RESEARCH ARTICLE

Determinants of zoogeographical boundaries differ between vertebrate groups

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Abstract

Aim: Worldwide distribution patterns of living animals are structured in multiple zoogeographical regions, characterized by faunas with homogeneous composition that are separated by sharp boundaries. These zoogeographical regions can differ depending on the considered animal group, probably because they have distinct characteristics such as dispersal, metabolism, or evolutionary history, and thus divergent responses to major biogeographical drivers, such as tectonic movements, abrupt climate transitions and orographic barriers. Here, we tested if the drivers of biogeographical boundaries are different between vertebrate classes with strongly divergent traits and evolutionary history.

Location: Global.

Time period: Present.

Major taxa studied: Amphibians, birds and mammals.

Methods: We focused on terrestrial biogeographical boundaries, considering multiple potential drivers: spatial heterogeneity of present-day climate, altitudinal variation, long-term tectonic movements and past climate change (temperature). We used spatially explicit regression models and geographically weighted regressions to select and quantify the factors explaining the position of the biogeographical boundaries between vertebrate classes.

Results: For mammals, tectonic movements, abrupt climatic transitions and orographic barriers jointly determined extant biogeographical boundaries, with tectonic movements being the most important. For birds, abrupt climatic transitions played the strongest role, while the effect of orographic barriers was weak. For amphibians, biogeographical boundaries mostly corresponded to areas with abrupt climatic transitions. The strongest transitions of amphibian faunas occur in areas with abrupt shifts of temperature and precipitation regimes.

Main conclusions: Our analyses confirmed that different drivers have jointly shaped the global vertebrate biogeographical regions, and highlight that taxa with different features show heterogeneous responses across the globe. Eco-physiological constraints likely increase the importance of spatial heterogeneity of climate, while

dispersal limitations magnify the relevance of physical barriers (mountain chains and long-term tectonic instability). Integrating among-taxa heterogeneity into analyses thus provides a more complete view of how different processes determine biodiversity variation across the globe.

1 | INTRODUCTION

Naturalists have long been aware that different areas of the world can host very different faunas: we neither have pandas in Europe nor salamanders in India, nor do we find ostriches in North America (Antonelli, 2017; Smith et al., 2018). These observations have stimulated biogeographers to define biogeographical regions (also called bioregions) since the 18th century, on the basis of increasingly refined distribution data (De Candolle, 1820; Fabricius, 1778; Wallace, 1876). Some bioregions, such as the Australian one, emerged consistently across analyses performed on multiple taxa. Nevertheless, comparison among these works soon revealed that biogeographical structure can vary strongly between taxonomic groups. For instance, analyses at the European level suggested the existence of a large number of subregions for amphibians and reptiles, while less distinct regions appeared for birds (Rueda et al., 2010).

Multiple factors have promoted the regionalization of faunas (Daru et al., 2017). First, physical barriers (e.g., sea or mountains) limit species dispersal and prevent the mixture of assemblages (e.g., Australia with the rest of the world). Still, many biogeographical boundaries cross continents, and some do not coincide with clear and visible physical barriers (Figure 1; Supporting Information Figure S1). Second, differences in eco-physiological requirements may cause environmental filtering and a high faunistic turnover in areas representing sharp climatic transitions (Buckley & Jetz, 2008; Daru et al., 2017; Melo et al., 2009; White et al., 2019). For instance, high turnover of bird communities has been observed in regions representing the transition from tropical to temperate climates (White et al., 2019). Third, tectonic movements have strongly modified the configuration of continents and determined biogeographical differences between regions due to limited dispersal (Lomolino et al., 2010). Finally, past climatic changes during the Pleistocene led to species extinctions and species range shifts that might still be visible in some present-day patterns of species ranges, richness, and endemism (Daru et al., 2017; Nogués-Bravo et al., 2010; Sandel et al., 2011). The complex nature of bioregions further challenges the identification of the driving factors. Some boundaries separate bioregions with limited dissimilarity between assemblages. These shallow bioregions (often referred to as 'subregions') are nested within deep bioregions (often referred to as 'realms'), which have strongly dissimilar assemblages and are separated by deep biogeographical boundaries (Holt et al., 2013; Wallace, 1876; Supporting Information

Figure S1). Biogeographical factors may thus have different roles in explaining shallow or deep boundaries, as shallow boundaries can be best explained by present-day ecological barriers (e.g., climatic heterogeneity), while deep boundaries are best explained by ancient processes such as tectonic movements (Ficetola et al., 2017).

An analysis of the factors determining the distributions of terrestrial biogeographical boundaries at the global scale showed that past tectonic movements, abrupt climatic transitions across regions, and orographic barriers determined the major zoogeographical boundaries (Ficetola et al., 2017). This work was based on biogeographical regions that were designed on the basis of phylogenetic dissimilarities of amphibians, birds and mammals (phylogenetic bioregions; Holt et al., 2013). In other words, analyses performed to date used bioregions built by averaging the beta diversity of different vertebrate clades (amphibians, birds and mammals), with regions and subregions distinguishing assemblages that were phylogenetically dissimilar for the three groups taken together. However, amphibians, birds and mammals have different life-history traits, including metabolism, eco-physiological tolerance, and dispersal abilities. Several analyses have shown that bioregions designed on the basis of different vertebrate clades show a significantly different structure, with clear variability in the number of regions and in the positions of boundaries (e.g., Rueda et al., 2010; Holt et al., 2013; Rueda et al., 2013; Edler et al., 2016; see Supporting Information Figure S1). It is likely that groups with different features (e.g., dispersal, metabolism, or evolutionary history) show divergent responses to biogeographical factors (Lomolino et al., 2010). Nevertheless, so far no study has tested this hypothesis, for instance by evaluating whether the positions of the biogeographical boundaries of these three vertebrate groups are influenced by different biogeographical factors.

