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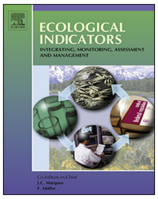

Local rise of phylogenetic diversity due to invasions and extirpations leads to a regional phylogenetic homogenization of fish fauna from Chinese isolated plateau lakes

Xiaoming Jiang[a,b], Chengzhi Ding[c,*], Sébastien Brosse[d], Baozhu Pan[a], Yan Lu[e], Zhicai Xie[b,*]

[a] State Key Laboratory of Eco-hydraulic in Northwest Arid Region of China, Xi'an University of Technology, Xi'an 710048, Shaanxi, China
[b] CAS Key Laboratory of Freshwater Ecology & Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China
[c] Yunnan Key Laboratory of International Rivers and Transboundary Eco-Security, Yunnan University, Kunming, Yunnan, China
[d] Laboratoire Evolution et Diversite Biologique (UMR5174 UPS-CNRS-IRD), University Paul Sabatier Toulouse 3, 31062 Toulouse, France
[e] Nanjing Hydraulic Research Institute, Nanjing 210029, China

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ABSTRACT

Human-mediated introductions of exotic species and extirpations of native species have modified the composition of biotic communities throughout the world, but the consequences of introductions and extirpations on local phylogenetic diversity (alpha-diversity) and on phylogenetic distinctiveness between sites (beta-diversity) remains poorly investigated. Here we analyze the long-term impacts of extirpations and invasions on both phylogenetic and taxonomic alpha and beta diversity of fish assemblages in Chinese isolated lakes. Data of fish assemblages in 15 lakes were grouped into three periods spanning the last 75 years: historical, intermediate and current periods. We partitioned phylogenetic beta diversity into turnover and nestedness component, and examined how introductions and extirpations led to temporal changes in alpha and beta diversity using linear regression and multiple regression models on distance matrices, respectively. Introductions and extirpations caused an increase of phylogenetic diversity (Δ^+) and phylogenetic unevenness (Λ^+) within the lakes, but the phylogenetic dissimilarity between lakes declined. Such trend, resulting from 60 years introductions and extirpations, was mainly due to a decline of the phylogenetic turnover, indicating that the replacement of native endemic species by widespread exotic species was the main driver of the observed phylogenetic homogenization. Temporal changes in phylogenetic and taxonomic dissimilarities were positively correlated, and taxonomic homogenization causes phylogenetic homogenization in ca. 60% of the lake pairs. Nevertheless, taxonomic homogenization turns to phylogenetic differentiation in one third of lake pairs due to the extirpation of the closely-related species and the introduction of distinct exotic species belonging to different lineages among lakes. Therefore, measuring phylogenetic diversity changes provides complementary information to taxonomy, and gives support to the Darwin's naturalization hypothesis stipulating that species distantly related to natives easily establish in their introduction range. Our results demonstrate that half a century of anthropogenic disturbance was sufficient to blur the phylogenetic distinctiveness among lakes that resulted from the last 5 million years evolutionary history of the Yun-Gui plateau.

1. Introduction

Human activities, such as harvesting, habitat degradation, pollution, land conversion, or biotic exchanges have modified faunas and floras throughout the world, resulting in a rapid and dramatic loss of global biodiversity, often coined as "the sixth mass extinction" (Barnosky et al., 2011; Wake and Vredenburg, 2008). Two fundamental processes, namely introductions of non-indigenous species and extirpations of indigenous species, are the result of all human disturbances and lead to the current biodiversity crisis (Sax and Gaines, 2008; Toussaint et al., 2018). Those two processes caused an alteration of local species richness (alpha diversity; Ceballos et al., 2017; Leprieur et al., 2008), but are also responsible from an increase in species similarity between species assemblages, called biotic homogenization (Liu et al., 2017; Rahel, 2000; Villéger et al., 2011). Nevertheless, to which extent those invasion and extirpation processes, affect others

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* Corresponding authors.
E-mail addresses: chzhding@ynu.edu.cn (C. Ding), zhcxie@ihb.ac.cn (Z. Xie).

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facets of biodiversity, such as functional or phylogenetic diversities remain little documented (e.g. Sobral et al., 2016; Villéger et al., 2014).

Phylogenetic diversity, which represents the evolutionary history of species within communities, is increasingly used in biodiversity studies because it reflects the diversity of a complex set of intrinsic (e.g. morphological, physiological and reproductive) and extrinsic (e.g. behavioral, growth and environmental tolerance) traits (Graham and Fine, 2008; Webb et al., 2002). Considering that functional traits of the species are conserved across the phylogeny, phylogenetic diversity has also been considered as an overall measure of the functional characteristics of species assemblages and has therefore been used to investigate ecosystem functioning and the associated provision of ecosystem services (e.g. Huang and Roy, 2013; Sol et al., 2017; Winter et al., 2013). Moreover, integrating phylogenetic information into community ecology frameworks has provided new insights on the roles of ecological and evolutionary processes in shaping assemblage structure (Safi et al., 2011). Indeed, species identity within a community largely depend on evolutionary history, reflecting adaptation to changing environmental conditions across ecological and evolutionary time scales (Ricklefs, 1987).

Human disturbances, by causing extirpations and invasions, are known to affect the phylogenetic structure of assemblages since extirpations and invasions are often non-random from a phylogenetic point of view (McKinney and Lockwood, 1999). Thus the loss of native species belonging to evolutionarily distinct or unique clusters (e.g. species-poor higher taxa) triggers phylogenetic diversity losses (Thuiller et al., 2011; Vamosi and Wilson, 2008). On the other hand, the gain of exotic species can also significantly alter the phylogenetic structure of local communities, as those successful invasive species usually from different lineages and exhibit distinct functional traits than the native species (Winter et al., 2009). Such phenomena of invasions are often coined as Darwin's naturalization hypothesis, which proposed that exotics distantly related to native species would be successful invaders because they compete little with the native species (Daehler, 2001; Strauss et al., 2006b).

In addition to the changes in phylogenetic structure of local assemblages (alpha diversity), the gain and loss of species can also cause changes in phylogenetic dissimilarity among assemblages, also coined as phylogenetic beta-diversity. (Graham and Fine, 2008; Morelli et al., 2016). Therefore, declines of phylogenetic distinctiveness between sites through extirpation and invasion trends indicate a regional loss of phylogenetic diversity (Cavender-Bares et al., 2009; Ives and Helmus, 2010). The changes in phylogenetic diversity experienced by ecosystems across exotic species introductions and native species extirpation trends had been reported over large scales. For instance, D'agata et al. (2014) reported a loss of phylogenetic diversity in the Pacific coral reef fish assemblages, and Winter et al. (2009) revealed a decline of the phylogenetic distinctiveness among European floras. Moreover, it has also been demonstrated that exotic species introductions do not compensate for phylogenetic losses for native species extinctions in bird assemblages (Sobral et al., 2016; Sol et al., 2017). Such phylogenetic changes through extirpation and invasions are often triggered in isolated ecosystems (islands, isolated lakes and endorheic rivers) which support high native species endemism rates due to their isolation that promoted species divergence. Moreover, such isolated communities are often closely related from a phylogenetic point of view because the restricted size of these ecosystems limits environmental heterogeneity (MacArthur and Wilson, 1967; Si et al., 2017), resulting in an imbalanced phylogeny (Ali and Huber, 2010). These isolated ecosystems faunas were little constrained by predation and competition and are often vulnerable to the introduction of exotic predators or competitors (Strauss et al., 2006a), leading to the extirpation of some native species and then to phylogenetic losses (Jiang et al., 2015; Sobral et al., 2016). Moreover, the pool of introduced species is limited to a few species (e.g. see Toussaint et al., 2016 for freshwater fish), leading to the introductions of the same species in all isolated ecosystems, which promotes taxonomic (and therefore probably phylogenetic) homogenization between isolated ecosystems (Ding et al. 2017).

Although those processes are documented for oceanic islands, our knowledge of isolated freshwater environments, such as isolated lakes and endorheic rivers is much less developed. To our knowledge, only Jiang et al. (2015) examined the changes in phylogenetic and functional alpha diversity in an isolated lake and Ding et al. (2017) investigated the changes in dissimilarity between freshwater isolated environments due to extirpations and invasions. Ding et al. (2017) demonstrated that fish extirpations and invasions that occurred during the last 60 years profoundly modified the taxonomic distinctiveness between fish faunas across a set of 15 isolated plateau lakes in Southwest China. Here we go further and investigate, in the same 15 lakes, how the last 60 years taxonomic changes modified the phylogenetic diversity of fish assemblages as well as the among-lake phylogenetic distinctiveness. To this aim, we compared the phylogenetic diversity across three time periods corresponding to the historical fauna before human mediated invasions and extirpations (1940–1957), an intermediate (1970–1985) and a current situation (2000–2015). Those three periods account for an increasing gradient in human disturbances and thus in introduction and extinction processes. We first quantified the relative effect of species introductions and the loss of native species on the changes of phylogenetic diversity patterns across the three time periods. We then examined how phylogenetic dissimilarity between isolated lakes was affected by species introductions and extirpations and to which extent those phylogenetic changes correlate with the taxonomic homogenization reported by Ding et al. (2017) on the same sites.

