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Dredging disturbance alleviating cyanobacterial blooms: weakening diversity maintenance of bacterioplankton community

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Abstract

Disentangling the ecological mechanisms in response to dredging disturbance is helpful to inform environmental policy for improving water quality. However, little is known about environmental adaptation and community assembly of bacterioplankton in response to dredging disturbance. Based on Illumine MiSeq sequencing and multiple statistical analyses, we have characterized interactions, functions, environmental breadth, phylogenetic signals and clustering, and the ecological assembly processes of a bacterioplankton community before and after dredging. We found distinct changes in community composition, comparable decreases in diversity, functional redundancy, conflicting interactions, lower phylogenetic clustering, and weak environmental adaptation after dredging. The bacterioplankton community assembly was affected by both stochastic and deterministic processes before dredging, but was dominated by stochasticity after dredging. Sediment total phosphorus was a decisive factor in balancing stochastic and deterministic processes for community assemblies of bacterioplankton before and after dredging. Consequently, taxonomic and phylogenetic α-diversities of the bacterioplankton exhibited a higher contribution to the water trophic level, as represented by chlorophyl α measurement, before rather than after dredging. Our results clarify the responses of bacterioplankton to environmental change caused by dredging disturbance, with nutrient loss and ecological drift playing important roles. The findings extend knowledge of the contribution of bacterioplankton diversity to the water trophic level and decipher the mechanisms of bacterioplankton diversity maintenance in response to dredging. The findings are also helpful for guiding cyanobacterial bloom mitigation.

Keywords: anthropogenic disturbance, environmental breadth, functional redundancy, phylogenetic clustering, phylogenetic signal, stochastic versus deterministic responses

1. Introduction

Bacterioplankton are important aquatic microorganisms and participate in nutrient biogeochemical cycles (Bunse and Pinhassi, 2017). Cyanobacteria, regarded as one of the most important members of bacterioplankton, generates massive blooms and cause worldwide environmental problems (Hamilton et al., 2016; Te et al., 2017). Cyanobacterial blooms threaten human health and the diversity of aquatic organisms via release of algal toxins and consuming oxygen (Huisman et al., 2018; Olson et al., 2020). Many studies have reported that the superfluous input of phosphorus (P) and nitrogen (N) leads to cyanobacterial blooms (Te et al., 2017; Zhang et al., 2017; Kim et al., 2020), and non-cyanobacterial bacterioplankton are reported to be responsible for the bloom of cyanobacteria (Berg et al., 2009; Te et al., 2017; Wan et al., 2020). Blocking nutrient input, especially N and P, into aquatic ecosystems and changing bacterioplankton interactions might mitigate cyanobacteria blooms.

Dredging can improve water quality and achieve environmental protection by changing both abiotic and biotic factors in water-sediment ecosystems (Liu et al., 2016; Zhang et al., 2017; Wan et al., 2020). Such large-scale anthropogenic disturbance has exhibited good performance for removing nutrients (e.g., N and P) from sediment (Liu et al., 2016). However, dredging affects bacterioplankton community composition (Zhang et al., 2017) and decreases bacterioplankton α-diversity (Wan et al., 2020). Deciphering maintenance of microbial diversity is of importance to estimate diversity-driven ecosystem processes and functions. However, the ecological mechanisms underlying bacterioplankton diversity maintenance as a result of dredging disturbance is poorly understood.

Microbial diversity maintenance is often clarified through two major aspects: environmental adaptation and community assembly (Jiao and Lu, 2020; Wan et al., 2021a, 2021b). Environmental adaptation of microorganisms involves two criteria: environmental breadth at a taxonomic level and phylogenetic signals at a phylogenetic level (Jiao and Lu, 2020; Wan et al., 2021c). Microbial environmental breadth reflects the distribution threshold of taxa along an environmental gradient over space or time (Baker and King, 2010). The phylogenetic signal is used to assess the strength of the microbial response to environmental preferences (Oliverio et al., 2017). This phylogeny-based trait characterizes how microorganisms interact with their environment, providing a solid foundation for predicting the preservation of microbial diversity (Martiny et al., 2015; Goberna and Verdú, 2016). Additionally, microbial responses to ongoing environmental change show phylogenetic conservatism, namely, species are not randomly distributed along the tree of life (Martiny et al., 2015). For instance, 30 isolated aerobic methane-oxidizing bacteria show strong phylogenetic conservatism to pH and temperature (Krause et al., 2014). Consequently, revealing environmental breadths and phylogenetic signals can explain major ecological phenomena, including species distribution patterns, seasonal succession, and responses to global environmental change (Thomas et al., 2016; Monk et al., 2017). However, environmental breadth and phylogenetic signals of bacterioplankton to environmental change has been rarely reported in eutrophic lakes.

