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► **To cite this version:**

Lin Cheng, Simon Blanchet, Géraldine Loot, Sebastien Villéger, Tanglin Zhang, et al.. Temporal changes in the taxonomic and functional diversity of fish communities in shallow Chinese lakes: the effects of river-lake connections and aquaculture. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 2014, 24 (1), pp.23-34. 10.1002/aqc.2418 . hal-02965442

HAL Id: hal-02965442

<https://ut3-toulouseinp.hal.science/hal-02965442>

Submitted on 15 Oct 2020

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Temporal changes in the taxonomic and functional diversity of fish communities in shallow Chinese lakes: the effects of river–lake connections and aquaculture

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ABSTRACT

1. Habitat modification by humans has severe impacts on the biotic and abiotic components of freshwater ecosystems. In China, shallow lakes in the Yangtze River basin are facing major habitat modification owing to the loss of their natural connections with rivers and the development of aquaculture.

2. In this study, temporal data (ranging from 1970 to 2010) from a set of lakes ($n = 8$) were used to quantify the abiotic and biotic consequences (i.e. taxonomic and functional diversity of fish communities) of such human activities. There were significant abiotic changes that mainly occurred after the 1990s. Specifically, water transparency decreased and the total nitrogen content of the lakes increased considerably.

3. A trend (although not significant) was detected towards a decrease in fish species richness over the period studied. The taxonomic dissimilarity (i.e. beta-diversity) among fish communities decreased significantly over the years, indicating a strong homogenization of the fauna across the lakes.

4. In addition, it was found that fish functional diversity has decreased in most lakes since the 1970s. In particular most migratory fish species with long life-spans and large body size disappeared from the lakes, hence contributing substantially to the observed decrease in functional diversity.

5. Based on the findings, it is argued that both the abiotic and biotic integrity of the lakes were seriously affected after the lakes lost their connections to the rivers. It would therefore be helpful to reconnect the lakes to rivers with wise sluice-gate management, and regulate fishery activities in those lakes to restore fish diversity.

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Received 3 August 2012; Revised 19 September 2013; Accepted 5 October 2013

KEY WORDS: biodiversity loss; functional richness; biotic homogenization; Yangtze River basin; lakes

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INTRODUCTION

Changes in biodiversity patterns resulting from human activities are acknowledged worldwide (Coles, 1997; Lodge *et al.*, 1998; Sala *et al.*, 2000; Millennium Ecosystem Assessment, 2005). The impact of humans on ecosystems is particularly obvious in freshwater ecosystems (Dudgeon *et al.*, 2006), as declines in biodiversity are far greater in freshwater ecosystems than in most terrestrial ecosystems (Sala *et al.*, 2000). Recent attention has focused on the effects of multiple stressors in freshwater ecosystems, among which habitat degradation, pollution and the introduction of non-native species are thought to be the main threats to biodiversity (Lodge *et al.*, 1998; Sala *et al.*, 2000; Dudgeon *et al.*, 2006). Habitat degradation involves direct effects when the habitat is destroyed or indirect effects when there are changes in physico-chemical parameters (Richter *et al.*, 1997; Dudgeon *et al.*, 2006). For instance, dam building imposes synergistic stresses on riverine ecosystems and leads to biotic and abiotic changes (Fahrig, 2003; Park *et al.*, 2003; Nilsson *et al.*, 2005; Tockner *et al.*, 2010b). Similarly, the loss of natural connections between ecosystems (e.g. between a lake and a river) could produce modifications in the physical habitat and hence decrease biodiversity by extirpating native species and facilitating the invasion of non-native species in the river floodplains (Power *et al.*, 1996). Although the effect of the loss of natural connections on the biotic and abiotic integrity of freshwater ecosystems has been investigated (Stanford and Ward, 1995; Stanford *et al.*, 1996; Tockner and Stanford, 2002; Tockner *et al.*, 2010a), very little is known about the coupled effect of connection losses and other human impacts such as aquaculture which can synergistically modify abiotic and biotic components of ecosystems.

The Central Yangtze ecoregion is characterized by vital ecological functions and unique biodiversity, and was therefore considered as one of the Global 200 priority ecoregions for conservation (Dudgeon, 1995; Olson and Dinerstein, 1998). In this region, lakes are naturally connected to rivers, and form a complex network of water systems characterized by high fish diversity (Chang and Cao, 1999; Xie and

Chen, 1999). However, in order to control floods, extensive water conservancy projects were implemented along the Yangtze River during the 1950s–1970s. As a consequence, most lakes have been disconnected from rivers by dams, locks or other water-regulating constructions, therefore potentially impeding the migration of fish between water bodies (Xie and Chen, 1999; Fang *et al.*, 2005). In parallel, considerable aquaculture has flourished in this area (Liang and Liu, 1995; Cui and Li, 2005). Before the loss of the river–lake connections, traditional fisheries exploited natural fish populations in those lakes. Then, after the loss of connections, intensive aquaculture developed in most of the lakes. The main aquaculture species are native carp (e.g. *Hypophthalmichthys molitrix*, *Hypophthalmichthys nobilis* and *Ctenopharyngodon idella*). Some valuable species (e.g. *Siniperca chuatsi* and *Eriocheir sinensis*), and some non-native species have also been cultured (e.g. *Oreochromis mossambicus* and *Oreochromis niloticus*) (Table 1). To date, there have been very few studies that have systematically examined the abiotic and biotic changes following such loss of connectivity between lakes and rivers, notably because of a lack of temporal data describing in detail those kinds of ecosystems (Power *et al.*, 1996; Wang *et al.*, 2005; Tockner *et al.*, 2010b). This is of prime importance, however, for developing efficient conservation programmes, especially in China where there are many endemic fish species (Fu *et al.*, 2003).

