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Global Patterns and Determinants of Multiple Facets of Freshwater Fishes Beta Diversity

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ABSTRACT

Aim: Global patterns of freshwater fish species diversity and their natural and anthropogenic determinants are relatively well documented. Yet, determinants of fish dissimilarity (beta diversity) across river basins remain poorly understood. Here, we quantify taxonomic, functional and phylogenetic beta diversity of freshwater fish across global river basins and identify the key environmental and historical drivers shaping these patterns.

Location: Global.

Time Period: 1960s–2000s.

Major Taxa Studied: Freshwater fish.

Methods: We used a global database of freshwater fishes, a trait database based on morphological descriptions and phylogenetic information calculated by phylogenetic distances. We assessed multiple facets of fish beta diversity and partitioned beta diversity into turnover and nestedness components to assess their contributions. Spearman correlation analysis was conducted to assess the relationships between them and their components. We then applied boosted regression trees (BRT) model to assess their relationships with key environmental, spatial and historical variables.

Results: We reported strong links between three facets of beta diversity, but species turnover contributed more strongly than nestedness to overall beta diversity, while functional and phylogenetic beta diversity exhibited contrasting patterns. We further found that geographic, climatic and historical factors all played significant roles in shaping beta diversity, with river basin area emerging as the most influential predictor.

Main Conclusions: Although the global patterns of the three facets of beta diversity are consistent, the contributions of turnover and nestedness are different. Our results suggest that distinguishing between turnover and nestedness dimensions of the taxonomic, functional and phylogenetic facets of biodiversity provides a comprehensive and insightful understanding of the mechanisms underlying global freshwater fish beta diversity.

1 | Introduction

In recent decades, an increasing number of studies have focused on the variation in biodiversity across different regions (i.e., beta diversity) and the environmental and geographical factors that may drive these patterns (Fitzpatrick et al. 2013; Leprieur et al. 2011; Ricklefs 2004). Beta diversity, which can be partitioned into two components: turnover and nestedness

(Baselga 2010), highlights the differences in biodiversity between sites rather than the simple species composition at a single site. It can be driven by multiple factors, including current and historical geographical isolation as well as spatiotemporal variations in environmental conditions (Baselga 2010; Jost 2007; Koleff et al. 2003; Whittaker 1960). Turnover between localities occurs when species differ between localities due to historical factors or changes in contemporary environmental conditions, while nestedness reflects differences in species richness between sites (Baselga 2010). These two processes are not only distinct but can even operate in opposing ways, collectively shaping the overall variation in beta diversity (Baselga 2010; Branco et al. 2020; Ulrich and Gotelli 2007; Williams 1997; Wright and Reeves 1992).

Traditional studies of beta diversity have primarily focused on differences in species composition between biological assemblages, such as taxonomic beta diversity (TBD). This approach effectively captures temporal and spatial changes in species composition and has been well studied, particularly in freshwater fish (Villéger et al. 2011; Toussaint et al. 2014). However, it overlooks the shared evolutionary history and functional similarities among species (Leprieur et al. 2011; Penone et al. 2016). Beyond TBD, functional beta diversity (FBD) and phylogenetic beta diversity (PBD) have gained wide acceptance and application as additional facets of biodiversity, which respectively assess the similarity of functional traits and the differences in evolutionary lineages between communities (Coleman et al. 2015; Leprieur et al. 2012; Mason et al. 2013; Qian et al. 2021; Su et al. 2022). Investigating taxonomic, functional and phylogenetic beta diversity facets simultaneously can hence provide a deeper understanding of the contemporary ecological and historical evolutionary mechanisms that shape changes in species diversity and composition within biological assemblages (Cavender-Bares et al. 2009; Xu et al. 2023).

The link between the three facets of beta diversity is not clear. Indeed, we can expect that they are correlated, as species identity often carries information about functional traits and phylogenetic history, and changes in TBD are frequently associated with variations in FBD and PBD (Penone et al. 2016; Safi et al. 2011; Swenson et al. 2012). Regional studies suggest that beta diversity tends to be higher when communities have been historically isolated and exposed to distinct environmental conditions. In contrast, it tends to be lower across all three facets when communities lack geographical isolation and share similar environmental conditions (Safi et al. 2011; Weinstein et al. 2014). Yet, they might also vary independently. For instance, environmental filtering may not necessarily act on phylogenetic lineages but rather select species with convergent traits adapted to specific conditions, resulting in lower FBD. For instance, Villéger et al. (2013) found that while taxonomic and functional nestedness were similar across European fish faunas, functional turnover was notably lower, leading to the overall lower FBD compared to TBD in the region. Thus, the different facets of beta diversity can provide unique insights into the causal mechanisms shaping biological composition though they are correlated.

Most previous studies have focused on one or more facets of biodiversity within specific regions, providing a well-understanding of how biodiversity operates at regional scales (Qian et al. 2021; Villéger et al. 2010, 2013; White et al. 2018; Wu et al. 2022). More recently, there has been a growing trend toward global-scale analyses, resulting in well-documented multidimensional beta diversity patterns across several taxonomic groups, including mammals (Penone et al. 2016), lake macrophytes (García-Girón et al. 2020), angiosperms (Xu et al. 2023) and reef fishes (Maxwell et al. 2022). In contrast, freshwater fish—despite their ecological importance and vulnerability—remain understudied in this context. To date, global studies have only explored their taxonomic beta diversity (Leprieur et al. 2011; Toussaint et al. 2014), with the phylogenetic and functional facets still largely unexplored. This is a significant knowledge gap, especially given the unique biogeographic characteristics of freshwater fishes (Villéger et al. 2011). High isolation among river basins coupled with limited dispersal ability has led to pronounced species turnover between river basins (Leprieur et al. 2011; Toussaint et al. 2014). Furthermore, local species richness is determined not only by the area and productivity of the basin, but also by the regional historical legacies (Guégan et al. 1998), which contribute primarily to species nestedness. Thus, TBD among rivers reflects a combined effect of turnover and nestedness (Baselga 2010). Understanding whether similar processes structure functional and phylogenetic beta diversity is essential, as it may uncover general mechanisms driving biodiversity patterns across ecosystems.

