

Global bioregions of reptiles confirm the consistency of bioregionalization processes across vertebrate clades

Mattia Falaschi¹  | Silvio Marta¹  | Elia Lo Parrino¹  | Uri Roll²  | Shai Meiri³  |
Gentile Francesco Ficetola^{1,4} 

¹Department of Environmental Science and Policy, Università degli Studi di Milano, Milan, Italy

²Mitrani Department of Desert Ecology, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University, Beersheba, Israel

³School of Zoology, & The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel

⁴Laboratoire d'Écologie Alpine, University Grenoble Alpes, University Savoie Mont Blanc, CNRS, LECA, Grenoble, France

Correspondence

Mattia Falaschi, Department of Environmental Science and Policy, Università degli Studi di Milano, Via Celoria 10, 20133 Milan, Italy.
Email: matt_fala@hotmail.it

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Abstract

Aim: The identification of biogeographical zones has been fundamental in broadscale biodiversity analyses over the last 150 years. If processes underlying bioregionalization, such as climatic differences, tectonics and physical barriers, are consistent across vertebrate clades, we expect that groups with more similar ecological characteristics would show more similar bioregions. Lack of data has so far hampered the delineation of global bioregions for reptiles. Therefore, we integrated comprehensive geographic distribution and phylogenetic data of lepidosaurian reptiles to delineate global reptile bioregions, compare determinants of biogeographical boundaries across terrestrial vertebrates and test whether clades showing similar responses to environmental factors also show more similar bioregions.

Location: Global.

Time Period: Present.

Major Taxa Studied: Reptiles, amphibians, birds, mammals.

Methods: For reptiles, we used phylogenetic beta diversity to quantify changes in community composition, and hierarchical clustering to identify biogeographic 'realms' and 'regions'. Then, we assessed the determinants of biogeographical boundaries using spatially explicit regression models, testing the effect of climatic factors, physical barriers and tectonics. Bioregions of reptiles were compared to those of other vertebrate clades by testing the overall similarity of the spatial structure of bioregions, and the match of the position of biogeographical boundaries.

Results: For reptiles, we identified 24 evolutionarily unique regions, nested within 14 realms. Biogeographical boundaries of reptiles were related to both climatic factors and past tectonic movements. Bioregions were very consistent across vertebrate clades. Bioregions of reptiles and mammals showed the highest similarity, followed by reptiles/birds and mammals/birds while amphibian bioregions were less similar to those of the other clades.

Main Conclusions: The overall high similarity among bioregions suggests that bioregionalization was affected by similar underlying processes across terrestrial vertebrates. Nevertheless, clades with different eco-physiological characteristics respond

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somewhat differently to the same environmental factors, resulting in similar but not identical regionalizations across vertebrate clades.

KEYWORDS

biogeographical boundaries, macroecology, phylogenetic beta diversity, squamates, tetrapod biogeography, vertebrates

1 | INTRODUCTION

We are approaching the 150th anniversary of 'The geographical distribution of animals' by Wallace (1876), which posed the bases for our understanding of the variation of life across geographical regions and may be seen as the foundation of modern biogeography. Wallace identified six main realms (Wallace, 1876) that delineate the major areas of the globe where animal assemblages are similar to each other but separated from adjacent regions by biogeographical boundaries (i.e. areas of transition between nearby bioregions) (Lomolino et al., 2010; Smith et al., 2018). Since then, knowing how different biota are related to each other and form bioregions has become fundamental for many ecological studies (Capinha et al., 2015; Sommeria-Klein et al., 2021). This knowledge helped to unravel evolutionary patterns and their drivers (Ficetola et al., 2021; He et al., 2020; Mazel et al., 2017) and even provided a basis for broadscale conservation planning (Dinerstein et al., 2017; Ennen et al., 2020; Whittaker et al., 2005).

Research on bioregions has remained a vital field of biogeography, and several bioregionalizations of the planet have been proposed during the last decades (e.g. Carta et al., 2022; Holt et al., 2013; Kreft & Jetz, 2010; Morrone, 2015; Procheş & Ramdhani, 2012; Rueda et al., 2013; Shen et al., 2021). Most historical regionalizations were based only on the geographic distribution of species. Nevertheless, it is also important to account for evolutionary processes that shaped these patterns over time (Daru et al., 2017). This enables delineating evolutionary distinct bioregions that would be overlooked by species-based approaches, but require the integration of species' geographic distribution and phylogenetic information with appropriate methods (Daru et al., 2017). Thanks to the increasing availability of both distributional and phylogenetic data, Holt et al. (2013) proposed the first global bioregionalization of amphibians, birds and mammals, using quantitative phylogenetic regionalization techniques.

Reptiles are the most species-rich group of terrestrial vertebrates, but data availability on reptiles lagged behind that of other terrestrial vertebrates, and global distribution ranges for most of the species have become available only recently (Roll et al., 2017). This lack of data hampered the delineation of global bioregions of reptiles, and most previous works were limited to regional- or continental-scale assessments, or focussed on specific clades (Ennen et al., 2020; Ficetola et al., 2018; Šmid et al., 2021; but see Procheş & Ramdhani, 2012). Reptiles were not included in the Holt et al. (2013) regionalization, but recent advances in the availability of distributional (Roll et al., 2017) and phylogenetic (Pyron et al., 2013;

Zheng & Wiens, 2016) data now allow biogeographic analyses at the global scale.

The compositional turnover of biotas is determined by the interplay between multiple processes: geological and geographic history, which represents past dispersal limitations; present geographical barriers; and climatic variation (Ficetola et al., 2017; White et al., 2019). In general, some key processes, such as the occurrence of major climatic or physical barriers that hamper dispersal and the homogenization of communities over large scales, probably affect the distribution of all vertebrates. However, different taxonomic groups show partially distinct responses to these factors (Ficetola et al., 2021). For instance, amphibians are strongly influenced by abrupt climatic transitions (especially precipitation-related), while mammals and birds show a strong response to both climatic and physical barriers (Ficetola et al., 2021). We hypothesize that the same environmental factors (i.e. climatic and physical barriers) acting on different vertebrate clades can result in slightly different bioregions, depending on the ecological features of each group. Hence, we expect that clades for which biogeographical boundaries are determined by similar factors will show a more similar structure of bioregions.

Rueda et al. (2013) highlighted the similarities between the recently delineated bioregions and the work of Wallace. To our knowledge, however, there are no quantitative tests of the similarity of bioregions across major vertebrate clades that also take into account phylogenetic information. For this reason, here, we integrated distributional and phylogenetic data of lepidosaurian reptiles (squamates plus Rhynchocephalia, i.e. *Sphenodon punctatus*, hereafter: reptiles), which constitute a monophyletic group including >96% of living reptiles (Uetz et al., 2022), with the aim to (Figure 1): (i) delineate global bioregions for reptiles; (ii) assess the determinants of biogeographical boundaries for reptiles and compare them to the ones of the other clades of terrestrial vertebrates. We assessed the effects of both climatic barriers (areas representing strong spatial heterogeneity of climate) and physical barriers (orographic barriers, major tectonic movements) following the framework of Ficetola et al. (2017, 2021); (iii) quantitatively test whether bioregions are consistent across terrestrial vertebrate clades, by comparing the bioregions of reptiles to the regionalizations of Holt et al. (2013) for amphibians, birds and mammals. This test enables assessing whether clades for which the geographic distribution is affected by similar processes would show more similar bioregions.

