**Heterogeneous geographic patterns of diversity dynamics across terrestrial vertebrates**

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**Abstract**

Diversity is distributed unevenly among lineages and regions and understanding the underlying process generating these global patterns is a key of evolutionary research. Here we use a combined approach to this central question characterizing the global patterns of geographic diversity in four major clades of living amniotes and explicitly incorporating their phylogenetic histories….

Evolutionary and ecological dynamics differ across regions of Earth and across clades of the tree of life.

**Introduction**

Understanding the evolutionary and ecological processes underlying biodiversity patterns has always been a central goal for natural historians and evolutionary biologists (de Candolle 1859; Matthew 1915; Moore 1920; Ruthven 1920; Allee 1926; Dobzhansky 1950; Fischer 1960; MacArthur 1965; Anderson 1974). In particular, the study of global geographic patterns of species diversity has occupied a prominent role in macroecological discussion from the very beginning of evolutionary biology as a discipline paving its way to modern evolutionary theory (Humboldt and Bonpland 1807; Darwin 1859; Wallace 1876). The biodiversity levels in a given geographic area are ultimately determined by three fundamental processes: lineage origination (generally represented by speciation in macroevolutionary studies of extant taxa), extinction, and dispersal (Ricklefs 2004; Mittelbach et al. 2007; Wiens 2011). These three basic generative processes and ultimately, the differences in species richness across geographic and phylogenetic contexts, might be mediated by variations in multiple biotic and abiotic factors operating at regional and local scales (Ricklefs 1987, 2006; Rabosky 2009), such as ecological interactions (Schemske et al. 2009), evolutionary time (Wallace 1878; Stephens and Wiens 2003), the relationship between organismal form and ecology (Heard and Hauser 1995; Freeman et al. 2022), environmental conditions (Currie et al. 2004; Allen et al. 2006), climatic trends (Thompson et al. 2023), or topography and plate tectonics (Hoorn et al. 2010; Badgley et al. 2017; Tejero-Cicuéndez et al. 2022).

In recent years, the emergence and development of what is known as spatial phylogenetics (Earl et al. 2021; Mishler 2023) has fostered the advancement of our understanding of macroecological dynamics by combining phylogenetic relatedness with the study of geographic biodiversity patterns. Specifically, the use of phylogeny-based metrics of biodiversity such as phylogenetic diversity (PD) allows for the investigation of the relatedness of the species that inhabit a given geographic area, such as that high PD values indicate the sympatric presence of distantly related species, while low PD values result from closely related species living together in a given area. The explicit inclusion of the phylogenetic dimension may greatly enhance our ability to understand the combined effects of evolutionary, ecological, and environmental factors acting on diversity dynamics (Davies and Buckley 2011; Tucker et al. 2017), as well as being an essential source of information for conservation purposes (Faith 1992; Redding and Mooers 2006).

In general, species richness and PD are positively correlated: regions showing high and low species richness are expected to have high and low levels of PD, respectively. The reason for this is that, if all the species and clades present at particular regions were subjected to homogeneous and constant diversification and dispersal rates, an increase (or decrease) in the number of species would be reflected in a proportional increase (or decrease) in the number of clades, such that the degree of phylogenetic relatedness would change accordingly and invariably across regions. However, geographic patterns of richness and PD are not necessarily coincidental (Tucker and Cadotte 2013). In other words, there are geographic regions where species are more distantly (high PD) or more closely (low PD) related than would be predicted by the number of species that these regions harbor (Fig. 1). Consequently, deviations from the expected relationship of PD to species richness (residual PD; Velasco and Pinto-Ledezma 2022) and their connection with biotic and abiotic factors are key research areas to further understand the processes underpinning geographic patterns of diversity and to proposing evolutionary scenarios consistent with such patterns.

Therefore, at local or regional scales, deviations from the expected relationship of PD to species richness (residual PD) might indicate the existence of biotic or abiotic factors affecting the community assembly. Low residual PD could reflect a species assembly governed by strong abiotic (e.g., habitat) filtering, leading to the coexistence of a higher proportion of closely related species than expected by the number of species which, considering niche conservatism principles, would presumably be ecologically similar (Romdal et al. 2013; Pyron et al. 2015; Chazot et al. 2021). In contrast, high residual PD may reflect the primacy of biotic (e.g., competition) filtering, resulting in the coexistence of species with different ecological affinities and likely more distantly related phylogenetically (Gause 1934; Hardin 1960; Macarthur and Levins 1967; Chesson 2000; HilleRisLambers et al. 2012).

At broader spatial scales, geographic differences in residual PD may also arise due to differences in the persistence of lineages through time, which can result in some regions having a greater proportion of older, more evolutionarily distinct lineages than other regions. The survivorship of lineages in an area, in turn, can be affected by a variety of factors, such as differences in habitat stability, dispersal events, or diversification rates. More specifically, species assemblages in regions with high residual PD values (i.e., species more distantly related to each other than predicted by species richness) might result from the gradual accumulation of species, either by dispersal from other areas (immigration) or by low levels of speciation and extinction (low turnover rate), acting as a reservoir of ancient lineages. This could reflect what has been commonly known in the evolutionary biology literature as a “museum” or “sanctuary” of biodiversity (Dobzhansky 1950; Stebbins 1974). However, high values of residual PD might also arise owing to a different combination of processes, such as high speciation rates in the past followed by low extinction rates of old lineages, or alternatively, exceptionally high extinction rates of younger lineages. Conversely, regions of low residual PD (i.e., with species more closely related than expected by richness) can result from exceptionally high speciation and extinction rates maintained through time (high turnover rate), which constitute the original conceptualization of a “cradle” of biodiversity (Stebbins 1974). However, low residual PD can also be the result of other scenarios, such as reduced extinction rates of young lineages or increased extinction of older clades.

The multiplicity of scenarios able to generate similar patterns of lineage and phylogenetic diversity highlights the importance of investigating the underlying evolutionary processes beyond solely focusing on elucidating whether specific geographic regions are cradles or museums of biodiversity (Vasconcelos et al. 2022).

