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RESEARCH ARTICLE

Global variation in the relationship between avian phylogenetic diversity and functional distance is driven by environmental context and constraints

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Abstract

Aim: If evolutionary distance is akin to evolutionary chance, then it follows that species assemblages that are distantly related will also be more disparate in terms of their traits, features and the niches they occupy. Yet, studies have found that the total phylogenetic distance of an assemblage, known as phylogenetic diversity, is an unreliable surrogate for functional diversity. We investigate global variation in the relationship between Faith's phylogenetic diversity (PD) and mean pairwise functional distance (MPFD) across latitude and the influence of migratory species on both these aspects of diversity.

Location: Global.

Time period: Present day.

Major taxa studied: Birds.

Methods: We measure PD and MPFD for over 9000 species of bird across more than 17,000 globally distributed assemblages. We obtain standardised effect sizes for both indices by simulating assemblage composition under an ecologically informed null model. We employ path analysis to characterize variation in the relationship between PD's and MPFD across latitude, elevation and with proportion of migratory species.

Results: Globally, assemblages that were phylogenetically diverse tended to be less functionally dispersed than expected; however, this relationship showed considerable variation across latitude decreasing with distance from the equator. The proportion of migratory species in an assemblage was found to be an important predictor of functional diversity, with migrant rich assemblages generally showing less functional diversity than expected. We identify the Andes and Hengduan Mountains as regions of exceptional bird functional diversity.

Main conclusions: The relationship between phylogenetic diversity and function diversity is context specific, varying across environmental gradients such as latitude, and influenced by ecological phenomena such as migration. Thus, care should be taken using phylogenetic diversity as a proxy for functional diversity, particularly in clades with sparse functional data. Instead, we recommend that studies consider how phylogenetic diversity's surrogacy for functional diversity may be impacted by environmental context and evaluate empirical observations against biogeographically constrained and ecologically informed null models.

1 | INTRODUCTION

Phylogenetic diversity quantifies the shared evolutionary history of an assemblage of taxa. In its original form as described by Faith (1992), for a given set of species, Faith's phylogenetic diversity (PD) is simply the sum of the length of the branches that connect those species on a phylogenetic tree. Faith (1992) originally proposed PD as way to capture the feature diversity of an assemblage, where feature is a catch-all term for any component of species' phenotype. Feature diversity is difficult to measure—it is not always clear how to delineate between features or how to quantify them—and problematic for comparisons: imagine trying to compare the feature diversity of frogs and wasps. Yet, measuring feature diversity as a component of biological diversity would be a valuable endeavour, particularly from the perspective of nature conservation, where it has been argued that preserving feature diversity is a hedge-betting strategy for protecting features that may be ecologically important (Cadotte et al., 2010; Safi et al., 2011) or have some future utility (Faith, 1992; Forest et al., 2007).

PD's surrogacy for feature diversity is predicated on the assumption that there is some relationship between how much evolutionary distance a group of species are separated by and how distinct they are from one another in terms of their traits and ecology. At face value, this seems a reasonable assumption. Longer branches, whether they represent genetic distance or time, indicate more opportunity for evolutionary change and thus more opportunity for acquiring unique traits and adapting to novel niches (Faith, 2018). Thus, all else being equal, we might expect that groups of species that are more phylogenetically diverse would also be more feature diverse.

Whether PD is a reliable surrogate of feature diversity remains an open question (Cadotte et al., 2017; Tucker et al., 2019), and empirical studies have found mixed support for the assumption (Kelly et al., 2014; Pollock et al., 2017). For example, Mazel et al. (2018) found that selecting assemblages of birds and mammals that maximized PD on average preserved 18% more functional diversity than selecting assemblages at random. However, the effect was inconsistent, as in more than one-third of their comparisons: the sets selected for maximum PD contained less functional diversity than the random sets. In contrast, Cadotte et al. (2008) found PD did predict the biomass production and the number of functional groups in grasslands, which is considered a proxy itself for functional diversity. However two subsequent works on similar study systems found only a weak association between PD, biomass productivity and functional diversity (Flynn et al., 2011; Venail et al., 2015).

It is important to note that these studies sought to identify a relationship between PD and functional diversity, rather than the feature diversity of Faith's original proposition (Faith, 1992). While feature diversity is a catch-all for all the constituent characteristics of a species, functional diversity generally refers specifically to the diversity of traits that are directly relevant to a species' ecological function (Naeem et al., 2012). This means that researchers must choose which traits they think are relevant to their measure of functional diversity. Thus, the traits selected in these studies may be too narrow a slice of a species' characteristics to reliably capture feature diversity (Owen et al., 2019). For example, a simulation study found that the more traits used to calculate functional diversity, the stronger its relationship with phylogenetic diversity (Tucker et al., 2018).

Instead of focusing on whether phylogenetic diversity is a universally good proxy for functional diversity, we consider why the relationship holds in some contexts and not in others. For example, it has been shown that PD's ability to predict functional diversity is weaker when the traits used to derive functional diversity have evolved under models with shifting rates and optima (Tucker et al., 2018). If evolutionary dynamics mediate the relationship between these two facets of diversity, then variation in the strength of the relationship may in part be determined by environmental and evolutionary context. Similarly, both PD and functional diversity have been shown to be structured along gradients of environmental harshness (Botero et al., 2014; Skeels & Cardillo, 2019; Skeels et al., 2020). Elevation determines the phylogenetic relationships among ant assemblages, with high-elevation assemblages tending to be on average more phylogenetically clustered than low-lying groups (Machac et al., 2011), and phylogenetically over-dispersed communities of hummingbirds in Ecuador are associated with low elevations and high humidity (Graham et al., 2009). Jarzyna et al. (2021) performed one of the largest studies to date on the relationship between PD and functional diversity in birds—an ideal system due to their global distribution and availability of spatial, phylogenetic and functional data. They found that both functional diversity and PD showed latitudinal and elevational trends and that the strength of their association was stronger at higher latitudes. This implies that PD's ability to act as a surrogate for functional diversity improves with distance from the equator. However, Jarzyna et al.'s study was limited to the world's mountainous regions and so it is unclear if their findings are generalizable to non-mountainous bird assemblages. Additionally, when estimating functional diversity, they used only a single morphological measurement, body mass, as well as three broad categorical ecological traits, nocturnality, diet and foraging niche. If the relationship between PD and functional diversity is determined by evolutionary and environmental context in birds, then we should expect to see these patterns hold on a global scale and when increasing the number of morphological characters used to define functional diversity.

