

# Global determinants of zoogeographical boundaries

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## *Author contributions*

The three authors conceived the study. GFF performed all analyses with the help of FM. GFF wrote the first version of the manuscript, with contribution of all authors

## *Competing interests*

The authors declare no competing financial interests

## *Data Deposition statement*

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

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

41

## 42 **Background**

43

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

64 We believe that this lack of knowledge comes from the complex nature and definition  
65 of biogeographical boundaries. Indeed, there is no single definition of boundary and they

66 appear to be hierarchically structured and spatially heterogeneous. For instance, Holt et al.<sup>11</sup>  
67 recently delineated the zoogeographical regions of the world by integrating species  
68 distribution data of terrestrial vertebrates with phylogenetic information. Measuring the  
69 phylogenetic turnover between vertebrate assemblages (taken at 200 × 200km resolution) and  
70 using a cluster algorithm, they delineated twenty zoogeographical regions of the world that  
71 explain most of variation in biodiversity while maximising the phylogenetic dissimilarities  
72 between them<sup>11</sup>. Interestingly, the nested nature of the dendrogram created from their cluster  
73 analysis also allowed Holt *et al.* to identify eleven regions, at a higher level, called realms  
74 (Fig. 1)<sup>11</sup>. However, the position of cut-off points is somehow arbitrary and, along the same  
75 dendrogram, if a deeper cut-off of similarity is used, some of Holt's realms collapse, resulting  
76 in a smaller number of realms that are mostly consistent with the original maps of Wallace's  
77 realms<sup>19</sup> (Fig. 1b). In other words, some boundaries separate highly dissimilar assemblages,  
78 while others separate regions with lower dissimilarities (Fig. 1). To refer to this  
79 biogeographical hierarchy, and since there is no clear terminology yet, we will use the terms  
80 shallow, intermediate and deep bioregions and boundaries. Clearly, complex determinants are  
81 responsible for this nested structure of biogeographical regions and we argue that some might  
82 explain deep bioregion boundaries, while others should be more related to intermediate and  
83 shallow boundaries. More specifically, we hypothesise that 1) climatic heterogeneity, 2)  
84 orographic barriers, 3) past tectonic history and 4) velocity of past climate change may play a  
85 major role in setting biogeographical boundaries. These factors may have a different role in  
86 explaining shallow or deep boundaries, as processes acting deeper in the past (e.g. plate  
87 tectonic movements) may be most important for deep boundaries, while factors representing  
88 present-day ecological barriers (e.g. climatic heterogeneity) may best explain shallow  
89 boundaries.

90 Climate is a major determinant of the present-day limits of species distributions <sup>20</sup>, and  
91 faunistic turnover is higher between regions with dissimilar environmental features <sup>21,22</sup>.  
92 Therefore, climate could have a major role, for instance for shallow boundaries <sup>18</sup>. However,  
93 climatic conditions have strongly shifted during the Quaternary, determining broad scale  
94 changes of species distributions and modifications of assemblages <sup>23-25</sup>. The velocity of past  
95 climate change since the last glacial maximum is known to be a major driver of endemism  
96 and biogeographical structure, with higher endemism of vertebrates in regions with more  
97 stable climate <sup>26</sup>. As endemism plays an important role in the definition of biogeographical  
98 regions <sup>19</sup>, quaternary climate changes have been potentially important to set boundaries  
99 representing shallow or intermediate dissimilarity among regions <sup>23</sup>. Tectonics have  
100 determined the long-term isolation of the biotas on some continental plates <sup>16</sup>, thus we expect  
101 that tectonic history (movements of plates during the Cenozoic) has determined some of the  
102 deepest boundaries <sup>7,27</sup>. While the role of tectonics on biogeographical patterns has long been  
103 recognized <sup>16</sup>, no global study has used plate-motion models to explicitly quantify  
104 determinants of biogeographical boundaries. Finally, mountains are major barriers to dispersal  
105 of terrestrial animals, thus we expect an overall role of orographic barriers.

106 Here, we build on Holt's zoogeographical regionalization by quantitatively measuring  
107 the relative importance of the above-mentioned four hypotheses across the nested structure of  
108 the global regions. First, we used spatial regression models to identify the factors best  
109 explaining the occurrence of boundaries. Second, we mapped their spatial heterogeneity, to  
110 identify global and regional variation of processes in function of climate and geological  
111 history. Third, we explored their relative importance through the nested structure of regions,  
112 to assess whether these processes play a consistent role on all the boundaries, or whether  
113 some are more important for boundaries representing deep or shallow dissimilarity. Finally,

114 we demonstrated the robustness of our conclusions to alternative classifications of  
115 zoogeographical regions<sup>6,10</sup>.

