RESEARCH PAPER

Global analysis of reptile elevational diversity

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ABSTRACT

Aim Latitudinal- and regional-scale studies of reptile diversity suggest a predominant temperature effect, unlike many other vertebrate richness patterns which tend to be highly correlated with both temperature and water variables. Here I examine montane gradients in reptile species richness with separate analyses of snakes and lizards from mountains around the world to assess a predominant temperature effect and three additional theories of diversity, including a temperature–water effect, the species–area effect and the mid-domain effect (MDE).

Location Twenty-five elevational gradients of reptile diversity from temperate, tropical and desert mountains in both hemispheres, spanning 10.3° N to 46.1° N.

Methods Elevational gradients in reptile diversity are based on data from the literature. Of the 63 data sets found or compiled, only those with a high, unbiased sampling effort were used in analyses. Twelve predictions and three interactions of diversity theory were tested using nonparametric statistics, linear regressions and multiple regression with the Akaike information criterion (AIC).

Results Reptile richness and, individually, snake and lizard richness on mountains followed four distinct patterns: decreasing, low-elevation plateaus, low-elevation plateaus with mid-elevation peaks, and mid-elevation peaks. Elevational reptile richness was most strongly correlated with temperature. The temperature effect was mediated by precipitation; reptile richness was more strongly tied to temperature on wet gradients than on arid gradients. Area was a secondary factor of importance, whereas the MDE was not strongly associated with reptile diversity on mountains.

Main conclusions Reptile diversity patterns on mountains did not follow the predicted temperature–water effect, as all diversity patterns were found on both wet and dry mountains. But the influence of precipitation on the temperature effect most likely reflects reptiles' use of radiant heat sources (sunning opportunities) that are more widespread on arid mountains than wet mountains due to lower humidity, sparser vegetation and less cloud cover across low and intermediate elevations.

Keywords
Climate, ectotherm, environmental gradient, lizards, mountains, snakes, species–area relationship, temperature, water availability.

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INTRODUCTION

Effective methods used to preserve biodiversity rely on a better comprehension of the mechanisms creating and maintaining biodiversity. Large-scale biodiversity patterns have shown a strong concordance with combined temperature and water variables, particularly for vertebrates (see the top part of Fig. 5; Mittelbach *et al.*, 2001; Hawkins *et al.*, 2003a; Currie *et al.*, 2004; Whittaker *et al.*, 2007). In contrast, large-scale diversity of rep-

tiles appears to be largely correlated with temperature alone (Kiester, 1971; Schall & Pianka, 1978; Currie, 1991; Meliadou & Troumbis, 1997; Hawkins *et al.*, 2003a; Rodríguez *et al.*, 2005; Whittaker *et al.*, 2007; Qian & Ricklefs, 2008). Reptile diversity is particularly high in arid regions of the world, for instance in North American deserts (Kiester, 1971; Schall & Pianka, 1978), southern Europe (Meliadou & Troumbis, 1997; Rodríguez *et al.*, 2005; Whittaker *et al.*, 2007) and inland Australia (Schall & Pianka, 1978). Recent population evidence for lizards in Europe

suggests that reptiles might benefit from increased temperatures from global warming (Chamaillé-Jammes *et al.*, 2006). Such results imply that the effects of climate change may be very different across vertebrate lineages.

Outliers to well-known patterns can lead to a better understanding of the mechanisms underlying a trend. Intuitively, a strong tie between reptile richness and ambient temperature is understandable given that ectotherms rely heavily on external temperature to regulate their body temperature (Porter & Gates, 1969). But reptile biodiversity is the least studied among terrestrial vertebrates, exhibited by lack of global diversity analyses recently published for birds (Hawkins *et al.*, 2003b; Orme *et al.*, 2005; Rahbek *et al.*, 2007), mammals (Ceballos & Ehrlich, 2006) and amphibians (Stuart *et al.*, 2004; Grenyer *et al.*, 2006). We know that reptile diversity increases with decreasing latitude, but most of these analyses do not extend into the lowest latitudes (Fischer, 1960; Kiester, 1971; Arnold, 1972; Schall & Pianka, 1978; Anderson, 1984; Currie, 1991; Gaston *et al.*, 1995; Meliadou & Troumbis, 1997; Reed, 2003; Whittaker *et al.*, 2007; Araújo *et al.*, 2008). It might be that the temperate skew in reptile analyses, which tend to end within arid latitudes, has led to a different view of diversity drivers from those in other groups.

A few regional analyses of reptile biodiversity have suggested an influence of evolutionary or regional climatic history (Vitt & Pianka, 2005; Araújo *et al.*, 2008; Qian & Ricklefs, 2008). At local spatial scales, climate (Heyer, 1967; Lambert & Reid, 1981; Fu *et al.*, 2007), spatial and habitat heterogeneity and length of growing season have been linked to reptile diversity (Heyer, 1967; Pianka, 1967), whereas topographic heterogeneity and seasonality have limited predictive ability in studies of reptile species richness at larger scales (Kiester, 1971; Rodríguez *et al.*, 2005; Qian & Ricklefs, 2008). One way to see if temperature is truly a pervasive driver of reptile diversity is to examine smaller spatial scales along multiple elevational gradients and to examine multiple diversity hypotheses simultaneously. Elevational tests benefit from a large number of replicates with contrasting environmental gradients in temperature, precipitation, area and seasonality from various latitudes and biogeographic regions. Here I test 12 predictions of four potential drivers of reptile biodiversity including temperature alone, a temperature–water effect, the species–area effect (also a surrogate for habitat heterogeneity) and the mid-domain effect (MDE). Three potential interactions among variables were also tested (Table 1). Similar analyses for birds, bats and small terrestrial mammals have shown a strong influence of the temperature–water effect on elevational diversity (McCain, 2005, 2007b, 2009), therefore a contrast with reptiles will uncover whether reptile trends are unique among terrestrial vertebrates.

Table 1 Currently testable hypotheses and predictions for reptile diversity on elevational gradients, including three possible interactions.

