Bird Phylogenetic Diversity Increases With Temperature Worldwide

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ABSTRACT

Aim: Temperature significantly influences the composition and structure of biotic communities at large scales. While its role in shaping taxonomic diversity is well-documented, its relationship with other facets of biodiversity, like phylogenetic diversity, remains poorly known. Understanding how and to which extent temperature contributes to global patterns of phylogenetic diversity compared to other biodiversity-structuring factors is crucial for comprehending how bird assemblages are structured worldwide, predicting their response to global-change drivers and supporting conservation policies focused on preserving bird genetic diversity and evolutionary history.

Location: Worldwide.

Methods: We analyse the role of temperature in predicting bird regional phylogenetic richness (PD) and divergence (MPD) worldwide, before and after controlling for the effect of species richness (SR). We also assess the shape of this relationship in different biogeographic realms and compare its explanatory power with other key biodiversity-structuring factors such as elevation, human impact index, net primary productivity and land use diversity.

Results: Our findings underscore the high significance and consistency of temperature as a key predictor positively associated with bird PD and MPD across the six main biogeographic realms, even after accounting for SR and latitude, suggesting that temperature modulates the intrinsic capacity of environments to support a diverse array of lineages. In addition, PD and MPD tended to increase at low elevations, but the human-impact index did not effectively predict bird phylogenetic diversity at this scale. Furthermore, high PD was linked to regions with high primary productivity and high land-use diversity, although both of these relationships were strongly mediated by SR.

Conclusions: This study unveils the key role of temperature in explaining bird phylogenetic diversity worldwide over other key biodiversity-structuring factors and points to the profound implications that climate change will have on the amount of evolutionary history held in bird assemblages, beyond species extinctions or range shifts alone.

1 | Introduction

Unravelling distribution patterns for Earth's biodiversity and the factors that shape them represents a fundamental, long-standing goal in the field of ecology. In recent decades, extensive research has analysed the global drivers of taxonomic diversity for various groups (Ceballos and Ehrlich 2006; Neate-Clegg, Blount, and Şekercioğlu 2021; Qian, Zhang, and Jiang 2023). However, traditionally, non-taxonomic components of biodiversity have received less attention. For instance, the limited availability of phylogenetic trees incorporating detailed genetic information has historically hindered our comprehension of the global distribution of phylogenetic diversity—a pivotal aspect of biodiversity—and its response to significant environmental determinants. This is highly relevant because the effects of global-change drivers on the phylogenetic structure of a community might be partly decoupled from its taxonomic richness, as, for instance, the presence of more species might not increase phylogenetic diversity if species within an assemblage show high evolutionary relatedness (Gumbs et al. 2023; McClure et al. 2023). More recently, extensive trait, phylogenetic and occurrence data for an ecologically important group such as birds are available (Jetz et al. 2012, 2014), and our knowledge about patterns in their functional and phylogenetic diversity has increased rapidly (Jarzyna, Quintero, and Jetz 2021; Martínez-Núñez, Martínez-Prentice, and García-Navas 2023a; Hughes et al. 2022; Voskamp et al. 2017). Nonetheless, our knowledge about the role played by temperature in structuring the phylogenetic diversity of bird assemblages at large scales remains poorly understood, which is a gap of knowledge particularly relevant in the context of past and ongoing climate change (Montaño-Centellas et al. 2023; Negro et al. 2022; Saupe et al. 2019; Voskamp et al. 2022).

The phylogenetic diversity of bird assemblages might be higher in warmer regions due to several mechanisms. First, the climatic stability of warm areas might promote that many species expand their range to warmer regions, evolving and changing their life histories and heat tolerance (Carbonell and Stoks 2020; Erwin 2009). Second, warmer climates have been associated with accelerated rates of climatic-niche evolution (Kozak and Wiens 2010), which could lead to higher speciation rates in warmer regions (Cardillo, Orme, and Owens 2005). In addition, most clades originated during warm periods, with their distribution range centred in warmer areas (Bennett et al. 2021), allowing more opportunities for speciation. Yet, although these speciation events might not increase phylogenetic divergence due to niche conservatism forces (Wiens et al. 2010), phylogenetic divergence could theoretically increase also as a result of species loss in warmer areas due to competition between species from close clades with similar niches (Tucker et al. 2018; Wang et al. 2022). These competition-driven local exclusions might cause a loss in species richness (SR), but increase phylogenetic divergence. Species-richness-dependent processes could also be involved (but see Pie, Divieso, and Caron 2023). Extreme temperature regions, both cold and hot, tend to have lower species diversity (Currie et al. 2004) due to the challenging environmental conditions that approach or exceed species' physiological limits, making it difficult for them to thrive. For instance, areas with low temperatures, such as the poles, have a reduced and climatically specialised set of species (i.e. species adapted to low temperatures), limiting the number of potential lineages that can adapt to or evolve in such environments. In contrast, hotter places like the tropics provide more climatic stability and available ecological niches and are considered to promote strong evolutionary radiation (Erwin 2009; Gaston 2000; Weir and Schluter 2007; but see Harvey et al. 2020).

