



## Geographic patterns of living tetrapod diversity reveal the signature of global diversification dynamics

Journal:	<i>Global Change Biology</i>
Manuscript ID	Draft
Wiley - Manuscript type:	Research Article
Date Submitted by the Author:	n/a
Complete List of Authors:	<p>Tejero-Cicuéndez, Héctor; Universidad Complutense de Madrid, Biodiversity, Ecology and Evolution</p> <p>Menéndez, Iris; Museum für Naturkunde - Leibniz-Institut für Evolutions- und Biodiversitätsforschung</p> <p>Steell, Elizabeth; University of Cambridge; University College London</p> <p>Navalón, Guillermo; University of Cambridge</p> <p>Blanco, Fernando; University of Gothenburg; Gothenburg Global Biodiversity Centre; Museum für Naturkunde - Leibniz-Institut für Evolutions- und Biodiversitätsforschung</p> <p>Šmíd, Jiří; Charles University; Národní muzeum</p>
Keywords:	phylogenetic diversity, species richness, biodiversity patterns, tetrapods, speciation
Abstract:	<p>Biodiversity is distributed unevenly among lineages and regions, and understanding the processes generating these global patterns is a central goal in evolutionary research, particularly in light of the current biodiversity crisis. Here, we integrate phylogenetic relatedness with species diversity patterns in four major clades of living tetrapods (amphibians, squamates, birds and mammals) to approach this challenge. We studied geographic patterns of richness-corrected phylogenetic diversity (residual PD), identifying regions where species are phylogenetically more closely or distantly related than expected by richness. We explored the effect of different factors in residual PD: recent speciation rates, temporal trends of lineage accumulation, and environmental variables. Specifically, we searched for evolutionary and ecological differences between regions of high and low residual PD. Our results reveal a nuanced relationship between recent speciation rates and residual PD, underscoring the role of recent speciation events in structuring current biogeographic patterns. Furthermore, we found differences between endothermic and ectothermic tetrapods in response to temperature and precipitation, highlighting the pivotal role of thermal physiology in shaping diversity dynamics. By illuminating the multifaceted factors underpinning global diversity patterns, our study represents a significant advancement towards more effective and holistic conservation approaches that are crucial to facing ongoing environmental challenges.</p>



# **Geographic patterns of living tetrapod diversity reveal the signature of global diversification dynamics**

Héctor Tejero-Cicuéndez<sup>1\*</sup>, Iris Menéndez<sup>2</sup>, Elizabeth M. Steell<sup>3,4</sup>, Guillermo Navalón<sup>3</sup>,  
Fernando Blanco<sup>2,5,6</sup>, Jiří Šmíd<sup>7,8</sup>

<sup>1</sup>Department of Biodiversity, Ecology and Evolution, Faculty of Biology, Universidad Complutense de Madrid, Madrid, Spain

<sup>2</sup>Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University Berlin, 10115 Berlin, Germany

<sup>3</sup>Department of Earth Sciences, University of Cambridge, Cambridge, United Kingdom

<sup>4</sup>Department of Earth Sciences, University College London, London, United Kingdom

<sup>5</sup>Department of Biological and Environmental Sciences, University of Gothenburg, Medicinaregatan 18, 405 30 Gothenburg, Sweden

<sup>6</sup>Gothenburg Global Biodiversity Centre, Box 461, Gothenburg, Sweden

<sup>7</sup>Department of Zoology, Faculty of Science, Charles University, Prague, Czech Republic

<sup>8</sup>Department of Zoology, National Museum, Prague, Czech Republic

\*Correspondence: hetejero@ucm.es

**Abstract**

Biodiversity is distributed unevenly among lineages and regions, and understanding the processes generating these global patterns is a central goal in evolutionary research, particularly in light of the current biodiversity crisis. Here, we integrate phylogenetic relatedness with species diversity patterns in four major clades of living tetrapods (amphibians, squamates, birds and mammals) to approach this challenge. We studied geographic patterns of richness-corrected phylogenetic diversity (residual PD), identifying regions where species are phylogenetically more closely or distantly related than expected by richness. We explored the effect of different factors in residual PD: recent speciation rates, temporal trends of lineage accumulation, and environmental variables. Specifically, we searched for evolutionary and ecological differences between regions of high and low residual PD. Our results reveal a nuanced relationship between recent speciation rates and residual PD, underscoring the role of recent speciation events in structuring current biogeographic patterns. Furthermore, we found differences between endothermic and ectothermic tetrapods in response to temperature and precipitation, highlighting the pivotal role of thermal physiology in shaping diversity dynamics. By illuminating the multifaceted factors underpinning global diversity patterns, our study represents a significant advancement towards more effective and holistic conservation approaches that are crucial to facing ongoing environmental challenges.

**Keywords:** phylogenetic diversity, species richness, biodiversity patterns, tetrapods, speciation

## Introduction

Clarifying the evolutionary and ecological processes underlying present-day patterns of biodiversity remains a central goal for natural historians and evolutionary biologists<sup>1–11</sup>. In particular, the study of global geographic patterns of species diversity (primarily, species richness) has occupied a prominent role in macroecological discussion since the infancy of evolutionary biology as a discipline<sup>12–14</sup> to modern evolutionary theory (e.g.,<sup>15</sup>). 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<sup>16–18</sup>. These three basic generative processes result in the unequal accumulation of species richness across geographic and phylogenetic contexts. Variations in these three processes may be influenced by differential biotic and abiotic factors operating at regional and local scales<sup>19–21</sup>, such as ecological interactions<sup>22</sup>, evolutionary time<sup>23,24</sup>, the relationship between organismal form and ecology<sup>25,26</sup>, environmental conditions<sup>27,28</sup>, climatic trends<sup>29</sup>, or topography and plate tectonics<sup>30–32</sup>.

In recent years, the emergence and development of spatial phylogenetics<sup>33,34</sup> has advanced our understanding of macroecological dynamics by combining phylogenetic relatedness with geographic biodiversity patterns. Specifically, the use of phylogeny-based metrics of biodiversity, such as Faith's phylogenetic diversity (PD<sup>35</sup>), enables investigations into the geographic distribution of species relatedness by considering the length of the phylogenetic branches connecting all the species present in a region. For instance, high PD values indicate the sympatric presence of distantly related species, while low PD values result from closely related species inhabiting a given geographic area. The explicit inclusion of the phylogenetic dimension may greatly improve our

ability to elucidate the synergistic effects of evolution, ecology, and the environment on diversity dynamics<sup>36,37</sup> in addition to providing an essential source of information for conservation purposes<sup>35,38</sup>.

In most cases, species richness and PD are positively correlated: regions showing high and low species richness have high and low levels of PD, respectively (e.g.,<sup>36,39</sup>). A positive linear relationship between richness and PD is expected under a null scenario of balanced phylogeny and species distributions: 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. This makes species richness a generally good proxy of PD<sup>40</sup>. However, geographic patterns of richness and PD are not necessarily congruent<sup>41</sup>. 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. 1a). These deviations from the expected relationship of PD to species richness (residual PD<sup>42</sup>) are the result of variations in the generative processes (i.e., speciation, extinction, and dispersal) across regions and clades, and therefore studying them is essential to understand the biotic and abiotic factors underpinning geographic patterns of species diversity.

For example, high residual PD values might represent the so-called “museums” or “sanctuaries” of biodiversity<sup>6,43</sup> resulting from the gradual accumulation of species, either by dispersal from other areas (immigration) or by low levels of speciation and extinction

(low turnover rate), but they 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, low residual PD can indicate “cradles” of biodiversity<sup>43</sup> resulting from high speciation and extinction rates maintained through time (high turnover rate), but it can also arise in 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 (e.g., Fig 1b) highlights the importance of investigating the underlying evolutionary processes beyond solely focusing on elucidating whether specific geographic regions are cradles or museums of biodiversity<sup>44</sup>.

