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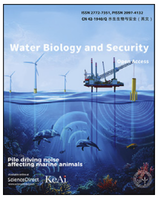

Research Article

Assessing fish taxonomic and functional β diversity to inform effective conservation strategies in a large reservoir of the Yangtze River Basin

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ABSTRACT

The determinants of local differences in species and functions matter for reservoir management but have seldom been investigated. To this aim, we explored fish taxonomic, and functional beta diversity between local assemblages in a large Chinese reservoir. Taxonomic β diversity was primarily driven by species richness differences (54%–72%), while functional β diversity was almost equally driven by turnover and nestedness components. Environmental characteristics of the sites were significant predictors of all facets of fish β diversity. Additionally, site contributions to taxonomic (LCBD) and functional (XLCBD) β diversity were significantly associated with human activity variables, suggesting that there is a pressing need to mitigate human-induced disturbances for the conservation of biodiversity. Species contributions to taxonomic (SCBD) and functional (XSCBD) β diversity exhibited positive correlations primarily with species occupancy and abundance, suggesting the potential uniqueness of certain common species. Priority conservation areas in the upstream area and rare but key species such as *Tachysurus* and *Siniperca* were identified based on site and species contributions. We thus propose to focus on habitat restoration actions to upstream areas by restricting sand mining, as the current mining activities in the river channel can directly alter riverbed morphology and damage the spawning grounds of fish. We also emphasize the necessity for increased conservation efforts through the development of sustainable recreational fishing policies and stock recovery programs for sensitive species such as *Pelteobagrus vachelli* and *Acheilognathus macropterus*. These species have lower SCBD or XLCBD values than others and possess unique feeding habits or high economic value, making them primary targets for recreational fishing. This research highlights the importance of integrating taxonomic and functional β diversity to effectively evaluate biodiversity changes and develop more comprehensive and sustainable conservation strategies for fish diversity conservation.

1. Introduction

Understanding the determinants of changes in species and functions between assemblages (β diversity) is recognized as a way to assess ecosystem health and stability (Olden et al., 2010). Historically, studies of β diversity have often concentrated on taxonomic diversity, which is grounded in species compositional variability (Mori et al., 2018), but it can be complemented by consideration of the differences in functions between species assemblages (Olden et al., 2010). Functional diversity, as a key component of biodiversity, offers a new perspective on the relationship between biodiversity and ecosystem functioning, serving as a better descriptor of ecosystem services and stability (Villéger et al., 2017). For instance, a study tracking fish communities over three decades noted that while taxonomic structures diverged, trait structures converged, indicating that environmental changes, such as warming, lead to convergence towards traits more adapted to new conditions, regardless of species composition (McLean et al., 2019). Moreover, understanding functional rarity and the role of functionally rare species in ecosystems can provide insights into conservation priorities and the development of effective management strategies (Grenié et al., 2018).

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Considering together both taxonomic and functional dissimilarities between assemblages enhances our capacity to elucidate the processes that shape biodiversity patterns (Jia et al., 2020; Zeni et al., 2019). The integration of taxonomic and functional diversity provides a more comprehensive understanding of community assembly and ecosystem functioning, revealing important patterns for understanding community responses to environmental change (Duffy et al., 2007). Therefore, when studying biodiversity, it is not only important to consider taxonomic diversity but also the functional diversity that underpins the ecosystem's capacity to provide services and maintain resilience.

Beta diversity can be partitioned into two distinct components: species replacement and species richness difference (Baselga, 2010). Species replacement reflects the interchange of species across various communities and reveals distinct habitats and/or distinct biogeographic histories, while species richness differences are attributable to natural or anthropogenic environmental filtering (Villéger et al., 2013). In addition, β diversity can be further complemented with site (local) and species contributions (Legendre and De Cáceres, 2013; Nakamura et al., 2020). Site contributions to β diversity (LCBD for taxonomic diversity and XLCBD for functional diversity) elucidate the extent to which individual sites contribute to the overall variation in β diversity, with higher values identifying the most unique habitats (Heino et al., 2022; Martelo et al., 2024). In addition, species contributions to β diversity (SCBD for taxonomic and XSCBD for functional diversity) reveal the individual impact of each species to β diversity, and although the most frequent or abundant species tend to present the highest SCBD, other species can still have a strong contribution due to their particular spatial distribution (Heino and Grönroos, 2017). Moreover, the extent to which these processes influence functional β diversity remains largely unexplored, particularly when considering species replacement and richness differences (Frasconi Wendt et al., 2021). This is particularly the case for freshwater fish communities, that were to date mainly considered over regional scales with only rare studies considering local and temporal patterns of taxonomic and functional biodiversity (Camara et al., 2023; Cheng et al., 2014).

Studying the factors influencing beta diversity and its components is of great significance for the conservation and restoration of ecosystems. The beta diversity pattern is generally believed to be jointly determined by environmental filtering, dispersal limitation, and other unknown historical processes (Baselga, 2010). Still, the environmental variables and the processes explaining β diversity appear inconsistent among studies, regions and aquatic ecosystems. For instance, Lima et al. (2024) reported environmental filtering as the primary structuring mechanism of local stream fish communities in the Brazilian Cerrado, regardless of the spatial scale. This is consistent with results from the Bita River in Colombia, which found that spatial variables were only weakly associated with beta diversity and its components (López-Delgado et al., 2020). Similar results were found in the Chishui River Basin (a major tributary of the Yangtze River), where fish LCBD was well explained by both environmental and spatial factors (Xia et al., 2022a), while Borges et al. (2020) found that dispersal variables were the main determinant of fish LCBD in the Neotropical ecoregion. In addition, a study on fish β diversity and its component patterns of fish in the middle and lower reaches of the Yangtze River identified river-lake connectivity, extent of riparian wetlands and fishing pressure as key drivers of fish β diversity, with the nestedness component of β diversity being mostly explained by the area of riparian wetlands and fishing pressure, while the turnover component was mainly associated with river-lake connectivity (Xiong et al., 2023).

Here we investigated the beta diversity patterns of fish assemblages from the Zhelin Reservoir, a large (302 km^2) canyon-type reservoir located in the middle reaches of the Yangtze River in China (Meng et al., 2023). Our aims were first to investigate the spatial and temporal patterns of fish community structure through the measure of β diversity, and their constituent components between 13 sites sampled at four occasions (spring, summer, autumn and winter). We then assessed the influence of natural characteristics and anthropogenic disturbances on fish β diversity and its components. Finally, we built on those results to identify priority areas and key species for fish diversity conservation in the Zhelin Reservoir.

2. Materials and methods

2.1. Study area

This study was conducted in the Zhelin Reservoir, a storage type reservoir located at coordinates 115°04′ to 115°40′ East and 29°03′ to 29°27′ North. It is the largest reservoir in Jiangxi Province, China, as illustrated in Fig. 1. The reservoir encompasses a water surface area of 308 km^2 and has a total storage capacity of 7.92×10^9 m^3. The average water depth is 16.3 m and the maximum depth reaches 45 m. The region experiences a subtropical monsoon climate, characterized by an average annual precipitation of 1611.8 mm. Fish community surveys were done from September 2020 through January, April, and July of 2021, spanning across the four seasons of autumn, winter, spring, and summer, respectively. These surveys were conducted at 13 strategically positioned sampling sites, extending from the upper to the lower reaches of the reservoir, as depicted in Fig. 1. Meanwhile, water quality and plankton surveys were also undertaken at these sampling locations.

