

# Composition, diversity, and environmental correlates of benthic macroinvertebrate communities in the five largest freshwater lakes of China

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**Abstract** China's five largest freshwater lakes (Poyang, Dongting, Taihu, Hongze, and Chaohu) are all located in lowland regions and differ greatly in lake morphology, hydrology, and water chemistry. However, basic knowledge of diversity patterns and factors driving macroinvertebrate community structure is lacking. We analyzed the composition and diversity of benthic macroinvertebrates and evaluated the roles of environmental factors and dispersal processes in determining beta diversity at both the lake and regional scales. The two Yangtze-connected lakes (i.e., Lakes Poyang and Dongting) were highest in taxonomic diversity. Differences in taxonomic composition were evident among the five lakes, with the

two Yangtze-connected lakes dominated by bivalves and/or gastropods, while Lake Taihu showed great changes in taxonomic composition among sites in accordance with its high habitat heterogeneity. Lake Hongze was dominated by polychaetes, crustaceans, and bivalves. The eutrophic–hypertrophic Lake Chaohu was exclusively dominated by chironomids and oligochaetes. At the lake scale, total  $\gamma$ -diversity was mainly attributed to  $\beta_1$ -diversity (among sites) ranging from 57.9 to 87.6%. The total  $\gamma$ -diversity at the regional scale was primarily related to higher  $\beta$ -diversity, with  $\beta_1$  and  $\beta_2$  (among lakes) accounting for 30.4 and 58.8% of total taxa richness, respectively. Environmental conditions appear to be important in structuring benthic macroinvertebrate communities at both the lake and regional scale. Dispersal does not appear to affect distribution of macroinvertebrates at the lake scale.

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## Introduction

Biological diversity is not homogeneously distributed on the Earth's surface (Abell et al., 2008; Boyero et al., 2012). One of the central topics in ecological research and conservation is the analysis of species diversity

patterns and composition (Crist et al., 2003). Biological diversity patterns in freshwater ecosystems may be regulated by different driving factors at different scales (Stendera et al., 2012; Heino et al., 2014). Assessing patterns of diversity over space and the factors that generate those patterns is crucial in understanding assembly rules underlying community structure and making informed management and conservation decisions.

Biological diversity in a region, termed  $\gamma$ -diversity, can be partitioned into two components (Crist et al., 2003). The first component is  $\alpha$ -diversity, which includes the diversity of species within a specific location. Alpha diversity can be measured either as species richness or using diversity indices. Another component,  $\beta$ -diversity, relates to change in the composition along gradients or the rate of species turnover among locations. Although early studies of biological diversity largely focused on comparing patterns of  $\alpha$ - and  $\gamma$ -diversity, over the past decade, there has been an increased focus on how diversity components, especially  $\beta$ -diversity, vary spatially and what factors may generate the patterns detected (Veech et al., 2002; Ligeiro et al., 2010; Francisco-Ramos & Arias-Gonzalez, 2013; Matsuda et al., 2015).

One way of assessing variation in diversity across scales is additive partitioning of diversity. Lande (1996) reviewed the subject and applied the additive approach to partition total species richness across multiple spatial scales. It consists of partitioning total species diversity ( $\gamma$ ) into additive components representing within-habitat diversity ( $\alpha$ ) and between-habitat diversity ( $\beta$ ), where diversity can be measured as species richness or using a diversity index. When multiple scales are available, total diversity can be partitioned into  $\alpha$  and multiple  $\beta$  components (Veech et al., 2002). One of the advantages of additive partitioning is that it allows evaluation of the relative importance of each scale on the total diversity in a region. In recent years, this method has been increasingly used to examine large-scale diversity patterns in freshwater ecosystems (Stendera & Johnson, 2005; Ligeiro et al., 2010; Hepp & Melo, 2013; Molozzi et al., 2013).

Species distributions are structured by local environmental conditions, spatial processes (dispersal, colonization-extinction dynamics), and spatial scales (Heino et al., 2014). Species diversity is generated by different factors operating at various scales and is therefore scale-dependent (Whittaker et al., 2001; Mykrä et al., 2007;

Stendera et al., 2012). In general, local environmental conditions, competition, and predation are more important at finer scales, while dispersal and historical factors are more evident at larger scales. For lake ecosystems, organisms are often thought to have greater chances to reach all habitats within a lake, resulting in communities that are not spatially structured. Despite this, recent studies have indicated that dispersal processes can considerably affect the distribution of organisms even at the lake scale (Specziar et al., 2013; Árvá et al., 2014; Vilmi et al., 2016). Hence, more research is needed to better understand the role of dispersal even at small spatial scales.

Benthic invertebrates play important roles in freshwater ecosystems, promoting nutrient cycling, facilitating energy flows of food webs, and altering the geochemical condition of sediments (Covich et al., 1999). Recent studies have pointed out the need to examine regional diversity patterns of freshwater invertebrates since their biodiversity is declining on a global scale (Lydeard et al., 2004; Strayer, 2006). Floodplain lakes are among the Earth's most distinctive landscapes and are characterized by high biodiversity and productivity (Tockner & Stanford, 2002). However, they are also among the most threatened ecosystems worldwide (Ward et al., 2002; Dudgeon et al., 2005), particularly those in lowland regions (Fang et al., 2006; Brauns et al., 2007; Ritterbusch et al., 2014). In the middle and lower reaches of the Yangtze and Huai Rivers, there are approximately 131 freshwater lakes with individual surface area  $>10$  km<sup>2</sup> and a total area about 19,055 km<sup>2</sup>, representing 68.7% of the total freshwater lake area ( $>10$  km<sup>2</sup>) in China (Jiang et al., 2009). The five largest freshwater lakes in China are all located in this region. These lakes are shallow lakes which are susceptible to disturbances by both natural and human activities (Le et al., 2010). Heightened eutrophication and habitat degradation resulting from anthropogenic disturbance has become the most prominent problem confronting these lakes. However, basic knowledge of diversity and environmental determinants of community composition in these lakes are lacking (Fu et al., 2003; Fang et al., 2006; Liu & Wang, 2010). In this regard, an improved understanding of the composition and distribution of biological communities in these lakes will be helpful for the development of management actions for conserving biodiversity.

