Ecological Gradients in Diversity and Abundance: A Search for Patterns and Processes in Small Mammal Communities

by Christy M. McCain

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BY C. McCAIN

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ABSTRACT

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One of the most fundamental questions in ecology is: what are the patterns of diversity and the mechanisms that produce them? Many biological theories have been proposed to explain latitudinal and elevational diversity gradients, but no accepted, general explanation for the distribution of biodiversity has surfaced. Two necessities for establishing a general diversity theory are utilizing more rigorous statistical methods to test hypotheses, and including more comparative analyses. With these aims in mind, I examine the predictability of null models and biological diversity hypotheses for latitudinal and elevational gradients in diversity and abundance of small mammals. The unimodal distribution of diversity in North American desert rodents was highly consistent with the mid-domain effect—a spatial constraint null model incorporating the overlap of variably sized ranges within a bounded region. Deviations from the null model demonstrated a localized pulse in richness caused by a local hard boundary, the Baja peninsula. The small mammal diversity along an elevational transect in Costa Rica was unimodal with species richness highest between 1000–1300 m. The spatial constraints of montane topography appear to influence the diversity pattern, although climatic conditions including an intermediate rainfall and temperature regime, and distance from the persistent cloud cap also are correlated with the pattern. The global analysis of elevational diversity trends for non-volant small mammals revealed a ubiquitous pattern of mid-elevational peaks in species richness. The mid-domain null model was not generally predictive across all datasets. Diversity peaks occurred at higher elevations on taller mountains (Massenerhebung effect), which is consistent with climatic factors working in concert to produce elevationally correlated habitat bands. Gamma diversity patterns demonstrated higher altitudinal peaks in species diversity as latitude increased. An examination of replicates in alpha diversity studies along elevational transects found high variability both temporally and spatially, emphasizing the necessity of replication in well-designed studies of diversity gradients. In an examination of range size-abundance trends no strong relationship was found between abundance or body size with elevational range size. Local and regional abundances across elevational ranges generally revealed a trend toward higher abundances at mid-range, although usually not centered at the range midpoint.

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INTRODUCTION

One of the most fundamental questions in ecology addresses biodiversity on earth: what are patterns of diversity and the mechanisms that produce them? Biodiversity patterns have been addressed scientifically since the revolutionary work of Darwin and Wallace who initially recognized the two most universal ecological gradients: latitudinal and elevational (Rosenzweig 1992, 1995). More recently, many other gradients have been considered, including productivity, disturbance, salinity, and bathymetric gradients. While mechanisms underlying patterns have been the emphasis of research efforts for decades, no accepted, general explanation for the distribution of biodiversity has surfaced, not even for the most studied gradients of latitude and elevation (Rosenzweig 1992, 1995; MacArthur 1972; Brown 2001; Lomolino 2001). The need to document and understand the mechanisms producing biodiversity patterns is urgent when biodiversity is being lost at unprecedented rates due to global habitat destruction, pollution, and climate change. To discern the most effective methods to preserve, protect and regenerate biodiversity, we need better comprehension of the mechanisms creating and maintaining biodiversity.

Eminent researchers in the fields of ecology, biogeography and evolutionary biology have asserted that we may be on the threshold of developing general theories for biodiversity (Brown 2001). Three branches of research offer promising results. The first emphasizes hypothesis testing by delineating specific predictions for the various diversity theories. Second is the application of new quantitative and statistical methods involving null models and simulation modeling of biodiversity data over various spatial scales in order to adequately test hypotheses. Third is the employment of synthetic and comparative analyses of large data sets of biodiversity information gathered over centuries of field research. These three tenets are employed in the diversity analyses presented herein.

As diversity theory progresses and empirical data accrue, it has become increasingly clear that many factors underlie large-scale diversity gradients (Brown

2001; Lomolino 2001). In the tangled complexity of biological factors affecting diversity gradients, a new null model, the mid-domain effect, could help to pare down the complexity. A mid-domain effect is predicted where spatial constraints like landmass boundaries such as oceans and mountaintops or edges on continents or islands limit species ranges and the simple overlap of many, variously sized ranges create a peak in species richness toward the middle of the bounded area (Colwell and Hurtt 1994; Colwell and Lees 2000). This prediction is based solely on geographic constraints and offers predictions against which empirical patterns can be compared. The utility of the null model approach for diversity patterns was tested for North American desert rodents across a latitudinal gradient (Chapter 1). Two different methodologies are used and compared to examine the predictions of the mid-domain effect, and several biological diversity theories are also compared to the empirical diversity pattern, including the species-area relationship, latitudinal gradients, productivity gradients, Rapoport's rule, habitat complexity, and adequacy of sampling.

Elevational gradients are excellent candidates for improving our understanding of patterns and processes of biodiversity. Montane topography is global—all continents and most islands vary elevationally—and climatic and ecological changes vary predictably along elevational gradients. Additionally, montane ecosystems are most likely to suffer extreme shifts in habitat distribution with global climate warming, as predicted by the seminal work of McDonald and Brown (1992). For these reasons, quantitative examination of elevational biodiversity patterns and processes would be applicable to understanding general production and maintenance of global biodiversity. Two separate analyses were used to assess the biodiversity patterns along elevational gradients. The first was a field study to comprehensively document and examine the alpha and gamma patterns of species richness in non-volant, small mammals (rodents, shrews, and mouse opossums) along a tropical elevational gradient in northwestern Costa Rica (Chapter 2). These data were used to determine the support for existing hypotheses of species richness encompassing mid-domain null models, as well as climatic, and community overlap hypotheses. The second was a comparative, synthetic analysis of all elevational gradients in small mammal diversity gathered from the literature (n = 51). Therein, I quantitatively test theoretical predictions of a null model and climatic factors, including the mountain mass effect, latitudinal trends, and species-area effects (Chapter 3).

The majority of elevational diversity studies in the literature assume that a single sampling transect is an accurate index to the species richness pattern for a mountain. This assumption was examined by assessing the consistency among temporal and spatial replicates in alpha diversity studies along elevational transects (Chapter 4). Lastly, many diversity patterns may be a result of underlying range size and abundance patterns of the species in the various communities. Chapter 5 is an assessment of the range size-abundance patterns for Costa Rican small mammals at a local and region scales along elevational gradients. Three predictions of range size theory were examined. First, species with larger ranges will have higher population density. Second, species with larger ranges will have greater body size. Third, populations will be highest at the center of elevational ranges.

CHAPTER 1.

NORTH AMERICAN DESERT RODENTS: A TEST OF THE MID-DOMAIN EFFECT IN SPECIES RICHNESS

ABSTRACT

Many biological theories have been proposed to explain latitudinal and elevational gradients of species richness, but only recently have theories been proposed that suggest that these patterns may be due solely to geographic constraints. These null models predict mid-domain peaks in species richness as a consequence of geometric patterns resulting from overlapping species ranges between 2 geographic boundaries. Desert rodents exhibit a marked mid-domain peak in species richness for boundaries defined by the latitudinal extent of North American deserts (19° N to 45° N). Empirical patterns are compared to predictions of 2 null models: an analytical-stochastic model and the binomial model. Empirical species richness occurs almost entirely within 95% prediction curves of the analytical-stochastic model. Observed species richness is highly correlated with predictions of the binomial model ($r^2 =$ 93%) but does not generally occur within 95% confidence intervals, in part because empirical range size distributions differ from predicted distributions. Other diversity theories, species-area relationships, productivity gradients, latitudinal gradients, and Rapoport's Rule, are evaluated; none is consistent with empirical patterns. These results demonstrate that the mid-domain effect is a consequence of overlap of variably sized ranges within a bounded region for both ecologically defined hard boundaries as well as boundaries determined by the shape of the earth. The significant deviations from null model predictions become the biological points of interest: skewed and/or localized pulses or depressions of species richness.

Deviations in the present analysis demonstrated a localized pulse in richness caused by a local hard boundary, the Baja peninsula.

INTRODUCTION

Robert H. MacArthur (1972:1) stated, “To do science is to search for repeated patterns, not simply to accumulate facts.” MacArthur is one of many ecologists who have investigated patterns of species diversity, specifically latitudinal and elevational gradients of species richness (MacArthur 1965; Rosenzweig 1995, and references therein). The latitudinal gradient, a negative relationship between latitude and richness with a peak in richness at the equator, is a pattern that is evinced by many taxa throughout the world. Numerous theories have been proposed to account for the gradient (MacArthur 1965; Pianka 1966; Terborgh 1971; Wilson 1973; Osman and Whitlatch 1978; Stevens 1989; Pagel et al. 1991; Rosenzweig 1992, 1995; Colwell and Hurtt 1994; Kaufman 1995; Willig and Lyons 1998; Lees et al. 1999). The less well-documented elevational gradient of species richness can have a mid-elevation peak in species richness, and several biological theories exist to explain this pattern (Graham 1983; Rosenzweig 1992, 1995; Stevens 1992; Colwell and Hurtt 1994; Patterson et al. 1996; Heaney 2001; Sanchez-Cordero 2001). The majority propose that the patterns result from an underlying biological process, although no single theory has widespread acceptance (Rosenzweig 1992; Colwell and Hurtt 1994; Kaufman 1995).

Recently, several independently derived models have emerged to explain these gradients based solely on geometric constraints on species ranges, without the incorporation of underlying biological mechanisms (Colwell and Hurtt 1994; Willig and Lyons 1998; Lees et al. 1999). These null models are derived from the geometric pattern that results from random range sizes and placements between the endpoints of 2 hard boundaries, a pattern termed the mid-domain effect (Colwell and Lees 2000).

Colwell and Lees (2000:72) defined the mid-domain effect as "the increasing overlap of species ranges toward the centre of a shared geographic domain due to geometric boundary constraints in relation to the distribution of species' range sizes and midpoints." Bounded range models assume that all species considered in the analysis share the same hard boundaries; therefore all species' ranges must be entirely within the bounded domain, and large ranges must be centered near the center of the domain. This results in increasing species richness toward the midpoint of the domain. An example of geographic boundaries limiting species ranges is that of terrestrial species on an island where distinct limits to the ranges are the edges of the island. Such range constraints can exist due to geographic features, such as continental boundaries, elevational boundaries, or the perimeter or depth of a body of water. Ecological range boundaries exist where species endemic to a specific ecological biome are constrained by the biotic and abiotic distribution of that ecosystem. All proposed null models—the fully stochastic and analytical-stochastic models (Colwell and Hurtt 1994), the binomial model (Willig and Lyons 1998), and the probabilistic model (Lees et al. 1999)—predict a mid-domain effect in species richness due solely to geometric constraints, although each employs distinct mathematical frameworks (Colwell and Lees 2000).

Null models suggest that underlying patterns in latitudinal and elevational gradients of species richness are the result of geographic boundaries such as coastlines and mountains (Colwell and Hurtt 1994). A diversity peak at the equator and at middle elevations was documented before the null models of mid-domain effect were proposed; therefore additional empirical examples of unknown species richness patterns within bounded range limits need to be examined to test the predictions of these null models. Two studies have confirmed the mid-domain effect outside the context of latitude or elevation. Pineda and Caswell (1998) examined bathymetric gradients and Lees et al. (1999) examined gradients across the island of Madagascar.

The North American desert biome has relatively distinct northern and southern ecological boundaries (as well as east-west boundaries) that limit the ranges of desert endemics—19° N to 45° N latitude (Fig. 1; MacMahon 1985). This ecological domain allows a valuable empirical test for null models of species richness because the latitudinal patterns of species richness within the bounded region have not been documented previously, and because the North American desert biome includes taxonomic groups with numerous endemic desert taxa (e.g. Heteromyidae). Herein, these desert endemics were employed in an empirical examination of the mid-domain effect. Null models predict a peak in species richness near the midpoint of the geographic limits of North American deserts, although several other patterns of species richness could be encountered. For example, if taxa were responding to environmental correlates of latitude, then species richness should increase toward lower latitudes, a pattern that has been shown for rodents in the New World (Kaufman 1995). Similarly, a uniform pattern could be encountered where species richness was uniformly distributed across the desert latitudinal gradient.

METHODS

An a priori delineation of North American deserts between 19° N and 45° N latitude was based on a combination of 2 maps in MacMahon (1985). One map depicts the classical ranges of North American deserts based on climate and plant distributions, and the 2nd was based on a combination of climate and on distributions of flora and fauna. The most expansive delineation based on these 2 maps was used in the present analysis (Fig. 1).

Thirty-seven rodent species endemic to North American deserts (Appendix I) were employed in an empirical examination of the latitudinal trends of species richness. Desert endemism was defined as those species with the majority (>90%) of their range occurring within the a priori desert delineation. The list of species and their ranges were compiled from Durrant (1952), Baker (1956), Ingles (1965), Anderson (1972), Findley et al. (1975), Hall (1981), Hoffmeister (1986), Jameson and Peeters (1988), and Davis and Schmidly (1994). Taxonomy from Wilson and Reeder (1993) was used to recognize species status. The latitudinal extent of the range of each species was calculated, producing 2 characteristics—the latitudinal midpoint and latitudinal range (Fig. 2). Species richness curves were then calculated by importing the empirical range sizes and midpoints into the computer program RangeModel (RangeModel: a Monte Carlo simulation tool for assessing geometric constraints on species richness. http:/viceroy.eeb.uconn.edu/RangeModel).

Two groupings of the desert rodent endemics were evaluated: (1) all endemics within the continental area of the North American deserts (*n* = 37), and (2) continental endemics excluding Baja endemics (*n* = 31). The 6 Baja endemics were excluded from the 2nd grouping to remove possible peninsular effects, which produce decreasing species richness towards the terminus of the peninsula (Brown and Lomolino 1998). Taylor and Regal (1978) detected a peninsular effect in Baja for various vertebrate groups including mammals and heteromyid rodents. Lawlor (1983) refuted these patterns for mammals in general and bats, but found some evidence that heteromyids rodents may show a peninsular effect.

Empirical patterns of species richness were compared to predictions of 2 null models—Colwell and Hurtt's analytical-stochastic model (1994) and Willig and Lyons' binomial model (1998). Colwell and Hurtt (Colwell and Hurtt 1994) created a group of null models with different parameters; some are fully stochastic, whereas others are capable of simulations using empirical data sets (see computer program RangeModel— http:/viceroy.eeb.uconn.edu/RangeModel). The 2 fully stochastic models, Model 2 and 3 of Colwell and Hurtt (1994), which correspond to the bivariate uniform range model and the uniform random range midpoint and range size models of the RangeModel program, are incapable of using empirical data. These models assume different underlying distributions of range sizes and placements of range midpoints; thus all variables except species number are predetermined. Model 2, the bivariate uniform model, is equivalent mathematically to the binomial model and MacArthur's two-hit broken stick model (Colwell and Lees 2000). Therefore, the ensuing discussion of the bivariate uniform model will be addressed in accordance with the binomial model. The uniform random models, 2 variations on Model 3, place 1 variable (either range size or range midpoint) within the domain boundaries according to a uniform probability distribution then randomly draw values for the 2 variable from geometrically feasible values with the bounded domain. These Model 3 variations are not employed in the current analysis because empirical values cannot be incorporated.

Unlike Models 2 and 3, the 2 forms of Colwell's analytical-stochastic model use empirical data from a system of interest, thus making the results "conditional" on the imported variables. The analytical-stochastic models sample with replacement from imported empirical (or hypothetical) data for 1 variable, and then randomize the placement of the other according to a modified uniform distribution for feasible values within 2 boundary endpoints to produce species richness curves. The first analytical-stochastic model uses empirical range sizes and creates randomized placements of midpoints between the boundaries, whereas the second form of the model uses the empirical midpoint locations and creates randomized range sizes constrained by the domain limits. These were the simulation models used in the current analysis because randomization using empirical data is better able to assess whether under random conditions, given either known range sizes or known range midpoints, a mid-domain effect occurs.

Empirical range sizes and midpoints of desert rodents were imported into RangeModel and were used to generate 600 simulations for each species group using random placement of empirical range sizes and again of empirical midpoints. Simulation results were then used to create 95% simulation prediction curves. The empirical species richness data were then compared to the 95% simulation prediction curves to assess the accuracy of the null model predictions. Random simulations were limited to 600 as each successive set of 200 simulations leads to minor changes in the 95% prediction curves.

The binomial null model is based on the joint probabilities of choosing 2 random points on a number line between zero and 1, such that the range spans a sampling point, p, on the unit domain (Willig and Lyons 1998). The probability of a randomly chosen range spanning the sampling point is 2pq, where q = 1-p. The resulting species richness curve has a mid-domain effect with the highest species richness at p = 0.5, with the predicted species richness being half of the total number of species in the analysis. This model allows for the calculation of standard deviations and 95% confidence intervals using a corrected version of the formula presented in Willig and Lyons (1998, pers. comm.) as follows: $\mathrm{Var}(2pqS) = \{2(S-1)/S^3\}\{(3-2S)(1-2pq)^2 + 2(S-2)(p^3 + q^3) + (1-2pq)\}$ from Nei (1975), and Nei and Roychoudhury (1974), where S is the number of range termini or twice the number of species in the analysis. Two standard deviations multiplied by species richness then give values to add and subtract from the predicted values to delineate approximate 95% confidence intervals of the binomial models predictions. Following Willig and Lyons (1998), I also tested for a linear association between richness and 2pq. The empirical values of species richness at each 1° of the desert domain were regressed against 2pq, and r^2 and 95% prediction curves were calculated to show how well the empirical data conform to the null model.

The binomial null model not only predicts a mid-domain effect, but also predicts an implicit distribution of range sizes based on the joint probability density function of pairs of uniformly distributed variables that delimit species' latitudinal ranges. This implicit frequency distribution of range sizes is a decreasing function from small to large ranges. Thus, implying that empirical species richness patterns that fit the binomial null model should consist of many small ranged species, few mid-ranged species and very few large ranged species. This was tested by comparing the cumulative number of range sizes produced via the null model with the cumulative distribution of range sizes in the empirical data using a Kolmogorov-Smirnov goodness-of-fit test (MINITAB 1996). This requirement of a particular distribution of range sizes is shared by the MacArthur's two-hit broken stick and the bivariate uniform random model (Colwell and Lees 2000), but not with the analytical-stochastic models. When the empirical distribution of range sizes differs from the underlying binomial model distribution (i.e. more larger ranged species), the empirical species richness curve will diverge from predicted curve.

Species richness frequently is correlated positively with area (Rosenzweig 1995). The North American desert biome does not have equal area throughout its latitudinal extent. An estimate of area per latitudinal degree was calculated by digitizing the desert boundaries into a geographic information system using the latest version of ArcInfo 8.1 (ESRI 2001). The area estimates were based on the Albers equal-area conic projections using 24° N and 41° N as the standard parallels which support a north-south extent of up to 30 –35° (25° extent for present analysis). The effect of area on the species richness pattern was assessed using regression analyses (MINITAB 1996). Species richness was regressed against 2pq alone, 2pq with area, and area alone. Experimental lack of fit tests (MINITAB 1996) produced no evidence for curvilinearity ($P > 0.10$) in regressions including 2pq with or without area.

RESULTS

Both species richness curves showed a strong mid-domain effect (Fig. 3). The concentration of small-ranged species endemic to the Baja Peninsula ($n = 6$) created a slight skew in the peak of species richness at 28° latitude, but otherwise was indistinguishable from the purely continental pattern. The continental species richness gradient also had a marked mid-domain peak, with the highest richness close to the center of the latitudinal domain at about 32°.

Six hundred RangeModel simulations (Colwell http:/viceroy.eeb.uconn.edu/RangeModel) using the empirical range sizes for each species grouping and randomized placement of midpoints all resulted in a mid-domain peak in species richness. A comparison of the empirical data to the 95% simulation prediction curves showed that the majority of empirical points (116/120) occurred within the predicted range of the analytical-stochastic null model (Fig. 3). The 600 RangeModel simulations with empirical range midpoints for each species grouping and randomized placement of range sizes also resulted in a mid-domain peaks in species richness. Again, the majority of empirical points (119/120) occurred within the 95% simulation prediction curves of the analytical-stochastic null model (Fig. 4).

Regressions of species richness per latitudinal band predicted by the binomial null model (2pq) against empirical values resulted in high r^2 for both species groupings: all desert rodent endemics, $r^2 = 0.88$; species excluding Baja peninsular endemics, $r^2 = 0.93$. Even when all rodent species inhabiting the North American deserts were included in the analyses ($n = 53$ including 22 non-endemics) a strong mid-domain effect still was observed ($r^2 = 0.90$). Regression analysis demonstrated high correlation between observed and the predicted species richness values, as all empirical data occurred within the 95% regression prediction curves (curves based solely on regression analysis). The empirical distributions did not coincide, however, with the specific predicted values of species richness, as 60% of the empirical data occurred outside the 95% confidence intervals based on the calculations of variance, which include the restrictions of underlying range distribution (Fig. 5). Observed species richness was higher than predicted by the binomial null model. This was partially a result of the deviation of the empirical range size distribution from that predicted by the binomial model. Although not significantly different in cumulative deviations (All species: $P > 0.2$; without Baja peninsular endemics: $P > 0.2$), the desert species had fewer small ranges, and more intermediate and large range sizes than predicted (Fig. 6). The small increase in numbers of species with larger range sizes leads to the peak in species richness deviating from the predicted value of n / 2.

The area estimates for each degree of latitude were not equal for all the latitudinal bands within North American deserts (Fig. 7A) or for the distribution excluding Baja (Fig. 7B). The greatest area occurred where the Sonoran and

Chihuahuan deserts overlapped between 29° and 33° N latitude, with a lower peak in area within the Great Basin Desert (39° to 42° N latitude). Plots of latitude versus area had 2 peaks whereas curves of species richness showed a single peak (Fig. 7). The regressions using 2pq alone to predict species richness had identical r^2 values to regressions including both 2pq and area (all species, 0.88 and 0.88; and species excluding Baja endemics, 0.93 and 0.93, respectively). The regression using area alone to predict species richness resulted in much lower r^2 values (all species, 0.47; and species excluding Baja endemics, 0.37, respectively).

DISCUSSION

Evaluation of null models supported the conclusion that the pattern of species richness for North American desert rodent endemics was a consequence of geometric constraints within a bounded environmental domain. A comparison of the predictions and deviations based on the 2 null models tested illustrated the differences between and strengths of the 2 models.

RangeModel null model.—Empirical patterns of species richness agree closely with predictions of analytical-stochastic models constrained by empirical range sizes or empirical range midpoints, with only 5 out of 240 data points occurring outside the 95% prediction limits (Figs. 3 and 4). All five outliers were associated with the curve that included the Baja peninsular endemics. The range midpoint simulations produced slightly lower richness than predicted towards the extreme limits of the desert latitudinal extent, and the range size simulations showed slightly higher than expected richness at 28°N. The peninsular effect could bias data sets that included peninsular species by creating an exaggerated decrease in species richness along the extent of the peninsula. Therefore, species richness curves including peninsular endemics may deviate from null model predictions at the southern extent of the peninsula. This was not the case in empirical analysis. The deviations of lower richness were outside the extent of the peninsula.

The influence of peninsular endemics was to shift the peak in richness towards the south, as the Baja endemics were all clustered within a small extent of the desert distribution. This is the likely reason for a slight deviation of higher than expected richness at 28° and slightly lower than expected towards the extremes of the distribution. In a comparison of the 2 simulation sets this reasoning becomes apparent, as the simulations using observed range sizes with random midpoint placement did not predict a cluster of species but a more even dispersion within the desert domain, while the simulations using empirical midpoint distributions, with the cluster of peninsular midpoints, predicted higher richness slightly south of the center. The lack of a peninsular effect for the desert endemics confirms the suspicions of Lawlor (1983) that the suggestion there is a peninsular effect in rodents is unfounded and that only weak patterns exist for heteromyid rodents. A more accurate description of Baja peninsula is that of a local hard boundary at the southern end of the peninsula. In such cases, a smaller, localized mid-domain peak would be expected towards the center of the local domain which may create pulses of higher richness in a broader diversity pattern. The local hard boundary at the southern end of Baja leads to more Baja endemics overlapping towards the center of Baja, thus creating a localized pulse in richness which led to the deviations from predictions across the entire desert domain.

In this analysis, a priori knowledge of the peninsular effect allowed for explicit evaluation of the factor. Analyses of patterns of species richness in less intensely investigated regions might identify such unusual patterns as significant deviations from predictions of the null model. Recognition of local hard boundaries within broader domains may clarify localized pulses in richness that appear in the analysis as deviations. A comparison of the simulations separately constrained by observed range sizes and observed range midpoints enables a more comprehensive evaluation of possible causes of divergent patterns than would use of models not constrained in such a manner (i.e. binomial model).

Binomial null model.—The binomial model serves as a null model for the mid-domain effect, as does the analytical-stochastic model of Colwell and Hurtt (1994), but the binomial has more specific predictions about the range size distribution. The generalized mid-domain effect predicts the shape of the richness gradient between 2 distinct domain boundaries. It predicts peak richness at the center of the domain with species richness decreasing towards the limits of the domain, but it does not assume any specific distribution of range sizes or any specific species richness values. All distributions of variable range sizes can produce mid-domain effects, but of different magnitude of curvature. A distribution of variable small range sizes placed randomly, but in a uniform distribution across the domain, will create a mid-domain peak with a flat and low curvature. A distribution of variable large and intermediate range sizes will produce a steep curve in species richness with a distinct peak. Colwell's models allow the testing for these different distributions of range sizes through simple dummy datasets imported into his RangeModel program.

Using confidence intervals from the variance calculation of 2pq (Willig and Lyons 1998) not only tests for a mid-domain effect but also tests for a specific number of species at that peak and elsewhere ($R_{predicted} = 2pqR_{total}$; R = species richness; i.e. peak species richness = $R_{total} / 2$). The strict form of the model assumes a triangular distribution of range sizes (Fig. 6), such that the majority of range sizes are small, few are intermediate-sized, and very few large range sizes exist. Such a distribution of range sizes between the 2 range constraints creates a mid-domain species-richness curve of a standardized low curvature, constraining the peak to be half of the total species richness. The more large and intermediate range sizes in the distribution, the greater the overlap of ranges toward the center of the domain, leading to a higher peak and a more pronounced curvature to the species richness pattern. This relationship between range sizes and curve shape is demonstrated clearly in both Colwell and Hurtt (1994) and Colwell and Lees (2000).

Therefore, empirical species richness patterns may be completely congruent with the null model predictions based on the geometric effects of bounded ranges but may not fall within the confidence intervals of the binomial model if the empirical distribution of ranges sizes includes more intermediate or large-sized ranges than the underlying distribution of the binomial model. This was the case with the desert rodent species richness pattern (as well as the species richness patterns for bats of Willig and Lyons 1998) as all indications supported the mid-domain effect while the 95% confidence intervals were consistently lower than the empirical curves. The distribution of range sizes for desert rodent endemics included more (but not significantly more) intermediate to large range sizes than predicted by the binomial distribution, resulting in more than half the species being present at mid-domain. By overlaying the 95% simulation prediction curves of the RangeModel and the predicted curve and associated 95% confidence curves of the binomial model it is apparent that the binomial species richness predictions are low, as the binomial prediction curve corresponds closely with the lower 95% simulation prediction curve of RangeModel. Additionally, half the points of the lower binomial 95% confidence curve were outside RangeModel predictions.

According to range size theory, many distributions of range sizes are strongly right-skewed and generally follow a log-normal distribution, although few empirical cases have been tested for fit to a log-normal distribution. Of those that have, many deviate significantly from this distribution (Gaston 1996). The binomial model assumes a triangular distribution of range sizes—a linearly decreasing function of sizes—although this is not a frequently cited distribution (Gaston 1996). Since range-size distribution has received relatively little investigation, and because the universality of a single range-size distribution among variously sized groups of taxa has yet to be shown, the assumption of the triangular range size distribution of the binomial model cannot yet be verified.

Biological theories.—Several biological theories have been proposed that also could produce peaks in species richness within a range domain, namely the species-area relationship, latitudinal gradients, productivity gradients, Rapoport's rule, habitat complexity, and inadequate sampling. As stated earlier, the species-area relationship is a pattern of increasing species richness with increasing area (Rosenzweig 1992, 1995; Willig and Lyons 1998; Lees et al. 1999). This pattern could produce a mid-domain peak in species richness if the greatest area were found towards the center of the distribution, and tapers to the extremes. In North American deserts, the area effect was small, and insignificant. Therefore, the species-area relationship or longitude (Bokma and Monkkonen 2000; Bokma et al. 2001) cannot be the primary underlying cause of the desert rodent species richness pattern.

With respect to the latitudinal species richness gradient, the desert-species richness pattern clearly does not follow a trend toward increasing richness with decreasing latitude since the lowest species richness was at the southernmost latitudes. Kaufman (1995) examined the latitudinal gradients of mammals by taxonomic orders, and the trend for all mammals was a strong peak in species richness at the equator. The pattern for rodents was an irregular hump-shaped curve with a general trend towards higher species richness near the equator but with several peaks and valleys between 45° N and 45° S latitude (Fig. 5; Kaufman 1995). Between 19° N and 45° N, her curve for rodents is concave, with the lowest local diversity at about 30°. This is opposite the pattern demonstrated in this study for the desert rodents at these latitudes, further indicating that the desert pattern is divergent from the overall rodent diversity gradient.

Productivity gradients frequently show hump-shaped relationships with species richness, with peaks in richness at intermediate productivity levels along a gradient from low to high productivity (Rosenzweig 1992, 1995; Waide et al. 1999; Mittelbach et al. 2001), although other studies show trends of increasing or decreasing species diversity with increasing productivity (Brown 1975; Rosenzweig 1992, 1995; Waide et al. 1999; Mittelbach et al. 2001). For deserts, productivity is relatively low, ranging from 0 to 600 g $m^{-2}yr^{-1}$, but has been shown to be highly variable spatially and temporally (Brown 1975; Waide et al. 1999). According to Waide et al. (1999), the relationship in arid ecosystems has not been investigated specifically, but they did note 2 general trends of particular value. They found that, for large-scale patterns among deserts across the world, those deserts with low to zero productivity have low species richness for various groups of taxa, whereas those with relatively high productivity had high species richness. However, at smaller scales, i.e. deserts within the same region, they did not find increased species richness with productivity (Fig. 8; Waide et al. 1999). In North America for instance, the Mojave Desert has the lowest productivity but high species richness while the Chihuahuan Desert has the highest productivity estimates but lower richness. If productivity were the primary underlying cause of the mid-domain peak in species richness in the North American deserts, then the prediction would be either that there is highest richness at intermediate productivity levels or that there is highest richness at high productivity levels. Neither of these cases is supported with the present productivity estimates available on the regional scale. Productivity-diversity trends appear to be strongly scale dependent (Waide et al. 1999; Scheiner et al. 2000; Mittelbach et al. 2001), and therefore productivity-diversity patterns at local scales may show divergent patterns from the regional scale studied here.