The increasing availability of both global distribution and phylogenetic data from species-rich clades allows for the exploration of large-scale diversity patterns and evolutionary processes. For example, in the last decade, the geographic distribution of residual PD has been addressed for the four major clades of living terrestrial vertebrates: mammals (Davies and Buckley 2011), amphibians (Fritz and Rahbek 2012), birds (Voskamp et al. 2017), and squamates (Gumbs et al. 2020; Vásquez-Restrepo et al. 2023).

This wealth of data opens an exciting, but unrealized, opportunity for the detailed comparison of geographic patterns of residual PD across the four major clades of amniotes including critically identifying differences and similarities in the biotic and abiotic factors underpinning global patterns of tetrapod biodiversity. In this study, we characterize geographic patterns of tetrapod species and phylogenetic diversity, and we test hypotheses related to the impact of multiple factors on regional levels of residual PD: recent speciation rates, evolutionary time, and environmental conditions. This allows us to identify key regions with different patterns of geographic diversity across tetrapod clades and shed light on the different processes underlying these patterns. Beyond informing our understanding of evolutionary dynamics producing global diversity patterns, our study ultimately aims to provide some insight into identifying priorities for conservation strategies in the face of the challenges imposed by the global environmental crisis.

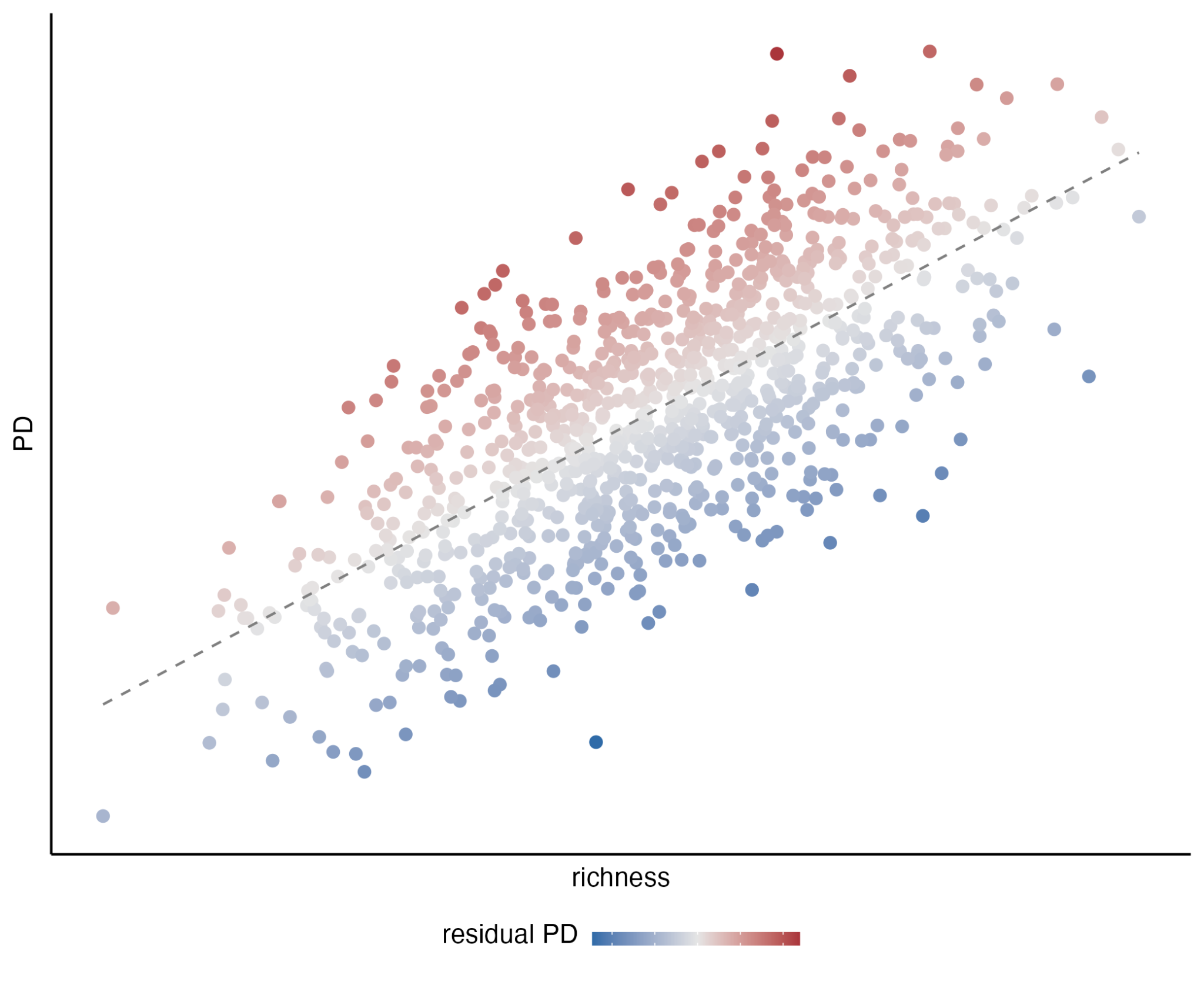


Fig. 1. Schematic representation of the relationship between species richness (X-axis) and phylogenetic diversity (Y-axis), with color representing residual phylogenetic diversity.

**Materials and Methods**

**Vertebrate data**. We obtained distribution vector data for amphibians and terrestrial mammals from IUCN (IUCN 2022), for birds from BirdLife International (http://www.birdlife.org/) and for squamates from Roll et al. (2021). Range maps for all groups were downloaded on 1 May 2022.

Phylogenetic data for all groups were downloaded from VertLife (<https://data.vertlife.org/>). This includes the consensus and posterior phylogenetic trees for amphibians (Jetz and Pyron 2018), birds (Jetz et al. 2012; we used the phylogeny built based on the backbone from Hackett et al. 2008), mammals (Upham et al. 2019), and squamates (Tonini et al. 2016).

