



Original research article

Complimentary analysis of metacommunity nestedness and diversity partitioning highlights the need for a holistic conservation strategy for highland lake fish assemblages



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ARTICLE INFO

Article history:

Received 15 September 2014

Received in revised form 7 December 2014

Accepted 8 December 2014

Available online 17 December 2014

Keywords:

Additive partitioning

Freshwater fish

Species turnover

Nestedness

Species invasion

Extinction

ABSTRACT

Metacommunity nestedness can be affected by both idiosyncratic species and species turnover, and diversity partitioning allows one to separate turnover and nested components within β -diversity. Thus, complimentary analysis of metacommunity nestedness and diversity partitioning allows for the identification of the underlying changes at both local and regional scales. We examined changes of fish assemblages in metacommunity nestedness and α -, β -, and γ -diversities resulting from the intense loss of native species and the invasion of nonnative species in Chinese highland lakes over the past 60 years. We found metacommunity nestedness rose markedly over time, following the loss of both β - and γ -diversity resulting from the loss of native species, and the increase of α diversity by the addition of nonnative species. This pattern is contradictory to the selective extinction leading to larger nestedness in natural ecosystems and indicates the human-induced negative effects on the metacommunity. However, β -diversity partitioning showed that the turnover component due to species replacement among lakes still contributes more than the nested component, suggesting the importance of avoiding setting conservation priorities based exclusively on metacommunity nestedness theory, but taking a more holistic metacommunity-approach to conservation instead.

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1. Introduction

Freshwater ecosystems cover just 0.8% of the Earth's surface and yet contain 41% of the world's known fish species (Daily, 1997). With over 50% of the world's population living closer than 3 km to a surface freshwater body (Kummu et al., 2011), the conflicts between human activities and the fragile characteristic of these ecosystems have resulted in the widespread deterioration and even collapse of many freshwater systems, with extinction rates five times higher than those of terrestrial and marine systems combined (Dudgeon et al., 2006; Sala et al., 2000). The introduction and spread of invasive

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fish species ranks amongst the greatest impacts to native freshwater ecosystems, particularly to areas where the highest proportion of threatened fish species are found (Leprieur et al., 2008). Invasive fish species may remain undiscovered for many years, with few discernible ecological impacts, until resulting in profound biological and economic changes (Klose and Cooper, 2013). Invasive species displace native species through predation, competition, disease and hybridization, while habitat loss, overfishing, and/or pollution synergistically drives loss of native species. Thus, on ecological timescales, changes in richness resulting from species loss (local extinction) and species gain (invasion) are among the key problems of nature conservation, and are expected to affect the composition of trophic interactions in communities, with important consequences for ecosystem function (Cardinale et al., 2012; Estes et al., 2011; Wardle et al., 2011).

Nestedness is a widely reported ecological pattern in metacommunities (Patterson and Atmar, 1986; Ulrich and Gotelli, 2007). It describes the hierarchical relationship between assemblages where the species present in species-poor units are proper subsets of those hosted by units with higher species richness (Darlington, 1957). High metacommunity nestedness is to be expected in metacommunities dominated by ubiquitous species with good dispersal capacities or widely-introduced effectively allowing their colonization of distant habitats. Additive partitioning provides a promising way to understand diversity patterns on regional scale (Veech et al., 2002) by segregating the total species diversity within a set of assemblages as the sum (γ -diversity) of the average diversity within an assemblage (α -diversity) and the diversity among the assemblages (β -diversity). Within β -diversity (variation of the species composition of assemblages across space or time), there are two components, i.e. true spatial turnover and nestedness (hereafter β_{turn} -diversity and β_{nest} -diversity), which result from two antithetic processes, namely species replacement and species loss (or gain), respectively (Baselga, 2012). Thus, additive partitioning of species richness allows for a direct comparison of α -, β - (including the components), and γ -diversities, and has particular relevance for testing ecological theory concerned with the determinants of species diversity at multiple spatial scales and potential applications in conservation biology. Both methods provide relative independent analyses of the complex aspects of community assembly from local to regional. However, the study of combined effect of species loss and gain on community assemblages in a changing environment context represents a large gap in our understanding of the relationship between species diversity and metacommunity patterns. Previous macroecological studies have addressed regional scale biotic homogenization as a consequences of species loss and gain (Rahel, 2000; Scott and Helfman, 2001). Nevertheless, few studies have examined the consequences of species loss and gain on diversity for metacommunity patterns across both spatial and temporal scales, which is a prerequisite for adopting sound conservation policies.

According to the concept of metacommunity nestedness, if species assemblages are completely nested, then the assemblages exhibit different α -diversity, but no species turnover (β_{turn} -diversity = 0). Thus, metacommunity nestedness can decline due to both idiosyncratic species and species turnover (Baselga, 2012). For this reason, β -diversity decomposition allows one to differentiate between the β_{nest} and β_{turn} -diversity components, which are indeed separated from α -diversity effects on metacommunity nestedness. Overall, while metacommunity nestedness analysis allows for the identification of the underlying pattern of regional assemblages, additive partitioning is necessary to complementarily assess what processes are driving observed changes in at both local and regional scales (Baselga, 2012). Thus, a combination of additive partitioning and metacommunity nestedness analysis can be a powerful tool to elucidate the effect of species loss and invasion on community assemblages at both local and regional scales.

