Nutrient enrichment homogenizes taxonomic and functional diversity of benthic macroinvertebrate assemblages in shallow lakes

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Running head: Eutrophication homogenizes lake macroinvertebrates

Keywords: eutrophication, beta diversity, functional homogenization, taxonomic homogenization, species traits, shallow lakes

Abstract

Eutrophication alters the trophic dynamics in lakes and may result in biotic homogenization. How nutrient enrichment drives patterns of taxonomic and functional (i.e. trait-based) homogenization of macroinvertebrate assemblages at within-lake (local) and among-lake (regional) scales is, however, not

well understood. Taxonomic and functional compositions of macroinvertebrate assemblages in 41 lakes of the middle and lower reaches of the Yangtze River and Huaihe River were analyzed at within-lake and among-lake scales. Our results indicated that there was a significant difference in macroinvertebrate assemblages among lakes under different trophic status, and that total phosphorus was the major environmental factor that regulated both taxonomic and functional beta diversity of macroinvertebrate assemblages. That the abundances of pollution-tolerant species (e.g. *Limnodrilus hoffmeisteri* and *Microchironomus tabarui*) increased with trophic state contributed the most to among-lake dissimilarity. Functional beta diversity was significantly positively correlated with taxonomic beta diversity, while functional beta diversity was on average lower than taxonomic beta diversity. A combination of univariate and multivariate techniques revealed that nutrient enrichment homogenized taxonomic and functional diversity of benthic macroinvertebrate assemblages in shallow lakes at within-lake and among-lake scales, and that there was an overall trend towards taxonomic homogenization that exceeded the trend of functional homogenization. Thus, taxonomic and functional compositions should be considered simultaneously to improve understanding of the response of aquatic communities to anthropogenic disturbance, as the loss and gain of species may be influenced by species-specific features, and functional composition may exhibit a relatively high correspondence with changes in environmental conditions.

Introduction

Focusing on species composition is the traditional approach to describe ecological communities, and it treats all species as functionally equivalent and phylogenetically independent (Petchey and Gaston 2006). The variation in species composition may thus sometimes fall short in providing a comprehensive picture of community assembly (Carmona et al. 2016; Devictor et al. 2010). Current research emphasizes that multiple facets of biodiversity (i.e., taxonomic, functional, and phylogenetic diversity) should be considered to provide a clearer picture of spatial patterning of ecological communities (Cai et al. 2018; Devictor et al. 2010). Functional (or trait-based) approaches can provide a more mechanistic perspective of the community-environment relationships and functioning of ecosystems in comparison to purely taxonomic approaches (Cadotte et al. 2011). This is because species primarily react to the environmental gradients through the specific functional traits and roles they play in an ecosystem (Carmona et al. 2016). Species composition may also be affected by dispersal and other stochastic forces (Heino et al. 2015b),

while traits may be phylogenetically conserved, with closely-related species being adapted to similar environmental conditions and having equivalent traits and being affected by environmental filtering (Heino and Tolonen 2017). Moreover, functional composition may exhibit a relatively high correspondence with changes in environmental conditions, reflecting resilience of ecosystems (Göthe et al. 2017; Laliberté et al. 2010).

Biodiversity can be divided into alpha, gamma and beta diversity (Whittaker 1960), of which beta diversity has gained increasing interest in recent years (Anderson et al. 2011). Beta diversity is a function of the compositional dissimilarity of biotic assemblages among sites or along environmental gradients (Donohue et al. 2009). The reduction in beta diversity leads to biotic homogenization, which is considered to be one of the most widespread forms of biotic impoverishment on the earth (Menezes et al. 2015). Biotic homogenization is the process by which biological differences of regional biotas in any organizational level decrease over time, in terms of genetic, taxonomic or functional features. It is a multifaceted process which involves environmental alterations, species invasions and extinctions (Petsch 2016; Olden and Rooney 2006). Homogenization of environmental conditions resulting from anthropogenic activities could contribute to biotic homogenization (Zorzalalmeida et al. 2017). Nevertheless, biotic homogenization is not random because the loss and gain of species may be influenced by species-specific features (Brice et al. 2017; McKinney et al. 1999). More sensitive species may be replaced by more tolerant species following environmental change, leading to increase of the similarity in species features, i.e. functional homogenization (Olden and Rooney 2006; McKinney et al. 1999). Although functional and taxonomic homogenization may occur simultaneously, patterns in these two processes might differ. Previous research indicated that functional homogenization exceeded taxonomic homogenization among European freshwater fish assemblages (Villéger et al. 2014), while Su et al. (2015) reported that taxonomic homogenization exceeded functional homogenization of fish assemblages in Yunnan, China. The relationship between taxonomic and functional homogenization varies greatly, depending on the initial habitat conditions and species composition (Su et al. 2015). If species of the original ecosystem status share similar traits, a decrease in species richness or a slight taxonomic homogenization may have no effect on the functional composition and subsequently on ecosystem function (Sonnier et al. 2014). Different responses of taxonomic and functional

homogenization to environmental changes should thus be assessed to better understand biotic homogenization.

Eutrophication resulting from nutrient enrichment, mainly driven by nitrogen and phosphorus, comprises a globally important anthropogenic threat to aquatic ecosystems (Heisler et al. 2008). The negative effects of nutrient enrichment on the ecosystem may be expected, wherever nutrient enrichment increases environmental degradation and decreases oxygen availability and habitat structural complexity (Wengrat et al. 2017; Donohue et al. 2009). Anthropogenic nutrient enrichment can alter community structure of aquatic organisms (Carvalho et al. 2006), e.g. through increase of phytoplankton biomass and algal blooms, and degradation of macrophyte cover, which would lead to consequent changes in the ecological functioning of lakes, e.g. energy flows, nutrient cycling and ecosystem services they provide to humans (Heisler et al. 2008; Schindler 2006). Many studies have focused on the impacts of eutrophication on species-based beta diversity and species richness (Zorzalalmeida et al. 2017; Dawson et al. 2016; Bini et al. 2014). For example, Donohue et al. (2009) found that nutrient enrichment led to taxonomic homogenization of lake benthic assemblages at both within-lake and among-lake scales. Menezes et al. (2015) found that fish species richness and diversity converged with progressive eutrophication, and eutrophication homogenized fish community composition in the littoral zone. However, current understanding of its effects on aquatic organisms has almost entirely focused on the change in taxonomic similarity between assemblages, whereas knowledge on functional diversity remains poor.

