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Global patterns in the shape of species geographical ranges reveal range determinants

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ABSTRACT

Aim Do species range shapes follow general patterns? If so, what mechanisms underlie those patterns? We show for 11,582 species from a variety of taxa across the world that most species have similar latitudinal and longitudinal ranges. We then seek to disentangle the roles of climate, extrinsic dispersal limitation (e.g. barriers) and intrinsic dispersal limitation (reflecting a species' ability to disperse) as constraints of species range shape. We also assess the relationship between range size and shape.

Location Global.

Methods Range shape patterns were measured as the slope of the regression of latitudinal species ranges against longitudinal ranges for each taxon and continent, and as the coefficient of determination measuring the degree of scattering of species ranges from the 1:1 line (i.e. latitudinal range = longitudinal range). Two major competing hypotheses explaining species distributions (i.e. dispersal or climatic determinism) were explored. To this end, we compared the observed slopes and coefficients of determination with those predicted by a climatic null model that estimates the potential range shapes in the absence of dispersal limitation. The predictions compared were that species distribution shapes are determined purely by (1) intrinsic dispersal limitation, (2) extrinsic dispersal limitations such as topographic barriers, and (3) climate.

Results Using this methodology, we show for a wide variety of taxa across the globe that species generally have very similar latitudinal and longitudinal ranges. However, neither neutral models assuming random but spatially constrained dispersal, nor models assuming climatic control of species distributions describe range shapes adequately. The empirical relationship between the latitudinal and longitudinal ranges of species falls between the predictions of these competing models.

Main conclusions We propose that this pattern arises from the combined effect of macroclimate and intrinsic dispersal limitation, the latter being the major determinant among restricted-range species. Hence, accurately projecting the impact of climate change onto species ranges will require a solid understanding of how climate and dispersal jointly control species ranges.

Keywords

Climatic envelopes, dispersal limitation, macroecology, neutral theory, niche determinism, range shape, species distribution modelling.

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INTRODUCTION

In a seminal paper, Brown & Maurer (1989) provided an influential research programme for the emerging field of

macroecology. Most of the questions listed have been subject to extensive research over the intervening 20 years (see Appendix S1 in Supporting Information). One exception is the documentation of patterns of species range shape and the

related investigation of what mechanisms cause them. These questions have been largely neglected by the macroecological community, with the exception of a small number of exploratory studies. For example, Brown & Maurer (1989), Brown (1995) and Brown *et al.* (1996) investigated the shape of species ranges for North American mammals, birds and reptiles, and found that most species with restricted ranges have distributions that are elongated in a north–south direction. Simultaneously, most species with large distributions were found to have elongated ranges in an east–west direction. The authors hypothesized that restricted-range species are limited mainly by topographical barriers (mountains, river valleys, coast lines), which, in North America, are oriented in a north–south direction. In contrast, widely distributed species should circumvent these barriers and instead be limited by macroclimate and the associated biomes, which generally run east–west in latitudinal bands. Examining range shapes for European birds and mammals, Brown & Maurer (1989) found that species with relatively restricted ranges in Europe have distributions that are east–west-oriented; they attributed this pattern to the longitudinal orientation of most European mountain chains (Brown & Maurer, 1989; Brown, 1995). Since the pioneer work of Brown and Maurer, only a few studies have examined elongation patterns in range shapes for different groups and territories (see Pfrender *et al.*, 1998; Hecnar, 1999; Rosenfield, 2002; Schlachter, 2010). Although not explicitly stressed in these studies, a striking pattern emerges from these analyses of range shapes: the apparently strong correlation between latitudinal and longitudinal ranges of species (see Figure 6 in Brown & Maurer, 1989). The critical question is how general these correlations are. Do they hold across different regions and organisms? If so, what mechanisms underlie the pattern? Can a correlation between latitudinal and longitudinal ranges be explained by dispersal (Hubbell, 2001) and/or climate (Hawkins *et al.*, 2003)?

Cain (1944) and Rapoport (1975) proposed that, in the absence of directional constraints on dispersal, random but spatially constrained dissemination of propagules and individuals would cause populations to expand isotropically (uniformly in all directions), leading to circular species ranges whose sizes would be basically determined by the intrinsic dispersal capacity of each species. Similar predictions arise from Hubbell's unified neutral theory of biodiversity and biogeography (Hubbell, 2001), which explains community assembly as the product of demographic stochasticity, random but spatially constrained dispersal, and speciation. Therefore, deviations from circularity in species distributions might be viewed as a consequence of the two main forces expected to hinder isotropic range expansion: macroclimate, which is likely to constrain expansion across latitude (Bailey, 1996); and dispersal barriers (i.e. extrinsic dispersal limitation) associated with major topographic features such as mountain chains, river valleys and coastlines (Cain, 1944; Rapoport, 1975; Brown & Maurer, 1989).

A taxon's tendency to have ranges elongated in south–north or east–west directions can be estimated from the slope of the

linear relationship between the latitudinal and longitudinal range extents (Y and X of the regression, respectively), because shapes in which these dimensions are equal would yield a slope ($b_{y,x}$) not statistically different from 1 (Fig. 1a). A second measure of range shapes is the dispersion of the ranges from the 1:1 line (Fig. 1b). If ranges fall close to the 1:1 line, range shape deviations from the latitudinal/longitudinal range equality are small. Here, range shape conformity to the 1:1 line was measured using a coefficient of determination (hereafter $r_{1:1}^2$) based on the residual sum of squares relative to the 1:1 line, instead of a classical fitted regression line (see Materials and Methods). Both measures provide relevant information regarding the potential determinants of species range shapes, as intrinsic dispersal limitation alone would generate ranges with equal latitudinal and longitudinal ranges, whereas extrinsic dispersal limitation and climatic restrictions would generate elongated ranges. However, the interpretation of $b_{y,x}$ and $r_{1:1}^2$ values is difficult because: (1) dispersal barriers can have any orientation, potentially deforming ranges in any direction (for discussion see Brown & Maurer, 1989; Brown, 1995); and (2) macroclimate does not run in perfect latitudinal bands (e.g. in North America; Bailey, 1996) and might therefore not always enlarge ranges in an east–west direction. Notably, macroclimate patterns may be influenced by the same major topographic features that act as barriers. To handle these complexities, we propose a climatic null model that estimates what species range shapes would be in the absence of dispersal limitation, that is, the shape of the potential distribution. The null expectation for range shapes that are fully determined by climate could then be estimated as the slope of the linear relationship between the potential latitudinal and longitudinal range extents ($b_{y,x-pot}$), and range shape deviations by the coefficient of determination relative to the 1:1 line for these potential ranges ($r_{1:1-pot}^2$). Using this approach (Fig. 1c,d), inferences regarding the determinants of species range shapes can be made based on four considerations, as follows.

