ELSEVIER

Contents lists available at ScienceDirect

## Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco



## Original research article

# Human impacts on functional and taxonomic homogenization of plateau fish assemblages in Yunnan, China



Guohuan Su<sup>a,b</sup>, Jun Xu<sup>a,\*</sup>, Munemitsu Akasaka<sup>c</sup>, Jorge García Molinos<sup>d</sup>, Shin-ichiro S. Matsuzaki<sup>e</sup>

- <sup>a</sup> Donghu Experimental Station of Lake Ecosystems, State Key Laboratory of Freshwater Ecology and Biotechnology of China, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, PR China
- <sup>b</sup> University of Chinese Academy of Sciences, Beijing 100080, PR China
- <sup>c</sup> Faculty of Agriculture, Tokyo University of Agriculture and Technology, Japan
- <sup>d</sup> Department of Ecology, Scottish Association for Marine Science, Scottish Marine Institute, Oban Argyll PA37 1QA, Scotland, UK
- <sup>e</sup> Center for Environmental Biology and Ecosystem Studies, National Institute of Environmental Studies, 16-2 Onogawa, Tsukuba, Ibaraki 305-8506, Japan

#### ARTICLE INFO

Article history:
Received 6 August 2015
Received in revised form 10 September 2015
Accepted 10 September 2015
Available online 23 October 2015

Keywords:
Beta-diversity
Extinction
Invasion
Non-native species
Taxonomic dissimilarity
Functional homogenization

#### ABSTRACT

Human activities and the consequent extinctions of native species and invasions of nonnative species have been changing the composition of species assemblages worldwide. These anthropogenic impacts alter not only the richness of assemblages but also the biological dissimilarity among them. However, much of the research effort to date has focused on changes in taxonomic dissimilarity (i.e. accounting for species composition) whether assessments of functional dissimilarity (i.e. accounting for the diversity of biological traits) are much more scarce, despite revealing important complimentary information by accounting for changes in the diversity of biological traits. Here, we assess the temporal (1950s against 2000s) changes in both taxonomic and functional dissimilarities of freshwater fish assemblages across lakes from the Yunnan Plateau in China. The laccard index to quantify the changes in both taxonomic and functional dissimilarity. We then partitioned dissimilarity to extract its turnover component and measured the changes in the contribution of turnover to dissimilarity. We found that functional and taxonomic homogenization occurred simultaneously. However, patterns between these two processes differed for some lakes. Taxonomic and functional homogenizations were stronger when the historical level of taxonomic dissimilarity among assemblages was high. The impact of extinctions of native species and invasions of non-native species on homogenization was otherwise complex to disentangle with no significant effect of any of the studied environmental factors. In agreement with other studies, our study proved that change in taxonomic dissimilarity cannot be used to predict changes in functional dissimilarity and, as an indicator of ecosystem functioning, functional dissimilarity should be used together with taxonomic dissimilarity to attain a more holistic understanding of human impacts on natural ecosystems.

© 2015 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

E-mail address: xujun@ihb.ac.cn (J. Xu).

<sup>\*</sup> Corresponding author.

#### 1. Introduction

Human activity and ecosystem disruption are strongly correlated, regardless of local fish biodiversity (Bellwood et al., 2003). Habitat alteration and biotic invasions are the two leading causes of global environmental change and biodiversity loss. As for freshwater ecosystems, fish extinction and invasion have occurred worldwide (Baxter et al., 2004; Seifert et al., 2015). Although species richness is decreasing on a global scale, species richness at the local and regional scales increases when the number of invasive non-native species greatly exceeds the number of native species becoming extinct (Sax et al., 2002; Winter et al., 2009; Matsuzaki et al., 2013).

The extinction of native species and invasion of non-native species should both lead to taxonomic homogenization (i.e. increase in the similarity of species composition among species assemblages over time), a trend documented for many other taxa across the world (Lockwood et al., 2000; Spear and Chown, 2008; Olden et al., 2011). However, much less evidence has been gathered on the impact of invasions and extinctions on the functional facet of biodiversity (Matsuzaki et al., 2013), or on its relationship with co-occurring changes in taxonomic dissimilarity among assemblages (Villéger et al., 2014). Therefore, it will provide a better understanding of the potential consequences of biodiversity change on ecosystem functioning by assessing the level of functional homogenization than just by measuring the level of taxonomic homogenization (Villéger et al., 2014).

