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Beta Diversity Partitioning and Drivers of Variations in Fish Assemblages in a Headwater Stream: Lijiang River, China

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Received: 21 January 2019; Accepted: 1 April 2019; Published: 2 April 2019



Abstract: Beta diversity partitioning has currently received much attention in research of fish assemblages. However, the main drivers, especially the contribution of spatial and hydrological variables for species composition and beta diversity of fish assemblages are less well studied. To link species composition to multiple abiotic variables (i.e., local environmental variables, hydrological variables, and spatial variables), the relative roles of abiotic variables in shaping fish species composition and beta diversity (i.e., overall turnover, replacement, and nestedness) were investigated in the upstream Lijiang River. Species composition showed significant correlations with environmental, hydrological, and spatial variables, and variation partitioning revealed that the local environmental and spatial variables outperformed hydrological variables, and especially abiotic variables explained a substantial part of the variation in the fish composition (43.2%). The overall species turnover was driven mostly by replacement (87.9% and 93.7% for Sørensen and Jaccard indices, respectively) rather than nestedness. Mantel tests indicated that the overall species turnover (β_{SOR} and β_{JAC}) and replacement (β_{SIM} and β_{JTU}) were significantly related to hydrological, environmental, and spatial heterogeneity, whereas nestedness (β_{SNE} or β_{JNE}) was insignificantly correlated with abiotic variables ($P > 0.05$). Moreover, the pure effect of spatial variables on overall species turnover (β_{SOR} and β_{JAC}) and replacement (β_{SIM} and β_{JTU}), and the pure effect of hydrological variables on replacement (β_{SIM} and β_{JTU}), were not important ($P > 0.05$). Our findings demonstrated the relative importance of interactions among environmental, hydrological, and spatial variables in structuring fish assemblages in headwater streams; these fish assemblages tend to be compositionally distinct, rather than nested derivatives of one another. Our results, therefore, indicate that maintaining natural flow dynamics and habitat continuity are of vital importance for conservation of fish assemblages and diversity in headwater streams.

Keywords: fish assemblages; abiotic variables; replacement; nestedness; headwater stream

1. Introduction

Fish assemblages in streams and rivers are, to a large degree determined by the prevailing spatial and environmental conditions, including physical, chemical, and biological characteristics [1,2]. Several studies have focused on the spatial variation of fish assemblages in rivers and their relationship to abiotic variables [3,4], and most of studies support the river continuum concept, description of the changes in fish composition from upstream to downstream [5,6]. However, temporal variations of fish assemblages occur in some sites [3,7], but not in others [5,8]. Although the relationship between fish assemblage and abiotic variables has been intensively investigated, the relative role of different variables contributing to fish assemblage variations remains poorly elucidated [9,10]. Some studies found that hydromorphologic variables (i.e., channel geometry, substrate, flow, vegetation, and land use in the riparian zone) were dominant regulating factors [11,12]. However, local environmental variables (e.g., nutrients, dissolved oxygen, pH, conductivity) and climate are more often considered to be the key determining factors [5,10]. It is, therefore, uncertain which of the abiotic variables (i.e., environmental, hydrological, and spatial variables) best explain the fish assemblage patterns on the regional scale [13,14]. Moreover, knowledge of the influence of regional constraints and historical processes on species contribution, abundance, and diversity remain superficial, although it has been considered critical for an advance in stream fish ecology and conservation [15,16].

Beta diversity (β -diversity) describes the variation in species composition among communities, measured by ecological dissimilarities between sampling units based on Jaccard or Sørensen indices [17,18]. β -diversity can be further partitioned into two additive components accounting for (i) the dissimilarity associated with the replacement of some species by others between assemblages (i.e., species replacement) and (ii) the dissimilarity associated with species losses in which an assemblage is a strict subset of another (i.e., nestedness-resultant dissimilarity of assemblages [19,20]). Some studies have revealed that replacement contributes more than nestedness to the overall species turnover (β -diversity) of fish assemblages in rivers and streams [21,22], while others have shown an equal contribution of replacement and nestedness to β -diversity [13,23]. Thus, the contribution of replacement or nestedness to β -diversity of fish assemblages may be area-specific.

Most Chinese studies of fish assemblages in rivers have focused on fish composition and its distribution, spatially and temporally, and on the role of environmental variables [24–27]. Recent studies indicate that fish assemblages correlate significantly with abiotic variables, such as river width, discharge, velocity, water temperature, dissolved oxygen, and altitude [27,28]. However, the question of which variables (i.e., physical variables, chemical variables, hydrological variables, and spatial variables) contribute most to fish assemblage variations is not well elucidated. In addition, in China, α -diversity within fish assemblages (i.e., species richness, Shannon index, Simpson's index, etc.) is widely studied [5,29,30], while β -diversity is poorly documented, especially β -diversity partitioning [30]. Exploring the two additive components of β -diversity, replacement and nestedness, can help with the acquisition of information about the underlying ecological mechanisms at different environmental conditions [20].

In the present study, we attempt to quantify the role of different abiotic variables in determining changes in fish assemblages through partitioning of β -diversity in the upstream Lijiang River, an area where information on freshwater fish diversity and distribution is currently poor. We address three questions: (i) What is most important for fish species composition: spatial variables, environmental variables, or hydrological variables? (ii) What are the major drivers of species and β -diversity of fish assemblages? (iii) Which factors contribute most to β -diversity: replacement or nestedness? The hypotheses were that (i) environmental, hydrological, and spatial variables interacted to determine species composition and β -diversity, and that (ii) spatial variables would be a key driver of β -diversity, but it was uncertain whether replacement or nestedness would prove to be of superior importance.