Ecological assembly processes mediate microbial community structure and coexistence patterns (Huber et al., 2020; Jiao et al.,2020), and have been found to be imperative in connecting microbial community structure with ecosystem function (Stegen et al., 2016; Wan et al., 2021c). Briefly, stochastic and deterministic processes adjust microbial community assembly (Yan et al., 2017; Huber et al., 2020). For instance, deterministic processes have great effects on bacterial community assembly in coastal waters of the East China Sea in autumn (Wang et al., 2020). Many studies have revealed that the balance between determinism and stochasticity is affected by environmental factors (Stegen et al., 2016; Huber et al., 2020). For example, pH was the major factor in determining bacterioplankton community assembly in 25 discrete freshwater lakes in Denmark (Ren et al., 2015). However, it remains unclear whether similar environmental variables regulate the balance between determinism and stochasticity of bacterioplankton communities in eutrophic freshwater lakes.

Freshwater lakes functioning for aquaculture, storing water, irrigating farmland, and providing recreation. However, freshwater lakes are facing severe challenges because of serious water eutrophication (Tao et al., 2017; Te et al., 2017), and dredging represents a massive human disturbance to enhance water quality. To investigate responses of bacterioplankton to dredging disturbance, we chose Lake Nanhu (Wuhan, China) as our study area. We selected nine representative sites in

Lake Nanhu (Fig. S1), and collected water and sediments samples before and after dredging. In a previous study, we found significant decreases in nutrients after dredging (Fig. S2), and our results demonstrated that cyanobacterial blooms can be mitigated by dredging via changing the interconnection between the bacterioplankton community and sediment biogeochemistry (Wan et al., 2020). In the present research, we aimed to (i) investigate contributions of taxonomic and phylogenetic diversity to the water trophic level before and after dredging, (ii) estimate environmental adaptation and community assembly processes before and after dredging, and (iii) decipher effects of community assembly on bacterioplankton interactions and functions. Since dredging led to nutrient loss, we hypothesized that dredging might weaken bacterioplankton environmental adaptation and intensify ecological drift. To achieve our goals and validate our hypothesis, we applied 16S rRNA gene amplicon sequencing and determined water and sediment physicochemical properties.

2. Materials and methods

2.1. Data collection

Detailed information about dredging procedures was described in prior research (Wan et al., 2020). In April and July, 2017 (before dredging) and in April and July, 2018 (after dredging), 36 water samples and 36 sediment samples were collected from 9 sites in Lake Nanhu (Wuhan, China). We estimated water physicochemical properties, including pH, turbidity (Tur), dissolved oxygen (DO), temperature (T), nutrient phosphorus PO_4^{3-}-P (PO4), nutrient nitrite NO_2^--N (NO2), nutrient nitrate NO_3^--N (NO3), and nutrient ammonia NH_4^+-N (NH4). Sediment physicochemical properties were also assessed, including total carbon (TC), total nitrogen (TN), total phosphorus (TP), Olsen P, inorganic phosphorus (IP), non-apatite inorganic phosphorus (NAIP), organic phosphorus (OP), and apatite phosphorus (AP). Sampling information and measurement of physicochemical properties have been previously described in detail (Wan et al., 2020). To assess the water trophic level, we estimated the content of chlorophyl α (Chl-α) based on a spectrophotometric method (Te et al., 2017).

Universal primers of 338F (5'- ACT CCT ACG GGA GGC AGC A-3') and 806R (5'- GGA CTA CHV GGG TWT CTA AT-3') were used to amplify bacterial 16S rRNA gene targeting V3–V4 regions (Mori et al., 2013). Illumina sequencing was performed at the Majorbio Bio-Pharm Technology Co., Ltd. Shanghai, China. Detailed description of bacterioplankton recovery from water samples, DNA extraction, and 16S rRNA gene amplification, and sequencing are reported in a previous study (Wan et al., 2020) and also summarized in the Supplementary materials (Supplementary method 1). The purified sequences were classified into operational taxonomic units (OTUs) at a 3% dissimilarity level against the SILVA v128 reference. The OTUs accounting for less than 0.001% of the total sequences were filtered out. The MiSeq raw reads were deposited in the NCBI Short Read Archive database under accession numbers PRJNA391223 (2017) and PRJNA541122 (2018). In addition, we also measured abundances of cyanobacteria and bacterioplankton using universal primers. The amplifications of 16S rRNA genes for assessing cyanobacteria and bacterioplankton abundance were reported in a prior study (Wan et al., 2020) and are also summarized in Supplementary materials (Supplementary method 2).