Hypothesis	Theory	Montane testable predictions
Area	Diversity is positively related to land area	1. Diversity at each 100-m elevation band will be positively related to area at that elevation for regional-scale studies 2. Removal of the area effect results in a large elevational diversity shift
Mid-domain effect (MDE)	Unimodal diversity within a bounded domain; highest diversity at the midpoint of the domain	1. Elevational diversity unimodal on all mountains 2. Empirical diversity at each 100-m band positively related to the MDE-predicted diversity at that elevation 3. Deviations of maximum diversity away from the midpoint of mountain are randomly distributed 4. Strong, significant relationship between MDE model fit (r^2 value) and average species range size/domain size ratio
Temperature	Diversity is positively related to temperature†	1. Elevational diversity decreasing on all mountains 2. Diversity at each 100-m band positively related to average annual temperature at that elevation 3. No statistical difference between the temperature–diversity relationship on humid and arid mountains
Temperature and H$_2$O (ECM*)	Diversity is positively related to productivity‡	1. Elevational diversity highest in warm, wet conditions: unimodal on arid mountains; decreasing or low-plateau on humid mountains 2. Diversity highly related to temperature on wet mountains, relationship weaker on arid mountains 3. On arid mountains, maximum diversity occurs with wetter, cooler conditions than at the mountain base
Interactions	I: Area–MDE II: Area–MDE–temperature III: Area–MDE–ECM	I. Area-corrected diversity improves fit to MDE II. Multiple regression and AIC quantify relative contribution III. If area is a primary factor in II above, then area-corrected data changes the fit to MDE and ECM

*ECM, elevational climate model. See text for definition. AIC, Akaike information criterion.
†Another temperature hypothesis is the metabolic theory of ecology; this was tested elsewhere (McCain & Sanders, 2010) (see Discussion).
‡A positive relationship with productivity and diversity would be the ideal montane hypothesis, but is currently not testable here given a lack of sufficiently small-scale, global data for net primary productivity or precipitation.

MATERIALS AND METHODS

Reptile elevational data

I found papers on reptile elevational diversity by searching BIOSIS and Web of Science using keyword combinations including reptile, herpetofauna, snakes, lizards, diversity, species richness, elevation (-al) and altitude (-inal). Only studies presenting the elevational diversity patterns or the elevational ranges of all reptiles, snakes or lizards were used in the quantitative analyses. Data sets were selected based on several a priori sampling criteria that have been used in previous analyses of small mammals (McCain, 2005), bats (McCain, 2007b) and birds (McCain, 2009) to ensure robust analyses (Rahbek, 2005; Nogués-Bravo et al., 2008; see Appendix S1 in Supporting Information). First, data sets were included in quantitative analyses only if sampling covered at least 70% of the elevational gradient. This is a critical restriction for studies with limited sampling at lower elevations, since discernment of pattern is strongly contingent on diversity estimates in the lowest 600 m (McCain, 2005; Nogués-Bravo et al., 2008). In contrast, limited sampling at the highest elevations is less critical since diversity always decreased monotonically above some threshold intermediate elevation. Second, the sampling effort needed to be substantial (many days or years per elevation and many elevations across the gradient) and not strongly elevationally biased. Elevational sampling bias was calculated by assessing the correlation between sampling (e.g. sampling days or hours) and elevation (100-m bands) when the appropriate data were published. In practice, sampling effort and bias could be difficult to assess due to the highly variable nature of sampling explanations in the published studies, particularly because many of these studies were regional compilations of the reptile fauna from varied researchers. Third, studies that discussed wide-scale habitat disturbance or elevationally correlated disturbance were not included in the analyses. Fourth, a gradient needed a minimum of seven species of reptiles, snakes or lizards to be included. In cases where the authors stated there were elevations at the top or bottom of the mountain which were undersampled, these elevations were not included in the analyses (as long as ≥ 70% of the gradient was well surveyed). No minimum mountain size was required a priori, although all the included studies did span large elevational gradients in reptile distributions (average 2800 m, minimum 1260 m, maximum 4600 m). Two studies conducted by Grinnell are quite old and may have some differences from modern classifications and therefore distributions (Grinnell & Storer, 1924; Grinnell et al., 1930). These were included in the analyses because of the strong sampling effort, the robustness of Grinnell's work to modern changes in taxonomy and range shifts (Moritz et al., 2008) and the negligible influence of small range changes on the overall species richness pattern in simulations (McCain, 2007b).

Most studies that calculated elevational diversity used range interpolation, which assumes a species was present between its highest and lowest reported elevations. For standardization, all additional compilations and analyses used the same method.

Interpolation aids in overcoming some limitations of under-sampling, but may also inflate estimates of species richness at mid-elevations (Colwell & Hurtt, 1994; Grytnes & Vetaas, 2002). Species richness was then calculated based on the number of ranges occurring within 100-m elevational bands from the lowest elevation to the highest elevation (e.g. 0–100 m, 100–200 m, etc.), unless a larger resolution was used in a particular study without raw data for reanalysis. For those studies that did not publish species elevational ranges, diversity patterns were extracted from figures or tables.

Four diversity patterns were clearly discernible: decreasing, low plateau, low plateau with a mid-elevation peak, and mid-elevation peak (see top of Fig. 1). Mid-elevation peaks have a unimodal diversity maximum, which includes at least 25% more species than at the lowest and highest elevations and occurs at least 400 m above the lowest elevation. Low-plateau patterns exhibit more than 300 m of consecutively high richness at the lowest elevations, and thereafter show monotonically decreasing species richness. Low-plateau patterns with a mid-elevation peak exhibit more than 300 m of high richness across low elevations with maximum diversity found more than 300 m above the lowest elevation, and they differ from the rest of the plateau by at least three species. Decreasing patterns exhibit generally declining species richness with increasing elevation. These four categories are easily calculated based on the diversity curve and are mutually exclusive; more patterns were possible but only these four were necessary with the current data.

Elevational gradients were studied at a local scale – field transects of standardized samples along single elevational gradients – or a regional scale, including data compiled from sight and capture records, specimen records and field notes for an entire mountain or mountainous region. Each scale has its benefits and drawbacks. For instance, regional richness may be highly influenced by area and sampling (Lomolino, 2001; Rickart, 2001; Rahbek, 2005; McCain, 2007b) whereas short-term transects may miss rare species or undersample elevational ranges. Therefore, the trends at the two scales could differ quantitatively and qualitatively. Like all analyses of existing data sets, there may be geographic, sampling and scale bias due to the uncoordinated nature of reptile diversity studies on mountains. Unfortunately, this cannot be remedied here.