2. Materials and Methods

2.1. Study Area

Lijiang River, which lies in Guangxi Zhuang Autonomous Region, southwest China (Figure 1), originates from the main peak of Mao'er Mountain (maximum altitude 2141.5 m) in the northeast of Guilin, and has a total length of 214 km and drainage area of 2173.29 km². Lijiang River has typical rain source characteristics and the bankfull discharge is 7810 m³/s, usually occurring in May and June [31]. The river has an extremely uneven flow during the year, mainly due to the huge heavy rainfall during the southeast monsoon in the upstream of the river flowing in a steep watershed. Ludong Stream, with a mean slope of 7.38‰, is one of the upstream tributaries to Lijiang River. The total length of Ludong Stream is 46 km with a total of drainage area of 314 km². All stream sections in the study area are mountainous with a turbulent waterflow and a large hydraulic gradient (31.7‰). The average annual discharge is 5.99×10^8 m³ and the average annual flow is 19 m³/s. However, the Fuzikou Reservoir was established in the Ludong Stream by means of a dam (with a total length of 239 m and a maximum height of 76.5 m) in January 2018 for the purpose of flood control, ecological hydration of Lijiang River, and power generation. The reservoir has a water storage capacity of 1.88×10^8 m³ with an impoundment level of 267 m, which can compensate water discharge to Lijiang River with a total of 1.114×10^8 m³ annually. The vegetation types on both sides of the stream are mixed, mostly consisting of coniferous forest, broad-leaved forest, and bamboo forest [32]. The fish community in most upstream areas of Lijiang River is dominated by *Zacco platypus*, *Pseudogastromyzon fangi*, *Erromyzon sinensis*, and *Opsariichthys bidens*, with little temporal variation in assemblages [33]. No floating and submerged vegetation was observed.

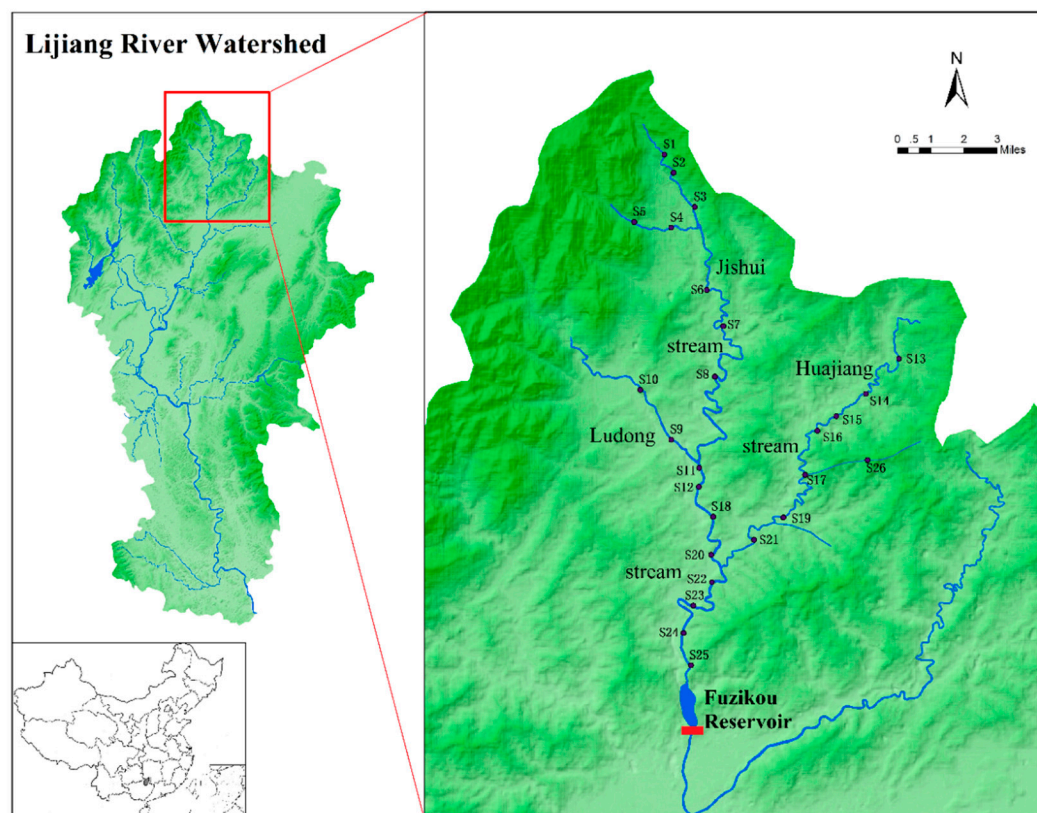


Figure 1. Study area and sampling sites in upstream of Lijiang River.

2.2. Field Sample Collection

Fish samples were collected from 26 sampling sites (Figure 1) from September to November 2016. All fish in each sampling reach, which was about 150 m long, were collected by a backpack electro-fisher (CWB-2000P, China; 12V import, 250 V export) downstream to upstream, with each ending of the reach blocked by block net. Fish specimens longer than 20 mm were identified to species, counted, and then returned to the river. Fish with total length smaller than 20 mm were not included and were released on site [34,35].

About 15 abiotic variables were measured at each sampling site, including physical and chemical parameters, such as water temperature, pH, dissolved oxygen, conductivity, turbidity, substrate size, and habitat structure character. Water temperature, pH, dissolved oxygen and conductivity were measured using a portable water quality analysis device (HACH HQ 40 d), and turbidity was measured applying a portable turbidimeter (HACH 2100 Q). Velocity was recorded at middle depth using a printing flow velocity meter (LJD-10 A). Latitude, longitude, and altitude were obtained from GPS (Garmin eTrex 10), and the distances of each sampling site to the dam of Fuzikou Reservoir were obtained from Google Earth. Measurements of stream wetted width and depth were taken at the widest and deepest section, and habitat percentage of habitat was estimated by walking along the stream reach after sampling and recording the types and relative proportions of the habitats (i.e., cascade, riffle, pool, step pool, run, glide). The same procedure was applied for substrate size, which was calculated by measuring the median particle diameter of thirty randomly chosen particles in each sampling reach [36].

2.3. Biotic and Abiotic Datasets

Two biotic datasets were applied in this study: (i) A species abundance data and species presence/absence data—a total of all 37 fish species recorded and their abundance were included and (ii) beta diversities (β -diversity). To calculate pairwise dissimilarities, we used the Sørensen dissimilarity index (β_{SOR}) and the Jaccard dissimilarity index (β_{JAC}) and two additive components (i.e., β_{SIM} , β_{NES} , and β_{SOR} for the Sørensen index and β_{JAC} , β_{JTU} , and β_{JNE} for the Jaccard index) [19,37]. Abbreviations used in the paper are explained in Table 1.

Table 1. Abbreviations used in this study.

