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Classic Hypotheses of Area, Time, and Climatic Stability Fall Short in Explaining High Tropical Species Richness

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Keywords: area | biogeography | climate change | latitudinal biodiversity gradient | Plio-Pleistocene | stability | time-for-speciation

ABSTRACT

Aim: Tropical biodiversity overshadows the number of species inhabiting other regions. Age, area, and stability constitute three classical ideas used to explain the higher richness in these warm and humid zones. In this study, we measured the global dynamics of tropical, arid, temperate, cold, and polar climate zones over the last 5 million years (Ma). We aimed to evaluate whether the age, area, and stability of these climate zones contribute to explain the observed differences in species richness.

Location: Global land.

Taxa: Amphibians, birds, and mammals.

Methods: We classified the paleoclimatic layers generated by the PALEO-PGEM climatic emulator—temperature and precipitation for the last 5 Ma at 1000-year intervals—into the main Köppen-Geiger climate zones: tropical, arid, temperate, cold, and polar. We then calculated three variables: age, area, and stability. Age represents the duration that each map cell has remained within its current climate zone since its last change (map cell-based measure). Area quantifies the total extent of each climate zone over time by summing all map cells corresponding to that climate zone (climate zone-based measure). Stability indicates the number of times a given map cell changed between climate zones over time (map cell-based measure). We implemented regression and correlation tests, Structural Equation Models, and decision trees to measure the relationship between these estimates and current global patterns of amphibian, bird, and mammal richness.

Results: Our results indicate that age, area, and stability do not account for the observed differences in species richness among the 5 climate zones.

Main Conclusions: None of these classical hypotheses alone can explain the high vertebrate tropical richness observed. Further investigation, incorporating additional taxa (e.g. invertebrates or plants), or integrating new perspectives (such as the influence of local variations in diversification processes) will provide a more comprehensive understanding of the factors shaping large-scale biodiversity patterns.

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1 | Introduction

Life on Earth is linked with climate, which influences species distribution, diversity, and the processes that lead to their diversification (Erwin 2009; Lomolino et al. 2016; Svenning et al. 2015). For example, studies about the effects of past climate on evolutionary processes have evidenced its relationship with species origination, dispersal, and extinction (e.g. Webb 2006; Chen and Benton 2012; Wilson 2014; Nogués-Bravo et al. 2018). Particularly, the current clustering of species at large geographic scales (i.e. biomes) is caused by the species' shared evolutionary history plus their adaptations to the surrounding geographical, geological, climatic, and biotic conditions (Benton 2009). With several classifications (e.g. Walter 1997; Olson et al. 2001; Peel et al. 2007), biomes have typically been described by a combination of functionality, physiognomy, and climate descriptors (Conradi et al. 2020), and have been frequently implemented in large-scale ecological and biogeographical studies (Mucina 2019). Moreover, due to the close relationship between climate and vegetation, climate-type classifications have been implemented as surrogates for biome schemes (Mucina 2019), on the basis that each climate type is usually dominated by one vegetation ensemble (Belda et al. 2014). Among other classical classifications (Holdridge 1947; Whittaker 1970), the Köppen-Geiger system is one of the most implemented and divides global climate into five main zones: tropical, arid, temperate, cold, and polar (Beck et al. 2018b; Köppen 1884).

On a global scale, species richness is concentrated in the tropics (hosting ~78% of terrestrial diversity; Barlow et al. 2018), and decreases towards the poles. This global pattern, known as the "Latitudinal Biodiversity Gradient" or "LBG" (Hillebrand 2004), have been described for most plant and animal species and higher taxa (Brown 2014), and has prompted several explanatory hypotheses. For instance, the greater time and area available in the tropics have been proposed as the main drivers for the higher richness of most taxa ("time-for-speciation effect" and "species-area relationship"; Rabosky 2012; Rohde 1992; Stephens and Wiens 2003). Thus, older and more widespread tropics would have provided a higher amount of space and time available for speciation, allowing lineages to accumulate and radiate towards surrounding environments (Fine and Ree 2006; Jetz and Fine 2012; Rohde 1992; Rosenzweig 1995). These ideas usually assume that most lineages originated in the tropics, and that species have a limited capability to disperse and adapt to other climates ("niche conservatism"; Erwin 1985; Jablonski et al. 2006; Wiens 2004).

Time and area are often related to the climatic stability hypothesis, which predicts that less perturbed and environmentally stable tropical regions would have led to greater specialisation, reduced extinction rates, and higher species richness (Fischer 1960; Hillebrand 2004; Schemske and Mittelbach 2017). Generally, stability refers to less variation in rainfall and temperature (Pianka 1966), which may contribute to the permanence of the existing tropical entity. In the Neotropics, for example, the long-term climatic stability would have favoured the gradual accumulation and preservation of lineages over time (Antonelli and Sanmartín 2011). This species' diversification and accumulation process, under this hypothesis, would be explained by processes of niche differentiation, adaptive radiation, and vicariance (Mannion et al. 2014; Pontarp et al. 2019). Moreover, due to this stability, several authors argue the role of the tropics as refuges for more disturbed periods (e.g. Quaternary Ice Ages), giving opportunities for allopatric speciation and the survival of newly formed species (Carnaval et al. 2009; Svenning et al. 2015). However, despite the strong support for the stability hypothesis, alternative explanations have also been proposed to explain tropical diversity (e.g. "resource-use hypothesis," by which more severe climate changes in the tropics may lead to higher diversification rates by fragmentation and vicariance episodes; Vrba 1993). In fact, Gamboa et al. (2024) tested this hypothesis under a 5 million-year scenario, finding that the tropics indeed present higher climatic fragmentation levels than other climate zones.

Previous works attempted to test the time, area, and climatic stability hypotheses to explain tropical biodiversity and the associated LBG for several groups. For example, Li and Wiens (2019) proposed colonisation time as the major factor explaining richness patterns within 15 plant, vertebrate, and invertebrate clades. On the contrary, Graham et al. (2006) found that historical stability can be as important as area in explaining spatial variation in tetrapod richness, whereas Cantidio and Souza (2019) claimed that it may act as a main driver of plant species' occurrences and abundances. Similarly, Brown et al. (2020) showed a strong association between climatic stability and contemporary global amphibian, bird, and mammal richness, and Colville et al. (2020) and Huntley et al. (2021) found past biome stability as the strongest predictor of diversity patterns for present plants and terrestrial vertebrates. Costa et al. (2018) also used a modelling approach to relate scenarios of past biome stability/variability with observed plant diversity patterns. However, these approaches have often relied on sparce temporal snapshots (Sepulchre et al. 2020) or specific regions (e.g. Neotropics, Australian Wet Tropics; but see Hagen et al. 2021), leaving the global dynamics of climate zones and their role in biodiversity largely unexplored (Antonelli et al. 2018; Maestri and Duarte 2020).

