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Role of Impoundments Created by Low-Head Dams in Affecting Fish Assemblages in Subtropical Headwater Streams in China

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Low-head dams are ubiquitous human disturbances that degrade aquatic ecosystem function worldwide. The localized effects of low-head dams have been relatively well documented; however, most previous studies have ignored the concealed process caused by native-invasive species. Based on fish assemblage data from the first-order streams of four basins in the Wannan Mountains, we used a quantitative approach to assess the effects of low-head dams on fish assemblages by distinguishing between native and native-invasive species using occurrence- and abundance-based data, respectively. Low-head dams significantly decreased native fish alpha diversity while favoring native-invasive fish. The opposite pattern between the two fish types partly masked changes in the whole fish assemblage. Meanwhile, the establishment of widespread native-invasive species and the loss of native species driven by low-head dams influenced the interaction network structure. The degree to which local fish assemblages were altered by low-head dams, i.e., beta diversity (β-diversity) was significantly higher for abundance-based approaches than for occurrence-based ones, suggesting that the latter underestimated the effects of low-head dams. Furthermore, the species contribution to β-diversity of native species was significantly higher than that of native-invasive species in both impoundments and free-flowing segments for abundance-based data. In communities or regions where native fish species are predominant, our results suggest that understanding which species contribute to β-diversity will offer new insights into the development of effective conservation strategies by taking the identities of native and native-invasive species into account.

Keywords: low-head dams, stream fish, diversity patterns, interaction networks, native-invasive species

INTRODUCTION

Habitat alteration and fragmentation resulting from anthropogenic disturbances greatly contribute to global freshwater biodiversity loss (Erős and Grant, 2015; Barbarossa et al., 2020; He et al., 2021). In a river network, headwaters have unique features and are extremely vulnerable to anthropogenic disturbances (Vannote et al., 1980; Meyer et al., 2007). Headwater streams not only export quantities of organic matter and nutrients to downstream ecosystems (Vannote et al., 1980; Eggert et al., 2012), but also provide heterogeneous habitats for a wide range of endemic species, which collectively contribute to the biodiversity of river networks (Meyer et al., 2007).

Low-head dams are ubiquitous human-made disturbances in mountainous headwater streams that are used for water supply, agricultural irrigation, and recreation (Yan et al., 2013; Jumani et al., 2020; Li et al., 2021). Dams can affect stream fish assemblages *via* multiple pathways, including blocking species dispersal between localities (Porto et al., 1999; Barbarossa et al., 2020) and changing the habitat and physicochemical conditions in streams (Smith et al., 2017; Hitchman et al., 2018; Turgeon et al., 2019). Specifically, the transformation from lotic to lentic conditions in impoundments can provide suitable conditions for potential invasive species to displace native species (Johnson et al., 2008; Liew et al., 2016; Turgeon et al., 2019). Further, habitat simplification can decrease resource and niche availability (Ruhí et al., 2016; Turgeon et al., 2019).

The localized effects of individual low-head dams have been relatively well documented, but the effects and conclusions differ among studies (see Fencl et al., 2017; Turgeon et al., 2019; Li et al., 2021). A potential reason for this inconsistency is that non-native or generalist native species can compensate for the difference in total local diversity in impoundments (Slawski et al., 2008; Liew et al., 2016; Turgeon et al., 2019). Invasions of non-native species caused by dams have a profound impact on global freshwater biodiversity and have drawn increasing attention from the public (Liew et al., 2016; Turgeon et al., 2019; Zhang et al., 2019). More importantly, in regions where native fish species are completely dominant, generalist native species that commonly occur in large streams would be potential invaders for upland streams and are usually termed as "native-invasive species" (Scott and Helfman, 2001; Dala-Corte et al., 2019). However, most previous studies on the ecological effects of low-head dams have ignored the invasion patterns of native-invasive species, as increased native diversity is generally viewed as a positive effect on ecosystem function.

Changes in species occurrences (i.e., local extinctions and colonizations) not only alter community α-diversity, but also affect community β-diversity and dynamics (Socolar et al., 2016; Erős et al., 2020), resulting in the formation of "novel communities" (Hobbs et al., 2006). A serious effect of native-invasive species invasion on native species is a change in trophic ecology through predation, competition, and the indirect effects in the context of environmental changes (Busst and Britton, 2017). Although the effects of low-head dams on habitat conditions and biodiversity have long been examined (Fencl et al., 2015, 2017; Turgeon et al., 2019), the responses in species interaction networks remain understudied. Recently, Momal et al. (2020) proposed a more robust method for inferring species interaction networks by incorporating environmental conditions (i.e., abiotic factors). Furthermore, native-invasive species typically have broad niches and environmental tolerances in headwater streams (Scott and Helfman, 2001). These native-invasive species with broad niches may contribute less to beta diversity than species with narrow or intermediate niches, because the latter species may occur in environmentally restricted conditions and contribute more to beta diversity (Heino and Grönroos, 2017). Therefore, exploring the contribution of each species to beta diversity may provide a platform for understanding the formation of community diversity patterns (Heino and Grönroos, 2017; Gavioli et al., 2019).