Classically, diversity indices used for measuring human impact on fish assemblages have mainly focused on the taxonomic identity of species (i.e. species richness and evenness of abundances) (Peet, 1974; Washington, 1984; Magurran, 2004). However, these indices failed to account for the diversity of biological characteristics among species. Indeed, beyond changes in taxonomic structure, a key question is to understand how environmental changes affect the functions of ecosystems through changes in the functional diversity of communities, i.e. the diversity of the biological attributes of the species (McGill *et al.*, 2006; Diaz *et al.*, 2007).

The aims of this study were threefold. First, changes in the abiotic characteristics of the lakes that followed the loss of lake–river connections

Table 1. Functional specialization of each species in the four-dimensional functional space and Generalized Linear Model (GLM) testing the temporal change in occurrence of each species ^{a,b}

Fish species	N/F ^c	Functional specialization	Null deviance	Residual deviance	P	sig. ^d
<i>Acheilognathus barbatulus</i>		0.2027	27.7259	27.2427	0.9226	
<i>Acheilognathus chankaensis</i>		0.1972	0.0000	0.0000	1.0000	
<i>Anguilla japonica</i>		0.6617	26.9205	21.1922	0.1256	
<i>Acheilognathus macropterus</i>		0.1969	7.9406	5.7416	0.5321	
<i>Aristichthy nobilis</i>	F	0.5536	0.0000	0.0000	1.0000	
<i>Abbottina rivularis</i>		0.1822	7.9406	5.7416	0.5321	
<i>Acheilognathus taenianalis</i>		0.1972	13.0030	10.2400	0.4296	
<i>Acheilognathus tonkinensis</i>		0.1997	22.4934	9.9054	0.0056	**
<i>Bottia superciliaris</i>		0.2681	20.0161	13.9210	0.1071	
<i>Channa argus</i>	F	0.3095	0.0000	0.0000	1.0000	
<i>Culter alburnus</i>		0.2735	13.0033	9.9054	0.3768	
<i>Cobitis arenae</i>		0.2164	0.0000	0.0000	1.0000	
<i>Carassius auratus</i>		0.3007	0.0000	0.0000	1.0000	
<i>Culter axycephalus</i>		0.3122	20.0161	16.6935	0.3445	
<i>Coilia brachygnathus</i>		0.2143	25.8979	22.7441	0.3685	
<i>Cyprinus carpio</i>	F	0.4742	0.0000	0.0000	1.0000	
<i>Culter dabry</i>		0.1735	0.0000	0.0000	1.0000	
<i>Coilia ectenes</i>		0.3443	13.0033	9.9054	0.3768	
<i>Culterichthys erythropterus</i>		0.1734	0.0000	0.0000	1.0000	
<i>Can Hemiculter</i>		0.1784	0.0000	0.0000	1.0000	
<i>Coreius heteroden</i>		0.1360	7.9406	4.4987	0.3284	
<i>Ctenopharyngodon idellus</i>	F	0.5626	0.0000	0.0000	1.0000	
<i>Culter mongolicus</i>		0.2484	25.8979	23.2852	0.4553	
<i>Coreosiniperca roulei</i>		0.1742	7.9406	5.7416	0.5321	
<i>Cobitis sinensis</i>		0.1948	20.0161	13.1833	0.0774	
<i>Distoechodon hupeinensis</i>		0.1410	27.5256	25.3782	0.5424	
<i>Distoechodon tumirostris</i>		0.1356	7.9406	4.4987	0.3284	
<i>Elopichthys bambusa</i>		0.7078	24.4350	18.7870	0.1300	
<i>Fugu ocellatus</i>		0.3078	7.9406	4.4987	0.3284	
<i>Gnathopogon guichenoti</i>		0.1812	13.0030	10.2400	0.4296	
<i>Hemiculter bleekeri</i>		0.1861	16.9084	14.9674	0.5848	
<i>Hemisanlanx brachyrostralis</i>		0.2796	16.9084	15.6470	0.7383	
<i>Hyporhamphus intermedius</i>	F	0.3741	22.4934	19.4661	0.3874	
<i>Hemibarbus labeo</i>		0.3845	7.9406	5.7416	0.5321	
<i>Hemibarbus maculatus</i>		0.1497	24.4350	12.8740	0.0091	**
<i>Hemibagrus macropterus</i>		0.2799	7.9406	4.4987	0.3284	
<i>Hypophthalmichthys molitrix</i>		0.4576	0.0000	0.0000	1.0000	
<i>Hypseleotris swinhonis</i>		0.2826	13.0033	9.9054	0.3768	
<i>Leiocassis longirostris</i>	F	0.2764	16.9080	14.0590	0.4155	
<i>Luciobrama macrocephalus</i>		0.4847	7.9406	4.4987	0.3284	
<i>Leptobotia taeniops</i>		0.1909	20.0161	17.8785	0.5443	
<i>Monopterus albus</i>		0.2768	7.9406	4.4987	0.3284	
<i>Megalobrama amblycephala</i>	F	0.1366	0.0000	0.0000	1.0000	
<i>Misgurnus anguillicaudatus</i>		0.2705	7.9406	5.7416	0.5321	
<i>Myxocyprinus asiaticus</i>		0.5216	7.9406	4.4987	0.3284	
<i>Macropodus chinensis</i>		0.2835	13.0033	9.9054	0.3768	
<i>Microphysogobio kiatingensis</i>		0.1827	13.0033	9.2258	0.2865	
<i>Mugilogobius myxodermus</i>		0.2892	27.7259	26.5631	0.7620	
<i>Mylopharyngodon piceus</i>		0.6317	0.0000	0.0000	1.0000	
<i>Macrura reevesi</i>		0.4308	7.9406	4.4987	0.3284	
<i>Mastacembelus sinensis</i>		0.1578	0.0000	0.0000	1.0000	
<i>Megalobrama skolkovii</i>		0.1419	27.7259	26.1962	0.6754	
<i>Neosalanx taihuensis</i>		0.2930	25.8979	22.7441	0.3685	
<i>Neosalanx taihuensis</i>		0.2922	26.9205	26.0578	0.8344	
<i>Opsariichthys bidens</i>		0.1817	16.9084	15.6470	0.7383	
<i>Ochetobius elongatus</i>		0.2488	24.4346	21.5591	0.4112	
<i>Oryzias latipes</i>		0.2117	27.5256	27.2427	0.9632	
<i>Oreochromis mossambicus</i>	N/F	0.3729	13.0033	9.5607	0.3283	
<i>Oreochromis niloticus</i>	N/F	0.3860	13.0033	9.5607	0.3283	
<i>Odontobutis obscurus</i>		0.1883	7.9406	5.7416	0.5321	
<i>Pseudobagrus albomarginatus</i>		0.1779	7.9406	4.4987	0.3284	