1. Intrinsic dispersal limitation alone is expected to yield circular shape distributions, because populations would expand isotropically owing to the absence of any directional extrinsic constraint. Thus, significant deviations from $b_{y,x} = 1$ provide an indication of the relevance of extrinsic limiting factors, such as the influence of strong climate gradients or major physical dispersal barriers.
2. Complete climatic determination of species ranges would cause observed species distributions to be identical to their potential distributions as inferred from the spatial projection of species niches. Thus, the existence of significant deviations from $b_{y,x} = b_{y,x-pot}$ suggests that non-climatic factors such as intrinsic dispersal limitation or physical barriers (extrinsic dispersal limitation) are important range constraints; intrinsic dispersal limitation would cause $b_{y,x}$ to be closer to 1 than $b_{y,x-pot}$, while barriers could cause deviations in either direction.
3. While intrinsic dispersal limitation reduces scatter around the equality line (equal longitudinal and latitudinal species ranges), extrinsic dispersal limitation and climatic determination increase scatter. Thus, if $r_{1:1}^2$ values are significantly larger

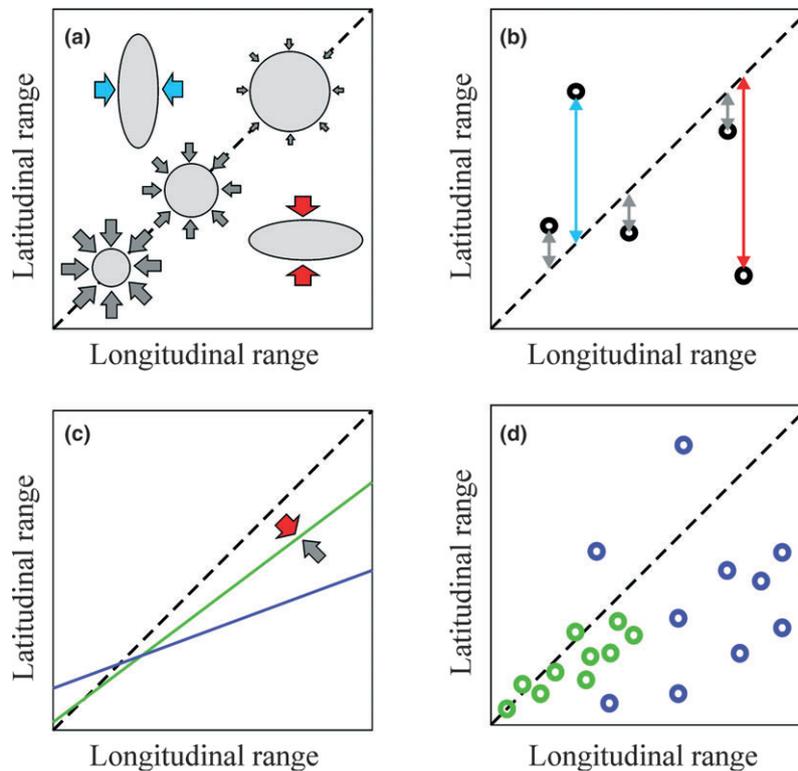


Figure 1 Hypothetical examples showing how various factors may control species range shapes and how these effects could influence $b_{y,x}$ (the slope of the linear relationship between the latitudinal and longitudinal range extents) and $r_{1:1}^2$ (the degree of scatter of species ranges from the 1:1 line). (a) Various hypothetical range shapes. When latitudinal and longitudinal ranges are equal, the points representing each species fall along the 1:1 line (dashed line). Ranges elongated in a north–south or east–west direction fall above or below this line, respectively. Intrinsic dispersal limitation alone (grey arrows) generates ranges with equal latitudinal and longitudinal ranges, whereas extrinsic dispersal limitation (blue arrows) and climatic restrictions (red arrows) generate elongated ranges. Note that the direction of climate restrictions and, especially, extrinsic dispersal limitation may vary among continents and cannot be generalized as a prediction. (b) The scattering of points from the 1:1 line depends on the shape of ranges. The existence of elongated ranges increases distances from points to the 1:1 line, thus decreasing $r_{1:1}^2$. (c) In real situations, extrinsic dispersal barriers and climatic bands may not be oriented in orthogonal directions; therefore, it is necessary to compare $b_{y,x}$ with those yielded by climatic potential distributions ($b_{y,x-pot}$). Significant differences between the realized $b_{y,x}$ (green line) and $b_{y,x-pot}$ (purple line) indicate the effects of intrinsic and/or extrinsic dispersal limitation. Notably, intrinsic dispersal limitation (grey arrow) would drive the $b_{y,x}$ closer to 1 (dashed line) than the $b_{y,x-pot}$. Likewise, significant differences between the realized $b_{y,x}$ and 1 indicate the effect of macroclimate and/or extrinsic dispersal limitation. (d) Comparison between the fit of realized ranges (green circles) to the 1:1 line ($r_{1:1}^2$) and the fit of potential ranges (purple circles) to the 1:1 line ($r_{1:1-pot}^2$) provides information about the relevance of intrinsic dispersal limitation versus extrinsic factors in shaping species distributions.

than $r_{1:1-pot}^2$, this is interpreted as indicating that intrinsic dispersal limitation has a discernible effect; that is, it suggests that observed distributions are not in equilibrium with current climate.

4. Within a given continent, the predominant direction of dispersal barriers (i.e. coastlines, mountains) will tend to modify the shape of species range in consistent directions. Thus, when observed patterns differ from expectation under intrinsic dispersal limitation ($b_{y,x} = 1$) and/or complete climate determination ($b_{y,x} = b_{y,x-pot}$), a consistent association between the predominant direction of barriers and the shape of species ranges across land masses and different taxa indicates the importance of extrinsic dispersal limitation.