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<sup>36</sup>, amphibians<sup>39</sup>, birds<sup>45</sup>, and squamates<sup>46,47</sup>. This wealth of data presents an exciting, but unrealized, opportunity for a detailed comparison of geographic patterns of residual PD across the four major clades of tetrapods, 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 enables the identification of key regions with different patterns of geographic diversity across tetrapod clades that shed light on the different processes underlying these patterns. Beyond informing our understanding of evolutionary

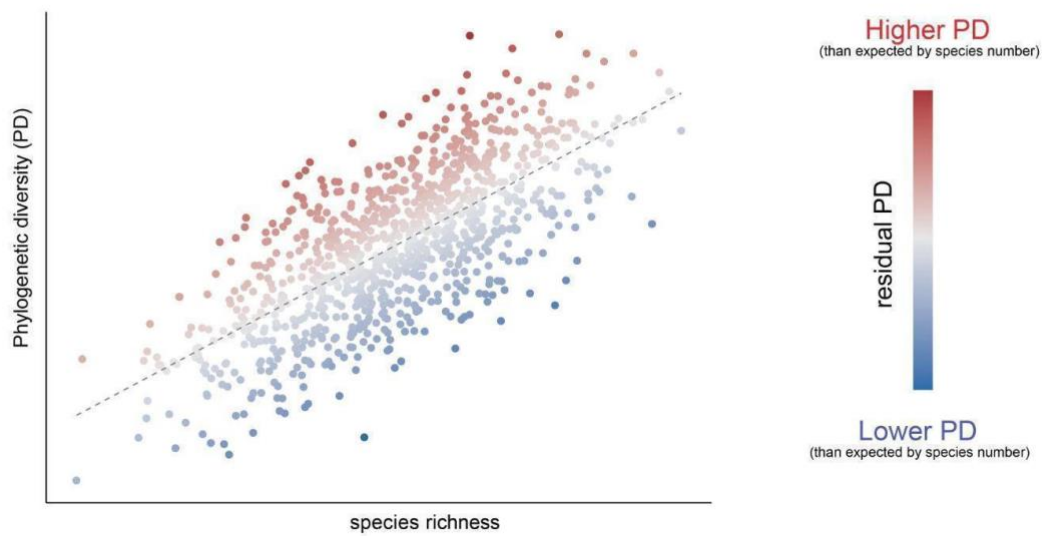
126 dynamics producing global diversity patterns, our study ultimately aims to provide some  
127 insight into identifying priorities for conservation strategies in the face of the challenges  
128 imposed by the global environmental crisis.

129

For Review Only



a) Theoretical relationship between phylogenetic diversity (PD) and species richness



b) Generative processes of phylogenetic diversity (PD)

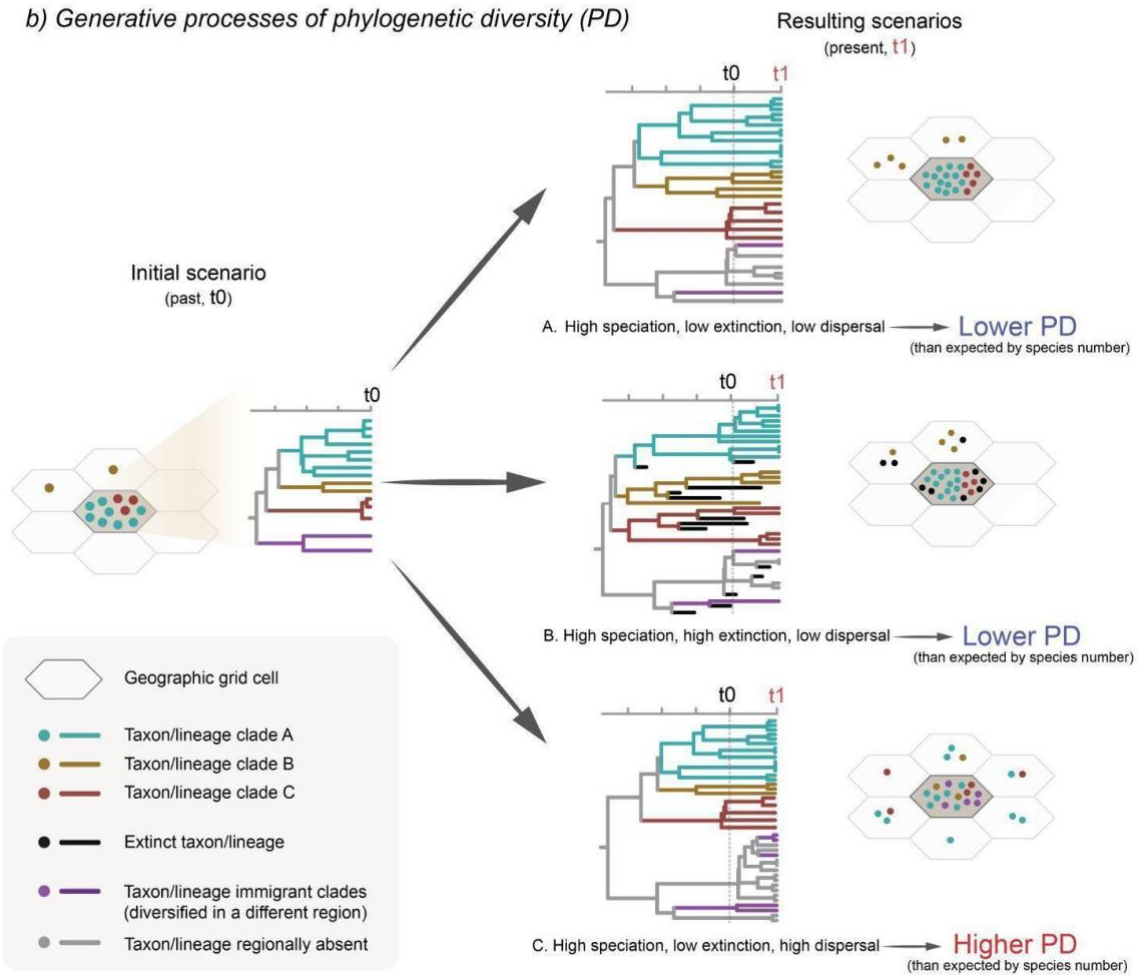


Fig. 1. Theoretical conceptualization of this study. of a) Schematic representation of the relationship between species richness (X-axis) and phylogenetic diversity (Y-axis). Each point represents a geographic grid cell with color representing residual phylogenetic

diversity: in red, the cells with more distantly related species (high PD) and in blue more closely related (low PD) than would be predicted by the number of species that these regions harbor. b) Hypothetical scenarios with different levels of PD produced by different combinations of speciation, extinction, and dispersal.

## Materials and Methods

**Vertebrate data.** We obtained distribution vector data for amphibians and terrestrial mammals from IUCN <sup>48</sup>, for birds from BirdLife International (<http://www.birdlife.org/>) and for squamates from <sup>49</sup>. 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 <sup>50</sup>, birds <sup>51</sup> (backbone from <sup>52</sup>), mammals <sup>53</sup>, and squamates <sup>54</sup>.

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 group, we first produced a hexagonal 100-km-resolution species richness grid using the *epm* package v1.1.1 <sup>55</sup> in R 4.3.0 <sup>56</sup>, 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 tetrapod group. These grids were produced with the functions `addPhylo` and `gridMetrics` in `epm`<sup>55</sup>, and they represent the sum of the branch lengths of the phylogenetic tree connecting all species in each cell (Faith's PD<sup>35</sup>). We used the R package `rlist` v0.4.6.2<sup>57</sup> to process the 'posterior' grids and ultimately obtaining a grid of average PD values. With the per-cell values of species richness and PD, we performed a local regression analysis (LOESS) with a smoothing parameter  $\alpha = 0.75$  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 elevated density of 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<sup>51</sup> 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<sup>58,59</sup>, 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<sup>60</sup>, with the aid of geiger v2.0.11<sup>61</sup> and phytools v1.5.1<sup>62</sup> 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 WorldClim v2.1 dataset<sup>63</sup>. Net primary productivity data summarized over the period between 1981 and 2015 was obtained at 5-arc-minute resolution from the NDVI3g time series<sup>64</sup>. The current topography data were based on<sup>65</sup> and obtained from the ENVIREM dataset<sup>66</sup> at a spatial resolution of 10 arc-minutes. 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 phylogenetic diversity (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 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 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).

