Regime transition Shapes the Composition, Assembly Processes, and Co-occurrence Pattern of Bacterioplankton Community in a Large Eutrophic Freshwater Lake

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Abstract
At certain nutrient concentrations, shallow freshwater lakes are generally characterized by two contrasting ecological regimes with disparate patterns of biodiversity and biogeochemical cycles: a macrophyte-dominated regime (MDR) and a phytoplankton-dominated regime (PDR). To reveal ecological mechanisms that affect bacterioplankton along the regime shift, Illumina MiSeq sequencing of the 16S rRNA gene combined with a novel network clustering tool (Manta) were used to identify patterns of bacterioplankton community composition across the regime shift in Taihu Lake, China. Marked divergence in the composition and ecological assembly processes of bacterioplankton community was observed under the regime shift. The alpha diversity of the bacterioplankton community consistently and continuously decreased with the regime shift from MDR to PDR, while the beta diversity presents differently. Moreover, as the regime shifted from MDR to PDR, the contribution of deterministic processes (such as environmental selection) to the assembly of bacterioplankton community initially decreased and then increased again as regime shift from MDR to PDR, most likely as a consequence of differences in nutrient concentration. The topological properties, including modularity, transitivity and network diameter, of the bacterioplankton co-occurrence networks changed along the regime shift, and the co-occurrences among species changed in structure and were significantly shaped by the environmental variables along the regime transition from MDR to PDR. The divergent environmental state of the regimes with diverse nutritional status may be the most important factor that contributes to the dissimilarity of bacterioplankton community composition along the regime shift.

Keywords Lake water · Regime shifts · Non-linear change · Bacterial community · Network analysis

Introduction
At certain eutrophic states, shallow lakes are generally characterized by two contrasting ecological regimes. These include a clear macrophyte-dominated regime (MDR) and a turbid phytoplankton-dominated regime (PDR) [1, 2]. The shift between the two alternative states is related to nutrient concentrations, specifically phosphorus and nitrogen. These nutrients maintain strong impacts on the structure and function of the ecosystem and are generally introduced through

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anthropogenic activities [3–5]. Once nutrient concentrations rise above a certain threshold, lakes may change from MDR to PDR and their ecosystems undergo drastic changes [6, 7]. These changes include phytoplankton blooms, gradual or rapid degradation of macrophytes, lower richness and diversity in the community of invertebrates and fishes, as well as the elevated water turbidity [2, 8–11]. These regimes may be alternative stable states, with the presence of a specific regime determined by a lake’s history. Previous studies have provided the evidences of such alternative stable state dynamics in small mesocosms [12, 13]. However, the evidence of alternative stable states in natural ecosystem is scarce due to the high complexity, as well as the temporal and spatial scale of the ecosystem [14].

This regime transition from MDR to PDR has been linked to changes in the nutritional status before, as the nutrients could alter the top-down effects on lower trophic levels by controlling the macrophyte and algal blooms [5, 15]. The composition of the bacterial communities in MDR and PDR may be different due to the contrasting decomposition products of algae and macrophytes, respectively [16]. Moreover, the bacterioplankton community composition may be shaped by the changed biotic interactions, such as predation and competition, due to the changed food webs in MDR and PDR [17, 18]. To date, there have been multiple studies establishing major differences in bacterioplankton community composition and diversity between these two regimes. For example, the alpha diversity of bacterioplankton community in MDR has been observed to be significantly higher than that in PDR [19]. The MDR appears to be dominated by Actinobacteria, Betaproteobacteria and Verrucomicrobia, whereas higher percentages of Alphaproteobacteria, Gammaproteobacteria, Cyanobacteria and Planctomycetes are observed in the PDR [20]. Dissolved organic carbon and macrophyte biomass are demonstrated to be important factors that driving the bacterioplankton community changes between these two regimes in Lake Taihu [21, 22]. Our previous study also found that bacterial community in the MDR maintained fewer functional genes (such as nitrogen cycling functional genes) but more microbial associations compared to the PDR regime [3]. The comparison of bacterial communities in MDR and PDR is important and has been well studied, but a continuous sampling along the regime transition seems to be also important but has not been well investigated. Whether bacterioplankton community composition (such as the relative abundance of bacterial species and diversity) changes linearly or non-linearly along the regime transition remains unknown. Here, we analyzed the dynamics of bacterioplankton communities and link them to the changes in physicochemical parameters. More specifically, we addressed whether bacterioplankton community composition changes linearly or non-linearly along the regime transition between MDR and PDR.

