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Global determinants of zoogeographical boundaries

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The distribution of living organisms on Earth is spatially structured. Early biogeographers identified the existence of multiple zoogeographical regions, characterized by faunas with homogeneous composition that are separated by biogeographical boundaries. Yet, no study has deciphered the factors shaping the distributions of terrestrial biogeographical boundaries at the global scale. Here, using spatial regression analyses, we show that tectonic movements, sharp changes in climatic conditions and orographic barriers determine extant biogeographical boundaries. These factors lead to abrupt zoogeographical transitions when they act in concert, but their prominence varies across the globe. Clear differences exist among boundaries representing profound or shallow dissimilarities between faunas. Boundaries separating zoogeographical regions with limited divergence occur in areas with abrupt climatic transitions. In contrast, plate tectonics determine the separation between deeply divergent biogeographical realms, particularly in the Old World. Our study reveals the multiple drivers that have shaped the biogeographical regions of the world.

Naturalists have long been fascinated by the variation of life across geographical regions and have described biogeographic areas since the eighteenth century[1–5]. Wallace[4] was one of the first mapping these biogeographical regions and identified some areas of transition between them (biogeographical boundaries). The analysis of biogeographical patterns has since remained an active research field[6–8] and, in recent years, the increasing availability of species distribution data has fostered quantitative studies on biogeographical regionalization at both global and regional scales, using macroecological and geospatial approaches[9–15]. On one hand, several biogeographical regions are clearly separated by barriers to dispersal[16]. For instance, Australia and Madagascar have unique terrestrial faunas, which clearly derive from the fact that they remained isolated from other land masses for tens of millions of years. On the other hand, many delineated biogeographical boundaries cross continents or correspond to narrow sea straits (Fig. 1). These terrestrial boundaries are assumed to be the consequence of multiple factors limiting the interchanges across regions, such as the presence of unfavourable climates, high turnover of environmental conditions, orographic barriers, and historical geological and climatic isolation[7,16,17]. Despite such qualitative statements, we do not know much about the relative importance of the determinants that delineate biogeographical boundaries[18] and no formal or comprehensive analyses have been carried out so far. Until now, studies on biogeographical boundaries generally have focused on one specific area, such as the Wallace line or the Nearctic–Neotropical transition zone[16,17], while a global analysis is still lacking.

We believe that this lack of knowledge comes from the complex nature and definition of biogeographical boundaries. Indeed, there is no single definition of boundary and they appear to be hierarchically structured and spatially heterogeneous. For instance, Holt *et al.* recently delineated the zoogeographical regions of the world by integrating species distribution data of terrestrial vertebrates with phylogenetic information[11]. Measuring the phylogenetic turnover between vertebrate assemblages (taken at 200 km × 200 km resolution) and using a cluster algorithm, they delineated 20 zoogeographical regions of the world that explain most of the variation in biodiversity, while maximizing the phylogenetic dissimilarities between the regions[11]. Interestingly, the nested nature of the dendrogram created from their cluster analysis also allowed the identification of 11 regions, at a higher level, called realms (Fig. 1)[11]. However, the position of cut-off points is arbitrary and, along the same dendrogram, if a deeper cut-off of similarity is used, some of the realms collapse, resulting in a smaller number of realms that are mostly consistent with the original maps of Wallace's realms[19] (Fig. 1b). In other words, some boundaries separate highly dissimilar assemblages, while others separate regions with lower dissimilarities (Fig. 1). To refer to this biogeographical hierarchy, since there is no clear accepted terminology, we use the terms shallow, intermediate and deep bioregions and boundaries. Clearly, complex determinants are responsible for this nested structure of biogeographical regions and we argue that some might explain deep bioregion boundaries, while others should be more related to intermediate and shallow boundaries. More specifically, we hypothesize that climatic heterogeneity, orographic barriers, past tectonic history and velocity of past climate change may play a major role in setting biogeographical boundaries. These factors may have a different role in explaining shallow or deep boundaries, as processes acting deeper in the past (for example, plate tectonic movements) may be most important for deep boundaries, while factors representing present-day ecological barriers (for example, climatic heterogeneity) may best explain shallow boundaries.