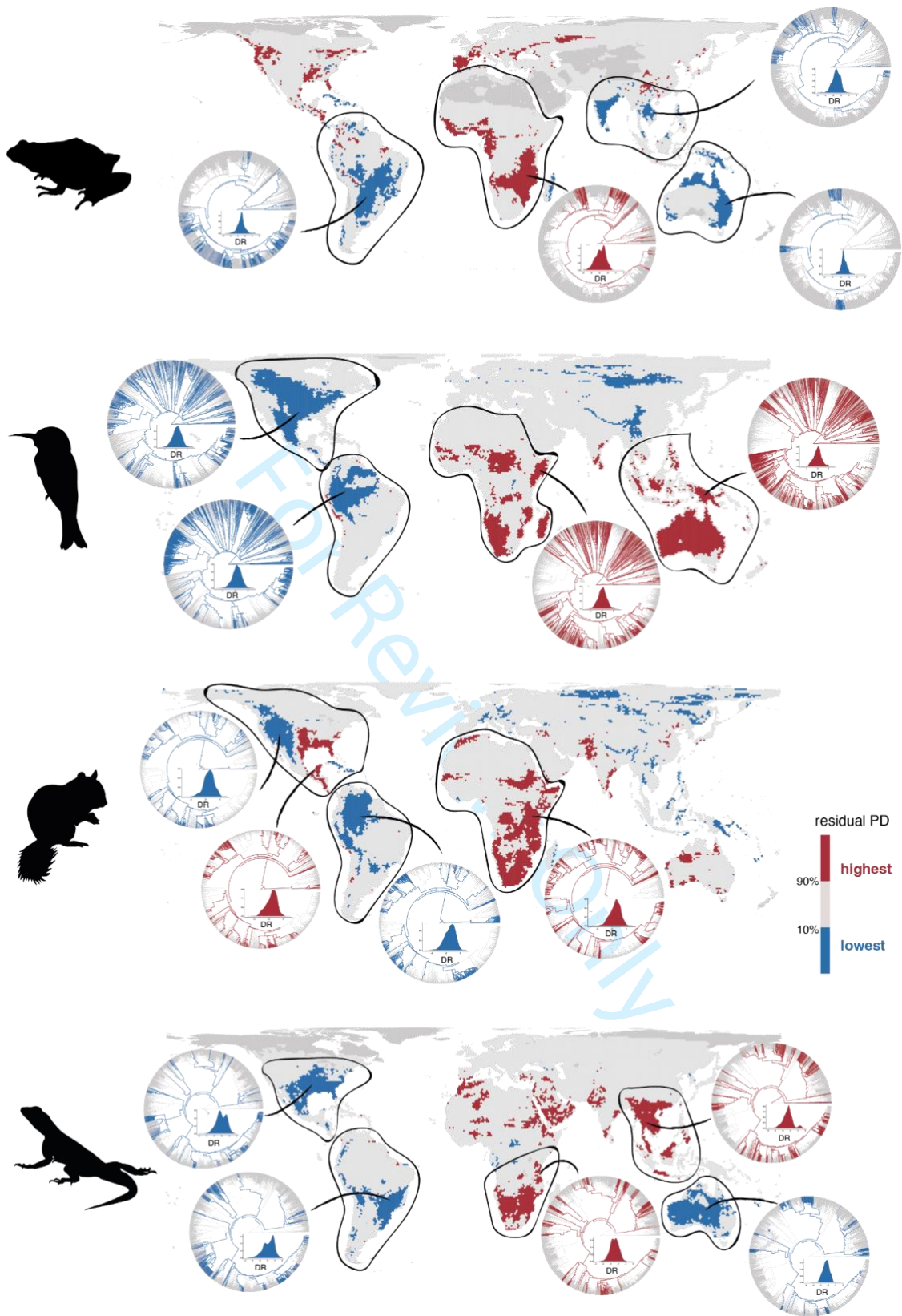
**The effect of speciation rates.** We found a statistically significant negative relationship between recent speciation rates (DR rates) and residual PD for all vertebrate clades ( $P < 0.001$ ; Fig. 3). In other words, lineages exhibit, on average, higher recent speciation rates in regions of low residual 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 generally have lower speciation rates. However, this negative relationship was found to be somewhat weak—with low  $R^2$  and slope coefficient values—and variable among

clades (Supp. Table 1;  $R^2_{\text{amphibians}} = 0.005$ ,  $R^2_{\text{birds}} = 0.047$ ,  $R^2_{\text{mammals}} = 0.076$ ,  $R^2_{\text{squamates}} = 0.13$ ).

When comparing only regions falling in the 10% lowest and 10% highest residuals, 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. Nonetheless, overall, these differences are 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). This indicates that the differences in DR rates between regions of high and low residual PD, though significant, are not of large magnitude.





280

281 Fig. 2. Geographic distribution of areas with the 10% lowest (in blue) and highest (in red)

282 residual PD for terrestrial vertebrates (amphibians, birds, mammals, and squamates). The

283 phylogenetic relationships of species present in focal regions, together with the density



plot of recent speciation rates (DR) of those species, are also shown to illustrate the evolutionary differences of regions with high and low residual PD. Silhouettes by Guillermo Navalón and Sergio M. Nebreda.

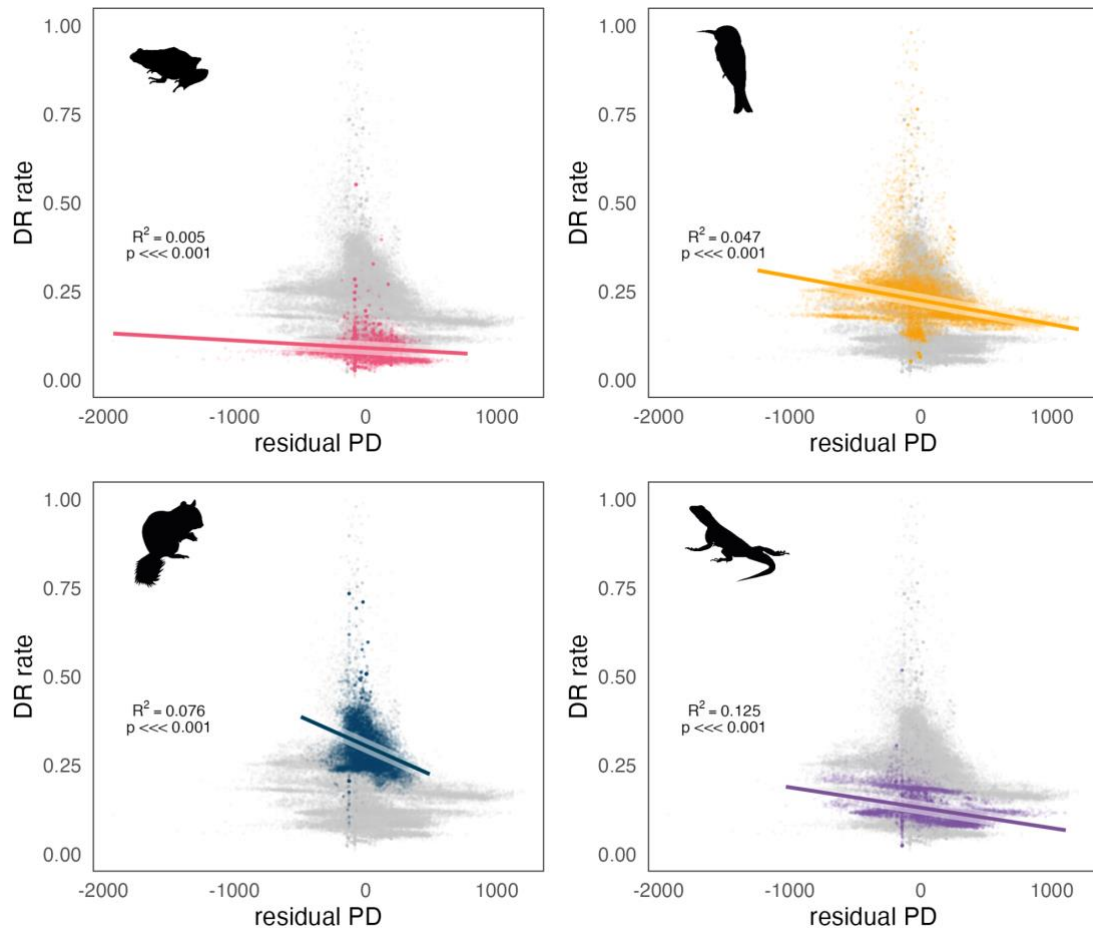


Fig. 3. Relationship between recent speciation rates (DR rates) and residual PD for all four clades of terrestrial vertebrates. The grey cloud of points in the background of each plot shows results for the four vertebrate groups combined.

