



Seventy-five years of biodiversity decline of fish assemblages in Chinese isolated plateau lakes: widespread introductions and extirpations of narrow endemics lead to regional loss of dissimilarity

Chengzhi Ding¹, Xiaoming Jiang^{2*}, Zhicai Xie² and Sébastien Brosse³

¹Yunnan Key Laboratory of International Rivers and Transboundary Eco-Security, Yunnan University, Kunming, Yunnan 650091, China, ²State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China, ³Laboratoire Evolution et Diversite Biologique (UMR5174 UPS-CNRS-ENFA), University Paul Sabatier Toulouse 3, 31062 Toulouse, France

ABSTRACT

Aim Introductions of exotic species have globally modified the structure and function of native assemblages and are recognized as one of the major threats to biodiversity. The current patterns, processes and consequences of invasion have been intensively studied globally, but studies reporting the long-term dynamics of invasions over large areas are rare. Here, we measured how the temporal changes in fish assemblage composition in a Chinese highland isolated-lake landscape drive taxonomic dissimilarity and its turnover component over three successive time periods spanning the last 75 years.

Location Yun–Gui Plateau, 15 isolated lakes.

Methods The Sørensen and Simpson indices were used to quantify changes in taxonomic dissimilarity and its turnover component over 1940–2015.

Results We report a decline of taxonomic dissimilarity between lakes through time, mainly due to a decrease in species turnover. Such a homogenization process was due to the combined effects of the invasion of the same non-native species in most lakes and of extirpation of narrow endemic species. The strong decline in species dissimilarity and turnover was triggered by a high historical level of dissimilarity among assemblages. At a regional scale, the combined effect of introductions and extirpations modified the distance decay of taxonomic similarity between lakes. Surprisingly, this beta-diversity gradient is currently no longer supported by biogeographic and evolutionary processes, but by the human-mediated introduction of distinct exotic species in some lakes. Moreover, an extinction debt process was evident as extirpations sometimes occurred many years after the introduction of non-native species.

Main conclusions Our study highlights that high historical differentiation of fishes in isolated lakes has turned to homogenization with dramatic loss of endemic species due to intensive introductions. This provides a striking example of human domination over an extended lake landscape and its associated irreparable biodiversity damages on isolated systems historically dominated by narrow endemic species.

Keywords

beta-diversity, endemism loss, exotic species introduction, isolated lakes, time-lag effect, turnover component.

*Correspondence: Xiaoming Jiang, State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China.
E-mail: jiangxm@ihb.ac.cn

INTRODUCTION

Anthropogenic activities and their subsequent environmental disturbances are recognized as the major drivers of the current biodiversity crisis (Vitousek *et al.*, 1997; Cardinale *et al.*, 2012). Multiple human disturbances, such as hydrologic alteration, habitat fragmentation, overexploitation and eutrophication, exacerbate species extinction risk (Dudgeon *et al.*, 2006). In addition, human-mediated exotic species introductions are considered as one of the major threats to biodiversity. Anthropogenic species introductions and extirpations have affected the richness and composition of local assemblages world-wide, and caused a decline in taxonomic dissimilarity, often coined biotic homogenization (Rahel, 2000; Olden & Poff, 2004; Villéger *et al.*, 2011; Toussaint *et al.*, 2014). For more than a decade, proof has been accumulating of a general trend towards biotic homogenization for various taxa in terrestrial, freshwater and marine ecosystems across the globe (e.g. Qian & Ricklefs, 2006; Winter *et al.*, 2009; Toussaint *et al.*, 2014).

Long-term studies examining the effects of introductions are needed because introductions might result in native extirpations several years, or decades, after the disturbance began (Gido & Brown, 1999; Rahel, 2000), a general process often called extinction debt (Rahel, 2002). As a result, extirpations might outpace introductions in the future and trigger biodiversity loss (Michael, 2002; Essl *et al.*, 2015).

Although most previous studies measured taxonomic homogenization as a change in dissimilarity (also coined beta-diversity) between two periods, dissimilarity (often measured using Jaccard or Sørensen indices) accounts for two independent components: the species replacement between assemblages (turnover component) and the difference in richness between assemblages (nestedness-resultant component). The turnover of dissimilarity reflects the species replacement induced by environmental sorting or spatial and historical constraints (Qian *et al.*, 2005), while the nestedness implies a non-random process of species loss caused by factors promoting the orderly disaggregation of assemblages (Gaston & Blackburn, 2000). The recent development of methods to partition beta-diversity (Baselga, 2010, 2012) hence provides a way to disentangle nestedness and turnover processes which has strong implications for understanding biotic patterns and their causes. Disentangling the two independent fractions of beta-diversity has already been achieved in spatial studies (e.g. Leprieur *et al.*, 2011; Boeiro *et al.*, 2013; Mouillot *et al.*, 2013), but the contribution of those two fractions to the change in dissimilarity across time (e.g. biotic homogenization or biotic differentiation) is less well understood (Toussaint *et al.*, 2014; Villéger *et al.*, 2014), especially over a time-scale spanning several decades (Angeler, 2013). However, long-term studies of the two processes would significantly help us understand metacommunity dynamics and shed light on the drivers of changes in beta-diversity.

Diversity patterns of isolated environments (e.g. islands, endorheic rivers and isolated lakes) provide ideal opportunities for examining and understanding biodiversity changes through anthropization. Indeed, geographical isolation leads to high level of species endemism and considerable taxonomic dissimilarity between those islands. The low species richness and the lack of interspecies predation or competition within these isolates make their fauna vulnerable to the introduction of exotic species that are often efficient predators or competitors (Snodgrass *et al.*, 1996; Magnuson *et al.*, 1998). Isolated environments are therefore likely to lose their native and endemic species through invasion and will in turn experience a decrease in taxonomic dissimilarity (also coined taxonomic homogenization) (Stohlgren *et al.*, 1999; Dudgeon *et al.*, 2006).

Isolated lakes are a particular case of isolated environment. They constitute aquatic islands surrounded by a sea of land (Rahel, 2007), and therefore strictly aquatic species such as fishes are under a particularly harsh isolation effect which promotes high levels of microendemism. However, compared to the abundant literature on islands, studies examining the effects of human disturbances on the change in dissimilarity in isolated lakes remain scarce (Lopes *et al.*, 2014). The Yun–Gui Plateau (or Yunnan–Guizhou Plateau), in south-west China, supports dozens of isolated freshwater lakes with high levels of fish endemism (Chu & Chen, 1990). During the past 75 years, these lakes have experienced drastic changes in fish assemblages because of intensive introductions of exotic fishes and extirpation of native endemic species (Chen *et al.*, 1998; Kang *et al.*, 2013; Jiang *et al.*, 2015). Here, we examined α -diversity (species richness in each lake) and γ -diversity (total species richness over the all lakes) of total and native fish assemblages, and analysed the changes in dissimilarity experienced by 15 large Yun–Gui Plateau lakes during the last 75 years. We therefore tested the change of dissimilarity across an increasing exotic species introductions and native extirpations trend.

Given the marked dissimilarity between isolated lakes fish fauna, and the increasing anthropogenic disturbance trend through time, that promotes exotic fish introduction and native species extirpation, we predict a decline of taxonomic dissimilarity due to a decline of the species turnover caused by a combined effect of the introduction of the same non-native species in several lakes and the extirpation of distinct narrow endemics in each lake. We also predict an accentuation of this trend through time, as the extinction debt paid for native species. Moreover, we speculate temporal changes in the distance decay of similarity as the introductions and extirpations will modify the relationship between fish faunal dissimilarity and geographical distance.