Here, we assess the temporal (1950s against 2000s) changes in both taxonomic and functional dissimilarities of freshwater fish assemblages across lakes from the Yunnan Plateau in China. These lakes have experienced high rates of extinction of native species and invasion of non-native species over the past 60 years. Based on historical (1950s, prior to extinctions and invasions) and current (2000s, after extinctions and invasions) comprehensive datasets of strictly freshwater fish assemblages for nine plateau lake basins of Yunnan China, we explored the effects of species extinctions and invasions on the taxonomic and functional dissimilarities between fish faunas assemblages following the methodological frameworks of Baselga (2012) and Villéger et al. (2013). From a macroecological perspective, our study had three primary objectives. First, we assessed the temporal changes in these biodiversity facets following invasions of non-native species and extinctions of native species. Second, we quantified the correlation between the change in functional dissimilarity and the change in taxonomic dissimilarity to test whether the latter could be used as a proxy for the former (i.e., redundancy between both metrics). Finally, we investigated the relative effects of historical dissimilarity and the number of extinctions and invasions on changes in taxonomic and functional dissimilarities.

#### 2. Materials and methods

#### 2.1. Measuring dissimilarity and contribution of turnover

Based on species composition, taxonomic dissimilarity can be defined as the percentage of species present only in one assemblage within a pair of assemblages, and it can be measured with the Jaccard index (Villéger et al., 2014).

$$\beta_{\rm diss} = \frac{b+c}{a+b+c}$$

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. However, only use this index could not describe the dissimilarity very exactly, thus Baselga (2012) partitioned the index into two parts: a nestedness and a turnover component. The turnover component accounts for the number of species replaced and the species richness in the poorest assemblage:

$$\beta_{\text{turnover}} = \frac{2 \times \min(b, c)}{a + 2 \times \min(b, c)}.$$

As turnover is a component of dissimilarity, its relative contribution to dissimilarity was more clear to measure, hereafter denoted  $P_{\text{turn}}$  (Toussaint et al., 2014):

$$P_{\text{turn}} = \frac{\beta_{\text{turnover}}}{\beta_{\text{diss}}} = \frac{2 \times \min(b, c)}{a + 2 \times \min(b, c)} \times \frac{a + b + c}{b + c}.$$

This partitioning of taxonomic dissimilarity has been recently transferred to functional dissimilarity (Villéger et al., 2013). Indeed, the functional richness of an assemblage can be measured as the volume of the convex hull shaping all the species in a multidimensional functional space (Villéger et al., 2008). The functional dissimilarity between two assemblages can thus be assessed using the percentage of overlap in this functional space. So it is possible to define the quantity a as the volume of the functional space shared by the two assemblages and b and c as the volume of the functional space they fill independently, respectively (Villéger et al., 2014).

### 2.2. Assessing changes in taxonomic and functional dissimilarities

The partitioning of taxonomic and functional dissimilarities can be used to describe biogeographic patterns at a given time (Baselga, 2012; Villéger et al., 2013). It also allows quantification of temporal changes in the taxonomic and functional facets of biodiversity following changes in species composition. Here we define e as the change from historical to current period in the diversity shared by two assemblages (e > -a), and f and g as the changes in the diversity unique to each of the two assemblages ( $f \ge -b$  and  $f \ge -c$ ). Change in dissimilarity and change in contribution of turnover to dissimilarity from a historical to a current period (after species extinctions and invasions occurred) can then be written as:

$$\begin{split} \Delta\beta_{\mathrm{diss}} &= \frac{b+f+c+g}{a+e+b+f+c+g} - \frac{b+c}{a+b+c} \\ \Delta p_{\mathrm{turn}} &= \frac{2\times \min(b+f,c+g)}{a+e+2\times \min(b+f,c+g)} \times \frac{a+e+b+f+c+g}{b+f+c+g} - \frac{2\times \min(b,c)}{a+2\times \min(b,c)} \times \frac{a+b+c}{b+c}. \end{split}$$

A decrease in dissimilarity (i.e. an increase in the percentage of species or functional space shared) means that assemblages became homogenized after their composition changed. On the contrary, an increase in dissimilarity indicates a differentiation. Interestingly, changes in taxonomic and functional dissimilarities are a priori independent of each other. For instance, a taxonomic homogenization could induce a functional differentiation if the species added to only one assemblage fill a unique portion of the functional space. Similarly, a taxonomic differentiation could induce a functional homogenization if the species introduced in only one of the two assemblages fill the same portion of the functional space (Villéger et al., 2014).

