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

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Corresponding Author:	Héctor Tejero-Cicuéndez, Ph.D. Complutense University of Madrid Madrid, SPAIN
First Author:	Héctor Tejero-Cicuéndez, Ph.D.
Order of Authors:	Héctor Tejero-Cicuéndez, Ph.D.
	Iris Menéndez
	Elizabeth M. Steell
	Guillermo Navalón
	Fernando Blanco
	Jiří Šmíd
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.
Suggested Reviewers:	Erin Saupe University of Oxford erin.saupe@earth.ox.ac.uk extensive background exploring the spatio-temporal dynamics of diversity gradients
	Sara Varela University of Vigo sara.varela@uvigo.es focuses on the relationship between biodiversity and the environment from a macroecological perspective
	Catalina Pimiento University of Zurich catalina.pimientohernandez@pim.uzh.ch main research topic is how past diversification dynamics have shaped current biodiversity

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Madrid, December 18, 2023

Dear Dr Geoffrey North
Editor-in-Chief, *Current Biology*

We would be grateful if you would consider the accompanying manuscript entitled "**Geographic patterns of living tetrapod diversity reveal the signature of global diversification dynamics**", for publication as an Article in *Current Biology*.

In recent years, advances in quantitative comparative methods and an increasing availability of large-scale datasets have bolstered our knowledge of global patterns of vertebrate biodiversity. However, our understanding of the evolutionary processes generating the uneven geographic distribution of biodiversity in modern ecosystems is still incipient.

In this study, we evaluate the links between diversification dynamics, environmental factors, and geographic patterns of species richness in the four main groups of living terrestrial vertebrates (amphibians, squamates, birds, and mammals)—which encompass more than 36,000 living species and span the last 350 million years of vertebrate evolution. Specifically, our approach integrates species richness and phylogenetic relatedness across geographic areas for more than 75% of extant tetrapod species to evaluate the generative evolutionary processes shaping modern day patterns of terrestrial vertebrate diversity. This study is the first of its kind in quantitatively comparing these patterns across major tetrapod clades.

Our results reveal common geographic regions with higher or lower phylogenetic diversity than expected across all tetrapod groups (in Africa and South America, respectively), as well as a widespread effect of recent speciation rates but a negligible effect of clade age. Furthermore, environmental variables differentially affect endotherm and ectotherm lineages. Our study contributes a completely novel global perspective of the generative processes of tetrapod biodiversity which could potentially guide the application of conservation measures and stimulate future studies focused on specific clades.

Our methodology, results and conceptual perspectives are relevant for macroecologists and evolutionary biologists working in the origination and preservation of current biodiversity, as evidenced by the interest generated from the submitted preprint of this article. The phylogenetic dimension of biodiversity also bears implications for conservation prioritisation and strategy, since preserving evolutionary history, and not only hotspots of species richness, has become a priority in the face of the challenges imposed by ongoing loss of biodiversity.

In selecting potential peer reviewers for our manuscript, we recommend well-recognised researchers that have made significant contributions to the study of evolutionary patterns and processes during the last decade. Prof. Erin Saupe (University of Oxford, UK), who has an extensive background exploring the spatio-temporal dynamics of diversity gradients. Dr Sara Varela (University of Vigo, Spain), whose research focuses on the relationship between biodiversity and the environment from a macroecological perspective. Prof. Catalina Pimiento (University of Zurich, Switzerland), whose main research topic is how past diversification dynamics have shaped current biodiversity. Additionally, Prof. Rampal Etienne (University of Groningen, The Netherlands), Dr Alexander Skeels (Australian National University, Australia), and Dr R. Alexander Pyron (The George Washington University, USA), all of whom study macroevolutionary patterns implementing phylogenetic comparative methods.

All authors have agreed to the content of the manuscript and its conclusions, and the paper is not under consideration elsewhere (please note that it has been recently posted in the preprint server *bioRxiv*: https://doi.org/10.1101/2023.11.03.565445).

