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ORIGINAL ARTICLE

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Nearly a decade-long repeatable seasonal diversity patterns of bacterioplankton communities in the eutrophic Lake Donghu (Wuhan, China)

Qingyun Yan[1,2] | James C. Stegen[3] | Yuhe Yu[2] | Ye Deng[4] | Xinghao Li[2] | Shu Wu[2] | Lili Dai[2] | Xiang Zhang[2] | Jinjin Li[2] | Chun Wang[2] | Jiajia Ni[2] | Xuemei Li[2] | Hongjuan Hu[2] | Fanshu Xiao[1] | Weisong Feng[2] | Daliang Ning[5] | Zhili He[1,5] | Joy D. Van Nostrand[5] | Liyou Wu[5] | Jizhong Zhou[5,6,7]

[1]Environmental Microbiome Research Center and the School of Environmental Science and Engineering, Sun Yat-sen University, Guangzhou, China

[2]Key Laboratory of Aquatic Biodiversity and Conservation of Chinese Academy of Sciences, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China

[3]Biological Sciences Division, Pacific Northwest National Laboratory, Richland, WA, USA

[4]CAS Key Laboratory of Environmental Biotechnology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, China

[5]Department of Microbiology and Plant Biology, Institute for Environmental Genomics, University of Oklahoma, Norman, OK, USA

[6]State Key Joint Laboratory of Environment Simulation and Pollution Control, School of Environment, Tsinghua University, Beijing, China

[7]Earth Sciences Division, Lawrence Berkeley National Laboratory, Berkeley, CA, USA

Correspondence
Qingyun Yan, Environmental Microbiome Research Center and the School of Environmental Science and Engineering, Sun Yat-sen University, Guangzhou, China.
Email: yanqy6@mail.sysu.edu.cn
and
Yuhe Yu, Key Laboratory of Aquatic Biodiversity and Conservation of Chinese Academy of Sciences, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China.
Email: yhyu@ihb.ac.cn
and
Jizhong Zhou, Institute for Environmental Genomics and Department of Microbiology and Plant Biology, University of Oklahoma, Norman, USA.
Email: jzhou@ou.edu

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Abstract

Uncovering which environmental factors govern community diversity patterns and how ecological processes drive community turnover are key questions related to understand the community assembly. However, the ecological mechanisms regulating long-term variations of bacterioplankton communities in lake ecosystems remain poorly understood. Here we present nearly a decade-long study of bacterioplankton communities from the eutrophic Lake Donghu (Wuhan, China) using 16S rRNA gene amplicon sequencing with MiSeq platform. We found strong repeatable seasonal diversity patterns in terms of both common (detected in more than 50% samples) and dominant (relative abundance >1%) bacterial taxa turnover. Moreover, community composition tracked the seasonal temperature gradient, indicating that temperature is a key environmental factor controlling observed diversity patterns. Total phosphorus also contributed significantly to the seasonal shifts in bacterioplankton composition. However, any spatial pattern of bacterioplankton communities across the main lake areas within season was overwhelmed by their temporal variabilities. Phylogenetic analysis further indicated that 75%–82% of community turnover was governed by homogeneous selection due to consistent environmental conditions within seasons, suggesting that the microbial communities in Lake Donghu are mainly controlled by niche-based processes. Therefore, dominant niches available within seasons might be occupied by similar combinations of bacterial taxa with modest dispersal rates throughout different lake areas.

KEYWORDS
community assembly, homogeneous selection, lake bacterioplankton, Lake Donghu, repeatable diversity patterns

1 | INTRODUCTION

Understanding natural biodiversity and determining the major factors regulating community diversity patterns (spatial or temporal) are central issues in predicting ecosystem response to environmental change (Chapin et al., 2000). Although we have a relatively mature understanding of the community assembly and environmental drivers of animal and plant communities, difficulties in examining and monitoring the "invisible" microbes have greatly limited our understanding of microbial communities. But by contrast, microorganisms are key components of ecosystem in terms of both relative abundance and their contributions to ecosystem functioning (Azam & Worden, 2004; Fuhrman, Sleeter, Carlson, & Proctor, 1989; Whitman, Coleman, & Wiebe, 1998). As such, it is vital to strengthen our understanding of the ecological processes controlling microbial community patterns at different spatial and temporal scales. Although recent studies suggested that some microbial patterns may mirror those found in plant and animal communities (e.g., species–area and species–time relationships, distance-decay, latitudinal diversity gradient), there also have fundamental distinctions between micro- and macro-organisms due to their differences in size, abundance, generation time, evolution rate and dispersal ability. Therefore, it is important to address the assembly mechanisms impacting microbial communities and work to make it equivalent to our knowledge of the plants and animals. Only in this way can we achieve a holistic understanding of the ecosystem structure and function and therefore can help us using both micro- and macro-organisms to provide better ecosystem services.

With rapid development and wide application of metagenome-based techniques in microbial ecology, our understanding of microbial diversity has been greatly enhanced in the past two decades (Fuhrman, 2009). Many lines of evidence suggest that aquatic microbial communities present different patterns at both spatial (from millimetres to kilometres to global) and temporal (e.g., monthly, seasonal, interannual) scales (Chow et al., 2013; Fortunato, Herfort, Zuber, Baptista, & Crump, 2012). For example, previous studies have assumed that aquatic microbial species are ubiquitously distributed (Finlay, 2002; Finlay & Clarke, 1999), but more recent work suggests that planktonic microbial communities in specific locations are primarily structured by niche-based processes (Eiler, Hayakawa, & Rappe, 2011; Langenheder, Berga, Ostman, & Szekely, 2012; Ren et al., 2015; Wang et al., 2013). Moreover, annually repeatable patterns in bacterial communities in the ocean suggest that community composition and abundance may be predictable based on the environmental parameters (Fuhrman et al., 2006). However, the ecological mechanisms controlling these diversity patterns are unclear and there is little consensus on how bacterioplankton are assembled in different aquatic ecosystems. For example, different environmental factors such as salinity (Logares et al., 2013), pH (Ren et al., 2015) and temperature (Fuhrman et al., 2008) found to be the key independent drivers of bacterioplankton in particular ecosystems. Moreover, decade long-term temporal patterns remain relatively unexplored, and only a few studies have examined bacterioplankton succession in marine ecosystems over decade time series (e.g., Chow et al., 2013; Cram et al., 2015).