Specifically, we expect that: (1) Biogeographical boundaries of reptiles respond strongly to climatic factors, particularly temperature, because they are ectotherms with often narrow thermal niches

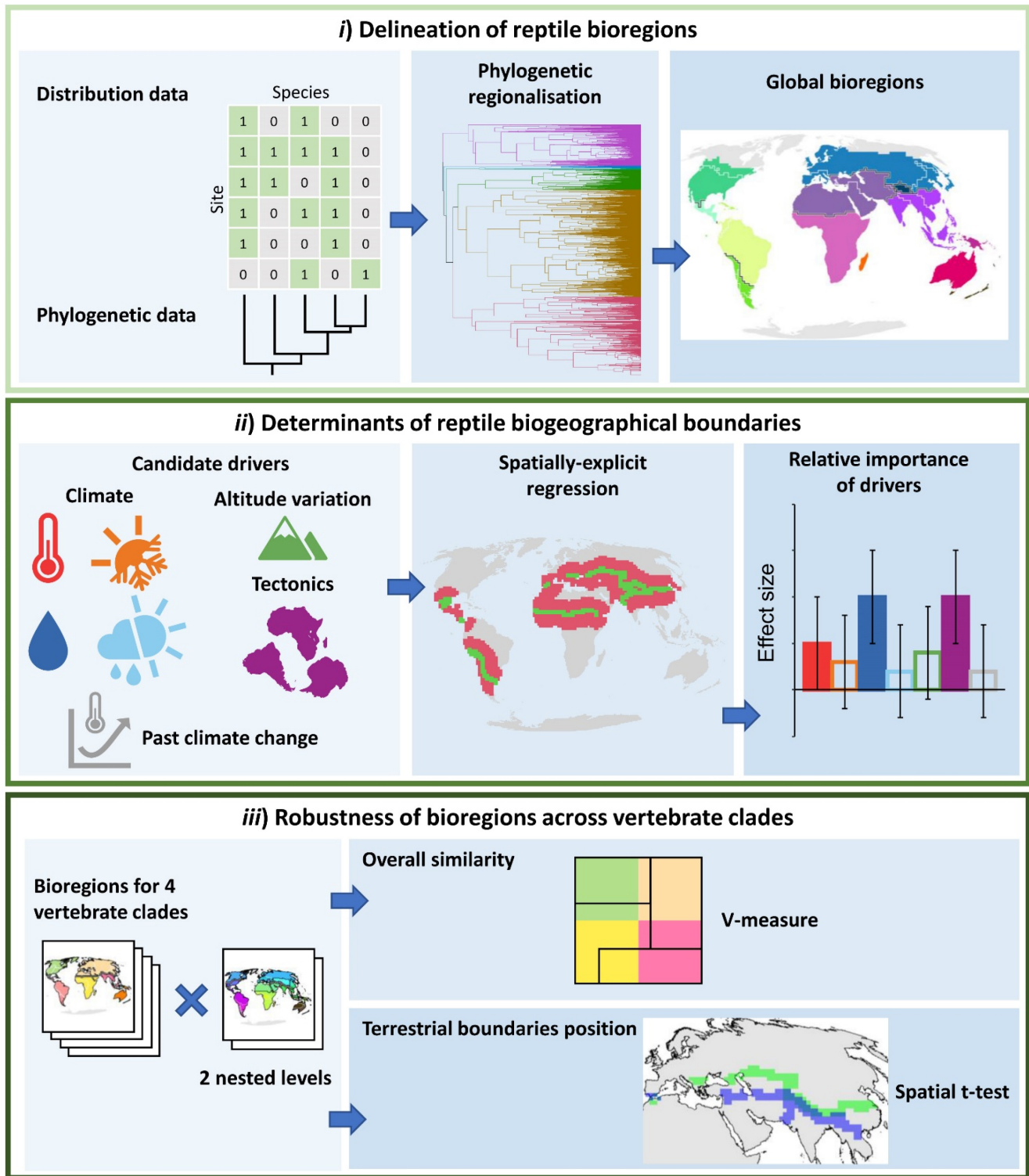


FIGURE 1 General outline of the study. (i) Global reptile bioregions were delineated by integrating distribution and phylogenetic data and using phylogenetic beta diversity ($p\beta_{sim}$) as a measure to quantify changes in community composition across different areas of the globe while taking into account phylogenetic relationships among species. We used hierarchical clustering to aggregate communities based on $p\beta_{sim}$ values and used two different thresholds to define biogeographic 'realms' and 'regions'. (ii) We assessed the determinants of biogeographical boundaries (i.e. boundaries between bioregions that are not separated by the sea at the 200-km resolution) of reptiles using spatially explicit regression models (Ficetola et al., 2017, 2021). (iii) Bioregions of reptiles were compared to Holt et al. (2013) regionalizations at the two nested levels of realms and regions, calculating the general similarity of the spatial structure of bioregions and the correlation between the occurrence of terrestrial boundaries across different clades.

(Sinervo et al., 2010). We further predict that reptiles are strongly affected by physical barriers due to their small size, low metabolic rates and lack of wings, all of which make them generally poor dispersers (Esquerré et al., 2019); (2) Amphibians respond to different factors compared with mammals and birds (see Ficetola et al., 2021). Climatic factors play a much stronger role than physical barriers in shaping amphibian biogeography compared with mammals and birds. Therefore, we expect a moderate similarity between amphibian bioregions and those of mammals, birds, and reptiles. At the same time, we expect good concordance between bioregions of mammals and birds because they are endotherms showing similar responses to climatic gradients and physical barriers (Ficetola et al., 2021; Melo et al., 2009); (3) If reptile boundaries are mainly related to climatic factors, we expect reptile bioregions to be more similar to bioregions of the other ectotherms (amphibians), while if also physical barriers have a strong influence on reptile boundaries, we expect reptile bioregions to resemble more closely bioregions of mammals and birds.

2 | MATERIALS AND METHODS

2.1 | Geographic distribution data

We focussed on Lepidosauria (i.e. lizards, snakes, amphisbaenians and the tuatara, *Sphenodon punctatus*) that represent the most species-rich clade of extant reptiles. Lepidosauria includes 11,350 of the 11,733 described species of reptiles [i.e. Lepidosauria + crocodiles and turtles (Uetz et al., 2022)]. We did not include crocodiles and turtles in our analyses because merging them with Lepidosauria would lead to a paraphyletic group. We used the distribution ranges of 10,214 reptiles from an updated version (version 1.5) of the Global Assessment of Reptile Distributions (Roll et al., 2017). Each map was rasterized at a resolution of 200 × 200 km in an equal-area projection (World Mollweide, ESRI:54009) to avoid changes in cell area at different latitudes. The 200-km resolution was selected because it is appropriate to study global-scale biodiversity patterns (Hurlbert & Jetz, 2007) and also to align with the work of Holt et al. (2013). A species was considered present in all cells intersecting its range polygon/s (i.e. containing any portion of the distribution range).