Climate is a major determinant of the present-day limits of species distributions[20] and faunistic turnover is higher between regions with dissimilar environmental features[21,22]. Therefore, climate could have a major role, for instance, for shallow boundaries[18]. However, climatic conditions have strongly shifted during the Quaternary period, determining broad-scale changes of species distributions and modifications of assemblages[23–25]. The velocity of past climate change since the last glacial maximum is known to be a major driver of endemism and biogeographical structure, with higher endemism of vertebrates in regions with more stable climate[26]. As endemism plays an important role in the definition of biogeographical regions[19], Quaternary climate changes have been potentially important to set boundaries representing shallow or intermediate

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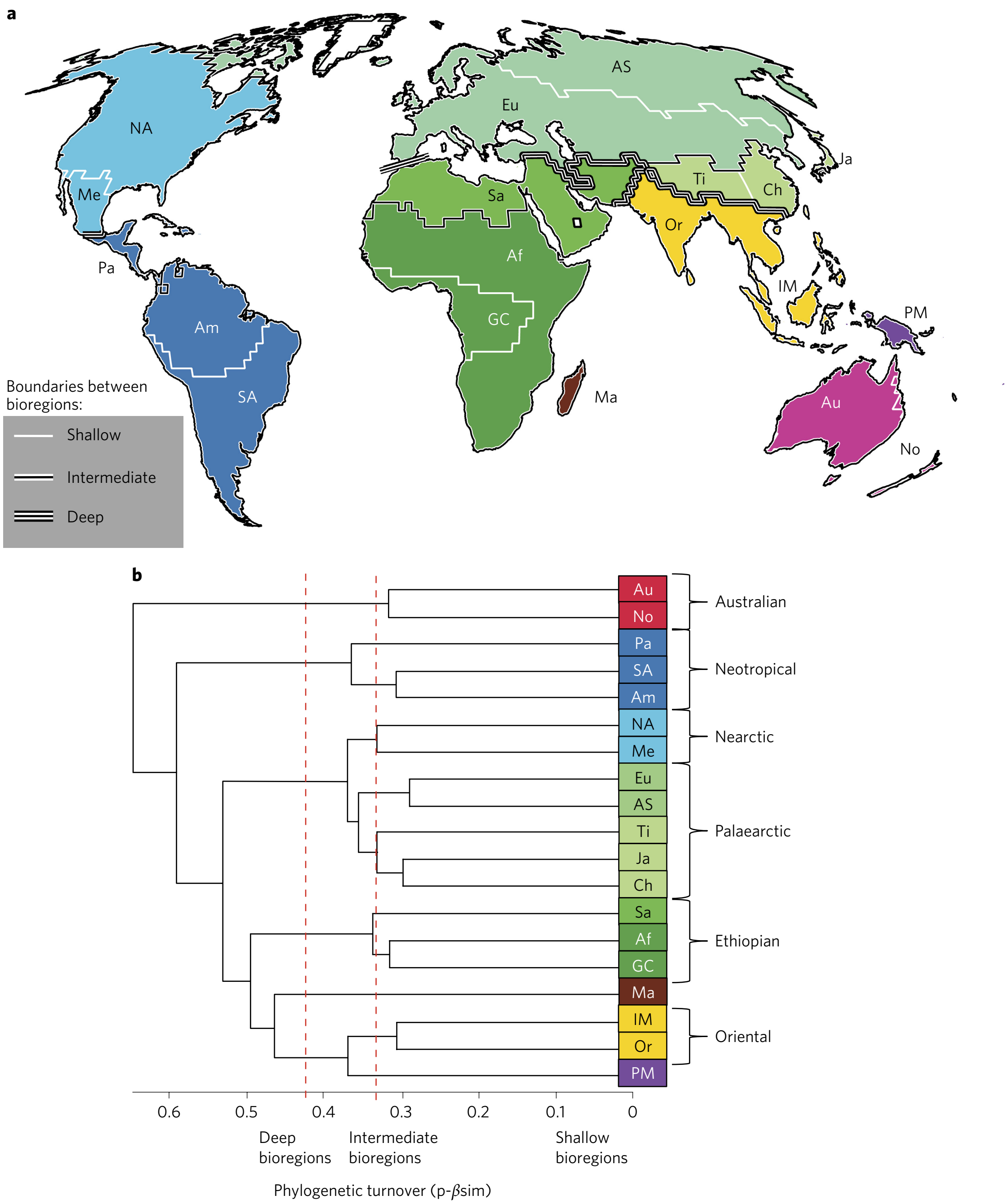