Here, we aimed to characterise the beta diversity patterns of freshwater fish at a global scale and to identify the key environmental and historical drivers shaping the taxonomic (TBD), functional (FBD) and phylogenetic (PBD) facets of beta diversity. To this purpose, we (1) mapped the spatial distribution of the three beta diversity facets at the river basin scale worldwide, (2) quantified their overall and component (turnover and nestedness), and (3) assessed their relationship with key environmental, spatial and historical variables. Given that species identity is often shaped by evolutionary history, and that environmental filtering and competitive exclusion primarily act on species traits rather than on their taxonomic identity or phylogenetic position (Cantera et al. 2023; Penone et al. 2016), we hypothesised that (H1) FBD exhibits weaker correlations with TBD and PBD, while TBD and PBD are more strongly correlated. In addition, since species geographical ranges and niche widths tend to increase at higher latitudes, leading to lower beta diversity in those regions (Soininen et al. 2018), we expect that (H2) the three facets of beta diversity exhibit a latitudinal decline. Furthermore, we hypothesised that (H3) both long-term climatic stability and contemporary environmental heterogeneity influence beta diversity, but historical stability will be a stronger predictor for phylogenetic and functional beta diversity due to evolutionary legacy (Sandel et al. 2011; Xu et al. 2023).

2 | Materials and Methods

2.1 | Freshwater Fish Occurrence Data

We used the most comprehensive global database of freshwater fish species distributions, available at http://data.freshwaterbiodiversity.eu (Tedesco et al. 2017). The database includes 3119 basins, covering about 80% of the Earth's surface and catalogues

14,953 fish species, which account for more than 83% of the globally recognised freshwater fish species (Tedesco et al. 2017). The fish occurrences were recorded at the basin level, which means the database includes all the freshwater fish species inhabiting the entire river network for each basin. According to Brosse et al. (2013) and Lévêque et al. (2008), each river basin was categorised into one of the six terrestrial biogeographic realms (i.e., Afrotropical, Australian (including Oceania), Nearctic, Neotropical, Oriental and Palearctic). Our analysis exclusively used the historical dataset of fish species from the preindustrial era—before the 18th century. This approach allowed us to avoid the confounding effects of the post-industrial influx of non-native species, ensuring that our assessment of fish assemblages accurately reflects the native species composition (Su et al. 2021).

2.2 | Functional Trait and Phylogeny

We used a trait database based on morphological descriptions of 10,705 species, derived from visual materials such as images and illustrations found in academic texts and online scientific resources (Su et al. 2021). Morphological assessment was conducted using 10 traits detailing the size and shape of body parts associated with feeding and movement (Tedesco et al. 2017; Toussaint et al. 2016). These morphological measures were based on lateral view images collected from a comprehensive review of literature, which included field data and scholarly sources, such as peer-reviewed journals, books and scientific websites. Fish size was described using maximum body length, while the remaining nine unitless morphological traits used for functional diversity analyses were calculated from 11 morphological metrics measured from lateral view images using ImageJ software (http://rsb.info.nih.gov/ij/index.html). For specific details on the sources of these traits, refer to Brosse et al. (2021). These traits were selected because they are commonly used to assess fish functional diversity (Su et al. 2019; Toussaint et al. 2016; Villéger et al. 2010). Concurrently, these traits are also associated with the feeding and locomotion functions of fish, which contribute to essential ecosystem processes, such as the regulation of food webs and nutrient cycles (Villéger et al. 2017). Because of image quality limitations, not all morphological traits could be measured reliably. For species exhibiting marked sexual dimorphism, the male morphology was considered due to the scarcity of female pictures for most species. We did not consider intraspecific morphological trait variation in this study because it has little influence on functional diversity at the large spatial resolution considered (Toussaint et al. 2018). Consequently, uncertain measurements were discarded, resulting in the morphological trait database with 24.2% missing data (ranging from 6.9% for maximum body length to 31.5% for relative maxillary length; Table S1). Missing values were imputed using the missForest package in R (Stekhoven and Bühlmann 2012), which employs a nonparametric random forest approach that accommodates mixed data types without distributional assumptions. Since most traits exhibited weak phylogenetic signal (Blomberg's $K < 0.25$) and the results of models with and without phylogenetic information were highly correlated (Spearman's Rho > 0.93, Table S1), we used the random forest model without phylogenetic information for imputation. Subsequently, a Principal Component Analysis (PCA) was executed on the 10 morphological traits across all species, and the first four PCA axes, which together explained 68.9% of the variance in global fish functions, were used to calculate the functional diversity indices.

Phylogenetic information for all species was obtained by calculating phylogenetic distances using a tree constructed by Rabosky et al. (2018), which includes 31,526 marine and freshwater ray-finned fishes. Positions for 11,638 species were estimated from genetic data, and the remaining 19,888 species were placed using stochastic polytomy resolution (Rabosky et al. 2018).

The three datasets were harmonised to include only those harbouring more than five species because functional diversity assessment based on four dimensions requires at least five species per river basin. In all our analyses we thus retained 10,682 fish species with both functional and phylogenetic information across 2456 basins containing at least five species. These species cover over 45% of known freshwater fish and spread in all major taxonomic orders (Froese and Pauly 2025; Table S2).

2.3 | Beta Diversity

We quantified taxonomic, functional and phylogenetic dissimilarity between each pair of fish communities using the Jaccard index, beta-FRic and UniFrac, respectively, and further partitioned these into turnover and nestedness components (Baselga 2010). These metrics were selected for their widespread use in ecological studies and their suitability for our species presence-absence data, effectively capturing spatial heterogeneity in fish communities and the underlying ecological drivers. Specifically, the Jaccard index calculates taxonomic dissimilarity based on species presence-absence (Baselga 2010), beta-FRic measures functional dissimilarity by comparing convex hulls in trait space (Villéger et al. 2008), and UniFrac assesses phylogenetic dissimilarity by comparing branch lengths in phylogenetic trees (Lozupone and Knight 2005). The turnover component reflects the replacement of species, traits and branches of the phylogenetic tree, excluding the effects of disparities in species richness, functional richness and phylogenetic richness across sites (Baselga 2010). Conversely, the nestedness component reflects the effects of variances in species richness, phylogenetic richness and functional richness; as differences in richness between assemblages increase, differences in nestedness also increase (Baselga 2010; Leprieur et al. 2011). Subsequently, since some basins lack adjacent basins or have few adjacent basins, we uniformly calculated the mean dissimilarity index values between each focal basin and its nearest neighbouring basins (based on their centroid distances from the focal basin) within the same biogeographic realm to represent taxonomic dissimilarity, functional dissimilarity and phylogenetic dissimilarity for each basin. To assess the robustness of this neighbourhood definition, we performed a sensitivity analysis by calculating the three facets of beta diversity using different numbers of nearest neighbouring basins ($k = 3$, 5 and 7) for each focal basin. A Spearman correlation analysis across these three scenarios revealed very high and consistent correlations (Rho > 0.8; Table S3) among the dissimilarity indices. Furthermore, examining the results on a global map showed that the spatial patterns were largely consistent across the three scenarios (Figure S1). Given this strong congruence in both correlation and spatial distribution, we conservatively chose five nearest neighbouring basins for all subsequent analyses, as this value adequately captured the spatial beta diversity pattern while maintaining a reasonable sample size for the neighbourhood comparison. All beta diversity calculations were performed using the R package 'betapart' (Baselga et al. 2023). Additionally, we calculated the proportion of the nestedness and turnover components contributing to total beta diversity for all three biodiversity facets, reflecting the relative importance of turnover and nestedness (Dobrovolski et al. 2012).

