



Dredging alleviates cyanobacterial blooms by weakening diversity maintenance of bacterioplankton community

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ABSTRACT

Disentangling ecological mechanisms behind dredging is meaningful to implement environmental policy for improving water quality. However, environmental adaptation and community assembly processes of bacterioplankton in response to dredging disturbance are poorly understood. Based on Illumine MiSeq sequencing and multiple statistical analyses, we estimated interactions, functions, environmental breadths, phylogenetic signals, phylogenetic clustering, and ecological assembly processes of bacterioplankton community before and after dredging. We found distinct change in community composition, comparable decreases in diversity, functional redundancy and conflicting interaction, relatively low phylogenetic clustering, and relatively weak environmental adaptation after dredging. The bacterioplankton community assembly was affected by both stochastic and deterministic processes before dredging, but dominated by stochasticity after dredging. Sediment total phosphorus was a decisive factor in balancing determinism and stochasticity for bacterioplankton community assembly before and after dredging. Consequently, taxonomic and phylogenetic α -diversities of bacterioplankton exhibited higher contributions to the water trophic level represented by chlorophyll α before dredging than afterwards. Our results emphasized bacterioplankton in response to environmental changes caused by dredging, with nutrient loss and ecological drift playing important roles. These findings extend knowledge of contribution of bacterioplankton diversity to water trophic level and decipher mechanisms of bacterioplankton diversity maintenance in response to dredging, which is useful for guiding mitigation of cyanobacterial blooms.

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, generate massive algal blooms and thus become worldwide environmental problems (Hamilton et al., 2016; Te et al., 2017). Cyanobacterial bloom threatens diversity of aquatic organisms via releasing 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) lead to cyanobacterial bloom

(Te et al., 2017; Zhang et al., 2017; Kim et al., 2020), and non-cyanobacterial bacterioplankton are also reported to be responsible for the bloom of cyanobacteria (Berg et al., 2009; Wan et al., 2020). Mitigation management of cyanobacterial blooms includes blocking nutrient inputs, especially N and P into aquatic ecosystems, and altering bacterioplankton interactions.

Dredging can improve water quality and achieve environmental protection purpose via modifying 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 internal nutrients (e.g., N and P) from

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sediments (Liu et al., 2016). 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 evaluate diversity-driven ecosystem processes and functions. However, ecological mechanisms underlying bacterioplankton diversity maintenance in response to dredging disturbance are still poorly understood.

Microbial diversity maintenance is always expounded 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 the taxonomic level and phylogenetic signal at the phylogenetic level (Jiao and Lu, 2020; Wan et al., 2021c). Microbial environmental distribution reflects the 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 microbial response to environmental preference (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 the ongoing environmental change show phylogenetic conservatism. 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 signal can explain major ecological phenomena, including species distribution pattern, seasonal succession, and response to global environmental change (Thomas et al., 2016; Monk et al., 2018). However, environmental breadth and phylogenetic signal of bacterioplankton to environmental changes, 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 functions they perform (Stegen et al., 2016; Wan et al., 2021c). Stochastic processes include random birth, death, and dispersal events that lead to species can co-occur with distinct overlapping niches (Jiao et al., 2020). Conversely, deterministic processes involve ecological selection forced by biotic and abiotic factors, which shape species environmental adaptation and therefore determine composition and relative abundance of species (Stegen et al., 2016; Huber et al., 2020). Both stochastic and deterministic processes shape community assembly of microorganisms (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 is the major factor in determining the bacterioplankton community assembly in 25 discrete freshwater lakes in Denmark (Ren et al., 2015). However, it remains unknown whether determinism and stochasticity of bacterioplankton communities are shaped by similar environmental factors in eutrophic freshwater lakes.

Freshwater lakes are functioning for aquaculture, source 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 representing a massive human disturbance is often used to enhance water quality. To investigate responses of bacterioplankton to dredging disturbance, we chose Lake Nanhu in Wuhan, China as our study area and nine representative sites in Lake Nanhu were selected for collecting water and sediment samples before and after dredging (Fig. S1). In our previous study, a significant decrease in nutrients after dredging was found (Fig. S2), and our results showed that cyanobacterial bloom could be mitigated by altering the interconnection between sediment biogeochemical processes and the bacterioplankton community (Wan et al., 2020). In the present research, we would like to: (i) investigate

contributions of taxonomic and phylogenetic diversity to water trophic level before and after dredging, (ii) explore mechanisms of microbial diversity maintenance before and after dredging, and (iii) decipher community assembly on bacterioplankton interaction and function. Considering dredging led to nutrient loss, we hypothesized that dredging might weaken bacterioplankton environmental adaptation and intensify ecological drift. To meet our targets and verify our hypothesis, 16S rRNA gene amplicon sequencing, and water and sediment physicochemical properties were determined for further analysis.