METHODS

Study area and lakes

Located in the south-west of China, the Yun–Gui Plateau (Fig. 1) is one of the five lake regions in China (Wang &

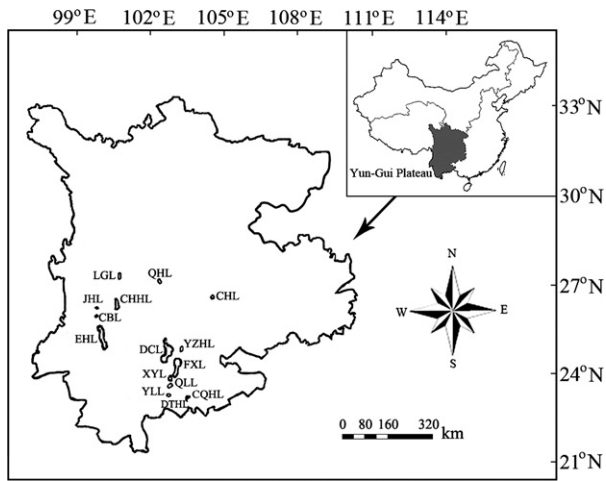


Figure 1 Map showing the location of the 15 studied lakes. DCL, Dianchi Lake; EHL, Erhai Lake; FXL, Fuxian Lake; CHHL, Chenghai Lake; LGL, Lugu Lake; QLL, Qilu Lake; XYL, Xingyun Lake; YZHL, Yangzonghai Lake; QHL, Qionghai Lake; CHL, Caohai Lake; YLL, Yilong Lake; DTHL, Datunhai Lake; CQHL, Changqiaohai Lake; CBL, Cibi lake; JHL, Jianhu Lake.

Dou, 1998). This area hosts 65 natural isolated lakes greater than 1 km², among which 13 lakes cover a surface greater than 10 km² (Ma *et al.*, 2011). The fish fauna inhabiting these lakes is characterized by a high level of fish endemism and considerable faunal dissimilarity between lakes (Li, 1982; Kottelat & Whitten, 1996). These isolated lakes supported species flocks of endemic congeneric fishes, with for instance, three species of *Schizothorax* in Lugu Lake; five species of *Cyprinus* in Erhai Lake; and two species of *Liobagrus* in Dianchi Lake (Li, 1982; Yang *et al.*, 1994).

While the first fish inventories made from 1940 to 1957 did not report changes in fish assemblages, these lakes have since experienced two successive waves of exotic fish introductions for aquaculture purposes. The first introduction wave occurred from 1958 to 1965 with the introductions of fast-growing fish species among which were black carp (*Mylopharyngodon piceus*), grasscarp (*Ctenopharyngodon idella*), silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Aristichthys nobilis*). Those commercial species introductions were accompanied by unintentional introductions of top-mouth gudgeon (*Pseudorasbora parva*), and gobies (*Rhinogobius giurinus*, and *Rhinogobius cliffordpopei*), which entered into these lakes as contaminants during the introduction of the commercial species (Chen *et al.*, 1998). The second introduction wave occurred from the late 1970s to the late 1980s with the introduction of icefish (*Neosalanx tangkahkeii*) to compensate for the decline in fishery yield observed in the early seventies (Kang *et al.*, 2015).

In addition to the exotic introductions, water quality of these lakes has declined rapidly due to increasing watershed pollution by urban and industrial effluents, causing an increase in nitrogen and phosphorus in most lakes (Yu *et al.*, 2010; Liu *et al.*, 2012). Hence, the combination of

overfishing, competition with exotic species and water quality degradation negatively affected the fish fauna, causing the extirpation of the most sensitive species.

We here focused on 15 lakes with sufficient data on fish fauna dynamics since the 1940s (including all 13 lakes greater than 10 km², Fig. 1). These lakes cover a wide range of morphometric characteristics, with lake surface area varying from 5.7 to 297.9 km², and lake elevations ranging from 1284 to 2691 m above sea level. The mean lake depth varied from 2.4 to 89.6 m, with a wide range of volume from 0.17 × 10⁸ to 189 × 10⁸ m³ (see details in Table S1 in Supporting Information). Among the 103 native species in these lakes, more than half were historically restricted to single lakes. Only one species (*Misgurnus anguillicaudatus*) occurred in all lakes, and six species (*M. anguillicaudatus*, *Carassius auratus*, *Monopterus albus*, *Cyprinus chilia*, *Oryzias sinensis* and *Channa argus*) occurred in over half of these lakes. Overall, there were 47 fish species only endemic to lakes in Yun-Gui Plateau.

Data collection and time periods

We collected fish occurrences in 15 lakes from published fish surveys (including scientific reports, books, online data and grey literature) at the lake scale since 1940s (Table S2). Data were then curated to homogenize taxonomy according to FishBase (Froese & Pauly, 2016).

We grouped these data into three periods corresponding to three series of about 15 years fish sampling, each separated by 10- to 15-year intervals during which sampling was more scarce: (1) historical period (1940–1957), (2) intermediate period (1970–1985), and (3) current period (2000–2015). For each period, we gathered all the data available from the literature (see details in Table S2) to build up exhaustive species lists (Tables S3–S5). Those data were derived from standardized fish inventories using castnets and electrofishing (most of the surveys before 1990s were conducted using castnets, whereas electrofishing was the main fishing method thereafter). These scientific inventories comprised several surveys per period by the Chinese fisheries institutes (detailed information for each lake and for each period is available in the literature cited in Table S2). From these species lists, we distinguished between native and exotic species and considered an exotic species as present in the lake only when the species was established.

Partitioning changes in taxonomic dissimilarity

Taxonomic dissimilarity was measured using the Sørensen index (β_{SOR}). β_{SOR} was calculated as follows:

$$\beta_{\text{SOR}} = \frac{b + c}{2a + b + c}$$

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

Taxonomic dissimilarity is an overall beta-diversity measure that accounts for two independent components, the replacement of species between assemblages (the turnover component) and the difference in richness between assemblages (the nestedness-resultant component). Those two components were measured using the beta-diversity decomposition proposed by Baselga (2010, 2012). According to Baselga (2010, 2012), turnover is quantified using the Simpson index (β_{sim}), which measures species replacement without being influenced by species richness differences (Lennon *et al.*, 2001; Koleff *et al.*, 2003). The β_{sim} index was calculated as follows:

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

where a , b and c are the same variables as defined for Sørensen dissimilarity.

β_{sor} and β_{sim} both range from 0 to 1, depicting a gradient from low dissimilarity (values close to 0) to high dissimilarity and turnover (values closer to 1).

Following Toussaint *et al.* (2014) and Villéger *et al.* (2014), we also calculated the relative contribution of turnover to dissimilarity, hereafter noted p_{turn} :

$$p_{\text{turn}} = \frac{\beta_{\text{sim}}}{\beta_{\text{sor}}} = \frac{\min(b, c)}{a + \min(b, c)} \times \frac{2a + b + c}{b + c}$$

The p_{turn} index cannot be defined when dissimilarity is null (i.e. when $b = c = 0$). However, such a situation of complete identity in species composition is rare in real cases and did not occur in this study. The p_{turn} ranges from 0 to 1. It is minimal and equals 0 when turnover is null ($\min(b, c) = 0$), which means that the poorest assemblage is a subset of the richest assemblage, and it is maximal and equals 1 when the two assemblages share no common species ($a = 0$), or when the two assemblages have the same richness ($b = c > 0$).