This study was based on surveys of benthic macroinvertebrates of 41 subtropical shallow lakes across the middle and lower reaches of the Yangtze River and Huaihe River system in China, for which eutrophication is one of the major environmental problems. In this study, we hypothesized that nutrient enrichment would lead to taxonomic and functional (i.e. inferred from static trait-based information) homogenization of lake benthic assemblages at both local (within-lake) and regional (among-lake) scales (Su et al. 2015; Villéger et al. 2014). Furthermore, we expected that taxonomic homogenization would be larger than functional homogenization since functional redundancy of some species exists (Baiser and Lockwood 2011). Specifically, the loss of some functions due to species loss in a community may be supplemented by the remaining species.

Materials and Methods

Study area and lakes

The middle and lower reaches of the Yangtze River and Huaihe River (MLYH) belong to the warm temperate monsoon and sub-humid climate region, with high density of freshwater lakes. This region is highly developed, with relatively high levels of urban and agricultural development. The middle and lower reaches of the Yangtze River and Huaihe River cover an area of 1,051,000 km^2, with a mean annual rainfall of above 1,000 mm, and contains approximately 655 (surface area > 1 km^2) freshwater lakes, with a total water area of 20,529 km^2 (Jiang et al. 2009). Many lakes in MLYH have experienced dramatic environmental degradation over the past three decades, due to the influence of human activities (Le et al. 2010). The sediments of these lakes were mainly composed of fine sediment, with relatively high background nutrient concentrations (Yang et al. 2010). In this study, 41 shallow lakes were investigated within this region, and six sampling sites of each lake were sampled, making up a total of 246 samples (Fig. 1, Table S1). Generally, the six sampling sites were randomly distributed in sublittoral zones since all the studied lakes were very shallow and without profundal zone (max water depth < 8.2 m, mean water depth < 5.2 m) (Table S1).

Field sampling and laboratory analyses

Macroinvertebrate samples were collected during April to June in 2012. Sampling was conducted with 1/16 m^2 modified Peterson grab, with six grabs comprising a sample. All materials collected from a site were pooled and rinsed in the field to remove fine sediments, and all remaining materials were fixed with a 7% buffered formaldehyde solution. In the laboratory, samples were sorted by hand on white enamel pans with the aid of a dissection microscope and preserved in 70% ethanol. The macroinvertebrates were identified to the lowest feasible taxonomic level under a dissection microscope (Olympus® SZX10) or a microscope (Olympus® BX53) using regional keys (Liu et al. 1979; Morse et al. 1994; Tang 2006; Wang 2002). When necessary (e.g., Oligochaeta, Polychaeta, and Diptera), microscope slides were prepared on Euparal. Macroinvertebrate abundance was obtained by counting all individuals and expressing the results as ind. m^{-2}.

Water temperature (WT), pH, dissolved oxygen (DO), electrical conductivity (COND), and turbidity were measured in situ, under-surface water (0.5 m below the water surface) using water quality analyzer

(YSI 6600 V2). Water depth and Secchi depth (SD) were also measured in the field. For each sampling site, water sample was collected from 0.5 m below the water surface, and surface sediment was also collected. The water and sediment samples were then kept at 4°C for further chemical analysis. The total nitrogen (TN), ammonium (NH_4^+-N), nitrate (NO_3^--N), total phosphorus (TP), orthophosphate (PO_4^{3-}-P), and permanganate index (COD_{Mn}) were measured in the laboratory based on standard methods (APHA 2012). In the field, the area of aquatic vegetation (Macrophyte cover) was estimated and divided into five classes 0, 0-5%, 5-25%, 26-50%, 51-75% and 76-100%, with assignment to classes from 0 to 5, respectively. Water area of each lake (surface area) was also taken into account in this study. The data of water area of each lake were provided by the Scientific Data Sharing Platform of Lake and Watershed (http://www.geodata.cn).

Trait information

As proxies for the functions of macroinvertebrates in lake ecosystems, we used a large number of species traits. Various species traits have been proposed for freshwater macroinvertebrates, including body size, mobility, reproductive characteristics, food source and feeding habits (Charvet et al. 2000; Usseglio-Polatera et al. 2000). In this study, 60 functional categories of 10 traits (i.e. maximal size, life cycle duration, aquatic stages, reproduction, dissemination, resistance form, respiration, locomotion and substrate relation, food, feeding habits) were considered (Table S2). Trait information was collected at the lowest feasible taxonomic level. That is, most trait information was obtained at the species level. When the trait information of a species was lacking, we used that of genera, and when the trait information of a genus was still lacking, we used that of family level instead. Recent studies have shown that functional composition based on fuzzy-coded traits can effectively indicate human disturbance on benthic macroinvertebrates (Charvet et al. 2000). In this study, 60 functional categories were calculated based on fuzzy-coded and affinities for each trait category were standardized as percentage affinities within a trait (Mondy and Usseglio-Polatera 2014). We multiplied the taxa-trait matrix by the taxa-site abundance matrix to obtain a traits-site matrix that included the relative abundance of each trait category in each site (Sarremejane et al. 2017).