## 2.3. Datasets and statistical analyses

Historical fish fauna data on the nine study lakes was collected from available presence/absence surveys published and unpublished before 1960s (supplement information, Table S2). Present-day fish fauna data was obtained through fish surveys conducted between 2008 and 2012 in the nine study lakes (Table S3) (Xu et al., 2015). The functional strategy of the 103 species present in the 9 assemblages studied was described using 7 functional traits commonly used in studies on fish functional diversity to describe the fish functional niche (Matsuzaki et al., 2013). Two traits were measured as continuous variables: maximum total body length and maturation. The remaining traits (mouth position, morphology, dietary traits, diet breadth, and vertical position in the water column), were coded as ordered traits (Table S1). All the functional traits were taken from the ichthyography (Chu and Chen, 1989, 1990) and Fishbase (Froese and Pauly, 2010).

Functional distances between each pair of species were computed using Gower's distance, which allowed different types of variables to be mixed while giving them equal weights (Gower, 1971). Then, a principal coordinates analysis (PCoA) was carried out on this functional distance matrix (Villéger et al., 2008). The indices of functional dissimilarity and turnover were computed in the functional space made by the first three principal axes of the PCoA, to achieve a necessary trade-off between information quality and computation time (Villéger et al., 2013). Indeed, the three-dimensional functional space provided an accurate representation of the functional dissimilarity between species (Villéger et al., 2014) (Mantel's test between Gower's distance on traits values and Euclidean distance in the three-dimensional functional space: r = 0.936, P < 0.001).

Indices of taxonomic and functional dissimilarity and contribution of turnover to dissimilarity between each pair of fish assemblages were computed for historical and current species composition. Temporal changes from the historical to the current period were computed for these four indices (a positive value indicates an increase in dissimilarity or in contribution of turnover from the historical to the current period). Correlations between changes in taxonomic dissimilarity and changes in functional dissimilarity were tested using Mantel's permutation test (Villéger et al., 2014).

In order to investigate the drivers of changes in taxonomic dissimilarity we used multiple regression on distance matrices (MRM) (Lichstein, 2007) with historical taxonomic dissimilarity, total number of invasive species, total number of extinct species, total number of common invasive species, total number of common invasive species and change in environmental factor in each pair of assemblages as explanatory matrices. *P*-values for MRM models were obtained by comparing each observed regression coefficient with a distribution of 10,000 permuted values. The same analysis was conducted to analyze changes in functional dissimilarity (Villéger et al., 2014).

We chose a significance level as  $\alpha = 0.05$ . Statistical analyses were carried out using R (R Core Team, 2012), including the libraries "betapart" for computing dissimilarity indices and "ecodist" for MRM analyses (Goslee and Urban, 2007; Villéger et al., 2014).

## 3. Results

The 9 plateau lakes considered in this study host 103 fish species. The number of native species extirpated from a basin was only weakly correlated with the total number of non-native species introduced (r=0.175, P=0.041). The species richness per lake basin increased on average by 14.4% from the historical to the current period (from 13.9  $\pm$  9.0 to 15.9  $\pm$  11.0).

**Table 1** Values (mean  $\pm$  SD, ranges in parentheses) of taxonomic and functional dissimilarities and contribution of turnover to dissimilarity in historical and current periods and the temporal changes (current value minus the historical one). Richness ratios (minimum richness/maximum richness for each pair of assemblages) are also indicated.