Yours sincerely,

Héctor Tejero-Cicuéndez
"Juan de la Cierva" postdoctoral researcher
Department of Biodiversity, Ecology and Evolution
Complutense University of Madrid (UCM)
C/ José Antonio Novais 12
28040 Madrid
hetejero@ucm.es

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

Héctor Tejero-Cicuéndez[1*], Iris Menéndez[2], Elizabeth M. Steell[3,4], Guillermo Navalón[3], Fernando Blanco[2,5,6], Jiří Šmíd[7,8]

[1]Department of Biodiversity, Ecology and Evolution, Faculty of Biology, Universidad Complutense de Madrid, Madrid, Spain

[2]Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University Berlin, 10115 Berlin, Germany

[3]Department of Earth Sciences, University of Cambridge, Cambridge, United Kingdom

[4]Department of Earth Sciences, University College London, London, United Kingdom

[5]Department of Biological and Environmental Sciences, University of Gothenburg, Medicinaregatan 18, 405 30 Gothenburg, Sweden

[6]Gothenburg Global Biodiversity Centre, Box 461, Gothenburg, Sweden

[7]Department of Zoology, Faculty of Science, Charles University, Prague, Czech Republic

[8]Department of Zoology, National Museum, Prague, Czech Republic

*Correspondence: hetejero@ucm.es

Summary

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[1–11]. 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[12–14] to modern evolutionary theory (e.g.,[15]). 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[16–18]. 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[19–21], such as ecological interactions[22], evolutionary time[23,24], the relationship between organismal form and ecology[25,26], environmental conditions[27,28], climatic trends[29], or topography and plate tectonics[30–32].

In recent years, the emergence and development of spatial phylogenetics[33,34] 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[35]), 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[36,37] in addition to providing an essential source of information for conservation purposes[35,38].

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.,[36,39]). 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[40]. However, geographic patterns of richness and PD are not necessarily congruent[41]. 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[42]) 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[6,43] 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[43] 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[44].

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[36], amphibians[39], birds[45], and squamates[46,47]. 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 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. 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 [48], for birds from BirdLife International (http://www.birdlife.org/) and for squamates from [49]. 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 [50], birds [51] (backbone from [52]), mammals [53], and squamates [54].

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 [55] in R 4.3.0 [56], 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 [55], and they represent the sum of the branch lengths of the phylogenetic tree connecting all species in each cell (Faith's PD [35]). We used the R package rlist v0.4.6.2 [57] 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 [51] 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 [58,59], 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 [60], with the aid of geiger v2.0.11 [61] and phytools v1.5.1 [62] 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 [63]. Net primary productivity data summarized over the period between 1981 and 2015 was obtained at 5-arc-minute resolution from the NDVI3g time series [64]. The current topography data were based on [65] and obtained from the ENVIREM dataset [66] 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; $R^2_{amphibians} = 0.005$, $R^2_{birds} = 0.047$, $R^2_{mammals} = 0.076$, $R^2_{squamates} = 0.13$).

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.

Fig. 2. Geographic distribution of areas with the 10% lowest (in blue) and highest (in red) residual PD for terrestrial vertebrates (amphibians, birds, mammals, and squamates). The 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 $R^2_{mammals}$ = 0.017; temperature $R^2_{mammals}$ = 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 [36] suggested that high residual PD found in Africa may reflect an African origin for many extant mammal clades [67]. 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., [68,69]), 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 [36,70–72]. 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 [36]. 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. The high vagility of birds likely contributed to higher residual PD values in Southeast Asia and Australia due to repeated colonization of islands in these regions [73,74]. In addition, the high dispersal ability of the majority of birds' main subclades resulted in the arrival and relictual permanence of lineages with widely different phylogenetic origins [75], as opposed to isolated radiations (and, therefore, lower PD), which may be more frequent in organisms with lower dispersal abilities [76,77]. High residual PD of squamates within Southeast Asia may be related to multiple waves of island colonization during intervals of low sea level and environmental change [78–81] , although this also affected mammals [82–84] and amphibians [80], 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., [85]).