The underlying mechanisms that drive the variations in bacterial community composition between sites are often summarized in two ways: niche-based selection and neutral processes [23, 24]. Nevertheless, there is a controversy about the relative importance of these two processes in driving microbial communities [25]. Stegen et al. (2013) developed a procedure for the quantitative estimation of the influence of ecological processes such as drift, selection and dispersal on bacterial community composition. This procedure demonstrated that both stochastic and deterministic processes appear to govern the assembly processes of bacterial communities [26, 27]. However, a more comprehensive understanding of the bacterioplankton community composition in the context of eutrophic lakes requires a thorough description of the abiotic drivers of co-occurrence patterns [28]. An inter-regime bacterioplankton co-occurrence network can demonstrate how clusters of organisms are driven by abiotic factors along regime shifts in freshwater lakes [29, 30]. Moreover, clusters in the species’ co-occurrence networks may be indicative of ecological processes governing community structure, such as niche filtering and habitat preference [31]. Additionally, microbial co-occurrence networks can predict hub species and potential interactions between species [32], thereby contributing to a deeper understanding of the underlying mechanisms that dominate the assembly processes of bacterioplankton communities along the regime shift in freshwater lakes.

Taihu Lake is a typical large shallow eutrophic lake composed of several connected lake zones that maintain different nutrition loadings [33]. It provides an ideal place to investigate the impact of regime transition on the bacterioplankton community. Although it is challenging to infer whether these are truly alternative stable states in the temporal sense in Taihu Lake, the physiochemical characteristics and the distribution of macrophytes in Taihu Lake could reflect the existence of MDR, PDR, and a transition between these two regimes [20]. High spatial heterogeneity in the abundance of macrophytes and phytoplankton suggests variation in the responses to eutrophication within the lake, which may be a result of a specific distribution pattern of critical nutrient loadings in Taihu Lake [34]. Studies on bacterioplankton communities across regime (spatial) shifts from MDR to PDR in Taihu Lake are of great significance to provide insights into the mechanism of biodiversity and regime maintenance in the lake ecosystem. In this study, high-throughput sequencing of the 16S rRNA genes was used to identify the patterns of bacterioplankton community composition across Taihu Lake, China. We addressed the following research questions (1) Does the diversity of bacterioplankton community and relative abundance of different bacterial species change linearly or non-linearly along the regime transition from MDR to PDR? (2) Which process dominates the bacterioplankton community assembly along
the regime transition? (3) Are there core factors that drive the changes in the bacterioplankton community composition along the regime transition?

**Materials and Methods**

**Sample Collection and High-Throughput Sequencing**

The samples and sequencing data in this study came from our previous study [3]. Briefly, six sampling sites across Taihu Lake (30°55′-31°32′58″N, 119°52′32″-120°36′10″E) were selected along the transition from the macrophyte-dominated regime (MDR) to the phytoplankton-dominated regime (PDR) (MDR-Core1, MDR-Core2, MDR-Edge, PDR-Edge, PDR-Core2, PDR-Core1) (Fig. S1) in August 2013. The dominant species of macrophytes in the MDR included *Potamogeton maackianus*, *Vallisneria natans*, and *Zizania latifolia* [35]. Water sampling, large plankton removal and bacterioplankton collection were described in our previous study [3]. A 5-L Schindler sampler was used to collect water samples at a depth of 0.5 m at each sampling point. After removing large plankton and other particles with 5-μm pore-sized polycarbonate filters, 0.22-μm polycarbonate filters were used to collect the bacterioplankton in the water samples. The physicochemical properties of the water samples, including the pH, dissolved oxygen (DO) and turbidity were measured in situ using a calibrated multifunction water quality sonde (YSI 6600, Yellow Springs, OH, USA). The concentrations of total nitrogen (TN), total phosphorus (TP), ammonium (NH₄⁺-N), nitrate (NO₃⁻-N), nitrite (NO₂⁻-N), orthophosphate (PO₄³⁻-P), dissolved total nitrogen (DTN) and dissolved total phosphorus (DTP), dissolved organic carbon (DOC) and concentrations of chlorophyll a (Chl a) were further determined [3].

The detailed information of DNA extraction, amplification, and high-throughput sequencing were described in our previous study [3]. In brief, microbial DNA was extracted, purified and the concentration and purity of the DNA was determined using the spectrophotometric method [36]. The bacterial 16S rRNA gene (V4 hypervariable region) was amplified and then sequenced using an Illumina MiSeq platform using the universal primers 515F (5′-GTG CCA GCMGCCGCGG-3′) and 806R (5′-GGACTACHVGGGT WTCTTAAAT-3′). The paired-end raw sequences were processed to control the quality by the Galaxy Pipeline (http://zhioulab5.rccc.ou.edu:8080/root/login?redirect=%2F) and then processed with QIIME v1.9.1 [36] as described in our previous study [3]. The raw reads were deposited into the NCBI Sequence Read Archive (SRA) database (BioProject: PRJNA511603).