Elements	Abbreviation
Environmental variables	Ev
Hydrological variables	Hv
Spatial variables	Sv
Dissimilarity matrices based on Euclidean distances for environmental variables	Evdis
Dissimilarity matrices based on Euclidean distances for hydrological variables	Hvdis
Dissimilarity matrices based on Euclidean distances for spatial variables	Svdis
Sørensen dissimilarity	β_{SOR}
Simpson dissimilarity (=turnover component of Sørensen dissimilarity)	β_{SIM}
Nestedness-resultant component of Sørensen dissimilarity	β_{NES}
Jaccard dissimilarity	β_{JAC}
Turnover component of Jaccard dissimilarity	β_{JTU}
Nestedness-resultant component of Jaccard dissimilarity	β_{JNE}

2.4. Abiotic Datasets

Three abiotic datasets were compiled as well including hydrological variables (Hv), environmental variables (Ev), and spatial variables (Sv). Hydrological variables (Hv) were in situ measured stream wet width, maximum depth, current velocity at the sampling sites, stream order, altitude, and the distance from the sampling sites to the dam of Fuzikou Reservoir. Environmental variables (Ev) were pH, water temperature (T), dissolved oxygen (DO), conductivity, turbidity and substrate size, hydrostatic habitats (%), fast-flow habitats (%), and slow-flow habitats (%). Except for the coordinates

(X: latitude, Y: longitude), Moran's eigenvector maps were used to generate the spatial variables (Sv) representing geographical positions and dispersal across the streams. A Euclidean distance matrix between each pair of sampling sites was calculated using the *earth.dist* function in the R package *fossil* (version 0.3.7). Then a principal coordinates of neighborhood matrix (PCNM) analysis was applied to compute the spatial variables representing geographical positions through the *pcnm* function in the R package *vegan* (version 2.5-3). The generated eigenvectors were considered as spatial variables (i.e., PCNMs), which could reflect unmeasured broadscale variation in the modern environment or historic factors, for example, natural dispersal-generated patterns demonstrating internal local-scale dispersal dynamics or regional-scale migration history [38]. Finally, a total of 17 PCNMs were generated, which were used in the following analyses (Table 2).

Table 2. Description of hydrological (Hv), environmental (Ev), and spatial (Sv) variables in upstream Lijiang River.

Abiotic Variables	Mean	Min.	Max.
Environmental variables (Ev)			
Water temperature (°C)	22.1	18.8	25.1
pH	7.8	6.9	9.7
Dissolved oxygen (mg/L)	8.4	6.1	9.8
Conductivity (µS/cm)	62.4	16.1	157.4
Turbidity (NTU)	3.1	0.2	18.4
Substrate size (cm)	10.2	7.2	15.9
% Hydrostatic habitat (pool, plunge)	28.4	0.0	76.9
% Fastflow habitat (riffle, cascade)	36.3	7.5	67.0
% Slowflow habitat (run, glide)	35.4	0.0	75.0
Hydrological variables (Hv)			
Wetted width (m)	14.2	2.4	63.5
Depth (cm)	34.3	16.1	53.5
Flow velocity (cm/s)	31.2	14.2	59.4
Distance from the dam of Fuzikou Reservoir (km)	20.4	2.2	35.6
Altitude (m)	324.4	226.6	469.8
Spatial variables (Sv)			
Latitude (°N)	25.78	25.70	25.88
Longitude (°E)	110.46	110.50	110.57
PCNM1: Principal coordinates of neighborhood matrix 1	0.00	−0.25	0.32
PCNM2: Principal coordinates of neighborhood matrix 2	0.00	−0.29	0.34
PCNM3: Principal coordinates of neighborhood matrix 3	0.00	−0.38	0.37
PCNM4: Principal coordinates of neighborhood matrix 4	0.00	−0.42	0.37
PCNM5: Principal coordinates of neighborhood matrix 5	0.00	−0.25	0.48
PCNM6: Principal coordinates of neighborhood matrix 6	0.00	−0.42	0.39
PCNM7: Principal coordinates of neighborhood matrix 7	0.00	−0.62	0.42
PCNM8: Principal coordinates of neighborhood matrix 8	0.00	−0.37	0.40
PCNM9: Principal coordinates of neighborhood matrix 9	0.00	−0.5	0.36
PCNM10: Principal coordinates of neighborhood matrix 10	0.00	−0.43	0.39
PCNM11: Principal coordinates of neighborhood matrix 11	0.00	−0.61	0.45
PCNM12: Principal coordinates of neighborhood matrix 12	0.00	−0.71	0.70
PCNM13: Principal coordinates of neighborhood matrix 13	0.00	−0.30	0.56
PCNM14: Principal coordinates of neighborhood matrix 14	0.00	−0.50	0.76
PCNM15: Principal coordinates of neighborhood matrix 15	0.00	−0.40	0.50
PCNM16: Principal coordinates of neighborhood matrix 16	0.00	−0.61	0.43
PCNM17: Principal coordinates of neighborhood matrix 17	0.00	−0.42	0.82

2.5. Data Analysis

To assess the species richness in the study area, species accumulation curves based on samples and individuals were applied. We used the *specpool* function in the R package *vegan* to get extrapolated species richness estimates based on presence/absence data, and species rarefaction curves were plotted based on abundance data with the *specaccum* function in the R package *vegan*.

To explore the potential impacts of spatial variables, hydrological variables and environmental variables on fish assemblages (question i), preliminary data analyses were conducted. Firstly, species composition with abundance was Hellinger-transformed using the function *decosdtand* in the R package *vegan*. Secondly, a detrended correspondence analysis (DCA) using the function *decorana* on the Hellinger-transformed species data produced the longest gradient length of 2.13 along the first axis, suggesting that redundancy analysis (RDA) was appropriate for further analyses [39]. We performed RDA with the *rda* function and tested the significance using the *anova* function. If significant, a forward selection using the function *ordistep* could be utilized to obtain reduced variables for the spatial variables, hydrological variables, and environmental variables, respectively. To eliminate factors with high collinearity, all abiotic variables were $\log(x+1)$ transformed, and variance inflation factors (VIF) using the *vif* function in the R package *car* were computed, and any factor with a VIF > 10 and a Spearman's rank correlation coefficient ($|r| > 0.75$) was removed from the analysis [40]. All the selected variables (i.e., Ev, Hv, and Sv) were used as explanatory variables and Hellinger-transformed fish composition data were used for the variation partitioning analysis using the function *varpart* in the R package *vegan* [41]. The significance of the fractions of variation explained was tested with 9999 permutations [42].