Another factor which could influence patterns of functional and phylogenetic diversity in birds is migration. One in five species of birds move twice yearly from breeding to non-breeding grounds, a phenomenon that vastly changes the species composition of communities all across the globe (Somveille et al., 2015). It is well-recognized that the contribution of migratory bird species to assemblage richness increases with latitude (Somveille et al., 2013) and peaks at the highest latitudes in the Northern Hemisphere. There are good reasons why we might expect migration to have an impact both on functional and phylogenetic diversity. While there is little consensus on exactly which traits are associated with migration in birds (Salewski & Bruderer, 2007; Soriano-Redondo et al., 2020), some traits have been shown to vary with migration. For example, migratory species of birds tend to have faster life histories and be smaller than resident species (Soriano-Redondo et al., 2020) and brain size relative to body size has been found to decline with distance migrated (Vincze, 2016). Thus, if migratory species tend to fall within particular regions of morphospace compared to non-migratory species, this could impact on patterns of functional diversity, particularly as the proportion of migratory species is expected to increase with latitude. While migration has arisen independently in birds several times, the majority of migratory species belong to three orders, the Anseriformes (waterfowl), Charadriiformes (shorebirds) and Passeriformes (Dufour et al., 2020), and so it may be that assemblages with a high proportion of migratory species are on average more phylogenetically clustered than assemblages with fewer migratory species. It is reasonable to ask whether migration itself plays a part in driving the effect of latitude on either functional or phylogenetic diversity.

Here, we set out to explore how the relationship between PD and functional diversity in bird assemblages varies across latitudinal gradients. Using the recently published AVONET dataset (Tobias et al., 2022) and a near complete phylogeny for birds (Jetz et al., 2012), we calculated the phylogenetic diversity and functional diversity for over 17,000 globally distributed bird assemblages (Weeks et al., 2022), to characterize the association between these indices across key environmental gradients and global regions.

2 | METHODS

2.1 | Assemblage, morphological and phylogenetic data

More than 17,000 bird assemblages were taken directly from Weeks et al. (2022). These were created from a 110 km x110 km grid (roughly 1° latitude and 1° longitude at the equator, Behrmann projection), and excluded all non-terrestrial cells (>50% ocean or >70% inland water) and all cells below 60° south. Species composition was determined using species range maps from Birdlife International, and included resident, breeding and non-breeding portions of species ranges. For measurements of functional disparity, morphological data for more than 10,000 species of bird were obtained from the AVONET database (Tobias et al., 2022). To measure PD, we used the same phylogeny as Weeks et al. (2022), which is a 50% majority rules consensus tree based on 1000 phylogenies taken from the posterior distribution of Jetz et al. (2012) with the Hackett et al. (2008) phylogeny used as a backbone.

2.2 | Phylogenetic diversity and functional disparity

We calculated mean pairwise functional distance (MPFD) and Faith's PD (Faith, 1992) for each of the 17,099 assemblages defined by Weeks et al. (2022). MPFD was estimated using the same six ecologically important functional effect traits used to characterize functional richness by Weeks et al. (2022), including total beak length, beak tip to the anterior edge of the nares, beak width, beak depth, tail length and tarsus length. All traits were corrected by dividing by species body mass. We elected to use these six morphological traits because it has been shown that at least four morphological trait axes are required to describe avian trophic niches and continuous morphological variables are better predictors of variation in dietary and behavioural niches than standard niche categories (Pigot et al., 2020). Trait data were then standardized to mean zero and standard deviation of one prior to analysis. MPFD was calculated by undertaking a principal coordinate analysis using the function 'quality.fspaces' from the R package *mFD* (Magneville et al., 2021; R Core Team, 2020). We elected to use MPFD because it is computationally efficient to calculate it for large datasets such as ours and it is statistically independent of species richness. Additionally we found that across all of our bird assemblages, MPFD was highly correlated with functional dispersion (Anderson, 2006; Laliberté & Legendre, 2010) another measure of functional diversity, which is statistically independent of species richness (Pearson's product–moment correlation, $r = 0.987$, $t = 804.71$, $\mathrm{df} = 17{,}097$, $p < 0.001$).

The *caper* package's 'calc.pd' function (Orme et al., 2018) was used to calculate PD. We elected to use Faith's PD rather than an alternative measure such as mean pairwise phylogenetic diversity because it was Faith's PD that was initially proposed as a proxy for feature diversity (Faith, 1992) and was routinely employed as a surrogate for functional diversity (Cadotte et al., 2008; Forest et al., 2007; Safi et al., 2011). We could have elected to use an index which was independent of species richness, such as mean pairwise phylogenetic diversity, but we believe that it is important that we remain consistent with the theoretical expectation of the literature. We note that the Jetz et al. (2012) phylogeny includes 3330 species whose phylogenetic position was estimated based on taxonomy and not molecular data. If the placement of these species in the majority rules consensus tree is biased this bias would likely carry over to measurements of PD. For example, if these species are consistently placed as the basal lineages of their genus, then this would inflate their branch length and thus the PD of any assemblage including them. While it is worth keeping this potential source of bias in mind, no other phylogeny of birds has the species coverage of the Jetz et al. (2012) tree and therefore for a global analysis of bird assemblages the advantage of being able to include almost all described species of birds outweigh the disadvantages of including this potential bias.

2.3 | Standardized effect sizes for PD and MPFD

PD is the sum length of the branches that connect a set of species on a phylogeny. Adding additional species to an assemblage will always increase the PD of the assemblage but the rate of increase will decline as species richness increases, simply because as species richness increases, more of the phylogeny is already represented by the species in the assemblage, and thus the amount of extra PD a new species can contribute shrinks. We expect the relationship between PD and species richness to be positive but with a rate of exponential decay. MPFD is a measure of central tendency, the average distance between all possible pairs of species in an assemblage in morphospace. While MPFD is statistically independent of species richness, all else being equal, variance in MPFD will decline with species richness, as it converges on the global average of all birds. Thus, we have a strong expectation about how both PD and MPFD will change with increased species richness. To understand the relationship between MPFD and PD we need to understand how they change above and beyond this expectation. The simplest way to do this would be to compare the MPFD or PD of a real assemblage to that of a synthetic assemblage, where species composition was entirely random and drawn from a pool of all possible birds. While this would correct for our expectations given differences in species richness among assemblages, it would fail to account for another set of expectations, those arising from the fact that our assemblages themselves are not statistically independent observations.

The composition of an assemblage is a consequence of biogeographic history, and therefore, we cannot treat our assemblages as independent entities: assemblages that are near one another may share similar compositions because of their shared history and environment. For example, if we observe very different values in the PD of two assemblages that are next to each other, we need to be able to say that this difference is more significant than a difference of the equivalent size between two assemblages that are on opposite sides of the planet; the difference is more important because it does not conform to our expectations based on the spatial distribution of the assemblages. Thus, we need a way of comparing our observed values of MPFD and PD to our expectations given both the richness of our assemblages and their shared biogeographic history.