Figure 1 | The global zoogeographical regions of the world. Regions defined by Holt *et al.*[11]. **a**, Biogeographical regions for vertebrates and their associated boundaries used in this study, as defined on the basis of phylogenetic faunistic turnover (ref. [11]). **b**, Phylogenetic turnover (p-βsim; ref. [11]) among bioregions. Regions may be clustered at different turnover thresholds. Clustering them at p-βsim = 0.33 results in bioregions corresponding to Holt *et al.*'s realms[11], while clustering them at deeper p-βsim values results in bioregions very similar to the traditional biogeographical realms[6,19]. Biogeographical regions are: Af, African; Am, Amazonian; AS, Arctico-Siberian; Au, Australian; Ch, Chinese; Eu, Eurasian; GC, Guineo-Congolian; IM, Indo-Malayan; Ja, Japanese; Ma, Madagascan; Me, Mexican; NA, North American (= Nearctic); No, Novozelandic; Or, Oriental; Pa, Panamanian; PM, Papua-Melanesian; SA, South American; Sa, Saharo-Arabian; Ti, Tibetan. The Polynesian region is not shown. Figure adapted from ref. [11], AAAS.

dissimilarity among regions[23]. Tectonics have determined the long-term isolation of the biotas on some continental plates[16]; thus, we expect that tectonic history (movements of plates during the Cenozoic era) has determined some of the deepest boundaries[7,27]. Although the role of tectonics on biogeographical patterns has long been recognized[16], no global study has used plate-motion models to explicitly quantify determinants of biogeographical boundaries. Finally, mountains are major barriers to the dispersal of terrestrial animals; thus, we expect an overall role of orographic barriers.

Here, we build on Holt *et al.*'s zoogeographical regionalization[11] by quantitatively measuring the relative importance of the above-mentioned hypotheses across the nested structure of the global regions. First, we used spatial regression models to identify the factors best explaining the occurrence of boundaries. Second, we mapped their spatial heterogeneity, to identify global and regional variation of processes in function of climate and geological history. Third, we explored their relative importance through the nested structure of regions, to assess whether these processes play a consistent role on all the boundaries or whether some are more important for boundaries representing deep or shallow dissimilarity. Finally, we demonstrated the robustness of our conclusions to alternative classifications of zoogeographical regions[6,10].

Results

The geographical position of terrestrial biogeographical boundaries was accurately predicted by the spatial models (Supplementary Table 1). When we analysed the factors related to the overall presence of boundaries (all boundaries in Fig. 1), we found support for a joint role of climatic heterogeneity, tectonic movements during the last 65 million years and orographic barriers (Fig. 2 and Supplementary Table 1). Temperature heterogeneity and tectonic movements were the variables with the strongest overall effect size, followed by orographic barriers and heterogeneity of temperature seasonality. We did not detect any relationship between biogeographical boundaries and the velocity of Late Quaternary climate change. Velocity of climate change is strongly related to topography[26] (Supplementary Table 2); however, it remained non-significant when altitude was excluded from the model (simultaneous autoregressive model; *t*-test of the regression coefficient: $t_{2191} = -0.73$, $P = 0.46$).

Geographically weighted regression (GWR) suggested that relationships between environmental features and boundaries were not homogeneous across the globe (Fig. 3a–d). Overall, temperature heterogeneity best explained the boundaries crossing Eastern Asia, Central America and North America, while heterogeneity of temperature seasonality best explained the boundaries of the Amazonian and Guineo–Congolian regions. Western Eurasia boundaries were best explained by tectonic movements, while orographic barriers best explained the Asiatic boundaries between the Arctico–Siberian, Eurasian, Tibetan and Oriental regions (Fig. 4a). Climatic variables were particularly important to define the boundaries of tropical and subtropical regions. Species turnover is the basis of biogeographical regionalization and is more strongly linked to environmental heterogeneity in the tropics than at the high latitudes[21]. This probably occurs because the limited short-term climatic variability in the tropics can favour physiological specialization, determining narrower niches and particularly strong responses to climate[28].

We then performed sequential analyses on boundaries representing different levels of faunistic dissimilarities. The boundaries representing the shallowest dissimilarities (white lines in Fig. 1) were strongly associated with heterogeneity of temperature seasonality and, to a lesser extent, with orographic barriers (Fig. 2 and Supplementary Fig. 1). Major equatorial regions (Guineo–Congolian and Amazonian) are areas with constant temperature through the year (Supplementary Fig. 2) and their limits, particularly in the south, are strongly related to shifts towards more seasonal climates. This strongly agrees with the idea that limited seasonal variability is a major determinant of the narrow niche of tropical animals[28].