The regional phylogenetic diversity of bird assemblages might also be explained by other ecosystem-structuring factors such as elevation, anthropisation, land-use diversity, or net primary productivity. These four factors also simultaneously moderate species' presence or absence, regulate ecological filtering and facilitate or hinder evolutionary relatedness and radiation based on the range of ecological niches they offer (Duflot et al. 2014; Jarzyna, Quintero, and Jetz 2021; Luo et al. 2012; Sanderson et al. 2002). Elevation and anthropisation (i.e. human impact index) have been described as important factors negatively correlated with bird SR at the landscape scale (Concepción et al. 2017; Matuoka et al. 2020), with potential impacts on phylogenetic diversity too (Price et al. 2014; Hanz et al. 2018). Bird communities in mountains tend to be phylogenetically clustered (Montaño-Centellas, McCain, and Loiselle 2020). This might be partly because elevation seems to be associated with recent diversification, particularly in species-poor communities (Quintero and Jetz 2018), leading to the accumulation of closely related species. However, several studies have shown complex and context-dependent responses of bird phylogenetic diversity to elevation worldwide (Jarzyna, Quintero, and Jetz 2021). Human-modified landscapes can drive the extinction of evolutionarily distinct species, impoverishing the phylogenetic diversity of bird assemblages in agricultural landscapes (Frishkoff et al. 2014) or urban areas (Sol et al. 2017). Yet, in raptors, intermediate or high levels of disturbance (i.e. human footprint) have been linked to increased phylogenetic diversity (Montaño-Centellas et al. 2023). Land-use diversity has recently been found to be a good predictor of high regional bird taxonomic and functional diversity at the global scale (Martínez-Núñez, Martínez-Prentice, and García-Navas 2023a), probably due to the homogenisation of species assemblages in regions dominated by a single type of land (Liang et al. 2019). Similarly, homogeneous regions dominated by a single or few habitat types (e.g. agriculture) might encourage the establishment of related lineages (e.g. open-habitat bird species) (Gaston 2000; Jetz and Fine 2012; Liang et al. 2019). Net primary productivity has often been positively related to SR (Cusens et al. 2012) and functional richness (Martínez-Núñez, Martínez-Prentice, and García-Navas 2023a) at a large scale, which is often attributed to a higher availability of ecological niches. There is also a positive relationship between net primary productivity and parrot phylogenetic diversity worldwide (Davies et al. 2007). Yet, its effect on phylogenetic diversity when accounting for most of the clades is unknown, as the availability of more ecological niches might not have a signal on phylogenetic diversity.

Regional bird phylogenetic diversity is probably affected not only by temperature, but also by several of these ecological factors simultaneously. By analysing and comparing the varying degrees of influence these factors exert on bird phylogenetic diversity

provides a scientific framework to refine predictive models, inform conservation decisions and safeguard avian biodiversity in a rapidly changing world.

In this study, we examined the link between mean temperature and regional bird phylogenetic diversity worldwide and compared the explanatory power of temperature with that of other important ecosystem-structuring factors, such as elevation, anthropisation, land-use diversity and net primary productivity. In this endeavour, we calculated phylogenetic richness (PD) and divergence (MPD) considering bird assemblages in more than 15,000 grid cells of ~110 km^2 size (i.e. regional scale) and tried to explain their variability using temperature and other possibly important environmental predictors calculated in the same grid cells. We hypothesise that: (i) temperature will be consistently and positively related to bird regional phylogenetic richness (PD) and divergence (MPD) across all the biogeographic realms after controlling for the effect of SR; (ii) given the numerous processes driven by temperature that can shape bird assemblages and phylogenetic diversity at large scales (e.g. range shifts, rates of diversification or opportunities for speciation among others) temperature will be a key factor explaining the variability in bird regional phylogenetic diversity worldwide, over elevation, anthropisation, land-use diversity and primary productivity; (iii) Elevation will tend to be negatively correlated with bird phylogenetic diversity worldwide; (iv) Human footprint will be negatively correlated with bird phylogenetic diversity worldwide; and (v) Net primary productivity and land-use diversity will be positively correlated with bird phylogenetic diversity worldwide.

2 | Materials and Methods

2.1 | Bird Spatial Data

We used the bird occurrence data matrix from the AVONET database (Tobias et al. 2022), whose data were obtained from BirdLife International (2019). The occurrence matrix used equal area grid cells based on the Behrmann projection with approximately one degree of resolution (around 110 km per cell side). Sites where species were classified as breeding native, breeding reintroduced, or resident were used to avoid noise from non-breeding or recently introduced species. At first, the matrix presented 18,710 grid cells covering the whole world. Subsequently, we excluded from the analysis those cells with less than 10% of land as well as cells representing regions with fewer than six species. We also excluded the biogeographic realms of Oceania and Antarctica because they had insufficient data points and would introduce bias to the analysis. After all these filters were applied, we had 15,714 grid cells, widely representing the six main biogeographic realms: Nearctic (2616 grid cells), Neotropic (2255 grid cells), Palearctic (6106 grid cells), Afrotropic (2462 grid cells), Australasian (1199 grid cells) and Indomalayan (1076 grid cells).

2.2 | Phylogenetic Tree

To calculate the phylogenetic diversity of bird assemblages, we retrieved phylogenetic information from Birdtree (www.birdtree.org), a validated phylogenetic tree containing all the extant bird species (9993 species) (Jetz et al. 2012). We obtained a set of 1000 equally plausible phylogenetic trees from Birdtree and generated a majority-rule consensus tree ($p = 0.5$) (Rubolini et al. 2015). Some species' names differed from those we had in the bird distribution occurrence matrix. To join both databases, we checked for the names in both databases in the GBIF tool: 'GBIF backbone', using the package 'rgbif' (Chamberlain and Boettiger 2017). Those species with non-matching synonyms ($n = 264$; e.g. those considered subspecies in one of the two databases) were removed. In total, 9729 species, which represent almost all the species of birds in the tree ($> 97\%$ from the initial number of species), were used to calculate phylogenetic diversity within each bird assemblage (i.e. grid cell).