Statistical methods

Taxonomic richness and functional richness were used to describe the taxonomic and functional

diversity of macroinvertebrates. Taxonomic richness (S) was the number of macroinvertebrate species. We standardized taxonomic richness to account for sampling effort, using the individual-based rarefaction (Colwell et al. 2012). Functional richness (Fric) was expressed as the richness of functional traits, and was calculated using the function *dbFD* in the R package *FD*. S and Fric values were based on mean values from each lake.

To test the compositional dissimilarity of macroinvertebrate assemblages, Permutational Analysis of Multivariate Dispersions (PERMDISP) was used as a measure of beta diversity. PERMDISP comprises a relative multivariate measure of variability in different groups of samples and is calculated by comparing ranked distance or similarity measures within and among groups in a similarity matrix. In this study, beta diversity (average distance to centroid) of taxonomic and functional compositions, i.e. taxonomic beta diversity (PERMDISPtaxa) and functional beta diversity (PERMDISPtraits), were calculated for each lake based on the six samples taken in each lake, based on Bray-Curtis similarity, using the function *betadisper* in the R package *vegan* (Oksanen et al. 2016).

Linear model (LM) was used to test the linear relationships between taxonomic diversity and functional diversity (i.e. taxonomic richness *vs.* functional richness, and taxonomic beta diversity *vs.* functional beta diversity). Mantel test was used to test the relationship between taxonomic and functional compositions, based on Bray-Curtis dissimilarity of taxonomic and functional abundances of the 246 samples.

Statistical analysis at regional scale

Previous studies indicated that pelagic productivity was mainly limited by the concentration of total phosphorus in these lakes (Xu et al. 2010; Wang et al. 2008). The 41 lakes were divided into three lake trophic groups based on the total phosphorus (TP) concentration. Mesotrophic (TP 0.01 mg/L - 0.05 mg/L) included 10 lakes, slightly eutrophic (TP 0.05 mg/L - 0.1 mg/L) included 19 lakes, and moderately eutrophic (TP 0.1 mg/L - 0.2 mg/L) included 12 lakes, according to technology regulations for surface water resources quality assessment in China (SL395-2007). For the detailed information of environmental variables of the three lake trophic groups, see the supplementary materials (Table S3).

Multivariate statistical analyses were performed to examine variation in assemblage structure among lake groups in different trophic status. Non-metric multidimensional scaling (NMDS) was performed based on a Bray-Curtis similarity matrix obtained from log(x+1)-transformed abundance data, using the function *vegdist* in the R package *vegan* (Oksanen et al. 2016). Macroinvertebrate assemblage structures, both taxonomic and functional compositions, were compared among the three lake trophic groups using permutational multivariate analysis of variance (PERMANOVA) and pairwise comparison (Anderson et al. 2017), based on a Bray-Curtis resemblance matrix with 999 permutations. The Bray-Curtis dissimilarities of taxonomic composition and functional composition among the three lake trophic groups were also calculated. Furthermore, similarity percentage (SIMPER) procedures were applied to determine the characteristic species for each lake trophic group using the software PRIMER 5.0.

At regional scale, beta diversity of taxonomic and functional compositions was calculated for each lake type. The ANOVA *F*-statistic was used to compare among-group differences in the distance from observations to their group centroid, and was performed using the function *betadisper* in the R package *vegan*. Significance of among-group differences was tested through permutation of least-squares residuals (Anderson et al. 2006). Besides, pairwise comparisons were also performed to test which groups were different, using the function *permutest* in the R package *vegan*.

Statistical analysis at local scale

Multiple linear regression (MLR) was employed to examine environmental drivers of taxonomic and functional beta diversity. In addition to environmental variables (e.g. TP, TN, and macrophyte cover, etc.), taxonomic and functional beta diversity may also be regulated by other factors such as environmental heterogeneity (Bini et al. 2014; Heino et al. 2015a). Hence, PERMDISP values, based on all the environmental variables, for each lake was calculated to represent environmental heterogeneity. Prior to the calculation of environmental heterogeneity, all environmental variables, except for pH, were log(x+1) transformed and standardized (Mean = 0, SD = 1) to improve normality. We next chose the final models using forward selection of explanatory variables based on Akaike's information criterion (AIC) that best accounted for variation in beta diversity and used adjusted coefficient of determination. MLR analysis was employed using the function *lm* in the R package *MASS*. Furthermore, the standardized regression coefficients of taxonomic and functional beta diversity in relation to TP were calculated, and

the absolute values were compared. The higher the value, the more susceptible beta diversity was to TP variation.

Spatial autocorrelation is commonly present in geographical data, resulting in non-independence of residuals and thus disobeying the assumption of standard regression analysis (Legendre and Legendre 2012). Moran's I correlograms were built to evaluate the degree of spatial autocorrelation of the response variables (i.e. taxonomic beta diversity, functional beta diversity, taxonomic richness and functional richness) and the predictor variables (e.g. TP) in relation to geographic distances. Moran I statistics were calculated using the function *correlog* in the R package *pgirmess* (Giraudoux 2016).

Results

Structure of macroinvertebrate assemblages

A total of 79 macroinvertebrate species were collected, including 9 Oligochaeta, 26 Chironomidae, 16 Bivalvia, 12 Gastropoda, 5 Hirudinea, 5 Crustacea, 4 Polychaeta and 2 other insects. Of the 60 functional categories, only 7 categories were not found in the 41 lakes. Taxonomic richness varied greatly among lakes, ranging from 7 to 23 in each lake, and functional richness varied even more profoundly, ranging from 4.7 to 44.8 in each lake. Moreover, Taxonomic richness was significantly positively related with functional richness ($R^2 = 0.35$, $P < 0.01$) (Fig. 2). Functional beta diversity varied between 0.066 and 0.271, and taxonomic beta diversity varied between 0.194 and 0.585. Although taxonomic beta diversity was also significantly positively related with functional beta diversity ($R^2 = 0.30$, $P < 0.001$), functional beta diversity was on average lower than taxonomic beta diversity (Fig. 2). In addition, Mantel test indicated a rather strong correlation between taxonomic and functional compositions ($r = 0.57$, $P < 0.001$).

