

# A new macroecological pattern: The latitudinal gradient in species range shape

Adrián Castro-Insua<sup>1</sup>  | Carola Gómez-Rodríguez<sup>1</sup> | Jens-Christian Svenning<sup>2,3</sup> |  
Andrés Baselga<sup>1</sup> 

<sup>1</sup>Departamento de Zoología, Facultad de Biología, Universidad de Santiago de Compostela, Rúa Lope Gómez de Marzoa, Santiago de Compostela, Spain

<sup>2</sup>Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Aarhus University, Aarhus C, Denmark

<sup>3</sup>Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, Aarhus C, Denmark

## Correspondence

Adrián Castro-Insua, Departamento de Zoología, Facultad de Biología, Universidad de Santiago de Compostela, Rúa Lope Gómez de Marzoa, Santiago de Compostela 15782, Spain.  
Email: adrian.castro@usc.es

## Funding information

Spanish Ministry of Economy and Competitiveness and European Regional Development Fund, Grant/Award Number: CGL2016-76637-P and IJCI-2014-20881; Xunta de Galicia, Grant/Award Number: ED481A-2015/074; VILLUM FONDEN, Grant/Award Number: 16549

Editor: Petr Keil

## Abstract

**Aim:** We analyse the latitudinal variation of range shape, testing whether ranges at higher latitudes or of larger size tend to be elongated in an east–west direction, as expected from climatic niche constraints. Additionally, we assess whether poleward range limits are less stochastic than equatorward limits.

**Location:** Global; all terrestrial areas except Antarctica.

**Time period:** Contemporaneous.

**Major taxa studied:** Birds and mammals.

**Methods:** We quantified the shape of the distribution ranges of 10,057 species of birds and 5,411 species of mammals, and assessed the relationship of range shape with latitude and range size using generalized additive models. The observed pattern was compared with that predicted by a null model, in which species ranges were constrained only by the shape of the landmasses. Furthermore, we divided each range in two polygons and measured their separate perimeters, to compare the limits of the poleward and equatorward portions of each range.

**Results:** In terrestrial mammals and birds, only species living at higher latitudes in the Northern Hemisphere and with large range sizes have ranges that consistently tend to be elongated in an east–west direction. The difference between observed and null range shapes increases from the Southern Hemisphere and the tropics towards the north. The difference between equatorward and poleward semi-perimeters was relevant only in the Southern Hemisphere, and it is probably explained by the shape of the continents.

**Main conclusions:** The existence of a latitudinal gradient in range shape is consistent with a different role of deterministic and stochastic processes in the tropics versus high latitudes. Specifically, the results are in line with a scenario in which tropical niche conservatism and relatively evolutionarily labile lower thermal tolerance increase the relevance of climate in determining range limits towards the poles, with stochastic factors (e.g., dispersal limitation) more relevant in shaping low-latitude range limits.

## KEYWORDS

birds, distribution ranges, macroecology, mammals, range shape, range size

## 1 | INTRODUCTION

What determines the limit of a species' distribution? Understanding the factors controlling these boundaries and discovering global regularities across taxa are fundamental for unveiling the mechanisms behind the

distribution of biodiversity and predicting how species will respond to global change. The geometry of species distributions can be characterized by their size and shape. Range size has received comparatively more attention (Gaston, 2003), for instance with studies showing that larger range sizes are associated with climatic instability (Morueta-

Holme et al., 2013) and revealing similar range size–latitude patterns among different classes of vertebrates (Davies, Purvis, & Gittleman, 2009; Orme et al., 2006; Whitton, Purvis, Orme, & Olalla-Tárraga, 2012). In contrast, little is known about the factors influencing the shape of species ranges and their geographical variation (but see Baselga, Lobo, Svenning, & Araújo, 2012; Brown & Maurer, 1989; Pigot, Owens, & Orme, 2010; Rosenfield, 2002), which is surprising given that range shape reflects the relative roles of niche limitation, dispersal barriers and intrinsic dispersal limitation (Baselga, Lobo, Svenning, & Araújo, 2012). In fact, here we show that unique predictions for range shape patterns can be derived from these alternative mechanisms, opening new avenues for assessing what determines species range limits.

Under neutral ecological dynamics (Hubbell, 2001), the expansion of the range after a speciation event would be equally probable in all directions (i.e., isotropic) and, therefore, species ranges would tend to be circular. In this situation, the intrinsic dispersal capability of species would control the size of isotropic ranges (Cain, 1944; Rapoport, 1975). Instead, extrinsic dispersal constraints (e.g., topographical barriers) or niche limitation (e.g., climatic requirements) would cause ranges to deviate from isotropy by determining differential probabilities for range expansion in different directions. Of course, in reality, all mechanisms could be acting simultaneously, with different relative relevance. A previous study on global range shape patterns of multiple taxa (plants, amphibians, birds and mammals) found that range shape patterns were intermediate between the predictions from either pure climatic or pure dispersal control (Baselga, Lobo, Svenning, & Araújo, 2012). However, when large-ranged species were removed, the observed ranges of small-ranged species (the vast majority of species) did not differ from neutral predictions, suggesting that range shapes might be determined by processes linked to range size, with small-ranged species more limited by dispersal and large-ranged species more limited by climate (Brown & Maurer, 1989).

Baselga, Lobo, Svenning, & Araújo (2012) did not analyse how range shape varies spatially (e.g., with latitude), but building on the finding that small- and large-ranged species have different range shapes, in the present study we assess whether variation in species range shape with latitude can provide new insights into the processes limiting species distributions. The motivation for such an analysis lies in five major sources of information:

1. Climatic zones at large scales are generally structured in latitudinal bands (Brown & Maurer, 1989; Peel, Finlayson, & McMahon, 2007), particularly in the Northern Hemisphere.
2. Most clades have tropical origins (i.e., in warm climates), with niche conservatism being an important mechanism behind the maintenance of the latitudinal richness gradient (Qian & Ricklefs, 2016; Smith, Bryson, Houston, & Klicka, 2012; Wiens & Donoghue, 2004).
3. Tolerance to heat is largely conserved across lineages, whereas tolerance to cold varies between and within species (Araújo et al., 2013). This suggests the existence of hard physiological boundaries constraining the evolution of tolerances to high temperatures, whereas evolution of tolerances to cold would be relatively more frequent (but still not very frequent, owing to niche conservatism, as stated above).
4. Distribution range size tends to increase with latitude (Rapoport, 1975; Ruggiero & Werenkraut, 2007), although there are many exceptions to this pattern (see, for example, Stevens, 1989), and some authors suggest that it might be a local phenomenon (Gaston, Blackburn, & Spicer, 1998).
5. Dispersal limitation has strong effects on large-scale species distributions (e.g., Baselga, Lobo, Svenning, & Araújo, 2012). Notably, dispersal has limited postglacial recolonization, with only good dispersers reaching high latitudes (e.g., Alsos et al., 2007), and poor dispersers remaining limited to relatively low latitudes (Baselga, Lobo, Svenning, Aragón et al., 2012; Svenning & Skov, 2007a, 2007b).

