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RESEARCH ARTICLE

Contemporary environment and historical legacy explain functional diversity of freshwater fishes in the world rivers

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Abstract

Aim: Regional taxonomic diversity (species richness) is strongly influenced by a joint effect of the current processes (habitat and energy availability) and historical legacies (past climate and geography), but it is still unclear how those historical and current environmental drivers have shaped the functional diversity of species assemblages.

Major taxa studied: Freshwater fish.

Location: Global.

Time period: 1960s–2000s.

Methods: We combined the spatial occurrences over 2,400 river basins world-wide and the functional traits measured on 10,682 freshwater fish species to quantify the relative role of the habitat, climate and historical processes on the current global fish functional diversity. To avoid any correlation between taxonomic diversity and functional diversity, we controlled for differences in the number of species (species richness) between rivers. Functional diversity was considered through three complementary facets: functional richness, functional dispersion and functional identity.

Results: The habitat-related variables explained most of the gradient in functional richness, verifying the habitat size–diversity hypothesis. In contrast, the historical climate–geography legacies markedly imprinted the functional dispersion and functional identity patterns, leading to a balanced influence of the current and historical processes. Indeed, the distribution of morphological traits related to fish dispersal was explained largely by the glaciation events during the Quaternary, leading to strong latitudinal gradients.

Main conclusions: This study provides new insights into the role of historical and current environmental determinants on the functional structure of fish assemblages and strengthens the proposal that the independence of facets of functional diversity from the species richness makes them essential biodiversity variables to understand the structure of communities and their responses to global changes.

Sébastien Villéger and Sébastien Brosse co-senior authorship.

KEYWORDS
climate–energy, functional dispersion, functional identity, functional richness, habitat size–diversity, historical climate–geography, morphological traits

1 | INTRODUCTION

Understanding the mechanisms that drive the global patterns of biodiversity is a central goal of biogeography and macroecology (Gaston, 2000). For most taxa, species richness (SR) is driven by the interaction between the current climate and energy, habitat diversity (i.e., the diversity of abiotic and biotic environments) and historical legacies (Buckley & Jetz, 2007; Guégan et al., 1998; Kerr & Packer, 1997; Kreft & Jetz, 2007; Tittensor et al., 2010), which put forward three non-mutually exclusive hypotheses. The habitat size–diversity hypothesis assumes that habitat size and diversity play a crucial role in extinction and colonization by species, leading to a positive relationship of species richness with the geographical area and diversity (MacArthur & Wilson, 1967). The contemporary climate–energy hypothesis considers that the species richness is positively correlated with the available energy within the ecosystem (Currie, 1991; Oberdorff et al., 2011; Wright, 1983). However, this hypothesis is ambiguous and can be expressed in two rather different processes. It can be treated as a factor that determines the resources available for a given biological community, hence as a productivity factor per se (e.g., net primary productivity), and it also can be treated as a factor that determines the physiological limits of the species (e.g., temperature) (Oberdorff et al., 2011). The historical hypothesis states that the pattern of species richness is closely related to the degree of stability in past climatic conditions and geographical contingencies, because geographical barriers, tectonic movements and climate stability could shape biodiversity patterns by means of dispersal limitation and evolutionary processes (He et al., 2020; Whittaker, 1977).

Besides the continuous progress of species-based biogeography, functional biogeography has been emerging in the last decade (Violle et al., 2014) to map patterns and disentangle the drivers of functional diversity. Functional diversity is a key facet of biodiversity that accounts for the diversity of biological and ecological features of organisms related to their responses to the environment and their effects on ecosystem processes. It has been studied for various taxa at local (i.e., site) and regional (i.e., river or ecoregion) scales (e.g., Blonder et al., 2018; Cai et al., 2018; Heino et al., 2013; Mason et al., 2007; Schleuter et al., 2012; Xu et al., 2019). Recently, global assessments of functional diversity have also been achieved, owing to the development of global-scale initiatives to measure functional traits in both plants and animals (e.g., Carmona et al., 2021; Diaz et al., 2016; Toussaint et al., 2016). For most taxa, the distribution of functional diversity is unequal across the world and not strongly related to that of species diversity, and its determinants are still largely unknown at broad scales (but see Barnagaud et al., 2017; Xu et al., 2020).

Functional diversity is multifaceted and therefore has to be described using sets of complementary indices (Mouillot et al., 2013; Villéger et al., 2008) measuring the distribution of functional traits (morphological, ecological, behavioural or physiological) in a multidimensional functional space (Villéger et al., 2008). Functional diversity indices account in different ways for the distribution of species in this space. For instance, functional richness (FRic) measures the portion of space filled by an assemblage, being driven by species with the most extreme trait values, whereas functional identity (FIde) and functional dispersion (FDis) are like multivariate average and deviation and therefore account for all species (Figure 1; Laliberté & Legendre, 2010; Toussaint et al., 2018; Villéger et al., 2008). A consideration of several functional diversity facets is therefore needed for a better understanding of how ecological processes shape the diversity of traits in species assemblages.

Freshwater fishes, which number *c.* 18,000 species, have colonized all freshwater habitats of the globe except the poles. They account for more than one-quarter of all the vertebrates on Earth (Su et al., 2021; Tedesco et al., 2017). Unlike terrestrial animals that can disperse freely across the land, freshwater fishes can only live and disperse through the river networks set by the drainage basins, which are separated from one another by natural barriers (i.e., oceans or land) and therefore constitute island-like systems (Oberdorff et al., 2011; Tedesco et al., 2012). Previous studies reported that patterns in fish species richness are driven by combinations of habitat conditions (e.g., structural complexity and basin area) and energy availability (e.g., primary productivity and temperature) and, to a lesser extent, historical legacy (e.g., climate fluctuations and geographical conditions) (Oberdorff et al., 1997, 2011). These processes could also drive the distribution of fish functional diversity, because functional traits reflect their roles in the ecosystems and respond to the environmental constraints and disturbances (Mouillot et al., 2013; Villéger et al., 2017). To date, such questions have been investigated for only a few regions (Rodrigues-Filho et al., 2018; Schleuter et al., 2012). For instance, Schleuter et al. (2012) reported that geographical isolation and climate had a strong imprint on the functional diversity of native European fish faunas. Even if marked differences in fish functional diversity have been reported among realms (Su et al., 2019; Toussaint et al., 2016), how the abovementioned historical and current environmental determinants shape the functional diversity of freshwater fishes over the world river basins remains unknown.