In this paper, the primary objectives were to (1) characterize the community structure of benthic

macroinvertebrates in the five lakes; (2) determine how diversity of macroinvertebrates varied across three different spatial scales (site, lake, and regional) using the additive components of total diversity; and (3) evaluate the importance of environmental conditions and dispersal processes in structuring benthic communities at the lake and regional scales.

## Methods

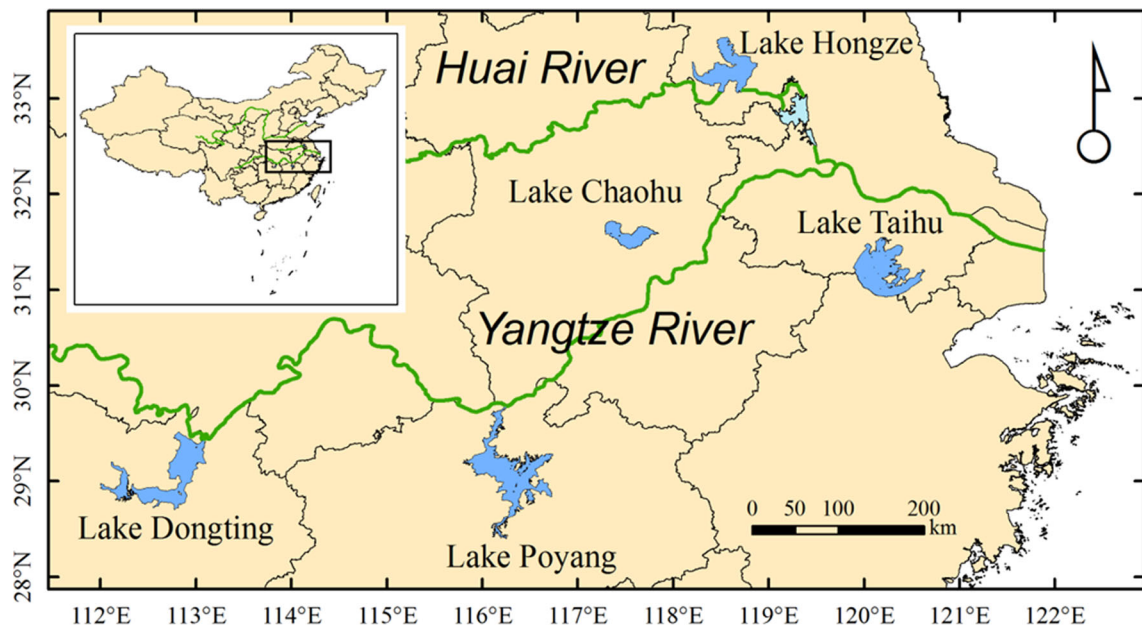
### Study area

The five lakes investigated in this study differ greatly in location, lake morphology, hydrology, and water chemistry (Fig. 1, Table 1). Four of the five lakes are distributed along the Yangtze River, with Lakes Dongting and Poyang being freely connected with the Yangtze mainstream and characterized by highly fluctuating water levels. Lakes Chaohu and Taihu are located in the lower reaches of the Yangtze system, and their outflow rivers to the Yangtze River are regulated by sluice gates. Lake Hongze is located in the lower reaches of the Huai River. The two Yangtze-connected lakes, Lakes Poyang and Dongting, are considered mesotrophic systems and have relatively low Chlorophyll-*a* (Chl-*a*) concentrations due to the

short residence time and relatively low nutrient concentrations of their waters (Yang et al., 2010). In contrast, the other three lakes have been classified as eutrophic or eutrophic-to-hypertrophic, according to their very high concentrations of Chl-*a* (Yang et al., 2010). Cyanobacterial blooms are the most serious environmental problem in Lakes Chaohu and Taihu (Fig. S1C), occurring annually and increasing in spatial extent, duration, and intensity over the past decades (Deng et al., 2007; Duan et al., 2014). Cyanobacterial blooms have also occurred occasionally in Lake Hongze in summer (Lei et al., 2010). Lakes Taihu and Chaohu both exhibit a nutrient load gradient (Fig. S1C, S1E) resulting from input of pollutants from inflow rivers.

### Macroinvertebrate sampling and measurement of environmental parameters

Field investigations were conducted between February 2007 and January 2014. Fifteen to thirty-five sites were selected for each lake taking account of lake morphology, environmental heterogeneity, and input and output rivers (Table 2; Fig. S1). These sampling sites were located in the limnetic zone, with most of the sampling sites being devoid of macrophytes except for sites in the east bays of Lake Taihu, where the substrate



**Fig. 1** Locations the five largest freshwater lakes in China

**Table 1** Lake morphology, hydrology, and water chemistry parameters of the five largest freshwater lakes in China

Parameters	Units	Poyang	Dongting	Taihu	Hongze	Chaohu
Surface area	km <sup>2</sup>	2933	2625	2425	1597	769.5
Lake storage <sup>a</sup>	10 <sup>8</sup> m <sup>3</sup>	149.6	167	51.4	30.4	20.7
Residence time	day	21	20	309	35	168
Water level change <sup>b</sup>	m	>9.7	>8.0	<2.5	<1.5	<5.0
Mean water depth <sup>a</sup>	m	5.1	6.4	2.1	1.9	2.7
Connectivity		Connected	Connected	Isolated	Isolated	Isolated
<b>pH<sup>c</sup></b>		8.28 (8.04–8.56)	8.80 (8.23–9.82)	8.38 (7.82–9.68)	8.84 (7.40–9.85)	8.85 (8.28–9.18)
<b>Conductivity<sup>c</sup></b>	μS cm <sup>-1</sup>	134 (95–199)	294 (205–370)	529 (427–693)	525 (462–618)	249 (183–321)
<b>Total dissolved solids<sup>c</sup></b>	g l <sup>-1</sup>	0.10 (0.06–0.29)	0.19 (0.13–0.24)	0.38 (0.29–0.51)	0.40 (0.36–0.48)	0.20 (0.18–0.28)
<b>Turbidity<sup>c</sup></b>	NTU	101 (33–173)	52 (4.1–220)	32 (0.6–117)	77 (45–155)	55 (25–220)
<b>Total nitrogen<sup>c</sup></b>	mg l <sup>-1</sup>	1.62 (1.22–2.26)	1.88 (0.92–2.86)	3.16 (1.20–7.60)	2.16 (1.59–2.93)	2.60 (1.17–8.81)
<b>Total phosphorus<sup>c</sup></b>	mg l <sup>-1</sup>	0.11 (0.06–0.21)	0.08 (0.03–0.30)	0.12 (0.04–0.32)	0.13 (0.11–0.16)	0.21 (0.07–0.75)
<b>Chlorophyll-a<sup>c</sup></b>	mg l <sup>-1</sup>	6.51 (3.28–14.66)	4.23 (1.16–13.39)	21.98 (3.74–60.23)	17.86 (9.94–27.88)	19.97 (4.87–41.96)
Trophic state <sup>d</sup>		Mesotrophic	Mesotrophic	Eutrophic-hypertrophic	Eutrophic	Eutrophic-hypertrophic

