area effect on elevational gradients. The semi-logarithmic area function tends to be used for species-area relationships mainly in the plant literature, so has been tested less. Because the power function is the basis for much of the species-area theory and is the pattern most supported in the literature and among the elevational diversity patterns tested here (Table 1), this appears to be the appropriate model. The difficultly with applying the power model is determining the appropriate z value.

The z value determines how rapidly diversity increases with increasing area (in log-log space; Rosenzweig 1995, Lomolino 2000 and references therein). Unfortunately, Rahbek's method for estimation of z is not widely applicable for several reasons. First, robust calculations of z values are quantified with a large number of regression points spread across a large range of area values (Conner and McCoy 1979, McGuinness 1984, Williamson 1988, Rosenzweig 1995, Lomolino 2000), both of which are limited in the Rahbek method (4–8 points). Second, Rahbek's method assumes that the change in diversity with area is more similar for bands of area at the same elevations from different mountain regions than it is across various elevational bands on the same mountain. The veracity of this assumption is unknown and untested. Third, for this method to work diversity must decrease with elevation on all mountains, which is rarely the case for most taxa and not the case for the elevational gradients of mammals considered here.

There are several alternative ways to estimate a z value for elevational gradients. The most obvious would be to use the z value calculated from the species-area regression for that particular mountain. This suffers from some of the same drawbacks as the Rahbek method: few points in the regression and a small spread of area values reduce the reliability of the z value estimation. This is illustrated by the spread in z values calculated for the 23 significant species-area gradients of NVSM and bats which range from 0.03–0.86 (Appendix D; mean = 0.40, sd = 0.25), 58% of which are well above or below values normally associated with z values (e.g. Rosenzweig 1995: 0.12–0.35). The spread in area values is twice as large in NVSM as that of bats, and area spread for individual mountains is low compared to the overall spread for the taxon (aver. NVSM = 36%, bats = 39%). In fact, for NVSM, z values are negatively related to the spread of area values; small z values are found on mountains with a large range in area between elevations ($r^2 = 0.29$, p 0.02).

Another z value that could be applied is the "canonical" value of z = 0.25 proposed by Preston (1962). But this seems a bit arbitrary given that we know empirically that z values can vary systematically for islands, continents, and taxonomic groups. I propose a taxon method: all the elevational area and diversity measures for each mammal group (NVSM, bats) that show significant log-log species area relationships are combined in a species-area analysis to estimate a taxon-specific, global z value for elevational gradients. This procedure covers the widest available set of area values and includes hundreds of data points in the regressions (NVSM = 399; bats = 140). Such a composite z value also eliminates the influence of extreme values resulting in a more conservative estimate than other potential estimators. To compare different species-area correction methods, I calculated curves using the power model with different z values, the semi-logarithmic method and the linear method (Appendix D; for details of methods see below). The z values tested with the power model included the taxon-specific z value (average, upper 95% confidence limit, and lower 95% confidence limit), the mountain z value, and the canonical value of 0.25 (Preston 1962).

The taxon-specific z value for NVSM was 0.22 with 95% confidence limits of 0.19–0.25 (Fig. 5A; log Species = -0.7152 + (0.2223) log Area), and 0.38 for bats with 95% confidence limits of 0.32–0.44 (Fig. 5B; log Species = -2.3803 + (0.3767) log Area). No trends in mountain-specific z values were detectable with species richness of the mountain ($r^2 = 0.0047$, $p = 0.7558$), mountain size by total area ($r^2 = 0.0260$, $p = 0.4625$), latitude ($r^2 = 0.0506$, $p = 0.3019$, or mountain type, for instance mountain range versus geopolitical elevational gradient (F ratio = 0.77, p = 0.3891).