2.3 | Phylogenetic Diversity

We selected two metrics to study birds' phylogenetic diversity: phylogenetic richness and phylogenetic divergence. We used Faith's phylogenetic diversity (PD) as a measure of phylogenetic richness. PD was estimated by the sum of all the branches of the phylogenetic tree encompassing the species in each bird assemblage and represents the amount of evolutionary history harboured in each grid cell (Tucker et al. 2017). Assemblages with more species will have a higher number of branches, often leading to higher PD. Yet closely related species will have shorter branches in the phylogeny, indicating lower phylogenetic richness. Therefore, we expect a higher phylogenetic richness if species are less related to each other. In addition to PD, we used the mean phylogenetic pairwise distance (MPD) as a measure of phylogenetic divergence. This metric was calculated as the mean of the phylogenetic distances between every pair of species within each assemblage in a grid cell (Tucker et al. 2017). As it measures divergence, the further away species are in the phylogenetic tree, the higher the MPD (Stevens et al. 2012). In this case, as the average is calculated and not the sum of the distances, the impact of SR on the metric is not expected to be significant. Yet, since the spectrum of the phylogenetic tree is limited, as the phylogenetic space becomes populated with species (i.e. more species occur in a grid cell), the more likely it is that some of these species are related, diminishing the MPD. The two phylogenetic metrics calculated (PD and MPD) varied widely across the 15,734 bird assemblages (i.e. grid cells) (PD ranged from 365 to 13,277. MPD ranged from 118 to 166). PD and MPD showed different distributions with little correlation between them (Pearson: $r = 0.04$, p-value < 0.001).

Due to the expected high correlation between species taxonomic richness (SR) and phylogenetic richness (PD), PD and MPD were corrected by SR to assess the variation in phylogenetic diversity and divergence that was not driven by SR alone (e.g. Voskamp et al. 2017). We conducted two methods to account for the effect of SR. First, we calculated standardised effect size measures of PD and MPD using the package picante (Kembel et al. 2010) with the functions ses.pd and ses.mpd for PD and MPD, respectively (swap algorithm for the null model with 999 runs and 1000 iterations). For random calculations, we considered the pool of species within each biogeographic realm to account for biogeographic and eco-evolutionary constraints across realms. Second,

we used the original (non-standardised) response variables of PD and MPD but included SR in the models as a covariate. The results obtained with these two procedures were very similar (see Table S1). Therefore, we present here the analyses where we included richness as a covariate, which is the alternative computationally less intensive and more replicable. The measures were calculated with the package 'picante' (Kembel et al. 2010).

2.4 | Temperature and Other Environmental Factors

To assess the relative importance of temperature compared to other relevant global-change factors in shaping bird phylogenetic diversity patterns, we calculated the median of the average annual temperature in each grid cell of ca. 100-km side. We used the median of the average temperature instead of maximum or minimum temperatures because, at this large scale, the median is more representative of the overall conditions and less sensitive to temporal and spatial outliers or extreme values. In addition, we also calculated for each grid cell: the coordinates at the centre of the grid (longitude and latitude), the median elevation as a central measure of the overall area that is little sensitive to outliers or extreme values, the median human footprint index (an index serving as a proxy for anthropisation) (Mu et al. 2022), the Shannon diversity index of land-use types (as a measure of regional land-use diversity) and the mean of the normalised difference vegetation index (NDVI). The NDVI is derived from satellite imagery and is based on the reflectance of vegetation at different wavelengths of light. This index is considered a proxy of net primary productivity, as higher values of NDVI signify greater photosynthetic activity and ecosystem productivity (Table S2 shows details about data sources and resolutions used).

Land-use diversity categories were determined using land cover maps from Copernicus (Table S3 provides information about all the categories of land use considered). Then, we calculated the Shannon diversity of land-use types for each grid.

We initially considered mean annual precipitation too, but we discarded it for being highly correlated with NPP (i.e. NDVI). We decided to maintain NDVI instead of precipitation, as this variable provides a more comprehensive assessment of habitat conditions and prioritises vegetation productivity as a more direct measure of habitat quality. After removing precipitation, Pearson correlation tests showed that correlations between explanatory variables were weak except for the relationship between NDVI and land-use diversity, which was moderate (Pearson: $r = 0.5$, p-value < 0.001, see Figure S1). Within each realm, correlations between explanatory variables were overall low too, with some exceptions (Figure S2).

2.5 | Statistical Analysis

First, we fitted one full generalised additive model (gam) for each response variable (PD and MPD), fitting independent intercepts (including realm as a covariate) and independent curves (using the 'by = realm' notation) for each biogeographic realm. The response variable used in each model was the phylogenetic metric (PD or MPD) normalised by the highest observed value (maximum = 1, minimum = 0). The five focal variables—temperature, elevation, human impact index, land-use diversity and NPP—were included as explanatory variables with smoothing terms. To account for spatial autocorrelation, the coordinates (longitude and latitude) of every grid cell entered the model as smoothed variables. In addition to the two first models, two additional models were fitted incorporating, in addition to all the explanatory variables, SR as a covariable with a smoothing term. Smoothing was done using a basis dimension of $k = 3$ (the same for all the variables) to avoid overfitting and a shrinkage version of the thin-plate regression spline to penalise 'wiggliness' (i.e. avoiding excessively complex functions) and thus improve interpretability (Pedersen et al. 2019). Similar specifications are common in ecology (e.g. Martínez-Núñez, Martínez-Prentice, and García-Navas 2023a). The models including only longitude, latitude and SR (only for models that intended to account for SR) were used as null models for both response variables (i.e. PD and MPD).

To assess the relative importance of each environmental factor, we ran five individual models for each response variable (PD and MPD; with and without SR as a covariate), each model containing one explanatory variable. These single-predictor models kept longitude and latitude as covariables, as well as biogeographic realm as a covariate to set the intercept and as a blocking factor ('by = realm') to calculate independent functions within each biogeographic realm. Variables were smoothed with $k = 3$ as in the full model. Then, we estimated the performance of each model and compared it to the others in terms of R squared (i.e. variance explained) and AIC. Finally, we observed the relationship between response variables and each explanatory variable by calculating and visualising the marginal effects in each single-predictor model (i.e. correcting for latitude, longitude and SR in standardised models). For this, we used the *visreg* package v.2.7.0 (Breheny and Burchett 2017). In addition, we observed the statistical significance (F-statistic and p-value) of the effect of each explanatory variable in each biogeographic realm. Full models were used to understand the added importance of all the variables and to check the relative importance of single-predictor models compared with competing models and the full model. All the models presented here met the assumptions of model residual normality and independence.

