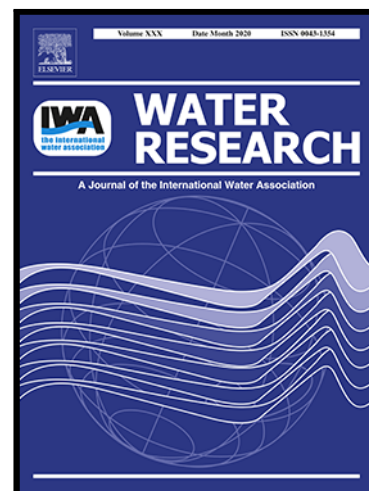


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**Highlights**

- Taxonomy and phylogeny were tightly correlated with environmental factors
- Rare taxa showed stronger environmental adaptation than abundant taxa
- Dissolved oxygen mediated balance between stochastic and deterministic processes

**Stronger environmental adaptation of rare rather than abundant bacterioplankton in response to dredging in eutrophic Lake Nanhu (Wuhan, China)**

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**Abstract**

Deciphering responses of rare versus abundant bacterioplankton to environmental change, crucial for understanding and mitigating of cyanobacterial blooms, is an important but poorly investigated subject. Using MiSeq sequencing, we investigated the taxonomic and phylogenetic diversity of rare and abundant bacterioplankton in eutrophic Lake Nanhu before and after dredging. We estimated environmental breadths and phylogenetic signals of ecological preferences of rare and abundant bacterioplankton, and investigated community function and bacterioplankton assembly processes. Both taxonomic and phylogenetic distances of rare and abundant bacterioplankton communities were significantly positively correlated with the dissimilarity of environmental factors. Threshold indicator taxa analysis and Blomberg's  $K$  statistic indicated that rare taxa held broader environmental thresholds and stronger phylogenetic signals for ecological traits than abundant taxa. Environmental adaptations of both rare and abundant taxa exhibited distinct changes after dredging. Higher functional redundancy occurred in the abundant compared to the rare bacterioplankton, with functions of rare bacterioplankton decreasing and for the abundant ones increasing after dredging. The null model revealed that dispersal limitation belonging to stochastic processes determined the abundant bacterioplankton community assembly, whereas variable selection belonging to deterministic processes drove the rare one. Rare bacterioplankton was more environmentally constrained than the abundant one. Dissolved oxygen was the decisive factor in determining the balance between stochasticity and determinism in both rare and abundant bacterioplankton. Our study extends our knowledge of environmental adaptation of rare versus abundant bacterioplankton to massive disturbing measures, i.e. dredging, and allows to estimate dredging performance for mitigating cyanobacterial blooms

from a molecular ecology viewpoint.

**Keywords:** community assembly; environmental breadth; environmental disturbance; heterotrophic bacteria; phylogenetic signal

## 1. Introduction

Heterotrophic bacteria play significant roles in key element cycling of aquatic systems (e.g., carbon degradation, nitrogen fixation, phosphorus solubilization, and sulfur transformation) (Lavik et al., 2009; Stegen et al., 2016; Wang et al., 2019), and represent important resources in aquatic food webs (Azam et al., 1983; Graham et al., 2014). Cyanobacteria, one of the most important members of bacterioplankton in both marine and freshwater ecosystems, are responsible for providing essential oxygen to most living organisms (Hamilton et al., 2016; Soo et al., 2017). Lately, excessive growth of cyanobacteria following eutrophication in freshwater ecosystems forms massive blooms, which become a global environmental issue leading to extensive oxygen depletion during bloom breakdown (Te et al., 2017). As a consequence, they directly affect the diversity of aquatic organisms and indirectly threaten environmental and human health by releasing algal toxins and causing lack of oxygen (Huisman et al., 2018). Cyanobacterial mass blooms in aquatic ecosystems are strongly correlated with the superfluous loading of nitrogen (N) and phosphorus (P) (Paerl et al., 2011; Li et al., 2020), and their seasonal massive growth mainly rely on the dynamic changes in nutrient and temperature (Bunse and Pinhassi, 2017; Yan et al., 2017a; Huisman et al., 2018). In addition, a prior study reveals that non-cyanobacterial bacterioplankton might also affect cyanobacterial biomass (Te et al., 2017). *Flavobacterium*, *Oxalobacteraceae*, and *Streptomyces* have positive effects on cyanobacterial growth, and *Arthrobacter*, *Gracilibacteria*, *Parcubacteria*, and *Pedobacter* exhibit negative

effects (Berg et al., 2009; Te et al., 2017; Wan et al., 2020a). Thereby, diversity, community composition, interactions, and function of the bacterioplankton are closely correlated with both water and sediment physicochemical properties, especially N and P sources (Zhang et al., 2017; Wan et al., 2020a). Consequently, understanding bacterioplankton community dynamics in response to environmental changes would provide mechanistic insights for cyanobacterial bloom mitigation.

Bacterioplankton  $\alpha$ - and  $\beta$ -diversity substantially vary along environmental gradients (e.g., nutrient, temperature, and oxygen) (Lindström et al., 2006; Lindström and Östman, 2011; Lindström and Langenheder, 2012; Shen et al., 2018). Several ecological theories that attempt to explain diversity-environment relationships mainly consider life strategies of species (e.g., competition and cooperation) and its *in-situ* resource (e.g., space and nutrient availability) (Niño-García et al., 2016; Lu et al., 2019; Huber et al., 2020). Heterogeneity in substrate preference and environmental stress adaptations of species result in differences in bacterioplankton growth rate and abundance (Li et al., 2011; Salcher et al., 2013). This can lead to an inhomogeneous distribution of bacterioplankton abundance in a local microbial community, with relatively few dominant and a large number of rare species (alternatively known as “rare biosphere”) (Sogin et al., 2006). Prior studies have described that rare and abundant species often exhibit distinct distribution patterns and functional traits (Liu et al., 2015; Jiao and Lu, 2020a). Therefore, deciphering the distribution pattern and community assembly process of rare and abundant species is vital for understanding microbe-driven ecosystem processes and functions.

Environmental heterogeneity is an important determinant in shaping species distribution patterns and affecting abundance in aquatic ecosystems (Pontarp et al., 2013; Marshall et al., 2019). Richness of a rare or abundant species is the result of a

balance between its growth and death rates (Pedrós-Alió, 2007; Ratzke et al., 2018), but both groups of microbial taxa show diverse responses to environmental change (Mo et al., 2018; Chen et al., 2020). Environmental thresholds of species reflect changes in taxa distributions along an environmental gradient over space or time (Baker and King, 2010). For example, environmental thresholds of bacterioplankton in streams and rivers along the Oklahoma-Arkansas border are evaluated by using the accumulated values of change points of all the species in a given bacterial community (LeBrun et al., 2018). Optional environmental thresholds rarely integrate the whole richness, occurrence, and directionality of microbial responses at the species level, and the limited research is concentrated on standardized phylogenetic and molecular evolutionary analysis of aquatic ecosystems affected by human activity. In addition, responses of microorganisms to environmental change reveal phylogenetic conservatism, with species being non-randomly distributed along the tree of life (Martiny et al., 2013; Martiny et al., 2015). For example, rare bacterioplankton show strong conservatism of negative responses to total nitrogen and total phosphorus, while abundant bacterioplankton exhibit strong conservatism of positive responses (Li et al., 2017). Salinity and pH are crucial determinants in shaping bacterial distribution patterns in aquatic ecosystems (Cottrel et al., 2005; Silveira et al., 2011; Bunse et al., 2016; Comte et al., 2017; Lu et al., 2019), and the response traits of pH and salinity preferences are reported to be relatively deeply conserved (Martiny et al., 2015). Therefore, evaluating the phylogenetic patterns of microbial response traits provides predictions for microbial distribution pattern and their responses to environmental change. However, phylogenetic pattern and response threshold of bacterioplankton communities to ongoing environmental change, especially rare and abundant taxa, have not been simultaneously studied in eutrophic lakes with massive cyanobacterial

blooms.