When we focused on deeper biogeographical relationships (intermediate bioregions, that is, boundaries among Holt *et al.*'s realms[11]), heterogeneity of temperature was the variable with the strongest effect size, followed by plate tectonic movements and orographic barriers (Fig. 2, Supplementary Fig. 1 and Supplementary Table 1). Finally, the deepest biogeographical boundaries were mostly related to plate tectonic motion, with a consistent effect through the boundaries crossing the whole Old World (Figs 2–4 and Supplementary Table 1). Nevertheless, significant local relationships remained with climatic parameters and orographic barriers (Fig. 3) and the position of the boundary between the Neotropics and the Nearctic corresponded to areas with strong heterogeneity of temperature (Fig. 3e and Fig. 4b). The optimal bandwidth detected by GWRs was 1,000 km in the analysis of shallow boundaries, 1,800 km when focusing on the intermediate boundaries and 4,800 km for deep boundaries. In these spatial regression models, the optimal bandwidth identifies the distance of neighbours to include into local regressions[29] and the shorter bandwidths of shallow and intermediate bioregions suggest that more local processes act on the boundaries representing limited dissimilarities.

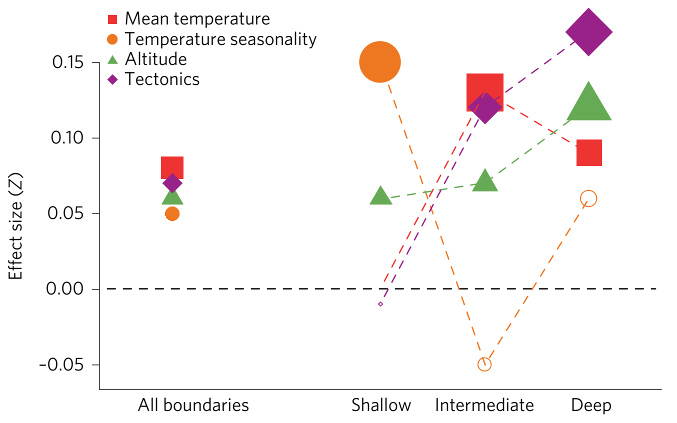

Figure 2 | Relative importance of plate tectonics, altitude and climate on the boundary positions of the biogeographical regions worldwide. The figure presents the effect sizes (obtained through autoregressive models) of each factor in explaining all boundaries and the boundaries between shallow, intermediate and deep bioregions (19, 11 and 6 bioregions, respectively). The size of symbols is proportional to effect size; empty symbols represent non-significant values. Effect size was measured using Fisher's *Z*, which allows for comparison among analyses, even if they have different sample sizes[62].

Discussion

Our analysis is a first attempt to tease apart the role of multiple factors in shaping zoogeographical boundaries at the global scale, and it shows that multiple factors often interplay to determine major transitions. For instance, past separation of tectonic plates led to long-term isolation and strong dissimilarity of faunas among continents, but biotic interchanges occurred when the movement of some plates brought isolated biotas in contact[30–32]. Clear biogeographical differences have remained even after contact among plates, probably maintained by the interplay with other processes. In the Old World, the collision between the African, Arabian, Eurasian and Indian plates has created major mountain chains, which are physical barriers that also determine sharp climatic transitions (Supplementary Fig. 4). In this region, plate tectonics, climate and orography have thus played a joint, and difficult to disentangle, role in shaping zoogeographical boundaries (Fig. 3).

Conversely, no sharp barriers exist between the Neotropics and the Nearctic; thus, the transition between these two realms is more blurred[7,19,33]. The northern distribution limit of Neotropical taxa is highly heterogeneous, with some Neotropical families of vertebrates limited to areas south of Panama and others ranging to Texas[16]. The formation of the Panama isthmus was a complex geological process, with multiple waves of dispersal of terrestrial organisms[32,34] and the deepest present-day faunistic transition does not always coincide with the narrowest isthmus or with the point of contact between plates (Uramita suture)[16,22,34]. The dispersal of organisms between North and South America was probably limited by the interplay between availability of land and suitable environmental conditions[32,34] and the transition from tropical to more temperate climates remains the most probable factor limiting biotic homogenization (Figs 3 and 4). A long-standing debate exists on the boundaries of some regions, such as the position of the southern limit of the Nearctic or the existence of the boundaries of the Sino–Japanese region; some of them have been proposed as possible transition zones[19,35],