Next, we ran Mantel tests in order to examine the changes in species composition along spatial, hydrological, and environmental gradients (question ii). The Mantel test has been utilized as a distance-based approach to study β -diversity in relation to distance matrices [40]. The significance of this distancedecay relationship, which measures how dissimilarity decays with increasing distance between pairwise sites, was determined using Mantel test with 9999 permutations [42]. We first calculated the total species turnover (β_{SOR} or β_{JAC}) and its two additive components (replacement (β_{SIM} or β_{JTU}) and nestedness (β_{NES} or β_{JNE})) based on presence/absence data with the function *beta.multi* in the R package *betapart* (version 1.5.1), and we used the function *beta.pair* to compute three dissimilarity matrices for β -diversity (i.e., β_{SIM} , β_{NES} , and β_{SOR} for *index.family* = "sørensen", and β_{JAC} , β_{JTU} , and β_{JNE} for *index.family* = "jaccard"). Dissimilarity matrices based on Euclidean distances for the spatial, hydrological, and environmental variables (i.e., Svdiss, Hvdis, and Evdis) were constructed. In addition to simple Mantel tests using six matrices, we applied partial Mantel tests to ease apart the pure effects of spatial, hydrological, and environmental variables on β -diversity matrices, and the significance was assessed using 9999 permutations. Mantel and partial Mantel tests were run using the functions *mantel* and *mantel.partial*, respectively, in the R package *vegan* [40,43]. All analyses were performed with the R software (version 3.5.1, R Development Core Team 2018).

3. Results

3.1. Variability of Abiotic Variables

The hydrological and environmental variables varied widely in the river (Table 2). For instance, stream wet width ranged from 2.4 m to 63.5 m (mean: 14.2 m), current velocity from 14.2 cm/s to 59.4 cm/s (mean: 31.2 cm/s), water temperature from 18.8 °C to 25.1 °C (mean: 22.1 °C), and conductivity from 16.1 $\mu\text{S}/\text{cm}$ to 157.4 $\mu\text{S}/\text{cm}$ (mean: 62.4 $\mu\text{S}/\text{cm}$). However, the spatial variables showed a small variation with latitude ranging from 25.70 to 25.88°N and longitude from 110.50 to 110.60°E, which reflects the small catchment (314 km²) studied.

3.2. Fish Assemblage Composition

A total of 2968 fish individuals were collected, comprising 37 fish species belonging to 11 families, most of which were native to the drainage area (Table 3). Cyprinidae, Balitoridae and Gobiidae contributed significantly to the typical fish assemblage composition, the proportions of individuals being 40.84%, 39.08%, and 14.82%, respectively. The dominant species were *Pseudogastromyzon fangi* (24.8%), *Zacco platypus* (21.0%), *Acrossocheilus parallens* (12.8%), and *Erromyzon sinensis* (10.5%). Of these species, 10 species were singleton species and 5 were doubleton species. Species richness ranged from

2 to 18 per site, and mean species richness was 11.19. In addition, the individuals ranged from 27 to 223 with an average of 114.15 individuals per site.

Table 3. Fish species and abundance collected in upstream Lijiang River.

Fish Species	Fish Abundance (N)
Bagridae	
1. <i>Tachysurus adiposalis</i> (Oshima, 1919)	7
2. <i>Tachysurus albomarginatus</i> (Rendahl, 1928)	34
Balitoridae	
3. <i>Erromyzon sinensis</i> (Chen, 1980)	312
4. <i>Pseudogastromyzon fangi</i> (Nichols, 1931)	736
5. <i>Vanmanenia lineata</i> (Fang, 1935)	26
6. <i>Vanmanenia pingchowensis</i> (Fang, 1935)	86
Cichlidae	
7. <i>Oreochromis niloticus</i> (Linnaeus, 1758) *	2
Cobitidae	
8. <i>Misgurnus anguillicaudatus</i> (Cantor, 1842)	36
Cyprinidae	
9. <i>Acrossocheilus kreyenbergii</i> (Regan, 1908)	19
10. <i>Acrossocheilus parallens</i> (Nichols, 1931)	381
11. <i>Carassius auratus</i> (Linnaeus, 1758)	1
12. <i>Cyprinus carpio</i> Linnaeus, 1758	5
13. <i>Microphysogobio chenhsienensis</i> (Fang, 1938)	29
14. <i>Microphysogobio kiatingensis</i> (Wu, 1930)	3
15. <i>Onychostoma barbatulum</i> (Pellegrin, 1908)	1
16. <i>Onychostoma gerlachi</i> (Peters, 1881)	1
17. <i>Opsariichthys bidens</i> Günther, 1873	88
18. <i>Parasinilabeo assimilis</i> Wu & Yao, 1977	16
19. <i>Pseudorasbora parva</i> (Temminck & Schlegel, 1846)	12
20. <i>Rhodeus ocellatus</i> (Kner, 1866)	1
21. <i>Squalidus atromaculatus</i> (Nichols & Pope, 1927)	27
22. <i>Zacco platypus</i> (Temminck & Schlegel, 1846)	623
Gobiidae	
23. <i>Rhinogobius duospilus</i> (Herre, 1935)	110
24. <i>Rhinogobius filamentosus</i> (Wu, 1939)	4
25. <i>Rhinogobius similis</i> Gill, 1859	143
26. <i>Rhinogobius leavelli</i> (Herre, 1935)	183
Mastacembelidae	
27. <i>Macrognathus aculeatus</i> (Bloch, 1786)	2
Nemacheilidae	
28. <i>Oreonectes platycephalus</i> Günther, 1868	2
29. <i>Schistura fasciolata</i> (Nichols & Pope, 1927)	22
30. <i>Schistura incerta</i> (Nichols, 1931)	9
31. <i>Traccatichthys pulcher</i> (Nichols & Pope, 1927)	1
Percichthyidae	
32. <i>Coreoperca whiteheadi</i> Boulenger, 1900	25
33. <i>Siniperca scherzeri</i> Steindachner, 1892	1
34. <i>Siniperca undulata</i> Fang & Chong, 1932	1
Siluridae	
35. <i>Pterocryptis anomala</i> (Herre, 1933)	2
36. <i>Pterocryptis cochinchinensis</i> (Valenciennes, 1840)	1
Sisoridae	
37. <i>Glyptothorax fokiensis</i> (Rendahl, 1925)	16

Notes: * exotic species.

