

ELEVATIONAL GRADIENTS IN DIVERSITY OF SMALL MAMMALS

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Abstract. A global analysis of elevational diversity trends for nonvolant small mammals revealed a clear pattern of mid-elevational peaks in species richness. Fifty-six data sets were used to test the predictions of a null model (the mid-domain effect) and climatic hypotheses. Very few data sets fit entirely within the predictions of the null model, and the average predictive power of the null model was low. Regional (gamma) diversity fit the null model better than did local (alpha) diversity. Diversity peaked at higher elevations on taller mountains, consistent with climatic factors producing elevationally correlated habitat bands (Massenerhebung effect). This positive, linear relationship was documented for all data sets but was particularly pronounced for alpha diversity. Gamma diversity, which is generally highly influenced by area, exhibited a trend of highest diversity shifting toward lower elevations, and higher elevational peaks in species diversity at higher latitudes. The elevation of temperate diversity peaks exhibited a negative association with latitude. These results are evidence for the importance of a suite of interacting climatic, area, and geometric factors on elevational diversity patterns, apparent in spite of noise associated with different sampling techniques, localities, and historical pressures.

Key words: alpha diversity; climate; elevational gradient; gamma diversity; mid-domain effect; Massenerhebung effect; small mammals; species density; species richness.

INTRODUCTION

In the past decade, a fundamental shift in understanding of diversity patterns resulted from a resurgence of elevational studies (Rahbek 1995, Brown 2001). Previously, diversity along elevational gradients was thought to decrease monotonically with increasing elevation, based on a few highly cited papers on birds in the tropics (Terborgh 1977, Brown and Gibson 1983, Brown 1988). However, a preliminary literature review for a wide variety of taxa found that only 20% of the studies supported a monotonically decreasing curve in diversity (Rahbek 1995). Many studies (49%) exhibited hump-shaped diversity curves with highest richness at mid-elevations, and 24% had a plateau of high richness across the lower elevations, which then declined at higher elevations. More recent elevational studies that focused on nonvolant small mammals found mid-elevational peaks of species richness in the Philippines (Heaney 2001 and references therein), Madagascar (Goodman and Carleton 1996, 1998, Goodman et al. 1996, 1999, Goodman and Rasolonandrasana 2001), Mexico (Sánchez-Cordero 2001), Nevada and Utah (Rickart 2001), and Costa Rica (McCain 2004).

Most elevational studies assess a particular taxon, but offer only anecdotal evidence about diversity hypotheses. Experimentation is not feasible, long-term climatic data are scarce, and many diversity hypotheses are interrelated and difficult to quantify from individual

transects (Brown 1995, Heaney 2001); hence, most factors influencing elevational diversity gradients are unresolved (Rosenzweig 1992, 1995, Brown 2001). Lomolino (2001) proposed a research agenda to improve understanding of these patterns advocating rigorous tests with comparisons of elevational diversity trends within and among both taxa and mountain ranges. Numerous elevational diversity studies for various taxa around the world represent a previously untapped source for comparative, quantitative analyses of biodiversity patterns. Here, I test theoretical predictions of a null model and other contributory factors based on 56 studies of elevational diversity of nonvolant small mammals from an extensive literature search.

One newly proposed null model, the mid-domain effect, predicts mid-elevational peaks in species richness based on spatial constraints of range placement between the hard boundaries of the sea and mountain summit (Colwell and Hurr 1994, Colwell and Lees 2000, Colwell et al. 2004, McCain 2003, 2004). These landmass boundaries limit species' ranges, and species with large and intermediate-sized ranges necessarily overlap at the center of the gradient, leading to a peak in species richness at the midpoint of the elevational gradient. Empirical support for this null model on elevational gradients exists for small mammals (McCain 2004), ants (Sanders 2002), and plants (Grytnes and Vetaas 2002, Grytnes 2003).