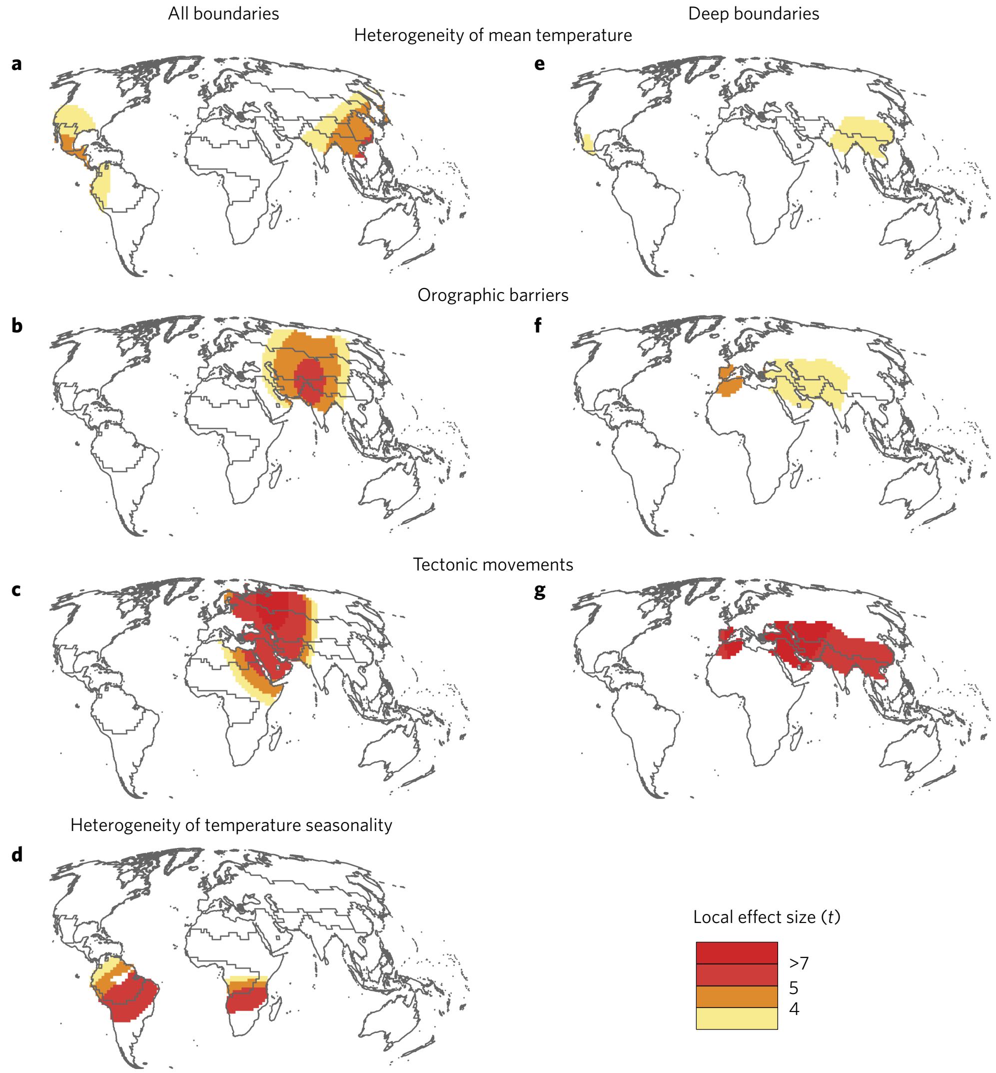

Figure 3 | Geographical variability of the importance of tectonics, altitude and climate on the position of biogeographical boundaries. Heterogeneity of local effect sizes (t) obtained through GWR. **a–d**, Analysis on all the boundaries. **e–g**, Analysis limited to the deep boundaries. Only local effect sizes significantly higher than zero are mapped. See Supplementary Fig. 1 for the results of analyses on shallow and intermediate boundaries.

even though they harbour many endemic taxa and maintain distinct biotas[16,36]. Temperature heterogeneity is the strongest correlate of the boundaries of these regions (Figs 3 and 4). Climatic, tectonic and orographic changes are often closely linked, but our results suggest that complex faunistic transitions may be associated with areas where climate does not act jointly with other processes.