(Continues)

Table 1. (Continued)

Fish species	N/F ^c	Functional specialization	Null deviance	Residual deviance	P	sig. ^d
<i>Parabotia banarescui</i>		0.1863	25.8979	18.9250	0.0728	.
<i>Paramisgurnus dabryanus</i>		0.2684	13.0030	10.2400	0.4296	
<i>Pseudolaubuca engraulis</i>		0.1974	13.0030	10.2400	0.4296	
<i>Parabotia fasciata</i>		0.1861	13.0033	9.9054	0.3768	
<i>Pelteobagrus fulvidraco</i>		0.2762	0.0000	0.0000	1.0000	
<i>Paracanthobrama guichenoti</i>		0.1354	26.9205	18.2812	0.0345	*
<i>Panacheilognathus imberbis</i>		0.2050	20.0161	18.2812	0.6292	
<i>Pseudobagrus nitidus</i>		0.2831	13.0033	9.9054	0.3768	
<i>Pseudorasbora parva</i>		0.1832	0.0000	0.0000	1.0000	
<i>Parabramis pekinensis</i>	F	0.1445	22.4934	19.8330	0.4470	
<i>Pseudolaubuca sinensis</i>		0.1936	26.9205	23.2852	0.3036	
<i>Pseudobrama simoni</i>		0.1768	22.4934	19.4661	0.3874	*
<i>Pelteobagrus vachelli</i>		0.2770	20.0161	12.1949	0.0499	
<i>Rhinogobius cliffordpopei</i>		0.2864	25.8979	21.6976	0.2406	
<i>Rhodeus fangi</i>		0.2073	20.0161	17.8785	0.5443	
<i>Rhinogobius giurinus</i>		0.2839	7.9406	4.4987	0.3284	
<i>Rhodeus lighti</i>		0.2081	25.8979	22.7441	0.3685	
<i>Rhodeus ocellatus</i>		0.2073	20.0161	17.8785	0.5443	
<i>Rhinogobio typus</i>		0.1358	7.9406	4.4987	0.3284	
<i>Squalidus argentatus</i>		0.1800	27.7259	23.2852	0.2176	
<i>Silurus asotus</i>		0.4185	20.0161	14.0594	0.1137	
<i>Siniperca chuatsi</i>	F	0.2063	0.0000	0.0000	1.0000	
<i>Squaliobarbus curriculus</i>		0.1443	27.5256	26.1962	0.7222	
<i>Saurogobio dabryi</i>		0.1433	20.0131	16.6935	0.3445	
<i>Saurogobio gymnocheilus</i>		0.1528	7.9406	4.4987	0.3284	
<i>Siniperca kneri</i>		0.2144	16.9084	13.7825	0.3726	
<i>Sarcocheilichthys nigripinnis</i>		0.1810	7.9406	5.7416	0.5321	
<i>Squalidus nitens</i>		0.1870	24.4350	14.0590	0.0156	*
<i>Siniperca scherzeri</i>		0.1759	20.0161	16.6935	0.3445	
<i>Sarcocheilichthys sinensis</i>		0.1607	22.4934	19.3277	0.3668	
<i>Silurus soldatovi</i>		0.3866	13.0030	11.1480	0.6030	
<i>Toxabramis swinhonis</i>		0.2119	7.9406	5.7416	0.5321	
<i>Xenocypris argentea</i>		0.1366	24.4346	17.8785	0.0875	.
<i>Xenocypris davidi</i>		0.1359	24.4346	23.2852	0.7652	
<i>Xenocypris microlepis</i>		0.1364	26.8205	24.3317	0.4595	

^aFor each species, presence/absence in each lake as the dependent variable and periods as the independent variable.

