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

3

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24 **Abstract**

25 Disentangling the ecological mechanisms in response to dredging disturbance is  
26 helpful to inform environmental policy for improving water quality. However, little is  
27 known about environmental adaptation and community assembly of bacterioplankton  
28 in response to dredging disturbance. Based on Illumine MiSeq sequencing and  
29 multiple statistical analyses, we have characterized interactions, functions,  
30 environmental breadth, phylogenetic signals and clustering, and the ecological  
31 assembly processes of a bacterioplankton community before and after dredging. We  
32 found distinct changes in community composition, comparable decreases in diversity,  
33 functional redundancy, conflicting interactions, lower phylogenetic clustering, and  
34 weak environmental adaptation after dredging. The bacterioplankton community  
35 assembly was affected by both stochastic and deterministic processes before dredging,  
36 but was dominated by stochasticity after dredging. Sediment total phosphorus was a  
37 decisive factor in balancing stochastic and deterministic processes for community  
38 assemblies of bacterioplankton before and after dredging. Consequently, taxonomic  
39 and phylogenetic  $\alpha$ -diversities of the bacterioplankton exhibited a higher contribution  
40 to the water trophic level, as represented by chlorophyl  $\alpha$  measurement, before rather  
41 than after dredging. Our results clarify the responses of bacterioplankton to  
42 environmental change caused by dredging disturbance, with nutrient loss and  
43 ecological drift playing important roles. The findings extend knowledge of the  
44 contribution of bacterioplankton diversity to the water trophic level and decipher the  
45 mechanisms of bacterioplankton diversity maintenance in response to dredging. The

46 findings are also helpful for guiding cyanobacterial bloom mitigation.

47

48 **Keywords:** anthropogenic disturbance, environmental breadth, functional redundancy,

49 phylogenetic clustering, phylogenetic signal, stochastic versus deterministic responses

50

## 51 **1. Introduction**

52 Bacterioplankton are important aquatic microorganisms and participate in nutrient

53 biogeochemical cycles (Bunse and Pinhassi, 2017). Cyanobacteria, regarded as one of

54 the most important members of bacterioplankton, generates massive blooms and cause

55 worldwide environmental problems (Hamilton et al., 2016; Te et al., 2017).

56 Cyanobacterial blooms threaten human health and the diversity of aquatic organisms

57 via release of algal toxins and consuming oxygen (Huisman et al., 2018; Olson et al.,

58 2020). Many studies have reported that the superfluous input of phosphorus (P) and

59 nitrogen (N) leads to cyanobacterial blooms (Te et al., 2017; Zhang et al., 2017; Kim

60 et al., 2020), and non-cyanobacterial bacterioplankton are reported to be responsible

61 for the bloom of cyanobacteria (Berg et al., 2009; Te et al., 2017; Wan et al., 2020).

62 Blocking nutrient input, especially N and P, into aquatic ecosystems and changing

63 bacterioplankton interactions might mitigate cyanobacteria blooms.

64 Dredging can improve water quality and achieve environmental protection by

65 changing both abiotic and biotic factors in water-sediment ecosystems (Liu et al.,

66 2016; Zhang et al., 2017; Wan et al., 2020). Such large-scale anthropogenic

67 disturbance has exhibited good performance for removing nutrients (e.g., N and P)

68 from sediment (Liu et al., 2016). However, dredging affects bacterioplankton

69 community composition (Zhang et al., 2017) and decreases bacterioplankton  
70  $\alpha$ -diversity (Wan et al., 2020). Deciphering maintenance of microbial diversity is of  
71 importance to estimate diversity-driven ecosystem processes and functions. However,  
72 the ecological mechanisms underlying bacterioplankton diversity maintenance as a  
73 result of dredging disturbance is poorly understood.

