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Taxonomic and functional diversity in a subtropical stream: A longitudinal pattern analysis

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Abstract

Identifying the spatial patterns of fish diversity in streams is basic for the conservation and management of stream fishes. The “upstream–downstream” patterns in the taxonomic α -diversity of stream fishes have been widely surveyed. However, the longitudinal patterns in the functional diversity and β -diversity of stream fishes have been given less attention. In this study, we surveyed fishes along an upstream–downstream gradient in a headwater stream of the Qiantang River, China, and examined the longitudinal variations in fish diversity. Our aims were to assess whether the longitudinal patterns in fish diversity were consistent between the taxonomic and functional metrics and between the α - and β -aspects of diversity. We found that both species richness and functional richness of fishes showed a hump-shaped relationship with the distance from headwaters, while both taxonomic and functional β -diversities presented the U-shaped distributions along the river continuum. Functional diversity related more to the distance from headwaters than taxonomic diversity. Despite their similar relationship with the distance from headwaters, taxonomic and functional β -diversities were dominated by species turnover and function nestedness components, respectively. Our results suggest that, along the river continuum in a subtropical stream, the α - and β -aspects of fish diversity present different longitudinal variations. Although the taxonomic and functional diversity shows similar relationships with distance from headwaters, their spatial variations are driven by different ecological processes.

KEYWORDS

taxonomic and functional diversities, the river continuum, turnover and nestedness, α and β -diversities

1 | INTRODUCTION

The distribution and abundance of stream fishes are influenced by historical events and abiotic and biotic factors (Poff & Allan, 1995; Schlosser, 1982). Due to the high spatial heterogeneity and temporal differentiation of stream environmental characteristics,

the composition and abundance of stream fish communities noticeably vary on spatial and temporal scales (Grossman, Dowd, & Crawford, 1990; Jackson, Peres-Neto, & Olden, 2001). On this basis, longitudinal patterns in diversity and the distribution of stream fish along upstream–downstream gradients have garnered the widespread attention of ecologists (Li, Tao, Chu, & Yan, 2018;

Suvarnaksha, Lek, Lek-Ang, & Jutagate, 2012; Torgersen, Baxter, Li, & McIntosh, 2006). Many researchers have found that the species richness of stream fishes increases gradually, reaching a maximum at the midstream and decreasing at the lower stream reaches (Li et al., 2018; Oberdorff, Guilbert, & Lucchetta, 1993; Torgersen et al., 2006). Nevertheless, traditional taxonomic diversity measures species-based cannot detect the effects of diversity on ecosystem processes along environmental gradients (Diaz & Cabido, 2001). Increasingly, approaches based on quantifying the functional traits of species are seen as a more useful way to understand biotic responses to environmental changes (Violle, Borgy, & Choler, 2015; Zbinden & Matthews, 2017). Functional traits reveal ecological differentiation between species and thus represent one of the most relevant components of biodiversity that can be considered to infer processes governing community assembly (Cécile et al., 2012; Swenson et al., 2012). Functional diversity embraces the composition of species traits and life-history strategies and also reveals more about the ecosystem responses to environmental changes (Kearney & Porter, 2009; Mayfield et al., 2010; Petchey & Gaston, 2006). According to the River Continuum Concept (RCC; Vannote, Minshall, Cumins, Sedell, & Cushing, 1980), changes in food sources along the river continuum constrain the trophic groups of aquatic organisms within communities. Fish species of generalised invertivores are expected in upstream areas, while omnivores, detritivores, herbivores and piscivores become more abundant in further downstream in a river basin (Schlosser, 1982; Vannote et al., 1980). These studies have provided theoretical expectations regarding functional diversity in streams along the environmental gradient (Pease, Gonzalez-diaz, Rodiles-hernandez, & Winemiller, 2012).

In addition to the number of species present in a given location (taxonomic α -diversity), β -diversity, which is defined as the degree to which species composition vary from place to place, is another key feature of biodiversity (Koleff, Gaston, & Lennon, 2003; Whittaker & Fernández-Palacios 2007). Taxonomic β -diversity represents the percentage of dissimilarity in species composition between communities, and functional β -diversity refers to dissimilarity in functional composition (Villéger, Grenouillet, & Brosse, 2013). According to Baselga (2010) and Villéger et al. (2013), taxonomic and functional β -diversity can be divided into nestedness and turnover components, representing two different modes of species/function changing between communities, that is species/functional loss or gain for the nestedness component and species/functional loss and gain for turnover. Due to the different meanings between α - and β -diversity, the two indices may show dissimilar spatial patterns along environmental gradients (Tylianakis, Klein, & Tscharnkte, 2008). In wadeable headwater streams, the general pattern may be that the α -diversity gradually increases downstream along the "upstream-downstream" gradient, but the β -diversity decreases (Jaramillo-Villa, Maldonado-Ocampo, & Escobar, 2010; Li et al., 2018; Zhang, Wan, Chu, & Yan, 2018). Moreover, the driving mechanisms for the spatial variation in taxonomic and functional β -diversity are dissimilar. For example, Zhang et al. (2018) reported that taxonomic β -diversity of

stream fishes was dominated by turnover, and functional β -diversity was dominated by nestedness.