2.2 | Biogeographical regionalization

To delineate bioregions of lepidosaurian reptiles, while maximizing the comparability of our results with the ones of previous studies, we identified bioregions following an already developed framework (Holt et al., 2013; Kreft & Jetz, 2010). First, we calculated a matrix of phylogenetic beta diversity ($p\beta_{sim}$) between each cell and all other cells through a modified version of the 'phylo.beta.pair' function from the betapart R package (Baselga et al., 2021) (the function and script used to run this analysis are available at figshare; Falaschi et al., 2023). Phylogenetic data were retrieved from an inference-based

phylogenetic tree including 9755 lepidosaurian species (Tonini et al., 2016). This tree was reconstructed with direct genetic data from 5415 species, and the position of unsampled species was estimated through Bayesian inference (Thomas et al., 2013). To allow the calculation of $p\beta_{sim}$ between cells, we resolved polytomies present in the phylogenetic tree as multiple dichotomies with a branch length of 0, using the 'multi2di' function from the R package ape (Paradis & Schliep, 2019). Cells with less than two species were excluded from analyses. Furthermore, to avoid artefacts due to the inclusion of species-poor cells on the borders of continents, cells for which the cover of emerged lands was less than 10% (i.e. >90% water) were excluded. The final data set included 9016 species (88% of the 10,214 species for which distribution ranges were available) across 3334 cells.

We tested different hierarchical clustering approaches to identify geographic clusters from the dissimilarity matrix (Kreft & Jetz, 2010). We compared the performance of five agglomerative hierarchical clustering methods: complete linkage, single linkage, unweighted pair-group arithmetic average, Ward's method, weighted average and divisive analysis clustering. To choose the best clustering method, we calculated the cophenetic correlation coefficient between each dendrogram obtained with the six clustering approaches and the dissimilarity matrix (Kreft & Jetz, 2010). Unweighted pair-group arithmetic average method showed the highest correlation (Supporting information Table S1); consequently, this method was selected as the best performing method to delineate bioregions (Holt et al., 2013; Kreft & Jetz, 2010).

The number of bioregions can potentially vary from one up to the number of cells considered in the regionalization and the criteria applied to set the threshold can vary according to the aim of the study (Kreft & Jetz, 2010). With the aim of comparing reptile bioregions to the previous bioregions of other vertebrate clades identified by Holt et al. (2013; Supporting Information Figure S1), we selected two different thresholds to define bioregions, corresponding to the minimum number of regions that explained 95% of between-cluster $p\beta_{sim}$ (sum of between-cluster $p\beta_{sim}$ /total $p\beta_{sim}$) and 90% of between-cluster $p\beta_{sim}$ (Holt et al., 2013). Bioregions explaining 95% of phylogenetic dissimilarity correspond to the 'regions' defined by Holt et al. (2013), while bioregions explaining 90% of dissimilarity correspond to the 'realms' by Holt. Following Holt et al. (2013), hereafter we defined these two levels as 'regions' and 'realms', generally referring to them as 'bioregions'.

All clusters formed by less than 10 cells were aggregated to the closest cluster in the phylogenetic regionalization. For the graphical representation, colours were selected by applying nonparametric multidimensional scaling (NMDS) to the realm-by-realm dissimilarity matrix. Starting from the cell-by-cell dissimilarity matrix, we calculated a realm-by-realm dissimilarity matrix averaging $p\beta_{sim}$ values within each realm. Then, we performed a three-dimension NMDS on the realm-by-realm dissimilarity matrix through the 'metaMDS' function from the R package vegan (Oksanen et al., 2020). The three values obtained for each realm were rescaled to vary between 0 and 255 and used as red, green and blue values to extract colours from the RGB colour space.

To test the robustness of our results to uncertainty in phylogenetic reconstruction (Tonini et al., 2016), all analyses were repeated using a different phylogenetic tree (Zheng & Wiens, 2016), which is based solely on genetic data, but includes fewer species (4162 species) compared with the other phylogenetic tree. This alternative regionalization returned very consistent results with those conducted using the Tonini et al., (2016) phylogeny (Supporting information Figure S2).

2.3 | Assessing determinants of reptile biogeographical boundaries

We used a previously developed framework to identify the factors related to the occurrence of biogeographical boundaries of reptiles (Ficetola et al., 2017, 2021). First, the boundaries of a bioregionalization were defined as the terrestrial cells for which at least one adjacent cell belongs to a different bioregion (Ficetola et al., 2017, 2021). We considered seven environmental variables that represent processes that can determine the occurrence of biogeographical boundaries (Ficetola et al., 2021); to compare drivers of reptile biogeographical boundaries to the ones of the other vertebrate clades, we considered variables used in previous studies (Ficetola et al., 2017, 2021). Four variables represented spatial heterogeneity of climate: heterogeneity of (1) mean annual temperature, (2) temperature seasonality, (3) annual precipitation and (4) precipitation seasonality. Three additional variables represented: (5) altitude variation (i.e. orographic barriers), (6) tectonic movements and (7) Quaternary climate change. Climatic variables were retrieved from WorldClim (Hijmans et al., 2005) [version 1.4, to be comparable with previous analyses (Ficetola et al., 2017, 2021); still, the correlation between WorldClim 1.4 and the most recent WorldClim 2.1 was nearly perfect (Pearson's $r \geq 0.99$ for all the considered variables)]. Heterogeneity of climatic variables was calculated as the coefficient of variation between each cell and the eight neighbouring cells. Altitude variation was expressed as the mean absolute difference between each 200 × 200 km cell and the eight neighbouring cells [terrain ruggedness index from the 'raster' R package (Hijmans, 2022)]. Tectonic movements were calculated as the variability in distance between each cell and its current neighbours over the last 65 million years, using the GPLATE software (Williams et al., 2012). Quaternary climate change was expressed as the average velocity of climate change for each cell during the late Quaternary (since 21,000 years ago) (Sandel et al., 2011). Additional details and examples are provided in previous studies (Ficetola et al., 2017, 2021).