After matching both distribution and phylogenetic data, the final datasets contained a total of 28,270 species: 5832 amphibians, 7995 birds, 5164 mammals, and 9279 squamates. These were the datasets used in subsequent analyses.

**Geographic grid and species richness**. For each amniote group, we first produced a hexagonal 100-km-resolution species richness grid using the epm package v1.1.1 (Title et al. 2022) in R 4.3.0 (R Core Team 2023), with the polygon distribution data transformed into an equal-area Behrmann projection as input and the ‘centroid’ approach. The resulting grid contains the information of the species present in each hexagonal cell, and was the base cell grid for all subsequent analyses.

**Residual phylogenetic diversity**. We obtained an average phylogenetic diversity (PD) grid after calculating PD grids for 100 trees from the posterior distribution for each amniote group. These grids were produced with the functions addPhylo and gridMetrics in epm (Title et al. 2022), and they represent the sum of the branch lengths of the phylogenetic tree connecting all species in each cell (Faith’s PD; Faith 1992). We used the R package rlist v0.4.6.2 (Ren 2021) to process the ‘posterior’ grids and ultimately obtaining a grid of average PD values. With the per-grid values of species richness and PD, we performed a local regression analysis (LOESS) and obtained the residuals from it. We then mapped these residuals again onto the original hexagonal grid to visualize the geographic distribution of the deviation of PD relative to richness (residual PD). High residual values indicate high PD for a given number of species (i.e., the species within a grid cell are more distantly related to each other than expected by the species richness of the grid cell), and, conversely, low residual PD indicates that the species present in a grid cell are more closely related to each other than predicted by species richness. To identify focal regions of particularly extreme values of residual PD, we set a threshold at 10% (i.e., lowest residual PD) and 90% (i.e., highest residual PD) from the total distribution of values from each vertebrate clade. We then visually identified regions of interest with contiguous high and low residual PD grid cells to investigate whether there are differences between them in speciation rates, lineage accumulation patterns, and environmental conditions.

**Recent speciation rates**. We estimated recent speciation rates (tip rates) calculating the average DR metric (Jetz et al. 2012) across 100 trees from the posterior distribution for each vertebrate clade. Then, we calculated mean DR values for each hexagonal grid cell. We plotted these per-cell mean DR values in the map and conducted a linear regression model of per-cell mean DR against residual PD (see above). To further understand the links between speciation rates and patterns of geographic diversity, we tested for differences in DR values between species present in regions of highest and lowest residual PD. To do this, we performed linear models with randomized residual permutations with the RRPP package v1.3.1 (Collyer and Adams 2018, 2022), first to globally compare grid cells of high and low residual PD and then to individually compare among the focal regions we identified (see above).

**Evolutionary time and lineage accumulation**. To explore whether there are differences in the age or the lineage accumulation patterns between regions of high and low residual PD, we calculated the number of lineages through time for extreme regions falling within the 10% lowest and 90% highest values of residual PD using the R package ape v5.7.1 (Paradis and Schliep 2019), with the aid of geiger v2.0.11 (Pennell et al. 2014) and phytools v1.5.1 (Revell 2012) for phylogenetic data handling. We then visually compared lineage-through-time (LTT) plots to determine whether our data reflect two main expectations: i) regions of high residual PD should exhibit comparatively older lineages than regions with low residual PD values, which might indicate that these regions acted as reservoirs of ancestral diversity, and ii) the pattern of lineage accumulation might be different between regions of high and low residual PD.

**Environmental variables**. One of the factors that may affect evolutionary processes and therefore shape geographic patterns of biodiversity is the environment in which species live. We tested the relationship between residual PD and different environmental variables: mean annual temperature, temperature seasonality, annual precipitation, precipitation seasonality, net primary productivity (NPP), and terrain roughness index (TRI, a variable representing the topographic complexity). Temperature and precipitation data were collected at a 10-minute spatial resolution (~18.5 km) from the summary data for the period between the years 1970 and 2000 contained in the WoldClim v2.1 dataset (Fick and Hijmans 2017). Net primary productivity data summarized over the period between 1981 and 2015 was obtained at 5-arc-minute resolution from the NDVI3g time series (Pinzon and Tucker 2014). The topography data were based on Wilson et al. (2007) and obtained from the ENVIREM dataset (Title and Bemmels 2018) at a spatial resolution of 10 arc-minutes. For the latter, we compared current topography values with estimated Holocene and Last Glacial Maximum values, and we did not find considerable differences, so we report only the analyses with the current values. All the environmental variables were resampled to match the spatial resolution of the hexagonal cell grid built for species richness and phylogenetic diversity (100 km), so that we could have per-cell values for every variable in order to implement regression models. Additionally, we generated three climatic spaces: one defined by temperature and precipitation, another one defined by temperature seasonality and precipitation seasonality, and a third one defined by NPP and TRI, and mapped the grid cells with lowest and highest 10% of the residual PD onto those climatic spaces to explore for potential segregation between them. Finally, we also explored how residual PD is distributed across the latitudinal gradient, to compare residual PD patterns with species richness.

**Results**

**Geographic patterns of residual phylogenetic diversity.** We found some regions with consistent patterns of residual PD across all four tetrapod clades (Supp. Fig. 1). The African continent harbors overall high residual PD (i.e., individual species more distantly related to each other than expected for the species richness of the assembly) for all the four amniote clades, except for the Sahara Desert for mammals and the rainforest in central Africa for squamates. Conversely, large areas of South America contain low residual PD (species more closely related to each other than predicted by the species richness of the assembly) for all clades. In fact, Africa and South America constitute focal regions of highest and lowest residual PD, respectively, for all vertebrate clades (Fig. 2).