2.2. Data collection

2.2.1. Fish sampling

Fish samples were collected utilizing multi-mesh composite gill nets and unbaited bottom traps. The composite gill net consisted of nine panels, each measuring 80 m in length and 5 m in height, featuring a gradation of mesh sizes: 2 cm, 4 cm, 6 cm, 8 cm, 10 cm, 12 cm, 14 cm, 16 cm, and 18 cm between opposite knots. Within a net, the mesh sizes were arranged in a randomized sequence, yet the sequence remained consistent across all gill nets (CEN, 2015). It should be noted that although we used multi-mesh composite netting for sampling, small fish may not be easily captured due to the minimum mesh size of 2 cm. The bottom trap, measuring 0.3 m in both width and height, was employed to capture benthic fish, with a trap length of 15 m and a mesh size of 1.2 cm. The relative abundance of fish at each sampling site during each period was ascertained by deploying two multi-mesh gill nets and four bottom traps, which were left in place for a 12-h exposure period, from 18:00 to 06:00 the following day. The collected fish were identified to the species level and weighed to the nearest 0.01 g. Immediately after measurements, fish were promptly returned to the water. The scientific name of the species collected was updated in accordance with FishBase (Forese and Panuly, 2021). The fish community abundance (com_ab) and species richness (sp_rich) are detailed in Table S1 (see Supplementary material).

2.2.2. Data collection of abiotic and biotic variables

We measured water temperature (WT, °C), pH, dissolved oxygen (DO, mg/L), and conductivity (Cond, μS/cm) of surface water (0.5 m below the surface) on-site using a portable multi-parameter water quality meter (HQ40D, Hach Love-land, USA). Water depth (WD, m) and Secchi disk transparency (SD, cm) were determined using a Depthmate Portable Sounder (SM-5) and a Secchi disk (SD20), respectively. At each sampling site, 1 L of water sample was collected for the subsequent analysis of total phosphorus (TP, mg/L), Phosphate (mg/L), total nitrogen (TN, mg/L), ammonium nitrogen (NH4, mg/L), nitrate (NO2, mg/L), nitrite (NO3, mg/L), and chemical oxygen demand (COD, mg/L). An additional 1 L of water sample was filtered through WHATMAN GF/C glass-fiber filters for Chlorophyll-a (Chl-a, μg/L) determination, as described by Yang et al. (2024). A third 1 L of water was collected and preserved with 15 mL of Lugol's solution. After 48 h of sedimentation, the supernatant was siphoned off, and the concentrate was reduced to 30 mL, from which 0.1 mL was used for the identification of phytoplankton species and the calculation of biomass (P_Bi, mg/L). 10 L of water were also collected and stored in a PE plastic bottle with a fixed volume of 50 mL containing 4%

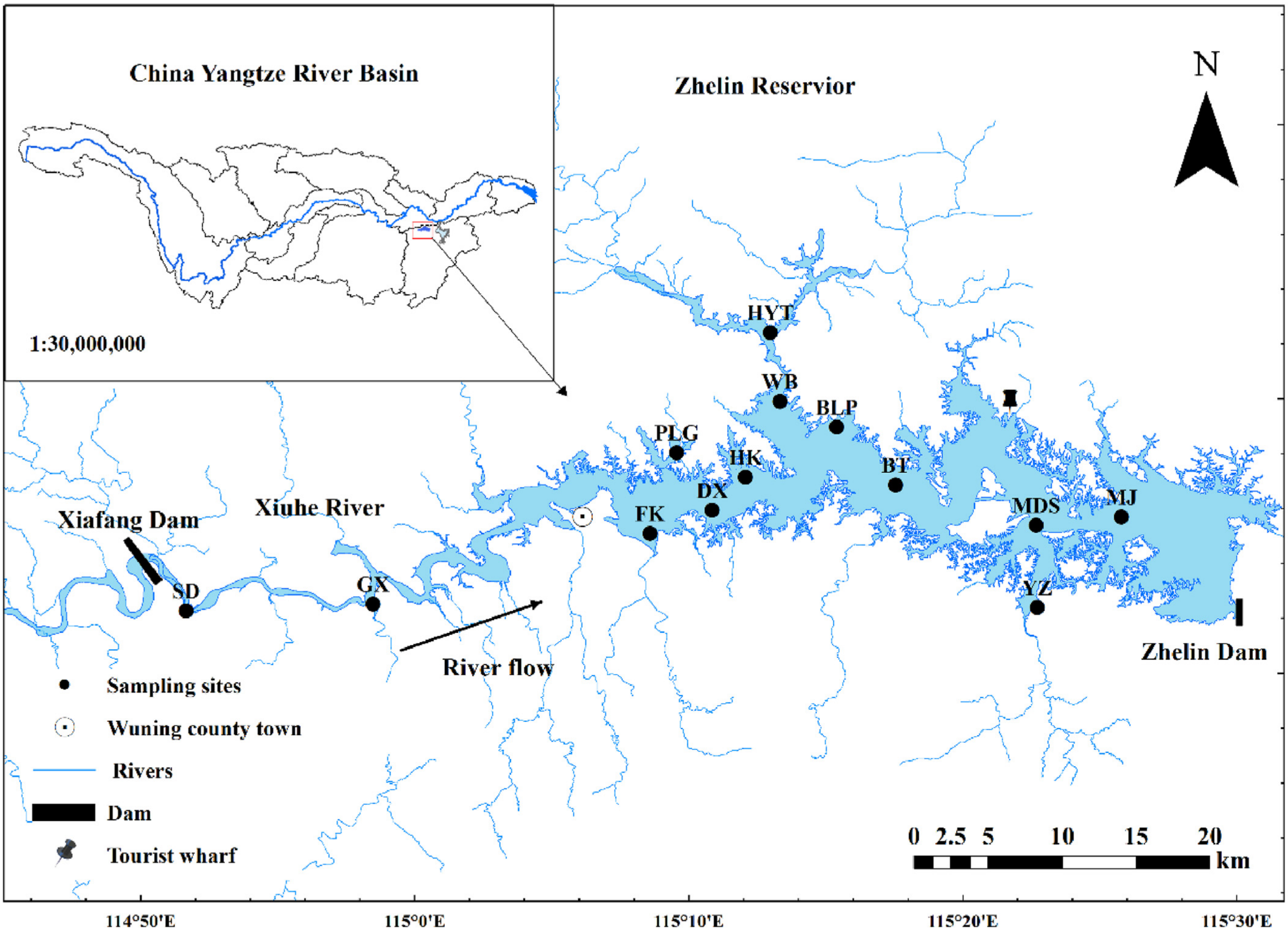

Fig. 1. Map of Zhelin Reservoir and location of sampling sites. Inset map indicates the location of the Zhelin Reservoir in the Yangtze River Basin. (Based on the national standard map with approval number GS (2019)4345).

formaldehyde solution for the identification of zooplankton species and biomass (Z_Bi, mg/L). We calculated the comprehensive nutrient index (NI) using Jin's (1995) method to assess water eutrophication (see Table S1). Furthermore, we measured and calibrated the longitude and latitude of Wuning county town, tourist wharf and sampling sites using a handheld GPS (G138BD, UniStrong, China) during the sampling period. We then calculated the geographic distances between sampling sites and Wuning county town (Dis_T, km) and tourist wharf (Dis_W, km) to quantify the impacts of human activities using the ‘distGeo’ function of the R package ‘geosphere’. Here we consider that a shorter distance to town and tourist wharfs indicates a stronger human disturbance. However, since both the town and tourist wharf are located in the lacustrine region, the effects of these human stressors may also reflect the impacts expected in the area due to reservoir construction (Thornton et al., 1991). Environmental, human activity and biotic variables in Zhelin Reservoir are detailed in Table S1 (Supplementary material).