The Wannan Mountains of China, characterized by low-head dams becoming ubiquitous features of the landscape (Li et al., 2021), offer an excellent opportunity to evaluate the effects of low-head dams on fish assemblages. Empirical evidence has shown that spatial patterns in the ecological effects of low-head dams can be quantified effectively by selecting free-flowing reference segments (Fencl et al., 2017; Hitchman et al., 2018; Li et al., 2021). Based on fish assemblage data collected in the impoundments created by low-head dams (i.e., comparison sites) and free-flowing segments (i.e., reference sites) in the first-order streams of the Wannan Mountains, we used a quantitative approach to assess the patterns in low-head dams affecting fish assemblages by considering the distinction between native and native-invasive species. We aimed to: (1) determine the effects of low-head dams on within-community (i.e., α-diversity) and between-community (i.e., β-diversity) diversities, (2) quantify the contributions of each species to the β-diversity for each habitat type, and (3) assess the difference in species interaction networks between the habitat types.

MATERIALS AND METHODS

Study Area

The Wannan mountainous region is located in the southern part of Anhui Province, China, and is composed of the Jiuhua, Huangshan, and Tainmu Mountains, with elevations of 1,342, 1,841, and 1,787 m, respectively. The study region is influenced by a subtropical monsoon climate, where the average annual temperature is approximately 17.8°C and the average annual rainfall is approximately 2,000 mm, with precipitation occurring mostly from May to September. Streams are abundant and extremely complex in this region, with major examples including the Qingyi, Qiupu, Chang, and Xin'an streams (Li et al., 2021).

Our study included 61 low-head dams in the first-order headwater streams (stream order, Strahler, 1957) of the Wannan Mountains, of which 16, 9, 9, and 27 low-head dams were located in the Qingyi, Qiupu, Chang, and Xin'an streams, respectively, (**Figure 1**). To properly identify and understand the effects of low-head dams, two types of sampling sites were set for each dam surveyed, comprising the impoundments created by low-head dams (i.e., comparison sites) and free-flowing segments (i.e., reference sites) far away from the dams. In this study, our criteria for selecting reference sites were as follows: (1) all sites should be wadable and accessible (i.e., first-order stream); (2) since the geomorphological footprints of low-head dams are less than 2 km, the free-flowing reference segments were ensured to be at least 2 km from each dam (Fencl et al., 2015); and (3) all the reference sites were located below dams to avoid confusion; references selected above the dams would ignore the blocking effects of the dam (Li et al., 2021).

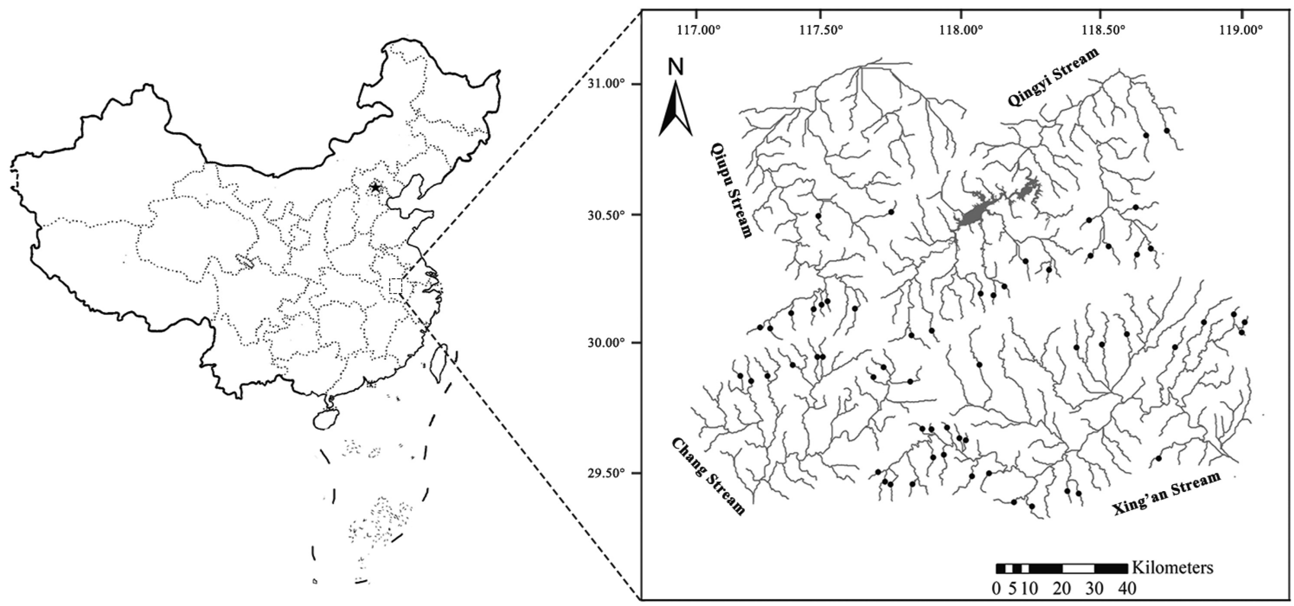

FIGURE 1 | Map showing the survey of low-head dams distributed among four basins in the Wannan Mountains, China. One impoundment area and one free-flowing segment were sampled for each dam.

Field Survey

Fish assemblages were collected from each site using a backpack electrofishing unit (CWB-2000 P, China; 12V import, and 250V export) by wading in two passes during August 2015. For more details on the fish sampling methods and sampling effects, see Li et al. (2021). The fish were identified to the species level using Nelson's (2006) classification method, counted, and released. Species were categorized as native and native-invasive species according to Scott and Helfman (2001), Chu et al. (2015); and Li et al. (2021).

The following local habitat conditions were measured at each site according to the methodology described by Li et al. (2021): (1) wetted width, (2) water depth, (3) current velocity, (4) dissolved oxygen, (5) substrate coarseness, and (6) heterogeneity. In addition, two dam metrics were used to quantify the size of each low-head dam: the dam height was estimated as the vertical height of the dam from the natural streambed to its lowest point on the dam crest, and the dam length was measured as the horizontal distance across the channel at the dam crest.

