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# Large-scale cascaded dam constructions drive taxonomic and phylogenetic differentiation of fish fauna in the Lancang River, China

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Received: 9 October 2018 / Accepted: 30 August 2019  
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**Abstract** The establishment of widespread non-native species and the loss of native species driven by multiple anthropogenic disturbances have led to a dramatic reconfiguration of current biodiversity. Trends towards homogenization or differentiation of fish fauna due to the impact of both introductions and extirpations on the taxonomic facet of biodiversity have been observed worldwide, while such effects on the phylogenetic facet have seldom been quantified. Here, we measured the spatio-temporal changes in taxonomic and phylogenetic dissimilarities of fish assemblages among 12 mainstream reaches of the Lancang River against the background of large-scale cascaded dam construction. We found that both the taxonomic and phylogenetic structures of fish assemblages exhibited heterogeneity due to the reduction in

the distribution area of common native species and imbalanced invasion by non-native species, which resulted from habitat fragmentation caused by the large-scale cascaded dam construction. Furthermore, changes in taxonomic and phylogenetic dissimilarities were highly correlated. Patterns of fish assemblage based on both taxonomic and phylogenetic structures showed clear spatio-temporal differences due to the imbalance of regional changes, namely, small changes upstream and large changes downstream. This study revealed that taxonomic and phylogenetic dissimilarities could increase in dam-fragmented habitats via imbalanced native species loss and non-native species invasion. Therefore, the risk of a generally positive interpretation of taxonomic and phylogenetic differentiation is highlighted, which should be highly important to ecologists and conservationists.

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**Keywords** Beta diversity · Taxonomic  
differentiation · Phylogenetic differentiation ·  
Hydropower construction · Non-native invasions ·  
International River

## Introduction

The construction and operation of dams for hydroelectric waterpower facilities are widely known to have negative effects on lotic biodiversity, leading to a series of undesirable responses in riverine ecosystems

(Humborg et al. 1997; Liermann et al. 2012; Santos et al. 2017; Wang et al. 2019). The influence of dams on fish diversity has become a primary environmental problem (Cooper et al. 2016; Ziv et al. 2012). Dams obstruct the dispersal and migration of organisms and destroy spawning habitats for certain species, both of which are directly linked to the loss of both populations and species of freshwater fishes (Gao et al. 2013; Nilsson et al. 2005; Petesse and Petrere 2012). In addition, human activities facilitate the establishment of non-native species via habitat transformation (Leprieur et al. 2008), and reservoirs are ideal pathways for the dispersal of non-native species (Havel et al. 2005). Changes in habitats have increased the risk of extirpation of specialists and invasion by non-native species (Moyle and Mount 2007; Rahel 2002). Studies have shown that environmental modifications provide more suitable conditions for non-native species, e.g., competitive advantages over native fishes for food, space and other resources, and tend to result in the extirpation of endemic species (Ding et al. 2017; Poff et al. 2007; Song et al. 2016).

The establishment of widespread non-native species and the loss of native species have affected the species richness and biological distinctiveness of communities worldwide and have led to a dramatic reconfiguration of the current biodiversity (Dudgeon and Smith 2006; Raghavan et al. 2008; Toussaint et al. 2014). Changes in species composition driven by the combined effects of invasions and extinctions can result in decreasing (i.e., homogenization), increasing (i.e., differentiation), or unchanged assemblage dissimilarities (Cassey et al. 2006; Olden and Poff 2003). Examining present-day and potential future variations in patterns of biodiversity can provide valuable information for prioritizing both species and areas essential for conservation (Olden and Poff 2004).

For more than a decade, trends towards taxonomic homogenization or differentiation driven by human-mediated disturbances such as habitat degradation, species invasion and hydroelectric development have been confirmed for fish assemblages in various freshwater ecosystems across the globe (Daga et al. 2015; Rahel 2000; Vileger et al. 2014; Vitule et al. 2012). In contrast, the impact of introductions and extirpations on the phylogenetic facet of biodiversity has seldom been quantified. The phylogenetic structure of an assemblage represents the evolutionary history of its members and reflects the diversity of its

genetic and thus morphological, physiological and behavioral characteristics (Webb et al. 2002). Phylogenies can also be used to predict the level of ecosystem function and the delivery of services and to guide conservation prioritization (Cadotte et al. 2008; Faith et al. 2010; Mouillot et al. 2011). Invasions and extinctions are not random processes from a phylogenetic perspective but are usually related to the life-history traits of species (Freville et al. 2007; Winter et al. 2009). Extinctions usually affect specialized endemic or rare species from species-poor families, while successful invaders are often ecological generalists that have wide distribution ranges and belong to species-rich families (Gaston 1998; Pysek et al. 2009; Vamosi and Wilson 2008). Hence, both the loss of native species and the gain of common non-native species should result in pronounced changes in phylogenetic structure (alpha diversity) and dissimilarity (beta diversity) between different regions. Therefore, assessing the level of phylogenetic dissimilarity can provide additional information that allows improved understanding of the mechanisms underlying changes in biodiversity patterns by connecting local processes with more regional processes, including trait evolution, speciation and dispersal (Bryant et al. 2008; Graham and Fine 2008; Leprieur et al. 2012; Morlon et al. 2011).

Previous reports of homogenization in fish fauna have involved mainly regional research, such as studies involving fish assemblages across rivers in Europe (Vileger et al. 2014), isolated plateau lakes (Ding et al. 2017; Jiang et al. 2019) and rivers (Liu et al. 2017) in China, and rivers in the USA (Cooper et al. 2017). However, studies investigating changes in fish biodiversity within a single river with cascade dams over time have focused almost exclusively on species richness, abundance and composition/structure (Cella-Ribeiro et al. 2017; Cheng et al. 2015; Kang et al. 2009), but very little is known about the change in beta diversity in terms of both taxonomic and phylogenetic facets. Cascade dams lead to habitat fragmentation, resulting in a loss of hydrological connectivity and marked alterations of fish assemblages via native extirpations and non-native invasions (Petesse and Petrere 2012). Therefore, there is a need to quantify multi-faceted changes in the dissimilarity of fish faunas in different reaches of cascade-dammed rivers.

Zhang et al. (2018) recently investigated changes in the taxonomic and phylogenetic alpha diversity of fish assemblages in the mainstream of the Lancang River (LCR), a large transboundary river that has experienced cascaded hydroelectric development and introductions of non-native species (Chen et al. 2015; Fan et al. 2015; Kang et al. 2009). Zhang et al. (2018) reported a significant loss of native species but an increase in phylogenetic alpha diversity over time. In the present study, we expand on this idea and investigate how the hydropower development and non-native invasions in the same 12 mainstream reaches have modified taxonomic and phylogenetic dissimilarities among reaches from a historical period to the current period. With this aim, we first determined the change trends in the taxonomic and phylogenetic facets of biodiversity. We then assessed the relationships between the changes in taxonomic and phylogenetic dissimilarities. Finally, we identified the determinants of the changes in taxonomic and phylogenetic dissimilarities.

## Materials and methods

### Study area

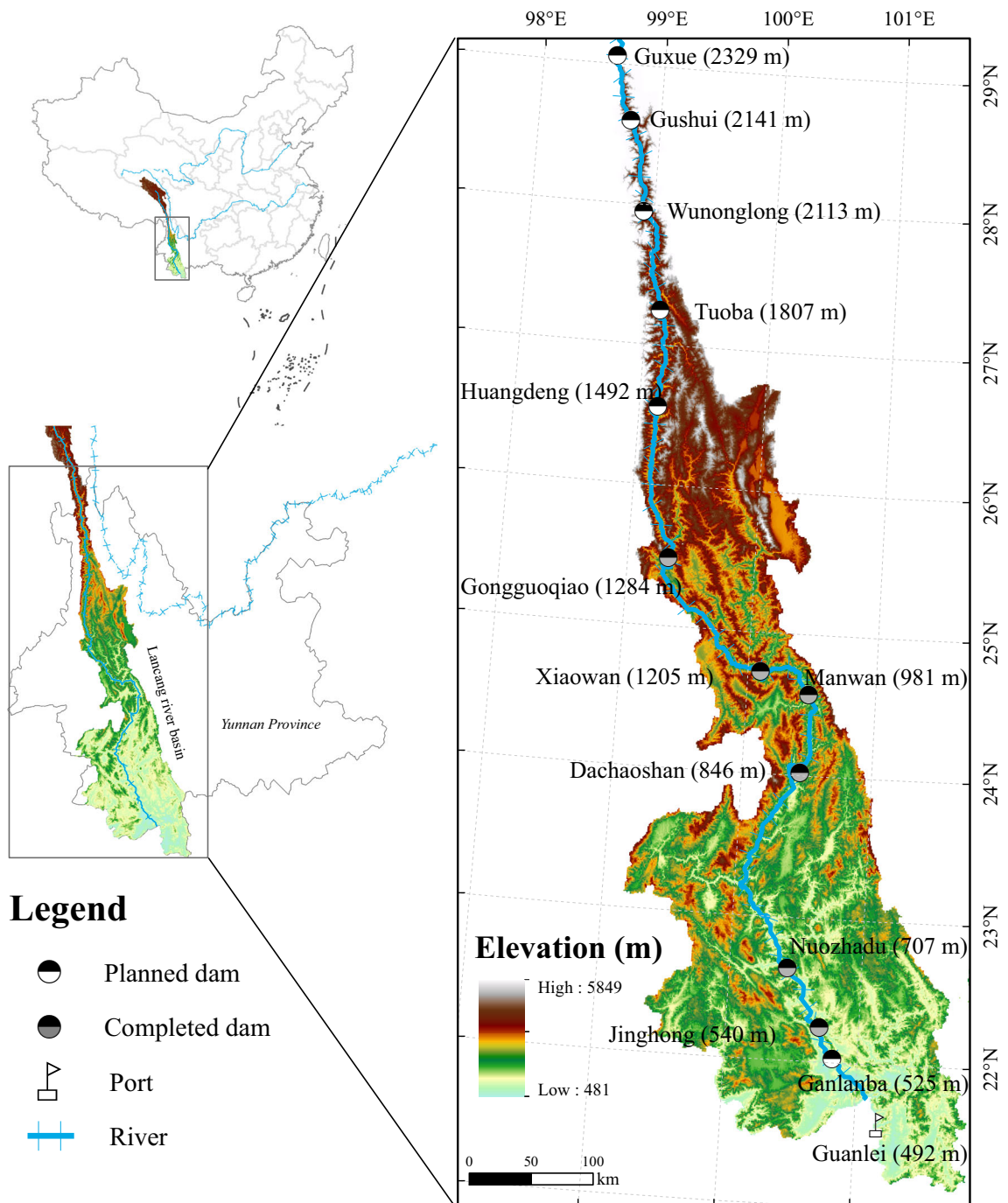
With a mainstream length of 2129 km, the LCR originates in the Tanggula Mountains on the Qinghai-Tibet Plateau and flows through Qinghai, Tibet and Yunnan provinces in China (He and Tang 2000). As a longitudinal river situated in western China, the LCR provides particular and diverse habitats for fishes (Baran et al. 2012). From the headwater of the LCR to the Nan'a River estuary, the riverbed altitude decreases from 5060 to 465 m, and the climate type changes from subarctic to temperate, subtropical and tropical (He 1995). Such complex and diverse environmental conditions support a high level of aquatic biodiversity in the river (Baran et al. 2012; Valbo-Jorgensen et al. 2009). The upstream LCR is characterized by high altitudes and low temperatures, and the fish assemblages consist mainly of cold-water species in the subfamilies Schizothoracinae (Cyprinidae) and Glyptosterninae (Sisoridae) and in the genus *Triplophysa* (Cobitidae) (Chen 2013; Guo et al. 2014). However, the downstream reaches are distributed mainly at low altitudes or in tropical mountains, and the representative fishes are warm-water fishes of

higher taxa such as the Barbinae, Labeoninae, Botiinae and the orders Siluriformes, Cyprinodontiformes, Perciformes and Tetraodontiformes (Liu et al. 2011). From upstream to downstream, the fish faunal composition gradually changes from simple to complex (Guo et al. 2014; Liu et al. 2011).