2. Materials and methods

2.1. Study area and lakes

Yun-Gui Plateau is one of the five lake regions in China. Located in the southwest of China, this plateau supports dozens of natural isolated lakes. The fish fauna inhabiting these lakes is characterized by a high level of endemism and considerable faunal dissimilarity between lakes (Kottelat and Whitten, 1996; Li, 1982). These isolated lakes supported species flocks of endemic congeneric fishes (Chu and Chen, 1990). During the past 60 years, fish assemblages in these lakes experienced dramatic changes due to two intensive successive waves of non-native fish introductions and native fish extirpations (Chen et al., 1998; Jiang et al., 2015). The first introduction wave occurred from 1958 to 1965, with the widespread introductions of fast-growing fish species, e.g. silver carp (*Hypophthalmichthys molitrix*), bighead carp (*Aristichthys nobilis*), grass carp (*Ctenopharyngodon idella*) and black carp (*Mylopharyngodon piceus*), for fisheries purposes. Those species were accompanied by unintentionally introduced small fishes such as top-mouth gudgeon (*Pseudorasbora parva*), gobies (*Rhinogobius giurinus*, *Rhinogobius cliffordpopei*, and *Micropercops swinhonis*), and mosquitofish (*Gambusia affinis*) (Chen et al., 1998). The second introduction wave occurred from the late 1970s to the late 1980s, mainly with the introduction of icefish (*Neosalanx tangkahkeii*) for fish farming and the unintentional introduction of bitterlings (e.g. *Rhodeus ocellatus*, *Rhodeus sinensis*) (Xiong et al., 2015). In addition to the pressures of exotic introductions, other human disturbances such as over-harvesting (Chen et al., 1998) and water eutrophication (Liu et al., 2012) also negatively affected the fish fauna, causing the extirpation of the most sensitive native species.

We here focused on 15 lakes with sufficient data on fish fauna dynamics since the 1940 s. Those lakes include the 13 larger lakes from the in Yun-Gui Plateau, with a surface greater than 10 km^2. They are located in an elevational range from 1284 to 2691 m above sea level, the lake surface area ranged from 5.7 to 297.9 km^2, with lake depth varying from 2.4 to 89.6 m and lake volume from 0.17×10^8 to $189 \times 10^8 m^3$. These isolated lakes historically supported 103 native fish species. More than half native species were restricted to a single lake. Those lakes acted as species flocks cradles, and are colonized by congeneric endemic species, with for instance, 5 species of *Cyprinus* and 4 species of *Schizothorax* in Erhai Lake; 3 species of *Yunanilus* and 2 species of *Liobagrus* in Dianchi Lake; 3 species of *Discogobio* and 3 species of *Yunanilus* in Fuxian lake; and 3 species of *Schizothorax* in Lugu Lake (Li, 1982; Yang et al., 1994).

2.2. Data collection and time periods

Fish occurrence data for the 15 lakes were collected from published fish surveys, including scientific reports, books, online data and grey literature since 1940s (see details in Table S1). Fish taxonomy was updated using FishBase (Froese and Pauly, 2016). As in Ding et al. (2017), data were then grouped into three periods: (i) historical period (1940–1957), (ii) intermediate period (1970–1985), and (iii) current period (2000–2015). The three periods all included about 15 years fish sampling, and were separated by 10–15 year intervals during which sampling was scarcer. On each period, there were several surveys for these lakes by the Chinese fisheries institutes (see Table S1 for details). Based on these species lists, we distinguished between native and non-native fish species and considered a non-native species as present in the lake only when it was established.

2.3. Measuring phylogenetic alpha and beta diversity

Due to the absence of a true phylogeny for the studied fish species, taxonomic distance based on the path lengths in the Linnaean taxonomic tree was used as a proxy of the phylogeny. This approach has been used in many studies dealing with phylogenetic diversity (Cai et al., 2018; Heino and Tolonen, 2017; Winter et al., 2013; Zhang et al., 2018). Higher taxonomic levels for each fish species were checked according to Nelson et al. (2016). As a result, there were 11 taxonomic levels (species, genus, subfamily, family, superfamily, suborder, order, series, superorder, subdivision and division) for our data.

We first calculated two indices of phylogenetic alpha diversity, namely average taxonomic distinctness (Δ^+, measuring the average taxonomic or phylogenetic distance between all pairs of species within an assemblage) and variation in taxonomic distinctness (Λ^+, reflecting the unevenness of the taxonomic tree for a given assemblage) (Clarke and Warwick, 1998), for fish faunas in the 15 lakes and the 3 time periods. Simple linear scaling was used in the calculations. The maximum distance through the tree is set at $\omega = 100$. As some taxonomic levels were not defined to all species (e.g. the subfamily level does not exist for some species), we weighted the branch lengths by the proportion of species at a given taxonomic level, following Tolimieri and Anderson (2010) and Jiang et al. (2015) (Table S2). The two indices were computed using the following equations:

$$\Delta^+ = [\Sigma\Sigma_{i<j}\omega_{ij}]/[S(S-1)/2]$$

$$\Lambda^+ = [\Sigma\Sigma_{i<j}(\omega_{ij} - \Delta^+)^2]/[S(S-1)/2]$$

where ω_{ij} is the weight given to the path length linking species i and j in the hierarchical taxonomic tree, and S is the number of species.

Phylogenetic beta diversity of fish fauna was measured using PhyloSør beta diversity index, a derivation of the Sørensen dissimilarity index, that measures the proportion of shared branch length among communities (Leprieur et al., 2012). Then we used an additive partitioning framework of phylogenetic beta diversity among these lakes to decompose beta diversity into two independent components: turnover (PhyloSim) and nestedness component (PhyloSne) (Baselga, 2010; Baselga, 2012). The turnover component accounts for phylogenetic turnover between assemblages induced by distinct combinations of phylogenetic lineages, whereas the nestedness component reflects phylogenetic dissimilarity caused by the difference in phylogenetic diversity between assemblages (Leprieur et al., 2012). We then calculated the relative contribution of turnover (turn%) and nestedness (nest%) components to dissimilarity since the relative importance of those two components provide insights on the different ecological processes ruling community assembly. The dominance of turnover over nestedness indicate that beta diversity is due to a different combination of phylogenetic lineages, whereas phylogenetic nestedness will dominate when changes in phylogenetic diversity are due to a difference in phylogenetic breadth (Heino and Tolonen, 2017).

2.4. Statistical analysis

For the 15 lakes, we first compared the differences in the phylogenetic alpha (Δ^+, Λ^+) and beta diversity (PhyloSør, PhyloSim, PhyloSne) of fish assemblages among three periods with repeated-measures ANOVAs using *aov*, *error* and *pairwise.t.test* functions in R. Multiple regression analyses were then used to examine the relationships between changes in Δ^+, Λ^+ and their respectively historical value, introductions and extirpations. Due to the varied historical native species richness among lakes (from 4 to 27 species), we used the percentage of exotic species (i.e., ratio of introduced species/entire species) and the percentage of extirpated species (extirpated/historical native species) as explanatory variables.

Then multiple regression on distance matrices (MRM, Lichstein, 2007) were used to disentangle the effects of historical dissimilarity (PhyloSør, PhyloSim, PhyloSne), introductions (percentage of exotic species in each pair of lakes) and extirpations (percentage of extirpated species in lake pairs) pressures on temporal changes (intermediate vs. historical and current vs. historical) in phylogenetic beta diversity. P-values of MRM models were calculated by comparing each observed regression coefficient with 10,000 permutations.

Finally, we assessed the relationships between temporal changes in phylogenetic dissimilarity and temporal changes in taxonomic dissimilarity. The overall taxonomic dissimilarity (Sørensen index) and its turnover (Simpson index) and nestedness (Nestedness) components were calculated according to the partitioning framework proposed by Baselga (2010, 2012), as Ding et al. (2017). We regressed the changes in phylogenetic and taxonomic dissimilarities, and the changes in turnover and nestedness components separately. The significance of the Pearson correlations were calculated using Mantel tests on 9999 permutations (Nekola and White, 1999).

We ran all calculations and analyses in R (R Developement Core team, 2017). R packages *vegan*, *betapart* and *ecodist* were used to compute Δ^+ and Λ^+ (*taxondive* in *vegan*), Mantel tests (*mantel* in *vegan*), dissimilarities and MRM analyses, respectively. All analyses were run on both the fish assemblages (i.e. native and exotic species) and only the native fish assemblages. Considering only native fish assemblages allowed measuring to which extent phylogenetic changes were due to native species extirpations, whereas considering entire fish assemblages mixed non-native species introduction and native species extirpation processes.