Data Statistics

The frequency of occurrence and relative abundance (*RA*) of each species were calculated for each habitat type. Species richness and abundance were regarded as the α-diversity. We used beta diversity to quantify the degree to which fish assemblages were altered by low-head dams. We calculated the temporal beta diversity (TBI) between the impoundment and free-flowing segment for each low-head dam for both occurrence and abundance data using the Sørensen dissimilarity index and its quantitative version, the Bray–Curtis dissimilarity index, respectively. The Sørensen indices, use occurrence-based data, which focus on species identities, i.e., abundant and rare species are treated equally (Koleff et al., 2003). However, abundance-based approaches give less weight to rare species, which means that they depend less on the sample size than occurrence-based approaches (Barwell et al., 2015).

For occurrence and abundance data, we obtained the fish community data (n site $\times$ p species) for two different habitat types, impoundments (*Im*) and free-flowing segments (*Fr*). We calculated the TBI between the impoundment and free-flowing reference segment for each dam. Specifically, we calculated the Sørensen ($\beta_{\text{Sør}}$) and Bray–Curtis dissimilarities (β_{BC}) for both occurrence- and abundance-based data (**Figure 2**). The TBI (i.e., beta diversity) was further partitioned into gain and loss components, based on the method of Legendre (2019). In addition, we first obtained the dissimilarity matrix ($n \times n$ site) for each habitat type separately using the Hellinger-transformed community data (n site $\times$ p species). Based on the dissimilarity matrix, we calculated the species contribution to beta diversity (SCBD) of individual species for each habitat type separately (**Figure 2**; Legendre and De Cáceres, 2013). All of the above diversity indices were calculated through the "*TBI*" function (Legendre, 2015) and "*adespatial*" package with the function "*beta.div*" (Legendre and De Cáceres, 2013) in R 4.0.2.

Using the standardized environmental variables, we employed principal component analysis (PCA) and permutational multivariate analysis of variance (PERMANOVA) to test the differences in habitat conditions between impoundments and free-flowing segments. The paired sample t-test was used to test the differences in species richness and abundance between the impoundments and free-flowing reference segments. Given that changes in the local diversities of whole species may not mean any change for native species (Turgeon et al., 2019), the

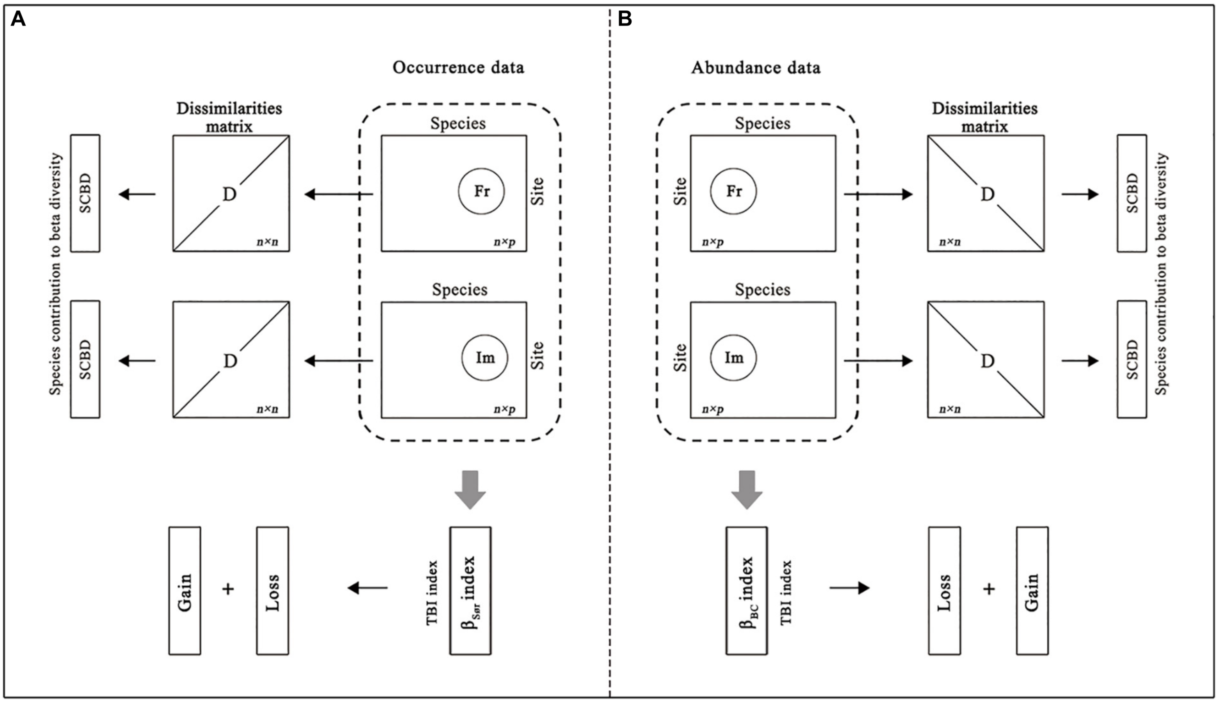

FIGURE 2 | Schematic diagram of the comparison of community data (n site × p species) for two different habitat types, impoundments (*Im*) and free-flowing segments (*Fr*). We calculated the temporal beta diversity (TBI) using the Sørensen dissimilarity index ($\beta_{Sør}$) for **(A)** occurrence data and the Bray-Curtis dissimilarity index (β_{BC}) for **(B)** abundance data. The TBI was further partitioned into gain and loss components, based on the method of Legendre (2019). In addition, we first obtained the dissimilarity matrix (n × n site) for each habitat type, and then we calculated the species contribution to beta diversity (SCBD) of individual species for each habitat type separately (adapted from Kuczynski et al., 2018).

paired samples t-test was conducted by distinguishing between native and native-invasive species. To determine whether the ecological effects of low-head dams depended on the data type, we used the paired samples t-test to test the differences in beta diversity for each dam between occurrence- and abundance-based measures. In addition, changes in local diversity associated with anthropogenic disturbances often depend on the relative number between the species lost and gained. As a complement to local diversity changes, we also used the paired samples t-test to test the differences between gain and loss components for each data type.