2.2. Data analysis

Significant differences in the data, if not otherwise stated, were analysed by the Student's t-test when data followed normal distributions ($p < 0.05$). Venn diagram and non-metric multidimensional scaling (NMDS) were used to reflect the community structure of bacterioplankton using the "VennDiagram" and "ggplot2" packages of R. Canonical analyses of the principal coordinates (CAP) were employed to investigate influences of environmental factors on bacterioplankton community structure by employing the "capscale" function in the "vegan" package of R. Permutational multivariate analysis of variance (PERMAVONA) and pairwise analyses of similarity (ANOSIM) were selected to quantitatively evaluate effects of physicochemical variables on community structure of bacterioplankton by applying the "adonis" and "anosim" function in the "vegan" package of R. The OTUs observed in more than 50% of samples before and after dredging (> 9 samples) were applied to construct a co-occurrence network. The co-occurrence networks were visualized employing Gephi v. 0.9.2 (https://gephi.org/) with a significance p value < 0.01 and Spearman's correlation coefficients (r) > 0.6. We used the ratio of positive edge (representssignificantly positive correlation) to negative edge (denotes noticeably negative correlation) to reflect bacterioplankton conflicting interactions (mainly competition and predation) (Wei et al., 2019). Functional profiling of the bacterioplankton community was conducted by employing the package ''Tax4Fun2" of R, and the functional redundancy index (FRI) of each sample was calculated based on sequence similarity of the 16S rRNA gene (Wemheuer et al., 2020). The FRI is estimated as the proportion of species capable of harbouring a particular KEGG function and their phylogenetic relationships to each other (Wemheuer et al., 2020). Structural equation modeling was applied to analyze systems involving multiple causal interconnections, including water trophic level, taxonomic diversity, phylogenetic diversity, physicochemical properties, and community function by employing IBM SPSS Amos v.21.

To evaluate the phylogenetic distance between communities, the beta mean nearest taxon distance (βMNTD) metric was employed by using the "comdistnt" function. To estimate whether species were clustering closer to the tips of the phylogeny, phylogenetic clustering based on standardised effect size measurement of the mean nearest taxon distance (SES.MNTD) was computed by applying the "ses.mntd" function in the "picante" package of R (Kembel et al., 2010). Threshold indicator taxa analysis (TITAN) was employed to estimate environmental breadth of bacterioplankton in response to environmental gradients by using the "TITAN2" package (Baker and King, 2010; Romero et al., 2019). A phylogenetic signal, reflecting phylogenetic conservation for traits that are closely correlated with microbial ecological preferences, can provide predictions for microbial evolutionary adaptation (Martiny et al., 2015). We used Blomberg's *K* statistic and the Fritz-Purvis *D* test to estimate phylogenetic signals of bacterioplankton taxa before and after dredging (Goberna and Verdú, 2016; Wan et al., 2021a). The Blomberg's *K* statistic reveals a phylogenetic signal that compares to the observed signal in a trait to the signal based on a Brownian motion-based metric of trait evolution on a phylogeny (Blomberg et al., 2003). We computed the *K* value by employing the "picante" package of R (Kembel et al., 2010):high *K* values imply strong phylogenetic signals (Goberna and Verdú, 2016). We estimated the phylogenetic signal of binary traits by employing the "phylo.D" function in the "caper" package of R (Orme et al., 2013). The Fritz-Purvis phylogenetic dispersion (*D*) value compares the observed sister-clade differences in the trait against those expected for a random phylogenetic pattern (Orme et al., 2013; Goberna and Verdú, 2016). We transformed the *D* value into $-D + 1$ to compare with Blomberg's *K* statistic (Goberna and Verdú, 2016). The evolution of a study trait (i) does not reflect a noticeable signal when $-D + 1 = 0$, (ii) is more conserved than expected by chance when $-D + 1 > 0$.