Rapoport's rule, the tendency for mean sizes of species ranges to decrease towards the equator and towards mid-elevations, predicts that as species richness increases range sizes decrease (Stevens 1989, 1992). Recently, Rapoport's rule has caused a flurry of investigative effort applied to understanding species richness gradients, including a test of the universality of the pattern (Lyons and Willig 1997) and theoretical modeling (Colwell and Hurtt 1994; Taylor and Gaines 1999). These studies suggest that the universality and robustness of Rapoport's rule are questionable. Similarly, Rapoport's Rule was not corroborated in the present analysis, as small range sizes were not clustered toward the area of highest species richness (Fig. 2).

Inadequate sampling has been shown to affect richness trends (Colwell and Hurtt 1994; Lees et al. 1999), although this most often is the case for tropical regions where species are not well documented and ranges may be far from accurate. In this case, the majority of species used in the study have been known since the beginning of the 1900s, and most have well-known ranges (Hall 1981). Thus, neither inadequate sampling, area, latitudinal species gradient, productivity, nor Rapoport's rule appear to explain the unimodal pattern of species richness observed for desert rodents.

Some authors assert that latitudinal, elevational, and even desert mid-domain peaks in species richness are the result of increased habitat complexity (MacArthur 1964; Pianka 1966). If habitat complexity is the result of higher diversity of plants and plant forms, and plant diversity is also highest at mid-domain, that pattern may just be a coincident mid-domain species-richness peak for plant endemics bounded by the same geographic or ecological boundaries as the animal kingdom. Thus, an interesting prediction of the mid-domain effect is that patterns of habitat complexity or plant species richness also would reflect geometric constraints. Of course, habitat complexity also may involve relationships with climatic variables and be intertwined with productivity hypotheses. To understand the explanatory power of these hypotheses, detailed empirical analyses are needed.

It has been suggested that the mid-domain null model limits analyses to endemics within the boundaries of specified limits and has biased the results by not including non-endemics, generalists of the same taxa also present within the same region (R. Holt, and J. Brown, pers. com.). Some critics argue that the mid-domain effect may be a result of this culling of the dataset and predict divergent patterns of species richness in analyses that include all species inhabiting the region. But when all rodent species inhabiting the North American deserts were included in the analyses ($n = 53$ including 22 non-endemics) a strong mid-domain effect still was observed ($r^2 = 0.90$). Since non-endemic species tend to be generalists, they have larger ranges that encompass more of the extent of the domain, which leads to a similarly shaped, but elevated, species richness curve with increased richness throughout the curve but particularly pronounced toward the center of the domain. Thus, adding non-endemics to the analysis does not lead to divergent patterns from the predictions of the null models.

The Mid-domain effect.—The mid-domain effect is an unavoidable consequence of bounded ranges of variable sizes. This is true for bounded latitudinal ranges, as well as for longitudinal or 3-dimensional ranges. As in any null model, it is the basis to which novel species-richness patterns should be compared. Significant deviations from the null model could then be biologically interesting patterns and indicate the need for analysis of such factors as distribution of abiotic resources, competition, evolutionary history, ecological history, and biome shifts.

Empirical diversity patterns that conform to predictions of the mid-domain effect based on randomizations of the empirical range sizes and midpoints do not signify that the diversity pattern is random. The empirical pattern consists of a distribution of species with different-sized overlapping ranges within limited boundaries that result in the mid-domain peak in species richness. Any random grouping of species with variably sized ranges within boundaries will show a mid-domain peak. The biological requirements and evolutionary history of each species has determined its range size and location within the bounded range of the North American deserts. The partitioning of the desert domain by each species and reasons for individual ranges distributions are biologically interesting on a finer community scale. Osman and Whitlatch (1978:52) addressed this general issue that diversity patterns "can exist regardless of any assumptions concerning the importance of competition, predation, species packing, niche characteristics, species ability to adapt, etc. Certainly, processes such as competition and predation may be important in determining the co-occurrence of particular suites of species . . ., but a diversity pattern could have resulted independent of these." Therefore, in the scope of the mid-domain effect, the diversity pattern may be a result of geometric boundaries, but species diversity in patches of the domain (alpha diversity) may be controlled by very different phenomenon that are predominately biological.

CHAPTER 2.

THE MID-DOMAIN EFFECT APPLIED TO ELEVATIONAL GRADIENTS: SPECIES RICHNESS OF SMALL MAMMALS IN COSTA RICA

ABSTRACT

The objective of this study was to comprehensively document and examine the alpha and gamma patterns of species richness in non-volant, small mammals (rodents, shrews, and mouse opossums) along a tropical elevational gradient. These data were used to determine the support for existing hypotheses of species richness encompassing mid-domain null models, as well as climatic, and community overlap hypotheses. Field studies were conducted along a Caribbean slope of the Río Peñas Blancas watershed in the northeastern region of Costa Rica between 750-1850 m at 10 sampling sites. Species richness and abundances of small mammals were surveyed for four seasons including three temporal replicates at each of five elevational sites: late wet season (2000), early wet season (2001), and dry season (2002), and one spatial replicate at five different sites within the same elevations during the late wet season (2001). Species richness at elevations below 700 m was compiled from specimen records from 23 U. S. national and international collections. Predictions of a null model based solely on geometric constraints were examined using a Monte Carlo simulation program, Mid-Domain Null. In 16,900 trap-nights, 1561 individuals from 16 species were captured. Both alpha and gamma species richness peaked at mid-elevation between 1000–1300 m, with richness declining both at higher and lower elevations. Most of the empirical curves of species richness occur within 95% prediction curves of the mid-domain model, although deviations from the null model exist. Regression of the empirical richness on the null model predictions explained nearly half of the variation observed ($r^2 = 0.45$, p = 0.002).

The geometric constraints of montane topography appear to influence the diversity pattern of small mammals, although climatic conditions including an intermediate rainfall and temperature regime, and distance from the persistent cloud cap also are correlated with the pattern of species richness. The predictions of productivity and community overlap hypotheses are not supported with the empirical data.

INTRODUCTION

The striking ecological changes that occur along elevational gradients drew the attention of early researchers, such as Darwin (1839, 1859), Wallace (1876, 1878), von Humboldt (1849), and Merriam (1890). Although latitudinal gradients in species richness have received more attention, elevational patterns have been addressed in the literature recently for various taxa. A recent issue of *Global Ecology and Biogeography* was dedicated to elevational patterns of species richness in mammals, with several authors discussing recently documented patterns as well as the possible mechanisms and theoretical guidelines for studies along elevational gradients (Heaney and Lomolino 2001). Rahbek (1995) reviewed 97 articles on elevational diversity patterns from a variety of taxa, and found that most studies detected the highest species richness at lower elevations, but almost half documented a mid-elevational peak in species richness. Most studies of elevational trends in non-volant small mammals, including rodents, insectivores, and sometimes marsupials, demonstrate mid-elevational peaks in species richness (Langham 1983; Yu 1994; Goodman and Carleton 1996, 1998; Goodman et al. 1996, 1999; Kelt 1999; Heaney 2001; Goodman and Rasolonandrasana 2001; Md. Nor 2001; Rickart 2001; Sánchez-Cordero 2001).

Numerous hypotheses exist to explain elevational species richness patterns; however, many are neither mutually exclusive nor independent, and none are consistently supported with empirical evidence (Brown 2001; Heaney 2001; Lomolino 2001). Historically, most diversity hypotheses attempted to explain entire gradients based on a single biological factor such as productivity, habitat complexity, habitat diversity, environmental stress, disturbance, resource diversity, or competition (Heaney 2001; Lomolino 2001). The elevational equivalent to the ecotone effect, or community overlap hypotheses, is another theoretical framework supported by empirical data, in which the greatest species richness exists in the areas of overlap between two distinct faunal communities (Lomolino 2001). Lastly, several hypotheses have been proposed that attempt to explain current species richness patterns by trends in historical factors, such as immigration, extinction, and speciation (Lomolino 2001 and see Myers and Giller 1988).

As diversity theory progresses and empirical data accrue, it has become increasingly clear that many factors underlie large-scale diversity gradients (Brown 2001; Lomolino 2001). In the tangled complexity of biological factors affecting diversity gradients, new null models of the mid-domain effect could help to pare down the complexity. A mid-domain effect is predicted where landmass boundaries such as oceans and mountaintops limit species ranges and the simple overlap of many, variously sized ranges create a peak in species richness at mid-elevation (Colwell and Hurtt 1994; Colwell and Lees 2000). This prediction is based solely on geographic constraints and offers predictions against which empirical patterns can be compared. Areas of significant deviation from the null predictions then enable researchers to search for specific biological factors that produce such skews, peaks or depressions in richness. This approach focuses attention on important areas of diversity and corresponding biological factors within a gradient. McCain (2003) detailed the utility of this approach for diversity patterns of North American desert rodents across a latitudinal gradient. The mid-domain effect along continental gradients has been supported to varying degrees with taxa ranging from plants, insects, birds, marsupials, and bats (see recent review of Colwell et al. in press and references therein).

Elevational diversity gradients can be broken into two general sampling types: gamma patterns and alpha patterns (or species-density patterns; Lomolino 2001).

Gamma diversity patterns include all elevational records for the taxa of interest from a mountain range or mountainous region. The majority of the gamma patterns are a compilation of species records from the literature—sampling records, field notes, and museum specimens. These invariably have sampling biases that may significantly influence the species richness pattern (Rickart 2001), and are highly influenced by area (Lomolino 2001). Several authors have documented the mid-domain effect for various non-mammalian taxa along elevational gradients of gamma diversity (Rahbek 1997; Lees et al. 1999; Grytnes and Vetaas 2002; Sanders 2002). In contrast, alpha diversity patterns detail species richness among equal-area samples along a single elevational transect; standardizing the area, sampling and slope effects. To date, only two studies of alpha diversity patterns in montane plants have attempted to assess the mid-domain effect with mixed results (Kessler 2001; Grytnes 2003). No alpha or gamma diversity patterns of mammalian taxa on elevational gradients have been tested using the mid-domain null models.

To fill this gap, the present study seeks to illustrate both the alpha and equal-sample gamma patterns of species richness along an elevational gradient for non-volant small mammals (rodents, shrews, and mouse opossums) in the mountainous region of Monteverde, Costa Rica, and determine the support for existing elevational species richness theories including null models, as well as climatic and community overlap theories.

METHODS

Study area

The Monteverde Cloud Forest Reserve sits within the larger Bosque Eterno de Los Niños; these two reserves encompass the majority of the Río Peñas Blancas watershed (Nadkarni and Wheelwright 2000). The known data on climate, geology, fauna, and flora of the Monteverde region, concentrating on the Monteverde community at the continental divide and Pacific slope, were compiled recently in an edited series of papers (Nadkarni and Wheelwright 2000). The Caribbean slope descends quickly from the highest peaks, Cerro Amigo (1840 m) and Cerro Chomogo (1799 m), with many ravines and steep slopes highly influenced by erosion and landslides. Slopes level off somewhat around 950–750 m, with an undulating topography between 700–1000 m (Fig. 9). Below 600 m, the flatter land is more accessible and desirable for agriculture, ranching, and human settlement.

The climate of this region represents a transition between the wet, humid Caribbean lowlands to the east, rising into the wet-cool highlands. Generally, the rainy season runs from May–December, with the peaks in precipitation occurring in June, September, and October, and the dry season extends from January–April (Clark et al. 2000). No Caribbean temperature data are available for the transect, but data along the Volcán Barva elevational cline (Caribbean) from northeastern Costa Rica indicate that temperature declines linearly with elevation at approximately 6° C per 1000 m a.s.l. (Lieberman et al. 1996). Rainfall data have only been collected sporadically both spatially and temporally on the Caribbean slope in the Monteverde region and may not be a reliable indication of pattern (Clark 1994; Clark et al. 2000), but the present data show that precipitation is highest at about 800 m and declines both above and below (Table 1; Unpublished data, ICE). Rainfall is clearly higher at 800 m than 1000–1300 m, although horizontal precipitation was not measured in the cloud cap above 1400 m. Horizontal precipitation can add substantially to standard rain gauge measurements (Clark et al. 2000), thus a secondary increase in rainfall is likely in the cloud cap, particularly at the lower edge at 1400–1550 m.

Three life zones are found along the Caribbean slope gradient (Bolaños and Watson 1993; Haber 2000). Lower montane rain forest, 1500–1850 m, is dominated by cloud forest vegetation with a variable and broken canopy at about 15–30 m high and showing pronounced epiphyte and moss growth. Premontane rain forest vegetation, 700–1400 m, is characterized by a lush evergreen forest, a high canopy (30–40 m) and heavy epiphyte growth. The premontane rain forest is variable elevationally, as canopy height and continuity decrease with elevation, while epiphyte and moss loads increase with elevation. The tropical wet forest dominates below 700 m elevation with a higher canopy punctuated by even taller emergent trees, with abundant lianas, vines, and buttress roots. Haber (2000) listed plant species and vegetative descriptions associated with each of these life zones and forest types for the Monteverde region. The elevational pattern of floristic diversity has not been sampled in Monteverde at present, but Lieberman et al. (1996) documented a unimodal peak in tree species diversity at 300 m elevation on a Caribbean transect in eastern Costa Rica.

Sampling

Non-volant small mammals [shrews (Sorcicidae), mouse opossums (Didelphidae), and heteromyid and murid rodents] were sampled along an elevational transect between 750–1840 m during 2000-2002 in the Monteverde region of Costa Rica. Five sampling sites along the Caribbean elevation transect were surveyed: 750–800 m, 1000–1050 m, 1250–1300 m, 1500–1550 m, and 1770–1840 m (Fig. 9). Ideally, lower elevations would have been surveyed, but no large fragments of intact forest exist below 600 m in this region of Costa Rica. All sampling sites were located in areas with the most undisturbed forest available at that elevation, and the forest was contiguous between all sites. I surveyed three temporal replicates at the original five elevational sites: late wet season, October–December 2000; early wet season, July–September 2001; and dry season, March–May 2002. One spatial replicate at the same elevations separated by 1–25 km from the original sites was then surveyed in the late wet season, October–December 2001 (Fig. 9). Trapping sites at the various elevations were sampled in a different order during each temporal replicate to reduce temporal autocorrelation among sites (Table 1). The late wet season spatial replicate was sampled in approximately the same elevational order and time of year as the first late wet season transect from 2000 (Table 1).

Trapping was standardized to include 130 traps: 7 pitfalls, 10 Victor snap traps set 1–3 m above ground on vines or in trees, 40 extra large folding Sherman live traps (3 x 3.75 x 12"), and 73 large folding Sherman live traps (3 x 3.5 x 9"; 20 extra large and 93 large Shermans were used in 2000). Sherman traps were placed on the ground or within 1 m of the ground on fallen logs, vines, or rocks. Pitfall traps of standardized diameters (3 of 14 cm; 2 of 10.2 cm; 2 of 7.6 cm) were placed in the soil so that the lips of the cups were level with the soil. Fallen woody debris was used to create artificial runways into pitfall cups. More species can be identified by using several trap types (Voss and Emmons 1996), but snap traps were placed only in the trees to decrease unnecessary collection of the abundant terrestrial species. This may have lead to inadvertent sampling biases, although Woodman et al. (1996) found no trapping bias between snap traps or live traps on the ground and in the trees for small mammals in Peru. Sherman traps were placed 15, 20, or 25 paces apart (ca. 8.5, 11.4, or 14.25 m) in lines designed to sample all microhabitats available at each elevation. Distance between traps was constant at a site, but varied among sites because slopes at some sites were so steep that the accessible area for trapping was reduced.

Each elevational site was trapped for seven consecutive nights except for the early wet season transect which was surveyed for five consecutive nights due to time limitations, for a total of 16,900 trap-nights. Each transect replicate was sampled for 4550 trap nights except for the early wet season transect, which was sampled for 3250 trap nights. Each elevation was surveyed a total of 3380 trap-nights (Table 1). Traps were checked once a day in the early morning and re-baited as needed. Victor traps were baited with peanut butter and oats. Pitfall traps were not baited. Half of the Sherman live traps were baited with peanut butter and oats, and the other half were baited with a mixture of grain sorghum, millet, sunflower seeds, and vanilla extract. The two bait types should have attracted all known species of small mammals in the area. Additionally, South American small mammals exhibited no significant capture biases between seed mixtures, and peanut butter and oats (Woodman et al. 1996). Each captured individual was identified to species, weighed with a Pesola scale, and trap location, reproductive condition, and abundance of mutalistic beetles were noted. Most animals were marked with a unique toe clip or ear tag (larger species, i.e. *Heteromys* spp., *Oryzomys albigularis*) and released. A limited number of voucher specimens were collected, mainly specimens of difficult field identification, rare species, and individuals caught in snap traps and pitfalls. Specimens are housed at The University of Kansas Natural History Museum or at the Museo Nacional de Costa Rica.

Analysis

A combined alpha diversity data set included species recorded for the three temporal replicates at the original elevational sites. The equal-sample gamma pattern was obtained by combining species records from each elevation across all four transect replicates, as well as a few elevational records from earlier collectors within the same region of the Peñas Blancas Valley (See Appendix 2 for included specimen records). In all cases, species were assumed to occur at an elevation if they were detected at both higher and lower elevations. Species-accumulation curves were used to assess how well species diversity was sampled at each site and elevation. An accurate estimate of species diversity for a sampling interval was assumed if the species-accumulation curve plateaued (Colwell and Coddington 1994). Additionally, I estimated species richness using non-parametric randomization estimators, Chao2 and Jack2, to evaluate potential variation in sampling-effort among elevations (Colwell and Coddington 1994; Colwell 2000). These two estimators, using both number of sampling occasions and species abundances, are the least biased estimates of species richness for small numbers of samples (Colwell and Coddington 1994). Because elevations below 600 m no longer contain adequately sized parcels of forest, I estimated the original species richness at low elevations by examining collection records of small mammals across the Caribbean slope of Costa Rica with particular emphasis on records from the Province of Alajuela. Collection records were compiled from 23 museum collections (see acknowledgments) and contained records of 5926 rodents, 69 mouse opossums, and 157 shrews from Costa Rica. The species predicted to occur below 700 m, their ranges, and the particular low- and high-elevation specimens used to make these estimates are listed in Appendix 2 for gamma and alpha diversity patterns. Because alpha diversity is by definition less than or equal to gamma diversity, the alpha estimation includes those species most likely to be trapped along the Peñas Blancas Valley.

The species richness data for the combined alpha diversity pattern and the gamma diversity pattern were compared to null model predictions with a Monte Carlo simulation procedure, Mid-Domain Null, which I wrote in Visual Basic for Excel (available upon request). This program simulates species richness curves based on empirical range sizes or range midpoints within a bounded domain based on the analytical-stochastic models of Colwell (1999) and Colwell and Hurtt (1994). The mid-domain null models describe the geometric pattern that results from random range sizes and placements between the endpoints of two hard boundaries that are shared by all species in the analysis. Therefore, all species' ranges must be entirely within the bounded domain, and large ranges must be centered near the midpoint of the domain. Such constraints result in increasing species richness toward the center of the domain (Colwell and Hurtt 1994; Willig and Lyons 1998; Lees et al. 1999; Colwell and Lees 2000; McCain 2003). The original analytical-stochastic model (RangeModel; Colwell 1999) sampled with replacement from imported empirical data for either range midpoints or range sizes, and then randomized the placement of the other according to a modified uniform distribution for feasible values within two boundary endpoints to produce species richness curves. Mid-Domain Null simulates species richness curves in the same way, but allows for sampling with or without replacement from empirical range sizes or midpoints. Additionally, this program is designed to run thousands of Monte Carlo simulations in a single session and offers various outputs including species richness curves, 95% simulation prediction curves, randomized data, among others.

Sampling with and without replacement from the empirical values determines the amplitude of the 95% prediction curves. When sampling without replacement, the empirical values for range size or midpoints in the simulation are constrained to actual empirical species distributions; sampling with replacement allows a set of species to be "created," which can be quite different from the original species complement. Sampling without replacement is a randomization technique, whereas sampling with replacement is a bootstrap method (Manly 1997). Manly (1997) states that randomization procedures are helpful in situations where "the hypothesis under investigation suggests that there will be a tendency for a certain type of pattern to appear in data, whereas the null hypothesis says that if this pattern is present then this is a purely chance effect of observations in a random order." This situation corresponds precisely to the mid-domain model. In contrast, bootstrapping of data is used in situations where "in the absence of any other knowledge about a population, the distribution of values found in a random sample . . . from the population is the best guide to the distribution in the population" (Manly 1997). The philosophical difference between bootstrapping and randomization is that bootstrapping should be applied to a data sample and randomization should be applied to the population pattern ("population" used here to indicate the community of species in an area). I contend that species richness curves are inherently "population" patterns, as the species are known and their ranges are known; slight inaccuracies in range size may exist and there is the possibility of a missing, low-density species, but for the most part the players are known. Bootstrapping assumes that the data are a sample from the actual "population"; thus the observed species and their ranges only represent a sample, and that the actual community could consist of very different species with different ranges. This is clearly not the general case in species diversity curves, especially in cases where sampling is complete or nearly so.

The practical difference between these two sampling procedures regards the width of the prediction intervals; the 95% prediction intervals based on sampling with replacement are wider than those sampled without replacement. I used randomization techniques, thus all 95% prediction curves were based on 50,000 simulations sampled without replacement from empirical range sizes. Regression of the empirical data on the predicted values, based on the average of the 50,000 simulations where mean = median = mode, gave r^2 estimates to the fit of the null model. Significant deviations from the null models pinpoint areas of biological interest and these areas were discussed in light of other potential causes. The expected general pattern according to other elevational diversity theories were also considered, including climatic correlates and community overlap.

RESULTS

Sixteen species, representing 3889 captures of 1561 unique individuals were trapped over the survey period (Table 1). The number of species encountered at a single elevational site within a 5–7 day period varied from 3 to 8, and the number of individual animals captured ranged from 15 to 154. The elevational range of each species and known presence localities are shown in Figure 10. The number of individuals captured for each species by elevation is listed in Appendix 3. All four replicates of the species richness curve for the Caribbean elevational transect showed mid-elevational peaks in species richness, but with some variation in species richness pattern (Fig. 11). The same shape of the species richness curve is seen in the late wet season 2000 and early wet season 2001 (Fig. 11a). The diversity curves of both of these replicates were consistent with the total pattern of species richness for all four replicates combined. Different species diversity patterns are seen, however, in the dry season 2002 replicate and the spatial replicate in late wet season 2001 (Fig. 11b).

Most species-accumulation curves at each elevational site reached a plateau in species richness before the end of the survey period (Fig. 12). A few curves did not plateau, most notably several surveys at 1000 m elevation, the elevation with the highest species richness, and those from the early wet season surveys, which were only 5 days long. All of the combined species-accumulation curves demonstrated plateaus, indicating that each elevation and most elevational replicates were sampled adequately to assess the species richness pattern for the Monteverde Caribbean slope. Adequate sampling is further supported by the fact that all previously documented species from the Monteverde region were trapped except for 1-3 species associated with high levels of disturbance or with the Pacific slope. Species richness estimators, Chao2 and Jack2 demonstrated the same overall pattern of species richness, although predicting slightly greater species richness at all elevations except 1800 m, and a more pronounced diversity peak at 1000 m.

Mid-domain analysis

The species richness curves including estimated species at lower elevations for the combined alpha diversity pattern and the combined gamma diversity pattern demonstrated mid-elevational peaks in species richness between 1000–1100 m and 1000–1300 m, respectively (Fig. 13). The 95% prediction curves from 50,000 simulations of Mid-Domain Null demonstrated a reasonable fit to the predictions of the null model, but with several deviations. Deviations occurred at the highest elevations and at mid-elevations for both the alpha and gamma species richness curves (Fig. 13). The moderate fit to the null model predictions were demonstrated by the low r^2 values (alpha: $r^2 = 0.452$; gamma: $r^2 = 0.454$), although both patterns were significant ($p = 0.002$). The gamma curve deviations for randomized midpoints were negative between 500–800m and positive at 1800 m. (Fig. 13a). The alpha curve deviations for randomized midpoints were negative between 600–800 m and positive at 1800 m with several points falling along the 95% simulation curves (Fig. 13b).

DISCUSSION

Clearly, the non-volant small mammal fauna demonstrated a mid-elevational peak in diversity; a pattern confirmed for all four transect replicates and the combined alpha and gamma diversity data sets. The question of importance then is what produces this diversity pattern? The mid-domain effect is an unavoidable consequence of bounded ranges of variable sizes. As in any null model, it is the baseline against which empirical species richness patterns should be compared (Colwell et al. in press and references therein). Significant deviations from the null pinpoint areas of particular biological interest, and indicate the need for analysis of the distribution of abiotic resources, species interactions, evolutionary history, and ecological history (McCain 2003; Colwell et al. in press). Deviations from null model predictions prompt examinations of two such areas: lower than predicted richness between 600–800 m and higher than expected richness above 1700 m. These deviations highlight the shift in the diversity peak towards higher elevations away from the predicted peak at one-half maximum altitude.

An evaluation of biological factors may explain this shift in the peak of richness. Community overlap theory predicts that species richness should peak at some intermediate elevation at the transition zone between two adjacent, species rich-communities. Further, small peaks in richness should exist at other transition zones between less speciose elevational communities (Lomolino 2001). The transition zones along the Monteverde transect are between the cloud forest vegetation of the lower montane forest and the premontane rain forest at 1400–1550 m, and between the premontane rain forest and the tropical wet forest at 700–600 m (gray shading in Fig. 13). Clearly, the predictions of this theory are not supported for my data set; the highest peak in richness does not occur at a transition zone between zonal communities but rather at the center of the premontane rain forest zone. Neither are there secondary peaks in richness at the transition zones. Lastly, the assumption that elevational bands exist as distinct communities with marked transition zones may not be the case for the small mammal species under analysis—as most species (11/18) are found in two or more of the forest communities and appear to be responding to species-specific elevational limits (Fig. 14a & 14b). Distinct vegetative communities may not exist as discrete units either, as Lieberman et al. (1996) found no evidence that tropical vegetation can be divided into floristic zones along their elevational transect in eastern Costa Rica. Their analysis demonstrated that species composition varied continuously with altitude, and that tree species were distributed by independent niche limitations. Hartshorn and Peralta (1988) also found evidence that transitions between life zones in Costa Rica were much broader and less discrete than predicted by life zone theory (Holdridge 1967, Holdridge et al. 1971).

Productivity gradients frequently demonstrate hump-shaped relationships in species richness, revealing peaks in richness at intermediate productivity levels along a gradient from low to high productivity (Rosenzweig 1992, 1995; Waide et al. 1999; Mittelbach et al. 2001). Actual forest productivity has not been measured along the elevational transect in Monteverde, nor elsewhere in Costa Rica. In such cases, correlates for productivity, such as temperature, precipitation, humidity etc. can be used to estimate areas of peak productivity. Unfortunately, the fundamental problem with climatic data on elevational gradients is that long-term, spatially diverse data are not available, and short-term data may be unreliable. According to the currently available data, temperature decreases monotonically with elevation, while rainfall appears to peak at mid-elevation with a secondary increase at the highest elevations due to cloud-driven precipitation. This would lead to a predicted peak in productivity at 800 m, as rainfall and temperature are both high. The peak in small mammal species richness is several hundred meters above this point. With the available climatic data, there does not appear to be a correspondence in species richness of small mammals with combined high rainfall and high temperature. Most tellingly, productivity theory predicts the richness peak in the area of strong negative deviations from the null model. The pattern of rainfall alone is not correlated with diversity either, as highest rainfall apparently exists at 800 m and 1400-1500m with a dip in rainfall at the intervening elevations where the diversity peak occurred.

In some cases, researchers identify the area of optimal ecological conditions as the region with the highest abundance of the focal species group (Terborgh 1977; Heaney 2001), especially in cases where productivity, climatic variables, and habitat diversity or complexity are difficult to measure. The elevation with the highest capture frequencies, an index of abundance, was 1500–1550 m elevation which averaged 123 individuals per survey as opposed to 73 at 1780–1840 m, 72 at 1250–1300 m, 62 at 1000–1050 m, and 61 at 800–750 m (Table 1, Appendix 3). For this study, capture frequency was not correlated with species richness ($r^2 = 0.0253$, p = 0.7982).

The peak in diversity is found at the elevations with intermediate rainfall and intermediate temperature, and a few hundred meters below the lower boundary of the persistent cloud cap, 1400-1550 m. This same pattern was identified by Goodman et al. (1999 and references therein) in a comparison of elevational transects on four mountains in Madagascar. They found mid-elevational peaks in diversity of small mammals, and in all cases the diversity peak was located at intermediate climatic conditions just below the lower boundary of perennial cloud cover. This ecological association is also supported by other research on tropical elevational gradients for small mammals in the Philippines (Heaney 2001 and references therein), in Borneo (Md. Nor 2001), and in Taiwan (Yu 1994). Additionally, Goodman et al. (1999) documented a positive, linear trend in which diversity peaks were located at higher elevations on taller mountains. Based on their regression, the predicted diversity peak for the Monteverde transect with a summit at 1840 m was 1165 m—startlingly close to that documented empirically. This trend is consistent with the Massenerhebung effect, which suggests that due to a suite of interacting climatic factors, elevationally-correlated habitat bands shift toward higher elevations on larger mountain masses (Flenley 1994; Lomolino 2001). Thus, evidence of a positive, linear trend in mid-elevational peaks supports a hypothesis of a suite of interacting climatic variables influencing the pattern of biodiversity.

Thus, there is evidence supporting geometric constraint effects and climatic influences on the mid-elevational peak in diversity. Several factors such as resource diversity, historical events, and biotic interactions could not be evaluated with present data, although they may be important. The best solution for testing the tentative correlations raised here is to replicate the elevational transect on several mountains within Costa Rica to look for similar diversity patterns and ecological associations in those small mammal communities. Such comparative studies of several mountains within a region were advocated by Lomolino (2001), and were successfully applied in Madagascar (Goodman et al. 1999) and Norway (Grytnes 2003) with productive results.

Replication

This is the first time an elevational analysis of small mammal diversity has been temporally replicated during three seasons and with a spatial replicate; therefore it provides valuable insight into the variability of such patterns. Two of the temporal replicates were consistent with the overall diversity pattern, but two replicates, the dry season and spatial replicate, differed considerably (Fig. 11a & 11b). The dry season pattern differed because fewer species were trapped at the 1000 m and 1500 m sites than during the three replicates in the wet season, probably due to lower capture rates in the dry season. Capture rates within the temporal replicates increased from the dry season (322 individuals) through the early wet season (386 individuals) and into the late wet season (416 individuals) when standardized for five days.