General additive models were run using the *mgcv* v.1.8-41 packages (Wood 2011). The package ggplot2 v.3.4 was used to draw plots (Wickham 2016). The packages *ape* v.5.6-2 (Paradis and Schliep 2019), *adephylo* v.1.1-13 (Jombart and Dray 2010) and *vegan* v.2.6-4 (Oksanen et al. 2022) were used for matching names in the phylogenetic tree and the occurrence matrix. For text modifications, we used *dplyr* v. 1.0.10 (Wickham et al. 2022).

Maps used to present global distributions were produced using QGIS 3.30 (QGIS Development Team 2021) with the complement of density analysis and the background maps from Mapzen Global Terrain and Open StreetMap. The data used to show the worldwide distribution of PD and MPD corrected by SR were the ones obtained from the *ses.pd* and *ses.mpd* functions of the package *picante* (Kembel et al. 2010).

All the analyses were done using R version 4.2.2 (R Core Team 2022).

3 | Results

From the total 9729 bird species considered, 861 species occurred in the Nearctic realm (23% unique species), 3804 species occurred in the Neotropic realm (83% unique species), 1683 species occurred in the Palearctic realm (24% unique species), 1978 species occurred in the Afrotropic realm (79% unique species), 1632 species occurred in the Australasian realm (80% unique species) and 1787 species occurred in the Indomalayan realm (41% unique species).

The Indomalayan region and the middle of South America (the Amazonian rainforest) had the highest values of phylogenetic diversity (PD). The lowest levels were found in arid regions like Patagonia and the Sahara Desert, as well as in cold regions such as Canada and the North of Russia (Figure 1). In contrast, we observed a more complex and heterogeneous distribution pattern for phylogenetic divergence (MPD), with higher values in Madagascar, Patagonia and islands from Central America, South Asia and Australasia. The lowest MPD values were found in areas in China, the EEUU and the Mediterranean region (Figure 1).

The global patterns of PD after accounting for SR had similarities with those of raw PD (Figure S3), although they showed a higher PD in Patagonia, Australasia and the tropics, with marked differences between the global north (lower PD values) and the global south (higher PD values). Additionally, particularly low values in northern Asia were observed (Figure S3).

All the environmental factors used showed some important explanatory power, and most effects were statistically significant (Tables S4 and S5), but mean annual temperature was the factor with the overall highest explanatory power. It was the second best for raw PD (only behind NPP), the best for standardised PD, the best for raw MPD and the second best for standardised MPD (just behind elevation) (Table 1; Figure S4). More importantly, the effects of temperature on PD and MPD after correcting for SR were positive and very consistent across the six biogeographic realms (Figure 2, all p-values < 0.001, Table S5). Temperature was also positively related to raw MPD in all the realms, while the patterns for raw PD were more variable and context-dependent (Figure 2). Except for temperature, the effects of the environmental factors on the phylogenetic richness and divergence often depended on the realm and the range of each specific factor in the realm (Figures 2 and 3; Figures S5, S6 and S7).

As expected, the best models were those that included all the predictors, and richness as a covariate. In particular, SR explained most of the variability in PD ($R^2 = 0.60$ without SR and $R^2 = 0.99$, including SR) (Table 1; Figure S4).

Elevation was also an important predictor of PD and MPD. It did not correlate with phylogenetic diversity in a consistent way worldwide. However, it showed an overall high explanatory power (Table 1) and a generally significant negative relationship with MPD and PD (after accounting for SR) (i.e. lower phylogenetic richness and divergence with increasing elevation) in the Indomalayan, Palearctic, Australasian and Neotropic realms (Figure 3; Tables S4 and S5, p-values < 0.001 in all the realms with the exception of the PD after accounting for SR in the Afrotropics: E.d.f = 0.863, Ref d.f. = 2.000, $F = 1.3$, $p = 0.082$).

The human impact index did not show any general substantial pattern at this large scale, being also one of the variables with lower explanatory power (Table 1; Figure S5). However, it still showed significant relationships with PD and MPD in most biogeographic realms (Tables S4 and S5).

Land-use diversity and NPP did not explain much variability in PD (after accounting for SR), yet both variables correlated positively with raw PD in all the biogeographic realms (i.e. when the effect of SR was not removed) (Figures S6 and S7, respectively). On the other hand, the MPD (raw and standardised by SR) did not show strong overall patterns, but raw MPD tended to decrease with NPP in all the biogeographic realms but Australasia (Figure S7).

Overall, there was high variability but a tendency towards significant positive effects of land-use diversity, NPP and temperature on raw PD and MPD across biogeographic realms (Tables S4 and S5). In contrast, human impact index and elevation tended to display non-significant or negative relationships with raw PD and MPD (Figure 4).