116

## 117 **Results**

118

119 The geographical position of terrestrial biogeographical boundaries was accurately predicted  
120 by the spatial models (Supplementary Table 1). When we analysed the factors related to the  
121 overall presence of boundaries (all boundaries in Fig. 1), we found support for a joint role of  
122 climatic heterogeneity, tectonic movements during the last 65 million years, and orographic  
123 barriers (Fig. 2, Supplementary Table 1). Temperature heterogeneity and tectonic movements  
124 were the variables with the strongest overall effect size, followed by orographic barriers and  
125 heterogeneity of temperature seasonality. We did not detect any relationship between  
126 biogeographical boundaries and the velocity of late quaternary climate change. Velocity of  
127 climate change is strongly related to topography<sup>26</sup> (Supplementary Table 2), still it remained  
128 non-significant if altitude was excluded from the model (simultaneous autoregressive model:  
129  $t_{2191} = -0.73, P = 0.46$ ).

130 Geographically weighted regression (GWR) suggested that relationships between  
131 environmental features and boundaries were not homogeneous across the globe (Fig. 3a-d).  
132 Overall, temperature heterogeneity best explained the boundaries crossing Eastern Asia,  
133 Central and North America, while heterogeneity of temperature seasonality best explained the  
134 boundaries of the Amazonian and Guineo-Congolian regions. Western Eurasia boundaries  
135 were best explained by tectonic movements while orographic barriers best explained the  
136 Asiatic boundaries between the Arctico-Sibirian, the Eurasian, the Tibetan and the Oriental  
137 regions (Fig. 4a). Climatic variables were particularly important to define the boundaries of

138 tropical and subtropical regions. Species turnover is the basis of biogeographical  
139 regionalization, and is more strongly linked to environmental heterogeneity in the tropics than  
140 at the high latitudes <sup>21</sup>. This probably occurs because the limited short-term climatic  
141 variability in the tropics can favour physiological specialization, determining narrower niches  
142 and particularly strong responses to climate <sup>28</sup>.

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

151 When we focused on deeper biogeographical relationships (intermediate bioregions,  
152 i.e. boundaries among Holt's realms), heterogeneity of temperature was the variable with the  
153 strongest effect size, followed by plate tectonic movements and orographic barriers (Fig. 2,  
154 Supplementary Fig. 1, Supplementary Table 1). Finally, the deepest biogeographical  
155 boundaries were mostly related to plate tectonic motion, with a consistent effect through the  
156 boundaries crossing the whole Old World (Figs. 2-4, Supplementary Table 1). Nevertheless,  
157 significant local relationships remained with climatic parameters and orographic barriers (Fig.  
158 3), and the position of the boundary between the Neotropics and the Nearctic corresponded to  
159 areas with strong heterogeneity of temperature (Fig. 3e, Fig. 4b). The optimal bandwidth  
160 detected by geographically weighted regressions was 1000 km in the analysis of shallow  
161 boundaries, 1800 km when focusing on the intermediate boundaries, and 4800 km for deep  
162 boundaries. In these spatial regression models, the optimal bandwidth identifies the distance

163 of neighbours to include into local regressions <sup>29</sup>, and the shorter bandwidths of shallow and  
164 intermediate bioregions suggest that more local processes act on the boundaries representing  
165 limited dissimilarities.

166

## 167 **Discussion**

168

169 Our analysis is a first attempt to tease apart the role of multiple factors in shaping  
170 zoogeographical boundaries at the global scale, and it shows that multiple factors often  
171 interplay to determine major transitions. For instance, past separation of tectonic plates led to  
172 long term isolation and strong dissimilarity of faunas among continents, but biotic  
173 interchanges have occurred when the movement of some plates brought isolated biotas in  
174 contact <sup>30-32</sup>. Clear biogeographical differences have remained even after the contact among  
175 plates, likely maintained by the interplay with other processes. In the Old World, the collision  
176 between the African, the Arabian, the Eurasian and the Indian plates has created major  
177 mountain chains, which are physical barriers that also determine sharp climatic transitions  
178 (Supplementary Fig. 4). In this region, plate tectonics, climate and orography have thus  
179 played a joint, and difficult to disentangle, role in shaping zoogeographical boundaries (Fig.  
180 3).