To our knowledge, at least at the scale of river continuum, previous studies on how stream fish diversity vary along the upstream-downstream gradient focus on the taxonomic diversity (e.g. Araújo, Pinto, & Teixeira, 2009; Sui, Lu, Yan, Chen, & Jia, 2014), and recently, increasing studies give attention to the longitudinal variations in the functional diversity of stream fishes (e.g. De Carvalho & Tejerinagarro, 2015; Pease et al., 2012; Troia & Gido, 2015). However, most of these studies focus on the traditional α -diversity of fish assemblages, whereas the β -diversity (especially the functional β -diversity) has been given less attention. In our study, we sampled fishes from 18 sites along the upstream-downstream gradient in the Shuaishui Stream, the headwater stream of the Qiantang River, China. Based on data collected on the fish and environment together with the functional traits measured for each fish species, we examined the spatial variations in environmental factors and the taxonomic and functional α - and β -diversities of fishes along the upstream-downstream gradient. We aimed to (a) examine the longitudinal variations in environmental factors and species compositions of fishes, (b) determine the relationships between each diversity index and the distance from headwaters, and (c) assess whether the longitudinal patterns in stream fish diversity depend on the taxonomic and functional metrics and the α - and β -aspects of diversity.

2 | MATERIALS AND METHODS

2.1 | Study area

The Shuaishui Stream is the headwater stream of the Qiantang River and originates on the Wugujian Mountain in the Xiuning County, Anhui Province, China. The Shuaishui Stream is approximately 110 km length with the drainage area being 1,512 km². Due to the subtropical monsoon climate, the annual precipitation is approximately 2,000 mm/year, of which approximately 80% occurs from April to September. According to the Xiuning county annals (1995), the environmental characteristics of the Shuaishui Stream change markedly along the longitudinal gradient from the Wugujian Mountain to the Huangshan city. The upstream segment is more than 22 km length, which begins at the headwaters and continues to the Xikou village. The habitats in the upstream environment are complicated, with high gradient and bending watercourse. The midstream (length: 53 km), from the Xikou village and to Chenxia County, is progressively more stable, with an expansive watercourse and a low velocity. Further downstream (length: 35 km) in the gradient, the habitat becomes more homogenous.

2.2 | Field data collection

We set sampling sites continuously with an interval of 3–6 km from headwaters to the downstream segments. The sampling

sites were selected in the field based on habitat representativeness and accessibility, and all of the sampling sites were set far from obvious human disturbances, such as dams, farms and urban areas. Because segment upstream showed more spatial variations between sites than that downstream, the sampling site upstream was more intensive than that downstream (Figure 1). A total of 18 sites were sampled, among which 7, 7 and 4 sites were located in the upstream, midstream and downstream segments, respectively. According to the annual precipitation data from Xiuning observatory (Appendix S1), we sampled the sites twice during May (representing the wetted season) and October (the dry season) 2017, respectively. Fish were collected using backpack electro-fishing gear (CWB-2000 P, China; 12 V import, 250 V export) by wading in two passes without block nets (30 min sampling time for each 100 m sampling segment). We identified the fish to species with reference to Chen (2013) and Chu, Zheng, and Dai (1999) and counted.

2.3 | Environmental characteristics

At each sampling site, 12 local habitat variables were collected (Table 1). The wetted width (m) was measured along three transects that were equally spaced across the stream channel. The water depth (m) was measured at three equal interval points along each transect. The current velocity (m/s) was taken at 60% of the water depth at each point (FP111, USA). The water temperature (°C), dissolved oxygen (mg/L), conductivity (mS/cm) and pH were measured using a handheld meter (YSI Pro). We characterised the substratum composition of each sampling site by using five variables, including

the percentages of large boulders (>256 mm in diameter), small boulders (64–256 mm), cobbles (15–63 mm), gravels (2–5 mm) and sand (<2 mm).

Using ArcGIS 10.0 and a digital elevation model (DEM) satellite layer with an accuracy of 30 m, we established sub-catchments for each sampling segment. According to the land use data set of Anhui Province with a scale of 1:100,000, we measured the relative areas of five types of land use/cover for each sampling sub-catchment, including forest, meadow, agriculture, wetland and urban. The distances from the headwater of each sampling site were also measured by using the same data.

2.4 | Functional traits

We measured 11 functional ratio traits related to trophic position, locomotion ability and habitat preference for each species (Table 2; Appendix S2). Considering that fishes often experience the shift in their feeding habits and habitat preference among different life stages (e.g. juvenile and adult), we only measured the functional traits for the adult individuals for each species. At least 30 specimens of each species were used to measure the traits, whereas all specimens were measured when the species were less than 30 individuals.

2.5 | Diversity index calculation

The taxonomic α -diversity was computed as the local species richness (SR).