Here, we assess diversity patterns in nine highland lake fish communities within the Yunnan Province in south-western China, using both additive partitioning and metacommunity nestedness analysis. Specifically, this study address three major objectives. First, we used null models to determine to what extent the fish assemblages show metacommunity nestedness and how metacommunity nestedness has changed over contemporary time scales (1950s to present day). Second, we examined temporal changes in α -, β -, and γ -diversities over the same period to elucidate the relatively contribution of species loss (local extinction) and gain (invasion) to these changes. Third, to complement the metacommunity nestedness analysis and better understand the mechanisms driving changes in fish assemblages, we further analyzed the contributions of β_{turn} and β_{nest} to β -diversity, and their changes via species loss and gain over the study period. Because highland lake ecosystems are vulnerable to external stressors (Chen et al., 2001; Yang et al., 2006, 1994), understanding of these patterns on an ecological time scale is crucial for effective conservation under pressing environmental change, and to inspire novel ways for ecosystem restoration and governance.

2. Material and methods

2.1. Description of study lakes

The lakes in Yunnan Plateau have attracted historically much ecological interest and are currently a Global 200 Priority Ecoregion of the Palearctic lake ecosystems (Olson and Dinerstein, 1998). The nine study lakes are located in the Yunnan Plateau, covering a wide range of latitude (27.716°–23.421°) though restricted in longitude (100.180°–103.306°) (Fig. 1). The altitude of these lakes ranges from 1053 to 2690 m above sea level with annual mean air temperature of 12.7–19.5 °C, and rainfall of 717–1056 mm (Li, 1982; Yang et al., 1994). Lake areas covered a wide range of 25.7–297 km² at ordinary water level, with a mean water depth of 2.4–89.6 m. These lakes are tectonic lakes with segregated evolutionary histories of fish communities. This unique combination of topographic complexity and climate conditions supports enormous biological diversity and high degrees of endemism within the region (Chen et al., 2001; Yang et al., 2006, 1994). Over the last century,

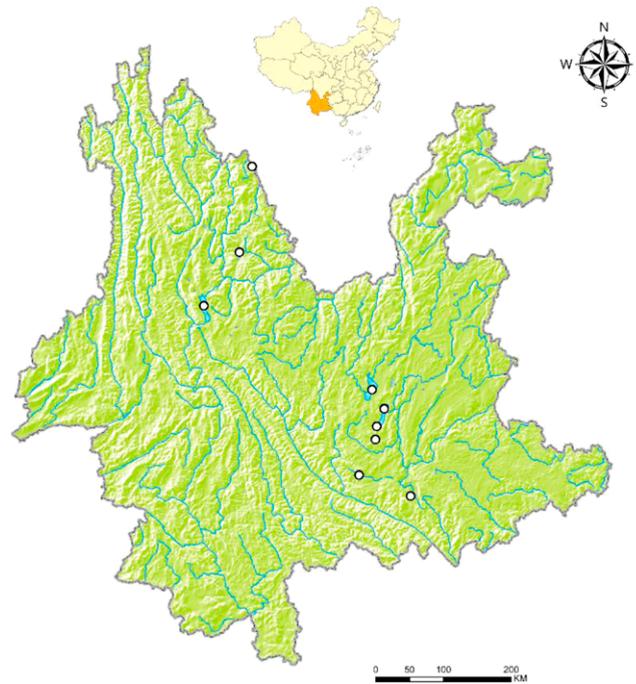


Fig. 1. Map showing the nine studied highland lakes (circles) in the Yunnan region of China.

however, ecosystem processes such as primary production and nutrient cycling have been severely altered by human activities (Whitmore et al., 1997). Fishery activities starting from the 1960s not only directly reduced the numbers and sizes of target and non-target species but also indirectly affected population dynamics through for example changes in reproductive output by removing potential spawners (Chen et al., 2001; Yang et al., 2006, 1994). Meanwhile, introduction of new species to these lakes also started from the 1960s for food production (Li, 1982; Yang et al., 1994).

2.2. Data acquisition and sampling

Historical fish fauna data on the nine study lakes was collected from available presence/absence surveys published and unpublished since the 1950s to 2007 (Supporting Information). After excluding those studies covering less than one year, we pooled all surveys conducted within each year for each lake. Present-day fish fauna data was obtained through fish surveys conducted between 2008 and 2012 in the nine study lakes. Fishes were caught by fish trap, gill net and trawl net according to the methods used in the historical surveys. We surveyed each lake by sampling 4–6 transects per 20 km² of lake surface. Transects were randomly allocated to ensure an adequate representation of the existing species richness in a lake. Fishes were collected as a part of routine commercial fishery in compliance with local fishery regulations. To keep consistency with the historical records only species presence/absence data was recorded. This was also a practical decision given the logical variability in the catchability of fishes by the different gears used in the surveys. To control the intra-annual variation in fish distribution, each lake was sampled during summer and autumn and visited at least twice during the studied period giving a total of 9 observations. After assessing the validity and concordance of the taxonomy of fish species identified in historical and present-day surveys using recent taxonomical monographs (Chen, 1998; Chu et al., 1999; Yue, 2000), a total of 152 species were recorded for these lakes including 100 native species, among which 95 were endemic species, and 52 nonnative species.