The species rarefaction curve showed no apparent asymptote, but a trend towards stabilization (Figure 2). Species richness in the areas was estimated to 47 ± 8 using the function *specpool* in the R package *vegan*, indicating that 78.7% of the expected richness were collected in this study.

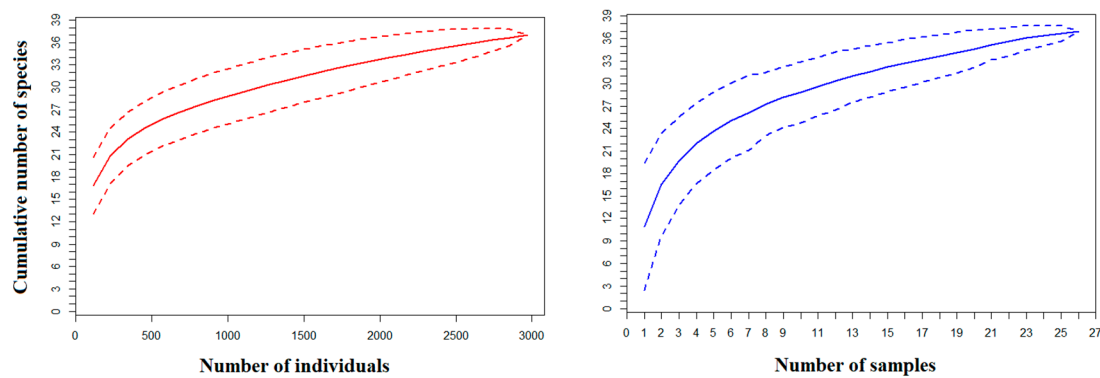


Figure 2. Species rarefaction curves in upstream Lijiang River. **Left:** Individual-based rarefaction curve; **right:** sample-based rarefaction curve.

3.3. Driver of Species Composition

In the RDA analysis for species composition, environmental, hydrological, and spatial variables all showed a significant relationship with composition. Two environmental variables, two hydrological variables, and four spatial variables were selected by forward selection (Table 4). According to variation partitioning analysis, the three abiotic variable sets explained 43.2% of species composition (Figure 3). The pure effect of environmental variables (7.1%) and spatial variables (4.0%) contributed more than the pure effect of hydrological variables (0.7%) on species variance, the joint effect of the three sets being the largest with 18.8%. The variation partitioning showed that fish composition was determined by the interaction of hydrological, environmental and spatial variables, thus supporting our first hypothesis.

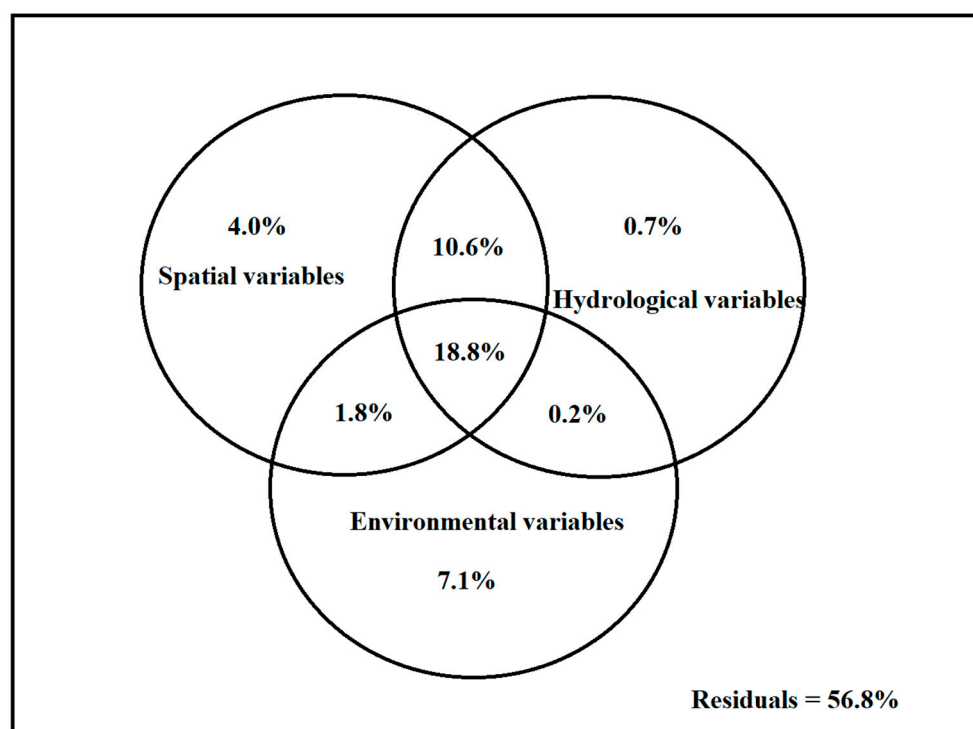


Figure 3. Contributions of the environmental, hydrological, and spatial variables to the variance in species composition in upstream of Lijiang River.

Table 4. Results of forward selection of environmental (Ev), hydrological (Hv), and spatial (Sv) variables for species composition in upstream Lijiang River.

Abiotic Variables	F	P	Abiotic Variables	F	P
Environmental variables (Ev)	4.52	<0.001	Spatial variables (Sv)	4.39	<0.001
Turbidity	4.55	0.005	PCNM1	9.61	0.005
Conductivity	3.93	0.005	PCNM2	3.81	0.01
Hydrological variables (Hv)	4.89	<0.001	PCNM3	2.77	0.025
Altitude	7.93	0.005	PCNM8	3.16	0.015
Depth	1.95	0.03			

3.4. Main Driver of β -Diversity

The partitioning total dissimilarity for the Sørensen and Jaccard indices showed that replacement (β_{SIM} or β_{JTU}) contributes more to the overall species turnover than nestedness (β_{SNE} or β_{JNE}). For example, the Sørensen indices ($\beta_{SIM} = 0.767$; $\beta_{SNE} = 0.096$; $\beta_{SOR} = 0.863$) suggested that replacement alone was responsible for 87.9% of the overall turnover of the species composition, and only 11.1% was accounted for by nestedness. Furthermore, the Jaccard indices ($\beta_{JTU} = 0.868$; $\beta_{JNE} = 0.058$; $\beta_{JAC} = 0.926$) showed that replacement alone was responsible for 93.7% of the overall turnover of the species composition, with only 6.3% being accounted for by nestedness.

