

Predicting broad-scale patterns in species distributions

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ABSTRACT

Species richness of virtually all high-level taxonomic groups is strongly statistically related to climatic variables such as temperature and precipitation, and consistently so across space and time. These observations are consistent with a causal link between the number of species that occur in a given region and its climate. Although dozens of hypotheses have been proposed, the main mechanisms underlying this pattern remain largely unresolved. And, few ecological studies have attempted to identify regularities in the individual species distributions that make up the richness–climate relationship. Despite the complexities of species’ biologies, I found that, to a first approximation, species’ probability of occupancy at continental scales were generally well statistically explained by a Gaussian function of temperature and precipitation. This simple model appeared general among species, taxa and regions. However, although individual species’ ranges are strongly statistically related to climate, spatial variations in richness cannot be explained by systematic variations in species’ climatic niches. And, individual species track changes in climatic variables through time much more weakly than species richness tracks these changes, suggesting that richness is at least partly constrained by mechanisms independent of species identities. Moreover, at macro-scales, species richness was also not strongly predictable from the temperature at which clades have originated, from historical variability in climatic variables nor from local short-term extirpation rates. In sum, I rejected several prominent hypotheses aiming to explain richness–climate relationship and found several lines of evidence inconsistent with the common idea that climatic constraints on individual species, by themselves, can explain richness–climate relationship. I propose a mechanism to explain, as a first approximation, the continental biogeography of species distributions that relies on neutral

processes of dispersal and local extinctions within species' broad deterministic thermal tolerances.

RÉSUMÉ

La richesse en espèces est fortement corrélée au climat, en particulier à des variables telles que la température et le niveau de précipitation, et ce, pour presque tous les grands groupes taxonomiques. Cette observation est conséquente avec l'hypothèse d'un lien de cause à effet entre le nombre d'espèces présentes dans une région et le climat de cette région. Par contre, bien que des douzaines d'hypothèses proposant un mécanisme qui pourrait expliquer la relation statistique entre richesse en espèces et climat fussent proposées, la cause de ce lien demeure un problème non-résolu. De plus, très peu d'études ont tenté d'identifier des régularités statistiques dans les distributions géographiques des espèces individuelles qui, une fois additionnées, forment les gradients de richesse en espèces. Ici, j'ai pu établir que, malgré la grande complexité et le caractère unique de chaque espèce, la distribution géographique d'une espèce à l'échelle continentale peut être très bien statistiquement décrite par une fonction normale de la température et du niveau de précipitation régional et ce, pour la grande majorité des espèces de différents groupes taxonomiques et sur différents continents. Malgré que la distribution géographique des espèces soit fortement liée au climat, j'ai constaté que les propriétés de la niche climatique des espèces ne varient pas de manière aussi prévisibles que la richesse en espèce et ne peuvent donc pas, à elles seules, expliquer les gradients de richesse en espèces. De plus, la richesse en espèces varie dans le temps tel que prédit par les changements climatiques et ce, beaucoup plus précisément que c'est le cas pour les espèces individuelles lorsque celles-ci migrent. Aux larges échelles géographiques dont il est ici question, j'ai aussi trouvé que la richesse en espèces n'est pas fortement prévisible à partir de la température d'origine du clade, de la variabilité historique du climat ni du taux d'extirpation local des espèces. En somme, j'ai pu rejeter de nombreuses hypothèses importantes visant à expliquer le lien entre richesse en

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NOTE

The chapters of this thesis have been submitted to scientific journals for their independent publication. Therefore, there is some degree of repetition amongst chapters and the formatting of each chapter slightly differs.

INTRODUCTION

My thesis is motivated by a simple question: why do species occur where they do? No species occurs everywhere on Earth, and most occur in very restricted areas. And, the number of species that occurs in a given area, i.e. species richness, varies by orders of magnitude over the surface of the globe. But, although there is lots of variance in species distributions that could potentially be explained, there is no agreed-upon general mechanism that has been shown to explain and predict the main patterns in species distributions. Through the test — and rejection — of hypotheses, my thesis attempts to identify the main mechanism(s) determining general ecological patterns and/or to exclude ones that appear unlikely to do so.

Throughout my thesis, I rely on the following guiding principles. First, I assume that most of the variance in ecological systems, just like physical systems, is tractable; i.e., that there are general laws that can be uncovered. Second, that hypotheses should be evaluated by testing their predictions and assumptions, and that predictive power is the operational way to evaluate our understanding of the natural world. Finally, I take a macroecological approach and study ecological patterns at large-scales in order to be able to make inferences at that scale and to encompass most of the variance in ecological patterns. I therefore ignore the details that are often the focus of ecological case studies in the hope to gain generality and predictive power.

Global variations in species richness arguably represent the most striking ecological pattern, and the first to be recognized. When 18th century European naturalists travelled to the New World, they were fascinated by the diversity of species found in the tropics and were the first to describe the general increase in species diversity towards the equator. Soon, species richness was hypothesized to be linked to variations in climate. Notably, in an 1807 essay, von Humboldt described the increase in the diversity of life towards the tropics and linked it to

climate and, in particular, to the availability of liquid water (Hawkins, 2001). However, the strong relationship between species richness and climatic variables was described statistically only in the 1980s (Currie & Paquin, 1987). At large spatial extents (continental) and regional grain sizes (thousands of km²), species richness correlates particularly strongly with temperature and precipitation (or variables highly collinear with these) for virtually all high-level taxonomic groups (i.e. class or higher) (Currie, 1991; Hawkins *et al.*, 2003; Field *et al.*, 2009). The statistical richness–climate relationship has also been shown to be highly congruent through space and time (Francis & Currie, 2003; H-Acevedo & Currie, 2003; Field *et al.*, 2005; Vázquez-Rivera & Currie, 2015). These observations are consistent with a causal link, either direct or indirect, between the number of species that occur in a given area and the climate in that area. Dozens of hypotheses have been proposed to account for this relationship, and the list keeps on growing (Hawkins *et al.*, 2003). My thesis aims to test several of these hypotheses, with the ultimate goal of elucidating the main mechanism(s) that links species richness to climate while closing as many doors as possible along the way.

Individual species' geographic ranges have also long been thought to be at least partially limited by climate. Hence, the first question I address is: Are species geographic distributions related to climate in a predictable way, just like species richness is (Chapter 1 and 2)? Then, my goal is to test whether species richness is predictably related to climate because individual species are related to climate in a systematic and predictable way. I derive specific predictions regarding how variations in species' climatic niches or geographic ranges could directly affect species richness. I then test these predictions at continental scales, using the geographic ranges of birds and mammals in the Americas (Chapter 3). To test the hypothesis that richness is predictably related to climate through climatic constraints on individual species ranges more

generally, I use migrating birds in the Americas as a natural experiment. I test whether consistent richness–climate relationships through time are due to individual species’ distributions closely tracking climatic variations (Chapter 4). If individual species’ generally closely track changes in climatic variables through time, it would be consistent with the hypothesis that richness–climate relationships simply emerge from the climatic constraints on individual species ranges. An alternate hypothesis that would account for the strong correlation between spatial variation in richness and climate would be that there are top-down, climatic limits on species richness that are generally more constraining than the climatic limits on species’ ranges.

It is often stated that the only processes that can change the number of species that occur in a given region are speciation, extinction and dispersal (Ricklefs, 1987). For some authors, this is taken to mean that the only factors that can explain and predict spatial patterns in species richness are these processes and that one cannot understand current diversity patterns without explicitly understanding how these processes generated them (e.g. (Wiens, 2011). Alternatively, it is possible that speciation, extinction and dispersal rates poorly predict species richness through space and time. This would be the case if these processes are highly diversity-dependent (i.e. that the rate of species’ accumulation slows down as diversity increases) such that some other factor largely controls species richness. Under this diversity-dependence scenario, the direct processes controlling richness (speciation, extinction, dispersal) would operate largely to fill some externally imposed equilibrium limit on species richness (Rabosky, 2009; Rabosky & Hurlbert, 2015). Indeed, speciation and extinction rates appear to have been highly variable through evolutionary times (Rabosky & Lovette, 2008; Rabosky & Hurlbert, 2015). And, although net diversification has certainly been higher in regions and clades that currently have high species richness (Jansson & Davies, 2008; Rolland *et al.*, 2014), speciation rate and

extinction rate, calculated over shorter units of time, are not necessarily higher in species-rich areas (Weir & Schluter, 2007; Rabosky & Lovette, 2008). Similarly, dispersal rates into, versus out of, species-rich regions are not necessarily higher either (Rolland *et al.*, 2014; Duchêne & Cardillo, 2015). Therefore, so far, there is little evidence that speciation, extinction or dispersal rates can be directly used to predict species richness through space and time.

I tested specific hypotheses that explicitly rely on the processes of speciation, extinction and/or dispersal to explain current-day global patterns in species richness. First, I used patterns of inter-annual non-reoccurrence of species in the North American breeding bird survey, to test the hypothesis that the contemporary richness–climate relationship is caused by contemporary climate-dependent local extinction rates (Chapter 5). Then, I tested a prediction of, perhaps, the most prominent hypothesis aiming to explain large-scale patterns in species richness, namely tropical niche conservatism (Chapter 6). Tropical niche conservatism proposes that most clades have originated at a time where the Earth was predominantly warm, with a climate generally resembling today’s tropics (Wiens & Donoghue, 2004). Most ancestral species have therefore evolved tolerances to warm tropical-like climates. The hypothesis proposes that physiological tolerances to climate are highly phylogenetically conserved, with speciation events that allow dispersal into novel climatic niches being rare. This hypothesis has risen to prominence likely because it is intuitive, its main assumption and prediction are well accepted (i.e, most clades have originated in warm climates and most contemporary species are adapted to warm tropical-like climates) and it relies on evolutionary processes. Moreover, the hypothesis makes multiple specific falsifiable predictions, a strength that, unfortunately, is shared by relatively few hypotheses aiming to explain richness gradients (Rohde, 1992; Currie *et al.*, 1999). I specifically tested the prediction that the sign and strength of current richness–temperature gradients in a

clade can be explained by the temperature of the Earth at the time at which the clade originated (Chapter 6). Another prominent hypothesis that aims to explain current richness gradients by relying on historical processes is the historic climate stability hypothesis. This hypothesis proposes that regions with historically variable climate during the Quaternary have had high local extinction rates with the range of many species retracting to warmer, more stable climates and that, due to low migration rates, many of these species have since failed to re-colonize (Svenning & Skov, 2007; Araújo *et al.*, 2008). Some authors have simply proposed that species richness depends on historic climate stability and have remained elusive about the underlying mechanisms (Hortal *et al.*, 2011). Since this hypothesis has also recently rose to prominence in the literature, with many studies finding supporting evidence, I revisit the literature regarding the climatic stability hypothesis to test the extent to which the available evidence is actually consistent with the hypothesis (Chapter 7).

The development of a simple, first-approximation model of the continental biogeography of species would represent an important leap forward for ecology. Simple models making specific predictions about natural systems, while being explicit about underlying assumptions, have had particularly important and lasting impacts on the field of ecology (e.g. the theory of island biogeography, the unified neutral theory of biodiversity and biogeography, the metabolic theory of ecology; optimal foraging theory). My thesis works towards a simple model that explicitly relies on the processes of speciation, extinction and dispersal to predict the main characteristics of species distributions, i.e. spatial variations in species richness, spatial turnover in species composition, species' occupancy-climate relationships (as described in Chapter 1 and 2) and spatial variations in species' range size, niche breadth and range filling (as described in Chapter 3). This would unify under the same general model major broad-scale ecological

patterns that have so far been considered mostly in isolation. To develop a model that would approximate the main characteristics of species distributions at broad scales, I take the approach that the simplest model, with the fewest free parameters, should be preferred. Complexity should only be added only when it is shown to be necessary to make better predictions. This is because, “if a theory needed to account for all the details of a system to yield predictions about its future behavior, gathering sufficient data to evaluate its predictions would require an inordinate amount of work. Such a theory would be inefficient, and as complex as the system it was attempting to describe” (Marquet *et al.*, 2014). An efficient theory is a way to look at the world that provides a compressed and simplified description of nature (Marquet *et al.*, 2014). In particular, neutral theories, ones that do not account for inter-specific differences, have been particularly efficient in ecology (Hubbell, 2001; Rosindell *et al.*, 2011). Although species differ in a nearly-infinite number of characteristics that can, and surely often do, affect their relative fitness, neutral models ignore this complexity to make predictions about natural systems that are robust to inter-specific differences. Neutral models can often predict real-life patterns surprisingly well (Hubbell, 2001). And, when and how they fail to predict natural patterns is especially informative.

To be efficient and useful, a first-approximation model of the continental biogeography of species should therefore be neutral, unless modelling inter-specific differences can be shown to improve predictive power. The literature is filled with accounts of inter-specific differences and how these ought to affect species distributions. And, although not accounting for these differences has been widely criticized, one must first show that inter-specific differences matter to the pattern of interest before making a model so complex that it has little practical use (Rosindell *et al.*, 2011). In particular, inter-specific differences are generally thought to be

particularly important determinants of species' range sizes, with species having broad tolerances (Slatyer *et al.*, 2013), being good dispersers (Nogués-Bravo *et al.*, 2014) or competitors (Pianka, 1989) or being able to tolerate widely available (Hanski *et al.*, 1993) or particularly harsh environments (Pither, 2003) would have wider geographic ranges. The evidence supporting these claims is mostly correlative (Morin & Lechowicz, 2013; Slatyer *et al.*, 2013; Nogués-Bravo *et al.*, 2014). However, it is not clear the extent to which correlations between range size and characteristics of species' distributions can be expected in the absence of causation. I therefore test the extent to which the correlations between range size and species' climatic niche characteristics are consistent with causal effects, versus equally consistent with a neutral model (Chapter 8).

Many hypotheses and ecological models also assume that species' geographic distributions are largely determined by, i.e. predictable from, their physiological tolerances (Sunday *et al.*, 2012; Araújo *et al.*, 2013). If these tolerances are important determinants of individual species distributions, then surely we should be accounting for them in models aiming to predict second-order patterns such as the range size frequency distribution and geographic variations in species richness. Several hypotheses aiming to explain broad-scale ecological patterns incorporate inter-specific differences in tolerances (Wiens & Donoghue, 2004; Slatyer *et al.*, 2013). But, it is still unclear the extent to which physiological thermal tolerances can explain species' distributions, inter-specific variations in range size and the richness–climate relationship.

By the test and rejection of hypotheses regarding broad-scale patterns in species distributions, my thesis progresses closer to a simple general, predictive model of the continental biogeography of (multicellular) species. I challenge prominent assumptions and hypotheses in

macroecology because I adhere to the view that science advances through the rejection of hypotheses, not through the accumulation of supporting evidence (Platt, 1964; Peters, 1991; as opposed to e.g. the Baconian method). In sum, my thesis seeks simplicity in a complex world through general ecological patterns.

CHAPTER 1 **How are tree species distributed in climatic space? A simple and general pattern**

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ABSTRACT

Aim Although many factors undoubtedly affect species' geographic distributions, can a single, simple model nonetheless capture most of the spatial variation in the probability of presence/absence in a large set of species? For 482 North American tree species that occur east of the Rocky Mountains, we investigated the shape(s) of the relationship between the probability of occupancy of a given location and macroclimate, and its consistency among species and regions.

Location North America

Methods Using Little's tree range maps, we tested four hypothetical shapes of response relating occupancy to climate: 1) high occupancy of all suitable climates; 2) threshold response (i.e., unsuitable climates exclude species, but within the thresholds, species presence is independent of climate); 3) occupancy is a bivariate normal function of annual temperature and precipitation; and 4) asymmetric limitation (i.e., abiotic factors set abrupt range limits in stressful climates only). Finally, we compared observed climatic niches with the occupancy of similar climates on off-shore islands as well as west of the Rockies.

Results i) Species' distributions in climatic space neither have strong thresholds, nor are they systematically skewed towards less stressful climates. ii) Occupancy can generally be described

by a bivariate normal function of temperature and precipitation, with little or no interaction between the two variables. This model, averaged over all species, accounts for 82% of the spatial variation in the probability of occupancy of a given area. iii) Occupied geographic ranges are typically ringed by unoccupied, but climatically suitable areas. iv) Observed climatic niche positions are largely conserved between regions.

Main conclusions We conclude that, despite the complexities of species' histories and biologies, to a first approximation, most of the variation in their geographic distributions relates to climate, in similar ways for nearly all species.

INTRODUCTION

Robert MacArthur (1972, p. 127), in his classic *Geographical Ecology*, wrote, “Patterns on islands (Chapter 5), of species diversity (Chapter 7), and of tropical communities (Chapter 8) are already clear and even moderately well understood, while patterns of single species’ ranges still seem to be catalogs of special cases.” Textbook wisdom indicates that species distributions can be affected by factors including climate, soil, competition, predation, parasitism, mutualism, historical events, land use, phylogeny, dispersal limitation, physical barriers, and more (MacArthur, 1972; Brown *et al.*, 1996; Gaston, 2003; Sexton *et al.*, 2009). Surprisingly few generalizations about how species are distributed in space are currently possible (Gaston, 2009).

Here we ask: can a single, general model, applied to a broad set of species (e.g., trees) account for the bulk of the variability in how those species are distributed in space? It is possible that much of the variability in the distributions of most species relates to a small number of driving variables (e.g., Hubbell, 2001), while a multitude of other factors have additional minor effects, or even major effects on a few species. Because a predictive model would be far more powerful than a catalog of possible influences on individual species’ ranges, our goal is to identify strong empirical consistencies of how species are distributed, as opposed to focusing on the biology of any particular species.

Climate has been recognized as the most obvious potential determinant of species’ distributions since von Humboldt (Hawkins, 2001). At the continental scale, geographical variation in species richness is strongly related to combined measures of temperature and precipitation (Field *et al.*, 2005, 2009), and individual species’ distributions often relate to similar variables (Gaston, 2003; Sexton *et al.*, 2009). Yet, the literature is replete with different hypotheses (or assumptions) about exactly *how* species’ distributions relate to climate.

Here, we tested four biologically plausible hypothetical relationships (Fig. 1.1) between the probability of occupancy of a region by a given species and macroclimate. Our approach differs from current species distribution models by restricting the shape of the response to only a few biologically relevant possibilities. Correlative niche models typically assume a given response function (e.g. BIOCLIM, DOMAIN) or a nearly unlimited set of response functions (e.g. CART, GAM, GARP, RTA, Maxent). The latter models typically suggest highly irregular species-specific functions (Elith *et al.*, 2010), have low transferability in space (Randin *et al.*, 2006; Peterson *et al.*, 2007), can be over-parameterized (Warren & Seifert, 2011) and can only be interpreted post-hoc.

First, consider the ‘tolerance hypothesis’ (Currie *et al.*, 2004). It proposes that physiological tolerance to abiotic factors is the principal limit to species’ geographic ranges (Grinnell, 1914; Pearson & Dawson, 2003). For example, a species range may be bounded by frost tolerance (Sakai & Weiser, 1973) or by conditions where primary productivity is greater than zero (Kleidon & Mooney, 2000). In principle, there are both upper and lower limits, but in practice, only one limit may be observable. At broad scales and coarse grain, the tolerance hypothesis predicts that species occur in all or most climatically suitable regions (Currie *et al.*, 2004). This is the assumed equilibrium-state of species distributions (Hutchinson, 1957; Svenning & Skov, 2004; Araújo & Pearson, 2005) and underlies simple climatic envelope models (e.g. BIOCLIM, DOMAIN, HABITAT).

Secondly, what we shall hereafter call the ‘threshold hypothesis’ postulates that climate imposes physiological limits to species’ ranges, but within those limits (again, in principle, both upper and lower), climate does not influence the probability of occurrence and other factors become important (Davis *et al.*, 1998; Guisan & Thuiller, 2005). The threshold hypothesis

predicts that, for a given species, climates outside the thresholds will be unoccupied but, within the climatic thresholds, regions may, or may not, be occupied (in contrast, the tolerance hypothesis predicted that all regions within the climatic thresholds will be occupied).

Thirdly, there is what might be called the ‘peaked suitability hypothesis’, whereby every species is maximally successful at a particular climate. This model predicts that suitability, and therefore the probability of occurring in a given region, decreases as a function of climatic distance from the species’ optimum (Gauch & Whittaker, 1972). The shape of the function and its parameters (mean, variance and height) may vary among species. Pigot *et al.* (2010) assumed that suitability declines exponentially from a species’ climatic optimum. Others assume a Gaussian response (Swan, 1970; Gauch & Whittaker, 1972; ter Braak & Looman, 1986).

Fourthly, what we call the ‘asymmetric limitation hypothesis’ (a.k.a. the “asymmetric abiotic stress limitation hypothesis”; Normand *et al.*, 2009) suggests that species distributions are abruptly limited by physical stress in cold and/or dry environments, while in less stressful environments, species’ distributions are limited by increasing biotic interactions (Dobzhansky, 1950; MacArthur, 1969, 1972; Brown *et al.*, 1996). If physiological tolerance imposes a sharp limit to range expansion only at the stressful end of the gradient (Root, 1988; Normand *et al.*, 2009), the asymmetric limitation hypothesis predicts that the probability of occupancy of a species is skewed towards the less stressful end of a climatic gradient, where biotic, rather than abiotic conditions limit distributions (Kaufman, 1995; Normand *et al.*, 2009). Normand *et al.* (2009) report that almost half of European plant species have significantly skewed distributions towards the less stressful end of at least one climatic variable, which they regarded as support for the hypothesis. Accordingly, species ranges often abut a temperature isotherm at their northern or upper-altitudinal limit (Root, 1988; Korner & Paulsen, 2004).

We also tested whether the climates occupied by a species are conserved across apparent dispersal barriers (the Rocky Mountains and ocean straits). If climate is the principal determinant of geographic ranges, species present on both sides of a dispersal barrier should occupy similar climatic conditions. Using coarse scale, mean annual climate data, is appropriate for such a test; making models more general by avoiding over-fitting, as suggested in a case study by Broennimann *et al.* (2007).

METHODS

Distribution and climate data

We used Little's range maps of 679 North American trees (U.S. Geological Survey, 1999) which are drawn for trees indigenous to the United States and Canada, including the parts of ranges that extend into Central America. However, Little's maps (and consequently our study) exclude Central American species whose ranges do not extend into the US. The maps were not drawn following isoclines and their grain, based on the smallest isolated patches of presence or absence, is approximately 10-20 km. Therefore, all the conclusions we present below apply to the presence or absence of species within regions of roughly 400 km².

Mean annual temperature and total annual precipitation were taken from WorldClim (Hijmans *et al.*, 2005). In the study region, all 19 bioclimatic variables from WorldClim are correlated with either the yearly average of temperature or precipitation we use here ($0.47 < r < 0.99$). Climate data were rasterized in 0.01° pixels.

To focus on the effects of climate on tree distributions, our study area included a single region with no major barriers to dispersal: mainland North America east of the Rocky Mountains (see Appendix S1.1). Operationally, we included all land east of the 1000 m elevation contour on

the east slope of the Rockies. All offshore islands were excluded. We then considered all 482 species that have at least parts of their range within this study area.

For all analyses, we distinguished narrowly and broadly-distributed species based on the size of their range (within the study region). We defined (arbitrarily, but qualitative results are not sensitive to the definition) narrowly-distributed species as those that occupy fewer than $\sim 5000 \text{ km}^2$ while the others were considered to have broad distributions. We report results separately for narrowly and broadly-distributed species only when there is a statistically significant difference.

Occupancy as a function of climate

We calculated occupancy Ω_{stp} , the proportion of the study region with a temperature t and precipitation p that falls within the range of species s . To do this, we first created 23 intervals of mean annual temperature, each 2°C wide. Because the frequency distribution of total annual precipitation (mm) in the study area is strongly positively skewed, we first square-root transformed precipitation. We then divided this range into 23 bins, each 3 units wide. Many $t \times p$ combinations do not occur anywhere in North America (specifically, areas with very low temperatures and high precipitation: the upper left quadrant of Fig. 1.2c, d) and some others are very rare. Combinations represented by <100 climate pixels were excluded from the analyses (these were all situated at the margin between existing and non-existing climates). This yielded 232 different existing $t \times p$ climate bins in continental eastern North America. Note that Ω_{stp} values, being proportions, are independent of map resolution and therefore so are all analyses.

We here define a species' observed climatic niche as all climate bins in which a species occurs anywhere in the study area (Fig. 1.2). This may not include all suitable climates (Pulliam,

2000; Kearney, 2006; Soberón, 2007). Conversely, sink populations (Pulliam, 2000) or false presences within the range map could lead to an overestimation of suitable climates. Next, we defined $\hat{T}_s$ and $\hat{P}_s$ as the $t \times p$ climate bin that species s occupies in the highest proportion or, in the case of more than one bin with equal Ω_{stp} , the most central.

We then tested whether the four hypotheses presented in Figure 1.1 and relating occupancy Ω_{stp} to temperature t and precipitation p , are consistent with the range of each of the 482 eastern North American trees here considered.

We first tested the tolerance hypothesis (i.e., that climatic tolerance alone determines presence/absence). Regions with tolerable climates were predicted to be entirely occupied and others unoccupied. Since a climate bin at the edge of a species climatic niche could include both tolerable and intolerable climatic conditions, it may or may not be occupied (e.g. 0°C may be suitable for species s and therefore occupied while -1°C is not, but they are considered in the same climate bin in the analysis). Therefore, the edges of each species' observed climatic niche were excluded from the test of this hypothesis (i.e., all occupied climate bins for which at least one of the four nearest-neighbors is unoccupied). We accepted the tolerance hypothesis if, in the remaining climate bins (hereafter referred to as the core climatic niche), occupancy $\Omega_{\text{stp}} \geq 0.75$ in all bins. This threshold is arbitrary but also fairly liberal and results are robust to the threshold definition (Appendix S1.2). For the 118 species without a core climatic niche (i.e. all occupied bins are adjacent to unoccupied bins), all occupied Ω_{stp} were considered.

We then tested the threshold hypothesis (i.e., that climate defines unsuitable areas, but Ω_{stp} is independent of climate within the thresholds). The threshold model predicts equal occupancy in all suitable climates, and zero occupancy elsewhere. Predicted occupancy was therefore taken as the average observed Ω_{stp} in occupied bins (as for the tolerance hypothesis, the

edges of the climatic niche were excluded), and zero in the ring of surrounding unoccupied cells. We then calculated the coefficient of determination between these predicted values and the observed occupancy values.

To test whether occupancy Ω_{stp} is consistent with the peaked suitability hypothesis, we modeled a bivariate normal function of temperature and precipitation (Appendix S1.3). We retained all bins in which $\Omega_{\text{stp}} > 0$, plus a ring of unoccupied climate bins directly adjacent to occupied ones. A bivariate normal model was used because it necessarily restricts the shape to a Gaussian function with only five parameters. We obtain the same qualitative results when using LOESS or polynomial functions instead.

Last, we tested the asymmetric limitation hypothesis. To determine whether individual species distributions are significantly skewed, we calculated μ_3 , the third statistical moment around the mean for temperature and precipitation. However, for 341 species, the climatic niche is truncated (i.e., the observed climatic niche abuts climate bins that do not exist in eastern North America). Skewness cannot be calculated directly in these cases. Therefore, we also tested, for all species, the prediction that there is a steeper decrease in occupancy towards the stressful end (cold and dry) of a climatic gradient with a binomial test. We calculated the difference in area under the curve computed for climates above and below the most occupied climate. The hypothesis predicts that this difference should generally be positive (Appendix S1.3).

Occupancy across dispersal barriers

Land areas located across dispersal barriers were used to evaluate the stability of species' observed climatic niches. Occupancy Ω_{stp} was determined for the western North American mainland (defined as all land areas situated west of the 1000 m elevation contour on the west

slope of the Rocky Mountains and Sierra Nevadas; Appendix S1.1). We considered only the 98 climatic bins that had >100 climate pixels both east and west of the Rockies. Similarly, we compared observed climatic niches on the eastern mainland versus those on the islands off the east coast of the continent (Appendix S1.1; 73 climatic bins).

For species present on both sides of the Rocky Mountains, we determined the Spearman's rank correlation between Ω_{stp} in the two regions. To determine whether the observed climatic niche position is retained across space, we also determined what we hereafter refer to as climatic nestedness: the proportion of the smaller climatic niche (in one region) that lies within the larger (in the other region). Last, to determine if climatic niches that are not entirely nested are nevertheless very similar, we calculated a buffered climatic nestedness. To do this, we slightly enlarged the largest climatic niche so it would encompass a ring of climate bins directly adjacent to (i.e., within 2°C and 3 precipitation units of) occupied bins, and we then recalculated nestedness.

RESULTS

For all species, occupancy Ω_{stp} depends significantly on temperature and precipitation ($p < 0.001$). On average, species geographically occupy only $29 \pm 22\%$ (SD) of their observed climatic niche (see Fig.1.2; 36% for the species in panel a and 60% for that in b), but this strongly increases with range size (Spearman's $\rho = 0.93$, $p < 0.001$, $n=426$ excluding species where Ω_{stp} is always < 0.01).

First, we reject the tolerance hypothesis, according to which species are predicted to occupy most of their climatic niche. No species has $\Omega_{\text{stp}} \geq 75\%$ in all bins of its core climatic

niche (Table 1.1) and this increases only to six species if we lower it to $\Omega_{\text{stp}} \geq 50\%$ (Appendix S1.2).

The threshold hypothesis (i.e., that occupancy Ω_{stp} is independent of climate within precipitation and temperature thresholds) explained as much, or more of the variance in the distributions of 55 species than the competing hypotheses (Table 1.1, Appendix S1.3). For these species, the threshold model accounts on average for $78 \pm 2\%$ (SE) of the variance in Ω_{stp} . The threshold model accounts for $55 \pm 1\%$ (SE), averaged over all species. Note that it was not possible to compare the competing models with standard information theoretic statistics (Appendix S1.3).

The peaked suitability model, according to which Ω_{stp} varies as a bivariate normal function of t and p , generally accounts for most, and on average $82 \pm 1\%$ (SE), of the variance in occupancy (Fig. 1.3). For most species, occupancy did not depend upon an interaction between t and p (Appendix S1.3). For 91% of the 482 species, the R^2 of the peaked suitability model was higher or equal to the R^2 of the threshold model (Table 1.1). Comparing the threshold and peaked suitability model based on R^2 rather than maximum likelihood, is more liberal in favor of the threshold model (Appendix S1.3). Moreover, the high R^2 values of the peaked suitability model remain high when climate bins with zero-occupancy are excluded (Appendix S1.4). For narrowly-distributed species, a bivariate normal function of temperature and precipitation accounts on average for 94% of the variability in Ω_{stp} versus 78% for broadly-distributed species. The coefficients obtained from the peaked suitability model are presented for all 482 species in Appendix S1.5.

Our results are inconsistent with the asymmetric limitation hypothesis. North American trees' observed climatic niches are not systematically skewed towards the less stressful end of

the climatic gradient (Fig. 1.4). The probability of exhibiting a right-skewed response is not greater than left-skew (one-sided binomial test; $p = 0.24$ for temperature and $p = 0.98$ for precipitation). We also reach the same conclusion when using only the 141 species whose climatic niches are not truncated, and for which we could calculate μ_3 . We observe statistically significant right-skewed distributions for the temperature and precipitation gradients for 21 and 11% of species respectively (Table 1.1). Left-skewed distributions occur in 15% of species for temperature and 23% for precipitation, which is as frequently as right-skewed distributions ($p = 0.16$ for t and $p > 0.99$ for p). We conclude that most species have a symmetric response to t and p . When the response is skewed, it can be skewed towards either end of the climatic gradient. We found that several other predictions of the asymmetric limitation hypothesis were also not supported (Appendix S1.6). Our conclusions are not affected by the climate bin delineation (Appendix S1.7).

Occupancy across dispersal barriers

The eastern North American mainland shares a much higher proportion of its species with off-shore islands (61%) than with the mainland west of the Rockies (13%). The Rockies apparently presented a greater barrier to dispersal than did ocean straights.

The relative occupancy of a climate bin is moderately conserved among geographic regions. For species occurring on both sides of a dispersal barrier, the relationship between occupancy and climate is usually similar in the two regions (Fig. 1.5a, b). Occupancy Ω_{stp} in the eastern mainland is significantly ($p < 0.05$) correlated to Ω_{stp} on western mainland and islands in 70% and 94% of species, respectively. Significant correlations are all positive and the average Spearman correlation coefficient (ρ) is 0.40 for western mainland and 0.53 for islands. For

islands, but not for western mainland, the mean ρ is 1.5 times larger for broadly- than narrowly-distributed species.

Similarly, maximum occupancy Ω_{stp} (a descriptor of a species' commonness within its climatic niche) is typically conserved among geographic regions. Maximum occupancy differs by less than 0.1 between regions for most species (Fig. 1.5c, d). The variation among species in maximum occupancy is moderately correlated between eastern and western North America ($r=0.36$) or between the eastern mainland and islands ($r=0.56$). Maximal Ω_{stp} is equally likely to be larger in eastern and western mainland (two-sided binomial test; $p=0.82$), but it is usually smaller off-shore ($p<0.001$).

Finally, climatic niche positions are strongly conserved among geographic regions, because the smaller climate niche is nearly always nested in the larger. Climatic nestedness is usually high (Fig. 1.5e, f) and even non-nested niches are quite similar to one another (Fig. 1.5g, h), with only 2 species having entirely non-nested climatic niches (Fig. 1.5g). These species are *Pinus hartwegii*, a species mostly occurring in the mountains of Mexico, and *Betula occidentalis*, a water-side species. Both species occupy only one climate bin with $\Omega_{\text{stp}}<0.001$ in eastern mainland (of the climates also existing in western mainland).

DISCUSSION

We have here demonstrated that, despite the “catalog of special cases” (MacArthur, 1972, p.172) that have been used to characterize them, tree species' geographic ranges are, to a first approximation, related to climate in quite a consistent, simple way. Observed climatic niches are never entirely occupied, yet unoccupied portions are predictable. The peaked suitability model was consistent with the distribution of nearly all species, narrow and broad-ranged, where the

probability of occupancy Ω_{sp} by species s is a bivariate normal function of temperature and precipitation. Averaged over all 482 species, the peaked suitability model accounts for 82% of the variance in species' regional occupancy (without interactions between climatic factors).

The utility of this finding is that it reduces species' macro-scale distributions from a very high dimensional problem (many different factors each operating in different ways on different species, and changing through space; Gaston, 2003) to, as a first approximation, a fairly low-dimensional problem. The probability of occupancy can be summarized by five parameters per species: mean temperature and precipitation, climatic niche breadth (temperature and precipitation variance of occupied areas), and maximum occupancy. We are currently investigating whether, among the species occupying a given location, the distribution of these parameters are predictable from climate, topography, etc.

Our goal was to identify the simplest model that captures the bulk of the variation in a broad set of species. Unquestionably, species' distributions can be affected by factors not included in our model (e.g., biotic interactions, other climatic variables, disturbances, historical legacies). More complicated models may make better predictions of individual species' distributions. Yet, studies using as many as 19 bioclimatic variables also found that realized/potential range size ratios of most species is very low (Svenning & Skov, 2004; Munguia *et al.*, 2008). Similarly, the realized/potential range size ratio of 16 North American tree species here considered was computed by Morin *et al.* (2007) using a process-based modeling approach. Our model predicts realized/potential range size ratios for these species that are only slightly lower than Morin *et al.* (56% vs 64%) and that are strongly correlated with theirs ($r=0.78$, $p<0.001$). We conclude that a Gaussian function of mean annual temperature and

precipitation does capture most of the variation in the probability of occurrence of North American trees.

We reject the asymmetric limitation hypothesis, based on the observation that right and left-skewed distribution occur equally frequently for North America trees (Fig. 1.4). Detection of skew was not the point here; for most species, occupancy is certainly not a perfectly symmetrical function of temperature and precipitation and with sufficient statistical power, one can always detect small departures from normality. More important is the effect size. A Gaussian function (without skew) explains an average of 82% of the variance in the probability of occurrence of a species (Fig. 1.3). Any residual skew is thus quite small and is frequently in the direction opposite to predicted. Our conclusion contrasts with that of Normand *et al.* (2009) even though our statistical results are quite similar. Normand *et al.* (2009) found that, among the 1577 European plant species they investigated, right-skewed responses (21%-26%) were more frequent than left-skew (6-12%), whereas we found 11%-21% right-skewed and 15-23% left-skewed. However, right-skewed responses to a given climatic gradient were not the norm among species in either study. Some additional predictions from the asymmetric limitation hypothesis are also inconsistent with observations (Appendix S1.6; Normand *et al.*, 2009). Biotic interactions may be more prominent in warmer/wetter climates (see Schemske *et al.*, 2009), but they apparently do not cause macro-scale distributions to be systematically skewed towards less stressful climates.

Given that we square-root transformed precipitation, it might be argued that the untransformed probability of occupancy is in fact right-skewed (i.e., toward wet climates). We transformed precipitation for two reasons. First, it was necessary for statistical reason: the frequency distribution of precipitation in North America is strongly positively skewed (i.e., there

are many mesic places and a few extremely wet ones). Second, the asymmetric limitation hypothesis assumes that biology scales linearly with climate; it is not couched in the raw climate variables. We argue that biological effects of precipitation scale less than linearly: the ecological difference between areas receiving 100 mm and 200 mm per year is much greater than that between 2100 mm and 2200 mm: Holdridge (1967) classified geographic variation in biomes as a function of the logarithm of precipitation; Whittaker (1975) did so as a function of approximately the square root of precipitation.

The shape of the response curve and the position (in climatic space) of the observed climatic niche is generally conserved among geographic regions, suggesting that these are species-specific traits. This is broadly consistent with other studies showing, as concluded by Randin *et al.* (2006), that most species "occupy similar niche positions in distinct regions". However, we found that climatic niche-breadth was not generally conserved. In species distribution models, this would cause abundant commission or omission errors in climatically suitable area, even with very similar niche positions and response curves. This may explain why the transferability of species distribution models in spatially distinct regions is variable and generally weak (Manel *et al.*, 2001; Randin *et al.*, 2006; Peterson *et al.*, 2007).

We find that species' geographic ranges are almost always entirely surrounded by unoccupied but apparently suitable climates, without obvious dispersal barriers. In this respect, the maps in Fig. 1.2 are typical of the tree distributions we examined. Svenning and Skov (2004, 2007) attribute the discrepancy between species' realized and potential distribution in European trees to slow dispersal from glacial refuges, causing species not to be in equilibrium with current climates. For North American trees, a similar explanation for low range filling would be

plausible if species occupied most climatically suitable areas on at least one edge of their geographic range (i.e., closest to the last glacial refuge). This is not typically the case.

The tree distribution data on which our conclusions are based (Little's maps: U.S. Geological Survey, 1999) are clearly imperfect. McKenney *et al.* (2007) found that, on average, 15% of tree locations fall outside Little's maps. Perhaps these were sink populations, deliberately excluded by Little, or perhaps they are simply false absences. There are also undoubtedly false presences in the data: local areas that are unoccupied within a species' range. These false absences and presences would have to be dependent on climate, and consistently so across species, in order to bias our main conclusion that the peaked suitability model accounts for most of the variance in species' occupancy. They are more likely responsible for some of the residual variance.

Why would occupancy Ω_{stp} be a peaked function of climate? This is the expected relationship if we simply assume (1) a Gaussian-like relationship between fitness and climate (McInerney *et al.*, 2009; Nogués-Bravo, 2009) and that (2) other factors affecting fitness such as extreme climatic events, sub-optimal soil quality or competition act independently and multiplicatively (Brown *et al.*, 1995) with climate. As the distance from the climatic optimum increases, fitness decreases and there is an increased likelihood that other factors make the locality uninhabitable. In other words, as the distance from the climatic optimum increases, the range would be increasingly restricted towards more specialized habitats (Austin, 1985; Brown *et al.*, 1995). Occupancy Ω_{stp} could also reflect the probability that a region with a given macroclimate bears suitable microclimates in which the species can persist.

But why do unoccupied but apparently climatically suitable areas typically encircle the entire distribution of species? It could arise from a dynamic equilibrium between colonization

and local extinction (Lennon *et al.*, 1997), if colonization probability depends upon the frequency of neighboring populations, and local extinction probability depends mainly (but not solely) upon climate. Specifically, we hypothesize that the probability of local extinction is proportional to $|t - \hat{T}_s|$ and $|p - \hat{P}_s|$ (thus, inversely related to occupancy Ω_{stp} , as demonstrated by Araújo *et al.*, 2002). High local extinction probability can lead to sink populations if gene flow from the population adapted to optimal climates prevents local adaptations to sub-optimal climates (Kirkpatrick & Barton, 1997; Case & Taper, 2000). Thus, a distributional limit can be attained even if the species' environment is relatively constant around that limit (Carter & Prince, 1981).

Finally, because both occupancy and climate are spatially autocorrelated, the null expectation, given no deterministic effect of climate on occupancy, is certainly not independence from climate (e.g. Beale *et al.*, 2008a). Therefore, spatial autocorrelation could be responsible for the symmetric decrease in occupancy around a species' most occupied climate we here observe. However, the observed relationship between species distributions and climate seems likely, at most, to be inflated by spatial autocorrelation. First, paleoecological (Williams *et al.*, 2002) and climate change studies (Parmesan, 2006) suggest that species distributions track changing climate. Second, we found that the majority of North American trees have similar observed climatic niches in different regions (i.e. west of the Rockies and on islands). But, regardless of whether the high explanatory power of the peaked suitability model arises because of deterministic effects of climate or not, the pattern appears general enough across species to be assumed in a general model of the continental biogeography of tree species.

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TABLES

Table 1.1 Percentage of species consistent with hypotheses relating the probability of occupancy Ω_{stp} of a region by species s to temperature t and precipitation p . Predictions for each hypothesis were tested on 482 eastern North American tree species.

Hypothesis	Tested prediction	Species consistent with an hypothesis
Tolerance	Most suitable climates are occupied (>75%)	0 %
Threshold	Climate defines unsuitable areas, but occupancy Ω_{stp} is independent of climate within the thresholds	11 %
Peaked suitability	Occupancy Ω_{stp} is a bivariate normal function of temperature and precipitation	91 %
Asymmetric limitation	The response curve is skewed towards hot or humid climates	- Temperature 21% ^a - Precipitation 11% ^a

^a Considering only the 141 species with non-truncated observed climatic niches

FIGURES

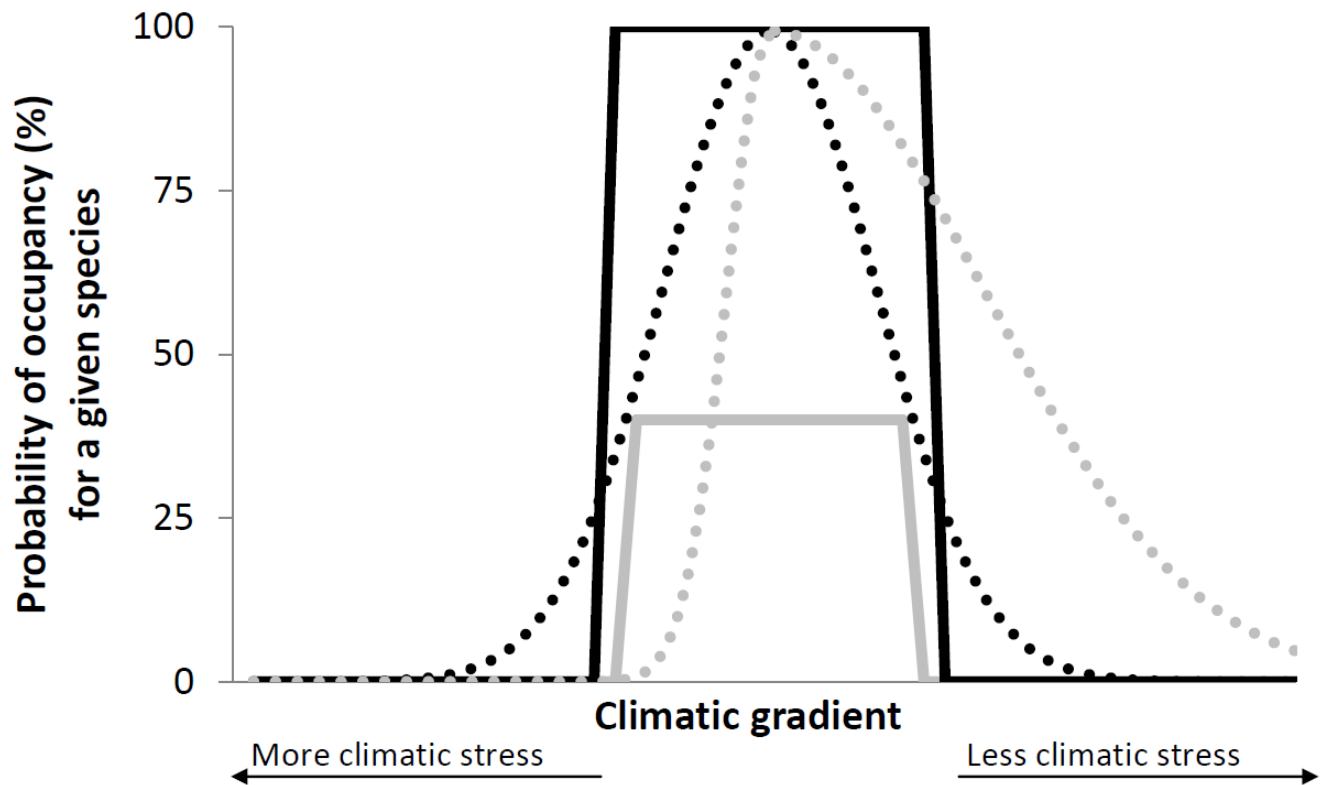


Figure 1.1 Hypothetical response curves of a species probability of occupancy along a climatic gradient. The ‘tolerance hypothesis’ (black line) predicts that regions with suitable climates will all be occupied. The ‘threshold hypothesis’ (grey line) predicts that climate only distinguishes unsuitable from potentially suitable habitat. The ‘peaked suitability hypothesis’ (black dots) predicts that the probability of occupancy will be normally distributed along a given climatic gradient. Finally, the ‘asymmetric limitation hypothesis’ (grey dots) predicts that the response curve will be skewed towards the less stressful end of the climatic gradient (i.e. towards warmer/wetter conditions).

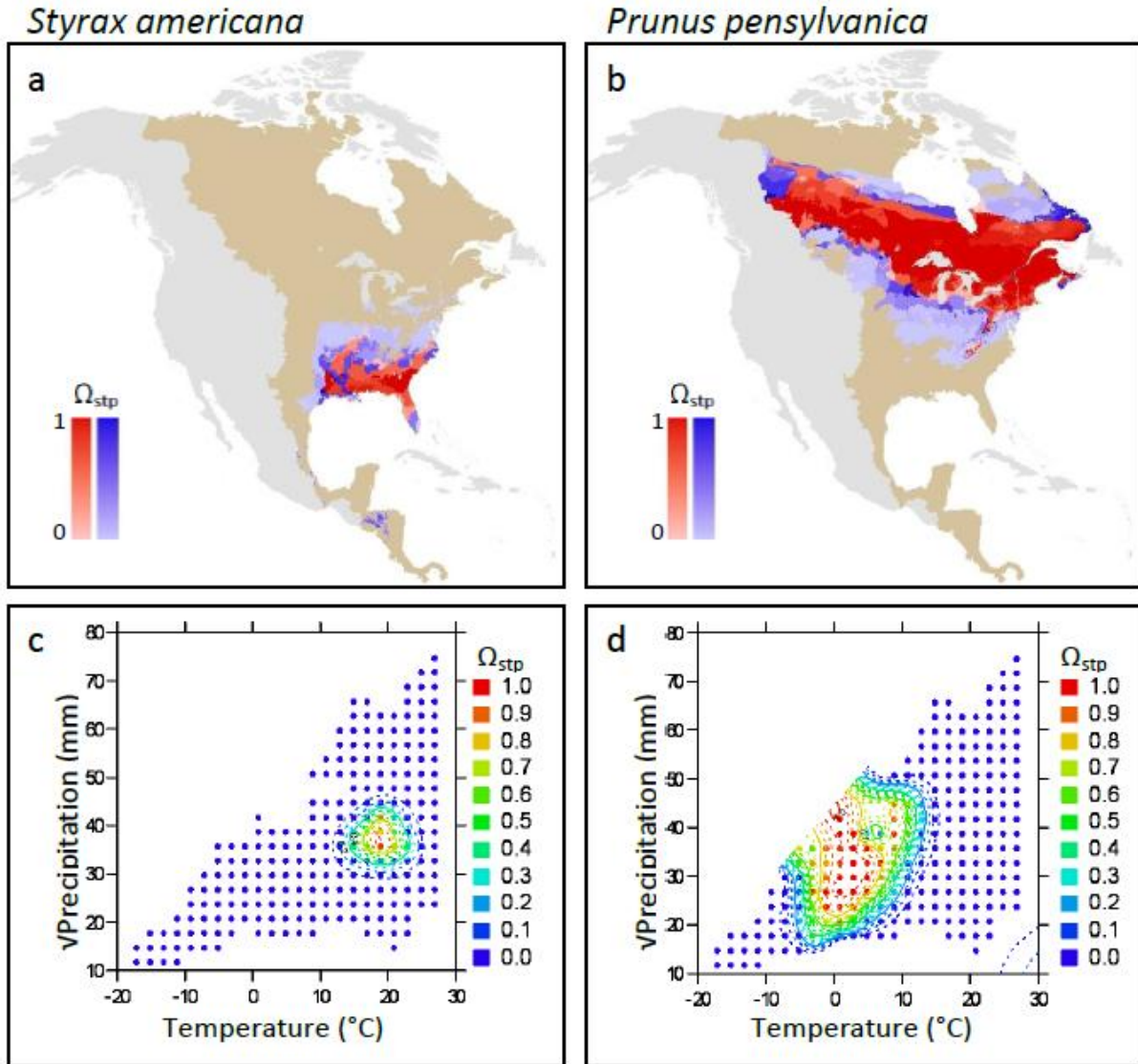


Figure 1.2 Examples of the observed climatic niches of trees in (a, b) geographic and (c, d) climatic space, shown for (a, c) *Styx americana* (American snowbell) and (b, d) *Prunus pensylvanica* (Pin cherry). In (a, b) the occupied range is red and unoccupied but climatically suitable regions are blue. The color intensity is proportional to occupancy Ω_{stp} ; the darker colors represent a proportion of occupancy closer to 1. Thus, a pale red area is occupied, but areas with the same climate elsewhere tend not to be occupied. A dark blue area is unoccupied, but areas elsewhere with the same climate are usually occupied. Beige areas are characterized by climates

never occupied by the species, while grey areas were excluded from analyses. Maps are in Mollweide projection, centered on -100° longitude. Panels (c, d) show the occupancy of the climate bins in the study region, in which each extant combination of temperature and precipitation (i.e. a climate bin) is represented by a dot. The color gradient indicates the occupancy Ω_{stp} of the climate bin $t \times p$ and the contour lines represent a DWLS smoothing of Ω_{stp} values at a tension of 0.1.

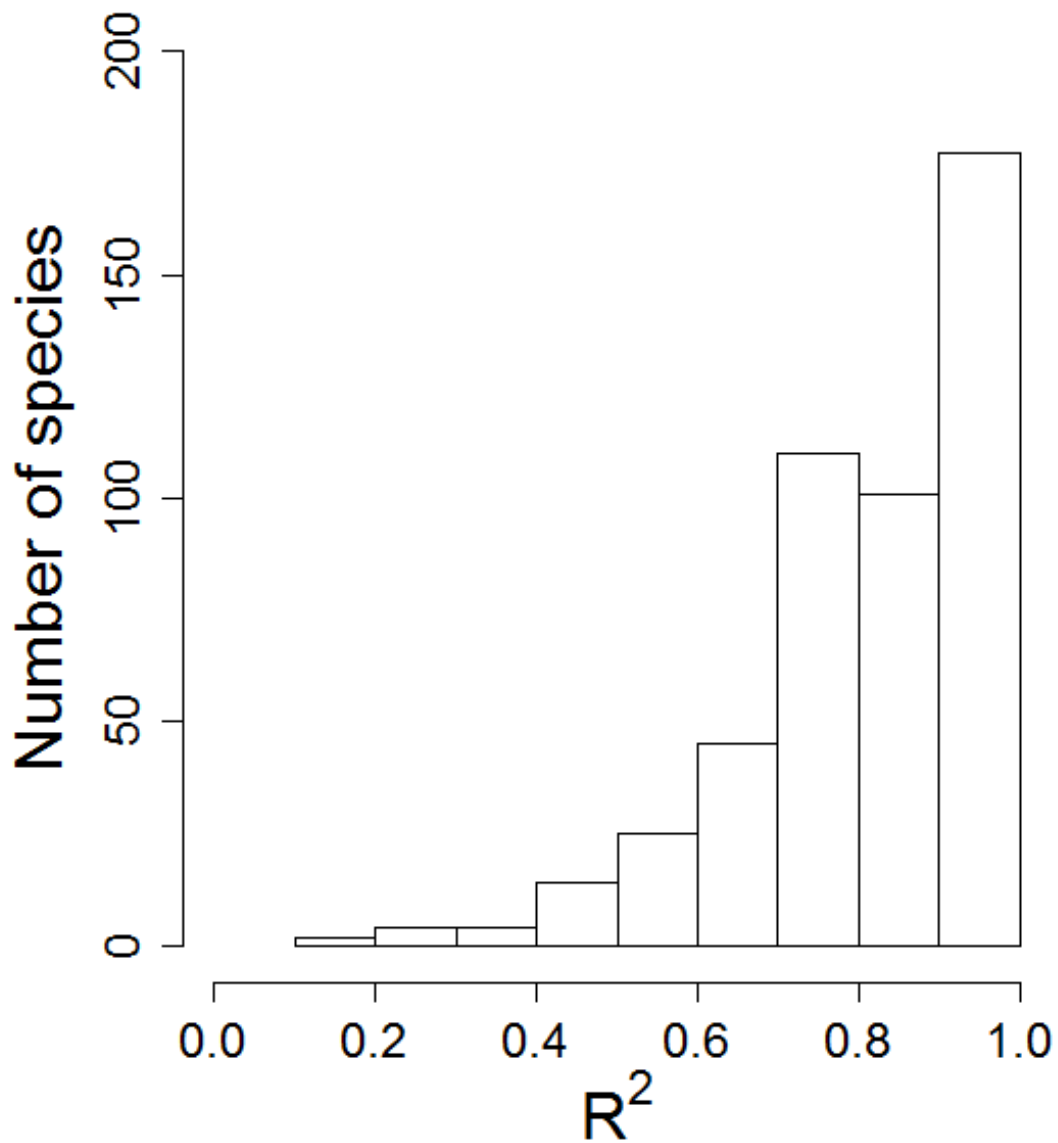


Figure 1.3 Distribution of the variability in occupancy Ω_{stp} of a region by species s explained by a bivariate normal function of temperature and precipitation. The model was fitted for each of 482 species climatic niche (i.e. all occupied climate bins) surrounded by a single ring of zero-occupancy.

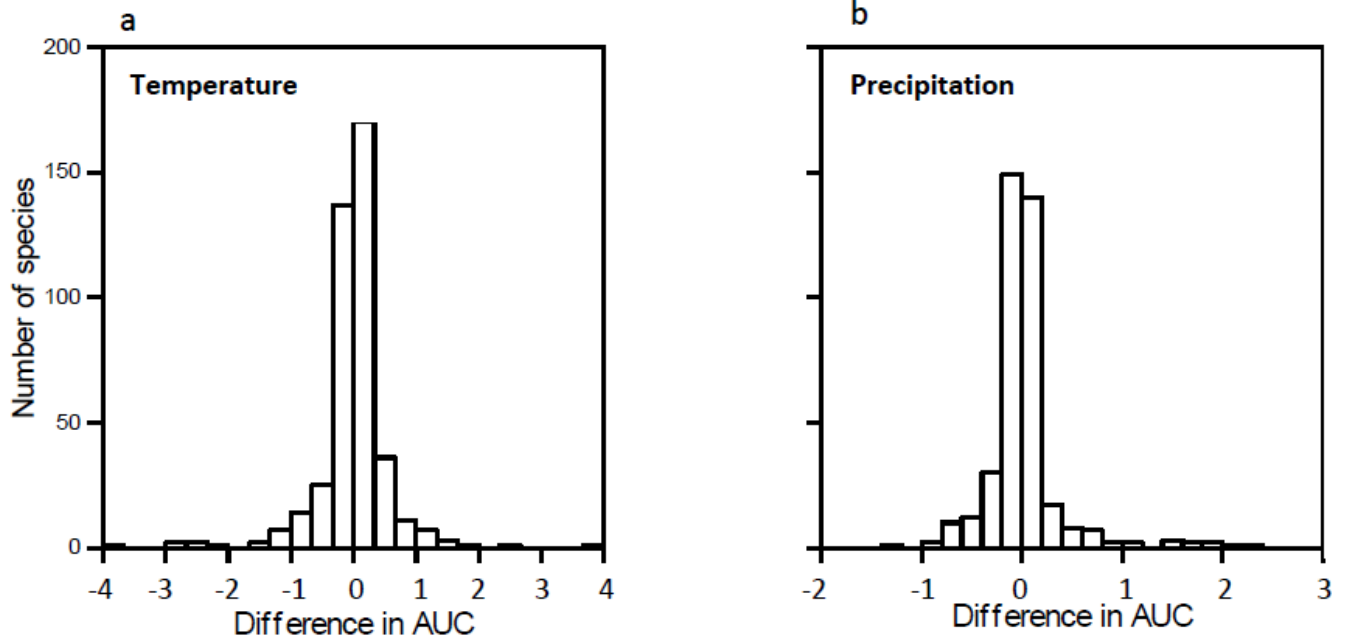


Figure 1.4 Distribution of the differences in area under the curve (AUC) on the benign, versus the stressful, sides of the most occupied climate for (a) temperature (AUC high temperature – AUC low temperature), 95% $CI_{mean} = [-0.058, 0.033]$ and $n=421$, and (b) precipitation (AUC high precipitation – AUC low precipitation), 95% $CI_{mean} = [-0.037, 0.044]$ and $n=389$. Results are shown for species for which occupied climate bins exist on both sides of the most occupied climate. The asymmetric limitation hypothesis predicts positive values.

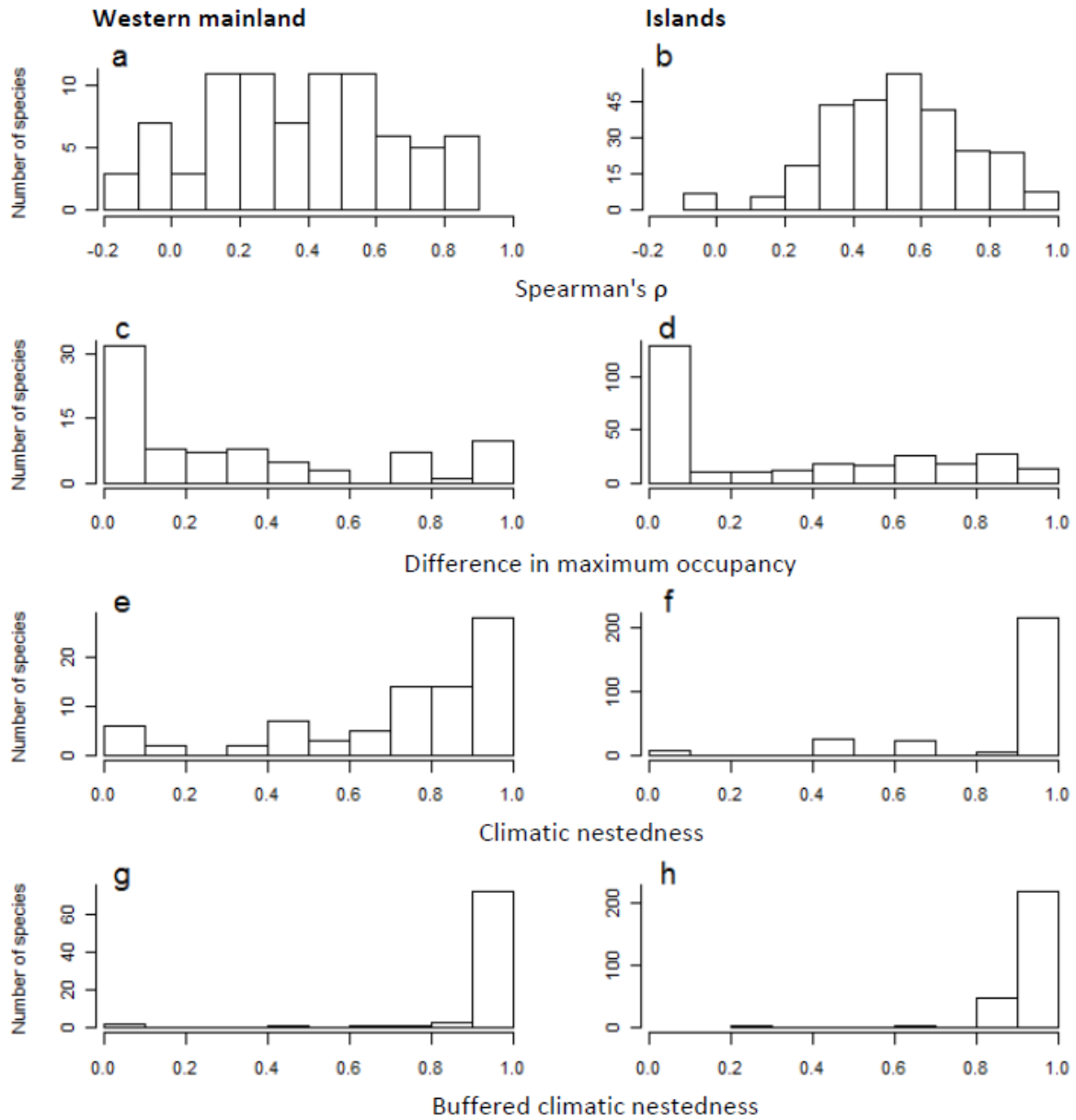


Figure 1.5 Distribution of four different measures of climatic niche similarity, comparing each species' eastern mainland distribution with that of western mainland (left) or islands (right). (a) and (b) are histograms of the Spearman's rank correlations between Ω_{stp} (the probability of occupancy of a climate bin $t \times p$ by species s) in (a) eastern versus western North America (for the 81 species that occur in both areas) and (b) the eastern mainland versus eastern off-shore islands (278 species). (c, d) For the same sets of species, Jaccard index of similarity, measuring

the overlap of a species' climatic niche in the two regions. (e, f) Climatic nestedness, i.e. the proportion of the smaller climatic niche nested within the largest. (g, h) Buffered climatic nestedness, where nestedness is calculated using climatic niches slightly enlarged to encompass neighboring climate bins.

CHAPTER 2 A consistent occupancy – climate relationship across birds and mammals of the Americas

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ABSTRACT

At broad spatial scales, species richness is strongly related to climate. Yet, few ecological studies attempt to identify regularities in the individual species distributions that make up this pattern. Models used to describe species distributions typically model very complex responses to climate. Here, we test whether the variability in the distributions of birds and mammals of the Americas relates to mean annual temperature and precipitation in a simple, consistent way. Specifically, we test if simple mathematical models can predict, as a first approximation, the geographical variation in individual species' probability of occupancy for 3277 non-migratory bird and 1659 mammal species. We find that a Gaussian model, where the probability of occupancy of a 10^4 km² quadrat decreases symmetrically and gradually around a species 'optimal' temperature and precipitation, was generally the best model, explaining an average of 35% of the deviance in probability of occupancy. The inclusion of additional terms had very small and idiosyncratic effects across species. The Gaussian occupancy-climate relationship appears general among species and taxa and explains nearly as much deviance as complex models including many more parameters. Therefore, we propose that hypotheses aiming to explain the broad-scale distribution

of species or species richness must also predict generally Gaussian occupancy-climate relationships.

INTRODUCTION

Surprisingly few ecological studies attempt to identify regularities in the organization of nature: Newtonian-style first-order laws for ecology. Ecology, and biology in general, is often perceived as being very complex and involving biological processes that are not universal (Quenette & Gerard, 1993; Beatty, 1996; Lawton, 1999) and that tend to vary through space (Jetz *et al.*, 2005) and time (Rickelfs *et al.*, 1999). Accordingly, much of ecology focuses on the intricacies and contingencies of nature: adaptations of particular species to particular environments, hyperdiversity of a taxon in a particular place, complex interspecific interactions, etc. Despite virtually no ecological laws being universal and perhaps contingencies being frequent, ecology would greatly benefit from identifying general patterns (Gaston & Blackburn, 1999; Lawton, 1999; Lange, 2005). As pointed out by Lawton (1999), a law is simply a widely observable pattern and does not need to be universal. It makes little sense to search for mechanisms and contingencies until general patterns have been identified.

Here, we are interested in broad-scale patterns describing the spatial distribution of species. Specifically we test whether a simple law, taking the form of a mathematical model, can predict, as a first approximation, the geographical variation in individual species' probability of occupancy. We are therefore purposely omitting much of the details thought to influence species' occupancy in favour of a general model.

In a previous study, we found that much of the variability in the distributions of North American tree species relates to mean annual temperature and precipitation in a quite consistent and simple way (Boucher-Lalonde *et al.*, 2012). The spatial variation in the probability of occupancy of a species was typically highly related to temperature and precipitation. A simple Gaussian function of climate, where species had a maximally occupied climate and the

probability of occupancy symmetrically decreased as the local climate increasingly diverged from this optimum, described very well the probability of occupancy of most species. This model is consistent with the hypothesis that species' occurrences are a probabilistic function of climate, with each individual species thriving at an optimal climate. This could be because climate as a strong effect on the fitness of individuals. As the climate of a region diverges from the species' optima, the fitness of individuals decreases and the species becomes increasingly likely to be excluded from the region by other constraints such as biotic interactions, extreme weather, food availability, dispersal limitation or source-sink population dynamics. In sum, a strong Gaussian occupancy-climate relationship is predicted if species are strongly limited by climate but also limited by a large number of factors affecting species multiplicatively (Brown, 1995; Boucher-Lalonde *et al.*, 2012).

Here, we ask: can most of the variability in the distributions of birds and mammals of the Western hemisphere be explained by a Gaussian response curve, as it can for North American tree species? To address this question, we test four biologically plausible hypothetical relationships between the probability of occupancy of a region by a given species and macroclimate following Boucher-Lalonde *et al.* (2012). Specifically we test and compare (1) the tolerance hypothesis where species' observed climatic niches are predicted to be almost fully occupied (Currie *et al.*, 2004), (2) the threshold hypothesis where, within climatic thresholds, species' presences are predicted to be unrelated to climate (e.g., Guisan & Thuiller, 2005), (3) the peaked suitability hypothesis where the probability of occupancy is predicted to have a Gaussian-shaped response to climate (Whittaker, 1965; Gauch & Whittaker, 1972; Austin 1980) and (4) the asymmetric limitation hypothesis where the probability of occupancy is predicted to

be skewed towards the warm and wet end of the climatic gradient (MacArthur, 1969; Kaufman, 1995; Normand *et al.*, 2009).

If the Gaussian occupancy-climate relationship that is general among North American trees (Boucher-Lalonde *et al.*, 2012) also appears to be general among birds and mammals of the Americas, the pattern could be used in the development of a predictive model of the broad-scale distribution of life on Earth. It could also be used as a secondary prediction in tests of hypotheses aiming to explain patterns in species richness (see Gotelli *et al.*, 2009). But, if species appear to respond to temperature and precipitation more idiosyncratically, then the richness-climate relationship could not be explained by a consistent occupancy-climate relationship.

METHODS

Distribution and climate data

The breeding ranges for birds and mammals of the Americas were obtained from NatureServe (Patterson *et al.*, 2003; Ridgely *et al.*, 2007) and converted into raster format. We divided the Americas into equal-area quadrats of 10,000 km² and removed those quadrats with <50% land area (Szabo *et al.*, 2009), leaving 4141 quadrats. A quadrat was considered occupied by a species when its breeding range overlapped at least partly the quadrat. The 3277 non-migratory birds and 1659 mammals with extant breeding ranges overlapping at least one quadrat were included in the study. The mean annual temperature and precipitation were obtained from the WorldClim database at a resolution of 30 arc-seconds (Hijmans *et al.*, 2005). The mean values of climate variables were calculated for each quadrat. We log-transformed precipitation because its frequency distribution is highly right-skewed, and the effects of precipitation on species' biology scale less than linearly (Holdridge, 1967; Whittaker, 1975; Boucher-Lalonde *et al.*, 2012).

Occupancy-climate models

For each species, we tested four hypothetical relationships between occupancy, here defined as the presence or absence of a given species within a quadrat, and climate (Fig. 2.1). For each hypothesized functional form, the probability of occupancy was modeled as a bivariate function of temperature and precipitation, using only quadrats that fall within the zoogeographic region(s) (Wallace, 1876) in which the species occurs. We fitted non-linear models assuming binomial error distributions using maximum likelihood and optimized with the Nelder–Mead method which allows the robust estimation of parameters in non-differentiable functions without making assumptions about the likelihood surface (Nelder & Mead, 1965). On average, species occupied 13% of the available quadrats, with a standard deviation of 0.17.

The first model (“Tolerance model”) proposes that species occur (with probability $p=1$) within a range of temperatures and precipitation, and not outside that range ($p=0$). The four fitted parameters are the minimum and maximum tolerance threshold for temperature and precipitation. The second model (“Threshold model”) proposes that the probability of occupancy within a range of tolerated temperature and precipitation is constant with $p \leq 1$ and $p=0$ outside that range. In addition to fitting tolerance thresholds on temperature and precipitation, this model adjusts a fifth parameters, the probability of occupancy within the thresholds. The third model (“Gaussian model”) proposes that the probability of occupancy is a bivariate normal function of temperature and precipitation following ter Braak and Looman (1986). This model has five fitted parameters: mean temperature and precipitation, temperature and precipitation variance of occupied areas and maximum occupancy, which can vary between 0 and 1. In this model, we also tested for a possible interaction between temperature and precipitation. The fourth

(“Skewed-normal model”) model proposes that the probability of occupancy of a species is a bivariate, skewed-normal function of temperature and precipitation. Here, the Gaussian response curve (ter Braak & Looman, 1986) is allowed to be skewed towards high or low temperatures and precipitations through modelled skewness terms (Azzalini, 1985).

For each hypothetical relationship between the probability of occupancy and climate, we calculated the total deviance, the explained deviance, and AIC. We compared each model to a null model where the probability of occupancy was constant and assumed to be unaffected by climate.

We also tested whether our relatively constrained models outperform other models. Perhaps other environmental variables or functional forms explain a higher proportion of the deviance in occupancy. To test whether our selected models fit significantly less well than models containing many other environmental variables and flexible relationships, we considered all 19 WorldClim Bioclimatic variables (Hijmans *et al.*, 2005) listed and described at <http://www.worldclim.org/bioclim>. For each species, we fitted occupancy as a function of the 19 variables through a generalized linear model (GLM) as well as through a generalized additive model (GAM). Both GLMs and GAMs are frequently used in species distribution models, and GAMs are among the best performing (Guisan *et al.*, 2007). For both GLMs and GAMs, we then used automated model selection to eliminate variables and retain a simplified model. For GLMs, we used both forward and backward selection based on AIC using the MASS package in R (Venables & Ripley, 2002). For GAMs, we used the defaults from the gam function in the mgcv package in R, but we added an extra penalty to each term so that it can be penalized to zero to allow terms to be entirely excluded from the models (Wood, 2011). For each species, we then

compared the explained deviance of the GLM and GAM to the explained deviance of our fitted climatic models.

RESULTS

The tolerance model was typically a very poor descriptor of species' occupancy. For 72% of species, the null model assuming that occupancy does not vary with temperature and precipitation explained as much of the deviance in occupancy (Fig. 2.2). The threshold model explained more of the deviance in occupancy, although still no better than the null model for 30% of species (Fig. 2.2). The Gaussian model, where occupancy is a bivariate normal function of temperature and precipitation, explained, on average, 35% of the deviance in occupancy and >50% of the deviance for 24% of species, but no more than the null model for 3% of species (Fig. 2.2). The skewed-normal model explained, on average, 36% of the deviance in occupancy (Fig. 2.2). The null model had the highest explained deviance mostly for extremely rare species: 82% occupied fewer than 10 quadrats.

Out of the hypothetical models here considered, the skewed-normal model was most often considered the best based on AIC (Table 2.1). However, averaged over all species, it increased the explained deviance by <1% compared to the Gaussian model. This is because, for most species, the statistical power to detect very small increases in explained deviance is very high. We therefore also based our model selection on explained deviance. Specifically, we considered that the 'best' model should increase the explained deviance by at least 1% per extra parameter. Doing so, we find that the Gaussian model is generally the best (Table 2.1). The Gaussian model is then selected as the 'best' for 69% of species versus 23% for the skewed-

normal model. Using this method, the tolerance and threshold models were selected as the 'best' models for 3% and 5% of species respectively.

The relationship between occupancy and climate (here, temperature and precipitation) was typically only very weakly skewed. But, most importantly, it was skewed towards low (cold and dry) and (hot and humid) climates nearly equally often (Fig. 2.3). The asymmetric limitation hypothesis predicts that species occupancy-climate relationships will typically be positively skewed, i.e. towards high temperatures and precipitations. For temperature, we find that this is the case for 65% of species, and typically very weakly so such that the skewness term, averaged over all species, is negative ($p < 0.01$). For precipitation, the skewness term is positive, as predicted, for 55% of species but skewness averaged over all species is not significantly different from 0 ($p = 0.45$).

Similarly, although an interaction between temperature and precipitation often explained a detectable amount of the deviance, its inclusion typically resulted in only a minuscule increase in explained deviance, and the sign of the interaction term was highly variable among species (Fig. 2.3). There was a slight tendency for positive interactions; 53% of species had positive interaction terms and the mean value for the interaction term among species was 0.08 ($p < 0.01$). In other words, the favourability of the environment with respect to one variable is largely independent of the favourability of the environment with respect to the other.

Allowing the inclusion of many additional variables and much more flexibility in the functional form resulted in only very small increases in explained deviance in occupancy relative to the Gaussian model. The selected GLMs and GAMs of occupancy as a function of climate, reduced from the 19 WorldClim Bioclimatic variables, nonetheless contained a high number of parameters. Averaged over all species, GLMs and GAMs had an effective number of parameters

of 13.6 and 17.9, respectively. GLMs and GAMs explained an average of 33.9% and 34.3% of the deviance in occupancy across species (Appendix S2.1). In fact, the explained deviance of GLMs and GAMs are correlated with an $r > 0.99$ such that including many additional climatic variables does capture some deviance, irrespective of the specific functional form. Although the AIC of both GLMs and GAMs are lower than that of the Gaussian models for 98% of species, the average increase in explained deviance are typically extremely small. Compared to Gaussian models, these much more complex models increase the explained deviance in species' occupancy by an average of only 1.4% for GLMs and 1.7% for GAMs (Appendix S2.1). Even when we only consider the cases where $\Delta AIC > 10$ such that the Gaussian model is deemed of much lower quality, we observe that GLMs increase the explained deviance of 4686 species by an average of only 1.5% (or 0.11% per extra parameter) while GAMs increased the explained deviance of 4705 species by an average of 1.8% (or 0.099% per extra parameter). We therefore consider that models including many more climatic variables (temperature and precipitation for the Gaussian model versus a potential of 19 bioclimatic variables for GLMs and GAMs) and allowing much flexibility in the relationships in the case of GAMs did not result in meaningful increases in explained deviance in occupancy.

Independently of the specific model selected, we observe that the vast majority of species have a large number of quadrats that are unoccupied but equally suitable, in term of mean annual temperature and precipitation, to those that are occupied. These patches of unoccupied but apparently suitable climates are typically directly adjacent to the occupied species range (Fig. 2.4); barriers to dispersal are not an obvious explanation. In fact, the unoccupied quadrats directly adjacent to occupied quadrats had significantly lower average probability of occupancy than within the species range for only 1.7% of species (one-tailed t-test, $p < 0.05$).

DISCUSSION

We have here found that, as a first approximation, the probability of occupancy of a quadrat (i.e., a 10^4 km^2 region) by a species of bird or mammal in the Americas can be described by a bivariate Gaussian function of temperature and precipitation. This response curve also generally explained the spatial variation in occupancy of North American trees well (Boucher-Lalonde *et al.*, 2012). Although the model poorly fits occupancy for some species, it explains much of the deviance in occupancy for the majority of species. Moreover, the Gaussian model typically shows little lack-of-fit, compared to the tolerance and threshold models. Adding additional terms such as an interaction between temperature and precipitation or a skewness term for temperature and precipitation, almost never resulted in a biologically meaningful increase in explained deviance (i.e. $>1\%$). Moreover, the sign of these terms are extremely variable among species, such that no general law emerges.

A Gaussian occupancy-climate relationship with mean annual temperature and precipitation as the independent variables appears to capture most of the variability in occupancy that can be explained by macro-climate. We found that including many more climatic variables and allowing flexible functional forms typically resulted in only very small increases in explained deviance. Our rather tightly constrained Gaussian models, relative to models with great flexibility and lots of predictor variables, are much simpler and consistent among species.

Ecologists have used Gaussian or Gaussian-like models to describe the distribution of species in relation to environmental variables for decades (Gauch & Whitakker, 1972; Austin, 1985; ter Braak & Looman, 1986; Pigot *et al.*, 2010). However, more recently, much more complex functions have been used. This is exemplified in the species distribution modelling

literature where automated processes are often used to fit several, often complex, models and select the best (based on AIC or else) to relate species presences to the environment (e.g., Artificial Neural Nets, MaxEnt, Boosted regression trees). These methods typically result in the selection of complex and highly species-specific occupancy-climate relationships (Elith *et al.*, 2011). Although these may give a marginally better description of species occupancy-climate relationships, they cannot be used to make predictions across sets of species, and they can have biologically implausible (or simply non-specified) response shapes.

A Gaussian relationship between occupancy and climate may reflect a biological mechanism. The fitness of a given species could be normally related to climate with species thriving at an optimal climate (McInerny *et al.*, 2009; Nogués-Bravo, 2009). If many factors, including climate, affect fitness and their effects are multiplicative (Brown *et al.*, 1995), we would expect the occupancy-climate relationship to be Gaussian just like the fitness-climate relationship. Under this hypothesis, as the climate of a region becomes increasingly divergent from the species' optimum, the stress imposed on the individuals increases. Hence, the probability that other factors prevent the species from occupying the region increases proportionally. These other limits on species' ranges can be multiple: food and resource availability, competition and predation pressures, weather and extreme climatic conditions, etc. The climatic breadth between a species' optimum and a near-zero probability of occupancy could be determined by its physiological tolerance. Species that occupy a large range of temperatures also tend to occupy a large range of precipitations and they also tend to have a high maximum occupancy (Appendix S2.1). But some species have a low probability of occupancy, even at their climatic optima. This could indicate that the climatic constraints on their range are relatively small compared to other limiting factors. Because we find that species' ranges are almost always

surrounded by unoccupied but climatically suitable areas, some of the other important factors affecting occupancy should be spatially structured.

Alternatively, the Gaussian relationship between occupancy and climate we have here observed may not be driven by a mechanistic link between climate and occupancy. Climate is highly spatially structured. Species ranges are also highly spatially cohesive. It is typically assumed that the former causes the latter (Diniz-Filho *et al.*, 2003). However, if factors other than climate, such as intrinsic dispersal limitation, cause the cohesiveness in species ranges, we would nevertheless observe that occupancy is highly correlated with climate (Bahn & McGill, 2007; Beale *et al.*, 2008a). A Gaussian occupancy-climate relationship with unoccupied but similar climates directly adjacent to occupied climate could be observed even without a causal relationship between occupancy and climate. However, in addition to being highly correlated with climate (Root, 1988; Sexton *et al.*, 2009), species ranges also appear to track temporal changes in environmental conditions (Parmesan *et al.*, 2006; Kharouba *et al.*, 2009; Tingley *et al.*, 2009; but see Boucher-Lalonde *et al.*, 2014a). Moreover, variation in bird species range shapes are better explained by mean annual temperature and precipitation than by a model that only assumes stochastic dispersal (Pigot *et al.*, 2010). Similarly, for North American mammals (but not for North American birds) variations in range shapes are better predicted by a climatic determination model than by intrinsic dispersal limitation (Baselga *et al.*, 2012).

Whether the Gaussian occupancy-climate relationship reflects a causal relationship or not, it appears to be general among species and taxa such that it is a predictable pattern that can be used to test hypotheses. Gotelli *et al.* (2009) proposed that, when testing competing hypotheses to explain the richness-climate relationship, predictions of secondary patterns, such as the turnover in species composition, should also be derived and tested to strengthen tests and

reject alternative hypotheses. We believe that mechanisms that predict a strong richness-climate relationship but do not predict Gaussian occupancy-climate relationships should be rejected. Prima facie, this is inconsistent with the “Tolerance”-type hypothesis of Kleidon and Mooney (2000), which proposes that species persist in areas where their net productivity is positive. Similarly, it seems unlikely that species’ distributions are more limited by abiotic factors on the climatically severe limits of their distribution, and by biotic interactions at the climatically benign side. Contrary to predictions (Kaufman, 1995; Normand *et al.*, 2009), the occupancy-climate relationship is not generally skewed towards high temperatures and precipitations.

We suggest the Gaussian occupancy-climate relationship is general enough across species that it should be used as a secondary pattern to test alternate hypotheses that aim to explain the broad-scale distribution of species. Hypothetical mechanisms should also account for the fact that the unoccupied portions of the climatic niches are typically spatially aggregated all-around the species’ range. We propose that these patterns could be generated by an equilibrium between extinction and colonization rates. The climate in a species’ range could affect the probability of local extinctions in an area and/or the probability of colonization of surrounding areas. For example, extinction rates could be positively related to the climatic distance from a species’ optimal climate. Meanwhile, colonization rates could be negatively related to the geographic distance to occupied regions but positively related to the abundance of the species in these occupied regions. Elsewhere, we sought climate-dependent local extinction probabilities in North American birds, but we only detected weak effects that were highly variable among species (Boucher-Lalonde *et al.*, 2013). We suggest that similar mechanisms that predict Gaussian occupancy-climate relationships should be empirically tested.

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TABLES

Table 2.1 Number of species for which each of the models considered is the best model based on AIC and on explained deviance, i.e. for which each extra parameters adds >1% of explained deviance.

	AIC		Explained deviance	
	Birds	Mammals	Birds	Mammals
Null model	148	109	NA	NA
Tolerance model	598	419	85	63
Threshold model	274	184	145	113
Gaussian model	1086	426	2302	1104
Skewed-normal model	1171	521	745	379

FIGURES

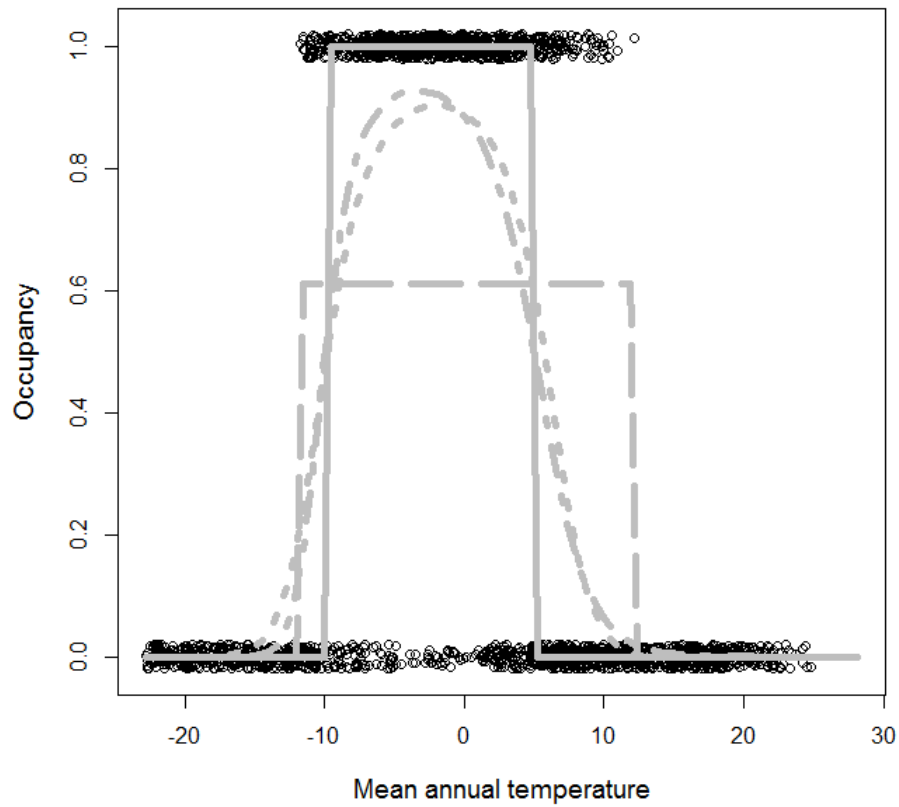


Figure 2.1 Occupancy of the Gray jay (*Perisoreus canadensis*), here shown as an example species, as a function of mean annual temperature (°C) in 10,000 km² quadrats in the Americas. Occupancy, measured as the presence (occupancy= 1) or absence (occupancy= 0) of the species within a quadrat, values have here been jittered by 0.1 for a better depiction of the frequency distribution of existing temperature (here, n= 2221). Only absences within zoogeographic regions in which the species occurs are included in the analysis. The fitted relationships for the four hypothetical models relating occupancy to climate that we test in the main text are here represented; the tolerance model (solid line), the threshold model (dashed line), the Gaussian model (dotted line) and the skewed-normal model (dot-dashed line). The models presented here in univariate space were fitted as a function of both temperature and log₁₀(precipitation) in mm.

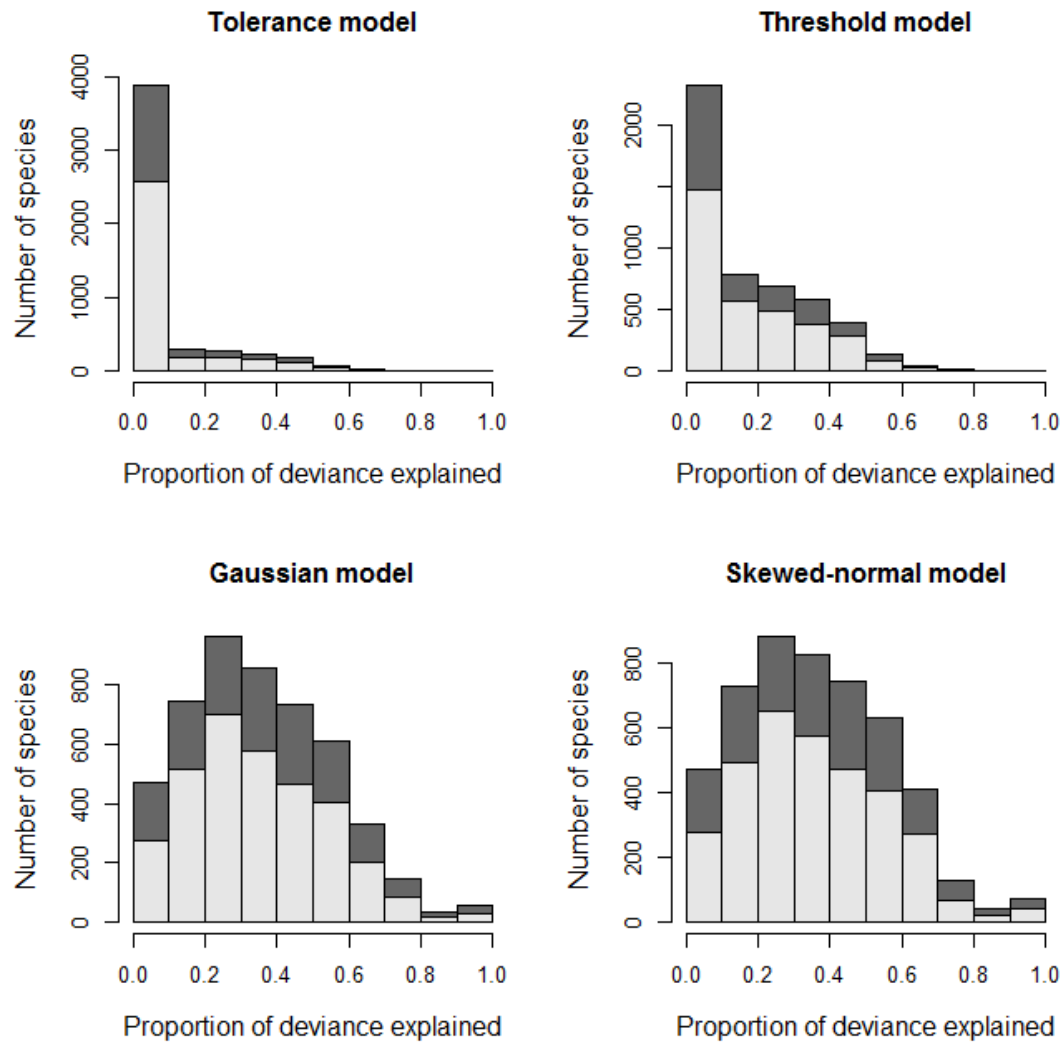


Figure 2.2 Frequency distribution of the proportion of deviance explained by the four tested models of occupancy as a function of temperature and precipitation for species of birds (light bars) and mammals (dark bars). The bars for birds and mammals are stacked such that the height of the bar represents the total number of species of both taxa. The threshold model is a modification of the tolerance model that includes an extra term such that, by definition, it must explain at least as much deviance in occupancy then the tolerance model. The skewed-normal model is a modification of the Gaussian model that includes an additional skewness term for temperature and for precipitation.

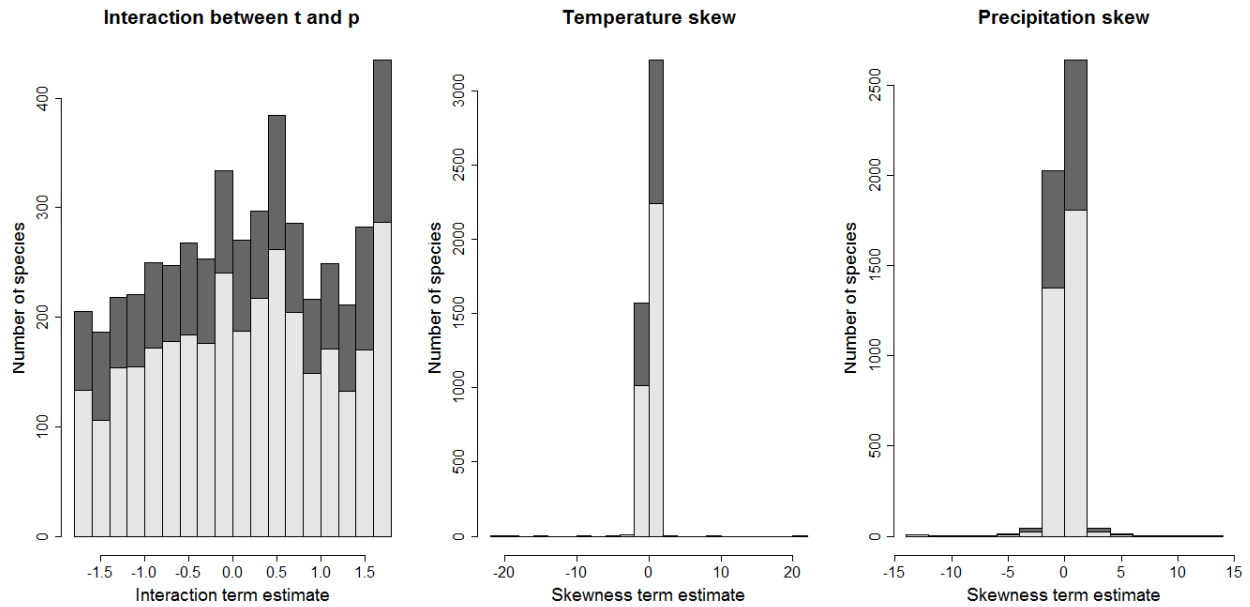


Figure 2.3 Frequency distribution among species for the estimates of the interaction between temperature and precipitation, the skewness of temperature and the skewness of precipitation. In all cases, the distribution of parameters has been standardized to a variance of 1. A positive interaction occurs when, as temperature increases, higher occupancy is achieved at higher precipitation. Inversely, a negative interaction occurs when, as temperature increases, higher occupancy is achieved at lower precipitation. A positive skewness term represents a right-skewed distribution, i.e. one with a longer tail at high values of temperature or precipitation and a sharper decline in occupancy at low values, while a negative interaction terms represents left skew. Across species, both the interaction and skewness terms are about as frequently positive than negative.