Disentangling different community assembly processes and their contributions is a key issue in microbial ecology (Stegen et al., 2016; Huber et al., 2020; Wan et al., 2021). Generally, stochastic and deterministic (i.e., species sorting) processes have been evaluated in respect to their contributions to microbial community assembly (Yan et al., 2017b; Wang et al., 2020). Thereby, rare bacterial taxa seem to be limited more by local environmental conditions than abundant ones, e.g. in Chinese inland freshwater ecosystems (Liu et al., 2015). In addition, in three subtropical bays of China, dispersal of rare bacterial taxa seems to be more limited than abundant ones (Mo et al., 2018). Environmental factors play important roles in balancing stochastic and deterministic processes (Jiao and Lu, 2020b; Wan et al., 2021). For example, availability of organic carbon can shift bacterial community assembly from stochastic to deterministic (Stegen et al., 2016). Yet, it remains unknown whether similar environmental factors mediate the governance of stochasticity and determinism in community assembly of rare versus abundant bacterioplankton in eutrophic aquatic ecosystems.

Lake Nanhu, located in Wuhan, China, plays important roles in providing entertainment, controlling flood, and supplying aquatic products. In the last decades, Lake Nanhu suffered from seasonally and periodically massive cyanobacterial blooms (Wuhan Water Authority 2014, <http://en.0430.com/cn/web113017/>). Many ecological restoration measures have been used to mitigate cyanobacterial blooms. Dredging, alternatively named as removal of sediment, has been reported and implemented to enhance the water quality of Lake Nanhu since July, 2017. Dredging represents a massive disturbance for the lake ecosystems and caught our interest in exploring the responses of both rare and abundant bacterioplankton. In a previous study, we



observed diversity losses in bacterioplankton communities after dredging, and noticeable declines in nutrient content of both water and sediment after dredging (Wan et al., 2020a). Additionally, our prior study also indicated that dredging could mitigate cyanobacterial bloom development by altering the interconnectivity between bacterioplankton communities in the overlying water and sediment biogeochemistry (Wan et al., 2020a). In the present study, we aimed to (i) estimate the potential environmental thresholds and phylogenetic distributions of rare and abundant bacterioplankton across diverse environmental gradients before and after dredging, (ii) investigate the major environmental variables influencing assembly processes of rare and abundant bacterioplankton, and (iii) determine relationships between community function and assembly before and after the disturbance event. Given the low competition potential and growth rate of rare taxa at natural sites (Pedrós-Alió, 2007; Campbell et al., 2011), we hypothesize that rare bacterioplankton taxa might be characterized by relatively narrow environmental thresholds and relatively weak phylogenetic signals for traits compared to abundant taxa. Community assembly processes can be imperative for coupling microbial community structure with their ecosystem functions (Bannar-Martin et al., 2017; Wan et al., 2021), we hypothesize community assembly could be indicative for bacterioplankton community function. To address our hypotheses, we performed 16S rRNA gene Illumina sequencing of rare versus abundant bacterioplankton in relation to 16 environmental factors, and we found rare bacterioplankton exhibited broader environmental thresholds and stronger phylogenetic signals for ecological traits than abundant bacterioplankton.

## 2. Materials and methods

### 2.1. Data collection

Dredging occurred in August, September, and November, 2017, and in January

and March, 2018, but no dredging was performed between April and July, 2018. A detailed description of dredging in the Lake Nanhu is given in our previous study (Wan et al., 2020a). A total of 36 each water and sediment samples were collected from nine sites located in eutrophic Lake Nanhu (Wuhan, China) before (April and July, 2017) and after (April and July, 2018) intensive lake dredging. We measured water physicochemical properties, such as pH, temperature (T), dissolved oxygen (DO), turbidity (Tur), free  $\text{PO}_4^{3-}\text{-P}$  ( $\text{PO}_4$ ), free  $\text{NH}_4^+\text{-N}$  ( $\text{NH}_4$ ), free  $\text{NO}_2^-\text{-N}$  ( $\text{NO}_2$ ), and free  $\text{NO}_3^-\text{-N}$  ( $\text{NO}_3$ ). Sediment physicochemical characteristics comprised total carbon (TC), total nitrogen (TN), inorganic phosphorus (IP), organic phosphorus (OP), non-apatite inorganic phosphorus (NAIP), apatite phosphorus (AP), total phosphorus (TP), and Olsen P were also determined. The detailed information about sampling, water processing, and measuring methods of physicochemical properties are described in detail by Wan et al. (2020a).

The V3–V4 regions of the 16S rRNA gene of bacterioplankton in water were amplified using the universal primer sets 338F (5'- ACT CCT ACG GGA GGC AGC A-3') and 806R (5'- GGA CTA CHV GGG TWT CTA AT-3') (Wan et al., 2020a). PCR products were purified and then sequenced on an Illumina MiSeq platform. Detailed procedures of the harvesting of bacterioplankton in water, DNA extraction, gene amplification, and raw data processing are described by Wan et al. (2020a) and also summarized in supplemental material (Experiment 1). The purified sequences were clustered into operational taxonomic units (OTUs) at a 97% similarity level against the SILVA v128 reference. The MiSeq sequencing raw data were deposited in the National Center for Biotechnology Information (NCBI, <https://www.ncbi.nlm.nih.gov/>) Short Read Archive (SRA) database under accession numbers PRJNA391223 (2017 water samples) and PRJNA541122 (2018 water samples).

## 2.2. Data analysis

A total of 1528 OTUs were identified from 1,201,742 purified reads. Based on the distribution patterns described in prior studies, OTUs with relative abundances less than 0.01% of the total sequences were named as “rare”, those with relative abundances above 0.1% were designated as “abundant”, and the remaining OTUs (0.01–0.1%) were defined as “intermediate” (Jiao and Lu., 2020a, 2020b).

To evaluate the pairwise phylogenetic distance between communities, beta mean nearest taxon distance ( $\beta$ MNTD) was calculated using the “comdistnt” function in the “picante” package. Functional profiling of bacterioplankton taxa was conducted by applying the package “Tax4Fun2” in R, and the functional redundancy index (FRI) of each sample was determined based on the similarity of the 16S rRNA gene sequences (Wemheuer et al., 2018; Wan et al., 2020b). The FRI refers to the proportion of species capable of possessing a particular Kyoto Encyclopedia of Genes and Genomes (KEGG, <https://www.kegg.jp/>) function and their phylogenetic relationship to each other (Wemheuer et al., 2018). Besides, we estimated the effects of physiochemical factors on bacterioplankton community composition by applying permutational multivariate analysis of variance (PERMANOVA).

To determine threshold values of rare and abundant bacterioplankton taxa in response to individual physicochemical factors, threshold indicator taxa analysis (TITAN) was carried out using the “TITAN2” package of R (Romero et al., 2019; Jiao and Lu, 2020b). Briefly, we determined upper and lower thresholds of difference in the rare and abundant bacterioplankton by calculating the sums of taxa scores for OTUs for each physicochemical variable. In addition, the phylogenetic signals were estimated for rare and abundant bacterioplankton to test the link between the environmental preference of a bacterioplankton’s OTU and its phylogeny, indicating

the response of phylogenetic conservatism to complex habitats (Martiny et al., 2015; Goberna and Verdú, 2016). Before achieving this analysis, we firstly determined the potential trait information about both rare and abundant bacterioplankton OTUs in response to each individual physicochemical variable. In brief, the ecological preferences for each OTU were assessed by computing Spearman correlations between physicochemical variables and relative abundances of bacterioplankton taxa according to prior studies (Oliverio et al., 2017; Jiao and Lu, 2020b). The OTUs positively or negatively correlated with pH were designated as “alkaline-preferred” or “acid-preferred”; the OTUs positively or negatively correlated with temperature were identified as “warm-preferred” or “cold-preferred”. In this study, we employed Blomberg’s  $K$  statistic to determine the phylogenetic signals for the environmental preference of rare and abundant bacterioplankton taxa (Goberna and Verdú, 2016; Oliverio et al., 2017). The Blomberg’s  $K$  statistical analysis describes a phylogenetic signal that compares the observed signal in a trait to the signal under a Brownian motion-based metric of trait evolution on a phylogeny (Blomberg et al., 2003). The  $K$  value was measured using the “multiPhylosigal” function in the “picante” package of R (Kembel et al., 2010), where  $K$  values closer to 0 represent a convergent or random pattern of evolution, and  $K$  values higher than 1 imply strong phylogenetic signals and conservatism of traits (Goberna and Verdú, 2016; Jiao and Lu, 2020b).