The partitioning of taxonomic dissimilarities was used to quantify temporal changes in pairwise taxonomic dissimilarity and the contribution of turnover to dissimilarity (hereafter called $\Delta\beta_{\text{sor}}$, $\Delta\beta_{\text{sim}}$ and Δp_{turn} , respectively) between the historical period (before human influence) and subsequent time periods (after human influence). The temporal changes in dissimilarity, turnover of dissimilarity and contribution of turnover to dissimilarity from a historical to a subsequent period were then calculated as:

$$\Delta\beta_{\text{sor}} = (\beta_{\text{sor}})_{\text{subsequent}} - (\beta_{\text{sor}})_{\text{historical}}$$

$$\Delta\beta_{\text{sim}} = (\beta_{\text{sim}})_{\text{subsequent}} - (\beta_{\text{sim}})_{\text{historical}}$$

$$\Delta p_{\text{turn}} = \frac{(\beta_{\text{sim}})_{\text{subsequent}}}{(\beta_{\text{sor}})_{\text{subsequent}}} - \frac{(\beta_{\text{sim}})_{\text{historical}}}{(\beta_{\text{sor}})_{\text{historical}}}$$

Statistical analysis

Within each period, we first quantified α -diversity (species richness in each lake) and γ -diversity (total species richness over the 15 lakes). Taxonomic dissimilarity (β_{sor}), turnover

component of dissimilarity (β_{sim}) and relative contribution of turnover to dissimilarity (p_{turn}) between fish assemblages of each pair of lakes were computed for the three periods. Temporal changes from historical to intermediate and current period were separately computed for these three indices.

Then non-metric multidimensional scaling (MDS) was separately performed based on Sørensen and Simpson indices to visualize patterns of fish assemblages during the three periods. Permutational analysis of multivariate dispersions (PERMDISP, Anderson, 2006) was used to test whether the fish compositional heterogeneity varied between the three periods. PERMDISP is similar to the Levene's test of homogeneity of variances and further uses the ANOVA F -statistic to compare among-group differences in the distance from observations to their group centroid. Significance of among-group differences is tested through permutation of least-squares residuals. The null hypothesis that there were no differences between the three periods was tested using a permutations test with 9,999 iterations.

We then assessed the relationships between assemblage dissimilarity and geographical distance between lakes (i.e. distance decay of similarity). The distance between pairs of lakes was measured between their centroids. We regressed the taxonomic dissimilarity (β_{sor}) and its turnover component (β_{sim}) on geographical distance between lake pairs for the three periods. As the lack of independence of observations (distances) precludes the test for significance by traditional regression procedures, significance of the Pearson correlations was calculated by Mantel permutation tests. Then, the frequency distributions of the parameters estimated by bootstrapping were used to compare whether the intercepts and slopes yielded by the two indices differed among historical, intermediate and current periods. A frequency distribution of 10,000 slopes and intercepts was retrieved by bootstrapping, using the `BOOT` package (Canty & Ripley, 2013).

Finally, we used multiple regression on distance matrices (MRM, Lichstein, 2007) to disentangle the drivers of temporal changes (intermediate vs. historical and current vs. historical) in taxonomic dissimilarity. Due to the varied historical native species richness between lakes (from 4 to 27 species), the same number of exotic species would denote quite different introduction pressure; hence, we defined total percentage of exotic species (i.e. ratio of introduced exotic/total species), and total percentage of extirpated species (extirpated/historically native species) in each pair of lakes as explanatory matrices in the MRM. P -values for MRM models were obtained by comparing each observed regression coefficient with a distribution of 10,000 permuted values.

We ran MDS and PERMDISP in `PRIMER 6` and `PERMANOVA+` for `PRIMER` package (Anderson *et al.*, 2008) and all other analyses in R (R Development Core Team, 2015), including calculating dissimilarity matrices in `BETAPART` package (Baselga & Orme, 2012), Mantel test in `VEGAN` package (Oksanen *et al.*, 2007), frequency distribution of slopes and intercepts in `BOOT` package (Canty & Ripley, 2012) and MRM

analyses in ECODIST package (Goslee & Urban, 2007). In our study, changes in fish assemblages were analysed across time both for the entire fish assemblages (i.e. native and exotic species) and for only the native fish assemblages.

RESULTS

Change in species composition through time

For total fish fauna in isolated lakes of Yun–Gui Plateau, α -diversity (species richness in individual lakes) experienced a significant increase in the intermediate and current periods compared to historical, while γ -diversity (total species richness) increased in the intermediate but declined in the current period (Fig. 2). For native species, α -diversity and γ -diversity both declined through time, suggesting that native taxa were extirpated both from individual lakes and from the region as a whole (Fig. 2).

Indeed, during the intermediate period, an average of 2.1 (14% of historical native species) native species were extirpated per lake, and 13 native species were not recorded in any lake for more than 30 years. Those species were therefore considered as extirpated from the regional species pool. On average, 8.7 (42%) exotic species were introduced and established per lake, and 27 exotic species as well as six species that were translocated between lakes were found at a regional scale (Table 1). In the current period, an average of 7.8 native species were extirpated and 13.1 exotic species were established per lake, whereas 59 native species were extirpated and 34 exotic and eight translocated species were established over all lakes (Table 1). Moreover, endemic species also experienced increasing loss through time. During the intermediate period, an average of 1.5 species per lake were extirpated (excluding three lakes without endemic

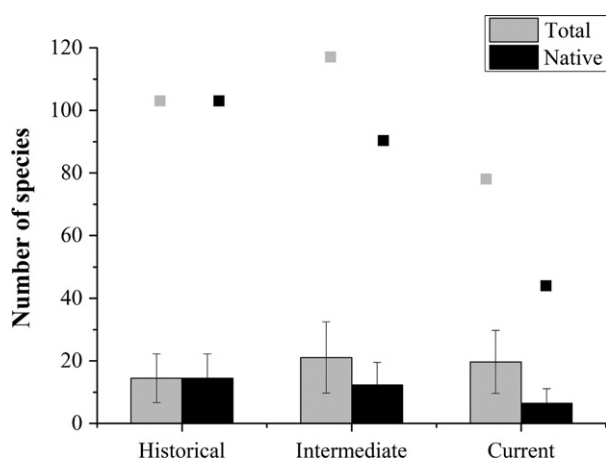


Figure 2 Alpha-diversity (mean value \pm SD of species richness; bars) and gamma-diversity (total species richness, squares) measured on the entire fish fauna (grey) and only on the native species (black) in the 15 studied lakes during historical (1940–1957), intermediate (1970–1985) and current (2000–2015) periods.

species in the historical period) and nine species were extirpated from the regional pool. During the current period, an average of 3.9 species per lake were extirpated (excluding three lakes without endemic species in the historical period) and 28 species were extirpated from the regional pool (Table 1). We also found there was no correlation between the percentages of introduced versus extirpated fish species within lakes ($r = 0.007$, $P = 0.491$) during the intermediate period, but such correlation turned to significant ($r = 0.456$, $P = 0.044$) during the current period.