2.4 | Environmental Variables

To evaluate the influence of climatic and geographical determinants on the beta diversity in freshwater fish species, we selected 23 variables representing climatic anomalies (historical climate), contemporary temperature, contemporary precipitation and geographical factors (Table S4). These selected factors encompass a comprehensive range of climatic and geographical factors that may influence beta diversity in freshwater fish species.

Climate anomalies were assessed using three predictors: Late Quaternary glacial–interglacial climate-change velocity (Velocity) and changes in mean annual temperature and precipitation between present and Last Glacial Maximum conditions (LGMT and LGMP). Velocity was measured as the local rate of displacement of climatic conditions over the Earth's surface since the Last Glacial Maximum (Sandel et al. 2011). LGMT and LGMP were measured as the average of two estimates from global circulation models, CCSM4 and MIROC-ESM (Hijmans et al. 2005). These predictors were selected because previous studies indicated that selective extinctions caused by Quaternary glaciations, along with limited time to recolonize glaciated regions, may shape contemporary species distribution (Hawkins and Porter 2003). Furthermore, areas that experienced smaller Quaternary Milankovitch oscillations tend to contain higher proportions of range-restricted species (Jansson 2003).

We selected nine predictors for contemporary temperature and seven predictors for precipitation (Fick and Hijmans 2017). Previous studies have found that these climatic factors not only play an important role in determining species distributions but also are correlated with large-scale patterns of freshwater biodiversity (Leprieur et al. 2009; Oberdorff et al. 1999). Since many variables within the contemporary temperature and contemporary precipitation categories are correlated, we used principal component analysis (PCA) for each group individually and extracted the first two axes representing synthetic variables for temperatures and precipitation. The first principal component axis of temperature (Temp_PCA1) accounted for 78.7% of the total variance and was negatively correlated with TSeasonality and TAnnualRange and positively correlated with the other contemporary temperature predictor variables (e.g., T and TColdest). The second principal axis (Temp_PCA2) accounted for 16.2%. For contemporary precipitation, the first (Prec_PCA1) and second principal component axes (Prec_PCA2) explained 53.1% and 27.5% of the total variance, respectively. Prec_PCA1 is negatively correlated with PSeasonality and directly related to the other variables, while Prec_PCA2 is negatively correlated with PDriest and PColdest and positively correlated with the other contemporary precipitation predictor (Figure S2).

Additionally, we also selected net primary productivity (NPP), mean slope (slope), elevational range (elevation) and river basin area (Area) as geographical factors. Area serves as an indicator of habitat diversity, and elevation reflects geographical isolation (Guégan et al. 1998; Leprieur et al. 2011). To match the spatial scale of beta diversity, environmental variables were calculated as the difference between basins. Specifically, we measured environmental variables for each basin as the average difference between the focal basin and its five neighbouring basins.

2.5 | Data Analysis

Since the three facets of beta diversity are interdependent and strongly correlated (Villéger et al. 2013; Wu et al. 2022), we used a null model to investigate whether FBD and PBD are influenced by the processes beyond those shaping TBD. These simulations were based on the observed TBD and the regional species pools to calculate the FBD and PBD. For each basin, we defined the species pool as the species occurring in it and its five nearest neighbouring basins within the same biogeographic realm. We then randomly shuffled the species identities in the trait pool and phylogenetic tree to calculate simulated FBD and PBD values. In this null model, the species richness, TBD and its components of turnover and nestedness remained constants as observed, since the species pool remained unchanged. We repeated the simulation 999 times and calculated the standardised effect size (SES) as the deviations of FBD and PBD.

To examine the congruence between taxonomic, functional and phylogenetic dissimilarity, as well as their components—turnover and nestedness—we used Spearman correlation and linear regression to assess the relationships between the different facets of beta diversity. This approach aimed to uncover potential associations and commonalities across the facets of beta diversity within freshwater fish assemblages.

We applied a boosted regression trees (BRT) model, which has been shown to be robust to extreme values (Su et al. 2023), to evaluate the relative importance of each environmental variable in shaping the patterns of TBD, FBD and PBD. We also used BRT to assess the relative importance of the same selected environmental variables in explaining the deviations of FBD and PBD.

While BRT are generally robust to collinearity among predictor variables, Parravicini et al. (2013) suggest excluding predictors with high absolute correlations before applying boosting methods, which improves the model accuracy and interpretability. Thus, we used Spearman correlation to examine the interrelationships among environmental predictor variables. We quantified the correlations among the environmental factors and found that Elevation and Temp_PCA1 were highly correlated ($\mathrm{Rho} > 0.7$), so we retained Temp_PCA1 and excluded Elevation (Figure S3). The final BRT models were constructed using a refined set of 11 predictors from the original 23 predictors. This selection process aimed to enhance model accuracy and interpretability by reducing collinearity among predictors. The refined predictor set is better suited to elucidating the relative importance of each variable on the patterns of TBD, FBD and PBD in freshwater fish communities.

BRT were chosen for their ability to accommodate a Gaussian distribution of the response variable (Elith et al. 2008). We used the 'gbm.step' function in the 'dismo' R package to fit the BRT models, which allow the selection of four key parameters: bag fraction, learning rate, tree complexity and the number of trees. A two-step optimization process was used to fine-tune the BRT model. First, 10-fold cross-validation (CV) was used to identify the optimal values for the four key parameters, ensuring model calibration and effective generalisation to new datasets. The model with the highest CV-D2 (the proportion of deviance explained) was selected as the most suitable. Subsequently, the robustness of the model was further reinforced by executing 100 iterations with varying random seeds (Su et al. 2023). This process involved calculating the average relative influence of predictors and the explained deviance (D2). This approach facilitated a thorough examination of the BRT model's efficacy and provided valuable insights into the dynamics among predictors affecting sustainability scores. In addition, several basins exhibit extreme environmental conditions due to their geographic location or limited area, which could potentially influence model performance. Therefore, we compared the results before and after excluding environmental outliers and found consistent patterns (Figure S4), confirming that our findings are robust and not driven by these extreme values.

All statistical analyses and data visualisation were conducted using R software version 4.3.