**Statistical Analyses**

The pipeline-based subsampled OTU table was used for the following statistical analyses. The OTU richness, Simpson evenness and Faith’s phylogenetic diversity were calculated with the QIIME scripts ‘alpha_diversity.py’ [37, 38]. Unweighted UniFrac [39] was calculated to quantify the phylogenetic beta diversity of bacterioplankton communities [27]. A principal coordinates analysis (PCoA) plot was constructed using the Bray–Curtis dissimilarity index and unweighted UniFrac matrices with the ‘vegan’ package (version 2.5-6) [40] in R software (version 3.6.1). Akaike information criterion values for linear-regression model and quadratic-regression of correlations between bacterial phylum and total phosphorus were calculated to select the proper models (Table S1). The bacterioplankton community composition along the regime transition was compared using analysis of similarity (ANOSIM) with the ‘vegan’ package (version 2.5-6) [41]. All environmental variables were standardized with the ‘scale’ function, prior to calculating the Euclidean distances of environmental variables with the ‘vegdist’ command in the ‘vegan’ (version 2.5-6) package of R software (version 3.6.1). We used centered log-ratio (clr) transformed abundance data with the ‘clr’ function in the ‘compositions’ (version 2.0-1) package in R software (version 3.6.1) during this step to ensure compositional coherence [42]. Mantel and partial Mantel tests were performed to determine if the differences in bacterioplankton community composition between the samples were correlated with environmental parameters using the ‘vegan’ package (version 2.5-6) in R [43].

A phylogenetic tree [44] was constructed based on the aligned sequences using the sequence analysis tools of the Galaxy Pipeline (http://zhioulab5.rccc.ou.edu:8080). The ‘picante’ package (version 1.8) in R software (version 3.6.1) was used to reveal changes in assembly processes of bacterial community along ecological gradients in Taihu Lake [27, 45]. The following measures were calculated with this package: MTND, ses.MNTD, betaMNTD and betaNTI. Significantly negative mean nearest taxon distance (MNTD) and standardized-effect size of the MNTD (ses.MNTD) values indicate that the bacterioplankton communities have a tendency to be more phylogenetically clustered than would be expected by chance [27, 46]. The beta mean nearest taxon distance metric (betaMNTD) is based on the phylogenetic turnover between communities in pairs [47, 48]. For the beta nearest taxon index (betaNTI) metrics, values between -2 and +2 are expected under stochastic process shaping community assembly; beyond that, betaNTI values are statistically significant [45, 48]. The betaNTI in combinations with the Bray–Curtis-based Raup-Crick (RCbray) was further assessed to examine the importance of major ecological processes (homogeneous selection, variable selection, dispersal
limitation, homogenizing dispersal and undominated) that drive the assembly of bacterioplankton communities along the regime transition, following the methods described in Stegen et al. (2013) [26].

Network Analysis

The pipeline-based OTU table was further used for network analysis. The samples were divided into six groups along the transition from macrophyte-dominated regime (MDR) to the phytoplankton-dominated regime (MDR-Core1, MDR-Core2, MDR-Edge, PDR-Edge, PDR-Core2, PDR-Core1) (Fig. S1). We constructed six co-occurrence networks from the six sampling sites along the regime transition and one global network based on all of the 54 samples. To avoid unreliable network inference on zero-rich taxa, only the most prevalent OTUs (those detected in at least 50% of samples in each regime, that is, 5 samples in one sampling site) were considered. In order to avoid the taxon number biases, we further trimmed each community dataset of sampling sites into the same taxon number, finally keeping the 527 most-abundant OTUs. CoNet was used to individually construct networks for the six sampling sites following the protocols described previously [49, 50] with minor modifications. In brief, the distribution of all pair-wise scores was calculated for each of five similarity measures (Bray–Curtis dissimilarity, Kullback–Leibler dissimilarity, Pearson and Spearman correlation, and Mutual Information), and the top 1000 positive and 1000 negative edges supported by at least two measures were retained initially. For each measurement and edge, 100 permutations (with renormalization for correlation measures) and bootstrap scores were generated, following the ReBoot routine. The measure-specific P-value was then computed, merged using Brown’s method and discarded applying Benjamini-Hochberg’s false discovery rate correction (edges with adjusted $P \geq 0.05$ were removed) [50]. Edges with scores outside the 95% confidence interval defined by the bootstrap distribution or not supported by at least two measures were discarded as well [50]. Topological properties of the networks were calculated in R software using ’igraph’ packages (version 1.2.4.1) [51], and networks were visualized using the Cytoscape software (version 3.6.1) [52]. Environmental variables were further integrated into the networks to reveal the relationship between nodes and environmental variables. Only correlations between environmental variables and species that were significant ($P < 0.05$, Benjamini–Hochberg adjust) and strong ($r \geq 0.75$ or $r \leq -0.75$) were considered. A novel microbial association network clustering algorithm (Manta) (version 1.0.1), which determines the optimal cluster number automatically, was used to separate the global network into clusters with default settings [28] after calculating the global network based on all 54 samples across the regime shift from MDR to PDR. Indexes, including modularity, clustering coefficient, average path length, network diameter, average degree and graph density were calculated using the ’igraph’ packages in R to describe the attributes of a network [53]. One thousand random networks were generated using the ’igraph’ packages in R, and all of the indexes of the random networks were calculated individually. A statistical Z-test was used to verify if the network indexes between the observed and random networks were significantly different.