The bacterioplankton are actually the most abundant types of microorganisms in both marine and freshwater ecosystems (Karner, DeLong, & Karl, 2001), and they are involved in almost all nutrient cycling and energy flow in aquatic ecosystems (Azam, 1998). Marine pelagic microbial communities have even been highlighted as the engines of marine carbon, nitrogen and sulphur cycles (Fuhrman, 2009). It is also very important to recognize that these biogeochemical processes result from complex interactions among community members—rather than from single populations (Strom, 2008). This highlights the necessity for community-level investigations of ecological processes involving bacterioplankton. The explosive increase in water microbiome studies has greatly enhanced our understanding of microbial diversity and its functional implications in aquatic ecosystems (Fuhrman, 2009; Fuhrman, Cram, & Needham, 2015). However, our understanding of the long-term turnover of bacterioplankton communities and its environmental drivers in freshwater lake ecosystems is very poor (e.g., Kara, Hanson, Hu, Winslow, & McMahon, 2013).

To determine how environmental factors regulate long-term community succession in freshwater ecosystems, here we focused on the bacterioplankton communities in a large eutrophic lake (Lake Donghu, Wuhan, China). Although Lake Donghu was well documented with systematic ecological work since 1955, most of these studies were performed with traditional ecological methods (e.g., taxonomical and physicochemical investigation) targeting different types of aquatic organisms (Liu, 1991, 1995). Only until 10 years ago, the culture-independent methods started to be used in examining the microorganisms in this well-studied urban lake (Yan, Yu, Feng, Deng, & Song, 2007; Yu, Yan, & Feng, 2008). Although the fingerprinting tools used were not well resolved, such studies have greatly enhanced our understanding of microbial communities in this ecosystem. Fortunately, the more recent high-throughput sequencing methods provide us with a much more in-depth look at bacterioplankton composition and its spatiotemporal dynamics. This knowledge will help us fill the gaps in understanding of the bacterioplankton community, and bring it to a level on par with other aquatic communities (e.g., phytoplankton, zooplankton, zoobenthos and fish) in Lake Donghu. Here we provide the first high-throughput sequencing data of

bacterioplankton in this lake ecosystem by investigating nearly a decade-long period using consistent procedures from sampling to data analysis. We hypothesize that (i) bacterioplankton community composition and abundance may vary repeatedly due to seasonal environmental changes in Lake Donghu; (ii) temperature would be the key factor modulate bacterioplankton community turnover in this lake system across long time periods due to the ecological processes of environmental filtering.

2 | MATERIALS AND METHODS

2.1 | Study area and experimental design

Lake Donghu in Wuhan, China (30°33′N, 114°23′E), is a shallow, eutrophic freshwater lake with an average depth of 2.5 m and a total surface area of 33.9 km^2 (Wuhan Water Authority 2014). It was generally regarded as the largest urban lake in China before 2014, but now it is replaced by the Tangxun Lake (47.6 km^2) due to the spread of urbanization (Wuhan Water Authority 2014). Lake Donghu is located near the middle reaches of the Yangtze River, and it originally had good water exchange with the Yangtze River, but this lake was cut off in 1902 to prevent the flooding that occurred frequently. It was further separated into several basins by artificial dikes in the late 1960s (Figure 1). Lake Donghu then experienced increasingly serious eutrophication due to the heavy discharge of urban sewage water and intensive aquaculture. In the last few decades, a series of ecological improvements and environmental protection were implemented to prevent the water environment from getting worse. The eutrophication in Lake Donghu therefore gradually improved after 1985, a turning point when the repeated cyanobacterial blooms ceased. In 2008, a large-scale integrated ecological project named the "Great Lake Donghu Ecological Water Network" was started to connect the six lakes around Lake Donghu and also connect to the Yangtze River. This ecological project will be finally finished in 2020 and mainly aimed to improve the water environment and enhance ecological services. However, Lake Donghu still remains relatively shallow, with similar to conditions before connection (Wuhan Water Authority 2014). Here we also want to use the pattern of bacterioplankton communities to reflect the general ecological effects from this project and some other actions performed in Lake Donghu during our investigating period. As significant change in ecological patterns may result from serious disturbance (Ferrenberg et al., 2013), the bacterioplankton pattern with insignificant change may suggest the effects of actions to the ecosystem are not significant.

In this study, we primarily targeted the community assembly and diversity dynamics of the bacterioplankton in Lake Donghu over nearly a decade. We selected five stations in the major lake areas (Figure 1) to represent a wide range of environmental conditions that may affect bacterioplankton communities within this lake ecosystem. Also, we selected a representative month (i.e., April, July, October, January) within each season to address the seasonal variability.

2.2 | Sampling

The same sampling procedure was applied for all 27 sampling events from April 2007 to January 2015 (five sampling stations for each event and totally 135 samples). During each sampling event, the fixed stations (Figure 1) were sampled within 2–4 hr between 8:00