^bEach GLM result indicated the null and the residual deviance, as well as the probability of rejecting the null hypothesis.

^c'N' stands for non-native species, and 'F' for the main fishery species in the lakes.

^dSignif. Codes: ** $P < 0.01$, * $P < 0.05$.

were assessed. Second, temporal variations in the taxonomic composition of fish communities were evaluated, both in terms of richness (alpha-diversity) and similarity among communities (beta-diversity). Third, changes in the functional diversity of the fish communities in the lakes were studied. This work was carried out using a unique spatio-temporal database summarizing abiotic and biotic conditions for eight lakes in the Yangtze River basin over a 30-year period. Drastic changes in the abiotic characteristics of the lakes were expected after the loss of the lake–river connections, notably because of the reduction in water exchange and the entry of exogenous nutrients from aquaculture. It was also expected that these changes would be followed by a strong turnover in the taxonomic diversity of the

fish communities, as well as a loss in the overall taxonomic diversity. Similarly, a decrease in the functional diversity of the fish communities was anticipated, due in part to the changes in the environmental characteristics and to the impossibility for some species to migrate between water bodies.

MATERIALS AND METHODS

Study area

The eight lakes (Figure 1) chosen for the study are located in the central zone of the Yangtze River basin (N: 29°49'–30°27'; E: 114°18'–116°32') in Hubei, China. This area is situated in the North Temperate Zone and has a large number of lakes

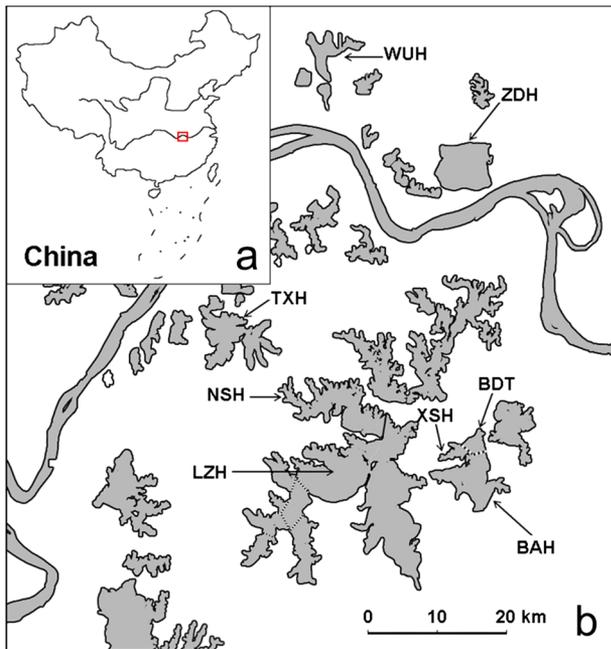


Figure 1. The eight lakes (b) and their location indicated by an empty square in the map of China (a). Lake names are coded: BAH: Bao'anhu Lake; BDT: Biandantang Lake; LZH: Liangzihu Lake; NSH: Niushanhu Lake; TXH: Tangxunhu Lake; WUH: Wuhu Lake; XSH: Xiaosihai Lake; ZDH: Zhangduhu Lake.

(Hubei alone has over 1300). All of the chosen lakes are relatively close to each other (within 200 km²), and share the same regional pool of fish species. They were all naturally connected to the Yangtze River before the 1970s but to control the floods the connections have been severed by dams, and all the lakes have now been used for aquaculture for several decades.

Data collection

Fish data were collected every 10 years from 1970 (i.e. directly after dam building) to 2010, and were classified in four periods to facilitate analyses: '1970s' (i.e. 1970–1979), '1980s' (i.e. 1980–1989), '1990s' (i.e. 1990–1999) and '2000s' (i.e. ≥ 2000). The fish species composition mainly came from historical records (unpublished data) by four-season surveys, and an investigation of commercial catch in each study year, adjusted by available data from publications (Liang and Liu, 1995; Cui and Li, 2005; Wang *et al.*, 2005; Cheng *et al.*, 2010).

Environmental data were collected every 10 years from 1980 to 2010. These data were not

available for the period directly following dam building (i.e. from 1970 to 1980), so environmental data were classified in three periods ('1980s', '1990s' and '2000s'). Environmental data included: water temperature (WT), water depth (WD), water transparency (TRA) measured by Secchi depth, total nitrogen (TN), pH, rigidity (RIG, the concentration of calcium and magnesium salts in water), conductivity (CON) and alkalinity (ALK). These data were based on previous studies in those lakes and are summarized by Liang and Liu (1995) and Cui and Li (2005).

Data analyses

Environment change analyses

Changes in the environmental conditions over the three periods were analysed using Non-metric Multidimensional Scaling (NMDS) based on Bray–Curtis dissimilarity matrices among lakes for each period. NMDS is an unconstrained ordination method for indirect gradient analysis in community ecology (Minchin, 1987). The NMDS ordination procedure can be used to visualize the similarities among samples (Devictor *et al.*, 2010). The NMDS result was summarized by a circle whose centroid represents the mean environmental conditions for each period, and area represents environmental similarity among study lakes for each period (smaller circles representing a higher between-lakes similarity than larger circles). Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson, 2001) was used to test for differences between centroids (i.e. differences in environmental conditions between periods). Environmental similarity among the three periods was tested by a multivariate permutation test, and by pairwise permutation tests between period pairs.

