

Global determinants of zoogeographical boundaries

Gentile Francesco Ficetola^{1,2*}, Florent Mazel^{1,3} and Wilfried Thuiller¹

¹ Univ. Grenoble Alpes, CNRS, Laboratoire d'Écologie Alpine (LECA), F-38000 Grenoble, France

² Department of Biosciences, Università degli Studi di Milano. Via Celoria 26, 20133 Milano, Italy

³ Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada

*e-mail : francesco.ficetola@gmail.com

Acknowledgements

We thank S. Ramdhani for providing high-resolution maps of bioregions. The research leading to these results has received funding from the European Research Council under the European Community's Seven Framework Programme FP7/2007-2013 Grant Agreement no. 281422 (TEEMBIO). All authors belong to the Laboratoire d'Écologie Alpine, which is part of Labex OSUG@2020 (ANR10 LABX56).

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 ¹⁻⁵. Wallace ⁴ 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 ⁶⁻⁸ 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 ⁹⁻¹⁵. On one hand, several
51 biogeographical regions are clearly separated by barriers to dispersal ¹⁶. 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 ^{7,16,17}. Despite those qualitative statements, we do
59 not know much about the relative importance of those determinants to delineate
60 biogeographical boundaries ¹⁸, 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 ^{16,17}, 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.¹¹
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 them¹¹. 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)¹¹. 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 realms¹⁹ (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 distributions²⁰, and
91 faunistic turnover is higher between regions with dissimilar environmental features^{21,22}.
92 Therefore, climate could have a major role, for instance for shallow boundaries¹⁸. However,
93 climatic conditions have strongly shifted during the Quaternary, determining broad scale
94 changes of species distributions and modifications of assemblages²³⁻²⁵. 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 climate²⁶. As endemism plays an important role in the definition of biogeographical
98 regions¹⁹, quaternary climate changes have been potentially important to set boundaries
99 representing shallow or intermediate dissimilarity among regions²³. Tectonics have
100 determined the long-term isolation of the biotas on some continental plates¹⁶, thus we expect
101 that tectonic history (movements of plates during the Cenozoic) has determined some of the
102 deepest boundaries^{7,27}. While the role of tectonics on biogeographical patterns has long been
103 recognized¹⁶, 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^{6,10}.

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 topography²⁶ (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 ²¹. 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 ²⁸.

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 ²⁸.

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 ²⁹, 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 ³⁰⁻³². 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 ^{7,19,33}. 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 ¹⁶. The formation of the
185 Panama Isthmus was a complex geological process, with multiple waves of dispersal of
186 terrestrial organisms ^{32,34}, 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) ^{16,22,34}. 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 ^{32,34}, 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 ^{19,35}, even though they harbour many endemic taxa and maintain distinct
195 biotas ^{16,36}. 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 ³⁷, a
202 pattern well recognized in the biogeographical literature ^{16,38,39}. 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 ^{37,38}. 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 ¹⁶. 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 ³⁷ (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 ³⁹. He, et al. ³⁹ 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 ³⁹, which corroborate our findings.

227 Here we focused on the biogeographical boundaries proposed by Holt et al ¹¹.
228 Alternative biogeographical structures have been proposed using both qualitative and
229 quantitative approaches ^{6,10,12-14,16}. 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 ⁴ 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 ^{6,10} 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 ¹³ and for
240 which different taxa can show non-congruent regionalization ¹⁰⁻¹². 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 ^{18,33,40,41}.
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 regions¹¹ 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^{42,43}. 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 dataset⁴⁴ 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 distribution⁴⁵. Furthermore,
276 mean annual temperature and precipitation seasonality are enough to explain most of climatic
277 variation at the global scale²¹, 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 maximum²⁶. 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 climates⁴⁶⁻⁴⁸, we preferred not including them in
289 our analyses. To test for the tectonic separation hypothesis⁷, 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^{49,50}. 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 analyses⁵¹. 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_{ERR}). SAR_{ERR} is considered
325 among the best-performing approaches to spatial regression⁵¹⁻⁵³. 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_{ERR} were built using hierarchical generalized linear mixed models
328 (HGGLM) with spatially correlated random effects⁵⁴. HGGLM provide results consistent with
329 other analytical approaches, e.g. spatial mixed models⁵⁵, but are more computationally
330 efficient, allowing to analyse large datasets in reasonable time⁵⁴. In all models, variance
331 inflation factor was ≤ 3 for all variables, indicating that collinearity among variables was not a
332 major issue⁵⁶. 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 spdep⁵⁷⁻⁶⁰. 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 ≤ 0 indicate that
341 performance is not better than random⁶¹.