3 | Results

3.1 | Global Patterns of Taxonomic, Phylogenetic and Functional Beta-Diversity and Their Components in Freshwater Fishes

By mapping the global multidimensional beta diversity of freshwater fishes, we showed that beta diversity depicted consistent spatial patterns across the three facets, gradually decreased from low latitudes to high latitudes, with high values primarily concentrated in low-latitude regions (Figure 1, Figure S5). Moreover, the three facets of beta diversity were positively correlated as expected (Figure 2), with a particularly strong correlation between TBD and PBD (Rho = 0.97). In contrast, FBD showed weaker correlations with both TBD and PBD (Rho < 0.8), indicating an incongruence between facets. For the turnover component, high taxonomic beta diversity mirrored the patterns of TBD, being concentrated in low-latitude regions. In contrast, turnover of FBD and PBD exhibited opposite patterns.

Additionally, when examining the relative contributions of turnover and nestedness, turnover dominated TBD in 62.7% of river basins. In contrast, the nestedness component accounted for a larger share in the majority of basins for FBD (78.9%) and

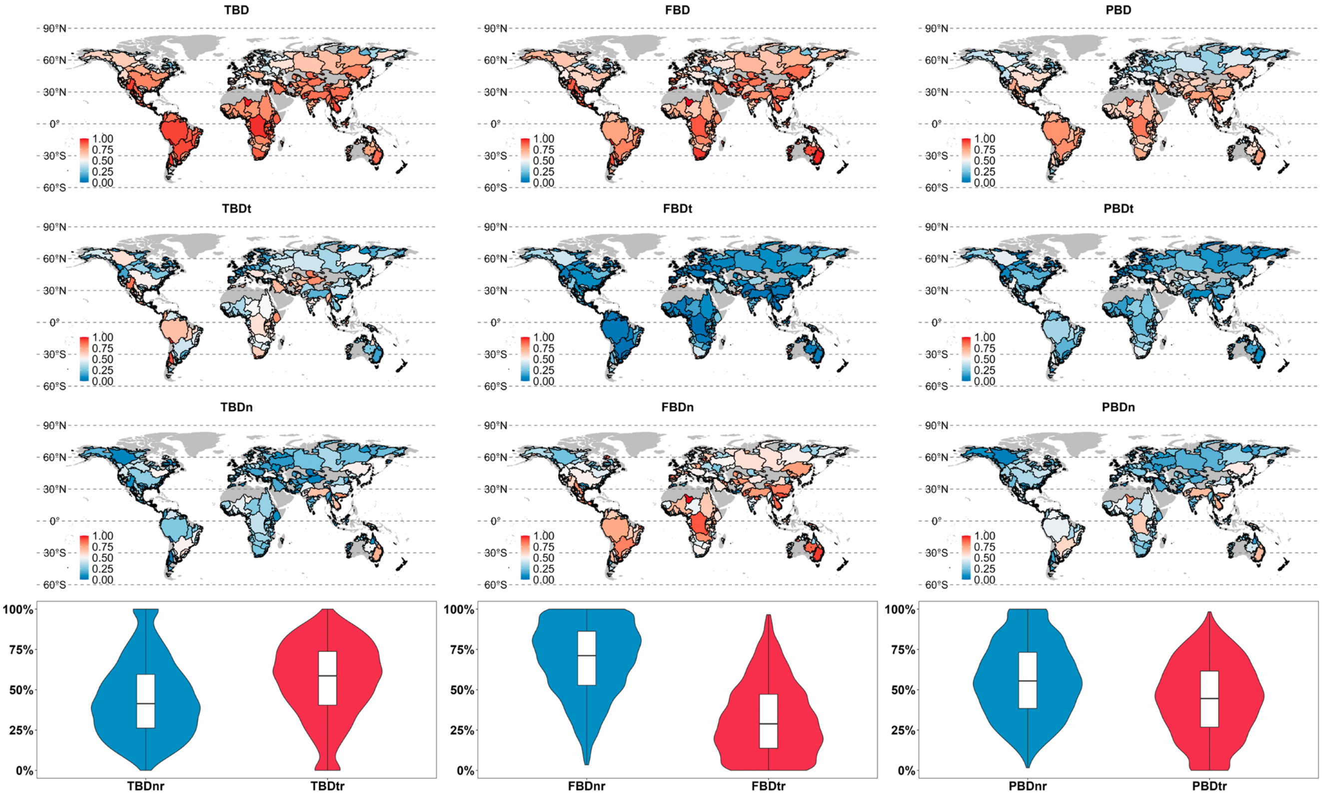

FIGURE 1 | Maps of freshwater fish taxonomic (TBD, TBDn and TBDt), functional (FBD, FBDn and FBDt), and phylogenetic beta diversity (PBD, PBDn and PBDt) in the global watersheds. The violin plots show the contribution of turnover (TBDtr, FBDtr and PBDtr) and nestedness (TBDnr, FBDnr and PBDnr) to total beta diversity. TBD, FBD and PBD are taxonomic, functional and phylogenetic diversities, respectively. TBDt, FBDt and PBDt account for the turnover components, whereas TBDn, FBDn and PBDn account for the nestedness components.