In contrast, the low residual PD of squamates in arid Australia, and of amphibians in the temperate woodlands of the northern and eastern coasts of Australia, likely resulted from a few extensive radiations (see the phylogenetic trees in Fig. 2). These radiations may be facilitated by adaptation and specialization within these unique biomes, leading to community assembly driven by proportionally more closely related species [86–91]. Finally,

geographic patterns of residual PD may be partially generated by ancient evolutionary lineages that inhabit certain regions. This could be the case of dibamid reptiles in Southeast Asia [92], palaeognath birds in Australia [93], or marsupial and xenarthran mammals in Australia and North America, respectively [94]. Additionally, passerine birds, that comprise ~60% of extant avian diversity, contribute to high residual PD in Australia due to the presence of numerous endemic lineages that are distantly related in comparison to the diverse, but generally closely related, passerine lineages inhabiting South America [95–97] (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 [98–103]. For instance, mountainous regions (a universally recognized driver of diversity and evolutionary processes [30,104,105]) 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 [106,107]), or induce dispersal barriers (e.g., [108]). Mountains may also generate important refugia and reserves of cold- or humid-adapted diversity during periods of climate warming and aridification [109,110]. 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 [111]) 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., [112,113]). 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 [114].

Apart from differences in trait- and environment-mediated speciation and dispersal, extinction may also be a major driver of diversity, diversification and biogeographic patterns [115,116]. Specifically, extinction events are known not only to underlie current

patterns of species richness [117,118], but also to substantially affect other facets of biodiversity [119–121]. Extinction may both increase and decrease phylogenetic diversity, depending on the age of the lineages that are more prone to extinction [122]. 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 [44]. 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 [123]. Integrating evolutionary relationships at a regional scale has been stated as a necessary step for global conservation efforts for decades [35]. 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 [124] 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 [125].

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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/gQEWAVjLIvl_b9oZEZdFULl4ousSOQojyBW8Kj1ckQ4

Author contributions (CRediT)

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

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Supplementary Table 1. Results from the linear model of recent speciation (DR) rates against residual phylogenetic diversity (PD).

Clade	Estimate	R.squared	p.value
amphibians	-2.09E-05	0.005	1.71E-16
birds	-7.24E-05	0.047	6.82E-209
mammals	-0.0001676	0.076	9.96E-274
squamates	-5.74E-05	0.125	0

Supplementary Table 2. Post-hoc analyses comparing DR rates between pairs of focal regions of high and low residual PD.