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
345⁶². 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 stationarity²⁹. GWR was performed after the SAR_{ERR} analyses, considering variables
351 significant in SAR_{ERR}. 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 GWR4.0.80⁶³; Local significance of GWR was adjusted for
356 multiple testing following⁶⁴.

357 References

358

- 359 1 Fabricius, J. C. *Philosophia Entomologica*. (Impensis Carol. Ernest. Bohnii, 1778).
- 360 2 De Candolle, A. P. *Essai élémentaire de géographie botanique*. (F. Levrault, 1820).
- 361 3 Swainson, W. *A treatise on the geography and classification of animals*. (Longman, Brown,
362 Green, and Longmans, 1835).
- 363 4 Wallace, A. R. *The geographical distribution of animals*. (Harper, 1876).
- 364 5 Sclater, P. L. On the general Geographical Distribution of the Members of the Class Aves.
365 *Journal of the Proceedings of the Linnean Society of London. Zoology* **2**, 130-145 (1858).
- 366 6 Cox, B. The biogeographic regions reconsidered. *J. Biogeogr.* **28**, 511-523,
367 doi:10.1046/j.1365-2699.2001.00566.x (2001).
- 368 7 Morrone, J. J. Biogeographical regionalisation of the world: a reappraisal. *Australian*
369 *Systematic Botany* **28**, 81-90 (2015).
- 370 8 Crisci, J. V., Cigliano, M. M., Morrone, J. J. & Roig-Junent, S. Historical Biogeography of
371 Southern South America. *Systematic Biology* **40**, 152-171 (1991).
- 372 9 Rueda, M., Rodriguez, M. A. & Hawkins, B. A. Towards a biogeographic regionalization of
373 the European biota. *J. Biogeogr.* **37**, 2067-2076, doi:10.1111/j.1365-2699.2010.02388.x
374 (2010).
- 375 10 Proches, S. & Ramdhani, S. The world's zoogeographical regions confirmed by cross-taxon
376 analyses. *Bioscience* **62**, 260-270, doi:10.1525/bio.2012.62.3.7 (2012).
- 377 11 Holt, B. *et al.* An update of Wallace's zoogeographic regions of the world. *Science* **339**, 74-78,
378 doi:DOI 10.1126/science.1228282 (2013).
- 379 12 Rueda, M., Rodriguez, M. A. & Hawkins, B. A. Identifying global zoogeographical regions:
380 lessons from Wallace. *J. Biogeogr.* **40**, 2215-2225, doi:10.1111/jbi.12214 (2013).
- 381 13 Vilhena, D. A. & Antonelli, A. A network approach for identifying and delimiting
382 biogeographical regions. *Nat. Commun.* **6**, doi:10.1038/ncomms7848 (2015).

