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ORIGINAL ARTICLE

The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica

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ABSTRACT

Aim 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.

Location Field studies were conducted along a Caribbean slope of the Río Peñas Blancas watershed in the north-eastern region of Costa Rica between 750 and 1850 m at 10 sampling sites.

Methods 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 US 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.

Results In 16,900 trap nights, 1561 individuals from 16 species were captured. Both alpha and gamma species richness peaked at mid-elevation between 1000 and 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 ($r^2 = 0.45$, $P = 0.002$).

Main conclusions 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.

Keywords

Costa Rica, elevational gradient, mid-domain effect, replication, small mammals, species richness.

INTRODUCTION

The striking ecological changes that occur along elevational gradients drew the attention of early researchers, such as Darwin (1839, 1859), von Humboldt (1849), Wallace (1876, 1878) 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 & 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 & Carleton, 1996, 1998; Goodman *et al.*, 1996, 1999; Kelt, 1999; Goodman & Rasolonandrasana, 2001; Heaney, 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). Finally, several hypotheses have been proposed that attempt to explain current species richness patterns by trends in historical factors, such as immigration, extinction and speciation (Myers & Giller, 1988; Lomolino, 2001).

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 & Hurtt, 1994; Colwell & Lees, 2000). This prediction is based solely on geographical 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.*, 2003).

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 & 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.

MATERIALS AND 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 & 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 & 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 and 1000 m (Fig. 1). 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 to December, with the peaks in precipitation occurring in June, September and October, and the dry season extends from January to April (Clark *et al.*, 2000). No Caribbean temperature data are available for the transect, but data

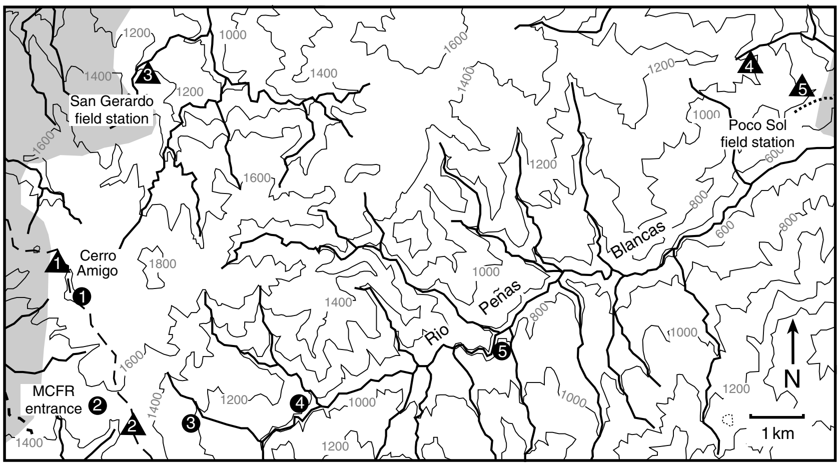

Figure 1 The Monteverde Cloud Forest Reserve and Bosque Eterno de los Niños (white) that protect the majority of the Peñas Blancas Valley. Trapping localities for the temporal replicates of the elevational gradient are shown in circles, and the spatial replicates are shown in triangles. The elevations 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.

along the Volcán Barva elevational cline (Caribbean) from north-eastern Costa Rica indicate that temperature declines linearly with elevation at *c.* 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; ICE, unpublished data). 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