	taxa	d	UCL (95%)	Z	Pr > d
cradle_australia_oceania:cradle_oriental	amphibians	0.00525528	0.00698079	1.10233047	0.15
cradle_australia_oceania:cradle_south_america	amphibians	0.01561991	0.00578026	3.57674856	0.001
cradle_australia_oceania:museum_africa	amphibians	0.0114298	0.0065061	2.74666907	0.003
cradle_oriental:cradle_south_america	amphibians	0.01036463	0.00647359	2.49136758	0.002
cradle_oriental:museum_africa	amphibians	0.01668508	0.00701332	3.55794931	0.001
cradle_south_america:museum_africa	amphibians	0.02704971	0.00531601	5.46148224	0.001
cradle_north_america:cradle_south_america	birds	0.00267518	0.01626041	-0.7325484	0.755
cradle_north_america:museum_africa_madagascar	birds	0.04391713	0.01936177	3.34503922	0.001
cradle_north_america:museum_australia_oceania_asia	birds	0.05353809	0.01732115	4.1915594	0.001
cradle_south_america:museum_africa_madagascar	birds	0.04124195	0.01537753	3.70799933	0.001
cradle_south_america:museum_australia_oceania_asia	birds	0.05086291	0.01456124	4.46237966	0.001
museum_africa_madagascar:museum_australia_oceania_asia	birds	0.00962096	0.01660227	0.69577414	0.257
cradle_north_america:cradle_south_america1	mammals	0.02791751	0.02450657	1.76948243	0.027
cradle_north_america:museum_africa	mammals	0.00283974	0.02563416	-0.9689377	0.827
cradle_north_america:museum_north_america	mammals	0.02831498	0.03051384	1.43523423	0.072
cradle_south_america:museum_africa1	mammals	0.03075725	0.01946118	2.5414738	0.004
cradle_south_america:museum_north_america	mammals	0.05623249	0.02699161	2.99347373	0.001
museum_africa:museum_north_america	mammals	0.02547524	0.02410014	1.6703083	0.044
cradle_australia:cradle_north_america	squamates	0.04805722	0.01229255	4.67906539	0.001
cradle_australia:cradle_south_america	squamates	0.09239165	0.00982233	7.93397381	0.001
cradle_australia:museum_south_africa	squamates	0.0168303	0.01091905	2.46286027	0.001
cradle_australia:museum_southeast_asia	squamates	0.01053019	0.0096155	1.74174676	0.029
cradle_north_america:cradle_south_america2	squamates	0.04433443	0.01151994	4.8334128	0.001
cradle_north_america:museum_south_africa	squamates	0.06488752	0.01223027	6.1095102	0.001
cradle_north_america:museum_southeast_asia	squamates	0.03752703	0.01114818	4.40339537	0.001
cradle_south_america:museum_south_africa	squamates	0.10922195	0.01094116	8.42007702	0.001
cradle_south_america:museum_southeast_asia	squamates	0.08186147	0.00954673	7.67088747	0.001
museum_south_africa:museum_southeast_asia	squamates	0.02736048	0.01060042	3.63286509	0.001

Supplementary Figure 1. Maps of residual phylogenetic diversity (PD) for all terrestrial vertebrate clades.

Supplementary Figure 2. Violin plots of recent speciation (DR) rates in the different focal areas identified as centers of high and low residual PD for all terrestrial vertebrate clades.

Supplementary Figure 3. Pairwise differences in DR rates (effect size Z) between specific regions of high and low residual PD, colored by taxa group. Left: differences between pairs of regions of low residual PD. Center: differences between regions of high residual PD and regions of low residual PD. Right: differences between pairs of regions of high residual PD.

Supplementary Figure 4. Lineage-through-time (LTT) plots for amphibian lineages in the different focal regions of low (in blue) and high (in red) residual PD.

Supplementary Figure 5. Lineage-through-time (LTT) plots for bird lineages in the different focal regions of low (in blue) and high (in red) residual PD.

Supplementary Figure 6. Lineage-through-time (LTT) plots for mammal lineages in the different focal regions of low (in blue) and high (in red) residual PD.

Supplementary Figure 7. Lineage-through-time (LTT) plots for squamate lineages in the different focal regions of low (in blue) and high (in red) residual PD.

Supplementary Figure 8. Relationship of annual precipitation (in mm) with residual PD in all tetrapod clades.

Supplementary Figure 9. Relationship of mean temperature (in ºC) with residual PD in all tetrapod clades.

Supplementary Figure 10. Relationship of precipitation seasonality and residual PD in all tetrapod clades.

Supplementary Figure 11. Relationship of temperature seasonality and residual PD in all tetrapod clades.

Supplementary Figure 12. Relationship of net primary productivity (NPP) and residual PD in all tetrapod clades.

Supplementary Figure 13. Relationship of terrain roughness index (TRI; a measurement of topographic complexity) and residual PD in all tetrapod clades.

Supplementary Figure 14. Climatic space defined by precipitation seasonality and temperature seasonality for all tetrapod clades, showing the geographic grid cells with the 10% lowest (in blue) and highest (in red) residual PD.

Supplementary Figure 15. Climatic space defined by net primary productivity (NPP) and terrain roughness index (TRI) for all tetrapod clades, showing the geographic grid cells with the 10% lowest (in blue) and highest (in red) residual PD.

Supplementary Figure 16. Latitudinal pattern of species richness (in the X-axis) and residual PD (in the color gradient) for all tetrapod clades.

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