However, increasing human impacts, e.g., construction of cascade dams, introduction of non-native species, water pollution and overfishing, are threatening fish assemblages in this river basin (Deng and Zeng 2004; Fan et al. 2015; He et al. 2007; Kang et al. 2009). A total of 21 hydropower dams were planned for the free-flowing main stream of the LCR in China, six of which have already been constructed, i.e., the Manwan Dam reservoir began filling in 1993, the Dachaoshan Dam began in 2001, the Jinghong Dam in 2008, the Xiaowan Dam in 2008, the Gongguoqiao Dam in 2011, and the Nuozhadu Dam in 2011. To assess the taxonomic and phylogenetic dissimilarities between different reaches, we selected 12 planned or operational dams as the site boundaries to divide the LCR from the Guxue Dam to Guanlei Port into 12 reaches, i.e., Guxue-Gushui, Gushui-Wunonglong, Wunonglong-Tuoba, Tuoba-Huangdeng, Huangdeng-Gongguoqiao, Gongguoqiao-Xiaowan, Xiaowan-Manwan, Manwan-Dachaoshan, Dachaoshan-Nuozhadu, Nuozhadu-Jinghong, Jinghong-Ganlanba and Ganlanba-Guanlei (Fig. 1). The upper 5 reaches (from Guxue-Gushui to Huangdeng-Gongguoqiao, altitude range: 2329–1284 m) that were not affected by the dams (the planned dams were not in construction until 2015) were defined as upstream regions. The lower 7 reaches (from Gongguoqiao-Xiaowan to Ganlanba-Guanlei, altitude range: 1284–492 m) that have been under the influence of hydropower stations were defined as downstream regions.

### Data collection

Fish species lists for the 12 reaches were constructed on the basis of published literature (Guo et al. 2014; Kang et al. 2010; Lei 2012; Liu et al. 2011), books (Chen 2013; Chu and Chen 1989; Chu and Chen 1990), scientific reports (environmental impact statements before and after the construction of each dam; Zhang 2001), information within online databases and data from our sampling surveys from 2008 to 2015. All scientific names were revised according to “Fishes of the World” (Nelson 2006). We grouped these data into



**Fig. 1** Study area. The 12 completed or planned dams selected as the region boundaries are displayed in the diagram, and the elevation information of each dam is shown in parentheses. The

historical (before the 1990s) and current (2006–2015) periods to quantify the temporal changes in taxonomic and phylogenetic dissimilarities. In reaches with

upstream reaches are from Guxue to Gongguoqiao; the downstream are from Gongguoqiao to Guanlei

operational dams, fish lists collected from each reservoir that had begun being filled prior to 2015 were used as current data. Enough fish collection

efforts were made in each reach to avoid data discrepancies caused by insufficient sampling in the current period. In both the historical and current periods, at least four-season investigations were carried out for each reach. Considering the varying water depth and flow velocity at different sampling sites of each reach, multiple types of fishing gears, including cast nets (mesh size 1 cm), drift gillnets (stretched mesh size 2.5 cm) and ground cages, were used during the surveys. We classified and imaged all specimens in the field and brought a few back to the laboratory for further research to avoid sampling effects on the fish community structure.

### Measuring taxonomic and phylogenetic dissimilarities

Beta diversity is a measure of the heterogeneity in assemblage composition between localities (Anderson et al. 2011) and can be used to examine multiple facets (i.e., taxonomic, phylogenetic and functional) of biodiversity (Villegier et al. 2013). These multiple-facet dissimilarities account for two additive components: the turnover component (replacement between assemblages) and the nestedness-resultant component (difference in richness between assemblages) (Baselga

$$\beta_{\text{sne.tax}} = \frac{\max(b, c) - \min(b, c)}{2a + b + c} \times \frac{a}{a + \min(b, c)} \quad (3)$$

where  $a$  is the number of species shared by two assemblages, and  $b$  and  $c$  are the number of species unique to each assemblage.

To calculate the phylogenetic dissimilarity, we used the PhyloSor beta diversity index, a derivation of the Sørensen dissimilarity index that is used to measure the proportion of total branch length shared among communities (Faith et al. 2009). According to Leprieur et al. (2012),  $PD_{Tot}$  represents the total branch length of the phylogenetic tree that contains all species present in both communities, and  $PD_k$  and  $PD_j$  are the total branch lengths of all species in each community. Hence,  $a = PD_k + PD_j - PD_{Tot}$  represents the branch length shared by two assemblages, and  $b = PD_{Tot} - PD_k$  and  $c = PD_{Tot} - PD_j$  represent the branch lengths unique to each assemblage. The phylogenetic dissimilarity and its turnover and nestedness components are formulated as follows:

$$\beta_{\text{sor.phy}} = \frac{2PD_{Tot} - PD_k - PD_j}{PD_k + PD_j} \quad (4)$$

$$\beta_{\text{sim.phy}} = \frac{\min(PD_{Tot} - PD_k, PD_{Tot} - PD_j)}{PD_k + PD_j - PD_{Tot} + \min(PD_{Tot} - PD_k, PD_{Tot} - PD_j)} \quad (5)$$

2010; Leprieur et al. 2012). Taxonomic dissimilarity was measured using the Sørensen index ( $\beta_{\text{sor}}$ ), and the taxonomic turnover ( $\beta_{\text{sim}}$ ) and nestedness ( $\beta_{\text{sne}}$ ) components were quantified in accordance with the beta diversity partitioning framework proposed by Baselga (2010); Baselga (2012). The taxonomic dissimilarity and its turnover and nestedness components are formulated as follows:

$$\beta_{\text{sor.tax}} = \frac{b + c}{2a + b + c} \quad (1)$$

$$\beta_{\text{sim.tax}} = \frac{\min(b, c)}{a + \min(b, c)} \quad (2)$$

$$\beta_{\text{sne.phy}} = \beta_{\text{sor.phy}} - \beta_{\text{sim.phy}} \quad (6)$$

### Statistical analysis

Indices of taxonomic and phylogenetic dissimilarity between each pair of fish assemblages were computed for each historical or current species composition. Paired  $t$  tests were applied to examine the temporal changes in taxonomic and phylogenetic dissimilarities and their turnover and nestedness components separately.



Using the Mantel permutation test, we then investigated the relationships between changes in taxonomic and phylogenetic dissimilarities. We assessed the changes in phylogenetic and taxonomic overall dissimilarities and their changes in turnover and nestedness components separately. The significance of each Pearson correlation was calculated using the Mantel test, with 9999 permutations (Nekola and White 1999).

To determine the drivers of changes in taxonomic and phylogenetic dissimilarities, we used multiple regressions on distance matrices (MRMs) (Lichstein 2007); the historical level of dissimilarity, total number of native species extirpations and total number of species introductions in each pair of reaches served as explanatory matrices. *P* values for the MRM models were obtained by comparing each calculated regression coefficient with a distribution of 10,000 permuted values.

Non-metric multidimensional scaling (nMDS) was then performed separately on the basis of the taxonomic and phylogenetic dissimilarity matrices to visualize the patterns of fish assemblages from the historical period to the current period. Two-way permutational analysis of variance (two-way PERMANOVA) with 999 permutations was used to investigate the effects of region (upstream and downstream reaches) and time (historical and current periods) on variance in fish assemblages.

We performed nMDS and two-way PERMANOVA via PRIMER version 6 (Clarke and Gorley 2006) and the PERMANOVA+ package (Anderson et al. 2008). All other analyses were performed by the use of R (R Development Core team, 2018), including the dissimilarity matrix calculations via the *betapart* package (Baselga 2012), Mantel tests via the *vegan* package (Canty and Ripley 2012) and MRM analyses via the *ecodist* package (Goslee and Urban 2007). In our study, analyses were run on both the entire fish assemblages (including native and non-native species) and assemblages including only native fish. Considering only the entire assemblages (native and non-native species) may induce a blurring effect of non-native invasions, as the introductions of non-native species could compensate in part for the loss of alpha and beta diversity due to the extirpation of native species (Ding et al. 2017; Toussaint et al. 2014).

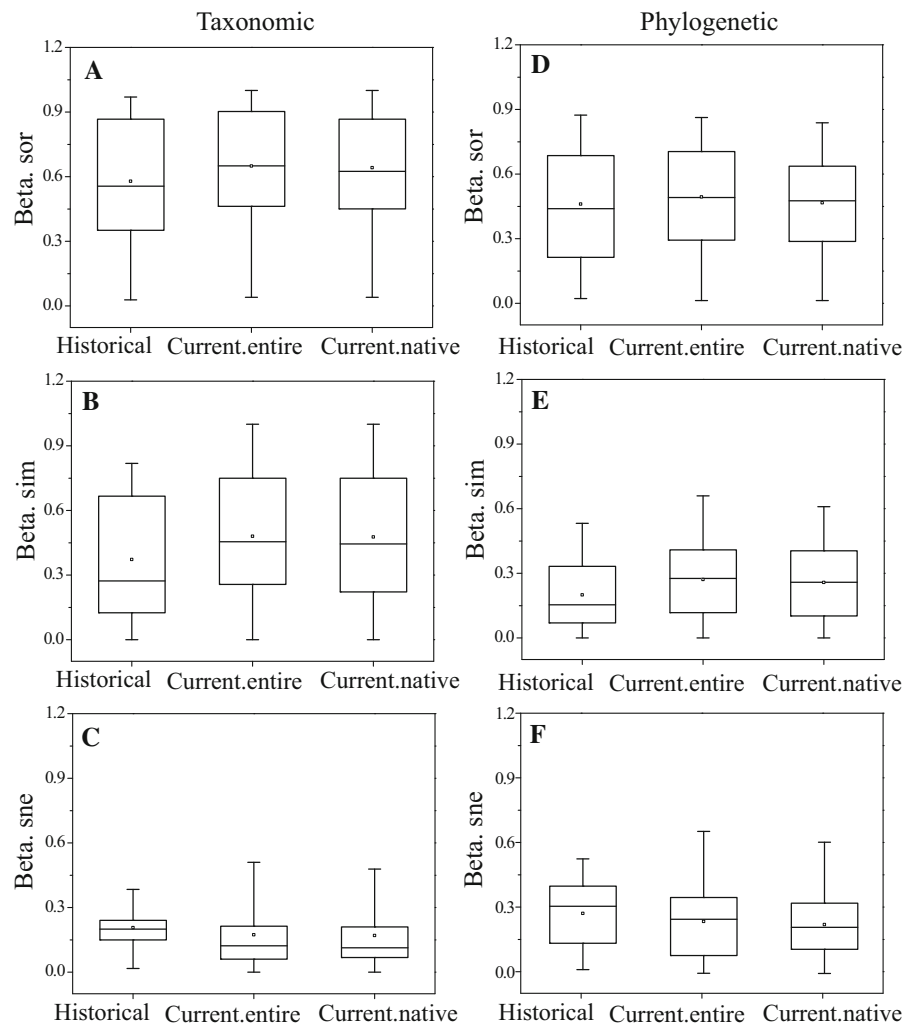
## Result

### Temporal changes in taxonomic and phylogenetic dissimilarities

In the historical period, the 12 reaches contained 162 fish species belonging to 89 genera, 21 families, 8 orders and 2 divisions. Among these species, Cypriniformes (72.2%) and Cyprinidae (43.8%) were the most species-rich order and family, respectively. In the current period, 135 species (including 22 non-native species) belonging to 88 genera (15 non-native), 24 families (5 non-native), 9 orders (3 non-native) and 1 division were found. Between the historical period and the current period, an average of 23.2 native species were extirpated per reach, whereas an average of 6.2 non-native species were established. In the five upstream reaches, 4 species, 2 genera were extirpated from the native species pool, and 4 non-native species (belonging to 4 genera and 1 family) were established. In the seven downstream reaches, 49 species, 13 genera, 2 families, 2 orders and 1 division were extirpated from the native species pool, and 21 non-native species (14 genera, 5 families and 3 orders) were established (Appendix 1).