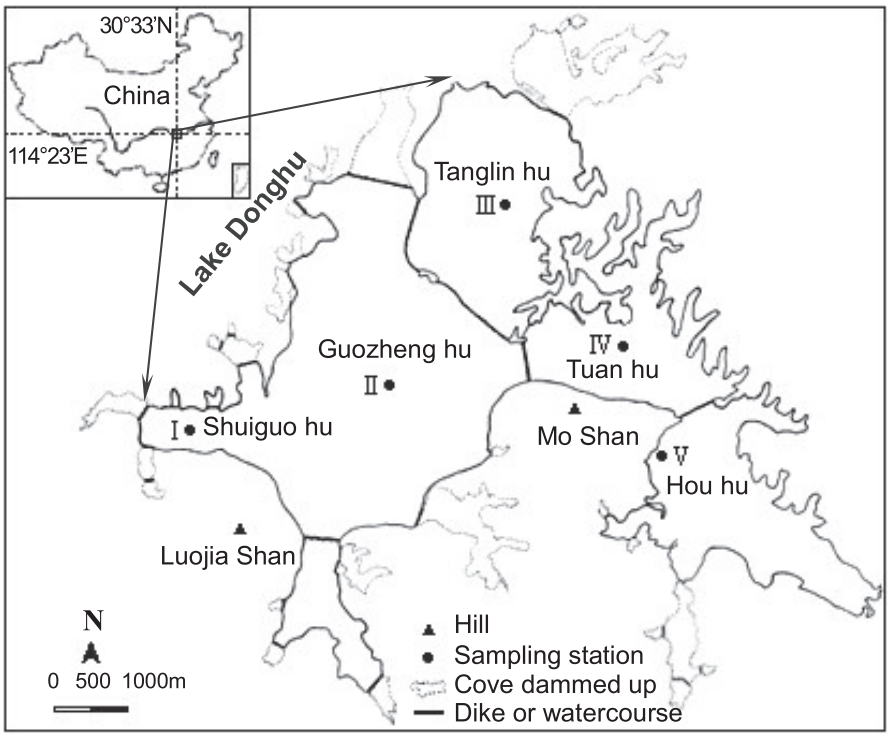

FIGURE 1 Location of sampling sites in the eutrophic Lake Donghu, Wuhan, China

a.m. and 12:00 a.m. on the same day to minimize daily variation. At each station, equal volumes of water (10 L) collected from the surface (10 cm below the water) and bottom (20 cm above the sediment) were mixed fully in a bucket, and then split for the following experiments. For DNA-based analysis, 1 L water was immediately filtered sequentially through 1.2-μm (Whatman, NJ, USA) and 0.22-μm filters (Millipore, MA USA) to collect bacterioplankton (particle-attached and free-living bacteria) and stored at −20°C for DNA extraction within 24 hr. Another litre of the mixed water samples were processed according to Huang (2000), kept at 4°C and transported to a laboratory for chemical analysis.

2.3 | Chemical analysis

Standard chemical analysis methods (Huang, 2000) were used for determining physicochemical factors including total nitrogen (TN), ammonium nitrogen (NH_4-N), nitrate nitrogen (NO_3-N), nitrite nitrogen (NO_2-N), total phosphorus (TP), phosphate phosphorus (PO_4-P), chemical oxygen demand (COD_{Mn}) and chlorophyll *a* (Chl-*a*). The concentrations of heavy metals including Cr, Cd, Pb, As, Cu and Hg were determined by graphite furnace atomic absorption spectrophotometry (GFAAS) using an Analyst 800 graphite furnace atomic absorption spectrometer (PerkinElmer, CT). Water temperature (WT), pH and transparency were determined in situ using a thermometer, Professional Plus Multi-Parameter Probe (YSI, OH, USA) and Secchi disc, respectively.

2.4 | DNA extraction

The 1.2- and 0.22-μm filters that collected the bacterial cells were used to extract DNA separately with a PowerWater® DNA extraction kit (Mo Bio, CA, USA) according to the manufacturer's instructions. Briefly, the filter was soaked in Solution PW1 (1 ml) was vortexed 5 min in PowerWater® bead tube, then centrifuged (4,000 *g*, 1 min) and transferred the supernatant to a new tube for an additional centrifugation (13,000 *g*, 1 min) to further remove all pellet. The supernatant was then purified and washed by solution PW2, PW3, PW4 and PW5 step by step. The DNA was dissolved in 100 μl DNA-free sterile water; DNA concentrations and quality were determined using a ND-1000 spectrophotometer (NanoDrop, DE, USA). The qualified DNAs were kept at −80°C for downstream analyses.

2.5 | 16S rRNA gene amplicon sequencing and phylogenetic analysis

Diversity of bacterioplankton was determined by analysing the V4 region of the 16S rRNA gene, which was amplified with the primer set 515f (5′-GTGCCAGCMGCCGCGGTAA-3′) and 806r (5′-GGACTACHVGGGTWTCTAAT-3′). All PCRs were conducted in triplicate for each sample with an initial 10 cycles of PCR amplification as we described previously (Yan et al., 2015, 2016). The products were then purified with Agencourt® Ampure® XP (Beckman Coulter, Inc., CA, USA) and further used as the template for the second PCR amplification (20 cycles) using the same primer set, but the reverse primer contained appropriate adapters and different barcodes to identify samples. PCR products were visualized using 1% agarose gels stained with ethidium bromide, and negative controls were always performed to make sure there was no contamination. The positive amplicons of the three technical replications of each sample were pooled and then quantified using the PicoGreen dsDNA Assay Kit (Invitrogen, CA, USA). All 134 samples (one sample failed to amplify so was not included in the following analysis) were equally combined and followed by gel purification before sequencing. The prepared DNA library was sequenced using an Illumina MiSeq platform with 2 × 250 bp kits at the Institute for Environmental Genomics according Wu et al. (2015).

Quality filtering and processing of the raw MiSeq reads were conducted on IEG's Galaxy pipeline (http://zhoulab5.rccc.ou.edu:8080/root). In brief, after trimming the primer and deleting sequences with Ns, the high-quality sequences with lengths of 245–260 bp were kept for subsequent analysis (Yan et al., 2016). As sequencing depth can affect the estimation of diversity (Fierer et al., 2012), all samples were rarefied to the same sequencing depth by randomly resampling (10,021 sequences per sample) before downstream analysis. Representative sequences from each OTU were assigned to a genus using the UPARSE method at 97% cut-off (Edgar, 2013), and these sequences were also used to align with 16S GreenGene sequences using PyNAST (Caporaso et al., 2010), and a maximum-likelihood tree was constructed using FASTTREE (Price, Dehal, & Arkin, 2009) for the following phylogenetic structure analysis.