2.2.3. *Functional traits*

Functional traits related to ecological types, including diet, maximum size, body shape, habitat location, presence of a sensory barbell, life span, and mobility (see Supplementary Table S2 for detail), were selected for the computation of functional diversity indices. These traits are associated with the functions of food acquisition (trophy), locomotion, habitat preference and life history strategies. For instance, fish size and body shape are pivotal determinants of fish function. Typically, larger fish exhibit superior speed and endurance compared to their smaller counterparts (Villéger et al., 2017). Diet, which reflects the predator-prey relationship between fish and their prey, plays a crucial role in shaping the structure and function of freshwater ecosystems by modulating the abundance of other aquatic organisms (Cheng et al., 2019). Moreover, habitat location, presence of a sensory barbell, and mobility are crucial factors that define their ecological niche. These elements significantly influence the fish's access to potential prey and the vertical transfer of nutrients between different water layers (Mouillot et al., 2014). Life history traits are crucial for explaining and predicting how different fish species respond to environmental stress, which are closely associated with their extinction risk and recovery potential (Winemiller, 2005). The trait values for each species were sourced from Fishbase (Forese and Panuly, 2021). The functional traits of 54 species collected from Zhelin Reservoir are listed in Table S2 (Supplementary material).

2.3. *Statistical analyses*

2.3.1. *Beta diversity partitioning*

Taxonomic β diversity (Tβ) and its components ($T\beta_{Repl}$ and $T\beta_{Rich}$) were calculated using the function 'beta.div.comp' in the R package 'adespatial', based on a species composition matrix (abundance data) that was previously transformed using Hellinger transformation to mitigate the influence of extreme values (Dray et al., 2018). Functional β diversity (Fβ, $F\beta_{Repl}$ and $F\beta_{Rich}$) were assessed with the function 'beta' in the R package 'BAT', using functional trait data. We computed inter-species trait distance with the function 'gowdis' in the R package 'FD', considering categorical and continuous traits (Laliberté et al., 2014; Maire et al., 2015).

We also assessed the contributions of sites (LCBD) or species (SCBD) to taxonomic β diversity with the function 'beta.div' in the R package 'adespatial' (Dray et al., 2018). Furthermore, the contributions of sites (XLCBD) and species (XSCBD) to functional β diversity were assessed with the approach developed by Nakamura et al. (2020). Permutation tests assessed LCBD and XLCBD differences among sites. To examine the differences in the components of β-diversity of species abundance and functional traits among seasons, the normal distribution of the components of β-diversity was first tested. For the diversity indices that conformed to the normal distribution, analysis of variance (ANOVA) was used to test differences, and the *t*-test was conducted for pairwise comparisons. For the diversity indices that did not conform to the normal distribution, the Kruskal-Wallis rank sum test was used to test differences, and the Wilcoxon test was conducted for pairwise comparisons. ArcGIS 10.5 was used to describe LCBD and XLCBD spatial patterns.

2.3.2. *Explaining variation in β diversity and its components*

We assessed the collinearity of explanatory variables by performing variable clustering using the function 'varclus' in the R package 'Hmisc', excluding highly correlated ones (Spearman's $\rho^2 > 0.7$) (Harrell and Dupont, 2021). TN, TP, and SD were both excluded because they all had high correlations with NI, and they were used to calculate NI (as mentioned in Section 2.2.2 above). Two variables (WD and WT) with missing values were both excluded. Thirteen explanatory variables (DO, pH, Conductivity, TSS, phosphate, NH4, NO2, NO3, NI, Dis_T, Dis_W, P_Bi, Z_Bi) were retained for the following analysis.

Multiple Regression on Matrix of Distances (MRM) were performed with the 'ecodist' R package to assess the relationships between β diversity variations (Tβ,$T\beta_{Repl}$, $T\beta_{Rich}$, Fβ, $F\beta_{Repl}$ and $F\beta_{Rich}$) and explanatory variables (Goslee and Urban, 2007). Before MRM, the explanatory variables distances were converted to standardized Euclidean distances. The permutation test was used to assess the significance ($P < 0.05$) of each variable in the model, with 999 permutations.

Variation Partitioning Analysis (VPA) was executed using the 'varpart' function in the R 'vegan' package to quantify contributions of explanatory variables to fish taxonomic (Tβ, $T\beta_{Repl}$, $T\beta_{Rich}$) and functional (Fβ, $F\beta_{Repl}$ and $F\beta_{Rich}$) diversity, respectively (Cristian, 2020). The thirteen explanatory variables were separated into three groups including water environmental (DO, pH, Conductivity, TSS, phosphate, NH4, NO2, NO3, NI), human activity (Dis_T, Dis_W) and biotic (P_Bi, Z_Bi) variables. By performing Monte Carlo tests (999 randomizations) with the function 'ordistep', the statistical significance of the pure effects was analyzed.

Beta regression, suitable for response variables with values restricted between 0 and 1, was applied to identify key factors for LCBD, XLCBD, SCBD, and XSCBD using the 'betareg' function in the R package 'betareg' (Zeileis et al., 2024). Four separate models for LCBD, XLCBD, SCBD and XSCBD were developed. For LCBD and XLCBD, species richness and community abundance along with the above thirteen variables were used as explanatory variables. Regarding SCBD and XSCBD, we incorporated species features such as niche width (i.e., the range of environmental conditions in which a species occurs), total abundance, and occupancy, along with their polynomial terms, as the explanatory variables. This approach is consistent with the methodology of Xia et al. (2022b). The inclusion of polynomial terms was deemed necessary because the relationships between species abundance, occupancy, and SCBD/XSCBD are unlikely to be linear, and polynomials can more effectively capture the complex nonlinear relationships between these variables. We utilized the classic Levins (1968) and Hutchinson (1957) framework, defining niche width as the range of resources or environmental conditions a species utilizes in a community. Although environmental variables were not directly measured, this approach is widely accepted in community ecology (Kraft et al., 2015). Niche width was calculated using the 'niche.width' function in the R package 'spaa', based on the species composition matrix (Zhang, 2013).