Based on the above considerations, we make the following hypotheses. First, we hypothesize (H1) that the effect of niche constraints should be stronger at higher latitudes because climatic conditions there are generally further from the ancestral tropical conditions of most lineages (point 2) and closer to their species-specific lower thermal limits (in contrast to the hard-boundary upper thermal limits, point 3). In addition, species living there have to be good dispersers, able to recolonize large areas quickly after the retreat of Pleistocene glaciations (points 4–5), hence occupying most suitable areas (i.e., distributions relatively close to equilibrium with current climatic conditions). This leads to the prediction that species ranges at higher latitudes should be elongated in an east–west direction, mirroring the geographical structure of climatic zones (particularly in the Northern Hemisphere, cf. point 1). Second, we hypothesize (H2) that the poleward limits of species ranges (associated with tolerance to cold) are likely to be more determined by climatic requirements (because, at higher latitudes, climatic conditions differ more from the ancestral tropical conditions of most lineages, cf. point 2), whereas equatorward limits are likely to be more determined by stochastic biotic processes (Normand et al., 2009), rather than by thermal niche constraints (as tolerance to heat is determined by hard boundaries, with smaller variation across lineages, cf. point 3). This leads to the prediction that poleward range limits should be more compact (i.e., less convoluted, hence shorter).

In order to test these predictions, we quantified the shape of the breeding ranges of 10,057 species of birds and 5,411 species of mammals worldwide. Specifically, to test H1 we assessed whether species at higher latitudes or with larger ranges are more elongated in an east–west direction by evaluating relationships between range shape and latitude and range extent, and whether the observed patterns could be accounted for by a null model in which species ranges are solely constrained by the shape of land masses. To test H2, we assessed whether the poleward semi-perimeters of the ranges are shorter than the equatorward semi-perimeters.

## 2 | METHODS

### 2.1 | Latitudinal and longitudinal ranges

We downloaded range maps of 5,411 mammal species (including 127 marine species) from the IUCN (2013) database and range maps of the breeding distributions of 10,057 bird species (including 332 marine

species) from the BirdLife International and NatureServe (2013) database. We analysed marine species separately, and the main results refer only to terrestrial species. We excluded non-native range polygons (i.e., zones where a species has been introduced). We calculated the maximal longitudinal and latitudinal extents of each polygon as the difference between their maximal and minimal longitude and latitude, respectively. The coordinates in these range maps were specified in degrees, and we transformed the maximal longitudinal and latitudinal extents in degrees to kilometres. One degree of latitude is equivalent to c. 110.6 km at the equator, and this length does not vary much at higher latitudes. However, the length of one degree of longitude varies significantly with latitude, so we estimated the longitudinal span in kilometres at the lowest latitude (closer to the equator) of the distribution, or at the mean latitude, in the cases in which this latitude was closer to the equator than the latitudinal extremes of the distribution range. For details of the calculations used to estimate the longitudinal range (in kilometres), see Supporting Information Appendix S1.

## 2.2 | Range shape

For simplicity, we considered that an isotropic distribution has equal latitudinal and longitudinal ranges, and based hereon we characterized the shape of ranges in two ways. First, in the relationship between latitudinal and longitudinal ranges, we measured the minimal distance between each point and the 1:1 line (in which latitudinal and longitudinal range are equal). Distribution ranges that are closer to this line should, in general, be more isotropic. This measure does not capture the directionality of deviations from isotropy or the proportion between latitudinal and longitudinal ranges, but it reflects the absolute magnitude of the deviation from exactly equal latitudinal and longitudinal ranges. Second, we calculated the scaled difference between latitudinal and longitudinal ranges:  $(\text{Lat} - \text{Lon})/(\text{Lat} + \text{Lon})$ , with 'Lat' being the latitudinal range and 'Lon' being the longitudinal range. When the latitudinal and longitudinal range are the same, this difference is equal to zero; when the latitudinal range is greater than the longitudinal one (the range is elongated in a north–south direction), this difference is positive; and when the range is elongated in an east–west direction, it is negative. Thus, this measure provides information about the direction of the elongation of the shape.

We fitted univariate generalized additive models (GAMs), with a normal error structure and identity link function, in order to assess the relationship of these measures of range shape (distance to the 1:1 line and latitude–longitude scaled difference as response variables), with latitude and with geographical range size as explanatory variables. This analysis was performed for terrestrial and marine species separately. In addition, we performed a variance partitioning analysis of the full models (i.e., latitude and range size as predictors) to partial out the effect of each variable.

## 2.3 | Null models

In order to assess the possible influence of geometrical constraints on range shapes (in particular, the shape of the continents might be

important at large scales), we compared the observed patterns in range shape with the patterns arising from a simple null model, in which species expand their ranges randomly from a starting cell. Each species starts in a random 50 km × 50 km cell (similar to those of Sastre, Roca, Lobo, & EDIT co-workers, 2009) and is allowed to occupy any of the cells neighbouring the already occupied cells, one at a time, until it reaches an area similar to its observed range size. If the species was not able to expand until reaching that area (e.g., because the starting cell was in an island smaller than the species' range size), we selected a different random starting cell.

We compared the latitudinal patterns in range shape of the null models with the observed patterns. We plotted the kernel density distribution of the latitude–longitude scaled difference of all species with their latitudinal midpoint falling in 10° latitudinal windows, both for the null model and for the real distributions. Then, we calculated the overlap between the observed distribution and the null model distribution.

## 2.4 | Range semi-perimeters

We tested the hypothesis that climatic factors can influence the degree of stochasticity in the limits of species ranges. As climatic conditions are generally further from the ancestral tropical conditions of most lineages at higher latitudes, it could be expected that the limits of species ranges are more constrained by climate there and, thus, less stochastic than at lower latitudes (Normand et al., 2009; Pellissier et al., 2013). To assess this, we compared the poleward and equatorward semi-perimeters (i.e., the perimeters of the poleward and equatorward portions of a polygon) of species ranges, predicting that the equatorward semi-perimeter of a polygon should be more stochastic (i.e., with a more uneven edge) if it is significantly longer than the poleward semi-perimeter.

To approach this question, we divided each range into two polygons by the latitudinal line that passed through the centroid of the range, and estimated the perimeter (in kilometres) of the resulting polygons (one to the north and the other to the south of the centroid). This estimation was done using the package *geosphere* (Hijmans, 2016) in R, which allows the computation of distances between angular coordinates (i.e., expressed in latitude/longitude). We tested whether the perimeter of the polygon closer to the equator (the equatorward semi-perimeter, ES) is longer than the perimeter of the polygon at a higher latitude (the poleward semi-perimeter, PS) for each species, by using a one-sided paired *t* test (that is, we tested whether  $ES > PS$ ). For this comparison, we standardized the semi-perimeters by dividing them by the sum of the semi-perimeters of both polygons for each species [thus, we compared  $ES/(PS + ES)$  and  $PS/(PS + ES)$ ]. The poleward polygon is the one above the centroid in the Northern Hemisphere and the one below the centroid in the Southern Hemisphere.