The relationships among reptile clades have undergone major changes within the last few decades based on differences in phylogenies using morphological and/or genetic data (Townsend et al. 2004 and references therein). The traditional split between lizards and snakes is no longer valid, because snakes are a monophyletic group nested within a lizard clade (e.g. anguimorphs). Nonetheless, many publications still contrast lizard and snake groupings in diversity studies, even recent works (e.g. Savage, 2002; Fu et al., 2007; Kryštufek et al., 2008). To encompass both a monophyletic perspective and a useful comparative tool, all elevational richness patterns will be presented for the monophyletic clades (reptiles, iguanids, geckos, anguimorphs and scincomorphs) and for the functional groupings of lizards and snakes. Tests of diversity hypotheses will be contrasted for combined reptiles, and individually for lizards
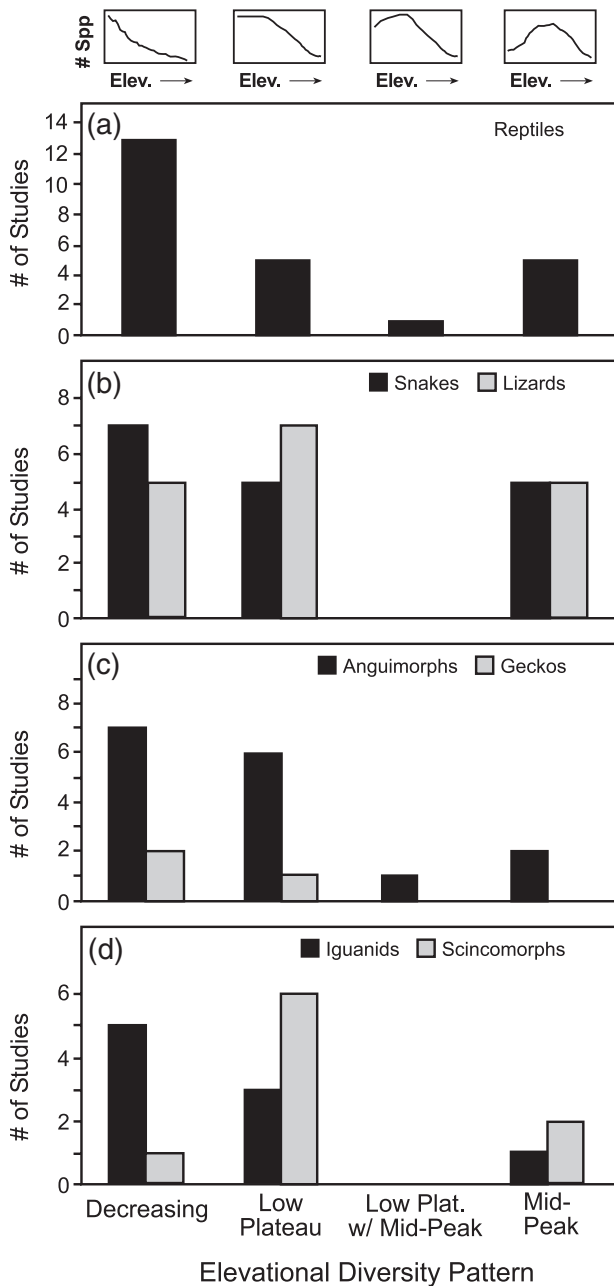
Figure 1 Reptile studies demonstrating four elevational richness patterns: decreasing, low plateau, low plateau with a mid-elevation peak and mid-elevation peak (a: *n* = 24; see text for definitions). Comparison of patterns for snakes and lizards (b: *n* = 17) and for monophyletic groups: anguimorphs (including snakes), geckos (c: *n* = 21 and 3, respectively), iguanids and scincomorphs (d: *n* = 9 and 9, respectively).

and snakes, due to the low sample sizes among monophyletic reptile clades.

Diversity hypotheses and testing methods

Many hypotheses proposed to explain large-scale patterns in species richness apply to elevational richness patterns. Several

are currently testable, including the species–area effect, the MDE, a temperature-only effect, a temperature–water effect (elevational climate model, ECM), and some combinations of these hypotheses (Table 1). Below I will briefly describe each hypothesis and its elevational predictions.

Area

The species–area relationship (SAR) asserts that as survey area increases, the number of species encountered increases (Terborgh, 1973; Rosenzweig, 1992, 1995). On mountains, the SAR predicts that elevational bands covering a greater area (e.g. low-lands) should harbour more species than elevational bands covering a smaller area (e.g. mountain tops) (Rahbek, 1997; McCain, 2007a). The SAR is based on the assumption that at regional and global scales extinction rates should decrease, and speciation rates should increase, with area due to the increased likelihood of barrier formation and increased population densities (Rosenzweig, 1995, and references therein). At small spatial scales, Rosenzweig (1995) argued that habitat diversity, and the strong ties of particular species to habitat, drive the local SAR. The elevational diversity patterns on mountains may fall somewhere on the continuum between these two scales and processes.

The SAR examines the influence of area between species richness samples from different spatial extents. In the context of elevational gradients, the regional-scale elevational gradients, where samples have been compiled from trapping records, specimen records and field notes for an entire mountain or mountainous region, could have a large area effect (Rahbek, 1997; Brown, 2001; Lomolino, 2001; Willig *et al.*, 2003; McCain, 2005). Local studies, in contrast, attempt to minimize the influence of area by estimating species richness among standardized samples along an elevational gradient (Lomolino, 2001; McCain, 2005). Local diversity analyses could be influenced by higher immigration from a larger regional community (e.g. a mass effect or indirect area effect; Romdal & Grytnes, 2007). This indirect effect is thought to be less pervasive (Lomolino, 2001), and empirical analyses found no general patterns (Romdal & Grytnes, 2007). Additionally, McCain (2005) found that the potential influence of area was markedly lower in local elevational gradients than in regional ones for terrestrial small mammals, and Sanders *et al.* (2003) found that area was negatively correlated with alpha diversity along three elevational gradients. For these reasons, and because of the different proposed drivers of the direct and indirect area effects, only regional data sets are considered in these analyses, as in previous work (McCain, 2007a, 2009).