		Taxonomic	Functional
Dissimilarity	Historical Current Change	$\begin{array}{c} 0.88 \pm 0.08 (0.60; 1.00) \\ 0.72 \pm 0.13 (0.41; 0.91) \\ -0.15 \pm 0.16 (-0.52; 0.18) \end{array}$	$\begin{array}{c} 0.82 \pm 0.14 (0.41; 1.00) \\ 0.77 \pm 0.22 (0.17; 1.00) \\ -0.05 \pm 0.23 (-0.67; 0.59) \end{array}$
Contribution of turnover to dissimilarity	Historical Current Change	$\begin{array}{c} 0.90 \pm 0.12 (1.00; 0.56) \\ 0.50 \pm 0.36 (1.00; 0.00) \\ -0.40 \pm 0.37 (-1.00; 0.39) \end{array}$	$\begin{array}{c} 0.59 \pm 0.34 (1.00; 0.03) \\ 0.32 \pm 0.38 (1.00; 0.00) \\ -0.27 \pm 0.51 (-0.98; 0.97) \end{array}$
Richness ratio	Historical Current Change	$\begin{array}{c} 0.53 \pm 0.26 (0.17; 1.00) \\ 0.47 \pm 0.24 (0.12; 1.00) \\ -0.06 \pm 0.34 (-0.82; 0.51) \end{array}$	$\begin{array}{c} 0.40 \pm 0.26 (0.05; 0.99) \\ 0.32 \pm 0.27 (0.00; 0.88) \\ -0.08 \pm 0.34 (-0.71; 0.72) \end{array}$

#### 3.1. Historical patterns of taxonomic and functional dissimilarities

Historical taxonomic dissimilarity among plateau fish assemblages was high with a value of  $0.88 \pm 0.08$  (mean  $\pm$  SD; Table 1). Contribution of turnover to the taxonomic dissimilarity was also high ( $0.90 \pm 0.12$ ). In contrast, historical functional dissimilarity was lower ( $0.82 \pm 0.14$ ), as was contribution of turnover to dissimilarity ( $0.59 \pm 0.34$ , Table 1). Difference in richness between assemblages was on average lower for species richness than for functional richness (minimum/maximum ratio of 0.53 and 0.40 respectively, Table 1).

#### 3.2. Temporal changes in taxonomic and functional dissimilarities

Overall, fish assemblages in plateau lakes showed a weak trend towards functional homogenization from the historical to the current period (mean change of  $-0.05 \pm 0.23$ ; Table 1). However, this low average value hid a great variability, with 63.9% of assemblage pairs showing homogenization while 36.1% showed no change or differentiation (Table 2). However contribution of turnover to functional dissimilarity showed a strong decrease ( $-0.27 \pm 0.51$ ; Table 1). However, there was strong variability of this index among assemblage pairs (Table 2). Among the 36.1% of pairs that showed functional differentiation, 22.2% also showed a decrease in the contribution of turnover while only 13.9% showed an increase. Among the 63.9% of functional homogenization cases, only 11.1% of assemblage pairs showing an increase in the contribution of turnover and 52.8% showing a decrease.

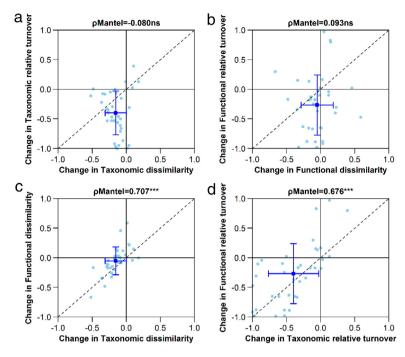
Change in taxonomic dissimilarity was on average higher than change in functional dissimilarity ( $-0.15\pm0.16$ ; Table 1). Cases of taxonomic homogenization (i.e. assemblages that became taxonomically more similar) were more frequent those of taxonomic differentiation (83.3% vs. 16.7%; Table 2). Contribution of turnover to taxonomic dissimilarity decreased stronger than the proportion of functional dissimilarity ( $-0.40\pm0.37$ ; Table 1). The ratio of species richness between the poorest and the richest assemblage in each pair decreased slightly ( $-0.06\pm0.34$ ; Table 1). While, the ratio of functional richness decreased on average by  $-0.08\pm0.34$  (Table 1).