The boundaries across Eurasia (for example, between the Palearctic and the Saharan region, and between the Sino–Japanese and the Oriental regions) were strongly related to tectonic movements, that is, the recent contact between the Eurasian, Arabian and Indian plates[37], a pattern well recognized in the biogeographical literature[16,38,39]. The importance of tectonic movements was particularly clear in western Asia (Fig. 3c). In this region, the boundary between the Saharan and the Eurasian bioregions matches the limits of the Arabian plate well, which remained isolated from Eurasia until the Miocene epoch[37,38]. The formation of major mountain chains (for example, the Zagros Mountains) after the collision between Arabia and Eurasia, and the harsh climatic conditions, probably contributed to the strong differentiation between the Arabian and Eurasian faunas[16]. The GWR analysis performed on all boundaries taken together suggested that tectonic movements have a very broad influence over western Eurasia, with apparent effects spanning northwards up to the Urals (Fig. 3c). However, this is probably an artefact of GWR analysis, which, in this case, overestimated the influence of tectonics across space, probably because of the very strong local effect of the movements of the Arabian plate. There is indeed no global effect of tectonics on shallow boundaries (such as the one between the Eurasian and the Arctico–Siberian plates; Fig. 2). Furthermore, no tectonic movements occurred inside the Eurasian plate during the last 100 million years[37] (Supplementary Fig. 4) and the boundary between the Eurasian and the Arctico–Siberian plates was clearly unrelated to tectonic movements if analysed separately (Supplementary Fig. 1).

Boundaries in eastern Asia and between the bioregions of central-northern America were related to the presence of a strong temperature gradient (Fig. 3a). Regional-scale analyses on eastern Asia yielded a similar pattern and showed that the interplay between present-day climate and elevational gradients is a strong determinant of zoogeographical boundaries in this area[39]. He *et al.* suggested that orographic barriers and tectonics were the most probable determinants of biogeographical structure in western China, while the transition from tropical to temperate and continental climates was a major determinant of the regionalization in eastern China[39], which corroborates our findings.

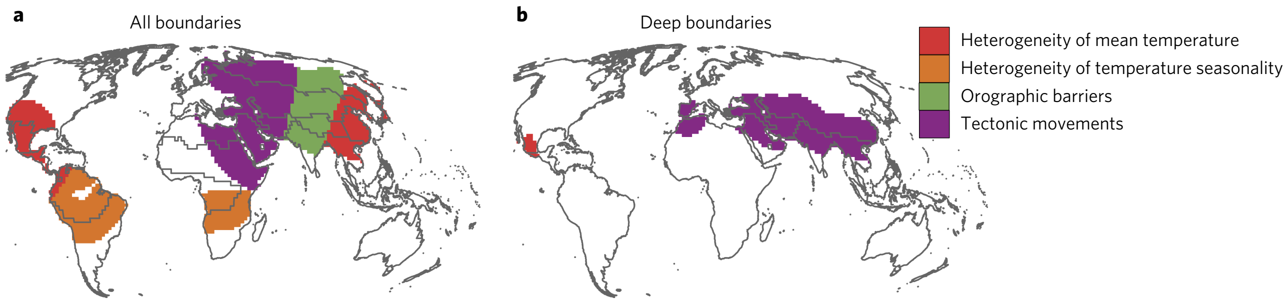

Figure 4 | Factors most strongly related to the presence of biogeographical boundaries. For each pixel, the map shows the factor with the highest local effect size according to GWR. **a**, Analysis on all the boundaries. **b**, Analysis limited to the deep boundaries. Only local effect sizes significantly higher than zero are mapped.