181         Conversely, no sharp barriers exist between the Neotropics and the Nearctic, thus the  
182 transition between these two realms is more blurred <sup>7,19,33</sup>. The northern distribution limit of  
183 Neotropical taxa is highly heterogeneous, with some Neotropical families of vertebrates  
184 limited to areas south of Panama, and others ranging until Texas <sup>16</sup>. The formation of the  
185 Panama Isthmus was a complex geological process, with multiple waves of dispersal of  
186 terrestrial organisms <sup>32,34</sup>, and the deepest present-day faunistic transition does not always



187 coincide with the narrowest isthmus or with the point of contact between plates (Uramita  
188 Suture) <sup>16,22,34</sup>. The dispersal of organisms between North and South America was likely  
189 limited by the interplay between availability of land and suitable environmental conditions  
190 <sup>32,34</sup>, and the transition from tropical to more temperate climates remains the most likely factor  
191 limiting biotic homogenisation (Figs. 3 & 4). A long standing debate exists on the boundaries  
192 of some regions, such as the position of the southern limit of the Nearctic, or the existence of  
193 the boundaries of the Sino-Japanese region, and some of them have been proposed as possible  
194 transition zones <sup>19,35</sup>, even though they harbour many endemic taxa and maintain distinct  
195 biotas <sup>16,36</sup>. Temperature heterogeneity is the strongest correlate of the boundaries of these  
196 regions (Figs 3 & 4). Climatic, tectonic and orographic changes are often closely linked, but  
197 our results suggest that complex faunistic transitions may be associated to areas where climate  
198 does not act jointly with other processes.

199         The boundaries across Eurasia (e.g. between the Palearctic and the Saharan region,  
200 between the Sino-Japanese and the Oriental regions) were strongly related to tectonic  
201 movements, i.e. the recent contact between the Eurasian, the Arabian and the Indian plate <sup>37</sup>, a  
202 pattern well recognized in the biogeographical literature <sup>16,38,39</sup>. The importance of tectonic  
203 movements was particularly clear in Western Asia (Fig. 3c). In this region, the boundary  
204 between the Saharan and the Eurasian bioregions matches well the limits of the Arabian plate,  
205 which remained isolated from Eurasia until the Miocene <sup>37,38</sup>. The formation of major  
206 mountain chains (e.g. the Zagros Mountains) after the collision between Arabia and Eurasia,  
207 and the harsh climatic conditions, have probably contributed to the strong differentiation  
208 between the Arabian and the Eurasian faunas <sup>16</sup>. The GWR analysis performed on all  
209 boundaries taken together suggested that tectonic movements have a very broad influence  
210 over Western Eurasia, with apparent effects spanning northward up to the Urals (Fig. 3c).  
211 However, this is likely an artefact of GWR analysis, which, in this case, overestimated the

212 influence of tectonics across space, probably because of the very strong local effect of the  
213 movements of the Arabian plate. There is indeed no global effect of tectonics on shallow  
214 boundaries (such as the one between the Eurasian and the Arctico-Siberian plates; Fig. 2).  
215 Furthermore, no tectonic movements occurred inside the Eurasian plate during the last 100  
216 million years <sup>37</sup> (Supplementary Fig. 4), and the boundary between the Eurasian and the  
217 Arctico-Siberian plate was clearly unrelated to tectonic movements if analysed separately  
218 (Supplementary Fig. 1).

219 Boundaries in Eastern Asia and between the bioregions of central-northern America  
220 were related to the presence of a strong temperature gradient (Fig. 3a). Regional scale  
221 analyses on Eastern Asia yielded a similar pattern, and showed that the interplay between  
222 present-day climate and elevational gradients is a strong determinant of zoogeographical  
223 boundaries in this area <sup>39</sup>. He, et al. <sup>39</sup> suggested that orographic barriers and tectonics were  
224 the most likely determinant of biogeographical structure in Western China, while the  
225 transition from tropical to temperate and continental climates was a major determinant of the  
226 regionalization in Eastern China <sup>39</sup>, which corroborate our findings.

227 Here we focused on the biogeographical boundaries proposed by Holt et al <sup>11</sup>.  
228 Alternative biogeographical structures have been proposed using both qualitative and  
229 quantitative approaches <sup>6,10,12-14,16</sup>. Although some differences exist, the overall pattern is  
230 consistent among studies, and differences are mostly for the shallow boundaries between  
231 subregions, while the deepest boundaries are strikingly similar between Wallace's <sup>4</sup> original  
232 classification and modern, data-demanding approaches. Interestingly, these boundaries that  
233 remain highly congruent among studies are the ones we showed that arise from several  
234 factors, such as the joint effect of tectonics, climate and orography in the Old World (Fig. 3f-  
235 g). Actually, our conclusions on how multiple processes act in concert to define the deepest  
236 biogeographical dissimilarities are robust, and do not strongly change if we use alternative