Prior to analysis, we recompiled data into four time periods: before 1960, 1960–1979, 1980–1999, and after 2000. The summed observations in each time periods were 12, 17, 16, 20, respectively, giving a total of 65 observations. Although historical surveys are relatively sparse, the durations are relatively long (4–5 year), which can compensate for the low number of observations. The relatively high number of observations in the recent period could also prevent underestimating the current situation of biodiversity. Although the current dataset may have lower detection probabilities for some native species in some lakes, the large number of losses of native species compared with historical records would dominate the results in this study. This temporal resolution was deemed as appropriate for detecting changes in metacommunity nestedness and diversity while effectively increasing survey effort to minimize the effect of false absences. Thus we conducted analysis on 4 presence–absence matrices, one for each period, each of dimensions $n \times s$, where n is the number of lakes (i.e. 9) and s is the number of species observed for the period (see Supplement information, Tables S1–S4).

2.3. Diversity partitioning and metacommunity nestedness

We defined γ -diversity as the total species richness found across all studied lakes and α -diversity corresponds to the species richness found in each lake over a specific period, then the variation in species richness among lakes (β -diversity) can be estimated as the difference between γ -diversity and the mean α -diversities across the lakes. The partitioning of β -diversity into β_{turn} -diversity and β_{nest} -diversity components was performed with “betapart” package (Baselga et al., 2013).

We used the recently developed NODF (nestedness measure based on overlap and decreasing fills) measure of metacommunity nestedness, which has better statistical properties, consistently rejects a nested pattern for different types of random matrices, and reduces the chance of overestimating the degrees of nestedness in metacommunities relative to other existing methods (Almeida-Neto et al., 2008). The measure of metacommunity nestedness (NODF) varies from 0 (no nestedness) to 100 (perfect nestedness). To test whether metacommunity nestedness in our assemblages differed significantly from that expected under simple assembly rules, we compared observed patterns against those resulting from fitting a constrained null model (999 replicates) where the probability of each cell in the matrix being occupied is the average of the probability of occupancy of its own row and column (Bascompte et al., 2003). More details about this type of analysis can be found in Almeida-Neto et al. (2008) and references therein. To disentangle the effects of native and nonnative species on metacommunity nestedness, we calculated this pattern separately for all species, native species, and nonnative species. NODFs were calculated with the “vegan” package (Oksanen et al., 2013).

2.4. Generalized linear mixed model

To study changes in species richness patterns over time, we conducted Poisson regression with a generalized linear mixed model (lake area as a random effect) in “lme4” package (Bates et al., 2014). For the multiple comparisons, function ‘glht’ in library “multcomp” was used (Hothorn et al., 2008). Calculation of indices and statistical analyses were carried out using R (version 3.1.0) statistical software (R-Development-Core-Team, 2011).

3. Results

3.1. Species richness patterns

Total species richness in the studied lakes ranged between 4 and 29 before 1960 (mean \pm standard deviation, 13.9 ± 9.0), with the regional species pool including 62 native and 16 invasive species (Fig. 2(A) and (B)). During the following period (1960–1979), the number of nonnative species more than doubled (39 species), while native richness remained fairly stable (65 species). During this period, number of species increased significantly, and mean species number was $19.4 (\pm 19.5, p < 0.05, \text{Fig. 2(B)})$. The native and nonnative species showed similar richness among lakes (11.4 ± 11.4 and 8.1 ± 6.4 ,