<sup>a</sup> Data cited from Gao & Jiang (2012)

<sup>b</sup> Difference of water levels between summer rainy season and winter dry season

<sup>c</sup> Values are mean (range) across all sampling occasions. Water chemistry parameters of Lake Taihu were provided by Taihu Laboratory for Lake Ecosystem Research (TLER)

<sup>d</sup> Trophic state was assessed using mean Chl-*a* by fixed boundary classification system for lake trophic state accepted by OECD (1982)

Bold font indicates significant differences among lakes in Kruskal–Wallis tests ( $P < 0.01$ )

**Table 2** Details about macroinvertebrates sampling of the five largest lakes in this study

	Poyang	Dongting	Taihu	Hongze	Chaohu
Number of sites	15	35	30	10	34
Sampling occasions	Jan. 2012	Aug. 2012	Feb. 2007/2008	Monthly	Apr. 2013
	Apr. 2012	Jan. 2013	May 2007/2008	Jan.–Dec. 2013	July 2013
	July 2012	July. 2013	Aug. 2007/2008		Oct. 2013
	Oct. 2012		Nov. 2007/2008		Jan. 2014
Sampling area	0.05 m <sup>2</sup> × 2	0.05 m <sup>2</sup> × 2	0.025 m <sup>2</sup> × 2	0.05 m <sup>2</sup> × 3	0.05 m <sup>2</sup> × 3
Number of samples	60	60 <sup>a</sup>	240	120	135 <sup>b</sup>

<sup>a</sup> Not all 35 sites were sampled three times because in some instances sites were dry

<sup>b</sup> One sample in April 2013 was lost

was covered by abundant macrophytes (Zhang et al., 2016; Fig S1C). Benthic macroinvertebrates were surveyed 3–12 times, and 60–240 samples were taken

for each lake (Table 2). Benthic samples were collected with a 0.025 or 0.05 m<sup>2</sup> modified Peterson grab, with two or three grabs comprising a sample at each site and

were pre-sieved in situ through a 250- $\mu\text{m}$  sieve. The materials retained on 250  $\mu\text{m}$  sieve were stored in a cooler box and transported to laboratory on the same day. In the laboratory, the samples were sorted on a white tray, and all specimens were picked out and preserved in 7% buffered formalin solution. Specimens were identified to the lowest feasible taxonomic level under a dissection microscope (Olympus<sup>®</sup> SZX10) or a microscope (Olympus<sup>®</sup> BX53) using regional keys (Liu et al., 1979; Yang & Sun, 1988; Morse et al., 1994; Wang, 2002; Tang, 2006). When necessary (e.g., Oligochaeta, Polychaeta, and Diptera), microscope slides were prepared on Euparal.

The environmental parameters, including pH, conductivity, total dissolved solids (TDS), and turbidity were measured in situ using a Hydrolab<sup>®</sup> DataSonde 5 sensor on all sampling dates. At each site, a vertically integrated water sample was collected and placed in acid-cleaned plastic containers which were kept cool and shaded before transportation to the laboratory. Total nitrogen (TN) and total phosphorus (TP) were measured using a combined persulfate digestion (Ebina et al., 1983), followed by spectrophotometric analyses (SHIMAD<sup>®</sup> UV-2550). Chl-*a* concentration was determined spectrophotometrically (SHIMAD<sup>®</sup> UV-2550) after extraction in 90% hot ethanol (Párista et al., 2002). Percentage cover of aquatic macrophytes was estimated visually and scored on an ordinal scale of 0–4 according to the total cover at each sampling site (0: 0%; 1: 1–25%; 2: 26–50%; 3: 51–75%; and 4: 76–100%).

#### Data analysis

In this study, we focus on spatial patterns of benthic macroinvertebrates within and among lakes. Hence, the environmental and biological data across different sampling occasions were averaged for each lake. The pooled data were used in all statistical analyses with the exception of estimation of taxa richness. Differences in environmental parameters among lakes were assessed by Kruskal–Wallis tests.

As variability in number of sites and samples were high among the five lakes, we standardized taxa richness thus allowing comparisons at the same sampling effort (Gotelli & Colwell, 2011). Species accumulation curves for each lake were generated to assess the adequacy of sampling effort by randomly subsampling the entire community 1000 times, therefore determining the number of species as a function of

sample size (Colwell, 2013). Given that only Lake Taihu approached the asymptote and the large differences in the number of individuals among lakes, we used Fisher's alpha diversity to compare diversity among lakes (Kheifits & Kheifitsy, 2013). In addition, we also estimated the total taxa richness for each lake using the first-order jackknife estimator. The jackknife is a general statistical technique for reducing the bias of an estimator by removing subsets of the data and recalculating the estimator with the reduced sample (Gotelli & Colwell, 2011).

To visualize taxonomic composition patterns in assemblages across lakes, we performed nonmetric multidimensional scaling (NMDS) based on a Bray–Curtis similarity matrix obtained from  $\log(x + 1)$  transformed abundance data. Analysis of similarities (ANOSIM) based on the same similarity matrix was employed to test differences of benthic assemblages among lakes, followed by pairwise comparisons using a Holm–Bonferroni sequential correction (Holm, 1979). ANOSIM is a nonparametric multivariate test of significant difference between two or more groups, and the difference between the within-group and between-group rank similarities is expressed as the global R value, with a score of 1 indicating complete separation and 0 indicating no separation (Clarke, 1993).