Here, we build on Ficetola et al. (2017) by quantifying the relative importance of abrupt climatic transitions, orographic barriers, tectonic movements, and past climate change to explain the zoogeographical regions defined for three classes of terrestrial vertebrates. We focused on phylogenetic regionalization, which can better represent processes acting in the past, is more appropriate to analyse strongly divergent bioregions, and can highlight patterns that are not evident in species- or genus-level analyses (Daru et al., 2017). Based on the differences between groups, we hypothesized that (a) amphibian boundaries are strongly affected by climatic transitions, since they are ectotherms with usually narrow bioclimatic niches, with limited tolerance to variation in water availability and
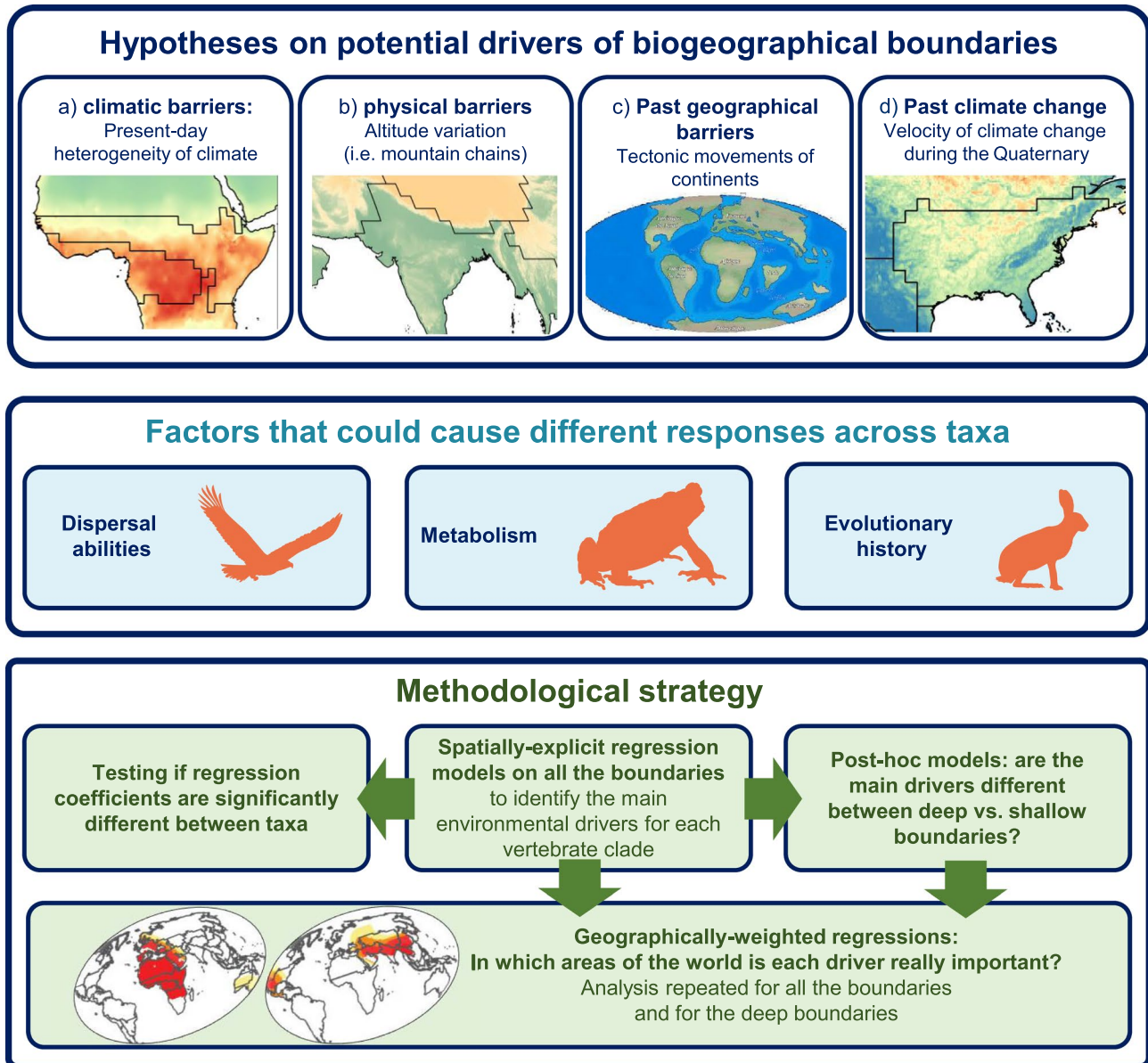
Hypotheses on potential drivers of biogeographical boundaries

a) climatic barriers:
Present-day
heterogeneity of climate

b) physical barriers
Altitude variation
(i.e. mountain chains)

**c) Past geographical
barriers**
Tectonic movements of
continents

d) Past climate change
Velocity of climate change
during the Quaternary

Factors that could cause different responses across taxa

**Dispersal
abilities**

Metabolism

**Evolutionary
history**

Methodological strategy

**Testing if regression
coefficients are significantly
different between taxa**

**Spatially-explicit regression
models on all the boundaries**
to identify the main
environmental drivers for each
vertebrate clade

**Post-hoc models: are the
main drivers different
between deep vs. shallow
boundaries?**

**Geographically-weighted regressions:
In which areas of the world is each driver really important?**
Analysis repeated for all the boundaries
and for the deep boundaries

FIGURE 1 Outline of study hypotheses and of the methods used. In the top panels, to exemplify our hypotheses we overlay boundaries of mammal bioregions (black lines) to maps of (a) temperature seasonality; (b) altitude; (c) a global plate reconstruction for 60 Myr ago and (d) velocity of temperature change during the Quaternary [Colour figure can be viewed at wileyonlinelibrary.com]

temperature (Buckley et al., 2012; Grenyer et al., 2006), and by physical barriers, due to their dispersal limitations. Within endotherms, we predict that (b) mammals have been strongly affected by physical barriers and tectonics during the last 65 Myr (Mazel et al., 2017) as most of the evolutionary history of placental mammals occurred in the Cenozoic (dos Reis et al., 2014; Halliday et al., 2019; O'Leary et al., 2013), while (c) birds are mostly affected by climatic transitions, as their expected higher dispersal ability would reduce the impact of physical barriers and often allow oversea movements (Mazel et al., 2017; White et al., 2019). We evaluate the importance of these factors for both deep and shallow boundaries, and map them to evaluate whether their importance varies spatially across biogeographical regions.

2 | METHODS

2.1 | Data

2.1.1 | Biogeographical regions

Our analyses were based on maps of biogeographical regions of mammals, birds and amphibians developed by Holt et al. (2013). Maps were rasterized at the 200-km resolution and projected to Mollweide equal-area. The 200-km resolution is generally adequate for analyses of species ranges at the global scale (Ficetola et al., 2014; Hurlbert & Jetz, 2007). Following previous works, we defined the 'terrestrial' boundaries as the boundaries separating

biogeographical regions that are not divided by water (e.g., sea) at the 200-km resolution (Supporting Information Figure S1; Ficetola et al., 2017). In the analysis of each vertebrate group, a raster cell was considered on the boundary between bioregions if at least one adjacent cell belongs to a different bioregion.