237 regionalizations <sup>6,10</sup> as baselines (Supplementary Table 3, Supplementary Fig. 3,  
238 Supplementary Discussion). The situation is more complex for boundaries representing  
239 shallow dissimilarities, which may be blurred by the presence of transition zones <sup>13</sup> and for  
240 which different taxa can show non-congruent regionalization <sup>10-12</sup>. Furthermore, responses to  
241 climatic factors may be strongly different among taxa, meaning that the parameters  
242 determining boundaries may vary not only among areas of the world, but also depending on  
243 the taxa on which biogeographical analyses are based. Fine resolution analyses, focusing on  
244 specific boundaries, can be important to reveal additional processes acting at more regional  
245 scale, and to understand when the biogeographical structure has originated <sup>18,33,40,41</sup>.  
246 Nevertheless, the analysis presented here paves the way for in-depth examination and  
247 comparative tests of the factors driving ecological and biogeographical transitions at multiple  
248 scales and for multiple taxa. The zoogeographical regions of the world have been shaped by  
249 multiple ecological and historical drivers. Using adequate spatial models, in combination with  
250 well-defined factors representing ecological expectations, allows to identify the complex and  
251 hierarchical processes determining zoogeographical boundaries, thus enabling a more  
252 objective understanding of biogeographical patterns.

253

254 **Methods**

255 **Data**

256 *Biogeographical regions* – We built on Holt's maps of biogeographical regions<sup>11</sup> that we  
257 converted in a raster grid at a 200 km resolution (Mollweide equal-area projection; see  
258 Supplementary Figs. 2 and 4 for Earth maps at this resolution), a scale generally appropriate  
259 for global analyses of species distribution<sup>42,43</sup>. The "terrestrial" biogeographical boundaries  
260 were defined as the boundaries between zoogeographical regions that are not separated by the  
261 sea at this resolution (Fig. 1). A cell was considered to be on the boundary if a nearby cell  
262 belongs to a different zoogeographical region / realm (depending on the analysis). A few  
263 boundaries were represented by narrow sea straits, that are not evident at the 200 km  
264 resolution (Gibraltar, Djibouti and La Pérouse Straits; see Fig. 1 and Supplementary Fig 2),  
265 and were also considered among the analysed boundaries.

266 *Predictors* - We considered four processes that might be related to the probability that a given  
267 world cell represents biogeographical boundaries: 1) areas of high climatic heterogeneity  
268 (climatic barriers); 2) orographic barriers; 3) tectonic separation; 4) instability of past climate.  
269 The climatic heterogeneity hypothesis proposes that boundaries correspond to areas where  
270 climatic parameters show strong spatial turnover (heterogeneity among neighbouring cells).  
271 We considered the heterogeneity for four climatic variables: annual mean absolute  
272 temperature, temperature seasonality, annual summed precipitation and precipitation  
273 seasonality; all climatic variables were extracted from the Worldclim dataset<sup>44</sup> up-scaled at a  
274 200 km resolution. These variables represent both average conditions and their variability  
275 across the year, and are simple major determinants of vertebrate distribution<sup>45</sup>. Furthermore,  
276 mean annual temperature and precipitation seasonality are enough to explain most of climatic  
277 variation at the global scale<sup>21</sup>, and other important variables (e.g. summer and winter

278 temperatures) are strongly related to linear combinations of the four climatic parameters  
279 considered in our analyses (Supplementary Table 4). To measure local heterogeneity, for each  
280 cell, we calculated the coefficient of variation (CV) between the focal cell and the  
281 neighbouring ones, using a queen connection scheme. Therefore, the values at a given cell are  
282 higher if the cell is strongly different from the neighbours (Supplementary Fig. 4). To test for  
283 the orographic barrier hypothesis, we calculated the mean absolute difference between the  
284 altitude of each cell and the neighbouring ones. To test for the potential effect of past climatic  
285 change/stability, for each cell we calculated the average velocity of climate change since the  
286 last glacial maximum<sup>26</sup>. Past climate change from the Cenozoic could also likely explain  
287 present-day biogeographical structure. However, given that paleoclimatic reconstructions are  
288 still unable to reliably reproduce deep past climates<sup>46-48</sup>, we preferred not including them in  
289 our analyses. To test for the tectonic separation hypothesis<sup>7</sup>, we calculated the variability in  
290 geographical distance between each cell and its neighbours during the last 65 million years  
291 (i.e. temporal variability of geographical distances averaged across neighbours; see  
292 Supplementary Fig. 4 for details and examples) using the GPLATE software<sup>49,50</sup>. This value  
293 is low for cells that did not change their position compared to neighbours (e.g. within  
294 continental shelves) and increases for cells that experienced tectonic movements (e.g. a  
295 continental collision) (Supplementary Figs. 4-5). All variables were log-transformed prior to  
296 analyses to improve normality and reduce skewness; pairwise correlations between the seven  
297 variables were  $< 0.7$ ; the strongest correlations were between mean temperature heterogeneity  
298 and altitude variation, and between velocity of past climate change and altitude variation  
299 (Supplementary Table 2).

