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Article *in* River Research and Applications · March 2019

DOI: 10.1002/rra.3412

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Received: 9 November 2018 | Revised: 21 January 2019 | Accepted: 26 January 2019
DOI: 10.1002/rra.3412

RESEARCH ARTICLE

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Effects of low-head dams on fish assemblages in subtropical streams: Context dependence on species category and data type

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Funding information
Anhui Provincial Key Laboratory; Earmarked Fund for the Anhui Fishery Research System, Grant/Award Number: 2016-84; National Natural Science Foundation of China, Grant/Award Numbers: 31872251, 31500452 and 31372227

Abstract

Anthropogenic disturbances may cause cosmopolitan species to replace endemic species, which will alter both the within-community diversities and between-community similarities of stream fish assemblages. In this study, we used data collected from headwater streams within the Xin'an basin, China, to evaluate the effects of low-head dams on the alpha diversity and community similarity of fish assemblages. Our aims were to determine whether the changes in fish diversities and similarities related to dam-associated disturbance are dependent on the species category (i.e., indigenous vs. native-invasive species) or data type (i.e., occurrence-based vs. abundance-based indices). We found that low-head dams significantly decreased the alpha diversity of the indigenous species in the impoundments but increased that of the native-invasive species. However, the magnitude of this change was weakened if the two categories of fishes were not distinguished. Additionally, low-head dams significantly decreased the occurrence-based similarities of the indigenous fishes but increased those of the native-invasive fishes. Despite the positive correlation between the occurrence-based and abundance-based indices, the former significantly overestimated the community similarities. Although most pairs of communities showed the same direction of changes for the two indices, some cases presented contrasting outcomes, including “perceived homogenization” (i.e., occurrence-based differentiation but abundance-based homogenization) and “perceived differentiation.” Our results suggest the importance of distinguishing indigenous and native-invasive species and considering both occurrence-based and abundance-based indices in future research on how anthropogenic activities affect fish diversities and similarities in streams.

KEYWORDS

biotic homogenization/differentiation, low-head dam, native-invasive species, occurrence/abundance-based similarity, species replacement

1 | INTRODUCTION

Anthropogenic activities have substantially altered the distributions of faunas and floras at the global, continental, regional, and local scales, causing cosmopolitan species to replace endemic species (Olden, Comte, & Giam, 2016; Sax & Gaines, 2003). Assessing the relationships between anthropogenic disturbances and biodiversity changes is a key topic in community ecology and is the basis for biodiversity conservation and management (Dudgeon et al., 2006).

Low-head dams through the overflow release, a common anthropogenic construction in upland streams, have lower dam height. They are often built for water consumption and agricultural irrigation and may modify local habitat conditions in streams by causing such effects as water deepening, velocity changes, and substrate-size decreasing in impoundments and may further alter the composition and abundance of local fish assemblages (Gillette, Daniel, & Redd, 2016; Yan, Wang, Zhu, Chu, & Chen, 2013). The degree to which fish assemblages are affected depends on dam size and function (Li, Zhang, et al., 2018), landscape conditions (Wang, Infante, Lyons, Stewart, & Cooper, 2011), the identity of the fish species and their behaviours (Smith, Meiners, Hastings, Thomas, & Colombo, 2017), and the size of the spatial scale and diversity index values (Fencl, Mather, Smith, & Hitchman, 2017). In addition, habitat modifications associated with dam impoundment may not only impact the indigenous fishes (Marchetti & Moyle, 2001) but also create favourable conditions for some cosmopolitan fishes, including "alien invasive species" (i.e., from other biogeographic regions) and "native-invasive species" (i.e., from the same region but other locations; Chu et al., 2015; Rahel, 2010; Scott & Helfman, 2001). In general, indigenous fishes occurred in small and small-to-mid-size streams prefer specific habitat conditions, such as relatively high-gradient, cold, clear, and lotic conditions. In contrast, cosmopolitan fishes occurred in relatively large rivers prefer relatively low-gradient, warm, turbid, and lentic conditions. The two types of fishes often show different responses to anthropogenic disturbances, which indicates the necessity to distinguish them when we assess the effects of human activities on stream fish assemblages.