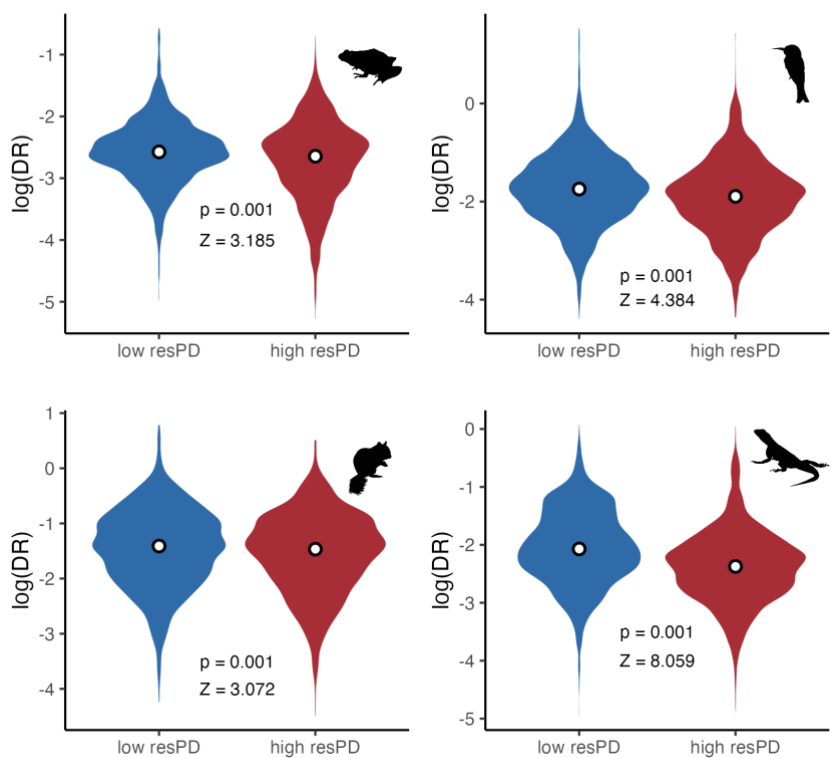


Fig. 4. Differences in recent speciation rates (DR rates) between areas of 10% lowest (in blue) and highest (in red) residual PD.

**The effect of evolutionary time and pattern of 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 lineages in regions of high residual PD to be as old as expected, and the pace of lineage accumulation is also not clearly distinguishable between regions of low and high residual PD. 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 younger ancestors than in low residual PD regions of North and South America, Supp. Fig. 6). In most cases, the age of origin of the

lineages leading to present-day species and the trajectories of the accumulation curves are 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 very weak negative 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  $R^2_{\text{mammals}} = 0.017$ ; temperature  $R^2_{\text{mammals}} = 0.138$ ). 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), whereas it is positive with temperature seasonality (Supp. Fig. 11). 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. There is no apparent segregation between high and low residual PD regions (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 no apparent latitudinal gradient in residual PD for any vertebrate clade, in contrast to species richness (Supp. Fig. 16). Notably, regions of high richness for birds across different latitudinal bands coincide with low residual PD levels (Supp. Fig. 16), although there appears to be no clear relationship between richness and residual PD (which is expected given that richness and PD are highly correlated).

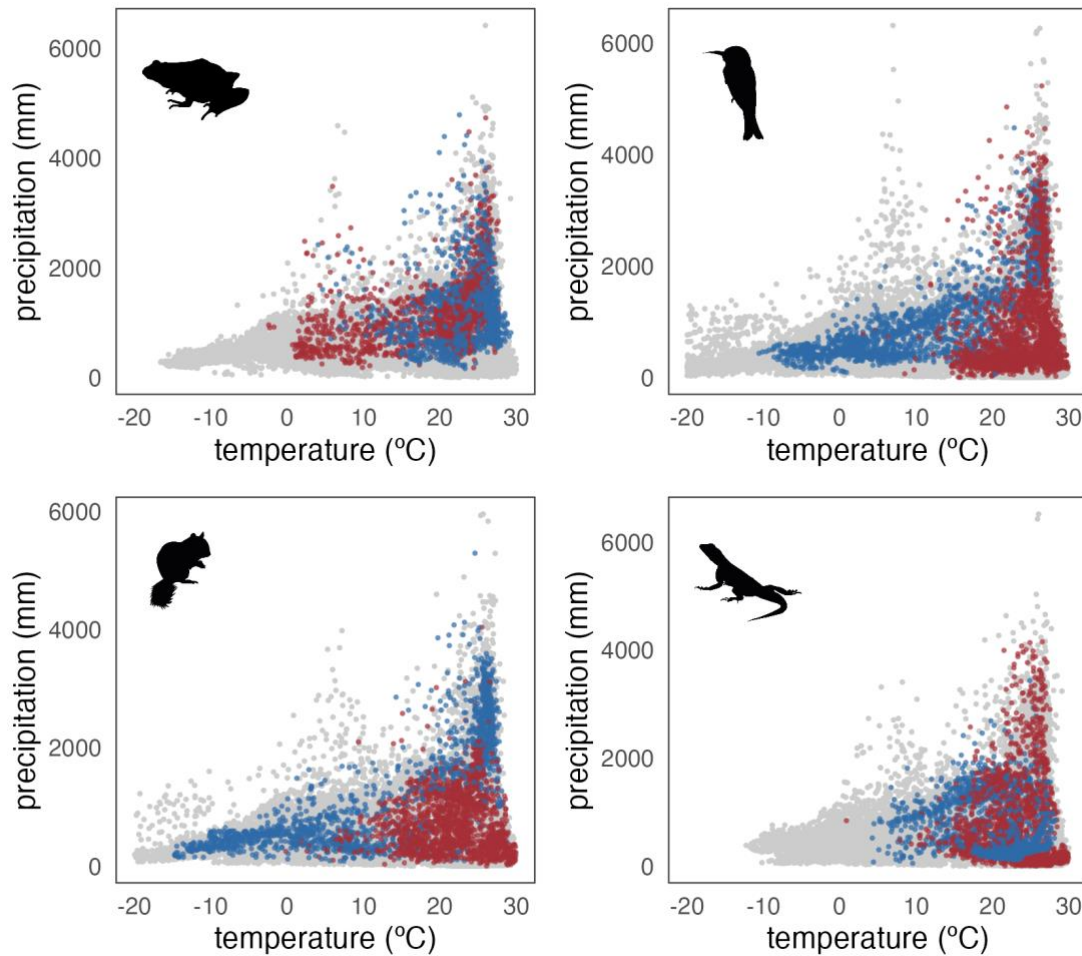


Fig. 5. Climatic space (mean annual temperature vs. annual precipitation) occupied by regions of 10% highest (in red) and lowest (in blue) residual PD for each vertebrate clade. The grey points are grid cells with residual PD values between the 10th and 90th percentiles.

## Discussion

Our results show that the integration of phylogenetic metrics with analyses of global geographic patterns of diversity among terrestrial vertebrates facilitates 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 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 (more distantly related species than predicted) levels for all four tetrapod groups (Fig. 2). Furthermore, we found a slight negative relationship of recent speciation rates with residual PD (Figs. 3 and 4), suggesting that recent speciation events helped generate present-day global biogeographic patterns. Finally, our results show that evolutionary time (i.e., clade/lineage age) as well as most climatic variables had low to no effect on the differentiation of regions with highest and lowest residual PD (Fig. 5). Nonetheless, we identified differences between endotherms (birds and mammals) and ectotherms (amphibians and squamates) when considering temperature and precipitation levels in regions with highest and lowest values of residual PD. This result indicates that thermal physiology may have influenced global diversity patterns among tetrapods.

We found that both American continents are regions of consistently low residual PD, meaning that regional assemblages are composed of species that are more closely related than expected by their richness. This applies to all the studied clades, with the exception of amphibians in North America and mammals in Eastern North America. In contrast, Africa consistently shows high levels of residual PD for all clades; in other words, it harbors species that are more distantly related than expected for all living tetrapods. Previous work on mammals<sup>36</sup> suggested that high residual PD found in Africa may reflect an African origin for many extant mammal clades<sup>67</sup>. While plausible for mammals, this

hypothesis does not explain this pervasive biogeographic patterning in Africa across other major terrestrial vertebrate clades that likely originated on different continents (e.g.,<sup>68,69</sup>), and instead may be indicative of other common factors related to the environmental and geological histories of the African continent. Similarly, the low residual PD for all groups observed in America, particularly in South America (Fig. 2), may have been influenced by recent diversification events in multiple extant clades, particularly following dispersal after the formation of the Isthmus of Panama, and coupled with the extinction of ancient endemic lineages<sup>36,70–72</sup>. 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 may be indicative of recent climatic or geographic events (e.g., reconfiguration of continents) as primary drivers of recent speciation rates that have consequently shaped spatial patterns of extant tetrapod diversity.

