Species endemism: Predicting broad-scale patterns and conservation priorities

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OFFICIAL STATEMENT OF WORK

Chapters in this thesis have been submitted to scientific peer-reviewed journals for publication with the participation of my supervisor (Chapter 1 and 3) and supervisor and one co-supervisor (Chapter 2) as co-authors. So, chapters presented here are written in first-person plural. Research ideas, written content, analyses and figures are my own work; the co-authors provided valuable guidance during the process. Anonymous reviewers and editors from journals (Ecography for Chapter 1 and Global Ecology and Biogeography for Chapter 2) suggested revisions that improved the clarity and flow of the manuscripts.

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Finally, I would like to mention that throughout my doctorate studies I have contributed in other research initiatives at Dr. Kerr and Dr. Currie’s labs. Some of the manuscripts ended up in publications:

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ABSTRACT

Do thermal barriers limit biotic composition and community similarity, potentially helping to shape biodiversity patterns at continental scales? Are environmental variables responsible for broad-scale patterns of species endemism? Are these patterns predictable? And, how can patterns of endemism can inform global conservation strategies? These are some of the questions that I attempted to answer during my doctoral research.

In the first chapter, I tested one of the most contentious hypotheses in ecology: Do thermal barriers, which grow stronger along elevational gradients across tropical mountains, create a dispersal barrier to organisms and consequently contribute to the isolation and divergence of species assemblages? If so, do patterns potentially generated by this mechanism detectably relate to dissimilarity of biotic assemblages along altitudinal gradients across the mountains in the Americas? We found that mountain passes are not only higher in tropical realms, as initially thought by Janzen (1967), and extensively popularized and assumed in further research, but they are also present in temperate regions along the western coast of North America. We also found that the stronger the thermal barrier, the higher the dissimilarity between communities. However, the variance explained was low, suggesting thermal barriers play a minor role in creating and maintaining patterns of biodiversity.

The second chapter raises the question of why are there more small-ranged species in some places than in others. I tested four macroecological hypotheses (*H1: climate velocity; H2: climate seasonality; H3: climate distinctiveness or rarity; and, H4: spatial heterogeneity in contemporary climate, topography or habitat*) to predict broad-scale patterns of species endemism, using a cross-continental validation approach. We found that there is no empirical reason, from the standpoint of model fitting, parameter estimates, and model validation, to claim

that any of these hypotheses creates and maintains broad-scale patterns of endemism. Although we found statistically significant relationships, they failed stronger tests of a causal relationship, namely accurate prediction. That is, the hypotheses did not survive the test of cross-continental validation, failing to predict observed patterns of endemism. Climate velocity was dropped from some models, suggesting that early correlations in some places probably reflect collinearity with topography. The effect of richness on endemism was in some cases negligible, suggesting that patterns of endemism are not driven by the same variables as total richness. Despite low explained variance, spatial heterogeneity in potential evapotranspiration was the most consistent predictor in all models.

The third chapter is aimed to evaluate the extent to which global protected areas (PAs) have included endemic species (species with small range size relative to the median range size). We measure the relative coverage of endemic species by overlapping species geographic ranges for amphibians, mammals, and birds, with the world database of PAs (1990-2016). Then we measure the rate of expansion of the global PA network and the rate of change in endemic species coverage.

We found that ~30% of amphibian, ~6% of bird and ~10% of mammal endemic species are completely outside PAs. Most endemic species' ranges intersect the PA network (amphibian species = 58%; birds = 83%; mammals = 86%), but it usually covers less than 50% of their geographic range. Almost 50% of species outside the PA network are considered threatened (critically endangered, endangered and vulnerable). We identified that ecoregions in tropical Andes, Mesoamerica, Pacific Islands (e.g., New Guinea, Solomon), Dry Chaco, and Atlantic forests are major conservation priorities areas.

The historic rates of new PAs added every year to the network is between ~6,000 to ~15,000. In contrast, we found that rates of including endemic species within the PA network have been fairly slow. Historic data shows that every year, the entire geographic range of 3 (amphibians) to 6 (birds and mammals) endemic species is 100% included inside the PA network (amphibians = from 162 to 233; mammals = 10 to 84; and, amphibians = 16 to 99). Based on these trends, it is very unlikely PAs will include all endemic species (14% total endemic species, that is ~1,508 out of 11,274) currently outside the PA network by 2020. It will require five times the effort made in the last two decades. However, projections also showed that is very likely that some portions of the geographic ranges for all endemic birds and mammals, but not for all endemic amphibians, will be covered by the future PA network.

I sum, I found that none of the hypotheses tested here can explain broad-scale patterns of total species richness and total species endemism. My main contribution on this research area is clearly rejecting these hypotheses from potential candidates that may explain biodiversity patterns. By removing them, we advance in this field and open possibilities to test new hypotheses and evaluate their mechanisms. I proposed that other drivers and mechanisms (whether biotic and biotic) acting at local scales, and escaping the detection of macroecological approaches, might be responsible for these patterns. Finally, in terms of conservation planning, I proposed that the international community has an opportunity to protect a great number of endemic species and their habitats before 2020, if they strategically create new PAs.

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GENERAL INTRODUCTION

Identifying broad-scale patterns of species distributions, and testing hypotheses aimed to explain the origin and maintenance of these patterns, is a main tenet in ecology (Hawkins *et al.*, 2003), with important implications in conservation (Myers *et al.*, 2000; Mittermeier *et al.*, 2005; Orme *et al.*, 2006). My thesis tests some of the most contentions hypotheses in ecology intended to explain broad-scale patterns in species distributions. I am also interested in using these biodiversity patterns to inform biodiversity conservation, in particular by investigating broad-scale patterns of species endemism. To do this, I use a macroecological approach that attempts to find generalities in species distributions, test important hypotheses with empirical data, and draw some recommendations for biodiversity conservation.

Geographical range size is one of the essential ecological and evolutionary traits of a species (Gaston, 2003), and spatial variation in species' range sizes has implication for the origin and maintenance of global diversity patterns (Orme *et al.*, 2006). Operationally, a terrestrial species is considered endemic if it has a small geographic distribution (also known as range-restricted species) (Jetz *et al.*, 2004; Ohlemüller *et al.*, 2008a; Pimm *et al.*, 2014), regardless of the size of the land surrounding it (Anderson, 1994). So, endemic species are not only expected in small and isolated islands, but also in large continental masses. Range-restricted species tend to be concentrated in particular regions in the world, creating the so called "centers of endemism" (Lamoreux *et al.*, 2006). How did some species successfully thrive while maintaining small range size? Janzen (1967) proposed an elegant mechanism to explain the origins and maintenance of this phenomenon: pronounced changes in climatic conditions along elevation gradients may facilitate allopatric speciation by limiting species dispersal, which in turn may promote species inhabiting tropical montane environments to constrain elevational distributions, resulting in small geographic ranges. So, in my first chapter, I attempt to measure and investigate the spatial variation of thermal barriers (differences in year-round thermal regimes between two locations, and the geographic space between them), along elevation gradients in mountain ranges, and test whether these thermal barriers predict gradients of assemblage similarity across the latitudinal extent of those mountain ranges. Janzen (1967) argues that organismal dispersal of organisms attempting to cross mountaintops might be limited by strong differences in thermal regimes between lowlands and highlands. This effect should be stronger in tropical realms because temperature seasonality is thought to be lower in tropical than temperate environments (Janzen, 1967). That is, a tropical species inhabiting a lowland area is less likely to encounter tolerable temperatures at high elevations. It is suggested that this mechanism may isolate species, promote allopatric speciation, and affect biodiversity patterns (Janzen, 1967; Ghalambor *et al.*, 2006; Mittelbach *et al.*, 2007). Here, I ask whether thermal barriers are widespread or exclusively present in tropical realms, and whether stronger thermal barriers in the tropics explains biotic dissimilarity along a latitudinal gradient across mountain systems in the Americas.

In Chapter 2, I investigate broad-scale patterns of endemism. High numbers of species with relatively small ranges are concentrated in some regions of the Earth (Jetz & Rahbek, 2002), creating broad-scale patterns of species endemism (Lamoreux *et al.*, 2006). For example, range-restricted species are more common on islands and mountain areas, predominantly in the southern hemisphere (Orme *et al.*, 2006). So, I ask why there are so many species with small geographic ranges (endemic species) in some places and not others? Although several mechanisms have been proposed to explain these patterns, including covariation with climate, spatial heterogeneity, the effect of historical factors, and biotic interactions (Fjeldså & Lovett, 1997; Jansson, 2003; Ohlemüller *et al.*, 2008a; Sandel *et al.*, 2011), their relative roles are still contentious. Here, we test the power of macroecological hypotheses (*H1: climate velocity; H2: climate seasonality; H3: climate distinctiveness or rarity; H4: spatial heterogeneity in contemporary climate, topography or habitat; and, H5: total species richness*) to predict broad-scale patterns of species endemism. I evaluate the robustness of the statistical models using cross-continental validation. We ask whether the strength of the signal is strong enough to yield informative predictions of numbers of endemic species in independent geographic areas, that is, whether the predictions are unbiased and consistently matched by observed trends. However, I begin by reviewing various methodological issues that complicate efforts to evaluate potential explanations and which may affect final conclusions. These include: (i) the spatial resolution of the analysis (Buckley & Jetz, 2008), (ii) the nature of metrics to measure species endemism (Crisp *et al.*, 2001), (iii) collinearity between predictors (Dormann *et al.*, 2013), (iv) the unusual statistical properties of spatial patterns of species endemism, such as zero-inflation (i.e., excess of zeros in data sets; Martin *et al.* (2005), (v) the strong correlation between metrics of species endemism and species richness, (vi) the way metrics are corrected for this effect (Crisp *et al.*, 2001), and (vii) the lack of taxonomic congruence in patterns of endemism (Lamoreux *et al.*, 2006).

In the third chapter, I evaluate whether endemic species are protected in the global Protected Areas (PA) network. In fact, endemism, along with other factors, has been used to identify global priorities for conservation. For instance, biodiversity hotspots (i.e., areas of high endemism undergoing severe habitat loss), are aimed to protect not only high number of species, but evolutionary process (Fjeldså *et al.*, 1999), and places with biodiversity vulnerability and irreparability (Myers *et al.*, 2000; Ricketts, 2001; Mittermeier *et al.*, 2004). Extensive evidence suggests that climate change is likely to have a negative effect on global biodiversity (Parmesan, 2006; Bellard *et al.*, 2012). In this context, species with small geographic ranges are more vulnerable to go extinct because they are unable to keep pace with climate change (Gaston, 1998; Thomas *et al.*, 2004; Malcolm *et al.*, 2006; Moritz & Agudo, 2013b), a phenomenon that can be modulated by the interaction between species' dispersal capabilities, habitat specialization, thermal adaptation, and interactions with other species (Malcolm *et al.*, 2002; Gilman *et al.*, 2010; Sinervo *et al.*, 2010). In general, biodiversity hotspots (Myers *et al.*, 2000) are projected to experience the disappearance of extant climates (Williams *et al.*, 2007; Bellard *et al.*, 2014), and the interaction between climate change and habitat loss may exacerbate extinction risk (Travis, 2003; Malcolm *et al.*, 2006; Moritz & Agudo, 2013a). So, in the third chapter, I ask whether the historical rate of change in endemic species coverage by the global PA network is likely to protect all endemic species by 2020. By 2020, the international community has pledged to increase terrestrial PAs to at least 17% of current Earth surface extent (Aichi biodiversity target 11) (CBD, 2010), so there is an opportunity to protect some features of biodiversity such as endemic species. More specifically, I ask when would full endemic coverage be achieved at present rates of change? In addition, I perform a comprehensive gap analysis to quantify the number of endemic species that are not covered by the PAs network, and their relative threatened status. I provide detailed information on endemic species and geographic areas for conservation that would help countries to meet Convention of Biological Diversity (CBD) targets.

CHAPTER 1. Over the top: do thermal barriers along elevation gradients limit biotic similarity?

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ABSTRACT

Organismal dispersal through mountain passes should be more constrained by temperature-related differences between lowland and highland sites in montane environments. This may lead to higher rates of diversification through isolation of existing lineages toward the tropics. This mechanism, proposed by Janzen (1967), could influence broad-scale patterns of biodiversity across mountainous regions and more broadly across latitudinal gradients. We constructed two complementary analyses to test this hypothesis. First, we measured topographically-derived thermal gradients using recently-developed climatic data across the Americas, reviewing the main expectations from Janzen's climatic model. Then, we evaluated whether thermal barriers predict assemblage similarity for amphibians and mammals along elevational gradients across most of their latitudinal extent in the Americas. Thermal barriers between low and high elevation areas, initially proposed to be unique to tropical environments, are comparably strong in some temperate regions, particularly along the western slopes of North American dividing ranges. Biotic similarity for both mammals and amphibians decreases between sites that are separated by elevation-related thermal barriers. That is, the stronger the thermal barrier separating pairs of sites across the latitudinal gradient, the lower the similarity of their species assemblages. Thermal barriers explain 10-35% of the variation in latitudinal gradients of biotic similarity, effects that were stronger in comparisons of sites at high elevations. Mammals' stronger dispersal capacities and homeothermy may explain weaker effects of thermal barriers on gradients of assemblage similarity than among amphibians. Understanding how temperature gradients have shaped gradients of montane biological diversity in the past will improve understanding of how changing environments may affect them in the future.

INTRODUCTION

Barriers to dispersal arising from pronounced changes in climatic conditions along elevation gradients may facilitate allopatric speciation by limiting species dispersal, which influences broad-scale patterns of species richness and composition (Janzen, 1967; Ghalambor *et al.*, 2006; Mittelbach *et al.*, 2007; Buckley *et al.*, 2013). Reduced temperature seasonality in tropical environments is also likely to cause species to specialize on narrower climatic conditions and reduce their capacity to acclimate to the wide range of temperatures that challenge organisms in temperate or cold environments (Stevens, 1989; Bonebrake, 2013). In other words, allopatric speciation rates in mountainous areas depend strongly on climate and particularly on temperature (Janzen, 1967). Because temperature seasonality is lower in tropical than temperate environments, a tropical species inhabiting a lowland area is unlikely to encounter tolerable temperatures at high elevations. In comparison, thermal regimes between lowland and highland areas overlap substantially in regions with more pronounced temperature seasonality. Organisms in such areas are, as a result, less likely to experience strong dispersal limitations arising from intolerance to temperature differences along elevation gradients (Ghalambor *et al.*, 2006).

Species inhabiting tropical montane environments occupy smaller elevational ranges (Wake & Lynch, 1976; Huey, 1978; Navas, 2002; Ghalambor *et al.*, 2006; Orme *et al.*, 2006; McCain, 2009) and show narrower thermal tolerances than species in temperate montane environments (Addo-Bediako *et al.*, 2000; Kozak & Wiens, 2007; Deutsch *et al.*, 2008; Cadena *et al.*, 2012). Colder temperatures at high elevations represent thermal barriers that limit dispersal rates among species with such narrow thermal tolerances, reducing gene flow between subpopulations and increasing allopatric speciation rates. While this process could contribute to the origin and maintenance of global gradients of species diversity, there is mixed evidence that tropical speciation rates exceed those of temperate regions (Graham *et al.*, 2004; Kozak & Wiens, 2006; Rissler & Apodaca, 2007; Peterson & Nyari, 2008; Hua & Wiens, 2010; Cadena *et al.*, 2012). Niche conservatism could reduce the capacity of taxa originating under warm conditions to establish populations in higher elevation, cooler areas (Moritz *et al.*, 2000; Wiens, 2004; Wiens *et al.*, 2010; Kozak & Wiens, 2012) and climate change-related extinction risk for some taxa (Deutsch *et al.*, 2008; Sinervo *et al.*, 2010; Kerr *et al.*, 2015). Understanding how climate interacts with species' physiological characteristics (Buckley *et al.*, 2013; Coristine *et al.*, 2014) and requirements for behavioral thermoregulation (Kearney *et al.*, 2009; Meiri *et al.*, 2013; Sunday *et al.*, 2014) will help assessments of emerging conservation challenges for which responses to climatic conditions play a role (White & Kerr, 2007).

Here, we test whether broad-scale gradients in assemblage similarity among mammals and amphibians relate to thermal barriers associated with dividing mountain ranges in western North and South America. We predict that increasing thermal barriers associated with gradients of temperature seasonality in mountainous areas across latitudes should lead to lower assemblage similarity among sites separated by those barriers. Population isolation is more likely in mountainous localities where temperature-related dispersal barriers are more persistent seasonally (Wiens & Graham, 2005; Ghalambor *et al.*, 2006; Kozak & Wiens, 2007; Mittelbach *et al.*, 2007; Buckley & Jetz, 2008; McCain, 2009; Cadena *et al.*, 2012), leading to higher allopatric speciation rates. The spatial relationship between assemblage similarity and thermal barriers should be more pronounced among taxa that are more strongly affected by environmental temperatures (i.e. ectotherms) and those with lower dispersal capacities (Angilletta, 2009).

MATERIAL AND METHODS

Topography and thermal barriers

We constructed detailed measurements of thermal overlap between thermal regimes among sites across the Americas. We define a thermal regime as the temperature range between maximum and minimum monthly temperature observed throughout the year for a particular site. Thermal overlap is the similarity between thermal regimes. In areas where thermal regimes differ substantially (i.e. there is little or no thermal overlap), thermal barriers to dispersal are likely to be present. We measured thermal regimes at the resolution of the climate data (~1 km^2) across mainland areas of the Americas using monthly temperature data from WorldClim for the 1951-2000 period. Cross-validated accuracy assessments of temperature measurements in the WorldClim dataset indicate that temperature normals for this period are usually within 0.3 ^{0}C of observed values, with uncertainties in temperature measures rising in the most sparsely sampled and mountainous areas, respectively (Hijmans *et al.*, 2005). The density of meteorological stations and availability of long term monitoring varies across the Americas and likely increases the uncertainty around estimates of thermal barriers that we hypothesize should limit species dispersal rates across mountainous regions. Geographic data were projected into Lambert Azimuthal Equal-Area projection and processed using ArcInfo Grid 10.3 (ESRI, 2014).

We selected 404 focal sites (Figure 1.1a) over which quadrats for biological measurements could be centred and temperature-related data extracted for subsequent analyses. This set of 404 focal sites includes 202 at low elevations (300 metres above sea level, m.a.s.l.) and 202 at high elevations (2000 m.a.s.l.). Low and high elevation focal sites were each divided into 101 east-west pairs, separated by dividing mountain ranges (e.g. Andes). Focal sites were situated from 69°N to 39°S with ~150 km latitudinal gaps between them (Figure 1.1a). The two sets of 202 focal sites were divided evenly between eastern and western areas, so 101 focal sites on the eastern slopes were paired with 101 focal sites on western slopes at both low and high elevations (Figure 1.1b). We computed the degree of thermal overlap between each focal site and all other pixels throughout the Americas, creating 404 thermal overlap surfaces relative to every focal site (e.g., thermal overlap map for an example focal site in Figure 1.1).

For all pixels in the Americas, we extracted the maximum temperature of the warmest month and minimum temperature of the coldest month (Figure 1.1c) (Hijmans *et al.*, 2005). We measured temperature in kelvins to avoid negative values in later calculations. Then, we used resulting thermal regimes values to parameterize Equation 1 (Figure 1.1d), which measures pairwise thermal overlap between each focal site and all other areas in the Americas:

$$Overlap\ value = \sum_{i=1}^{12} \frac{d_i}{\sqrt{R_{1i} R_{2i}}},\ (1)$$

where d_i is the temperature overlap between the focal site and each other site in the Americas for the ith month. R_{1i} is the difference in kelvins between the monthly mean maximum and minimum for the ith month of the focal site and R_{2i} is the corresponding value for each other site in the Americas. The maximum thermal overlap value is 12 if thermal regimes between two sites share identical monthly minimum and maximum temperatures throughout the year (Figure 1.1e). Thermal overlap decreases as thermal regimes between sites grows more dissimilar. Zero values are possible if there is no overlap between thermal regimes between a focal site and another site and negative values will be observed if there is an annually persistent temperature difference (e.g., the maximum temperature of one site is always lower than the minimum temperature of another, Figure 1.1e). Finally, we measured how thermal overlap changes along altitudinal gradients across the Americas by regressing observed thermal overlap values against elevation using ordinary least squares regression. We use the slope of these regressions to evaluate how thermal regimes vary with respect to elevation across the Americas. All data are available freely from http://www.macroecology.ca/ and Supplementary Materials, Appendix 1 (Figure S1.1).

Assemblage similarity

We used distribution data for 1771 terrestrial mammal species (Patterson *et al.*, 2007) from IUCN (http://www.iucnredlist.org) and 3131 amphibian species from Natureserve (http://www.natureserve.org/) in the western hemisphere. Distribution maps generally have fewer false absences than presence-only datasets but contain many false presences; compositional similarity between pairs of quadrats may appear misleadingly high using range map data. In addition, species distributions are less certain in tropical regions, a trend that is likely to be more pronounced at high elevations, where local distribution differences due to topographical complexity may be undetected. To our knowledge, this uncertainty has not yet been directly tested and is beyond the scope of this paper. Our results should be considered conservative (i.e., errors of commission in species range data are more common and increase apparent assemblage similarity among paired quadrats).

We measured species presences within quadrats of ~100 km^2 centered on each of the 404 focal sites, described above. A species was considered present if any portion of its range intersected a quadrat. We centered quadrats at 300 and 2000 m.a.s.l. (and focal sites for thermal overlap calculations) to overcome two constraints. First, elevation contours at 2000 m.a.s.l. are generally present across the study region of North and South America, while elevations greater than this are not. Second, some areas in Central America are narrow and have very small land areas near sea level, with steep slopes rising quickly above. In these areas, placing quadrats at 300 and 2000 m.a.s.l., respectively, eliminated spatial overlap between adjacent quadrats, which would have misled measurements of similarity.

Pairwise similarity between species assemblages in site pairs was measured using the Sørensen coefficient in EstimateS version 9 (Colwell, 2013). We constructed a presence/absence matrix for mammals and amphibians within each quadrat. We created two sets of pairwise comparisons: first between pairs of lowland quadrats (300 m.a.s.l.) and a second between pairs of highland quadrats (2000 m.a.s.l.) at the same latitude to the east and west of the dividing mountain range (Figure 1.1f). We compared east-west pairs of quadrats (i.e. separated by dividing ranges, Figure 1.1b) at the same elevation, which are more likely to represent biologically independent measurements, reducing potential area effects on biodiversity patterns that can mislead analyses in mountainous regions (Romdal & Grytnes, 2007).

The Sørensen index uses presence-absence data and gives double weight to presences in two quadrats (Legendre & Legendre, 1998). This measure is calculated as:

$$S_{ij} = \frac{2A}{2A+B+C}, \quad (2)$$

where A is the number of species common to both quadrats i and j; B is the number of species present only at quadrat i; and C is the number of species present only at quadrat j (Chao *et al.*, 2005). Values range between 0 and 1, where 1 indicates that the two quadrats have the same species composition, and 0 means the two quadrats share no species.

Thermal barriers separating assemblages

We used the maximum difference in thermal regimes separating paired sites as an index of thermal barriers that organisms would encounter while moving from one quadrat to another across the dividing range. The biological impact of a thermal barrier should be greater if a dispersing organism encounters temperatures that are rarely or never present in the area from which it moved. Thermal barriers, as measured here (and described in Janzen, 1967), measure the difference in thermal regimes between points of origin for dispersal (at low or high elevations) and the mountain passes that separate this point of origin from a quadrat at the same elevation across the dividing mountain range.

Statistical Analysis

We constructed ordinary least squares regression models to test whether thermal overlap may limit assemblage similarity among pairs of quadrats across the Americas. Spatial autocorrelation normally influences broad-scale analyses across gridded sampling networks profoundly, which diminishes reliability of their probability tests by violating the assumption of independence of regression errors and biases predictor coefficients (Bini *et al.*, 2009). Analyses here rely on assemblage similarity, a characteristic shared between paired sites separated by known distances. This pairwise distance measurement accounts for the extent to which purely spatial effects predict similarity, which decreases with geographic distance (Soininen *et al.*, 2007). We included pairwise site separation as a covariate in all analyses. Distance and similarity were square root-transformed to improve normality and homoscedasticity of residuals (Nekola & White, 1999).

We analyzed two sets of quadrats, which were centred on pairs of focal sites. First, we compared lowland quadrats (300 m.a.s.l.; East-West, *EW* and West-East, *WE,* Figure 1.1e) and, separately, highland quadrats on opposing sides of dividing ranges (2000 m.a.s.l.; *ew* and *we*, Figure 1.1e). The first letter indicates which focal site was used as the basis for thermal overlap calculations. For instance, *EW* pairwise comparisons of similarity as a function of thermal overlap use the thermal overlap value calculated from a site to the east (*E*, at 300 m.a.s.l.). Finally, we tested for differences between regression slopes for similarity in paired quadrats in lowland and highland areas. Statistical analyses were performed in R v 3.2.1. (R Core Team, 2012).

RESULTS

Thermal overlap along altitudinal and latitudinal gradients shows considerable variability. While the rate of change of thermal overlap with elevation is usually linear (Figure 1.2; Table S1.1; and Figure S1.2a), there is a region between 33°N and 48°N along the eastern side of the continental divide where that relationship is clearly nonlinear (Figure 1.2; see also Table S1.1 and Figure

S1.2b). With respect to latitude, the greatest rates of change of temperature with respect to elevation are in the tropics, decreasing toward sub-tropical areas, and stabilizing between 20-40°S and 30-50°N (Figure 1.2 and 1.3). Thermal regimes change similarly with elevation across the tropics and when measured from coastal areas of North America around 60°N (e.g., model estimates for a tropical region: $y = -6.6 \text{ X } 10^{-3}$ Elevation + 12.005; and model estimates for western North America at 60°N: $y = -6.7 \text{ X } 10^{-3}$ Elevation + 12.312; Figure 1.2 and Figure S1.3). Thermal barriers along elevation gradients vary considerably more than simple latitudinal expectations suggest, so latitude cannot be used as a surrogate for the magnitude of thermal barriers (or as an indicator of the absence of thermal overlap between low and high elevation areas). Explicit measurements of thermal barriers are needed to test for their potential effects on gradients of similarity across the Americas (see Figure S1.4).

Broadly, mammal and amphibian assemblages become less similar when separated by more substantial thermal barriers imposed by the steep elevation gradients of mountain ranges in the Americas. That is, the stronger the thermal barrier separating them, the lower the similarity of species composition between paired quadrats becomes (amphibians: $R^2 = 0.11 – 0.33$; mammals: $R^2 = 0.17 – 0.34$; Table 1.1). For pairwise comparisons of high elevation quadrats (i.e. at 2000 m.a.s.l.), this result remains robust after accounting for separation distances between quadrats (amphibians: $R^2 = 0.33$; $F = 26.4$; $df = 2,99$; $p<0.05$; and mammals: $R^2 = 0.34$; $F = 26.9$; $df = 2,99$; $p < 0.05$; Table 1.1a; Figure 1.4a). However, the effect of thermal barriers on similarity is more variable when measured from west to east (amphibians: $R^2 = 0.20$; $F = 14.0$; $df = 2,99$; $p < 0.05$; and mammals: $R^2 = 0.25$; $F = 18.3$; $df = 2,99$; $p < 0.05$; Table 1.1b). For pairwise comparisons of low elevation quadrat pairs, the effect of thermal barriers on similarity decreases (amphibians: $R^2 = 0.22$; $F = 15.4$; $df = 2,99$; $p < 0.05$; and mammals: $R^2 = 0.26$; $F = 19.2$; $df =$

2,99; $p<0.05$; Table 1.1c; Figure 1.4b). The relationship between thermal barriers and biotic similarity at low elevations is not significant for mammals if measured from west-to-east (F = 12.1; df = 2,99; p = 0.17; Table 1.1d) but is weakly significant for amphibians ($R^2 = 0.11$; F = 7.5; df = 2,99; $p < 0.05$).

DISCUSSION

Mechanisms governing the origin and maintenance of gradients of biological diversity remain the focus of intense interest in ecology and evolution (Currie *et al.*, 2004; Hawkins *et al.*, 2004; Hillebrand, 2004; Kozak & Wiens, 2010; Wiens *et al.*, 2010). If mountain passes are "higher" in the tropics (Janzen, 1967), then population isolation and subsequent increase in speciation rate could contribute to gradients of species richness and turnover on a continental scale (Mittelbach *et al.*, 2007; Buckley & Jetz, 2008). Here, we measured and investigated spatial variation in thermal barriers along elevation gradients in mountain ranges and tested whether these barriers predict gradients of assemblage similarity across the latitudinal extent of those mountain ranges.

Mountain passes are "higher" in biological terms when they are associated with strong thermal barriers, but these effects are not limited to the tropics. That is, the similarity of species assemblages decreases in comparisons of sites separated by more substantial thermal barriers associated with higher elevations. These effects are stronger for amphibians, which likely have lower effective dispersal rates than many mammal species and greater susceptibility to temperature fluctuations associated with ectothermy. However, we found robust evidence that thermal barriers, initially thought to be uniquely strong in tropical environments, can be comparably steep in temperate regions, particularly in western North America (Figure 1.2 and

1.3). We find no evidence that thermal barriers are uniquely strong in tropical environments, although they are more widespread there.

Our results suggest that thermal barriers associated with mountain ranges limit species dispersal and increase potential for allopatric speciation. Comparisons between species assemblages in paired, highland sites showed a detectable and consistent effect of thermal barriers on assemblage similarity for both mammals and amphibians (Figure 1.4 and Table 1.1). Temperature-related limitations on dispersal across high elevation areas could contribute to explanations of why patterns of assemblage similarity across broad areas converge among different taxa (Buckley & Jetz, 2008). Field measurements of thermal barriers can reflect sophisticated, location-specific information that reflect the operative temperature in an environment for a particular organism. Emerging techniques for measuring operative temperature account for factors such as incident solar radiation, wind speed, humidity, and ground temperature. Such approaches improve understanding of how short term environmental conditions influence species' behavioral thermoregulation requirements (Sunday *et al.*, 2014) or species' dispersal and acclimation capacities in particular environments (Buckley et al. 2013a, Buckley et al. 2013b). Integrating such sophisticated metrics with spatially explicit dispersal rates estimates would enable tests of their potential effects on diversification rates and provide insight into processes that shape gradients of diversity.

Patterns of thermal overlap interact with species' dispersal capacities differently than suggested in simple tropical-temperate comparisons. For example, temperature-related dispersal barriers can be large if a species attempts to move inland from coastal North America, where areas with temperate rainforest have little or no thermal overlap with high elevation areas further inland. Nevertheless, mammal and amphibian species may filter around or through mountain ranges and the thermal barriers they impose. Many lowland species in tropical regions have broad geographical ranges spanning the Andes and these ranges were likely established as organisms dispersed through inter-Andean valleys at low altitude (Haffer, 1967; Brumfield & Capparella, 1996; Ron, 2000; Miller *et al.*, 2008). Lineages inhabiting neotropical lowlands may have experienced initial isolation as a result of Andean uplift (Weir & Price, 2011). However, trans-Andean dispersal events after Andean uplift reestablished contact among many such populations (Miller *et al.*, 2008). Lowlands with similar thermal regimes near the northern limits of the Andes in Venezuela may have connected cis-Andean (east of the Andes) and trans-Andean (west of the Andes) biotas (Haffer, 1967; Ron, 2000). The Andalucia pass in Colombia and the Marañón and Porculla valleys in Peru, where thermal regimes differ by only small margins from neighboring lowlands, provide effective dispersal corridors connecting Amazonian, Pacific and Central American biotas (Haffer, 1967; Vuilleumier, 1971; Miller *et al.*, 2008)) (Supplementary Materials Appendix 1, Figure S1.5).

Thermal barriers are weaker or absent at low elevations (Wright *et al.*, 2009; Salisbury *et al.*, 2012) and our results cannot readily explain variation in species assemblages within such areas. Alternative explanations must be sought. It is possible that species within regions with relatively stable seasonal climates have lower dispersal capacities, making speciation more likely in the presence of any kind of barrier, thermal or otherwise (Jocque *et al.*, 2010). If so, the intrinsic dispersal ability of species (Kodandaramaiah, 2009; Smith & Klicka, 2010) could generate structured gradients of species richness across regions independently of *in situ* speciation rates (Cadotte, 2006; Wiens, 2011). Dispersal capacity also determines how rapidly organisms can track shifting environmental conditions (Ronce, 2007; Leroux *et al.*, 2013).

To the extent that thermal barriers limit species dispersal and contribute to the origins and maintenance of diversity gradients, rising temperatures in mountains that force upslope shifts in species' ranges (Dimitrov *et al.*, 2012; Kerr *et al.*, 2015) could erode species' geographical isolation and potentially confront distinctive, high elevation populations with influxes of individuals from historically disjunct areas. Such effects seem more likely for species in areas where thermal barriers associated with elevation are largest, which are most common in, but not restricted to, the tropics (Tewksbury *et al.*, 2008; Dillon *et al.*, 2010; Sinervo *et al.*, 2010). If so, recently diverged populations may recombine. Mountainous areas have provided microrefugia for organisms during historical climatic changes (Jansson, 2003; Willis & Bhagwat, 2009; Scherrer & Korner, 2011) and could improve species persistence following anthropogenic climate change (Ashcroft, 2010; Moritz & Agudo, 2013a; Robillard *et al.*, 2015). The role of such areas in maintenance, or erosion, of population isolation and allopatry relative to changing thermal barriers could be significant. Climate change offers pseudo-experimental opportunities (Kerr *et al.*, 2007) to test how thermal barriers associated with elevation gradients shape broad-scale gradients of assemblage similarity.

Processes intrinsic to the classic "mountain passes" hypothesis (Janzen 1967) appear to contribute to the origins and maintenance of broad-scale gradients of biological diversity. This mechanism helps explain how environmental conditions shaped regionally-distinctive species assemblages in the past, integrating ecological perspectives on dispersal with evolutionary consequences for speciation. Yet, thermal barriers in some temperate regions are comparably strong to those observed in tropical areas. Differences in species assemblages across mountainous regions likely reflect some effect of those barriers, but other factors, whether historical or contemporary, must contribute to gradients of biological diversity. Understanding of such mechanisms will inform predictions of how assemblages may change in the future.

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TABLES

Table 1.1. Compositional similarity (COMP) as a function of tha maximum thermal overlap (TOV) and accounting for geographical distance (DIST) for pairwise comparison of quadrats in the highlands (*a*, *b*) and lowlands (*c*, *d*) in the Americas.

Amphibians								***Mammals***						
Predictor	Estimate	Std. E.	t value	Pr(>t)	R^2Adj	*F*	*p*	Estimate	Std. E.	t value	Pr(>t)	R^2Adj	*F*	*p*
a. Quadrats at HIGHLANDS (2000-2000m), using TOV from EAST slope (ew†)														
Intercept	0.4466	0.0542	8.233	***	0.33	26.4	***	0.8953	0.0359	24.93	***	0.34	26.9	***
TOV	0.0339	0.0049	6.844	***				0.0167	0.0032	5.11	***			
DIST	-0.0094	0.0030	-3.121	**				-0.0115	0.0020	-5.74	***			
b. Quadrats at HIGHLANDS (2000-2000m), using TOV from WEST slope (we)														
Intercept	0.4384	0.5941	7.379	***	0.20	14.0	***	0.8917	0.0381	23.34	***	0.25	18.3	***
TOV	0.0303	0.0063	4.815	***				0.0141	0.0040	3.48	***			
DIST	-0.010	0.0033	-2.99	**				-0.0117	0.0021	-5.45	***			
c. Quadrats at LOWLANDS (300-300m), using TOV from EAST slope (EW)														
Intercept	0.6873	0.0782	8.782	***	0.22	15.4	***	1.0020	0.0642	15.59	***	0.26	19.2	***
TOV	0.0180	0.0039	4.521	***				0.0109	0.0032	3.36	**			
DIST	-0.0126	0.0023	-5.270	***				-0.0121	0.0019	-6.18	***			
d. Quadrats at LOWLANDS (300-300m), using TOV from WEST slope (WE)														
Intercept	0.5541	0.0766	7.230	***	0.11	7.58	***	0.8478	0.0622	13.61	***	0.17	12.1	***
TOV	0.0109	0.0044	2.436	*				0.0002	0.0036	0.07	0.94			
DIST	-0.008	0.0022	-3.790	***				-0.0083	0.0018	-4.49	***			

Signif. Codes (Pr(>t)): 0 '***' 0.001 '**' 0.01 '*' (Df=(2, 99) degrees of freedom)

† the first letter indicates which focal site was used to construct thermal overlap measurements for the linear model analysis. For instance, *ew* uses the thermal overlap value calculated from a focal quadrat *e* located in the eastern slope at 2000 m.a.s.l.

FIGURES

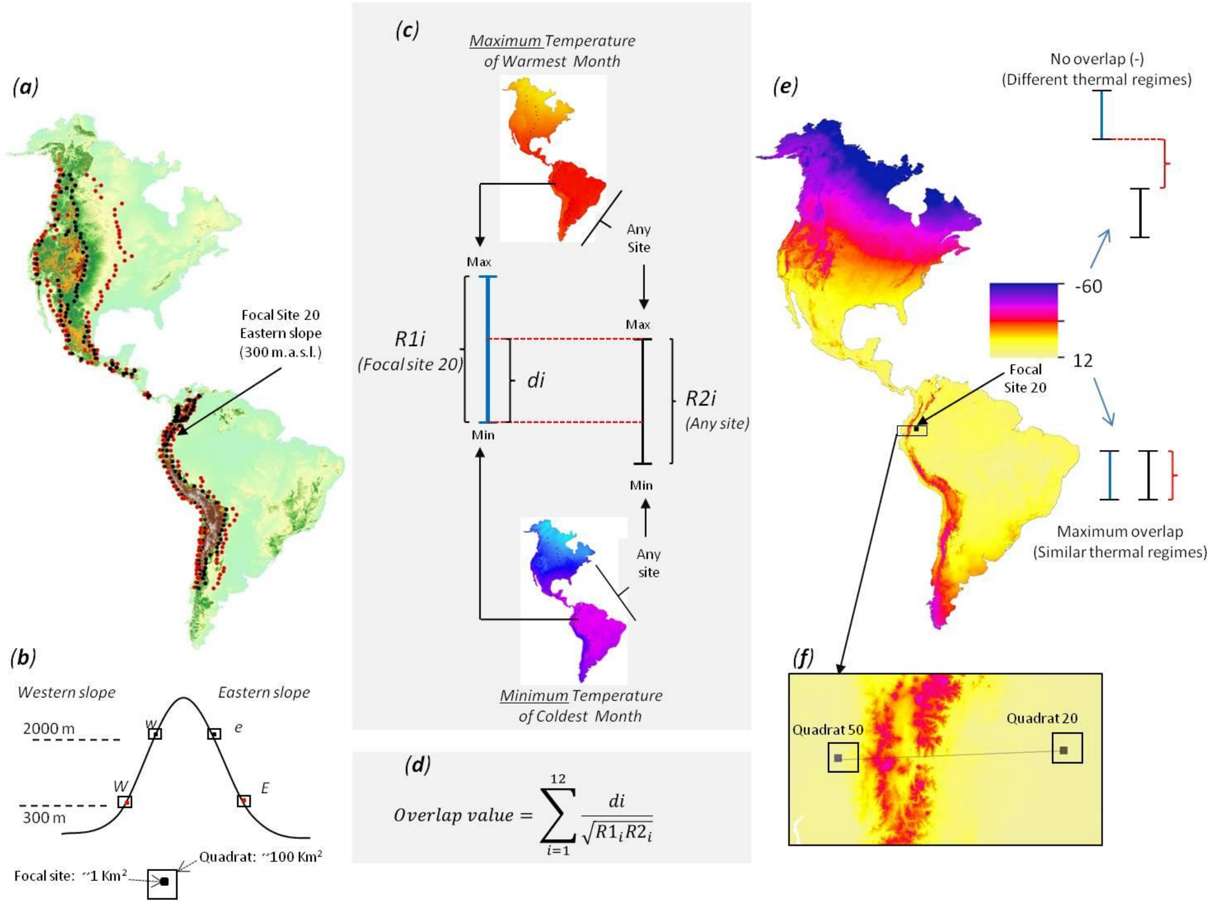

Figure 1.1. Conceptual diagram showing Janzen’s approach (Janzen, 1967), as adapted to measure the overlap between thermal regimes of 404 focal sites (a ~1 km^2 pixel) relative to all other sites in the Americas *(a)*. These were divided into two sets of 101 focal site pairs at identical latitudes and elevations: the first set of 101 focal site pairs is at high elevation (2000 metres above sea level), and the second set is at low elevation (300 metres above sea level). The sites in each pair are separated by the dividing mountain ranges of the western Americas *(b)*. We placed ~100 km^2 quadrats over each of focal sites to assess that area’s assemblage of mammals and amphibians. Minimum and maximum monthly temperatures were extracted, pixel by pixel, throughout the Americas *(c)*. We used these values to quantify thermal overlap between each

focal site and all others using Janzen's equation *(d)*. R_{1i} is the seasonal thermal regime of a focal site, R_{2i} is the thermal regime for a compared site, and d_i is the overlap between them. This resulted in 404 thermal overlap maps of the Americas, relative to each focal site *(e)*. Thermal overlap ranges from pale yellow, which represents complete overlap between two thermal regimes for every month (a value of 12) to purple, which represents maximum observed separation between thermal regimes (i.e., areas with negative values indicates a substantial thermal regime difference with respect to this example focal site). A thermal barrier between two sites is the maximum difference in thermal overlap encountered between them (*f*).