The topological roles of certain nodes were determined by within-cluster connectivity ($Z_i$) and connectivity among clusters ($P_i$), which reflect the connection between a node to nodes within its cluster and those in other clusters [53, 54]. $Z_i$ and $P_i$ are calculated according to Guimerà and Amaral (2005). The nodes in a network are divided into four subcategories according to the simplified classification: peripheral nodes, connectors, cluster hubs and network hubs [54, 55]. The topological properties of nodes in a co-occurrence network can reveal species that correlate in their responses to the environment and may therefore be indicators of these responses. The topological role of each OTU was determined according to the scatter plot of within-cluster connectivity ($Z_i$) and among-cluster connectivity ($P_i$) [56]; including: Peripheral nodes ($Z_i \leq 2.5, P_i \leq 0.62$) that have only a few links and seldom connect to other clusters; connectors ($Z_i \leq 2.5, P_i > 0.62$) that are highly linked to several clusters; cluster hubs ($Z_i > 2.5, P_i \leq 0.62$) that are highly connected to nodes in their own clusters; network hubs ($Z_i > 2.5, P_i > 0.62$) that act as both cluster hubs and connectors.

Results

Environmental Heterogeneity in the Sampling Sites Across the Regime Transition

The geographic distance was significantly correlated with Euclidean distance of environmental parameters (Fig. S2, $P < 0.001$), indicating that more distant samples were more dissimilar in terms of their environmental parameters. TP concentrations were significantly different along the regime transition from the macrophyte-dominated regime (MDR) to the phytoplankton-dominated regime (PDR) (Fig. S3). Furthermore, almost all of the environmental parameters at six sampling sites across the transition from MDR to PDR were significantly correlated with TP (Fig. S4). The concentrations of TN, $\text{NO}_2^-$-N, TP, DTP, $\text{PO}_4^{3-}$-P, DOC, and Chl a continuously increased with the regime shift from MDR to PDR, while the concentrations of DTN and $\text{NO}_2^-$-N significantly decreased with the regime shift (Fig. S4).
Community Composition and Assembly Processes of Bacterioplankton Altered Along the Regime Shift from MDR to PDR

In total, we obtained 1,877,021 high-quality sequences from 54 samples. To correct bias due to the different sequencing depths, we randomly subsampled the minimum amount of sequences (13,368 sequences) from each sample. The total OTU richness was 18,655 at a 97% similarity level for all samples. Indices of the OTU richness, phylogenetic diversity and Pielou’s evenness of the bacterioplankton community significantly decreased along the regime shift from MDR to PDR (Fig. 1a). The NMDS plot revealed that based on both of the taxonomy and phylogeny, the bacterioplankton community clustered together for each site, along the regime transition from MDR to PDR and were significantly different from each other (Fig. 1b and Table S2). As the regime shifted from MDR to PDR, the beta diversity of macrophyte-dominated regime (MDR) and phytoplankton-dominated regime (PDR) in Taihu Lake (a). Nonmetric multidimensional scaling plots based on the taxonomic dissimilarity (Bray–Curtis distance) and phylogenetic dissimilarity (UniFrac) (b)

Fig. 1 Spearman correlations between operational taxonomic units (OTUs) richness, phylogenetic diversity of the bacterioplankton community and Pielou’s evenness index of the bacterioplankton community and total phosphorus (TP) along the regime shift from macrophyte-dominated regime (MDR) and phytoplankton-dominated regime (PDR) in Taihu Lake (a). Nonmetric multidimensional scaling plots based on the taxonomic dissimilarity (Bray–Curtis distance) and phylogenetic dissimilarity (UniFrac) (b)
bacterioplankton community increased and reached its peak at the PDR-Edge site (Fig. S5 and S6). The average relative abundance of bacterial phyla and genera changed along the regime shift from MDR to PDR (Fig. 2 and Fig. S7). *Bacteroidetes*, *Betaproteobacteria* and *Actinobacteria* dominated the bacterioplankton community at the MDR-Core1 site (Fig. 2a). As opposed to a gradual change of communities along the environmental gradient of regime transition from MDR to PDR, the results demonstrate that the relative abundance of all taxa changed with increased TP concentration linearly or non-linearly (Fig. 2b, $P < 0.001$ in all cases). Moreover, the non-linear model fit better for

![Fig. 2](image_url)

**Fig. 2** Relative abundances of bacterial phyla in samples along the regime shift from macrophyte-dominated regime (MDR) to phytoplankton-dominated regime (PDR) in Taihu Lake (a). Spearman correlations between the relative abundances of bacterial phyla and total phosphorus (TP) (b). Akaike information criterion values were calculated to select the proper models (Table S7).
most taxa (Table S1). Typically, as the regime shifted from MDR to PDR, the relative abundance of *Betaproteobacteria* decreased non-linearly and gradually, whereas abundance of *Actinobacteria* increased non-linearly and reached its peak at the MDR-Edge site. *Firmicutes* and *Gammaproteobacteria* became abundant at the PDR-Edge site, and respectively dominated the PDR-Core sites with a linear and non-linear tendency, respectively.