- 383 14 Kreft, H. & Jetz, W. A framework for delineating biogeographical regions based on species
384 distributions. *J. Biogeogr.* **37**, 2029-2053, doi:DOI 10.1111/j.1365-2699.2010.02375.x (2010).
- 385 15 Edler, D., Guedes, T., Zizka, A., Rosvall, M. & Antonelli, A. Infomap Bioregions: Interactive
386 mapping of biogeographical regions from species distributions. *Systematic Biology*,
387 doi:10.1093/sysbio/syw1087 (2016).
- 388 16 Lomolino, M. V., Riddle, B. R., Whittaker, R. J. & Brown, J. H. *Biogeography*. Fourth
389 Edition edn, 878 (Sinauer Associates, 2010).
- 390 17 Riddle, B. R. & Hafner, D. J. Integrating pattern with process at biogeographic boundaries: the
391 legacy of Wallace. *Ecography* **33**, 321-325, doi:10.1111/j.1600-0587.2010.06544.x (2010).
- 392 18 Glor, R. E. & Warren, D. Testing ecological explanations for biogeographic boundaries.
393 *Evolution* **65**, 673-683, doi:10.1111/j.1558-5646.2010.01177.x (2011).
- 394 19 Kreft, H. & Jetz, W. Comment on "An Update of Wallace's Zoogeographic Regions of the
395 World". *Science* **341**, 343, doi:DOI 10.1126/science.1237471 (2013).
- 396 20 Sexton, J. P., McIntyre, P. J., Angert, A. L. & Rice, K. J. in *Annu. Rev. Ecol. Evol. Syst.* Vol.
397 *40 Annual Review of Ecology Evolution and Systematics* 415-436 (Annual Reviews, 2009).
- 398 21 Buckley, L. B. & Jetz, W. Linking global turnover of species and environments. *Proc. Natl.*
399 *Acad. Sci. USA* **105**, 17836-17841, doi:10.1073/pnas.0803524105 (2008).
- 400 22 Melo, A. S., Rangel, T. F. L. V. B. & Diniz-Filho, J. A. F. Environmental drivers of beta-
401 diversity patterns in New-World birds and mammals. *Ecography* **32**, 226-236,
402 doi:10.1111/j.1600-0587.2008.05502.x (2009).
- 403 23 Graham, R. W. *et al.* Spatial response of mammals to late quaternary environmental
404 fluctuations. *Science* **272**, 1601-1606 (1996).
- 405 24 Davis, M. B. & Shaw, R. G. Range shifts and adaptive responses to Quaternary climate
406 change. *Science* **292**, 673-679, doi:10.1126/science.292.5517.673 (2001).
- 407 25 Taberlet, P., Fumagalli, L., Wust-Saucy, A. G. & Cosson, J. F. Comparative phylogeography
408 and postglacial colonization routes in Europe. *Mol. Ecol.* **7**, 453-464, doi:DOI 10.1046/j.1365-
409 294x.1998.00289.x (1998).

- 410 26 Sandel, B. *et al.* The influence of late quaternary climate-change velocity on species
411 endemism. *Science* **334**, 660-664 (2011).
- 412 27 Mao, K. S. *et al.* Distribution of living Cupressaceae reflects the breakup of Pangea. *Proc.*
413 *Natl. Acad. Sci. USA* **109**, 7793-7798, doi:10.1073/pnas.1114319109 (2012).
- 414 28 Chan, W.-P. *et al.* Seasonal and daily climate variation have opposite effects on species
415 elevational range size. *Science* **351**, 1437-1439 (2016).
- 416 29 Bivand, R., Pebesma, E. J. & Gómez-Rubio, V. *Applied spatial data analysis with R.*
417 (Springer, 2008).
- 418 30 Vermeij, G. J. When Biotas Meet: Understanding Biotic Interchange. *Science* **253**, 1099-1104
419 (1991).
- 420 31 Simpson, G. G. S. *Splendid Isolation: The Curious History of South American Mammals.*
421 (Yale University Press, 1980).
- 422 32 Bacon, C. D. *et al.* Biological evidence supports an early and complex emergence of the
423 Isthmus of Panama. *Proceedings of the National Academy of Sciences* **112**, 6110-6115 (2015).
- 424 33 Daza, J. M., Castoe, T. A. & Parkinson, C. L. Using regional comparative phylogeographic
425 data from snake lineages to infer historical processes in Middle America. *Ecography* **33**, 343-
426 354, doi:10.1111/j.1600-0587.2010.06281.x (2010).
- 427 34 Montes, C. *et al.* Middle Miocene closure of the Central American Seaway. *Science* **348**, 226
428 (2015).
- 429 35 Müller, P. *Aspects of Biogeography.* (Dr. W. Junk b.v. Publishers, 1974).
- 430 36 Holt, B. G. *et al.* Response to Comment on "An Update of Wallace's Zoogeographic Regions
431 of the World". *Science* **341**, 343, doi:DOI 10.1126/science.1237541 (2013).
- 432 37 Seton, M. *et al.* Global continental and ocean basin reconstructions since 200 Ma. *Earth-*
433 *Science Reviews* **113**, 212-270, doi:10.1016/j.earscirev.2012.03.002 (2012).
- 434 38 Briggs, J. C. *Biogeography and plate tectonics.* (Elsevier, 1987).
- 435 39 He, J., Kreft, H., Gao, E., Wang, Z. & Jiang, H. Patterns and drivers of zoogeographical
436 regions of terrestrial vertebrates in China. *J. Biogeogr.*, doi: 10.1111/jbi.12892,
437 doi:10.1111/jbi.12892 (2016).

438 40 Smith, B. T. & Klicka, J. The profound influence of the Late Pliocene Panamanian uplift on
439 the exchange, diversification, and distribution of New World birds. *Ecography* **33**, 333-342,
440 doi:10.1111/j.1600-0587.2009.06335.x (2010).