Using a functional trait database providing information on food acquisition and locomotion for >10,000 freshwater fish species (Su et al., 2021), we evaluated the contributions of the three potential groups of processes known to affect species diversity to three complementary facets of functional diversity (FRic, FDis and FIde) in 2,453 river basins covering almost the entire continental area of the globe. Our aim was to disentangle the interplay between species richness, climate–energy-, habitat size–diversity- and historical

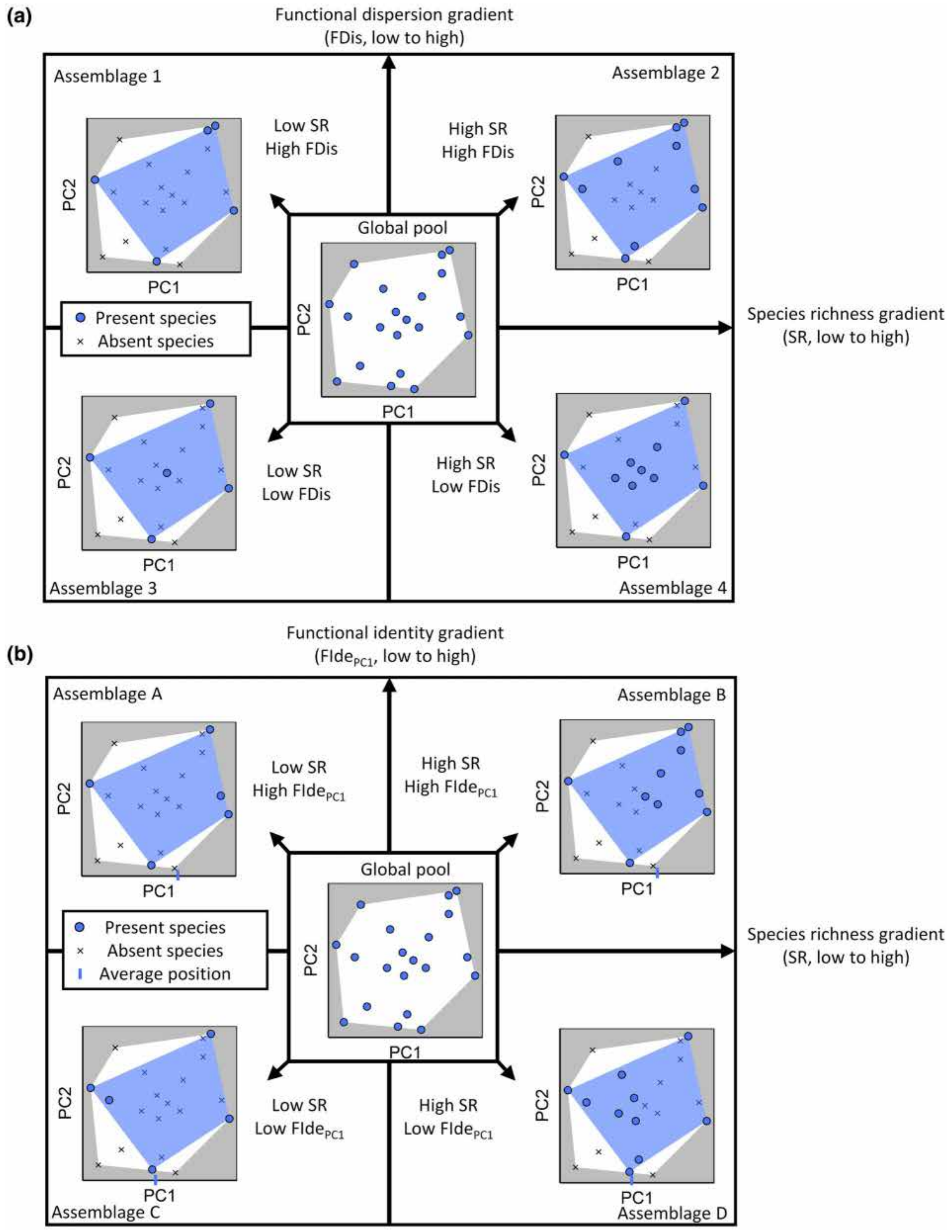

FIGURE 1 Contrasted situations of functional dispersion (FDis) and functional identity (FIde) with the same functional richness (FRic) and two levels of species richness (SR). Species are represented as blue dots. The functional space is represented here in two dimensions (PC1 and PC2). The global species pool is indicated in the centre of each plot. The white area represents the global functional richness. Eight theoretical species assemblages (e.g., fish fauna from eight river basins) illustrate (a) four contrasted situations of FDis and (b) four contrasted situations of FIde. They are characterized by different species richness (low on the left side, high on the right side) but identical functional richness (blue polygons). The FDis is measured as the average distance of species from the centroid of the species present in an assemblage. The FIde is measured as the average of the position of species along each functional axis (illustrated here only for PC1)

climate–geography-related variables on the global patterns of freshwater fish functional diversity. More precisely, we predicted: (1) that FRic patterns are congruent with species richness patterns, hence driven mostly by the same drivers (habitat, climate and energy); (2) that FDis increases nonlinearly with both habitat area and energy availability because, beyond a threshold, a greater diversity of habitats or higher energy, although promoting extreme morphologies (high FRic values), does not promote dominance by opposite trait combinations (i.e., most species have the same core trait values); and (3) that FIde is driven by both habitat and energy because different environments will favour different trait values. Nevertheless, these assumptions might depend to a large extent on the legacies of historical climate and geography, with rivers subjected to ancient isolation or recent glaciations having their fauna filtered for a particular trait, irrespective of other traits, and therefore promoting high FDis. For instance, we expect that Quaternary climate oscillations will favour species with high dispersal ability, but distinct in other respects, hence tending to have particular trait combinations resulting from the postglacial recolonization of distinct habitats and niches within drainage basins, ensuring an increased FDis of the assemblages.

2 | MATERIALS AND METHODS

2.1 | Occurrence data

We used the most comprehensive database of freshwater fish species distributions across the world (Tedesco et al., 2017; available at http://data.freshwaterbiodiversity.eu). The fish occurrence database gathers the occurrence of 14,953 species (>90% of the freshwater fish species) in 3,119 drainage basins, covering >80% of the surface of the Earth (Tedesco et al., 2017). We considered only the historical occurrence (i.e., records for native species).

