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

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ORIGINAL RESEARCH

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

Chao Zhang · Chengzhi Ding · Liuyong Ding · Liqiang Chen · Jinming Hu · Juan Tao · Xiaoming Jiang

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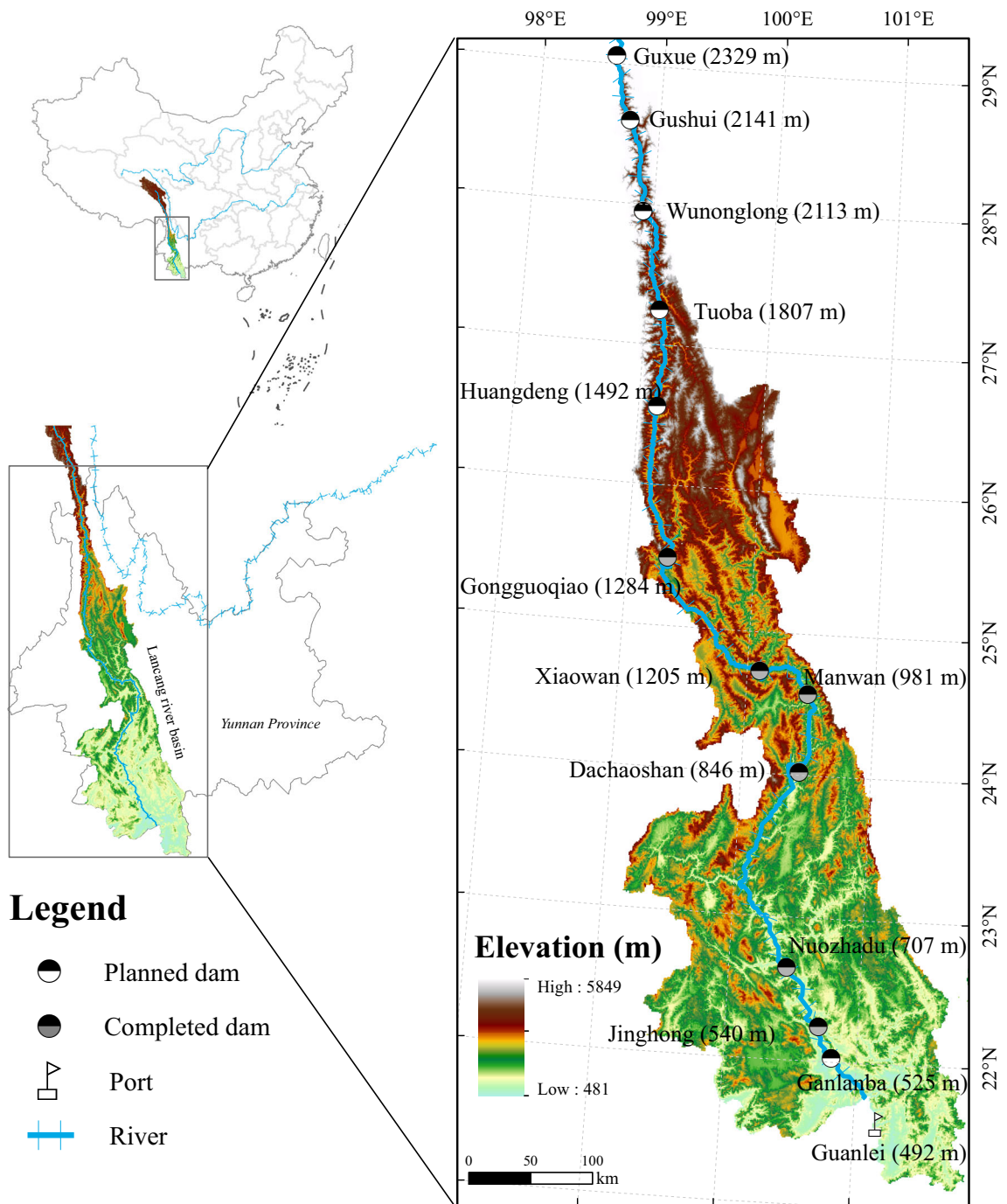
Fig. 1 Study area. The 12 completed or planned dams selected as the region boundaries are displayed in the diagram, and the elevation information of each dam is shown in parentheses. The

