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ENVIRONMENTAL BIOTECHNOLOGY

The heterogeneity of composition and assembly processes of the microbial community between different nutrient loading lake zones in Taihu Lake

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Abstract To investigate the differences in the microbial community composition and assembly process in two lake zones (Meiliang Bay (MLB) and Xukou Bay (XKB) in Taihu Lake, China) with different nutrient loadings, water samples were collected. Both the 16S ribosomal RNA (rRNA) gene for the bacterial community and the 18S rRNA gene for the microeukaryote community were investigated using the Illumina second-generation sequencing platform (2 × 250 paired-end). The results indicated that both the bacterioplankton and microeukaryote community composition derived from the two lake zones were significantly different. Significantly higher operational taxonomic unit (OTU) richness ($P < 0.01$) and phylogenetic diversity ($P < 0.05$) were found for the bacterioplankton community of MLB. However, a comparable alpha diversity was found between the microeukaryote communities of MLB and XKB ($P > 0.05$). Environmental factors significantly affected the community compositions in XKB for both the bacterioplankton and microeukaryotes. However, they did not significantly influence the microbial community composition in MLB, except for a weak correlation between dissolved organic carbon (DOC) and the microeukaryote community. The microbial communities tended to be more phylogenetically clustered than expected by chance in the two lake zones. Moreover, the results of the phylogenetic structure suggest that deterministic processes played overwhelming roles in driving the assembly of both the bacterioplankton and microeukaryote community in XKB.

Keywords Community composition · Assembly process · Nutrient loading · Bacterioplankton · Microeukaryotes · Taihu Lake

Dayong Zhao and Xinyi Cao contributed equally to this work.

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Introduction

In freshwater ecosystems, microorganisms, including bacterioplankton and microeukaryotes, have received increasing attention as important components of aquatic ecosystems (Grossart and Ploug 2001; Newton et al. 2011). It has been a longstanding challenge to understand the mechanisms governing the diversity, community composition, and assembly of microbial communities in freshwater ecosystems (Ren et al. 2015).

Previous studies have indicated that eutrophic shallow freshwater lakes could form particularly stable states that are ecologically different from each other under high and low nutrient loading levels (Scheffer et al. 1993). In the relatively low nutrient loading state, the stable state is characterized by a large amount of macrophytes and higher biodiversity of plants and animals, whereas the high nutrient loading state maintains

a large number of phytoplankton and lower biodiversity (Wetzel and Søndergaard 1998). Previous studies have found that the microbial community composition differed in various ecological habitats (Wu et al. 2007). It has also been observed that the community structure of bacterioplankton changed in response to the addition of nutrients to the ecosystem (Zhou et al. 2014). The high nutrient levels could affect the composition of bacterioplankton (Haukka et al. 2006). However, studies evaluating the response of the microeukaryote community assembly and the differences between the community assembly of bacterioplankton and microeukaryotes to changes in the nutrient loading level in freshwater lakes are not available.

Characterizing the processes that underlie spatial variation in biotic communities across an ecosystem is another major theme of ecological research (Martiny et al. 2006; Anderson et al. 2011; Wang et al. 2013). Niche-related processes refer to deterministic processes, including environmental filtering and interspecific competition, whereas neutral effects include unpredictable disturbances, probabilistic dispersal, and other stochastic processes (Hubbell 2001; Cavender-Bares et al. 2009; Hanson et al. 2012; Zhou et al. 2013). It has been demonstrated that the community structure of microorganisms is influenced by both deterministic and stochastic processes in freshwater lakes (Logares et al. 2013; He et al. 2014; Ren et al. 2015). However, little is known about the relative importance of deterministic and stochastic processes in the assembly of bacterioplankton and microeukaryote communities in natural freshwater lakes. Phylogenetic studies have been frequently used to evaluate the biodiversity patterns, which span plants, animals, and microbes (Cavender-Bares et al. 2009; Vamosi et al. 2009; Auguet et al. 2010; Jones and Hallin 2010). However, studies on the assembly processes of microbial communities in freshwater lakes are lacking (Bryant et al. 2008).

In this study, two natural freshwater lake zones of Taihu Lake (Meiliang Bay and Xukou Bay) in China were selected to assess the impacts of ecosystem conversion from a high nutrient level to a low nutrient level on the diversity, composition, and assembly processes of both the bacterioplankton and microeukaryote communities. The aims of the present study focused on the following three aspects: (i) Does the microbial community (including bacterioplankton and microeukaryotes) of freshwater lakes differ between the different nutrient loading lake zones? (ii) Do environmental factors impact the microbial communities differently in the two lake zones? (iii) What are the differences between the deterministic and stochastic processes that play a role in the assembly of microbial communities in the two lake zones? As far as we know, this is the first study to evaluate the roles of deterministic and stochastic processes in the assembly of both bacterioplankton and microeukaryote communities in freshwater lake ecosystems.

Materials and methods

Study area, sample collection, and physicochemical analyses

Taihu Lake (30° 55′ 40″–31° 32′ 58″ N, 119° 52′ 32″–120° 36′ 10″ E) is one of the largest freshwater and eutrophic lakes in China. The lake covers a total area of 2427.8 km^2 with a mean depth of 1.9 m and a watershed area of 19,000 km^2. Meiliang Bay (MLB) and Xukou Bay (XKB) are two distinct ecological zones in Taihu Lake. MLB is a turbid lake zone with a high biomass of algae (Qin et al. 2007; Cai et al. 2012). It supplies irrigation, drinking water, and industrial water for Wuxi City. At the same time, domestic and industrial wastewater from the surrounding areas is discharged into this zone (Qiao et al. 2006; Zeng et al. 2012b). However, XKB is a clear zone dominated by a variety of aquatic macrophytes (Qin et al. 2007; Zeng et al. 2012a).