Temporal changes in beta-diversity of fish assemblages

Multidimensional scaling plots of total species based on taxonomic dissimilarity (Sørensen index) showed a clear pattern of greatest dispersion among the lakes during the historical period, followed by a trend towards increased similarity between the lake faunas in the intermediate and current periods (Fig. 3a). Such a trend was also verified for turnover (Simpson index), which decreased with time (Fig. 3b). Considering only the native species provided a less marked trend, but native dissimilarity and turnover appeared less marked in the current period than in the former periods (Fig. 3c,d).

According to PERMDISP analyses, patterns of dissimilarity and turnover showed a similar decreasing trend from historical to intermediate and current periods (Fig. 4). For the entire fish assemblages, the average distance to the group centroid based on Sørensen ($F = 10.20$, $P < 0.001$) and Simpson ($F = 9.75$, $P < 0.001$) coefficients both significantly differed among the three periods. The historical period showed a significantly higher average distance to the group centroid than intermediate and current periods (Fig. 4). Nevertheless, when considering only the native fauna, the average distance to the group centroid for the Sørensen index did not differ significantly among three periods, whereas the results of Simpson index differ significantly ($F = 4.40$, $P = 0.038$) with higher average distances to the group centroid in historical and intermediate periods than in the current period. The changes of fish composition of Lugu Lake (circle and square at the right side of Fig. 3d) partly induced the results of Simpson index, as this lake only harboured one widespread native and three endemic species of *Schizothorax* in the historical and intermediate periods, whereas it experienced a loss of the three endemic species in the current period.

Historical fish assemblage dissimilarity (β_{SOR}) among isolated lakes was high with a mean value of 0.68 (SD \pm 0.15, Table 2). The turnover (β_{SIM} , 0.52 \pm 0.19) and its contribution to dissimilarity (p_{TURN} , 0.75 \pm 0.22) were also high. Those values declined for both the entire fish fauna and the native fishes from the historical to the subsequent periods, therefore depicting a significant trend towards taxonomic homogenization. Such a homogenization trend was more marked during the intermediate period for the entire fish assemblages than for the native assemblage: $\Delta\beta_{\text{SOR}}$

Table 1 The number of native and endemic fish species in studied lakes for historical period (1940–1957), and the number and percentage of extirpated native, extirpated endemic and introduced exotic fish species in intermediate (1970–1985) and current periods (2000–2015). Values are percentage of extirpated and introduced in brackets. The percentage of extirpated native, extirpated endemic and introduced exotic fish species are defined as extirpated native/historically native, extirpated endemic/historically endemic and introduced exotic/total species, respectively. Ex-Na = extirpated native, Ex-En = extirpated endemic, In-Ex = introduced exotic. Total means extant or extirpated fish species across all studied lakes.

Lake name	Historical		Intermediate			Current		
	Native	Endemic	Ex-Na	Ex-En	In-Ex	Ex-Na	Ex-En	In-Ex
Dianchi	27	10	3 (11.1%)	1 (10.0%)	22 (47.8%)	16 (59.3%)	7 (70.0%)	16 (59.3%)
Erhai	17	8	0 (0)	0 (0)	14 (45.2%)	7 (41.2%)	5 (62.5%)	24 (70.6%)
Fuxian	25	15	5 (20.0%)	4 (26.7%)	7 (25.9%)	7 (28.0%)	5 (33.3%)	25 (58.1%)
Chenghai	18	0	1 (5.6%)	–	5 (22.7%)	13 (72.2%)	–	6 (54.5%)
Lugu	4	3	0 (0)	0 (0)	3 (42.9%)	3 (75.0%)	3 (100%)	13 (92.9%)
Qilu	11	5	1 (9.1%)	1 (20.0%)	16 (61.5%)	5 (45.5%)	4 (80.0%)	14 (70.0%)
Xingyun	15	9	7 (46.7%)	6 (66.7%)	9 (52.9%)	8 (53.3%)	7 (77.8%)	21 (75.0%)
Yangzonghai	19	7	4 (21.1%)	3 (42.9%)	5 (25.0%)	10 (52.6%)	4 (57.1%)	18 (66.7%)
Qionghai	26	2	1 (3.8%)	0 (0)	15 (37.5%)	15 (57.7%)	2 (100%)	8 (42.1%)
Caohai	10	1	0 (0)	0 (0)	4 (28.6%)	4 (40.0%)	1 (100%)	3 (33.3%)
Yilong	15	5	4 (26.7%)	2 (40.0%)	7 (38.9%)	13 (86.7%)	5 (100%)	12 (85.7%)
Datunhai	7	0	0 (0)	–	7 (50.0%)	6 (85.7%)	–	10 (90.9%)
Changqiaohai	4	0	0 (0)	–	8 (66.7%)	1 (25.0%)	–	12 (75.0%)
Cibi	8	2	3 (37.5%)	1 (50.0%)	4 (44.4%)	4 (50.0%)	2 (100%)	4 (50.0%)
Jianhu	9	2	3 (33.3%)	0 (0)	5 (45.5%)	5 (55.6%)	2 (100%)	11 (73.3%)
Total	103	47	13	9	33	59	28	42

(-0.13 ± 0.09 vs. -0.02 ± 0.07), $\Delta\beta_{\text{sim}}$ (-0.17 ± 0.15 vs. -0.05 ± 0.11), Δp_{turn} (-0.12 ± 0.23 vs. -0.05 ± 0.14) (Table 2). In contrast, in the current period, native assemblages showed a stronger homogenization trend than the entire fish assemblages in β_{sim} (-0.29 ± 0.27 vs. -0.26 ± 0.19) and p_{turn} (-0.37 ± 0.36 vs. -0.19 ± 0.31), and a weaker homogenization trend in β_{sor} (-0.09 ± 0.15 vs. -0.20 ± 0.15) (Table 2). Moreover, β_{sim} all decreased faster than β_{sor} across two subsequent periods based on both the entire and the native fishes.

Temporal changes of distance decay of similarity

Measuring the distance decay of similarity according to the geographical distance between lake pairs showed that fish assemblage dissimilarity was positively related to geographical distance for the three periods considering both dissimilarity and turnover (all the relationships were significant except for turnover in the intermediate period which was marginally significant ($P = 0.073$; Fig. 5a,b, Table 3). The intercept was significantly higher in historical than in intermediate ($P = 0.030$ and $P = 0.050$ for β_{sor} and β_{sim} , respectively) and current periods ($P < 0.001$ for both β_{sor} and β_{sim}). Slopes did not significantly differ among three periods for both indices (Table 3).

For native fish fauna, the relationship between assemblage dissimilarity and geographical distance was significantly related to geographical distance in historical and intermediate periods, but such relationships vanish in the current period for both β_{sor} and β_{sim} (Fig. 5c,d, Table 3). The

regression lines of β_{sor} did not significantly differ between historical and intermediate periods ($P > 0.05$).

Determinants of changes in assemblage dissimilarity

Multiple regression on distance matrices analyses significantly predicted changes in β_{sor} and β_{sim} based on historical level of dissimilarity, and introduction and extirpation pressures for both the entire fauna and native assemblages. Considering both native and exotic species, the MRM model explained 20.2% ($P < 0.001$) and 61.6% ($P < 0.001$) of the variation in change in β_{sor} in the intermediate and current periods, respectively. The historical β_{sor} had a significant negative effect, indicating lake pairs with high historical dissimilarity tended to be more homogenized (Table 4). The percentage of introduced species in a pair of lakes also had a significant negative effect on change in β_{sor} , meaning that pairs of lakes that received more exotic species tended to be more homogenized. In contrast, percentage of extirpated species did not contribute significantly to the overall homogenization trend (Table 4). The turnover (β_{sim}) of entire assemblages was determined by historical dissimilarity, percentage of introduced species and percentage of extirpated species together. The predictive power of MRM models predicting turnover (intermediate period: $R^2 = 0.457$, $P < 0.001$; current period: $R^2 = 0.647$, $P < 0.001$) was higher than that of models predicting overall change in beta-diversity (Table 4).