In summary, to date, the role of time, area, and climatic stability in global species distributions has been partially tested, primarily due to the still underdocumented spatial and temporal changes in climate zones' history (Cracraft et al. 2020). Here, we leverage PALEO-PGEM, a paleoclimate emulator with a 5 million years (Ma) temporal framework and fine spatial resolution (Holden et al. 2019), to provide the first comprehensive analysis of climate zone dynamics across time and its influence on biodiversity. We aim to answer the following questions (Figure S1): (1) Are tropical zones older than others? We aim to test the "time-for-speciation" effect (Rohde 1992; Stephens and Wiens 2003), measuring the time that each present map cell has been a specific climate zone. (2) Were the tropics the largest region over time? We aim to test the "area" related hypothesis (Rosenzweig 1995), measuring the total area occupied by each of the climate zones through time, as well as its accumulated area. (3) Have tropical zones been more climatically stable than others? We tested the climatic stability hypothesis (Fischer 1960), where "stability" refers to the extent to which a particular map cell has been continuously occupied by the same climate zone (McDonald-Spicer et al. 2019). (4) Are age, area, and stability metrics linked to observed vertebrate richness? We tested if calculated estimates of age, area, and stability are linked to current amphibian, bird, and mammal species richness. We chose amphibians, birds, and mammals because (1) they represent well-studied, monophyletic vertebrate clades, (2) their LBGs have been extensively investigated, and (3) high-resolution distribution data are available (IUCN 2021); making them well-suited model groups for testing our hypotheses.

2 | Methods

2.1 | Climate Data

We focused on the last 5 Ma, encompassing the Pliocene (5.3–2.6 Ma), Pleistocene (2.6–0.01 Ma) and Holocene (0.01 Ma ago to the present day; Cohen et al. 2021). This period started with a subtle warming trend in the early Pliocene (until 3.2 Ma), continuing with successive cooling pulses that culminated in the establishment of continental northern hemisphere glaciations (Zachos et al. 2001). Moreover, orographic and tectonic events occurred during this period, such as the gradual uplift of the Andes (Gregory-Wodzicki 2000).

To examine how these climatic changes influence biogeographic patterns, we used the high-resolution climate emulator PALEO-PGEM (Holden et al. 2019), which provides global temperature and rainfall monthly data with 1000-year temporal resolution and 0.5° spatial resolution (Figure 1). Using monthly mean temperature (°C) and total rainfall (mm) data from PALEO-PGEM, we created 10,002 arrays representing each time step over the past 5 Ma (two arrays of 12 matrices per time step). These data were classified based on the Köppen-Geiger climate classification system (Beck et al. 2018b) into five primary climate zones (tropical, arid, temperate, cold, and polar), since the present (pre-industrial, ca. 1760) to 5 Ma ago. This classification was implemented through the "KoppenGeiger" MATLAB function (Beck et al. 2018a) adapted for use in R (Galván et al. 2023). This results in 5001 final matrices, representing climate zones distribution at 1000-year intervals. As other biomes classifications differ in their ways to categorise them, which can influence the conclusions of the study (Donoghue and Edwards 2014), we selected the Köppen-Geiger classification due to its exclusive reliance on climatic parameters (Beck et al. 2018b).

2.2 | Biodiversity Data

We obtained terrestrial mammals and amphibians range maps from IUCN website on 24th January 2022 and 1st of March 2022 (https://www.iucnredlist.org/resources/spatial-data-download; IUCN 2021), and birds range maps from BirdLife International on 4th of March 2022 (http://datazone.birdlife.org/species/requestdis; BirdLife International and Handbook of the Birds of the World 2021). Mammals and amphibians range maps were provided as shapefiles, so we loaded them in R using the 'rgdal' package (Bivand et al. 2021). Birds range maps were provided as an ESRI file geodatabase, so we dissolved the polygons corresponding to a single species and exported them as a shapefile in QGIS (QGIS Development Team 2021). Then, for all groups, we excluded species range polygons with "presence" values 3 ("possibly extant") and 6 ("presence uncertain"), as well as with "origin" values 3 ("introduced") and 4 ("vagrant"), avoiding highly uncertain records and keeping the natural range of each species (Miraldo et al. 2016). We rasterized these polygon data at 0.5°, creating presence/absence raster files per species and richness maps for each group, using the 'terra' package (Figures S1 and S2; Hijmans 2022).

2.3 | Hypotheses Testing and Statistical Analyses

Once matrices of climate zones distribution were created, we rasterized and reprojected the maps to the Mollweide equal area projection (minimising area distortion and enabling the calculation of global and regional metrics; Videos S1 and S2). Then, we performed the following measures using the 'raster' package (Figure 1; Hijmans 2023): (1) For the "time-for-speciation effect" hypothesis, we measured the "age" of a climate zone in each map cell as the number of time steps, with each step representing a thousand years, that the map cell has been part of the current climate zone since its last change. For example, if a map cell is currently part of the tropical climate zone, and it has been so since it changed from arid to tropical 50 steps ago, the age of the tropical zone in that cell will be 50000 years. (2) For the area-related hypothesis, we measured the total "area" of each climate zone as the sum of the area of all map cells corresponding to the same climate zone in each time step (in km^2). To do so, we used the "lsm_c_ca" function of the 'landscapemetrics' package (Hesselbarth et al. 2019). In addition, as the importance of integrating time into area measurements has been demonstrated for several plant and animal groups (Belmaker and Jetz 2015; Fine and Ree 2006; Jetz and Fine 2012), we measured the "accumulated area" of a climate zone through all the time steps as the area under the curve of this temporal trend (using the "sintegral" function of the 'Bolstad2' package; Curran 2013). (3) For the stability-related hypothesis, we considered stability as the extent to which an entity is continuously the same through a period of time (Cantidio and Souza 2019; Carnaval et al. 2014; Costa et al. 2018; Graham et al. 2006; Terribile et al. 2012). We measured the stability of a climate zone using two metrics: (a) number of changes ("N° changes"), measured as the total number of changes between climate zones per map cell, and (b) total number of different climate zones per map cell ("N° climate zones"). In both cases, the lower the value, the higher the degree of stability. These stability metrics accounts for the change in both climatic conditions and "climate-zone" entity properties (McDonald-Spicer et al. 2019).

We worked at the map-cell level except for area measures, for which we worked at the climate-zone level (Figure S1; Hesselbarth et al. 2019). Although we calculated these metrics globally, for the following analyses we selected study units divided by landmass (America, Africa, and Eurasia + Oceania ["EurOc"]) and animal clades (amphibians, birds, and mammals), to maximise the number of replicates and differentiate potential responses among geographically distant climate zones. We based our decision on Hagen et al. (2021), who found that tropical biodiversity is driven by different paleoenvironmental and tectonic processes in each landmass. In this sense, individual statistical analyses were applied for each metric (Age, Area, N° changes, and N° climate zones) and each study unit