The diversity of the spatial replicate peaked at a much higher elevation, 1500 m, and had lower richness at the 1000 m and 1300m sites than the combined species richness pattern and than the original, temporally-replicated transect. Beta diversity changes (species turnover) were apparent in the lower two elevations, 1000 m and

800 m, where two novel species (*Heteromys desmarestianus* and *Oryzomys bolivaris*) were the common species caught. These differences may reflect differences in the microhabitats sampled or differences due to slope as the elevational profiles between the two transects differed. Additionally, the spatial transect may have been influenced by aspect differences and edge effects as the 1250–1300 m site was on a north-facing slope while all others were east-facing. The lower three sites were within contiguous forest that abutted fragmented second growth and clear-cut regions nearby. These three sites also had dramatically lower numbers of captures and individuals than any previously trapped site on the mountain (213 individuals in 5 days), which is consistent with a hypothesis of lower populations of small mammals in and near habitat fragmentation. It is apparent from the four replicates that no single survey was adequate to document the entire fauna of the gradient. Such results stress the importance of replication in spatial examinations of diversity, and challenge the ability of single surveys to conclusively document elevational patterns of species richness. If single surveys are the only feasible possibility, sampling for small mammals in the Central American forests would be most fruitful during the wet season and at sites with high rates of capture.

CHAPTER 3.

ELEVATIONAL GRADIENTS IN DIVERSITY OF SMALL MAMMALS: MID-ELEVATION PEAKS AND THE EFFECTS OF CLIMATE, LATITUDE AND AREA

ABSTRACT

One reason the factors underlying elevational diversity patterns are still unresolved is a lack of hypothesis testing. A global analysis of elevational diversity trends for non-volant small mammals revealed a ubiquitous pattern of mid-elevational peaks in species richness. Fifty-one elevational data sets were used to test the predictions of a null model—the mid-domain effect—and climatic hypotheses. Each data set was compared to predictions of the null model with 50,000 Monte Carlo simulations of randomly placed range sizes to clarify how much of each observed pattern was a result of simple spatial constraints. Very few data sets fit entirely within the 95% prediction curves of the null model, as the average predictive power of the null model was low (r^2 = 38%). Gamma data fit predictions of the null model better than alpha data (70% and 33% significant r^2 values, respectively).

Diversity peaks occurred at higher elevations on taller mountains (Massenerhebung effect), which is consistent with climatic factors working in concert to produce elevationally correlated habitat bands. Such a positive, linear relationship was documented for the combined data sets (r^2 = 44%, P = 0.0000) and for tropical, island, and continental sets, but was particularly pronounced in alpha data sets (r^2 = 70%, P = 0.0001). The mid-domain effect predicts the diversity peak at the elevational midpoint, and is therefore, necessarily correlated with mountain height as well. But the predictions of geometric constraint were tested across the entirety of the elevational span, and were only significant for 33% of the alpha data sets. Gamma diversity studies, which are highly influenced by increased area at lower elevations; exhibited a negative, linear trend of diversity peaks shifting to lower elevations on

taller mountain ranges ($r^2 = 28\%$, $P = 0.01$). Gamma diversity patterns also demonstrated higher altitudinal peaks in species diversity as latitude increased ($r^2 = 26\%$, $P = 0.02$). These results are evidence for the importance of a suite of interacting climatic factors on elevational diversity patterns that is apparent even with the noise from different sampling techniques, localities, and historical pressures.

INTRODUCTION

Biodiversity patterns have been addressed scientifically since the revolutionary work of Darwin and Wallace who initially recognized the two most universal ecological gradients: latitudinal and elevational (Rosenzweig 1992, 1995). While the underlying factors producing and maintaining biodiversity have been the emphasis of research efforts for decades, no accepted, general explanation for the distribution of biodiversity has surfaced, not even for the most studied gradients of latitude and elevation (Brown 2001, Lomolino 2001). The need to document and understand the mechanisms producing biodiversity patterns is urgent when biodiversity is being lost at unprecedented rates due to global habitat destruction, pollution, and climate change. To discern the most effective methods to preserve, protect, and regenerate biodiversity, we need better comprehension of the factors creating and maintaining biodiversity.

Elevational gradients are excellent candidates for improving our understanding of patterns and processes of biodiversity. Montane topography is global—all continents and most islands vary elevationally—and climatic and ecological changes vary predictably along elevational gradients. Biodiversity changes are of the same order of magnitude as along other ecological gradients, but occur over much smaller spatial scales. Superimposed on elevational gradients are the influences of latitude, species-area relationships, and clines in environmental factors (temperature, precipitation, energy, humidity, etc.; Lomolino 2001). Additionally, montane ecosystems are most likely to suffer extreme shifts in habitat distribution with global climate warming, as predicted by the seminal work of McDonald and Brown (1992). Thus, the underlying mechanisms determining elevational biodiversity patterns are critical to understanding general trends in production and maintenance of global biodiversity.

In the past decade, a fundamental shift in our understanding of diversity patterns resulted from a global resurgence of elevational studies for various taxa (Rahbek 1995, Brown 2001). Previously, diversity along elevational gradients was thought to simply decrease monotonically with increasing elevation (Terborgh 1977, Brown and Gibson 1983, Brown 1988). This viewpoint was based on a few highly cited papers on birds in the tropics. However, a preliminary overview of the literature for a wide-variety of taxa including plants, invertebrates, and vertebrates found that only 20% of the studies examined supported a monotonically decreasing curve in diversity (Rahbek 1995). Many of the studies (49%) exhibited a hump-shaped curve with highest richness at mid-elevations, and 24% had a plateau of high richness across most of the lower elevations, which then declined above some mid-elevation. A resurgence of elevational studies on the diversity of non-volant small mammals (rodents, shrews, and marsupials) 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 in press).

Most studies of elevational diversity assess the biodiversity of a taxon, but only offer anecdotal evidence supporting alternative diversity hypotheses. As with other large-scale ecological patterns, 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 diversity on elevational gradients are still unresolved (Rosenzweig 1992, 1995, Brown 2001). Lomolino (2001) proposed a research agenda to improve understanding of these patterns advocating the development of statistically rigorous tests of pattern for comparisons of elevational trends in diversity within and among taxa and mountain ranges, and expanding analyses of clines in environmental variables. Numerous empirical studies along elevational gradients for various taxa around the world are a previously untapped source for comparative, quantitative analyses of biodiversity patterns. Herein, I quantitatively test theoretical predictions of a null model and climatic factors by comparing global elevational gradients in diversity of non-volant small mammals (n = 51) collected in an extensive literature search (Appendix 4).

One newly-proposed null hypothesis, the mid-domain effect, predicts mid-elevational peaks in species richness based on geometric constraints of range placements between the hard boundaries of the sea and mountain summit (Colwell and Hurtt 1994, Colwell and Lees 2000, Colwell et al. in press, McCain 2003, in press). These landmass boundaries limit species' ranges, and species with large and intermediate-sized ranges necessarily must overlap at the center of the gradient. The simple overlap of many variously sized ranges leads to a predicted peak in species richness at the midpoint of the elevational gradient. Empirical support for the null model on elevational gradients exists for small mammals (McCain in press), ants (Sanders 2002), and plants (Grytnes and Vetaas 2002, Grytnes 2003). The null model provides an objective test of non-biological factors that may underlie the diversity pattern. The predictions of the null model can be tested for each elevational data set to evaluate the effect of geometric constraint on diversity patterns (McCain 2003, in press).

The most frequently cited explanations for patterns of elevational diversity are climatic hypotheses proposing single factor predictors such as rainfall, temperature, productivity, and habitat complexity or diversity (Heaney 2001, Lomolino 2001 and references therein). Current theory recognizes the complex interrelatedness of climatic factors, which can work in concert to influence diversity trends across ecological gradients (Brown 2001, Lomolino 2001 and references therein). The most striking physical attribute of elevational gradients is the succession of habitat changes that occur along the gradient, which are directly related to climatic variables. Habitat bands of physiognomically and floristically similar vegetation shift to higher elevations on larger mountains compared to smaller mountains; a pattern known as the Massenerhebung effect or mountain mass effect (Schroeter 1908, Martin 1963, Flenley 1994). If combinations of climatic factors similarly highly influence patterns of elevational diversity, then one would predict that the highest species richness would occur at higher elevations on larger mountains than on small mountains. A stronger trend would be predicted for datasets from mountain ranges on islands, as the mountain mass effect is more pronounced on isolated island or mountain peaks near the sea (Schroeter 1908, Martin 1963, Flenley 1994). Because the mid-domain effect predicts the highest diversity occurring at the elevational midpoint, a similar positive relationship with mountain height is predicted. Fortunately, the predictions of the null model are tested across the entirety of the gradient, allowing distinctions between the two hypotheses. If an interacting group of climatic factors affected species diversity, latitudinal trends would also be predicted. Citing downward shift in climatic regimes, Lomolino (2001) predicted peaks in elevational diversity shifting to lower elevations on mountains at higher latitudes.

The aims of the current study are (1) to determine the pervasiveness of mid-elevational peaks in species richness for non-volant small mammals, (2) test the generality of the mid-domain effect on elevational gradients, and (3) determine support for theoretical predictions of climatic hypotheses including mountain mass effect and latitudinal trends. To facilitate discriminatory hypothesis testing, elevational data sets for non-volant small mammals (NVSM) were partitioned into categories according to climate—tropical or temperate, location—island or continent, and sampling method—alpha or gamma diversity patterns.

METHODS

I searched the literature for documented patterns of species richness for non-volant small mammals along elevational gradients. All diversity data sets were re-analyzed assuming species occurred at an elevation if they were detected at both higher and lower elevations. Analyses were conducted using the elevational range of each species. In some cases where the lowest or highest elevations were unsampled, all details provided in the results and discussions of each publication were used to estimate upper and lower range limits. In cases where several alpha diversity data sets existed, Oaxaca, Madagascar, and Taiwan, I compiled gamma diversity curves. The lower elevational range boundaries for the Oaxaca species were augmented by elevational range data in Hall (1981). Data sets were grouped into regions based on climate: tropical or temperate, by biogeographic units: islands or continents, and lastly by diversity data: alpha or gamma. Alpha diversity patterns are species-density estimates taken from field transects along an elevational gradient for a particular mountain, ideally standardized for sampling effort. Gamma data sets are 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. The species richness patterns of such elevational summary patterns are highly influenced by area (Lomolino 2001), and may have significant sampling biases within the elevational gradient (Rickart 2001). The data used in alpha and gamma diversity patterns are qualitatively and quantitatively different, thus the factors producing these patterns will not necessarily coincide.

In hypothesis testing, data sets were employed only if sampling occurred across the majority of the elevational gradient (>80%), and if sampling did not exhibit substantial elevational biases. Elevational gradients are inherently constrained by geographic boundaries of the sea and the mountaintop. To test the influence of geographic boundaries, all diversity patterns were compared to the predictions of a null model with a Monte Carlo simulation procedure, Mid-Domain Null, a program which I wrote that is available upon request. This program simulates species richness curves based on empirical range sizes (or range midpoints) within a bounded domain based on the analytical-stochastic models of Colwell and Hurtt (1994) and Colwell (1999). For additional details on simulation procedures see McCain (2003, in press). 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 geometric constraints on the elevational diversity gradients. Regression of the empirical data on the predicted values, based on the average of the 50,000 simulations where mean = median = mode, gave r^2 estimates to the fit of the null model. Consistent deviations from predictions of the null model among data sets suggests influences of climatic, historical, or other factors important in determining species richness.

Climatic influences on the elevational diversity patterns should produce trends consistent with mountain mass and latitudinal effects (Lomolino 2001). The mountain mass effect when applied to peaks in elevational diversity predicts a shift in diversity peaks to higher elevations on taller mountains. Linear regressions were used to detect a positive, linear relationship between mountain height and the elevation with maximum species diversity. The mid-domain effect always predicts the diversity peak at the elevational mid-point, which is necessarily correlated with mountain height as well. Therefore, a positive relationship with mountain height and the diversity peak also is predicted by the null model. A mountain mass effect attributable to the mid-domain effect can be distinguished with two methods. The first method involves determining the fit of the mid-domain predictions across the entire shape of the diversity curve, as the null model predicts not only the peak in diversity at the mid-point of the elevational range but as a smooth, hump-shaped curve that nears zero at either end point. If the null predictions are not supported consistently across the diversity curves for the various data sets then this factor is eliminated as the cause of the mountain mass effect. Secondly, because the mid-domain effect always predicts the diversity peak at the elevational midpoint, a regression of the diversity peak as a percentage of mountain height against mountain height should be non-significant. Additionally, the regression line should be a straight line with the average diversity peak for all samples falling at 50% of mountain height. Large deviations from the average 50% of mountain height would indicate ecological influences not consistent with the mid-domain null model.

Gamma diversity patterns are highly influenced by area because in most cases area and habitat diversity decline with elevation; therefore predisposing peaks in gamma diversity to low elevations. In these cases, no linear pattern between peak richness and mountain mass would be expected, but a negative linear relationship between the diversity peak (measured as the percentage of the mountain height) and mountain range size should be demonstrated. Lomolino (2001) predicted a negative linear trend in the elevation of the diversity peak with increasing latitude. Linear regressions were also used to examine latitudinal trends in maximum diversity along elevational gradients.

RESULTS

Fifty-one elevational gradients in small mammal diversity were found in 33 studies (Appendix 4). Data sets were grouped into regions based on climate: tropical (31) or temperate (20); biogeographic units: islands (21) or continents (30); and data method: alpha (24) or gamma (27). Groupings were not independent, as most gamma data sets are from continental and temperate areas, whereas most alpha data sets are from the tropics and islands. All but four of the elevational gradients had maximum species richness at mid-elevation. Two exhibited a bimodal pattern and two studies had no recognizable pattern of species richness with elevation. The two studies, both alpha diversity transects, which found no pattern in species richness had substantial portions of the gradient that were unsampled—33 to 64% (Patterson et al. 1989, Bonvicino et al. 1997). The two studies that demonstrated a distinct bimodal pattern of highest diversity at the lowest and highest elevations either lacked sampling along the entire elevational gradient (42% sampled; Kelt 1999) or the authors emphasized the lack of sampling at mid-elevations (Patterson et al. 1998). On small islands with low species richness (≤ 8 species) mid-elevational peaks were relatively flat and variable depending on inclusion of exotics, and with richness differing by only one or two species at elevations where species were documented (Heaney et al. 1989, Rickart 1993, Heaney 2001). Thus, diversity patterns of small mammals along most elevational gradients demonstrated pronounced mid-elevational peaks in species richness with the only exceptions being studies where sampling was low on portions of the elevational gradient or for depauperate island faunas. Twelve elevational gradients with significant sampling biases or insufficient sampling, including the four listed above, were not used in the quantitative analyses.

Even though diversity peaked at mid-elevations, there was high variability in the shape of the diversity curves and the elevation with maximum richness. The 95% prediction curves based on 50,000 simulations of Mid-domain Null were used to assess the impact of geometric constraints on the elevational gradients (n = 38). The fit to the null model of geometric constraints ranged from highly predictive—explaining 84.2% of the variability—to not predictive at all—explaining 0.2% of the variation (see Fig. 15 for examples). The average predictability was 37.7% (Table 2). Slightly more than half of the data sets had slopes significantly different from zero (53%; indicated by stars in Appendix 4). The null model had greater predictive ability for gamma, continental, and temperate data sets than for alpha, island, and tropical data sets. Only 33% of the alpha data sets had significant r^2 values, while 70% of r^2 for gamma sets were significant. There was no consistent pattern of deviations from the null model for all data sets combined; maximum diversity was shifted toward higher elevations for 13 data sets and towards lower elevations for 15 data sets. There was a trend of more deviations toward higher elevations for alpha, tropical, and island data sets (9 to 3, 6 to 3, 10 to 5, respectively), while gamma, continental, and temperate data sets had more deviations toward lower elevations (4 to 12, 7 to 11, 3 to 9).

Linear regression of mountain height on the elevation of maximum species richness showed a significant positive relationship (Table 3; Fig. 16a). This positive linear trend was significant for tropical, island, and continental data sets, and was particularly pronounced for alpha data sets (Table 3; Fig. 16b). The regression equation for the mountain mass effect for alpha diversity transects is: Y = -62.6253 + 0.6497X, where Y is the elevation of the diversity peak and X is elevation of the mountain summit. The slope for all datasets (alpha and gamma) was slightly lower: 0.4199. The regression for islands with gamma data sets removed was significant also with the highest overall r^2 value (0.7014, p = 0.0001). The linear trend for a fixed zone of high diversity as a percentage of the mountain height predicted by the mountain summit was less predictive but negative (Table 3; Fig. 17a). This negative trend was significant only for tropical and gamma data sets (Table 3; Fig. 17b). The tendency for gamma data sets to have diversity peaks shifted toward the lower elevations is evident also in the fact that 11 of 12 data sets with a peak in diversity in the lower third of the elevational gradient were gamma data sets (Table 4). Additionally, three gamma data sets had a secondary peak in diversity at the lowest elevations. Diversity peaks in alpha data measured as a percentage of mountain height demonstrated no trend with mountain height and were not consistently centered at 50% of the mountain height (Table 3; Fig. 17C). The average diversity peak was located above 62% of mountain height. Lastly, the diversity peaks of the combined and gamma data sets had significant positive, linear trends with latitude (Table 3; Fig. 18).

DISCUSSION

Elevational patterns of non-volant small mammals demonstrated strong support for pervasive mid-elevational peaks in species richness. Mid-elevational peaks in diversity have been documented previously for several other taxa including several invertebrate groups (Janzen 1973, Janzen et al. 1976, Olson 1994, Lees et al. 1999, Richardson et al. 2000, Sanders 2002), plants (Lieberman et al. 1996, Kessler 2001, Md. Nor 2001, Grytnes and Vetaas 2002, Grytnes 2003), and amphibians (Lees et al. 1999). Nonetheless, some researchers consider mid-elevational peaks in species richness to be aberrant patterns resulting from biased sampling, area effects on small islands where lowland area is substantially reduced, or historical or current disturbance of lowlands by humans. In so far as I could assess, I used only those data sets with equal or unbiased sampling regimes. Of those, all demonstrated mid-elevational peaks in diversity, although depauperate island faunas showed only shallow mid-elevation patterns. As for sampling completeness for each data set, only a few of the studies were replicated, or presented species accumulation curves. In alpha transects, it is assumed that equal sampling among elevations results in an index of species richness, in which the overall pattern in richness is retained, even if undersampling exists. My impression is that any shifts in the diversity peak resulting from undersampling would only be a few hundred meters, higher or lower, not wholesale changes.

The well-known positive relationship of diversity and area is clearly important in gamma data sets but should not be an issue in alpha studies as they are standardized for effort and area (Lomolino 2001). Gamma diversity data sets from islands with reduced lowland area still demonstrate diversity peaks shifted toward lower elevations, but it is true that, taken together, mid-elevations could have greater area than a narrow strip of lowlands at the base. Nonetheless, all continental gamma data sets also demonstrated mid-elevational peaks and only 36% of those had maximum diversity shifted toward the lower 1/3 of the gradient, so area alone cannot account for the mid-elevational peaks in diversity. Lastly, if disturbance was the factor creating a deviant mid-elevational pattern from an inherently monotonically-declining pattern of richness, then the expectation would be for diversity to peak at the lowest undisturbed elevation and decline monotonically above that elevation.

Only 27% of all of the data sets demonstrated the peak in diversity in the lower 1/3 of the elevational gradient, indicating that disturbance at the lowest elevations is not creating the overall pattern. Only if you invoke large elevational range shifts or entire lowland biota extinctions would lowland disturbance be related to the overall pattern of mid-elevational peaks, and neither is indicated by the data and descriptions in the compiled studies. Given that mid-elevational peaks in species richness are real patterns, the critical question is what produces the pattern?

Mid-Domain Effect

The geometric constraints of the mid-domain null model were not generally predictive across all the elevational data sets as, of the 38 data sets selected for analysis, 73% had r^2 values less than 50% and only 24% had r^2 values greater than 60%. In only half of the studies was the relationship significant, in that the regression slope was distinguishable from zero. As seen in Appendix 4, the entire continuum of r^2 values was demonstrated for the null model analysis. This wide scatter in the predictability of geometric constraints diminishes the validity of the model as an explanation for elevational diversity patterns of non-volant small mammals. Additionally, there appeared to be no consistent trend in deviations toward higher or lower elevations from the diversity peak predicted by the null model for all data sets combined. Differences between sampling method were apparent as gamma data followed the predictions of the null model more consistently, 70% significant, than alpha data with only 33% significant r^2 values. Gamma data had more diversity peaks shifted toward lower elevations indicating an area effect, whereas peaks shifted more toward higher elevations in alpha data sets indicating the climatic effect. The better fit of the null model to gamma data may indicate that the method of summing elevational ranges across different slopes and aspects reflects more geometric constraint due to the extending or generalizing of elevational ranges.

Mountain Mass Effect

A strong climatic signal is apparent despite noise associated with divergent sampling techniques, historical factors, and biogeography. Maximum diversity was at a higher elevation on taller mountains; evidence supporting a mountain mass effect produced by a group of interacting climatic factors. The trend is significant for all data sets combined, but is most highly validated for alpha data (Table 3) and is not significant for gamma data. It then follows that those data sets with more alpha transects, islands and tropical, were significant, and those with more gamma data were not significant or were significant but less predictive (temperate and continents, respectively). The mountain mass effect tends to be most noticeable on islands or mountains near the ocean (Schroeter 1908, Martin 1963, Flenley 1994). This also was the case for small mammals as the island-alpha data sets had the highest r^2 value explaining over 70% of the variation.

The mid-domain null model also predicts the peak in diversity at the mid-point of the elevational range; hence predicting a diversity peak highly correlated with the height of the mountain. Fortunately, the null model predictions can be more finely tested across the entire elevational gradient, and those tests, as stated above, were not generally supportive of the null model. Alpha data sets most strongly corroborate the mountain mass effect, but only 33% had significant r^2 values for the null model. Secondly, the alpha data did not demonstrate maximum diversity consistently at the mid-point of the elevational gradient; the average peak was located at 62% of the mountain height (Fig. 17C). Therefore, geometric constraint does not appear to be the cause of the mountain height trend.

Maximum diversity for alpha data sets was at a higher elevation on taller mountains, but the increase was not proportional. A proportional increase would have demonstrated peak diversity at a higher percentage of mountain height on taller mountains; no linear trend in percentage of mountain height was demonstrated (Fig. 17C). This suggests that the largest mountains have less hospitable habitat at the highest elevations from possible snow effects, vertical habitat reduction, or more extreme climatic conditions like cloud caps, which pushes diversity peaks proportionally lower. There is evidence of such a correlation across several of the tropical, alpha data sets where maximum diversity of small mammals was consistently a few hundred meters below the persistent cloud cover at the top of the mountain. This correlation was documented on the five mountains across Madagascar (Goodman et al. 1999), several mountains in the Philippines (Heaney 2001 and references therein), two mountains on Taiwan (Yu 1994), and in Borneo (Md. Nor 2001), and Costa Rica (McCain in press). This would be in accordance with the trends in alpha diversity peaks of small mammals, if the cloud cap was consistently larger on taller mountains; such a size trend would also show a non-proportional, mountain mass effect for the lower limit of the cap.

Area Effect

Because gamma diversity data are summaries of elevational ranges across a mountain range, Lomolino (2001) predicted that these diversity studies would demonstrate discernable area effects. Diversity peaks of gamma data (% of mountain) were at proportionally lower elevations on larger mountain ranges (Fig. 17B). Two other data sets showed this negative trend, island and tropical, but when the gamma data sets were removed these trends were not significant. This negative trend implies an area effect: larger mountain ranges have even greater lowland area surrounding them, resulting in a diversity peak shifted toward lower elevations. Additionally, many gamma data sets had maximum diversity within the lower 1/3 of the elevational gradient and several exhibited a secondary peak in diversity at low elevations. Previous studies found that area effects account for substantial portions of variability in elevational diversity patterns, and when removed, the 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 or other mechanisms contributing to the diversity pattern.

Latitudinal Trend

Lomolino (2001) predicted that if climatic factors were driving diversity patterns on elevational gradients then a latitudinal trend should be demonstrated. Invoking "downward shifts in climatic regimes and zonal communities", he predicted a negative, linear trend with increasing latitude. The gamma data sets demonstrated a significant latitudinal effect, which was also significant for all data sets combined but not for tropical, temperate, island, continental, or alpha data sets individually. The elevation of maximum diversity for gamma data sets was found to be higher on mountains at higher latitudes, counter to predictions. It is probable that there are very different climatic influences at different latitudes for non-volant small mammal communities. For instance, in many of the tropical transects the entire gradient is forested from lowland tropical rainforest thru montane forests and finally cloud forest and sometimes dwarf forest and páramo. In contrast, many of the western North American mountains begin in harsher lowland environments of deserts or desert scrub with desert dominated ecosystems throughout the lower mid elevations, which then grade into piñon-juniper then coniferous forests sometimes culminating in low-stature habitats above treeline. The case could be made that these harsher conditions at the lower elevations on higher latitude mountains may shift diversity peaks toward higher elevations. Unfortunately, the latitudinal trend is complicated by geographic bias—most high latitude studies are gamma data sets from large mountains, specifically from the western US. Another complicating factor is that many of these mountains rise from higher initial elevations, for example the lowlands around the Uinta Mountains are at 1500 m, predisposing such mountain ranges to diversity maxima at elevations above that limit.

Since the examination of latitudinal trends is hindered by sampling biases, it would be advantageous for future researchers to document gamma and alpha diversity patterns along more temperate mountain ranges including gradients starting at elevations nearer to sea level and on shorter mountains. Elevational data sets for non-volant small mammals in Europe and on the non-tropical portions of the Asian continent are noticeably absent and needed.

Future Directions

An examination of elevational data compilations for various taxa will determine whether the trends in elevational diversity demonstrated in this analysis are general phenomena. Unlike latitudinal gradients, elevational gradients in diversity are less universal across taxonomic groups (Rahbek 1995). The climatic factors underlying diversity patterns are taxon-dependent. Thus, the location of maximum diversity along an elevational gradient should vary predictably within a taxon (Lomolino 2001). For instance, bats are known to exhibit monotonically decreasing pattern of species richness on the same mountains where small mammals exhibited mid-elevational peaks (Graham 1983, Heaney et al. 1989, Patterson et al. 1998, Sánchez-Cordero 2001). Similarly, aspects of the ecology and history of different taxonomic groups may reveal divergent responses to elevational gradients. Thus, examining those taxa with similar elevational diversity trends may lead to general explanations based on convergent influences. Comparing the factors influencing diversity in taxa with contrasting patterns will expose important factors that cause differences among taxonomic groups. Such an analysis applied across taxa promises to substantially extend our understanding of diversity patterns along elevational gradients and provide powerful insight into general mechanisms underlying elevational diversity (Brown 2001).

CHAPTER 4.

ELEVATIONAL GRADIENTS IN SPECIES RICHNESS: IS REPLICATION NECESSARY?

ABSTRACT

The objective of this study was to assess consistency among temporal and spatial replicates in alpha diversity studies along elevational transects. The majority of elevational diversity studies in the literature assume that a single sampling transect is an accurate index to the species richness pattern for a mountain. Species richness estimates from six studies in the literature were reanalyzed by seasonal and spatial replication. All six of the studies replicated temporally, either for two or three seasons, while only two studies replicated spatially. Each diversity replicate was compared to other replicates and to the aggregate diversity pattern for that mountain. Standardized abundances of small mammals were compared among replicates and examined for correlations between diversity estimates. Lastly, sampling effort was examined to determine its possible impact on abundance or diversity trends in replicates. No individual replicate was identical to another replicate or aggregate diversity pattern. The majority of replicates, 9 out of 14, demonstrated generally consistent patterns of species richness with aggregate patterns and with other replicates. Seasonal effects are apparent in many of the studies with a general trend toward decreased species richness and decreased number of individuals in the dry season. In three cases, the drier season had elevational patterns in species richness that differed from other seasons and the aggregate. Both spatial replicates demonstrated diversity patterns very different from the aggregate diversity patterns and the other elevational transects. Two of studies with inconsistent diversity patterns were those with the lowest sampling effort. Replicated species richness patterns are found to be variable both temporally and spatially. Diversity studies with

robust diversity estimates were from the wet season, based on the highest capture rates, and with the highest sampling effort. The evidence supports replication as a necessary component of well-designed studies of diversity gradients.

INTRODUCTION

Understanding global biodiversity is a priority in ecology due to the unprecedented extinction rates associated with habitat loss, climate change, and pollution. To improve our conservation efforts designed to maintain and promote biodiversity, we need accurate descriptions of diversity patterns and precise comprehension of mechanisms producing them (Brown 2001; Lomolino 2001). Three global diversity patterns have generated substantial scientific interest since the research of Darwin and Wallace: latitudinal gradients, species-area relationships, and elevational gradients (Rosenzweig 1992, 1995; Rahbek 1995, 1997; Brown and Lomolino 1998; Brown 2001). All landforms on earth exhibit elevational variation; thus an accurate understanding of global diversity, at least in part, relies on precise discernment of altitudinal diversity. The initial intention of elevational diversity research needs to be first documenting accurate patterns along gradients, and then searching for the specific mechanisms underlying these patterns. Currently, we do not have an accurate picture of the elevational pattern of diversity for most taxa (Rahbek 1995). A fundamental shift in the scientific perception of elevational diversity patterns has occurred in the last decade. The generally accepted pattern of monotonically decreasing diversity with increasing elevation has been shown to be false in almost half the studies reviewed (Rahbek 1995; Brown 2001). Many taxa, including plants (Whittaker and Niering 1965; Lieberman et al. 1996; Md. Nor 2001; Grytnes and Vetaas 2002; Grytnes 2003), insects (Janzen 1973; Janzen et al. 1976; McCoy 1990; Olson 1994; Lees et al. 1999; Sanders 2002) and birds (Terborgh 1977; Rahbek 1997; Young et al. 1998), demonstrate mid-elevational peaks in species richness. This pattern is consistently exhibited by small mammals globally for both alpha and gamma diversity data (McCain submitted).

Alpha diversity patterns detail species richness among equal area samples along a single altitudinal transect. Field studies along alpha diversity transects usually are designed to standardize area and slope effects. Gamma diversity data sets are species richness patterns compiled from trapping records, specimen records, and field notes for an entire mountain or mountainous region regardless of slope or area, generally without standardized trapping effort across elevations. The diversity patterns of such elevational summaries are highly influenced by area (Lomolino 2001), and may have significant sampling biases within the elevational gradient (Rickart 2001). Data used in alpha and gamma diversity patterns are qualitatively and quantitatively different, thus the factors producing these patterns will not necessarily coincide. A resurgence in elevational diversity studies has occurred in the last decade for various taxa, but we still need to assess whether these documented diversity patterns are consistent among seasons and sites. The precision of an alpha diversity pattern on a single mountain can be improved by increasing sampling effort or by replication both temporally and spatially.