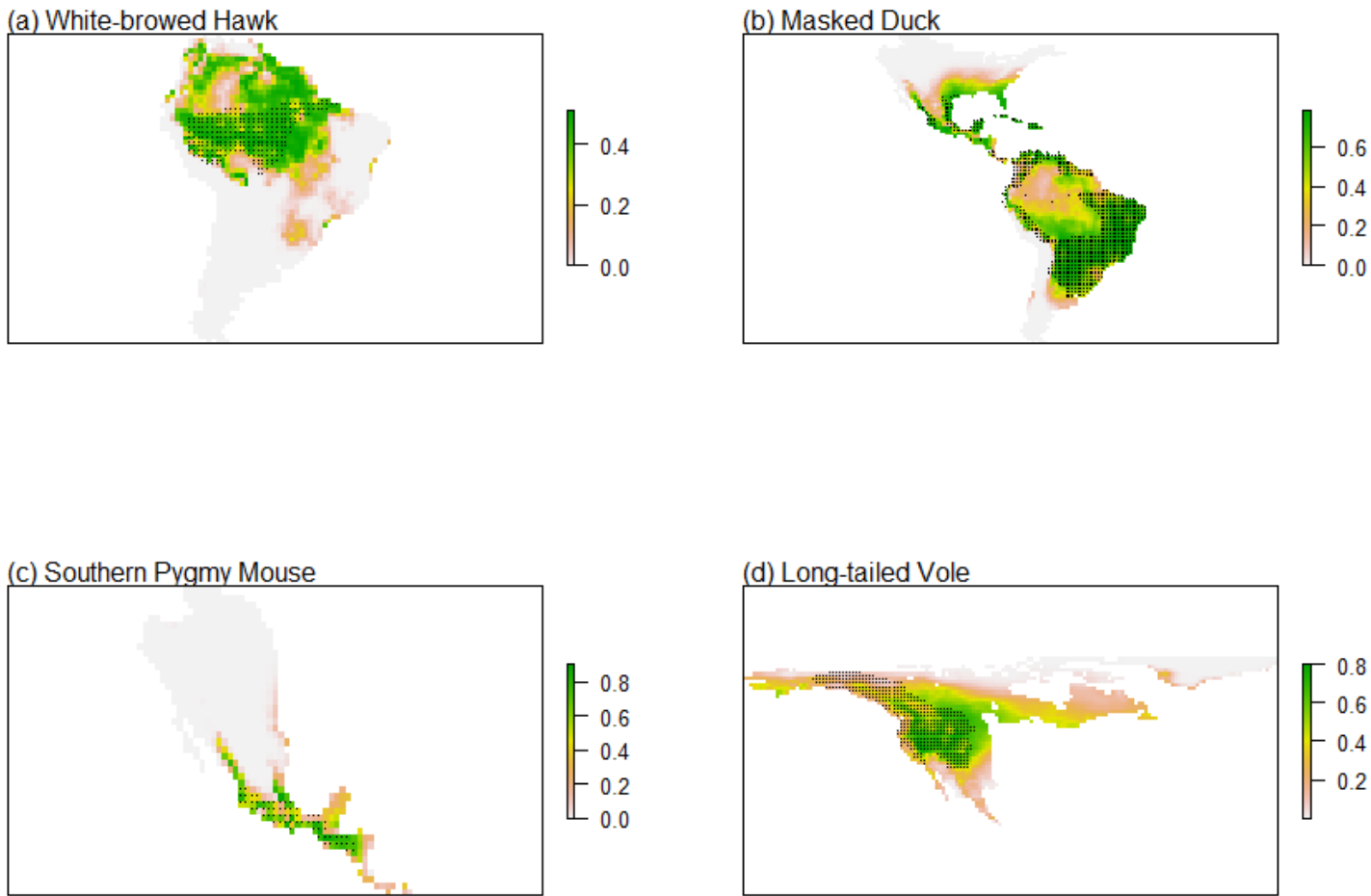


Figure 2.4 Predicted probability of occupancy estimated from the Gaussian occupancy-climate model and which can vary from zero (in gray) to one, within the zoogeographical region in which the species is present. Four example species are presented; (a) White-browed Hawk (*Leucopternis kuhli*); (b) Masked Duck (*Nomonyx dominicus*); (c) southern pygmy mouse (*Baiomys musculus*); and (d) long-tailed vole (*Microtus longicaudus*). The probability of occupancy of each 10 000 km² quadrat was fitted by a bivariate normal function of mean annual temperature (°C) and the log of precipitation in mm. Occupied quadrats are here marked with a black point.

CHAPTER 3 Can the richness–climate relationship be explained by systematic variations in how individual species’ occurrences relate to climate?

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ABSTRACT

Aim At large spatial extents, species richness of high-level taxa is generally strongly positively correlated with temperature and precipitation, and consistently so across space and time. Here, we test whether this richness–climate relationship is driven by systematic associations between climate and characteristics of individual species’ geographic ranges. Specifically, we test the hypotheses that spatial variations in richness are driven by variations in species’ mean range size, climatic niche-breadth, climatic range filling, frequency distribution of climatic niche position and/or frequency distribution of extant climatic conditions.

Location Americas

Methods We tested hypothetical effects of climatically-constrained ranges on species richness using the breeding ranges of 3277 birds and 1659 mammals. We tallied species richness in 10^4 km² quadrats in the Americas, as well as summary statistics describing the geographic ranges and climatic niches of the species occurring in each quadrat. We then used regression models to relate species richness to those characteristics.

Results We found that species' mean range size, climatic niche-breadth and range filling were generally, but inconsistently, negatively related to species richness. As predicted, species richness per quadrat increased with the number of species having their climatic niches centered in the climatic conditions of the quadrats and with the geographic extent of those conditions, although these relationships were relatively weak.

Main conclusion The richness–climate relationship appears largely decoupled from systematic variations in characteristics of species' climatic niches. Species generally have larger geographic ranges, wider climatic niches and higher range filling in species-poor areas, each of which, all else being equal, should generate a richness–climate relationship inversed from what we observed in nature. More species have their ranges centered on warm, wet and common climatic conditions. However, temperature and precipitation variables themselves explain substantially more of the variance in species richness than characteristics of species' climatic niche.

INTRODUCTION

At large spatial extents, species richness is strongly related to climate for virtually all higher-level taxa, such that the warmest and wettest regions on Earth typically harbour orders of magnitude more species than the coldest or driest regions. At large geographic extents (continents) and coarse grains (e.g. 10^4 km^2), the strong richness–climate relationship is congruent across time, from seasons to millennia (Yasuhara *et al.*, 2012; Boucher-Lalonde *et al.*, 2014a; Vazquez-Rivera & Currie, 2015), and space, from regions to globally (Francis & Currie, 2003; Hawkins *et al.*, 2003; Field *et al.*, 2009). Yet, the mechanism(s) underlying this ubiquitous relationship are still contentious (Rabosky, 2009; Brown, 2014).

The size of species geographic ranges, as well as the characteristics of species' realized climatic niches, also varies geographically. For example, at broad spatial scales, there is a general tendency, “Rapoport’s rule” (Stevens, 1989), of an increase in mean range size with latitude. The pattern is however far from universal, and appears mostly restricted to the Northern Hemisphere (Gaston *et al.*, 1998; Orme *et al.*, 2006). The different hypothetical mechanisms that have been proposed to explain large scale variations in range size, including Rapoport’s rule, typically invoke an effect of climate on individual species’ distributions. Harsh or temporally variable climates are hypothesized to favour species with large climatic niche breadth (Janzen, 1967; Stevens, 1989) or high dispersal ability, allowing them to occupy wider geographic ranges (Svenning *et al.* 2008; Baselga *et al.*, 2012). Climatic harshness is often defined by low temperatures and water availability (Currie *et al.*, 2004; Adams, 2009), since fewer physiological combinations would allow the maintenance of populations in such conditions (Kleidon & Mooney, 2000) and fewer species are adapted to cold or dry environments (Adams, 2009; Araújo *et al.*, 2013).

Since species richness as well as the characteristics of the geographic ranges of species both show strong spatial variations that are hypothesized to be largely climate-driven, we ask: Could richness–climate relationships occur largely as a consequence of the effect of climate on the geographic ranges of individual species (Fig. 3.1)? Perhaps richness is climate-limited merely as a consequence of individual species’ probabilities of occurrence being climate-limited (see Boucher-Lalonde *et al.*, 2014a). Indeed, the niche concept unifies many ecological and evolutionary hypotheses aiming to explain richness gradients (Lamanna *et al.*, 2014). A plethora of hypotheses either assume or predict that spatial variations in species richness arise from systematic variations in the mean characteristics of species niches, e.g. higher niche packing (Lamanna *et al.* 2014), smaller niche breadth (Stevens 1989), lower (Schemske *et al.* 2009) or higher (Svenning *et al.* 2008) filling of the potential abiotic niche have all been hypothesized to increase species richness. Different hypotheses sometimes assume contradictory relationships between richness and species’ niche characteristic (examples below). And, although relationships between species’ climatic niches and richness gradients are a common theme in the literature, few have explicitly tested whether richness gradients can be predicted by variations in species’ mean niche characteristics (see Orme *et al.*, 2006; Weiser *et al.* 2007).

Here, we derive explicit predictions regarding how spatial variations in the mean climatic niche characteristics of species could directly cause variations in species richness. We test whether species richness in 10,000 km² quadrats can be statistically explained by a positive effect of (H1) mean range size, (H2) the frequency distribution of niche position along a climatic gradient, (H3) mean climatic niche-breadth, (H4) mean climatic range filling and (H5) the frequency distribution of extant climatic conditions. We quantify the extent to which these variables can predict spatial variations in species richness; whether their predictive power holds

across taxonomic groups (birds and mammals) and continents (North and South America); and whether accounting for them reduces the residual effects of climatic variables to zero (see Table 3.1).

Most simply, (H1) increases in species' mean range size should increase species richness. This is because, all else being equal, larger ranges should overlap more, thus promoting species richness (Šizling *et al.*, 2009). This hypothesis assumes a direct causal link between range size and richness. Note that this is contrary to Stevens' (1989) hypothesis suggesting that decreased range size increases richness. In order for Stevens' hypothesis to allow species' mean range size and species richness to positively covary, an independent mechanism (e.g. increased speciation rate) that would affect both of these variables would necessarily need to be invoked since, alone, smaller species' ranges cannot be responsible for greater richness (Šizling *et al.*, 2009). Note that the relationship between richness and species' range size has already been shown to be weak and inconsistent for birds (Orme *et al.*, 2006) and plants (Weiser *et al.*, 2007), but it is still unclear the extent to which variations in range size contribute to the richness–climate relationship.

Other hypotheses propose that the richness–climate relationship arises through variation in species' climatic niche characteristics along climatic gradients (Fig. 3.2). First, (H2) warm and wet areas could be species-rich simply as a consequence of more species being able to thrive in, or having their climatic niche centered on, such conditions. For example, tropical niche conservatism proposes that the richness–climate relationship is driven by the phylogenetically conserved tolerances of species to the tropical-like warm and wet conditions in which most clades have originated (Wiens *et al.*, 2005; Romdal *et al.*, 2013). Other tolerance-type hypotheses of species richness (e.g. Kleidon & Mooney, 2000) propose that the distribution of species' niches along an environmental gradient directly drives variations in species richness.

Second, (H3) climatic niche breadth could generate the observed richness-climate relationship if species occurring in species-rich warm and wet regions generally occur in a wider range of climates, therefore enhancing the probability that those regions are occupied by many species (see Okie *et al.*, 2015). This is a possibility we here consider, despite the fact that others have argued that the richness–niche breadth relationship is actually in the opposite direction, i.e. negative (Stevens, 1989; Vazquez & Stevens, 2004; Jocque *et al.*, 2010; Chejanovski & Wiens, 2014). If niche width is actually narrower in warm wet areas (Ghalambor *et al.* 2006; Deutsch *et al.* 2008), then some other independent mechanism would have to give rise to greater richness (see Šizling *et al.*, 2009). Third, (H4) inter-specific variations in climatic range filling, the proportion of the potential climatic range that is occupied by the species (Svenning & Skov, 2004), could contribute to the richness–climate relationship if range filling decreases with decreasing temperature and precipitation. This could involve a direct causal link or be due to, for example, post-glacial migration lags (Svenning *et al.*, 2008; Normand *et al.*, 2011), assuming that cold and dry regions have generally been deglaciated more recently and have not been fully recolonized. This hypothesis predicts a positive richness–range filling relationship. Again, there is an alternate hypothesis that would predict a negative richness–range filling relationship: that favourable climates increase biotic interactions and species’ niche packing, which reduces climatic range filling (e.g. Dobzansky, 1950); however, under this hypothesis, range filling is not the direct cause of richness gradients.

Undoubtedly, more species can survive in warm and wet conditions (Adams, 2009; Araújo *et al.*, 2013), which is consistent with H2, but this need not be the primary constraint on richness (Boucher-Lalonde *et al.*, 2014a). Constraints on species occurrences are likely scale-dependent; e.g. climate may explain the absence of a species from entire regions, but not species

absences within climatically favourable regions. Thus, there could be constraints on richness more proximate than the constraints imposed by species' climatic tolerances. This is particularly plausible since many species appear to occupy only a small subset of the climates they can tolerate (see Araújo *et al.*, 2013; Gouveia *et al.*, 2014). Additionally, mechanisms predicting a strong richness-climate relationship, even when neutral (i.e. assuming all species have the same characteristics), can predict that more species' geographic ranges are centered in warm and wet conditions, but with the causal pathway in the opposite direction. For example an increased carrying-capacity (i.e. the number of individuals that can occur in a given area) could lead to an increase in species richness and consequently allow more species' to have their realized climatic niches in warm and wet areas without any climatic constraints imposed directly on species (Hurlbert & Stegen, 2014).

As such, even if there is no causal relationship between the frequency distribution of climatic niche positions and species richness, there may nevertheless be a statistical correlation. The lack of a statistical correlation would actually be surprising, but it could occur if, as proposed above, species occurring in species-rich environments generally have larger climatic niche breadth or range filling (Fig. 3.2). Finally, (H5) species richness could increase with the size of the area over which climates extend (Rosenzweig, 1995), for example, through increased diversification rates (Ricklefs, 2006), by increasing the range size of the species that occur in common conditions (Tomašových *et al.*, 2015), etc.

Our aim is to provide a test of these hypothesized causal links between species' climatic niches and richness gradients (Table 3.1). If the characteristics of species' climatic niches systematically vary along environmental gradients (e.g. Fig. 3.2), and if these relationships were similar in North and South America, then the richness–climate relationship could be simply

described as an emergent property of the climatic constraints on individual species' ranges. Alternatively, if the richness–climate relationship appears stronger than the sum of the climatic constraints on species ranges, it would be consistent with (although not a test of) the hypothesis that there are important top-down climatic constraints on richness, independent of those imposed on individual species (see Boucher-Lalonde *et al.* 2014a). Undoubtedly, factors other than macroclimate contribute to variations in species richness and to individual species' ranges (e.g. habitat, isolation, biotic interactions, history); here, we only test hypotheses that could explain the richness–climate relationship through systematic variations in the characteristics of species' ranges.

METHODS

We divided the Americas into equal-area quadrats of 10,000 km², which is roughly the effective resolution at which range maps can be considered accurate (Hurlbert & Jetz, 2007). We removed quadrats with <50% land area, leaving 4141 quadrats following Boucher-Lalonde *et al.* (2014b). A quadrat was considered occupied by a species when its breeding range at least partly overlapped the quadrat. We obtained from Nature Serve the breeding ranges of 3277 non-migratory birds and 1659 mammals breeding in the Americas (Patterson *et al.*, 2007; Ridgely *et al.*, 2007). Mean annual temperature and precipitation were obtained from WorldClim at 30 arc-seconds resolution (Hijmans *et al.*, 2005). The WorldClim data have been generated through interpolation of average monthly climate data from weather stations with at least 10 years of data between 1960 and 1990 (or up to year 2000 in some areas with few records; available at <http://worldclim.org/>; Hijmans *et al.*, 2005). Precipitation was log-transformed, following Boucher-Lalonde *et al.* (2014b) since it is strongly positively skewed, making a few quadrats

having disproportionate weight on the results, and that the effect of precipitation on species likely scales less than linearly (see Appendix S3.1 for results with untransformed precipitation). Mean temperature and precipitation were then calculated for each quadrat. Throughout the text, we therefore focus exclusively on the relationship between species richness and macroclimatic variables at coarse grains.

We measured the properties of species' realized niches as follow. Range size was simply taken to be the number of quadrats occupied by a species. We measured niche breadth as the range of occupied climate. We measured climatic range filling as the realized/potential range size ratio following Svenning & Skov (2004), where we assume that the potential range consists of all quadrats in the Americas with temperature and precipitation levels that exist somewhere within the geographic range occupied by the species. We calculated a second measure of range filling, by restricting the potential range to the zoogeographic regions (from Holt *et al.*, 2013) in which the species occur. This either had no effect on, or reduced the size of, the (unoccupied) potential range, thereby increasing estimated range filling. Across all species, the correlation between range filling calculated over the entire Americas versus within species' zoogeographic regions was high ($r = 0.81$). This choice had no effect on the qualitative patterns we observed; we therefore only present range filling calculated over the entire Americas. Niche position is the environmental centroid (Soininen *et al.*, 2011), which here is simply calculated as the mean climate of quadrats occupied by a species. We estimated the above niche properties for mean annual temperature and total annual precipitation. Temperature and precipitation are amongst the two strongest and most consistent predictors of species richness gradients (Hawkins *et al.*, 2003; O'Brien, 2006), and they are also generally strongly statistically related to the probability of

occurrence of individual species of birds and mammals at large spatial scales (Boucher-Lalonde *et al.*, 2014b).

We then tallied the number of species occurring in a quadrat to obtain species richness. We also calculated the mean and standard deviation of the range sizes of these co-occurring species. To test whether the distribution of species in climate space could give rise to patterns of species richness (see Fig. 3.2), we additionally calculated the mean climatic niche breadths and range filling of all species for which the potential range, instead of the realized range, overlapped the quadrat (results for realized instead of potential ranges were similar; see Appendix S3.1). For each quadrat, we then calculated the number of species that have their climatic niche centered on climatic conditions similar to that of the quadrat (climatic “niche position”), as well as the geographic extent of those climates throughout the Americas (climatic “availability”). To do this, we binned temperature and precipitation values. We varied bin size (by 1°C and by 0.05 log-precipitation units), and we picked (below) the bin sizes that maximised the strength of the empirical relationships between species richness and the independent variable (i.e. either frequency of climatic niche position or of extant conditions). The size of the bins did not affect our qualitative conclusions. For each quadrat, we tallied the number of species that have their climatic niche centred within 3°C and 0.5 units of the logarithm of precipitation (mm) of the climate of this focal quadrat (which represent ~6% of the range of extant temperature and precipitation in the Americas). We also tallied the number of quadrats that have climatic conditions within 3°C and 0.15 units of the logarithm of precipitation (mm) of the focal quadrat (as a measure of the commonness of the climate). Because areas with similar climates may be separated by large distances, we also considered the possibility that richness in a given quadrat depends upon the number of quadrats with similar climates within a distance X of the focal

quadrat. We allowed distance X to vary between 1 000 km and 15 000 km by intervals of 1 000 km. Restricting our measure of climatic availability to these distance classes did not affect our qualitative conclusions, so we only present results for the availability of conditions within the entire Americas.

We used ordinary least square models (OLS) to test whether species richness is related to spatial variations in range size, climatic niche breadth, range filling, the frequency of climatic niche position and the frequency of extant climatic conditions. Because some degree of spatial autocorrelation always remained in the residuals, we also used simultaneous autoregressive error models (SARs) following Kissling & Carl (2008), which removed this residual spatial autocorrelation. All statistical analyses were carried in R 3.1.0 (R Core Team, 2014) using the *nnls* (Mullen & Stokkum, 2012), *spdep* (Bivand *et al.*, 2013) and *ncf* (Bjornstad, 2013) packages.

RESULTS

Bird and mammal species richness are strongly related to temperature and precipitation throughout the Americas (Table 3.2; Fig. 3.3). Together, temperature and precipitation explain 83% of the variance in bird and 73% in mammal species richness (Table 3.2). This richness–climate relationship is similar, although statistically distinguishable, for North and South America (see also Francis & Currie 2003; Boucher-Lalonde *et al.* 2014a). Here, allowing the coefficients of the relationship to vary by continent increases the explained variance in richness by 7% for birds and 5% for mammals. Below, we tested whether this richness–climate relationship could be explained by the distribution of individual species' climatic niche and geographic range size.

First, if high species richness per quadrat is primarily a consequence of an increased probability of range overlap due to increased mean range size, then geographical variations in richness must be positively correlated with the mean range size of species occurring in the region (H1). In our data set, like elsewhere (Jetz & Rahbek 2002), large-ranged species contribute substantially more to the overall richness gradient than do small-ranged species (Fig. S3.3). However, total species richness is generally negatively correlated with the mean range size of species occurring in the quadrat (Table 3.2, Fig. 3.4a and 3.5a). Thus, although small-ranged species contribute little to the overall richness gradient, they can substantially reduce the mean range size of species in species-rich areas. This is the case in North America; the average range size of both birds and, to some extent, mammals decreases with species richness ($R^2 = 0.59$ for birds and 0.07 for mammals). In South America, the relationship is positive ($R^2 = 0.17$ for birds and 0.45 for mammals), thus in the direction predicted from H1, but irregularly shaped (see also Orme *et al.*, 2006; Weiser *et al.* 2007).

If spatial variation in mean climatic niche breadth (H3) or range filling (H4) generate the richness–climate relationship, then species richness must be positively related to spatial variation in these variables (Fig. 3.2), and consistently so between continents. Rather, the relationships were generally negative (Table 3.2, Fig. 3.4b-d and 3.5b-d). Specifically, species richness systematically decreases with mean temperature niche breadth (Fig. 3.4b and 3.5b). For precipitation niche breadth, the relationship was very weakly positive (direction consistent with H2) in North America ($R^2 = 0.002$ for birds and 0.13 for mammals), but was negative in South America (Fig. 3.4c and 3.5c). Species richness increases with mean range filling (direction consistent with H3) only in South America, and only weakly ($R^2 = 0.20$ for birds and 0.03 for

mammals); the relationship is inversed in North America ($R^2 = 0.24$ for birds and 0.66 for mammals; Fig. 3.4d and 3.5d).

Of all predictor variables of richness we considered (H1-H5 in Table 3.1), temperature niche breadth was the strongest predictor of bird richness and the second strongest predictor of mammal richness (Table 3.2), approaching the variance in richness that can be attributed to mean annual temperature. The strong negative relationship was also roughly consistent between continents (Fig. 3.4b and 3.5b). Most of the explained variance in richness could be equally attributed to either the mean temperature niche breadth of species or to the mean annual temperature of the quadrats. When these two variables are included together, the marginal effect of temperature niche breadth (0.05 for birds and 0.01 for mammals) and of mean annual temperature (0.08 for birds and 0.07 for mammals) were both small.

As expected, a generally increasing number of species have their climatic niches centered on warmer and wetter conditions (H2). Accordingly, species richness per quadrat is positively related to the number of species that have their climatic niche positioned in a climate similar to that of the quadrat, especially for temperature (Fig. 3.4e-f and 3.5e-f). However, the relationship is not congruent between continents, with South American quadrats systematically having higher richness than in North America, after accounting for the number of species with their climatic niches centered on a given climate (Fig. 3.4e-f and 3.5e-f), such that models fitted in one continent have no predictive power in the other continent ($R^2 \leq 0$, where $R^2 = 1 - \frac{SS_{residuals}}{SS_{total}}$ and SS_{total} is calculated from the mean richness in the continent and $SS_{residuals}$ is calculated for the regression model fitted in the other continent). Temperature and precipitation variables themselves explain much more variance in species richness than does climatic niche position (Table 3.2). Moreover, the marginal effect of climatic niche position becomes negligible once we

account for the main effect of temperature or precipitation (Table 3.2). In contrast, the effect of temperature and precipitation is relatively high after having accounted for the frequency of climatic niche positions. Specifically, while temperature and frequency of temperature niche position together explain 82% and 70% of the variance in richness for birds and mammals respectively, 20% (birds) and 17% (mammals) is uniquely explained by temperature while <1% by the frequency of temperature niche position. Similarly, while precipitation and the frequency of precipitation niche position together explain 48% of the variance in bird and 47% in mammal richness, 6% (birds) and 17% (mammals) is uniquely explained by precipitation while <1% (birds) and 3% (mammals) can be uniquely explained by precipitation niche position.

Warm and, to some extent, wet climates (when precipitation is log-transformed) also tend to span larger areas in the Americas than cold or dry climates (Fig. S3.4). Therefore, total species richness in a climatic bin can also be statistically related to the total area span by the climatic conditions (H5). But, the relationship is strong only for temperatures with relatively small geographic extents, and it is only weakly congruent between continents (Fig. 3.4g-h and 3.5g-h). Throughout the Americas, the number of quadrats in a given temperature bin steeply increases with temperature up until mean annual temperatures of roughly 20°C: particularly rare climatic conditions are also particularly harsh. And, temperature and precipitation explain more variance in species richness than the total area over which they extend (Table 3.2). The effect of temperature and precipitation area also becomes negligible once included along with climate as a covariate in the model (Table 3.2), while the marginal effect of climate remains relatively large (marginal $R^2 = 0.15$ for birds and 0.11 for mammals, $p < 0.001$).

For all models of richness considered (see Table 3.1), strong spatial autocorrelation remained in the residuals. Accounting for spatial autocorrelation in the first-order neighbouring

grid cells through SAR error models eliminated spatial autocorrelation in the residuals. The SAR models explained nearly all of the variance in richness, with Nagelkerke pseudo- R^2 of 0.99 for bird and 0.98 for mammal richness in all models; nearly all of the variance could be attributed to spatial structure in the spatially dependent error term. This spatial autocorrelation is very likely inflated here due to our use of range maps which were constructed by spatial interpolation. The standardized coefficients of the various predictor variables (Table 3.2) estimated from OLS and SAR models were highly correlated ($r=0.8$), although coefficient shifts did occur (see Bini *et al.*, 2009). Model choice did not affect our conclusions. We present results from OLS models which allowed straightforward variance partitioning. Note that richness was not generally more strongly, nor more consistently, related to the standard deviation than to the mean niche characteristics (Fig. S3.5).

DISCUSSION

A strong and consistent richness–climate relationship at coarse grains and large spatial extents (Fig. 3.3) could, in principle, arise because the characteristics of individual species’ geographic ranges are strongly related to climate (Fig. 3.1, 3.2; Stevens, 1989; Morueta-Holme, 2013). However, we did not find strong evidence that this is the case (Table 3.1). We conclude that richness patterns are not determined by aggregating the niche characteristics of sets of species under none of the hypotheses we here considered. Moreover, to generate the observed richness gradients in a simple and direct way, mean range size, climatic niche breadth and range filling would need to be positively related to richness, but we generally observed the opposite trend, although inconsistently. Thus, the observed spatial variations in mean range size, climatic niche breadth and range filling should, by themselves, cause an inverse richness–climate relationship.

Alternative hypotheses could explain the generally negative empirical relationships between richness and range size, climatic niche breadth and range filling. In particular, harsh, temporally variable climates, could select for species with large climatic niche breadth and large geographic ranges, whereas the more temporally stable climates of the tropics could select for small-ranged specialists (Janzen, 1967; Quintero & Wiens, 2013; Morueta-Holme *et al.*, 2013), creating strong physiological barriers to dispersal which would enhance allopatric speciation (Janzen, 1967) and/or reduce extinction rates (Jocque *et al.*, 2010). This could explain the observed negative relationships between richness and both mean range size and climatic niche breadth. However, the effect of climate per se remained non-negligible after having accounted for these niche characteristics, suggesting an independent effect of climate on richness. And, although the relationship between richness and mean range size is inconsistent (see also Gaston *et al.* 1998; Orme *et al.*, 2006; Weiser *et al.*, 2007; Morueta-Holme *et al.*, 2013), we note that the negative relationship between richness and temperature niche breadth was indeed consistently strong, which would deserve tests of potential underlying mechanisms. There are also alternative hypotheses that could explain a negative relationship between richness and species' range filling. In particular, tropical-like climates could offer more exploitable niche dimensions, create higher niche packing or be home to stronger biotic interactions, which could lead to both higher species richness and lower range filling of any given climatic axis (Dobzhansky, 1950). But, these hypotheses imply that another mechanism affects both richness and range filling, not that they are directly linked.

We did find that more species have their climatic niches centered towards warmer and wetter conditions. Yet, niche position alone is insufficient to account for the empirical richness–climate relationship. The fact that the richness–climate relationship is stronger than predicted

from the sum of species' climatic niche positions, suggests that climate somehow (directly or indirectly) imposes an additional constraints on species richness. Moreover, there is evidence inconsistent with the hypothesis that niche position imposes a primary constraint on richness: species' realized climatic niches can vary substantially through time (Veloz, *et al.* 2012; Ordonez, 2013; Boucher-Lalonde *et al.*, 2014a) while richness tracks temporal changes in climate much more closely (Boucher-Lalonde *et al.*, 2014a; Vazquez-Riviera & Currie, 2015).

Species richness in a quadrat generally increased with the geographic extent of similar climatic conditions throughout the Americas. However, the effect of area on species richness became negligibly small once we accounted for the much larger effect of climate per se. Thus, it seems unlikely that the tropics are species-rich mainly because they extend over large geographic areas (Rosenzweig, 1995). Fine & Ree (2006) and Jetz & Fine (2012) have shown that the area occupied by a biome integrated over geological time is a good predictor of biome-level species richness. Biomes that have extended over broad areas for long periods of time presumably have experienced higher net diversification, and more species are now adapted to their environments (Fine & Ree, 2006; Jetz & Fine, 2012). This hypothesis surely merits attention, although it is still unclear whether such a mechanism could explain spatial variations in species richness at finer spatial grains (e.g. 10^4 km^2 in this study).

Our results are inconsistent with an effect of climate on species richness mediated by an effect of climate on simple characteristics of individual species ranges and suggest either a direct effect of climate on species richness, or an indirect effect mediated through other variables. A strict ecologically determined carrying-capacity on species richness also seems highly unlikely because communities are not saturated with species (Wiens, 2011): invasive species (Sax & Gaines, 2008) and experimental species introductions (Menéndez *et al.*, 2006) frequently

increase species richness, and richness appears to be moderately increasing over evolutionary time-scales (Cornell, 2013). Nevertheless, it is possible that climate sets an equilibrium limit on regional species richness, independently of the factors that affect the composition of species assemblages (Rabosky, 2009; Boucher-Lalonde *et al.*, 2014a, Hurlbert & Stegen, 2014). For example, climate could affect the equilibrium between species' local extinction and colonization rates (Boucher-Lalonde *et al.*, 2014c) or the minimum population size of species in the community (Walker, 2013). Historical and evolutionary variables such as time for diversification, diversification rates, or niche conservatism are also widely regarded as potentially important variables to explain current large-scale richness gradients (Mittelbach *et al.*, 2007; Stevens, 2011; Rolland *et al.*, 2014). It is also possible that the apparent effect of current climate on species richness partly reflect collinearities with other variables that affect species richness such as temporal stability in conditions, trophic stability, historical climate, etc. (Gouveia *et al.* 2013; Valentine & Jablonski, 2015). Thus, although we found that the richness–climate relationship is not directly mediated through an effect of climate on the mean characteristics of species' ranges, it is possible that other variables mediate the richness–climate relationship itself and/or that climate affects species ranges in more complex ways or along with other important factors.

An important caveat to our conclusions is that, as in other studies (e.g. Svenning & Skov, 2004), potential range was estimated from observed geographic ranges. The macroclimatic conditions occupied by the species may however poorly reflect the species' temperature and precipitation tolerances (Gouveia *et al.*, 2014). Although physiological tolerance and realized climatic ranges are at least moderately positively correlated for plants and insects (Hawkins *et al.*, 2014; Hoffmann *et al.*, 2012; Nogués-Bravo *et al.*, 2014), this is not necessarily the case in

other groups, including birds and mammals (see Sunday *et al.*, 2011; Araújo *et al.*, 2013). It is therefore possible that we have here simply failed to measure species' climatic niches in a biologically meaningful way. However, for this to have affected our conclusions there would need to be strong, systematic biases in the unoccupied portions of a species' physiologically suitable climates that we failed to include in our measure of potential range. For example, migration-lags could have excluded many species from all cold regions, leading to low range filling and therefore low species richness in these regions (Svenning *et al.*, 2008); but, being entirely unoccupied, these cold regions would not have been considered part of the species' potential range. If this were the case, it would inflate our measured range filling in cold regions and eliminate what would have otherwise been a strong positive richness–range filling relationship. We cannot eliminate this possibility here. That being said, measuring realized niches is the most common technique to estimate species' climatic niche (Early & Sax, 2014), and has been used to support a variety of hypotheses (e.g. Slatyer *et al.*, 2013; Nogués-Bravo *et al.*, 2014), including the hypothesis that low range filling is caused by high post-glacial migration lags (Normand *et al.* 2011). Alternative methods to measure the climatic niche also have major caveats: physiological tolerance data are scarce and in-lab measurements may poorly translate to natural environments (Hoffmann *et al.*, 2013); occurrences points are not as comprehensive and can be biased (Barry & Elith, 2006).

In conclusion, the richness–climate relationship does not appear to be primarily driven by systematic variations in simple metrics of species' geographic ranges or climatic niche characteristics. Although the limits on individual species' ranges may have a strong climatic component, the climatic effects on species richness appear to be largely decoupled from the climatic constraints on individual species' ranges (see also Weiser *et al.* 2007; Boucher-Lalonde

et al., 2014a). This is inconsistent with several prominent hypotheses in the literature (e.g. Kleidon & Mooney, 2000; Wiens *et al.*, 2005; Svenning *et al.*, 2008; Romdal *et al.*, 2013). Note that we came to this conclusion from the premise that a consistent pattern likely has common underlying explanation (Rohde, 1992) and have therefore tested for consistent predictors of species richness (but see e.g. Gouveia *et al.*, 2013 who do not share this premise). The main processes driving the strong and nearly ubiquitous richness–climate relationship do not appear to depend upon simple, predictable, climatic constraints on individual species ranges that operate at macro-scales.

ACKNOWLEDGMENTS

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TABLES

Table 3.1 Summary table of the test of the predictions of each of our proposed hypotheses (H1-H5) to explain large-scale spatial variations in species richness. We denote whether each prediction was consistent (“yes”) or inconsistent (“no”) with empirical data. Using the geographic ranges of bird and mammal species in the Americas, we tested whether the hypothesized relationships (1) were in the predicted direction (i.e. positive), (2) were strong (R^2 stronger, or within 15% of that of current climate), (3) whether the extrapolative predictive power held across North and South America, (4) whether the relationships, within continents, had the same sign (positive or negative) for birds and mammals and (5) whether the marginal R^2 of richness as a function of the climate (temperature and precipitation) in the quadrat became lower than 5% once the predictor variable was included.

Hypotheses	Predicted direction (i.e. positive)?	Strong relationship (i.e. similar to current climate?	Consistency across continents?	Consistency across taxa?	Negligible marginal effect of current climate?
H1 - Range size	No	No	No	Yes	No
H2 - Climatic niche positions	Yes	Yes	No	Yes	No
H3 - Climatic niche breadth	No	Yes	Yes	Yes	No
H4 - Climatic range filling	No	No	No	Yes	No
H5 - Distribution of extant climates	Yes	No	Yes	Yes	No

Table 3.2 Proportion of the variance in bird and mammal species richness explained by each of the predictor variables. Positive relationships could contribute to the observed positive richness–climate relationship, while negative relationships (†) cannot involve a direct causal link. In the model containing all eight niche characteristics, coefficients were either constrained to be positive, or not. The marginal R^2 for climatic variables is calculated as the increase in R^2 when the climatic variable is added to a model that contains all eight niche characteristics. The marginal R^2 for niche characteristic variables is calculated as the increase in R^2 when the variable is added to a model containing temperature (temp) and precipitation (prec). NS denotes coefficients with associated p-values < 0.05.

		OLS R ²	Marginal R ²
Birds			
	Climate		
	Observed temp	0.81	0.06
	Observed prec	0.46	<0.01
	Observed temp*prec	0.83	0.06
	Niche characteristics		
	Range size	0.41†	0.05†
	Temp niche breadth	0.79†	0.05†
	Prec niche breadth	0.21†	<0.01†
	Range filling	0.60†	0.07†
	Temp niche position	0.65	<0.01
	Prec niche position	0.42	NS
	Temp availability	0.67	<0.01
	Prec availability	0.06	<0.01†
	All niche characteristics (positive coefficients)	0.84	<0.01
	All niche characteristics (unconstrained)	0.92	0.09
Mammals			
	Climate		
	Observed temp	0.70	0.09
	Observed prec	0.47	<0.01
	Observed temp*prec	0.73	0.11
	Niche characteristics		
	Range size	0.04	0.01
	Temp niche breadth	0.58†	<0.01†
	Prec niche breadth	0.24†	<0.01†
	Range filling	0.28†	<0.01†
	Temp niche position	0.51	NS
	Prec niche position	0.30	0.01†
	Temp availability	0.60	0.01
	Prec availability	0.09	<0.01†
	All niche characteristics (positive coefficients)	0.73	<0.01
	All niche characteristics (unconstrained)	0.80	0.07

FIGURES

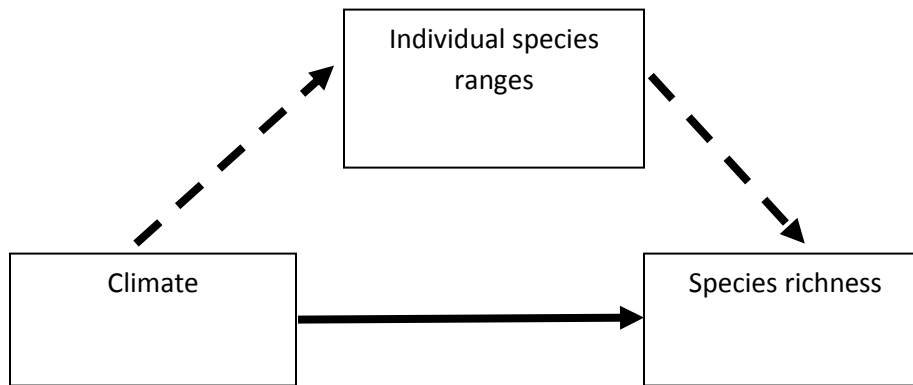


Figure 3.1 Hypothesized causal pathways between climate and species richness. Climate (here, temperature and precipitation) could affect species richness directly (plain arrow) by limiting the number of species, or the rate of their accumulation, in a region. If so, the factors that affect species richness would be largely independent of the factors that limit individual ranges. Climate could also largely determine the geographic range of individual species such that the overall richness–climate relationship would result from the sum of the species-specific constraints (dashed arrows). If climatic constraints on individual species’ ranges are non-randomly distributed across climates, then the sum of individual species climatically-constrained geographic ranges would lead to an indirect correlation between climate and species richness. In the text, we test different ways in which systematic variations in the distribution of species’ climatic constraints could affect richness.

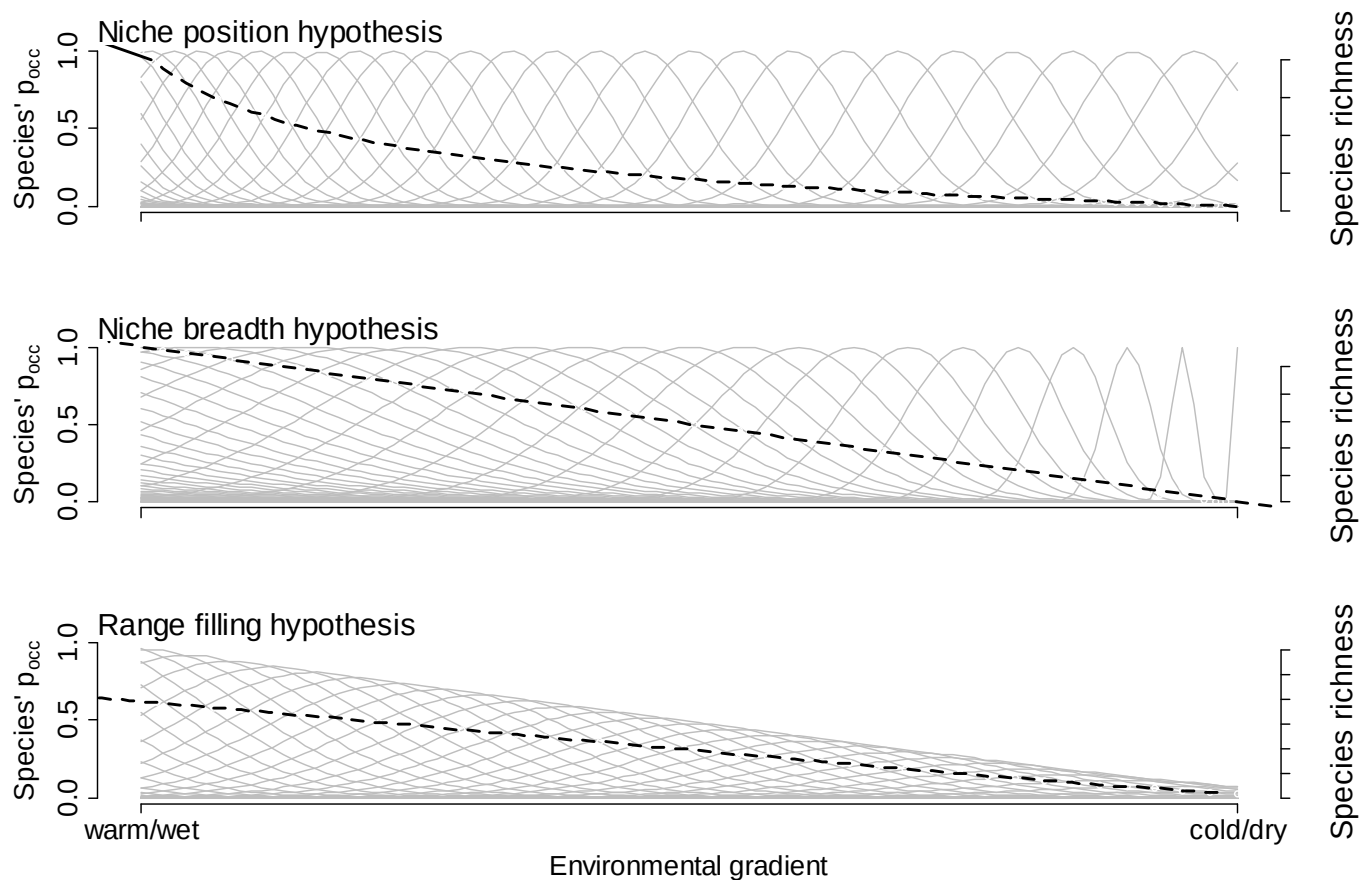


Figure 3.2 Conceptual representations of hypotheses proposing that the richness–climate relationship is determined by predictable constraints on individual species’ climatic niches. The gray curves represent the probability of occurrence (p_{occ}) of individual species (left axis) along an environmental gradient. For illustrative purposes only, we present individual species’ response curves as Gaussian functions. The niche position hypothesis (top panel, H4) proposes that a decreasing number of species have their climatic niches centered towards harsher environmental conditions. The niche breadth hypothesis (middle panel, H2) proposes that species’ climatic niche widths decrease along the environmental gradient. The range filling hypothesis (lower panel, H3) proposes that the filling of species’ potential range, here represented by the maximum probability of occurrence, decreases along the environmental gradient, which means that any given quadrat within the potential niche has a decreased

probability of being occupied and contributing to species richness. These hypotheses all predict that species richness (right axis) decreases along the environmental gradient. Predicted species richness was here calculated as the sum of individual species' probability of occurrences (dashed line).

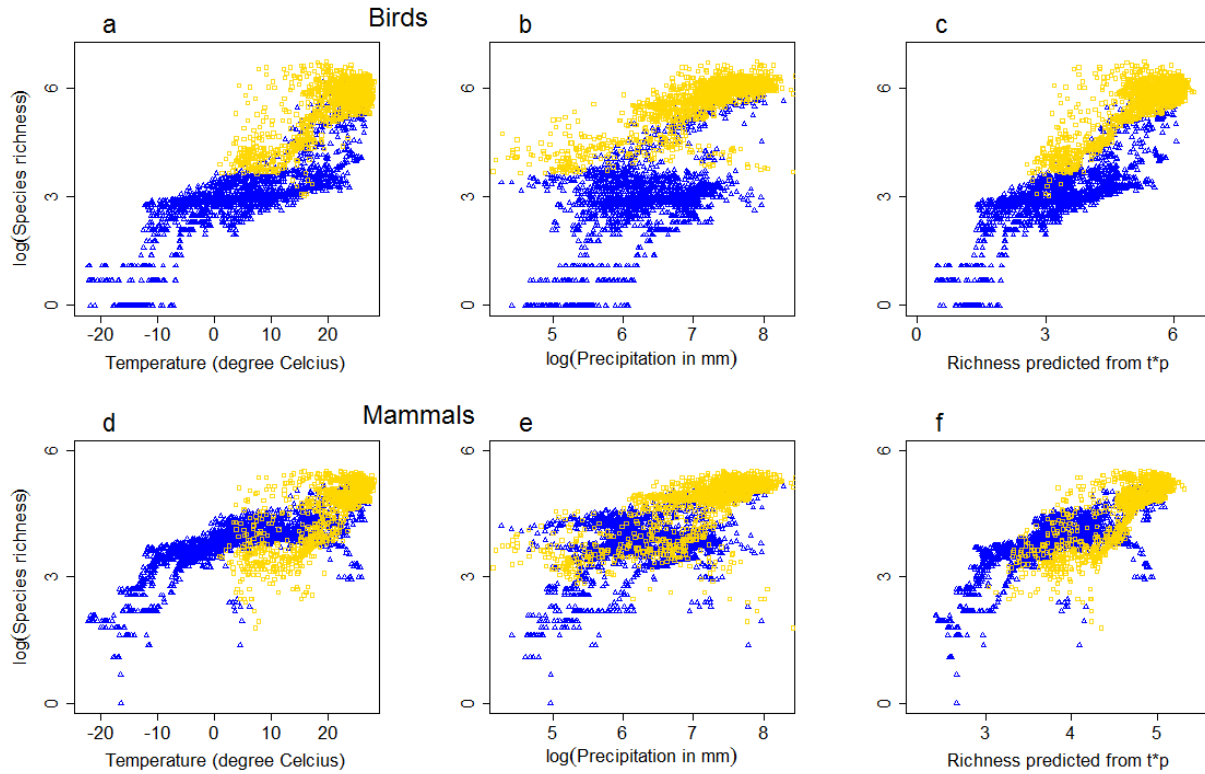


Figure 3.3 Species richness per 10^4 km^2 quadrat in North (triangles) and South (squares) America as a function of (a, d) mean annual temperature, (b, e) total annual precipitation and (c, f) temperature, precipitation and their interaction for (a, b, c) 3277 bird and (d, e, f) 1659 mammal species.

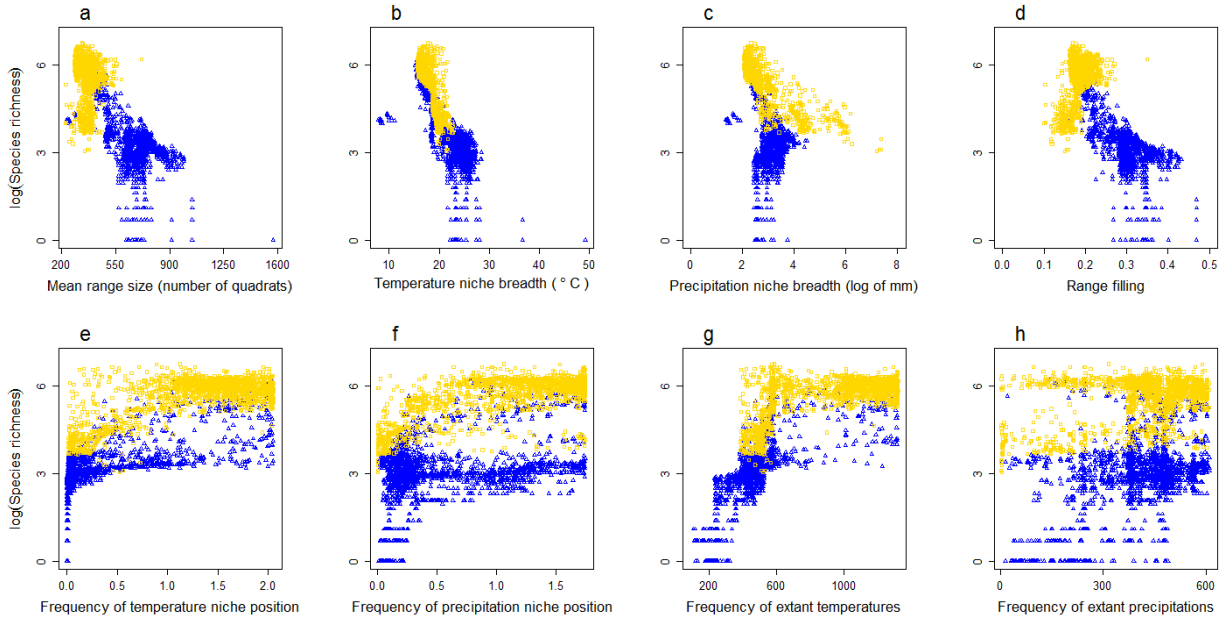


Figure 3.4 Bird species richness in 10^4 km^2 quadrats in North (dark triangles) and South (pale squares) America as a function of characteristics of individual species' distributions. If climate affects species richness through its effect on the niche of individual species, species richness is predicted to be positively correlated with these explanatory variables (a-h). The predictor variables are (a) mean range size, measured as the number of occupied 10^4 km^2 quadrats of all species occurring in the quadrat; mean (b) temperature niche breadth in $^{\circ}\text{C}$; (c) logarithm of precipitation niche breadth in mm; and (d) range filling of all species with potential ranges overlapping the quadrat; (e) number of species with a climatic niche centered on a temperature within 3°C or (f) a precipitation within 0.5 units of the focal quadrat scaled to a variance of 1; and the number of quadrats with (g) extant temperatures within 3°C and (h) extant precipitation levels within 0.15 units (in log mm), of the focal quadrat. Data are from the breeding ranges of 3277 bird species.

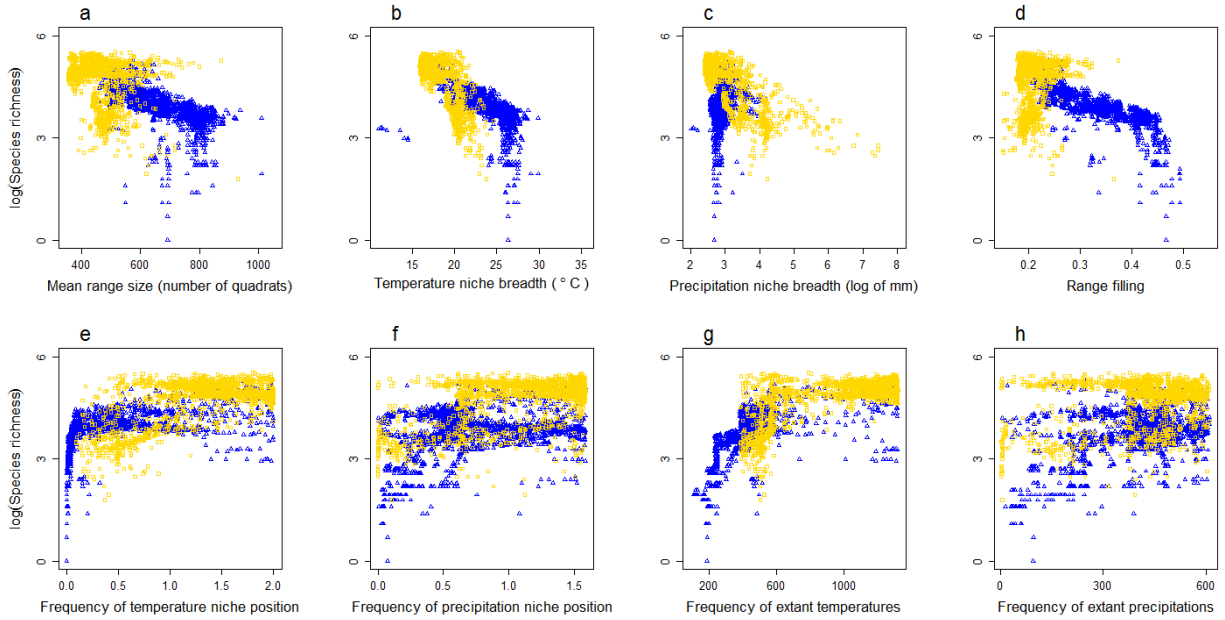


Figure 3.5 Mammal species richness in 10^4 km^2 quadrats in North (dark triangles) and South (pale squares) America as a function of characteristics of individual species' distributions. If climate affects species richness through its effect on the realized niche of individual species, species richness is predicted to be positively correlated with these explanatory variables (a-h). The predictor variables are (a) mean range size, measured as the number of occupied 10^4 km^2 quadrats of all species occurring in the quadrat; mean (b) temperature niche breadth in $^{\circ}\text{C}$; (c) logarithm of precipitation niche breadth in mm; and (d) range filling of all species with potential ranges overlapping the quadrat; (e) number of species with a climatic niche centered on a temperature within 3°C or (f) a precipitation within 0.5 units of the focal quadrat scaled to a variance of 1; and the number of quadrats with (g) extant temperatures within 3°C and (h) extant precipitation levels within 0.15 units (in log mm), of the focal quadrat. Data are from the breeding ranges of 1659 mammal species.

CHAPTER 4 Does climate limit species richness by limiting individual species' ranges?

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ABSTRACT

Broad-scale geographic variation in species richness is strongly correlated with climate, yet the mechanisms underlying this correlation are still unclear. We test two broad classes of hypotheses to explain this pattern. Bottom-up hypotheses propose that the environment determines individual species' ranges. Ranges then sum up to yield species richness patterns. Top-down hypotheses propose that the environment limits the number of species that occur in a region, but not which ones. We test these two classes of hypotheses using a natural experiment: seasonal changes in environmental variables and seasonal range shifts of 625 migratory birds in the Americas. We show that richness seasonally tracks the environment. In contrast, individual species' geographic distributions do not. Rather, species occupy different sets of environmental conditions in two seasons. Our results are inconsistent with extant bottom-up hypotheses. Instead, a top-down mechanism appears to constrain the number of species that can occur in a given region.

INTRODUCTION

Broad-scale geographic variation in species richness is strongly correlated with climate. At regional scales, across continents and globally, species richness of most taxa covaries strongly with climate (Currie, 1991; Field *et al.* 2009). Richness-climate relationships are largely consistent among continents (Currie & Francis, 2004), suggesting a mechanistic link between climate and species richness that applies very broadly. This hypothesized causal effect of climate on species richness is highly debated in the literature because the high correlation between climate and richness could be due to covariance with other factors, particularly historical ones (Latham & Ricklefs, 1993; Fine & Ree, 2006).

Natural experiments can be used to test for a causal link between environment and species richness. For example, H-Acevedo & Currie (2003) found that the relationship between bird species richness and environmental variables is congruent between the winter and summer season in North America (see also Hurlbert & Haskell, 2003). Similarly, the spatial relationship between climate and butterfly species richness across Canada accurately predicts how richness changes through time due to recent climate changes (Algar *et al.*, 2009b). The relationship between woody plant richness and water-energy variables at a site in Hungary has remained constant over the past 320 000 years while climate oscillated (Willis *et al.*, 2007). These results are consistent with a causal link, either direct or indirect, between species richness and contemporaneous environment.

The environment could impose top-down limits on species richness, independently of species identities. For example, species-energy theory proposed that primary productivity imposes a carrying capacity on the number of individuals and therefore on species richness (Wright, 1983). Metabolic theory of biodiversity predicts species richness from a mechanism

involving temperature-dependent metabolic rate and a cap on the total number of individuals in a region (Brown *et al.*, 2004). Classic island biogeography theory proposed that richness depends upon an equilibrium between colonization and extinction rates (MacArthur & Wilson, 1967). Regardless of their specific mechanism, top -down hypotheses of species richness predict that the richness-environment relationship is congruent through time and space because the mechanism operates independently of factors that vary spatially or temporally, other than climate (Brown *et al.*, 2001). In other words, these hypotheses require that the environment limits the number of species that can occur in a given region (Brown *et al.*, 2001; O'Brien, 1998) or determines stochastic immigration and extinctions rates (MacArthur & Wilson, 1967).

Alternatively, the environment could control species richness bottom-up by constraining individual species' ranges. Bottom-up hypotheses attribute richness gradients to mechanisms that create individual species' environmental niches. These hypotheses predict that the richness-environment relationship is congruent through time and space because individual species' realized environmental niches are fixed, and they track geographical variations in climatic constraints (Tingley *et al.*, 2009; LaSorte & Jetz, 2012). This is a critical assumption of species distribution models (Guisan & Thuiller, 2005; Kharouba *et al.*, 2009) and of the approach of stacking these individual models to predict richness (Algar *et al.*, 2009b; Guisan & Rahbek, 2011). The environment could control richness bottom-up by, for example, constraining the number of different physiological configurations that are viable at any given location (Kleidon & Mooney, 2000; Kleidon *et al.*, 2009). Another prominent example is the tropical niche conservatism hypothesis, which is the maintenance of ancestral tolerances to tropical (warm and productive) environments in daughter species (Wiens & Donoghue, 2004; Wiens *et al.*, 2010).

One way to distinguish between top-down versus bottom-up hypotheses is to investigate a group of species where richness is known to track environmental variables as those variables change temporally, and to ask whether individual species' ranges also shift in response to the same environmental variables. Bottom-up hypotheses predict that richness-environment relationships persist when environment changes because species geographically track their occupied environmental niche (*sensu* Pearson, 2007); the main constraint on species ranges is each species' abiotic niche (Soberon & Nakamura, 2009) such that a species' occupied niche must either be close to or a predictable subset of its fundamental niche. Top-down hypotheses, on the other hand, do not predict that species temporally track environmental variables. Migratory species could instead occupy different parts of larger fundamental niches when environmental variables change, showing marked differences in habitat use between seasons (Hagan & Johnston, 1992; Nakazawa *et al.*, 2009).

To test those competing hypotheses, we analysed the summer and winter geographic ranges of birds in the Americas. The environment in many regions changes dramatically between seasons, and many birds apparently respond to this change by migrating between summer and winter ranges. As a consequence of the migration of these species, total bird species richness in any given location varies seasonally, but the overall richness-environment relationship remains approximately constant through time (H-Acevedo & Currie, 2003; Hurlbert & Haskell, 2003).

Here, we modeled the environments occupied by 625 migratory bird species from December to February and from May to July. We then measured the overlap of the occupied environmental niche between the two seasons. We tested whether, as predicted by bottom-up hypotheses, this overlap is (a) higher than if species had migrated independently of their occupied environmental niche in the previous season, and (b) higher than if species had not

migrated at all. Although top-down and bottom-up hypotheses are not necessarily mutually exclusive, we can test whether bottom-up mechanisms in isolation are sufficient to account for patterns of richness.

We focus on temperature and enhanced vegetation index (EVI; similar to NDVI but not likely to saturate when leaf area index is high) as our measures of environment. Of all environmental variables considered, temperature and EVI contributed the most to the seasonal richness-environment relationship (see Methods). Temperature tolerance is generally an important constraint on species ranges (Root, 1988; Gaston, 2003). Similarly, it is commonly believed that birds migrate because of changes in resource or food availability (Berthold, 1995), with EVI likely reflecting plant productivity and insect abundance (Szep *et al.*, 2006).

METHODS

Occupancy and climate data

We divided the Americas into equal-area quadrats of 10,000 km² using a Behrmann projection. After removing quadrats with <50% land area, 4141 quadrats remained. For each quadrat, we calculated a fifty-year averaged mean temperature and total precipitation for the months of May, June and July (season 1) as well as for the months of December, January and February (season 2) from WorldClim (Hijmans *et al.*, 2005). For both seasons, we also calculated the standard deviation of temperature and precipitation (Hijmans *et al.*, 2005), a twenty-five year averaged mean Normalized Difference Vegetation Index (NDVI) from the Advanced Very High Resolution Radiometer (AVHRR) data series (Pinzon *et al.*, 2005; Tucker *et al.*, 2005), a two-year averaged Enhanced Vegetation Index (EVI) from Moderate Resolution Imaging

Spectroradiometer (MODIS) on Terra (Justice *et al.*, 1998) as well as the mean and range in elevation of each quadrat (Hijmans *et al.*, 2005).

Breeding and non-breeding ranges for birds of the Americas were obtained from NatureServe (Ridgely *et al.*, 2007). A quadrat was considered occupied by a species when its range overlapped any part of the quadrat. The 3902 bird species with extant ranges overlapping at least one quadrat of the Americas were included.

The richness-environment relationship

For season 1 (May to July) as well as for season 2 (December to February), we tallied the total number of species whose ranges overlapped each quadrat, thus obtaining species richness per quadrat. All species whose geographic ranges include a particular quadrat during the season were included. Species that stayed year round in a particular quadrat were therefore counted in both seasons (H-Acevedo & Currie, 2003). For migratory species whose breeding ranges only occurred in the Northern hemisphere ($n= 474$) or did not occur south of the tropic of Capricorn ($n= 2$), we considered season 1 to be the breeding season and season 2 to be the non-breeding season. Inversely, for species whose breeding ranges only occurred in the Southern hemisphere ($n= 121$) or did not occur north of the tropic of Cancer ($n= 19$), we considered season 1 to be the non-breeding season, and season 2, the breeding season.

We then fitted richness in both seasons as a single function of temperature, precipitation, their standard deviation, NDVI, mean and range in elevation, as these were the variables considered by H-Acevedo & Currie (2003). Additionally, we included EVI, as a substitute measure of vegetation density and productivity because it remains sensitive to increases in canopy density beyond the density at which NDVI becomes saturated (Huete *et al.*, 2002). We

also included season as a categorical variable in the model to test whether richness-environment relationships remain constant between seasons. All second order interaction terms were considered. We also considered second and third order polynomial terms for temperature (H-Acevedo & Currie, 2003). We then reduced this model to include only variables with substantial biological effects by sequentially eliminating terms for which the partial r^2 was less than 0.01. We did not use p- or AIC-values in model selection because the very high statistical power of our data set ($n = 7810$) leads to inclusion of many variables that account for miniscule amounts of variance. To fit the models, we $\log_{10}$ transformed richness to improve homoscedasticity and normality of the residuals. Thus, there are 4141 quadrats represented in each of the two seasons minus a total of 472 quadrats with zero richness (mostly Arctic islands) that were excluded for a total sample size of 7810 quadrats in the richness-environment analyses. We have excluded quadrats with richness values of zero to eliminate both the statistical and ecological bound in richness (i.e., richness reaches zero in some harsh climates, but it cannot be lower than zero in more extreme climates). Note that none of our qualitative conclusions are affected by excluding zero richness quadrats.

Because of high multicollinearity among independent variables, many models had nearly equivalent statistical fits as measured by the R^2 and AIC. However, temperature and EVI were uniformly present in the high-performing models. Since richness apparently most strongly tracks temperature and EVI, we then measured the occupied environmental niche of individual species considering only those variables. It is certainly possible that individual species' distributions are constrained by environmental variables other than those retained in our richness-environment model. However, if individual species track variables that richness does not apparently track, then bottom-up hypotheses proposing that richness patterns result from individual species'

environmental tolerances are nevertheless refuted. Precipitation and the standard deviation of temperature were also sometimes retained in the richness-environment model. We therefore present in Appendix S4.1 results where the occupied environmental niche of species is modelled with these variables.

Environmental niche overlap

For the 625 migratory species that had distinct ranges in season 1 and season 2, we fitted a model relating occupancy to the seasonal environment independently for season 1 and season 2. We related the probability of occupancy (presence or absence in a quadrat) in a given season to the seasonal environmental variables using Gaussian models (e.g. in Figure 4.1). We first fitted occupancy as a Gaussian function of each environmental variable independently (here, temperature and EVI) assuming a binomial error distribution. These models contain three terms: the mean, which represents the optimal environment for the species based on occupancy; the standard deviation of the Gaussian curve, which measures occupied environmental breadth; and a scaling constant that adjusts for the height of the curve which can vary between 0 and 1. Based on Boucher-Lalonde *et al.* (2012), we assumed that this function generally explains the geographic distribution of species well. There was no pattern in the residuals and all models were highly statistically significant (n= 4141 quadrats). Note that, when presences for a species peak near the limits of existing environmental conditions, the parameters of the Gaussian model are impossible to estimate. Therefore, 32% of the univariate Gaussian models failed to converge (see Appendix S4.1 for measures of the occupied niche that do not rely on a fitted model).

We then measured the overlap in environmental space between the Gaussian models fitted for season 1 and season 2 for each environmental variable. We measured the overlap in

occupied environments by what we hereafter refer to as (a) integral overlap, which is the proportion of the integral of the fitted Gaussian curves for the two seasons that is shared between seasons, and (b) integral nestedness, which is the maximal proportion of the integral of the fitted relationship for one season that is nested within the integral of the other season. Values of 0 represent no environmental overlap between seasons, while values of 1 represent full overlap between seasons. We also used other measures of overlap which are presented in Appendix S4.1.

Null models of overlap

Bottom-up hypotheses for the richness–environment relationship predict that species’ occupied environmental niches will be stable, i.e. fully overlap, between season 1 and season 2. Top-down hypotheses predict that the species that occur in a particular climate are independent of the species that occupied that climate in the opposite season. The challenge here is that environmental niches in the two seasons may be independent and nevertheless overlap substantially. Conversely, environmental niches may be highly stable between seasons, but the coarse climate and occupancy data used here as well as the spatial distribution of particular environmental conditions may introduce error in the degree of overlap of environmental niches. Therefore, to test statistically whether occupied environments are seasonally stable, as predicted by bottom-up hypotheses, or are independent, as predicted by top-down hypotheses, we developed null expectations for the measures of overlap.

The null models must retain (a) the extant range of environmental variables, (b) the cohesive spatial structure of geographic ranges and (c) the richness–environment relationship which has to be maintained between seasons. We therefore treated the set of observed ranges of all species as the set of possible ranges for any given species. For each species, we tested if

environmental overlap between its range in season 1 and season 2 was greater than the expected environmental overlap with the ranges of other migratory species in the opposite season. When a species' occupied environmental niche in one season overlapped its own niche in the opposite season more than it overlapped with the niche other species, we considered that the species is tracking its individual environmental niche and that the observed overlap is not merely due to richness tracking climate. Another key prediction of bottom-up hypotheses is that migratory species must conserve a higher niche overlap by migrating than if they had not migrated. Top-down hypotheses do not make this prediction. We therefore used a t-test to test whether migration generally increase niche overlap, with the prediction that the difference between overlap with versus without migration is positive.

To demonstrate that our results and conclusions are robust to the specific type of model used and are unaffected by the description of occupied environments in univariate space, we also fitted a MaxEnt model (Phillips *et al.*, 2006) with four environmental variables for all species: temperature, EVI, precipitation and the standard deviation of temperature. MaxEnt is the most widely used species distribution model (SDM) and has been shown to perform among the best when compared to other SDMs (Elith *et al.*, 2006). Although MaxEnt was built to model true presence data (Phillips *et al.*, 2006), there is a precedent of use with range maps (e.g. Hof *et al.*, 2011). Using the Bray-Curtis distances between MaxEnt suitability scores as our measure of overlap, we confirmed our findings that niche overlap between seasons is typically low, no better than expected under our null model and generally not higher than if species had not migrated (see Appendix S4.1).

All statistical analyses were performed in R 2.14 (R Development Core Team, 2012); MaxEnt models were fitted with the "dismo" package (Hijmans, 2012) and AUC with the "verification" package (NCAR - Research Application Program, 2012).

RESULTS

The relationship between bird species richness and environment in the Americas is congruent between season 1 (May to July) and season 2 (December to February) (Fig. 4.2). Temperature and EVI together explain 90% of the variance in richness in both seasons, throughout the Americas. Season and its interaction with temperature and EVI are statistically significant, but explain <1% of additional variance in richness. Similarly, we found that there is no residual effect of continent (North versus South America) in the model, despite the residuals being spatially autocorrelated (Moran's $I = 0.57$). Moreover, the seasonal change in temperature and EVI explains very well the change in seasonal species richness and spatial autocorrelation can be eliminated by fitting a simultaneous autoregressive error model (see Appendix S4.1). Because the seasonal congruence of the richness–environment relationship holds true for the entire Western Hemisphere (Fig. 4.2), as expected (H-Acevedo & Currie, 2003; Hurlbert & Haskell, 2003), we can proceed with the question: is this because of bottom-up or top-down limits on species richness?

Temperature and EVI describe individual species' niches reasonably well. We used univariate Gaussian models of temperature and EVI to model the niche of each species in each season (e.g. Fig. 4.1), and we found no apparent lack-of-fit. The area under the receiver operating curve (AUC) was generally high and comparable to that of other studies that have modelled species distribution-environment relationships. For temperature, AUC was higher than

0.5 for all species and higher than 0.8 for 70% of species in season 1 and 97% of species in season 2. For EVI, AUC was higher than 0.8 for only 34% and 13% of species in season 1 and 2 respectively. The average explained deviance of the models was 0.30 (0.006 SE) for temperature and 0.18 (0.005 SE) for EVI. Note that, if species distributions consistently relate poorly to temperature and EVI, which predict species richness very well, that is, in itself, inconsistent with the hypothesis that individual species' tolerances drive the richness–environment relationship.

For the 625 migratory bird species, we found that environmental niche overlap between seasons was generally low (Fig. 4.3). Niche overlap was not higher than expected under the null hypothesis that individual species do not track their occupied environmental niches when richness tracks the environment (Fig. 4.4). Additionally, niche overlap was not typically higher than if species had not migrated (Fig. 4.5). Other measures of niche and niche overlap are presented in Appendix S4.1 and lead to the same conclusions.

Specifically, the occupied temperature niche of most species only partially overlaps in the two seasons, although one is nearly always nested within the other (Fig. 4.3a). For a given species, the overlap of its observed temperature niches between the two seasons was generally not higher than the overlap with the occupied temperature niches of other species (Fig. 4.4a). We tested whether this is an artefact caused by many species having similar climatic niches. If this were the case, then niche overlap for a pair of species between seasons should be strongly related to their overlap within a given season, with a slope of 1 and an intercept of 0. However, we find that the overlap of species pairs within a season poorly predicts their overlap between seasons ($R^2 = 0.13$), with a slope of only 0.37 and an intercept of 0.44. Thus, species that do not overlap at all within a given season (i.e. share none of their climate niche as here defined) still have, on average, 44% overlap between season 1 and 2. The predictive power of nestedness as a measure

of overlap is only slightly higher (Table 4.1). We also found that most species would conserve a similar niche overlap if they did not migrate (Fig. 4.5a). Migration increases the average integral overlap and nestedness for temperature by only 8 and 23% respectively.

EVI niche overlap was also typically very low (Fig. 4.3b) and was not higher than expected under our null model (Fig. 4.4b). Additionally, for all pairs of species, within-season overlap was a very poor predictor of between-season overlap (Table 4.1). Finally, species would on average conserve higher niche overlap for EVI if they stayed year round in either their May to July or December to February range instead of migrating (Fig. 4.5b). Migration decreases average integral niche overlap and nestedness for EVI by 19 and 40% respectively. Therefore, we reject the hypothesis that species generally strongly track the environmental variables that richness is tracking. Instead, species migrate largely independently of their occupied niches in the previous season.

DISCUSSION

We have here found that, while richness strongly tracks seasonal changes in temperature and productivity measured by EVI, the vast majority of species do not strongly track these variables. Temperature and EVI apparently impose top-down limits on species richness independently of either factor's effect on the location of individual species' ranges boundaries. Bottom-up hypotheses proposing that richness tracks the environment through the sum of the effects on individual species' environmental tolerances (e.g. tropical niche conservatism) may explain, for example, why entire biogeographic provinces have differing numbers of species, and contribute to understanding the origins of species pools, but we found no evidence that they account for

regional variations in richness such as those commonly represented in global maps of species richness.

Although the environmental niches of most species at least partly overlapped between seasons, this overlap was no greater than expected under the null hypothesis that species migrate independently of their previously occupied environmental niche. Like other studies (Nakazawa *et al.*, 2004; Martinez-Meyer *et al.*, 2004; Papes *et al.*, 2012), we find that, for the majority of species, the overlap between seasons is higher than if presences were randomly located within the study region (see Appendix S4.1). However, we extend these findings and show that species seasonal niches can partly overlap simply because this is what is expected when species migrate within a bounded environmental space with a species richness gradient that is controlled top-down by the environment. Moreover, contrary to predictions from bottom-up hypotheses, the seasonal overlap between species environmental niches' was typically not higher than if the species had stayed year round in either its breeding or non-breeding range.

Species' ranges may nevertheless be constrained by tolerances to environmental variables. Perhaps species require different environmental conditions at different stages of their life history, such as between spring breeding and overwintering periods (Hagan & Johnston, 1992). Or, perhaps individual species' ranges are constrained by different environmental variables than those we considered here. For example, temperature extremes, rather than mean temperatures, could constrain species richness and/or species ranges (Simova *et al.*, 2011). Here, it would be difficult to distinguish their partial effects because the spatial variation of seasonal mean, minimum, or maximum temperatures across the Americas is very highly correlated ($r=0.99$). We acknowledge that we have not, nor did we intend to, model all dimensions of a species' environmental niche.

That said, recall that bottom-up hypotheses propose that spatial variation in species richness is very strongly correlated with temperature and EVI because individual species' ranges are strongly constrained by their tolerances for those variables. If, instead, individual species track different set of conditions during the breeding and non-breeding seasons, and if richness variation reflects such tolerances, then richness must correlate with different sets of variables in the two seasons. We observed the opposite: species' ranges do not seasonally track temperature and EVI, but richness does. For illustrative purposes, imagine that species were strongly constrained by soil type. This cannot possibly explain why richness is strongly related to temperature. Similarly, if species ranges are constrained by temperature during the breeding season but by soil type during the non-breeding season, these limits could not explain why richness seasonally tracks temperature. Finally, one could argue that bottom-up hypotheses could explain richness–environment relationships at other temporal or spatial scales. However, the most parsimonious explanation for richness patterns that prove consistent across temporal (H-Acevedo & Currie, 2003; Hurlbert & Haskell, 2003; Yasuhara *et al.*, 2012) and spatial scales [2, 49], and across continents [50, 51] and taxa [49], is that they share a common explanation.

There is a great deal of evidence consistent with the most general prediction of top-down hypotheses: that the richness–environment relationship should be consistent across space and time [6, 7, 48–51]. However, specific top-down mechanisms have been less successful. Consider, for example, the “species–energy hypothesis”: that energy determines the number of individuals that can occur in a region, and thereby the number of species [10]. It has been shown that richness is more highly correlated with climate than with abundance, including for American birds [52, 53]. Thus, the specific mechanism is insufficient [47, 52, 53]. Similarly, other top-

down hypotheses [13, 14] implicitly raise the question: why more species and not more individuals?

One example of a broadly successful top-down hypothesis is the equilibrium theory of island biogeography [12]. According to this theory, species richness on islands represent the equilibrium between immigration and local extinction rates. The species involved are not individually distinguished. It is possible that a similar mechanism operates on continents. Evolution may have provided pools of species within biogeographic provinces that are much larger than regional species assemblages. If rates of immigration to, and local extinction within, regions are climate-dependent, then correlations between richness and climate would result.

Here, we have rejected both predictions derived from the hypothesis that bottom-up mechanisms explain contemporary richness–environment relationships among birds in the Americas. This cannot be because our test was too conservative because our conclusions do not depend on the threshold used, i.e. the vast majority of species are not tracking their own occupied niche better than the niche of other species (Fig. 4.4). But perhaps, the environmental niches of migratory birds of the Americas are simply all too similar for our test to be valid. However, if this were the case, then species' environmental niches could not account for seasonal variations in species richness.

Niche conservatism may largely determine the identities of the species occurring in a given region without strongly affecting species richness. For instance, Algar *et al.* [54] showed that Hylid frog phylogenetic structure is independent of the environmental factors that best explain richness. Similarly, Hawkins *et al.* [55] have shown that the relationship between richness and contemporary climate is highly congruent for birds and mammals, but that it cannot be explained by similar evolutionary trajectories. Here, we do not argue that evolutionary or

historical [56] processes are never important, but rather that the numbers of species in regional species assemblages are apparently primarily (but not necessarily exclusively) controlled by contemporary top-down effects. We conclude that environmental change leads to a reorganisation of species where the warmest and most productive environment can sustain more species, regardless of their identities.

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TABLES

Table 4.1 Linear regression models of the overlap of species pairs between seasons as a function of their overlap within a given season. For all pairs of species, the overlap between season 1 and season 2 is therefore predicted by their overlap within season 1 and within season 2 (i.e, two x values for each y value). If all species fully conserved their niches between seasons, the regression would have a slope of 1, an intercept of 0 and an R^2 of 1. Here we present the observed coefficients of the fitted relationships for the environmental variables temperature and enhanced vegetation index (EVI) and for two different measures of niche overlap; integral overlap and integral nestedness. The standard errors are in parenthesis.

	Temperature		EVI	
	Integral overlap	Integral nestedness	Integral overlap	Integral nestedness
Slope	0.37 (0.0018)	0.43 (0.00037)	0.49 (0.0019)	0.34 (0.0014)
Intercept	0.44 (0.0014)	0.09 (0.0016)	0.25 (0.0017)	0.03 (0.00026)
R^2	0.13	0.22	0.22	0.17

FIGURES

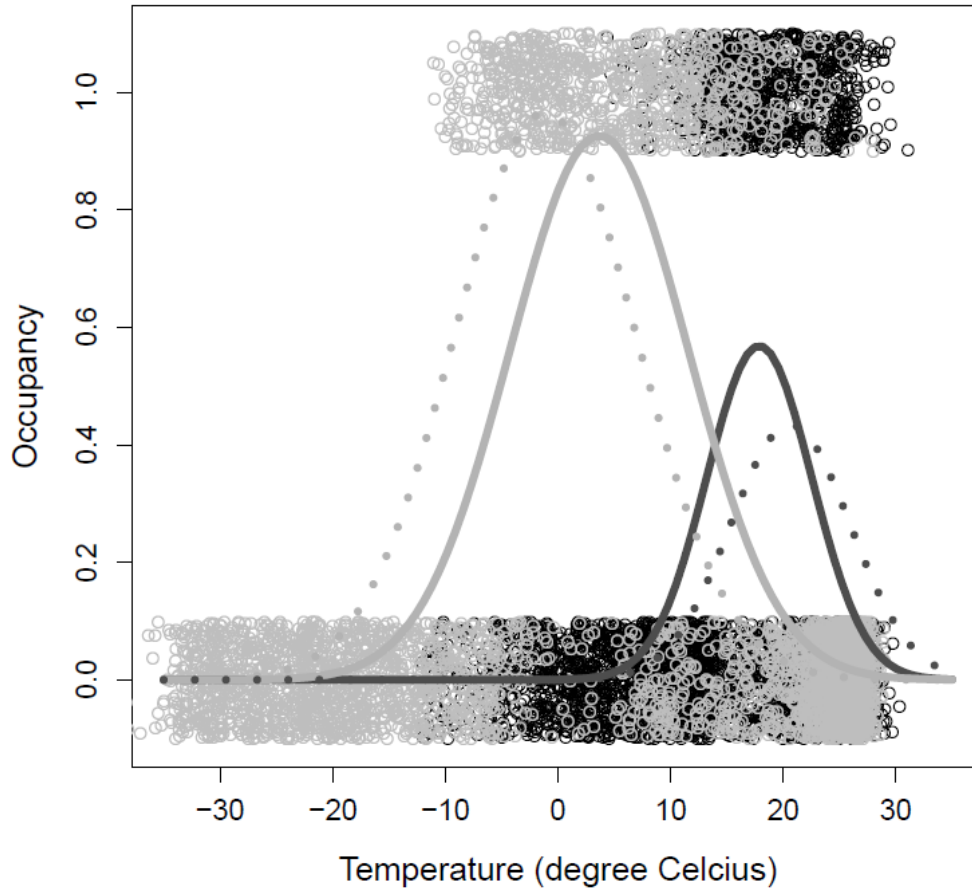


Figure 4.1 Occupancy of 10,000 km² quadrats (n= 4141) in the Americas by *Accipiter cooperii* (Cooper's hawk) in May to July (black dots) and in December to February (gray dots). Presences (occupancy = 1) and absences (occupancy = 0) have here been jittered by 0.1. Seasonal occupancy was related to seasonal temperature by a Gaussian model. The fitted relationship is presented for May to July (dark curve) and December to February (pale curve) and explains respectively 21% and 54% of the deviance in occupancy. We also present the fitted relationships assuming no migration, i.e. if the species had stayed in its May to July (pale dotted curve) or in its December to February range (dark dotted curve) instead of migrating.

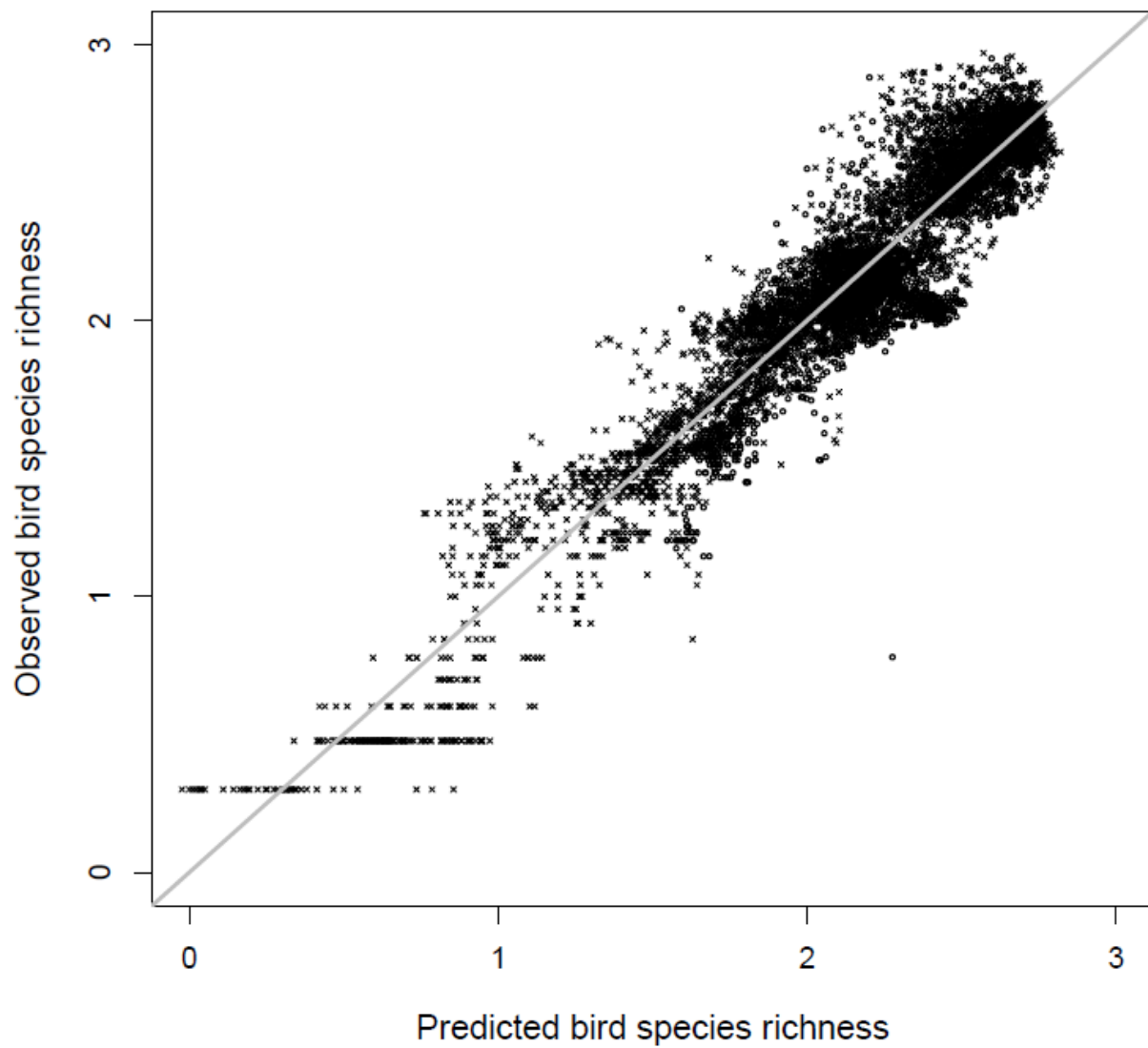


Figure 4.2 Observed $\log_{10}$ transformed bird species richness versus predicted richness from temperature and enhanced vegetation index (EVI). Richness for each 10,000 km² quadrat is represented for the season of May to July (o) and of December to February (x) and is calculated from range maps of 3902 birds in the Americas. The 1:1 line is shown in gray.

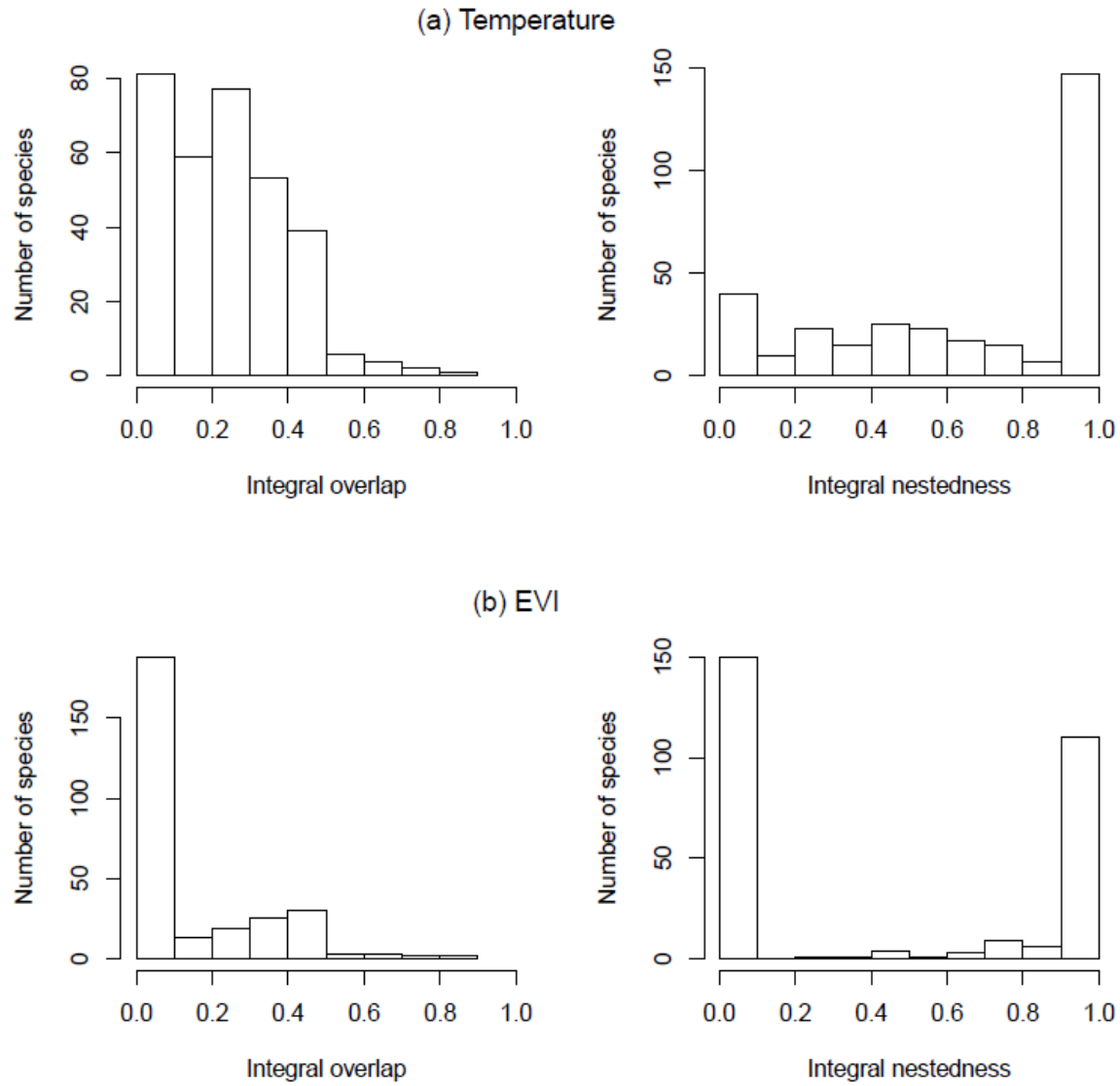


Figure 4.3 Distribution of measures of environmental niche overlap between May to July and December to February for (a) temperature and (b) enhanced vegetation index (EVI). The niche of a species in a given season is modelled by a univariate Gaussian function of the environmental variable (e.g. Fig. 4.1). We used two different measures of overlap described in the main text; integral overlap (left column) and integral nestedness (right column). Values of 0 indicate no niche overlap while values of 1 represent perfect niche overlap between seasons. By definition, integral nestedness will always be equal to or higher than integral overlap.

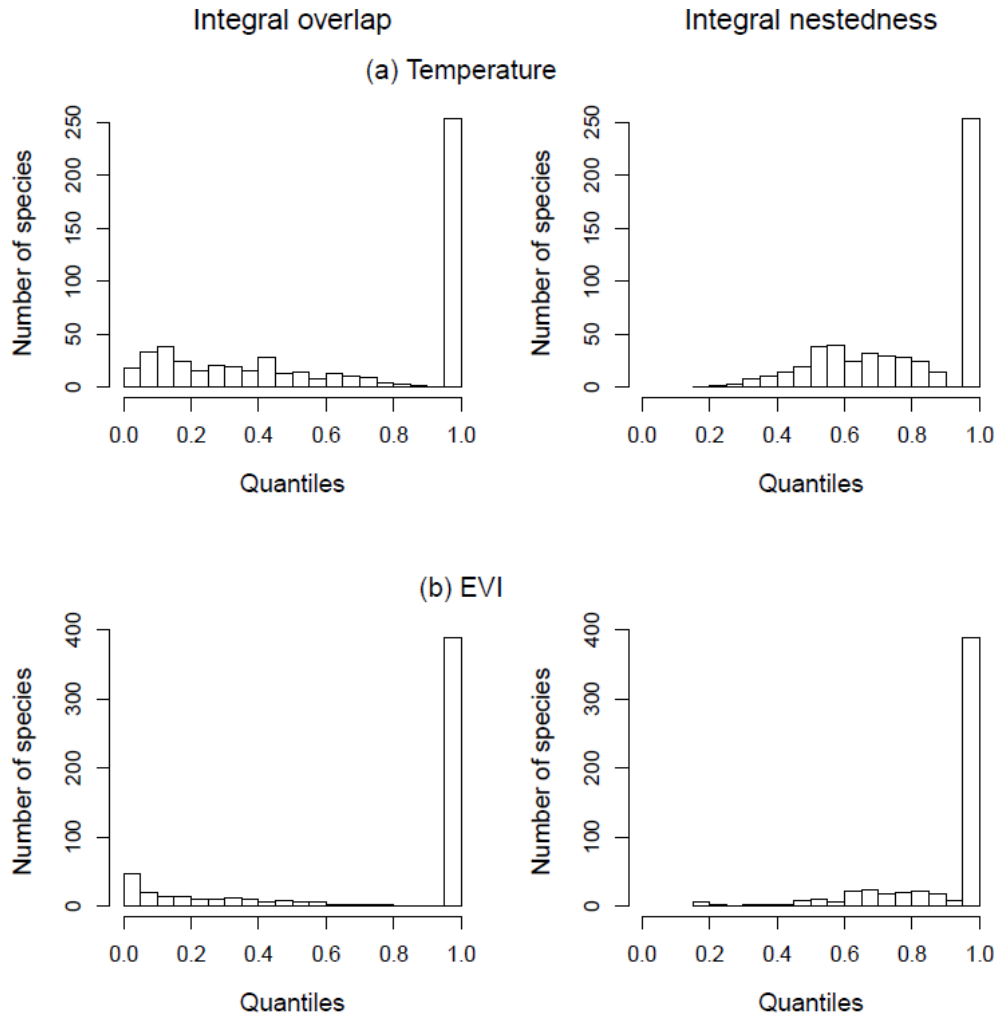


Figure 4.4 Assume that, when a species migrates between seasons, it could potentially move to the post-migration range of any species. Here, we test whether the environmental conditions in a species' pre-migration geographic range are more similar to the conditions in its own post-migration range than to the conditions in the ranges occupied by other species post-migration for (a) temperature and (b) enhanced vegetation index (EVI). For a given species, the quantile is calculated as the proportion of species for which the occupied niche overlap is equal to or greater than the observed seasonal niche overlap for the species. The quantiles are calculated for two different measures of niche overlap: integral overlap (left column) and integral nestedness (right column).