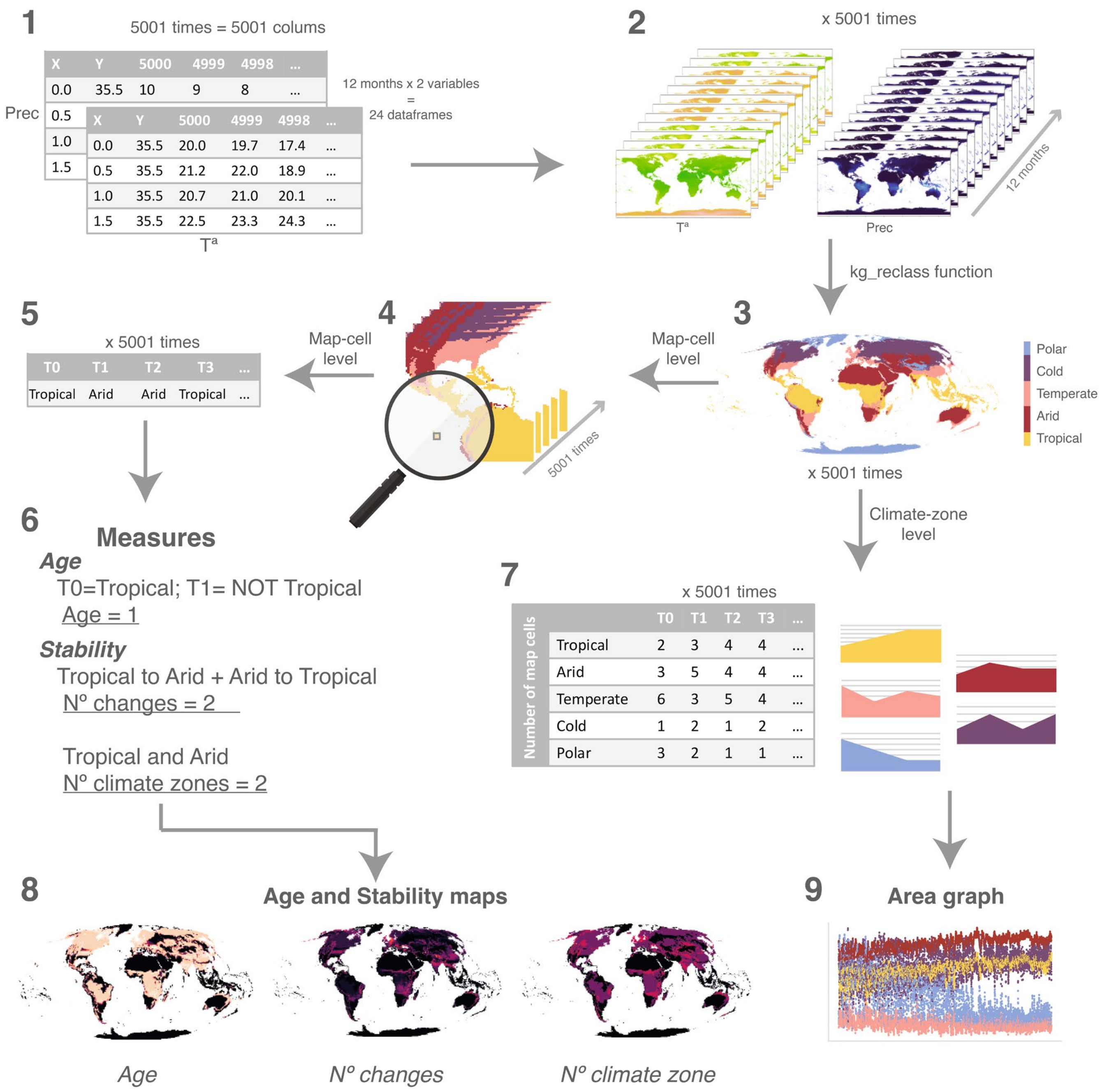

FIGURE 1 | Schematic methodological workflow used in this study. (1) From PALEO-PGEM (Holden et al. 2019), we obtained 24 databases containing monthly mean temperature (°C) and total rainfall (mm) data for 5001 time steps (each step representing 1000 years). (2) For each time step, we converted these databases into two arrays of 12 matrices (representing temperature and precipitation data for 12 months). In total, we obtained 10002 arrays. (3) For each time step, we used these arrays and Köppen-Geiger climate classification (Beck et al. 2018b) to classify them into main climate zones: Tropical, arid, temperate, cold, and polar. In total, we obtained 5001 classified maps. (4) In order to perform map-cell level metrics, (5) we focus on the temporal evolution of each map cell and (6) calculated the age (number of time steps, with each step representing a thousand years, that the map cell has been part of the current climate zone since its last change), the N° changes (total number of changes between climate zones per map cell), and the N° climate zones (total number of different climate zones per map cell). For the example map cell (T0 = Tropical, T1 = Arid, T2 = Arid, T3 = Tropical), Age = 1, N° changes = 2, and N° climate zones = 2. (7) On the contrary, in order to perform climate-zone level metrics, we calculated the total area of each climate zone as the sum of the area of all map cells corresponding to the same climate zone in each time step (in km^2). As a result, we obtained (8) maps for age and stability (N° changes and N° climate zones), and (9) a temporal graph for the area of each climate zone throughout 5 Ma.

(e.g. amphibians in America tropical climate zone). The masks for the landmasses were created in QGIS (QGIS Development Team 2021), and the criteria used for these divisions can be found in Appendix S1.

To analyse the relationship between climate metrics (Age, Area, N° changes, and N° climate zones) and species richness, we created a database with geographic data of species presence/absence for each map cell using the "as.data.frame" function in the 'terra' package (Hijmans 2022). Then, regarding the relationship between area and species richness, we divided it into landmasses and climate zones and calculated the richness in each zone. Lastly, we performed Spearman correlation tests, linear models, and Structural Equation Models (SEM) between the accumulated area of a climate zone and species richness for each animal clade; using the "cor" function in the 'stats' package (R Core Team 2022), "lmp" function in the 'lmPerm' package (Wheeler and Torchiano 2016), and "sem" function in the 'lavaan' package (Rosseel 2012).

For testing the per-cell relationship between age/stability metrics and biodiversity levels, we independently used three explanatory variables: Age, N° changes, and N° climate zones. In addition, we independently include amphibian, bird, and mammal species richness as response variables. Then, we performed per-clade generalised least squares (GLS) regressions for each climate zone and landmass, using the 'nlme' and 'gstat' packages (Pebesma 2004; Pinheiro et al. 2021). To do so, we implemented two sampling approaches: a random sampling, for which we randomly sampled 500 map cells of the original data set; and a stratified sampling, for which we divided the original set into subsequent categories and performed a random sampling in each of them (either selecting 50 map cells or 10% map cells per category). For this stratified sampling, we selected 10 categories for "Age" (every 500000 years), eight categories for "N° changes" (every 200 changes), and four categories for "N° climate zones" (one per each value of distinct climate zones). Following Tejero-Cicuéndez et al. (2022), variables were scaled, so that coefficients may range from −1 to 1. In addition, we included an exponential autocorrelation structure in the models to account for the non-independence of the data (Beguería and Pueyo 2009), and we applied a bootstrapping procedure of 1000 replicates to determine 95% models' confidence intervals. Lastly, we selected as significant those cases were more than 95% of their replicates are significant (p-value ≤ 0.05).

Finally, we performed decision trees and a random forest to identify the variables better explaining the number of species per map cell on the three taxa. A decision tree is a binary recursive partitioning algorithm that classifies a data set according to the homogeneity of subgroups data. Starting with the entire data set at the tree root, and through the branches, data are divided in each of the nodes according to one of the explicative variables (Steinberg 2009). Furthermore, random forest is a machine-learning algorithm that classifies data by combining the predictions of many decision trees generated by random samples of map cells (Costa et al. 2018). We constructed 500 trees including previous variables (Age, N° changes, and N° climate zones), and "Landmass" ("America," "Africa" or "EurOc") and "Climate zone at time 0" ("Tropical," "Arid," "Temperate," "Cold" or "Polar") as factor variables. We excluded "Area" variable due to its close relationship with "Landmass" and "Climate zone at time 0," and we used the 'rpart', 'rpart.plot', and 'randomForest' packages (Liaw and Wiener 2002; Milborrow 2019; Therneau et al. 2019).