On the other hand, some geographic regions exhibit very contrasting patterns of residual PD among the four amniote clades. Australia is a low-residual-PD region for amphibians and especially squamates, while it harbors high residual PD for birds and mammals. Residual PD in the Indomalayan region is generally high for birds and squamates but relatively low for amphibians, while for mammals it is a very heterogeneous area with high levels in India but regions of low and high levels in Southeast Asia. North America is a region of low residual PD for birds and squamates, and of relatively high residual PD for amphibians. For mammals, there is a clear segregation in residual PD patterns between eastern (high values) and western (low values) North America. Eurasia is also a heterogeneous region across vertebrates, with generally low levels of residual PD for mammals and birds, high levels for amphibians, and areas of high and low levels for squamates. The Arabian Peninsula contains exclusively high levels of residual PD for squamates, but for mammals and birds it shows relatively low levels across the interior and high levels in the mountainous regions of the south and west (Supp. Fig. 1).

**The effect of speciation rates**. We found a statistically significant negative relationship between recent speciation rates and residual PD for all vertebrate clades (*P* <<< 0.001; Fig. 3). In other words, lineages exhibit in average higher recent speciation rates in regions of low residual PD (i.e., regions where species are more related to each other than predicted by the richness of the assembly), while regions of high residual PD have in general lower speciation rates. However, this negative relationship was found to be somewhat weak - with low R2 and slope coefficient values - and variable among clades (Supp. Table 1; R2amphibians = 0.005, R2birds = 0.047, R2mammals = 0.076, R2squamates = 0.13).

For all clades, we found significantly lower speciation rates in the lineages present in grid cells with the lowest residual PD relative to those present in cells with the highest residual PD (*P* = 0.001 in all cases), especially for squamates, although, attending to the effect sizes (*Z*) and the overall distribution of DR values, this difference appears to be mild (Fig. 4).

Likewise, we found significant differences in species’ DR rates among focal regions of highest and lowest residual PD, with low residual PD broadly corresponding to higher speciation rates, but these differences are overall not prominently apparent (Supp. Fig. 2, Supp. Table 2). Furthermore, we did not find clearly greater differences in DR effect size (*Z*) between focal regions of highest and lowest residual PD than between different regions of high residual PD and between different regions of low residual PD (*P* = 0.467; Supp. Fig. 3), indicating that the differences in DR rates between regions of high and low residual PD, though significant, are not of large magnitude.

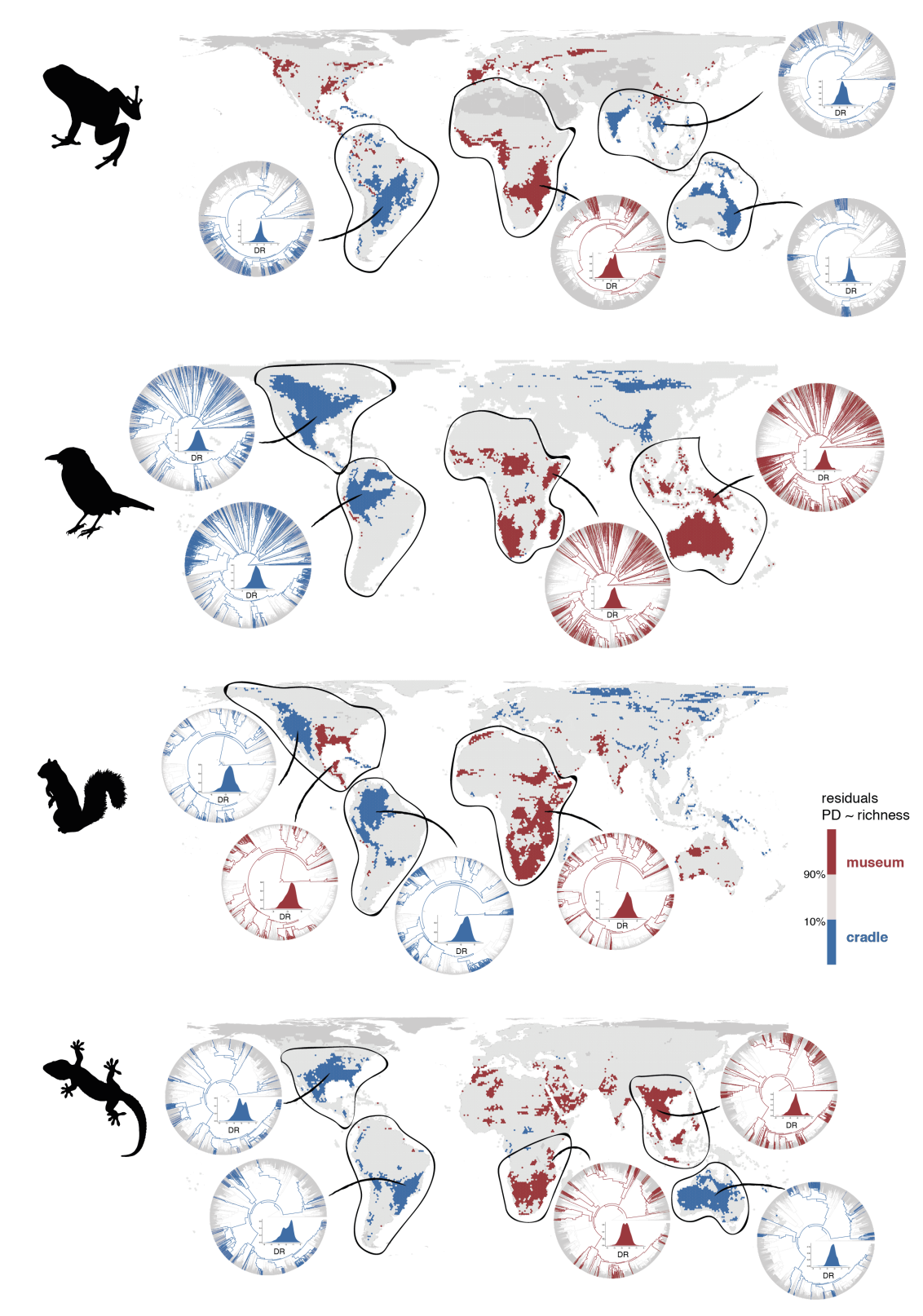


Fig. 2. Geographic distribution of areas with the 10% lowest (in blue) and highest (in red) residual PD for terrestrial vertebrates. The phylogenetic relationships of species present in focal regions are also shown to illustrate the evolutionary differences of regions with high and low residual PD. Silhouettes extracted from 'phylopic' (www.phylopic.org).