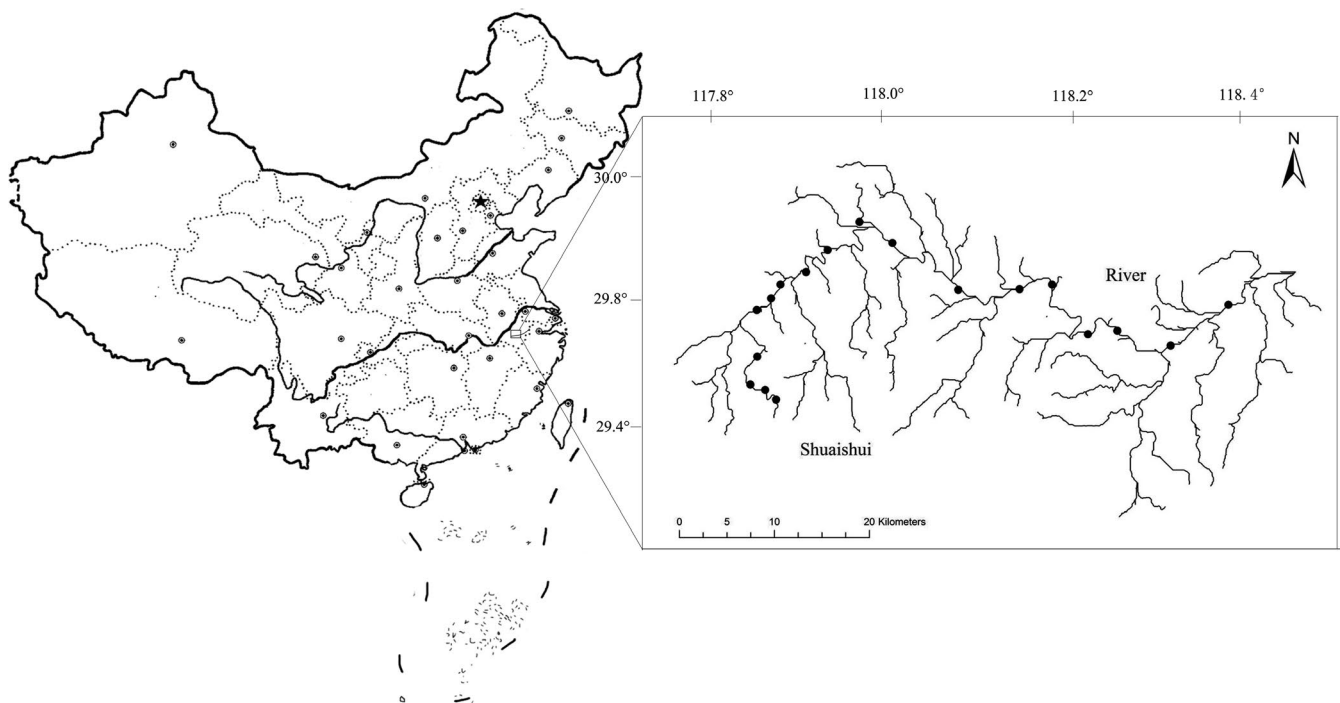


FIGURE 1 Map of the study region; the Shuaishui Stream, Xin'an Basin, Anhui, China. (Black circles indicate the sampling sites.)

TABLE 1 Environmental variables measured in the Shuaishui Stream

Category	Environmental variable	Abbrev.	Variable
Local-scale variables	Water depth (m)	WD	Average depth of stream
	Wetted width (m)	WW	Average width of stream
	Conductivity (mS/cm)	CO	Specific conductivity
	Dissolved oxygen (mg/L)	DO	Dissolved oxygen of stream by YSI
	Water temperature (°C)	WT	Water temperature of stream by YSI
	Current velocity (m/s)	CV	Average velocity of stream
	pH	PH	pH of stream by YSI
	Large boulder (%)	LB	Percentage of large boulders in the substratum
	Small boulder (%)	SB	Percentage of small boulders in the substratum
	Cobble (%)	COB	Percentage of cobbles in the substratum
	Gravel (%)	GR	Percentage of gravels in the substratum
	Sand (%)	SA	Percentage of sand in the substratum
Landscape-scale variables	Forest area (%)	FA	Percentage of forest area in the landscape
	Meadow area (%)	MA	Percentage of meadow area in the landscape
	Agriculture area (%)	AA	Percentage of agriculture area in the landscape
	Wetland area (%)	WA	Percentage of wetland area in the landscape
	Urban area (%)	UA	Percentage of urban area in the landscape

We used a broad suite of measurable, quantitative traits to characterise multiple niche dimensions and to allow the use of a recently developed multidimensional method of estimating functional diversity (Laliberté & Legendre, 2010; Pease et al., 2012; Villéger, Mason, & Moullot, 2008). The functional richness ($FRic$, functional space occupied), functional evenness ($FEve$, the weighted distribution of functional traits) and functional divergence ($FDiv$, the dispersion of functional traits) were regarded as the functional α -diversity (Appendix S3). The “FD” package for R 3.4.1 was used to calculate the functional α -diversity (Laliberté & Legendre, 2010).

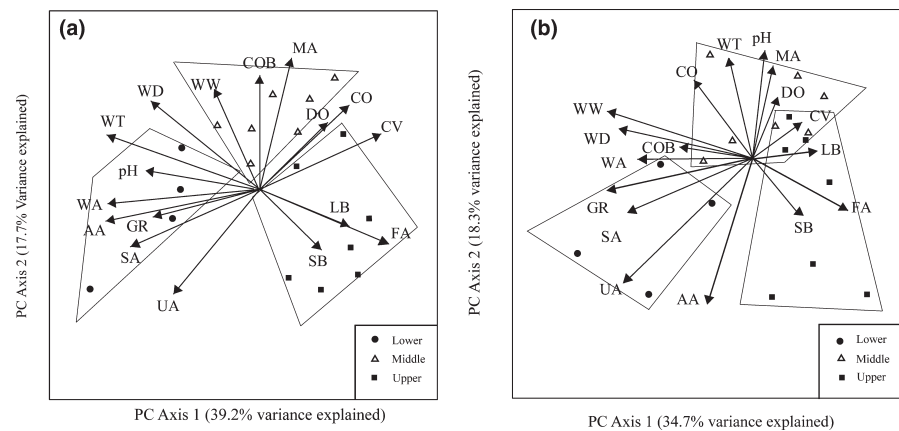
To quantify the magnitude of species change between communities, we used the Sørensen index (β_{sorr}) to calculate the β -diversity of the pairwise assemblages, and the analogous calculation for functional β -diversity developed by Villéger et al. (2013). According to Baselga (2010), we partitioned the taxonomic β -diversity ($\beta_{tax-sorr}$) into two components, including nestedness ($\beta_{tax-nest}$) and turnover ($\beta_{tax-tur}$). Only species occurrence data were used. For the functional

composition, the functional β -diversity ($\beta_{fun-sorr}$) was also partitioned into nestedness ($\beta_{fun-nest}$) and turnover ($\beta_{fun-tur}$) based on Villéger et al. (2013) and Villéger, Miranda, Hernández, and Moullot (2010) (Appendix S3). To determine how β -diversity varied along the longitudinal gradient of the stream, we calculated β -diversity for site i as the mean of pairwise comparisons between site i and all other sites (Baselga & Orme, 2012). The taxonomic and functional β -diversity measures were calculated using the “ape” package (Paradis, 2010) and “betapart” package (Baselga & Orme, 2012) in R 3.4.1.