4 | Discussion

Understanding how global change drivers can reshape the phylogenetic diversity of species assemblages at large scales is essential for biodiversity conservation because the amount of PD and MPD in a community sets the basis for its adaptive potential and ecological singularity/redundancy (Gumbs
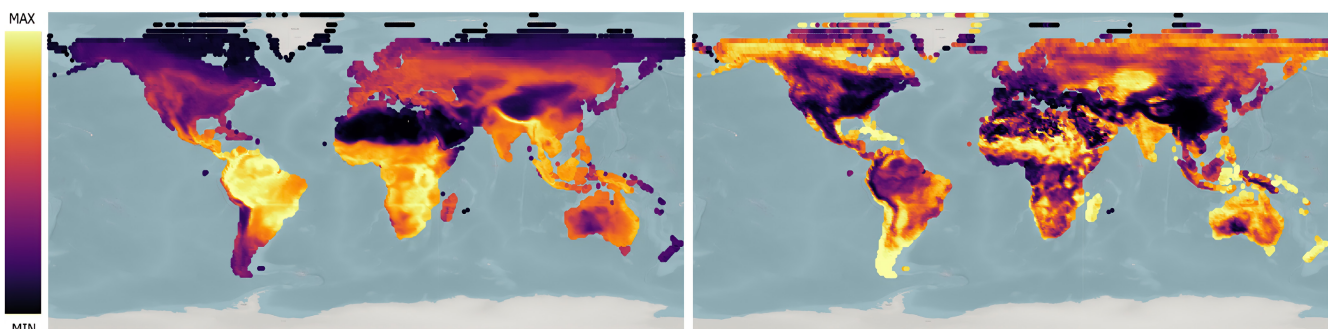

FIGURE 1 | Global distribution of bird raw phylogenetic richness (PD) and raw phylogenetic divergence (MPD). Base map made with QGIS. On the left, PD distribution map, and on the right, MPD distribution map.

TABLE 1 | Relative importance of environmental predictors to explain PD and MPD (raw and standardised by SR).

Response variable	Environmental predictor	R-sq	AIC
Raw PD	Null model	0.605	−23,139
Raw PD	Elevation	0.634	−24,321
Raw PD	Human Impact	0.690	−26,934
Raw PD	Land-use diversity	0.730	−29,137
Raw PD	**Temperature**	**0.759**	**−30,922**
Raw PD	**NPP**	**0.766**	**−31,332**
Raw PD	All the predictors	0.988	−37,924
PD_SR	Null model with SR	0.988	−77,512
PD_SR	NPP	0.988	−77,016
PD_SR	Elevation	0.988	−78,363
PD_SR	Land-use diversity	0.989	−79,403
PD_SR	**Human Impact**	**0.990**	**−80,756**
PD_SR	**Temperature**	**0.990**	**−81,370**
PD_SR	All the predictors	0.992	−84,119
Raw MPD	Null model	0.253	−65,995
Raw MPD	Human Impact	0.281	−66,551
Raw MPD	Land-use diversity	0.287	−66,528
Raw MPD	NPP	0.302	−66,677
Raw MPD	Elevation	0.382	−68,972
Raw MPD	**Temperature**	**0.419**	**−69,948**
Raw MPD	All the predictors	0.564	−72,633
MPD_SR	Null model with SR	0.351	−68,220
MPD_SR	Land-use diversity	0.362	−68,244
MPD_SR	Human Impact	0.363	−68,470
MPD_SR	NPP	0.384	−68,623
MPD_SR	**Temperature**	**0.452**	**−70,872**
MPD_SR	**Elevation**	**0.463**	**−71,166**
MPD_SR	All the predictors	0.590	−73,715

Note: Response variables are raw PD (Fath's Distance), raw MPD (Mean pairwise distance), as well as standardised PD and MPD when models include SR as a covariate. Marginal R-squared (R-sq) and AIC show the goodness of fit of each gam model. Models are ordered by response variable and sorted from least to most explicative. The most explicative variable in every metric is highlighted in bold (two are highlighted when differences in R-sq are very low).

et al. 2023; McClure et al. 2023). In this study, we unveil the generalised and consistent role of temperature and the importance of other factors on bird regional phylogenetic diversity worldwide. These results are valuable for understanding macroecological biodiversity patterns, anticipating global-change impacts (e.g. climate change) and guiding conservation strategies.

The SR of many taxa has been linked to global latitudinal patterns. In this regard, the higher richness of species towards the tropics has been attributed to climate, how climate is distributed in the world (i.e. the biogeography of climate) (Coelho et al. 2023) or the higher energy and net primary productivity