The historical mean value of the taxonomic dissimilarity of fish assemblages among the 12 reaches was 0.58 (range 0.03–0.97; Fig. 2a), mainly because of its turnover component (mean value: 0.37, accounting for 63.8%; Fig. 2b). In the current period, the mean value of the taxonomic dissimilarity among the 12 reaches was 0.65 (range 0.04–1.00) for the entire assemblages and 0.64 (range 0.04–1.00) for the native assemblages (Fig. 2a). Considering the temporal changes, the  $\beta_{\text{sor,tax}}$  increased on average by 0.07 (12.1%) for the entire assemblages and 0.06 (10.3%) for the native assemblages, respectively (Table 1); the assemblages exhibited significant taxonomic differentiation across the 12 reaches (paired *t* test:  $t = -6.09$ ,  $P < 0.001$  for entire assemblages and  $t = -5.29$ ,  $P < 0.001$  for native assemblages; Table 2). Furthermore, these taxonomic differentiation trends occurred mainly in pairs of downstream reaches (D–D pairs) (mean increase of 0.14 for entire assemblages and 0.16 for native assemblages, Table 1). In addition, the increase in taxonomic dissimilarity was mainly due to the increase in its turnover component, whereas the nestedness component decreased (Fig. 2b, c; Table 1).

**Fig. 2** Boxplots of the different components of taxonomic and phylogenetic dissimilarities for historical period and current period on the basis of entire and native assemblages. The bottom and top of the box represent the 25th and 75th percentiles, the middle line represents the median, the middle open squares represent average values, and the whiskers represent 1.5 interquartile ranges beyond the boxes. The results of paired *t* tests are provided in Table 2



However, the historical value of phylogenetic dissimilarity among the 12 reaches was lower than that of taxonomic facets, with a mean value of 0.48 (range 0.02–0.87; Fig. 2d). Compared with the taxonomic dissimilarity component, the phylogenetic nestedness component (mean value: 0.28, 58.3%) contributed more (Fig. 2f). In the current period, the mean value of the phylogenetic dissimilarity was 0.51 (range 0.02–0.87; Fig. 2d) for the entire assemblages and 0.48 (range 0.01–0.83; Fig. 2d) for the native assemblages. Considering the temporal changes, the  $\beta_{\text{sor.phy}}$  increased by an average of 0.03 (6.3%) for the entire assemblages and 0.006 (1.3%) for the native assemblages, respectively (Table 1), showing a weaker trend of differentiation than that of taxonomic dissimilarity (paired *t* test:  $t = -3.02$ ,  $P = 0.004$  for

entire assemblages and  $t = -0.50$ ,  $P > 0.05$  for native assemblages; Table 2). The phylogenetic differentiation also occurred mainly in the D–D pairs (mean increase of 0.09 for entire assemblages and 0.10 for native assemblages; Table 1), and the increase in phylogenetic dissimilarity was also due to the increase in its turnover component (Fig. 2e).

#### Correlations between changes in taxonomic dissimilarity and phylogenetic dissimilarity

Changes in taxonomic dissimilarity and its turnover and nestedness components were highly correlated with their corresponding changes in phylogenetic facet for both entire and native assemblages (all Mantel tests:  $r > 0.80$ ,  $P < 0.001$ ; Fig. 3). Apart from



**Table 1** Temporal changes in taxonomic and phylogenetic dissimilarities from the historical period to the current period for entire assemblages and native assemblages

	Changes in taxonomic dissimilarity			Changes in phylogenetic dissimilarity		
	$\beta_{\text{sor.tax}}$	$\beta_{\text{sim.tax}}$	$\beta_{\text{sne.tax}}$	$\beta_{\text{sor.phy}}$	$\beta_{\text{sim.phy}}$	$\beta_{\text{sne.phy}}$
<i>Entire</i>						
All pairs	0.07 ± 0.09	0.11 ± 0.11	− 0.04 ± 0.11	0.03 ± 0.09	0.08 ± 0.09	− 0.04 ± 0.10
U–U pairs	0.06 ± 0.08	0.002 ± 0.02	0.06 ± 0.09	0.04 ± 0.06	− 0.003 ± 0.01	0.04 ± 0.06
U–D pairs	0.03 ± 0.05	0.11 ± 0.09	− 0.07 ± 0.08	− 0.002 ± 0.05	0.07 ± 0.07	− 0.07 ± 0.08
D–D pairs	0.14 ± 0.12	0.16 ± 0.12	− 0.02 ± 0.14	0.09 ± 0.12	0.13 ± 0.10	− 0.04 ± 0.13
<i>Native</i>						
All pairs	0.06 ± 0.10	0.10 ± 0.11	− 0.04 ± 0.11	0.006 ± 0.10	0.06 ± 0.07	− 0.06 ± 0.11
U–U pairs	0.04 ± 0.05	0.002 ± 0.02	0.03 ± 0.06	0.01 ± 0.02	− 0.003 ± 0.01	0.01 ± 0.03
U–D pairs	0.02 ± 0.05	0.11 ± 0.09	− 0.09 ± 0.06	− 0.05 ± 0.05	0.07 ± 0.06	− 0.12 ± 0.07
D–D pairs	0.16 ± 0.11	0.15 ± 0.13	0.01 ± 0.15	0.10 ± 0.11	0.09 ± 0.09	0.01 ± 0.14

The values are means ± standard deviations. All pairs: 66 dissimilarity values between the 12 reaches paired with each other, U–U pairs: 10 dissimilarity values between the 5 upstream reaches paired with each other, U–D pairs: 35 values between the 5 upstream reaches paired with 7 downstream reaches, D–D pairs: 21 between the 7 downstream reaches paired with each other

**Table 2** Results of paired *t* tests of the taxonomic and phylogenetic dissimilarities for entire assemblages and native assemblages between the historical period and current period for the 12 reaches

	Taxonomic dissimilarity			Phylogenetic dissimilarity		
	<i>t</i>	<i>p</i>	<i>df</i>	<i>t</i>	<i>p</i>	<i>df</i>
<i>Entire assemblages</i>						
Sor <sub>h</sub> − Sor <sub>c</sub>	− 6.09	<b>&lt; 0.001</b>	65	− 3.02	<b>0.004</b>	65
Sim <sub>h</sub> − Sim <sub>c</sub>	− 8.08	<b>&lt; 0.001</b>	65	− 7.18	<b>&lt; 0.001</b>	65
Sne <sub>h</sub> − Sne <sub>c</sub>	2.70	<b>0.009</b>	65	3.28	<b>0.002</b>	65
<i>Native assemblages</i>						
Sor <sub>h</sub> − Sor <sub>c</sub>	− 5.29	<b>&lt; 0.001</b>	65	− 0.50	0.619	65
Sim <sub>h</sub> − Sim <sub>c</sub>	− 7.91	<b>&lt; 0.001</b>	65	− 6.92	<b>&lt; 0.001</b>	65
Sne <sub>h</sub> − Sne <sub>c</sub>	2.96	<b>0.004</b>	65	4.01	<b>&lt; 0.001</b>	65

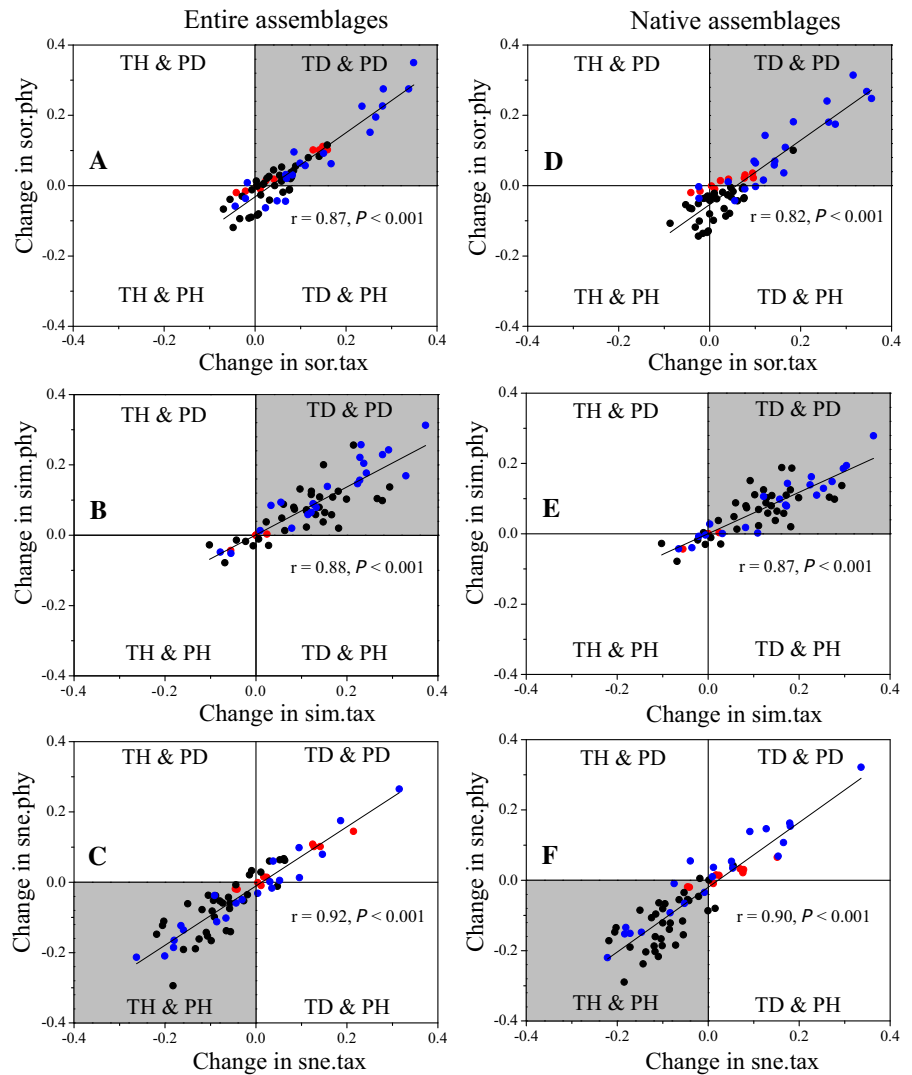
*P* values < 0.05 are bolded

the major trends towards taxonomic and phylogenetic differentiation for overall changes in dissimilarity, some reach pairs also exhibited taxonomic and phylogenetic homogenization (18.2% for entire assemblages and 27.3% for native assemblages; Fig. 3a, d). In addition, some pairs showed opposite patterns between taxonomic and phylogenetic metrics (21.2% for entire assemblages and 36.4% for native assemblages; Fig. 3a, d). These patterns were also observed for changes in turnover components (Fig. 3b, e). With respect to changes in nestedness components, the major trends were taxonomic and phylogenetic homogenization (Fig. 3c, f).