At the regional scale, the process of species replacement may alter the idiosyncrasy of local communities, causing biotic homogenization or differentiation in a region (Dar & Reshi, 2014). The results of studies addressing whether dams alter the similarities of river fish communities and induce biotic homogenization through the replacement of endemic species by common introduced species have been inconsistent (Clavero & Hermoso, 2011), and species replacements may also induce biotic differentiation (Olden & Poff, 2003). Furthermore, the effects may depend on the spatial/temporal scale (Marchetti, Lockwood, & Light, 2006), initial similarity (Rosenblad & Sax, 2017), and modes of species replacement (Olden & Poff, 2003). In general, two types of data are used to identify such effects, which are species occurrence and abundance data, that is, the presence–absence and number of individuals of a single species in a certain area, respectively. In addition, changes in community similarities may differ depending on whether occurrence-based or abundance-based indices are used, even for uniform data (La Sorte & McKinney, 2007), because the former account for the patterns of species compositional variation (i.e., turnover and nestedness), whereas the latter account for the patterns of abundance-based variation (i.e., balanced variation in abundance and abundance gradients, Baselga, 2017). Considering the difficulty of obtaining abundance data, occurrence-based indices have been widely adopted (Daga et al., 2015), which may result in the overestimation of community similarities because of the existence of dominant and rare species, and abundance-based indices may provide more precise information on community similarities (La Sorte & McKinney, 2007; Mckinney & La Sorte, 2007). As we know, despite the differences in their abundance from that in the free-flowing segments, lotic indigenous and lentic native-invasive fishes can coexist in the impoundments created by low-head dams (Chu et al., 2015; Yan et al., 2013). From this perspective, low-head dams may provide a platform for comparing biotic homogenization/differentiation processes between occurrence-based and abundance-based indices.

In this study, we used data collected from the impoundments created by low-head dams and the free-flowing segments within the headwater streams of the Xin'an River basin in China to examine the effects of low-head dams on the alpha diversity and community similarity of fish assemblages. Our aims were to determine whether the changes in fish diversities and similarities were dependent on the (a) species category (i.e., indigenous vs. native-invasive species) or (b) data type (i.e., occurrence-based vs. abundance-based indices).

2 | METHODS

2.1 | Study area

The Xin'an River originates from the Wugujian at the Huaiyu Mountains in China, flows east towards its confluence with Qiandao Lake, then flows through the Qiantang River, and finally pours into the East China Sea. This basin is 240 km in length and 6,500 km^2 in area. Because of the subtropical monsoon climate, the Xin'an basin is characterized by asymmetric seasonal temperature and precipitation distributions. The mean monthly air temperature during the past three decades has ranged from 4.2°C (January) to 27.9°C (July). The annual rainfall is approximately 1,800 mm/year, and approximately 80% of the rainfall occurs during the period from April to September.

2.2 | Field sampling

A total of 29 comparable low-head dams within the Xin'an River were surveyed in this study (Figure 1). All the surveyed dams were selected from the first-order (Strahler, 1957) streams. Two sampling sites were established for each dam, which were the impoundments created by the dam and a free-flowing segment (i.e., the reference site) at least 1-km upstream or downstream from the dam. A segment of 50 m in length was sampled for each impoundment and free-flowing segment. The entire impoundment was sampled when the impoundment was less than 50-m length.

During August 2015, fishes were collected using a backpack electro-fishing unit (CWB-2000 P, China; 12-V import, 250-V export) by wading in two passes. All electro-fishing passes were conducted using a uniform sampling effort, with approximately 30 min of sampling time for each 50-m segment performed by the same three persons. Fishes were identified to species (except for *Ctenogobius* fish due to the lack of identifying tools), counted, and returned to the sampling sites if alive. Voucher specimens were stored in an 8% formaldehyde solution for further identification in the laboratory.