In October of 2015, 10 water samples were collected from each of the two lake zones of Taihu Lake (Meiliang Bay and Xukou Bay). The sampling stations were in the same geographical area and were generally distributed uniformly. The location of each sampling station was recorded with a global positioning system (GPS), which was used for calculating the pairwise distances between sampling stations.

Water samples were collected at a depth of 0.5 m in the water column at each sampling site using a sampler (DSC2500, Xiamen Dengxun Instruments, Fujian, China). Large plankton and other particles in the samples were removed by passing the sample through a 5-μm polycarbonate filter (Millipore, Billerica, MA, USA). Bacterioplankton was collected by passing the sample through a 0.22-μm polycarbonate filter (Millipore, Billerica, MA, USA).

The temperature, pH, oxidation reduction potential (ORP), and conductivity of the water samples were measured in situ with a water quality sonde (YSI 6600, Yellow Springs Instruments, OH, USA). Total nitrogen (TN) and total phosphorous (TP) were investigated according to Rice et al. (2012). Dissolved inorganic nitrogen, including ammonia nitrogen (NH_4^+–N), nitrate nitrogen (NO_3^-–N), and nitrite nitrogen (NO_2^-–N), were measured with continuous colorimetric flow analysis (Skalar SAN PLUS system, Skalar Analytical BV, Breda, the Netherlands). Chlorophyll *a* was extracted with ethanol and investigated with a spectrophotometer (Jespersen and Christoffersen 1987).

DNA extraction, amplification, and pyrosequencing

The extraction and purification of microbial DNA was performed according to Wu et al. (2006). The bacterial 16S ribosomal RNA (rRNA) gene and microeukaryotic 18S rRNA gene were PCR amplified and sequenced using the Illumina MiSeq platform (San Diego, CA, USA). The V4–V5

hypervariable regions of the bacterial 16S rRNA gene (Caporaso et al. 2012) and the V9 hypervariable region of the microeukaryotic 18S rRNA gene (Logares et al. 2014) were amplified. PCR reactions (total volume of 20 μL) contained 0.4 μM of each of the universal primers, 10 ng template of DNA, 2 μL of 2.5 mM dNTPs, and 0.4 μL of FastPfu Polymerase (TransGen Biotech, Beijing, China). Cycling parameters were as follows: an initial denaturation step at 95 °C for 2 min, followed by 25 cycles at 95 °C for 30 s, 55 °C for 30 s, and 72 °C for 30 s, with a final extension at 72 °C for 5 min. All samples were amplified with three replicates. The PCR products were pooled together and purified with the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA) according to the manufacturer's instructions.

Purified PCR products were quantified by Qubit®3.0 (Life Invitrogen, Carlsbad, CA, USA) and every 24 amplicons whose barcodes were different were mixed equally. The pooled DNA was used to construct an Illumina paired-end library following the Illumina genomic DNA library preparation procedure. The amplicon library was paired-end sequenced on the Illumina MiSeq platform (San Diego, CA, USA) at Shanghai BIOZERON Co., Ltd. according to the standard protocols. The raw reads were deposited into the NCBI Sequence Read Archive (SRA) database (Accession Number: SRP090623).

Pyrosequencing data analysis

Raw reads of the bacterial 16S rRNA gene and microeukaryotic 18S rRNA gene sequences were analyzed with Mothur v.1.37.0 (Schloss et al. 2009). In brief, the raw reads were denoised, trimmed, quality filtered, and aligned using Mothur (Quast et al. 2013; Zhao et al. 2014; Ren et al. 2015). To build the operational taxonomic unit (OTU) matrix, first, the "dist.seqs" command in Mothur was used to generate a distance matrix; then, the "cluster" command based on the furthest-neighbor algorithm method was employed to cluster the clean sequences into OTUs. Finally, the "make.shared" command was used to generate an OTU-shared file at the cutoff of 0.03.

To correct bias due to the different sequencing depths, we randomly subsampled the minimum amount of sequences (for example, 23,247 sequences for the 16S rRNA gene) from each sample for the alpha and beta diversity analysis. The "remove.rare" command in Mothur was used to exclude OTUs with fewer than four sequences from the OTU table (Bokulich et al. 2013). The FastTree algorithm (v.2.1.3) was employed to construct a phylogenetic tree (command used in FastTree: -fastest, -gtr, and -nt) (Price et al. 2009).

Alpha diversity was computed using the command "summary.single" in Mothur. The phylogenetic diversity (PD) of Faith (1992) was calculated based on the phylogenetic tree using the "pd" function in the "picante" package (Kembel et al. 2010) of R (R Core Team 2013). Differences in the microbial community composition were examined using both the taxonomy-based Bray-Curtis distance and the phylogeny-based UniFrac distance with the "vegan" package (Oksanen et al. 2013) and "picante" package (Kembel et al. 2010) of R (R Core Team 2013).