3. Results

3.1. *Temporal variation of β diversity and its components*

A total of 5440 individuals, representing 54 fish species from 5 orders, 12 families and 36 genera, were captured in the Zhelin reservoir during the survey (Table S2). Cypriniformes, with 38 species, accounted for 70.37% of the total number of species, followed by Perciformes and Siluriformes, with eight and six species, respectively. Considering seasons, the highest number of species was captured in autumn (34 species), and the lowest in summer (29). Fourteen species from 13 genera, 3 families, 2 orders were present across all four seasons, among which 12 species were Cyprinids. In contrast, 14 species, belonging to 4 orders, 8 families and 12 genera, occurred only in a single season.

Overall, the mean value of Tβ was higher in autumn (0.59 ± 0.11) compared to Fβ (0.48 ± 0.12), as illustrated in Table 1. Conversely, in other seasons, Fβ exceeded Tβ. Throughout the four seasons, taxonomic β diversity was mainly driven by the richness difference component, which accounted for 69%, 69%, 72% and 54% of the β diversity in autumn, winter, spring and summer, respectively. In contrast, the values of $F\beta_{Repl}$ in autumn and spring were notably higher. The $T\beta_{Rich}$ values were significantly higher in spring (0.33 ± 0.1) and summer (0.34 ± 0.08) compared to winter (0.25 ± 0.07), while all of them were lower than those recorded in autumn (0.41 ± 0.09). Significant differences in $T\beta_{Repl}$ values were detected between winter (0.21 ± 0.17) and summer (0.13 ± 0.1), whereas no significant differences were observed when compared with spring and autumn ($P > 0.05$). Notably, $F\beta_{Rich}$ in summer and $F\beta_{Repl}$ in spring reached the highest levels across all seasons, with values of 0.62 ± 0.26 and 0.33 ± 0.2, respectively.

3.2. *Spatiotemporal patterns of sites and species contributions to β diversity*

The contributions of species to β diversity, as measured by SCBD, XSCBD, and XLCBD, did not exhibit significant seasonal differences, as illustrated in Fig. 2 ($P > 0.05$). However, the LCBD values show significant seasonal variation, with the highest values observed in summer (0.14 ± 0.06) and the lowest in autumn (0.09 ± 0.04) ($P < 0.05$), as shown in Fig. 2c. Species including *Hemiculter leucisculus* (Basilewsky, 1855), *Acheilognathus taenianalis* (Bleeker,1859), *Aristichthys nobilis* (Richardson,1845), *Hemiculter bleekeri* (Warpachowski, 1887) and *Squalidus argentatus* (Sauvage and Dabry de Thiersant, 1874) exhibited SCBD values exceeding 0.1, as detailed in Table 2. Notably, *H. leuciscuclus* was the most significant contributor to taxonomic β diversity across spring, summer, and winter, with respective values of 0.22, 0.31, and 0.14. In autumn, the species *Acheilognathus nobilis* (Günther, 1868) displayed the highest SCBD value of 0.13. Mirroring the SCBD findings, the same two species (*H. leuciscuclus* and *S. argentatus*) had XSCBD values

Table 1

Seasonal variation in taxonomic and functional β diversity and their components. The percentage of contribution of each component in parentheses.

		Autumn (n = 55)	Spring (n = 28)	Summer (n = 21)	Winter (n = 28)
Taxonomic	$T\beta_{Rich}$	0.41 ± 0.09^{a} (69%)	0.33 ± 0.10^{b} (69%)	0.34 ± 0.08^{b} (72%)	0.25 ± 0.07^{c} (54%)
	$T\beta_{Repl}$	0.18 ± 0.14^{ab} (31%)	0.15 ± 0.09^{ab} (31%)	0.13 ± 0.10^{b} (28%)	0.21 ± 0.17^{a} (46%)
	$T\beta$	0.59 ± 0.10^{a}	0.48 ± 0.12^{b}	0.47 ± 0.13^{b}	0.46 ± 0.16^{b}
Functional	$F\beta_{Rich}$	0.24 ± 0.15^{c} (49%)	0.32 ± 0.23^{c} (49%)	0.62 ± 0.26^{a} (80%)	0.45 ± 0.24^{b} (59%)
	$F\beta_{Repl}$	0.24 ± 0.12^{ab} (51%)	0.33 ± 0.20^{a} (51%)	0.15 ± 0.12^{c} (20%)	0.31 ± 0.19^{ab} (41%)
	$F\beta$	0.48 ± 0.12^{c}	0.65 ± 0.19^{b}	0.77 ± 0.17^{a}	0.76 ± 0.12^{a}

Note: Values represent mean ± standard deviation. Different lowercase letters in the same row indicate significant differences between seasons ($p < 0.05$).

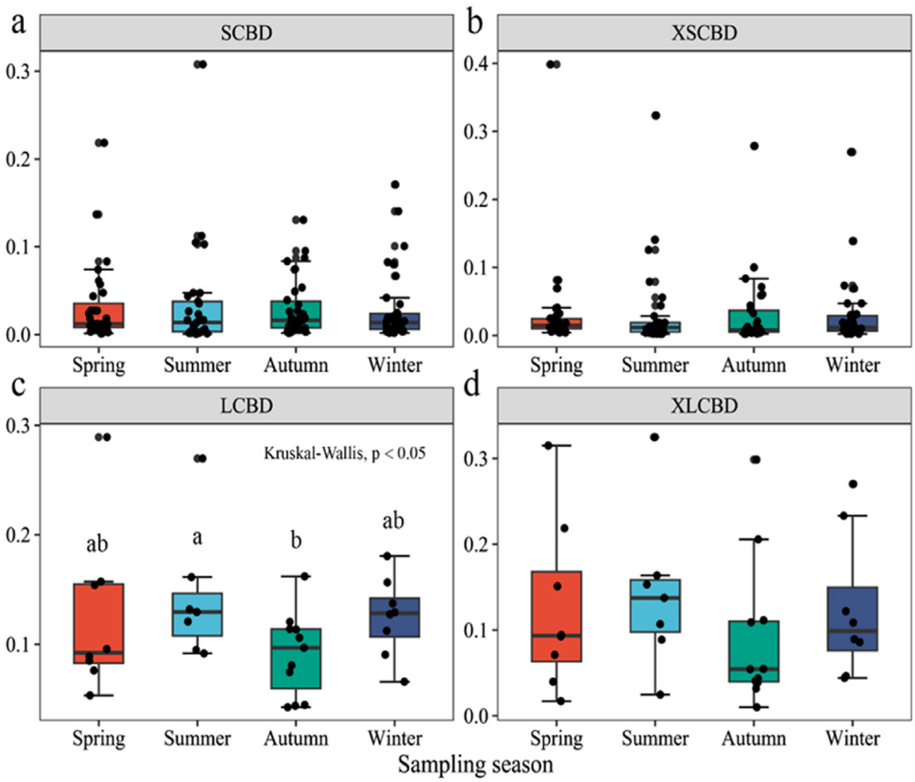

Fig. 2. Seasonal variation in species and site contribution to taxonomic (panel **a** and **c**) and functional β diversity (panel **b** and **d**). Boxes represent interquartile ranges (25% and 75%), solid blue lines within boxes present median values, and whiskers above and below represent 1.5 times the interquartile range. Different letters indicate significant differences in ranks based on pairwise Wilcoxon-tests.