In addition to abiotic processes influencing spatial patterning of diversity, biotic factors likely drove some of these observable patterns<sup>36</sup>. In particular, heterogeneous geographic residual PD patterns among clades (e.g., in Eurasia and Australia; Fig. 2) may indicate that intrinsic biological characteristics (i.e., physiological, ecological, or morphological) have played a role in the generation of the observed clade-specific geographic patterns. For example, the Malay Archipelago shows particularly high residual PD for birds relative to other vertebrates, whereas parts of Australia present low residual PD for amphibians and squamates but high residual PD for mammals and birds (Fig. 2). It is plausible that these differences have arisen due to ecological and functional differences among clades, which may have determined their biogeographic and evolutionary history.

413 The high vagility of birds likely contributed to higher residual PD values in Southeast  
414 Asia and Australia due to repeated colonization of islands in these regions <sup>73,74</sup>. In  
415 addition, the high dispersal ability of the majority of birds' main subclades resulted in the  
416 arrival and relictual permanence of lineages with widely different phylogenetic origins <sup>75</sup>,  
417 as opposed to isolated radiations (and, therefore, lower PD), which may be more frequent  
418 in organisms with lower dispersal abilities <sup>76,77</sup>. High residual PD of squamates within  
419 Southeast Asia may be related to multiple waves of island colonization during intervals  
420 of low sea level and environmental change <sup>78-81</sup>, although this also affected mammals  
421 <sup>82-84</sup> and amphibians <sup>80</sup>, which do not show comparable patterns of residual PD (perhaps  
422 due to a greater effect of environmental fluctuations promoting turnover in these taxa;  
423 e.g., <sup>85</sup>).

424  
425 In contrast, the low residual PD of squamates in arid Australia, and of amphibians in the  
426 temperate woodlands of the northern and eastern coasts of Australia, likely resulted from  
427 a few extensive radiations (see the phylogenetic trees in Fig. 2). These radiations may be  
428 facilitated by adaptation and specialization within these unique biomes, leading to  
429 community assembly driven by proportionally more closely related species <sup>86-91</sup>. Finally,  
430 geographic patterns of residual PD may be partially generated by ancient evolutionary  
431 lineages that inhabit certain regions. This could be the case of dibamid reptiles in  
432 Southeast Asia <sup>92</sup>, palaeognath birds in Australia <sup>93</sup>, or marsupial and xenarthran  
433 mammals in Australia and North America, respectively <sup>94</sup>. Additionally, passerine birds,  
434 that comprise ~60% of extant avian diversity, contribute to high residual PD in Australia  
435 due to the presence of numerous endemic lineages that are distantly related in comparison  
436 to the diverse, but generally closely related, passerine lineages inhabiting South America  
437 <sup>95-97</sup> (Fig. 2). These contrasting patterns are somewhat paradoxical considering that



passerines are generally competent fliers, suggesting that there may be additional factors driving spatial diversity patterns among birds.

Previous work has identified that diversity dynamics are strongly influenced by both extrinsic (e.g., the paleogeographic history) and intrinsic (e.g., ecomorphological or niche-related) factors<sup>98–103</sup>. For instance, mountainous regions (a universally recognized driver of diversity and evolutionary processes<sup>30,104,105</sup>) serve multiple functions during biodiversity generation; mountains can promote speciation due to habitat heterogeneity across an elevational gradient (acting as a source of diversity, particularly in the tropics<sup>106,107</sup>), or induce dispersal barriers (e.g.,<sup>108</sup>). Mountains may also generate important refugia and reserves of cold- or humid-adapted diversity during periods of climate warming and aridification<sup>109,110</sup>. 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<sup>111</sup>) may harbor low levels of residual PD, as our results show in Australia for squamates and North America for birds, mammals and squamates (Fig. 2). In many cases, this may reflect large radiations of certain clades adapted to the arid conditions (e.g.,<sup>112,113</sup>). This ecological versatility of physiographic features may 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). This may be explained by fundamental physiological differences between endotherms and ectotherms<sup>114</sup>.

Apart from differences in trait- and environment-mediated speciation and dispersal, extinction may also be a major driver of diversity, diversification and biogeographic

patterns<sup>115,116</sup>. Specifically, extinction events are known not only to underlie current patterns of species richness<sup>117,118</sup>, but also to substantially affect other facets of biodiversity<sup>119–121</sup>. Extinction may both increase and decrease phylogenetic diversity, depending on the age of the lineages that are more prone to extinction<sup>122</sup>. High residual PD regions may result from higher extinction rates of species from relatively recent radiations, mainly reducing species assemblages to taxa with more distant evolutionary relationships, whereas low residual PD may arise in regions where extinction rates are higher for relatively old diversity<sup>44</sup>. The exploration of extinction dynamics and, critically, the inclusion of fossil data (which enables better estimates of extinction and deeper speciation events), will help to further disentangle the factors underpinning geographic patterns of vertebrate diversity. Likewise, our results show no apparent relationship between the residual PD of a region and the age of the biota within it or the pattern of lineage accumulation (Supp. Figs. 4–7), but the inclusion of fossil information would enhance our ability to investigate such a relationship.

Moving forward, our methodology to quantify spatial phylogenetic diversity may help to inform conservation policies beyond the species-richness-hotspot and endemism strategies<sup>123</sup>. Integrating evolutionary relationships at a regional scale has been stated as a necessary step for global conservation efforts for decades<sup>35</sup>. Assessing patterns of residual PD for focal clades would inform on which regions harbor the highest lineage diversity (highest residual PD), facilitating efforts to maximize conservation of phylogenetically distinct lineages and help to preserve larger portions of the evolutionary history of entire clades. Additionally, regions with the lowest residual PD that may be acting as sources of diversity<sup>124</sup> can be considered in conservation initiatives as priority areas in order to safeguard the generation of new biodiversity. Furthermore, integrating

paleontological data into our method would facilitate a novel, multidisciplinary approach for utilizing deep time data for species conservation prioritization<sup>125</sup>.

## Acknowledgments

HT-C is supported by a "Juan de la Cierva - Formación" postdoctoral fellowship (FJC2021-046832-I) funded by MCIN/AEI/10.13039/501100011033 and by the European Union NextGenerationEU/PRTR. IM was funded by the Alexander von Humboldt Foundation through a Humboldt Postdoctoral Fellowship. GN was funded by UKRI grant MR/X015130/1. FB was funded by Gothenburg University via the Swedish Research Council (VR: 2019-04739). JŠ was supported by the Czech Science Foundation (GAČR) under grant number 22-12757S and by the Charles University Research Centre under grant number 204069.

## Competing interests

The authors declare no competing interests.

## Data availability

All data and scripts used will be deposited in a repository for public access and will be made available upon acceptance. Private link for peer review:

[https://datadryad.org/stash/share/gQEWAVjLIvI\\_b9oZEZdFULl4ousSOQojyBW8Kj1c\\_kQ4](https://datadryad.org/stash/share/gQEWAVjLIvI_b9oZEZdFULl4ousSOQojyBW8Kj1c_kQ4)

## 513 **Author contributions (CRediT)**

514 Conceptualization: HT-C, JŠ. Methodology: HT-C, IM, EMS, GN, FB, JŠ. Software: HT-  
 515 C, IM. Formal analysis: HT-C, IM. Data curation: HT-C, JŠ. Writing – Original draft:  
 516 HT-C, IM. Writing – Review and editing: EMS, GN, FB, JŠ. Visualization: HT-C, IM,  
 517 EMS, GN.