300

### 301 **Statistical analyses**

302 We used spatially-explicit regression models to assess the factors that may explain the  
303 position of biogeographical boundaries. We first analysed the factors related to the overall  
304 presence of boundaries (all boundaries in Fig. 1, global analysis). The dependent variable was  
305 whether a grid cell is in contact with a terrestrial biogeographical boundary (Y/N; Fig. 1),  
306 while the seven environmental variables, scaled to mean = 0 and variance = 1, were the  
307 independent ones. We then performed three analyses, to assess the factors related to  
308 boundaries representing different values of phylogenetic turnover: shallow phylogenetic  
309 turnover (boundaries between shallow bioregions but not between realms; white lines in Fig.  
310 1), deep turnover (boundaries between intermediate and deep bioregions, i.e. Holt's realms)  
311 and very deep turnover (boundaries between deep bioregions, i.e. Wallace's realms). These  
312 analyses were performed to assess the relative importance of variables identified by the global  
313 analysis in determining boundaries representing specific levels of turnover, thus we used  
314 variables significant in the global analysis as independent. Each analysis was limited to within  
315 1000 km from the target biogeographical boundaries, to avoid an excessive number of zeros.

316 The residuals of preliminary ordinary least squares regression showed significant  
317 spatial autocorrelation (global analysis: Moran's  $I = 0.357$ ; analysis on shallow boundaries:  $I$   
318 = 0.374; analysis on intermediate boundaries:  $I = 0.361$ ; analysis on deep boundaries:  $I =$   
319 0.366; all  $P < 0.001$ ), and failure in taking into account spatial autocorrelation may bias the  
320 result of regression analyses<sup>51</sup>. Therefore, we used simultaneous autoregressive spatial  
321 models (SAR) with binomial error distribution to identify the environmental features related  
322 to the occurrence of biogeographical boundaries. SAR-models are spatially-explicit regression  
323 techniques that deal with spatial autocorrelation; in our models, spatial autocorrelation was  
324 incorporated in the error term using neighbourhood matrices (SAR<sub>ERR</sub>). SAR<sub>ERR</sub> is considered  
325 among the best-performing approaches to spatial regression<sup>51-53</sup>. We used a neighbourhood of  
326 566 km, which is the shortest distance allowing to keep all study cells connected to at least

327 another cell. Binomial SAR<sub>ERR</sub> were built using hierarchical generalized linear mixed models  
328 (HGGLM) with spatially correlated random effects<sup>54</sup>. HGGLM provide results consistent with  
329 other analytical approaches, e.g. spatial mixed models<sup>55</sup>, but are more computationally  
330 efficient, allowing to analyse large datasets in reasonable time<sup>54</sup>. In all models, variance  
331 inflation factor was  $\leq 3$  for all variables, indicating that collinearity among variables was not a  
332 major issue<sup>56</sup>. Nevertheless, moderate correlation existed between altitude variation and mean  
333 temperature heterogeneity (Supplementary Table 2). We thus repeated analyses by removing  
334 the correlated variables; coefficients obtained removing the correlated variables were in good  
335 agreement with the ones of the full models (Supplementary Table 5), confirming the  
336 robustness of our analyses. Analyses were performed on the R environment with the packages  
337 car, hglm, maptools, raster and spdep<sup>57-60</sup>. The capability of SAR models to correctly predict  
338 the position of biogeographical boundaries was assessed using the maximum true skill  
339 statistics, which is a measure of predictive accuracy ranging from -1 to +1, where +1 indicates  
340 perfect agreement between observed and predicted values, and values  $\leq 0$  indicate that  
341 performance is not better than random<sup>61</sup>.

342 SAR models provide one single coefficient per each independent variable,  
343 representing the overall relationship (global analysis), but biogeographical and ecological  
344 relationships can often vary as a function of the location, showing strong spatial heterogeneity  
345<sup>62</sup>. We thus used geographically weighted regression (GWR) to assess the spatial  
346 heterogeneity of relationships between environmental features and boundaries. GWR is an  
347 exploratory technique that pinpoints where non-stationarity occurs within the geographical  
348 space, i.e. where locally-weighted regression coefficients deviate from their global values. If  
349 the local coefficients vary across space, this may be considered as an indication of non-  
350 stationarity<sup>29</sup>. GWR was performed after the SAR<sub>ERR</sub> analyses, considering variables  
351 significant in SAR<sub>ERR</sub>. We used a binomial model and standardized independent variables.

352 The best bandwidth was identified through a fixed Gaussian Kernel; to identify the best  
353 bandwidth, we built all the models with bandwidths from 5000 to 1000 km at intervals of 200  
354 km, and selected the one with lowest corrected Akaike's Information Criterion (AICc). GWR  
355 was run using the software GWR4.0.80<sup>63</sup>; Local significance of GWR was adjusted for  
356 multiple testing following<sup>64</sup>.