2. Materials and methods

2.1. Samples and data collection

Detailed information about dredging was described in a 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 in Wuhan of China (Wan et al., 2021c). We estimated water physicochemical properties, including pH, turbidity (Tur), dissolved oxygen (DO), temperature (T), nutrient phosphorus $\text{PO}_4^{3-}\text{-P}$ (PO_4), nutrient nitrite $\text{NO}_2\text{-N}$ (NO_2), nutrient nitrate $\text{NO}_3\text{-N}$ (NO_3), and nutrient ammonia $\text{NH}_4^+\text{-N}$ (NH_4), based on standard approaches (APAH, 1998). 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 described previously (Wan et al., 2020). Chlorophyll α (Chl- α) content was quantified using spectrophotometric method (Te et al., 2017).

Universal primers of 338F (5'-ACT CCT ACG GGA AGC A-3') and 806R (5'-GGA CTA CHV GGG TWT CTA AT-3') were applied 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 sequence processing are reported previously (Wan et al., 2020) and also summarized in the Supplementary materials (Supplementary method 1). The validated 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, abundances of cyanobacteria and bacterioplankton were also measured using universal primers. The amplifications of 16S rRNA genes for assessing cyanobacteria and bacterioplankton abundances are reported in a previous study (Wan et al., 2020) and also summarized in the Supplementary materials (Supplementary method 2).

2.2. Data analysis

Venn diagram and non-metric multidimensional scaling (NMDS) were used to reveal the community structure of bacterioplankton using the "VennDiagram" and "ggplot2" packages of R (Wan et al., 2021d). Permutational multivariate analysis of variance (PERMANOVA) and pairwise analyses of similarity (ANOSIM) were selected to quantitatively evaluate pure effects of single physicochemical variables on community structure of bacterioplankton by using the "adonis" and "anosim" function in the "vegan" package of R (Wan et al., 2020). 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 (Wan et al., 2020). 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 (represent significantly positive correlation) to negative edge (denote noticeably negative correlation) to reflect bacterioplankton conflicting interaction (mainly including competition and predation) (Wei et al., 2019). We performed functional prediction based on sequence similarity of the bacterioplankton 16S rRNA gene by employing the package "Tax4Fun2" of R, and calculated the functional redundancy index (FRI) of each sample (Wemheuer et al., 2020; Wan et al., 2021c). 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 assess the phylogenetic distance between communities, the beta mean nearest taxon distance (β MNTD) 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 measure 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 the phylogenetic conservation for traits that are closely correlated with microbial ecological preference, can provide predictions for microbial evolutionary adaptation (Martiny et al., 2015). We used Blomberg's K statistic and 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 contrasts the observed signal to the signal under a Brownian motion-based metric of trait evolution on a phylogeny (Blomberg et al., 2003). The K values were computed by applying the "picante" package of R (Kembel et al., 2010), and 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; Goberna and Verdú, 2016). The D value was transformed 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 (β NTI) and null model-based Bray-Curtis-based Raup-Crick (RC_{bray}) were applied to compute the differences in diversities at both phylogenetic and taxonomic levels (Stegen et al., 2016; Wan et al., 2021a). If $|\beta\text{NTI}| > 2$, this demonstrates the dominance of deterministic processes, with significantly more (i.e., variable selection; $\beta\text{NTI} > 2$) and less (i.e., homogeneous selection; $\beta\text{NTI} < -2$) phylogenetic turnover than expected. If $|\beta\text{NTI}| < 2$, $RC_{\text{bray}} < -0.95$ and $RC_{\text{bray}} > 0.95$, this represents the relative contributions of homogenizing dispersal and dispersal limitation, respectively. If $|\beta\text{NTI}| < 2$ and $|RC_{\text{bray}}| < 0.95$, this indicates the influence of "undominated" assembly, which mainly comprise diversification, ecological drift, weak selection, and/or weak dispersal (Stegen et al., 2016; Jiao et al., 2020; Huber et al., 2020). The detailed algorithm is described in prior literature (Stegen et al., 2016). The neutral model analysis was employed to further reflect the contribution of a stochastic 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 significantly positively correlated with pH ($p < 0.05$) and DO ($p < 0.01$), while noticeably negatively correlated with NH_4 before and after dredging ($p < 0.05$) (Table 1). Linear regressions reflected significant correlations between Chl- α content and cyanobacterial abundance before and after dredging ($p < 0.001$), but no apparent correlation was found between Chl- α content and bacterioplankton abundance ($p > 0.05$) (Fig. 1b). This suggests that algae blooms in eutrophic Lake Nanhu were mainly dominated by cyanobacterial blooms 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). All OTUs were classified into 33 phyla. *Actinobacteria*, *Proteobacteria*, and *Bacteroidetes* dominated the communities before and after dredging, with a total relative abundance of higher than 85%. The relative abundances of *Proteobacteria* and *Bacteroidetes* decreased significantly after dredging (Wilcoxon rank-sum test, $p < 0.05$). The NMDS plot reflected distinct difference in community structure of bacterioplankton 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 PERMANOVA results, N (e.g., TN and NH_4) and P (e.g., AP and TP) exhibited significant contributions to 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, NH_4 , and NO_3) had significant effects on taxonomic or phylogenetic α -diversity before dredging rather than after dredging (Table 1). Additionally, the taxonomic α -diversity showed significant correlation with Chl- α before dredging ($p < 0.05$), but it not after dredging ($p > 0.05$) (Fig. 1b). The phylogenetic α -diversity was slightly more correlated with Chl- α before dredging than afterwards ($p > 0.05$). 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 β MNTD) of bacterioplankton were significantly correlated with physicochemical factor dissimilarity before and after dredging ($p < 0.001$; Figs. S5 and S6). Subsequently, environmental adaptation of bacterioplankton were evaluated at both taxonomic and phylogenetic levels (Fig. 2). The bacterioplankton showed a broader range of environmental thresholds for almost all environmental factors except T, NH_4 , IP and AP before dredging than after dredging (Fig. 2a). This suggests that weakening of bacterioplankton adaptation to environment in general and also enhancing of preferences to some unique environmental factors after dredging. Furthermore, the bacterioplankton exhibited stronger phylogenetic signals for almost all environmental parameters before dredging than after dredging based on Blomberg's K statistic (Fig. 2b) and Fritz-Purvis