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 (m)	Dates	Trap nights	Species	Unique individuals	Average annual rainfall (years)
MCFR, Cerro Amigo (east)	1840–1780	LW: 25–31 Oct. 2000	910	6	94	NA
		EW: 21–25 July 2001	650	5	61	
		DRY: 21–27 Mar. 2002	910	6	69	
MCFR, Cerro Amigo (west)	1840–1790	LW2: 21–27 Oct. 2001	910	5	67	NA
MCFR, Investigator's trail	1550–1500	LW: 15–21 Oct. 2000	910	6	154	2498 mm (1983–99)*
		EW: 29 July to 2 Aug. 2001	650	6	122	
		DRY: 24–30 Apr. 2002	910	4	93	
MCFR, Brillante trail	1550–1500	LW2: 9–15 Oct. 2001	910	8	122	NA
MCFR, Peñas Blancas trail	1300–1250	LW: 4–10 Nov. 2000	910	7	94	NA
		EW: 31 Aug. to 4 Sep. 2001	650	5	64	
		DRY: 10–16 Mar. 2002	910	7	85	
BEN: SGFS, Congo rail	1300–1250	LW2: 3–9 Nov. 2001	910	4	44	3426 mm (1975–99)†
MCFR, Peñas Blancas trail	1050–1000	LW: 14–20 Nov. 2000	910	8	82	3524 mm (1995–99)‡
		EW: 21–25 Aug. 2001	650	7	81	
		DRY: 14–20 Apr. 2002	910	5	70	
BEN: PSFS, above Zambia trail	1050–1000	LW2: 25 Nov. to 1 Dec. 2001	910	4	15	NA
MCFR, Sendero Ticodendron	800–750	LW: 26 Nov. to 2 Dec. 2000	910	4	106	5135 mm (1994–98)§
		EW: 8–12 Aug. 2001	650	3	58	
		DRY: 3–9 Apr. 2002	910	3	60	
BEN: PSFS, Zambia trail	800–750	LW2: 16–22 Nov. 2001	910	4	20	4642 mm (1979–99)¶
		Total	16,900	16	1561	

MCFR, Monteverde Cloud Forest Reserve; BEN, Bosque Eterno de Los Ninos; 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.

*Monteverde, Pacific Slope: 1500 m.

†San Gerardo Field Station: 1220 m.

‡MCFR, Aleman Refuge: 925 m.

§MCFR, Eladios Refuge: 850 m.

¶Poco Sol Field Station: 700 m.

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 & 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 (Soricidae), mouse opossums (Didelphidae), and heteromyid and murid rodents] were sampled along an elevational transect between 750 and 1840 m during 2000–02 in the Monteverde region of Costa Rica. Five sampling sites along the Caribbean elevation transect were surveyed: 750–800, 1000–1050, 1250–1300, 1500–1550 and 1770–1840 m (Fig. 1). 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. 1). 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: seven pitfalls, 10 Victor snap traps set 1–3 m above ground on vines or in trees, 40 extra large folding Sherman live traps (3 × 3.75 × 12″), and 73 large folding Sherman live traps (3 × 3.5 × 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 & 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 (*c.* 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 because of 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 1 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 & Coddington, 1994). Additionally, I estimated species richness using nonparametric randomization estimators, Chao2 and Jack2, to evaluate potential variation in sampling-effort among elevations (Colwell & 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 & Coddington, 1994). As 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 1 for gamma (A) and alpha (B) diversity patterns. As 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 with 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 & 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 centred near the midpoint of the domain. Such constraints result in increasing species richness toward the centre of the domain (Colwell & Hurtt, 1994; Willig & Lyons, 1998; Lees *et al.*, 1999; Colwell & 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 the 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 three to eight, and the