518

## 519 **References**

- 520 1. de Candolle, A. L. P. P. On the Causes which Limit Vegetable Species Towards the  
 521 North, in Europe and Similar Regions. *Annual Report of the Board of Regents of the*  
 522 *Smithsonian Institution for the Year 1858* 237–245 (1859).
- 523 2. Matthew, W. D. Climate and evolution. *Annals of the New York Academy of*  
 524 *Sciences* **24**, 171–318 (1915).
- 525 3. Moore, B. The Ecological Society and Its Opportunity. *Science* **51**, 67–68 (1920).
- 526 4. Ruthven, A. G. The Environmental Factors in the Distribution of Animals.  
 527 *Geographical Review* **10**, 241–248 (1920).
- 528 5. Allee, W. C. Distribution of Animals in a Tropical Rain-Forest with Relation to  
 529 Environmental Factors. *Ecology* **7**, 445–468 (1926).
- 530 6. Dobzhansky, T. Evolution in the tropics. *American Scientist* **38**, 209–221 (1950).
- 531 7. Fischer, A. G. Latitudinal variations in organic diversity. *Evolution* **14**, 64–81  
 532 (1960).
- 533 8. MacArthur, R. H. Patterns of Species Diversity. *Biological Reviews* **40**, 510–533  
 534 (1965).
- 535 9. Anderson, S. Patterns of Faunal Evolution. *The Quarterly Review of Biology* **49**,  
 536 311–332 (1974).

- 537 10. Harmon, L. J. An Inordinate Fondness for Eukaryotic Diversity. *PLoS Biology* **10**,  
538 8–11 (2012).
- 539 11. Saupe, E. E. Explanations for latitudinal diversity gradients must invoke rate  
540 variation. *Proceedings of the National Academy of Sciences* **120**, e2306220120  
541 (2023).
- 542 12. Humboldt, A. von & Bonpland, A. *Essai sur la géographie des plantes*. (Schoell,  
543 1807).
- 544 13. Darwin, C. *On the Origin of Species by Means of Natural Selection, or the*  
545 *Preservation of Favoured Races in the Struggle for Life*. (John Murray, 1859).
- 546 14. Wallace, A. R. *The geographical distribution of animals*. (Harper and Brothers,  
547 1876).
- 548 15. Futuyma, D. J. Can Modern Evolutionary Theory Explain Macroevolution? in  
549 *Macroevolution: Explanation, Interpretation and Evidence* (eds. Serrelli, E. &  
550 Gontier, N.) vol. 2 (Springer International Publishing, 2015).
- 551 16. Ricklefs, R. E. A comprehensive framework for global patterns in biodiversity.  
552 *Ecology Letters* **7**, 1–15 (2004).
- 553 17. Mittelbach, G. G. *et al.* Evolution and the latitudinal diversity gradient: Speciation,  
554 extinction and biogeography. *Ecology Letters* **10**, 315–331 (2007).
- 555 18. Wiens, J. J. The causes of species richness patterns across space, time, and clades  
556 and the role of ‘ecological limits’. *Quarterly Review of Biology* **86**, 75–96 (2011).
- 557 19. Ricklefs, R. E. Community Diversity: relative roles of local and regional processes.  
558 *Science* **235**, 167–171 (1987).
- 559 20. Ricklefs, R. E. Evolutionary diversification and the origin of the diversity-  
560 environment relationship. *Ecology* **87**, 3–13 (2006).

- 561 21. Rabosky, D. L. Ecological limits and diversification rate: alternative paradigms to  
562 explain the variation in species richness among clades and regions. *Ecology Letters*  
563 **12**, 735–743 (2009).
- 564 22. Schemske, D. W., Mittelbach, G. G., Cornell, H. V., Sobel, J. M. & Roy, K. Is There  
565 a Latitudinal Gradient in the Importance of Biotic Interactions? *Annual Review of*  
566 *Ecology, Evolution, and Systematics* **40**, 245–269 (2009).
- 567 23. Wallace, A. R. *Tropical nature, and other essays*. (Macmillan and Company, 1878).
- 568 24. Stephens, P. R. & Wiens, J. J. Explaining species richness from continents to  
569 communities: The time-for-speciation effect in emydid turtles. *American Naturalist*  
570 **161**, 112–128 (2003).
- 571 25. Heard, S. B. & Hauser, D. L. Key evolutionary innovations and their ecological  
572 mechanisms. *Historical Biology* **10**, 151–173 (1995).
- 573 26. Freeman, B. G., Weeks, T., Schluter, D. & Tobias, J. A. The latitudinal gradient in  
574 rates of evolution for bird beaks, a species interaction trait. *Ecology Letters* **25**, 635–  
575 646 (2022).
- 576 27. Currie, D. J. *et al.* Predictions and tests of climate-based hypotheses of broad-scale  
577 variation in taxonomic richness. *Ecology Letters* **7**, 1121–1134 (2004).
- 578 28. Allen, A. P., Gillooly, J. F., Savage, V. M. & Brown, J. H. Kinetic effects of  
579 temperature on rates of genetic divergence and speciation. *Proceedings of the*  
580 *National Academy of Sciences of the United States of America* **103**, 9130–9135  
581 (2006).
- 582 29. Thompson, J. B., Davis, K. E., Dodd, H. O., Wills, M. A. & Priest, N. K. Speciation  
583 across the Earth driven by global cooling in terrestrial orchids. *Proceedings of the*  
584 *National Academy of Sciences* **120**, e2102408120 (2023).

- 585 30. Hoorn, C. *et al.* Amazonia Through Time: Andean Uplift, Climate Change,  
586 Landscape Evolution, and Biodiversity. *Science* **330**, 927–931 (2010).
- 587 31. Badgley, C. *et al.* Biodiversity and Topographic Complexity: Modern and  
588 Geohistorical Perspectives. *Trends in Ecology and Evolution* **32**, 211–226 (2017).
- 589 32. Tejero-Cicuéndez, H. *et al.* Reconstructing Squamate Biogeography in Afro-Arabia  
590 Reveals the Influence of a Complex and Dynamic Geologic Past. *Systematic Biology*  
591 **71**, 261–272 (2022).
- 592 33. Earl, C. *et al.* Spatial phylogenetics of butterflies in relation to environmental drivers  
593 and angiosperm diversity across North America. *iScience* **24**, 102239 (2021).
- 594 34. Mishler, B. D. Spatial phylogenetics. *Journal of Biogeography* **50**, 1454–1463  
595 (2023).
- 596 35. Faith, D. P. Conservation evaluation and phylogenetic diversity. *Biological*  
597 *Conservation* **61**, 1–10 (1992).
- 598 36. Davies, T. J. & Buckley, L. B. Phylogenetic diversity as a window into the  
599 evolutionary and biogeographic histories of present-day richness gradients for  
600 mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*  
601 **366**, 2414–2425 (2011).
- 602 37. Tucker, C. M. *et al.* A guide to phylogenetic metrics for conservation, community  
603 ecology and macroecology. *Biological Reviews* **92**, 698–715 (2017).
- 604 38. Redding, D. W. & Mooers, A. O. Incorporating evolutionary measures into  
605 conservation prioritization. *Conservation Biology* **20**, 1670–1678 (2006).
- 606 39. Fritz, S. A. & Rahbek, C. Global patterns of amphibian phylogenetic diversity.  
607 *Journal of biogeography* **39**, 1373–1382 (2012).
- 608 40. Rodrigues, A. S. L., Brooks, T. M. & Gaston, K. J. Integrating phylogenetic  
609 diversity in the selection of priority areas for conservation: does it make a

- 610 difference? in *Phylogeny and Conservation* (eds. Purvis, A., Gittleman, J. L. &  
 611 Brooks, T.) (Cambridge University Press, 2005).
- 612 41. Tucker, C. M. & Cadotte, M. W. Unifying measures of biodiversity: understanding  
 613 when richness and phylogenetic diversity should be congruent. *Diversity and*  
 614 *Distributions* **19**, 845–854 (2013).
- 615 42. Velasco, J. A. & Pinto-Ledezma, J. N. Mapping species diversification metrics in  
 616 macroecology: Prospects and challenges. *Frontiers in Ecology and Evolution* **10**,  
 617 951271 (2022).
- 618 43. Stebbins, G. L. *Flowering plants: evolution above the species level*. (Harvard  
 619 University Press, 1974).
- 620 44. Vasconcelos, T., O'Meara, B. C. & Beaulieu, J. M. Retiring “Cradles” and  
 621 “Museums” of Biodiversity. *The American Naturalist* **199**, 195–204 (2022).
- 622 45. Voskamp, A., Baker, D. J., Stephens, P. A., Valdes, P. J. & Willis, S. G. Global  
 623 patterns in the divergence between phylogenetic diversity and species richness in  
 624 terrestrial birds. *Journal of Biogeography* **44**, 709–721 (2017).
- 625 46. Gumbs, R. *et al.* Global priorities for conservation of reptilian phylogenetic diversity  
 626 in the face of human impacts. *Nat Commun* **11**, 2616 (2020).
- 627 47. Vásquez-Restrepo, J. D., Ochoa-Ochoa, L. M., Flores-Villela, O. & Velasco, J. A.  
 628 Deconstructing the dimensions of alpha diversity in squamate reptiles (Reptilia:  
 629 Squamata) across the Americas. *Global Ecology and Biogeography* **32**, 250–266  
 630 (2023).
- 631 48. IUCN. The IUCN Red List of Threatened Species. Version 2022-2.  
 632 <https://www.iucnredlist.org> (2022).