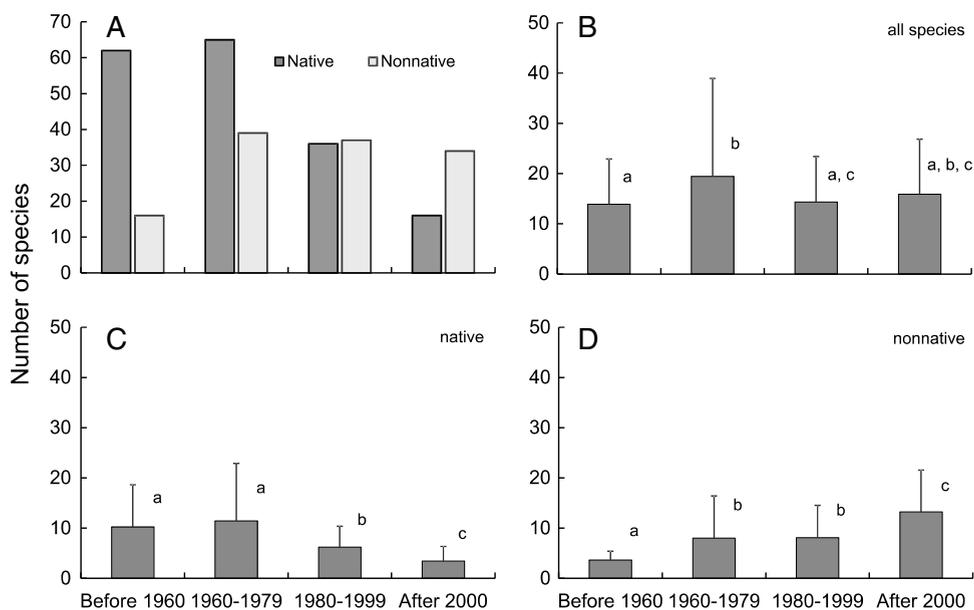


Fig. 2. Species richness in highland fish assemblages over the different time periods. (A) Species numbers of native and nonnative species in the species pool. Mean (\pm 1 SD; $n = 9$) numbers of (B) fish species, (C) native fish species in the lakes, and (D) nonnative fish species in the lakes. Periods under the same letter are not statistically significant from each other (multiple comparison with GLMM at 0.05 significant-level).

Table 1

Null model test for significant metacommunity nestedness for highland fish assemblages over the 4 different time periods. The measure of metacommunity nestedness (NODF) varies from 0 (no nestedness) to 100 (perfect nestedness). The metacommunities in different time periods are significantly nested under the constrained null model ($p < 0.001$, bold text) when the observed values fall outside the 95% confidence intervals.

Period	NODF	Mean (sim.)	95% confidence interval (sim.)	P value (sim.)
All species				
Before 1960	24.2	15.993	1.916	0.001
1960–1979	32.6	15.962	1.494	0.001
1980–1999	6.6	17.210	1.932	0.001
After 2000	61.3	32.242	3.371	0.001
Native species				
Before 1960	22.0	13.08	1.813	0.001
1960–1979	28.1	14.552	2.038	0.001
1980–1999	21.0	14.337	2.755	0.001
After 2000	22.5	17.883	5.829	0.169
Nonnative species				
Before 1960	31.4	22.084	6.270	0.017
1960–1979	42.7	18.478	3.160	0.001
1980–1999	40.0	20.349	3.530	0.001
After 2000	71.5	39.924	5.074	0.001

respectively, Fig. 2(C) and (D)), and nonnative species significantly increased ($p < 0.005$). Interestingly, the rise in the number of nonnative species was followed by a dramatic decrease in native richness over the next 20 years (1980–1999), with only 36 species recorded, while nonnative richness remained unchanged (37 species). Species numbers in the lakes during this period ($4\text{--}30$; 14.0 ± 9.1 species) significantly decreased compared with those in period 1960–1979 ($p < 0.05$), and were similar to those reported for the first period, with a significant decrease of native species ($p < 0.005$). This trend continued into the current period (after 2000), with the native species further decreasing to just 16 species (3.4 ± 2.9) while the number of nonnative species was reduced slightly to 34 species (13.2 ± 8.3). Overall, number of native species significantly decreased ($p < 0.01$) and number of nonnative species significantly increased ($p < 0.01$) among the lakes.

3.2. Metacommunity nestedness

We found consistent statistically significant metacommunity nestedness among the highland fish assemblages across all periods. When all species were considered (Table 1), the calculated NODFs were 22.4, 32.6, 26.6 and 61.3, which were significantly higher than expected under the constrained null model. Interestingly, the NODF in the most recent period (after 2000) was between two to three-fold higher than that existing during the previous three periods. Although NODFs for native species were also statistically significant (with one exception for the recent period), they showed relatively low values compared to those observed for the whole assemblages and nonnative assemblages during the study periods (Table 1). In contrast, nonnative assemblages registered the highest and significant NODFs values for each period, compared with the whole and native assemblages (Table 1). Again, the NODF for the last period (71.49) approximately doubled those of the other three periods.

3.3. Diversity partitioning

Species richness was relatively high in 1960–1979, with a mean of 19 species per lake and a β diversity of 86 species adding to a γ diversity of 104 species (Fig. 3(A)). After 2000, although mean α diversity was still higher than the periods before 1960 and 1980–1999, both β and γ diversity decreased to the lowest levels, with values of 35 and 50, nearly half of the historical maxima, coincident with the maximum NODF (61.32; Table 1).

Decomposition of fish species into native and nonnative indicated that current (after 2000) native mean α - and β -diversity decreased strikingly by more than 76% and 75%, compared with the historical maxima of native species, also reached during 1960–1979, while the γ -diversity dropped by more than 79% (Fig. 3(B)) matching the lowest NODF (Table 1). For nonnative species, mean α diversity in the current period reached 11 species, the highest across periods (Fig. 3(C)). However, γ -diversity of nonnative species peaked (39 species) during the period of 1960–1979, and decreased slightly until the present period though only by 5 species. β -diversity of nonnative species also decreased 31% during this period.