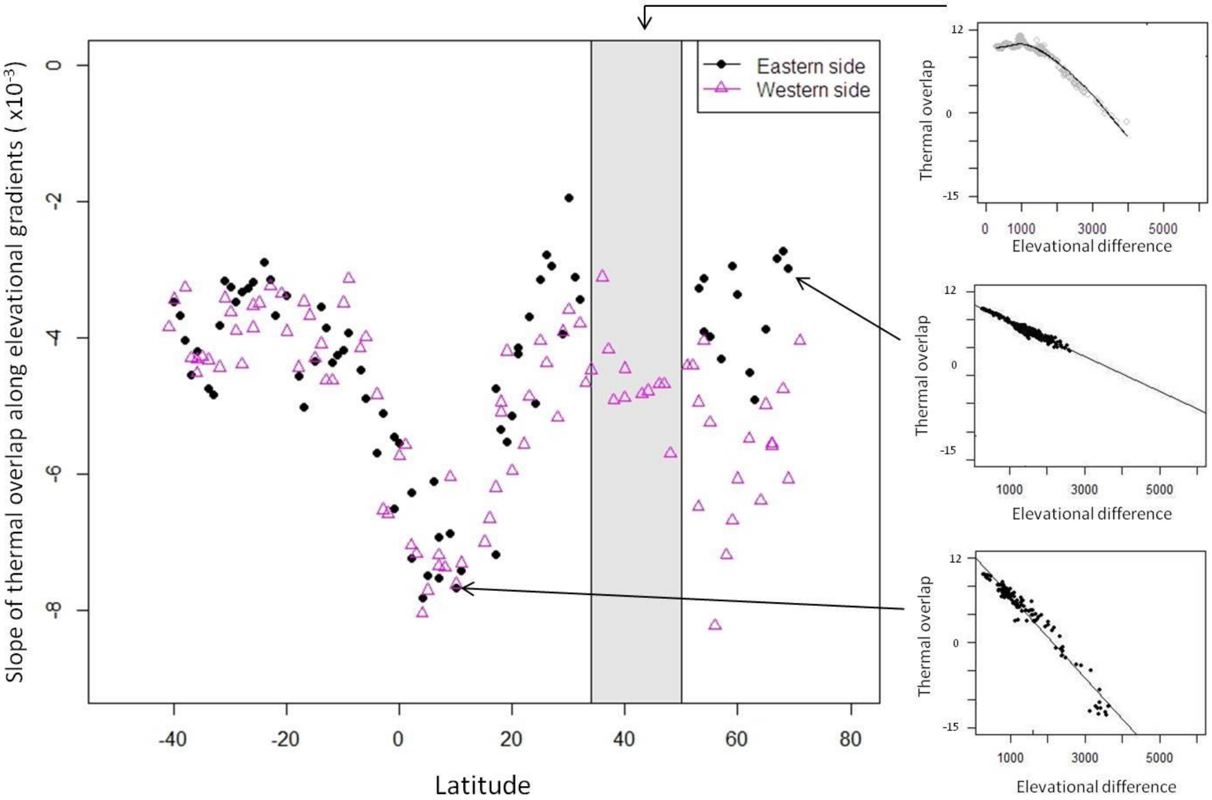

Figure 1.2. Changing thermal overlap relative to latitude along elevational gradients in the mountain ranges of the Americas. Black dots (left panel) represent slopes of thermal overlap relative to elevation measured from east of the dividing mountain ranges to the peak elevation within them, while magenta triangles represent same trend measured from the west. The gray region indicates an area where thermal overlap is not linearly related to elevation and linear regression slope values are consequently not shown. Two panels on the right give detailed examples showing how thermal overlap changes apparently linearly from low with elevation in many areas. The middle panel on the right shows a shallow thermal overlap slope (s= - 2.97 X 10^{-3}) for temperate zones and the third panel shows the steepest thermal overlap slope (s= -7.23 X 10^{-3}) for tropical regions.

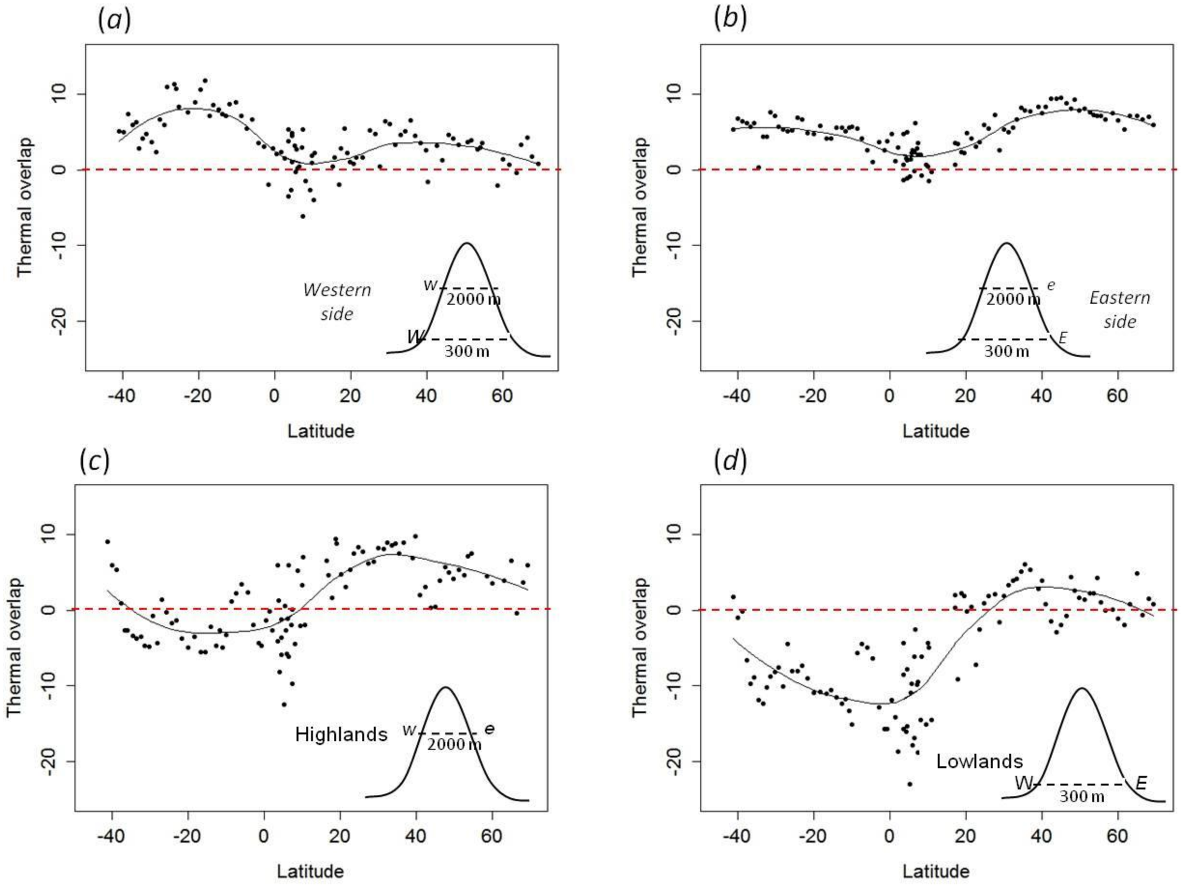

Figure 1.3. Maximum difference in thermal overlap between two sites across dividing mountain ranges in the Americas. Focal sites being compared along an elevational gradient are (*a*) low to high elevation focal sites on the western slopes of mountain ranges shown in Figure 1.1a, (*b*) low to high elevation focal sites along the eastern slopes of those mountain ranges, (*c*) focal sites between high elevations and (*d*) focal sites between low elevations. For instance, (*a*) shows the maximum difference in thermal overlap encountered between a low elevation focal site at 300 m (*W*) and a nearby high elevation focal site at 2000 m (*w*). This difference in thermal overlap represents the thermal barrier that an organism must overcome when dispersing between focal sites. Scatterplots with Loess curves are shown. Dashed lines show the point at which thermal overlap declines to zero.

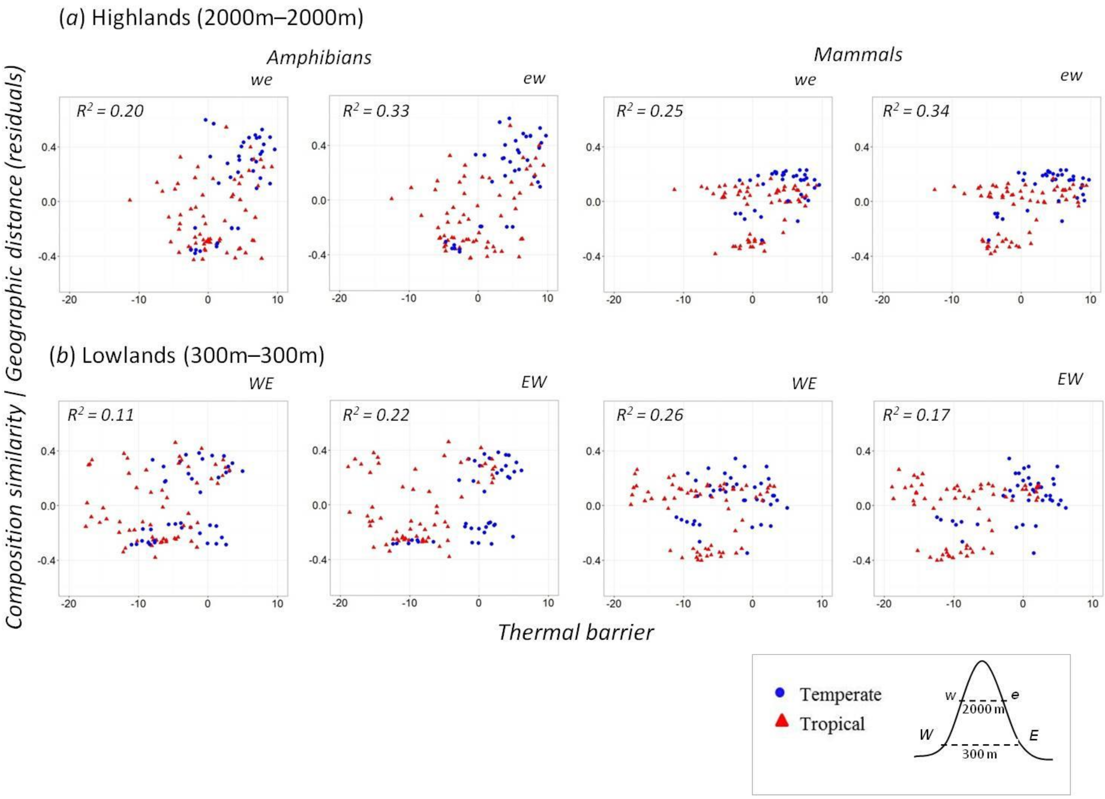

Figure 1.4. Relationships between assemblage similarity for amphibians and mammals as a function of the maximum thermal overlap (controlling for pairwise geographic distances) between quadrats located at (*a*) high elevations (2000 m) and (*b*) low elevations (300 m). Red triangles represent tropical pairwise comparisons and blue dots represent temperate ones. Letters in the top right of each graph indicate the focal site from which the thermal overlap was measured (note that quadrats are centered on each focal site). For instance, in the first graph, *we* indicates focal sites located at 2000 m, one set in the west (*w*) and the other set in the east (*e*). The first letter indicates which focal site was used to initiate thermal overlap measurements. For instance, *we* uses the thermal overlap value calculated from a focal site located to the west (*w*, at 2000 m), whereas in the second graph (*ew*), the thermal overlap value used is from a focal site located to the east of the dividing range (*e*, at 2000 m). Stronger thermal barriers between sites are suggested by negative thermal overlap values.

CHAPTER 2. The origins and maintenance of global species endemism

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Note: this paper was submitted to Global Ecology and Biogeography and the editor invited submission of a revised version of the manuscript.

ABSTRACT

Aim

We test macroecological hypotheses (*H1: climate stability; H2: climate seasonality; H3: climate distinctiveness or rarity; and, H4: spatial heterogeneity in contemporary climate, topography or habitat*) to predict broad-scale patterns of total species endemism.

Location

Continental areas worldwide and zoogeographic realms.

Methods

Using species distributions maps for mammals and amphibians, we calculated five metrics of species endemism at different spatial resolutions, based on range sizes cut-offs and inverse and median range size. We performed regression analyses, and we tested the accuracy of fitted models using a cross-continental approach, comparing observed vs. predicted values of endemism.

Results

Simple correlations with all variables were statistically significant, but the variance explained was low to moderate. Endemism was not consistently related to metrics of climate stability. This was complicated by the fact that measurements of climate stability were highly collinear with spatial heterogeneity an effect that increased at coarser resolutions. Endemism was not systematically higher in areas of high species richness. Despite low variance explained, spatial heterogeneity in potential evapotranspiration was the most consistent predictor in all models. The relationships were not predictive across zoogeographic realms.

Main conclusions

Our results do not consistently indicate that any of the hypothesized processes creates and maintains global patterns of endemism. Although we found significant relationships, they failed the stronger test of a causal relationship: accurate prediction in independent data. The inconsistent effect of richness in our models suggests that patterns of endemism are not driven by the same variables as total richness. Neither were patterns of endemism consistently related to measurements of climatic stability, suggesting that earlier correlations in some places probably reflect collinearity with spatial heterogeneity.

INTRODUCTION

Exceptional numbers of species with relatively small ranges are concentrated in some regions of the Earth (Jetz & Rahbek, 2002), creating broad-scale patterns of species endemism (Lamoreux *et al.*, 2006). Although several factors have been proposed to explain these patterns, including climate, spatial heterogeneity, historical factors, and biotic interactions (Fjeldså & Lovett, 1997; Jansson, 2003; Ohlemüller *et al.*, 2008b; Sandel *et al.*, 2011), their relative roles are still contentious.

One prominent hypothesis invoking the effect of historical climate on species endemism (H1: *climate stability hypothesis*) (Dynesius & Jansson, 2000; Jansson & Dynesius, 2002) suggests that recurrent and rapid climatic shifts, caused by periodic changes in the orbit of the Earth during the Quaternary (i.e., Milankovitch oscillations over 10-100 thousand year periods; Berger (1988)), have led to significant changes in the size and the location of the geographical distributions of clades. Orbitally-forced species range dynamics may contribute to present-day gradients of endemism in three ways (Dynesius & Jansson, 2000). First, areas of high climatic instability may select for species with high dispersal abilities that enable them to track rapid spatial displacement of climatic conditions, resulting in species with broader distributions. Second, climatic instability may reduce the likelihood of specialization on a narrow array of climatic conditions, which could reduce speciation rates and limit the evolution of novel clades. Third, areas with unstable climates may have higher extinction rates, with small-ranged species facing greater extinction risks because of challenges of surviving stronger climatic variability. In contrast, areas of high climatic stability select for species with low dispersal capabilities, offering opportunities for persistence and further diversification. Sandel *et al.* (2011) show that species with broad geographical ranges are associated with areas of high climate-change velocity (a variable that measures climate stability) during the Last Glacial Maximum (LGM - 21,000 years ago). They further argue that species with small range sizes and low dispersal capabilities have gone extinct in areas with high climate velocity, most likely because they were unable to cope with strong climate displacement prevalent in these areas (Sandel *et al.*, 2011). Fjeldså and Lovett (1997) offer another perspective: environmentally-stable areas may have enabled survival and concentration of young species with small ranges, and also of relictual taxa with comparably narrow ranges. Extinction in climatically unstable areas is not essential to explain macroecological patterns in this model of endemism (Fjeldså & Lovett, 1997).

A second set of hypotheses proposes that contemporary climate shapes the spatial distribution of endemism. First, great seasonal variation in temperature may select for species that can tolerate a wider temperature range (Sunday *et al.*, 2011), resulting in species with wider climatic niches and therefore larger geographic ranges. In contrast, low seasonality may select for species with narrower thermal tolerances, resulting in species with smaller geographic ranges (H2: *climate seasonality hypothesis*) (Addo-Bediako *et al.*, 2000). Second, areas that are climatically distinct from their regional surroundings may select for species adapted to these conditions, which in turn may promote small range sizes in those localities (H3*: climate distinctiveness or rarity*) (Ohlemüller *et al.*, 2008b).

Another hypothesis proposes that spatial heterogeneity (H4: *Spatial heterogeneity in contemporary climate, topography or habitat*) is the main factor that creates and maintains patterns of species endemism. Spatial heterogeneity creates more ecological niche opportunities and resource partitioning in a given region (Chesson, 2000), and it promotes the persistence, adaptation and diversification of range-restricted species (Jetz & Rahbek, 2002; Ohlemüller *et al.*, 2008b).

In sum, several environmental drivers (climate – whether past or current - and/or spatial heterogeneity) could shape spatial variation in the richness of range-restricted species. If one or more of these are the drivers of global variation in endemic richness, they must not only be statistically significant and explain substantial variance in gradients of endemic species richness (Møller & Jennions, 2002), but also how well the model makes predictions for data against which it has not yet been tested (i.e., whether the model can only be fit retrospectively to existing data or predict trends successfully in independent areas). A model's greatest test is in whether it is rigorously validated (Wenger & Olden, 2012). Notwithstanding that the hypotheses mentioned above have received some support, tests of those models against independent data have not yet been undertaken. If such factors drive global variation in endemic richness, then consistent relationships between predictor variables and endemic richness should be observed (Møller & Jennions, 2002) and models should predict the response variable (Rykiel, 1996). That is, patterns of endemism should relate consistently to geographic variation of these drivers and models should be not only an adequate representation of broad-scale patterns of endemism but an indication of how much confidence we can place in inferences about the real system that are based on models' outcomes. This is important because the core purpose of this work is to identify meaningful potential determinants of endemism and the extent to which these determinants are consistent across regions (Wenger & Olden, 2012).

Here, we test each of these hypotheses by examining to what extent broad-scale patterns of endemism related to the aspects of temporal and spatial climatic stability and heterogeneity using different metrics of endemism. We evaluate the robustness of the statistical models using cross-continental validation. Finally, we ask whether the strength of the signal is strong enough to yield informative predictions of numbers of endemic species in independent geographic areas, that is, whether the predictions are unbiased.

MATERIAL AND METHODS

Species distributions

We used worldwide species distribution maps (IUCN, 2014) for terrestrial mammals (n=5291) and amphibians (n=6312) and projected them onto the World-Behrmann projection to preserve area across the extent of the analysis.

Spatial resolution

To test for the effect of spatial resolution, we used various spatial resolutions. First, we overlaid vector maps of species distributions onto grids of approximately 1 degree (*c.* 110 km X 110 km), the finest spatial resolution that is appropriate for this broad scale analysis (Hurlbert & Jetz, 2007; Buckley & Jetz, 2008). Given the likelihood of scale dependence in patterns of species endemism (Belmaker & Jetz, 2011), and given that other studies have reported results at coarser spatial resolutions (Sandel *et al.*, 2011), we repeated analyses at three additional spatial resolutions (*c.* 200 X 200, 500 X 500 and 1000 X 1000 km). We included only grid cells consisting of more than 50% land area.

Measuring species endemism

We constructed five metrics of endemism for each amphibian and mammal assemblage in a quadrat. Our operational definition of endemism is: a concentration of species with small geographic range size. For the first three metrics, we ordered species by range size, from smallest to largest, and we retained species when their range sizes fell within one of three cut-offs. First, we counted species as endemic if their ranges fell within the smallest quartile (25%) of the taxon's range size (Jetz & Rahbek, 2002). The second cut-off was an arbitrary, but commonly selected, range size of 50,000 km^2 (e.g., BirdLife International), which includes 71% of amphibians ($n_{\text{small-ranged}}$ = 4527) and 34% of mammals ($n_{\text{small-ranged}}$ = 1815). The third threshold was 250,000 km^2, which includes 85% of amphibians ($n_{\text{small-ranged}}$ = 5354) and 54% of mammals ($n_{\text{small-ranged}}$ = 2854), which we used to compare differences among regions in the endemism-climate relationship (Sandel *et al.*, 2011). We overlaid the species' ranges that satisfied each of these criteria, and we summed up the number of endemic species of mammals and amphibians in each grid cell. For the fourth metric of endemism, we wished to avoid defining arbitrary range-size cut-offs (as described above), so we calculated species endemism by counting all species within each grid cell, but we weighted the count by the inverse of each species' range size (hereafter, WE or weighted endemism) (Crisp *et al.*, 2001). The final metric is based on median range size (hereafter Median) of all species occurring in a grid cell. Because range size distributions are positively skewed, median range size is recommended instead of mean range size (Orme *et al.*, 2006).

Spatial taxonomic congruence of patterns of endemism

To measure the spatial taxonomic congruence of patterns of endemism, we compared the geographic variation of endemism for mammals and amphibians (i.e., taxonomic congruence) (Lamoreux *et al.*, 2006). For metrics based on range-size cut-offs (first quartile, 50,000 km^2, 250,000 km^2), we compared the proportions of endemics in each of the four quartiles of range size (smallest quartile, etc.) between the two taxonomic groups. For WE and Median, we calculated the difference between amphibians and mammals' endemism values.

Climate and geographical predictors

To test the role of past and present climatic conditions on endemism, we used a set of variables from various sources. From WorldClim (Hijmans *et al.*, 2005) at 2.5 arc-minute resolution we used mean annual temperature (MAT), temperature seasonality (TS), total annual precipitation (PT), precipitation seasonality (PS, the distribution of precipitation throughout the year), mean annual temperature during Last Glacial Maximum (LGM, from the Community Climate System Model: CCSM4), and altitude. Potential evapotranspiration (PET) at 30 arc-second resolution was obtained from Trabuco and Zommer (2009) and the global dataset of yearly actual evapotranspiration (AET, 5 arc-minutes) was downloaded from the Food and Agriculture Organization of the United Nations (http://www.fao.org/geonetwork). Glaciated areas were extracted from the broad-scale vegetation map representing the Last Glacial Maximum (LGM) period (Ray & Adams, 2001). We projected all grids to the World-Behrmann equal area projection.

To measure climate stability we used climate velocity (CV) as a metric that represents the displacement of climate in units of distance (meters) per time (years) (Loarie *et al.*, 2009). So, CV is the ratio between the temporal and spatial components of mean annual temperature (MAT and MAT_LGM). The temporal component is the absolute difference between current MAT and past MAT_LGM (in °C/year) in a cell. The spatial component is the change of MAT relative to distance, that is the change of MAT from grid cell to grid cell (in °C/m). We derived the spatial component from the calculated slope using the 'slope' function in ArcGIS 10.3 (ESRI, 2014).

We adjusted areas with slopes equal to zero to small values (0.00001) to circumvent the issue of dividing by zero (Sandel *et al.*, 2011).

To measure climate seasonality, we used two proxies for temperature and precipitation seasonality (TS and PS respectively). Climate distinctiveness (CD), or rarity, was calculated for mainland grid cells at each spatial resolution to assess the area across which climatic conditions were comparable within a moving window of 11 grid cells (Ohlemüller *et al.*, 2008b). We searched for similar climates within a moving window for each climatic measurement using four thresholds for each climatic metric. These were 1. MAT: ±0.5°C, ±1°C, ±2°C and ±4°C; 2. PT±10mm, ±100mm, ±200mm, ±500mm; 3. PS: ±5mm, ±10mm, ±20mm and ±50mm; 4. TS: ±10mm, ±100mm, ±500mm, ±1000mm. For each metric and threshold, we added up the number of cells with climates outside these ranges, and we standardized this sum by the total number of cells in that window. For example, a grid cell surrounded by areas with distinctive climatic conditions has a regionally rare climate (CD values approaching 1). In contrast, CD values approaching 0 indicate climates similar to surrounding areas. We also tested for effects of different moving windows (5, 11 and 15 cells for each resolution). We excluded islands because they were sensitive to this moving window. For instance, a measurement of CD for a grid cell on a Caribbean island, based on a large moving window, is affected by continental cell values (which clearly are not connected with the island in question). Therefore, we included only mainland areas for each continent.

To measure spatial heterogeneity (SH), we calculated and compared four metrics that account for most of the spatial variability in climate (AET, PET, and MAT) and topography (ALT, we used elevation from WorldClim). We calculated heterogeneity as both the range and standard deviation for each of these measurements within each grid cell.

Finally, we included variables that may exert effects on patterns of endemism and alter model fit, such as total species richness (Kerr, 1997; Crisp *et al.*, 2001), the area of the continent available for species to disperse (hereafter, Area) (Jetz *et al.*, 2004), and glaciated areas from LGM that may have affected species presence and dispersal (Whittaker *et al.*, 2001) on which each grid cell fell. We aimed to evaluate how suggested mechanisms can drive patterns of species endemism independently of these covariates.

Statistical analysis

Endemism-climate relationship: first approximation

To explain the extent to which patterns of endemism relate to each predictor, we first explored nonparametric correlations coefficients between all metrics of endemism and each predictor. We used Spearman's rank correlation coefficients (r_s) to describe monotonic, often non-linear, relationships.

Model fitting

To explore the relationships between endemism and all predictors, we used conventional ordinary least squares (OLS). We first transformed the dependent variables (WE and Median were the only metrics that allowed transformation, see results) to improve homoscedasticity and normality, and the independent variables to improve linearity and the distributions of the underlying data. We constructed single models that match all four working hypotheses and then evaluated multiple regression models, implementing a model selection approach that identify the best model using the Akaike Information Criterion (AIC) score. For multiple regression models we progressively identified and removed the variable with the highest Variance Inflation Factor value (VIF, a measure of the strength of collinearity between variables) (Griffith, 2003;

Dormann *et al.*, 2013). We retained only variables with VIF<2.5. We evaluated the contribution of each variable using variation partitioning (Legendre & Legendre, 2012). Because we were interested in variables contributing substantially to the total variance explained, we removed variables that explained <2% of the variance and tested interaction for remaining variables. We tested how stable the conclusions were after controlling for spatial autocorrelation using simultaneous autoregressive models (SAR) (Kissling & Carl, 2008). For variables retained in models, we also constructed path analyses to test whether each predictor directly or indirectly affects endemism. To compare and contextualize our results we used the well-documented statistical relationship between AET and richness (Currie, 1991; Hawkins *et al.*, 2003), without implying a causal relationship. We standardized all variables (mean of zero and standard deviation 1) to allow the comparison of path coefficients.

Cross-continental analysis: estimating accuracy of models

To evaluate the capability of models describe above on independent data, we used a cross-continental validation approach (Wenger & Olden, 2012). We split the data into training and testing samples: we used the training sample to build the model and the test sample to evaluate whether the model successfully predicts species endemism in the hold out portion (Olden & Jackson, 2000; Francis & Currie, 2003). Here, we used zoogeographic realms (ZRs) from Holt *et al.* (2013) to split the dataset because they reflect phylogenetic relationships of the major vertebrate taxa (i.e., taxa within a ZR share a similar evolutionary history and differentiate from other ZRs). Using ZRs may inform us whether processes from the hypotheses presented above might have operated leading to different regional patterns of endemism (Ricklefs, 2004). So, we constructed models using data from all ZRs except one, and we then predicted endemism on the hold-out ZR. We repeated this cross-validation procedure for all ZRs. Predicted values of endemism were compared with observed values of endemism for each ZR.

Zero-inflated issue

Metrics of endemism based on range size cut-offs (i.e., QE, 50K km^2 and 250K km^2) tend to contain a large proportion of zero values, representing the absence of species with small geographic ranges. This zero-inflation issue can mislead statistical inferences because zero-inflated datasets do not fit standard distributions (Martin *et al.*, 2005). One way to correct this is by transforming species endemism. However, this process usually does not spread out the zero values, so to deal with this issue we applied two part models, also known as conditional or hurdle models to explain patterns of endemism (Martin *et al.*, 2005). Hurdle models assume that zeroes originate from a single process. The first component (the zero-hurdle component) evaluates species presence or absence and the second component (the count component) counts values using a Poisson error distribution (Stefánsson, 1996). We compared hurdle models with Zero-Inflated Poisson (ZIP) and Poisson models as null hypotheses. So, our purpose here is to test for whether the environmental process described in the hypotheses tested here can explain broad-scale patterns of endemism, using zero-inflated metrics. We considered zero values to be ‘true zeroes’ because we are using species’ ranges resolved at the finest spatial resolution at which it is reasonable to ascertain species’ presence/absence (Buckley & Jetz, 2008).

All statistical analyses were performed in R v 3.2.1 (R Core Team, 2017).

RESULTS

Spatial distribution of broad scale patterns of endemism

As reported in previous studies (Jetz *et al.*, 2004; Lamoreux *et al.*, 2006) range-restricted amphibians and mammals' species are concentrated in tropical and subtropical regions (Figure 1a, Figure S1, S2). However, geographic congruence of mammal and amphibian endemism is not the general rule, and it depends upon the metric used to measure endemism (Figure 1b and Figure S3). The most general pattern is that high numbers of range-restricted species in both taxa are found in tropical mountains but the variation within mountainous regions is quite high (Figure S4a). Range-restricted species often occur in areas of complex spatial heterogeneity, but topographically complex places do not necessarily have higher richness of range-restricted species. Although, range-restricted species thrive in mountainous environments they are also found in low elevations (Figure S4b). Finally, the proportion of range-restricted species within areas of high species richness varies highly and it also depends upon the metric used to measure endemism (Figure S5).

Metrics of endemism

Different metrics of endemism yield divergent patterns. Correlations among metrics of endemism vary considerably (amphibians $|r| = 0.29 – 0.839$; and, mammals $|r| = 0.295$ to 0.859; Table 1a, b). Median and WE showed more spatial similarities ($|r| = 0.731$ and 0.685 for amphibians and mammals respectively). In addition, metrics of endemism at broad spatial scales were correlated with species richness (Table 1c), an effect that increased dramatically at coarser spatial resolutions (Figure S6). Not surprisingly, WE was strongly correlated with total species richness (|r| = 0.85 – 0.74 for amphibians and mammals respectively) and in lower degree Median ((|r| = 0.40 – 0.34).

Endemism and predictors relationships

Endemism among amphibians and mammals relates to all predictors (Table S1). However, the strength of the correlation varied among metrics and generally grew stronger as the range size cut-off increased. Similarly, the strength of correlations increased at coarser spatial resolution, although these relationships varied unexpectedly (Tables S2 and S3).

Single regression models

Variance explained for all predictors ranged from low to moderate, depending on the metric of endemism used in models, taxonomic group, and zoogeographic realm (Table 2). Climate seasonality and climate distinctiveness showed the highest values of variance explained (ranging from 0.306 to 0.408), followed by climate stability and spatial heterogeneity (ranging from 0.161 to 0.301). Climate seasonality models tended to explain more variance in temperate ZRs than tropical ones; but the effect is not consistent across metrics and taxonomic groups. On the other hand, models for climate distinctiveness and spatial heterogeneity tended to show similar variance across ZRs and global models, but some of them showed contrasting values (Table 2). So, there is not a clear signal to claim that similar realms in terms of low seasonality will respond similarly, or vice versa, realms under contrasting seasonality will respond differently.

Cross-continental analyses showed that single-variable models failed to predict broad-scale patterns of endemism (Figure 2). Despite moderate variance explained by some models, they predict poorly areas of high endemism. For instance, cross-continental validation showed that climate seasonality tends to best predict areas with high numbers of species with large ranges, but predict poorly in areas where range-restricted species are concentrated (Figure 2).

Multiple regression models

SH_PET (*Spatial heterogeneity*, *H4*) and Richness consistently arose as the main predictors from the best multiple regression models relating to endemism among amphibians (Table 3 and Figure 3a). In contrast, the best models for mammal endemism varied substantially in that other variables emerged to explain patterns of mammals' endemism, such as CV and MATS, and SH_PET and Richness were dropped from the best models. In addition, models including predictors from different hypotheses, for example: SH_PET and CV (which happened to be highly collinear; VIF = 3-4; Figures S7 and S8) were not more informative (based on AIC; Table 3). Interaction terms did little to render models more informative. In sum, the leading role of climate seasonality in single models is replaced by spatial heterogeneity and, sometimes, by climate stability in multiple regression models (Figure S9 and S10). The fact that in some multiple regression models, total species richness does not appear within the best model and a weak relationship in path analysis, suggest that its role and the processes behind broad-scale patterns of total species richness are decoupled from broad-scale patterns of total species endemism (Figure 3a, 4a and S11).

The effect of SH_PET appeared to be consistent across all path analyses (Figure 3b and 4b). The effect of Richness on Median endemism almost disappeared in the relationship with mammals (Figure 3b), suggesting a minor role of Richness on species endemism. The strong effect of Richness on WE endemism is the result of the autocorrelation between WE and Richness (Figure 4b). Path analysis for the best models showed that AET has strong and direct effects on amphibians and mammals' Richness (Figure 3b and 4b), as reported in previous studies, allowing in some way to calibrate and contextualize our results.

Cross continental validation showed that there is no correlation between the best model and validation correlation. Models tended to overestimate observed values of endemism for both mammals and amphibians, effects that are particularly pronounced in areas of high endemism (Figure 3c and 4c). Finally, OLS models tended to overestimate predicted values of endemism compared to SAR models (Figure S12). However, both OLS and SAR failed to predict broad-scale patterns of endemism (Figure S13). Misspecification of the model most likely arises from the omission of key variable (variables let out from the model) driving endemism. That is, climate and topography may have a role, but other drivers not included in multiple models may have a preponderant role in shaping broad scale patterns of endemism.

Two part models: addressing zero-inflation

Hurdle models better captured the observed zero counts (Table S4 and Figure S14) and predicted places where should be not species at all. However, some models did not predict all observed zero values in cross-continental validation (Figure S15). Models also showed differences ZRs and did not predict well how many endemics should be there. While some models overestimated values of endemic species others underestimated them (Figure S15).

DISCUSSION

There is no empirical reason, from the standpoint of model fitting, parameter estimates and model validation, to claim that any of the hypotheses or combinations of them (*H1, H2, H3 or H4*) adequately account for broad-scale patterns of species endemism among mammals and amphibians. Although all relationships are statistically significant, most of the variance remains unexplained and cross-continental tests of spatial models do not accurately predict observed patterns of endemism in spatially independent continental mainland areas (i.e., ZRs). It suggests that regression models between predictors and endemism do not capture fundamental processes that generate endemism.

We showed that processes tested here are unlikely to create and maintain broad-scale patterns of total species endemism. However, these models suggest that these climatic factors may directly influence endemism within zoogeographical realms. This may explain the signal we have detected for each mechanism and realm-specific differences. Metrics of climate stability (CV) and spatial heterogeneity in climate (SH_PET) are highly collinear and variance explained is low and similar between them, so patterns of endemism can be related to either one or the other. However, what is noteworthy here is that in the model selection approach the best models tend to select for metrics of spatial heterogeneity instead of climate stability. So, the reported influence of climate stability (measured as climate velocity, CV) on global endemism patterns (Sandel *et al.*, 2011) plays a secondary and very small role, at most, after accounting for possible effects of spatial heterogeneity (SH_PET) on numbers of endemic species. That CV dropped out from model selection suggests that CV might be a surrogate of spatial heterogeneity with an element of climate in there. Disentangling the relative roles of long-term climatic stability and spatial heterogeneity in climate on patterns of endemism, even if small, may be consequential in the context of climate change effects on biological diversity. Two-part models including climate stability showed that there are many sites that are predicted to have zero endemic species but have many. Regardless of possible measurement errors or limitations of these data, longterm climate stability may have exerted small, perhaps even undetectable, effects on within-region extinction of endemics, contrary to predictions for that hypothesis (Sandel *et al.*, 2011). So, elevated extinction rates in areas where postglacial climate velocities were high do little to distinguish areas with high endemism from those where endemic species are absent. Palaeoecological studies have shown that biological responses to postglacial climate changes are primarily through changes in species abundance and distributions, rather than on species extinctions (Willis & MacDonald, 2011). Moreover, models based on palaeorecords suggest that many taxa are unlikely to become extinct due to longterm, and presumably relatively gradual, climate changes (Nogués-Bravo *et al.*, 2016).

Although seasonality has also been proposed to influence processes generating endemism, models including seasonality failed a stronger validation test. This mechanism was thought to be amplified in mountainous regions at low-latitudes, where thermal regimes' differences between low and high were considered to be stronger than in mountain ranges in temperate realms (Janzen, 1967). However, recent evidence shows that thermal barriers limiting organismal dispersal are present in temperate realms (Zuloaga & Kerr, 2017), challenging the idea that this mechanism operates exclusively in tropical regions. Future research may explore whether this mechanism might help explain the origins and maintenance of gradients of endemism.

Despite the coincidence of some areas of endemism with rare climates, models based on climatic rarity predict endemism poorly, suggesting that rare climatic combinations do not play a leading role in creating or maintaining patterns of endemism.