2.6 | Data analysis

According to the ratio of the number of occurrences of a species to the total number of samples, the frequency of occurrence of the species (F_i) is determined. And the relative abundance (P_i) is determined by the ratio of the number of individuals in a species to the

FIGURE 2 PCA ordination of Shuaishui Stream reaches based on local-scale and landscape-scale environmental variables, the abbreviations of environmental variables are shown in Table 1



total number of catches at that samples site. The three stream segments are analysed independently.

A principal component analysis (PCA) was performed on log-transformed ($\log_{10}(X + 1)$) environmental variables (local and landscape scales) to identify the primary environmental gradients among stream sites. May and October were analysed independently to examine differences between seasons. To determine the spatial variation in both the taxonomic and functional α - and β -diversity patterns along the upstream–downstream gradient, we used curve estimation to test the correlation between the diversity indices and the distance from the headwaters. The optimal model was determined based on the R^2 value of each model. The SPSS 22.0 statistics package was used to perform the statistical analysis, and statistical significance was accepted at $p < .05$.

TABLE 2 The functional ratio traits measured for each fish species collected in this study

Functional trait	Measure	Ecological meaning
Relative eye size	Ed/Hd	Visual scope to food
Mouth gape shape	Md/Mw	Shape of food
Relative gut length	Gl/Bl	Ability to digest food
Relative eye position	Eh/Hd	Vertical position in water
Body shape I	Bd/Bw	Locomotion
Body shape II	Bd/Bl	Locomotion
Relative head length	Hi/Bl	Food resource use
Relative head depth	Hd/Bd	Food resource use
Contribution of caudal peduncle to the swimming capability	Cfd/CPd	Sustained swimming ability
Relative body length	Bl/Si	Habitat use, feeding, and life-history strategy

Note: The trait definitions and functional categories followed Gatz, 1979; Webb, 1984; Kramer & Bryant, 1995; Sibbing & Nagelkerke, 2001; Karpouzi & Stergiou, 2003; and Boyle & Horn, 2006.

Abbreviations: Bd , body depth; Bl , body length; Bw , body width; Cfd , maximum caudal fin depth; CPd , caudal peduncle depth; Ed , eye diameter; Eh , eye height; Gl , gut length; Hd , head depth; Hi , head length; Md , mouth height; Mo , mouth orientation; Mw , mouth width; Si , maximum standard length.

3 | RESULTS

3.1 | Environmental characteristics

The two axes of PCA of environmental characteristics in May explained 56.9% of variation among site. The first PC axis (explained 39.2%) was strongly associated with water temperature (WT), wetted width (WW), agriculture area (AA) and gravel (GR). Sampling sites with high scores on PC1 showed relatively high water temperature and large wetland and agriculture areas. These sites were located at the downstream segment of Shuaishui Stream. Sampling sites upstream were characterised by relatively high current velocity, more boulders and large forest area. The second PC axis explained 17.7% of the variation, and the environmental factors with high scores on PC2 were meadow area (MA), cobble (COB), conductivity (CO) and pH (Figure 2a). Also, the environmental characteristics varied spatially during October. The first and second axes of PCA explained 34.7% and 18.3% of the variance, respectively, and the WW, WD, WA and %SA changed substantially from upstream to downstream (Figure 2b).

3.2 | Overview of fish composition

A total of 35 species were collected in this study, representing 9 families and 4 orders. 33 and 32 species were collected in May and October, respectively. Cyprinidae fishes represented 61.8% of the total species richness; 13, 25 and 24 species were collected from the upper, middle and downstream segments, respectively. *Onychostoma barbatulum* and *Phoxinus oxycephalus* were only collected the upper streams with high elevation. *Cyprinus carpio*, *Hemiculterella sauvasi*, *Pseudorasbora parva* and *Sinibrama macrops* only occurred in the downstream. *Zacco platypus*, *Acrossocheilus fasciatus*, *Cobitis rarus*, *Vanmanenia stenosoma* and *Rhinogobius* spp. were abundant in communities in the upper stream ($F_i > 40\%$), among which *Rhinogobius* spp. reach 100% frequency of occurrence. *Microphysogobio fukiensis*, *Acheilognathus*, *Sarcocheilichthys parvus* and *Pseudobagrus truncatus* occurred most frequently in the middle stream, whereas more abundant species including *Hemiculter leuciscus*, *Carassius auratus* and *Cyprinus carpio* were collected in the downstream (Table 3).

TABLE 3 The frequency of occurrence (F_i %) and the relative abundance (P_i %) of fishes collected in the Shuaishui Stream