### Variation in patterns of fish assemblages

nMDS ordination plots of entire fish assemblages based on both taxonomy and phylogeny showed a clear separation between upstream and downstream reaches, but the separation between the upstream historical period and the current period is less evident than downstream one (Fig. 4a, c). Two-way PERMANOVA revealed that both time (historical or current) ( $F = 3.18$ ,  $P = 0.014$  for taxonomic and  $F = 2.95$ ,  $P = 0.019$  for phylogenetic) and region (upstream or downstream) ( $F = 37.17$ ,  $P = 0.001$  for taxonomy and  $F = 42.24$ ,  $P = 0.001$  for phylogeny) were significant sources of taxonomic and phylogenetic variation in the fish assemblages, whereas the interaction effect was not significant (Table 3).

**Fig. 3** Changes in taxonomic beta diversity (sor.tax, sim.tax, sne.tax) versus changes in phylogenetic diversity (sor.phy, sim.phy, sne.phy) among the 12 reaches for entire (a–c) and native (d–f) fish assemblages. The Pearson correlation ( $r$ ) and significance ( $P$  value) of the Mantel tests are provided in each panel. The red circles represent pairs of upstream reaches, the blue circles represent pairs of downstream reaches, and the black circles represent pairs of upstream and downstream reaches. The shaded areas indicate the major trend. *TH* taxonomic homogenization, *PH* phylogenetic homogenization, *TD* taxonomic differentiation, *PD* phylogenetic differentiation

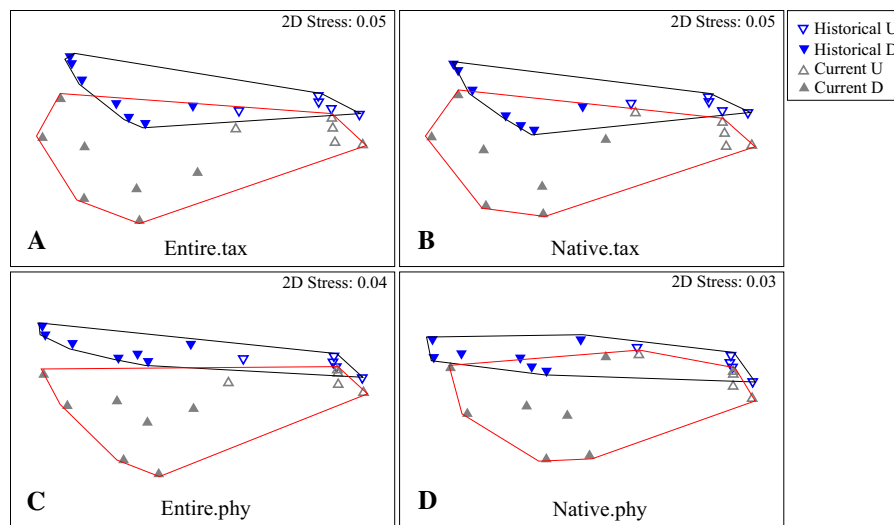


With respect to the native assemblages, the nMDS plots revealed a pattern similar to that for the entire assemblages for both taxonomy and phylogeny (Fig. 4b, d). Two-way PERMANOVA revealed that only region ( $F = 36.35$ ,  $P = 0.001$  for taxonomy and  $F = 40.58$ ,  $P = 0.001$  for phylogeny) was a significant source of variation, whereas time and the interaction effects were not significant (Table 3).

#### Determinants of changes in taxonomic dissimilarity and phylogenetic dissimilarity

MRM showed that changes in both taxonomic dissimilarity and phylogenetic dissimilarity were significantly predicted by historical values and introduction

and extirpation pressures for entire fish assemblages ( $R^2 = 0.11$ ,  $P < 0.001$  for taxonomy and  $R^2 = 0.10$ ,  $P < 0.001$  for phylogeny; Appendix 3). The historical levels of dissimilarity had a significant negative effect (Std  $b < 0$ ,  $P < 0.001$ ; Fig. 5a, d); i.e., pairs of assemblages with a low historical dissimilarity tended to be more differentiated than those with a high historical dissimilarity. The total number of native species extirpations from the pair of assemblages had a significant positive effect (Std  $b > 0$ ,  $P < 0.05$ ; Fig. 5b, e), i.e., pairs with relatively high numbers extirpated native species tended to be more differentiated than those with relatively low numbers of extirpated native species. However, the total number of species introductions in a pair of assemblages did



**Fig. 4** nMDS analysis of entire assemblages and native assemblages for taxonomic and phylogenetic facets. *U* upstream reaches, *D* downstream reaches. The black and red polygons indicate the degree of dispersion for the historical and current periods, respectively

**Table 3** Results of two-way permutational analysis of variance (two-way PERMANOVA) in taxonomic and phylogenetic facets for entire assemblages and native assemblages

Source	Total		Native	
	F	P (perm)	F	P (perm)
<i>Taxonomy</i>				
Time	3.184	<b>0.014</b>	2.071	0.077
Region	37.17	<b>0.001</b>	36.35	<b>0.001</b>
Time × Region	1.757	0.106	1.216	0.301
<i>Phylogeny</i>				
Time	2.948	<b>0.019</b>	2.001	0.106
Region	42.24	<b>0.001</b>	40.58	<b>0.001</b>
Time × Region	1.557	0.164	1.174	0.301

Time: historical and current. Region: upstream and downstream

*P* values < 0.05 are bolded

not contribute significantly (Std  $b > 0$ ,  $P > 0.05$ ; Fig. 5c, f).

For native assemblages, MRM showed that changes in both taxonomic and phylogenetic dissimilarities were predicted by the historical values and extirpation pressures ( $R^2 = 0.12$ ,  $P < 0.001$  for taxonomy and  $R^2 = 0.14$ ,  $P < 0.001$  for phylogeny; Appendix 3). The historical levels of dissimilarity had significant negative effects (Std  $b < 0$ ,  $P < 0.001$ ; Fig. 6a, c),

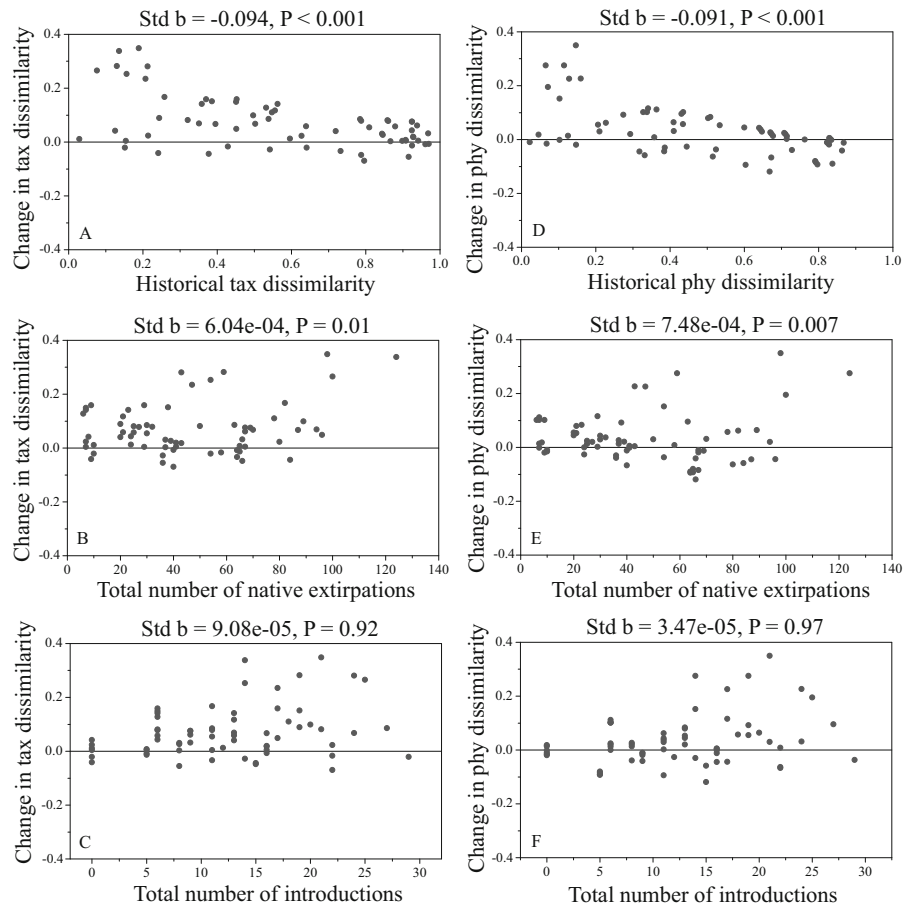
and the total number of native species extirpations had a significant positive effect on the change in both taxonomic and phylogenetic dissimilarities (Std  $b > 0$ ,  $P < 0.05$ ; Fig. 6b, d).

## Discussion

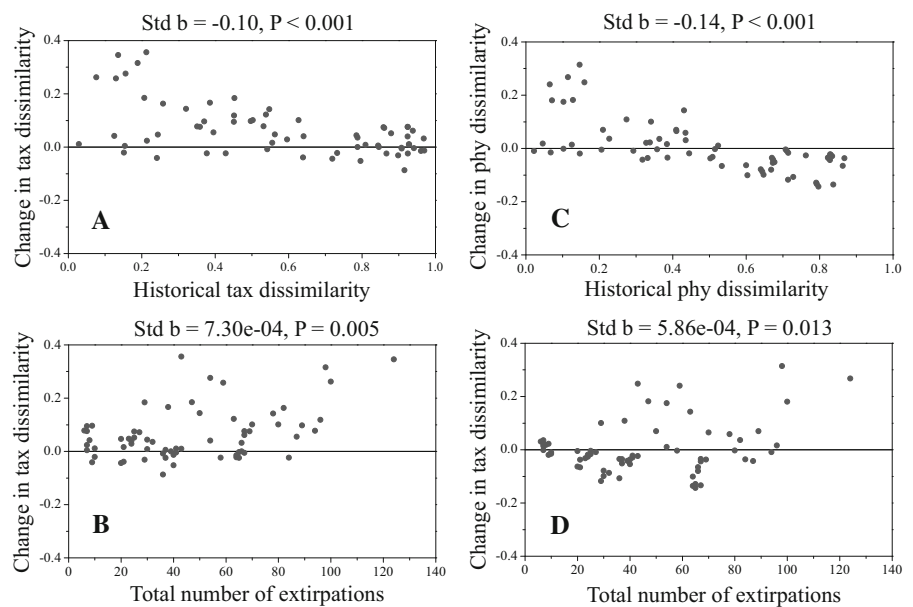
The high environmental heterogeneity among different reaches in the LCR resulted in a relatively high level (approximately 0.60) of taxonomic dissimilarity in the historical period. The considerable difference in the number of higher taxa in fish assemblages between the upstream region (five reaches) and downstream region (seven reaches) (orders: 3 vs. 8; families: 5 vs. 21) resulted in a considerable among-reach difference in the branch lengths of phylogenetic trees, leading to a moderate phylogenetic dissimilarity (approximately 0.50) in the historical period. The historical value of the taxonomic dissimilarity was higher than that of the phylogenetic dissimilarity, indicating that even if fish assemblages of different regions comprise distinct species and different numbers of species, they still share a proportion of the total branch length of the phylogenetic tree.