Considering only the native species, change in β_{sor} in the intermediate period was negatively related to historical β_{sor} ,

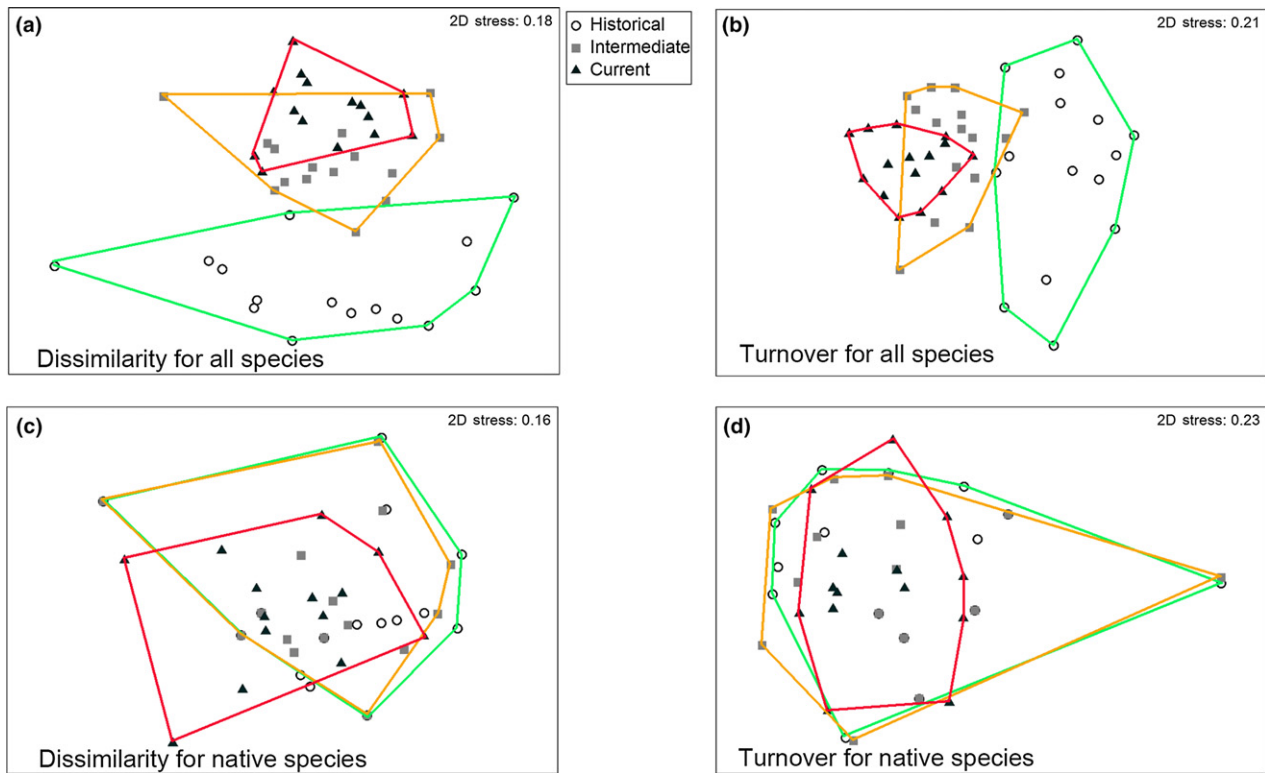


Figure 3 Non-metric multidimensional scaling (MDS) plots of fish assemblages from the 15 lakes in the three periods based on taxonomic dissimilarity (Sørensen index, a, c) and turnover (Simpson index (b, d). Entire species assemblages were considered in a and b, whereas only the native species were considered on c and d. The solid coloured lines represent the convex hull encapsulating the 15 lakes for each period. Green: historical period (1940–1957); orange: intermediate period (1970–1985); and red: current period (2000–2015). Colour figure can be viewed at wileyonlinelibrary.com

and total percentage of introductions and extirpations, with 25.5% explained variation, whereas current change in β_{sor} was not significantly predicted by the above variables (Table 4). Change in β_{sim} in the intermediate period was negatively related to historical β_{sim} and total percentage of extirpations, whereas the current β_{sim} -change was additionally related to total percentage of introductions (Table 4).

DISCUSSION

The lake landscape of Yun–Gui Plateau results from a series of neotectonic activities including the plateau upraise, fluvial incision and elevation differences since the late Pliocene period. These physical barriers isolated the lakes that are characterized by a low richness in species compared to lakes connected to rivers (Snodgrass *et al.*, 1996; Magnuson *et al.*, 1998). In the absence of human disturbances, low species exchange and local adaptive radiation led to a historically high level of endemism and high level of between-lake dissimilarity of fish assemblages (Kottelat & Whitten, 1996; Dudgeon *et al.*, 2006). The fish fauna of the 15 Yun–Gui plateau lakes considered here hence had a low fish α -diversity with on average 14.5 native species per lake before human disturbances modified those assemblages (i.e. historical richness, Fig. 2). This species diversity is much lower than that

found in non-isolated lakes from the Yangtze Floodplain that are inhabited by 60–70 native species (Li, 1982; Chu & Chen, 1990). Moreover, more than 65% of the native species were historically restricted to one lake and most of them are endemic to the Yun–Gui Plateau (60 species) or endemic to one or a few of the Yun–Gui Plateau lakes (47 species). Among the 15 considered lakes, there was a high historical level of taxonomic dissimilarity (almost 70% dissimilarity between lakes pairs, on average) that was mainly due to the marked species turnover between lakes, that accounted for 75% of the observed dissimilarity before those assemblages were modified by anthropogenic disturbances (i.e. historical period, Table 2).

Half a century of intensive exotic species introductions for aquaculture purposes and of multicausal native species extirpation (including overfishing, competition with non-natives and water quality degradation, Chen *et al.*, 1998; Lu & Song, 2003) profoundly modified the historical patterns. Indeed, since the late 1950s those lakes experienced a strong exotic species introduction pressure, with a percentage of exotic species that reached on average 42% (range 23–67%) of the fauna in the 1970s and 1980s and that currently peaks to an average value of 66% (33–93%). Such invasion level is much higher than that found at the global and continental scales. For instance, Leprieur *et al.* (2008b) showed that exotic