in these regions. In line with our first hypothesis, our results unveil that mean annual temperature is a key predictor, consistently and positively associated with bird PD and MPD across the six main biogeographic realms (after removing the effect of SR and latitude). Several mechanisms might explain why warmer regions can support bird assemblages with higher phylogenetic diversity. Among the most important ones are: (i) higher climatic stability in warm areas can promote species range expansions (Carbonell and Stoks 2020; Erwin 2009); (ii) accelerated rates of climatic-niche evolution (Kozak and Wiens 2010) and (iii) and the fact that most clades originated during warm periods (Bennett et al. 2021), allowing more opportunities for speciation. These results are
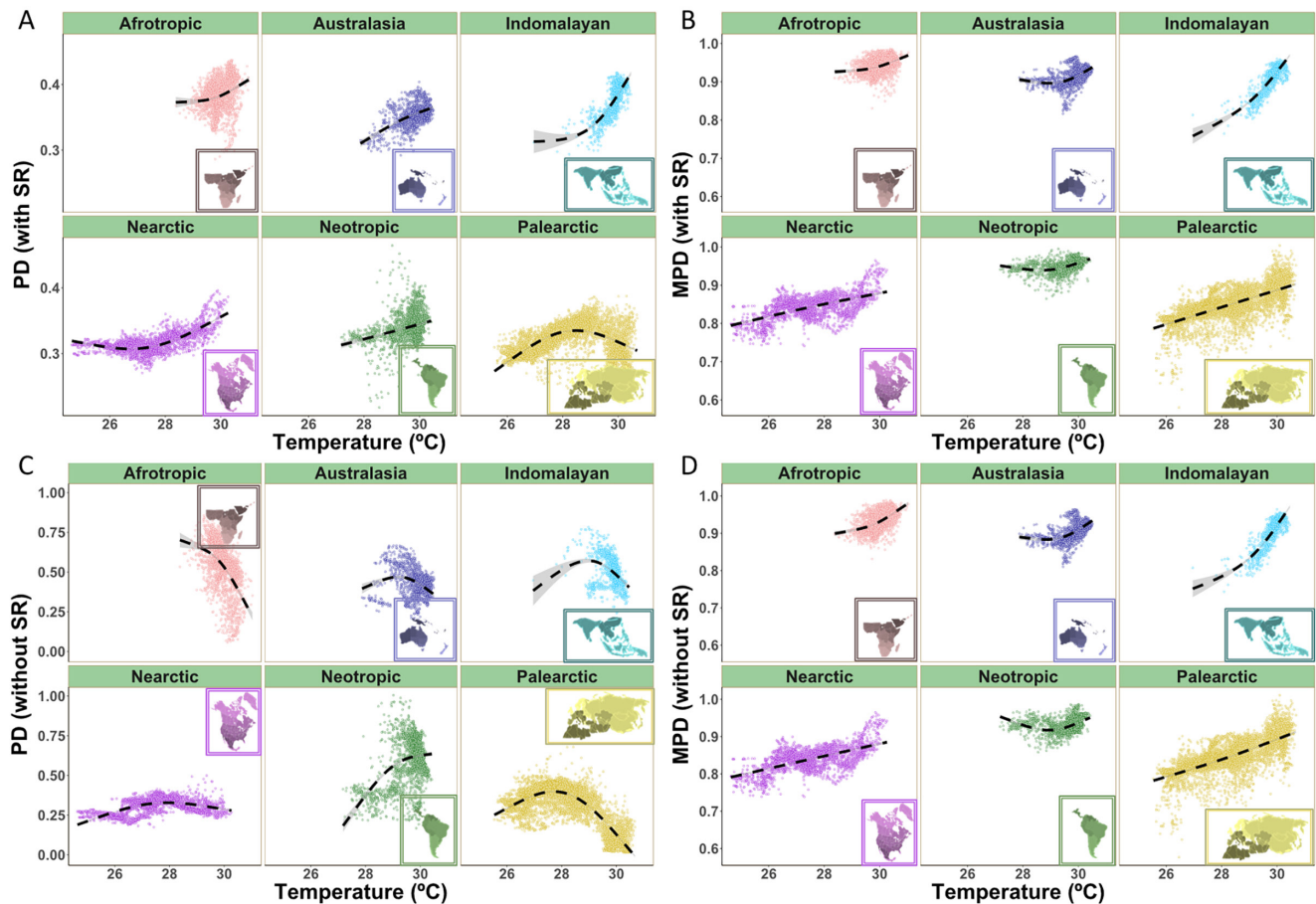
FIGURE 2 | Relationship between mean annual temperature (°C) and bird regional phylogenetic diversity across biogeographic realms (PD and MPD raw and standardised by SR). The plots in A and B represent PD and MPD values with SR in model (standardised by SR). Pannels C and D show raw PD and MPD (without standardising by SR). Pannels A and C explain variation in PD, while B and D represent variation in MPD. Metrics have been normalised between 0 and 1 (dividing their value by the maximum value). Every point represents the effect of the average annual temperature on the corresponding metric. The black line shows the model fit, and the line shadows represent the 95% confidence interval. There are 2616 grid cells (i.e. points) in the Nearctic, 2255 grid cells in the Neotropic, 6106 grid cells in the Palearctic, 2462 grid cells in the Afrotropic, 1199 grid cells in the Australasian and 1076 grid cells in the Indomalayan. Icons from biogeographic realms were obtained and modified from Wikimedia Commons, shared by user Carolspears under Creative Commons licence (CC BY-SA 3.0).

in line with ecological hypotheses developed for other groups and should be considered in order to protect and study warmer areas. Particularly, because they could be a shelter for phylogenetic diversity (Pollock, Thuiller, and Jetz 2017), with relatively low vulnerability to future scenarios of species extinctions (Martínez-Núñez, Martínez-Prentice, and García-Navas 2023b; Weeks et al. 2022). Nonetheless, the fact that raw PD decreased in regions with very high temperatures (especially in the Afrotropic realm) raises alarms about the possible negative impacts of climate change in already dry and warm areas (Saladin et al. 2020). Particularly in the Afrotropic, where the lack of water availability associated with these hot regions might pose extreme conditions and hard ecological constraints (Šímová et al. 2011). The fact that temperature was one of the most important predictors and the only one that showed consistent trends across the studied biogeographic realms partly supports our second hypothesis and raises alarms about the generalised potential impact of climate change on the phylogenetic structure of bird assemblages worldwide. In effect, a recent study has suggested that likely climate change scenarios could have profound impacts on bird

phylogenetic diversity globally, with stronger losses in tropical and subtropical areas (Voskamp et al. 2022). However, our second hypothesis was not fully sustained because the other studied factors also showed high, and sometimes similar, predicting capacities as temperature.