Both taxonomic and phylogenetic dissimilarity of bacterioplankton community were significantly correlated with environmental distance along the regime shift (Fig. S8, \( P < 0.05 \)). Concentrations of TP along the MDR and PDR showed significant negative correlations with the alpha diversity of the bacterioplankton community (Fig. 1a), indicating that the alpha diversity decreased with increasing nutrient concentration under the regime shift. Significant positive correlations between the TP dissimilarity and beta diversity of bacterioplankton community were also observed (Fig. S9), indicating that the differences of TP concentration between the samples contribute to the heterogeneity of bacterioplankton communities along the regime shift from MDR to PDR. Based on the Mantel test and partial Mantel test results (Table S3), the bacterioplankton community was significantly correlated with most of the environmental parameters along the regime shift (\( P < 0.05 \)), especially for TP (\( R = 0.7645 \) and 0.5377 for Mantel test and partial Mantel test, respectively). The PCoA plot further highlighted that the community composition aligned well to environmental parameters (Fig. 3).

Almost all of the betaNTI values were considerably less than \(-2\) (Fig. S10a). This suggests that deterministic processes dominate in shaping the bacterioplankton communities along the two regimes [48]. Moreover, as the regime shifted from MDR to PDR, the contribution of deterministic processes first decreased in the edge sites and then increased again closer to the PDR. Furthermore, the assembly analysis revealed the quantitative importance of variable selection (selection under heterogeneous abiotic and biotic environmental conditions leading to more dissimilar structures among communities; also called variable selection), homogeneous selection (selection under homogeneous abiotic and biotic environmental conditions leading to more similar structures among communities), dispersal limitation, homogeneous dispersal, and other processes in shaping the community patterns of the bacterioplankton community along the two regimes (Fig. S10b). At a relative importance of more than 60%, variable selection contributed the most to the assembly processes of bacterioplankton communities.

**Fig. 3** Bray–Curtis dissimilarity based PCoA plot from six sampling sites across regime shift from macrophyte-dominated regime (MDR) to phytoplankton-dominated regime (PDR) in Taihu Lake. TN, total nitrogen; DTN, dissolved total nitrogen; \( \text{NH}_4^+ \)-N, ammonium nitrogen; \( \text{NO}_2^- \)-N, nitrite nitrogen; \( \text{NO}_3^- \)-N, nitrate nitrogen; TP, total phosphorus; DTP, dissolved total phosphorus; \( \text{PO}_4^{3-} \)-P, phosphate; DOC, dissolved organic carbon; DO, dissolved oxygen; Chl \( \alpha \), chlorophyll a
in these six sites. At 28.58%, homogenizing dispersal was the second-most important assembly process of the bacterioplankton community.

**Co-occurrence Patterns of the Bacterioplankton Community Along the Regime Shift**

Before constructing the global network from all of the 54 samples, we constructed six co-occurrence networks from the six sampling sites along the regime transition. These sampling sites, located along the regime transition from MDR to PDR, were labelled MDR-Core1, MDR-Core2, MDR-Edge, PDR-Edge, PDR-Core2 and PDR-Core1. The derived co-occurrence networks featured environment-specific species co-occurrence relationships (Fig. 4 and Fig. S11). Subnetworks inferred from datasets trimmed into uniform number of OTUs contained distinct co-occurrence patterns in terms of species composition (Fig. 4). Moreover, these regime-specific co-occurrence relationships displayed network characteristics that were significantly different compared to random networks (Table 1). The Z-test results comparing a variety of indexes of the observed correlation-based network with those of random networks, including Modularity, Transitivity and Network diameter, indicated that the networks among species along the regime shift from PDR and MDR were all nonrandom ($P < 0.001$ in all cases, Table 1). Based on the size and taxonomic information, the bacterioplankton community network changed along the regime transition from MDR to PDR (Table 1 and Fig. S11). Bacteroidetes, Betaproteobacteria and Actinobacteria dominated and clustered in the MDR sites, whereas Firmicutes and Gammaproteobacteria dominated and clustered in the PDR sites.