2.2 | Functional traits

The functional database was obtained from Su et al. (2021), which encompasses 10 morphological traits for 10,682 freshwater fish species present in the occurrence database. It covers almost 60% of the documented world freshwater fish fauna. The 10 traits describe the size and shape of body parts involved in food acquisition and locomotion (Villéger et al., 2017). Among them, the body size is a key trait related to functions driven by metabolism (Blanchet et al., 2010) and was estimated as the maximum body length registered on FishBase (www.fishbase.org; Froese & Pauly, 2018). In addition to size, the 11 morphological measures were assessed on side view pictures (Supporting Information Figure S1a) collected during an extensive literature review, including our field data and scientific literature sources made up of peer-reviewed articles, books and scientific websites (for details on the sources, see Brosse et al., 2021). We collected at least one picture (photograph or scientific drawing) per species. Only good-quality pictures and scientific side view drawings of entire adult animals, with confirmed species identification, were kept. For species with marked sexual dimorphism, we considered male morphology, because pictures of females are scarce for most species (especially for Perciformes and Cyprinodontiformes). Intraspecific morphological trait variability was not considered in the present study because it hardly affects functional diversity at the large spatial resolution considered (Toussaint et al., 2018). The nine unitless traits describing the morphology of the fish head (including mouth and eye), body, pectoral and caudal fins (Supporting Information Figure S1b) were computed as ratios between 11 morphological measures made using IMAGEJ software (http://rsb.info.nih.gov/ij/index.html). The 10 morphological traits (nine unitless ratios and body size) selected are commonly used in assessments of fish functional diversity (e.g., Bellwood et al., 2014; Su et al., 2019, 2020, 2021; Toussaint et al., 2016, 2018; Villéger et al., 2010) and are linked to the feeding and locomotion functions of fish that themselves determine their contribution to key ecosystem processes, such as controlling food webs and nutrient cycles (Villéger et al., 2017). Overall, 24.1% of the values were missing in the original dataset (from 6.9% for maximum body length to 31.4% for relative maxillary length). We filled these missing values by using a phylogenetic generalized linear model, which includes phylogenetic information to improve the imputation performance (Bruggeman et al., 2009; Penone et al., 2014). Phylogenetic information was obtained from the R package “fishtree” (Chang et al., 2019; Rabosky et al., 2018), and the model was performed using the “phylopars” function from the R package “Rphylopars” (Bruggeman et al., 2009). The efficiency of this model at filling in missing values was tested on a random set of 1,000 species with complete values for all 10 traits. We randomly set 25% of the values for the 1,000 species as missing values and then filled them with simulated values. We then compared the simulated values with the real values. This procedure was repeated 1,00 times. Spearman's ρ between the real and simulated data was used to measure the efficiency of the procedure. The average value of Spearman's ρ varied from .86 to .95, demonstrating the efficiency of the method. As a comparison with a classical imputation method, filling the gaps using the average trait value of the 75% species with data, the average values of Spearman's ρ varied from .79 to .85, showing that the “phylopars” procedure outperforms the classical imputation method (Supporting Information Figure S2). The maps of the average values of the 10 traits for the fish assemblages in 2,453 river basins over the world are provided in the Supporting Information (Figure S3).

We then computed a principal components analysis (PCA) using the 10 morphological traits for all the species. The first five axes, accounting for 78.4% of the total variance and having eigenvalues greater than one for each axis, were kept to build a five-dimensional functional space (Supporting Information Figure S4) that faithfully represented the trait-based functional distance between species (Maire et al., 2015). The principal component (PC)1 axis is controlled mainly by fish mouth size and position and therefore reflects trophic level; the PC2 axis is controlled mainly by fish eye vertical position and body lateral shape and therefore reflects fish position in the water column; the PC3 axis is controlled mainly by fish body elongation and fin size and therefore reflects habitat type and locomotion; the PC4 axis is controlled mainly by fish body elongation and body size and therefore reflects fish size and hydrodynamism; and the PC5 axis is controlled mainly by fish caudal peduncle throttling and therefore reflects locomotion (Supporting Information Figures S1b and S4). Overall, PC1, PC2 and PC4 accounted for both nutrition and locomotion, whereas PC3 and PC5 accounted mainly for locomotion.

2.3 | Functional diversity indices

We calculated three complementary indices (FRic, FDis and FIde) to assess the functional diversity of fish assemblages in each river basin.

Functional richness measures the volume occupied by the species from an assemblage (i.e., convex hull) and has frequently been used to describe the functional diversity of assemblages (Díaz et al., 2016; Su et al., 2021; Villéger et al., 2008). Functional richness provides more information than species richness because two assemblages with the same number of species can host species with distinct functional traits, whereas two assemblages with contrasted species richness can host species with similar extreme trait values and thus have the same FRic. In this case, considering the environmental determinants of functional diversity might reveal the influence of some variables hidden in the species richness facet (Mouchet et al., 2010). However, FRic is often positively correlated with species richness and does not inform on the species position/distribution within the functional space, because it considers only the species with the most extreme traits (Villéger et al., 2008). Hence, functional metrics complementing FRic are needed to provide a more comprehensive description of the functional diversity of species assemblages.

Functional dispersion (FDis; Laliberté & Legendre, 2010) measures the mean distance of species in the five-dimensional functional space to the centroid of all species in the assemblage. Here, we scaled it between zero and one by dividing its raw value by half of the maximum distance among all the species present in the global species pool, which is the maximum value possible given species trait values (Mouillot et al., 2013).

In addition, the position of the species assemblage in the functional space can be assessed by the functional identity, which measures the average position of species on each functional axis (Mouillot et al., 2013), therefore providing an FIde value for each axis.

These three indices are complementary, because FDis and FIde can take contrasted values for a given FRic (Figure 1). For instance, two species assemblages with the same FRic owing to similar extreme species can have low FDis when most of the non-extreme species are located around the centroid (Figure 1a, assemblages 1 and 3) or have high FDis when most of the non-extreme species have almost extreme trait values and disperse to the margins of the functional space (Figure 1a, assemblages 2 and 4).

2.4 | Predictor variables

Overall, 16 original predictor variables were selected to evaluate the effect of the three groups of drivers (i.e., climate–energy, habitat size–diversity and historical climate–geography) on the variation in freshwater fish diversity.

Climate–energy was assessed by five predictors: mean annual temperature (TEM); mean annual precipitation (PRE); mean annual evapotranspiration (EVP); mean annual runoff (ROF); and mean annual net primary productivity (NPP).

Habitat size–diversity was assessed using four predictors: river basin area (RBA); elevational range (ALR); mean slope (MSP); and river basin diversity (RBD). The RBD was estimated by applying Shannon's diversity index to proportions of biomes (i.e., vegetation types associated with regional variations in climate) within river basins (Oberdorff et al., 2011).

Historical climate–geography was assessed by six predictors: temperature anomaly during the Quaternary period (TEA); past temperature trend (PTT); past precipitation trend (PPT); past climate-change velocity (PCV); basin median latitude (BML); and the endorheic/exorheic status (EOC) of the river that relates to the level of isolation of the river basin. The TEA was measured as the change in the mean annual temperature between the present and Last Glacial Maximum conditions (the average values based on two global circulation models; Supporting Information Table S1; Dias et al., 2014). The PTT and PPT were measured as the centennial trend of temperature and precipitation changes since the Last Glacial Maximum, reflecting the consistent spatio-temporal changes in climatic stability (Brown et al., 2020). The PCV was measured as the local rate of displacement of climatic conditions over the surface of the Earth since the Last Glacial Maximum (Sandel et al., 2011). See the Supporting Information (Table S1) for a list of the variables, corresponding references and units. A list of the data sources is also given in the Supporting Information (Appendix S1).