49. Roll, U. *et al.* GARD 1.5 range shapefiles used in: Global diversity patterns are explained by diversification rates at ancient, not shallow, timescales. (2021) doi:10.5683/SP2/913A8L.
50. Jetz, W. & Pyron, R. A. The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nature Ecology and Evolution* **2**, 850–858 (2018).
51. Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in space and time. *Nature* **491**, 444–448 (2012).
52. Hackett, S. J. *et al.* A Phylogenomic Study of Birds Reveals Their Evolutionary History. *Science* **320**, 1763–1768 (2008).
53. Upham, N. S., Esselstyn, J. A. & Jetz, W. Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biology* **17**, 1–44 (2019).
54. Tonini, J. F. R., Beard, K. H., Ferreira, R. B., Jetz, W. & Pyron, R. A. Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biological Conservation* **204**, 23–31 (2016).
55. Title, P. O., Swiderski, D. L. & Zelditch, M. L. EcoPhyloMapper: An r package for integrating geographical ranges, phylogeny and morphology. *Methods in Ecology and Evolution* **13**, 1912–1922 (2022).
56. R Core Team. *R: A Language and Environment for Statistical Computing*. (R Foundation for Statistical Computing, 2023).
57. Ren, K. rlist: A toolbox for non-tabular data manipulation. (2021).
58. Collyer, M. L. & Adams, D. C. RRPP: An r package for fitting linear models to high-dimensional data using residual randomization. *Methods in Ecology and Evolution* **9**, 1772–1779 (2018).

- 658 59. Collyer, M. L. & Adams, D. C. RRPP: Linear Model Evaluation with Randomized  
659 Residuals in a Permutation Procedure. (2022).
- 660 60. Paradis, E. & Schliep, K. ape 5.0: an environment for modern phylogenetics and  
661 evolutionary analyses in R. *Bioinformatics* **35**, 526–528 (2019).
- 662 61. Pennell, M. W. *et al.* Geiger v2.0: An expanded suite of methods for fitting  
663 macroevolutionary models to phylogenetic trees. *Bioinformatics* **30**, 2216–2218  
664 (2014).
- 665 62. Revell, L. J. phytools: An R package for phylogenetic comparative biology (and  
666 other things). *Methods in Ecology and Evolution* **3**, 217–223 (2012).
- 667 63. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate  
668 surfaces for global land areas. *International Journal of Climatology* **37**, 4302–4315  
669 (2017).
- 670 64. Pinzon, J. E. & Tucker, C. J. A non-stationary 1981-2012 AVHRR NDVI3g time  
671 series. *Remote Sensing* **6**, 6929–6960 (2014).
- 672 65. Wilson, M. F. J., O’Connell, B., Brown, C., Guinan, J. C. & Grehan, A. J. Multiscale  
673 Terrain Analysis of Multibeam Bathymetry Data for Habitat Mapping on the  
674 Continental Slope. *Marine Geodesy* **30**, 3–35 (2007).
- 675 66. Title, P. O. & Bemmels, J. B. ENVIREM: an expanded set of bioclimatic and  
676 topographic variables increases flexibility and improves performance of ecological  
677 niche modeling. *Ecography* **41**, 291–307 (2018).
- 678 67. Lillegraven, J. A., Thompson, S. D., McNab, B. K. & Patton, J. L. The origin of  
679 eutherian mammals. *Biological Journal of the Linnean Society* **32**, 281–336 (1987).
- 680 68. Benson, R. B. J. *et al.* Cretaceous tetrapod fossil record sampling and faunal  
681 turnover: Implications for biogeography and the rise of modern clades.  
682 *Palaeogeography, Palaeoclimatology, Palaeoecology* **372**, 88–107 (2013).

- 683 69. Claramunt, S. & Cracraft, J. A new time tree reveals Earth history's imprint on the  
684 evolution of modern birds. *Sci. Adv.* **1**, e1501005 (2015).
- 685 70. Webb, D. S. Mammalian faunal dynamics of the great American interchange.  
686 *Paleobiology* **2**, 220–234 (1976).
- 687 71. Weir, J. T., Bermingham, E. & Schluter, D. The Great American Biotic Interchange  
688 in birds. *Proceedings of the National Academy of Sciences* **106**, 21737–21742  
689 (2009).
- 690 72. Carrillo, J. D. *et al.* Disproportionate extinction of South American mammals drove  
691 the asymmetry of the Great American Biotic Interchange. *Proceedings of the*  
692 *National Academy of Sciences* 1–7 (2020) doi:10.1073/pnas.2009397117.
- 693 73. Jönsson, K. A. & Fjeldså, J. Determining biogeographical patterns of dispersal and  
694 diversification in oscine passerine birds in Australia, Southeast Asia and Africa.  
695 *Journal of Biogeography* **33**, 1155–1165 (2006).
- 696 74. Sheldon, F. H., Lim, H. C. & Moyle, R. G. Return to the Malay Archipelago: the  
697 biogeography of Sundaic rainforest birds. *J Ornithol* **156**, 91–113 (2015).
- 698 75. Jönsson, K. A., Fjeldså, J., Ericson, P. G. P. & Irestedt, M. Systematic placement of  
699 an enigmatic Southeast Asian taxon *Eupetes macrocerus* and implications for the  
700 biogeography of a main songbird radiation, the Passerida. *Biology Letters* **3**, 323–  
701 326 (2007).
- 702 76. Inger, R. F. & Voris, H. K. The biogeographical relations of the frogs and snakes of  
703 Sundaland. *Journal of Biogeography* **28**, 863–891 (2001).
- 704 77. Siler, C. D. *et al.* Did geckos ride the Palawan raft to the Philippines? *Journal of*  
705 *Biogeography* **39**, 1217–1234 (2012).
- 706 78. How, R. A. & Kitchener, D. J. Biogeography of Indonesian snakes. *Journal of*  
707 *Biogeography* **24**, 725–735 (1997).

- 708 79. Voris, H. K. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river  
709 systems and time durations. *Journal of Biogeography* **27**, 1153–1167 (2000).
- 710 80. Brown, R. M. *et al.* Evolutionary Processes of Diversification in a Model Island  
711 Archipelago. *Annual Review of Ecology, Evolution, and Systematics* **44**, 411–435  
712 (2013).
- 713 81. Husson, L., Boucher, F. C., Sarr, A.-C., Sepulchre, P. & Cahyarini, S. Y. Evidence  
714 of Sundaland's subsidence requires revisiting its biogeography. *Journal of*  
715 *Biogeography* **47**, 843–853 (2020).
- 716 82. Van Den Bergh, G. D., De Vos, J. & Sondaar, P. Y. The Late Quaternary  
717 palaeogeography of mammal evolution in the Indonesian Archipelago.  
718 *Palaeogeography, Palaeoclimatology, Palaeoecology* **171**, 385–408 (2001).
- 719 83. Meijaard, E. Mammals of south-east Asian islands and their Late Pleistocene  
720 environments. *Journal of Biogeography* **30**, 1245–1257 (2003).
- 721 84. Mercer, J. M. & Roth, V. L. The Effects of Cenozoic Global Change on Squirrel  
722 Phylogeny. *Science* **299**, 1568–1572 (2003).
- 723 85. Wilting, A., Sollmann, R., Meijaard, E., Helgen, K. M. & Fickel, J. Mentawai's  
724 endemic, relictual fauna: is it evidence for Pleistocene extinctions on Sumatra?  
725 *Journal of Biogeography* **39**, 1608–1620 (2012).
- 726 86. Pianka, E. R. Diversity and adaptive radiations of Australian desert lizards. in  
727 *Ecological biogeography of Australia* 1376–1392 (1981).
- 728 87. Rabosky, D. L., Donnellan, S. C., Talaba, A. L. & Lovette, I. J. Exceptional among-  
729 lineage variation in diversification rates during the radiation of Australia's most  
730 diverse vertebrate clade. *Proceedings of the Royal Society B: Biological Sciences*  
731 **274**, 2915–2923 (2007).