Mantel tests showed that the overall turnover of species composition, based on both the Sørensen and Jaccard indices (β_{SOR} and β_{JAC}), increased significantly with hydrological and environmental distances, and the relationships between the overall species turnover (β_{SOR} and β_{JAC}) and hydrological distances were similar to the relationships between the overall turnover (β_{SOR} and β_{JAC}) and environmental distances. The weakest relationships were found for spatial distances (Table 5). The replacement based on both indices (β_{SIM} and β_{JTU}) increased significantly with hydrological, spatial, and environmental distances (excepting β_{JTU}) (Figures 4 and 5), and the relationships between replacement (β_{SIM} and β_{JTU}) and hydrological distances were similar to the relationships between replacement (β_{SIM} and β_{JTU}) and spatial distances. The weakest relationships were those for environmental distances (Figures 4 and 5). In contrast, there were no significant relationships between nestedness (β_{SNE} or β_{JNE}) and environmental, hydrological, and spatial distances ($P > 0.05$) (Table 5).

Table 5. Results of Mantel and partial Mantel test for the correlation between β -diversity and dissimilarity matrices based on Euclidean distances for spatial (Svdis), hydrological (Hvdis), and environmental variables (Evdiss) in upstream Lijiang River. For other abbreviations: see Table 1.

Index	Evdiss	Hvdis	Svdis	Evdiss ^a	Hvdis ^a	Svdis ^a
β_{SIM}	0.269 **	0.155 *	0.232 ***	0.188 *	0.034	0.128
β_{SNE}	0.033	0.150	−0.058	0.047	0.162	−0.085
β_{SOR}	0.356 ***	0.366 ***	0.200 **	0.281 *	0.255 *	0.042
β_{JTU}	0.226 **	0.135	0.225 ***	0.154 *	0.028	0.139
β_{JNE}	−0.010	0.097	−0.091	0.018	0.126	−0.099
β_{JAC}	0.346 ***	0.373 ***	0.213 **	0.264 *	0.264 *	0.061

^a The pure effect while controlling for the other two distances. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Based on partial Mantel tests, the pure effects of hydrological and environmental distances on the overall species turnover (β_{SOR} and β_{JAC}) were significant, whereas the pure effect of spatial distances was not significant ($P > 0.05$). The pure effect of environmental distances on replacement (β_{SIM} and β_{JTU}) was significant ($P < 0.05$), while the pure effects of hydrological and spatial distances were insignificant. Similarly, there were no significant relationships between nestedness (β_{SNE} or β_{JNE}) and environmental, hydrological, and spatial distances ($P > 0.05$) (Table 5).

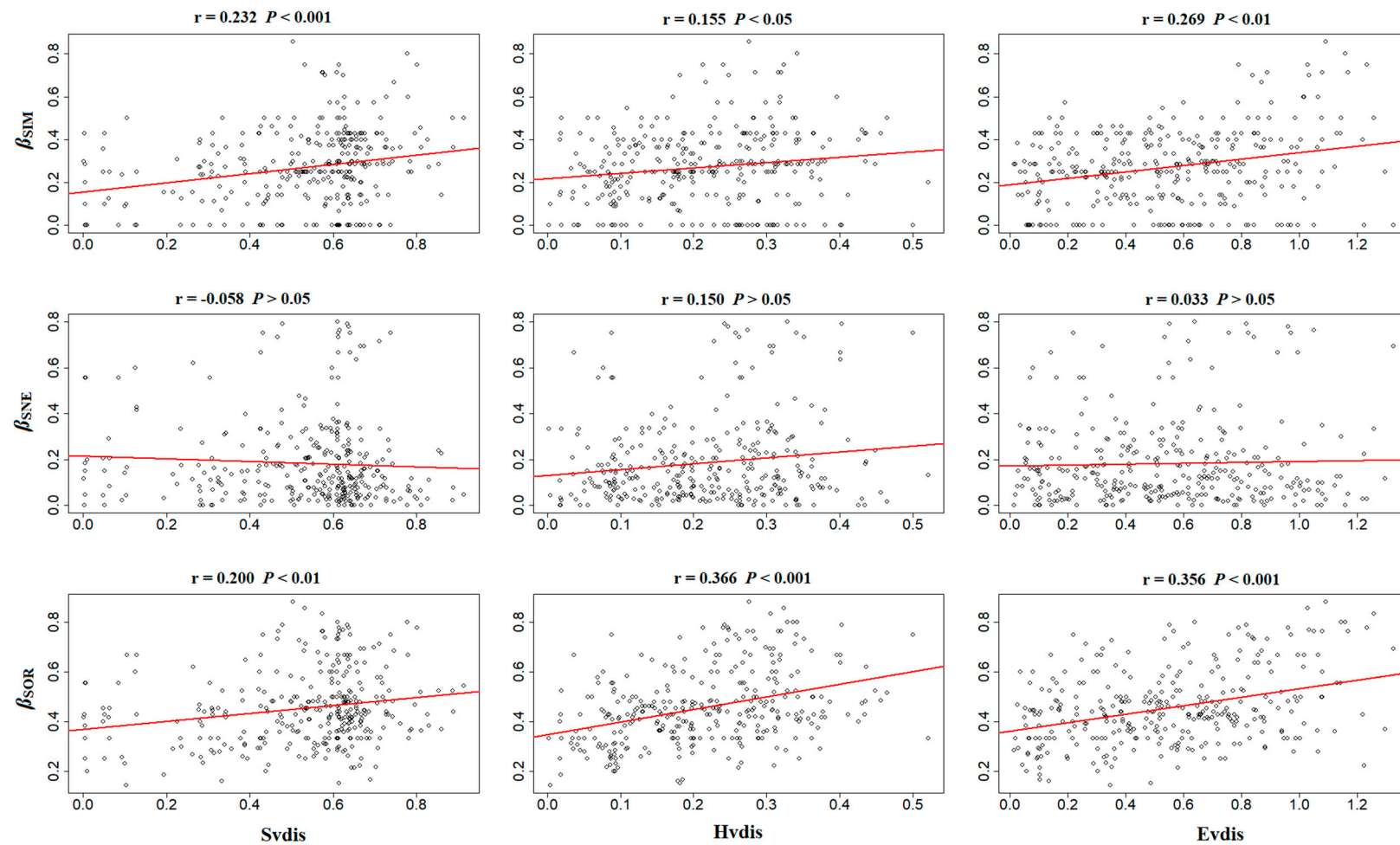


Figure 4. Relationship between Sørensen indices (β_{SIM} , β_{SNE} , and β_{SOR}) and dissimilarity matrices based on Euclidean distances for spatial (Svdis), hydrological (Hvdis), and environmental (Evdis) variables in upstream Lijiang River. For other abbreviations see Table 1.