The ecological community assembly processes of rare and abundant bacterioplankton were estimated by applying the null model (Stegen et al., 2016; Yan et al., 2017b; Huber et al., 2020). The null model analysis was carried out to calculate the relative contributions of four ecological processes, namely, homogeneous selection, homogenizing dispersal, dispersal limitation, and variable selection (Yan et al., 2017b; Huber et al., 2020; Wang et al., 2020). Briefly, differences in taxonomic

and phylogenetic diversities were calculated according to the null model-based Bray-Curtis-based Raup-Crick ( $RC_{\text{bray}}$ ) and  $\beta$ -nearest taxon index ( $\beta\text{NTI}$ ) using the “picante” package of R (Stegen et al., 2012; Wan et al., 2021).  $\beta\text{NTI}$  values  $< -2$  reflect significantly less than the expected phylogenetic turnover (homogeneous selection), whereas  $\beta\text{NTI}$  values  $> +2$  indicate noticeably more than the expected phylogenetic turnover (variable selection) (Stegen et al., 2012). The relative contribution of dispersal limitation was assessed as the proportion of pairwise comparisons with  $|\beta\text{NTI}| < 2$  and  $RC_{\text{bray}} > 0.95$ , whereas the relative contribution of homogenizing dispersal was evaluated as the percentage of pairwise comparisons with  $|\beta\text{NTI}| < 2$  and  $RC_{\text{bray}} < -0.95$ . The remaining categories of  $|\beta\text{NTI}| < 2$  and  $|RC_{\text{bray}}| < 0.95$  were estimated as the effect of “undominated” assembly, namely, no single process drives the variations in community structure (Stegen et al., 2012). Effects of physicochemical factors on the assemblies of rare and abundant bacterioplankton communities were estimated using the Mantel test, where physicochemical factor dissimilarities were calculated using Euclidean distance matrices. The linear regression between change in FRI and  $\beta\text{NTI}$  was generated based on ordinary least-squares.

### 3. Results

#### 3.1. Distribution patterns of rare and abundant bacterioplankton

Before dredging, a total of 553,327 reads were classified into 1280 OTUs. Rare bacterioplankton comprised 60.5% of the total community richness, but their total relative abundance accounted for only 2.3% of the whole community. Abundant bacterioplankton comprised 12.5% of the total community richness, but their total relative abundance accounted for 86.3% of the whole community. In contrast, a total of 648,415 reads were gained after dredging, and these reads were assigned to 1274

OTUs. After dredging, rare bacterioplankton accounted for 68.4% of the total bacterioplankton community richness, but their total relative abundance comprised only 2.1% of the entire community. Abundant bacterioplankton taxa represented 9.9% of the total bacterioplankton community richness, but their total relative abundance accounted for 88.5% of the entire community.

Both rare and abundant OTUs occupancies were significantly positively correlated with corresponding reads numbers in water samples taken before (Fig. 1A) and after dredging (Fig. 1B). Abundant OTUs were more widespread than rare ones in water samples taken before and after dredging. Before dredging, 98.8% of abundant OTUs and only 22.8% of the rare ones were detected in more than 50% of all samples. After dredging, 100% of abundant OTUs and only 24.5% of the rare ones were found in more than 50% of all samples. Of the retained sequences, 99.9% were classified at the phylum level before and after dredging. Before dredging, 30 and 13 phyla were assigned to rare and abundant bacterioplankton, respectively. The rare bacterioplankton was dominated by *Proteobacteria*, *Bacteroidetes*, and *Firmicutes*, with corresponding relative abundances of 38.9%, 19.0%, and 14.8%, respectively. The abundant bacterioplankton was mainly comprised of *Proteobacteria* (41.8%), *Actinobacteria* (29.1%), and *Bacteroidetes* (16.7%) (Fig. 1C). After dredging, 32 and 12 phyla were attributed to rare and abundant bacterioplankton, respectively. Rare bacterioplankton was dominated by *Proteobacteria* (40.8%) and *Bacteroidetes* (20.0%) and the abundant one was dominated by *Actinobacteria* (51.1%), *Proteobacteria* (23.9%), and *Bacteroidetes* (12.8%) (Fig. 1D).

We estimated both taxonomic and phylogenetic distances for both rare and abundant bacterioplankton in water samples taken before and after dredging (Fig. 2). The community distances based on Bray-Curtis dissimilarity (Fig. 2A) and the

phylogenetic distances based on  $\beta$ MNTD matrices (Fig. 2B) of rare and abundant bacterioplankton showed significantly positive correlations with the dissimilarities of environmental factors in water samples taken before and after dredging. These results indicated that environmental factors had strong effects on taxonomic and phylogenetic diversity of the bacterioplankton community. Additionally, community (Fig. 2C) and phylogenetic distances (Fig. 2D) of rare bacterioplankton were significantly higher than of the abundant one before and after dredging ( $p < 0.001$ ). Redundancy analysis indicated that environmental factors explained 69.77% and 60.83% variations in abundant bacterioplankton community composition before and after dredging, respectively (Fig. S1). In contrast, environmental factors explained relatively less variations in rare bacterioplankton community composition, with 53.81% and 52.1% of the variations before and after dredging, respectively. PERMANOVA results showed that both water and sediment physicochemical variables revealed different effects on rare and abundant bacterioplankton composition before and after dredging (Table S1). For instance, DO exhibited significant effects on the compositions of rare ( $R^2 = 14.65\%$ ,  $F = 2.75$ ;  $p < 0.01$ ) and abundant ( $R^2 = 23.81\%$ ,  $F = 5.00$ ;  $p < 0.01$ ) bacterioplankton. This implied that rare and abundant bacterioplankton taxa might respond differently to environmental changes.

### 3.2. Environmental responses of rare and abundant bacterioplankton

Abundances of the top 10 rare and abundant bacterioplankton taxa showed different correlations with both water and sediment physicochemical variables before and after dredging (Table S2–S5). For example, OTU1205 belonging to *Bacteroidetes* occurred in water samples taken before the dredging and was significantly positively correlated with DO. Environmental threshold analysis was employed to investigate the responses of rare versus abundant bacterioplankton to each of the studied

environmental factors based on calculations of  $z^+$  and  $z^-$  (Fig. S2–S5). The rare bacterioplankton exhibited a broader range of environmental thresholds compared to the abundant bacterioplankton for almost all tested variables in the same period (Fig. 3A). It is worth noting that environmental thresholds of rare and abundant taxa in response to some variables declined and in response to some others increased after dredging. For instance, the environmental thresholds of both rare and abundant taxa decreased for ammonia, but increased for nitrate (Fig. 3A). This suggested shifts in the adaptation of rare and abundant bacterioplankton to environmental change. Thus, the strength of the relationship between environmental preferences and phylogeny of rare and abundant bacterioplankton was measured to estimate whether ecological traits are predictive for phylogenetic diversity (Fig. 3B). Blomberg's  $K$  statistic revealed that rare bacterioplankton showed stronger phylogenetic signals for most environmental variables than the abundant bacterioplankton in the same period. This suggested that within the rare bacterioplankton community, closely correlated taxa exhibited similar ecological preferences to the measured environmental factors. In addition, phylogenetic signals of both rare and abundant bacterioplankton declined for most environmental variables after dredging.

### *3.3. Ecological assembly processes and functions of rare and abundant bacterioplankton*

Based on our null model analysis, the relative contribution of community assembly processes differed between rare and abundant bacterioplankton before and after dredging (Fig. 4). Dispersal limitation belonging to stochastic processes determined community assembly of the abundant bacterioplankton before and after dredging, with corresponding relative contributions of 75.8% and 72.5%, respectively. Variable selection belonging to deterministic processes had much smaller effects on



community assembly of the abundant bacterioplankton before (24.2%) and after (26.1%) dredging. Variable selection (35.9%) exhibited relatively larger effects on the community assembly of rare bacterioplankton than homogenizing dispersal (22.9%) and dispersal limitation (29.4%) before dredging. Similarly, variable selection (33.3%) showed relatively larger effects on the community assembly of rare bacterioplankton than homogenizing dispersal (24.8%) and dispersal limitation (22.2%) after dredging. Differentiating processes dominated both rare and abundant bacterioplankton community assembly before and after dredging, while homogenizing processes contributed partially to rare bacterioplankton community assembly. Stochastic processes in rare bacterioplankton slightly increased, but weakly decreased for abundant bacterioplankton after dredging (Fig. 4). Deterministic processes in rare bacterioplankton decreased, but increased for abundant bacterioplankton after dredging. The ratios of sorting/dispersal limitation in rare bacterioplankton were higher than that in the abundant one before and after dredging (Fig. S6). This indicated that rare bacterioplankton is more environmentally constrained than the abundant ones.