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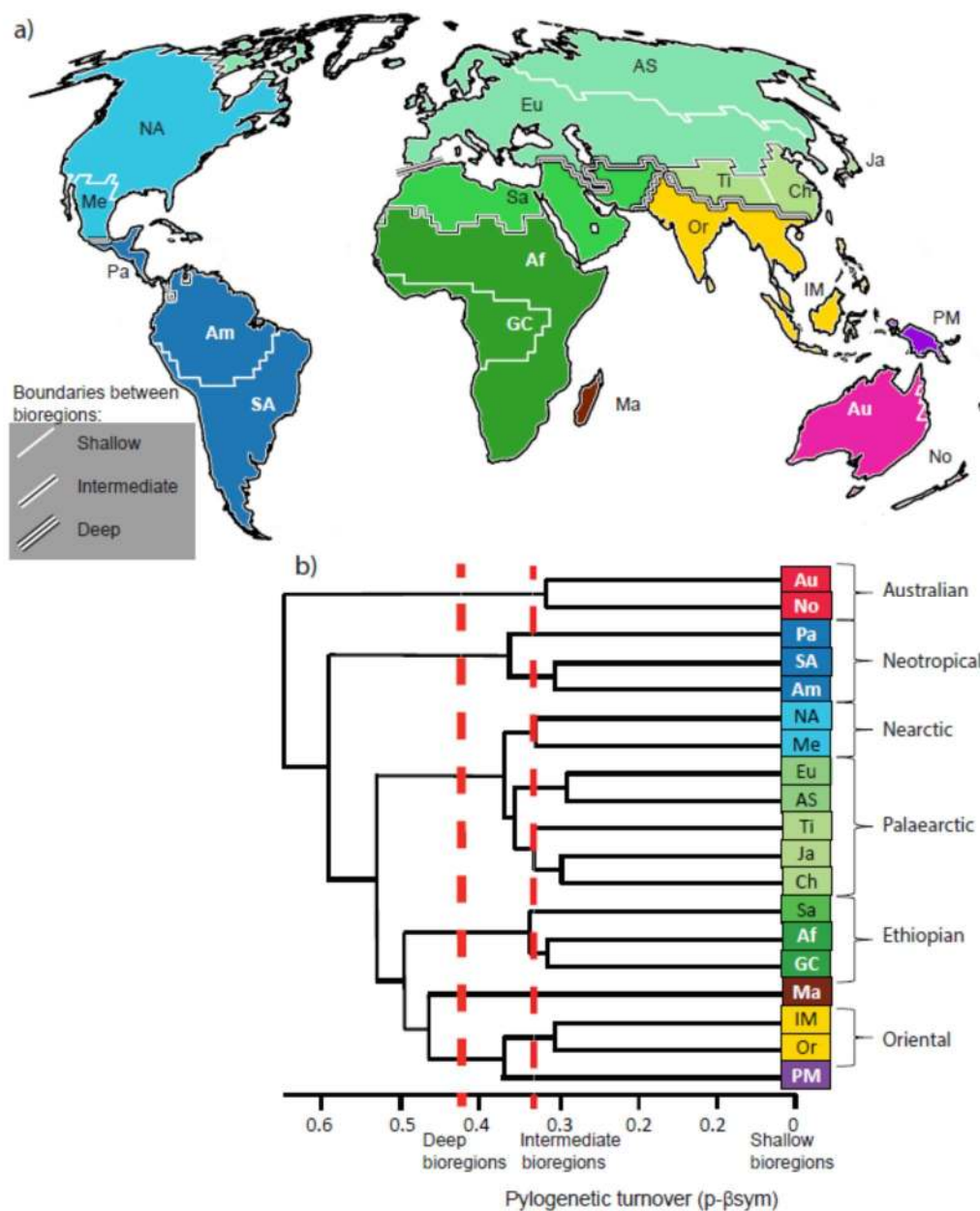
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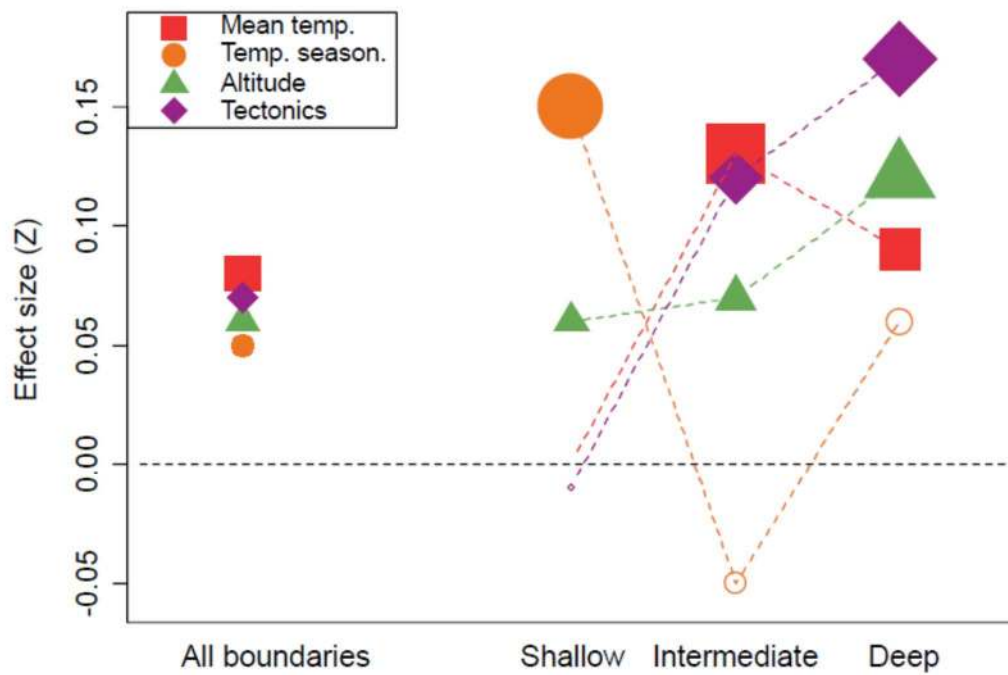