We performed this analysis separately for each hemisphere in order to assess the influence of the shape of land masses on the length of semi-perimeters, as most continents taper to the south (i.e., taper to the pole in the Southern Hemisphere but to the equator in the Northern Hemisphere). This could create an artefactual pattern, confounding the effect of the shape of the continents with that of the different

climatic determinism between poleward and equatorward semi-perimeters. Thus, separating both hemispheres should allow us to identify whether such a confounding effect is taking place. We assigned each species to the Northern or Southern Hemisphere (2,905 and 2,379 species of mammals and 4,717 and 5,008 species of birds in the Northern and Southern Hemisphere, respectively). If the range of the species crossed the equator, we used its mean latitude to assign it to one of the hemispheres. Additionally, in order to assess whether these differences depend on range size, we also conducted this analysis using only the species with the smallest and largest range sizes (first and fourth range size quartiles, respectively), as species with small ranges are more likely to be limited by dispersal, and the main factors that determine their range shape might differ from more widely distributed species. Note that, as the semi-perimeters were standardized, range size should not influence the magnitude of the difference between semi-perimeters.

The main problem with this approach is that it is possible to find that the lower-latitude portions have longer perimeters simply because, as latitudinal belts with equivalent latitudinal span increase in area towards the equator (and owing to the way we divide the polygons), these halves are larger, particularly in very large polygons. To account for this, we flipped the polygons on their east–west axis and repeated the same measures described above. If the lower-latitude portions of the original polygons have effectively longer perimeters, we should find that after flipping them, the upper-latitude polygons have longer

perimeters. However, if the perimeters of lower-latitude portions remain longer in the flipped polygons, we cannot conclude that there are any significant differences between perimeters.

All GIS and statistical analyses were conducted in R (R Core Team, 2016; version 3.2.4) using the package *mapproj* (Bivand & Lewin-Koh, 2016; package version 0.8.39) to read shapefiles, the package *rgeos* (Bivand & Rundel, 2016; package version 0.3.17) to manipulate polygons, and the package *geosphere* (Hijmans 2016; package version 1.5.1) to estimate the geographical range size (in square kilometres) and to measure the perimeters (in kilometres) of each species. GAMs were fitted with the package *mgcv* (Wood, 2011; package version 1.8.12), using penalized cubic regression splines. The R code for manipulating range polygons (with an example polygon included) and the C++ code we used to implement the null model are available in Supporting Information Appendix S2.

### 3 | RESULTS

The latitudinal and longitudinal extent of the geographical ranges are positively correlated (Spearman's  $\rho = .90$ ,  $p < .001$  in mammals and  $\rho = .87$ ,  $p < .001$  in birds; Figure 1), with species deviating more from the 1:1 line with increasing longitudinal extent in both mammals and birds. Moreover, there is a triangular pattern in the relationship between mean latitude of the distributions and distance to the 1:1 line

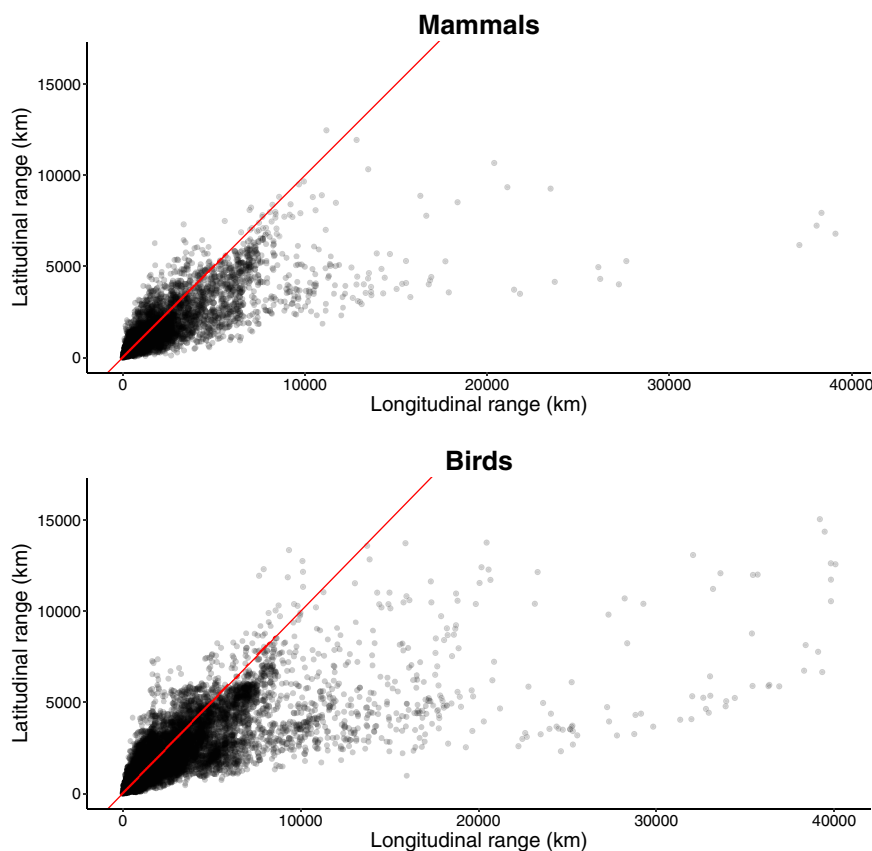
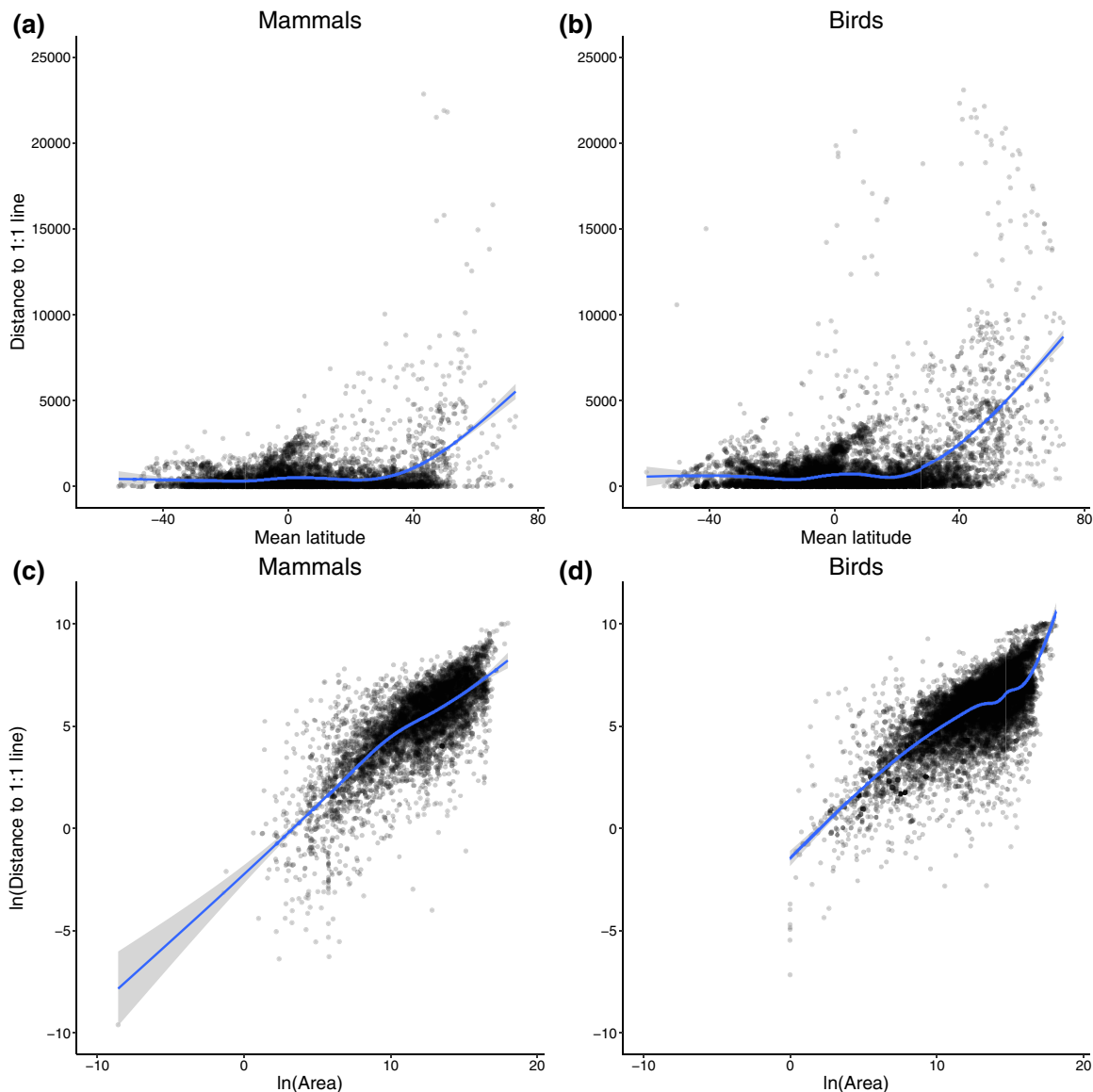