74 Microbial diversity maintenance is often clarified through two major aspects:  
75 environmental adaptation and community assembly (Jiao and Lu, 2020; Wan et al.,  
76 2021a, 2021b). Environmental adaptation of microorganisms involves two criteria:  
77 environmental breadth at a taxonomic level and phylogenetic signals at a phylogenetic  
78 level (Jiao and Lu, 2020; Wan et al., 2021c). Microbial environmental breadth reflects  
79 the distribution threshold of taxa along an environmental gradient over space or time  
80 (Baker and King, 2010). The phylogenetic signal is used to assess the strength of the  
81 microbial response to environmental preferences (Oliverio et al., 2017). This  
82 phylogeny-based trait characterizes how microorganisms interact with their  
83 environment, providing a solid foundation for predicting the preservation of microbial  
84 diversity (Martiny et al., 2015; Goberna and Verdú, 2016). Additionally, microbial  
85 responses to ongoing environmental change show phylogenetic conservatism, namely,  
86 species are not randomly distributed along the tree of life (Martiny et al., 2015). For  
87 instance, 30 isolated aerobic methane-oxidizing bacteria show strong phylogenetic  
88 conservatism to pH and temperature (Krause et al., 2014). Consequently, revealing  
89 environmental breadths and phylogenetic signals can explain major ecological  
90 phenomena, including species distribution patterns, seasonal succession, and

91 responses to global environmental change (Thomas et al., 2016; Monk et al., 2017).  
92 However, environmental breadth and phylogenetic signals of bacterioplankton to  
93 environmental change has been rarely reported in eutrophic lakes.

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

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

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

126

## 127 **2. Materials and methods**

### 128 **2.1. Data collection**

129 Detailed information about dredging procedures was described in prior research  
130 (Wan et al., 2020). In April and July, 2017 (before dredging) and in April and July,  
131 2018 (after dredging), 36 water samples and 36 sediment samples were collected from  
132 9 sites in Lake Nanhu (Wuhan, China). We estimated water physicochemical  
133 properties, including pH, turbidity (Tur), dissolved oxygen (DO), temperature (T),  
134 nutrient phosphorus  $\text{PO}_4^{3-}\text{-P}$  (PO4), nutrient nitrite  $\text{NO}_2^-\text{-N}$  (NO2), nutrient nitrate  
135  $\text{NO}_3^-\text{-N}$  (NO3), and nutrient ammonia  $\text{NH}_4^+\text{-N}$  (NH4). Sediment physicochemical

136 properties were also assessed, including total carbon (TC), total nitrogen (TN), total  
137 phosphorus (TP), Olsen P, inorganic phosphorus (IP), non-apatite inorganic  
138 phosphorus (NAIP), organic phosphorus (OP), and apatite phosphorus (AP).  
139 Sampling information and measurement of physicochemical properties have been  
140 previously described in detail (Wan et al., 2020). To assess the water trophic level,  
141 we estimated the content of chlorophyll  $\alpha$  (Chl- $\alpha$ ) based on a spectrophotometric  
142 method (Te et al., 2017).

143 Universal primers of 338F (5'- ACT CCT ACG GGA GGC AGC A-3') and 806R  
144 (5'- GGA CTA CHV GGG TWT CTA AT-3') were used to amplify bacterial 16S rRNA  
145 gene targeting V3–V4 regions (Mori et al., 2013). Illumina sequencing was performed  
146 at the Majorbio Bio-Pharm Technology Co., Ltd. Shanghai, China. Detailed  
147 description of bacterioplankton recovery from water samples, DNA extraction, and  
148 16S rRNA gene amplification, and sequencing are reported in a previous study (Wan  
149 et al., 2020) and also summarized in the Supplementary materials (Supplementary  
150 method 1). The purified sequences were classified into operational taxonomic units  
151 (OTUs) at a 3% dissimilarity level against the SILVA v128 reference. The OTUs  
152 accounting for less than 0.001% of the total sequences were filtered out. The MiSeq  
153 raw reads were deposited in the NCBI Short Read Archive database under accession  
154 numbers PRJNA391223 (2017) and PRJNA541122 (2018). In addition, we also  
155 measured abundances of cyanobacteria and bacterioplankton using universal primers.  
156 The amplifications of 16S rRNA genes for assessing cyanobacteria and  
157 bacterioplankton abundance were reported in a prior study (Wan et al., 2020) and are



158 also summarized in Supplementary materials (Supplementary method 2).