NMDS showed that lakes under different trophic status harbored distinct communities, with a low stress value (0.16) (Fig. 3). The results of PERMANOVA and the pairwise tests also indicated significant differences in taxonomic and functional compositions of macroinvertebrate assemblages among the three lake trophic groups (Table 1, Fig. 4). *Limnodrilus hoffmeisteri* and *Microchironomus tabarui* were characteristic species that had the most contribution to among-group dissimilarity (Table 2). *L. hoffmeisteri* and *M. tabarui* were most abundant in moderately eutrophic lakes, followed by slightly eutrophic lakes and mesotrophic lakes. Based on the analysis of all the lakes, it was found that Bivalvia

were more abundant in mesotrophic and slightly eutrophic lakes than in moderately eutrophic lakes, whereas Oligochaeta and Chironomidae were more abundant in moderately eutrophic lakes than in mesotrophic and slightly eutrophic lakes (Fig. S1).

Regarding functional composition, relative abundance of both "diapause or dormancy" in the trait of "resistance form" and "crawler" in the trait of "locomotion and substrate" relation decreased with increasing trophic status. For the feeding habits, relative abundance of deposit feeders increased with increasing trophic status, while those of shredders and scrapers decreased with increasing trophic status, following the opposite pattern. Functional composition based on other traits (e.g. locomotion and substrate relation, respiration, dissemination, aquatic stages, etc.) showed no significant differences among the three lake trophic groups (Fig. S2).

Homogenization at regional scale

There were significant differences in beta diversity among the three lake trophic groups, both for taxonomic ($P < 0.001$, $F = 30.36$) and functional data ($P < 0.001$, $F = 10.59$). Pairwise comparisons also indicated that there were significant differences in taxonomic and functional beta diversities among the three lake trophic groups (Fig. 5). Taxonomic beta diversity of mesotrophic lakes (0.60) was the highest, followed by slightly eutrophic lakes (0.55), and that of moderately eutrophic lakes was the least (0.47). As for functional beta diversity, mesotrophic lakes still had the highest value (0.23), followed by slightly eutrophic lakes (0.18), whereas moderately eutrophic lakes had the lowest value (0.15). The results showed that the higher nutrient enrichment, the lower beta diversity of taxonomic composition and functional composition, indicating that nutrient enrichment would lead to taxonomic homogenization and functional homogenization at regional scale. In addition, the Bray-Curtis dissimilarities of taxonomic composition among the three lake trophic groups were much higher than that of functional composition (Table 1).

Homogenization at local scale

Multiple linear regression found several significant environmental variables closely related with taxonomic and functional beta diversity of macroinvertebrate assemblages (Table S4). Based on AIC, the explanatory variables that best accounted for taxonomic beta diversity were TP ($P < 0.01$) and SD ($P < 0.05$), both of which were significantly related to taxonomic beta diversity. The explanatory variables that

best accounted for functional beta diversity were TP, macrophyte cover and water area. Nevertheless, only TP was significantly ($P < 0.05$) related to functional beta diversity, and macrophyte cover showed marginally significant ($P = 0.095$) relationship with functional beta diversity. Moran I statistics showed very weak spatial autocorrelation for the response variables (i.e. taxonomic beta diversity, functional beta diversity, taxonomic richness and functional richness) and the predictor variable (i.e. TP) (Fig. S3), suggesting spatial independence between adjacent lakes.

As shown in Fig. 5, taxonomic beta diversity was negatively correlated with TP ($R^2 = 0.29$, $P < 0.01$), and functional beta diversity also showed a negative relationship with TP ($R^2 = 0.08$, $P < 0.05$). As the standardized regression coefficient of taxonomic beta diversity model ($b = -0.54$) was much higher than that of functional beta diversity model ($b = -0.28$), suggesting that taxonomic beta diversity was more susceptible to nutrient enrichment than functional beta diversity.

Discussion

Nutrient enrichment leads to both taxonomic and functional homogenization

Enhanced anthropogenic activities can exclude sensitive species and thereby create taxonomic and functional homogenization at the community level (McKinney et al. 1999). Our results indicated strongly that both taxonomic and functional compositions of benthic macroinvertebrate assemblages, at both local and regional scales, generally became more homogeneous with increasing nutrient concentration. This finding is congruent with Menezes et al. (2015) who documented similar patterns for fish community homogenization. Donohue et al. (2009) also indicated a negative relationship between taxonomic beta diversity of macroinvertebrates and nutrient concentrations.

Two primary mechanisms may account for these patterns. Firstly, eutrophication tends to alter habitat structure and reduce macrophyte cover. Habitat heterogeneity is an important factor generating beta diversity in freshwater ecosystems (McGoff et al. 2013), and decreased habitat heterogeneity owing to anthropogenic disturbance can significantly reduce beta diversity. Habitat alteration may directly cause the extirpation of sensitive species that cannot tolerate the new abiotic conditions (Williams et al. 1993). With increasing nutrient concentration, the importance of trophic heterogeneity within and among benthic habitats often decreases, which could also reduce taxonomic and functional dissimilarity of macroinvertebrate assemblages (Hayford et al. 2015). In this study, *L. hoffmeisteri* (Oligochaeta)