Analyses of taxonomic composition

Fish species richness was first compared among the four periods using Kruskal–Wallis rank sum tests followed by multiple comparison tests. Then, changes in fish composition and similarity among fish communities were analysed using NMDS as described above for environmental data. PERMANOVA was used to test for differences

between centroids (i.e. species composition of communities) and taxonomic similarity between lakes was tested using a multivariate permutation test followed by pairwise permutation tests.

In order to evaluate how the presence of non-native fish species affected changes in community composition and similarity, the same tests were carried out on the fish community without including the non-native species.

Analyses of the functional diversity of fish communities

Measuring the functional diversity of communities requires, as a first step, the functional characterization of the species pool using a set of relevant functional traits (Violle *et al.*, 2007), and values for seven traits were recorded from FishBase (Froese and Pauly, 2010, <http://fishbase.org>). This set of traits aims to assess the functional niche of each species and account for the following: migration status (migratory or sedentary species), maximum body length, maximum age, body length at maturity, age at maturity, trophic guild (carnivorous, herbivorous and invertivorous) and habitat preference (pelagic, benthopelagic and demersal).

As this set of traits gathered both qualitative and quantitative parameters, a multidimensional functional space was built in two steps following Villéger *et al.* (2008). First, functional pairwise distances between species were computed using the Gower's distance, which allows different types of variables to be mixed while giving them equal weights. Then, using this functional distance matrix, a Principal Coordinates Analysis (PCoA) was carried out. PCoA provided coordinates for each species in a multidimensional space, the axes of which may be considered as independent synthetic functional traits (Villéger *et al.*, 2008). Following a trade-off between information quality and interpretability, only the four first axes (representing 34%, 25%, 17% and 12% of the total variance, respectively) were retained, which globally summarize 89% of the total variance. Distribution of species in this four-dimensional functional space according to their respective traits is illustrated in Figure 5. Specialization of a

focal species can be defined as its Euclidean distance to the centre of gravity of all the species in the four-dimensional functional space (Bellwood *et al.*, 2006; Devictor *et al.*, 2010).

Functional diversity gathers three independent facets, of which functional richness (i.e. range of functional traits present) is the only one that does not require species abundances to be computed (Villéger *et al.*, 2010). When considering a multidimensional framework, functional richness is measured as a multidimensional range using convex hull volume (Cornwell *et al.*, 2006). The convex hull is defined by the following condition: if two points belong to the convex hull, any point on the segment between these points also belongs to it. The convex hull thus depends on the most extreme points, called vertices, i.e. species with extreme trait combinations. In other words, functional richness of an assemblage is represented by the combination of all species within the extreme points of the convex hull – relative to the convex hull volume filled by all species in the study.

Functional richness was computed for all communities (each lake and each period), based on the PCoA coordinates of the species present. These raw values were then standardized to a percentage by dividing by the convex hull volume filled by the whole set of species.

All the analyses were carried out in R software (R Development Core Team, 2008) under the packages: *vegan* (Oksanen *et al.*, 2010), *ade4* (Chessel *et al.*, 2004; Dray and Dufour, 2007; Dray *et al.*, 2007), *geometry* (Grasman and Gramacy, 2010) and *cluster* (Maechler *et al.*, 2005).

Changes in species occurrence over time

As a final analysis, tests were carried out to determine whether the presence/absence (i.e. the occurrence) of each species had significantly changed over recent decades in the eight lakes. Generalized Linear Models (GLMs) were used with binomial error terms for each species independently, and with the presence/absence of the species as the dependent variable and the four periods as the independent variable.

RESULTS

Environmental changes in the lakes

Significant environmental changes were found among the three periods (PERMANOVA, $P < 0.001$). The lakes' environmental conditions were similar in the 1980s and 1990s, while significant changes were detected since the 2000s. Specifically, there was a significant decrease in water transparency and a significant increase in total nitrogen in the recent 10-year period (Table 2, Figure 2). The water depth also decreased whereas the rigidity, the conductivity and the alkalinity increased significantly (Figure 2). A slight (but not significant) decrease in environmental similarity over time was also found, with lakes tending to be more dissimilar after the 1990s.

Changes in the taxonomic diversity of fish

Changes in species richness

A non-significant trend was detected toward a decrease in local fish species richness since the 1970s ($P = 0.39$). There was a sharp decrease in the total number of species found in the eight lakes since the 1980s with a drop from more than 90 species in the 1970s to fewer than 80 species thereafter (Supplementary Data, Figure S1).

Changes in the composition and similarity of fish communities among lakes

According to the NMDS analyses of fish communities, significant changes in species composition were not detected during the four periods (i.e. no difference between the position of the centroids in the four circles, PERMANOVA, $P > 0.05$, Figure 3(A)). However, significant increases in the similarity among fish communities within each period were found (Figure 3(A) and (B)), multivariate permutation test $P < 0.001$).