3. Results

3.1. Temporal changes in phylogenetic alpha diversity and their determinants

In historical period, before human mediated introductions and extirpations, 103 fish species belonging to 42 genera, 10 families, 5 orders and 2 subdivisions occurred across the 15 lakes. Among them, Cypriniformes (89 species) and Cyprinidae (72 species) were the species-richest order and family, respectively (Table 1). In the intermediate period, there were 117 species (including 27 non-native species), belonging to 59 genera (17 non-native), 16 families (6 non-native), 7 orders (2 non-native) and 2 subdivisions. In the current period, 78 species (including 34 non-native), 49 genera (21 non-native), 18 families (9 non-native), 8 orders (3 non-native) and 3 subdivision (1 non-

Table 1
List of families, order and subdivision, and number of genera and species within each families in the 15 studied lakes during historical (1940–1957), intermediate (1970–1985) and current (2000–2015) periods. Introduced taxa are bolded and indicated by "+"; Extirpated taxa are italicized and indicated by "−"

			Historical period		Intermediate period		Current period	
Subdivision	Order	Family	No. genera	No. species	No. genera	No. species	No. genera	No. species
Ostarioclupeomorpha	Cypriniformes	Cyprinidae	27	72	38 (**11**$^{+}$)	84 (**18**$^{+}$, *6*$^{-}$)	28 (**10**$^{+}$, *9*$^{-}$)	48 (**17**$^{+}$, *41*$^{-}$)
		Balitoridae	4	15	4	11 (*4*$^{-}$)	2 (*2*$^{-}$)	5 (*10*$^{-}$)
		Cobitidae	2	2	2	2	2 (**1**$^{+}$, *1*$^{-}$)	2 (**1**$^{+}$, *1*$^{-}$)
	Siluriformes	Bagridae	3	4	3	3 (*1*$^{-}$)	2 (*1*$^{-}$)	2 (*2*$^{-}$)
		Siluridae	1	3	1	4 (**1**$^{+}$)	1	3 (**1**$^{+}$, *1*$^{-}$)
		Amblycipitidae^{-}	1	3	1	1 (*2*$^{-}$)	0 (*1*$^{-}$)	0 (*3*$^{-}$)
		Clariidae	1	1	1	2 (**1**$^{+}$)	1	2 (**2**$^{+}$, *1*$^{-}$)
Euteleostei	Beloniformes	Adrianichthyidae	1	1	1	1	1	1
		Hemirhamphidae^{+}	–	–	1 (**1**$^{+}$)	1 (**1**$^{+}$)	1 (**1**$^{+}$)	1 (**1**$^{+}$)
	Perciformes	Channidae	1	1	1	1	1	1
		Gobiidae^{+}	–	–	1 (**1**$^{+}$)	2 (**2**$^{+}$)	1 (**1**$^{+}$)	3 (**3**$^{+}$)
		Odontobutidae^{+}	–	–	1 (**1**$^{+}$)	1 (**1**$^{+}$)	1 (**1**$^{+}$)	1 (**1**$^{+}$)
		Percichthyidae^{+}	–	–	1 (**1**$^{+}$)	1 (**1**$^{+}$)	–	–
		Cichlidae^{+}	–	–	–	–	1 (**1**$^{+}$)	2 (**2**$^{+}$)
		Osphronemidae^{+}	–	–	–	–	1 (**1**$^{+}$)	1 (**1**$^{+}$)
	Synbranchiformes	Synbranchidae	1	1	1	1	1	1
	Cyprinodontiformes^{+}	**Poeciliidae**$^{+}$	–	–	1 (**1**$^{+}$)	1 (**1**$^{+}$)	1 (**1**$^{+}$)	1 (**1**$^{+}$)
	Osmeriformes^{+}	**Osmeridae**$^{+}$	–	–	1 (**1**$^{+}$)	1 (**1**$^{+}$)	2 (**2**$^{+}$)	2 (**2**$^{+}$)
		Salangidae^{+}	–	–	–	–	1 (**1**$^{+}$)	1 (**1**$^{+}$)
Elopomorpha^{+}	**Anguilliformes**$^{+}$	**Anguillidae**$^{+}$	–	–	–	–	1 (**1**$^{+}$)	1 (**1**$^{+}$)

native) were recorded (Table 1). Overall, 13 species, but no genera or family were extirpated from the native species pool between historical and intermediate periods. Between intermediate and current periods, 46 species, 14 genera, and 1 family were extirpated from the native species pool.

Considering entire fish fauna, both the Δ^+ and Λ^+ increased through time, with highest values in current period (Fig. 1, Table S3), indicating fish assemblages became more phylogenetically diverse and variable among lakes. For native fish species, Δ^+ and Λ^+ did not significantly changed between historical and intermediate periods, but Δ^+ significantly increased and Λ^+ significantly declined between intermediate and current periods (Fig. 1, Table S3). Except changes in Λ^+ in intermediate period, temporal changes in Δ^+ and Λ^+ of entire assemblages were significantly predicted by historical state, fish invasion rate

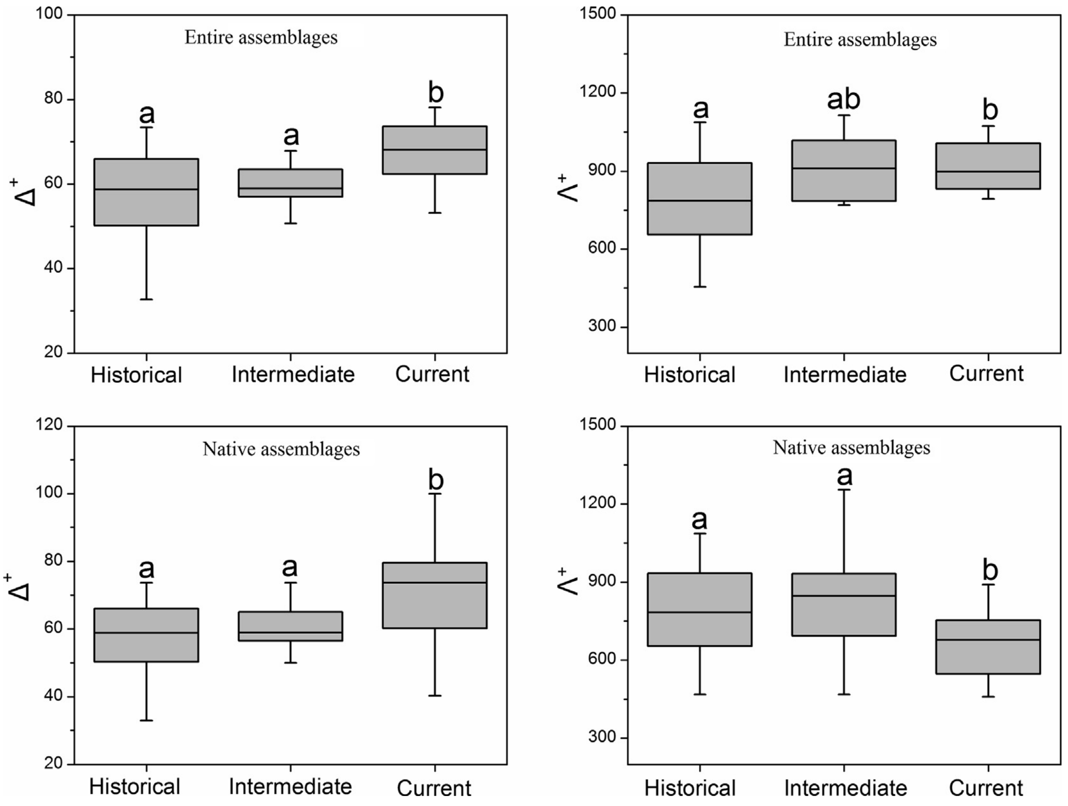

Fig. 1. Box plots of average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) for the entire fish fauna (top panels) and only on the native species (bottom panels) of the 15 studied lakes during historical (1940–1957), intermediate (1970–1985), and current (2000–2015) periods. Different letters indicate significant differences ($p < 0.05$) among periods (see Tables S3 for detailed results of repeated-measures ANOVA and paired-*t* test).

Table 2

Results of multiple regression models for changes in average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) of intermediate and current periods based on entire assemblages and native assemblages. Std b: standardized regression coefficient.

		Std b	t	P	Model Stats
Entire assemblages					
Intermediate	Change in Δ^+				
	Historical Δ^+	**−0.619**	**−2.784**	**0.018**	
	Invasion	−0.184	−0.831	0.424	F = 3.387, P = 0.058
	Extirpation	−0.100	−0.460	0.655	Adj. R^2 = 0.337
	Change in Λ^+				
	Historical Λ^+	−0.131	−0.418	0.684	
	Invasion	−0.027	−0.089	0.931	F = 0.086, P = 0.967
	Extirpation	0.095	0.309	0.763	Adj. R^2 = -0.244
Current	Change in Δ^+				
	Historical Δ^+	**−0.745**	**−7.138**	**< 0.001**	
	Invasion	**0.619**	**5.382**	**< 0.001**	F = 28.17, P < **0.001**
	Extirpation	**−0.320**	**−2.749**	**0.019**	Adj. R^2 = 0.853
	Change in Λ^+				
	Historical Λ^+	**−0.756**	**−7.277**	**< 0.001**	
	Invasion	0.085	0.780	0.452	F = 32.12, P < **0.001**
	Extirpation	**0.308**	**2.716**	**0.020**	Adj. R^2 = 0.870
Native assemblages					
Intermediate	Change in Δ^+				
	Historical Δ^+	−0.439	−1.999	0.069	F = 4.397, P = **0.037**
	Extirpation	0.504	2.293	**0.041**	Adj. R^2 = 0.327
	Change in Λ^+				
	Historical Λ^+	0.028	0.100	0.922	F = 0.478, P = 0.632
	Extirpation	0.264	0.924	0.374	Adj. R^2 = -0.081
Current	Change in Δ^+				
	Historical Δ^+	0.170	0.652	0.527	F = 1.661, P = 0.231
	Extirpation	−0.402	−1.542	0.149	Adj. R^2 = 0.086
	Change in Λ^+				
	Historical Λ^+	−0.377	−1.864	0.087	F = 8.039, P = **0.006**
	Extirpation	**−0.805**	**−3.982**	**0.002**	Adj. R^2 = 0.501

The models of entire assemblages included historical value, percentage of invasion and percentage of extirpation as explanatory variables, while the models of native assemblages included historical value and percentage of invasion only. Significant variables are bolded.

and extirpation rate (Table 2). Historical state had a significant negative effect, indicating that lakes with low Δ^+ and Λ^+ became more phylogenetically diverse and variable across time. In contrast, invasion pressure had a positive effect on changes in Δ^+ and Λ^+ between historical and current periods, meaning that the lakes which received more exotic fishes experienced higher increase in phylogenetically average distance and unevenness. Moreover, the percentage of extirpated native species had no effect between historical and intermediate period, whereas it caused a decline of Δ^+ and an increase of Λ^+ between historical and current periods (Table 2).