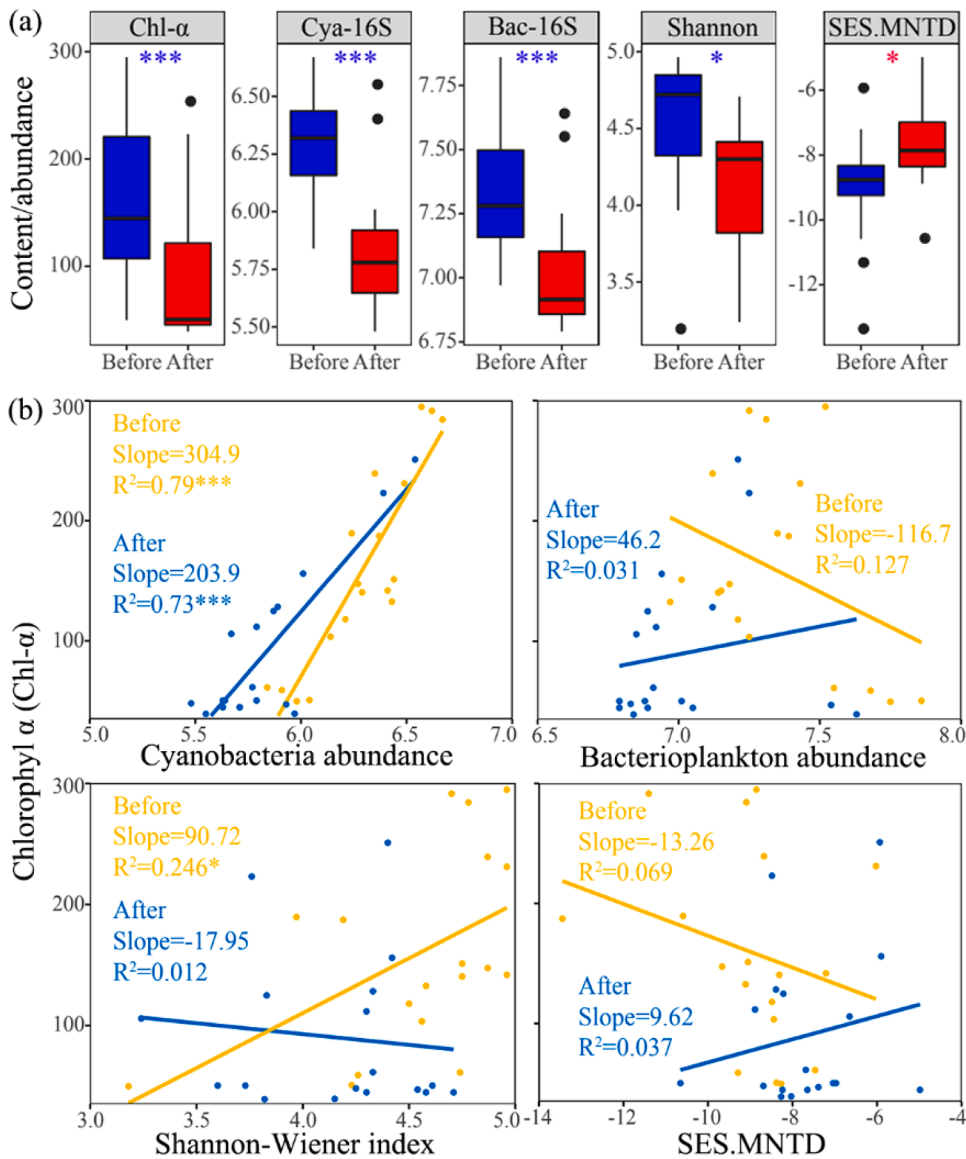


Fig. 1. (a) Boxplot showing differences in chlorophyll α (Chl- α ; $\mu\text{g/L}$), cyanobacteria abundance (Cya-16S; log10 copies/L water), bacterioplankton abundance (Bac-16S; log10 copies/L water), taxonomic diversity (Shannon-Wiener index), and phylogenetic diversity (SES.MNTD index) between before and after dredging. (b) Linear regressions between Chl- α and cyanobacteria abundance, bacterioplankton abundance, taxonomic diversity, and phylogenetic diversity before and after dredging. Asterisks represent significance (*, $p < 0.05$; ***, $p < 0.001$).