Given the above considerations, our specific goals are (1) to test for the generality of the relationship between latitudinal and longitudinal ranges; and (2) to compare the observed

patterns of range shape with predicted patterns obtained with neutral models that assume random, but spatially constrained, dispersal, and models that assume pure climatic control of species distributions. In addition, we examine how the relative roles played by the potential distribution determinants vary with range size.

MATERIALS AND METHODS

Biological and climate data

Species ranges were derived from expert-drawn range maps for the world amphibians (IUCN, 2009), the New World birds and mammals (Ridgely *et al.*, 2007), and the New World palms (Henderson *et al.*, 1995), as well as from atlases of presence–absence for European mammals (Mitchell-Jones *et al.*, 1999),

trees (Jalas & Suominen, 1972–1996) and herbs (families Brassicaceae and Caryophyllaceae) (Jalas & Suominen, 1972–1996). The range map data were analysed at a 1° resolution, while the atlas data were analysed at 0.5° resolution, that is, close to their original $c. 50 \times 50$ km resolution. In total, 18 datasets were examined (taxonomic group \times continent combinations), covering a total of 11,582 species. As the climate data available from WorldClim (Hijmans *et al.*, 2005) have a spatial resolution of 30 arcsec ($c. 1$ km), we calculated the averaged climatic values for each grid cell according to the resolution of the relevant biological data. We used mean annual temperature and annual precipitation as macroclimatic descriptors, as these variables are usually reported to be major determinants of species diversity (Hawkins *et al.*, 2003; Whittaker *et al.*, 2007) and are also strongly correlated with alternative climatic variables such as growing degree-days or evapotranspiration (Baselga & Araújo, 2009; Fløjgaard *et al.*, 2009).

Measuring ranges

Species latitudinal and longitudinal ranges were measured in kilometres after projecting the geographical coordinates of cells onto a UTM (Universal Transverse Mercator) grid system using IDRISI (Clark Labs, 2000). This procedure is necessary because longitudinal ranges cannot be measured as Euclidean distances between the westernmost and easternmost extremes, as these two points could be at different latitudes, thus yielding a diagonal measure instead of the longitudinal range. Therefore, the ranges have to be measured as the sides of a square that circumscribes the species range. Using a UTM grid, the sides of such a square are directly expressed in kilometres. This projection produces a certain degree of distortion in large continents (especially in Eurasia), but this effect is negligible when estimating the species range metrics used here as we are only using maximum and minimum coordinates. Alternative procedures would yield much more serious problems: (1) measuring ranges in degrees makes ranges at different latitudes incomparable, and (2) computing longitudinal ranges with geographical coordinates and then transforming them into kilometres, according to the mean latitude of the range, generates some longitudinal range estimates that are much greater than the real width of the continents, especially at higher latitudes.

Estimating potential distributions

The same procedure was used to measure longitudinal and latitudinal ranges of potential distributions. These were estimated using a rectilinear climatic envelope for each species analogous to BIOCLIM (Busby, 1991); the working assumption is that observed occurrences of species are often expected to represent the range of climate values that the species can tolerate (Soberón & Nakamura, 2009; Jiménez-Valverde *et al.*, 2011), although the degree to which this expectation is true varies with the degree to which the species current distribution is in equilibrium with contemporary climate (Araújo & Pearson,

2005; Baselga & Araújo, 2010). Mean annual temperature and annual precipitation (minimum and maximum limits) were computed for each species in a given continent, and the species' climatic potential distribution was estimated as all grid cells in the continent falling within these climatic ranges. The longitudinal and latitudinal extents of these potential distributions were computed. To assess the robustness of our results, we performed a second analysis using an alternative modelling procedure for estimating potential distributions. This procedure uses the Mahalanobis distance (MD) to rank potential sites according to their distance to a vector expressing the mean environmental conditions of all the observed presences in the environmental space. This algorithm produces an elliptic envelope that can be related directly to the unimodal bell-shaped response of species to climate predictors (Farber & Kadmon, 2003). Here, MD scores below the 95th percentile (increasing MD scores implies decreasing climatic suitability) were mapped as representing the potential range of species (see also Nogués-Bravo *et al.*, 2008). The longitudinal and latitudinal extents of these potential distributions were computed.

Assessing range shape patterns

Thereafter, latitudinal species ranges were regressed against longitudinal ranges, for both observed and potential ranges, and the slopes ($b_{y:x}$) were computed for each taxon and continent, as a measure of range shapes (perfect equivalence between latitudinal and longitudinal ranges would yield $b_{y:x} = 1$). A second measure, the coefficient of determination, was computed to assess the degree of scatter of species ranges from the equality line. Therefore, we did not use the ordinary r^2 , as it measures the dispersion of points with respect to the fitted regression line, but computed $r_{1:1}^2$, measuring the residual sum of squares with respect to the 1:1 line (perfect equality between latitudinal and longitudinal ranges would yield $r_{1:1}^2 = 1$). This parameter, as other coefficients of determination used in atypical regressions (Exner & Zvara, 1999), can take negative values when the fit between observed data and the 1:1 is poor. We selected these two measures of range shape based just on the latitudinal and longitudinal ranges instead of more complex measures (e.g. Maurer, 1994; Pigot *et al.*, 2010) for the following reasons.

1. Latitudinal and longitudinal axes of species ranges provide a fixed system of reference, allowing direct comparison between observed and potential distributions, which is not possible with the above-mentioned alternatives as axes defining the shape are rotated and thus incomparable.
2. This reference system is easily interpretable, as climatic gradients are much more marked across latitudes than across longitudes (Bailey, 1996), with some local exceptions as in North America, so it is a straightforward expectation that climatic determination should generally yield low $b_{y:x}$ and $r_{1:1}^2$.
3. The slope of latitudinal versus longitudinal range regression ($b_{y:x}$) provides a summary of how the relationship between the longitudinal and latitudinal range dimensions changes across range sizes.