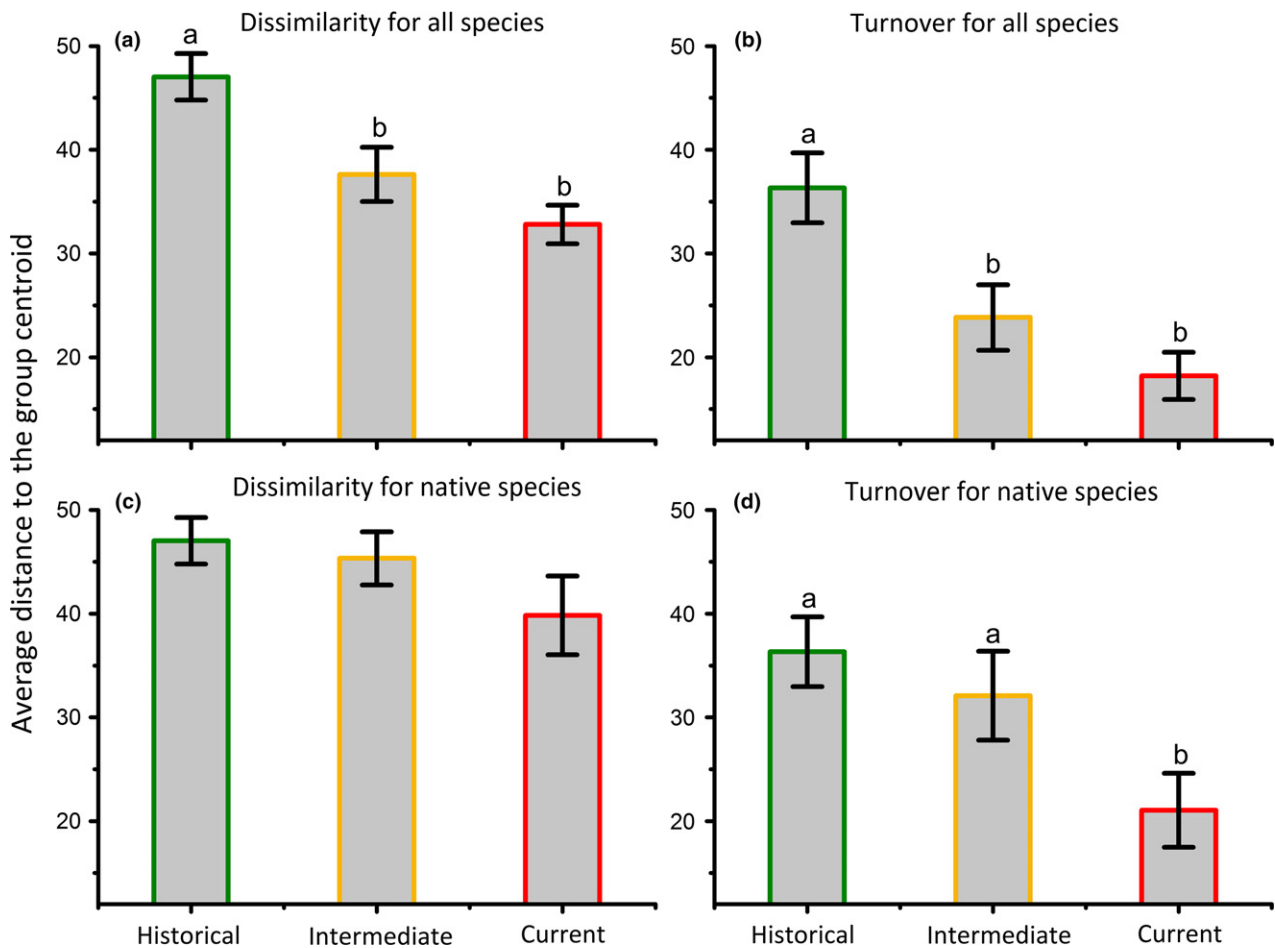


Figure 4 Permutational analysis of multivariate dispersions (PERMDISP) showing mean \pm SE distances to the group centroid based on dissimilarity (Sørensen index, a) and turnover (Simpson index, b) of entire assemblages, and dissimilarity (Sørensen index, c) and turnover (Simpson index, d) of native assemblages among historical (1940–1957; green), intermediate (1970–1985; orange) and current (2000–2015; red) periods. Different letters denoted significant differences ($P < 0.05$) among the periods. Colour figure can be viewed at wileyonlinelibrary.com

species account for <5% of the fauna in more than half of the world's river basins. Our results also largely exceed the exotic fish invasion levels found in river basins from the Oriental (*c.* 5%) and Palaearctic (*c.* 16%) realms (Brosse *et al.*, 2013). The threatened situation of native and endemic species was also severe; on average, 55% (25–87%) of the native species have been extirpated from at least one lake, leading to the classification of more than 50% of the 47 lake endemic species as critically endangered in the Chinese Red List.

Human disturbances causing exotic species introductions and native extirpations are known as key drivers pushing freshwater fishes towards global homogenization (Rahel, 2000; Olden & Rooney, 2006; Toussaint *et al.*, 2014). However, beyond this overall decreasing trend of dissimilarity, both homogenization and differentiation of fish assemblages have been observed in North America (Rahel, 2000, 2002), Europe (Leprieur *et al.*, 2008a; Villéger *et al.*, 2014) and on a global scale (Toussaint *et al.*, 2014). The partitioning of assemblage dissimilarity into turnover and nestedness-resultant components provides an opportunity to explore the mechanism of β -diversity changes following human

disturbance (Baselga, 2012; Villéger & Brosse, 2012). Our results showed that assemblage dissimilarity (β_{sor}), turnover component of dissimilarity (β_{sim}) and contribution of turnover to the dissimilarity (p_{turn}) based on both entire and native assemblages all dramatically decreased through time.

The introductions of exotic species usually have a time-lag effect on native species: most recent introductions do not result in extirpations of native fishes and initially show an increase in biodiversity (Griffiths, 1997; Gido & Brown, 1999; Rahel, 2000). However, the extinction process actually needs a relatively long time to complete its course (Scott & Helfman, 2001; Michael, 2002; Rahel, 2002). This appears to be the case for lake fishes in our study. Even if most introduced fishes are known as harmful to native species, due to increased competition for food (Qin & Xie, 2007), native fish egg predation (Du & Li, 2001) and hybridization (Tang & Chen, 2012), the percentages of introduced versus extirpated fish species within lakes were not correlated during the intermediate period (10–20 years after the first introduction wave). Moreover, there were much fewer extirpated species than introduced species during this period (Table 1), and

Table 2 Taxonomic dissimilarity (Sørensen index), turnover (Simpson index) and contribution of turnover to dissimilarity (p_{turn}) for historical (1940–1957), intermediate (1970–1985) and current periods (2000–2015) based on entire assemblages (all species) and considering only native species. Values are mean \pm standard deviation with range in brackets.

		All species	Native species
Dissimilarity	Historical	0.68 \pm 0.15 (0.18 to 0.94)	0.68 \pm 0.15 (0.18 to 0.94)
	Intermediate	0.55 \pm 0.14 (0.08 to 0.89)	0.66 \pm 0.14 (0.27 to 0.93)
	Current	0.48 \pm 0.11 (0.20 to 0.73)	0.59 \pm 0.18 (0 to 1)
	Intermediate vs. Historical	-0.13 \pm 0.09 (-0.32 to 0.19)	-0.02 \pm 0.07 (-0.27 to 0.20)
	Current vs. Historical	-0.20 \pm 0.15 (-0.55 to 0.26)	-0.09 \pm 0.15 (-0.40 to 0.36)
Turnover	Historical	0.52 \pm 0.19 (0 to 0.82)	0.52 \pm 0.19 (0 to 0.82)
	Intermediate	0.35 \pm 0.15 (0 to 0.60)	0.48 \pm 0.20 (0 to 0.82)
	Current	0.26 \pm 0.13 (0 to 0.56)	0.23 \pm 0.26 (0 to 1)
	Intermediate vs. Historical	-0.17 \pm 0.15 (-0.42 to 0.17)	-0.05 \pm 0.11 (-0.30 to 0.24)
	Current vs. Historical	-0.26 \pm 0.19 (-0.68 to 0.29)	-0.29 \pm 0.27 (-0.75 to 0.34)
Contribution of turnover to dissimilarity	Historical	0.75 \pm 0.22 (0 to 1)	0.75 \pm 0.22 (0 to 1)
	Intermediate	0.64 \pm 0.23 (0 to 1)	0.71 \pm 0.23 (0 to 1)
	Current	0.56 \pm 0.27 (0 to 1)	0.38 \pm 0.39 (0 to 1)
	Intermediate vs. Historical	-0.12 \pm 0.23 (-0.66 to 0.43)	-0.05 \pm 0.14 (-0.47 to 0.25)
	Current vs. Historical	-0.19 \pm 0.31 (-0.71 to 0.92)	-0.37 \pm 0.36 (-1 to 0.33)