Table 1

Pearson's correlations between physicochemical factors and Chl-a content, taxonomic diversity (Shannon-Wiener index), and phylogenetic diversity (SES.MNTD index), and Mantel's correlations 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 significance (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$)

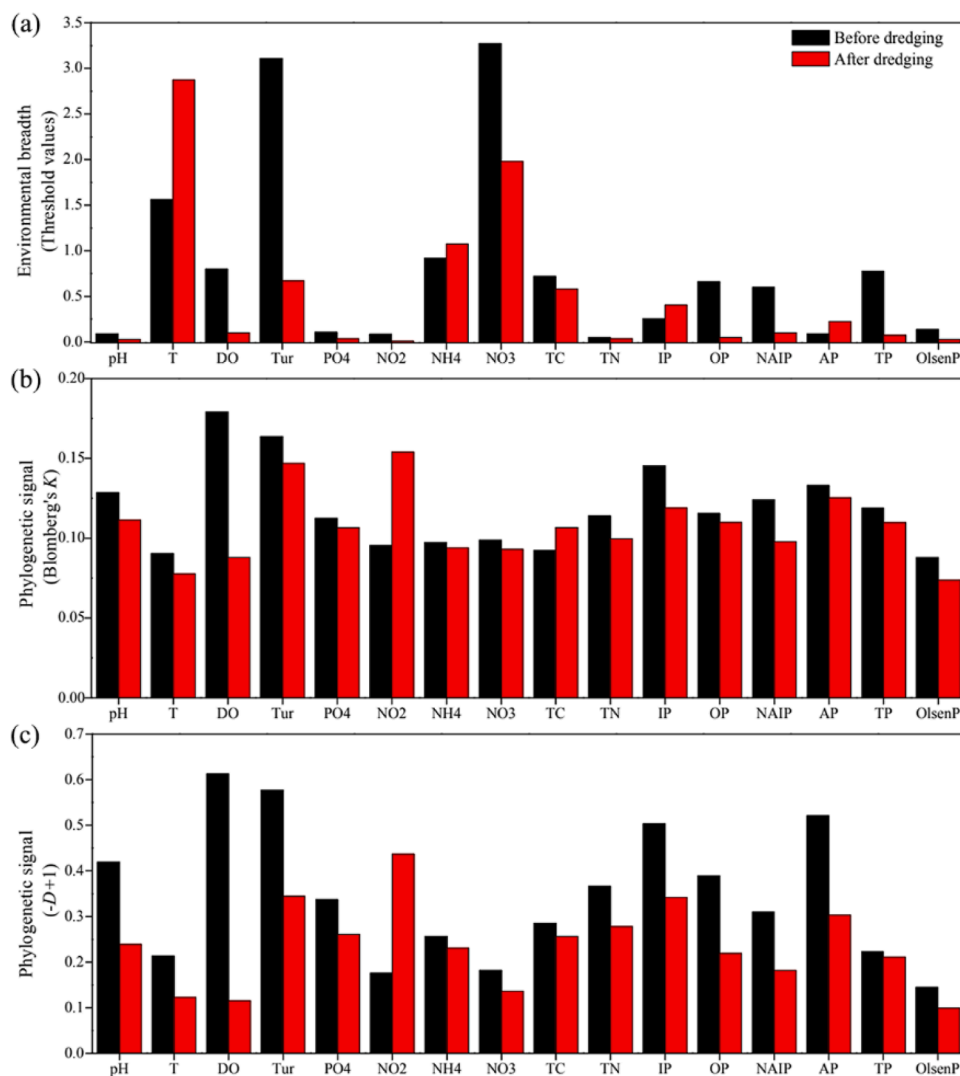


Fig. 2. Environmental adaptation of bacterioplankton in eutrophic Lake Nanhu before and after dredging. (a) Environmental breadth assessed by the threshold values of taxa in response to environmental factors determined by using threshold indicator taxon analyses. (b and c) Phylogenetic signal demonstrating trait conservatism for the environmental preferences of bacterioplankton before and after dredging employing Blomberg's K statistic (b) and the Fritz-Purvis D test (c). The abbreviations for the environmental factors are defined in the "Materials and methods" section.

D test (Fig. 2c). These results supported that bacterioplankton taxa showed a stronger environmental adaptation at both taxonomic and phylogenetic levels before rather than after dredging.