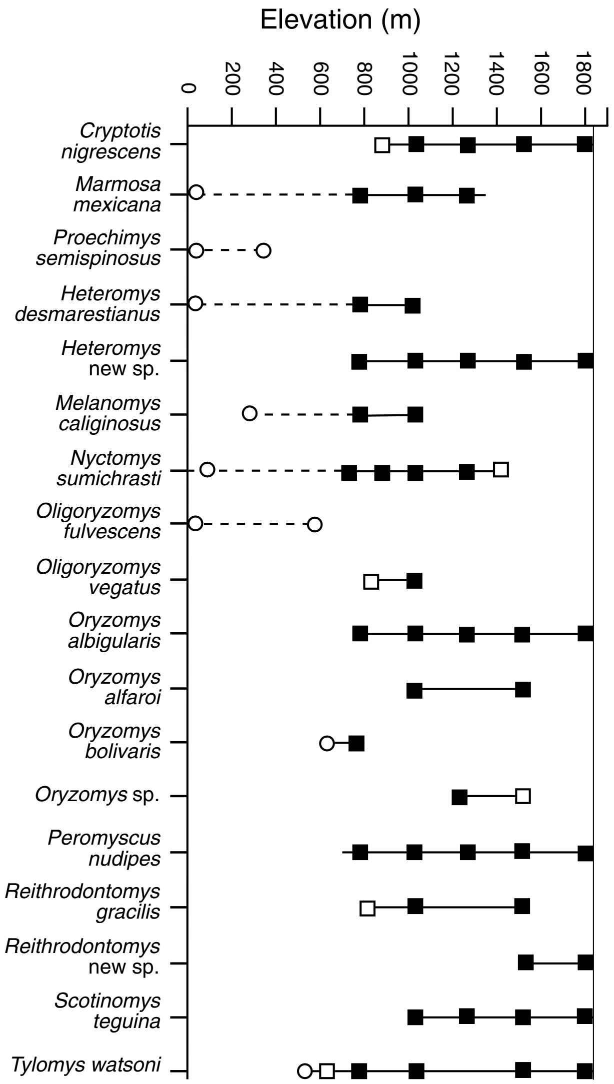

Figure 2 Elevational ranges of each species documented along the Río Peñas Blancas transects. Black boxes indicate locations where individuals were trapped or sighted from 2000 to 2002, and white boxes indicate localities from specimens collected previously in the same areas, and the white circles are the lower and upper localities for species from the Costa Rican specimen database.

number of individual animals captured ranged from 15 to 154. The elevational range of each species and known presence localities are shown in Fig. 2. The number of individuals captured for each species by elevation is listed in Appendix 2. 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. 3). The same shape of the species richness curve is seen in the late wet season 2000 and early wet season 2001 (Fig. 3a). 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. 3b).

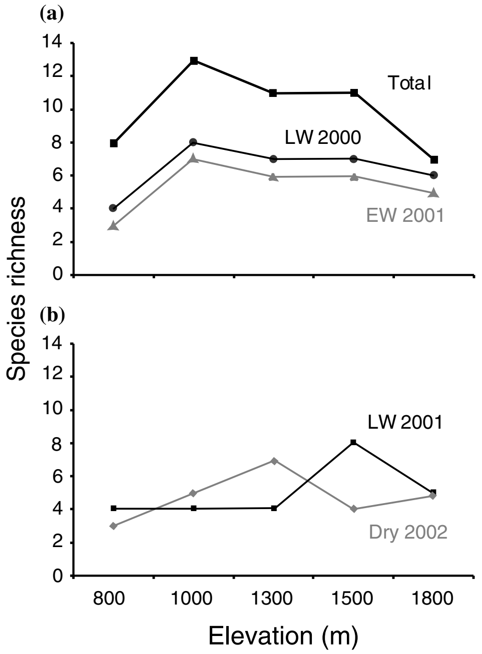

Figure 3 Species richness patterns for the four replicates: (a) late wet season (2000), and early wet season (2001); (b) dry season (2002), and the spatial replicate from the late wet season (2001). The combined species richness pattern including species ranges documented in any of the four transects is shown in the total species richness curve.

Most species accumulation curves at each elevational site reached a plateau in species richness before the end of the survey period (Fig. 4). 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 one to three 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 and 1000–1300 m, respectively (Fig. 5). 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

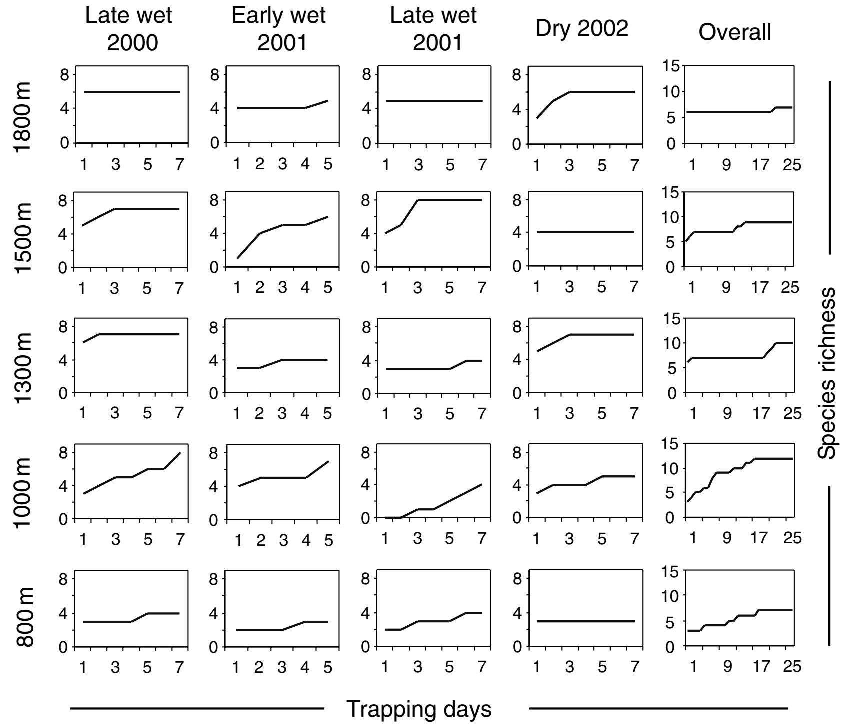

Figure 4 Species accumulation curves for each site, and overall species accumulation curves for each elevation using the combined data from all replicates.