Species/family/order	Upper stream (F_i %/ P_i %)	Middle stream (F_i %/ P_i %)	Downstream (F_i %/ P_i %)
Cypriniformes			
Cobitidae			
<i>Cobitis rarus</i>	71.43/7.41	71.43/5.45	50.00/3.37
<i>Leptobotia guilinensis</i>	28.57/ 0.56	57.14/3.32	/
<i>Misgurnus anguillicaudatus</i>	/	42.86/1.42	50.00/2.25
<i>Cobitis sinensis</i>	/	57.14/3.32	/
Homalopteridae			
<i>Vanmanenia stenosoma</i>	85.71/21.82	85.71/16.82	25.00/8.24
Cyprinidae			
<i>Onychostoma barbatulum</i>	14.29/0.28	/	/
<i>Phoxinus oxycephalus</i>	14.29/0.70	/	/
<i>Acrossocheilus fasciatus</i>	85.71/26.43	85.71/8.22	100/16.10
<i>Zacco platypus</i>	85.71/18.60	71.43/10.46	50.00/1.50
<i>Acheilognathus chankaensis</i>	/	14.29/0.27	25.00/1.50
<i>Cyprinus carpio</i>	/	/	75.00/2.62
<i>Carassius auratus</i>	/	/	50.00/1.12
<i>Abbottina rivularis</i>	28.57/1.96	28.57/1.40	75.00/3.75
<i>Acheilognathus barbatulus</i>	/	71.43/6.16	75.00/2.62
<i>Gnathopogon taeniellus</i>	/	14.29/0.18	50.00/2.62
<i>Hemiculter leuciscus</i>	/	14.29/0.24	/
<i>Hemiculterella sauvagi</i>	/	/	25.00/0.37
<i>Microphysogobio fukiensis</i>	/	71.43/5.05	50.00/3.00
<i>Microphysogobio tafangensis</i>	14.29/0.28	42.86/1.90	25.00/0.75
<i>Opsarichthys bidens</i>	38.86/0.84	/	50.00/1.50
<i>Pseudorasbora parva</i>	/	/	50.00/1.12
<i>Sinibrama macrops</i>	/	/	25.00/1.25
<i>Rhodeus ocellatus</i>	14.29/0.28	14.29/0.24	100/7.12
<i>Sarcocheilichthys parvus</i>	/	57.14/3.08	100/6.74
<i>Sarcocheilichthys sinensis</i>	/	14.29/0.24	/
<i>Squalidus argentatus</i>	/	/	25.00/0.25
<i>Squalidus nitens</i>	/	42.86/1.18	/
Siuriformes			
Bagridae			
<i>Pseudobagrus truncatus</i>	39.86/1.68	85.71/2.84	/
<i>Pelteobagrus fulvidraco</i>	/	14.29/0.24	/
Synbranchiformes			
Sybranchidae			
<i>Monopterus albus</i>	/	28.57/0.47	50.00/0.75
Mastacembelidae			
<i>Sinobdella sinensis</i>	/	42.86/1.42	75.00/5.63
Perciformes			
Odontobutidae			
<i>Odontobutis potamophila</i>	/	14.29/0.47	50.00/1.12
Sinipercidae			

(Continues)

TABLE 3 (Continued)

Species/family/order	Upper stream ($F_i\%/P_i\%$)	Middle stream ($F_i\%/P_i\%$)	Downstream ($F_i\%/P_i\%$)
<i>Siniperca chuatsi</i>	/	57.14/1.18	/
<i>Siniperca scherzeri</i>	/	14.29/0.24	25.00/0.37
Gobiidae			
<i>Ctenogobius</i> sp.	100/19.16	85.71/24.17	75.00/9.36

3.3 | Taxonomic and functional α -diversity

According to the curve estimation, SR and $FRic$ increased with the distance from the headwaters, and the peaks occurred midstream before declining, producing a hump-shaped relationship along the gradient ($R^2 = 0.725$, $p < .01$ in May and $R^2 = 0.542$, $p < .05$ in October for SR ; $R^2 = 0.751$, $p < .01$ in May and $R^2 = 0.617$, $p < .01$ in October for $FRic$). And the correlation coefficient R^2 for SR was relatively lower than that for $FRic$ during each season. Both $FDiv$ and $FEve$ were not significantly correlated with the gradient ($p > .05$; Figure 3).

3.4 | Taxonomic and functional β -diversity

After curve estimation, both taxonomic and functional β_{sor} in May decreased with increasing distance from the headwaters; the minimum values were recorded midstream, and the values increased with the gradient heading downstream. Both showed U-shaped relationships from the headwaters to the downstream area ($R^2 = 0.459$, $p < .05$ for

$\beta_{tax-sor}$; $R^2 = 0.608$, $p < .05$ for $\beta_{fun-sor}$). This U-shaped distribution was also observed for $\beta_{tax-sor}$ ($R^2 = 0.444$, $p < .05$), not $\beta_{fun-sor}$ ($p > .05$) in October (Figure 4a).

For the taxonomic β_{sor} , the percentages of $\beta_{tax-nes}$ and $\beta_{tax-tur}$ were 26.6% and 73.4% in May and 37.5% and 62.5% in October, respectively. And the mean $\beta_{tax-nes}$ value was significantly lower than $\beta_{tax-tur}$ value during two seasons (paired t test, $t = -6.53$, $p < .01$ in May; $t = -2.80$, $p < .01$ in October). However, for $\beta_{fun-sor}$, the percentages of $\beta_{fun-nes}$ and $\beta_{fun-tur}$ were 62.4% and 37.6% in May and 74.5% and 25.5% in October, respectively, and $\beta_{fun-nes}$ was significantly higher than $\beta_{fun-tur}$ ($t = 3.62$, $p < .01$ in May; $t = 4.82$, $p < .01$ in October).