Spatial heterogeneity in habitat systematically was the strongest correlate of endemism in all models, but models failed to accurately predict unseen data. We have shown that endemic species are *often* found in mountainous regions (high spatial heterogeneity in habitat (Fjeldså *et* *al.*, 2012)) but they are not *exclusively* present in mountainous areas. Rapid expansion of ranges among endemics since the last LGM might have contributed to endemic becoming more wide-spread. Alternatively, other factors that are contingent and historical, but as yet unmeasured, may be needed to explain where centres of endemism are situated. In addition, historical processes (as well as contemporary climate) may be collinear with some surrogates of spatial heterogeneity (e.g., topography measured as altitudinal range) (Jetz *et al.*, 2004), complicating prospects for distinguishing between historical and contemporary processes along topographical gradients.

Gradients of species endemism can be clearly distinguished from underlying gradients of species richness, suggesting that the two patterns arose from different processes. The facts that models incorporating richness explained little variance of endemism for amphibians (except for metrics that are by nature correlated with Richness) and that their effects tend to disappear in path analyses reinforces the idea that species endemism is not a consequence of species richness. Globally, the richness of small-ranged species is not well correlated with total species richness (Rahbek *et al.*, 2007). So, processes creating and maintaining broad-scale patterns of endemism must be decoupled from those of species richness. Total species richness is unlikely to be an effective surrogate or indicator of biotic interactions. Research into metrics that can capture local biotic interactions and scale them up for broad scale analyses would be valuable in efforts to explain and predict gradients of endemic species.

If existing hypotheses do not explain the origin and maintenance of broad-scale patterns of endemism simply or consistently and drivers and processes explaining the origins and maintenance of species richness are distinct from those contributing to endemism, how are centres of high endemicity formed? It is likely that local factors, whether biotic or abiotic, contribute to patterns of endemism and broad-scale analyses do not account for such relatively localized effects. Species responses to climate are strongly scale-dependent (Schweiger & Beierkuhnlein, 2016). Even though abiotic factors predominantly operate at larger scales (Willis & Whittaker, 2002) some climatic variables acting at local scales may shape species distributions more strongly than factors commonly measured in macroecological analyses (Lennon *et al.*, 2011; Opedal *et al.*, 2015). For instance, microclimates reduce species exposure to broad-scale climatic trends that dominate a region, potentially permitting their persistence in areas that are generally no longer suitable (Maclean *et al.*, 2015). Indeed, temperature, precipitation and radiation can be modulated by topography and/or vegetation (De Frenne *et al.*, 2013). Secondly, it has been also suggested that biotic factors may have a strong influence on species distribution at local scales (Jablonski, 2008) and some studies have shown macroecological signals of species interactions acting locally (Gotelli *et al.*, 2010). Further research may integrate biotic factors, such as competition (Mordecai *et al.*, 2016) and local coexistance (Godsoe *et al.*, 2015), specialization (Fjeldså & Lovett, 1997), population and community dynamics (Locey & Lennon, 2016; Ralston *et al.*, 2016), and niche differentiation (Brown *et al.*, 2013). So, biotic and abiotic factors operating at local scales may interact contingently in small areas, spurring opportunities for diversification or reducing local extinction rates or both. That so many centres of endemism are located in mountainous areas suggests that such combinations of local conditions and/or intrinsic biotic traits are more likely to occur in those areas.

Region-specific responses also suggest that historical contingency or the distinct origin of continental biotas may play an important role in modulating the number of endemic species in areas of high endemism. These include distinct historical factors (Haffer, 1969; Rahbek *et al.*, 2007) and biogeographical asymmetry (biota origin effects) between regions (Fjeldså *et al.*, 1997) or processes (other than environmental filtering) that may lead to the geographic accumulation of phylogenetically distinct and range restricted species (Rosauer & Jetz, 2015). Further research might evaluate whether region-specific historical factors might alter potential effects of contemporary or historical environmental conditions (e.g., spatial heterogeneity of climate, or climate velocity) on endemism. Lack of congruence of patterns of species endemism between taxonomic groups also suggests that local biotic and abiotic conditions may lead to taxon-specific responses.

Dispersal is another intrinsic species trait that likely contributes to present-day species distributions (Leroux *et al.*, 2013). This study did not attempt to evaluate potential roles for dispersal limitation in shaping patterns of endemism. We note that other methodological challenges complicate efforts to distinguish historical and contemporary influences on endemism. We demonstrate that these obstacles can be overcome to enable clear tests of causal hypotheses. Challenges include: (i) the spatial resolution of the analysis (Buckley & Jetz, 2008) (ii) the nature of metrics to measure species endemism (Crisp *et al.*, 2001) (iii) collinearity between predictors (Dormann *et al.*, 2013) (iv) the unusual statistical properties of spatial patterns of species endemism, such as zero-inflation (i.e., excess of zeros in data sets) (Martin *et al.*, 2005) and (v) the strong correlation between metrics of species endemism and species richness, and the way metrics are corrected for this effect (Crisp *et al.*, 2001). In addition to these issues, conclusions around the roles any of these hypotheses in shaping gradients of endemism typically emphasize statistical significance of models or the strength of observed signals (variance explained), rather than the capacity of models to predict endemism in spatially independent areas, such as on different continents.

Generating accurate predictive models on how species might persist at small population sizes and in spatially restricted areas is needed to improve predictions for how changing environmental conditions will affect the origins and maintenance of the world’s centres of endemism. Models from macroecological hypotheses tested here have failed to pass stronger tests, suggesting that broad-scale main mechanism and drivers are yet to be discovered.

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TABLES

Table 2.1. Spearman's rank correlation coefficients among metrics of endemism for a) amphibians and b) mammals; and, c) between total species richness and five metrics of endemism. Metrics of endemism were constructed using range size cut-offs (first quartile, 50K km^2 and 250K km^2), inverse range size (Weighted endemism, WE) and median range size (Median). Note that the negative correlations involving Median are to be expected: larger median range size implies fewer range-restricted species.

a) Correlation coefficients among metrics of amphibians' endemism

	Quartile	50K km^2	250K km^2	WE
Quartile				
50K km^2	0.537			
250K km^2	0.423	0.765		
WE	0.413	0.708	0.839	
Median	-0.279	-0.485	-0.611	-0.731

b) Correlation coefficients among metrics of mammals' endemism

	Quartile	50K km^2	250K km^2	WE
Quartile				
50K km^2	0.731			
250K km^2	0.501	0.665		
WE	0.549	0.683	0.859	
Median	-0.295	-0.391	-0.517	-0.685

c) Correlation coefficients between endemism and total species richness

Metric of Endemism	Amphibians total richness	Mammals total richness
Quartile	0.29	0.31
50,000 Km2	0.48	0.36
250,000 Km2	0.61	0.55
WE	0.85	0.74
Median	-0.40	-0.34

Table 2.2. Estimates from the relationship between endemism for a) amphibians and b) mammals and various predictors. We presented results for two metrics of endemism that we could transform: Median range size = Sqrt(Median) and Weighted endemism = Log_{10}(WE). For predictors, we used: CV = Log10(Climate velocity); MATS = Seasonality in mean annual temperature; CD_PT = Climate distinctiveness (rarity) in total precipitation; and, SH_PET = Log_{10}(Spatial heterogeneity in potential evapotranspiration).

		Amphibians $^{\pounds}$		Mammals §	
Hypotheses (Model)	Model	Sqrt (Median)	Log_{10} (WE)	Sqrt (Median)	Log_{10} (WE)
H1: Climate stability	Global model	0.188	0.188	0.181	0.301
(Endemism ~ CV)	*Afrotropical*	0.208	0.306	0.148	0.321
	Australian	0.264	0.324	0.369	0.325
	Nearctic	0.086	0.065	0.235	0.428
	Neotropical	0.362	0.189	0.216	0.168
	Oriental	0.399	0.326	0.368	0.310
	Palearctic	0.159	0.101	0.162	0.310
	Panamanian	0.487	0.609	0.114	0.289
	Saharo-Arabian	0.022	0.272	0.474	0.377
	Sino-Japanese	0.495	0.138	0.422	0.192
H2: Climate seasonality	Global model	0.198	0.408	0.205	0.345
(Endemism ~ MATS)	*Afrotropical*	0.226	0.273	0.331	0.343
	Australian	0.256	0.357	0.447	0.272
	Nearctic	0.733	0.615	0.669	0.659
	Neotropical	0.256	0.040	0.412	0.004**
	Oriental	0.364	0.296	0.520	0.229
	Palearctic	0.387	0.449	0.312	0.260
	Panamanian	0.045*	0.136	0.149	0.022.
	Saharo-Arabian	0.138	0.026	NS	NS
	Sino-Japanese	0.529	0.314	0.297	0.254
H3: Climate distinctiveness	Global model	0.120	0.306	0.153	0.334
(Endemism ~ CD_PT)	*Afrotropical*	0.056	0.197	0.257	0.328
	Australian	0.300	0.462	0.478	0.262
	Nearctic	0.177	0.131	0.070	0.111
	Neotropical	0.372	0.094	0.412	0.037
	Oriental	0.111	0.104	0.156	0.094
	Palearctic	0.153	0.145	0.064	0.151
	Panamanian	NS	0.025.	0.063*	NS
	Saharo-Arabian	0.017**	0.204	0.523	0.370
	Sino-Japanese	0.034	0.137	NS	0.189
H4: Spatial heterogeneity	Global model	0.222	0.161	0.179	0.239
(Endemism ~ SH_PET)	*Afrotropical*	0.144	0.209	0.075	0.206
	Australian	0.267	0.361	0.349	0.294
	Nearctic	0.207	0.163	0.354	0.489
	Neotropical	0.373	0.169	0.204	0.180
	Oriental	0.180	0.162	0.137	0.168

Palearctic	*0.239*	*0.170*	*0.238*	*0.340*
Panamanian	*0.240*	*0.387*	*0.221*	*0.213*
Saharo-Arabian	*0.009**	*0.200*	*0.424*	*0.421*
Sino-Japanese	*0.381*	*0.080*	*0.292*	*0.194*

All r^2 signifiant (***) unless other specified

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1 and *NS* =No significant

[£] sample size for full models (n=9273)

[§] sample size for full models (n=10443)

Table 2.3. Model selection for amphibians (a, b) and mammals' (c, d) endemism (Weighted endemism = *WE* (*a*, *c*); and Median range size (*b*, *d*)) as a function of various predictors: *CV* = Log10(Climate velocity for); MATS = seasonality in mean annual temperature; *CD_PT* = Climate distinctiveness (rarity) in total precipitation; *SH_PET* = Log$_{10}$(*Spatial heterogeneity* in potential evapotranspiration); and, *Richness* = Total species richness. In bold best model.

a) Amphibians (Weighted Endemism, WE)

Model WE ~	R^2	Rank by AICc	AICc	Delta AICc (Δ_i)	Weight AIC
SH_PET + Richness	**0.710**	**1**	**21204.6**	**0.00**	**1**
CV + Richness	0.699	2	21555.0	350.42	0
CD_PT + Richness	0.603	3	24136.0	2931.41	0
Richness	0.586	4	24506.7	3302.10	0
SH_PET + MATS	0.506	5	26145.9	4941.29	0
CV + MATS	0.481	6	26618.5	5413.85	0
MATS + CD_PT	0.463	7	26921.1	5716.48	0
MATS	0.408	8	27830.6	6626.00	0
SH_PET + CD_PT	0.372	9	28384.4	7179.77	0
CV + CD_PT	0.368	10	28436.3	7231.73	0
CD_PT	0.306	11	29310.8	8106.15	0
SH_PET + CV	0.198	12	30644.6	9440.01	0
CV	0.188	13	30761.4	9556.82	0
SH_PET	0.161	14	31063.2	9858.60	0

b) Amphibians (Median Endemism)

Model Median ~	R^2	Rank by AICc	AICc	Delta AICc (Δ_i)	Weight AIC
SH_PET + Richness	**0.379**	**1**	**146645.0**	**0.00**	**1**
SH_PET + MATS	0.368	2	140864.1	159.13	0
CV + Richness	0.327	3	147396.1	751.11	0
CV + MATS	0.304	4	147708.0	1063.00	0
SH_PET + CD_PT	0.273	5	148108.8	1463.85	0
SH_PET + CV	0.234	6	148591.2	1946.25	0
CV + CD_PT	0.230	7	148640.8	1995.81	0
SH_PET	0.223	8	148725.6	2080.67	0
MATS + CD_PT	0.212	9	148858.9	2213.91	
MATS	0.198	10	149119.7	2374.75	0
CD_PT + Richness	0.195	11	149050.3	2405.29	0
CV	0.189	12	149123.9	2478.96	0
Richness	0.181	13	149213.5	2568.56	0
CD_PT	0.120	14	149874.8	3229.79	0

c) Mammals (Weighted Endemism, WE)

Model WE ~	R^2	Rank by AICc	AICc	Delta AICc (Δ_i)	Weight AIC
CV + Richness	**0.585**	**1**	**14594.1**	**0.00**	**1**
SH_PET + Richness	0.582	2	14676.8	82.62	0
SH_PET + MATS	0.512	3	16288.5	1694.34	0
CV + MATS	0.509	4	16349.5	1755.35	0
CD_PT + Richness	0.502	5	16514.6	1920.49	0
Richness	0.472	6	17127.3	2533.13	0
CV + CD_PT	0.466	7	17230.4	2636.25	0
MATS + CD_PT	0.448	8	17579.8	2985.68	0
SH_PET + CD_PT	0.448	9	17591.3	2997.16	0
MATS	0.345	10	19370.8	4776.68	0
CD_PT	0.334	11	19550.3	4956.19	0
SH_PET + CV	0.309	12	19923.9	5329.81	0
CV	0.301	13	20044.4	5450.30	0
SH_PET	0.238	14	20947.5	6353.39	0

d) Mammals (Median Endemism)

Model Median ~	R^2	Rank by AICc	AICc	Delta AICc (Δ_i)	Weight AIC
SH_PET + MATS	**0.337**	**1**	**188533.8**	**0.00**	**1**
CV + MATS	0.304	2	189035.1	501.32	0
SH_PET + CD_PT	0.259	3	189696.0	1162.26	0
CV + CD_PT	0.260	4	189882.8	1349.01	0
MATS + CD_PT	0.239	5	189976.5	1442.72	0
SH_PET + Richness	0.234	6	190047.6	1513.84	0
CV + Richness	0.220	7	190237.4	1703.59	0
MATS	0.205	8	190430.8	1897.01	0
SH_PET + CV	0.202	9	190472.8	1939.02	0
CV	0.181	10	190736.7	2202.88	0
SH_PET	0.180	11	190758.1	2224.31	0
CD_PT + Richness	0.162	12	190979.1	2445.28	0
CD_PT	0.153	13	191095.4	2561.57	0
Richness	0.107	14	191639.4	3105.60	0

FIGURES

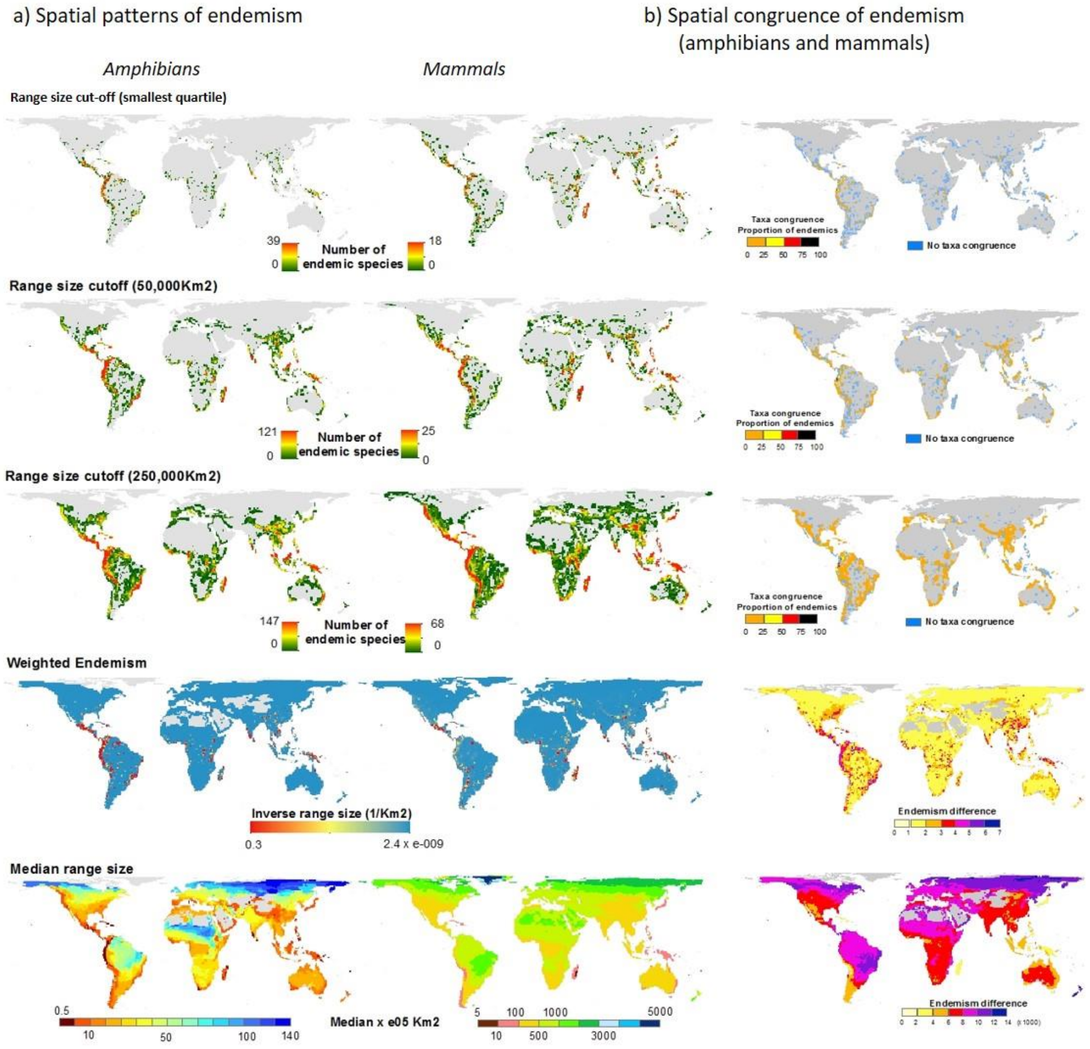


Figure 2.1. Broad-scale patterns of endemism (a) spatial distribution of mammals and amphibians' endemism, and (b) areas of taxonomic congruence within major centers of endemism (i.e., overlapping areas of endemics species for mammals and amphibians at 100 km x 100 km spatial resolution). Taxonomic congruence was measured as follows: for metrics based on range size cut-offs (smallest quartile, 50,000 km^2, 250,000 km^2) we used four bins for proportion of endemics (0-25%, 25-50%, 50-75% and 75-100%). For metrics based on inverse range size (weighted endemism, WE) and median range size (Median), we calculated the difference between amphibians and mammals' endemism values.

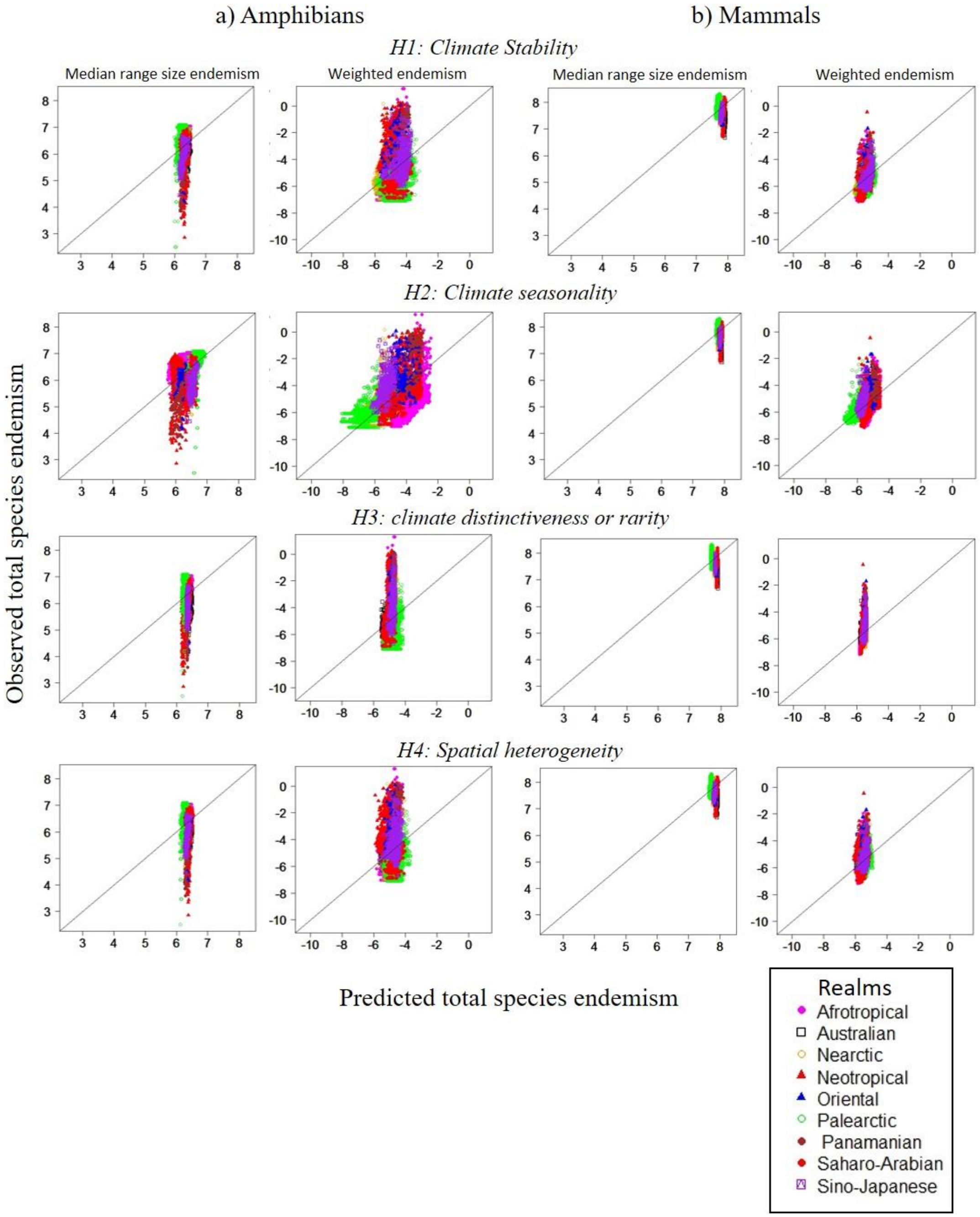
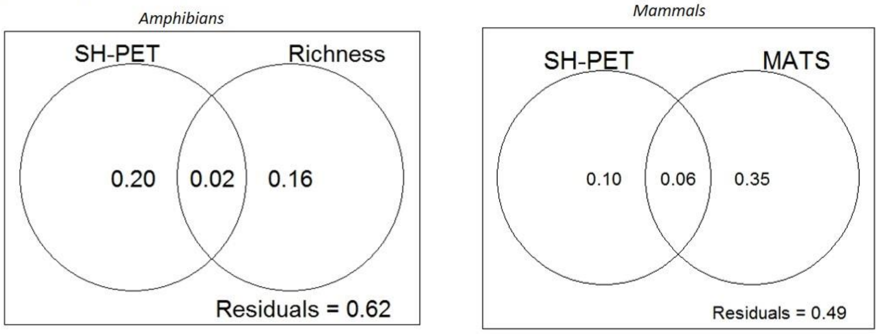


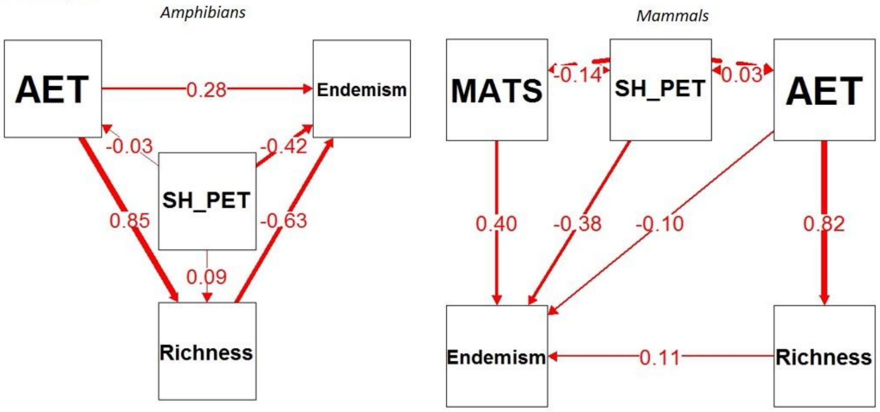
Figure 2.2. Observed vs predicted values of broad-scale patterns of total species endemism (Log_{10}) for a) amphibians and b) mammals using a cross-continental approach (i.e., models used the data from all zoogeographic realms from Holt *et al.* (2013) except one to then predict endemism on the hold-out continent). We tested four *hypotheses* (predictors): *H1: Climate*

stability (Climate velocity); *H2: Climate seasonality* (Seasonality in mean annual temperature); *H3*: *Climate distinctiveness* (in total precipitation, CD_PT); and, *H4: Spatial heterogeneity* (in potential evapotranspiration SH_PET)). We tested two metrics of endemism: median range size and weighted endemism. Results are shown for SAR models.

a) Variance partitioning



b) Path analysis



c) Cross-continental validation

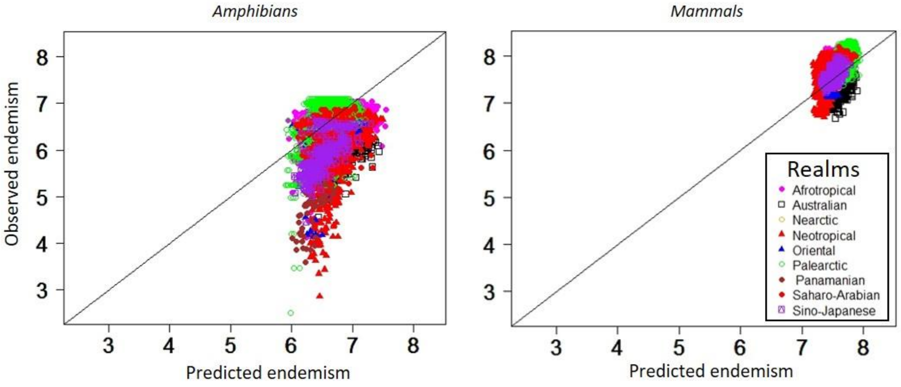


Figure 2.3. Best models predicting broad scale patterns of Endemism (using Median range size as a metric of endemism) for amphibians (graphs on the left) and mammals (graphs on the right). a) variance partitioning, b) path analysis and c) Cross-continental validation for best models. MATS = Seasonality in mean annual temperature; SH_PET = Spatial heterogeneity in potential evapotranspiration; AET = Actual evapotranspiration; and, Richness = Total species richness.

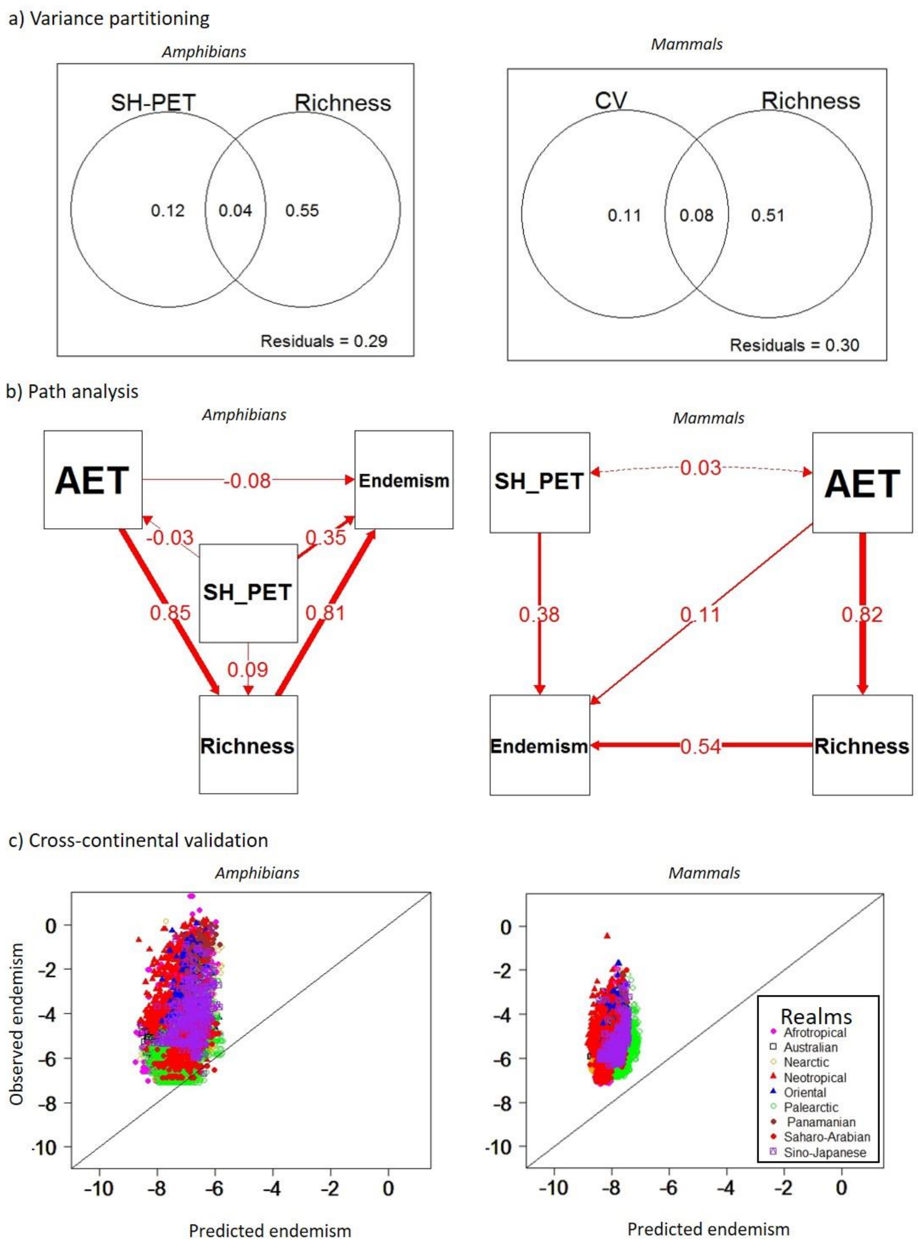


Figure 2.4. Best models predicting broad scale patterns of endemism, using log(Weighted Endemism) as a metric of endemism for amphibians (graphs on the left) and mammals (graphs on the right). a) variance partitioning, b) path analysis and c) Cross-continental validation for best models. Seasonality = Seasonality in mean annual temperature; SH_PET = Spatial heterogeneity in potential evapotranspiration; AET = Actual evapotranspiration; and, Richness = Total species richness.

CHAPTER 3. Endemic species coverage by the global protected areas network

ABSTRACT

Protected areas (PAs) are one of the main tools for halting habitat degradation and biodiversity loss worldwide. By 2020, governments have agreed to expand the terrestrial protected area network from 13% to 17% of the Earth's surface (Convention on Biological Biodiversity, CBD - Aichi Target 11, 2010). However, it is not clear to what extent this global strategy has protected endemic species. As CBD-Aichi Target 11 deadlines approach, we provide a comprehensive assessment of the impact of terrestrial PAs on endemic species protection. We measure the relative coverage of endemic species (i.e. species with small range size) by overlapping species geographic ranges for amphibians, mammals and birds with a global database of PAs (1990-2016). Then we measure the rate of expansion of the global PA network, and the rate of change in endemic species coverage.

We found that ~30% of amphibian, ~6% of bird, and ~10% of mammal endemic species are completely outside PAs. Most endemic species' ranges intersect the PA network (amphibian species = 58%; birds = 83%; mammals = 86%), but PAs usually cover less than 50% of the geographic range. Almost 50% of species outside the PA network are considered threatened (critically endangered, endangered and vulnerable).

The historic rates of new PAs added every year to the network is between ~6,000 to ~15,000. In contrast, we found that rates of including endemic species within the PA network have been fairly slow. Historic data shows that annually, additions to the PA network result in 3 (amphibians) to 6 (birds and mammals) endemic species having their entire geographic ranges covered by the PA network.

Based on these trends, it is very unlikely the global PA network will include all endemic species (14% total endemic species, that is ~1,508 out of 11,274) currently outside the PA network by 2020. It will require five times the effort made in the last two decades - or a century if current rates of inclusion persist - to include all endemic species currently outside the PA network. However, projections also showed that is very likely that some portions of the endemic species geographic ranges for birds and mammals, but not for amphibians, will be covered by the future PA network.

INTRODUCTION

One of the major challenges in the 21st century is the conservation and sustainable use of biological diversity (CBD, 2104). Land use change (LUC) is the leading factor of habitat and biodiversity loss (Foley *et al.*, 2005; Newbold *et al.*, 2016) and has already degraded more than 60% of ecological systems worldwide (Millennium Ecosystem Assessment, 2005). Protected areas (PAs) represent a global strategy to halt habitat loss and reduce fragmentation and overexploitation of natural resources (Butchart *et al.*, 2012; Le Saout *et al.*, 2013). PAs also aim to protect not only species, but habitats, and ecosystem functions (Duncan *et al.*, 2015) and services (Parrish *et al.*, 2003). By 2020, countries signatories of the Aichi biodiversity target 11 nations have pledged to increase terrestrial PAs to at least 17% of current Earth surface extent (CBD, 2010). Preliminary assessments showed some improvements toward this target (2010 = 14% and 2016 = 15.4%) (UNEP-WCMC & IUCN, 2016).

Species with small geographic ranges (an operational definition of endemic species (Jetz *et al.*, 2004; Ohlemüller *et al.*, 2008a; Pimm *et al.*, 2014)) are of special conservation concern. Range-restricted species tend to be concentrated in some regions in the world (Lamoreux *et al.*, 2006), and have been widely used in conservation planning to prioritize highly irreplaceable regions (“hotspots”) and to halt massive biodiversity loss (Myers *et al.*, 2000; Orme *et al.*, 2005; Brooks *et al.*, 2006). These hotspots represent not only concentrations of young and relictual taxa (Fjeldså & Lovett, 1997), but topographically complex regions that offer valuable ecosystem services (Naidoo *et al.*, 2008), and unique biotas in islands and archipielagos (Myers *et al.*, 2000). Preliminary assessments revealed a big gap in covering hotspots of high endemism within the global network of PAs, calling the attention to include biodiversity patterns in conservation planning to increase the likelihood of protecting biological diversity as a whole (Rodrigues *et al.*, 2004; Joppa *et al.*, 2013). Terrestrial endemic species are constrained to ~25 hotspots in no more than 1.4% of the land surface and they are severely threatened by loss of habitat (Myers *et al.*, 2000). Hotspots capture between 44% (Myers *et al.*, 2000) to 59% endemic species in ~17.4 million km^2 (Joppa *et al.*, 2013), and the level of protection that the global PA network offer to these hotspots is likely less than 20% coverage for all three major taxonomic groups: amphibians, birds and mammals (Jenkins *et al.*, 2013).

Extinction rates are accelerating (Pimm *et al.*, 2014; Ceballos *et al.*, 2015), wild population still in decline (WWF, 2016), and drivers of species declines show sustained increases (Butchart *et al.*, 2010). On average, 52 species from vertebrate groups, like amphibians, birds, and mammals, move one category closer to extinction every year (Hoffmann *et al.*, 2010). However, conservation efforts, through systematic conservation planning (Margules & Pressey, 2000; Meir *et al.*, 2004; Pressey *et al.*, 2007), have also made quantifiable improvements to the status of biological diversity, preventing species from declining toward extinction (Hoffmann *et al.*, 2010), and facilitating species recovery by reducing habitat loss (Geldmann *et al.*, 2013). Coordinated efforts to increase PA network extent, such as the Aichi Biodiversity Target 11 (CBD, 2010), including patterns of biodiversity in conservation planning (Rodrigues *et al.*, 2004), and preventing the extinction of known threatened species (CBD Aichi Target 12) (CBD, 2010), should pave the way to effectively protect global biodiversity. In theory, increasing the global network of PAs to 17% has the potential to increase the average protection of high number of species geographic ranges (totally or partially), but it will require to require coordinated international efforts (Pouzols *et al.*, 2014). However, it is still unclear whether this strategy will protect endemic species. Preliminary projections show that expected extinction rates in hotspots for the next century should be significantly reduced if there is an increase in the PA network on those hotspots currently unprotected (Pimm & Raven, 2000). Quantifying the extent to which PAs have protected endemic species over recent decades also will elucidate the likelihood of protecting endemic species before 2020. Temporal analysis can be complemented by a spatial analysis, identifying geographic areas, and species to focus conservation efforts that would help countries to make informed and effective decisions.

Here we ask whether the historical rate of change of endemic species coverage by the global PA network is likely to protect endemic species by 2020. More specifically, we ask at present rates of change, when would full endemic coverage be achieved? In addition, we performed a comprehensive gap analysis to quantify the number of endemic species that are not covered by the PAs network and their relative threatened status. We provide detailed information on endemic species and geographic areas for conservation that would help countries to meet CBD targets.

METHODS

We used global vector distribution maps (only native species = 22,191) for terrestrial mammals (n = 5,276), and amphibians (n = 6,428) from IUCN (2014), and birds (n = 10,487) from BirdLife (2016). We used median range size as an operational proxy of endemic species (Pimm *et al.*, 2014), resulting in 11,273 species in total (and mammals = 2,636; amphibians=3,214; and, birds = 5423). To measure the extinction risk, we used all categories from the IUCN red list (IUCN, 2014).

We used the world database of PAs (WDPA, n = 214,809) and selected only terrestrial areas (n = 210,483) worldwide (IUCN & UNEP-WCMC, 2017). Our final PA data set includes entirely terrestrial PAs (field 'MARINE' = 0; n = 200,155) and PAs having some portion of coastal area (field 'MARINE' = 1; n = 10,328). We merged all PA polygons into a single layer for a total area of 20,518,653 km^2, representing 15.2% of the Earth terrestrial surface.

To measure the relative location of each species' geographic distribution with respect to the extent of any PA, we overlapped species with the boundaries of PAs. We categorized this overlap as follows: (i) species geographic ranges that are totally or at least 95% within any PA boundary (inside); (ii) species whose ranges fall only partially (<95%) within the PA; and, (iii) species completely outside any PA boundary (outside). For species with ranges only partially within PAs, we created three categories measuring relative protection afforded by PAs: poor (>50%), medium (50-75%), and strong proportional range inclusion (75-95% of the species' range falls within the boundaries of protected areas).

The extent to which endemic species have benefited from progressive expansion of protected areas networks was measured by counting the number endemic species within PAs annually over a period of 26 years (1990-2016).

We also assessed how many species are currently threatened (e.g., critically endangered, endangered, and vulnerable from IUCN categories) but that are found outside the boundaries of protected areas. To evaluate the degree of land cover change within the geographic range of endemic species and their relative location with respect to PAs (inside, intersect, and outside

PAs), we used the land cover change map from the Millennium Ecosystem Assessment (2005) (Lepers *et al.*, 2005). This data set shows areas of rapid land-cover change worldwide world between 1981-2000, synthetizing major forest-cover changes, dry-land degradation, and changes in human extent. Finally, we summarized our results using terrestrial ecoregions of the world (Olson *et al.*, 2001) and countries' administrative divisions from CIESIN - Columbia University *et al.* (2011).