441 41 Pomara, L. Y., Ruokolainen, K. & Young, K. R. Avian species composition across the
442 Amazon River: the roles of dispersal limitation and environmental heterogeneity. *J. Biogeogr.*
443 **41**, 784-796, doi:10.1111/jbi.12247 (2014).

444 42 Hurlbert, A. H. & Jetz, W. Species richness, hotspots, and the scale dependence of range maps
445 in ecology and conservation. *Proc. Natl. Acad. Sci. USA* **104**, 13384-13389, doi:DOI
446 10.1073/pnas.0704469104 (2007).

447 43 Ficetola, G. F. *et al.* An evaluation of the robustness of global amphibian range maps. *J.*
448 *Biogeogr.* **41**, 211–221 (2014).

449 44 Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. High resolution
450 interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965-1978 (2005).

451 45 Boucher-Lalonde, V., Morin, A. & Currie, D. J. A consistent occupancy–climate relationship
452 across birds and mammals of the Americas. *Oikos* **123**, 1029-1036, doi:10.1111/oik.01277
453 (2014).

454 46 Harrison, S. P., Bartlein, P. J. & Prentice, I. C. What have we learnt from palaeoclimate
455 simulations? *Journal of Quaternary Science* **31**, 363-385, doi:10.1002/jqs.2842 (2016).

456 47 Harrison, S. P. *et al.* Evaluation of CMIP5 palaeo-simulations to improve climate projections.
457 *Nat. Clim. Chang.* **5**, 735–743 (2015).

458 48 Mauri, A., Davis, B. A. S., Collins, P. M. & Kaplan, J. O. The influence of atmospheric
459 circulation on the mid-Holocene climate of Europe: a data-model comparison. *Climate of the*
460 *Past* **10**, 1925-1938 (2014).

461 49 Williams, S., Muller, R., Landgrebe, T. & Whittaker, J. An open-source software environment
462 for visualizing and refining plate tectonic reconstructions using high-resolution geological and
463 geophysical data sets. *GSA Today* **22**, 4-9, doi:10.1016/j.earscirev.2012.03.002 (2012).

464 50 Boyden, J. A. *et al.* in *Geoinformatics: Cyberinfrastructure for the Solid Earth Sciences* (eds
465 Keller G.R. & C. Baru) 99-113 (Cambridge University Press, 2011).

466 51 Beale, C. M., Lennon, J. J., Yearsley, J. M., Brewer, M. J. & Elston, D. A. Regression analysis
467 of spatial data. *Ecol. Lett.* **13**, 246-264 (2010).

468 52 Dormann, C. F. *et al.* Methods to account for spatial autocorrelation in the analysis of species
469 distributional data: a review. *Ecography* **30**, 609-628 (2007).

470 53 Kissling, W. D. & Carl, G. Spatial autocorrelation and the selection of simultaneous
471 autoregressive models. *Global Ecol. Biogeogr.* **17**, 59-71 (2008).

472 54 Alam, M., Roennegard, L. & Shen, X. Fitting Conditional and Simultaneous Autoregressive
473 Spatial Models in hglm. *R Journal* **7**, 5-18 (2015).

474 55 Rousset, F. & Ferdy, J.-B. Testing environmental and genetic effects in the presence of spatial
475 autocorrelation. *Ecography* **37**, 781-790, doi:10.1111/ecog.00566 (2014).

476 56 Dormann, C. F. *et al.* Collinearity: a review of methods to deal with it and a simulation study
477 evaluating their performance. *Ecography* **36**, 27-46, doi:DOI 10.1111/j.1600-
478 0587.2012.07348.x (2013).

479 57 Hijmans, R. J. *raster: Geographic data analysis and modeling. R package version 2.5-2.*
480 (<http://CRAN.R-project.org/package=raster>, 2015).

481 58 Ronnegard, L., Shen, X. & Alam, M. hglm: A Package for Fitting Hierarchical Generalized
482 Linear Models. *R Journal* **2**, 20-28 (2010).

483 59 Fox, J. & Weisberg, S. *An R companion to applied regression.* (Sage, 2011).

484 60 Bivand, R. & Lewin-Koh, N. *maptools: Tools for reading and handling spatial objects.*
485 (www.r-project.org, 2014).

486 61 Allouche, O., Tsoar, A. & Kadmon, R. Assessing the accuracy of species distribution models:
487 prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* **43**, 1223-1232 (2006).