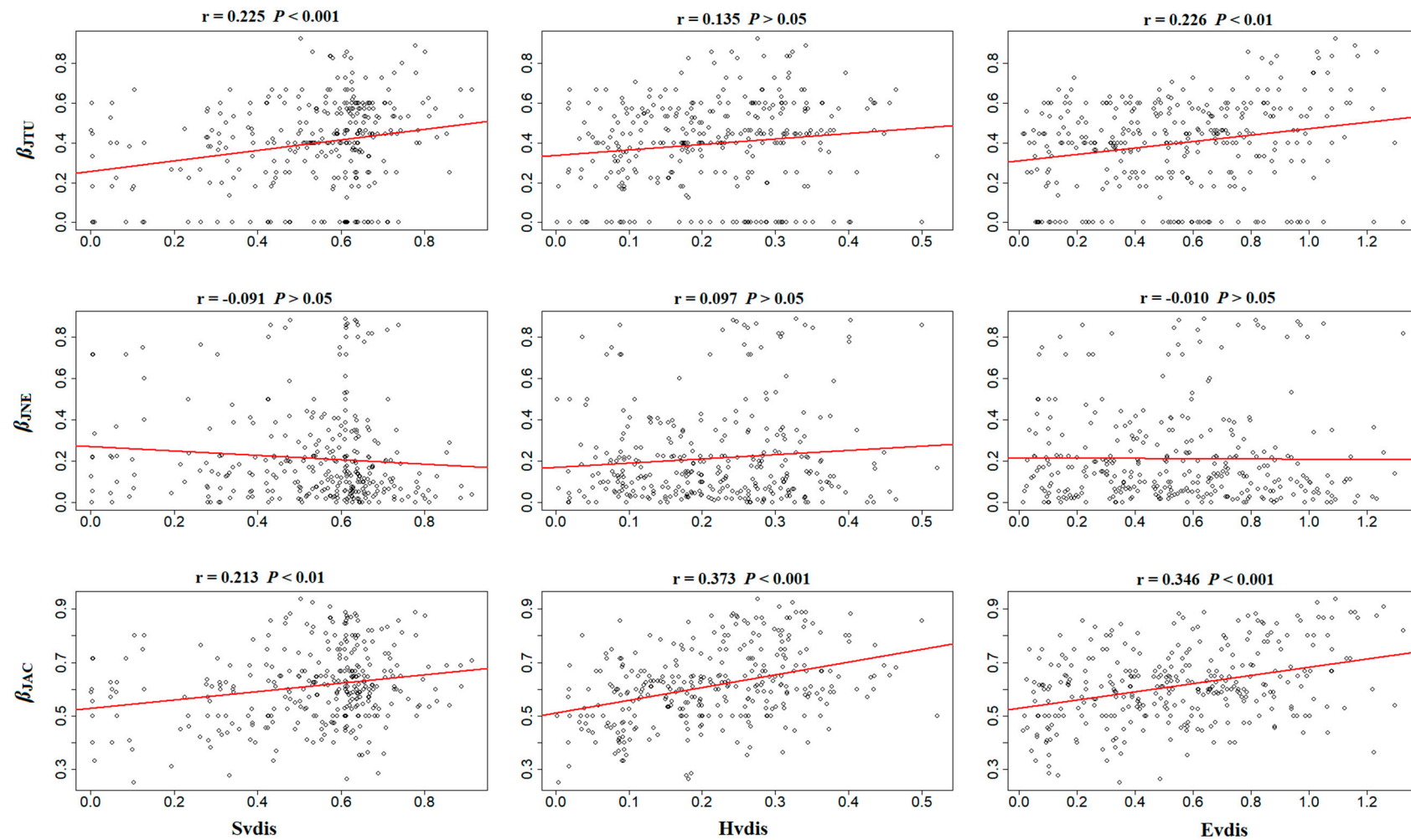


Figure 5. Relationship between Jaccard indices (β_{JTU} , β_{JNE} , and β_{JAC}) and dissimilarity matrices based on Euclidean distances for spatial (Svdis), hydrological (Hvdis), and environmental (Evdis) variables in upstream Lijiang River. For other abbreviations see Table 1.

4. Discussion

An important task in ecology is to explore the variables controlling the abundance and distribution patterns of aquatic organisms and the underlying causes [40]. Our results suggest that environmental filtering is a significant force structuring fish assemblage. The environmental, hydrological and spatial variables together explained approximately 43.2% of the total variation in fish composition. The most significant factors determining fish assemblages in upstream Lijiang River were the interactions among environmental variables, hydrological variables, and spatial variables accounting in total for 18.8% of the variation. Moreover, the pure environmental variables contributed much more than the pure spatial and hydrological variables (Figure 3). This concurs with other studies showing environmental variables to be more important than spatial variables in explaining fish composition. Earlier studies have revealed that the amount of variation explained by environmental variables, including elevation and stream width, among others, ranged from 17.3% to 34.9% [14,44–46]. However, we found the amount of variation explained by environmental variables to be lower (i.e., 7.1%) than recorded in these previous studies, which might reflect that we separated various hydrological variables (i.e., stream width, depth, flow velocity, altitude, etc.) from environmental variables, potentially increasing the overall interactions among the three different abiotic sets.

Longitudinal patterns in fish species richness and assemblage structure have been well studied in American and European streams [47,48], as well as in China [5,24,49,50]. In wadable headwater streams, local fish species richness usually increases downstream, which is due to the general increase in stream size and habitat diversity and complexity downstream [5,47,51]. We found that fish species richness, abundance, and Shannon index increased downstream, but exhibiting maximum values in the second stream order followed by a decrease towards third stream order (Figure 6), as found also in other Chinese headwater streams [50]. A subsequently lower fish species richness, abundance and Shannon index values in the third stream order might reflect anthropogenic disturbances, most importantly construction of the Fuzikou Reservoir dam (i.e., three sampling sites in the third stream order being located less than 4 km from the dam). Besides, many rare species were found in the present study area, resulting in no apparent asymptote in species rarefaction curves (Figure 2) [52,53]. A total of 14 fish species were collected from just one or two locations, representing as much as 37.8% of all species found.