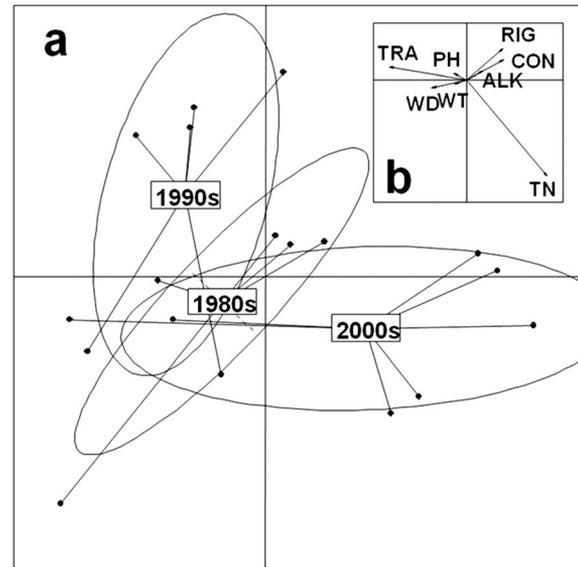


Figure 2. Output of a Non-metric Multidimensional Scaling (NMDS) analysis used to test for changes in the environmental conditions over three periods (1980s, 1990s and 2000s) in eight Chinese lakes. (a) Graphical summary of the NMDS analysis. Results are summarized by a circle whose centroid represents the mean environmental conditions for each period, and area represents environmental dissimilarity among study lakes for each period (smaller circles representing a smaller between-lakes dissimilarity than larger circles). Each circle represents a period and each dot a lake. (b) Vector plots showing the correlation of environmental variables (WT: water temperature, WD: water depth, TRA: water transparency, TN: total nitrogen, PH: pH, RIG: rigidity, CON: conductivity and ALK: alkalinity).

There were significant differences between the 1970s and 1990s and between the 1970s and 2000s (Permutation tests, $P < 0.05$), but not between the 1990s and 2000s or between the 1970s and 1980s (Permutation tests, $P < 0.4$). Lakes were more similar to each other in species composition in recent decades.

The main non-native and aquaculture species are highlighted in Table 1. Two non-native species (*Oreochromis mossambicus* and *Oreochromis niloticus*) were found in some lakes, which have been introduced for aquaculture. All these results were not significantly affected when the analyses were carried out without non-native species.

Table 2. Average values of environmental parameters over the three periods (WT: water temperature, WD: water depth, TRA: water transparency, TN: total nitrogen, PH: pH, RIG: rigidity, CON: conductivity and ALK: alkalinity)

Period	WT	WD	TRA	PH	CON	RIG	ALK	TN
1980s	19.7 ± 16.4	2.3 ± 0.5	1.6 ± 0.2	8.03 ± 0.2	191.3 ± 3750.0	6.4 ± 6.3	55.8 ± 32.6	0.9 ± 0.3
1990s	19.8 ± 2.0	2.2 ± 0.4	1.5 ± 0.3	8.05 ± 0.0	207.6 ± 2213.5	6.3 ± 2.3	53.1 ± 115.5	0.3 ± 0.1
2000s	22.8 ± 1.9	2.2 ± 0.3	0.8 ± 0.2	8.3 ± 0.1	314.5 ± 14276.9	8.1 ± 13.8	67.3 ± 195.5	1.8 ± 0.9

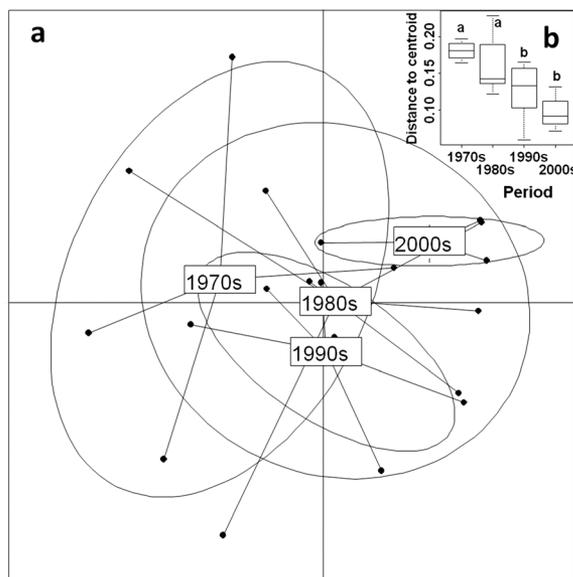


Figure 3. Output of a Non-metric Multidimensional Scaling (NMDS) analysis used to test for changes in the taxonomic composition and dissimilarity among eight Chinese lakes over four decades (1970s, 1980s, 1990s and 2000s). (a) Graphical summary of the NMDS analysis. Results are summarized by a circle whose centroid represents the mean taxonomic composition for each period, and area represents taxonomic dissimilarity among study lakes for each period (smaller circles representing a smaller between-lakes dissimilarity than larger circles). Each circle represents a period and each dot a lake. (b) Boxplot detailing changes in taxonomic dissimilarity from the 1970s to 2000s (the letters above the boxplots show the results of pairwise Permutation test). The median represents the median distance (measured from a Bray–Curtis dissimilarity matrix) from each dot to the centroid of each circle.

Changes in functional richness

Most of the lakes that showed a decrease in species richness were also affected by a loss of functional richness, but the magnitude of this loss varied considerably. For example, in both Biandangtang Lake and Niushanhu Lake species richness decreased by seven species, while functional richness decreased by 37% in Biandangtang Lake, but only decreased by 7% in Niushanhu Lake (Figure 4). Among the lakes showing an increased species richness some also showed an increase in their functional richness but others showed a decrease. For instance, species richness had increased in Liangzihu Lake by three species, but functional richness decreased by 2% (Figure 4). This last finding is determined by a non-random functional turnover, with generalist species replacing original ones (which historically contributed to a high functional richness).