2.5 | Statistical analysis

We applied boosted regression trees (BRTs) to assess the relative importance of each considered variable in shaping the patterns of FRic, FDis and FIde. In addition to the 16 predictor variables, we also considered the total number of native species [i.e., species richness (SR)] present in each river basin as a predictor in all the BRT models. Furthermore, we also performed a linear regression between FRic and species richness and compared the result with a piecewise regression to test whether the slope of this relationship changes beyond a species richness breaking point. Piecewise regression was computed using the "segmented" function in the "segmented" package in R (Muggeo, 2008).

Although BRTs were considered relatively robust to collinearity among predictor variables, it has recently been shown that removing predictor variables with an absolute Pearson correlation coefficient >.7 is a desirable practice with techniques based on boosting

(Parravicini et al., 2013). We therefore removed PRE and PCV from the BRT models because they were strongly correlated with EVP and TEA (Supporting Information Figure S5). From the 16 initial predictors, the remaining 14 predictors were kept in the original BRT models. All the models were conducted twice, including species richness as a variable and excluding it, to check whether species richness affected the influence of other environmental variables on the three facets of functional diversity.

The BRTs were fitted using the "gbm.step" function in the "dismo" package in R (Elith et al., 2008). This technique allows for the specification of four main parameters: bag fraction (*bf*), learning rate (*lr*), tree complexity (*tc*) and the number of trees (*nt*). The *bf* is the proportion of samples used at each step; *lr* is the contribution of each fitted tree to the final model; *tc* is the number of nodes of each fitted tree, determining the extent to which statistical interactions were fitted; and *nt* represents the number of trees, corresponding to the number of boosting iterations.

The optimal setting of the parameters was chosen using 10-fold cross-validation (CV). The procedure provides a parsimonious estimate, CV – D^2 (i.e., the cross-validated proportion of the deviance explained), representing the expected performance of the model when fitted to new data (Elith et al., 2008). Using CV, we explored different combinations of the parameters to be set, and we retained the model showing the highest CV – D^2 (Supporting Information Table S2).

The relative influence of predictor variables in the final optimal BRT models was evaluated with the contribution to model fit attributable to each predictor, averaged across all the trees fitted (Friedman, 2001). To account for uncertainty around these estimates, the relative influence of each predictor variable was calculated on 1,000 bootstrap replicates of the original dataset to compute 95% confidence intervals by using the "gbm.fixed" function in the "dismo" package and the "boot" function in the "boot" package. We also estimated the interactions between each pair of predictors by using the "gbm.interactions" function in the "dismo" package (Elith et al., 2008).

Spatial autocorrelation has become an important issue in geographical ecology and macroecology over recent decades (Leprieur et al., 2011; Rangel et al., 2010). Given that BRTs do not account for spatial autocorrelation in both the dependent and predictor variables, we also performed autoregressive error ($\mathrm{SAR}_{\mathrm{error}}$) models and compared the results of $\mathrm{SAR}_{\mathrm{error}}$ models to check whether spatial autocorrelation influenced the BRT results. We scaled the 14 predictor variables to a zero mean and unit variance to ensure equal weighting in the models. Quadratic terms were included in the $\mathrm{SAR}_{\mathrm{error}}$ models to consider nonlinear relationships. The spatial autocorrelation analysis was performed using the "spatialreg" and "spdep" packages (Bivand & Piras, 2015). The results of $\mathrm{SAR}_{\mathrm{error}}$ models are provided in the Supporting Information (Table S3). Functional diversity drivers identified by BRT models were confirmed overall by $\mathrm{SAR}_{\mathrm{error}}$ models.

All statistical analyses were performed with R software v.3.5.1 (R Core Team, 2019).

3 | RESULTS

We first mapped FRic, FDis (Figure 2) and FIde (measured on PC1–PC5; Figure 3) of freshwater fish assemblages at the global scale. Those three facets of functional diversity were not strongly correlated with each other (|Pearson's r| < .51; Supporting Information Figure S6). Besides, they varied greatly among river basins between and within the six realms. The highest values of FRic were concentrated disproportionately in river basins located in the Neotropical realm (e.g., the Amazon River reached the highest FRic value, at 44% of the world FRic) and some large basins from other realms, whereas low values were located mostly in the two northern realms (i.e., Nearctic and Palaearctic) and the Australian realm (Figure 2a). The patterns of FDis and FRic were weakly correlated with each other (Pearson's $r = .11$). The FDis values ranged from .06 to .38, with the highest values concentrated in river basins from Europe (Figure 2b). The patterns of FIde showed latitudinal gradients for some axes of the functional space. Specifically, FIde on PC1 increased from the Equator to the poles, FIde on PC2 and PC3 decreased with latitude from south to north, and FIde on PC4 and PC5 increased with latitude from south to north (Figures 3 and 4).

The final BRT model for FRic explained 77.5% of the total variation (cross-validation procedure; Supporting Information Table S2). The relationship between the observed and predicted FRic was remarkably high ($R^2 = .984$ for a regression of slope one and zero intercept; Supporting Information Figure S8). As expected, species richness was found to be the best predictor of FRic, with a relative contribution to the BRT model reaching 71.4%. However, all remaining variables related to the three hypotheses did not play strong roles (i.e., relative contribution <5.2%) in shaping the pattern of FRic (Figure 2a). For FDis, the BRT model explained 48.8% of the total variation (cross-validation procedure; Supporting Information Table S2). The relationship between observed and predicted FDis was also high ($R^2 = .994$ for a regression of slope one and zero intercept; Supporting Information Figure S8). Together, the historical climate–geography-related variables contributed the most to the FDis pattern (36.3%), followed by the habitat-related variables (30%) and climate–energy (25.2%). Among them, basin median latitude was the most influential variable (14.8%), followed by the net primary productivity (11.7%). All the other variables had a contribution <10% (Figure 2a).

The BRT models explained *c*. 65% of the total deviance for FIde on PC1–PC5 (Supporting Information Table S2). The relationships between observed and predicted FIde on the five PC axes remained high, with R^2 values > .9 (Supporting Information Figure S8). However, FIde on the five PC axes displayed contrasting relationships with variables related to the different hypotheses. The results of FIde on PC1 and PC5 were under a balanced influence of habitat- and historical-related variables, with group contribution ranging from 34.7 to 42.3%, among which, basin median latitude and annual runoff contributed the most to FIde on both axes (Figure 3a,e). In contrast, FIde on PC2 and PC3 was under a balanced influence of the three groups of variables, with