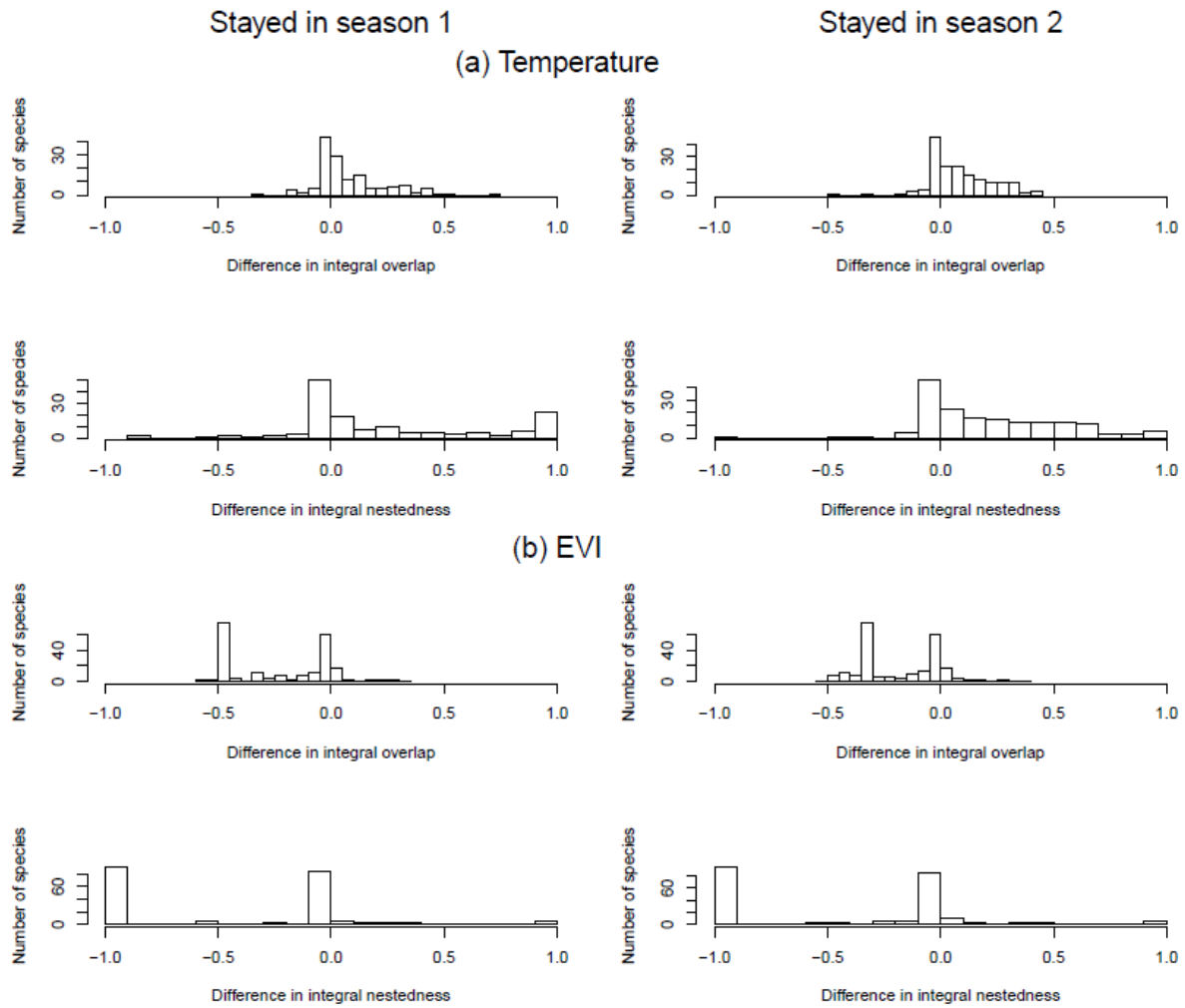


Figure 4.5 Distribution of the differences in niche overlap if migratory species had stayed year round in either the range they occupy from May to July (left column) or from December to February (right column) instead of migrating. Specifically, we measured overlap given migration minus overlap assuming no migration. If species migrate to track their environmental niche, positive values are predicted. Results are presented for (a) temperature and (b) enhanced vegetation index (EVI) and two measures of overlap; integral overlap and integral nestedness.

CHAPTER 5 Can climate explain interannual local extinctions among bird species?

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ABSTRACT

Aim Geographical variations in species richness are strongly related to temperature and precipitation. On ecological time-scales, these variations in species richness should reflect rates of immigration and local extinction (extirpation). Here we ask whether the probability of local extinction in passerine birds covaries with climate. Specifically, we test whether local extinctions increase with climatic harshness or with the climatic distance from a species' optimal climate.

Location USA and Canada.

Methods We obtained bird counts from the North American Breeding Bird Survey (BBS) from 1967 to 2012. For each BBS route, we calculated the probability of interannual local extinction for each of 206 passerine birds. We then used linear mixed-effects models and structural equation modelling to relate local extinction rates to our hypothesized predictor variables: temperature, precipitation and their distance from the species' most occupied temperature and precipitation.

Results We found that local extinctions are nearly independent of temperature and precipitation: no climate is inherently more extinction-prone than any other. Similarly, the climatic distance

from a species' maximally occupied temperature and precipitation has only an extremely weak positive effect on the probability of local extinction. We found that only abundance has a strong negative effect on the probability of local extinction.

Main conclusions Although variations in local extinctions are typically spatially structured, we conclude that they are not related to contemporary climate in a consistent way among species. Broad-scale geographical gradients of species richness are unlikely to be driven by higher extinction rates in climatically harsh areas.

INTRODUCTION

Are local extinctions of species predictable? This question is important for conservation management because the extinction of a species is ultimately the culmination of many local extinction events (Soulé, 1983). It is also important to biogeography (Hanski, 1998); MacArthur & Wilson's (1967) island biogeography theory proposed that island richness is determined by a dynamic equilibrium between rates of immigration and extinction, where the rate of extinction is inversely related to island size. Similarly, it has been argued that large-scale biogeographical patterns can only be explained by explicitly accounting for processes such as extinction and immigration (Hanski, 1998; Goldberg *et al.*, 2005; He *et al.*, 2005; Ricklefs, 2007).

Consider continental variation in species richness. Coarse-grained, broad-extent geographical variation in species richness is strongly correlated ($r^2 \approx 0.8$) with contemporary climatic variables (Field *et al.*, 2009): richness in most species groups increases with mean annual temperature and/or precipitation, sometimes with a negative interaction between the two. The mechanisms underlying these patterns are still contentious (Willig *et al.*, 2003; Mittelbach *et al.*, 2007). Geographical variation in richness and its correlation with contemporary climate could arise if rates of immigration and/or extinction depended strongly upon contemporary climatic variables (Chown & Gaston, 2000; Mora *et al.*, 2003; Goldberg *et al.*, 2005). In the present study, we test whether local extinctions can be linked to climate. For the purposes of the present study, we define 'extinction' in a manner analogous to MacArthur & Wilson's (1967) usage: the presence of a species in a locality at time t , followed by its absence in a subsequent census at $t+1$.

How might extinction depend upon climate? A first hypothesis is that local extinctions increase with climatic harshness (Fig. 5.1a). Specifically, we hypothesize that extinction rates are

greater at lower temperatures and levels of precipitation. Cold and dry climates are broadly recognized as imposing strong range limits (MacArthur, 1972; Parmesan, 2006) and physiological constraints (Kleidon & Mooney, 2000) on species, which could be reflected by a higher local extinction rate (Holt & Keitt, 2000). If such climate-dependent extinctions are general across species, it could explain why species richness is typically low in cold and dry areas. A generally higher extinction probability could be generated by: (1) species occurring in harsh climates having higher extinction rates over their entire range, relative to species occurring in wetter or warmer conditions; (2) species generally having a higher extinction rate at the cold and dry end of their range; or a combination of (1) and (2). If variations in local extinctions are not strongly negatively related to temperature and precipitation (in principle, with $R^2 > c. 0.8$, because the proposed causal chain is: climate $\rightarrow$ extinction rate $\rightarrow$ richness), then climate-dependent extinctions cannot be the primary factor responsible for spatial variations in species richness. Low rates of colonization or speciation in cold and dry regions might then explain the richness–climate relationship.

A second hypothesis (below) is a variant of the abundant-centre hypothesis, which proposes that populations are most abundant at the geographical centre of a species' range where environmental conditions are presumably optimal, whereas the species' smallest populations are found at range edges where less favourable environmental conditions occur (Brown, 1984; Sagarin & Gaines, 2002). According to the small-population paradigm, small populations get trapped in a positive feedback loop, where genetic drift, inbreeding and stochasticity further decrease their numbers (Caughley, 1994; Tanaka, 2000). Larger populations are less affected by these processes. Combining the abundant-centre hypothesis and the small-population paradigm, one would expect local extinctions to be more frequent at the edge than at the core of a species'

range (Yackulic *et al.*, 2011). Furthermore, declining species should see their ranges shrink towards their cores (Rodríguez, 2002), where local populations are presumably more abundant and less likely to become extinct (Channell & Lomolino, 2000).

However, the abundant-centre hypothesis is poorly supported by empirical studies. Many authors report that the ranges of declining species collapse towards their edges, with core populations not being the most persistent in the face of local extinction (Channell & Lomolino, 2000; Turvey *et al.*, 2010). A meta-analysis performed by Sagarin & Gaines (2002) revealed that the abundant-centre hypothesis itself is only supported by 39% of the empirical studies testing its predictions. It cannot be assumed that, as a general rule, species are most abundant at the geographical centre of their ranges and that their abundance declines gradually and uniformly towards all edges.

We propose what we shall call the ‘climate-centre hypothesis’. Abundance and extinction risk could depend not on the geographical distance from the centre of a species’ geographical range, but rather on distance in climatic space from a species’ optimal climate (Fig. 5.1b). A species’ optimal climate need not be at the geographical centre of its range. We operationally define ‘optimal climate’ following Boucher-Lalonde *et al.* (2012) – the precipitation and temperature that a species occupies with the highest probability. If suitability and, accordingly, abundance do decrease with distance from a species’ optimal climate (Gauch & Whittaker, 1972; Vetaas, 2002), then local extinctions should increase accordingly.

Most recent studies of local extinctions have focused on threatened species. These species may decline because some particular process, such as human-related disturbance, reduces their abundance (Channell & Lomolino, 2000). The purpose of the present study is specifically

not to focus on the decline of threatened species; rather, we ask whether local extinctions in species in general may relate predictably to the same climatic variables that variation in species richness is strongly correlated with. We are also not primarily concerned with the question of whether there is a detectable correlation between richness and extinction rates. Rather, we would like to know if climate-dependent rates of local extinction may be a major driver of continental patterns of richness.

METHODS

We test the two hypotheses outlined above using data from the North American Breeding Bird Survey (BBS), an extensive dataset that includes annual counts of breeding birds on 5030 routes across the USA and southern Canada (USGS, 2013). In June of every year since 1967, experienced volunteer ornithologists survey these 40-km routes, stopping every 0.8 km for 3 min to identify and count the birds seen or heard. Volunteers rely more heavily on hearing than on eyesight for species identification and songbirds therefore have a higher probability of being detected than non-passerines (Cunningham *et al.*, 1999). We limited our study to the 206 passerine species included in BBS records between 1967 and 2012. We excluded routes sampled during fog, precipitation or high winds, because these conditions reduce the likelihood of detecting birds along the route (Ziolkowski *et al.*, 2010).

We characterized each BBS route in terms of its average annual mean temperature and precipitation by overlaying climatic maps obtained from WorldClim (Hijmans *et al.*, 2005) with a map of BBS routes. Although we acknowledge that mean annual temperature and precipitation may not have direct effects on local extinctions of birds, these are commonly good predictors of

species richness (Currie, 1991), which is the focus of the present study. Moreover, the continental variation in annual mean and extremes for climatic variables are highly correlated. For example, on BBS routes, the yearly minimum and maximum temperature and precipitation, calculated from WorldClim (Hijmans *et al.*, 2005), correlate with the annual means with an r of 0.78 and 0.47 for temperature and 0.64 and 0.75 for precipitation.

We calculated interannual local extinction probability e_{si} as the number of local extinctions of species s on route i , divided by the number of potential extinctions of the same species on the same route (Fig. 5.2). A local extinction is defined here as an apparent absence on a route where the species had been observed the previous year. A potential local extinction is either a presence or an apparent absence on a route where the species had been observed in the previous year. This definition of e_{si} can overestimate true local extinction probabilities because of false absences. A species that is present but undetected would be falsely recorded as an extinction. Here, extinction is operationally defined as an observed presence followed by (apparent) absence in the following year. Species with low detection probability will rarely be observed as being present; they will therefore rarely be falsely observed to have gone extinct. Although this artefact may increase our extinction estimates, it will only influence our conclusions if the frequency of false extinctions is correlated with climate. However, climate per se is unlikely to be a source of bias in bird census, but habitat type and vegetation density may be (Bibby, 2000).

To test whether the detectability of local extinctions affects our results, we recalculated e_{si} , where a local extinction was defined as the absence of a species on a given route for x consecutive years following a presence on that route. Routes that had both presences and absences in the x consecutive years were excluded. We allowed x to vary between one and three

years and we repeated all the analyses discussed below with these different e_{si} estimates. We found that the relationships between different measures of e_{si} and climate were qualitatively very similar under the different values of χ . This is because the different measures of e_{si} were all highly correlated with one another (all $r \geq 0.92$). The operational definition of extinction did not affect our conclusions, and we therefore present results only for the one-year threshold.

To test our first hypothesis – that local extinction probability increases with climatic harshness – we modelled e_{si} as a function of temperature and precipitation using a linear mixed-effects model, where species is treated as a random variable. Both the slope and intercept of e_{si} as a function of climate are treated as random effects of species. The prediction is that e_{si} decreases with temperature and precipitation, cold and dry environments generally being considered harsh for species. Note that we have used climate means rather than minima, but their partial effects are not distinguishable here. Moreover, processes such as extinction could be driven by cumulative measures of climate, and not necessarily by extremes (e.g. Kleidon & Mooney, 2000).

We then tested our second hypothesis – that local extinctions increase with the distance from a species' optimal climate. First, we determined the maximally occupied temperature and precipitation for each species. To do this, we overlaid NatureServe's breeding range maps (Ridgely *et al.*, 2007) for each species onto our climate data. We then binned temperatures into intervals of 2 °C. Precipitation was square-root transformed and binned into intervals, each three units wide (Boucher-Lalonde *et al.*, 2012). We then tallied the number of cells in each temperature and precipitation bin that fell within the species' range, and the number in each bin that fell outside the range. The maximally occupied climate for that species is the temperature and precipitation with the highest proportion of occupied cells throughout North America (e.g. in

Appendix S5.1). Very rare climate bins (those with less than 10,000 km² total area) were eliminated from the analysis. We then set each species' optimum to the temperature and precipitation on the BBS route that is the closest to the maximally occupied climate estimated from range maps. For each species on each BBS route, we computed the absolute difference between its optimal climate and the local climate. We then divided this absolute difference by the maximum climatic difference observed for that species. Climatic distances therefore vary from 0 at a species' optimum, to 1 at the limit of the species' climatic niche. We used linear mixed-effects models to test whether the probability of local extinction increases with climatic distance. We similarly tested absolute (rather than relative) climatic distance. Because the two sets of results were very similar, we only present those with relative climatic distance.

We compare how well our climate-centre hypothesis accounts for spatial variation in the probability of local extinction in the BBS data with the abundant-centre hypothesis. For the latter, we measured the geographical distance separating each BBS route from the nearest edge of each of the 206 species' range maps. For this analysis, we excluded BBS observations that fell outside the NatureServe range, leaving $n = 220,116$ species–route combinations. We estimated abundance a_{si} as the count of individuals for species s and route i averaged over the number of years where it was present. We then included geographical distance and abundance in our mixed-effects models, to test for the partial effect of climatic distance once these variables were accounted for.

Finally, we used structural equation modelling to investigate how three parameters – climatic distance from the optimum, location within the geographical range, and abundance – influence extinction rates. We hypothesized a positive relationship between the probability of local extinction and climatic distance from the optimum of temperature and precipitation. This

positive relationship could either be direct or through a negative effect on abundance (Fig. 5.1b). We also considered the effect of geographical distance from range edges in the model. We tested the alternative hypothesis that geographical distance has a direct effect on abundance (i.e. the abundant-centre hypothesis), versus acting indirectly through its effect on the temperature and precipitation distance (i.e. the climate-centre hypothesis; Fig. 5.1b). Because statistical power is extremely high and because there is both spatial and phylogenetic autocorrelation in the data, it is pointless to test for the statistical significance of links in the structural models: even very weak links appear to be significant. Instead, we retained links in the model for which the parameter estimate is at least 0.1, because we were interested in identifying important drivers of extinction, rather than statistically detectable ones.

Statistical analyses were performed with R (R Development Core Team, 2012), using the nlme package (Pinheiro *et al.*, 2012) for mixed-effects models and the sem package for structural equation modelling (Fox *et al.*, 2012).

RESULTS

Climate effects

The probability of local extinction is typically spatially structured (Fig. 5.2), but it does not generally increase with climatic harshness. Interannual extinctions, e_{si} , are independent of temperature ($P = 0.30$; $n = 228,502$) and very weakly dependent on precipitation ($P < 0.01$; $n = 228,502$), with the fixed effect of precipitation explaining $< 1\%$ of the variance in e_{si} (Fig. 5.3a and 5.3b). The random effects (groups = 206 species) of temperature and precipitation are normally distributed and centred on zero; together, they explain 22% of the variance in e_{si} . In

other words, most of the variability in local extinctions is explained at the species level, with an extremely weak tendency for extinction probabilities to be higher in dry areas. When linear models of interannual local extinction probabilities are fitted independently for each species, only 50% have the predicted negative relationship with temperature and 61% with precipitation. At the species level, the majority of species have significant relationships with temperature and precipitation, but low R^2 and shallow slopes.

The probability of local extinction also cannot be explained by the climatic distance from a species' optimal climate. Geographical variation in interannual extinction rate is not related to the climatic distance from the species' temperature optimum ($P = 0.43$; $n = 228,502$) and increases with the climatic distance from the species' precipitation optimum ($P < 0.01$; $n = 228,502$) from a species' optimal climate, as estimated from the fixed effects of temperature and precipitation in mixed-effects models (Fig. 5.3c and 5.3d). The probability of local extinction increases by 0.14 between a species' optimum precipitation and the further precipitation level from that optimum, but this difference explains only 1% of the total variation among species and sites. Nearly all of the 23% of variance in e_{si} that is explained by climatic distance is at the level of individual species. Accordingly, when linear models of interannual local extinctions as a function of climatic distance from the species' climatic optimum are fitted independently for each species, only 50% of species have the predicted positive relationship for temperature distance and 62% for precipitation distance. In other words, the effect of distance from the climatic optimum is significant but very weak for the majority of species, and is not consistently positive.

Distance and abundance effects

The probability of interannual local extinctions, e_{si} , generally increases by 0.07 from the centre to the edge of species' ranges ($P < 0.01$), but this relationship is extremely weak, with the fixed effect of geographical distance explaining 0.1% of the variance in local extinctions. It is highly variable among species, with the random effects of geographical distance explaining 17% of the variance.

In contrast, abundance has a strong effect on the probability of local extinction. In a mixed-effects model, abundance explains 57% of the variance in e_{si} ($P < 0.01$), of which 47% of the total variance is explained by the fixed effects. All of the 206 species showed the predicted negative effect of abundance, with a mean R^2 of 47% across species. Temperature, precipitation and geographical distance together explain less than 1% of additional variance when included alongside abundance in a mixed-effects model.

Structural models

Using structural equation modelling, we found that our climate-centre model was not supported. From the starting model depicted in Fig. 5.1b, the selected model only included a strong negative relationship between abundance and local extinctions ($r = -0.7$; $P < 0.01$) and a positive relationship between geographical distance and precipitation distance ($r = 0.23$; $P < 0.01$). The relationships between local extinctions and the climatic distance from a species' optimum were weak and were therefore excluded from the model ($r = 0.03$ for temperature; $r = 0.07$ for precipitation; $P < 0.01$), as were the relationships between climatic distance and abundance ($r = -0.07$ for temperature; $r = -0.05$ for precipitation; $P < 0.01$). Neither geographical nor climatic

distance can explain abundance or local extinctions across all 206 passerine bird species (i.e. $r < 0.1$). We obtained the same structural model when we logit-transformed the probability of local extinction to improve its distribution.

DISCUSSION

The probability of local extinction in North American passerine birds is poorly predicted by contemporary temperature and precipitation. For any given species, local extinction rates are typically highly variable and spatially structured (e.g. Fig. 5.2), but the climatic and geographical variables considered here explain virtually none of that variance in a consistent way among species. Species' extinctions appear to relate to climate in highly idiosyncratic ways. For most species, local extinction significantly relates to climate and/or climatic distance from the optimum, but the relationships are extremely variable among species and are often not in the predicted direction.

Our results are inconsistent with the hypothesis that continental patterns of species richness result from a stochastic equilibrium between immigration and extinction, where local extinctions are higher in climatically harsh areas, specifically cold and dry regions (Fig. 5.1a). The observed climate effects are simply too weak (Fig. 5.3a and 5.3b). Species do have high probabilities of local extinctions in some areas (Fig. 5.2), but those areas are not related to mean temperature and precipitation in any consistent way. Extinctions may have shaped regional species pools (which this study does not examine) if, historically, harsh climates had higher extinction probability, all else being equal (Wallace, 1878; Roy & Goldberg, 2007).

Our climate-centre hypothesis (Fig. 5.1b) was also unsupported for North American

passerines. Although local extinctions significantly relate to climatic distance, its effect is extremely variable among species and explains a minuscule amount of the variance. It cannot, therefore, be an important factor affecting species richness at contemporary time-scales (Fig. 5.3c and 5.3d). We cannot exclude the possibility that these small observed differences in local extinctions driven by the climatic distance from a species' optimum might add up over longer (e.g. evolutionary) time-scales and become important drivers of species' range limits (Holt & Barfield, 2011).

Not surprisingly, local extinction probabilities correlate strongly with local abundance. Local extinctions decrease with abundance for biological reasons (Leigh, 1981; Hanski, 1982) as well as statistical ones; the probability of observing a species that is present depends on the number of individuals of that species that are present in the region (Karl *et al.*, 2000). It appears that the factors that explain abundance – for example niche requirements (Brown *et al.*, 1995) – are likely to be the ones that will also best explain intraspecific geographical variation in local extinctions. The fact that we find a strong relationship between extinction probability and local abundance is also an important finding methodologically. It indicates that the variability in BBS data is not so strong that it obscures expected relationships. Like Martínez-Meyer (2013), we find that the relationship between abundance and climatic distance is significantly negative, although we argue that the effect is negligibly small and highly variable among species.

Perhaps the climate warming throughout the past half century is the main factor driving local extinctions (Thomas *et al.*, 2006). The mean change in temperature throughout the BBS routes was $0.02\text{ }^{\circ}\text{C yr}^{-1}$, with a maximum of $0.11\text{ }^{\circ}\text{C yr}^{-1}$ (Gibbs, 2012). However, the relationship between abundance and change in temperature was very weak – explaining less than 3% of the total variance in mean abundance across routes and species – and negative, such that

increased temperatures decreased mean abundance (Gibbs, 2012). Because we have found here that abundance is a relatively good predictor of species local extinctions, it is unlikely that such a weak link between abundance and change in temperature could modify our conclusions.

It is possible that other aspects of climate, such as extreme weather events, affect local extinctions in passerine birds. In case studies, successive harsh winters have been shown to decrease abundance and increase local extinctions towards range edges (Mehlman, 1997). Here, this would have been reflected in our geographical distance variable. We also recognize that other measures of macro-scale climate could be more directly related to bird physiology. The climate of the breeding season could have been used rather than the annual average, but these measures are too highly correlated with mean annual temperature and precipitation ($r = 0.96$ and 0.87 , respectively) to partition their respective effects.

Noise in the data generated by sampling error, the lack of a control and confounding factors are recurring concerns with macroecological studies in general, and particularly in studies that show the absence of a pattern (Gaston & Blackburn, 1999; Paine, 2010). We have used this approach, sampling and analysing our data at a broad spatial scale, because this is the scale at which we wish to be able to make inferences. We explicitly aimed to test whether variations in local extinction rates could explain coarse-grained continental patterns such as the richness–climate relationship and species’ geographical ranges. These are highly related to the climatic variables we have used here (e.g. Currie, 1991; Araújo *et al.*, 2005). If variation in local extinction rates was an important mechanism to explain these patterns, we would expect to observe strong relationships between local extinctions and climate, despite the presence of other potential effects such as habitat fragmentation (Boulinier *et al.*, 1998, 2001) or isolation (MacArthur & Wilson, 1967; Harrison, 1991). These factors only weakly affect bird local

extinctions and their effects vary greatly across species and regions (Boulinier *et al.*, 2001; Sallabanks, 2002; Ferraz *et al.*, 2007). Such confounding factors can introduce noise to the local extinction–climate relationship, which reduces the ability to detect effects, but not the observed effect size. Here, we did detect effects but these were extremely weak.

Could spatial variation in detection probability have obscured a relationship between extinction probability and climate? Detection probability is likely to be related to abundance. In principle, abundance might be lower in warm areas, leading to a higher apparent rate of extinction, offsetting a true higher extinction rate in cold areas. This seems unlikely. First, the correlation between abundance and climate in our data was very low ($r < 0.14$). Second, intraspecific extinction rates are strongly spatially structured, albeit not in ways that relate to climate. It would require an extraordinary coincidence for the detection probability to covary with climate such that the net correlation between extinction rate and climate is near zero and that it does so without destroying other spatial structure in extinction rates. Third, requiring a species to be unobserved for three years before it is regarded as absent did not change our conclusions. Large systematic biases in our estimates of extinction rates seem unlikely.

We conclude that patterns of local extinctions in passerine birds do relate to contemporary climate. The observed effects are, however, extremely weak and highly variable among species, such that contemporary climate has virtually no predictive power in explaining variation in local extinctions.

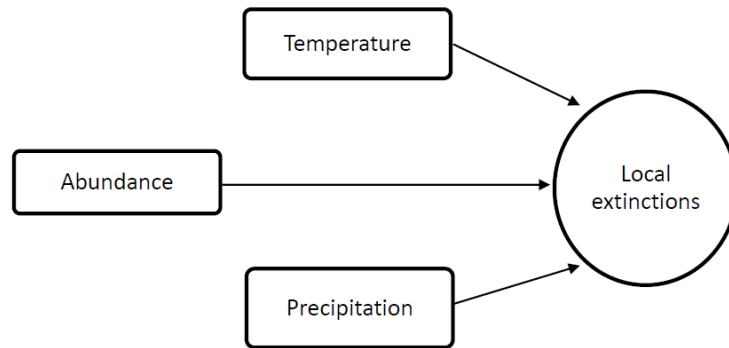
ACKNOWLEDGEMENTS

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FIGURES

Climatic harshness hypothesis



Climate-centre hypothesis

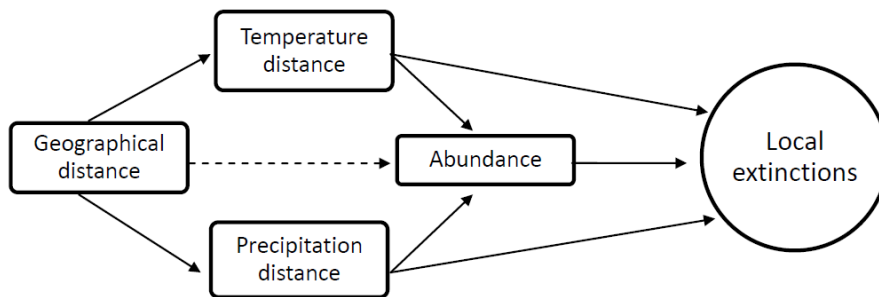


Figure 5.1 graphical representations of two hypotheses proposing an effect of climate on the probability of local extinction, *sensu* MacArthur & Wilson (1967). The climatic harshness hypothesis proposes that local extinctions are more frequent in areas with harsh temperature and precipitation. The climate-centre hypothesis proposes that the difference between a species' optimal temperature and the temperature in a region in which the species occurs (i.e. temperature distance) affects the rate of local extinction, either directly, or by reducing the species' abundance. A similar effect is postulated for precipitation. The geographical distance from the centre of a species' distribution may affect abundance directly (i.e. the abundant-centre hypothesis; dashed line) or indirectly by affecting climatic distance.

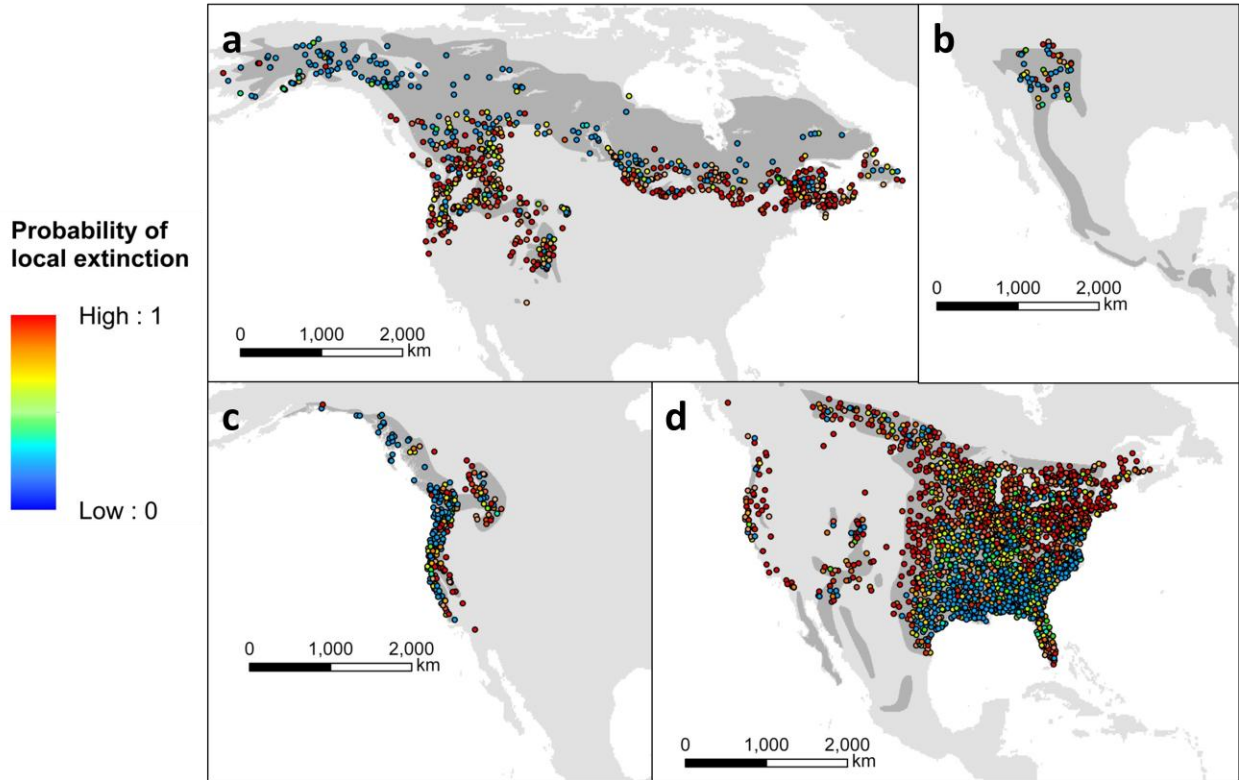


Figure 5.2 Spatial variation in the probability of local extinction for selected bird species in North America: (a) grey jay (*Perisoreus canadensis*); (b) Grace's warbler (*Setophaga graciae*); (c) chestnut-backed chickadee (*Poecile rufescens*); and (d) purple martin (*Progne subis*). The probability of local extinction varies from 0 in blue (presences on a route are always followed by a presence) to 1 in red (presences on a route are always followed by absences). The breeding range of the species is represented in dark grey. Maps are in Eckert IV projection with a central meridian of 100° W.

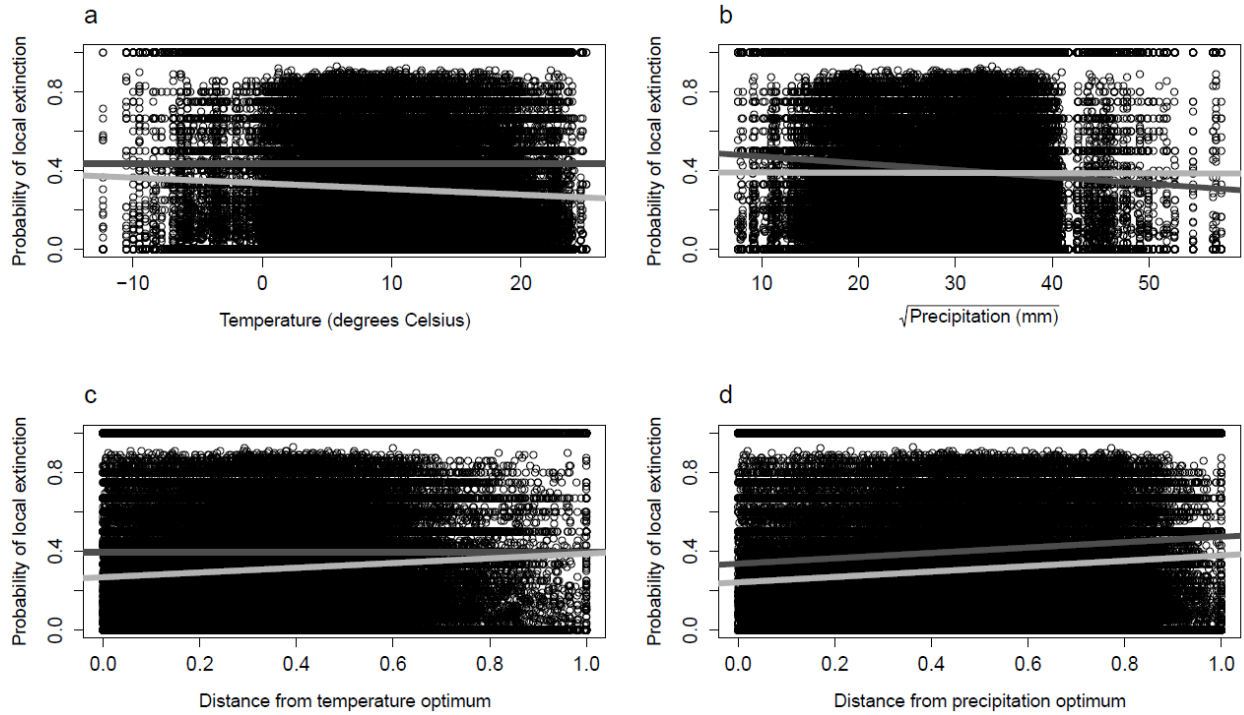


Figure 5.3 The probability of local extinction among 206 passerine birds in North America as a function of (a) the observed mean annual temperature, (b) the observed square root of total annual precipitation, (c) the climatic distance from a species' temperature optimum and (d) the climatic distance from a species' precipitation optimum. Each datum represents the probability of local extinction on a given route of the Breeding Bird Survey for a given species ($n = 228,502$). The dark grey lines represent the fixed effect of the independent variable (climate in (a) and (b) and climatic distance from the optimum in (c) and (d)) on the probability of local extinction when fitted with a linear mixed-effects model, where species is treated as a random effect. The pale grey lines represent the fitted relationship of a simple linear regression fitted through all data ($R^2 < 0.01$ for panels (a), (b) and (c) and $R^2 = 0.01$ for panel (d); $P < 0.01$ in all cases); species occurring on more routes have more weight in the regression

CHAPTER 6 The weakness of evidence supporting tropical niche conservatism as a main driver of current richness–temperature gradients

Citation: Boucher-Lalonde, V., De Camargo, R. X., Fortin, J.-M., Khair, S., So, R. I., Vázquez Rivera, H., Watson, D., Zuloaga, J. & Currie, D. J. (2015) The weakness of evidence supporting tropical niche conservatism as a main driver of current richness–temperature gradients. *Global Ecology and Biogeography*, **24**, 795–803. doi: 10.1111/geb.12312

ABSTRACT

Aim Geographical variations in species richness are highly correlated with current temperature. The tropical niche conservatism hypothesis proposes that this relationship is driven by the evolutionary conserved ancestral tolerances of species to the warm environments in which most clades have originated. The hypothesis predicts that the slope of the richness–temperature gradient is positively related to the temperature of the period during which the clade originated. Here, we test this prediction for bird and mammal families in the Americas and by revisiting a global analysis of 343 groups of organisms.

Location The Americas and world-wide

Methods We computed the slope of the species richness–current temperature relationship within each bird and mammal family in the Americas. We used palaeo-climate reconstructions to estimate temperature at the time of the family's origination, taken from the fossil record. We then tested how much of the among-family variance in the richness–temperature slope could be explained by the temperature at the family's origination. We repeated this test for 343 groups of

organisms presented in a study by Romdal *et al.* (*Global Ecology and Biogeography*, **22**, 344-350).

Results Contrary to the prediction of tropical niche conservatism, the temperature at which bird and mammal families originated does not explain variations in the richness–temperature relationships. Similarly, we show that, although the predicted relationship can be statistically detected in a broad range of groups of organisms (Romdal *et al.*, 2013, *Global Ecology and Biogeography*, **22**, 344-350), it in fact statistically explains only 1.2–2.9% of the variance among groups in the slope of richness gradients.

Main conclusions We found evidence inconsistent with the hypothesis that tropical niche conservatism is the main mechanism underlying the ubiquitous richness–climate relationship.

INTRODUCTION

At broad spatial scales, the geographic variation in species richness of virtually all higher-level species groups (e.g. angiosperms, vertebrates, insects) is highly correlated with current climatic variables, especially temperature (Hawkins *et al.*, 2003; Hillebrand, 2004; Field *et al.*, 2009; Buckley *et al.*, 2012). This strong correlation between richness and climate (hereafter richness–climate relationship) is highly consistent across space and time for high-level taxonomic groups, such that, given the climatic conditions of a region, contemporaneous species richness of a taxon can be predicted, irrespective of the continent (Francis & Currie, 2003), season (Boucher-Lalonde *et al.*, 2014a) or millennium (Willis *et al.*, 2007; Vazquez-Rivera & Currie, 2014) of interest. Although a large fraction of the explained variance in the richness–climate relationship is congruent across space and time, detectable differences typically remain amongst time periods (Boucher-Lalonde *et al.*, 2014a; Vazquez-Rivera & Currie, 2014), regions (Francis & Currie, 2003; Jiménez & Ricklefs, 2014), taxonomic groups (Wolters *et al.*, 2006) and as a function of species traits (e.g. Tello & Stevens, 2010). Moreover, the species richness–climate relationship does not hold consistently within lower taxonomic groups such as families, as opposed to within higher taxonomic groups such as classes (Currie, 1991; Buckley *et al.*, 2010). But, for large groups of organisms, at large geographic extents and coarse grain, the strong species richness–climate relationship is nearly ubiquitous, such that it "must have a common explanation" (Rohde, 1992; but see e.g. Tello & Stevens, 2010; Gouveia *et al.*, 2013 who argue for multiple causality). Although dozens of hypotheses have been proposed to tackle the causal link underlying the richness–climate relationship, the causal mechanisms underlying the pattern remain largely unresolved (Rodhe, 1992; Mittelbach *et al.*, 2007; Brown, 2014) because, we propose, too few attempts have been made to prune hypotheses out of the literature.

Niche conservatism is increasingly often proposed to be a main driver of broad-scale richness gradients (Hawkins, 2008; Buckley *et al.*, 2010; Wiens *et al.*, 2010; Stevens, 2011; Romdal *et al.*, 2013). The tropical niche conservatism hypothesis proposes that species distribution patterns are "by and large" (Romdal *et al.*, 2013, p. 344) governed by evolutionary conserved ancestral tolerances to warm and wet environments (Wiens & Graham, 2005; Wiens *et al.*, 2010). This hypothesis proposes that (1) most clades of multicellular organisms originated in periods with widespread tropical-like conditions, and that (2) most species in these clades have at least partly retained their ancestral physiological tolerances, (3) leading to a strong current richness–climate relationship. Because (1) and (2) are generally accepted (Ricklefs & Schuler, 1993; Wiens & Donoghue, 2004; Wiens *et al.*, 2010; Jansson *et al.*, 2013), it has been argued that, as a consequence, niche conservatism can explain the observed richness–climate relationship (Wiens & Graham, 2005; Hawkins, 2008).

Although the tropical niche conservatism hypothesis predicts that species' evolved physiological tolerances to climate should lead to a positive richness–temperature relationship, this prediction provides, at best, the weakest possible test of the hypothesis. It was the observation that the hypothesis was developed to explain in the first place. It is possible that factors other than species' evolved physiological tolerances may constrain regional richness to a much greater extent. Since most species tolerate the climates of many more regions than they actually occupy (Svenning & Skov, 2004; Araújo *et al.*, 2013; Gouveia *et al.*, 2014), there could be more stringent constraints on richness (Boucher-Lalonde *et al.*, 2014a).

A strength of the tropical niche conservatism hypothesis is that it does make other explicit predictions (Wiens & Graham, 2005; Wiens *et al.*, 2010). Specifically relating to species richness patterns, tropical niche conservatism predicts that the temperature during the period in

which a clade originated influenced the sign and strength of the richness–temperature relationship. Clades that originated during particularly warm geological periods should have steep positive richness–temperature relationships, whereas clades that originated in colder climatic conditions should have shallower or even negative richness–temperature relationships (Wiens & Donoghue, 2004; Buckley *et al.*, 2010).

Romdal *et al.* (2013) recently provided evidence consistent with this prediction of the tropical niche conservatism hypothesis. They found that, in a large sample of varied groups of organisms, the slope of the richness–latitude relationship is statistically significantly related to the temperature at which the group originated. However, Romdal *et al.* (2013) do not report the strength of the relationship. Thus, although the relationship predicted by niche conservatism is statistically detected, it remains unclear whether it is consistent with the interpretation that tropical niche conservatism is “by and large” (Romdal *et al.*, 2013, p. 344) responsible for the strong and nearly ubiquitous richness–climate relationship. Several other studies have also detected signals of niche conservatism and argued that it could explain both the classical richness–climate relationship as well as exceptions to the pattern (Pyron & Burbrink, 2009; Wiens *et al.*, 2009; Buckley *et al.*, 2010; Giehl & Jarenkow, 2012).

Here, rather than test whether any signal predicted by niche conservatism is statistically detectable, we ask how strong it is. If niche conservatism is the main mechanism causing broad-scale spatial variation in species richness, then the signal should be strong.

We first re-examined the data of Romdal *et al.* (2013) to assess how much of the variance in richness can be attributed to niche conservatism. The answer, we show below, is: not much. We then asked: could the observed relationship in Romdal *et al.* (2013) be so weak because the data are very heterogeneous and sometimes consist of polyphyletic groups of organisms (e.g.

trees, macroalgae, macroinvertebrates)? The statistical signal of tropical niche conservatism should be stronger for lower-level monophyletic clades because the conservatism of the climatic niche should decrease through time, and thus towards the base of the phylogeny (Wiens & Donoghue, 2004; Wiens & Graham, 2005), although it is also possible that niche conservatism has been relaxed in recent time periods (Buckley *et al.*, 2010). We therefore used data on bird and mammal families within the Americas. Moreover, the predictor variable used by Romdal *et al.* (2013) – temperature at the time of origination of the clade – was a very coarse three-level categorical variable. We therefore asked whether using a more precise continuous measure of temperature increases the amount of the variance in the slope of the current richness–temperature relationship that can be statistically related to the temperature at the time of the family's origination.

METHODS

First, we reanalysed the data of Romdal *et al.* (2013). Romdal *et al.* (2013) considered the slope of the richness–latitude relationship of the 343, sometimes polyphyletic, groups of organisms from around the world compiled in the meta-analysis of Hillebrand (2004). We modelled the slopes of these richness–latitude relationships as a function of the climate at which the group originated using general linear non-parametric models. Romdal *et al.* (2013) distinguished between five broad palaeoclimatic categories: (1) 'snowball earth'; (2) full glaciation; (3) partial glaciation; (4) transitional/warm; and (5) warm. They then grouped these original categories into three by grouping the two coldest and two warmest categories (Romdal *et al.*, 2013). We treated this explanatory variable as either categorical, following Romdal *et al.* (2013), or as an ordinal variable with linear contrasts.

Second, we assessed how much of the variance in the slopes of richness–temperature relationships, among bird and mammal families in the Americas, can be attributed to the temperature at which the families originated. Breeding ranges of bird and mammal species in the Americas were obtained from NatureServe (Ridgely *et al.*, 2007; Patterson *et al.*, 2007; Data available from <http://www.natureserve.org>, accessed January 2010). We divided the Americas into equal-area quadrats of 10,000 km² and removed those quadrats with <50% land area, leaving 4141 quadrats (following Boucher-Lalonde *et al.*, 2014b). A quadrat was considered occupied by a species when its breeding range overlapped the quadrat at least partly. We included zero richness quadrats, but this choice did not affect our qualitative conclusions. We estimated the mean current temperature of each quadrat from WorldClim 30 arc-seconds mean annual temperature (Hijmans *et al.*, 2005). For each family, we computed the slope of the richness–current temperature relationship using a linear model. Prior to this, we standardized the data for each family by subtracting richness in each quadrat by the mean across all quadrats and by dividing by the standard deviation, so that the slopes of these relationships would not depend upon species richness per quadrat. We did the same analyses without standardizing the data, and we found qualitatively very similar results to those presented below (data in Appendix S6.1 and Appendix S6.2). Species were assigned to families based on the classification of NatureServe.

Following Romdal *et al.* (2013), the geological period of origination of each bird and mammal family was estimated from the fossil record in Benton (1993). Dates of origination ranged from < 1 to 100 million years ago (Ma). Bird families first appeared in the fossil record, on average, during the early Miocene, and mammal families, during the early Oligocene. When the origin was considered uncertain, we analyzed the data using both the earliest and latest origin period proposed by Benton (1993). We restricted the data to families that were present in both

NatureServe and Benton (1993), such that we carried out our analyses on 64 bird and 43 mammal families, each comprising between 1 and 336 species (Appendix S6.1 and Appendix S6.2). In order to verify that our conclusions are robust to the method used to estimate origination time (here, the fossil record), we also estimated the divergence time of each family based on the molecular phylogenetic time tree of Jetz *et al.* (2012) for birds and Meredith *et al.* (2011) for mammals (details in Appendix S6.3).

We estimated the temperature at the time of origination from several sources (Appendix S6.3). First, we used the climate categories of Romdal *et al.* (2013) described above. Second, we used the temperature reconstructions of Cramer *et al.* (2011), digitized from their Figure 9. Third, we digitized both the global and tropical temperature estimates from Figure 1 in Crowley and Berner (2001). Finally, we used the inverse of the 5-point running average data of Zachos *et al.* (2001) on deep-sea oxygen isotope ($\delta^{18}\text{O}$) as a proxy for global temperature (data available from <http://www.ncdc.noaa.gov/palaeo/pubs/ipcc2007/fig61.html>). This dataset goes back only 65 Myr, so its use resulted in the exclusion of two families. Given the uncertainty around the temperature estimates, we also wanted to assert that our conclusions did not depend on our specific choice of temperature reconstruction. For all temperature data sets, we considered the minimum, maximum and median temperature during the period of origin. As this choice did not affect our conclusions, we present the results for the median temperature during the period of origin.

We used linear regression models to test the hypothesized effect of the temperature at the family's origination on the slope of the richness–current temperature relationship. Tropical niche conservatism predicts that the temperature during the geological period at which the family originated has a positive effect on the slope of the richness–temperature relationship; i.e.

increasingly positive slopes in clades that originate during warmer periods. We also tested whether temperature at origination could predict the sign (irrespective of the strength) of the richness–temperature relationship using generalized linear model with a binomial error distribution and a logit link function.

Using non-parametric models (as did Romdal *et al.*, 2013) led to the same conclusions, so we only present the results for the parametric models. Since the slope of the richness–temperature relationship can be estimated more precisely in families with larger numbers of species, we also used weighted linear models where each family was weighted by the number of species in the family. However, this also had no effect on our qualitative conclusions. Hence, we only present the results for the non-weighted regressions. Note that Romdal *et al.* (2013) used the slope of the richness–latitude relationship in their analyses, instead of the richness–temperature relationship. We did our analyses both ways and our conclusions were unchanged (see Appendix S6.1 and S6.2 for data and S6.3 for results). We only present the results for temperature, as the predictions from the tropical niche conservatism hypothesis are specific to temperature rather than latitude. Finally, we also carried out the analyses separately for families with a South American versus North American origin, using the data compiled by Smith *et al.* (2012); see Appendix S6.3. Analyses were carried out in R 3.1.0 (R Core Team, 2014).

RESULTS

Although variations in the slope of the latitudinal gradient in richness among groups of organisms is significantly related to the temperature category at which the group originated in the data of Romdal *et al.* (2013), the relationship explains very little of the variance in slopes among taxonomic groups (Fig. 6.1). Specifically, the original five categories explained only 1.2% ($p=$

0.04) of the variance, while the reduced 3 climate categories explained 2.4% ($p = 0.04$) of the variance in the slopes, when we treat the climatic categories as an ordinal explanatory variable (and respectively 2.6% and 2.9% of the variance when we treat it as categorical, but the observed effects are not systematically in the predicted direction across the five categories; see Figure 2a in Romdal *et al.*, 2013).

Using more homogeneous and monophyletic taxonomic groups, i.e. bird and mammal families, did not increase the proportion of the variance that could be attributed to tropical niche conservatism. On the contrary, the slope of the species richness–temperature relationships within families was not significantly related to the temperature at which the clade originated (Fig. 6.2a, b). The relationship was slightly negative (albeit non-significant) for mammals, while tropical niche conservatism predicts a positive relationship. When we use a more precise and continuous estimate of temperature at family origination such as the temperature reconstruction of Cramer *et al.* (2011), the relationship remains non-significant (Fig. 6.2c, d and Appendix S6.3).

For both birds and mammals, the relationship between the slope of the richness–temperature relationship and temperature at the family's origin was non-significant for all five different estimates of historic temperatures considered, as well as for the different possible time of origination (latest or earliest appearance in the fossil record; Appendix S6.3). In all cases, the slope was near zero ($p > 0.12$), often negative, and explained very little of the variance ($R^2 < 4\%$). When we separately analyzed families with North American origin (where climates have been sometimes tropical-like, and sometimes cooler) versus South American origin (predominately tropical) in order to reduce the noise in our estimate of temperature at origination that would be due to inter-continental differences, we found the predicted positive relationship only for South American mammals and only three families were driving this pattern (Appendix S6.3).

Temperature at the family's origination period could not explain the sign (positive versus negative) of the family's richness–temperature relationship either ($p > 0.07$ and explained deviance $< 8\%$ in all 20 models considered). When we repeated all analyses using phylogeny-based divergence time estimates (rather than Benton's origination times based on fossils), all relationships remained very weak and non-significant, except when using the tropical temperature estimates of Crowley and Berner (2001), in which case the relationships became statistically significant, but in the direction opposite to that predicted by tropical niche conservatism (Appendix S6.3).

DISCUSSION

Niche conservatism of ancestral temperature tolerances statistically explains, at best, only very small amounts of variations in current richness–temperature gradients. Often, it explains none, or the relationships are in the wrong direction. While Romdal *et al.* (2013) have shown that the slope of the richness–latitude relationship is detectably steeper with increasing temperature at which a group of organisms originated, as predicted by tropical niche conservatism, the relationship in their data explained only 1.2% of the variance. We applied their methodology to bird and mammal families in order to increase the homogeneity in the dependent variable. We used several reconstructions of historical climate that provided greater precision in the independent variable. These refinements did not reveal stronger relationships between richness–temperature slopes and temperature at the time of origination of the clade (Fig. 6.2 and Appendix S6.3; see also Huang *et al.*, 2014 for marine bivalves). If "the niche conservatism hypothesis proposes that species distribution patterns are, by and large, governed by ancestral climatic affinities" (Romdal *et al.*, 2013), then a strong relationship should have been observed.

Simulation models have demonstrated that, given niche conservatism and no ecological limit on richness, small subclades representing 1% of the phylogeny should exhibit strong correlations with temperature, with the sign determined by the region of origin (Hurlbert & Stegen, 2014). Thus, the fact that the species richness within most families is poorly related to temperature is in itself inconsistent with niche conservatism (Appendix S6.1 and S6.2). The empirical evidence is therefore inconsistent with the hypothesis that tropical niche conservatism is a main determinant of current species richness gradients.

In our data, and as reported by others (Currie, 1991; Field *et al.*, 2009), species richness within higher-level taxonomic groups is strongly related to current temperature, with an R^2 of 83% for birds and 64% for mammals. Tropical niche conservatism predicts that this overall strongly positive richness–temperature gradient emerges from aggregating within-clade species richness–temperature gradients, which are often steeply positive (Buckley *et al.*, 2010). Therefore the variance in species richness explained by current temperatures is predicted to be higher within-families than among-families, which is not the case. The mean R^2 of the within-family richness–current temperature relationship is only 30% (maximum 71%) for birds and 21% (maximum 68%) for mammals (Appendix S6.1 and S6.2). Moreover, if tropical niche conservatism were the main driver of such variation (Wiens, 2011; Romdal *et al.*, 2013), then the strong richness–current temperature correlation must reflect an indirect effect resulting from collinearity between current climate and the direct effect of evolutionary radiation in the clades examined. The direct correlation should be stronger than the indirect correlation. But in fact, the reverse is true: the richness–current temperature correlation is very strong, and the relationship between the slope of the richness–temperature relationship and the temperature at the origination of the clade is weak to vanishing (Fig. 6.1; Fig. 6.2; Appendix S6.3).

Might the weak relationship between the slope of the richness–temperature relationship and temperature at the origination of the clade be due to error in the temperature estimates? There are undoubtedly errors, both in the estimated time of origination of clades and in the temperature reconstructions, which would weaken any existing correlations. Although our three continuous measures of temperature at origination, estimated from independent global temperatures data sets, were all highly correlated ($r = 0.92\text{--}0.99$ for birds and $0.92\text{--}0.98$ for mammals), the origination times estimated from the fossil record were only weakly correlated with those estimated from molecular phylogenies ($r = 0.43\text{--}0.45$ for birds and 0.28 for mammals). We carried out a small simulation to determine to what extent errors in the independent variable can weaken an otherwise strong correlation (Appendix S6.4). We found that the uncertainties around the temperature at origination estimates would need to be very large to have masked the effect of temperature at origination, if there were such an effect (viz.: the correlation between real and estimated temperature at origination would have to be c. $r < 0.25$; Appendix S6.4). It therefore appears unlikely that the temperature at origination is measured with so much error that it completely masks a strong correlation.

A potential caveat is that the tropical temperature data of Crowley and Berner (2001) over the past 100 Myr were not so strongly correlated with the global estimates ($0.40 < r < 0.80$), such that the global estimates of temperatures may poorly reflect the actual temperatures experienced by individuals in the specific region in which the clade originated. If global and regional variations in temperatures are in fact very poorly correlated (c. $r < 0.25$), it could explain the lack of effect we have observed here (Appendix S6.4). If the errors around the temperature at origination estimates are that large, it would however similarly invalidate the conclusions of Romdal *et al.* (2013) and would currently prevent a strong test of tropical niche

conservatism, here or elsewhere, as the main driver of richness gradients. To reduce the error in our predictor variable due to regional differences in temperature, we analyzed the data separately for families with South American and North American origin. Our conclusion, that the bulk of the evidence is inconsistent with tropical niche conservatism as a main explanation of current richness gradients, remained unchanged (Appendix S6.3).

We have also not tested different models of niche conservatism. For example, it is possible that there was early niche divergence at the root of the phylogeny (> 50 Myr), followed by strong niche conservatism (Buckley *et al.*, 2010). We only tested whether variations in the slopes of the species richness–temperature relationship at low taxonomic levels could be explained by tropical niche conservatism, leading to a strong positive richness–temperature relationship at higher taxonomic levels. This was not the case.

The extent to which ecological niches are conserved through phylogenies may have been overstated in the literature (Losos, 2008). But, even if species do have a strong tendency to retain their ancestral tolerances to warm conditions (Wiens & Graham, 2005; Araújo *et al.*, 2013), broad-scale geographical gradients in species richness may have little to do with individual species' climatic tolerances. Species' fundamental niches tend to be much larger than their realized niches (Araújo *et al.*, 2013). Specifically, throughout their range, species' occupy only a small subset of the temperatures at which they can survive, which is not necessarily predictable from their fundamental niche (Gouveia *et al.*, 2014). So, even if many species can tolerate warm environments and few can tolerate cold (Araújo *et al.*, 2013), predictions of species richness based on tolerances to temperature may systematically greatly overestimate richness.

It is often argued that species richness can only be modified through the processes of speciation, extinction and dispersal; therefore any explanation for species richness patterns must

ultimately appeal to these processes (Wiens & Donoghue, 2004; Wiens, 2011). One of the strengths of the tropical niche conservatism hypothesis is that its mechanism relies on these processes (Wiens & Donoghue, 2004; Wiens, 2011). However, ecological factors can influence these processes (Wiens, 2011), which could simply operate to fill-up an ecologically-determined equilibrium richness gradient (Rabosky, 2009; Hurlbert & Stegen, 2014). If so, different evolutionary rates could lead to roughly equal number of species in similar environments (Rabosky, 2009). Several hypothesized mechanisms that would lead to a top-down ecological control on species richness have been empirically rejected (Currie *et al.*, 2004; Hawkins *et al.*, 2007); however, refutation of a given mechanism is not positive evidence for another (Wiens, 2011). Other hypotheses regarding geographic variation in species richness that make explicit predictions beyond a positive richness–climate relationship remain to be tested (Mittlebach *et al.*, 2007; Brown, 2014). Tropical niche conservatism may determine the distribution of taxa among biomes or biogeographic provinces (e.g., Fig. 1 in Wiens & Donoghue, 2004; Table 1 in Wiens *et al.*, 2009), but we found no evidence that it determines richness gradients at finer grains.

Other evidence is also inconsistent with the hypothesis that niche conservatism explains spatial gradients in species richness at grains of $\sim 10^4$ km² over continental to global extents. First, species richness closely tracks seasonal changes in climatic variables even though individual species do not (Boucher-Lalonde *et al.*, 2014a). A niche conservatism explanation for richness gradients postulates that species richness tracks climate *because* individual species do (Boucher-Lalonde *et al.*, 2014a). In contrast, individual species' realized niches tend to shift temporally (Veloz *et al.*, 2012; Boucher-Lalonde *et al.*, 2014a). Second, lineages frequently adapt to new climatic conditions long before they occupy these climates (Jansson *et al.*, 2013; Zanne *et al.*, 2014). This suggests that climatic tolerances are not the primary constraints on

species distributions as assumed by the hypothesis that niche conservatism is the main determinant of species richness. Third, while tropical niche conservatism predicts that richness is limited by which species can tolerate the environment, this does not generally appear to be the case (Algar *et al.*, 2009a; Boucher-Lalonde *et al.*, 2014a). Fourth, assemblages that have similar geographic gradients of richness can have very different evolutionary trajectories (Hawkins *et al.*, 2012), suggesting either remarkable coincidence or ecological rather than evolutionary limits on richness (Rabosky, 2009). Fifth, studies that have attempted to relate spatial variation in species richness to measures of evolutionary derivedness have found weak relationships or none at all. Examples include: Cicindelidae (tiger beetles), Percidae (perches and darters), Catastomidae (suckers), Cyprinidae (minnows) (Kerr & Currie, 1999), butterflies (Hawkins & DeVries, 2009), Muscidae (flies) (Lowenberg-Neto *et al.*, 2011), Phyllostomidae (leaf-nosed bats) (Stevens, 2006) and angiosperm families (Hawkins *et al.*, 2011).

In sum, although niche conservatism may explain the phylogenetic structure of species assemblages and which species are excluded from species pools (Algar *et al.*, 2009a; Moen *et al.*, 2013), it cannot explain among-clade variations in the richness–temperature relationship. This could be because there is no such relationship or because the errors around the temperature at origination estimates are so large that they mask the existing relationship. Current climate has been repeatedly found to be a strong and consistent predictor of species richness of higher-level taxonomic groups across space and time. But, here and elsewhere in the literature, we found evidence inconsistent with the hypothesis that tropical niche conservatism is the main mechanism underlying the ubiquitous richness–climate relationship. The evidence that nominally supports the hypothesis is much weaker than first meets the eye.

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FIGURES

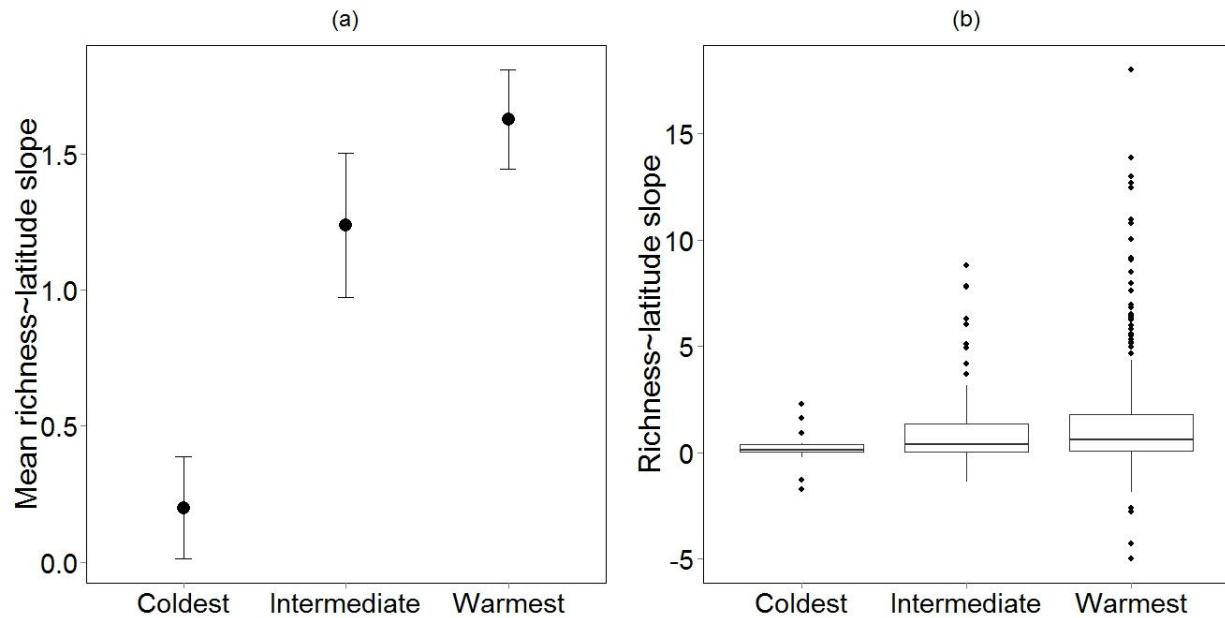


Figure 6.1 (a) The mean slope of the latitudinal diversity gradients in 343 groups of organisms as a function of the temperature at the group's origination, as shown in Figure 1b in Romdal *et al.* (2013). Error bars represent the standard error of the mean. (b) Boxplots representing the variation in the underlying data. The tropical niche conservatism hypothesis deals with the variation in slope among taxonomic groups, as opposed to the variation in mean slope among sets of species (panel a).

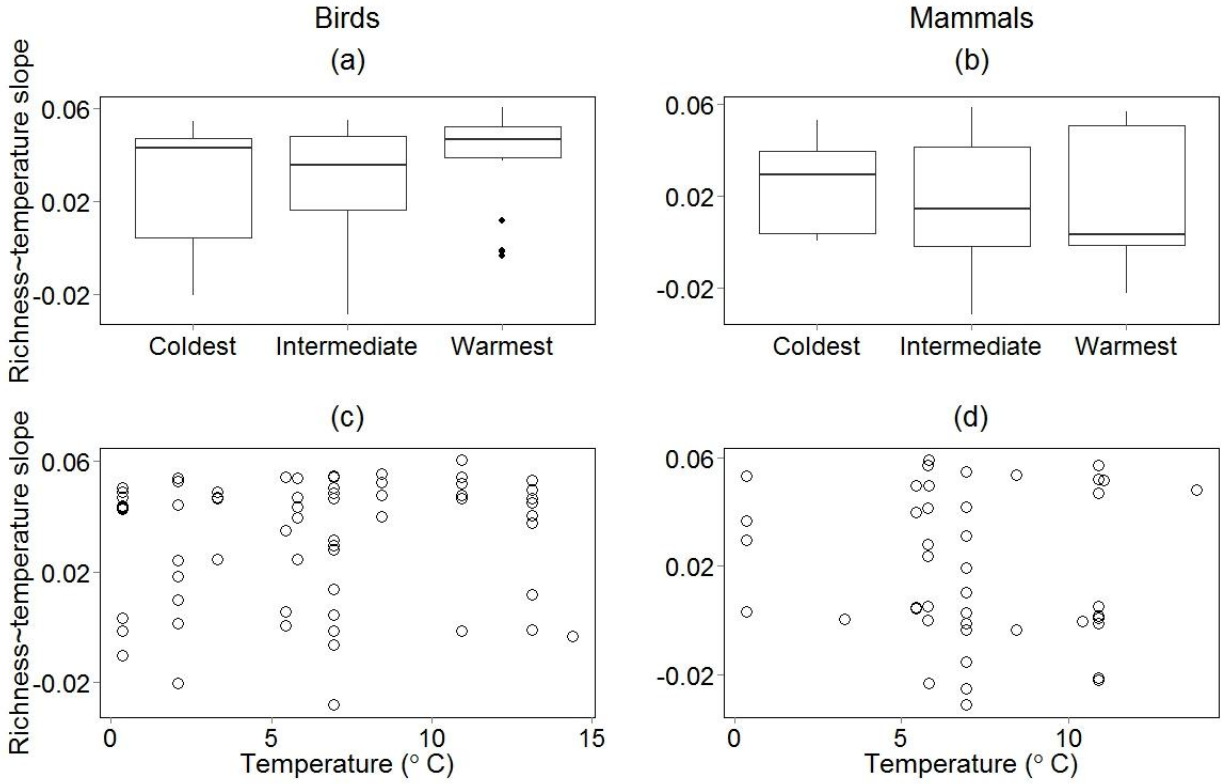


Figure 6.2 Standardized slope of the species richness–temperature (spatial grain: 10,000 km²) relationship in the Americas for (a, c) 64 bird and (b, d) 43 mammal families as a function of the temperature at which the family originated. We here estimated the temperature at family origination using (a, b) the palaeoclimate categories of Romdal *et al.* (2013) as well as (c, d) the temperature reconstructions of Cramer (2011). All relationships are non-significant ($p > 0.25$). Here, when uncertain, the earliest origin period was taken.

CHAPTER 7 A critical re-examination of historic climate stability and its hypothesized effect on species richness

Citation: Boucher-Lalonde, V. & Currie, D. J. (Unpublished) A critical re-examination of historic climate stability and its hypothesized effect on species richness.

ABSTRACT

It is commonly argued that broad-scale geographic variation in species richness reflects major influences of both current climate and historic climate stability. Here, we examine the strength of the published tests of these two propositions. Both current and historic climate are strongly statistically related to spatial variation in species richness. More importantly, the richness–current climate relationship has survived strong tests: models calibrated in one region or one temporal period accurately predict patterns of richness in other regions and other temporal periods. In contrast, published evidence regarding effects of historical climate stability is quite mixed. Historic climate stability typically explains little additional variance in species richness, beyond that explained by current climate. Correlations reported in the literature between richness and climate stability are sometimes in the predicted direction, and sometimes in the opposite direction. A prominent recent study by Hortal *et al.* (2011 *Ecology Letters* 14: 741-748) reported spatial variation in the slope of the richness–climate stability relationship, which the authors interpreted as evidence of effects of historical climate. Re-analysing their data, we found that controlling for current climate completely changes those patterns. Fitting alternative models does as well. We found no study in which a model of species richness fitted as a function of climate stability was shown to accurately predict richness in independent data. We highlight that the

statistical effects of historic climate stability could potentially arise from collinearities and spatial autocorrelation. Current evidence suggests that any effect of historic climate stability on richness gradients is likely small and idiosyncratic, such that it does not improve our predictive ability across space and time. Stronger tests must be carried before one can argue that historic climate stability is an important driver of current richness patterns.

Introduction

Species richness varies strikingly over broad spatial extents (regional to global) and coarse grains (e.g. 10^4 km^2). Some authors have argued that this variation in richness reflects mainly variations in contemporary environmental conditions; e.g. (Currie, 1991). Others have emphasized major historical events such as climatic oscillations; e.g. (Dynesius & Jansson, 2000). Many argue that these are both important to our understanding of diversity gradients (Ricklefs *et al.*, 1999; Hawkins *et al.*, 2005; Hortal *et al.*, 2011; Gouveia *et al.*, 2013). The purpose of this study is to ask what is the actual evidence that spatial variation in richness is related to both contemporary and historical climate? How strong are the published tests of these hypotheses?

The perceived strength of hypothesis tests depends, in part, on one's philosophical stance. We take the philosophical view that predictive ability is the operational way to measure understanding (Platt, 1964; Peters, 1991; Gottfried & Wilson, 1997). Hypotheses are supported not by marshalling evidence that is consistent with the hypothesis (i.e., the “problem of induction” (Russell, 1949; Popper & Miller, 1983), but rather by subjecting the hypotheses to strong tests (Platt, 1964). Tests are provided by deducing predictions from the hypothesis: predictions are things that *must* be observed if the hypothesis is true. Predictions are not simply speculations about things that *might* be observed, under the given hypothesis. *Strong predictions* are those that are precise and highly unlikely to occur unless the hypothesis is true (Platt, 1964). In this light, a hypothesis that predicts a detectable correlation between two variables has provided only a relatively weak prediction, because correlations may arise for reasons other than a causal link between the two variables. A hypothesis that predicts specific values for the dependent variable provides a much stronger test.

Let us begin with the influence of contemporary environment on broad-scale variations in species richness. Variations in richness are strongly statistically related to climatic variables such as temperature and precipitation (e.g. $R^2 = 0.76$ in (Currie, 1991); 0.80 in (O'Brien, 1998); 0.90 in (Boucher-Lalonde *et al.*, 2014a). Consistent with the hypothesis of a causal relationship between contemporary climate and richness, the richness–climate relationship is highly consistent through space (Francis & Currie, 2003; Field *et al.*, 2009), through seasonal changes in climatic variables (Hurlbert & Haskell, 2003; Boucher-Lalonde *et al.*, 2014a), through climate warming during the Holocene (Vázquez-Rivera & Currie, 2015), through the recent glacial periods (Willis *et al.*, 2007), and it holds for virtually all high-level taxonomic groups (Hillebrand, 2004). Thus, the richness–contemporary climate relationship has survived a large number of strong tests by natural experiment (Table 7.1): richness patterns are not merely correlated to contemporary environment; those correlations (models) accurately predict richness variation through time and space in data sets independent of the data used to develop the original correlations. Other environmental variables beside climate also statistically account for (generally smaller) amounts of variation in species richness: in particular, primary and secondary productivity (Waide *et al.*, 1999; Waring *et al.*, 2006), environmental heterogeneity (Kerr & Packer, 1997; Field *et al.*, 2009), isolation (Kalmar & Currie, 2007) and edaphic factors (Field *et al.*, 2009; Dubuis *et al.*, 2013). The hypothesis that contemporary environmental conditions affect richness gradients has thus survived multiple strong tests, although specific mechanisms underlying the relationship are still unclear, and some of the variance in richness is clearly related to other factors, or is left unexplained (~25%).

Consider now historical variables that have been hypothesized to affect observed geographical patterns in species richness. Factors such as historical contingency (Ricklefs *et al.*,

1999), time and area for diversification (Fine & Ree, 2006), phylogenetic conservatism of ancestral climatic niches (Wiens *et al.*, 2010) or migration lag since the last ice-age (Svenning & Skov, 2007) could exert strong influences on current species distributions. And, indeed, variations in richness can be strongly statistically related to these historical variables (e.g. max $r^2 = 0.57$ in (Fine & Ree, 2006); 0.54 in (Araújo *et al.*, 2008); 0.39 in (Sandel *et al.*, 2011). Many studies have modelled richness as a function of both current climate and historical effects. These studies have generally found that simple correlations between richness and historical variables statistically account for significant amounts of variation in richness, but historical variables only account for very small amounts of additional variation, after accounting for contemporary climate (Hawkins & Porter, 2003; Currie & Francis, 2004; Hawkins *et al.*, 2006; Montoya *et al.*, 2007; Dunn *et al.*, 2009; Gouveia *et al.*, 2013; Lima-Ribeiro *et al.*, 2013). This is because historical factors and current climate are often highly collinear, such that their partial statistical effects are both very small (Hawkins *et al.*, 2006; Araújo *et al.*, 2008). Correlations rarely distinguish convincingly between hypothesized effects of contemporary and historical variables. And, correlations between highly spatially autocorrelated variables are likely to be strong and statistically significant even in the absence of causal relationships and regardless of whether such a causal link appears biologically sensible or not; see (Beale *et al.*, 2008a).

However, the fact that richness–contemporary climate models accurately predict changes in richness in natural experiments in which contemporary climate is changed, but historical climate is unchanged, or uncontrolled (Table 7.1), suggests that the shared statistical effect of history and contemporary climate is largely due to the latter. We are not aware of any study in which richness was modelled as a function of historical climate, and this model then successfully

predicted richness in an independent data set. In other word, richness–historical climate relationships have been fitted, but the resulting models have not yet been independently tested.

Climate stability since the Last Glacial Maximum

Here, we consider specifically the historic climate stability hypothesis, which has recently gained momentum in the literature (Araújo *et al.*, 2008; Fløjgaard *et al.*, 2011; Hortal *et al.*, 2011; Normand *et al.*, 2011; Gouveia *et al.*, 2013; Mathieu & Davies, 2014). The historic climate stability hypothesis proposes that temporal variations in climate regimes during glacial and interglacial cycles caused local extinctions, which in turn reduced species richness (Dynesius & Jansson, 2000; Araújo *et al.*, 2008). During glacial periods, species are hypothesized to have been confined to refuge areas, mostly, but not exclusively, at lower latitudes than their current distributions (Svenning *et al.*, 2008). When the glaciers retreated, species then re-colonized areas with suitable climates, but with slow migration rates, leading to disequilibrium between current climatic conditions and species distributions (Svenning & Skov, 2007).

Several studies have related current species richness to the difference between current climate and climate during the last glacial maximum (LGM, 21,000 years ago). These studies have detected statistically significant correlations between species richness and climate stability since the LGM (Araújo *et al.*, 2008; Normand *et al.*, 2011; Gouveia *et al.*, 2013). Correlations of this sort do represent a test of the climate stability–richness hypothesis. However, these do not represent strong tests of a causal link between richness and historical climate because: 1) they have not excluded the possibility that richness–historical climate correlations are due to collinear contemporary variables (e.g., by testing the relationships in areas where historical and contemporary climate are not collinear); 2) they have not shown that the correlations are

predictive in independent data sets (e.g., by calibrating on one continent and predicting on another); or 3) they have not shown that changes in the independent variable lead to changes in the dependent variable (e.g., by examining changes in richness as climate changes).

Critical tests of genuine predictions?

Now, let us examine more closely the specific evidence that has been presented as supporting the historic climate stability hypotheses. In a recent paper, Hortal *et al.* (2011), p. 742, "attempt to disentangle the contributions of past and current climate on current diversity of Scarabaeinae (Coleoptera: Scarabaeidae) dung beetles in Europe". They hypothesized that phylogenetic conservatism of cold intolerance in Scarabaeinae led to virtually no species surviving beyond the LGM 0°C isotherm (Hortal *et al.*, 2011). They postulated that, north of the LGM 0°C isotherm, species richness should be determined by "the establishment of new assemblages following the change in environmental conditions as the climate warmed", while south of this limit, richness should be determined by "environmental changes since the LGM and long-term historical and community assembly processes" (Hortal *et al.*, 2011), p.742. From this hypothesis, Hortal *et al.* (2011) presented two predictions that relate to geographical patterns in species richness (other predictions related to species composition): first, that the slope of the relationship between species richness and climate variability since the LGM changes at the LGM 0°C isotherm. Second, they predicted that the relationship between species richness and current environmental conditions is stronger in the northern part of the continent.

The first weakness of this hypothesis is its predictions. Although they are not unreasonable, it is not obvious that they are logically necessary, given the hypothesis. It is not clear that they would refute the hypothesis if they turned out not to be true. Hortal *et al.* (2011)

preceded their predictions with explanations of how historical climate “may” have affected current richness gradients. Thus, if Hortal *et al.* (2011) did not view their stated predictions as critical tests with the potential to refute their hypothesis, but rather as historical interpretations of observed patterns, it could explain our divergent conclusions (below).

Nonetheless, let us treat the predictions of Hortal *et al.* (2011) as critical hypothesis tests. We repeated the analyses of Hortal *et al.* (2011), using the same data, and the same analytical methods. We asked what is the strength of the evidence consistent with the predictions and whether the data are equally consistent with interpretations other than the historical hypothesis they propose. Specifically, we modelled current patterns of richness as a function of the 14 current and historical environmental variables from their study, given that they argue (p. 741) that richness depends upon both contemporary and historical climate, and that current climate is a well-supported predictor of richness gradients (Table 7.1). Details of our analyses are given in Appendix S7.1.

First, we found that temperature variability since the LGM uniquely accounted for only a small amount of the variance in Scarabaeinae richness. Among the 14 current and historic environmental variables considered, richness is most strongly linked to PET and current temperature, explaining respectively 78% and 72% of the variance. In comparison, temperature variability statistically explains 50% of the variance in richness. When included together, current temperature uniquely explains 32% and temperature variability 10% of the variance in richness, while together explaining 82%. An additive global regression model containing all 14 current and historic environmental variables explains 91% of the variance in richness, 5% of which is uniquely explained by current temperature and 0.5% by temperature variability. All 14 variables are statistically significant ($p < 0.05$), which is unsurprising due to the large sample size ($n =$

1056). Current temperature had the largest standardized effect size while historical temperature variability had the 11th largest.

Second, we found that any geographic variation in the slope of the richness–temperature variability relationship depends very strongly on the method used. Hortal *et al.* (2011), p.742, “predict that the relationship between species richness and climate variability since the LGM will change its shape roughly around the past location of this [the 0°C] isotherm”. They tested this prediction using a geographically weighted regression (GWR) (Table 7.2). The slope of the local regression of richness as a function of temperature variability varied substantially through space (Figure 7.1). But, the LGM temperature at which a breakpoint in the richness–temperature variability local slopes is fitted strongly depends on the weighting function used in the GWR (Gaussian or bisquared), how a breakpoint in the linear relationship is fitted (e.g. fitting a change in intercept, versus fitting a change in slope, versus fitting a change in both, see Table S7.1).

The variation in the slope of the richness–temperature variability relationship also depends strongly on which other predictors are included as covariates. Depending on the methods, the local slopes of richness as a function of temperature variability alone can be found to have a breakpoint at LGM temperatures of -12.37°C to -0.17°C (Table S7.1). If we include current temperature as a covariate (given that Hortal *et al.* (2011), p. 741, argue that richness depends upon both contemporary and historical climate), then the partial slope of richness as a function of temperature variability then shows a mostly east-west pattern of increasingly negative coefficients, instead of a north-south pattern (Figure 7.1d). This pattern is qualitatively inconsistent with the explanation proposed by Hortal *et al.* (2011). A breakpoint added to the model nonetheless is significant, falling between -5.81°C to +2.95°C (Table S7.1). If we include all environmental variables as covariates, the breakpoint falls between -20.64°C to +4.16°C

(Table S7.1). With some methods, fitted breakpoints are around the LGM 0°C isotherm, and others not (Figure 7.1 and Table S7.1).

We also used a more direct way to test the prediction, by simply fitting richness as a function of temperature variability and fitting a breakpoint based on LGM temperatures (without first fitting a GWR model). Again, depending on how we model a change of shape in the richness–temperature variability linear relationship, and whether we include other environmental variables as covariates, breakpoints vary between -16.48°C and +0.49°C (Table S7.1). To verify whether breakpoints in the relationship could potentially be artefactual, we simulated a linear richness–temperature variability relationship, with no breakpoint in the data. We then fitted models that estimate a breakpoint. These models often fitted a breakpoint around LGM temperatures of -5 to 0°C, near the mid-point of the data (Figure S7.2). In other words, in a large data set with high statistical power, models that include a breakpoint term often fit one, even in the absence of any real breakpoint in the data. We also found that models that fit a breakpoint to latitude and longitude often provide better fit than models as a function of temperature variability (Figure 7.1).

Finally, Hortal *et al.* (2011) predicted that the relationship between species richness and current environmental conditions should be stronger in the northern part of the continent. Although the R^2 of the relationship between richness and current environmental variables is indeed higher in the North, as predicted, we note that the slopes tend to be less steep (Figure 7.2, Table 1 and S1 in (Hortal *et al.*, 2011). It is not clear to us if and why this was predicted. Although one can clearly detect statistically significant differences between the North and South of Europe (Hortal *et al.* 2011), the observed richness–current climate relationship appears continuous around the LGM 0°C isotherm transition (Figure 7.2).

To summarize, although it is possible to develop descriptions of a richness data set (model fitting, e.g. with GWR) that include the hypothesized effect of historic climate variability, other equally strong descriptions of the same data can be developed that do not show the hypothesized effect. Changes in the model assumptions and in the variables included dramatically change the apparent effects of historical climate variability. And, no independent test of the predictive ability of a model based on historical climate variability has yet been carried out. Thus, we argue, the data are in fact not unambiguously consistent with the authors' hypothesis.

A critical review of the strength and direction of effects of historic climate stability

Evidence consistent with the historic climate stability hypothesis is similarly weak or equivocal in many other studies. First, many studies have found that species richness is only weakly related to historic climate stability after accounting for current climate (Dunn *et al.*, 2009; de Souza Lima-Ribeiro *et al.*, 2010; Kissling *et al.*, 2012b; Lima-Ribeiro *et al.*, 2013; Cabral *et al.*, 2014). Fløjgaard *et al.* (Fløjgaard *et al.*, 2011) removed climatic stability since the LGM from their statistical model of European mammal species richness because the observed correlations were inconsistent with the prediction of the historic climate hypothesis.

Moreover, the observed relationship between richness and historic climate stability is not always in the direction predicted by the hypothesis. Araújo *et al.* (Araújo *et al.*, 2008) modelled reptile and amphibian species richness in Europe as a function of both current climate and climate anomaly since the LGM (i.e., the difference between LGM climate and current climate). Note that Araújo *et al.* (Araújo *et al.*, 2008) refer to this anomaly as climate “stability”, but it is in fact a measure of variability; the historic climate stability hypothesis therefore predicts a

negative relationship. They found that the partial R^2 of temperature and precipitation variability is higher than that of current temperature and precipitation; see also Werneck (Werneck *et al.*, 2012). While most of the explained variance in species richness is shared between historic and current climate (i.e., 39% for reptiles and 21% for amphibians), the partial R^2 of historic climate stability is 12% for reptiles and 19% for amphibians but is only 5% for current climate (Araújo *et al.*, 2008). However, only one out of four of their richness–climatic variability correlations is negative, as predicted. Specifically, reptiles show the predicted negative relationship between richness and precipitation variability. In contrast, reptile richness is a polynomial function of historic temperature variability that is positive over the range of temperature variability observed in Europe (i.e., the wrong direction). Amphibian richness varies as a peaked function of temperature variability with a maximum near the mean temperature variability. The amphibian richness–precipitation variability relationship is positive (i.e., the wrong direction). Thus, the bulk of the evidence appears to be inconsistent with the historic climate hypothesis, although Araújo *et al.* (Araújo *et al.*, 2008) do not discuss this point.

Other studies have also included both current and historic climate in their models of species richness and have reported statistically significant effects of historic climate stability and a generally stronger effect of current climate on species richness (Dalsgaard *et al.*, 2011; Sandel *et al.*, 2011; Abellán & Svenning, 2014). But, the variance in richness explained uniquely by historical climate, versus the variance related to the collinearity of current and historic climate, is not explicitly reported. Effects in the opposite direction to predictions of the historic climate stability hypothesis have been observed in some instances (Kissling *et al.*, 2012b; Abellán & Svenning, 2014).

Evidence in support of a hypothesized effect of historic climate stability on current species distributions has also been drawn from studies of individual species ranges (rather than richness) but appears to us similarly equivocal (see details in Appendix S7.1).

Secondary predictions

Opposite observations have sometimes been cited as supporting evidence for the historic climate stability hypothesis. Consider: the observation that historical climate variability has the greatest effect on current distributions in regions where climate changed the least has been regarded as support for the historic climate stability hypothesis (Hortal *et al.*, 2011; Normand *et al.*, 2011). But, the opposite effect has also been observed and regarded as support for the hypothesis in other studies (Svenning *et al.*, 2008; Gouveia *et al.*, 2013). If the specific relationship cannot be deduced from the hypothesis, we argue that simply detecting a correlation is a very weak test, especially in the presence of collinearities. And, *a priori*, we know that strongly spatially autocorrelated variables are highly likely to be strongly correlated, even in the absence of a causal link (Lennon, 2000; Beale *et al.*, 2008a).

Moreover, secondary predictions derived from the historic climate stability hypothesis are also inconsistent with the evidence. First, if the effect of historic climate stability is through post-glacial migration lag, range filling should be high at the edge closest to LGM refuge and low at the opposite edge (Svenning *et al.*, 2008). However, we have observed elsewhere (Boucher-Lalonde *et al.*, 2014b) that regions with unoccupied but suitable macro-climate typically entirely surround species' ranges. Normand *et al.* (Normand *et al.*, 2009) reported that species occupy a *larger* proportion of their potential range at the cold edge, whereas the historic climate hypothesis argues that species should experience a migration lag and generally have *less*

range filling at the historically more variable, i.e. generally the cold, edge of their potential range (Svenning & Skov, 2007; Svenning *et al.*, 2008). Second, it is possible that migration rates are much higher than assumed under the historic climate stability hypothesis (Clark *et al.*, 1998; Nathan *et al.*, 2002; Ordonez & Williams, 2013) although this is highly debated (Svenning & Skov, 2007; Feurdean *et al.*, 2013). Note that Hortal *et al.* (2011) do not specify the mechanism by which historic climate stability affects richness, i.e. dispersal limitation is not assumed. Third, the historic climate stability hypothesis assumes that species track suitable climates through time, albeit with a migration or extinction lag. Although species' ranges often shift in the general direction predicted by climate change (Parmesan & Yohe, 2003; Lenoir *et al.*, 2008; Chen *et al.*, 2011), some species shift to very different climatic niches when climate changes (Veloz *et al.*, 2012) and species richness temporally tracks climate a lot more closely than individual species' ranges do (Boucher-Lalonde *et al.*, 2014a).

Conclusion

In sum, we suggest that tests of the hypothesis that historic climatic stability has affected current patterns of richness suffer from a common fault: they have looked for evidence to support the hypothesis, as opposed to asking whether the hypothesis survives multiple strong tests. Historic climate stability can statistically explain some of the residual variance in richness that is not explained by current climate (e.g. 1% in (Lima-Ribeiro *et al.*, 2013); 1-5% in (Gouveia *et al.*, 2013); 8% in (Dunn *et al.*, 2009); 12-19% in (Araújo *et al.*, 2008); 47% in (Werneck *et al.*, 2012)), perhaps especially so for small-ranged species with low dispersal abilities (Svenning & Skov, 2007; Mathieu & Davies, 2014). It may also explain the composition of species assemblages (Hortal *et al.*, 2011; Kissling *et al.*, 2012a; Moen *et al.*, 2013). Nonetheless, much

of the extant evidence is inconsistent with historic climate stability as a major driver of current patterns in species richness. Moreover, so far as we know, no study has tested whether richness–historical climate relationships successfully predict richness patterns outside the original data. Although the hypothesis, as currently formulated, appears not to withstand critical tests, modified hypotheses could be formulated and tested, and we cannot reject the general hypothesis that history has affected current richness patterns. But, if there is an effect of climate stability since the LGM, it appears to be small and idiosyncratic, such that it does not necessarily improve our predictions of species richness across space and time.

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TABLES

Table 7.1 Predictions derived from the hypothesis that current climate is a main driver of gradients in species richness at coarse grains and large spatial extents. We provide a non-exhaustive list of references that have tested and failed to reject these predictions.

Prediction	References
Current climate predicts richness in independent regions, biomes and continents	(O'Brien, 1998; Francis & Currie, 2003; Field <i>et al.</i> , 2009)
Contemporaneous climate predicts richness through seasonal changes in climatic variables	(Turner <i>et al.</i> , 1987; H-Acevedo & Currie, 2003; Hurlbert & Haskell, 2003; Boucher-Lalonde <i>et al.</i> , 2014a)
Contemporaneous climate predicts richness through recent climate change	(Menendez <i>et al.</i> , 2006; Algar <i>et al.</i> , 2009b; La Sorte <i>et al.</i> , 2009)
Contemporaneous climate predicts richness through recent glacial periods	(Willis <i>et al.</i> , 2007; Yasuhara <i>et al.</i> , 2012; Blois <i>et al.</i> , 2013; Vázquez-Rivera & Currie, 2015)
The richness–current climate relationship is similar in most taxonomic groups	(Currie, 1991; Hawkins <i>et al.</i> , 2003; Field <i>et al.</i> , 2009)
The richness–current climate relationship is consistent across elevational and latitudinal gradients	(McCain, 2009)
The richness–current climate relationship is consistent on islands and continents	(Kalmar & Currie, 2007)

Table 7.2 Statistical results of geographically weighted regression (GWR) models of European Scarabaeinae species richness as a function of temperature variability since the last Glacial maximum (LGM) presented in Figure 7.1 and the corresponding linear regression models (OLS). The GWR models include either temperature variability alone or along with current temperature as a covariate or also with precipitation variability since the LGM and 12 current environmental variables as covariates. The GWR were fitted using either a bi-squared or Gaussian weighting function and a 5% bandwidth. For all models, we present the R^2 , effective number of parameters and AIC of the OLS and GWR.

	Temperature variability alone		Current temperature and temperature variability since the LGM		All environmental variables	
	bi-squared	Gaussian	bi-squared	Gaussian	bi-squared	Gaussian
R^2 of OLS	50.0%		82.2%		90.8%	
Number of parameters in OLS	2		3		15	
AIC of OLS	7936.9		6847.3		6176.4	
R^2 of GWR	98.7%	95.5%	99.0%	95.8%	99.7%	98.3%
Number of parameters in GWR	66.8	15.8	88.4	20.7	502.3	108.5
AIC of GWR	4221.6	5476.6	4004.7	5370.4	4429.1	4604.3

FIGURES

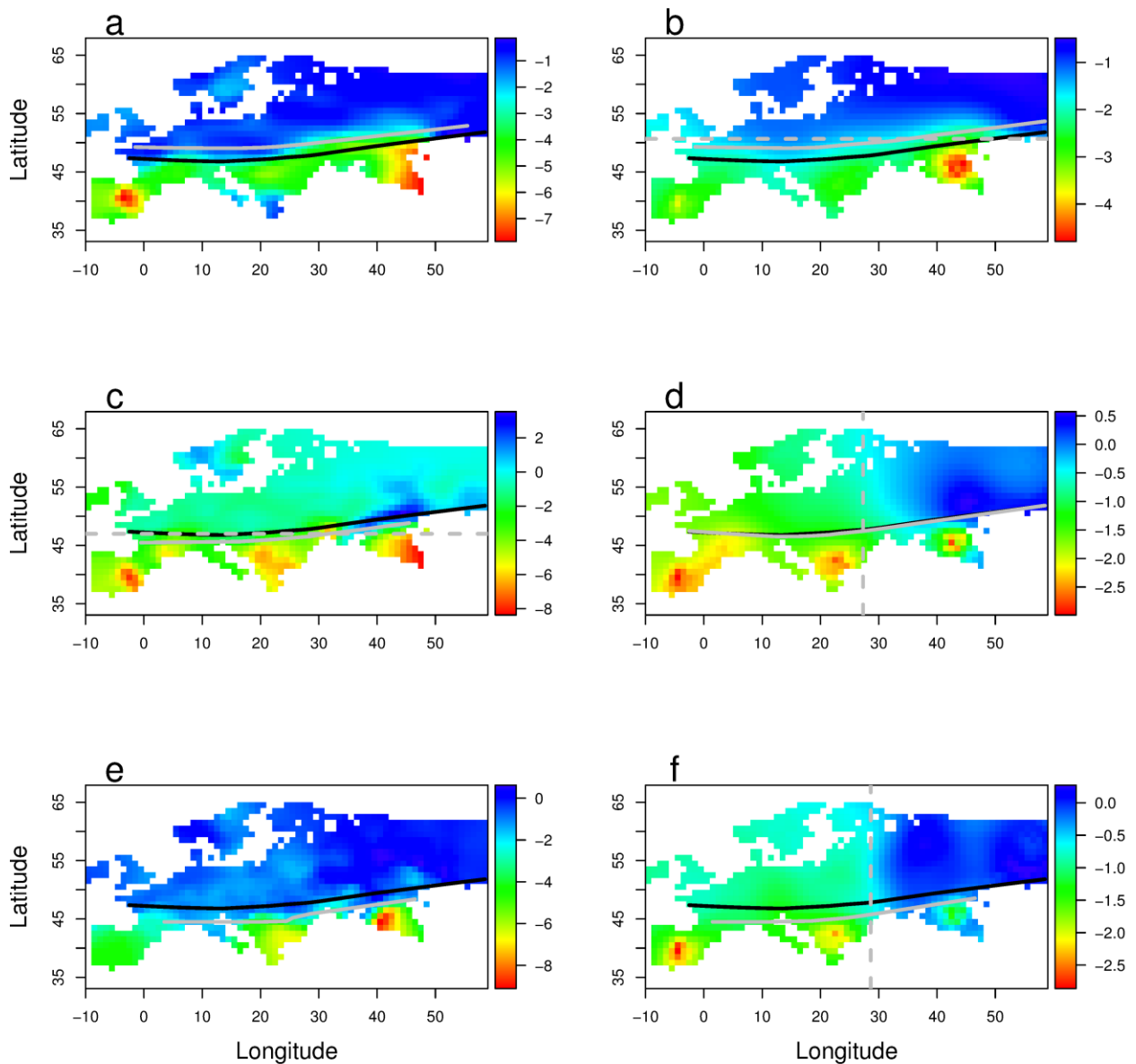


Figure 7.1 Non-stationarity in the relationship between Scarabaeinae species richness and temperature variability since the last glacial maximum (LGM, 21 000 years ago). The maps show the distribution of the local slope of the richness–temperature variability relationship fitted through geographically weighted regression (GWR) models using either a bi-squared (left) or Gaussian (right) weighting function of the 5% neighbouring grid cells. The GWR models have

been fitted including different independent variables, either (a,b) only temperature variability, (c,d) temperature variability and current temperature, or (e,f) 14 historic and current environmental variables. The solid black lines represent the location of the LGM 0°C isotherm. The solid gray lines represent the LGM isotherm that was identified by fitting a breakpoint in the mean local slopes of richness–temperature variability based on LGM temperatures (a: -3.17°C, b: -3.76°C, c: 2.95°C , d: 0.40°C , e: 4.16°C, f: 3.87°C; see Table S7.1). When a fitting a breakpoint based on either latitude or longitude, instead of LGM temperatures, increased the explained variance of the model, we identify this breakpoint with dashed lines.