For native fish assemblages, only the change in Δ^+ in intermediate period and change in Λ^+ in current period were significantly explained. The historical values of Δ^+ and Λ^+ both had a marginally significant negative effect, but the extirpation rate had a positive effect on change in Δ^+ but a negative one on change in Λ^+ (Table 2).

3.2. Temporal changes in phylogenetic beta diversity and their determinants

Historical phylogenetic dissimilarity (PhyloSør, with an average value of 0.425) among isolated lakes resulted from a balanced contribution of turnover (PhyloSim, average = 0.203; turn% = 50.4%) and nestedness (PhyloSne, average = 0.222; nest% = 49.6%). For the entire fish assemblages, the overall dissimilarity and turnover component both significantly declined from the historical to the subsequent periods, whereas nestedness component did not significantly changed through time (Fig. 2, Table S3). For native fishes, overall dissimilarity did not significantly changed, but turnover significantly decreased and nestedness increased (Fig. 2, Table S3). During the phylogenetic homogenization process, the relative contribution of nestedness (nest%) increased at the expense of contribution of turnover component (turn%).

All but one MRM models significantly predicted temporal changes in phylogenetic dissimilarity (PhyloSør), turnover (PhyloSim) and nestedness (PhyloSne) for both the entire and native fish fauna, based on historical level of dissimilarity, extirpation and/or introduction pressures (to the exception of PhyloSim for the native fauna). For entire fishes, the MRM models explained 32.2% ($P < 0.001$) and 65.8% ($P < 0.001$) of the variance in changes in PhyloSør, 32.7% ($P = 0.002$) and 40.6% ($P < 0.001$) of the variance in changes in PhyloSim, 23.2% ($P = 0.006$) and 52.7% ($P < 0.001$) of the variance in changes in PhyloSne in the intermediate and current periods, respectively (Table 3). Their respective historical values all had a markedly negative effect, suggesting lake pairs with high levels of historical dissimilarity tended to be more homogenized (PhyloSør, PhyloSim) or more nested (PhyloSne). For only native species, changes in PhyloSør and PhyloSne in the intermediate period were both negatively related to historical dissimilarity, with 18.6% and 11.6% explained variation, respectively. In the current period, changes in PhyloSør and PhyloSne were also negatively affected by historical dissimilarity but also positively related to the percentage of extirpations (Table 3). Temporal changes in PhyloSim, however, were not significantly predicted by historical dissimilarity and extirpation strength.

3.3. Relationships between changes in phylogenetic and taxonomic beta diversity

With extirpations and invasions in the two subsequent periods, changes in phylogenetic beta diversity (PhyloSør, PhyloSim and PhyloSne) were all strongly correlated with their corresponding taxonomic beta diversity for entire and native fishes: the correlation coefficients (r) of Mantel tests range from 0.714 to 0.888 and the models were all significant ($P < 0.001$). PhyloSør and PhyloSim decreased linearly with decreasing their taxonomic dissimilarities, whereas PhyloSne increased with increasing taxonomic nestedness component (Figs. 3, 4). Apart from those major trends toward taxonomic and phylogenetic homogenization for overall change in dissimilarity and change in turnover, for both entire assemblages and native fish fauna, some lake pairs also differentiate both from a taxonomic and a phylogenetic point of view. Such a trend is rare for entire fish assemblages (less than 10% of the lake pairs; Fig. 3a, d), but more common considering only the native fauna, particularly in the current period (ca. 28% of the lake pairs, Fig. 4d). For some lake pairs we also observed opposite patterns between taxonomic and phylogenetic metrics. Such a situation was rare for the natives and did not exceed 15% of the pairs, but it was more common for the entire fauna, where a phylogenetic differentiation and a taxonomic homogenization was detected in ca. one third of the lake pairs (Fig. 3a,d). Such pattern was also observed for turnover, particularly during the current period (Fig. 3e).

4. Discussion

The historical fish taxonomic structure (the number of higher taxa, e.g. families and orders) in the Yun-Gui Plateau lakes was characterized by a few orders and families (5 orders and 10 families), but also by high levels of endemism compared to river-connected lakes in the Yangtze Floodplain. Indeed, the latter lakes are historically colonized by ca. 10 orders and 20 families and do not count endemic species (Ji et al., 2017;

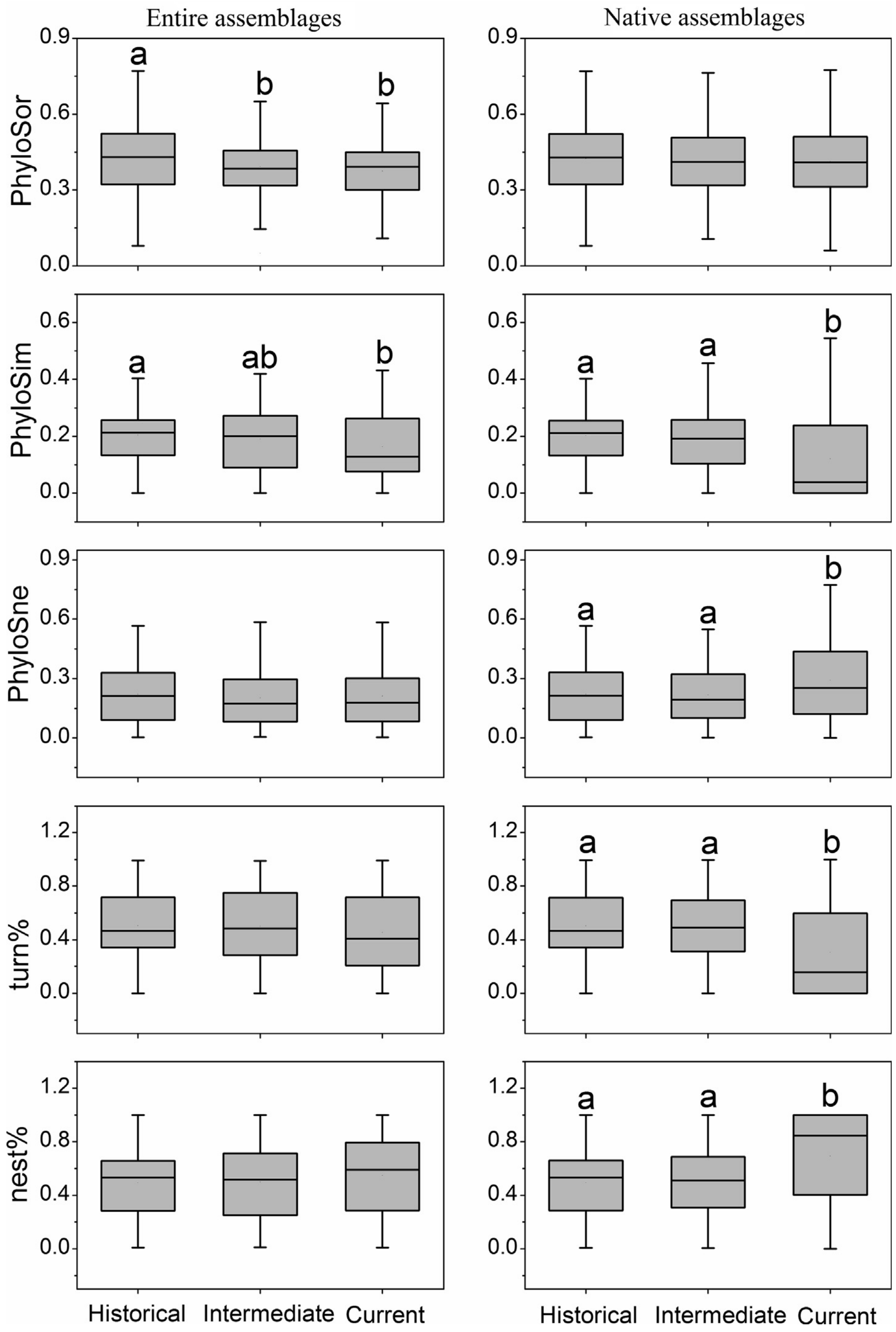

Fig. 2. Box plots of phylogenetic dissimilarity (PhyloSør), turnover (PhyloSim), nestedness (PhyloSne) and contributions of turnover (turn%) and nestedness (nest%) to dissimilarity for historical (1940–1957), intermediate (1970–1985), and current (2000–2015) periods based on entire assemblages (left panels) and on native-only species (right panels). Different letters indicate significant differences among periods (see Tables S3 for detailed results of repeated-measures ANOVA and paired-*t* test).

Liu and Wang, 2010). In the Yun-Gui Plateau lakes, some orders frequently occurring in the Yangtze Floodplain, e.g. Osmeriformes, Anguilliformes and Clupeiformes, were absent, and the Perciformes are only represented by a single native species. Moreover, these isolated lakes support widespread flocks of closely-related fish species (congeneric species) due to long-term adaptive radiation evolution (Chu and Chen, 1990; Li, 1982). The limited number of higher taxa and the high proportion of congeneric species thus resulted in low phylogenetic diversity (Δ^+) and high phylogenetic unevenness (Λ^+) of the native fauna within each lake.

