



Could temperature and water availability drive elevational species richness patterns? A global case study for bats

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ABSTRACT

Aim A global meta-analysis was used to elucidate a mechanistic understanding of elevational species richness patterns of bats by examining both regional and local climatic factors, spatial constraints, sampling and interpolation. Based on these results, I propose the first climatic model for elevational gradients in species richness, and test it using preliminary bat data for two previously unexamined mountains.

Location Global data set of bat species richness along elevational gradients from Old and New World mountains spanning 12.5° S to 38° N latitude.

Methods Bat elevational studies were found through an extensive literature search. Use was made only of studies sampling $\geq 70\%$ of the elevational gradient without significant sampling biases or strong anthropogenic disturbance. Undersampling and interpolation were explicitly examined with three levels of error analyses. The influence of spatial constraints was tested with a Monte Carlo simulation program, Mid-Domain Null. Preliminary bat species richness data sets for two test mountains were compiled from specimen records from 12 US museum collections.

Results Equal support was found for decreasing species richness with elevation and mid-elevation peaks. Patterns were robust to substantial amounts of error, and did not appear to be a consequence of spatial constraints. Bat elevational richness patterns were related to local climatic gradients. Species richness was highest where both temperature and water availability were high, and declined as temperature and water availability decreased. Mid-elevational peaks occurred on mountains with dry, arid bases, and decreasing species richness occurred on mountains with wet, warm bases. A preliminary analysis of bat richness patterns on elevational gradients in western Peru (dry base) and the Olympic Mountains, WA (wet base), supported the predictions of the climate model.

Main conclusions The relationship between species richness and combined temperature and water availability may be due to both direct (thermoregulatory constraints) and indirect (food resources) factors. Abundance was positively correlated with species richness, suggesting that bat species richness may also be related to productivity. The climatic model may be applicable to other taxonomic groups with similar ecological constraints, for instance certain bird, insect and amphibian clades.

Keywords

Bats, climate, diversity, elevational gradient, mammals, mid-domain effect, species richness, temperature, water availability.

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INTRODUCTION

One fundamental goal of ecology and conservation is to determine what factors drive global biodiversity. The latitudinal

increase in species richness towards the equator has been used repeatedly in attempts to uncover important mechanisms (e.g. Pianka, 1966; Rohde, 1992; Hawkins *et al.*, 2003). Studies along elevational gradients can also be insightful (Brown, 2001;

Lomolino, 2001), particularly because they occur across smaller spatial scales making field studies more feasible, and because there are more mountains for independent replication than there are latitudinal gradients. A decade ago species richness was thought to show a single elevational pattern: richness decreasing with increasing elevation (Brown, 1988; Rahbek, 1995; Brown & Lomolino, 1998). Since then it has become increasingly clear that many, if not most, elevation patterns show highest species richness at mid-elevations (Rahbek, 1995, 2005).

We now know that species richness can decrease with elevation, peak at mid-elevation, or in a few cases increase with elevation (Rahbek, 1995, 2005). This variation may be informative. Certain richness patterns may be a consequence of a particular climatic regime or historical contingency, or certain patterns may be represented only by particular taxonomic groups driven by their ecological constraints. If such predictable patterns exist within taxa and among climates they will pinpoint driving factors in species richness (Brown, 2001; Lomolino, 2001; McCain, 2005). Such meta-analyses of elevational richness studies are needed for each taxonomic group from a global perspective. Only one exists to date. Small mammals (non-flying) consistently show mid-elevational peaks along montane gradients regardless of regional climate, latitude or scale of analysis (McCain, 2005). Available evidence suggests a climatic mechanism involving a complex interplay between rainfall, temperature and cloud cover.

Many potential mechanisms for elevational patterns in species richness have been proposed spanning aspects of climate, area, history, sampling and spatial constraints (Heaney, 2001; Lomolino, 2001). Climatic mechanisms include temperature, precipitation, humidity, cloud cover and productivity, which parallel these hypotheses along latitudinal gradients (e.g. Pianka, 1966; Rohde, 1992; Hawkins *et al.*, 2003). Unfortunately, most support for climatic mechanisms rests on correlative generalizations from a single season of climatic measurements at a few elevational sites on a single elevational gradient. The lack of quality, long-term data on climate factors like rainfall, humidity, cloud cover and productivity on the small-scaled elevational gradients have hampered the development of a quantitative theory. No climatic models have been proposed yet due to these limitations.

A quantitative null model exists to examine the influence of spatial constraints on elevational gradients in species richness: the mid-domain effect (MDE). The MDE predicts mid-elevational peaks in species richness based on spatial constraints of range placement between the hard boundaries of the sea and mountain summits (Colwell & Hurtt, 1994; Colwell & Lees, 2000; McCain, 2003, 2004; Colwell *et al.*, 2004). Landmass boundaries limit species ranges and species with large and intermediate-sized ranges necessarily overlap at the centre of the gradient. This leads to a peak in species richness at the mid-point of the elevational gradient. Thus, the MDE predicts highest richness at mid-elevations with a monotonic decline towards the base and top of the mountain, regardless of ecological gradients. Although theoretically controversial (Colwell *et al.*, 2004, 2005; Hawkins *et al.*, 2005; Zapata *et al.*, 2005), empirical support for the MDE on elevational gradients exists in varying degrees for small mammals (McCain,

2004, 2005), ants (Sanders, 2002; Sanders *et al.*, 2003) and plants (Grytnes & Vetaas, 2002; Grytnes, 2003).

Sampling may also have important consequences for species richness patterns along elevational gradients (Terborgh, 1977; Colwell & Hurtt, 1994; Grytnes & Vetaas, 2002; Rahbek, 2005). All studies suffer from some degree of undersampling, although proper sampling design attempts to minimize biases. Elevational richness patterns are estimated from either point samples or by interpolation, which assumes that a species occurs at all elevations between the highest and lowest documented record. Grytnes & Vetaas (2002) found that interpolation may create an artificially strong decrease in species richness towards the ends of the gradient. Thus, interpolation may bias species richness patterns towards mid-elevational peaks.

The aim of this article is to elucidate a mechanistic understanding of elevational gradients in species richness by examining not only climatic factors (both regional and local), but also influences of spatial constraints, undersampling and interpolation. With the current paucity of small-scale climatic data, global meta-analyses offer a natural experimental setting to test the generality of potential drivers. I use a global data set of elevational patterns for bat species richness from Old and New World mountains spanning 12.5° S to 38° N latitude. Bats are ideal study organisms for such a global analysis because they are a species-rich taxon occurring across a broad range of latitudes and they have clear ecological constraints due to their adaptations to flight. I examine whether the trends are upheld for major trophic groups (e.g. insectivores, frugivores) and the two main families of bats: the Vespertilionidae, which dominate temperate bat communities, and the Phyllostomidae, which dominate tropical bat communities (see Stevens, 2004). Lastly, I propose the first climatic model for elevational gradients in species richness and test the predictions with preliminary bat data for two previously unexamined mountains.

MATERIALS AND METHODS

I found papers on bat species richness along elevational gradients, searching BIOSIS and Web of Science using various combinations of keywords: bat, Chiroptera, diversity, species richness, elevation(-al), altitude(-inal). For grey literature, I searched the US Forest Service publication website, the EPA/DOE GrayLit site and National Park Service websites with the keywords listed above. I compiled and reanalysed these data using the methods of a similar analysis on nonvolant small mammals (McCain, 2005). For all papers, species richness patterns were assigned to three categories: decreasing, lower plateau and mid-elevation peak (more patterns were possible but only three were necessary with these data). Decreasing richness patterns are those in which species numbers decline with increasing elevation. Lower plateaus have several 100-m bands at the mountain base with similarly high species richness and declining species richness at upper elevations. Mid-elevational peaks have 25% or more species than at the base and top of the mountain.