To test the hypothesis that environmental filtering may dominate the ecological processes governing bacterioplankton community turnover, we first quantify phylogenetic diversity of communities between a given pair of samples (Yan et al., 2016). Briefly, we applied the R package to calculate the weighted beta nearest taxon index (βNTI, Webb, Ackerly, McPeek, & Donoghue, 2002) separating OTUs into two pairwise communities. The βNTI in combination of Bray–Curtis-based Raup-Crick (RC_{bray}) (Stegen et al., 2013) was further used to quantify the influence of major ecological processes governing the bacterioplankton communities. The relative influence of community turnover determined by the variable selection and homogeneous selection were indicated by the fraction of communities with $\beta NTI > +2$ and $\beta NTI < -2$, respectively (Dini-Andreote, Stegen, van Elsas, & Salles, 2015). If $|\beta NTI| < 2$, but with $RC_{bray} > +0.95$ or <-0.95 suggested that the community turnover is governed by dispersal limitation or homogenizing dispersal, respectively. However, $|\beta NTI| < 2$ and $|RC_{bray}| < 0.95$, indicates a situation where composition turnover is not dominated by any single process as described above (Stegen, Lin, Fredrickson, & Konopka, 2015).

2.6 | Statistical analysis

To test the hypothesis that bacterioplankton may vary repeatedly due to seasonal environmental changes, discriminant function analysis (DFA) was performed to determine changes in community composition and the time series analysis was used to identify significant

autocorrelations and cyclical patterns among seasons as evidence of a repeating pattern. The canonical correspondence analysis (CCA) was further performed to determine which environmental variables were most strongly related to community composition. In addition, the 16S rRNA gene amplicon sequence data were also analysed using the following statistical methods: (i) alpha diversity (e.g., Shannon, Chao 1, Pielou evenness, OTU richness) and beta diversity (based on the Jaccard or Bray–Curtis distance) comparison; (ii) Bray–Curtis-based DCA and UniFrac-based PCoA ordination to show the community similarity according to taxonomic and phylogenetic characteristics, respectively (Yan et al., 2016); (iii) nonparametric tests including multiple-response permutation procedure (MRPP), and permutational multivariate analysis of variance (PERMANOVA) to test whether community dissimilarity are significant or not; (iv) significance tests of any two compared objectives were performed using analysis of variance (ANOVA) with least-significant-difference (LSD) tests; (v) generalized linear models (GLM) for revealing potential spatial and temporal effects on the communities; and (vi) permutational analysis of multivariate dispersion and null deviation analysis according to the method proposed by Chase, Kraft, Smith, Vellend, and Inouye (2011) to reveal whether the taxonomic composition of community is indistinguishable from the null expectation. All the above statistics except the DFA were performed using the "VEGAN," "PHYLOSEQ" and "PICANTE" R programs (R Foundation for Statistical Computing, Vienna, Austria), and the SYSTAT 13 (Systat Software Inc., CA, USA) was used for DFA analysis.

3 | RESULTS

3.1 | Overall community diversity and turnover

Our sequencing effort (rarefied to 10,021 sequences per sample) detected 6639 OTUs (UPARSE at 97% cut-off) from the 134 samples. Among all detected taxa, Proteobacteria accounted for 32.6% of the OTUs. The relative abundance suggested that Proteobacteria (28.3%–37.6% ± 1.5%–2.2%) and Cyanobacteria (19.3%–31.8% ± 2.1%–3.1%) were the most abundant phyla in all four seasons (Fig. S1A), and these two phyla as well as the other relative dominant phylum (Bacteroidetes) generally showed significant shifts between the relatively colder (spring–winter) and hotter (summer–autumn) seasons (Fig. S1B). Briefly, the Proteobacteria and Bacteroidetes decreased significantly ($p < .05$) from spring to summer and then showed no significant shift until autumn, but significantly ($p < .05$) increased in winter. However, the Cyanobacteria showed different trends with an increase in autumn that was maintained until winter.

The OTU richness and Pielou evenness all showed significant (ANOVA, $p < .05$) increases from spring to summer, then remained relatively stable until autumn, and significantly ($p < .05$) decreased in winter (Fig. S2). Interestingly, the alpha-diversity indices (OTU richness and Pielou evenness) significantly (regression models, $p < .05$) increased as the temperature increased (Figure 2). The beta diversity analysis based on the overall community also showed significant ($p < .05$) differences among seasons. For example, both Jaccard and Bray–Curtis dissimilarity tests indicated that the overall composition of bacterioplankton were significantly (MRPP and PERMANOVA, $p < .05$) different between any two compared seasons (Table 1). Such seasonal community patterns (at least those of the summer–autumn and winter-spring trends) were also observed with the Bray–Curtis-based DCA (Figure 3a) and UniFrac-based PCoA ordination (Figure 3b), which generally separated the communities into groups according to the seasons with relative higher (summer–autumn) or lower temperature (spring–winter).

3.2 | Common and dominant bacterial members varied across seasons

The common (detected in more than 50% samples) and simultaneously dominant (relative abundance >1%) OTUs (i.e., OTU_1-6, OTU_8, OTU_11, OTU_43) and genera (i.e., *Albidiferax*, *Polynucleobacter*, *Bacillariophyta*, *Cryptomonadaceae*, *Flavobacterium*, *Haliscomenobacter*) also differed considerably between seasons ($p < .05$), except OTU_1 (Fig. S3A). However, not all of these members showed similar responses to the seasonal variations in Lake Donghu. For example, some OTUs significantly ($p < .05$) increased in summer and remained at relatively high abundance until autumn (e.g., OTU_6 (Cyanobacteria), OTU_11 (Proteobacteria)), but in spring and winter were much lower; some others showed an almost opposite trend and significantly ($p < .05$) decreased their relative abundance in summer and autumn (e.g., OTU_3 (Actinobacteria), OTU_8 (Proteobacteria)). Similarly, at the genus level the relative abundance of *Albidiferax* (Proteobacteria), *Flavobacterium* (Bacteroidetes) in spring

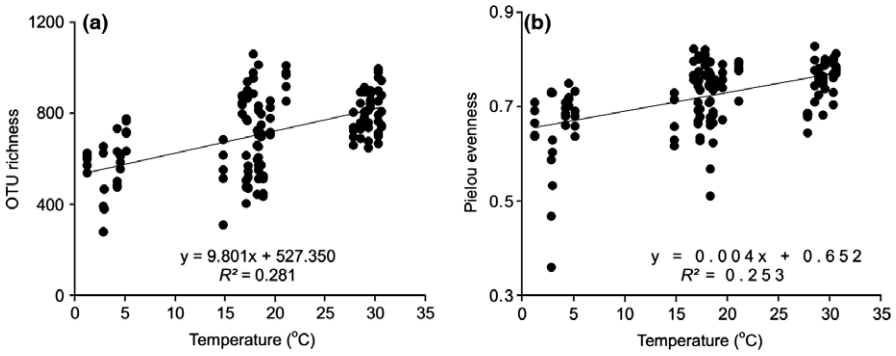

FIGURE 2 Relationship between the bacterial alpha diversity and temperature

TABLE 1 Dissimilarity test showing the differences of bacterioplankton composition between each of two compared seasons