Results of Mantel test demonstrated that changes in dissolved oxygen (DO) in the water was noticeably correlated with  $\beta$ NTI of rare ( $r = 0.499$ ;  $p < 0.01$ ) and abundant ( $r = 0.221$ ;  $p < 0.01$ ) bacterioplankton before the dredging (Table 1). This also applied to rare ( $r = 0.230$ ;  $p < 0.01$ ) and abundant ( $r = 0.127$ ;  $p < 0.05$ ) bacterioplankton after the dredging (Table 1). This suggested that DO serve as a good predictor of assembly processes in both rare and abundant bacterioplankton in eutrophic Lake Nanhu. In addition, pairwise comparisons of  $\beta$ NTI values for rare and abundant bacterioplankton before and after dredging were significantly positively correlated with changes in DO (Fig. S7). This indicated that an increasing divergence in dissolved oxygen resulted in

an increase in stochasticity in the assembly of both rare and abundant bacterioplankton communities before and after dredging. To further explore the interconnections between DO and phylogenetic turnover ( $\beta$ NTI), water samples were clustered into subgroups based on DO content. With increasing dissolved oxygen, the relative contributions of stochasticity first increased and then decreased in the rare bacterioplankton before dredging, and first declined and then increased in the abundant bacterioplankton before dredging (Fig. S8). Similarly, the relative contributions of stochasticity increased and then decreased in both rare and abundant bacterioplankton after dredging.

Based on functional profiling results at level 3 KEGG Orthology, functional numbers in the abundant bacterioplankton was comparably higher than that in the rare bacterioplankton before and after dredging (Fig. S9). Additionally, 5835 functions including C-, N-, P-, and S-cycling-related enzymes or proteins, displayed a higher functional redundancy in the rare bacterioplankton before dredging, whereas 2711 functions showed a higher redundancy in the rare bacterioplankton after dredging. Similarly, 3304 and 4355 functions were separately found in abundant bacterioplankton before and after dredging, suggesting functions increase in abundant bacterioplankton after dredging. Some functions were unique (value = 10 and value = -10) in the corresponding communities and sampling period (Fig. S9). For instance, 73 functions (e.g., phosphothreonine lyase (EC: 4.2.3.-), phosphonopyruvate hydrolase (EC: 3.11.1.3), and daptidamide synthase (EC: 6.3.2.47)) were exclusively found in rare bacterioplankton before dredging (value = 10), and 193 functions (e.g., urease (EC: 3.5.1.5), arginine decarboxylase (EC: 4.1.1.19), sulfinoalanine decarboxylase (EC: 4.1.1.29), and phosphatidylinositol-4,5-bisphosphate 4-phosphatase (EC: 3.1.3.78)) occurred exclusively in rare bacterioplankton after

dredging (value = -10). This suggested the gain of several specific bacterioplankton functions after dredging. Additionally,  $\beta$ NTI was slightly and positively correlated with changes in FRI of the rare ( $R^2 = 0.0045$ ,  $p > 0.05$ ; Fig. 5A) and abundant ( $R^2 = 0.0068$ ,  $p > 0.05$ ; Fig. 5B) bacterioplankton before dredging. Interestingly,  $\beta$ NTI was significantly positively correlated with changes in FRI of the rare ( $R^2 = 0.077$ ,  $p < 0.001$ ; Fig. 5C) and abundant ( $R^2 = 0.013$ ,  $p < 0.05$ ; Fig. 5D) bacterioplankton after dredging. This implies that ecological community processes have strong effects on functions of both rare and abundant bacterioplankton after dredging.

## 4. Discussion

### 4.1. Broader environmental adaptations of rare than abundant bacterioplankton taxa

Environmental filtering governs microbial diversity and as a consequence influences microbial and ecosystem functioning (Wagg et al., 2014). A large number of studies have explored the effects of environmental variables on bacterioplankton community composition (e.g., Lindström et al., 2006; Lindström and Östman, 2011; Lindström and Langenheder, 2012; Zhang et al., 2017; Shen et al., 2018), very few of them have investigated the community structures of rare and abundant bacterioplankton. Though some researches have reported that physical and chemical factors (e.g., temperature, pH, DO, turbidity), in particular nutrients (e.g., nitrogen and phosphorus sources) affect community composition of the rare and/or abundant bacterioplankton (Liu et al., 2015; Liao et al., 2017; Nyirabuhoro et al., 2020), only very few studies have reported on adaptations to environmental change of rare versus abundant bacterioplankton.

These studies have addressed the potential of adaptation to environmental drivers of rare and abundant bacterioplankton community by using two different measures: i) environmental breadth applying TITAN analysis (Baker and King, 2010; Romero et

al., 2019) and ii) strengths of phylogenetic signals to ecological preference employing Blomberg's  $K$  statistic (Blomberg et al., 2003; Goberna and Verdú, 2016). Environmental breadth can reveal species niche breadth, and phylogenetic signals could provide predictions for species evolutionary adaptation in response to environmental changes (Goberna and Verdú, 2016; Jiao and Lu, 2020b).

Firstly, the rare bacterioplankton exhibited broader response thresholds to most physicochemical factors than the abundant bacterioplankton, which is inconsistent with the finding that abundant fungi in agricultural soils present broader response thresholds to environmental factors (Jiao and Lu, 2020b). This is opposite to our hypothesis and this discrepancy might be greatly due to the higher richness of rare contrary to abundant bacterioplankton. Additionally, abundant bacterioplankton taxa were rather ubiquitous compared to the rare ones before and after dredging. This agrees well with several previous findings (Liu et al., 2015; Chen et al., 2020; Mo et al., 2020; Jiao and Lu, 2020a). In contrast, rare bacterioplankton taxa were not distributed evenly and most occurred only in a few water samples, which is in accordance with prior reports (Liu et al., 2015; Liao et al., 2017; Chen et al., 2020; Mo et al., 2020). This phenomenon might be driven by the specific environmental condition (mass blooms of cyanobacteria; Wan et al., 2020a) and rapid environmental changes in human activities, e.g., dredging (leading to nutrient loss). This may promote the rapid adaptation of the rare bacterioplankton, which shows a high phylogenetic and consequently functional richness. Microorganisms adapting to environmental changes have been characterized for both genetic and physicochemical level (Chen and Zhang, 2020). A previous study has revealed that non-acidophilic and non-thermophilic *Bacillus subtilis* are capable to adapting to extreme temperatures (100°C for up to 8 h) and acidic environments (pH = 1.50 for over 2 years) and can

maintain their activity by using an extracellular electron transfer (Chen et al., 2019). In addition, denitrifying phosphorus-accumulating bacterium *Enterobacter cloacae* HW-15 adapts to low nutrient conditions by hydrolyzing their intracellularly accumulated polyphosphate (Wan et al., 2017). Environmental threshold analysis using TITAN has been reported in some aquatic biodiversity-related research (Monk et al., 2017; LeBrun et al., 2018; Romero et al., 2019). For example, total phosphorus in streams and rivers along the Oklahoma-Arkansas border are correlated to the structure and functional capability of the bacterioplankton and archaeal communities (LeBrun et al., 2018). Findings of environmental breadths of microorganisms using environmental threshold analysis are appealing, but are also controversially discussed regarding implications to the real field situation. Therefore, confirmatory experiments are required to applying such statistical results for advising environmental policy. Nevertheless, our results provide a solid statistical hint for the potentially broader environmental breadths of rare bacterioplankton taxa compared to abundant bacterioplankton taxa in eutrophic lakes. These findings are, to our knowledge, novel and have not been reported before.