The most frequently cited explanations for patterns of elevational diversity relate to gradients in single factors, such as rainfall, temperature, productivity, competition, resource abundance, habitat complexity,

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or habitat diversity (Heaney 2001, Lomolino 2001, Rickart et al. 1991 and references therein). Current theory recognizes the complex interrelatedness of climatic factors, which can work in concert to influence diversity trends (Brown 2001, Lomolino 2001 and references therein). A striking feature of elevational gradients is the succession of habitats that occurs across the gradients, which are directly related to climatic variables. Physiognomically similar vegetation types are found at higher elevations on taller mountains, a pattern known as the Massenerhebung effect or mountain mass effect (Flenley 1994 and references therein). For example, the lower boundaries of cloud forest vegetation on mountains of Indonesia exhibit a positive, linear trend with mountain height (van Steenis [1972]; $r^2 = 0.9999$, $P < 0.0001$). If combinations of climatic factors influence elevational patterns of small mammal diversity similarly, then highest species richness would occur at higher elevations on taller mountains than on shorter mountains for taxa exhibiting mid-elevational diversity peaks. As the mountain mass effect is more pronounced on isolated island or mountain peaks near the sea (Flenley 1994 and references therein), stronger trends would be expected for diversity patterns in these places. Small mammals may be responding to climatic factors directly (i.e., tracking temperature) or indirectly by tracking vegetative traits responding to climate. Both may be important, but cannot be separated herein. Thus, discussions of climatic factors imply both direct and indirect effects. If interacting climatic factors affect species diversity, latitudinal trends would also be predicted (Lomolino 2001).

The mid-domain null model predicts that highest species richness should occur at the elevational midpoint and decline symmetrically toward sea level and the mountaintop regardless of mountain height or latitude. Climatic influences on elevational patterns of species diversity should produce trends consistent with mountain mass and latitudinal effects (Lomolino 2001). A climatically driven mountain mass effect predicts a positive linear trend in the elevation of highest diversity with mountain height. The mid-domain effect similarly predicts positive peak diversity and mountain height relationships, since the midpoint of an elevational gradient and the height of the mountain are necessarily positively correlated. Two methods are employed to detect a positive linear trend in highest diversity and mountain height due to a mid-domain effect: (a) the null model predictions are examined across the entire elevation gradient of diversity assessing the overall fit to the mid-domain effect, and (b) statistical comparisons are made between the elevation of highest diversity and the elevational midpoint.

The current study aims to (1) determine the pervasiveness of mid-elevational peaks in species richness for nonvolant small mammals, (2) test the generality of the mid-domain effect on elevational gradients, and

(3) assess predictions of climatic hypotheses including mountain mass effect and latitudinal trends.

METHODS

I searched the literature for studies of species richness along elevational gradients for nonvolant small mammals. Data sets were grouped into tropical vs. temperate, islands vs. continents, and alpha or gamma diversity. Alpha diversity patterns are local species-density samples taken from field transects along single elevational gradients; gamma data sets are more comprehensive species richness patterns compiled from trapping records, specimen records, and field notes for an entire mountain or mountainous region regardless of slope, area, or standardized trapping effort across elevations. Gamma diversity may be highly influenced by area (Lomolino 2001), and may have significant sampling biases (Rickart 2001). As the data in alpha and gamma patterns are qualitatively and quantitatively different, the factors producing these patterns will not necessarily coincide. All diversity data from the literature were reanalyzed, assuming that species occurred at an elevation if they were detected at both higher and lower elevations. Analyses were based on elevational ranges of each species. In cases where several alpha diversity data sets existed (Oaxaca, Madagascar, Taiwan, Qilian), I compiled gamma diversity curves. Lower elevational range boundaries for Oaxacan species were augmented by elevational range data from Hall (1981).