Statistical analyses

The taxonomy-based and phylogeny-based distances were visualized using nonmetric multidimensional scaling (NMDS) to compare the microbial community composition among samples with R (R Core Team 2013). The differences in microbial community composition of different lake zones were tested with analyses of similarity (ANOSIM) with the "anosim" function in R (R Core Team 2013). Canonical correspondence analysis (CCA) was calculated using the "vegan" package (Oksanen et al. 2013) in R (R Core Team 2013) to explore the roles of environmental factors in structuring the microbial community of the different lake zones. Heatmap figures were made using the HemI 1.0.3.3 software (Deng et al. 2014). The Mantel test in R (R Core Team 2013) was conducted to examine the significance of the correlations between dissimilarities of the microbial community composition and the geographic distances or environmental heterogeneity (Legendre and Legendre 2012).

Community phylogenetic structure and the analysis of assembly processes of the microbial community

Mantel correlograms with 9999 randomizations were conducted to examine the phylogenetic signal between the pairwise matrix of OTU phylogenetic distances and OTU ecological niche distances as previously described (Andersson et al. 2010; Wang et al. 2013). The mean nearest taxon distance (MNTD) and the standardized effect size of the MNTD (ses.MNTD) (Webb et al. 2002) were also calculated with the "picante" package (Kembel et al. 2010) of R (R Core Team 2013). Unweighted Unifrac (Lozupone and Knight 2005) and the betaMNTD (Fine and Kembel 2011; Stegen et al. 2012) were used to quantify phylogenetic turnover in microbial community composition between samples (phylogenetic beta diversity) (Wang et al. 2013). The standardized effect size of the betaMNTD was calculated for each lake zone based on random shuffling of the OTU labels across the tips of the phylogeny (Hardy 2008; Stegen et al. 2012; Wang et al. 2013).

To investigate the underlying processes of microbial community assembly, the relative importance of the deterministic and stochastic processes were assessed according to Wang et al. (2013). Partial Mantel tests were performed to investigate the relationships between spatial or environmental distance and phylogenetic turnover (Unifrac, betaMNTD or ses.betaMNTD) after controlling for spatial or environmental

distance. These analyses were performed with the "vegan" (Oksanen et al. 2013) and "picante" (Kembel et al. 2010) packages in R (R Core Team 2013).

Results

Differences in environmental attributes between the two lake zones

The two lake zones differed significantly (two-tailed paired Student *t* test: $P < 0.05$) in many environmental parameters (Table 1), including pH and the concentrations of TN, TP, ammonia nitrogen (NH_4^+–N), and nitrite (NO_2^-–N). The MLB lake zone maintained a significantly higher pH (8.53), concentrations of TN (1.98 mg/L), TP (0.22 mg/L), NH_4^+–N (0.06 mg/L), and NO_2^-–N (0.006 mg/L) than those of the XKB lake zone, indicating a higher level of nutrients.

Description of the overall sequences obtained

After the pre-processing of the obtained sequences, 702,730 and 720,458 quality sequences were obtained for the 16S rRNA gene and the 18S rRNA gene, respectively. The total OTU richness was 3247 and 2059 at a 97% similarity level of all the rarefied samples for the 16S rRNA gene and the 18S rRNA gene, respectively. The minimum number of sequences obtained in one sample was 24,824 and 24,960 for the 16S and 18S rRNA genes, respectively. Fourteen OTUs consisted of more than 10,000 sequences (the maximum was 45,813) for the 16S rRNA gene sequences, and seven OTUs consisted of more than 10,000 sequences (the maximum was 156,654) for the 18S rRNA gene sequences. Additionally, the numbers of OTUs containing ≥1000, ≥100, and ≥4 sequences were 90, 430, and 2713 for the 16S rRNA gene sequences and 44, 221, and 1788 for the 18S rRNA gene sequences, respectively. The rarefaction curves of the bacterioplankton and microeukaryote communities were approximately planar (Supplementary Fig. S1), and the relative abundances of the bacterioplankton phyla/subphyla are shown in Supplementary Fig. S2.

The bacterioplankton community of MLB exhibited higher OTU richness than in XKB for each specific phylum, except *Gammaproteobacteria*, *Firmicutes*, and *Cyanobacteria* (Supplementary Fig. S3). For OTU richness, there was significantly higher OTU richness in bacterial groups of *Bacteroidetes*, *Betaproteobacteria*, *Chloroflexi*, *Acidobacteria*, and unclassified bacterioplankton in MLB ($P < 0.05$) (Supplementary Fig. S3). For the average relative abundance, significantly higher relative abundances of *Actinobacteria*, *Alphaproteobacteria*, *Betaproteobacteria*, *Bacteroidetes*, *Acidobacteria*, *Gemmatimonadetes*, *Chloroflexi*, and unclassified bacteria were found in MLB ($P < 0.05$) (Supplementary Fig. S3).