All analyses were run in R version 4.2.2 (specific R packages are available in Appendix S2; R Core Team 2022), and computationally demanding sections were carried out on the FinisTerrae-III supercomputer (CESGA 2021). Landmasses were plotted using Natural Earth data (https://www.naturalearthdata.com/).

3 | Results

3.1 | Age of the Climate Zones

Globally, there is a great difference between the age patterns of the arid and polar zones and the remaining ones (Figure 2). In this sense, these climate zones are the oldest, with their median values at 5 Ma (median values are indicated, and then first and third quartiles are displayed within brackets; arid = 5 [1.37–5] Ma, polar = 5 [2.04–5] Ma; Figure S3). On the other side, the cold and temperate climate zones present lower median values (cold = 0.019 [0.012–1.32] Ma, temperate = 0.14 [0.010–4.22] Ma), whereas the tropical climate zone shows an accumulation of points around 20,000 years and 5 Ma (median = 0.71 [0.016–5] Ma).

When separating by landmasses (Figure S3), the pattern changes for some climate zones. The arid zone continues to be the oldest (median near 5 Ma for all landmasses), the temperate zone varies between landmasses (America = 1.56 [0.014–5] Ma, Africa = 0.24 [0.005–3.38] Ma, EurOc = 0.071 [0.08–3.17] Ma), and the cold climate zone is maintained as the youngest just in America (0.012 [0.011–0.017] Ma). Africa is characterised by a general lack of cold and polar climate zones. However, the tropical climate zone maintains its bimodal distribution in America and Africa (America = 0.42 [0.018–5] Ma, Africa = 0.021 [0.014–0.51] Ma), whereas it presents a higher age in EurOc (5 [0.70–5] Ma). The opposite occurs for the polar climate zone, which is maintained as old in America (3.22 [0.006–5] Ma) but turns out to be younger in EurOc (0.10 [0.007–2.57] Ma). These results showed that EurOc tropics are the oldest compared with their American and African counterparts, although other climate zones also present an elevated age.

3.2 | Total Area of the Climate Zones

Globally (Figure 3), it is possible to see three clear trends belonging to the tropical, arid, and temperate climate zones. These climate zones suffered less variance over time, with the arid zone presenting the highest accumulated area (2.20×10^{11} km^2) followed by the tropical and temperate zones (1.83×10^{11} and 1.04×10^{11} km^2, respectively). Furthermore, the cold and polar climate zones suffered a greater variance through time due to glaciation periods and their continuous exchanging (cold = 1.89×10^{11} km^2, polar = 1.38×10^{11} km^2).

However, the pattern changes when focusing on each landmass (Figure 3). In America, the tropical zone presents the highest accumulated area (6.97×10^{10} km^2), together with the cold (5.72×10^{10} km^2) and polar climate zones (5.42×10^{10} km^2). In this case, the temperate and arid climate zones are the less extensive (3.38×10^{10} and 3.07×10^{10} km^2, respectively). Regarding Africa, the pattern is similar to the global approach, in which the arid zone is the most extensive through time (8.71×10^{10} km^2),

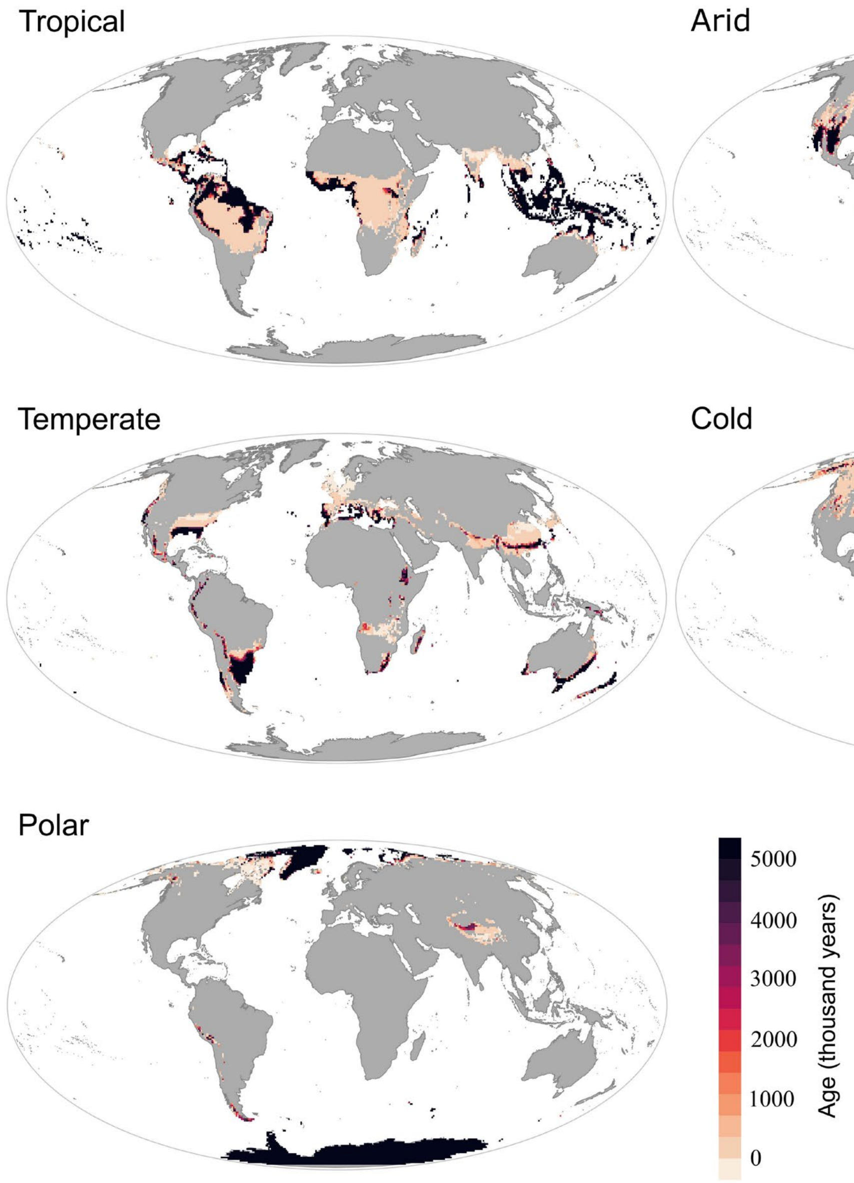

FIGURE 2 | Spatial distribution of the age of the climate zones (in thousand years, Mollweide equal area projection). For each map cell, age was calculated as the number of time steps, with each step representing a thousand years, that the map cell has been part of the current climate zone since its last change. Individual maps for current map cells corresponding to tropical, arid, temperate, cold, and polar climate zones.

followed by tropical and temperate zones (5.41×10^{10} and $1.68\times10^{10}\,\mathrm{km}^2$). There are a few cold and polar map cells with a lower accumulated area (4.85×10^{7} and $3.24\times10^{6}\,\mathrm{km}^2$). Lastly, in EurOc, the global pattern is also generally maintained, with the arid and cold climate zones as the largest (1.02×10^{11} and $1.32\times10^{11}\,\mathrm{km}^2$), well ahead of the tropical, temperate, and polar zones (5.96×10^{10}, 5.37×10^{10}, and $2.31\times10^{10}\,\mathrm{km}^2$). In this sense, the importance of the area in tropical biodiversity would be only observed in American tropics, although other climate zones also present a great area.