Data sets were grouped by climate (tropical, temperate or transitional between tropical and temperate), landmass (island

or continent) and alpha (local) or gamma (regional) species richness. Alpha richness refers to local samples taken from field transects along single elevational gradients. 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. Gamma richness may be highly influenced by area (Rahbek, 1997, 2005; Brown, 2001; Lomolino, 2001; Willig *et al.*, 2003; McCain, 2005), and may have significant sampling biases (Rickart, 2001). As the scales of the data in alpha and gamma patterns are qualitatively and quantitatively different, the factors producing these patterns will not necessarily coincide (Rahbek, 2005). Such a dichotomy was seen in local and regional elevational gradients in small mammals (McCain, 2005).

Data sets were selected based on several sampling criteria, since sampling is of utmost importance in detecting unbiased patterns in comparative analyses (McCain, 2005; Rahbek, 2005; see Appendix S1 in Supplementary Material). First, data sets were included in the quantitative analyses only if sampling covered at least 70% of the elevational gradient. Secondly, I classified sampling effort as low, medium or high based on the number of months or years and intensity (e.g. number of mist nets per night) of study along the transect, quantity of sampling methods used (i.e. misting netting, bat detectors, etc.), and the scope of the museum specimens and systematic literature assessed. This was necessarily qualitative due to the highly variable nature of the explanations of sampling in the text of the studies. Thirdly, assessments were made (or noted if discussed by authors) of elevational correlations in sampling intensity with species richness, since few studies had standardized sampling effort among elevations. Finally, I considered whether study sites were subject to wide-scale disturbance (e.g. the Philippine Islands). The comparison of trends among bat families and trophic groups was limited to the New World since only one Old World data set, from New Guinea, was sufficiently sampled.

All of the regional studies are based on interpolating a species elevational range between the highest and lowest records. To facilitate comparisons of species richness patterns between point samples in the local scale analyses with regional analyses, local samples were interpolated. Interpolation aids in overcoming some limitations of undersampling, but may also inflate species richness estimates at mid-elevations (Grytnes & Vetaas, 2002). I explicitly examined the influence of undersampling and interpolation with an error analysis by range augmentation for each gradient. Interpolation allows ranges to increase between sampling points but not beyond them; thus, adding range segments simulates interpolation beyond the current sampling sites. I increased range sizes using three different procedures: (1) uniform augmentation for all ranges, (2) uniform range augmentation by size categories and (3) probability simulations with randomized range augmentation for each range size class. All range augmentations are percentages of the total length of the montane gradient with half of the error added to the lower range limit and half to the upper range limit until the base or top of the mountain was reached (e.g. gradient = 2000 m; 10% range

augmentation would add 100 m to the upper and lower range ends for a total of 200 m). The augmentations by size category assume that smaller ranges are more likely to be undersampled; therefore they have larger amounts of error. The range size categories are (1) small, < 26% of gradient, (2) medium, 26% to < 51% of gradient, and (3) large, ≥ 51% of gradient. The probability simulations add an additional element of realism by assuming that not all species ranges are undersampled but varying those that are randomly. Four levels of uniform range augmentation were applied to all ranges, [10, 30, 50, 70%]. Four levels of size-specific, uniform range augmentation were applied with augmentation decreasing from small to medium to large ranges: [20, 10, 0%], [30, 20, 10%], [50, 25, 10%], [70, 50, 30%]. The simulations are similar but with decreasing probabilities of error with range size: [30, 20, 10%], [50, 30, 10%], [70, 50, 20%], [100, 60, 40%] and decreasing percentages of augmentation with size: [20, 10, 0%], [40, 30, 10%], [50, 40, 20%], [70, 50, 30%]. For each probability and percentage error combination I used 1000 simulations to calculate 95% confidence intervals.

To test the influence of geographical boundaries, species richness patterns were compared to null model predictions with a Monte Carlo simulation procedure (Mid-Domain Null; McCain, 2004). This procedure simulates species richness curves using empirical range sizes within a bounded domain, based on analytical-stochastic models (Colwell & Hurtt, 1994; Colwell *et al.*, 2004; see McCain, 2003, 2004, 2005). Simulation boundaries were mountain summit and lowest elevation for the mountain range. Species richness data were then examined in 100-m increments. For each data set, 95% prediction curves based on 50,000 simulations sampled without replacement from empirical range sizes were used to assess the impact of spatial constraints on the elevational richness gradients. Regressions of the empirical values on predicted values, based on the average of the 50,000 simulations, gave r^2 estimates of the fit of the null model. Consistent deviations from null model predictions suggest that climatic, historical or other factors are important in determining species richness.

To test the proposed climate model, two preliminary species richness data sets, for western Peru and the Olympic Mountains, WA, were compiled from bat specimen records from 12 US museum collections in the MaNIS Database (<http://elib.cs.berkeley.edu/manis/>). The elevation of each specimen was based on the data base information or was estimated from the collecting locality through maps, digital elevation models and/or gazetteers. For western Peru, all data from western departments were included except Tumbes, which contains lowland tropical forest unlike the lowlands of other departments that are mostly desert or desert scrub. For the Olympic Mountains, bat specimens were included from the four counties that encompass the mountain range and surrounding coastal counties. The bat classifications were based on those of Wilson and Reeder (1993).

RESULTS

Twenty-seven elevational gradients in bat species richness were found in 24 published studies (see Appendix S1 in Supplementary

Material). Twenty bat species richness gradients had analysable data included in the publication, four presented only the richness curve (Tamsitt, 1965; Medway, 1972; Juste & Pérez del Val, 1995; Navarro & Leon-Paniagua, 1995), two discussed general elevational species richness in a region (Hoffmeister, 1986; Adams, 2003) and one presented generalized elevational range data in a mountainous region (Timm & LaVal, 2000). Of the studies that didn't provide raw data, several sampled too few sites or species, or were too general to be informative in this context. Thus, in discussions of species richness patterns only Tamsitt (1965) and Navarro & Leon-Paniagua (1995) are included herein with the 20 studies with data. Study effort on bats was concentrated where bats are most diverse: the tropics (60% of studies) and continental mountains (74%). All island studies were from the Old World tropics, specifically the Philippines and New Guinea.

For all studies, regardless of sampling effort, most elevational gradients in species richness of bats peaked mid-slope (13/22; 59%), whereas 8/22 (36%) demonstrated a decreasing pattern, and one revealed a low-elevation plateau in species richness (Tamsitt, 1965). The 20 elevational gradients with data are detailed in Fig. 1. The number of mid-elevation peaks is inflated here by studies with low sampling effort, sampling effort highly skewed towards a few elevations, sampling less than 70% of the elevational gradient and/or sampling in areas that were highly impacted by wide-scale, low-elevation human disturbance (Heaney *et al.*, 1989, 1999; Fawcett, 1994; Cerveny, 1998; Rickart *et al.*, 1999; Barataud, 2004). Carrera-E.'s (2003) transect from the eastern slopes of Ecuador also sampled less than 70% of the slope (67%), but the unsampled area occurred towards the mountain top, where species richness had already been shown to be declining for 1800 m (Fig. 1). For this reason, Ecuador was included in the quantitative analyses. The strong effect of lowland disturbance and sampling effort for bats in the Philippine islands was noted by the authors (Heaney *et al.*, 1989, 1999; Rickart *et al.*, 1999). The areas of strongest human disturbance are depicted in Fig. 1 by grey shading. The authors pointed out that within undisturbed forest bat species richness declined with elevation. Because of the strong influences of human disturbance, these studies are unable to provide a definitive indication of elevational species richness and are not considered in the quantitative analyses. Similarly, two studies with decreasing species richness patterns had low sampling effort or too little methodological description, and therefore were not considered further in the analyses (Tamsitt, 1965; Navarro & Leon-Paniagua, 1995). Thus, when considering only those data sets without large sampling effects or influences of human disturbance, half of the richness patterns had mid-elevation peaks (6/12: Ecuador, Jalisco, Mazateca, Utah, White-Inyo, Yosemite) and half decreased with elevation (6/12; Colombia, Manu, Mixteca, New Guinea, Peru, Venezuela). These 12 citations and study details are listed in Table 1 and Appendix S1 in Supplementary Material.