To quantify the contributions of native and native-invasive species to the β-diversity for each habitat type, we first obtained the SCBD of individual species that reflected the relative importance of species for a region (Legendre and De Cáceres, 2013; Heino and Grönroos, 2017). Analysis of variance was used to test the difference in SCBD values between the native and native-invasive species in impoundments and free-flowing segments. Statistical analyses were performed for occurrence- and abundance-based data separately.

Poisson log-normal (PLN) models are joint species distribution models that can be used to infer species interactions while controlling for environmental factors and sampling efforts (Chiquet et al., 2019). Following Chiquet et al. (2019), we constructed a suite of PLN models to infer the species interaction network of fish assemblages in each habitat type using environmental factors and species abundance data. Here, we built 13 PLN models that included different combinations for the free-flowing reference segments, and 17 PLN models were built for the impoundments by considering the dam height and length (**Supplementary Appendix 1**). Additionally, the sampling effort (i.e., the total number of fish caught at each site) was included in our models to control for differences in fish abundance at different sites (Chiquet et al., 2019; Brimacombe et al., 2021). The PLN models were evaluated to determine the best model using non-traditional Bayesian information criterion (BIC) and cumulative root-mean-square error. Generally, higher BIC scores indicate better-fitting models. If the PLN models showed the same BIC scores, the model with the lowest RMSE score was selected as the best model. Furthermore, we inferred the fish interaction networks for each habitat type using the EMtree method proposed by Momal et al. (2020). The EMtree method, which represents a single undirected connection between species nodes, can infer both potential direct and indirect interactions between species. A criterion for assessing the reliability of species connections is to use a higher threshold such that at least one node (i.e., species) has at least one connection to build the network (Bassett et al., 2006). We created networks with the highest threshold that remained connected. PLN models were performed using the "*PLN models*" package (Chiquet et al., 2019), and EMtree (EMtree version 1.1.0) was accomplished using the "*EMtree*" package (Momal et al., 2020).

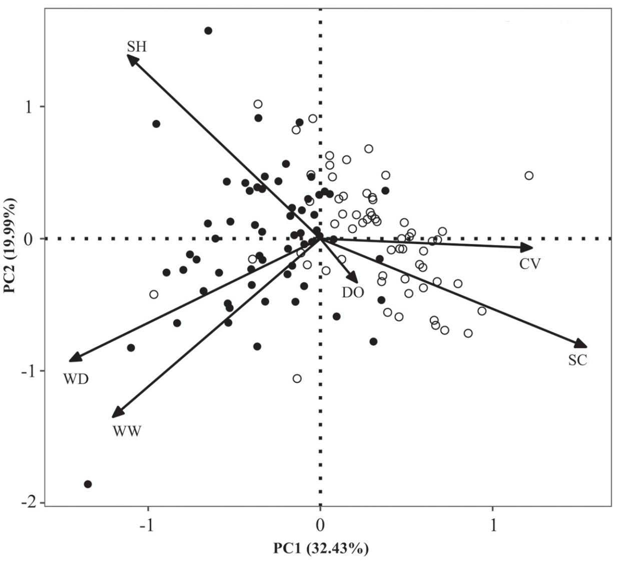

FIGURE 3 | Ordination plots of the principal component analysis (PCA) between impoundments and reference free-flowing segments. Solid and hollow circles represent the impoundments and free-flowing segments, respectively. WW, wetted width; WD, water depth; SH, substrate heterogeneity; SC, substrate coarseness; DO, dissolved oxygen; and CV, current velocity.

RESULTS

Habitat Conditions

The first and second axes of PCA explained 32.43 and 19.99% of the habitat variance, respectively. Sampling sites were scattered at the right section of the ordination plot for the impoundments and at the left section for the free-flowing segments (**Figure 3**). PERMANOVA revealed that habitat conditions significantly differed between impoundments and free-flowing segments (R^2 = 0.15, P < 0.001). Compared with free-flowing segments, conductivity, water width, and water depth were higher, and current velocity and substrate coarseness were lower in impoundments (**Figure 3**).

Community Composition

Thirty-two species belonging to 11 families and 5 orders were collected. Thirty and 29 species were collected in impoundments and free-flowing segments, respectively, of which the two habitat types shared 27 species, including 14 native and 13 native-invasive species. Additionally, two native-invasive species (*Micropercops swinhonis* and *Pelteobagrus fulvidraco*) were only collected in impoundments, whereas two native (*Leptobotia guilinensis* and *Parasinilabeo assimilis*) and one native-invasive (*Silurus asotus*) species only occurred in free-flowing segments (**Table 1**).

Changes in α- and β-Diversity

Regarding the whole assemblages, the paired samples t-test showed that the mean species abundance significantly decreased in impoundments compared to that in free-flowing segments (P < 0.05), whereas the species richness did not significantly vary between the two habitat types (**Table 1**). After distinguishing the two categories of fish assemblages, the species richness and abundance of native assemblages significantly varied between the two habitat types (P < 0.05), both of which were significantly lower in impoundments than in free-flowing segments. In addition, when only native-invasive assemblages were considered, the species richness was significantly higher in impoundments than in free-flowing segments (P < 0.05), whereas no significant difference was observed for species abundance (**Table 2**).