Curve estimation showed that the quadratic model agreed with the " β_{nes} -distance" relationship for $\beta_{tax-nes}$ in May and October ($R^2 = 0.357$, $p < .05$ in May; $R^2 = 0.281$, $p < .05$ in October), and for $\beta_{fun-nes}$ in May ($R^2 = 0.786$, $p < .05$), not $\beta_{fun-nes}$ in October ($p > .05$; Figure 4b). The taxonomic and functional β_{tur} patterns differed in their responses to changing distance. $\beta_{fun-tur}$ did not change with distance from the headwaters ($p > .05$), whereas the taxonomic turnover displayed a U-shaped relationship with distance in May

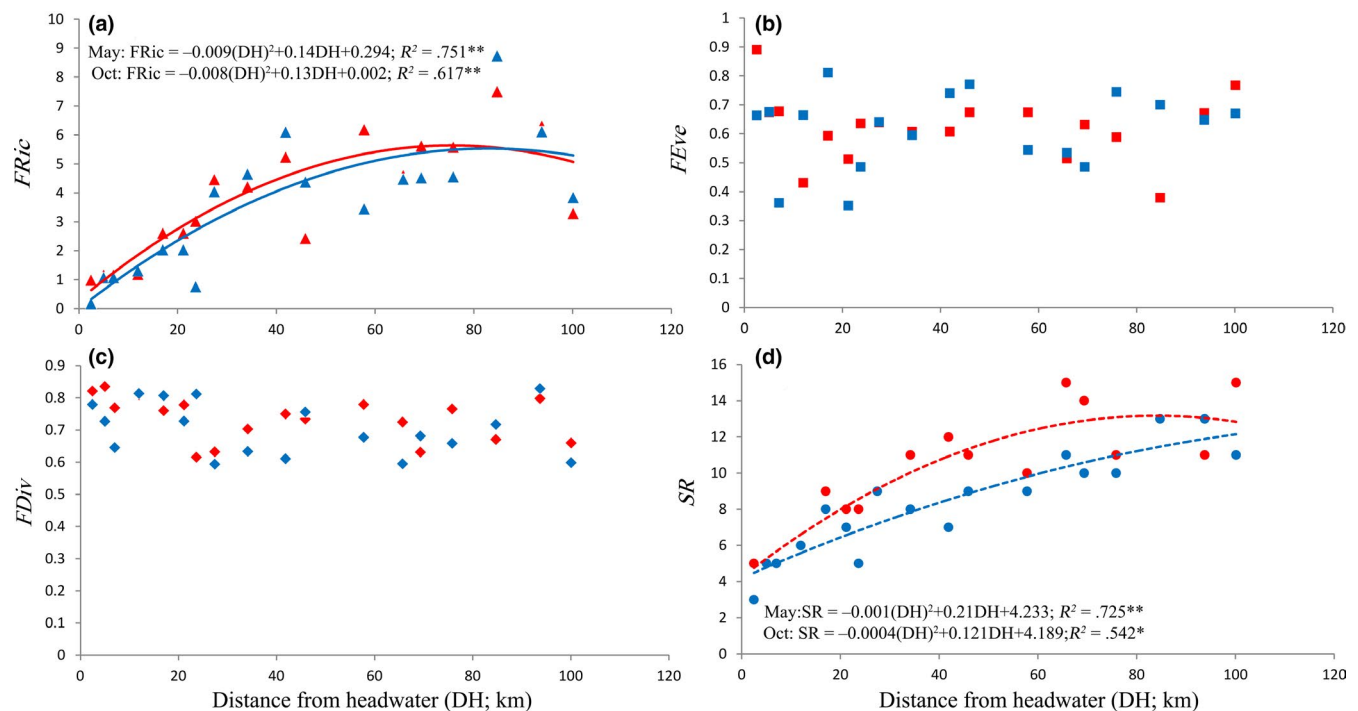


FIGURE 3 Relationships between α diversities and the distance from headwaters. Red and blue signs represented May and October, respectively

($R^2 = 0.393$, $p < .05$) and a hump-shaped relationship in October ($R^2 = 0.501$, $p < .05$; Figure 4c).

3.5 | The relationship between taxonomic and functional diversity

According to the results of curve estimation, there was a positive linear relationship between functional richness and species richness in both seasons ($R^2 = 0.614$, $p < .01$ in May; $R^2 = 0.697$, $p < .01$ in October; Figure 5a). Similarly, the taxonomic turnover and functional turnover had a strong positive linear relationship ($R^2 = 0.291$, $p < .05$; $R^2 = 0.386$, $p < .01$ in October; Figure 5b).

4 | DISCUSSION

From the headwaters to downstream areas, the species richness of stream fishes often increases, peaks in intermediate stream segments, and eventually decreases downstream, producing a hump-shaped relationship (Li et al., 2018; Mazzoni & Lobón-Cerviá, 2000; Oberdorff et al., 1993; Roberts & Hitt, 2010). We found that the taxonomic α -diversity (i.e. species richness) of fishes in the Shuaishui Stream had a hump-shaped distribution along the distance from the headwaters, which is consistent with the above-mentioned pattern. On one hand, stream size, habitat diversity and complexity often increase along a longitudinal gradient to reach a maximum in mid-elevation reaches of streams (Resh et al., 1988), which may be one of the reasons explaining the spatial variations in the taxonomic α -diversity of fishes in the Shuaishui Stream. On the other hand, more anthropogenic disturbances occur and populations are denser in downstream areas than upstream and midstream areas, which leads to a decrease in fish species richness (especially species that are extremely sensitive to anthropogenic disturbance) in lower stream reaches (Li et al., 2018; Oberdorff et al., 1993).