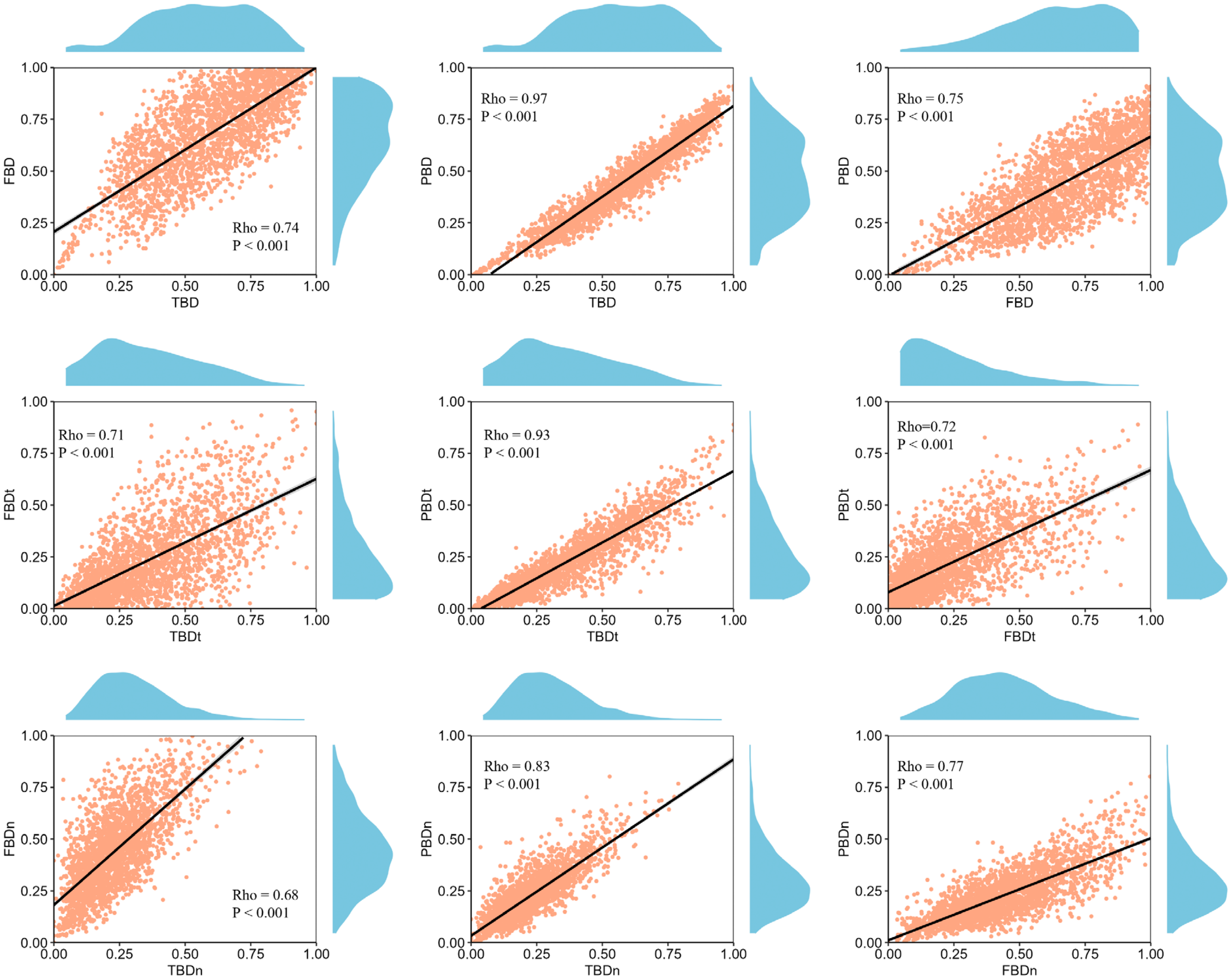

FIGURE 2 | Correlation plots of fish taxonomic (TBD, TBDn and TBDt), functional (FBD, FBDn and FBDt) and phylogenetic (PBD, PBDn and PBDt) beta diversity in the global watersheds. Correlation coefficients (Rho) are shown for each relationship based on the Spearman test.

PBD (58.6%). These results indicate that turnover is the primary driver of TBD, while nestedness plays a more prominent role in shaping FBD and PBD.

3.2 | Effects of Geographical and Climate Factors on Beta-Diversity

Based on a cross-validation procedure, the BRT models explained 63.8%, 50% and 63.5% of the variation in TBD, FBD and PBD, respectively. The fitted functions from the BRT model were often nonlinear and varied in shape, as shown in the dependency plots (Figures 3–5). All variables related to climate anomalies, contemporary temperature and precipitation, as well as geographical factors, contributed significantly to the three facets of beta diversity, with relative influences ranging from 16.8% (Basin area) to 5.6% (Temp_PCA1).

No single environmental predictor explained more than 20% of the variances in all three models, with basin area being the most influential predictor, followed by predictors representing contemporary precipitation and climate anomalies. For TBD, basin area contributed 16.8% and showed a strong positive effect, with Prec_PCA2 (12.2%) and velocity (11.0%) as the next most influential predictors. In contrast, the temperature-related axes (Temp_PCA1 and Temp_PCA2) had limited influence, accounting for only 5.9% and 6.7% of the variance, respectively (Figure 3). PBD mirrored TBD in both the ranking and direction of predictor effects, albeit with slightly different contribution values (Figure 5). FBD, however, displayed a distinct pattern (Figure 4): while basin area remained the most influential variable (11.7%), Velocity (10.9%) and Prec_PCA1 (10.4%) were the second and third most important predictors.

Some general patterns were observed across the three facets. For instance, beta diversity decreased as velocity increased, stabilising beyond a certain threshold. A similar pattern was also observed for runoff and Prec_PCA1. Nonetheless, distinct differences were also evident. Specifically, both TBD and PBD increased with basin area, whereas FBD remained relatively unchanged.

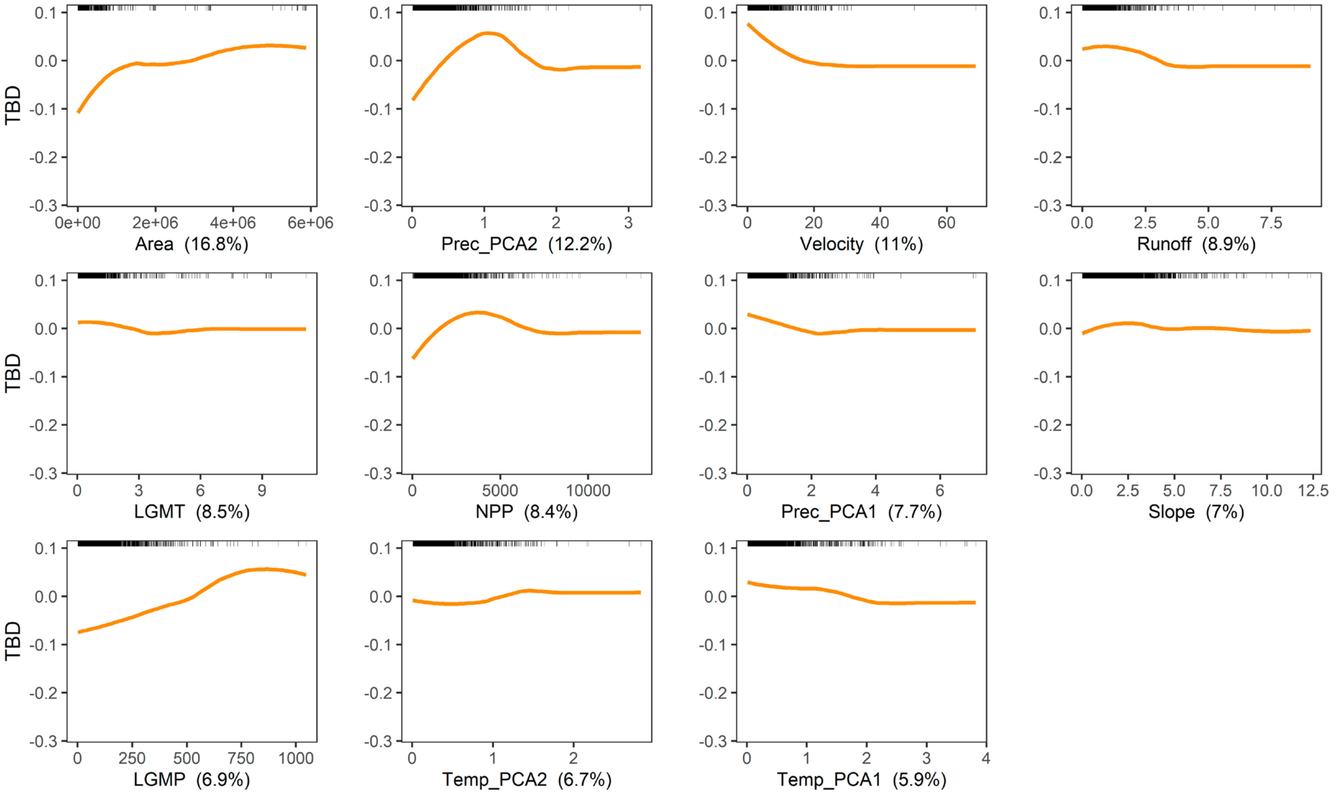

FIGURE 3 | Results of boosted regression trees showing the partial dependency between taxonomic beta diversity (TBD) and predictors. The plots are ranked according to the relative importance of each predictor variable, and the value in parentheses in each panel shows the percentage of contribution of each predictor considered in the model.