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501 **Figure 1. The global zoogeographical regions of the world**, as defined by Holt et al. <sup>11</sup>. a) Biogeographical  
 502 regions for vertebrates and their associated boundaries used here, as defined on the basis of phylogenetic  
 503 faunistic turnover <sup>11</sup>. b) Phylogenetic turnover ( $p\text{-}\beta\text{sim}$ ; <sup>11</sup>) among bioregions. Regions may be clustered at  
 504 different turnover thresholds. Clustering them at  $p\text{-}\beta\text{sim} = 0.33$  results in bioregions corresponding to the Holt's  
 505 realms <sup>11</sup>, while clustering them at deeper  $p\text{-}\beta\text{sim}$  values results in bioregions very similar to the traditional  
 506 biogeographical realms <sup>6,19</sup>. The figure has been redrawn on the basis of Holt et al. <sup>11</sup>. Biogeographical regions  
 507 are: Au, Australian; No, Novozelandic; Pa, Panamanian; SA, South American; Am, Amazonian; NA, North  
 508 American (=Nearctic); Me, Mexican; Eu, Eurasian; AS, Arctico-Siberian; Ti, Tibetan; Ja, Japanese; Ch, Chinese;  
 509 Sa, Saharo-Arabian; Af, African; GC, Guineo-Congolian; Ma, Madagascan; IM, Indo-Malayan; Or, Oriental;  
 510 PM, Papua-Melanesian. The Polynesian region is not shown.