The SAR leads to two predictions: (1) a positive, significant relationship between reptile diversity and area across 100-m elevational bands (Rahbek, 1997; McCain, 2007a), and (2) area standardization should result in a large change in the elevational diversity pattern (McCain, 2007a). Area estimates were derived from the original study (i.e. Nathan & Werner, 1999; Fu *et al.*, 2007) or calculated using ArcGIS (following McCain, 2007a). The SAR follows a curvilinear relationship in arithmetic space:

diversity increases rapidly over small areas but, once successively large areas are examined, diversity plateaus (e.g. Preston, 1962; Conner & McCoy, 1979; Rosenzweig, 1995). Conner & McCoy (1979) found that some SARs were better characterized by linear relationships; therefore, I tested both a linear [no. of species = constant × area ($S = cA$)] and a curvilinear ($\log S = z \log A + \log c$) area relationship using linear regression (e.g. Conner & McCoy, 1979; Rosenzweig, 1995; McCain, 2007a).

Area standardization was based on calculating area-corrected diversity curves using the power function ($S = cA^z$) with a comparison of two z-values: an average reptile, snake or lizard z-value and the canonical z-value proposed by Preston [0.25; Preston, 1962 (0.262)]. The average z-value is calculated from log–log SAR regression using all estimates of diversity for each 100-m band across all gradients from each reptile group. This was found to be a robust estimate of taxonomic group z-values, as it reduces the influence of some steep slopes on some montane gradients (McCain, 2007a). SAR regressions on individual mountains can be very steep, encompassing z-values much higher than common z-values (e.g. 0.12–0.35; Rosenzweig, 1995). For instance, over 40% of the reptile z-values are greater than 0.6. The area adjustment simply involves solving the power function equation for the constant (c) when using known values for z, number of species, and the area estimate at each 100-m elevational band (McCain, 2007a).

The MDE

The MDE assumes that spatial boundaries (e.g. the lowest and highest elevation in a region; or the base and top of a mountain) cause more overlap of species ranges toward the centre of an area where many large- to medium-sized ranges must overlap but are less likely to abut the edge of the area (Colwell et al., 2004, 2005, and references therein). On mountains, MDE predicts (McCain, 2004, 2005, 2007a,b): (1) predominantly unimodal diversity curves with maximum diversity at the midpoint of the mountain (point midway between the lowest and highest elevation; chi-square goodness of fit test); (2) strong, positive associations between predicted diversity based on 50,000 Monte Carlo simulations (mid-domain null; McCain, 2004) and empirical diversity at each 100-m elevational band (linear regression); (3) deviations in maximum diversity away from the midpoint of the mountain should be randomly distributed among gradients (Student's t-test); and (4) strong, significant relationships between MDE fit (r^2 value from linear regression) and a ratio of the average range size to elevational gradient length (linear regression; e.g. Dunn et al., 2007).

Climate I: temperature

A positive relationship between temperature and diversity has been shown for many large-scale diversity patterns, although underlying mechanistic hypotheses differ (e.g. Pianka, 1966; Hawkins et al., 2003a; Evans et al., 2005; Storch et al., 2005). On mountains, temperature decreases monotonically by an average of 0.6 °C per 100-m elevational gain (moist adiabatic lapse rate;

Barry, 1992). If temperature is a main determinant of reptile diversity, then the predictions are: (1) predominantly decreasing patterns in diversity (chi-square goodness of fit test); (2) strong, positive correlations between elevational diversity and temperature (linear regressions); (3) similarly strong and positive temperature–diversity relationships on arid and wet mountains (Mann–Whitney U-test; McCain, 2009). The metabolic theory of ecology (MTE) also predicts a linear relationship between diversity and temperature with a specific slope of 0.65 (e.g. Allen et al., 2002), but this relationship is tested elsewhere for snakes and lizards (see McCain & Sanders, 2010).

Climate II: temperature and water

Productivity has also been strongly and positively linked to diversity (e.g. Mittelbach et al., 2001; Hawkins et al., 2003a; Evans et al., 2005; Storch et al., 2005). Several mechanisms attempt to explain this relationship and are nicely summarized in Evans et al. (2005); many of these are not testable directly here due to a lack of abundance data and small-scale productivity/water data. However, an elevational climate model (ECM) was recently proposed (McCain, 2007b) and supported for bats and birds (McCain, 2007b, 2009), where, in a verbal construct, separate gradients in temperature and water availability on mountains in different climatic regimes predict divergent elevational diversity patterns (McCain, 2007b, 2009). Temperature decreases with elevation on all mountains, while rainfall and water availability involve more complex relationships with elevation depending on the local climate (see ahead to the top of Fig. 5). On arid mountains (e.g. south-western US mountains), water availability is highest at intermediate elevations where rainfall and soil water retention is highest and evaporation lowest. Water availability drops off dramatically towards the low elevations where high temperature and high evaporation exceed rainfall inputs, leading to arid habitats. Towards the upper elevations water availability also drops toward the mountain top, although less dramatically, as runoff is high due to shallow soils and exposed rock, and precipitation is seasonally inaccessible as snow and ice. On humid mountains (e.g. the eastern Andes), water availability is high across a broad base of lower elevations and only decreases toward the tops of the mountains, again due to higher runoff and decreases in rainfall. Under the ECM, reptile species richness is predicted to be positively related to the warmest and wettest conditions elevationally, predicting: (1) mid-elevation peaks in reptile species richness on arid mountains, and decreasing and low plateaus in diversity on warm, wet mountains (chi-square test of homogeneity), and (2) a stronger relationship between diversity and temperature on mountains in humid climates compared with mountains in arid climates (linear regressions and Mann–Whitney U-test; see Climate I: temperature above). Each mountain is assigned an arid or humid mountain classification depending on its base vegetation (arid = humidity index < 0.50, wet > 0.50 humidity index; UNEP's (1997) World Atlas of Desertification classification).

Interactions

Three hypothesis interactions can be tested for variables quantified at the same scale as reptile diversity (i.e. 100-m elevational bands): area, MDE and temperature. An interaction of area and the MDE predicts that: (1) maximum diversity is consistently skewed from the mountain midpoint toward elevations with the most area (paired Student's *t*-test), and (2) once diversity has been standardized for area, then the fit to the MDE should be significantly improved (Mann–Whitney *U*-test) (Sanders, 2002; McCain, 2007a, 2009). Interactions of area, the MDE and temperature can be simultaneously tested using all possible multiple regression models and fits compared using the Akaike information criterion (AIC). The AIC weighs both model fit and parameter complexity, thus determining models that parsimoniously detect the strongest relationships (Burnham & Andersen, 2002). Models with the highest AIC weight identify the strongest relationships between measured variables and elevational diversity. I use multi-model inference to assess the importance of each variable by summing the Akaike weights across all models (Burnham & Andersen, 2002). Finally, if area is more related to reptile diversity than temperature and MDE in multiple regressions, then the precedence of the area effect is established. In that case, area-corrected diversity curves can be used to reassess the relative fits of the ECM and MDE. Lastly, spatial autocorrelation exists both in reptile elevational diversity and environmental data, which may influence the results of these analyses, although not necessarily (Diniz-Filho *et al.*, 2003). Due to the length and complexity of the current analyses, spatial autocorrelation analyses and influences of multiple tests (e.g. Bonferroni corrections) will be treated in a separate paper.