Partitioning of β -diversity into β_{turn} -diversity and β_{nest} -diversity components showed that, when all species were considered (Fig. 3(D)), β_{nest} -diversity reached 38.5% during the current period (after 2000). Despite this increase in the nested component of total β diversity, we found that β_{turn} -diversity has still a relatively high contribution (%) towards β -diversity

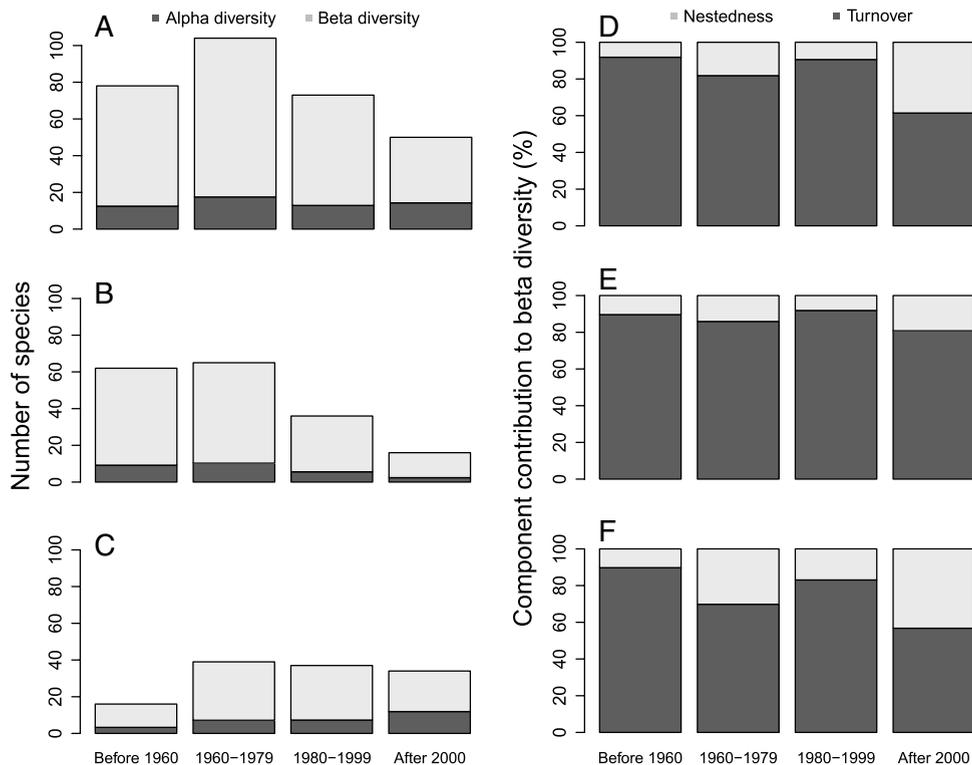


Fig. 3. (A)–(C) Diversity partitioning (α -, β -, and γ -diversity) and (D)–(F) decomposition of total β -diversity into spatial turnover and nested components for highland fish assemblages in the different time periods for (A, D) all fishes, (B, E) native and (C, F) nonnative fish assemblages.

in present-day assemblages. The β_{nest} -diversity in native and nonnative species communities was 80.8% and 56.8% of their β -diversities, respectively, in current period (after 2000, Fig. 3(E) and (F)).

4. Discussion

4.1. Species loss and gain

Human activities have had significant impacts on species loss and gain in these lakes. The dramatic loss of native species is likely a result of the interaction between the multiple anthropogenic pressures affecting these lakes, such as species invasion, overfishing, reclamation or pollution (Chen et al., 2001). For example, in Lake Datunhai, fishery production of native fishes was 25×10^4 kg in 1966, but decreased to 3×10^4 kg in 1981, and native species has never been recorded again since the 1990s (Chen et al., 2006). Fishery activities not only directly reduced the numbers and size of target and non-target native species but also indirectly affected population dynamics by removing potential spawners (Chen et al., 2001; Yang et al., 2006, 1994). A typical example for reclamation is Lake Dianchi, in which littoral habitat of native species decreased about 15% of lake total area, and species including *Anabarilius alburnops*, *A. polylepis*, and *Xenocypris yunnanensis* are near extinction in the current period (Chen et al., 2006).

The impacts of the fishery industry on lakes are not only restricted to local native populations, but also act as an important vector of species addition. The widespread introduction of nonnative species for enhancing local fishery production through the development of local fisheries is undoubtedly a key driver for species invasion (Gao et al., 1981). For instance, grass carp (*Ctenopharyngodon idellus*), black carp (*Mylopharyngodon piceus*), silver carp (*Hypophthalmichthys molitrix*), and bighead (*Hypophthalmichthys nobilis*), all Chinese economically important species for food protein, were introduced in the period of 1950s and 1960s (Chen et al., 2006; Chu and Chen, 1989; Xiong et al., 2008). The repeated introduction of some economically-important species (e.g. reinforcement or restock of carps mentioned above) is another important mechanism for colonization of invaders as a result of the development of local fisheries over the last 60 years (Li, 2006). Meanwhile, invasive species negatively affect local native species in a variety of ways. First, invasive species can outcompete native species through food competition. For example, populations of the native species *Anabarilius sgrahami* have decreased sharply after the invasion of the icefish (*Neosalanx taihuensis*) in the 1980s, with which shares diet and foraging strategies (Li, 2006; Xiong et al., 2008). Secondly, invasive species can affect native population dynamics through changes in reproductive output by consuming their eggs in the littoral/benthic zones. For instance, *Abbottina rivularis*, *Pseudorasbora parva*, and *Ctenogobius*

giurinus invaded these lakes as non-target fishery species. These invaders overlap their habitat with many native species in the littoral area and consume eggs of native species (Li, 2006; Xiong et al., 2008). Finally, some invasive species, such as *Pelteobagrus fulvidraco*, *Cultrichthys erythropterus*, and *Clarias fuscus* are larvae predators of native species (Xiong et al., 2008).