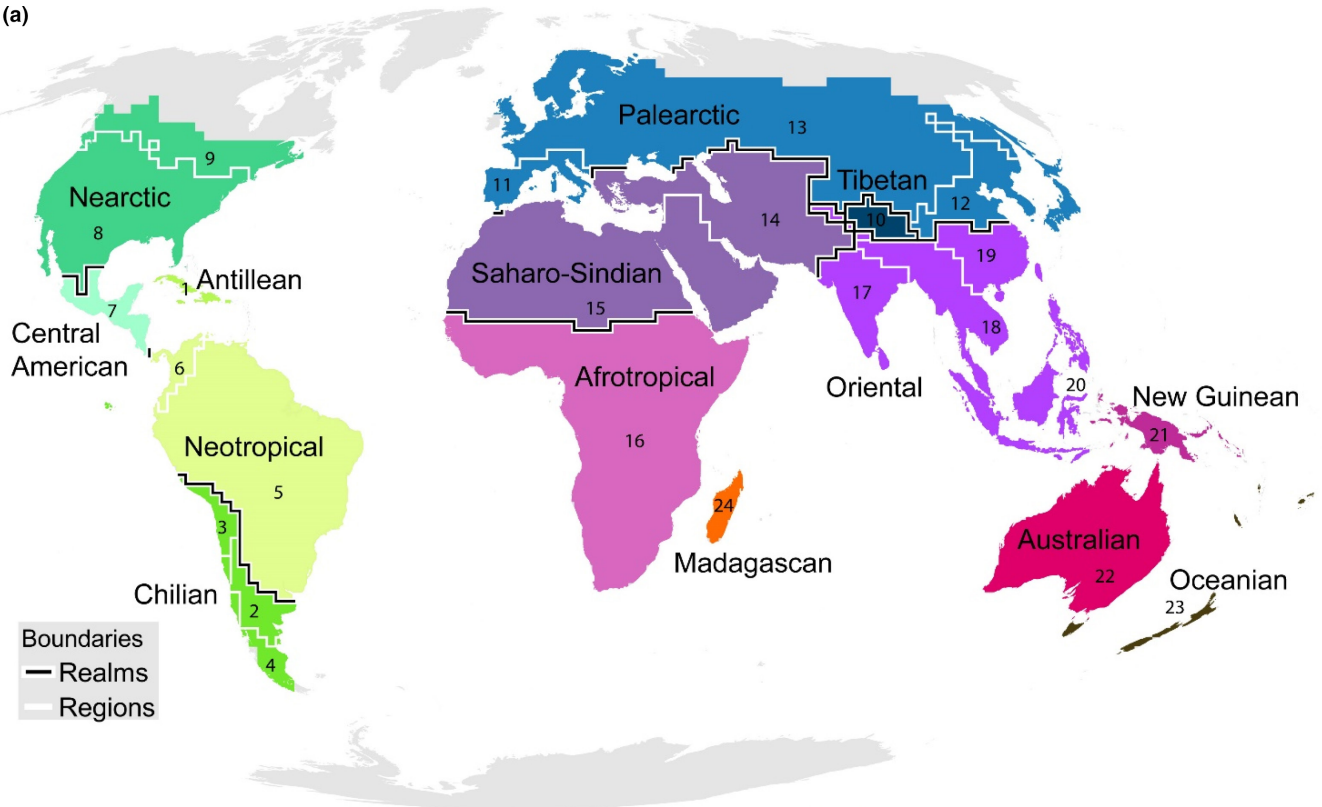
Spatial autocorrelation of environmental data can strongly bias inference based on the analysis of distribution patterns, potentially determining spatially similar patterns and causing misleading inferences about the importance of underlying drivers (Beale et al., 2010; McIntire & Fajardo, 2009; Warren et al., 2014). To limit these issues, we tested our a priori hypotheses using statistical tools that enable incorporating the spatial structure into models (McIntire & Fajardo, 2009; Warren et al., 2014). We used simultaneous autoregressive spatial (SAR) models with binomial error distribution to assess relationships between the position of biogeographical boundaries and the candidate drivers while taking into account spatial autocorrelation. For this analysis, the dependent variable was whether a given grid cell was in contact with a biogeographical boundary (Y/N). To avoid an excessive number of zeros, cells >1000 km from any boundary were excluded from analyses. Initially, we assessed the drivers of the overall presence of boundaries (all boundaries up to the 95% $p\beta_{sim}$ threshold), using all seven candidate drivers as independent variables. All independent variables were scaled (mean = 0 and standard deviation = 1) to allow the comparison of effect sizes. Then, we ran an additional analysis selecting as dependent variables only the boundaries of realms. To limit type II error, we only considered potential predictor variables that showed a significant effect in the global model. In both analyses, spatial autocorrelation was incorporated in the error term using neighbourhood matrices, with a neighbourhood distance of 566 km (which is the minimum distance that kept all cells connected to at least one other cell). Simultaneous autoregressive spatial models were built using hierarchical generalized linear mixed models (HGLMs; Alam et al., 2015) with spatially autocorrelated random effects. Analyses were performed in the R environment using the packages raster (Hijmans, 2022), spdep (Bivand & Wong, 2018), spatialreg (Bivand et al., 2021) and hglm (Ronnegard et al., 2010). For each variable, the effect estimates obtained in HGLMs were transformed to Fisher's z. Fisher's z is a measure of effect size that is independent of sampling size, and thus enables robust comparisons of effects estimated in different models. Values of Fisher's z were calculated from the t-values of HGLMs (see Rosenthal, 1994 and Hartung et al., 2008 for detailed procedures) using the 'tes' function from the compute.es R package (del Re, 2013).

2.4 | Comparison of regionalizations across vertebrate clades

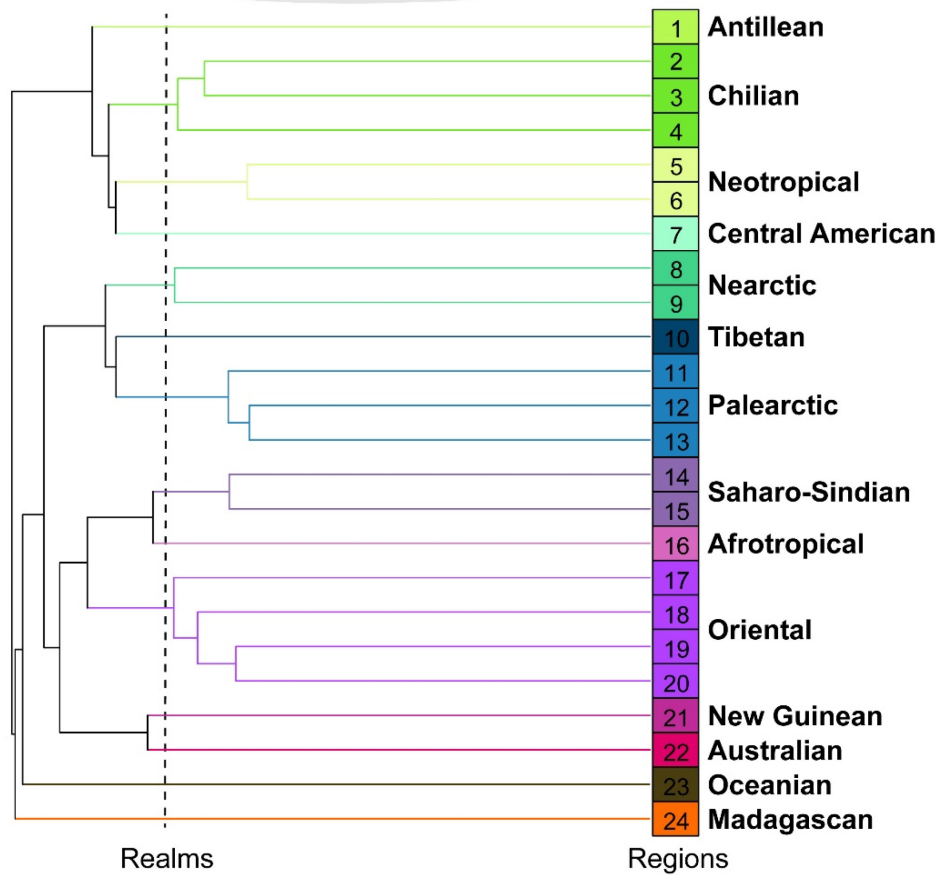
To test whether clades showing similar responses to environmental factors also have more similar bioregions, we compared the reptile