Different from α -diversity, β -diversity quantifies the degree to which species compositions vary from one community to another (Kessler et al., 2009; Whittaker, 1972). Therefore, α -diversity and β -diversity of fishes may show different spatial patterns along environmental gradients (Tylianakis et al., 2008). For example, Li et al. (2018) found that β -diversity of stream fishes showed a U-shaped relationship with distance from the headwaters, while α -diversity showed a hump-shaped pattern. Jaramillo-Villa et al. (2010) found that β -diversity of stream fishes decreased but α -diversity increased with elevation decreasing from 1,750 to 1,000 m at the Colombian Andes. We found that the taxonomic β -diversity of fishes in the Shuaishui Stream showed a U-shaped relationship with the distance from headwaters, which was different from the longitudinal pattern in the taxonomic α -diversity. This U-shaped distribution in β -diversity of stream fishes along the longitudinal was also observed by Li et al. (2018) and Zhang et al. (2018). These authors explained this pattern by two

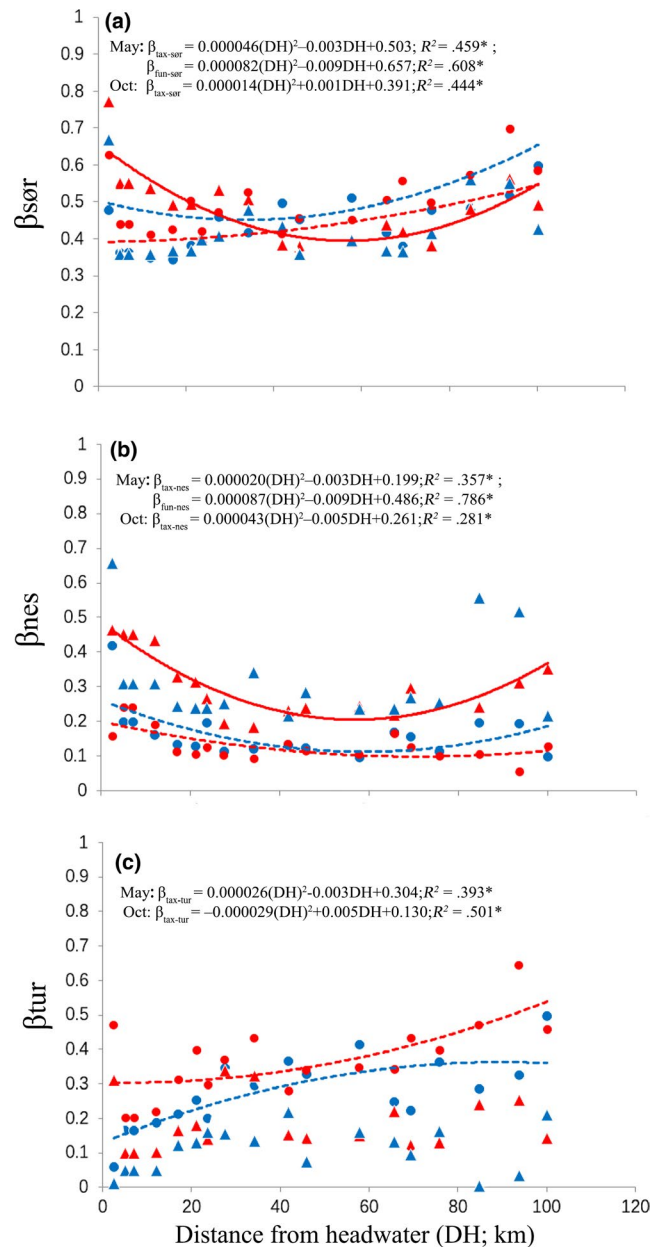


FIGURE 4 Relationships between β diversities and the distance from headwaters. Circle and triangle represented taxonomic and functional diversities, and red and blue signs represented May and October, respectively

ecological processes, including the gradual loss of the upstream species, which caused β -diversity decreasing from headwaters to midstream, and the gradual gain of the downstream species causing β -diversity decreasing from midstream to lower reaches. We believed that the two processes may be the causative mechanisms explaining the longitudinal pattern in β -diversity of fishes observed in this study. First, by comparing the fish assemblages between the upstream and midstream areas, we found that some endemic species (cold-water and lotic species) in the headwaters, such as *Onychostoma barbatulum*, *Phoxinus oxycephalus* and *Vanmanenia stenostoma*, gradually decreased downstream, which should cause the decrease in the idiosyncrasy of midstream

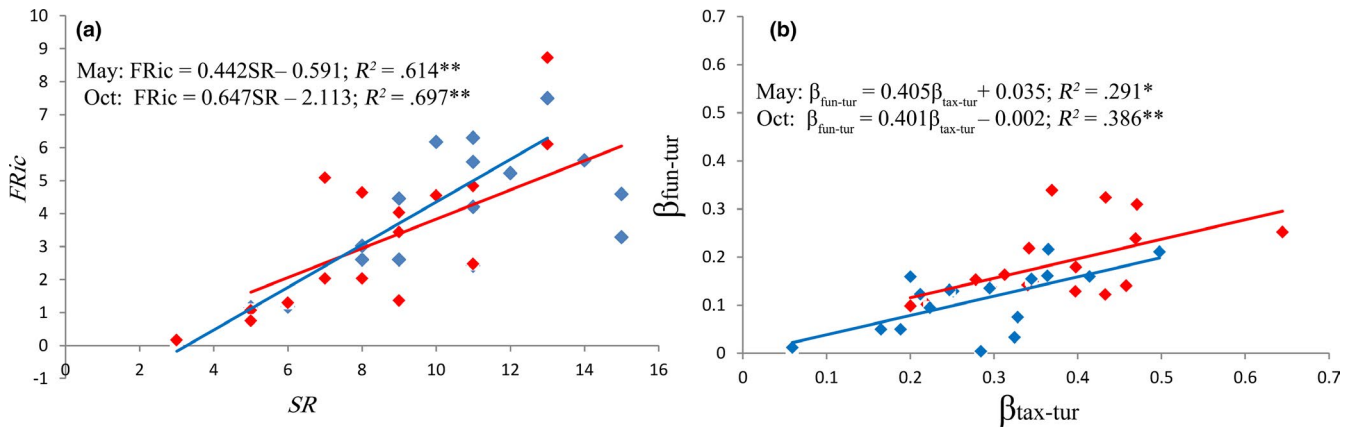


FIGURE 5 Relationships between taxonomic and functional diversities. Red and blue signs represented May and October, respectively

assemblages. Second, due to the spatial changes in food sources along the fluvial continuum, the carnivorous and herbivorous species, such as *Siniperca chuatsi*, *Rhodeus ocellatus* and *Acheilognathus barbatulus*, gradually increased in the downstream areas, leading to the increase in β -diversity of downstream assemblages relative to midstream assemblages.