Additive partitioning was applied to taxa richness involving three hierarchical spatial scales: site, lake, and the whole region (Fig. S2). At the lowest spatial scale, the between-site diversity ( $\beta_1$ ) is determined by subtracting the within-site diversity ( $\alpha_1$ ) from the  $\alpha$  diversity at the next highest scale (i.e., the within-lake diversity,  $\alpha_2$ ). Similarly, the between-lake diversity ( $\beta_2$ ) is determined by subtracting the within-lake diversity ( $\alpha_2$ ) from the  $\alpha$  diversity at the highest spatial scale (i.e., the total diversity,  $\gamma$ ). In this study, the total taxa richness was partitioned at the lake scale ( $\gamma = \alpha_1 + \beta_1$ ) and the regional scale ( $\gamma = \alpha_1 + \beta_1 + \beta_2$ ). The magnitudes of observed alpha and beta components are dependent on the number and size of sampling units. Accordingly, a proper assessment of the importance of each fraction can be done using a null model (Crist et al., 2003). We used individual-based randomization to assess the significance of diversity components. We randomized the data according to the null model 9999 times, to generate a distribution of expected values. The observed diversity component value at a given spatial level was then compared to the respective random distribution, to determine if it was greater or less than expected value.

We evaluate the effects of dispersal and environmental conditions in structuring beta diversity using a distance-based approach. We assessed the relationships through a Standard Mantel correlation between community similarity and either environmental distance (reflecting environmental conditions) or geographical distance (as a proxy for dispersal). Considering the relationship between environmental and geographical distance is often statistically significant, partial Mantel tests were run to assess the influence of geographical distance on community similarity while controlling the effect of environmental distance and vice versa. Mantel correlations were analyzed for individual lake sites and for entire lakes. For each analysis, the three different matrices were constructed as follows: (1) the community similarity matrix between pairs of sites or lakes based on Sorensen coefficient (presence–absence data) and Bray–Curtis coefficient (abundance data that were previously log-transformed); (2) the matrix of geographical distances between sites of each individual lake was derived from their corresponding longitudinal and latitudinal coordinates, while geographical distances between lakes were generated from watercourse distances. Watercourse distances between lakes were used because they provided better representations of the spatial patterns generated by dispersal (Landeiro et al., 2011); (3) the environmental explanatory matrix based on Euclidean distance. All measured environmental parameters (z-score standardization) were included in the analysis. When considering the entire lakes, biological and environmental data were pooled within a lake. The significance of the Mantel test was based on a Monte Carlo procedure with 9999 permutations.

Species accumulation curves and the jackknife estimator were produced with EstimateS 9.1 (<http://viceroy.eeb.uconn.edu/EstimateS/index.html>). Fisher's alpha diversity, NMDS, and ANOSIM analyses were conducted using PAST 3.05 (Hammer et al., 2001). Additive diversity partitioning and Mantel tests were performed using the *vegan* package in R version 3.2.3 (R Development Core Team, 2015).

## Results

### Environmental characterization

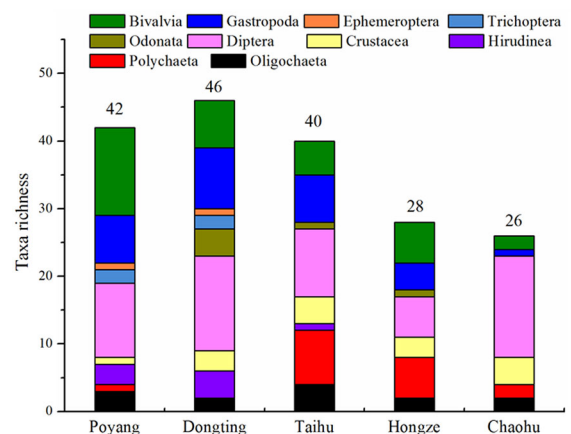
Kruskal–Wallis tests indicated that all seven measured environmental parameters differed significantly among

the five lakes ( $P < 0.001$ , Table 1). Conductivity and total dissolved solids in the two lower river lakes (i.e., Taihu and Hongze) were significantly higher than those in the two upper Yangtze-connected lakes, with Lake Poyang presented the lowest values. Lakes Taihu and Chaohu registered the most eutrophic state with high concentrations of nutrients and Chl-*a*. Lakes Poyang and Dongting were mesotrophic according to their lower concentrations of Chl-*a*.

Environmental conditions also varied greatly among sites at the lake scale, as seen by the large range in values between sites (Table 1). For example, within-lake variability in TP ranged from 1.5-fold to tenfold for the five lakes. Conductivity, total dissolved solids, turbidity, total nitrogen, and Chl-*a* also showed great within-lake variation. These results highlight the strong spatial heterogeneity in environmental conditions of these lakes.

### Taxa richness and community composition

A total of 89 taxa were recorded from the studied lakes, including 18 Bivalvia, 12 Gastropoda, 7 Oligochaeta, 5 Polychaeta, 7 Hirudinea, 4 Crustacea, 29 Diptera (26 were Chironomidae), 4 Odonata, 2 Trichoptera, and 1 Ephemeroptera (Table S1). Of the 89 taxa, six taxa (6.7%) were found in all lakes and 40 taxa (44.9%) were confined to specific lakes. The two Yangtze-connected lakes were more abundant in the richness of Gastropoda, Bivalvia, and Hirudinea, while the other isolated lakes had more species of Polychaeta (Fig. 2). The species accumulation curve