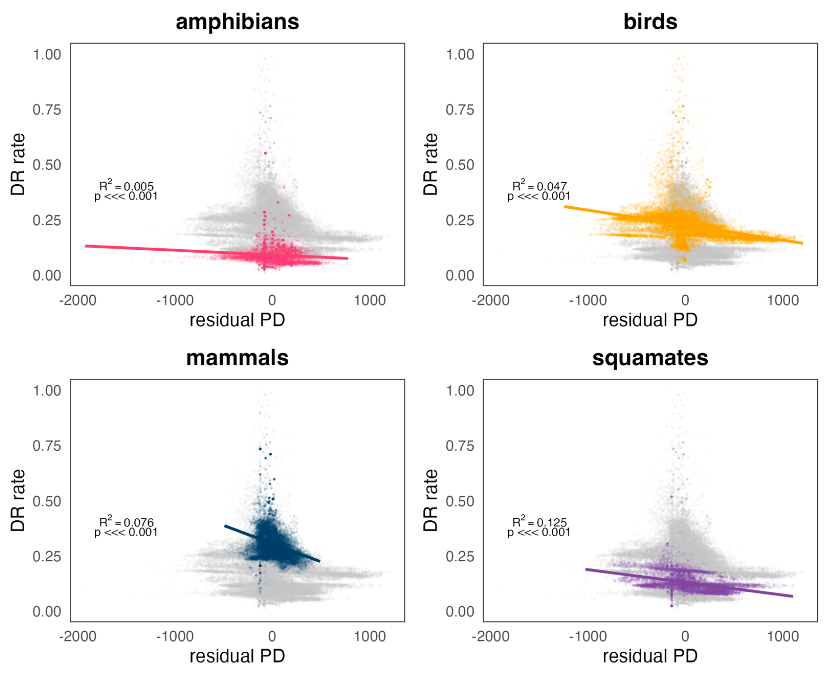


Fig. 3. Relationship between DR rates (recent speciation rates) and residual PD for all four clades of terrestrial vertebrates.

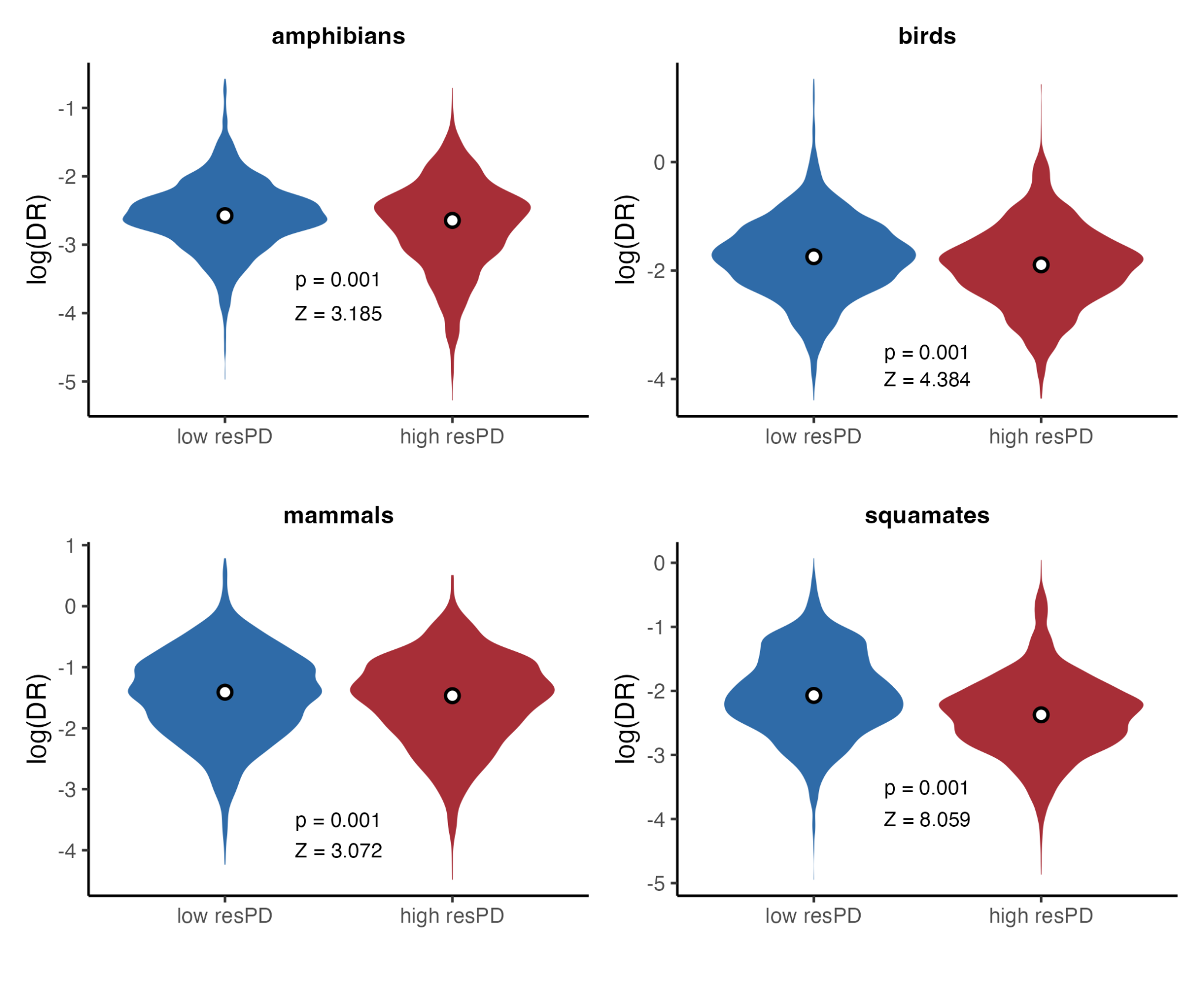


Fig. 4. Differences in DR rates (recent speciation rates) between areas of 10% lowest (in blue) and highest (in red) residual PD.