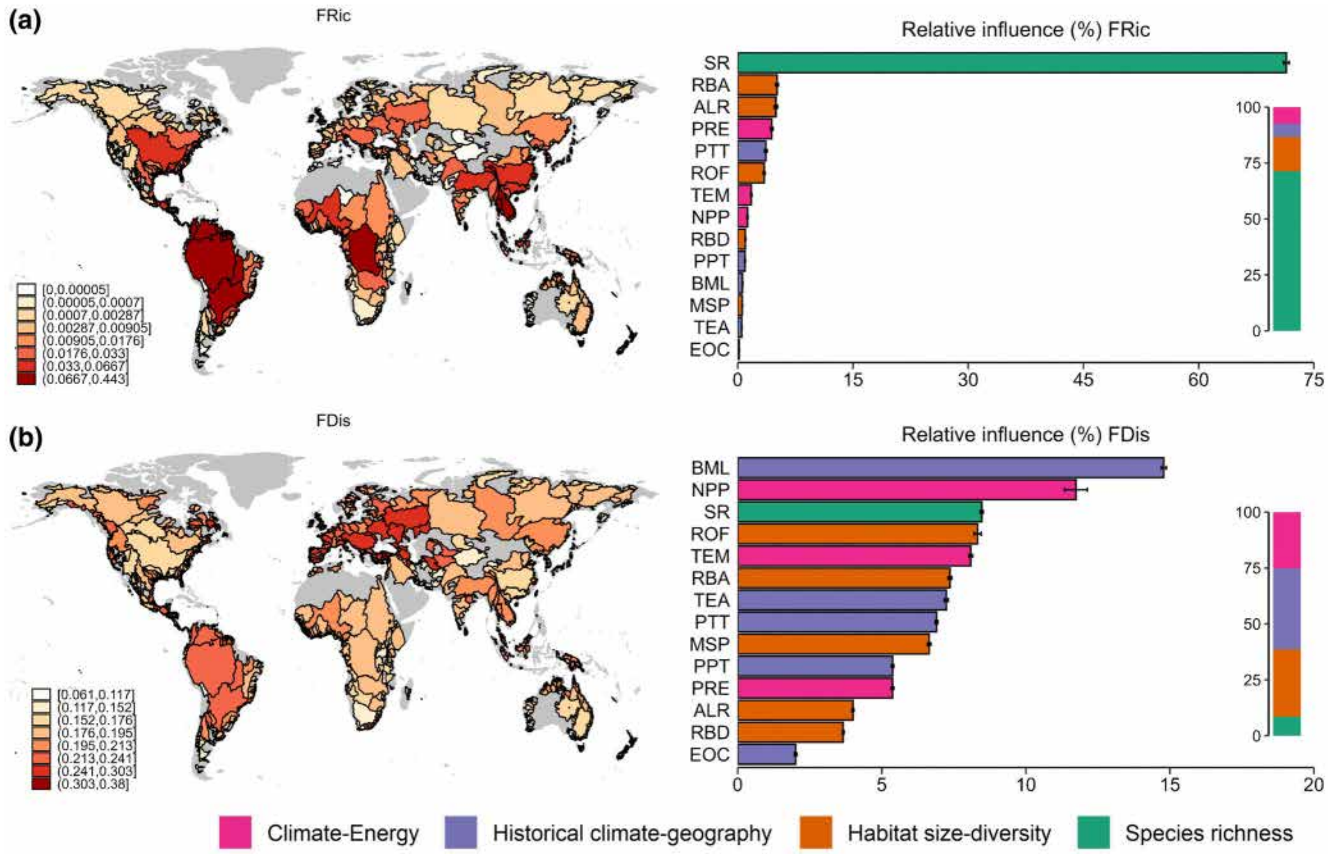

FIGURE 2 Global distribution of fish functional richness (FRic) and functional dispersion (FDis) (left panels; gradient of colour shows the percentage of basins with the highest values to the lowest values) and the relative influence of the 14 predictor variables in the boosted regression trees (BRT) models (right panels). Coloured horizontal bars in the right panels indicate the influence of each predictor variable, accounting for current climate, past climate, geography, habitat–energy and species richness, on (a) FRic and (b) FDis. Coloured vertical bars on the right summarize the overall influence of the current climate-, past climate-, geography-, habitat–energy- and species richness-related variables on FRic and FDis. ALR: elevational range; BML: basin median latitude; EOC: endorheic; MSP: mean slope; NPP: net primary productivity; PPT: past precipitation trend; PRE: precipitation; PTT: past temperature trend; RBA: river basin area; RBD: river basin diversity; ROF: runoff; SR: species richness; TEA: temperature anomaly; TEM: temperature

the group contribution ranging from 25.2 to 35.4% (Figure 3b,c). Among them, net primary productivity (24%, PC2), runoff (21.8%, PC3) and temperature (21.6%, PC3) were the most influential variables. The results of FIde on PC4 showed that historical climate–geography-related variables (51.1%), especially the median latitude (33.6%), contributed the most to the pattern (Figure 3a), following by the habitat (27%) and climate–energy (17.4%) groups (Figure 3d).

Interactions between predictors would affect the performance of the BRTs (Supporting Information Table S2). Although interactions between variables were weak in the models for FRic and FDis (Figure 5a,b), models taking interactions into account still performed better than the simpler ones (Supporting Information Table S2). Especially, some interactions of variables were very strong in the models for FIde on the five PC axes (Figure 5c–g). Basin median latitude, in particular, had relatively strong interactions in most of the models for FIde, especially with temperature and runoff, highlighting that these factors have different effects in basins located in different latitudes (Figure 5c–g).

4 | DISCUSSION

A consideration of three complementary facets of functional diversity (Figure 1) allowed us to quantify the roles of climate–energy, habitat size–diversity and historical climate–geography processes on the functional diversity of the world freshwater fish faunas. We revealed that the relative roles of those processes differ from those known for species richness (Guégan et al., 1998; Oberdorff et al., 2011). Functional richness was, nevertheless, influenced strongly by the species richness, which is per se governed primarily by habitat diversity and energy availability (Guégan et al., 1998; Oberdorff et al., 2011). The habitat size–diversity and climate–energy hypotheses together explained almost 80% of the FRic (Supporting Information Figure S9a), which thus confirmed the strong effect of contemporary habitat and energy availability on FRic, but also the tight linkage between taxonomic richness and functional richness. The positive relationship between species and functional richness could be explained, in part, by the expected increase of the range of traits with an increasing number