Comparing observed and potential parameters

Observed $b_{y,x}$ values were compared with predicted values assuming that species distributions are determined purely by (1) intrinsic dispersal limitation ($b_{y,x} = 1$) or (2) climate ($b_{y,x} = b_{y,x-pot}$). Observed $r_{1:1}^2$ values were also compared with predicted values yielded by potential ranges. To do this analysis, we bootstrapped the regression parameters 1000 times using the 'boot' package (Canty & Ripley, 2008) in R (R Development Core Team, 2006), obtaining the estimated distributions of $b_{y,x}$ and $r_{1:1}^2$. The significance of differences between observed ($b_{y,x}$ and $r_{1:1}^2$) and potential ($b_{y,x-pot}$ and $r_{1:1-pot}^2$) parameters was estimated by comparing the parameter distributions empirically, that is, by computing the number of times that the opposed relationship between observed and potential parameters could be obtained by chance. The alternative would be to use parametric tests, but, in our opinion, the comparison of the bootstrapped distributions is more robust, as it avoids assumptions regarding the distribution of parameters.

Assessing the relationship between range size and shape

Finally, the linear regression models of latitudinal against longitudinal species ranges described above were compared with piecewise regressions, allowing $b_{y,x}$ to change above a given breakpoint. The existence of a significant breakpoint would indicate a relationship between range shape and range size. Piecewise regressions were fitted for each dataset considering all possible breakpoints at 500-km intervals, and the one yielding a smaller residual standard error was selected (Crawley, 2007). The selected piecewise regression models were compared against the respective linear regression models by means of ANOVA tests.

RESULTS

In 78% of the datasets examined (taxonomic group \times continent combinations; $n = 18$), the results supported the existence of a close relationship between latitudinal and longitudinal ranges, with $b_{y,x} > 0.7$ and $r_{1:1}^2 > 0.4$ (Figs 2–4). The $b_{y,x}$ range was 0.40–1.01 (mean = 0.72 ± 0.24 SD; median = 0.78; $n = 18$) and was always significantly higher than 0 ($P < 0.001$), except for European bats ($b_{y,x} = -0.06$; $P = 0.610$). At the same time, $b_{y,x}$ differed significantly from 1 ($P < 0.001$) in all groups and continents, except for European non-volant mammals ($P = 0.263$) and North American birds ($P = 0.826$). In fact, $b_{y,x}$ exhibited a consistent downward deviation from 1; it was < 1 in all significant cases, a proportion (16 of 16) that differed significantly from the null expectation of $b_{y,x}$ deviations to either side of 1 with equal probability ($\chi^2 = 14.06$, d.f. = 1, $P < 0.001$). Deviations from the equality line were, however, moderate: the $r_{1:1}^2$ range was 0.40–0.75 in the majority of datasets, except for African ($r_{1:1}^2 = 0.27$) and Australian ($r_{1:1}^2 = 0.14$) amphibians, Euro-

pean bats ($r_{1:1}^2 = -2.20$) and North American palms ($r_{1:1}^2 = -1.09$) (mean = 0.32 ± 0.75 SD; median = 0.56; $n = 18$).

In the majority of cases, range shapes also deviated from the null expectation under complete climatic determination. Notably, $b_{y,x-pot}$ differed significantly from $b_{y,x}$ in 12 of 18 datasets, the exceptions being New World palms, African and Australian amphibians, and European and South American bats. For datasets with significantly different $b_{y,x}$ and $b_{y,x-pot}$ values, $b_{y,x}$ was closer to 1 than $b_{y,x-pot}$ in 11 of 12 cases, with North American non-volant mammals as the exception. This proportion differed significantly from the null expectation that $b_{y,x}$ and $b_{y,x-pot}$ would be closest to 1 with equal frequency ($\chi^2 = 6.75$, d.f. = 1, $P = 0.009$). We note that $b_{y,x-pot}$ was sometimes > 1 . This was the case for three of five North American groups, but not for the other datasets. Similar differences were found between $r_{1:1}^2$ and $r_{1:1-pot}^2$ (Figs 2–4): $r_{1:1-pot}^2$ differed significantly from $r_{1:1}^2$ in 13 of 18 datasets; exceptions were North American non-volant mammals, bats and birds, as well as African and Australian amphibians. Among datasets with significantly different $r_{1:1}^2$ and $r_{1:1-pot}^2$, the fit to the 1:1 line was higher for the realized ranges in 12 of 13 cases. This proportion significantly differed from the null expectation that $r_{1:1-pot}^2$ would be higher or lower than $r_{1:1}^2$ in the same number of cases ($\chi^2 = 7.69$, d.f. = 1, $P = 0.006$). We note again that North America formed a special case: $r_{1:1}^2$ did not differ significantly from $r_{1:1-pot}^2$ for four of five North American groups, with palms as the exception.

These findings were not dependent on the specific method used for estimating potential ranges in the climatic null model. Using an alternative modelling procedure based on Mahalanobis distances (see Materials and Methods), all previously reported significant differences between $b_{y,x}$ and $b_{y,x-pot}$ or between $r_{1:1}^2$ and $r_{1:1-pot}^2$ were again recovered, as were five new significant cases that were non-significant in the main results (see Appendix S2 for a detailed description of this complementary set of results).

Range size was significantly related to range shape patterns in 13 of 18 datasets, for which piecewise regressions significantly decreased the residual standard error compared with linear regressions (Table 1). The exceptions included European herbs and mammals, and South American bats (although differences between piecewise and linear regression were also marginally significant in South American bats and European Caryophyllaceae and mammals). Among datasets showing significant or marginally significant breakpoints, $b_{y,x}$ was shallower above the breakpoint in 13 of 16 cases. This proportion significantly differed from the null expectation that $b_{y,x}$ would be higher or lower above the breakpoint in the same number of cases ($\chi^2 = 5.06$, d.f. = 1, $P = 0.024$). Within these 16 datasets, breakpoints separated the most widespread species from the rest, as most species fell below the breakpoint (8519 of 11,000; see Table 1). Among these datasets, $b_{y,x}$ below the breakpoint was not significantly different from 1 (neutral expectation) in nine cases (4461 species) and was closer to 1 than above the breakpoint in 13 datasets.