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

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

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 (Villeger 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

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

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:

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

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

2010; Leprieur et al. 2012). Taxonomic dissimilarity was measured using the Sørensen index (β_{sor}), and the taxonomic turnover (β_{sim}) and nestedness (β_{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:

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

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

$$\beta_{\text{sne.phy}} = \beta_{\text{sor.phy}} - \beta_{\text{sim.phy}} \tag{6}$$

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 $\beta_{sor.tax}$ 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
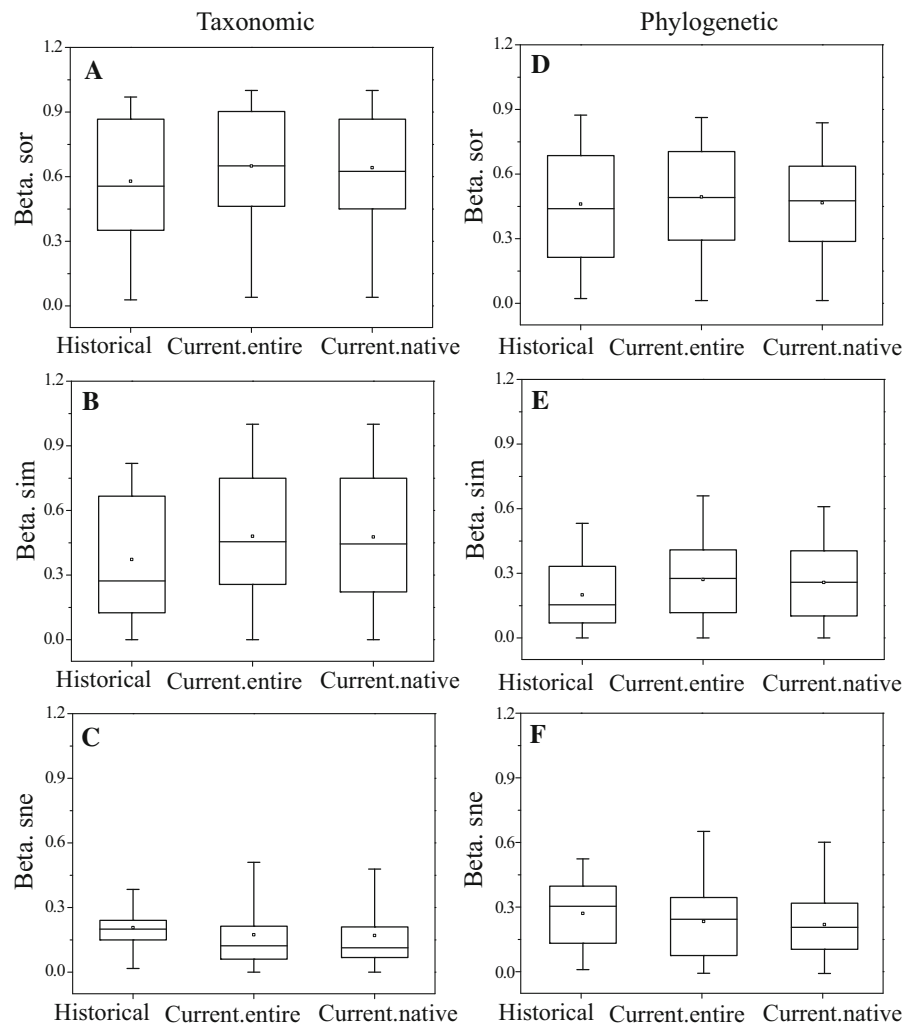
However, the historical value of phylogenetic dissimilarity among the 12 reaches was lower than that of taxonomic facets, with a mean value of 0.48 (range 0.02–0.87; Fig. 2d). Compared with the taxonomic dissimilarity component, the phylogenetic nestedness component (mean value: 0.28, 58.3%) contributed 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 $\beta_{sor.phy}$ 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		