Data sets were included in tests only if sampling covered most (>70%) of the elevational gradient, and if sampling did not exhibit substantial elevational biases. To test the influence of geographic boundaries, diversity patterns were compared to null model predictions with a Monte Carlo simulation procedure (Mid-Domain Null; McCain 2004). This procedure simulates species richness curves using empirical range sizes within a bounded domain, based on analytical-stochastic models (Colwell and Hurtt 1994, Colwell and Lees 2000; see McCain 2003, 2004). Simulation boundaries were mountain summit and lowest elevation for the mountain range. Diversity data were simulated in 100-m increments. For each data set, 95% prediction curves based on 50 000 simulations sampled without replacement from empirical range sizes were used to assess the impact of spatial constraints on the elevational diversity gradients. Regressions of the empirical values on predicted values, based on the average of the 50 000 simulations where mean \approx median \approx mode, gave r^2 estimates of the fit of the null model. Consistent deviations from null model predictions suggest influences of climatic, historical, or other factors also important in determining species richness.

Linear regressions were used to test for positive, linear relationships between mountain height and the elevation with maximum species diversity. Two methods were used to distinguish whether or not the positive

linear trend was due to the mid-domain model: (1) determining the fit of the mid-domain predictions across the entire shape of the diversity curve (the null model predicts not only the peak in diversity at the midpoint of the elevational range but as a smooth, hump-shaped curve that nears zero at either end point); and, (2) because the mid-domain effect always predicts diversity peaks at elevational midpoints, a paired *t* test should show whether there is a statistical difference between the elevational midpoint and the elevation of highest diversity.

Gamma diversity patterns are highly influenced by area, because area and habitat diversity generally decline with elevation, therefore biasing gamma diversity peaks toward low elevations. Area was not measured for each mountain, but the area effect in mountain ranges is a well-documented phenomenon (Körner 2000, Lomolino 2001). In these cases, no linear relationship is expected between peak richness and mountain mass, but peak richness is expected to shift toward lower elevations. The latitudinal trends were examined with two linear regressions: (1) elevation of maximum diversity against latitude, and (2) the residuals from the regressions of maximum diversity and mountain height against latitude.

RESULTS

Fifty-six elevational gradients in small mammal diversity were found in 35 published studies (Appendix A). Data sets were grouped into tropical (32) or temperate (24), island (21) or continental (35), and alpha (27) or gamma diversity (29); groupings were not independent (most gamma data sets from continental temperate areas, most alpha data sets from the tropics and islands). All but four data sets had maximum species richness at mid-elevation. Two exhibited bimodal patterns and two studies had no recognizable trends. These latter two studies, both alpha diversity transects, had substantial portions of the gradient unsampled (33–64%; Patterson et al. 1989, Bonvicino et al. 1997). The two studies that demonstrated bimodal patterns of peak diversity at the lowest and highest elevations either lacked sampling along the entire elevational gradient (42% sampled; Kelt 1999) or emphasized lack of sampling at mid-elevations (Patterson et al. 1998). On small islands with low species richness (≤ 8 species), diversity peaks were relatively flat and variable depending on inclusion of exotics, and with richness differing by only one or two species among elevations (Heaney et al. 1989, Rickart 1993, Heaney 2001). Three gamma diversity patterns had plateaus of richness at low elevations, as diversity declined toward the mountain base by less than 25%. Similarly, two alpha patterns demonstrated plateaus of high elevation richness, as diversity declined toward the summit by less than 25%. In general, diversity patterns of small mammals along most elevational gradients demonstrated pronounced mid-elevational peaks in species richness.

Seventeen studies with elevationally biased or insufficient sampling, including the four not exhibiting mid-elevational peaks discussed above, were not used in the quantitative analyses.

Even though diversity peaked at intermediate elevations, shapes of diversity curves and elevations with maximum richness were highly variable. The 95% prediction curves based on 50 000 simulations were used to assess the impact of spatial constraints on 39 elevational gradients. Fit to the null model ranged from highly predictive to not predictive at all (0.0–79.1% of variation; Appendix A; Fig. 1), and r^2 values were generally low (average $r^2 = 0.238$; Appendix B). The null model had greater predictive ability for gamma, continental, and tropical data sets than for alpha, island, and temperate data sets. Alpha data sets had lower average r^2 values, than gamma data ($r^2 = 0.156$ and $r^2 = 0.295$, respectively). No consistent pattern of deviations from null predictions existed for all data sets combined: maximum diversity was shifted toward higher elevations for 20 data sets and lower elevations for 18 data sets. Deviations tended toward higher elevations for alpha, tropical, and island data sets, whereas gamma, continental, and temperate data sets tended toward lower elevations.