FIGURE 1 Scatterplot of the relationship between longitudinal range and latitudinal range. The 1:1 line is shown

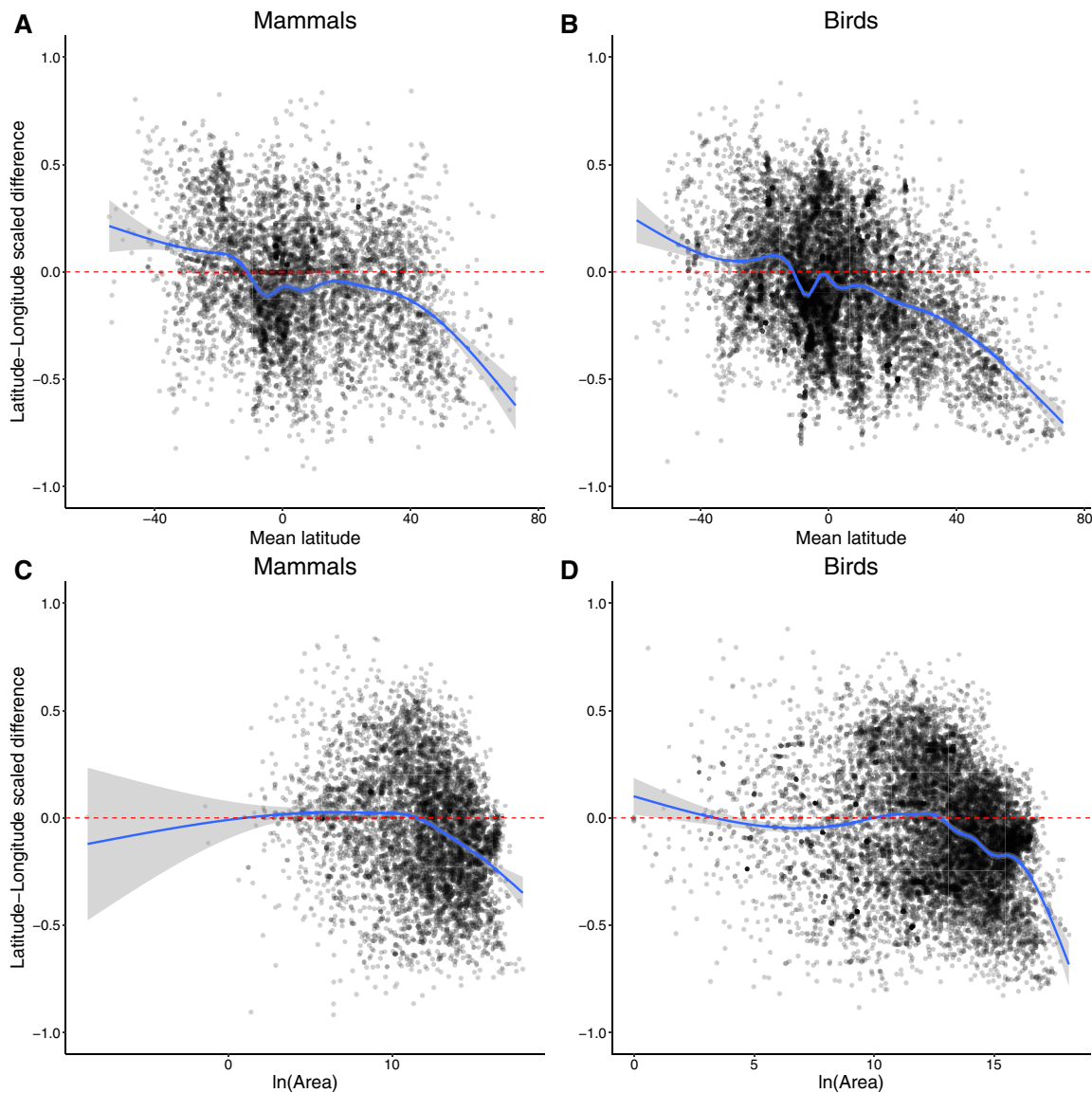


**FIGURE 2** Relationship between the distance to the 1:1 line of Figure 1 (ranges with more similar latitudinal and longitudinal ranges are closer to the 1:1 line) and (a, b) the mean latitude of the range or (c, d) range extent (in square kilometres). In the scatterplots against range extent, both variables are ln-transformed. The fitted single-term generalized additive model (GAM) is superimposed, with a 95% confidence interval

(Figure 2a,b). In other words, most of the species have range shapes that are isotropic or close to isotropy (closer to the 1:1 line), but the species that deviate the most from isotropy occur, in general, at higher latitudes in the Northern Hemisphere. Likewise, the species with the largest geographical extents tend to deviate more from the 1:1 line (Figure 2c,d); and there is a strong positive correlation between distance to the 1:1 line and range area (Pearson's  $r = .75$  in mammals and  $r = .70$  in birds, all  $p < .001$ , both variables ln-transformed). Hence, species with large range sizes deviate more from equal latitudinal and longitudinal ranges. A GAM including mean absolute latitude and range size explains about half of the variability in the distance to the 1:1 line ( $r^2 = .50$  for mammals,  $r^2 = .61$  for birds, all  $p < .001$ ). Most of this variation is explained uniquely by range size [unique contribution of range size = 34% (mammals) and 32% (birds); unique contribution of mean

absolute latitude = 7% (mammals) and 14% (birds)], and only a small proportion of this explained variation is shared between both variables.