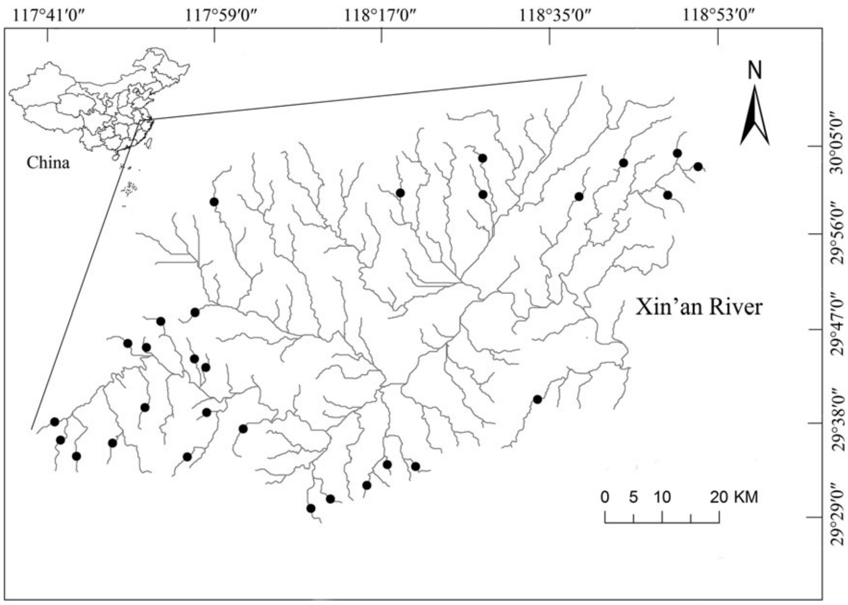

FIGURE 1 Sampling diagram of the Xin'an basin in Anhui Province, China. Black circles represent the spatial positions of the low-head dams surveyed in this study. One impoundment and one free-flowing segment were sampled for each dam

Five habitat variables were measured in each surveyed segment, including the wetted width, water depth, current velocity, substrate coarseness, and heterogeneity. The wetted width (m) was measured along three equally spaced transects that ran across the surveyed stream channel. The water depth (cm) was measured at three equally spaced points along each transect. The current velocity (m/s) was quantified at 60% of water depth at each point using FP111 (USA). The substrate was evaluated using a 1-m lead core divided into 10-cm sections based on the size-class frequency method of Bain and Stevenson (1999): particle size 0 = 0–0.059 mm, 1 = 0.06–1 mm, 2 = 2–15 mm, 3 = 16–63 mm, 4 = 64–256 mm, and 5 > 256 mm. The mean and standard deviation of the substrate values were used as the indices of substrate coarseness and heterogeneity, respectively.

2.3 | Species categories

Because all the sampling sites were established in first-order headwater streams within this study basin, the indigenous fishes are highly adapted to the lotic conditions in mountain streams. Therefore, according to Chu et al. (2015), we considered the species that naturally prefer clear, cool, high-gradient, and lotic conditions as the indigenous fishes in the small and small-to-mid-sized streams and those that naturally prefer more turbid, warmer, lowland, and lentic conditions as the native-invasive species in the larger streams.

2.4 | Data analysis

Multivariate methods were used to test the differences in habitat conditions between the impoundments and free-flowing segments (Heino, 2013). First, distance-based redundancy analysis was conducted using principal coordinate analysis based on the Euclidean distance and redundancy analysis to visualize the distribution of all sampling sites. Second, a canonical analysis of principal coordinates (CAP) supplemented the results from the principal coordinate analysis to test the average differences in habitat conditions. Third, a permutational analysis of multivariate dispersions (PERMDISP) was used to test the difference in habitat heterogeneity using the analysis of variance F-statistic. The multivariate analyses were conducted in a PRIMER 7.0 software.

The frequency of occurrence (*FO*) and the relative abundance (*RA*) were estimated for each species as $FO_i = 100\ (S_i/S)$ and $RA_i = 100\ (N_i/N)$, where S_i and S are the number of samples in which species *i* was collected and the number of the total samples, and N_i and N are the abundances of species *i* and of all the fish species, respectively (Krebs, 1989). $FO_i \geq 40\%$, $10\% \leq FO_i < 40\%$, and $FO_i < 10\%$ represent the common species, incidental species, and rare species, respectively. In addition, $RA_i \geq 10\%$ represents the dominant species (Chu et al., 2015; Krebs, 1989).

The Jaccard index based on the species presence–absence information was calculated to evaluate compositional similarity (CS_J) using the following formula: $CS_J = a/\ (a + b + c)$, where *a* is the number of shared species, and b and c are the numbers of unshared species at the two sampling sites (Rahel, 2010). Analogously, the Bray–Curtis coefficient was calculated using the species abundance data (CS_{BC}) with the formula $CS_{BC} = 1 - \sum_{i=1}^{n} | Yij - Yik | / \sum_{i=1}^{n} | (Yij + Yik) | \sum_{i=1}^{n} |Yij - Yik| / \sum_{i=1}^{n} | (Yij + Yik) |$, where *Yij* and *Yik* are the abundances of species *i* at study sites *j* and *k*, respectively (Cassey, Lockwood, Olden, & Blackburn, 2008). The above indices were calculated for composition similarity between the two sampling sites in PRIMER 7.0 software, and the calculations were independently conducted for the impoundments and free-flowing segments.