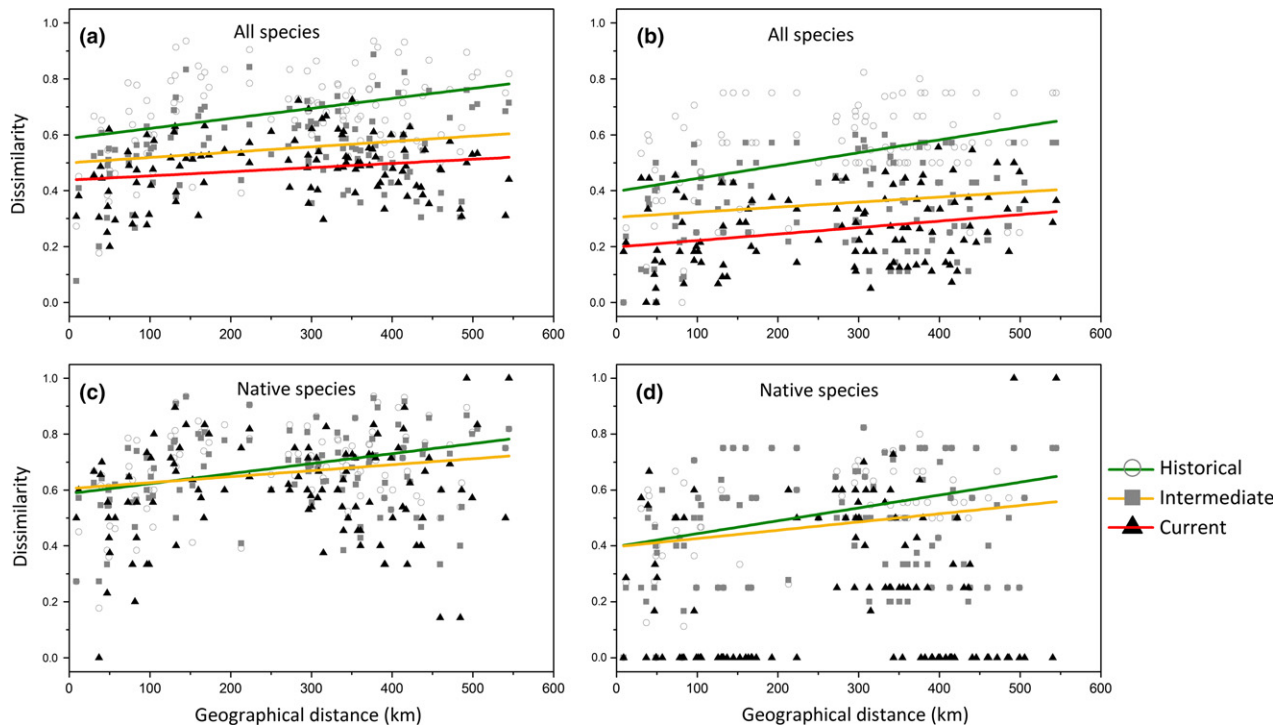


Figure 5 Relationships between taxonomic dissimilarity (a, c) and turnover (b, d) and geographical distance. Distance decay of similarity was calculated on entire assemblages (a, b) and on native assemblages (c, d). The regression lines for each period are represented with colours according to the considered period. Green: historical period (1940–1957); orange: intermediate period (1970–1985); and red: current period (2000–2015). Regression lines were represented only for significant regressions ($P < 0.05$). The Pearson correlation coefficients, significance (P -value computed using Mantel tests), and differences among intercept and slope of regression lines between the three periods are given in Table 2. Colour figure can be viewed at wileyonlinelibrary.com

the β_{SOR} , β_{SIM} and p_{turn} based on native species only slightly decreased in this period (Table 2, Fig. 5), supporting the assertion that introductions did not cause native species extirpation over a short time span. However, in the current period, that is over 50 years after the first introduction, the

percentage of exotic species turned to a positive correlation with percentage of extirpations, and the number of extirpated species was close to or exceeded the number of exotic species. Such findings confirm the extinction debt concept (Rahel, 2002; Essl *et al.*, 2015) and highlight the time-lag

Table 3 Distance decay of similarity measured using the Pearson correlation coefficients (r), significance (P computed using Mantel tests), intercept and slope of regression lines between dissimilarity (Sorensen index) and distance between sites, or turnover (Simpson index) and distance between sites for the historical, intermediate and current periods. The analyses were achieved on entire assemblages (all species) and on native species only. Intercepts and slopes with different letters indicate significant differences ($P < 0.05$) between periods.

		Historical	Intermediate	Current
Dissimilarity of all species	r	0.363	0.200	0.200
	P	< 0.001	0.047	0.041
	Intercept	0.587 ^a	0.500 ^b	0.438 ^b
	Slope ($\times 10^{-4}$)	3.58 ^a	1.91 ^a	1.49 ^a
Turnover of all species	r	0.362	0.173	0.263
	P	< 0.001	0.073	0.009
	Intercept	0.398 ^a	0.305 ^b	0.198 ^b
	Slope ($\times 10^{-4}$)	4.60 ^a	1.80 ^a	2.32 ^a
Dissimilarity of native species	r	0.363	0.221	0.139
	P	< 0.001	0.035	0.130
	Intercept	0.587 ^a	0.605 ^a	0.547 ^a
	Slope ($\times 10^{-4}$)	3.58 ^a	2.14 ^a	1.69 ^a
Turnover of native species	r	0.362	0.220	0.085
	P	< 0.001	0.033	0.216
	Intercept	0.398 ^a	0.397 ^a	0.192 ^b
	Slope ($\times 10^{-4}$)	4.60 ^a	2.96 ^{ab}	1.51 ^b

Those P -value < 0.05 are bold.

Table 4 Results of multiple regression on distance matrices (MRM) analyses disentangling effects of historical dissimilarity, exotic species introduction (percentage of introduced species) and native species extirpation (percentage of extirpated species) on intermediate versus historical and current versus historical changes in dissimilarity (Sørensen index) and turnover (Simpson index). The same analyses were run for intermediate and current and on both entire assemblages and native assemblages. Std b: standard partial regression coefficient.