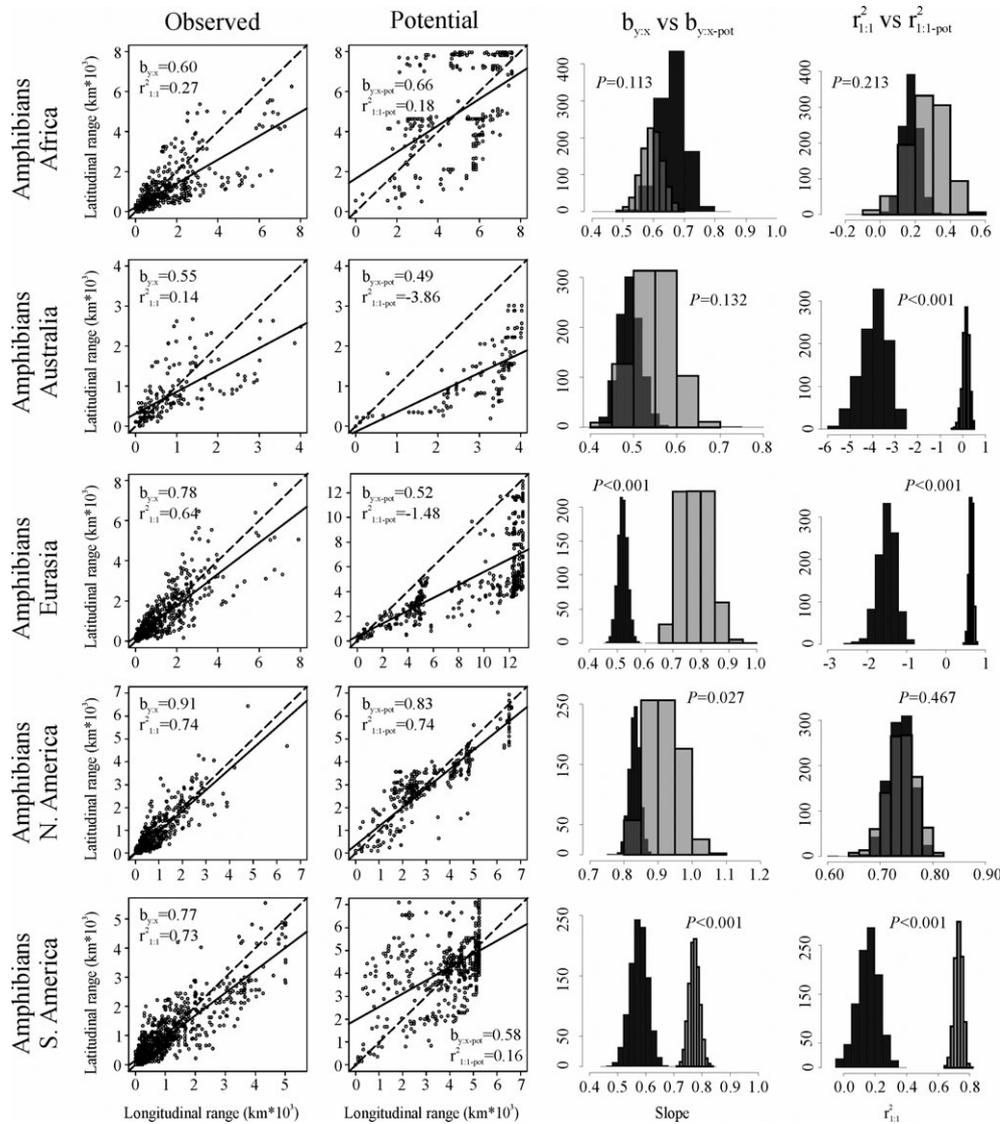


Figure 2 Relationship between latitudinal and longitudinal dimensions of species ranges for observed and potential distributions of amphibians on all continents. Dashed lines represent the 1:1 line. Histograms show the bootstrapped distribution of $b_{y:x}$ and $r^2_{1:1}$ for the observed (grey) and potential (black) ranges, used to assess whether differences between them are significant (P -values are shown).

DISCUSSION

Our study provides the most extensive analysis of species range shapes to date, and it shows that latitudinal and longitudinal ranges are of similar extent for most species and regions. The recurrence of this pattern in our dataset supports the interpretation that climate and dispersal limitation are both critical determinants of species ranges across a wide variety of taxonomic groups and regions.

Previous studies of range shape patterns are scarce. Early work by Rapoport (1975) was focused on the factors forcing species ranges to be elongated and implicitly assumed isotropic dispersal as a null model. Rapoport also found evidence that climate and topographic barriers were responsible for range elongations in North American mammals and South American birds. A small number of later studies focused

on the same range shape pattern described by Brown & Maurer (1989) that was assessed here, but they were restricted to specific taxa and regions, such as world turtles (Hecnar, 1999), North American freshwater fishes (Rosenfield, 2002), mosquitoes, amphibians and reptiles (Pfenner *et al.*, 1998), or trees (Schlachter, 2010). Other analyses investigated different aspects of range shapes, such as how geometric constraints influence range circularity (Sandell, 2009), or how the spatial distribution of range shapes in birds can be explained by environmentally deterministic or stochastic models (Pigot *et al.*, 2010). However, our study is the first investigating range shapes for a large dataset including different taxa and all continents except Antarctica, as well as the first to assess comparatively the roles played by climatic factors and dispersal limitation as range determinants using range shapes. Specifically, our results can be discussed in the light of the