To do this, we compared the observed values of PD and MPFD to those simulated under a biogeographically constrained null model of community assembly (Gotelli, 2000; Miller et al., 2017). We developed our *regional null model* by dividing the world into 65 regions based on the intersection of Dinerstein et al.'s (2017) description of global biomes and geographic realms. For each assemblage, we could then sample *n* species at random from the relevant regions' species pool, where *n* is the empirical species richness. Importantly, these regions showed considerable variation in geographic size ranging from 236 to 17,023,070 km^2, with larger regions tending to occur at higher latitudes, although a Spearman's rank correlation test did not find this relationship to be significant (Rho = 0.242, $S = 347$, p-value = 0.052).

For each of the ~17,000 sites used in this study, we simulated 999 synthetic species assemblages under each of the null models and calculated the PD and MPFD of each. We then used these simulated values to obtain standardized effect sizes (SES) for each of the assemblages, such that

$$\mathrm{MPFD}_{\mathrm{SES}} = \frac{\mathrm{MPFD}_{\mathrm{observed}} - \mathrm{mean}\left(\mathrm{MPFD}_{\mathrm{simulated}}\right)}{SD\left(MPFD_{simulated}\right)} \tag{1}$$

$$\mathrm{PD}_{\mathrm{SES}} = \frac{\mathrm{PD}_{\mathrm{observed}} - \mathrm{mean}\left(\mathrm{PD}_{\mathrm{simulated}}\right)}{\mathrm{SD}\left(\mathrm{PD}_{\mathrm{simulated}}\right)} \tag{2}$$

An assemblage with $\mathrm{PD}_{\mathrm{SES}}$ score greater than zero is more phylogenetically diverse than expected under the null model, while a score of less than zero is less phylogenetically diverse than expected under the null model. Similarly, where an assemblage's $\mathrm{MPFD}_{\mathrm{SES}}$ is greater than zero it is more functionally dispersed than expected and, where it is less than zero, more functionally concentrated.

2.4 | Modelling the relationship between MPFD and PD

We are specifically interested in the relationship between MPFD and PD and the relationship between the standardized effect size of each. However, to isolate the direct effects of these aspects of biodiversity on each other, it is important that we account for biotic and abiotic effects that may act to confound our analysis (hereafter, indirect effects). For example, Jarzyna et al. (2021) showed that elevation influences both the functional and phylogenetic diversity of bird assemblages, and thus, it is essential that any analysis of the relationship of MPFD and PD or $\mathrm{MPFD}_{\mathrm{SES}}$ and $\mathrm{PD}_{\mathrm{SES}}$ takes into account the effect of elevation on both. Additionally, species richness itself may have an influence on both PD and MPFD beyond the direct statistical expectations outlined above which would carry through to our standardized effect sizes. For example, if negative interspecific interactions (such as reproductive interference or resource competition) between close relatives influence the assembly of communities, then functionally divergent and distantly related species might be preferentially selected for in diverse communities. Thus, even though we have corrected for the direct effect of species richness on PD and MPFD by using standardized effect sizes, it is still expedient to investigate its indirect effects on these indices. Additionally, the latitudinal biodiversity gradient means we can reliably assume that an assemblage's richness can be predicted in part by its distance from the equator. However, there are good reasons to suspect that absolute latitude may influence both PD and MPFD independently of its relationship via species richness. For example, differences in resource availability across the latitudinal gradient combined with the influence of past global temperature fluctuations on the expansion and contraction of the tropics, and the dispersal of species from the tropics to higher latitudes, all may mean that latitude influences both PD and MPFD independently of its relationship with species richness. Certainly, Jarzyna et al. (2021) showed not only that the latitude of a montane bird assemblage affected its PD and functional diversity, but that the relationship between the two itself varied with latitude. Thus, it is important that we consider both how latitude independently affects both MPFD and PD and also how its interaction with these two indices might affect the direct relationship between them. Finally, migratory species richness may independently drive MPFD and PD if migration enforces functional constraints and morphologies that are more common in particular lineages. All of these indirect effects may not be corrected for simply using standardized effect sizes, and so it important that when analysing the relationship between MPFD_{SES} and PD_{SES}, we also model the influence of these variables on these two facets of diversity.

Given the complex interplay of different predictors, we elected to employ path analysis. Path analysis is an extension of multiple regression that allows for situations where some predictor variables in a statistical model are dependent on other predictors in the model. Thus, our path analysis included four paths, for four different outcome variables, the MPFD_{SES}, PD_{SES}, proportion of migratory and species richness for each of our bird assemblages. Additionally, some of these paths will include the absolute latitude and average elevation of the grid cells as predictor variables. Absolute latitude was simply taken from the centroid of every grid cell while the average altitude was obtained for 16,979 of the assemblages from a summary of Bioclim data for each grid cell published by Weeks et al. (2022). To ascertain the proportion of migratory species within each of our grid cells, we used Dufour et al.'s (2020) list of migration characteristics for 9819 species of birds and treated any species which was recorded as strictly or partially migratory (some proportion of the population migrates) as a migratory species. We then calculated the proportion of species in each grid cell that were defined as migratory. We opted to use the Dufour et al. (2020) list of migratory species because it has good coverage and was recently published. Also, its taxonomy can be easily matched to that of the Jetz et al.'s (2012) phylogeny and the AVONET database (Tobias et al., 2022). All variables were scaled and standardized to a mean of zero and a standard deviation of one before the path analysis was conducted.

To isolate the direct effect between PD_{SES} and MPFD_{SES} while evaluating the relative influence of latitude on that relationship compared to the direct effect of migratory species, we fit three different versions of our model. In the most complex model, the MPFD_{SES} path includes both the proportion of migratory species and an interaction between PD_{SES} and absolute latitude as predictors. We then fit two reduced models, one which does not include an interaction between PD and latitude and one which does not include the proportion of migratory species as a predictor variable. These path analysis models were fit using the cfa function from the 'lavaan' package in R (Rosseel, 2012). We assessed model support using Bayesian information criteria (BIC).

We also considered the possibility that our observations show spatial autocorrelation beyond what can be accounted for using the biogeographically constrained null models. Therefore, we compared non-spatial path analysis to two spatially explicit path analyses that included one and two spatial bins for the data with a lag distance upper limit of 10% of the total distance between our assemblages. These models were implemented using the 'runModels' function in the R package *sesem* (Lamb et al., 2014) and great circle distances among each pair of sites was calculated using the 'rdist.earth' function in the R package *fields* (Nychka et al., 2021) and the grid cell's centroid.

3 | RESULTS

3.1 | Geographic distributions of function and phylogenetic diversity and relationships to geographic variables

Raw MPFD and PD scores are positively correlated (Figure 1a.) and this most likely reflects PD's dependency on species richness because, as expected, PD shows a quadratic relationship with species richness, with an overall increase with species richness but a decline in the rate of increase. Further, we can see that with increased PD, and thus increased species richness, the variance in MPFD declines as larger assemblages approach the global average of avian functional distance. In contrast, the standardized effect scores derived from the regional null show an overall negative relationship (Figure 1c) and a majority of assemblages (9609) were less functionally diverse ($\text{MPFD}_{\text{SES}} < 0$) but more phylogenetically diverse ($\text{PD}_{\text{SES}} > 0$) than expected. As expected, the relationships between MPFD and MPFD_{SES} and PD and PD_{SES} are positive (Figure S1).