All polygons and grids were projected using the World-Behrmann projection to preserve area across the extent of the analysis. Analyses were performed using ArcGIS (ESRI, 2014) and R (R Core Team, 2017). The datasets analysed during the current study are available from citations provided above and results of our analyses can be found at http://www.macroecology.ca.

RESULTS

Temporal analysis: measurement of the rate of change

Between 1990 and 2016, ~6,000 to ~15,000 PAs were added annually to the global PA network, but this number has declined in recent years (Figure 1). However, the rates of inclusion of endemic species within the PA network have been fairly slow in the last two and a half decades. For instance, the rates of wholly including endemic amphibian species inside the PA network was about 9 species per year (S/Y), far from doubling the number of endemic species since the 1990 baseline (from 162 to 233; Figure 2). For mammals and birds, the rate at which new endemic species were added to global PA networks was lower (3 S/Y), leading to a 6-8-fold increase in numbers of these species whose ranges were fully included in the PA network (mammals = 10 to 84; and, amphibians = 16 to 99).

Completely including all endemic species currently outside the PA network before 2020 (~4 years), within the network, requires a roughly 5-fold increase in rates of new PA establishment relative to progress observed over the 1990-2016 period. This is especially challenging for amphibians, a taxon for which 943 species currently fall entirely outside PA boundaries. In contrast, birds and mammals have fewer species outside the PA network (303 and 262 species, respectively). On the other hand, if conservation objectives are partial inclusion of endemic species' ranges, rather than inclusion of species' entire ranges, then rates of progress are considerably higher (Figure 2). If current trends persist, most endemic bird and mammal species currently outside PAs will be receiving at least partial protection within PA boundaries by 2020. In contrast, rates of partial inclusion for endemic amphibians that had no prior presence within PAs are lower (Figure 2). Challenges also remain in protecting the whole extent of these endemic species, safeguarding single areas between 10 Km^2 to 10,000 Km^2. The average extent of PAs added to the network is far smaller (~2 orders of magnitude) than the size of these species' geographical ranges (Figure 3).

Coverage

We found that only 3% of the geographic ranges for all major terrestrial vertebrates are completely inside the PA network (~6% of endemic species) and around 7% (~14% of endemic species) are entirely outside the PA network (Table 1, Figure 4a). For amphibians, almost 30% of all endemic species are not covered by any PA, and 58% of species are partially covered by the PA network (Table 1). Nearly 80% of the geographic ranges for birds and mammals are somewhat covered by the PA network.

Extinction risk

Depending on taxon, between 50-60% of endemic species inside PAs are considered threatened (i.e., aggregating IUCN red list categories: critically endangered, endangered and vulnerable). Surprisingly, the number of endemic species threatened and not included (outside) by the PA network is slightly lower (between 40-50%) than endemic species inside the PA network (Figure 4b). Birds showed the highest number of endemic species threatened inside PAs and the lowest number of endemic species threatened in partially covered (intersect) by PAs.

Extinct species

We found that the geographic range of a high number of endemic bird species that went extinct (n = 44; using IUCN status = ‘Extinct’) were not covered by the PA network (Figure 4c). Numbers for mammals and amphibians were comparative lower (2 and 6, respectively).

Countries

Endemic species that are not currently covered by the PA network (outside) are concentrated in some countries (Figure 5), including for amphibians: Brazil, Mexico, Colombia, and Peru; and Papua New Guinea; for birds: Bolivia, Australia and Costa Rica; and, for mammals: Indonesia, Argentina and Papua New Guinea (Table 2). Papua New Guinea harbors the highest number of endemic species for each of the three taxonomic groups.

Ecoregions

Most amphibians outside protected terrestrial areas are concentrated in the ecological regions along the tropical Andes and in New Guinea, while areas with high concentrations of endemic bird species are particularly among islands in the Pacific. Endemic mammals are especially concentrated in the dry Chaco region in southern South America (Figure 6).

Land cover/land use

For birds and amphibians, the dominant land cover within the geographical ranges of endemic species completely inside PAs is primary forest (Figure 7). In contrast, secondary forest and pastures dominate the geographic ranges of mammals' endemic species within the PA network. Geographic ranges of endemic species for birds and mammals outside the PA network are mainly cover by pastures and secondary forest, and by primary forest for amphibians (Figure 7). For species' geographic ranges intersecting the PA network, land use/land cover changes take various forms (i.e. from urban areas to primary forest).

DISCUSSION

The rate of change in endemic species coverage has been very slow in the last two and half decades (1990-2016), making if very unlikely, if the rate is maintained, that the world's endemic species can be wholly included within protected areas 2020. Between 1990 and 2016, the rate of endemic species coverage was very low (3 to 9 species per year, depending on the taxonomic group). So, maintaining these rates of change, more than a century will be required to include ~1508 endemic species currently outside the PA network. Projections based on historic data showed that is very likely that some portions of the geographic ranges of birds and mammals' endemic but not amphibians species will be covered by the future PA network.

Despite the slow historic rate of endemic species coverage, the Aichi target that nations are working toward represent an opportunity to include and protect high numbers of endemic species within the global PA network. An optimistic scenario could be including the total number of geographic ranges of endemic species currently outside the PA network (n=1,508) within it. Expanding the PA network to include all these species before 2020 will require five times the effort made in the last two decades. It will be likely because the historic rate of new PAs added every year is between ~6,000 to ~15,000. This will fill the gap and lack of protection of species with small range sizes and associated niches (Gray *et al.*, 2016). However, it will require an effort to leveraging financial resources, encouraging political will and trading-off with other biodiversity and ecological features to include these species.

If protecting endemic species is worthwhile because they represent a group of desirable and strategic features in biodiversity conservation (Myers *et al.*, 2000; Orme *et al.*, 2005; Brooks *et al.*, 2006; Naidoo *et al.*, 2008), then international community (local, regional and national governments, international cooperation agencies, NGOs, etc.) might focus on prioritizing them to be part of the PA network by 2020. So, expanding the PA network to cover the full extent of endemic species currently outside the PA network will protect almost 14% total endemic species (1,508 out of 11,274). For amphibians, it will impact the most, around 30% of total endemic species will be covered (943).

Systematic conservation planning is needed to solve some issues emerging from different scenarios. For example, it is likely that many new species, with small geographic ranges, remain to be describe (Scheffers *et al.*, 2012). New discoveries are more likely to occur for amphibians than for others groups (Pimm *et al.*, 2010); and some estimates, for other dominant groups such as flowering plants, indicate a high percentage (~15%) of species that still likely undiscovered (Joppa *et al.*, 2011). Some areas may be “hotspots” of endemism for particular or multiple taxa, so targeting such hotspots for protection would lead to substantial progress in endemic species conservation. Under current trend it is expected that some endemic species of mammals and birds (and less likely amphibians) will be covered in some way for a PA in the next 4 years, so it will be a priority to evaluate the effectiveness of this partial protection. Challenges also emerge in protecting the whole extent of each endemic species, because it requires safeguarding single areas between 10 Km^2 to 10,000 Km^2 and restoring natural habitats which have dramatically changed in land cover use (from forest to secondary forest and pastures), specially for mammals and birds' geographic distributions.

One of the assumptions in conservation is that creating PAs will secure species and associated ecosystem functions. We evaluate only one dimension of biodiversity that can offer quantitative information of the effectiveness of the PAs (Chape *et al.*, 2005). A comprehensive assessment of biodiversity, oriented to set global conservation priorities must also consider other facets and metrics (Brum *et al.*, 2017; Pollock *et al.*, 2017), such as rarity (Possingham & Wilson, 2005), and other dimension of biodiversity (Hoekstra *et al.*, 2005) and ecosystem services (Turner *et al.*, 2007). However, the expansion PA network covering the extent of species with small range size seems to offer not only highly cost-effective protection of areas of high biodiversity (Balmford *et al.*, 2002; Venter *et al.*, 2014), but sustained provision of ecosystems services basic for human activities.

Areas within and surrounding PAs have experienced land change use and exploitation of natural resources, resulting in biodiversity loss (Laurance *et al.*, 2011) and degradation of ecosystem services (Foley *et al.*, 2005), such as climate and air quality regulation. We found that areas outside the PA network, harboring endemic species, have experience changes in land cover use (from forest to secondary forest, pastures and crops); especially for mammals and birds' geographic distributions. LUC projections also show that this trend of ecosystems degradation will continue in the next two decades (Pouzols *et al.*, 2014). In fact, habitat fragmentation has been associated as a major driver for mammal extinction risk and endemic species have suffered significant losses of critical habitat from within their geographic range (Crooks *et al.*, 2017). Land use change in countries with particularly high diversity (e.g., Indonesia, Papua New Guinea and Colombia) accelerates extinctions and the erosion of other aspects of biological diversity, such as phylogenetic diversity (Chaudhary *et al.*, 2018). Expanding the PA network rapidly into remaining intact habitats would significantly improve conservation prospects for tropical species (Gibson *et al.*, 2011; Dinerstein *et al.*, 2017; Watson & Venter, 2017).

Expanding PAs to areas where endemic species are currently unprotected will require restoration efforts, whether active or passive, that recover habitat quality (Birch *et al.*, 2010). We showed that almost 50% of the endemic species outside the PA network are threatened (i.e., critically endangered, endangered and vulnerable) and at least 180 species are reportedly extinct based on IUCN red lists, most of them birds. This risk factor can increase if detailed spatial data are incorporated within the analysis (Ocampo-Peñuela *et al.*, 2016) and environmental stressors persist. Biological diversity has been eroded at rates never experienced (Ceballos *et al.*, 2015) and range-restricted species have lost their historic range area due to intensive human activities (Ceballos & Ehrlich, 2002). Moreover, vertebrate population has showed 25% average decline in abundance (Dirzo *et al.*, 2014).and habitat loss and fragmentation may compromise maintenance of healthy populations and species stocks in the future (Brooks & Balmford, 1996; Brooks *et al.*, 1999). Reducing extinction risk of endemic species effectively requires also targeting the places very precisely in the landscape (Akasaka *et al.*, 2017).

Endemic species outside the PA network are located mainly in areas previously identified as biodiversity hotspots (Myers *et al.*, 2000): the Andes, Choco, Pacific Islands (e.g., New Guinea, Solomon), Mesoamerica, Dry Chaco and Atlantic forests. And, they also occupy ecoregions where habitat conversion exceeds habitat protection (Hoekstra *et al.*, 2005) and species losses may most likely occur (Manne *et al.*, 1999). Within these ecoregions, it is necessary to refine conservation priorities (Jenkins *et al.*, 2010) and monitoring PAs (Nagendra *et al.*, 2013) using new technological tools such as remote sensing (Rose *et al.*, 2015; Pettorelli *et al.*, 2016).

Persistence of species, habitats and ecosystems services depends not only on including biological and ecological factors but on coordinating and translating generalized, global drives toward international conservation agreements into achievable goals within nations and the societies that comprise them (Pouzols *et al.*, 2014). Global, regional and local realities may emerge in the attempt to implement conservation goals. Reconciling conservation and development targets may increase land use efficiency and minimize habitat and biodiversity loss (Lambin & Meyfroidt, 2011). Similarly, attempts to combine and reconcile interests of different stakeholders into national and local policies could help to minimize poverty, redefine local economic development and protect biological diversity (Adams *et al.*, 2004; Naughton-Treves *et al.*, 2005; Berkes, 2007; Palmer & Di Falco, 2012; Mishra *et al.*, 2017).

Protecting endemic species requires coordinated efforts to expand a large and dispersed network of PAs and implement regional conservation management to mitigate environmental stressors and enhance biological and ecological processes (Ceballos *et al.*, 2005). Increasing the number of PAs globally must also be accompanied by reducing PA removal from the global network (Lewis *et al.*, 2017). Coordinating global targets, governments efforts and local implementation require a new aggressive campaign to protect biodiversity and ecosystem services. New PAs and areas buffering them should be managed by national and regional agencies in coordination with local communities and NGOs. Local stakeholders could adopt these areas and obtain tangible social and economic benefits.

Aichi target 11 offers a unique opportunity to include all endemic species currently outside the global PA network within it. However, historical data showed that current rates of change in including endemic species are very slow. So, a call to the international community (local, regional and national governments, international agencies, NGOs, etc.) is made to focus and establish an international strategy to include more than 1500 endemic vertebrate species (amphibians, birds and mammals) within the current PA network before 2020. It will preserve not only a substantial number of species but also habitats and ecosystem functions and services.

ACKNOWLEDGEMENTS

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TABLES

Table 3.1. Number of endemic species that overlap (inside or intersect) or not (outside) with Protected Areas (PAs). Values in parenthesis represent the proportion (%) of species in each category within that taxon. Endemic species are based on median range size. “Inside” indicates that polygons of species’ ranges are 95% or more contained within the PA network; “outside” indicates species ranges totally outside the PA network; “intersect” indicates overlap of species geographic ranges with the PA network in three categories: between 75% - 95%, 50% - 75% and less than 50%.

			Species location with respect to Protected Terrestrial Areas				
Taxon	Total species	Endemic species	Inside	Intersect			Outside
				75% - 95%	50%-75%	< 50%	
Amphibians[1]	6,428	3,214	395	243	344	1,289	943
		(50%)	(6%)	(4%)	(5%)	(20%)	(15%)
Birds[2]	10,487	5,423	84	133	322	4,581	303
		(52%)	(1%)	(1%)	(3%)	(38%)	(3%)
Mammals[3]	5,276	2,636	99	126	211	1,938	262
		(50%)	(2%)	(2%)	(4%)	(37%)	(5%)
Total species	22,191	11,274	578	502	877	7,808	1,508
		(51%)	(3%)	(2%)	(4%)	(35%)	(7%)

Cut-off median range size:

[1] Amphibians = 4,478 Km^2

[2] Birds = 421,151 Km^2

[3] Mammals = 182,722 Km^2

Table 3.2. Top 20 countries harboring the highest number of endemic species outside the protected terrestrial areas (PAs) network for amphibians, birds and mammals. Countries holding high numbers of endemic species for: three taxonomic groups (red), two taxa (blue), and one taxon (black).

	Country	Amphibians	Country	Birds	Country	Mammals
1	Papua New Guinea	99	Bolivia	239	Indonesia	33
2	Brazil	93	Australia	160	Argentina	24
3	Mexico	88	Costa Rica	117	Papua New Guinea	22
4	Peru	84	Burundi	74	Mexico	18
5	Colombia	74	United States of America	68	Philippines	12
6	India	57	Belize	63	Solomon Islands	12
7	Ecuador	56	Bhutan	57	India	10
8	Indonesia	42	Guatemala	54	Madagascar	10
9	China	31	Venezuela	51	Ethiopia	8
10	Haiti	28	Brunei Darussalam	47	Sudan	8
11	Cameroon	25	Solomon Islands	44	China	7
12	Bolivia	16	French Polynesia	43	Congo, Democratic Republic	7
13	Argentina	15	Cameroon	41	Somalia	7
14	Congo, Democratic Republic	15	Papua New Guinea	40	Iran	5
15	Guatemala	15	Ethiopia	39	Russia	4
16	Venezuela	15	Cuba	35	Turkey	4
17	United Rep. of Tanzania	14	Dominican Republic	34	Angola	3
18	Angola	13	Chile	33	Cuba	3
19	Chile	13	Jamaica	33	Federated State of Micronesia	3
20	Madagascar	13	Sri Lanka	33	South Africa	3

FIGURES

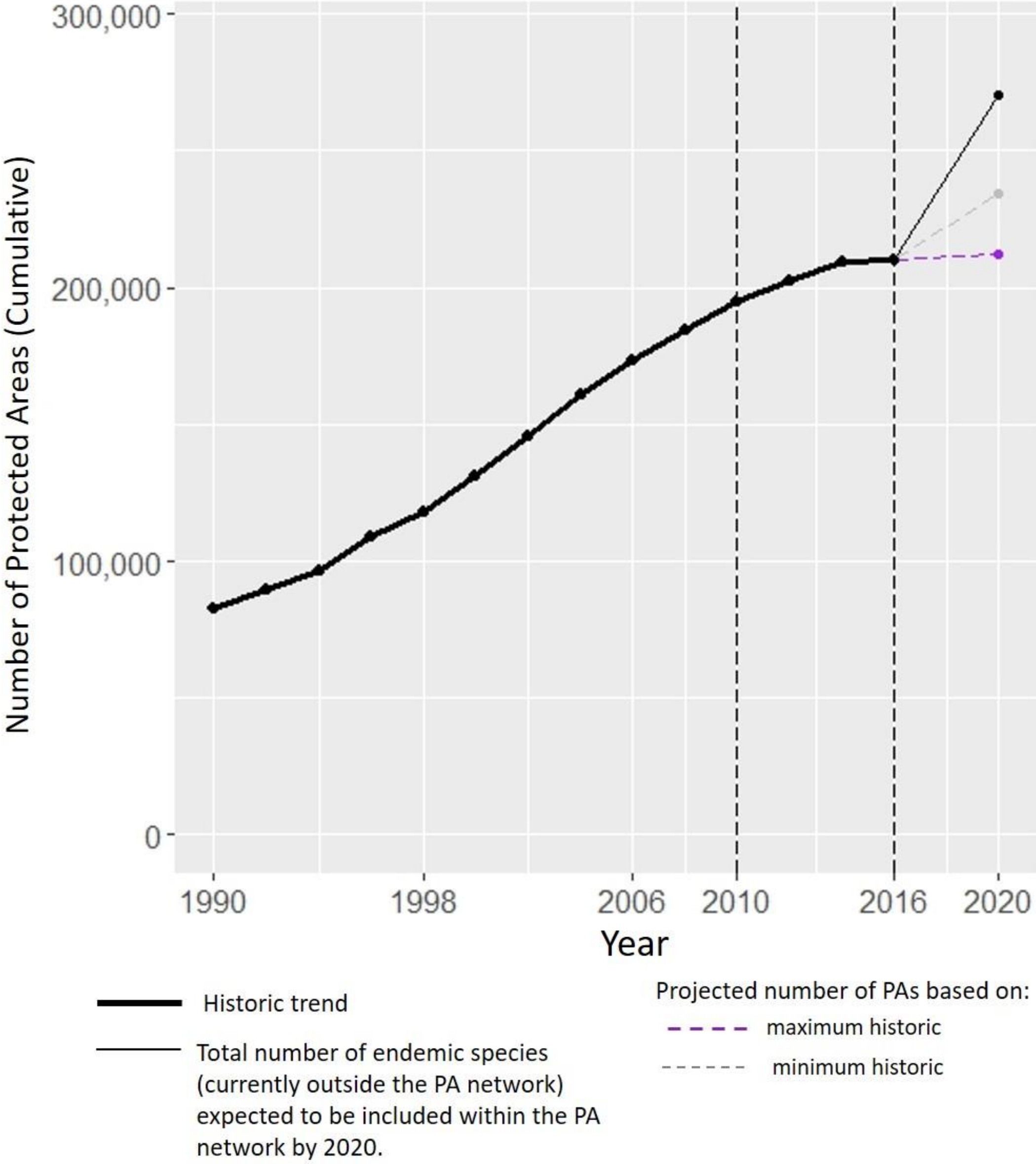


Figure 3.1. Number of protected terrestrial areas (PAs) included in the global network since 1990 (thick black line), and projections to include all endemic species currently outside the PA network (n = 1,580, black thin line) by 2020. Two additional projections are calculated using two rates of change of endemic species coverage: low rate, purple dashed line; and high rate, green dashed line. Projected trends of PA coverage by 2020, using minimum (grey dashed line) and maximum (thin black line) historical rates.

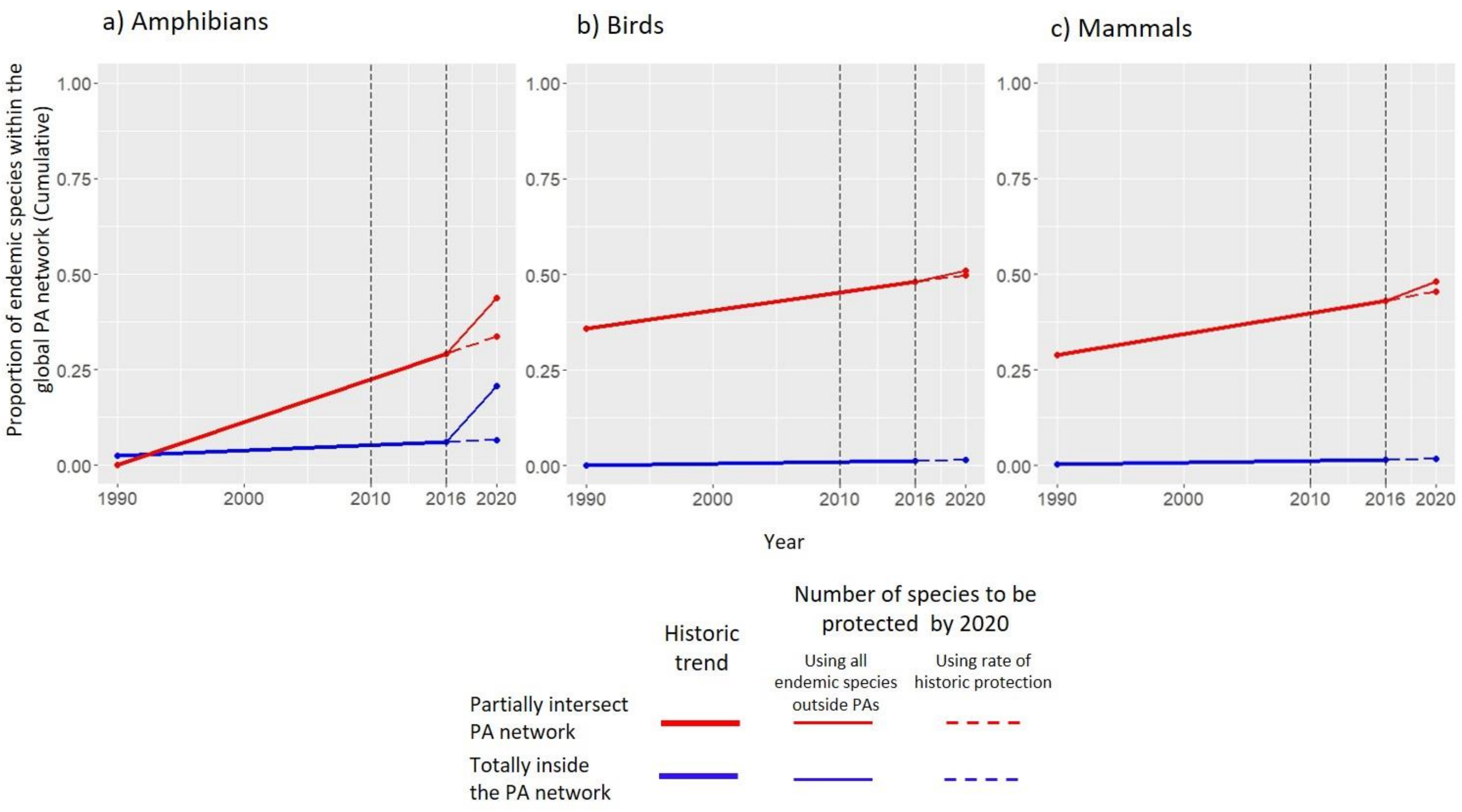


Figure 3.2. Number of endemic species that are inside (blue line) or intersect (red line) protected terrestrial areas (PAs) for a) amphibians, b) birds and c) mammals. Historic trend represented by thick lines. Two projections aimed to include endemic species within the PA network: using total number of endemic species outside current (2016) PA network (thin line) and using the historic rate of change for species coverage (dotted line).

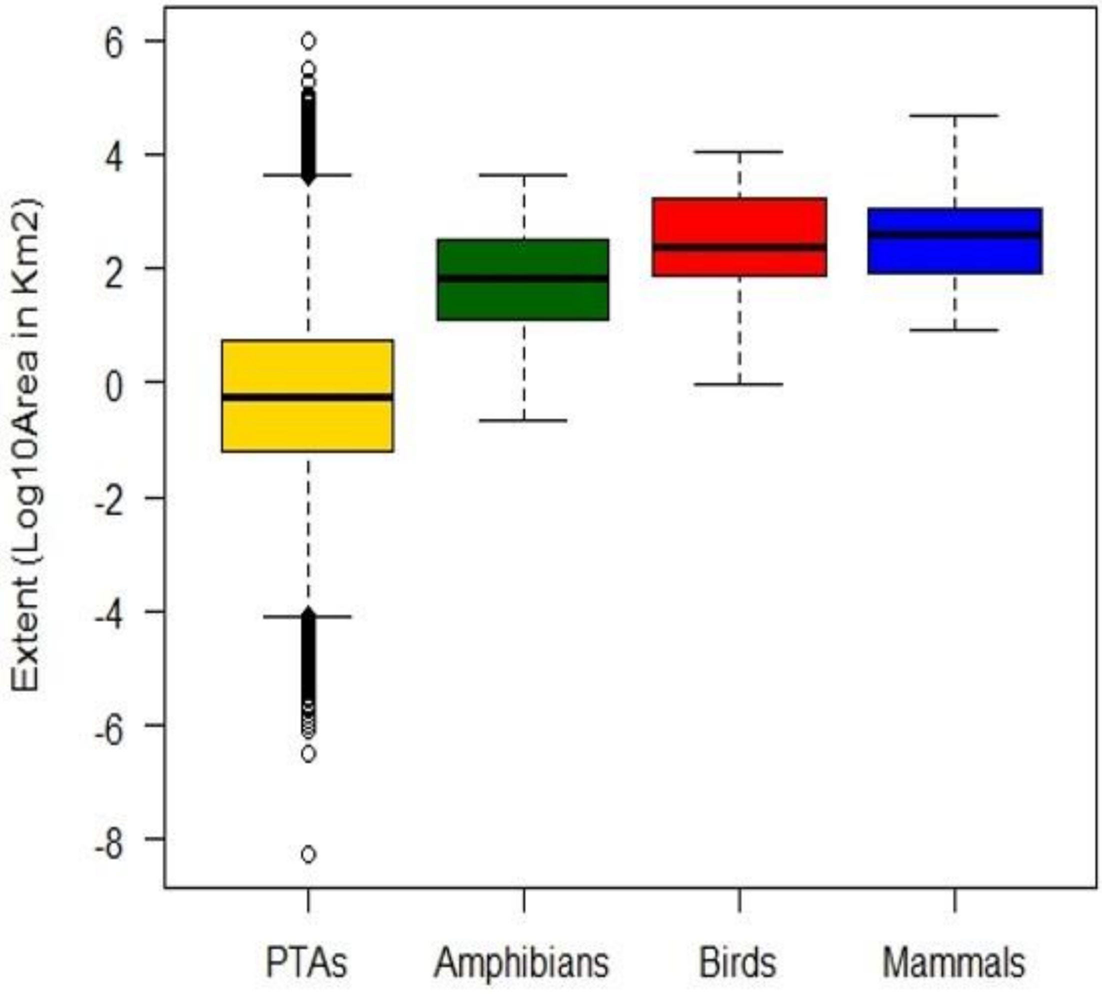
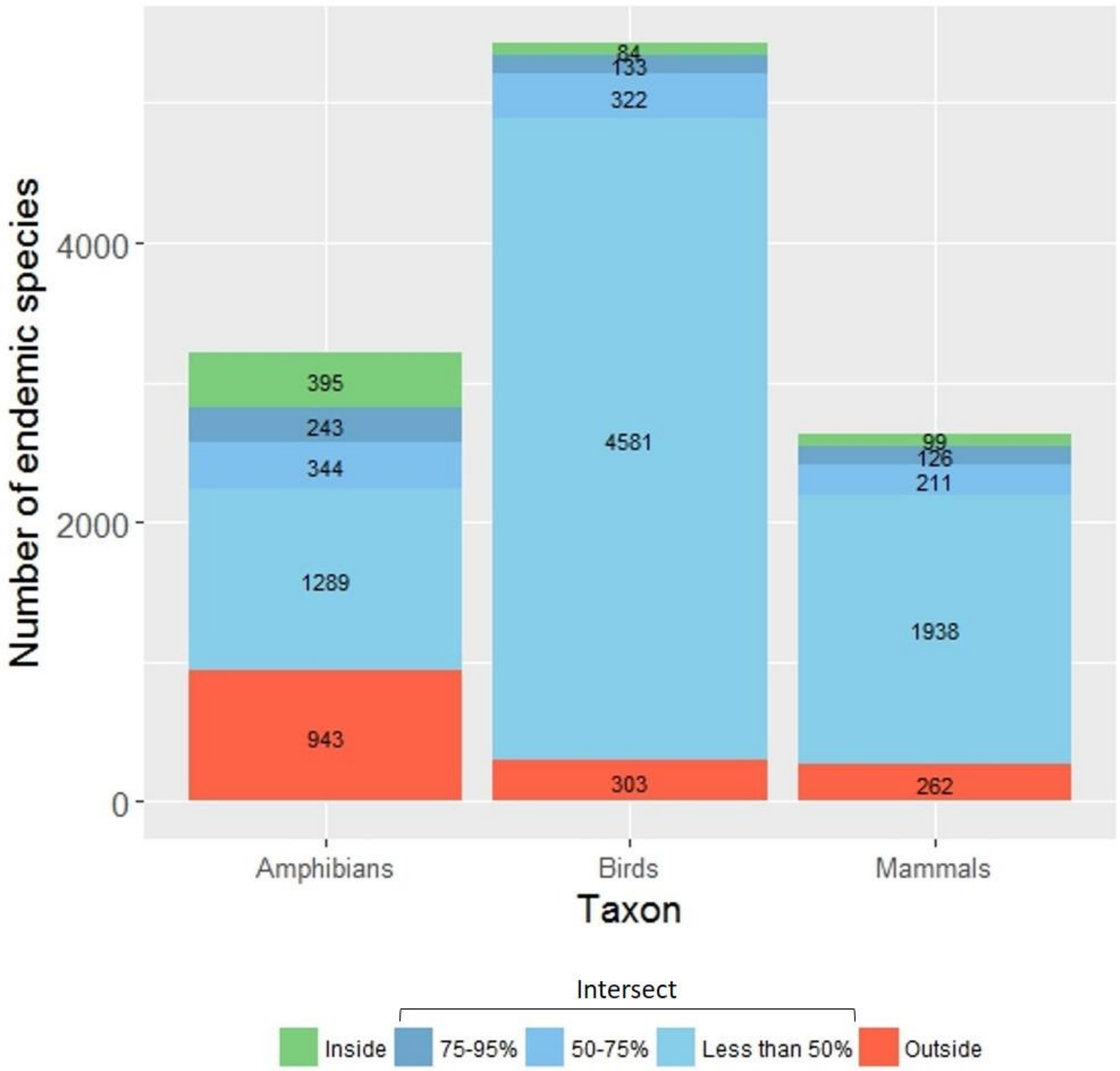
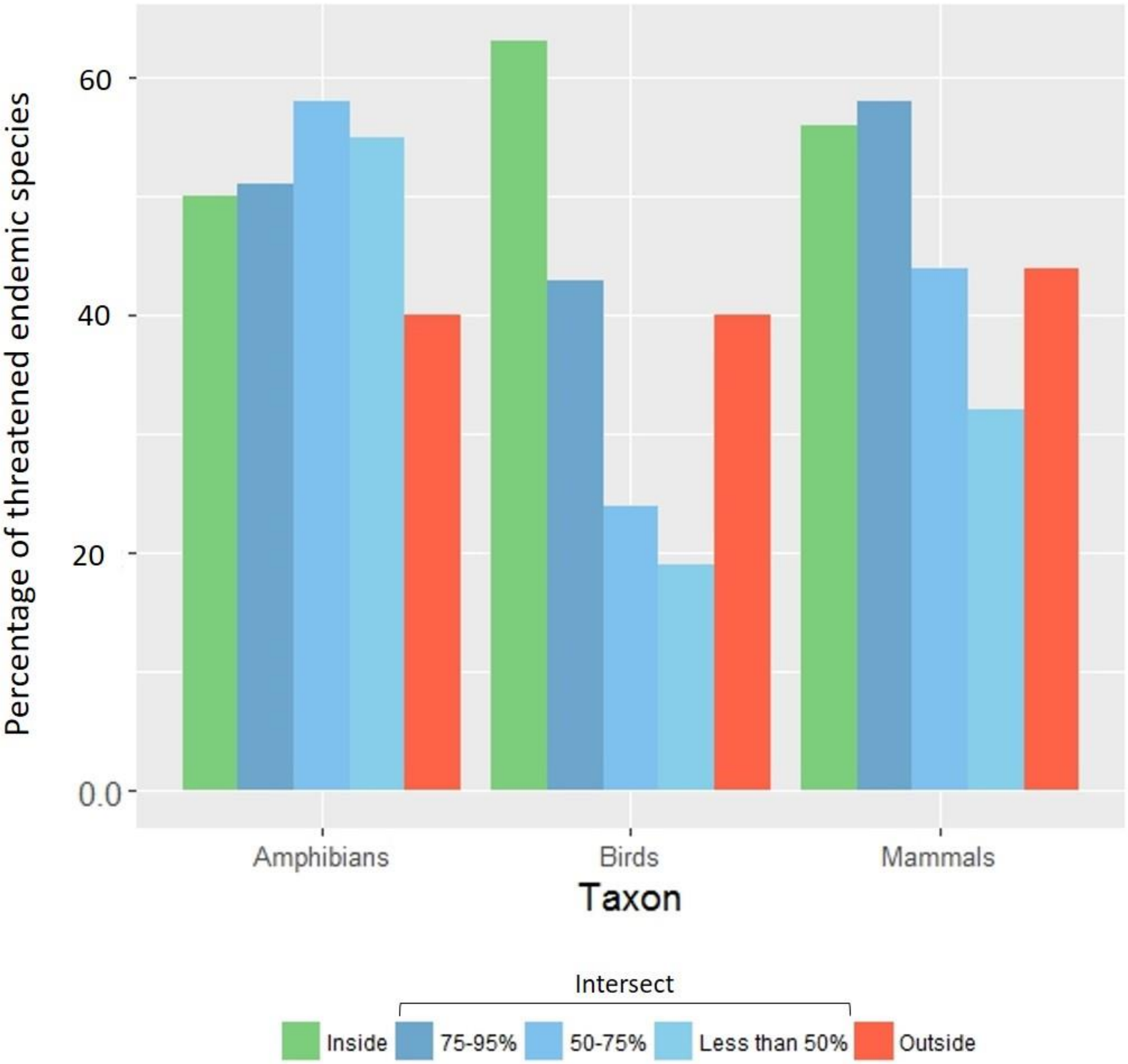


Figure 3.3. Extent of protected terrestrial (PAs) areas (yellow) and geographic range size extent endemic species outside the PA network for amphibians (green), birds (red) and mammals (blue).

a) Total endemic species



b) Percentage of threatened endemic species



c) Extinct species

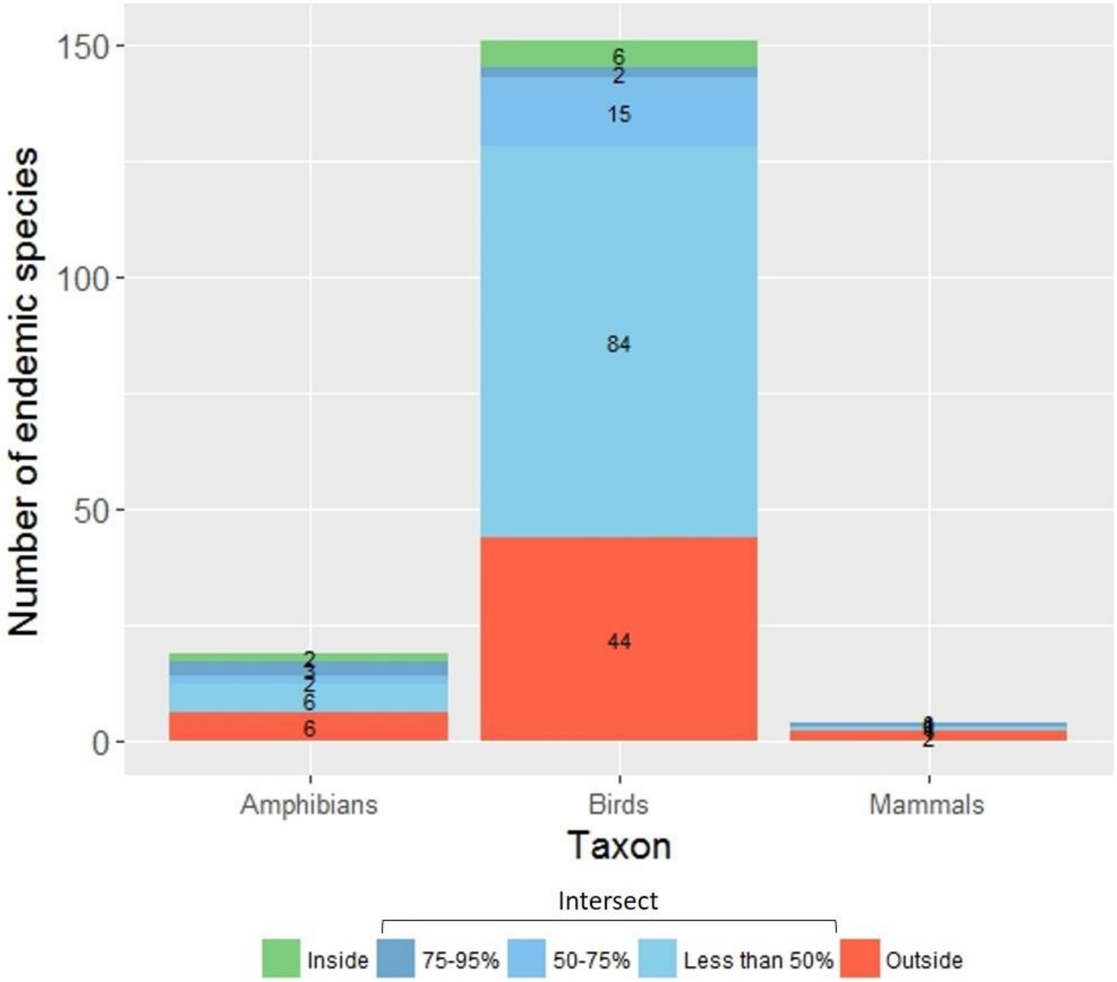
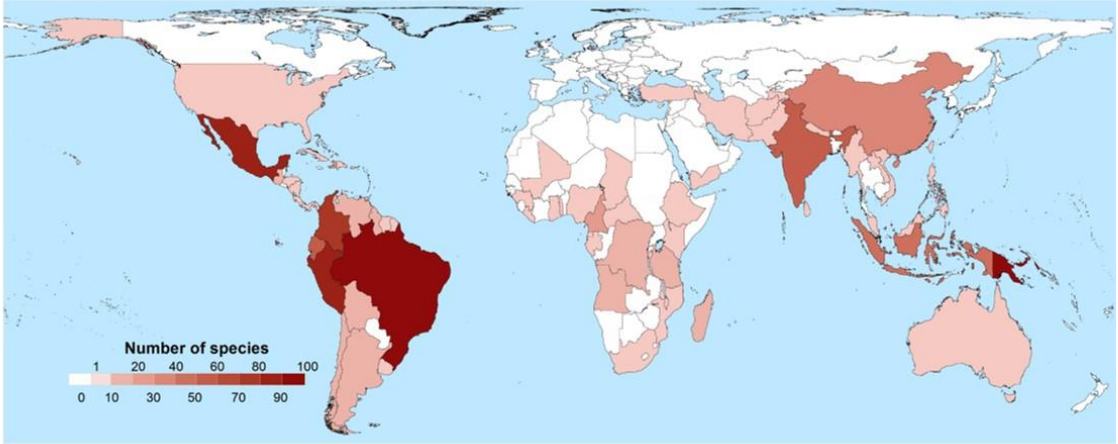
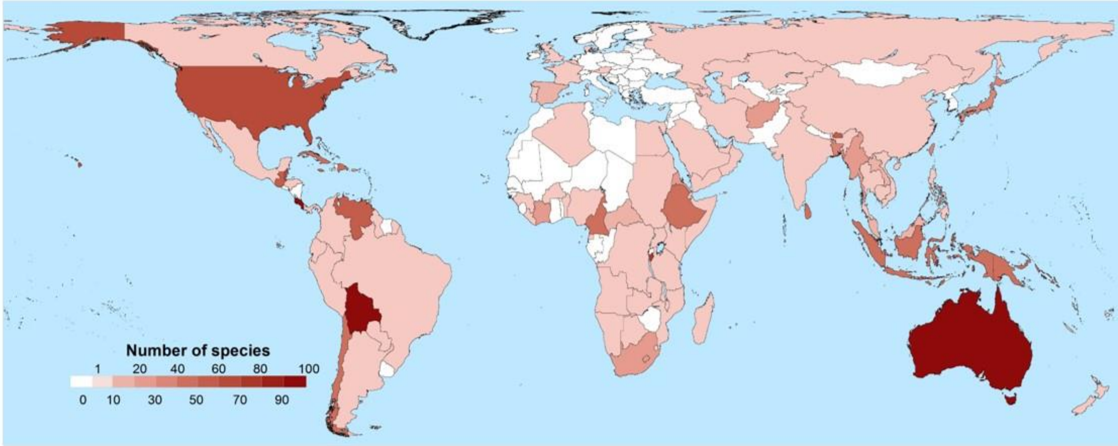