To explore the effects of environmental factors on taxon-taxon association networks, all taxa and environmental factors were added to obtain the global network (Fig. 4). The bacterioplankton community of the six sampling sites along regime transition from MDR to PDR was grouped into three clusters, with cluster 1 and cluster 3 surrounded by specific nodes of cluster 2, respectively (Fig. 4). Compared with the environmental variables in the MDR-associated cluster (cluster 1), those in the PDR-associated cluster (cluster 3) had greater positive effects on OTUs, especially for TP. We also observed that environmental factors such as turbidity, pH, DTP, DOC, PO$_4^{3-}$-P and NO$_2^{-}$-N were hubs in these networks, indicating that the changes in the concentrations of nutrients are driving the bacterioplankton community interactions along the regime shift from MDR to PDR. Of note, taxa assigned to cluster 2 are grouped with both cluster 1 and cluster 3 in the visualization. Few connections were

Fig. 4 CoNet-based network of all samples along the regime shift from the macrophyte-dominated regime (MDR) and phytoplankton-dominated regime (PDR) in Taihu Lake clustered with manta. The red solid lines indicate positive correlations and the black lines indicate negative correlations. Different phyla and environmental factors are represented with different colors (a). Cluster identity is further represented by different node shapes and colors (b).
Table 1: Topological properties of the empirical network and associated random network for bacterioplankton community along the regime transition from macrophyte-dominated regime (MDR) to phytoplankton-dominated regime (PDR) in Lake Taihu.

| Sites            | Nodes | Edges | Modularity | Transitivity | Network diameter | Average degree | Modularity (SD) | Transitivity (SD) | Network diameter (SD) |
|------------------|-------|-------|------------|--------------|------------------|----------------|-----------------|-------------------|----------------------|
| Global network   | 614   | Overall positive | 2150       | 0.464\(^a\)  | 0.269\(^a\)  | 9\(^b\)        | 12.65           | 0.243             | 0.021                | 4.227                |
|                  |       | negative       | 1734       |              |                  |                |                 | (0.004)           | (0.001)             | (0.495)              |
|                  | Cluster1 positive | 697       | 0.791\(^a\)  | 0.360\(^a\)  | 13\(^b\)        | 3.535          | 0.542           | (0.008)           | 0.011                | 9.933                |
|                  |       | negative       | 179        |              |                  |                |                 | (0.004)           | (0.001)             | (0.807)              |
|                  | Cluster2 positive | 691       | 0.454\(^a\)  | 0.291\(^a\)  | 19\(^b\)        | 1.624          | 0.850           | (0.013)           | 0.003                | 25.63                |
|                  |       | negative       | 15         |              |                  |                |                 | (0.003)           | (0.003)             | (3.385)              |
|                  | Cluster3 positive | 422       | 0.671\(^a\)  | 0.301\(^a\)  | 21\(^b\)        | 2.275          | 0.721           | (0.010)           | 0.005                | 16.472               |
|                  |       | negative       | 0          |              |                  |                |                 | (0.003)           | (0.003)             | (1.617)              |
| MDR-Core1        | 301   | positive       | 353        | 0.791\(^a\)  | 0.360\(^a\)  | 13\(^b\)        | 3.535           | 0.542             | 0.011                | 9.933                |
|                  |       | negative       | 179        |              |                  |                |                 | (0.008)           | (0.004)             | (0.807)              |
| MDR-Core2        | 517   | positive       | 241        | 0.454\(^a\)  | 0.291\(^a\)  | 19\(^b\)        | 1.624           | 0.850             | 0.003                | 25.63                |
|                  |       | negative       | 179        |              |                  |                |                 | (0.013)           | (0.003)             | (3.385)              |
| MDR-Edge         | 429   | positive       | 286        | 0.671\(^a\)  | 0.301\(^a\)  | 21\(^b\)        | 2.275           | 0.721             | 0.005                | 16.472               |
|                  |       | negative       | 202        |              |                  |                |                 | (0.010)           | (0.003)             | (1.617)              |
| PDR-Edge         | 431   | positive       | 1439       | 0.878\(^a\)  | 0.453\(^a\)  | 21\(^b\)        | 7.360           | 0.337             | 0.017                | 6.003                |
|                  |       | negative       | 147        |              |                  |                |                 | (0.005)           | (0.002)             | (0.308)              |
| PDR-Core2        | 381   | positive       | 1143       | 0.964\(^a\)  | 0.411\(^a\)  | 11\(^b\)        | 8.661           | 0.303             | 0.023                | 5.134                |
|                  |       | negative       | 507        |              |                  |                |                 | (0.005)           | (0.002)             | (0.341)              |
| PDR-Core1        | 269   | positive       | 419        | 0.691\(^a\)  | 0.425\(^a\)  | 21\(^b\)        | 3.777           | 0.516             | 0.014                | 9.231                |
|                  |       | negative       | 89         |              |                  |                |                 | (0.009)           | (0.005)             | (0.739)              |

\(^a\)Significant difference between the empirical network and the random network \((P<0.001, \text{Z-test})\)