Holt et al. (2013) identified bioregions representing the clusters required to explain an amount of phylogenetic turnover (pβ_{sim}) > 95% of the total sum of all the pβ_{sim} values. This led to the identification of 19 bioregions for amphibians and birds, and 34 bioregions for mammals (Supporting Information Figure S1). Broader bioregions ('realms') can be identified by cutting the dendrograms at higher dissimilarity values, and setting lower cut-off values. Using a 90% cut-off led to 14 'realms' for amphibians, 7 realms for birds and 12 for mammals (Holt et al., 2013; Supporting Information Figure S1).

2.1.2 | Environmental features

We assessed the role of four processes that can increase the probability of a given cell of representing a biogeographical boundary (Ficetola et al., 2017): (a) areas of high spatial heterogeneity of climate (hereafter: climatic barriers); (b) orographic barriers (such as mountain chains); (c) long-term tectonic movements; (d) velocity of climate change in the past. The hypothesis of climatic heterogeneity suggests that boundaries occur in areas where climate shows abrupt transitions (high heterogeneity among adjacent raster cells). We considered four bioclimatic features (O'Donnell & Ignizio, 2012): absolute annual mean temperature, seasonality of temperature (i.e., standard deviation of monthly temperature averages), mean annual precipitation, and seasonality of precipitations (i.e., the ratio between the standard deviation of the monthly precipitation and the mean monthly precipitation). These variables are key determinants of the distribution of vertebrates (Boucher-Lalonde et al., 2014) and, in global-scale analyses, they explain the majority of climatic variation (Buckley & Jetz, 2008). Other important climatic parameters (e.g., temperatures during the coldest and warmest seasons) are strongly related to linear combinations of these four variables (Pearson's correlations > .9; Ficetola et al., 2017). We extracted climatic variables from WorldClim version 1.4 (Hijmans et al., 2005). For each cell, local heterogeneity was calculated as the coefficient of variation (CV) between the cell of interest and the eight neighbouring ones. Heterogeneity values are thus higher for cells having climate extremely different from the nearby ones (Ficetola et al., 2017; see Supporting Information Figure S2). To assess the role of orographic barriers, we calculated the averaged altitude difference (mean of absolute values) between each cell and the eight neighbouring ones. To evaluate the role of tectonic separation (Morrone, 2015), we used GPLATES (Boyden et al., 2011; Williams et al., 2012) to assess the variation of geographical distance between each cell and the neighbouring ones during the last 65 million years [average variability through time of geographical distances between neighbours; see Ficetola et al. (2017) for examples and additional details]. Tectonic movements are low for cells within continental shelves and are higher

for cells undergoing tectonic movements (Supporting Information Figure S2). To assess the role of the past climate change, we calculated the mean velocity of temperature change during the late Quaternary for each cell (Sandel et al., 2011). Strong uncertainty remains for palaeoclimatic reconstructions across the Cenozoic and for precipitation values (Harrison et al., 2015, 2016; Mauri et al., 2014), thus we decided not to include Cenozoic-scale climatic variation and past precipitation in our analyses. Before analyses, all variables were log-transformed to reduce skewness and improve normality, and then scaled and normalized (mean = 0 and variance = 1); pairwise Pearson's correlations between environmental variables were always < .7.

2.2 | Statistical analyses

Spatially explicit regression models were used to evaluate the factors related to the position of biogeographical boundaries between vertebrate groups. First, we assessed the factors affecting the overall presence of boundaries between bioregions of each clade (all the boundaries in Supporting Information Figure S1, global analysis). As the dependent variable, we considered if a cell is in contact with a boundary (Y/N; Supporting Information Figure S1), while the seven environmental variables (four variables representing present-day climate plus altitude variation, tectonics and past climate change; Figures 1 and 2) were the independent ones. For this analysis, the number of predictors (seven) was small compared to the number of analysed cells (> 1,500); therefore we did not perform model selection. Analyses were then repeated for the deep bioregions ('realms'), to pinpoint the factors determining large phylogenetic turnover, and for the boundaries occurring between shallow bioregions but not between deep bioregions (white lines in Supporting Information Figure S1; hereafter shallow boundaries). The analyses of realms and of shallow boundaries can be viewed as post-hoc tests, evaluating the relative role of globally important variables in determining deep versus shallow boundaries; thus here we only considered variables found to be significant in the global analysis (Figure 1; see also Ficetola et al., 2017). Analyses were limited to < 1,000 km from biogeographical boundaries (i.e., five cells from the boundary), to avoid a too large proportion of zeros.