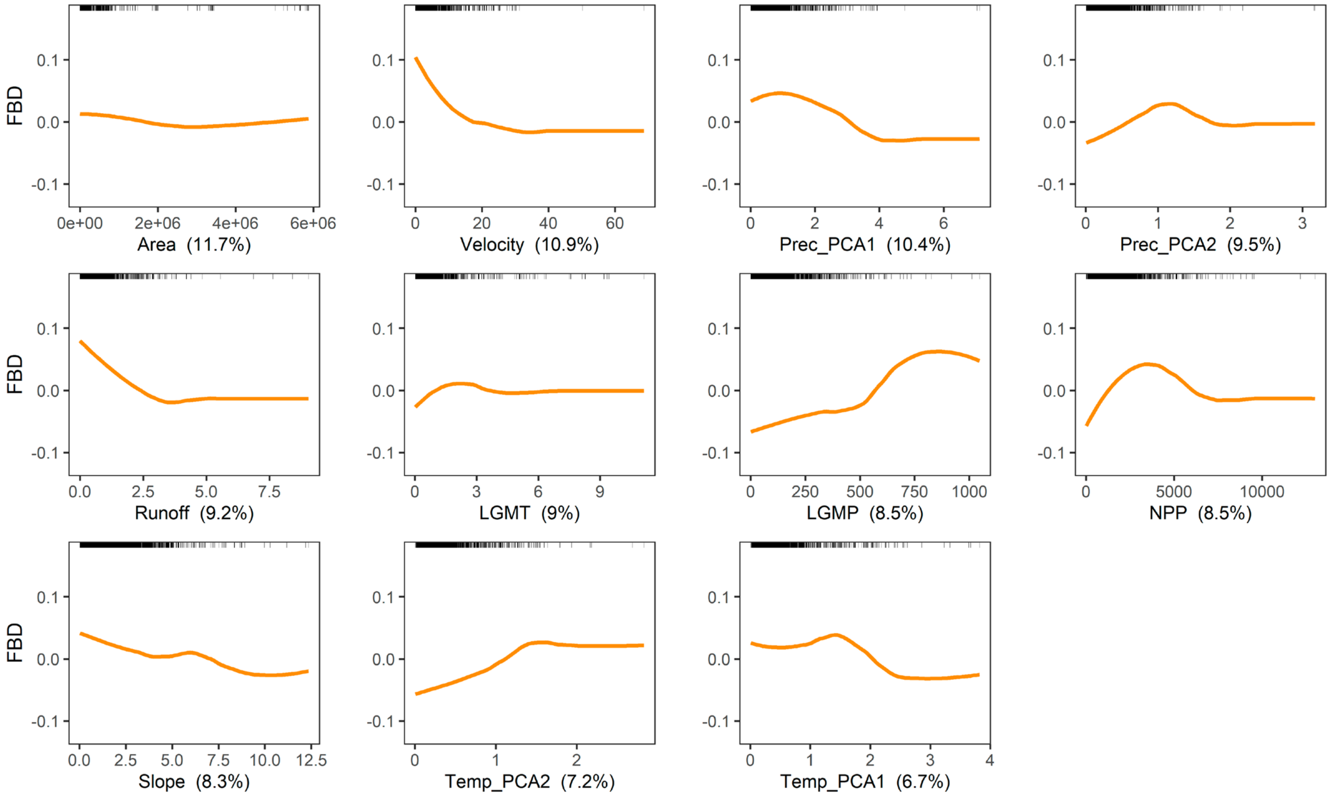

FIGURE 4 | Results of boosted regression trees showing the partial dependency between functional beta diversity (FBD) and predictors. The plots are ranked according to the relative importance of each predictor variable, and the value in parentheses in each panel shows the percentage of contribution of each predictor considered in the model.