Our third hypothesis was partly supported by our results, because elevation tended to be negatively associated with regional bird phylogenetic richness (PD) (after controlling for SR) and with MPD (i.e. with and without SR) in all the biogeographic regions. The Afrotropic realm, where there were very few regions with a median elevation above 1000 m, was an exception. Elevation has shown a variable but often negative association with bird diversity (Hanz et al. 2018; Hoiss et al. 2012; Jarzyna, Quintero, and Jetz 2021; McCain 2009; Montaño-Centellas, McCain, and Loiselle 2020). The interplay between water and food availability, temperature, vegetation type and cover, and radiation in different regions can explain the complexity of relationships between elevation and bird communities found in different mountain systems across the world (Jarzyna, Quintero, and Jetz 2021). The prevailing
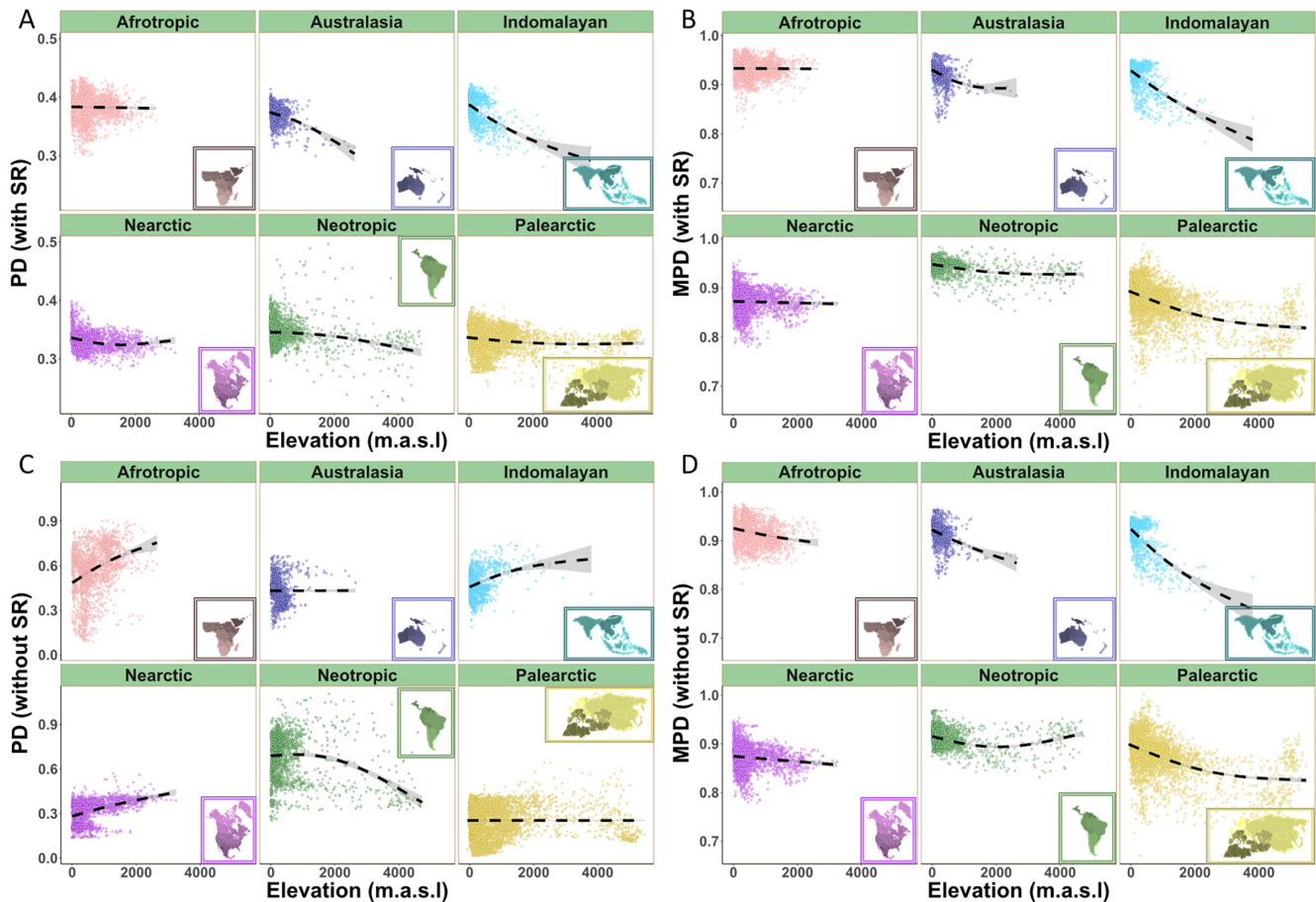
FIGURE 3 | Relationship between median elevation (meters above sea level) and bird regional phylogenetic diversity across biogeographic realms (PD and MPD, raw and standardised by SR). The plots in A and B represent PD and MPD values with SR in the model (standardised by SR). Panels C and D show raw PD and MPD (without standardising by SR). Panels A and C explain variation in PD, while B and D represent variation in MPD. Metrics have been normalised between 0 and 1 (dividing their value by the maximum value). Every point represents the effect of elevation in the corresponding metric. The black line shows the model fit, and the line shadows represent the 95% confidence interval. There are 2616 grid cells (i.e. points) in the Nearctic, 2255 grid cells in the Neotropic, 6106 grid cells in the Palearctic, 2462 grid cells in the Afrotropic, 1199 grid cells in the Australasian and 1076 grid cells in the Indomalayan. Icons from biogeographic realms were obtained and modified from Wikimedia Commons, shared by user Carolspears under Creative Commons licence (CC BY-SA 3.0).

negative associations have been attributed to environmental filtering (i.e., solar radiation, extreme temperatures and water availability) (Cavender-Bares et al. 2009; Hanz et al. 2018; Hoiss et al. 2012). Regions in high elevations (e.g. mountains) can behave in a similar way to islands from an ecological perspective due to their isolation and the prevailing strong ecological constraints. Hence, apart from species filtering, limited speciation might contribute to explaining why we found less PD and MPD at higher elevations, although some important studies report high diversification rates (of related lineages) in such constraining environments (Quintero and Jetz 2018). Lastly, non-random patterns of invasion and extinction can contribute to reduced phylogenetic diversity in bird assemblages on island-like ecosystems (Baiser et al. 2018).

The human impact index has often been negatively associated with bird phylogenetic diversity in many studies at local or landscape scales (Concepción et al. 2017; Matuoka et al. 2020). Loss of species and biotic homogenisation could be the main mechanisms reducing phylogenetic diversity at these levels (Sol et al. 2017; Clergeau et al. 2006). Our fourth hypothesis was

not fully met since we found a negative correlation between human impact index and raw PD, with a unique exception in the Afrotropic region, where we found a positive pattern. This response is likely explained by the loss of species and evolutionary history in highly anthropised areas. Nonetheless, the exception in the Afrotropics could be explained by a lower intensity of human impact in these areas, where human impact at the regional scale may even increase the availability of niches instead of decreasing them, resembling the intermediate perturbation hypothesis (Molino and Sabatier 2001). A global study found a similar humped-shaped pattern on raptor phylogenetic diversity as a response to human perturbation (Montaño-Centellas, 2023). However, we did not observe any significant relationship with MPD or PD after controlling for SR, probably because the human impact index has stronger local or landscape effects (Frishkoff et al. 2014; Sol et al. 2017) that may not be significant at these bigger scales.