Ecological community assembly processes were assessed using null and neutral model analyses (Sloan et al., 2006; Stegen et al., 2016). β-nearest taxon index (βNTI) and null model-based Bray-Curtis-based Raup-Crick (RC_{bray}) were applied to calculate the differences in phylogenetic and taxonomic diversities. If $|\beta NTI| > 2$, this demonstrates the dominance of deterministic processes, with significantly more (i.e., variable selection; $\beta NTI > 2$) and less (i.e., homogeneous selection; $\beta NTI < -2$) phylogenetic turnover than expected. If $|\beta NTI| < 2$, $RC_{bray} < -0.95$ and $RC_{bray} > 0.95$, this represents the relative contributions of homogenizing dispersal and dispersal limitation, respectively. If $|\beta NTI| < 2$ and $|RC_{bray}| < 0.95$, this indicates the influence of "undominated" assembly, which mostly comprises diversification, ecological drift, weak selection, and/or weak dispersal (Stegen et al., 2016; Huber et al., 2020). The detailed algorithm for this is described in prior literature (Stegen et al., 2016). The neutral model analysis was employed to further reflect the contribution of astochastic process to the bacterioplankton community assembly by predicting the interconnection between species abundance distribution and species area (Zhou and Ning, 2017). In this model, the migration rate of "*m*" and model fitness of "R^2" were calculated by applying the "stats4" and "hmisc" packages in R (Sloan et al., 2006).

3. Results

3.1. Abundance, composition, and diversity of bacterioplankton community before and after dredging

Significant decreases in the Chl-α content and abundance of bacterioplankton and cyanobacteria were found after dredging (Wilcoxon rank-sum test, $p < 0.001$; Fig. 1a). The Chl-α content was strongly positively correlated with pH and DO, while noticeably negatively correlated with NH4 before and after dredging ($p < 0.05$ or $p < 0.01$) (Table 1). Linear regressions reflected significant correlations between Chl-α content and cyanobacterial abundance before and after dredging ($p < 0.001$), while no significant correlation was found between Chl-α content and bacterioplankton abundance ($p > 0.05$) (Fig. 1b). This might suggest that the blooms in eutrophic Lake Nanhu were mainly dominated by cyanobacteria before and after dredging.

We identified 1528 OTUs from the retained 1,201,742 high-quality sequences at 97% sequence similarity. The bacterioplankton communities shared 1026 OTUs before and after dredging (Fig. S3), and the OTUs were classified into 33 phyla. *Actinobacteria*, *Proteobacteria*, and *Bacteroidetes* dominated before and after dredging, with total relative abundances higher than 85%. The relative abundances of *Proteobacteria* and *Bacteroidetes* significantly decreased after dredging (Wilcoxon rank-sum test, $p < 0.05$). The NMDS plot reflected distinct differences in bacterioplankton community composition before and after dredging, and ANOSIM further confirmed that the difference was significant (R = 0.415, $p < 0.001$) (Fig. S3). The 16 physicochemical variables explained 62.95% and 53.57% of total variations in community composition before and after dredging, respectively (Fig. S4). According to the PERMANOVA results, N (e.g., TN and NH4) and P (e.g., AP and TP) exhibited significant effects on bacterioplankton community structure (Fig. S4). These results suggest that nutrient loss caused by dredging affected bacterioplankton community composition.

The taxonomic α-diversity represented by the Shannon-Wiener index for the bacterioplankton was significantly higher before dredging than afterwards ($p < 0.05$; Fig. 1a), suggesting bacterioplankton diversity loss caused by the dredging event. The phylogenetic α-diversity represented by SES.MNTD was noticeably lower before dredging than afterwards, and were all less than zero and all at $p < 0.001$ (Wilcoxon rank-sum test, $p < 0.05$; Fig. 1a). Relatively more physicochemical factors (e.g., TP, AP, NH4, and NO3) had significant effects on taxonomic or phylogenetic α-diversity before rather than after dredging (Table 1). Additionally, the taxonomic α-diversity was significantly correlated with Chl-α before dredging ($p < 0.05$), but was not after dredging ($p > 0.05$) (Fig 1b). The phylogenetic α-diversity was slightly correlated with Chl-α before rather than after dredging ($p > 0.05$). These results indicate that the bacterioplankton diversity contributed differently to the water trophic level before and after dredging.