Change in dissimilarity and change in contribution of turnover to dissimilarity were not significant correlated with each other for both taxonomic and functional facets (Fig. 1(a), (b)). Changes in taxonomic and functional dissimilarity were positively correlated (Spearman's correlation coefficient  $\rho=0.707$ ; Mantel test P<0.001; Fig. 2(c)). Changes in the contribution of turnover to taxonomic and functional dissimilarities were also positively correlated ( $\rho=0.676$ ; P<0.001; Fig. 1(d)).

## 3.3. Determinants of changes in taxonomic and functional dissimilarities

Change in taxonomic dissimilarity could be significantly predicted from historical period and invasion and extinction pressures (MRM, R2 = 0.847, P < 0.01; Fig. 2). The historical level of taxonomic dissimilarity had a significant negative effect, i.e. pairs of assemblages with a high historical dissimilarity tended to be more homogenized (Fig. 2). The total number of extinct species from the pair of assemblages did not have a significant contribution. The total number of invasive species in a pair of assemblages had a significant positive effect on change in taxonomic dissimilarity, i.e. pairs that received more species tended to be less homogenized. The total number of common invasive species in a pair of assemblages also had a significant negative effect on change in taxonomic dissimilarity, i.e. pairs that received more common species tended to be more homogenized. However, the total number of common extinct species had no effect on change in taxonomic dissimilarity, the environmental factor did not show a significant effect either. Factors that influenced changes in functional dissimilarity were almost same as the former, but had a little differentiation (MRM, R2 = 0.638, P < 0.01; Fig. 2). The total number of extinct species from the pair of assemblages had a significant contribution.

deviation of change in functional dissimilarity.	al dissimilarity.						
	Functional homogenization	ıtion		Functional differentiation	ion		Total taxonomic change
	Total	Decrease in contribution of turnover	Increase in contribution of turnover	Total	Decrease in contribution of turnover	Increase in contribution of turnover	
Taxonomic homogenization $58.3\%(-0.19\pm0.16)$ Taxonomic differentiation $5.6\%(-0.02\pm0.03)$ Total functional change $63.9\%(-0.18\pm0.16)$	$58.3\%(-0.19 \pm 0.16)$ $5.6\%(-0.02 \pm 0.03)$ $63.9\%(-0.18 \pm 0.16)$	$50.0\%(-0.16 \pm 0.13)$ $2.8\%(-0.04 \pm 0.00)$	$8.3\%(-0.39 \pm 0.25)$ $2.8\%(0.00 \pm 0.00)$	$25.0\%(0.11 \pm 0.14)$ $11.1\%(0.29 \pm 0.20)$ $36.1\%(0.17 \pm 0.18)$	$13.9\%(0.06 \pm 0.05)$ $8.3\%(0.34 \pm 0.21)$	$11.1\%(0.17 \pm 0.20)$ $2.8\%(0.15 \pm 0.00)$	$83.3\%(-0.10 \pm 0.21)$ $16.7\%(0.19 \pm 0.23)$



**Fig. 1.** Changes in taxonomic and functional dissimilarity versus changes in contribution of turnover to dissimilarity. Spearman's correlation coefficient and associated Mantel permutation test are provided at the top of each panel (\*\*\*P < 0.001, \*\*P < 0.01, ns not significant). The mean value and associated standard deviation among pairs of fish faunas are shown in each panel.