Table 1 Environmental attributes of the MLB and XKB lake zones

Attributes	MLB	XKB
TN (mg/L)	*1.98 ± 0.97***	0.61 ± 0.09
TP (mg/L)	*0.22 ± 0.10****	0.04 ± 0.01
NH_4^+–N (mg/L)	*0.06 ± 0.04**	0.02 ± 0.02
NO_3^-N (mg/L)	0.06 ± 0.04	0.03 ± 0.01
NO_2^-–N (mg/L)	*0.006 ± 0.004**	0.002 ± 0.001
DOC (mg/L)	4.29 ± 1.32	4.24 ± 1.47
pH	*8.53 ± 0.37**	8.25 ± 0.24
T (°C)	18.1 ± 0.1	18.2 ± 0.2
EC (mS/cm)	*0.382 ± 0.007****	0.354 ± 0.011
ORP (mV)	17.2 ± 4.4	20.98 ± 9.8

The higher environmental attributes which show significant differences between the two lake zones are indicated in italics

TN total nitrogen, *TP* total phosphorus, NH_4^+ *–N* ammonium nitrogen, NO_3^- *–N* nitrate nitrogen, NO_2^- *–N* nitrite nitrogen, *DOC* dissolved organic carbon, *T* temperature, *EC* electrical conductivity, *ORP* oxidation reduction potential, *MLB* Meiliang Bay, *XKB* Xukou Bay

Significant difference (two-tailed paired Student *t* test $P < 0.05$) between MLB and XKB lake zones. ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$

Differences in microbial community composition between the two lake zones

The richness and alpha diversity of bacterioplankton and microeukaryote communities, including both Chao1 and phylogenetic diversity, were compared between the two lake zones (Fig. 1). Significantly higher OTU richness ($P < 0.01$) and phylogenetic diversity ($P < 0.05$) were found in the bacterioplankton community of MLB than those of the bacterioplankton community of XKB. However, the richness and alpha diversity of the microeukaryote communities were comparable for MLB and XKB ($P > 0.05$).

The NMDS plot revealed that the taxonomic (OTUs) and phylogenetic composition of both bacterioplankton and microeukaryote communities clustered according to lake zone (Fig. 2), suggesting that there are differences in community composition for the bacterioplankton and microeukaryotes in the two different lake zones. The differences in the community composition of the bacterioplankton and microeukaryotes were also confirmed by the results of ANOSIM (Table 2).

Linking environmental and spatial factors to the bacterioplankton and microeukaryote community

Table 3 illustrates that environmental factors play different roles in controlling the microbial community composition for the MLB and XKB lake zones. Both nutrient variables (TN and TP) and pH significantly affected the microbial community compositions in XKB ($P < 0.05$) for

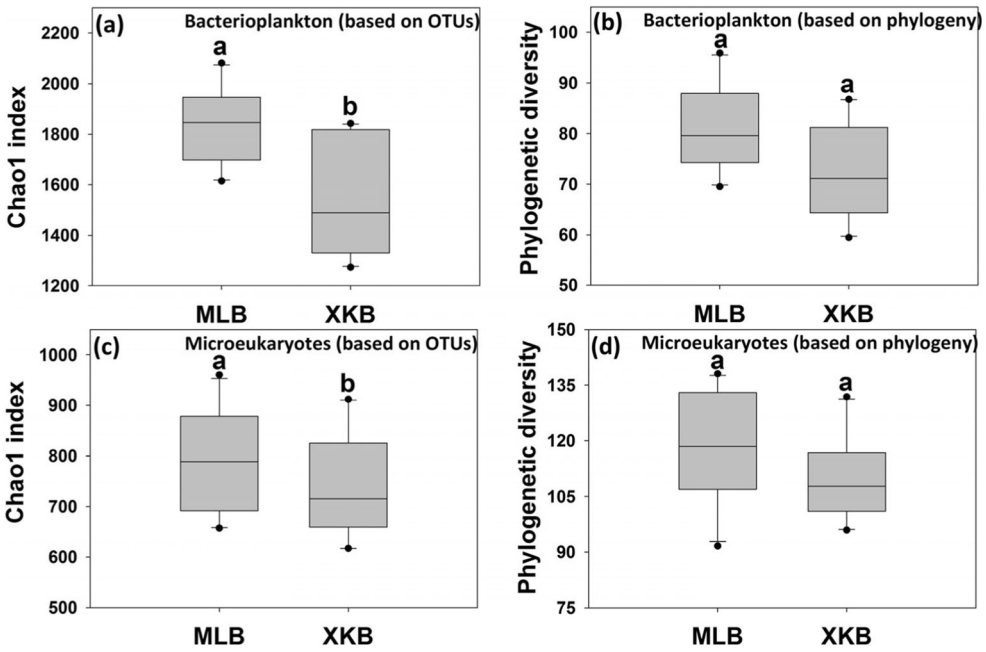

Fig. 1 The richness and alpha diversities based on both taxonomic (**a**, **c**) and phylogenetic indexes (**b**, **d**) of bacterioplankton (**a**, **b**), and microeukaryotes (**c**, **d**). *Different letters above columns* indicate significant differences between the Meiliang Bay (MLB) and Xukou Bay (XKB) lake zones

both the bacterioplankton and microeukaryotes, whereas environmental factors did not show a significant correlation with the microbial community composition in MLB, except for the weak correlation between DOC and the microeukaryote community. These results were also confirmed by the CCA results at $P < 0.05$ (Supplementary Fig. S4) and the curve fitting of environmental variable dissimilarity and taxonomic dissimilarity (Supplementary Fig. S5). Furthermore, the relative abundance of the dominant groups of bacterioplankton communities along the different environmental attributes were depicted by a heatmap (Supplementary Fig. S6). Compared with MLB,