**Evolutionary time and lineage accumulation**. We did not find notable differences between focal regions of high and low residual PD in the time of origin or the pattern of accumulation of the lineages they harbor (Supp. Figs. 4-7). Specifically, we did not find the expected older age in regions of high residual PD, and the pace of lineage accumulation is also not clearly distinguishable between regions of both types. Even though some regions of low residual PD do harbor younger diversity than regions of high residual PD (e.g., amphibians in Oceania relative to amphibians in Africa, Supp. Fig. 4), this is the opposite in other cases (e.g., mammals in high residual PD Africa have actually younger ancestors than in low residual PD regions of North and South America, Supp. Fig. 6), and in most cases the age of origin of the lineages leading to the current species is similar in regions of high and low residual PD.

**Environmental variables**. We found an overall low to no linear relationship between residual PD and environmental variables (Supp. Figs. 8-13). There is a negative but very weak relationship between annual precipitation and residual PD for all groups (Supp. Fig. 8), while the relationship with mean annual temperature is negative for amphibians and positive for the rest of vertebrate clades (Supp. Fig. 9), with mammals showing the highest amount of residual PD variance explained in both cases (precipitation R2mammals = 0.017; temperature R2mammals = 0.138). For precipitation seasonality and temperature seasonality, amphibians show an opposite trend to that of the other clades, although the variance explained is very low overall (Supp. Figs. 10 and 11). In amphibians, the correlation of residual PD with precipitation seasonality is negative (Supp. Fig. 10) and with temperature seasonality positive (Supp. Fig. 11), while for the rest of vertebrates these correlations are positive and negative, respectively. There is an extremely low correlation of residual PD with net primary productivity (NPP) for all clades (Supp. Fig. 12). With current topographic complexity (terrain roughness index, TRI), the correlation is also very low overall, but there is a somewhat clearer negative trend in birds and mammals (Supp. Fig. 13).

However, in the environmental space defined by mean annual temperature and annual precipitation, we found some segregation between regions of low and high PD for birds and mammals, but substantial overlap for amphibians and squamates (Fig. 5). In both birds and mammals, extremely low residual PD regions are characterized by two combinations: low precipitation with low to moderate temperature (which roughly correspond to areas of tundra, cold deserts and temperate grasslands; Whittaker 1975), and high precipitation with high temperature (i.e., tropical rainforest and savannah). Most of the high residual PD regions for birds and mammals, on the other hand, are found in environments with both low to moderate precipitation and high temperature (i.e., subtropical desert and savannah). However, highest residual PD regions for birds, unlike in mammals, are also found in areas with high precipitation and temperature (i.e., tropical rainforest and savannah).

The patterns of distribution of regions with high and low residual PD across the environmental space defined by precipitation seasonality and temperature seasonality, or by NPP and TRI, do not follow clearly interpretable trends, and there is not an apparent segregation of high and low residual PD regions in neither of them (Supp. Figures 14 and 15), except perhaps for birds in the climate seasonality space, where high residual PD regions tend to be at lower temperature seasonality than regions of low residual PD (Supp. Fig. 14). Likewise, there is not an apparent latitudinal gradient in residual PD for any vertebrate clade, in contrast to species richness (Supp. Fig. 16). Notably, although there appears to be no clear relationship between richness and residual PD (which is expected given that richness and PD are highly correlated), for birds regions of high richness across different latitudinal bands coincide with low residual PD levels (Supp. Fig. 16).