The sampling effort varied among these 12 studies (Table 1), and some have higher probabilities of sampling error (e.g. Utah, Ecuador) than others. The error analyses show that substantial

amounts of sampling error are needed to produce a different richness pattern (see Appendix S2 in Supplementary Material). Decreasing richness patterns become low-elevation plateaus with moderate to high levels of range augmentation (Fig. 2a). The exception is Colombia, which had mid-elevation peaks in a few high-error regimes [16% of error analyses (EA)]. Ranges from mid-elevation peaks also needed high amounts of error to become a low-elevation plateau (Fig. 2b). Most error levels broaden the richness peak, while some high-error procedures produced low-elevation plateaus. No error procedures were able to change the mid-elevation peaks of Mazateca and Jalisco, while only very high levels of error changed White-Inyo and Utah to low-elevation plateaus. Ecuador was the least robust to error, becoming low plateau with uniform error scenarios $\geq 30\%$ and some randomizations above 50% (50% EA). Yosemite plateaued in richness at low elevations after errors above 70% in all but uniform scenarios applied to all ranges (33% EA). The average range size at Yosemite is large (2053 m; see Appendix S1 in Supplementary Material), therefore adding a uniform percentage to large ranges quickly expands most ranges to the mountain base. On average, for mid-elevation peaks to become low plateaus species ranges need to be undersampled by 63.3–73.3% (1941–2248 m) of the montane gradient in the various error scenarios.

The 95% prediction curves based on 50,000 simulations of spatial constraints for the 20 elevational gradients with data are shown in Fig. 1. Null model regressions were only calculated for data sets without sampling effects or disturbance effects (no stars in Fig. 1). Fits to the null model varied widely: r^2 values ranged from 0 to 0.854 with an average of 0.156 ($n = 12$). There were only three data sets, all temperate with unimodal patterns, that had r^2 values $> 10\%$ (85.4% Utah, 44.5% White-Inyo, 48.3% Yosemite). Thus, not surprisingly, temperate data show greater fits to the null model than either tropical or tropical–temperate transition data (mean $r^2 = 0.591, < 0.001$ and 0.034, respectively). Alpha data sets had higher average r^2 values than gamma data (0.233 and 0.117, respectively). The majority of deviations from null predictions were shifts in peak richness to elevations significantly lower than the mountain mid-point (75%; $t = -3.33, P = 0.003, n = 12$).

The main dichotomy in species richness patterns was between climates: the majority of tropical data sets (83%) show decreasing species richness with elevation, while all three temperate data sets are unimodal (Fig. 1). Two of three data sets from a tropical–temperate transition in western Mexico show unimodal richness patterns (Mazateca, Jalisco). Alpha and gamma species richness demonstrated equal numbers of decreasing and unimodal richness patterns (alpha 2 and 2, gamma 4 and 4, respectively). Two unimodal patterns were alpha transects, one in the temperate zone (Utah) and one in Mexico (Mazateca); the other two alpha studies that had decreasing richness were from Ecuador and Mexico (Jalisco).

Peak elevational species richness of bats demonstrated a positive trend with latitude (Fig. 3a; $r^2 = 0.461, P = 0.015$): temperate zones showed richness peaks at higher elevations than the tropics (mean elevations of 1796 m and 333 m, respectively).

Table 1 Listing of elevational transects of bat species richness used in the quantitative analyses. Each denoted by study site (citation), abbreviation used in text, data method (A = alpha; G = gamma), diversity pattern (DP; D = decreasing; M = mid-elevation peak), sampling effort category (percentage of gradient sampled), sampling explanation (L = if literature assessed for range data) and range description. If specimen data were examined the number of museums are given in parentheses after specimens. If field data were included, the methods used are listed in parentheses (N = mist netting; H = hunting; R = roost captures/surveys; V = visual detection; A = acoustic detection)

Study site	Abbreviation	Data	DP	Sampling effort	Sampling explanation	Ranges
Central Peru (Graham, 1983)	Peru	G	D	High (85%)	Specimens (5), 17 months field (N, H, R)	Interpolated
Manu, Peru (Patterson <i>et al.</i> , 1996)	Manu	G	D	High (95%)	Specimens (2), 292 days field (N, H, R), L	Interpolated*
Eastern Ecuador (Carrera-E., 2003)	Ecuador	G	M	Low-med. (67%)	Specimens (3), 14 days field (N), L	14 sites and interpolated
Colombia (Muñoz Arango, 1990)	Colombia	A	D	Low-med. (85%)	12 months field (N, H, R)†	8 sites
Venezuela (Handley, 1976)	Venezuela	G	D	High (76%)	39 months field (N, H, R)	Interpolated
Mazateca, Mexico (Sánchez-Cordero, 2001)	Mazateca	A	M	Medium (91%)	480 days field (N), 40 days/site	5 sites
Mixteca, Mexico (Sánchez-Cordero, 2001)	Mixteca	A	D	Medium (92%)	480 days field (N), 40 days/site	7 sites
Jalisco, Mexico (Iñiguez Dávalos, 1993)	Jalisco	G	M	Low-med. (84%)	14 months field (N, H, R)‡, L	Interpolated
White-Inyo, CA–NV (Szewczak <i>et al.</i> , 1998)	White-Inyo	G	M	Medium (79%)	Specimens (4), 325+ person-days field (N, R, V, A)§	Interpolated
Henrys, UT (Mollhagen & Bogan, 1997)	Utah	A	M	Medium (79%)	33 days field (N: 94 net-nights)¶	22 sites and interpolated
Sierra Nevada, CA (Pierson <i>et al.</i> , 2001)	Yosemite	G	M	Medium (100%)	9 years field (N, R, A)**	40 sites and interpolated
New Guinea (Flannery, 1990)	New Guinea	G	D	High (100%)	Specimens (13), L	Interpolated

*Range data grouped by level of accuracy in ranges.

†Sampling effort not quantified per site in manuscript (ms).

‡Sampling effort not quantified per site in ms, but for three habitat types for low, mid and high elevation (221, 125, 154.25 h of netting, respectively).

§Sampling effort not quantified per elevation in ms; additional records and sampling added in summer 2002 (Szewczak, unpublished data).

¶Sampling effort quantified per site in ms; interpolated richness not significantly correlated with sampling ($P > 0.05$); site richness significantly correlated with sampling ($P < 0.01$).

**Sampling effort quantified per site in ms; interpolated richness not significantly correlated with sampling ($P > 0.05$); same diversity curve identified by Grinnell & Storer (1924).