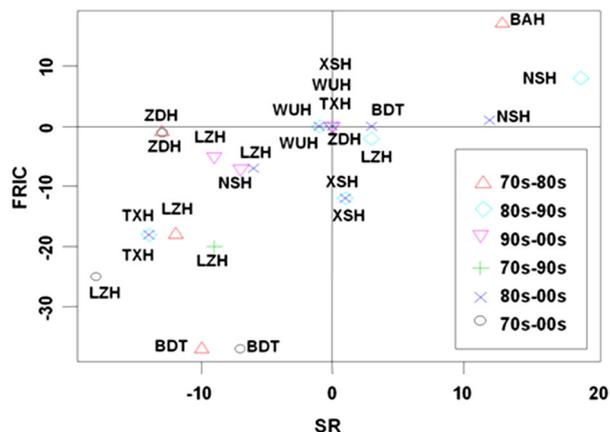


Figure 4. Species richness (SR) changes and the corresponding functional richness (FRic) changes in each lake for each period (lake names are coded as in Figure 1). A positive value indicates an increase in species or functional richness over time. Different symbols denote different periods (see the legend in Figure 1).

The occurrence of several lacustrine species (e.g. *Acheilognathus tonkinensis*, *Hemibarbus maculatus*, *Paracanthobrama guichenoti* and *Pseudobrama simony*) significantly increased over time, indicating that they were more frequent in recent decades in the lakes studied. Most of them had low values of functional specialization (Table 1), and were close to each other in the functional space (Figure 5).

DISCUSSION

Significant environmental changes in recent decades were detected that matched the loss of the natural connections between this set of lakes and the Yangtze River system. This loss in connectivity limits the possibility of water exchange between water bodies, and hence explained such abrupt environmental changes (Power *et al.*, 1996; Tockner *et al.*, 2010b). However, the increase in total nitrogen and conductivity could also be ascribed to the input of nutrients inherent in aquaculture practices (Liang and Liu, 1995; Cui and Li, 2005). Given that these two pressures (loss of connectivity and aquaculture) are acting simultaneously on the lakes (Xie and Chen, 1999; Wang *et al.*, 2005), teasing apart the relative effect of each is a difficult task and would require additional data. Nonetheless, these changes co-vary with a considerable increase in the nutrient

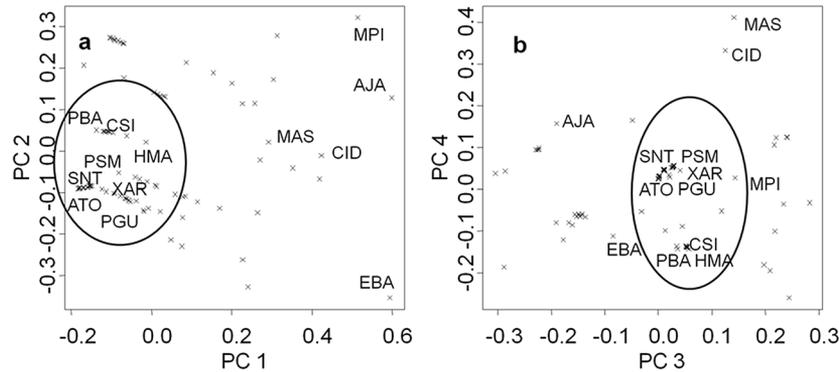


Figure 5. Functional space. Species are plotted in the four-dimensional functional space according to their respective traits (a: Axes 1 vs Axes 2; b: Axes 3 vs Axes 4). Species with high value of functional specialization are noted with their codes (MPI: *Mylopharyngodon piceus*; AJA: *Anguilla japonica*; MAS: *Myxocyprinus asiaticus*; CID: *Ctenopharyngodon idellus*; EBA: *Elopichthys bambusa*); species that had low values are noted and shown in circle (PBA: *Parabotia banarescui*; CSI: *Cobitis sinensis*; HMA: *Hemibarbus maculatus*; PSM: *Pseudobrama simoni*; SNT: *Squalidus nitens*; ATO: *Acheilognathus tonkinensis*; XAR: *Xenocypris argentea*; PGU: *Paracanthobrama guichenoti*).

concentration in the water and a disappearance of macrophytes, thereby decreasing the water transparency markedly over the last 10 years. Indeed, macrophyte cover was found to be positively related to water transparency in these shallow lakes (Cheng *et al.*, 2010). The increase of nutrients increases the risk of harmful algal blooms (Xie and Chen, 1999; Fang *et al.*, 2005); therefore, preventing the increase of nutrient input to lakes should be a priority for the management of lake ecosystems in this area. In addition, restricting the exchange of water between lake and river probably caused the observed decrease in average depth of the lakes since they had always been supplied with water especially in the flooding season before loss of connection to the river.