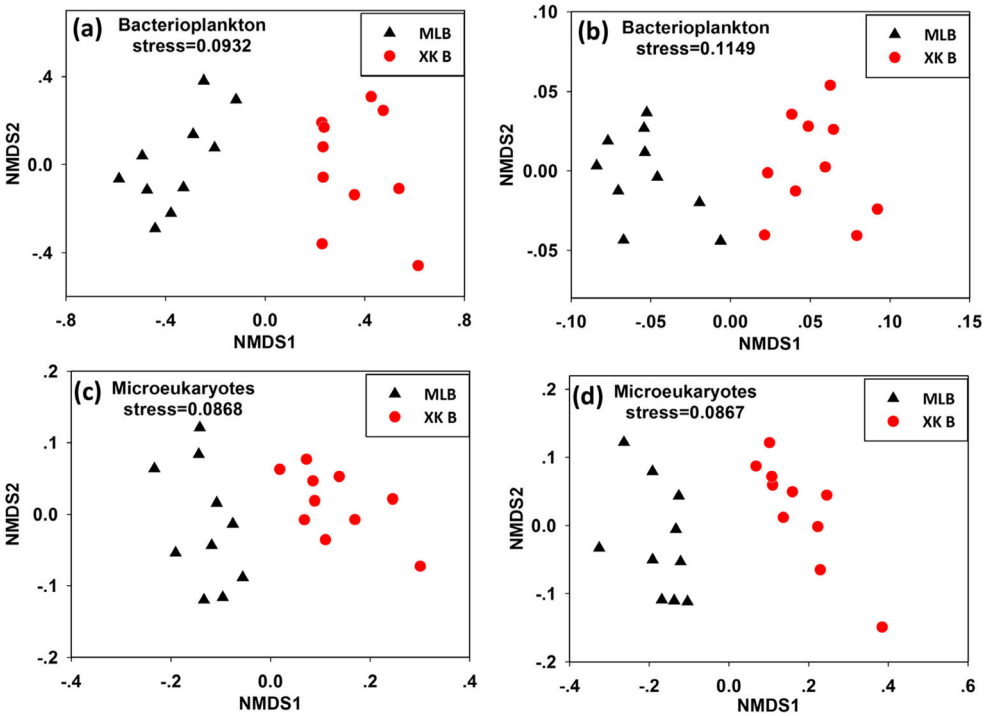

Fig. 2 Non-parametric multidimensional scaling (NMDS) plots derived from the taxonomy-based on Bray-Curtis distance (**a**, **c**) and the phylogeny-based UniFrac distance (**b**, **d**) of community composition of bacterioplankton (**a**, **b**), and microeukaryotes (**c**, **d**). *MLB* Meiliang Bay lake zone, *XKB* Xukou Bay lake zone

Table 2 Differences of microbial community composition between the Meiliang Bay (MLB) and Xukou Bay (XKB) lake zones investigated by analysis of similarity (ANOSIM)

	Microbial community	*R*	*P*
Taxonomic based	Bacterioplankton	0.8002	<0.001
	Microeukaryotes	0.5058	<0.001
Phylogeny based	Bacterioplankton	0.7091	<0.001
	Microeukaryotes	0.9013	<0.001

the environmental factors maintained stronger correlations with the relative abundance of the main phyla/subphyla of bacterioplankton in XKB (Supplementary Fig. S6).

Phylogenetic structure and assembly processes of the microbial community

Mantel correlograms consistently showed significant positive correlation across short phylogenetic distances for all sample groups ($P < 0.05$) (Supplementary Fig. S7), indicating closely related taxa (OTUs) possess niche conservatism and that there might be strong interactions between closely related taxa.

Figure 3 shows that the mean nearest taxon distance (MNTD) and the standardized effect sizes of MNTD (ses.MNTD) of bacterial communities derived from MLB were significantly higher than those of XKB ($P < 0.05$). However, the MNTD and ses.MNTD of the microeukaryote communities were comparable between the two different lake zones ($P > 0.05$). Boxplots based on ses.betaMNTD (Supplementary Fig. S8) show that the ses.betaMNTD of the bacterial community derived from MLB were significantly higher than those of XKB ($P < 0.05$). However, the betaMNTD of bacterioplankton and microeukaryote communities were comparable between the two different lake zones ($P > 0.05$) (Supplementary Fig. S8). The results of the nonmetric multidimensional scaling based on the betaMNTD showed that samples were phylogenetically segregated by different lake zones for both bacterioplankton and microeukaryotes (Fig. 4), indicating differences in community composition for the bacterioplankton and microeukaryotes in the two different lake zones. To compare the assembly processes of the microbial communities in the two different lake zones, partial Mantel tests were performed and the results are shown in Table 4. After controlling for environmental distance, spatial distance was not significantly correlated with ses.betaMNTD for samples collected from both lake zones for both bacterioplankton and microeukaryote communities. Spatial distance was not significantly correlated with the unweighted Unifrac and betaMNTD for samples collected in MLB after controlling for environmental distance. Moreover, environmental distance was not significantly correlated with unweighted Unifrac and betaMNTD for samples collected in MLB after controlling for spatial distance, whereas it was significantly correlated with both unweighted Unifrac and betaMNTD for samples collected in XKB for both bacterioplankton and microeukaryote communities. Therefore, as Wang et al. (2013) previously described, the assembly of both the bacterioplankton and microeukaryote communities collected in XKB was governed by deterministic processes of measured environmental variables, whereas the microbial communities derived from the MLB lake zone were assembled by unknown processes.