Regression of the elevation of peak species richness on mountain height showed a significant positive relationship (Appendix C; Fig. 2A). This positive linear trend was significant for gamma, tropical, island, and continental data sets, and was particularly pronounced for alpha data sets (Appendix C; Fig. 2B and C; regression equation for alpha transects $Y = 78.1939 + 0.5998X$). The base of many mountains in the gamma and temperate data sets occur at intermediate elevations, thus when standardized for height from base temperate data also demonstrate a significant, positive linear trend with mountain height ($r^2 = 0.573$, $P = 0.0007$), and gamma data demonstrate a stronger trend ($r^2 = 0.323$, $P = 0.0072$). Locations of highest diversity and elevational midpoints were indistinguishable for all data sets combined ($t = -0.427$, $P = 0.672$). But peak diversity occurred at significantly higher elevations for alpha and island data ($t = 3.291$, $P = 0.002$; $t = 2.267$, $P = 0.017$, respectively), and significantly lower elevations for gamma and continental data ($t = -2.498$, $P = 0.011$; $t = -2.010$, $P = 0.028$, respectively) than mountain midpoints. Diversity peaks of combined, alpha, and gamma data sets had significant positive, linear trends with latitude, and temperate data had a negative, linear trend (Appendix C; Fig. 3). Temperate data showed a significant, negative trend with latitude regardless of whether temperate Peru (16° S) was included (Fig. 3C, D). All other data sets showed no trend. Significant latitudinal trends were demonstrated only for gamma and temperate data with the regression of residuals from peak diversity and summit height against latitude (Appendix C).

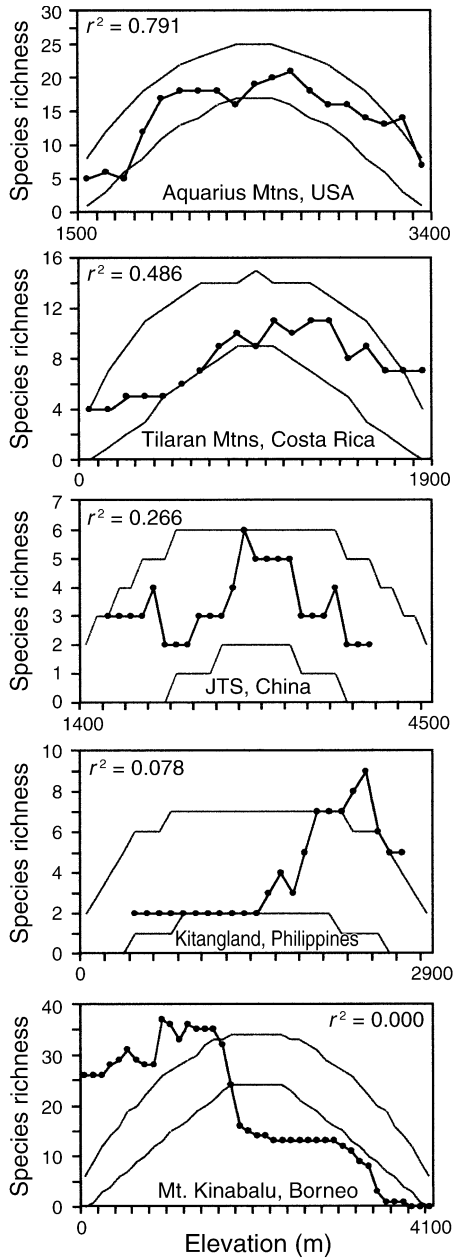


FIG. 1. Five examples of the mid-domain analysis including the 95% confidence limits (lines without data points) from 50 000 range size simulations using Mid-Domain Null (McCain 2004) and the empirical diversity pattern (data points and lines). Coefficients of determination for the fit to the null model are shown in the upper corners. JTS = Jingtshang Station, Mt. Qilian.