Spatial autocorrelation can bias the result of regression analyses (Beale et al., 2010); thus we used simultaneous autoregressive spatial regression (SAR) models (binomial error). SAR models are spatially explicit models that allow spatial autocorrelation to be taken into account. We used neighbourhood matrices to incorporate spatial autocorrelation in the error term, as this approach produces good results in spatial regression (Beale et al., 2010; Dormann et al., 2007; Kissling & Carl, 2008). We selected a 566-km neighbourhood; this is the minimum distance allowing all study cells to be connected to another cell. We built SAR models using hierarchical generalized linear mixed models (HGLM) with spatially autocorrelated error (Figure 1; Alam et al., 2015). The variance inflation factor was ≤ 4 in all the models and for all the variables, indicating limited multicollinearity
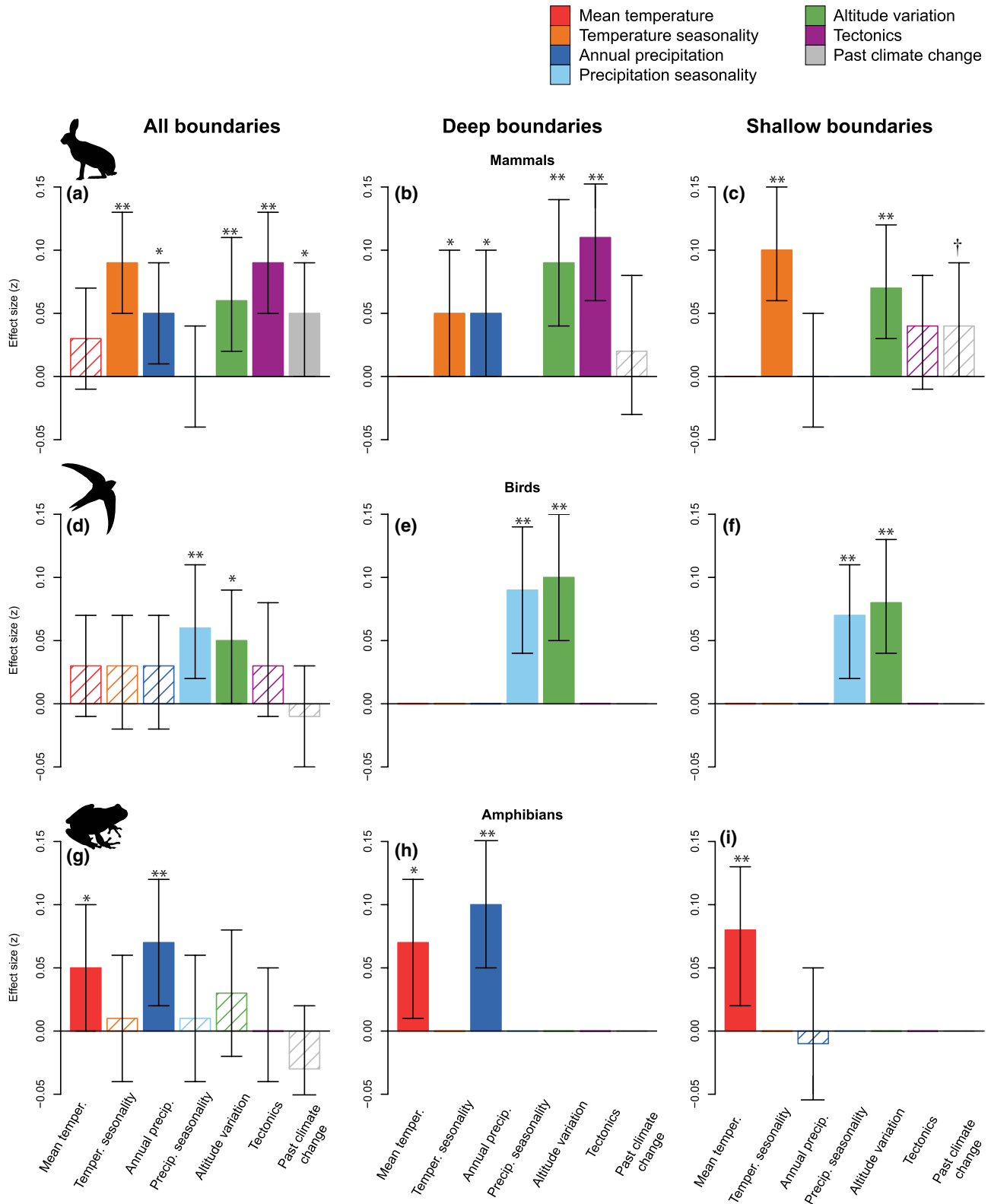
FIGURE 2 Relationships between environmental variables and the position of biogeographical boundaries of mammals (a-c), birds (d-f) and amphibians (g-i). Bars represent the effect sizes (from autoregressive regression models) of each variable in explaining all the boundaries (left panels), the boundaries between deep bioregions only (central panels), and the boundaries between shallow bioregions only (right panels); filled bars indicate significant effects, asterisks represent significance levels ($^{†}p < .1$; $^{*}p < .05$; $^{**}p < .01$). Effect size was assessed using Fisher's z; error bars are 95% confidence intervals of z [Colour figure can be viewed at wileyonlinelibrary.com]

(Dormann et al., 2013). We used two approaches to evaluate the fit of mixed models. First, we calculated the difference in conditional Akaike's information criterion (cAIC) between each SAR model and the respective model including spatial random effects but not environmental variables (ΔcAIC). We then calculated the evidence ratio E of models, compared to the ones with the spatial random effect only: $E = w_i/w_j$, where w_i is the Akaike's weight of the model including both environmental predictors and spatial random effects, and w_j is the weight of the model only including spatial random effects. E can be interpreted as the empirical support of the model including environmental predictors, compared to the model without them; models showing E values > 10 have good support, while models showing E values > 100 have strong support (Burnham & Anderson, 2002; Lukacs et al., 2007). Second, we calculated the amount of variation of the dependent variables that is predicted by the fixed terms in the model, when taking into account the spatial random effect (Zhang, 2017) as a measure of pseudo-r^2.

We used a Z-test to evaluate whether regression coefficients (slopes) are significantly different between taxa (Figure 1; Paternoster et al., 1998). This test was limited to the coefficients of the main analysis (all biogeographical regions). Analyses were performed in the R environment (R Core Team 2019) with the packages car, hglm, maptools, raster, rsq and spdep (Bivand & Lewin-Koh, 2014; Fox & Weisberg, 2011; Hijmans, 2015; Ronnegard et al., 2010; Zhang, 2020); the data and the associated code are provided in figshare (Ficetola et al., 2021).

Classical models only provide one single regression coefficient for each predictor, which represents the overall relationship. Since ecological and biogeographical relationships frequently vary across locations and can show heterogeneity across the geographical space (Mellin et al., 2014), we also used geographically weighted regression (GWR) to evaluate whether relationships between independent variables and boundaries are heterogeneous in space. GWR allows identification of areas where local regression coefficients are different from the global average. Non-stationarity can be present if GWR coefficients vary across space (Bivand et al., 2008). We performed the GWR analysis after SAR, only considering the variables significant in SAR, using standardized environmental variables and binomial error. To identify the appropriate bandwidth, we used a fixed Gaussian kernel. We built models with bandwidths of 1,000–5,000 km at intervals of 200 km, and we selected the one with the lowest corrected AIC. We ran GWR using GWR 4.0.80 (Nakaya et al., 2005); we followed da Silva and Fotheringham (2016) to adjust the local significance of GWR for multiple testing.

3 | RESULTS

For all the taxonomic groups, spatially explicit models of biogeographical boundaries showed a good fit (pseudo-r^2 values ≥ .28 and evidence-ratio > 40 for all the models; Table 1). The support was generally very strong for models considering all biogeographical boundaries and deep boundaries only, and tended to be weaker for

models on shallow boundaries. The support of models was particularly strong for mammals (evidence ratio always > 10,000).

When we analysed the factors related to the biogeographical boundaries of mammals (Supporting Information Figure S1a), we found support for a joint role of multiple processes. Biogeographical boundaries of mammals were associated with areas that underwent strong tectonic movements during the last 65 million years, that represent sharp transitions of seasonality of temperature and precipitation, with orographic barriers, and that underwent rapid climate change during the Quaternary. Tectonic movements were the variable with the strongest effect size, followed by heterogeneity of temperature seasonality and orographic barriers (Figure 2a, Table 1). When we only considered the deep boundaries, the role of tectonic movements was particularly strong, while the role of present-day climatic transitions became weaker, and there was no effect of late Quaternary climate change anymore (Figure 2b, Table 1). Conversely, when we only focused on shallow boundaries, the role of tectonics become weak and non-significant, while the role of present-day climatic transitions showed the highest effect size values (Table 1, Figure 2c).