	Jaccard distance-based test				Bray–Curtis distance-based test			
	MRPP		PERMANOVA		MRPP		PERMANOVA	
	Delta	*p*	*F*	*p*	*Delta*	*p*	*F*	*p*
Spring vs. Summer	0.669	**.001**	17.152	**.001**	0.619	**.001**	26.462	**.001**
Spring vs. Autumn	0.680	**.001**	13.359	**.001**	0.613	**.001**	22.122	**.001**
Spring vs. Winter	0.725	**.001**	3.561	**.001**	0.669	**.001**	4.659	**.001**
Summer vs. Autumn	0.631	**.001**	3.582	**.001**	0.555	**.001**	4.872	**.001**
Summer vs. Winter	0.673	**.001**	15.287	**.001**	0.605	**.001**	24.277	**.001**
Autumn vs. Winter	0.685	**.001**	11.338	**.001**	0.597	**.001**	19.402	**.001**
Spring vs. Summer	0.669	**.001**	17.152	**.001**	0.619	**.001**	26.462	**.001**

MRPP, multiple-response permutation procedure; PERMANOVA, permutational multivariate analysis of variance.
p values <.05 in bold.

and winter were significantly ($p < .05$) higher than that in summer and autumn. However, the common and dominant Cyanobacteria genera (i.e., *Bacillariophyta* and *Cryptomonadaceae*) seemed to have more diverse responses to environmental shifts (Fig. S3B).

To further determine whether the seasonal patterns observed for the bacterioplankton communities were repeatable across the sampling period, we applied an eigenvector technique—discriminant function analysis (DFA)—to evaluate the changes in common and dominant OTUs. Results indicated that the first discriminant function (DFA1) of each data set (i.e., common or dominant OTUs) showed highly repeatable patterns through time. Time series analysis based on the DFA1 scores indicated that the compositional pattern of communities tended to be distinct in different seasons, but were very similar within the same season (Figure 4). This pattern was repeated year by year, indicating strong, repeatable seasonal fluctuations of bacterioplankton communities in Lake Donghu for both common and dominant OTUs (Figure 4).

3.3 | Ecological processes governing the assembly of bacterioplankton communities

Bray–Curtis distance-based permutational analysis of bacterioplankton communities indicated that the observed β-diversity was significantly (PERMDISP, $p < .05$) different from a randomly permutated community within each season (Table S1). Using null deviation analysis (keep alpha and gamma diversity of the whole/group data constant, Chase et al., 2011), we also found that the observed community similarities within seasons were significantly ($p < .05$) higher than those from random permutations. The analysis with the presence/absence-based Jaccard distance also suggested that the observed communities were significantly ($p < .05$) different from the null random expectation in all seasons (data not shown). These results suggested that the community composition of bacterioplankton in Lake Donghu could be primarily governed by deterministic processes (e.g., environmental filtering or competition) rather than stochastic ones.

We further applied phylogenetic analysis to determine how the bacterioplankton communities assembled and to clarify which ecological processes governed the communities as described previously (Stegen et al., 2013; Yan et al., 2016). As microbial communities often have a relatively small number of high-abundance members coupled with a long tail of low abundance members (Shafquat, Joice, Simmons, & Huttenhower, 2014; Sogin et al., 2006), here we focused only on the abundance-weighted relatives (i.e., using weighted βNTI in combination with RC_{bray}) to quantify the ecological processes that influence bacterioplankton composition. As expected, the deterministic process of homogeneous selection, which causes community composition to be similar under consistent environmental conditions (Dini-Andreote et al., 2015), was largely responsible for the assembly and turnover of bacterioplankton communities in Lake Donghu (75%–82%, Figure 5), while dispersal limitation, which causes divergence in community composition due to limited exchange of microbes (Stegen et al., 2013), only contributed 12%–23% to the community assembly.

3.4 | Environmental factors affecting the bacterioplankton community

Generalized linear models (GLM) were used to evaluate spatial and temporal shifts in both biotic and abiotic features of the ecosystem. Our results suggested that both biotic (e.g., bacterioplankton community diversity, abundance of particular bacterial genus or phylum) and abiotic factors (e.g., nutrient, temperature, pH, heavy metals) almost all significantly ($p < .05$) differed between seasons (Table 2). However, there was no significant ($p > .05$) interactive effect of season*station for any of the investigated factors. It should be noted that temperature, which shows significant and positive relationship with the OTU richness and Pielou evenness, appears to have an important influence over alpha diversity of the bacterioplankton in Lake Donghu (Figure 2). From the CCA ordination (Figure 6), we found that the investigated communities were significantly distributed across the water temperature gradient (ANOVA, $F = 3.226$, $p = .01$), indicating microbial composition seems to be mainly affected by the temperature or attribute to environmental factors that are directly or indirectly correlated with the temperature. For example, although TP only showed a weak correlation with the temperature (regression models, $R^2 = .20$, $p < .05$), its relatively long