RESULTS

Of the 87 studies of reptiles on mountains found in the literature, 54 studies detailed elevational diversity along 63 montane gradients. Only 25 combined reptile gradients and 17 snake and lizard gradients met a priori sampling criteria and had robust content for quantitative analyses (Appendices S1 & S2). Some of the combined reptile gradients could not be separated into snake and lizard analyses ($n = 8$). To adequately portray reptile patterns, all possible combined analyses are presented. For 17 of those data sets, snakes and lizards could be analysed separately.

Robust gradients covered mountainous regions from various climates (tropical, subtropical, arid, temperate), latitudes (10.3° N to 46.1° N), longitudes (121.5° W to 100° E), mountain heights (1260–7556 m) and scales (local and regional) (Fig. 2).

Four reptile diversity patterns were represented (Fig. 1a): 54% decreasing, 21% low-elevation plateaus (LP), 4% low-elevation plateaus with mid-elevation peaks (LPMP) and 21% unimodal with mid-elevation peaks (MP) for combined reptiles. There were significantly more decreasing patterns and fewer LPMP than expected ($\chi^2 = 12.67$, d.f. = 3, $P = 0.0054$). Snakes exhibited a similar distribution to all reptiles, whereas lizards exhibited more LP patterns than reptiles or snakes (Fig. 1b; $n = 17$ and 17, respectively), although not significantly more ($X^2 = 4.66$, d.f. = 6, $P = 0.5851$). Elevational diversity patterns varied among monophyletic reptile groups (Fig. 1c,d). Iguanids (e.g. iguanas, anoles) and anguimorphs (e.g. monitor lizards, snakes) exhibited a similar distribution of patterns to combined reptiles. Geckos exhibited predominantly decreasing and LP patterns, whereas scincomorphs (e.g. skinks, whiptails) predominately exhibited LP patterns. Due to low sample sizes for monophyletic groups, further quantitative analyses will be restricted to combined reptiles, and individually for the functional groups of snakes and lizards.

The distribution of elevational diversity patterns differed slightly between the Western and Eastern hemispheres (Fig. 2). Eastern-hemisphere reptiles displayed more mid-elevation peaks in diversity, although not significantly more than the Western Hemisphere ($X^2 = 2.08$, d.f. = 3, $P = 0.5560$). There was no relationship between the elevation of maximum diversity and latitude ($r^2 = 0.0322$, $P = 0.4017$, $n = 24$), even when examined for snakes and lizards individually. Unfortunately, there were few sufficiently sampled data sets from tropical latitudes, but among those ($n = 6$) five were decreasing and one was a LP pattern. There were few local data sets that met the sampling criteria ($n = 4$; Appendix S2), so both scales are combined in the presented analyses. The justification for combining scales was based on statistical tests corrected for unequal sample sizes, which showed no significant differences between the scales. The local- and regional-scale data sets were not significantly different in their distribution of elevational diversity patterns ($X^2 = 0.13$, d.f. = 3, $P = 0.988$), as each had about 50% decreasing, 20% LP, 20% MP and 5% or fewer LPMP. And the reptile data sets at the local and regional scale were not significantly different in their
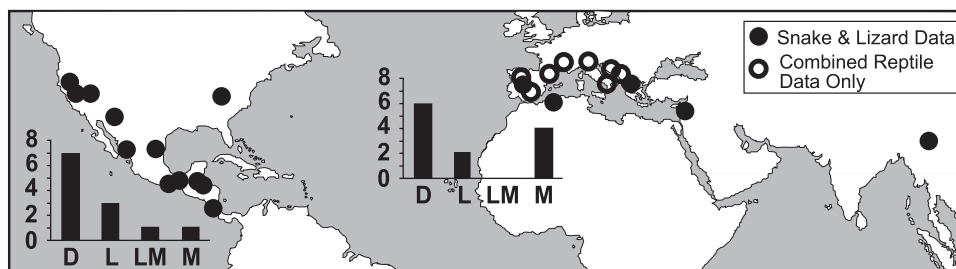

Figure 2 The distribution of reptile study sites and a comparison of the four main elevational richness patterns in the western and eastern hemispheres (D = decreasing, L = low plateau, LM = low plateau with mid-elevation peak, M = mid-elevation peak; see text for definitions).

fits to the predictions of area, MDE or temperature (area, $t = -0.73$, d.f. $= 3.72$, $P = 0.51$; MDE, $t = 0.98$, d.f. $= 3.6$, $P = 0.39$; temperature, $t = -1.78$, d.f. $= 3.12$, $P = 0.17$). Tests of hypothesis predictions and interactions (Table 1) are detailed sequentially below:

Area

Support for the area predictions was mixed (Table 2). Positive, significant SARs were detected in most studies (Fig. 3a). The average r^2 value for linear SAR in reptiles was 0.38 and for curvilinear analyses was 0.65, with nearly identical values for snakes and lizards (Appendix S3). Significant changes in diversity pattern with area-corrected diversity curves occurred in over half of reptile gradients, half of snake gradients and less than half of lizard gradients (Table 2, Appendix S3). Lastly, among area-corrected curves, large shifts (> 300 m) in the location of maximum diversity were only detected in about a quarter of the studies (Table 2, Appendix S3).

The MDE

Reptile, snake and lizard diversity had low concordance with the four MDE predictions. Elevational diversity was not uniformly unimodal (Fig. 1). Fits to the MDE were generally poor: average r^2 value $= 0.11$ for reptiles, 0.03 for snakes and 0.04 for lizards (Fig. 3b, Appendix S4). Deviations in maximum diversity were not randomly distributed around the mountain midpoint, but were shifted to significantly lower elevations (reptiles, $t = -9.42$, $P < 0.0001$, $n = 24$; snakes, $t = -9.12$, $P < 0.0001$, $n = 17$; lizards, $t = -7.80$, $P < 0.0001$, $n = 17$). Lastly, there was no significant relationship between average snake and lizard range size relative to gradient length and fit to MDE (snakes, $r^2 = 0.0115$, $P = 0.69$; lizards, $r^2 < 0.0001$, $P = 0.98$). Reptiles were significant, although

the relationship was not particularly predictive (reptiles, $r^2 = 0.2302$, $P = 0.04$).