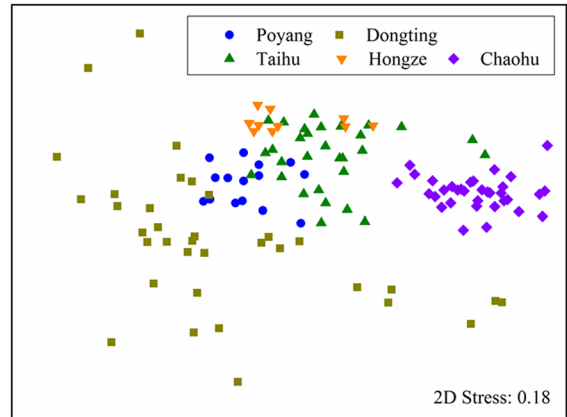


**Fig. 2** Taxa richness and composition of macroinvertebrate in the five largest freshwater lakes in China

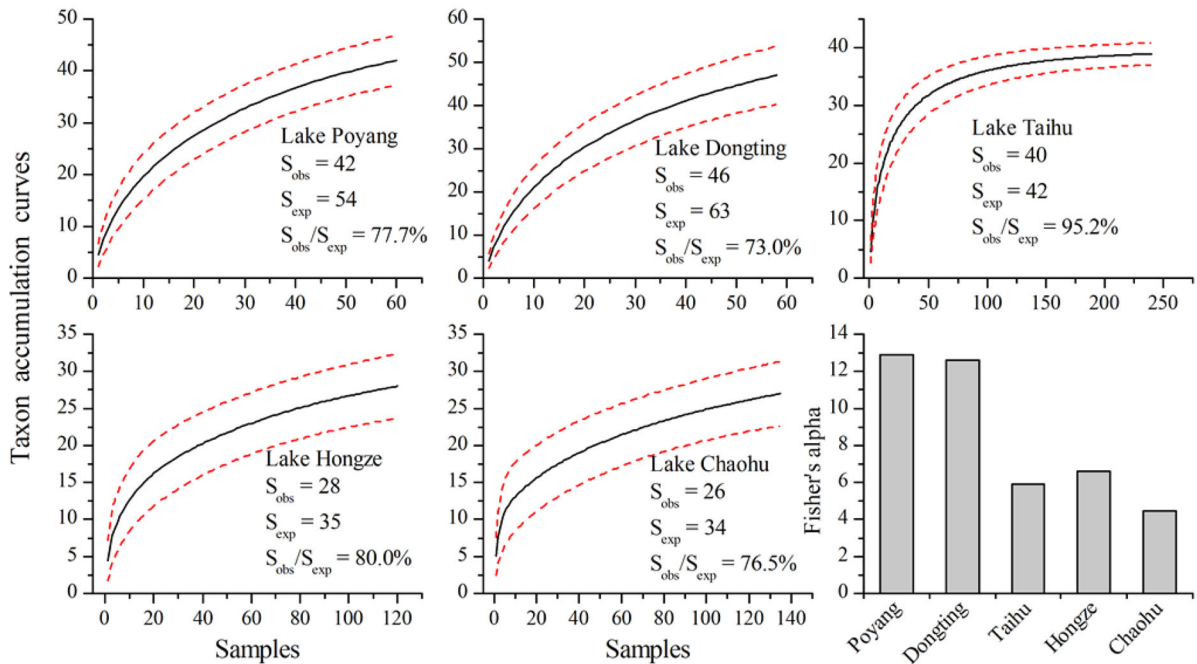
for Lake Taihu approached the asymptote, showing that our richness estimate derived from samples was an accurate representative of the total taxa richness in the lake. In contrast, the accumulation curves for the other four lakes did not reach asymptotes, indicating that our sampling was unlikely to have covered their full taxonomic diversity (Fig. 3). First-order jackknife estimates showed that the observed richness represented 95% of the estimated total richness in Lake Taihu, while lower than 80% in the other four lakes. Fisher’s alpha diversity values in Lakes Poyang and Dongting were almost two-fold that of the other lakes. The Jackknife taxa richness was also highest in Lakes Poyang and Dongting, followed by Lake Taihu, and lowest in Lakes Hongze and Chaohu.

Differences in taxonomic composition were evident among the five lakes (Fig. 4). Pairwise comparisons in one-way ANOSIM analyses indicated that the benthic community differed significantly between lakes for all pairwise comparisons ( $R$ : 0.35–0.98,  $P < 0.001$ ), with the exception of Lakes Poyang and Dongting ( $R = 0.07$ ,  $P = 0.13$ ). The taxonomic composition of total macroinvertebrate abundance differed

among the five lakes. Most sites in Lake Poyang were dominated by bivalves [mainly *Corbicula fluminea* (O. F. Müller, 1774)], a crustacean (Gammaridae sp.), and the polychaeta *Nephtys* sp. (Fig. S3A). Bivalves accounted for 24.27–86.75% of the total abundance and were highly abundant in the northern part of the



**Fig. 4** Nonmetric multidimensional scaling analysis (NMDS) of macroinvertebrate assemblage in the five lakes. Ordination of the 124 sites according to species composition based on Bray–Curtis similarity matrix

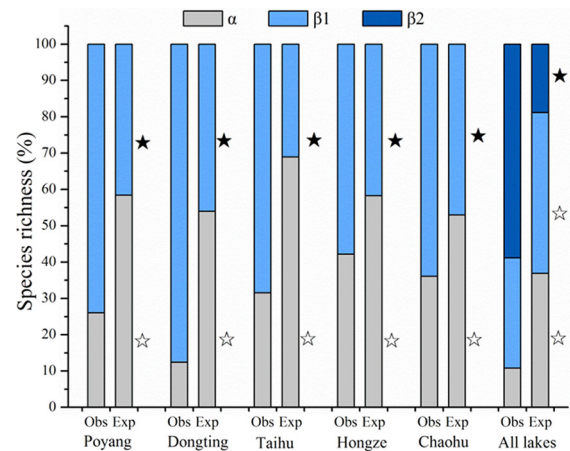


**Fig. 3** Species accumulation curves and Fisher’s alpha diversity for the five studied lakes. Dashed lines represent the 95% confidence intervals.  $S_{obs}$  indicates that observed and  $S_{exp}$  estimated taxa richness based on first-order jackknife estimator, respectively