Among the 15 considered isolated lakes, phylogenetic dissimilarity during the historical period (i.e. before species introduction and extirpation occurred) was moderate (an average of ca. 40% dissimilarity between lake pairs), with a balanced contribution of turnover and nestedness components, which markedly differs from the taxonomic beta-diversity reported by Ding et al. (2017). Indeed, historical taxonomic dissimilarity between lakes was high (about 68.0%), due to a strong contribution of species turnover (accounting for 75% of overall dissimilarity). The low phylogenetic dissimilarity compared to taxonomic dissimilarity and the low contribution of turnover to phylogenetic dissimilarity suggests that while species composition differed greatly between lakes, those species belong to the same higher taxa

Table 3

Results of multiple regression on distance matrices (MRM) analyses for changes in overall phylogenetic dissimilarity (PhyloSør), phylogenetic turnover (PhyloSim) and phylogenetic nestedness (PhyloSne) components. The same analyses were run for intermediate and current periods and on both entire and native only assemblages. Historical value, native species extirpation (percentage of extirpated species and/or exotic species introduction (percentage of introduced species) were considered as explanatory variables.

Entire assemblages	Change in PhyloSør				Change in PhyloSim				Change in PhyloSne			
	Intermediate		Current		Intermediate		Current		Intermediate		Current	
	Std b	P-value	Std b	P-value	Std b	P-value	Std b	P-value	Std b	P-value	Std b	P-value
Historical dissimilarity	**−0.377**	**< 0.001**	**−0.790**	**< 0.001**	**−0.667**	**< 0.001**	**−0.891**	**< 0.001**	**−0.383**	**< 0.001**	**−0.912**	**< 0.001**
Introduction	−0.016	0.780	**−0.226**	**0.006**	−0.034	0.751	−0.129	0.121	−0.047	0.694	−0.093	0.504
Extirpation	−0.057	0.226	0.135	0.108	−0.141	0.109	**0.263**	**< 0.001**	0.060	0.542	−0.117	0.352
R^2	**0.322**	**< 0.001**	**0.658**	**< 0.001**	**0.327**	**0.002**	**0.406**	**< 0.001**	**0.232**	**0.006**	**0.527**	**< 0.001**
Native assemblages	Change in PhyloSør				Change in PhyloSim				Change in PhyloSne			
	Intermediate		Current		Intermediate		Current		Intermediate		Current	
	Std b	P-value	Std b	P-value	Std b	P-value	Std b	P-value	Std b	P-value	Std b	P-value
Historical dissimilarity	**−0.228**	**< 0.001**	**−0.505**	**< 0.001**	−0.169	0.066	−0.340	0.072	**−0.158**	**0.007**	**−0.420**	**0.016**
Extirpation	−0.074	0.102	**0.240**	**0.014**	−0.089	0.096	−0.046	0.618	0.029	0.540	**0.268**	**0.039**
R^2	**0.186**	**< 0.001**	**0.304**	**< 0.001**	0.102	0.078	0.066	0.167	**0.116**	**0.015**	**0.194**	**0.011**

Std b: standard partial regression coefficient. Significant variables are bolded.

(orders and families). They therefore share a large amount of evolutionary history, leading to a low phylogenetic clustering among lakes (Graham and Fine, 2008). The isolation of Yun-Gui Plateau lakes lasts for the late Pliocene period, and such short isolation time (< 5 million years) permitted the differentiation of several endemic genera and species (Li, 1982), that remain clustered in a few higher taxa (more than 70% of the endemic species belong to the Cyprinidae family and more than 95% belong to the Cypriniformes order). Therefore, fish assemblages among these lakes have a large amount of shared branch length in the phylogenetic tree, despite a strong species turnover among lakes, resulting in low levels of both among-lake dissimilarity in phylogenetic composition and a low contribution of phylogenetic turnover compared to taxonomic dissimilarity and turnover (Heino and Tolonen, 2017).

Native species extirpations and non-native species introductions that occurred for half a century caused a marked increase in phylogenetic diversity in all the lakes. As shown by Jiang et al. (2015) in Erhai lake, the loss of some congeneric native species (e.g. species from *Cyprinus*, *Schizothorax Yunanilus* and *Liobagrus*), and the introductions of exotic distant-related species from new orders (e.g. Anguilliformes, Osmeriformes and Cyprinodontiformes), led to a marked increase in phylogenetic diversity. Such a trend observed in Erhai lake (Jiang et al., 2015), also holds for the other isolated lakes of the Yun-Gui Plateau, whatever their size or location. Moreover, the phylogenetic alpha diversity increased in each lake turn toward a decline of phylogenetic beta-diversity between lakes. Such phylogenetic homogenization process is explained by the extirpation of native endemic species and/or by the introduction of the same exotic species in all the lakes. Here those two processes act together since extirpation and invasion together explain phylogenetic homogenization and both processes might negatively affect ecosystem structure and function. For instance, the loss of unique species from a phylogenetic point of view will probably impoverish the range of functional responses of species assemblages to environmental changes, which might in turn trigger functional homogenization among lakes (Jackson et al., 2015; Winter et al., 2009).

The differences in temporal changes in phylogenetic unevenness (Λ^+) between entire and native-only assemblages are explained by two antagonistic processes. Introductions increased the phylogenetic unevenness by adding distant branches to the phylogenies, whereas native species loss reduced unevenness by reducing phylogenetic clustering due to the presence of congeneric species and the reduction in the number of higher taxa (families and orders, Jiang et al., 2014; Zintzen et al., 2011). Therefore the loss of some cyprinid native species and the decrease in the number of native families (5.5 vs 3.9 families per lake on average for historical and current periods, respectively) and orders (3.6 vs 2.7 orders per lake on average for historical and current periods, respectively) reduced phylogenetic unevenness (decrease of Λ^+) within native species, but such trend was not sufficient to counteract the strong increase of higher taxa (families, orders) due to exotic species introductions, leading to an overall increase of phylogenetic unevenness (increase of Λ^+).

From a conservation point of view, the increase of Δ^+ has frequently been considered as a positive change for biotic communities, since it denotes phylogenetically diverse assemblages (Clarke and Warwick, 1998). In the same way, Helmus et al. (2010) showed that disturbed assemblages host more related species than undisturbed ones, since disturbance is supposed to exclude the species that cannot survive to the disturbance. Nevertheless, in isolated environments characterized by a reduced historical phylogenetic diversity made of closely related species, extirpations reduce phylogenetic clustering and therefore increase phylogenetic diversity. Similarly, exotic species introductions provide phylogenetic distant species to assemblages and therefore also increase local phylogenetic diversity. Although counterintuitive, increasing phylogenetic diversity in such isolated environments cannot be considered as a positive trend for species conservation, but contrarily, depicts a decline of the native fauna and a replacement by non-native exotic species. Similarly, high level of unevenness in taxonomic structure is often considered to be a result of high environmental heterogeneity (Leira et al., 2009). In other word, more heterogeneous habitat should support more families and orders and enhance phylogenetic diversity and unevenness. Thus, a decline in Λ^+ in native fishes, partly due to the loss of some families and orders, may reflect a decline of habitat heterogeneity in these lakes, probably due to increasingly serious lakes eutrophication (Liu et al., 2012). Overall, in isolated environments such as isolated lakes hosting closely-related species, phylogenetic diversity trends through extirpation and invasion are contrary to those reported in the literature for less isolated environments (Helmus et al., 2010). We therefore call for caution when analyzing phylogenetic changes through time in isolated ecosystems.

Such apparent opposite trends between our study and the literature probably lies in the “Darwin’s naturalization conundrum” (Diez et al., 2008; Qian and Sandel, 2017), stipulating that invasion success lies in two opposite processes called “naturalization and pre-adaptation hypotheses”. According to the “naturalization hypothesis”, exotic species