Figure 3.4. Coverage of endemic species by protected terrestrial areas (PAs, data 1990-2016). a) Total endemic species; b) Threatened endemic species (aggregated IUCN categories: Critically endangered, Endangered and Vulnerable) from total; and, c) Extinct species. Species geographic ranges that intersect any PA (categories in blues hues) where subdivided according to their percentage of overlap with PAs' extent (i.e., 75% - 95%, 50% - 75% and less than 50% of overlap). Notice that species that overlapped more than 95% with any PAs where considered inside PAs.

a) Amphibians



b) Birds



c) Mammals

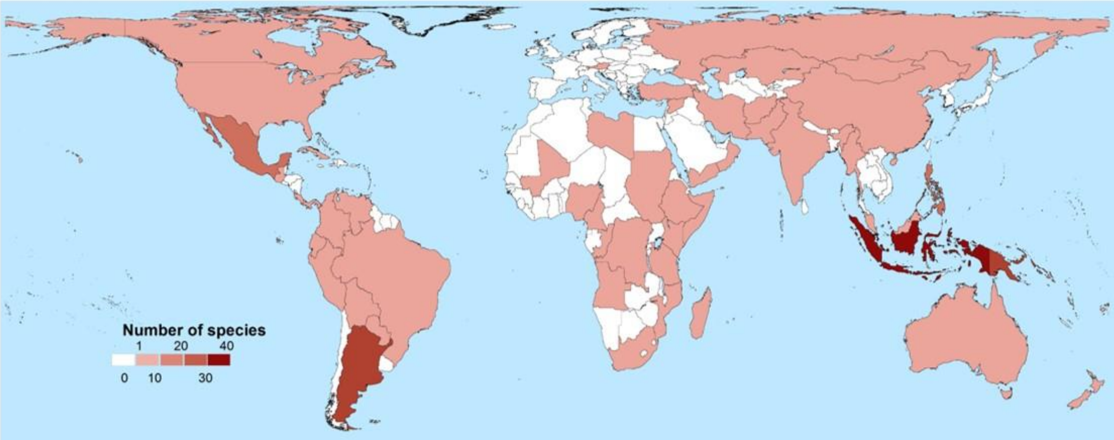
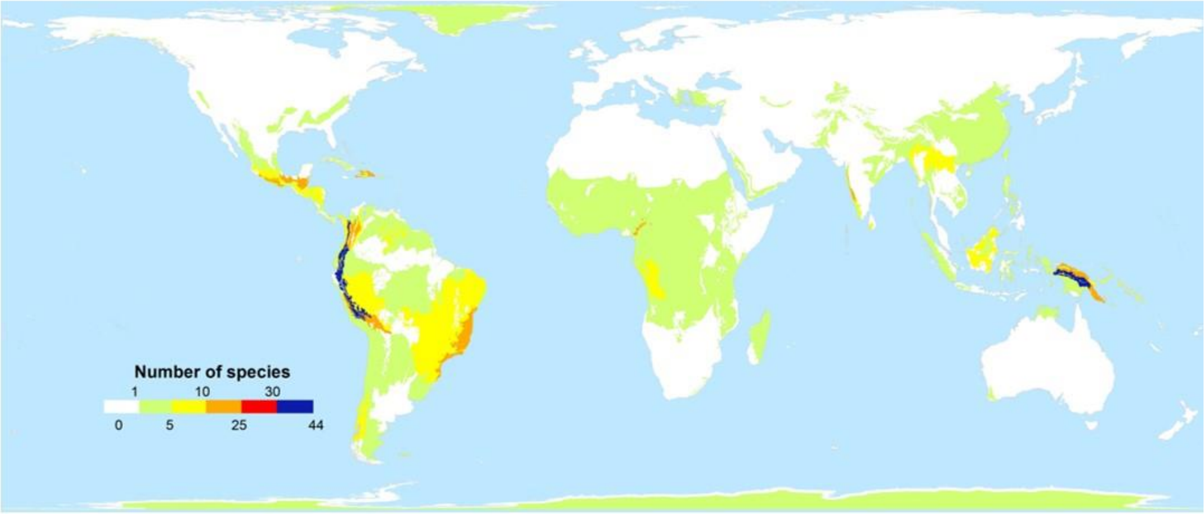
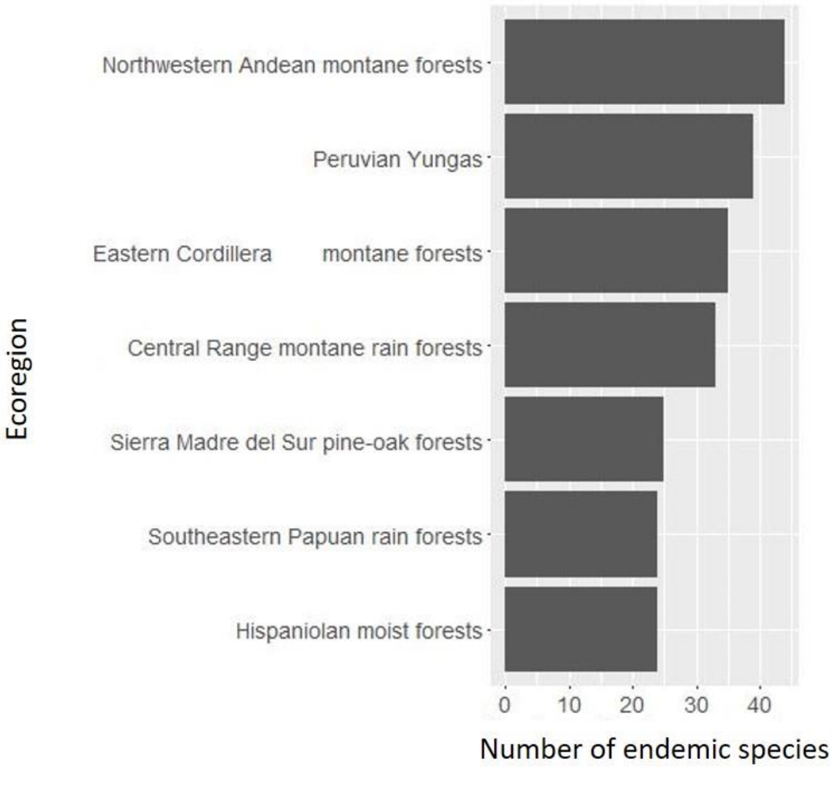


Figure 3.5. Number of endemic species outside Protected Areas (PAs) per country for a) amphibians, b) birds and c) mammals.

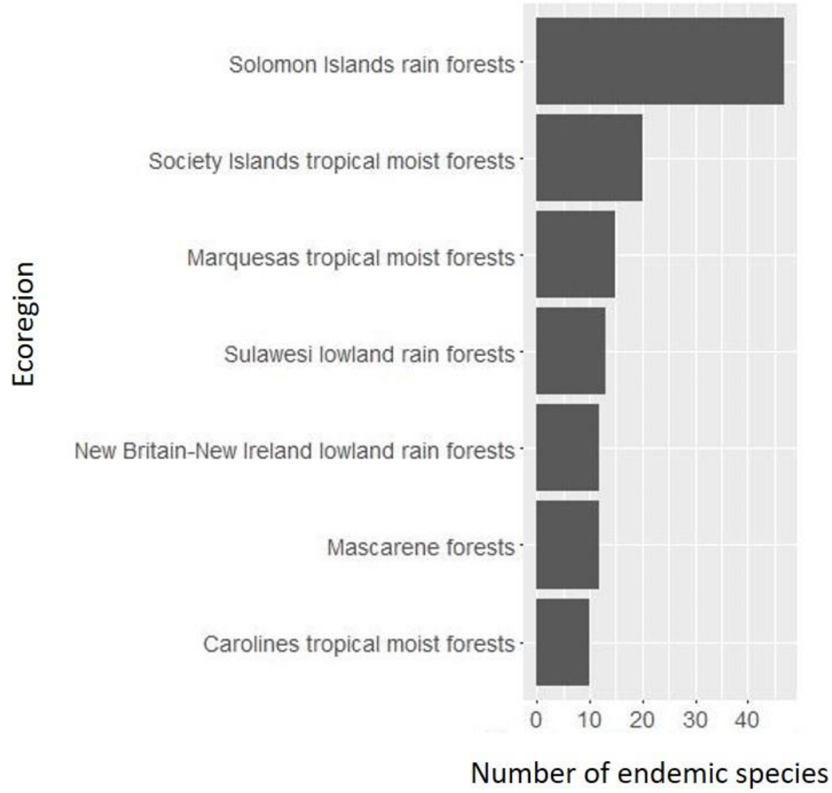
a) Amphibians





b) Birds


Number of species
1
10
30
0
5
25
47


Solomon Islands rain forests
Society Islands tropical moist forests
Marquesas tropical moist forests
Sulawesi lowland rain forests
New Britain-New Ireland lowland rain forests
Mascarene forests
Carolines tropical moist forests
Ecoregion
0
10
20
30
40
Number of endemic species

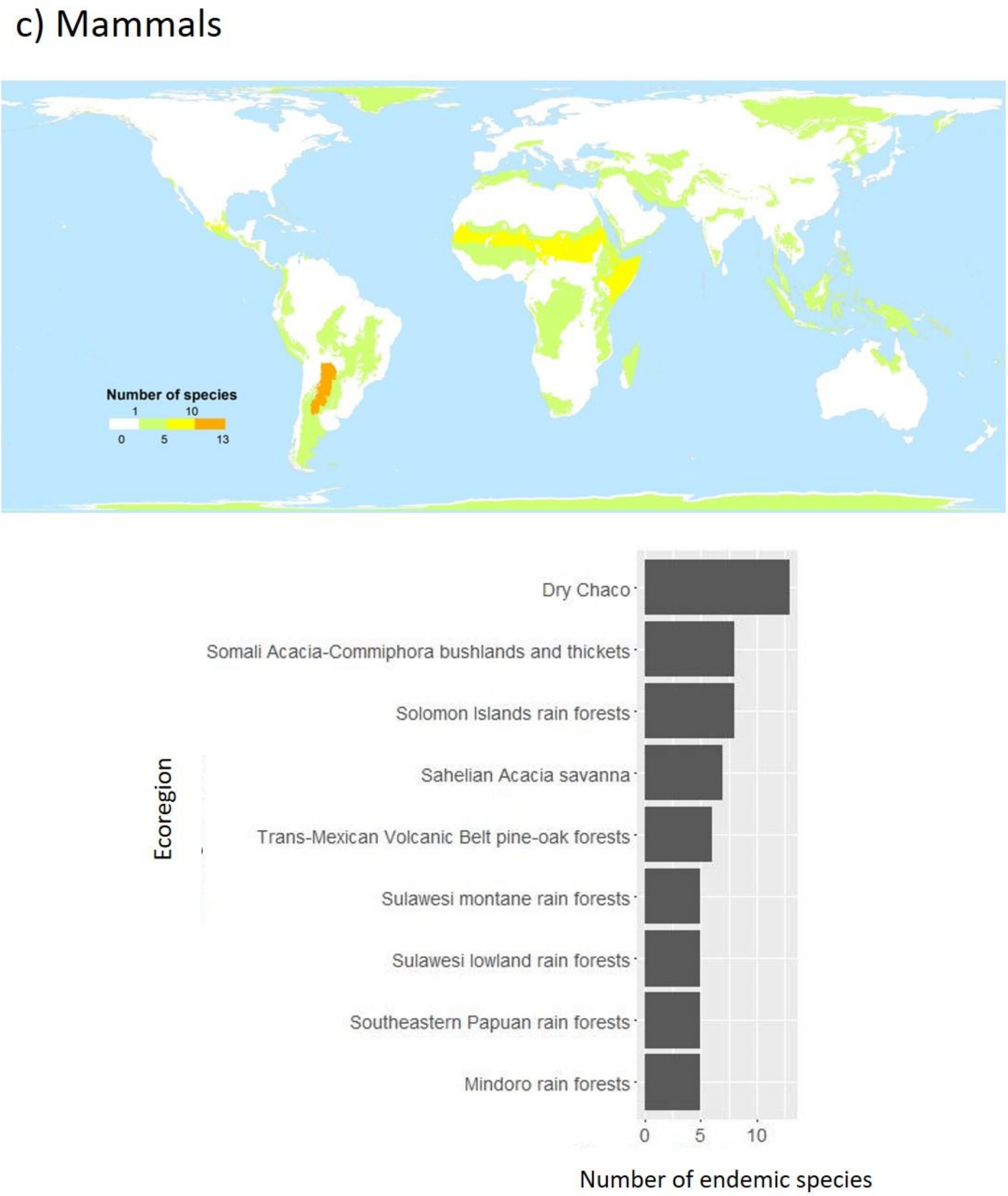
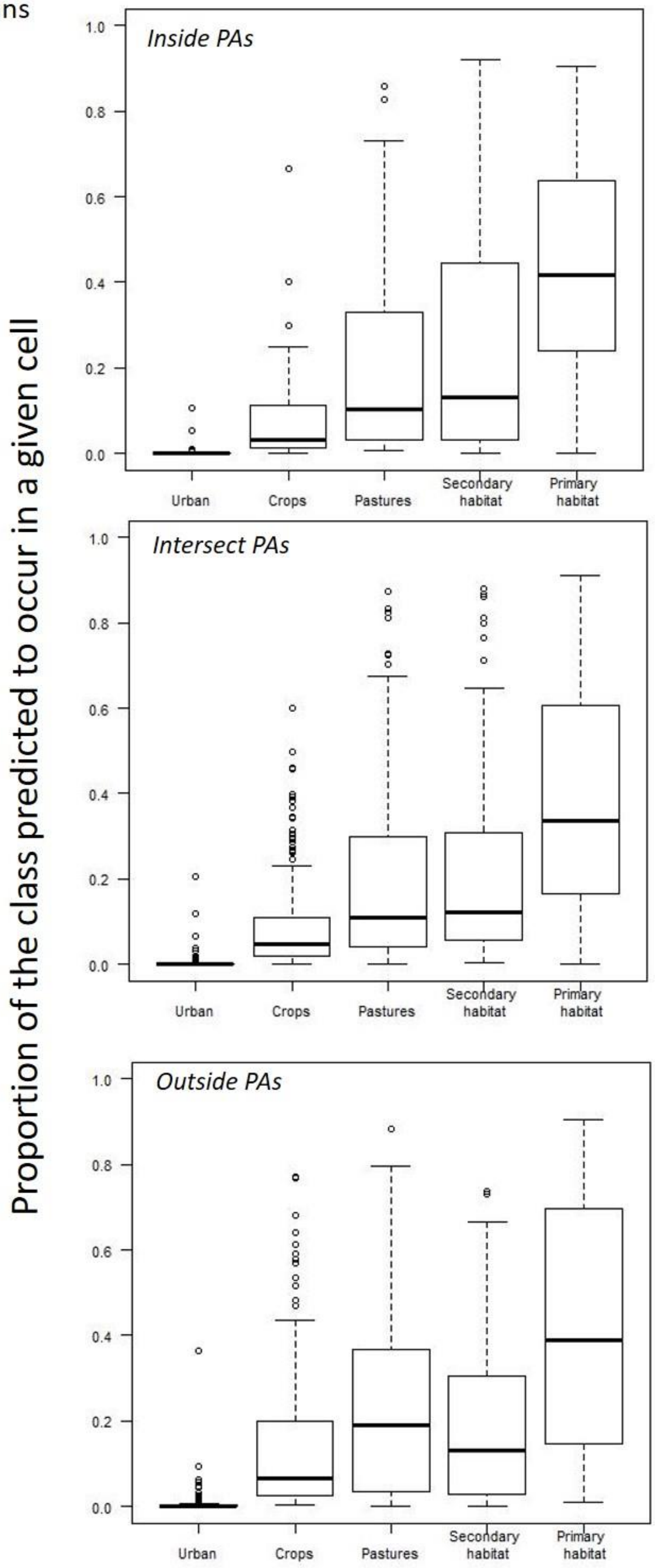
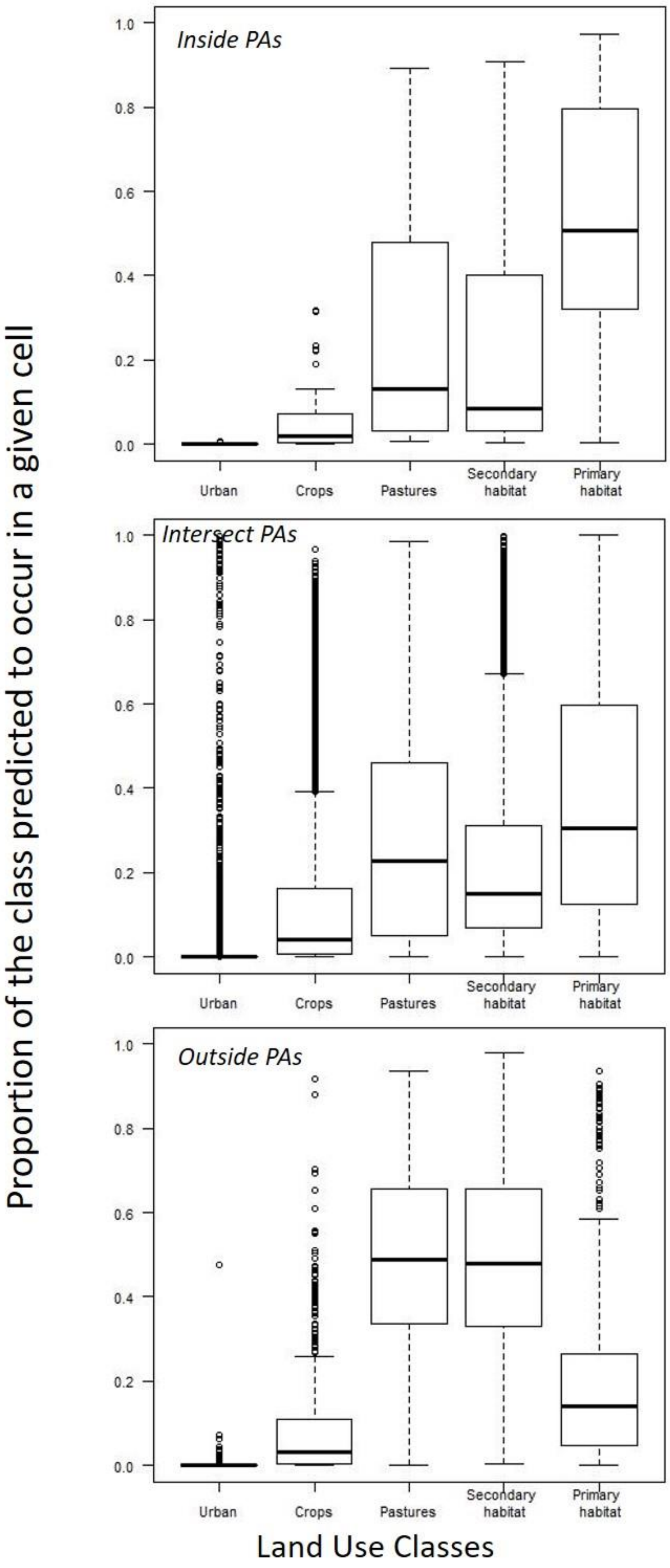


Figure 3.6. Ecoregions and number of endemic species completely outside protected terrestrial areas for a) amphibians, b) birds and c) mammals. Bars represent a sample of ecoregions with highest number of endemic species.

a) Amphibians



b) Birds


Proportion of the class predicted to occur in a given cell
Inside PAs
Intersect PAs
Outside PAs
1.0
0.8
0.6
0.4
0.2
0.0
Urban
Crops
Pastures
Secondary habitat
Primary habitat
Land Use Classes

c) Mammals

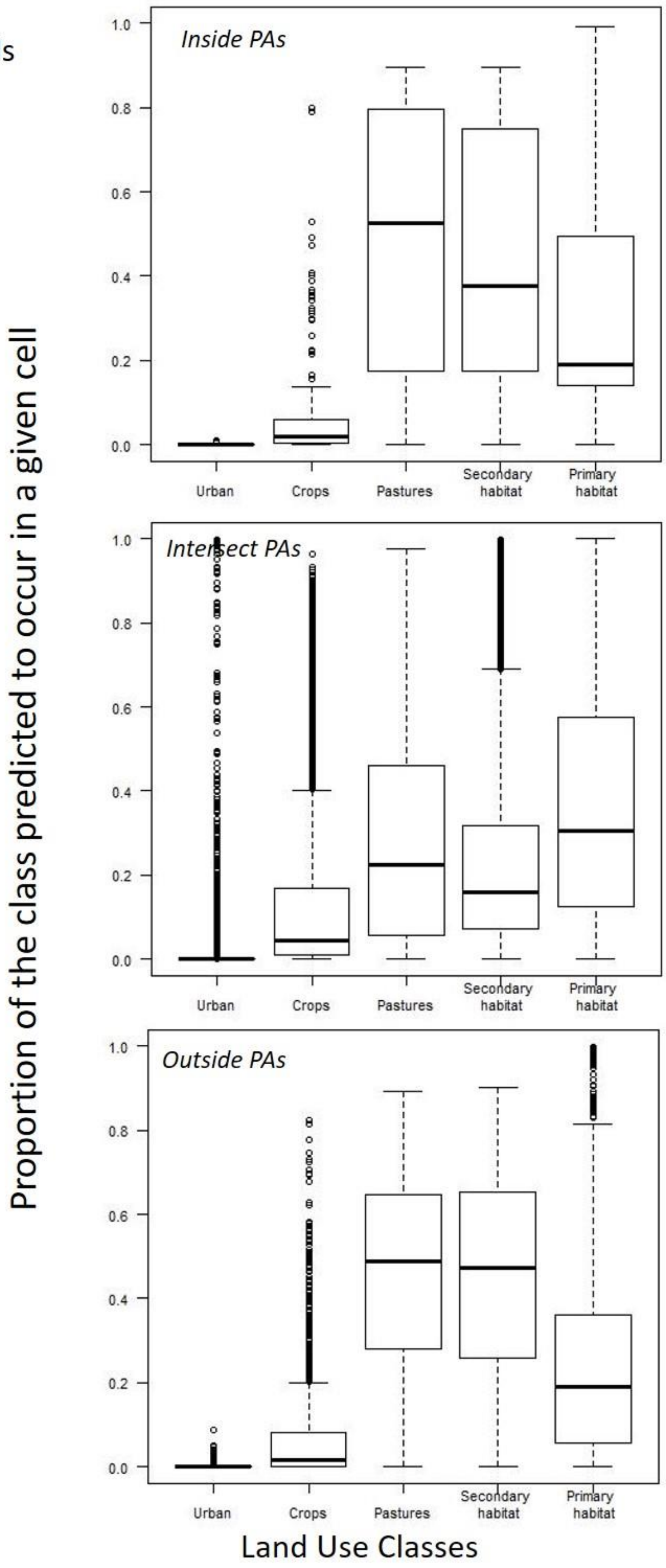

Inside PAs
Intersect PAs
Outside PAs
Proportion of the class predicted to occur in a given cell
0.0
0.2
0.4
0.6
0.8
1.0
Urban
Crops
Pastures
Secondary habitat
Primary habitat
Land Use Classes

Figure 3.7. Proportion of the class predicted to occur within a given cell within the extent of the species geographic range (i.e., inside, outside or intersect the protected area network, PAs); for a) amphibians, b) birds, and c) mammals.

GENERAL CONCLUSION

My thesis attempted to test some hypotheses that can explain broad-scale patterns of species endemism, and to inform conservation planning about the likelihood of protecting endemic species under a global conservation initiative (Aichi target 11, Convention of Biological Diversity).

I found that thermal barriers proposed to characterize differences between tropical and temperate realms are not accurate. Thermal barriers might be more complex than a latitudinal climate gradient. I also found that hypotheses tested here failed to provide a reliable explanation of macroecological patterns. In terms of conservation, I found that it is very unlikely to protect all endemic species at the present rates endemics are being covered by PAs.

In Chapter 1, I found that thermal barriers between low and high elevation areas, initially proposed to be unique to tropical environments, are comparably strong in some temperate regions, particularly along the western slopes of North American dividing ranges. I also found that biotic similarity for both mammals and amphibians decreases between sites that are separated by elevation-related thermal barriers. That is, the stronger the thermal barrier separating pairs of sites across the latitudinal gradient, the lower the similarity of their species assemblages. Thermal barriers explain 10-35% of the variation in latitudinal gradients of biotic similarity, effects that were stronger in the comparisons of sites at high elevations. Thermal barriers are weaker or absent at low elevations (Wright et al. 2009, Salisbury et al. 2012), and our results cannot readily explain variation in species assemblages within such areas. So, processes intrinsic to the classic ‘mountain passes’ hypothesis (Janzen 1967) appear to contribute in some way to the origins and maintenance of broad-scale gradients of biological diversity. However, other factors, whether historical or contemporary, must be the main drivers of gradients of biological diversity. My findings also have significant implications. If mountains passes are also high in temperate regions, it is unlikely that the mechanism proposed by Janzen (1967) may explain broad-scale patterns of total species richness, as this hypothesis predicts a significant peak of richness in some temperate regions in western North America which is not supported by empirical evidence (Currie, 2017). Based on this, we should reject Janzen's hypothesis and its main mechanism as a candidate to explain broad-scale patterns of total species richness.

In Chapter 2, I found that there is no empirical reason, from the standpoint of model fitting, parameter estimates and model validation, to claim that any tested process, individually or in combination, creates and maintains global patterns of endemism. Although, I found significant relationships, they failed the stronger test of a causal relationship: accurate prediction. Although all relationships are statistically significant, most of the variance remains unexplained, and cross-continental tests of spatial models did not accurately predict observed patterns of endemism in spatially independent zoogeographic realms. This suggests that regression models between predictors and endemism do not capture fundamental processes that generate endemism. That the effect of richness almost disappeared in some models, suggests that patterns of endemism are not driven by the same variables as total richness. Patterns of endemism were not consistently related to climatic velocity, suggesting that early correlations in some places probably reflect collinearity with topography instead. Local combinations of biotic and abiotic conditions that are essentially unpredictable by any macroecological approach might be responsible for patterns of endemism.

In Chapter 3, I found that 30% of amphibians, 6% of birds and 10% of mammals' endemic species are completely outside Protected Areas (PAs). Almost 50% of species outside

PAs, and partially covered by the PA network, are considered threatened (critically endangered, endangered and vulnerable). Between 1990 and 2016, 3 to 6 endemic species have been completely covered every year by the PA network (# included amphibian species = 162 to 233; mammals = 10 to 84; and, amphibians = 16 to 99). Based on these trends, including all endemic species currently outside the PA network completely within it is very unlikely by 2020. However, projections also showed that is very likely that some portions of all endemic species' geographic ranges for birds and mammals, but not for amphibians, will be covered by the 2020 PA network. If protecting endemic species is worthwhile, because they represent a strategic feature in biodiversity conservation, then international community and local governments might focus on prioritizing them to be part of the PA network by 2020. Expanding the PA network to cover the full extent of endemic species currently outside the PA network will protect almost 14% total endemic species (1,508 out of 11,274), safeguarding not only endemic species but the habitats, historical processes, and ecosystem services associated with them. Ecoregions in tropical Andes, Mesoamerica, Pacific Islands (e.g., New Guinea, Solomon), Dry Chaco, and Atlantic forests are major priorities. Challenges remain in protecting the whole extent of each endemic species, because it requires safeguarding single areas between 10 Km^2 to 10,000 Km^2, and restoring natural habitats which have dramatically changed in land cover use (from forest to secondary forest and pastures), especially for mammals' and birds' geographic distributions.

Finally, my main contribution to this research area is clearly rejecting these hypotheses from potential candidates that may explain biodiversity patterns. By removing them, I advance in this field and open possibilities to test new ideas and gather new evaluate their mechanisms. By investigating rates of endemic species inclusion in PAs, I provide detailed information and methodologies that can help countries to strategically conserve biodiversity and meet CBD target requirements.

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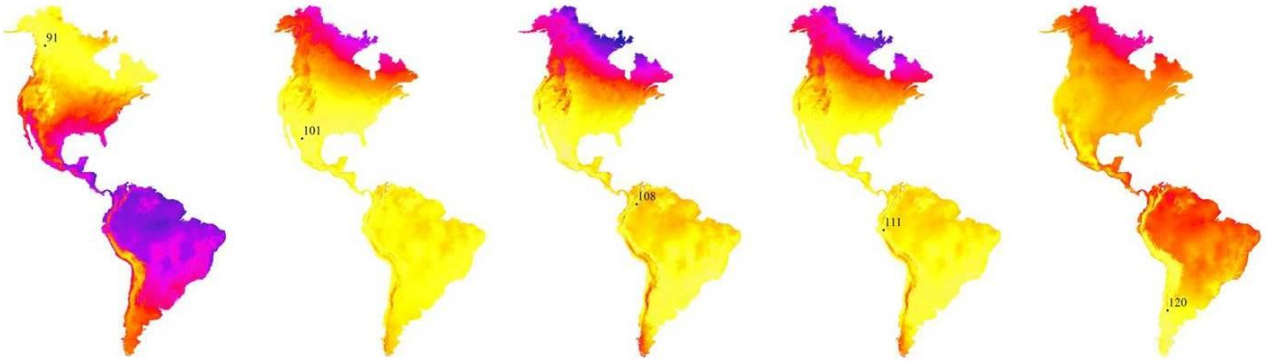
APPENDICES CHAPTER 1

Table S1.1. Models for thermal overlap (y) as a function of elevation (x) in the Americas. Coordinates indicate the focal site at 300 masl used to compare measurements of thermal regimes with all sites encounter towards the highest elevation in the mountaintop.

		Western	side				Eastern side	
	Latitude	Longitude	Model	R2	Latitude	Longitude	Model	R2
	7075030	-3805520	y = -4.0427E-03x + 11.914	0.7821	6924190	-3075140	y = -2.9672E-03x + 12.758	0.7723
2	6636390	-3890880	y = -5.5827E-03x + 14.181	0.8256	6508520	-2832130	y = -3.8689E-03x + 13.319	0.6929
3	6355640	-3966410	y = -6.2727E-03x + 12.713	0.8901	6006140	-2321130	y = -3.3734E-03x + 12.727	0.8705
4	5858640	-3818730	y = -6.6783E-03x + 12.312	0.8250	5547640	-2249130	y = -3.9905E-03x + 13.936	0.7689
5	5465050	-3875530	y = -5.244E-03x + 13.959	0.9655	5267090	-2200570	y = -3.2967E-03x + 13.376	0.9144
6	5267260	-4283520	y = -6.487E-03x + 14.804	0.9031	4867110	-2061600	y = -0.0013E-03x^2 + 1.9382E-03x + 11.260	0.9211
7	4834640	-4460130	y = -5.6956E-03x + 13.518	0.9624	4514770	-2314000	y = -0.0015E-03x^2 + 2.2707E-03x + 11.251	0.9485
8	4418120	-4462130	y = -4.7839E-03x + 14.154	0.9898	4106400	-2473370	y = -0.0011E-03x^2 + 0.417E-03x + 11.956	0.984
9	3974940	-4126420	y = -4.8802E-03x + 13.721	0.9736	3808640	-2714380	y = -2.9666E-03x + 13.242	0.8706
10	3567640	-4067530	y = -3.1102E-03x + 13.306	0.9283	3453700	-2785420	y = -0.0018E-03x^2 + 2.4733E-03x + 11.038	0.5755
11	3179370	-3872130	y = -3.7919E-03x + 12.822	0.9776	3136340	-3090820	y = -3.1158E-03x + 12.768	0.9411
12	2766890	-3705880	y = -5.1708E-03x + 13.560	0.9450	2757040	-3009730	y = -2.9475E-03x + 12.706	0.9559
13	2307480	-3640130	y = -4.8647E-03x + 14.160	0.9508	2368150	-2931130	y = -4.9641E-03x + 13.597	0.9468
14	1908340	-3042820	y = -4.2007E-03x + 12.437	0.9487	2037110	-2791660	y = -4.2453E-03x + 12.751	0.8816
15	1688310	-2393470	y = -6.1983E-03x + 14.354	0.9867	1786520	-2262260	y = -5.351E-03x + 13.469	0.9916
16	1057900	-1540130	y = -7.3075E-03x + 14.777	0.9582	1107640	-1439510	y = -7.42E-03x + 14.216	0.9594
17	755800	-399651	y = -7.3721E-03x + 13.231	0.9634	737130	-192130	y = -6.9312E-03x + 15.656	0.9745
18	468643	-523130	y = -7.7117E-03x + 14.498	0.9952	467260	-371130	y = -7.4971E-03x + 15.106	0.9752
19	168259	-920514	y = -7.0457E-03x + 14.299	0.9698	145047	-657462	y = -7.2321E-03x + 15.451	0.9495
20	-154781	-1039710	y = -6.5807E-03x + 12.005	0.9744	-143357	-754130	y = -5.7991E-03x + 13.369	0.9699
21	-590357	-1108130	y = -3.9943E-03x + 12.883	0.9766	-581357	-793130	y = -4.8577E-03x + 12.937	0.9522

22	-1020750	-924130	y = -3.4936E-03x + 13.455	0.8934	-986357	-592130	y = -3.523E-03x + 12.794	0.9603
23	-1383800	-734684	y = -4.0904E-03x + 14.917	0.9658	-1260130	17092	y = -3.8576E-03x + 13.656	0.9456
24	-1712360	-526776	y = -3.4718E-03x + 14.507	0.8927	-1664780	312818	y = -5.0148E-03x + 13.269	0.9852
25	-2080210	-22130	y = -3.3546E-03x + 15.773	0.9678	-2147160	931870	y = -3.6806E-03x + 13.269	0.9891
26	-2584220	-43130	y = -3.6027E-03x + 16.911	0.8483	-2560540	618870	y = -3.1806E-03x + 12.382	0.9808
27	-2906120	-54364	y = -3.8919E-03x + 13.918	0.9871	-2918360	583870	y = -3.4772E-03x + 12.955	0.9794
28	-3232190	-117130	y = -4.4388E-03x + 13.616	0.9885	-3224360	412870	y = -3.8112E-03x + 13.348	0.9648
29	-3564730	-125761	y = -4.5198E-03x + 13.649	0.9621	-3572360	599727	y = -4.2064E-03x + 14.219	0.9562
30	-3841040	-112451	y = -3.2651E-03x + 12.810	0.9567	-3860360	454870	y = -3.6746E-03x + 13.429	0.9904

(a) Highlands (2000 masl)



(b) Lowlands (300 masl)

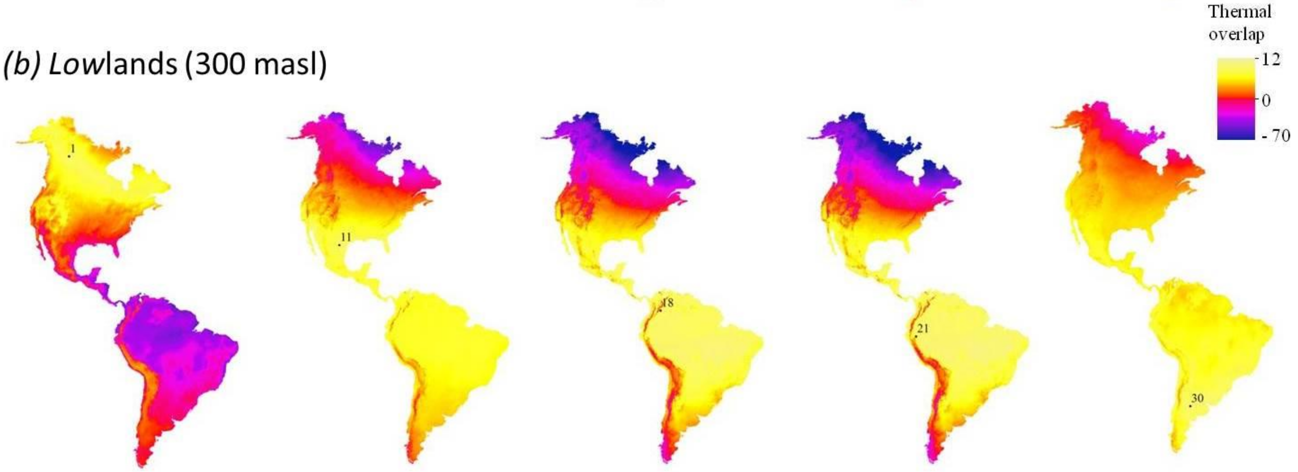
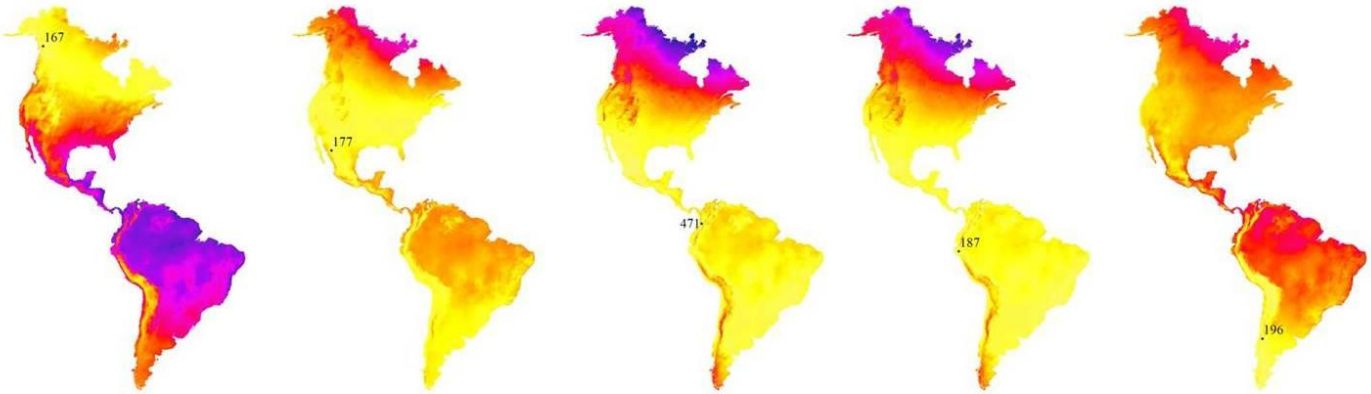


Figure S1.1a. Thermal Overlap (TOV) between focal sites and their surrounding environmental space in the eastern side of the Americas. Figure shows a selected group of sites in the *(a)* highlands *(b)* lowlands.