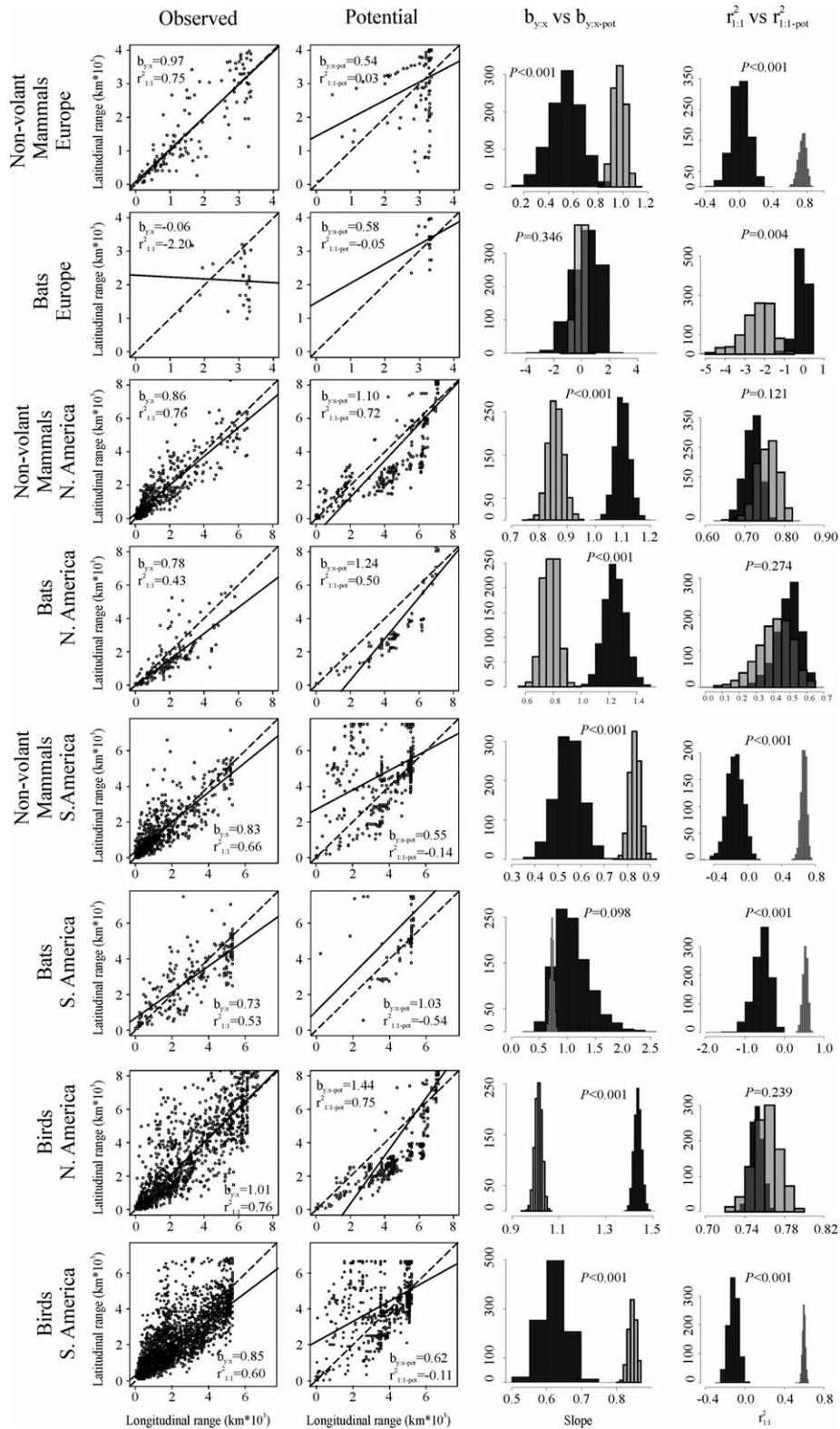


Figure 3 Relationship between latitudinal and longitudinal dimensions of species ranges for observed and potential distributions in European and New World mammals and birds. Dashed lines represent the 1:1 line. Histograms show the bootstrapped distribution of $b_{y:x}$ and $r^2_{1:1}$ for the observed (grey) and potential (black) ranges, used to assess whether differences between them are significant (P -values are shown).