Looking at the geographic distribution of the MPFD_{SES} (Figure 2), we see that those few assemblages with positive values tend to be concentrated in areas such as the northern Andes, the Hengduan mountains, as well as high latitude regions in North America and Eurasia. We also note that the Amazon basin appears to show remarkably low MPFD_{SES}, suggesting it is much more functionally concentrated than the expectations of our regional null model. When MPFD_{SES} is plotted against latitude (Figure 1d), we can see that it reaches its lowest just south of the equator, likely reflecting the effect of the Amazon basin, and shows a number of peaks which coincide with the latitude of the Northern Andes, Hengduan Mountains and the aforementioned regions of North America and Eurasia. Areas with higher than expected PD were much more widespread compared to MPFD, including much of South and Central America, South and East Asia, and sub-Saharan Africa. Again, we can see the impact of these regions when PD_{SES} is plotted against latitude. What is of particular interest here is that at the same northern latitudes where we see a peak in MPFD_{SES}, we also see a lot of assemblages with low PD_{SES}. This suggests that at these high latitudes in North America and Eurasia we have a set of assemblages which are made up of functionally distinct but closely related. These are the same assemblages where we see the proportion of migratory species in an assemblage consistently exceeding 75% (Figure 2).

We find no evidence that average regional PD_{SES} or species richness are influenced by region size (see Figure S2). Average regional MPFD_{SES} showed a statistically significant association with region size ($ß = -0.223$, 95% CI [−0.436 to −0.009], $p = 0.041$), however with considerable unexplained variance (Adjusted $R^2 = 0.068$). As only one of these indices showed some association with region size, we can be confident that differences in the size of our regions are not driving the results of our null model. To ensure that the species composition of our simulated assemblages showed a realistic relationship to distance, we fit non-linear decay models of beta diversity to both the simulated and empirical assemblages (see Figure S3).

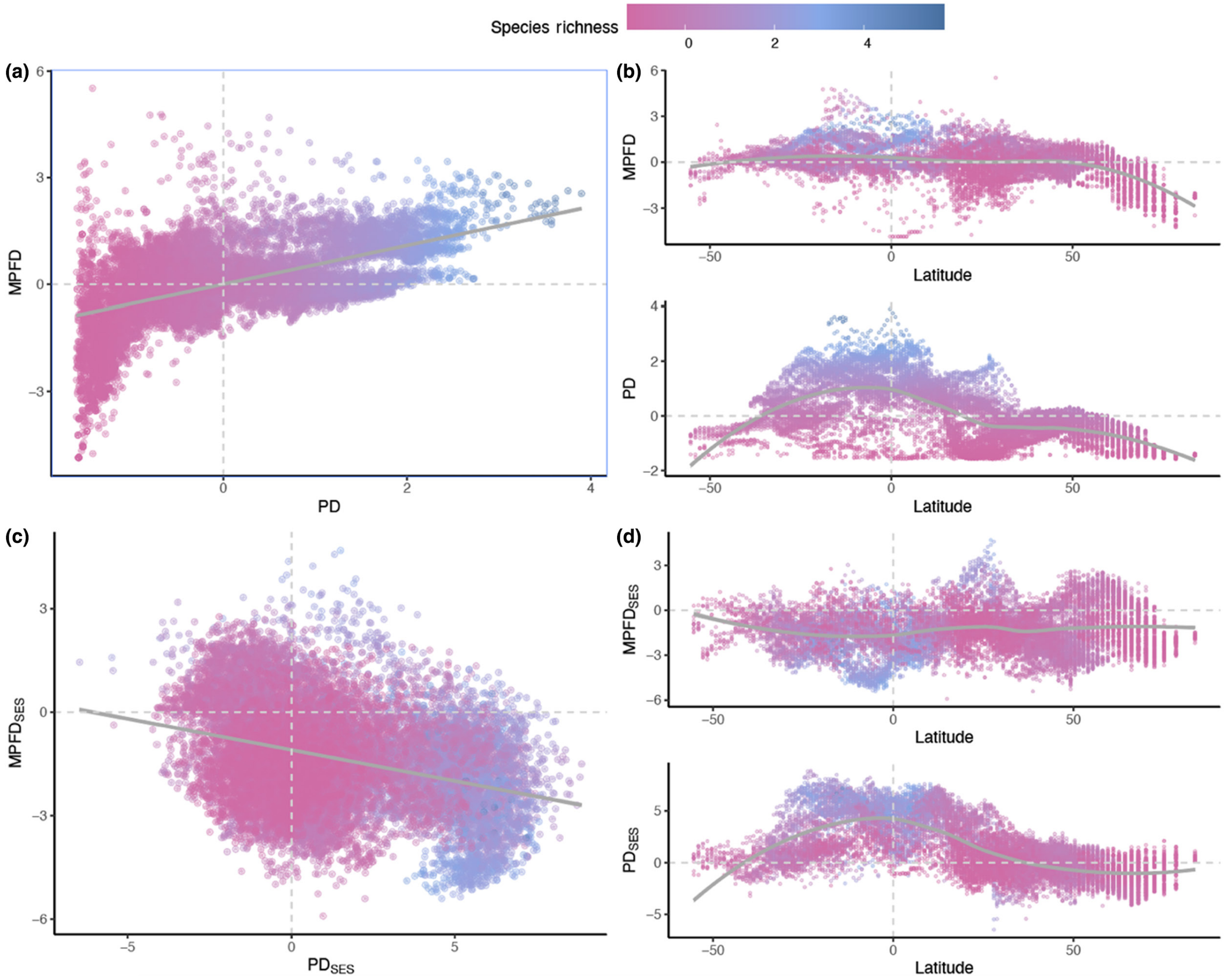

FIGURE 1 Scatterplots of the standardized phylogenetic diversity and mean pairwise functional distance ($\mu = 0$, $\sigma = 1$) values plotted against each other (a) and latitude (b), and the standardized effect scores of the two indices plotted against each other (c) and latitude (d). Colours of the points are universal between the plots and show the standardized species richness ($\mu = 0$, $\sigma = 1$) of each assemblage.

3.2 | Drivers of functional and phylogenetic diversity

Among the non-spatial path analyses, the model with the lowest BIC was the model which included both the proportion of migratory species and the interaction between PD$_{\text{SES}}$ and latitude as predictors of MPFD$_{\text{SES}}$ (Table S1). Figure 3 shows path diagrams for this model, including the unstandardized coefficients for each of the predictors, while Figure 4 shows the same coefficients for each model, their confidence intervals and the impact of the interaction between PD$_{\text{SES}}$ and latitude on the relationship between MPFD$_{\text{SES}}$ and PD$_{\text{SES}}$ (model coefficients are also provided in Table S2). All predictor coefficients reported in the text hereafter are taken from the best-fitting model, unless otherwise noted.