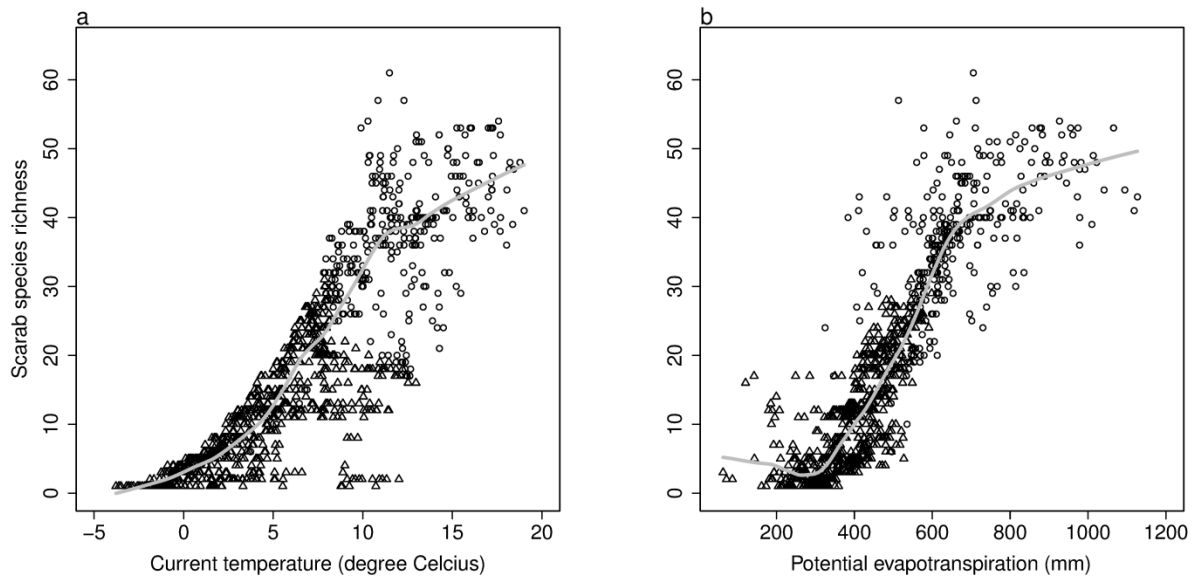


Figure 7.2 European Scarabaeinae species richness as a function of (a) current temperatures and (b) potential evapotranspiration. A LOWESS curve with a smoother span of 0.2 has been fitted through the data. The shape and strength of the relationships around the transition between quadrats north (triangles) and south (circles) of the last glacial maximum 0°C isotherm northern appear continuous.

CHAPTER 8 Range size is strongly correlated to climatic niche breadth – Biology or artefact?

Citation: Boucher-Lalonde, V. & Currie, D. J. (Submitted) Range size is strongly correlated to climatic niche breadth – Biology or artefact?

ABSTRACT

Species' geographic ranges could primarily be physiological tolerances drawn in space. Alternatively, geographic ranges could be only very broadly constrained by physiological climatic tolerances: there could generally be much more proximate constraints on species' ranges (dispersal limitation, biotic interactions, etc.) such that species only occupy a small and unpredictable subset of tolerable climates. In the literature, species' climatic tolerances are typically estimated from the set of conditions observed within their geographic range. Using this method, recent studies have concluded that broader climatic niches permit larger ranges. Others have investigated the biological causes of incomplete range filling. But, since climatic constraints were measured directly from species' ranges in these cases, are correlations between species' range size and climate necessarily consistent with a causal link? We evaluated the extent to which variation in range size among 3277 bird and 1659 mammal species occurring in the Americas is statistically related to characteristics of species' realized climatic niches. We then compared how these relationships differed from the ones expected in the absence of a causal link. We created a null model that randomizes the predictor variables (climate), while retaining their spatial autocorrelation structure, thereby removing any causal relationship between range size and climate. We found that, although range size is strongly positively related to climatic niche breadth, range filling and, to a lesser extent, niche position in nature, the observed

relationships are not stronger than expected from spatial autocorrelation alone. Thus, these correlations alone are insufficient to invoke a causal link between range size and climate. We conclude that equally strong relationships between range size and climate would result from any processes causing ranges to be highly spatially autocorrelated.

INTRODUCTION

Species' geographic ranges have long been thought to be strongly limited by their tolerances of climate (Andrewartha & Birch, 1954). Temperature and water availability, in particular, are generally thought to be important axes of the fundamental niche (Kearney & Porter, 2004), which encompasses all environmental conditions in which a species can survive (Hutchinson, 1957). The realized niche, i.e. the environmental conditions experienced within the species' range, is set by the fundamental niche and reduced, or expanded, by dispersal, biotic interactions and the available set of conditions (Peterson *et al.*, 2011; Sax *et al.*, 2013). At macro-scales and coarse grains, climate is generally assumed to be an important range determinant, with range limits close to the species' climatic tolerances (Bozinovic *et al.*, 2011; Chejanovski & Wiens, 2014; Strubbe *et al.*, 2015).

Strong climatic constraints on individual species' ranges are also thought to lead to higher-order patterns in nature such as the richness-climate relationship (Wiens & Graham, 2005; Romdal *et al.*, 2013) and inter-specific variations in range size (Morin & Lechowicz, 2013; Slatyer *et al.*, 2013). In particular, species that are able to tolerate broader environmental conditions are hypothesized to be more widely distributed: niche breadth positively affects range size (Stevens, 1989; Slatyer *et al.*, 2013) through an increase in species' potential range size. Biotic interactions (e.g., greater parasitism in warm climates) and dispersal limitation (e.g., colonization lags following glaciation) are hypothesized to exclude species from occurring in all suitable climatic conditions, such that species whose biology allows them to fill a greater proportion of their fundamental niche should have larger ranges (Svenning & Skov, 2004; 2007; Soberón & Peterson, 2005; Nogués-Bravo *et al.*, 2014). Last, niche position, i.e. where species'

niche occurs along a given climatic gradient, has also been hypothesized to affect range size through various mechanisms (Pither, 2003; Barnagaud *et al.*, 2012; Laube *et al.*, 2013).

Tests of these hypotheses relating range size to species' biological characteristics typically rely on measuring climatic tolerances from observed geographic ranges. Early and Sax (2014) noted that “the use of species' distributions to measure species' environmental tolerances is one of the most fundamental techniques in biogeography”. Physiological climatic tolerances are costly and time-consuming to measure (but see Calosi *et al.*, 2010; Sunday *et al.*, 2011; Araújo *et al.*, 2013), and in-lab measurements are not necessarily transferable to natural settings because of behaviour, habitat complexity or other confounding factors (Hoffmann *et al.*, 2014; Sunday *et al.*, 2014). It is therefore appealing to measure climatic tolerances from the observed species' ranges themselves (Svenning & Skov, 2004; Early & Sax, 2014; Warren *et al.*, 2014).

In particular, to test the hypothesis that wider tolerances increase species' range size, species' environmental or habitat niche breadths have generally been measured from the same geographic data as range size was calculated (Slatyer *et al.*, 2013; Morin & Lechowicz, 2013). As predicted, range size consistently increases with species' realized niche breadth (Slatyer *et al.*, 2013; Morin & Lechowicz, 2013). Slatyer *et al.*'s (2013) meta-analysis concluded “Niche breadth predicts geographical range size: a general ecological pattern” and called for a deeper investigation of the underlying ecological and evolutionary causes. Yet, in most of the studies compiled by Slatyer *et al.* (2013), niche breadth was measured from the same macro-scale data as range size; not independently. And, the studies in which niche breadth has been measured independently of range size did not consistently detect the predicted positive effect. Specifically, while four out of the five studies in Slatyer *et al.*'s (2013) meta-analysis that measured range size and “environmental tolerance breadth” from the same species' distribution data found the

predicted positive relationship, this was true for only two out of six studies that used independent data (i.e. calcium requirement in Briers, 2003; germination temperature in Calosi *et al.*, 2010; see Slatyer *et al.*, 2013). The results for “habitat breadth” in Slatyer *et al.* (2013) were similar: 24/26 studies measuring range size and habitat breadth from the same species’ distribution data detected the predicted positive relationship, while only 7/18 studies that used independent data (e.g. microhabitat use, field guide classification, independent census data) did so. Therefore, in the literature, the conclusion that climatic niche breadth explains range size mostly relies on correlative studies where range size and niche breadth are measured from the same macro-scale data.

Similarly, range-filling, the proportion of a species’ potential range that is occupied, has also been measured directly from the observed range of occupied climates, assuming that species can tolerate the macroclimatic conditions anywhere within this potential range, but not beyond it (Svenning & Skov, 2004, but see Sunday *et al.*, 2012). Hypotheses have then been proposed about the biological factors that could affect the extent of range-filling, e.g. post-glacial migration (Svenning & Skov, 2004; 2007; Svenning *et al.*, 2008), competition (Pearson & Dawson, 2003) or colonization ability (Schurr *et al.*, 2007). Cold- and drought-tolerance have also been measured directly from species’ ranges, to reach conclusions about potential causal mechanisms explaining variations in range size (Stephenson, 1990; Pither, 2003).

Measuring climatic tolerance directly from species geographic ranges to test hypotheses about the biological determinants of species’ ranges rests on the critical assumption that species’ occupied climatic niche is generally closely related to physiological tolerances (Warren *et al.*, 2014). Although physiological climatic limits beyond which any given species can no longer survive undoubtedly exist (Araújo *et al.*, 2013), the extent to which they actually impose range

boundaries is less clear (Bahn & McGill, 2013; Ordonez, 2013; Sax *et al.*, 2013; Hargreaves *et al.*, 2014; Gouveia *et al.*, 2014; Boucher-Lalonde *et al.*, 2014a; 2014b). Most species occupy only a fraction of apparently suitable climates (Svenning & Skov, 2004; Boucher-Lalonde *et al.*, 2012; 2014b). And, terrestrial species' geographic ranges often fall short of (or beyond) the species' physiological climatic limits (Sunday *et al.*, 2011; Hargreaves *et al.*, 2014).

If a circumscribed area such as a species' range is placed randomly on a continent, it will encompass a range of climatic conditions — a realized climatic niche — even if there were no deterministic relationship between that range and the climate on which it was placed. It is already well recognized that the observed niche breadth of widespread species are taken from more locations than that of small-ranged species, which can generate an artifactual positive relationship between range size and niche breadth (Brown, 1984). Slayter *et al.* (2013) found that the relationship between range size and niche breadth holds even after correcting for this sampling bias (see also Boulangeat *et al.*, 2012; Morin & Lechowicz, 2013). But, what has been underappreciated is that species' ranges, as well as extant climatic conditions, are highly spatially autocorrelated. Superimposing two spatially autocorrelated surfaces can lead to a correlation between the two, even if there is no causal relationship (Beale *et al.*, 2008a; Chapman, 2010).

Here, we evaluate the extent to which inter-specific variations in range size would be statistically related to species' occupied climatic niches (i.e., climatic niche breadth, range filling and niche position) in the absence of any mechanistic connection between these variables. We then ask whether real (i.e. observed) range size–climatic niche relationships are stronger than expected from a randomization of the predictor variable (i.e., climatic niche breadth, range filling or niche position). To do this, we studied the breeding ranges of 3277 non-migratory birds and

1659 mammals occurring in the Americas. Note that, although animals may adjust their behaviour to occupy microclimatic conditions that are very different from the regional average, much of the literature on variation in range size and species' climatic niche (e.g. Munguía *et al.*, 2008; Slatyer *et al.*, 2013) largely relies on coarse-grained environmental and animal distribution data, with birds and mammals sometimes showing amongst the strongest effect sizes (Table S3 in Slatyer *et al.*, 2013). We used macro-scale data on species' geographic ranges, and we measured (macro)climatic niche characteristics from these, a method used in the majority of studies that have found a relationship between range size and climate. We constructed a null model that randomizes the relationship between the measured climatic niche and range size, while maintaining spatial autocorrelation (Beale *et al.*, 2008a; Chapman, 2010). This allowed us to assess the extent to which inter-specific variations in range size can be deterministically explained by the climatic niche, versus spatial autocorrelation alone. Relationships stronger than the null expectations would be consistent with deterministic effects of climatic tolerances on species ranges, validating the assumption that is implicit elsewhere in the literature.

METHODS

The breeding ranges of 3277 non-migratory birds and 1659 mammals of the Americas were obtained from NatureServe (Patterson *et al.*, 2007; Ridgely *et al.*, 2007) and converted into raster format. We divided the Americas into 4141 equal-area quadrats of 10,000 km² following Boucher-Lalonde *et al.* (2014b), which is roughly the effective resolution of expert-drawn range maps (Hurlbert & Jetz, 2007). Conclusions about the relationship between species' range size and environmental niche have often relied on range maps and/or on data with a similar resolution (Slatyer *et al.*, 2013 and references therein; Nogués-Bravo *et al.*, 2014). A quadrat was

considered occupied by a species when its breeding range overlapped the quadrat at least partly. Mean annual temperature and total precipitation were obtained from the WorldClim database at a 30 arc-seconds resolution (Hijmans *et al.*, 2005). Their means were calculated for each quadrat.

We measured the properties of species' occupied temperature and precipitation niche as follows. We measured niche breadth as the range of occupied climate (Pannek *et al.*, 2013; Quintero & Wiens, 2013; Nakazawa, 2013). We measured climatic range filling as the realized/potential range size ratio following Svenning and Skov (2004) where the potential range is assigned to include all quadrats within the range of climates occupied by the species somewhere. We restricted the potential range to be within the zoogeographical region(s) in which the species occurs (i.e. North American, Mexican, Panamanian, Amazonian, South American and/or Artico-Siberian; Holt *et al.*, 2013), such that climatically suitable areas outside the zoogeographic regions in which the species occurs do not affect the measured potential range (see Fig. S8.6 in Appendix S8.1 for results where the potential range is not restricted). We measured niche position as the environmental centroid (Soininen *et al.*, 2011), which is here simply the mean climate of occupied quadrats. We also calculated the minimum and maximum occupied temperature and precipitation.

We generated null expectations for the empirical relationships between range size and measures of the climatic niche (described below). This was done by randomizing the climatic variables, while maintaining their autocorrelation structure among quadrats (Chapman, 2010). The method is a simple extension of a resampling test, where the climate values are randomly rearranged among quadrats, but where the resampled gradient is constrained to have a similar spatial correlation structure (estimated by empirical variograms) as the real gradients. This procedure removes any deterministic link between species' ranges and climate. In principle, this

could have also been done by placing species' ranges randomly on the observed climatic gradients in North America (Beale *et al.*, 2008a). However, relocating species' ranges is less computationally efficient (Chapman, 2010), creates an artificial mid-domain effect (Beale *et al.*, 2008a) and appears to be sensitive to methodological details (Beale *et al.*, 2008b).

We then assessed how inter-specific variation in range sizes is related to species' climatic niche properties, using general linear models. We then compared each range size–niche property relationship to the null expectation based on randomized climates (i.e. in which there is no causal link between range size and climatic niches). Since hypotheses in the literature, and logic, clearly predict a positive effect of climatic niche breadth and range filling on range size, we performed a one-tailed significance test to maximize power. Since hypotheses about the effect of climatic niche position on range size vary and are not all clearly directional, we performed a two-tailed test to allow for both positive and negative effects. Similarly, we assessed how species' climatic niche properties (niche breadth, range filling and niche position) covary among species, and we tested whether these correlations were different than those expected from spatial autocorrelation alone (two-tailed tests). In the literature, niche properties are sometimes correlated, and potential causal mechanisms are then inferred from these correlations (e.g. Chejanovski & Wiens, 2014). Our aim here was therefore to test whether these correlations are different than what we can expect from spatial autocorrelation alone.

We used Chapman's (2010) procedure to generate randomized gradients in temperature and precipitation. We first quantified spatial autocorrelation in temperature and precipitation in the Americas, at the spatial grain of 10^4 km^2 . For both temperature and precipitation, we modelled the spatial correlation structure of the data through an empirical variogram, using a powered-exponential function in the 'geoR' package (Ribeiro & Diggle, 2001) in R (R Core

Team, 2013). Then, we created a new variable that reproduced this spatial structure using stationary Gaussian Random Fields generated in the 'RandomFields' package (Schlather *et al.* 2014). This is a stochastic process by which random numbers are generated and mapped in space and where the probability that a given value is assumed depends on the neighboring values through the variogram model. We then adjusted for the observed mean difference between coastal and inland cells following Chapman (2010). The values for each quadrat generated by the Gaussian Random Fields were then ranked such that the random value generated in each quadrat could be replaced with the exact value that has the same rank order in the real variable. A detailed description of the algorithm and the R code to generate the simulated null gradients is available in Chapman's (2010) Appendix S3. We created a thousand iterations of these randomized null variables for temperature and precipitation within the Americas to serve as a null model in our analyses (Fig. S8.1). Correlations between real and randomized variables varied greatly, but were centered on zero, as were the correlations between the randomized temperature and precipitation variables (Fig. S8.13).

We then superimposed the observed breeding ranges of North American birds and mammals on each set of randomized climatic variables, and we calculated the niche properties for each species on the randomized climatic surfaces. Since the potential range was restricted to the zoogeographic region(s) in which each species occurs, our null model for the distribution of range filling was calculated by randomizing the climatic variables only within the zoogeographic region(s) in which the species occurs (but see Fig. S8.6, in which we relax this constraint). We then compared the slope and R^2 of the observed relationships to those obtained from our set of randomizations. Because some randomizations produced climate surfaces that were strongly correlated with observed climate, we repeated all our analyses with a set of 1000 randomizations

in which we excluded all randomized climatic surfaces that were correlated with $|r| > 0.2$, with the real climatic variables. By restricting the randomizations to be uncorrelated with the real variables, we increase our ability to distinguish the real relationships from the null model. These results are presented in Fig. S8.9-S.812 and were qualitatively similar to those obtained from the full set of randomizations.

To test whether our approach has sufficient power to detect a signal of climate on species' ranges and whether this is affected by intrinsic (endogenous) spatial autocorrelation (i.e. that arises from spatial processes specific to the species, such as dispersal), we simulated species' ranges that are causally related to climate. Specifically, we performed two different simulation models in which we simulated species' geographic range. In these, each species kept its measured range size and range of occupied climates. Consequently, the simulated niche characteristics were highly correlated to those observed ($0.71 \leq r \leq 0.99$). In the first simulation model, we did not incorporate intrinsic spatial autocorrelation, such that all quadrats that fell within the species' climatic niche had an equal probability of being occupied by the species. In this model, climate deterministically explains species' ranges; any spatial autocorrelation in the range is solely induced from the spatially autocorrelated climatic variables (i.e. exogenous spatial autocorrelation only). In the second simulation model, we additionally modelled strong intrinsic spatial autocorrelation in the species' range through a simple spreading-dye model. Amongst the quadrats that fell within the species' climatic niche, one was randomly seeded, and neighboring quadrats that fell within the species' climatic niche were then sequentially selected to be occupied until the species' range size was attained (if all neighboring quadrats within the species' climatic niche were occupied and total range size was not yet attained, a new quadrat was randomly seeded). For both simulation models, we then compared the range size–climatic

niche properties relationships and tested whether they are stronger than those that would have been observed in the 1000 randomizations of the climatic surfaces. This allowed us to test whether, given the variance in the data, a causal relationship between species' ranges and climate could have been detected in the presence of, versus in the absence of, intrinsic spatial autocorrelation.

RESULTS

Correlations among niche properties

Temperature and precipitation niche position are highly positively correlated for mammals ($r = 0.68$) and for birds ($r = 0.64$) in the Americas (see also Chejanovski & Wiens, 2014), which presumably at least partly reflects the fact that temperature and precipitation in the Americas are highly correlated ($r = 0.62$). Additionally, temperature and precipitation niche breadth are highly correlated ($r = 0.77$ for mammals and 0.65 for birds; see also Chejanovski & Wiens, 2014), as well as range filling of the temperature and precipitation niches ($r = 0.91$) (Table 8.1). Climatic niche breadth is weakly negatively related to temperature and precipitation niche position (Table 8.1). The strongest observed correlations were between niche breadth and the minimum temperature or precipitation occupied by the species (Fig. 8.1). However, all the observed correlations presented in Table 8.1 and Figure 8.1 fall either within the range expected from the randomization procedure, or are weaker than expected (Table 8.1; Fig. 8.1).

Correlations with range size

Variations in range sizes are, by definition, entirely explained by the interaction of potential range size (i.e. the spatial extent of climates that are suitable based on occupancy) and range filling. Thus, it is unsurprising that observed range size was positively related to both species' range filling ($r^2 = 0.41$ for temperature and 0.38 for precipitation, $p < 0.001$) and climatic niche breadth ($r^2 = 0.34$ for temperature and 0.22 for precipitation, $p < 0.001$). Inter-specific variations in range size were only very weakly positively related to niche position ($r^2 = 0.01$, $p < 0.001$ for both temperature and precipitation). The minimum temperature and maximum precipitation occupied by a species' were, however, substantially stronger correlates of range size ($r^2 = 0.17$ and 0.16 respectively, $p < 0.001$) than mean niche position.

However, comparing the above results to null expectations, we found that these observed relationships all fell within, or were weaker than, the relationships expected from a randomization of the predictor variables. Specifically, the observed slopes (Fig. 8.2) and coefficients of determination (Fig. 8.3) were not stronger than expected under a null model in which there is no causal link between range size and the characteristics of the climatic niche, but which conserves the spatial structure in both species' ranges and climatic conditions. These conclusions were maintained when we analyzed the bird and mammal data separately (Fig. S8.2-S8.5). When we restricted our set of randomizations to be uncorrelated with the real climatic variables, we also found very similar results; see Figure S8.9-S8.12. In sum, we cannot reject the null hypothesis that the observed correlation between range size and niche breadth arose from spatial autocorrelation alone.

Given the variance in the data and the observed effect sizes, if species geographic ranges were indeed causally linked to climate, our randomization procedures did have the statistical

power to detect some of the relationships between range size and climatic niche characteristics as being significantly stronger than expected under our null model, especially in the absence of intrinsic spatial autocorrelation (Fig. 8.4 and 8.5). Specifically, when we simulated species' ranges that are probabilistically determined by climate, while maintaining both range size and the range of climates occupied, the slopes and R^2 of relationships between range size and temperature niche breadth, temperature niche position as well as temperature and precipitation range filling were higher than those obtained by randomizing these simulated ranges (Fig. 8.4 and 8.5). However, when we simulated species' ranges through a spreading-dye model that introduces strong intrinsic spatial autocorrelation (again, maintaining species' range size and the range of occupied climates), the expected relationships between range size and the climatic niche that are expected from spatial autocorrelation alone become much stronger. Therefore, the observed slopes and R^2 of range size as a function of temperature niche breadth becomes undistinguishable from those obtained from the randomization procedure (Fig. 8.4a and 8.5a). In other words, intrinsic spatial autocorrelation makes the causal relationships between range size and species' climatic niches more difficult to distinguish from those expected in the absence of causality. In the absence of intrinsic spatial autocorrelation, most observed relationships were strong enough that they would have been detected as significant.

DISCUSSION

Temperature and precipitation are considered to be among the major factors determining species' range boundaries, especially at broad spatial scales (Wiens, 2011), and they statistically explain much of the variation in the probability of occupancy of a region by a species (Boucher-Lalonde *et al.*, 2012; 2014b). Species richness is also strongly related to temperature and precipitation

(Hawkins *et al.*, 2003), as is interspecific variation in range size (Stevens, 1989; Pither, 2003). Consistent with earlier literature, we find that the range size of bird and mammals species in the Americas is positively correlated with their climatic niche breadth, their range filling and their niche position.

However, contrary to the assumptions of previous studies (e.g. Svenning & Skov, 2004; Slatyer *et al.*, 2013), we found that there is no need to postulate that range size and species' climatic niche properties (climatic niche breadth, niche position, and range filling) are causally linked. Although species' physiological climatic tolerances must set an upper limit on range size, it is possible that species' range sizes rarely approach this limit in practice. In the presence of strong spatial autocorrelation, correlations between a species' range size and the climate niche characteristics that one can extract from this range are expected, regardless of any causal link, therefore providing an inconclusive test of causality.

Of course, species' ranges could be highly spatially autocorrelated in the first place because they are limited by climate (Brown, 1984; Diniz-Filho *et al.*, 2003). However, geographic ranges could also be highly spatially autocorrelated because of processes that are independent of climate such as dispersal limitation. Here, we simply argue that the observed correlations between range sizes and niche properties cannot be used to support hypothesized causal link with climatic tolerance. This is because, although the relationships are significantly steeper than a slope of zero, they are not statistically different than a null model that retains spatial autocorrelation. To perform a strong test of the hypothesis that inter-specific differences in climatic niches' characteristics cause variations in range size, one needs to measure tolerances independently of species' ranges (e.g. in-lab measurements). Such tests are less common and the

tested correlations have often been weak or absent (e.g. Calosi *et al.*, 2008; Luna & Moreno, 2010; Sunday *et al.*, 2012; Bates *et al.*, 2013).

The conflation of environment and geography is a common problem in ecology that can often lead to spurious inferences about the importance of deterministic processes in generating spatial patterns in species distributions (Warren *et al.*, 2014). It had already been noted that, in the presence of strong spatial autocorrelation, strong relationships are expected between species' geographic distributions and climate (Beale *et al.*, 2008a; Chapman, 2010), making evidence of a strong statistical link between the two (e.g. Boucher-Lalonde *et al.*, 2012; 2014b) weak evidence of a causal relationship. Similarly, the common conclusion that range size depends on climate (Slatyer *et al.*, 2013) mostly rests on evidence of a statistical relationship where a species' range size and climate niche are measured from the same coarse scale data, which also provides particularly weak evidence of causality. If the observed relationships between range size and climate were indeed causal, and in the absence of intrinsic spatial autocorrelation, our resampling tests would generally have been powerful enough to detect it. In the presence of intrinsic spatial autocorrelation, many causal relationships are indistinguishable from those expected in the absence of causality.

Although it seems logical that climatic tolerances (either directly or indirectly) would determine species geographic ranges, it is not necessarily the case. Occupied climates are often not highly predictable from physiological climatic tolerances alone (Kellermann *et al.*, 2012; Araújo *et al.*, 2013; Gouveia *et al.*, 2014; Khaliq *et al.*, 2014). Despite species' distributions (Bahn & McGill, 2013; Boucher-Lalonde *et al.*, 2012; 2014b) and range limits (Cahill *et al.*, 2014) being highly correlated to environmental variables, species distribution models often poorly extrapolate in spatially segregated regions (Randin *et al.*, 2006; Bahn & McGill, 2013;

Early & Sax, 2014) and through time (Pearman *et al.*, 2008; Boucher-Lalonde *et al.*, 2014a; but see Kharouba *et al.*, 2009). Moreover, transplant experiments have shown that transplants can be self-sustaining beyond the species' geographic range limits for 83% of species (Table 3 in Hargreaves *et al.*, 2014). Many species have evolved physiological tolerances to conditions beyond the range they occupied (Zanne *et al.*, 2014). In sum, although species are constrained to occupy climates in which they can survive, or persist as a sink population (Pulliam, 2000), there could often be more stringent limits on geographic ranges than those imposed by physiological tolerances to macroclimate.

If it were the case that species generally have realized climatic niches that poorly reflect their climatic tolerances (i.e. other factors more proximately set range limits), then what could possibly explain variations in range size? One possibility is that geographic ranges are determined by a large set of factors. If the importance of these factors varies a lot across species, space and time, variations in range size could be largely unpredictable by any single predictor. Alternatively, variations in range size may be highly predictable, even if they are not driven directly by the characteristics of a species' climatic niche. First, range size generally increases with local abundance, such that locally abundant species tend to have large ranges and vice versa. This abundance-range size relationship has been widely documented for a large array of taxa, habitats and regions and across temporal and spatial scales (Gaston *et al.*, 1997). Most species are locally rare, but species with large ranges reach high abundances in some locations (Murray & Lepschi, 2004). Second, local abundance has a strong negative effect on extinction rates (Boucher-Lalonde *et al.*, 2014c) and a positive effect on colonization rates of surrounding regions (Hubbell, 2001). Therefore, species that reach high abundances are more likely to expand their geographic ranges and are less likely to become locally extinct. Third, species abundances

within local assemblages are known to be roughly log-normally distributed, such that, within a given community, most species are relatively rare while only a few are abundant (Preston, 1962; Ulrich *et al.*, 2010). Combining these general patterns, we propose that inter-specific variations in range size could partly be driven by the ability of species to maintain high abundances in local communities (which could be climate-dependent).

When relating range size to potential predictor variables, it is already common practice to account for the fact that wide-ranging species are sampled from more locations than small-ranging species, such that positive relationships are expected in the absence of any causal relationship. We propose that future studies should also explicitly account for spatial autocorrelation in the independent variable (when present). We have here shown that correlations that appear to be strong are, in fact, not different from a null model where climate has no effect on species' range (Fig. 8.1-8.3). Yet, we found that in some cases (e.g. Fig. S8.7-S8.8), the observed relationships were weaker than one would expect from spatial autocorrelation alone. Using data independent from species' ranges to measure the climatic niche would provide much stronger tests of the hypothesis of a causal link (e.g. Calosi *et al.*, 2008; 2010; Sunday *et al.*, 2012).

We have here shown that the relationship between range size and climate in the range could be explained by the spatial autocorrelation of the climate variables themselves and of the species' ranges. Spatial autocorrelation greatly inflates the observed relationships between geographic ranges and climate (Beale *et al.*, 2008a). In sum, while climate obviously excludes many species from occurring in some areas (Sunday *et al.*, 2011), other factors could be more proximately determining species' ranges and we would nonetheless observe strong correlations between geographic ranges and climate. Climate could definitely be a major determinant of

species' range and range size, but we caution that the correlations commonly presented in the literature (e.g. Boucher-Lalonde *et al.*, 2014b) do not provide strong evidence of this.

ACKNOWLEDGEMENTS

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TABLES

Table 8.1 Correlation coefficients from pairwise correlations between the different occupied niche properties for n= 3277 bird and 1659 mammal species within their American breeding range. The measured niche properties are the temperature (T) and precipitation (P) breadth and mean (position) of occupied climates along with range filling, i.e. the proportion of quadrats with suitable climates in the zoogeographical region(s) in which the species occurs that fall within the species range. The two-tailed p-value, calculated from a randomization test that controls for spatial autocorrelation, for each correlation coefficient is presented in parentheses. Here, the significant correlations with $p \leq 0.02$ all represent correlations weaker, i.e. closer to zero (not stronger), than expected from spatial autocorrelation alone. No corrections were made for multiple comparisons.

	T breadth	P breadth	T position	P position	T filling	P filling
Birds						
P breadth	0.65 (0.39)					
T position	-0.23 (0.87)	-0.33 (0.21)				
P position	-0.11 (0.60)	-0.45 (0.34)	0.64 (0.14)			
T filling	0.12 (<0.001)	0.13 (<0.001)	0.15 (0.41)	0.04 (0.80)		
P filling	0.11 (<0.001)	0.03 (<0.001)	0.28 (0.03)	0.12 (0.45)	0.91 (<0.001)	
Range size	0.53 (0.01)	0.40 (<0.001)	0.19 (0.49)	0.09 (0.70)	0.66 (0.68)	0.65 (0.34)
Mammals						
P breadth	0.77 (0.80)					
T position	-0.27 (0.47)	-0.19 (0.25)				
P position	-0.20 (0.26)	-0.27 (0.70)	0.68 (0.07)			
T filling	0.22 (<0.001)	0.21 (0.01)	-0.01 (0.79)	0.03 (0.74)		
P filling	0.17 (<0.001)	0.12 (<0.001)	0.11 (0.23)	0.14 (0.04)	0.91 (<0.001)	
Range size	0.65 (0.06)	0.59 (0.02)	0.01 (0.97)	0.06 (0.59)	0.61 (0.15)	0.57 (0.01)

FIGURES

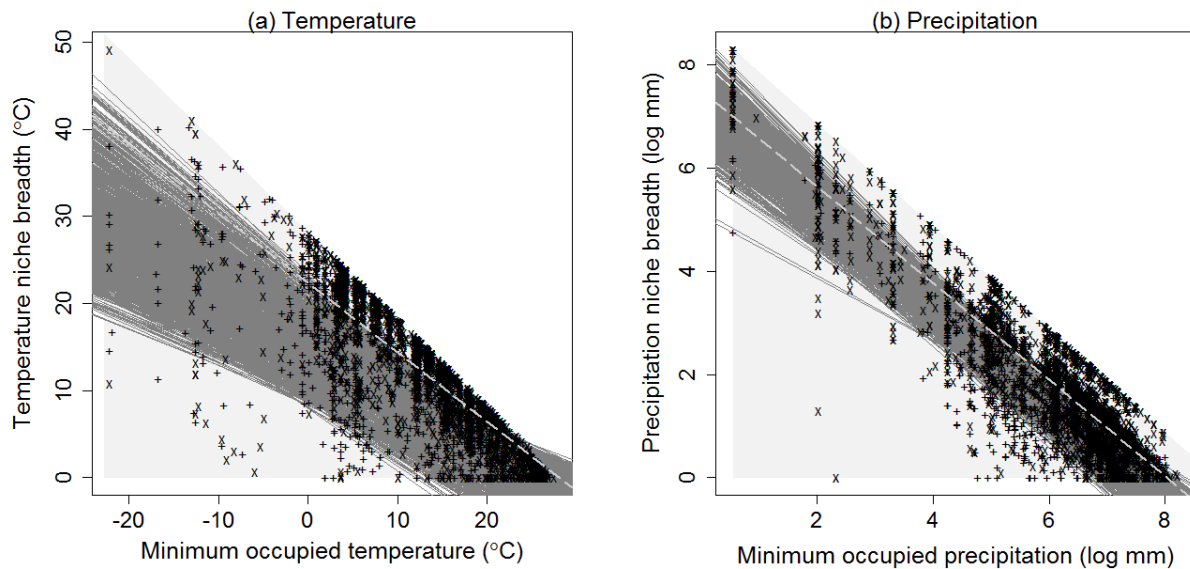


Figure 8.1 Relationship between the occupied (a) temperature (°C) and (b) precipitation (logarithm of precipitation in mm) breadth and the minimum value occupied by the species. The points represent 3277 non-migratory bird (x) and 1659 mammal (+) species with breeding ranges in the Americas. The fitted regression is represented by the dashed line. These relationships are constrained, since species occupying a low minimum temperature or precipitation can have large niche breadth, whereas species with high minimum temperature or precipitation must have a small niche breadth. The triangular constraints are depicted in light gray. The dark gray lines represent the linear relationships obtained under one thousand randomizations of the independent variable that conserve its spatial structure. The observed correlations (the dashed lines) are stronger than (a) 90.4% and (b) 52.7% of the randomizations.

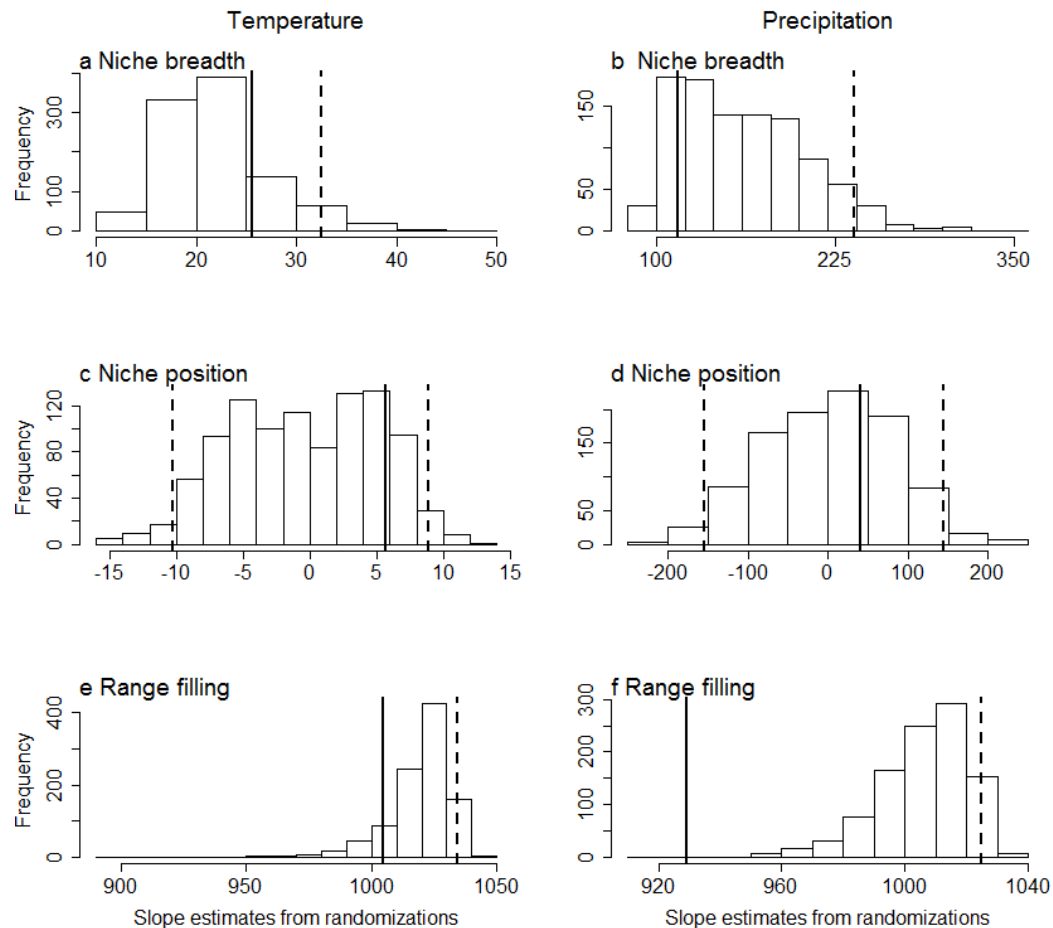


Figure 8.2 Histograms of expected distribution of slopes between range size and a set of climatic niche characteristics under the null model. The observed slope of the relationship between range size, measured in number of 10^4 -km² quadrats occupied, and (a, b) niche breadth, (c, d) niche position and (e, f) range filling of the occupied (a, c, e) temperature (°C) and (c, d, f) precipitation (mm) is shown by a vertical solid line. The data are from the American geographic ranges of 3277 non-migratory bird and 1659 mammal species. The expected distribution of slopes was generated by randomizing the predictor variable, while maintaining spatial autocorrelation in the climatic variables. The vertical dashed line represents the 5% threshold of the randomizations (two-tailed for niche position; one-tailed for niche breadth and range filling such that values higher than the dashed line would be considered statistically significant).

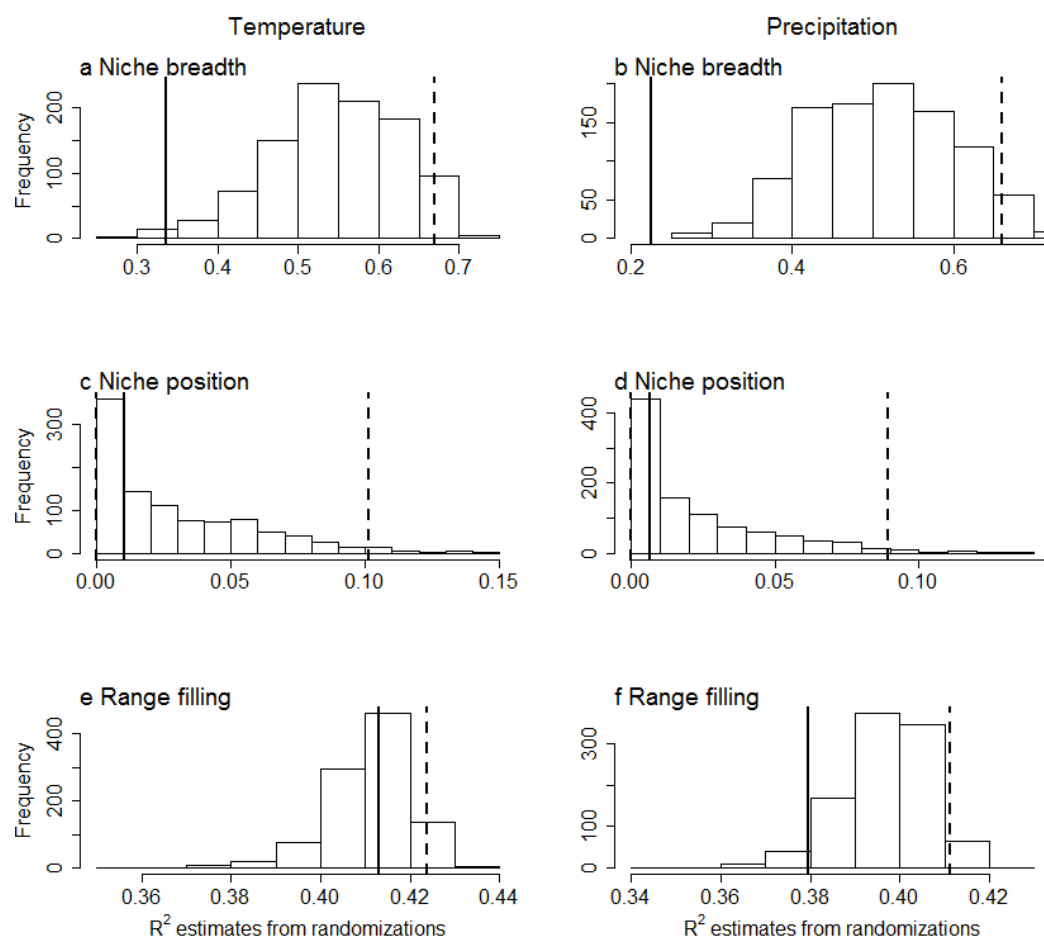


Figure 8.3 Histograms of expected distribution of coefficients of determination (R^2) between range size and a set of climatic niche characteristics under the null model. The observed R^2 of the relationship between range size and (a, b) niche breadth, (c, d) niche position and (e, f) range filling of the occupied (a, c, e) temperature (°C) and (c, d, f) precipitation (mm) is shown by a vertical solid line. The data are from the American geographic range of 3277 non-migratory bird and 1659 mammal species. The expected distribution of R^2 has been generated by randomizing the predictor variable, while maintaining spatial autocorrelation in the climatic variables. The vertical dashed line represents the 5% threshold of the randomizations (two-tailed for niche position; one-tailed for niche breadth and range filling such that values higher than the dashed line would be considered statistically significant).

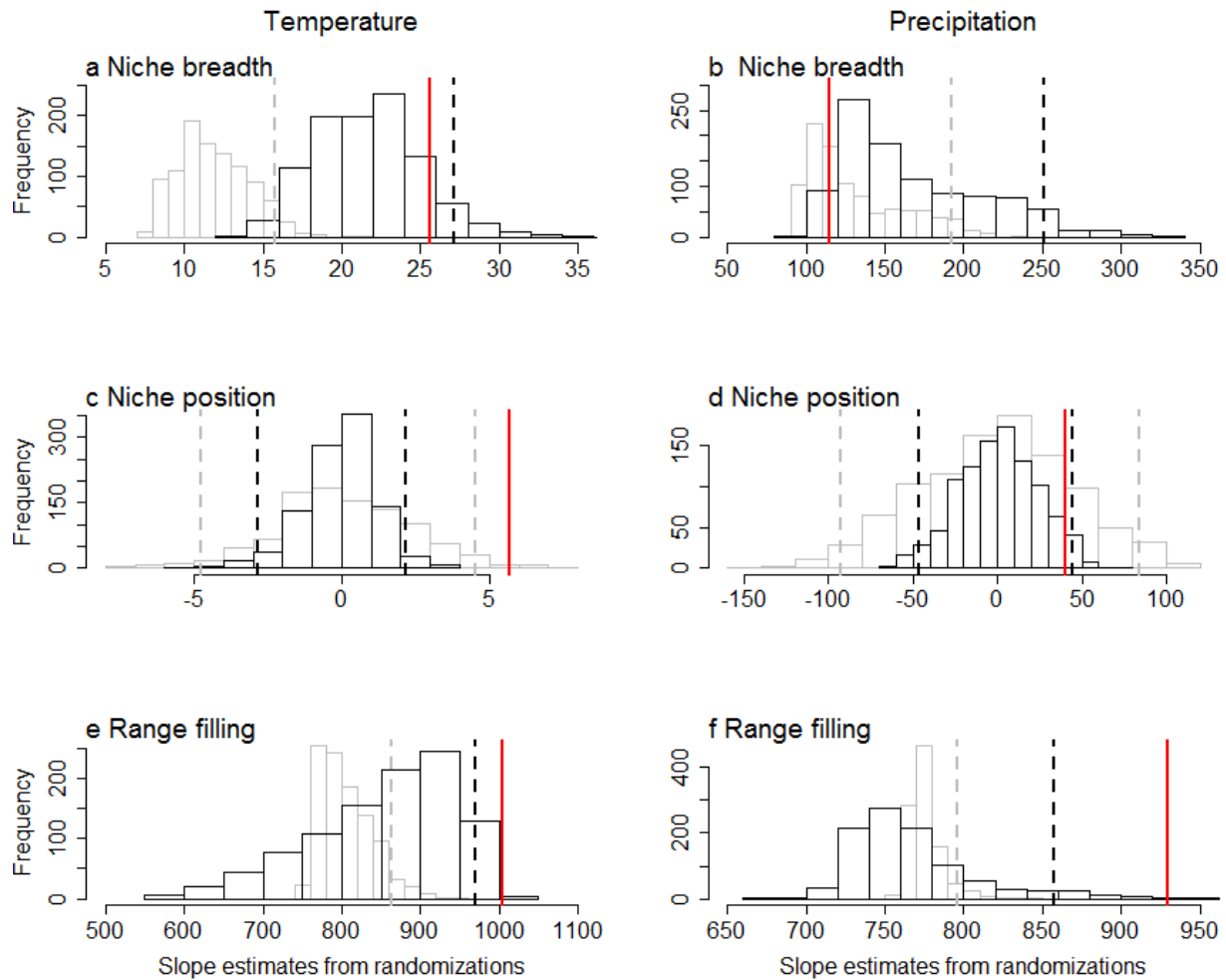


Figure 8.4 Histograms of expected slopes from power analyses that either incorporate intrinsic spatial autocorrelation (black) or not (gray). Species geographic ranges were simulated to be deterministically explained by temperature and precipitation while maintaining the range size and climatic niche of real species. The observed slope of the relationship between range size, measured in number of quadrats occupied, and (a, b) niche breadth, (c, d) niche position and (f, g) range filling of the occupied (a, c, f) temperature (°C) and (c, d, g) precipitation (mm) are shown by a vertical solid line. Quadrats within a species' climatic niche either had an equal probability of being occupied (i.e., ranges are not necessarily cohesive, shown in gray) or intrinsic spatial autocorrelation was modelled through a spreading-dye algorithm (black). For each of the two simulations, we then generated a histogram of the expected distribution of slope

values by randomizing the predictor variable, while maintaining its spatial autocorrelation. The vertical dashed line represents the 5% threshold of the randomizations (one-tailed for niche breadth and range filling to test whether observed values are larger than the dashed line; two-tailed for niche position to test whether observed values are either smaller or larger than the dashed line). This figure is equivalent to Figure 8.2, but for geographic ranges that have been simulated to be causally linked to macroclimatic variables.

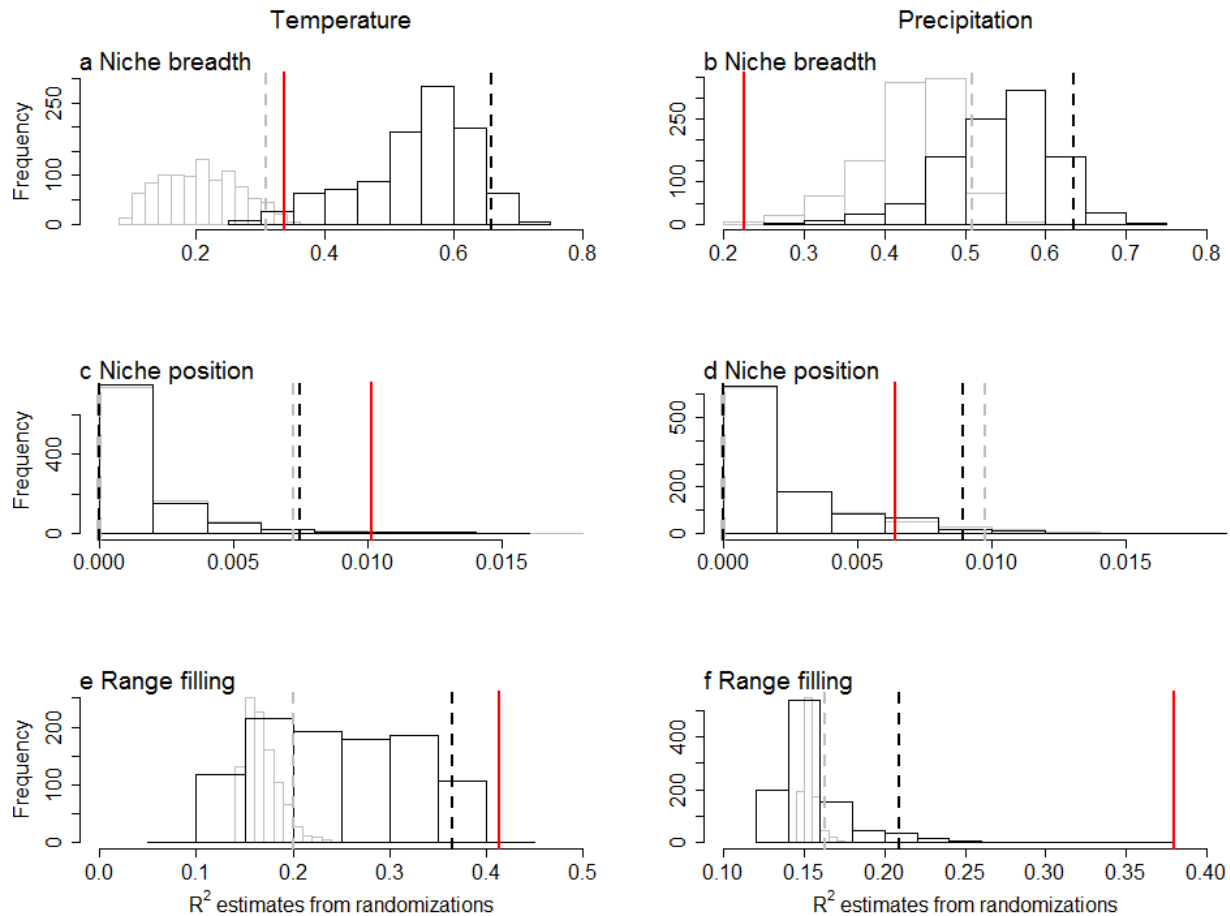


Figure 8.5 Histograms of expected R^2 from power analyses that either incorporate intrinsic spatial autocorrelation (black) or not (gray). Species geographic ranges that are deterministically explained by temperature and precipitation and that maintain the range size and climatic niche of real species were simulated. The observed R^2 of the relationship between range size, measured in number of quadrats occupied, and (a, b) niche breadth, (c, d) niche position and (f, g) range filling of the occupied (a, c, f) temperature ($^{\circ}\text{C}$) and (c, d, g) precipitation (mm) are shown by a vertical solid line. Quadrats within a species' climatic niche either had an equal probability of being occupied (gray) or intrinsic spatial autocorrelation was modelled through a spreading-dye algorithm (black). For each of the two simulations, we then generated a histogram of the expected distribution of slope values by randomizing the predictor variable, while maintaining its

spatial autocorrelation function. The vertical dashed line represents the 5% threshold of the randomizations (one-tailed for niche breadth and range filling to test whether observed values are larger than the dashed line; two-tailed for niche position to test whether observed values are either smaller or larger than the dashed line). This figure is equivalent to Figure 8.3, but for geographic ranges that have been simulated to be causally linked to macroclimatic variables.

GENERAL CONCLUSION

My thesis attempted to identify regularities in species' distributions at large geographic scales in order to predict broad, consistent patterns in the geographic distribution of multicellular terrestrial species. In particular, through the test and falsification of hypotheses, I set out to identify the main mechanism(s) that links species richness to climate. I found that prominent hypotheses to explain richness–climate relationships did not survive critical tests and showed that widely-held assumptions in macroecology sometimes rely almost exclusively on weak supporting evidence. I consider that how the tested hypotheses have failed will be useful to the development of new models and hypotheses. I have identified broad-scale patterns in distributions that need to be predicted by hypotheses aiming to provide a unified explanation for richness gradients and have shown that some processes are unlikely to provide such an explanation.

I found that none of the hypotheses I tested aiming to explain richness–climate relationships could account for the strength and generality of the relationship between species richness and climatic variables at coarse grains and broad spatial extents. I therefore conclude that the hypotheses I tested can be provisionally falsified since they provide poorer predictive power, and no novel predictions consistent with empirical data, versus the simple hypothesis that contemporaneous climatic variables affect species richness. Although different epistemological models can have scientific value and that induction is at the basis of fundamental theories in ecology and evolution, the empirical falsification of hypotheses nevertheless represents a useful idealized view of the process of science which can allow rapid scientific progress and arguably provides the most rationale way to evaluate hypotheses (Platt, 1964; Lakatos, 1999; Popper, 2002). Before the literature gets filled with supporting evidence for virtually all proposed

hypotheses, it is useful to critically assess the hypotheses, test their predictive power and verify if any evidence is inconsistent with the hypotheses. This is what I tried to accomplish in this thesis. Even if one's goal were to partition the variance to multiple working hypotheses (Chamberlain, 1965), my thesis is useful in that it has shown that little of the variance in richness and in richness–climate relationships can be accounted by climatic-constraints on individual species, tropical niche conservatism, climatic variability since the Last Glacial Maximum or short-term interannual extinction probability, while most of the variance is left to explained by other predictors/mechanisms.

The next step will be to develop a simple model of the continental biogeography of species from which multiple predictions can be deduced and tested and that explicitly relies on the processes that can directly change species richness. My thesis has provided insights to develop such a model. First, I have shown that prominent hypotheses such as tropical niche conservatism (Chapter 6) and the historic climatic stability hypotheses (Chapter 7) have poor predictive power to explain broad-scale patterns in species richness. Second, I have shown that the richness–climate relationship cannot be well and consistently explained as a direct effect of variation in species' climatic niche characteristics (Chapter 3), nor does it arise simply as a consequence of individual species being strongly constrained by climatic variables (Chapter 4). In fact, variations in species' range size, climatic niche breadth and, to a lesser extent, range filling should, by themselves, generate richness–climate relationships that are inversed compared to what we consistently observe in nature (Chapter 3). I also found that differential local extirpation rates over short time scales could not explain the richness–climate relationship either (Chapter 5). Climate-dependent speciation or dispersal rates also appear to be poor predictors of the richness–climate relationship (Currie *et al.*, 2004; McPeck & Brown, 2007; Rabosky &

Hurlbert, 2014; Duchêne & Cardillo, 2015). And, although species' geographic ranges strongly and consistently statistically relate to climatic variables (Chapter 1 and Chapter 2), there is little evidence that climate can causally explain inter-specific variations in range size (Chapter 8). Physiological thermal tolerances poorly predict species' geographic distributions and predict a richness–climate relationship substantially steeper than what we observe empirically (Sunday *et al.*, 2011; Araújo *et al.*, 2013; Boucher-Lalonde, Unpublished). My thesis suggests that it is unlikely that a single characteristic of species climatic niches or a single climate-dependent evolutionary process would be largely responsible for the strong and consistent richness–climate relationship.

A model that aims to approximate the real-world variation in the characteristics of species distributions will need to explain the nearly ubiquitous richness–climate relationship, spatial turnover in species composition, Gaussian occupancy-climate relationships (as described in Chapter 1 and 2) and spatial variations in species' range size, niche breadth and range filling (as described in Chapter 3). I found no evidence that species-specific evolutionary histories, historical variations in climate or variations in evolutionary processes needed to be accounted for to explain richness gradients. However, although the number of species occurring in an area increases with temperature and precipitation, the number of species that could occur there (estimated from their tolerances) appears to increase much faster. I therefore would now like to test a near-neutral model relying on the processes of extinction and dispersal, with species only differing in their thermal tolerance. I suggest that two constraints should be imposed: (1) thermal tolerances beyond which species cannot survive; and (2) a maximum number of individuals that can occur in a fixed-sized area, that perhaps should be a decelerating function of the availability of liquid water (O'Brien, 2006). This model would make multiple falsifiable predictions, which

could then be rigorously tested with the goal of developing a simple model with high predictive power.

By attempting to identify the regular, broad-scale predictable patterns in nature and their underlying causes emerging from the tremendous variation in ecological systems, my thesis has largely ignored the unique characteristics of species, communities and ecosystems. But, what I did find is that macro-climatic variables could predict much of the variance in several characteristics of species distributions. Therefore, we can make reliable first-approximation predictions regarding the distribution of species without any knowledge of the particularities of the system involved. The specific mechanism(s) remain unresolved, but I was able to reject some of the most prominent and intuitive hypotheses as mainly responsible for the observed macro-scale richness–climate relationships. If predictive power is the operational way to assess understanding, we can state that we have a good understanding that climate affects how many species can occur in a region and some of the general characteristics of the geographic ranges of the species' occurring there. Yet, we do not understand the historical and evolutionary processes that have given rise to these patterns nor the species composition of communities. We might achieve this understanding in the near future if we stop looking for supporting evidence for hypotheses that provide no predictive power. Instead, I suggest focusing on refining current models that do have high predictive power and test the extent to which adding elements of complexity improves predictions of how species are distributed through space and through time.

REFERENCES

- Abellán, P. & Svenning, J.-C. (2014) Refugia within refugia – patterns in endemism and genetic divergence are linked to Late Quaternary climate stability in the Iberian Peninsula. *Biological Journal of the Linnean Society*, **113**, 13-28.
- Adams, J. (2009) *Species richness - Patterns in the diversity of life*. Praxis, Chichester, UK.
- Aitken, S. N., Yeaman, S., Holliday, J. A., Wang, T. & Curtis-McLane, S. (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, **1**, 95-111.
- Algar, A.C., Kerr, J.T. & Currie, D.J. (2009a) Evolutionary constraints on regional faunas: whom, but not how many. *Ecology Letters*, **12**, 57-65.
- Algar A.C., Kharouba, H.M., Young, E.R. & Kerr, J.T. (2009b) Predicting the future of species diversity: macroecological theory, climate change, and direct tests of alternative forecasting methods. *Ecography*, **32**, 22-33.
- Andrewartha, H. G. & Birch, L. C. (1954) The Distribution and Abundance of Animals. *The University of Chicago Press*, Chicago, Illinois.
- Araújo, M. B., & Pearson, R. G. (2005) Equilibrium of species' distributions with climate. *Ecography*, **28**, 693-695.
- Araújo, M. B., Williams, P. H. & Fuller, R. J. (2002) Dynamics of extinction and the selection of nature reserves. *Proceedings of the Royal Society of London Series B*, **269**, 1971-1980.
- Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. (2005) Validation of species-climate impact models under climate change. *Global Change Biology*, **11**, 1504-1513.

- Araújo, M.B., Nogues-Bravo, D., Diniz-Filho, J.A.F., Haywood, A.M., Valdes, P.J. & Rahbek, C. (2008) Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography*, **31**, 8-15.
- Araújo, M.B., Ferri-Yanez, F., Bozinovic, F., Marquet, P.A., Valladares, F. & Chown, S.L. (2013) Heat freezes niche evolution. *Ecology Letters*, **16**, 1206-1219.
- Austin, M. P. (1980) Searching for a model for use in vegetation analysis. *Vegetatio*, **42**, 11-21.
- Austin, M. P. (1985) Continuum concept, ordination methods, and niche theory. *Annual Review of Ecology and Systematics*, **16**, 39-61.
- Austin, M. P., Cunningham, R. B. & Fleming, P. M. (1984) New approaches to direct gradient analysis using environmental scalars and statistical curve-fitting procedures. *Vegetatio*, **55**, 11-27.
- Austin, M. P., Nicholls, A. O., Doherty, M. D. & Meyers, J. A. (1994) Determining species response functions to an environmental gradient by means of a β -function. *Journal of Vegetation Science*, **5**, 215-228.
- Azzalini, A. (1985) A class of distributions which includes the normal ones. *Scandinavian Journal of Statistics*, **12**, 171-178.
- Bahn, V. & McGill, B. J. (2007) Can niche-based distribution models outperform spatial interpolation? *Global Ecology and Biogeography*, **16**, 733-742.
- Bahn, V. & McGill, B. J. (2013) Testing the predictive performance of distribution models. *Oikos*, **122**, 321–331.
- Barnagaud, J.-Y., Devictor, V. , Jiguet, F. , Barbet-Massin, M. , Le Viol, I. & Archaux, F. (2012) Relating Habitat and Climatic Niches in Birds. *Plos One*, **7**, e32819.

- Barry, S. & Elith, J. (2006) Error and uncertainty in habitat models. *Journal of Applied Ecology*, **43**, 413–423.
- Baselga, A., Lobo, J. M., Svenning, J. C. & Araújo, M. B. (2012) Global patterns in the shape of species geographical ranges reveal range determinants. *Journal of Biogeography*, **39**, 760–771.
- Beale, C. M., Lennon, J. J. & Gimona, A. (2008a) Opening the climate envelope reveals no macroscale associations with climate in European birds. *Proceedings of the National Academy of Sciences USA*, **105**, 14908–14912.
- Beale, C. M., Lennon, J. J. & Gimona, A. (2008b) European bird distributions still show few climate associations. *Proceedings of the National Academy of Sciences USA*, **106**, E41–E43.
- Beatty, J. (1996) Why biologists argue like they do? *Philosophy of science*, **64**, S432–S443.
- Benton, M.J. (1993) *The fossil record 2*. Chapman & Hall, London.
- Bibby, C. (2000) Bird census techniques. Academic Press, London.
- Berthold, P. (1995) *Control of bird migration*. London: Chapman & Hall.
- Bini, M.L., Diniz-Filho, J. A. F., Rangel, T. F. L. V. B., Akre, T. S. B., Albaladejo, R. G., Albuquerque, F. S., Aparicio, A., Araújo, M. B., Baselga, A., Beck, J., Isabel Bellocq, M., Böhning-Gaese, K., Borges, P. A. V., Castro-Parga, I., Khen Chey, V., Chown, S. L., De Marco, Jr, P., Dobkin, D. S., Ferrer-Castán, D., Field, R., Filloy, J., Fleishman, E., Gómez, J. F., Hortal, J., Iverson, J. B., Kerr, J. T., Daniel Kissling, W., Kitching, I. J., León-Cortés, J. L., Lobo, J. M., Montoya, D., Morales-Castilla, I., Moreno, J. C., Oberdorff, T., Olalla-Tárraga, M. Á., Pausas, J. G., Qian, H., Rahbek, C., Rodríguez, M. Á., Rueda, M., Ruggiero, A., Sackmann, P., Sanders, N. J., Carina Terribile, L., Vetaas,

- O. R. & Hawkins, B. A. (2009) Coefficient shifts in geographical ecology: an empirical evaluation of spatial and non-spatial regression. *Ecography*, **32**, 193–204.
- Bivand, R. S., Hauke, J., & Kossowski, T. (2013) Computing the Jacobian in Gaussian spatial autoregressive models: An illustrated comparison of available methods. *Geographical Analysis*, **45**, 150-179.
- Bjornstad, O.N. (2013) ncf: spatial nonparametric covariance functions. R package version 1.1-5. <http://CRAN.R-project.org/package=ncf>
- Blackburn, T. M., & Gaston, K. J. (1997) The relationship between geographic area and the latitudinal gradient in species richness in New World birds. *Evolutionary Ecology*, **11**, 195-204.
- Boucher, F. C., Thuiller, W., Davies, T. J. & Lavergne, S. (2014) Neutral biogeography and the evolution of climatic niches. *The American Naturalist*, **183**, 573-584.
- Boucher-Lalonde, V., Morin, A. & Currie, D.J. (2012) How are tree species distributed in climatic space? A simple and general pattern. *Global Ecology and Biogeography*, **21**, 1157-1166.
- Boucher-Lalonde, V., Thériault F. & Currie D.J. (2013) Can climate explain interannual local extinctions among bird species? *Journal of Biogeography*, **41**, 443-451.
- Boucher-Lalonde, V., Kerr, J.T. & Currie, D.J. (2014a) Does climate limit species richness by limiting individual species' ranges. *Proceedings of the Royal Society B*, **281**, 20132695.
- Boucher-Lalonde, V., Morin, A. & Currie, D. (2014b) A consistent occupancy – climate relationship across birds and mammals of the Americas. *Oikos*, **123**, 1029–1036.
- Boucher-Lalonde, V., Thériault, F.L. & Currie, D.J. (2014c) Can climate explain interannual local extinctions among bird species? *Journal of Biogeography*, **41**, 443-451.

- Boulangeat, I., Gravel, D. & Thuiller, W. (2012) Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters*, **15**, 584-593.
- Boulinier, T., Nichols, J.D., Hines, J.E., Sauer, J.R., Flather, C.H. & Pollock, K.H. (1998) Higher temporal variability of forest breeding bird communities in fragmented landscapes. *Proceedings of the National Academy of Sciences USA*, **95**, 7497-7501.
- Boulinier, T., Nichols, J.D., Hines, J.E., Sauer, J.R., Flather, C.H. & Pollock, K.H. (2001) Forest fragmentation and bird community dynamics: Inference at regional scales. *Ecology*, **82**, 1159-1169.
- Bozinovic, F., Calosi, P. & Spicer, J. I. (2011) Physiological Correlates of Geographic Range in Animals. *Annual Review of Ecology, Evolution, and Systematics*, **42**, 155-179.
- Broennimann, O., Treier, U.A., Muller-Scharer, H., Thuiller, W., Peterson, A.T. & Guisan, A. (2007) Evidence of climatic niche shift during biological invasion. *Ecology Letters*, **10**, 701-709.
- Brown, J.H. (1984) On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255-279.
- Brown, J.H. (2014) Why are there so many species in the tropics? *Journal of Biogeography*, **41**, 8-22.
- Brown J.H., Ernest, S.K.M., Parody, J.M. & Haskell, J.P. (2001) Regulation of diversity: maintenance of species richness in changing environments. *Oecologia*, **126**, 321-332.
- Brown J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771-1789.

- Brown, J. H., Mehlman, D. W. & Stevens, G. C. (1995) Spatial variation in abundance. *Ecology*, **76**, 2028-2043.
- Brown, J. H., Stevens, G. C. & Kaufman, D. M. (1996) The geographic range: Size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, **27**, 597-623.
- Buckley, L.B., Davies, T.J., Ackerly, D.D., Kraft, N.J.B., Harrison, S.P., Anacker, B.L., Cornell, H.V., Damschen, E.I., Grytnes, J.A., Hawkins, B.A., McCain, C.M., Stephens, P.R. & Wiens, J.J. (2010) Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proceedings of the Royal Society B*, **277**, 2131-2138.
- Buckley, L.B., Hurlbert, A.H. & Jetz, W. (2012) Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography*, **21**, 873-885.
- Cabral, J.S., Weigelt, P., Kissling, W.D. & Kreft, H. (2014) Biogeographic, climatic and spatial drivers differentially affect α -, β - and γ -diversities on oceanic archipelagos. *Proceedings of the Royal Society B*, **281**, 20133246.
- Cahill, A. E., Aiello-Lammens, M. E., Fisher-Reid, M.C, Hua, X., Karanewsky, C. J. , Ryu, H. Y. , Sbeglia, G. C., Spagnolo, F., Waldron, J. B. & Wiens, J. J. (2014) Causes of warm-edge range limits: systematic review, proximate factors and implications for climate change. *Journal of Biogeography*, **41**, 429-442.
- Calosi, P., Bilton, D.T. , Spicer, J.I & Atfield, A. (2008) Thermal tolerance and geographical range size in the *Agabus brunneus* group of European diving beetles (Coleoptera: Dytiscidae). *Journal of Biogeography*, **35**, 295–305.

- Calosi, P., Bilton, D.T. , Spicer, J.I, Votier, S.C. & Atfield, A. (2010) What determines a species' geographical range? Thermal biology and latitudinal range size relationships in European diving beetles (Coleoptera: Dytiscidae). *Journal of Animal Ecology*, **79**, 194-204.
- Carter, R. N. & Prince, S. D. (1981) Epidemic models used to explain biogeographical distribution limits. *Nature*, **293**, 644-645.
- Case, T. J. & Taper, M. L. (2000) Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *American Naturalist*, **155**, 583-605.
- Caughley, G. (1994) Directions in conservation biology. *Journal of Animal Ecology*, **63**, 215-244.
- Channell, R. & Lomolino, M.V. (2000) Trajectories to extinction: spatial dynamics of the contraction of geographical ranges. *Journal of Biogeography*, **27**, 169-179.
- Chapman, D. S. (2010) Weak climatic associations among British plant distributions. *Global Ecology and Biogeography*, **19**, 831-841.
- Chejanovski, Z. A., Wiens, J. J. (2014) Climatic niche breadth and species richness in temperate treefrogs. *Journal of Biogeography*, **41** 1936–1946.
- Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024-1026.
- Chown, S.L. & Gaston, K.J. (2000) Areas, cradles and museums: the latitudinal gradient in species richness. *Trends in Ecology & Evolution*, **15**, 311-315.
- Clark, J.S., Fastie, C., Hurtt, G., Jackson, S.T., Johnson, C., King, G.A., Lewis, M., Lynch, J., Pacala, S., Prentice, C., Schupp, E.W., Webb, T. & Wyckoff, P. (1998) Reid's paradox of rapid plant migration - Dispersal theory and interpretation of paleoecological records. *Bioscience*, **48**, 13-24.

- Cornell, H.V. (2013) Is regional species diversity bounded or unbounded? *Biological Reviews*, **88**, 140-165.
- Cramer, B.S., Miller, K.G., Barrett, P.J. & Wright, J.D. (2011) Late Cretaceous–Neogene trends in deep ocean temperature and continental ice volume: Reconciling records of benthic foraminiferal geochemistry ($\delta^{18}\text{O}$ and Mg/Ca) with sea level history. *Journal of Geophysical Research: Oceans*, **116**, C12023.
- Crowley, T.J. & Berner, R.A. (2001) Paleoclimate - CO₂ and climate change. *Science*, **292**, 870-872.
- Cunningham, R.B., Lindenmayer, D.B., Nix, H.A. & Lindenmayer, B.D. (1999) Quantifying observer heterogeneity in bird counts. *Australian Journal of Ecology*, **24**, 270-277.
- Currie, D.J. (1991) Energy and large-scale patterns of animal-species and plant-species richness. *American Naturalist*, **137**, 27-49.
- Currie, D.J. & Paquin, V. (1987) Large-scale biogeographical patterns of species richness of trees. *Nature*, **329**, 326-327.
- Currie, D.J. & Francis, A.P. (2004) Taxon richness and climate in angiosperms: Is there a globally consistent relationship that precludes region effects? Reply. *American Naturalist*, **163**, 780-785.
- Currie, D.J., Francis, A.P. & Kerr, J.T. (1999) Some general propositions about the study of spatial patterns of species richness. *Ecoscience*, **6**, 392-399.
- Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guégan, J., Hawkins, B. A., Kaufman, D. M., Kerr, J. T., Oberdorff T., O'Brien, E. & Turner, J. R. G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7**, 1121-1134.

- Chamberlain, T.C. (1965) The method of multiple working hypotheses. *Science*, 144, 754-759.
- Dalsgaard, B., Magård, E., Fjeldså, J., Martín González, A.M., Rahbek, C., Olesen, J.M., Ollerton, J., Alarcón, R., Cardoso Araújo, A., Cotton, P.A., Lara, C., Machado, C.G., Sazima, I., Sazima, M., Timmermann, A., Watts, S., Sandel, B., Sutherland, W.J. & Svenning, J.-C. (2011) Specialization in Plant-Hummingbird Networks Is Associated with Species Richness, Contemporary Precipitation and Quaternary Climate-Change Velocity. *Plos One*, **6**, e25891.
- Davis, A. J., Lawton, J. H., Shorrocks, B. & Jenkinson, L. S. (1998) Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *Journal of Animal Ecology*, **67**, 600-612.
- de Souza Lima-Ribeiro, M., Felizola Diniz-Filho, J.A. & Barberi, M. (2010) Climate stability and the current patterns of terrestrial vertebrate species richness on the Brazilian Cerrado. *Quaternary International*, **222**, 230-236.
- Diniz-Filho, J. A., Bini, L. M. & Hawkins, B. A. (2003) Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography*, **12**, 53-64.
- Dobzhansky, T. (1950) Evolution in the Tropics. *American Scientist*, **38**, 209-221.
- Dubuis, A., Giovanettina, S., Pellissier, L., Pottier, J., Vittoz, P. & Guisan, A. (2013) Improving the prediction of plant species distribution and community composition by adding edaphic to topo-climatic variables. *Journal of Vegetation Science*, **24**, 593-606.
- Duchêne, D.A. & Cardillo, M. (2015) Phylogenetic patterns in the geographic distributions of birds support the tropical conservatism hypothesis. *Global Ecology and Biogeography*, **24**, 1261–1268.

- Dunn, R.R., Agosti, D., Andersen, A.N., Arnan, X., Bruhl, C.A., Cerdá, X., Ellison, A.M., Fisher, B.L., Fitzpatrick, M.C., Gibb, H., Gotelli, N.J., Gove, A.D., Guenard, B., Janda, M., Kaspari, M., Laurent, E.J., Lessard, J.-P., Longino, J.T., Majer, J.D., Menke, S.B., McGlynn, T.P., Parr, C.L., Philpott, S.M., Pfeiffer, M., Retana, J., Suarez, A.V., Vasconcelos, H.L., Weiser, M.D. & Sanders, N.J. (2009) Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. *Ecology Letters*, **12**, 324-333.
- Dynesius, M. & Jansson, R. (2000) Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences USA*, **97**, 9115-9120.
- Early, R. & Sax, D. F. (2014) Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. *Global Ecology and Biogeography*, **23**, 1356-1365.
- Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L. G., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. M., Peterson, A. T., Phillips, S. J., Richardson, K., Scachetti-Pereira, R., Schapire, R. E., Soberon, J., Williams, S., Wisz, M. S. & Zimmermann, N. E. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129-151.
- Elith, J., Phillips, S. J., Hastie, T., Dudik, M., Chee, Y. E. & Yates, C. J. (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, **17**, 43-57.
- Ferraz, G., Nichols, J.D., Hines, J.E., Stouffer, P.C., Bierregaard, R.O. & Lovejoy, T.E. (2007) A large-scale deforestation experiment: Effects of patch area and isolation on Amazon birds. *Science*, **315**, 238-241.

- Feurdean, A., Bhagwat, S.A., Willis, K.J., Birks, H.J.B., Lischke, H. & Hickler, T. (2013) Tree Migration-Rates: Narrowing the Gap between Inferred Post-Glacial Rates and Projected Rates. *Plos One*, **8**
- Field, R., O'Brien, E.M. & Whittaker, R.J. (2005) Global models for predicting woody plant richness from climate: Development and evaluation. *Ecology*, **86**, 2263-2277.
- Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guegan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G. (2009) Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, **36**, 132-147.
- Fine, P.V.A. & Ree, R.H. (2006) Evidence for a time-integrated species-area effect on the latitudinal gradient in tree diversity. *American Naturalist*, **168**, 796-804.
- Fløjgaard, C., Normand, S., Skov, F. & Svenning, J.-C. (2011) Deconstructing the mammal species richness pattern in Europe – towards an understanding of the relative importance of climate, biogeographic history, habitat heterogeneity and humans. *Global Ecology and Biogeography*, **20**, 218-230.
- Fox, J., Nie, Z., Byrnes, J., Culbertson, M., Friendly, M., Kramer, A. & Monette, G. (2012) Sem: Structural equation models. R package version 3.0-0. <http://CRAN.R-project.org/package=sem>
- Francis, A.P. & Currie, D.J. (2003) A globally consistent richness-climate relationship for angiosperms. *American Naturalist*, **161**, 523-536.
- Gaston, K.J., Blackburn, T.M. & Spicer, J.I. (1998) Rapoport's rule: time for an epitaph? *Trends in Ecology & Evolution*, **13**, 70-74.
- Gaston, K. J. & Blackburn, T. M. (1999) A critique for macroecology. *Oikos*, **84**, 353-368.

- Gaston, K. J. (2003) *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, New York.
- Gaston, K. J. (2009) Geographic range limits: achieving synthesis. *Proceedings of the Royal Society B*, **276**, 1395-1406.
- Gauch, H. G. & Whittaker, R. H. (1972) Coenocline simulation. *Ecology*, **53**, 446-451.
- Gibbs, K. (2012) Examining patterns of species distribution, abundance, variability and conservation status in relation to anthropogenic activities. PhD thesis, University of Ottawa, Ottawa.
- Goldberg, E.E., Roy, K., Lande, R. & Jablonski, D. (2005) Diversity, endemism, and age distributions in macroevolutionary sources and sinks. *American Naturalist*, **165**, 623-633.
- Gotelli, N. J., Anderson, M. J., Arita, H. T., Chao, A., Colwell, R. K., Connolly, S. R., Currie, D. J., Dunn, R. R., Graves, G. R., Green, J. L., Grytnes, J. A., Jiang, Y. H., Jetz, W., Lyons, S. K., McCain, C. M., Magurran, A. E., Rahbek, C., Rangel, T., Soberon, J., Webb, C. O. & Willig, M. R. (2009) Patterns and causes of species richness: a general simulation model for macroecology. *Ecology Letters*, **12**, 873-886.
- Gottfried, K. & Wilson, K.G. (1997) Science as a cultural construct. *Nature*, **386**, 545-547.
- Gouveia, S. F., Hortal, J., Cassemiro, F.A.S., Rangel, T.F. & Diniz-Filho, J.A. (2013) Nonstationary effects of productivity, seasonality, and historical climate changes on global amphibian diversity. *Ecography*, **36**, 104-113.
- Gouveia, S.F., Hortal, J., Tejedo, M., Duarte, H., Cassemiro, F.A.S., Navas, C.A. & Diniz-Filho, J.A.F. (2014) Climatic niche at physiological and macroecological scales: the thermal tolerance–geographical range interface and niche dimensionality. *Global Ecology and Biogeography*, **23**, 446–456.

- Giehl, E.L.H. & Jarenkow, J.A. (2012) Niche conservatism and the differences in species richness at the transition of tropical and subtropical climates in South America. *Ecography*, **35**, 933-943.
- Grinnell, J. (1914) Barriers to distribution as regards birds and mammals. *The American Naturalist*, **48**, 248-254.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993-1009.
- Guisan, A., Graham, C. H., Elith, J., Huettmann, F. & the NCEAS Species Distribution Modelling Group. (2007) Sensitivity of predictive species distribution models to change in grain size. *Diversity and Distributions*, **13**, 332-340.
- Guisan A. & Rahbek, C. (2011) SESAM - a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. *Journal of Biogeography*, **38**, 1433-1444.
- H-Acevedo, D. & Currie, D.J. (2003) Does climate determine broad-scale patterns of species richness? A test of the causal link by natural experiment. *Global Ecology and Biogeography*, **12**, 461-473.
- Hagan J. M. & Johnston, D. W. (1992) *Ecology and conservation of neotropical migrant landbirds*. Washington DC: Smithsonian Institution Press.
- Hanski, I. (1982) Dynamics of regional distribution - The core and satellite species hypothesis. *Oikos*, **38**, 210-221.
- Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41-49.
- Hanski, I., Kouki, J. & Halkka, A. (1993) Three explanations of the positive relationship between distribution and abundance of species. *Species diversity in ecological*

- communities: historical and geographical perspectives* (ed. by R.E.a.S. Ricklefs, D.), pp. 108-116. University of Chicago Press, Chicago.
- Hargreaves, A. L., Samis, K. E. & Eckert, C. G. (2014) Are Species' Range Limits Simply Niche Limits Writ Large? A Review of Transplant Experiments beyond the Range. *American Naturalist*, **183**, 157-173.
- Harrison, S. (1991) Local extinction in a metapopulation context - An empirical evaluation. *Biological Journal of the Linnean Society*, **42**, 73-88.
- He, F.L., Gaston, K.J., Connor, E.F. & Srivastava, D.S. (2005) The local-regional relationship: Immigration, extinction, and scale. *Ecology*, **86**, 360-365.
- Hawkins, B.A. (2001) Ecology's oldest pattern? *Trends in Ecology & Evolution*, **16**, 470-470.
- Hawkins, B.A. (2008) Recent progress toward understanding the global diversity gradient. *International Biogeography Society Newsletter*, **6**, 5-7.
- Hawkins, B.A, Albuquerque, F.S., Araújo, M.B., Beck, J., Binin, L.M., Cabrero-Sañudo, F.J., Castro-Parga, I., Diniz-Filho, J.A.F., Ferrer-Castán, D., Field, R., Gómez, J.F., Hortal, J., Kerr, J.T., Kitching, I.J., León-Cortés, J.L., Lobo, J.M., Montoya, D., Moreno, J.C., Olalla-Tárraga, M.A., Pausas, J.G., Qian, H., Rahbek, C., Rodríguez, M.A., Sanders, N.J. & Williams, P. (2007) A global evaluation of metabolic theory as an explanation for terrestrial species richness gradients. *Ecology*, **88**, 1877-1888.
- Hawkins, B.A. & DeVries, P.J. (2009) Tropical niche conservatism and the species richness gradient of North American butterflies. *Journal of Biogeography*, **36**, 1698-1711.
- Hawkins, B.A., Diniz-Filho, J.A.F. & Soeller, S.A. (2005) Water links the historical and contemporary components of the Australian bird diversity gradient. *Journal of Biogeography*, **32**, 1035-1042.

- Hawkins, B.A., Diniz-Filho, J.A., Jaramillo, C.A. & Soeller, S.A. (2006) Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. *Journal of Biogeography*, **33**, 770-780.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105-3117.
- Hawkins, B.A., McCain, C.M., Davies, T.J., Buckley, L.B., Anacker, B.L., Cornell, H.V., Damschen, E.I., Grytnes, J.A., Harrison, S., Holt, R.D., Kraft, N.J.B. & Stephens, P.R. (2012) Different evolutionary histories underlie congruent species richness gradients of birds and mammals. *Journal of Biogeography*, **39**, 825-841.
- Hawkins, B.A. & Porter, E.E. (2003) Relative influences of current and historical factors on mammal and bird diversity patterns in deglaciated North America. *Global Ecology and Biogeography*, **12**, 475-481.
- Hawkins, B.A., Rodriguez, M.A. & Weller, S.G. (2011) Global angiosperm family richness revisited: linking ecology and evolution to climate. *Journal of Biogeography*, **38**, 1253-1266.
- Hawkins, B. A., Rueda, M., Rangel, T. F., Field, R., Diniz-Filho, J. A. F. (2014) Community phylogenetics at the biogeographical scale: cold tolerance, niche conservatism and the structure of North American forests. *Journal of Biogeography*, **41**, 23–38.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965-1978.

- Hijmans, R., Phillips, S., Leathwick, J. & Elith, J. (2012) dismo: Species distribution modeling. R package version 0.7-17. <http://CRAN.R-project.org/package=dismo>.
- Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *The American Naturalist*, **163**, 192-211.
- Hof C., Araújo, M.B., Jetz, W. & Rahbek, C. (2011) Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature*, **480**, 516-U137.
- Hoffmann, A. A., Chown, S. L., Clusella-Trullas, S. (2013) Upper thermal limits in terrestrial ectotherms: how constrained are they? *Functional Ecology*, **27**: 934–949.
- Holdridge, L. R. (1967) Life zone ecology. *Tropical Science Center*, San Jose, Costa Rica.
- Holt, B.G., Lessard, J.-P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D., Fabre, P.-H., Graham, C.H., Graves, G.R., Jonsson, K.A., Nogues-Bravo, D., Wang, Z., Whittaker, R.J., Fjeldsa, J. & Rahbek, C. (2013) *Science*, **339**, 74-78.
- Holt, R.D. & Keitt, T.H. (2000) Alternative causes for range limits: A metapopulation perspective. *Ecology Letters*, **3**, 41-47.
- Holt, R.D. & Barfield, M. (2011) Theoretical perspectives on the statics and dynamics of species' borders in patchy environments. *American Naturalist*, **178**, S6-S25.
- Hortal, J., Diniz-Filho, J.A.F., Bini, L.M., Angel Rodriguez, M., Baselga, A., Nogues-Bravo, D., Rangel, T.F., Hawkins, B.A. & Lobo, J.M. (2011) Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. *Ecology Letters*, **14**, 741-748.
- Huang, S., Roy, K. & Jablonski, D. (2014) Do past climate states influence diversity dynamics and the present-day latitudinal diversity gradient? *Global Ecology and Biogeography*, **23**, 530-540.

- Huete, A., Didan, K., Miura, T., Rodriguez, E.P., Gao, X., Ferreira, L.G. (2002) Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing and Environment*, **83**, 195-213.
- Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. In. Princeton University Press, Princeton, N.J.
- Hurlbert, A.H. (2004) Species-energy relationships and habitat complexity in bird communities. *Ecology Letters*, **7**, 714-720.
- Hurlbert, A. & Jetz, W. (2007) Species richness, hotspots and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences USA*, **104**, 13384–13389.
- Hurlbert, A. & Stegen, J. (2014) When should species richness be energy limited, and how would we know? *Ecology Letters*, **17**, 401-413.
- Hutchinson, G. (1957) Concluding remarks. *Cold Spring Harbour Symposia on Quantitative Biology*, **22**, 415-427.
- Jansson, R. & Davies, T.J. (2008) Global variation in diversification rates of flowering plants: energy vs. climate change. *Ecology Letters*, **11**, 173-183.
- Jansson, R., Rodriguez-Castaneda, G. & Harding, L.E. (2013) What can multiple phylogenies say about the latitudinal diversity gradient? A new look at the tropical conservatism, out of the tropics, and diversification rate hypotheses. *Evolution*, **67**, 1741-1755.
- Janzen, D.H. (1967) Why mountain passes are higher in the tropics. *American Naturalist*, **101**, 233-249.

- Jetz, W. & Fine, P.V.A. (2012) Global Gradients in Vertebrate Diversity Predicted by Historical Area-Productivity Dynamics and Contemporary Environment. *Plos Biology*, **10**, e1001292.
- Jetz, W., Rahbek, C. & Lichstein, J. W. (2005) Local and global approaches to spatial data analysis in ecology. *Global Ecology and Biogeography*, **14**, 97-98.
- Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012) The global diversity of birds in space and time. *Nature*, **491**, 444-448.
- Jiménez, I. & Ricklefs, R. E. (2014) Diversity anomalies and spatial climate heterogeneity. *Global Ecology and Biogeography*, **23**, 988-999.
- Jocque, M., Field, R., Brendonck, L. & De Meester, L. (2010) Climatic control of dispersal-ecological specialization trade-offs: a metacommunity process at the heart of the latitudinal diversity gradient? *Global Ecology and Biogeography*, **19**, 244-252.
- Justice, C.O., Vermote, E., Townshend, J.R.G., Defries, R., Roy, D.P., Hall, D.K., Salomonson, V.V., Privette, J.L., Riggs, G., Strahler, A., Lucht, W., Myneni, R. B., Knyazikhin, Y., Running, S. W., Nemani, R. R., Wan, Z. M., Huete, A. R., van Leeuwen, W., Wolfe, R. E., Giglio, L., Muller, J. P., Lewis, P. & Barnsley, M. J. (1998) The Moderate Resolution Imaging Spectroradiometer (MODIS): Land remote sensing for global change research. *Ieee Transactions on Geoscience and Remote Sensing*, **36**, 1228-1249.
- Kalmar, A. & Currie, D.J. (2007) A unified model of avian species richness on islands and continents. *Ecology*, **88**, 1309-1321.
- Karl, J.W., Heglund, P.J., Garton, E.O., Scott, J.M., Wright, N.M. & Hutto, R.L. (2000) Sensitivity of species habitat-relationship model performance to factors of scale. *Ecological Applications*, **10**, 1690-1705.

- Kaufman, D. M. (1995) Diversity of New-World mammals - Universality of the latitudinal gradients of species and bauplans. *Journal of Mammalogy*, **76**, 322-334.
- Kearney, M. (2006) Habitat, environment and niche: what are we modeling? *Oikos*, **115**, 186-191.
- Kearney, M. & Porter, W. P. (2004) Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology*, **85**, 3119-3131.
- Kellermann, V., Overgaard, J. , Hoffmann, A. A. , Fløjgaard, C. , Svenning, J.-C. & Loeschcke, V. (2012) Upper thermal limits of *Drosophila* are linked to species distributions and strongly constrained phylogenetically. *Proceedings of the National Academy of Sciences USA*, **109**, 16228-16233.
- Kerr, J.T. & Currie, D.J. (1999) The relative importance of evolutionary and environmental controls on broad-scale patterns of species richness in North America. *Ecoscience*, **6**, 329-337.
- Kerr, J.T. & Packer, L. (1997) Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature*, **385**, 252-254.
- Khalid, I., Hof, C., x Prinzinger, C., Böhning-Gaese, K. & Pfenninger, M. (2014) Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proceedings of the Royal Society B*, **281**, 20141097.
- Kharouba, H. M., Algar, A. C. & Kerr, J. T. (2009) Historically calibrated predictions of butterfly species' range shift using global change as a pseudo-experiment. *Ecology*, **90**, 2213-2222.
- Kirkpatrick, M. & Barton, N. H. (1997) Evolution of a species' range. *American Naturalist*, **150**, 1-23.

- Kissling, W.D. & Carl, G. (2008) Spatial autocorrelation and the selection of simultaneous autoregressive models. *Global Ecology and Biogeography*, **17**, 59-71.
- Kissling, W.D., Eiserhardt, W.L., Baker, W.J., Borchsenius, F., Couvreur, T.L.P., Balslev, H. & Svenning, J.-C. (2012a) Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide. *Proceedings of the National Academy of Sciences USA*, **109**, 7379-7384.
- Kissling, W.D., Baker, W.J., Balslev, H., Barfod, A.S., Borchsenius, F., Dransfield, J., Govaerts, R. & Svenning, J.-C. (2012b) Quaternary and pre-Quaternary historical legacies in the global distribution of a major tropical plant lineage. *Global Ecology and Biogeography*, **21**, 909-921.
- Kleidon, A., Adams, J., Pavlick, R. & Reu, B. (2009) Simulated geographic variations of plant species richness, evenness and abundance using climatic constraints on plant functional diversity. *Environmental Research Letters*, **4**, 5.
- Kleidon, A. & Mooney, H. A. (2000) A global distribution of biodiversity inferred from climatic constraints: results from a process-based modelling study. *Global Change Biology*, **6**, 507-523.
- Korner, C. & Paulsen, J. (2004) A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, **31**, 713-732.
- Kreyling, J., Schmid, S. & Aas, G. (2014) Cold tolerance of tree species is related to the climate of their native ranges. *Journal of Biogeography*, **42**, 156-166.
- La Sorte, F.A. & Jetz, W. (2012) Tracking of climatic niche boundaries under recent climate change. *Journal of Animal Ecology*, **81**, 914-925.