Secondly, based on Blomberg's  $K$  statistic, we found that rare bacterioplankton taxa exhibited stronger phylogenetic signals for environmental preference than the abundant ones. This result is inconsistent to previous findings highlighting that abundant bacteria in Chinese agricultural soils show stronger phylogenetic signals for environmental preference than rare ones (Jiao and Lu, 2020a). This discrepancy can be partially explained by differences in bacterial community composition and environment heterogeneity, e.g., soils are usually much more complex than aquatic ecosystems. Several previous studies have reported that functional traits derived from the ecological preferences of a species rely on its evolutionary history (Graham and

Fine, 2008; Saladin et al., 2009). For example, traits of bacteria in four forest ecosystems are to a higher degree constrained by evolutionary history than environmental heterogeneity (e.g., temperature, precipitation, and dominant vegetation) (Morrissey et al., 2019). This notion is confirmed by more specific differences in evolution history of two novel ammonia oxidizing bacteria of canonical *Nitrospira* and comammox *Nitrospira* which leads to distinct responses to external nitrogen sources (Palomo et al., 2018). High phylogenetic conservatism of microbial response traits to environmental preference has been studied earlier (Martiny et al., 2015). Thereafter, microbial response traits to salinity and pH preferences are deeply phylogenetically conserved, indicated generally by the decisive roles of salinity and pH in determining microbial distribution pattern (Cottrel et al., 2005; Silveira et al., 2011; Bunse et al., 2016; Comte et al., 2017). In our study, the rare bacterioplankton taxa showed stronger phylogenetic signals for ecological preferences, which might indicate that rare taxa possess higher phylogenetic niche conservatism with respect to evolutionary history of environmental adaptation (Bennett et al., 2010). The stronger phylogenetic signals of the rare bacterioplankton for ecological preferences could explain why rare bacterioplankton taxa have broader environmental breadths and distinct distribution patterns than the abundant ones. In summary, our results of environmental breadth and phylogenetic signal analyses indicate that rare and abundant bacterioplankton possess distinct adaptations to various environmental conditions in a eutrophic lake. Following environmental disturbance by dredging, we found clear shifts (decrease or increase) in environmental adaptations of both rare and abundant bacterioplankton based on both environmental breadth and phylogenetic signal analyses.

#### 4.2. Different assembly processes dominate rare and abundant bacterioplankton

Microbial community composition and functions are regarded as being governed by different ecological mechanisms and therefore it is important to estimate the relative contributions of stochastic and deterministic processes to microbial community assembly (Stegen et al., 2016; Bannar-Martin et al., 2017). In the assemblies of abundant bacterioplankton communities, stochastic processes (i.e., dispersal limitation) dominated before and after dredging. For the assemblies of abundant bacterioplankton communities, deterministic processes (i.e., variable selection) were more important than dispersal limitation and homogenizing dispersal before and after dredging. These results are in line with findings that rare bacterial taxa are more constrained by environmental factors than abundant ones in agricultural soils (Jiao and Lu, 2020a) and inland freshwater ecosystems (Liu et al., 2015). These findings, however, differ from previous studies describing that dispersal of rare bacterial taxa is more limited than that of abundant ones in three subtropical bays of China (Mo et al., 2018) and in wetland soils (Ji et al., 2020). These discrepancies might be attributed to differences in habitat characteristics and geography (Jiao and Lu, 2020b). For example, it has been shown that stochastic processes increase with higher nutrient condition, while deterministic processes seem to be more related to low nutrient conditions (Chase, 2010; Zhou et al., 2014). Bacteria in aquatic ecosystems can easier disperse and hence reach nutrient rich conditions or escape from unfavorable conditions (e.g., predator and high temperature) than those in a solid medium (e.g., soil) (Ariel et al., 2015; Simon et al., 2016). The observed divergence in different ecological processes governing assemblies of rare versus abundant bacterioplankton communities might be also due to the environmental heterogeneity in general and the individual capability of taxa to handling environmental changes (Palomo et al., 2018; Morrissey et al., 2019). Abundant taxa are more generalists and

rare taxa more specialists. The high richness of rare taxa represents a high spectrum of specialist species which are doing quite well under different environmental conditions hence their high ecological breadth (Pedrós-Alió, 2007). Our findings, however, still support a prior report demonstrating that abundant microbial taxa are more limited by dispersion than rare taxa in inland freshwater ecosystems (Liu et al., 2015).

To understand microbial community assembly mechanisms, it is critical to disentangle environmental factors influencing the relative contributions of both stochastic and deterministic processes (Stegen et al., 2016; Jiao et al., 2020; Wan et al., 2021). Yet, there are only a few studies addressing environmental factors affecting the relative contributions of stochastic versus deterministic processes and their roles for bacterial community assembly in aquatic ecosystems. Using the null model analysis, we found that  $\beta$ NTI of both rare and abundant bacterioplankton is more closely correlated with dissolved oxygen than other variables before and after dredging. This might indicate that dissolved oxygen represents a crucial factor adjusting the balance between stochastic and deterministic processes for both rare and abundant bacterioplankton in eutrophic aquatic ecosystems.

The critical role of dissolved oxygen in determining assembly processes of both rare and abundant bacterioplankton might be to a large extent attributed to the oxygen requirement for most living heterotrophic microorganisms (Soo et al., 2017). Oxygen availability is greatly determining the redox state of an ecosystem and hence is essential as the most potent electron acceptor for microbial respiration (Cao et al., 2016; Zhang et al., 2017). Yet, oxygen can be also a poison for some functional, anaerobic bacteria in participating in key element cycling in aquatic ecosystems (Yan et al., 2018). For instance, nitrogen fixation and denitrification processes, and methane and phosphine formation require anoxic or anaerobic condition for bacteria



(Jenkins et al., 2000; Lavik et al., 2009; Kobayashi et al., 2019). Therefore it is likely that dissolved oxygen might determine bacterioplankton community assembly via its impact on both aerobic and anaerobic respiration and growth. Considering the importance of photosynthesis for oxygen generation, factors directly or indirectly related to photosynthesis (e.g., light intensity, nutrient, and metal ions) might also be decisive for stochastic and deterministic processes. Future work needs to explore the precise role of various environmental factors for community assembly processes of bacterioplankton in more differing aquatic ecosystems.

Ultimately, we have constructed a conceptual framework to describe the environmental adaptation and community assembly processes of rare versus abundant bacterioplankton in eutrophic lake (Fig. 6). Rare bacterioplankton exhibited broader environmental breadths and stronger phylogenetic signals of ecological preference than the abundant one before and after dredging. However, environmental adaptations of rare and abundant bacterioplankton varied differently after dredging. The abundant bacterioplankton exhibited a higher functional redundancy than the rare bacterioplankton, and functions of rare bacterioplankton decreased while functions of abundant bacterioplankton increased after dredging. Stochastic processes governed the abundant bacterioplankton community and deterministic processes dominated in the rare community before and after dredging. Dissolved oxygen was the crucial factor in determining community assembly processes of rare and abundant bacterioplankton, indicating distinct changes in stochasticity with higher dissolved oxygen content.

## 5. Conclusions

In this study, we characterized taxonomic and phylogenetic diversity, and environmental adaptations of rare and abundant bacterioplankton along environmental

gradients in the eutrophic Lake Nanhu. To our knowledge, our DNA-based datasets and statistical analysis is the first to reveal that rare bacterioplankton are more environmentally constrained than the abundant bacterioplankton, and rare bacterioplankton have better environmental adaptation potentials than abundant one. Dissolved oxygen exhibits a decisive role in mediating the balance between stochastic and deterministic processes in community assemblies of both rare and abundant bacterioplankton. Dredging as a disturbance could result in functional changes in bacterioplankton community, and thus imply dredging is a useful approach in mitigating cyanobacterial blooms. Community assembly could be a bio-indicator for evaluating the bacterioplankton community function. Our findings are of significance for understanding the maintenance of bacterioplankton diversity, and offer a way to predict the response of bacterioplankton to environmental changes caused, e.g., by dredging in eutrophic freshwater ecosystems. Considering the importance of bacterioplankton for health of aquatic ecosystems, experimental validation of the model should be implemented in more differing freshwater and marine ecosystems.