DISCUSSION

Elevational patterns of nonvolant small mammals demonstrated strong support for pervasive intermediate elevational peaks in species richness. Such mid-elevational diversity peaks have been documented previously for other taxa, including several invertebrate groups, plants, and amphibians (Rahbek 1995 and ref-

erences therein). In my analyses, biased sampling, area effects on small islands where lowland area is substantially reduced, or historical or current disturbance of lowlands by humans do not underlie mid-elevational peaks in diversity. Thus, given that intermediate elevational peaks in species richness appear to be the dominant pattern, the critical question is what produces them.

Mid-domain effect

The spatial constraints assumed by the mid-domain null model were not highly predictive in this review: of the 39 data sets analyzed, 59% had $r^2 < 30\%$, only 15% had $r^2 > 50\%$. This wide scatter and low predictive ability diminishes the generality of the model as the sole explanation for elevational diversity patterns of nonvolant small mammals. No consistent trend existed in deviations toward higher or lower elevations from the diversity peak predicted by the null model for all data sets combined. Effects of different sampling meth-

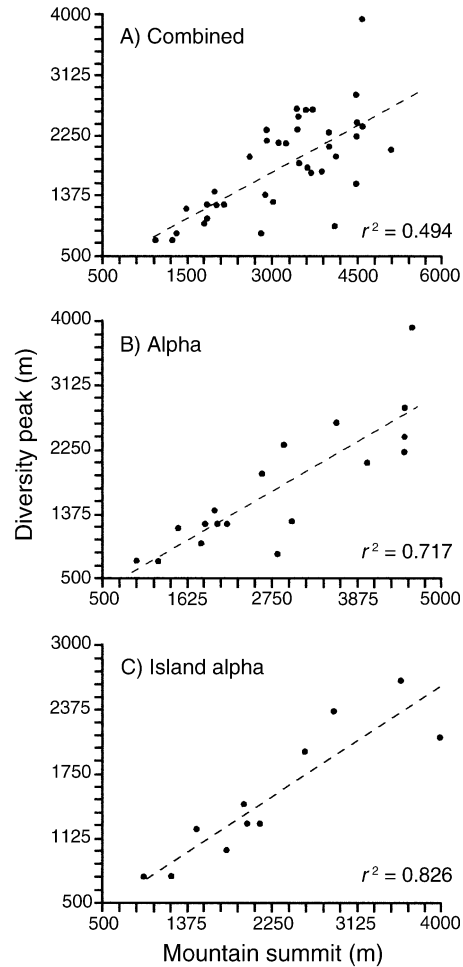


FIG. 2. Positive, linear trend of the maximum diversity of nonvolant small mammals with mountain height for (A) all data sets combined, (B) alpha data sets, and (C) island alpha data.