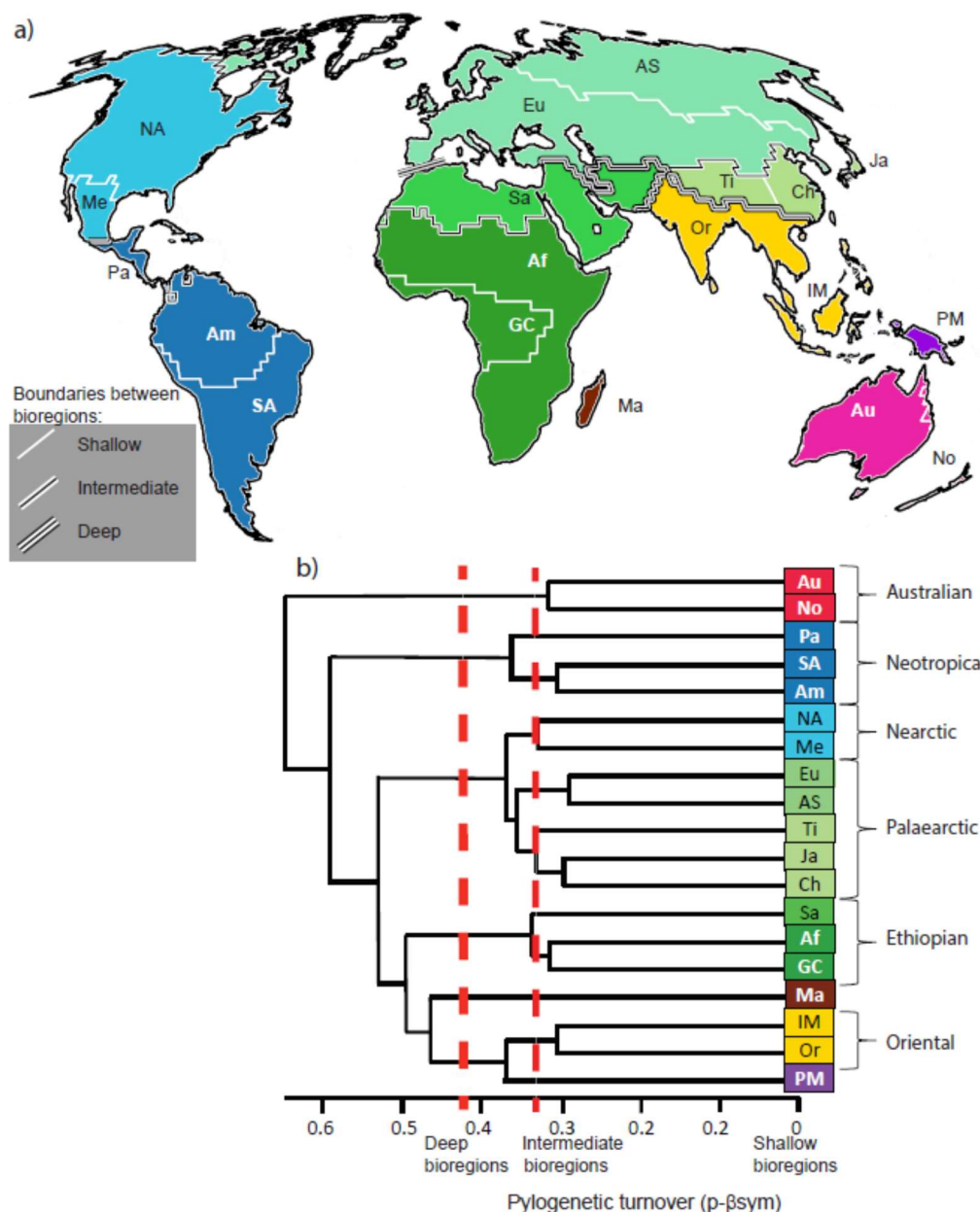
488 62 Mellin, C., Mengersen, K., Bradshaw, C. J. A. & Caley, M. J. Generalizing the use of
489 geographical weights in biodiversity modelling. *Global Ecol. Biogeogr.* **23**, 1314-1323,
490 doi:10.1111/geb.12203 (2014).

491 63 Nakaya, T., Fotheringham, A. S., Brunsdon, C. & Charlton, M. Geographically weighted
492 Poisson regression for disease association mapping. *Stat. Med.* **24**, 2695-2717,
493 doi:10.1002/sim.2129 (2005).