Table 3 Mantel test for the correlations between community composition and environmental variables for bacterioplankton and microeukaryotes in the MLB and XKB lake zones of Taihu Lake

Sites	Bacterioplankton		Microeukaryote	
	MLB	XKB	MLB	XKB
Environmental variables	*R* values			
All factors	−0.082	*0.768***	0.156	*0.776****
TN	0.060	*0.723****	0.001	*0.633****
TP	0.232	*0.757****	0.129	*0.592***
NH_4^+–N	0.023	0.070	0.217	0.176
NO_3^-–N	0.092	−0.150	−0.078	-0.155
NO_2^-–N	−0.220	−0.080	−0.037	0.053
DOC	−0.103	0.242	*0.420**	0.444
pH	−0.138	*0.553****	−0.023	*0.351**
T	−0.254	0.362	0.104	*0.672****
EC	−0.028	*0.446**	−0.060	*0.385**
ORP	−0.249	*0.774****	0.105	*0.591****

Significant correlations are indicated in italics

TN total nitrogen, *TP* total phosphorus, NH_4^+ *–N* ammonium nitrogen, NO_3^- *–N* nitrate nitrogen, NO_2^- *–N* nitrite nitrogen, *DOC* dissolved organic carbon, *T* temperature, *EC* electrical conductivity, *ORP* oxidation reduction potential, *MLB* Meiliang Bay, *XKB* Xukou Bay

***$P < 0.001$; **$P < 0.01$; *$P < 0.05$

Discussion

In this study, we examined the discrepancies in community composition of freshwater bacterioplankton and microeukaryotes and the relative importance of deterministic and stochastic processes across two lake zones with different nutrient loading levels. Clear differences in diversity, composition, phylogenetic structure, and assembly process of the microbial communities were observed across the two lake zones.

Significant differences were observed in the water characteristics of the two different lake zones (Table 1). The nutrient loading level in MLB was significantly higher than that of XKB, which could be attributed to the discharge of domestic and industrial wastewater from the surrounding area (Qiao et al. 2006). Most pollutant inflow rivers are located in the

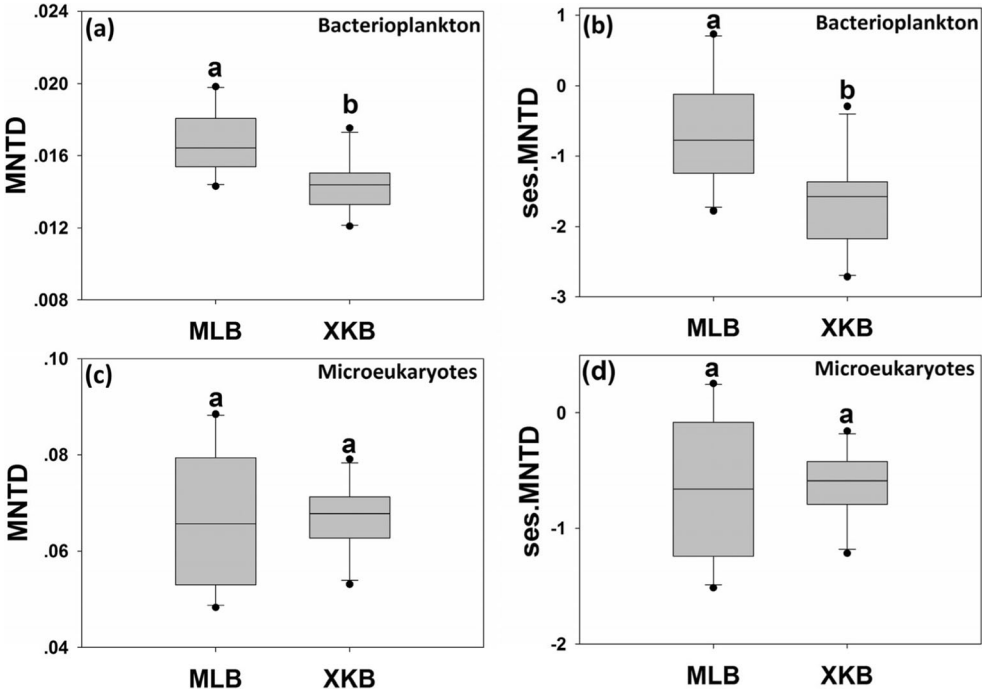

Fig. 3 Comparison of the mean nearest taxon distance (MNTD) (**a**, **c**) and the standardized effect sizes of MNTD (ses.MNTD) (**b**, **d**) of community composition of bacterioplankton (**a**, **b**), and microeukaryotes (**c**, **d**) in the Meiliang Bay (MLB) and Xukou Bay (XKB) lake zones. *Different letters above columns* indicate the significant differences between two lake zones ($P < 0.05$)

west or northwest part of Taihu Lake (Qin et al. 2007). Some previous studies have also reported the higher concentrations of metals (Zeng et al. 2012c) and organic pollutants (Liu et al. 2009) in the MLB lake zone.