	$\beta_{sor.tax}$	$\beta_{sim.tax}$	$\beta_{sne.tax}$	$\beta_{sor.phy}$	$\beta_{sim.phy}$	$\beta_{sne.phy}$
Entire						
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
Native						
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 $\pm$ 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		
	t	*p*	*df*	*t*	*p*	*df*
Entire assemblages						
$Sor_h - Sor_c$	-6.09	**< 0.001**	65	-3.02	**0.004**	65
$Sim_h - Sim_c$	-8.08	**< 0.001**	65	-7.18	**< 0.001**	65
$Sne_h - Sne_c$	2.70	**0.009**	65	3.28	**0.002**	65
Native assemblages						
$Sor_h - Sor_c$	-5.29	**< 0.001**	65	-0.50	0.619	65
$Sim_h - Sim_c$	-7.91	**< 0.001**	65	-6.92	**< 0.001**	65
$Sne_h - Sne_c$	2.96	**0.004**	65	4.01	**< 0.001**	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
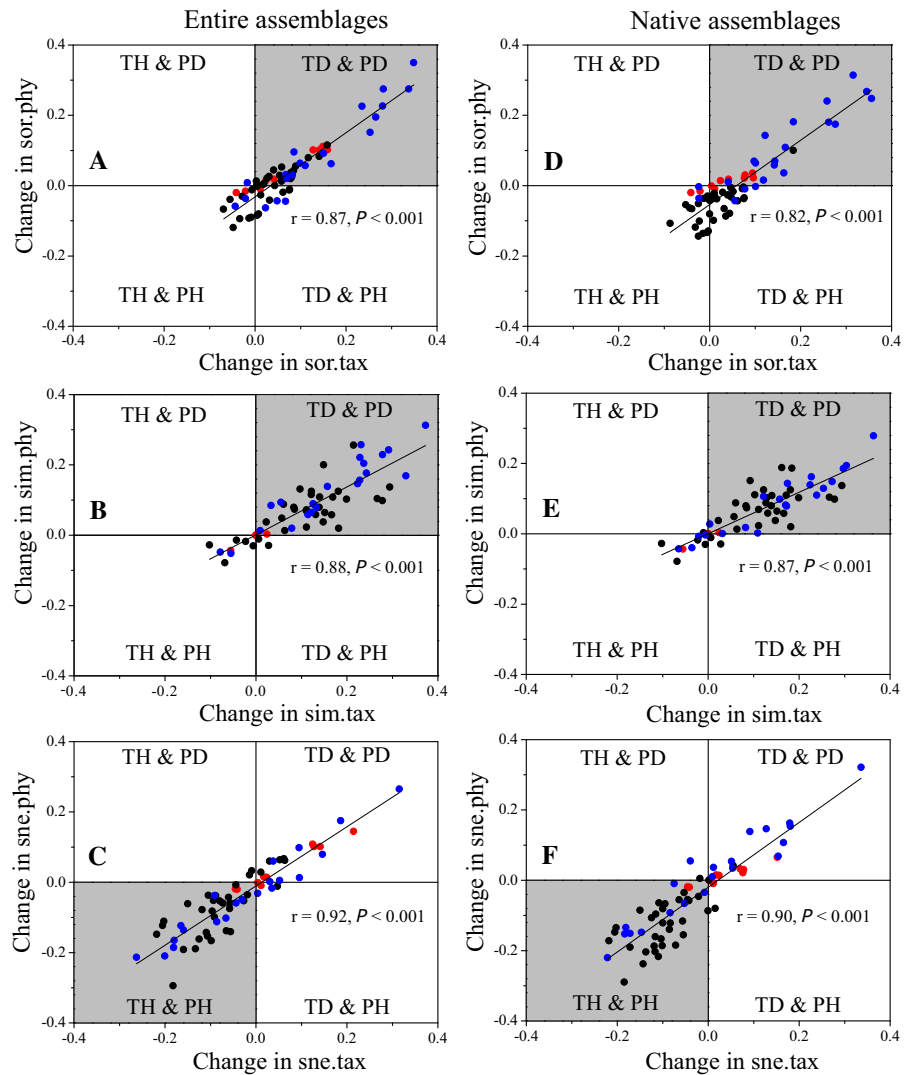
With respect to the native assemblages, the nMDS plots revealed a pattern similar to that for the entire assemblages for both taxonomy and phylogeny (Fig. 4b, d). Two-way PERMANOVA revealed that only region (F = 36.35, *P* = 0.001 for taxonomy and F = 40.58, *P* = 0.001 for phylogeny) was a significant 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
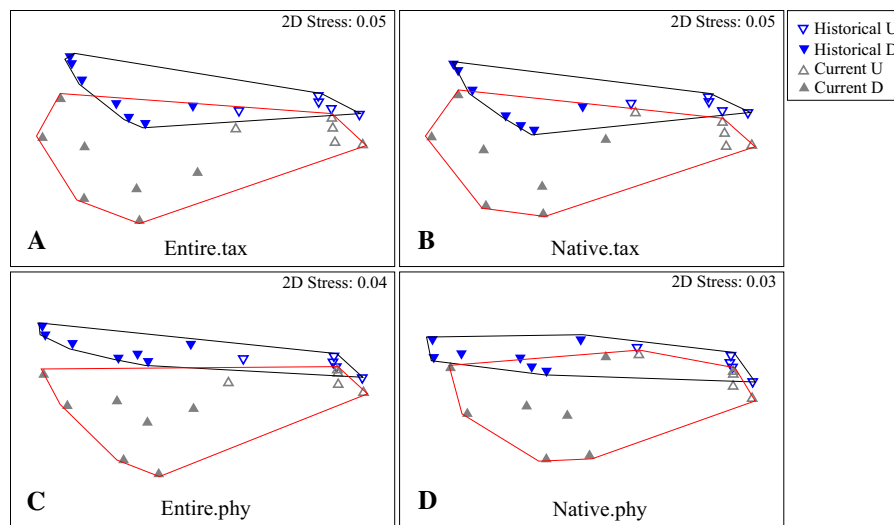
Fig. 4 nMDS analysis of entire assemblages and native assemblages for taxonomic and phylogenetic facets. *U* upstream reaches, *D* downstream reaches. The black and red polygons indicate the degree of dispersion for the historical and current periods, respectively