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### **Conflict of interest**

The authors declare that they have no conflicts of interest.

### **Ethical statement**

This article does not contain any studies with human or animal subjects.

### **CREDIT AUTHOR STATEMENT**

Yuyi Yang, Wenjie Wan, and Wenke Yuan provided data analysis ideas. Wenjie Wan analyzed the data and wrote the manuscript. Yuyi Yang, Donglan He, and Hans Peter Grossart revised the manuscript, and Yuyi Yang submitted the manuscript.

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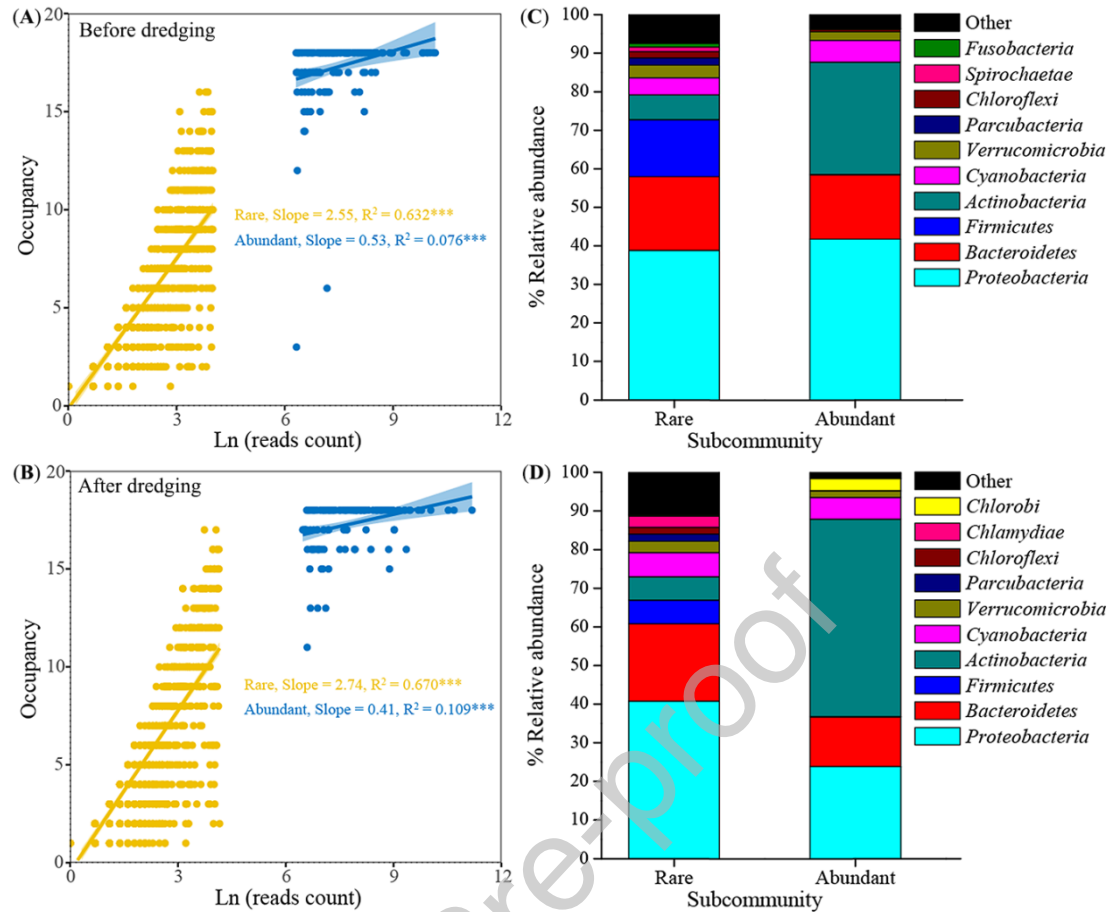