In addition, the mean β-diversity using occurrence-based approaches ($\beta_{sør}$) was significantly lower than that using abundance-based approaches (β_{BC}; P < 0.05). Meanwhile, the abundance-based approaches detected a higher loss component (0.34 ± 0.22) than the gain component (0.20 ± 0.19) for all assemblages (P < 0.05), but no significant difference was observed for occurrence-based approaches (**Table 3**).

Species Contribution to β-Diversity for Native and Native-Invasive Species

When using occurrence data, there was no significant difference in SCBD values between native and native-invasive species in either the impoundments or free-flowing segments (P > 0.05, **Figure 4A**). However, abundance data showed significant differences in SCBD values between native and native-invasive species in both habitat types (P < 0.05, **Figure 4B**). Specifically, the SCBD values were significantly higher for native fish species than for native-invasive ones in both the impoundments and free-flowing segments (**Figure 4B**).

Inferred Species Interaction Networks From EMtree

Within each habitat type, the best-fit PLN model was selected to infer the species interaction networks. Specifically, the PLN model with "Site name" was chosen for both habitat types, which had the highest BIC scores (free-flowing segments: -2,503.34; impoundments: -2,315.86; **Supplementary Appendix 1**). Meanwhile, native species, such as *Zacco platypus* and *Cobitis sinensis*, showed the highest betweenness centrality values (larger nodes in the figures) in the free-flowing segments (**Figure 5A**). However, native-invasive species, such as *Sarcocheilichthys parvus* and *Acheilognathus taenianalis*, achieved the highest betweenness centrality values in the impoundments (**Figure 5B**).

DISCUSSION

As a common anthropogenic disturbance in headwater streams, low-head dams may modify the local habitat in stream, including deeper water, slower flow, smaller substrate in impoundments upstream, and faster flow and larger substrate in the plunging areas downstream (Tiemann et al., 2004; Yan et al., 2013; Fencl et al., 2015). Due to the backwater effect of dams, the wetted width and water depth are greater in impoundments than that in free-flowing segments (Fencl et al., 2015). As

TABLE 1 | Species compositions, occurrence of frequency (*FO*), and relative abundance (*RA*) of fishes collected in impoundments (*Im*) and free-flowing segments (*Fr*).

Order/Family/Species	Abbreviation	Abundance data				Occurrence data			
		RA (%)		SCBD (%)		FO (%)		SCBD (%)	
		Im	*Fr*	*Im*	*Fr*	*Im*	*Fr*	*Im*	*Fr*
Cypriniformes									
Cobitidae									
Cobitis sinensis	*C. sinensis*	4.54	0.09	4.57	0.31	9.84	3.28	2.29	0.80
Cobitis rarus	*C. rarus*	6.49	4.55	9.63	9.31	39.34	29.51	9.14	6.69
*Misgurnus anguillicaudatus**	*M. anguillicaudatus*	4.04	1.94	8.03	5.03	45.90	31.15	9.67	7.04
Leptobotia guilinensis	*L. guilinensis*	0.00	0.12	0.00	0.20	0.00	4.92	0.00	1.23
Homalopteridae									
Vanmanenia stenosoma	*V. guilinensis*	2.04	9.52	3.41	8.71	31.15	72.13	6.38	8.18
Cyprinidae									
Zacco platypus	*Z. platypus*	30.50	35.54	15.30	19.56	83.61	80.33	7.20	7.75
Acrossocheilus fasciatus	*A. fasciatus*	10.74	9.07	12.81	12.02	62.30	55.74	10.84	9.58
Opasrrichthys bidens	*O. bidens*	0.42	0.30	0.78	0.45	9.84	9.84	2.10	2.18
Belligobio nummifer	*B. nummifer*	0.67	0.12	1.46	0.34	11.48	3.28	2.69	1.25
*Rhodeus ocellatus**	*R. ocellatus*	5.41	7.31	5.68	6.82	26.23	26.23	5.40	5.42
Acheilognathus chankaensis	*A. chankaensis*	0.58	0.97	0.41	1.53	1.64	3.28	0.24	0.68
Rhynchocypris oxycephalus	*R. oxycephalus*	4.95	4.91	2.48	7.18	6.56	18.03	2.34	6.12
*Carassius auratus**	*C. auratus*	2.70	0.64	3.27	0.69	16.39	11.48	4.02	2.66
*Abbottina rivulars**	*A. rivulars*	1.58	0.42	1.25	0.35	9.84	4.92	2.05	0.94
Aphyocypris chinensis	*A. chinensis*	0.42	0.85	0.83	1.64	8.20	4.92	1.57	0.94
*Sarcocheilichthys parvus**	*S. parvus*	0.54	0.61	1.29	1.09	4.92	4.92	1.00	1.17
*Squalidus argentatus**	*S. argentatus*	0.21	0.55	0.42	1.60	8.20	4.92	1.04	1.88
*Pseudorasbora parva**	*P. parva*	1.33	1.06	1.89	0.80	18.03	8.20	4.06	1.74
*Acheilognathus taenianalis**	*A. taenianalis*	0.04	0.06	0.11	0.12	1.64	1.64	0.57	0.51
Onychostoma barbatula	*O. barbatula*	0.08	0.18	0.79	0.51	1.64	6.56	0.41	2.10
Parasinilabeo assimilis	*P. assimilis*	0.00	0.09	0.00	0.10	0.00	3.28	0.00	1.03
Siluriformes									
Amblycipitidae									
Liobagrus styani	*L. styani*	0.29	1.15	0.45	1.82	4.92	16.39	0.98	4.43
Bagridae									
Pseudobagrus truncates	*P. truncates*	0.87	0.55	0.99	1.25	9.84	18.03	2.41	5.31
*Pelteobagrus fulvidraco**	*P. fulvidraco*	0.04	0.00	0.32	0.00	1.64	0.00	0.57	0.00
Siluridae									
*Silurus asotus**	*S. asotus*	0.00	0.03	0.00	0.14	0.00	1.64	0.00	0.61
Beloniformes									
Adrianichthyidae									
*Oryzias sinensis**	*O. sinensis*	0.37	0.06	0.29	0.06	3.28	1.64	0.51	0.28
Synbranchiformes									
Synbranchidae									
*Monopterus albus**	*M. albus*	0.54	0.09	0.79	0.13	11.48	4.92	2.91	1.44
Mastacembelidae									
*Sinobdella sinensis**	*S. sinensis*	0.17	0.24	0.33	0.40	6.56	9.84	1.51	2.43
Perciformes									
Odontobutidae									
*Odontobutis potamophila**	*O. potamophila*	3.54	1.46	6.20	3.29	29.51	22.95	6.40	6.28
*Micropercops swinhonis**	*M. swinhonis*	0.08	0.00	0.09	0.00	3.28	0.00	0.51	0.00
Gobiidae									
Ctenogobius sp.	*Ctenogobius* sp.	16.77	17.34	16.78	13.73	60.66	75.41	10.19	7.30
Percichthyidae									
*Siniperca chuatsi**	*S. chuatsi*	0.04	0.18	0.08	0.80	1.64	4.92	0.95	2.05