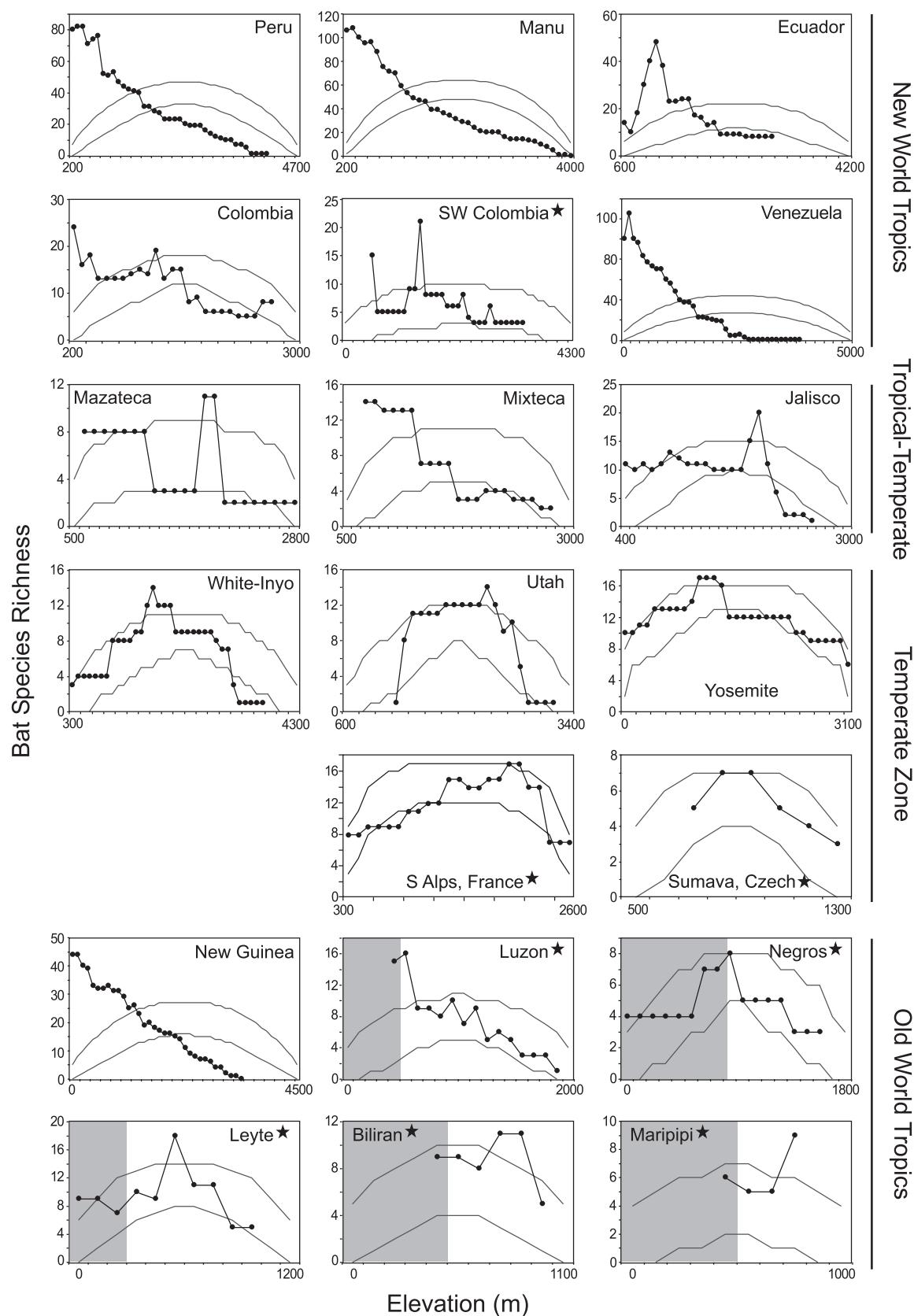


Figure 1 Twenty bat species richness patterns along elevational gradients (black circles and lines) including 95% simulation limits (lines only) of the mid-domain analysis from 50,000 range size simulations using Mid-Domain Null. Stars by gradient locality indicate data sets not used in the quantitative analyses due to sampling or lowland disturbance issues. Grey shading indicates elevations with high levels of habitat disturbance.

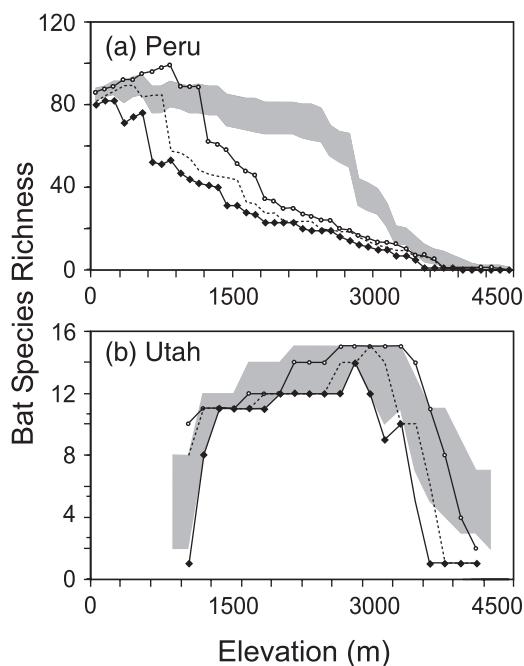


Figure 2 Effects of different levels and scenarios of sampling error for two montane bat gradients: (a) Peru and (b) Henry Mountains, Utah. Black diamonds = observed species richness; dashed line = 10% uniform range augmentation; white dots = uniform error by size [30, 20, 10%]; grey shading = error simulations at different probabilities of error [70, 50, 20%] and different percentages of error [50, 40, 20%] by size. See text for details of error regimes.

Species richness of all bat communities declined dramatically above a threshold elevation, and the threshold increased monotonically from the tropics to the temperate zone (833, 1867, 2100 m). The positive latitudinal trend in elevational richness was found for the two largest bat families, Vespertilionidae (Fig. 3b; $r^2 = 0.416$, $P = 0.032$) and Phyllostomidae (not shown), although the Phyllostomidae was not a significant result ($r^2 = 0.131$, $P = 0.379$). Latitudinal trends in elevational richness were not found for the other less diverse bat families (i.e. Molossidae, Emballonuridae, etc.). Vespertilionids differed significantly from the overall bat pattern: all but one elevational richness peak was at mid-elevation, although at lower elevations towards the tropics (Fig. 3b). In contrast, the tropical and subtropical Phyllostomids showed the same richness pattern as the overall elevational pattern for bats, regardless of latitude. Thus, the peaks in species richness for the Vespertilionids were significantly higher than those of the tropical Phyllostomid family (paired $t = 5.701$, $P = 0.0004$), and the upper and lower range boundaries of Vespertilionids were higher than those for Phyllostomids (paired $t = 2.766$, $P = 0.014$; and paired $t = 3.560$, $P = 0.005$, respectively). Only the insectivorous clade of bats showed the strong latitudinal trend in elevation of peak richness (Fig. 3c; $r^2 = 0.589$, $P = 0.006$), which strongly mirrored that of the overall bat richness pattern. The other trophic groups (frugivores, carnivores/sanguivores and omnivorous nectivores) that are mainly tropical in distribution showed no trends in elevational species richness with latitude