Environmental conditions play an important role in structuring lacustrine fish communities (Amarasinghe and Welcomme, 2002). Many studies have shown that the fish communities in these Chinese lakes were closely related with environmental parameters, such as water transparency, water depth, and water temperature (Xie *et al.*, 2000; Ye *et al.*, 2006; Cheng *et al.*, 2010). Thus, we expected that environmental changes induced by losing lake–river connections would also indirectly affect the fish taxonomic composition. Species richness tended to decrease over the last four decades, although this decline was not statistically significant. However, change in species richness was extremely irregular during this period, perhaps due to a combination of the collapse of native fish species, the

establishment of some non-native species, such as *Oreochromis mossambicus* and *Oreochromis niloticus* (in the 1990s) and the stocking of native commercial species (Table 1). Functional analysis of fish diversity showed that changes in biodiversity cannot be expressed only by the use of taxonomic information. Indeed, changes in fish species richness and functional richness were sometimes inconsistent. This can happen, for example, when species turnover is such that a new species with original functional traits replaces a generalist species (in that case, species richness stagnates while functional richness increases). Conversely, when species richness increases, functional richness can decrease, for example when species loss is directed toward generalist species. In Xiaosihai Lake, for instance, species richness increased by one species whereas functional richness decreased by 12% in the 2000s. The increase in species richness resulted from the appearance of six species and the disappearance of five species. The six species that appeared (*Acheilognathus tonkinensis*, *Culter mongolicus*, *Siniperca kneri*, *Parabramis pekinensis*, *Neosalanx taihuensis* and *Rhodeus lighti*) were near the central part of the functional space, and all of them are small-bodied lacustrine fish. In contrast, two of the five species that disappeared were closer to the edge of the functional space (Figure 5, *Hemiculter bleekeri* and *Silurus asotus*), meaning that their functional traits were original compared with the whole set of species. They were

indeed larger than the species that appeared recently in the lakes, and needed riparian habitat during their life-cycle. As a result, the disappearance of these original species caused functional diversity to decrease by 12% because of the loss of these traits. The results clearly illustrated the need to consider biodiversity within a multi-facet framework, since an increase in taxonomic diversity can sometimes mask a decrease in functional diversity (Villéger *et al.*, 2010).

The results showed significant changes in the similarity of fish communities over the last four decades. Dissimilarity steeply decreased since the 1980s, indicating a strong decrease in beta-diversity. Specifically, significant changes were detected in the 10 years from the 1980s to the 1990s, while there were no significant changes before the 1980s and after the 1990s. The finding that fish communities did not significantly change during the first decade following the loss of lake–river connections could be explained by a biological delay between the effects of human disturbances and the response of fish populations. In addition, the results might indicate that the fish community tended to be more stable in the recent 10-year period, even if the beta-diversity of the fish communities was still slightly decreasing.

A decrease in beta-diversity over time indicates a homogenization of communities. In general, community homogenization is ascribed to the loss of native species and the establishment of a common pool of non-native species (Olden and Rooney, 2006). The effect of non-native species was tested by performing all the analyses without including non-native species (see Table 1 for the list of non-native species). The NMDS gave similar results when only native species were considered. This indicates that, as shown by others (La Sorte and Boecklen, 2005; Keith *et al.*, 2009; Lôbo *et al.*, 2011), the introduction of non-native species was not the main driver of change in dissimilarity in these communities. Even without the non-native species, the analysis still failed to detect a significant decrease in species richness. Therefore, it can reasonably be assumed that change in environmental conditions caused by the loss of connectivity and the development of aquaculture probably led to a turnover within the native species pool that has increased the

similarity between communities. For instance, some small lacustrine fish were relatively rare in the past (such as *Squalidus nitens*, *Rhodeus lighti* and *Rhinogobius cliffordpopei*), and are now distributed in all lakes owing to accidental introduction by aquaculture activities. On the other hand, it is also probable that the disappearance of rare species (such as *Anguilla japonica*, *Culter axycephalus* and so on) has increased homogenization.

The functional diversity analysis also shed light on the processes behind such homogenization. As shown in the fish functional spaces, the homogenization of fish communities could mainly be ascribed to the disappearance of migratory fish species and an increase in lacustrine fish species. Specifically, migratory fish with long life-spans and large size were mainly affected by the changes reported here. These species are distributed at the edge of the functional space and can therefore be defined as specialist species (Devictor *et al.*, 2010). For instance, 10 fish species disappeared after the 1970s; their maximum length was greater than 50 cm and three of them (*Fugu ocellatus*, *Myxocyprinus asiaticus* and *Elopichthys bambusa*) were migratory species.

We argue, therefore, that the time is ripe to develop wide-ranging, effective conservation plans to restore (or at least preserve) such biodiversity. We propose, first, that a key measure will be to restore the water network and establish wise sluice-gate management methods to revive a healthy river–lake ecosystem. Specifically, we propose to make operational use of sluice gates and to involve all potential users in setting an adequate functioning of these sluice gates. This study has shown that migratory fish were seriously affected and the opening of sluice gates may help to favour migration. Other conservation actions should be taken to assist fish migration between the lakes and the river system, such as installing fish passes or starting assisted migration programmes for large fish species. In addition, aquaculture programmes should be designed to favour the rearing of native rather than non-native fish species, to limit the continuing tendency to homogenization. In parallel, we propose the development of supportive breeding programmes

that would preserve the biological integrity of native species that are not targeted by aquaculture and fisheries activities (e.g. small native fish species) to avoid a loss of species richness in the future. We suggest also that a social and economic monitoring plan should be devised together with appropriate sluice-gate management, as restoring river–lake connectivity or seasonal water fluctuations may alter human activities, such as agriculture, fisheries, flood control and drinking water supply in the area.

ACKNOWLEDGEMENTS

We are grateful to Dr Gaël Grenouillet for his help with statistical analyses, and John Woodley for correcting the English. Thanks to the CAS-CNRS programme for providing PhD grants and the National Science and Technology Supporting Program of China (No. 2012BAD25B08) from the R and D project of the Ministry of Agriculture of China. We sincerely thank two anonymous referees for comments that greatly improved the manuscript.

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