3.2. Environmental adaptation of bacterioplankton at taxonomic and phylogenetic levels

Both community distance (represented by Bray-Curtis dissimilarity) and phylogenetic distance (represented by βMNTD) of bacterioplankton were significantly correlated with physicochemical factor dissimilarity before and after dredging (p < 0.001; Fig. S5, S6). Subsequently, we evaluated environmental adaptation of bacterioplankton at both taxonomic and phylogenetic levels (Fig. 2). The bacterioplankton exhibited a broader range of environmental thresholds for almost all environmental factors before dredging than after dredging (Fig 2a). Furthermore, the bacterioplankton showed stronger phylogenetic signals for almost all environmental parameters before dredging than after dredging based on Blomberg's *K* statistic (Fig 2b) and Fritz-Purvis *D* test (Fig 2c). These results indicated that bacterioplankton taxa showed stronger environmental adaptation before rather than after dredging.

3.3. Ecological processes and influence on bacterioplankton community assembly

Based on the null model, dispersal limitation (47.7%) and variable selection (28.1%) contributed most to community assembly before dredging (Fig. 3a). However, "undominated" processes (51.0%) and dispersal limitation (41.8%) contributed most to community assembly after dredging. Homogenizing dispersal and homogeneous selection contributed less to community assembly. Consequently, stochastic and differentiating processes dominated bacterioplankton community assembly, and both processes were higher before dredging than after dredging (Fig. 3a). The neutral community model revealed that the bacterioplankton community was more affected by neutral processes after dredging (m = 0.303, R^2 = 0.731) than before dredging (m = 0.262, R^2 = 0.717) (Fig. 3b). These results revealed that dredging led to an increase in "undominated" processes probably via increasing ecological drift, which in turn increased stochasticity.

The results of the Mantel test showed that changes in TP, AP, and Tur were significantly correlated with βNTI compared to other environmental factors before and after dredging (Table 1). Additionally, βNTI was significantly negatively correlated with a change in TP before dredging (Fig. S7), suggesting that an increasing divergence in TP led to a decrease in stochasticity. In contrast, βNTI was noticeably positively correlated with the change in TP after dredging (Fig. S7), demonstrating an increasing difference in TP resulted in an increase in stochasticity. We divided these samples into groups based on TP content, and found that increasing TP led to the relative contributions of stochasticity first decreasing and then increasing before dredging, and first increased and then declined after dredging (Fig. S8).

Subsequently, we used co-occurrence networks and function profiling to reflect outcomes of stochasticity-dominated assembly of bacterioplankton community (Fig. 4). We observed relatively more nodes and edges before dredging (node = 644, edge = 51,082) than after dredging (node = 528, edge = 12,508) (Fig. 4a; Table S1). The ratio of positive to negative edges was relatively low before (ratio = 3.38) than after dredging (ratio = 8.06) (Table S1), suggesting relatively less conflicting interactions between bacterioplankton after dredging. The core nodes in each network module were affiliated with *Bacteroidetes*, *Cyanobacteria*, *Firmicutes*, *Planctomycetes*, and *Proteobacteria* before dredging (Table S2), and were affiliated with *Actinobacteria*, *Bacteroidetes*, *Chloroflexi*, and *Proteobacteria* after dredging (Table S3). The core microorganisms represented by core nodes showed differing correlations with physicochemical variables (Table S2, S3). These results demonstrated that comparable divergence in bacterioplankton interactions before and after dredging. According to function profiling results, 8608 functions at KEGG pathway level 3 were detected before and after dredging, and these shared 8504 functions (Fig. S9). Among these, 5632 functions showed higher functional redundancy before dredging, while 1108 functions exhibited higher functional redundancies after dredging (Fig. S9). More unique functions were found after dredging, such as cytokinin dehydrogenase (EC: 1.5.99.12), creatinine deaminase (EC: 3.5.4.21), and c-di-GMP phosphodiesterase (EC: 3.1.4.52). At KEGG pathway level 2, some functions (e.g., amino acid metabolism, carbohydrate metabolism, lipid metabolism, and environmental adaptation) were significantly higher before dredging than after dredging (Fig. 4b). These results suggested that a general functional decrease in the bacterioplankton community and a gain of some unique functions occurred after dredging. According to the PERMANOVA results, sediment TP showed significantly higher effects on bacterioplankton community function compared to other physicochemical factors before and after dredging (Fig. S10). This implies that the phosphorus resource is the determinant affecting bacterioplankton community function.