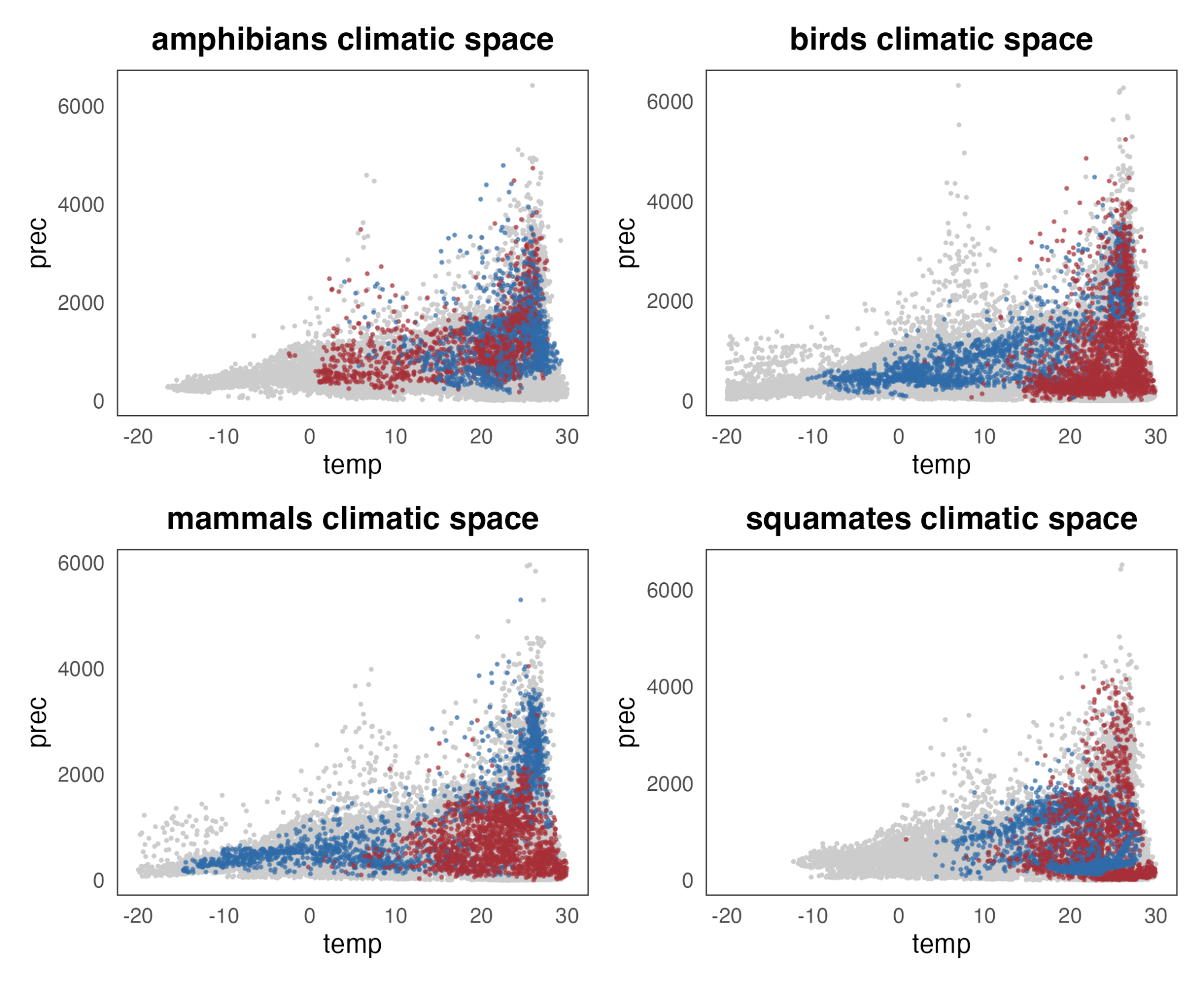


Fig. 5. Climatic space (mean annual temperature vs. annual precipitation) occupied by regions of highest (in red) and lowest (in blue) residual PD for each vertebrate clade.

**Discussion**

Our results shows that the integration of phylogenetic metrics with the analysis of global geographic patterns of diversity in amniotes, enables a more holistic approach to exploring the evolutionary and ecological processes underlying current spatial patterns of biodiversity. Here we addressed the global geographic distribution of richness-corrected phylogenetic diversity (residual PD) for four major terrestrial vertebrate clades (amphibians, birds, mammals, and squamates).

We identified the areas of greatest concentration of high and low residual PD and found entire regions with consistently low (more closely related species than predicted by their species assemblage richness) and high levels (more distantly related species than predicted) for all four groups (Fig. 2). Furthermore, we found a negative but weak relationship of recent speciation rates with residual PD (Figs. 3 and 4), indicating some role, though limited, of recent speciation events in generating global biogeographic patterns. Finally, our results show low to no effect of evolutionary time and most climatic variables on the differentiation of regions with highest and lowest residual PD (Fig. 5), although some tantalizing differences between homeotherms (birds and mammals) and poikilotherms (amphibians and squamates) in the temperature and precipitation of regions with highest and lowest values of residual PD might point to some role of species thermal physiology in defining the global patterns of diversity in amniotes.

We found that the American continent is consistently a region of low residual PD (species in regional assemblages are more closely related than expected by their richness) across vertebrate clades and Africa consistently harbors high levels of residual PD (species more distantly related than expected) for all groups. Previous work on mammals (Davies and Buckley 2011) suggested that the high residual PD found in Africa might reflect that many of the extant mammal clades have an African origin (Lillegraven et al. 1987). While this is a plausible explanation, it does not explain the pervasiveness of this biogeographic pattern across major terrestrial vertebrate clades with very disparate biogeographic origins and might indicate common factors related with the environmental and geologic histories of this region. Similarly, America, and particularly South America, exhibits low levels of residual PD relative to the consistently high values in Africa for all groups (Fig. 2) which might be connected with the recent diversification of multiple current clades following migrations after the formation of the Isthmus of Panama and coupled with the extinction of ancient endemic lineages (Webb 1976; Weir et al. 2009; Davies and Buckley 2011; Carrillo et al. 2020). This is also consistent with the ubiquitous negative relationship observed between residual PD and recent speciation rates which, although weak, reflects that recent speciation is likely one of the processes governing the geographic dimension of vertebrate diversity dynamics (Fig. 3). Taken together, these results might point at recent climatic or geographic events (e.g., reconfiguration of continents) as a primary driver of spatial patterns of diversity dynamics in some regions by affecting, at least in part, recent levels of speciation.

Despite overall patterns, there is a multiplicity of processes that can drive global patterns of residual PD, and the specific generative processes underlying such patterns are likely variable from one region to another and among different taxonomic groups (Davies and Buckley 2011). Specifically, the heterogeneity in residual PD patterns among vertebrate groups in other parts of the world (e.g., Eurasia and Australia; Fig. 2) indicates that species’ intrinsic characteristics (i.e., physiological, ecological, or morphological) might also have a role in the generation of the observed clade-specific geographic patterns. For example, the Malay Archipelago shows especially high residual PD for birds relative to the other vertebrates, while parts of Australia present low residual PD for amphibians and squamates but high residual PD for mammals and especially birds (Fig. 2). One explanation for these differences may reside in the ecological and functional differences among clades, which may have determined their biogeographic and evolutionary history. The high vagility of birds, which enabled the repeated colonization of the islands in Southeast Asia and Australia (Jønsson and Fjeldså 2006; Sheldon et al. 2015), might be the cause of the higher values of residual PD found in the region for this clade resulting from the arrival and relictual permanence of lineages with different phylogenetic origins (Jønsson et al. 2007), as opposed to isolated radiations which might be more frequent in organisms with lower dispersal abilities (Inger and Voris 2001; Siler et al. 2012). High residual PD of squamates in this area might be related to multiple waves of island colonization during intervals of low sea levels and environmental change (How and Kitchener 1997; Voris 2000; Brown et al. 2013; Husson et al. 2020), although this also affected mammals (Van Den Bergh et al. 2001; Meijaard 2003; Mercer and Roth 2003) and amphibians (Brown et al. 2013), which do not show comparable patterns of residual PD (perhaps due to a greater effect of environmental fluctuations promoting turnover in these taxa; e.g., Wilting et al. 2012).