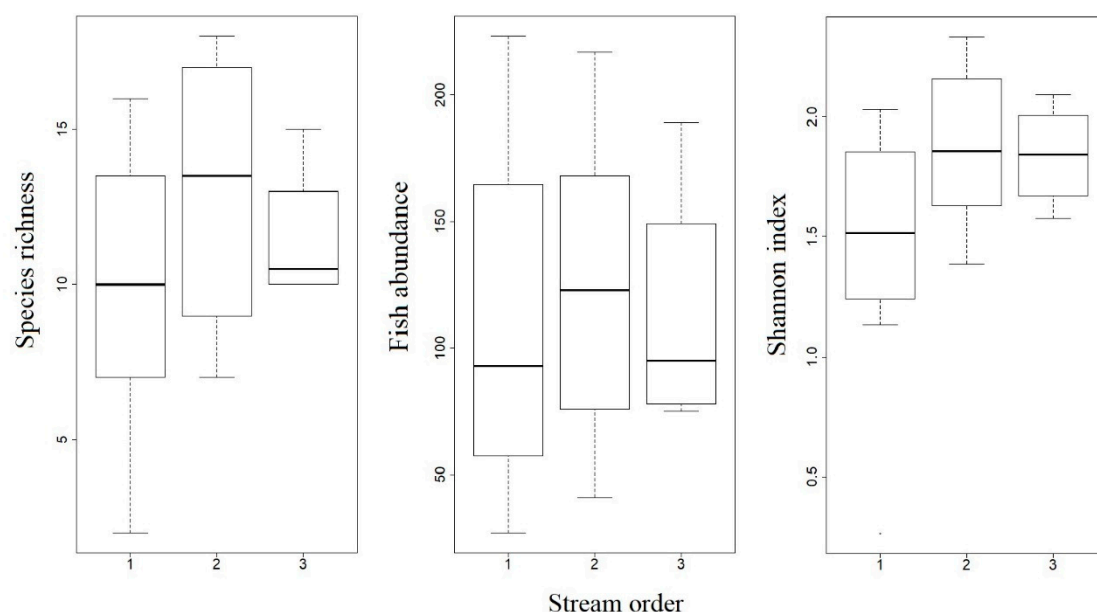


Figure 6. Species richness, fish abundance, and Shannon index in different stream orders in upstream Lijiang River.

We used two approaches to calculate the overall species turnover and its two additive components (replacement and nestedness) based on the Sørensen and the Jaccard indices. Replacement was more important than nestedness in explaining the overall species turnovers, implying that species replacement was responsible for the pattern in species turnover in the upstream Lijiang River. This indicates that the variation in species between sampling sites and the compositional difference in individual assemblages were the main drivers of diversity at a watershed scale [14,43]. The pattern in species turnover concurs with other recent findings from studies on β -diversity of stream fish assemblages [14,22,30].

Additionally, identifying the mechanisms underlying the spatial patterns of biodiversity is a major task in community ecology, especially with regards to biodiversity conservation and stream restoration [30,40,54]. The relative roles of different distances showed considerable variability for β -diversity and the additive components. For instance, Mantel tests suggested that the following rank of importance of the variables accounting for the among-site differences in species based on both indices (β_{SOR} or β_{JAC}): Environmental variables \approx hydrological variables $>$ spatial variables, while the importance for replacement in species (β_{SIM} or β_{JTU}) was: Environmental variables \approx spatial variables $>$ hydrological variables. In contrast, nestedness (β_{SNE} or β_{JNE}) was not significantly correlated with the environmental, hydrological, and spatial variables (Table 5). Our results revealed a clear distancedecay of fish assemblage dissimilarity with increasing environmental and hydrological distances (Figures 4 and 5), which indicated that maintaining various habitats continuously in streams are of vital importance.

The Fuzikou Reservoir started to be impounded in January 2018 and when filled it will have a storage capacity of $1.88 \times 10^8 \text{ m}^3$. By then, all sampling sites in the third stream order and most sampling sites in the second stream order will potentially be affected, which may reduce the fish species richness due to the increase of permanent lentic habitats and the decrease in hydrological connectivity [28,55–57]. Moreover, the dam may weaken the influence of stream spatial position on fish species richness [28], which could lead to the replacement of species turnover by nestedness [22,55].

In conclusion, the present study reveals that the importance of different abiotic variables in constructing fish assemblage composition and β -diversity patterns. Maintenance of naturally existing β -diversity patterns is of vital importance in the conservation of regional species diversity pool [58]. Our findings identified the key drivers of fish composition being the interactions between environmental, hydrological, and spatial variables, and further revealed that species replacement contributes more than nestedness in maintaining β -diversity. Our results, therefore, indicate that maintaining natural flow dynamics and habitat continuity are of vital importance for conservation of fish assemblages and diversity in headwater streams and that the dam construction in such areas, therefore, induces conservation problems.

Author Contributions: This paper received individual contributions from each author as specified: L.H., J.H. and Q.Z. developed the basic idea and designed the investigation. J.H., L.H., Y.M., Z.W. and Q.Z. performed the sampling collection and processing. L.H., Y.M., N.W. performed the data analyses. L.H. and J.H. led the original writing. E.J., Z.W. and N.W. reviewed and made corrections to improve the paper. All authors read the full paper and agreed to its publication.

Acknowledgments: This study was supported by National Natural Science Foundation of China (Grant/Award Number: 51509042), Guangxi Natural Science Foundation (Grant/Award Numbers: 2016GXNSFAA380104; 2018GXNSFAA281022), Guangxi ‘Bagui Scholar’ Construction Project (Grant/Award Number: 2016A10), and Guangxi Science and Technology Planning Project (GuiKe-AD18126018). Erik Jeppesen was supported by WATEC-Centre for Water Technology, Aarhus University. We also thank Anne Mette Poulsen for English revision, and two anonymous reviewers’ constructive comments which greatly improved our manuscript.

Conflicts of Interest: The authors declare that there is no conflict of interest regarding this publication.

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