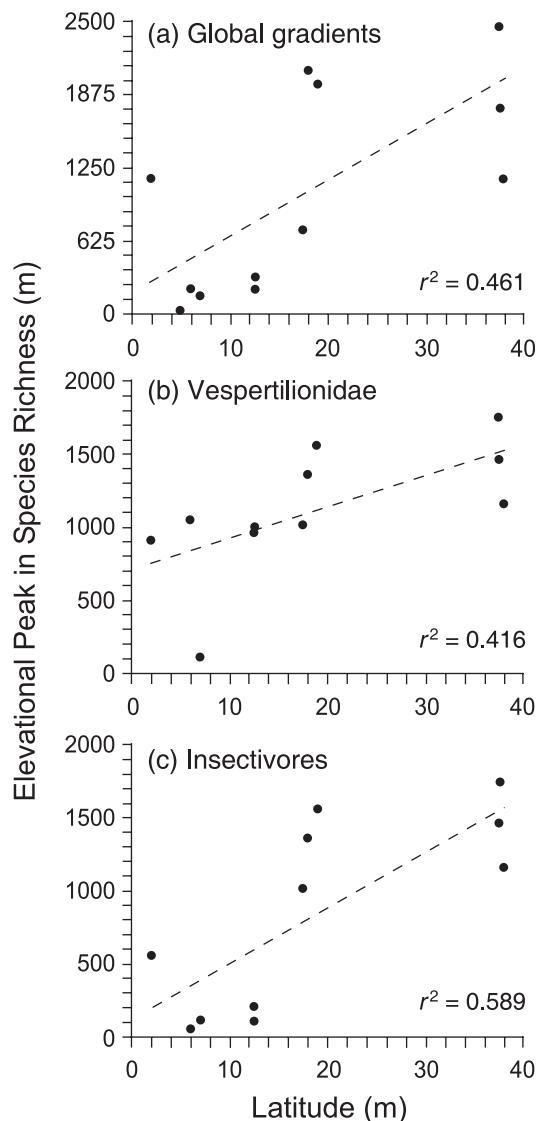


Figure 3 Positive, linear trend in elevation of maximum bat species richness with latitude for all species and gradients ($P = 0.015$, $n = 12$), for the family Vespertilionidae ($P = 0.032$, $n = 11$) and for insectivores ($P = 0.006$, $n = 11$) from the Americas.

as most richness peaks were towards the lower elevations on all gradients where they occurred.

The abundance of bats was correlated positively with species richness except for three Philippine islands, which had high levels of deforestation (see Appendix S3 in Supplementary Material). Several of the correlations were not significant because they were based on few sampling points. Abundance declined with elevation, except for some of the Philippine Islands and Utah where the highest abundances were at mid-elevations. Most of these correlations were based on abundances corrected for sampling effort. Sampling corrected abundance was calculated by the authors, or in some cases by me if the data was provided in the manuscript, as the number of individuals captured per site divided by a standardized sampling effort (e.g. number of sampling nights, number of mist-net hours, etc.).

Climate model

All studies found that temperature decreased linearly with increasing elevation, although at varying rates (0.38–0.68 °C for every 100 m), which could be due to differences in duration and number of sites sampled. Based on the data or citations, temperature decreased with each 100-m increase in elevation by 0.56 °C in Peru, 0.38 °C in Ecuador, 0.68 °C in Colombia and 0.51 °C in Mexico. These were in accordance with data for the Old World tropical mountains (0.5–0.55 °C for every 100 m; Md. Nor, 2001) and the average environmental lapse rate of 0.6 °C for every 100 m (Barry, 1992). Precipitation trends with elevation were highly variable: the highest precipitation was at the lowest elevations with a secondary peak at upper elevations in Ecuador, whereas Colombia, Jalisco, Mixteca and Peru had mid-elevation peaks in precipitation. Mazateca, Utah and White-Inyo noted increasing precipitation with elevation. Studies from other regions have also found the highest precipitation at mid-elevations (i.e. Costa Rica, Borneo), although all studies on precipitation suffer from sampling of only few sites, over relatively short time-scales (Barry, 1992), and do not always account for horizontal precipitation from low-lying clouds. All of the tropical mountains occurred on wet slopes (e.g. eastern versant of the Andes), thus rainfall was high at low to mid-elevations, even if slightly higher rainfall was noted at mid-slope. In contrast, all of the temperate and two of the Mexican mountains (Jalisco, Mazateca) had arid or seasonal drought conditions at the mountain base. On these mountains, rainfall was highest at upper elevations, and rainfall was very low at the base (i.e. < 10 cm year⁻¹ at the base of White-Inyo, 5 cm at the base of Utah (Henry's) and 15 cm at the base of Mazateca) with high rates of evapotranspiration.

Bat elevational species richness was strongly correlated with temperature for the wet, tropical mountains (average $r = 0.887$, SE = 0.0392), less correlated on the subtropical, Mexican mountains (average $r = 0.7580$, SE = 0.0870) and not significantly correlated on temperate mountains (average $r = 0.2483$, SE = 0.0007). The threshold temperature for bat activity was documented to be 2–10 °C (Cerveny, 1998; Pierson *et al.*, 2001; references therein). Such a strong temperature constraint was noted at the coldest temperatures, as no bats were found above some limit between 2600 and 4100 m on the various mountains. The temperate data sets and two elevational gradients from Mexico, which all had dry, arid conditions at the mountain base, demonstrated highest bat richness at mid-slope. This trend appears to be correlated with water availability. The highest water availability on these temperate or subtropical mountains is at mid-slope, where higher rainfall is paired with runoff from steep slopes, and shallow soils at the highest elevations, where most precipitation is in the form of ice and snow. On these mountains most streams are seasonal and intermittent at the lowest elevations (Mollhagen & Bogan, 1997).

A climate model based on these results demonstrates that bat elevational species richness appears to be responding to two contrasting gradients up mountain slopes: the temperature gradient and moisture availability gradient (Fig. 4). The proposed shape

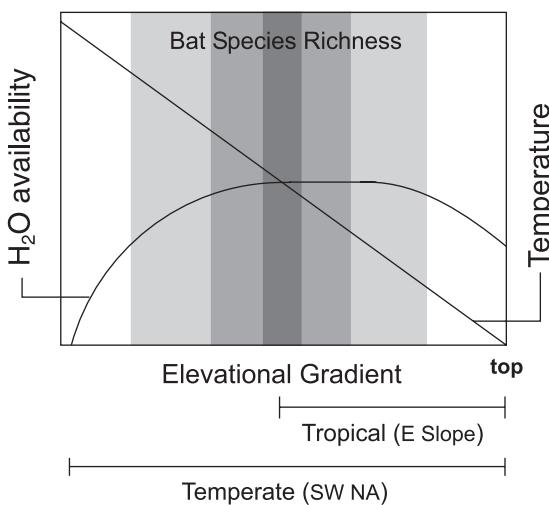


Figure 4 Generalized climatic model for elevational gradients in species richness of bats, incorporating a linearly decreasing temperature gradient and a unimodal water availability gradient. Bat species richness is depicted in grey tones with darker tones indicating more species. The placements of generalized tropical and temperate elevational gradients are shown below the x-axis.

of the water availability curve reflects not just trends in rainfall but what is known about evapotranspiration and runoff. Because exact rainfall trends are unknown as of yet, I propose that for a broad band of elevations (tropical, low to mid-elevations; dry temperate, mid to high elevations) water availability is high. Rainfall may peak mid-slope or above, but runoff to lower elevations tends to even out water availability at these elevations. And at the highest elevations water availability declines as precipitation declines, runoff is highest due to the steepest slopes and shallowest soils, and seasonal snow and ice are inaccessible water resources. Water availability along a gradient with an arid base should have declining species richness where there is low rainfall and high evapotranspiration. Thus, on mountains with arid conditions at the mountain base (as seen here in the American Southwest and north-west Mexico) bat richness should be highest at the mid-elevation point where temperature and water availability are highest and decline at the highest elevations due to extreme cold temperatures. However, on mountains with wet, warm conditions at the base (eastern Andes, New Guinea) you would expect bat richness to decline as temperature declines and secondarily as water availability declines.