There was little difference in the area-corrected diversity curves with the four different z values, as the location of the diversity peak was the same as the taxon value for 79% of data sets (Fig. 4; Appendix D). Most deviations occurred with the mountain z values, which as stated above were highly variable. Diversity peak shifts among the z values averaged ~750 m for the mountain z values and ~400 m for all other z values. There were larger differences in the location of peak diversity when comparing curvilinear methods to either semi-logarithmic or linear correction methods. For instance, 48% of the semi-logarithmic and 35% of the linear had different locations of peak diversity with an average shift of ~525 m away from the peak of the curvilinear methods using the taxon z value (Fig. 4; Appendix D). The semi-logarithmic correction methods altered the empirical diversity curves the least. In only 4 cases was semi-logarithmic diversity peak different from the empirical peak, whereas about half were changed with the other correction methods. Nonetheless, the species diversity curves resulting from all area correction methods and the multiple z values were highly correlated (Fig. 4; Appendix E): taxon-specific value with lower 95% CL ($r = 0.994$), with upper 95% CL ($r = 0.994$), with canonical value ($r = 0.988$), with semi-logarithmic ($r = 0.840$), and linear correction ($r = 0.858$). The only non significant correlations were NVSM of the Great Smoky Mountains (linear, mountain specific z, and semi-logarithmic), and NVSM of the Uinta Mountains (mountain specific z).

Regardless of the area-correction method, the fit to the mid-domain effect did not improve appreciably after removing the area effect (Table 1). All correction methods (best model fit (Table 1), curvilinear with taxon z, mountain specific z, or canonical z; semi-log; and linear) found similar numbers of MDE fits that increased (9–13), decreased (6-8) or did not change (4–6). The magnitudes of increases and decreases were also very similar (average increase: 0.17–0.26; average decrease: 0.12–0.23), except for the semi-logarithmic correction which were much lower (increase 0.03, decrease 0.06). Thus, the resulting average fits to MDE were very similar: best fit ($r^2 = 0.27$); taxon z ($r^2 = 0.29$); mountain z ($r^2 = 0.33$); canonical z ($r^2 = 0.29$); semi-logarithmic ($r^2 = 0.26$); and linear ($r^2 = 0.30$).

I advocate using the power model, $S = cA^z$, first used by Rahbek (1997) and used for latitudinal gradients (Lyons and Willig 1999, Romdal et al. 2004), since it accounts for the strong curvilinear shape of most species-area relationships and because it is the basis of the species-area theory (Rosenzweig 1995 and references therein). I suggest that a taxon-specific z value (and is confidence limits) is the most comprehensive and conservative estimation method for elevational data. Since the taxon z value is estimated from hundreds of points it limits the effects of extreme values resulting in an average species-area correction (Fig. 3).

Nonetheless, my comparison of various values of z found the resulting area-corrected curves to be very similar and highly correlated ($r = 0.84$–0.99). In general, z values ranging from 0.1–0.4 tend to produce very similar diversity curve shapes with little variation in the location of the peak in diversity (≤250m, Appendix D & E; not all analyses shown). The magnitude of the z value has the least effect on patterns of decreasing diversity paired with a strongly decreasing area profile, since all values of z caused peak diversity to shift to the same mid-elevation (e.g. 4G). Thus, a range of z values appears to be robust for use in mammalian area-corrected diversity curves, and most likely for other taxonomic groups. Therefore, I would advocate using the power model with (1) a taxon-specific z value and its upper and lower confidence limits if the data is available, or (2) a spread of possible z values including the canonical value (i.e. 0.15, 0.25, 0.35). Using a range of z values concedes that there is error in estimation of the true z value and therefore examines the possible error effects on the diversity curves within a range of probable z values. Such an error analysis seems the most robust method for using the power model since a single estimated value is unlikely to be the true value. The suggested range of z values (and those from the taxon specific calculations) is also consistent with research on continental and island species-area curves which usually range between 0.12–0.35 (Rosenzweig 1995: pg. 17) and with the z values calculated by Rahbek (1997) for birds on South American mountains.

The linear and semi-logarithmic methods of constructing area-corrected diversity curves are the simplest methods to calculate. The inconsistency with the linear method is that most species-area relationships are not linear (Table 1; Preston 1962, Conner and McCoy 1979). The drawback seen with the semi-logarithmic corrections is that it is relatively insensitive to area effects (see above; Appendix D), and is less supported by theory. Nonetheless, both types of area-corrected curves are still highly correlated with the power model in most cases (r = 0.84–0.86; Fig. 4, Appendix E). Thus, previous analyses using linear and semi-logarithmic methods are most likely robust, but I would advocate these methods only if the power method with a variety of z values gives highly conflicting results or if the species-area relationships are strongly linear or semi-logarithmic.

Examples of Methodology:

(1) Curvilinear Method:

The empirical number of species (S) and the estimated area (A) for each 100m elevational band plus the appropriate z value are entered in the power model and solved for the constant c ($c = S / A^{z}$). C then becomes the area-corrected diversity estimate for that particular elevational band. In order to rescale c to similar values as the empirical diversity each c estimate is multiplied by a constant.