*SCBD, species contribution to beta diversity. *indicates native-invasive fish species based on Scott and Helfman (2001); Chu et al. (2015); and Liu et al. (2019).*

TABLE 2 | Spatial variations in species richness and fish abundance (mean ± standard deviation) between the impoundments (*Im*) and free-flowing segments (*Fr*) for whole, native, and native-invasive assemblages based on the paired samples *t*-test.

Assemblages types	Diversity	Habitat type		t	P
		Im	*Fr*		
Whole assemblages	Species richness	5.26 ± 2.51	5.48 ± 2.13	1.24	0.22
	Abundance	39.39 ± 30.43	54.07 ± 40.64	2.89	**0.005**
Native assemblages	Species richness	3.41 ± 1.81	4.05 ± 1.49	3.02	**0.004**
	Abundance	31.26 ± 28.75	46.15 ± 34.41	3.89	**0.000**
Native-invasive assemblages	Species richness	1.85 ± 1.92	1.43 ± 1.70	-2.73	**0.008**
	Abundance	8.13 ± 14.40	7.92 ± 16.45	-0.15	0.88

Values in bold indicate significant differences.

TABLE 3 | Variation in beta diversity (β-diversity) between the data types and the difference between losses and gains components for each data type based on paired samples *t*-test.

Diversity	Occurrence data	Abundance data	
β-diversity	0.37 ± 0.20	0.54 ± 0.21	*t* = 7.33, *P* = **0.000**
Loss	0.20 ± 0.19	0.34 ± 0.22	
Gain	0.16 ± 0.14	0.20 ± 0.19	
	t = -1.30, *P* = 0.20	*t* = -2.98, *P* = **0.004**	

Values in bold indicate significant differences.

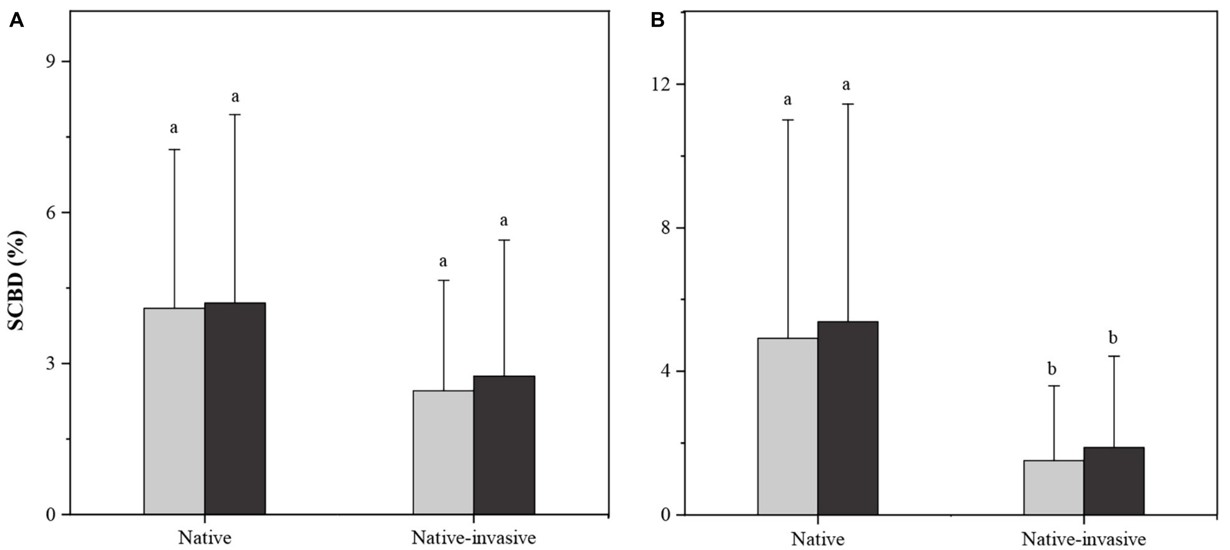

FIGURE 4 | Bar plots showing the mean ± SD of the species contribution to β-diversity (SCBD) of native species and native-invasive species in impoundments (black) and free-flowing segments (gray). Different letters represent significant differences ($P < 0.05$). **(A)** occurrence-based SCBD, **(B)** abundance-based SCBD.