\(^b\)Random networks were generated by rewiring all of the links with the same numbers of nodes and edges to the corresponding empirical network. The numbers in parentheses indicate the standard deviation (SD) of structural properties of 1000 random networks.
observed between the taxa in cluster 2 and environmental variables, suggesting these taxa in cluster 2 may respond weakly (or not at all) to nutrient concentrations compared with taxa in cluster 1 and cluster 3. The bacterial hub nodes in the global bacterioplankton community networks belonged to the dominant phyla in the MDR, edge area and PDR, respectively (Fig. S12 and Table S4). A total of 47 hubs were identified (Table S4), which were mainly from phyla Betaproteobacteria, and Actinobacteria in cluster 1, from phyla Betaproteobacteria, Gammaproteobacteria and Actinobacteria in cluster 2, from phyla Cyanobacteria in cluster 3.

Discussion

**Phosphorus Concentrations as an Indicator of Regime Transition**

This and previous studies demonstrated that the lake water displays significant environmental heterogeneity along the regime transition from the macrophyte-dominated regime (MDR) to the phytoplankton-dominated regime (PDR) [20, 57]. Certain environmental parameters have been suggested to be responsible for the observed differences in bacterioplankton community, such as pH [58] and nutrients [5], as well as the occurrence of phytoplankton [59–61]. The mechanisms of the regime shift can involve multiple drivers and may include interactions of macrophytes, phytoplankton, nutrients, and herbivorous waterfowl [62]. Here, we focused on the phosphorus concentration because it is commonly targeted to mitigate eutrophication. Previous studies have suggested that regime shifts from MDR to PDR in shallow lakes are commonly induced by the increased nutrients, especially phosphorus [2, 59, 62]. In the present study, we found that most of the environmental parameters at six sampling sites across the transition from MDR to PDR were significantly correlated with TP, especially turbidity (Fig. S4). Turbidity is a measure of water transparency, which is mainly influenced by the concentrations of phytoplankton and re-suspended sediment particles [15]. The wind-driven process of sediment re-suspension is much stronger in PDR-Core sites than that of the MDR-Core sites in Taihu Lake because the submerged macrophytes in MDR have a calming effect on the water column and sediment turbulence [8, 63], which is consistent with the results found in this study.

**Compositional Dissimilarity of Bacterioplankton Communities Differed Along Regime Transition**

Our results indicate that the bacterioplankton community was significantly correlated with environmental factors at the regime transition, especially TP, which is regarded as a limiting nutrient in the freshwater ecosystem [64–66]. Significant differences in alpha and beta diversities of the bacterioplankton communities have been widely observed in other lake ecosystems with disparate environmental variables [67, 68]. Decreased alpha diversity of the bacterioplankton communities along the regime transition from MDR to PDR was observed. It significantly and linearly correlated with TP, which is consistent with the observation that bacterial community diversity is negatively affected by phytoplankton blooms [69]. In general, when the evenness of bacterioplankton community decreases with the regime shift, the diversity does so too, suggesting that particular species become more dominant with the regime transition [70]. Moreover, several taxonomic groups displayed substantial changes in abundance as the regime shifted (Fig. 2 and Fig. S7). Regime shifts provide a mechanism for selection, as abundant OTUs become rare or even more abundant due to their sensitivity to environmental changes [1, 3]. Intriguingly, these changes were occasionally non-linear, suggesting that taxa had different optima along the MDR-PDR gradient. For a number of taxa, e.g., Acidobacteria and Cyanobacteria, the relationships between concentrations of TP and their abundance were described by quadratic functions. Previous research has shown that Betaproteobacteria tends to be the dominant group in relatively oligotrophic lakes [20], whereas Firmicutes appear to be involved in DOC degradation [71], often become dominant in eutrophic lakes [72]. Our results are consistent with these findings, as Betaproteobacteria and Firmicutes were negative and positive linearly correlated with TP. Therefore, these taxa might be used as indicator taxa for the different regimes.