For example, if you had three elevational bands with species richness values of 40, 40, 10, and area estimates of 100, 50, 25 million m^2 with an estimated z value of 0.25 then the calculations would be the following:

A. $c1 = 40 / 100{,}000{,}000^{0.25}$
$c1 = .400$
$c1 = .400 * 100 = 40$

B. $c2 = 40 / 50{,}000{,}000^{0.25}$
$c2 = 0.476$
$c2 = 0.476 * 100 = 47.6$

C. $c3 = 10 / 25{,}000{,}000^{0.25}$
c3 = 0.141
c3 = 0.141 * 100 = 14.1

(2) Linear Method:

This method assumes that if each 100m elevational band had the same area then diversity would increase by a factor equal to the lesser amount of area. Thus, each elevational band is compared to the elevational band of greatest area. The proportion less is multiplied by the diversity in the band with the greatest area, and this additional diversity is added to the empirical diversity for the band.

For example, using the same three areas in the curvilinear example, the calculations would be the following:

A. Proportion of largest area missing:

elev.1: area = 100,000,000 / 100,000,000 = 1.0 → 0
elev.2: area = 50,000,000 / 100,000,000 = 0.5 → 0.5
elev.3: area = 25,000,000 / 100,000,000 = 0.25 → 0.75

B. Multiply proportion of largest area missing by greatest area's diversity:

elev.1: area = 100,000,000 / 100,000,000 = 1.0 → 0 * 40 = 0
elev.2: area = 50,000,000 / 100,000,000 = 0.5 → 0.5 * 40 = 20
elev.3: area = 25,000,000 / 100,000,000 = 0.25 → 0.75 * 40 = 30

C. Add proportional increase in diversity to empirical diversity:

elev.1: area = 100,000,000 / 100,000,000 = 1.0 → 0 * 40 = 0 + 40 = 40
elev.2: area = 50,000,000 / 100,000,000 = 0.5 → 0.5 * 40 = 20 + 40 = 60
elev.3: area = 25,000,000 / 100,000,000 = 0.25 → 0.75 * 40 = 30 + 10 = 40

Appendix D. The elevation of the diversity peak for the empirical diversity curve and for the area-corrected diversity curves using curvilinear ($S=cA^z$), semi-logarithmic (S/log A) and linear corrections. The curvilinear correction method is calculated for the mountain specific z value, the taxon specific z value and its 95% upper & lower confidence limits, and the canonical z-value of 0.25. The canonical value is also the upper 95% CL for NVSM so is not repeated. Bold values show changes in peak location among z values >50m. [Mountains ordered by latitude S-N.]

	Mtn Z value	Empirical	Curvilinear (z values)					Semi-Log.	Linear
NVSM Transects			***Mtn z***	***0.19***	***0.22***	***0.25***			
Madagascar	0.13	1300	**1750**	1950	1950	1950		1300	1300
New Guinea	0.56	1550	**2250**	1550	1550	1550		1550	1550
Rwenzori Mtns, Uganda	0.31	2250	2550	2500	2500	2500		2450	2400
Mt. Kinabalu, Sabah, Borneo	0.39	950	1550	1550	1550	1550		950	950
Costa Rica	0.24	1250	1250	1250	1250	1250		1250	1250
Great Smokey Mtns, TN & NC, USA	0.06	650	**550**	2050	2050	2050		650	550
Abajo Mtns, UT, USA†	0.14	2550	2550	2550	2550	2550		2550	2550
Yosemite NP, CA, USA	0.22	1150, 1850	1850	1850	1850	1850		1150, 1850	1850
Henry Mtns, UT, USA†	0.29	1850, 2450	2450	2450	2450	2450		2450	2450
Tushar Mtns, UT, USA	0.40	2650	**3150**	2650	2650	2650		2650	2650
La Sal Mtns UT & CO, USA	0.53	1750	**3050**	2850	2850	2850		1750, 3000	2850
Pavant Mtns, UT, USA	0.51	2050	**2750**	2050	2050	2050		2050	2050
Wasatch Plateau, UT, USA	0.36	2350	3100	3100	3050	3100		3050	3050
Deep Creek Mtns, NV & UT, USA	0.28	1550, 1850	1850, **2450**	1850	1850	1850, **2450**		1550, 1850	1550, 1850
Ruby Mtns, NV, USA*	0.77	1850	**2950**	2200	2200	**2300**		1850	2200
Wasatch Range, UT, USA	0.30	1800	2250, 2750	2250	2250	2250		1800	1950
Uinta Mtns, UT, USA	0.86	1950	**3050**	2500	2500	2500		1950	2550
Bat Transects			***Mtn z***	***0.32***	***0.38***	***0.44***	***0.25***		
SE Peru (E Slope)*	0.09	400	750	750	750	750	750	450, 750	750
Manu National Park Region, Peru*	0.03	350	**350**	650	650	650	650	350	650
New Guinea*	0.81	100	**1250**	850	850	**950**	**750**	150	150
Venezuela*	0.56	150	**2150**	750	750	**1550**	**350**	150	350
Sierra de Manantlan, Jalisco, Mexico	0.61	1950	**450**	1950	1950	**450**, 1950	1950	1950	1950
White and Inyo Mtns, CA & NV, USA	0.77	1750	**3050**	1750	1750	**2750**	1750	1750	1750