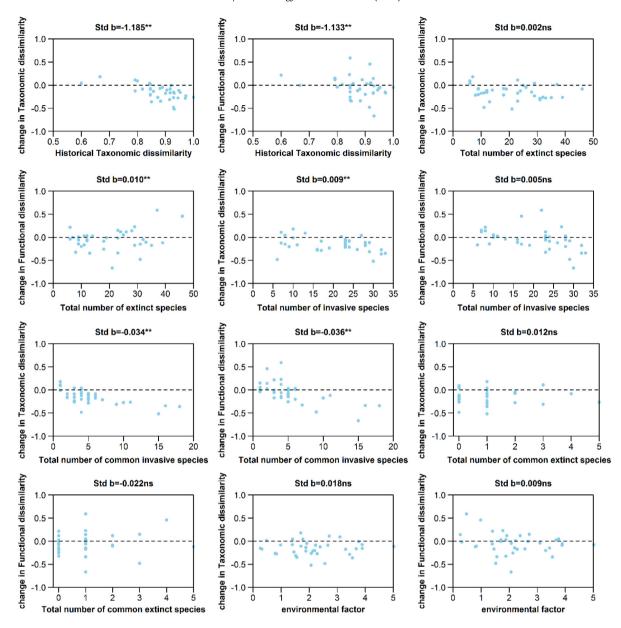
#### 4. Discussion

The formation time of Yunnan plateau lakes can be traced back to the Pliocene epoch, they randomly distributed in the Yunnan Plateau, located in the source of each basin or branch, belonging to four different hydrographic networks (Dianchi Lake, Chenghai Lake and Luguhu Lake belong to Jinshajiang River; Fuxianhu Lake, Qiluhu Lake, Xingyunhu Lake, Yangzonghai Lake and Datun Lake belong to Nanpanjiang River; Erhai Lake belong to Lancang River; Yilonghu Lake belong to Yuanjiang River (Yang, 1984)). Because of the complex historical and geological conditions (Chen et al., 2001; Xu et al., 2015), there was a high historical level of taxonomic dissimilarity between fish assemblages. Furthermore, the high level of taxonomic dissimilarity observed among the 9 lakes was mainly due to species replacement, as the contribution of turnover to taxonomic dissimilarity was also high (Table 1). However, despite being marginally lower than taxonomic dissimilarity, functional dissimilarity also maintained a high level, while having a comparatively lower contribution of turnover to dissimilarity, though still played a dominant role.

These results show that functional dissimilarity as similar high degree as taxonomic dissimilarity but had lower contribution of turnover to functional dissimilarity. Therefore, the freshwater fish assemblages in these lakes contain distinct species (and different numbers of species) also possessing different combinations of trait values.

Over recent years, human activities had significant impacts on biodiversity in these lakes. These anthropogenic impacts have modified the richness of assemblages as well as the biological dissimilarity among them. Due to the high demand for recreational fishing and aquaculture activities, and to the high commercial activity within these plateau lakes, the number of invasive species has increased rapidly dominating the assemblages (Chen, 1991; Xiong et al., 2008). For example, a total of 12 new invasive species have been reported from Fuxianhu Lake between 1995 and 2008 (Xiong et al., 2008). These invasions not only change the intrinsic composition of the fish assemblages, but also have a profound negative effect on native species. Meanwhile, anthropogenic pressures on freshwater ecosystems, such as pollution, habitat modification and over fishing, have led some fish species towards local extinction (Chen, 1991; Yang, 1996). The direction and intensity of change in taxonomic dissimilarity among pairs of fish assemblages was variable, but on average we found a distinct trend towards taxonomic homogenization (Tables 1 and 2, Fig. 1). We also found that the contribution of turnover to dissimilarity decreased strongly, but this change was characterized by a high variability among pairs of assemblages (Tables 1 and 2), a pattern also found at the global scale (Toussaint et al., 2014). Furthermore, the change in taxonomic dissimilarity was independent of the change in the contribution of turnover (Fig. 1). This independence could be explained by the lack of a clear trend in the ratio of richness difference among assemblages. Indeed, the ratio between species richness of assemblage pairs decreased slightly from the historical to the current period but this average value hid a high variability (Table 1).

The change in functional dissimilarity was lower than taxonomic change, with a global trend towards functional homogenization of 0.05. However, functional differentiation remained frequent (36.1% of assemblage pairs) but of lower magnitude than homogenization. More importantly, even if there was a significant positive correlation between changes



**Fig. 2.** Effect of historical dissimilarity, extinction/invasion and environment pressures on changes in taxonomic and functional dissimilarities. Standard partial regression coefficient (Std b) and associated *P*-value from multiple regression on distance matrices (MRM) are given for each panel.

in taxonomic and functional dissimilarities (Fig. 1), in more than 30% of assemblage pairs the changes were in the opposite direction (Table 2). For instance, 5.6% of the assemblage pairs that showed taxonomic differentiation were actually functionally homogenized and 25% of the assemblage pairs taxonomically homogenized were functionally differentiated (Table 2). For the remaining cases where taxonomic and functional dissimilarities changed in the same direction, the change in taxonomic dissimilarity was most often of higher magnitude than the change in functional dissimilarity, despite a high variability in the magnitude of this difference (Fig. 1). This discrepancy highlights the need to consider explicitly the functional facet of biodiversity, as changes in functional dissimilarity cannot be predicted by the change in taxonomic dissimilarity.