- Lakatos, I. (1999) *Lectures on Scientific Method*. In: For and Against Method (Editor: M. Motterlini). The University of Chicago Press, Chicago & London, pp. 459.
- Lamanna, C., Blonder, B., Violle, C., Kraft, N. J., Sandel, B., Simova, I., Donoghue, J.C. II, Svenning, J. C., McGill, B. J., Boyle, B., Buzzard, V., Dolins, S., Jorgensen, P. M., Marcuse-Kubitza, A., Morueta-Holme, N., Peet, R. K., Piel, W. H., Regetz, J., Schildhauer, M., Spencer, N., Thiers, B., Wiser, S. K. & Enquist, B. J. (2014) Functional trait space and the latitudinal diversity gradient. *Proceedings of the National Academy of Sciences USA*, **111**, 13745-13750.
- Lange, M. (2005) Ecological laws: what would they be and why would they matter? *Oikos*, **110**, 394-403.
- Latham R.E. & Ricklefs, R.E. (1993) Global patterns of tree species richness in moist forests - Energy-diversity theory does not account for variation in species richness. *Oikos*, **67**, 325-333.
- Laube, I., Graham, C. H. & Boehning-Gaese, K. (2013) Intra-generic species richness and dispersal ability interact to determine geographic ranges of birds. *Global Ecology and Biogeography*, **22**, 223-232.
- Lawton, J. H. (1999) Are there general laws in ecology? *Oikos*, **84**, 177-192.
- Leigh, E.G. (1981) The average lifetime of a population in a varying environment. *Journal of Theoretical Biology*, **90**, 213-239.
- Lennon, J.J. (2000) Red-shifts and red herrings in geographical ecology. *Ecography*, **23**, 101-113.
- Lennon, J. J., Turner, J. R. G. & Connell, D. (1997) A metapopulation model of species boundaries. *Oikos*, **78**, 486-502.

- Lenoir, J., Gégout, J., Marquet, P., De Ruffray, P. & Brisse, H. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**, 1768-1771.
- Lima-Ribeiro, M., Faleiro, F. & Silva, D. (2013) Current and historical climate signatures to deconstructed tree species richness pattern in South America. *Acta Scientiarum*, **35**, 219-231.
- Loehle, C. (1998) Height growth rate tradeoffs determine northern and southern range limits for trees. *Journal of Biogeography*, **25**, 735-742.
- Losos, J.B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, **11**, 995-1003.
- Lowenberg-Neto, P., de Carvalho, C.J.B. & Hawkins, B.A. (2011) Tropical niche conservatism as a historical narrative hypothesis for the Neotropics: a case study using the fly family Muscidae. *Journal of Biogeography*, **38**, 1936-1947.
- Luna, B., & Moreno, J.M. (2010) Range-size, local abundance and germination niche-breadth in Mediterranean plants of two life-forms. *Plant Ecology*, **210**, 85-95.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Oxford.
- MacArthur, R.H. (1969) Patterns of communities in the tropics. *Journal of the Linnean Society*, **1**, 19-30.
- MacArthur, R. H. (1972) *Geographical ecology; patterns in the distribution of species*. Harper & Row, New York.
- Manel, S., Williams, H. C. & Ormerod, S. J. (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology*, **38**, 921-931.

- Marquet, P.A., Allen, A.P., Brown, J.H., Dunne, J.A., Enquist, B.J., Gillooly, J.F., Gowaty, P.A., Green, J.L., Harte, J., Hubbell, S.P., O'Dwyer, J., Okie, J.G., Ostling, A., Ritchie, M., Storch, D. & West, G.B. (2014) On Theory in Ecology. *Bioscience*, **64**, 701-710.
- Martinez-Meyer, E., Peterson, A.T. & Navarro-Siguenza, A.G. (2004) Evolution of seasonal ecological niches in the Passerina buntings (Aves: Cardinalidae). *Proceedings of the Royal Society B*, **271**, 1151-7.
- Mathieu, J. & Davies, J. (2014) Glaciation as an historical filter of below-ground biodiversity. *Journal of Biogeography*, **41**, 1204–1214.
- Mehlman, D.W. (1997) Change in avian abundance across the geographic range in response to environmental change. *Ecological Applications*, **7**, 614-624.
- Menéndez, R., Megias, A.G., Hill, J.K., Braschler, B., Willis, S.G., Collingham, Y., Fox, R., Roy, D.B. & Thomas, C.D. (2006) Species richness changes lag behind climate change. *Proceedings of the Royal Society B*, **273**, 1465-1470.
- Meredith, R.W., Janečka, J.E., Gatesy, J., Ryder, O.A., Fisher, C.A., Teeling, E.C., Goodbla, A., Eisirik, E., Simão, T.L.L., Stadler, T., Rabosky, D.L., Honeycutt, R.L., Flynn, J.J., Ingram, C.M., Steiner, C., Williams, T.L., Robinson, T.J., Burk-Herrick, A., Westerman, M., Ayoub, N.A., Springer, M.S. & Murphy, W.J. (2011) Impacts of the Cretaceous terrestrial revolution on KPg extinction on mammal diversification. *Science*, **334**, 521-524.
- McInerney, G. J., Turner, J. R. G., Wong, H. Y., Travis, J. M. J. & Benton, T. G. (2009) How range shifts induced by climate change affect neutral evolution. *Proceedings of the Royal Society B*, **276**, 1527-1534.

- McKenney, D. W., Pedlar, J. H., Lawrence, K., Campbell, K. & Hutchinson, M. F. (2007) Potential impacts of climate change on the distribution of North American trees. *Bioscience*, **57**, 939-948.
- McPeck, M.A. & Brown, J.M. (2007) Clade Age and Not Diversification Rate Explains Species Richness among Animal Taxa. *The American Naturalist*, **169**, E97-E106.
- Mittelbach, G. G., Schemske, D. W., Cornell, H. V., Allen, A. P., Brown, J. M., Bush, M. B., Harrison, S. P., Hurlbert, A. H., Knowlton, N., Lessios, H. A., McCain, C. M., McCune, A. R., McDade, L. A., McPeck, M. A., Near, T. J., Price, T. D., Ricklefs, R. E., Roy, K., Sax, D. F., Schluter, D., Sobel, J. M. & Turelli, M. (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**, 315–331.
- Moen, D.S., Irschick, D.J. & Wiens, J.J. (2013) Evolutionary conservatism and convergence both lead to striking similarity in ecology, morphology and performance across continents in frogs. *Proceedings of the Royal Society B*, **280**, 20132156.
- Montoya, D., Rodriguez, M.A., Zavala, M.A. & Hawkins, B.A. (2007) Contemporary richness of holarctic trees and the historical pattern of glacial retreat. *Ecography*, **30**, 173-182.
- Mora, C., Chittaro, P.M., Sale, P.F., Kritzer, J.P. & Ludsin, S.A. (2003) Patterns and processes in reef fish diversity. *Nature*, **421**, 933-936.
- Morin, X., Augspurger, C. & Chuine, I. (2007) Process-based modeling of species' distributions: What limits temperate tree species' range boundaries? *Ecology*, **88**, 2280-2291.
- Morin, X. & Chuine, I. (2006) Niche breadth, competitive strength and range size of tree species: a trade-off based framework to understand species distribution. *Ecology Letters*, **9**, 185-195.

- Morin, X. & Lechowicz, M.J. (2013) Niche breadth and range area in North American trees. *Ecography*, **36**, 300-312.
- Moruet-Holme, N., Enquist, B.J., McGill, B.J., Boyle, B., Jørgensen, P.M., Ott, J.E., Peet, R.K., Šímová, I., Sloat, L.L., Thiers, B., Violle, C., Wiser, S.K., Dolins, S., Donoghue, J.C., Kraft, N.J.B., Regetz, J., Schildhauer, M., Spencer, N. & Svenning, J.-C. (2013) Habitat area and climate stability determine geographical variation in plant species range sizes. *Ecology Letters*, **16**, 1446-1454.
- Mullen, K.M., & Stokkum, I.H.M. (2012) nnls: The Lawson-Hanson algorithm for non-negative least squares (NNLS). R package version 1.4. <http://CRAN.R-project.org/package=nnls>
- Munguia, M., Peterson, A. T. & Sanchez-Cordero, V. (2008) Dispersal limitation and geographical distributions of mammal species. *Journal of Biogeography*, **35**, 1879-1887.
- Murray, B. R. & Lepschi, B. J. (2004) Are locally rare species abundant elsewhere in their geographical range? *Austral Ecology*, **29**, 287-293.
- Nakazawa, Y. (2013) Niche breadth, environmental landscape, and physical barriers: their importance as determinants of species distributions. *Biological Journal of the Linnean Society*, **108**, 241-250.
- Nakazawa, Y., Peterson, A. T., Martinez-Meyer, E. & Navarro-Siguenza, A. G. (2004) Seasonal niches of Nearctic-Neotropical migratory birds: Implications for the evolution of migration. *Auk*, **121**, 610-618.
- Nathan, R., Katul, G.G., Horn, H.S., Thomas, S.M., Oren, R., Avissar, R., Pacala, S.W. & Levin, S.A. (2002) Mechanisms of long-distance dispersal of seeds by wind. *Nature*, **418**, 409-413.

- NCAR - Research Application Program. (2012) verification: Forecast verification utilities. R package version 1.32. <http://CRAN.R-project.org/package=verification>.
- Nelder, J. A. and Mead, R. (1965) A simplex algorithm for function minimization. *Computer Journal*, **7**, 308–313.
- Nogués-Bravo, D. (2009) Predicting the past distribution of species climatic niches. *Global Ecology and Biogeography*, **18**, 521-531.
- Nogués-Bravo, D., Pulido, F., Araújo, M.B., Diniz-Filho, J.A.F., García-Valdés, R., Kollmann, J., Svenning, J.-C., Valladares, F. & Zavala, M.A. (2014) Phenotypic correlates of potential range size and range filling in European trees. *Perspectives in Plant Ecology, Evolution and Systematics*, **16**, 219-225.
- Normand, S., Ricklefs, R.E., Skov, F., Bladt, J., Tackenberg, O. & Svenning, J.-C. (2011) Postglacial migration supplements climate in determining plant species ranges in Europe. *Proceedings of the Royal Society B*, **278**, 3644-3653.
- Normand, S., Treier, U. A., Randin, C., Vittoz, P., Guisan, A. & Svenning, J. C. (2009) Importance of abiotic stress as a range-limit determinant for European plants: insights from species responses to climatic gradients. *Global Ecology and Biogeography*, **18**, 437-449.
- O'Brien, E.M. (1998) Water-energy dynamics, climate, and predicting of woody plant species richness: An interim general model. *Journal of Biogeography*, **25**, 379-398.
- O'Brien, E. M. (2006) Biological relativity to water-energy dynamics. *Journal of Biogeography*, **33**, 1868-1888.
- Oksanen, J. & Minchin, P. R. (2002) Continuum theory revisited: what shape are species responses along ecological gradients? *Ecological Modelling*, **157**, 119-129.

- Ordóñez, A. (2013) Realized climatic niche of North American plant taxa lagged behind climate during the end of the Pleistocene. *American Journal of Botany*, **100**, 1255-1265.
- Ordóñez, A. & Williams, J.W. (2013) Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. *Ecology Letters*, **16**, 773-781.
- Paine, R.T. (2010) Macroecology: Does it ignore or can it encourage further ecological syntheses based on spatially local experimental manipulations? *American Naturalist*, **176**, 385-393.
- Pannek, A., Ewald, J. & Diekmann, M. (2013) Resource-based determinants of range sizes of forest vascular plants in Germany. *Global Ecology and Biogeography*, **22**, 1019-1028.
- Papes, M., Peterson, A.T. & Powell, G.V.N. (2012) Vegetation dynamics and avian seasonal migration: clues from remotely sensed vegetation indices and ecological niche modelling. *Journal of Biogeography*, **39**, 652-64.
- Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, **37**, 637-669.
- Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37-42.
- Patterson, B., Ceballos, G., Sechrest, W., Tognelli, M., Brooks, T., Luna, L., Ortega, P., Salazar, I. & Young, B. (2007) Digital Distribution Maps of the Mammals of the Western Hemisphere, version 3.0.
- Pearman, P. B., Randin, C. F., Broennimann, O., Vittoz, P., van der Knaap, W. O., Engler, R., Le Lay, G., Zimmermann, N. E. & Guisan, A. (2008) Prediction of plant species distributions across six millennia. *Ecology Letters*, **11**, 357-369.

- Pearson, R. (2007) Species' distribution modeling for conservation educators and practitioners. Synthesis. *American Museum of Natural History*.
- Pearson, R. G. & Dawson, T. P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361-371.
- Peters, R.H. (1991) *A critique for Ecology*. Cambridge University Press, Cambridge.
- Peterson, A. T., Papes, M. & Eaton, M. (2007) Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. *Ecography*, **30**, 550-560.
- Peterson, A. T. P., Soberón, J., Pearson, R. G., Anderson, R. P., Martínez-Meyer, E., Nakamura, M. & Araújo M. B. (2011) Ecological Niches and Geographical Distributions: A Modeling Perspective. *Princeton University Press*.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231-259.
- Pianka, E.R. (1989) Latitudinal gradients in species diversity: A review of concepts. *The American Naturalist*, **100**, 13.
- Pigot, A. L., Owens, I. P. F. & Orme, C. D. L. (2010) The environmental limits to geographic range expansion in birds. *Ecology Letters*, **13**, 705-715.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R development core team (2012) nlme: Linear and nonlinear mixed effects models. R package version 3.1-105.
- Pinzon J., Brown, M.E. & Tucker, C.J. (2005) Satellite time series correction of orbital drift artifacts using empirical mode decomposition. In Hilbert-Huang Transform: Introduction and Applications (ed. N. Huang). College Park: Global land cover facility, University of Maryland.

- Pither, J. (2003) Climate tolerance and interspecific variation in geographic range size. *Proceedings of the Royal Society of London Series B*, **270**, 475-481.
- Platt, J.R. (1964) Strong inference – Certain systematic methods of scientific thinking may produce much more rapid progress than others. *Science*, **146**, 347-353.
- Popper, K.R. (2002) *Conjectures and Refutations: The Growth of Scientific Knowledge*. Psychology Press, pp 582.
- Popper, K. & Miller, D. (1983) A proof of the impossibility of inductive probability. *Nature*, **302**, 687-688.
- Preston, F. W. (1962) Canonical distribution of commonness and rarity.1. *Ecology*, **43**, 185-215.
- Pulliam, H.R. (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349-361.
- Pyron, R.A. & Burbrink, F.T. (2009) Can the tropical conservatism hypothesis explain temperate species richness patterns? An inverse latitudinal biodiversity gradient in the New World snake tribe Lampropeltini. *Global Ecology and Biogeography*, **18**, 406-415.
- Quenette, P. & Gerard, J. (1993) Why biologists do not think like Newtonian physicists. *Oikos*, **68**, 361-363.
- Quintero, I. & Wiens, J.J. (2013) What determines the climatic niche width of species? The role of spatial and temporal climatic variation in three vertebrate clades. *Global Ecology and Biogeography*, **22**, 422-432.
- R development Core Team (2012) *R: A language and environment for statistical computing*. R Foundation for Statistical computing, Vienna. URL <http://www.R-project.org/>.
- R Core Team (2013) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

- R Core Team (2014) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Rabosky, D.L. (2009) Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. *Ecology Letters*, **12**, 735-743.
- Rabosky, D.L. & Lovette, I.J. (2008) Explosive evolutionary radiations: decreasing speciation or increasing extinction through time? *Evolution*, **62**, 1866-1875.
- Rabosky, D.L. & Hurlbert, A.H. (2015) Species Richness at Continental Scales Is Dominated by Ecological Limits. *The American Naturalist*, **185**, 572-583.
- Randin, C. F., Dirnbock, T., Dullinger, S., Zimmermann, N. E., Zappa, M. & Guisan, A. (2006) Are niche-based species distribution models transferable in space? *Journal of Biogeography*, **33**, 1689-1703.
- Ribeiro, P.J. & Diggle, P.J. (2006) geoR: a package for geostatistical analysis. *R-NEWS*, **1**, 15-18.
- Ricklefs, R.E. (1987) Community Diversity: Relative Roles of Local and Regional Processes. *Science*, **235**, 167-171.
- Ricklefs, R.E. (2006) Evolutionary diversification and the origin of the diversity-environment relationship. *Ecology*, **87**, S3-S13.
- Ricklefs, R.E. (2007) History and diversity: Explorations at the intersection of ecology and evolution. *American Naturalist*, **170**, S56-S70.
- Ricklefs, R.E. & Schluter, D. (1993) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago.

- Ricklefs, R. E., Latham, R. E & Qian H. (1999) Global patterns of tree species richness in moist forests: distinguishing ecological influences and historical contingency. *Oikos*, **86**, 369-373.
- Ridgely, R. S., Allnutt, T. F., Brooks, T., McNicol, D. K., Mehlman, D. W., Young, B. E. & Zook, J. R. (2007) Digital Distribution Maps of the Birds of the Western Hemisphere, version 3.0.
- Rodriguez, J.P. (2002) Range contraction in declining North American bird populations. *Ecological Applications*, **12**, 238-248.
- Rohde, K. (1992) Latitudinal gradients in species diversity — The search for the primary cause. *Oikos*, **65**, 514-527.
- Rolland, J., Condamine, F.L., Jiguet, F. & Morlon, H. (2014) Faster Speciation and Reduced Extinction in the Tropics Contribute to the Mammalian Latitudinal Diversity Gradient. *PLoS Biol*, **12**, e1001775.
- Romdal, T.S., Araùjo, M.B. & Rahbek, C. (2013) Life on a tropical planet: niche conservatism and the global diversity gradient. *Global Ecology and Biogeography*, **22**, 344-350.
- Root, T. (1988) Energy constraints on avian distribution and abundances. *Ecology*, **69**, 330-339.
- Rosenzweig, M.L. (1995) Species diversity in space and time. In, p. 436. Cambridge University Press, New York.
- Rosindell, J., Hubbell, S.P. & Etienne, R.S. (2011) The Unified Neutral Theory of Biodiversity and Biogeography at Age Ten. *Trends in Ecology & Evolution*, **26**, 340-348.
- Roy, K. & Goldberg, E.E. (2007) Origination, extinction, and dispersal: Integrative models for understanding present-day diversity gradients. *American Naturalist*, **170**, S71-S85.
- Russell, B. (1949) *History of Western Philosophy*. George Allen & Unwin, London.

- Sagarin, R.D. & Gaines, S.D. (2002) The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecology Letters*, **5**, 137-147.
- Sakai, A. & Weiser, C. J. (1973) Freezing resistance of trees in North America with reference to tree regions. *Ecology*, **54**, 118-126.
- Sallabanks, R. (2002) Effects of forest fragmentation on breeding bird populations: Conflicting views from North America. *Avian Landscape Ecology: Pure and Applied Issues in the Large-Scale Ecology of Birds*, 3-14.
- Sandel, B., Arge, L., Dalsgaard, B., Davies, R.G., Gaston, K.J., Sutherland, W.J. & Svenning, J.-C. (2011) The influence of Late Quaternary climate-change velocity on species endemism. *Science*, **334**, 660-664.
- Sax, D.F., Early, R. & Bellemare, J. (2013) Niche syndromes, species extinction risks and management under climate change. *Trends in Ecology and Evolution*, **28**, 517-523.
- Sax, D.F. & Gaines, S.D. (2008) Species invasions and extinction: The future of native biodiversity on islands. *Proceedings of the National Academy of Sciences USA*, **105**, 11490-11497.
- Schlather, M., Malinowski, A., Oesting, M., Boecker, D., Stokorb, K., Engelke, S., Martini, J., Menck, P., Gross, S., Burmeister, K., Manitz, J., Singleton, R., Pfaff, B. & R Core Team (2014) RandomFields: Simulation and Analysis of Random Fields. R package version 3.0.10. <http://CRAN.R-project.org/package=RandomFields>.
- Schemske, D. W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M. & Roy, K. (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology Evolution and Systematics*, **40**, 245-269.

- Schurr, F. M., G. F. Midgley, A. G. Rebelo, G. Reeves, P. Poschlod, and S. I. Higgins. 2007. Colonization and persistence ability explain the extent to which plant species fill their potential range. *Global Ecology and Biogeography*, **16**, 449-459.
- Sexton, J. P., McIntyre, P. J., Angert, A. L. & Rice, K. J. (2009) Evolution and ecology of species range limits. *Annual Review of Ecology Evolution and Systematics*, **40**, 415-436.
- Simova, I., Storch, D., Keil, P., Boyle, B., Phillips, O.L. & Enquist, B.J. (2011) Global species-energy relationship in forest plots: role of abundance, temperature and species climatic tolerances. *Global Ecology and Biogeography*, **20**, 842-856.
- Šizling, A.L., Storch, D. & Keil, P. (2009) Rapoport's rule, species tolerances, and the latitudinal diversity gradient: geometric considerations. *Ecology*, **90**, 3575-3586.
- Slatyer, R.A., Hirst, M. & Sexton, J.P. (2013) Niche breadth predicts geographical range size: a general ecological pattern. *Ecology Letters*, **16**, 1104-1114.
- Smith, B.T., Bryson, R.W., Houston, D.D. & Klicka, J. (2012) An asymmetry in niche conservatism contributes to the latitudinal species diversity gradient in New World vertebrates. *Ecology Letters*, **15**, 1318–1325
- Sobéron, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, **10**, 1115-1123.
- Sobéron, J. & Nakamura, M. (2009) Niches and distributional areas: Concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences USA*, **106**, 19644-19650.
- Sobéron, J. & Peterson, A.T. (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, **2**, 1-10.

- Soininen, J., Heino, J., Lappalainen, J. & Virtanen, R. (2011) Expanding the ecological niche approach: Relationships between variability in niche position and species richness. *Ecological Complexity*, **8**, 130-137
- Soulé, M. (1973) The Epistasis Cycle: A Theory of Marginal Populations. *Annual review of ecology and systematics*, **4**, 165-187.
- Stephenson, N. L. (1990) Climatic control of vegetation distribution - The role of the water-balance. *American Naturalist*, **135**, 649-670.
- Stevens, G.C. (1989) The latitudinal gradient in geographical range - How so many species coexist in the tropics. *American Naturalist*, **133**, 240-256.
- Stevens, R.D. (2006) Historical processes enhance patterns of diversity along latitudinal gradients. *Proceedings of the Royal Society B*, **273**, 2283-2289.
- Stevens, G.C. (2011) Relative effects of time for speciation and tropical niche conservatism on the latitudinal diversity gradient of phyllostomid bats. *Proceedings of the Royal Society B*, **278**, 2528-2536.
- Strubbe, D., Beauchard, O. & Matthysen, E. (2015) Niche conservatism among non-native vertebrates in Europe and North America. *Ecography*, **38**, 321-329.
- Sunday, J. M., A. E. Bates & Dulvy, N.K. (2011) Global analysis of thermal tolerance and latitude in ectotherms, *Proceedings of the Royal Society B*, **278**, 1823-1830.
- Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2012) Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, **2**, 686-690.
- Sunday, J. M., Bates, A. E., Kearney, M. R., Colwell, R. K., Dulvy, N. K., Longino, J. T. & Huey, R. B. (2014) Thermal-safety margins and the necessity of thermoregulatory

- behavior across latitude and elevation. *Proceedings of the National Academy of Sciences USA*, **111**, 5610-5615.
- Svenning, J. C. & Skov, F. (2004) Limited filling of the potential range in European tree species. *Ecology Letters*, **7**, 565-573.
- Svenning, J.-C., Normand, S. & Skov, F. (2008) Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. *Ecography*, **31**, 316-326.
- Svenning, J.C. & Skov, F. (2007) Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecology Letters*, **10**, 453-460.
- Swan, J. M. A. (1970) An examination of some ordination problems by use of simulated vegetational data. *Ecology*, **51**, 89-102.
- Szabo, N. D., Algar, A. C. & Kerr, J. T. (2009) Reconciling topographic and climatic effects on widespread and range-restricted species richness. *Global Ecology and Biogeography*, **18**, 735-744.
- Szep T., Moller, A.P., Piper, S., Nuttall, R., Szabo, Z.D. & Pap, P.L. (2006) Searching for potential wintering and migration areas of a Danish Barn Swallow population in South Africa by correlating NDVI with survival estimates. *Journal of Ornithology*, **147**, 245-253.
- Tanaka, Y. (2000) Extinction of populations by inbreeding depression under stochastic environments. *Population Ecology*, **42**, 55-62.
- Tello, S. & Stevens, R. D. (2010) Multiple environmental determinants of regional species richness and effects of geographic range size. *Ecography*, **33**, 796-808.
- ter Braak, C.J.F & Looman, C.W.N (1986) Weighted averaging, logistic regression and the Gaussian response model. *Vegetatio*, **65**, 3–11.

- Thomas, C.D., Franco, A.M.A. & Hill, J.K. (2006) Range retractions and extinction in the face of climate warming. *Trends in Ecology & Evolution*, **21**, 415-416.
- Tingley, M. W., Monahan, W. B., Beissinger, S. R. & Moritz C. (2009) Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences USA*, **106**, 19637-19643.
- Tingley, R., Vallinoto, M., Sequeira, F. & Kearney, M. R. (2014) Realized niche shift during a global biological invasion. *Proceedings of the National Academy of Sciences USA*, **111**, 10233-10238.
- Tomašových, A., Jablonski, D., Berke, S. K., Krug, A. Z. and Valentine, J. W. (2015) Nonlinear thermal gradients shape broad-scale patterns in geographic range size and can reverse Rapoport's rule. *Global Ecology and Biogeography*, **24**: 157–167.
- Tucker, C.J., Pinzon, J.E., Brown, M.E., Slayback, D.A., Pak, E.W., Mahoney, R., Vermote, E.F. & El Saleous, N. (2005) An extended AVHRR 8-km NDVI dataset compatible with MODIS and SPOT vegetation NDVI data. *International. Journal of Remote Sensing*, **26**, 4485-4498.
- Turvey, S.T., Barrett, L.A., Hart, T., Collen, B., Hao, Y.J., Zhang, L., Zhang, X.Q., Wang, X.Y., Huang, Y.D., Zhou, K.Y. & Wang, D. (2010) Spatial and temporal extinction dynamics in a freshwater cetacean. *Proceedings of the Royal Society B*, **277**, 3139-3147.
- Ulrich, W., Olrik, M. & Ugland, K. I. (2010) A meta-analysis of species-abundance distributions. *Oikos*, **119**, 1149-1155.
- U.S Geological Survey (1999) *Digital representation of "Atlas of United States Trees" by Elbert L. Little, Jr.* <<http://esp.cr.usgs.gov/info/veg-clim/>>

- USGS Patuxent Wildlife Research Center (2013) North American Breeding Bird Survey ftp data set, version 2013.0, <ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/datafiles/>
- Vazquez, D.P. & Stevens, R.D. (2004) The latitudinal gradient in niche breadth: Concepts and evidence. *American Naturalist*, **164**, E1-E19.
- Vázquez-Rivera, H. & Currie, D.J. (2015) Contemporaneous climate directly controls broad-scale patterns of woody plant diversity: a test by a natural experiment over 14,000 years. *Global Ecology and Biogeography*, **24**, 97–106.
- Velòz, S.D., Williams, J.W., Blois, J.L., He, F., Otto-Bliesner, B. & Liu, Z. (2012) No-analog climates and shifting realized niches during the late quaternary: implications for 21st-century predictions by species distribution models. *Global Change Biology*, **18**, 1698-1713.
- Venables, W. & Ripley, B. (2002) Modern Applied Statistics with S. Fourth Edition. *Springer*, New York, pp. 508.
- Vetaas, O.R. (2002) Realized and potential climate niches: A comparison of four *Rhododendron* tree species. *Journal of Biogeography*, **29**, 545-554.
- Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P. & Parmenter, R. (1999) The Relationship between Productivity and Species Richness. *Annual Review of Ecology and Systematics*, **30**, 257-300.
- Walker, K. (2013) *Climatic dependence of terrestrial species assemblage structure*. PhD thesis, University of Ottawa, Ottawa.
- Wallace, A. (1876) The geographic distribution of animals. *Harper & Brothers*, New York.
- Wallace, A.R. (1878) *Tropical nature and other essays*, MacMillan, London.

- Waring, R.H., Coops, N.C., Fan, W. & Nightingale, J.M. (2006) MODIS enhanced vegetation index predicts tree species richness across forested ecoregions in the contiguous U.S.A. *Remote Sensing of Environment*, **103**, 218-226.
- Warren, D. L., Cardillo, M., Rosauer, D. F. & Bolnick, D. I. (2014) Mistaking geography for biology: inferring processes from species distributions. *Trends in Ecology & Evolution*, **29**, 572-580.
- Warren, D., & Seifert, S. (2011) Environmental niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications*, **21**, 335-342.
- Weir, J.T. & Schluter, D. (2007) The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science*, **315**, 1574-1576.
- Werneck, F.P., Nogueira, C., Colli, G.R., Sites, J.W. & Costa, G.C. (2012) Climatic stability in the Brazilian Cerrado: implications for biogeographical connections of South American savannas, species richness and conservation in a biodiversity hotspot. *Journal of Biogeography*, **39**, 1695-1706.
- Whittaker, R. (1965) Dominance and diversity in land plant communities: Numerical relations of species express importance of competition in community function and evolution. *Science*, 147-250.
- Whittaker, R. H. (1975) *Communities and Ecosystems*, 2nd ed. MacMillan, New York.
- Wiens, J.J. (2011) The causes of species richness patterns across space, time and clades and the role of "ecological limits". *Quarterly Review of Biology*, **86**, 75-96.
- Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Davies, T.J., Grytnes, J.A., Harrison, S.P., Hawkins, B.A., Holt, R.D., McCain, C.M.

- & Stephens, P.R. (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, **13**, 1310-1324.
- Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*, **19**, 639-644.
- Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology Evolution and Systematics*, **36**, 519-539.
- Wiens, J.J., Sukumaran, J., Pyron, R.A. & Brown, R.M. (2009) Evolutionary and biogeographic origins of high tropical diversity in Old World frogs (Ranidae). *Evolution*, **63**, 1217-1231.
- Williams, J.W., Post, D.M., Cwynar, L.C., Lotter, A.F. & Levesque, A.J. (2002) Rapid and widespread vegetation responses to past climate change in the North Atlantic region. *Geology*, **30**, 971-974.
- Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology Evolution and Systematics*, **34**, 273-309.
- Willis, K.J., Kleczkowski, A., New, M. & Whittaker, R.J. (2007) Testing the impact of climate variability on European plant diversity: 320,000 years of water–energy dynamics and its long-term influence on plant taxonomic richness. *Ecology Letters*, **10**, 673-679.
- Wolters, V., Bengtsson, J. & Zaitsev, A. (2006) Relationship among the species richness of different taxa. *Ecology*, **87**, 1886–1895.
- Wood, S. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society B*, **73**, 3-36.

- Yackulic, C.B., Sanderson, E.W. & Uriarte, M. (2011) Anthropogenic and environmental drivers of modern range loss in large mammals. *Proceedings of the National Academy of Sciences USA* **108**, 4024-4029.
- Yasuhara, M., Hunt, G., Dowsett, H., Robinson, M. & Stoll, D. (2012) Latitudinal species diversity gradient of marine zooplankton for the last three million years. *Ecology Letters*, **15**, 1174–1179.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. (2001) Trends, rhythms, and aberrations in global climate 65 Ma to Present. *Science*, **292**, 686-693.
- Zanne, A.E., Tank, D.C., Cornwell, W.K., Eastman, J.M., Smith, S.A., FitzJohn, R.G., McGlinn, D.J., O'Meara, B.C., Moles, A.T., Reich, P.B., Royer, D.L., Soltis, D.E., Stevens, P.F., Westoby, M., Wright, I.J., Aarssen, L., Bertin, R.I., Calaminus, A., Govaerts, R., Hemmings, F., Leishman, M.R., Oleksyn, J., Soltis, P.S., Swenson, N.G., Warman, L. & Beaulieu, J.M. (2014) Three keys to the radiation of angiosperms into freezing environments. *Nature*, **506**, 89-92.
- Ziolkowski, D.J., Pardieck, K. & Sauer, J. (2010) On the road again - For a bird survey that counts, *Birding*, **32**, 32-40.

APPENDICES CHAPTER 1

Appendix S1.1



Figure S1.1 Map of the study area: continental eastern North and Central America (black). The eastern islands (white) and mainland west of the Rocky Mountains (dashed) were used as independent regions to evaluate the spatial stability of climatic niches. Grey areas are excluded from all analyses.

Appendix S1.2

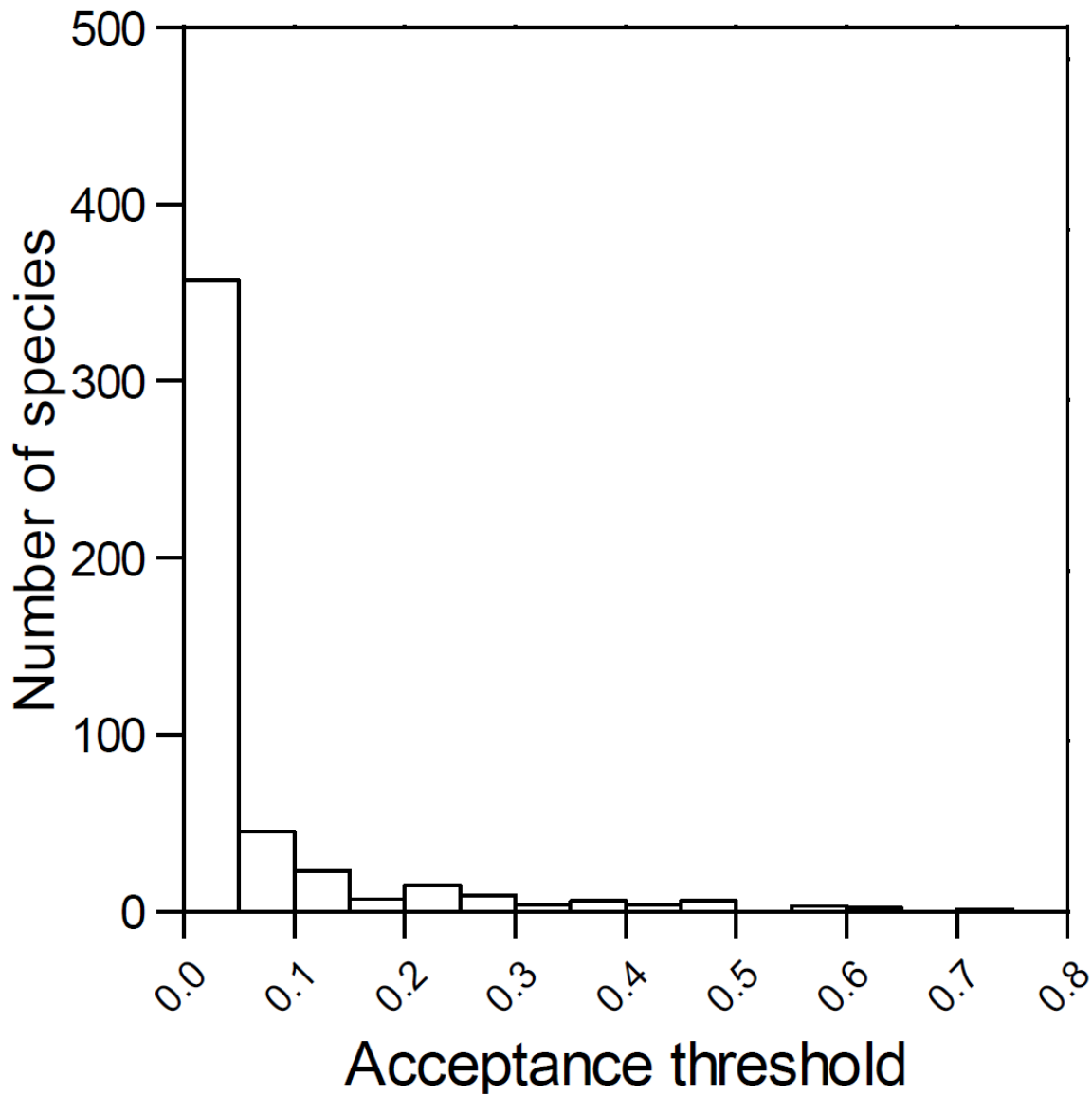


Figure S1.2 Number of additional species for which the tolerance hypothesis is accepted depending on the acceptance threshold. The tolerance hypothesis predicts that, within the core climatic niche, all combinations of temperature t and precipitation p are occupied at a proportion of at least x , where x is the acceptance threshold. In the text, we accepted the hypothesis when all Ω_{stp} within the core climatic niche are ≥ 0.75 .

Appendix S1.3

We tested whether species distributions are independent of temperature and precipitation, with Chi-squared cross-tabulations. Species were here predicted to occur in each climate bin proportionally to its availability in the study area.

The peaked suitability hypothesis could imply either that Ω_{stp} responds independently to t and p , or that Ω_{stp} responds to a $t \cdot p$ interaction. We first fitted occupancy Ω_{stp} as a bivariate normal function of t and p , including an interaction term (eq. 1).

$$\Omega_{stp} = \frac{1}{2\pi\sigma_t\sigma_p\sqrt{1-i^2}} \exp \left[-\frac{\left(\frac{(t-\mu_t)^2}{\sigma_t^2} - \frac{2i(t-\mu_t)(p-\mu_p)}{\sigma_t\sigma_p} + \frac{(p-\mu_p)^2}{\sigma_p^2} \right)}{2(1-i^2)} \right] h$$

eq.1

Where σ_t and σ_p are the estimated variance for temperature and precipitation respectively; μ_t and μ_p are the estimated mean; h is a scaling constant; and i is the correlation between temperature and precipitation (interaction term). Because this model fitted occupancy Ω_{stp} of all species reasonably well (Fig. S1.3), we used it to test whether occupancy depends upon an interaction between temperature and precipitation. A positive interaction occurs when, as temperature increases, higher occupancy is achieved at higher precipitation. A negative interaction occurs when, as temperature increases, higher occupancy is achieved at lower precipitation. We concluded that species' climatic niches depended on such an interaction when the interaction term i was significant ($p < 0.05$) and its inclusion in the model increased the R^2 by $>5\%$.

We found that, for most species, occupancy Ω_{stp} responds independently to t and p . Among the 374 broadly distributed species, 26% have a significant interaction term which increases the R^2 of the model by $>5\%$, and 11% among the 108 narrowly-distributed species. Altogether, 109 of 482 species have a distribution consistent with a response to climate that depends upon a $t \cdot p$ interaction. For these species, the interaction term increased the R^2 by an average of $13\% \pm 1\%$, relative to the peaked suitability model with no interaction. Equal numbers of significant interactions are positive, versus negative (binomial test; $p = 1.00$). The bivariate normal model with no interaction (eq.2) was therefore used to model the peaked suitability hypothesis in the main text.

$$\Omega_{\text{stp}} = \frac{1}{2\pi\sigma_t\sigma_p} \exp \left[-\frac{\left(\frac{(t - \mu_t)^2}{\sigma_t^2} + \frac{(p - \mu_p)^2}{\sigma_p^2} \right)}{2} \right] h$$

eq.2

The peaked suitability model (eq.2) was compared to the threshold model based on the R^2 (observed versus predicted). Because the two models are not fitted with the same subset of climate bins, they are not strictly comparable. Thus, eq.2 was also fitted only for the core climatic niche and the surrounding ring of zero-occupancy (as for the threshold model) and, if the R^2 of the threshold model was higher or equal, the threshold hypothesis was considered consistent with the species distribution. Because the threshold model does not have a specified number of parameters, the models cannot be compared using maximum likelihood methods. To make the models comparable in such a way, the threshold model would have had to be fitted without excluding climate bins, therefore decreasing the explained variance, and using five

parameters (as many as the peaked suitability model). As a consequence, less species would have been selected as consistent with the threshold hypothesis.

For all species, including those with truncated observed climatic niches, we tested the prediction of the asymmetric limitation hypothesis that the decrease in occupancy should be steeper at the cold and dry end of the climatic gradient. We first identified the largest rectangular matrix of $t \times p$ bins for which $\Omega_{stp} > 0.01$. We then calculated row and column occupancy: i.e., $\Omega_{st\bullet}$, the proportion of occupied cells in each temperature bin, averaged over all precipitation bins within the rectangle, and $\Omega_{s\bullet p}$, occupancy averaged over temperature bins. Next, we plotted $\Omega_{st\bullet} = f(t - \hat{T}_s)$ and $\Omega_{s\bullet p} = g(p - \hat{P}_s)$ (Fig. S3.2). The asymmetric limitation hypothesis predicts that, generally, for equal ranges of $|t - \hat{T}_s|$ on both sides of $\hat{T}_s$, $AUC_{t < \hat{T}_s}$ should be less than $AUC_{t > \hat{T}_s}$. Similarly, for equal ranges of $|p - \hat{P}_s|$, $AUC_{p < \hat{P}_s}$ should be less than $AUC_{p > \hat{P}_s}$.

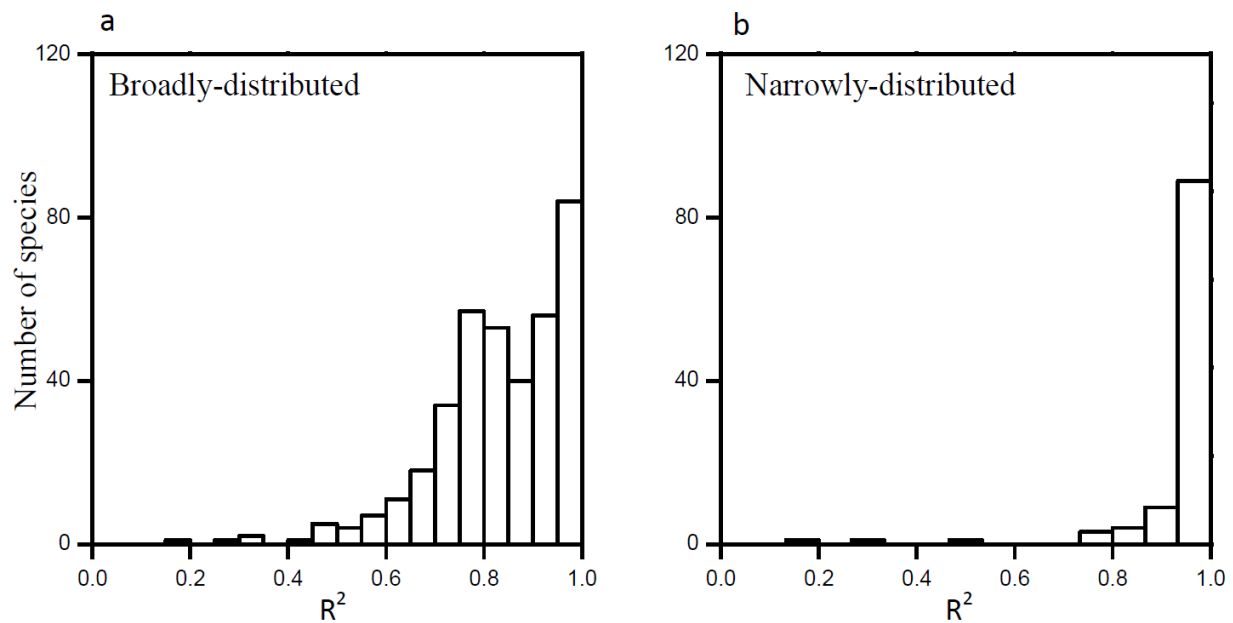


Figure S1.3 Distribution of the R^2 values obtained for the (a) 374 broadly- and (b) 108 narrowly-distributed species, where the probability of occupancy is fitted as a bivariate normal function of temperature and precipitation, including an interaction term (eq.1); $p < 0.005$ for all but one species where $p = 0.08$.

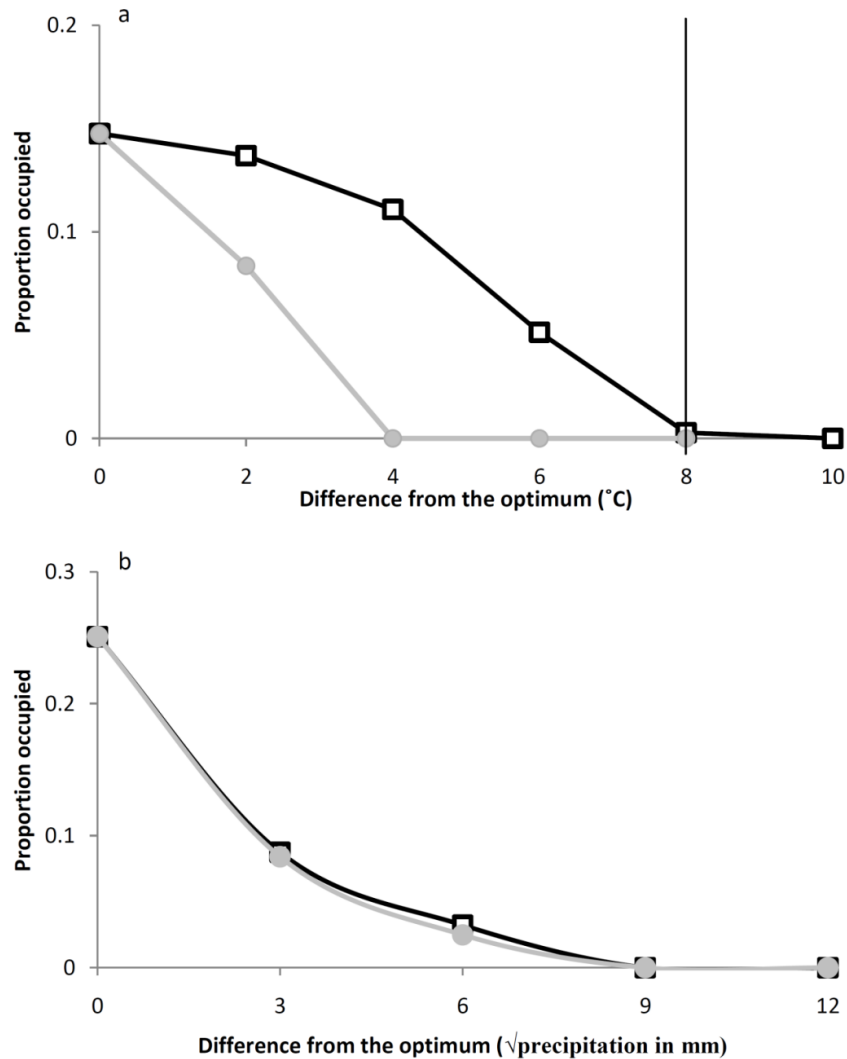


Figure S1.4 Example species, *Carya texana* (Black hickory), showing the decrease in Ω_{stp} from the most occupied climate on the benign edge (grey circles) and stressful edge (black squares) for the (a) temperature and (b) precipitation gradients. When more climate bins are available on one side of the most occupied climate, they are excluded. Accordingly, in Panel (a), occurrence points right of the vertical black line are excluded. The occupied proportions are averaged across the other climatic variable. For this species, the difference in AUC is -0.43 for temperature and -0.02 for precipitation; i.e. in the opposite direction to the prediction from the asymmetric limitation hypothesis.

Appendix S1.4

The high R^2 values we obtain are generally not 'forced' by climate bins with zero-occupancy. While including all zeros increased the average R^2 by 4%, excluding the ring of zero-occupancy surrounding the observed climatic niche from the R^2 calculation decreased the average R^2 by 7% (Fig. S3) and keeping only the core climatic niche decreased the average R^2 by 4%. However, most of the extremely high R^2 are obtained from species with very small climate niches. Of the 89 species with an $R^2 > 99\%$, 69 occupy <5 climate bins. For these species, the ring of zero-occupancy clearly has a large weight in the model.

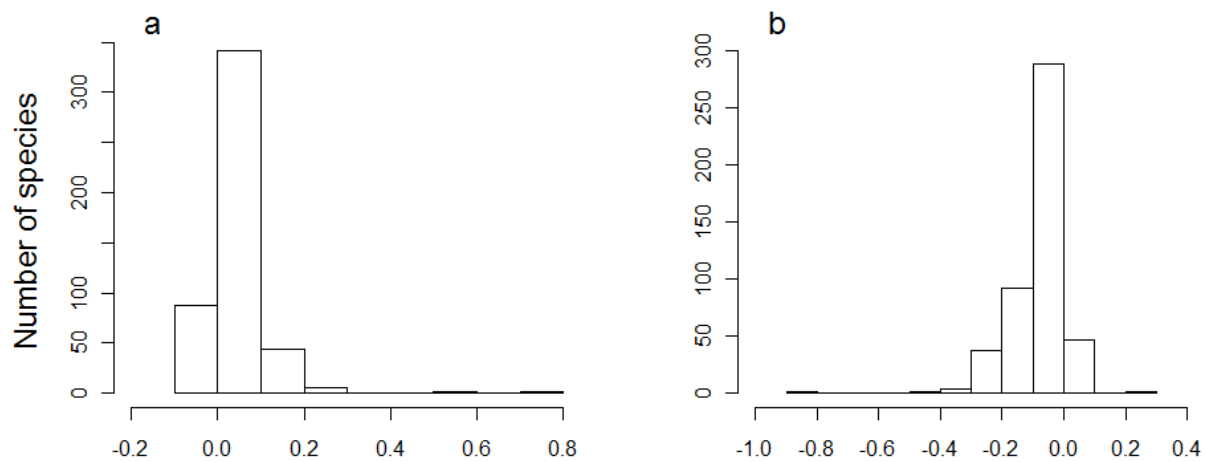


Figure S1.5 Change in R^2 , relative to the peaked suitability model presented in Figure 3, (a) when all climate bins are used to model occupancy, rather than only the observed climate niche and the surrounding ring of zero-occupancy ($n = 482$); and (b) when only occupied climate bins are included (i.e., the ring of zero-occupancy is excluded); the coefficients obtained from the peaked suitability model are used to explain occupancy of the observed climatic niche only.

Appendix S1.5

Table S1.1 Coefficient estimates for each parameter of the peaked suitability model fitting occupancy Ω_{stp} of a species s as a bivariate normal function of temperature t and precipitation p (without an interaction term), obtained in Systat13. Here, σ_t and σ_p are the estimated variance and μ_t and μ_p are the estimated mean for temperature in °C and squared root of precipitation in mm respectively, while h is a scaling constant. The R^2 is also presented along with the number of climate bins used for modeling (i.e. occupied climate bins and the surrounding ring of zero-occupancy). All 482 North American trees included in the study are here presented. The hypotheses (Fig. 1, Table 1) for which the species showed support is also presented: "T" for support of the threshold hypothesis, "G" for support of the peaked suitability hypothesis and "I" for an interaction between temperature and precipitation.

Scientific name	Common name	σ_t	σ_p	μ_t	μ_p	h	R2	n	Support
<i>Abies balsamea</i>	balsam fir	4.85	8	0.43	34.21	316.67	0.85	79	G
<i>Abies fraseri</i>	Fraser fir	1.38	0.68	1.88	22.38	3.61	0.84	27	G,I
<i>Abies lasiocarpa</i>	subalpine fir	1.71	1.81	7.38	43.01	23.66	0.97	30	G
<i>Acacia berlandieri</i>	Berlandier acacia	1.73	6.85	22.08	19.26	96.99	0.95	64	G
<i>Acacia farnesiana</i>	sweet acacia	1.98	8.78	22.78	17.6	137.27	0.9	68	G,I
<i>Acacia greggii</i>	catclaw acacia	2.74	5.98	21.44	19.26	128.1	0.91	49	G
<i>Acacia rigidula</i>	blackbrush acacia	1.78	5.64	22.94	22.61	73.41	0.93	68	G
<i>Acacia roemeriana</i>	Roemer acacia	2.08	2.85	21.34	19.72	37.08	0.84	31	G,I
<i>Acacia tortuosa</i>	twisted acacia	1.09	4.24	22.16	23.68	41.06	0.79	114	G
<i>Acacia wrightii</i>	Wright acacia	1.74	5.53	21.91	20.53	55.3	0.75	47	G,I
<i>Acer barbatum</i>	Florida maple	1.69	2.13	17.1	36.97	17.16	0.85	53	T
<i>Acer glabrum</i>	Rocky Mountain maple	1.77	4.51	11	5.46	104.09	0.99	20	G
<i>Acer grandidentatum</i>	bigtooth maple	0.94	1.08	18.87	27.34	0.68	0.97	31	G
<i>Acer leucoderme</i>	chalk maple	1.5	1.65	16.36	37.35	5.15	0.97	40	G
<i>Acer negundo</i>	boxelder	5.88	131.47	10.63	0	3900.37	0.33	114	T,I
<i>Acer nigrum</i>	black maple	2.38	4.08	10.02	32.15	48.03	0.69	52	T,I
<i>Acer pensylvanicum</i>	striped maple	3.84	6.98	5.49	41.96	250.66	0.89	67	G
<i>Acer rubrum</i>	red maple	7.3	6.36	8.64	37.83	368.38	0.71	119	T
<i>Acer saccharinum</i>	silver maple	4.74	7.96	10.23	37.21	270.56	0.66	94	T
<i>Acer saccharum</i>	sugar maple	4.56	6.46	6.29	35.48	234.17	0.79	78	T
<i>Acer spicatum</i>	mountain maple	3.87	10.26	4.41	40.06	330.64	0.85	79	G
<i>Acoelorrhaphe wrightii</i>	paurotis palm	1.07	0.5	23	35.5	0.02	0.94	12	G
<i>Aesculus glabra</i>	Ohio buckeye	3.66	2.52	14.66	31	57.77	0.82	61	G
<i>Aesculus octandra</i>	yellow buckeye	2.5	4.58	11.08	41.92	90.37	0.9	42	G
<i>Aesculus parviflora</i>	bottlebrush buckeye	1.11	1.24	17.16	37.94	2.47	0.92	27	G,I
<i>Aesculus pavia</i>	red buckeye	1.77	3.65	18.29	37.05	39.26	0.65	63	G
<i>Aesculus sylvatica</i>	painted buckeye	1.18	3.95	14.75	38.45	9.24	0.76	35	G
<i>Alnus maritima</i>	seaside alder	0.49	0.53	16.48	32.5	0.05	0.77	15	G
<i>Alnus rugosa</i>	speckled alder	5.35	121.69	-0.26	81	3375.83	0.67	95	T,I
<i>Alnus serrulata</i>	hazel alder	4.23	5.21	11.79	39.14	160.5	0.75	76	G
<i>Alnus sinuata</i>	Sitka alder	0.76	0.98	2.33	22.52	0.13	0.99	19	G
<i>Alnus tenuifolia</i>	thinleaf alder	1.8	2.3	-2.06	18.61	26.97	0.72	38	G,I
<i>Alvaradoa amorphoides</i>	Mexican alvaradoa	0.36	0.75	23	37.26	0.02	1	12	G
<i>Amelanchier alnifolia</i>	western serviceberry	5.14	2.1	3.3	21.64	86.02	0.82	66	G
<i>Amelanchier arborea</i>	downy serviceberry	5.72	7.13	8.41	38.08	331.22	0.77	94	T
<i>Amelanchier interior</i>	inland serviceberry	0.87	0.89	3	26.5	1.72	0.96	30	G
<i>Amelanchier sanguinea</i>	roundleaf serviceberry	2.55	14.34	2.63	68.86	1253.72	0.61	61	G,I
<i>Amphitecna latifolia</i>	black calabash	0.36	0.54	25	35.5	0	1	9	G,T
<i>Amyris balsamifera</i>	balsam torchwood	0.36	0.79	25	37	0	1	12	G
<i>Amyris elemifera</i>	torchwood	0.51	0.75	23.78	37.46	0.18	1	18	G
<i>Annona glabra</i>	pond apple	0.41	0.99	23.77	37.04	18.83	1	19	G

<i>Aralia spinosa</i>	devils walkingstick	4.22	4.37	12.83	39.46	135.95	0.72	79	G,I
<i>Arbutus texana</i>	Texas madrone	0.54	0.94	19.6	28.29	1.42	0.98	29	G
<i>Ardisia escallonioides</i>	marlberry	0.65	0.99	23.42	37.04	5.84	1	23	G
<i>Artemisia tridentata</i>	big sagebrush	1.22	1.22	8.14	18.04	13.01	0.97	17	G
<i>Asimina parviflora</i>	smallflower pawpaw	0.77	2.96	19.57	39.51	8.18	0.81	38	G
<i>Asimina triloba</i>	pawpaw	3.12	6.14	12.16	38.66	149.89	0.79	67	G
<i>Avicennia germinans</i>	black mangrove	3.34	26.56	31	81	670.53	0.62	110	G
<i>Baccharis halimifolia</i>	eastern baccharis	2.45	3.84	19.48	37.01	53.18	0.69	66	T
<i>Betula alleghaniensis</i>	yellow birch	4.27	10.52	5.79	43.57	428.29	0.82	77	G
<i>Betula lenta</i>	sweet birch	2.52	6.56	10.21	41.33	126.72	0.88	64	G
<i>Betula nana</i>	dwarf birch	3.63	9.52	-8.25	16.86	264.88	0.88	59	G
<i>Betula nigra</i>	river birch	3.35	3.83	15.04	36.65	89.23	0.83	82	G
<i>Betula occidentalis</i>	water birch	1.11	3.23	1.72	16.97	27.1	0.98	30	G
<i>Betula papyrifera</i>	paper birch	5.26	18.32	-0.37	37.18	719.12	0.75	106	G
<i>Betula populifolia</i>	gray birch	2.99	4.8	4.34	39.43	107.42	0.75	55	G,I
<i>Betula uber</i>	Ashe birch	0.47	0.76	10.31	34	0.04	1	15	G
<i>Bourreria ovata</i>	Bahama strongbark	0.71	0.69	20.22	18.35	0.22	1	9	G,T
<i>Bumelia celastrina</i>	saffron plum	1.36	3.71	23.64	26.57	35.01	0.97	105	G
<i>Bumelia lanuginosa</i>	gum bumelia	3	8.19	19.64	27.27	170.53	0.6	73	G,I
<i>Bumelia lycioides</i>	buckthorn bumelia	2.12	1.41	15.99	37.53	16.4	0.95	47	G
<i>Bumelia tenax</i>	tough bumelia	1.47	1.07	21.07	35.7	2.26	1	30	G
<i>Bursera fagaroides</i>	fragrant bursera	5.57	11.93	31	26.94	50.37	0.27	98	G,I
<i>Bursera simaruba</i>	gumbo limbo	0.48	0.74	23.77	37.12	11.11	1	16	G
<i>Byrsonima lucida</i>	key byrsonima	0.43	0.64	23.77	37.38	0.8	1	16	G
<i>Caesalpinia mexicana</i>	Mexican poinciana	1.21	3.28	23.98	27.94	26.44	0.97	85	G
<i>Calyptanthus pallens</i>	pale lidflower	0.48	0.73	23.99	36.98	0.43	0.94	16	G,I
<i>Calyptanthus zuzygium</i>	myrtle of the river	0.49	0.72	24.09	37.18	0.09	0.91	16	G,I
<i>Canella winterana</i>	canella	0.5	0.53	24.01	35.5	0.01	1	12	G
<i>Capparis cynophallophora</i>	Jamaica caper	0.44	0.71	23.7	37.09	0.24	0.99	15	G
<i>Capparis flexuosa</i>	limber caper	0.4	0.65	23.51	37.33	0.31	1	15	G
<i>Carpinus caroliniana</i>	American hornbeam	4.71	6.17	11.75	37.69	214.97	0.74	166	G
<i>Carya aquatica</i>	water hickory	1.38	3.6	18.84	37.8	33.57	0.76	52	G
<i>Carya cordiformis</i>	bitternut hickory	3.92	6.71	11.9	36.84	209.56	0.75	88	G
<i>Carya floridana</i>	scrub hickory	0.43	0.68	22.64	36.46	2.44	1	16	G
<i>Carya glabra</i>	pignut hickory	4.01	5.47	12.32	38.32	171.5	0.76	88	G
<i>Carya illinoensis</i>	pecan	2.85	3.43	17.62	31.52	58.71	0.81	76	G
<i>Carya laciniosa</i>	shellbark hickory	1.86	2.82	12.24	33.43	22.43	0.78	54	G,I
<i>Carya myristicaeformis</i>	nutmeg hickory	0.81	2.45	17.74	35.02	1.37	0.87	29	G
<i>Carya ovata</i>	shagbark hickory	3.3	6.58	11.27	37.8	177.62	0.84	123	G
<i>Carya pallida</i>	sand hickory	2.91	3.2	11.67	42.37	67.67	0.73	51	G,I
<i>Carya texana</i>	black hickory	2.68	2.08	17.34	32.55	26.76	0.86	51	G
<i>Carya tomentosa</i>	mockernut hickory	4.29	5.15	12.97	38.04	172.86	0.74	87	G,I
<i>Castanea alnifolia</i>	Florida chinkapin	1.08	2.25	19.73	38.25	1.98	0.75	44	G

<i>Castanea dentata</i>	American chestnut	2.73	5.9	10.83	40.31	128.64	0.89	69	G
<i>Castanea ozarkensis</i>	Ozark chinkapin	0.96	2.32	14.79	34.41	2.49	0.98	29	G
<i>Castanea pumila</i>	Allegheny chinkapin	4.77	4.71	12.34	41.09	113.86	0.53	72	T,I
<i>Catalpa bignonioides</i>	southern catalpa	0.85	1.22	17.82	37.84	5.74	0.96	22	G
<i>Catalpa speciosa</i>	northern catalpa	1.1	0.62	14.56	34.35	3.8	0.97	21	G
<i>Celtis laevigata</i>	sugarberry	2.79	5.97	17.75	33.08	128.87	0.8	89	G
<i>Celtis lindheimeri</i>	Lindheimer hackberry	0.71	0.69	20.22	18.35	0.22	0.84	23	G
<i>Celtis occidentalis</i>	hackberry	3.38	5.99	10.99	28.71	148.29	0.74	88	G,I
<i>Celtis reticulata</i>	netleaf hackberry	2.13	2.89	16.38	25.26	39.72	0.76	71	G
<i>Celtis tenuifolia</i>	Georgia hackberry	2.46	2.85	15.41	35.3	18.7	0.79	62	G,I
<i>Cephalanthus occidentalis</i>	common buttonbush	7.91	6.9	14.46	36.22	384.96	0.61	173	G
<i>Cercidium macrum</i>	border paloverde	1.31	2.5	23.61	26.17	21.39	0.99	56	G
<i>Cercis canadensis</i>	eastern redbud	4.24	6.48	13.79	36.17	199.69	0.51	120	G,I
<i>Cercocarpus breviflorus</i>	hairy cercocarpus	0.33	0.79	21	21.98	0.05	1	12	G
<i>Chamaecyparis thyoides</i>	Atlantic white cedar	1.11	0.63	9.77	34.28	12.8	0.57	50	G
<i>Chilopsis linearis</i>	desert willow	2.83	3.49	21.04	16.62	72.92	0.93	49	G
<i>Chionanthus virginicus</i>	fringetree	3.45	4.24	11.66	41.69	97.8	0.63	76	G,T,I
<i>Chrysobalanus icaco</i>	cocoplum	0.47	0.75	23.74	37.11	16.84	1	16	G
<i>Chrysophyllum oliviforme</i>	satinleaf	0.47	0.74	23.75	37.12	16.86	1	16	G
<i>Citharexylum berlandieri</i>	Berlandier fiddlewood	1.02	3.1	24.27	27.61	18.97	0.95	51	G
<i>Citharexylum fruticosum</i>	Florida fiddlewood	0.43	0.65	23.81	37.29	1.42	0.99	16	G
<i>Cladrastis kentukea</i>	yellowwood	1.99	1.93	9.57	42.18	15.08	0.89	39	G
<i>Clethra acuminata</i>	cinnamon clethra	2.23	4.53	10.42	44.01	69.51	0.9	40	G
<i>Cliftonia monophylla</i>	buckwheat tree	0.59	3.18	19.61	39.83	8.82	0.75	26	G
<i>Coccoloba diversifolia</i>	pigeon plum	0.43	0.66	23.78	37.14	7.95	1	16	G
<i>Coccoloba uvifera</i>	seagrape	0.46	0.68	23.96	37.08	3	1	19	G
<i>Coccothrinax argentata</i>	Florida silverpalm	0.49	0.67	23.97	37.32	1.6	0.99	16	G
<i>Colubrina arborescens</i>	coffee colubrina	0.42	0.66	23.63	37.26	0.5	0.99	15	G
<i>Colubrina cubensis</i>	Cuba colubrina	0.33	0.78	23	37.17	0.01	1	12	G
<i>Condalia hookeri</i>	bluewood	1.85	3.98	22.46	26.08	57.91	0.92	64	G
<i>Conocarpus erectus</i>	button mangrove	0.46	0.71	23.9	36.97	4.24	0.97	19	G
<i>Cordia boissieri</i>	anacahuita	1.26	3.64	23.87	27.26	30.06	0.78	89	G
<i>Cordia sebestena</i>	Geiger tree	0.47	0.71	24.09	36.84	0.28	0.96	15	G
	alternate leaf								
<i>Cornus alternifolia</i>	dogwood	4.45	9.13	6.65	40.91	338.21	0.81	85	G
<i>Cornus drummondii</i>	roughleaf dogwood	4.37	3	15.22	29.65	87.68	0.78	77	G
<i>Cornus florida</i>	flowering dogwood	4.53	5.13	12.99	37.82	180.85	0.77	126	G
<i>Cornus racemosa</i>	gray dogwood	2.32	3.53	8.68	31.43	55.47	0.83	68	G
<i>Cornus rugosa</i>	roundleaf dogwood	2.98	6.45	4.56	34	106.4	0.57	64	G,I
<i>Cornus stolonifera</i>	red osier dogwood	4.71	10.79	2.23	29.43	380.86	0.75	98	G
<i>Cornus stricta</i>	stiffcornel dogwood	2.04	2.5	17.68	37.51	32.02	0.86	68	G
<i>Corylus cornuta</i>	beaked hazel	4.39	15.98	5.32	53.94	869.7	0.73	95	G
<i>Cotinus obovatus</i>	American smoketree	0.91	2.82	14.54	33.84	1.37	0.48	42	G

<i>Crataegus chrysocarpa</i>	fireberry hawthorn	1.98	3.59	3.7	22.2	36.57	0.73	35	G
<i>Crataegus columbiana</i>	Columbia hawthorn	0.92	0.69	1.86	19.15	0.35	0.73	16	G
<i>Crataegus douglasii</i>	black hawthorn	0.82	0.77	3.6	18.95	2.22	0.92	36	G
<i>Crataegus succulenta</i>	fleshy hawthorn	2.11	2.9	6.13	23.23	46.2	0.91	52	G
<i>Crataegus tracyi</i>	Tracy hawthorn	0.76	1.55	18.84	26.84	0.51	1	21	G
<i>Crossopetalum rhacoma</i>	Florida crossopetalum	0.48	0.7	23.88	36.7	0.08	1	15	G
<i>Cyrilla racemiflora</i>	swamp cyrilla	1.11	3.56	18.76	37.98	18.75	0.8	48	G
<i>Diospyros texana</i>	Texas persimmon	2.19	6.38	21.68	21.43	107.34	0.93	53	G
<i>Diospyros virginiana</i>	common persimmon	4.6	5.06	14.38	37.54	177.85	0.68	86	G,I
<i>Dipholis salicifolia</i>	willow bustic	0.45	0.67	23.94	37.25	2.26	1	16	G
<i>Dodonaea viscosa</i>	hopbush	0.9	4.83	20.69	0	2469.91	0.7	126	G
<i>Drypetes lateriflora</i>	Guiana plum	0.45	0.68	23.85	37.21	0.58	1	16	G
<i>Ehretia anacua</i>	anaqua	1.87	2.87	23.26	27.98	33.59	0.92	90	G
<i>Elliottia racemosa</i>	elliottia	0.51	0.65	18.19	34.54	0.2	0.99	15	G
<i>Erythrina herbacea</i>	eastern coralbean	2.41	5.81	22.82	32.31	51.21	0.52	101	G,I
<i>Esenbeckia berlandieri</i>	Berlandier esenbeckia	0.57	1.47	24.29	29.32	3.96	0.8	65	G,I
<i>Eugenia axillaris</i>	white stopper	0.47	0.76	23.74	37.1	16.66	1	16	G
<i>Eugenia confusa</i>	redberry stopper	0.48	0.53	24.09	35.5	0.01	1	12	G
<i>Eugenia foetida</i>	boxleaf stopper	0.44	0.65	23.81	37.19	26.14	1	16	G
<i>Euonymus atropurpureus</i>	eastern wahoo	2.32	3.61	12.08	31.87	54.77	0.89	70	G
<i>Exothea paniculata</i>	inkwood	0.5	0.75	23.87	37.38	0.91	0.99	19	G
<i>Eysenhardtia polystachya</i>	kidneywood	1.85	9.22	23.12	39.38	11.54	0.53	101	G,I
<i>Eysenhardtia texana</i>	Texas kidneywood	1.85	6.36	21.67	19.64	94.77	0.94	61	G
<i>Fagus grandifolia</i>	American beech	6.18	5.9	8.77	38.77	291.72	0.79	98	G
<i>Ficus aurea</i>	Florida strangler fig	0.43	1	23.74	36.97	16.33	1	19	G
<i>Ficus citrifolia</i>	shortleaf fig	0.42	0.65	23.7	37.35	0.57	1	16	G
<i>Forestiera acuminata</i>	swamp privet	1.59	1.86	17.5	37.66	13.09	0.87	49	G,I
<i>Forestiera angustifolia</i>	Texas forestiera	1.96	8.01	22.5	19.83	124.83	0.91	65	G
<i>Forestiera segregata</i>	Florida privet	0.85	1.13	23.33	36.88	2.44	0.97	29	G
<i>Franklinia alatamaha</i>	franklinia	0.36	0.54	19	35.5	0	1	9	G,T
<i>Fraxinus americana</i>	white ash	6.23	6.19	9.42	37.53	313.51	0.79	98	T
<i>Fraxinus berlandieriana</i>	Berlandier ash	1.09	7.58	22.26	18.02	69.97	0.91	46	G
<i>Fraxinus caroliniana</i>	Carolina ash	1.22	3.48	18.96	38.16	19.81	0.61	51	G
<i>Fraxinus cuspidata</i>	fragrant ash	3.26	1.72	29.17	16.72	29.53	0.97	22	G
<i>Fraxinus greggii</i>	Gregg ash	1.16	9.36	20.95	0	208.06	0.76	54	G
<i>Fraxinus nigra</i>	black ash	3.31	7.26	4.44	34.52	192.19	0.84	69	G
<i>Fraxinus pennsylvanica</i>	green ash	6.52	14.29	9.58	33.4	663.39	0.54	118	T
<i>Fraxinus profunda</i>	pumpkin ash	1.43	1.7	15.25	34.59	4.53	0.64	65	G,I
<i>Fraxinus quadrangulata</i>	blue ash	1.71	3.04	11.96	32.35	12.9	0.62	42	G,I
<i>Fraxinus texensis</i>	Texas ash	0.96	1.19	19.33	28.36	3.71	0.99	32	G
<i>Fraxinus velutina</i>	velvet ash	0.64	1.32	21.68	20.12	0.42	1	21	G
<i>Genipa clusiifolia</i>	seven year apple	0.33	0.79	25	36.96	0.03	1	12	G
<i>Gleditsia aquatica</i>	waterlocust	1.47	2.35	18.49	36.4	10.43	0.8	51	G

<i>Gleditsia triacanthos</i>	honeylocust	4.46	4.82	14.64	33.34	122.79	0.68	86	G
<i>Gordonia lasianthus</i>	loblolly bay	2.13	1.54	20.66	35.91	14.68	0.96	44	G
<i>Guaiacum angustifolium</i>	Texas lignumvitae	2.17	6.62	22.29	18.88	112.68	0.92	54	G
<i>Guapira discolor</i>	blolly	0.45	0.66	23.77	37.22	1.07	0.98	16	G
<i>Guettarda elliptica</i>	elliptic leaf velvetseed	0.49	0.74	24.01	37.03	0.2	1	16	G
<i>Guettarda scabra</i>	roughleaf velvetseed	0.46	0.67	23.94	37.32	1.44	0.98	16	G
<i>Gymnanthes lucida</i>	oysterwood	0.48	0.73	23.85	37.08	0.12	0.89	16	G
<i>Gymnocladus dioicus</i>	Kentucky coffeetree	2.65	2.09	12.55	30.52	33.12	0.92	56	G,I
<i>Halesia carolina</i>	Carolina silverbell	2.78	2.94	11.04	42.56	66.47	0.9	55	G
<i>Halesia diptera</i>	two wing silverbell	0.83	2.8	18.74	39.48	12.42	0.92	30	G
<i>Halesia parviflora</i>	little silverbell	0.86	1.92	19.02	39.81	1.1	0.97	26	G
<i>Hamamelis virginiana</i>	witch hazel	5.64	6.21	9.63	39.18	244.87	0.72	100	G
<i>Hamelia patens</i>	scarletbush	0.42	0.99	23.74	36.9	18.7	1	22	G
<i>Helietta parvifolia</i>	barreta	1.29	4.02	23.58	25.29	24.11	0.92	84	G
<i>Hippomane mancinella</i>	manchineel	0.49	0.52	24.02	35.5	0.02	1	12	G
<i>Hypelate trifoliata</i>	hypelate	0.34	0.79	23	36.94	0.01	1	12	G
<i>Ilex ambigua</i>	Carolina holly	1.14	3.49	18.79	38.09	23.1	0.81	51	G
<i>Ilex amelanchier</i>	sarvis holly	0.46	1.28	19	41.5	0.92	0.99	26	G
<i>Ilex cassine</i>	dahoon	0.88	1.36	22.67	36.71	9.11	0.86	47	G
<i>Ilex coriacea</i>	large gallberry	1.1	3.53	19	38.63	15.14	0.75	45	G
<i>Ilex decidua</i>	possumhaw	2.6	4.31	17.77	35.08	77.89	0.72	71	G
<i>Ilex krugiana</i>	tawnyberry holly	0.36	0.7	23	37.43	0.04	1	12	G
<i>Ilex laevigata</i>	smooth winterberry	5.89	13.01	1.89	70.96	2019.71	0.33	44	G
<i>Ilex longipes</i>	Georgia holly	0.49	0.85	19.66	40.08	1.15	1	16	G
<i>Ilex montana</i>	mountain winterberry	2.63	4.18	10.78	42	87.39	0.93	67	G
<i>Ilex myrtifolia</i>	myrtle dahoon	1.12	3.22	19.21	37.39	9.54	0.74	41	G
<i>Ilex opaca</i>	American holly	4.99	4.24	13.3	39.67	140.74	0.61	72	T,I
<i>Ilex verticillata</i>	common winterberry	5.09	7.79	8.31	39.66	292.57	0.74	82	T
<i>Ilex vomitoria</i>	yaupon	1.3	5.45	19.65	36.65	33.02	0.48	54	T,I
<i>Illicium floridanum</i>	Florida anise tree	0.61	1.2	18.43	40.33	8.38	0.96	48	G
<i>Illicium parviflorum</i>	yellow anise tree	0.44	0.61	23	35.51	0.01	1	12	G,T
<i>Jacquinia keyensis</i>	joewood	0.49	0.71	23.97	36.84	0.2	0.99	16	G
<i>Juglans cinerea</i>	butternut	3.06	7.99	9.68	38.21	165.23	0.75	68	G
<i>Juglans major</i>	Arizona walnut	0.77	0.51	18.39	26.52	0.23	1	15	G
<i>Juglans microcarpa</i>	little walnut	0.9	1.45	19.17	23.4	2.21	0.63	44	G,I
<i>Juglans nigra</i>	black walnut	3.8	7.18	12.99	35.75	209.33	0.72	93	G
<i>Juniperus ashei</i>	Ashe juniper	1.11	2.65	18.99	27.38	5.78	0.93	46	G
<i>Juniperus communis</i>	common juniper	5.66	27.53	-3.16	30.27	1037.94	0.77	114	G
<i>Juniperus deppeana</i>	alligator juniper	0.65	0.63	17.9	46.6	0.82	0.87	34	G
<i>Juniperus erythrocarpa</i>	redberry juniper	0.44	0.51	20.34	17.5	0.02	1	9	G
<i>Juniperus flaccida</i>	drooping juniper	1.63	1.1	23.53	18.23	2.52	0.58	83	G
<i>Juniperus horizontalis</i>	creeping juniper	3.91	14.5	-2.96	26.06	424.42	0.84	88	G
<i>Juniperus monosperma</i>	one seed juniper	0.46	1.13	22.33	30	0.57	0.52	39	G

<i>Juniperus pinchotii</i>	Pinchot juniper	1.6	1.49	16.59	23.08	11.58	0.97	34	G
<i>Juniperus scopulorum</i>	Rocky Mountain juniper	5.42	1.58	11.17	19.95	2.2	0.33	36	G
<i>Juniperus silicicola</i>	southern redcedar	2.26	2.57	21.16	37.28	7.64	0.44	45	G,I
<i>Juniperus virginiana</i>	eastern redcedar	4.08	8.22	12.42	34.47	271.9	0.76	101	G
<i>Kalmia latifolia</i>	mountain laurel	3.1	5.66	11.01	40.16	135.55	0.86	71	G
<i>Koeberlinia spinosa</i>	allthorn	1.36	11.3	22.48	5.17	205.12	0.89	68	G
<i>Krugiodendron ferreum</i>	leadwood	0.46	0.68	23.9	37.2	0.74	1	16	G
<i>Laguncularia racemosa</i>	white mangrove	0.45	0.71	23.87	36.95	3.22	0.98	19	G
<i>Larix laricina</i>	tamarack	5.85	14.86	-1.17	34.63	667.61	0.75	94	G,I
<i>Larrea divaricata</i>	creosote bush	2.91	4.05	20.38	17.17	91.59	0.91	48	G
<i>Leitneria floridana</i>	corkwood	0.52	0.67	20.45	37.99	0.44	0.75	25	G
<i>Leucaena pulverulenta</i>	great leadtree	1.23	3.31	23.91	27.71	28.02	0.85	101	G
<i>Leucaena retusa</i>	littleleaf leadtree	1.01	2.73	19.99	19.94	16.89	0.85	27	G,I
<i>Licaria triandra</i>	Florida licaria	0.34	0.8	25	36.97	0.01	1	12	G
<i>Liquidambar styraciflua</i>	sweetgum	3.72	4.7	16.14	38.5	121.76	0.8	136	G
<i>Liriodendron tulipifera</i>	yellow poplar	3.91	5.37	12.04	39.01	158	0.76	87	G
<i>Lyonia ferruginea</i>	tree lyonia	0.85	1.29	22.71	36.43	5.52	0.71	45	G
<i>Lysiloma latisiliquum</i>	Bahama lysiloma	0.49	0.78	23.73	36.97	1.14	0.99	16	G
<i>Lysiloma microphylla</i>	littleleaf lysiloma	1.87	10.73	31	1.77	7251.98	0.94	47	G
<i>Maclura pomifera</i>	Osage orange	1.77	1.68	19.29	31.18	15.85	0.86	32	G,I
<i>Magnolia acuminata</i>	cucumbertree	2.59	5.48	10.87	41.65	109.14	0.92	64	G
<i>Magnolia ashei</i>	Ashe magnolia	0.42	0.64	19.73	39.64	1.21	1	15	G
<i>Magnolia fraseri</i>	Fraser magnolia	2.62	3.89	10.49	42.5	79.34	0.88	40	G
<i>Magnolia grandiflora</i>	southern magnolia	1	3.53	19.04	38.3	21.34	0.85	42	G
<i>Magnolia macrophylla</i>	bigleaf magnolia	3.48	1.57	16.01	38.91	12.22	0.58	43	G,I
<i>Magnolia pyramidata</i>	pyramid magnolia	0.45	1.47	18.28	40.38	4.95	0.98	19	G
<i>Magnolia tripetala</i>	umbrella magnolia	2.35	3.1	10.56	39.64	29.63	0.69	51	G,I
<i>Magnolia virginiana</i>	sweetbay	2.04	3.1	18.65	37.74	34.65	0.62	70	G
<i>Malus angustifolia</i>	southern crab apple	3.9	3.66	15.06	39.55	41.84	0.47	57	G,I
<i>Malus coronaria</i>	sweet crab apple	1.57	8.4	9.62	37.73	43.64	0.79	54	G
<i>Malus ioensis</i>	prairie crab apple	1.66	1.3	11.01	30.51	11.36	0.85	63	G,I
<i>Manilkara bahamensis</i>	wild dilly	0.36	0.79	25	36.94	0	1	12	G
<i>Mastichodendron foetidissimum</i>	false mastic	0.44	0.66	23.89	37.15	3.95	1	16	G
<i>Maytenus phyllanthoides</i>	Florida mayten	0.48	0.52	24.09	35.5	0.02	1	12	G
<i>Metopium toxiferum</i>	Florida poison-tree	0.49	0.72	23.86	37.4	1.44	1	16	G
<i>Morus microphylla</i>	Texas mulberry	1.36	1.83	18.19	24.74	4.46	0.96	42	G
<i>Morus rubra</i>	red mulberry	4.97	6.73	14.68	35.07	262.31	0.67	110	T,I
<i>Myrcianthes fragrans</i>	twinberry stopper	0.76	0.65	23.62	37.18	2.49	1	20	G
<i>Myrica cerifera</i>	southern bayberry	1.38	4.4	18.92	36.44	37.94	0.64	58	T
<i>Myrica heterophylla</i>	evergreen bayberry	1.03	3.8	18.66	38.02	15.22	0.7	41	G
<i>Myrica inodora</i>	odorless bayberry	0.45	0.99	19.7	40.39	9.7	0.98	19	G

<i>Myrica pensylvanica</i>	northern bayberry	2.31	2.08	7.43	36.33	15.76	0.77	46	G,I
<i>Nectandra coriacea</i>	Florida nectandra	0.49	0.73	23.71	37.38	0.81	1	19	G
<i>Nemopanthus collinus</i>	mountain holly	1.02	1.35	8.99	38.88	3.24	1	31	G
<i>Nyssa aquatica</i>	water tupelo	1.36	2.9	19.11	39.38	23.08	0.74	38	T,I
<i>Nyssa ogeche</i>	Ogeechee tupelo	0.43	1.44	19.85	36.41	10.63	0.81	27	G,I
<i>Nyssa sylvatica</i>	black tupelo, blackgum	4.58	5.08	12.85	38.07	179.64	0.72	93	G
<i>Osmanthus americanus</i>	devilwood	1.05	3.45	19.11	38.89	16.11	0.73	45	G
<i>Ostrya virginiana</i>	eastern hophornbeam	5.91	7.63	9.1	37.21	326.7	0.68	184	G
<i>Oxydendrum arboreum</i>	sourwood	3.48	4.22	11.76	40.65	111.91	0.76	58	G,I
<i>Parkinsonia aculeata</i>	Jerusalem thorn	1.95	12.5	23.29	9.63	220.05	0.85	68	G
<i>Persea borbonia</i>	redbay	2.8	2.98	19.95	37.31	30.91	0.51	57	T
<i>Picea engelmannii</i>	Engelmann spruce	0.36	0.54	5	20.5	0	1	9	G,T
<i>Picea glauca</i>	white spruce	5.21	18.05	-1.92	31.57	662.27	0.68	86	G,I
<i>Picea mariana</i>	black spruce	6.52	59.96	-2.22	81	2410.5	0.7	91	T,I
<i>Picea rubens</i>	red spruce	3.26	5.9	4.56	41.97	180.1	0.87	57	G
<i>Picramnia pentandra</i>	bitterbush	0.35	0.79	25	37.11	0	1	12	G
<i>Pinckneya pubens</i>	pinckneya	0.64	1.73	19.16	35.5	2.39	0.99	26	G
<i>Pinus ayacahuite</i>	Mexican white pine	0.97	1.88	15.65	45.53	1.72	0.88	67	G,I
<i>Pinus banksiana</i>	jack pine	3.68	5.88	0.09	26.08	134.96	0.61	83	G,I
<i>Pinus caribaea</i>	Caribbean pine	2.69	8.75	24.16	44.2	17.62	0.41	82	T,I
<i>Pinus cembroides</i>	Mexican pinyon	1.32	2.08	19.56	24.28	1.15	0.25	86	G
<i>Pinus clausa</i>	sand pine	0.64	0.96	22.81	36.52	3.49	0.99	25	G
<i>Pinus contorta</i>	lodgepole pine	1.38	0.99	1.49	22.41	7.67	0.77	34	G
<i>Pinus echinata</i>	shortleaf pine	4.01	4.6	12.45	39.95	128.58	0.7	66	G,I
<i>Pinus elliottii</i>	slash pine	0.84	3.54	19.45	39.09	13.67	0.55	46	G
<i>Pinus flexilis</i>	limber pine	0.8	0.71	5.17	19.14	0.08	0.97	14	G
<i>Pinus glabra</i>	spruce pine	0.89	3.59	18.76	38.7	14.22	0.82	31	G
<i>Pinus greggii</i>	Gregg pine	2.21	4.33	20.89	57.37	4.05	0.43	47	T,I
<i>Pinus hartwegii</i>	Hartweg pine	0.56	1.52	15.82	45.58	2.55	0.95	28	G
<i>Pinus lawsonii</i>	Lawson pine	1.63	1.28	29.95	29.46	1.1	1	22	G
<i>Pinus michoacana</i>	Michoacán pine	0.98	1.49	27	25.38	2.01	0.8	78	G
<i>Pinus montezumae</i>	Montezuma pine	0.77	1.55	22.38	29.67	0.75	0.98	50	G
<i>Pinus nelsonii</i>	Nelson pinyon	0.5	0.75	20.15	27.78	0.01	0.99	15	G
<i>Pinus oocarpa</i>	Nicaraguan pitch pine	3.22	2.7	17.57	43.89	36.61	0.55	116	G
<i>Pinus palustris</i>	longleaf pine	1.21	3.36	18.7	38.29	24.17	0.75	52	G
<i>Pinus patula</i>	Mexican weeping pine	1.08	21.71	21.82	50.32	0.27	0.3	63	G
<i>Pinus ponderosa</i>	ponderosa pine	0.9	5.93	8.46	0	775.17	0.97	51	G
<i>Pinus pringlei</i>	Pringle pine	0.65	2.45	24.34	31.98	0.02	0.9	28	G
<i>Pinus pseudostrobus</i>	False Weymouth pine	3.87	6.21	20.97	43.72	16.07	0.41	122	G
<i>Pinus pungens</i>	Table Mountain pine	2.43	3.78	10.48	43.31	68.41	0.91	44	G
<i>Pinus resinosa</i>	red pine	2.61	7.4	3.65	34.18	123.85	0.71	61	G,I
<i>Pinus rigida</i>	pitch pine	2.28	6.7	10.28	41.48	116.39	0.9	63	G

<i>Pinus serotina</i>	pond pine	1.25	1.74	18.51	35.83	9.49	0.84	48	G,I
<i>Pinus strobiformis</i>	southwestern white pine	1.02	1.94	20.85	28.34	0.07	0.87	26	G
<i>Pinus strobus</i>	eastern white pine	4.67	10.75	6.07	43.21	456.75	0.76	78	G,I
<i>Pinus taeda</i>	loblolly pine	2.18	3.37	17.84	37.06	47.4	0.74	60	G
<i>Pinus teocote</i>	Twisted leaves pine	2.53	1.81	31	25.32	22.3	0.81	81	G
<i>Pinus virginiana</i>	Virginia pine	2.63	5.19	11.19	41.06	108.8	0.91	52	G
<i>Piscidia piscipula</i>	Florida fishpoison tree	0.48	0.53	23.93	35.5	0.03	1	12	G
<i>Pistacia texana</i>	Texas pistache	0.49	0.83	21	19.28	0.5	0.98	18	G
<i>Pithecellobium flexicaule</i>	ebony blackbead	1.22	3.72	23.79	27.04	33.59	1	66	G
<i>Pithecellobium guadalupense</i>	Guadeloupe blackbead	0.5	0.69	24.03	37.15	0.84	0.96	16	G
<i>Pithecellobium pallens</i>	huajillo	1.18	6.33	23.08	21.02	46.5	0.93	59	G
<i>Pithecellobium unguis-cati</i>	catclaw blackbead	0.46	0.51	23.83	35.5	0.03	1	12	G
<i>Planera aquatica</i>	planertree	1.06	3.21	18.38	38.45	20.77	0.82	46	G
<i>Platanus occidentalis</i>	American sycamore	4.72	5.92	13.06	36.67	221.4	0.73	108	G
<i>Populus angustifolia</i>	narrowleaf cottonwood	0.79	0.68	4.65	19.11	0.37	0.19	17	T
<i>Populus arizonica</i>	Arizona cottonwood	0.71	0.95	19.67	18.19	0.13	0.71	35	G,I
<i>Populus balsamifera</i>	balsam poplar	4.78	23.3	-0.1	40.93	819.54	0.77	101	G
<i>Populus deltoides</i>	eastern cottonwood	5.48	8.96	12.6	25.81	338.34	0.52	112	T,I
<i>Populus fremontii</i>	Fremont cottonwood	0.52	0.73	18.07	16.35	0.42	1	8	G
<i>Populus grandidentata</i>	bigtooth aspen	3.68	6.39	5.09	34.3	192.83	0.83	77	G
<i>Populus heterophylla</i>	swamp cottonwood	3.05	1.69	15.25	35.1	7.15	0.78	48	G,I
<i>Populus tremuloides</i>	quaking aspen	5.6	17.05	0.93	35.67	669.27	0.59	100	T,I
<i>Populus trichocarpa</i>	black cottonwood	0.47	0.73	6.15	19.01	0.24	0.94	12	G,I
<i>Prosopis juliflora</i>	mesquite	5.01	7.51	22.07	21.48	298.65	0.86	69	G
<i>Prosopis pubescens</i>	screwbean mesquite	0.45	0.62	20.08	18.48	1.24	1	12	G
<i>Prunus alleghaniensis</i>	Allegheny plum	1.1	1.62	8.75	33.4	0.64	0.81	28	G,I
<i>Prunus americana</i>	American plum	3.13	13.69	10.87	36.28	304.35	0.7	98	G
<i>Prunus angustifolia</i>	Chickasaw plum	2.76	7.16	16.21	30.72	121.35	0.71	87	G
<i>Prunus caroliniana</i>	Carolina laurelcherry	1.12	3.7	18.95	38.05	22.15	0.84	47	G
<i>Prunus hortulana</i>	hortulan plum	1.16	1.55	12.94	32.14	4.81	0.94	35	G
<i>Prunus mexicana</i>	Mexican plum	3.01	2.57	17.38	31.43	47.01	0.76	79	G
<i>Prunus munsoniana</i>	wildgoose plum	1.24	1.99	13.09	32.09	5.58	0.93	50	G
<i>Prunus myrtifolia</i>	West Indies cherry	0.44	0.64	23.83	37.39	0.93	0.99	16	G
<i>Prunus nigra</i>	Canada plum	2.6	15.51	3.4	69.79	1029.84	0.42	51	T,I
<i>Prunus pensylvanica</i>	pin cherry	5.51	11.69	2.08	35.42	462.07	0.7	102	G,I
<i>Prunus serotina</i>	black cherry	6.16	6.38	10.57	36.91	301.09	0.74	166	G
<i>Prunus umbellata</i>	flatwoods plum	1.19	3.61	18.62	37.5	24.7	0.79	46	G
<i>Prunus virginiana</i>	common chokecherry	4.61	13.58	5.34	23.52	482.18	0.81	109	G
<i>Pseudotsuga menziesii</i>	Douglas fir	0.45	0.5	20.39	17.5	0.04	0.77	27	G
<i>Psidium longipes</i>	long stalk stopper	0.35	0.74	23	37.24	0.03	1	12	G