3.3 | Stability of the Climate Zones

Regarding the N° changes between climate zones in each map cell (Figure 4 and Figure S5A), all climate zones present high global stability (i.e. smaller N° changes). Polar, arid, and tropical present the highest values (polar = 0 [0; 33] changes, arid = 0 [0; 56] changes, tropical = 11 [0; 196] changes). In general, less stable zones consist of transition zones between climate zones (Figure 4). Separating by landmasses (Figure S5A), the general pattern holds for America and Africa, with arid, polar, and tropical as the most stable (arid: America = 46 [0–370], Africa = 0 [0; 0]; polar: America = 8 [0–570] changes; tropical: America = 10 [0–82], Africa = 120 [15–375]). In EurOc, arid and tropical climate zones are also the most stable (0 [0–64] changes and 0 [0–49] changes, respectively), together with the cold (77 [2–290] changes). In this case, the polar climate zone turns out to be the least stable (363 [35–614] changes).

Then, for the number of different climate zones per map cell (Figures S4 and S5B) results agree with the previous metric. Arid and polar climate zones present the least number of past climate

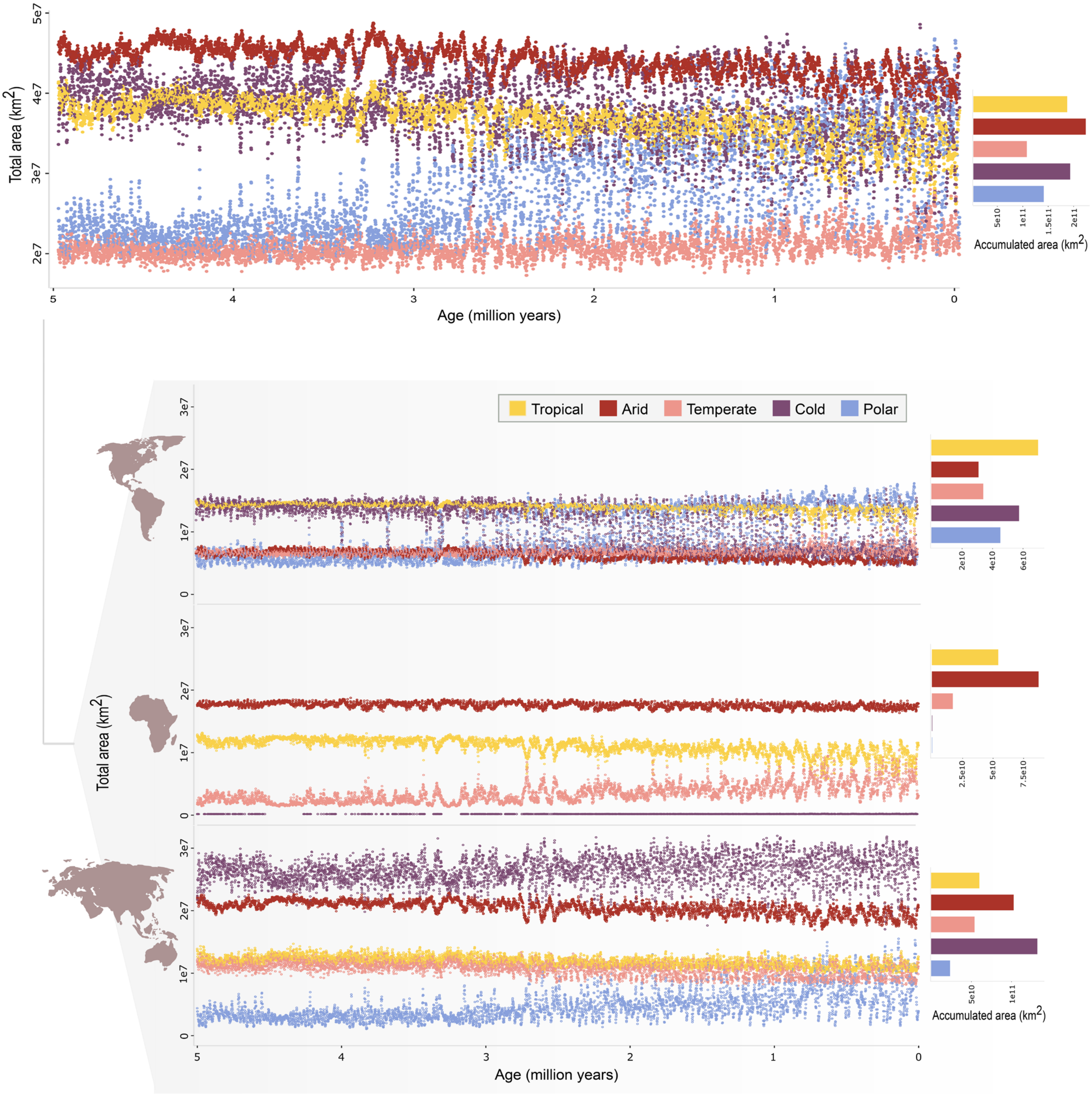

FIGURE 3 | Total area of the climate zones through time (km^2). The first graph shows the global evolution of the total area of the climate zones throughout the 5 Ma. Each point represents the total area of that climate zone in a given time step. The following graphs show the evolution of the total area of the climate zones in each landmass: America, Africa, and EurOc. In addition, barplots on the right show the corresponding total accumulated area of each climate zone for each graph.

zones (a higher proportion of map cells holding 1 climate zone), followed by the remaining climate zones. Similarly, transition regions are the zones presenting the highest N° climate zones. When separating by landmasses, the arid climate zone is maintained as the most stable (with its highest proportion of map cells containing 1 climate zone for all landmasses), together with America polar and EurOc tropical zones. In this case, EurOc tropics are more stable than their American and African counterparts, although the arid and polar climate zones are the most stable in the general scenario.

3.4 | Age, Area, and Stability Relationship With Species Richness

There is no significant correlation between the area of a climate zone and its number of species for any of the animal groups (Figure 5, Tables S1 and S2). Moreover, SEM and linear models show no significant effect of the area on species richness (Table S2).

Globally, we did not detect a clear effect of the age of a climate zone's cell map and its biodiversity levels for none of the clades

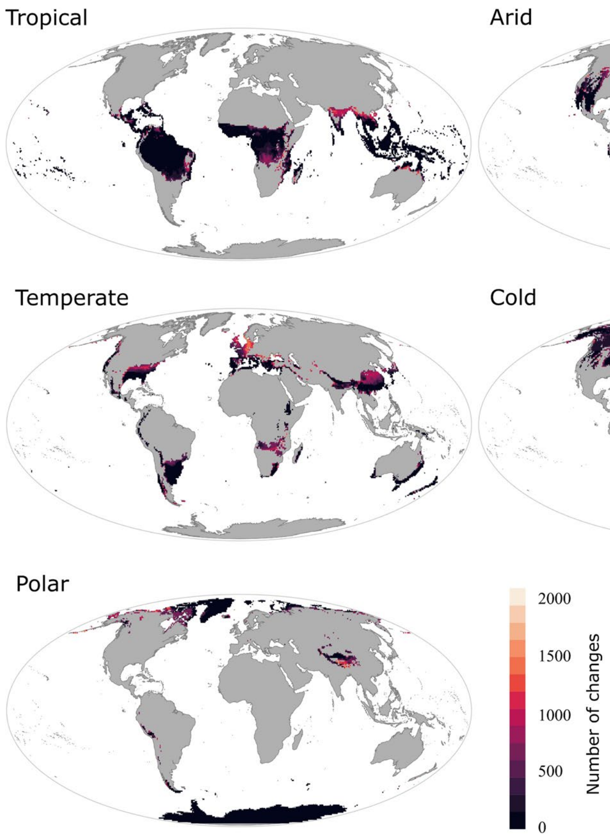

FIGURE 4 | Spatial distribution of the stability (N° changes) of the climate zones (Mollweide equal area projection). For each map cell, "N° changes" was calculated as the total number of changes between climate zones. Individual maps for current map cells corresponding to tropical, arid, temperate, cold, and polar climate zones.