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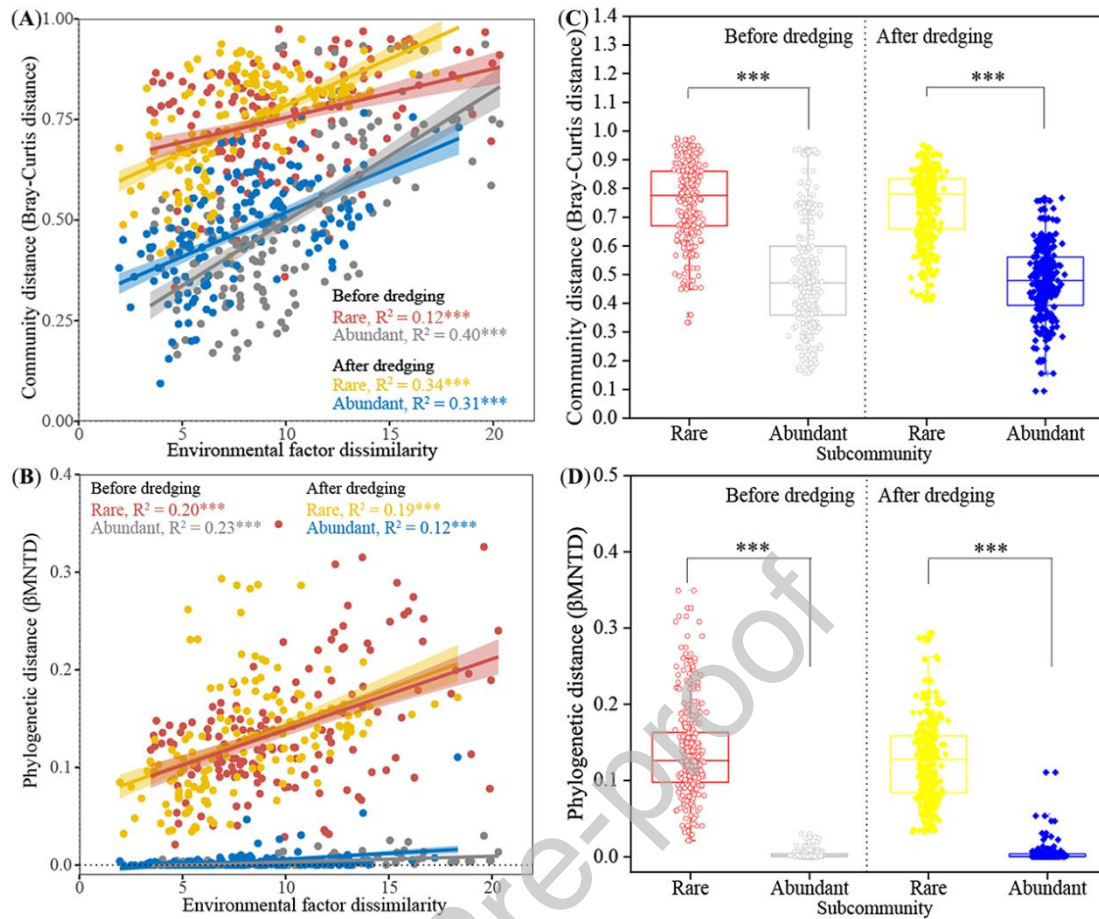
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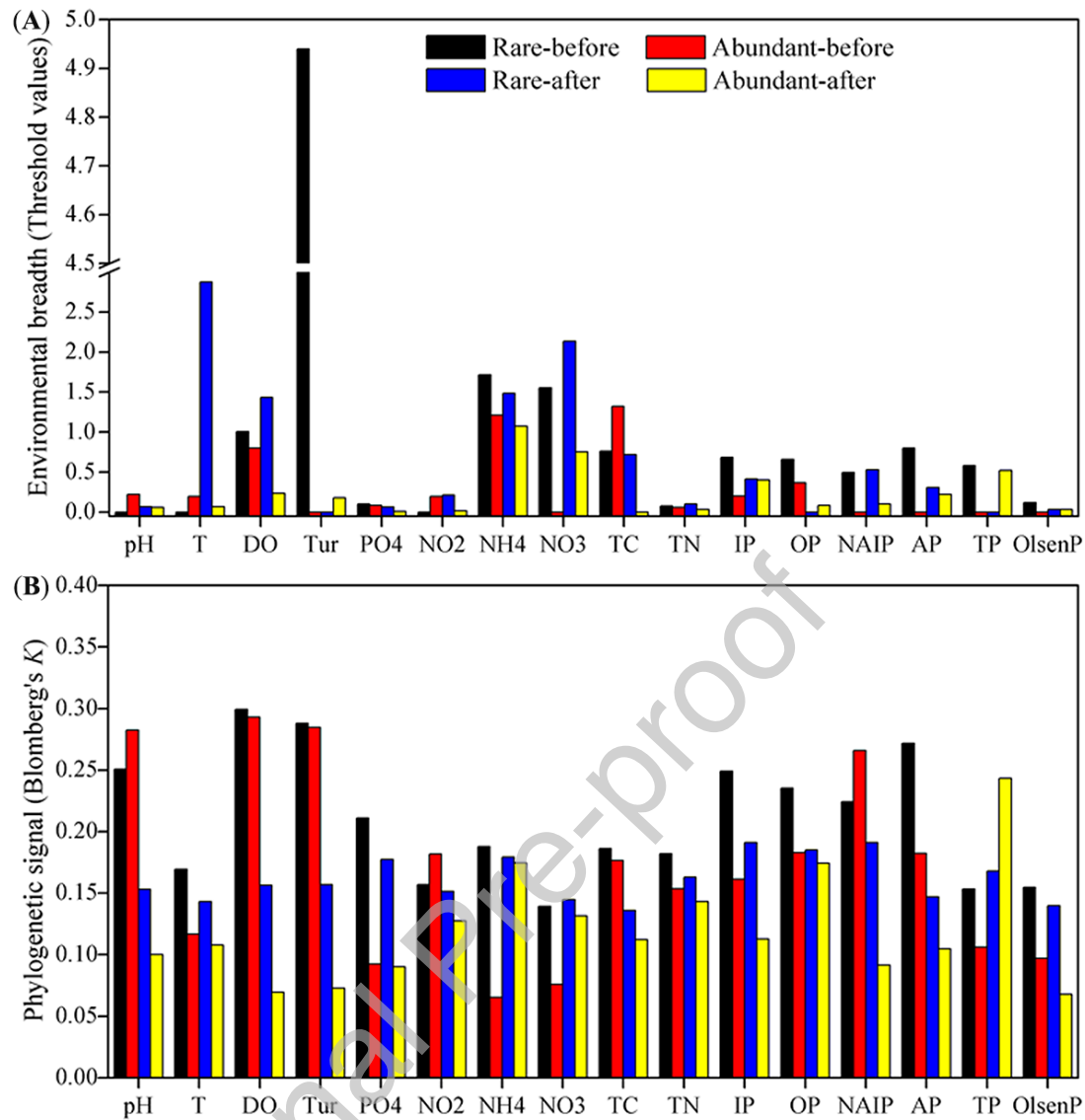
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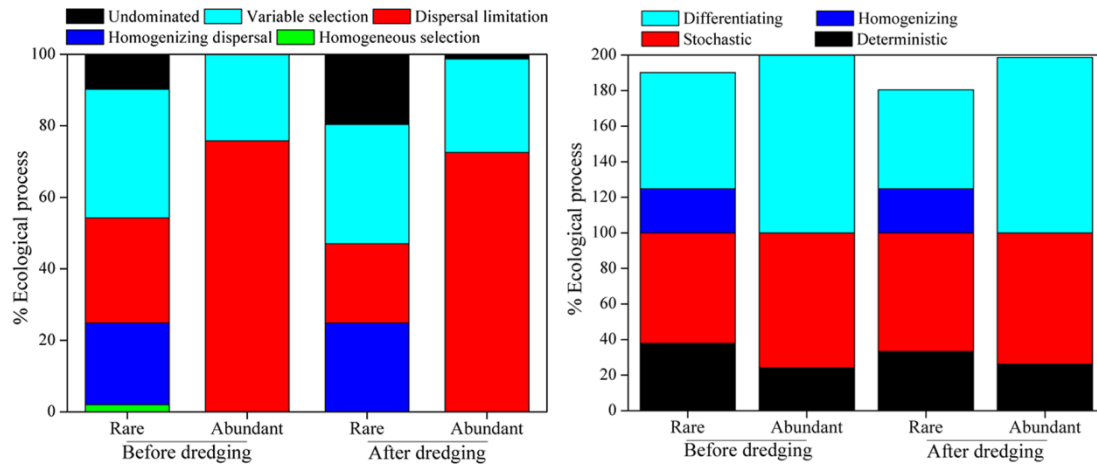
**Fig. 1.** The abundance-occupancy relationships of rare and abundant bacterioplankton OTUs in water samples taken before (A) and after (B) dredging, and the taxonomic composition of rare and abundant bacterioplankton at the phylum level in water samples taken before (C) and after (D) dredging. Asterisks denote significance ( $^{***}$ ,  $p < 0.001$ ).



**Fig. 2.** The taxonomic and phylogenetic distances of rare and abundant bacterioplankton before and after dredging. Linear regressions between environmental factor dissimilarity and community distance (A) and phylogenetic distance (B) of rare and abundant bacterioplankton. Differences in community distance (C) and phylogenetic distance (D) between rare and abundant bacterioplankton. Asterisks denote significance (\*\*\*,  $p < 0.001$ ).