Table 2
Species contributions to taxonomic (SCBD) and functional (XSCBD) dissimilarity among different seasons.

	SCBD				XSCBD			
	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer
Hemiculter leucusculus	0.074	**0.140**	**0.218**	**0.308**	**0.279**	**0.270**	**0.398**	**0.323**
Parabramis pekinensis	0.095	/	0.027	/	**0.100**	/	/	/
Acheilognathus gracilis	0.084	/	/	/	0.083	/	/	/
Pseudorasbora parva		/	/	/	0.071	0.069	/	/
Xenocyopris davidi	0.075	**0.101**	0.074	0.044	0.060	0.047	0.028	/
Hypophthalmichthys molitrix	/	/	/	/	0.059	0.026	/	0.019
Aristichthys nobilis	**0.131**	0.067	0.057	0.047	0.059	/	/	0.019
Hyporhamphus intermedius	/	/	/	/	0.044	/	0.069	0.079
Carassius auratus	0.053	0.080	/	/	0.038	0.030	/	/
Megalobrama amblycephala	/	/	/	0.026	0.032	/	/	/
Channa argus	/	0.082	/	/	/	**0.139**	/	/
Acheilognathus taenianalis	/	**0.171**	/	/	/	0.073	/	/
Xenocypris argentea	/	0.035	/	/	/	0.047	/	/
Acheilognathus chankaensis	/	/	0.044	/	/	0.031	0.025	/
Hemiculter bleekeri	/	/	**0.137**	0.035	/	0.031	0.081	0.056
Saurogobio dabryi	/	/	0.048	/	/	/	0.041	/
Acheilognathus macropteru	/	/	0.083	0.038	/	/	0.040	/
Chanodichthys mongolicus	0.039	/	0.061	0.048	/	/	0.032	/
Acheilognathus barbatulus	/	/	/	/	/	/	0.024	/
Leporinus punctatus	/	/	/	/	/	/	0.023	/
Tachysurus fulvidraco	/	0.021	/	/	/	/	/	**0.141**
Squalidus argentatus	/	0.042	/	**0.103**	/	/	/	**0.126**
Silurus meridionalis	/	/	/		/	/	/	0.044
Culter oxycephaloides	/	/	/	**0.112**	/	/	/	0.019
Gnathopogon imberbis	0.034	/	/	/	/	/	/	/
Cultrichthys erythropterus	0.049	/	/	/	/	/	/	/
Pseudobrama simoni	0.087	/	0.027	/	/	/	/	/
Rhodeus sinensis	/	0.025	/	/	/	/	/	/

Note:The top 10 contributing species for each season are listed. Contributions with values greater than 0.1 are highlighted in bold. A forward slash ('/') indicates that the species was not captured during that particular season.

above 0.1 during winter. Furthermore, *H. leucisculus* was identified as the species with the highest XSCBD value across all seasons, underscoring its consistent influence on β diversity.

As depicted in Fig. 3, LCBD and XLCBD values ranged from 0.04 to 0.29 and 0.01 to 0.33, respectively. Three sites exhibited significant LCBD and XLCBD values across spring, summer, and autumn. The proportion of sites with LCBD values exceeding the average contribution was highest in winter (62.5%) and lowest in summer (28.6%). By contrast, 42.9% of sites in summer showed a larger XLCBD value than average contribution, marking the highest percentage across all seasons. In contrast, only 25.0% of sites in winter had an XLCBD value above the average. In addition, sites located in the middle and lower regions of the reservoir contributed substantially to both taxonomic and functional β diversity compared to those in the upper region. This suggests that the middle and lower region sites harbor greater taxonomic and functional uniqueness.

3.3. *Key drivers of β diversity and its components*

The MRM models revealed a significant correlation between taxonomic and functional β diversity and environmental and human activity variables (Table 3 and Fig. S1). However, no significant link was detected between β diversity and Phytoplankton and Zooplankton biomasses). Taxonomic β diversity ($T\beta_{Repl}$ and Tβ) significantly increased ($P < 0.05$) DO, pH and Dis_W. In contrast, conductivity showed a significant negative correlation with $T\beta_{Repl}$. Functional β diversity (Fβ and $F\beta_{Rich}$), increased significantly ($P < 0.05$) with Dis_T. Similarly, $F\beta_{Rich}$ increased with Dis_W whereas $F\beta_{Repl}$ decreased.

The relative importance of three variable groups (i.e., environmental, human activities and biotic variables) varied among diversity facets and components (Fig. 4), with a contribution ranging from 0.02% to 14.34% per considered variable. For taxonomic β diversity, the environmental, human activities and biotic variables collectively explained 10.84%, 12.70% and 15.92% of the total variation in Tβ, $T\beta_{Rich}$ and $T\beta_{Repl}$, respectively (Fig. 4a, b and c). The explained variation in $F\beta_{Rich}$ was 18.18%, nearly double that of Fβ, which was 9.33%. In terms of pure effects, environment variables were generally more influential in Tβ and Fβ, accounting for 8.14% and 7.36% of the explained variation, respectively (Fig. 4a and d). Human activities variables contributed nearly equally to $F\beta_{Repl}$ (7.90%) and $F\beta_{Rich}$ (6.67%) (Fig. 4e and f). Biotic variables had a weaker contribution, explaining less than 1.5%, except for $T\beta_{Rich}$, which accounted for 7.57% of the explained variation (Fig. 4b).

The outcomes of beta regression analyses indicated that the collective set of variables accounted for 58.5% and 56.3% of the variation in the contribution of sites to taxonomic (LCBD) and functional (XLCBD) beta diversity, respectively (Table 4). Among the environmental variables considered, phosphate and pH were significantly and positively related to XLCBD, while conductivity exhibited a significant negative relationship with LCBD ($P < 0.05$). Furthermore, a significant positive correlation was observed between the distance to Wuning city (Dis_T) and both LCBD and XLCBD ($P < 0.05$). Community abundance was found to have a significant negative relationship with LCBD ($P < 0.05$). Considering the species contribution to beta diversity, all predictors jointly explained 78.6% and 46.5% of the variation in SCBD and XSCBD, respectively. SCBD was significantly associated with total species abundance, occupancy and their second-order terms, while XSCBD showed a significant positive correlation only with total abundance and its second-order term. There was a strong but non-significant relationship between SCBD and niche width, as was the case with XSCBD (Table 5).

4. Discussion

4.1. *Taxonomic and functional β diversity and its components*

The distinct seasonal patterns we measured in both taxonomic and functional β diversity were linked to temporal changes in species richness that led to functional diversity turnover throughout the year, indicating that variations in species composition have a distinct influence on the functional trait structure of the fish community. This divergence may be attributed to variations in species functional traits that do not necessarily align with fish taxonomy, highlighting the importance of considering both taxonomic and functional perspectives when assessing biodiversity (Villéger et al., 2012). Seasonal fish migration may indirectly enhance $T\beta_{Rich}$ and reduce $T\beta_{Repl}$, influencing the spatial distribution of homogeneity of fish stocks throughout the reservoir, aligning with findings from other lakes in the middle and lower reaches of the Yangtze River (Jiang et al., 2020). Environmental and human activities variables were also a significant predictor of taxonomic and functional β diversity indicating that human activities are contributing to shape the spatial and temporal patterns of the fish assemblages in the Zhelin Reservoir, as already reported by Liang et al. (2024) in five Chinese impounded lakes (Gaoyou Lake, Hongze Lake, Luoma Lake, Nansi Lake, and Dongping Lake). We nevertheless report a non-significant correlation between functional diversity and eutrophication (NI, see Table 3 and Table S1) that contrasts with previous studies (Feng et al., 2023).