the water depth increases in impoundments, current velocity is reduced and its sediment transport ability in the water column increases, generally resulting in an increase of sediment deposition (Tiemann et al., 2004; Yan et al., 2013). In this study, we found that low-head dams significantly decreased substrate coarseness, current velocity, and increased water depth, wetted width, and substrate heterogeneity in impoundments, which is consistent with the findings of other studies (Yan et al., 2013; Fencl et al., 2015).

Habitat modifications associated with anthropogenic activities not only cause the native species population to decline and even cause local extinctions, but also facilitate the invasion of alien/native-invasive species into upland streams (Slawski et al., 2008; Dala-Corte et al., 2019; Turgeon et al., 2019). A serious consequence associated with low-head dams is the addition of native-invasive species and exclusion of native species (Liew et al., 2016; Smith et al., 2017; Liu et al., 2019). Our study clearly documented that the species richness of native species significantly decreased in impoundments, while that of native-invasive species increased (**Table 2**). Changes in local diversities associated with anthropogenic activities often depend on the relative number of lost and gained species and their abundances

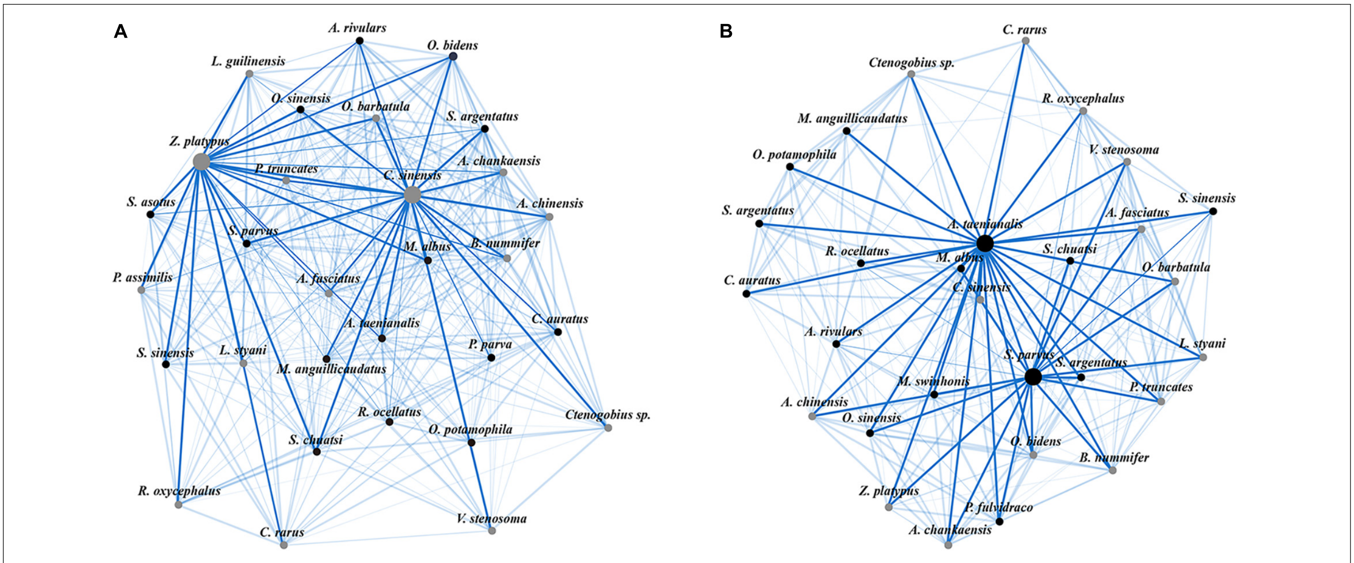

FIGURE 5 | Species interaction networks of stream fish assemblages in the free-flowing segments **(A)** and impoundments **(B)**. Each species is represented by a node, and each edge width is proportional to its conditional probability. The native (gray) and native-invasive species (black) are marked differently. For more details about species abbreviations, see **Table 1**.

(Turgeon et al., 2019). Unsurprisingly, increases in native-invasive species richness can largely compensate for the loss of native species, which could explain this pattern of changes in the total species richness in impoundments; this effect masked changes in the whole fish assemblage. When the loss of native species (abundance change: 14.89) outnumbers the gain of native-invasive species (abundance change: 0.21), changes in the species abundance patterns of whole assemblages may be driven by native species (**Table 2**). Overall, low-head dams favor native-invasive species, while negatively affecting native species with high sensitivity to environmental change (Slawski et al., 2008; Liu et al., 2019).