lake. Gammaridae sp. and *Nephtys* sp. represented 0–31.58% and 0–36.41% of the total abundance, respectively. In Lake Dongting, gastropods and bivalves (mainly *C. fluminea*) were the dominant taxa at most sampling sites (Fig. S3B). Gastropods constituted 0–100% of the total abundance with an average value of 44.76%. The relative abundance of bivalves ranged from 0 to 100% with an average value of 20.57%. Oligochaetes and crustaceans dominated the total abundance only at three sites (S13, S23, and S41). Benthic assemblages in Lake Taihu showed high spatial heterogeneity in abundance and taxonomic composition, with total abundance ranging from 200 to 35,340 ind m<sup>-2</sup> (Fig. S3C). Particularly, high abundance was recorded at sites in Meiliang Bay, Zhushan Bay and site 10# (2785–35,340 ind m<sup>-2</sup>), always dominated by pollution-tolerant oligochaetes (62.32–98.76%). Relatively low abundance was found in other areas (<2135 ind m<sup>-2</sup>), with bivalves (5.07–68.98%) and polychaetes (2.44–75.95%) dominating the communities in Gonghu Bay, Central Region, and Western Region, while gastropods were the dominant taxa in East Bays (23.91–76.67%). In Lake Hongze, the most abundant taxa were polychaetes, crustaceans, and bivalves, accounting for 27.93–91.65%, 1.04–28.08%, and 2.95–56.59% of the total macroinvertebrates abundance, respectively (Fig. S3D). Oligochaetes only showed high relative abundance at two sites (S2 and S3). For Lake Chaohu, benthic fauna were exclusively dominated by chironomids and oligochaetes, which represented 6.47–98.83% and 1.17–93.53% of total macroinvertebrates abundance (Fig. S3E), respectively.

### Additive diversity partitioning

Partitioning of the  $\alpha$ - and  $\beta$ -diversity components showed similar patterns across the five lakes (Fig. 5). In general, the  $\beta$ -diversity component (expressed as percentage of the total diversity) was much higher than the  $\alpha$ -diversity component. The diversity percentage explained by  $\beta_1$  (among sites) diversity ranged from 57.9% in Lake Hongze to 87.6% in Lake Dongting, which were all significantly higher than expected from random ( $P < 0.001$ ). Conversely, the  $\alpha$  component accounted for a small fraction of the total diversity, 12.4–42.1%, and were all significantly lower than expected from random ( $P < 0.001$ ). The total  $\gamma$ -



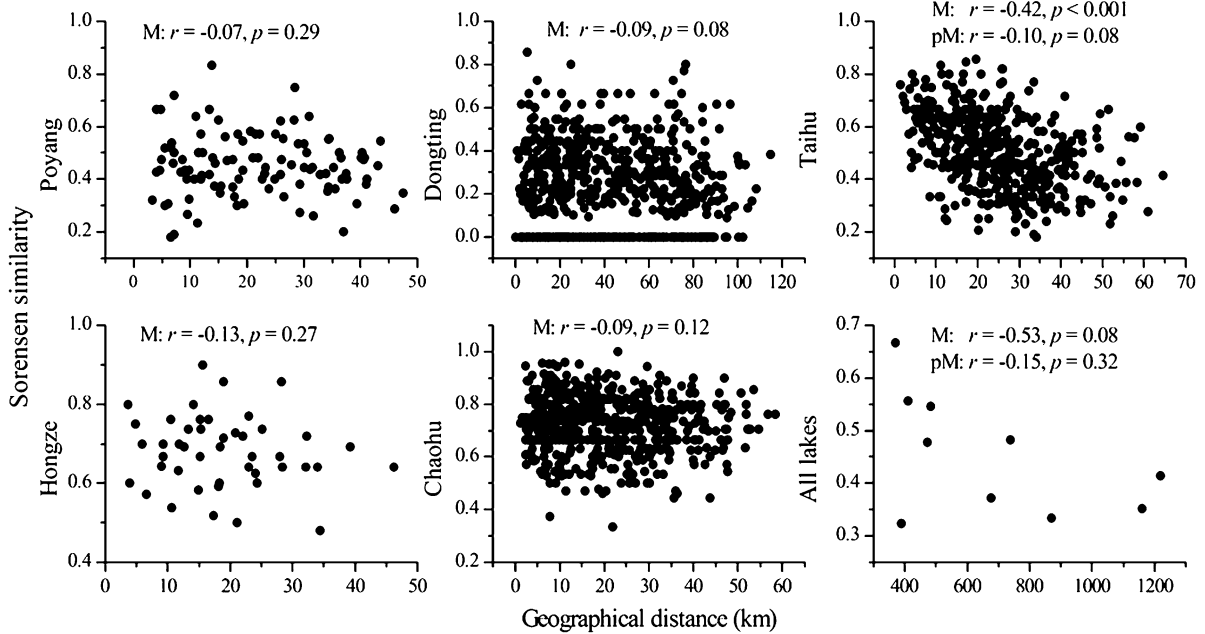
**Fig. 5** Additive partitioning of macroinvertebrate diversity at the lake and the regional scales. Contributions of average  $\alpha$ -diversity and two  $\beta$ -diversity components:  $\beta_1$  among sites and  $\beta_2$  among lakes. The observed partitions (Obs) are compared with the expected values (Exp) as predicted by the null model based on 9999 randomizations. Open star symbols Obs < Exp,  $P < 0.0001$ . Filled star symbols Obs > Exp,  $P < 0.0001$

diversity at the whole region was mainly attributed to  $\beta$ -diversity, with  $\beta_1$  and  $\beta_2$  accounted for 30.4 and 58.8% of total taxa richness, respectively. The  $\alpha$ -diversity explained a very small proportion (10.8%) of the total  $\gamma$ -diversity. The observed  $\alpha$  and  $\beta_1$  diversities were significantly lower than expected ( $P < 0.001$ ), while  $\beta_2$  component was much greater than expected from random prediction ( $P < 0.001$ ).