several deviations. Deviations occurred at the highest elevations and at mid-elevations for both the alpha and gamma species richness curves (Fig. 5). 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 and 800 m and positive at 1800 m. (Fig. 5a). The alpha curve deviations for randomized midpoints were negative between 600 and 800 m and positive at 1800 m with several points falling along the 95% simulation curves (Fig. 5b).

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.*, 2003). 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 (Colwell *et al.*, 2003; McCain, 2003). Deviations from null model predictions prompt examinations of two such areas: lower than predicted richness between 600 and 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 (grey shading in Fig. 5). 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 centre of the premontane rain forest zone. Neither are there secondary peaks in richness at the transition zones. Finally, 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 of 18) are found in two or more of the forest communities and appear to be responding to species-specific elevational limits (Fig. 6a,b). 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 & 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).

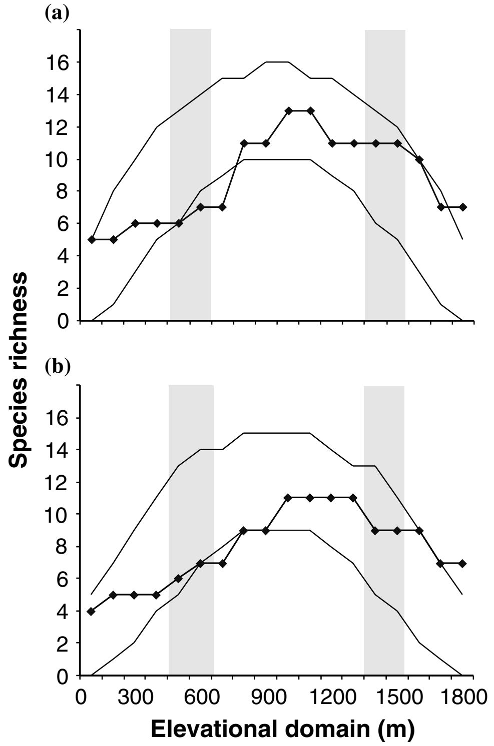

Figure 5 Species richness curves (lines with data points), and the 95% prediction curves sampled without replacement from program Mid-Domain Null (50,000 simulations each). (a) Gamma analysis using empirical range sizes and simulated range midpoints. (b) Alpha analysis using empirical range sizes and simulated range midpoints. Shaded regions represent regions of transition between habitat types.