4.2. Metacommunity nestedness

Metacommunity nestedness analysis does not make any assumptions about the possible causal factors that reorganize sites and species, but the differential rates of extinction and colonization are considered its ultimate causes (Atmar and Patterson, 1993; Wright et al., 1997; Wright and Reeves, 1992). Our results seem to agree with this view. Metacommunity nestedness for historical native assemblages are relative low but significant in these lakes, which could be explained by high endemicity of fish assemblages. For instance, there are many species from genus *Anabarilius*, *Cyprinus*, *Sinocyclocheilus* and *Schizothorax* that were recorded in only one of these lakes (Chen et al., 2006). The significant pattern of metacommunity nestedness in these assemblages could be that some lakes are located in the same large river basin, and there are several widely distributed native species in this region. For example, Lakes Fuxian, Xingyun, Qilu, Yangzonghai, Datunhai belong to Nanpanjing river basin (Yang, 1984); some species (e.g. *Carassius auratus*, *Cyprinus carpio chilia*, *Misgurnus anguillicaudatus*), are native species that are distributed in several lakes (Chen et al., 2006). Our results also indicate that the gradual loss of species over the last 60 years from the regional community progressively decreased the metacommunity nestedness of native assemblages, which contradicts the expected effect of selective extinction leading to larger nestedness (Bruun and Moen, 2003; Patterson and Atmar, 1986). The endemic species from the genus *Anabarilius*, *Cyprinus*, *Sinocyclocheilus* and *Schizothorax* are prone to loss from these assemblages (Tables S1–S4), having so-called extinction-prone attributes, including long lifecycle, large body size, low reproductive capacity, low dispersal ability, small geographical range, and high specialization level of habitat (Chen et al., 2001; Chu and Chen, 1989; Yang et al., 2006, 1994).

Metacommunity nestedness among these highland lake assemblages has increased significantly over the last decade relative to historical levels. This pattern seems to be driven by the higher metacommunity nestedness characteristic of nonnative species. The marked increase in invasive species that these lakes experienced during the 1980s and 90s led to present-day assemblages in which invasive species are double in number to native species, which account for just 25% of the maximum historical native richness. Introduction of nonnative species was implemented as a regional fishery attempt and can thus promote metacommunity nestedness in receiving communities through the homogenization of the regional assemblage, because economic fish species were introduced and persisted in all these lakes (Chen et al., 2001; Yang et al., 2006, 1994). Our results suggest that, although the loss of native species eroded the historically significant metacommunity nestedness of native assemblages, the gain of nonnative species from the development of local fisheries enhanced the level of metacommunity nestedness observed in present-day communities.

4.3. Additive partitioning of diversity

Although metacommunity nestedness reveals that species loss and gain ultimately leads to a highly nested pattern of these assemblages, diversity additive partitioning further provides complementary information that the loss of both β - and γ -diversity are mainly driven by loss of native (mostly endemic) species, and the increase in α -diversity is driven by the gain of invasive species. The increase of α -diversity by the species introduction of fishery activities can be viewed as the selective colonization (Darlington, 1957; Wethered and Lawes, 2005) and selective environmental tolerances (Driscoll, 2008; Greve et al., 2005), which are important mechanisms to enhance the metacommunity nestedness. However, effect of species introduction on metacommunity nestedness is weak during the early stages (before 1970's) with an increase of γ -diversity in this period, indicating that high numbers of native species appear to have buffered against the development of high metacommunity nestedness, until the reduction in native species lagged approximately 20 years behind the peak in invasive species (Fig. 3).

By partitioning β -diversity into β_{turn} -diversity and β_{nest} -diversity components, we further found that the contribution of β_{nest} -diversity systematically increased. The main cause for this pattern is the widespread introduction of nonnative species into some of these lakes and the loss of native species as discussed above (see Tables S1–S4). However, despite the observed increase in the relative contribution of β_{nest} -diversity, we found that the contribution of β_{turn} -diversity was still at relatively high levels for both native and nonnative assemblages. These results indicate that there are still high levels of endemism in this region, a former Pleistocene glacial refugia and center of speciation (Li et al., 2011). In the case of nonnative species, the effect of selective introduction of specific commercial species into some of these lakes, together with the colonization failure and dispersal limitation of some introduced species, might have also contributed towards the observed β_{turn} -diversity (see Tables S1–S4).

4.4. Holistic conservation strategy

Metacommunity nested structures are observed in many types of habitat and in many taxa, and also it has been suggested to have implications for biological conservation (Cutler, 1994; Patterson, 1987). For example, in a perfectly nested metacommunity, a large, species-rich assemblage would necessarily conserve more species than any combination of smaller

ones. This idea is particularly in connection with the 'single large or several small' (SLOSS) debate regarding nature reserve design (Cutler, 1994; Patterson, 1987). Our results however, stress the importance of assessing the relative contribution of species extinctions and invasions when considering the implications of metacommunity nestedness for biodiversity conservation by complementary information on diversity partitioning.