494 64 da Silva, A. R. & Fotheringham, A. S. The multiple testing Issue in geographically weighted
495 regression. *Geogr. Anal.* **DOI: 10.1111/gean.12084**, doi:10.1111/gean.12084 (2016).

496 65 Rosenthal, R. in *The Handbook of Research Synthesis* (eds H. Cooper & L.V. Hedges) 231-
497 244 (Russel Sage Foundation, 1994).

498

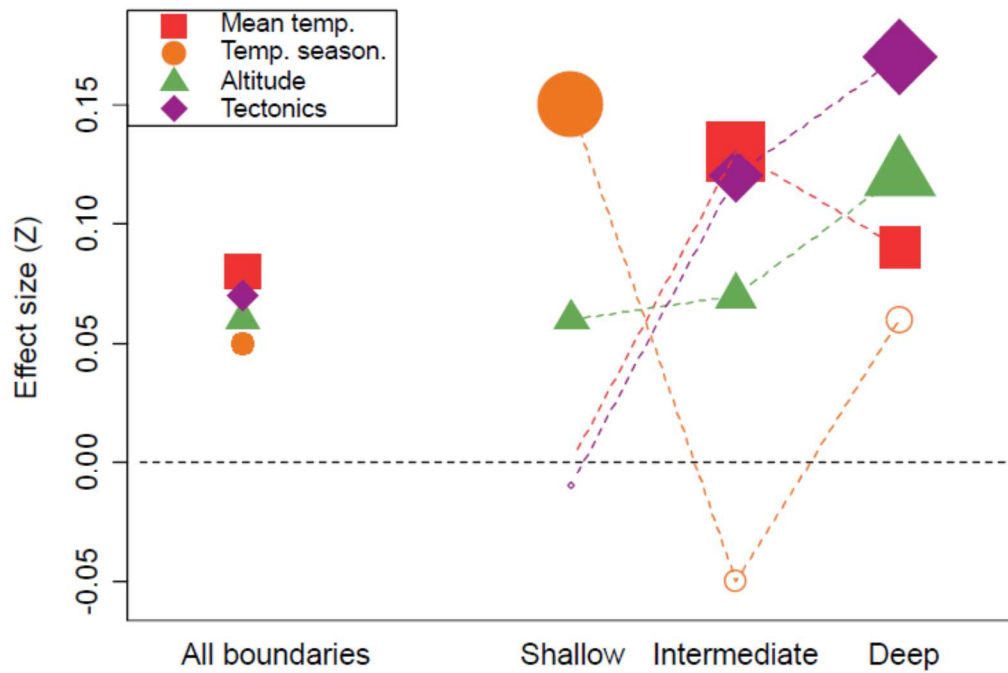


499

500

501 **Figure 1. The global zoogeographical regions of the world**, as defined by Holt et al. ¹¹. a) Biogeographical
 502 regions for vertebrates and their associated boundaries used here, as defined on the basis of phylogenetic
 503 faunistic turnover ¹¹. b) Phylogenetic turnover ($p\text{-}\beta\text{sim}$; ¹¹) 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 ¹¹, while clustering them at deeper $p\text{-}\beta\text{sim}$ values results in bioregions very similar to the traditional
 506 biogeographical realms ^{6,19}. The figure has been redrawn on the basis of Holt et al. ¹¹. 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.