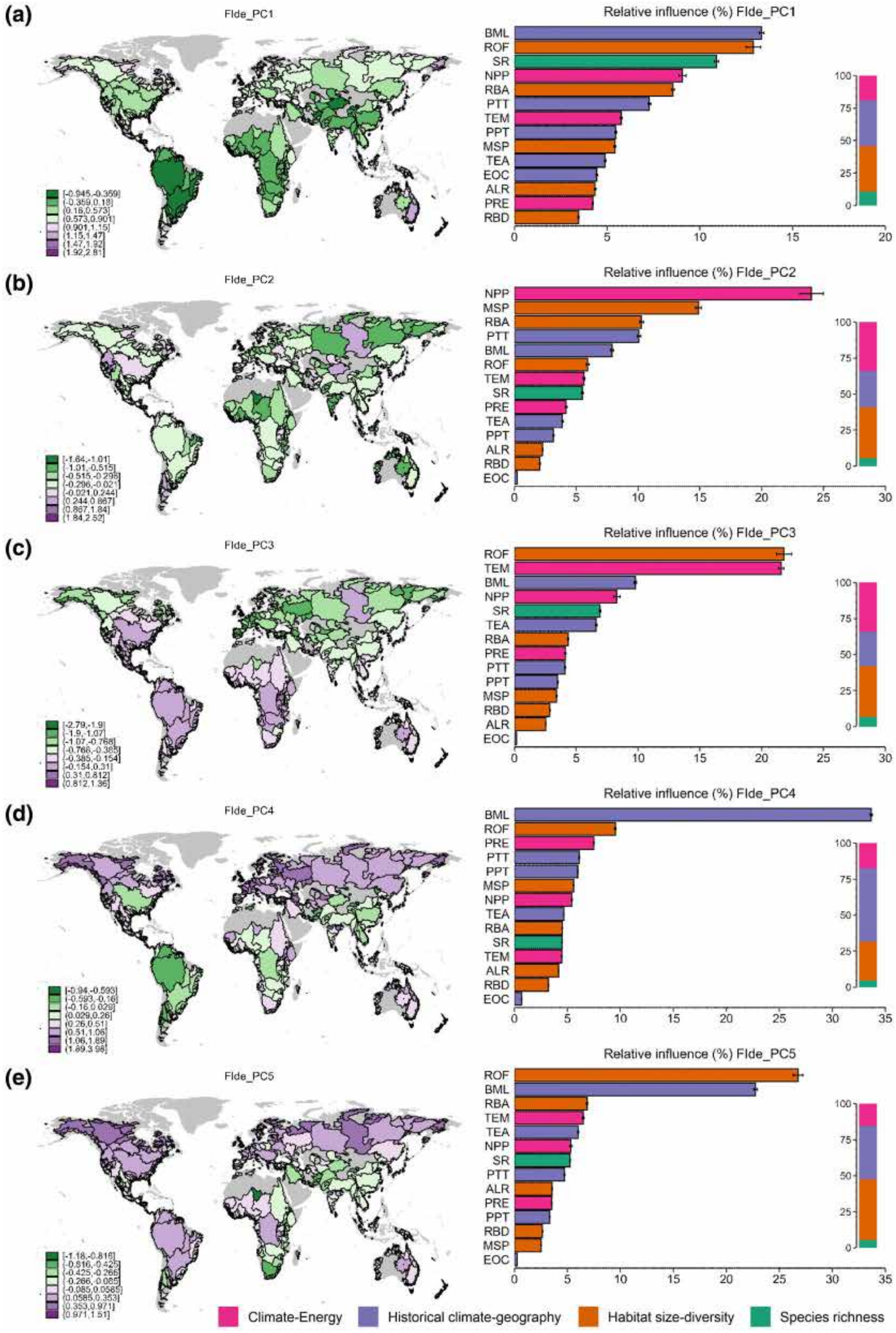

FIGURE 3 Global distribution of fish functional identity (FIde) on PC1–PC5 (left panels; gradient colours from purple to green show the percentage of basins with the highest to the lowest FIde values) and the relative influence of the 14 predictor variables in the boosted regression trees (BRT) models (right panels). Coloured horizontal bars in the right panels indicate the influence of each predictor variable, accounting for current climate, past climate, geography, habitat–energy and species richness, on (a–e) functional identity on axes PC1–PC5. Coloured vertical bars on the right summarize the overall influence of the current climate-, past climate-, geography-, habitat–energy- and species richness-related variables on the five FIde dimensions. ALR: elevational range; BML: basin median latitude; EOC: endorheic; MSP: mean slope; NPP: net primary productivity; PC, principal component; PPT: past precipitation trend; PRE: precipitation; PTT: past temperature trend; RBA: river basin area; RBD: river basin diversity; ROF: runoff; SR: species richness; TEA: temperature anomaly; TEM: temperature