The dominance of taxonomic turnover over taxonomic nestedness (63.8% vs. 36.2%) indicates that the fish assemblage heterogeneity was largely due to species replacement rather than a difference in

**Fig. 5** Effects of historical dissimilarity and extirpation/introduction pressures on changes in taxonomic and phylogenetic dissimilarities for entire assemblages. Standard partial regression coefficient (Std  $b$ ) and associated  $P$  value from MRM are given for each variable



**Fig. 6** Effects of historical dissimilarity and extirpation pressures on changes in taxonomic and phylogenetic dissimilarities for native assemblages. Standard partial regression coefficient (Std  $b$ ) and associated  $P$  value from MRM are given for each variable



richness; i.e., the proportion of species numbers shared by different assemblages was low (Baselga 2010). As is well known, taxonomic turnover provides information about deterministic niche-related processes (e.g., filtering of different species by prevailing environmental features) related to species replacements between different environmental conditions (Nunes et al. 2016). These results may be due to the high habitat heterogeneity among the 12 reaches. Although high habitat heterogeneity also resulted in a great difference in richness between the upstream and downstream reaches, very few common species were shared by reaches in the two different regions. Hence, the value of taxonomic turnover was still higher than that of taxonomic nestedness. In contrast, phylogenetic nestedness contributed more (58.3%) than phylogenetic turnover in the historical period, indicating a strong difference in phylogenetic richness (Baselga 2010; Villeger et al. 2013). In addition, there were many more high taxa in the downstream reaches than that in the upstream reaches; species in the upstream reaches mainly belonged to the orders Cypriniformes (59.1%) and Siluriformes (40.4%), which were also included in the downstream fish fauna (72.9% of species in Cypriniformes and 19.1% in Siluriformes). Hence, fish assemblages in the upstream and downstream reaches shared a large proportion of total branch length, and the unique branch length of the upstream reaches was much smaller than that of the downstream reaches. As a result, we observed higher phylogenetic nestedness than phylogenetic turnover.

From the historical period to the current period, cascaded hydropower construction in the mainstream of the LCR has led to habitat fragmentation. The barriers formed by the cascade dams can limit the living space and natural distribution range of dispersed and migratory species (Cheng et al. 2015; Petesse and Petrere 2012), which is also the case in the LCR. In the historical period, 132 of all the 162 native species were present in at least two of the 12 reaches. However, in the current period, 109 of them experienced a reduction in distribution area, especially species in the downstream reaches (e.g., *Tor sinensis*, *Discherodonius parvus*, and *Pangasius sanitwongsei*). The extensive reduction in the distribution area of native species resulted in a decrease in the proportion of species shared by different reaches and led to an increase in taxonomic turnover. In addition, an increase in non-native species may generally lead to homogenization

(Toussaint et al. 2014; Villeger et al. 2014). However, the invasions of non-native species did not occur in each of the 12 reaches because of substantial regional environmental differences, such as those in water temperature, depth and flow velocity. Non-native species are likely to be successful invaders if they are introduced into a habitat that is similar to their native habitats (Moyle and Marchetti 2006). In the upstream reaches, high altitude and harsh environmental conditions (e.g., low temperature and strong radiation) may prevent the establishment of non-native species (Kang et al. 2009; Zefferman et al. 2015), but in the downstream reaches, suitable environments and anthropogenic activities provide conditions for the successful establishment of many non-native species (Fan et al. 2015; Kang et al. 2009; Zhang et al. 2018). Moreover, the invasions of non-native species somewhat differed among the downstream reaches. For example, *Oreochromis nilotica* was established in three reaches; *Gambusia affinis* and *Neosalanx taihuensis*, in two reaches; and *Prochilodus lineatus*, *Macropodus chinensis*, *Cultrichthys erythropterus* and *Pseudolaubuca sinensis*, in one reach. Hence, the discrepancy in invasions of non-native species resulted in a further decrease in the proportion of species shared by different reaches, leading to an increase in taxonomic turnover.

The imbalance of human disturbances resulted in an imbalance of regional changes. In the upstream reaches, only a few native species were extirpated (Zhang et al. 2018) because of the fish assemblages experiencing weak human disturbances, e.g., low human population density and hydropower dams not under construction (Kang et al. 2009). However, cascaded hydropower development, non-native invasions, overfishing and water pollution have significantly affected fish assemblages in the downstream reaches (Deng and Zeng 2004; Fan et al. 2015; Kang et al. 2009), resulting in considerable declines in species richness (average: 36.9 species, i.e., 47.2% of total native species per downstream reach) (Zhang et al. 2018). Overall, the downstream reaches, with high historical species richness, experienced a greater decrease in species numbers than did the upstream reaches, where historical species numbers were low. Such uneven changes in species richness led to a considerable decrease in the difference in species richness between the upstream and downstream reaches. Despite the introduction of non-native species

in the downstream reaches leading to the increase in the difference in species richness between the upstream and downstream reaches, there were many fewer introduced non-native species than extirpated native species (9.7 vs. 36.9 per downstream reach). Hence, the taxonomic nestedness component ultimately decreased.

With respect to the phylogenetic facet, Cyprinidae, Balitoridae and Sisoridae were the most species-rich families in the historical period, accounting for an average of 34.9%, 26.5% and 23.6% of the total species per reach, respectively. Hence, different reaches shared a large proportion of total branch length at the family level. In contrast, in the current period, the extirpated species in the downstream reaches were also concentrated mainly in the same three families (on average, 37% of extirpated species were members of the Cyprinidae; 33%, the Balitoridae; and 12%, the Sisoridae). Thus, the extirpations of these native species also caused a large reduction in common branch lengths shared by different reaches, leading to an increase in the phylogenetic turnover component. Furthermore, the uneven invasions by non-native species resulted in a further decrease in the shared evolutionary branch lengths among reaches. Some of the non-native species that belong to historically absent orders and families were distantly related to native species (e.g., *Gambusia affinis* from the order Cyprinodontiformes, *Neosalanx taihuensis* from Osmeriformes and *Prochilodus lineatus* from Characiformes; *Micropercops swinhonis* from the family Odontobutidae; and the genus *Oreochromis* from Cichlidae), resulting in a significant increase in the unique branch lengths in those invaded reaches. Therefore, the phylogenetic turnover component between different reaches increased further.

Normally, the increase in unique branch lengths in the downstream reaches should have led to an increase in the difference in phylogenetic richness (i.e., nestedness component) between the upstream and downstream reaches. However, in the studied river, there was a considerable decline in phylogenetic branch length in the downstream reaches over time because of the extirpation of several native orders (e.g., the historically occurring orders Beloniformes, Anguilliformes, Myliobatiformes and Tetraodontiformes disappeared in some downstream reaches). In contrast, the upstream reaches, although having a low historical levels of phylogenetic branch length, experienced few

extirpations of higher taxa. Therefore, the difference in phylogenetic richness between the upstream and downstream reaches (U-D pairs) decreased markedly and led to a decrease in phylogenetic nestedness.

Although phylogenetic differentiation is correlated with taxonomic differentiation, approximately 20–35% of reach pairs experienced phylogenetic homogenization while they differentiated from a taxonomic point of view. Therefore, measuring the phylogenetic facet of beta diversity should be used as a complement to taxonomic beta diversity, as this metric can help to better understand the mechanism of change in fish diversity patterns (Graham and Fine 2008; Jiang et al. 2019).

It is generally believed that the ecological effect of homogenization is negative, while that of differentiation is positive (Marchetti et al. 2006; Scott and Helfman 2001). In the present study, habitat fragmentation due to hydropower development led to both taxonomic and phylogenetic differentiation, but the result was caused by the reduction in the distribution area of common native species and invasion by ecologically narrow species in specific suitable habitats. Therefore, the differentiation in this study should not be misinterpreted. The results were consistent with those of previous studies involving individual dams, where the differences in fish assemblages between the areas upstream and downstream of the dams also increased (Agostinho et al. 2008; Ding et al. 2019; Sa-Oliveira et al. 2015). Cascade dams, however, are expected to have spatially and temporally cumulative effects on fish assemblages, which may be much stronger than those caused by individual dams and further strengthened over time. In our study, the time since completion of the cascade dams is still short. A study on the variation in fish assemblages in the cascade reservoir system of the Tietê River Basin in Brazil by Petesse and Petrere (2012) revealed taxonomic differentiation in the first decade but homogenization in the second decade. In addition, introductions of non-native species usually initially result in an increase in biodiversity and require relatively long periods of time to exert negative effects on native species (Ding et al. 2017; Rahel 2000). Therefore, the observed taxonomic and phylogenetic differentiations are probably an early warning of further homogenization, as demonstrated by

\_ENREF\_59Petesse and Petrere (2012).



## Conclusion

The fish assemblages in the LCR showed differentiation trends in both taxonomic and phylogenetic facets of biodiversity because of habitat fragmentation driven by large-scale cascaded hydropower dam construction. However, such differentiation was caused by a reduction in the distribution area of widespread native species and imbalanced invasions by non-native species in specific suitable habitats. Therefore, the differentiation in this study should not be misinterpreted. Furthermore, the imbalanced cascaded hydropower development and non-native invasions were sufficient to blur taxonomic and phylogenetic patterns of fish diversity in the LCR resulting from long-term evolution and adaptation. Although the changes in taxonomic and phylogenetic dissimilarities were highly correlated, our study still showed an inconsistency in the changes between them, indicating that phylogenetic diversity should be used as a complementary metric to taxonomy. Moreover, the difference in changes in turnover and nestedness

components for both taxonomic and phylogenetic dissimilarities indicated the importance of the partitioning of beta diversity.

**Acknowledgements** This study was financially supported by the National Natural Science Foundation of China (Grants 41867072, 41807402), the Biodiversity Survey and Assessment Project of the Ministry of Ecology and Environment, China (2019HJ2096001006), the National Key Research and Development Program of China (2016YFA0601601), and the Yunnan University “Double First-class” Construction Project (Grants C176210215, C176240208002).

## Appendix 1

A list of families, orders and the number of genera and species with each families detected in the 12 reaches of the LCR during the historical (before 1990s) and current (2006–2015) periods. Those taxa and numbers bold with “+” mean they were non-native to the studied reaches.