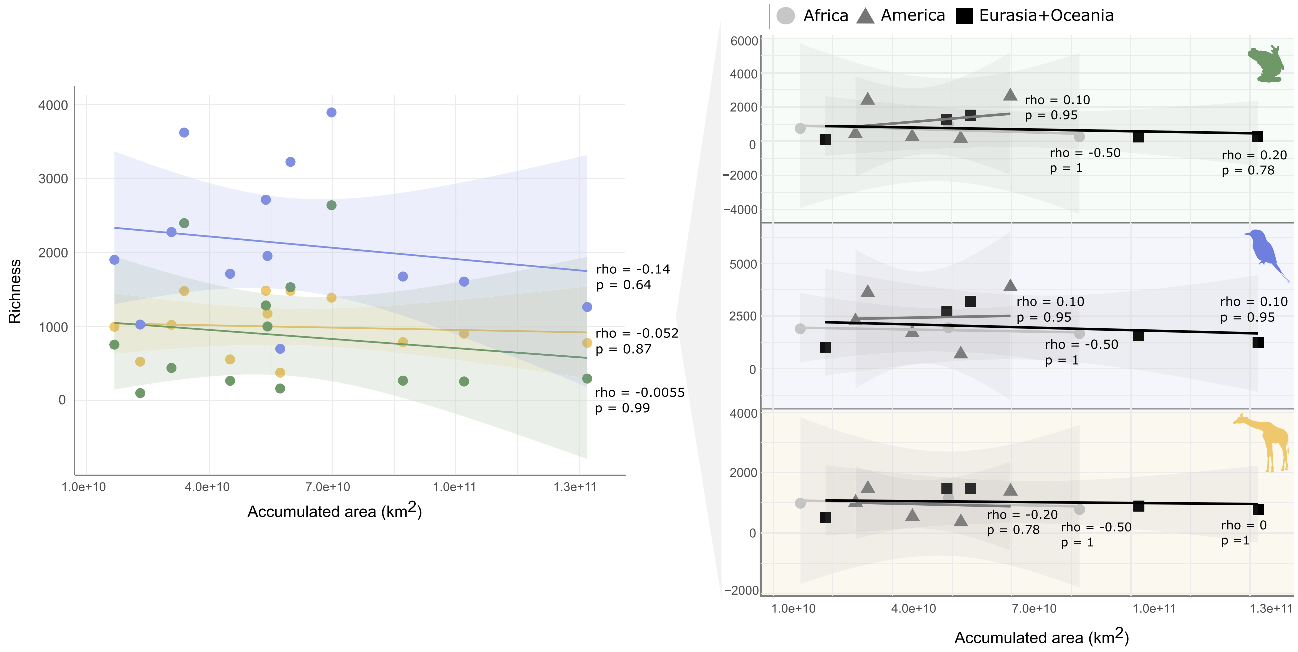

FIGURE 5 | Relation between the accumulated area of the climate zones (km^2) and amphibian, bird, and mammal richness. Each point represents a climate zone in a specific landmass. Graphs are shown globally (on the left) and split by landmasses (on the right) for each animal group. rho = Spearman correlation coefficient; p = p-value.

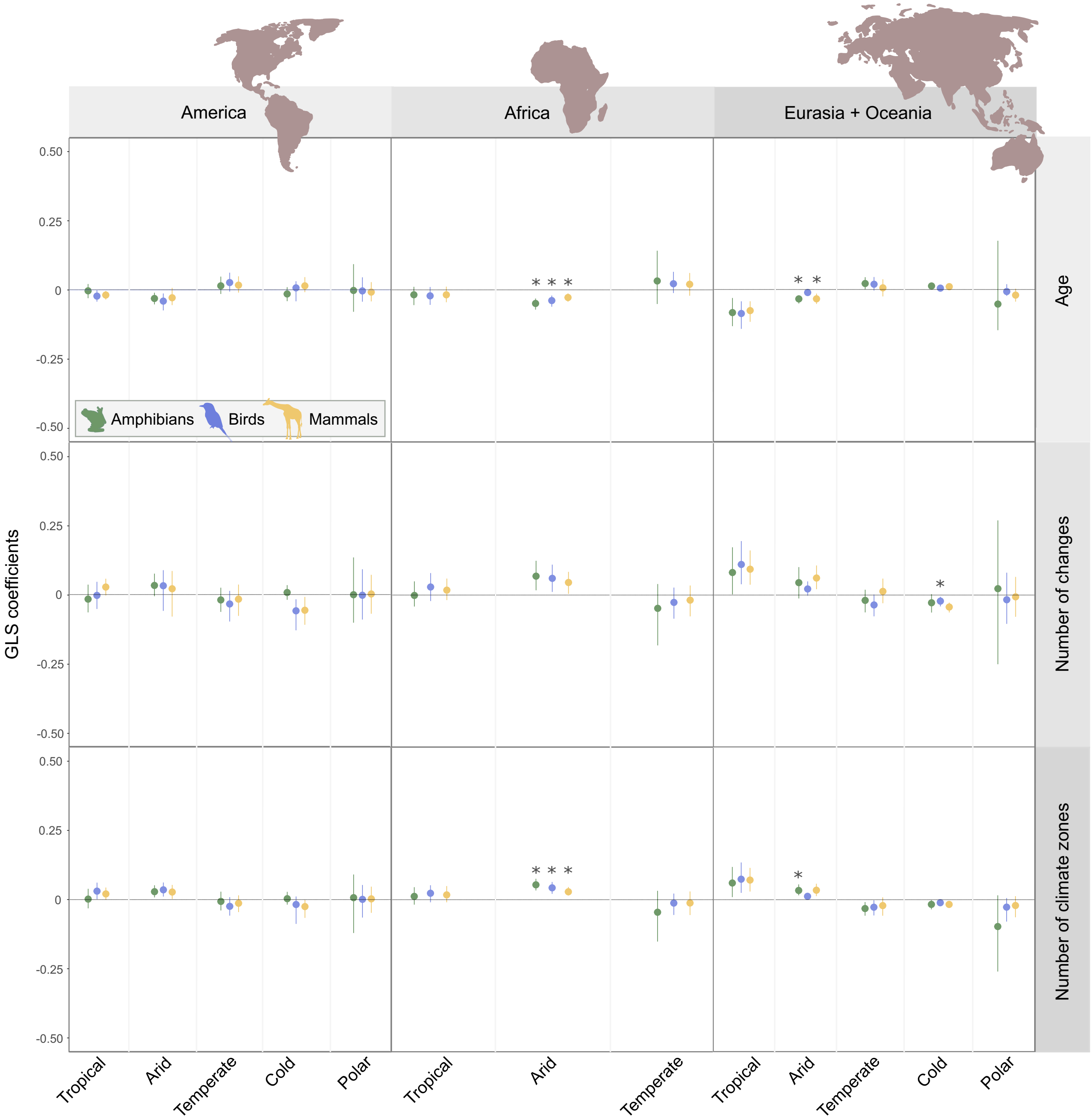

FIGURE 6 | GLS regression coefficients when randomly selecting 10% map cells of each variable subcategory (see Section 2). Coefficients of the GLS regressions (median values and 95% confidence interval) between the studied variables (Age, N° changes, and N° climate zones) and amphibian, bird, and mammal richness for each climate zone and landmass. Significant cases are indicated with an asterisk (> 95% of their replicates show a p-value ≤ 0.05).