3.3. Ecological processes of bacterioplankton community assembly

Based on the null model, dispersal limitation (47.7%) and variable selection (28.1%) contributed the most to community assembly before dredging (Fig. 3a). However, "undominated" processes (51.0%) and dispersal limitation (41.8%) contributed the most to community assembly after dredging. Homogenizing dispersal and homogeneous selection contributed limitedly to community assembly. Consequently, stochastic and differentiating processes dominated bacterioplankton community assembly, and both were apparently higher before dredging than after dredging (Fig. 3a). The neutral community model revealed that 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 increase in "undominated" process probably via increasing ecological drift, which in turn increased stochasticity.

Results of the Mantel's tests showed that changes in TP, AP, and Tur were significantly correlated with β NTI compared to other environmental factors before and after dredging (Table 1). Additionally, β NTI was significantly negatively correlated with the change in TP before dredging (Fig. S7), suggesting that an increasing divergence in TP led to

a decrease in stochasticity. By contrast, β NTI was noticeably correlated with the change in TP positively 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 decreased first and then increased before dredging, and increased first 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 dredging (ratio = 3.38) than afterwards (ratio = 8.06) (Table S1), suggesting relatively less conflicting interaction 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). Those core microorganisms represented by core nodes showed differing correlations with physicochemical variables (Tables S2, S3). These results supported that a comparable divergence in bacterioplankton interactions between before dredging 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

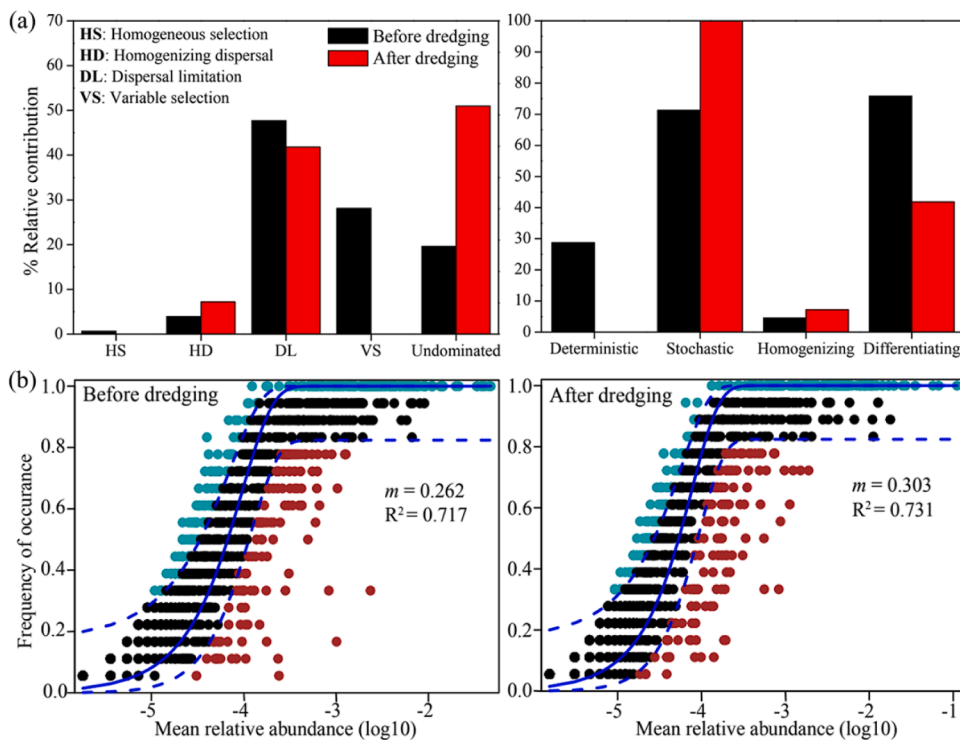


Fig. 3. Community assembly of bacterioplankton before and after dredging. (a) Null model analysis showing relative contributions of ecological processes to the assemblies of bacterioplankton communities before and after dredging. Stochastic = Homogenizing dispersal + Dispersal limitation + Undominated processes; Deterministic = Homogeneous selection + Variable selection; Homogenizing = Homogenizing dispersal + Homogeneous selection; Differentiating = Dispersal limitation + Variable selection. (b) Fit of the neutral community model showing bacterioplankton community assembly before and after dredging. The solid blue lines indicate the best fit to the neutral model, and the dashed blue lines represent 95% confidence intervals around the model prediction. OTUs that occur more or less frequently than predicted by the neutral community model are shown in different colors.

(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 suggest that a functional decrease in bacterioplankton community in general and also gaining of unique functions after dredging. According to PERMANOVA results, sediment TP showed significantly greater effects on community function than other physicochemical parameters before and after dredging (Fig. S10). This implies that phosphorus resource might be the determinant factor shaping the bacterioplankton community function.

Ultimately, we quantitatively estimated the 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 β NTI and 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 affected more by community assembly after dredging. We also found significant correlation between β NTI and change in Chl- α content before dredging ($R^2 = 0.10$, $p < 0.001$) than after dredging ($R^2 = 0.012$, $p > 0.05$) (Fig. 5b). This suggests that dredging disturbance might reduce the effect of bacterioplankton community assembly on the water trophic level.