The latitude–longitude scaled difference, a proxy for shape directionality, starts to decrease with mean latitude above a point c. 30–40° N, such that at high latitudes the ranges tend to be elongated in an east–west direction (Figure 3a,b). Near the equator, most species ranges tend to have similar latitudinal and longitudinal ranges (the local central tendency of the scaled difference is negative, but close to zero), as evidenced by the high density of points. At high latitudes in the Southern Hemisphere, species tend to have north–south elongated ranges. This latitudinal pattern also appears if we plot the mean of the latitude–longitude scaled difference of all species present in 100 km × 100 km cells against latitude (Figure 4; see figures in Supporting Information Appendix S3). The latitude–longitude scaled difference also



**FIGURE 3** Relationship between latitude–longitude scaled difference (ranges with more similar latitudinal and longitudinal ranges are closer to zero, indicated by a dashed line) and (a, b) mean latitude of the ranges or (c, d) range extent (square kilometres, ln-transformed). The fitted single-term generalized additive model (GAM) is shown, with a 95% confidence interval

varies with range size, with ranges being isotropic on average when geographical range size is small, but tending to be elongated in an east–west direction when it is large (Figure 3c,d). Remarkably, only a low proportion of variance of the latitude–longitude scaled difference is explained by a GAM including mean absolute latitude and range size ( $r^2 = .16$  in mammals,  $r^2 = .21$  in birds, all  $p < .001$ ). This implies that, although these variables largely explain deviations from isotropy, these predictors do not explain the direction of these deviations (i.e., north–south or east–west elongation). The fact that there are not systematic range shape deviations associated with these predictors would be in accordance with the hypothesis that only a small fraction of the species (widespread or high-latitude species) would be constrained by their niche requirements. Again, a variance partitioning analysis shows that most of the variance is explained uniquely by either mean latitude or area [unique contribution of mean absolute latitude = 8% (mammals

and 11% (birds); unique contribution of range size = 5% (mammals and birds)]. At low latitudes no pattern is observed for the direction of the deviation from isotropy, but it should be noted that the shape of the continents and regional topography seem to influence the latitude–longitude scaled difference in particular cases. For example, ranges are generally north–south elongated in southern South America (where the Andes probably act as both a climatic constraint and a dispersal barrier), as well as in Madagascar (where the shape of the island is likely to be the factor behind this elongation) or eastern Australia for mammals (probably owing to climatic constraints, in this case; see Figure 4).

Additionally, we performed the same analyses using a more conservative estimate of longitudinal range (calculating longitudinal span in kilometres at the mean latitude of the distribution), finding similar patterns to those described above (see Supporting Information Appendix S4).

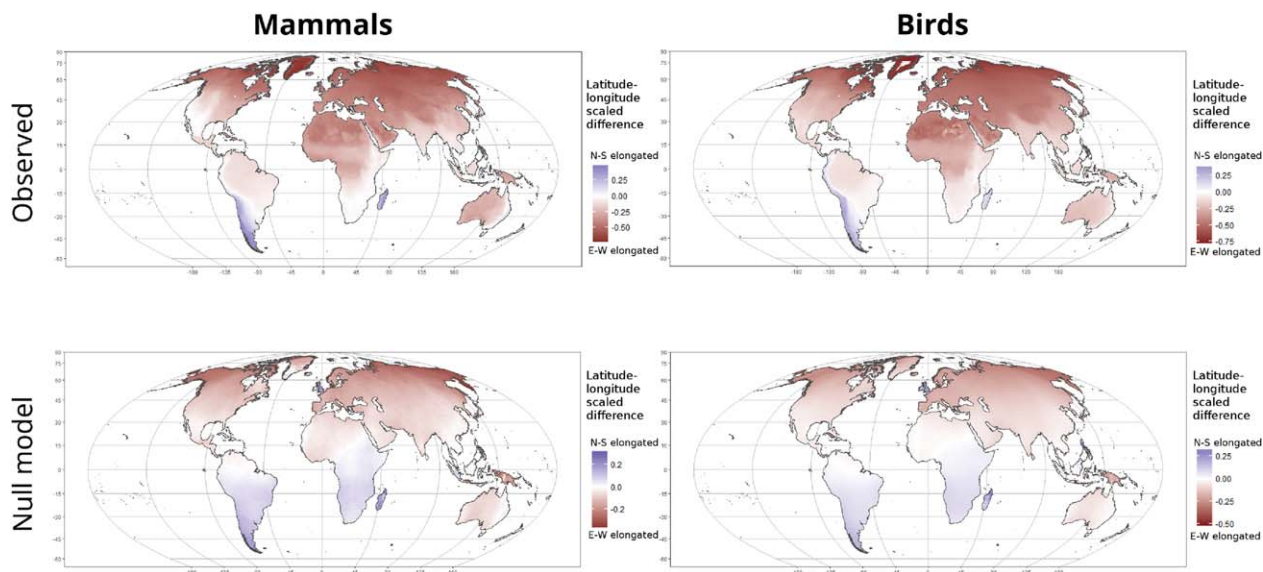


FIGURE 4 Maps showing the mean latitude-longitude scaled difference of all species present in each 100 km × 100 km cell. A blue colour indicates that the mean is positive (i.e., many species in those cells have ranges elongated north-south), whereas red indicates that the mean is negative (i.e., ranges are generally elongated east-west). The maps of the first row are those of the observed distribution ranges, and the maps of the second row correspond to the null model distribution ranges

There are broad similarities between the maps of mean range shape elongation of the null models and the observed distributions (Figure 4). For example, the null models predict north-south elongated ranges in the southern end of South America or Madagascar, and east-west elongated ranges at high latitudes in the Northern Hemisphere. However, the null models do not show the same latitudinal pattern in range shape (Supporting Information Figure S5.1); that is, we do not find strong deviations from isotropy at high latitudes in the Northern Hemisphere. There is a slight tendency at the highest latitudes towards east-west elongated ranges in the Northern Hemisphere and towards north-south

elongated ranges in the Southern Hemisphere. This tendency might be explained in part by the shape of the continents, particularly in the Southern Hemisphere. However, the tendency towards east-west elongated ranges in the Northern Hemisphere is much stronger in the empirical patterns (they are more elongated than predicted by the null model; see Figure 3a,b), as the difference between the observed pattern and the null model is greater at high latitudes (less overlap in the distributions) in the Northern Hemisphere (see Figure 5).