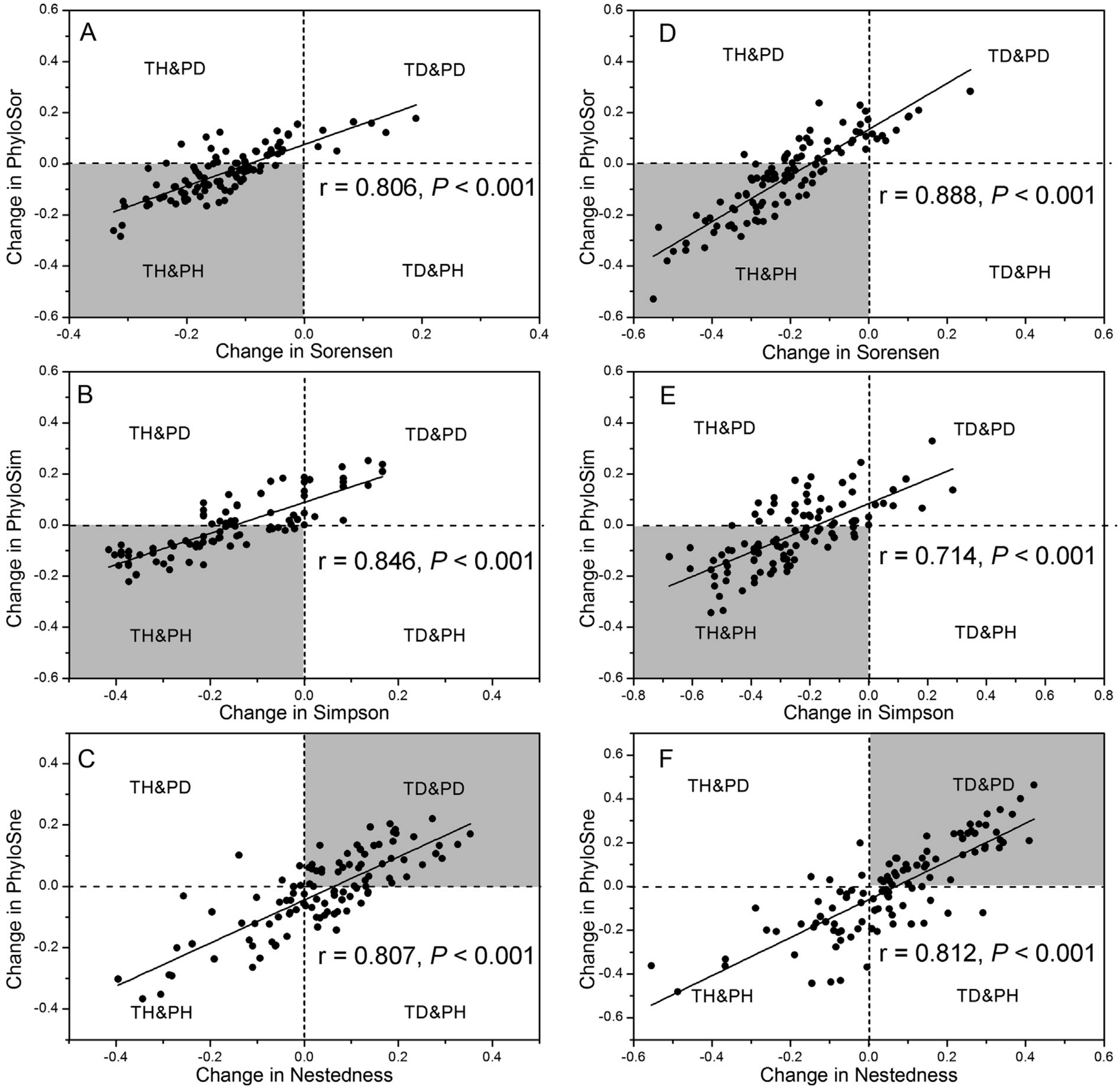

Fig. 3. Change in phylogenetic beta diversity (PhyloSør, PhyloSim, PhyloSne) vs. changes in taxonomic beta diversity (Sørensen, Simpson, Nestedness) among isolated lakes in intermediate (A, B, C) and current (D, E, F) periods based on entire fish fauna. The Pearson correlation (r) and significance (*P* value) of Mantel tests are also given. TH = taxonomic homogenization, TD = taxonomic differentiation, PH = phylogenetic homogenization, PD = phylogenetic differentiation. Grey areas indicate the major trend.

distantly related to native species should be successful invaders as they should little compete with native species (Daehler, 2001; Strauss et al., 2006b), whereas according to the “pre-adaptation hypothesis”, exotic species closely related to native species should be successful invaders as close relatives share similar traits and could adapt to similar environments (Qian and Sandel, 2017; Ricciardi and Mottiar, 2006). Although previous works often provided a balanced contribution of both hypotheses (Ricciardi and Mottiar, 2006), our results clearly supports the naturalization hypothesis. Indeed, the most successful invasive species, established in over half of the 15 lakes, belong from orders (Cyprinodontiformes for *Gambusia affinis*, Osmeriformes for *Neosalanx taihuensis*), subfamilies or genera (e.g. *Ctenopharyngodon idellus*, *Aristichthys nobilis*, *Hypophthalmichthys molitrix*) historically absent from the lakes. In contrast, the invasive species from genera present in the native fauna (e.g. *Acheilognathus*, *Cyprinus*, *Silurus*) were less successful. The naturalization hypothesis also stipulates that the original traits of non-native species make them efficient predators or competitors for the native fauna and they are therefore predicted to have deleterious effects on the native fauna (Ricciardi and Atkinson, 2004). This was for instance experienced after the introduction of brown trout in New Zealand rivers where Salmonids were historically absent (Townsend and Crowl, 1991). We therefore encourage forthcoming studies to quantify the impact of non-native species on the remaining endemic fauna, to buffer the current trend towards endemic species extirpation in the Yun-Gui Plateau lakes.

At the regional scale, phylogenetic dissimilarity of fish assemblages decreased through time. Such trend, mainly due to a decline in phylogenetic turnover, indicates a loss of evolutionarily unique species in the lakes and/or a gain of the same non-native species across the entire region (Olden and Poff, 2004). In the Yun-Gui Plateau lakes, different non-native species were introduced and distinct native species were extirpated from each lake. Therefore, the loss of phylogenetic turnover caused by native extirpations was stronger than the differentiation effect of non-native species introductions. Nevertheless, phylogenetic differentiation was not rare, within the entire faunas but also within the natives. Such differentiation being linked to an increase in phylogenetic

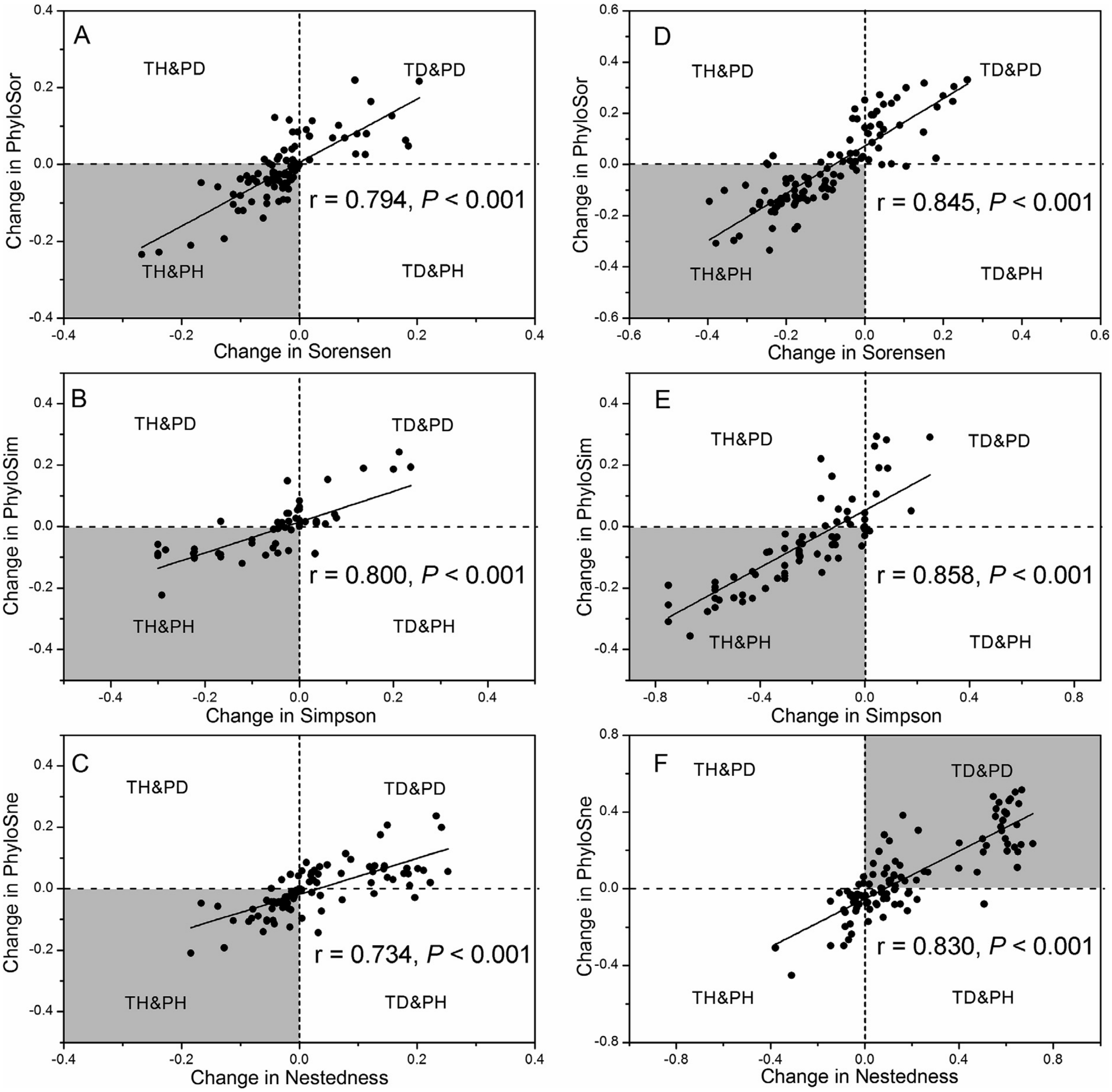

Fig. 4. Changes in phylogenetic beta diversity (PhyloSør, PhyloSim, PhyloSne) vs. changes in taxonomic beta diversity (Sørensen, Simpson, Nestedness) of native fish species in intermediate (A, B, C) and current (D, E, F) periods. See the meanings of abbreviations in Fig. 3. Grey areas indicate the major trend.

nestedness, it means that extirpating different endemic species also modifies the evolutionary breath of assemblages (Leprieur et al., 2012), such differential breath being responsible of a pronounced effect of nestedness in explaining differentiation cases. Moreover, although phylogenetic homogenization is correlated to taxonomic homogenization, as the increase in shared species is expected to generate an increase in phylogenetic overlap (Graham and Fine, 2008; Winter et al., 2009), about a third of lake pairs phylogenetically differentiated although they homogenize from a taxonomic point of view. This is due to the interplay between the extirpation of closely-related species and the establishment of phylogenetically distinct non-native species in the different lakes. For instance, *Anguilla japonica* (Anguilliformes) only established in two lakes. Such phylogenetic uniqueness between lakes due to the introduction of distantly-related exotic species might turn to homogenization in the future since introduced species will probably spread over lakes. So the observed phylogenetic differentiation is probably an early warning of a future phylogenetic homogenization, as demonstrated by Toussaint et al. (2014) for taxonomic homogenization of the global fish fauna.