(Data S1 and S2; Figure 6, Figures S6 and S7). GLS coefficients for this variable are low, varying from −0.08 to 0.04. The highest effect (−0.08) is detected for EurOc amphibians in the tropical climate zone (Figure 6). Similarly, a general absence of a relationship was found for the two variables related to the stability of a map cell (N° changes and N° climate zones), although some of the coefficients were higher (varying from −0.07 to 0.17). The highest coefficients were positive for EurOc birds in the tropical climate zone and negative for African amphibians in the temperate one (Figure 6 and Figure S6). Also, different sampling techniques give, in general, similar median coefficients (Data S2, Figures S6 and S7), with the stratified percentage sampling showing the larger 95% confidence intervals (Figure 6).

Lastly, random forests showed that the climate zone and the landmass are the most important variables explaining richness (Figure S8, Table S3). For the three clades, the highest number of species is explained by the fact of belonging to tropical or temperate climate zones, especially in America. In addition, N° changes and age are important variables in the last tree subdivisions. Thus, focusing on the decision trees performed with the entire data set (Figure S8), a lower age explains a higher richness, which agrees with some results of GLS regressions (Figure 6, Figures S6 and S7).

4 | Discussion

In this study, we tested classical hypotheses linking global biodiversity patterns to differences in the age, area, and stability of climate zones, defending that tropical climates are generally older, larger, and more stable. We used the PALEO-PGEM climate emulator to map the evolution of the main climate zones over the last 5 Ma (Holden et al. 2019). We first measured global age, area, and stability metrics for each climate zone for comparative purposes. Then, dividing by climate zones, landmasses, and animal clades, we tested the relationship between these metrics and richness. Specifically for age and stability, we analysed how they relate to local richness values in a given map cell (see Section 2). This is the reason why, for example, a climate zone could be labelled as "stable" based on its median "N° changes" (global perspective) and, within this zone, a higher number of local changes could be associated with a higher richness (map-cell perspective). Overall, our results suggest that none of these hypotheses, at least individually, explain the higher levels of tropical richness observed in amphibians, birds, and mammals.

First, results show that the age of the map cells within each climate zone is not related to their current richness, regardless of the climate zone, landmass, or taxonomic group analysed. To independently test this effect, we controlled for other potential drivers of biodiversity differences and conducted 1000 independent replicates per climate zone, landmass, and taxon. Historically, age has been proposed as a key hypothesis to explain the high biodiversity of the tropics ("age-diversity relationship"; Pianka 1966), either relying on the antiquity of these zones or on the greater evolutionary time of their inhabiting species ("time-for-speciation" effect; Fischer 1960; Rohde 1992; Stephens and Wiens 2003). In this sense, these warm and humid environments may have facilitated species accumulation under the premise of niche conservatism and differential rates of species colonisation across climates (Wiens and Donoghue 2004). However, here, we did not incorporate explicit evolutionary processes, but rather focused on analysing large-scale biogeographic richness patterns. Nevertheless, several studies provided similar results to ours, not finding an age-diversity relationship for our studied clades (amphibians, birds, and mammals; Pyron et al. 2013; Quintero and Jetz 2018; Tenorio et al. 2023), and reptiles (Tejero-Cicuéndez et al. 2022).

The last 5 Ma have been characterised by global cooling, glaciations, community turnovers, and shifts in species distributions (Appendix S3). In this context, our results demonstrate that, at a map-cell scale, older zones do not necessarily support higher species richness than younger ones (i.e. those that remained as the current climate zone for a shorter period). However, when comparing tropical regions across landmasses, we observed that EurOc tropics are older than their American and African counterparts. This aligns with the observed higher biodiversity in EurOc tropics compared to those in the American and African tropics (known as the "pantropical diversity disparity," Hagen et al. 2021). While our study does not establish a causal link, it suggests that the relative age of tropical climate zones may play a role in shaping regional differences in species richness and should be considered in future investigations. Further, GLS results showed a small effect of the age on richness, suggesting that, in case the age is truly playing a role in biodiversity levels, this may be limited or complementary to other factors. Age only appears as an important factor in the last subdivisions of the clades' decision trees, which agrees with the idea of its potentially secondary effect on configurating species richness in some groups or zones. This has also been defended by recent papers, suggesting that time effects would be more prevalent in some taxa (like those with narrower geographic ranges; Cerezer et al. 2022), or at shorter timescales (Etienne et al. 2019).

We are aware that we are not considering the age of the species or the time that they have been occupying each of these zones (i.e. their "evolutionary time"; Stephens and Wiens 2003). Several authors have studied these factors (for a review see Li and Wiens 2019), with most of them supporting an effect of this evolutionary time on richness patterns (but see bird and mammal results in Igea and Tanentzap 2019). Even so, recent work found a lack of relationship between lineage ages and lizard richness, arguing against the simple role of time in explaining biodiversity heterogeneity (Tejero-Cicuéndez et al. 2022). These contradictory results point to the importance of the chosen variable because, as explained by these authors, they are not directly inferring the true timing of diversification in each zone. Species are dynamic and can disperse across different regions, making it challenging to assume that species currently inhabiting a particular zone necessarily diversified within that region. Thus, disentangling the contributions of in situ diversification and dispersal is complex and requires explicit evolutionary analyses, although it would complement the current study.

Second, geographical area has been historically proposed as one of the main determinants of species richness (Rosenzweig 1995), with larger regions containing more species and larger population sizes (Fine 2015). However, other authors have put in doubt these ideas, arguing that not all tropical regions have a larger area than cold-temperate zones (Rohde 1992), or have directly not detected a species-area relationship in several environments (trees: Silva de Miranda et al. 2022; reptiles: Tejero-Cicuéndez et al. 2022; amphibians, birds, and mammals: Tenorio et al. 2023).

Our results show that the time-integrated area of a climate zone does not have a global role on species richness (measured as gamma diversity). Here, arid zones present a greater global area and, although the tropical zone is bigger in America, these values are shared with other climate zones. In this sense, other factors seem to be more relevant for configuring biodiversity at the macroscale, such as dispersal events or other multiple-source disturbances (Vrba 1993). Chown and Gaston (2000) also claim that other aspects, such as low productivity at high latitudes, may reduce the richness they would gain from its area alone. However, as pointed out by Fine (2015), concerns may arise about how to choose the accurate window of time to evaluate the effect of time-integrated area. This concern may be applied to our study, as we are not explicitly measuring the area of the climate zones in the timeframe where extant species were supposed to inhabit in the past. However, we consider our estimation as a proxy of the available extent for species to diversify and a way of explicitly testing the area-diversity relationship. For that reason, the lack of effect of the area at this spatiotemporal scale does not neglect its potential role at local or regional scales, as well as at longer timeframes (Mittelbach et al. 2007).