The alpha diversity of bacterioplankton collected from MLB was significantly higher than that of XKB. Compared with XKB, MLB exhibits higher nutrient loading. Such a nutrient state could weaken niche selection by reducing competition for resources and providing more diverse resources to some microbial species, which may contribute to the higher diversity (Monier et al. 2015; Zhou et al. 2014). However, the alpha diversity of the microeukaryotes in the two lake zones was comparable. Microeukaryotes are a group of extremely diverse organisms that possess a wide range of distinct morphologies (Caron et al. 2012; Landry and Calbet 2004; Sherr and Sherr 1994), physiologies, and links to higher trophic levels (Caron et al. 2012; Bik et al. 2012; Calbet and Saiz 2005). Very few studies have attempted to identify and enumerate all protist taxa because of their complexities (Caron et al. 2009; Gifford and Caron 2000; Tomas and Haste 1997). Therefore, it is still uncommon to delineate microeukaryotic species based on their genetic signatures. In this study, more than 50% of the detected OTUs were categorized in unclassified groups (Supplementary Table S1), which may contribute to the comparable alpha diversity of microeukaryotes in the two lake zones. In addition, it is suggested that bacterial and eukaryotic microbes have similar cellular-mineral-environmental constraints (Worden and Allen 2010). Although the relatively less favorable nutrient conditions could be considered stress factors that would influence species composition in XKB, the ability of microeukaryotes to adapt to environmental perturbations and compete with each other is stronger (Worden and Allen 2010).

Different roles of environmental factors in controlling the microbial community composition were observed for the MLB and XKB lake zones. Both nutrient factors (TN and TP) and pH significantly affected the community compositions of bacterioplankton and microeukaryotes in XKB

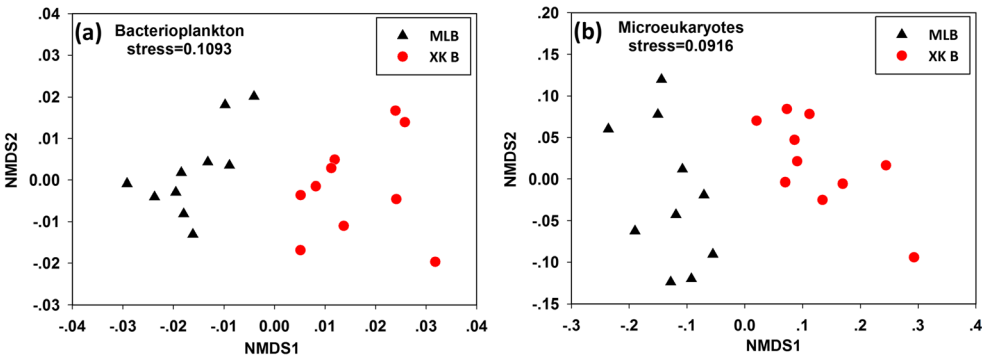

Fig. 4 Nonmetric multidimensional scaling plots of microbial community dissimilarities of bacterioplankton (**a**) and microeukaryotes (**b**) based on betaMNTD. *MLB* Meiliang Bay lake zone, *XKB* Xukou Bay lake zone

Table 4 Partial Mantel tests for the correlations between unweighted Unifrac and the explanatory distances (spatial and environmental distance) based on the Spearman correlation coefficient for the MLB and XKB lake zones

Correlation of		Controlling for	Bacterioplankton		Microeukaryotes	
			MLB	XKB	MLB	XKB
ses.beta MNTD	Spatial distance		0.0942	*0.6628***	−0.1214	*0.7730****
ses.beta MNTD	Environmental distance		−0.3045	*0.6789****	−0.0463	*0.6795***
ses.beta MNTD	Spatial distance	Environmental distance	0.1521	0.2651	−0.0274	0.1487
Unifrac	Spatial distance	Environmental distance	−0.0398	0.2793	0.0823	*0.4036**
betaMNTD	Spatial distance	Environmental distance	−0.0385	0.2596	0.0290	0.0625
Unifrac	Environmental distance	Spatial distance	−0.2997	*0.5414****	−0.3052	*0.6883****
betaMNTD	Environmental distance	Spatial distance	−0.2034	*0.4211***	−0.3115	*0.5698****

MLB Meiliang Bay, *XKB* Xukou Bay

The significances are tested based on 9999 permutations. ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$

($P < 0.05$). However, environmental factors did not significantly affect the microbial community composition in MLB, except for the weak correlation between DOC and the microeukaryote community. Hydrochemical gradients have been identified as environmental barriers in previous microbial surveys (Stock et al. 2013) including the Cariaco Basin (Stoeck et al. 2003), Framvaren Fjord (Behnke et al. 2006), Mariager Fjord (Zuendorf et al. 2006), Baltic Sea (Stock et al. 2009), the Black Sea (Wylezich and Jurgens 2011), and stratified lakes (Casamayor et al. 2008). Therefore, the significant distinction of microbial communities in the two lake zones is not an unexpected result. However, it is surprising that the environmental variables only exhibited minor effects on the microbial community of MLB.

The different nutrient loadings mean differing extents of environmental stress that would influence species composition and turnover within the lake zones (Shen et al. 2014; Zhou et al. 2014). Therefore, it is reasonable that the relationship between the microbial community and the environmental factors in MLB is weaker than in XKB. This would be attributed to the niche selection that was weakened by reducing competition for resources and by providing more diverse resources. Moreover, although the pH of XKB was significantly higher than that of MLB, the direct or indirect filtering effects of pH were similar in the two lake regions, as they belong to the same acceptable pH range for the microbes (Ren et al. 2015). Furthermore, DOC has been shown to affect microbial species directly. These interactions are different in prokaryotes and eukaryotes (Bährs et al. 2012; Prokhotskaya and Steinberg 2007). The weak correlation between DOC and the microeukaryote community in MLB may be connected to the larger organism volume and higher nutrient demand of microeukaryotes.