4.2. *Species and site contributions to taxonomic and functional β diversity*

Our findings indicate that the contribution of species and sites to taxonomic and functional beta diversity exhibit predictable patterns according to environmental and anthropogenic characteristics. For instance, the sites MDS, MJ and DX contribute the most to taxonomic and functional beta diversity, suggesting that fish species composition at those sites was significantly different from the other sites and support unique functional traits (Heino et al., 2022). The functional uniqueness of those sites may be linked to their situation within the core area of a National Reserve, where fish communities are less subjected to disturbance than in others sites. LCBD was found to be significantly and negatively correlated with conductivity, consistent with the results from the Chishui River Basin, located upstream in the Yangtze River, indicating that fish community structures may be more unique at sites with lower conductivity. This may be related to the specific environmental conditions of these sites, which may limit the distribution of certain fish species, thus affecting the composition of fish communities (Xia et al., 2022b). Sites with low conductivity therefore host unique biological communities, which may be more sensitive to environmental changes and should thus be considered in biodiversity conservation plans. Moreover, the LCBD value was correlated with water conductivity, which can be considered as a link between LCBD and water quality. Within a region, conductivity is supposed to be mainly influenced by human activities such as urban effluent and agricultural practices, and thus represents a synthetic measure of water quality degradation (da Silva et al., 2020; Wang et al., 2013). Moreover, high conductivity levels can also filter out sensitive species, thus reducing species diversity in high conductivity areas (Cheng et al., 2024). At the same time, species adapt to different conductivity levels by occupying distinct ecological niches, increasing differences in species composition (Chen et al., 2014; Liu et al., 2016). Furthermore, human activities, such as urbanization, may affect the relationship between species richness and LCBD by reducing ecologically unique assemblages (Camara et al., 2022). Despite inconsistencies in the literature on the link between LCBD and species richness (Borges et al., 2020; Hill et al., 2021; Legendre and De Cáceres, 2013; Ngor et al., 2018), lower LCBD or XLCBD values here suggest a higher degree of human disturbance, with closer proximity to towns (indicated by smaller Dis_T values in our study) associated with smaller LCBD and XLCBD values. Therefore, the structure and type of data used and the combined effect of other factors should be fully considered to better understand the potential relationship between LCBD and species richness.

Regarding the species contributions to β diversity (i.e. SCBD and XSCBD), the pivotal species for maintaining both taxonomic and

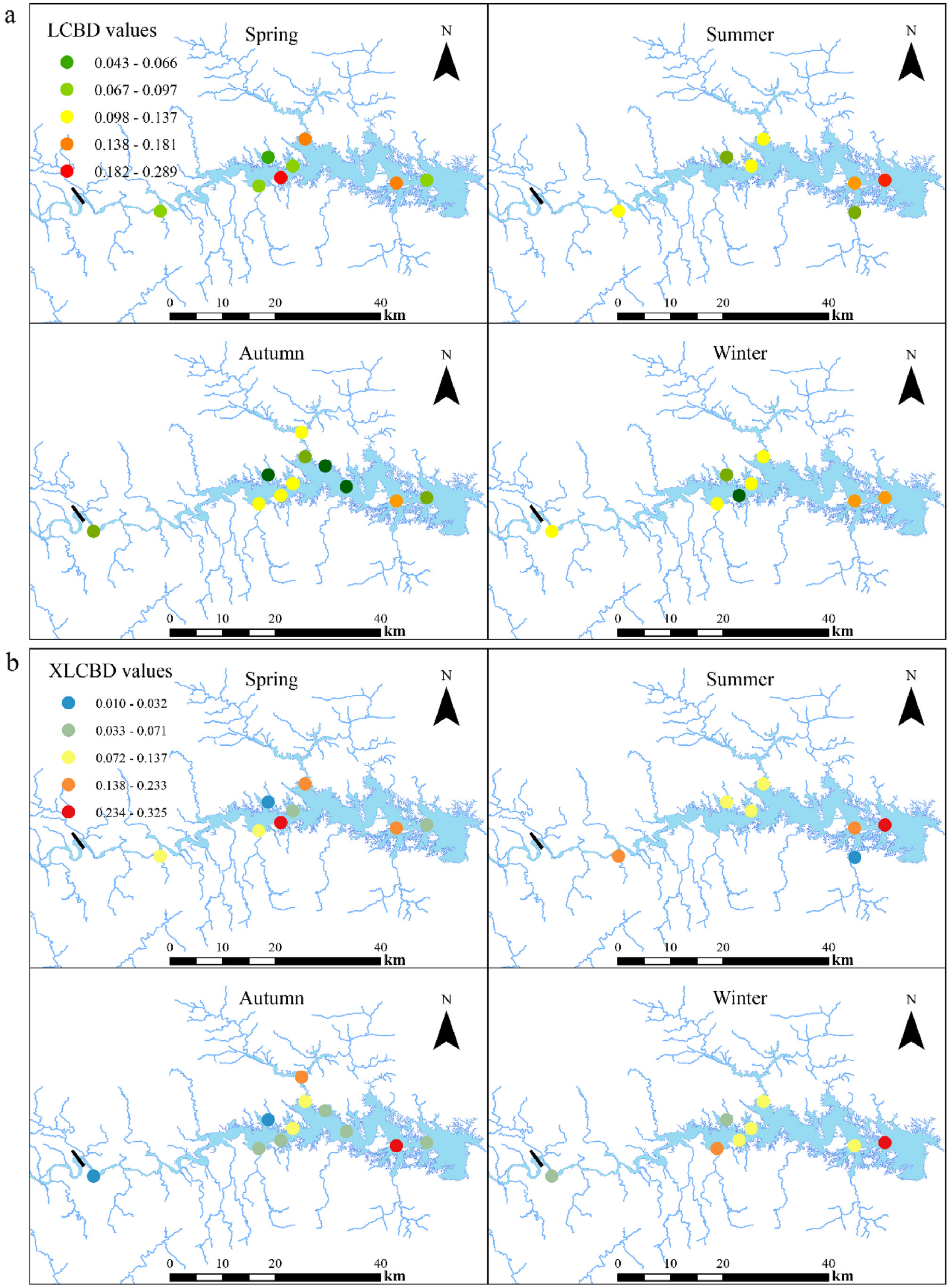

Fig. 3. Spatiotemporal variation in site contributions to taxonomic (panel **a**) and functional β diversity (panel **b**).

Table 3
Results of the multiple regression analysis on matrices analysis (MRM) for taxonomic and functional beta diversity with environment, human activities and biotic variables.