Regarding range edge evenness, in the observed range polygons equatorward semi-perimeters tend to be longer than poleward semi-

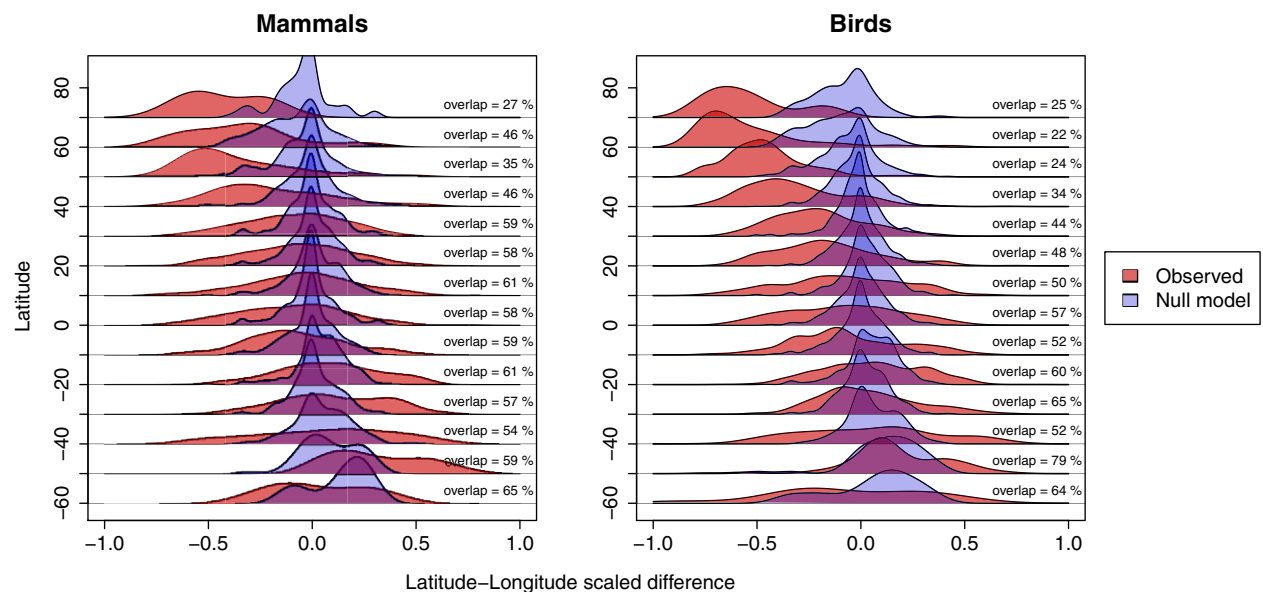


FIGURE 5 Comparison between the observed distribution of range shapes and the distribution in the null model. For each 10° latitudinal band, we show the observed distribution of range shapes in red and the distribution in the null model in blue of all the species with their distribution centred in that particular latitudinal band. More similar distributions overlap more

**TABLE 1** Results of the paired one-sided *t* tests comparing the length of the equatorward and poleward semi-perimeters (standardized; see main text) of the ranges

		Hemisphere	<i>t</i>	d.f.	<i>p</i>	Mean of the differences	<i>r</i> <sup>2</sup>
Mammals	All species	North	2.56	2,904	.010	.008 ± .006	–
		South	9.48	2,378	< .001	.032 ± .007	.036
	Fourth area quartile	North	2.76	725	.006	.021 ± .015	.010
		South	15.31	594	< .001	.108 ± .014	.283
	First area quartile	North	–.54	725	.59	–.003 ± .011	–
		South	–.16	594	.87	–.001 ± .012	–
Birds	All species	North	4.79	4,716	< .001	.014 ± .006	.005
		South	24.54	5,007	< .001	.067 ± .005	.107
	Fourth area quartile	North	6.24	1,178	< .001	.045 ± .014	.032
		South	31.08	1,251	< .001	.182 ± .012	.436
	First area quartile	North	–.02	1,178	.98	–.0001 ± .009	–
		South	1.15	1,251	.25	.006 ± .010	–

Note. A positive difference (significantly different from zero) means that the poleward semi-perimeters are shorter. We present the results for all species, for the species with larger geographical range extents (fourth area quartile), and for the species with smaller geographical range extents (first area quartile). The last two columns show the mean difference between the equatorward and the poleward semi-perimeter, with a 95% confidence interval and a measure of the effect size (*r*<sup>2</sup>) when the difference is statistically significant. Significant values of *p* (< .01) are marked in bold.

perimeters in both hemispheres, with a greater difference in the Southern Hemisphere (mean of the differences .008 ± .006 in the Northern Hemisphere and .032 ± .007 in the Southern Hemisphere for mammals; and .030 ± .010 in the Northern Hemisphere and .141 ± .010 in the Southern Hemisphere for birds; see Table 1). Results are again similar for mammals and birds. These differences are driven by large-ranged species, as they are not significant for species in the first geographical range size quartile and are greater for species in the fourth geographical range size quartile. However, after flipping the polygons on their horizontal axis we found that these differences seem to be significant only in the Southern Hemisphere (see Supporting Information Appendix S6), as only in this case poleward semi-perimeters become longer than equatorward semi-perimeters (see the negative mean of the differences).

## 4 | DISCUSSION

Our results unveil a latitudinal pattern in range shape elongation, with widespread and high-latitude species in the Northern Hemisphere systematically elongated in an east–west direction. The deviation of observed patterns from null expectations systematically increases to the north. In turn, low-latitude and small-range species do not show any consistent bias towards east–west or north–south elongated ranges. These low-latitude species (below 30°) constitute the vast majority of mammal (83.4%) and bird species (88.7%) and, remarkably, most of them have ranges with similar latitudinal and longitudinal extents (see Figure 2a,b). This is consistent with range expansion of most species at low latitudes being largely driven by isotropic processes not expected under niche control of species distributions (however, note that isotropic ranges could appear under niche constraints if environmental gradients along longitudinal and latitudinal directions were similar). Isotropy would be a macroscopic property of systems under neutral dynamics (i.e., stochastic dispersal equal in latitudinal and

longitudinal directions, speciation and extinction). In contrast, niche constraints seem to dominate at higher latitudes, as inferred from the systematic elongation in an east–west direction in the small proportion of species centred above 30° in the Northern Hemisphere. The deviation from what is expected from null models simulating isotropic distributions increases towards the North (see Figure 5), suggesting an increasing relevance of climatic forcing when the climatic conditions differ more from the ancestral tropical conditions in which most clades have originated (Wiens & Donoghue, 2004). Thus, although climate is structured in latitudinal belts all across the globe, these belts force species ranges to be elongated in east–west direction only when they occur at high latitudes. In other words, only species in colder regions would reach their climatic niche limits, and thus their range limits would be mostly niche driven. In turn, the low-latitude species would not reach their upper thermal limits, because these are a hard boundary (Araújo et al., 2013). As a consequence, differences across species in upper thermal limits are less likely to be responsible for differences in species distributions. Thus, the ranges of low-latitude species are probably less constrained by thermal niches, but are likely to be subject to other processes; probably stochastic or biotic processes (Normand et al., 2009), given the lack of any systematic deviation from isotropic ranges. These results are also consistent with the findings of previous studies that show that the thermal tolerance limits of species predict their latitudinal range limits well in many cases (particularly in ectotherms; e.g., Sunday, Bates, & Dulvy, 2012).