Biogeographical boundaries of birds (Supporting Information Figure S1b) were mostly related to sharp transitions of precipitation seasonality and to orographic barriers; these factors had a comparable role. The role of these variables remained similar in the analysis of deep and shallow boundaries (Figure 2d-f, Table 1). Finally, biogeographical boundaries of amphibians (Supporting Information Figure S1c) were mostly related to climate, being associated with areas that represent sharp transitions of temperature and precipitation; precipitation was more important than temperature in the analyses considering either all the boundaries or only the deep boundaries, while in the analysis of shallow boundaries temperature was the only significant variable (Figure 2g-i, Table 1, Supporting Information Table S1).

The comparison of model coefficients showed significant differences between the coefficients of mammals and the ones of birds/amphibians (Supporting Information Table S1). Differences were particularly strong for tectonics, where mammals showed higher positive regression coefficients, compared to both birds and amphibians. Mammals also showed the strongest responses to temperature seasonality and, to a lesser extent, past temperature changes. Conversely, birds showed the strongest response to precipitation seasonality. We did not detect significant differences between the regression coefficients of birds and amphibians (Supporting Information Table S1).

For the three vertebrate groups, the relative importance of predictors varied spatially across the globe. For mammals, abrupt transitions in temperature seasonality were particularly important for biogeographical transitions crossing Africa and western Eurasia, while instead annual sums of precipitation were particularly relevant for transitions in Asia and Africa; orographic barriers were extremely important both in the Americas and in Eurasia and tectonic movements were important between Africa and Eurasia, while past climate change was important at the global scale, even though the

TABLE 1 Spatially explicit regression models (binomial simultaneous autoregressive models) measuring the strength of the relationships between the position of biogeographical boundaries and potential covariates

			B	SE	t	df	p
All boundaries							
Mammals	Climate heterogeneity	Mean temperature	.161	.111	1.455	2,256	.146
		Temp. seasonality	.475	.113	4.186	2,256	<.001
		Annual precipitation	.255	.110	2.313	2,256	.021
		Prec. seasonality	.005	.091	0.056	2,256	.955
		Altitude variation	.394	.130	3.036	2,256	.002
		Tectonic movements	.346	.081	4.293	2,256	<.001
		Past climate change	.266	.123	2.164	2,256	.031
ΔcAIC = −102.3	E > 10,000	$r^2_{fixed} = .56$					
Birds	Climate heterogeneity	Mean temperature	.156	.113	1.384	2,139	.166
		Temp. seasonality	.148	.117	1.266	2,139	.206
		Annual precipitation	.129	.109	1.178	2,139	.239
		Prec. seasonality	.292	.097	3.000	2,139	.003
		Altitude variation	.292	.134	2.184	2,139	.029
		Tectonic movements	.129	.080	1.612	2,139	.107
		Past climate change	−.046	.111	−0.414	2,139	.679
ΔcAIC = −46.1	E > 10,000	$r^2_{fixed} = .63$					
Amphibians	Climate heterogeneity	Mean temperature	.299	.152	1.967	1,581	.049
		Temp. seasonality	.069	.143	0.485	1,581	.628
		Annual precipitation	.383	.138	2.773	1,581	.006
		Prec. seasonality	.066	.117	0.564	1,581	.573
		Altitude variation	.202	.175	1.153	1,581	.249
		Tectonic movements	.019	.103	0.185	1,581	.853
		Past climate change	−.172	.147	−1.168	1,581	.243
ΔcAIC = −13.2	E = 742	$r^2_{fixed} = .65$					
Realms							
		Temp. seasonality	.327	.162	2.019	1,468	.044
Mammals		Annual precipitation	.303	.148	2.049	1,468	.041
		Altitude variation	.517	.156	3.325	1,468	.001
		Tectonic movements	.486	.113	4.287	1,468	<.001
		Past climate change	.159	.173	0.922	1,468	.357
ΔcAIC = −61.9	E > 10,000	$r^2_{fixed} = .70$					
Birds		Prec. seasonality	.429	.130	3.302	1,438	.001
		Altitude variation	.529	.143	3.707	1,438	<.001
ΔcAIC = −36.3	E > 10,000	$r^2_{fixed} = .53$					
Amphibians		Mean temperature	.321	.132	2.425	1,289	.015
		Annual precipitation	.537	.149	3.607	1,289	<.001
ΔcAIC = −16.3	E = 3,448	$r^2_{fixed} = .60$					
Shallow	**boundaries**						
		Temp. seasonality	.605	.135	4.468	1,904	<.001
Mammals		Annual precipitation	.014	.133	0.102	1,904	.919
		Altitude variation	.441	.137	3.215	1,904	.001
		Tectonic movements	.170	.101	1.685	1,904	.092
		Past climate change	.245	.138	1.783	1,904	.075

(Continues)

TABLE 1 (Continued)

			B	SE	t	df	p
ΔcAIC = −47.7	E > 10,000	r^2_{fixed} = .49					
Birds		Prec. seasonality	.339	.117	2.901	1,932	**.004**
		Altitude variation	.426	.118	3.618	1,932	**< .001**
ΔcAIC = −7.0	E = 43	r^2_{fixed} = .28					
Amphibians		Mean temperature	.747	.274	2.722	458	**.007**
		Annual precipitation	−.056	.276	−0.204	458	.838
ΔcAIC = −7.7	E = 47	r^2_{fixed} = .59					

Note: B = regression coefficients; SE = standard error of B; ΔcAIC = difference in conditional Akaike's information criterion between each model and the respective model including spatial random effects but not environmental variables; E = evidence ratio of the model; r^2_{fixed} = amount of variation explained by the fixed terms in the model.

effect size was generally weak (Figure 3). For birds, precipitation seasonality was particularly important for transitions crossing Africa and western Eurasia, while orographic barriers had a major role both in Eurasia and in the Americas (Figure 4). For amphibians, heterogeneity of both temperature and precipitation were particularly relevant for transitions crossing Eurasia, Africa, and South America (Figure 5).

4 | DISCUSSION

A wide range of processes affects global biogeographical patterns. Notably, species ranges are determined by the interplay between ecological, historical and geographical factors (Lomolino et al., 2010). Some biogeographical boundaries (e.g., between the Sino-Japanese and the Oriental bioregions) are evident across all vertebrate groups. Nevertheless, strong variations exist between vertebrates (Supporting Information Figure S1). Our analysis suggests that these differences can be partly explained by their contrasting responses to environmental and geographical factors, as expected on the basis of their general ecology. In summary, the biogeographical boundaries of mammals align more closely with geographical features (mountains and tectonic sutures) than those of amphibians, which correspond more closely to sharp temperature and precipitation transitions. Bird boundaries are related to both geographical and climatic factors.