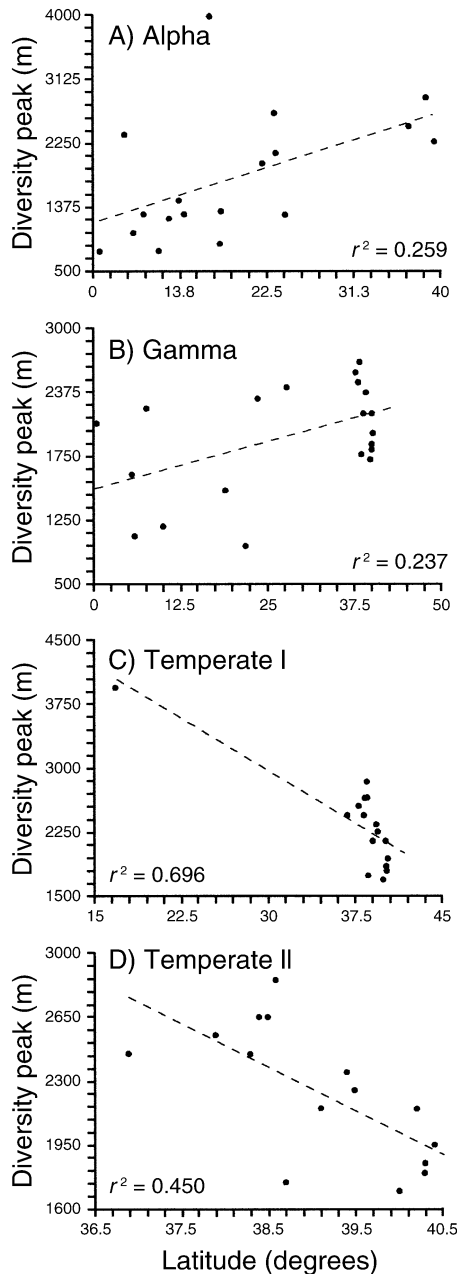


FIG. 3. Linear regressions of the diversity peak of non-volant small mammals with latitude for (A) alpha data, (B) gamma data, (C) temperate data (all), and (D) temperature data without southwestern Peru at 16° S latitude.

ods were apparent, as gamma data followed null model predictions more consistently (higher average r^2 values). Gamma data had diversity peaks shifted toward lower elevations indicating an area effect; peaks shifted toward higher elevations in alpha data sets indicated climatic effects. The consistency of these deviations from the null model predictions may indicate that the underlying mid-domain effects are modified by area and climate trends, either resulting in peak diversity

shifting downward with area or upward with climate. The better fit of the null model with gamma data may indicate that summing elevational ranges more broadly across different slopes and aspects reflects more spatial constraints due to the extending or generalizing of elevational ranges.

Mountain mass effect

A climatic signal was apparent in spite of noise associated with divergent sampling techniques, historical factors, and biogeography. Maximum diversity was at higher elevations on taller mountains, evidence supporting a mountain mass effect produced by interacting climatic factors. The trend is highly significant for alpha data and is significant for all other data sets except temperate data, which is significant only if standardized for absolute mountain height. The mountain mass effect tends to be most noticeable on islands or mountains near the ocean (Flenley 1994 and references therein). This effect was noted for small mammals in the present study as island alpha data had the highest r^2 value, explaining over 82% of the variation (Fig. 2C).

The mid-domain null model predicts peak diversity at the mid-point of the elevational range, hence predicting diversity peaks highly correlated with mountain height. The null model predictions can be tested more finely across the entire elevational gradient; those tests were not generally supportive of the null model as the sole contributory factor. Alpha data sets most strongly corroborated the mountain mass effect, but spatial constraints only explained about 16% of the variability, on average. Alpha data demonstrated maximum diversity significantly above the mid-point of the elevational gradient, with an average near 61% of mountain height. Hence, spatial constraint alone does not appear to be an adequate explanation for the mountain height trend in alpha data. Both climatic and geometric factors could be important to determining the alpha diversity patterns, as climatic effects shifting the diversity peak toward higher elevations modify the underlying unimodal diversity curve of the mid-domain effect.

The climatic trend in diversity peaks with mountain height suggests that small mammals are responding to a climatic optimum. Evidence from several of the tropical alpha data indicates that this optimum may be at intermediate climatic conditions, a few hundred meters below the persistent cloud cover at the top of the mountain (e.g., on five mountains across Madagascar [Goodman et al. 1999], several mountains in the Philippines [Heaney 2001], two mountains in Taiwan [Yu 1994], in Borneo [Md. Nor 2001], and in Costa Rica [McCain 2004]).