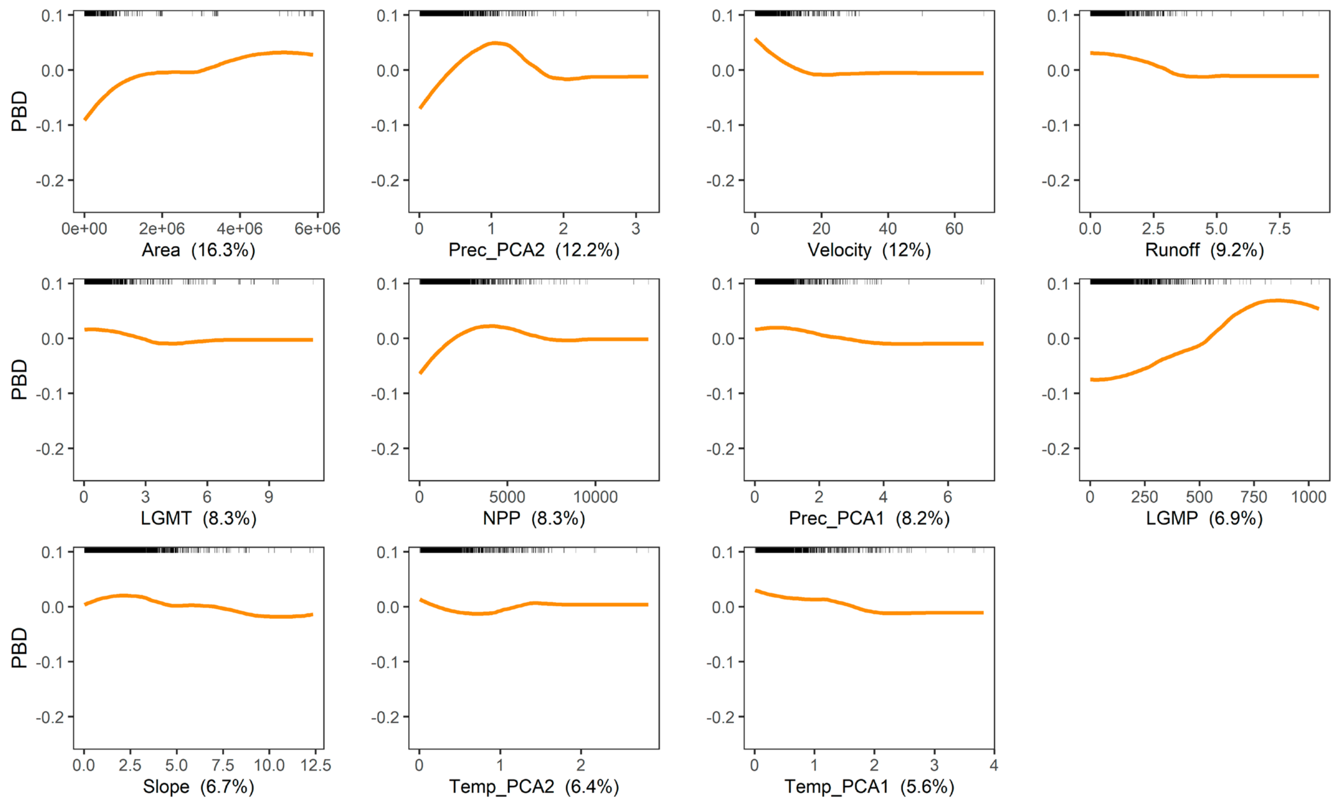

FIGURE 5 | Results of boosted regression trees showing the partial dependency between phylogenetic beta diversity (PBD) and predictors. The plots are ranked according to the relative importance of each predictor variable, and the value in parentheses in each panel shows the percentage of contribution of each predictor considered in the model.

3.3 | Deviation of Functional and Phylogenetic Beta-Diversity and Associated Factors

Null model analyses revealed that deviations from observed functional and phylogenetic beta diversity, including both turnover and nestedness, were spatially heterogeneous (Figure S6). Globally, more than 50% of basins exhibited a positive deviation in FBD, whereas for other metrics, the majority of basins showed negative deviations.

Based on a cross-validation procedure, the BRT models explained 33% and 39% of the deviation in FBD and PBD, respectively (Figures S7 and S8). Consistent with findings for total beta diversity, Area emerged as the primary predictor for both FBD and PBD deviations, explaining 12.4% and 12% of the variance, respectively. Area showed a nonlinear relationship with PBD deviation and a negative correlation with FBD deviation. Meanwhile, Slope (11.9%) and Runoff (10.6%) ranked as the second and third most important factors for FBD deviation. For PBD deviation, the top four predictor factors (Area, Runoff, Velocity and Prec_PCA2) matched those identified for overall PBD, underscoring their pivotal roles in shaping global PBD patterns.

4 | Discussion

In this study, we analysed a comprehensive global dataset of freshwater fish assemblages to examine patterns of taxonomic, functional and phylogenetic beta diversity, and to evaluate their associations with geographic and climatic determinants. Our findings revealed substantial regional variations in freshwater fish beta diversity, with distinct relationships identified with climatic, historical and geographic variables.

4.1 | The Relationship and Composition of Taxonomic, Functional and Phylogenetic Beta Diversity

Exploring the correlations among taxonomic, functional and phylogenetic beta diversity can provide valuable insights into how different facets of beta diversity vary globally and interact with each other. Although this study reveals significant positive correlations among the three biodiversity facets (Figure 2), the varying contributions of their decomposed components suggest that each facet captures some unique aspects of community dissimilarity. Supporting our first hypothesis, we observed the strongest correlation between taxonomic and phylogenetic beta diversity, likely due to their shared evolutionary basis. In contrast, both showed weaker correlations with functional beta diversity. This pattern may stem from species being closely related taxonomically and phylogenetically but functionally divergent (Cantera et al. 2023; Penone et al. 2016), or from convergent evolution driving trait similarity across distinct lineages (Cavender-Bares et al. 2009).

Environmental filtering acted on species traits rather than their taxonomic or phylogenetic positions, with similar environmental conditions imposing selective pressures that favour species with convergent morphological strategies to exploit ecological niches

(Cantera et al. 2023; Penone et al. 2016; Swenson et al. 2012). Furthermore, in cases of functional redundancy across lineages, species turnover can occur without substantial changes in community-level traits (Tsianou et al. 2021; Villéger et al. 2013; White et al. 2018). This may explain the weak correlations of FBD with both TBD and PBD, which align with previous findings (Mazel et al. 2018; Villéger et al. 2013). In addition, the strong correlation between TBD and PBD is also expected, as species formation and differentiation are often driven by evolutionary processes, a similar pattern observed in prior research (Qian et al. 2021; Tsianou et al. 2021).

By decomposing beta diversity into turnover and nestedness we revealed multiple aspects of dissimilarity between communities—details that may not be detected when using overall beta diversity alone (Baselga 2010; Soininen et al. 2018; Tsianou et al. 2021). TBD was predominantly characterised by turnover, a well-known pattern. The assemblages are highly distinct due to high turnover caused by isolation between river basins (Leprieur et al. 2011) and the analysis of TBD in our study confirmed existing patterns. In contrast, FBD was dominated by nestedness, which may result from similar environmental conditions in adjacent basins. Indeed, environmental filtering selects fish species with similar traits, leading to greater overlap in functional traits, trait convergence, and consequently low turnover (Tsianou et al. 2021; Villéger et al. 2013). Additionally, communities with higher functional richness may encompass those with lower functional richness, contributing to high nestedness. Similar to FBD, nestedness contributed more to PBD than turnover. This could be attributed to the limited colonisation and dispersal abilities of freshwater fish, which are significantly influenced by geographical features, such as mountain barriers, fragmented river networks and altitudinal gradients (Radinger et al. 2018). Their distribution may be confined to regions with greater phylogenetic diversity, while other areas contain only subsets of these lineages, resulting in higher nestedness. Furthermore, similar environmental conditions in adjacent basins may lead to lower lineage dispersion, thus reducing turnover (Peixoto et al. 2017; Penone et al. 2014). Overall, the strong links between taxonomic, functional and phylogenetic facets of biodiversity, should not hide distinct contributions of the turnover and nestedness components, probably linked to environmental and evolutionary determinants affecting in different ways the three facets of biological diversity.

4.2 | Geographic Patterns of Beta Diversity

The null model analysis indicated a deviation between functional and phylogenetic beta diversity and their null expectations, thus suggesting that global patterns are shaped by specific factors rather than random assembly. It may result from the geographical isolation of basins or the difference in environmental conditions. Notably, positive deviations in functional turnover were mainly concentrated in high-latitude regions such as North America, while positive deviations in phylogenetic turnover were primarily observed in Brazil and North America. These positive deviations in turnover may indicate that species replacement among assemblages predominantly involved distantly related lineages and species with contrasting functional traits. In contrast, negative turnover deviations reflected the replacement of more recently diverged lineages and species with similar functional traits, and these patterns were concentrated in western Russia, China, and parts of Africa for both FBD and PBD.