normally preferring fine organic-rich sediments, occurred more abundantly in moderately eutrophic lakes than slightly eutrophic lakes and mesotrophic lakes; thus, it contributed the most to the dissimilarity among different lake trophic status. A previous study of McGoff et al. (2013) found that habitat alteration plays a crucial role in taxonomic homogenization of littoral macroinvertebrate assemblages across Europe. Structural habitat alteration and water quality changes might occur concomitantly. Additionally, aquatic vegetation also has an important role in structuring macroinvertebrate assemblages (Zhang et al. 2014), and the result of MLR indicated that there was significant negative relationship between macrophyte cover and the total phosphorus concentration ($R^2 = 0.28$, $P < 0.01$) (Fig. S4), which evidenced the effects of eutrophication on macrophyte cover. In freshwater ecosystems, aquatic vegetation promotes beta diversity of macroinvertebrates via producing multiple environmental gradients, providing living space and refuge and selecting species traits related to population dynamics and feeding habits (Céréghino et al. 2008; Heino 2008). Furthermore, the roots of some macrophytes may provide dissolved oxygen to benthic macroinvertebrates (Takamura et al. 2009). In this study, the results of MLR indicated macrophyte cover was one of the main factors that regulated the functional composition of macroinvertebrate assemblages, suggesting that decreased macrophyte cover had contributed to the observed homogenization of macroinvertebrate assemblages.

Secondly, anthropogenic eutrophication acts as "an ecological filter", which may reduce the compositional dissimilarity of biotic assemblages among sites via decreasing the importance of random processes in structuring biotic communities (Chase 2007). The mechanism behind this process can be explained by "niche selection" that strong environmental filtering would exclude species that are less adapted to high-nutrient environments, which may occur independently of changes in habitat heterogeneity (Chase 2007). However, whether compositional dissimilarity increases or decreases with nutrient enrichment depends on the initial site productivity (Chalcraft et al. 2008). Besides, the gradual increase in productivity caused by natural eutrophication over a relatively long timescale allows the biotic assemblages to adapt to the increasingly productive conditions. On the contrary, anthropogenic nutrient enrichment likely leads to a rapid increase in productivity, which may act as a deterministic filter allowing only a few species to survive in eutrophic environments. In this study, the abundances of two Oligochaeta species (*L. hoffmeisteri* and *Branchiura sowerbyi*) were positively related with trophic status,

i.e. they were the most abundant in moderately eutrophic lakes and the least abundant in mesotrophic lakes. *M. tabarui* (Chironomidae) also showed a similar pattern. These taxa are reported to be pollution tolerated and be able to live in stressful environments (Wang et al. 2012). However, *Corbicula fluminea* (Bivalvia) was dominant in mesotrophic and slightly eutrophic lakes, but not a characteristic species in moderately eutrophic lakes, as this species is reported to be sensitive to increased nutrient enrichment and associated hypoxia (Saloom and Duncan 2005). The result that Oligochaeta and Chironomidae were much more abundant than Bivalvia in moderately eutrophic lakes might result from the effects of strong ecological filters.

The low explanatory power of TP (max R^2 = 0.29) indicated that other potentially important environmental variables might also be responsible for taxonomic and functional homogenization, e.g. number of habitat types, sediment composition, sediment grain size and organic matter content of sediments. Habitat conditions do have strong effects on macroinvertebrate community composition (Cai et al. 2012; Heino 2008): the more habitat types there are, the more living space there is for different species of macroinvertebrates (McGoff et al. 2013; Heino 2008). The decrease of habitat heterogeneity would lead to habitat homogenization within or among lakes, resulting in taxonomic and functional homogenization of macroinvertebrate assemblages. Sediment conditions strongly affect benthic macroinvertebrate assemblages (Donohue and Irvine 2003). In our studied lakes, the sediment mainly comprised of silty and clay grains, with the proportion of silt varying from 50% to 70%. Thus, it seems that the grain size composition of sediments is unlikely to be a dominant factor regulating beta diversity of macroinvertebrate assemblages (Yang et al. 2010). Besides, we could not consider organic matter contents and nutrients in sediments, which may be responsible for the low explanatory power of our models. In addition to physical and chemical factors, biotic factors (e.g. competition, predation, and dispersal etc.) could also be responsible for the homogenization of macroinvertebrate assemblages (Rahel 2002). These factors should be better integrated into future studies, which would benefit from concomitant experimental manipulations of nutrient levels and biotic interactions.

There was a significant positive correlation between changes in taxonomic beta diversity and functional beta diversity, indicating they followed similar patterns, as also found by Baiser and Lockwood (2011). This is likely because functional composition is especially pertinent to changing spatial patterns

of taxonomic composition, and the loss and gain of species driving homogenization and differentiation are heavily influenced by the traits that these species possess (Brice et al. 2017; Capellini et al. 2015). In this study, significant differences existed in both taxonomic and functional compositions of macroinvertebrate assemblages among the three lake trophic groups. However, the functional similarity was relatively higher than taxonomic similarity. This indicated that taxonomic and functional beta diversity shared the same trend with TP variation, but the degree of change might differ.

Different responses of taxonomic versus functional beta diversity

Our results indicated that the effects of nutrient enrichment on taxonomic homogenization were greater than those on functional homogenization. In this study, functional beta diversity remained moderate despite high level of taxonomic beta diversity, i.e. lower functional homogenization than taxonomic homogenization. This finding is congruent with Su et al. (2015) who reported that historical functional dissimilarity of fish assemblages in Yunnan, China, was lower than taxonomic dissimilarity, and the change in functional dissimilarity was also lower than the taxonomic change. Sonnier et al. (2014) also reported although upland forests in Wisconsin have experienced taxonomic homogenization, they have not undergone functional homogenization. If species of the original status share similar traits, a decrease in species richness or a slight taxonomic homogenization may have no effect on ecosystem function. However, Villéger et al. (2014) documented that functional homogenization exceeded taxonomic homogenization among European freshwater fish assemblages. There might be three main reasons for different patterns of taxonomic and functional homogenization. Firstly, the discrepancy could be explained by different dispersal ability among species (e.g. macroinvertebrates, fish and plants) (Zhang et al. 2018; Sonnier et al. 2014; Baiser and Lockwood 2011). Secondly, study scales could also have effect on the results (Baiser and Lockwood 2011). Translocated species played a strong role in the homogenization process of fish assemblages in the scale of the whole Europe, while at smaller scales, translocation might have little impacts on the homogenization process, as species may belong to the same species pool. Thirdly, species extirpation did not play a significant role in the homogenization process of European fish assemblages (Villéger et al. 2014); however, homogenization process of fish assemblages in Yunnan was mainly due to invasive species and extinction of native fish species (Su et al. 2015). In our study, the elimination of the sensitive species under the impacts of eutrophication may have a profound