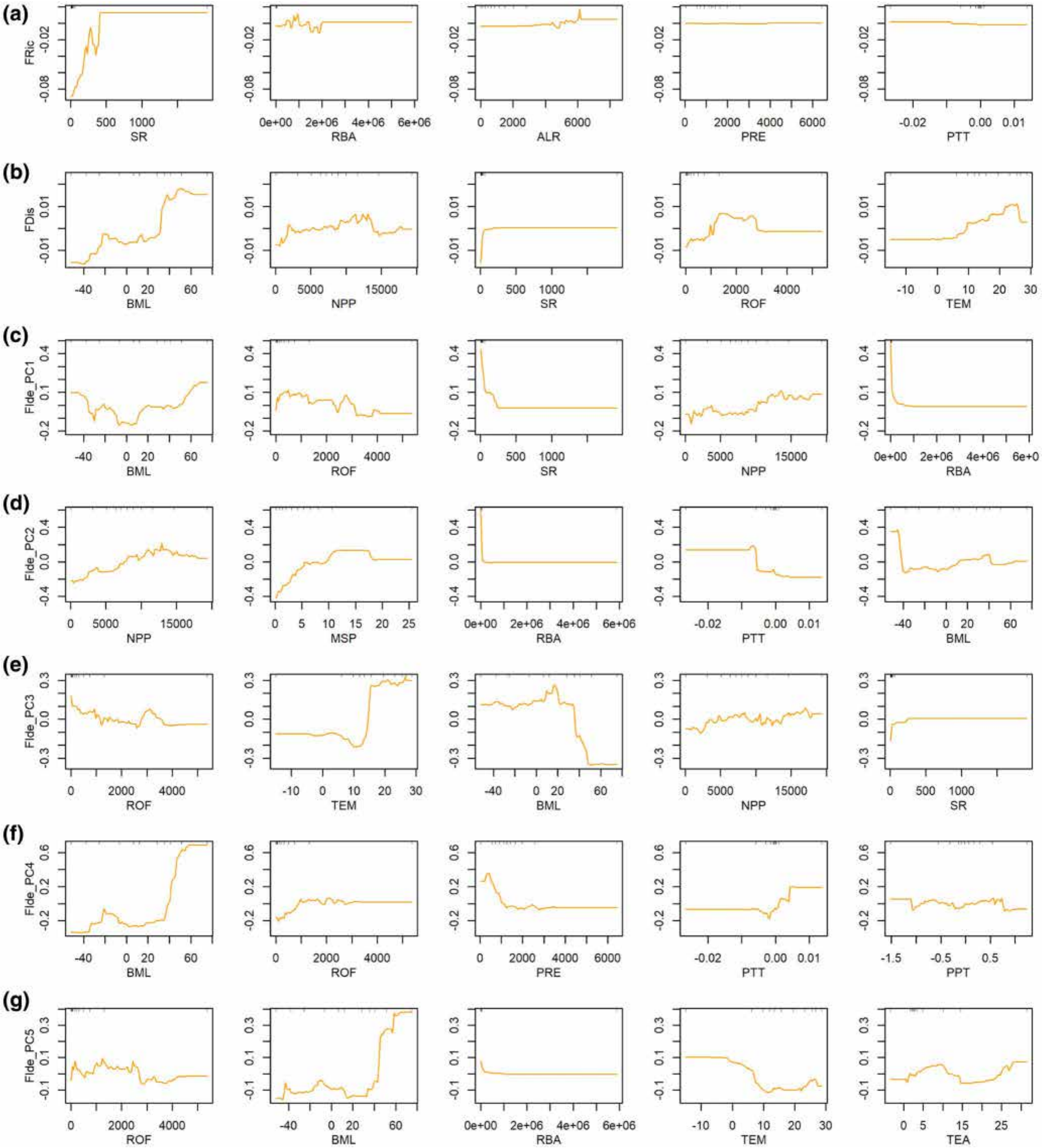

FIGURE 4 Results of boosted regression trees showing the partial dependence between each functional diversity facet and the corresponding five most influential predictor variables (for the remaining variables, see Supporting Information Figure S7). The *y*-axis in each panel represents the zero-centred fitted function of the corresponding functional diversity index: (a) functional richness, (b) functional dispersion and (c–g) functional identity on PC1–PC5. ALR: elevational range; BML: basin median latitude; MSP: mean slope; NPP: net primary productivity; PPT: past precipitation trend; PRE: precipitation; PTT: past temperature trend; RBA: river basin area; ROF: runoff; SR: species richness; TEA: temperature anomaly; TEM: temperature

of species in an assemblage (Villéger et al., 2008). Nevertheless, we did not detect any saturation effect of functional richness with an increase in species (Supporting Information Figure S10), which is inconsistent with current knowledge on the functional diversity of plants (Ordonez & Svenning, 2017) and on the species richness of North American mammals (Kerr & Packer, 1997), where the limited pool of the range (or categories) of traits explained the saturation of functional richness. Instead, we showed that FRic

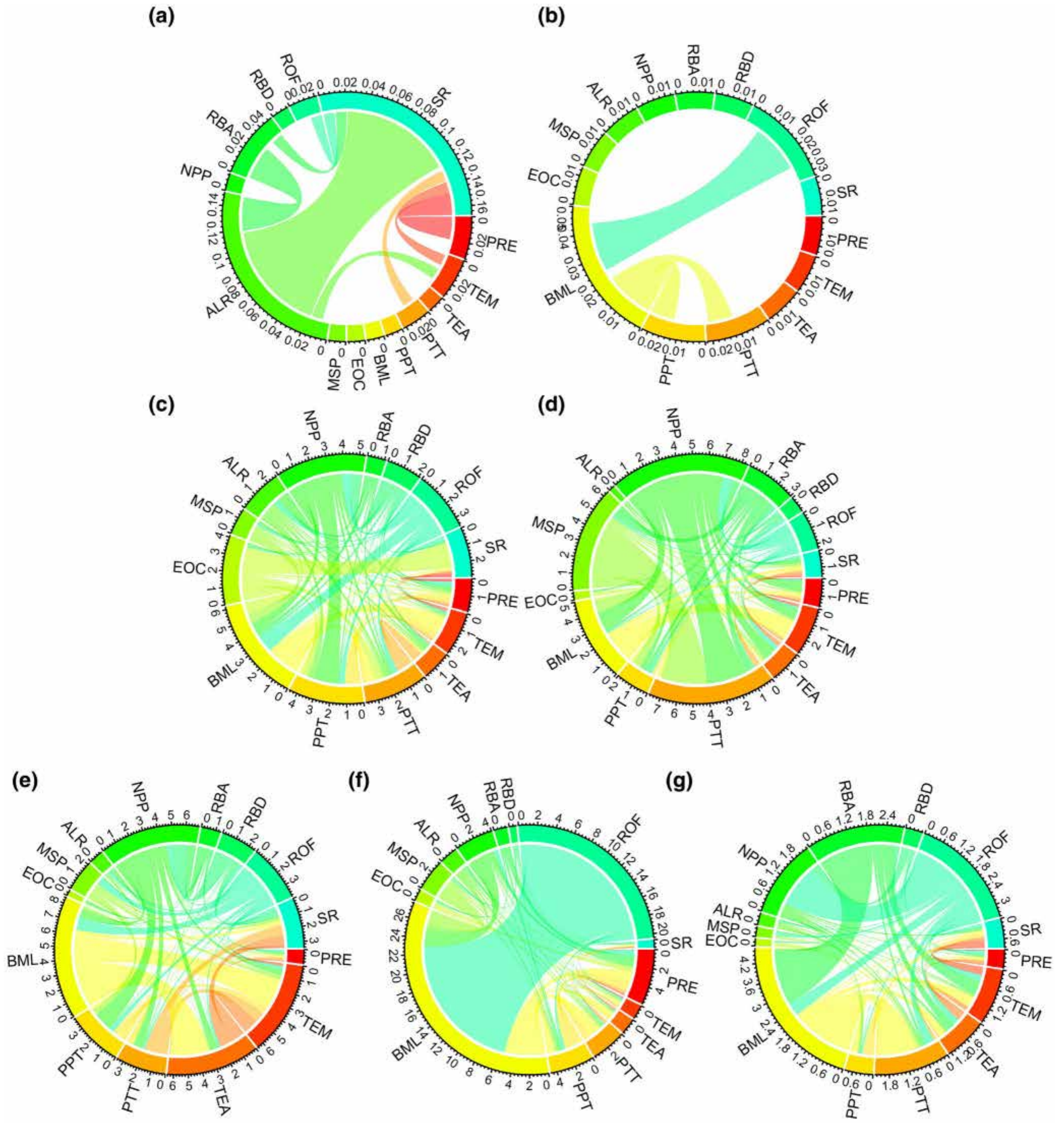

FIGURE 5 Interactions between the 14 predictors for each boosted regression trees (BRT) model. The width of the bands represents the strength of interaction between pairs of the predictors used to build the BRT models for (a) functional richness, (b) functional dispersion and (c–g) functional identity on PC1–PC5. ALR: elevational range; BML: basin median latitude; EOC: endorheic; MSP: mean slope; NPP: net primary productivity; PPT: past precipitation trend; PRE: precipitation; PTT: past temperature trend; RBA: river basin area; RBD: river basin diversity; ROF: runoff; SR: species richness; TEA: temperature anomaly; TEM: temperature

overall increased linearly with species richness, associated with an increase in heterogeneity of functional richness among the most species-rich river basins, which can be explained by differences in the overall pool of functional traits supported by each biogeographical realm (Toussaint et al., 2016).