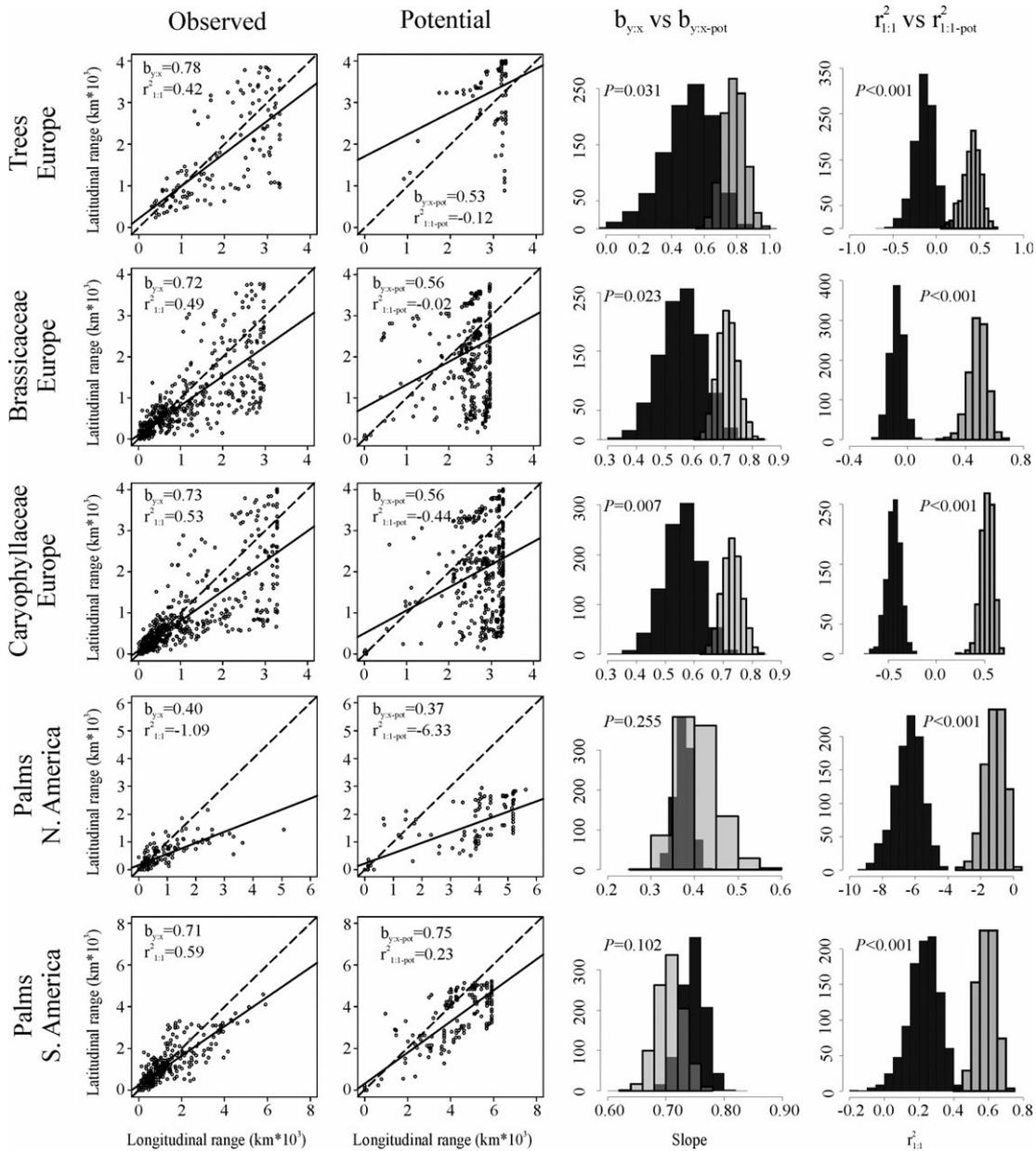


Figure 4 Relationship between latitudinal and longitudinal dimensions of species ranges for observed and potential distributions in European trees and herbs, and New World palms. Dashed lines represent the 1:1 line. Histograms show the bootstrapped distribution of $b_{y:x}$ and $r^2_{1:1}$ for the observed (grey) and potential (black) ranges, used to assess whether differences between them are significant (P -values are shown).

three major factors that have been proposed to control species ranges at macroecological scales (Fig. 1): (1) intrinsic dispersal limitation of each species, reflecting functional traits (Bullock *et al.*, 2002) and the amount of time available for dispersal (Paul *et al.*, 2009); (2) extrinsic dispersal limitation resulting from topographic barriers (Brown & Maurer, 1989); and (3) macroclimatic limitations imposed by species thermal, water- and biome-related niches (Hutchinson, 1957; Whittaker *et al.*, 2001). Biotic interactions (both facilitative and competitive) may also influence species ranges, notably by modifying the response of species to climate (e.g. climate-driven shifts in the competitive ability of species and life forms) (Callaway *et al.*,

2002). Such effects could be considered a component of macroclimatic limitations (Normand *et al.*, 2009). However, biotic interactions can also limit distributions independently of climate (Case *et al.*, 2005; Araújo & Luoto, 2007). Such effects are often thought to be important mainly at the level of the fine structure of species distributions (Connor & Bowers, 1987), although they can also – at least theoretically – affect range limits (Case & Taper, 2000; Price & Kirkpatrick, 2009; Araújo *et al.*, 2011). In any case, we assume that non-climatically driven biotic interactions probably affect range shapes idiosyncratically, that is, without a consistent effect on range shape.

Table 1 Comparison between linear ($b_{y,x}$) and piecewise ($b_{y,x\text{-bel}}$ and $b_{y,x\text{-abo}}$ for slopes below and above the breakpoint, respectively) regression slopes accounting for changes in the relationship between latitudinal and longitudinal ranges across species range sizes. The significance of differences between piecewise and linear regressions [F , d.f. and $P(\text{break})$] and between the slope below the breakpoint and the neutral prediction [$P(b_{y,x\text{-bel}} = 1)$; empirical P derived by bootstrapping] are shown, as well as the total number of species (S_{tot}) and those included below the breakpoint (S_{bel}), when applicable.

Dataset	$b_{y,x}$	Break	$b_{y,x\text{-bel}}$	$b_{y,x\text{-abo}}$	F	d.f.	$P(\text{break})$	$P(b_{y,x\text{-bel}} = 1)$	S_{bel}	S_{tot}
Amphibians – Africa	0.60	4000	0.71	1.27	32.79	2, 587	< 0.001	< 0.001	555	591
Amphibians – Australia	0.55	1500	0.98	0.57	17.69	2, 186	< 0.001	0.402	160	190
Amphibians – Eurasia	0.78	4000	0.94	0.69	39.08	2, 632	< 0.001	0.072	618	636
Amphibians – North America	0.91	4500	0.91	-1.05	12.17	3, 663	< 0.001	0.009	666	668
Amphibians – South America	0.77	2000	0.89	0.88	19.07	3, 1483	< 0.001	< 0.001	1355	1488
Mammals – Europe	0.97	3000	0.99	-1.39	6.34	2, 123	0.083	0.471	98	127
Bats – Europe	-0.06	1500	0.12	-2.61	6.34	2, 26	0.277	n.a.	n.a.	30
Mammals – North America	0.86	500	1.65	0.81	2.66	2, 465	0.001	< 0.001	158	469
Bats – North America	0.78	5000	0.69	-0.37	20.06	2, 183	< 0.001	< 0.001	182	187
Mammals – South America	0.83	2500	0.93	1.08	22.85	2, 691	< 0.001	0.119	582	695
Bats – South America	0.73	2000	1.15	0.75	2.54	2, 208	0.053	0.204	66	212
Birds – North America	1.01	6000	0.98	2.60	3.31	2, 1476	< 0.001	0.174	1325	1480
Birds – South America	0.85	2000	1.15	0.96	6.81	2, 2952	< 0.001	< 0.001	1766	2956
Trees – Europe	0.78	3000	0.96	-1.78	7.60	2, 121	0.002	0.310	99	125
Brassicaceae – Europe	0.72	500	1.06	0.67	10.48	2, 548	0.153	n.a.	n.a.	552
Caryophyllaceae – Europe	0.73	1000	0.96	0.75	2.98	2, 581	0.071	0.262	387	585
Palms – North America	0.40	1500	0.55	0.02	16.18	3, 175	< 0.001	< 0.001	154	180
Palms – South America	0.71	2000	1.04	0.73	45.54	3, 406	< 0.001	0.775	348	411