Here, we focused on the biogeographical boundaries proposed by Holt *et al.*[11]. Alternative biogeographical structures have been proposed using both qualitative and quantitative approaches[6,10,12–14,16]. Although some differences exist, the overall pattern is consistent among studies and differences are mostly present for the shallow boundaries between subregions, while the deepest boundaries are strikingly similar between Wallace's original classification[4] and modern, data-driven approaches. Interestingly, these boundaries that remain highly congruent among studies are the ones we showed that arise from several factors, such as the joint effect of tectonics, climate and orography in the Old World (Fig. 3f,g). Actually, our conclusions on how multiple processes act in concert to define the deepest biogeographical dissimilarities are robust and do not strongly change if we use alternative regionalizations[6,10] as baselines (Supplementary Table 3, Supplementary Fig. 3 and Supplementary Discussion). The situation is more complex for boundaries representing shallow dissimilarities, which may be blurred by the presence of transition zones[13] and for which different taxa can show non-congruent regionalization[10–12]. Furthermore, responses to climatic factors may be strongly different among taxa, meaning that the parameters determining boundaries may vary not only among areas of the world, but also depending on the taxa on which biogeographical analyses are based. Fine-resolution analyses, focusing on specific boundaries, can be important to reveal additional processes acting at more regional scales and to understand when the biogeographical structure originated[18,33,40,41]. Nevertheless, the analysis presented here paves the way for in-depth examination and comparative tests of the factors driving ecological and biogeographical transitions at multiple scales and for multiple taxa. The zoogeographical regions of the world have been shaped by multiple ecological and historical drivers. Using adequate spatial models, in combination with well-defined factors representing ecological expectations, allows identification of the complex and hierarchical processes determining zoogeographical boundaries, thus enabling a more objective understanding of biogeographical patterns.

Methods

Data. *Biogeographical regions.* We built on Holt *et al.*'s maps of biogeographical regions[11] that we converted into a raster grid at a 200 km resolution (Mollweide equal-area projection; see Supplementary Figs 2 and 4 for Earth maps at this resolution), a scale generally appropriate for global analyses of species distribution[42,43]. The 'terrestrial' biogeographical boundaries were defined as the boundaries between zoogeographical regions that were not separated by the sea at this resolution (Fig. 1). A cell was considered to be on the boundary if a nearby cell belonged to a different zoogeographical region or realm (depending on the analysis). A few boundaries were represented by narrow sea straits that are not evident at the 200 km resolution (Gibraltar, Djibouti and La Pérouse Straits; see Fig. 1 and Supplementary Fig. 2) and were also considered among the analysed boundaries.

Predictors. We considered four processes that might be related to the probability that a given world cell represents biogeographical boundaries: (1) areas of high climatic heterogeneity (climatic barriers); (2) orographic barriers; (3) tectonic separation; and (4) instability of past climate. The climatic heterogeneity hypothesis proposes that boundaries correspond to areas where climatic parameters show strong spatial turnover (heterogeneity among neighbouring cells). We considered the heterogeneity for four climatic variables: annual mean absolute temperature, temperature seasonality, annual summed precipitation and precipitation seasonality; all climatic variables were extracted from the WorldClim dataset[44] up-scaled at a 200 km resolution. These variables represent both average conditions and their variability across the year, and are simple major determinants of vertebrate distribution[45]. Furthermore, mean annual temperature and precipitation seasonality are enough to explain most of the climatic variation at the global scale[21] and other important variables (for example, summer and winter temperatures) are strongly related to linear combinations of the four climatic parameters considered in our analyses (Supplementary Table 4). To measure climate heterogeneity, for each cell, we calculated the coefficient of variation between the focal cell and its neighbouring cells, using a queen connection scheme. Therefore, the values at a given cell are higher if the cell is strongly different from its neighbours (Supplementary Fig. 4). To test for the orographic barrier hypothesis, we calculated the mean absolute difference between the altitude of each cell and its neighbouring cells. To test for the potential effect of past climatic change or stability, for each cell we calculated the average velocity of climate change since the last glacial maximum[26]. Past climate change from the Cenozoic could also probably explain present-day biogeographical structure. However, given that paleoclimatic reconstructions are still unable to reliably reproduce deep past climates[46–48], we preferred to not include them in our analyses. To test for the tectonic separation hypothesis[7], we calculated the variability in geographical distance between each cell and its neighbours during the last 65 million years (that is, temporal variability of geographical distances averaged across neighbours; see Supplementary Fig. 4 for details and examples) using GPLATE software[49,50]. This value is low for cells that did not change their position compared with their neighbours (for example, within a continental shelf) and increases for cells that experienced tectonic movements (for example, a continental collision) (Supplementary Figs. 4 and 5). All variables were log-transformed before analyses to improve normality and reduce skewness. Pairwise correlations between the seven variables were <0.7; the strongest correlations were between mean temperature heterogeneity and altitude variation, and between velocity of past climate change and altitude variation (Supplementary Table 2).