Across all three models we see several consistent relationships between MPFD$_{\text{SES}}$ and its predictors. For example, both altitude and species richness have very little effect on MPFD$_{\text{SES}}$ (Altitude, ß = 0.032, 95% CI [0.018 to 0.047], $p < 0.001$; Species richness, ß = −0.012, 95% CI [−0.032 to 0.007], $p = 0.205$), while latitude and its interaction with PD$_{\text{SES}}$ both showed a moderate and negative relationship (Latitude, ß = 0.108, 95% CI [0.072 to 0.143], $p < 0.001$; Latitude:PD$_{\text{SES}}$, ß = −0.15, 95% CI [−0.167 to −0.134], $p < 0.001$). The two most important predictors of MPFD$_{\text{SES}}$ were PD$_{\text{SES}}$ and migration. Both predictors were found to have a negative relationship with MPFD$_{\text{SES}}$ (PD$_{\text{SES}}$, ß = −0.323, 95% CI [−0.346 to −0.23], $p < 0.001$; Migration, ß = −0.298, 96% CI [−0.329 to −0.267], $p < 0.001$). The only predictor which did not have a consistent effect on MPFD$_{\text{SES}}$ across models was latitude. Latitude was found to be positively related to MPFD$_{\text{SES}}$ only in the models which included migration as an additional predictor. In the model which did not include migration, latitude was found to be negatively related to MPFD$_{\text{SES}}$ (ß = −0.159, 95% CI [−0.181 to −0.137], $p < 0.001$). This suggests that any decline in MPFD$_{\text{SES}}$ at higher latitude assemblages is better explained by the increase in the proportion of migratory species than latitude itself.

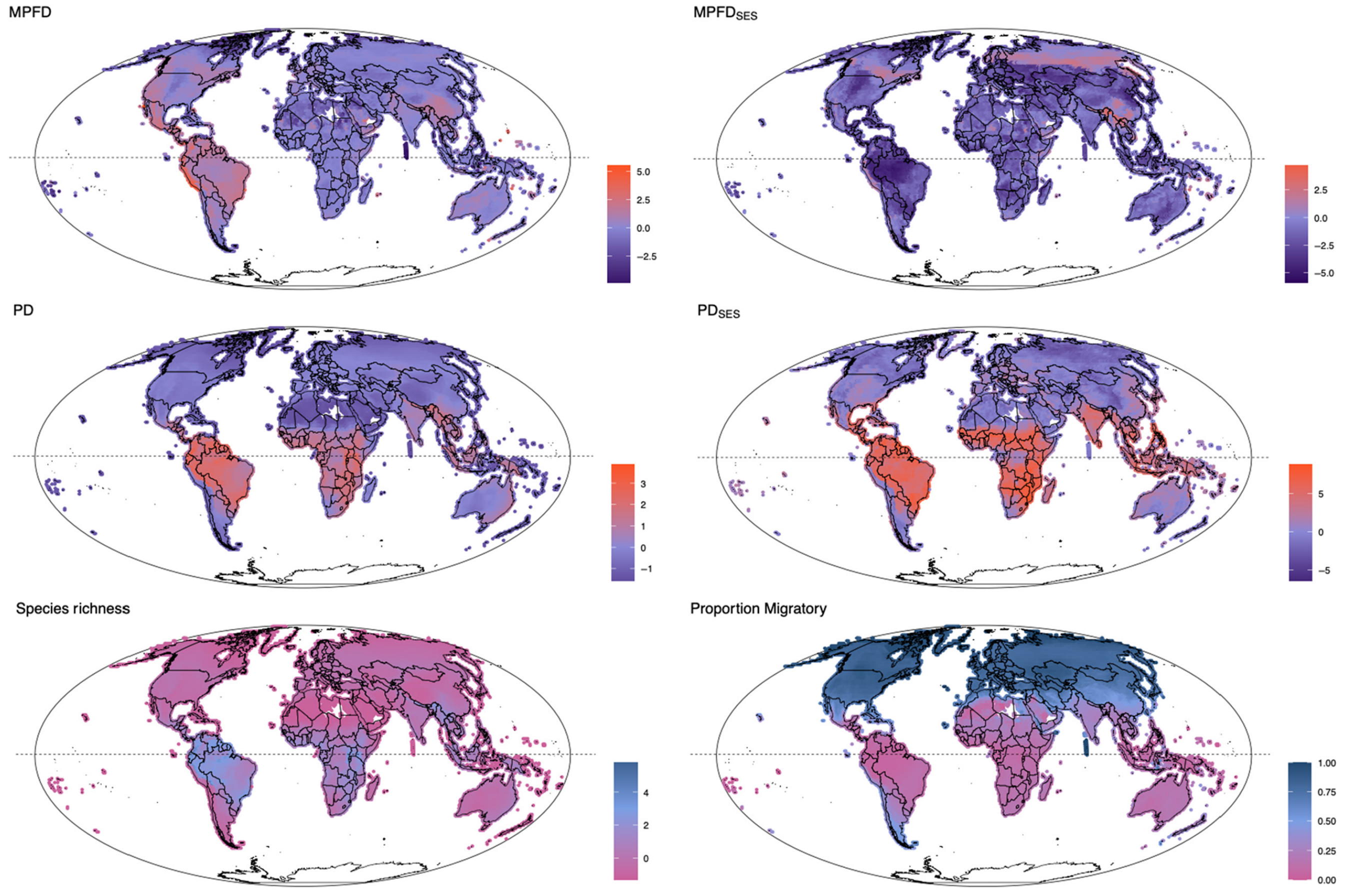

FIGURE 2 Geographical distributions of standardized phylogenetic diversity, mean pairwise functional distance ($\mu = 0$, $\sigma = 1$), standardized effect scores derived from the regional null model and the standardized species richness ($\mu = 0$, $\sigma = 1$) and proportion of migratory species for each of the grid cells.

The change of the $MPFD_{SES}$ ~ latitude relationships from positive to negative with the exclusion of migration as a predictor has important bearing on how we understand the effect of the interaction between latitude and PD_{SES}. Figure 4 shows the predicted slope of the $MPFD_{SES}$ ~ PD_{SES} relationship across different absolute latitudes. We can see here that while the slope of the two models which include the interaction term is almost identical, the intercept is different. In practice, while both models with interaction terms predict the relationship between these two indices to get lower with distance from the equator, only the model which also includes migration expects the relationship to be positive at some latitudes, anything less than approximately 50°. Under the model which does not include migration, the relationship between $MPFD_{SES}$ and PD_{SES} is negative at all latitudes.