It should be noted that in the Southern Hemisphere ranges tend to be elongated in a north–south direction, particularly at higher latitudes. The most probable explanation for this is that the shape of the continents constrains ranges to be elongated in this direction, as the null models do predict north–south elongation. In turn, in marine species, which mostly have ranges elongated in an east–west direction, we find the same tendencies in elongation in both hemispheres, with ranges being more elongated in an east–west direction at higher latitudes, also in the Southern Hemisphere (see Supporting Information Appendix S7).



This is what would be expected when continent shape does not influence range shape elongation, further supporting the idea that the gradient in range shapes reflects the increasing relevance of climatic niches towards the poles in constraining species ranges. The general result we found does not preclude the possibility that climate might be one of the main factors determining local range limits in some small-range, low-latitude species (Morueta-Holme, Fløjgaard, & Svenning, 2010), whereas historical range constraints might be more important for the broad-scale distribution (e.g., Araújo et al., 2008). Likewise, specific lineages of organisms might show patterns that differ from the general one (Pfrender, Bradshaw, & Kleckner, 1998).

We also found that species with larger range sizes tend to have east–west elongated ranges (Figure 3c,d). This could be consistent with the proposition that the variation of climate at larger scales (continental or regional) is a more important determinant of range limits in those species that are more widely distributed (Pearson & Dawson, 2003). The patterns of variation of range shape with latitude and with range size might be related, because species of birds and mammals at high latitudes tend to have larger range sizes and latitudinal ranges (Davies et al., 2009; Orme et al., 2006; Tomašových et al., 2016). However, the variance partitioning analysis we performed shows that most of the variance in latitude–longitude scaled difference (proxy for shape directionality and relative elongation) explained by the GAM is not jointly explained by latitude and range size, and that the unique contribution of latitude to the explained variance is slightly larger.

We found that equatorward semi-perimeters are longer than poleward ones. However, these differences are generally not large, with small effect sizes in most cases (see Table 1). After flipping the polygons on their horizontal axis, we would expect that poleward semi-perimeters become longer, but this is not the case. The only exceptions are the species with the largest range sizes (fourth quartile) in the Southern Hemisphere (in this case, the mean of the differences becomes negative; see Supporting Information Table S6.1). This suggests that, in most cases, the reason why we find that equatorward semi-perimeters are longer is that, because the Earth is a sphere, latitudinal bands near the equator are larger, and thus we find that equatorward semi-perimeters are longer. However, in the species with large range sizes in the Southern Hemisphere, the shorter poleward semi-perimeters cannot be explained solely by the shape of the Earth. Here, the shape of the continents is the most plausible explanation, given that in the Southern Hemisphere they taper toward the poles, enforcing smaller poleward range limits. In any case, with this approach our results do not support previous suggestions that biotic interactions are more important at lower latitudes, where abiotic conditions are less stressful (Brown, Stevens, & Kaufman, 1996; Loehle, 1998; Pellissier et al., 2013).

Our inferences are subject to several caveats. First, estimating longitudinal extents of species ranges is not straightforward. The method used (measuring the longitudinal range at lowest latitude of the distribution) may overestimate longitudinal span consistently, particularly at higher latitudes, but when we used a more conservative estimate (calculating the longitudinal span at the mean latitude of the

distribution) we found the same patterns (see Supporting Information Appendix S4). Second, we used simple measures of range shape based on the difference between latitudinal and longitudinal range extents instead of more complex measures (see, for example, Pigot et al., 2010). However, we did this because fixed longitudinal and latitudinal axes allow direct comparison of the direction of elongation of the ranges between species and, given that climatic variation is generally more marked across latitudes, the patterns of elongation can be interpreted in relationship to unique predictions (Baselga, Lobo, Svenning, & Araújo, 2012). Third, we are aware that the high variation in range shape at low latitudes might be caused by many different processes, and our analyses do not rule out the possibility that, in some cases, small-scale variation in climate or high spatial heterogeneity of abiotic factors at low latitudes could be among the main determinants of range shape in these regions. For instance, lower climatic variability and narrower physiological tolerances would make topographical barriers more effective at low latitudes (Ghalambor, Huey, Martin, Tewksbury, & Wang, 2006; Janzen, 1967). This being true, the variation in the orientation of mountain ranges would cause more irregular deviations from isotropy in low latitudes compared with high latitudes. This is difficult to assess because disentangling the effects of climatic variation and topography is problematic, but future studies should try to address this question. In any case, we are assessing macroscopic patterns arising from variation across a high number of species and regions, so these particular cases are expected to have little weight in the results.

To conclude, a novel macroecological pattern becomes apparent when latitudinal variation in the shape of species ranges is assessed, with isotropic ranges at the tropics, and anisotropic ranges at high latitudes. This pattern is consistent with stochastic processes being more important in driving species ranges at low latitudes, and deterministic processes (related to latitudinal climatic variation) stronger at higher latitudes. One plausible explanation for this is that the majority of species living at high latitudes must unavoidably have high dispersal ability (because they have recolonized those regions in a short period of time; i.e., since Last Glacial Maximum), allowing them to reach their physiological limits. At lower latitudes, most distributions have similar latitudinal and longitudinal ranges, an isotropic pattern expected if species distributions are predominantly controlled by intrinsic dispersal limitation, which probably does not allow most of these species to reach their physiological limits.

## ACKNOWLEDGMENTS

We are grateful to P. Keil, A. Tomašových and one anonymous referee for insightful comments on a previous version of this paper. A. C.-I., C.G.-R. and A.B. were supported by the Spanish Ministry of Economy and Competitiveness and the European Regional Development Fund (grant CGL2016–76637-P, and fellowship IJCI-2014–20881 to C.G.-R.) and Xunta de Galicia (fellowship ED481A-2015/074 to A.C.-I.). J.-C.S. considers this work a contribution to his VILLUM Investigator project funded by VILLUM FONDEN (grant 16549).

## DATA ACCESSIBILITY

Range maps of mammals are available at <http://www.iucnredlist.org/technical-documents/spatial-data>, and range maps of birds are available upon request at <http://datazone.birdlife.org/species/requestdis>.

