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Responses of species and phylogenetic diversity of fish communities in the Lancang River to hydropower development and exotic invasions

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ABSTRACT

Multiple anthropogenic disturbances have been modifying the structure and diversity of local assemblages worldwide through both introductions of nonnative species and disappearance of native species. Most previous studies have concentrated on the effects of human disturbances on species diversity, but their effects on phylogenetic diversity have been relatively seldom documented. Here, we measured the temporal changes in species and phylogenetic alpha diversity in 12 mainstream regions of the Lancang River (LCR) in the context of hydropower development and widespread exotic invasions. We found that disturbances by dams and widespread introductions of exotic fishes have induced a marked loss of native species (average 36.8 species disappeared per region, accounting for 47.2% of the historical native species) in the downstream regions over time, whereas few native species were disappeared (average 4 species disappeared, accounting for 23.8% of the historical native species) in the upstream regions. In terms of phylogenetic diversity, however, the average taxonomic distinctness (Δ^+, a taxonomic proxy for phylogenetic diversity) of the entire assemblages significantly increased (an increase of 4.4% compared to historical Δ^+) in all regions, while native Δ^+ insignificantly decreased in downstream regions, and the variation in taxonomic distinctness (Λ^+, a proxy for variation in phylogenetic diversity) of the entire assemblages significantly increased (24.6%) in downstream regions, while native Λ^+ significantly decreased (12.0%) in all regions. Such changes in phylogenetic diversity were triggered by invasions by distantly related exotic species and disappearances of congeneric endemic species. Across the LCR, the relationships between species richness, Δ^+, and Λ^+ and altitude all became obscure due to the combined effect of introductions and disappearances. In dammed regions, the disappearance rate and rate of change in the taxonomic distinctness of native assemblages showed negative correlations with the distances of cascade dams. Our study showed that intensive hydropower development and exotic invasions have significantly affected both the taxonomic and phylogenetic diversity of fish assemblages in the LCR, especially in its downstream region. However, the response of phylogenetic diversity to human disturbance was inconsistent with that of species diversity, implying that examining the response of phylogenetic diversity could provide additional information for assessing the impacts of human domination.

1. Introduction

The accelerated extinction of species due to the increasing anthropogenic impacts on ecosystems, especially through habitat changes, pollution and the overexploitation of populations, has become the preeminent characteristic of the current biodiversity crisis (Cardinale et al., 2012). A growing number of studies showed that dam construction and operation for hydroelectric waterpower facilities led to a series of undesirable ecological responses in rivers (Nadon et al., 2015, Santos et al., 2017), and the influence of dams on fish diversity has become one of the main environmental problems (Ziv et al., 2012). Cascade dams lead to habitat fragmentation, obstructing the dispersal and migration of organisms and destroying spawning habitats for certain species, which are directly linked to the loss of populations and species of freshwater fishes (Nilsson et al., 2005, Petesse and Petrere, 2012, Gao et al., 2013).

In addition to extinction, human activities have also promoted the introduction of exotic species (Strayer, 2012). Changes in habitats have increased the risk of extirpation of habitat specialists and invasion by exotic species (Cheng et al., 2015). Studies have shown that exotic

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species are likely to find modified habitats more suitable, giving them an advantage in competition with native fishes for food, space and other resources (Poff et al., 2007) and tending to result in the extirpation of endemic species (Rahel, 2002, Ding et al., 2017). Anthropogenic nonnative introduction and native extirpation processes have acted together to affect the composition and richness of local assemblages worldwide as well as their functional and phylogenetic structure (Olden and Poff, 2004, Villeger et al., 2014, Liu et al., 2017), increasing the level of similarity among faunas (i.e., biotic homogenization) (Dudgeon and Smith, 2006, Olden et al., 2008, Raghavan et al., 2008).

Most previous studies examining the effects of human-mediated introductions of exotic species and dam construction on fish diversity focused on the level of species diversity (i.e., species richness and species composition among assemblages) (Agostinho et al., 2004, Agostinho et al., 2008, Limburg and Waldman, 2009, Cheng et al., 2016). In contrast, effects of human disturbances on the phylogenetic diversity of fish assemblages have been relatively seldom documented (Jiang et al., 2015). Phylogenetic diversity, or the average phylogenetic distance of species assemblages, has been acknowledged to represent the evolutionary history of species within an assemblage and can reflect the ecological differences among species (Webb et al., 2002). The invasions and extirpations of species are not random processes that occur within a hierarchical taxonomic tree but rather a reflection of species life history responses to environmental change (Freville et al., 2007, Winter et al., 2009). Extinctions usually befall specialized endemic or rare species, often from species poor families, which form distinct parts of biotas (Gaston, 1998, Vamosi and Wilson, 2008). Invasive species are often ecological generalists with wide distributional ranges, belonging to species-rich families (Pysek et al., 2009). Hence, the loss of native species and the gain of exotic species should result in an alteration of phylogenetic diversity. Therefore, examining the effects of extirpations and invasions on phylogenetic diversity can significantly enhance the understanding of how evolutionary and ecological processes drive biodiversity patterns (Graham and Fine, 2008, Winter et al., 2009).