FIGURE 2 Global bioregions of reptiles. (a) Regions obtained based on distribution and phylogenetic data of 9016 lepidosaurian reptiles. Different colours represent distinct realms; black and white lines separate biogeographic realms, while white lines separate regions. (b) Phylogenetic similarity among the 24 regions (95% $p\beta_{sim}$ threshold). Vertical dotted lines represent the threshold used to obtain realms (90% explained $p\beta_{sim}$). Numbers correspond to the following biogeographic regions: 1, Antillean; 2, Pampas; 3, Andean; 4, Patagonia; 5, Brazilian; 6, Panamanian; 7, Central American; 8, Southern Nearctic; 9, Northern Nearctic; 10, Tibetan; 11, Mediterranean; 12, Sino-Japanese; 13, Northern Palearctic; 14, Zagros; 15, Saharo-Sindian; 16, Afrotropical; 17, Indian; 18, Southeastern Asia; 19, Southern China; 20, Indo-Malayan; 21, New Guinean; 22, Australian; 23, Oceanian; 24, Madagascan.

(a)



(b)



regionalization obtained here with the regionalizations of amphibians, birds and mammals from Holt et al. (2013). Before comparisons, all the regionalizations were projected in equal-area World Mollweide. We used two approaches to assess the similarity between regionalizations.

First, we used the V-measure, a method specifically developed to compare the spatial association between regionalizations (Nowosad & Stepinski, 2018). The V-measure compares two categorical maps and returns values between 0 (no association) and 1 (perfect association). We used the R package *sabre* (Nowosad & Stepinski, 2018) to obtain similarity values for each pairwise comparison between the reptile regionalizations and the three previously published ones. Each regionalization proposed using the Holt's framework has a nested structure; we considered the two levels of the nested structure that allow considering different depths of biogeographical divergence: regions nested within realms (Ficetola et al., 2017, 2021). The V-measure framework does not provide a significance test. We therefore used a randomization approach to test whether the similarity between regionalizations was significantly higher than expected by chance. For each pairwise comparison, we calculated the V-measure values for the comparison of a given regionalization with 499 randomly created regionalizations, and calculated a *p* value representing the proportion of random comparisons showing a V-measure value higher than the true regionalizations. Random regionalizations were created by (1) randomly sampling a number of terrestrial cells corresponding to the number of random bioregions needed, (2) creating Voronoi polygons from that set of points through the 'voronoi' function of the R package *dismo* (Hijmans et al., 2021) and then (3) cutting the Voronoi polygons using the outline of global landmasses. The complete script, including examples to run null-models, is available at figshare (Falaschi et al., 2023). Regionalization at the same nested level (e.g. 90% $p\beta_{sim}$) for different clades can identify a different number of bioregions. In null models, each regionalization was compared with randomly generated regionalizations showing the same number of bioregions of the regionalization against which it was compared to. For instance, regionalization of amphibians yielded 14 realms (bioregionalization A) while mammal regionalization yielded 12 realms (bioregionalization B). We created 499 random regionalizations (random-A) with 14 bioregions and 499 random regionalizations with 12 bioregions (random-B). Then, V-measure values were calculated for the comparison between amphibians and the 499 random-B regionalizations, and for the comparison between mammals and the 499 random-A regionalizations. As a result, for each pairwise comparison among true regionalizations, we calculated two *p* values (A vs. random-B and B vs. random-A; Figure 4).

Second, we compared the position of terrestrial boundaries across regionalizations at the two nested levels. For each regionalization and each nested level, we generated a raster map representing the distance of each cell from the closest boundary (Supporting information Figure S3). We then used a modified version of the *t*-test that is appropriate to test the correlations between spatial processes

(Vallejos et al., 2020) to assess whether the distance of each cell from the biogeographical boundary is similar among the bioregions of different clades. If two bioregions are similar, boundaries cross the same areas of the planet and a given cell shows a similar distance from the boundary in the two maps. Before testing the correlations, distance values in km were divided by 200 (side length of the cells, in km) and log+1 transformed.

3 | RESULTS

3.1 | Bioregions of lepidosaurian reptiles

We identified 24 regions nested within 14 realms (Figure 2). The realms identified for reptiles were overall consistent with the ones identified for other vertebrate clades (Holt et al., 2013). For instance, despite minor discrepancies, the six classical Palearctic, Nearctic, Neotropical, Afrotropical, Oriental and Australian realms were clearly identifiable. Additionally, our analyses confirmed a highly differentiated Madagascan realm (Figure 2; Supporting information Figure S1). Furthermore, similar to Holt et al. (2013), we identified a Saharo-Sindian realm (here including Northern Africa, much of South-Western Asia and South Eastern Europe), and a Central American realm, which was similar to the Holt's Panamanian realm but here did not include Panama (Figure 2). These are realms located in transition zones between highly differentiated bioregions (Kreft & Jetz, 2013; Müller, 1986b). Differences from bioregions developed for other vertebrates included the well-separated Antillean and Chilean realms, a Tibetan realm between the Palearctic and the Oriental regions (but more closely affiliated with the Palearctic), and a New Guinean realm (Figure 2). Other differences with Holt et al. (2013) included the lack of a Sino-Japanese realm, and the separation between Australian and Oceanian realms, the latter here including New Zealand and other Pacific islands (Figure 2; Supporting information Figure S1). Neither Holt et al.'s scheme nor ours recovered Wallace's line (Figure 2).

3.2 | Determinants of the boundaries between reptile bioregions

Spatially explicit models, assessing the factors related to the presence of biogeographical boundaries for reptiles, showed that terrestrial boundaries occur in areas with strong spatial heterogeneity for climatic parameters (particularly for annual precipitation, followed by mean annual temperature) and that underwent strong tectonic movements in the last 65 million years (Figure 3a; Supporting information Table S2a). Heterogeneity of precipitation and tectonic movements were the main determinants of the presence of boundaries when we focussed on boundaries of realms only (Figure 3b; Supporting information Table S2b).