To better understand variation in species function in an ecosystem, functional diversity has been suggested for explaining when, where and how species can live and interact with each other, using complementarity or redundancy of their morphological, physiological and ecological attributes (Cadotte, Carscadden, & Mirotchnick, 2011; Diaz & Cabido, 2001; Kang, Huang, Yan, Yan, & Lin, 2018; McGill, Enquist, Weiher, & Westoby, 2006). Covariance between functional diversity and species richness helps us to know the dynamic utilisation of food and living space (Kang et al., 2018). Corresponding to different spatial scale, functional diversity may show a positive linear, nonlinear or asymptotic relationship with species richness (Petchey and Gaston, 2002; Petchey & Gaston, 2006; Stuart-Smith et al., 2013). In this study, we found that the functional richness of fishes linearly related to species richness, and both of the two indices showed a hump-shaped relationship with the distance from headwaters. Our results confirm the river continuum concept expectations that functional diversity should increase within a drainage basin as resource diversity increasing, which promotes the trophic diversity of fishes increasing and the interspecific functional trait differentiating (Pease et al., 2012; Thorp, Thoms, & Delong, 2008). The slight decrease in functional richness of fishes in the lower reaches can be explained by the linear relationship between functional richness and species richness, which is due to the similar decrease in species richness of fish assemblages downstream. Also, more anthropogenic disturbances and human populations occur in downstream areas of the Shuaishui basin. Habitat modifications associated with anthropogenic activities may result in the cosmopolitan fishes replacing the endemic fishes (Li et al., 2018), and this species replacement may decrease the functional diversity of fishes when the gaining cosmopolitan fishes bring less or no new functional traits (Pease et al., 2012), which may be responsible for that functional richness decrease more than species richness of

fishes in the last sampling sites downstream as shown in Figure 3. As an important determinant of ecosystem processes, functional diversity is more sensitive to environmental stress or disturbance than taxonomic diversity (Norberg et al., 2001; Suding & Goldstein, 2008). According to the R^2 values of the "α-diversity-distance from headwaters" relationships, we found that the functional richness related more intensively to the distance from headwaters than species richness during each season; the R^2 values were 0.751 (May) and 0.617 (October) for functional richness and 0.725 (May) and 0.542 (October) for species richness, respectively. In addition, we also found that the taxonomic turnover rates linearly related to the functional turnover, and both the taxonomic and functional β -diversity of fishes showed the similar U-shaped distributions along the longitudinal gradient. However, the taxonomic β -diversity was dominated by species turnover, while the functional β -diversity was dominated by functional nestedness. This discrepancy in the modes of assemblage changing (i.e. turnover versus nestedness) along environmental gradients between the functional and taxonomic organisations has also been observed for stream fishes (e.g. Zhang et al., 2018) and other terrestrial taxons (e.g. Bishop, Robertson, Ransburg, & Parr, 2015). The warm-water species (such as *Zacco platypus* and *Acrossocheilus fasciatus*) replacing the old-water species (such as *Rhynchocypris oxycephalus*) in the upstream-midstream areas, and the lentic species (such as *Carassius auratus* and *Rhodeus ocellatus*) replacing the lotic species (such as *Zacco platypus* and *Vanmanenia stenostoma*) in the midstream-downstream areas result in the relatively high species turnover along the longitudinal gradient of the Xin'an River, into which the Shuaishui Stream flows (Chen, Meng, Zhang, Chu, & Yan, 2019). However, the functional organisations of stream fishes may vary longitudinally as a nestedness mode (Zhang et al., 2018). Taking an example of the trophic traits of fishes, detritivores, omnivores, herbivores and piscivores often gradually occur downstream in turn along the river continuum (Pouilly, Barrera, & Rosales, 2006; Zhu et al., 2012). Comparing with fish assemblages upstream, the gain of herbivores and piscivores species without the loss of detritivores species for the fish assemblages downstream indicate that the trophic guilds of upstream assemblages show as a subset of the downstream assemblages (Chen et al., 2019; Zhang et al., 2018).

Therefore, our results suggest that the most spatial variations in stream fish assemblages are driven by species turnover and functional nestedness along the river continuum.

In summary, we found that, in this study area, both species richness and functional richness of fishes showed a hump-shaped relationship with the distance from headwaters, while both taxonomic and functional β -diversities presented the U-shaped distributions along the river continuum. Functional diversity related more to the distance from headwaters than taxonomic diversity. Despite their similar relationship with the distance from headwaters, taxonomic and functional β -diversities were dominated by species turnover and function nestedness components, respectively. Our results suggest that, along the upstream–downstream gradient in a subtropical stream, the α - and β -aspects of fish diversity may show different spatial patterns. Although the taxonomic and functional metrics of fish diversity may present similar spatial patterns, the β -diversity indicates that fish assemblages vary longitudinally through species turnover but functional nestedness.

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AUTHORS' CONTRIBUTION

D.Z., Y.Y. and B.K. conceived and designed the investigation. D.Z., W.H. and L.C. performed field and/or laboratory work. D.Z. analysed the data. D.Z., W.H., D.X. and B.K. contributed materials, reagents and/or analysis tools. D.Z. and Y.Y. wrote the paper.

DATA AVAILABILITY STATEMENT

The raw/processed data required to reproduce these findings cannot be shared at this time due to legal or ethical reasons. The data used to support the findings of this study are available from the corresponding author upon request.

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SUPPORTING INFORMATION

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

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