Finally, we quantitatively estimated effects of bacterioplankton community assembly on community function and water trophic level before and after dredging (Fig 5). A more significant correlation was found between βNTI and the functional redundancy index after dredging ($R^2 = 0.11$, $p < 0.001$) than before dredging ($R^2 = 0.04$, $p < 0.001$) (Fig. 5a), suggesting bacterioplankton community function was more affected by community assembly after dredging. We also found a significant correlation between βNTI and changes in Chl-α content before dredging ($R^2 = 0.10$, $p < 0.001$) rather than after dredging ($R^2 = 0.012$, $p > 0.05$) (Fig. 5b). This suggested that dredging disturbance might reduce the effects of bacterioplankton community assembly on water trophic level.

3.4. Relationships between trophic level, environmental factors, diversity and function of bacterioplankton

Structural equation modeling was used to reflect interconnection among five components, including water trophic level, environmental factors, taxonomic diversity, phylogenetic diversity, and community function (Fig. 6). Before dredging, physicochemical factors had a significant positive effect on bacterioplankton taxonomic diversity, which in turn noticeably positively affected the water trophic level ($p < 0.05$; Fig. 6a, 6c). Physicochemical factors also showed a dramatic directly positive influence on water trophic level. The model exhibited a good fit to our data, as reflected by the non-significant $\chi 2$ test ($N = 18$, $\chi 2 = 0.15$, d.f. = 1, $p = 0.903$; Fig.

6a). In contrast, physicochemical factors showed limited direct or indirect effects on water trophic level after dredging ($p > 0.05$; Fig. 6b, 6d). The model also exhibited a good fit to the data, as indicated by the non-significant $\chi2$ test (N = 18, $\chi2 = 0.75$, d.f. = 1, $p = 0.387$; Fig. 6b). Bacterioplankton community function showed significant positive effects on both taxonomic and phylogenetic diversities, while phylogenetic diversity exhibited limited effects on the water trophic level before and after dredging ($p < 0.01$; Fig. 6a, 6b). Direct effects of physicochemical factors, community function, taxonomic diversity, and phylogenetic diversity on water trophic level were stronger than indirect effects of corresponding components (Fig. 6c, 6d). These results suggested that water trophic level, environmental factors, taxonomic diversity, phylogenetic diversity, and community function were more closely connected before dredging than after dredging.

4. Discussion

Dredging can be regarded as a large-scale anthropogenic disturbance and can alter abiotic environmental conditions and biotic community diversity and function (Manap and Voulvoulis, 2016; Zhang et al., 2017; Wan et al., 2020). It has been routinely applied for environmental protection for purifying eutrophic lakes and rivers. Many attempts have been made to reveal ecological mechanisms behind dredging to inform environmental governance. However, most studies investigate the effects of environmental variables on abundance, diversity, and structure of the bacterioplankton community (Su et al., 2017; Te et al., 2017), rather than environmental adaptation and community assembly. In this work, we investigated the responses of bacterioplankton to environmental change. Unexpectedly, we found distinct shifts in diversity, composition, interactions, function, environmental adaptation, and ecological assembly processes of the bacterioplankton community after dredging.

4.1. Smaller contributions of bacterioplankton diversity to the water trophic level after dredging

Published literature has reported that both taxonomic and phylogenetic α-diversities contribute significantly to multiple functions in terrestrial ecosystems (Jing et al., 2015; Luo et al., 2018). This might be also applied to aquatic ecosystems in terms of water trophic level. Unexpectedly, we found higher contributions of taxonomic and phylogenetic α-diversities to the water trophic level before dredging than after dredging. This phenomenon might be due to differences in diversity maintenance at both taxonomic and phylogenetic levels before and after dredging.

4.2. Weaker environmental adaptation of bacterioplankton after dredging

Environmental adaptations of bacterioplankton before and after dredging were estimated by applying two different approaches: environmental breadth at taxonomic level based on TITAN analysis (Baker and King, 2010; Romero et al., 2019) and phylogenetic signals at a phylogenetic level based on Blomberg's K statistic and the Fritz-Purvis D test (Goberna and Verdú, 2016; Wan et al., 2021a). We found that bacterioplankton exhibited broader environmental breadths and stronger phylogenetic signals before dredging than after dredging, suggesting stronger environmental adaptation before dredging.