There are direct predictions of this model: mountains with arid conditions at the base regardless of latitude are predicted to have the highest bat species richness mid-slope, whereas warm, wet mountains, even at high latitudes, should have the highest bat species richness at or near the base. Two candidate test mountains would be the western slope of the Andes in Peru, which is characterized by arid lowland conditions, and the wet mountain region of the Olympics in the Pacific Northwest of Washington State. Elevational studies of the bat fauna on these mountains do not exist, but specimen records from the last 100 years have been collected in these regions. A preliminary

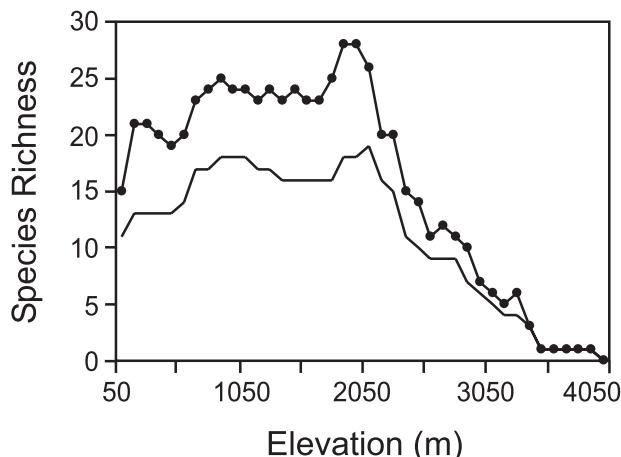


Figure 5 Preliminary elevational species richness patterns for bats of western Peru based on specimen data from 12 US museum collections in the MaNIS database. The line with circles represents the pattern for all species and the smooth line represents the pattern for only those species with ≥ 10 specimens.

analysis of these bat richness patterns shows strong support for the proposed climate model. Species richness appears to be highest at mid-slope of the western slope of the Peruvian Andes (Fig. 5). The upper elevations for the Olympic Mountains were not extensively sampled to detail an elevational richness pattern, but all 10 species occurring on the mountain were present at the lowest elevations (0–100 m). Thus, species richness is either decreasing with elevation or has a low-elevation plateau, both of which support the predictions of the climate model.

DISCUSSION

Bat species richness on mountains clearly follows two patterns: decreasing with elevation and peaking at mid-elevation (Fig. 1). Bat species richness decreased with elevation on tropical elevational gradients and peaked at mid-elevation on temperate gradients (Fig. 3). Elevational species richness of Phyllostomids, other tropical bat families and the insectivore guild directly mirrored the overall species richness patterns. The Vespertilionids, which dominate temperate communities, consistently demonstrated mid-elevational peaks although shifted towards lower elevations at low latitudes. The other trophic groups, mainly tropical, were most diverse at lower elevations. Error analyses demonstrate the patterns are not likely to be a consequence of undersampling or interpolation (Fig. 2). Null model analyses reveal that bat elevational species richness is not responding simply to spatial constraints (Fig. 1). Climatic mechanisms acting at both regional and local scales appear to be the important drivers of elevational richness of bats. Meta-analyses pinpoint the combination of temperature and water availability as the key driving factors (Fig. 4). I will discuss undersampling and interpolation, spatial constraints, regional and local climate and their influence on elevational richness of bats sequentially.

Sampling and interpolation

All empirical studies have sampling limitations due to the very nature of field studies — limitations in time and money, personnel, trapping methodologies and taxonomic variation in capture rates, etc. Certain sampling designs may lead to biased species richness patterns (McCoy, 1990; Colwell & Hurtt, 1994; Grytnes & Vetaas, 2002). To address sampling concerns, first, for the quantitative analyses I considered only those data sets without obvious sampling biases or disturbance trends (44% meet my criteria, see Table 1 and Appendix S1 in Supplementary Material). Second, for the remaining studies, I explicitly examined the influence of general undersampling and interpolation with various range augmentation regimes (see Appendix S2 in Supplementary Material). The error regimes ranged from least realistic with uniform undersampling to most realistic with randomizations based on decreasing probabilities of error and decreasing magnitudes of error from smaller to larger range sizes. With all error regimes, decreasing species richness patterns remained decreasing with elevation — either unchanged in shape or plateauing at the lower elevations (Fig. 2a). Colombia was the only exception in a few error scenarios (2.8% of the cases).

The amount of error needed to change a mid-elevational species richness pattern to a decreasing or low plateau was large (Fig. 2b). On average, a decreasing richness pattern occurred after adding nearly 2000–3000+ m to ranges in the various error regimes. Such large errors are highly unlikely. Ecuador and Yosemite showed the most response to large errors. The error necessary for bat richness in Ecuador and Yosemite to decrease with elevation is to add 1080 m and 1962 m, respectively, for uniform error, 1080 m and 2170 m, respectively, for uniform error by range size (small) and more for the randomized simulations. Ecuador could be undersampled sufficiently that the true pattern is decreasing, but this further supports the temperature–water relationship, whereas the Yosemite richness pattern is independently verified by Grinnell's early work on the mountain, as he found the same elevational pattern in bat richness (Grinnell & Storer, 1924) when only sampling bats with shotguns. Thus, both decreasing and unimodal patterns for bats are supported even given a basic level of undersampling.

Spatial constraints

Spatial constraints on species ranges have been theoretically implicated and, in some cases, empirically supported to be a contributing factor to mid-elevational peaks in species richness (Colwell *et al.*, 2004 and references therein). Regardless of size, latitude or climatic regime of the mountain, the mid-domain effect (MDE) predicts species richness to peak at the middle of the gradient. Elevational richness of bats does not coincide with the predictions of the MDE: only three of the gradients had $r^2 > 40\%$ while the other nine had $r^2 < 7\%$ (Fig. 1; Appendix S1 in Supplementary Material). Wide scatter and low predictive ability diminish the generality of the null model as an explanation for elevational richness patterns of bats (average $r^2 = 0.156$). Additionally, latitudinal trends in the MDE — temperate, elevational

richness fit MDE predictions more than tropical — expose the fact that richness patterns do change in relation to latitude and climate so that the simple assumption of the MDE cannot be upheld.

The average MDE fit is lower than that found for non-volant small mammals on elevational gradients globally ($r^2 = 0.238$; McCain, 2005). Thus, for the two most speciose groups of mammals, elevational patterns are not directly consistent with the MDE. Species richness peaks were shifted consistently towards lower elevations with only three higher than the mountain mid-point. There was a slight effect of sampling scale, as alpha data fit null model predictions slightly better than did gamma data. This was in contrast to small mammals which demonstrated higher fits to null models in gamma rather than alpha data. Overall, the consistent deviations from null model predictions and latitudinal richness trends patterns suggest underlying climatic drivers.

Climatic drivers

The elevation of highest species richness was positively related to latitude (Fig. 3): highest richness was at low elevations in the tropics, but at mid-slope in the temperate zone. Intermediate latitudes in Mexico, which show an overlap of temperate and tropical habitats and species, demonstrate both richness patterns on mountainsides. This suggests that regional climate determines the elevational species richness pattern of bats. But this strong latitudinal trend is misleading, because of differences in the local climatic regime of mountains sampled in each latitudinal zone. In the temperate zone, only mountains with dry or arid conditions at the bases were surveyed, whereas in the tropics only warm, wet mountains were surveyed.