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)
Taxonomy				
Time	3.184	**0.014**	2.071	0.077
Region	37.17	**0.001**	36.35	**0.001**
Time × Region	1.757	0.106	1.216	0.301
Phylogeny				
Time	2.948	**0.019**	2.001	0.106
Region	42.24	**0.001**	40.58	**0.001**
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
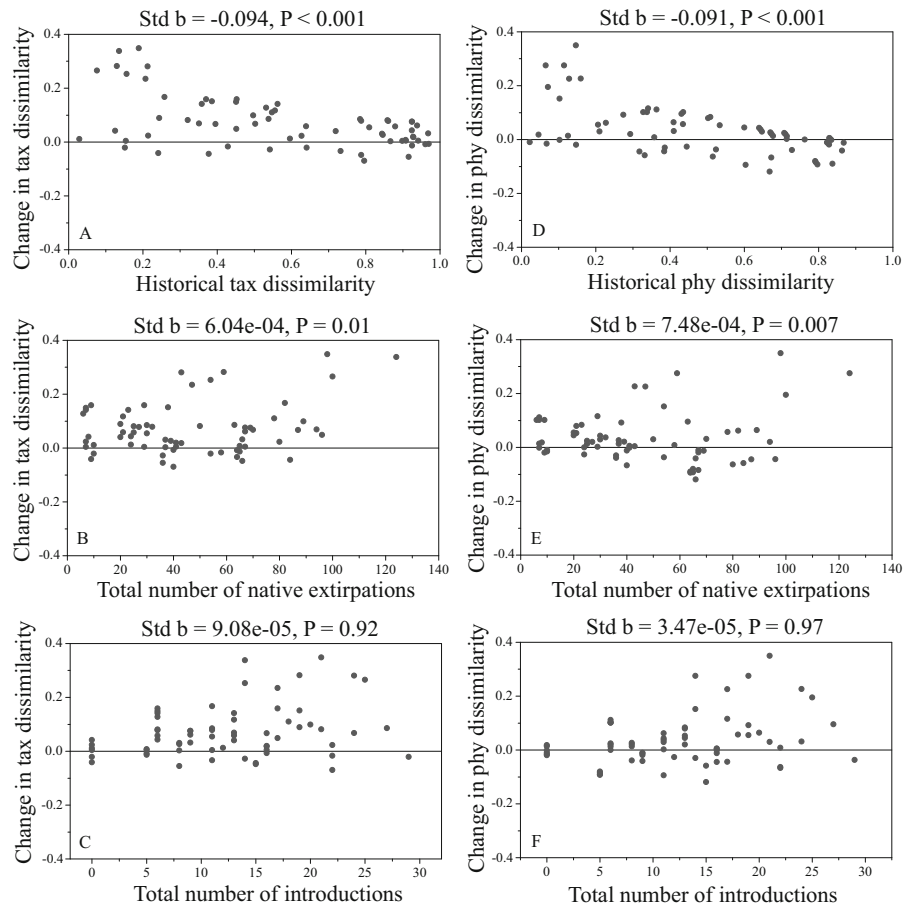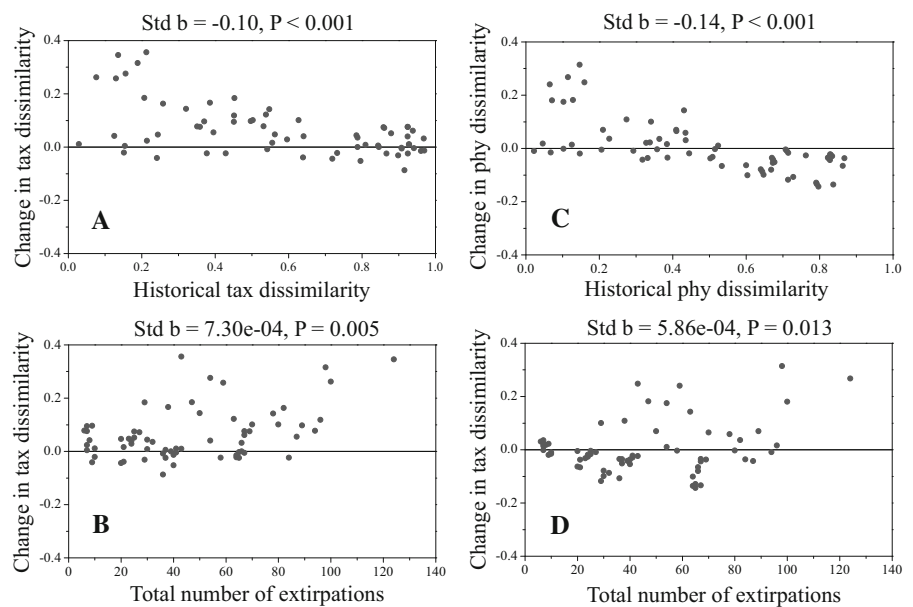