Paired-samples *t* tests were used to test the differences in alpha diversities between the impoundments and free-flowing segments based on the local species richness and fish abundance. Additionally, paired-samples *t* tests were also used to test the differences between CS_J and CS_{BC} and the between-site-type differences for CS_J and CS_{BC}.

Because we aimed to assess whether the indigenous and native-invasive fishes differed in their responses to dam perturbation, the above *t* tests were conducted for the indigenous fishes, the native-invasive fishes, and all fishes. Prior to the analysis, all variables were $\log_{10}$ (X + 1) transformed to meet the assumptions of normality and homogeneity of variance. The SPSS 20.0 software was used to perform the statistical analysis, and statistical significance was accepted at $p < 0.05$.

In addition, we calculated the difference in similarity indices ($\triangle CS$) between impoundments (CS_{Im}) and free-flowing segments (CS_{Fs}) as follows: $\triangle CS = CS_{Im} - CS_{Fs}$. $\triangle CS$ was calculated independently for CS_J and CS_{BC}. A $\triangle CS$ value greater than zero indicated the homogenization of fish assemblages in impoundments, whereas a $\triangle CS$ value less than zero indicated differentiation (Rahel, 2000).

3 | RESULTS

3.1 | Habitat conditions

The paired-samples *t* tests showed that the current velocity and substrate coarseness significantly decreased and that the wetted width and water depth significantly increased in the impoundments relative to the free-flowing segments ($p < 0.05$), whereas the substrate heterogeneity showed no significant change ($p = 0.07$; Table 1).

In the distance-based redundancy analysis, axis-1 and axis-2 explained 54.4% and 24.0% of the variance in habitat conditions, respectively. The wetted width was positively related to axis-1, and the water depth and substrate coarseness were correlated with axis-2 (Figure 2). The CAP showed no significant difference in habitat conditions between the impoundments and free-flowing segments (*trace* = 0.90, $p = 0.10$). Additionally, the PERMDISP showed that the two site types did not significantly differ in their mean habitat Euclidean distances (impoundments, 0.33 ± 0.03; free-flowing segments, 0.32 ± 0.02; $F = 0.11$, $p = 0.75$).

3.2 | Fish composition

A total of 1,883 fishes were collected, representing 24 species, eight families, and four orders. The 24 species included 13 indigenous and 11 native-invasive species (Table 2). Nineteen species were collected from the impoundments, with an average of 4.8 ± 2.3 (mean ± SD) species and 29.0 ± 18.8 fishes per sample, and 20 species were collected from the free-flowing segments, with 5.0 ± 2.0 species and

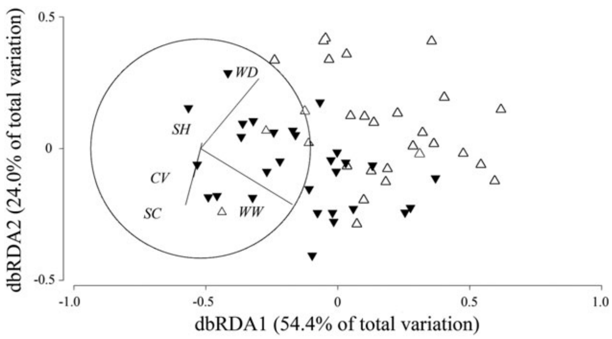

FIGURE 2 The biplot shows the distance-based redundancy analysis. Open triangles represent the impoundments, and black triangles represent the free-flowing segments. Vectors represent Spearman's correlations of the local habitat variables with the distance-based redundancy analysis axis. *CV*, *SC*, *SH*, *WD*, and *WW* represent current velocity, substrate coarseness, substrate heterogeneity, water depth, and wetted width, respectively

35.9 ± 23.4 fishes per sample. The two sampling site types shared 15 species, including eight indigenous and seven native-invasive species.

The common species were *Vanmanenia stenosoma*, *Acrossocheilus fasciatus*, *Zacco platypus*, and *Rhinogobius* sp. (*FO* > 40%). All these species were also abundance-dominant (*RA* > 10%) except for *V. stenosoma*. Three native-invasive (*Pseudorasbora parva*, *Abbottina rivularis*, and *Pelteobagrus fulvidraco*) and one indigenous species (*Belligobio nummifer*) were only found in the impoundments. Four indigenous (*Leptobotia guiiinensis*, *Phoxinus oxycephalus*, *Onychostoma barbatulum*, and *Liobagrus styani*) and one invasive species (*Monopterus albus*) were only collected from the free-flowing segments.