Climate I: temperature

Support for the three temperature predictions was mixed. Reptile diversity did exhibit predominantly decreasing diversity patterns, as predicted by decreasing temperature on mountains, but the frequencies of decreasing, LP, and MP patterns among lizards and snakes were more even (Fig. 1). Reptile elevational diversity was positively and significantly related to temperature on most gradients, although the strength of the relationship was highly variable, ranging from r^2 values of 0–0.97 (Fig. 4, Appendix S5). And, contrary to temperature predictions, the strength of the temperature–diversity relationship was contingent upon precipitation regime. The temperature–diversity relationship was significantly stronger on wet mountains than dry mountains (reptiles, Mann–Whitney U-test $Z = 3.15$, $P < 0.001$, $n = 23$; snakes, $Z = 2.93$, $P = 0.002$, $n = 16$; lizards, $Z = 1.84$, $P = 0.033$, $n = 16$).

Climate II: temperature and water (ECM)

The predictions of the ECM were not consistently supported. All diversity patterns were represented on wet and dry mountains
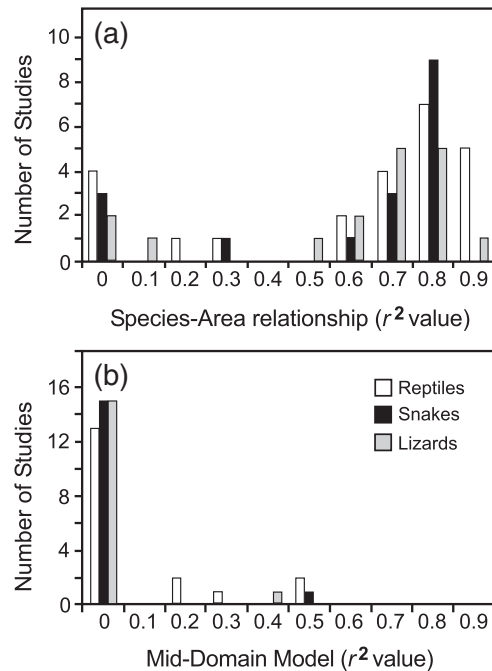

Figure 3 The number of studies with various strengths of fit to the species–area relationship and mid-domain effect using elevational richness of reptiles, snakes and lizards. Strength of fit is measured with r^2 values from linear regression analyses. (a) The variation in fit to the log–log species–area relationship among studies of reptiles (mean $r^2 = 0.65$), snakes (mean $r^2 = 0.65$) and lizards (mean $r^2 = 0.64$). (b) The variation in fit to the mid-domain model among studies of reptiles (mean $r^2 = 0.11$), snakes (mean $r^2 = 0.04$) and lizards (mean $r^2 = 0.04$).
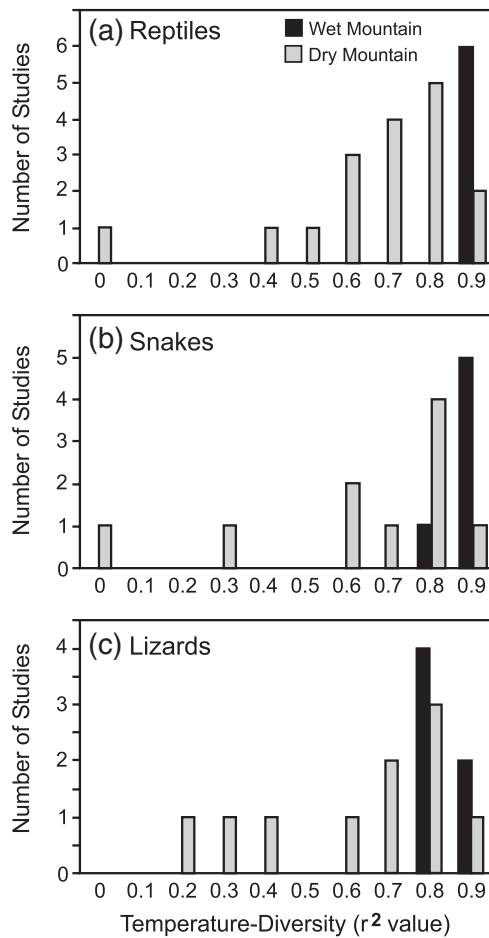
Table 2 The percentage of reptile studies on elevational gradients that show positive species–area effects, including a significant, positive log area–log richness relationship, a large change in the elevational diversity pattern with area standardization (e.g. a decreasing trend changes to a mid-elevation peak), and a large (> 300 m) shift in the location of maximum diversity with area standardization

Taxon	% Significant log–log	% Diversity change		% Large shift in maximum diversity	
	Area effect	Taxon z	z = 0.25	Taxon z	z = 0.25
Reptiles	79.2%	57.9%	73.7%	21.1%	31.6%
Snakes	82.3%	50.0%	50.0%	21.4%	35.7%
Lizards	76.5%	15.4%	61.5%	0.0%	38.5%

The analyses for area standardization among elevational bands contrasts two z-values in the species–area equation: an average z-value for all gradients of a taxonomic grouping (taxon z), and the z-value based on Preston, 1962 (z = 0.25). See text for more description of the area analyses and Appendix S3 for species–area statistics of individual gradients.

Figure 4 The number of studies with various strengths of fit to the temperature–diversity relationship using elevational patterns for reptiles, snakes and lizards. Strength of fit is measured with r^2 values from linear regression analyses. This relationship is stronger on humid mountains than dry mountains: (a) reptiles humid $r^2 = 0.93$, $n = 6$; dry $r^2 = 0.71$, $n = 17$; (b) snakes humid $r^2 = 0.92$, $n = 6$; dry $r^2 = 0.66$, $n = 10$; (c) lizards humid $r^2 = 0.87$, $n = 6$, dry $r^2 = 0.67$, $n = 10$.

for combined reptiles, snakes and lizards (Fig. 5). Decreasing and LP patterns were not predominantly found on wet mountains and mid-elevation peaks were not predominantly found on dry mountains for reptiles ($X^2 = 2.19$, d.f. = 3, $P = 0.54$), snakes ($\chi^2 = 0.03$, d.f. = 2, $P = 0.98$) or lizards ($X^2 = 0.03$, d.f. = 2, $P = 0.98$). But, as predicted, the temperature–diversity relationship was stronger on humid rather than dry mountains (Fig. 4).