	Change in dissimilarity				Change in turnover			
	Intermediate		Current		Intermediate		Current	
	Std b	P -value	Std b	P -value	Std b	P -value	Std b	P -value
Entire assemblages								
Historical dissimilarity	-0.298	< 0.001	-0.670	< 0.001	-0.554	< 0.001	-0.905	< 0.001
Introduction	-0.034	0.090	-0.012	0.029	-0.124	0.039	-0.009	0.022
Extirpation	-0.078	0.217	0.090	0.114	-0.205	0.071	0.257	0.044
R^2	0.202	< 0.001	0.616	< 0.001	0.457	< 0.001	0.647	< 0.001
Native assemblages								
Historical dissimilarity	-0.226	< 0.001	-0.314	0.016	-0.190	0.028	-0.351	0.041
Introduction	-0.038	0.010	0.002	0.787	-0.026	0.440	-0.033	0.002
Extirpation	-0.118	0.016	0.166	0.204	-0.260	0.006	-0.014	0.017
R^2	0.255	< 0.001	0.154	0.116	0.269	0.014	0.392	< 0.001

Those P -value < 0.05 are bold.

effects of introductions. The combined effect of introduction and extirpation explained the decline of dissimilarity and turnover between the intermediate and current periods (Table 2, Fig. 5). Such results show that long-term studies, encompassing several decades, are needed to examine faunistic changes caused by human activities. It is indeed a crucial research agenda for conservation biology to determine the change of future biodiversity and how introduction/extirpation processes are influenced by the historical composition of communities, the characteristics of introduced species and

the degree of habitat alteration (Moyle & Light, 1996; Kolar & Lodge, 2001).

The steep and consistent decreasing trends of β_{SOR} , β_{SIM} and p_{TURN} through time contrast with two recent studies on nine isolated lakes from the same region (Su *et al.*, 2015; Xu *et al.*, 2015). Those studies reported an inconsistent homogenization of fish assemblages through time, but such discrepancy might be explained by differences in the time window considered (these studies consider a shorter time frame) and the establishment status of the exotic species considered.

Hence, considering not only established exotic species but all the species introduced (whatever establishment success), as in Su *et al.* (2015) and Xu *et al.* (2015) blurred the patterns shown here, testifying that the patterns we show actually reflect the impact of established non-natives on the taxonomic dissimilarity between lakes.

Turnover (β_{sim}) experienced greater temporal decrease than the overall dissimilarity (β_{sor}) (Table 2). The introduction of the same exotic species and the extirpation of distinct species in lake pairs led to a decrease in both taxonomic dissimilarity and its turnover component, especially for those dissimilar pairs (Toussaint *et al.*, 2014). This also caused a decline in the contribution of turnover to dissimilarity (p_{turn}), meaning that the fish metacommunity gradually changed from spatially structured by distinct endemic species to a more homogeneous state, where fish assemblages are dominated by a few widespread exotic species. The studied lakes historically experienced relative unique fish assemblages, resulting in high levels of β_{sim} and p_{turn} , denoting a low state of nestedness of beta-diversity in the historical period. However, when the lakes received the same non-native species introductions (a increase), accompanied by the extirpations of distinctive species (both b and c decrease), the turnover component experienced greater decrease than total dissimilarity and p_{turn} also decreased (Baselga, 2012; Toussaint *et al.*, 2014), indicating fish assemblages in the lakes became more homogenized by becoming more nested. Nevertheless, considering exclusively the effects of extirpations on the change in dissimilarity and turnover revealed that the decrease of β_{sim} and p_{turn} when considering only the native fauna (i.e. considering only the effect of extirpations) were greater than when considering the entire assemblages (i.e. considering both extirpations and introductions) from the intermediate to current periods (Table 2). Hence, although similar exotic fishes were introduced to the lakes, there are still several invasive species established in a single or a few lakes (e.g. *Acheilognathus macropterus* and *Toxabramis hoffmanni* only established in Dianchi Lake, *Tinca tinca* and *Clarias leather* only established in Fuxianhu Lake and *Protosalanx hyalocranius* established only in Lugu Lake). As previously demonstrated over the world river basins (Toussaint *et al.*, 2014), such discrepancy in exotic species establishment increases the species distinctiveness between lakes, and therefore compensates in part for the loss of dissimilarity due to the extirpation of native species. We hence suggest to not only consider the change of dissimilarity of the entire faunas, but also to consider only the native fish fauna to avoid a blurring effect of some non-native species that pushes assemblages towards differentiation.

Over the plateau landscape, we report a pronounced homogenized trend of fish assemblages through time, with a decline of the distance decay of dissimilarity, which is currently sustained only by the non-native species. Excluding non-native species from our analyses revealed that the distance decay of similarity is currently absent. This means that the anthropogenic changes experienced by the Yun-Gui

plateau lakes were so harsh that they erased the distance decay of similarity, a general biogeographic trend known for almost all organisms and ecosystems on earth (Nekola & White, 1999; Soininen *et al.*, 2007). Such a result parallels recent studies demonstrating that over only a few decades, human activities, through invasions and extirpations, were able to modify the historical patterns of biodiversity (Leprieur *et al.*, 2008b; Villéger *et al.*, 2011) but also the functional structure of fish assemblages (Blanchet *et al.*, 2010). Moreover, the distance decay reported when considering the entire fauna was only attributable to the differences in exotic species established in the different lakes, that likely refers to the strength in introduction pressure in each lake (Leprieur *et al.*, 2008b). In addition to the changes in species composition, a recent study reported the dramatic changes in functional and phylogenetic diversity of fish assemblages in one of the studied lake under long-term introduction pressures (Jiang *et al.*, 2015). Other studies also highlighted the consistent degradations of vascular hydrophyte (Xu & Jin, 2006; Wang *et al.*, 2013), molluscs (Song *et al.*, 2013) and plankton (Liu *et al.*, 2014) in Yun-Gui Plateau lakes during the past 60 years, due to increasing human disturbances. Our results hence represent a striking example of the so-called human domination on earth ecosystems (Vitousek *et al.*, 1997).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Physical characteristics of the 15 studied lakes.

Table S2 Literature used to build up fish species lists in historical (1940–1957), intermediate (1970–1985), and current (2000–2015) periods in the 15 studied lakes of Yun–Gui Plateau.

Table S3 Species occurrence in the 15 lakes during the historical period (1940–1957). 1 account for the presence of the species as native in the lake during the considered period, 0

means the species is absent from the lake, 2 means the species is present in the lake, but non-native from this lake. Lake codes are as follows: DCL, Dianchi Lake; FXL, Fuxian Lake; XYL, Xingyun Lake; QLL, Qilu Lake; YZHL, Yangzonghai Lake; YLL, Yilong Lake; EHL, Erhai Lake; CQHL, Changqiaohai Lake; DTHL, Datunhai Lake; CBL, Cibi lake; JHL, Jianhu Lake, CHHL, Chenghai Lake; CHL, Caohai Lake; LGL, Lugu Lake; QHL, Qionghai Lake.

Table S4 Species occurrence in the 15 lakes during the intermediate period (1970–1985). 1 account for the presence of the species as native in the lake during the considered period, 0 means the species is absent from the lake, 2 means the species is present in the lake, but non-native from this lake. Lakes codes as in Table S3.

Table S5 Species occurrence in the 15 lakes during the current period (2000–2015). 1 account for the presence of the species as native in the lake during the considered period, 0 means the species is absent from the lake, 2 means the species is present in the lake, but non-native from this lake. Lakes codes as in Table S3.

BIOSKETCH

Chengzhi Ding is an Assistant Professor at Yunnan University. His interests include the ecology and conservation of native species, biogeography of freshwater fishes and the development of conservation strategies towards restoring disturbed aquatic ecosystems.

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