Taxonomic distinctness (TD) indices developed by Clarke and Warwick (1998), quantifying the relatedness of the species within a sample based on Linnaean classification tree distances between species, have been widely used as a proxy for phylogenetic diversity in the absence of evolutionary data based on molecular phylogenies (Heino et al., 2005, Srivastava et al., 2012, Griffin et al., 2013, Jiang et al., 2015). TD indices is based on presence/absence data insensitivity to sampling methods and efforts (Clarke and Warwick, 1998, Clarke and Warwick, 2001a), and they have been applied in terrestrial, marine and freshwater environmental assessments and biological conservation (Jiang et al., 2014, Hu and Zhang, 2016) during the past 20 years.

In this study, we selected the Lancang River (LCR), one of the largest rivers in the world, to examine the changes in the species-level and phylogenetic diversity of fish assemblages during the past three decades. As one of the richest rivers in the world in terms of its fish diversity, the LCR supports a high level of endemism (Baran et al., 2012). However, in recent years, its fish fauna has experienced serious biodiversity loss due to increasing human disturbances (e.g., hydroprojects, nonnative invasions, overfishing, land use change, and pollution) (Kang et al., 2009, Fan et al., 2015). There have been contested plans for 21 hydropower dams on the free-flowing main stream of the LCR, and more than 20 exotic species have been found (Liu et al., 2011). High levels of fish diversity and endemism, as well as its transboundary location, make human disturbance to the LCR of great concern to the public. Therefore, assessments of the impacts of anthropogenic disturbances on the species and phylogenetic diversity were urgently necessary. Our research aimed to (1) examine the temporal changes in species and phylogenetic diversity, (2) characterize whether the diversity-environmental (species and phylogenetic diversity) relationships changed over time, and (3) estimate the influence of different dammed regions on fish species and phylogenetic diversity.

2. Materials and methods

2.1. Study area

The LCR, or Upper Mekong River (UMKR), is one of the largest rivers in the world and is characterized by a high level of fish biodiversity (Valbo-Jorgensen et al., 2009). With a mainstream length of 2129 km, the river 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 north–south flowing river situated in western China, the LCR watershed covers different kinds of landscapes, various climates and a wide range of altitudes, which provides particular and diverse habitats for fishes (Baran et al., 2012).

In recent years, however, an increase in anthropogenic disturbances has affected the fish diversity of the LCR. Since 1993, cascade dams have been built in succession in the mainstem, and the commissioned dams have led to changes in the riverine communities and fish assemblages (Fan et al., 2015). In addition, an increase in exotic species tends to result in the loss of native species; for instance, *Oryzias minutillus* and *Oryzias sinensis* in the LCR have become endangered due to the extensive invasion of *Pseudorasbora parva* and *Rhinogobius* (He et al., 2007). In addition, the fishing intensity continues to increase with the increase in population in the LCR Basin and the efficiency of fishing gear and destructive sampling (Kang et al., 2009). Water pollution has increased due to sewage discharge from both agriculture and industry, especially dredging and mining (Deng and Zeng, 2004). In addition, dwindling forest area and the extensive planting of cash crops (e.g., banana trees) in the downstream of the LCR may affect the habitat for both fish and fish food due to increasing soil erosion.

To date, six dams have begun in operation along the mainstream: *Manwan Dam* in 1993, *Dachaoshan Dam* in 2001, *Jinghong Dam* in 2008, *Xiaowan Dam* in 2009, *Gongguoqiao Dam* in 2011, and *Nuozhadu Dam* in 2012 (key parameters of the six commissioned dams are listed in Table 1), while 15 additional dams will be completed in the next decades. Here, we selected 12 planned or operational dams and *Guanlei Port* as the site boundary to divide the study area into 12 parts: *Guxue-Gushui* (*GX-GS*), *Gushui-Wunonglong* (*GS-WNL*), *Wunonglong-Tuoba* (*WNL-TB*), *Tuoba-Huangdeng* (*TB-HD*), *Huangdeng-Gongguoqiao* (*HD-GGQ*), *Gongguoqiao-Xiaowan* (*GGQ-XW*), *Xiaowan-Manwan* (*XW-MW*), *Manwan-Dachaoshan* (*MW-DCS*), *Dachaoshan-Nuozhadu* (*DCS-NZD*), *Nuozhadu-Jinghong* (*NZD-JH*), *Jinghong-Ganlanba* (*JH-GLB*) and *Ganlanba-Guanlei* (*GLB-GL*) (Fig. 1). These 12 regions represent different kinds of fish habitats, covering a great variation of altitudes and latitudes. From the *GX-GS* region to the *GLB-GL* region, the average altitude decreases from 2235 m to 508.5 m. Furthermore, regions from *Gongguoqiao Dam* to *Ganlanba Dam* have been under the operation of the hydropower station.

Table 1
Key parameters of the six commissioned dams in the study area.

Dam	Normal water storage level (m)	Dam height (m)	Reservoir filling
Gongguoqiao	1319	130.0	Sep. 2011
Xiaowan	1240	292.0	Dec. 2008
Manwan	994	132.0	Mar. 1993
Dachaoshan	899	120.5	Nov. 2001
Nuozhadu	812	260.0	Nov. 2011
Jinghong	602	107.0	Apr. 2008