effect on the taxonomic and functional homogenization of macroinvertebrate assemblages. There is no direct relation between change in taxonomic homogenization and change in functional homogenization (Su et al. 2015; Villéger et al. 2014). Therefore, the changes in functional homogenization cannot be predicted by the changes in taxonomic homogenization.

The finding that taxonomic homogenization exceeded functional homogenization in this study may also result from the different properties of taxonomic and functional beta diversity, as functional redundancy was not considered in this study, and functional redundancy often exists in some species with similar traits (Petchey and Gaston 2006). In this study, the lower functional dissimilarity than taxonomic dissimilarity suggested that there was relatively high functional redundancy, which may explain why functional beta diversity declined slowly along with increased TP level, while clear changes was detected for taxonomic beta diversity (Sonnier et al. 2014). We base this reasoning on the results obtained by Baiser and Lockwood (2011), who found that the relationship between changes in taxonomic and functional similarity among communities depends on the amount of functional redundancy in the species pool. In this case, even if some species may be eliminated with increasing nutrient enrichment, functional traits may also be conserved with closely related species being adapted to similar environmental conditions and having equivalent traits. Thus, there should be a more moderately smaller decrease of functional beta diversity than taxonomic beta diversity. Furthermore, no reduction in functional beta diversity with the reduction in taxonomic beta diversity does not mean it is good for the ecosystem: what if the ecosystem is on the brink of the loss of critical functions contributed by some species? When functional redundancy is high, losing or gaining species from an assemblage tells us little about changes in functions (Baiser and Lockwood 2011). For instance, if there are several species sharing the same trait in an assemblage, taxonomic beta diversity would decrease with the loss of any of the species, while functional beta diversity might remain stable. However, when most of the species disappeared, the function would still preserved but it would be on the brink of functional loss. In this case, the ecosystem would be particularly vulnerable, as the loss of a special function may exhibit low resilience to disturbance (Laliberté et al. 2010). Although we failed to show this quantitatively, it should be worthy of attention because a few thousand years of human imprint on the earth have become a major process structuring biodiversity patterns at various scales (Ellis 2016). There is an urgent need for ecologists to

measure functional redundancy and ecosystem resilience to detect early signals of ecological change before abrupt shifts occur (Laliberté et al. 2010).

Another potential reason for the trend that taxonomic homogenization exceeded functional homogenization in this study might be that not all trait information was based on species level data. Trait information based on genus or family level would result in lower beta diversity than that based on species level, because higher taxonomic levels (i.e. genus or family) could provide less applicable information (Sarremejane et al. 2017).

Conclusion

In line with our hypothesis, our results indicated that eutrophication was clearly associated with reduced taxonomic and functional beta diversity of macroinvertebrate assemblages at both local (within-lake) and regional (among-lake) scales. Additionally, there was an overall trend towards the fact that taxonomic homogenization exceeded that of functional homogenization in response to eutrophication. Hence, taxonomic and functional compositions should be considered simultaneously to improve understanding of the effects of eutrophication and other anthropogenic disturbance on aquatic communities. This is because the changes in functional composition cannot be predicted by the changes in taxonomic composition, while functional diversity has been proven to be closely related to ecosystem functioning. Moreover, taxonomic and functional homogenization of macroinvertebrate assemblages may cause important and unanticipated impacts on freshwater ecosystems, with potentially considerable ecological, evolutionary and socio-economic consequences.

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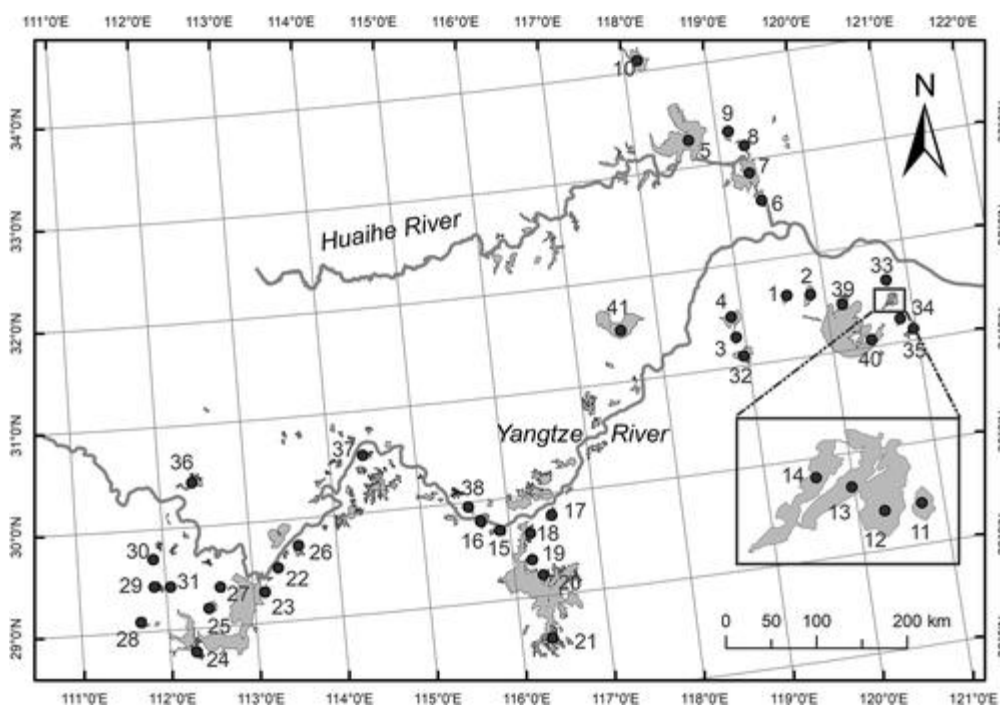spatial extent and productivity. Hydrobiologia **800:** 7-16.