On the other hand, the low residual PD of squamates in arid Australia, and of amphibians in the temperate woodlands of the northern and eastern coasts of Australia, is likely the result of a few extensive radiations (see the phylogenetic trees in Fig. 2) facilitated by the adaptation to the environmental conditions and specialization within those biomes, which have led to a community assembly driven by proportionally more closely related species (Pianka 1981; Rabosky et al. 2007; Skinner et al. 2011; Vidal-García and Keogh 2015; Brennan et al. 2023). Finally, geographic patterns of residual PD might also be partially generated by ancient evolutionary lineages that inhabit certain regions. This could be the case of dibamid reptiles in Southeast Asia (Townsend et al. 2011), palaeognath birds in Australia (Yonezawa et al. 2017), or marsupial mammals in Australia and North America (May-Collado et al. 2015).

Apart from differences in trait- and environment-mediated speciation and dispersal, extinction might also be a major driver of diversity, diversification and biogeographic patterns (Jablonski 2001; Seeholzer and Brumfield 2023). Specifically, extinction events are known not only to underlie current patterns of species richness (Pyron 2014a; Meseguer and Condamine 2020) but also to importantly affect other facets of biodiversity (Erwin 2008; Pimiento et al. 2020; Brocklehurst et al. 2021). Extinction might both increase and decrease phylogenetic diversity, depending on the age of the lineages more prone to experience extinction (Daru et al. 2017). High residual PD regions might result from the higher extinction rates of species from relatively recent radiations, mainly reducing species assemblages to taxa with more distant evolutionary relationships, while low residual PD may arise in regions where extinction2 rates are higher for relatively old diversity (Vasconcelos et al. 2022). The exploration of extinction dynamics and, critically, the inclusion of fossil data (which allows to better estimate extinction and critically, deeper speciation events), will help to further disentangle the factors underlying this and other geographic patterns of vertebrate diversity.

The variety of factors that might be generating residual PD geographic patterns is consistent with previous results indicating that the distribution of diversity is strongly subjected both to extrinsic (e.g., the paleogeographic history) and intrinsic (e.g., ecomorphological or niche-related) factors (Pyron 2014b; Menéndez et al. 2021). In this sense, mountainous regions (an universally recognized driver of diversity and evolutionary processes; Hoorn et al. 2010; Rahbek et al. 2019; Perrigo et al. 2020) can have very different ecological roles depending on how the species’ ecological preferences relate to environmental features. Namely, they can act as a source of new diversity, promoting speciation due to habitat diversity across an elevational gradient (especially in the tropics; Cadena et al. 2011) or constituting dispersal barriers (e.g., Miller et al. 2008), and they have also been reported as important refugia and reserves of cold- or humid-adapted diversity during periods of climate warming and aridification events (Hampe and Jump 2011; Fjeldså et al. 2012). Likewise, deserts, which have been recurrently considered sinks of diversity (i.e., regions harboring distantly related species due to a lack of within-system diversification; Crisp et al. 2009) might in fact harbor low levels of residual PD, like the Australian deserts for squamates and the North American deserts for birds, mammals and squamates (Fig. 2), which in many cases might reflect large radiations of certain clades adapted to the arid conditions (e.g., Wiens et al. 2013; Rabosky et al. 2014). This ecological versatility of physiographic features might be responsible for the lack of a clear relationship between environmental variables and residual PD (Supp. Figs. 8-13), although some segregation is apparent in the climate space between the regions of highest and lowest residual PD, especially in birds and mammals (Fig. 5), which might be explained by fundamental physiological differences between endotherms and ectotherms (Buckley et al. 2012).

Additionally, the fact that multiple processes can lead to similar patterns of residual PD probably explains why we did not find a straightforward effect of evolutionary time or lineage accumulation dynamics on the differences between regions of highest and lowest residual PD (Supp. Figs. 4-7). While time has been reported as a primary driver of diversity gradients in some systems (e.g., Miller and Román-Palacios 2021) and might be reflected in age differences among biotas in different regions (ref?), here we did not find the expected relationship between more closely related species assemblages (low residual PD) and younger origination ages. Likewise, a differential pattern of lineage accumulation between regions of high and low residual PD would be a plausible expectation. Specifically, as potential scenarios, we could expect a relatively linear or constant accumulation of species in regions of high residual PD, maybe resulting in the maintenance of ancient lineages, while in regions of low residual PD we might expect a community build-up marked by alternating periods of high diversification and stasis in lineage dynamics. However, our results show an ambiguous pattern in this respect, without a clear segregation between regions of low and high residual PD. This, together with the mild differences in recent speciation between species from low and high residual PD regions (Figs. 3 and 4), might be an indicative that the phylogenetic patterns of extant species alone cannot account for the evolutionary dynamics we found across vertebrate clades, which in turn suggests that dispersal and/or deep-time diversification might be key for understanding these results (and therefore highlights the need of fossil data to further disentangle diversity dynamics).

The study of phylogenetic diversity patterns and their underlying causes is not only important to understanding how different factors operate and shape the evolutionary history. Our results might also be especially relevant from a conservation perspective. In fact, the need of integrating the evolutionary relationships of the species at the regional scale to inform conservation policies has been stated for decades (Faith 1992), in opposition to conservation approaches that solely focus on hotspots of species richness and geographic endemism (Myers et al. 2000). The geographic deviations of phylogenetic diversity from species richness (i.e., patterns of residual PD) might provide essential information to develop proper conservation strategies. Regions with highest residual PD maximize the conservation of phylogenetically distinct lineages, helping to preserve larger portions of the evolutionary history of entire clades. However, it might not be sufficient to prioritize those areas, since regions with lowest residual PD, on the other hand, potentially act like sources of diversity, where new species are originating (Meseguer et al. 2020). Thus, combining the conservation of regions both with high and low residual PD might be an effective way to attend to past as well as future diversification arenas. Considering additional factors, such as the stability or turnover of communities, and therefore the degree of opportunity for their permanence or demise, might prove a critical practice to integrate in the decision of where to invest conservation resources. Studying geographic patterns of diversity dynamics is the baseline to carry out these practices, which in turn might stand as the only valid approach to mitigate the effects of the undergoing global environmental change.

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