### Effects of dispersal limitation and environmental conditions

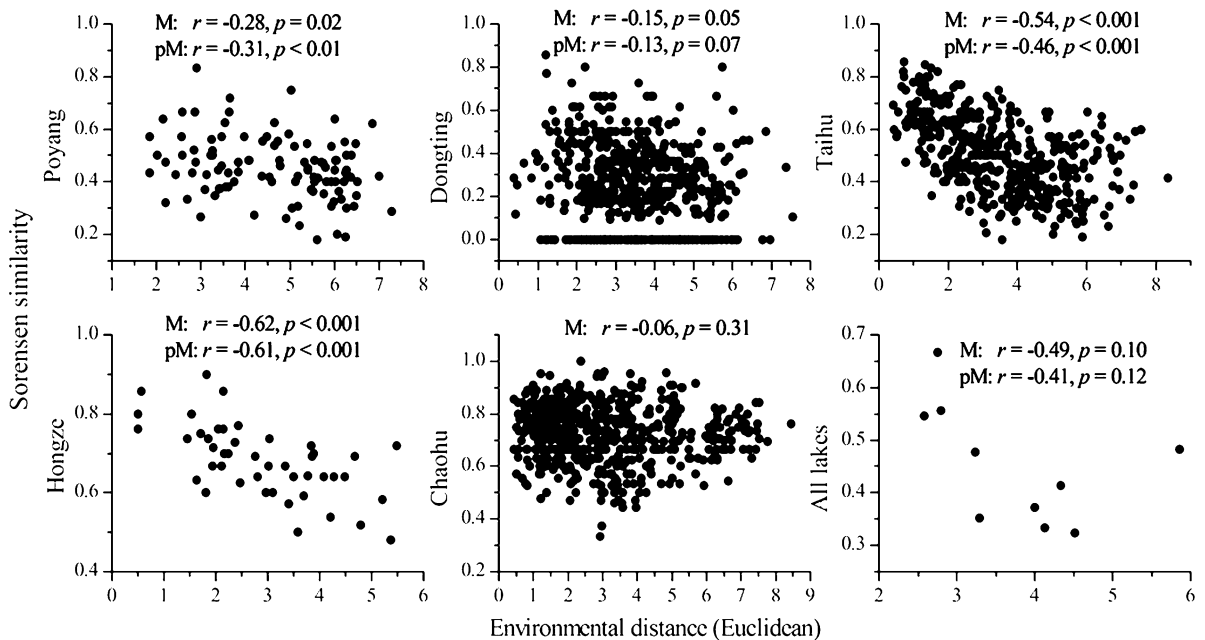
For individual lakes, community similarity decreased significantly with geographical distance only in Lake Taihu (Fig. 6,  $r = -0.42$ ,  $P < 0.001$ ). However, if the role of environmental distances was removed, the effect of geographical distance in Lake Taihu was not significant ( $r = -0.42$ ,  $P = 0.08$ ). By contrast, Sorensen similarity for three lakes was highly correlated with environmental distance when geographical distance was controlled (Fig. 7). The effect of environmental distance was significant for all five lakes when Bray–Curtis similarity was used (Fig. S4). At the regional scale, no significant correlation was detected between community similarity and geographical distance or environmental distance in spite of relatively high correlation coefficient.





**Fig. 6** Standard (M) and partial Mantel correlations (pM) between community similarity (Sorensen) and geographical distance. The significance of the Mantel test was based on a

Monte Carlo procedure with 9999 permutations. For individual lakes, partial Mantel tests were employed only when significant correlations were detected in Standard Mantel tests



**Fig. 7** Standard (M) and partial Mantel correlations (pM) between community similarity (Bray–Curtis) and environmental distance (Euclidean). The significance of the Mantel test was

based on a Monte Carlo procedure with 9999 permutations. For individual lakes, partial Mantel tests were employed only when significant correlations were detected in Standard Mantel tests

## Discussion

### Taxa richness and composition

Species accumulation curves indicated that taxa richness was underestimated in the two Yangtze-connected lakes (Lakes Poyang and Dongting). This result may be partially attributed to the fact that the sampling sites in these two lakes were restricted to the main river courses, and therefore a large proportion of the extensive body of seasonal flooded wetland was left uninvestigated. Several studies have shown that the invertebrate diversity on floodplain wetland can be orders of magnitude higher than in the associated channel (Shiel et al., 1998; Reese & Batzer, 2007). The macroinvertebrate communities of Lakes Poyang and Dongting are highly diverse. A previous study indicated that more than 150 taxa have been recorded in Lake Poyang by combining historical data from 1962 to 2012 (Cai et al., 2014). A compiled data from 1950 to 2010 showed that 46 species of gastropods and 62 species of bivalves have been recorded in Lake Poyang representing 21 and 72% of the total gastropods and bivalves, respectively, in the Yangtze Basin; 21 of the gastropod species and 46 of the bivalve species are endemic to China and a large proportion only occur in Yangtze-connected lakes (Lakes Poyang and Dongting, Zhang et al., 2013). Further studies of the benthic fauna and other aquatic biota should focus on seasonal flooded wetland of these two lakes.

Taxa richness in Lakes Poyang and Dongting, despite of the likely underestimation, was higher than that in the other three lakes. Difference in trophic state between lakes may be one factor explaining the variation in taxa richness. Conditions for Lakes Poyang and Dongting remain mesotrophic, while the other three lakes have become eutrophic or eutrophic–hypertrophic. Water and sediment chemistry variables relating to trophic state have often been cited as important factors depressing diversity of benthic fauna (Donohue et al., 2009a). Previous studies indicate that long-term eutrophication has substantially decreased  $\alpha$  diversity of macrozoobenthos in Lake Taihu and Chaohu (Cai et al., 2012a, b, c). High concentrations of nutrients and associated algal blooms and hypoxia at the lake bottom will reduce survivorship of some sensitive benthic species (Rosset et al., 2014). Indeed, species of Trichoptera and Ephemeroptera (sensitive

groups) were only detected in the two mesotrophic lakes (Lakes Poyang and Dongting). On the other hand, the distinctive hydrologic conditions of the two Yangtze-connected lakes may play a very important role in maintaining diversity. Water velocity varies greatly in space inducing high heterogeneity in substrate composition that can support diverse taxonomic groups (Cai et al., 2014). In addition, a large area (e.g., over 2,700 km<sup>2</sup> in Lake Poyang) was seasonally flooded, which may help increasing habitat diversity (Dai et al., 2016). The positive effects of hydrological conditions on invertebrate diversity have been documented in several studies (Davidson et al., 2012; Nielsen et al., 2012).