## ORCID

Adrián Castro-Insua  <http://orcid.org/0000-0003-4184-8641>

Andrés Baselga  <http://orcid.org/0000-0001-7914-7109>

## REFERENCES

- Alsos, I. G., Eidesen, P. B., Ehrich, D., Skrede, I., Westergaard, K., Jacobsen, G. H., ... Brochmann, C. (2007). Frequent long-distance plant colonization in the changing Arctic. *Science*, *316*, 1606–1609.
- Araújo, M. B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P. A., Valladares, F., & Chown, S. L. (2013). Heat freezes niche evolution. *Ecology Letters*, *16*, 1206–1219.
- Araújo, M. B., Nogués-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.
- Baselga, A., Lobo, J. M., Svenning, J.-C., Aragón, P., & Araújo, M. B. (2012). Dispersal ability modulates the strength of the latitudinal richness gradient in European beetles. *Global Ecology and Biogeography*, *21*, 1106–1113.
- 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.
- BirdLife International & NatureServe. (2013). *Bird species distribution maps of the world*. Cambridge, U.K.; Arlington: BirdLife International; NatureServe.
- Bivand, R., & Lewin-Koh, N. (2016). *mapproj: Tools for reading and handling spatial objects* (R package version 0.8–39). Retrieved from <https://cran.r-project.org/package=mapproj>
- Bivand, R., & Rundel, C. (2016). *rgeos: Interface to geometry engine - open source (GEOS)* (R package version 0.3–17). Retrieved from <https://cran.r-project.org/package=rgeos>
- Brown, J. H., & Maurer, B. A. (1989). Macroecology: The division of food and space among species on continents. *Science*, *243*, 1145–1150.
- 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.
- Cain, S. A. (1944). *Foundations of plant geography*. New York, NY: Harper & Brothers.
- Davies, T. J., Purvis, A., & Gittleman, J. L. (2009). Quaternary climate change and the geographic ranges of mammals. *The American Naturalist*, *174*, 297–307.
- Gaston, K. J. (2003). *The structure and dynamics of geographic ranges*. Oxford, U.K.: Oxford University Press.
- Gaston, K. J., Blackburn, T. M., & Spicer, J. I. (1998). Rapoport's rule: Time for an epitaph? *Trends in Ecology and Evolution*, *13*, 70–74.
- Ghalambor, C. K., Huey, R. B., Martin, P. R., Tewksbury, J. J., & Wang, G. (2006). Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology*, *46*, 5–17.
- Hijmans, R. J. (2016). *geosphere: Spherical trigonometry* (R package version 1.5-1). Retrieved from <https://cran.r-project.org/package=geosphere>
- Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton, NJ, U.S.A.: Princeton University Press.
- IUCN. (2013). *IUCN red list of threatened species* (Version 2013.2). Retrieved from <http://www.iucnredlist.org/technical-documents/spatial-data>
- Janzen, D. H. (1967). Why mountain passes are higher in the tropics. *The American Naturalist*, *101*, 233–249.
- Loehle, C. (1998). Height growth rate tradeoffs determine northern and southern range limits for trees. *Journal of Biogeography*, *25*, 735–742.
- Morueta-Holme, N., Enquist, B. J., McGill, B. J., Boyle, B., Jørgensen, P. M., Ott, J. E., ... Svenning, J.-C. (2013). Habitat area and climate stability determine geographical variation in plant species range sizes. *Ecology Letters*, *16*, 1446–1454.
- Morueta-Holme, N., Fløjgaard, C., & Svenning, J.-C. (2010). Climate change risks and conservation implications for a threatened small-range mammal species. *PLoS One*, *5*, e10360.
- 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.
- Orme, C. D. L., Davies, R. G., Olson, V. A., Thomas, G. H., Ding, T.-S., Rasmussen, P. C., ... Gaston, K. J. (2006). Global patterns of geographic range size in birds. *PLoS Biology*, *4*, e208.
- 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.
- Peel, M. C., Finlayson, B. L., & McMahon, T. A. (2007). Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences Discussions*, *4*, 439–473.
- Pellissier, L., Bräthen, K. A., Vittoz, P., Yoccoz, N. G., Dubuis, A., Meier, E. S., ... Guisan, A. (2013). Thermal niches are more conserved at cold than warm limits in arctic-alpine plant species. *Global Ecology and Biogeography*, *22*, 933–941.
- Pfrender, M. E., Bradshaw, W. E., & Kleckner, C. A. (1998). Patterns in the geographical range sizes of ectotherms in North America. *Oecologia*, *115*, 439–444.
- 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.
- Qian, H., & Ricklefs, R. E. (2016). Out of the tropical lowlands: Latitude versus elevation. *Trends in Ecology and Evolution*, *31*, 738–741.
- R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rapoport, E. H. (1975). *Areografía: estrategias geográficas de las especies*. México, D.F.: Fondo de Cultura Económica.
- Rosenfield, J. A. (2002). Pattern and process in the geographical ranges of freshwater fishes. *Global Ecology and Biogeography*, *11*, 323–332.
- Ruggiero, A., & Werenkraut, V. (2007). One-dimensional analyses of Rapoport's rule reviewed through meta-analysis. *Global Ecology and Biogeography*, *16*, 401–414.
- Sastre, P., Roca, P., & Lobo, J. M. & EDIT co-workers. (2009). A geoplatform for improving accessibility to environmental cartography. *Journal of Biogeography*, *36*, 568–568.
- 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.
- Stevens, G. C. (1989). The latitudinal gradient in geographical range: How so many species coexist in the tropics. *The American Naturalist*, *133*, 240–256.

- Sunday, J. M., Bates, A. E., & Dulvy, N. K. (2012). Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, 2, 686–690.
- Svenning, J.-C., & Skov, F. (2007a). Ice age legacies in the geographical distribution of tree species richness in Europe. *Global Ecology and Biogeography*, 16, 234–245.
- Svenning, J.-C., & Skov, F. (2007b). Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecology Letters*, 10, 453–460.
- Tomašových, A., Kennedy, J. D., Betzner, T. J., Kuehnle, N. B., Edie, S., Kim, S., . . . Jablonski, D. (2016). Unifying latitudinal gradients in range size and richness across marine and terrestrial systems. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20153027.
- Whitton, F. J. S., Purvis, A., Orme, C. D. L., & Olalla-Tárraga, M. Á. (2012). Understanding global patterns in amphibian geographic range size: Does Rapoport rule? *Global Ecology and Biogeography*, 21, 179–190.
- Wiens, J. J., & Donoghue, M. J. (2004). Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution*, 19, 639–644.
- Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear

models: Estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 73, 3–36.

#### BIOSKETCH

ADRIÁN CASTRO-INSUA is a PhD student interested in macroecology and macroevolution of vertebrates.

#### SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**How to cite this article:** Castro-Insua A, Gómez-Rodríguez C, Svenning J-C, Baselga A. A new macroecological pattern: The latitudinal gradient in species range shape. *Global Ecol Biogeogr.* 2018;27:357–367. <https://doi.org/10.1111/geb.12702>