Replication (repetition of the experiment) assesses the amount of variation due to ecological and environmental stochasticity in space and time. It insures against the "intrusion of chance events on ecological experiments" (Krebs 1989:272). The importance of replication in field and laboratory studies is emphasized in statistical texts and discussions of experimental design (Hurlbert 1984; Krebs 1989; Sokal and Rohlf 1995; Oksanen 2001). Replication is vital not only for measuring experimental error in manipulative studies, but also for assessing consistency and accuracy of descriptive patterns among sampling periods and plots. For elevational diversity studies, two scales of replication exist, replication of the diversity pattern on a single mountain, and between mountains. Replication of elevational gradients between mountain ranges assesses the generality of diversity patterns and is a synthetic analysis that is the only replication option for gamma diversity patterns (i.e., Goodman and Rasolonandrasana 2001 and reference therein; Grytnes 2003). However, for alpha diversity patterns, temporal and spatial replication on a single mountainside would be replication in the traditional sense; answering how much variability is there in diversity patterns among seasons on the same elevational transect and among different transects along the same elevational gradient. Without an estimation of the temporal and spatial variability of elevational diversity patterns, we are unable to assess the consistency and generality of these patterns.

In a recent review of elevational diversity patterns for small mammals, I found that only 6 of 24 alpha diversity studies replicated spatially or temporally. Four studies replicated during two seasons (Yu 1994; Kelt 1999; Md. Nor 2001; Sánchez-Cordero 2001) and one sampled during three seasons (McCain in press). Only two studies replicated spatially (Yu 1994; McCain in press). In all other cases, the diversity pattern was reported with a single transect of sampling. Rarely are specific sites sampled exhaustively due to time and financial limitations, therefore such studies assume that the species richness documented for a particular site is a true representation of the actual number of species inhabiting the area. In this sense, the local snap shot of species richness is assumed to be an index to true species richness at the site. This assumption has not been formally tested because in most cases researchers do not know the extent of temporal and spatial variability in elevational surveys.

An index of species richness needs to be constant over space and time to provide meaningful comparisons among regions (Nichols and Conroy 1996). Many factors can affect the probability of capture of a specific species, and such effects can be marked in rarely caught species. Spatial and temporal variability in population sizes, habitat quality, behavior, and movement patterns all affect the probability of capture in a survey. The robustness of an index may vary geographically or among species. Comparisons among several temporal and spatial replicates of the same alpha diversity transect allow us to test the prediction that each individual transect would be an accurate index. By comparing several alpha diversity transects, the robustness of a single transect can be demonstrated if replicate transects across seasons, years, or sites show similar patterns of species richness. Additionally, a comparison of aggregate data for all the replicates to each individual replicate can directly test the robustness of the index of species richness for that mountain. The six replicated studies for small mammals are re-analyzed to address the question of whether a single elevational transect is a sufficient index to the species richness pattern or whether replication is necessary.

METHODS

Of the six replicated studies of elevational diversity of small mammals: five gradients were located in tropical areas and one was from the southwestern U.S. Yu (1994) surveyed rodents and shrews across three elevational transects on the island of Taiwan: two transects on Yushan Mountain represented spatial replicates. The first transect on Yushan was sampled in both the wet and dry seasons, and thus provided temporal replication. Md. Nor (2001) sampled an elevational transect on Mount Kinabalu, Malaysia during two seasons—the later somewhat drier than the first—for both rodents and shrews. Sánchez-Cordero (2001) documented small mammal diversity on two elevational transects in Oaxaca, Mexico (Sierra Mazateca and Sierra Mixteca) during both wet and dry seasons. The two Oaxaca transects were not considered spatial replicates because they were located on different mountains. Kelt (1999) documented the species richness pattern of rodents during summer and winter on a portion of the Deep Canyon transect in southern California. McCain (in press) detailed the elevational diversity pattern of rodents, shrews, and marsupial mice in the Tilirán Mountains, Costa Rica during early wet, late wet, and dry seasons, and also sampled a spatial replicate. Each study sampled a different percentage of the elevational gradient, but the span of elevations was consistent among replicates within a study.

Sampling effort differed substantially among studies, and some replicates were sampled less than others (Fig. 19). Each site on the Oaxacan transects was uniformly sampled for 1000 trap nights (t.n. = # traps x # nights) for each replicate. The wet season replicate in Taiwan was sampled for 1008 t.n. per site, but the dry season and spatial replicate had 720 t.n. per site. Costa Rican sites were all sampled for 910 t.n. except during early wet season which was trapped for 650 t.n. Mt. Kinabalu was sampled for 405 t.n. and 225 t.n. at each site during the wet and dry season, respectively. The Deep Canyon transect was sampled for 137 t.n. at each site for both summer and winter.

Besides sampling intensity, plateauing of species accumulation curves indicates thorough sampling (Colwell and Coddington 1994). Only Yu (1994), Md. Nor (2001), and McCain (in press) published species accumulation curves. The majority of these plateaued several days before termination of trapping. Because the quality of the diversity pattern is based not only on replication but sampling effort, I predict that those studies with less sampling will have greater variability among replicates.

Two studies, Yu (1994) and McCain (in press), address the issue of replication, and thus graphically display or evaluate differences among diversity patterns of replicates. For this study, each diversity replicate was re-analyzed assuming species occurred at an elevation if they were detected at both higher and lower elevations. The diversity pattern of each replicate is compared with other temporal replicates and with aggregate diversity patterns. Similarities between replicates were quantified using correlation analyses. Aggregate diversity patterns were based on the overall elevational ranges of each species detected for the replicates combined. An aggregate pattern for temporal replicates only included replicates along the same elevational transect, while an aggregate for spatial replicates included both the spatial and temporal replicates. Lastly, published abundance of captures or individuals for each replicate was quantified and examined for correlations between diversity estimates.

RESULTS

All replicates and summaries of diversity patterns showed mid-elevational peaks in species richness. The obvious pattern consistent across all studies examined (Yu 1994; Kelt 1999; Md. Nor 2001; Sánchez-Cordero 2001; McCain in press) is that no replicate had a species richness pattern identical to another replicate or to the combined pattern (Fig. 20). The shape of the diversity pattern was consistent among most temporal replicates: Mazateca (Fig. 20A; $r = 0.853$), Mixteca (Fig. 20B; $r = 0.760$), Deep Canyon (Fig. 20D; $r = 0.925$), Taiwan (Fig. 20E; $r = 0.888$), and for the wet seasons in Costa Rica (Fig. 20F; $r = 1.0$). Major deviations among replicates occurred between temporal replicates on Kinabalu (Fig. 20C; $r = 0.194$) and for the dry season in Costa Rica (Fig. 20F; $r = 0.600$). Nine of the 13 temporal replicates had diversity patterns consistent with the aggregate pattern: both replicates on Mazateca, wet season replicate on Mixteca, wetter season on Kinabalu, summer on Deep Canyon, both seasons in Taiwan, and the two wet seasons in Costa Rica. The inconsistent patterns were the dry seasons on Kinabalu (Fig. 20C), in Costa Rica (Fig. 20F), and on Mixteca (Fig. 20B), and the winter season on Deep Canyon (Fig. 20D). In these cases, either there was no discernable peak in diversity or the peak was shifted away from the highest peak in richness documented in the aggregate pattern. The two spatial replicates from Costa Rica (Fig. 20G; average r = 0.030) and Taiwan (Fig. 20H; average r = 0.200) differed dramatically from other replicates and the combined patterns. In both, the diversity peak was shifted toward higher elevations and considerably less diversity was documented at the lower elevations than for aggregate patterns.

For replicates with highly variable diversity patterns, the differences were attributable to one or two elevational sites, which had decreased diversity estimates. In several cases low estimates occurred at the elevation of peak diversity in the aggregate pattern: 1200 m site in dry season on Mixteca, at 1700 m on Kinabulu in the drier season, and 1250 m site in Deep Canyon during the winter. Three other deviant patterns were attributable to low diversity estimates at two sites also including the diversity peak of the aggregate pattern: dry season in Costa Rica at 1000 m and 1500 m, spatial replicate in Costa Rica at 1000 m and 1300 m, and on the spatial replicate in Taiwan at the two lowest elevations. In general, drier seasons had lower diversity than other seasons (Fig. 20), and the majority of deviant diversity replicates occurred during the dry season (or winter). As stated earlier, several replicates within a study had differing sampling effort, and in two of these cases, Mt. Kinabalu (Md. Nor 2001) and Deep Canyon (Kelt 1999), inconsistent species richness patterns were in evidence in the lesser-trapped replicate. Moreover, these two studies had lower trapping effort overall than the other studies (Fig. 19).

Total abundances of individuals (Yu 1994; Kelt 1999; McCain in press) or captures (Md. Nor 2001) for each replicate were published for all studies except those from the Oaxacan mountains (Sánchez-Cordero 2001). Large variation existed in abundances seasonally and spatially (Fig. 21). Only the three wet seasons (including the spatial transect) in Costa Rica showed roughly the same pattern in abundances across the elevational gradient (Fig. 21D). The number of captures was somewhat similar for the Kinabalu replicates, although the drier season lacked the pronounced peak in captures present in the wetter season (Fig. 21C). All replicates in Taiwan (Fig. 21A) and Deep Canyon (Fig. 21B), as well as the dry season in Costa Rica, produced very different patterns in numbers of individuals captured. With regard to diversity, inconsistent diversity patterns were associated with lower capture rates for the dry season in Costa Rica and Malaysia, and the winter in Deep Canyon. The two spatial transects had less diversity at the lower elevations than the temporal replicates, although only the Costa Rica transect showed low abundances at these sites (Fig. 21D). The Yushan spatial transect actually had an abundance peak at the elevations of divergently low diversity from the temporal transects (Fig. 21A). Again, there was a general trend of fewer individuals and captures during the dry (and winter) seasons.

DISCUSSION

The ability of a single replicate to converge on the actual species richness pattern for mountain is not consistent temporally or spatially in these studies. Nonetheless, the majority of replicates, 9 out of 14, revealed generally consistent patterns of species richness with aggregate patterns and with other replicates, albeit with ubiquitous minor differences. Seasonal effects are apparent in many of the studies with a general trend toward decreased species richness and decreased number of individuals in the dry season. In some cases, the drier season also had inconsistent elevational patterns in species richness (Md. Nor 2001; Sánchez-Cordero 2001; McCain in press). Drier conditions may decrease food availability leading to lower populations of small mammals and a concomitant reduced probability of capture especially for rarer species. Many tropical rodent species are known to reproduce mainly during the rainy seasons, thus the lowest population sizes would be expected during the non-reproductive season. This may account for fewer captures in the dry season and possibly the lower diversity estimates. Another possibility is that the dry conditions influence movement patterns. Individuals may decrease movement in the non-breeding season, hence, be less susceptible to capture. Such behavioral changes may decrease probabilities of capture for some species leading to lower diversity estimates. Similar trends in food resources, reproduction, and movement patterns may exist in the winter for montane systems in the desert like Deep Canyon, California, where Kelt (1999) also found lowered diversity, fewer animals, and a different diversity pattern in winter.

Of the five temporal replicates that documented inconsistent patterns of species richness, two had lower trapping effort per site than most of the other studies (Deep Canyon transect, Kelt 1999; and Mt. Kinabalu, Md. Nor 2001). The inconsistent diversity pattern from the drier season on Kinabalu (Md. Nor 2001) also had lower trapping effort than the first session, and resulted in fewer captures. In contrast, the early wet season replicate in Costa Rica (McCain in press) also had lower trapping effort than the other temporal replicates and had three sites where species-accumulation curves did not level off; however, the species richness pattern was consistent with the overall pattern. The main difference between these two studies is that the trapping effort on Kinabalu in the dry season was only 36% of the sampling effort of the early wet replicate in Costa Rica. Inconsistent patterns of species richness could be the result of the decreased trapping effort. Still the association between trapping effort, animal abundance, and influence of rarely caught species on these patterns is complex and incompletely understood. These relationships warrant further evaluation, but it is clear that caution should be used in interpretation of diversity analyses with low sampling effort.

The two spatial replicates from Taiwan (Yu 1994) and Costa Rica (McCain in press) both exhibit patterns of species richness inconsistent with temporal replicates, and in both cases the peak in species richness shifted from mid-elevations to higher mid-elevations with decreased richness at the lower elevations. The Yushan spatial replicate found a similar peak in species richness which was broader, but was missing a secondary peak at lower elevations found in the other two replicates. The diversity for the Costa Rican spatial replicate peaked at a much higher elevation, 1500m, and had dramatically lower richness at lower elevations than either the combined species richness pattern or the temporally replicated transects. Because of spatial heterogeneity of microhabitats and populations on different slopes and aspects, these changes may reflect real differences in the elevational profiles between the two transects. This is most likely the case for the spatial replicate detailed by Yu (1994) on Yushan Mountain in Taiwan. However, it is probably not the only cause for the differences seen in Costa Rica. The spatial transect in Costa Rica may have been influenced by aspect differences at one site, 1250–1300m, which was on a north-facing slope while all others were east facing. Anthropogenic edge effects also appeared to influence this transect however. The lower three sites were within contiguous forest in a park that abutted fragmented second growth and clear-cut regions. These three sites also had dramatically lower numbers of captures and individuals than any previously trapped site on the mountain. They averaged 47.3 captures and 26.3 individuals, whereas all other sites averaged 220.4 captures and 87.2 individuals with the same trapping effort. Lower species richness and low abundances of many taxa have been demonstrated in areas of forest fragmentation (Laurance and Bierregaard 1997); a pattern documented for small mammals (Lynam 1997 and references therein). Because of the possible influence of edge effects not present in the other replicates, I do not consider this spatial replicate an accurate representation of the small mammal pattern for the Tilirán region.

Another expectation of spatial replication is that as you move across space, new species will be documented and other species, documented previously, will not be encountered. This was shown clearly by the spatial replicates of Yu (1994), and on the spatial replicate at the two lowest elevations in Costa Rica. This spatial heterogeneity of populations, ß diversity, when summed over the entire mountain is what leads to greater species richness at elevations with the largest area and most habitat types. This same process is seen on a smaller scale when species richness from spatial replicates is combined. For example, if four species are encountered at the lowest elevation at site one and four different species are encountered at the same elevation on site two, then the combined species richness pattern would have eight species even though at both sites species-density never exceeded four species. The addition of spatial transects involves expanded variation, and may be more helpful in studies of ß diversity than in detailing a particular transect trajectory and environmental correlations with species richness. The existence of extreme differences in patterns of species richness among spatial transects down the same mountain slope may highlight important issues in elevational species richness patterns themselves, i.e. that no single pattern exists but that the pattern is in fact highly variable. Studies designed to specifically document this variability would be extremely valuable to our understanding of elevational patterns in diversity.

Replication allows the researcher to get a more reliable estimate of diversity patterns with more samples, and can demonstrate how patterns vary temporally and spatially. The veracity of the index assumption, that a single sampling transect along an elevational gradient is an accurate assessment of the diversity pattern, was shown to be true in some circumstances. Those single transects with apparently accurate diversity patterns had high sampling effort and consistently high capture success. Seasonal effects were apparent: dry seasons and the season with reduced reproductive activity had lower capture rates and a greater probability of variable diversity patterns. The recommended route toward accurate diversity patterns along ecological gradients is implementing an experimental design to maximize sampling effort and replication. If restricted time and resources make several replicates impossible, it appears that two replicates along the same transect during two seasons will yield the most valuable information. If only one transect can be conducted then the wet season in the tropics, or the known season of highest abundances and reproduction will give the most accurate estimation of the species richness pattern given adequate sampling. Less confidence should be placed in patterns of species richness with high temporal and spatial variability, or in those situations where some sites have dramatically lower capture rates and/or appear to be affected by edge effects of fragmentation or other anthropogenic disturbance factors. These results are based on studies spanning only a year or two, but long-term studies are necessary to adequately improve our comprehension of variability in diversity or abundance along elevational gradients.

CHAPTER 5.

PATTERNS IN ELEVATIONAL RANGE SIZE AND ABUNDANCE AT A LOCAL AND REGIONAL SCALE FOR RODENTS IN COSTA RICA

ABSTRACT

The objective of this study was to test several predictions of range size-abundance theory at the local and regional scales for elevational ranges of rodents in Costa Rica. The hypotheses examined were that larger ranges will be correlated with (a) higher abundances and (b) greater body size, and that (c) abundances will be highest at the center of elevational ranges. The local scale analyses were conducted along a Caribbean elevational transect from 750–1840 m in the Tilarán mountain range of northwestern Costa Rica. The regional scale analysis was conducted for the combined elevational relief of Costa Rica. Local elevational ranges and abundances were based on mark-recapture trapping at five elevational sites during late wet season, early wet season, and dry season in 2000–2002. Regional elevational ranges and abundances were based on a database of 5926 rodent specimens from Costa Rica. A linear relationship between abundance and elevational range size was not significant at the local scale, but was significant at the regional scale although not highly predictive. Body size and elevational range size were not related at the local or regional scale. Local and regional abundances across the elevational ranges generally revealed a trend toward higher abundances at mid-range, although usually not centered at the range midpoint. Lowland species had decreasing abundance with increasing elevation. Most species were rare locally and regionally regardless of elevational range size, geographic range in Costa Rica, or body size. This simply may be a consequence of the generally smaller range sizes and lower abundances of tropical species compared to temperate species. Highest abundances occurred near the center of elevational ranges but not precisely at the midpoint.

INTRODUCTION

The mechanisms underlying the realized geographic range of a species are fundamental to our understanding of evolution, range expansion and contraction, community diversity and abundance, and ecological affinities. In the last few decades, researchers have documented several patterns that appear to be generally applicable to geographic ranges. First, species' ranges are located in space independently of other species ranges (McGill and Collins 2003 and references therein; McCain in press). Second, range size is variable among species (Gaston 1990; Brown et al. 1996; and reference therein). Range size varies by more than 12 orders of magnitude; most species have small or moderately sized ranges, and very large ranged species are rare (Brown et al. 1996). Third, range size and body size are positively correlated (Gaston 1990; Brown et al. 1996). Larger sized species tend to have more expansive ranges, and smaller species are more restricted geographically. Lastly, larger ranged species tend to have greater population density at peak abundances than smaller-ranged species (Hengeveld and Haeck 1982; Brown 1984; Gaston 1990; Brown et al. 1995; Brown et al. 1996; McGill and Collins 2003).

The theory of geographic ranges also encompasses elevational ranges of species (defined as the elevational extent) as some of the first studies were from gradient analyses along montane transects (Whittaker 1952, 1956, 1960, 1967; Whittaker and Niering 1965). Whittaker's studies revealed that population densities are highest at the center of the elevational range of a species. This pattern has since been documented for many species, especially birds, across their geographic ranges (Hengeveld and Haeck 1982; Brown 1984; Gaston 1990; Brown et al. 1995; Brown et al. 1996; McGill and Collins 2003). Centered abundances across species' ranges are predicted if the optimum ecological conditions for that species are centered within the range (Gaston 1990; Brown et al. 1996 and reference therein). Species displaying this centered population pattern have abundance distributions that have been proposed to follow either normal (Gaussian) curves or 'peak-and-tail' distributions across their geographic range. A 'peak-tail' pattern as defined by McGill and Collins (2003) describes an abundance distribution across a range characterized by a few peaks of high abundance that drop off towards the periphery of the range. Abundances across a species' range are highly variable (Brown 1984), thus the peak-and-tail pattern is a better descriptor than the normal curve in many cases since it includes this variation in the distribution. Greater population size at the center of a species' range has several important implications for evolution, range expansion, and extinction probabilities (Channell and Lomolino 2000a, b).

The majority of range studies documenting geographic patterns have examined the better-known species of the Northern Hemisphere, with an emphasis on birds and some evidence from insects, plants, and mammals (Gaston 1990 and references therein). Birds are well studied because of the copious and valuable long-term data on abundances across ranges in the US and Canada from breeding bird surveys. However, less work has focused on small mammals, elevational ranges or different scales of range predictions. Patterns along elevational gradients may vary depending on whether ranges are defined regionally or locally. Local elevational ranges are detailed along transects up a mountainside, and local abundance patterns enumerated through mark-recapture techniques. Regional elevational patterns can be summarized from all elevational records of a species for a particular area or country. Regional abundance patterns can be estimated through documented population studies or specimen records. Of course, population studies and geographic sampling over large spatial scales are likely to have biases or inadequacies. Nonetheless, they offer valuable data that may suggest patterns for poorly known species ranges, particularly in the tropics where long-term population data do not exist.

Herein, several predictions are made regarding geographic ranges tested at the local and regional scales for the elevational ranges of rodents in Costa Rica. First, species with larger ranges will have higher population density. Second, species with larger ranges will have greater body size. Third, populations will be highest at the center of elevational ranges.

METHODS

Data on a local spatial scale were collected along a Caribbean elevational transect in the Tilarán mountain range in northwestern Costa Rica. Detailed descriptions of the study site and climate are available in McCain (in press). Rodents were sampled along an elevational transect between 750–1840 m during 2000–2002. Five sampling sites along the Caribbean elevation transect were surveyed: 750–800 m, 1000–1050 m, 1250–1300 m, 1500–1550 m, and 1770–1840 m (see Fig. 1, McCain in press). All sampling sites were located in areas with the most undisturbed forest available at that elevation, and the forest was contiguous between all sites. All five elevational sites were trapped during three seasons: late wet season, October–December 2000; early wet season, July–September 2001; and dry season, March–May 2002. Sites at the various elevations were sampled in a different order during each replicate to reduce temporal autocorrelation among sites. Trapping was standardized to include 130 traps: 7 pitfalls, 10 Victor snap traps set 1–3 m above ground on vines or in trees, 40 extra large folding Sherman live traps, and 73 large folding Sherman live traps. Each elevational site was trapped for seven consecutive nights except for the early wet season transect which was surveyed for five consecutive nights, for a total of 12,350 trap-nights. Animals were marked with a unique toe clip or ear tag, and released; selected vouchers were retained. For more details on trapping procedures see McCain (in press).

Local elevational ranges are defined as the distance between the lowest and highest captures for a species. Local abundances are measured either as a simple count or as a population estimate. Only species with consistently high numbers of recaptures are amenable to population estimation. Population estimates are based on mark and recapture histories imported in program CAPTURE (Rexstad and Burnham 1991). The Jackknife procedure is used because it has been shown to have the most robust population estimates for small samples (Burnham and Overton 1979).

Regional spatial scale analyses were conducted using a database of 5926 rodent specimens from Costa Rica compiled from 23 collections (see acknowledgments). All small rodents were used in the analyses except squirrels and pocket gophers, which may show biased abundance patterns because they are not easily captured with traditionally used live or snap traps. Other rare species may have similar biases, but since we know so little about them it is necessary to make the simplifying assumption that their low capture rates are due to their low abundance. Elevational ranges were determined from the highest and lowest elevational record in Costa Rica. Records with suspect localities, elevations, or species identifications were not used. Two species, *Heteromys sp.* and *Oligoryzomys vegetus*, are recently recognized species, thus many collections have specimens of these species identified as *H. desmarestianus* or *O. fulvescens*, respectively. The systematic monographs (Anderson and Timm ms; Carleton and Musser 1995, respectively) were used to determine which specimens belonged to each species. Only the specimens enumerated in the systematic revisions, those from the same localities, or those clearly above or below the elevational range of the other species were included in the present analysis.

Relative population sizes at the regional scale were inferred from the number of specimens taken from each elevational interval. Ideally, population studies across the elevational range of each species would be employed, but such data do not exist for these species. Prior to this study, only *H. desmarestianus* (Fleming 1974), *Liomys salvini* (Fleming 1974), and *Peromyscus nudipes* (Anderson 1982) have been examined in short-term studies at one site each. Using specimen numbers to estimate abundance patterns involves assumptions about sampling equalities across the elevational range. In Costa Rica, several sites have experienced higher trapping intensity than others, most notably La Selva (70 m), Monteverde (1300–1700 m), Cerro de la Muerte (2100–3200 m), Turrialba (650 m), and Volcán Irazú (1650–2900 m). Nonetheless, sites along the majority of the elevational relief in Costa Rica have been sampled and numbers of specimens should give a rough estimate of abundance patterns along each species' range.

To determine if species with larger ranges have larger populations, linear regressions of elevational range against abundance were run at both the local and regional scales. Local abundance for each species was the total number of individuals captured summed across the five sampling localities for all three seasons (see Appendix 2 in McCain in press). Regional abundance is the total number of specimens for each species collected in Costa Rica. Area of the species' range within Costa Rica and total latitudinal range was regressed against regional abundance. Latitudinal range and range area in Costa Rica (% coverage) were based on maps from Hall (1981) and Reid (1997). Linear regressions were used to determine if a positive relationship exists between range size and body size. Average body size (weight in grams) of each species was taken from the literature (Hall 1981; Reid 1997). The abundance pattern across the elevational range for each species was assigned to one of five descriptive categories: (1) decreasing with elevation, (2) peak-and-tail pattern shifted toward lower elevations, (3) peak-and-tail pattern centered near elevational range midpoint, (4) peak-and-tail pattern shifted toward higher elevations, and (5) increasing with elevation. Only species with more than 10 captures at the local scale or 20 specimens at the regional scales were examined, as fewer did not allow meaningful discernment of pattern. To examine location of peak abundance and eliminate some sampling effort bias, each species' range was divided into 5 equal segments, and cumulative abundance determined in each elevational range per species. Highest abundance was then assigned to one of the five elevational segments. Chi-square goodness of fit tests were used to test whether significantly greater abundance occurred near the center of a species' elevational range as opposed to the periphery.

RESULTS

Elevational range size and placement were variable across both the local and regional scales (Table 5). Elevational range size varied from 100 to 1340 m at the local scale (n = 12) and 150 to 3800 m at the regional scale (n = 34). Abundances also are highly variable (Table 5), as 4 species are known from fewer than 5 individuals on the elevational transect, while *Peromyscus nudipes*, the most common species, had 859 individuals caught in the same sampling period. A similar spread in abundances was seen in the regional data. Eight species are known in Costa Rica from fewer than 10 specimens, while others are very common in collections (i.e. *P. nudipes* = 990 specimens). The community abundance pattern at both scales follows the commonly documented lognormal distribution.

The linear regression of abundance by elevational range was insignificant at the local scale (r^2 = 0.206, p-value = 0.1386, n = 12; Fig. 22a), but significant at the regional scale (r^2 = 0.297, p-value = 0.0009, n = 34; Fig. 22b). Abundance regressed against area of range in Costa Rica (r^2 = 0.310, p-value = 0.0740, n = 35; Fig. 22c) and latitudinal range (r^2 = 0.029, p-value = 0.3305, n = 35) were not significant. Species that were rare locally were rare regionally also (r^2 = 0.954, p-value = 0.000, n = 12).

No linear relationship was found between body size and range size at the local (r^2 = 0.270, p-value = 0.083, n = 12; Fig. 23a) or regional scale (r^2 = 0.077, p-value = 0.1250, n = 32; Fig. 23b). The slope was positive in the local analysis, but negative in the regional analysis. In both cases, the regressions were heavily influenced by body size of one or two species with large ranges (Fig. 23a & b); otherwise there appeared to be no noticeable pattern in elevational range size with body size for these rodent species. Body size and regional abundance also appear unrelated (r^2 = 0.016, p-value = 0.485, n = 34).

Local abundance across elevational range generally followed a trend of higher abundance at mid-range, as seen in the four most abundant species (Fig. 24).

However, none of the species followed a normal, or even symmetrical, curve. All abundance patterns were better described by the peak-and-tail pattern. The highest abundances were shifted toward higher elevations for *Heteromys* sp. and *P. nudipes*. *Oryzomys albigularis* and *Scotinomys teguina* appeared to have the highest abundance closer to the range midpoint, but *S. teguina* displayed a more bimodal pattern. The same general trends in abundance were seen at the regional scale for these four species as in the abbreviated range of elevations for the local transect (Fig. 25 a–d). Overall, abundance patterns across the range of the 12 locally documented species included two with peak-and-tail pattern centered near elevational range midpoint, two with peak-and-tail pattern skewed toward higher elevations, and two increasing with elevation. Six species had no discernable pattern because they were caught too infrequently or at only one elevation.

The majority, 15 of 22, of species in the regional analysis had highest abundances at mid-range although many not centered at the range midpoint (i.e. Fig. 25 a–d). Five species displayed a peak-and-tail pattern shifted toward lower elevations, three with peak-and-tail pattern centered near elevational range midpoint, and seven with peak-and-tail pattern shifted toward higher elevations. No species increased monotonically in abundance with elevation. Seven species, lowland specialists, had their highest abundance at the lowest elevations in the range (i.e. Figure 25e). Nonetheless, the probability of the highest abundance occurring in one of the five equal elevational segments of its range was indistinguishable from random ($X^2 = 9.24$, $df = 4$, $p > 0.05$).

DISCUSSION

Range size-abundance:

The assumption that a linear relationship occurs between range size and abundance is ubiquitous across taxonomic groups and continents. However, this pattern does not hold for elevational ranges of tropical rodents in Costa Rica at a local scale, and is only marginally predictive at a regional scale. Correlations of regional abundances with geographic range coverage in Costa Rica or with latitudinal range also were insignificant. Most of the highly cited papers on the positive range-abundance pattern are based on data from birds, plants, and insects from the US, Britain, and Europe (Brown 1984, 1995; Lacy and Bock 1986; Blackburn et al. 1997; Gaston et al. 1997a, b; Quinn et al. 1997), although there are exceptions. The relationship at a local scale between range size and abundance of plants was not significant in eastern Australia (Hunter 2003) nor central England (Thompson et al. 1998). Geographic range size and abundance were insignificantly related for birds in New Zealand (Blackburn et al. 2001), for butterflies in Britain (Dennis et al. 2000), and for plants in central England (Thompson et al. 1998). Thus, mammals or perhaps many organisms from tropical regions may not conform to the pattern expected in northern hemisphere birds.

Two range-abundance studies on mammals both found significant relationships between geographic range size and abundance in England (Blackburn et al. 1997) and Australia (Johnson 1998). Interestingly, Johnson (1998) found that the relationship depends on latitude, such that tropical species have low population density relative to range size; thus, a less predictive relationship occurs between range size and abundance. This seems to be consistent with the result seen in Costa Rican small mammals. Of the other tropical range-abundance studies in the literature, one found no significant relationship between range size and local abundance in a pair of Neotropical tree species (Buckley and Kelly 2003). The other found a significant relationship between geographic range size and abundance of insects in the dry tropical forest of Tanzania (Kruger and McGavin 2000). More tropical studies are needed to assess whether or not the non-significant pattern reported herein is more general at these latitudes.