3.3 | Alpha diversity of fishes

The paired-samples *t* tests showed that there were no significant differences in either the species richness or abundance of all fishes between the impoundments and free-flowing segments ($p > 0.05$). However, when the two categories of species were distinguished, the species richness and abundance of indigenous fishes in the impoundments were significantly lower than those in the free-flowing segments ($p < 0.05$). In addition, for the native-invasive fishes, their abundances and species richness increased in the impoundments, but significant variation was only observed for species richness ($p = 0.02$; Table 3).

TABLE 1 Differences in habitat variables between the impoundments and the free-flowing segments based on the paired-samples *t* test

Habitat variables	*Im*	*Fs*	*t*	*p*
Wetted width	11.81 ± 7.40	7.15 ± 4.64	6.99	<0.001
Water depth	48.45 ± 21.69	31.00 ± 12.20	4.62	<0.001
Current velocity	0.20 ± 0.26	0.63 ± 0.57	−5.77	<0.001
Substrate heterogeneity	0.38 ± 0.22	0.28 ± 0.16	1.91	0.07
Substrate coarseness	2.25 ± 0.98	3.95 ± 1.24	−7.43	<0.001

TABLE 2 Species composition, frequency of occurrence, and relative abundance of fishes collected in the impoundments and free-flowing segments

	FO (%)		RA (%)	
Order/family/species	*Im*	*Fs*	*Im*	*Fs*
Cypriniformes				
Cobitidae				
Cobitis sinensis	6.90	3.45	0.24	0.19
Cobitis rarus	37.93	31.03	5.11	5.47
Misgurnus anguillicaudatus [a]	51.72	31.03	6.06	3.17
Leptobotia guiiinensis	/	6.90	/	0.19
Homalopteridae				
Vanmanenia stenosoma	41.38	72.41	4.04	8.64
Cyprinidae				
Acrossocheilus fasciatus	82.76	82.76	21.28	21.59
Zacco platypus	79.31	79.31	24.02	23.80
Carassius auratus [a]	6.90	3.45	2.14	0.29
Opsariichthys bidens	13.79	13.79	0.95	0.58
Phoxinus oxycephalus	/	6.90	/	0.19
Rhodeus ocellatus [a]	13.79	17.24	1.31	3.55
Pseudorasbora parva [a]	10.34	/	0.36	/
Sarcocheilichthys parvus [a]	10.34	10.34	1.55	1.92
Squalidus argentatus [a]	10.34	13.79	0.59	1.25
Belligobio nummifer	6.90	/	0.59	/
Onychostoma barbatulum	/	10.34	/	0.48
Aphyocypris chinensis [a]	6.90	6.90	0.71	2.50
Abbottina rivularis [a]	3.45	/	0.12	/
Siluriformes				
Bagridae				
Pseudobagrus truncatus	6.90	13.79	0.36	0.58
Pelteobagrus fulvidraco [a]	3.45	/	0.12	/
Amblycipitidae				
Liobagrus styani	/	3.45	/	0.10
Synbranchiformes				
Synbranchidae				
Monopterus albus [a]	/	3.45	/	0.10
Perciformes				
Odontobutidae				
Odontobutis potamophila [a]	27.59	10.34	4.99	0.67
Gobiidae				
Rhinogobius sp.	62.07	75.86	25.45	24.76

Note.

[a]Native-invasive fish species.

TABLE 3 Variation in species richness and fish abundance between impoundments and free-flowing segments for all fishes, indigenous fishes, and native-invasive fishes based on the paired-samples *t* test

Species types	Habitat types	Species richness	Fish abundance
All fishes	*Im* *Fs*	4.83 ± 2.27 4.97 ± 2.01	29.00 ± 18.81 35.93 ± 23.44
		$t = -0.39$, $p = 0.696$	$t = -1.80$, $p = 0.083$
Indigenous fishes	*Im* *Fs*	3.38 ± 1.68 4.00 ± 1.46	23.79 ± 17.48 31.10 ± 22.29
		$t = -2.35$, $p = 0.026$	$t = -2.08$, $p = 0.047$
Native-invasive fishes	*Im* *Fs*	1.45 ± 1.50 0.97 ± 1.43	5.21 ± 7.35 4.83 ± 9.52
		$t = 2.54$, $p = 0.017$	$t = 0.20$, $p = 0.840$