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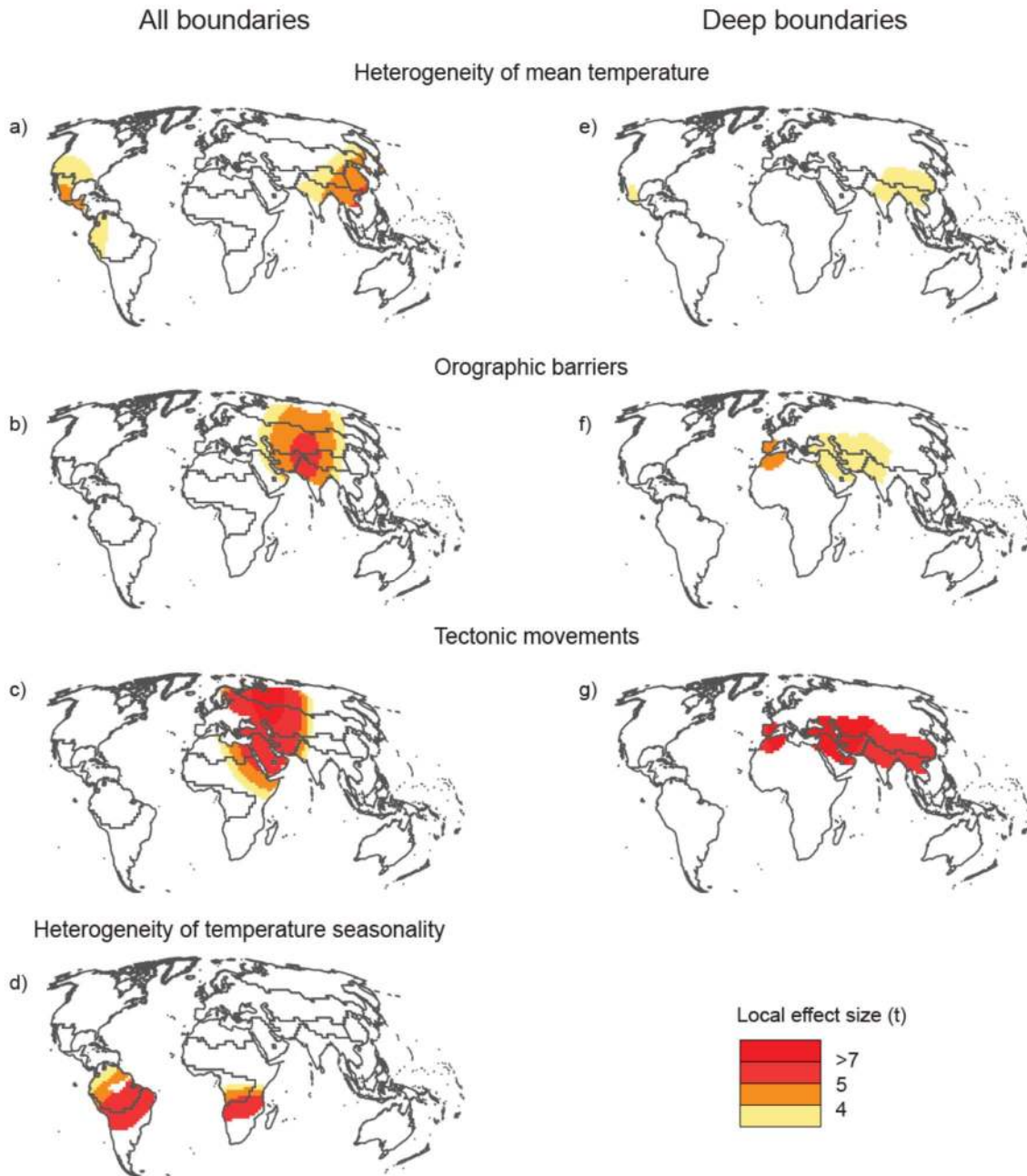
513

514 **Figure 2. Relative importance of plate tectonics, altitude and climate on the**  
 515 **biogeographical regions boundaries position worldwide.** The figure presents the effect  
 516 sizes (obtained through autoregressive models) of each factor in explaining all boundaries,  
 517 and boundaries between shallow, intermediate and deep bioregions (19, 11 and 6 bioregions,  
 518 respectively). The size of symbols is proportional to effect size; empty symbols represent non-  
 519 significant values. Effect size was measured using Fisher's Z, which allows the comparison  
 520 among analyses even though they have different sample size <sup>65</sup>.

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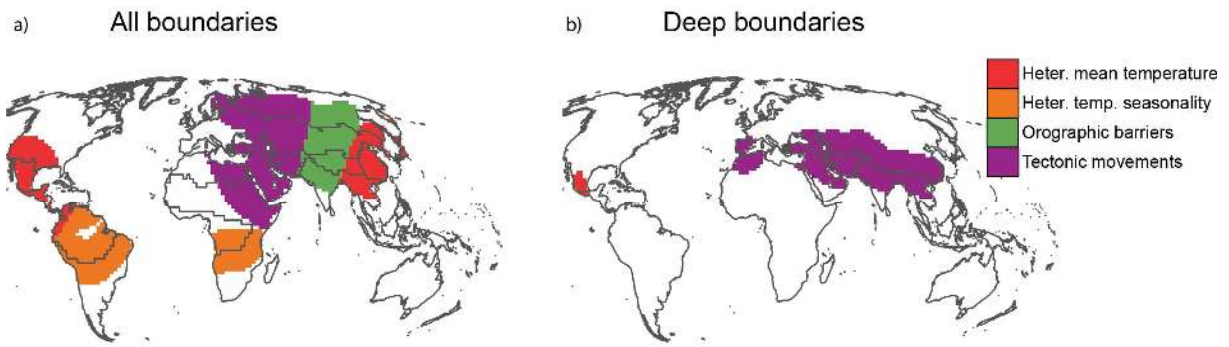




523  
524 **Figure 3. The geographical variability of the importance of tectonics, altitude and**  
525 **climate on the position of biogeographical boundaries: heterogeneity of local effect sizes**  
526 obtained through geographically weighted regression. Left-panels: analysis on all the  
527 boundaries; right-panels: analysis limited to the deep boundaries. Only local effect sizes  
528 significantly higher than zero are mapped. See Supplementary Fig. 1 for the results of  
529 analyses on shallow and intermediate boundaries.

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533

534 **Figure 4. Factors most strongly related to the presence of biogeographical boundaries.**  
 535 For each pixel, the map shows the factor with the highest local effect size according to  
 536 geographically weighted regression. Only local effect sizes significantly higher than zero are  
 537 mapped.