Tectonics had a particularly strong role for mammals, as expected on the basis of their limited ability for overseas dispersal (at least compared to birds), and in agreement with the observation that the β-diversity (turnover in species assemblage composition) of mammals is heavily determined by present-day geographical distance and past tectonics (Lomolino et al., 2010; Mazel et al., 2017). However, we detected a significant impact of multiple processes for mammals, including present-day climate and climate change during the Quaternary (Figure 2a). Climatic variation after the end of glaciations caused major changes in the distribution of mammals, determining range shifts and extinctions (Nogués-Bravo et al., 2010; Taberlet et al., 1998). Still, such past climatic changes are known to have affected all taxa, including birds and amphibians (Hewitt, 2000; Sandel et al., 2011; Taberlet et al., 1998). It is thus unclear why relationships

between biogeographical boundaries and environmental features are particularly strong for mammals, as shown by the largest effect sizes (Figure 2). We based our analyses on the bioregions defined by Holt et al. (2013), who identified 19 regions for birds and amphibians, and 34 regions for mammals. It is possible that the larger number of bioregions and of boundaries between them improved the likelihood of identifying the factors driving bioregionalization. Additional factors that could explain the more clear-cut results for mammals include a better knowledge of species ranges compared to amphibians (compare Ficetola et al., 2014; Rondinini et al., 2011), which might allow a more accurate definition of bioregions. Furthermore, the dispersal limitations of mammals in comparison to birds might make more evident the effects of past processes and barriers.

For birds, biogeographical boundaries were associated with orographic barriers, and with areas where climatic seasonality strongly increases. Recent analyses suggested that temperature (freezing line) was a major determinant of biogeographical transitions of birds (White et al., 2019). Even though the role of temperature was not particularly evident here, our conclusions and the ones by White et al. (2019) are not mutually exclusive. White et al. (2019) mostly focused on the Himalayas, which represents one of the strongest environmental gradients in the world, and where major orographic barriers coexist with steep environmental gradients of temperature and precipitation (Pan et al., 2016; Rana et al., 2019; Sharma et al., 2019; White et al., 2019). We analysed boundaries at a coarse resolution (200 km), as is appropriate for global analyses, and at this grain distinguishing between the role of temperature and altitude can be tricky. Furthermore, unlike White et al. (2019) we considered the temperature gradient rather than the temperature mean. Only fine-scale analyses can identify the processes that are at work locally. Indeed, global and local scale analyses are complementary, and the integration of their conclusions is necessary for a better understanding of eco-geographical processes (Brown, 1995; Ficetola, Lunghi, et al., 2018; White et al., 2019). Finally, the importance of precipitation seasonality might be linked to migratory behaviours and variation in resources. For birds, biogeographical boundaries were based on breeding ranges. High climate seasonality requires animals either to be adaptive enough to stay even during the unfavourable seasons, or to move and then to develop migration capabilities. In
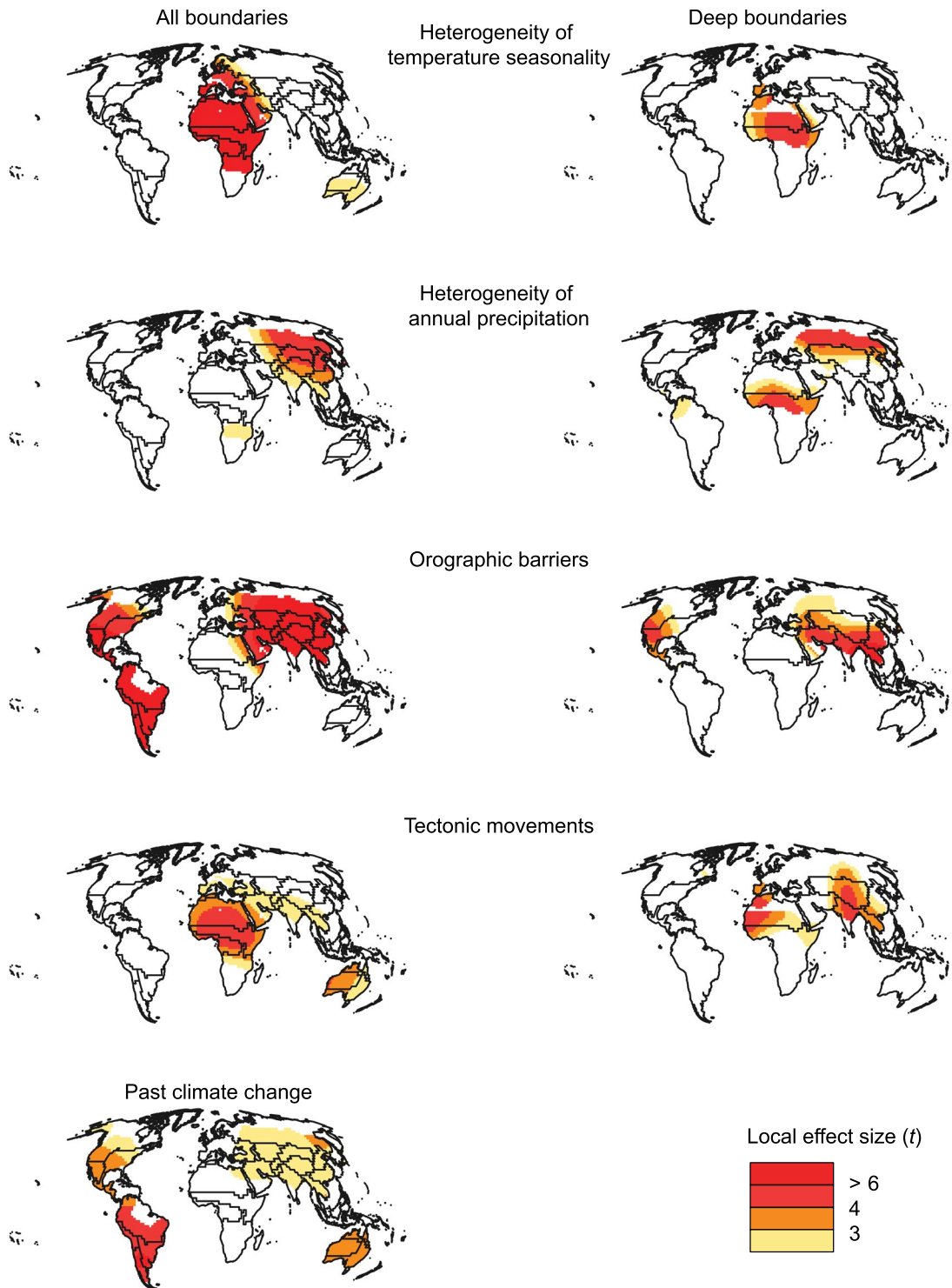
Mammals

FIGURE 3 Geographical variation of the relationships between present/past climate, tectonics, altitude, and the position of biogeographical boundaries of mammals. Maps show heterogeneity of local effect sizes obtained through geographically weighted regression. Left panels: analysis on all the boundaries; right panels: analysis of the deep boundaries. We only map local effect sizes significantly larger than zero. Effect sizes > 3 are also significant after multiple tests corrections (da Silva & Fotheringham, 2016) [Colour figure can be viewed at wileyonlinelibrary.com]

fact, temporal variation of available resources predicts well the variation of distribution and abundance of several birds, including

many species living in Eurasia and Africa (Beresford et al., 2019; Newton, 2008; compare with Figure 4).