Fig. 6 Effects of historical dissimilarity and extirpation pressures on changes in taxonomic and phylogenetic dissimilarities for native assemblages. Standard partial regression coefficient (Std *b*) and associated *P* value from MRM are given for each variable

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*, *Discherodontus 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.

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
	Siluriformes	Sisoridae	4	5	3	3
GS-WNL	Cypriniformes	Cobitidae	1	1	1	1
		Balitoridae	3	5	3	4
		Cyprinidae	1	3	1	3
	Siluriformes	Sisoridae	4	6	3	3
WNL-TB	Cypriniformes	Cobitidae	1	1	1	1
		Balitoridae	3	5	3	3
		Cyprinidae	2	4	1	3
	Siluriformes	Sisoridae	4	8	4	5
TB-HD	Cypriniformes	Cobitidae	1	1	1	1
		Balitoridae	3	5	3	4
		Cyprinidae	1	3	1	3
	Siluriformes	Sisoridae	4	8	4	5
HD-GGQ	Cypriniformes	Cobitidae	3	3	3	3
		Balitoridae	7	13	6	10
		Cyprinidae	6	10	10 (**4⁺**)	14 (**4⁺**)
	Siluriformes	Sisoridae	5	9	5	9
	Synbranchiformes	Synbranchidae	1	1	1	1
	Perciformes	Gobiidae			**1⁺**	**2⁺**