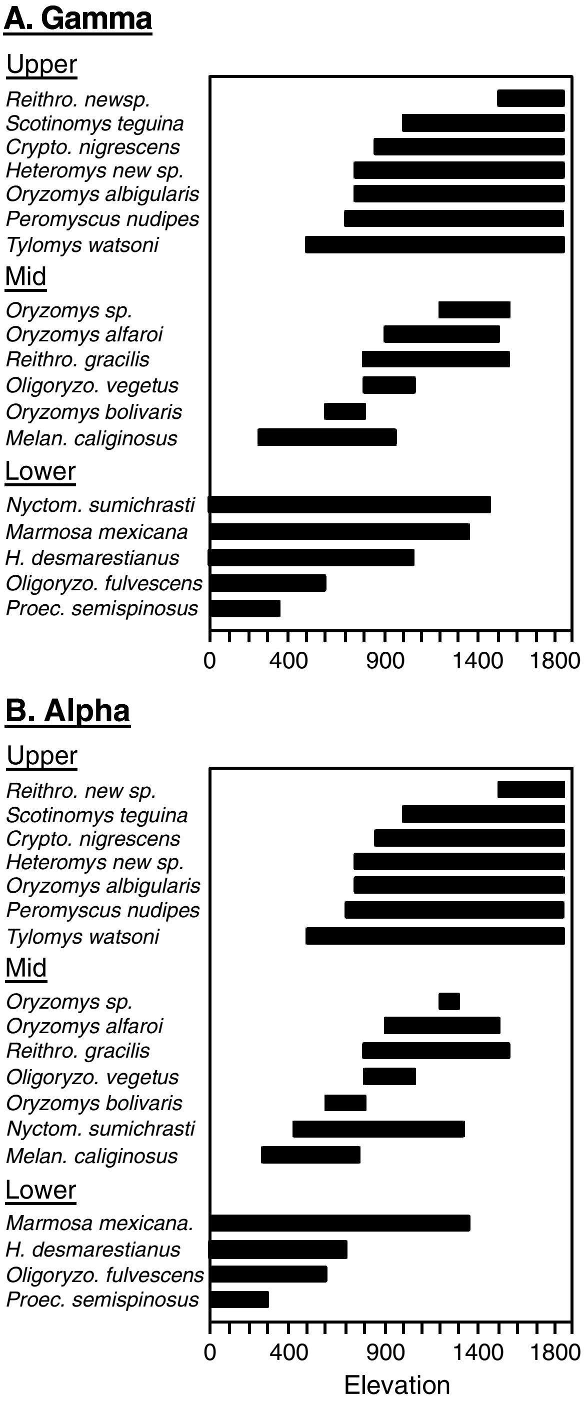

Figure 6 Elevational ranges of each species of small mammal for the Río Peñas Blancas elevational gradient. Aggregations of range termini would indicate areas of community overlap. (a) Gamma diversity ranges. (b) Alpha diversity ranges.

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 neither 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 because of 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 metres 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 and 1400–1500 m 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, 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 2). 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 metres 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. 3a,b). The dry season pattern differed because fewer species were trapped at the 1000 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 5 days.

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

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BIOSKETCH

Christy McCain is an ecologist and evolutionary biologist focusing on large-scale ecological patterns of mammals with particular emphasis on species richness, abundance, and distribution patterns along ecological gradients. She is also interested in null models, ecological modelling of species ranges, montane biogeography, and theoretical and empirical aspects of the causes and maintenance of species diversity.

Appendix 1A Summary of gamma elevational distribution extensions based on the literature and specimens.

	Peñas Blancas Valley specimen					
Species	Documented range (m)	Range extension (m)	Specimen	Estimated lower range (m)	Alajuela low elevation (s) (m)	Specimen (s)
Cryptotis nigrescens	1000–1840	870	KU 143381			
Marmosa mexicana	750–1350			0–750	8*	Dickey 14248
Proechimys semispinosus				0–350	8*–267	FMNH 44012, MVZ 164965
Heteromys desmarestianus	750–1050			0–750	25*	MVZ 164851
Melanomys caliginosus	750–1050			200–750	267	FMNH 44001
Nyctomys sumichrasti	1000–1300	700–900 1400–1450	Sighted by CMM USNM 559055	0–600	100	AMNH (McPherson 85)
Oligoryzomys fulvescens				0–600	45	KU 142729
Oligoryzomys vegetus	1000–1050	840–950	KU 159040, KU 159042			
Oryzomys bolivaris	700–800			600–700	670	FMNH 44005
Oryzomys sp.	1200–1300	1550	KU 159021			
Reithrodontomys gracilis	1200–1550	840–950	KU 159089, KU 159093			
Tylomys watsoni	1000–1840	600	Reported in houses	500–600	560*	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 1B Summary of alpha elevational distribution extensions based on the literature and specimens.

	Peñas Blancas Valley					
Species	Documented range (m)	Range extension (m)	Specimen	Estimated lower range (m)	Alajuela low elevation (s) (m)	Specimen (s)
Cryptotis nigrescens	1000–1840	870	KU 143381			
Marmosa mexicana	750–1350			0–750	8*	Dickey 14248
Proechimys semispinosus				0–300	8*–267	FMNH 44012, MVZ 164965
Heteromys desmarestianus				0–700	25*	MVZ 164851
Melanomys caliginosus				200–700	267	FMNH 44001
Nyctomys sumichrasti	1000–1300	700–900	Seen by CMM	400–700		
Oligoryzomys fulvescens				0–600	45	KU 142729
Oligoryzomys vegetus	1000–1050	840–950	KU 159040, KU 159042			
Oryzomys bolivaris	700–800			600–700	670	FMNH 44005
Reithrodontomys gracilis	1200–1550	840–950	KU 159089, KU 159093			
Tylomys watsoni	1000–1840	600	Reported in houses	500–600	560*	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 2 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	1050–1000 m	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.