Region	Order	Family	Historical		Current	
			No. genera	No. species	No. genera	No. species
GX-GS	Cypriniformes	Balitoridae	2	3	2	2
		Cyprinidae	1	3	1	3
GS-WNL	Siluriformes	Sisoridae	4	5	3	3
		Cobitidae	1	1	1	1
	Cypriniformes	Balitoridae	3	5	3	4
		Cyprinidae	1	3	1	3
WNL-TB	Siluriformes	Sisoridae	4	6	3	3
		Cobitidae	1	1	1	1
	Cypriniformes	Balitoridae	3	5	3	3
		Cyprinidae	2	4	1	3
TB-HD	Siluriformes	Sisoridae	4	8	4	5
		Cobitidae	1	1	1	1
	Cypriniformes	Balitoridae	3	5	3	4
		Cyprinidae	1	3	1	3
HD-GGQ	Siluriformes	Sisoridae	4	8	4	5
		Cobitidae	3	3	3	3
	Cypriniformes	Balitoridae	7	13	6	10
		Cyprinidae	6	10	10 (4 <sup>+</sup> )	14 (4 <sup>+</sup> )
	Siluriformes	Sisoridae	5	9	5	9
	Synbranchiformes	Synbranchidae	1	1	1	1
	Perciformes	Gobiidae			1 <sup>+</sup>	2 <sup>+</sup>

Region	Order	Family	Historical		Current	
			No. genera	No. species	No. genera	No. species
GGQ-XW	Cypriniformes	Cobitidae	3	3	3	3
		Balitoridae	9	16	6	7
		Cyprinidae	11	15	16 (8 <sup>+</sup> )	20 (9 <sup>+</sup> )
	Siluriformes	Clariidae	1	1	1	1
		Bagridae	1	1	1	1
		Sisoridae	4	8	2	5
	Beloniformes	Adrianichthyidae	1	1		
	Synbranchiformes	Synbranchidae	1	1	1	1
	Perciformes	Cichlidae			1 <sup>+</sup>	1 <sup>+</sup>
		Gobiidae			1 <sup>+</sup>	2 <sup>+</sup>
		Odontobutidae			1 <sup>+</sup>	1 <sup>+</sup>
XW-MW	Cypriniformes	Cobitidae	3	3	3	3
		Balitoridae	8	13	1	2
		Cyprinidae	16	19	16 (4 <sup>+</sup> )	18 (5 <sup>+</sup> )
	Siluriformes	Clariidae	1	1		
		Schilbeidae	1	2	1	2
		Sisoridae	4	7	1	1
	Beloniformes	Adrianichthyidae	1	1		
	Synbranchiformes	Synbranchidae	1	1		
	Perciformes	Channidae	1	1		
		Gobiidae			1 <sup>+</sup>	3 <sup>+</sup>
		Odontobutidae			1 <sup>+</sup>	1 <sup>+</sup>
	Osmeriformes	Osmeridae			1 <sup>+</sup>	1 <sup>+</sup>
	Cyprinodontiformes	Poeciliidae			1 <sup>+</sup>	1 <sup>+</sup>
MW-DCS	Cypriniformes	Cobitidae	3	3	1	1
		Balitoridae	7	14	4	5
		Cyprinidae	18	26	16 (6 <sup>+</sup> )	19 (6 <sup>+</sup> )
	Siluriformes	Clariidae	1	1	1	1
		Schilbeidae	1	2	1	2
		Sisoridae	5	11	2	3
	Beloniformes	Adrianichthyidae	1	1		
	Synbranchiformes	Synbranchidae	1	1	1	1
	Perciformes	Channidae	1	1	1	1
		Cichlidae			1 <sup>+</sup>	1 <sup>+</sup>
		Gobiidae			1 <sup>+</sup>	1 <sup>+</sup>
DCS-NZD	Cypriniformes	Cobitidae	3	3	3	3
		Balitoridae	9	18	5	9
		Cyprinidae	22	32	20 (3 <sup>+</sup> )	28 (3 <sup>+</sup> )
	Siluriformes	Clariidae	1	1		
		Bagroidea	1	2	1	2
		Sisoroidea	4	8	4	6
	Beloniformes	Adrianichthyidae	1	1		
	Synbranchiformes	Synbranchidae	1	1	1	1
	Perciformes	Cichlidae			1 <sup>+</sup>	2 <sup>+</sup>

Region	Order	Family	Historical		Current	
			No. genera	No. species	No. genera	No. species
NZD-JH	Gobiidae	1	1	1 <sup>+</sup>	1 <sup>+</sup>	
	Channidae	1	1	1	1	
	Cypriniformes	Cobitidae	6	6	3	3
		Balitoridae	7	15	1	3
	Siluriformes	Cyprinidae	27	42	15 (3 <sup>+</sup> )	18 (3 <sup>+</sup> )
		Clariidae	1	1		
		Siluridae	4	4		
		Schilbeidae	1	2	1	2
		Sisoridae	3	7	2	5
		Bagridae	1	1		
		Akysidae	1	1		
	Beloniformes	Adrianichthyidae	1	1		
	Synbranchiformes	Synbranchidae	1	1		
		Mastacembelidae	1	1		
	Perciformes	Gobiidae	1	1	1 <sup>+</sup>	1 <sup>+</sup>
		Anabantidae	1	1		
		Osphronemidae	2	2		
		Channidae	1	3	1	1
JH-GLB	Tetraodontiformes	Tetraodontidae	1	1		
	Osmeriformes	Osmeridae			1 <sup>+</sup>	1 <sup>+</sup>
	Anguilliformes	Anguillidae	1	1		
		Cyrinocheilidae	1	1		
	Cypriniformes	Cobitidae	7	7	4	4
		Balitoridae	7	18	3	6
		Cyprinidae	35	56	26 (5 <sup>+</sup> )	35 (6 <sup>+</sup> )
	Siluriformes	Clariidae	1	1		
		Siluridae	4	4	1	1
		Schilbeidae	1	2	1	2
		Pangasiidae	1	3		
		Bagridae	1	1	1	1
		Sisoridae	3	7	2	4
		Akysidae	1	2		
	Beloniformes	Adrianichthyidae	1	2	1	1
	Synbranchiformes	Synbranchidae	1	1	1	1
		Mastacembelidae	1	1	1	1
	Perciformes	Gobiidae	1	1	1 <sup>+</sup>	1 <sup>+</sup>
		Anabantidae	1	1		
		Osphronemidae	2	2	1	1
		Channidae	1	3	1	1
		Cichlidae			1 <sup>+</sup>	2 <sup>+</sup>
	Tetraodontiformes	Tetraodontidae	1	1		

Region	Order	Family	Historical		Current	
			No. genera	No. species	No. genera	No. species
GLB-GL	Myliobatiformes	Dasyatidae	1	1		
		Cypriniformes				
		Cyrinocheilidae	1	1	1	1
		Cobitidae	7	7	7	7
		Balitoridae	9	24	6	13
		Cyprinidae	36	56	34 (7 <sup>+</sup> )	45 (9 <sup>+</sup> )
	Characiformes	Prochilodontidae			1 <sup>+</sup>	1 <sup>+</sup>
	Siluriformes	Clariidae	1	1	1	1
		Siluridae	4	4	2	2
		Schilbeidae	1	2	1	2
		Pangasiidae	1	3	1	2
		Bagridae	1	1	1	1
		Sisoridae	3	7	3	7
		Akysidae	1	2	1	2
		Adrianichthyidae	1	2	1	1
	Cyprinodontiformes	Poeciliidae			1 <sup>+</sup>	1 <sup>+</sup>
	Synbranchiformes	Synbranchidae	1	1	1	1
		Mastacembelidae	1	1	1	1
	Perciformes	Gobiidae	1	1	1 <sup>+</sup>	2 <sup>+</sup>
		Anabantidae	1	1	1	1
		Osphronemidae	2	2	2	3 (1 <sup>+</sup> )
		Channidae	1	3	1	3
		Tetraodontidae	1	1	1	1

## Appendix 2

A list of species occurrences in the 12 reaches of the Lancang River (LCR). The term “non-native” represents non-LCR species and “exotic” represents non-China species.

Species		Occurrence	Species		Occurrence
1	<i>Dasyatis laosensis</i>	Native	93	<i>Cosmochilus nanlaensis</i>	Native
2	<i>Anguilla bicolor</i>	Native	94	<i>Puntioplites falcifer</i>	Native
3	<i>Gyrinocheilus aymonieri</i>	Native	95	<i>Puntioplites waandersi</i>	Native
4	<i>Sinibotia longiventralis</i>	Native	96	<i>Poropuntius carinatus</i>	Native
5	<i>Syncrossus beauforti</i>	Native	97	<i>Poropuntius huangchuchieni</i>	Native
6	<i>Ambastaia nigrolineata</i>	Native	98	<i>Poropuntius krempfi</i>	Native
7	<i>Acantopsis dialuzona</i>	Native	99	<i>Barbonymus gonionotus</i>	Native
8	<i>Lepidocephalichthys berdmorei</i>	Native	100	<i>Sikukia flavicaudata</i>	Native
9	<i>Acanthopsoidea gracilis</i>	Native	101	<i>Sikukia gudgeri</i>	Native
10	<i>Misgurnus anguillicaudatus</i>	Native	102	<i>Sikukia longibarbata</i>	Native

continued

Species			Occurrence		
Species			Occurrence		
11	<i>Vanmanenia serrilineata</i>	Native	103	<i>Myastacoleucus lepturus</i>	Native
12	<i>Vanmanenia sp.</i>	Native	104	<i>Myastacoleucus marginatus</i>	Native
13	<i>Balitora lancangjiangensis</i>	Native	105	<i>Hypsibarbus vernayi</i>	Native
14	<i>Hemimyzon elongatus</i>	Native	106	<i>Percocypris retrodorsalis</i>	Native
15	<i>Hemimyzon pengi</i>	Native	107	<i>Luciocyprinus striolatus</i>	Native
16	<i>Hemimyzon tchangi</i>	Native	108	<i>Bangana brevirostris</i>	Native
17	<i>Balitoropsis vulgaris</i>	Native	109	<i>Bangana lippa</i>	Native
18	<i>Balitoropsis yunnanensis</i>	Native	110	<i>Bangana yunnanensis</i>	Native
19	<i>Homatula acuticephala</i>	Native	111	<i>Bangana zhui</i>	Native
20	<i>Homatula anguillioides</i>	Native	112	<i>Labeo pierrei</i>	Native
21	<i>Homatula pycnolepis</i>	Native	113	<i>Crossocheilus reticulatus</i>	Native
22	<i>Homatula wuliangensis</i>	Native	114	<i>Henicorhynchus lineatus</i>	Native
23	<i>Homatula variegata</i>	Native	115	<i>Lobocheilus melanotaenia</i>	Native
24	<i>Pteronemacheilus meridionalis</i>	Native	116	<i>Labiobarbus leptocheila</i>	Native
25	<i>Physoschistura raoi</i>	Native	117	<i>Cirrhinus molitorella</i>	Native
26	<i>Physoschistura shuangjiangensis</i>	Native	118	<i>Garra fasciacauda</i>	Native
27	<i>Schistura amplizona</i>	Native	119	<i>Garra cambodgiensis</i>	Native
28	<i>Schistura bannaensis</i>	Native	120	<i>Garra imberba imberba</i>	Native
29	<i>Schistura breviceps</i>	Native	121	<i>Garra mirofronitis</i>	Native
30	<i>Schistura bucculenta</i>	Native	122	<i>Garra orientalis</i>	Native
31	<i>Schistura conirostris</i>	Native	123	<i>Mekongina lancangensis</i>	Native
32	<i>Schistura cryptofasciata</i>	Native	124	<i>Schizothorax lantsangensis</i>	Native
33	<i>Schistura fasciolata</i>	Native	125	<i>Schizothorax lissolabiatus</i>	Native
34	<i>Schistura vinciguerrae</i> Hora	Native	126	<i>Schizothorax nudiventris</i>	Native
35	<i>Schistura kengtungensis</i>	Native	127	<i>Schizothorax yunnanensis</i>	Native
36	<i>Schistura kloetzliae</i>	Native	128	<i>Ptychobarbus kaznakovi</i>	Native
37	<i>Schistura latifasciata</i>	Native	129	<i>Gymnocypris firmispinatus</i>	Native
38	<i>Schistura macrocephalus</i>	Native	130	<i>Cyprinus carpio</i>	Native
39	<i>Schistura poculi</i>	Native	131	<i>Carassius auratus</i>	Native
40	<i>Schistura porthos</i>	Native	132	<i>Prochilodus lineatus</i>	Exotic
41	<i>Schistura schultzi</i>	Native	133	<i>Clarias fuscus</i>	Native
42	<i>Schistura sexnubes</i>	Native	134	<i>Micronema moorei</i>	Native
43	<i>Schistura waltoni</i>	Native	135	<i>Phalacrodonotus bleekeri</i>	Native
44	<i>Sectoria heterognathos</i>	Native	136	<i>Wallago attu</i>	Native
45	<i>Triplophysa brevicecauda</i>	Native	137	<i>Hemisilurus mekongensis</i>	Native
46	<i>Triplophysa stenura</i>	Native	138	<i>Clupisoma longianalis</i>	Native
47	<i>Triplophysa anterodorsalis</i>	Native	139	<i>Clupisoma sinense</i>	Native
48	<i>Vanmanenia striata</i>	Native	140	<i>Pangasius djambal</i>	Native
49	<i>Rasbora atridorsalis</i>	Native	141	<i>Pangasius micronemus</i>	Native
50	<i>Rasbora septentrionalis</i>	Native	142	<i>Pangasius sanitwongsei</i>	Native
51	<i>Danio apopyris</i>	Native	143	<i>Hemibagrus wyckioides</i>	Native
52	<i>Danio browni</i>	Native	144	<i>Pelteobagrus vachelli</i>	Native
53	<i>Danio chrysotaeniatus</i>	Native	145	<i>Bagarius bagarius</i>	Native
54	<i>Gymnodanio strigatus</i>	Native	146	<i>Bagarius yarrelli</i>	Native
55	<i>Raiamas guttatus</i>	Native	147	<i>Glyptothorax deqingensis</i>	Native