Statistical analyses. We used spatially explicit regression models to assess the factors that may explain the position of biogeographical boundaries. We first analysed the factors related to the overall presence of boundaries (all boundaries in Fig. 1; global analysis). The dependent variable was whether a grid cell was in contact with a terrestrial biogeographical boundary (Y/N; Fig. 1), while the seven environmental variables, scaled to mean = 0 and variance = 1, were the independent variables. We then performed three analyses to assess the factors related to boundaries representing different values of phylogenetic turnover: shallow phylogenetic turnover (boundaries between shallow bioregions but not between realms; white lines in Fig. 1), deep turnover (boundaries between intermediate and deep bioregions, that is, Holt *et al.*'s realms[11]) and very deep turnover (boundaries between deep bioregions, that is, Wallace's realms[4]). These analyses were performed to assess the relative importance of variables identified by the global analysis in determining boundaries representing specific levels of turnover; therefore, we used variables significant in the global analysis as independent variables. Each analysis was limited to within 1,000 km from the target biogeographical boundaries, to avoid an excessive number of zeros.

The residuals of preliminary ordinary least squares regression showed significant spatial autocorrelation (global analysis: Moran's $I = 0.357$; analysis on shallow boundaries: $I = 0.374$; analysis on intermediate boundaries: $I = 0.361$; and analysis on deep boundaries: $I = 0.366$; all analyses $P < 0.001$) and failure in taking into account spatial autocorrelation may bias the result of regression analyses[51]. Therefore, we used simultaneous autoregressive spatial (SAR) models with binomial error distribution to identify the environmental features related to the occurrence of biogeographical boundaries. SAR models are spatially explicit regression techniques that deal with spatial autocorrelation; in our models, spatial autocorrelation was incorporated in the error term using neighbourhood matrices (SAR_{ERR}). SAR_{ERR} are considered among the best-performing approaches to spatial regression[51–53]. We used a neighbourhood of 566 km, which was the shortest distance allowed that kept all study cells connected to at least another cell. Binomial SAR_{ERR} were built using hierarchical generalized linear mixed models (HGLMs) with spatially correlated random effects[54]. HGLMs provide results consistent with other analytical approaches, for example, spatial mixed models[55], but are more computationally efficient, allowing the analysis of large datasets in reasonable time[54]. In all models, the variance inflation factor was ≤3 for all variables, indicating that collinearity among variables was not a major issue[56]. Nevertheless, moderate correlation existed between altitude variation and mean temperature heterogeneity (Supplementary Table 2). We thus repeated analyses by removing the correlated variables; coefficients obtained after removing the correlated variables were in good agreement with the ones of the full models (Supplementary Table 5), confirming the robustness of our analyses. Analyses were performed in the R environment with the packages car, hglm, maptools, raster and spdep[57–60]. The capability of SAR models to correctly predict the position of biogeographical boundaries was assessed using the maximum true skill statistics, which is a measure of predictive accuracy ranging from −1 to +1, where +1 indicates perfect agreement between observed and predicted values and values ≤0 indicate that performance is not better than random[61]. Effect size of HGLM coefficients was measured using Fisher's Z, which allows for comparison among analyses, even if they have different sample sizes[62].

SAR models provide one single coefficient per each independent variable, representing the overall relationship (global analysis), but biogeographical and ecological relationships can often vary as a function of the location, showing strong spatial heterogeneity[63]. We thus used GWR analysis to assess the spatial heterogeneity of relationships between environmental features and boundaries. GWR analysis is an exploratory technique that pinpoints where non-stationarity occurs within the geographical space; that is, where locally-weighted regression coefficients deviate from their global values. If the local coefficients vary across space, this may be considered as an indication of non-stationarity[29]. GWR analysis was performed after the SAR_{ERR} analyses, considering variables significant in SAR_{ERR}. We used a binomial model and standardized independent variables. The best bandwidth was identified through a fixed Gaussian kernel; to identify the best bandwidth, we built all the models with bandwidths from 5,000 to 1,000 km at intervals of 200 km, and selected the one with lowest corrected Akaike information criterion. GWR was run using the software GWR4.0.80 (ref. [64]); local significance of GWR was adjusted for multiple testing following ref. [65].

Data availability. The data and the scripts that support the findings of this study are available from the corresponding author on request.

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Author contributions

G.F.F., F.M. and W.T. conceived the study. G.F.F. performed all analyses with the help of F.M. G.F.F. wrote the first version of the manuscript, with contributions from F.M. and W.T.

Additional information

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Competing interests

The authors declare no competing financial interests.