(a) Highlands (2000 masl)



(b) Lowlands (300 masl)

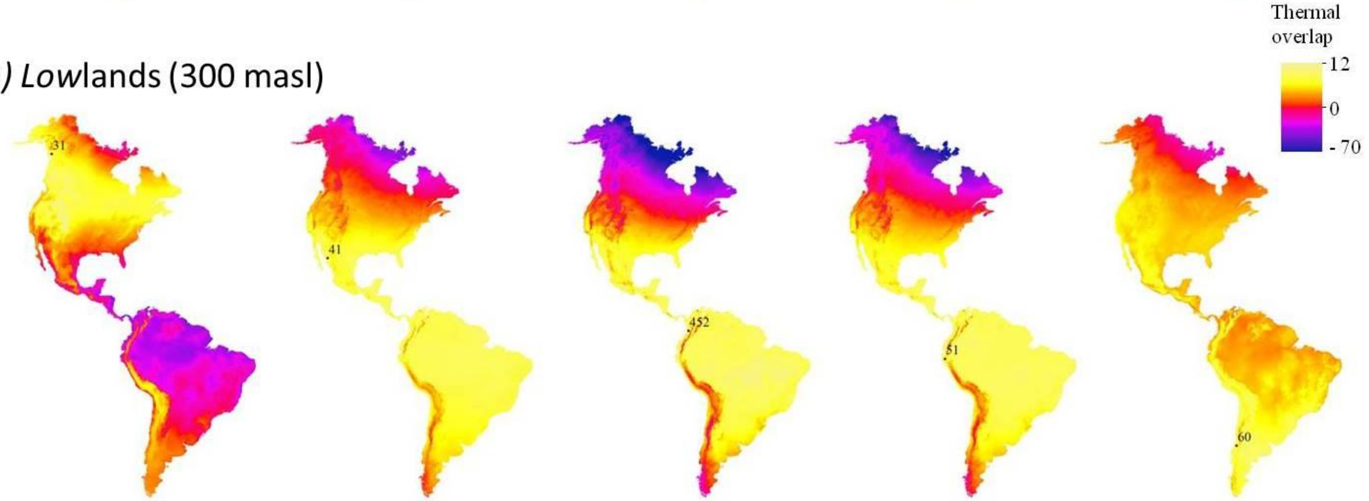


Figure S1.1b. Thermal Overlap (TOV) between focal sites and their surrounding environmental space in the western side of the Americas. Figure shows a selected group of sites in the *(a)* highlands *(b)* lowlands.

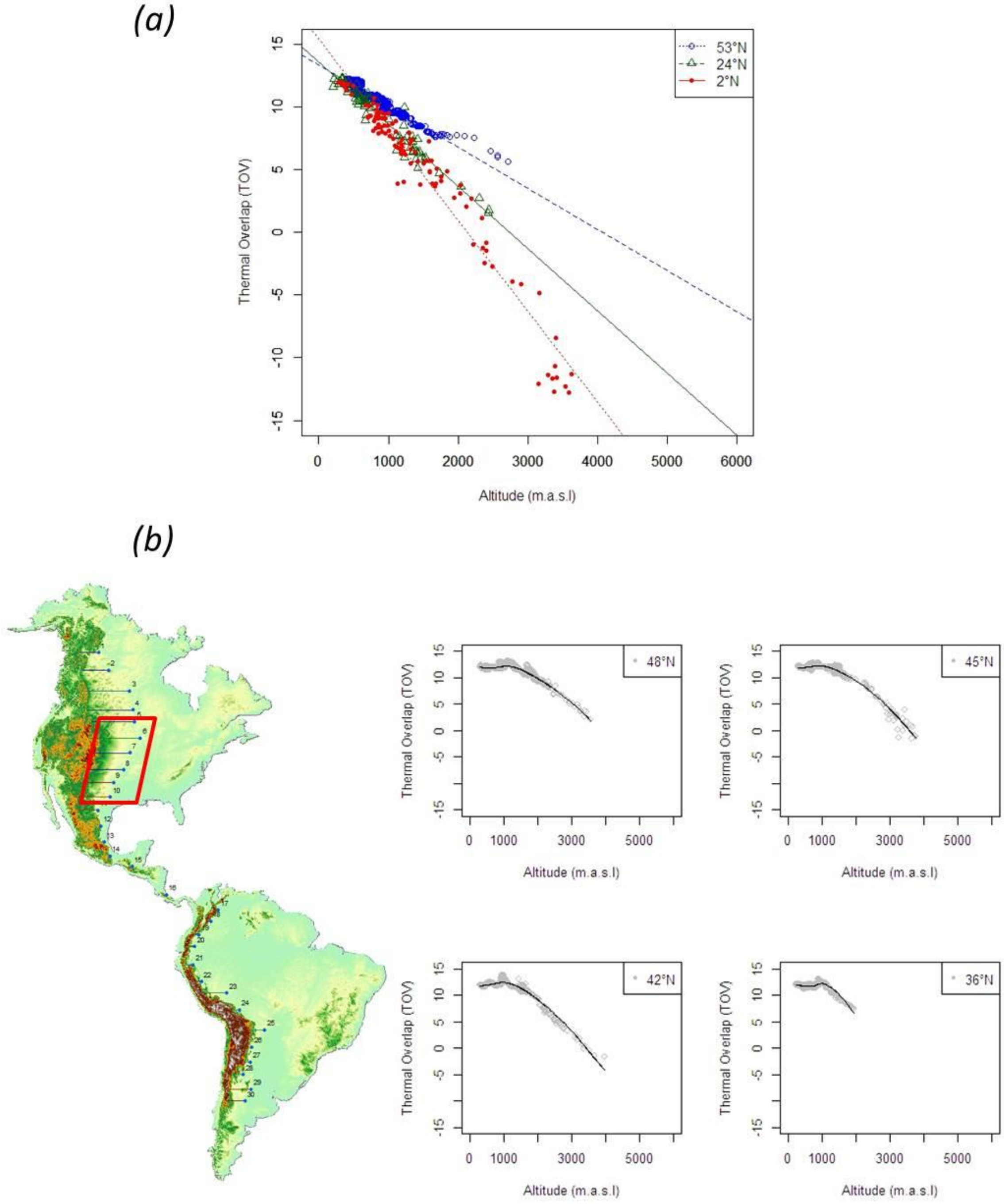


Figure S1.2. Thermal overlap as a function of altitude: *(a)* This relationship is linear for most of the Americas (three sites in eastern side), but is non-linear in some regions east of the Rockies in North America between 33°N and 48°N *(b).*

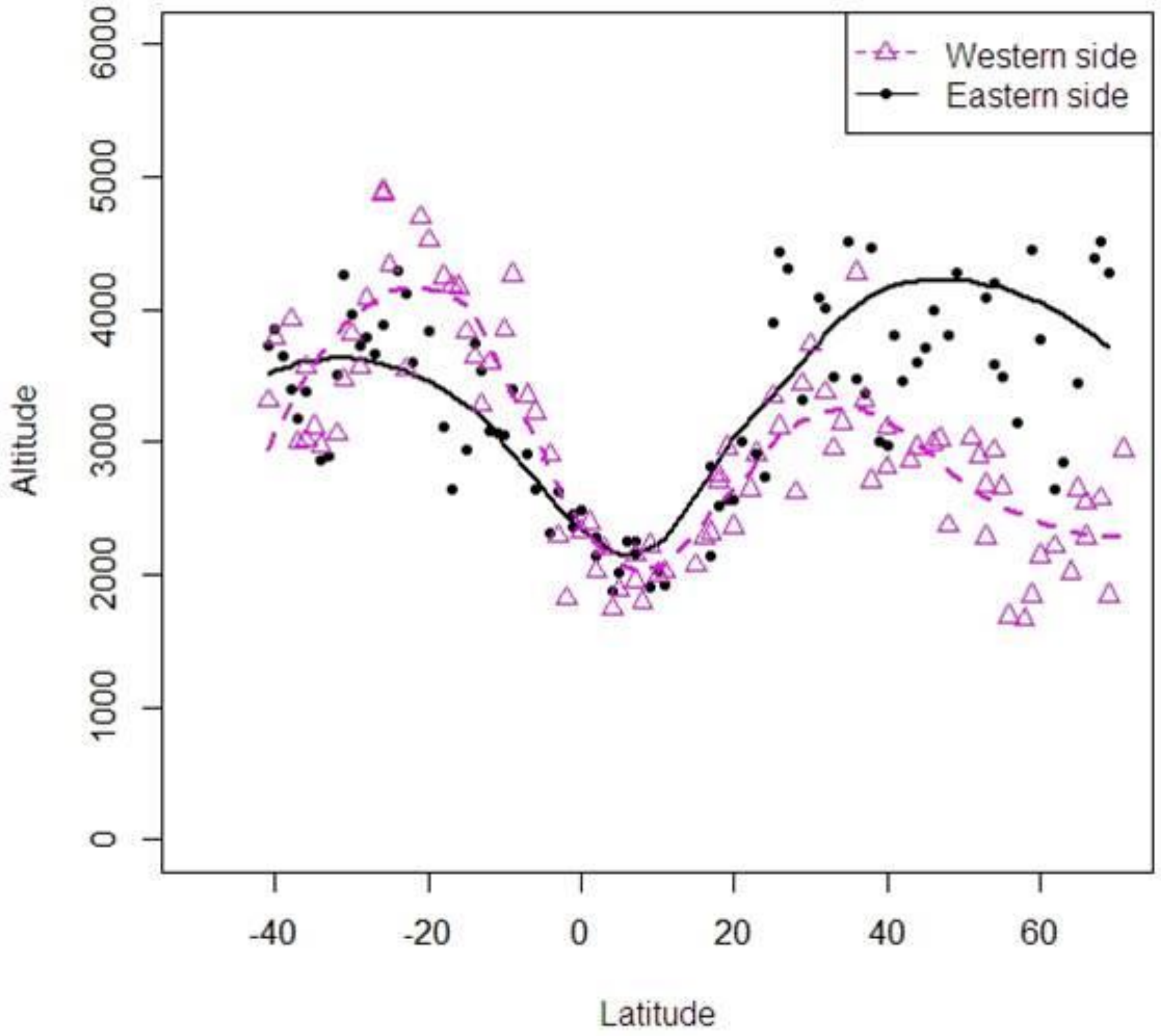


Figure S1.3. Elevation at which thermal overlap decreases to zero at all locations across the Americas.

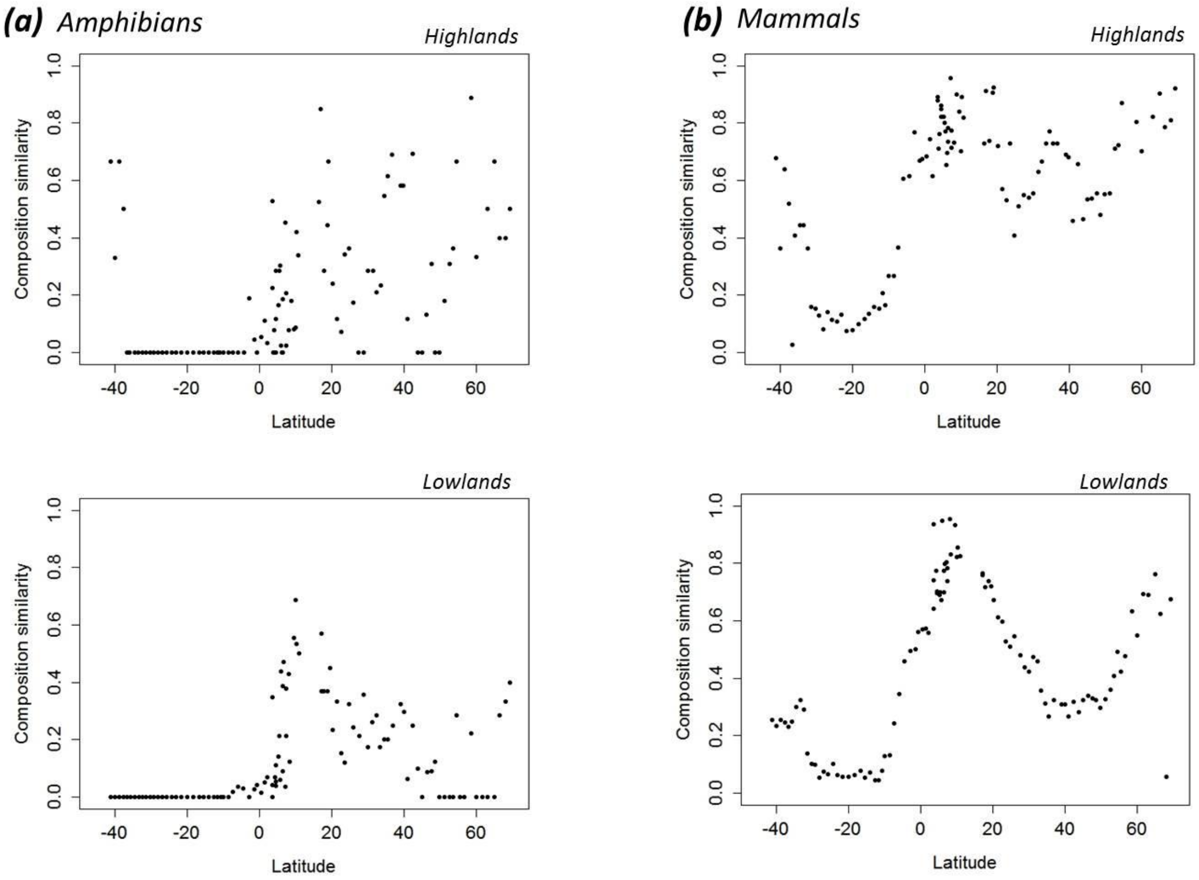


Figure S1.4. Compositional similarity between pairwise comparisons of quadrats across a latitudinal gradient in the Americas' mountains. (*a*) Amphibians and (*b*) Mammals. Upper panel shows pairwise comparisons of sites between sites in the highlands and lower panel in lowlands

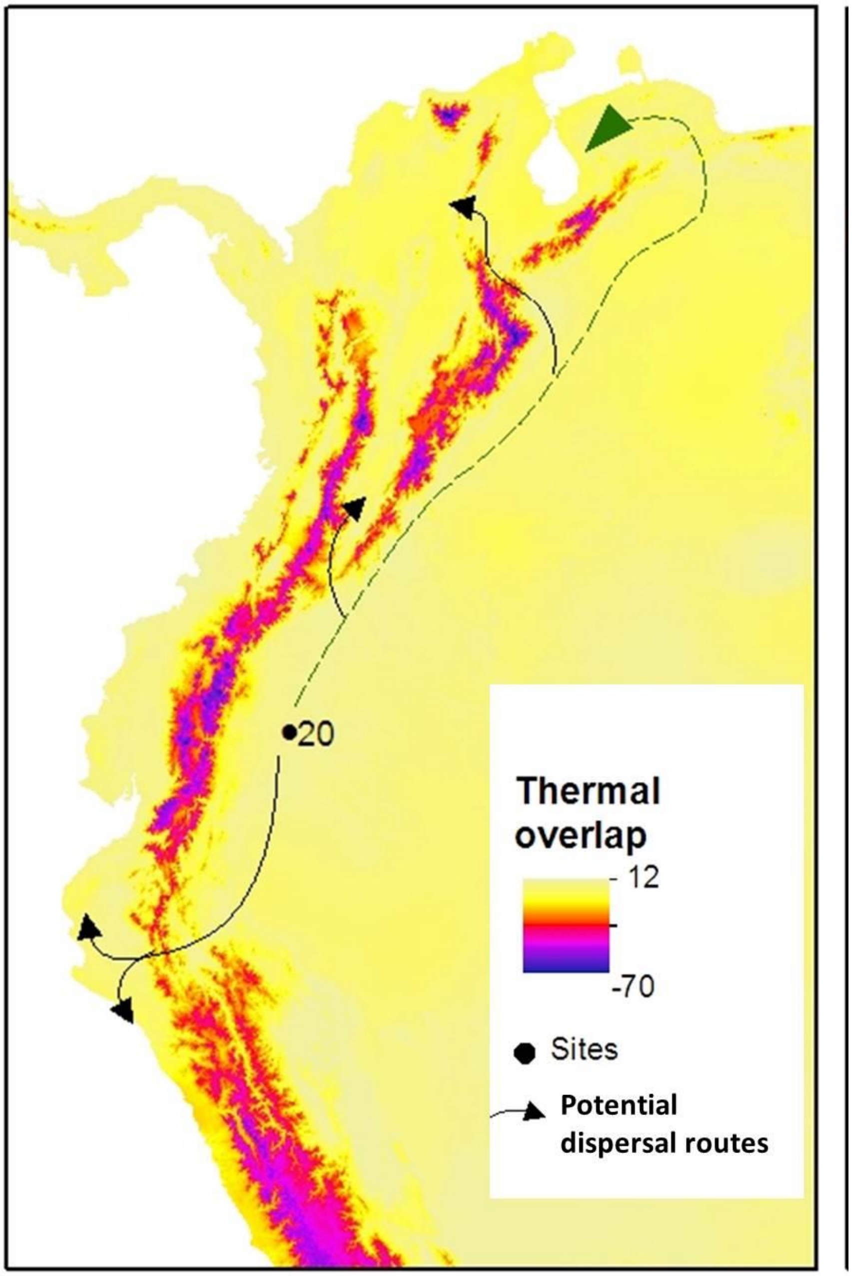


Figure S1.5. Potential ‘passes’ in northern South America that could allow species to circumvent thermal barriers imposed by differences in thermal regimes between focal sites. Arrows represent potential dispersal routes.

APPENDICES CHAPTER 2

Table S2.1. Non-parametric correlations coefficients (Spearman rank, r_s) between endemism for mammals and amphibians and environmental predictors. Metrics of endemism based on species range size cut-offs (QE = first quartile; 50K = 50,000 km^2 and 250K = 250,000 km^2), inverse range size (WE = Weighted Endemism) and median range size (Median). Results shown are for *c.* 110 km x 110 km spatial resolution.

Hypothesis/Predictors	**Amphibians**					**Mammals**				
	QE	50K	250K	WE	Median	QE	50K	250K	WE	Median
H1: ***Climate velocity***	-0.26	-0.42	-0.50	-0.39	0.43	-0.32	-0.40	-0.51	-0.56	0.43
H2: ***Climate seasonality***										
Mean temperature	-0.26	-0.37	-0.44	-0.70	0.42	-0.27	-0.31	-0.42	-0.66	0.45
Total precipitation	0.001	0.02	0.02	0.02	-0.02	0.03	0.05	0.08	0.11	-0.16
H3: ***Climate distinctiveness (rarity)***										
Mean temperature	0.06	0.06	0.06	-0.17	-0.05	0.09	0.09	0.06	-0.09	-0.00003
Total precipitation	0.27	0.42	0.49	0.62	-0.34	0.29	0.34	0.41	0.63	-0.39
Precipitation seasonality	0.09	0.13	0.19	0.20	-0.28	0.11	0.19	0.27	0.27	-0.28
Temperature seasonality	-0.14	-0.12	-0.14	-0.32	0.06	-0.10	-0.09	-0.10	-0.26	0.04
H4: ***Spatial heterogeneity***										
in climate:										
Mean temperature	0.21	0.30	0.34	0.13	-0.24	0.25	0.30	0.33	0.27	-0.19
in topography:										
Elevation	0.22	0.32	0.37	0.18	-0.29	0.27	0.32	0.37	0.32	-0.24
in habitat										
Actual evapotranspiration	0.14	0.20	0.18	0.25	-0.14	0.18	0.21	0.23	0.32	-0.17
Potential evapotranspiration	0.23	0.39	0.48	0.37	-0.47	0.30	0.39	0.48	0.49	-0.43
H5: ***Total species richness***	0.29	0.45	0.51	0.84	-0.40	0.29	0.32	0.37	0.74	-0.34
Other predictors										
Productivity:										

Potential evapotranspiration	0.06	0.11	0.17	0.41	-0.30	0.07	0.09	0.19	0.33	-0.33
Actual evapotranspiration	0.24	0.35	0.39	0.69	-0.26	0.22	0.23	0.26	0.58	-0.29
Precipitation total	0.26	0.39	0.41	0.66	-0.21	0.22	0.21	0.20	0.50	-0.18
Current - Mean temperature	0.11	0.18	0.24	0.49	-0.30	0.10	0.13	0.23	0.40	-0.32
Past mean temperature (LGM)	0.12	0.20	0.26	0.49	-0.30	0.12	0.16	0.28	0.45	-0.35
Area	-0.11	-0.14	-0.18	-0.28	0.25	-0.10	-0.11	-0.15	-0.20	0.18
Glaciated areas (LGM)	-0.05	-0.13	-0.19	-0.29	0.22	-0.07	-0.13	-0.23	-0.40	0.33

Table S2.2. Spearman correlation coefficients (r) between *amphibians'* endemism and several predictors at different spatial resolutions. We used four metrics to calculate endemism based on range size (QE= first quartile; 50K=50,000 km^2 and 250K=250,000 km^2), inverse range size (WE = Weighted Endemism), and median range size.

		Spatial resolution																						
		100 km X 100 km						200 km X 200 km						500 km X 500 km						1,000 km X 1,000 km				
Predictors	#	QE	50K	250K	WE	Median	x	QE	50K	250K	WE	Median	x	QE	50K	250K	WE	Median	x	QE	50K	250K	WE	Median
Climate velocity	1	-0.26	-0.42	-0.50	-0.39	0.43		-0.35	-0.47	-0.55	-0.44	0.47		-0.45	-0.58	-0.62	-0.50	0.55		-0.53	-0.51	-0.49	-0.45	0.49
Climate distinctiveness in MAT (t=0.5, wind=5)	2	0.12	0.14	0.14	-0.05	-0.12		0.03	0.02	0.05	-0.11	-0.06		-0.08	0.01	0.06	-0.09	-0.14		0.12	0.17	0.23	0.07	-0.18
Climate distinctiveness in MAT (t=0.5, wind=11)	3	0.06	0.07	0.07	-0.14	-0.07		-0.01	-0.03	0.00	-0.19	-0.06		-0.07	0.04	0.06	-0.10	-0.12		0.00	0.07	0.10	0.00	-0.05
Climate distinctiveness in MAT (t=0.5, wind=15)	4	0.04	0.05	0.04	-0.18	-0.06		-0.03	-0.01	0.02	-0.18	-0.10		-0.08	0.01	0.03	-0.14	-0.09		-0.05	0.00	0.05	-0.06	0.00
Climate distinctiveness in MAT (t=1, wind=5)	5	0.12	0.14	0.15	-0.07	-0.10		0.03	0.02	0.03	-0.15	-0.06		-0.09	0.00	0.09	-0.12	-0.15		0.09	0.03	0.09	-0.08	-0.03
Climate distinctiveness in MAT (t=1, wind=11)	6	0.06	0.06	0.06	-0.17	-0.05		-0.02	-0.02	0.00	-0.20	-0.07		-0.08	0.00	0.05	-0.15	-0.10		-0.07	-0.05	-0.01	-0.12	0.08
Climate distinctiveness in MAT (t=1, wind=15)	7	0.03	0.04	0.03	-0.20	-0.04		-0.03	-0.02	0.01	-0.20	-0.09		-0.09	-0.01	0.02	-0.18	-0.06		-0.09	-0.12	-0.06	-0.19	0.12
Climate distinctiveness in MAT (t=2, wind=5)	8	0.12	0.16	0.18	-0.05	-0.10		0.00	0.00	0.02	-0.21	-0.01		-0.13	-0.05	0.01	-0.17	-0.10		0.17	0.08	0.17	-0.05	-0.11
Climate distinctiveness in MAT (t=2, wind=11)	9	0.05	0.06	0.06	-0.19	-0.04		-0.04	-0.05	-0.03	-0.25	-0.03		-0.10	-0.02	0.02	-0.16	-0.11		-0.03	-0.09	-0.02	-0.18	0.06
Climate distinctiveness in MAT (t=2, wind=15)	10	0.02	0.03	0.02	-0.22	-0.04		-0.06	-0.04	-0.01	-0.23	-0.07		-0.10	-0.02	0.01	-0.19	-0.07		-0.09	-0.18	-0.12	-0.29	0.15
Climate distinctiveness in MAT (t=4, wind=5)	11	0.12	0.18	0.23	0.03	-0.15		0.00	0.01	0.03	-0.18	0.01		-0.19	-0.15	-0.11	-0.27	0.03		0.25	0.00	0.14	-0.09	-0.16
Climate distinctiveness in MAT (t=4, wind=11)	12	0.02	0.04	0.05	-0.21	-0.01		-0.08	-0.07	-0.05	-0.27	-0.01		-0.12	-0.04	0.00	-0.19	-0.07		0.00	-0.11	-0.02	-0.21	0.04
Climate distinctiveness in MAT (t=4, wind=15)	13	-0.01	0.00	0.00	-0.25	0.00		-0.09	-0.06	-0.03	-0.25	-0.05		-0.09	-0.02	0.01	-0.19	-0.04		-0.06	-0.21	-0.11	-0.32	0.14
Climate distinctiveness in Prec.Tot. (t=10, wind=5)	14	0.16	0.23	0.29	0.41	-0.20		0.13	0.24	0.27	0.37	-0.17		0.11	0.14	0.14	0.23	-0.13		0.15	0.23	0.21	0.29	-0.20
Climate distinctiveness in Prec.Tot. (t=10, wind=11)	15	0.20	0.31	0.37	0.49	-0.25		0.22	0.33	0.37	0.49	-0.26		0.29	0.29	0.27	0.41	-0.26		0.11	0.25	0.18	0.33	-0.25

Climate distinctiveness in Prec.Tot. (t=10, wind=15)	16	0.21	0.33	0.40	0.52	-0.28	0.25	0.38	0.41	0.54	-0.30	0.34	0.34	0.32	0.45	-0.28	0.08	0.31	0.23	0.42	-0.28
Climate distinctiveness in Prec.Tot. (t=100, wind=5)	17	0.28	0.43	0.51	0.62	-0.34	0.32	0.45	0.48	0.58	-0.32	0.46	0.54	0.46	0.62	-0.39	0.30	0.64	0.58	0.71	-0.58
Climate distinctiveness in Prec.Tot. (t=100, wind=11)	18	0.27	0.42	0.49	0.62	-0.34	0.32	0.46	0.49	0.61	-0.36	0.52	0.56	0.48	0.67	-0.43	0.17	0.58	0.47	0.66	-0.49
Climate distinctiveness in Prec.Tot. (t=100, wind=15)	19	0.26	0.42	0.49	0.62	-0.35	0.31	0.47	0.49	0.62	-0.37	0.55	0.58	0.49	0.68	-0.44	0.13	0.56	0.47	0.65	-0.46
Climate distinctiveness in Prec.Tot. (t=200, wind=5)	20	0.29	0.46	0.53	0.65	-0.38	0.35	0.48	0.50	0.62	-0.36	0.48	0.57	0.47	0.64	-0.39	0.37	0.68	0.60	0.74	-0.61
Climate distinctiveness in Prec.Tot. (t=200, wind=11)	21	0.27	0.44	0.50	0.64	-0.37	0.34	0.48	0.49	0.63	-0.38	0.52	0.56	0.47	0.67	-0.42	0.22	0.65	0.53	0.73	-0.58
Climate distinctiveness in Prec.Tot. (t=200, wind=15)	22	0.27	0.44	0.49	0.64	-0.37	0.34	0.49	0.49	0.64	-0.39	0.54	0.57	0.48	0.67	-0.43	0.18	0.62	0.51	0.69	-0.53
Climate distinctiveness in Prec.Tot. (t=500, wind=5)	23	0.30	0.41	0.43	0.47	-0.29	0.34	0.41	0.41	0.52	-0.30	0.52	0.53	0.43	0.63	-0.39	0.34	0.65	0.55	0.72	-0.54
Climate distinctiveness in Prec.Tot. (t=500, wind=11)	24	0.27	0.40	0.44	0.59	-0.36	0.35	0.48	0.48	0.64	-0.43	0.52	0.51	0.45	0.64	-0.42	0.13	0.56	0.44	0.66	-0.50
Climate distinctiveness in Prec.Tot. (t=500, wind=15)	25	0.26	0.41	0.44	0.61	-0.39	0.35	0.49	0.49	0.66	-0.45	0.53	0.51	0.43	0.61	-0.39	0.11	0.54	0.44	0.63	-0.48
Climate distinctiveness in Prec.Seas. (t=1, wind=5)	26	0.11	0.15	0.21	0.20	-0.27	0.10	0.13	0.17	0.19	-0.24	0.08	0.16	0.16	0.17	-0.20	0.22	0.34	0.29	0.32	-0.28
Climate distinctiveness in Prec.Seas. (t=1, wind=11)	27	0.08	0.13	0.18	0.20	-0.27	0.11	0.15	0.18	0.22	-0.26	0.04	0.10	0.11	0.09	-0.13	-0.10	0.01	-0.05	-0.01	0.05
Climate distinctiveness in Prec.Seas. (t=1, wind=15)	28	0.07	0.12	0.17	0.21	-0.27	0.11	0.16	0.20	0.24	-0.29	0.05	0.07	0.10	0.06	-0.11	-0.11	-0.05	-0.09	-0.07	0.10
Climate distinctiveness in Prec.Seas. (t=2, wind=5)	29	0.13	0.17	0.22	0.19	-0.27	0.12	0.15	0.19	0.20	-0.27	0.12	0.18	0.18	0.18	-0.23	0.33	0.35	0.34	0.30	-0.34
Climate distinctiveness in Prec.Seas. (t=2, wind=11)	30	0.09	0.13	0.19	0.20	-0.28	0.12	0.16	0.19	0.23	-0.28	0.07	0.13	0.14	0.11	-0.19	0.05	-0.03	0.00	-0.05	-0.02

Climate distinctiveness in Prec.Seas. (t=2, wind=15)	31	0.07	0.13	0.18	0.21	-0.28	0.11	0.17	0.20	0.24	-0.30	0.07	0.10	0.13	0.07	-0.16	0.01	-0.04	-0.04	-0.03	0.00
Climate distinctiveness in Prec.Seas. (t=3, wind=5)	32	0.12	0.16	0.19	0.13	-0.23	0.15	0.17	0.20	0.18	-0.25	0.17	0.21	0.21	0.21	-0.24	0.40	0.33	0.34	0.29	-0.37
Climate distinctiveness in Prec.Seas. (t=3, wind=11)	33	0.09	0.14	0.19	0.19	-0.28	0.12	0.16	0.19	0.21	-0.28	0.07	0.12	0.15	0.11	-0.20	0.17	0.04	0.06	0.03	-0.12
Climate distinctiveness in Prec.Seas. (t=3, wind=15)	34	0.07	0.13	0.17	0.20	-0.28	0.10	0.16	0.20	0.22	-0.31	0.05	0.08	0.12	0.05	-0.15	0.06	0.03	0.05	0.04	-0.08
Climate distinctiveness in Prec.Seas. (t=4, wind=5)	35	0.09	0.12	0.11	0.04	-0.13	0.06	0.05	0.07	-0.01	-0.06	-0.03	0.00	-0.01	-0.02	-0.02	0.16	-0.09	-0.09	-0.13	0.05
Climate distinctiveness in Prec.Seas. (t=4, wind=11)	36	0.05	0.06	0.08	0.05	-0.13	0.05	0.07	0.08	0.06	-0.15	-0.06	-0.03	0.02	-0.05	-0.05	-0.04	-0.17	-0.19	-0.20	0.19
Climate distinctiveness in Prec.Seas. (t=4, wind=15)	37	0.04	0.07	0.09	0.09	-0.17	0.04	0.06	0.09	0.08	-0.19	-0.09	-0.10	-0.04	-0.12	0.04	-0.09	-0.14	-0.16	-0.15	0.18
Climate distinctiveness in Temp.Seas. (t=1, wind=5)	38	-0.11	-0.16	-0.19	-0.22	0.11	-0.20	-0.23	-0.24	-0.23	0.18	-0.17	-0.18	-0.13	-0.10	0.09	0.20	-0.03	-0.05	-0.04	0.03
Climate distinctiveness in Temp.Seas. (t=1, wind=11)	39	-0.14	-0.15	-0.17	-0.26	0.10	-0.18	-0.18	-0.18	-0.22	0.11	-0.16	-0.18	-0.11	-0.18	0.07	0.11	-0.04	-0.09	-0.08	0.06
Climate distinctiveness in Temp.Seas. (t=1, wind=15)	40	-0.13	-0.13	-0.15	-0.25	0.08	-0.17	-0.15	-0.15	-0.20	0.07	-0.14	-0.15	-0.10	-0.19	0.08	0.20	0.04	-0.02	0.01	-0.04
Climate distinctiveness in Temp.Seas. (t=2, wind=5)	41	-0.13	-0.11	-0.12	-0.31	0.05	-0.20	-0.18	-0.18	-0.30	0.09	-0.17	-0.12	-0.06	-0.15	0.00	0.23	-0.06	-0.04	-0.12	-0.01
Climate distinctiveness in Temp.Seas. (t=2, wind=11)	42	-0.14	-0.12	-0.14	-0.33	0.06	-0.19	-0.17	-0.18	-0.29	0.06	-0.13	-0.14	-0.10	-0.19	0.03	0.07	-0.14	-0.14	-0.21	0.13
Climate distinctiveness in Temp.Seas. (t=2, wind=15)	43	-0.15	-0.13	-0.15	-0.33	0.07	-0.16	-0.15	-0.16	-0.27	0.05	-0.12	-0.14	-0.10	-0.22	0.06	0.10	-0.17	-0.17	-0.25	0.14
Climate distinctiveness in Temp.Seas. (t=3, wind=5)	44	-0.13	-0.11	-0.11	-0.36	0.06	-0.21	-0.19	-0.17	-0.36	0.07	-0.21	-0.20	-0.16	-0.28	0.07	0.10	-0.09	-0.06	-0.17	-0.02
Climate distinctiveness in Temp.Seas. (t=3, wind=11)	45	-0.16	-0.14	-0.15	-0.37	0.08	-0.20	-0.19	-0.19	-0.33	0.07	-0.15	-0.16	-0.13	-0.26	0.06	-0.06	-0.13	-0.15	-0.25	0.16

Climate distinctiveness in Temp.Seas. (t=3, wind=15)	46	-0.16	-0.14	-0.17	-0.37	0.08	-0.18	-0.17	-0.17	-0.31	0.06	-0.14	-0.17	-0.15	-0.30	0.10	-0.17	-0.32	-0.30	-0.43	0.31
Climate distinctiveness in Temp.Seas. (t=4, wind=5)	47	-0.11	-0.11	-0.10	-0.36	0.10	-0.22	-0.22	-0.19	-0.40	0.10	-0.22	-0.22	-0.18	-0.31	0.09	0.04	-0.10	-0.07	-0.15	-0.01
Climate distinctiveness in Temp.Seas. (t=4, wind=11)	48	-0.17	-0.16	-0.17	-0.41	0.09	-0.21	-0.22	-0.22	-0.38	0.09	-0.15	-0.17	-0.14	-0.27	0.07	-0.10	-0.22	-0.22	-0.30	0.23
Climate distinctiveness in Temp.Seas. (t=4, wind=15)	49	-0.17	-0.16	-0.18	-0.40	0.10	-0.19	-0.19	-0.20	-0.35	0.08	-0.14	-0.16	-0.14	-0.29	0.10	-0.15	-0.37	-0.32	-0.45	0.35
Habitat heterogeneity (Range) in AET	50	0.14	0.19	0.18	0.24	-0.14	0.17	0.23	0.26	0.36	-0.29	0.20	0.31	0.38	0.39	-0.43	0.47	0.45	0.43	0.48	-0.48
Habitat heterogeneity (Range) in PET	51	0.24	0.41	0.50	0.39	-0.48	0.33	0.46	0.56	0.45	-0.54	0.37	0.56	0.64	0.51	-0.62	0.66	0.67	0.69	0.60	-0.70
Habitat heterogeneity (Range) in MAT	52	0.22	0.32	0.36	0.16	-0.26	0.28	0.33	0.38	0.19	-0.29	0.21	0.31	0.38	0.17	-0.32	0.33	0.22	0.27	0.08	-0.24
Habitat heterogeneity (Range) in Altitude	53	0.22	0.33	0.38	0.19	-0.29	0.29	0.36	0.42	0.25	-0.34	0.30	0.41	0.49	0.32	-0.43	0.52	0.47	0.50	0.35	-0.47
Habitat heterogeneity (Sd) in AET	54	0.14	0.20	0.18	0.25	-0.14	0.20	0.27	0.27	0.35	-0.25	0.29	0.40	0.39	0.46	-0.35	0.41	0.55	0.45	0.61	-0.50
Habitat heterogeneity (Sd) in PET	55	0.23	0.39	0.48	0.37	-0.47	0.31	0.43	0.53	0.41	-0.52	0.31	0.48	0.56	0.40	-0.56	0.47	0.41	0.48	0.36	-0.53
Habitat heterogeneity (Sd) in MAT	56	0.21	0.30	0.34	0.13	-0.24	0.26	0.30	0.35	0.15	-0.26	0.11	0.20	0.27	0.04	-0.23	0.11	-0.04	0.03	-0.14	-0.06
Habitat heterogeneity (Sd) in Altitude	57	0.22	0.32	0.37	0.18	-0.29	0.28	0.35	0.41	0.23	-0.34	0.28	0.41	0.48	0.30	-0.44	0.53	0.44	0.46	0.32	-0.47
Seasonality in MAT	58	-0.26	-0.37	-0.44	-0.70	0.42	-0.36	-0.44	-0.48	-0.70	0.43	-0.54	-0.55	-0.50	-0.71	0.44	-0.34	-0.67	-0.56	-0.77	0.57
Seasonality in Prec. Tot.	59	0.00	0.02	0.02	0.02	-0.02	0.03	0.02	0.01	0.03	-0.04	0.05	0.07	0.05	0.08	-0.07	0.32	0.16	0.09	0.16	-0.15
Climate relict in MAT (wind=5)	60	0.09	0.08	0.07	0.02	-0.04	0.12	0.09	0.11	0.02	-0.06	0.08	0.03	0.00	-0.07	0.05	-0.20	-0.23	-0.29	-0.24	0.22
Climate relict in MAT (wind=11)	61	0.12	0.10	0.11	0.00	-0.04	0.15	0.08	0.08	-0.04	0.00	-0.09	-0.13	-0.14	-0.23	0.17	-0.23	-0.25	-0.30	-0.29	0.28
Climate relict in MAT (wind=15)	62	0.13	0.10	0.11	-0.01	-0.02	0.13	0.04	0.04	-0.09	0.03	-0.14	-0.16	-0.16	-0.27	0.19	-0.24	-0.25	-0.28	-0.29	0.28
Productivity in PET	63	0.06	0.11	0.17	0.41	-0.30	0.11	0.17	0.19	0.40	-0.29	0.21	0.24	0.24	0.38	-0.27	0.38	0.43	0.36	0.51	-0.41
Productivity in AET	64	0.24	0.35	0.39	0.69	-0.26	0.32	0.42	0.42	0.69	-0.27	0.53	0.53	0.43	0.72	-0.31	0.07	0.64	0.55	0.74	-0.44
Area	65	-0.12	-0.14	-0.18	-0.28	0.25	-0.13	-0.16	-0.19	-0.28	0.24	-0.19	-0.20	-0.19	-0.28	0.24	0.04	-0.21	-0.27	-0.31	0.28
Glaciated areas	66	-0.05	-0.13	-0.19	-0.29	0.22	-0.06	-0.16	-0.20	-0.28	0.24	-0.17	-0.24	-0.25	-0.29	0.25	-0.41	-0.28	-0.26	-0.29	0.28
MAT	67	0.11	0.18	0.24	0.49	-0.30	0.17	0.24	0.26	0.49	-0.30	0.30	0.31	0.30	0.47	-0.30	0.34	0.52	0.43	0.60	-0.47
MAT-Past	68	0.12	0.20	0.26	0.49	-0.30	0.19	0.26	0.29	0.49	-0.31	0.32	0.34	0.32	0.48	-0.31	0.38	0.54	0.45	0.60	-0.47
Precipitation total	69	0.26	0.39	0.40	0.66	-0.21	0.34	0.44	0.42	0.65	-0.22	0.54	0.52	0.40	0.66	-0.27	0.01	0.61	0.50	0.69	-0.42

Altitude	70	0.10	0.13	0.17	0.06	-0.19	0.13	0.15	0.21	0.11	-0.24	0.15	0.24	0.30	0.18	-0.32	0.47	0.28	0.32	0.22	-0.35
Richness	71	0.29	0.45	0.51	0.85	-0.40	0.41	0.54	0.56	0.85	-0.43	0.65	0.70	0.63	0.88	-0.52	0.32	0.83	0.76	0.93	-0.70

Table S2.3. Spearman correlation coefficients (r) between *mammals'* endemism and several predictors at different spatial resolutions. We used five metrics to calculate endemism based on range size (QE= first quartile; 50K=50,000 km^2 and 250K=250,000 km^2), inverse range size (WE = Weighted Endemism) and median range size (Median).