		Taxonomic β diversity			Functional β diversity		
		Tβ	$T\beta_{Rich}$	$T\beta_{Repl}$	Fβ	$F\beta_{Rich}$	$F\beta_{Repl}$
		$R^2 = 0.13$	$R^2 = 0.15$	$R^2 = 0.19$	$R^2 = 0.11$	$R^2 = 0.20$	$R^2 = 0.17$
Environment variables	DO	0.12	−0.11	**0.16** *	−0.02	0.01	−0.04
	pH	**0.18** *	0.04	0.08	0.06	−0.02	0.09
	Conductivity	−0.15	0.27	**−0.32** *	−0.08	−0.04	−0.02
	TSS	0.01	0.03	−0.02	0.05	0.07	−0.06
	Phosphate	0.06	−0.11	0.13	0.17	0.23	−0.17
	NH4	−0.07	0.07	−0.1	−0.15	−0.22	0.17
	NO2	−0.10	−0.06	−0.01	−0.05	0.03	−0.08
	NO3	−2.79	−1.39	−0.53	−2.27	0.04	−2.14
	NI	−0.01	0.04	−0.04	−0.01	−0.04	0.05
Human activities variables	Dis_T	**0.18** **	0.00	0.11	**0.15** *	**0.14** *	−0.06
	Dis_W	−0.01	−0.03	0.02	0.08	**0.25** *	**−0.28** *
Biotic variables	P_Bi	0.09	0.03	0.03	0.03	−0.08	0.14
	Z_Bi	0.05	0.16	−0.1	0.06	0.03	0.02

Note:The variation (R^2) of beta diversity that is explained by these variables. The partial regression coefficients and associated *P*−values of the final model are reported from permutation test (nperm = 9999), *$P < 0.05$, **$P < 0.01$.

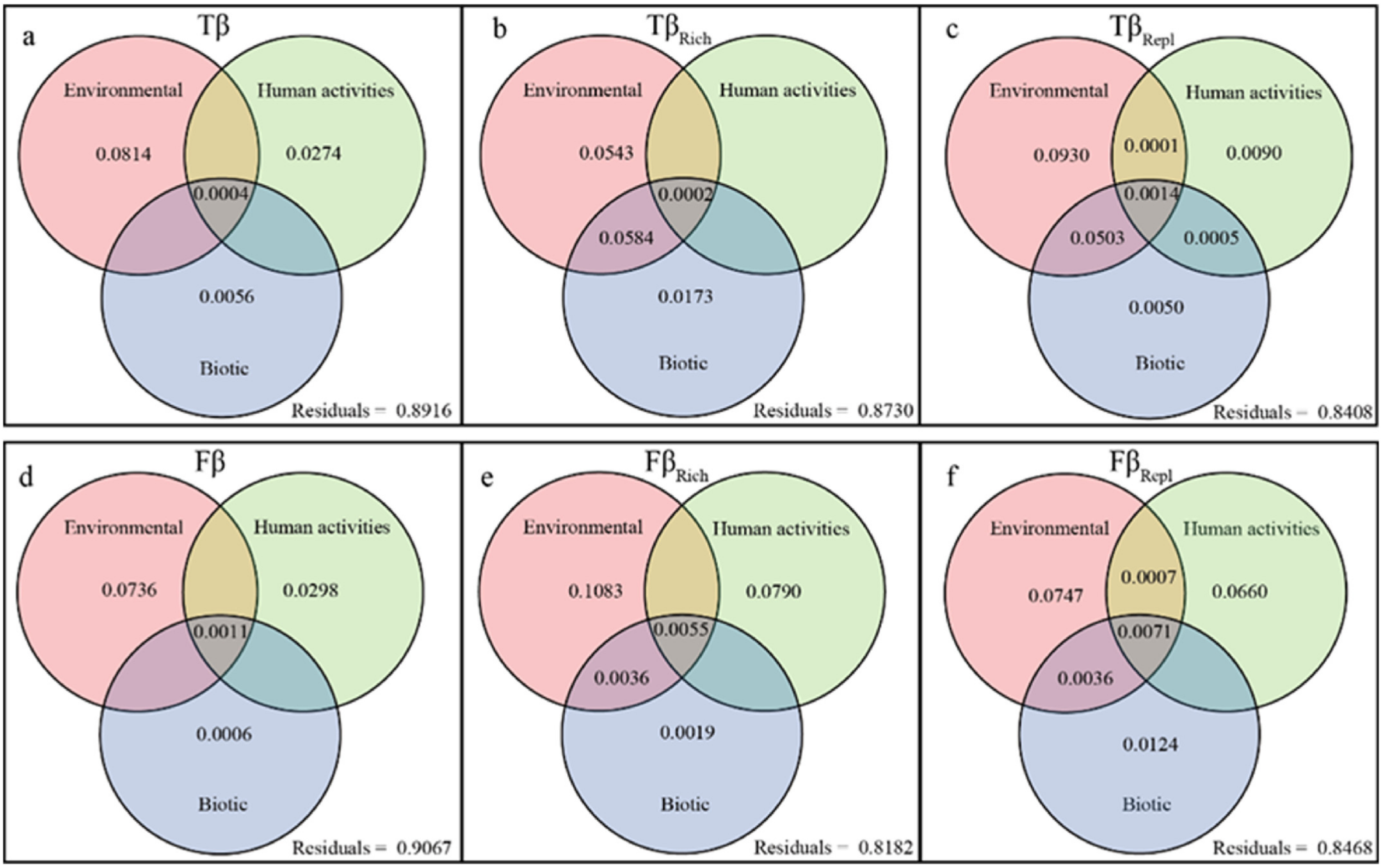

Fig. 4. Variation Partitioning Analysis assessing distances for taxonomic (panel **a**–**c**) and functional (panel **d**–**f**) β diversity and its components, and selected groups of environmental, human activities and biotic variables. The values shown represent the adjusted R^2, indicating the proportion of variance explained by each variable set. Negative values, which would indicate a decrease in explanatory power, are omitted from this presentation.

functional β diversity varied across seasons. *Hemiculter leucusculus* consistently showed high values in contributing to taxonomic and functional β diversity. This species is indeed characterized by opportunistic strategies and a rapid generation turnover rate (Gu et al., 2022), as its life history traits, such as growth, sex ratio, and maturation rate, also play a role in its ecological success and contribution to β diversity (Huang et al., 2022). Other species, like *A. nobilis*, *Acheilognathus taenianalis*, also played significant roles at different times. Interestingly, species with higher contributions to taxonomic diversity did not always have higher contributions to functional diversity, indicating that different factors influence these aspects (Leão et al., 2020). As anticipated, our findings corroborate the idea that SCBD is predictable from species characteristics, especially for species occupancy, which is an important concept in ecology and is commonly used to assess the presence of a species within a particular area and is one of the key indicators for biodiversity monitoring and conservation (Liu et al., 2024). For instance, high SCBD values

Table 4

Beta regression analyses of LCBD and XLCBD with community metrics (i.e., community abundance (com_ab) and species richness (sp_rich)), environmental, human activities and biotic variables. *N* = 34 sites. Significant p values ($p < 0.05$) are indicated by bold font.