Changes in taxonomic and functional dissimilarity were both significantly related to the historical level of taxonomic dissimilarity. This historical contingency is intuitive for extreme levels of taxonomic dissimilarity; for instance a pair of assemblages that historically had few species in common cannot experience a high taxonomic differentiation. The number of extinct species had a significant positive effect on change in functional dissimilarity but not on taxonomic. In contrast, the number of invasive species introductions played a significant positive role in explaining the change in taxonomic dissimilarity though not in functional dissimilarity. This pattern was completely different from the studies on European

river basins (Villéger et al., 2011, 2014). However, when we decomposed the extinct and invasive species into unique and common parts, then add the common part in the MRM analysis, the result showed the number of common invasive species of each pair had a negative effect whereas the number of common extinct species of each pair had no effect on both taxonomic and functional dissimilarities.

Indeed, despite their history of isolation, speciation in these lakes have occurred under similar ecological conditions, resulting in similar traits shared amongst the different species. As a result, the disappearance of the native species decreased the homogenization in functional dissimilarity to a certain extent. More importantly, invasive species are mainly concentrated in some lakes, and there are a lot of single invasive species (e.g. *Acheilognathus macropterus* and *Toxabramis swinhonis* only established in Dianchi Lake, *Anguilla anguilla* and *Hemibarbus maculatus* only establish in Fuxianhu Lake), as for other lakes the phenomenon was not obvious, and thus invasive species as a result of decrease the homogenization in taxonomic dissimilarity. This also can explain why the number of common invasive species is much less than the total number and lead to increase homogenization in both taxonomic and functional dissimilarity. We also considered the change of environmental factors (lake area, fish catch and water quality) as a complex factor added into the model but it had no significant effect on the dissimilarity. This weak effect could be explained by the complex topography and geology and the influence of special events, such as the arsenic contamination accident in Yangzonghai Lake in 2008 (Wang et al., 2010).

Simultaneously assessing changes in taxonomic and functional dissimilarities as well as the changes in their turnover components made it possible for us to understand the consequences of non-native species invasion and native species extinction on the biodiversity of assemblages.

Since there are few studies that concentrate on the taxonomic and functional dissimilarities among plateau lake fish assemblages, our study highlight the importance of assessing the effects of non-native species invasion and native species extinction on ecosystem function in these lakes. More importantly, in agreement with the results of a former study (Villéger et al., 2014), we found that the taxonomic dissimilarity cannot be used as a proxy for the functional dissimilarity. Thus, the latter would be a very useful method to understand, predict and mitigate the effects of global change on aquatic ecosystems.

## Acknowledgments

This research was supported by the National Natural Science Foundation of China (Grant Nos. 31170439, 31370473), and the Water Pollution Control and Management Project of China (Grant Nos. 2012ZX07101-001 and 2008ZX07101-001).

#### Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2015.09.002.

#### References

Baselga, A., 2012. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. Glob. Ecol. Biogeogr. 21, 1223–1232.

Baxter, C.V., Fausch, K.D., Murakami, M., Chapman, P.L., 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology 85, 2656–2663.

Bellwood, D.R., Hoey, A.S., Choat, J.H., 2003. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. Ecol. Lett. 6, 281–285.

Chen, Y., 1991. Fish resources and its utilization and protection in Yunnan. Resour. Sci. 13, 25–33.

Chen, Z., Yang, J., Su, R., Chen, X., 2001. Present status of the indigenous fishes in Dianchi Lake, Yunnan. Chin. Biodivers. 9, 407–413.

Chu, X., Chen, Y., 1989. The Fishes of Yunnan, China, Part I. Science Press, Beijing.

Chu, X., Chen, Y., 1990. The Fishes of Yunnan, China, Part II. Science Press, Beijing.

Froese, R., Pauly, D., 2010. FishBase. International Center for Living Aquatic Resources Management.

Goslee, S.C., Urban, D.L., 2007. The ecodist package for dissimilarity-based analysis of ecological data. J. Stat. Softw. 22, 1–19.