The PD_{SES} pathway is highly consistent between models. The strongest predictor of PD_{SES} is latitude, which shows a negative relationship (ß = −0.417, 95% CI [−0.438 to −0.396], $p < 0.001$), followed by species richness, which shows a positive relationship. Altitude also shows a moderate negative relationship with PD_{SES} (beta = −0.167, 95% CI [−0.176 to −0.158], $p < 0.001$). Migration's impact on PD_{SES} is limited (ß = −0.078 m, 95% CI [−0.098 to −0.057)], $p < 0.001$). For our other two paths, the findings are unsurprising and consistent between models. Latitude is a very strong positive predictor of the proportion of migratory species in an assemblage (ß = 0.896, 95% CI [0.0889 to 0.902)], $p < 0.001$) but shows a negative relationship with its overall species richness. Altitude was found to have a marginal effect on species richness (ß = −0.567, 95% CI [−0.579 to −0.554], $p < 0.001$).

When these models were refit using the spatially explicit path analysis from the *sesem* package, we observed only slight changes in the coefficients between the non-spatial model and the two bins with different lag distances. Certainly, we did not observe any changes in the coefficient values between lag distance bins which would lead to a different interpretation than that provided for the results of the non-spatial model. This suggests that our findings are largely robust to the impacts of spatial autocorrelation, likely due to our use of a biogeographically constrained null model. Model fit summary statistics for the spatially explicit path analysis are provided in Table S3 and coefficient values are illustrated in Figure S4 and Table S4.

4 | DISCUSSION

Overall, sites with greater PD than expected tend to have lower MPFD than expected and vice versa, meaning that when distantly related species co-occur they tend to be functionally more similar to one another than our expectations, given a biogeographically constrained null model of community assembly. However, this global relationship belies the role that geography plays in mediating the relationship between functional and phylogenetic diversity, as we found strong evidence that latitude plays a role in mediating the strength and direction of the relationships between both PD_{SES} and $MPFD_{SES}$. Under a model which includes both the proportion of migratory species and the interaction between PD_{SES} and latitude as predictors, the relationship between PD_{SES} and $MPFD_{SES}$ shows a moderate positive relationship in the tropics. However, as we move away from the equator, that relationship weakens. At approximately 50° latitude this model predicts that there is no relationship between PD_{SES} and $MPFD_{SES}$, while at latitudes above this the relationship becomes increasingly negative. Put simply, in the tropics, PD_{SES}'s relationship to $MPFD_{SES}$ conforms to our theoretical expectations; assemblages which contain distantly related species tend to also be morphologically diverse. However, by the time we reach roughly the middle of the temperate zone, this relationship has broken down—an assemblage's PD_{SES} has no bearing on its functional diversity. At higher latitudes, where biomes shift from temperate forests and grasslands towards tundra in the northern hemisphere, we observed the opposite pattern to that of the tropics: assemblages made of distantly related species on average tend to be formed of morphologically similar birds. We also found that including migration as a predictor, drastically alters the effect of latitude on $MPFD_{SES}$, shifting it from a negative relationship to a positive one. This suggests that the apparent decline in $MPFD_{SES}$ at higher latitudes is largely explained by the increase in the proportion of migratory bird species in these regions. Once that effect is captured by another variable, it reveals a countervailing effect of latitude; that in fact, all else being equal, assemblages at higher latitudes will tend to be more functionally diverse.

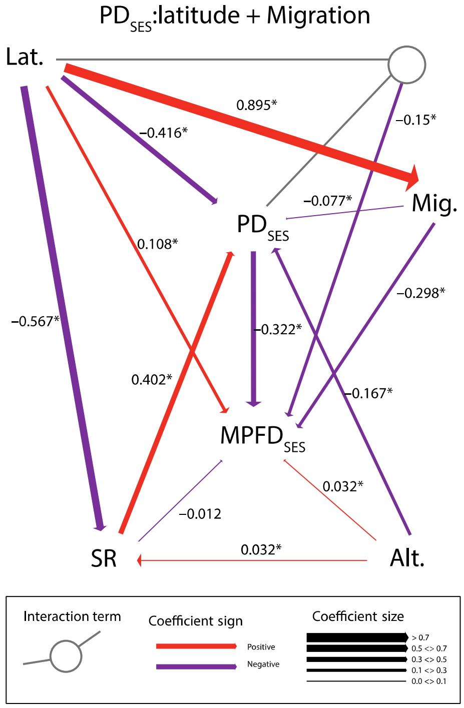

FIGURE 3 Path diagram of the best fitting non-spatial model. Numbers adjacent to arrows are the unstandardized regression coefficients of each predictor and an * indicates that the effect was significant (*p*-value <0.05).

Jarzyna et al. (2021) also found strong latitudinal variation in the relationship between richness-corrected functional diversity and phylogenetic diversity in their analysis of bird assemblages. However, their findings differ in terms of where the surrogacy of phylogenetic diversity for functional diversity was strongest. At low latitudes, Jarzyna et al. (2021) found that phylogenetically clustering

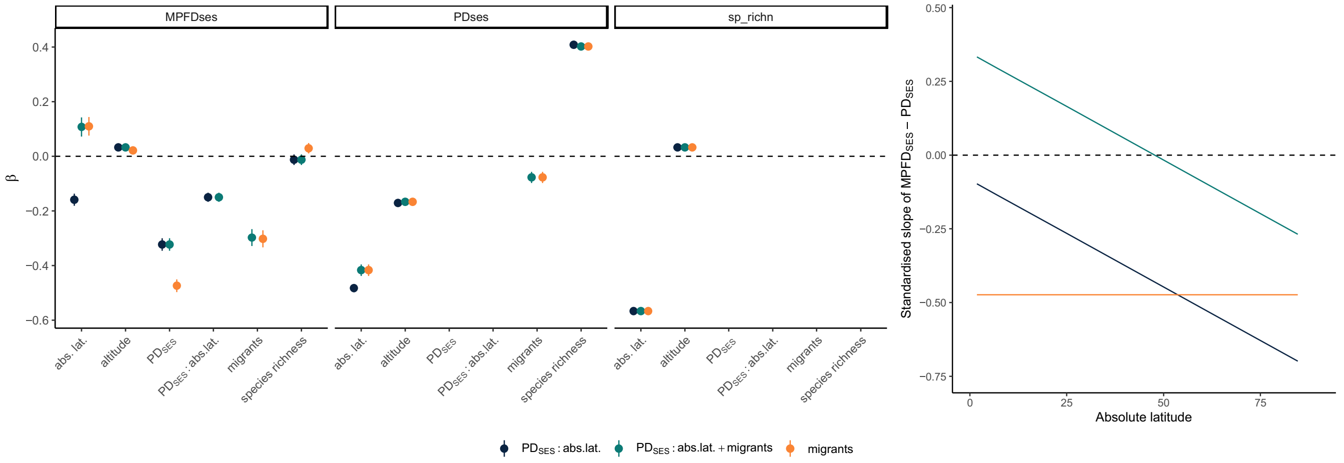

FIGURE 4 Results for the non-spatial path analyses for PD_{SES}-$MPFD_{SES}$ under the regional null. The first three windows show the estimated coefficients (points) and 95% confidence intervals (bars) for all predictors variables for the outcome variables $MPFD_{SES}$, PD_{SES} and species richness. The rightmost windows visualize the interaction, showing how the slope between PD_{SES}-$MPFD_{SES}$ changes with absolute latitude. The colours are universal across the figures and distinguish between the three different models, the model including the interaction effect between PD_{SES} and latitude (blue), the model including the interaction effect and proportion of migratory species (teal), and the model including just proportion of migratory species (orange).

