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 (a) Species' distributions in climatic space do not have strong thresholds, nor are they systematically skewed towards less stressful climates. (b) 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. (c) Occupied geographic ranges are typically ringed by unoccupied, but climatically suitable areas. (d) 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.

Keywords

Abiotic stress, ecological niche, Gaussian response curve, geographic range, habitat suitability, northern range limit, plants, potential range size, probability of occurrence, species distribution modelling.

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INTRODUCTION

Robert MacArthur (1972, p. 127), in his classic work *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 catalogues of special cases'. Textbook wisdom indicates that species distribu-

tions can be affected by factors including climate, 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 catalogue of possible influences on the ranges of individual species, our goal is to identify strong empirical consistencies of how species are distributed, as opposed to focusing on the biology of any particular species.

Since von Humboldt (Hawkins, 2001), climate has been recognized as the most obvious potential determinant of species distributions. At the continental scale, geographic variation in species richness is strongly related to combined measures of temperature and precipitation (Field *et al.*, 2005, 2009), and the distributions of individual species 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) 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.*, 2011), 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 occurrence 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' (also known as 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; Körner & Paulsen, 2004).

Figure 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).

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. The use of 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 (US 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 USA. 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 km^2.

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 in Supporting Information). 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 *c*. 5000 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 pixels with a temperature *t* and precipitation *p* that fall 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 (in mm) in the study area is strongly positively skewed, we first square-root transformed precipitation. We then divided this range into 23 bins, each three

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. 2c,d) and some others are very rare. Climatic combinations represented by fewer than 100 pixels were excluded from the analyses (these were all situated at the margin between existent and non-existent 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. 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 T_s and 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 Fig. 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 the observed climatic niche of each species were excluded from the test of this hypothesis (i.e. all occupied climate bins for which at least one of the four nearest neighbours is unoccupied). We accepted the tolerance hypothesis if, in the remaining climate bins (hereafter referred to as the core climatic niche), occupancy $\Omega_{stp} \geq 0.75$ in all bins. This threshold is arbitrary but also fairly liberal, and results are robust to the threshold definition (Appendix S2). 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 modelled a bivariate normal function of temperature and precipitation (Appendix S3). We retained all bins in which $\Omega_{stp} > 0$, plus a ring of unoccupied climate bins directly adjacent to occupied ones. A bivariate normal model
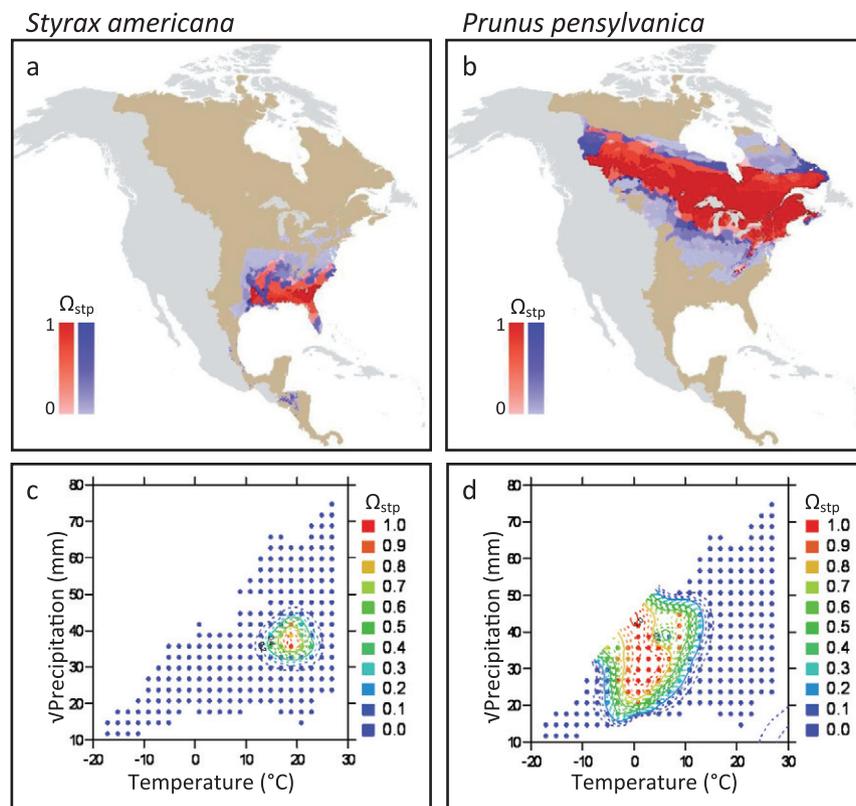
Figure 2 Examples of the observed climatic niches of trees in (a, b) geographic and (c, d) climatic space, shown for (a, c) *Styrax americana* (American snowbell) and (b, d) *Prunus pensylvanica* (pin cherry). In (a, b) the occupied range is red, and unoccupied but climatically suitable regions are blue. The colour intensity is proportional to occupancy Ω_{stp}; the darker colours 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, centred on −100° longitude. Panels (c) and (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 colour gradient indicates the occupancy Ω_{stp} of the climate bin $t \times p$ and the contour lines represent a distance-weighted least squares smoothing of Ω_{stp} values at a tension of 0.1.