Few abundance-range size studies have focused on elevational ranges. Brown (1984) reanalyzed Whittaker's North American plant and insect data along elevational gradients (1956, 1960) and found significant relationships between abundance and range size. No previous elevational gradient studies in the tropics exist. Thus, it appears that small mammals in the tropics may not exhibit an abundance-range size relationship due to small ranges coupled with generally low abundances. This may stem from characteristics unique to tropical rodent biology where most species are rare regardless of geographic or elevational range. The few species that are quite abundant (*Heteromys desmarestianus*, *Liomys salvini*, *Melanomys caliginosus*, *Peromyscus nudipes*, *Scotinomys teguina*, *S. xerampelinus*, and *Sigmodon hirsutus*) vary in elevational and geographic range size. The only consistent factor among them may be flexibility to habitat disturbance, although only some would be considered trophic generalists (*M. caliginosus*, *P. nudipes*, and *S. hirsutus*).

Range Size and Body Size:

Most studies of range size find that it is positively correlated with body size, and many studies have also found higher abundances in larger species (Brown et al. 1996 and references therein). Neither of these relationships was supported with tropical rodents in Costa Rica. Many recent studies examining this relationship have also failed to find significant relationships. No relationship was found for body size with abundance, range size, or latitude for mammals in Australia (Johnson 1998). No relationship between body size and range size or abundance was significant for birds in Finland (Solonen 1994). A negative relationship between body size and range size was found for the global distribution of waterfowl (Gaston and Blackburn 1996). And global waterfowl (Gaston and Blackburn 1996) and protozoans in Scotland (Finlay and Fenchel 2001) had negative relationships between body size and abundance. This relationship between body size and range size may not be as general as first perceived; taxonomic level or phylogenetic history of clades may cause variation in strength of this correlation.

Tropical rodent species varied in size, but the spread was not as great as variation in birds across clades or for mammals in general. In Costa Rica, the largest species at the regional scale were rare, and only widely ranging species in the local analysis was large bodied. In general, most species had small ranges and low abundances regardless of body size. Again, this may be a reflection of tropical biology, as tropical species tend to have smaller ranges (Brown et al. 1996), but also may reflect rodent biology. Body size in rodents may not be a good predictor of range size or abundance, as other factors such as dispersal, intrinsic rate of increase, response to disturbance, and trophic generalization may be more important than for other groups for which strong relationships with body size and range size or abundance exist.

Centralized Abundance Pattern:

Abundances were generally higher in the middle of the species' ranges at both the local and regional scales, corroborating a trend that has been documented for many species both elevationally and geographically. The majority of patterns were better described by the peak-and-tail pattern, which encompasses the variability in abundance estimates across the range (McGill and Collins 2003). Only one or two species displayed a pattern resembling a normal curve (i.e. *P. nudipes*, Fig. 25). The lowland species did not display a centered abundance pattern, but had decreasing richness with increasing elevation (i.e. *Melanomys caliginosus*, Fig. 25). Lowland species are best adapted to the environmental conditions at the lowest elevations. The hypothesis most commonly proposed to explain the centered abundance pattern is that detailed by Brown (1984): species are most common at the most ideal biological conditions and decrease in abundance gradually toward their niche limits. From an elevational perspective, the lowland adapted species would be expected to display exactly the pattern shown in Costa Rica, since the biological conditions along the elevational gradient most ideal for those species are the lowest.

The theoretical treatment of the centered abundance pattern in the literature implies that the peak abundance is located at the midpoint of the range. However, the location of peak abundance was not consistently at the elevational range mid-point for these species. Regionally, 12 of 15 species with centered abundances had the peak abundance shifted either towards lower or higher elevations. Locally, the species had abundance peaks either near the range midpoint, shifted toward higher elevations, or demonstrated increasing abundance with elevation. The difference between the two scales is mainly attributable to two factors. First, most of the local species were primarily montane thus more likely to be abundant at higher elevations. Second, the entire elevational range wasn't sampled due to deforestation at lower elevations, so that lower elevation species range were not included in the local analysis. Another important point is that the local population estimates were susceptible to the influences of site-specific differences. *Heteromys sp.* had much higher abundances at the two relatively flat sites (1500 m and 800 m), while *S. teguina* was more abundant at the two sites with steepest slopes that also had the most edge habitat (1800 m and 1000 m). Such, species-specific attributes of different sites may have had been highly influential in the local abundance patterns but with the current data are inextricable from the elevational gradient.

There was good concordance between the range-abundance patterns of the species documented both locally and regionally for the subset of elevations that overlapped at the two spatial scales. It may be possible to improve the regional abundance data by attempting to standardize trapping effort either by number of sampling localities per elevation or number of collecting bouts based on dates. Both will not directly assess sampling effort in terms of traps/nights, but may eliminate some dependency in peak abundances to highly studies sites. Future analyses will attempt such comparisons of abundance patterns with different formulations of specimen data.

The elevational range-abundance studies of Whittaker (1952, 1956, 1960, 1967) showed similar shifts in the peak abundance away from the range midpoint, but still somewhat centered, when the raw data were analyzed as in Brown (1984). Peak abundances shifted away from the range midpoint are shown also in the location of highest abundance for many of the bird data (i.e. Brown 1984). Thus, the centered abundance pattern across species ranges is a general pattern but with high variability in the degree of "centeredness". This has implications for theoretical applications of the centered abundance pattern. For instance, Channell and Lomolino (2000a, b) have used this general pattern of highest abundances centered within the range and decreasing towards the range peripheries to model extinction probabilities across species ranges assuming the highest abundances and thus lowest threat index existed at the midpoint of the range. They found greater extinction risk toward range peripheries, both geographically and elevationally. But incorporating the shifting of peak abundance away from the range midpoint into theoretical and simulation models may produce different results.

CONCLUSION

This collection of analyses detailing latitudinal and elevational diversity of small mammals have shown that despite the variation among ecological gradients and geographical localities some clear, general trends were apparent. The systematic employment of and improvements made to the mid-domain null model (and associated programs) have shown that diversity null models are valuable additions to the statistical rigor and quantification of diversity analyses.

The utility of the mid-domain null model is demonstrated in the first three chapters. The diversity pattern of North American desert rodents (a symmetrical, unimodal curve with highest diversity at 31 degrees N latitude) appeared to be highly influenced by spatial constraints of the ecological boundaries of the desert ecosystem at a large spatial scale. The biological theories including productivity hypotheses, species-area relationships, endemic bias, or sampling bias were able to predict the observed pattern in diversity of desert rodents. The elevational diversity analyses in Costa Rica and globally appeared to be less responsive to spatial constraint. The fit to the null model predictions were equivocal for elevational data sets as many demonstrated r^2 values between 30 and 40 %, and the Costa Rica data sets had r^2 values of 44%. Some elevational datasets showed highly significant fits to the mid-domain effect, for instance the gamma diversity pattern for Madagascar had an r^2 value of 88%. The variability in values is evidence of some influence of spatial constraints of montane systems, but clearly indicated that other biological factors also influenced the diversity patterns. Additionally, some systems, single diversity patterns and gamma diversity patterns as a whole, appear to be more influenced by spatial constraint. This disparity in the significance of spatial constraint could be related to the range size distribution and to the number of species in each analysis—patterns that warrant further investigation. Similarly, improvements can be made to the mid-domain null model predictions by increasing the specificity of range size distributions, and incorporating more biological information to make more complex predictions of diversity pattern.

All of the unbiased analyses of elevational diversity in Costa Rica and globally demonstrated unimodal diversity curves with the highest diversity at some middle elevation. The elevational diversity analyses of small mammals reinforced the perceived importance of a suite of interacting climatic factors. The highest diversity was documented at intermediate climatic conditions—intermediate rainfall, temperature and productivity—at mid-elevations a few hundred meters below the persistent cloud cap found at the mountaintop. This trend supported the predictions of the mountain mass effect where the highest diversity was found at higher elevations on taller mountains and at lower elevations on shorter mountains. This linear relationship was strongest for alpha diversity studies (single transects along a mountain side), and for tropical and island data. The gamma data sets (summaries of diversity pattern for a mountain or mountain range) had stronger spatial constraint and area effects with little support for the mountain mass effect. One interesting pattern that deserves further study is that the gamma data sets had a positive, linear relationship between the elevation of peak diversity and latitude. Peaks in diversity were at higher elevations for mountains at greater latitudes. Unfortunately, this trend is hindered by sampling bias—most high latitude elevational studies focused on tall mountains and mountains emerging from higher elevations. More datasets are needed to detect strong support for the latitudinal-elevational diversity pattern. Area is another factor that warrants further study, especially for the gamma diversity studies, to interpret the degree of fit to spatial constraints, climatic influences, and other diversity hypotheses without the strong species-area effects.

Additional avenues of importance for delineating a generalizable diversity theory—particularly for elevational diversity patterns—are three-fold. First, better quantitative tests are need for other biological theories like the community overlap hypothesis, habitat complexity hypotheses, and hypotheses based on historical factors. Simulation, null models, and theoretical modeling should clarify testing these hypotheses in future analyses. Second, more synthetic, comparative approaches are needed for a variety of taxa at various spatial scales to determine generalizable trends and pinpoint taxon-specific contrasts, which should lead to a better understanding of the complex nature of elevational diversity patterns. Third, more experimental approaches are needed to determine specific mechanisms producing elevational diversity. Such studies will need to be long-term and combine taxonomic diversity surveys with concomitant, detailed climatic monitoring. Experimental manipulations like enclosures with both species and diversity removals and introductions will also be invaluable in pinpointing mechanisms. The temporal and spatial variability in diversity patterns revealed in the replication chapter emphasize the need for such long-term studies to adequately quantify the nature of elevational diversity patterns.

Range-size distributions of small mammals along ecological gradients, particularly elevational gradients, might be a key to understanding the ubiquitous unimodal diversity patterns and deserves closer examination. If small mammal assemblages have a general range-size distribution within an ecological gradient, they may be predisposed to show certain diversity patterns. For instance, a distribution of range sizes characterized by mostly midsize ranges and fewer small and large ranges may tend towards a unimodal diversity pattern, whereas a range size distribution including mostly large and midsize ranges may tend toward greater skew in the diversity pattern toward either end of the gradient. Lastly, abundance patterns along ecological gradients may be important not only in diversity patterns but also in dispersal trends, population stability, and species extinction probabilities. My analyses of abundance and range size patterns in Costa Rica emphasize that most rodent species are rare locally and regionally regardless of body size, elevational range size, and geographic range size. A general trend of higher abundances at mid-elevations was noted, although many abundance peaks were skewed toward higher and lower elevations but not coincident with diversity peaks. Longer studies are needed to adequately assess the spatial and temporal variability in trends in elevational abundance patterns and their influence on diversity patterns.

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Figure 1. The North American desert biome including the Great Basin, Mojave, Sonoran, and Chihuahuan Deserts. The biome extends from 45°N to 19°N latitude (modified from MacMahon, 1985).

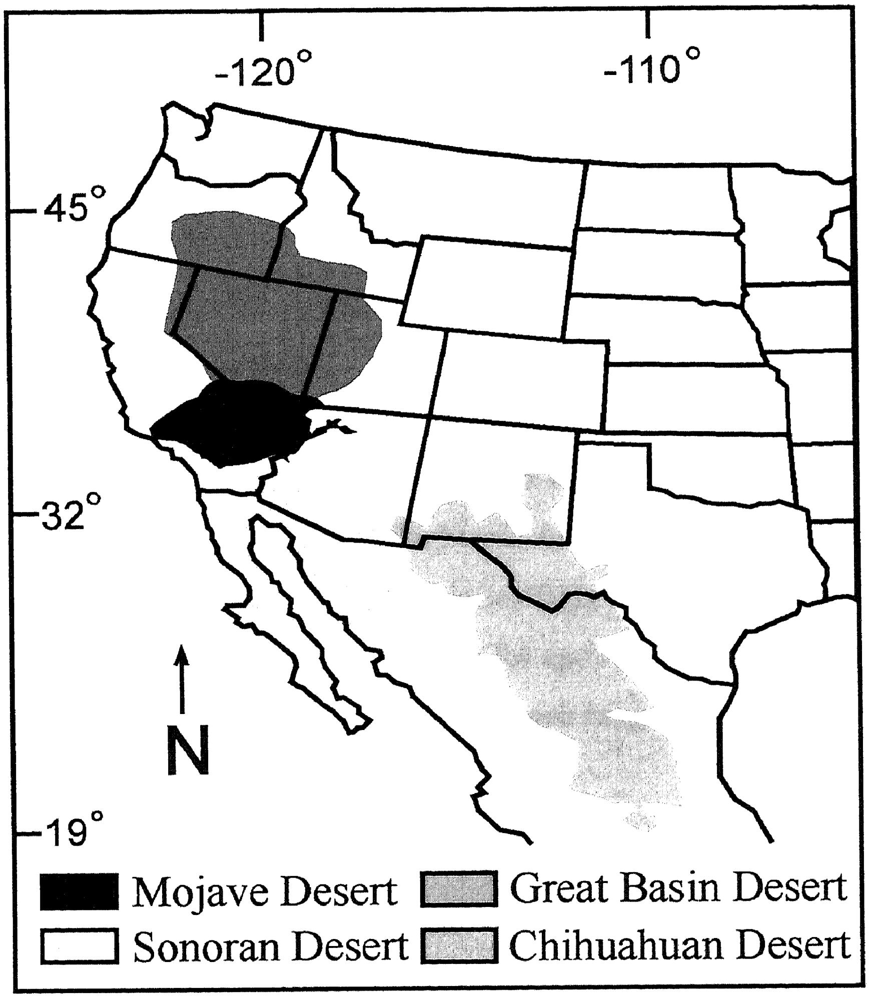

-120°
-110°
45°
32°
19°
N
Mojave Desert
Great Basin Desert
Sonoran Desert
Chihuahuan Desert

Figure 2. A graphical representation of range size of each desert rodent compared to range midpoint and latitudinal range in the North American desert biome. Solid circles represent continental species, open circles Baja peninsular endemics. Horizontal lines are extent of latitudinal range for each species, and triangle represents limits of possible range midpoint for each range size.

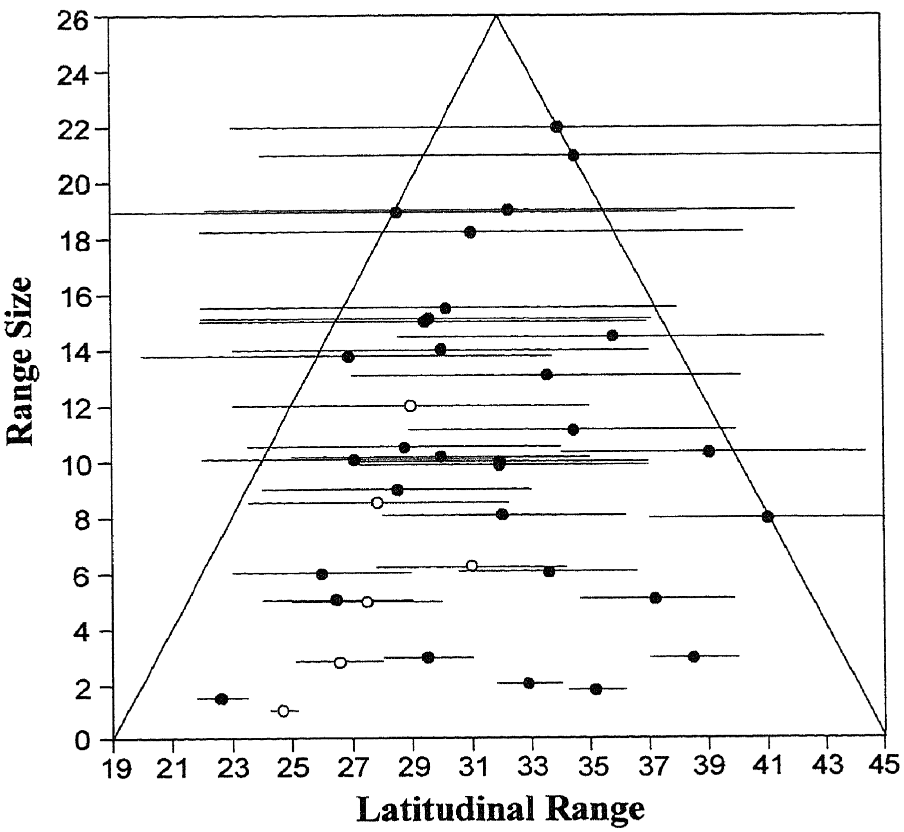

Range Size
26
24
22
20
18
16
14
12
10
8
6
4
2
0
19
21
23
25
27
29
31
33
35
37
39
41
43
45
Latitudinal Range

Figure 3. Empirical species richness curves for North American desert rodent endemics plotted with 95% simulation prediction curves from RangeModel (http:/viceroy.eeb.uconn.edu/RangeModel) based on empirical range sizes. Curves for A) all species ($n = 37$) and B) excluding Baja peninsular endemics ($n = 31$).

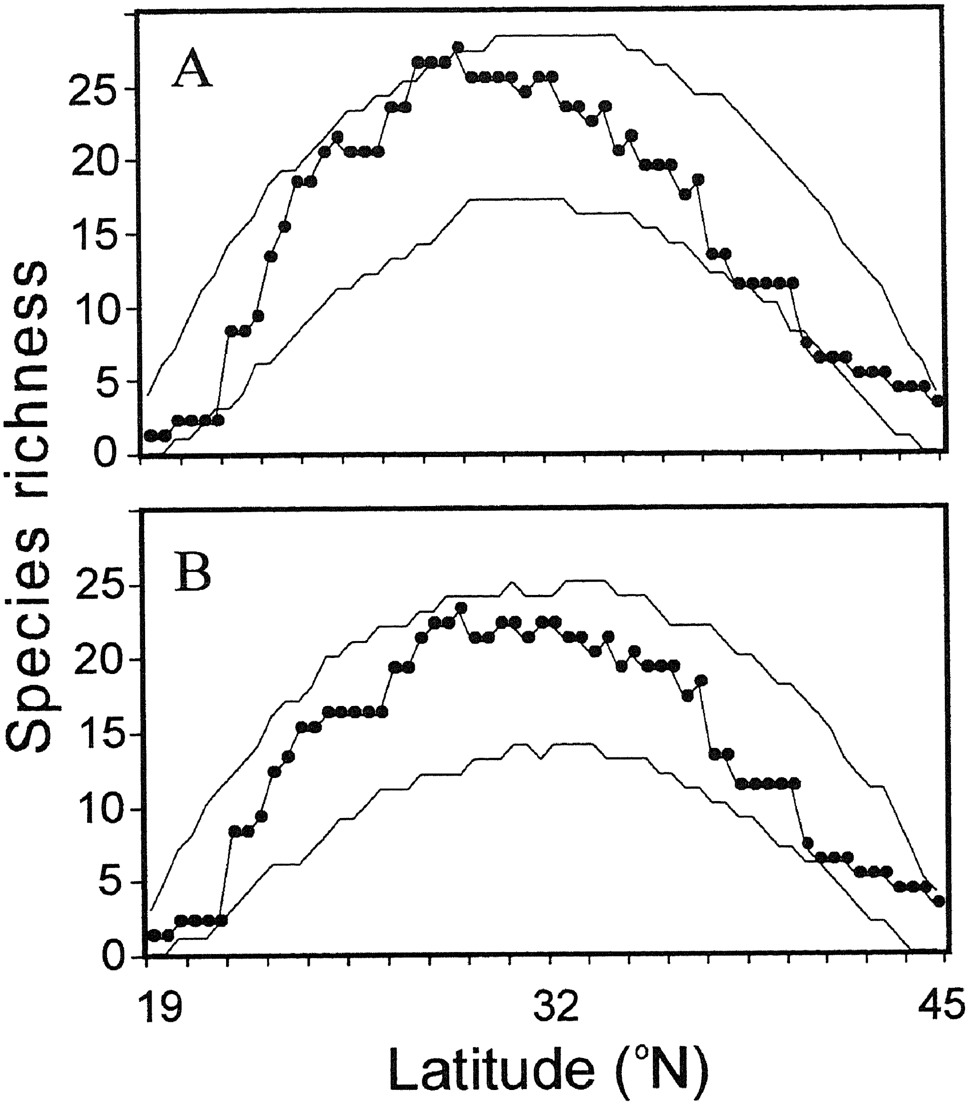

A
B
Species richness
0
5
10
15
20
25
0
5
10
15
20
25
19
32
45
Latitude (°N)

Figure 4. Empirical species richness curves for North American desert rodent endemics plotted with 95% simulation prediction curves from RangeModel (http:/viceroy.eeb.uconn.edu/RangeModel) based on empirical range midpoints. Curves for A) all species (*n* = 37) and B) excluding Baja peninsular endemics (*n* = 31).

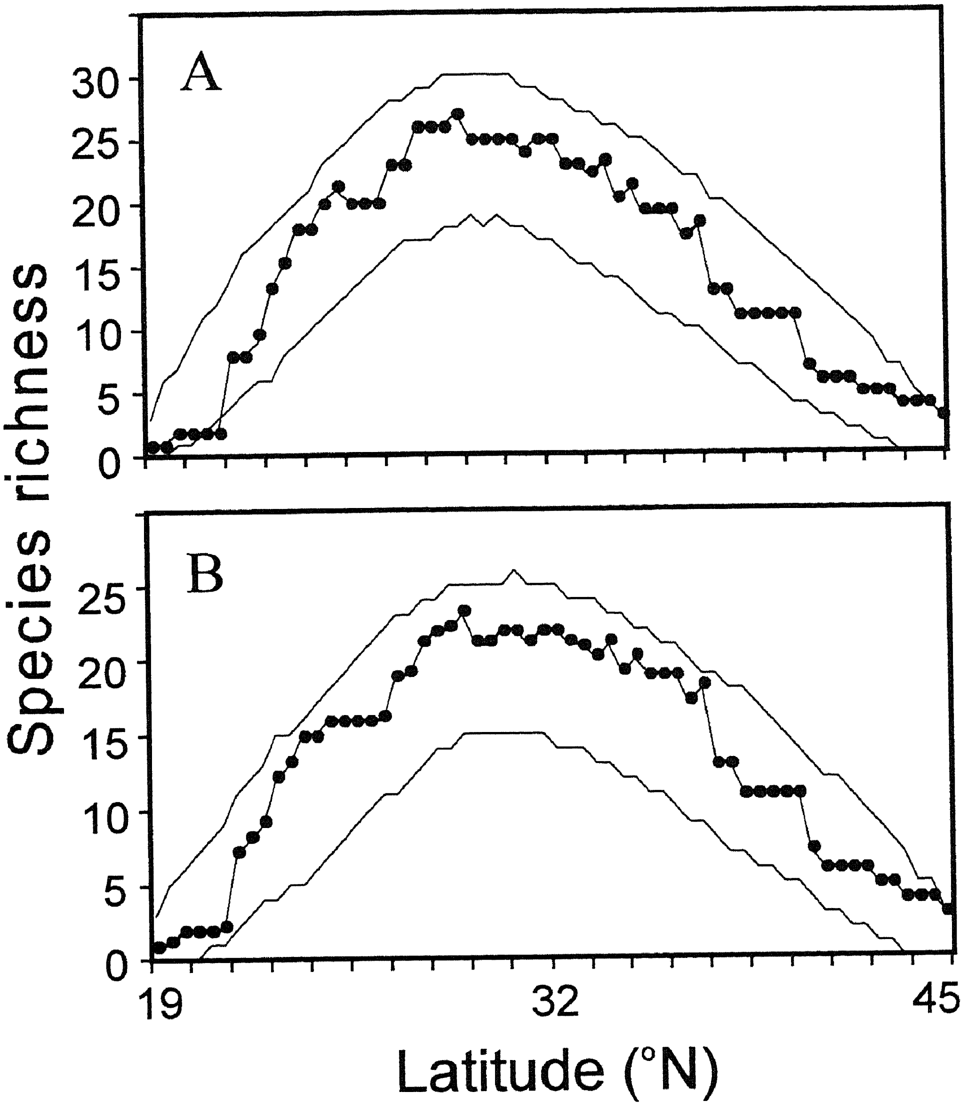

A
B
Species richness
0
5
10
15
20
25
30
0
5
10
15
20
25
19
32
45
Latitude (°N)

Figure 5. Empirical species richness curves for North American desert rodent endemics plotted with 95% confidence interval from the binomial null model (Willig and Lyons, 1998). Curves for A) all species ($n = 37$) and B) excluding Baja peninsula endemics ($n = 31$).

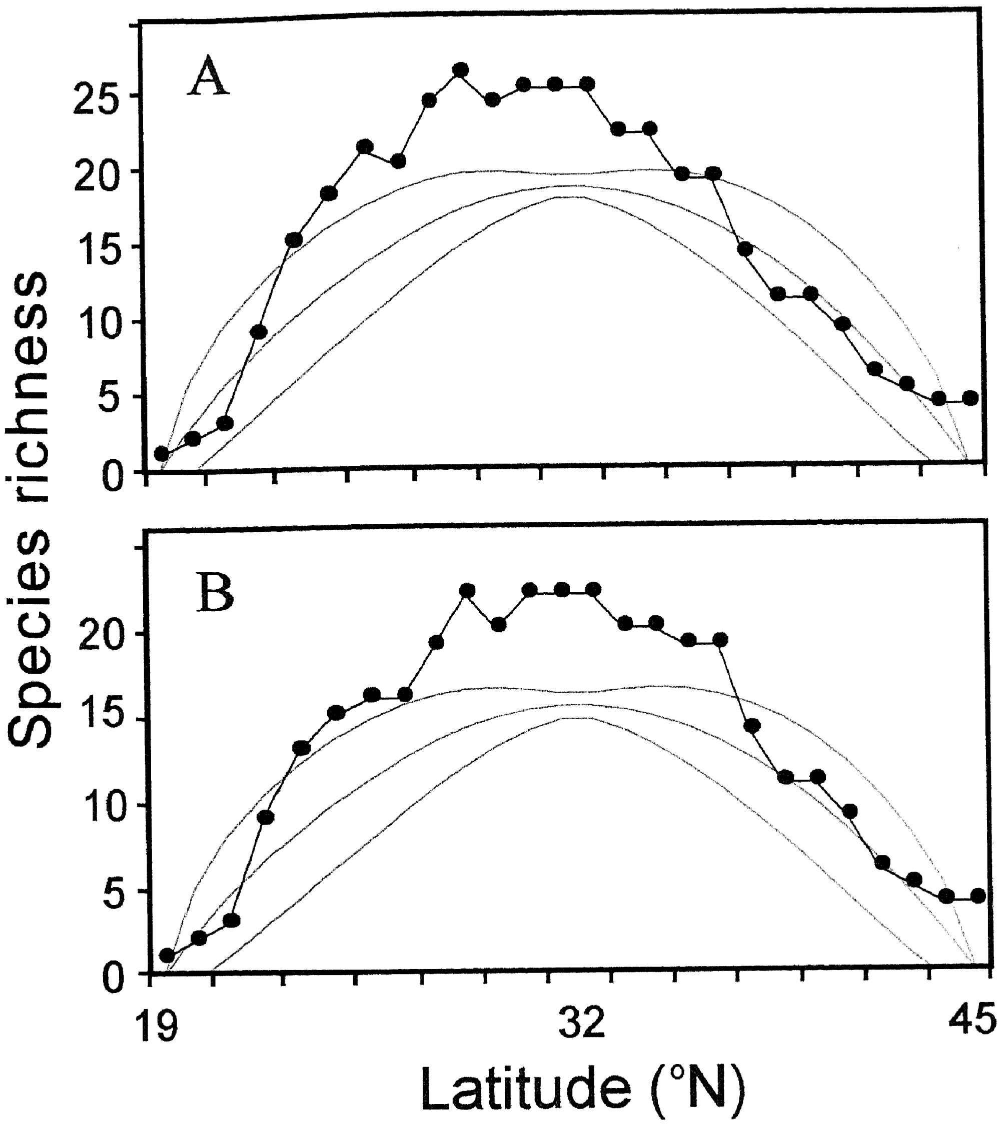

A
B
Species richness
0
5
10
15
20
25
Latitude (°N)
19
32
45

Figure 6. Probability-density functions for range sizes of the binomial model compared to empirical distribution of range size for North American desert rodents. Probability-density function (gray) and empirical range sizes (black) for A) all rodent endemics and B) excluding Baja peninsular endemics.

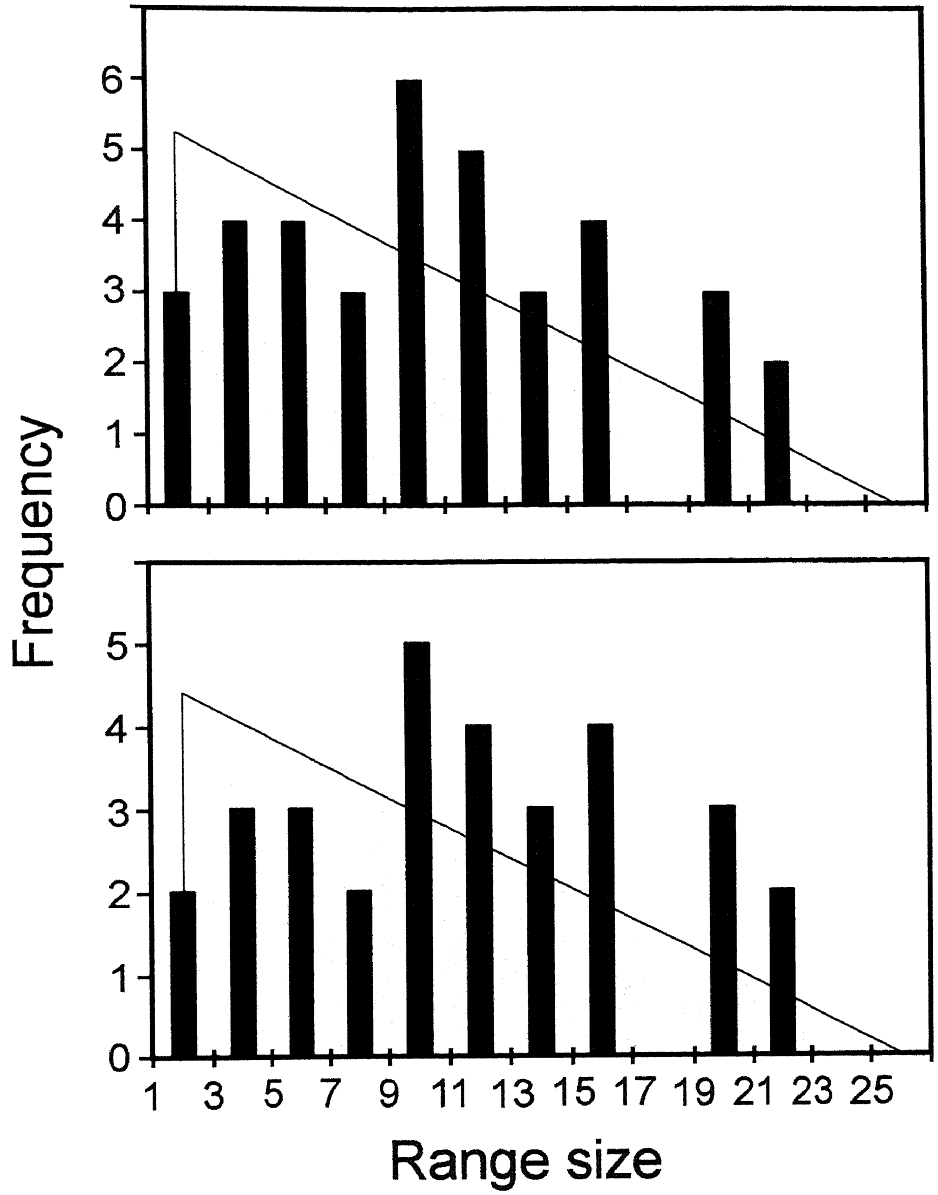

Frequency
6
5
4
3
2
1
0
5
4
3
2
1
0
1
3
5
7
9
11
13
15
17
19
21
23
25
Range size

Figure 7. Comparison between species richness curves of desert rodents and area associated with each degree of latitude for geographical distribution of North American deserts. Area and richness of species for A) all deserts and B) deserts excluding Baja peninsula.