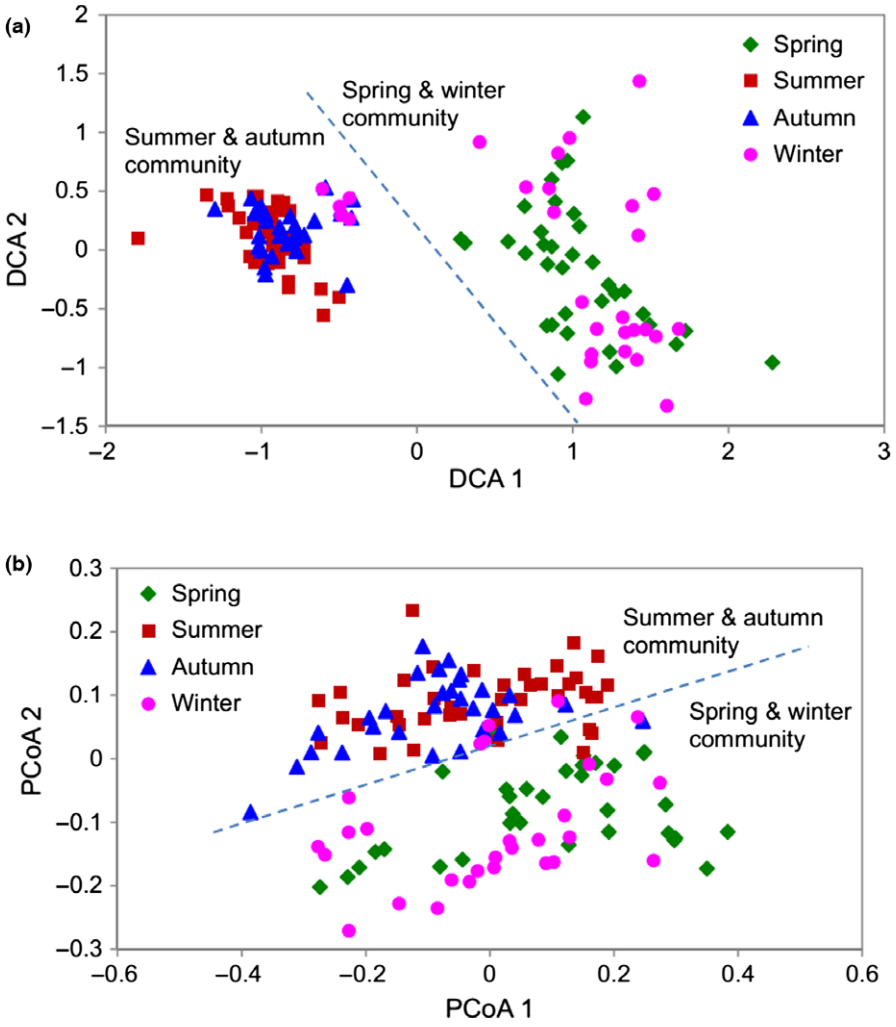

FIGURE 3 Detrended correspondence analysis (a) and principal coordinates analysis (b) illustrating the bacterial community dissimilarity among seasons, which were calculated according to the weighted Bray–Curtis distance and UniFrac phylogenetic distance, respectively

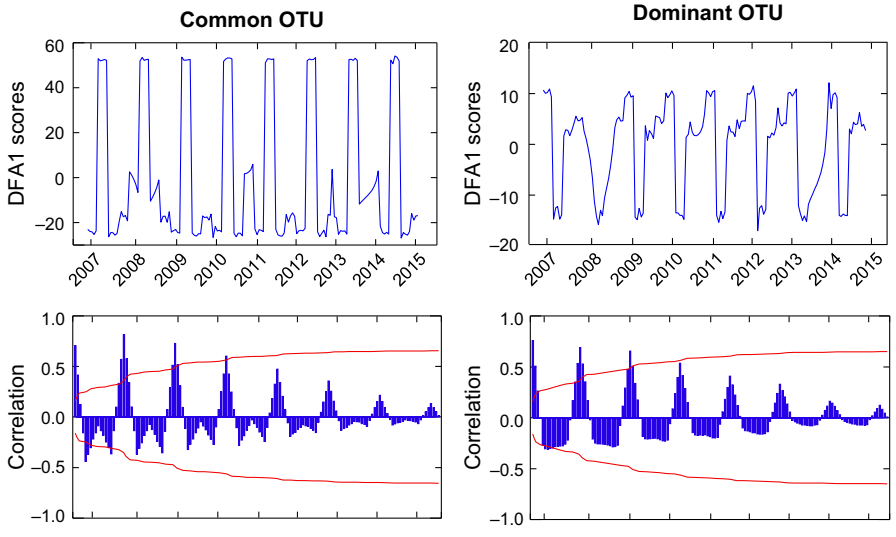

FIGURE 4 Annually repeating patterns of bacterioplankton communities sampled seasonally in Lake Donghu as determined by discriminant function analysis (DFA). Upper panel shows the time series analysis of the first discriminant function (DFA1) scores; lower panel shows the autocorrelation of the discriminant function across all time lags. The red lines in the lower panel represent correlations with $p < .05$

arrow and very small angle with the water temperature as visualized in the CCA ordination (ANOVA, $F = 2.507$, $p = .01$) suggest significant effects on the seasonal bacterioplankton community patterns. On the other hand, the transparency (ANOVA, $F = 3.349$, $p = .01$) and As (ANOVA, $F = 2.546$, $p = .01$) also showed strong (indicated by relatively long arrows) and significant relationship with the community composition, but it did not contribute much to the seasonal variation in community composition.

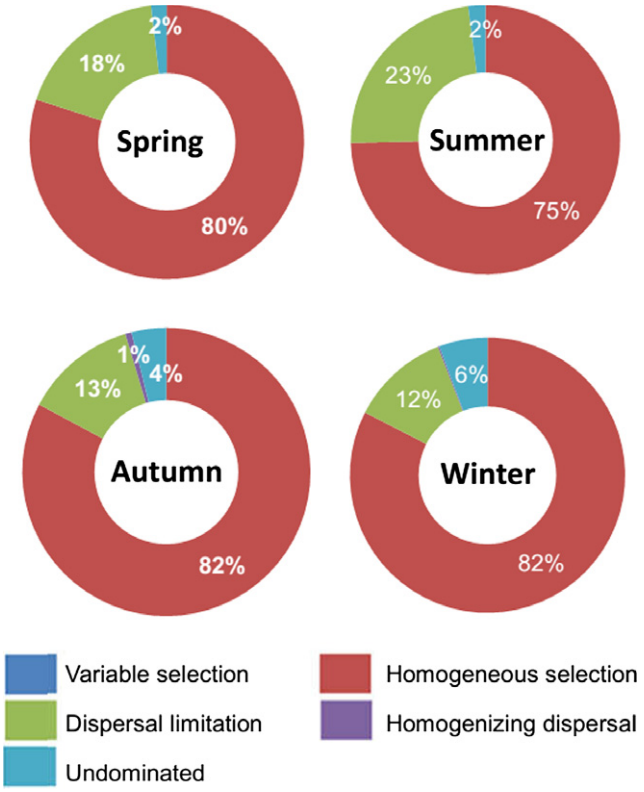

FIGURE 5 Summary of ecological processes govern the bacterioplankton community turnover within each season. The percentages are given the relative contribution of each process to the community turnover as indicated by different colours