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.

Lastly, 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 S3).

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). We considered only the 98 climatic bins that had more than 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; 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

Table 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%*; precipitation 11%*

*Considering only the 141 species with non-truncated observed climatic niches.

one (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 three 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 ± 22% (SD) of their observed climatic niche (see Fig. 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 $\Omega_{stp} \geq 75\%$ in all bins of its core climatic niche (Table 1) and this increases only to six species if we lower it to $\Omega_{stp} \geq 50\%$ (Appendix S2).

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, Appendix S3). For these species, the threshold model accounts on average for 78 ± 2% (SE) of the variance in Ω_{stp}. The threshold model accounts for 55 ± 1% (SE), averaged over all species. Note that, for several reasons (Appendix S3), it was not possible to compare the competing models with standard information theoretic statistics.

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 ± 1% (SE), of the variance in occupancy (Fig. 3). For most species, occupancy did not depend upon an interaction between t and p (Appendix S3). For 91% of the 482 species, the R^2 of the peaked suitability model was higher than or equal to the R^2 of the threshold model (Table 1). Comparing the threshold and peaked suitability model based on R^2 rather than maximum likelihood is more liberal in favour of the threshold model (Appendix S3). Moreover, the high R^2 values of the peaked suitability model remain high when climate bins
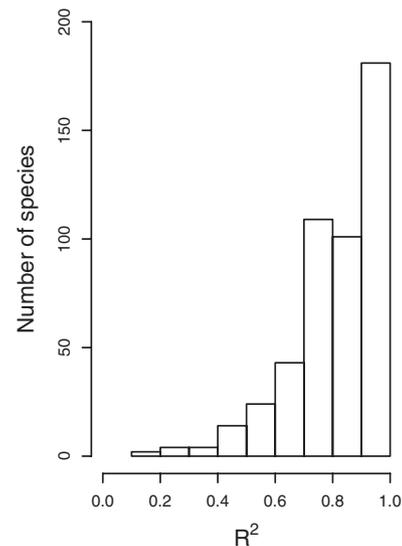
Figure 3 Distribution of the variability in occupancy Ω_{stp} of a region by species s explained by a bivariate normal function of temperature and precipitation. The model was fitted for each of 482 species climatic niche (i.e. all occupied climate bins) surrounded by a single ring of zero-occupancy.

with zero-occupancy are excluded (Appendix S4). 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 S5.

Our results are inconsistent with the asymmetric limitation hypothesis. The observed climatic niches of North American trees are not systematically skewed towards the less stressful end of the climatic gradient (Fig. 4). The probability of exhibiting a right-skewed response is not greater than a left-skewed one (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). Left-skewed distributions occur in 15% of species for temperature and 23% for precipitation, which is as
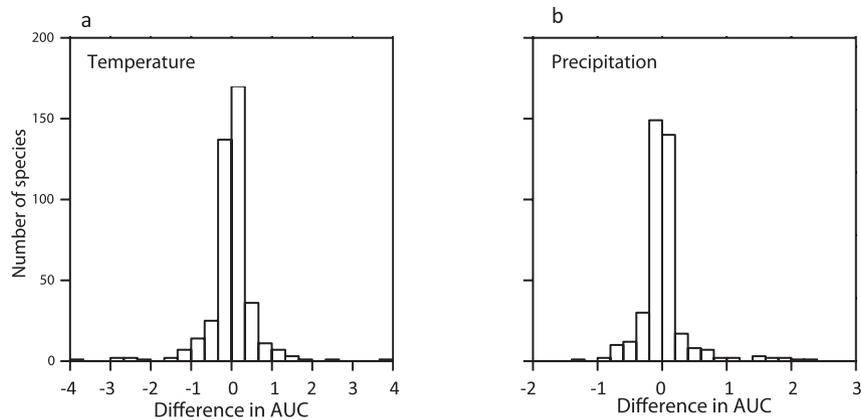
Figure 4 Distribution of the differences in area under the curve (AUC) on the benign versus the stressful sides of the most occupied climate for (a) temperature (AUC high temperature – AUC low temperature), 95% confidence interval (CI_{mean}) = [−0.058, 0.033] and n = 421, and (b) precipitation (AUC 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.

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 S6). Our conclusions are not affected by the climate bin delineation (Appendix S7).

Occupancy across dispersal barriers

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

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. 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 the western mainland and 0.53 for islands. For islands, but not for the western mainland, the mean ρ is 1.5 times larger for broadly than for 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. 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 the eastern and western mainland (two-sided binomial test; $P = 0.82$), but it is usually smaller offshore ($P < 0.001$).

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. 5e, f) and even non-nested niches are quite similar to one another (Fig. 5g, h), with only two species having entirely non-nested climatic niches (Fig. 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 $\Omega_{stp} < 0.001$ in the eastern mainland (of the climates also existing in the western mainland).