Birds

All boundaries

Heterogeneity of precipitation seasonality

Deep boundaries

Orographic barriers

Local effect size (*t*)

> 6
4
3.3
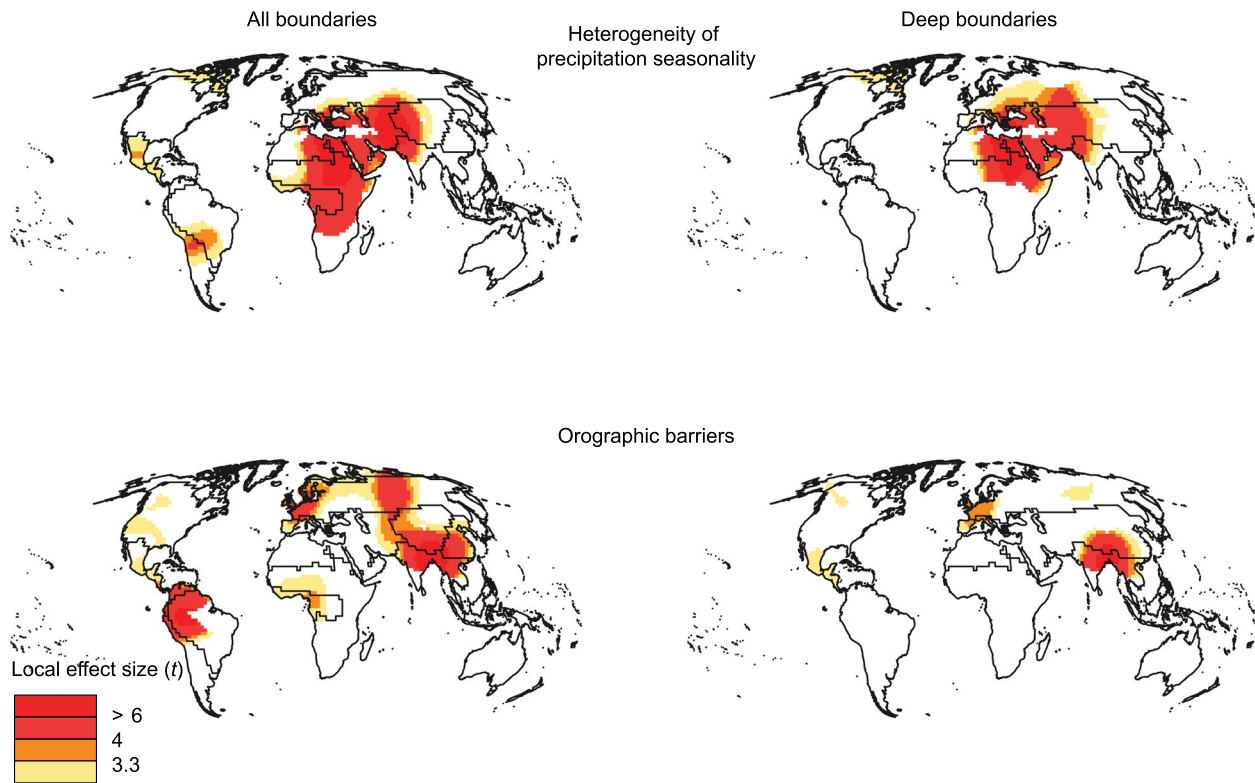
FIGURE 4 Geographical variation of the relationships between climate, altitude, and position of biogeographical boundaries of birds. Maps show heterogeneity of local effect sizes obtained through geographically weighted regression. Left panels: analysis on all the boundaries; right panels: analysis of the deep boundaries. We only map local effect sizes significantly larger than zero. Effect sizes > 3.3 are also significant after multiple tests corrections (da Silva & Fotheringham, 2016) [Colour figure can be viewed at wileyonlinelibrary.com]

For amphibians, climate was the key factor, as expected on the basis of their metabolism and physiology. Moreover, amphibians are ectotherms, heavily relying on ambient energy for their metabolism, and even closely related species can show a different response to temperature (Buckley et al., 2012; Ficetola, Lunghi, et al., 2018; Quintero & Wiens, 2013). Thus, for many amphibians, cold tolerance is a major determinant of range limits (Wiens et al., 2006). Nevertheless, the role of precipitation was stronger than the one of temperature. This is not surprising given that water availability is extremely important for amphibian activity and reproduction, and multiple studies have identified precipitation as a major climatic driver of their ecological patterns. For instance, precipitation changes affected population trends of amphibians more strongly than temperature changes (Ficetola & Maiorano, 2016). Furthermore, despite both temperature and precipitation determining the range limits of amphibians, precipitation-related variables are often the most important variables (Cunningham et al., 2016).

The nested structure of the biogeographical regions and the joint analysis of deep and shallow boundaries can help disentangle the processes that act at different temporal scales (Daru et al., 2017). It must be remarked that deep branches in biogeographical dendrograms represent high turnover, and not directly time; still the strongest phylogenetic dissimilarities are generally observed between