<i>Ptelea trifoliata</i>	common hoptree	3.73	4.7	17.4	33.42	99.09	0.46	141	G
<i>Quercus alba</i>	white oak	4.31	6.26	11.66	37.49	209.86	0.72	87	G
<i>Quercus arkansana</i>	Arkansas oak	0.81	1.4	17.67	37.04	0.45	0.98	22	G
<i>Quercus bicolor</i>	swamp white oak	1.98	3.32	9.99	32.04	39.38	0.9	55	G
<i>Quercus chapmanii</i>	Chapman oak	0.77	1.18	22.76	36.16	2.7	0.79	40	G
<i>Quercus coccinea</i>	scarlet oak	2.88	5.61	11.25	39.74	132.44	0.89	64	G
<i>Quercus durandii</i>	Durand oak	1.14	2.53	18.75	27.02	15.91	0.91	48	G
<i>Quercus ellipsoidalis</i>	northern pin oak	1.63	1.79	5.73	27.15	12.56	0.74	36	G,I
<i>Quercus falcata</i>	southern red oak	3.6	4.26	15.27	38.05	108.92	0.61	67	G,I
<i>Quercus georgiana</i>	Georgia oak	0.45	1.78	16.2	35.01	0.25	1	18	G
<i>Quercus glaucoides</i>	Lacey oak	1.4	1.71	19.09	26.2	2.92	0.97	37	G
<i>Quercus gravesii</i>	Graves oak	1.2	1.91	20.79	19.44	0.17	0.9	20	G
<i>Quercus grisea</i>	gray oak	0.93	1.99	19.03	20.45	0.12	0.98	19	G
<i>Quercus havardii</i>	Havard oak	1.32	4.16	16.22	19.32	18.01	0.89	27	G,I
<i>Quercus ilicifolia</i>	bear oak	1.46	1.8	9.16	34.6	15.5	0.99	51	G
<i>Quercus imbricaria</i>	shingle oak	2.02	3.2	11.79	32.72	27.66	0.61	51	G,I
<i>Quercus incana</i>	bluejack oak	1.21	4.03	18.79	37.5	21.02	0.72	48	G
<i>Quercus laevis</i>	turkey oak	1.3	3.58	18.83	37.53	17.46	0.59	46	G
<i>Quercus laurifolia</i>	laurel oak	1.33	3.37	19.13	38.61	27.37	0.7	57	T
<i>Quercus lyrata</i>	overcup oak	1.97	3.23	18.04	37.16	47.29	0.82	62	G
<i>Quercus macrocarpa</i>	bur oak	6.37	4.29	10.45	28.16	169.2	0.58	108	T,I
<i>Quercus marilandica</i>	blackjack oak	4.21	6.48	15.18	36.02	188.62	0.54	83	T,I
<i>Quercus michauxii</i>	swamp chestnut oak	2.24	2.79	17.76	37.49	45.83	0.8	64	G,I
<i>Quercus mohriana</i>	Mohrs oak	1.11	2.19	18.35	21.28	11.2	0.86	37	G,I
<i>Quercus muehlenbergii</i>	chinkapin oak	3.48	7.56	12.63	37.56	173.21	0.68	94	G,I
<i>Quercus myrtifolia</i>	myrtle oak	0.81	1.24	22.74	36.45	4.8	0.89	40	G
<i>Quercus nigra</i>	water oak	2.47	3.73	17.78	36.91	66.56	0.75	65	G
<i>Quercus nuttallii</i>	Nuttall oak	1.54	2.24	18.15	38.66	13.56	0.76	30	G,I
<i>Quercus oglethorpensis</i>	Oglethorpe oak	0.4	0.48	16.44	35.5	0.07	1	12	G
<i>Quercus palustris</i>	pin oak	2.45	2.84	11.94	32.92	42.44	0.85	52	G,I
<i>Quercus phellos</i>	willow oak	2.64	2.9	16.54	37.02	54.13	0.78	57	G
<i>Quercus prinus</i>	chestnut oak	2.8	5.58	11.14	40.07	127.51	0.9	66	G
<i>Quercus pungens</i>	sandpaper oak	0.77	1.55	18.95	23.89	3.58	0.99	31	G
<i>Quercus rubra</i>	northern red oak	5.46	7.74	7.93	37.73	353.3	0.78	92	T
<i>Quercus rugosa</i>	netleaf oak	1.86	11.95	20.68	59.37	26.89	0.67	104	G,I
<i>Quercus shumardii</i>	Shumard oak	3	4.81	17.25	34.45	98.74	0.71	72	G
<i>Quercus stellata</i>	post oak	4.45	6.96	14.94	35.63	223.96	0.54	81	T,I
<i>Quercus velutina</i>	black oak	3.95	6.09	12.25	37.31	193.47	0.76	81	G
<i>Quercus virginiana</i>	live oak	1.67	7.72	20.39	29.64	76.73	0.67	67	G,I
<i>Rapanea punctata</i>	Florida rapanea	0.41	1	23.75	36.99	18	1	22	G
<i>Rhamnus betulaefolia</i>	birchleaf buckthorn	1.4	1.85	22.37	29.19	0.22	0.89	35	G
<i>Rhamnus caroliniana</i>	Carolina buckthorn	2.87	2.28	15.5	37.55	38.7	0.71	87	G
<i>Rhizophora mangle</i>	mangrove	2.29	3.52	31	81	44.46	0.82	64	G,T

	Catawba									
<i>Rhododendron catawbiense</i>	rhododendron rosebay	2.67	3.47	10.5	42.73	53.52	0.89	42	G	
<i>Rhododendron maximum</i>	rhododendron	2.56	5.51	10.59	41.7	110.04	0.89	61	G	
<i>Rhus copallina</i>	shining sumac	4.78	5.43	13.33	37.34	197.53	0.73	100	G,I	
<i>Rhus glabra</i>	smooth sumac	3.97	9.19	11.72	34.79	278.4	0.74	119	G	
<i>Rhus lanceolata</i>	prairie sumac	2.71	5.26	20.28	25	33.82	0.42	100	G	
<i>Rhus microphylla</i>	littleleaf sumac	1.62	3.95	19.27	20.38	43.3	0.92	36	G	
<i>Rhus typhina</i>	staghorn sumac	3.91	6.97	6.56	37.08	177.82	0.72	71	G	
<i>Robinia kelseyi</i>	Kelsey locust	1.74	1.59	10.47	39.03	1.37	0.87	28	G,I	
<i>Robinia pseudoacacia</i>	black locust	2.55	5.05	11.03	41.43	102.45	0.93	58	G	
<i>Robinia viscosa</i>	clammy locust	1.27	5.02	9.79	46.15	21.08	0.84	38	G,I	
<i>Roystonea elata</i>	Florida royalpalm	0.26	0.37	23	35.46	0	1	12	G,T	
<i>Sabal mexicana</i>	Mexican palmetto	2.94	9.38	24.19	39.52	9.87	0.21	86	G,I	
<i>Sabal minor</i>	dwarf palmetto	1.58	4.49	19.27	36.45	42.02	0.61	53	T	
<i>Sabal palmetto</i>	cabbage palmetto	0.84	1.22	22.81	36.72	8.68	0.96	41	G	
<i>Salix alaxensis</i>	feltleaf willow	1.77	9.07	-9.09	0	213.48	0.78	44	G,I	
<i>Salix amygdaloides</i>	peachleaf willow	4.67	6.88	8.22	20.21	254.41	0.82	81	G,I	
<i>Salix arbusculoides</i>	peachleaf willow	3.81	3.55	-4.87	17.4	97.02	0.86	56	G	
<i>Salix bebbiana</i>	Bebb willow	4.65	150	2.06	73.4	3516.04	0.65	100	G,I	
<i>Salix bonplandiana</i>	Bonpland willow	1.65	11.03	31	0	13749.91	0.59	108	G	
<i>Salix caroliniana</i>	Coastal Plain willow	4.68	2.32	19.52	36.39	27.25	0.43	83	G,I	
<i>Salix discolor</i>	pussy willow	3.99	7.68	3.17	31.46	224.38	0.73	91	G	
<i>Salix exigua</i>	coyote willow	6.12	7.21	7.68	21.39	346.22	0.81	143	G,I	
<i>Salix floridana</i>	Florida willow	0.88	1.02	20.28	37.64	0.08	0.83	23	G,I	
<i>Salix lasiandra</i>	Pacific willow	2.32	2.64	-1.18	19.78	32.13	0.79	48	G,I	
<i>Salix lasiolepis</i>	arroyo willow	1.01	0.67	20.26	18.86	0.83	0.84	18	G	
<i>Salix lucida</i>	shining willow	4.68	7.64	1.94	34.08	284.13	0.84	86	G	
<i>Salix mackenzieana</i>	Mackenzie willow	1.47	2.18	-2.01	18.68	22.69	0.77	40	G,I	
<i>Salix nigra</i>	black willow	5.61	7.28	13.68	34.67	318.08	0.61	110	T,I	
<i>Salix pellita</i>	satiny willow	3.33	4.73	-1.59	33.17	116.04	0.82	65	G	
<i>Salix petiolaris</i>	meadow willow	3.14	61.55	3.06	0	800.46	0.44	81	T,I	
<i>Salix pyrifolia</i>	balsam willow	3.93	12.72	0.1	35.31	301.68	0.61	78	G	
<i>Salix scouleriana</i>	Scouler willow	2.16	2.64	-1.68	19.95	40.23	0.86	46	G,I	
<i>Salix sericea</i>	silky willow	4.67	7.67	7.33	40.6	203.76	0.59	72	G,I	
<i>Salix sitchensis</i>	Sitka willow	0.58	0.55	1.83	23.1	0.11	0.81	19	G,I	
<i>Salix taxifolia</i>	yewleaf willow	1.82	10.56	31	0	10585.89	0.84	112	G	
<i>Sambucus canadensis</i>	American elder	6.98	6.54	11.13	36.26	368.04	0.73	124	T	
<i>Sambucus glauca</i>	blueberry elder	0.36	0.55	4.96	20.6	0	0.99	14	G	
<i>Sambucus mexicana</i>	Mexican elder	2.98	7.02	19.76	49.39	19.31	0.44	110	G	
<i>Sapindus drummondii</i>	western soapberry	2.34	6.14	17.98	24.6	97.41	0.74	72	G	
<i>Sapindus saponaria</i>	wingleaf soapberry	0.88	1.12	23.53	36.35	0.1	0.92	29	G	
<i>Sassafras albidum</i>	sassafras	4.56	5.19	12.94	37.8	188.5	0.74	87	G	

<i>Schoepfia chrysophylloides</i>	graytwig	0.45	0.66	23.92	37.25	2.36	0.99	19	G
<i>Serenoa repens</i>	saw palmetto	0.88	1.32	22.73	36.7	9.06	0.75	42	G
<i>Shepherdia argentea</i>	silver buffaloberry	2.67	3.8	6.36	19.05	81.78	0.91	36	G
<i>Simarouba glauca</i>	paradise tree	0.49	0.63	23.81	37.39	1.56	1	16	G
<i>Solanum erianthum</i>	mullein nightshade	2.36	9.65	26.29	30.15	140.6	0.82	120	G,I
<i>Sophora affinis</i>	Texas sophora	1.15	2.05	18.92	28.39	9.79	0.88	39	G,I
<i>Sophora secundiflora</i>	mescalbean	2.23	6.39	21.58	14.99	98.59	0.91	43	G
<i>Sorbus americana</i>	American mountain ash	4.93	9.5	2.53	39.94	352.3	0.78	77	G
<i>Sorbus decora</i>	showy mountain ash	5.13	6.97	-0.97	35.27	289.32	0.84	69	G
<i>Sorbus scopulina</i>	Greene mountain ash	1.57	1.52	0.66	22	2.69	0.77	34	G
<i>Sorbus sitchensis</i>	Sitka mountain ash	1.07	0.51	1.55	23.51	0.11	1	15	G
<i>Staphylea trifolia</i>	American bladdernut	2.64	3.66	11.85	33.23	61.01	0.84	75	G,I
<i>Stewartia malacodendron</i>	Virginia stewartia	0.51	1.64	18.36	40.42	5.37	0.9	40	G
<i>Stewartia ovata</i>	mountain stewartia	1.97	3.1	12.13	42.24	39.1	0.89	37	G
<i>Styrax americana</i>	American snowbell	1.67	3.15	18.48	37.75	33.87	0.78	67	G
<i>Styrax grandifolia</i>	bigleaf snowbell	1.36	3.09	18.3	37.85	23.28	0.79	61	G
<i>Styrax platanifolia</i>	sycamore leaf snowbell	0.92	1.4	19.75	28.12	3.26	1	23	G
<i>Suriana maritima</i>	baycedar	0.46	0.69	23.92	37.21	1.32	1	16	G
<i>Swietenia mahagoni</i>	West Indies mahogany	0.63	0.89	23.88	36.51	0.2	0.91	15	G,I
<i>Symplocos tinctoria</i>	common sweetleaf	4.74	4.06	13.28	41.86	78.72	0.4	65	G,I
<i>Taxodium distichum</i>	baldcypress	2.54	4.09	19.04	36.89	58.41	0.64	61	T
<i>Taxodium mucronatum</i>	Montezuma baldcypress	0.61	4.94	22.4	25.46	4.76	0.77	76	G,T
<i>Taxus canadensis</i>	Canada yew	5.13	5.87	1.82	34.69	247.49	0.83	69	T
<i>Taxus floridana</i>	Florida yew	0.36	0.54	19	38.5	0	1	9	G,T
<i>Tetrazygia bicolor</i>	Florida tetrazygia	0.35	0.72	23	37.48	0.07	1	12	G
<i>Thrinax radiata</i>	Florida thatchpalm	0.48	0.53	24.08	35.5	0.01	1	12	G
<i>Thuja occidentalis</i>	northern white cedar	2.54	6.93	2.82	33.26	129.39	0.78	78	G
<i>Tilia americana</i>	American basswood	4.05	6.1	7.46	32.24	172.92	0.61	80	T
<i>Tilia caroliniana</i>	Carolina basswood	1.42	2.95	18.35	36.18	28.88	0.78	69	G
<i>Tilia heterophylla</i>	white basswood	2.81	4.7	11.25	41.1	104.73	0.9	54	G
<i>Torreya taxifolia</i>	Florida torreya	0.36	0.54	19	38.5	0.01	1	9	G,T
<i>Toxicodendron vernix</i>	poison sumac	6.07	7.75	11.12	40.96	78.61	0.19	73	T
<i>Trema lamarckiana</i>	West Indies trema	0.34	0.76	25	37.24	0.01	1	12	G
<i>Trema micrantha</i>	Florida trema	0.44	0.67	23.83	37.14	18.28	1	16	G
<i>Tsuga canadensis</i>	eastern hemlock	4.41	7.36	6.88	40.78	280.93	0.83	70	G
<i>Tsuga caroliniana</i>	Carolina hemlock	2.08	5.78	10.74	46.97	67.99	0.86	37	G
<i>Ulmus alata</i>	winged elm	2.87	3.52	16.22	35.81	74.71	0.83	71	G
<i>Ulmus americana</i>	American elm	7.13	9.61	9.46	34.08	554.31	0.68	126	T
<i>Ulmus crassifolia</i>	cedar elm	1.99	3.92	19.96	29.33	53.7	0.73	54	T,I
<i>Ulmus rubra</i>	slippery elm	4.42	7.72	11.49	35.44	263.68	0.74	105	G

<i>Ulmus serotina</i>	September elm	1.72	2.7	15.22	36.92	2.27	0.75	33	G
<i>Ulmus thomasii</i>	rock elm	2.25	2.04	8.2	29.14	29.39	0.83	62	G
<i>Ungnadia speciosa</i>	Mexican buckeye	0.86	1.45	19.34	28.65	2.14	0.86	53	G
<i>Vaccinium arboreum</i>	tree sparkleberry	3.54	4.23	16.06	37.92	89.39	0.59	76	G,I
<i>Viburnum lentago</i>	nannyberry	2.59	5.59	6.7	30	80.88	0.56	69	T,I
<i>Viburnum nudum</i>	possumhaw viburnum	1.84	1.5	20.82	35.85	12.72	0.98	63	G
<i>Viburnum obovatum</i>	Walter viburnum	2.67	1.83	20.53	35.99	9.18	0.46	36	G
<i>Viburnum prunifolium</i>	blackhaw	2.24	3.84	11.03	34.22	52.51	0.76	57	G
<i>Viburnum rufidulum</i>	rusty blackhaw	2.64	4.44	16.92	33.97	82.51	0.84	65	T
<i>Viburnum trilobum</i>	American cranberrybush	2.49	10.46	4.49	37.94	191.72	0.79	65	T
<i>Ximenia americana</i>	tallowwood	0.65	0.68	23.16	36.79	10.25	1	20	G
<i>Yucca aloifolia</i>	aloe yucca	1.15	1.17	23.21	37.22	1.9	0.87	37	G
<i>Yucca carnerosana</i>	Carneros yucca	0.8	1.26	19.68	18.21	0.13	0.68	29	G,I
<i>Yucca elata</i>	soaptree yucca	1.18	0.68	17.54	18.1	1.87	1	14	G
<i>Yucca gloriosa</i>	moundlily yucca	0.53	0.77	18.16	36.53	0.44	0.92	18	G
<i>Yucca rostrata</i>	beaked yucca	1.34	1.96	22.71	18.39	1.28	0.58	18	G
<i>Yucca torreyi</i>	Torrey yucca	0.78	2.63	20.28	19.16	13.77	0.96	25	G
<i>Yucca treculeana</i>	Trecul yucca	1.76	4.41	22.88	24.77	55	0.78	68	G
<i>Zanthoxylum americanum</i>	common prickly ash	2.9	2.72	9.61	29.68	44.12	0.83	80	G,I
<i>Zanthoxylum clava-herculis</i>	Hercules club	1.42	5.17	19.51	34.71	28.35	0.66	55	G
<i>Zanthoxylum coriaceum</i>	Biscayne prickly ash	0.49	0.52	24.03	38.5	0.02	1	12	G
<i>Zanthoxylum fagara</i>	lime prickly ash	1.7	7.76	23.32	27.72	65.62	0.68	99	G
<i>Zanthoxylum hirsutum</i>	Texas Hercules club	2.24	1.75	19.73	27.8	20.22	0.87	35	G,I

Appendix S1.6

We calculated the potential species richness $\hat{S}_{tp}$ in each climate bin as the sum of species for which $\Omega_{stp} > 0.01$. Similarly, we calculated $\Omega_{\bullet tp}$, the proportion of occupied pixels in a climate bin averaged over all species that occupy that climate somewhere in their range. Finally, we tested whether the percentage of variance in Ω_{stp} explained by climate (peaked suitability model) increases with climatic stress (coldest and driest occupied Ω_{stp}), using only species with ≥ 50 occupied climatic bins.

The asymmetric limitation hypothesis predicts that skewed responses towards hot and humid conditions should be more prevalent in extreme climates (Kaufman, 1995). In contrast, we observed that the proportion of such right-skewed responses increases with temperature (GLM with logit link and binomial error distribution; explained deviance = 0.73, $p < 0.001$) and was unrelated to precipitation ($p = 0.06$). If species' distributions are primarily limited by climate at the stressful end of the gradient, then the realised/potential species richness ($R/\hat{S}_{tp}$) should be higher in stressful climates (low t and p). These climates should also, on average, be highly occupied by the few species able to tolerate them. Thus, occupancy of a given climatic bin averaged over all species ($\Omega_{\bullet tp}$) should decrease with temperature and precipitation. In contrast, we observe that both $R/\hat{S}_{tp}$ and $\Omega_{\bullet tp}$ peak at middle-range climates (Fig. S1.6) and are best described by a second order polynomial function of temperature and precipitation (R^2 increases by 0.17 for $R/\hat{S}_{tp}$ and by 0.21 for $\Omega_{\bullet tp}$ when a second order term is included; $p < 0.001$). Finally, the asymmetric limitation hypothesis predicts that occupancy is more closely related to climate (i.e. higher R^2) for species occurring in climatically stressful regions (Kaufman, 1995). The distribution of North American trees is consistent with this prediction for precipitation ($r^2 = 0.52$,

$p < 0.001$) but not temperature ($p = 0.45$). In sum, virtually none of the predictions derived from the asymmetric limitation hypothesis are supported.

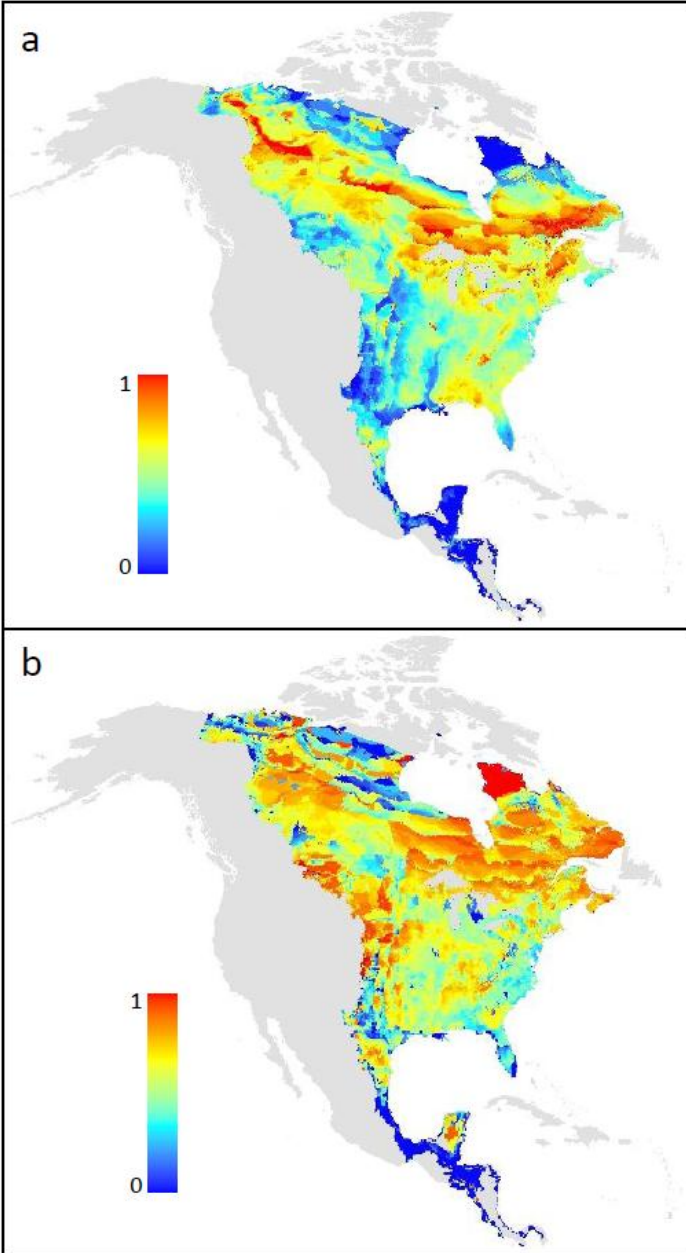


Figure S1.6 Map of the (a) Realized/Potential richness ($R/\hat{S}_{tp}$, the ratio of observed richness to the number of species whose observed climatic niche includes the climate of the region) and (b) average occupancy ($\Omega_{\bullet tp}$, occupancy Ω_{stp} averaged over species occurring in a given pixel). Grey areas are either excluded from analyses or have a tree species richness of zero; $n = 482$ species.

Appendix S1.7

The delineation of climate bins did not influence our general conclusions. The binning does make the parameters of the fitted relationships (Appendix S1.5) imprecise, but not biased. The fitted climatic niches (e.g. Fig. 1.2c, d) are qualitatively the same when different climate bins are used (Fig. S1.7). All tested predictions from the different hypotheses are robust to the bins delineation. Creating narrower (more) climate bins would have increased our power to detect more complex responses and would have lowered the R^2 of the fitted models (the opposite is true for larger (less) climate bins; Fig. S1.8). However, since the binning does not generate any bias in the results, our conclusion that left and right skewed responses occur as frequently would have remained, despite detecting statistically significant skewness for more species. An interaction between temperature and precipitation would have also been significant for more species, but positive and negative interactions would have remained as frequent.

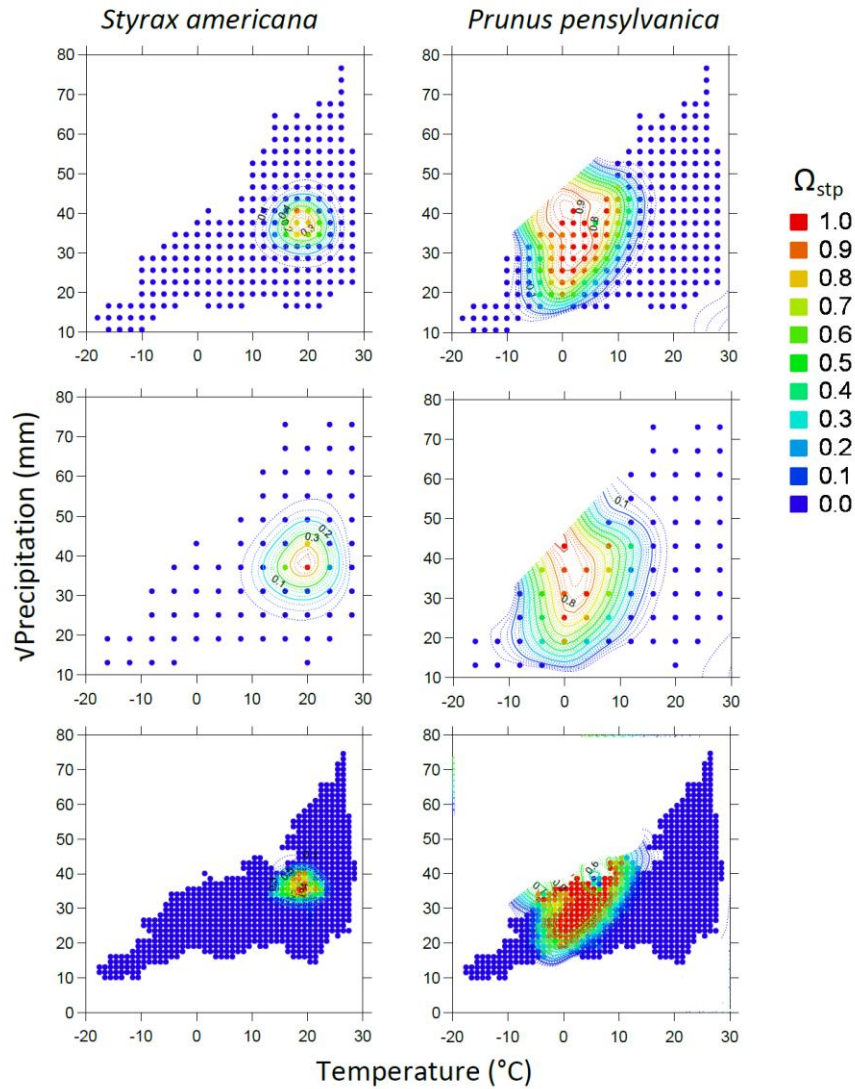


Figure S1.7 Examples of the observed climatic niches of *Styx americana* (American snowbell) and *Prunus pensylvanica* (Pin cherry) with different climate bin delineation (to be compared with Figure 2 in the main text). Occupancy of the climate bins in the study region, in which each extant combination of temperature and precipitation (i.e. a climate bin) is represented by a dot. Top row: temperature by 2°C and the square root of precipitation (mm) by 3, but all climate bins are offset compared to Figure 2. Middle row: temperature by 4°C and the square root of precipitation (mm) by 6. Bottom row: temperature by 1°C and the square root of precipitation (mm) by 1.5.

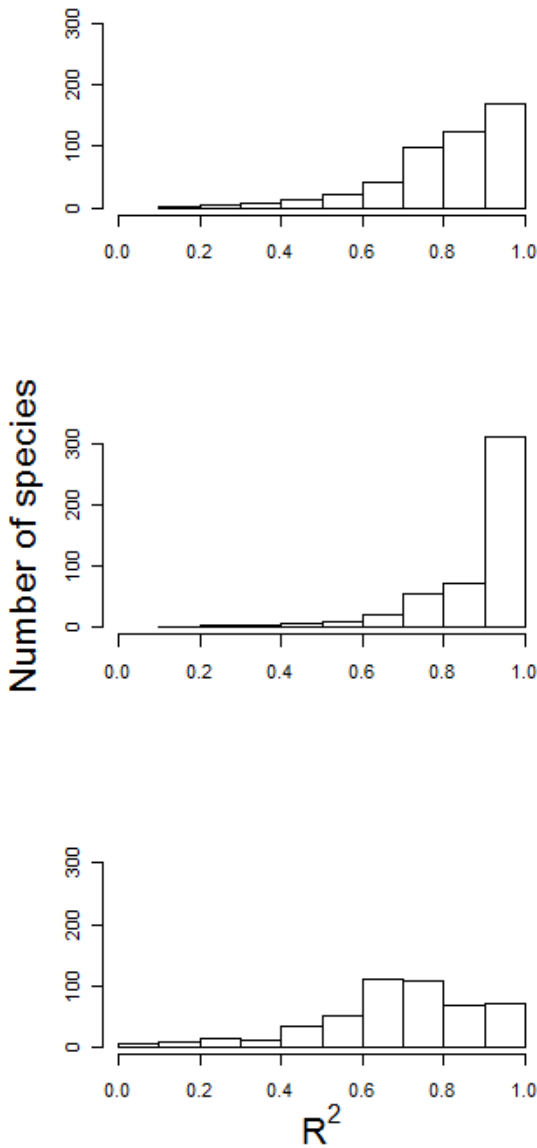


Figure S1.8 Distribution of R^2 for 482 species when occupancy is fitted as a bivariate normal function of temperature and precipitation, for different climate bin delineation (to be compared with Figure 3 in the main text). Top row: temperature by 2°C and the square root of precipitation (mm) by 3, but all climate bins are offset compared to Figure 2. Middle row: temperature by 4°C and the square root of precipitation (mm) by 6. Bottom row: temperature by 1°C and the square root of precipitation (mm) by 1.5.

APPENDICES CHAPTER 2

Appendix S2.1

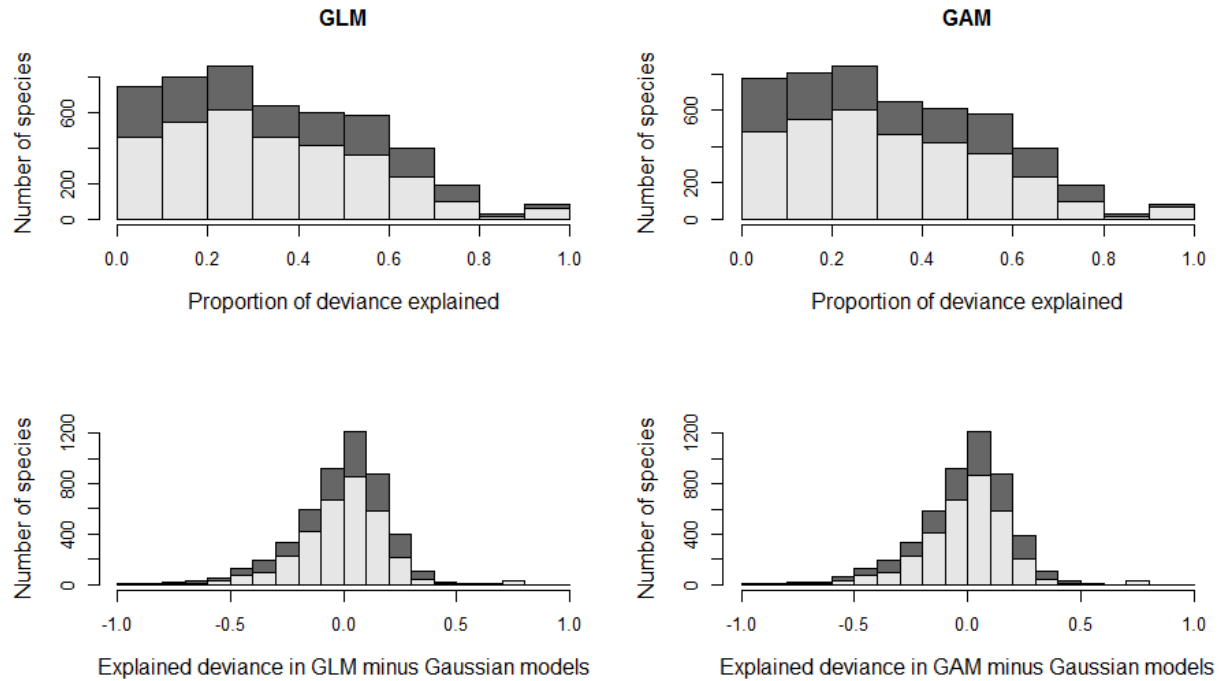


Figure S2.1 Frequency distribution among 3277 bird (light bars) and 1659 mammal (dark bars) species of the proportion of the deviance in occupancy explained by generalized linear (GLM) and generalized additive (GAM) models where a set of 19 bioclimatic variables are included as independent variables. In the bottom panel, we also show the frequency distribution of the difference in the explained deviance in occupancy between the GLMs and GAMs presented in the upper panel minus that of the Gaussian occupancy-climate relationship presented in Figure 2 of the main text. The bars for birds and mammals are stacked such that the height of the bar represents the total number of species of both taxa.

Table S2.1 Pairwise correlations among the parameters of the Gaussian occupancy-climate model for bird and mammal species in the Americas. The parameters of the bivariate Gaussian model are maximum occupancy which can vary between 0 and 1, mean temperature and precipitation which represent the climatic optima for the species and the standard deviation (SD) in occupied areas for temperature and precipitation. The parameters are only weakly colinear.

	Maximum occupancy	Temperature optimum	Precipitation optimum	Temperature SD	Precipitation SD
Maximum occupancy	1.00	-0.24	0.47	0.21	0.19
Temperature optimum	-0.24	1.00	-0.20	-0.25	-0.36
Precipitation optimum	0.47	-0.20	1.00	0.25	0.30
Temperature SD	0.21	-0.25	0.25	1.00	0.12
Precipitation SD	0.19	-0.36	0.30	0.12	1.00

APPENDICES CHAPTER 3

Appendix S3.1

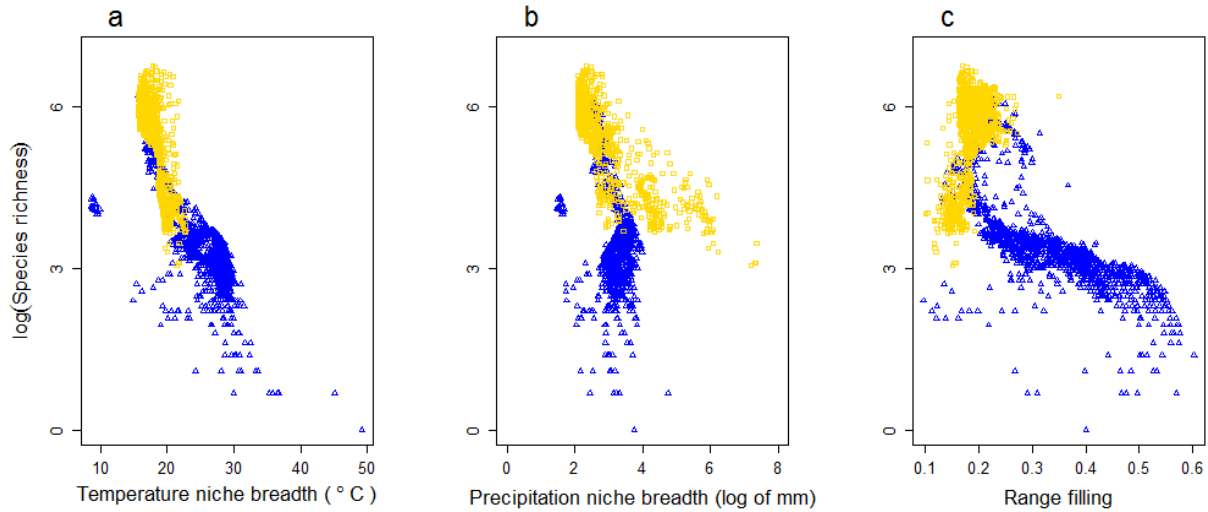


Figure S3.1 The common logarithm of bird species richness in 10^4 km^2 quadrats in North (dark triangles) and South (pale squares) America as a function of (a) mean temperature niche breadth in $^{\circ}\text{C}$; (b) logarithm of precipitation niche breadth in mm; and (c) range filling of all species with realized geographic ranges overlapping the quadrat. Positive relationships were predicted. Data are from the breeding ranges of 3277 bird species. This figure presents the same data as Fig. 4b-d, but here the mean climatic niche characteristics are calculated across all species occurring in a quadrat, whereas in Fig. 4b-d, it is calculated for all species whose potential range (defined in climatic space) overlaps the quadrat.

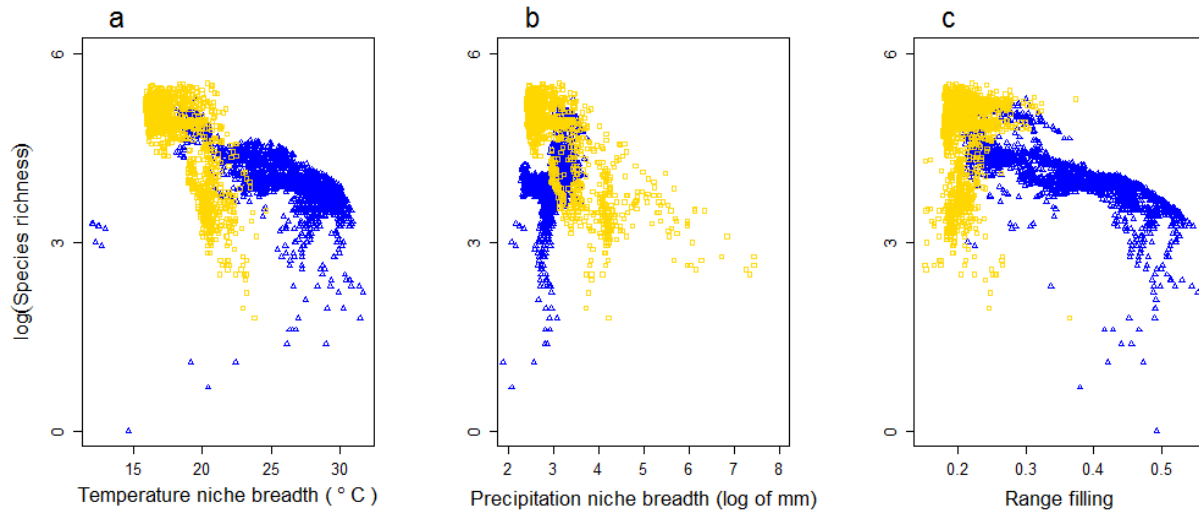


Figure S3.2 The common logarithm of mammal species richness in 10^4 km^2 quadrats in North (dark triangles) and South (pale squares) America as a function mean (a) temperature niche breadth in $^{\circ}\text{C}$; (b) logarithm of precipitation niche breadth in mm; and (c) range filling of all species with realized geographic ranges overlapping the quadrat. Positive relationships were predicted. Data are from the breeding ranges of 1659 mammal species. This figure presents the same data as Fig. 5b-d, but here the mean climatic niche characteristics are calculated across all species occurring in a quadrat, whereas in Fig. 5b-d, it is calculated for all species whose potential range (defined in climatic space) overlaps the quadrat.

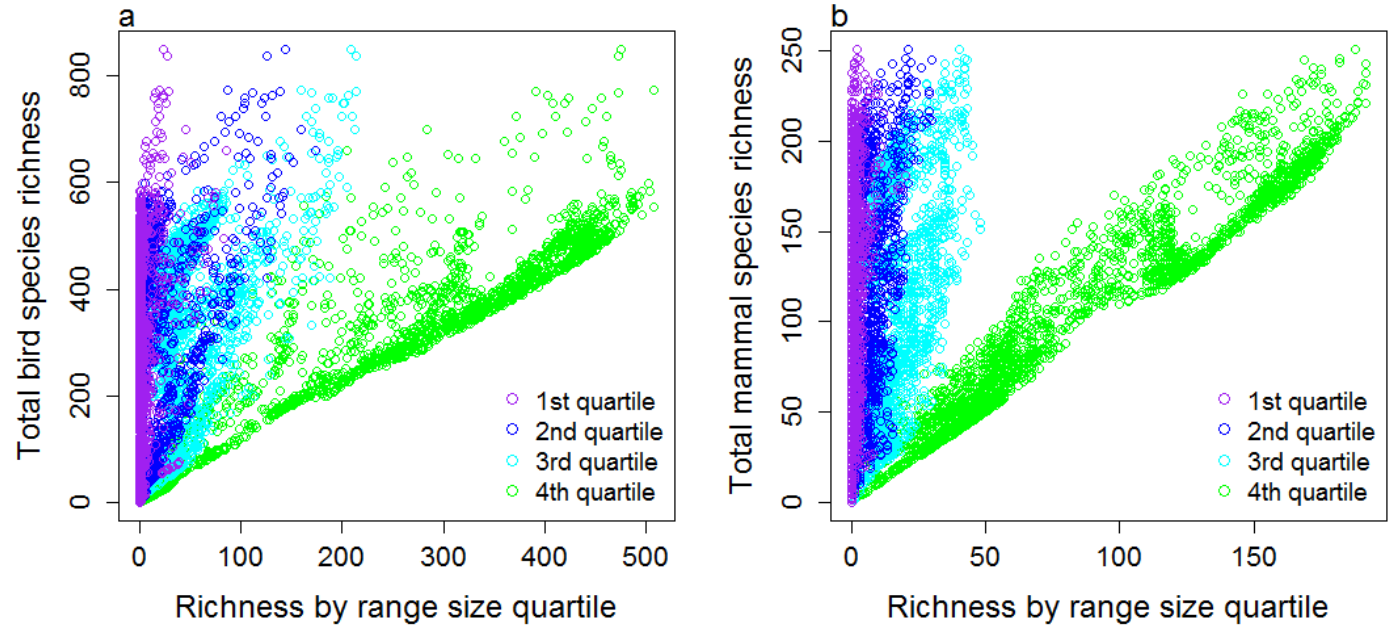


Figure S3.3 Total (a) bird and (b) mammal species richness as a function of the richness when only species of a given range size quartile are included.

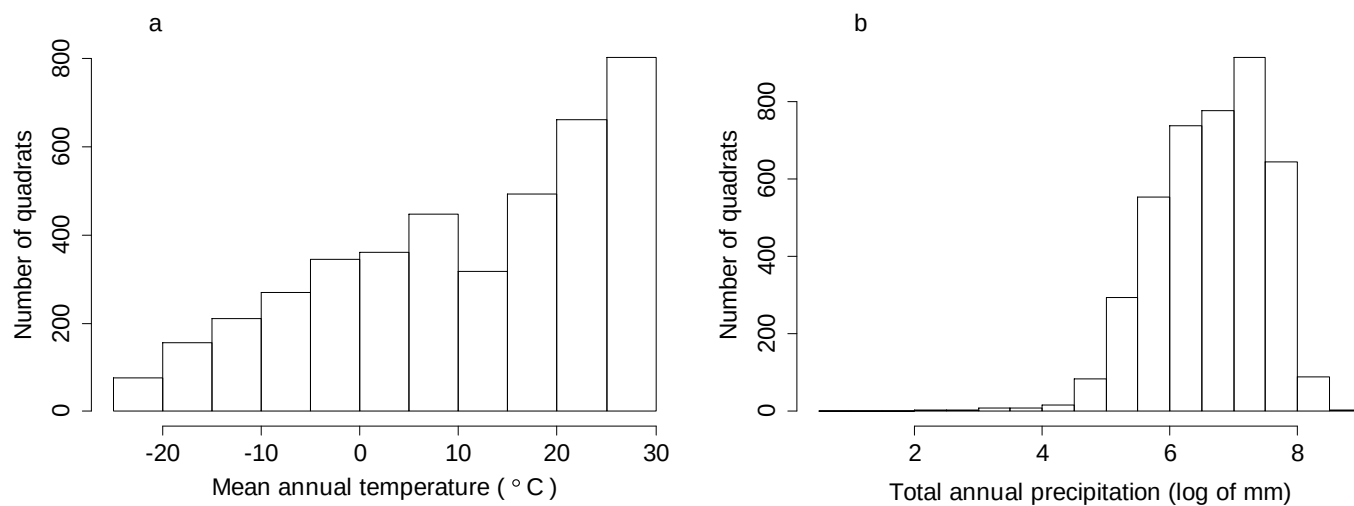


Figure S3.4 Frequency distribution of the number of 10,000 km² quadrats in the Americas with given (a) mean annual temperature (°C) and (b) logarithm of total annual precipitation (mm).

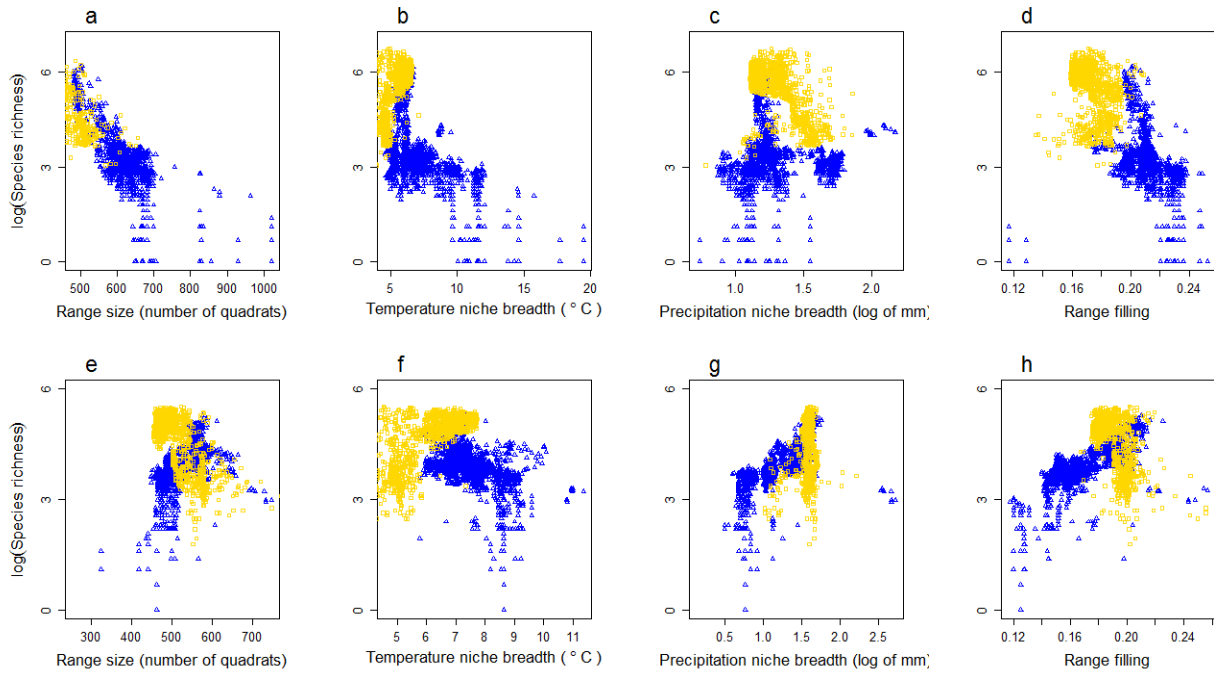


Figure S3.5 Species richness of (a-d) bird and (e-h) mammal species richness in 10^4 km^2 quadrats in North (dark triangles) and South (pale squares) America as a function of the standard deviation in the niche characteristics of the species occurring in the quadrat. The predictor variables are the standard deviation in (a,e) range size, measured as the number of occupied 10^4 km^2 quadrats of all species occurring in the quadrat; (b,f) temperature niche breadth in °C; (c,g) logarithm of precipitation niche breadth in mm; and (d,h) range filling of all species with potential ranges overlapping the quadrat. Panels a-d correspond to panels a-d in Figure 4, and panels e-h correspond to panels a-d in Figure 5, but using the standard deviation, instead of the mean, of species' niche characteristics.

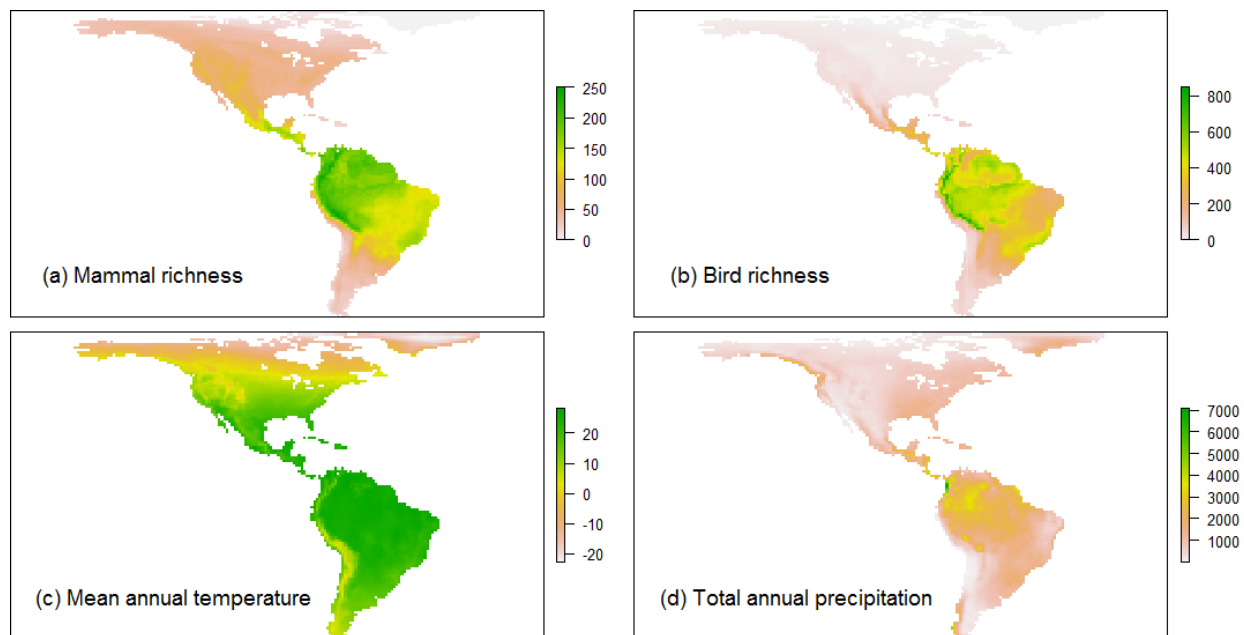


Figure S3.6 Maps of the response variables, i.e. (a) mammal and (b) bird species richness calculated as the total number of species whose breeding range overlapped the quadrat, and climatic predictor variables, i.e. (c) mean annual temperature in °C and (d) total annual precipitation in mm.

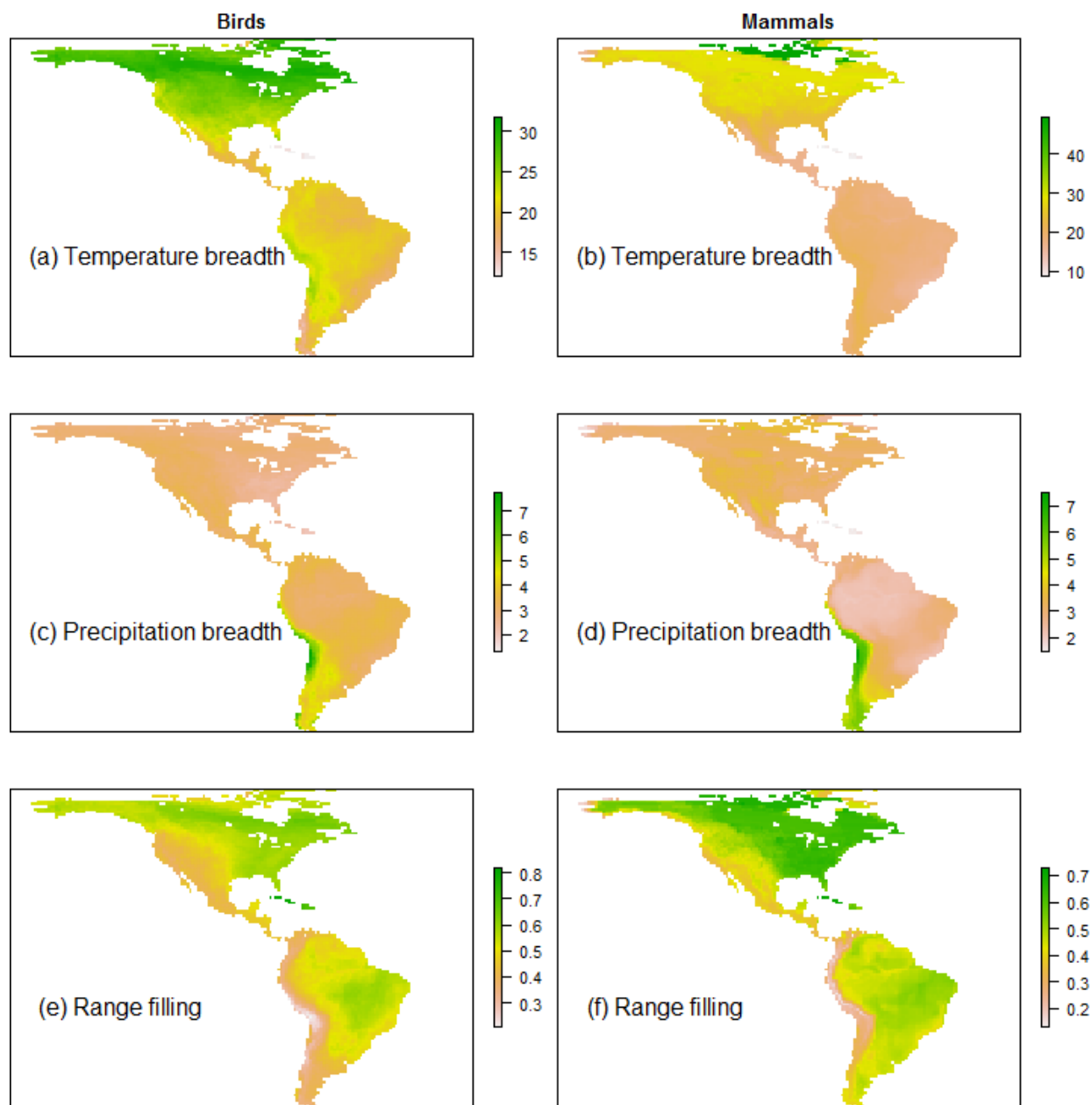


Figure S3.7 Maps of mean species niche characteristics for (a, c, e) birds and (b, d, f) mammals; (a-b) mean temperature niche breadth in °C; (b) logarithm of precipitation niche breadth in mm; and (c) range filling of all species with realized geographic ranges overlapping the quadrat.

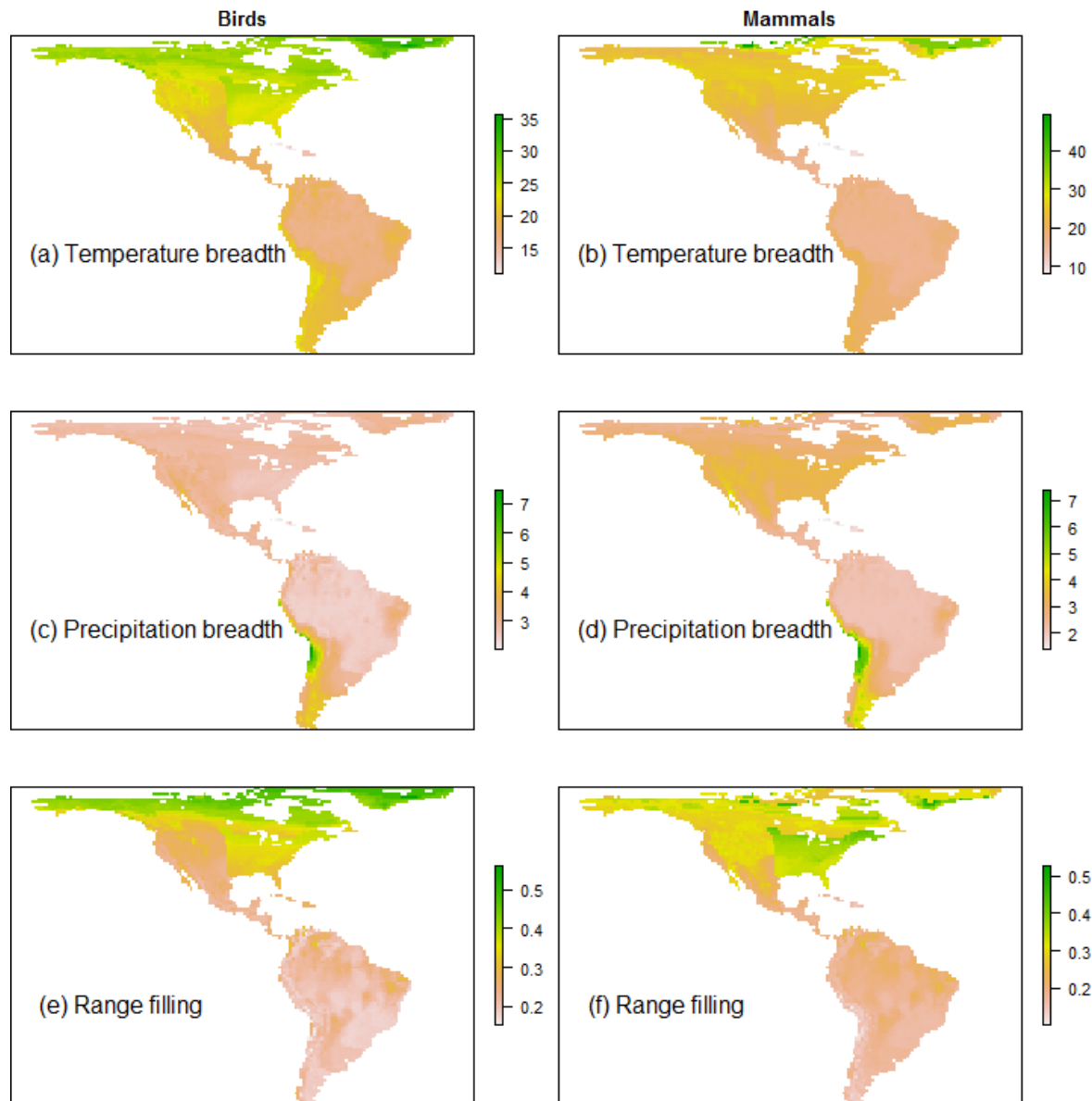


Figure S3.8 Maps of mean species niche characteristics for (a, c, e) birds and (b, d, f) mammals; (a-b) mean temperature niche breadth in °C; (b) logarithm of precipitation niche breadth in mm; and (c) range filling of all species with potential geographic ranges overlapping the quadrat. This figure presents the same data as Figure S3.7, but in Figure S3.7 the mean climatic niche characteristics are calculated across all species occurring in a quadrat, whereas here, it is calculated for all species whose potential range (defined in climatic space) overlaps the quadrat.

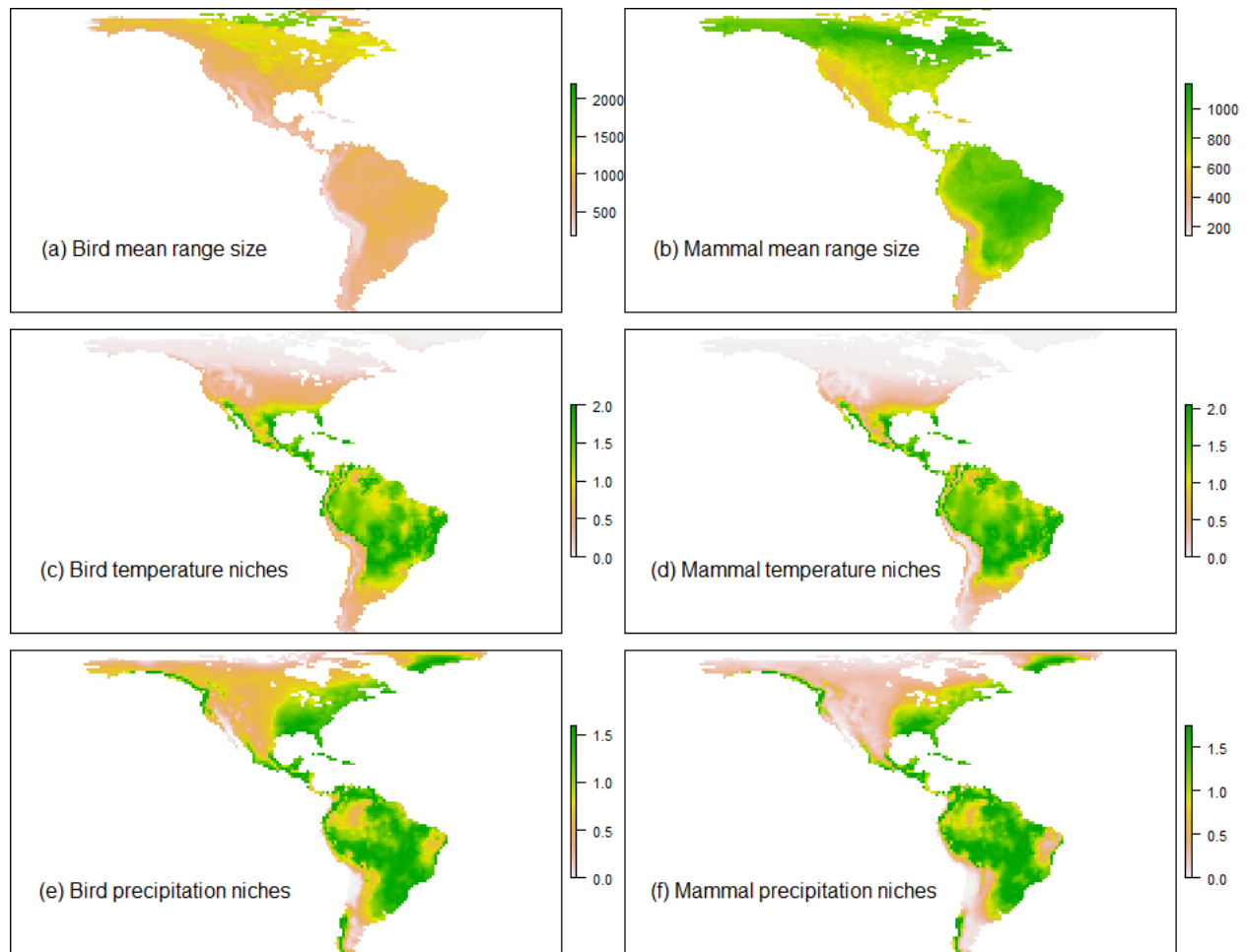


Figure S3.9 Maps of species' niche characteristics of (a, c, e) birds or (b, d, f) mammals used as predictor variables, i.e. (a-b) mean range size, measured as the number of quadrats within the species breeding range, of all species occurring in a quadrat; (c-d) number of species with a climatic niche centered on a temperature within 3°C or (e-f) a precipitation within 0.5 units of the focal quadrat scaled to a variance of 1.

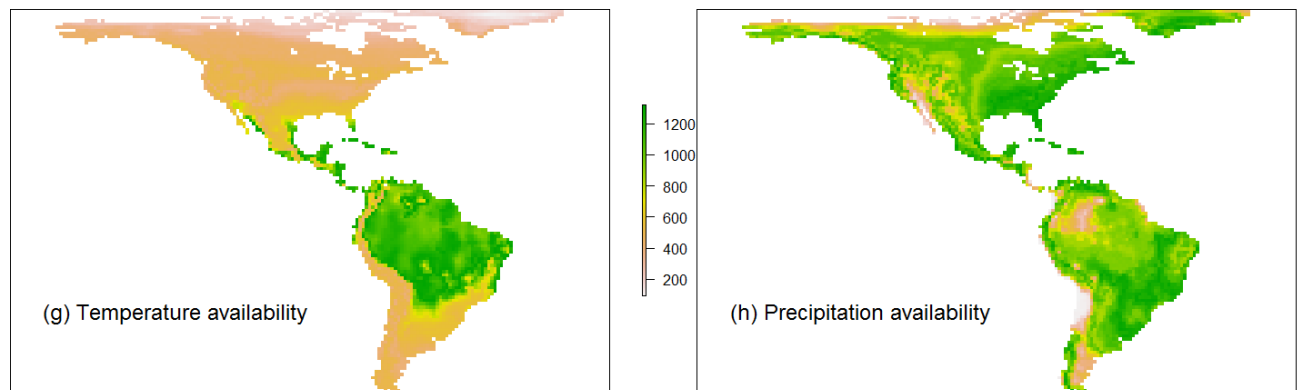


Figure S3.10 Maps of the number of quadrats with (a) extant temperatures within 3°C and (h) extant precipitation levels within 0.15 units (in log mm), of the focal quadrat.

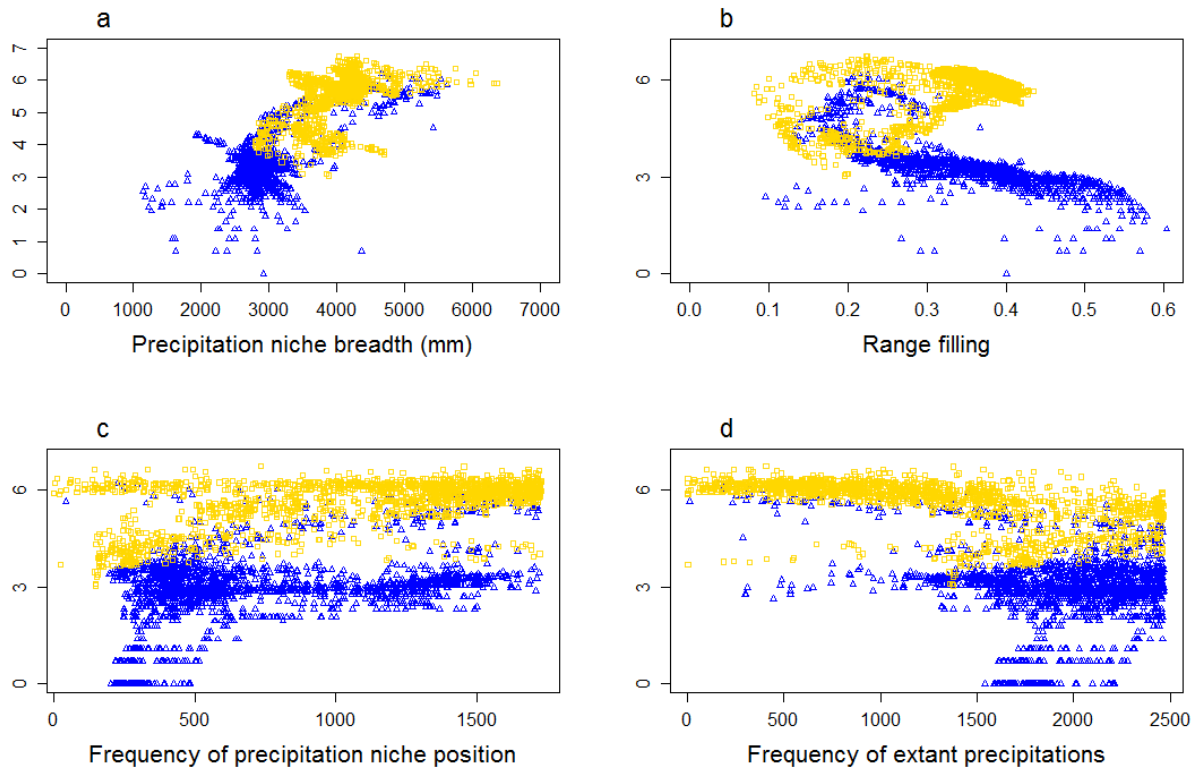


Figure S3.11 Bird species richness in 10^4 km^2 quadrats in North (dark triangles) and South (pale squares) America as a function of characteristics of individual species' distributions, when precipitation values are not transformed (i.e. in mm). If climate affects species richness through its effect on the realized niche of individual species, species richness is predicted to be positively correlated with these explanatory variables (a-d). The predictor variables are (a) mean precipitation niche breadth in mm and (b) mean range filling of all species with ranges overlapping the quadrat; (c) number of species with a climatic niche centered on precipitation values within 500 mm of that of the focal quadrat; and the number of quadrats with (d) extant precipitation levels within 500 mm of the focal quadrat.

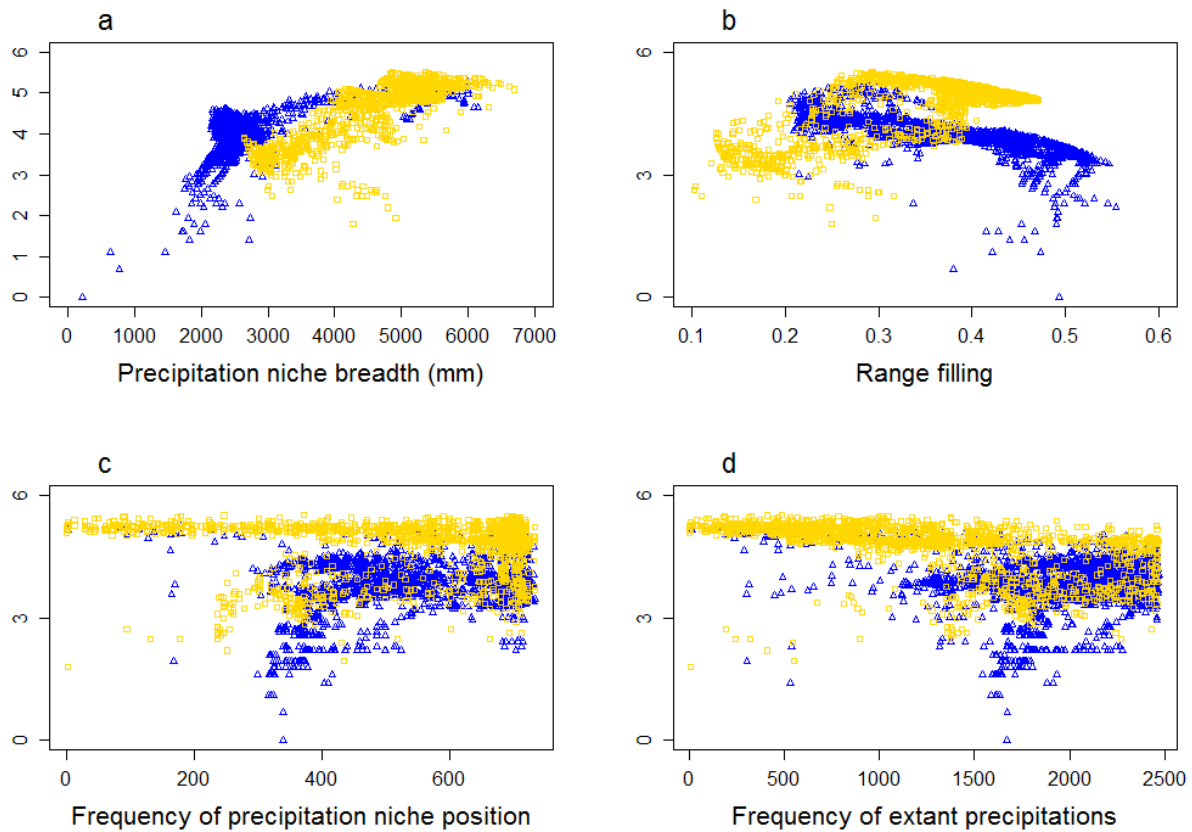


Figure S3.12 Mammal species richness in 10^4 km^2 quadrats in North (dark triangles) and South (pale squares) America as a function of characteristics of individual species' distributions, when precipitation values are not transformed (i.e. in mm). If climate affects species richness through its effect on the realized niche of individual species, species richness is predicted to be positively correlated with these explanatory variables (a-d). The predictor variables are (a) mean precipitation niche breadth in mm and (b) mean range filling of all species with ranges overlapping the quadrat; (c) number of species with a climatic niche centered on precipitation values within 500 mm of that of the focal quadrat; and the number of quadrats with (d) extant precipitation levels within 500 mm of the focal quadrat.

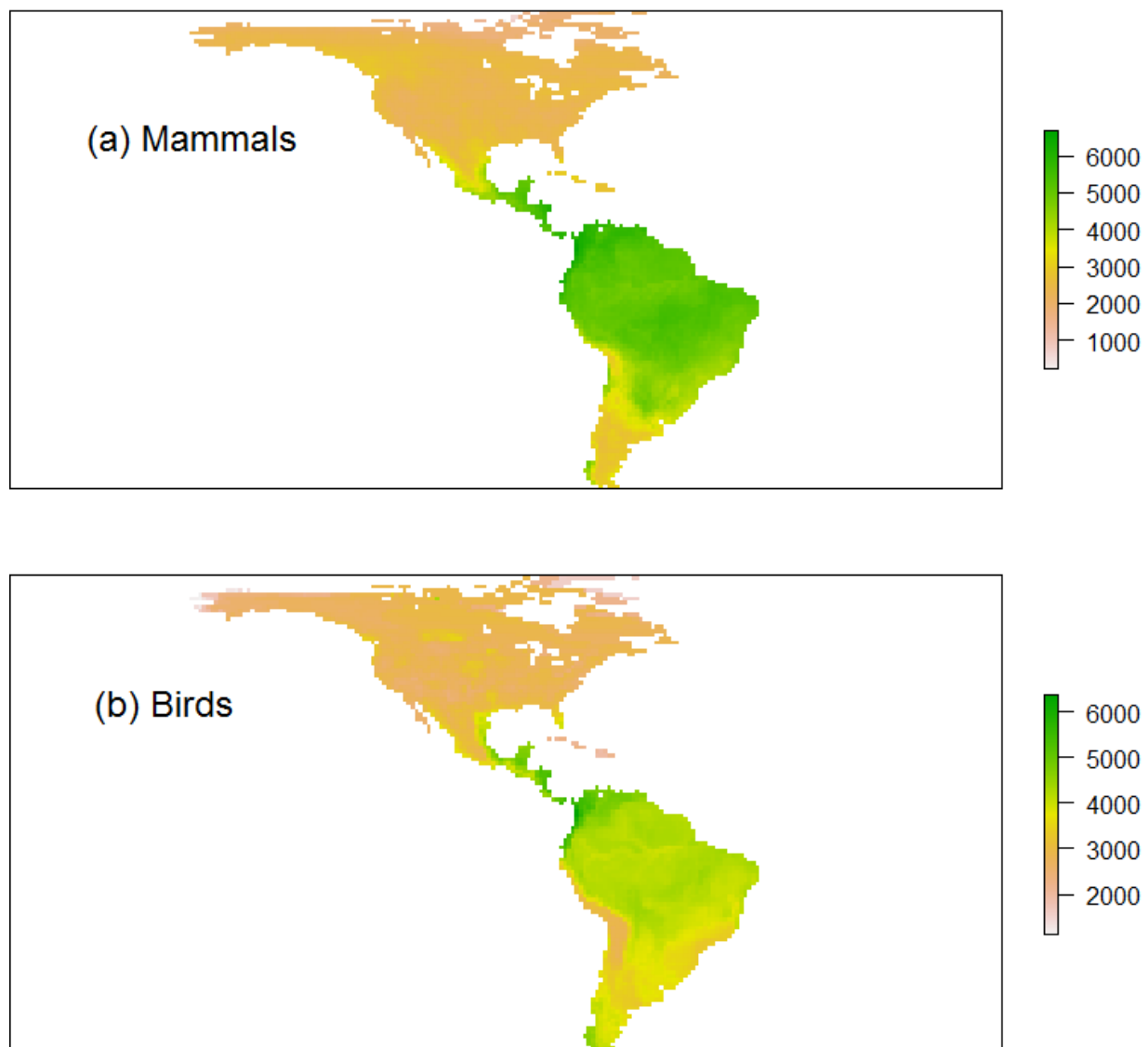


Figure S3.13 Maps of mean precipitation niche breadth (in mm) of all species occurring in a quadrat for (a) mammals and (b) birds.

Table S3.1 Proportion of the variance in bird and mammal species richness explained by the predictor variables, when precipitation is not transformed (i.e. in mm per year). Positive relationships are predicted as negative relationships (†) cannot involve a direct causal link. NS denotes coefficients with associated p-values < 0.05.

	OLS R ²	Marginal R ² of niche variable, after accounting for precipitation	Marginal R ² of niche variable, after accounting for climatic variables	Marginal R ² of precipitation, after accounting for niche variable	Marginal R ² of climatic variables, after accounting for niche variable
Birds					
Prec niche breadth	0.67	0.26	0.03	0.05	0.19
Range filling	0.12†	0.07†	<0.01	0.48	0.71
Prec niche position	0.30	<0.01	NS	0.18	0.83
Prec availability	0.37†	0.05†	<0.01†	0.14	0.46
Mammals					
Prec niche breadth	0.65	0.22	0.03	0.04	0.11
Range filling	0.04†	0.03†	<0.01	0.45	0.70
Prec niche position	0.01	<0.01	<0.01†	0.46	0.72
Prec availability	0.28†	0.19†	<0.01	0.20	0.46

APPENDICES CHAPTER 4

Appendix S4.1

To test whether species richness seasonally tracks the environment because individual species do, we measured overlap between migratory species' environmental niches between two seasons in the Americas and we tested whether this overlap is (a) higher than if the species had migrated to the geographic range of a randomly chosen species (i.e. independently of the environmental niche occupied in the previous season), and (b) higher than if the species had not migrated. We used seven measures of overlap (Table S4.1) to ensure that our conclusions do not depend on the specific measure used. We found that all measures of overlap considered lead to the same qualitative conclusions. We presented the results for two of the measures in the main text; integral overlap and integral nestedness. Here, we also present results for breadth overlap and breadth nestedness (Table S4.1), which are similar but with the advantages that they do not rely on parameters estimated from a fitted models, and that all 625 species can be included. The disadvantage is that absences are not considered. Additionally, because one end of the species' environmental niche (e.g. low temperatures) could be generally tracking seasonal climate more closely than the other (e.g. high temperatures), we also included two measures of skewness in the overlap (Table S4.1).

Here, we present the results for the measures of overlap that we did not present in the main text as well as skewness in overlap. We found that the occupied environmental niche of a species only partially overlaps in the two seasons, although one is nearly always nested within the other (Fig. S4.1). Occupancy modelled by a Gaussian model for season 1 was typically positively correlated with the modelled occupancy for season 2, although almost never strongly so (Fig. S4.1). Similarly, niche agreement, measured by the AUC of a model for one season

tested on the other season, was generally relatively low (Fig. S4.1): model performance decreases substantially when predictions are made in the other season. The non-overlapping portions of the temperature niches between the two seasons were typically slightly larger at low than at high temperatures, meaning that the warm end of the niche tends to track more closely between seasons than the cold end (Fig. S4.2). No such trend was observed for the enhanced vegetation index (EVI; Fig. S4.2).

Most importantly, the observed temperature niche overlap was no better than expected under our null model (Fig. S4.3). For most measures of niche overlap, the quantiles were frequently very high, indicating that the species' seasonal niche overlap was not higher than its overlap with other species' niches (Fig. S4.3). Additionally, most species would conserve very similar environmental niche overlap if they were to stay year-round in the range they occupy from May to July (Fig. S4.4) or from December to February (Fig. S4.5).

Richness could track additional environmental variables, apart from temperature and EVI. When fitting our richness–environment relationship, and showing its congruence between seasons, we found that, in addition to temperature and EVI, precipitation and the standard deviation (SD) of temperature were also sometimes retained in the best performing richness–environment models. We find that the seasonal change in richness can be predicted by the seasonal change in temperature and EVI with an R^2 of 0.62 (Fig. S4.6). This shows that richness really does temporally track these environmental variables (or variables strongly correlated with them), and that they account for most of the variability in the change in richness. Residuals are, however, highly spatially autocorrelated (Moran's $I = 0.9$). In principle, this could indicate that some spatially-structured environmental variables have not been accounted for. Including the seasonal change in precipitation and temperature SD, along with temperature and EVI, and their

interactions in a linear model increases the R^2 to 0.76 (Fig. S4.6). The inclusion of precipitation and temperature SD also corrects for the lack of fit in the relationship (Fig. S4.6). However, the residuals remain highly spatially autocorrelated (Moran's $I = 0.85$). Fitting the seasonal change in richness with a simultaneous autoregressive error model can eliminate residual spatial autocorrelation and improve model fit (Fig. S4.6). Moran's I and SAR models were calculated with the 'spdep' package in R (Bivand, 2013 <http://CRAN.R-project.org/package=spdep>) following Kissling & Carl (2007) with a neighbourhood of 1.5 such that the 8 quadrats adjacent to the focal quadrat are included in the local neighbourhood. Modelling the proportional seasonal change in species richness, rather than the raw values, gives very similar results (Fig. S4.6). Altogether, these results suggest that the environmental variables in our models account for autocorrelation at the characteristically broad extents over which climate varies and that the residual spatial autocorrelation is not mainly due to other spatially-structured environmental variables. Rather, it seems like localized autocorrelation remains, probably due to intrinsic population processes.

To account for the fact that richness may also track precipitation and the yearly standard deviation in temperature, we also measured niche overlap between seasons for these additional environmental variables that richness may also track. Here, we present the results of all our measures of overlap (Table S4.1) for precipitation and the seasonal temperature SD. Our conclusions for those environmental variables are the same than the conclusions for temperature and EVI. Specifically, we find that niche overlap between seasons is typically low (Fig. S4.7, Fig. S4.8), no better than expected under our null model (Fig. S4.9, Fig. S4.10) and only slightly higher than if species had not migrated (Fig. S4.11, Fig. S4.12, Fig. S4.13, Fig. S4.14).

Finally, to demonstrate that our results and conclusions are robust to the specific type of model used and are unaffected by the description of occupied environments in univariate space, we also fitted a MaxEnt model with four environmental variables for all species: temperature, EVI, precipitation and the standard deviation of temperature. We here present the seasonal overlap using the Bray-Curtis distances between MaxEnt suitability scores for all quadrats (see Rödder & Engler, 2011). The Bray-Curtis distances vary between 0 (no overlap) and 1 (complete overlap). This confirmed our findings that niche overlap between seasons is typically low (Fig. S4.15), no better than expected under our null model (Fig. S4.16) and generally not higher than if species had not migrated (Fig. S4.17). Although suffering less biases than some other metrics, Bray-Curtis distances are inflated by the inclusion of a high number of grid cells where the species are absent because the species then share lots of unoccupied environmental space (Rödder & Engler, 2011). This could definitely be a concern in our data that span the entire Americas. However, we did not pre-process the data to eliminate low occurrence probabilities because it would result in (1) many species-season pairs being incomparable and (2) a varying sample size between comparisons. Note that using the measures of overlap that we could calculate from Table S4.1 also leads to the same conclusions.

Table S4.1 Measures of environmental niche overlap. We present the names of these measures as they are used in the text, along with a short description. For breadth similarity, breadth nestedness, integral similarity and integral nestedness, measures range from 0 to 1, with 0 representing no niche overlap and 1 complete niche overlap. The correlation coefficient can range between -1 and 1; -1 being perfect negative correlation between model predictions from the two seasons, 0 no correlation and 1 perfect positive correlation. For the AUC tested on season 1 and on season 2, values below 0.5 indicate that the overlap is poorer than random. Measures of skewness (breadth skewness and integral skewness) range from 0 to 1, with values below 0.5 meaning that the non-overlapping portion of the niche tends to be at low environmental values whereas values above 0.5 mean that non-overlapping portion of the niche is at high environmental values. The example refers to calculated niche overlap values for *Accipiter cooperii* (see Figure 1 in the main text).

Measure of niche overlap	Description	Example
Breadth similarity	Proportion of the total environmental space occupied in either season that is shared in both season	0.61
Breadth nestedness	Proportion of the environmental space occupied in a season that is nested within the environmental space occupied in the other season	0.88
Breadth skewness	Proportion of the environmental space not shared between the season that is at low environmental values	0.81
Integral similarity	Proportion of the total area under the fitted curve in either season that is shared in both season	0.14
Integral nestedness	Proportion of the total area under the fitted curve of a season that is nested within the fitted curve of the other season	0.46
Integral skewness	Proportion of the area under the fitted curve not shared between the seasons that is at low environmental values	0.81
Correlation coefficient	Correlation coefficient of a Spearman rank correlation between the predicted values of the models of the two seasons	0.45
AUC tested on season 2	Area under the receiver operating characteristic curve (AUC) of the model fitted for season 1 and evaluated on season 2	0.46
AUC tested on season 1	Area under the receiver operating characteristic curve (AUC) of the model fitted for season 2 and evaluated on season 1	0.59

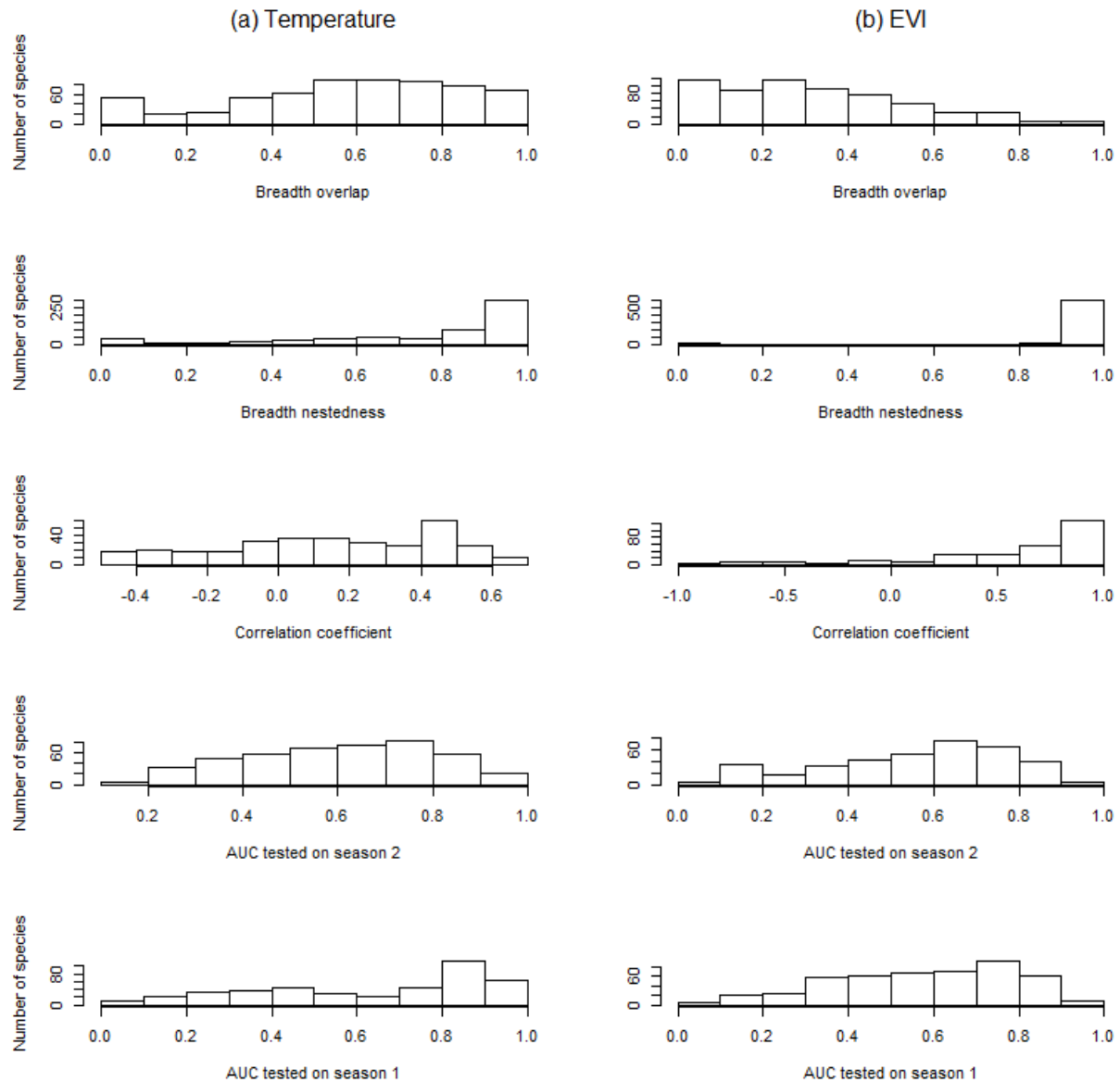


Figure S4.1 Distribution among species of five different measures of environmental niche overlap between May to July and December to February for (a) temperature and (b) enhanced vegetation index (EVI). In all cases, bottom-up hypotheses of species richness predict high occupied niche overlap between seasons, i.e. values close to 1. For breadth overlap, breadth nestedness, AUC tested on season 1 and AUC tested on season 2, values of 0 indicate no niche overlap, while values of 1 represent perfect niche overlap between seasons. By definition, breadth nestedness will always be equal or higher than breadth overlap (Table S4.1). The

correlation coefficient can range between -1 and 1; -1 being perfect negative correlation between model predictions from the two seasons, 0 no correlation and 1 perfect positive correlation. For the AUC tested on season 1 and on season 2, values below 0.5 indicate that the overlap is poorer than random.

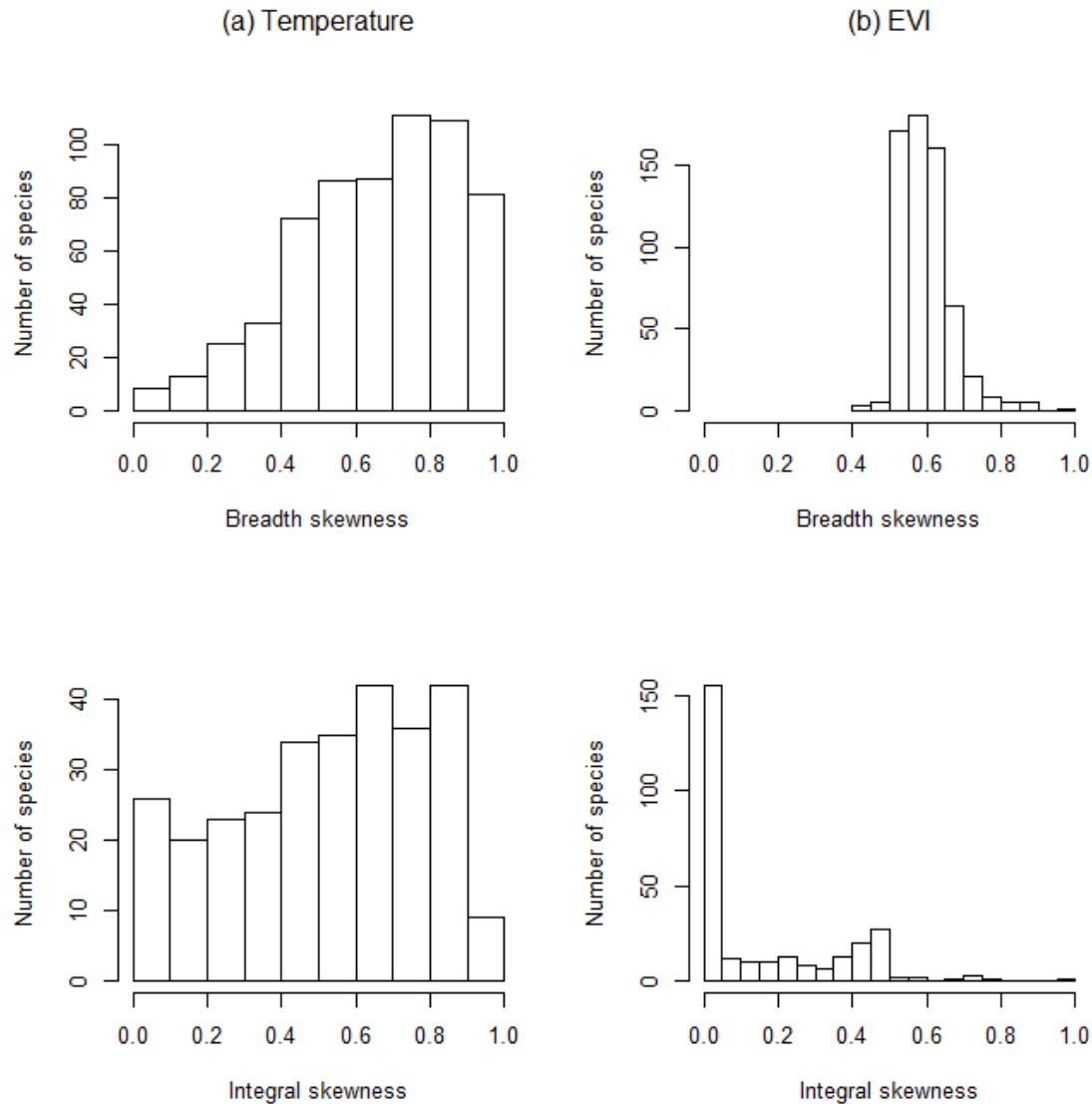


Figure S4.2 Distribution among species of two measures of skewness in niche overlap between seasons; integral skewness and breadth skewness. The skewness in environmental niche overlap was measured for (a) temperature and (b) enhanced vegetation index (EVI). Values below 0.5 mean that the non-overlapping portion of the niche tends to be at low environmental values, i.e. that the warm or more productive end of the niche is more closely conserved between seasons. Inversely, values above 0.5 mean that non-overlapping portion of the niche is at high environmental values.