3.4 | Community similarities

According to the paired-samples *t* tests, the mean CS_J values were significantly higher than the mean CS_{BC} values ($p < 0.001$) across the two species categories and two site types and that both the CS_J and CS_{BC} of the native-invasive fishes in the impoundments were significantly higher than those in the free-flowing segments ($p < 0.001$). For the indigenous fishes, the CS_J significantly decreased in the impoundments, whereas the CS_{BC} significantly increased ($p < 0.01$). When the two species categories were not distinguished, the between-site changes in both the CS_J and CS_{BC} values agreed with those for the indigenous fishes (Table 4).

For all fishes, $\triangle CS_J$ was significantly related to $\triangle CS_{BC}$ ($r = 0.41$, $p < 0.01$, $n = 406$). Among all 406 pairwise comparisons of assemblages, 56.7% ($n = 230$) showed uniform changes between $\triangle CS_J$ and $\triangle CS_{BC}$; of these, 27.8% ($n = 113$) assemblages pairs presented homogenization ($\triangle CS > 0$; the first quadrant in Figure 3), and 28.9% ($n = 117$) showed differentiation ($\triangle CS < 0$; the third quadrant in Figure 3). However, 33.7% ($n = 137$) of assemblage pairs showed difference between $\triangle CS_J$ and $\triangle CS_{BC}$. Among which, 101 showed occurrence-based differentiation ($\triangle CS_J < 0$) and abundance-based homogenization ($\triangle CS_{BC} > 0$; the second quadrant in Figure 3), and only 36 assemblage pairs presented the opposite changes (the fourth quadrant in Figure 3).

4 | DISCUSSION

Low-head dams may substantially modify the local habitat in impoundments by causing deeper water, slower flows, and smaller substrate particles (Gillette, Tiemann, Edds, & Wildhaber, 2005; Yan et al., 2013). Additionally, as large dams do, low-head dams may decrease the spatial variation in habitat features and cause habitat homogenization in impoundments (Bu, Li, Zhu, Ling, & Yan, 2017). In this study, our CAP and PERMDISP results showed that the local habitat and spatial heterogeneity in impoundments did not significantly differ from those in free-flowing segments, and slight habitat differentiation even occurred in the former. This discrepancy may be associated with the different spatial scales at which samples were collected among the different studies. Streams are characterized by high spatial heterogeneity in habitat conditions along the upstream–downstream gradient (Vannote, Minshall, Cummins, Sedell, & Cushing, 1980; Li, Tao, Chu, & Yan, 2018; Zhang, Wan, Chu, & Yan, 2018), which suggests that the reference sites (i.e., free - flowing segments) in both Bu et al. (2017) and this study should

TABLE 4 Variation in community similarities between CS_J and CS_{BC} and between impoundments and free-flowing segments based on the paired-samples *t* test

Species types	Habitat types	CS_J	CS_{BC}	
All fishes	*Im*	0.34 ± 0.20	0.29 ± 0.18	$t = 6.22$, $p < 0.001$
	Fs	0.40 ± 0.22	0.27 ± 0.18	$t = 13.46$, $p < 0.001$
		$t' = -4.98$, $p < 0.001$	$t' = 2.49$, $p = 0.013$	
Indigenous fishes	*Im*	0.43 ± 0.25	0.32 ± 0.21	$t = 10.91$, $p < 0.001$
	Fs	0.46 ± 0.25	0.29 ± 0.19	$t = 16.25$, $p < 0.001$
		$t' = -3.08$, $p = 0.002$	$t' = 2.81$, $p = 0.005$	
Native-invasive fishes	*Im*	0.12 ± 0.21	0.09 ± 0.17	$t = 4.41$, $p < 0.001$
	Fs	0.04 ± 0.13	0.03 ± 0.11	$t = 3.90$, $p < 0.001$
		$t' = 6.51$, $p < 0.001$	$t' = 6.58$, $p < 0.001$	

Note. *t* values represent the differences between CS_J and CS_{BC}; *t'* values represent the differences between impoundments and free-flowing segments