We found that 16 out of 18 dataset ranges extended more broadly across longitude than across latitude. Of these 16 datasets, nine correspond to northern temperate zones and seven to the Southern Hemisphere. This pattern is consistent with the proposition that macroclimate is an important range determinant (Whittaker, 1975), as macroclimates (particularly temperature) tend to be distributed in latitudinal bands. However, our results also show that observed latitudinal and longitudinal range extents were more similar than expected from macroclimate alone, suggesting that climatic restrictions and intrinsic dispersal limitation interact in controlling species ranges in most cases. In line with recent studies of community patterns and dynamics (Gravel *et al.*, 2006; Adler *et al.*, 2007; Svenning *et al.*, 2008), these findings lend support to the view that realized species distributions are the result of species-intrinsic and potentially neutral dynamics (random speciation, isotropic dispersal and stochastic extinction), and extrinsic driving factors (notably macroclimate). The relative influence of neutral (intrinsic dispersal limitation) and environmental (extrinsic dispersal limitation and climatic restrictions) drivers is expected to vary across species with different range sizes (e.g. Jetz & Rahbek, 2002; Svenning & Skov, 2007; McInnes *et al.*, 2009). As for range shape, it has been shown that the determining factors may differ among range size classes (Pigot *et al.*, 2010). Here, we explored an alternative approach to test for the relationship between range shape and range size. If the relative influence of intrinsic dispersal limitation and environmental control changes with range size, the effect should be detected as a breakpoint in the regression of latitudinal against longitudinal ranges. Our results show such a change for most

taxa, with slopes tending to be steeper and closer to 1 below the breakpoint. This result suggests that intrinsic dispersal limitation is more important for restricted-range species and that macroclimate is more important as a determinant of widespread species.

It could be argued that restricted-range species may be responding to climate gradients at smaller scales (Hawkins & Diniz-Filho, 2006; Ohlemüller *et al.*, 2008), such as those associated with elevational gradients, but there is no particular justification why mesoscale climatic gradients would yield ranges equally elongated in longitude and latitude, especially taking into account that mountain ranges tend to be elongated. In fact, in half of the analysed datasets, the observed slopes were not significantly different from the neutral expectation (observed slope = 1) when the most widespread species were removed from the analyses. We note that this finding applies to a large proportion – about 40% – of the species ($n = 4461$). This result also implies that restricted-range species are more likely to show reduced levels of equilibrium with current climate than widespread species; this being true, our inferences about the potential distributions of restricted species are probably less accurate than those for widespread species, and differences between observed and potential distributions (if these could be derived from actual physiological data) could be more marked than estimated. In other words, the relevance of non-climatic factors in determining species distributions could be even higher than inferred in this study.

The relative influence of neutral and environmental drivers could also differ among land masses (Brown & Maurer, 1989).

For example, within a single taxon, it is reasonable to expect that (1) the lowest observed slopes will be found in continents with sharp latitudinal climatic gradients (notably where gradients from warmer to colder conditions coincide with gradients from wetter to drier conditions), whereas (2) the highest slopes will be found in regions with large north–south-oriented mountain ranges or coastlines. Because amphibian data are available for the five land masses, they provide an excellent opportunity for comparing patterns across land masses. With these data we found a clear imprint of intrinsic dispersal limitation on the shape of species ranges for Eurasia, South America and North America. However, this was not the case for the amphibians in Africa and Australia, which showed the lowest slopes. Australia and Africa harbour particularly large regions that are very unsuitable (too dry) for such highly water-dependent organisms, and the main suitable areas in both continents (Central African rain forest, northern Australia) occur as relatively narrow longitudinal stretches. In other words, in Africa and Australia latitudinal climatic gradients are particularly strong, at least relative to the climate requirements of amphibians, causing a much stronger constraint on ranges than elsewhere (e.g. very few species of amphibians can live in the Sahara). Therefore, it is unsurprising that climate plays the dominant role in these continents.

Our framework sought to identify deviations from pure intrinsic dispersal limitation and pure climatic determination with the use of two null models. However, disentangling the effect of extrinsic dispersal limitation (barriers) from these alternative drivers was difficult, as no general prediction can be made a priori owing to the idiosyncratic orientation of topographic barriers in different land masses. However, after comparing the observed slopes in continents with the different major orientations of their topographic barriers, we found little evidence for a relevant role of dispersal barriers (including mountain ranges, coastlines and land mass shapes) in controlling range shapes, despite the importance that Rapoport (1975) and Brown & Maurer (1989) attributed to them. For example, for amphibians, the observed slope was highest in North America (suggesting an effect of north–south-oriented mountains) but, in contrast, the slope was not higher in South America than in Eurasia (as would be predicted by the major respective orientations of mountain chains and coastlines). Likewise, the same patterns are observed in non-volant mammals when North America, South America and Europe are compared. We suggest two potential and non-exclusive explanations: (1) despite general macroscale orientation patterns on each continent, physical barriers are at smaller scales heterogeneously oriented also within continents and, as a result, do not appear to drive species ranges towards consistent shapes; and (2) large mountain chains and coastlines modify the macroclimate, with the result that any major topographic influences are largely subsumed into the macroclimate effects. The weak signal of dispersal barriers in species range shapes is perhaps most evident in North America. Here, despite mountains being oriented in north–south directions and the

potential slope often being > 1 , contrary to the general expectation of macroclimate being structured in latitudinal bands (Brown & Maurer, 1989; Brown, 1995), observed slopes were still < 1 . Therefore, the marked tendency of observed ranges to have similar longitudinal and latitudinal range extents, independently of the structure of climatic bands and the orientation of barriers, seems to be clearly linked to intrinsic dispersal limitation.

CONCLUSIONS

We have shown that observed species range shapes do not correspond to the shapes that ranges would have if they were determined mainly by intrinsic dispersal limitation, nor do they conform to the range shapes that would be expected if macroclimate were the main factor controlling ranges. Confirming causation through the analysis of macroecological patterns is not possible, but our results support, using a different methodological framework and metrics, previous contributions suggesting that range shapes are the joint product of these two drivers. The consequence of these joint effects is that species ranges are simultaneously sensitive to climate and far from in equilibrium with it. This lack of equilibrium with contemporary climate is so marked that range shape patterns cannot be distinguished from neutral predictions when the most widespread species are removed from the analyses.

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SUPPORTING INFORMATION

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

Appendix S1 Trends in publication of key issues of macroecology as identified by Brown & Maurer (1989).

Appendix S2 Complementary set of results using an alternative modelling procedure.

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BIOSKETCH

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