continued					
	Species	Occurrence		Species	Occurrence
56	<i>Barilius caudiocellatus</i>	Native	148	<i>Glyptothorax fuscus</i>	Native
57	<i>Barilius koratensis</i>	Native	149	<i>Glyptothorax laosensis</i>	Native
58	<i>Barilius pulchellus</i>	Native	150	<i>Glyptothorax longinema</i>	Native
59	<i>Opsariichthys bidens</i>	Native	151	<i>Glyptothorax macromaculatus</i>	Native
60	<i>Macrochirichthys macrochirius</i>	Native	152	<i>Pseudecheneis immaculatus</i>	Native
61	<i>Rhodeus ocellatus</i>	Non-native	153	<i>Pseudecheneis sulcatoides</i>	Native
62	<i>Rhodeus spinalis</i> Oshima	Non-native	154	<i>Pareuchiloglanis abbreviatus</i>	Native
63	<i>Acheilognathus barbatulus</i>	Native	155	<i>Pareuchiloglanis gracilicaudata</i>	Native
64	<i>Metzia lineata</i>	Native	156	<i>Glyptothorax zanaensis</i>	Native
65	<i>Hemiculter leucisculus</i>	Non-native	157	<i>Pareuchiloglanis myzostoma</i>	Native
66	<i>Hemiculterella macrolepis</i>	Native	158	<i>Pareuchiloglanis prolixidorsalis</i>	Native
67	<i>Paralaubuca barroni</i>	Native	159	<i>Creteuchiloglanis longipectoralis</i>	Native
68	<i>Cultrichthys erythropterus</i>	Non-native	160	<i>Oreoglanis jingdongensis</i>	Native
69	<i>Pseudolaubuca sinensis</i>	Non-native	161	<i>Oreoglanis setiger</i>	Native
70	<i>Hemibarbus maculatus</i>	Native	162	<i>Akysis brachybarbatus</i>	Native
71	<i>Pseudorasbora parva</i>	Non-native	163	<i>Akysis sinensis</i>	Native
72	<i>Abbotina rivularis</i>	Non-native	164	<i>Oryzias minutillus</i>	Native
73	<i>Gobiobotia yuanjiangensis</i>	Native	165	<i>Oryzias sinensis</i>	Native
74	<i>Ctenopharyngodon idella</i>	Non-native	166	<i>Gambusia affinis</i>	Exotic
75	<i>Mylopharyngodon piceus</i>	Non-native	167	<i>Monopterus albus</i>	Native
76	<i>Tinca tinca</i>	Exotic	168	<i>Mastacembelus armatus</i>	Native
77	<i>Hypophthalmichthys molitrix</i>	Non-native	169	<i>Oreochromis mossambica</i>	Exotic
78	<i>Hypophthalmichthys nobilis</i>	Non-native	170	<i>Oreochromis nilotica</i>	Exotic
79	<i>Tor laterivittatus</i>	Native	171	<i>Rhinogobius cliffordpopei</i>	Non-native
80	<i>Tor polylepis</i>	Native	172	<i>Rhinogobius giurinus</i>	Non-native
81	<i>Tor sinensis</i>	Native	173	<i>Rhinogobius maculicervix</i>	Native
82	<i>Tor tambra</i>	Native	174	<i>Rhinogobius brunneus</i> (Temminck et Schlegel)	Non-native
83	<i>Tor tambroides</i>	Native	175	<i>Micropercops swinhonis</i>	Non-native
84	<i>Folifer brevifilis</i>	Native	176	<i>Anabas testudineus</i>	Native
85	<i>Hampala macrolepidota</i>	Native	177	<i>Macropodus opercularis</i>	Native
86	<i>Puntius semifasciolatus</i>	Native	178	<i>Macropodus chinensis</i>	Non-native
87	<i>Puntius ticto</i>	Native	179	<i>Trichogaster trichopterus</i>	Native
88	<i>Onychostoma gerlachi</i>	Native	180	<i>Channa gachua</i>	Native
89	<i>Scaphiodonichthys acanthopterus</i>	Native	181	<i>Channa striata</i>	Native
90	<i>Discherodontus parvus</i>	Native	182	<i>Channa lucius</i>	Native
91	<i>Cyclocheilichthys repasson</i>	Native	183	<i>Monotretre turgidus</i>	Native
92	<i>Cosmochilus cardinalis</i>	Native	184	<i>Neosalanx taihuensis</i>	Non-native



## Appendix 3

Results of multiple regressions on distance matrices (MRM) analyses for changes in taxonomic and phylogenetic dissimilarities for entire and native assemblages. Historical value, total number of native extirpation and total number of introduction were considered as explanatory variables.

	Change in tax dissimilarity		Change in phy dissimilarity	
	Std b	P value	Std b	P value
<i>Entire assemblages</i>				
Historical dissimilarity	− 0.094	< <b>0.001</b>	− 0.091	< <b>0.001</b>
Introduction	9.08e−05	0.92	3.47e−05	0.97
Extirpation	6.04e−04	<b>0.01</b>	7.48e−04	<b>0.007</b>
R <sup>2</sup>	0.11	< <b>0.001</b>	0.10	< <b>0.001</b>
<i>Native assemblages</i>				
Historical dissimilarity	− 0.10	< <b>0.001</b>	− 0.14	< <b>0.001</b>
Extirpation	7.30e−04	<b>0.005</b>	5.86e−04	<b>0.013</b>
R <sup>2</sup>	0.12	< <b>0.001</b>	0.14	< <b>0.001</b>

## References

- Agostinho AA, Pelicice FM, Gomes LC (2008) Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. *Braz. J Biol* 68:1119–1132
- Anderson M, Gorley R, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth
- Anderson MJ et al (2011) Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. *Ecol Lett* 14:19–28. <https://doi.org/10.1111/j.1461-0248.2010.01552.x>
- Baran E, Chum N, Fukushima M, Hand T, Hortle KG, Jutagate T, Kang B (2012) Fish biodiversity research in the Mekong Basin. In: The biodiversity observation network in the Asia-Pacific Region Spring, Japan, pp 149–164
- Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. *Glob Ecol Biogeogr* 19:134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Baselga A (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Glob Ecol Biogeogr* 21:1223–1232. <https://doi.org/10.1111/j.1466-8238.2011.00756.x>
- Bryant JA, Lamanna C, Morlon H, Kerkhoff AJ, Enquist BJ, Green JL (2008) Microbes on mountainsides: contrasting elevational patterns of bacterial and plant diversity. *Proc Natl Acad Sci USA* 105:11505–11511. <https://doi.org/10.1073/pnas.0801920105>
- Cadotte MW, Cardinale BJ, Oakley TH (2008) Evolutionary history and the effect of biodiversity on plant productivity. *Proc Natl Acad Sci USA* 105:17012–17017. <https://doi.org/10.1073/pnas.0805962105>
- Canty A, Ripley B (2012) Boot: Bootstrap R (S-Plus) functions. In: R package version
- Cassey P, Blackburn TM, Lockwood JL, Sax DF (2006) A stochastic model for integrating changes in species richness and community similarity across spatial scales. *Oikos* 115:207–218. <https://doi.org/10.1111/j.2006.0030-1299.15223.x>
- Cella-Ribeiro A, Doria CRD, Dutka-Gianelli J, Alves H, Torrente-Vilara G (2017) Temporal fish community responses to two cascade run-of-river dams in the Madeira River, Amazon basin. *Ecohydrology*. <https://doi.org/10.1002/Eco.1889>
- Chen XY (2013) Checklist of fishes of Yunnan. *Zool Res* 34:281–343
- Chen SQ, Chen B, Fath BD (2015) Assessing the cumulative environmental impact of hydropower construction on river systems based on energy network model. *Renew Sust Energ Rev* 42:78–92. <https://doi.org/10.1016/j.rser.2014.10.017>
- Cheng F, Li W, Castello L, Murphy BR, Xie SG (2015) Potential effects of dam cascade on fish: lessons from the Yangtze River. *Rev Fish Biol Fish* 25:569–585. <https://doi.org/10.1007/s11160-015-9395-9>
- Chu XL, Chen YR (1989) The fishes of Yunnan, China. Part I: Cyprinidae. Science Press, Beijing
- Chu XL, Chen YR (1990) The fishes of Yunnan, China. Part II. Cyprinidae. Science Press, Beijing
- Clarke KR, Gorley R (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth
- Cooper AR, Infante DM, Wehrly KE, Wang LZ, Brenden TO (2016) Identifying indicators and quantifying large-scale effects of dams on fishes. *Ecol Indic* 61:646–657. <https://doi.org/10.1016/j.ecolind.2015.10.016>
- Cooper AR, Infante DM, Daniel WM, Wehrly KE, Wang LZ, Brenden TO (2017) Assessment of dam effects on streams and fish assemblages of the conterminous USA. *Sci Total Environ* 586:879–889. <https://doi.org/10.1016/j.scitotenv.2017.02.067>
- Daga VS, Skora F, Padial AA, Abilhoa V, Gubiani EA, Vitule JRS (2015) Homogenization dynamics of the fish assemblages in Neotropical reservoirs: comparing the roles of introduced species and their vectors. *Hydrobiologia* 746:327–347. <https://doi.org/10.1007/s10750-014-2032-0>
- Deng Q, Zeng GQ (2004) Research of countermeasures for ecologically environment protection in Lancang jiang watershed Yunnan Province. *Yunnan Environ Sci* 23:135–136
- Ding CZ, Jiang XM, Xie ZC, Brosse S (2017) Seventy-five years of biodiversity decline of fish assemblages in Chinese isolated plateau lakes: widespread introductions and extirpations of narrow endemics lead to regional loss of dissimilarity. *Divers Distrib* 23:171–184