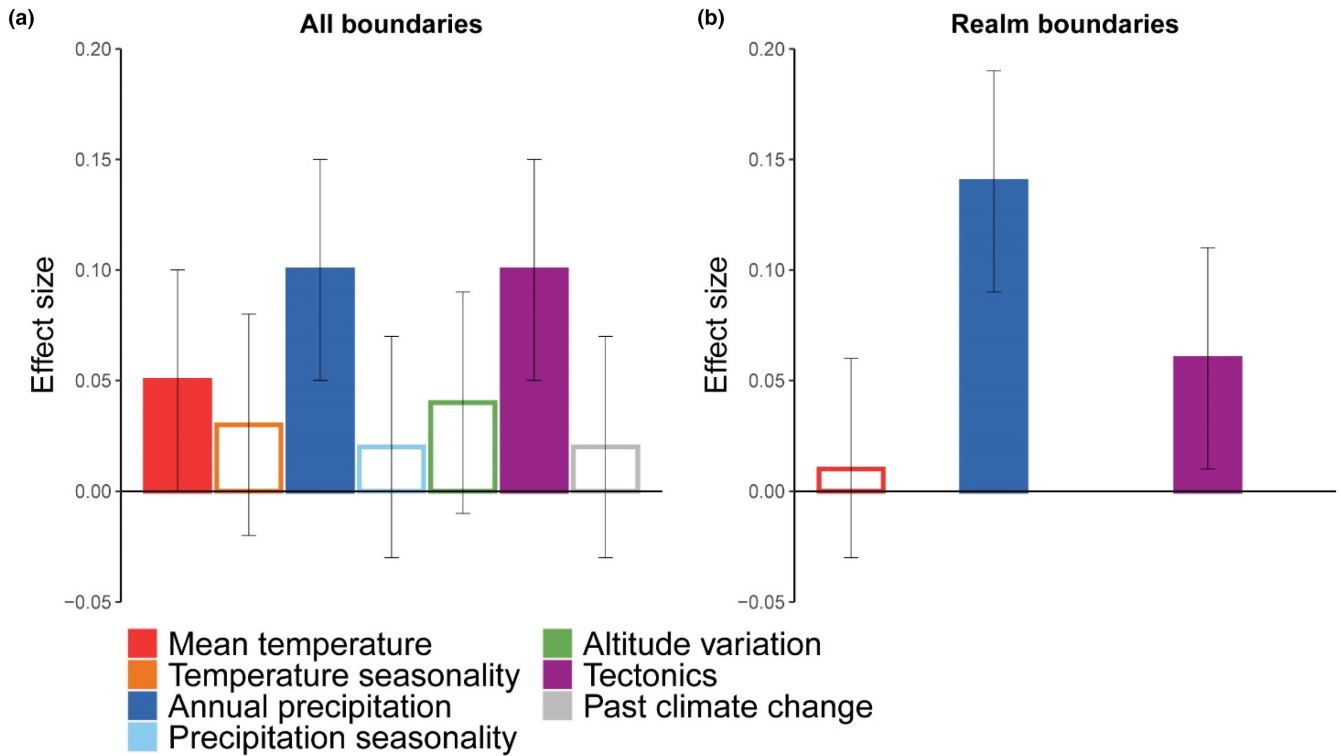
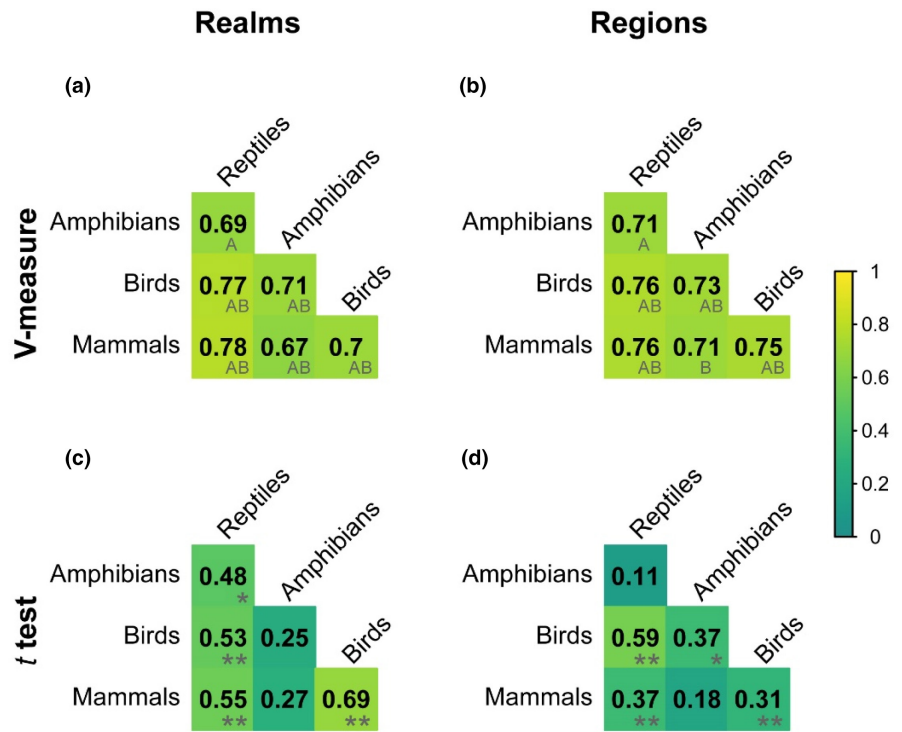


FIGURE 3 Drivers of biogeographical boundaries of reptiles. Effect of candidate drivers in determining (a) the general occurrence of terrestrial boundaries (boundaries of realms + regions), (b) the occurrence of boundaries of realms. Coloured bars indicate effect sizes (Fisher's z) with full bars being significant and empty ones not significant. Error bars represent the 95% confidence intervals of z. Only variables showing significant associations in (a) are used for subsequent model of boundaries of realms. Climatic variables are intended as heterogeneity of climate (see section 2.3).

FIGURE 4 Similarities among regionalizations at two levels across the nested structure of bioregions. Top panels (a, b) are V-measure values for realms (a) and regions (b). Capital grey letters in panels a and b indicate p values < 0.05. 'A' indicates that actual bioregions for the clades on the rows are more similar to clades on the columns than random bioregions; 'B' indicates that actual bioregions for the clades on the columns are more similar to clades on the rows than random bioregions. Bottom panels (c, d) are correlation coefficients of spatial t-tests for realms (c), and region (b), with * indicating p values < 0.05, and ** < 0.01.



3.3 | Similarity of bioregions across vertebrate clades

The V-measure method (Nowosad & Stepinski, 2018) provided a quantitative estimate of the similarity across different regionalizations at the two different levels (regions and realms) and generally showed high similarity between the bioregions of different clades.