Interactions

An area–MDE interaction was not supported. There was no significant increase in MDE fit when calculated with area-corrected diversity; mean r^2 values were nearly identical (Appendix S4). Reptile MDE fits slightly decreased with area correction (lowered by 0.03–0.05). Snake and lizard MDE fits slightly increased with area correction (increased by 0.01–0.07 and

0.002–0.004, respectively). Akaike weights determined that the best multiple regression model for reptile elevational diversity included temperature, area and MDE (interaction II; all variables log-transformed for normality) with temperature contributing the most to the model, followed by area then MDE [$r^2 = 0.49$, $P < 0.0001$, $n = 449$ (elevation bands)]. The best models for snakes and lizards also included all three variables, with temperature emerging as the strongest single factor, followed by MDE, then area (snakes, $r^2 = 0.49$, $P < 0.001$; lizards, $r^2 = 0.30$, $P < 0.001$, respectively). In all cases, summed AIC weights (> 0.90) indicated that all variables were important. Since temperature – not area – was shown to be the strongest single factor, there is no statistical or biological foundation for testing interaction III (area–MDE–ECM).

DISCUSSION

Patterns of reptile richness on mountains are diverse, exhibiting four general patterns: decreasing, low plateau, low plateau with a mid-elevation peak, and unimodal with a mid-elevation peak (Fig. 1). The distribution of diversity patterns changes depending on the group (monophyletic groups, namely reptiles, geckos, anguimorphs, iguanids, or scincomorphs, or functional groups, namely snakes and lizards; Fig. 1) but wasn't significantly different due to scale or hemisphere (eastern and western; Fig. 2). The elevational variability in diversity patterns may be attributable to particular proposed drivers of biodiversity. The strongest single factor was temperature, with secondary support for a humidity effect and an area effect. There was little support for the MDE or the ECM.

Area

Some predictions of the SAR, a surrogate for habitat heterogeneity at this scale (Rosenzweig, 1992, 1995), were supported for montane reptiles. Many studies showed a significant, positive relationship of diversity with elevational area, and more than half of the significant SAR studies showed a substantial change in diversity pattern with area corrections (Fig. 3a, Table 2, Appendix S3). Other SAR predictions, however, were not supported, as peak diversity only shifted by 300 m or more for about a quarter to a third of the studies. Following temperature and MDE, area had the least influence on lizard and snake diversity in combined multivariate analyses (interaction II).

Mixed support for the area effect on mountains is consistent with similar analyses of terrestrial small mammals, bats and birds (McCain, 2007a, 2009), which also found strong area effects in only about half, or fewer, of the elevational gradients. Other taxonomic groups, including plants, ants and fish, also show mixed SAR effects on mountains, both supportive (Sanders, 2002; Jones *et al.*, 2003; Bachman *et al.*, 2004; Fu *et al.*, 2004) and not supportive (Odland & Birks, 1999; Vetaas & Grytnes, 2002; Sanders *et al.*, 2003; Bhattarai *et al.*, 2004; Oommen & Shanker, 2005). Such mixed effects emphasize that area cannot be the main driver of elevational diversity, but is instead a secondary factor of importance. Therefore,

methodologies that promote the initial removal of area effects, before examining other potential drivers of diversity, are not advisable (e.g. Rahbek, 1997).

The MDE

Spatial constraints on species ranges are theoretically implicated and, in some cases, empirically supported to be a contributing factor to mid-elevation peaks in species richness (e.g. Colwell *et al.*, 2004; Colwell *et al.*, 2005; but see Hawkins *et al.*, 2005; Zapata *et al.*, 2005). None of the four MDE predictions were supported for reptile elevational gradients. Fits to MDE simulations were negligible (average $r^2 = 0.3$–0.11; Fig. 3b, Appendix S4). Deviations of maximum diversity away from the mountain midpoint were significantly skewed toward lower elevations, not randomly distributed as expected. A positive relationship between average lizard and snake range sizes and the MDE fit was not supported. MDE fits were not improved when area and MDE were tested together. Similar trends in low MDE fits, skewed deviations and lack of an area–MDE interaction were documented along elevational gradients globally for terrestrial small mammals (McCain, 2005, 2007a), bats (McCain, 2007a,b) and birds (McCain, 2009). For most vertebrate groups and other taxa examined so far (Dunn *et al.*, 2007), elevational patterns are not consistent with the MDE. Thus, spatial factors (SAR or MDE) are not supported as the main drivers of reptile diversity on mountains.