Area effect

Because gamma diversity data are summaries of elevational ranges across an entire mountain range, Lomolino (2001) predicted that these studies would show discernable area effects. Indeed, gamma diversity peaks

were shown to be significantly lower than the midpoint of the mountain. Many gamma data sets had maximum diversity in the lower third of the elevational gradient, and several exhibited secondary peaks or plateaus in richness at low elevations. Previous studies found that area effects account for substantial portions of variability in elevational diversity patterns; when area effects were removed, support for other hypotheses was strengthened (Rahbek 1997, Sanders 2002). Thus, it is possible that the species–area effect is masking the mountain mass effect, a stronger fit to spatial constraints, or hindering the detection of latitudinal diversity patterns.

Latitudinal trends

Lomolino (2001) predicted that if climatic factors were driving diversity patterns on elevational gradients, then latitudinal trends should exist. Invoking “downward shifts in climatic regimes and zonal communities,” he predicted negative, linear trends in elevation of peak richness with increasing latitude. The gamma, alpha and temperate data sets demonstrated significant latitudinal effects, but not tropical, island, or continental data sets. The elevation of maximum diversity for gamma and alpha data sets, however, was higher on mountains at higher latitudes, counter to expectations. Temperate data supported the decline in diversity peaks with latitude. It is probable that different climatic influences affect non-volant small mammal communities at different latitudes or that latitudinal patterns are scale dependent. Unfortunately, the latitudinal trend is complicated by geographic bias—most high-latitude studies are gamma data sets from tall mountains, specifically from the western United States. Although when controlling for mountain height, gamma data still show a significant, positive latitudinal trend, but the combined, and alpha data did not (Appendix C). Another complicating factor is that many of high latitude mountains rise from higher initial elevations predisposing such mountain ranges to diversity maxima at elevations above that limit. Controlling for elevational at base of mountain resulted in a nonsignificant latitudinal trend in gamma data ($r^2 = 0.154$, $P = 0.079$), but temperate data retained a significant, negative latitudinal trend ($r^2 = 0.913$, $P = 0.000$). Therefore, when both mountain height and base elevation are controlled, only temperate data sets exhibit a latitudinal trend—the expected decrease in the diversity peaks with latitude. This suggests that temperate clines in latitude may be more pronounced than clines within the tropical region and that the latitudinal pattern may not be a simple linear pattern, both of which are trends seen in montane treelines and snow lines latitudinally (Körner 1998 and references therein).

General conclusions

Alpha and gamma diversity data demonstrate divergent trends in spatial constraint, area, climate, and latitudinal effects. Alpha data show strong effects of cli-

mate shifting maximum diversity toward higher elevations on taller mountains and minor effects of spatial constraint. This mirrors the general conclusions of elevational patterns of small mammals in Costa Rica (McCain 2004), where spatial constraint could explain a general mid-elevational trend in diversity, but the skew in maximum diversity towards higher elevations indicated strong influences of climate. Gamma data exhibit greater influence of spatial constraint and area effects, as peaks in diversity are found significantly lower than the elevational midpoints. Thus, it appears that several factors are important in determining elevational diversity patterns in small mammals: spatial constraint effects modified by the area and climate. Temperate data demonstrated latitudinal trends robust to mountain height and base elevations not seen in other data sets, and not predicted by spatial constraint alone. Since sampling biases hinder examinations of latitudinal trends, it would be advantageous for future researchers to document gamma and alpha diversity patterns along a wider latitudinal span, including gradients starting at elevations nearer to sea level and on the lowest and tallest mountains. More detailed climatic data for a range of mountain heights and latitudes is a pressing need to specifically evaluate the influence of particular climatic factors.

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APPENDIX A

A table listing all elevational data sets of small-mammal diversity, including data specifics, null model and analysis values, and a list of data sources used in the review is available in ESA's Electronic Data Archive: *Ecological Archives* E086-019-A1.

APPENDIX B

A table of average linear regression statistics for null model analyses of elevational diversity patterns is available in ESA's Electronic Data Archive: *Ecological Archives* E086-019-A2.

APPENDIX C

A table of linear regression statistics for elevational diversity peak by mountain height, diversity peak by latitude, and residuals (from the regression of diversity peak and mountain height) by latitude is available in ESA's Electronic Data Archive: *Ecological Archives* E086-019-A3.