Similar to the microbial community composition based on taxonomic and phylogenetic dissimilarities, the results of NMDS based on the betaMNTD show that the samples were phylogenetically segregated by different lake zones (Fig. 4). Consistent with the alpha diversity, the MNTD and ses.MNTD results of the bacterioplankton community in the XKB lake zones are significantly different from those results observed in MLB (Fig. 3).

Almost all the ses.MNTD obtained using the null model were significantly negative, which indicates that the microbial communities tended to be more phylogenetically clustered than expected by chance in the two lake zones (Wang et al. 2013). Furthermore, samples in XKB were more likely to be clustered than samples in MLB, as the ses.MNTD values were more significantly negative (Fig. 3). In addition, it is necessary to propose that the more clustered boxplot in XKB (Fig. 3) may be due to the relatively low nutrient loading level. This may lead to stronger niche selection due to the increased competition for resources (Zhou et al. 2014).

Previous studies have indicated that the community composition of microorganisms is influenced by both deterministic and stochastic processes (Jones and McMahon 2009; Lindström and Langenheder 2012; Sloan et al. 2006; Örjan et al. 2010). In this study, the phylogenetic information and the procedure proposed by Wang et al. (2013) were used to investigate the relative importance of deterministic and stochastic processes across the two lake zones. The first step was to examine whether the distributions of ses.betaMNTD deviate significantly from zero. Deviating significantly from zero suggests strong influences of deterministic processes (Wang et al. 2013). The mean values of ses.betaMNTD for both of the two lake zones were negative (less than −4). Additionally, the mean value of ses.betaMNTD for the bacterioplankton community in XKB was lower than that of MLB (Supplementary Fig. S8), suggesting that deterministic processes governed the microbial community composition in both lake zones, especially for the XKB lake zone. Severe eutrophication imposes strong environmental filtering on microbial communities (Wang et al. 2013). Additionally, spatial distances were not significantly related to ses.betaMNTD after controlling for the

measured environmental variables in the two lake zones in the present study (Table 4). Wang et al. (2013) indicated that the partial Mantel coefficient related to spatial distance reflected the deterministic processes governed by unmeasured environmental variables. The obtained results suggested that the unmeasured environmental variables maintained only small effects on the bacterioplankton and microeukaryote community composition in the two lake zones.

Next, we evaluated the roles of the deterministic and stochastic processes on microbial community assembly in freshwater lakes of different nutrient loading levels. The partial Mantel coefficients from the analyses of Unifrac and betaMNTD were used. For both the bacterioplankton and microeukaryote community in XKB, the partial Mantel coefficients were higher for environmental distance (bacterioplankton, $R = 0.5414$ for UniFrac and $R = 0.4211$ for betaMNTD; microeukaryotes, $R = 0.6883$ for UniFrac and $R = 0.5698$ for betaMNTD; all $P < 0.01$) than for spatial distance (bacterioplankton, $R = 0.2793$ for UniFrac and $R = 0.2596$ for betaMNTD; microeukaryotes, $R = 0.4036$ for UniFrac and $R = 0.0625$ for betaMNTD) (Table 4). This indicates that deterministic processes governed by measured environmental variables are more important than stochastic processes.

The results characterized by partial Mantel tests for the bacterioplankton and microeukaryotes in MLB did not provide any clear ecological inferences. Stochastic processes were overwhelmed by deterministic processes governed by the measured environmental variables in XKB, whereas this was not the case for the MLB lake zone (higher nutrient loadings). Previous studies have also reported greater determinism in extreme or low resource environments (Chase 2010; Gerisch et al. 2011; Kembel et al. 2011; van der Plas et al. 2012; Zhou et al. 2014). We infer that the stochastic processes played a more important role in controlling microbial community assembly in higher nutrient loading lake zones, which was consistent with the study of the phytoplankton-dominated and macrophyte-dominated lake zones in Dianchi Lake (Wang et al. 2017).

In this study, significant heterogeneity of composition and assembly processes of the bacterioplankton and microeukaryote communities was observed between the two lake zones of Taihu Lake. Nutrient loadings were identified as the important driving forces of the observed differences in bacterioplankton and microeukaryote community composition and assembly. The higher nutrient loading lake zone (MLB) maintained higher diversity of the bacterioplankton community and a significantly different community composition compared with the XKB lake zone. Although environmental filtering was the most important determinant of microbial community assembly in both lake zones, an enhanced importance of stochastic processes was observed in the higher nutrient loading lake zone (MLB). It is worth noting that only two sets of lake zones were examined in this study. Further studies are needed to determine the impacts of spatial and temporal factors.

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Author contributions Dayong Zhao, Jin Zeng, and Zhongbo Yu designed the experiments. Dayong Zhao, Xinyi Cao, Rui Huang, Jin Zeng, Sichen Wang, and Huimin Xu did the field sampling. Huimin Xu and Xiaowei He did the analysis of the water characteristics. Dayong Zhao, Xinyi Cao, and Jin Zeng was responsible for the performance of the molecular experiments. Dayong Zhao, Xinyi Cao, Rui Huang, Jin Zeng, and Feng Shen did the data analysis. Dayong Zhao, Xinyi Cao, Jin Zeng, Huimin Xu, and Zhongbo Yu wrote the paper. Dayong Zhao, Xinyi Cao, Jin Zeng, and Zhongbo Yu revised the paper.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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