Bioregions were generally very similar, with most pairwise comparisons (i.e. V-measure scores) > 0.7, and usually higher similarities than expected by chance (Figure 4a,b). Still, bioregions showed some differences. In general, reptiles, mammals and birds were more similar to each other compared to amphibians (Figure 4a,b).

We also found strong similarities across clades for the position of terrestrial boundaries (Figure 5), measured as the correlation

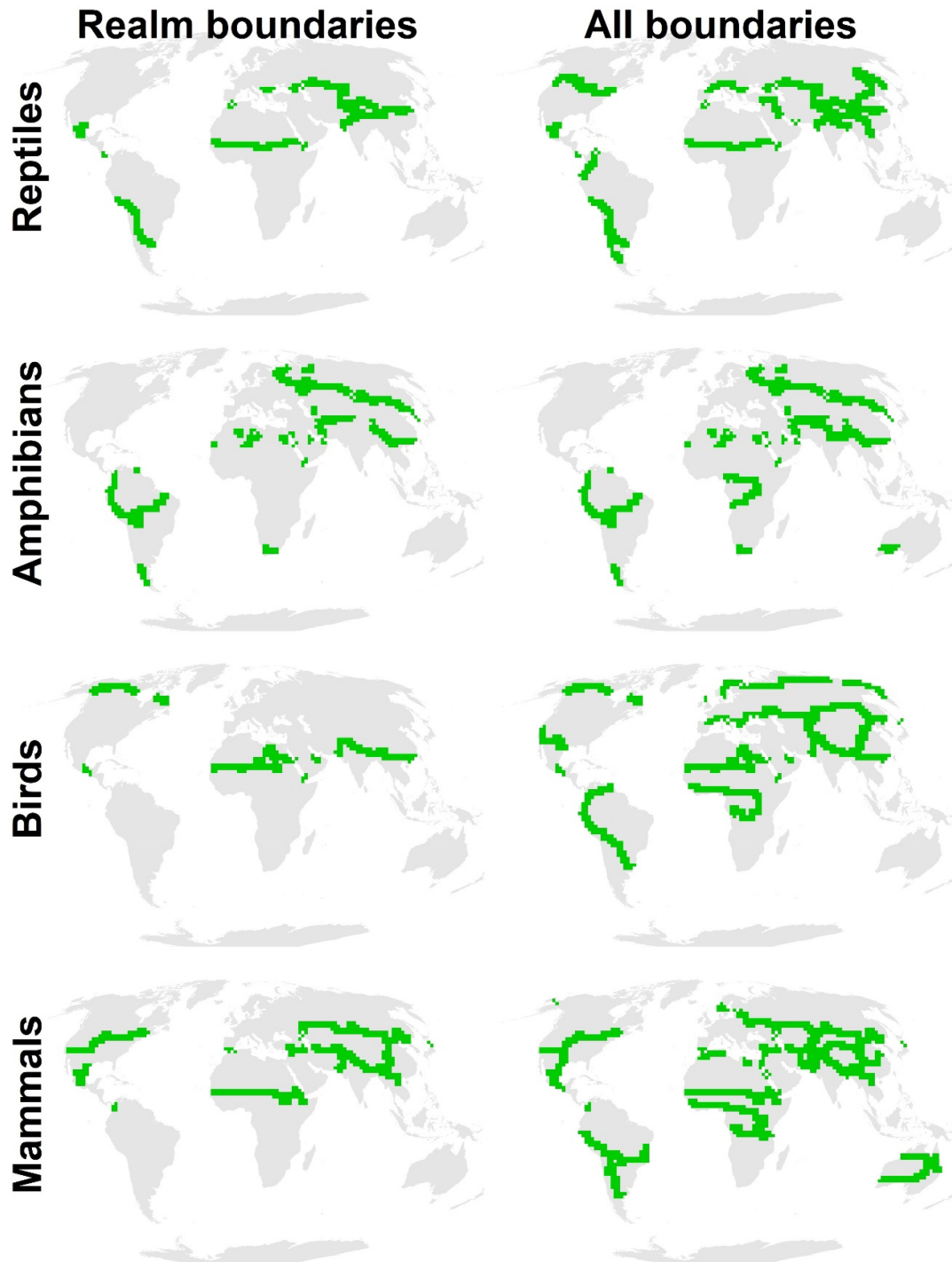


FIGURE 5 Terrestrial boundaries of regions and realms for different vertebrate clades. Realm boundaries: boundaries at the 90% $p\beta_{sim}$ threshold; all boundaries: boundaries at the 95% $p\beta_{sim}$ threshold (regions). Reptile bioregions come from this work; amphibians, birds and mammals are from Holt et al. (2013).

between the distance of each cell from the closest boundary of each taxon. Correlations (Pearson's r) were significant in most cases but, also in this case, amphibians often showed lower similarities (Figure 4c,d).

4 | DISCUSSION

A global regionalization of reptiles, integrating phylogenetic data with the geographic distribution of most species, was so far lacking due to data gaps. Our novel analysis of reptile bioregions showed strong similarities with patterns for other land-vertebrates, particularly with mammals and birds. The significant agreement between the bioregions of the four clades of terrestrial vertebrates supports the idea that similar key drivers, such as climate and tectonic movements, have strongly shaped the distribution ranges of all terrestrial vertebrates. Nevertheless, ecological differences across clades determine different responses to ecogeographical drivers, and determine strong variation in the degree of cross-clade biogeographical coherence.

4.1 | Global bioregions of reptiles

Overall, bioregions of reptiles matched well those of other vertebrates. Differences included a sharper differentiation of some regions such as the Madagascan and Oceanian. The case of Madagascar is exemplary. Here, a few clades produced multiple recent radiations, resulting in a megadiverse bioregion with a highly endemic fauna (98% of reptile species are endemic; Antonelli et al., 2022). In our work, the Oceanian region contained the highly differentiated New Zealand (100% of endemic genera), sharing several gecko and skink clades with Oceanian islands. The clustering of Tasmania with New Zealand and the Pacific islands, and not with Australia, is surprising. All the genera and even some species present in Tasmania also inhabit Australia, while no genus is shared between Tasmania and either New Zealand or the Pacific islands (Roll et al., 2017). While the Tasmanian fauna is clearly a subset of the Australian one, both shared and nonshared taxa concur in defining relationships among bioregions on the basis of beta diversity. The huge diversity of mainland Australia, together with the low species richness of Tasmania, may thus have contributed to limiting the similarity between them. Additionally, clustering algorithms have recognized issues with species-poor bioregions that show similarities with multiple neighbouring regions (Kreft & Jetz, 2013). The clustering of Tasmania with New Zealand by the best-performing algorithm probably occurs because both regions are rather far from Australia and share a locally widespread subclade of skinks (Eugongylinae).