On all mountains temperature decreased with elevation. Water availability was highest at mid-elevation on arid mountains and high across a broad zone of low to mid-elevations on mountains in warm, wet climates. Highest bat species richness occurred in the elevational zone where water and temperature are simultaneously maximized (Fig. 4). This is illustrated by the three Mexican mountains: the two with more arid conditions at the base (Sierra Mazateca, Oaxaca and Sierra Manantlán, Jalisco) had mid-elevational peaks in richness, while the wetter-based mountain (Sierra Mixteca, Oaxaca) had a decreasing richness pattern. Bat elevational studies also indicate a correlation between species richness and abundance (Appendix S3 in Supplementary Material). The most productive environments are predicted to harbour both the highest abundance and the highest species richness (Terborgh, 1977). Thus, the optimal combination of temperature and water availability gradients may also indicate that these are the most productive sites elevationally for bats. Unfortunately, neither primary productivity nor an index of productivity was measured in these studies.

To test the locally driven climate model further, I examined bat faunas on an arid montane gradient at low latitude, western Peru, and a warm, wet mountain at high latitude, the Olympics, WA. The preliminary data for western Peru (Fig. 5) demonstrate a mid-elevational peak as predicted. Bats on the Olympic Mountains, WA, demonstrate the highest species richness at low

elevations, as predicted. Both inference from the meta-analyses and support from test mountains identify local climate conditions of temperature and water availability as the main drivers of bat elevational species richness.

O'Brien (1993) demonstrated that species richness of woody plants across southern Africa is a positive function of water and a parabolic function of energy, and a variety of water-energy models have since been shown to have explanatory power across multiple large-scale geographical studies for plants and animals (Hawkins *et al.*, 2003; references therein). Additionally, water and energy/temperature are correlated with elevational species richness of epiphytes (Andes; Krömer *et al.* 2005) and ferns (Himalayas; Bhattacharai *et al.*, 2004). Brown and Lomolino (1998) also noted that highest species richness of most organisms in the American Southwest was found at intermediate elevations, and this may be due to the lack of water in arid environments at the base. Clearly, water and energy regimes are essential to the physiology of plants and directly influence distribution and species richness (O'Brien, 1993; Hawkins *et al.*, 2003; Bhattacharai *et al.*, 2004; Krömer *et al.*, 2005); but for animal richness patterns, the question of interest becomes the relative importance of direct (physiological) and indirect (resource) effects of water and temperature on species richness patterns (Hawkins *et al.*, 2003).

Bats are thought to be directly limited by the physiological/thermoregulatory constraints of mammalian adaptations to flight at cold temperatures (McNab, 1982; Graham, 1983; Patterson *et al.*, 1996; and references therein). Such studies stress that these energetic constraints act as a 'filter barrier' to upward elevational range expansion, and result in the hard limits of bat distributions on mountain tops (Graham, 1983). Bat abundance, capture rates and detection rates decrease with elevation and colder temperatures (Appendix S3 in Supplementary Material; Terborgh, 1977; Graham, 1983; Cerveny, 1998). Similarly, males are more abundant than females at higher elevations, presumably because females have greater energetic needs for gestation, lactation and rearing of young (Grindal *et al.*, 1999; Cryan *et al.*, 2000). Temperature could also influence bat species richness indirectly through food resources and availability (Graham, 1983; Szewczak *et al.*, 1998). Insect abundance, fruit and nectar production and abundances of many small vertebrates are all predicted to be low under cold temperature regimes (e.g. Janzen, 1973; Janzen *et al.*, 1976; Fauth *et al.*, 1989; Loiselle & Blake, 1991; Navas, 2003).

Successful exploitation of desert ecosystems necessitates the evolution of adaptations to extreme temperatures for water conservation and salt balance. These adaptations can be behavioural, such as occupation of cool, subterranean caves, fluctuation in activity levels or physiological adaptations for waste and water regulation in the excretory system (McNab, 1982); but the arid environment may have strong ecological constraints on the abundance of food resources. Most arid plants occur in low abundances and limit fruit, nectar and seed output due to water limitations (e.g. Noy-Meir, 1973; MacMahon, 1997). Similarly, insect abundances must be limited by water availability and therefore are likely to be much more patchily distributed in arid environments (e.g. Janzen, 1973; MacMahon, 1997; Perrin &

Boyer, 2000). Thus, it appears that the optimal conditions for bat species richness — warm and wet — may be the most optimal conditions for their food resources.

General conclusions

From the data sets on bat species richness along elevational gradients collected so far, two different patterns are supported: decreasing richness with increasing elevation, and richness peaks at mid-elevation. Null model analyses indicate that climatic factors, not spatial constraints, are most consistent with elevational richness trends. Two factors, temperature and water availability, explain a large amount of variation in bat species richness. A generalized model of these overlapping climatic gradients (Fig. 4) leads to testable predictions for unexamined mountain slopes and other taxonomic groups. Preliminary results for bats on two new mountains strongly support the predictions of the proposed climatic model. Shapes of the temperature and particularly moisture functions can be modified to allow for variation seen in different regions and climates. For example, plateaus in water availability at warm temperatures would predict corresponding plateaus in bat species richness. For those taxa that may respond similarly to these climatic factors, similar elevational richness patterns would be expected. Some candidate taxa are birds, particularly small-bodied clades tied to insect, fruit or nectar food resources, some insect clades, for instance moths, and possibly certain amphibian clades. Other taxonomic groups may need additional environmental factor(s) included in the model. The trends found herein present opportunities for tests on empirical gradients in the future that applied in a systematic fashion should lead to a deeper understanding of how elevational gradients in species richness are structured.

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BIOSKETCH

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SUPPLEMENTARY MATERIAL

The following material is available online at www.blackwell-synergy.com/loi/geb

Appendix S1 Listing of all elevational transects of bat species richness.

Appendix S2 Species richness error simulations using uniform and randomized probabilities of range augmentation.

Appendix S3 Correlation statistics of abundance and species richness estimates, and linear regression statistics for abundance with elevation along elevational gradients of bats.

APPENDIX S1. Listing of all elevational transects of bat species richness. Each denoted by study site (reference), data method, climate, richness pattern, sampling effort (% of gradient sampled), null model r^2 values, and average elevational range size. 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	Data	Climate	Richness	Sampling effort	null r^2	Range Size
1. Central Peru (Graham, 1983)	gamma	tropical	decreasing	high (85%)	0.00	1105 m
2. Manu, Peru (Patterson <i>et al.</i> , 1986)	gamma	tropical	decreasing	high (95%)	0.00	1087 m
3. Eastern Ecuador (Carrera-E., 2003)	gamma	tropical	unimodal	low-med (67%)	0.00	540 m
4. Colombia (Muñoz Arango, 1990)	alpha	tropical	decreasing	low-med (85%)	0.00	639 m
5. SW Colombia (Fawcett, 1994)	alpha	tropical	unimodal	low (66%)	N/A	
6. Venezuela (Handley, 1976)	gamma	tropical	decreasing	high (76%)	0.00	769 m
7. Mazateca, Mexico (Sánchez-C., 2001)	alpha	temp.-trop.	unimodal	med (91%)	0.0198	577 m
8. Mixteca, Mexico (Sánchez-C., 2001)	alpha	temp.-trop.	decreasing	med (92%)	0.0601	735 m
9. Jalisco, Mexico (Iñiguez Dávalos, 1993)	gamma	temp.-trop.	unimodal	low-med (84%)	0.0216	704 m
10. White-Inyo, CA & NV (Szewczak, <i>et al.</i> , 1998)	gamma	temperate	unimodal	med (79%)	0.4347	1596 m
11. Henrys, UT (Mollhagen & Bogan, 1997)	alpha	temperate	unimodal	med (79%)	0.8538	1017 m
12. Sierra Nevada, CA (Pierson <i>et al.</i> , 2001)	gamma	temperate	unimodal	med (100%)	0.4833	2053 m
13. Southern Alps, France (Barataud, 2004)	gamma	temperate	unimodal	med (85%)*	NA	
14. Sumava, Czech (Cerveny, 1998)	alpha	temperate	unimodal	low (59%)	NA	