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**$^+$)	20 (**9**$^+$)
	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**$^+$	**1**$^+$
		Gobiidae			**1**$^+$	**2**$^+$
		Odontobutidae			**1**$^+$	**1**$^+$
XW-MW	Cypriniformes	Cobitidae	3	3	3	3
		Balitoridae	8	13	1	2
		Cyprinidae	16	19	16 (**4**$^+$)	18 (**5**$^+$)
	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**$^+$	**3**$^+$
		Odontobutidae			**1**$^+$	**1**$^+$
	Osmeriformes	Osmeridae			**1**$^+$	**1**$^+$
	Cyprinodontiformes	Poeciliidae			**1**$^+$	**1**$^+$
MW-DCS	Cypriniformes	Cobitidae	3	3	1	1
		Balitoridae	7	14	4	5
		Cyprinidae	18	26	16 (**6**$^+$)	19 (**6**$^+$)
	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**$^+$	**1**$^+$
		Gobiidae			**1**$^+$	**1**$^+$
DCS-NZD	Cypriniformes	Cobitidae	3	3	3	3
		Balitoridae	9	18	5	9
		Cyprinidae	22	32	20 (**3**$^+$)	28 (**3**$^+$)
	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**$^+$	**2**$^+$

Region	Order	Family	Historical		Current	
			No. genera	No. species	No. genera	No. species
	Gobiidae	1	1	**1+**	**1+**	
	Channidae	1	1	1	1	
NZD-JH	Cypriniformes	Cobitidae	6	6	3	3
		Balitoridae	7	15	1	3
		Cyprinidae	27	42	15 (**3+**)	18 (**3+**)
	Siluriformes	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+**	**1+**
		Anabantidae	1	1		
		Osphronemidae	2	2		
		Channidae	1	3	1	1
	Tetraodontiformes	Tetraodontidae	1	1		
	Osmeriformes	Osmeridae			**1+**	**1+**
JH-GLB	Anguilliformes	Anguillidae	1	1		
	Cypriniformes	Cyrinocheilidae	1	1		
		Cobitidae	7	7	4	4
		Balitoridae	7	18	3	6
		Cyprinidae	35	56	26 (**5+**)	35 (**6+**)
	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+**	**1+**
		Anabantidae	1	1		
		Osphronemidae	2	2	1	1
		Channidae	1	3	1	1
		Cichlidae			**1+**	**2+**
	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**[+])	45 (**9**[+])
	Characiformes	Prochilodontidae			**1**[+]	**1**[+]
	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
	Beloniformes	Adrianichthyidae	1	2	1	1
	Cyprinodontiformes	Poeciliidae			**1**[+]	**1**[+]
	Synbranchiformes	Synbranchidae	1	1	1	1
		Mastacembelidae	1	1	1	1
	Perciformes	Gobiidae	1	1	**1**[+]	**2**[+]
		Anabantidae	1	1	1	1
		Osphronemidae	2	2	2	3 (**1**[+])
		Channidae	1	3	1	3
	Tetraodontiformes	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	*Dasyatis laosensis*	Native	93	*Cosmochilus nanlaensis*	Native
2	*Anguilla bicolor*	Native	94	*Puntioplites falcifer*	Native
3	*Gyrinocheilus aymonieri*	Native	95	*Puntioplites waandersi*	Native
4	*Sinibotia longiventralis*	Native	96	*Poropuntius carinatus*	Native
5	*Syncrossus beauforti*	Native	97	*Poropuntius huangchuchieni*	Native
6	*Ambastaia nigrolineata*	Native	98	*Poropuntius krempfi*	Native
7	*Acantopsis dialuzona*	Native	99	*Barbonymus gonionotus*	Native
8	*Lepidocephalichthys berdmorei*	Native	100	*Sikukia flavicaudata*	Native
9	*Acanthopsoides gracilis*	Native	101	*Sikukia gudgeri*	Native
10	*Misgurnus anguillicaudatus*	Native	102	*Sikukia longibarbata*	Native