Figure legends

Figure 1
Open in figure viewerPowerPoint
Locations of the 41 shallow lakes in the middle and lower reaches of Yangtze River and Huaihe River, China. The corresponding relation of numerical order and the name of each lake can be found in the supplementary materials.
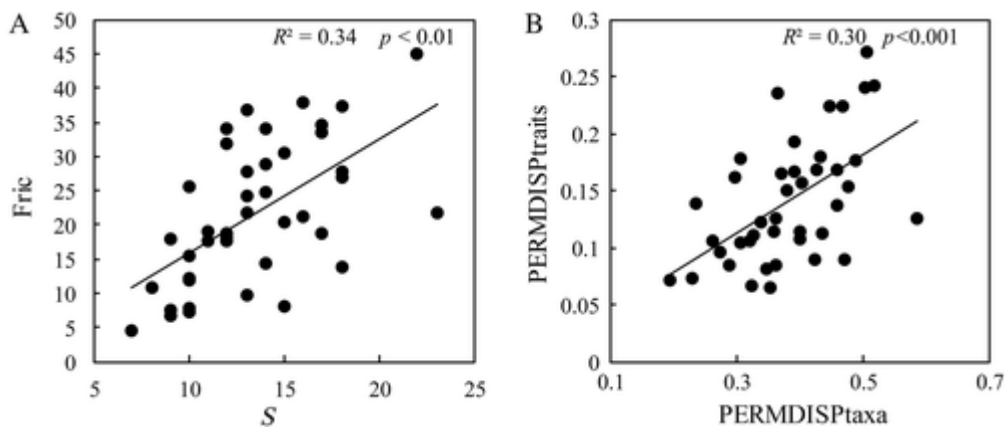
Figure 2

Linear regression of the relationship between taxonomic diversity and functional diversity at local scale: (**A**) taxonomic richness vs. functional richness, and (**B**) taxonomic beta diversity vs. functional beta diversity. *b* stands for the standardized regression coefficient. *S* and Fric stand for taxonomic richness and functional richness, respectively, and PERMDISPtaxa and PERMDISPtraits stand for taxonomic beta diversity and functional beta diversity, respectively.