Though no generalization can be made about the causality of community assemblages, our results highlight that introduction of invasive species promoted metacommunity nestedness in receiving communities with extinction of endemic species, which is contradictory to the traditional biological conservation ideas based on the metacommunity nestedness theory. The fact that fish assemblages in our study lakes currently exhibit a higher degree of metacommunity nestedness could be misinterpreted from a conservation point of view as suggesting that conservation efforts directed towards those lakes hosting higher richness (α -diversity) will effectively preserve the biodiversity of these highland lake communities. Even if the metacommunity nestedness is driven by invasive species, our partitioning of β -diversity of native and nonnative species suggested both of them actually contributed towards high species turnover in present-day assemblages, suggesting there are chances to conserve more native species and to prevent further biotic homogenization in these assemblages. Meanwhile, native species assemblages show some resilience or buffering capacity to biotic homogenization by invasive species. This phenomenon also suggests that combining metacommunity nestedness and diversity partitioning analysis can offer important insights to improve our understanding of how differences in the antithetic processes of species gain and loss affect community assembly and thus help prioritizing conservation efforts. We therefore stress the importance of avoiding setting conservation priorities based exclusively on metacommunity nestedness theory in these assemblages but taking a holistic metacommunity-approach to conservation instead, i.e. multiple-assemblage species-based conservation strategy.

4.5. Concluding remarks

The main purpose of our study is to contribute to improve our current understanding of the consequences of species loss and gain on regional assemblages. Our study highlights the challenges of elucidating the interacting effect of species loss and gain on metacommunity nestedness in ecological time scale. We demonstrated that the changing of metacommunity nestedness may emerge from the combined effect of different levels of species losses and gains. That is the loss of both β - and γ -diversity by local extinction of native species, and the increase of α -diversity by the addition of invasive species. Even if the assemblages are nested over space in the current period, our partition of β -diversity of native and nonnative species indicate both of them still can contribute towards high species turnover of the present-day regional community assembly in these highland lakes, suggesting the prevention of further community homogenization is still possible. Our study thus lends strong empirical support for prioritizing conservation efforts in this nested metacommunity.

Acknowledgments

For data compiling and sampling we wish to thank Yingying Chen and Yi Yang at the Huazhong aquaculture Univ., and Xiaohu Huang at Hubei Univ. We also thank local volunteer fishermen, who provided invaluable help in sampling. This research was supported by the National Natural Science Foundation of China (Grant Nos. 31170439, 31200359, 31370473), and the Water Pollution Control and Management Project of China (Grant Nos. 2012ZX07101-001 and 2008ZX07101-001). This study was also supported by the Environment Research and Technology Development Fund of the Ministry of the Environment, Japan (S-9-4). There are no actual or potential competing financial interests. The funders had no role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2014.12.004>.

References

- Almeida-Neto, M., Guimaraes, P., Guimarões, P.R., Loyola, R.D., Ulrich, W., 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117, 1227–1239.
- Atmar, W., Patterson, B.D., 1993. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* 96, 373–382.
- Bascompte, J., Jordano, P., Melián, C.J., Olesen, J.M., 2003. The nested assembly of plant–animal mutualistic networks. *Proc. Natl. Acad. Sci.* 100, 9383–9387.
- Baselga, A., 2012. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Glob. Ecol. Biogeogr.* 21, 1223–1232.
- Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieux, F., 2013. betapart: Partitioning beta diversity into turnover and nestedness components. R package version 1.3. <http://CRAN.R-project.org/package=betapart>.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-6, <http://CRAN.R-project.org/package=lme4>.
- Bruun, H.H., Moen, J., 2003. Nested communities of alpine plants on isolated mountains: relative importance of colonization and extinction. *J. Biogeogr.* 30, 297–303.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., 2012. Biodiversity loss and its impact on humanity. *Nature* 486, 59–67.
- Chen, Y., 1998. *Fauna Sinica, Osteichthyes, Cypriniformes II*. Science Press, Beijing, China.
- Chen, Y., Yang, J., Li, Z., 2006. The diversity and present status of fishes in Yunnan Province. *Chinese Biodivers.* 6, 272–277.