3.4. Relationships among 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 factor, taxonomic diversity, phylogenetic diversity, and community function (Fig. 6). Before dredging, physicochemical factors had significantly positive effect on bacterioplankton taxonomic diversity, which in turn noticeably positively affected the water trophic level ($p < 0.05$;

Fig. 6a,c). Physicochemical factors also showed the dramatic directly positive influence on water trophic level. The model exhibited a good fit to our data, as reflected by the non-significant χ^2 test ($N = 18$, $\chi^2 = 0.15$, d.f. = 1, $p = 0.903$; Fig. 6a). By contrast, physicochemical factors showed the limitedly direct or indirect effect on water trophic level after dredging ($p > 0.05$; Fig. 6b,d). The model also exhibited a good fit to the data, as indicated by the non-significant χ^2 test ($N = 18$, $\chi^2 = 0.75$, d.f. = 1, $p = 0.387$; Fig. 6b). Bacterioplankton community function showed significant positive effects on both taxonomic and phylogenetic diversities, but phylogenetic diversity exhibited limited effects on the water trophic level before and after dredging ($p < 0.01$; Fig. 6a,b). Direct effects (one factor directly affects another) of physicochemical factor, community function, taxonomic diversity, and phylogenetic diversity on water trophic level were stronger than indirect effects (one factor indirectly influences another) of corresponding component (Fig. 6c,d). 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 regarded as a large-scale anthropogenic intervention in environmental management 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 perform environmental governance. However, most studies investigate 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 changes caused by dredging. Unexpectedly, we found distinct shifts in diversity, composition, interaction, function, environmental adaptation, and ecological assembly processes of the bacterioplankton community after dredging.