In contrast, species richness had a limited influence (<10%) on the functional dispersion and functional identity patterns. Instead, variables related to historical climate–geography hypothesis primarily explained the patterns of FDis and FIde (mostly on PC1, PC4 and PC5). We revealed a latitudinal gradient in FDis (Figure 4b), whereby values increased from south to north and reached maximal values in the high-latitude basins of the Northern Hemisphere, especially in European basins (Figure 2b). Those basins experienced a larger amplitude of Quaternary climatic oscillations and higher temperature anomaly (Jansson, 2003; Leprieur et al., 2011). Each Quaternary glaciation caused the extinction of most small-sized species with low dispersal ability (Griffiths, 2006), then glacier retreat opened available habitats, which were recolonized preferentially from southern refuge areas (e.g., the Mississippi and Danube river basins in the Nearctic and Palaearctic realms, respectively) through intermittent inter-basin connections during the postglacial period (Leprieur et al., 2011; Reyjol et al., 2007). This process was particularly important in Europe, where the high extinction levels during Quaternary glaciations were little compensated by the recolonization from southern refuges owing to the dominant east–west orientation of river basins (Oberdorff et al., 1997). Those historical processes selected species with extreme dispersal traits (e.g., large body size) among the pool of species that survived in the glacial refuges, explaining the overdominance of locomotion-related extreme trait values in the fish assemblages of the temperate and cold areas of the Northern Hemisphere. The interplay of these two processes therefore explains, in part, why fish assemblages in temperate and cold rivers of the Northern Hemisphere have a lower functional richness (with the exception of some refuge areas during glaciations) in comparison to the tropical areas that were less impacted by glaciations. The areas recently recolonized after the last Quaternary glaciations primarily received few species with traits associated with high dispersal ability (e.g., body size; Blanchet et al., 2010), but with contrasted suites of traits related to feeding, hence promoting higher functional dispersion. On the contrary, glacial refugia host fish faunas with higher functional richness and dispersion, paralleling recent results on the role of glaciations in the spatial distribution of plant functional diversity in Europe (Ordonez & Svenning, 2017).

Dispersal and locomotor ability are strongly linked to body size (Griffiths, 2006; Tedesco et al., 2012) and caudal fin size (Radinger & Wolter, 2014; Su et al., 2020; Webb, 1984), which are strongly influential variables on PC4 and PC5 of the functional space (maximum body length and caudal peduncle throttling; see Supporting Information Figure S4), explaining the latitudinal gradient in functional identity observed for those PC axes. This finding parallels the patterns observed for functional dispersion, testifying that species with high dispersal abilities tend to have extreme trait values within assemblages (FDis) and in the global functional space (FIde). The functional traits of those species underline the high functional dispersal ability of fishes in the assemblages found in previously glaciated river basins of the Northern Hemisphere. These results are in line with those of Blanchet et al. (2010), who found that large-bodied fish species dominate in higher latitudes of the Northern Hemisphere. Nevertheless, this trend was not verified in the Southern Hemisphere, probably because of the limited surface of continental areas in the temperate and cold regions, and only a few rivers flowing in the extreme southern part of the hemisphere were affected by the glaciations (Blanchet et al., 2010; Wright et al., 1993). Moreover, those southern temperate faunas are mainly composed of marine lineages that colonized freshwaters secondarily (e.g., Gobiidae and Galaxidae in southern South America, South Australia and New Zealand; Blanchet et al., 2010; Lévêque et al., 2008), probably relating the colonization process to physiological constraints (e.g., the ability of fish to deal with gradients of salinity).

Our findings also suggest that variables related to the climate–energy and habitat size–diversity hypotheses contributed to shaping the patterns of FDis and FIde. For instance, FIde on PC2 and PC3, which mostly represent the fish body elongation and shape, are most influenced by climate–energy- and habitat-related variables (Figure 3b,c). The shifts of species position in the functional space along the climate–energy-related variables might be explained by two different mechanisms: (1) divergent traits make the fishes from a given assemblage more efficient in using the highly diversified food resources present in more productive regions (e.g., with high NPP values; Wright, 1983); and (2) the functional traits reflect the physiological limits of the species that are constrained by climate-related variables (e.g., temperature; Hawkins et al., 2003). Likewise, the shifts of species position in the functional space along the habitat diversity-related variables might reflect morphological adaptations to habitat types. For instance, low runoff and low-slope rivers promote slow-flowing water habitats, which are inhabited preferentially by the less elongated fish species (Haas et al., 2010; Su et al., 2020).

It should, nevertheless, be noticed that the river basin spatial grain used here does not capture the entire spatial and environmental variability of rivers. Indeed, sub-basin fish faunas could be constrained by distinct environmental determinants and historical legacies (e.g., for the Amazon drainage, see Oberdorff et al., 2019). We therefore encourage further studies to investigate the determinants of fish functional diversity at sub-basin spatial grains to obtain a more comprehensive picture of the processes responsible for current functional diversity patterns. Likewise, considering more local grains would permit an approach to the relative roles played by environmental characteristics and biotic processes, as previously done by Cilleros et al. (2016) for Amazonian and European rivers. Moreover, although the 10 morphological traits we used are currently the most comprehensive trait dataset for freshwater fishes of the globe (Brosse et al., 2021; Su et al., 2021), they do not cover the entire functional range of fishes (e.g., reproductive traits) or fully replace life-history traits (Kuczynski et al., 2018). We therefore appeal for the development of a global database on fish traits, as done already for the other vertebrate groups (Myhrvold et al., 2015; Oliveira et al., 2017). This will provide us with a better understanding of how the historical and current ecological processes jointly shaped the functional diversity of global freshwater fishes and how future climate change and human activities will modify those biodiversity patterns.

4.1 | Conclusion

To conclude, our study shows that the historical legacy has played a significant role in the global FDis and FIde patterns of freshwater fish, providing insights into the relative roles of historical and current environmental determinants in the functional structure of fish assemblages. In contrast, the FRic was determined mainly by the habitat size–diversity hypothesis, owing to its strong dependence on species richness. More generally, our results strengthen the assertion that the independence of facets of functional diversity from the species richness makes them essential biodiversity variables (*sensu* Pereira et al., 2013) to understand the structure of communities and their changes through global changes. Global hotspots of species richness have been widely used to determine priority areas for conservation, and other facets of biological diversity are still under consideration (but see Su et al., 2021). Our results provide evidence of the distinct processes shaping taxonomic and functional facets of biodiversity and thus advocate for consideration of functional diversity measures in global freshwater conservation priorities.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Fish occurrence data can be retrieved freely from https://doi.org/10.6084/m9.figshare.c.3739145, and metadata are available in the paper by Tedesco et al. (2017). Fish functional trait data can be retrieved freely from https://doi.org/10.6084/m9.figshare.13383170, and metadata are available in the paper by Su et al. (2021). Data sources for environmental variables are given in the Supporting Information (Table S1). Core data and codes used for analyses are available at https://doi.org/10.6084/m9.figshare.17062010.

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BIOSKETCH

Guohuan Su is interested in the macroecology and diversity of freshwater fish. He is currently investigating the relationship between global fish biodiversity and river networks and the influence of global changes on global fish biodiversity patterns.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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