Third, authors have defended the higher stability of the tropics in comparison to the greater record of fragmentation, bottlenecks, and founder effect at higher latitudes (Lawrence and Fraser 2020; Mittelbach et al. 2007). This would explain the hypothetical higher tropical rates of net diversification (although recently questioned in plants by Tietje et al. 2022), and the current LBG (Mannion et al. 2014). Here, as we performed with age analyses, we conducted 1000 independent replicates per climate zone, landmass, and taxon. Our results show that the tropics presented similar stability levels to other zones such as arid or polar (map-cell level). This means that, although we detected a general tropical stability as in other studies (Cantidio and Souza 2019; Colville et al. 2020; Costa et al. 2018; Graham et al. 2006), this would not be applied just to this climate zone. Therefore, we cannot directly relate this variable to the remarkably higher tropical richness. In fact, Tietje et al. (2022) found that species richness was not higher in more stable zones. Furthermore, a recent study implementing the same climate emulator found that, although the tropics experienced fewer events of fragmentation, they indeed presented higher general fragmentation values (Gamboa et al. 2024). In this sense, despite their higher general stability, it seems that the tropics may have experienced similar environmental shifts to those occurring outside the tropics (Bush et al. 2011; Rull 2011). Also, in agreement with our results, there is evidence of changes in the placement and length of tropical regions over time (Jaramillo and Cárdenas 2013). This would emphasise a link between some degree of historical instability and biodiversity patterns (Gamboa et al. 2024; Renema et al. 2008). For example, specific shifts in tropical biomes were detected during the Quaternary period, with contraction and expansion episodes (Hopkins et al. 1993; Moritz et al. 2000). This likely affected processes such as dispersal and diversification (Rull 2020), which may contribute to the extant biological richness. Equally, the observed high stability of other zones, like arid ones, may be related to other biological characteristics, such as the distribution of mammal climate specialists (Gamboa et al. 2024).

In addition, our results showed no effect of both stability variables (N° changes and N° climate zones) on species richness, with coefficients close to 0. Although the trend is minimal, most significant cases showed that N° changes and N° climate zones have a positive effect on richness. Normally, an increase in instability has been related to decreased speciation, increased extinction, and dispersal episodes (Colville et al. 2020; Fei et al. 2017). However, other authors have defended the important role of different scales of disturbance in promoting diversification. For example, the classical "turnover-pulse hypothesis" claims that past global climate changes drove pulses of species turnover (Vrba 1993). The mechanism behind this idea is that, although climate fragmentation can lead to extinction, this also can promote new dispersion, adaptation, and speciation opportunities. As an example, Gamboa et al. (2024) found that high mammal richness in the tropics is indeed linked to higher fragmentation values. Also, at greater temporal scales, unstable periods within longer stable periods are associated with increased evolutionary rates for tetrapods and plants, contributing to the assembly of tropical diversity (Meseguer et al. 2020). Lastly, Furness et al. (2021) pointed out that, although broad scale instability may reduce biodiversity, localised levels of instability may increase it along permanent homogeneous environments. Thus, instability pulses may promote diversification under a longer term stability scenario.

Comparing landmasses, map cells classified as the same climate zone show distinct climatic dynamics over the last 5 Ma, and also differential species richness. Other authors discussed the differences in plants and tetrapod diversity and possible explanations between global tropical (Couvreur 2015; Hagen et al. 2021), temperate (Qian and Ricklefs 2000), or arid systems (Tejero-Cicuéndez et al. 2022). This disparity can also be observed in our random forest, in which the entity per se (e.g. "being" tropical in America) explained most of the species richness for all groups. Tietje et al. (2022) also detected the importance of the biome (in their case, "tropical rainforest") in hosting a greater plant richness. Altogether, this suggests that there may be other factors shaping global biodiversity apart from broad climate limits (Hagen et al. 2021; Pontarp et al. 2019). For instance, contrasting timings of lineages' origin and diversification (deeper in time), together with differences in dispersal, extinction, and environmental pressures, can lead to these discrepancies (Silva de Miranda et al. 2022). In this regard, Igea and Tanentzap (2019) investigated birds and mammals and found that tropical hotspots, except for the Afrotropics, generated and exported species at higher rates than their nearby regions. In contrast, the Afrotropics, subjected to higher aridity and contraction/expansion episodes since the Miocene, may have followed other routes (Anhuf et al. 2006; Igea and Tanentzap 2019; Kissling et al. 2012). This is also appreciated in our results, in which African tropics show lower stability levels and a higher area decrease by its exchange with the temperate zone (especially in the last Ma).

The fact that we found a small effect of generally proposed drivers on global amphibian, bird, and mammal biodiversity also emphasises the likely complexity of factors affecting diversity across landmasses and taxonomic groups (Cerezer et al. 2022). Although we discussed the potential limitations of our variables (further discussion is available in Appendix S3), there are other non-mutually exclusive hypotheses that can be relevant. Ecological hypotheses, focusing on the mechanisms underlying species' coexistence, maintenance, and responses to the environment (e.g. thermal physiologies), may be plausible explanations (Buckley et al. 2012; Lawrence and Fraser 2020). For example, higher productivity and kinetics at lower latitudes would result in more species by increasing speciation and reducing extinction (Brown 2014; Hawkins et al. 2003; Pianka 1966), with some studies focusing on these animal groups pointing in this direction (Fritz et al. 2016; Jetz and Fine 2012). Also, biotic interactions may play an important role (Schemske et al. 2009), and other aspects setting diversification or dispersal constraints may explain the lower diversity of zones such as arid or temperate (Mittelbach et al. 2007). Thus, these constraints would not be directly related to stability or time-area factors, but to other aspects such as niche conservatism or dispersal limits.

Lastly, our approach also suggests that global biodiversity patterns should be examined at broader spatial scales, as the influence of climate (at least within an evolutionary timescale) may not be directly tied to temporal dynamics of local map cells. Instead, a continental-scale assessment would provide insight into how long-term past climatic changes have shaped present-day biodiversity patterns (Gamboa et al. 2024). In conclusion, our study shows that none of the classical hypotheses—age, area, climatic stability—alone can fully explain the high vertebrate tropical richness observed, neither the differences in diversity observed within climate zones. Further investigation, incorporating additional taxa (e.g. invertebrates or plants) to explore the complexity of community assembly rules, or integrating new perspectives (such as the influence of local variations in diversification processes) will expand on the findings of this study and provide a more comprehensive understanding of the factors shaping biodiversity patterns.

Author Contributions

Sofía Galván: data curation; formal analysis; investigation; methodology; software; visualisation; writing – original draft; writing – review and editing. **Sara Varela:** conceptualisation; funding acquisition; investigation; methodology; project administration; resources; supervision; writing – review and editing. **Sara Gamboa:** conceptualisation; data curation; investigation; methodology; software; supervision; visualisation; writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and scripts that support the findings of this study are available in Dryad: https://doi.org/10.5061/dryad.h70rxwdv4.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.