- Ding CZ et al (2019) Fish assemblage responses to a low-head dam removal in the Lancang River. *Chin Geogr Sci* 29:26–36. <https://doi.org/10.1007/s11769-018-0995-x>
- Dudgeon D, Smith REW (2006) Exotic species, fisheries and conservation of freshwater biodiversity in tropical Asia: the case of the Sepik River. *Papua New Guinea Aquat Conserv* 16:203–215. <https://doi.org/10.1002/aqc.713>
- Faith DP, Lozupone CA, Nipperess D, Knight R (2009) The cladistic basis for the phylogenetic diversity (PD) measure links evolutionary features to environmental gradients and supports broad applications of microbial ecology's "Phylogenetic Beta Diversity" framework. *Int J Mol Sci* 10:4723–4741. <https://doi.org/10.3390/ijms10114723>
- Faith DP, Magallon S, Hendry AP, Conti E, Yahara T, Donoghue MJ (2010) Ecosystem services: an evolutionary perspective on the links between biodiversity and human well-being. *Curr Opin Environ Sustain* 2:66–74. <https://doi.org/10.1016/j.cosust.2010.04.002>
- Fan H, He DM, Wang HL (2015) Environmental consequences of damming the mainstream Lancang-Mekong River: a review. *Earth Sci Rev* 146:77–91. <https://doi.org/10.1016/j.earscirev.2015.03.007>
- Freville H, McConway K, Dodd M, Silvertown J (2007) Prediction of extinction in plants: interaction of extrinsic threats and life history traits. *Ecology* 88:2662–2672. <https://doi.org/10.1890/06-1453.1>
- Gao X, Li MZ, Lin PC, Duan ZH, Liu HZ (2013) Environmental cues for natural reproduction of the Chinese sturgeon, *Acipenser sinensis* Gray, 1835, in the Yangtze River, China. *J Appl Ichthyol* 29:1389–1394. <https://doi.org/10.1111/jai.12363>
- Gaston KJ (1998) Species-range size distributions: products of speciation, extinction and transformation. *Philos Trans R Soc Lond B Biol Sci* 353:219–230
- Goslee SC, Urban DL (2007) The ecodist package for dissimilarity-based analysis of ecological data. *J Stat Softw* 22:1–19
- Graham CH, Fine PVA (2008) Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. *Ecol Lett* 11:1265–1277. <https://doi.org/10.1111/j.1461-0248.2008.01256.x>
- Guo ZF, Li L, He WP, Li HL (2014) Research on fish resource in the upstream of Lancang River. *Mod Agric Sci Technol* 14:337
- Havel JE, Lee CE, Vander Zanden MJ (2005) Do reservoirs facilitate invasions into landscapes? *Bioscience* 55:518–525. [https://doi.org/10.1641/0006-3568\(2005\)055%5b0518:drfiil%5d2.0.co;2](https://doi.org/10.1641/0006-3568(2005)055%5b0518:drfiil%5d2.0.co;2)
- He DM (1995) Analysis of hydrological characteristics in Lancang-Mekong River Yunnan. *Geogr Environ Res* 7:58–74
- He DM, Tang QC (2000) Chinese International River. Science Press, Beijing
- He DM, Feng Y, Hu JM (2007) Water resources utilization and ecological protection of International River in southwest China. Science Press, Beijing, pp 180–189
- Humborg C, Ittekkot V, Cociasu A, Vonbodungen B (1997) Effect of Danube River dam on Black Sea biogeochemistry and ecosystem structure. *Nature* 386:385–388
- Jiang XM, Ding CZ, Brosse S, Pan BZ, Lu Y, Xie ZC (2019) Local rise of phylogenetic diversity due to invasions and extirpations leads to a regional phylogenetic homogenization of fish fauna from Chinese isolated plateau lakes. *Ecol Indic* 101:388–398
- Kang B, He DM, Perrett L, Wang HY, Hu WX, Deng WD, Wu YF (2009) Fish and fisheries in the Upper Mekong: current assessment of the fish community, threats and conservation. *Rev Fish Biol Fish* 19:465–480. <https://doi.org/10.1007/s11160-009-9114-5>
- Kang B, Hu WX, Qi WL, Yang CM, Li JH (2010) Research on fish species diversity in the Buyuan River. *Progr Fish Sci* 31:03–06
- Lei CY (2012) The influence and protection of hydropower construction on fish in the mainstream of Lancang River: a case study of Jinghong, Xiaowan and Gongguoqiao Dams Yunnan University
- Leprieur F, Beauchard O, Blanchet S, Oberdorff T, Brosse S (2008) Fish invasions in the world's river systems: when natural processes are blurred by human activities. *PLoS Biol* 6:404–410. <https://doi.org/10.1371/journal.pbio.0060028>
- Leprieur F, Albouy C, De Bortoli J, Cowman PF, Bellwood DR, Mouillot D (2012) Quantifying phylogenetic beta diversity: distinguishing between 'true' turnover of lineages and phylogenetic diversity gradients. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0042760>
- Lichstein JW (2007) Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecol* 188:117–131. <https://doi.org/10.1007/s11258-006-9126-3>
- Liermann CR, Nilsson C, Robertson J, Ng RY (2012) Implications of dam obstruction for global freshwater fish diversity. *BioScience* 62:539–548
- Liu MD, Chen DQ, Duan XB, Wang K, Liu SP (2011) Ichthyofauna composition and distribution of fishes in Yunnan section of Lancang River. *Fish Sci China* 18:156–170
- Liu CL, He DK, Chen YF, Olden JD (2017) Species invasions threaten the antiquity of China's freshwater fish fauna. *Divers Distrib* 23:556–566. <https://doi.org/10.1111/ddi.12541>
- Marchetti MP, Lockwood JL, Light T (2006) Effects of urbanization on California's fish diversity: differentiation, homogenization and the influence of spatial scale. *Biol Conserv* 127:310–318
- Morlon H et al (2011) Spatial patterns of phylogenetic diversity. *Ecol Lett* 14:141–149. <https://doi.org/10.1111/j.1461-0248.2010.01563.x>
- Mouillot D et al (2011) Protected and threatened components of fish biodiversity in the Mediterranean Sea. *Curr Biol* 21:1044–1050. <https://doi.org/10.1016/j.cub.2011.05.005>
- Moyle PB, Marchetti MP (2006) Predicting invasion success: freshwater fishes in California as a model. *Bioscience* 56:515–524
- Moyle PB, Mount JF (2007) Homogenous rivers, homogenous faunas. *PNAS* 104:5711–5712
- Nekola JC, White PS (1999) The distance decay of similarity in biogeography and ecology. *J Biogeogr* 26:867–878. <https://doi.org/10.1046/j.1365-2699.1999.00305.x>
- Nelson JS (2006) Fishes of the world. Wiley, New York
- Nilsson C, Reidy CA, Dynesius M, Revenga C (2005) Fragmentation and flow regulation of the world's large river systems. *Science* 308:405–408. <https://doi.org/10.1126/science.1107887>

- Nunes CA, Braga RF, Figueira JEC, Neves FD, Fernandes GW (2016) Dung Beetles along a tropical altitudinal gradient: environmental filtering on taxonomic and functional diversity. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0157442>
- Olden JD, Poff NL (2003) Toward a mechanistic understanding and prediction of biotic homogenization. *Am Nat* 162:442–460. <https://doi.org/10.1086/378212>
- Olden JD, Poff NL (2004) Ecological processes driving biotic homogenization: testing a mechanistic model using fish faunas. *Ecology* 85(7):1867–1875
- Pettesse ML, Petrere M (2012) Tendency towards homogenization in fish assemblages in the cascade reservoir system of the Tiete river basin, Brazil. *Ecol Eng* 48:109–116. <https://doi.org/10.1016/j.ecoleng.2011.06.033>
- Poff NL, Olden JD, Merritt DM, Pepin DM (2007) Homogenization of regional river dynamics by dams and global biodiversity implications. *Proc Natl Acad Sci USA* 104:5732–5737. <https://doi.org/10.1073/pnas.0609812104>
- Pysek P et al (2009) The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. *Divers Distrib* 15:891–903. <https://doi.org/10.1111/j.1472-4642.2009.00602.x>
- Raghavan R, Prasad G, Anvar-Ali PH, Pereira B (2008) Exotic fish species in a global biodiversity hotspot: observations from River Chalakudy, part of Western Ghats, Kerala, India. *Biol Invasions* 10:37–40. <https://doi.org/10.1007/s10530-007-9104-2>
- Rahel FJ (2000) Homogenization of fish faunas across the United States. *Science* 288:854–856
- Rahel FJ (2002) Homogenization of freshwater faunas. *Annu Rev Ecol Syst* 33:291–315
- Santos RMB, Fernandes LFS, Cortes RMV, Varandas SGP, Jesus JJB, Pacheco FAL (2017) Integrative assessment of river damming impacts on aquatic fauna in a Portuguese reservoir. *Sci Total Environ* 601–602:1108–1118
- Sa-Oliveira JC, Hawes JE, Isaac-Nahum VJ, Peres CA (2015) Upstream and downstream responses of fish assemblages to an eastern Amazonian hydroelectric dam. *Freshw Biol* 60:2037–2050. <https://doi.org/10.1111/fwb.12628>
- Scott MC, Helfman GS (2001) Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. *Fisheries* 26:6–15
- Song MY, Lee WO, Kim KH, Park YS, Bae MJ (2016) The impact of the Goesan dam on fish communities up- and downstream. *Ann Limnol Int J Limnol* 52:151–162. <https://doi.org/10.1051/limn/2016002>
- R Core Team (2018) R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical computing. Retrieved from <https://www.R-project.org/>
- Toussaint A, Beauchard O, Oberdorff T, Brosse SVS (2014) Historical assemblage distinctiveness and the introduction of widespread non-native species explain worldwide changes in freshwater fish taxonomic dissimilarity. *Glob Ecol Biogeogr* 23:574–584
- Valbo-Jorgensen J, Coates D, Hurtle KG (2009) The Mekong: fish diversity in the Mekong River Basin. Biophysical environment of an International River basin. Academic Press, London, pp 161–196
- Vamosi JC, Wilson JR (2008) Nonrandom extinction leads to elevated loss of angiosperm evolutionary history. *Ecol Lett* 11:1047–1053. <https://doi.org/10.1111/j.1461-0248.2008.01215.x>
- Villegger S, Grenouillet G, Brosse S (2013) Decomposing functional -diversity reveals that low functional-diversity is driven by low functional turnover in European fish assemblages. *Glob Ecol Biogeogr* 22:671–681. <https://doi.org/10.1111/geb.12021>
- Villegger S, Grenouillet G, Brosse S (2014) Functional homogenization exceeds taxonomic homogenization among European fish assemblages. *Glob Ecol Biogeogr* 23:1450–1460. <https://doi.org/10.1111/geb.12226>
- Vitule JRS, Skora F, Abilhoa V (2012) Homogenization of freshwater fish faunas after the elimination of a natural barrier by a dam in Neotropics. *Divers Distrib* 18:111–120. <https://doi.org/10.1111/j.1472-4642.2011.00821.x>
- Wang J, Ding LY, Tao J, Ding CZ, He DM (2019) The effects of dams on macroinvertebrates: global trends and insights. *River Res Appl* 35:1–12
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ (2002) Phylogenies and community ecology. *Annu Rev Ecol Syst* 33:475–505
- Winter M et al (2009) Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proc Natl Acad Sci USA* 106:21721–21725. <https://doi.org/10.1073/pnas.0907088106>
- Zefferman E et al (2015) Plant communities in harsh sites are less invaded: a summary of observations and proposed explanations. *Aob Plants*. <https://doi.org/10.1093/aobpla/plv056>
- Zhang R (2001) Post-evaluation of ecological environment of manwan hydroelectric station on the Lancang River. *Design of Hydroelectric Power Station* 17
- Zhang C, Ding LY, Ding CZ, Chen LQ, Sun J, Jiang XM (2018) Responses of species and phylogenetic diversity of fish communities in the Lancang River to hydropower development and exotic invasions. *Ecol Indic* 90:261–279
- Ziv G, Baran E, Nam S, Rodriguez-Iturbe I, Levin SA (2012) Trading-off fish biodiversity, food security, and hydropower in the Mekong River Basin. *Proc Natl Acad Sci USA* 109:5609–5614. <https://doi.org/10.1073/pnas.1201423109>

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