15. New Guinea (Flannery, 1990)	gamma	tropical	decreasing	high (100%)	0.00	864 m
16. Luzon, Philippines (Heaney <i>et al.</i> , 1999)	alpha	tropical	decreasing	med (71%)	NA	
17. Negros, Philippines (Heaney <i>et al.</i> , 1989)	alpha	tropical	unim./decr.	med (84%)	NA	
18. Leyte, Philippines (Heaney <i>et al.</i> , 1989)	alpha	tropical	unim./decr.	med (78%)	NA	
19. Biliran, Philippines (Rickart <i>et al.</i> , 1999)	alpha	tropical	unim./decr.	low-med (45%)	NA	
20. Maripipi, Philippines (Rickart <i>et al.</i> , 1999)	alpha	tropical	unim./decr.	low-med (64%)	NA	
21. Eastern Mexico (Navarro & L., 1995)	alpha	temp.-trop	decreasing	low	No data	
22. Eastern Colombia (Tamsitt, 1965)	gamma	tropical	plateau-decr.	med?	No data	
23. Bioko Island, Africa (Juste & P., 1995)	alpha	tropical	decreasing	low	No data	
24. Malay Peninsula (Medway, 1972)	alpha	tropical	decreasing	low	No data	
25. Arizona, USA (Hoffmeister, 1986)	general	temperate	unimodal			
26. Rocky Mtn. West, USA (Adams, 2003)	general	temperate	unimodal			
27. Monteverde, C. Rica (Timm & L., 2000)	general	tropical	NA			

*significant correlation between sampling and species richness

APPENDIX S2. Richness error simulations using uniform and randomized probabilities of range augmentation. A percentage of the montane gradient (m) is added as a uniformly or increasing with range size (small, medium, large). Half is added to each range endpoint until the montane boundaries are reached. Abbreviations: D = decreasing; LP = low plateau (* indicates a mid-elevation peak that is less than 25% greater than the lower limit); MP = mid peak. **Bold** indicates a significant change in richness pattern (i.e. decreasing to mid peak or mid peak to decreasing or low plateau).

Probability	Percentage ¹	Peru	Manu	Ecu	Col	Ven	Maz	Mix	Jal	WI	UT	Yos	NG
Empirical		D	D	MP	D	D	MP	D	MP	MP	MP	MP	D
All	10	D*	D	MP	D	LP	MP	D	MP	MP	MP	MP	D
	30	LP	LP	LP	LP	LP	MP	LP	MP	MP	MP	LP*	LP*
	50	LP	LP	LP	MP	LP	MP	LP	MP	MP	LP*	LP*	LP
	70	LP	LP	LP	MP	LP	MP	LP	MP	LP*	LP*	LP*	LP
All	20, 10, 0	D	D	MP	LP	LP	MP	D	MP	MP	MP	MP	D
	30, 20, 10	LP*	LP*	LP	LP	LP	MP	LP	MP	MP	MP	MP	LP
	50, 25, 10	LP*	LP*	LP	LP*	LP	MP	LP*	MP	MP	LP*	MP	LP
	70, 50, 30	LP	LP	LP	LP*	LP	MP	LP*	MP	LP*	LP*	LP*	LP*
30, 20, 10	20, 10, 0	D	D	MP	D	D	MP	LP	MP	MP	MP	MP	D
	40, 30, 10	D	D	MP	D	D	MP	LP	MP	MP	MP	MP	LP
	50, 40, 20	LP	LP	MP	LP	LP	MP	LP	MP	MP	MP	MP	LP
	70, 50, 30	LP*	LP*	MP	LP	LP*	MP	LP	MP	MP	MP	MP	LP*
50, 30, 10	20, 10, 0	D	D	MP	LP*	D	MP	LP	MP	MP	MP	MP	D
	40, 30, 10	D	D	MP	LP*	D	MP	LP	MP	MP	MP	MP	LP
	50, 40, 20	LP	LP	LP*	LP*	LP	MP	LP*	MP	MP	MP	MP	LP
	70, 50, 30	LP	LP*	LP	MP	LP	MP	LP*	MP	MP	MP	MP	LP*

70, 50, 20	20, 10, 0	D	D	MP	LP	D	MP	LP	MP	MP	MP	MP	D
	40, 30, 10	D	D	MP	LP	D	MP	LP	MP	MP	MP	MP	LP
	50, 40, 20	LP	LP	LP*	LP*	LP	MP	LP*	MP	MP	MP	MP	LP
	70, 50, 30	LP	LP	LP	MP	LP	MP	LP*	MP	MP	MP	MP	LP*
100, 60, 40	20, 10, 0	D	D	MP	LP	D	MP	LP	MP	MP	MP	LP*	D
	40, 30, 10	D	D	MP	LP	D	MP	LP*	MP	MP	MP	LP*	LP
	50, 40, 20	LP	LP	LP*	LP	LP	MP	LP*	MP	MP	MP	LP*	LP
	70, 50, 30	LP	LP	LP	LP*	LP	MP	LP*	MP	LP*	MP	LP*	LP

[†]Percent of Montane Gradient, for example 10% for each gradient is equal to 450m (Peru), 380m (Manu), 360m (Ecuador), 280m (Colombia), 500m (Venezuela), 230m (Mazateca), 250m (Mixteca), 260m (Jalisco), 400m (White-Inyo), 280m (Henrys), 310 (Yosemite), and 450m (New Guinea).

APPENDIX S3. Correlation statistics of abundance and species richness estimates, and linear regression statistics for abundance with elevation along elevational gradients of bats, emphasizing that elevations with higher abundances tend to have higher richness and that generally abundance decreases with elevation for those data sets with decreasing richness.

Data Set	Abundance & Richness		Abundance & Elevation	
	r	p	r^2	p
Ecuador (Carrera-E., 2003)	0.9350	0.0197	-0.5243	0.1666
SW Colombia (Fawcett, 1994)	0.4725*	0.4217	-0.9761*	0.0016
Peru (Graham, 1983)	correlated	NA	-0.80*	< 0.01
Manu, Peru (Patterson <i>et al.</i> , 1986)	0.9200	NA	-0.63	NA
Leyte (Heaney <i>et al.</i> , 1989)	0.1401*	0.8222	-0.5270*	0.1649
Negros (Heaney <i>et al.</i> , 1989)	-0.0067*	0.9914	-0.8939*	0.0152
Luzon (Heaney <i>et al.</i> , 1999)	0.7942*	0.0592	-0.7700*	0.0216
Utah (Mollhagen & Bogan, 1997)	0.6155*	0.1913	0.0064*	0.8807
Colombia (Muñoz Arango, 1990)	0.9533	0.0032	-0.6364	0.0572
E Mexico (Navarro & Leon, 1995)	correlated	NA	-0.8630*	0.0260
Biliran (Rickart <i>et al.</i> , 1993)	-0.1030*	0.8970	-0.9160*	0.0840
Maripipi (Rickart <i>et al.</i> , 1993)	-0.3556*	0.7685	-0.5789*	0.4495

*Corrected for sampling effort by authors or herein (e.g. # of captures / # days of sampling)
NA = not available in publication