continued

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

continued

	Species	Occurrence		Species	Occurrence
56	*Barilius caudiocellatus*	Native	148	*Glyptothorax fuscus*	Native
57	*Barilius koratensis*	Native	149	*Glyptothorax laosensis*	Native
58	*Barilius pulchellus*	Native	150	*Glyptothorax longinema*	Native
59	*Opsariichthys bidens*	Native	151	*Glyptothorax macromaculatus*	Native
60	*Macrochirichthys macrochirius*	Native	152	*Pseudecheneis immaculatus*	Native
61	*Rhodeus ocellatus*	Non-native	153	*Pseudecheneis sulcatoides*	Native
62	*Rhodeus spinalis Oshima*	Non-native	154	*Pareuchiloglanis abbreviatus*	Native
63	*Acheilognathus barbatulus*	Native	155	*Pareuchiloglanis gracilicaudata*	Native
64	*Metzia lineata*	Native	156	*Glyptothorax zanaensis*	Native
65	*Hemiculter leucisculus*	Non-native	157	*Pareuchiloglanis myzostoma*	Native
66	*Hemiculterella macrolepis*	Native	158	*Pareuchiloglanis prolixdorsalis*	Native
67	*Paralaubuca barroni*	Native	159	*Creteuchiloglanis longipectoralis*	Native
68	*Cultrichthys erythropterus*	Non-native	160	*Oreoglanis jingdongensis*	Native
69	*Pseudolaubuca sinensis*	Non-native	161	*Oreoglanis setiger*	Native
70	*Hemibarbus maculatus*	Native	162	*Akysis brachybarbatus*	Native
71	*Pseudorasbora parva*	Non-native	163	*Akysis sinensis*	Native
72	*Abbotina rivularis*	Non-native	164	*Oryzias minutillus*	Native
73	*Gobiobotia yuanjiangensis*	Native	165	*Oryzias sinensis*	Native
74	*Ctenopharyngodon idella*	Non-native	166	*Gambusia affinis*	Exotic
75	*Mylopharyngodon piceus*	Non-native	167	*Monopterus albus*	Native
76	*Tinca tinca*	Exotic	168	*Mastacembelus armatus*	Native
77	*Hypophthalmichthys molitrix*	Non-native	169	*Oreochromis mossambica*	Exotic
78	*Hypophthalmichthys nobilis*	Non-native	170	*Oreochromis nilotica*	Exotic
79	*Tor laterivittatus*	Native	171	*Rhinogobius cliffordpopei*	Non-native
80	*Tor polylepis*	Native	172	*Rhinogobius giurinus*	Non-native
81	*Tor sinensis*	Native	173	*Rhinogobius maculicervix*	Native
82	*Tor tambra*	Native	174	*Rhinogobius brunneus (Temminck et Schlegel)*	Non-native
83	*Tor tambroides*	Native	175	*Micropercops swinhonis*	Non-native
84	*Folifer brevifilis*	Native	176	*Anabas testudineus*	Native
85	*Hampala macrolepidota*	Native	177	*Macropodus opercularis*	Native
86	*Puntius semifasciolatus*	Native	178	*Macropodus chinensis*	Non-native
87	*Puntius ticto*	Native	179	*Trichogaster trichopterus*	Native
88	*Onychostoma gerlachi*	Native	180	*Channa gachua*	Native
89	*Scaphiodonichthys acanthopterus*	Native	181	*Channa striata*	Native
90	*Discherodontus parvus*	Native	182	*Channa lucius*	Native
91	*Cyclocheilichthys repasson*	Native	183	*Monotrete turgidus*	Native
92	*Cosmochilus cardinalis*	Native	184	*Neosalanx taihuensis*	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
Entire assemblages				
Historical dissimilarity	− 0.094	**< 0.001**	− 0.091	**< 0.001**
Introduction	9.08e−05	0.92	3.47e−05	0.97
Extirpation	6.04e−04	**0.01**	7.48e−04	**0.007**
R^2	0.11	**< 0.001**	0.10	**< 0.001**
Native assemblages				
Historical dissimilarity	− 0.10	**< 0.001**	− 0.14	**< 0.001**
Extirpation	7.30e−04	**0.005**	5.86e−04	**0.013**
R^2	0.12	**< 0.001**	0.14	**< 0.001**

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