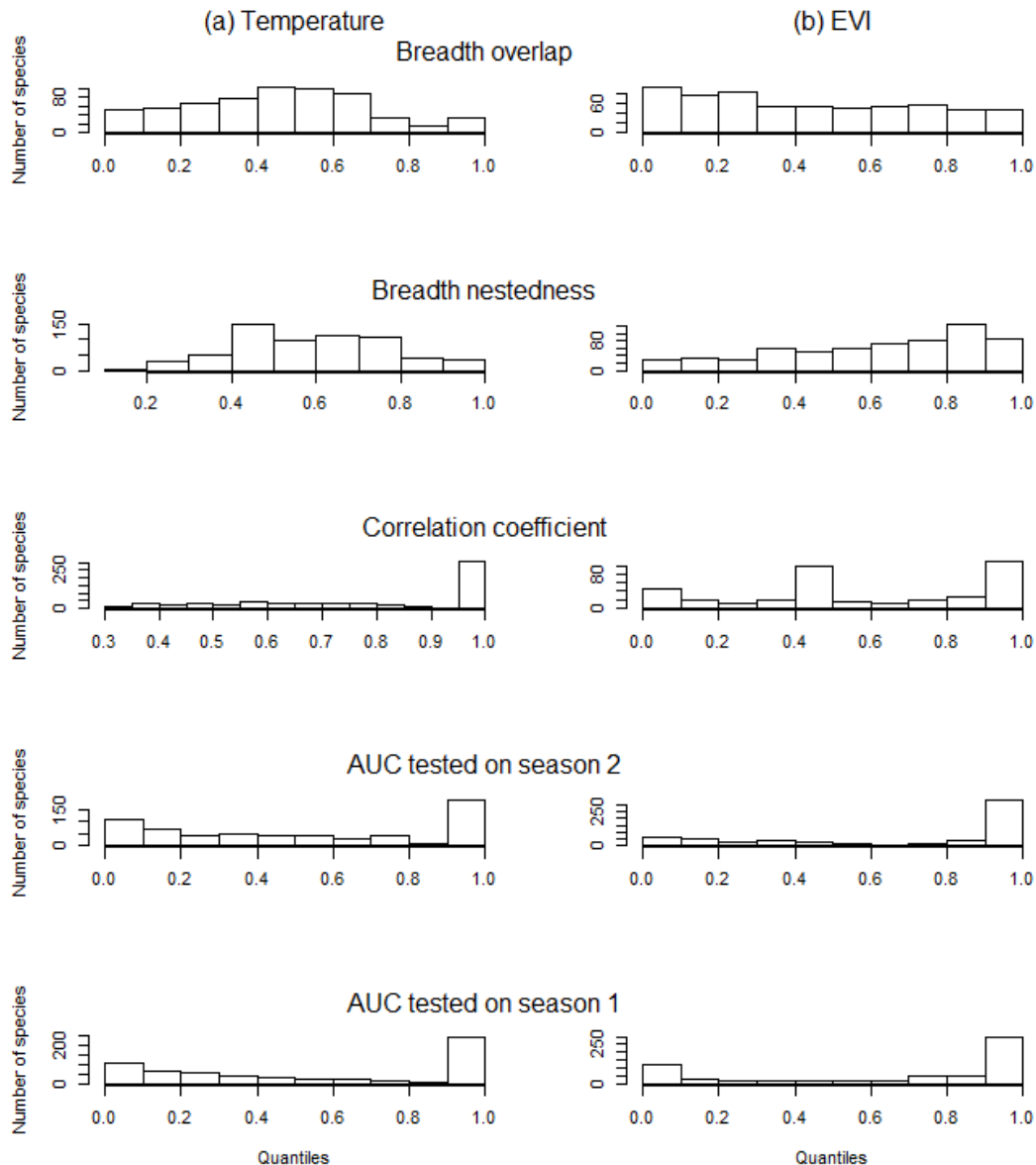


Figure S4.3 Distribution of quantiles among species under the null hypothesis that species migrate independently of their occupied environmental niche in a given season (i.e., by occupying the off-season range of a randomly chosen species, versus than their own off-season range). In all cases, low values indicate a higher niche overlap then predicted under the null hypothesis and therefore in accordance with bottom-up hypotheses of species richness. This is shown for (a) temperature and (b) enhanced vegetation index (EVI). We calculated the quantiles for a given species A by first calculating the climatic overlap between its geographic

distributions in the two seasons. We then calculated the overlap of the climatic niche of species A in one season with the climatic niches of every other species in the opposite season. The value of the quantile is the proportion of species in the opposite season for which the range overlap is equal to or greater than the observed seasonal range overlap for species A. The quantiles are calculated for five different measures of niche overlap (see Table S4.1).

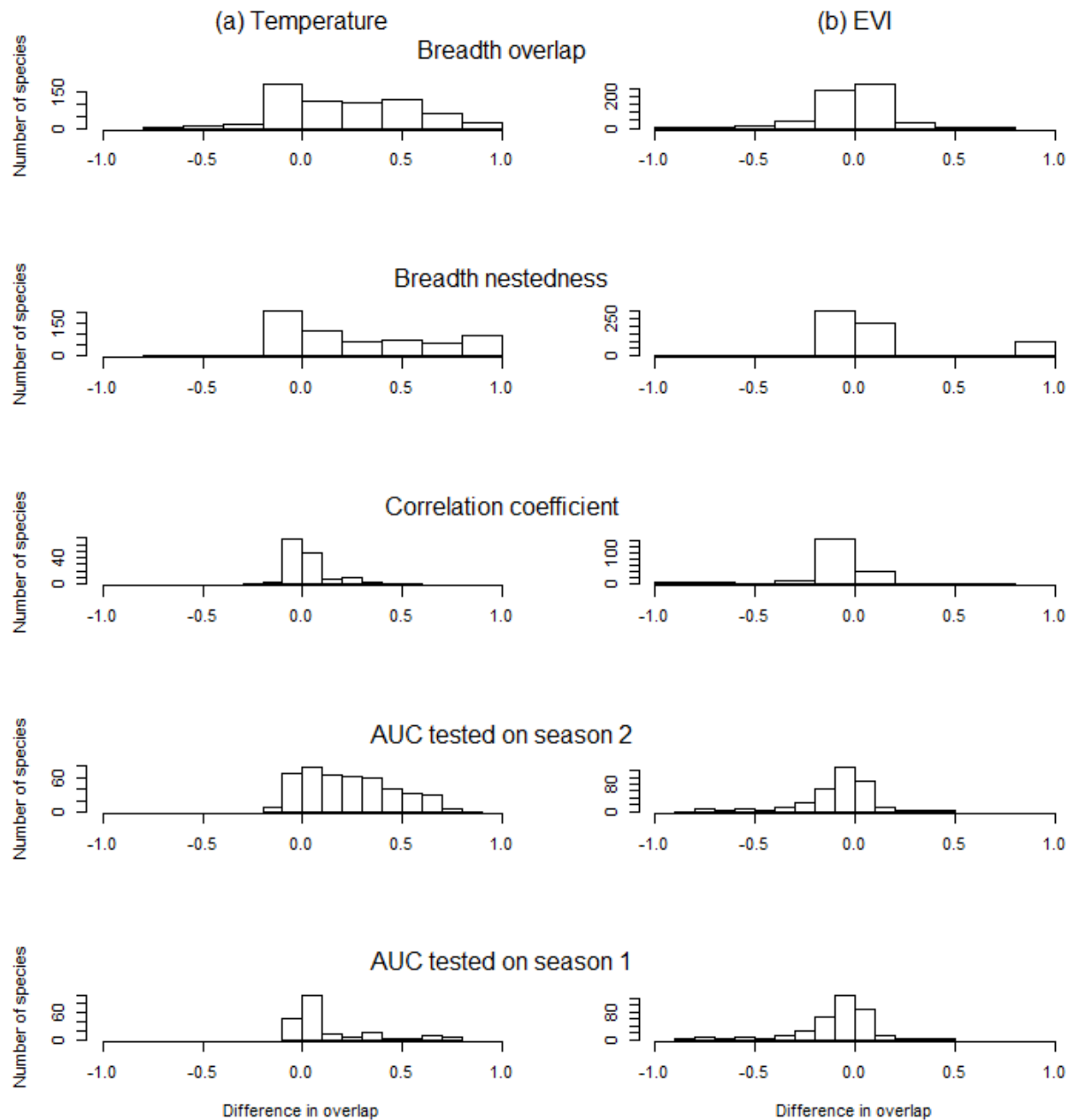


Figure S4.4 Distribution of the differences in temperature niche overlap if migratory species had stayed year round in the range they occupy from May to July instead of migrating. If species migrate to track their environmental niche, positive values are predicted. Results are presented for (a) temperature and (b) enhanced vegetation index (EVI) and five measures of overlap (see Table S4.1).

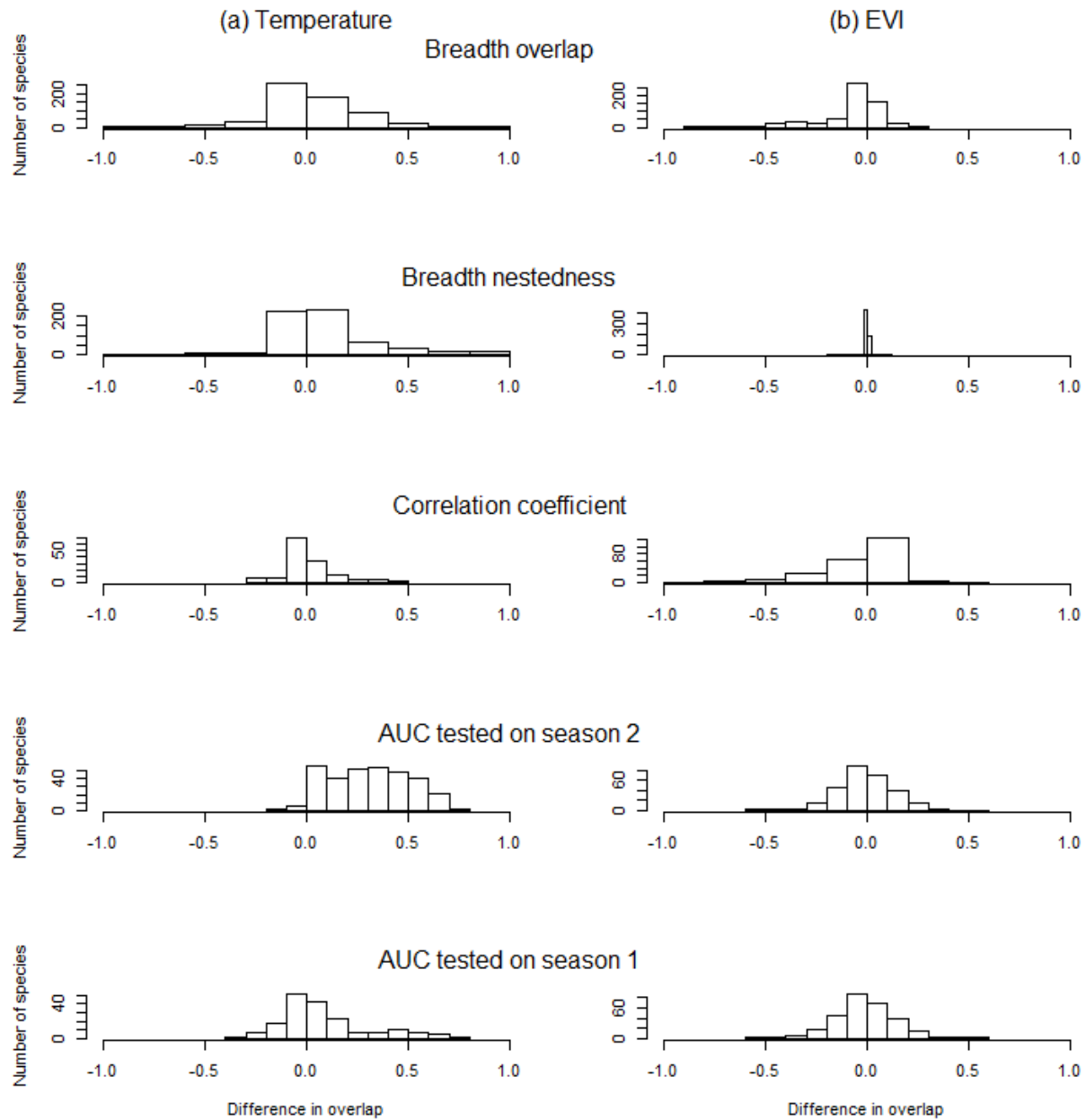


Figure S4.5 Distribution of the differences in temperature niche overlap if migratory species had stayed year round in the range they occupy from December to February instead of migrating. If species migrate to track their environmental niche, positive values are predicted. Results are presented for (a) temperature and (b) enhanced vegetation index (EVI) and five measures of overlap (see Table S4.1).

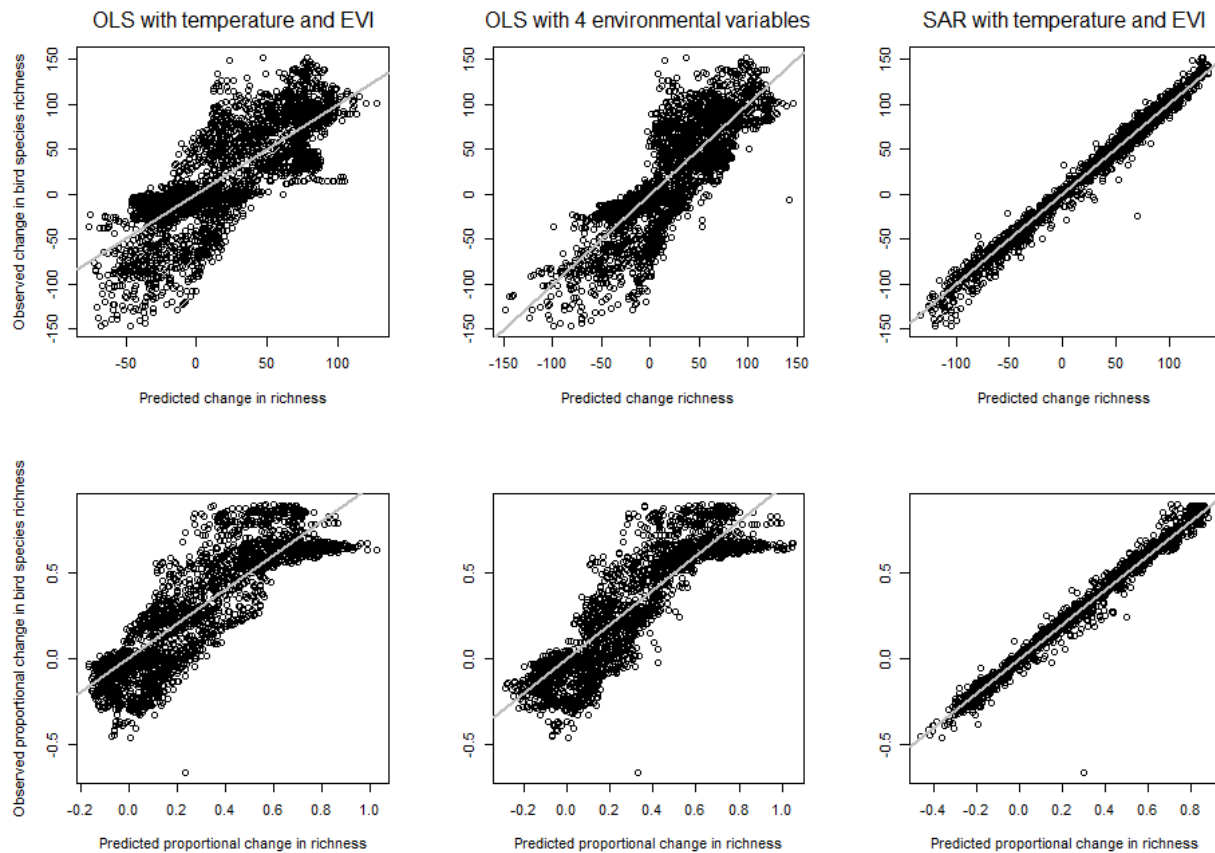


Figure S4.6 Observed seasonal change in bird species richness as a function of the change in richness predicted by the seasonal change in environment. Left panel: richness is predicted by mean annual temperature and enhanced vegetation index (EVI) in a linear regression model. Middle panel: richness is predicted by temperature, EVI, the standard deviation of temperature and precipitation in a linear regression model. Right panel: richness is predicted by temperature and EVI in a simultaneous autoregressive error model, with a neighborhood of 1.5. Top row: models are fitted on the raw seasonal change in richness data, i.e. richness in season 1 minus richness in season 2. Bottom row: models are fitted on the proportional seasonal change in richness, i.e. the raw change in richness is divided by the total richness in both seasons. The 1:1 lines are shown in gray.

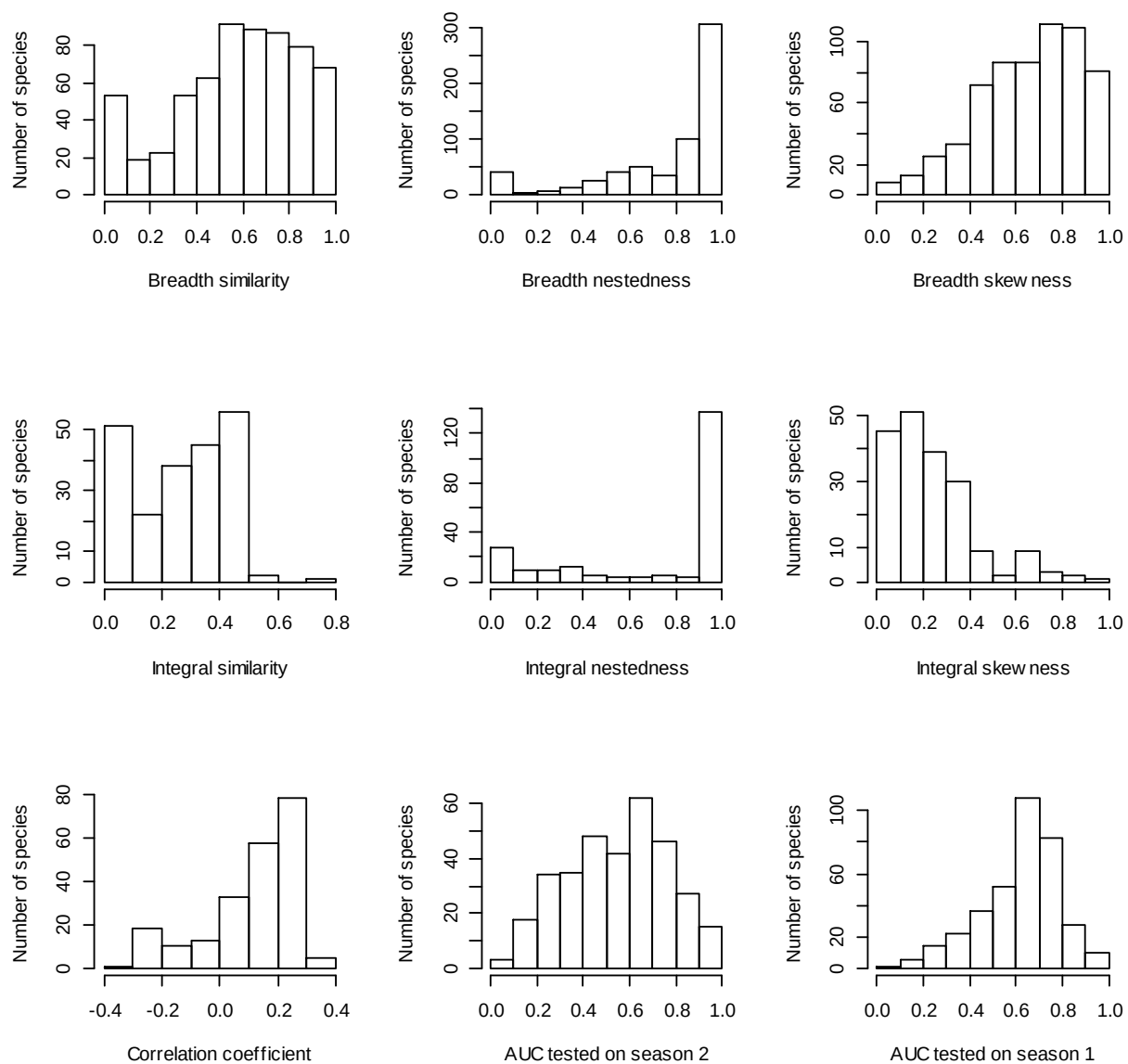


Figure S4.7 Distribution among species of the different measures of precipitation niche overlap between May to July (Season 1) and December to February (Season 2), see Table S4.1.

Generally, high values indicate that species track their precipitation niche between seasons as predicted by bottom-up hypotheses of species richness. The exception is for breadth skewness and integral skewness where high values indicate that the wet end of the niche is more closely conserved between seasons, while low values mean that the dry end is more conserved.

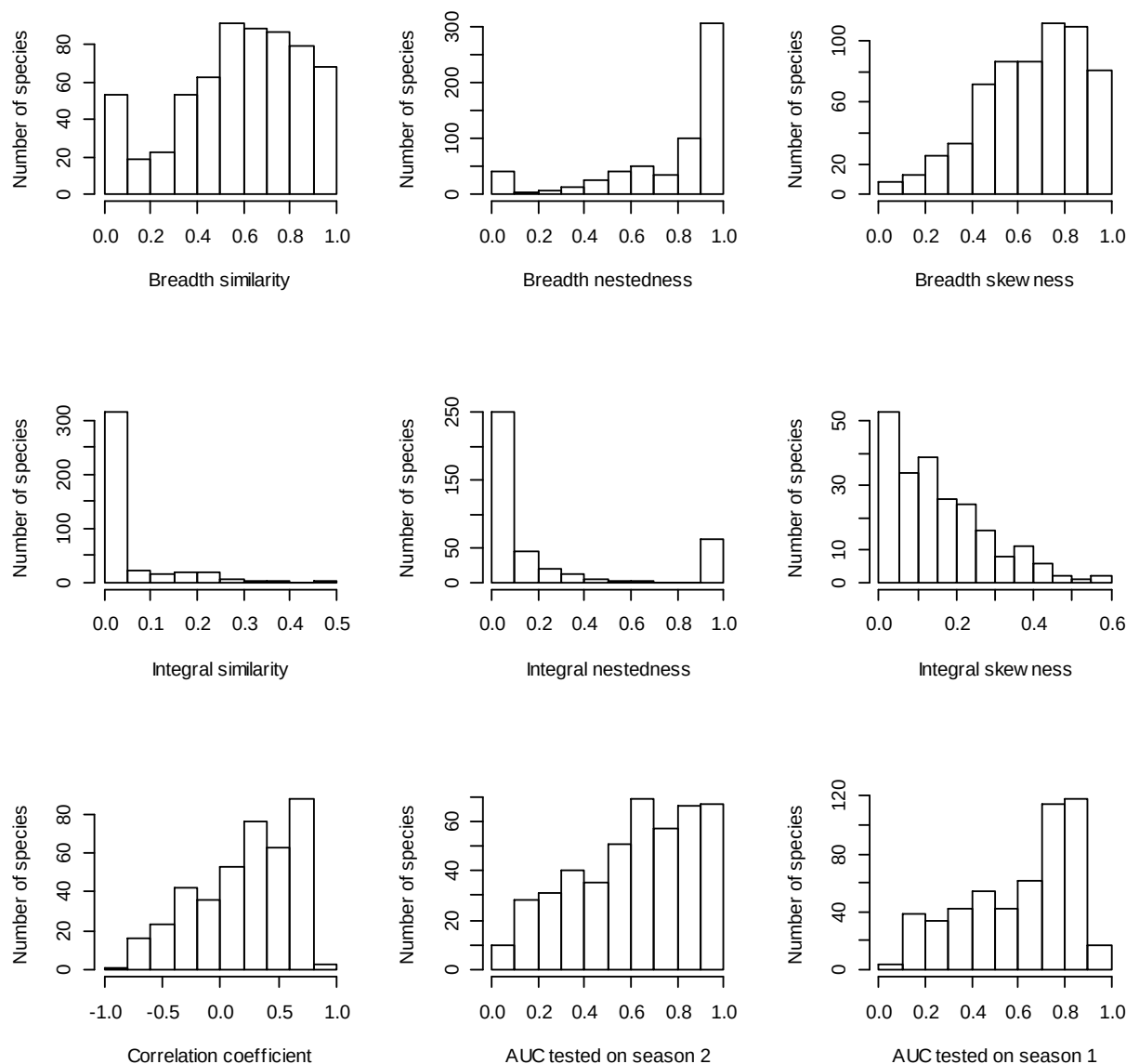


Figure S4.8 Distribution among species of the different measures of niche overlap in the standard deviation in temperature between May to July (Season 1) and December to February (Season 2), see Table S4.1. Generally, high values indicate that species track their precipitation niche between seasons as predicted by bottom-up hypotheses of species richness. The exception is for breadth skewness and integral skewness where high values indicate that the highly seasonally variable end of the niche is more closely conserved between seasons, while low values mean that the least variable end of the niche is more conserved.

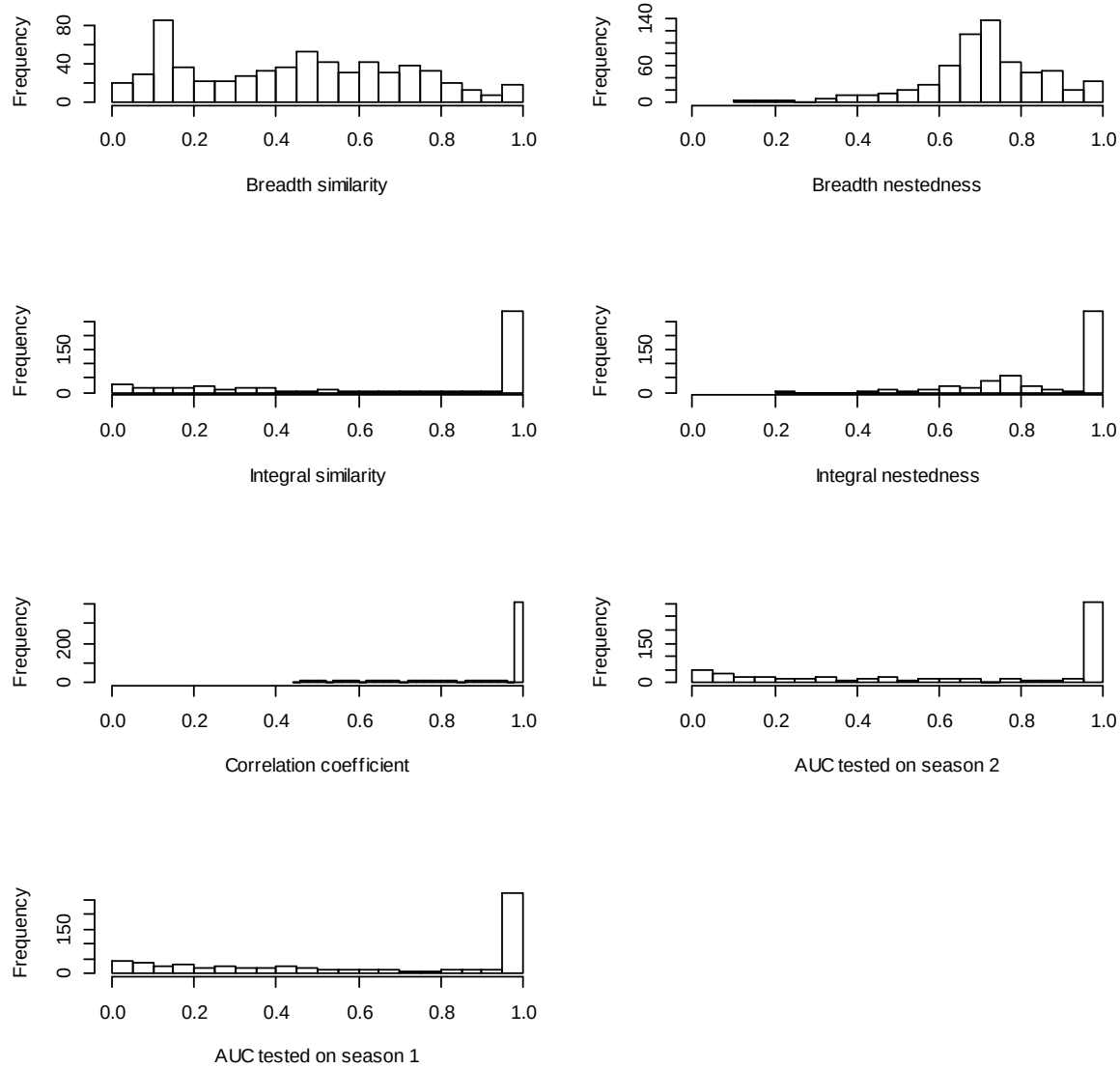


Figure S4.9 Distribution among species of the quantiles of range overlap for different measures of precipitation range overlap between seasons, see Table S4.1. For a given species, the value of the quantile is calculated as the proportion of species in the opposite season for which the range overlap is equal to or greater than the observed seasonal range overlap for the species. Bottom-up hypotheses of species richness predict that species temporally track their own occupied niche more than the niches occupied by other species, hence low quantiles values are predicted.

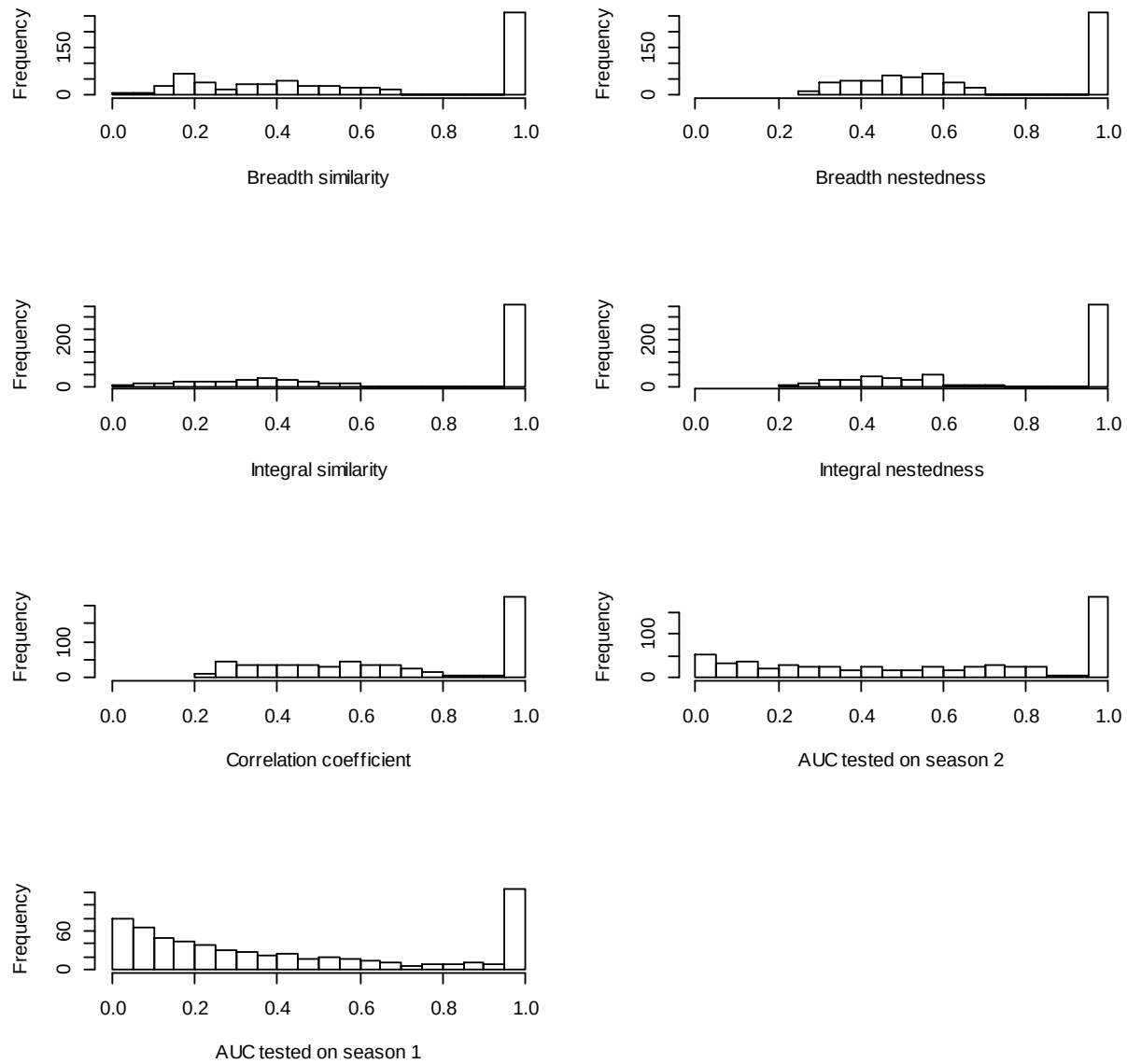


Figure S4.10 Distribution among species of quantiles of overlap for different measures of seasonal range overlap in the standard deviation of temperature. For a given species, the value of the quantile is calculated as the proportion of species in the opposite season for which the range overlap is equal to or greater than the observed seasonal range overlap. Low values are predicted from bottom-up hypotheses of species richness.

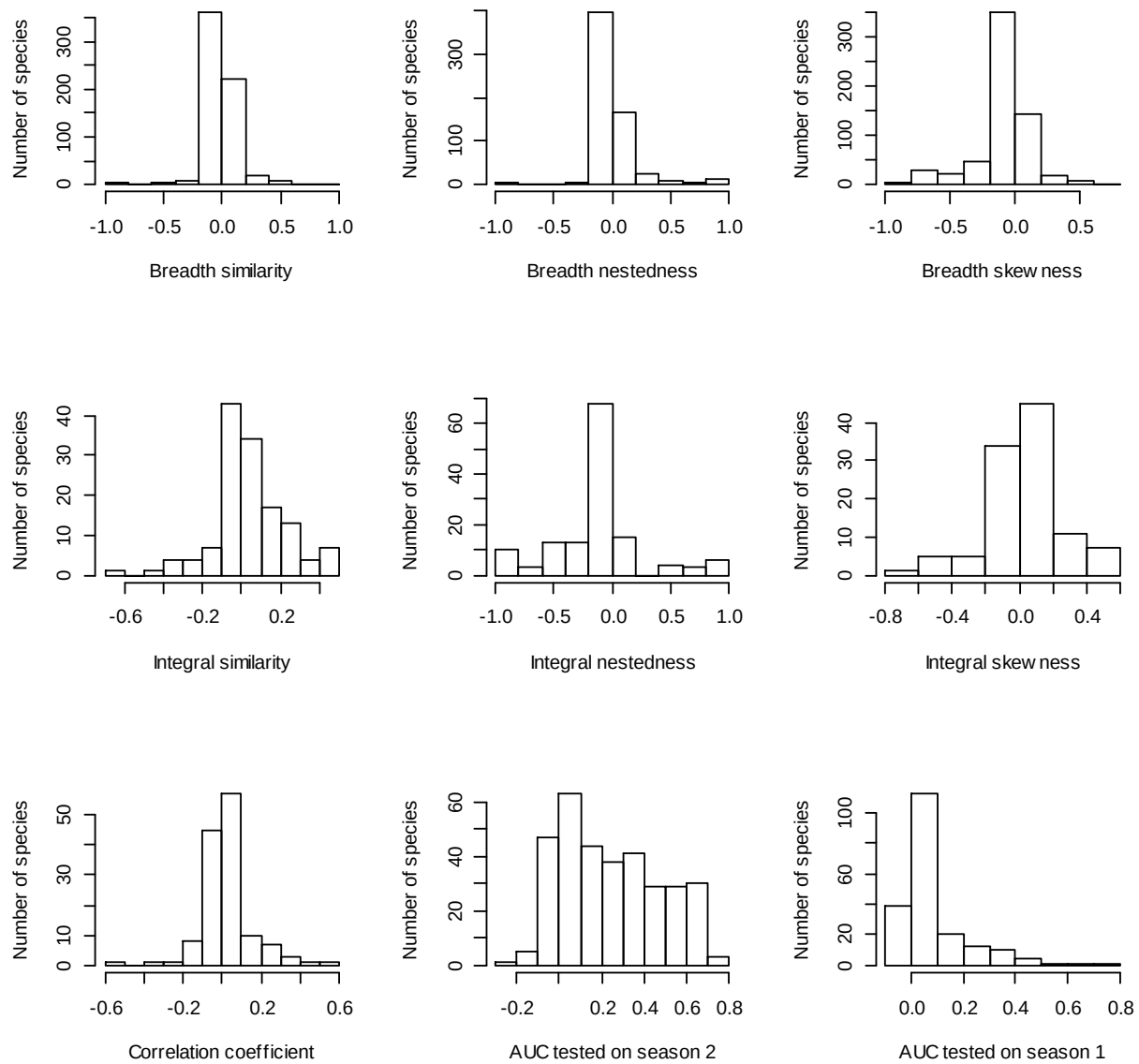


Figure S4.11 Distribution among species of the differences in precipitation niche overlap if migratory species had stayed year round in the range they occupy from May to July instead of migrating. Bottom-up hypotheses of species richness predict that species maintain higher niche overlap by migrating, hence positive values are predicted.

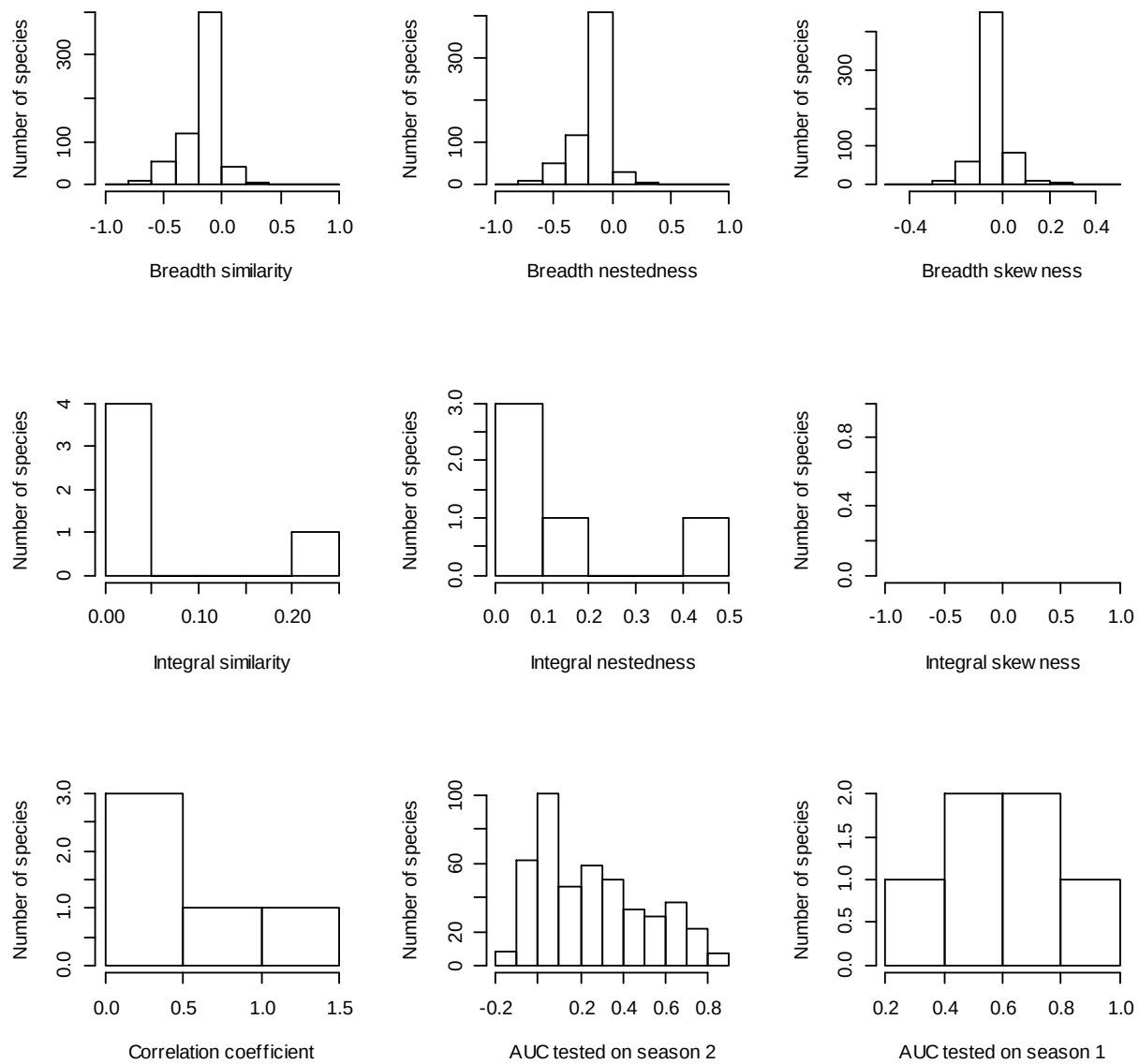


Figure S4.12 Distribution of the differences in niche overlap for the standard deviation of seasonal temperature if migratory species had stayed year round in the range they occupy from May to July instead of migrating. Bottom-up hypotheses of species richness predict that species maintain higher niche overlap by migrating, hence positive values are predicted.

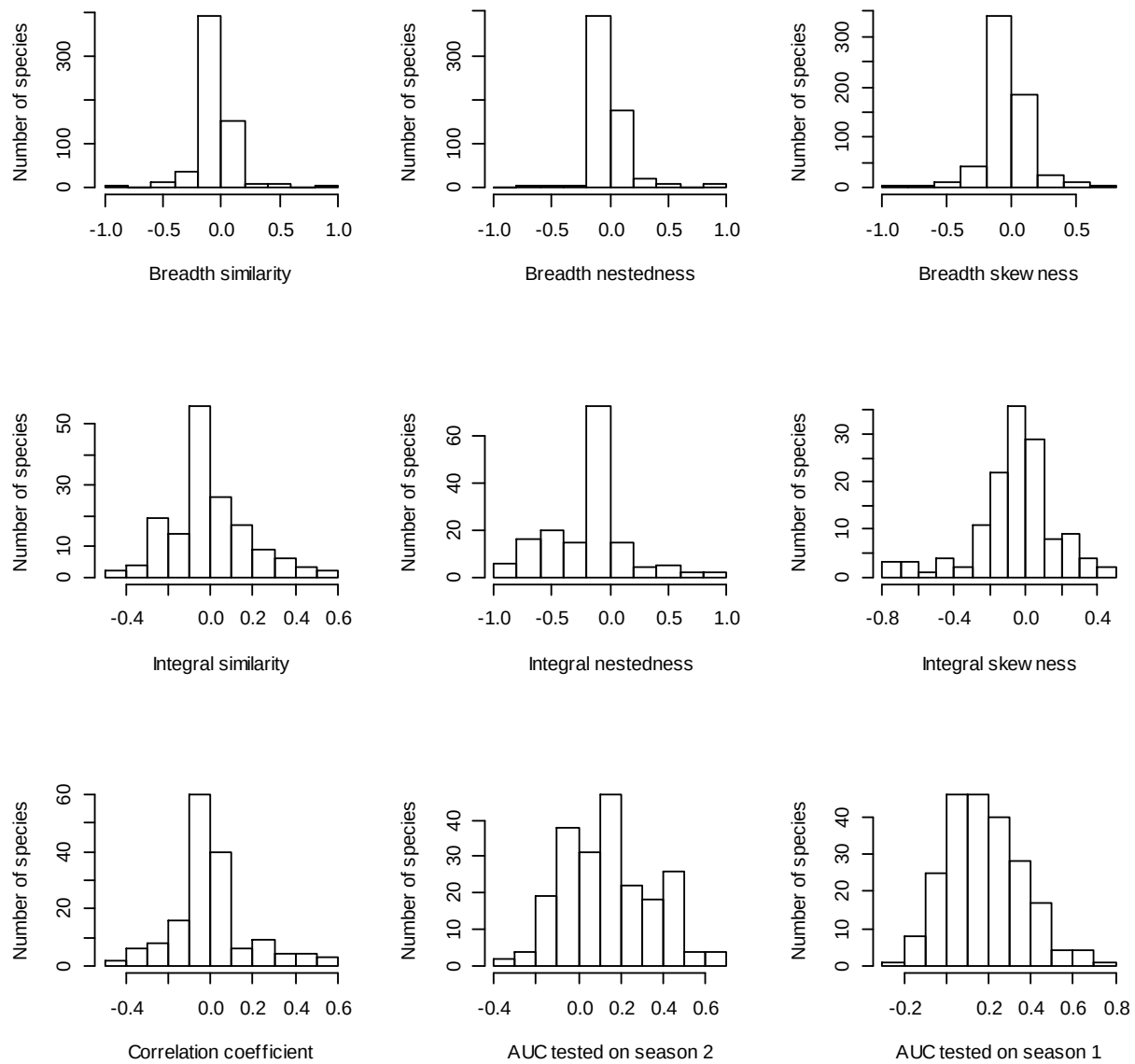


Figure S4.13 Distribution of the differences in precipitation niche overlap if migratory species had stayed year round in the range they occupy from December to February instead of migrating. Bottom-up hypotheses of species richness predict that species maintain higher niche overlap by migrating, hence positive values are predicted.

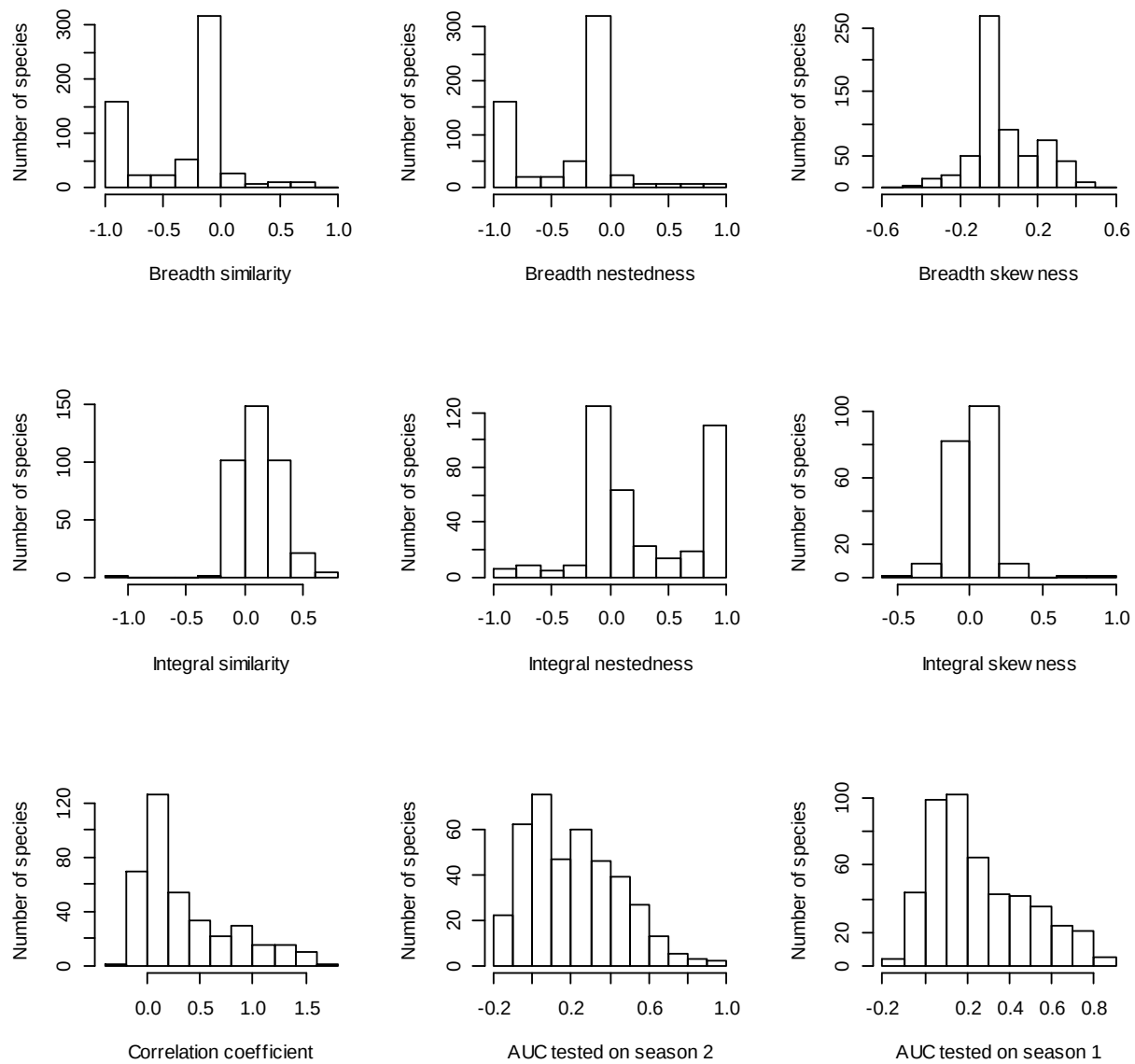


Figure S4.14 Distribution of the differences in niche overlap for the standard deviation of seasonal temperature if migratory species had stayed year round in the range they occupy from December to February instead of migrating. Bottom-up hypotheses of species richness predict that species maintain higher niche overlap by migrating, hence positive values are predicted.

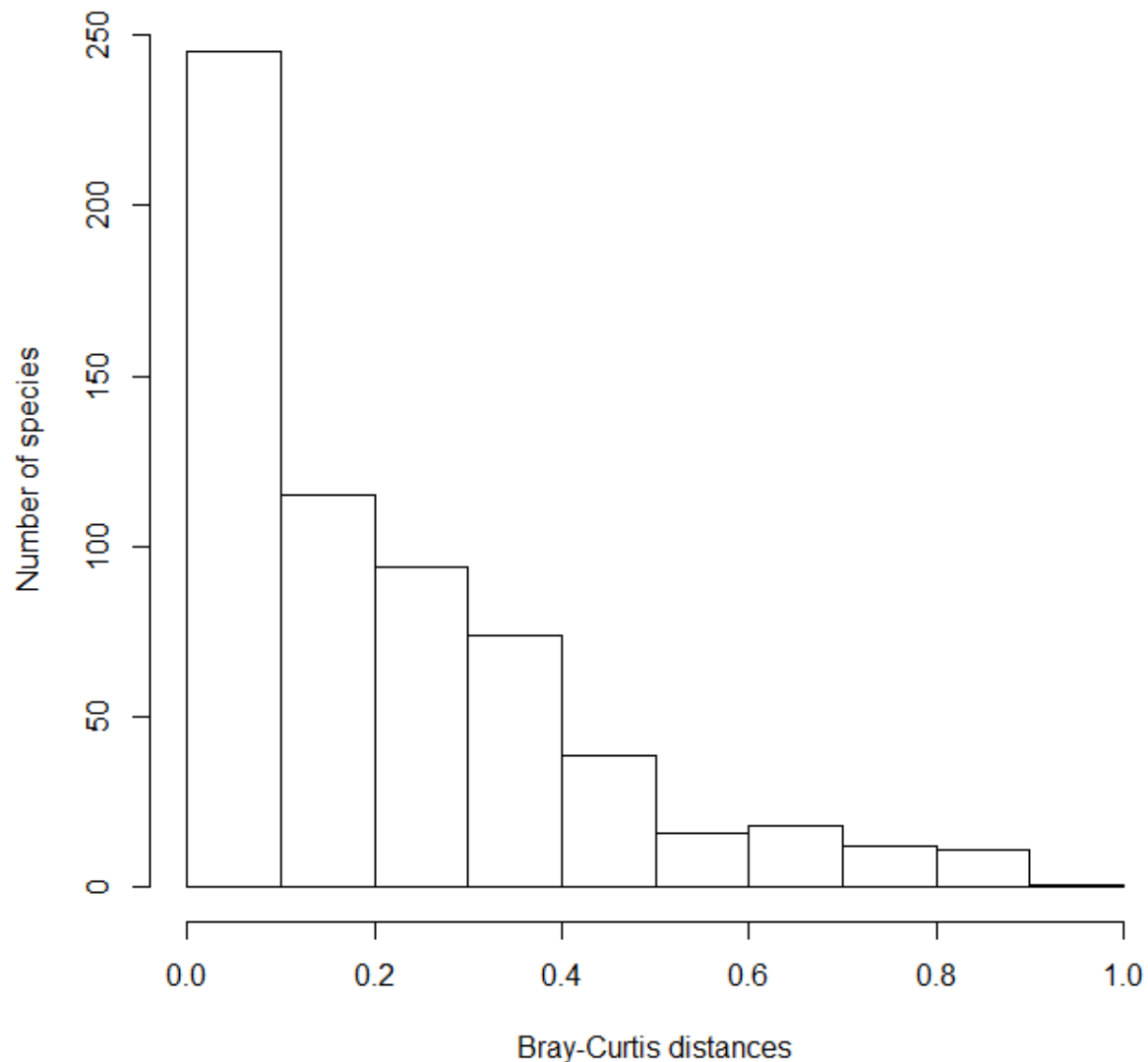


Figure S4.15 Frequency distribution among species seasonal overlap between occupied climatic niches. The climatic niche is here modelled by MaxEnt where temperature, enhanced vegetation index (EVI), precipitation and the standard deviation of temperature are included in the model. Seasonal niche overlap is measured by the Bray-Curtis distance between predicted suitability scores for all quadrats in both season. The Bray-Curtis distance can vary between 0 (no overlap) and 1 (full overlap). Bottom-up hypotheses of species richness predict that species occupied environmental niches should be similar between seasons, hence values close to one are predicted.

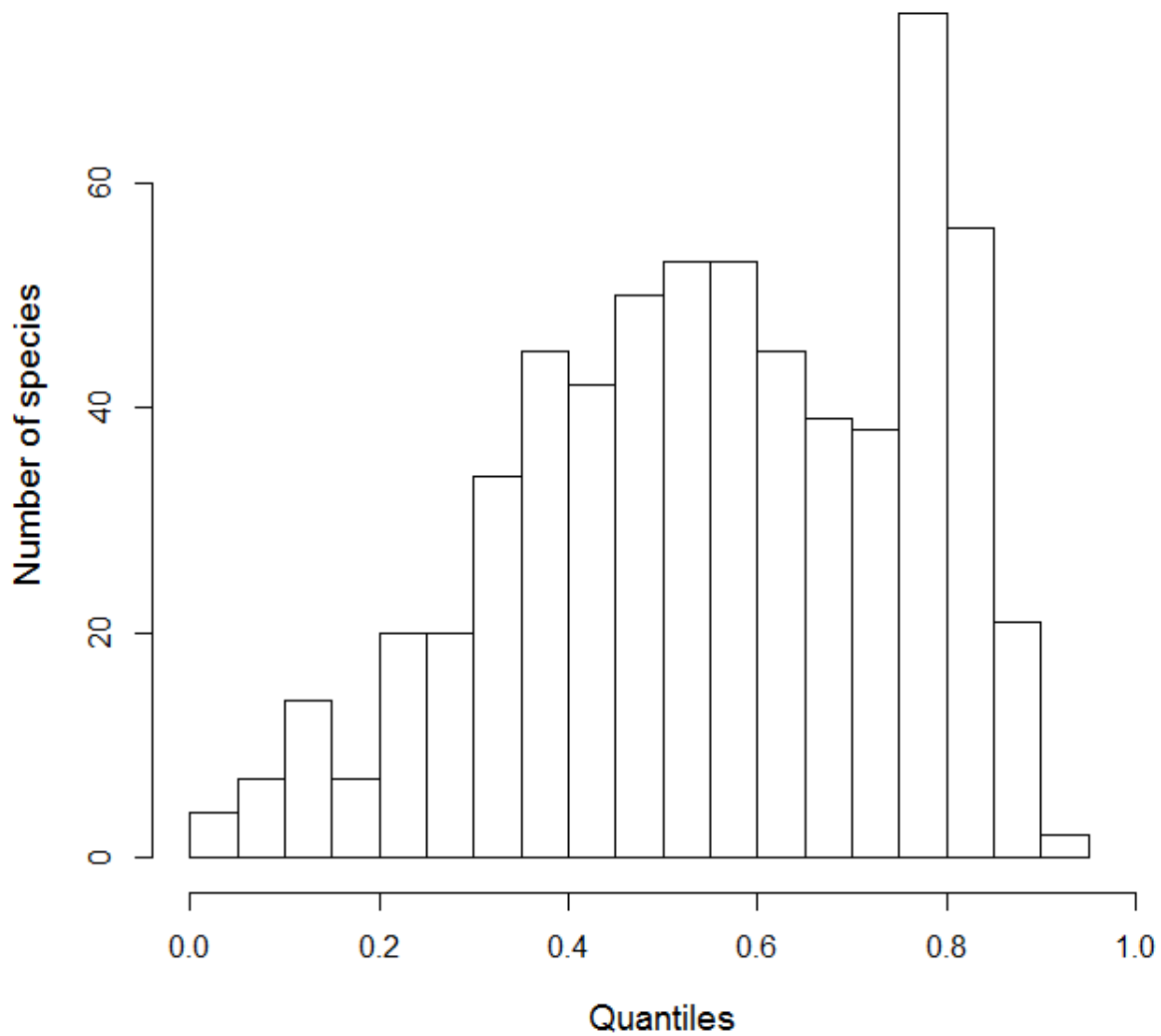


Figure S4.16 Frequency distribution among species of the quantiles of occupied niche overlap estimated from MaxEnt models. We tested whether the environment in a species' pre-migration range is more similar to the conditions in its own post-migration range than to the conditions in the ranges occupied by other species post-migration. For a given species, the quantile is calculated as the proportion of species for which the occupied environmental overlap is equal to or greater than the observed overlap for the species, hence bottom-up hypotheses of species richness predict low quantile values. Niche overlap is here calculated as the Bray-Curtis distance between predicted MaxEnt suitability scores for all quadrats in both seasons.

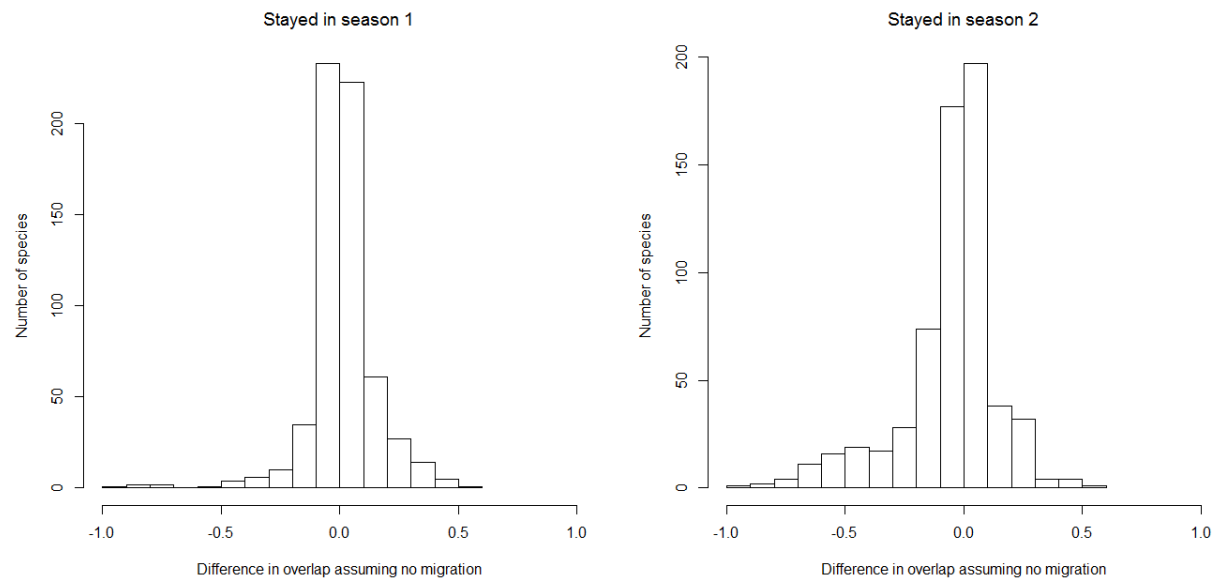


Figure S4.17 Frequency distribution of the difference in seasonal niche overlap with migration minus the overlap that would have been observed if species had stayed year-round in the geographic range they occupy from May to July (season 1; left panel) or from December to February (season 2; right panel). Overlap in species climatic niche is measured by the Bray-Curtis distance between suitability scores predicted from MaxEnt models. Positive values represent an increase in climatic niche overlap with migration as predicted by bottom-up hypotheses of species richness whereas negative values indicate that a higher climatic niche overlap would have been observed without migration. On average, species increase their niche overlap by migrating away from their May to July range (mean= 0.013, $P= 0.03$) but decrease their overlap by migrating away from their December to February geographic range (mean= - 0.057, $P< 0.01$).

APPENDICES CHAPTER 5

Appendix S5.1

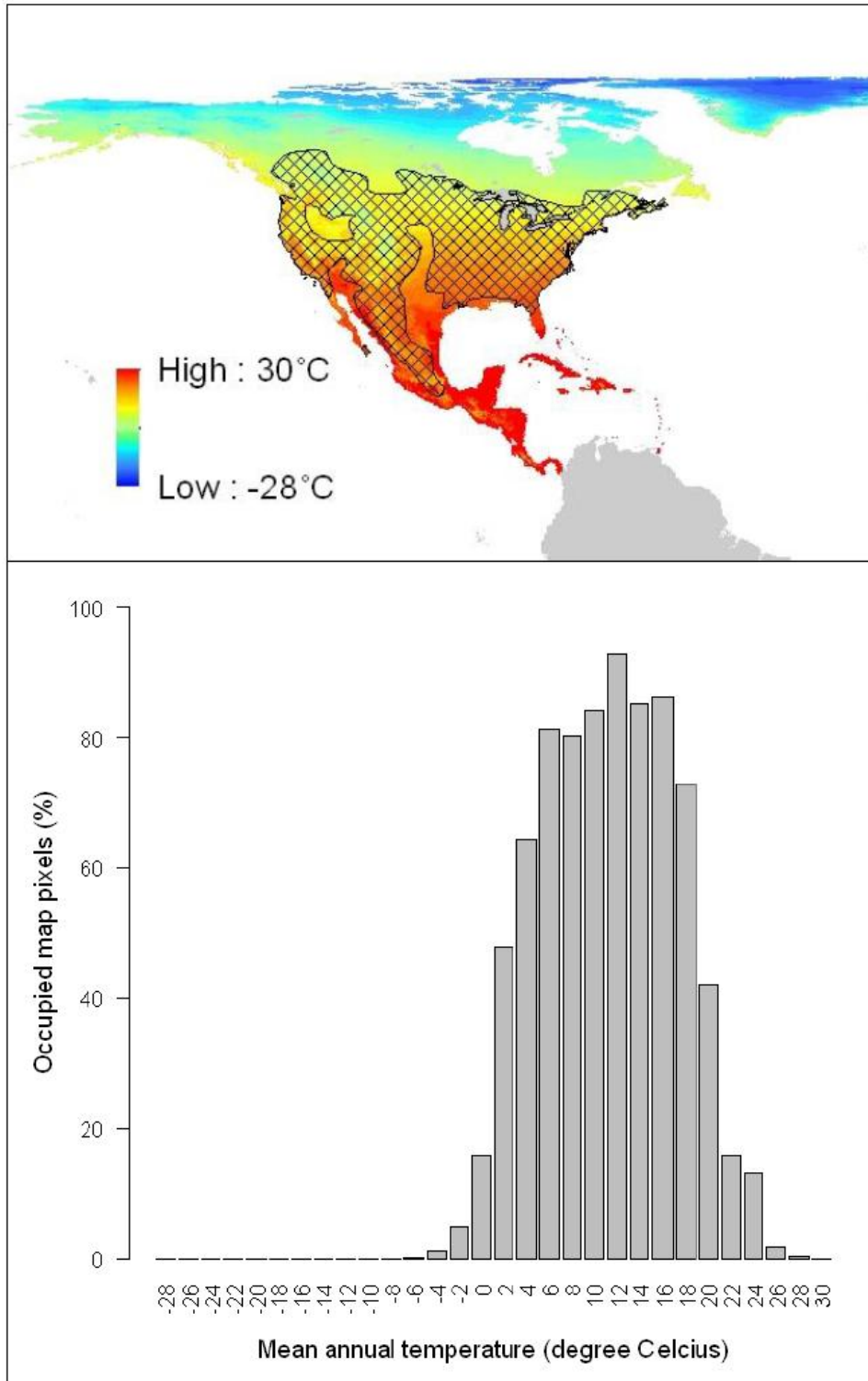


Figure S5.1 An example of the determination of the maximally occupied temperature for *Sitta carolinensis* (White-breasted Nuthatch). Top panel: the breeding range of *S.carolinensis* (black grid) layered over a map of North America, where the average annual temperature has been binned by 2° C. The map is in Behrmann projection. Bottom panel: bar graph of *S.carolinensis*' relative occupancy of each temperature bin, i.e. the proportion of the pixels in a given temperature bin that fall within *S.carolinensis*' breeding range. Here the temperature optima is 12° C.

APPENDICES CHAPTER 6

Appendix S6.1

Table S6.1 Bird families used in the study, along with the number of species per family (N) breeding in the Americas based on NatureServe (Ridgely *et al.* 2003), the slope and standardized slope of species richness as a function of mean annual temperature and the estimated earliest and latest origin based on Benton (1993). For both the earliest and latest possible origin, we present the median temperature of the period from several proxies: Romdal *et al.* (2013) paleoclimatic categories, Cramer *et al.* (2011) temperature reconstructions in degree Celcius, Crowley and Berner (2001) global and tropical temperature anomalies in degree Celcius and Zachos *et al.* (2001) inverse of $\delta^{18}\text{O}$ in perthousand.

	Family	N	Slope richness ~ temperature	Slope standardized richness ~ temperature	R ²
1	Accipitridae	49	0.54	0.05	0.57
2	Alcidae	4	0.00	-0.01	0.01
3	Anatidae	28	0.13	0.04	0.28
4	Anhimidae	3	0.02	0.05	0.40
5	Anhingidae	1	0.03	0.05	0.57
6	Apodidae	30	0.12	0.05	0.44
7	Aramidae	1	0.02	0.05	0.43
8	Ardeidae	12	0.16	0.05	0.53
9	Bucconidae	35	0.16	0.04	0.37
10	Burhinidae	2	0.00	0.01	0.04
11	Capitonidae	14	0.02	0.03	0.15
12	Caprimulgidae	37	0.17	0.05	0.53
13	Cariamidae	2	0.01	0.02	0.12
14	Charadriidae	7	0.06	0.05	0.50
15	Ciconiidae	1	0.01	0.02	0.12
16	Cinclidae	3	0.00	-0.01	0.02
17	Columbidae	58	0.26	0.05	0.59
18	Corvidae	45	0.01	0.01	0.01
19	Cracidae	48	0.10	0.05	0.46
20	Cuculidae	26	0.22	0.06	0.60
21	Dulidae	1	0.00	0.00	0.00
22	Emberizidae	181	0.32	0.05	0.42
23	Eurypygidae	1	0.02	0.04	0.32
24	Falconidae	20	0.20	0.05	0.55
25	Furnariidae	281	0.73	0.05	0.47
26	Gaviidae	1	0.00	0.00	0.00
27	Haematopodidae	1	0.00	0.00	0.00

28	Hirundinidae	19	0.11	0.05	0.54
29	Icteridae	71	0.27	0.05	0.57
30	Jacanidae	2	0.03	0.05	0.57
31	Laridae	7	0.04	0.05	0.43
32	Momotidae	9	0.04	0.04	0.31
33	Motacillidae	10	0.02	0.02	0.07
34	Nyctibiidae	7	0.05	0.05	0.44
35	Opisthocomidae	1	0.01	0.04	0.24
36	Paridae	12	-0.02	-0.02	0.08
37	Phalacrocoracidae	3	0.00	0.00	0.00
38	Phasianidae	12	-0.04	-0.03	0.16
39	Phoenicopteridae	2	0.00	0.00	0.00
40	Picidae	114	0.27	0.05	0.58
41	Podicipedidae	6	0.03	0.03	0.17
42	Psittacidae	140	0.38	0.05	0.48
43	Psophiidae	3	0.01	0.03	0.19
44	Rallidae	42	0.15	0.05	0.42
45	Ramphastidae	35	0.11	0.04	0.36
46	Recurvirostridae	1	0.00	0.00	0.00
47	Rheidae	2	0.01	0.02	0.11
48	Rostratulidae	1	0.00	0.01	0.02
49	Scolopacidae	9	0.03	0.04	0.31
50	Sittidae	3	0.00	0.00	0.00
51	Steatornithidae	1	0.00	0.01	0.03
52	Strigidae	59	0.14	0.05	0.43
53	Sylviidae	15	0.05	0.05	0.43
54	Thamnophilidae	209	0.66	0.04	0.36
55	Thinocoridae	3	0.00	0.00	0.00
56	Timaliidae	1	0.00	0.00	0.00
57	Tinamidae	47	0.16	0.05	0.46
58	Todidae	3	0.00	0.00	0.00

59	Trochilidae	304	0.48	0.04	0.37
60	Troglodytidae	69	0.11	0.04	0.39
61	Trogonidae	25	0.10	0.04	0.37
62	Tyrannidae	336	1.35	0.05	0.50
63	Tytonidae	2	0.03	0.06	0.71
64	Vireonidae	33	0.10	0.05	0.43

Continued

Earliest estimated origin						
Origin		Romdal et al	Zachos et al.	Crowley & Berner		Cramer et al.
				Global	Tropical	
1	Lutetian	Warmest	-0.82	4.27	-0.45	10.92
2	Priabonian	Intermediate	-1.78	3.28	-0.57	6.95
3	Ypresian	Warmest	-0.16	5.00	-0.22	13.11
4	Ypresian	Warmest	-0.16	5.00	-0.22	13.11
5	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
6	Lutetian	Warmest	-0.82	4.27	-0.45	10.92
7	Rupelian	Intermediate	-2.53	2.81	-0.75	5.82
8	Bartonian	Warmest	-1.33	3.04	-0.52	8.45
9	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
10	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
11	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
12	Lutetian	Warmest	-0.82	4.27	-0.45	10.92
13	Rupelian	Intermediate	-2.53	2.81	-0.75	5.82
14	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
15	Upper Miocene	Coldest	-2.76	1.46	-0.45	3.31
16	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
17	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
18	Middle Miocene	Coldest	-1.98	2.30	-0.59	5.45
19	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95

20	Bartonian	Warmest	-1.33	3.04	-0.52	8.45
21	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
22	Upper Miocene	Coldest	-2.76	1.46	-0.45	3.31
23	Ypresian	Warmest	-0.16	5.00	-0.22	13.11
24	Ypresian	Warmest	-0.16	5.00	-0.22	13.11
25	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
26	Cenomanian	Warmest	NA	7.25	0.79	14.40
27	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
28	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
29	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
30	Rupelian	Intermediate	-2.53	2.81	-0.75	5.82
31	Priabonian	Intermediate	-1.78	3.28	-0.57	6.95
32	Rupelian	Intermediate	-2.53	2.81	-0.75	5.82
33	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
34	Bartonian	Warmest	-1.33	3.04	-0.52	8.45
35	Middle Miocene	Coldest	-1.98	2.30	-0.59	5.45
36	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
37	Priabonian	Intermediate	-1.78	3.28	-0.57	6.95
38	Priabonian	Intermediate	-1.78	3.28	-0.57	6.95
39	Lutetian	Warmest	-0.82	4.27	-0.45	10.92
40	Middle Miocene	Coldest	-1.98	2.30	-0.59	5.45
41	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
42	Ypresian	Warmest	-0.16	5.00	-0.22	13.11
43	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
44	Ypresian	Warmest	-0.16	5.00	-0.22	13.11
45	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
46	Ypresian	Warmest	-0.16	5.00	-0.22	13.11
47	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
48	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
49	Bartonian	Warmest	-1.33	3.04	-0.52	8.45
50	Middle Miocene	Coldest	-1.98	2.30	-0.59	5.45

51	Ypresian	Warmest	-0.16	5.00	-0.22	13.11
52	Lutetian	Warmest	-0.82	4.27	-0.45	10.92
53	Upper Miocene	Coldest	-2.76	1.46	-0.45	3.31
54	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
55	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
56	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
57	Upper Miocene	Coldest	-2.76	1.46	-0.45	3.31
58	Priabonian	Intermediate	-1.78	3.28	-0.57	6.95
59	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
60	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
61	Rupelian	Intermediate	-2.53	2.81	-0.75	5.82
62	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
63	Lutetian	Warmest	-0.82	4.27	-0.45	10.92
64	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36

Continued

Latest estimated origin						
Origin		Romdal et al.	Zachos et al.	Crowley & Berner		Cramer et al.
				Global	Tropical	
1	Priabonian	Intermediate	-1.78	3.28	-0.57	6.95
2	Rupelian	Intermediate	-2.53	2.81	-0.75	5.82
3	Priabonian	Intermediate	-1.78	3.28	-0.57	6.95
4	Ypresian	Warmest	-0.16	5.00	-0.22	13.11
5	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
6	Bartonian	Warmest	-1.33	3.04	-0.52	8.45
7	Rupelian	Intermediate	-2.53	2.81	-0.75	5.82
8	Chattian	Intermediate	-2.13	2.52	-0.81	5.80
9	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
10	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
11	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95

12	Bartonian	Warmest	-1.33	3.04	-0.52	8.45
13	Chattian	Intermediate	-2.13	2.52	-0.81	5.80
14	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
15	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
16	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
17	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
18	Upper Miocene	Coldest	-2.76	1.46	-0.45	3.31
19	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
20	Chattian	Intermediate	-2.13	2.52	-0.81	5.80
21	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
22	Upper Miocene	Coldest	-2.76	1.46	-0.45	3.31
23	Lutetian	Warmest	-0.82	4.27	-0.45	10.92
24	Ypresian	Warmest	-0.16	5.00	-0.22	13.11
25	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
26	Maastrichtian	Warmest	NA	5.84	0.27	9.42
27	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
28	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
29	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
30	Rupelian	Intermediate	-2.53	2.81	-0.75	5.82
31	Rupelian	Intermediate	-2.53	2.81	-0.75	5.82
32	Rupelian	Intermediate	-2.53	2.81	-0.75	5.82
33	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
34	Chattian	Intermediate	-2.13	2.52	-0.81	5.80
35	Middle Miocene	Coldest	-1.98	2.30	-0.59	5.45
36	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
37	Rupelian	Intermediate	-2.53	2.81	-0.75	5.82
38	Rupelian	Intermediate	-2.53	2.81	-0.75	5.82
39	Lutetian	Warmest	-0.82	4.27	-0.45	10.92
40	Middle Miocene	Coldest	-1.98	2.30	-0.59	5.45
41	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
42	Lutetian	Warmest	-0.82	4.27	-0.45	10.92

43	Middle Miocene	Coldest	-1.98	2.30	-0.59	5.45
44	Ypresian	Warmest	-0.16	5.00	-0.22	13.11
45	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
46	Ypresian	Warmest	-0.16	5.00	-0.22	13.11
47	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
48	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
49	Bartonian	Warmest	-1.33	3.04	-0.52	8.45
50	Upper Miocene	Coldest	-2.76	1.46	-0.45	3.31
51	Ypresian	Warmest	-0.16	5.00	-0.22	13.11
52	Bartonian	Warmest	-1.33	3.04	-0.52	8.45
53	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
54	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
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56	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
57	Upper Miocene	Coldest	-2.76	1.46	-0.45	3.31
58	Rupelian	Intermediate	-2.53	2.81	-0.75	5.82
59	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
60	Pliocene	Coldest	-3.02	1.22	-0.23	2.09
61	Rupelian	Intermediate	-2.53	2.81	-0.75	5.82
62	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
63	Bartonian	Warmest	-1.33	3.04	-0.52	8.45
64	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36

Continued

Molecular phylogeny-based estimated diversification time						
Divergence	Romdal et al.		Zachos et al.	Crowley & Berner		Cramer et al.
				Global	Tropical	
1	154.18	Intermediate	NA	8.56	-1.74	NA
2	39.16	Coldest	-1.41	3.04	-0.52	8.36
3	126.23	Coldest	NA	7.79	-0.74	NA

4	142.71	Coldest	NA		8.48	-1.55	NA	
5	66.19	Coldest	NA		4.84	0.35		9.50
6	101.20	Coldest	NA		7.38	0.11		13.52
7	57.44	Coldest		-0.85	4.71	0.12		10.86
8	117.77	Coldest	NA		7.59	-1.20	NA	
9	93.07	Coldest	NA		7.13	0.74		16.53
10	105.32	Coldest	NA		7.55	-0.36		13.74
11	44.57	Coldest		-0.99	4.42	-0.44		10.24
12	148.48	Intermediate	NA		8.33	-1.66	NA	
13	157.78	Intermediate	NA		8.91	-1.79	NA	
14	86.59	Coldest	NA		6.69	0.59		15.95
15	130.47	Coldest	NA		7.97	-0.59	NA	
16	56.65	Coldest		-0.85	4.71	0.12		11.66
17	144.33	Coldest	NA		8.48	-1.55	NA	
18	24.66	Intermediate		-1.73	2.64	-0.79		5.95
19	107.75	Coldest	NA		7.59	-0.94		13.04
20	132.48	Coldest	NA		8.24	-0.80	NA	
21	74.38	Coldest	NA		6.74	0.12		10.74
22	0.69	Coldest		-3.78	1.20	0.00		0.09
23	73.48	Coldest	NA		6.49	0.22		10.68
24	156.33	Intermediate	NA		8.83	-1.76	NA	
25	4.25	Coldest		-3.34	1.22	-0.23		2.18
26	133.49	Coldest	NA		8.24	-0.80	NA	
27	56.61	Coldest		-0.85	4.71	0.12		11.77
28	59.65	Coldest		-0.71	4.45	0.21		9.99
29	30.16	Intermediate		-2.51	2.60	-0.82		5.64
30	45.84	Coldest		-0.65	4.42	-0.44		11.25
31	42.88	Coldest		-0.91	4.13	-0.47		9.62
32	92.19	Coldest	NA		7.13	0.74		16.11
33	60.72	Coldest		-0.61	4.45	0.21		10.31
34	154.56	Intermediate	NA		8.83	-1.76	NA	

35	139.69	Coldest	NA		8.69	-1.44	NA	
36	72.37	Coldest	NA		6.49	0.22		10.43
37	66.19	Coldest	NA		4.84	0.35		9.50
38	56.90	Coldest		-0.85	4.71	0.12		11.43
39	102.83	Coldest	NA		7.38	0.11		12.51
40	62.10	Coldest		-0.62	4.45	0.28		10.77
41	102.83	Coldest	NA		7.38	0.11		12.51
42	153.82	Intermediate	NA		8.56	-1.74	NA	
43	88.45	Coldest	NA		6.69	0.59		15.29
44	19.49	Intermediate		-2.28	2.67	-0.67		6.54
45	72.71	Coldest	NA		6.49	0.22		10.52
46	56.61	Coldest		-0.85	4.71	0.12		11.77
47	97.67	Coldest	NA		7.26	0.81		13.62
48	86.37	Coldest	NA		6.69	0.59		16.06
49	44.70	Coldest		-0.99	4.42	-0.44		10.33
50	19.55	Intermediate		-1.98	2.65	-0.73		6.54
51	155.00	Intermediate	NA		8.83	-1.76	NA	
52	128.29	Coldest	NA		7.97	-0.59	NA	
53	1.59	Coldest		-3.75	1.33	-0.11		0.63
54	7.08	Coldest		-2.74	1.43	-0.38		3.22
55	75.85	Coldest	NA		6.74	0.12		11.42
56	1.53	Coldest		-3.75	1.33	-0.11		0.63
57	161.72	Intermediate	NA		8.84	-1.81	NA	
58	103.38	Coldest	NA		7.38	0.11		12.59
59	124.03	Coldest	NA		7.65	-0.90	NA	
60	48.30	Coldest		-0.38	4.74	-0.40		12.89
61	147.99	Intermediate	NA		8.33	-1.66	NA	
62	62.51	Coldest		-0.81	4.45	0.28		11.00
63	128.29	Coldest	NA		7.97	-0.59	NA	
64	33.62	Intermediate		-1.75	3.02	-0.69		6.13

Appendix S6.2

Table S6.2 Mammal families used in the study, along with the number of species per family (N) breeding in the Americas based on NatureServe (Patterson *et al.* 2007), the slope and standardized slope of species richness as a function of mean annual temperature and the estimated earliest and latest origin based on Benton (1993). For both the earliest and latest possible origin, we present the median temperature of the period from several proxies: Romdal *et al.* (2013) paleoclimatic categories, Cramer *et al.* (2011) temperature reconstructions in degree Celcius, Crowley and Berner (2001) global and tropical temperature anomalies in degree Celcius and Zachos *et al.* (2001) inverse of $\delta^{18}\text{O}$ in perthousand.

	Family	N	Slope richness ~ temperature	Slope standardized richness ~ temperature	R ²
1	Abrocomidae	9	0.00	0.00	0.00
2	Antilocapridae	1	0.00	0.00	0.00
3	Aplodontiidae	1	0.00	0.00	0.00
4	Bovidae	4	-0.01	-0.02	0.11
5	Caenolestidae	6	0.00	0.01	0.01
6	Camelidae	2	0.00	0.00	0.00
7	Canidae	17	0.01	0.01	0.02
8	Capromyidae	7	0.00	0.00	0.00
9	Castoridae	1	-0.01	-0.03	0.12
10	Caviidae	16	0.05	0.04	0.31
11	Cebidae	53	0.08	0.04	0.34
12	Cervidae	18	0.03	0.02	0.11
13	Chinchillidae	6	0.00	0.00	0.00
14	Dasypodidae	18	0.12	0.05	0.52
15	Didelphidae	76	0.20	0.05	0.45
16	Dinomyidae	1	0.00	0.02	0.07
17	Dipodidae	4	-0.01	-0.02	0.09
18	Echimyidae	77	0.12	0.04	0.33
19	Emballonuridae	19	0.18	0.05	0.43
20	Erethizontidae	16	0.02	0.03	0.15
21	Felidae	14	0.14	0.06	0.68
22	Geomyidae	40	0.00	0.01	0.01
23	Leporidae	24	0.00	0.00	0.00
24	Megalonychidae	2	0.01	0.03	0.19
25	Microbiotheriidae	1	0.00	0.00	0.00
26	Molossidae	35	0.37	0.06	0.63
27	Mormoopidae	8	0.05	0.04	0.26

28	Mustelidae	19	0.01	0.00	0.00
29	Myrmecophagidae	4	0.07	0.05	0.53
30	Natalidae	4	0.01	0.03	0.17
31	Noctilionidae	2	0.05	0.05	0.55
32	Ochotonidae	2	0.00	-0.02	0.05
33	Octodontidae	12	0.00	0.00	0.00
34	Phyllostomidae	153	1.17	0.05	0.48
35	Procyonidae	14	0.08	0.06	0.64
36	Sciuridae	101	-0.01	0.00	0.00
37	Solenodontidae	2	0.00	0.00	0.00
38	Soricidae	74	-0.05	-0.02	0.10
39	Talpidae	7	0.00	0.00	0.00
40	Tapiridae	3	0.02	0.05	0.48
41	Tayassuidae	3	0.05	0.05	0.58
42	Ursidae	3	-0.02	-0.03	0.19
43	Vespertilionidae	79	0.25	0.05	0.56

Continued

Fossil-based earliest estimated origin						
Origin		Romdal et al.	Zachos et al.	Crowley & Berner		Cramer et al.
				Global	Tropical	
1	Upper Miocene	Coldest	-2.76	1.46	-0.45	3.31
2	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
3	Lutetian	Warmest	-1.33	4.27	-0.45	10.92
4	Rupelian	Intermediate	-2.22	2.81	-0.75	5.82
5	Chattian	Intermediate	-2.22	2.52	-0.81	5.80
6	Lutetian	Warmest	-0.82	4.27	-0.45	10.92
7	Priabonian	Intermediate	-1.78	3.28	-0.57	6.95
8	Middle Miocene	Coldest	-1.98	2.30	-0.59	5.45
9	Priabonian	Intermediate	-2.53	3.28	-0.57	6.95

10	Middle Miocene	Coldest	-1.98	2.30	-0.59	5.45
11	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
12	Chattian	Intermediate	-2.13	2.52	-0.81	5.80
13	Middle Miocene	Coldest	-1.98	2.30	-0.59	5.45
14	Thanetian	Warmest	-0.83	4.71	0.12	11.07
15	Campanian	Warmest	NA	6.73	0.19	13.86
16	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
17	Lutetian	Warmest	-2.53	4.27	-0.45	10.92
18	Chattian	Intermediate	-2.22	2.52	-0.81	5.80
19	Lutetian	Warmest	-1.33	4.27	-0.45	10.92
20	Chattian	Intermediate	-2.22	2.52	-0.81	5.80
21	Rupelian	Intermediate	-2.53	2.81	-0.75	5.82
22	Lutetian	Warmest	-1.33	4.27	-0.45	10.92
23	Lutetian	Warmest	-1.33	4.27	-0.45	10.92
24	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
25	Danian Palaeogene Cainozoic	Warmest	-0.71	4.45	0.28	10.43
26	Lutetian	Warmest	-1.33	4.27	-0.45	10.92
27	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
28	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
29	Lutetian	Warmest	-0.82	4.27	-0.45	10.92
30	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
31	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
32	Priabonian	Intermediate	-2.53	3.28	-0.57	6.95
33	Chattian	Intermediate	-2.22	2.52	-0.81	5.80
34	Middle Miocene	Coldest	-1.98	2.30	-0.59	5.45
35	Chattian	Intermediate	-2.13	2.52	-0.81	5.80
36	Priabonian	Intermediate	-1.78	3.28	-0.57	6.95
37	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
38	Lutetian	Warmest	-1.33	4.27	-0.45	10.92
39	Bartonian	Warmest	-1.78	3.04	-0.52	8.45
40	Rupelian	Intermediate	-2.53	2.81	-0.75	5.82

41	Priabonian	Intermediate	-1.78	3.28	-0.57	6.95
42	Priabonian	Intermediate	-1.78	3.28	-0.57	6.95
43	Bartonian	Warmest	-1.33	3.04	-0.52	8.45

Continued

Fossil-based latest estimated origin						
Origin		Romdal et al.	Zachos et al.	Crowley & Berner		Cramer et al.
				Global	Tropical	
1	Upper Miocene	Coldest	-2.76	1.46	-0.45	3.31
2	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
3	Bartonian	Warmest	-0.82	3.04	-0.52	8.45
4	Lower Miocene Neogene	Intermediate	-2.53	2.66	-0.70	6.95
5	Lower Miocene Neogene	Intermediate	-2.13	2.66	-0.70	6.95
6	Lutetian	Warmest	-0.82	4.27	-0.45	10.92
7	Priabonian	Intermediate	-1.78	3.28	-0.57	6.95
8	Middle Miocene	Coldest	-1.98	2.30	-0.59	5.45
9	Rupelian	Intermediate	-1.78	2.81	-0.75	5.82
10	Middle Miocene	Coldest	-1.98	2.30	-0.59	5.45
11	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
12	Chattian	Intermediate	-2.13	2.52	-0.81	5.80
13	Middle Miocene	Coldest	-1.98	2.30	-0.59	5.45
14	Thanetian	Warmest	-0.83	4.71	0.12	11.07
15	Campanian	Warmest	NA	6.73	0.19	13.86
16	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
17	Rupelian	Intermediate	-0.82	2.81	-0.75	5.82
18	Lower Miocene Neogene	Intermediate	-2.13	2.66	-0.70	6.95
19	Bartonian	Warmest	-0.82	3.04	-0.52	8.45
20	Lower Miocene Neogene	Intermediate	-2.13	2.66	-0.70	6.95
21	Rupelian	Intermediate	-2.53	2.81	-0.75	5.82
22	Bartonian	Warmest	-0.82	3.04	-0.52	8.45

23	Bartonian	Warmest	-0.82	3.04	-0.52	8.45
24	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
25	Danian Palaeogene Cainozoic	Warmest	-0.71	4.45	0.28	10.43
26	Bartonian	Warmest	-0.82	3.04	-0.52	8.45
27	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
28	Lower Miocene Neogene	Intermediate	-2.22	2.66	-0.70	6.95
29	Lutetian	Warmest	-0.82	4.27	-0.45	10.92
30	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
31	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
32	Rupelian	Intermediate	-1.78	2.81	-0.75	5.82
33	Lower Miocene Neogene	Intermediate	-2.13	2.66	-0.70	6.95
34	Middle Miocene	Coldest	-1.98	2.30	-0.59	5.45
35	Chattian	Intermediate	-2.13	2.52	-0.81	5.80
36	Priabonian	Intermediate	-1.78	3.28	-0.57	6.95
37	Pleistocene Quaternary	Coldest	-3.76	1.33	-0.11	0.36
38	Bartonian	Warmest	-0.82	3.04	-0.52	8.45
39	Priabonian	Intermediate	-1.33	3.28	-0.57	6.95
40	Rupelian	Intermediate	-2.53	2.81	-0.75	5.82
41	Priabonian	Intermediate	-1.78	3.28	-0.57	6.95
42	Priabonian	Intermediate	-1.78	3.28	-0.57	6.95
43	Bartonian	Warmest	-1.33	3.04	-0.52	8.45

Continued

Molecular phylogeny-based estimated diversification time						
	Divergence	Romdal et al.	Zachos et al.	Crowley & Berner		Cramer et al.
				Global	Tropical	
1	24.79	Intermediate	-1.73	2.64	-0.79	5.85
2	18.70	Intermediate	-2.28	2.67	-0.67	6.91
3	51.58	Warmest	0.01	5.26	-0.29	13.71
4	17.07	Intermediate	-2.19	2.67	-0.67	7.44

5	13.07	Coldest		-2.48	1.90	-0.57	4.12
6	65.38	Warmest		-0.63	4.84	0.35	9.85
7	47.31	Warmest		-0.43	4.74	-0.40	12.28
8	18.07	Intermediate		-2.30	2.67	-0.67	7.16
9	58.39	Warmest		-0.79	4.71	0.12	10.05
10	17.61	Intermediate		-2.30	2.67	-0.67	7.35
11	13.53	Coldest		-1.75	2.69	-0.62	4.60
12	18.70	Intermediate		-2.28	2.67	-0.67	6.91
13	25.70	Intermediate		-2.18	2.41	-0.83	5.05
14	67.47	Warmest	NA		4.84	0.35	9.32
15	21.88	Intermediate		-1.85	2.65	-0.73	6.66
16	25.70	Intermediate		-2.18	2.41	-0.83	5.05
17	50.94	Warmest		0.07	5.26	-0.29	13.81
18	14.62	Intermediate		-1.48	2.69	-0.62	6.16
19	51.67	Warmest		0.01	5.26	-0.29	13.68
20	36.50	Intermediate		-1.64	3.28	-0.57	7.30
21	28.97	Intermediate		-2.58	2.60	-0.82	5.49
22	31.42	Intermediate		-2.52	2.60	-0.82	5.82
23	48.40	Warmest		-0.38	4.74	-0.40	12.95
24	25.88	Intermediate		-2.18	2.41	-0.83	4.96
25	67.84	Warmest	NA		5.19	0.33	9.23
26	48.76	Warmest		-0.11	4.74	-0.40	13.18
27	34.05	Intermediate		-1.75	3.02	-0.69	6.39
28	29.15	Intermediate		-2.58	2.60	-0.82	5.50
29	40.50	Warmest		-1.26	3.04	-0.52	8.91
30	51.67	Warmest		0.01	5.26	-0.29	13.68
31	33.69	Intermediate		-1.75	3.02	-0.69	6.17
32	48.40	Warmest		-0.38	4.74	-0.40	12.95
33	20.70	Intermediate		-2.22	2.65	-0.73	6.46
34	34.05	Intermediate		-1.75	3.02	-0.69	6.39
35	29.15	Intermediate		-2.58	2.60	-0.82	5.50

36	51.58	Warmest		0.01	5.26	-0.29	13.71
37	74.65	Warmest	NA		6.74	0.12	10.79
38	66.56	Warmest	NA		4.84	0.35	9.45
39	66.56	Warmest	NA		4.84	0.35	9.45
40	51.49	Warmest		0.07	5.26	-0.29	13.73
41	30.42	Intermediate		-2.51	2.60	-0.82	5.69
42	37.41	Intermediate		-1.64	3.28	-0.57	7.40
43	45.22	Warmest		-0.99	4.42	-0.44	10.79

Appendix S6.3

Historical temperature estimates

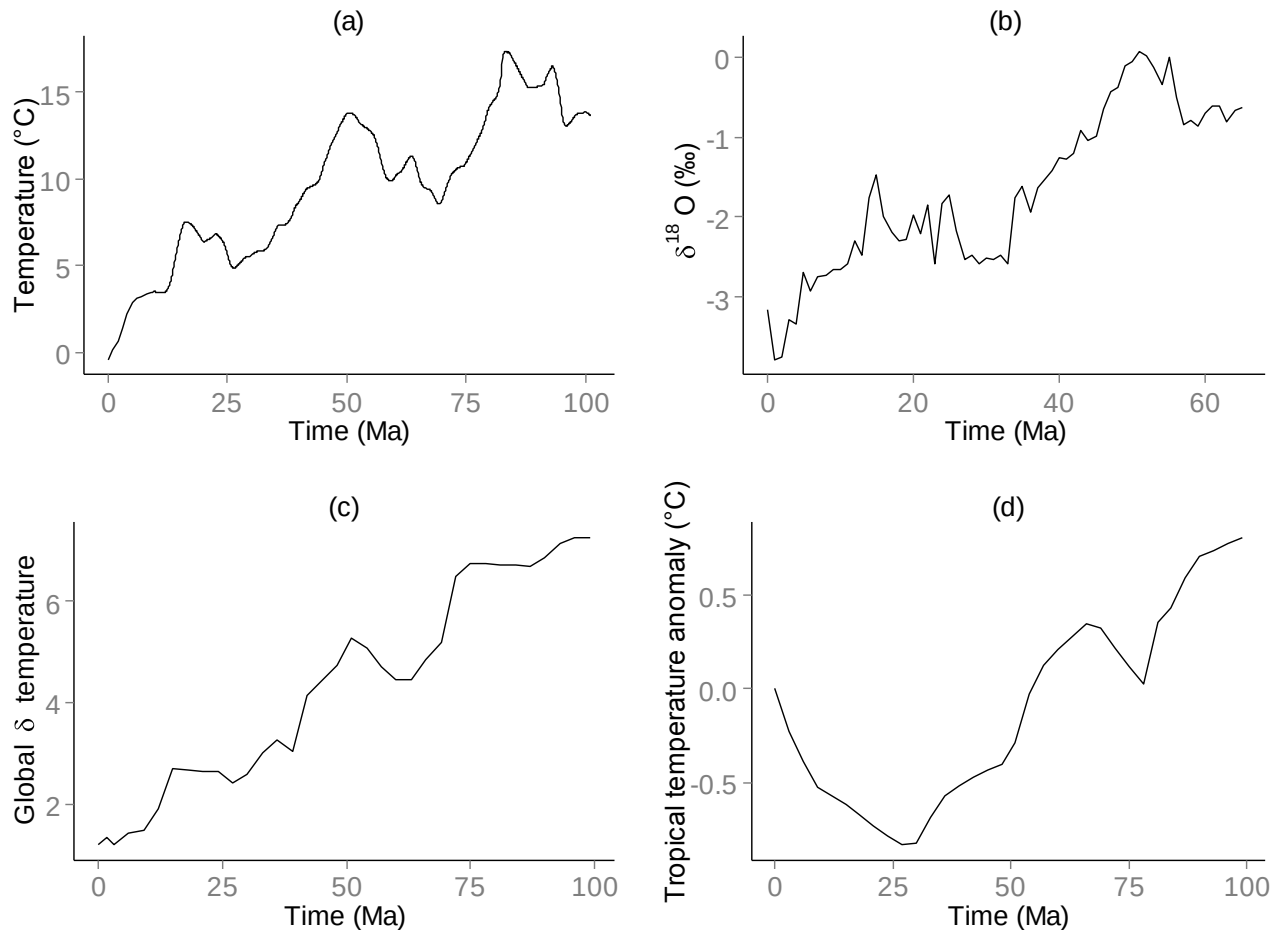


Figure S6.1 Estimates of past temperatures over the last 100 million years (Ma). (a) The data represent global temperature reconstructions over 100 Ma, and have been digitized from the upper panel of Figure 9 in Cramer *et al.* (2009). (b) Negative value of deep-sea benthic foraminiferal oxygen isotope ($\delta^{18}\text{O}$) records over the last 65 Ma, as a proxy for global temperature (Zachos *et al.*, 2001). Values represent a 5 point running average of raw data (Zachos *et al.*, 2001), and have been downloaded from <http://www.ncdc.noaa.gov/paleo/pubs/ipcc2007/fig61.html>. (c) Global δ temperature variation

over the last 100 Ma, as scaled from deep-sea oxygen isotope records (Crowley and Berner, 2001). Data have been digitized from the panel b of Figure 1 in Crowley and Berner (2001). (d) Mean tropical temperature anomaly over the last 100 Ma, as scaled from oxygen isotope records at low latitudes (Crowley and Berner, 2001). The data have been digitized from the panel c of Figure 1 in Crowley and Berner (2001). In all four panels, the data have been linearly interpolated.