A possibly issue in the present study is that the phylogeny of fish fauna is based on Linnaean taxonomic distance rather not molecular phylogenetic data. Taxonomic classification only reflects the evolutionary relationships among species to a certain extent, and thus may resulted in an imprecise calculation of true phylogenetic diversity. However, in Yun-Gui Plateau lakes, DNA data of many endemic fish species are sorely lacking, making the true phylogeny unavailable. When the true phylogenetic data is not available, taxonomy is usually considered as a reasonable surrogate for phylogeny (Saito et al., 2015) and this approach has been successfully applied in many recent studies (e.g. Cai et al., 2018; Zhang et al., 2018).

In summary, our study showed that intensive introductions of exotic species and extirpations of native species in Yun-Gui Plateau isolated lakes during the past 60 years have significantly altered the phylogenetic alpha- and beta-diversity, leading to a decline of lake fauna uniqueness, from both taxonomic and phylogenetic point of views. Half a century of human mediated introductions and extirpations were sufficient to blur evolutionary patterns resulting from the independent evolution of the fish fauna during the last ca. 5 million years. Although taxonomic and phylogenetic metrics were often correlated, we here show that the interplay between extirpation of closely-related species and introduction of phylogenetically distant species can generate opposite taxonomic and phylogenetic patterns. This demonstrates that phylogenetic diversity should be used as a complementary metric to taxonomy. Moreover, phylogenetic diversity is often considered as a proxy for the overall functional properties of organisms (Gerhold et al., 2015; Vitousek et al., 1997), pending functional traits are conserved along the phylogeny, which is often the case in freshwater fish (Comte et al., 2014; Helmus et al., 2007). Therefore, the phylogenetic homogenization, mainly ruled by a loss of phylogenetic turnover, experienced by the Yun-Gui Plateau lakes, suggests that the functional identity of each lake is currently declining. In the same time, the introduction of distinct non-native species in each lake gives way to functionally richer, but less unique ecosystems. This constitutes an irremediable loss of biodiversity, since the extirpation of endemic species is definitive. We therefore appeal to control the spread of non-native species in those still unique ecosystems.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.01.041.

References

Ali, J.R., Huber, M., 2010. Mammalian biodiversity on Madagascar controlled by ocean currents. Nature 463, 653–656. https://doi.org/10.1038/nature08706.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., 2011. Has the Earth's sixth mass extinction already arrived? Nature 471, 51–57. https://doi.org/10.1038/nature09678.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecol. Biogeogr. 19, 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.

Baselga, A., 2012. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. Global Ecol. Biogeogr. 21, 1223–1232. https://doi.org/10.1111/j.1466-8238.2011.00756.

Cai, Y., Zhang, M., Xu, J., Heino, J., 2018. Geographical gradients in the biodiversity of Chinese freshwater molluscs: implications for conservation. Divers. Distrib. 24, 485–496. https://doi.org/10.1111/ddi.12695.

Cavender-Bares, J., Kozak, K.H., Fine, P.V., Kembel, S.W., 2009. The merging of community ecology and phylogenetic biology. Ecol. Lett. 12, 693–715. https://doi.org/10.1111/j.1461-0248.2009.01314.

Ceballos, G., Ehrlich, P.R., Dirzo, R., 2017. From the Cover: PNAS Plus: Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proc. Natl. Acad. Sci. U.S.A. 114, E6089. https://doi.org/10.1073/pnas.1704949114.

Chen, Y., Yang, J., Li, Z., 1998. The diversity and present status of fishes in Yunnan Province. Biodiversity Sci. 6, 272–277. https://doi.org/10.1111/j.1752-1734.2007.00003.x.

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

Clarke, K., Warwick, R., 1998. A taxonomic distinctness index and its statistical properties. J. Appl. Ecol. 35, 523–531. https://doi.org/10.1046/j.1365-2664.1998.

Comte, L., Murienne, J., Grenouillet, G., 2014. Species traits and phylogenetic conservatism of climate-induced range shifts in stream fishes. Nat. Commun. 5, 5023. https://doi.org/10.1038/ncomms6053.

D'agata, S., Mouillot, D., Kulbicki, M., Andréfouët, S., Bellwood, D.R., Cinner, J.E., Cowman, P.F., Kronen, M., Pinca, S., Vigliola, L., 2014. Human-mediated loss of phylogenetic and functional diversity in coral reef fishes. Curr. Biol. 24, 555–560. https://doi.org/10.1016/j.cub.2014.01.049.

Daehler, C.C., 2001. Darwin's naturalization hypothesis revisited. Am. Nat. 158, 324–330. https://doi.org/10.1086/321316.

Diez, J.M., Sullivan, J.J., Hulme, P.E., Edwards, G., Duncan, R.P., 2008. Darwin's naturalization conundrum: dissecting taxonomic patterns of species invasions. Ecol. Lett. 11, 674–681.

Ding, C., Jiang, X., Xie, Z., Brosse, S., 2017. 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. Divers. Distrib. 23, 171–184. https://doi.org/10.1111/ddi.12507.

Froese, R., Pauly, D., 2016. FishBase. World Wide Web Electronic Publication. Available at: http://www.fishbase.org.

Gerhold, P., Cahill, J.F., Winter, M., Bartish, I.V., Prinzing, A., 2015. Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). Funct. Ecol. 29, 600–614. https://doi.org/10.1111/1365-2435.12425.

Graham, C.H., Fine, P.V., 2008. Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. Ecol. Lett. 11, 1265–1277. https://doi.org/10.1111/j.1461-0248.2008.01256.

Heino, J., Tolonen, K.T., 2017. Ecological drivers of multiple facets of beta diversity in a lentic macroinvertebrate metacommunity. Limnol. Oceanogr. 62, 2431–2444. https://doi.org/10.1002/lno.10577.

Helmus, M., Savage, K., Diebel, M., Jt, Ives, A., 2007. Separating the determinants of phylogenetic community structure. Ecol. Lett. 10, 917–925. https://doi.org/10.1111/j.1461-0248.2007.01083.x.

Helmus, M.R., Keller, W.B., Paterson, M.J., Yan, N.D., Cannon, C.H., Rusak, J.A., 2010. Communities contain closely related species during ecosystem disturbance. Ecol. Lett. 13, 162–174. https://doi.org/10.1111/j.1461-0248.2009.01411.x.

Huang, D., Roy, K., 2013. Anthropogenic extinction threats and future loss of evolutionary history in reef corals. Ecol. Evol. 3, 1184–1193. https://doi.org/10.1002/ece3.527.

Ives, A.R., Helmus, M.R., 2010. Phylogenetic metrics of community similarity. Am. Nat. 176, E128–E142. https://doi.org/10.1086/656486.

Jackson, H., Jones, C.G., Agapow, P.M., Tatayah, V., Groombridge, J.J., 2015. Microevolutionary diversification among Indian Ocean parrots: temporal and spatial changes in phylogenetic diversity as a consequence of extinction and invasion. Ibis 157, 496–510. https://doi.org/10.1111/ibi.12275.

Ji, L., He, P., Jia, Y., Peng, S., 2017. The taxonomic distinctness diversity of fish community in Lake Honghu during the past 50 years. J. Lake Sci. 29, 932–941. https://doi.org/10.18307/2017.0417.

Jiang, X., Song, Z., Xiong, J., Xie, Z., 2014. Can excluding non-insect taxa from stream macroinvertebrate surveys enhance the sensitivity of taxonomic distinctness indices to human disturbance? Ecol. Indic. 41, 175–182. https://doi.org/10.1016/j.ecolind.2014.01.036.

Jiang, Z., Brosse, S., Jiang, X., Zhang, E., 2015. Measuring ecosystem degradation through half a century of fish species introductions and extirpations in a large isolated lake. Ecol. Indic. 58, 104–112. https://doi.org/10.1016/j.ecolind.2015.05.040.

Kottelat, M., Whitten, T., 1996. Freshwater biodiversity in Asia with special reference to fish. World Bank Technical Paper 343, 1–59.

Leira, M., Chen, G., Dalton, C., Irvine, K., Taylor, D., 2009. Patterns in freshwater diatom taxonomic distinctness along an eutrophication gradient. Freshwater Biol. 54, 1–14. https://doi.org/10.1111/j.1365-2427.2008.02086.x.

Leprieur, F., Albouy, C., De Bortoli, J., Cowman, P.F., Bellwood, D.R., Mouillot, D., 2012. Quantifying phylogenetic beta diversity: distinguishing between 'true' turnover of lineages and phylogenetic diversity gradients. PLoS One 7, e42760. https://doi.org/10.1371/journal.pone.0042760.

Leprieur, F., Beauchard, O., Blanchet, S., Oberdorff, T., Brosse, S., 2008. Fish invasions in the world's river systems: when natural processes are blurred by human activities. Plos Biol. 6, 404–410. https://doi.org/10.1371/journal.pbio.0060028.

Li, S., 1982. Fish fauna and its differentiation in the upland lakes of Yunnan. Acta Zool. Sinica 28, 169–176.