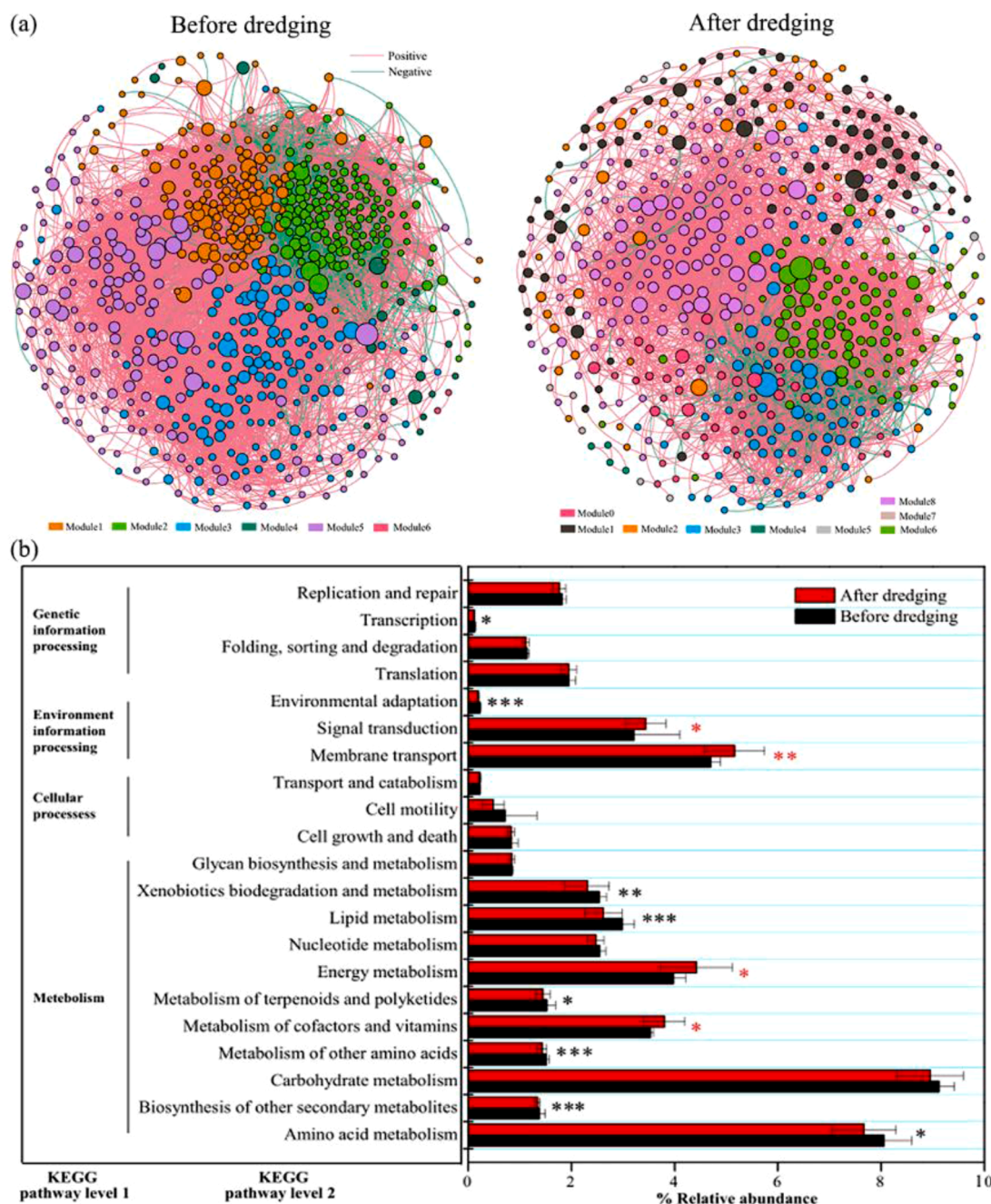


Fig. 4. Co-occurrence networks of OTUs (a) and function profiling of bacterioplankton community (b) before and after dredging. Asterisks denote significance (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). The nodes (circles) in the networks denote OTUs, and the size of the node reflects the value of betweenness centrality. The red and green edges (lines) in the networks represent significant positive and negative correlations, respectively.

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

Published literatures have reported that both taxonomic and phylogenetic α -diversities contribute significantly to multiple functions in terrestrial ecosystems (Jing et al., 2015; Luo et al., 2018; Wan et al., 2021a). This might be also applied to aquatic ecosystems in term of the water trophic level. Unexpectedly, we found greater 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, namely environmental breadth and phylogenetic signal at taxonomic and phylogenetic levels, respectively (Wan et al., 2021a, 2021b). We found that bacterioplankton showed 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 (Wan et al., 2021a). For instance, a previous study has reported that *Proteobacteria*, *Actinobacteria* and *Cyanobacteria* are regarded as indicator taxa in wastewater

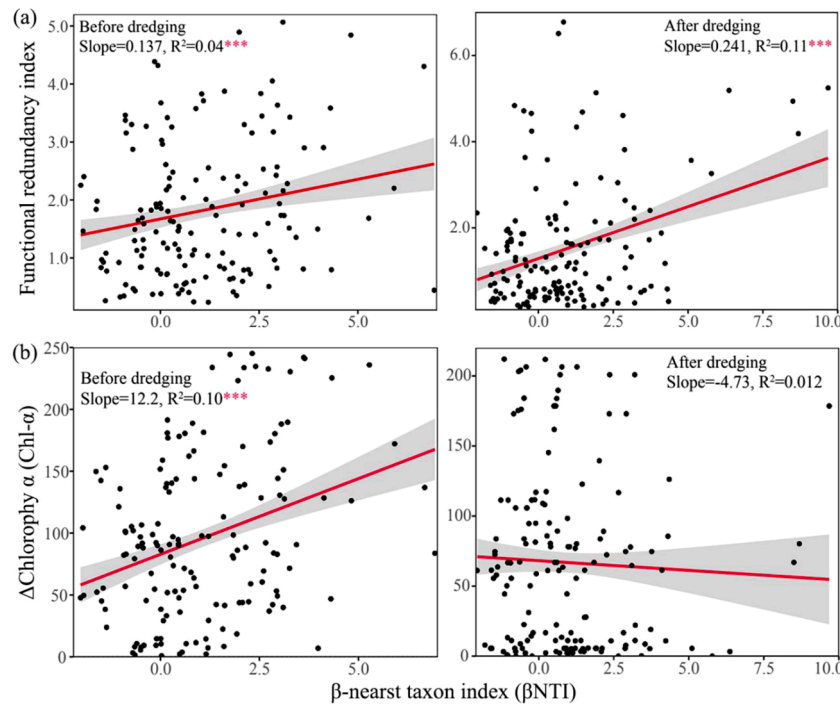


Fig. 5. Linear regressions between β NTI and functional redundancy index (a) and change in chlorophyll α content (b) before and after dredging. Asterisks denote significance (***, $p < 0.001$).