4 | DISCUSSION

Previous studies on bacterioplankton diversity patterns were mainly restricted to single dimensions such as short time periods (1 or 2 years) or horizontal/vertical profiles across particular environmental gradients (Fortunato et al., 2012). However, comparisons of both spatial and temporal dimensions over a long time period (e.g., ~10 years) remain rarely explored. In this study, we presented bacterioplankton communities in a well-documented shallow eutrophic lake (Lake Donghu, Wuhan, China) across two dimensions: spatially across the five major lake areas (Figure 1) and temporally across nearly one decade with seasonal interval. Although planktonic microbes in Lake Donghu have been found to be significantly different among seasons within a single year (Yu et al., 2008; Zhang, Yan, Yu, & Dai, 2014), it was unknown whether bacterioplankton communities displayed similar seasonal patterns year after year, especially during the construction of ecological projects. Interestingly, the present study showed very clear, repeatable patterns in the composition of both common and dominant OTUs across 2007 to 2015 (Figure 4), suggesting that the dynamics of bacterioplankton in Lake Donghu may be primarily governed by environmental factors that change seasonally. This finding differs from previous studies of bacterial community temporal patterns in some other lake systems. For example, in a boreal forest lake, there was no clear seasonal pattern but just a gradual change over time (Lindström, 1998); in a humic lake, there was little similarity from year to year (Kent et al., 2004); in temperate lakes, no recurring seasonal changes were observed (Yannarell, Kent, Lauster, Kratz, & Triplett, 2003). The sharp contrast between repeatable patterns shown here and lack of repeatable patterns in previous studies could be due to methodological differences and/or local characteristics of the different lake systems. However, our results agree with more recent studies in marine ecosystems showing clear seasonal variability of microbial communities (Chow et al., 2013; Cram et al., 2015; Gilbert et al., 2012).

The extent to which microbial composition is driven by the same environmental factors across different systems (e.g., marine vs. freshwater) is currently uncertain (Fortunato et al., 2012). For example, salinity and depth (and covarying features) appear to be major factors that affect bacterioplankton in marine ecosystems (Fuhrman et al., 2015), but pH (Ren et al., 2015) and productivity (Kara et al., 2013) seem to be more important in freshwater ecosystems. On the other hand, there are also some common factors (e.g., temperature, nutrients) that showed significant effects on both marine and freshwater bacterioplankton. As expected, our results are consistent with an important influence of temperature over bacterioplankton composition, including OTU richness, evenness and temporal turnover in composition (Figures 2 and 6). However, there was no significant spatial effect on the observed community patterns, which is likely due to consistent environmental conditions across sampling stations (Table 2). However, at much greater spatial scales with clearer environmental gradients, such as across river to ocean ecosystems, the spatial variability would likely overwhelm seasonal patterns of the bacterioplankton communities (Fortunato et al., 2012).

Findings from our present study and previous work (e.g., Crump & Hobbie, 2005; Fortunato et al., 2012) suggest that bacterioplankton communities are not assembled randomly, and are mainly determined by environmental conditions. We found that 75%–82% of community turnover in Lake Donghu was governed by the deterministic process of homogeneous selection, which causes the community composition to be similar under consistent environmental conditions (Dini-Andreote et al., 2015). This may partly due to the most abundant phylum of Proteobacteria, as their rapid growth can quickly lead to this group becoming abundant under suitable conditions (Fuhrman & Hagström, 2008). However, different members of the Proteobacteria showed different responses to seasonally changing factors, with some peaking in colder seasons while others peaking at relatively higher temperature seasons (Fig. S3). Our time series analyses (Figure 4) also provide evidence that repeatable environmental conditions—most likely temperature—impose repeatable selective environments that deterministically govern community composition.

The alpha diversity (OTU richness and Pielou evenness) in hotter seasons (summer and autumn) were significantly higher than that in colder seasons (spring and winter) (Fig. S2), and temperature may be responsible for this. Indeed, we found temperature was positively correlated (regression models, $p < .05$) with the alpha diversity metrics (Figure 2). This temperature effect may be similar to mechanisms leading to the latitudinal diversity gradient of planktonic bacteria

TABLE 2 Summary of generalized linear models (GLM) showing the statistical significance of the bacterial and environmental characteristics

		Season		Station		Season*station	
Parameters	**No. valid values**	***F***	***p***	***F***	***p***	***F***	***p***
Alpha diversity							
Shannon	134	29.729	**<.001**	2.518	**.045**	0.661	.785
Pielou evenness	134	19.945	**<.001**	2.676	**.035**	0.678	.769
Chao 1	134	25.223	**<.001**	2.291	.064	0.996	.457
OTU richness	134	48.626	**<.001**	0.985	.419	0.712	.737
Dominant phyla							
Proteobacteria	134	4.411	**.006**	0.783	.539	0.759	.691
Cyanobacteria	134	4.708	**.004**	1.737	.147	0.745	.705
Bacteroidetes	134	17.248	**<.001**	0.844	.500	0.371	.971
Actinobacteria	134	0.757	.520	0.179	.949	0.091	1.000
Common and dominant genera							
Albidiferax	134	57.024	**<.001**	0.809	.522	0.299	.988
Polynucleobacter	134	8.783	**<.001**	2.040	.093	0.306	.987
Bacillariophyta	134	3.264	**.024**	5.726	**<.001**	0.620	.822
Cryptomonadaceae	134	7.742	**<.001**	1.219	.307	0.575	.859
GpIIa	134	40.087	**<.001**	0.688	.602	0.914	.535
Flavobacterium	134	16.169	**<.001**	0.511	.728	0.338	.980
Haliscomenobacter	134	3.697	**.014**	1.901	.115	0.547	.879
Environmental characteristics[a]							
TN (mg/L)	115	3.476	**.019**	0.991	.416	0.515	.900
TP (mg/L)	125	9.300	**<.001**	0.226	.923	0.065	1.000
COD_{Mn}	134	4.700	**.004**	0.349	.844	0.102	1.000
pH	100	4.121	**.009**	0.409	.802	0.224	.997
Water temperature (°C)	100	356.21	**<.001**	0.839	.504	0.261	.993
As (μg/L)	123	8.521	**<.001**	6.075	**<.001**	0.263	.993
Cr (μg/L)	134	3.013	**.033**	0.577	.680	0.040	1.000

TN, total nitrogen; TP, total phosphorus; COD_{Mn}, chemical oxygen demand; As, arsenic; Cr, chromium.
p values <.05 in bold.
[a]There have some missing values due to environmental samples were not collected or failed in measurement for some sampling events.