**Changes in Assembly Processes of Bacterioplankton Communities were Attributed to Regime Transition**

Although the deterministic processes were observed to dominate in shaping the bacterioplankton communities in both the MDR-Core and PDR-Core sites, the deterministic processes in the assembly of bacterial community of MDR-Core sites were stronger compared to those of the PDR-Core sites. Competition among bacterial species could be reduced in more productive environments, hence weakening the selection and strengthening the stochasticity of the assembly of bacterial communities [5, 73]. Previous study also showed that the relative importance of deterministic processes in the assembly of bacterial community increased in extreme or harsh environments [74–77]. The stronger deterministic processes in the assembly of bacterial community in the MDR-Core sites may be due to the lower nutrient concentrations compared to PDR-Core sites [57]. The decreased contribution of deterministic processes in the edge sites of MDR and PDR could be attributed to multiple causes. On the one hand, edge sites could provide a more...
favorable living environment because of the higher nutrient concentrations compared to the MDR-Core sites and lower microcystins pressure compared to the PDR-Core sites [69, 72]. On the other hand, water disturbance driven by strong wind in the edge sites of the two regimes in Lake Taihu could also result in the elevated passive dispersal of bacterial species, therefore, increasing the stochasticity of the assembly of bacterioplankton community [65]. While the comparable relative importance of deterministic processes in the assembly of bacterioplankton community in PDR-Core sites may be attributed to the microcystins originated from Cyanobacteria blooms [78, 79]. For the main ecological processes, variable selection contributed the most to the assembly of bacterioplankton community (Fig. S10b). In freshwater lakes, both the composition and assembly processes of bacterioplankton community were intensively influenced by nutrient loadings [57, 80, 81] as well as submerged macrophytes [8, 20]. The heterogeneous assembly pattern of bacterioplankton community in the present study could be attributed to the different nutrient loadings along the regime shift (Fig. 5).

Regime Transition Revealed by Network Clusters and Hub Species

In the ecosystems, coexistence is potentially supported by niche processes like environmental filtering, as the different filters lead to establishment of different communities [23, 48]. Species that share the similar ecological niches may compete or cooperate to resist environmental pressure when resources are scarce [82, 83]. Compared to the MDR-core sites, the Cyanobacteria bloom in PDR-Core sites strengthen the effects of selection due to the microcystins [84]. The modularity of the site-specific co-occurrence network varied along the regime shift (Table 1). Previous studies have shown the existence of modules that driven by environmental attributes [85, 86]. In the present study, we also found that closely related taxa tended to be positively inter-connected and clustered together (Fig. 4). Moreover, we found several hub OTUs in the three network clusters, which are likely to reflect the response of the bacterioplankton community to the regime shift (mainly from phyla Betaproteobacteria, and Actinobacteria in cluster 1, from phyla Betaproteobacteria, Gammaproteobacteria and Actinobacteria in cluster 2, from phylum Cyanobacteria in cluster 3). The clusters 1 and 3 contain taxa that dominated the MDR or PDR regime, respectively. These were also taxa that consistently increased or decreased across the environmental gradient (Fig. 2). The taxa in cluster 2 showed more subtle patterns. The relative abundance of Actinobacteria firstly increased and then decreased with the increasing concentration of TP, which was different from the pattern of relative abundance of Firmicutes along the regime shift from MDR to PDR, whereas the abundance of Gammaproteobacteria increased with TP but then saturated. Thus, taxa in the cluster 2 may benefit from increased TP, but only up to a point. Given that clusters

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**Fig. 5** Conceptual model of the shift in the bacterioplankton community composition along the regime shift from macrophyte-dominated regime (MDR) to phytoplankton-dominated regime (PDR) in a freshwater shallow lake. The unconfirmed dynamic process of regime transition is indicated by thick black dotted line. The changes in alpha and beta diversity of bacterioplankton community are indicated by the orange and brown lines, respectively. The relative contribution of stochastic assembly processes of bacterioplankton community is indicated by the pink line. The arrows in x-axis and y-axis indicate the direction of the increase of environmental attributes (bottom x-axis: nutrient loading, left y-axis: abundance of macrophyte, top x-axis: turbidity, right y-axis: abundance of phytoplankton). The histogram attached in right y-axis indicates the hub species along regime transition.
in the microbial co-occurrence networks may represent different niches [29], the clusters indicated high similarity in response of species to the environmental variations, especially concentrations of TP, along the regime shift (Fig. 5).

**Conclusion**

The data obtained in the present study suggested that the ecological regimes drove a marked divergence in the composition of bacterioplankton community. The alpha diversity and evenness indexes linearly decreased, indicating that particular bacterial species became dominant with the regime transition. The hub species that could reflect the regime conditions belonged to *Betaproteobacteria* and *Actinobacteria* in the MDR-Core sites, *Betaproteobacteria*, *Gammaproteobacteria* and *Actinobacteria* in the edge sites and *Cyanobacteria* in the PDR-Core sites (Fig. 5). The relative importance of deterministic processes in the assembly of bacterioplankton community decreased at the edge sites when the regime shifted from MDR to PDR. The bacterioplankton co-occurrence networks were clearly linked to environmental variables and were divided into three clusters that reflected the regime shift. The different nutrient loadings may be the most important factor that contributes to the dissimilarity of bacterioplankton community composition along the regime shift. Our results provide useful information for better understanding the relationships between nutrients and bacterioplankton community in macrophyte- and phytoplankton-dominated freshwater regimes.

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**Data Availability** The raw reads were deposited into the NCBI Sequence Read Archive (SRA) database (BioProject: PRJNA511603).

**Code Availability** Not applicable.

**Declarations**

**Conflict of Interest** The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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

**Consent to Participate** Not applicable.

**Consent for Publication** The publisher has the authors’ permission to publish the content presented herein.

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