		Spatial resolution																			
		100 km X 100 km					200 km X 200 km					500 km X 500 km					1,000 km X 1,000 km				
Predictors	#	QE	50K	250K	WE	Median	QE	50K	250K	WE	Median	QE	50K	250K	WE	Median	QE	50K	250K	WE	Median
Climate velocity	1	-0.32	-0.40	-0.51	-0.55	0.43	-0.41	-0.47	-0.55	-0.59	0.45	-0.54	-0.57	-0.63	-0.62	0.49	-0.57	-0.52	-0.55	-0.58	0.48
Climate distinctiveness in MAT (t=0.5, wind=5)	2	0.14	0.16	0.15	0.05	-0.07	0.07	0.08	0.07	-0.02	-0.05	0.08	0.06	0.09	0.00	-0.12	0.19	0.10	0.10	0.06	-0.13
Climate distinctiveness in MAT (t=0.5, wind=11)	3	0.09	0.10	0.07	-0.07	-0.02	0.02	0.01	0.00	-0.14	-0.01	0.06	0.06	0.05	-0.04	-0.08	0.08	-0.03	-0.02	-0.01	0.01
Climate distinctiveness in MAT (t=0.5, wind=15)	4	0.07	0.07	0.03	-0.12	0.00	0.01	0.02	0.01	-0.14	-0.03	0.02	0.04	0.02	-0.07	-0.03	0.02	-0.10	-0.08	-0.10	0.05
Climate distinctiveness in MAT (t=1, wind=5)	5	0.15	0.16	0.15	0.03	-0.04	0.07	0.06	0.04	-0.07	-0.02	0.07	0.08	0.08	-0.02	-0.09	0.07	0.01	0.00	-0.06	-0.06
Climate distinctiveness in MAT (t=1, wind=11)	6	0.09	0.09	0.06	-0.09	0.00	0.03	0.02	-0.01	-0.15	-0.01	0.01	0.03	0.01	-0.08	-0.03	-0.05	-0.12	-0.12	-0.12	0.11
Climate distinctiveness in MAT (t=1, wind=15)	7	0.07	0.06	0.03	-0.14	0.01	0.02	0.02	0.00	-0.16	-0.02	0.00	0.02	-0.01	-0.11	0.01	-0.08	-0.18	-0.16	-0.20	0.14
Climate distinctiveness in MAT (t=2, wind=5)	8	0.16	0.19	0.20	0.08	-0.06	0.06	0.05	0.03	-0.12	0.04	-0.02	-0.01	-0.01	-0.11	-0.03	0.15	0.02	0.02	-0.03	-0.07
Climate distinctiveness in MAT (t=2, wind=11)	9	0.09	0.09	0.07	-0.10	0.00	0.00	-0.01	-0.03	-0.20	0.04	-0.01	0.00	-0.01	-0.11	-0.04	-0.04	-0.13	-0.13	-0.15	0.16
Climate distinctiveness in MAT (t=2, wind=15)	10	0.06	0.06	0.02	-0.15	0.02	-0.01	-0.01	-0.02	-0.19	0.01	-0.02	0.01	-0.02	-0.14	-0.01	-0.12	-0.22	-0.22	-0.26	0.24
Climate distinctiveness in MAT (t=4, wind=5)	11	0.18	0.23	0.28	0.18	-0.14	0.06	0.07	0.07	-0.07	0.03	-0.12	-0.14	-0.14	-0.24	0.11	0.19	0.02	0.03	-0.02	-0.06

Climate distinctiveness in MAT (t=4, wind=11)	12	0.07	0.08	0.06	-0.11	0.04	-0.03	-0.04	-0.05	-0.22	0.05	-0.05	-0.04	-0.05	-0.17	0.03	-0.01	-0.14	-0.14	-0.18	0.16
Climate distinctiveness in MAT (t=4, wind=15)	13	0.03	0.04	0.00	-0.18	0.06	-0.04	-0.04	-0.05	-0.22	0.02	-0.04	-0.01	-0.03	-0.16	0.03	-0.11	-0.23	-0.22	-0.29	0.23
Climate distinctiveness in Prec.Tot. (t=10, wind=5)	14	0.19	0.24	0.29	0.49	-0.28	0.17	0.22	0.25	0.42	-0.27	0.18	0.17	0.18	0.31	-0.22	0.20	0.05	0.09	0.22	-0.14
Climate distinctiveness in Prec.Tot. (t=10, wind=11)	15	0.23	0.28	0.34	0.54	-0.33	0.23	0.27	0.32	0.50	-0.33	0.29	0.25	0.23	0.41	-0.28	0.22	0.11	0.10	0.25	-0.10
Climate distinctiveness in Prec.Tot. (t=10, wind=15)	16	0.24	0.29	0.35	0.56	-0.34	0.26	0.30	0.33	0.52	-0.36	0.29	0.26	0.26	0.42	-0.28	0.24	0.17	0.15	0.29	-0.18
Climate distinctiveness in Prec.Tot. (t=100, wind=5)	17	0.31	0.37	0.44	0.65	-0.37	0.33	0.37	0.41	0.58	-0.37	0.41	0.38	0.39	0.53	-0.44	0.54	0.46	0.44	0.54	-0.56
Climate distinctiveness in Prec.Tot. (t=100, wind=11)	18	0.30	0.35	0.42	0.63	-0.38	0.33	0.36	0.40	0.58	-0.40	0.43	0.39	0.38	0.56	-0.44	0.44	0.38	0.36	0.47	-0.43
Climate distinctiveness in Prec.Tot. (t=100, wind=15)	19	0.29	0.34	0.41	0.63	-0.39	0.32	0.35	0.39	0.58	-0.41	0.43	0.39	0.37	0.55	-0.40	0.41	0.39	0.36	0.40	-0.38
Climate distinctiveness in Prec.Tot. (t=200, wind=5)	20	0.33	0.40	0.47	0.68	-0.40	0.35	0.39	0.43	0.61	-0.40	0.40	0.38	0.38	0.52	-0.43	0.62	0.59	0.55	0.62	-0.61
Climate distinctiveness in Prec.Tot. (t=200, wind=11)	21	0.30	0.36	0.44	0.66	-0.42	0.33	0.36	0.40	0.59	-0.43	0.40	0.38	0.35	0.53	-0.40	0.54	0.49	0.47	0.54	-0.50
Climate distinctiveness in Prec.Tot. (t=200, wind=15)	22	0.29	0.35	0.42	0.64	-0.42	0.32	0.35	0.39	0.58	-0.44	0.41	0.38	0.34	0.51	-0.37	0.49	0.48	0.45	0.48	-0.47
Climate distinctiveness in Prec.Tot. (t=500, wind=5)	23	0.29	0.34	0.39	0.49	-0.28	0.31	0.34	0.39	0.52	-0.35	0.39	0.40	0.41	0.53	-0.47	0.54	0.55	0.50	0.60	-0.55

Climate distinctiveness in Prec.Tot. (t=500, wind=11)	24	0.30	0.34	0.44	0.63	-0.44	0.32	0.37	0.43	0.60	-0.50	0.37	0.38	0.37	0.52	-0.43	0.44	0.41	0.39	0.47	-0.47
Climate distinctiveness in Prec.Tot. (t=500, wind=15)	25	0.28	0.34	0.43	0.64	-0.48	0.32	0.36	0.42	0.59	-0.50	0.36	0.35	0.32	0.48	-0.35	0.42	0.41	0.40	0.40	-0.45
Climate distinctiveness in Prec.Seas. (t=1, wind=5)	26	0.14	0.21	0.28	0.25	-0.23	0.15	0.20	0.25	0.25	-0.25	0.16	0.19	0.23	0.25	-0.29	0.31	0.19	0.20	0.35	-0.18
Climate distinctiveness in Prec.Seas. (t=1, wind=11)	27	0.12	0.19	0.26	0.25	-0.26	0.13	0.19	0.26	0.27	-0.30	0.09	0.15	0.15	0.18	-0.19	-0.04	-0.11	-0.11	0.00	0.16
Climate distinctiveness in Prec.Seas. (t=1, wind=15)	28	0.10	0.18	0.25	0.26	-0.27	0.14	0.20	0.27	0.28	-0.33	0.07	0.14	0.13	0.14	-0.13	-0.10	-0.14	-0.15	-0.05	0.18
Climate distinctiveness in Prec.Seas. (t=2, wind=5)	29	0.15	0.23	0.30	0.25	-0.23	0.15	0.22	0.28	0.27	-0.27	0.20	0.22	0.23	0.25	-0.32	0.38	0.31	0.31	0.41	-0.27
Climate distinctiveness in Prec.Seas. (t=2, wind=11)	30	0.12	0.20	0.28	0.26	-0.28	0.14	0.19	0.28	0.28	-0.32	0.12	0.20	0.18	0.20	-0.25	0.05	0.01	-0.01	0.08	0.04
Climate distinctiveness in Prec.Seas. (t=2, wind=15)	31	0.11	0.19	0.27	0.27	-0.29	0.13	0.19	0.27	0.28	-0.34	0.10	0.18	0.16	0.16	-0.20	0.02	-0.03	-0.05	0.06	0.04
Climate distinctiveness in Prec.Seas. (t=3, wind=5)	32	0.13	0.21	0.26	0.19	-0.17	0.14	0.23	0.29	0.26	-0.25	0.20	0.25	0.26	0.28	-0.36	0.41	0.43	0.40	0.40	-0.40
Climate distinctiveness in Prec.Seas. (t=3, wind=11)	33	0.12	0.20	0.28	0.26	-0.28	0.12	0.19	0.28	0.27	-0.33	0.10	0.18	0.20	0.19	-0.28	0.12	0.14	0.10	0.16	-0.11
Climate distinctiveness in Prec.Seas. (t=3, wind=15)	34	0.11	0.18	0.27	0.26	-0.30	0.12	0.19	0.28	0.26	-0.35	0.07	0.17	0.17	0.14	-0.20	0.06	0.07	0.05	0.12	-0.05
Climate distinctiveness in	35	0.07	0.08	0.11	0.00	0.00	0.05	0.09	0.12	0.03	-0.01	0.03	0.10	0.12	0.07	-0.17	0.00	0.08	0.05	0.00	-0.08

Prec.Seas. (t=4, wind=5)																					
Climate distinctiveness in Prec.Seas. (t=4, wind=11)	36	0.06	0.11	0.16	0.09	-0.10	0.05	0.11	0.19	0.14	-0.22	0.00	0.10	0.12	0.06	-0.17	-0.17	-0.07	-0.12	-0.10	0.13
Climate distinctiveness in Prec.Seas. (t=4, wind=15)	37	0.05	0.11	0.18	0.14	-0.19	0.06	0.12	0.21	0.16	-0.27	-0.04	0.04	0.03	-0.02	-0.06	-0.17	-0.07	-0.13	-0.12	0.13
Climate distinctiveness in Temp.Seas. (t=1, wind=5)	38	-0.10	-0.12	-0.16	-0.17	0.02	-0.16	-0.18	-0.23	-0.18	0.06	-0.10	-0.13	-0.14	0.00	0.00	0.01	0.01	0.00	0.06	0.02
Climate distinctiveness in Temp.Seas. (t=1, wind=11)	39	-0.11	-0.11	-0.15	-0.21	0.04	-0.14	-0.14	-0.16	-0.15	0.02	-0.12	-0.08	-0.11	-0.07	0.07	-0.06	-0.01	-0.05	0.05	0.13
Climate distinctiveness in Temp.Seas. (t=1, wind=15)	40	-0.10	-0.10	-0.14	-0.21	0.03	-0.13	-0.11	-0.13	-0.14	0.00	-0.15	-0.11	-0.12	-0.11	0.11	0.03	0.10	0.05	0.19	-0.01
Climate distinctiveness in Temp.Seas. (t=2, wind=5)	41	-0.08	-0.07	-0.08	-0.24	0.04	-0.13	-0.13	-0.14	-0.24	0.05	-0.04	-0.07	-0.10	-0.06	-0.02	0.07	0.07	0.00	0.05	0.00
Climate distinctiveness in Temp.Seas. (t=2, wind=11)	42	-0.10	-0.09	-0.10	-0.26	0.04	-0.12	-0.11	-0.11	-0.21	0.01	-0.08	-0.08	-0.12	-0.11	0.03	-0.09	-0.04	-0.12	-0.02	0.15
Climate distinctiveness in Temp.Seas. (t=2, wind=15)	43	-0.10	-0.09	-0.11	-0.27	0.04	-0.11	-0.10	-0.10	-0.20	0.00	-0.12	-0.11	-0.14	-0.15	0.09	-0.06	-0.03	-0.10	-0.01	0.13
Climate distinctiveness in Temp.Seas. (t=3, wind=5)	44	-0.07	-0.05	-0.03	-0.24	0.06	-0.14	-0.11	-0.09	-0.27	0.05	-0.16	-0.15	-0.19	-0.19	0.05	0.02	-0.07	-0.08	-0.09	0.04
Climate distinctiveness in Temp.Seas. (t=3, wind=11)	45	-0.11	-0.09	-0.09	-0.29	0.06	-0.14	-0.11	-0.10	-0.24	0.02	-0.15	-0.14	-0.16	-0.19	0.05	-0.16	-0.17	-0.19	-0.13	0.23
Climate distinctiveness in Temp.Seas. (t=3, wind=15)	46	-0.11	-0.09	-0.11	-0.29	0.06	-0.12	-0.10	-0.09	-0.22	0.01	-0.14	-0.14	-0.17	-0.21	0.10	-0.29	-0.36	-0.36	-0.33	0.39

Climate distinctiveness in Temp.Seas. (t=4, wind=5)	47	-0.06	-0.03	0.00	-0.21	0.10	-0.15	-0.12	-0.10	-0.29	0.09	-0.18	-0.18	-0.21	-0.23	0.08	-0.03	-0.12	-0.15	-0.08	0.03
Climate distinctiveness in Temp.Seas. (t=4, wind=11)	48	-0.12	-0.10	-0.10	-0.32	0.08	-0.16	-0.13	-0.12	-0.28	0.05	-0.16	-0.15	-0.17	-0.20	0.07	-0.21	-0.27	-0.31	-0.24	0.25
Climate distinctiveness in Temp.Seas. (t=4, wind=15)	49	-0.12	-0.10	-0.12	-0.32	0.07	-0.14	-0.13	-0.12	-0.26	0.03	-0.16	-0.15	-0.18	-0.22	0.10	-0.31	-0.40	-0.43	-0.39	0.37
Habitat heterogeneity (Range) in AET	50	0.17	0.20	0.24	0.33	-0.18	0.22	0.26	0.33	0.41	-0.34	0.34	0.40	0.49	0.45	-0.52	0.50	0.59	0.60	0.55	-0.62
Habitat heterogeneity (Range) in PET	51	0.31	0.40	0.49	0.52	-0.45	0.40	0.49	0.55	0.57	-0.50	0.53	0.58	0.64	0.60	-0.56	0.72	0.68	0.71	0.69	-0.66
Habitat heterogeneity (Range) in MAT	52	0.26	0.31	0.35	0.30	-0.21	0.31	0.36	0.37	0.33	-0.22	0.34	0.34	0.39	0.30	-0.21	0.29	0.21	0.27	0.19	-0.15
Habitat heterogeneity (Range) in Altitude	53	0.27	0.32	0.37	0.34	-0.25	0.33	0.38	0.42	0.39	-0.29	0.42	0.44	0.50	0.44	-0.34	0.51	0.47	0.54	0.51	-0.43
Habitat heterogeneity (Sd) in AET	54	0.18	0.21	0.23	0.32	-0.17	0.24	0.28	0.30	0.39	-0.29	0.38	0.40	0.44	0.48	-0.45	0.54	0.55	0.58	0.59	-0.58
Habitat heterogeneity (Sd) in PET	55	0.30	0.39	0.48	0.49	-0.43	0.38	0.47	0.53	0.52	-0.47	0.46	0.51	0.57	0.48	-0.50	0.52	0.44	0.47	0.36	-0.44
Habitat heterogeneity (Sd) in MAT	56	0.25	0.30	0.33	0.27	-0.19	0.29	0.32	0.34	0.27	-0.19	0.23	0.21	0.27	0.15	-0.12	0.08	-0.07	-0.02	-0.09	0.07
Habitat heterogeneity (Sd) in Altitude	57	0.26	0.32	0.37	0.32	-0.24	0.32	0.37	0.41	0.37	-0.28	0.40	0.42	0.49	0.43	-0.34	0.53	0.44	0.50	0.48	-0.42
Seasonality in MAT	58	-0.27	-0.31	-0.42	-0.65	0.45	-0.33	-0.37	-0.44	-0.64	0.46	-0.44	-0.47	-0.48	-0.61	0.48	-0.57	-0.64	-0.63	-0.64	0.62
Seasonality in Prec. Tot.	59	0.03	0.05	0.08	0.11	-0.16	0.03	0.08	0.11	0.14	-0.16	0.09	0.14	0.11	0.20	-0.17	0.16	0.28	0.22	0.32	-0.24
Climate relict in MAT (wind=5)	60	0.09	0.09	0.07	0.04	0.00	0.13	0.13	0.09	0.05	0.01	0.04	0.00	-0.05	-0.09	0.12	-0.29	-0.31	-0.33	-0.31	0.34
Climate relict in MAT (wind=11)	61	0.12	0.12	0.08	0.03	0.02	0.13	0.10	0.02	-0.03	0.08	-0.02	-0.07	-0.11	-0.19	0.20	-0.30	-0.32	-0.33	-0.35	0.39
Climate relict in MAT (wind=15)	62	0.12	0.12	0.06	0.00	0.05	0.10	0.07	-0.02	-0.09	0.13	-0.04	-0.08	-0.12	-0.20	0.20	-0.30	-0.31	-0.32	-0.34	0.38
Productivity in PET	63	0.07	0.09	0.19	0.33	-0.32	0.10	0.14	0.23	0.33	-0.33	0.18	0.24	0.28	0.34	-0.36	0.42	0.53	0.50	0.52	-0.54

Productivity in AET	64	0.22	0.23	0.26	0.58	-0.29	0.27	0.26	0.25	0.55	-0.29	0.39	0.30	0.27	0.52	-0.32	0.46	0.39	0.38	0.49	-0.45
Area	65	-0.10	-0.11	-0.15	-0.20	0.17	-0.12	-0.11	-0.16	-0.17	0.19	-0.15	-0.12	-0.18	-0.10	0.23	-0.24	-0.16	-0.22	-0.06	0.28
Glaciated areas	66	-0.07	-0.13	-0.22	-0.35	0.33	-0.10	-0.17	-0.25	-0.36	0.34	-0.22	-0.27	-0.29	-0.38	0.36	-0.32	-0.39	-0.36	-0.43	0.43
MAT	67	0.10	0.13	0.23	0.40	-0.32	0.13	0.18	0.26	0.39	-0.33	0.23	0.28	0.30	0.39	-0.35	0.46	0.55	0.52	0.54	-0.54
MAT-Past	68	0.12	0.16	0.28	0.45	-0.35	0.17	0.22	0.31	0.45	-0.36	0.27	0.32	0.36	0.45	-0.39	0.48	0.58	0.57	0.58	-0.56
Precipitation total	69	0.22	0.21	0.20	0.50	-0.17	0.27	0.23	0.19	0.46	-0.18	0.36	0.26	0.20	0.44	-0.20	0.42	0.32	0.31	0.41	-0.34
Altitude	70	0.13	0.16	0.19	0.22	-0.28	0.16	0.20	0.24	0.26	-0.29	0.24	0.25	0.30	0.31	-0.31	0.39	0.32	0.35	0.44	-0.39
Richness	71	0.29	0.32	0.37	0.74	-0.34	0.37	0.39	0.40	0.74	-0.38	0.55	0.50	0.49	0.75	-0.48	0.68	0.63	0.66	0.76	-0.68

Table S2.4. Poisson, Hurdle and Zero-Inflated Poisson (ZIP) models form amphibians and mammals’ endemism.

	Amphibians Models			Mammals Models Estimate (Standard error)		
	Poisson	Hurdle-Poisson	ZIP	Poisson	Hurdle-Poisson	ZIP
Climate stability						
Df	2	4	4	2	4	4
AIC	8511	6018	6135	11691	10016	10014
Zeros obs. ₤	9558	9882	9863	9558	9224	9214
Climate seasonality						
Df				2	4	4
AIC	8503	5993	5971	12236	10273	10246
Zeros obs. ₤	9283	9882	9883	8549	9224	9227
Climate distinctiveness						
Df	2	4	4	2	4	4
AIC	8428	6012	6016	11724	10042	10054
Zeros obs. ₤	9282	9882	9882	8576	9224	9222
Climate heterogeneity						
Df	2	4	4	2	4	4
AIC	8801	6177	6162	11996	10128	10110
Zeros obs. ₤	9348	9882	9883	8641	9224	9227

Log *L* = maximized log-likelihood

AIC = Akaike Information Criterion

₤ Total Zero obs. for amphibians = 9882; Non-zeros obs.=564; Total obs. 10446
Total Zero obs. for mammals = 9224; Non-zeros obs.= 1222; Total obs. 10446

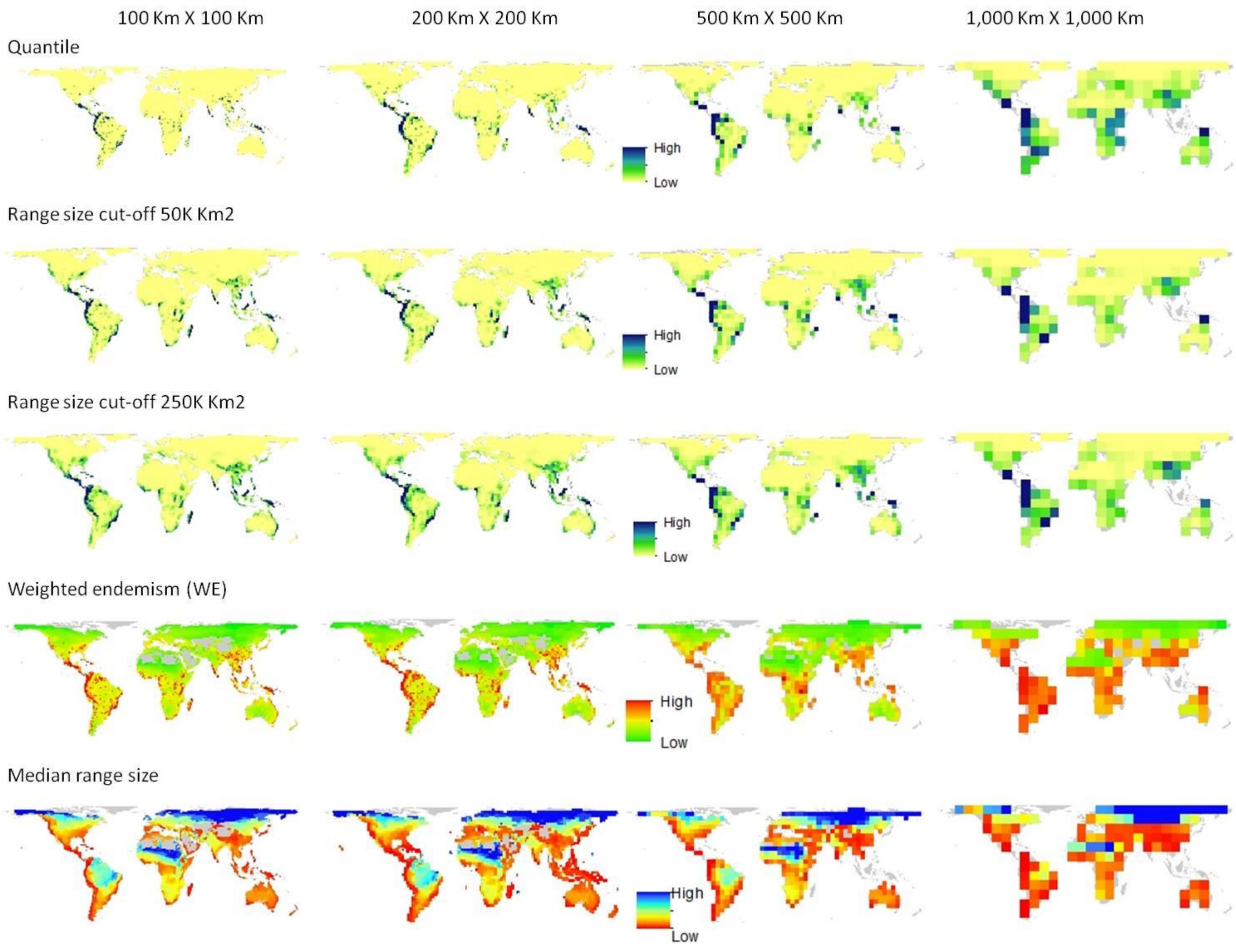


Figure S2.1. Broad scale patterns of amphibian endemism using five metrics and four spatial resolutions. Metrics were constructed using range size cut-offs (first quartile, 50K km^2 and 250K km^2), inverse range size (Weighted Endemism, WE) and median range size.

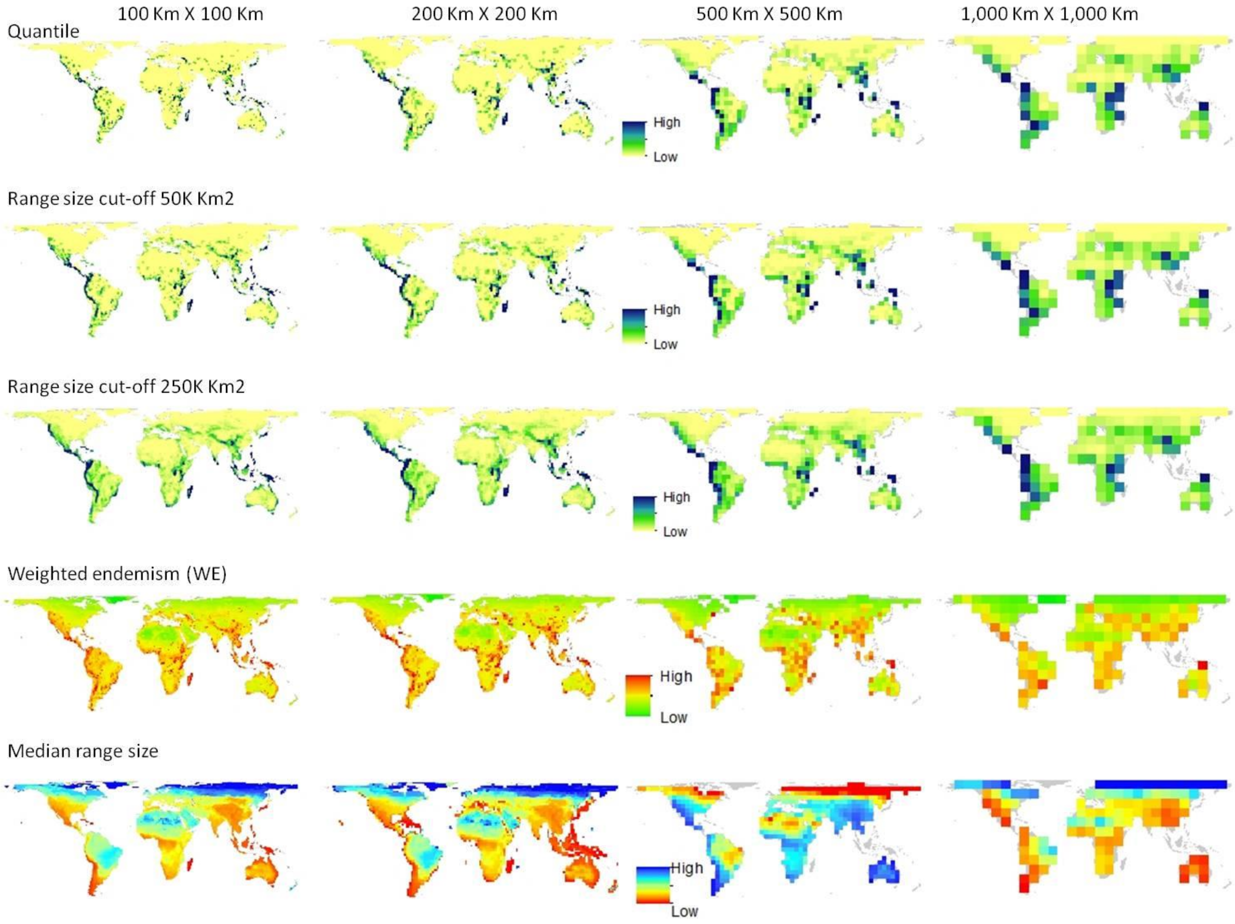
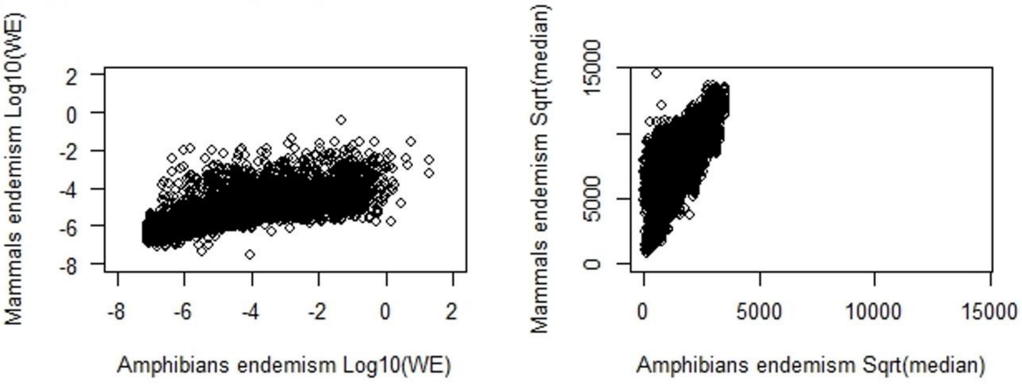


Figure S2.2. Broad scale patterns of mammal endemism using five metrics and four spatial resolutions. Metrics were constructed using range size cut-offs (first quartile, 50K km^2 and 250K km^2) and inverse range size (Weighted Endemism, WE), and median range size.

a) Inverse range size (Weighted endemism, WE)



c) Quartile (Range size threshold = Smallest quartile)

Range size threshold (<50,000 Km^2)

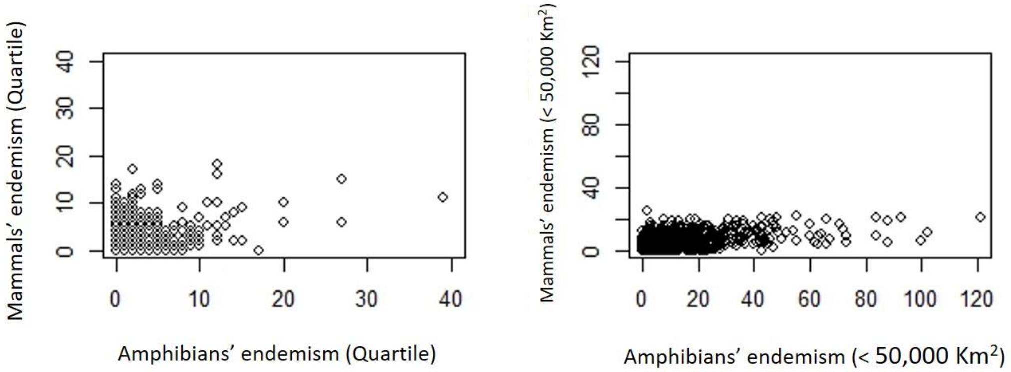


Figure S2.3. Spatial congruence between mammals and amphibians using various metrics of endemism a) Inverse range size, b) Median range size, c) Range size threshold (smallest quartile), and d) Range size threshold (<50,000 Km2).

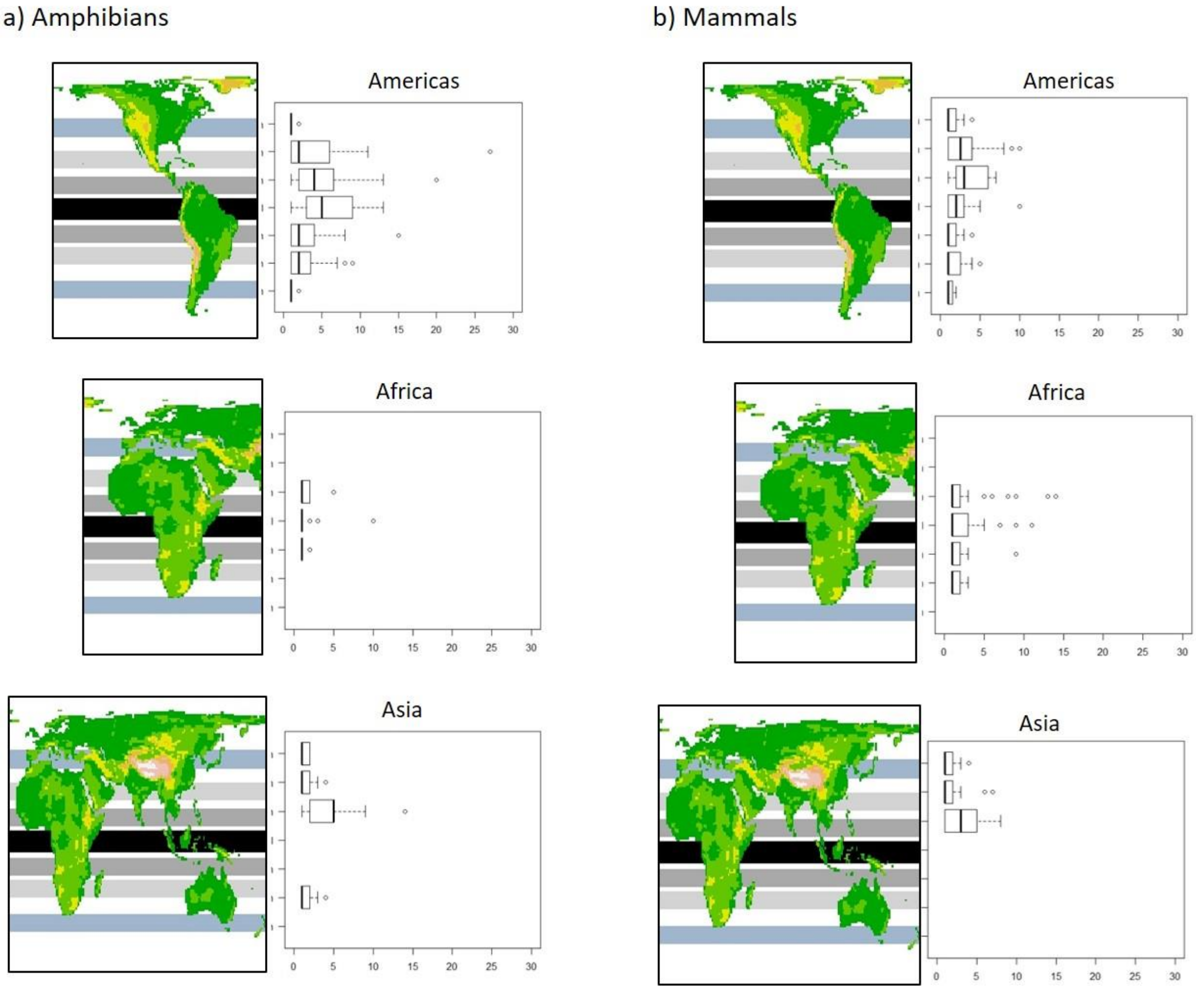


Figure S2.4a. Number of endemic species (boxplots) in mountain systems (300 to 2,500 meters above the sea level) along a latitudinal gradient (greyscale bands represent approximately 10 degrees) for a) amphibians and b) mammals.