Environmental breadth and phylogenetic signal analyses are useful to reflect microbial environmental adaptation (Jiao and Lu, 2020; Wan et al., 2021a). For instance, a previous study reported that *Proteobacteria*, *Actinobacteria* and *Cyanobacteria* are regarded as indicator taxa in wastewater treatment plants by applying TITAN analysis (Romero et al., 2019). Abundant bacteria and/or fungi exhibit stronger phylogenetic signals than corresponding rare taxa (Jiao and Lu, 2020; Wan et al., 2021a, 2021b). Microbial functional traits for ecological preferences rely on the evolutionary history of the species (Morrissey et al., 2019). For instance, bacterial functional traits in four forest soils in North America were mainly determined by evolutionary history and less affected by environmental filtering (e.g., vegetation type, precipitation, and temperature) (Morrissey et al., 2019). Species are not randomly distributed along the tree of life due to phylogenetic conservatism (Martiny et al., 2015), and the tree of life can provide information about evolutionary diversification, speciation and extinction rates (Stadler and Bokma, 2013). However, the stronger phylogenetic signals of bacterioplankton before dredging than afterwards might not be due to the shift in evolutionary history, since evolutionary diversification, speciation and extinction are strongly correlated with long-term environmental change (Lu et al., 2019). The stronger phylogenetic signals of bacterioplankton for functional traits before dredging might be via two pathways: (i) dredging-caused nutrient loss which in turn affected bacterioplankton community composition, and (ii) microbial ecological drift caused by removing sediment. It has been reported that exchanges of microorganisms and nutrients occurs between water and the sediment surface (Liao et al., 2020; Wan et al., 2020). Additionally, microbial responses to different environmental variables are phylogenetically conserved at different taxonomic levels (Martiny et al., 2015). For instance, in *Acidobacteria*, pH preference is reported to be deeply phylogenetically conserved at the phylum level, while in *Cyanobacteria* and *Actinobacteria*, temperature preference appears to be shallowly conserved at the species level (Martiny et al., 2015). In the present study, bacterioplankton showed stronger phylogenetic signals before rather than after dredging which might suggest that the bacterioplankton exhibit more phylogenetic niche conservatism (Bennett et al., 2010). This is similar to the results that showed that bacterioplankton exhibited closer phylogenetic clustering before dredging than after dredging. Additionally, the disturbance events of dredging can lead to an unstable ecosystem, which in turn could affect the bacterioplanktonic resistance to environmental change and the resilience to return to the original state or reach a new stable state (Pimm, 1984; Zhang et al., 2017). The significant change in bacterioplankton community composition might reflect that the bacterioplankton did not possess strong resistance to disturbance, and could not recover to the initial stable state after dredging. These findings might also explain why higher contributions of taxonomic and phylogenetic α-diversities to the water trophic level occur before dredging than after dredging.

4.3. Stochasticity community assembly after dredging

Before dredging, both stochastic and deterministic processes had a relatively large influences on community assembly. These results differ from the findings of homogeneous selection referring to deterministic processes dominating bacterioplankton community assembly in Lake Donghu across four seasons (Yan et al., 2017) and in coastal waters in the East China Sea across three seasons (i.e., spring, summer, and autumn) (Wang et al., 2020). A microbial community tends to be a stochasticity-dominated assembly in nutrient-rich conditions, and inclines to be a deterministic-dominated assembly in nutrient-poor conditions (Chase, 2010). After dredging, the relative contribution of “undominated” processes to bacterioplankton community assembly increased, which is similar to a report describing that “undominated” processes show a greater contribution to bacterioplankton community assembly in a flood-occurring period than in a dry season (Huber et al., 2020). These findings indicate that both anthropogenic (i.e., dredging) and natural (i.e., flood) disturbances increase microbial ecological drift.

Before and after dredging, βNTI values of bacterioplankton community were more strongly correlated with sediment total phosphorus than other environmental variables. The decisive role of sediment total phosphorus in affecting community assembly might be partially due to the high phosphorus demand for living organisms (Canfield et al., 2020). Sediment total phosphorus is an important phosphorus source for bacterioplankton growth via release from sediment (Taylor et al., 2018). Because the phosphorus cycle is coupled with carbon and nitrogen cycles (Canfield et al., 2020), sediment organic carbon and organic nitrogen might also affect stochastic and deterministic processes. We will investigate the effects of multiple environmental variables onbacterioplankton community assembly in differing aquatic ecosystems in future research.