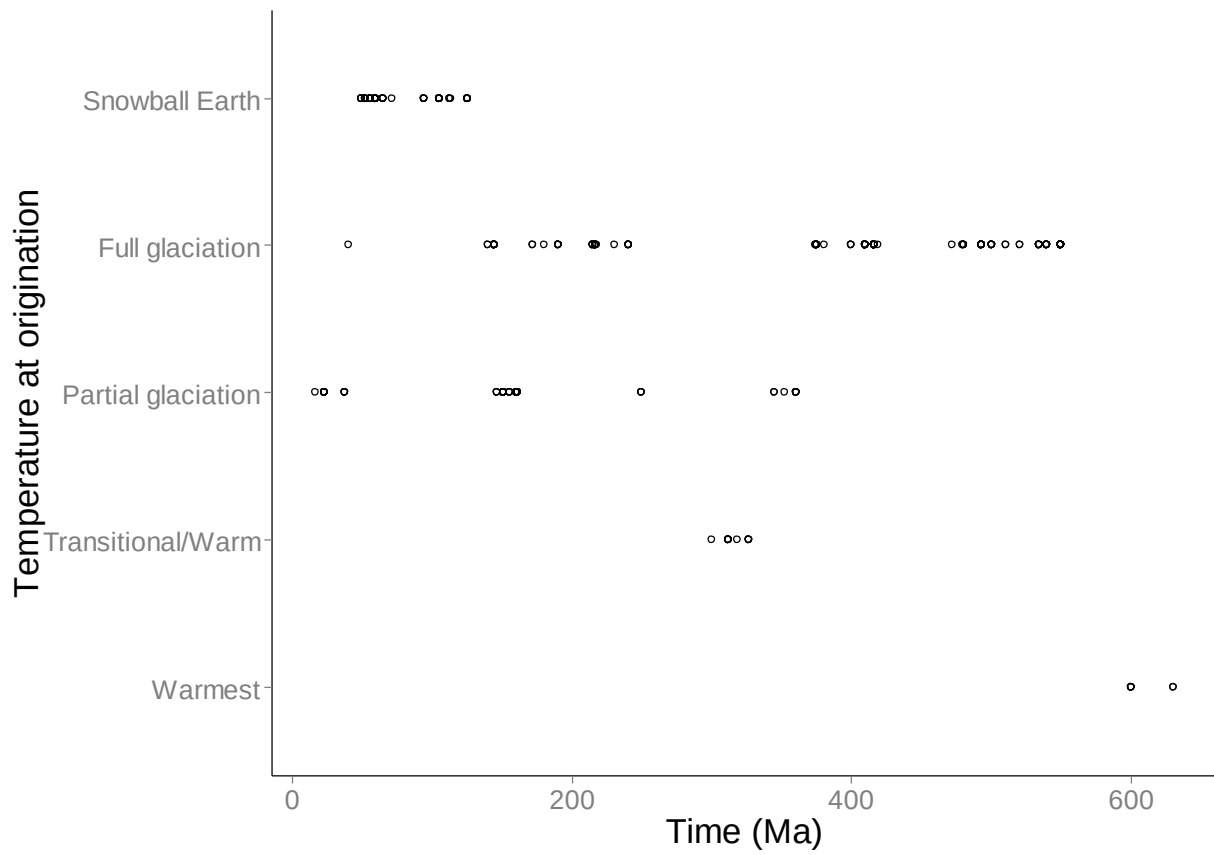


Figure S6.2 Origination time in millions of years ago (Ma) and associated temperature at origination of the 343 groups of organisms included in Romdal *et al.* (2013).

Results with alternative measures of temperature at origination

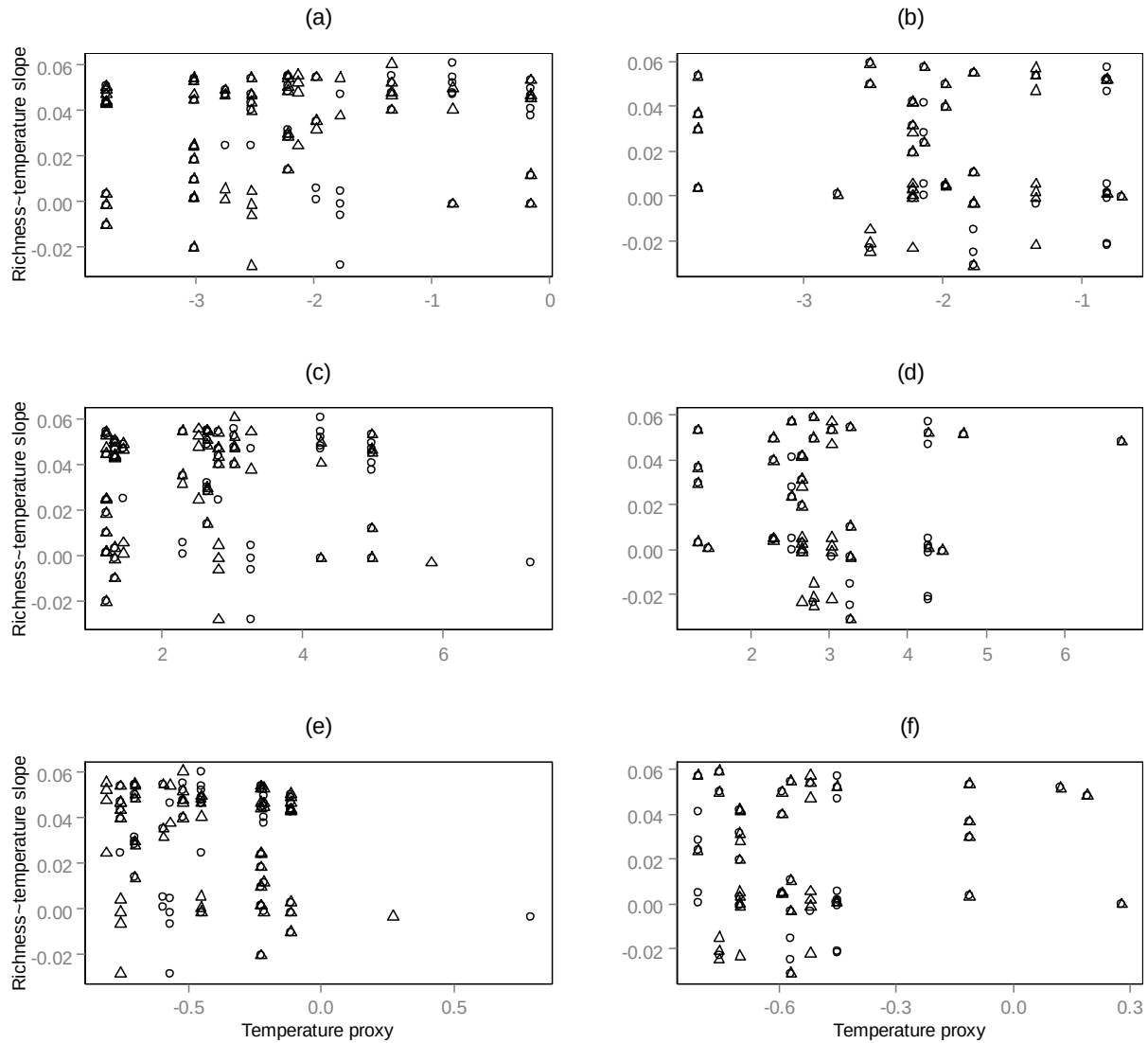


Figure S6.3 Standardized slope of the richness–temperature relationship in the Americas for (a, c, e) 64 bird and (b, d, f) 43 mammal families as a function of the temperature at which the family originated. We considered both the earliest (circles) and latest (triangles) possible origination for each species. We here estimated the temperature at family origination using (a, b) the data of Zachos (2001) presented in Figure S6.1a as well as the global (c, d) and tropical (e, f) temperature estimates of Crowley and Burner (2001) presented in Figure S6.1c and d respectively. All relationships are non-significant ($p > 0.13$).

Results using richness–latitude gradients as the dependent variable

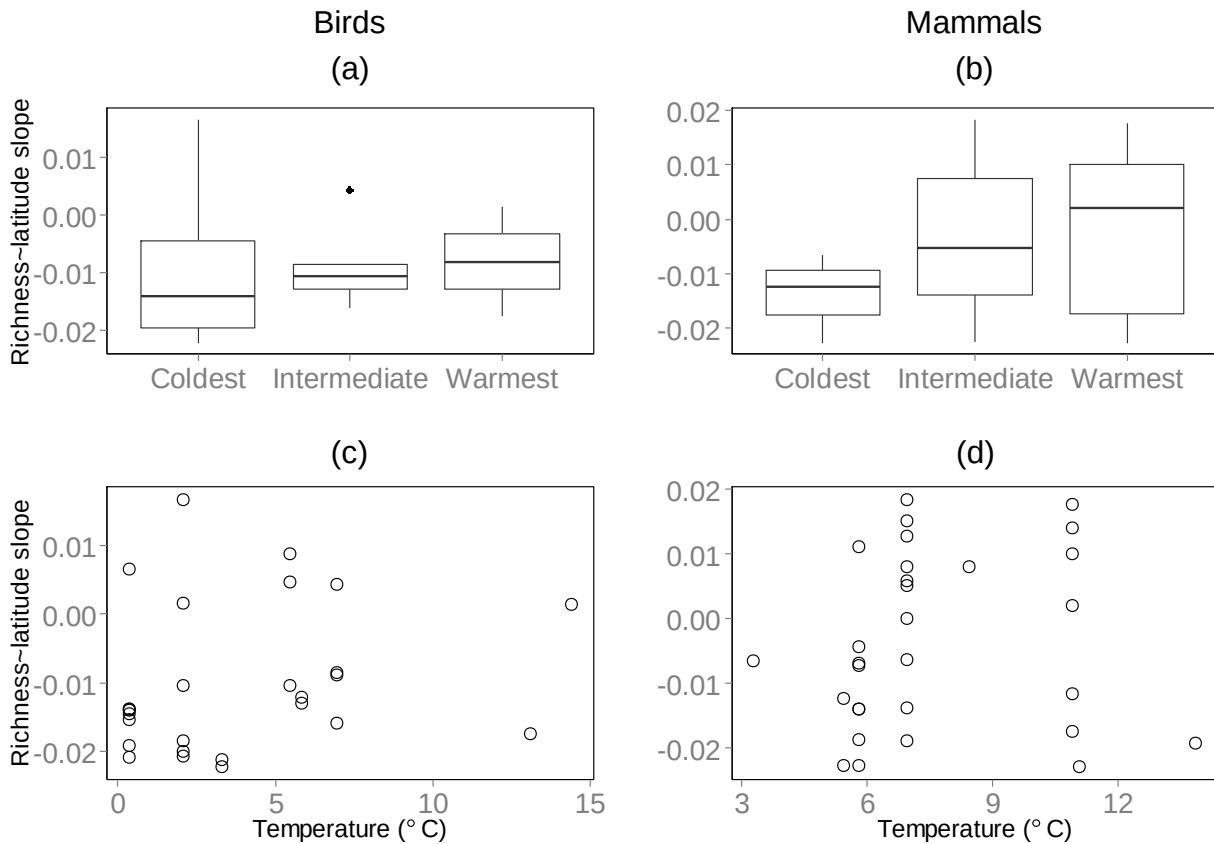


Figure S6.4 Standardized slope of the richness–latitude relationship in the Americas for (a, c) 64 bird and (b, d) 43 mammal families as a function of the temperature at which the family originated. The lack of a relationship is observable whether we use the slopes of richness–temperature relationships as the dependent variable (Figure 2 in the main text) or of richness–latitude relationships (here). We here estimated the temperature at family origination using (a, b) the palaeoclimate categories of Romdal *et al.* (2013) as well as (c, d) the temperature reconstructions of Cramer *et al.* (2011). All relationships are non-significant ($p > 0.15$). Here, when uncertain, the earliest origin period was taken.

Analyses separated by continent of origin

We also analyzed the data separately for families with North American versus South American origin. Global temperatures are imprecise estimates of the actual temperatures in the region in which the families originated, which adds an unknown amount of noise to our predictor variable (i.e. temperature at origination). Unfortunately, data on the regions in which bird and mammal families have originated are very sparse and data on palaeo regional temperatures are not available. To nevertheless account for spatial differences in temperatures, we divided the data by continental origin. This allowed us to reduce potential noise in our predictor variable that would be caused by continental differences in temperature. We used the data compiled by Smith *et al.* (2012), where bird and mammal families have been assigned to an ancestral origin in either North or South America. Since not all families were represented in the data of Smith *et al.* (2012), our sample size was reduced to 43 bird families and 36 mammal families. We repeated our analyses testing the effect of temperature at origination on the slopes of current richness–temperature gradients, using our 5 estimates of historical temperatures and our 2 fossil-based estimates of time of origination (10 different estimates of temperature at origination). We restricted our analyses to either (1) 23 bird families with an origin in North America, (2) 22 mammal families with an origin in North America, (3) 21 bird families with an origin in South America and (4) 15 mammal families with an origin in South America. For (1) birds with a North American origin, relationships were all negative (i.e. in the wrong direction) with $p > 0.05$ (Fig. S6.5). For (2) mammals with a North American origin, all relationships were also negative (i.e. in the wrong direction) and 9/10 had $p > 0.05$ while one had $p = 0.018$ (Fig. S6.5). For (3) birds with a South American origin the slope estimate was close to 0, with the estimate shifting between positive and negative values depending on the estimate of temperature at origination,

always with $p > 0.05$. For (4) mammals with a South American origin, the relationship was always positive (i.e. predicted direction), with $0.014 < p < 0.15$ (Fig. S6.6). This positive relationship between current richness–temperature gradients and temperature at origination for mammal families with South American origin, explained up to 50% of the variance (i.e. when using the estimates of temperature of Cramer *et al.* 2011). This observed positive effect is entirely driven by 3 mammal families with steep current richness–temperature gradients that have originated in a substantially warmer period than the other mammal families with South American origin (i.e. >45 Ma). Eliminating these 3 families makes the relationships non-significant in all cases. The bulk of the evidence is therefore inconsistent with tropical niche conservatism as a main explanation for current richness–temperature gradients.

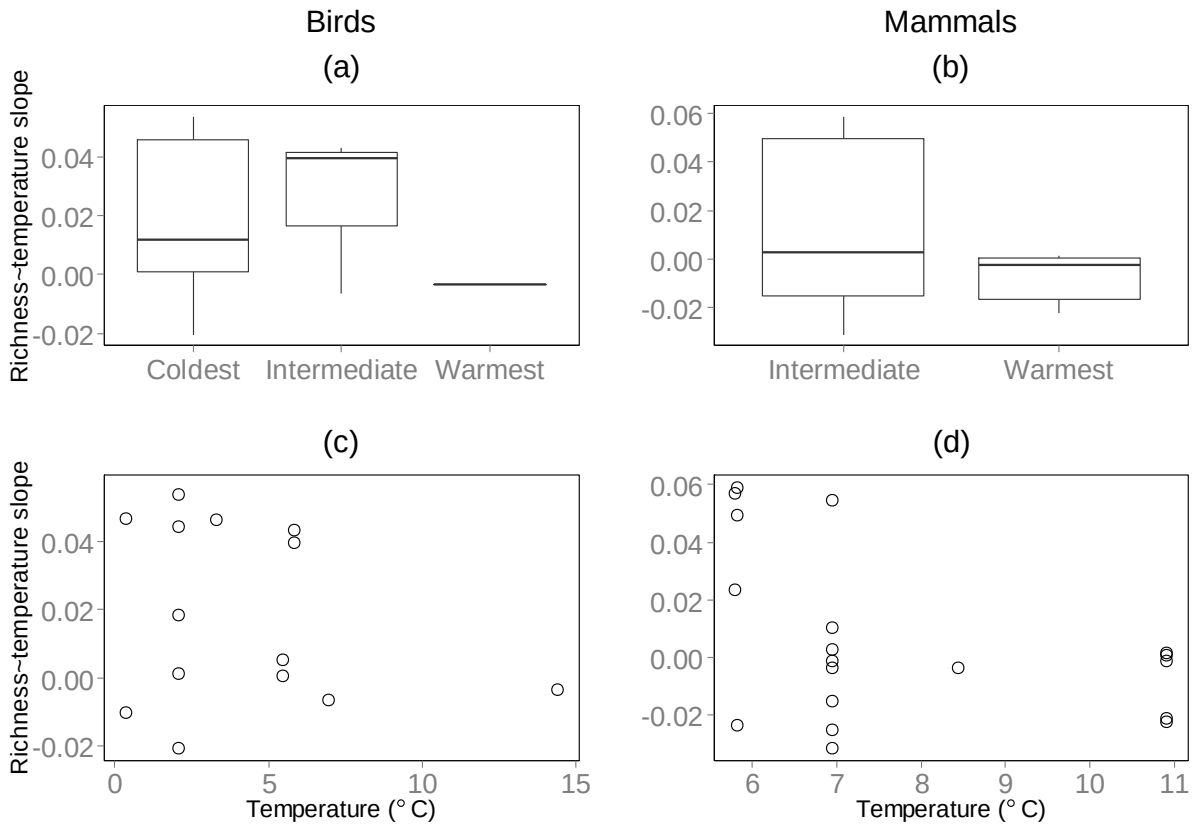


Figure S6.5 Standardized slope of richness–temperature gradients as a function of temperature at origination for (a, c,) 23 bird and (b, d) 22 mammal families with a North American origin. We here estimated the temperature at family origination using (a, b) the palaeoclimate categories of Romdal *et al.* (2013) as well as (c, d) the temperature reconstructions of Cramer *et al.* (2011). Here, when uncertain, the earliest origin period was taken. These are a subset of the data (i.e. North American origination only) of the data presented in Figure 2 of the main text.

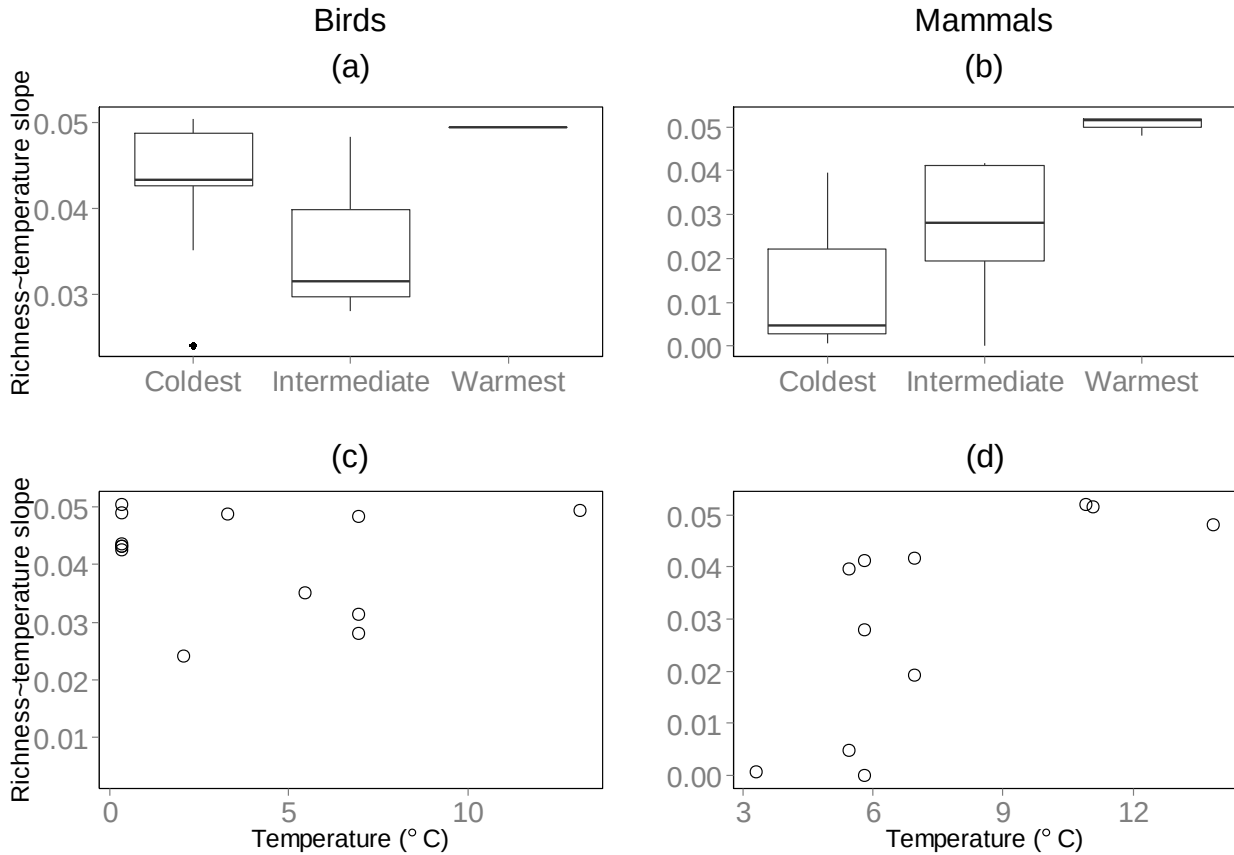


Figure S6.6 Standardized slope of richness–temperature gradients as a function of temperature at origination for (a, c,) 21 bird and (b, d) 15 mammal families with a South American origin. We here estimated the temperature at family origination using (a, b) the palaeoclimate categories of Romdal *et al.* (2013) as well as (c, d) the temperature reconstructions of Cramer *et al.* (2011). Here, when uncertain, the earliest origin period was taken. These are a subset of the data (i.e. South American origination only) of the data presented in Figure 2 of the main text.

Phylogeny-based divergence time estimates

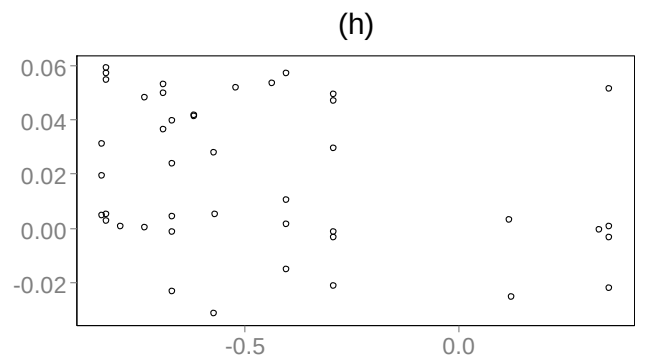
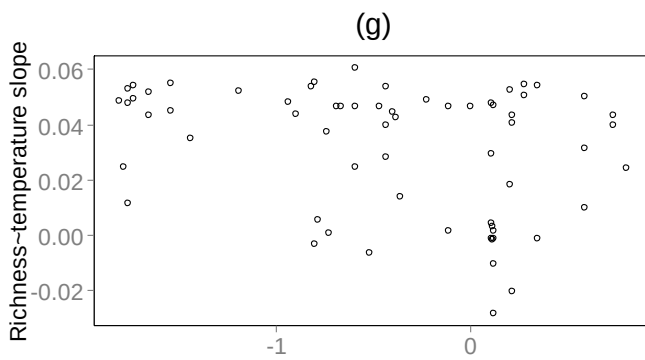
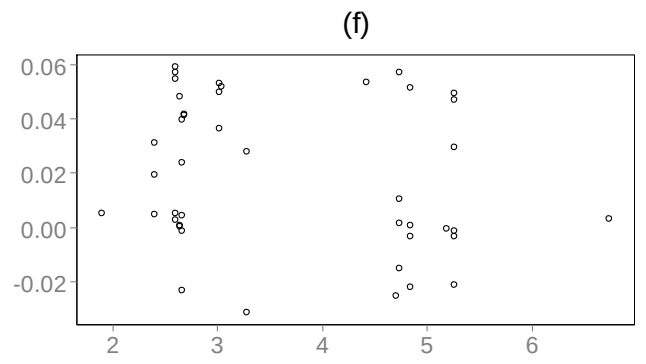
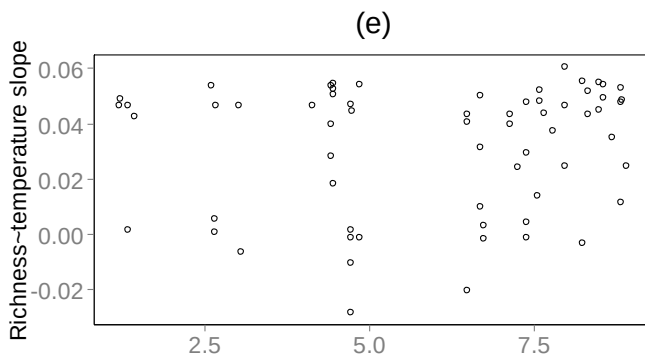
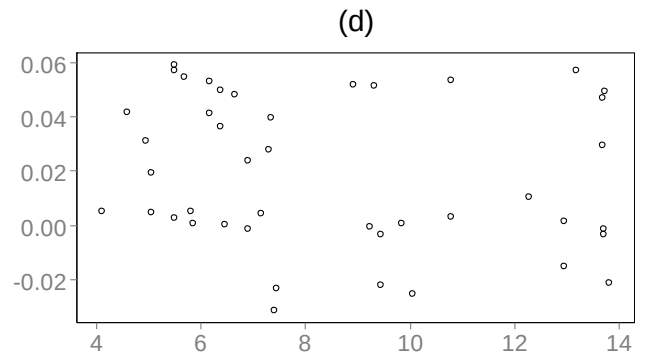
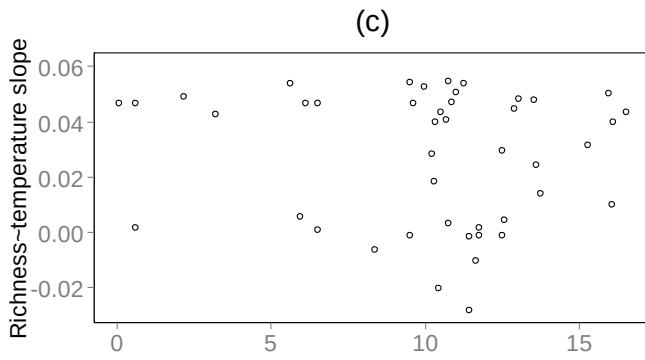
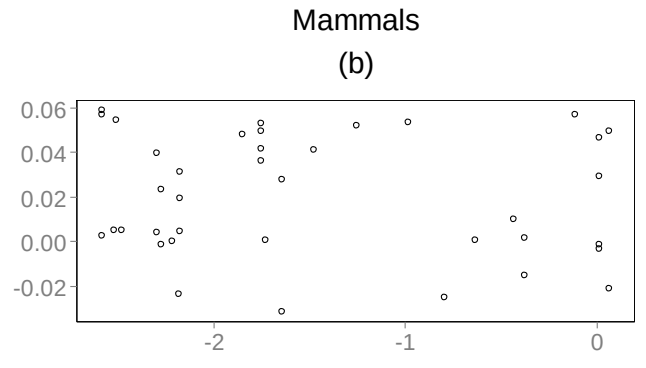
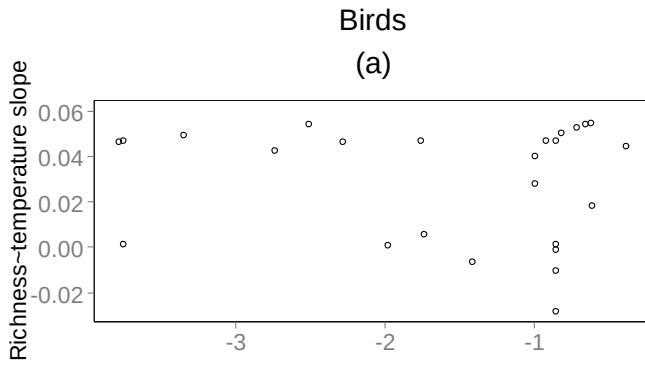
We estimated the divergence time of each of family from its more closely related ancestor based on molecular time-clock phylogenies.

For birds, we used the dated phylogeny of all 9,993 extant species of birds from Jetz *et al.* (2012), including species with and without genetic data. We used a sample of 1000 trees from the pseudo-posterior samples of complete trees assembled by Jetz *et al.* (2012) using the backbone phylogeny of Hackett *et al.* (2008). We estimated the divergence time of each bird family by determining the time it diverged from the more closely related taxonomic unit. We then averaged these divergence times across the 1000 sample trees to obtain a mean divergence time for each of the 64 bird families. The minimum and maximum family divergence time, estimated across the 1000 sample trees, were highly correlated ($r = 0.81$).

For mammals, we simply digitized the molecular phylogenetic time tree of mammalian families presented Meredith *et al.* (2011, Figure 1). We then estimated the divergence time of each family from its sister taxon. The data of Cramer *et al.* (2011) only extend to 110 Ma, resulting in the exclusion of 20 bird families with earlier divergence times, while the data of Zachos *et al.* (2001) only extend to 65 Ma, resulting in the exclusion of 39 bird and 5 mammal families (see Appendix S6.1 and S6.2).

For both bird and mammal families, we then estimated the temperature at the time of the diversification from the five temperature reconstructions presented in the main text. Then, we repeated all analyses presented in the main text, testing whether the slope of richness–temperature relationships is positively related to the temperature at the time the family diverged from its most recent common ancestor (instead of the fossil-based time at origination). We found that there were no such effects (Fig. S6.4) and thus our qualitative conclusions remain

unchanged. All relationships, either using the standardized or non-standardized slopes of richness as a function of either temperature or latitude, or doing a logistic regression using the sign of standardized temperature slopes, were non-significant ($p > 0.05$). Some exceptions are detailed below where the relationship was statistically significant, but always in the direction opposite to that predicted by tropical niche conservatism. Specifically, when using the standardized slopes of richness as a function of temperature at origination with the temperature data of Crowley and Burner (2001), the relationship was significantly negative for both birds and mammals ($p = 0.02$ for birds and 0.05 for mammals), while tropical niche conservatism predicts a positive relationship (Fig. S6.4). Similarly, when we only considered the sign of the richness–temperature slope as the dependent variable, the relationship, for mammals only, was significantly negative for four of the five temperature proxies ($p < 0.05$ and explained deviance between 0.10 – 0.19). Our qualitative conclusions remained unchanged when we weighted the above regressions by the number of species in the family or when we used non-parametric tests. We did not adjust for multiple comparisons.



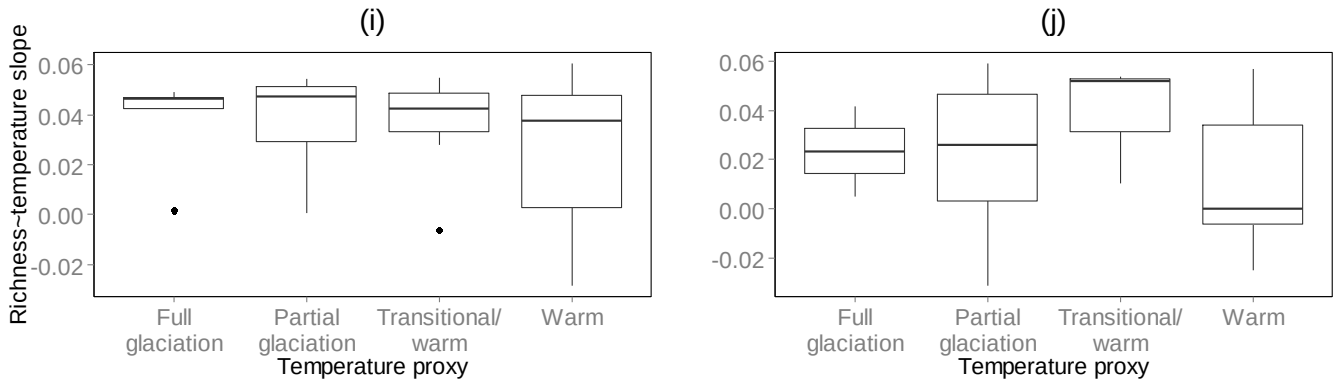


Figure S6.7 Standardized slope of the richness–temperature relationship in the Americas for (a, c, e, g) 64 bird and (b, d, f, h) 43 mammal families as a function of the temperature at time the family diverged from its most recent ancestor, as estimated from phylogenetic time trees. We here estimated the temperature at the time family diversification from (a, b) the data of Zachos (2001) presented in Figure S6.1a, (c, d) of Cramer *et al.* (2009) presented in Figure S6.1b, as well as the (e, f) global and (g, h) tropical temperature estimates of Crowley and Burner (2001) presented in Figure S6.1c and d respectively and (i, j) the temperature categories of Romdal *et al.* (2013). All relationships are non-significant ($p > 0.05$), except for (g) and (h) where the relationship is significantly negative ($p = 0.02$ for birds and 0.05 for mammals) while tropical niche conservatism predicts a positive relationship.

Appendix S6.4

We ran a statistical power analysis to assess the probability of detecting an existing relationship between the slope of richness–temperature relationships and temperature at origination as statistically significant, given $\alpha = 0.05$. We assumed that either all of the variance, or half of the variance, in the richness–temperature slopes can be accounted for by the temperature at origination. We then introduced random normally distributed errors in the independent variable, for which we varied the standard deviation. We then ran a linear regression and tested for statistical significance for 10000 simulated independent variables with such normally distributed errors. We report the statistical power as the percentage of these relationships that were detected as statistically significant ($p < 0.05$).

Table S6.3 Statistical power to detect the effect of temperature at origination on the slopes of the richness–temperature relationship among bird (n= 63) and mammal (n= 43) families in the Americas as statistically significant, given $\alpha= 0.05$, a specified relationship and a specified error in the independent variable. We report the statistical power to detect such an effect, assuming that the relationship explains either all or half of the variance in richness–temperature slopes. We further assumed normally distributed errors, with a standard deviation equal to either the range of variability in x, denoted Rx, half that range Rx/2 or a quarter of that range Rx/4. In parentheses, we report the observed mean coefficient of correlation between the true values of x and its error-introduced estimate.

Explained variance	Standard deviation of the errors		
	Rx/4	Rx/2	Rx
Birds (n= 64)			
All	100% (r= 0.72)	98% (r= 0.46)	52% (r= 0.25)
Half	98% (r= 0.46)	52% (r= 0.25)	18% (r= 0.13)
Mammals (n= 43)			
All	100% (r= 0.77)	97% (r= 0.52)	49% (r= 0.29)
Half	97% (r= 0.52)	49% (r= 0.29)	16% (r= 0.15)

APPENDICES CHAPTER 7

Appendix S7.1

Methods

We used the data of Hortal *et al.* (2011) on species richness estimated from range maps of 106 European Scarabaeinae species in mainland Europe and binned into a 1°x1° grid. Data on present and LGM temperature and precipitation were extracted from the same Atmosphere–Ocean General Circulation Model (Hortal *et al.* 2011). The historical variability in temperature and precipitation was calculated as the difference between current and LGM values, such that small climate variability values represent stable climates (Hortal *et al.* 2011). Species richness is predicted to relate negatively to temperature and precipitation variability while positively relating to current temperature and precipitation (Hortal *et al.* 2011).

We first directly tested the prediction that the richness–temperature variability relationship changes in shape around LGM temperatures of 0°C by fitting a piecewise regression of richness as a function of temperature variability, with a breakpoint estimated from LGM temperatures. We then reproduced Hortal's *et al.* (2011) analyses by including only temperature variability as the predictor variable in a geographically weighted regression (GWR) model of species richness (Figure 1a). Then, we also included current mean annual temperature in the model to explicitly account for its effect. To ensure that our conclusions were not affected by the exclusion of other environmental variables that affect species richness, we additionally considered current precipitation and its variability since the LGM as well as the 10 additional environmental variables included in Hortal *et al.* (2011), namely altitudinal range, actual evapotranspiration (AET), potential evapotranspiration (PET), water balance, current spring and

summer precipitation, amount of organic matter and pH in the surface horizons of the soil, diversity of land-cover categories and the proportion of agricultural land in each grid cell (Hortal *et al.* 2011). We ran both global regressions and GWRs for each set of independent variables considered. In the GWRs, we allowed the bandwidth to be selected from 5 to 20%, as in Hortal *et al.* (2011). In all cases, a bandwidth of 5% achieved the lowest AIC and was selected. We used both a Gaussian and bi-square weighting function in the program SAM 4.0 (Spatial Analysis in Macroecology, Rangel *et al.* 2010 *Ecography*, 33, 46–50.).

To provide another test of the prediction that the richness–temperature variability relationship changes in shape around LGM temperatures of 0°C, we fitted a piecewise regression on the local slopes of richness–temperature variability relationships, estimated by the GWR models, with a breakpoint fitted from LGM temperatures. These analyses were carried out in R version 3.0.1 (R core team 2013) using the ‘nls’ function for piecewise regressions and optimizing the breakpoint (constrained to be within the range of observed values) by minimising the residual sums of squares with the ‘optimize’ function (see formulas and results in Table S7.1).

Effect of historic climate stability on individual species ranges

The historic climate stability hypothesis predicts that species' whose geographic ranges are closer to their LGM geographic range should currently fill a greater proportion of their potential range (Svenning and Skov 2007). Conversely, species that had to migrate larger distances to track climate change should experience a migration lag. In general, range filling should therefore be higher in areas where climate since the LGM has been most stable leading to higher species richness (Svenning and Skov 2007). Consistent with the historic climate stability hypothesis, range filling decreases with distance from LGM refugia (mean deviance uniquely explained= 4% in Dullinger *et al.* 2012), as does species' probability of occurrence (mean partial r^2 = 3% Svenning *et al.* 2008) and species richness (r^2 = 78% in Svenning and Skov 2007). Normand *et al.* (2011) also found a positive relationship between current and LGM distributions for 65% of species of European plants, with 55% showing a significant positive effect beyond that of current climate. On average, the partial R^2 of current climatic variables was 28.5%, and 5.8% for distance from LGM refugia (Normand *et al.* 2011).

However, Dullinger *et al.* (2012) identified species' LGM refugia by regressing current distributions as a function of a set of potential LGM refugia. They then determined which of the potential LGM refugia was the most likely for a given species by selecting the model with the lowest AIC. However, for 51 of 183 species (28%) the 'best model' showed a positive effect of distance from putative LGM refugia with $\Delta AIC < 10$, whereas the historic climate hypothesis predicts a negative effect. The article does not state what proportion of the best models had correlations in the opposite direction to the prediction with $\Delta AIC < 0$, but it is not implausible that it could be close to half of the species. Dullinger *et al.* (2012) discarded these models based on the argument that they "cannot think of a plausible, or at least parsimonious, explanation" for

these positive effects and instead select the model with the lowest AIC among the ones with negative signs for each species. This may be a way to identify potential refugia, but it cannot be viewed as a test of the historic climate stability hypothesis, since plausible refugia are identified by assuming that the hypothesis is true. The logic is circular. Similarly, Normand *et al.* (2011) estimated potential LGM refugia by hind-casting models of current occurrence–climate relationships onto LGM climates. They then tested how distance from refugia predicts current distributions. But, if climate had not changed since the LGM, LGM distributions would be estimated to be roughly equal to current distributions. Distance from these estimated refugia would therefore be a very good statistical predictor of current distribution, although this apparent effect could not possibly be due to historical climate change. And, in fact, Normand *et al.* (2011) observed that distance from refugia explained current distributions mostly in southern Europe where climate change since the LGM is close to zero (Fløjgaard *et al.* 2011); ~15% of the variation in species' occurrences is uniquely explained by distance from LGM refugia in southern Europe and ~0% in northern Europe (Normand *et al.* 2011).

Therefore, in the absence of independent information regarding LGM species ranges, any conclusions about spread from LGM refugia should be treated cautiously. Note that species distribution models have failed to accurately predict genetically-based (Worth *et al.* 2014) and fossil-based (Davis *et al.* 2014) evidence of LGM refugia. And, Lima-Ribeiro *et al.* (2010) have used palynological data and found that the effect of historic climate stability on species richness in the Brazilian Cerrado was non-significant, although this could arguably be due to the fact climatic oscillations have been relatively small in that region (Gouveia *et al.* 2013).

Estimations of a LGM temperature breakpoint in the richness–temperature variability relationship

Table S7.1 Estimates a LGM temperature breakpoint in the linear richness–temperature variability relationship fitted through different models.

For each model, the formula is provided along with the estimated LGM breakpoint (°C), the variance in the dependent variable explained and the AIC. Results within black boxes are comparable has the boxes encompass models that have been fitted to the same dependent variable.

Eq	Dependent variable (y)	Predictor variable (x)	Breakpoint variable (x1)	Non-linear least-square formula		Other predictor variables		
						None	Current Temperature	All
Species richness								
1	Temperature variability	LGM temperature	$y \sim (x1 \leq f) * (i1 + s1 * x) + (x1 > f) * ((i1 + s1 * f) + s2 * (x - f))$ +(slopes of other predictor variables)	Breakpoint (°C)	-0.39	-16.00	-16.48	
				Expl. variance	0.85	0.95	0.97	
				AIC	7639	6587	5969	
2	Temperature variability	LGM temperature	$y \sim (x1 \leq f) * (i1 + s1 * x) + (x1 > f) * (i2 + s2 * x)$ +(slopes of other predictor variables)	Breakpoint (°C)	0.39	-0.10	0.49	
				Expl. variance	0.93	0.96	0.98	
				AIC	6926	6340	5596	
3	Temperature variability	LGM temperature	$y \sim (x1 \leq f) * (i1 + s1 * x) + (x1 > f) * ((i1 + s1 * f) + s2 * x1)$ +(slopes of other predictor variables)	Breakpoint (°C)	-14.94	-12.12	-4.29	
				Expl. variance	0.94	0.95	0.97	
				AIC	6748	6517	5835	

Local slopes of richness~temperature variability (GWR of richness~predictor variable(s), bisquare weighting function)

4	NA	LGM temperature	$y \sim (x1 \leq f) * i1 + (x1 > f) * i2$	Breakpoint (°C)	-3.17	2.95	4.16
				Expl. variance	0.82	0.75	0.81
				AIC	3369	3522	2910
5	Temperature variability	LGM temperature	$y \sim (x1 \leq f) * (i1 + s1 * x) + (x1 > f) * ((i1 + s1 * f) + s2 * x)$	Breakpoint (°C)	-0.71	1.17	-20.64
				Expl. variance	0.81	0.59	0.56
				AIC	3413	4032	3786
6	Temperature variability	LGM temperature	$y \sim (x1 \leq f) * (i1 + s1 * x) + (x1 > f) * (i2 + s2 * x)$	Breakpoint (°C)	-4.04	1.19	1.46
				Expl. variance	0.86	0.80	0.86
				AIC	3093	3293	2586
7	LGM temperature	LGM temperature	$y \sim (x1 \leq f) * (i1 + s1 * x) + (x1 > f) * ((i1 + s1 * f) + s2 * (x - f))$	Breakpoint (°C)	-10.24	-2.67	-2.34
				Expl. variance	0.85	0.77	0.82
				AIC	3161	3437	2829
8	LGM temperature	LGM temperature	$y \sim (x1 \leq f) * (i1 + s1 * x) + (x1 > f) * (i2 + s2 * x)$	Breakpoint (°C)	-0.59	1.18	3.06
				Expl. variance	0.86	0.78	0.83
				AIC	3091	3379	2806

Local slopes of richness~temperature variability (GWR of richness~predictor variable(s), Gaussian weighting function)

9	NA	LGM temperature	$y \sim (x1 \leq f) * i1 + (x1 > f) * i2$	Breakpoint (°C)	-3.76	0.40	3.87
				Expl. variance	0.92	0.71	0.71
				AIC	1583	2059	1420
10	Temperature variability	LGM temperature	$y \sim (x1 \leq f) * (i1 + s1 * x) + (x1 > f) * ((i1 + s1 * f) + s2 * x)$	Breakpoint (°C)	-0.94	-0.20	0.60
				Expl. variance	0.91	0.67	0.66
				AIC	1771	2185	1598
11	Temperature variability	LGM temperature	$y \sim (x1 \leq f) * (i1 + s1 * x) + (x1 > f) * (i2 + s2 * x)$	Breakpoint (°C)	-4.13	0.40	0.40
				Expl. variance	0.94	0.73	0.74
				AIC	1319	1990	1325
	LGM temperature	LGM temperature	$y \sim (x1 \leq f) * (i1 + s1 * x) + (x1 > f) * ((i1 + s1 * f) + s2 * (x - f))$	Breakpoint (°C)	-12.37	-5.81	-5.12

12				Expl. variance	0.94	0.73	0.75
				AIC	1231	1974	1283
				Breakpoint (°C)	-12.34	-5.06	-5.26
13	LGM temperature	LGM temperature	$y \sim (x1 \leq f) * (i1 + s1 * x) + (x1 > f) * (i2 + s2 * x)$	Expl. variance	0.94	0.73	0.75
				AIC	1233	1975	1285

Local slopes of richness–precipitation variability

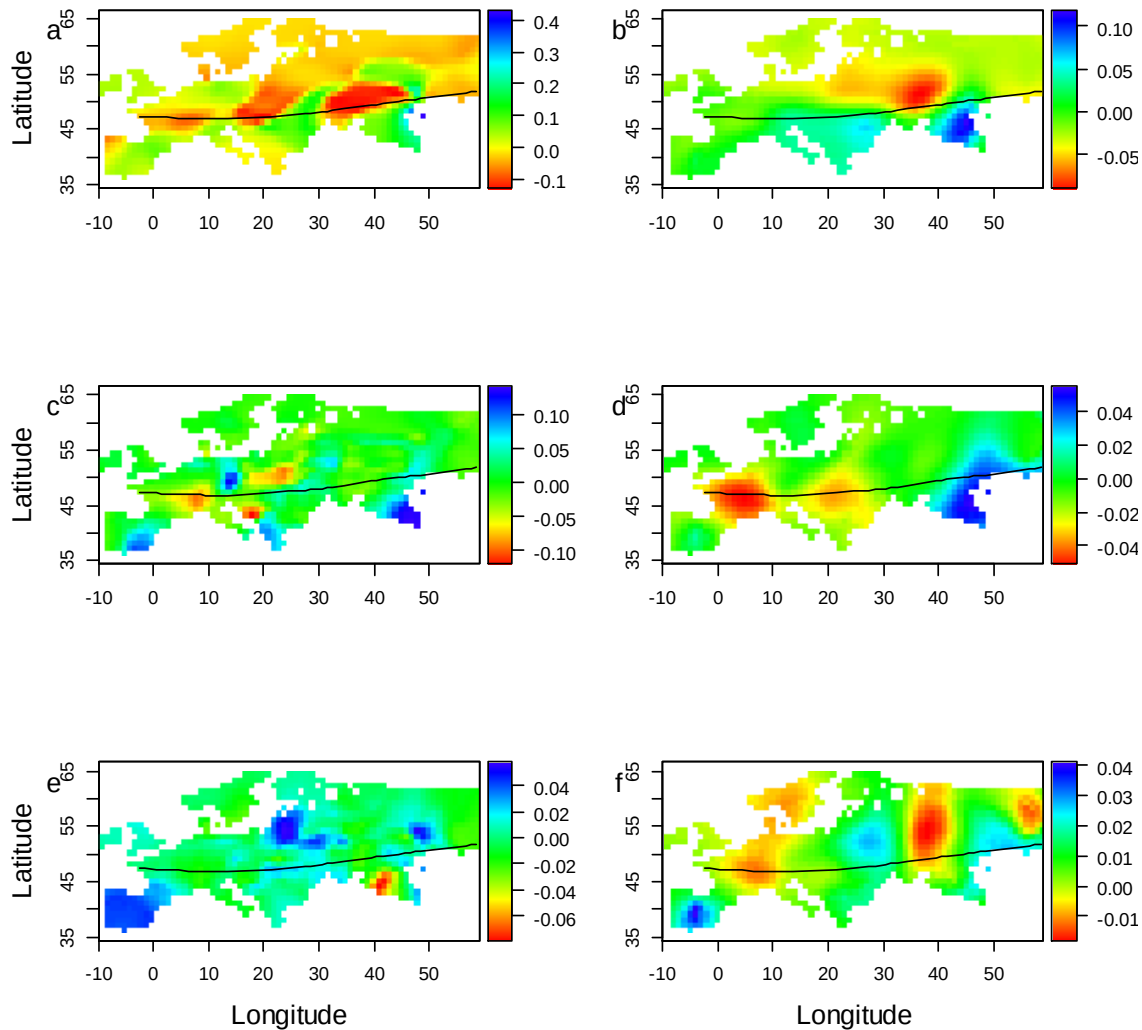


Figure S7.1 Non-stationarity in the relationship between Scarabaeinae richness and precipitation variability since the last glacial maximum (LGM). The maps show the distribution of the local slope of the richness–precipitation variability relationship fitted through geographically weighted regression (GWR) models using either a bi-squared (left) or Gaussian (right) weighting function of the 5% neighbouring grid cells. The GWR models have been fitted including different independent variables, either (a,b) only precipitation variability, (c,d) precipitation variability and current temperature and precipitation or (e,f) 14 historic and current environmental variables. The black lines represent the location of the LGM 0°C isotherm.

Null distribution of expected breakpoints

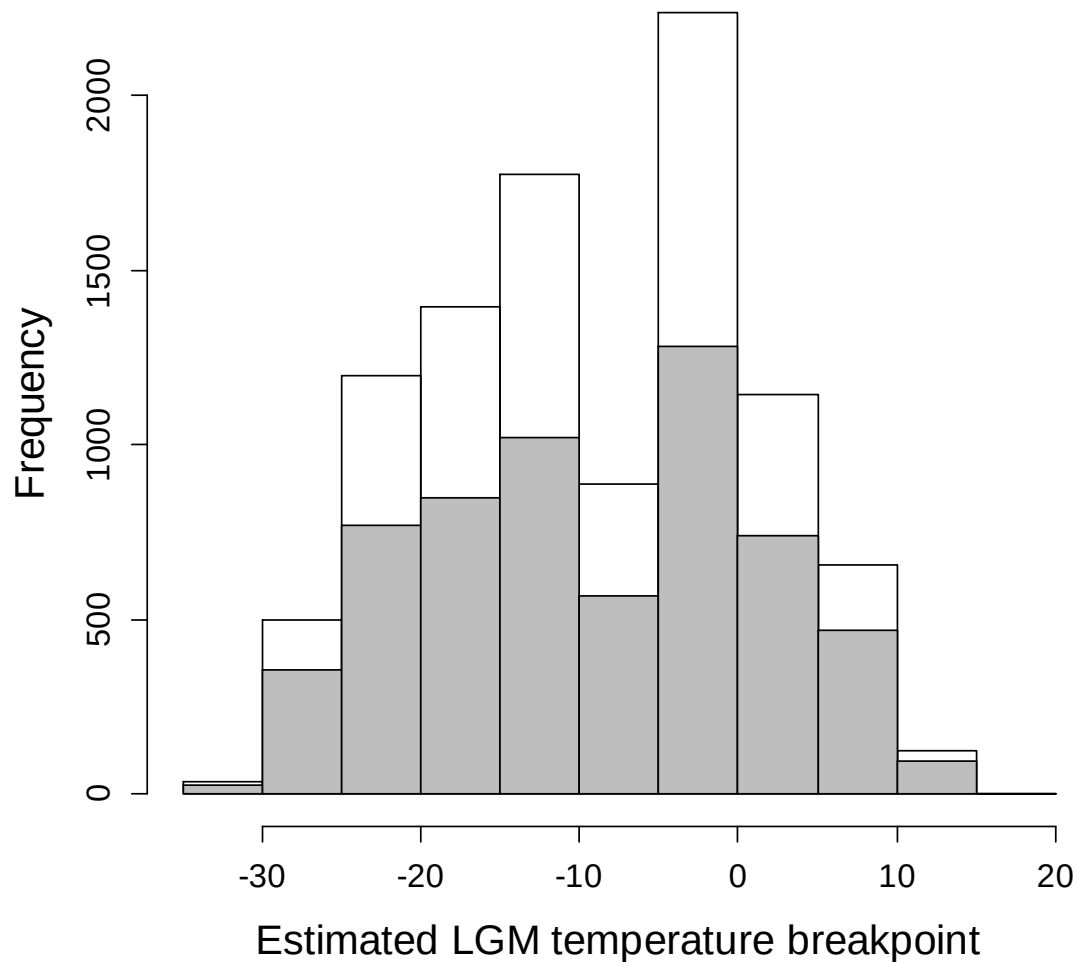


Figure S7.2 Frequency distribution of estimated breakpoints when species richness is simulated to be a negative linear function of observed temperature variability since the LGM in Europe with normally distributed error (mean=0, sd=8, mean R^2 of simulated richness–temperature variability linear relationship= 0.51). Richness has been simulated 10,000 times and fitted by a piecewise function of temperature variability, where an independent slope and intercept is fitted above and below a fitted LGM temperature (Eq 1 in Table S7.1). The shaded portions of the bars represent piecewise models for which the AIC was lower than that of a simple linear model (62% of simulations). Breakpoints at LGM temperatures between -5 and 0°C are most frequently estimated.

Additional references

- Davis, E.B., McGuire, J.L. & Orcutt, J.D. (2014) Ecological niche models of mammalian glacial refugia show consistent bias. *Ecography*, **37**, 1133–1138.
- Dullinger, S., Willner, W., Plutzer, C., Englisch, T., Schratt-Ehrendorfer, L., Moser, D., Ertl, S., Essl, F. & Niklfeld, H. (2012) Post-glacial migration lag restricts range filling of plants in the European Alps. *Global Ecology and Biogeography*, **21**, 829–840.
- Worth, J.R.P., Williamson, G.J., Sakaguchi, S., Nevill, P.G. & Jordan, G.J. (2014) Environmental niche modelling fails to predict Last Glacial Maximum refugia: niche shifts, microrefugia or incorrect palaeoclimate estimates? *Global Ecology and Biogeography*, **40**, 126–138.

APPENDICES CHAPTER 8

Appendix S8.1

Examples of simulated climatic gradients

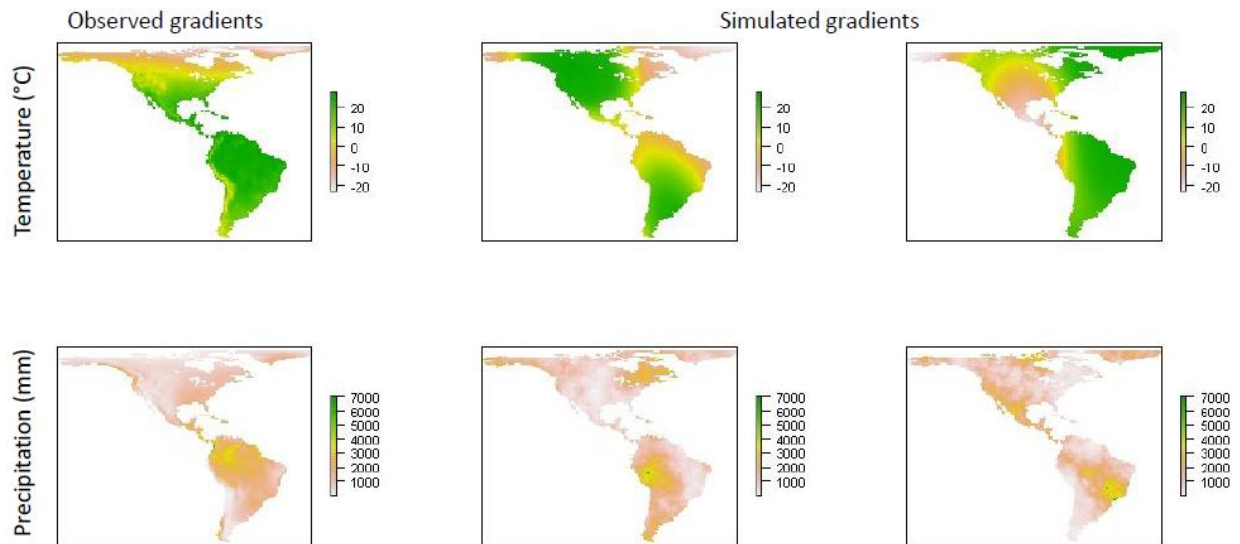


Figure S8.1 Observed mean annual temperatures (°C) and total annual precipitations (mm) along with two examples of simulated climatic gradients that randomize observed values while keeping the same spatial autocorrelation structure as in the observed data following Chapman (2010).

Results from the randomizations of temperature in birds only

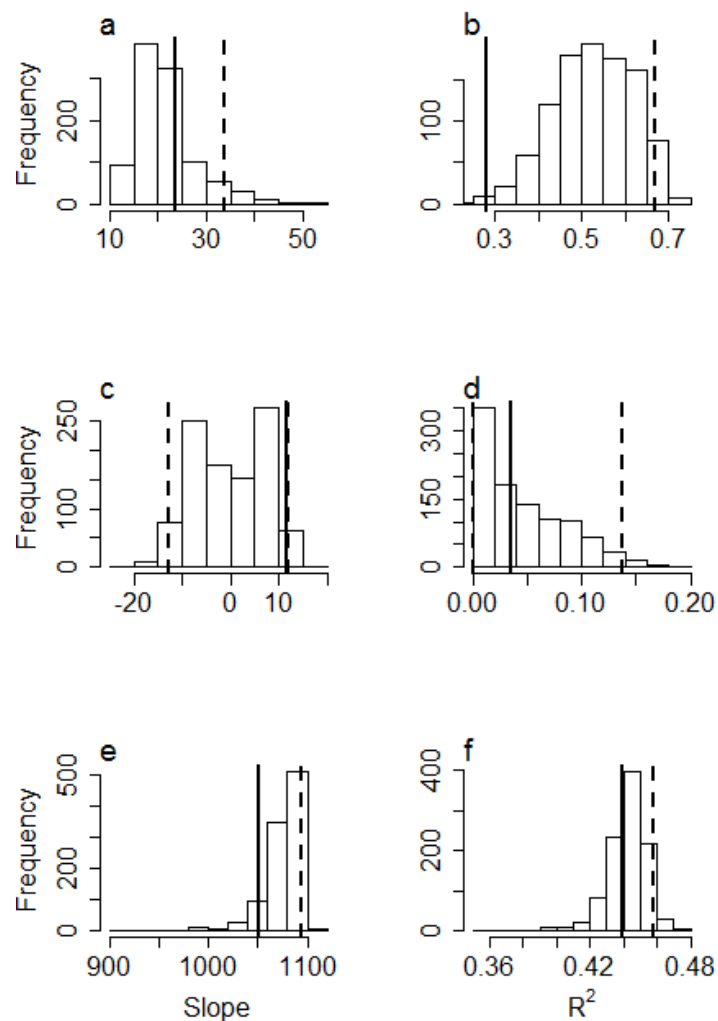


Figure S8.2 Distribution of (a, c, e) slope and (b, d, f) R^2 values of bird range size as a function of temperature niche properties obtained from 1000 randomizations of temperatures throughout the Americas (e.g. Fig. S8.1). For each randomization, range size was regressed against temperature (a-b) niche breadth, (c-d) niche position and (e-f) range filling. The observed coefficients obtained from 3277 non-migratory bird species are represented by a solid line. Dashed lines represent the threshold of the 5% most extreme values obtained from randomizations (one-tailed for niche breadth and range filling; two-tailed for niche position).

Results from the randomizations of precipitation in birds only

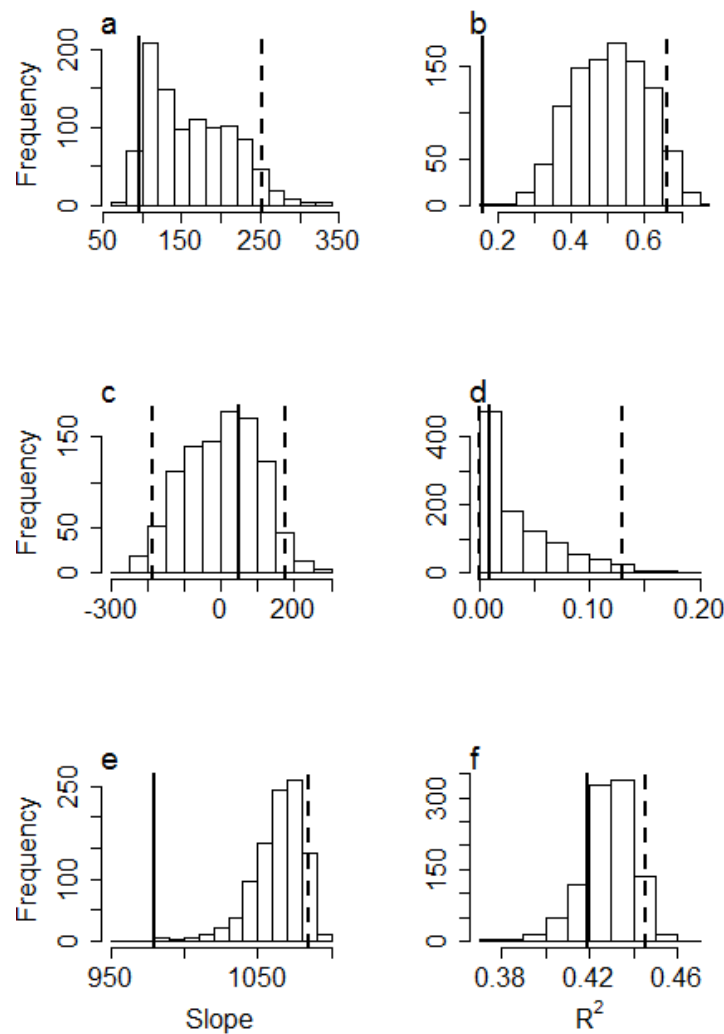


Figure S8.3 Distribution of (a, c, e) slope and (b, d, f) R^2 values of bird range size as a function of precipitation niche properties obtained from 1000 randomization of precipitations throughout the Americas (e.g. Fig. S8.1). For each randomization, range size was regressed against precipitation (a-b) niche breadth, (c-d) niche position and (e-f) range filling. The observed coefficients obtained from 3277 non-migratory bird species are represented by a solid line. Dashed lines represent the threshold of the 5% most extreme values obtained from randomizations (one-tailed for niche breadth and range filling; two-tailed for niche position).

Results from the randomizations of temperature in mammals only

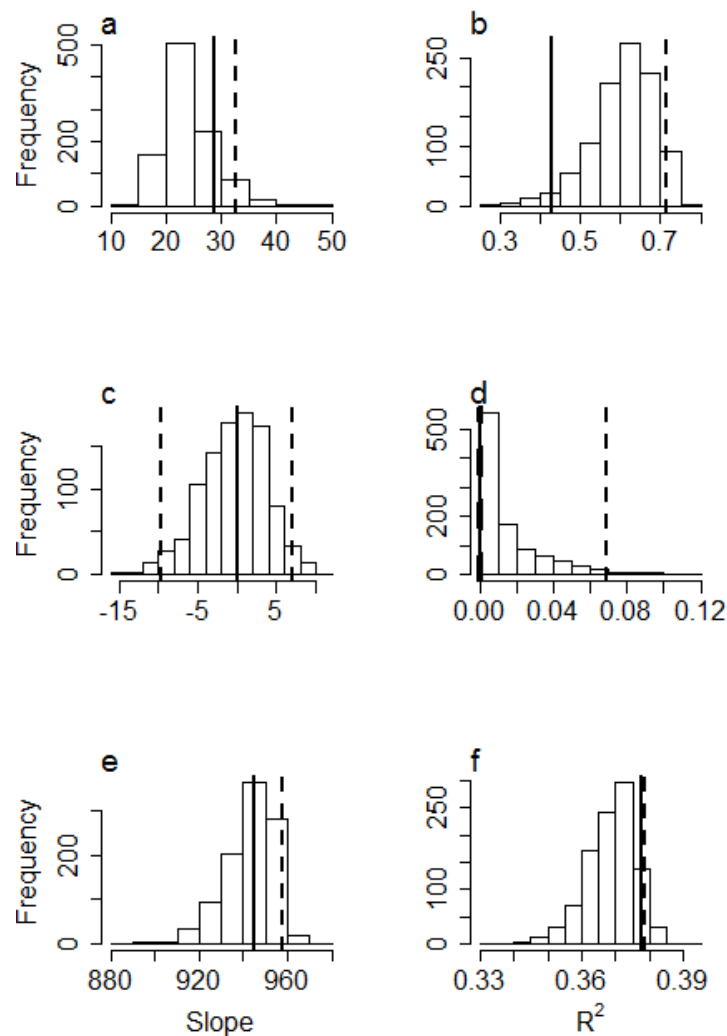


Figure S8.4 Distribution of (a, c, e) slope and (b, d, f) R^2 values of mammal range size as a function temperature niche properties obtained from 1000 randomization of temperatures throughout the Americas (e.g. Fig. S8.1). For each randomization, range size was regressed against temperature (a-b) niche breadth, (c-d) niche position and (e-f) range filling. The observed coefficients obtained from 1659 non-migratory mammal species are represented by a solid line. Dashed lines represent the threshold of the 5% most extreme values obtained from randomizations (one-tailed for niche breadth and range filling; two-tailed for niche position).

Results from the randomizations of precipitation in mammals only

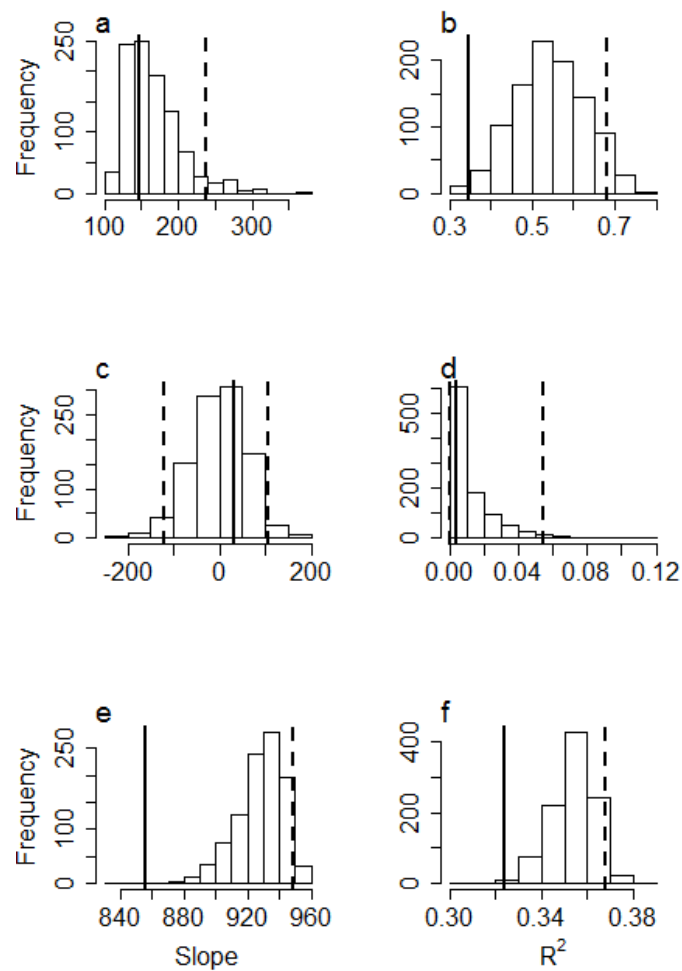


Figure S8.5 Distribution of (a, c, e) slope and (b, d, f) R^2 values of mammal range size as a function of precipitation niche properties obtained from 1000 randomization of precipitations throughout the Americas (e.g. Fig. S8.1). For each randomization, range size was regressed against precipitation (a-b) niche breadth, (c-d) niche position and (e-f) range filling. The observed coefficients obtained from 1659 mammal species are represented by a solid line. Dashed lines represent the threshold of the 5% most extreme values obtained from randomizations (one-tailed for niche breadth and range filling; two-tailed for niche position).

All results for the range size–range filling relationship, when the potential range is unconstrained

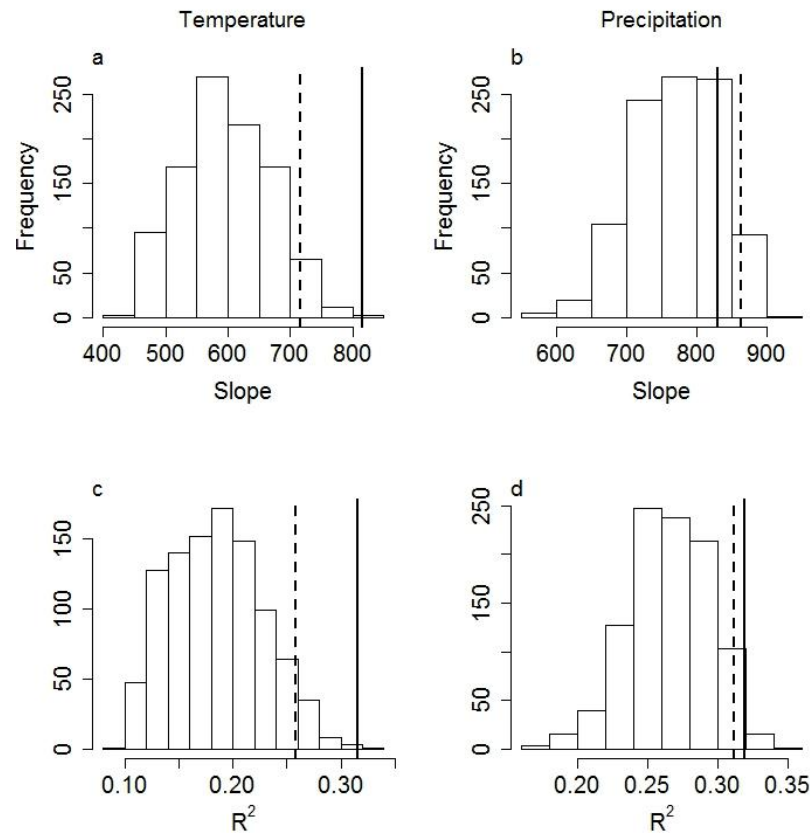


Figure S8.6 Distribution of (a, b) slope and (c, d) R^2 values of range size as a function range filling obtained from 1000 randomizations of temperature and precipitation within the Americas. Range filling is the realized/potential range size ratio. Here, the potential range is calculated as all quadrats within the Americas that fall within the species' occupied climatic niche. In the main text, the potential range is calculated within the zoogeographic region(s) in which the species occur such that the geographical extent of climatic conditions in distant regions does not affect the potential range (see Figure 2e-f and Figure 3e-f in the main text for comparison). Range filling is calculated for (a, c) temperature and (b, d) precipitation. In each panel, the observed slope obtained from 3277 bird and 1659 mammal species is represented by a solid line. The upper 5% threshold from the set of randomizations is shown by a dashed line.

Correlations among niche properties (Table 1) compared to expectations from randomizations for birds only

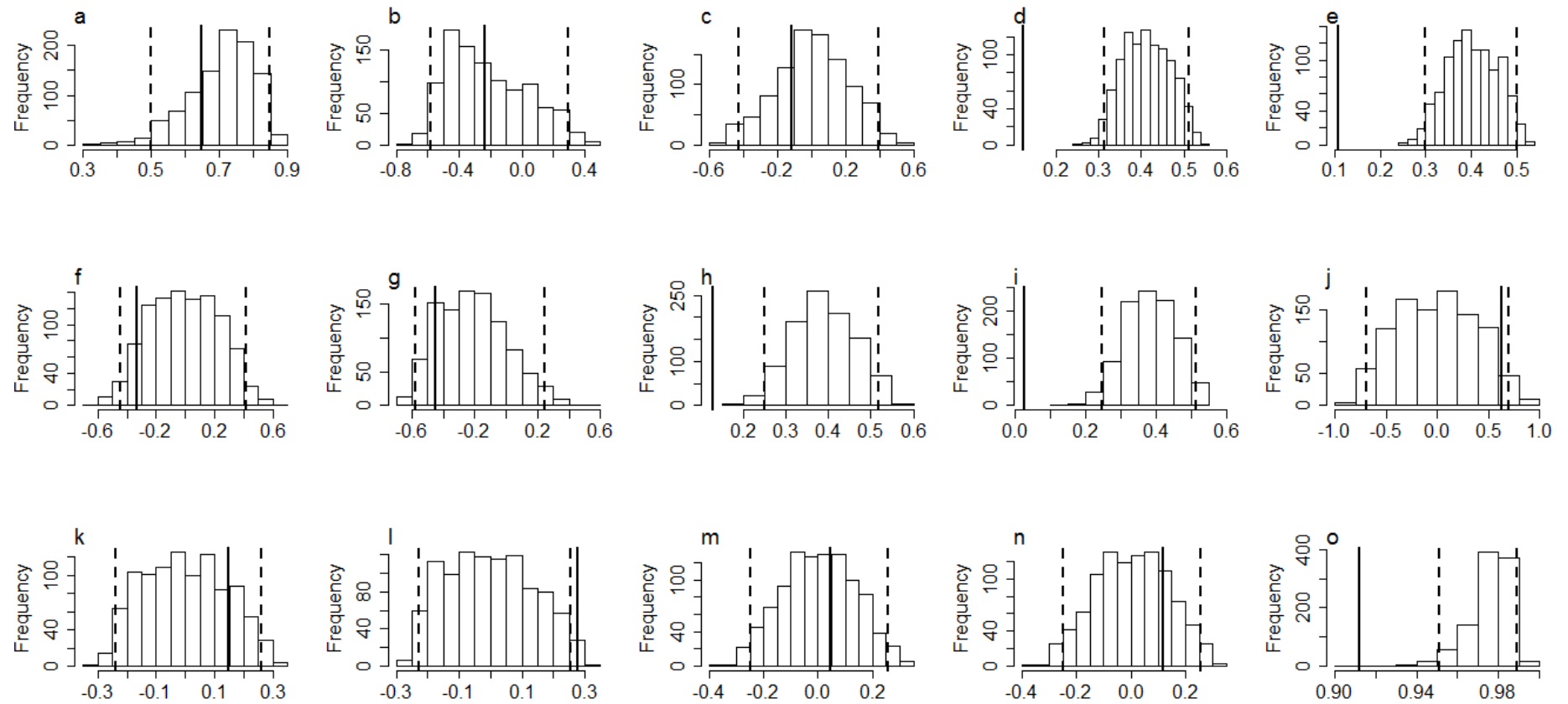


Figure S8.7 Distribution of correlation coefficients between all pairwise combinations of niche properties of 3277 bird species presented in Table 1 obtained from 1000 randomization of temperature and precipitation within the Americas. The correlations coefficients are presented for (a) temperature and precipitation niche breadth; (b) temperature niche breadth and temperature niche position; (c) temperature niche breadth and precipitation niche position; (d) temperature niche breadth and temperature range filling; (e) temperature niche breadth and precipitation range filling; (f) precipitation niche breadth and temperature niche position; (g) precipitation niche breadth and precipitation niche position; (h) precipitation niche breadth and temperature range filling; (i) precipitation niche breadth and precipitation range filling; (j) temperature and precipitation niche position; (k) temperature niche position and temperature range filling; (l) temperature niche position and precipitation range filling; (m) precipitation niche position and temperature range filling; (n) precipitation niche position and precipitation range filling; and (o) temperature and precipitation range filling. The observed correlation coefficients (presented in Table 1 of the main text) are represented by a vertical solid line. The dashed lines represent the 5% most extreme correlation coefficients obtained from the randomizations (two-tailed).

Correlations among niche properties (Table 1) compared to expectations from randomizations for mammals only

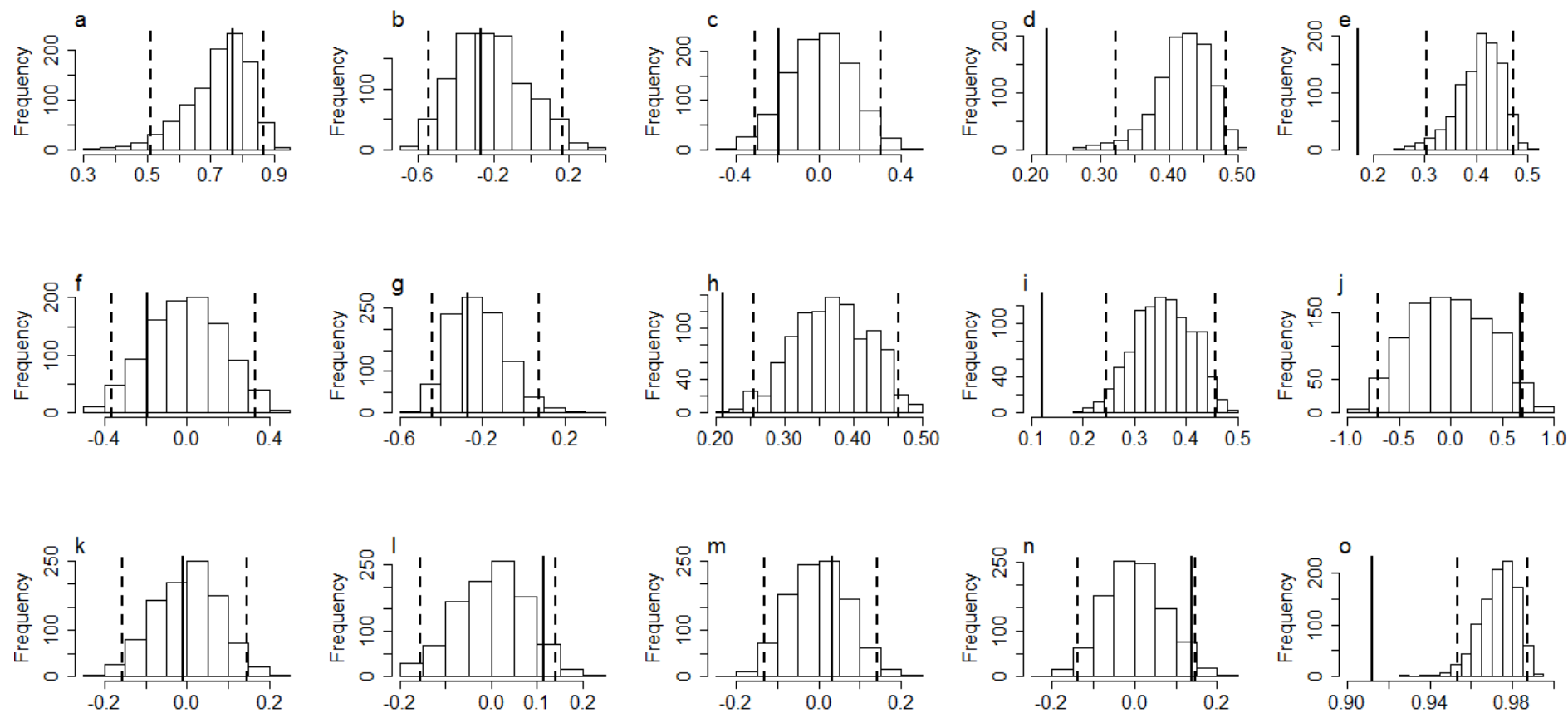


Figure S8.8 Distribution of correlation coefficients between all pairwise combinations of niche properties of 1659 mammal species presented in Table 1 obtained from 1000 randomization of temperature and precipitation within the Americas. The correlations coefficients are presented for (a) temperature and precipitation niche breadth; (b) temperature niche breadth and temperature niche position; (c) temperature niche breadth and precipitation niche position; (d) temperature niche breadth and temperature range filling; (e) temperature niche breadth and precipitation range filling; (f) precipitation niche breadth and temperature niche position; (g) precipitation niche breadth and precipitation niche position; (h) precipitation niche breadth and temperature range filling; (i) precipitation niche breadth and precipitation range filling; (j) temperature and precipitation niche position; (k) temperature niche position and temperature range filling; (l) temperature niche position and precipitation range filling; (m) precipitation niche position and temperature range filling; (n) precipitation niche position and precipitation range filling; and (o) temperature and precipitation range filling. The observed correlation coefficients (presented in Table 1 of the main text) are represented by a vertical solid line. The dashed lines represent the 5% most extreme correlation coefficients obtained from the randomizations (two-tailed).

Results from a restricted set of randomizations of temperature in birds

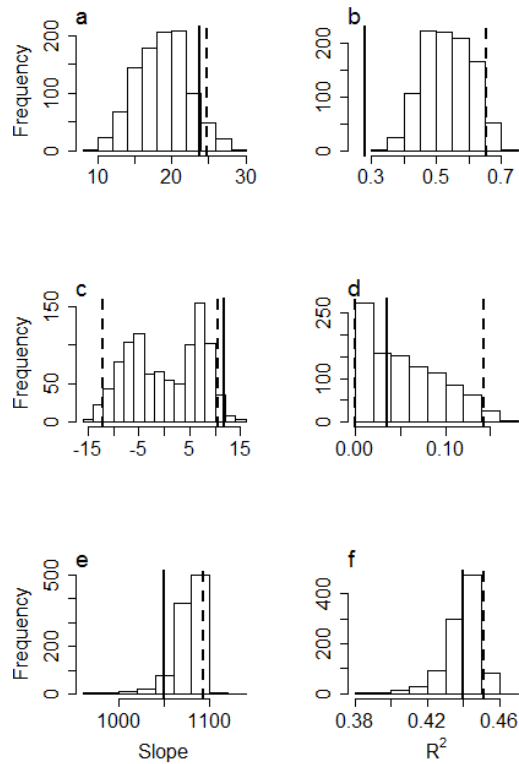


Figure S8.9 Distribution of (a, c, e) slope and (b, d, f) R^2 values of bird range size as a function of temperature niche properties obtained from 1000 randomizations of temperatures throughout the Americas. Here, the set of temperature randomizations was constrained to be correlated with the real temperature data with $|r| < 0.2$. For each randomization, range size was regressed against temperature (a-b) niche breadth, (c-d) niche position and (e-f) range filling. The observed coefficients obtained from 3277 non-migratory bird species are represented by a solid line. Dashed lines represent the threshold of the 5% most extreme values obtained from randomizations (one-tailed for niche breadth and range filling; two-tailed for niche position). This figure is equivalent to Figure S8.2, but uses a more liberal null model by restricting the set of possible randomizations.

Results from a restricted set of randomizations of precipitation in birds

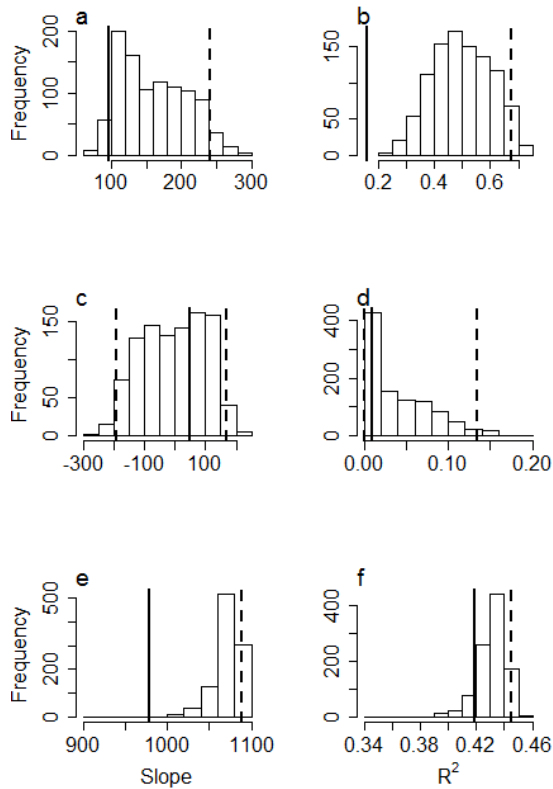


Figure S8.10 Distribution of (a, c, e) slope and (b, d, f) R^2 values of bird range size as a function of precipitation niche properties obtained from 1000 randomizations of temperatures throughout the Americas. Here, the set of precipitation randomizations was constrained to be correlated with the real precipitation data with $|r| < 0.2$. For each randomization, range size was regressed against precipitation (a-b) niche breadth, (c-d) niche position and (e-f) range filling. The observed coefficients obtained from 3277 non-migratory bird species are represented by a solid line. Dashed lines represent the threshold of the 5% most extreme values obtained from randomizations (one-tailed for niche breadth and range filling; two-tailed for niche position). This Figure is equivalent to Figure S8.3, but uses a more liberal null model by restricting the set of possible randomizations.

Results from a restricted set of randomizations of temperature in mammals

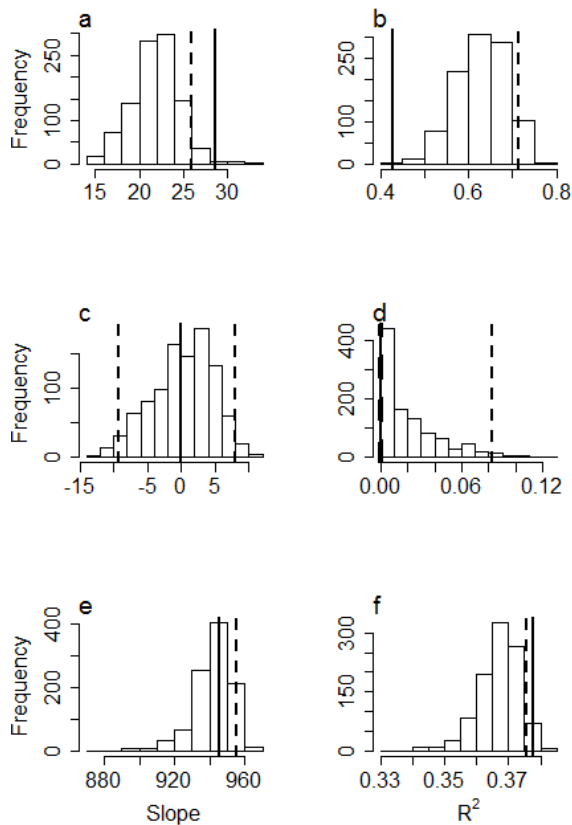


Figure S8.11 Distribution of (a, c, e) slope and (b, d, f) R^2 values of mammal range size as a function of temperature niche properties obtained from 1000 randomizations of temperatures throughout the Americas. Here, the set of temperature randomizations was constrained to be correlated with the real temperature data with $|r| < 0.2$. For each randomization, range size was regressed against temperature (a-b) niche breadth, (c-d) niche position and (e-f) range filling. The observed coefficients obtained from 1659 mammal species are represented by a solid line. Dashed lines represent the threshold of the 5% most extreme values obtained from randomizations (one-tailed for niche breadth and range filling; two-tailed for niche position). This Figure is equivalent to Figure S8.4, but uses a more liberal null model by restricting the set of possible randomizations.

Results from a restricted set of randomizations of precipitation in mammals

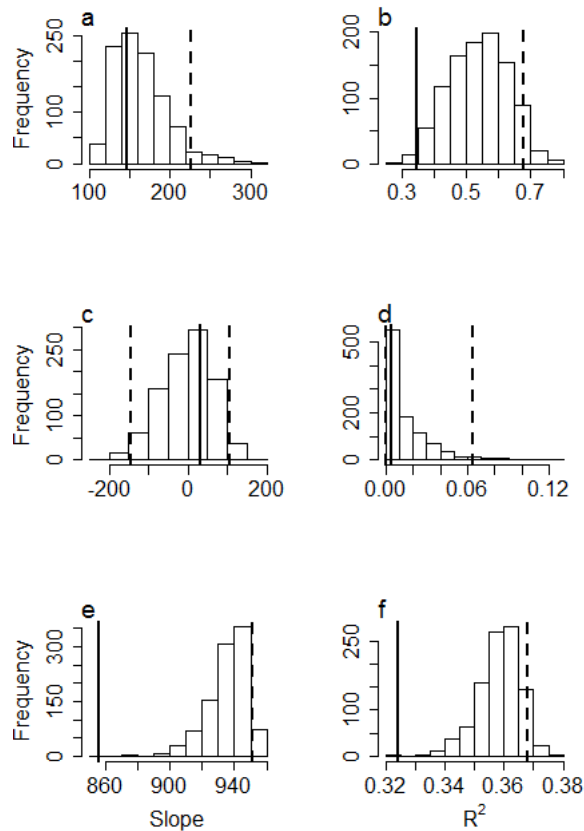


Figure S8.12 Distribution of (a, c, e) slope and (b, d, f) R^2 values of mammal range size as a function of precipitation niche properties obtained from 1000 randomizations of precipitation throughout the Americas. Here, the set of precipitation randomizations was constrained to be correlated with the real precipitation data with $|r| < 0.2$. For each randomization, range size was regressed against precipitation (a-b) niche breadth, (c-d) niche position and (e-f) range filling. The observed coefficients obtained from 1659 mammal species are represented by a solid line. Dashed lines represent the threshold of the 5% most extreme values obtained from randomizations (one-tailed for niche breadth and range filling; two-tailed for niche position). This Figure is equivalent to Figure S8.4, but uses a more liberal null model by restricting the set of possible randomizations.

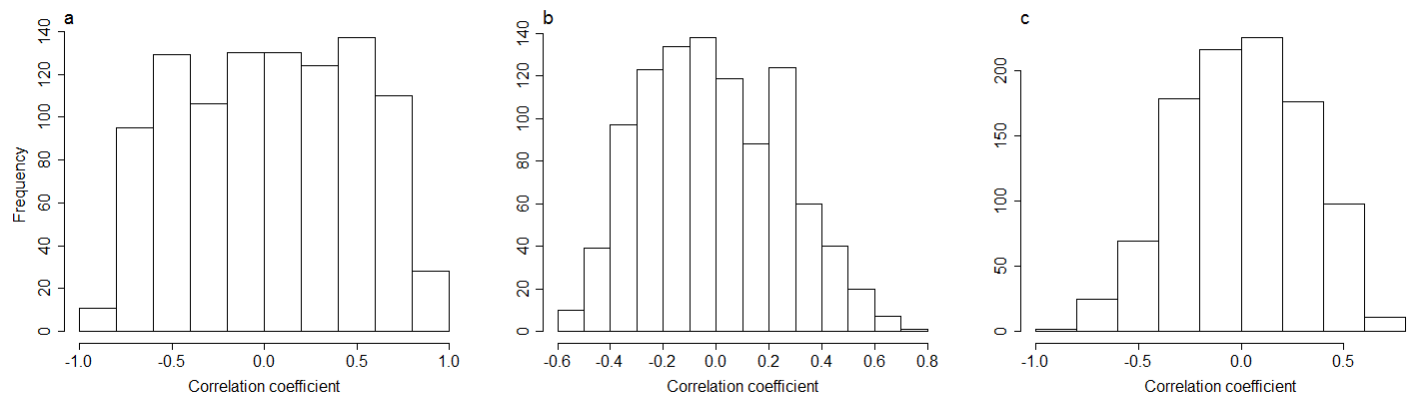


Figure S8.13 Frequency distribution of the correlation coefficients between (a) real and 1000 iterations of randomized temperature gradients, (b) real and 1000 iterations of randomized precipitation gradients and (c) 1000 iterations of randomized precipitation and temperature gradients.