88. Skinner, A., Hugall, A. F. & Hutchinson, M. N. Lygosomine phylogeny and the origins of Australian scincid lizards. *Journal of Biogeography* **38**, 1044–1058 (2011).
89. Vidal-García, M. & Keogh, J. S. Convergent evolution across the Australian continent: ecotype diversification drives morphological convergence in two distantly related clades of Australian frogs. *Journal of Evolutionary Biology* **28**, 2136–2151 (2015).
90. Tejero-Cicuéndez, H., Tarroso, P., Carranza, S. & Rabosky, D. L. Desert lizard diversity worldwide: Effects of environment, time, and evolutionary rate. *Global Ecology and Biogeography* **31**, 776–790 (2022).
91. Brennan, I. G. *et al.* Populating a Continent: Phylogenomics Reveal the Timing of Australian Frog Diversification. *Systematic Biology* syad048 (2023) doi:10.1093/sysbio/syad048.
92. Townsend, T. M., Leavitt, D. H. & Reeder, T. W. Intercontinental dispersal by a microendemic burrowing reptile (Dibamidae). *Proceedings of the Royal Society B: Biological Sciences* **278**, 2568–2574 (2011).
93. Yonezawa, T. *et al.* Phylogenomics and Morphology of Extinct Paleognaths Reveal the Origin and Evolution of the Ratites. *Current Biology* **27**, 68–77 (2017).
94. May-Collado, L. J., Kilpatrick, C. W. & Agnarsson, I. Mammals from ‘down under’: a multi-gene species-level phylogeny of marsupial mammals (Mammalia, Metatheria). *PeerJ* **3**, e805 (2015).
95. Moyle, R. G. *et al.* Tectonic collision and uplift of Wallacea triggered the global songbird radiation. *Nature Communications* **7**, 12709 (2016).
96. Oliveros, C. H. *et al.* Earth history and the passerine superradiation. *Proceedings of the National Academy of Sciences* (2019) doi:10.1073/pnas.1813206116.

- 757 97. Harvey, M. G. *et al.* The evolution of a tropical biodiversity hotspot. *Science* **370**,  
758 1343–1348 (2020).
- 759 98. James, C. D. & Shine, R. Why are there so many coexisting species of lizards in  
760 Australian deserts? *Oecologia* **125**, 127–141 (2000).
- 761 99. Jetz, W. & Rahbek, C. Geographic range size and determinants of avian species  
762 richness. *Science* **297**, 1548–1551 (2002).
- 763 100. Badgley, C. Tectonics, topography, and mammalian diversity. *Ecography* **33**, 220–  
764 231 (2010).
- 765 101. Pyron, R. A. Biogeographic analysis reveals ancient continental vicariance and  
766 recent oceanic dispersal in amphibians. *Systematic Biology* **63**, 779–797 (2014).
- 767 102. Menéndez, I. *et al.* A multi-layered approach to the diversification of squirrels.  
768 *Mammal Review* **51**, 66–81 (2021).
- 769 103. Jiang, K. *et al.* Evolutionary history and global angiosperm species richness–climate  
770 relationships. *Global Ecology and Biogeography* **32**, 1059–1072 (2023).
- 771 104. Rahbek, C. *et al.* Building mountain biodiversity: Geological and evolutionary  
772 processes. *Science* **365**, 1114–1119 (2019).
- 773 105. Perrigo, A., Hoorn, C. & Antonelli, A. Why mountains matter for biodiversity.  
774 *Journal of Biogeography* 315–325 (2020) doi:10.1111/jbi.13731.
- 775 106. Cadena, C. D. *et al.* Latitude, elevational climatic zonation and speciation in New  
776 World vertebrates. *Proceedings of the Royal Society B: Biological Sciences* **279**,  
777 194–201 (2011).
- 778 107. Šmíd, J. *et al.* Diversity patterns and evolutionary history of Arabian squamates.  
779 *Journal of Biogeography* **48**, 1183–1199 (2021).

- 780 108. Miller, M. J. *et al.* Out of Amazonia again and again: episodic crossing of the Andes  
781 promotes diversification in a lowland forest flycatcher. *Proceedings of the Royal*  
782 *Society B: Biological Sciences* **275**, 1133–1142 (2008).
- 783 109. Hampe, A. & Jump, A. S. Climate Relicts: Past, Present, Future. *Annual Review of*  
784 *Ecology, Evolution, and Systematics* **42**, 313–333 (2011).
- 785 110. Fjeldså, J., Bowie, R. C. K. & Rahbek, C. The Role of Mountain Ranges in the  
786 Diversification of Birds. *Annual Review of Ecology, Evolution, and Systematics* **43**,  
787 249–265 (2012).
- 788 111. Crisp, M. D. *et al.* Phylogenetic biome conservatism on a global scale. *Nature* **458**,  
789 754–756 (2009).
- 790 112. Wiens, J. J., Kozak, K. H. & Silva, N. Diversity and niche evolution along aridity  
791 gradients in North American lizards (Phrynosomatidae). *Evolution* **67**, 1715–1728  
792 (2013).
- 793 113. Rabosky, D. L., Hutchinson, M. N., Donnellan, S. C., Talaba, A. L. & Lovette, I. J.  
794 Phylogenetic disassembly of species boundaries in a widespread group of Australian  
795 skinks (Scincidae: *Ctenotus*). *Molecular Phylogenetics and Evolution* **77**, 71–82  
796 (2014).
- 797 114. Buckley, L. B., Hurlbert, A. H. & Jetz, W. Broad-scale ecological implications of  
798 ectothermy and endothermy in changing environments. *Global Ecology and*  
799 *Biogeography* **21**, 873–885 (2012).
- 800 115. Jablonski, D. Lessons from the past: Evolutionary impacts of mass extinctions.  
801 *Proceedings of the National Academy of Sciences* **98**, 5393–5398 (2001).
- 802 116. Seeholzer, G. F. & Brumfield, R. T. Speciation-by-Extinction. *Systematic Biology*  
803 syad049 (2023) doi:10.1093/sysbio/syad049.

- 804 117. Pyron, R. A. Temperate extinction in squamate reptiles and the roots of latitudinal  
805 diversity gradients. *Global Ecology and Biogeography* **23**, 1126–1134 (2014).
- 806 118. Meseguer, A. S. & Condamine, F. L. Ancient tropical extinctions at high latitudes  
807 contributed to the latitudinal diversity gradient. *Evolution* **74**, 1966–1987 (2020).
- 808 119. Erwin, D. H. Extinction as the loss of evolutionary history. *Proceedings of the*  
809 *National Academy of Sciences* **105**, 11520–11527 (2008).
- 810 120. Pimiento, C. *et al.* Selective extinction against redundant species buffers functional  
811 diversity. *Proceedings of the Royal Society B: Biological Sciences* **287**, 20201162  
812 (2020).
- 813 121. Brocklehurst, N., Panciroli, E., Benevento, G. L. & Benson, R. B. J. Mammaliaform  
814 extinctions as a driver of the morphological radiation of Cenozoic mammals.  
815 *Current Biology* **31**, 2955–2963.e4 (2021).
- 816 122. Daru, B. H., Elliott, T. L., Park, D. S. & Davies, T. J. Understanding the Processes  
817 Underpinning Patterns of Phylogenetic Regionalization. *Trends in Ecology &*  
818 *Evolution* **32**, 845–860 (2017).
- 819 123. Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J.  
820 Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
- 821 124. Meseguer, A. S., Antoine, P.-O., Fouquet, A., Delsuc, F. & Condamine, F. L. The  
822 role of the Neotropics as a source of world tetrapod biodiversity. *Global Ecology*  
823 *and Biogeography* **29**, 1565–1578 (2020).
- 824 125. Pimiento, C. & Antonelli, A. Integrating deep-time palaeontology in conservation  
825 prioritisation. *Frontiers in Ecology and Evolution* **10**, (2022).
- 826