or overdispersion appeared to have little relationship to the functional structure of an assemblage, while towards high latitudes functional and phylogenetic clustering became increasingly associated, although not in functionally over-dispersed assemblages. In contrast, we found that PD_{SES}'s surrogacy for $MPFD_{SES}$ was strongest at the lowest and highest latitudes, but weak in the temperate regions. Thus, a researcher might feel confident making predictions about a bird assemblage's functional diversity based on its phylogenetic diversity in the tropics where the relationship is positive, or the arctic where it is negative, but should be cautious in temperate regions where the relationship is weak to negligible.

Of course, there are a number of ways in which Jarzyna et al.'s (2021) study differs from ours that may explain the inconsistency between our findings and theirs. Their study was restricted to 46 mountainous regions while ours was global, and the spatial resolution of their data was much finer than our study. They also used a different measure of functional diversity (dendogram-based functional diversity and functional distinctiveness), which was estimated from body mass, nocturnality, diet and foraging niche, as opposed to our measure of functional dispersion, which was estimated solely from body mass corrected morphological traits.

Taken collectively our findings show that the surrogacy of PD_{SES} for $MPFD_{SES}$, largely depends on the geographical context of the assemblage being studied. At face value, our findings suggest it would be reasonable to use PD_{SES} to predict functional diversity at high-latitudes and in the tropics but not in the temperate regions of the planet, so long as the direction of the relationship is accounted for. However, we caution against such an interpretation. It is our strong suspicion that the importance of the interaction term in our model really reflects the inadequacy of imposing a linear model onto a non-linear relationship.

4.1 | Regions of exceptional MPFD and PD

When we look at the geographical distribution of our standardized effect scores for MPFD, we can see that the vast majority, ~81%, are less morphologically disparate than our expectations under the null model. This supports a recent study which found a similar pattern of widespread functional clustering in the global distribution of squamate reptile clades (Skeels et al., 2020). The remaining 19% of sites, those which are more morphologically diverse than expected, are geographically clustered in just a handful of regions, namely the northern Andes, the Hengduan Mountains and in a long band which covers much of southern Canada and Russia. Compare this to PD_{SES}, where we can clearly see that the majority of regions that are more phylogenetically diverse than expected fall within the tropics (56%) and become increasingly rare at higher latitudes, a phenomenon which is clearly captured by the importance of both latitude and species richness in predicting PD_{SES} in of all of our models. Thus, while the geographic distribution of PD_{SES} shows a latitudinal gradient consistent with the modelling approach we employed, $MPFD_{SES}$ does not: its relationship to latitude and the interaction between latitude and PD_{SES} likely reflects the impact of these exceptional regions with greater than expected $MPFD_{SES}$.

For at least two of these regions, it is unsurprising that they show such exceptional functional diversity. The Tropical Andes and the Hengduan Mountains are two megadiverse regions that encompass recognized biodiversity hotspots (Mittermeier et al., 2011). To give some context, the Hengduan Mountains is home to one of the richest temperate floras, with over twelve thousand recognized species of plant, including 3300 endemics (Sun et al., 2017) while the Tropical Andes are one of the most biodiverse and unique terrestrial ecosystems on the planet, and home to 1743 endemic or nearly endemic vertebrate species (Bax & Francesconi, 2019). Interestingly, both regions were also less phylogenetically diverse than expected under the null model. This is consistent with Jarzyna et al. (2021), who found that assemblages in tropical and temperate highlands with the most closely related species were often functionally dissimilar.

Tropical mountains are known to show remarkable species richness (Rahbek et al., 2019). Species elevational ranges are very narrowly defined compared to temperate regions, and in some cases, there is complete turnover of community composition from the base of a mountain to its peak (Cadena et al., 2012; McCain, 2009; Quintero & Jetz, 2018). While recent work suggests that this pattern in birds is likely to be driven by high-interspecific competition rather than as an adaptive response to the sharp thermal clines of mountainous regions (Freeman et al., 2022), both processes could lead to the higher-than-expected MPFD we observed. If interspecific competition is driving species towards specializing in narrow elevational ranges, it may also be driving adaptation in the traits we used to measure MPFD. Similarly, if elevational environmental gradients mean that grid cells on mountains contain on average more environments than a low-land grid cells, then we would expect them to include a more functionally disparate assemblage of species. Of the six traits used in our analyses, three relate to beak shape and, as this largely determines how a bird interacts with resources in its habitat, our measure could reflect adaptive divergence in these traits among co-occurring birds.

It should be noted that there are other tropical mountainous regions where we do not find any evidence of higher MPFD than expected, such as the Eastern Rift mountains in Africa. However, what makes the Andes and the Hengduan Mountain ranges unique is their recent uplift and their extreme topographic complexity (Rahbek et al., 2019). Mountain uplift events have been associated with evolutionary radiations (Eronen et al., 2015; Favre et al., 2015), as they make the landscape more heterogenous, providing novel niches for adaptation and creating barriers to geneflow that encourage speciation. Thus, the exceptionally high $MPFD_{SES}$ under our null is likely a consequence of repeated colonizations and radiations of birds within these recently uplifted and topographically complex tropical mountain ranges.

We also found regions of exceptionally high $MPFD_{SES}$ throughout the North American and Eurasian Taiga biome. These hotspots for $MPFD_{SES}$ are less straightforward to explain due to the low diversity and environmental homogeneity of these regions compared to known biodiversity hotspots such as the northern Andes and Hengduan regions. However, this could be explained by an environmental harshness model (Skeels et al., 2020), which predicts a negative relationship between functional diversity and diversity or a positive relationship between functional diversity and measures of environmental harshness, such as latitude and the underlying temperature gradient, as harsh environments might place very strong constraints on species co-existence. Under this model, low resource abundance supports low population sizes and very few species can share a common resource while maintaining a viable population size. Instead, we expect a small number of species but each of these performing very distinct ecological roles, with very little or no redundancy. Due to the large size of the Taiga biome in both North America and Eurasia, the model for community assembly will likely sample allopatric species from different parts of this biome which fulfil similar ecological roles leading to increased functional similarity beyond anything that is observed. This could explain why we do not see this hotspot extending even further northward into the northern polar regions, as so few species occur here that any functional diversity measure on null communities will approach a similar minimal value as that observed in the data. This highlights how a biogeographically constrained null model emphasizes ecologically interesting patterns that may be obscured when using global randomization.