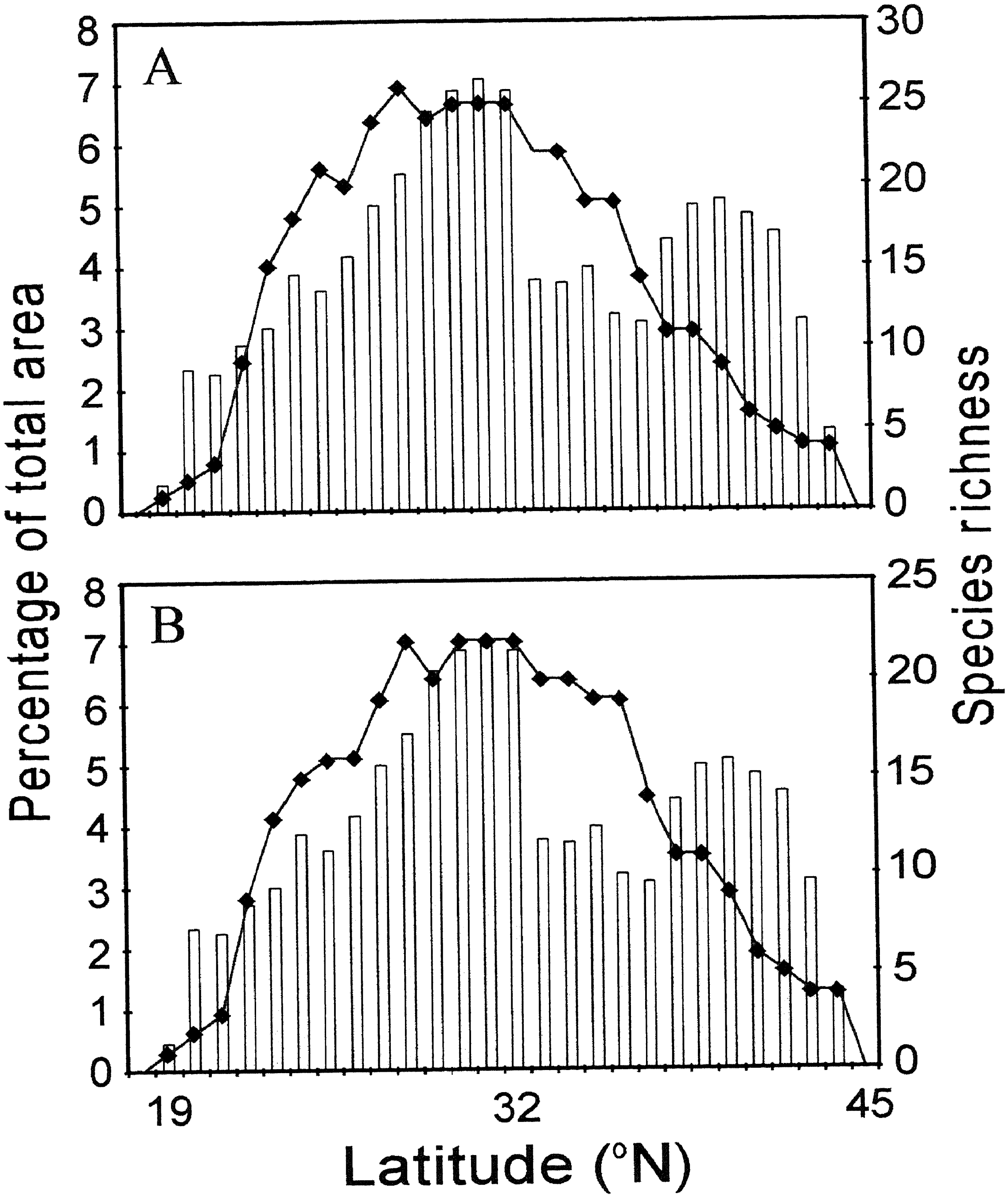
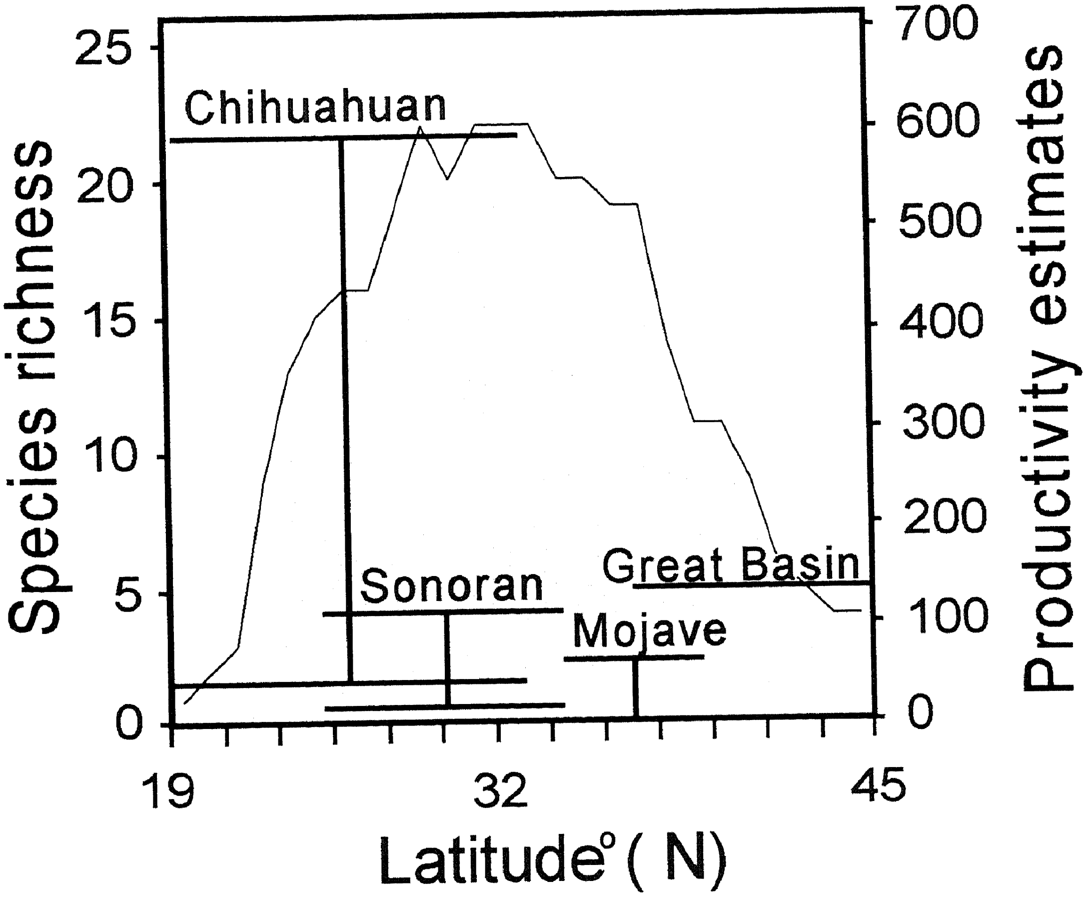

A
B
Percentage of total area
Species richness
Latitude (°N)
0
1
2
3
4
5
6
7
8
0
5
10
15
20
25
30
19
32
45

Figure 8. Range of estimates of primary productivity (productivity / ($gm^{-2}yr^{-1}$)) for each desert within the North American desert ecosystem compared with species richness of desert rodent endemics (data from Waide et al. 1999 and references therein). Extent of each desert shown with horizontal bars. Range of productivity estimates shown with vertical bars (with only a single estimate for the Great Basin).



Species richness
Productivity estimates
Latitude° (N)
Chihuahuan
Sonoran
Great Basin
Mojave
0
5
10
15
20
25
0
100
200
300
400
500
600
700
19
32
45

Figure 9. The Monteverde Cloud Forest Reserve and Bosque Eterno de los Niños (white) that protect the majority of the Peñas Blancas Valley. Trapping localities for the temporal replicates of the elevational gradient are shown in circles, and the spatial replicates are shown in triangles. The elevations of the sites are 1) 1770–1840 m, 2) 1500–1550 m, 3) 1250–1300 m, 4) 1000–1050 m, and 5) 750–800 m.

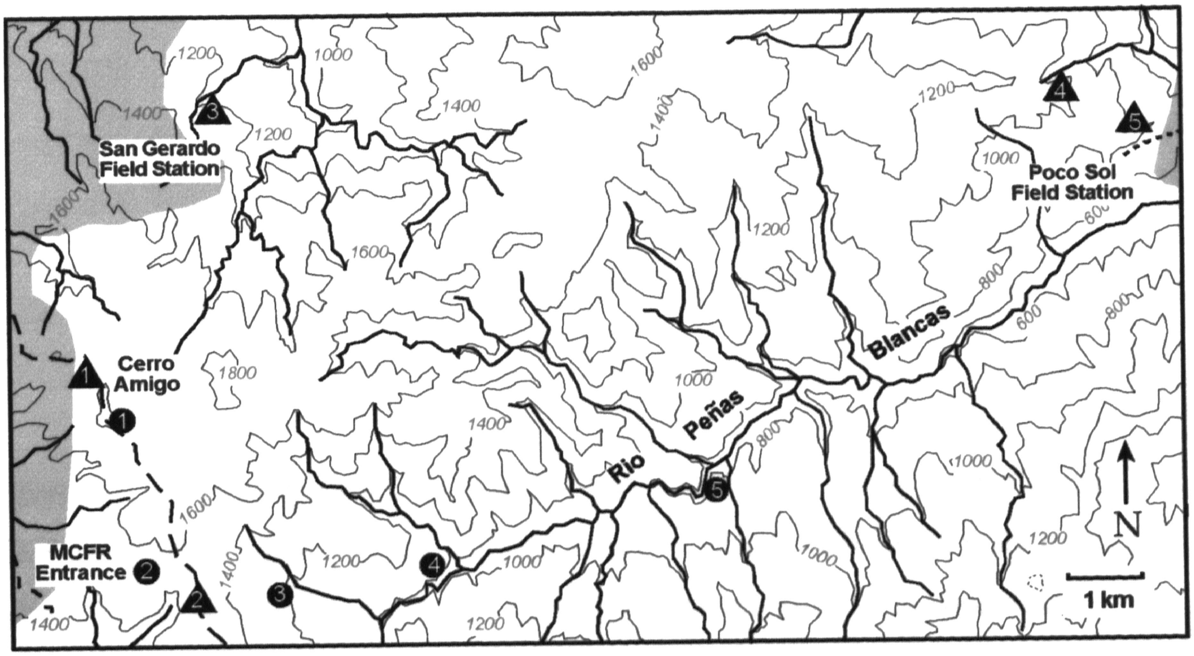

San Gerardo Field Station
Poco Sol Field Station
Cerro Amigo
MCFR Entrance
Rio Peñas Blancas
1 km
N
1
2
3
4
5
1200
1000
1400
1600
1800
800
600

Figure 10. Elevational ranges of each species documented along the Río Peñas Blancas transects. Black boxes indicate locations where individuals were trapped or sighted from 2000–2002, and white boxes indicate localities from specimens collected previously in the same areas, and the white circles are the lower and upper localities for species from the Costa Rican specimen database.

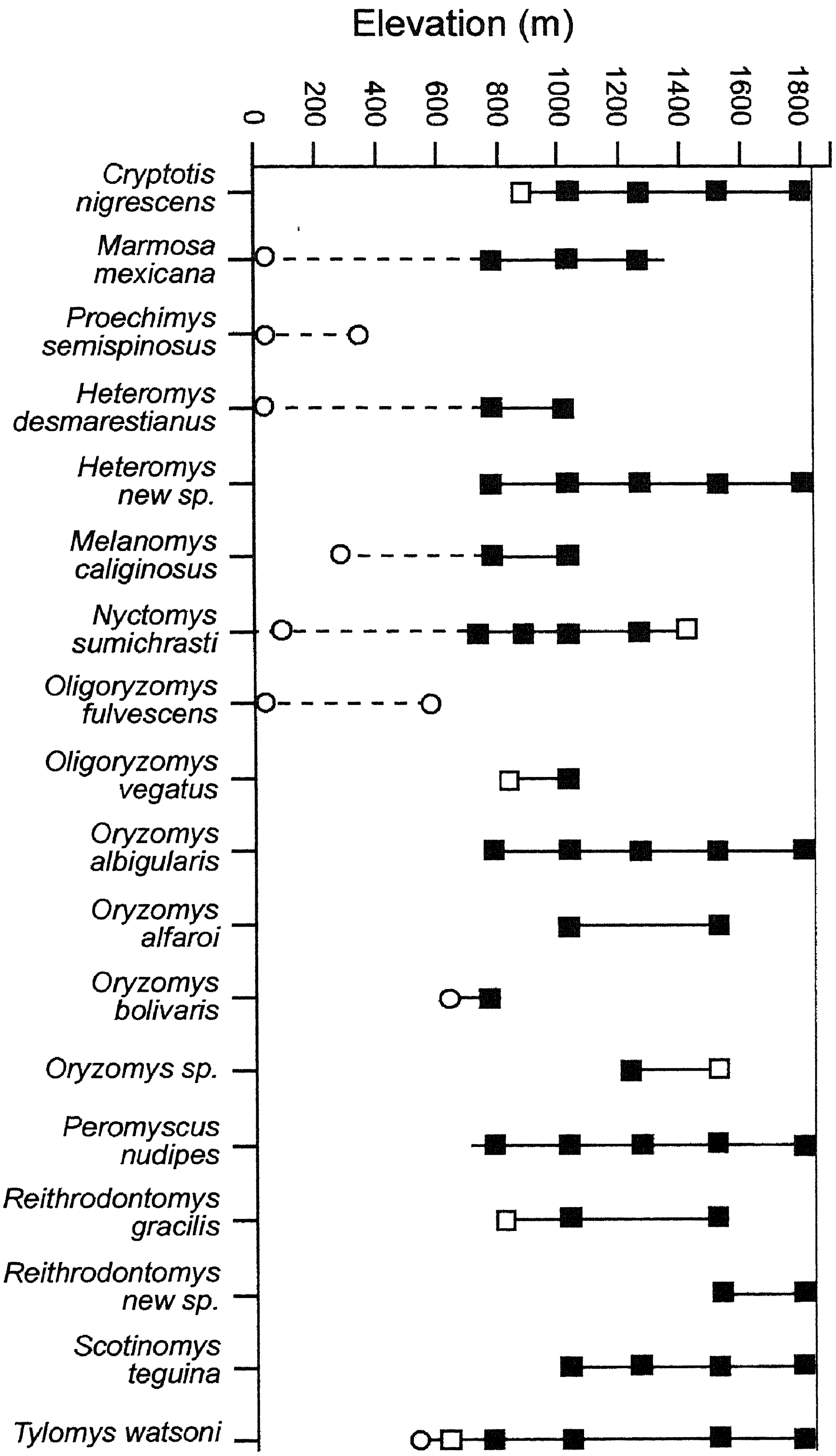

Elevation (m)
0
200
400
600
800
1000
1200
1400
1600
1800
Cryptotis nigrescens
Marmosa mexicana
Proechimys semispinosus
Heteromys desmarestianus
Heteromys new sp.
Melanomys caliginosus
Nyctomys sumichrasti
Oligoryzomys fulvescens
Oligoryzomys vegatus
Oryzomys albigularis
Oryzomys alfaroi
Oryzomys bolivaris
Oryzomys sp.
Peromyscus nudipes
Reithrodontomys gracilis
Reithrodontomys new sp.
Scotinomys teguina
Tylomys watsoni

Figure 11. Species richness patterns for the four replicates: (A) late wet season, 2000 and early wet season, 2001, (B) dry season, 2002, and the spatial replicate from the late wet season, 2001. The combined species richness pattern including species ranges documented in any of the four transects is shown in the total species richness curve.

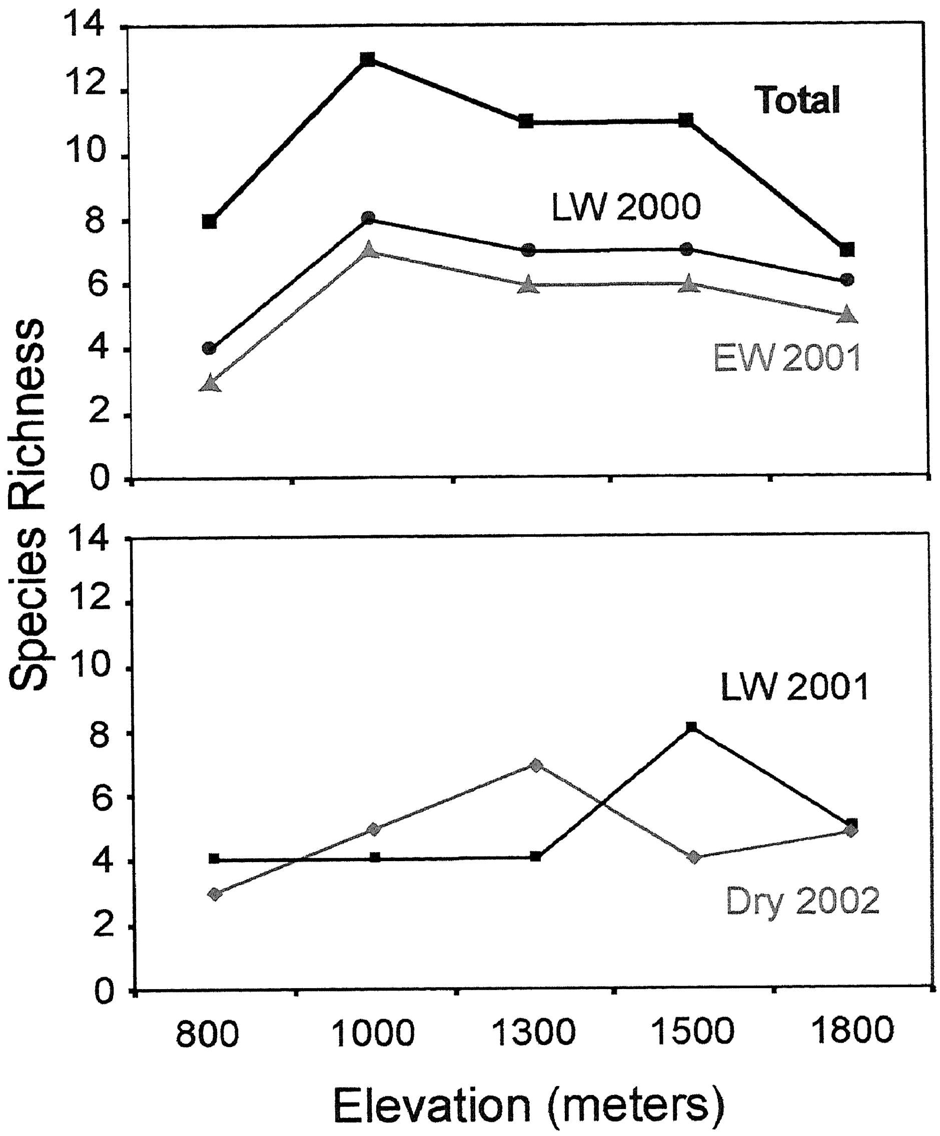

Total
LW 2000
EW 2001
LW 2001
Dry 2002
Species Richness
0
2
4
6
8
10
12
14
800
1000
1300
1500
1800
Elevation (meters)

Figure 12. Species-accumulation curves for each site, and overall species-accumulation curves for each elevation using the combined data from all replicates.

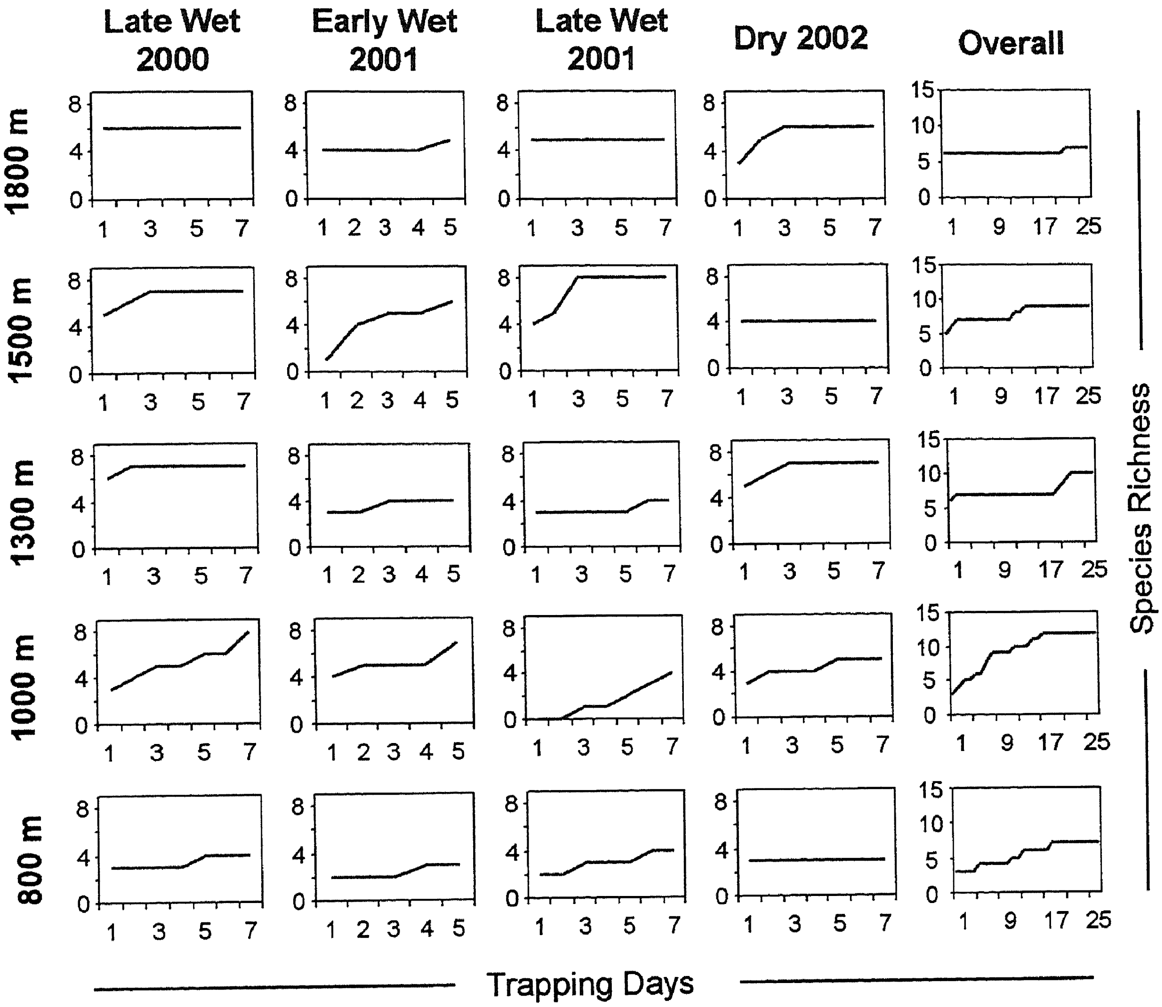

Late Wet 2000
Early Wet 2001
Late Wet 2001
Dry 2002
Overall
1800 m
1500 m
1300 m
1000 m
800 m
0
4
8
0
5
10
15
1
3
5
7
1
2
3
4
5
1
9
17
25
Species Richness
Trapping Days

Figure 13. Species richness curves (lines with data points), and the 95% prediction curves sampled without replacement from program Mid-Domain Null (50,000 simulations each). A. Gamma analysis using empirical range sizes and simulated range midpoints. B. Alpha analysis using empirical range sizes and simulated range midpoints. Shaded regions represent regions of transition between habitat types.

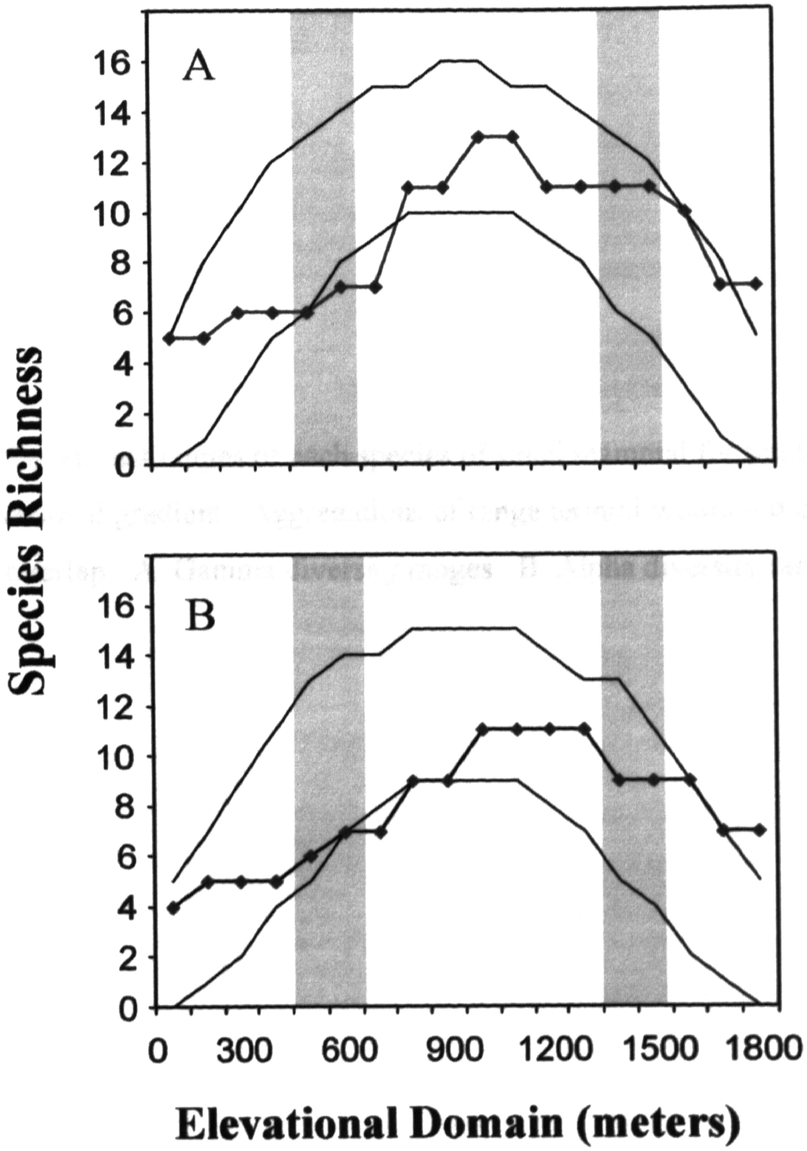

A
B
Species Richness
0
2
4
6
8
10
12
14
16
0
300
600
900
1200
1500
1800
Elevational Domain (meters)

Figure 14. Elevational ranges of each species of small mammal for the Río Peñas Blancas elevational gradient. Aggregations of range termini would indicate areas of community overlap. A. Gamma diversity ranges. B. Alpha diversity ranges.