Climate

Temperature was the strongest single factor supported with the elevational richness patterns of reptiles (Fig. 4). This is consistent with earlier regional-scale studies emphasizing the importance of temperature in reptile biodiversity (Kiester, 1971; Schall & Pianka, 1978; Currie, 1991; Meliadou & Troumbis, 1997; Hawkins *et al.*, 2003a; Rodríguez *et al.*, 2005; Whittaker *et al.*, 2007; Qian & Ricklefs, 2008). In contrast to bats and birds, the temperature–water predictions of the ECM were not supported for reptiles (Fig. 5). All diversity patterns occurred on both humid and arid montane gradients. But not all predictions of the temperature model were consistently supported. There were more mid-elevation peaks in reptile diversity on mountains than would be expected if temperature alone drove montane diversity. Temperature had the strongest effect in multivariate analyses, but a substantial portion of variation in diversity remained unexplained. Additionally, the temperature–diversity relationship was significantly stronger on humid mountains than dry mountains (Fig. 4, Appendix S5). Water appears to be important in mediating the temperature effect, but in a divergent way than predicted by the ECM. On humid forested mountains, reptiles are very dependent on the warmest temperatures in the lowest 300 m (80%) whereas, on arid mountains, reptile diversity is less constrained to the lowest elevations. On arid gradients, 50% of maximum reptile diversity occurs between 600 and 1200 m, and 50% occurs below 300 m.
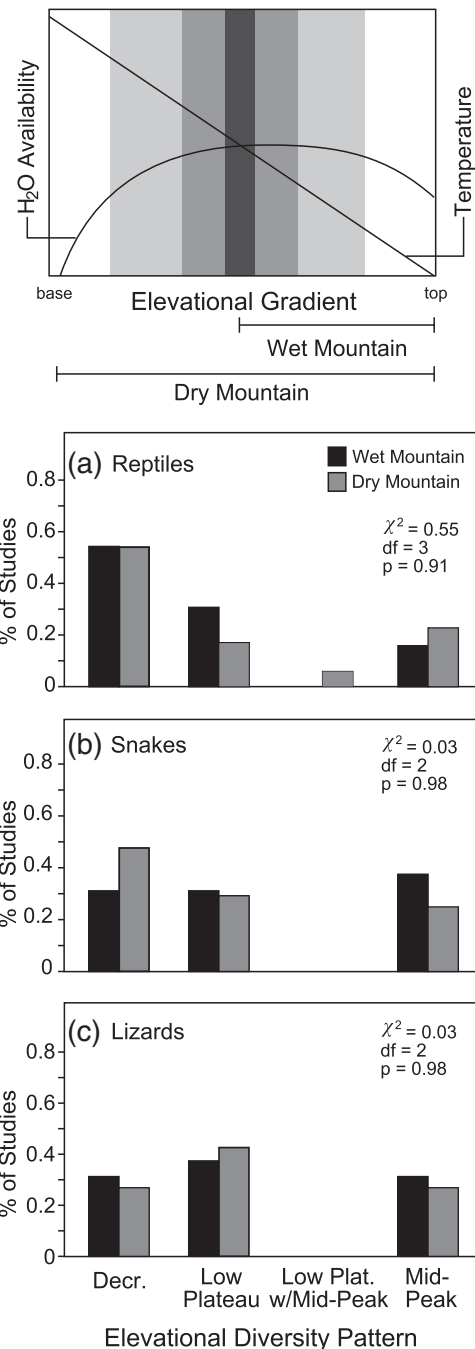

Figure 5 The elevational climate model (ECM) incorporates a linearly decreasing temperature gradient and a water availability gradient that differs between wet and dry mountains, and predicts maximum richness at mid-elevations on dry mountains, and decreasing or low plateaus in richness on wet mountains. Reptile species richness is depicted in grey tones, the darker shade indicating more species. The ECM was not supported for reptiles (a), snakes (b) or lizards (c), as each of the elevational diversity patterns consisted of nearly equal percentages of wet and dry gradients.

The significant variation in temperature relationships, and the many different locations of maximum diversity on arid mountains, may be due to the use by reptiles of direct sunlight to regulate their body temperature (Porter & Gates, 1969). Since the body temperatures of ectotherms rely on air temperature, radiant heat, wind and humidity, the trends in air temperature alone may not predict reptile species distributions and diversity patterns (Porter & Gates, 1969). On wet forested mountains, the opportunities to regularly use radiant heat are limited due to higher humidity, greater cloud cover and greater vegetative cover. Therefore, most species occur at the lower elevations with the warmest ambient temperatures. In contrast, the opportunities to use radiant heat on arid mountains are much greater, at both low and mid-elevations, due to low humidity, less cloud cover and sparser vegetation coverage. Therefore, it may be the case that reptiles on arid mountains are weighing the conditions influencing body temperature – air temperature, radiant heat, humidity and wind – such that the optimum conditions occur at the locations of highest reptile diversity (Porter & Gates, 1969). Much finer climatic data on these gradients than are currently available are needed to more precisely discern such trends. But this would be a fruitful future direction of research.

Evolutionary history

Evolutionary hypotheses are less developed elevationally than latitudinally, although recent analyses are breaking new ground (e.g. Wiens *et al.*, 2007). Due to a lack of species-level, time-calibrated phylogenetic trees, many phylogenetic trends like the time-for-speciation effect are not yet testable (Stephens & Wiens, 2003; Wiens *et al.* 2007). But some general, simplistic predictions can be discussed. Static evolutionary models propose a region on mountains where conditions promote speciation and dampen extinction risk and therefore predict a single diversity optimum (e.g. Brown, 2001, p.107; Heaney, 2001, hypothesis 12; Lomolino, 2001, Fig. 3). Such models can be rejected for montane reptiles due to the four distinct patterns in elevational diversity. If evolutionary factors generating montane diversity are strongly contingent on local fauna, conditions and biogeographic history, then only regionally consistent patterns would be predicted. But for montane reptiles, the different trends are not regionally consistent, as all patterns occur in each region: North America, Central America, Europe and Asia. Lastly, niche conservatism proposes that climatic conditions within which a taxon evolved – tropical-like conditions for most modern groups and species – should be conserved in the present (Wiens & Donoghue, 2004). Thus, niche conservatism predicts maximum reptile diversity in the warmest, wettest conditions, the same general pattern as that of the ECM. The lack of a divergent diversity pattern between wet and humid mountains (ECM) also negated support for this simple prediction of niche conservatism.

Summary

In summary, montane gradients in reptile, snake and lizard diversity follow four distinct patterns: decreasing, low plateau, mid-elevation peaks and, occasionally, low plateaus with mid-elevation peaks. The single largest correlate with these trends is temperature. The temperature trend is stronger along wet mountain gradients where opportunities to use radiant heat are limited. On arid gradients, however, the temperature effect is mediated by access to radiant heat which is, in turn, influenced by rainfall, soil and vegetative density. Tests also revealed that area is of secondary importance, whereas MDE and historical factors were the least consistent with the reptile diversity trends. Finer-scale climate data on precipitation, humidity and radiant heat at ground level will enable detailed analysis of the climatic factors mediating the ambient temperature effects. Additionally, the temperate bias in these studies highlights the need for more extensive elevational studies of reptiles at tropical latitudes. These analyses also pinpoint a stronger temperature effect for reptiles over birds, bats and terrestrial small mammals. This may suggest that reptiles will also respond to increasing temperatures and aridity differently than birds and mammals.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Details and citations of reptile elevational gradients used in analyses.

Appendix S2 Details and citations of reptile elevational gradients not used in analyses.

Appendix S3 Area and elevational gradients in reptile diversity.

Appendix S4 Mid-domain effect and elevational gradients in reptile diversity.

Appendix S5 Temperature and elevational gradients in reptile diversity.

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