- Chen, Z., Yang, J., Su, R., Chen, X., 2001. Present status of the indigenous fishes in Dianchi Lake, Yunnan. *Biodivers. Sci.* 9, 407–413.
- Chu, X., Chen, Y., 1989. Biological characteristics of fish fauna in lakes of Yunnan Plateau and the method of fishery utilization. *Resour. Dev. Mark.* 5, 3–8.
- Chu, X., Zheng, B., Dai, Y., 1999. *Fauna Sinica, Osteichthyes, Siluriformes*. Science Press, Beijing, China.
- Cutler, A.H., 1994. Nested biotas and biological conservation: metrics, mechanisms, and meaning of nestedness. *Landsc. Urban Plann.* 28, 73–82.
- Daily, G., 1997. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press.
- Darlington, P.J., 1957. *Zoogeography: The Geographical Distribution of Animals*. Wiley.
- Driscoll, D.A., 2008. The frequency of metapopulations, metacommunities and nestedness in a fragmented landscape. *Oikos* 117, 297–309.
- Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, M.L., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev.* 81, 163–182.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B., 2011. Trophic downgrading of planet earth. *Science* 333, 301–306.
- Gao, C., Zhuang, D., Zhang, K., Guo, Q., 1981. Preliminary investigation of abundance changes on economic fishes in highland lakes, Yunnan. *Chinese J. Zool.* 1, 31–34.
- Greve, M., Gremmen, N.J., Gaston, K.J., Chown, S.L., 2005. Nestedness of Southern Ocean island biotas: ecological perspectives on a biogeographical conundrum. *J. Biogeogr.* 32, 155–168.
- Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. *Biom. J.* 50, 346–363.
- Klose, K., Cooper, S.D., 2013. Complex impacts of an invasive omnivore and native consumers on stream communities in California and Hawaii. *Oecologia* 945–960.
- Kummu, M., de Moel, H., Ward, P.J., Varis, O., 2011. How close do we live to water? A global analysis of population distance to freshwater bodies. *PLoS One* 6, e20578.
- 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, e28.
- Li, K., 2006. Studies on biology and genetic diversity of two endemic fishes in lakes of Yunnan Plateau, In Institute of Hydrobiology, Chinese Academy of Sciences. University of Chinese Academy of Sciences, Hubei Wuhan.
- Li, S., 1982. Fish fauna and its differentiation in the upland lakes of Yunnan. *Acta Zool. Sin.* 28, 169–176.
- Li, Y., Zhai, S.-N., Qiu, Y.-X., Guo, Y.-P., Ge, X.-J., Comes, H.P., 2011. Glacial survival east and west of the 'Mekong-Salween Divide' in the Himalaya-Hengduan Mountains region as revealed by AFLPs and cpDNA sequence variation in *Sinopodophyllum hexandrum* (Berberidaceae). *Mol. Phylogenet. Evol.* 59, 412–424.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, L.G., Solymos, P., Stevens, M.H.H., Wagner, H., 2013. *vegan: Community Ecology Package*. R package version 2.0-10. <http://CRAN.R-project.org/package=vegan>.
- Olson, D.M., Dinerstein, E., 1998. The Global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. *Conserv. Biol.* 12, 502–515.
- Patterson, B.D., 1987. The principle of nested subsets and its implications for biological conservation. *Conserv. Biol.* 1, 323–334.
- Patterson, B.D., Atmar, W., 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol. J. Linn. Soc.* 28, 65–82.
- R-Development-Core-Team, 2011. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rahel, F.J., 2000. Homogenization of fish faunas across the United States. *Science* 288, 854–856.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., 2000. Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Scott, M.C., Helfman, G.S., 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. *Fisheries* 26, 6–15.
- Ulrich, W., Gotelli, N.J., 2007. Null model analysis of species nestedness patterns. *Ecology* 88, 1824–1831.
- Veech, J.A., Summerville, K.S., Crist, T.O., Gering, J.C., 2002. The additive partitioning of species diversity: recent revival of an old idea. *Oikos* 99, 3–9.
- Wardle, D.A., Bardgett, R.D., Callaway, R.M., Van der Putten, W.H., 2011. Terrestrial ecosystem responses to species gains and losses. *Science* 332, 1273–1277.
- Wethered, R., Lawes, M.J., 2005. Nestedness of bird assemblages in fragmented Afrotropical forest: the effect of plantation forestry in the matrix. *Biol. Conserv.* 123, 125–137.
- Whitmore, T., Brenner, M., Jiang, Z., Curtis, J., Moore, A., Engstrom, D., Wu, Y., 1997. Water quality and sediment geochemistry in lakes of Yunnan Province, southern China. *Environ. Geol.* 32, 45–55.
- Wright, D.H., Patterson, B.D., Mikkelsen, G.M., Cutler, A., Atmar, W., 1997. A comparative analysis of nested subset patterns of species composition. *Oecologia* 113, 1–20.
- Wright, D.H., Reeves, J.H., 1992. On the meaning and measurement of nestedness of species assemblages. *Oecologia* 92, 416–428.
- Xiong, F., Li, W., Pan, J., 2008. Present status of alien fishes and analysis of relative problems in Lake Fuxian in Yunnan Province. *Acta Agric. Jiangxi* 20, 92–94.
- 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., Chen, Y., Be, Y., 1994. Studies on fish diversity in plateau lakes of the central Yunnan. *Chinese Biodivers.* 3, 04.
- Yang, H., Xie, P., Xu, J., Zheng, L., Deng, D., Zhou, Q., Wu, S., 2006. Seasonal variation of microcystin concentration in Lake Chaohu, a shallow subtropical lake in the People's Republic of China. *Bull. Environ. Contam. Toxicol.* 77, 367–374.
- Yue, P., 2000. *Fauna Sinica, Osteichthyes, Cypriniformes III*. Science Press, Beijing, China.