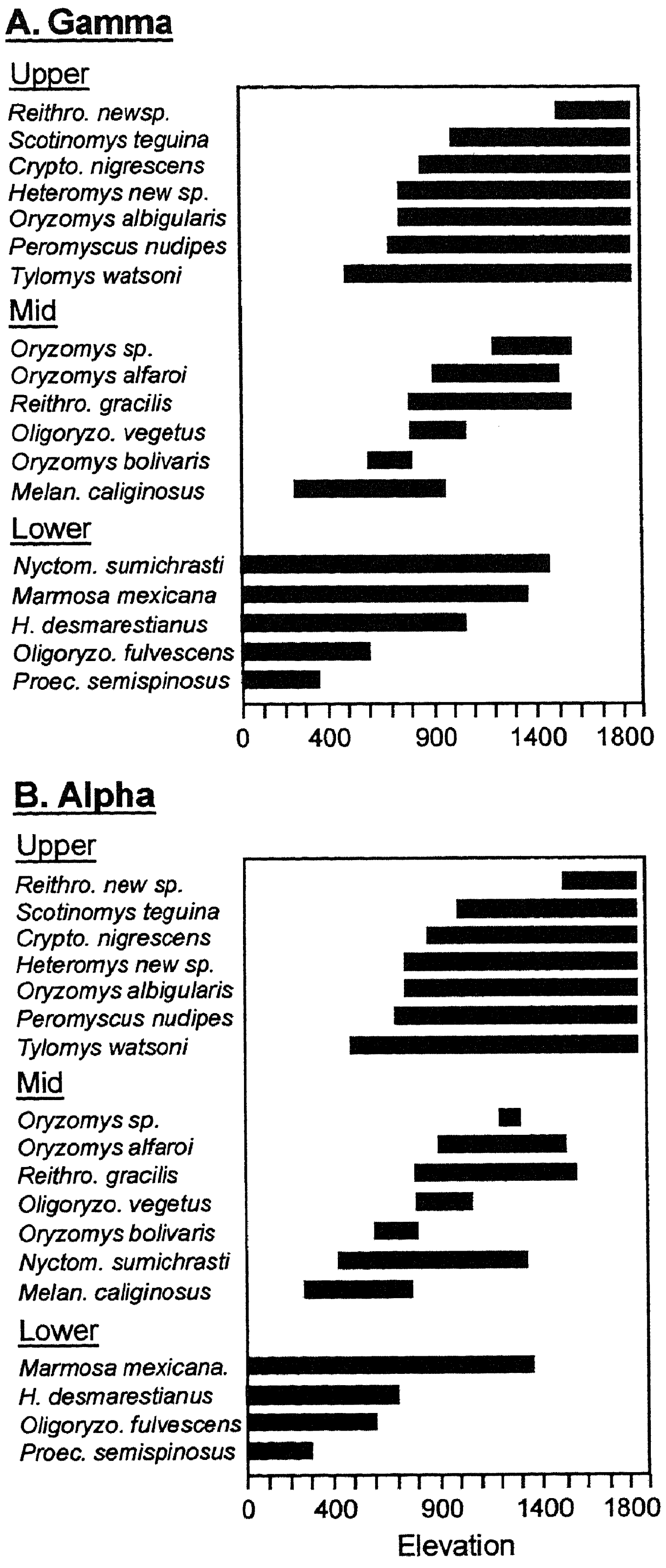
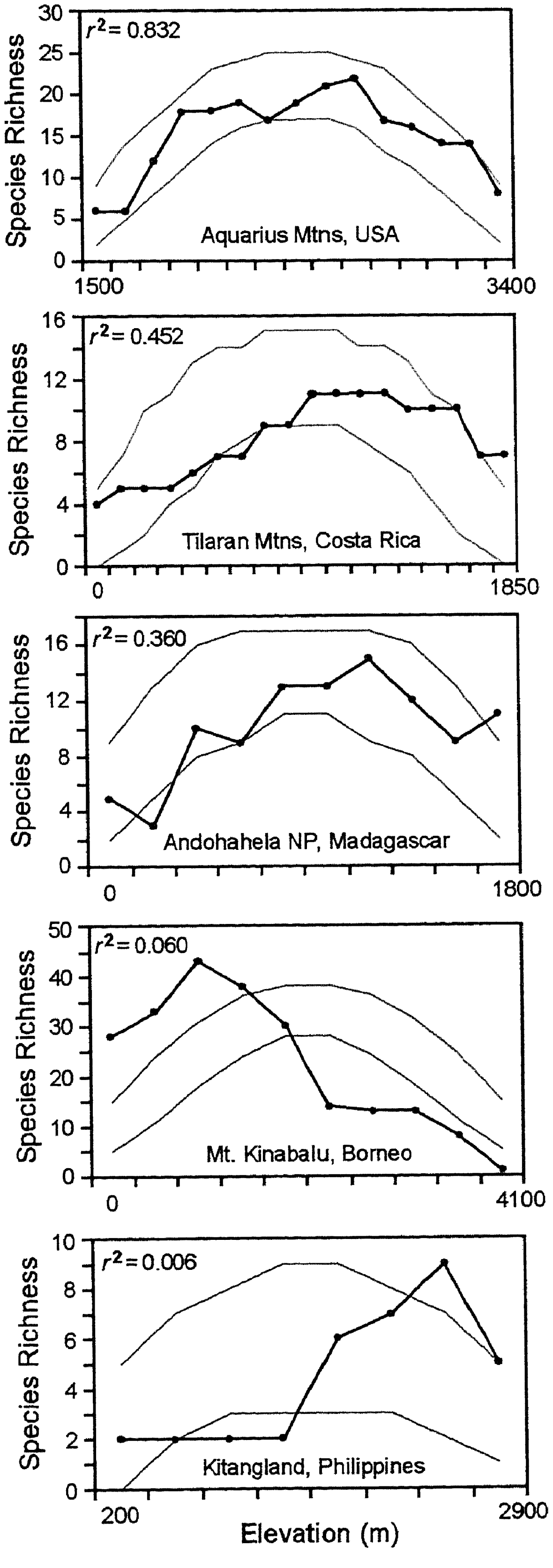

A. Gamma
Upper
Reithro. newsp.
Scotinomys teguina
Crypto. nigrescens
Heteromys new sp.
Oryzomys albigularis
Peromyscus nudipes
Tylomys watsoni
Mid
Oryzomys sp.
Oryzomys alfaroi
Reithro. gracilis
Oligoryzo. vegetus
Oryzomys bolivaris
Melan. caliginosus
Lower
Nyctom. sumichrasti
Marmosa mexicana
H. desmarestianus
Oligoryzo. fulvescens
Proec. semispinosus
0
400
900
1400
1800
B. Alpha
Upper
Reithro. new sp.
Scotinomys teguina
Crypto. nigrescens
Heteromys new sp.
Oryzomys albigularis
Peromyscus nudipes
Tylomys watsoni
Mid
Oryzomys sp.
Oryzomys alfaroi
Reithro. gracilis
Oligoryzo. vegetus
Oryzomys bolivaris
Nyctom. sumichrasti
Melan. caliginosus
Lower
Marmosa mexicana.
H. desmarestianus
Oligoryzo. fulvescens
Proec. semispinosus
0
400
900
1400
1800
Elevation

Figure 15. Five examples of the mid-domain analysis including the 95% confidence limits (grey lines) from 50,000 range size simulations using Mid-Domain Null, and the empirical diversity pattern (black circles and lines). Coefficients of determination for the fit to the null model are shown in the upper left corners.



Species Richness
$r^2 = 0.832$
Aquarius Mtns, USA
0
5
10
15
20
25
30
1500
3400
$r^2 = 0.452$
Tilaran Mtns, Costa Rica
0
4
8
12
16
0
1850
$r^2 = 0.360$
Andohahela NP, Madagascar
0
4
8
12
16
0
1800
$r^2 = 0.060$
Mt. Kinabalu, Borneo
0
10
20
30
40
50
0
4100
$r^2 = 0.006$
Kitangland, Philippines
0
2
4
6
8
10
200
2900
Elevation (m)

Figure 16. Positive, linear trend of the maximum diversity of non-volant small mammals with mountain height exemplifying the mountain mass effect for A. all data sets combined, and B. alpha data sets.

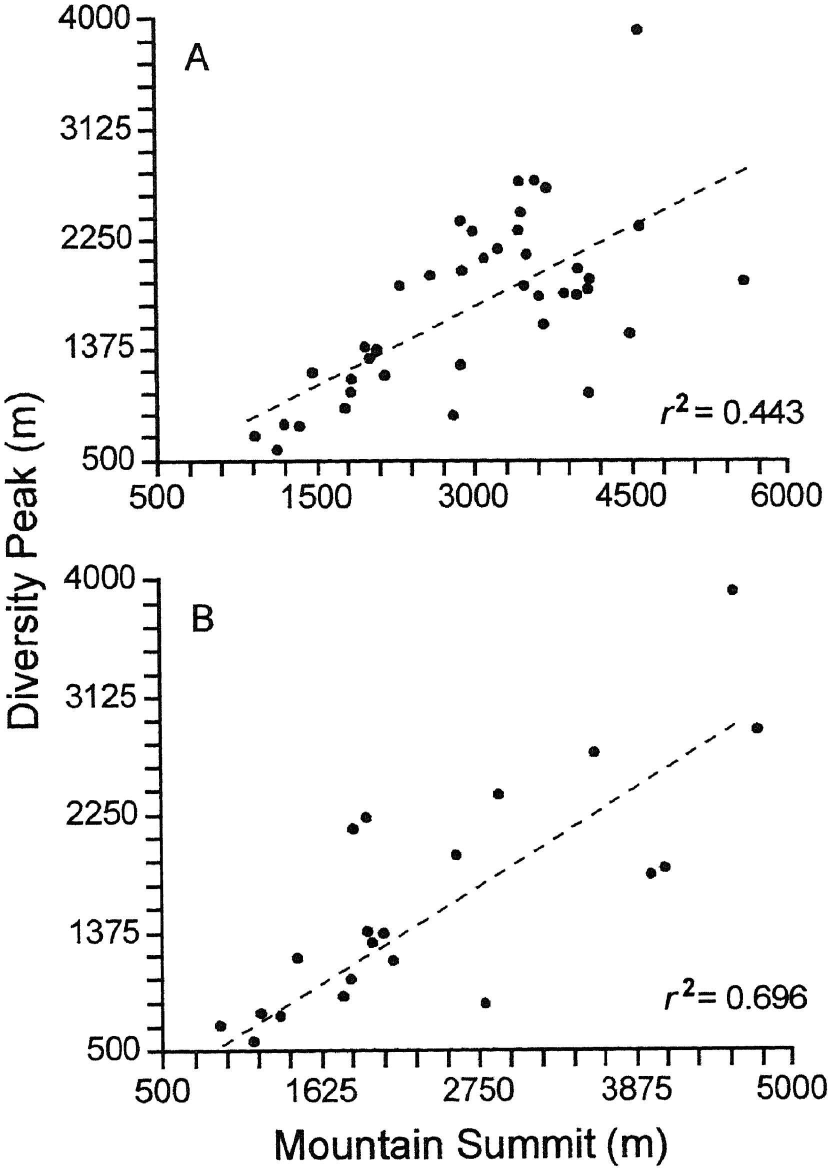

A
B
r² = 0.443
r² = 0.696
Diversity Peak (m)
Mountain Summit (m)
4000
3125
2250
1375
500
500
1500
3000
4500
6000
1625
2750
3875
5000

Figure 17. Linear regressions of the diversity peak of non-volant small mammals expressed as a percentage of the mountain height with mountain height for A. all data sets combined, B. gamma data, and C. alpha data.

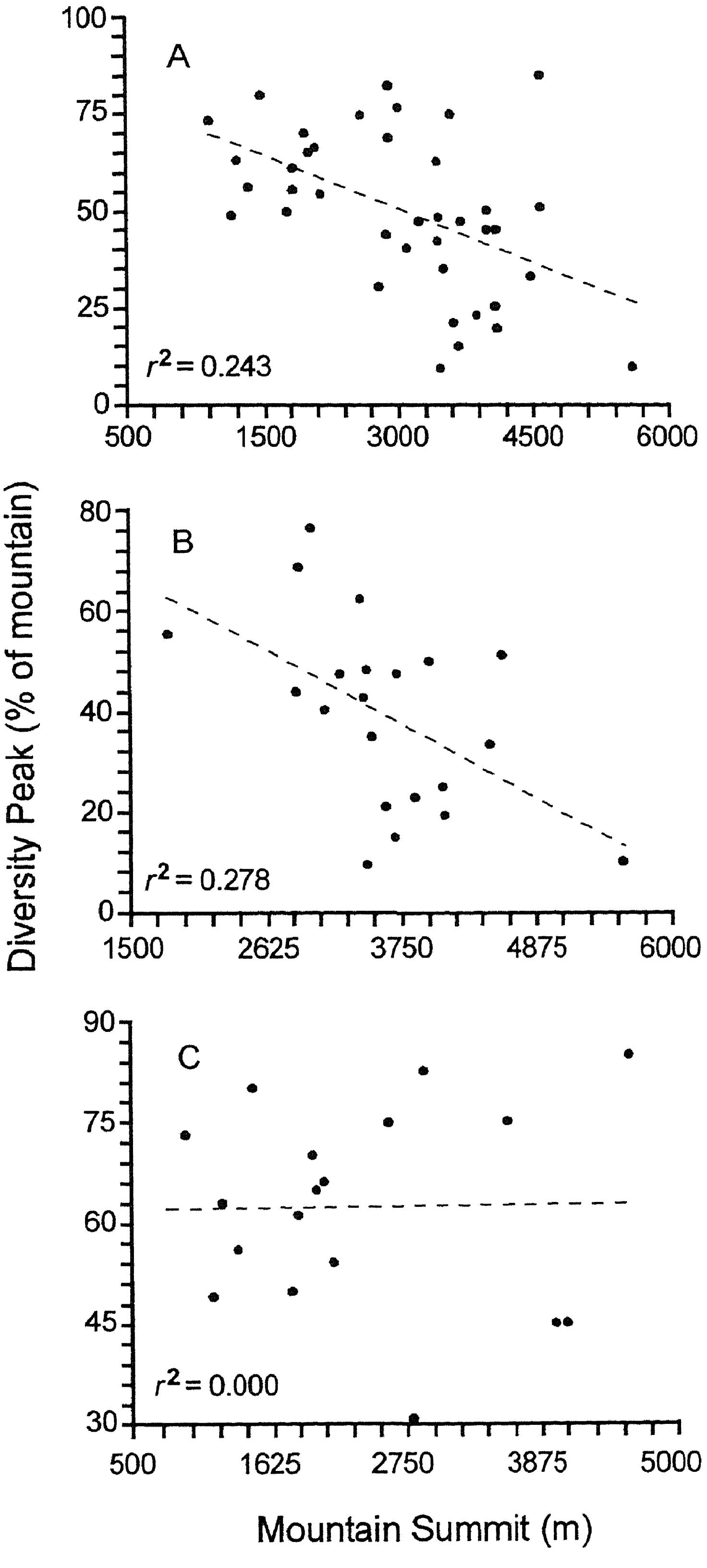

A
$r^2 = 0.243$
100
75
50
25
0
500
1500
3000
4500
6000
B
$r^2 = 0.278$
80
60
40
20
0
1500
2625
3750
4875
6000
C
$r^2 = 0.000$
90
75
60
45
30
500
1625
2750
3875
5000
Diversity Peak (% of mountain)
Mountain Summit (m)

Figure 18. Positive, linear trend of the maximum diversity of non-volant small mammals with latitude for gamma data sets.

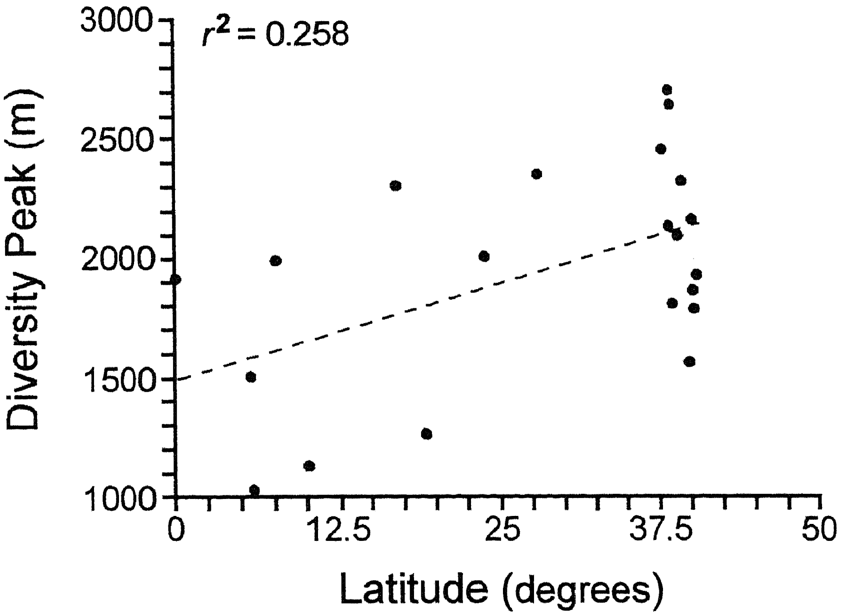

r^2 = 0.258
Diversity Peak (m)
3000
2500
2000
1500
1000
0
12.5
25
37.5
50
Latitude (degrees)

Figure 19. Sampling effort for each replicate (wet, dry, spatial) in each study measured in trap nights (# of traps x # nights). The summer and winter on the Deep Canyon transect are depicted as wet and dry seasons respectively.

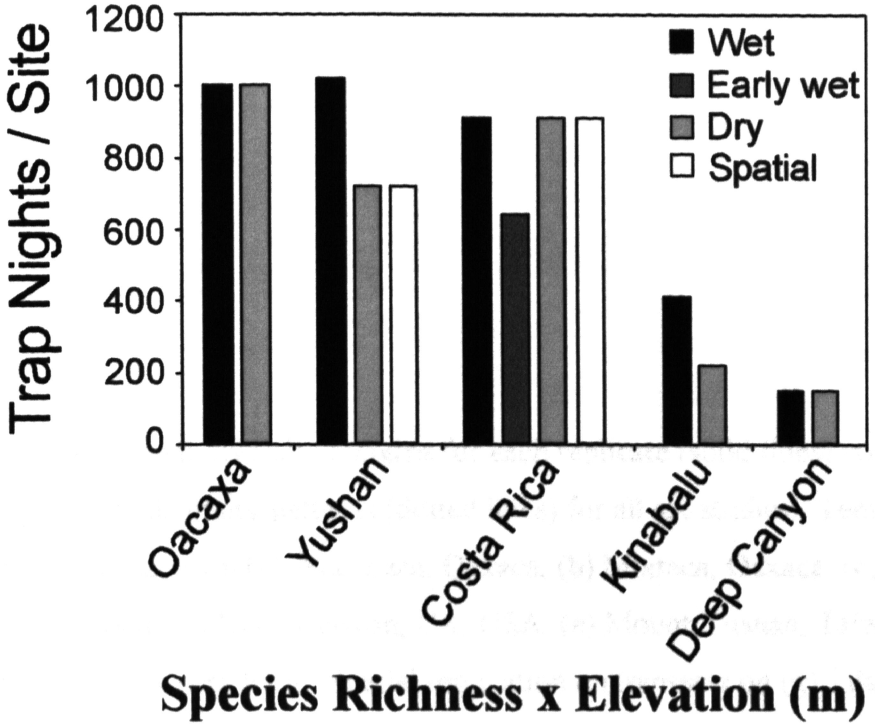
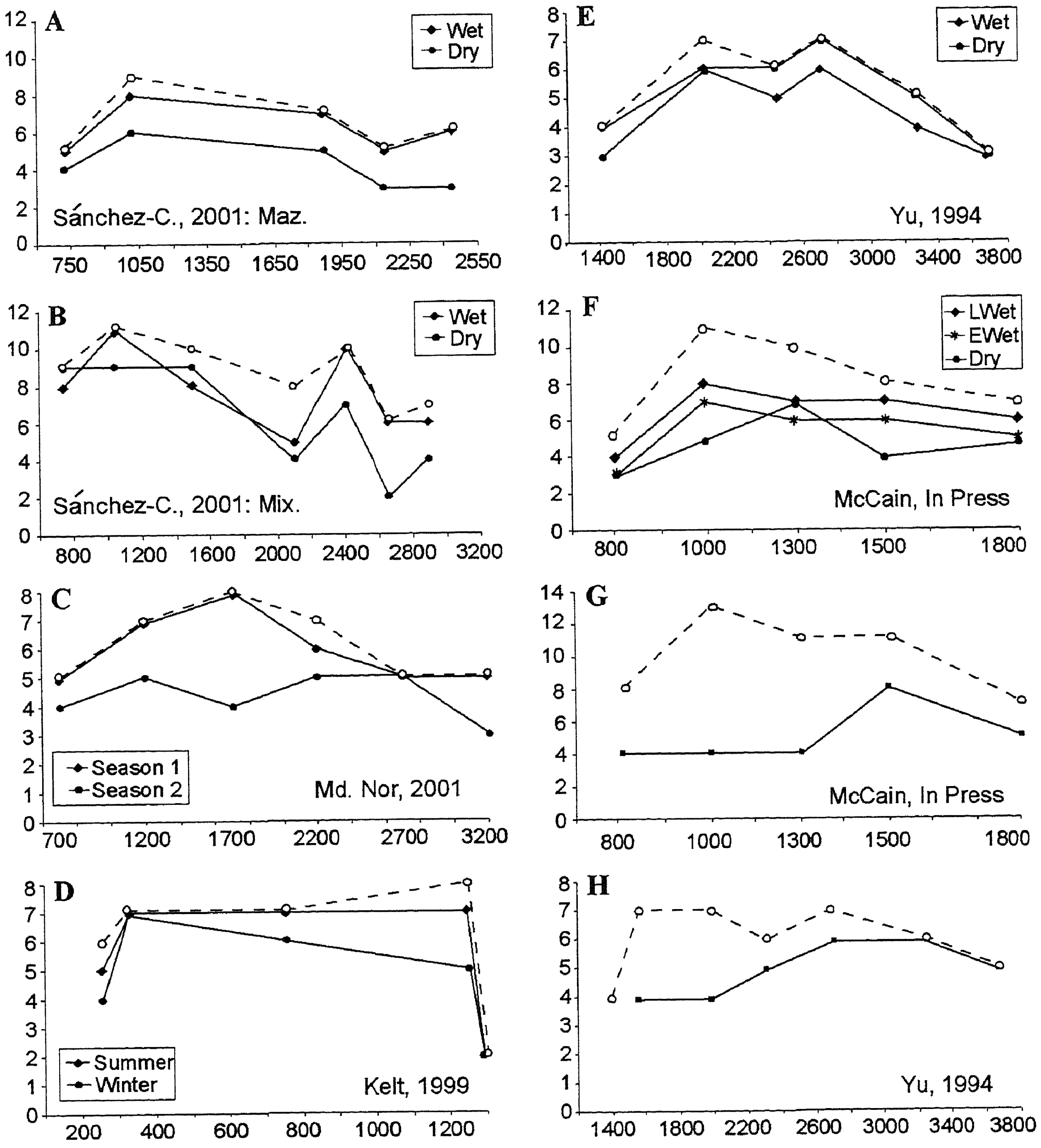

Trap Nights / Site
1200
1000
800
600
400
200
0
■ Wet
■ Early wet
▨ Dry
☐ Spatial
Oacaxa
Yushan
Costa Rica
Kinabalu
Deep Canyon
Species Richness x Elevation (m)

Figure 20. Elevational diversity patterns for each replicate (solid lines) compared with the aggregate diversity patterns (dotted lines) for all six studies. Temporal replication of transects on (a) Mazateca, Oaxaca, (b) Mixteca, Oaxaca, (c) Mount Kinabalu, Malaysia, (d) Deep Canyon, CA, USA, (e) Mount Yushan, Taiwan, and (f) Tilarán Mountains, Costa Rica. Spatial replication on transects on (g) Tilarán Mountains, Costa Rica, and (h) Mount Yushan, Taiwan.



Species Richness x Elevation (m)

Figure 21. Abundance estimates of individuals for the temporal replicates and spatial replicates on (a) Mount Yushan, Taiwan, and (d) Tilarán Mountains, Costa Rica. Number of individuals on temporal replicates of (b) Deep Canyon, CA, USA, and number of captures on temporal replicates of (c) Mount Kinabalu, Malaysia.

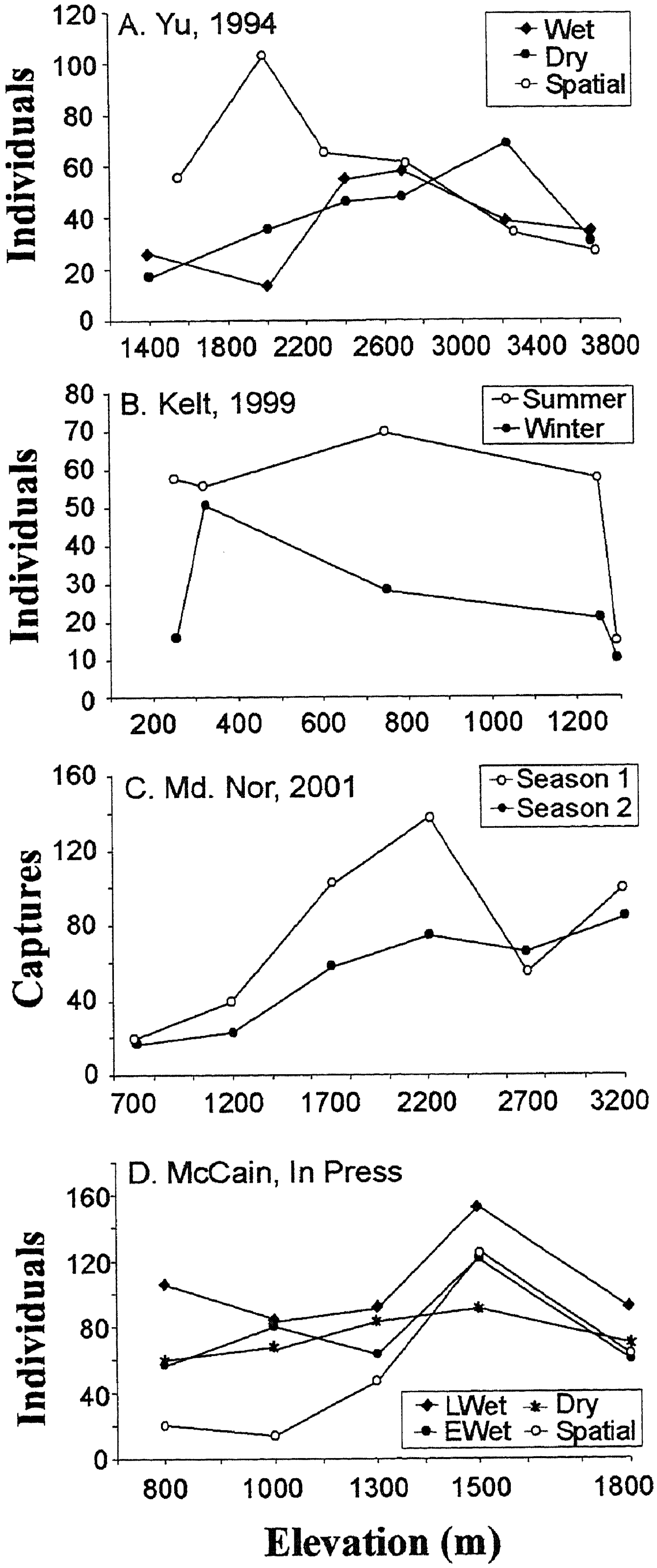

A. Yu, 1994
Individuals
0
20
40
60
80
100
120
1400
1800
2200
2600
3000
3400
3800
Wet
Dry
Spatial
B. Kelt, 1999
Individuals
0
10
20
30
40
50
60
70
80
200
400
600
800
1000
1200
Summer
Winter
C. Md. Nor, 2001
Captures
0
40
80
120
160
700
1200
1700
2200
2700
3200
Season 1
Season 2
D. McCain, In Press
Individuals
0
40
80
120
160
800
1000
1300
1500
1800
LWet
Dry
EWet
Spatial
Elevation (m)

Figure 22. Linear relationships between abundance and elevational range size for rodents in Costa Rica at (a) local scale ($r^2 = 0.206$, p = 0.1386) and (b) regional scale ($r^2 = 0.297$, p = 0.0009), and (c) for geographic ranges measured as a percentage of coverage in Costa Rica at a regional scale ($r^2 = 0.310$, p = 0.0740).

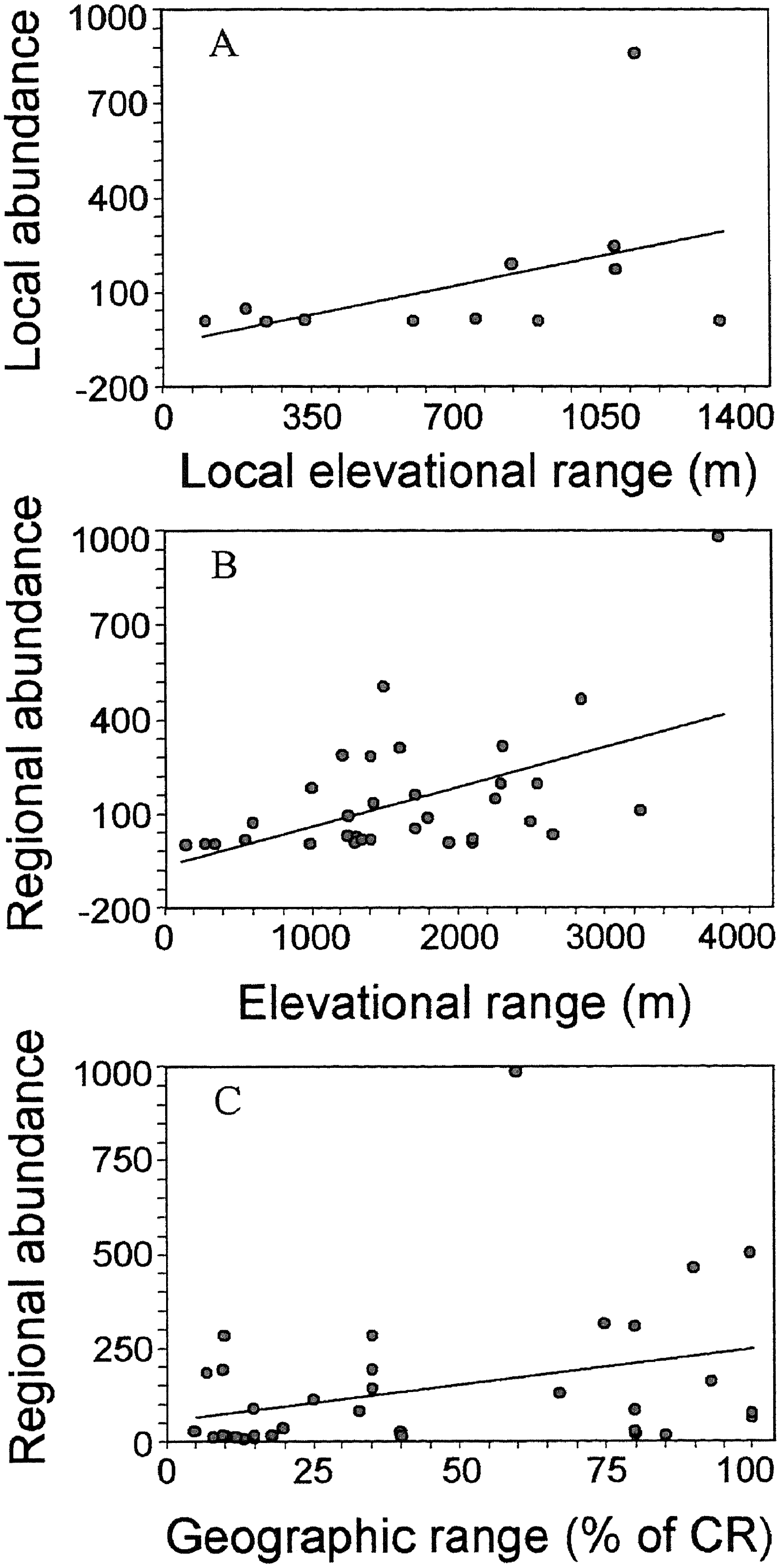

A
Local abundance
1000
700
400
100
-200
0
350
700
1050
1400
Local elevational range (m)
B
Regional abundance
1000
700
400
100
-200
0
1000
2000
3000
4000
Elevational range (m)
C
Regional abundance
1000
750
500
250
0
0
25
50
75
100
Geographic range (% of CR)

Figure 23. Linear relationships between body size and elevational range size for rodents in Costa Rica at a (a) local scale ($r^2 = 0.270$, $p = 0.083$) and (b) regional scale ($r^2 = 0.077$, $p = 0.1250$).