The geographic variation in total taxonomic, functional and phylogenetic beta diversity of global freshwater fish was highly consistent, exhibiting latitudinal gradients, with high values predominantly concentrated in low-latitude regions (Figure 1 and Figure S5). This aligns with our second hypothesis and corroborates a pattern of decreasing beta diversity with increasing latitude, as previously observed by Leprieur et al. (2011). The formation of this latitudinal pattern has long been a subject of debate. According to Rapoport's rule (Stevens 1989), species' geographic ranges and niche widths increase with latitude, potentially driving a decline in beta diversity at higher latitudes (García-Girón et al. 2020; Soininen et al. 2018). Kirk et al. (2022) proposed that this phenomenon results from environmental filtering across latitudes, where equilibrium strategies (low fecundity, high juvenile survivorship) diminish along latitudinal gradients, thereby explaining the reduced functional beta diversity between adjacent river basins at high latitudes. Furthermore, Miller and Román-Palacios (2021) argued that the most plausible explanation lies in the evolutionary time of species, suggesting that high diversity is more likely achieved through long-term diversification rather than rapid bursts. Additionally, the tropical niche conservatism hypothesis (TNC; Wiens and Donoghue 2004) posits that the tropics have provided longer timescales for speciation, with most species originating in tropical regions; their dispersal and adaptation to temperate zones are limited, resulting in higher phylogenetic beta diversity in the tropics. Overall, the latitudinal gradients of all three beta diversity facets showed consistent patterns, exhibiting a decline with increasing latitude, which may be driven by geographic isolation, environmental filtering and long-term evolutionary processes.

4.3 | Environmental and Historic Determinants of Beta Diversity

Furthermore, according to the results of the BRT model, none of the four groups of environmental factors—climatic stability, environmental heterogeneity, geographic isolation and basin area—were clearly more important than the others in shaping beta diversity patterns globally (Figures 3–5). The contribution of all environmental variables was no more than 20%, indicating that each plays an important role in explaining the patterns of three facets of beta diversity on the global scale, but basin area was the most influential predictor, which was not consistent with our third hypothesis.

Area was a predominant predictor of all three beta diversity facets because larger river basin areas typically offer more habitats and resources, supporting a greater variety and abundance of species (Guégan et al. 1998; Tisseuil et al. 2013). This probably facilitates the accommodation of more diverse functional groups, potentially resulting in higher richness. Consequently, species in a smaller basin may be a subset of those inhabiting larger adjacent basins, which could contribute to nestedness. Moreover, basin area also affects regional extinctions, with larger populations being less prone to extinction than smaller ones (Hugueny et al. 2011). The influence of area and other geographical factors has also been previously reported to contribute to the maintenance of spatial gradients in freshwater diversity (Guégan et al. 1998; Oberdorff et al. 1999; Tisseuil et al. 2013). The result of BRT for the deviations of FBD and PBD further confirmed this. Meanwhile, slope, as one of the geographical factors, also contributes to the pattern of beta diversity in fish. The change in river slope and flow determines the cost of upstream movement for fish and thus selects fish with distinct morphologies (Carvajal-Quintero et al. 2019; Waters 1996), that belong to distinct species and are also part of distinct lineages.

Additionally, the interactions and contributions of contemporary precipitation and certain historical factors related to Quaternary glaciation were similar across the three facets of total beta diversity. Changes in precipitation patterns can influence water quality, disrupt watershed linkages, and impact nutrient availability, thereby affecting beta diversity across different watersheds (Häder and Barnes 2019). Moreover, severe rainfall can trigger flooding, which fosters the emergence of extensively interconnected aquatic habitats. These environments facilitate fish dispersal and the recurrent restructuring of fish communities across a spatially diverse spectrum (Oliveira et al. 2015; Thomaz et al. 2007). In addition, long periods of low rainfall may lead to reduced water levels, which can intensify competitive exclusion and potentially result in further local extinctions (Thomaz et al. 2007). Velocity, referring to the rate of Late Quaternary climate change, is also a key driver of total beta diversity, particularly FBD. Rapid climate-change velocity indicates swift environmental shifts and is closely linked to elevated extinction risks, often pushing endemic species toward local extirpation (Sandel et al. 2011). In contrast, regions with low climate-change velocities—typically in climatically stable, low-latitude zones—serve as refugia for many small-bodied species and often support faunas with high endemism (Sandel et al. 2011). These stable regions exhibit greater in situ species persistence compared to areas that experienced intense climatic fluctuations during glacial–interglacial cycles (Leprieur et al. 2011; Sandel et al. 2011; Su et al. 2022). Moreover, Quaternary glaciation contributed to the extinction of small-sized species with limited dispersal abilities, while post-glacial recolonization processes further reshaped fish diversity patterns (Carvajal-Quintero et al. 2019; Griffiths 2006; Leprieur et al. 2011). Overall, the global patterns of the three facets of beta diversity are driven by multiple environmental factors, including geographic factors and long-term climate stability, with river basin area emerging as the most influential predictor.

4.4 | Limitations

Although we used a comprehensive global database of freshwater fish distributions, which shows no apparent taxonomic bias (covering more than 45% of the major taxonomic orders), some regional gaps remain. Specifically, regions such as the Indonesian islands and coastal rivers of Peru are underrepresented in the current database (Tedesco et al. 2017). This uneven spatial coverage may be related to the low number of local researchers. Hughes et al. (2021) also reported that high sampling coverage is largely confined to developed countries, highlighting the global disparity in research effort and data availability. Such geographical sampling bias may influence our results to some extent, but it is difficult to determine the strength of this bias on beta diversity measures. We thus recommend increasing sampling and data collection in poorly surveyed regions to improve spatial data balance.

5 | Conclusions

To conclude, our findings indicate that contemporary and historical environmental factors play equally important roles in shaping the global patterns of freshwater fish beta diversity. Although the overall spatial patterns are consistent across taxonomic, functional and phylogenetic facets, the relative contributions of turnover and nestedness differ. Specifically, taxonomic beta diversity is primarily driven by turnover, whereas functional and phylogenetic beta diversity are more influenced by nestedness. Overall, despite an overall consistency between beta diversity facets, distinguishing between turnover and nestedness dimensions of the taxonomic, functional and phylogenetic facets of biodiversity provides a comprehensive and insightful understanding of the mechanisms underlying global freshwater fish beta diversity.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and R code used for this paper are included in Dryad https://doi.org/10.5061/dryad.dncjsxmbh (DOI link).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** geb70181-sup-0001-Supinfo.docx.