		LCBD, Pseudo−R^2 = 0.585				XLCBD, Pseudo−R^2 = 0.563			
		Estimate	SE	z	p	Estimate	SE	z	p
Environmental variables	DO	0.04	0.059	0.68	0.494	0.029	0.091	0.32	0.749
	pH	−0.067	0.138	−0.49	0.625	**−0.428**	**0.206**	**−2.08**	**0.038**
	Conductivity	**−0.017**	**0.008**	**−2.05**	**0.040**	**−0.029**	**0.011**	**−2.5**	**0.012**
	TSS	−0.013	0.049	−0.27	0.790	0.107	0.076	1.41	0.159
	Phosphate	−0.315	0.489	−0.64	0.520	**−1.600**	**0.788**	**−2.04**	**0.042**
	NH4	−8.225	7.386	−1.11	0.265	−11.80	11.90	−0.98	0.325
	NO2	−0.089	0.287	−0.31	0.756	−0.417	0.432	−0.97	0.334
	NO3	−1.205	3.246	−0.37	0.711	−7.530	5.18	−1.45	0.146
	NI	−0.011	0.008	−1.27	0.205	0.003	0.012	0.23	0.819
Human activities variables	Dis_T	**0.022**	**0.008**	**2.83**	**0.005**	**0.028**	**0.012**	**2.31**	**0.021**
	Dis_W	0.003	0.011	0.25	0.800	−0.018	0.018	−1.02	0.310
Biotic variables	P_Bi	−0.003	0.019	−0.15	0.879	−0.009	0.029	−0.32	0.747
	Z_Bi	0.118	0.118	1.00	0.318	0.239	0.174	1.37	0.170
Fish community variables	com_ab	**−0.003**	**0.001**	**−3.63**	**0.000**	−0.001	0.001	−0.65	0.519
	sp_rich	0.025	0.020	1.27	0.204	−0.036	0.029	−1.27	0.204

Table 5

Beta regression analyses of SCBD and XSCBD with species metrics (i.e., species occupancy and total abundance) and niche width. *N* = 54 species. Significant *p* values ($p < 0.05$) are indicated by bold font.

	SCBD, Pseudo−R^2 = 0.786				XSCBD, Pseudo−R^2 = 0.465			
	Estimate	SE	z	p	Estimate	SE	z	p
Occupancy	0.300	0.058	5.190	**0.000**	0.032	0.076	0.420	0.670
Occupancy^2	0.010	0.001	8.290	**0.000**	0.002	0.002	1.460	0.140
Total abundance	0.014	0.002	8.220	**0.000**	0.011	0.002	4.510	**0.000**
Total abundance^2	0.000	0.000	7.960	**0.000**	0.000	0.000	4.080	**0.000**
Niche width	0.298	0.256	1.170	0.240	0.234	0.300	0.780	0.440

are associated here with species that do not need conservation measures owing to high abundance and wide distribution, thus paralleling Gavioli et al. (2019) results on fish faunas from an Italian river.

4.3. Implications fish diversity conservation

LCBD and XLCBD could serve to identify distinct assemblages within a region or a lake, and guide the design of protected areas (Hill et al., 2021). Here we underscore the practical value of these metrics for conserving fish diversity. We observed that sites with higher LCBD and XLCBD values are predominantly found within a Natural Reserve, suggesting that the protected area plays a role in safeguarding unique habitats. Concurrently, the upstream sites showed lower LCBD or XLCBD values, possibly due to the significant impact of human activities in these areas. Therefore, we recommend implementing more protection measures in upstream areas, particularly by enforcing restrictions on sand mining to prevent habitat degradation and loss (Cao et al., 2024). In addition, a combined approach to the protection of sites with high uniqueness and those rich in species may not only preserve a significant proportion of regional species diversity but also safeguard functional diversity, which is crucial for ecosystem function and the provision of ecosystem services. Furthermore, we underscore the importance of assessing and conserving species with restricted distributions, such as those belonging to the genera *Tachysurus* and *Siniperca*, whose XSCBD values, along with their abundance and occupancy, are significantly below 5% (Acreman et al., 2020). Despite the Yangtze River Basin's 10-year fishing moratorium, these initiatives are not widely implemented. Rare species like *Tachysurus* and *Siniperca*, with low XSCBD values, require targeted conservation, including habitat restoration and captive breeding programs, as experienced with *Gymnocypris przewalskii* in Lake Qinghai (Weng et al., 2023). Although the Chinese government has established nature reserves and a 10-year fishing ban in the Yangtze River Basin to protect and restore fish populations and their habitats, recreational fishing for *Tachysurus* persists, necessitating a balance between fishery development and biodiversity conservation by developing and implementing a sustainable recreational fishery development plan. Last but not least, it is undoubtedly critical and essential to obtain continuous, long-term monitoring data to enable a more comprehensive assessment of biodiversity conservation policies and strategies. This is particularly important in the face of growing demands and impacts on ecosystems and the services they provide (Iacarella, 2022).

5. Conclusions

In conclusion, our research advocates for the concurrent use of taxonomic and functional traits to better understand fish community dynamics. This integrated approach helps in identifying spatiotemporal patterns and informs conservation strategies. Our findings suggest that prioritizing conservation in distinct areas and for unique species could be an efficient conservation strategy. Moreover, it is necessary to undertake habitat restoration and implement protective measures, including enforcement of restrictions on sand mining in upstream areas. For key species, targeted conservation measures such as stock recovery programs for *Tachysurus* and *Siniperca*, along with sustainable recreational fishing policies, need to be developed to ensure the preservation of biodiversity in the Zhelin Reservoir. We anticipate that our findings will progress collective understanding of fish diversity conservation and will help in developing targeted and pragmatic conservation and management strategies for fish diversity under the 10-year fishing ban in the Yangtze River Basin. To do that, incorporating both taxonomic and functional β diversity into the assessment of biodiversity would help gauge the dynamics of fish diversity and, in turn, devise sustainable strategies that are not only more comprehensive but also sustainable in the long run. This integrated approach is essential for the effective preservation of fish diversity, ensuring ecological integrity and resilience of aquatic ecosystems.

CRediT authorship contribution statement

Zihao Meng: Writing – original draft, Visualization, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Sébastien Brosse:** Writing – original draft, Methodology, Conceptualization. **Miao Xiang:** Methodology, Investigation, Data curation. **Feifei Hu:** Investigation, Data curation. **Xinye Wang:** Investigation, Data curation. **Xuejun Fu:** Resources, Methodology, Investigation, Data curation. **Deguo Yang:** Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Xuemei Li:** Writing – review & editing, Writing – original draft, Resources, Project administration, Funding acquisition, Formal analysis, Conceptualization.

Ethics statement

This study strictly adhered to China's Regulations on the Management of Yangtze River Aquatic Biological Conservation. Field sampling was approved by the Ethical Committee for Institute of Yangtze River Fisheries Research, Chinese Academy of Fishery Sciences. Non-lethal methods were prioritized to minimize ecological impact. All fish were released after data collection. Data handling followed IUCN ethical guidelines.

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Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.watbs.2025.100407.

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