Our analyses confirmed the presence of some transition zones, already suggested by Müller (1974, 1986a), which are areas of the globe where highly differentiated biotas mix, producing unique biotas, yet not phylogenetically distinct (Kreft & Jetz, 2013; Vermeij, 2001). However, approaches devoted to the identification

of transition zones based on phylogenetic data are still challenging (Daru et al., 2017; Edler et al., 2017; Vilhena & Antonelli, 2015) because clustering algorithms can assign samples to clusters with low confidence, resulting in arbitrary boundaries (Kreft & Jetz, 2013). Some regions, such as the Central American and Saharo-Sindian, match very well-proposed transition zones (Müller, 1986a; Wallace, 1876). For instance, in the Saharo-Sindian region, an impoverished tropical fauna coexists with temperate lineages, delineating Afrotropical-Palaearctic transitions (Kreft & Jetz, 2013). This is also the case for our Tibetan region, which does not hold endemic species and might represent a transition zone between the Palaearctic and the Oriental realms (Figure 2).

4.2 | Drivers of biogeographical boundaries

Biogeographical boundaries of reptiles were associated with areas currently representing sharp transitions of temperature and precipitation and that underwent strong tectonic movements (Figure 4). This pattern shows clear similarities with amphibian boundaries, which are strongly associated with sharp transitions of precipitation and temperature (Ficetola et al., 2021). Sharp climatic transitions are a major physiological constraint for ectotherms such as amphibians and reptiles, as they often have narrow climatic niches. Ectotherm metabolism is more dependent on climate compared with endothermic vertebrates, and variation in temperature and water availability poses major constraints to their activity and to embryonic development (Buckley et al., 2012; Cunningham et al., 2016; Ma et al., 2018; Sinervo et al., 2010). Nevertheless, reptile biogeographical boundaries were also strongly related to physical barriers, resembling mammals and birds (see Figure 3 and Ficetola et al., 2021). The geological history of our planet strongly shaped the composition of communities (He et al., 2020; Mazel et al., 2017) and plate tectonics is one of the strongest determinants of zoogeographical boundaries of reptiles (Figure 3). Tectonic movements can be particularly important in shaping the geographic distribution and evolutionary history of organisms with low dispersal abilities, such as reptiles and terrestrial mammals, which are not as good oversea dispersers as bats and birds (Mazel et al., 2017).

4.3 | Similarity of bioregions across vertebrates

We tested the assumption that similar underlying processes shape the biogeography of vertebrates, leading to good agreement of regionalizations for different clades. We found generally high similarities between the bioregions of all four clades, and similarity was particularly high when biogeographic realms, that might represent more ancient processes compared with regions, are considered (Figure 4a,b). At the realm-level, the highest similarity was found between reptiles and mammals, followed by reptiles and birds (Figure 4a). At a shallower level (regions), the highest similarities were between reptiles and both birds and mammals, followed by mammals and birds (Figure 4b). We

obtained a very similar pattern when we assessed the position of terrestrial boundaries among the different clades (Figure 4c,d). While the absolute values of spatial correlation coefficients were generally lower than the general similarity index (i.e. V-measure values), most of them were much higher than expected by chance, and were also much stronger than expected just on the basis of the spatial structure of data (Warren et al., 2014). Only for amphibians, the similarity in the position of boundaries was often nonsignificant. Overall, birds, mammals and reptiles were more similar to each other than to amphibians. On the one side, the strong similarities between bioregions of birds, mammals and reptiles support our hypothesis that consistent bioregionalizations are associated with mostly consistent responses to the same processes, since bioregions for these clades show strong responses to both climatic factors and physical barriers. Consequently, as amphibians mostly respond to climatic drivers, they show bioregions less similar to the ones of other vertebrates. On the other side, the limited similarity between bioregions of amphibians and reptiles was somehow unexpected. In principle, we expected bioregions of amphibians to be more closely related to reptiles than to birds or mammals. However, besides the generally limited similarities, we found that the clade most similar to amphibians was sometimes reptiles and sometimes birds (Figure 4). The limited similarity showed by amphibians might also be caused by uncertainty on the position of boundaries over large areas of the globe. For instance, in amphibians, the position of the boundary separating the Palearctic from the Palaeotropics is very uncertain across large parts of the Sahara Desert and the Tibetan Plateau, where amphibians are absent (Supporting information Figure S1a).

Reptile and mammal bioregions showed the highest overall similarity (Figure 4). While birds also respond to both climatic and physical barriers, reptiles and mammals are the two groups showing the strongest response to plate tectonics (see Figure 3 and Ficetola et al., 2021). Reptiles and mammals are two groups of amniotes that are predominantly nonflying and, unlike amphibians, are not strongly dependent on aquatic habitats for reproduction. For reptiles, orographic barriers were not detected as a significant factor in determining the occurrence of biogeographic boundaries, as would be expected given the high similarity with mammals. This might occur because, in several areas, there is a very strong correspondence between orography, tectonics and temperature. Specifically, the Himalayas is both the major mountain chain of the world, and one of the places with the strongest tectonic movements; the spatial concordance of the three factors might limit the possibility of teasing apart their role. However, while not significant for reptiles, the effect size of orographic barriers (average Fisher's $z=0.04$; p value=0.085) was similar to the statistically significant factors, such as temperature (Supporting information Table S2). Additionally, for mammals, tectonics is also a stronger predictor compared with orography (Ficetola et al., 2021), supporting the similarity between these two groups.

By comparing global bioregions at different levels, we found that bioregions developed for different vertebrate clades are strongly consistent. Despite 150 years of methodological innovations, data

collection and discovery of new species, the conclusions of Wallace and other seminal biogeographers (Müller, 1974) did not drastically change. More complete data on the geographic distribution and phylogeny of analysed clades now enable a more precise delineation of bioregions compared with previous studies, and future advances will soon allow detailed analyses at finer scales. For instance, the most complete reptile phylogenetic tree currently includes only <50% of known species (Zheng & Wiens, 2016), and a complete phylogeny for this group is still largely unavailable. Furthermore, significant uncertainty exists on the geographic distribution of many vertebrates (Ficetola et al., 2012, 2014; Hughes et al., 2021), hampering fine-scale biogeographic analyses in regions where data are more scarce. Given the robustness of broadscale analyses obtained in the last 150 years, we do not expect significant changes in broadscale patterns (Holt et al., 2013), still, new data will provide a rich resource to identify fine-scale biodiversity patterns and assess the possible consequences of the alteration of biogeographical patterns by anthropogenic activities (Bernardo-Madrid et al., 2019; Capinha et al., 2015; Helmus et al., 2014).

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

All data, scripts and the shapefile of obtained bioregions are available at figshare: <https://doi.org/10.6084/m9.figshare.19844755> (Falaschi et al., 2023).

ORCID

Mattia Falaschi  <https://orcid.org/0000-0002-4511-4816>

Silvio Marta  <https://orcid.org/0000-0001-8850-610X>

Elia Lo Parrino  <https://orcid.org/0000-0001-9619-9568>

Uri Roll  <https://orcid.org/0000-0002-5418-1164>

Shai Meiri  <https://orcid.org/0000-0003-3839-6330>

Gentile Francesco Ficetola  <https://orcid.org/0000-0003-3414-5155>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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