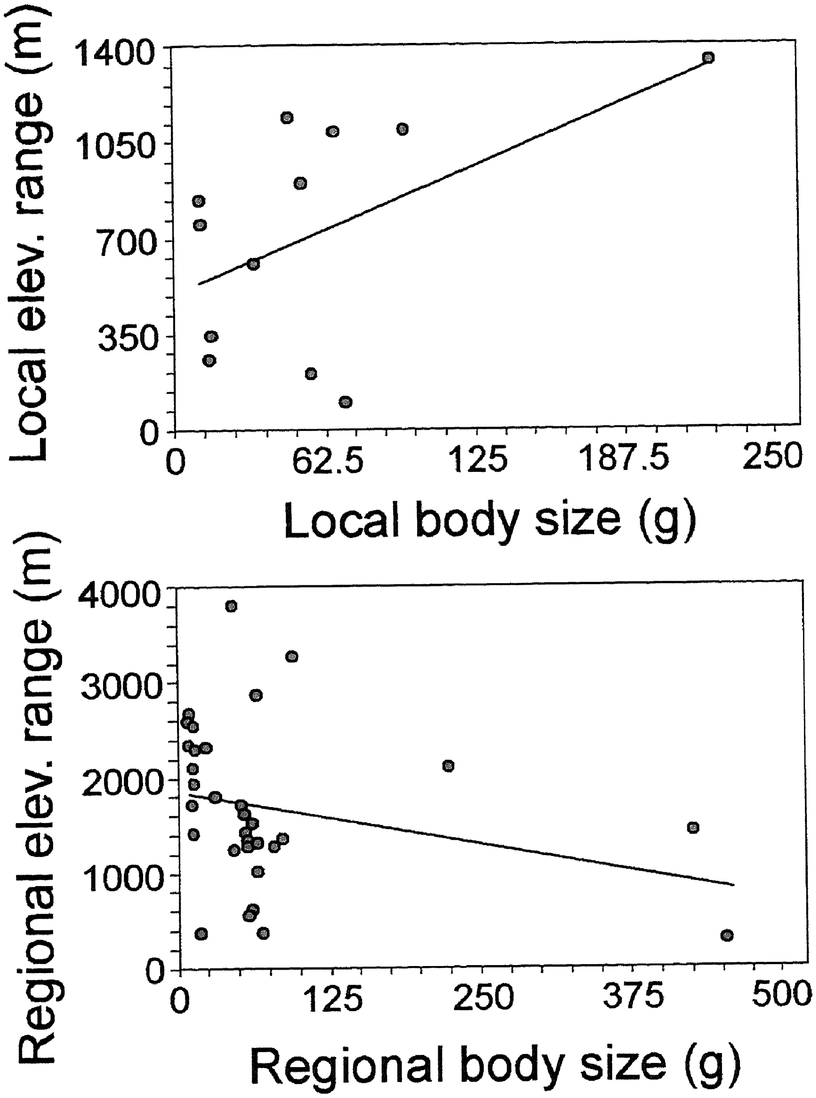

Local elev. range (m)
1400
1050
700
350
0
0
62.5
125
187.5
250
Local body size (g)
Regional elev. range (m)
4000
3000
2000
1000
0
0
125
250
375
500
Regional body size (g)

Figure 24. Population size fluctuations among three seasons and five elevations across a Caribbean transect in the Tilarán mountain range for the four most common rodent species (a) *Heteromys* sp., (b) *Oryzomys albigularis*, (c) *Peromyscus nudipes*, and (d) *Scotinomys teguina*.

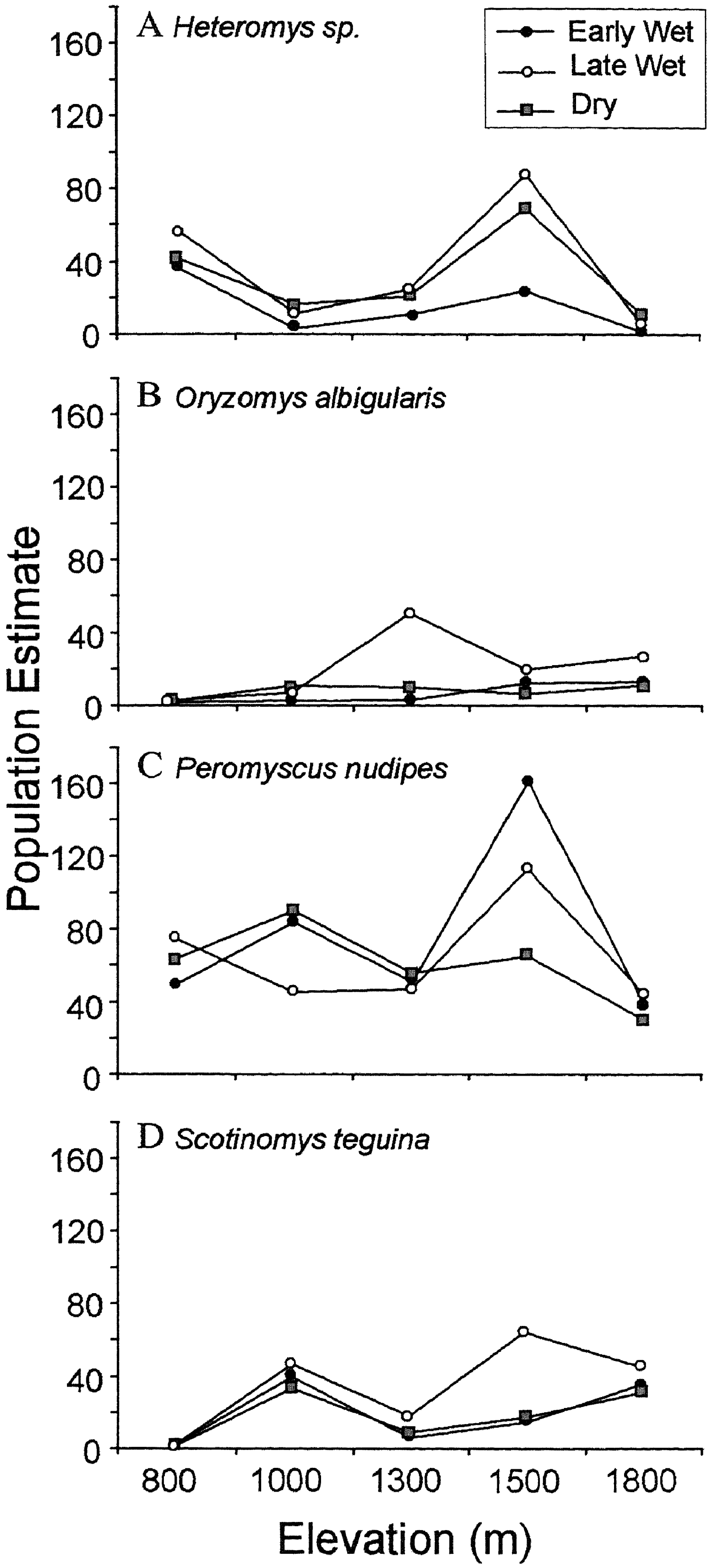
A Heteromys sp.
B Oryzomys albigularis
C Peromyscus nudipes
D Scotinomys teguina
Early Wet
Late Wet
Dry
Population Estimate
0
40
80
120
160
800
1000
1300
1500
1800
Elevation (m)

Figure 25. Abundance patterns of five species across their elevational ranges in Costa Rica measured from numbers of specimens in 23 national and international collections (see acknowledgments) (a) *Heteromys* sp., (b) *Oryzomys albigularis*, (c) *Peromyscus nudipes*, (d) *Scotinomys teguina*, and (e) *Melanomys caliginosus*.

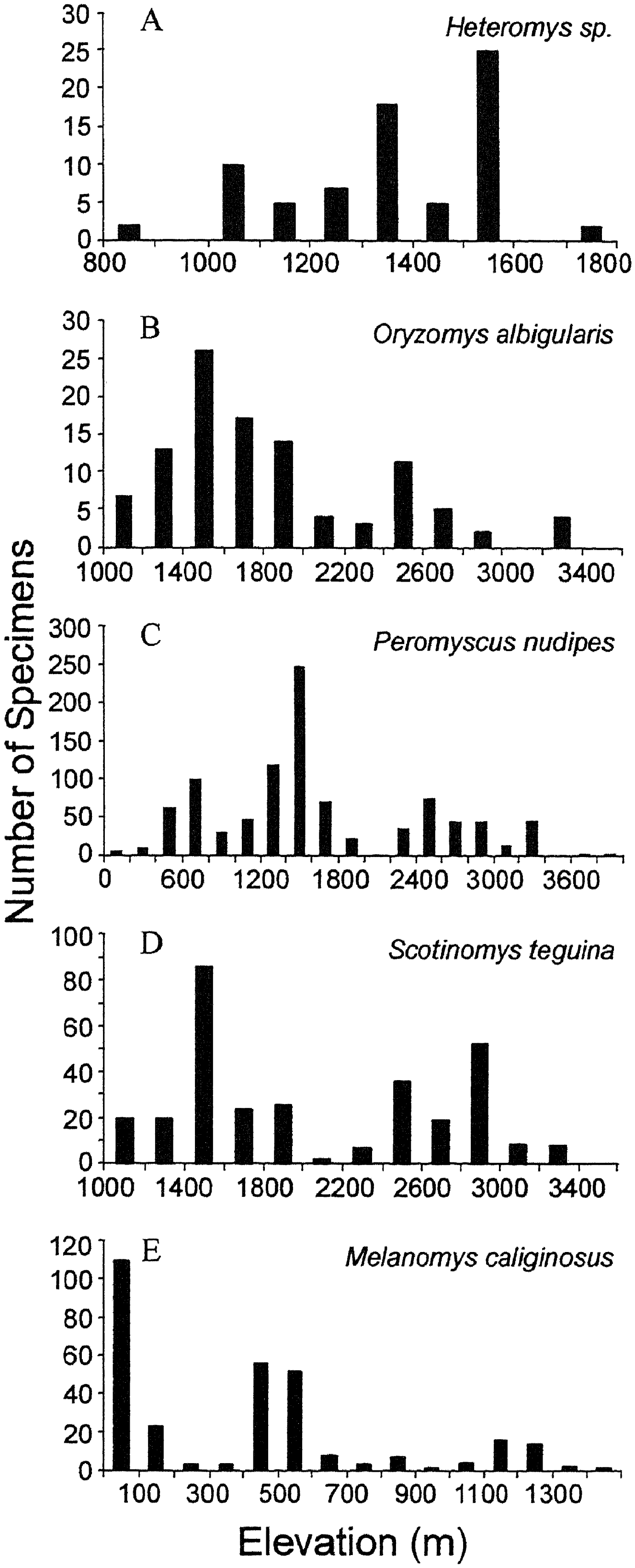

A
Heteromys sp.
B
Oryzomys albigularis
C
Peromyscus nudipes
D
Scotinomys teguina
E
Melanomys caliginosus
Number of Specimens
Elevation (m)
0
5
10
15
20
25
30
800
1000
1200
1400
1600
1800
1000
1400
1800
2200
2600
3000
3400
0
50
100
150
200
250
300
0
600
1200
1800
2400
3000
3600
0
20
40
60
80
100
120
100
300
500
700
900
1100
1300

Table 1. Schedule of trapping along elevational transects for each replicate including trapping effort, species richness, number of individuals captured, and rainfall data available for individual sites (ICE: unpublished data).

Site	Elevation	Dates	Trap Nights	Species	Unique Individuals	Aver. Annual Rainfall (years)
MCFR, Cerro Amigo (east)	1840–1780m	LW: 25–31 Oct. 2000	910	6	94	N/A
		EW: 21–25 July 2001	650	5	61	
		DRY: 21–27 Mar. 2002	910	6	69	
MCFR, Cerro Amigo (west)	1840–1790m	LW2: 21–27 Oct. 2001	910	5	67	N/A
MCFR, Investigator's trail	1550–1500m	LW: 15–21 Oct. 2000	910	6	154	2498 mm (83-99) [1]
		EW: 29 July–2 Aug. 2001	650	6	122	
		DRY: 24–30 Apr. 2002	910	4	93	
MCFR, Brillante Trail	1550–1500m	LW2: 9–15 Oct. 2001	910	8	122	N/A
MCFR, Peñas Blancas trail	1300–1250m	LW: 4–10 Nov. 2000	910	7	94	N/A
		EW: 31 Aug.–4 Sept. 2001	650	5	64	
		DRY: 10–16 Mar. 2002	910	7	85	
BEN: SGFS, Congo Trail	1300–1250m	LW2: 3–9 Nov. 2001	910	4	44	3426 mm (75-99) [2]
MCFR, Peñas Blancas trail	1050–1000m	LW: 14–20 Nov. 2000	910	8	82	3524 mm (95-99) [3]
		EW: 21–25 Aug. 2001	650	7	81	
		DRY: 14–20 Apr. 2002	910	5	70	
BEN: PSFS, above Zambia Trail	1050–1000m	LW2: 25 Nov. – 1 Dec. 2001	910	4	15	N/A
MCFR, Sendero Ticodendron	800–750m	LW: 26 Nov.–2 Dec. 2000	910	4	106	5135 mm (94-98) [4]
		EW: 8–12 Aug. 2001	650	3	58	
		DRY: 3–9 Apr. 2002	910	3	60	
BEN: PSFS, Zambia Trail	800–750m	LW2: 16–22 Nov. 2001	910	4	20	4642mm (79-99) [5]
		TOTAL:	16,900	16	1561	

MCFR: Monteverde Cloud Forest Reserve; BEN: Bosque Eterno de Los Niños; SGFS: San Gerardo Field Station; PSFS: Poco Sol Field Station. LW: late wet season; EW: early wet season; DRY: dry season: LW2: late wet season spatial replicate.

[1]: Monteverde, Pacific Slope: 1500m

[2]: San Gerardo Field Station: 1220m;

[3]: MCFR, Aleman Refuge: 925m

[4]. MCFR, Eladios Refuge: 850m

Table 2. Average linear regression statistics for null model analyses of elevational diversity patterns for non-volant small mammals using Mid-Domain Null.

Data Sets	Aver. r^2	% significant	n
Combined	0.376	53%	38
Alpha	0.317	33%	18
Gamma	0.431	70%	20
Island	0.350	37%	19
Continent	0.403	68%	19
Tropical	0.345	44%	25
Temperate	0.438	69%	13

Table 3. Linear regression statistics for elevational diversity peak of non-volant small mammals including r^2 values and p-values in parentheses for diversity peak by mountain height (Mt. Mass), diversity peak measured as % of mountain height by mountain height (% Mt. Mass), and diversity peak by latitude.

Data Set	Mt. Mass	% Mt. Mass	Latitude	n
Combined	0.443 (0.000)	0.243 (0.001)	0.208 (0.003)	39
Alpha	0.697 (0.000)	0.000 (0.968)	0.121 (0.157)	18
Gamma	0.012 (0.637)	0.278 (0.014)	0.258 (0.019)	21
Island	0.431 (0.002)	0.246 (0.026)	0.135 (0.111)	20
Continent	0.282 (0.019)	0.088 (0.218)	0.045 (0.383)	19
Tropical	0.437 (0.000)	0.324 (0.002)	0.117 (0.087)	26
Temperate	0.245 (0.085)	0.064 (0.404)	N/A*	13

*Inadequate latitudinal spread in the data sets to have a meaningful regression statistic.

Table 4. The number of diversity data sets for non-volant small mammals with the peak in species richness occurring in the lower, middle, or upper 1/3 of the elevational gradient grouped by scale—alpha and gamma sampling, location—island or continent, and climate—temperate (TM) or tropical (TP).

	Lower Peak		Middle Peak		Upper Peak	
	TM	TP	TM	TP	TM	TP
Alpha Patterns:						
Islands	0	0	0	11	0	5
Continents	0	1	0	1	1	1
Total Alpha	1		12		7	
Gamma Patterns:						
Islands	1	1	0	2	0	0
Continents	8	1	8	2	1	1
Total Gamma	11		12		2	
Total	12		24		9	

Table 5. Elevational extents (m), range sizes, and abundances of rodent species from Costa Rica from several spatial scales: local scale documented along an elevational transect in the Tilarán Mountains, and regional scale of all elevational relief in Costa Rica, geographic range coverage in Costa Rica, and latitudinal range size (degrees) of each species.

Species	Local: Range	Range Size	Abundance	Regional: Range	Range Size	Abundance	% in CR	Latitudinal Range
H. desmarestianus				0–2850	2850	459	90	15
H. new sp.	750–1840	1090	242	800–1800	1000	183	7	1.5
H. oresterus				1860–3110	1250	27	5	1
H. gymnurus				0–280	280	8	85	17
L. salvini				0–1220	1200	286	35	8.5
M. caliginosus				0–1600	1600	306	80	21
N. sumichrasti	400–1300	900	6	0–1700	1700	54	100	12
O. trinitatis				0–1300	1300	5	15	24.5
O. fulvecens				0–1700	1700	159	93	26
O. vegatus	800–1050	250	2	840–3400	2500	77	33	2
O. albigularis	750–1840	1090	176	100–3340	3250	111	25	15.5
O. alfaroi	900–1500	600	5	500–2300	1800	81	80	25
O. bolivaris	750–800	50	44	0–1400	1400	18	40	16
O. couesi				0-600	600	67	21	62.5
O. phyllotis				0–1300	1300	21	80	9.75

O. talamancae				0–525	525	13	15	4
P. nudipes	700–1840	1140	859	150–3950	3800	990	60	14
P. semispinosus				0–1425	1425	129	67	21
R. brevirostrus				500–2590	2100	8	12	3.75
R. creper				1400–3670	2300	193	35	1.5
R. gracilis	800–1550	750	10	100–2750	2650	33	20	11.5
R. mexicanus				860–3110	2260	145	35	15
R. sp.	1500–1840	340	17	1500-1840	340	15*	2	1
R. paradoxus				50–1000	1000	2	13	2.1
R. rodriguezi				1500–3440	1940	8	18	1
R. sumichrasti				1200–3733	2550	193	10	11.5
R. raptor				1400–1750	350	8	10	3
R. underwoodi				2000–2150	150	4	8	1.75
S. teguina	1000–1840	840	191	1100–3400	2300	312	75	10.5
S. xerampylinus				2350–3700	1400	281	10	1.5
S. hirsutus				0–1500	1500	504	100	8
S. alfari				0–1350	1350	13	40	8.5

S. aphrastus	1200–1300	100	1	1200–1550	350	3	10	2
T. watsoni	500–1840	1340	5	0–2100	2100	18	80	3.75
Z. brevicauda				0–1250	1250	92	15	9

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*approximately (new species to be described)

Appendix 1. Rodent species endemic to North American deserts including desert affiliation (GB = Great Basin Desert, M = Mojave Desert, S = Sonoran Desert, C = Chihuahuan Desert) and latitudinal range limits (degrees and minutes N). Species endemic to the Baja Peninsula indicated by Baja in parentheses after latitudinal range.

Sciuridae—*Spermophilus atricapillus*, S, 25°10′–28°00′ (Baja); *S. mohavensis*, M, 34°20′–36°10′; *S. tereticaudus*, M, S, 27°00′–37°00′; *Ammospermophilus harrisii*, S, 28°00′–36°10′; *A. interpres*, *C*, 25°00′–35°00′; *A. leucurus*, GB, M, 24°00′–45°00′. Geomyidae—*Geomys arenarius*, C, 31°50′–34°00′; *Pappogeomys castanops*, C, 22°30′–38°00′.

Heteromyidae—*Dipodomys agilis*, S, 25°00′–30°00′ (Baja); *D. deserti*, GB, M, S, 29°00′–40°10′; *D. merriami*, GB, M, S, C, 22°00′–41°50′; *D. microps*, GB, 34°00′–44°20′; *D. nelsoni*, C, 24°00′–29°00′; *D. panamintinus*, GB, M, S, 34°40′–39°50′; *D. spectabilis*, S, C, 22°00′–37°00′; *Microdipodops megacephalus*; GB, 37°00′–45°00′; *M. pallidus*, GB, 37°00′–40°00′; *Chaetodipus arenarius*, S, 23°30′–32°10′ (Baja); *C. baileyi*, S, 23°30′–34°00′; *C. fallax*, M, S, 27°50′–34°10′ (Baja); *C. formosus*, GB, M, S, 27°00′–40°10′; *C. intermedius*, S, C, 27°00′–37°00′; *C. lineatus*, S, 21°50′–23°30′; *C. nelsoni*, C, 22°00′–32°10′; *C. penicillatus*, M, S, C, 23°00′–37°00′; *C. spinatus*, S, 23°00′–35°00′ (Baja); *Perognathus amplus*, S, 30°30′–36°40′; *P. longimembris*, GB, M, S, 28°30′–43°00′.

Muridae—*Neotoma albigula*, C, 19°00′–38°00′; *N. goldmani*, C, 23°00′–29°00′; *N. lepida*, GB, M, 23°00′–45°00′; *Onychomys torridus*, GB, M, S, C, 22°00′–40°20′; *Peromyscus eremicus*, M, S, C, 22°00′–37°10′; *P. eva*, S, 24°10′–25°20′ (Baja); *P. merriami*, S, 24°00′–33°00′; *P. pectoralis*, C, 20°00′–33°50′; *P. polius*, C, 28°00′–31°00′.

Appendix 2A. Summary of gamma elevational distribution extensions based on literature and specimens.

	Peñas Blancas Valley					
Species	Documented Range	Range Extension	Specimen	Estimated Lower Range	Alajuela Low Elevation(s)	Specimen(s)
Cryptotis nigrescens	1000–1840m	870m	KU 143381			
Marmosa mexicana	750–1350m			0–750m	8m*	Dickey 14248
Proechimys semispinosus				0–350m	8*–267m	FMNH 44012, MVZ 164965
Heteromys desmarestianus	750–1050m			0–750m	25m*	MVZ 164851
Melanomys caliginosus	750–1050m			200–750m	267m	FMNH 44001
Nyctomys sumichrasti	1000–1300m	700–900m	Sighted by CMM	0–600m	100m	AMNH (McPherson 85)
		1400–1450m	USNM 559055			
Oligoryzomys fulvescens				0–600m	45m	KU 142729
Oligoryzomys vegetus	1000–1050m	840, 950m	KU 159040, KU 159042			
Oryzomys bolivaris	700–800m			600–700m	670m	FMNH 44005
Oryzomys sp.	1200–1300m	1550m	KU 159021			
Reithrodontomys gracilis	1200–1550m	840, 950m	KU 159089, KU 159093			
Tylomys watsoni	1000–1840m	600m	Reported in houses	500-600m	560m*	KU 143335

* Low-elevation specimens from eastern provinces, but not from Alajuela

AMNH = American Museum of Natural History; Dickey = Dickey Collection; FMNH = Field Museum; KU = Natural History Museum, University of Kansas; MVZ = Museum of Vertebrate Zoology, Berkeley.

Appendix 2B. Summary of alpha elevational distribution extensions based on literature and specimens.

	Peñas Blancas Valley					
Species	Documented Range	Range Extension	Specimen	Estimated Lower Range	Alajuela Low Elevation(s)	Specimen(s)
Cryptotis nigrescens	1000–1840m	870m	KU 143381			
Marmosa mexicana	750–1350m			0–750m	8m*	Dickey 14248
Proechimys semispinosus MVZ				0–300m	8*–267m	FMNH 44012, 164965
Heteromys desmarestianus				0–700m	25m*	MVZ 164851
Melanomys caliginosus				200–700m	267m	FMNH 44001
Nyctomys sumichrasti	1000–1300m	700–900m	Seen by CMM	400–700m		
Oligoryzomys fulvescens				0–600m	45m	KU 142729
Oligoryzomys vegetus	1000–1050m	840, 950m	KU 159040, KU 159042			
Oryzomys bolivaris	700–800m			600–700m	670m	FMNH 44005
Reithrodontomys gracilis	1200–1550m	840, 950m	KU 159089, KU 159093			
Tylomys watsoni	1000–1840m	600m	Reported in houses	500-600m	560m*	KU 143335

* Low-elevation specimens from eastern provinces, but not from Alajuela

AMNH = American Museum of Natural History; Dickey = Dickey Collection; FMNH = Field Museum; KU = Natural History Museum, University of Kansas; MVZ = Museum of Vertebrate Zoology, Berkeley.

Appendix 3. Numbers of individuals of each species trapped at each elevation in the Río Peñas Blancas Valley, Costa Rica.

Species	1840-1760 m	1550-1500 m	1300-1250 m	1050-1000m	800-750
Crypotis nigrescens	7	6	2	2	0
Marmosa mexicana	0	0	2	2	2
*Heteromys desmarestianus**	0	0	0	10	11
Heteromys new sp.	13	85	58	18	68
*Melanomys caliginosus**	0	0	0	2	1
Nyctomys sumichrasti	0	2	1	3	0
Oligoryzomys vegatus	0	0	0	1	0
Oryzomys albigularis	72	57	31	15	1
Oryzomys alfaroi	0	1	0	4	0
Oryzomys bolivaris	0	0	0	0	44
Oryzomys sp.	0	0	1	0	0
Peromyscus nudipes	117	300	169	142	131
Reithrodontomys gracilis	0	7	2	1	0
Reithrodontomys new sp.	16	1	0	0	0
Scotinomys teguina	67	55	22	47	0
Tylomys watsoni	1	seen	0	1	seen

* Species only caught on spatial replicate

Appendix 4. Listing of all elevational transects for diversity of non-volant small mammals used in the review. Each denoted by study site, sampling method, climate, location, elevation of diversity maximum, and null model r^2 values. Significant r^2 values designated with an asterisk. Those data sets with N/A under the null model were deemed to have sampling biases or insufficient data for the quantitative analyses.

Study site	Method	Climate	Location	Diversity peak	Null Model: r^2
1. Mt. Kinabalu, Borneo[23]	gamma	tropical	island	1025 m	0.060
2. Mt. Kinabalu, Borneo[23]	alpha	tropical	island	1845 m	0.548*
3. Caparaó, Brazil[2]	alpha	tropical	continent	no pattern	N/A
4. Colorado Desert, CA[18]	alpha	temperate	continent	bimodal	N/A
5. La Picada, Chile[25]	alpha	temperate	continent	no pattern	N/A
6. Monteverde, Costa Rica[22]	gamma	tropical	continent	1124 m	0.454*
7. Monteverde, Costa Rica[22]	alpha	tropical	continent	1022 m	0.452*
8. d'Ambre, Madagascar[10, 15]	alpha	tropical	island	1181 m	0.364
9. d'Andohahela, Madagascar[11]	alpha	tropical	island	1300 m	0.360
10. d'Andringitra, Mad.[4, 8, 10, 17]	alpha	tropical	island	1950 m	0.712*
11. d'Anjanaharibe-Sud, Mad.[5, 6]	alpha	tropical	island	1365 m	0.272
12. Marojejy, Madagascar[3, 7]	alpha	tropical	island	1155 m	0.666*

13. Madagascar[3-11, 17]	gamma	tropical	island	1260 m	0.842*
14. Gunong Benom, Malaya[24]	alpha	tropical	continent	219 m	N/A
15. Kedah, Malaysia[21]	alpha	tropical	island	764 m	0.669*
16. Mazateca, Oaxaca[32]	alpha	tropical	continent	840 m	0.163
17. Mixteca, Oaxaca[32]	alpha	tropical	continent	mid- elev. bimodal	N/A
18. Oaxaca[12, 32]	gamma	tropical	continent	2300 m	0.450*
19. Central Nepal[1]	gamma	tropical	continent	2350 m	0.447*
20. Deep Creek, Nevada, USA[30]	gamma	temperate	continent	1566 m	0.189
21. Oquirrh, Nevada, USA[30]	gamma	temperate	continent	2162 m	0.623*
22. Raft River, Nevada, USA[30]	gamma	temperate	continent	2039 m	N/A
23. Ruby, Nevada, USA[30]	gamma	temperate	continent	1869 m	0.321*
24. Snake, Nevada, USA[30]	gamma	temperate	continent	2112.5 m	N/A
25. Stansbury, Nevada, USA[30]	gamma	temperate	continent	1847 m	N/A
26. Papua New Guinea[28]	gamma	tropical	island	1500 m	N/A
27. Papua New Guinea[20]	alpha	tropical	island	mid-elevation	N/A

28. Manu, Peru[26]	gamma	tropical	continent	bimodal	N/A
29. SW Peru[27]	alpha	temperate	continent	3909 m	0.037
30. Biliran, Philippines[29]	alpha	tropical	island	750 m	0.004
31. Isarog, Philippines[13, 15, 31]	alpha	tropical	island	1375 m	0.020
32. Kitanglad, Philippines[13]	alpha	tropical	island	2393 m	0.006
33. Leyte, Philippines[14, 29]	alpha	tropical	island	563 m	0.020
34. Maripipi, Philippines[29]	alpha	tropical	island	675 m	0.413
35. Mindanao, Philippines[13]	gamma	tropical	island	1993 m	0.217
36. Negros, Philippines[14, 16]	alpha	tropical	island	893 m	0.348
37. Guanshan, Taiwan[33]	alpha	tropical	island	2700 m	0.006
38. Yushan, Taiwan[33]	alpha	tropical	island	1800 m	0.468*
39. Central Taiwan[33]	gamma	tropical	island	2000 m	0.491*
40. Rwenzori, Uganda[19]	gamma	tropical	continent	1910 m	0.002
41. Abajo, Utah, USA[30]	gamma	temperate	continent	2450 m	0.444
42. Aquarius, Utah, USA[30]	gamma	temperate	continent	2703 m	0.832

43. Fishlake, Utah, USA[30]	gamma	temperate	continent	2259 m	N/A
44. Henry, Utah, USA[30]	gamma	temperate	continent	2133 m	0.135
45. La Sal, Utah, USA[30]	gamma	temperate	continent	1806 m	0.303*
46. Markagunt, Utah, USA[30]	gamma	temperate	continent	2475 m	0.720*
47. Pavant, Utah, USA[30]	gamma	temperate	continent	2092 m	0.797*
48. Tushar, Utah, USA[30]	gamma	temperate	continent	2649 m	0.625*
49. Uinta, Utah, USA[30]	gamma	temperate	continent	1919 m	0.195
50. Wasatch Range, Utah, USA[30]	gamma	temperate	continent	2323 m	0.434*
51. Wasatch Plateau, Utah, USA[30]	gamma	temperate	continent	1789 m	0.756*

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1. Abe, H. 1982; 2. Bonvicino et al., 1997; 3. Carleton and Goodman, 2000; 4. Goodman and Carleton, 1996; 5. Goodman and Carleton, 1998; 6. Goodman and Jenkins, 1998; 7. Goodman and Jenkins, 2000; 8. Goodman and Rasolonandrasana, 2001; 9. Goodman et al., 1996a; 10. Goodman et al., 1996b; 11. Goodman et al, 1999: a, b; 12. Hall, 1981; 13. Heaney, 2001; 14. Heaney et al., 1989; 15. Heaney et al., 1999; 16. Heideman et al., 1987; 17. Jenkins et al., 1996; 18. Kelt, 1999; 19. Kerbis Peterhans et al., 1996; 20. Kikkawa and Dwyer, 1992; 21. Langham, 1983; 22. McCain, in press; 23. Md. Nor, 2001; 24. Medway, 1972; 25. Patterson et al., 1989; 26. Patterson et al., 1998; 27. Pearson and Ralph, 1978; 28. Rahbek, 1995; 29. Rickart, 1993; 30. Rickart, 2001; 31. Rickart et al., 1999; 32. Sánchez-Cordero, 2001; 33. Yu, 1994.