areas that experienced very long periods of independent evolution. Therefore, comparing the drivers of deep and shallow boundaries might help to distinguish between recent processes (e.g., present-day climate), and processes that acted over geological periods (Ficetola et al., 2017; Mazel et al., 2017). Our analysis confirmed this idea. For mammals and birds, the importance of climatic drivers decreased when we focused just on deep boundaries while, at least for mammals, the importance of tectonics increased (Figure 2). These differences were also evident for climate change during the Quaternary. Quaternary climate change showed a generally limited role, and was only important for shallow boundaries of mammals. Quaternary climatic change is a relatively recent process, compared to the complexity of factors that have determined mammal distribution during the last 65 Myr, and this explains its weak relationship with the deep boundaries. Furthermore, relationships between boundaries and environmental variables showed strong heterogeneity across the globe (Figures 3–5). For instance, in mammals, temperature seasonality was particularly important in Africa, where boundaries match areas of transitions from extremely stable to more seasonal climate (compare Supporting Information Figure S1a; Figure 3). Conversely, in other areas of the world mountain chains have the strongest role. This highlights that, despite the fact that all these processes can jointly influence biogeographical structure, the
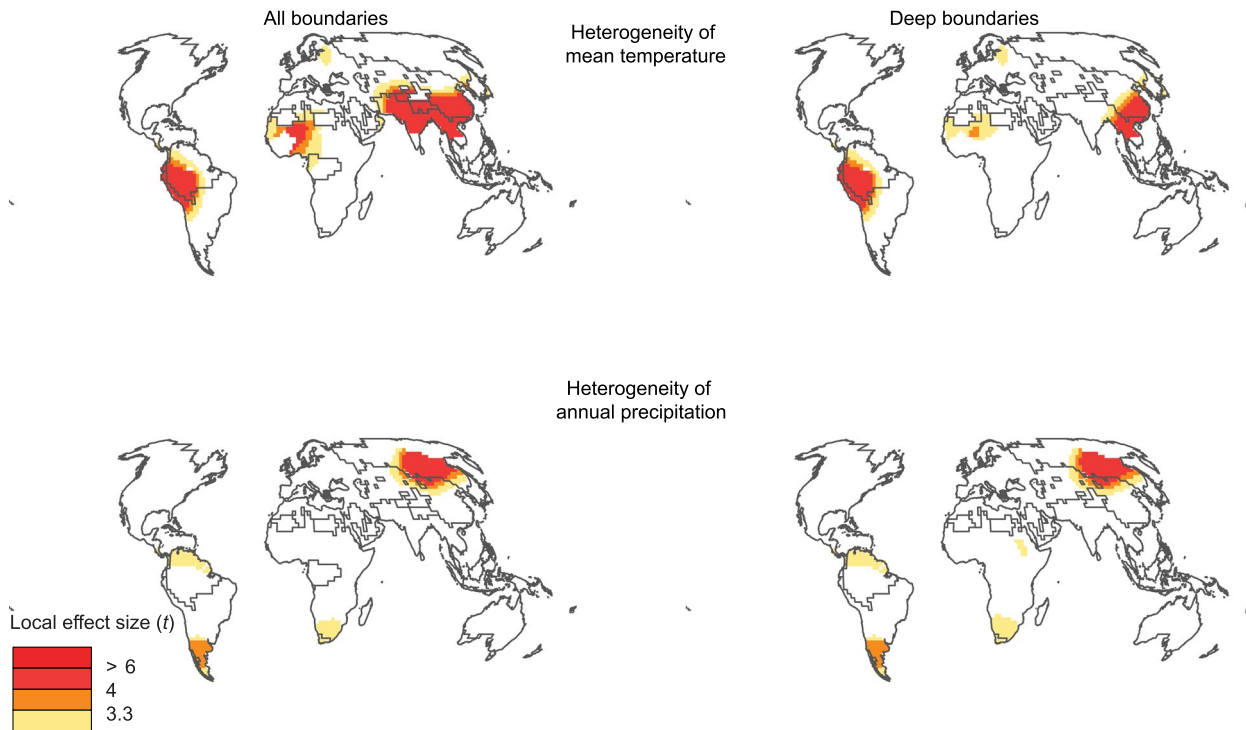
Amphibians

FIGURE 5 Geographical variation of the relationships between climate and the position of biogeographical boundaries of amphibians. Maps show heterogeneity of local effect sizes obtained through geographically weighted regression. Left panels: analysis on all the boundaries; right panels: analysis of the deep boundaries. We only map local effect sizes significantly larger than zero. Effect sizes > 3.3 are also significant after multiple tests corrections (da Silva & Fotheringham, 2016) [Colour figure can be viewed at wileyonlinelibrary.com]

importance of drivers shows strong spatial variation. Geographically weighted regression is a powerful tool to identify the areas where each factor is important (Figures 3–5), and its results can be used to generate hypotheses that can be tested in regional studies.

Our analyses focused on three main groups of vertebrates, assuming a coherent biogeographical response within each of them. However, this simplifies the complexity of biogeographical responses within each group (Mazel et al., 2017). For instance, different clades of mammals have varying dispersal abilities that could lead to different bioregionalizations (Kreft & Jetz, 2010). Thus, we expect different importance of biogeographical factors had we analysed separately volant and non-volant mammals. For instance, orographic or past geographical barriers might be less important for bats than for the other mammals, even though available data suggested limited differences between the bioregionalization of volant and non-volant mammals (Kreft & Jetz, 2010). Analyses performed with a finer taxonomic extent (e.g., comparing orders) could allow explicit tests of how differences in life-history traits can determine the response to major biogeographical forces. We acknowledge that available global-scale phyloregions are based on relatively old phylogenetic data (Fritz et al., 2009; Fritz & Rahbek, 2012; Pyron & Wiens, 2011), with many polytomies and incomplete branch length estimates (Holt et al., 2013), and this could create uncertainties. Nevertheless, the consistency between these phyloregions and regional analyses using more recent phylogenetic data

suggests robustness of patterns, at least at our coarse study scale (He et al., 2020).

Different responses to eco-geographical factors between vertebrates likely determined their present-day biogeographical patterns, and these effects can be evident at both local (White et al., 2019) and global scales. Until now, broad-scale (phylo) regionalizations have been limited to the best studied groups of vertebrates or plants. However, knowledge of species ranges is improving at an impressive rate (e.g., Phillips et al., 2019; Roll et al., 2017; van den Hoogen et al., 2019), paving the way for a detailed knowledge of biogeographical patterns for an unprecedented number of clades (Daru et al., 2018; Ficetola, Falaschi, et al., 2018; Iversen et al., 2019; Roll et al., 2017). The increased availability of accurate geographical ranges can allow the identification of the drivers of biogeographical processes across the whole tree of life (Daru et al., 2017). Moreover, human activities and climate change currently cause rapid shifts of ranges through extinctions and colonization (Bernardo-Madrid et al., 2019). The analysis of bioregionalization can thus allow better understanding of relationships between ongoing environmental changes and biodiversity shifts.

ACKNOWLEDGMENTS

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BIOSKETCH

G. Francesco Ficetola is a researcher combining multiple approaches (field activities, landscape ecology, macroecology, evolutionary ecology and environmental DNA) to improve knowledge on biodiversity. His research focuses on the determinants of biodiversity patterns, and on the long-term effects of human activities at multiple scales, from micro-habitat to global.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.