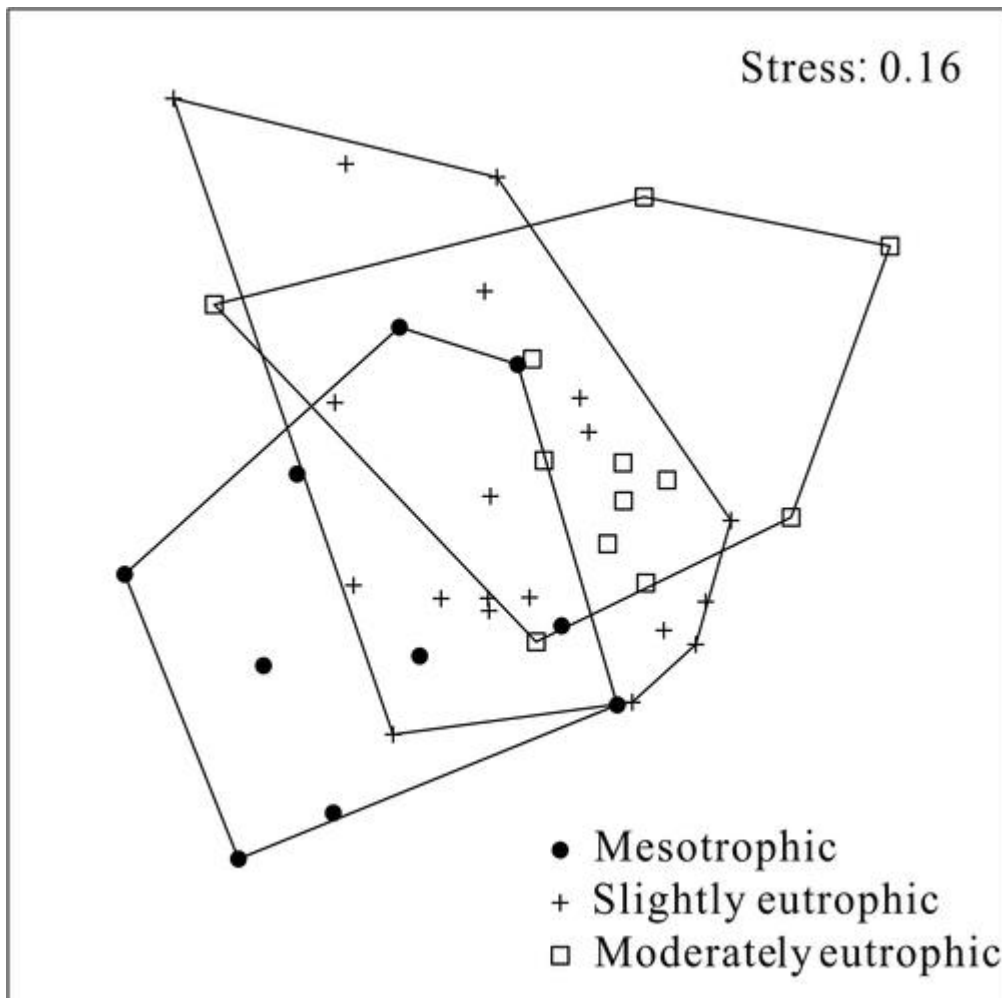**Figure 3**

Nonmetric multidimensional scaling of macroinvertebrate assemblages based on Bray-Curtis similarity coefficients, showing the differences in assemblage structure among the three lake trophic groups.
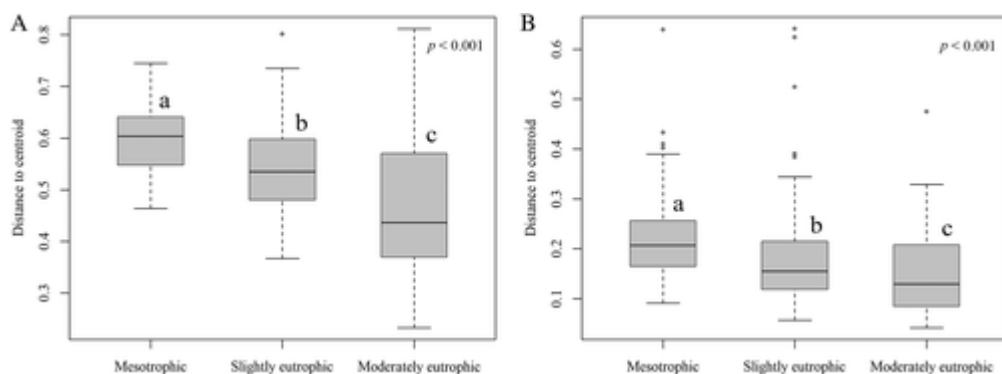
Figure 4

Boxplots based on tests of homogeneity of dispersion analysis representing mean distances from group centroids for community data at regional (among-lake) scales: (**A**) taxonomic composition and (**B**) functional composition. Boxplots' horizontal lines denote median values, boxes represent interquartile ranges (25–75% percentiles), range bars show maximum and minimum extreme values, and hollow circles represent outliers. Each group differing in the pairwise comparison was given by a different letter (a, b, or c).
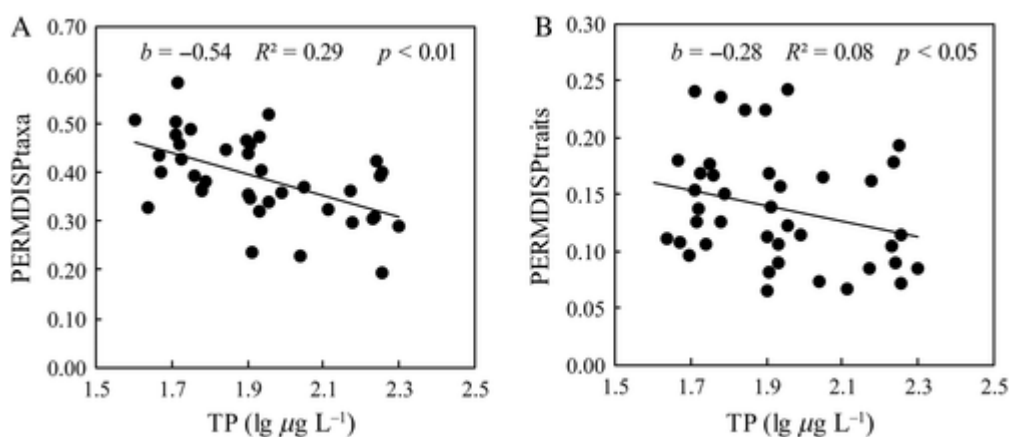

Figure 5

Linear regression relationships between taxonomic and functional beta diversity and the TP concentration at local (within-lake) scale: (**A**) taxonomic beta diversity and (**B**) functional beta diversity.

Table 1 PERMANOVA and pairwise comparison showing significance levels in both taxonomic and functional community of macroinvertebrate assemblages among the three lake trophic groups. Upper triangular matrix shows the Bray-Curtis dissimilarity of taxonomic composition, and lower triangular matrix shows that of functional composition; **$P < 0.01$.

	Mesotrophic	Slightly eutrophic	Moderately eutrophic
Mesotrophic		81.06%**	82.42%**
Slightly eutrophic	30.08%**		74.33%**
Moderately eutrophic	30.90%**	24.86%**	

Table 2 Characteristic species for lakes under different trophic status identified by SIMPER procedure, their contributions (contr., %) to among-group dissimilarity and within-group similarity (both up to a cumulative percentage of 80%), and average abundance (abun., ind./m^2) under each trophic status were calculated.

Species	Contr.	Mesotrophic		Slightly eutrophic		Moderately eutrophic	
		Abun.	Contr.	Abun.	Contr.	Abun.	Contr.
Limnodrilus hoffmeisteri	18.30	35.66	6.77	91.83	18.04	753.69	32.70
Microchironomus tabarui	12.17	39.92	8.67	114.38	6.73	124.98	13.56
Propsilocerus akamusi	10.90						
Tanypus chinensis	6.54					89.52	6.44
Bellamya aeruginosa	6.16	44.32	25.91	48.99	13.71		
Branchiura sowerbyi	6.13	19.03	16.33	39.46	23.03	78.40	21.57
Chironomus fslaviplumus	6.05	16.08	4.95	46.51	9.83		
Corbicula fluminea	5.01	11.09	6.38	58.68	6.62		
Nephtys oligobranchia	4.62	13.73	8.35				
Procladius choreus	3.26			15.56	3.66	45.38	7.12
Rhyacodrilus sinicus	3.18						
Cryptochironomus sp.	1.10	8.36	3.43				
Total	**83.42**	**188.19**	**80.79**	**415.41**	**81.62**	**1091.97**	**81.39**