Gower, J.C., 1971. A general coefficient of similarity and some of its properties. Biometrics 857–871.

Lichstein, J.W., 2007. Multiple regression on distance matrices: a multivariate spatial analysis tool. Plant Ecol. 188, 117–131.

Lockwood, J.L., Brooks, T.M., Mckinney, M.L., 2000. Taxonomic homogenization of the global avifauna. Anim. Conserv. 3, 27–35.

Matsuzaki, S.i.S., Sasaki, T., Akasaka, M., 2013. Consequences of the introduction of exotic and translocated species and future extirpations on the functional diversity of freshwater fish assemblages. Glob. Ecol. Biogeogr. 22, 1071–1082.

Olden, J.D., Lockwood, J.L., Parr, C.L., 2011. Biological invasions and the homogenization of faunas and floras. In: Conservation Biogeography. Wiley-Blackwell, Oxford, pp. 224–244.

R Core Team, 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Sax, D.F., Gaines, S.D., Brown, J.H., 2002. Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. Am. Nat. 160, 766–783.

Seifert, L.I., Weithoff, G., Gaedke, U., Vos, M., 2015. Warming-induced changes in predation, extinction and invasion in an ectotherm food web. Oecologia 1–12.

Spear, D., Chown, S.L., 2008. Taxonomic homogenization in ungulates: patterns and mechanisms at local and global scales. J. Biogeogr. 35, 1962–1975. Toussaint, A., Beauchard, O., Oberdorff, T., Brosse, S., Villéger, S., 2014. Historical assemblage distinctiveness and the introduction of widespread non-native species explain worldwide changes in freshwater fish taxonomic dissimilarity. Glob. Ecol. Biogeogr. 23, 574–584.

Villéger, S., Blanchet, S., Beauchard, O., Oberdorff, T., Brosse, S., 2011. Homogenization patterns of the world's freshwater fish faunas. Proc. Natl. Acad. Sci. 108, 18003–18008.

Villéger, S., Grenouillet, G., Brosse, S., 2013. Decomposing functional  $\beta$ -diversity reveals that low functional  $\beta$ -diversity is driven by low functional turnover in European fish assemblages. Glob. Ecol. Biogeogr. 22, 671–681.

Villéger, S., Grenouillet, G., Brosse, S., 2014. Functional homogenization exceeds taxonomic homogenization among European fish assemblages. Glob. Ecol. Biogeogr. 23, 1450–1460.

- Villéger, S., Mason, N.W., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290–2301.
- Wang, Z., He, B., Pan, X., Zhang, K., Wang, C., Sun, J., Yun, Z., Jiang, G., 2010. Levels, trends and risk assessment of arsenic pollution in Yangzonghai Lake, Yunnan Province, China. Sci. China Chem. 53, 1809–1817.
- Winter, M., Schweiger, O., Klotz, S., Nentwig, W., Andriopoulos, P., Arianoutsou, M., Basnou, C., Delipetrou, P., Didžiulis, V., Hejda, M., 2009. Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. Proc. Natl. Acad. Sci. 106, 21721–21725.
- Xiong, F., Li, W., Pan, J., 2008. Present status of a lien fishes and analysis of relative problems in Fuxian Lake in Yunnan Province. Acta Agric. Jiangxi 20,
- Xu, J., Su, G., Xiong, Y., Akasaka, M., Molinos, J.G., Shin-ichiro, S.M., Zhang, M., 2015. Complimentary analysis of metacommunity nestedness and diversity partitioning highlights the need for a holistic conservation strategy for highland lake fish assemblages. Glob. Ecol. Conserv. 3, 288–296.
   Yang, L., 1984. The preliminary study on the original classification and distribution law of lakes on the Yunnan Plateau. Trans. Oceanol. Limnol. 1, 34–39.
- Yang, L., 1984. The preliminary study on the original classification and distribution law of lakes on the Yunnan Plateau. Trans. Oceanol. Limnol. 1, 34–39. Yang, J., 1996. Nonnative and native fish of Yunnan: study of the type and extent of influence and related problem. In: Protect Biodiversity in China(II). China Environmental Science Press, Beijing, p. 138.