* decreasing diversity; † low elevation plateau

Appendix E. The *r* values for correlations between the area-corrected diversity curves using the taxon value and for other values of z, as well as for the linear and semi-logarithmic methods. Canonical z calculations for non-volant, small mammals (NVSM) are the same as upper CL because z values are equal. Non-significant correlations are shown in bold. [Mountains ordered by latitude S-N.]

		Curvilinear Corrections				
NVSM Transects	Linear	Mtn z	lower CL	upper CL	canonical	Semi-Log.
Madagascar	0.8249	0.9336	0.9915	0.9937	0.9937	0.7969
New Guinea	0.9614	0.7442	0.9984	0.9988	0.9988	0.9515
Rwenzori Mtns, Uganda	0.9528	0.9721	0.9969	0.9974	0.9974	0.9410
Mt. Kinabalu, Sabah, Borneo	0.9280	0.8205	0.9940	0.9953	0.9953	0.8815
Costa Rica	0.7952	0.9861	0.9712	0.9721	0.9721	0.6553
Great Smokey Mtns, TN & NC, USA	**0.0726**	**0.1124**	0.9946	0.9981	0.9981	**0.2054**
Abajo Mtns, UT, USA†	0.9439	0.9194	0.9895	0.9938	0.9938	0.6610
Yosemite NP, CA, USA	0.7020	0.9995	0.9826	0.9820	0.9820	0.8166
Henry Mtns, UT, USA†	0.8922	0.9800	0.9941	0.9962	0.9962	0.8353
Tushar Mtns, UT, USA	0.9275	0.9507	0.9978	0.9985	0.9985	0.9341
La Sal Mtns UT & CO, USA	0.5867	0.7996	0.9971	0.9980	0.9980	0.9235
Pavant Mtns, UT, USA	0.9208	0.9162	0.9987	0.9991	0.9991	0.9650
Wasatch Plateau, UT, USA	0.9757	0.9419	0.9976	0.9981	0.9981	0.9475
Deep Creek Mtns, NV & UT, USA	0.9660	0.9966	0.9989	0.9992	0.9992	0.9736
Ruby Mtns, NV, USA*	0.8340	0.7084	0.9978	0.9985	0.9985	0.9356
Wasatch Range, UT, USA	0.9504	0.9808	0.9966	0.9975	0.9975	0.9190
Uinta Mtns, UT, USA	0.9757	**0.3982**	0.9991	0.9993	0.9993	0.9974
Bat Transects						
SE Peru (E Slope)*	0.9650	0.9040	0.9967	0.9972	0.9832	0.8672
Manu National Park Region, Peru*	0.9613	0.8762	0.9973	0.9977	0.9861	0.8869
New Guinea*	0.9273	0.8109	0.9955	0.9957	0.9783	0.8453
Venezuela*	0.8000	0.7188	0.9724	0.9658	0.8943	0.6151
Sierra de Manantlan, Jalisco, Mexico	0.9476	0.9470	0.9953	0.9957	0.9777	0.8664
White and Inyo Mtns, CA & NV, USA	0.9222	0.8101	0.9961	0.9958	0.9826	0.9087
Average *r* =	**0.8580**	**0.8360**	**0.9935**	**0.9941**	**0.9877**	**0.8404**

* decreasing diversity

† low elevation plateau