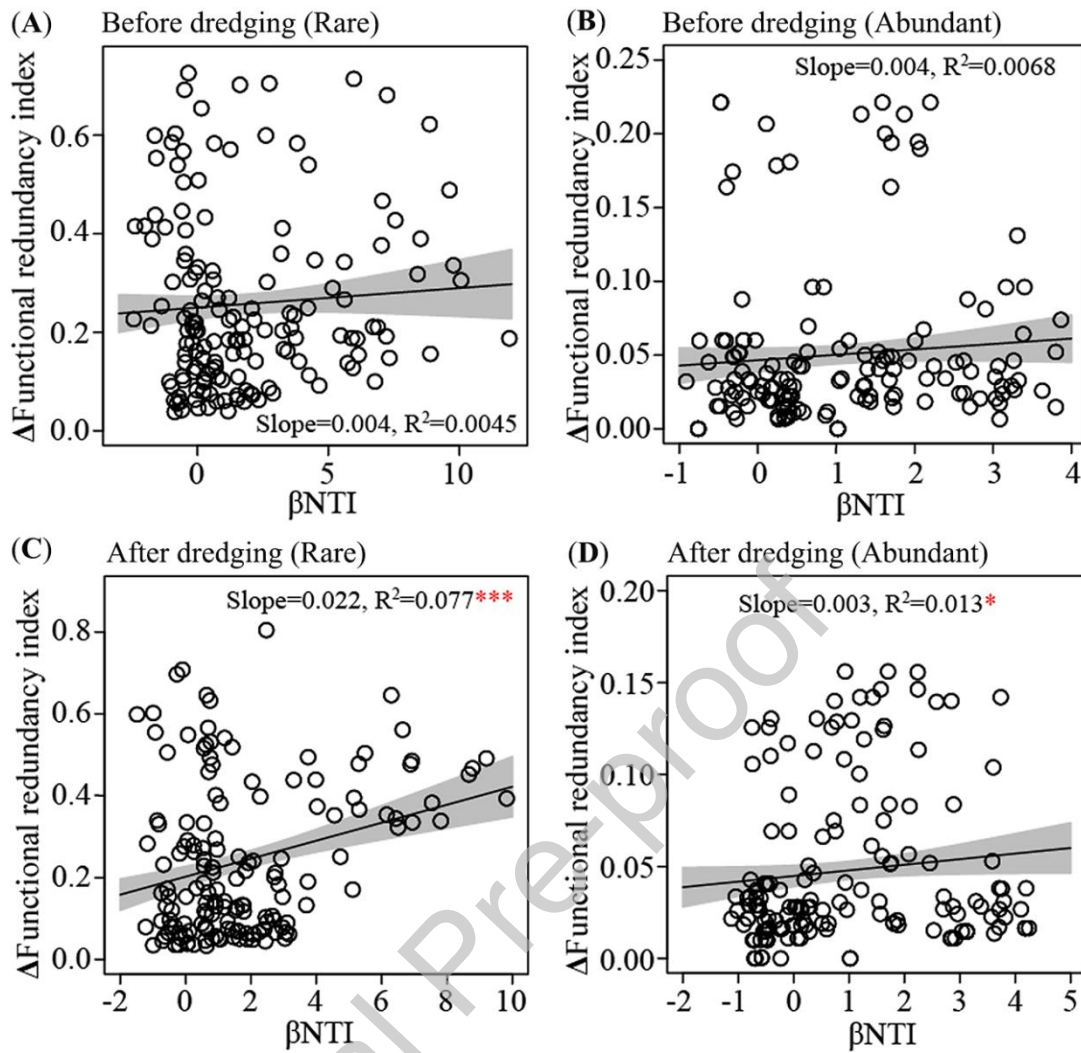


**Fig. 3.** Environmental adaptations of rare and abundant bacterioplankton before and after dredging. Environmental breadths of bacterioplankton estimated by the threshold values of rare and abundant taxa in response to environmental factors were calculated applying TITAN (A). Phylogenetic signals of bacterioplankton reflecting the trait conservatism for environmental preferences of the rare and abundant bacterioplankton were determined using Blomberg's *K* statistic (B). Units for parameters: mg/L (DO,  $\text{PO}_4^{3-}\text{-P}$ ,  $\text{NO}_2^{-}\text{-N}$ ,  $\text{NO}_3^{-}\text{-N}$ , and  $\text{NH}_4^{+}\text{-N}$ ), mg/g (IP, OP, NAIP, AP, TP, and Olsen P), °C (temperature: T), pH (pH), FTU (turbidity: Tur), and % (TC and TN). The abbreviations of environmental factors are defined in Section 2.

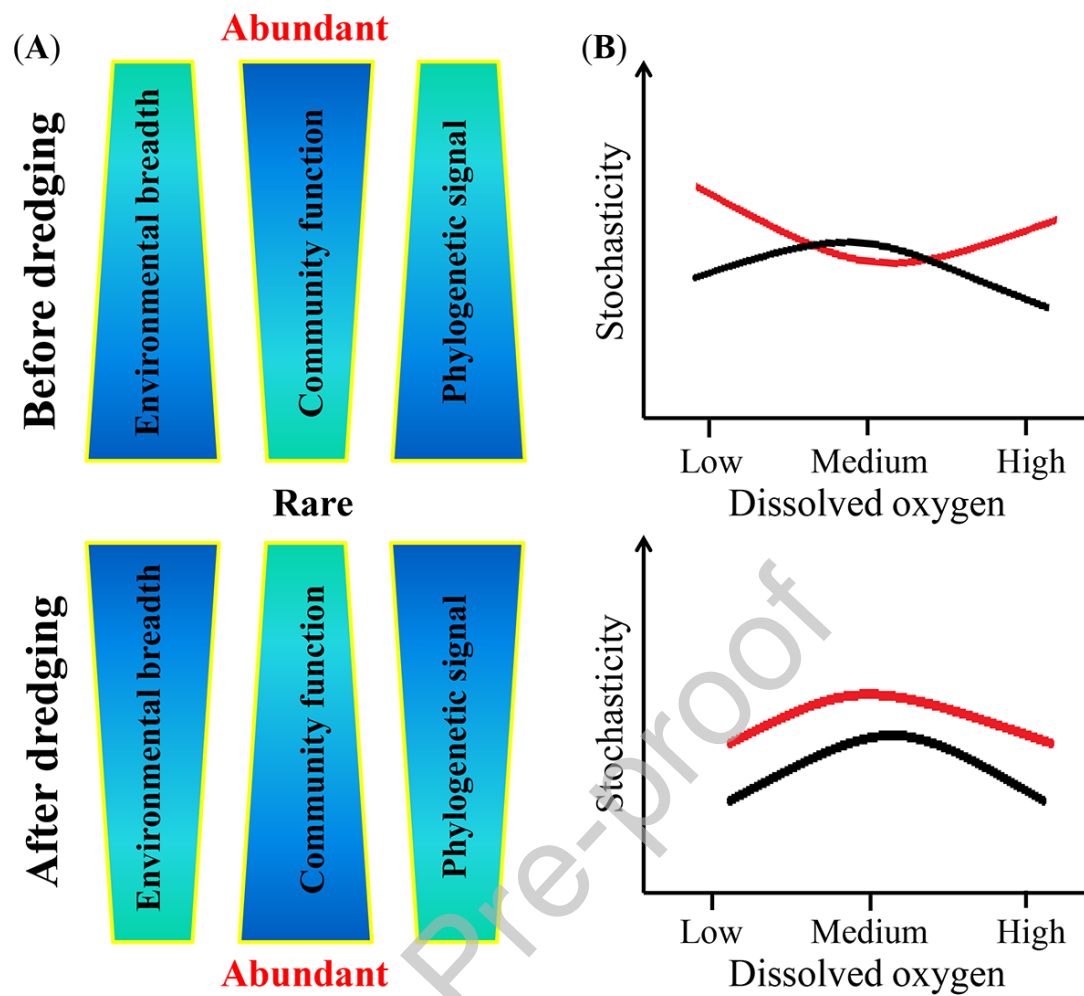


**Fig. 4.** The relative contributions of ecological processes to the assemblies of both rare and abundant bacterioplankton communities in water samples taken before and after dredging. Stochastic = Dispersal limitation + Homogenizing dispersal + Undominated processes; Deterministic = Variable selection + Homogeneous selection; Homogenizing = Homogeneous selection + Homogenizing dispersal; Differentiating = Variable selection + Dispersal limitation.





**Fig. 5.** Linear regressions between  $\beta$ NTI and function redundancy index in rare (A) and abundant (B) bacterioplankton before dredging, in rare (C) and abundant (D) bacterioplankton after dredging. Asterisks represent significance (\*,  $p < 0.05$ ; \*\*\*,  $p < 0.001$ ).



**Fig. 6.** Conceptual models revealing environmental adaptation (A) and stochastic processes (B) in the assemblies of rare and abundant bacterioplankton sub-communities under the influence of dissolved oxygen.

**Table 1.** Mantel tests of environmental factors against the  $\beta$ NTI of rare and abundant bacterioplankton sub-communities in water samples taken before and after dredging. Asterisks denote significance (\*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ).

Property	Before dredging (Mantel's $r$ )		After dredging (Mantel's $r$ )	
	Rare	Abundant	Rare	Abundant
pH	0.419**	0.359**	-0.077	0.177**
T	0.027	0.036	-0.016	0.023
DO	0.499**	0.221**	0.230**	0.127*
Turbidity	0.549**	0.153**	0.062	0.221**
PO <sub>4</sub>	0.502**	0.015	0.034	0.122*
NO <sub>2</sub>	-0.134*	-0.062	0.003	-0.046
NH <sub>4</sub>	0.105	0.174**	0.587**	0.105
NO <sub>3</sub>	0.263**	0.178**	-0.084	0.124*
TC	0.220**	0.057	-0.050	-0.099
TN	0.271**	0.125*	-0.092	-0.112*
IP	0.008	-0.070	0.014	-0.027
OP	0.131*	-0.051	0.003	-0.090
NAIP	0.123*	0.011	0.401**	-0.037
AP	0.002	-0.092	0.495**	0.000
TP	-0.093	0.049	0.105	0.236**
Olsen P	-0.182**	0.064	-0.056	-0.203**

Note: T, DO, PO<sub>4</sub>, NO<sub>2</sub>, NH<sub>4</sub>, and NO<sub>3</sub> represent water physicochemical properties of temperature, dissolved oxygen, free PO<sub>4</sub><sup>3-</sup>-P, free NO<sub>2</sub><sup>-</sup>-N, free NH<sub>4</sub><sup>+</sup>-N, and free NO<sub>3</sub><sup>-</sup>-N, respectively. TC, TN, IP, OP, NAIP, AP, and TP denote total carbon, total nitrogen, inorganic phosphorus, organic phosphorus, non-apatite inorganic phosphorus, apatite phosphorus, and total phosphorus, respectively.

## GRAPHICAL ABSTRACT