511



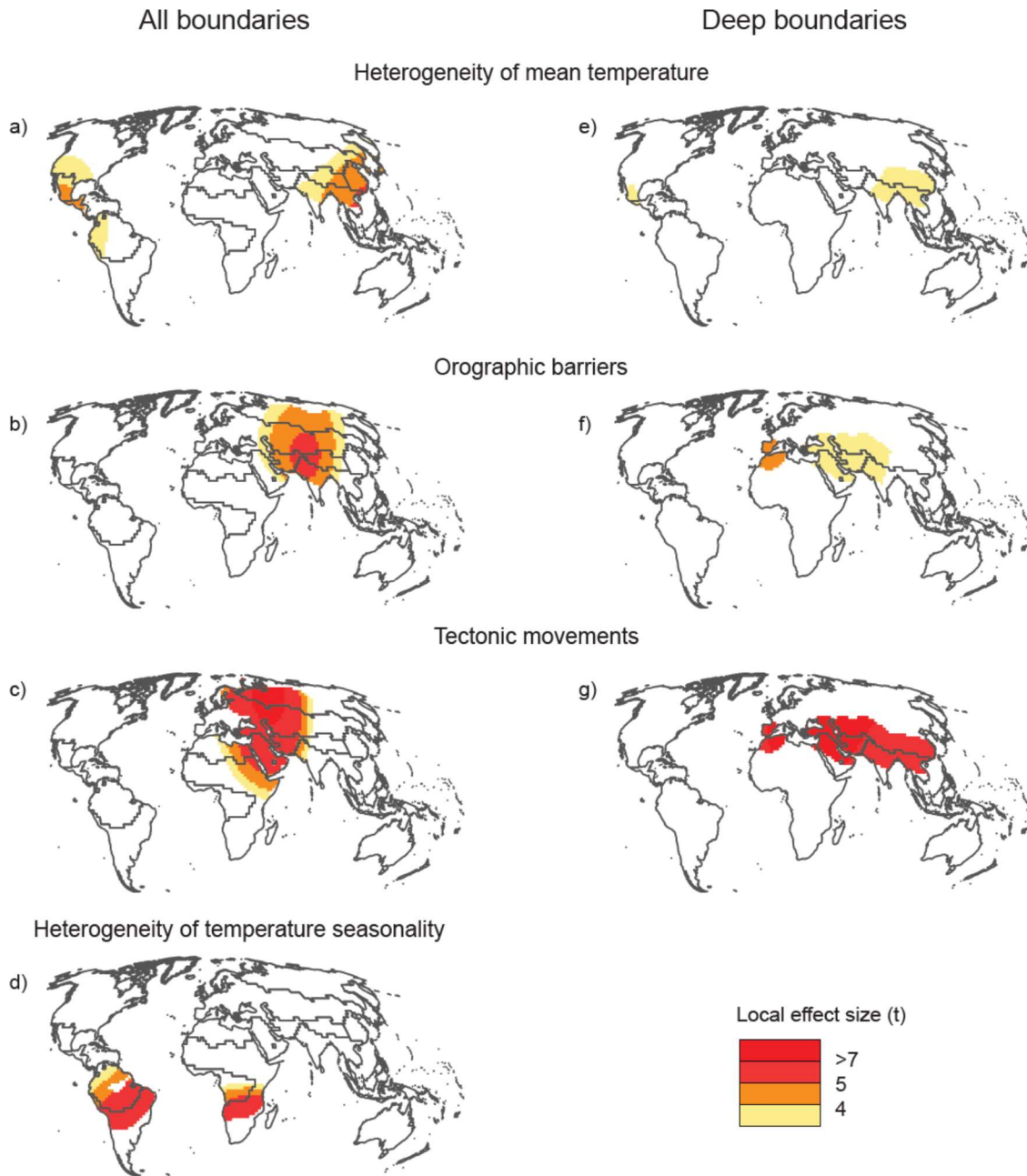
512

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 ⁶⁵.

521

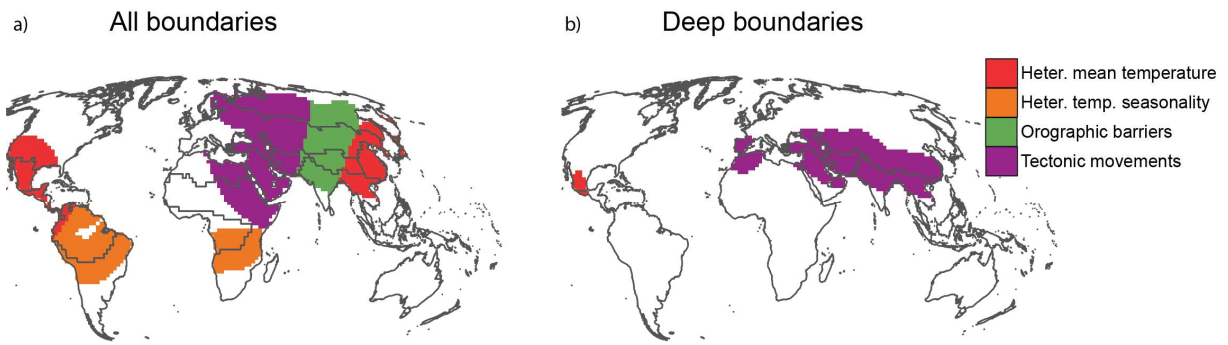
522



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.

530

531



532

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.