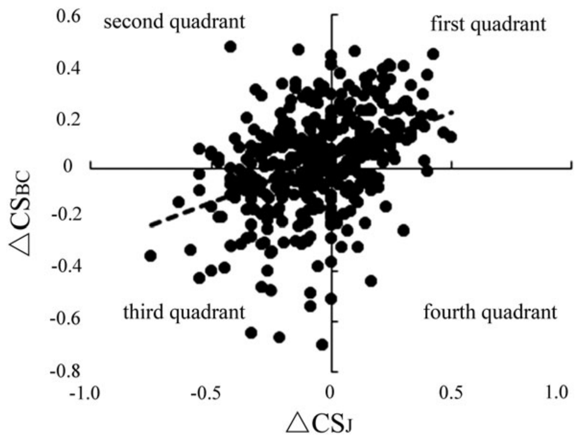

FIGURE 3 Bivariate diagram of the changes in assemblage similarities between the occurrence-based indices and abundance-based indices; black circles indicate the results from 406 pairwise comparisons, and the dashed line represents the fitted line

have different habitat dissimilarity (which can be viewed as the “initial dissimilarity” before damming).” Because Bu et al. (2017) collected samples from first-order to third-order steams, but we sampled from only the first-order streams, the “former habitat dissimilarity” observed by Bu et al. (2017) should be relatively high, but that should be relatively low in this study. In addition, the degree to which local habitat is modified by low-head dams often depends on the dam size and function (Li, Zhang, et al., 2018). Given the different sizes and function of low-head dams, the surveyed impoundments should also show habitat dissimilarity (which can be viewed as the “current dissimilarity” after damming). At a large scale, for the example of Bu et al. (2017), habitat homogenization in impoundments could occur because the former dissimilarity is relatively high (i.e., higher than the current dissimilarity). In contrast, at a smaller scale, for the example of this study, the relatively low former dissimilarity (i.e., lower than the current dissimilarity) could cause the habitat differentiation.

Habitat modifications associated with low-head dams may decrease the fitness of indigenous fishes, which will alter the fish species composition and abundance in local assemblages (Dorobek, Sullivan, & Kautza, 2015). However, habitat changes may also create favourable conditions for cosmopolitan fishes (Chu et al., 2015; Marchetti & Moyle, 2001). In this study, we found that low-head dams significantly decreased the alpha diversity of the indigenous fishes and increased that of the native-invasive fishes in impoundments, but a significant change was only observed for species richness in the latter. In terms of specific fishes, both the *FO* and *RA* of some indigenous species (e.g., *V. stenosoma*) decreased, but that of the native-invasive fishes (e.g., *Misgurnus anguillicaudatus*) increased in the impoundments relative to the free-flowing segments. The opposite changes in alpha diversity between the two fish types may explain why no significant change in alpha diversity was observed when the two fish types were not distinguished. As an example, the decrease in the mean local species richness for indigenous fishes (0.62 species) was similar to the increase in the mean local species richness for native-invasive fishes (0.48 species). Therefore, our results suggest that indigenous and native-invasive fishes differ in their responses to low-head dams (i.e., decrease/loss in indigenous species and increase/gain in invasive species), which highlights the necessity to distinguish indigenous and native-invasive species when we assess how anthropogenic disturbances affect the alpha diversity of stream fishes.

At the regional scale, both a loss in indigenous species and a gain in invasive species may alter between-community similarities (Rahel, 2002). Among pairs of communities, the loss of unshared species and/or the gain of shared species can increase community similarity and cause biotic homogenization. Conversely, biotic differentiation occurs with a loss in shared species and/or a gain in unshared species (Olden, Lockwood, & Parr, 2011; Olden & Poff, 2003). In this study, we found that low-head dams significantly decreased the mean CS_J of indigenous fishes in impoundments, indicating the differentiation of species composition. Considering that species composition changes among indigenous fishes following dam perturbations are mainly driven by species loss, composition differentiation among indigenous fishes should result from the loss of shared species. The slight habitat differentiation in the impoundments observed in this study may possibly explain the composition differentiation of indigenous fishes. However, we also found that low-head dams significantly increased the mean CS_J of native-invasive fishes in the impoundments, suggesting that composition homogenization had occurred. It has been revealed that biotic homogenization or differentiation may depend on the initial similarities of the former assemblages (Rosenblad & Sax, 2017). Furthermore, despite the occurrence of habitat homogenization, both homogenization and differentiation in species compositions may be observed in fishes occurring in impoundments. The former will occur when the initial pairwise similarity is relatively low, and the latter occurs when the initial similarity is high (Bu et al., 2017). We found that the mean CS_J for indigenous fishes in the free-flowing segments (in which similarity coefficients can be viewed as the initial similarity) was 0.46, whereas that of native-invasive fishes was less than 0.10. Therefore, we believe that the different initial similarities are responsible for the different changes in composition similarities between the indigenous and native-invasive fishes.