DISCUSSION

We have here demonstrated that, despite the 'catalogue of special cases' (MacArthur, 1972, p. 172) that have been used to characterize them, the geographic ranges of tree species 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_{stp} 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 macroscale 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

Figure 5 Distribution of four different measures of climatic niche similarity, comparing each species' eastern mainland distribution with that of the western mainland (left) or islands (right). (a), (b) 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). Correlations to the right of the dotted line are significant at $\alpha = 0.05$. (c), (d) For the same sets of species, the 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 neighbouring climate bins.
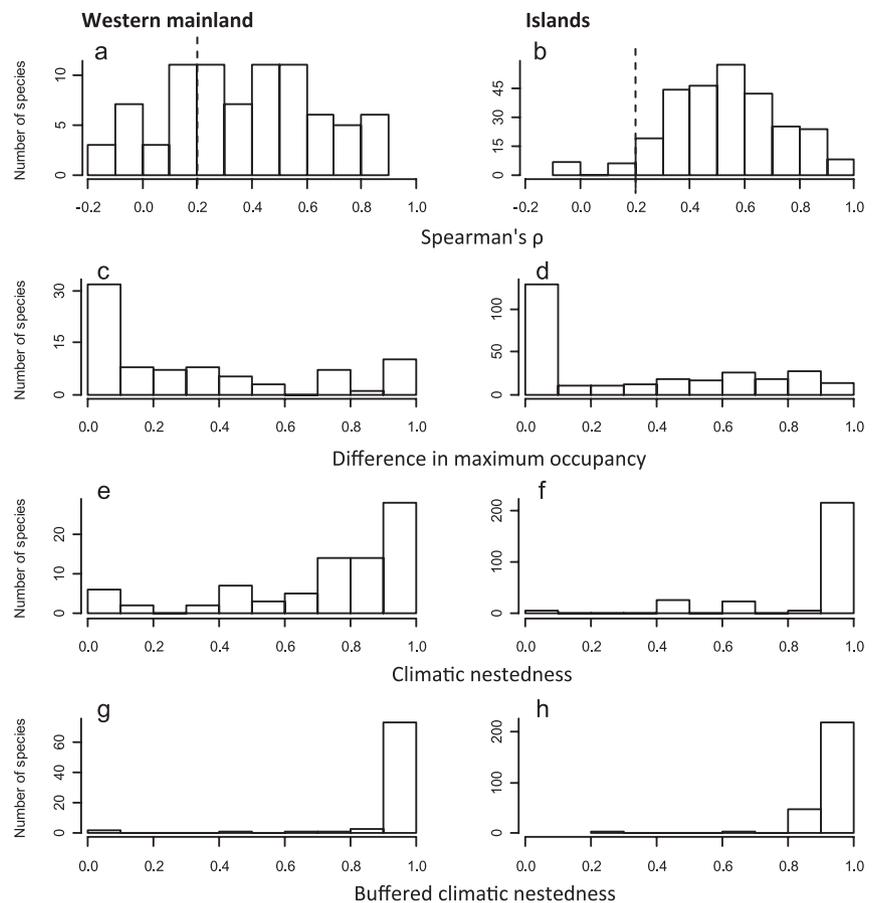
whether, among the species occupying a given location, the distribution of these parameters is predictable from climate, topography, etc.

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 the 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 considered here was computed by Morin et al. (2007) using a process-based modelling approach. Our measured realized/potential range size ratios for these species that are only slightly lower than Morin et al.'s (56 vs. 64%) and 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. 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. 3). Any residual skew is thus quite small and is frequently in the direction opposite to that 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%) where more frequent than left skewed (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 S6; 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 macroscale 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 reasons: 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 and 200 mm year^{-1} is much greater than that between 2100 and 2200 mm year^{-1}: Holdrige (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 errors of commission or omission in climatically suitable areas, 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. 2 are typical of the tree distributions we examined. Svenning & 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; US 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 (McInerny *et al.*, 2009; Nogués-Bravo, 2009) and (2) that other factors affecting fitness such as extreme climatic events, suboptimal soil quality or competition act independently and multiplicatively (Brown *et al.*, 1998) 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.*, 1998). 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 neighbouring populations, and local extinction probability depends mainly (but not solely) upon climate. Specifically, we hypothesize that the probability of local extinction is proportional to $|t - T_s|$ and $|p - P_s|$ (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 suboptimal 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 independent of climate (e.g. Beale *et al.*, 2008). Therefore, spatial autocorrelation could be responsible for the symmetric decrease in occupancy around a species' most occupied climate we observe here. However, the observed relationship between species distributions and climate seems likely, at most, to be inflated by spatial autocorrelation. First, palaeoecological (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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SUPPORTING INFORMATION

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

Appendix S1 Map of the study area.
Appendix S2 Robustness of the tolerance hypothesis to the acceptance level.
Appendix S3 Methodological details.
Appendix S4 Robustness of the peaked suitability model to zero-occupancy.
Appendix S5 Coefficients obtained from the peaked suitability model.
Appendix S6 Additional results for the asymmetric limitation hypothesis.
Appendix S7 Effect of the climate bin delineation on the results.

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