Lichstein, J.W., 2007. Multiple regression on distance matrices: a multivariate spatial analysis tool. Plant Ecol. 188, 117–131. https://doi.org/10.1007/s11258-006-9126-3.

Liu, C., He, D., Chen, Y., Olden, J.D., 2017. Species invasions threaten the antiquity of China's freshwater fish fauna. Divers. Distrib. 23, 556–566. https://doi.org/10.1111/ddi.12541.

Liu, W., Li, S., Bu, H., Zhang, Q., Liu, G., 2012. Eutrophication in the Yunnan Plateau lakes: the influence of lake morphology, watershed land use, and socioeconomic factors. Environ. Sci. Pollut. Res. 19, 858–870. https://doi.org/10.1007/s11356-011-0616-z.

Liu, X., Wang, H., 2010. Estimation of minimum area requirement of river-connected lakes for fish diversity conservation in the Yangtze River floodplain. Divers. Distrib. 16, 932–940. https://doi.org/10.1111/j.1472-4642.2010.00706.

MacArthur, R.H., Wilson, E.O., 1967. Theory of Island Biogeography. Princeton University Press, Princeton, NJ, USA.

McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends. Ecol. Evol. 14, 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1.

Morelli, F., Benedetti, Y., Ibáñez-Álamo, J.D., Jokimäki, J., Mänd, R., Tryjanowski, P., Møller, A.P., 2016. Evidence of evolutionary homogenization of bird communities in urban environments across Europe. Global Ecol. Biogeogr. 25, 1284–1293. https://doi.org/10.1111/geb.12486.

Nekola, J.C., White, P.S., 1999. The distance decay of similarity in biogeography and ecology. J. Biogeogr. 26, 867–878. https://doi.org/10.1046/j.1365-2699.1999.00305.

Nelson, J.S., Grande, T.C., Wilson, M.V., 2016. Fishes of the World. John Wiley & Sons.

Olden, J.D., Poff, L.R., 2004. Ecological processes driving biotic homogenization: testing a mechanistic model using fish faunas. Ecology 85, 1867–1875. https://doi.org/10.1890/03-3131.

Qian, H., Sandel, B., 2017. Phylogenetic relatedness of native and exotic plants along climate gradients in California, USA. Divers. Distrib. 23, 1323–1333. https://doi.org/10.1111/ddi.12620.

R Development Core team, 2017. R: a language and environment for statistical computing. Vienna, Austria: Foundation for Statistical Computing. http://www.R-project.

org.

Rahel, F.J., 2000. Homogenization of fish faunas across the United States. Science 288, 854–856. https://doi.org/10.1126/science.288.5467.854.

Ricciardi, A., Atkinson, S.K., 2004. Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecol. Lett. 7, 781–784. https://doi.org/10.1111/j.1461-0248.2004.00642.x.

Ricciardi, A., Mottiar, M., 2006. Does Darwin's naturalization hypothesis explain fish invasions? Biol. Invasions 8, 1403–1407. https://doi.org/10.1007/s10530-006-0005-6.

Ricklefs, R.E., 1987. Community diversity: relative roles of local and regional processes. Science 235, 167–171. https://doi.org/10.1126/science.235.4785.167.

Safi, K., Cianciaruso, M.V., Loyola, R.D., Brito, D., Armourmarshall, K., Dinizfilho, J.A., 2011. Understanding global patterns of mammalian functional and phylogenetic diversity. Proc. R. Soc. B-Biol. Sci. 366, 2536–2544. https://doi.org/10.1098/rstb.2011.0024.

Saito, V.S., Siqueira, T., Fonseca-Gessner, A.A., 2015. Should phylogenetic and functional diversity metrics compose macroinvertebrate multimetric indices for stream biomonitoring? Hydrobiologia 745, 167–179. https://doi.org/10.1007/s10750-014-2102-3.

Sax, D.F., Gaines, S.D., 2008. Species invasions and extinction: the future of native biodiversity on islands. Proc. Natl. Acad. Sci. 105, 11490–11497. https://doi.org/10.1073/pnas.0802290105.

Si, X., Cadotte, M.W., Zeng, D., Baselga, A., Zhao, Y., Li, J., Wu, Y., Wang, S., Ding, P., 2017. Functional and phylogenetic structure of island bird communities. J. Anim. Ecol. 86, 532–542. https://doi.org/10.1111/1365-2656.12650.

Sobral, F.L., Lees, A.C., Cianciaruso, M.V., 2016. Introductions do not compensate for functional and phylogenetic losses following extinctions in insular bird assemblages. Ecol. Lett. 19, 1091–1100. https://doi.org/10.1111/ele.12646.

Sol, D., Bartomeus, I., González-Lagos, C., Pavoine, S., 2017. Urbanisation and the loss of phylogenetic diversity in birds. Ecol. Lett. 20, 721–729. https://doi.org/10.1111/ele.12769.

Strauss, S.Y., Lau, J.A., Carroll, S.P., 2006a. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? Ecol. Lett. 9, 357–374. https://doi.org/10.1111/j.1461-0248.2005.00874.x.

Strauss, S.Y., Webb, C.O., Salamin, N., 2006b. Exotic taxa less related to native species are more invasive. Proc. Natl. Acad. Sci. U.S.A. 103, 5841–5845. https://doi.org/10.1073/pnas.0508073103.

Thuiller, W., Lavergne, S., Roquet, C., Boulangeat, I., Lafourcade, B., Araujo, M.B., 2011. Consequences of climate change on the tree of life in Europe. Nature 470, 531. https://doi.org/10.1038/nature09705.

Tolimieri, N., Anderson, M.J., 2010. Taxonomic distinctness of demersal fishes of the California current: moving beyond simple measures of diversity for marine ecosystem-based management. PLoS One 5, e10653. https://doi.org/10.1371/journal.pone.0010653.

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. Global Ecol. Biogeogr. 23, 574–584. https://doi.org/10.1111/geb.12141.

Toussaint, A., Beauchard, O., Oberdorff, T., Brosse, S., Villéger, S., 2016. Worldwide freshwater fish homogenization is driven by a few widespread non-native species. Biol. Invasions 18, 1295–1304. https://doi.org/10.1007/s10530-016-1067-8.

Toussaint, A., Charpin, N., Beauchard, O., Grenouillet, G., Oberdorff, T., Tedesco, P.A., Brosse, S., Villéger, S., 2018. Non-native species led to marked shifts in functional diversity of the world freshwater fish faunas. Ecol. Lett. 21, 1649–1659. https://doi.org/10.1111/ele.13141.

Townsend, C.R., Crowl, T.A., 1991. Fragmented population structure in a native New Zealand fish: an effect of introduced brown trout? Oikos 61, 347–354. https://doi.org/10.2307/3545242.

Vamosi, J.C., Wilson, J.R., 2008. Nonrandom extinction leads to elevated loss of angiosperm evolutionary history. Eco. Lett. 11, 1047–1053. https://doi.org/10.1111/j.1461-0248.2008.01215.x.

Villéger, S., Blanchet, S., Beauchard, O., Oberdorff, T., Brosse, S., 2011. Homogenization patterns of the world's freshwater fish faunas. P. Natl. Acad. Sci. U.S.A. 108, 18003–18008. https://doi.org/10.1073/pnas.1107614108.

Villéger, S., Grenouillet, G., Brosse, S., 2014. Functional homogenization exceeds taxonomic homogenization among European fish assemblages. Global Ecol. Biogeogr. 23, 1450–1460. https://doi.org/10.1111/geb.12226.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. Science 494–499. https://doi.org/10.1007/978-0-387-73412-5_1.

Wake, D.B., Vredenburg, V.T., 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. Proc. Natl. Acad. Sci. U.S.A. 105, 11466–11473. https://doi.org/10.1073/pnas.0801921105.

Webb, C.O., Ackerly, D.D., McPeek, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. Annu. Rev. Ecol. Evol. Systematics 33, 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448.

Winter, M., Devictor, V., Schweiger, O., 2013. Phylogenetic diversity and nature conservation: where are we? Trends. Ecol. Evol. 28, 199–204. https://doi.org/10.1016/j.tree.2012.10.015.

Winter, M., Schweiger, O., Klotz, S., Nentwig, W., Andriopoulos, P., Arianoutsou, M., Basnou, C., Delipetrou, P., DidžIulis, V., Hejda, M., Hulme, P.E., Lambdon, P.W., Pergl, J., Pyšek, P., Roy, D.B., Kühn, I., 2009. Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. Proc. Natl. Acad. Sci. U.S.A. 106, 21721–21725. https://doi.org/10.1073/pnas.0907088106.

Xiong, W., Sui, X., Liang, S.-H., Chen, Y., 2015. Non-native freshwater fish species in China. Rev. Fish Biol. Fish. 25, 651–687. https://doi.org/10.1007/s11160-015-9396-8.

Yang, J., Chen, Y., Yuanhui, B., 1994. Studies on fish diversity in plateau lakes of the central Yunnan. Biodiv. Sci. 2, 204–209.

Zhang, C., Ding, L., Ding, C., Chen, L., Sun, J., Jiang, X., 2018. Responses of species and phylogenetic diversity of fish communities in the Lancang River to hydropower development and exotic invasions. Ecol. Indic. 90, 261–279. https://doi.org/10.1016/j.ecolind.2018.03.004.

Zintzen, V., Anderson, M.J., Roberts, C.D., Diebel, C.E., 2011. Increasing variation in taxonomic distinctness reveals clusters of specialists in the deep sea. Ecography 34, 306–317. https://doi.org/10.1111/j.1600-0587.2010.06546.x.