The variation in both the identity and abundance of species between different habitats can also affect the degree to which local fish community compositions differ (Barwell et al., 2015; Li et al., 2021). More importantly, our results showed that the local community changes in fish assemblages (i.e., the total β-diversity) associated with low-head dams were significantly higher for abundance-based approaches than for occurrence-based approaches (**Table 3**), suggesting that the latter could underestimate the localized effects of individual low-head dams. As low-head dams are less likely to result in local-scale species extinctions than large dams, most of the remaining species often experience changes in abundance (decreased, increased, or unchanged; Yan et al., 2013; Fencl et al., 2017). Previous studies have shown that changes in fish diversity patterns may be primarily driven by changes in the abundance of native species (Tiemann et al., 2004; Liu et al., 2019) in communities or regions where native-invasive species are still not predominant. If the number of shared species between communities does not change, but the abundance does, the dissimilarity index based on abundance approaches will show changes that depend on the magnitude of shifts in abundance (Cassey et al., 2008; Baselga, 2013; Legendre, 2014). In this study, 29 of the 32 species were found in both impoundments and free-flowing segments. However, besides the variations in the abundances of dominant native species, we also found that some native species (e.g., *Vanmanenia stenosoma* and *Aphyocypris chinensis*) drastically decreased and other native-invasive species (e.g., *Carassius auratus* and *Odontobutis potamophila*) markedly increased in abundance in the impoundments compared to in the free-flowing segments (**Table 1**). Therefore, the results of our study are not surprising when formerly rare species become dominant or *vice versa*, given that species abundances can change drastically enough to produce large differences relative to the changes in species composition from one community to another.

For occurrence- and abundance-based approaches, we also found that native species had higher SCBD values than native-invasive species in both habitat types, but significant variation was observed only in abundance-based approaches (**Figure 4**). Headwater streams with highly heterogeneous habitats nourish unique species assemblages (Meyer et al., 2007), where native species with small niche breadths occurring under environmentally restricted conditions may contribute more to β-diversity (Heino and Grönroos, 2017). As is generally observed in natural ecosystems, communities often exhibit heterogeneous species–abundant distributions (Magurran et al., 2011). In this study, the *RA* of most native species across sites was higher than that of native-invasive species, especially in regions where native fish species were completely predominant. Previous studies have shown that species with high total abundance across sites contribute most to the abundance-based β-diversity (Heino and Grönroos, 2017; Gavioli et al., 2019). When the identities of native and native-invasive species are considered, the high SCBD values can reveal which native-invasive species are the most abundant and widespread, whereas the low SCBD values can identify rare native species. Although some rare native species have a relatively lower contribution to β-diversity, such species may still need conservation actions owing to their local extinction risk (Gavioli et al., 2019). Meanwhile, the native-invasive species with high abundance should be strictly controlled to mitigate the ecological consequences of low-head dams.

Complex ecological networks of interacting species are crucial for maintaining biodiversity in local ecosystems and the effects of species interactions can differ either spatially or temporally (Tylianakis and Morris, 2017). Normally, a fraction of native species may primarily contribute to local community dynamics (Meyer et al., 2007), especially in headwater streams where native-invasive fish species are still not predominant. However, changes in species diversity and basal food resources resulting from habitat modifications can affect the species interaction networks (Brimacombe et al., 2021; Danet et al., 2021). Previous studies have shown that impoundments created by dams can act as powerful environmental filters that may select sets of species that are better adapted to particular habitat conditions (Liew et al., 2016). In this study, we found that the betweenness centrality of native-invasive species (i.e., omnivorous fish) was the highest in the impoundments (**Figure 5**), which reflected the importance of species for the interaction network structure. Indeed, betweenness centrality measures the ability of nodes (i.e., species) to act as a bridge in the interaction network, which can efficiently identify the "keystone species" in ecosystems (González et al., 2010; Momal et al., 2020). High betweenness centrality values of species represent high network connectance among species, which can strengthen the importance of species interaction networks (Thébault and Fontaine, 2010). In addition, the transformation of natural lotic habitats into artificial lentic habitats not only facilitate the establishment of native-invasive species (Chu et al., 2015; Liew et al., 2016), but also greatly change basal food resources (Ruhí et al., 2016). Feeding habits can play a crucial role in maintaining the stability of species interactions, and tropical streams are typically dominated by omnivorous mechanisms (Ruhí et al., 2016; Brimacombe et al., 2021). Therefore, native-invasive species (omnivorous fish) can take full advantage of niches specific to lentic habitats in impoundments, which are essential for maintaining the stability of interaction networks.

CONCLUSION

In this study, we used a quantitative approach to assess the patterns of low-head dams affecting stream fish assemblages by distinguishing between native and native-invasive species. Our results suggest that low-head dams affect stream fish diversity in two ways: by adding native-invasive species and by excluding native species typical of headwaters. However, changes in species richness and abundance not only alter the local community composition (Barwell et al., 2015; Li et al., 2021), but also affect the community stability (Brimacombe et al., 2021). Although species interactions were not directly observed in our system, we provide initial evidence that low-head dams influence the interaction network structure. Additionally, we found that occurrence-based approaches could underestimate the localized effects of low-head dams when fish assemblages differ primarily in abundance rather than species composition. SCBD values can determine which species contribute the most to β-diversity (Legendre and De Cáceres, 2013). We found that the abundance-based SCBD values were significantly higher for native fish species than for native-invasive ones in both habitat types. In communities or regions where native fish species are predominant, our results suggest that understanding which species contribute to β-diversity will offer new insights into the development of effective conservation strategies, by taking the identities of native and native-invasive species into account.

DATA AVAILABILITY STATEMENT

The original contributions presented in this study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding authors.

ETHICS STATEMENT

The animal study was reviewed and approved by the Animal Ethics Committee of the Anhui Normal University.

AUTHOR CONTRIBUTIONS

YY and QL designed the study. QL, XL, KT, CZ, and YY conducted the field and/or laboratory work. QL, XL, and CZ analyzed data. LC, HF, and YG contributed materials, reagents, and analytical tools. QL drafted the manuscript with the assistance of CZ and YY. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.916873/full#supplementary-material

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