4.4. Less conflicting interactions and weaker functions after dredging

Ecological community assembly processes determine microbial interaction patterns and functions (Xun et al., 2019; Jiao et al., 2020; Wan et al., 2021c). Bacterioplankton community functions decreased after dredging and sediment total phosphorus was essential for community functions. Phosphorus limitationaffected bacterioplankton community function in our and other studies (Yeh et al., 2020), which might be partially due to phosphorus effects on bacterioplankton community assembly. Co-occurrence networks showed that edges and nodes decreased after dredging, which is a similar finding for a flood-occurring river ecosystem in Paraná (Huber et al., 2020). The bacterioplankton community presented less conflicting interactions (mainly competition and predation) after dredging, which might be partially due to nutrient loss in water-sediment ecosystems. Sediments are important nutrient pool (Liu et al., 2016; Wan et al., 2020), and dredging-caused nutrient loss affects bacterioplankton growth, which in turn affects their abundance (Zhang et al., 2017). In addition, dredging can cause microbial ecological drift, which in turn affects the exchange of bacteria between water and sediment (Liao et al., 2020), thereby influencing bacterioplankton community stability and interactions. It is worth noting that the core bacterioplankton changed in the network module after dredging, which might lead to a community functional shift. For example, the phylum *Chloroflexi*, reported to be responsible for production of cobalamin (amicrobial growth factor) (Mehrshad et al., 2018), was found to be one of the core nodes in the network module after dredging. Consequently, bactererioplankton function generally decreased after dredging, although more unique functions were gained after dredging. From the perspective of water quality improvement, dredging should be performed promptly and efficiently to decouple bacterioplankton from their growth environment.

5. Conclusions

To our knowledge, our study is the first that shows that higher contributions of bacterioplankton taxonomic and phylogenetic α-diversities to water trophic level occur before dredging than after dredging. Bacterioplankton showed decreases in conflicting interactions, functional redundancy, phylogenetic clustering, and environmental adaptation after dredging. Both determinism and stochasticity governed bacterioplankton community assembly before dredging, while stochasticity dominated bacterioplankton community assembly after dredging. Sediment total phosphorus was a good indicator for bacterioplankton community assembly. Dredging could lead to nutrient loss, cause microbial ecological drift, and weaken relationships between abiotic and biotic factors, therefore implying that dredging is an effective means to improve water quality. Our findings reveal ecological mechanisms associated with dredging and also provide a guide for informing environmental protection policy.

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Conflict of interest

The authors declare that they have no conflicts of interest.

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Table 1 Pearson correlations between physicochemical factors and Chl-a content, taxonomic diversity (Shannon-Wiener index), and phylogenetic diversity (SES.MNTD index), and Mantel's correlation between changes in physicochemical factors and phylogenetic turnover represented by βNTI.

Property	Chl-a content		Taxonomic diversity		Phylogenetic diversity		Community assembly	
	Before	After	Before	After	Before	After	Before	After
pH	0.552*	0.519*	0.187	–0.129	–0.510*	0.027	0.291**	0.029
T	–0.223	–0.287	–0.268	0.250	–0.020	–0.010	0.090	–0.104
DO	0.693***	0.634**	0.535*	0.087	–0.037	–0.071	0.261***	0.042
Tur	–0.726***	–0.414	–0.480*	0.091	0.300	–0.084	0.201**	0.189***
PO4	–0.298	–0.214	–0.508*	0.145	0.250	0.085	0.189***	0.052
NO2	–0.308	0.137	0.101	–0.144	0.544*	–0.017	–0.021	0.415***
NH4	–0.517*	–0.560*	–0.542*	–0.019	–0.027	0.154	0.019	0.522***
NO3	–0.189	–0.098	–0.518*	0.101	–0.144	–0.227	0.071	0.008
TC	–0.390	–0.235	–0.316	0.049	0.138	0.000	0.103	0.008
TN	–0.385	–0.181	–0.234	0.041	0.256	0.083	0.160**	–0.020
IP	–0.442	–0.080	–0.551*	–0.308	–0.273	–0.179	0.030	0.294***
OP	0.276	0.287	–0.005	0.109	0.099	0.137	0.172**	0.051
NAIP	0.287	–0.300	–0.281	0.249	–0.310	–0.115	0.087	0.216***
AP	–0.485*	–0.011	–0.543*	–0.270	–0.064	0.225	–0.177**	0.181**
TP	–0.247	0.002	–0.543*	–0.450	–0.175	–0.265	–0.213***	0.342***
Olsen P	–0.258	–0.086	0.012	–0.253	–0.118	0.340	–0.041	0.027

Note: The abbreviations of environmental factors are defined in Section 2. Asterisks represent significant level (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$).