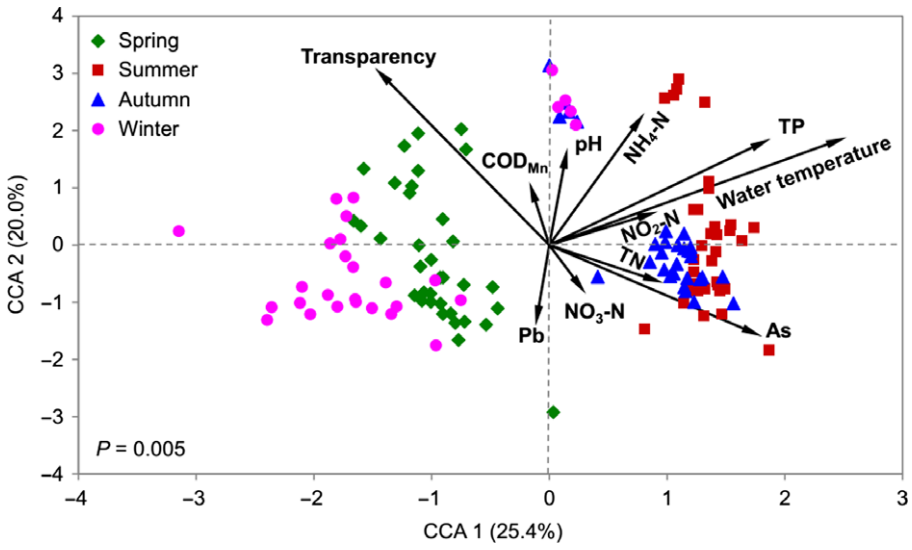

FIGURE 6 Canonical correspondence analysis (CCA) showing the relationships between bacterioplankton communities (response variables) and environmental factors (explanatory variables). Only the factors that significantly ($p < .05$) correlated with the communities were kept in the final analysis, and the given *p* value was determined by ANOVA

(Fuhrman et al., 2008). Of course, there may also have other environmental factors that vary with temperature will contribute to the observed repeatable seasonal patterns. The nutrient exchange between water and sediments, for example, can be enhanced with an increase in temperature due elevated biological activity (Boström, Andersen, Fleischer, & Jansson, 1988). This could result in the observed high concentration of TP in summer (Fig. S4, Table S2), and in turn, such nutrient variation among seasons may also contribute somewhat to the seasonal differences of bacterioplankton community as discussed above (Figure 6).

Findings of the present study together with our previous investigations (Yan et al., 2007; Yu et al., 2008) performed at the same stations in Lake Donghu all suggested that the seasonal variability of the bacterioplankton communities overwhelms any spatial patterns within this eutrophic urban lake in the past decade. Although the "Great Lake Donghu Ecological Water Network" project started a couple of years after our first sampling time (March 2006 in Yan et al., 2007), we did not detect any clear disturbance in bacterioplankton composition at the seasonal scale. Therefore, connecting the six lakes around Lake Donghu at least did not change the seasonally repeatable patterns of the bacterial communities. Significant changes in ecological patterns may occur only with serious disturbance (Ferrenberg et al., 2013). However, the six lakes around Lake Donghu are only connected by an ecological water network, which is expected to greatly enhance natural water purification and ecological restoration in Lake Donghu. This should make the "Great Lake Donghu" ecosystem more stable and therefore maintain the seasonally repeatable patterns of the observed bacterioplankton communities. Further monitoring should go ahead and determine whether such seasonal patterns will continue. However, results generated by analysing samples collected from multiple locations across the lake suggest that there is little spatial variation, so one or two sampling sites may be enough to reflect the seasonal variability of bacterioplankton in Lake Donghu.

In summary, the repeatable seasonal bacterioplankton patterns that were dominated by strong homogeneous selection with modest dispersal limitation suggest that the bacteria in this lake system are mainly controlled by deterministic processes, and can disperse throughout the lake system within a season. In other words, when there has turnover in community membership, ecologically similar (and closely related) taxa in the community are interchanged, suggesting functional (or least ecological) redundancy within a season. However, the microbial taxa are more specialized among seasons due to environmental filtering (e.g., temperature, nutrient availability and heavy metal contamination) and some related biological interactions (e.g., predation and symbiosis), which caused community composition vary among seasons. Therefore, the dominant bacterial niches available in each season are occupied by similar combinations of bacterial taxa and show repeatable seasonal patterns across nearly a decade-long period. These repeatable seasonal patterns shown here indicate strong environmental control over bacterioplankton communities. Just as Fuhrman et al. (2006) reported that annually reoccurring bacterial communities in ocean ecosystems are predictable based on environmental factors, the present study may improve our ability to use process-based models to predict ecosystem response to environmental change in freshwater ecosystems.

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DATA ACCESSIBILITY

All Illumina MiSeq raw sequence data were deposited under NCBI BioProject Accession no. PRJNA380987.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Q.Y. and Y.Y. designed the study; Q.Y. generated the data, performed the analyses and wrote the manuscript; Y.D., X.L., S.W., L.D., X.Z., J.L., C.W., J.N., X.L., H.H., F.X., W.F., D.N. and L.W. assisted with the analytic tools or with sample preparation; J.C.S., Z.H., J.D.V.N. and J.Z. provided comments and edited the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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