### Determinants of diversity and composition at the lake scale

In this study, a single site represented on average 12.4–42.1% of the total macroinvertebrate richness of the five lakes. This figure is slightly higher than the  $\alpha$ -diversity values reported in another study on diversity partitioning of freshwater lakes macroinvertebrates (6–16% in Stendera & Johnson, 2005). This comparison is, however, complicated by the fact that samples collection in this study was seasonally restricted to autumn (Stendera & Johnson, 2005). In contrast, the sampling sites in our study lakes were surveyed 3–12 times, which means that more species could be detected in a single site. Indeed, Crist & Veech (2006) found that varying survey efforts could modify the component of  $\alpha$ -diversity. In a 3-year study, Suurkuukka et al. (2012) also observed a relatively higher contribution of  $\alpha$ -diversity to total macroinvertebrate diversity (23%). The partitioning of total taxa richness indicated  $\alpha$ -diversity at the lake scale was lower than expected by chance, indicating that species are spatially distributed in an aggregated way. This finding agrees with most previous studies analyzing the partition diversity of macroinvertebrates in lakes (Flach et al., 2012; Suurkuukka et al., 2012), streams (Ligeiro et al., 2010; Hepp & Melo, 2013; Massoli & Callil, 2014), rivers (Gray & Harding, 2009; Głowacki et al., 2011), and reservoirs (Molozzi et al., 2013).

Within lakes,  $\beta_1$ -diversity was the major component of total diversity and significantly higher than expected by chance. The high contribution of  $\beta_1$  could result from well-known aggregative distribution of

freshwater macroinvertebrates (Stoffels et al., 2003). On the other hand,  $\beta_1$ -diversity of Lakes Poyang (74.0%), Dongting (87.6%), and Taihu (68.5%) were relatively higher than that of Lakes Hongze (57.9) and Chaohu (63.9%). The lower  $\beta_1$  diversities in Lakes Hongze and Chaohu may be attributed to their relatively small changes in nutrient conditions among sites. All sampling sites in these two lakes were in a eutrophic or hypertrophic state, something that should increase the homogenization of littoral benthic assemblages in Ireland lakes (Donohue et al., 2009b). This relationship might be caused by nutrient-promoted homogenization of habitat structure, mainly through the loss of macrophytes due to increased eutrophication and degraded light climate (Zhang et al., 2016). The sampling sites in Lakes Hongze and Chaohu were almost devoid of macrophytes (Cai et al., 2012c). In contrast, Lake Taihu presents a longer trophic gradient from mesotrophic to hypertrophic and is covered by a large area of macrophytes in the East Bays characterized by high habitat heterogeneity and stability (Zhang et al., 2016). For the two Yangtze-connected lakes, distinctive hydrological conditions and seasonal flooding also help increase habitat diversity (Gao & Jiang, 2012; Cai et al., 2014).

Environmental conditions appeared to be more important in shaping beta diversity within lakes, illustrated by significant correlations between community similarity and environmental distance after removing the effects of geographical distance. High correlation coefficients in Mantel tests were observed in Lakes Poyang, Taihu, and Hongze, indicating our measured environmental parameters are major drivers of beta diversity in these lakes. A previous study also indicated that spatial patterns of macroinvertebrate community composition in Lake Taihu were highly correlated to nutrient concentrations, total suspended solids, and macrophyte coverage (Cai et al., 2012a). Meanwhile, the diversity of macroinvertebrates in Lake Poyang is known to be strongly affected by changes in substrate composition associated with water velocity (Cai et al., 2014). In Lakes Dongting and Chaohu, relatively low values for the Mantel correlation coefficients may be due to some potentially important environmental variables not accounted for in our study (e.g., nutrient and grain size of sediments and dissolved oxygen at bottom layer). Dispersal processes seemed not to be important within lakes. The lack of significant distance–decay relationship

therefore suggests high connectivity among sampling sites.

#### Determinants of diversity and composition at the regional scale

Contrary to our a priori expectation, diversity patterns in the five lakes across three scales were not random. We found high correlation coefficients between community composition and geographical distance and environmental distance. However, the correlation coefficient between community similarity and geographical distance declined greatly when the effect of environmental distance was controlled for, but the correlation coefficient between community similarity and environmental distance showed little change regardless of whether geographical distance was removed or not. This result suggests strongly that environmental conditions can be more important than dispersal processes in shaping beta diversity among these large shallow Chinese lakes. A result that is likely driven by great differences in environmental conditions among the five lakes (e.g., hydrology, trophic state, and salinity). The two Yangtze-connected lakes (Poyang and Dongting), characterized by lower salinity and nutrient concentrations, were more abundant in species of bivalves and gastropods. The high richness of bivalves is likely related to the prevalence of sandy bottoms (Karatayev et al., 2003). In contrast, species of polychaetes (estuarine and marine species) mainly survived in downstream Lakes with relatively higher salinity. Five and four species of polychaetes were found in the more saline Lakes Taihu and Hongze, respectively, while less saline lakes Poyang and Dongting had only one and no species of polychaetes.

The high beta component among these lakes may be due not only to differences in environmental conditions, but could also have resulted from the known dispersal that has been observed in other studies for a range of freshwater organisms (Astorga et al., 2012; Wetzel et al., 2012; Hepp & Melo, 2013; Goldenberg Vilar et al., 2014). An interesting result is that no polychaetes were detected in the upstream Lake Dongting despite its salinity being higher than Lake Poyang. An alternative explanation is that watercourse distance from lake to Yangtze estuary may also restrict the distribution of polychaetes. Previous studies conducted at multiple scales observed

high variability in benthic communities related to dispersal processes across broad scales (>100 km, Mykrä et al., 2007). In our study, the watercourse distances between lakes, ranging from 369 to 1220 km, are considerably longer than is comparable to the maximum distances (1100 km) reported in previous studies of dispersal in freshwater macroinvertebrates (Astorga et al., 2012; Hepp & Melo, 2013; Warfe et al., 2013). Hence, we speculate that dispersal is also an important mechanism generating high beta diversity among the five lakes. However, more lakes along the Yangtze River should be investigated to produce a more robust evaluation of the relative importance of dispersal processes and environmental conditions in determining beta diversity among lakes.

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