Due to the limitations of abundance data, most recent studies on biotic homogenization have focused on occurrence-based indices, which ignore the different weights for rare and abundance-dominant species (reviewed in Olden et al., 2016). We found that the mean CS_J was significantly higher than the mean CS_{BC}, indicating an overestimation of similarity by the occurrence-based indices (Cassey et al., 2008). We also found that although the native-invasive fishes showed homogenization based on both the occurrence-based and abundance-based indices, the indigenous fishes presented occurrence-based differentiation but abundance-based homogenization. McKinney and La Sorte (2007) introduced the perceived homogenization concept to describe this mismatch between occurrence-based differentiation and abundance-based homogenization. Compared with rare species, abundance-dominant species are easily perceived by humans. If abundance-dominant species are uniform in abundance across assemblages, pairwise comparisons of assemblages will be considered to be more similar to one another despite the fact that the identity of rare species may be quite different (Cassey et al., 2008). We consider that, for indigenous fishes in impoundments, the unshared rare species may contribute to occurrence-based differentiation and that the shared dominant species can cause abundance-based homogenization. In this study, we found that some rare indigenous species (e.g., *L. guiiinensis* and *Pseudobagrus truncatus*; less than 5% of the RA) decreased in their frequencies of occurrence in impoundments compared with those in free-flowing segments. However, the dominant species (e.g., *A. fasciatus*, *Z. platypus*, and *R.* sp.; more than 20% of the RA) did not show an obvious change in the FO between the impoundments and the free-flowing segments. We found that approximately 25% of all 406 fish assemblage pairs presented occurrence-based differentiation and abundance-based homogenization, which can also be explained by the perceived homogenization concept. Additionally, we found that approximately 9% of the assemblage pairs showed occurrence-based homogenization and abundance-based differentiation, which can be explained by the perceived differentiation concept offered by Cassey et al. (2008). The loss of unshared indigenous species and/or the gain of shared invasive species can cause occurrence-based homogenization, whereas the abundance differentiation of the formerly shared dominant species can cause abundance-based differentiation. In addition, we found that more than half of all 406 paired assemblages showed similar trends between changes in the occurrence-based indices and changes in the abundance-based indices. Similar results were also found by McKinney and Lockwood (2005) and Cassey et al. (2008). The differences in the occurrence-based and abundance-based indices may be limited because the index values are mainly determined by the number of shared species in the assemblages (Koleff, Gaston, & Lennon, 2003).

In conclusion, our results suggest that low-head dams significantly decrease the alpha diversity of indigenous fishes but increase that of native-invasive fishes; whereas, the changes in alpha diversity will be weakened when the two fish categories are not distinguished. Due to their different initial similarities, biotic differentiation occurs for indigenous fishes, and biotic homogenization occurs for native-invasive fishes. Although most pairs of assemblages show the uniform changes between the occurrence-based and the abundance-based indices, partial pairs present the contrasting outcomes for the two indices, including the perceived homogenization (i.e., occurrence-based differentiation but abundance-based homogenization) and the perceived differentiation (i.e., occurrence-based homogenization but abundance-based differentiation). Therefore, in future, to accurately assess how anthropogenic disturbances affect species diversities of stream fishes, we should not only distinguish the indigenous and native-invasive fishes but take into account occurrence-based and abundance-based methods.

ACKNOWLEDGEMENTS

This study was funded by the National Natural Science Foundation of China (31372227, 31500452, and 31872251) and the Earmarked Fund for the Anhui Fishery Research System (2016-84). We acknowledge the support from the Anhui Provincial Key Laboratory of the Conservation and Exploitation of Biological Resources, and we also thank all colleagues for their performance of field surveys and fish identifications. This research was approved by the Anhui Normal University Animal Ethic Committee.

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How to cite this article: Liu Y, Wang Y, Zhu Q, et al. Effects of low-head dams on fish assemblages in subtropical streams: Context dependence on species category and data type. *River Res Applic*. 2019;35:396–404. https://doi.org/10.1002/rra.3412