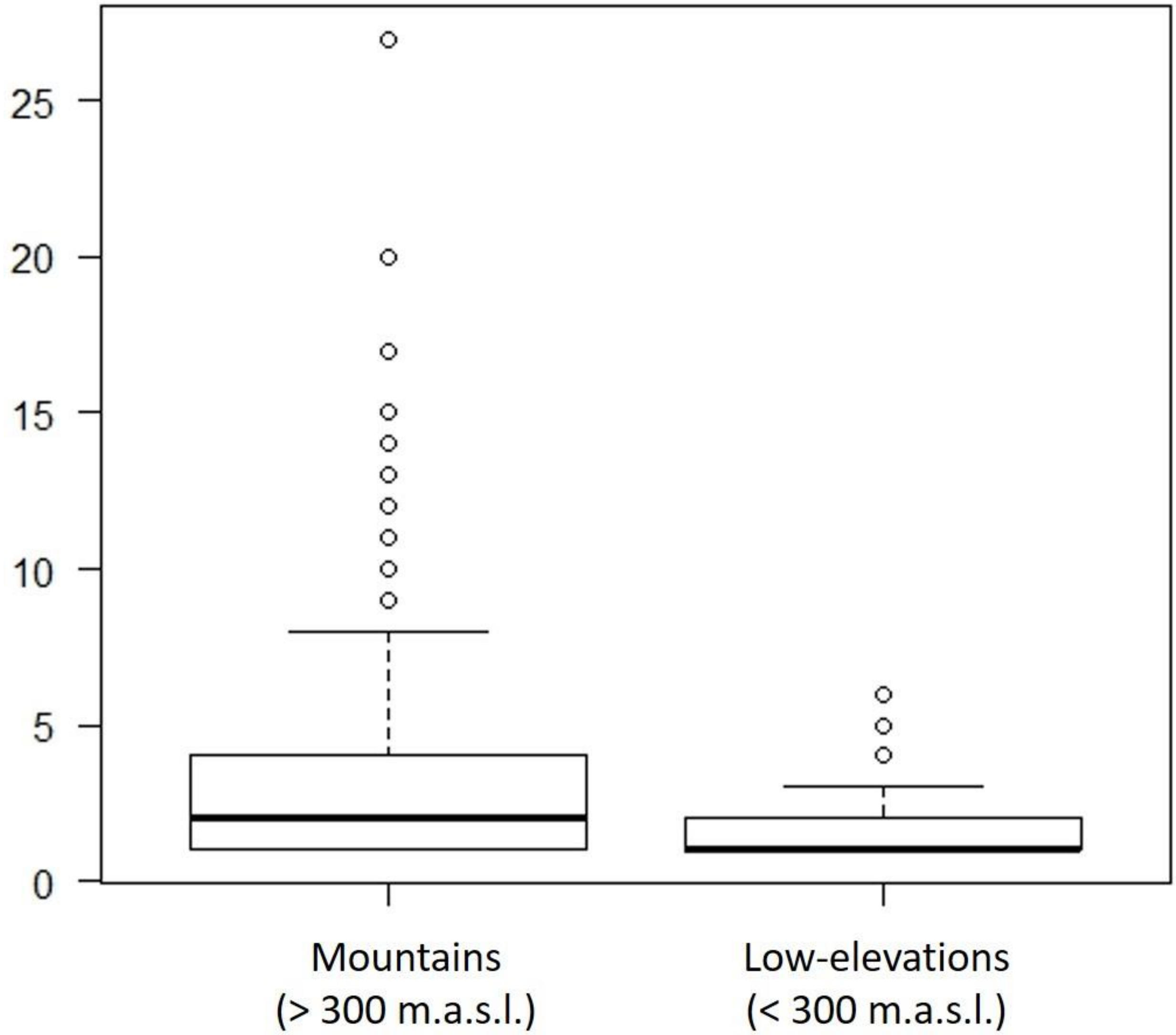
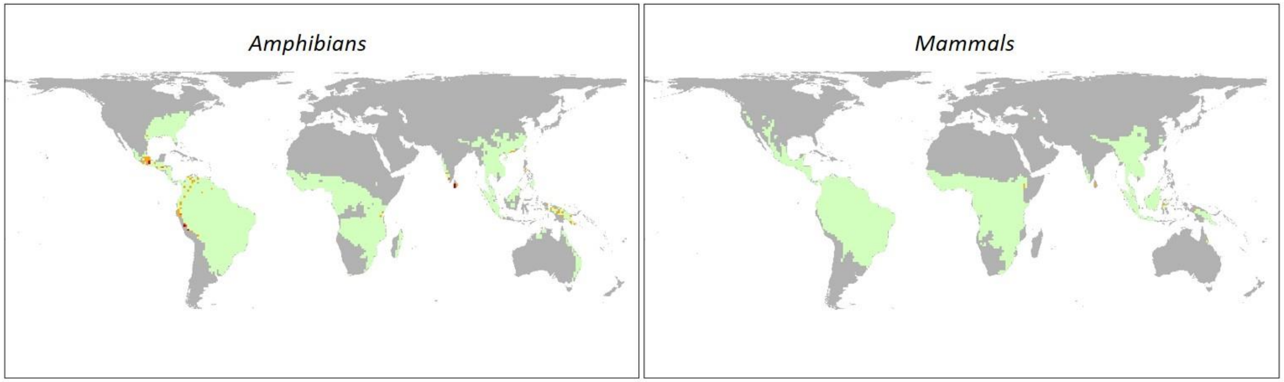


Figure S4b. Number of range-restricted species in mountains (>300 meters above sea level, m.a.s.l) and low elevations (< 300m).

a) Range size cut-off (Quartile)



b) Range size cut-off (50,000 Km^2)

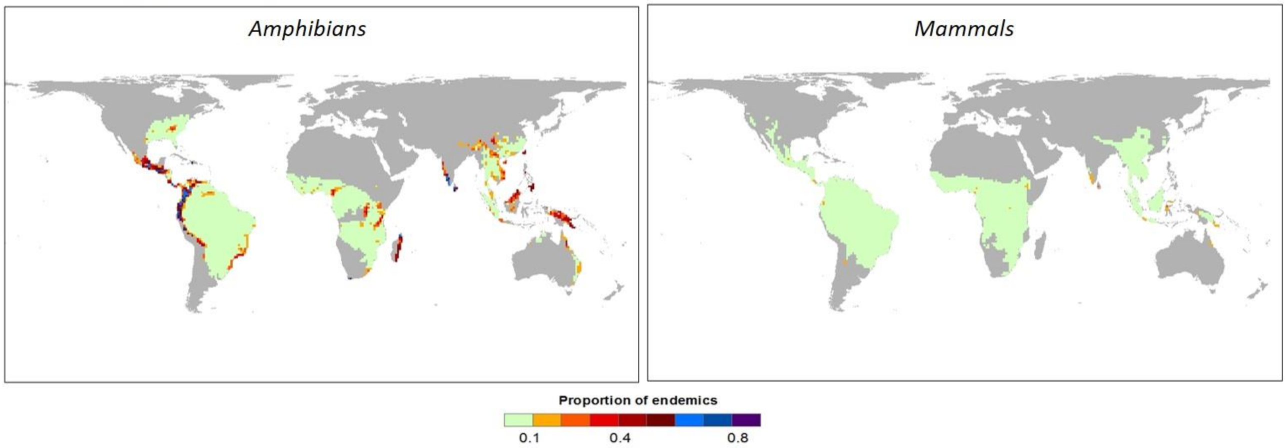


Figure S2.5. Proportion of species with small range size within areas of high species richness (highest quantile) for amphibians (left graphs) and mammals (right graphs), using the highest quartile of two metrics of species endemism a) range size cut-off = Quantile and b) range size cut-off = 50,000 Km2.

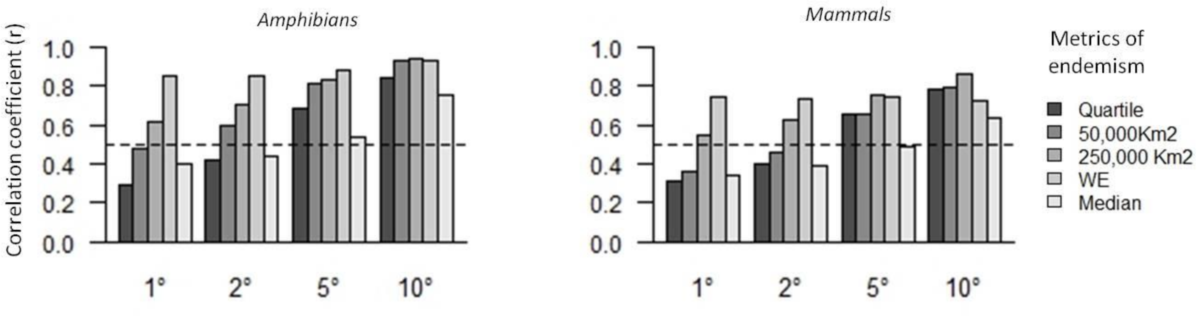
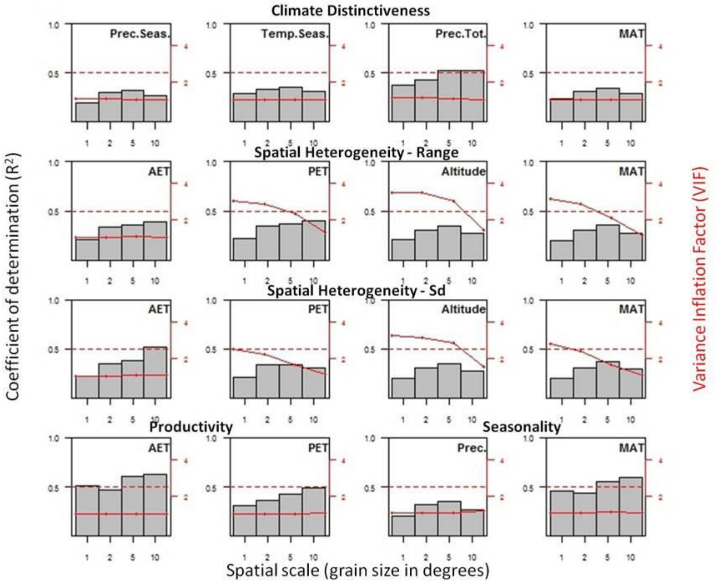


Figure S2.6. Spearman's rank correlation coefficient (*r*, dotted line indicates *r* = 0.5) among metrics of species endemism and total species richness. Metrics were constructed using range size cut-offs (first quartile, ranges smaller than $5x10^4$ km^2, and ranges smaller than $2.5x10^5$ km^2), inverse range size (Weighted Endemism, WE) and median range size.

a) Weighted endemism (WE)



b) Median range size

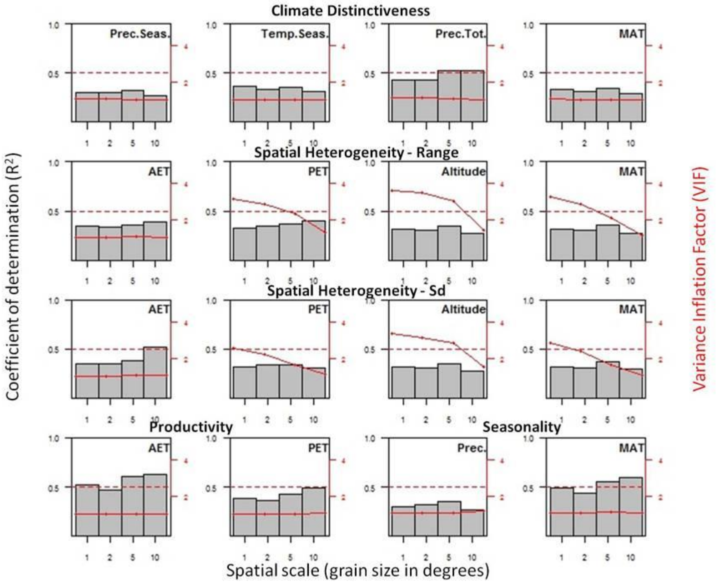
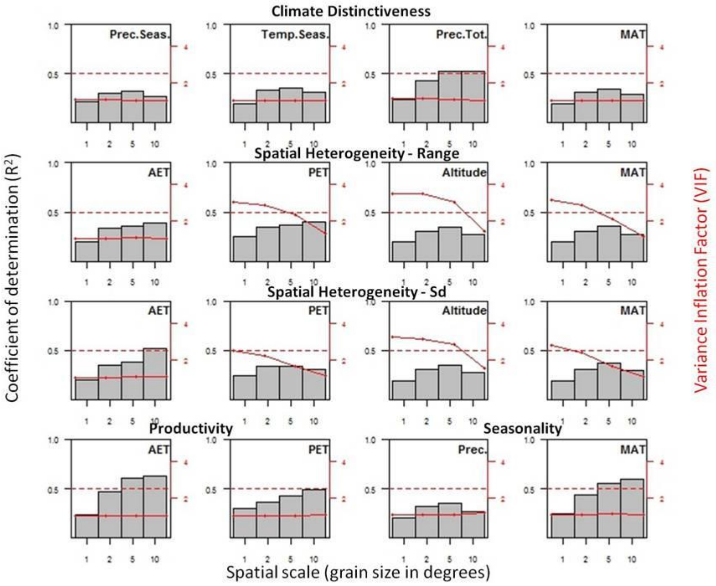


Figure S2.7. Coefficient of determination (grey bars, R^2) and collinearity (red lines, Variance Inflation Factor, VIF) between amphibians' endemism as a function of climate velocity (CV) plus each other predictor, using two metrics of endemism a) Weighted endemism (WE), and b) Median range size. Red dashed line represents VIF = 2.5 (above this line is high concern regarding collinearity between variables). MAT = Mean annual temperature, AET = Actual evapotranspiration, PET = Potential evapotranspiration, Prec. = Total precipitation.

a) Weighted endemism (WE)



b) Median range size

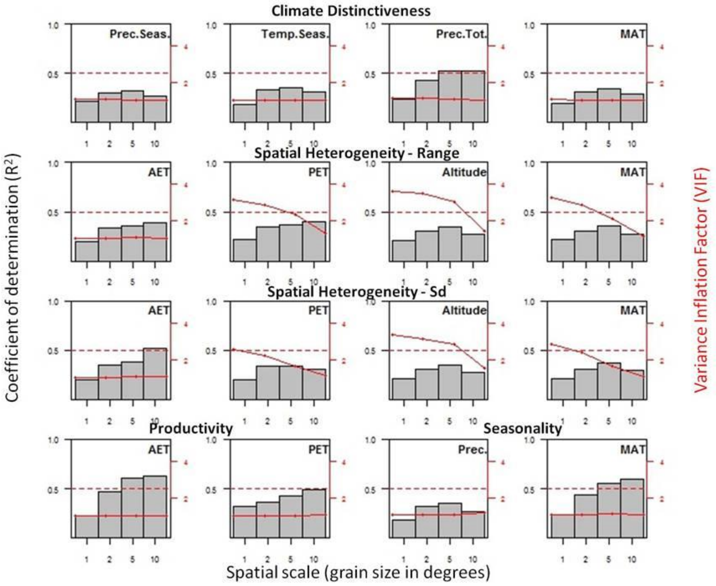
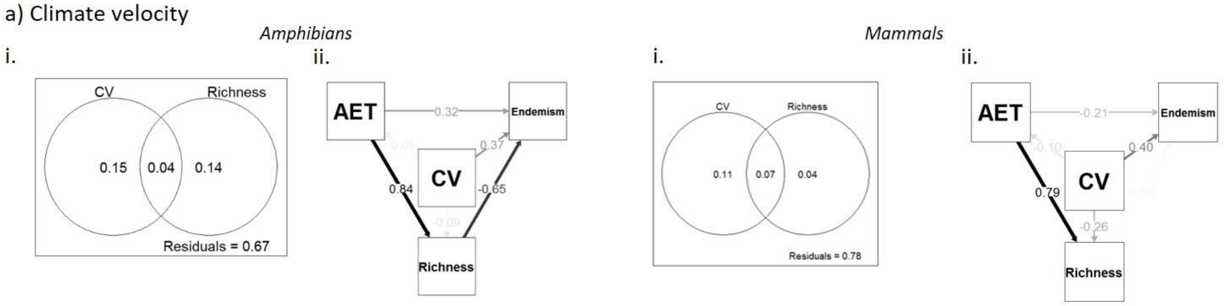


Figure S2.8. Coefficient of determination (grey bars, R^2) and collinearity (red lines, Variance Inflation Factor, VIF) between *mammals*' endemism as a function of climate velocity (CV) plus each other predictor, using two metrics of endemism a) Weighted endemism (WE), and b) Median range size. Red dashed line represents VIF = 2.5 (above this line is high concern regarding collinearity between variables). MAT = Mean annual temperature, AET = Actual evapotranspiration, PET = Potential evapotranspiration, Prec. = Total precipitation.

a) Climate velocity



b) Spatial heterogeneity

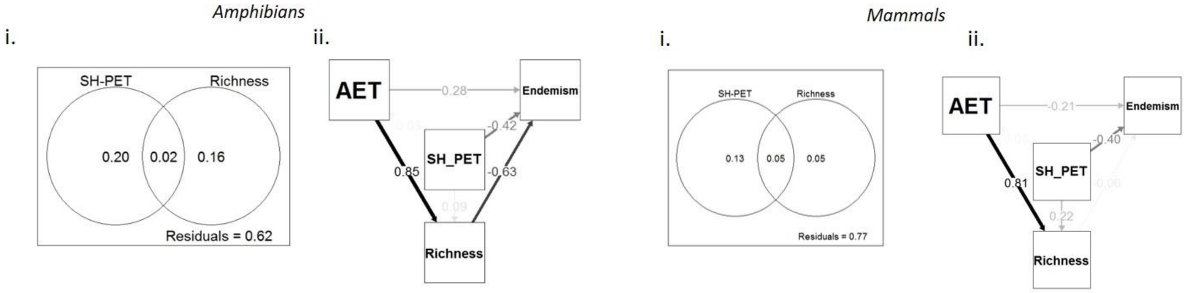


Figure S2.9. Models predicting endemism (using Median range size) for a) Climate velocity and b) Spatial heterogeneity. (i) Variance partitioning (variance contribution of each predictor and shared variance) and (ii) path analysis (the darker the line the stronger the effect on that relationship);. AET = Actual evapotranspiration; CV = Climate velocity; SH-PET = Spatial heterogeneity in potential evapotranspiration; PET = potential evapotranspiration; Richness = Total species richness.

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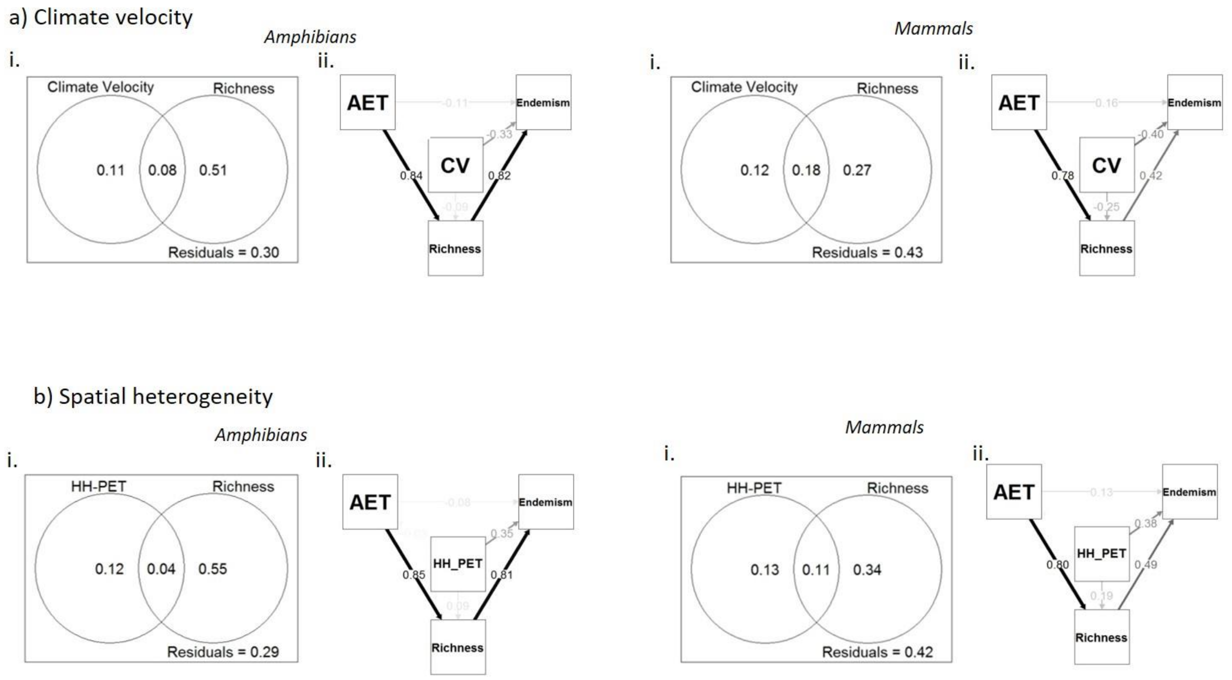
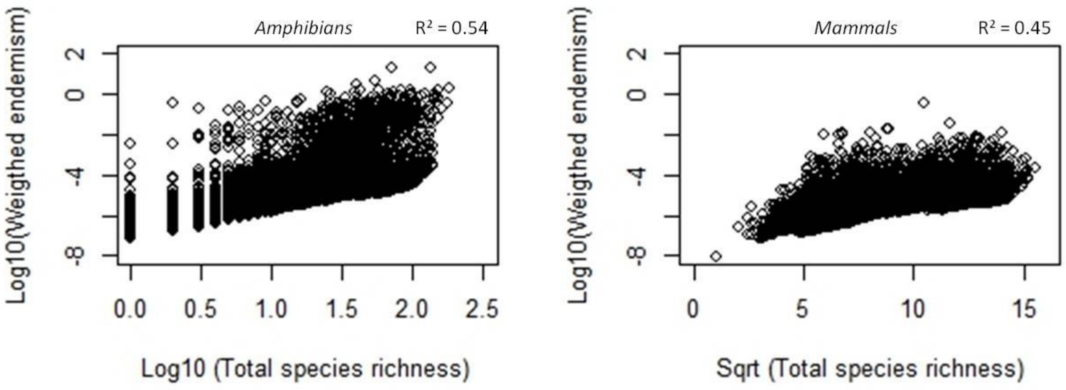


Figure S2.10. Models predicting endemism (using Weighted Endemism, WE) for a) Climate velocity and b) Spatial heterogeneity. (i) Variance partitioning (variance contribution of each predictor and shared variance) and (ii) path analysis (the darker the line the stronger the effect on that relationship);. AET = Actual evapotranspiration; CV = Climate velocity; SH-PET = Spatial heterogeneity in potential evapotranspiration; PET = potential evapotranspiration; Richness = Total species richness.

a) Total species richness ~ Weighted endemism



b) Total species richness ~ Median range size

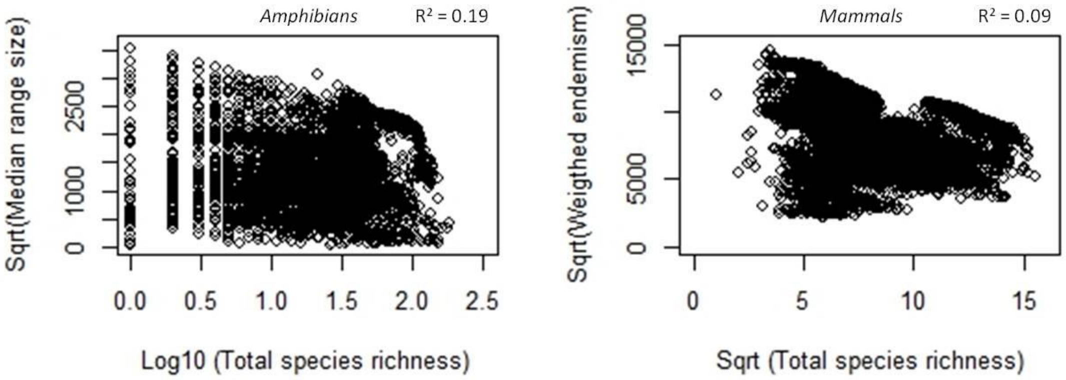


Figure S2.11. Total species richness as a function of endemism a) Weighted endemism (WE) and b) Median range size for amphibians and mammals. Variance explained is shown (R^2).

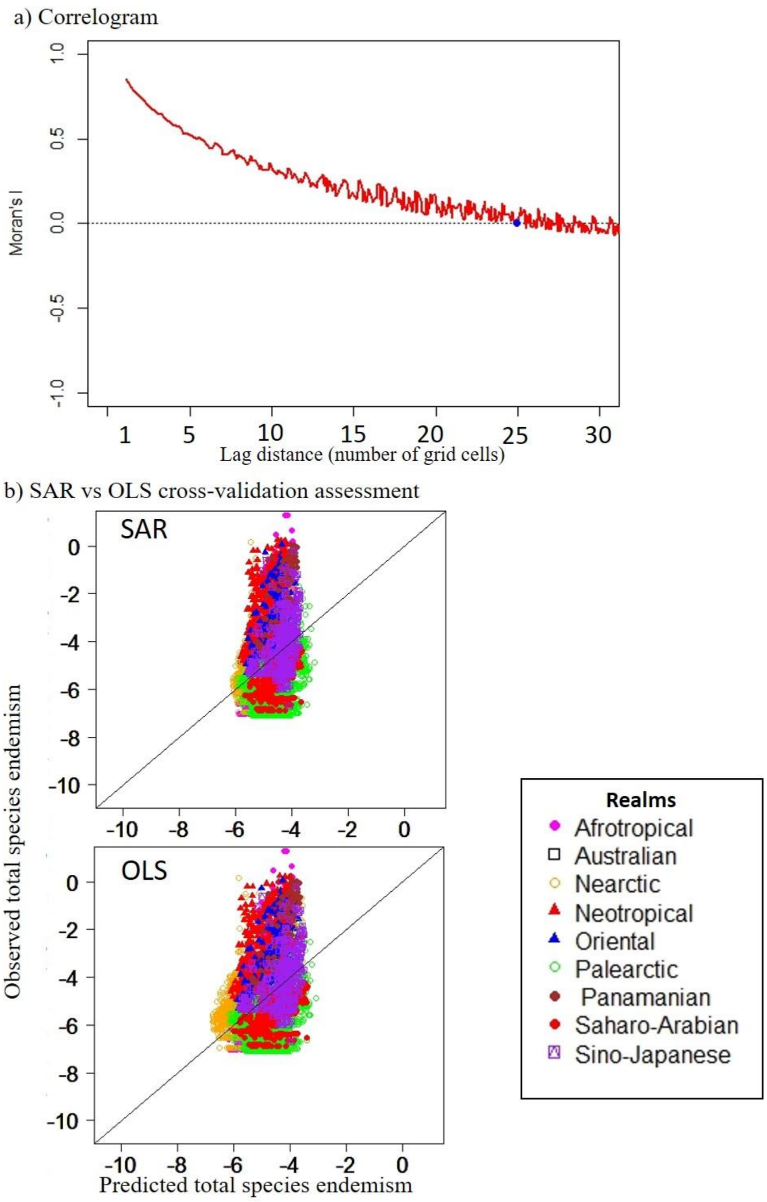


Figure S2.12. Cross-continental validation from best Ordinary least squares (OLS) and spatial autoregressive (SAR) models predicting broad scale patterns of endemism for amphibians and mammals, using two metrics of endemism a) Median range size and b) Weighted endemism. SH-PET = Spatial heterogeneity in potential evapotranspiration; PET = potential evapotranspiration; CD-PT = Climate distinctiveness in Total precipitation; and, Richness = Total species richness.

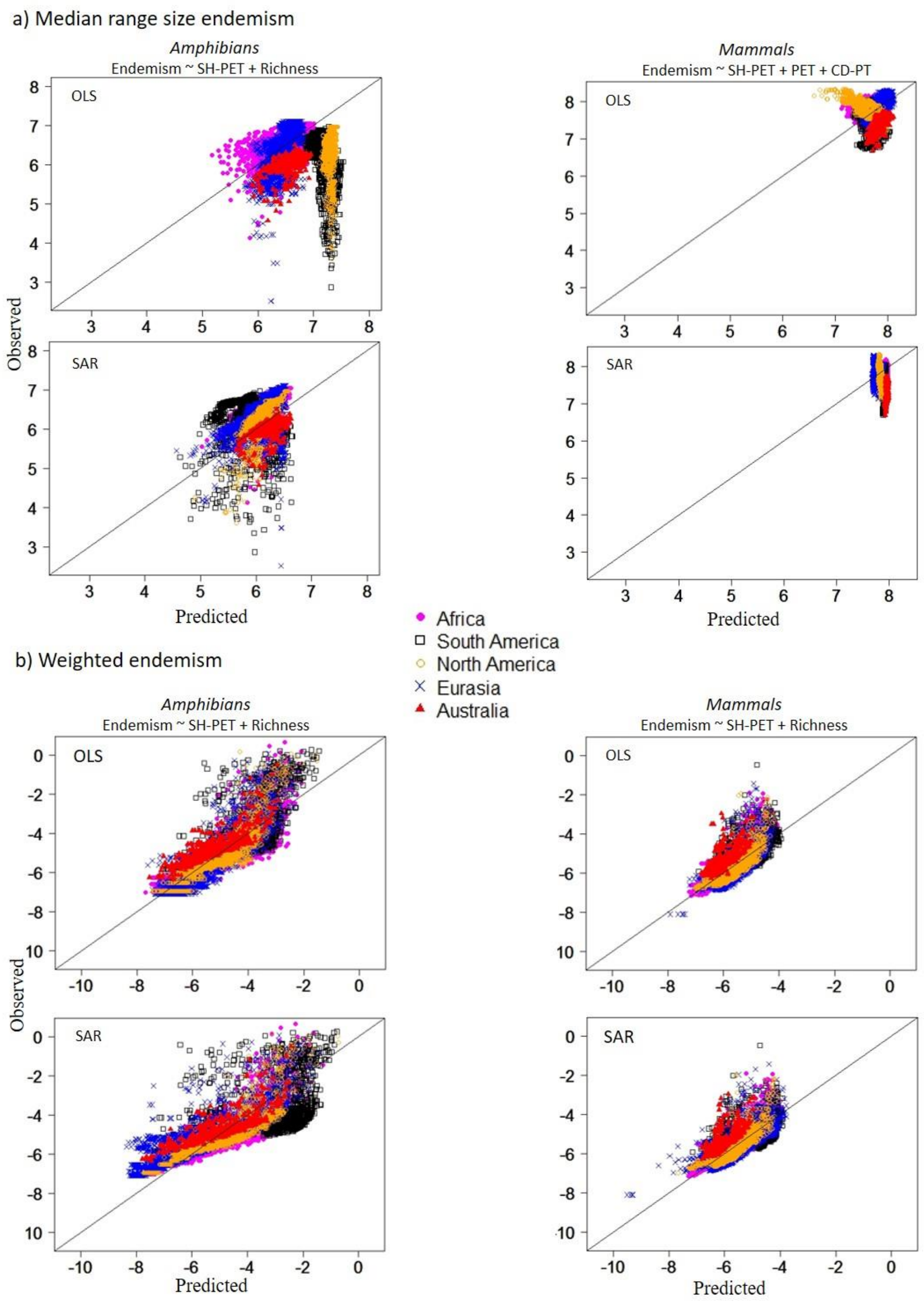


Figure S2.13. Cross-continental validation from best Ordinary least squares (OLS) and spatial autoregressive (SAR) models predicting broad scale patterns of endemism for amphibians and mammals, using two metrics of endemism a) Median range size and b) Weighted endemism. SH_PET = Spatial heterogeneity in potential evapotranspiration; PET = potential evapotranspiration; CD_PT = Climate distinctiveness in Total precipitation; and, Richness = Total species richness. Here we used some continental masses instead of realms to demonstrate that models failed to predict endemism in various geographic settings.

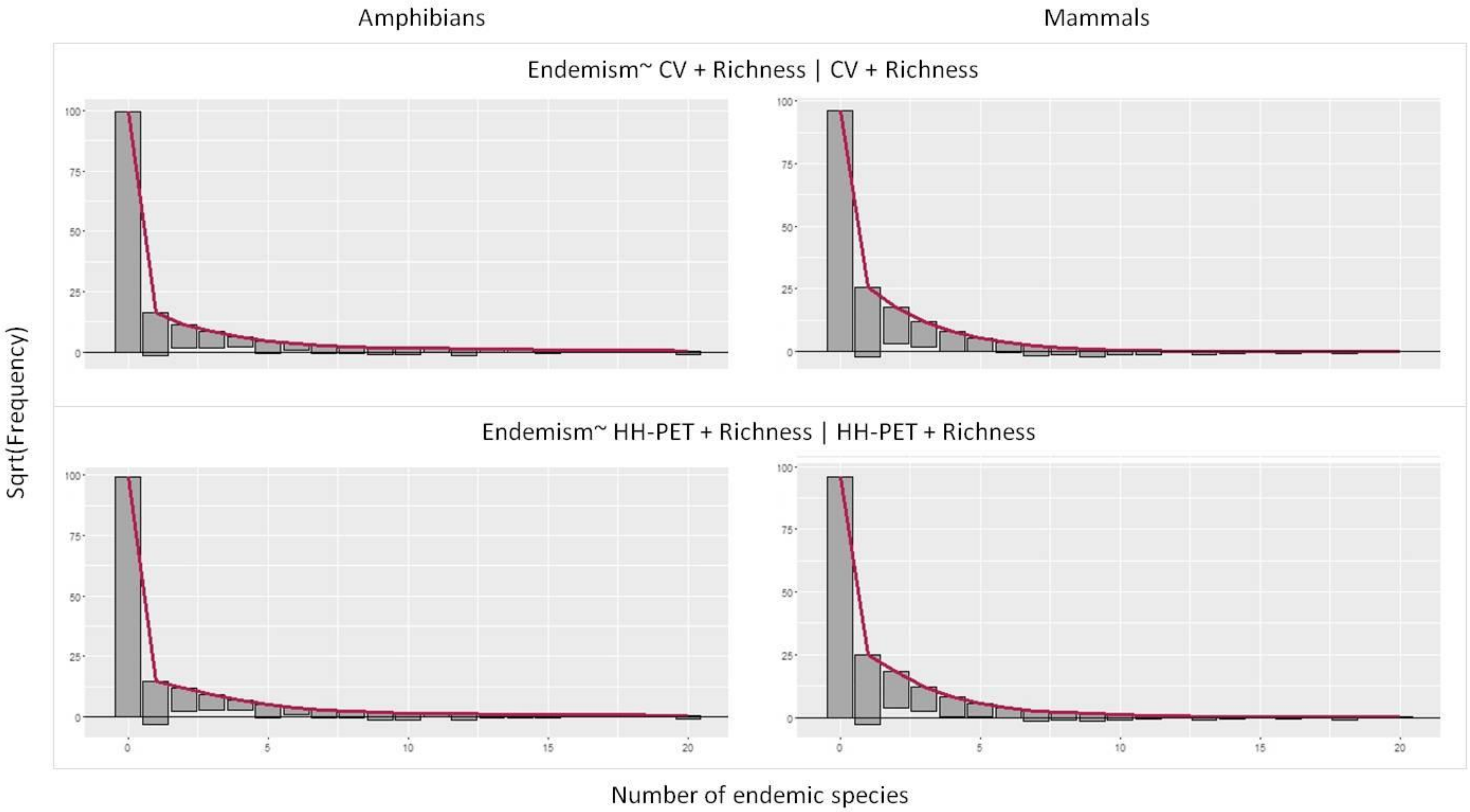


Figure S2.14. Hanging rotograms from hurdle models (amphibians and mammals) for past climate (top graphs) and current climate (bottom graphs).

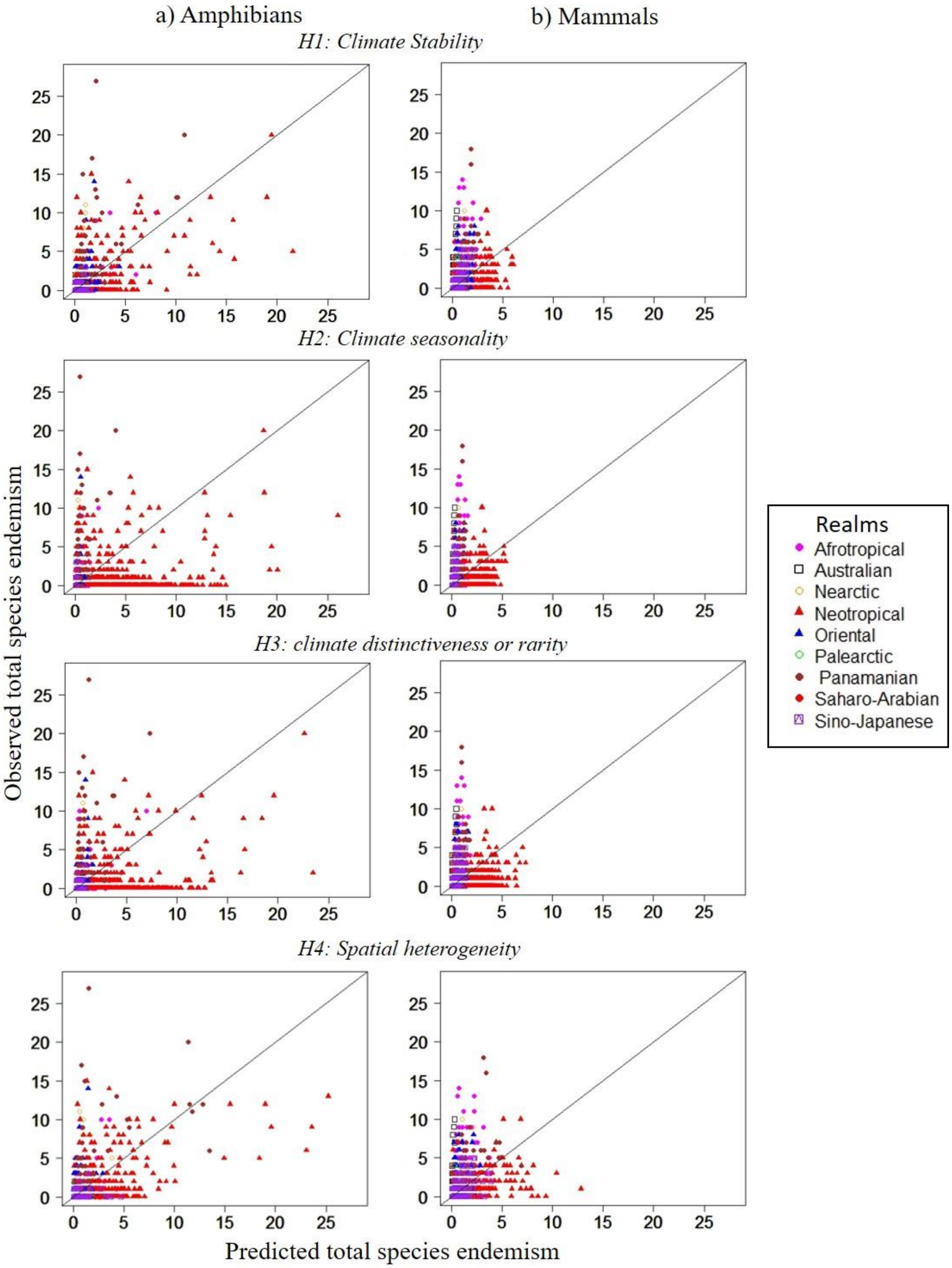


Figure S2.15. Predicted vs. observed endemic species (amphibians and mammals) from hurdle models for a) climate velocity; and b) Spatial heterogeneity in potential evapotranspiration.