Regions with high net primary productivity and land-use diversity (which are two variables relatively correlated at a global scale: Pearson: $r = 0.5$, p-value < 0.001) can provide a high number
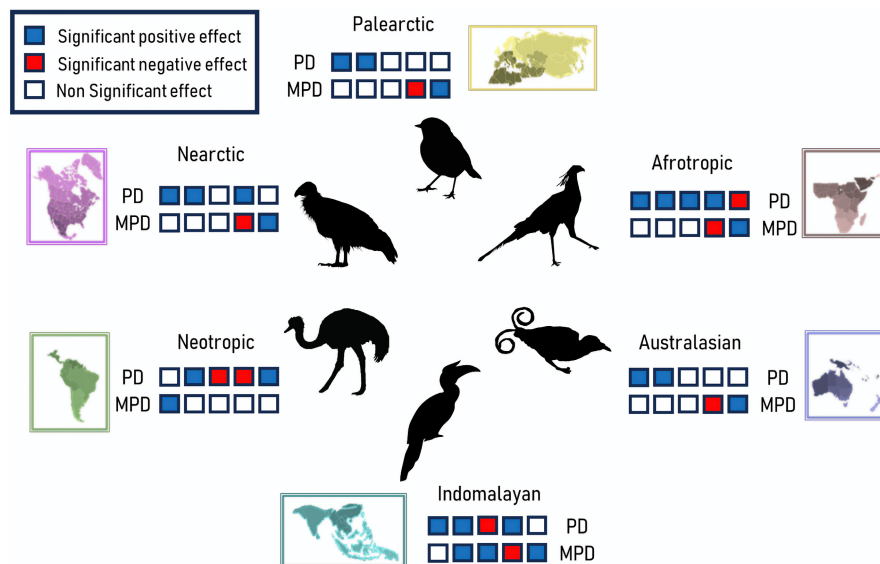
FIGURE 4 | Effect of each studied environmental factor on raw PD and MPD across biogeographic regions. The order of the variables is: Land-use diversity, NDVI, human impact index, elevation and mean annual temperature. Bird species profiles were obtained from http://phylopic.org and represent (ordered clockwise from the palearctic): *Erithacus rubecula*, *Sagittarius serpentarius*, *Diphyllodes respublica*, *Buceros rhinoceros*, *Rhea americana* and *Gymnogyps californianus*. Images from biogeographic realms were obtained and modified from Wikimedia Commons by user Carolspears under a Creative Commons licence (CC BY-SA 3.0).

of habitats, resources and available niches (Tucker et al. 2018), increasing bird taxonomic and functional diversity worldwide (Martínez-Núñez, Martínez-Prentice, and García-Navas 2023a). As species that use similar niches are often more functionally and phylogenetically related to each other than species that exploit very different niches (i.e. niche conservatism) (Stevens et al. 2012), it is expected that a higher NPP and land-use diversity will increase the phylogenetic diversity of birds in the region (Rurangwa et al. 2021; Stein, Gerstner, and Kreft 2014). Our results partly supported our fifth hypothesis, as while raw PD was positively associated with these environmental factors, there was no overall pattern with MPD or PD after controlling for SR. This suggests that the mechanism by which PD increases in regions with high NPP and land-use diversity relies mainly on the accumulation of more species that use the different habitats and niches. However, these species are to some extent phylogenetically similar to the ones already present in more homogeneous regions (at least not more different than a random accumulation of species), since raw and standardised MPD did not show a generalised positive association. This limitation in phylogenetic distance due to the availability of more diverse niches or habitats could be explained by larger scale restrictions such as climatic or biogeographic constraints.

In conclusion, this study unveils the critical role that temperature and other factors play in modulating the global evolutionary diversity of birds and highlights the necessity for coordinated conservation efforts that take into account these multiple environmental factors. The clear, consistent and widespread effect of temperature contrasts with the realm-dependent links observed with other biodiversity-structuring factors such as elevation, human impact index, land-use diversity and net primary productivity, suggesting that warm (but not extremely hot and arid) regions can concentrate a higher amount of evolutionary history worldwide, independently from SR. The processes by which temperature modulates the intrinsic capacity of environments to

support more diverse lineages of species still need to be further explored. However, we now know that intense and fast changes in mean temperatures driven by climate change could have deep moderating impacts on the amount of bird phylogenetic diversity that different regions can support across the globe, beyond species-specific extinctions or range shifts. In addition, the insights we provide here, showing the general large-scale association between key environmental factors and the amount of bird evolutionary history accumulated at the regional scale, have important implications for guiding conservation strategies and underscore the urgency of preserving Earth's avian diversity in the face of ongoing global change. Future studies should delve into the mechanisms driving these associations and the influence of likely scenarios of global change on the capacity of regions to support a complex phylogenetic structure in bird assemblages. As we navigate an era of unprecedented global change, the preservation of genetic diversity and evolutionary history within bird assemblages becomes increasingly paramount for the resilience and adaptability of these communities in the face of evolving environmental challenges.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code used to support the findings of this study are openly available in 'Figshare' at https://doi.org/10.6084/m9.figshare.24224263.v1.

Peer Review

The peer review history for this article is available at https://www.webof science.com/api/gateway/wos/peer-review/10.1111/ddi.13930.

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Supporting Information

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