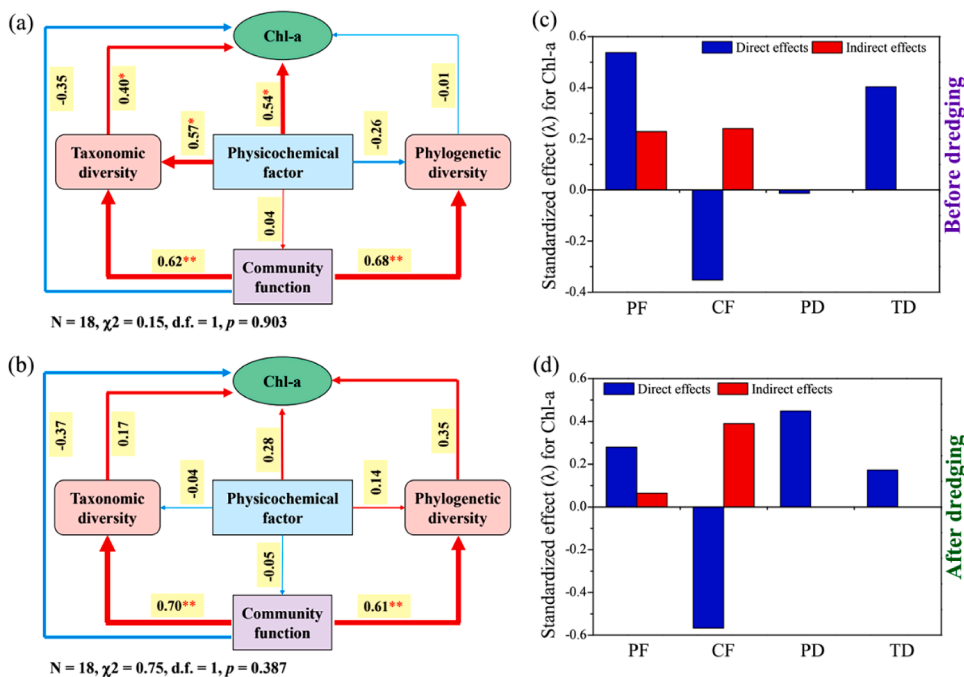


Fig. 6. Structural equation models showing hypothesized causal relationships among components including Chl- α , taxonomic diversity, phylogenetic diversity, community function, and physicochemical factor (the first axis of principal component analysis based on the physicochemical factor matrix) (a) before dredging and (b) after dredging. The width of the arrows indicates the strength of the standardized path coefficient. The red lines represent positive path coefficients, and the blue lines denote negative path coefficients. Values above the lines indicate path coefficients between two parameters. Asterisks indicate parameters with a significant correlation (*, $p < 0.05$; **, $p < 0.01$). The direct and indirect effects of biotic and abiotic factors on the water trophic level (represented by Chl- α content) before (c) and after (d) dredging. Abbreviations: PF, physicochemical factor; CF, community function; PD, phylogenetic diversity; TD, taxonomic diversity.

treatment plant 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 depend on the evolutionary history of the species (Martiny et al., 2015; Morrissey et al., 2019). Species are not distributed randomly 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 species 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) the microbial ecological drift caused by removing sediment. It has been reported that exchanges of

microorganisms and nutrients occur between water and the sediment surface (Liao et al., 2020; Wan et al., 2020). In addition, microbial responses to different environmental variables are phylogenetically conserved at different taxonomic levels (Martiny et al., 2015). For example, 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 show more phylogenetic niche conservatism (Bennett et al., 2010). This is similar to the results in which bacterioplankton exhibited closer phylogenetic clustering before dredging than afterwards. Additionally, the disturbance events of dredging can lead to an unstable ecosystem, which in turn affect the bacterioplanktonic resistance to environmental change and the resilience to return to the original status or establish a new stable state (Pimm, 1984; Zhang et al., 2017). The significant change in bacterioplankton community composition might reflect that the bacterioplankton did not show strong resistance to dredging disturbance, and could not recover to the initial stable state after dredging, at least not in a short period of time. These findings mentioned above might explain why larger contributions of taxonomic and phylogenetic α -diversities to the water trophic level occur before dredging rather than after dredging.

4.3. Stochasticity community assembly post dredging

Before dredging, both stochastic and deterministic processes had 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 over four seasons (Yan et al., 2017) and in coastal waters in the East China Sea for three seasons (i.e., spring, summer, and autumn) (Wang et al., 2020). Microbial community tends to be stochasticity-dominated assembly in nutrient-rich conditions, and incline to be determinism-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, β NTI 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. In the future, we plan to investigate the effects of multiple environmental variables for bacterioplankton community assembly in differing aquatic ecosystems with more sampling sites.

4.4. Less conflicting interaction and weaker function after dredging

Ecological community assembly processes determine microbial interaction patterns and functions (Jiao et al., 2020; Wan et al., 2021c). Bacterioplankton community functions decreased after dredging and sediment total phosphorus was essential for community functions. Phosphorus limitation affected bacterioplankton community functions in this and also 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 interaction (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 bacterioplanktonic 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 surface sediment (Liao et al., 2020), thereby influencing bacterioplankton community stability and interactions. It is worth noting that the core bacterioplankton changed in 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 (a key microbial growth factor) (Mehrshad et al., 2018), was found to be one of the core nodes in the network module after dredging. Consequently, bacterioplankton function decreased in general after dredging, however, more unique functions gained after dredging. From the perspective of water quality improvement, dredging should be performed promptly and efficiently to decouple bacterioplankton from their living environment.

5. Conclusion

To our knowledge, our study is the first that shows a greater contribution of bacterioplankton taxonomic and phylogenetic α -diversities to the water trophic level occur before rather than after dredging. Bacterioplankton show decreases in conflicting interaction, functional redundancy, phylogenetic clustering, environmental adaptation after dredging. Both determinism and stochasticity govern bacterioplankton community assembly before dredging, but stochasticity dominates bacterioplankton community assembly after dredging. Sediment total phosphorus can be a key 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 performing environmental protection policy.

Declaration of Competing Interest

The authors declare that they have no conflicts of interest.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:[10.1016/j.watres.2021.117449](https://doi.org/10.1016/j.watres.2021.117449).

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