Regions which have exceptionally high $\mathrm{PD}_{\mathrm{SES}}$ null tend to fall within tropical latitudes and this could be explained by the evolutionary and climatic history of the globe. The tropical conservatism hypothesis makes the explicit prediction that tropical regions should be more phylogenetically overdispersed and temperate regions more phylogenetically clustered because the warm humid climate found in tropical latitudes today is much older than the cooler and drier climate found in temperate latitudes. Due to the late emergence of the temperate climate around the Eocene–Oligocene boundary, temperate clades must be younger and clustered within tropical clades. There is strong evidence for this in birds (Duchêne & Cardillo, 2015). Another contributing factor to high tropical $\mathrm{PD}_{\mathrm{SES}}$ could be the presence of important biogeographic convergence zones between long-separated biotas. For example, we see many assemblages with high $\mathrm{PD}_{\mathrm{SES}}$ across the Indo-Australian archipelago, in the Wallacean islands between the Sunda and Sahul continental shelves, probably the most well-known contact zone between two regions with evolutionary distinct fauna (Holt et al., 2013). Recent phylogenetic and biogeographical studies have suggested that crown Passerines first radiated in what is now Australia and New Zealand ~47 Ma and then dispersed into the rest of the world via the island uplifting in Wallacea ~20–30 Ma (Moyle et al., 2016; Oliveros et al., 2019) and birds in the region show a highly complex biogeographic history of exchange and colonization dynamics across lineages (Prasetya et al., 2023). The high $\mathrm{PD}_{\mathrm{SES}}$ observed in this region may reflect this history, with bird assemblages comprised of a Eurasian constituency, as well as an Australasian constituency that may well represent some of the deepest branches of the Passerine clade.

4.2 | The impact of migration on $\mathrm{MPFD}_{\mathrm{SES}}$ and $\mathrm{PD}_{\mathrm{SES}}$

We have already discussed the interdependencies of migration and latitude, and how this affects the $\mathrm{PD}_{\mathrm{SES}}$, $\mathrm{MPFD}_{\mathrm{SES}}$ and the relationship among the two variables. But it is worth considering the global effects of migration on functional and phylogenetic diversity. Migration plays an important role in determining the functional diversity of an assemblage. For example, a recent study by Jarzyna and Stagge (2023) showed that migration creates pronounced temporal changes in the functional diversity of bird assemblages across the mainland of the United States. In our study, assemblages with a greater proportion of migratory species tended to be more morphologically constrained than those with fewer migratory species (with the exception of the boreal taiga biome, discussed above). Migration is an extreme behaviour and has been associated with various morphological changes to facilitate long-distance flight (Salewski & Bruderer, 2007; Soriano-Redondo et al., 2020; Vincze, 2016) and also suggested that it is associated with a number of evolutionary tradeoffs (Winger et al., 2019). While we did not use any traits associated with wing shape or size in our analysis, focusing instead on traits associated with a bird's ecological niche (Weeks et al., 2022), it is possible that being migratory places a constraint on a bird's ability to adapt traits associated with foraging strategy. For example, if niche space is more limited at higher latitudes, it may necessitate certain beak shapes, limiting the evolutionary avenues available to an evolving species. It has been shown that birds show high levels of morphological convergence within trophic niches (Pigot et al., 2020).

It is also interesting that $\mathrm{PD}_{\mathrm{SES}}$ showed only a marginal relationship with migration. Migration has arisen independently in birds several times, although the majority of migratory bird species belong to three orders the Anseriformes (waterfowl), Charadriiformes (shorebirds) and Passeriformes (Dufour et al., 2020). If the capacity to adapt to higher latitude environments through migration is not particular to any clades, the phylogenetical signal is low, then we might not expect the presence of migratory birds to influence the phylogenetic diversity of an assemblage beyond that which is expected just from adding an extra species to an assemblage.

5 | CONCLUSION

Globally, we found a negative relationship between our two standardized indices, that is when assemblages were more phylogenetically diverse than expected they tended to be less functionally diverse than expected. However, this relationship is context specific and shows considerable variation across latitudes. Overall, the relationship between phylogenetic diversity and functional dispersion decreases with distance from the equator, becoming negative at higher latitudes. We also show that migration plays an important role in shaping the functional diversity of bird assemblages, with the inclusion of migratory species leading to more morphologically clustered assemblages of birds.

Our study shows that the relationship between phylogenetic diversity and functional diversity is context specific and attempts to evaluate the surrogacy of one for the other must consider their interaction with environmental gradients such as latitude. This is important for studying other clades for which comprehensive morphological databases like AVONET are not available. The fact that the relationship between MPFD_{SES} and PD_{SES} shows such variation across environmental gradients, such as latitude, means that phylogenetic diversity cannot be treated as an 'off-the-shelf' proxy for functional diversity. Instead, we recommend that future studies consider how phylogenetic diversity's surrogacy for functional diversity may be impacted by environmental context and compare its empirical observations to expectations derived from biogeographically constrained and ecologically informed null models. Doing so will not only allow conservationists to better utilize these indices, it also may offer unique insights into the macroecology and evolutionary history of other clades.

AUTHOR CONTRIBUTIONS

Keaghan Yaxley: Conceptualization (lead), data curation (lead), formal analysis (lead), investigation (lead), methodology (lead), project administration (lead), software (lead), visualization (lead), writing—original draft (lead) and writing—review and editing (lead). **Alexander Skeels**: Conceptualization (support), methodology (support), writing—original draft (support) and writing—review and editing (support). **Robert A Foley**: Conceptualization (support), methodology (support), project administration (support), writing—original draft (support) and writing—review and editing (support).

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data produced from this study and the R code to reproduce the analysis and figures are available on the Dryad Digital Repository at https://doi.org/10.5061/dryad.05qfttf8t.

Data used to conduct the analyses in this manuscript can be accessed via the following sources:

- Tobias et al.'s (2022) avian morphological database AVONET is available in the Figshare digital repository at https://figshare.com/s/b990722d72a26b5bfead.
- Dufour et al.'s (2020) list of migratory bird species is available via the publication's supporting information at https://doi.org/10.1111/jbi.13700.
- Weeks et al.'s (2022) presence–absence matrix of global bird assemblages and associated bioclimatic data and their majority rules consensus bird phylogeny are available in the Zenodo digital repository at https://zenodo.org/record/5139951.
- Dinerstein et al.'s (2017) map of global ecoregions is available via the publication's supporting information at https://doi.org/10.1093/biosci/bix014.

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SUPPORTING INFORMATION

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