159

## 160 **2.2. Data analysis**

161 Significant differences in the data, if not otherwise stated, were analysed by the  
162 Student's t-test when data followed normal distributions ( $p < 0.05$ ). Venn diagram and  
163 non-metric multidimensional scaling (NMDS) were used to reflect the community  
164 structure of bacterioplankton using the "VennDiagram" and "ggplot2" packages of R.  
165 Canonical analyses of the principal coordinates (CAP) were employed to investigate  
166 influences of environmental factors on bacterioplankton community structure by  
167 employing the "capscale" function in the "vegan" package of R. Permutational  
168 multivariate analysis of variance (PERMANOVA) and pairwise analyses of similarity  
169 (ANOSIM) were selected to quantitatively evaluate effects of physicochemical  
170 variables on community structure of bacterioplankton by applying the "adonis" and  
171 "anosim" function in the "vegan" package of R. The OTUs observed in more than 50%  
172 of samples before and after dredging (> 9 samples) were applied to construct a  
173 co-occurrence network. The co-occurrence networks were visualized employing  
174 Gephi v. 0.9.2 (<https://gephi.org/>) with a significance  $p$  value  $< 0.01$  and Spearman's  
175 correlation coefficients ( $r$ )  $> 0.6$ . We used the ratio of positive edge  
176 (represent significantly positive correlation) to negative edge (denotes noticeably  
177 negative correlation) to reflect bacterioplankton conflicting interactions (mainly  
178 competition and predation) (Wei et al., 2019). Functional profiling of the  
179 bacterioplankton community was conducted by employing the package "Tax4Fun2"  
180 of R, and the functional redundancy index (FRI) of each sample was calculated based

181 on sequence similarity of the 16S rRNA gene (Wemheuer et al., 2020). The FRI is  
182 estimated as the proportion of species capable of harbouring a particular KEGG  
183 function and their phylogenetic relationships to each other (Wemheuer et al., 2020).  
184 Structural equation modeling was applied to analyze systems involving multiple  
185 causal interconnections, including water trophic level, taxonomic diversity,  
186 phylogenetic diversity, physicochemical properties, and community function by  
187 employing IBM SPSS Amos v.21.

188 To evaluate the phylogenetic distance between communities, the beta mean  
189 nearest taxon distance ( $\beta$ MNTD) metric was employed by using the “comdistnt”  
190 function. To estimate whether species were clustering closer to the tips of the  
191 phylogeny, phylogenetic clustering based on standardised effect size measurement of  
192 the mean nearest taxon distance (SES.MNTD) was computed by applying the  
193 “ses.mntd” function in the “picante” package of R (Kembel et al., 2010). Threshold  
194 indicator taxa analysis (TITAN) was employed to estimate environmental breadth of  
195 bacterioplankton in response to environmental gradients by using the “TITAN2”  
196 package (Baker and King, 2010; Romero et al., 2019). A phylogenetic signal,  
197 reflecting phylogenetic conservation for traits that are closely correlated with  
198 microbial ecological preferences, can provide predictions for microbial evolutionary  
199 adaptation (Martiny et al., 2015). We used Blomberg’s  $K$  statistic and the Fritz-Purvis  
200  $D$  test to estimate phylogenetic signals of bacterioplankton taxa before and after  
201 dredging (Goberna and Verdú, 2016; Wan et al., 2021a). The Blomberg’s  $K$  statistic  
202 reveals a phylogenetic signal that compares to the observed signal in a trait to the

203 signal based on a Brownian motion-based metric of trait evolution on a phylogeny  
204 (Blomberg et al., 2003). We computed the  $K$  value by employing the “picante”  
205 package of R (Kembel et al., 2010): high  $K$  values imply strong phylogenetic signals  
206 (Goberna and Verdú, 2016). We estimated the phylogenetic signal of binary traits by  
207 employing the “phylo.D” function in the “caper” package of R (Orme et al., 2013).  
208 The Fritz-Purvis phylogenetic dispersion ( $D$ ) value compares the observed sister-clade  
209 differences in the trait against those expected for a random phylogenetic pattern  
210 (Orme et al., 2013; Goberna and Verdú, 2016). We transformed the  $D$  value into  $-D +$   
211 1 to compare with Blomberg’s  $K$  statistic (Goberna and Verdú, 2016). The evolution  
212 of a study trait (i) does not reflect a noticeable signal when  $-D + 1 = 0$ , (ii) is more  
213 conserved than expected by chance when  $-D + 1 > 0$ .

214 Ecological community assembly processes were assessed using null and neutral  
215 model analyses (Sloan et al., 2006; Stegen et al., 2016).  $\beta$ -nearest taxon index ( $\beta$ NTI)  
216 and null model-based Bray-Curtis-based Raup-Crick ( $RC_{\text{bray}}$ ) were applied to  
217 calculate the differences in phylogenetic and taxonomic diversities. If  $|\beta\text{NTI}| > 2$ ,  
218 this demonstrates the dominance of deterministic processes, with significantly more  
219 (i.e., variable selection;  $\beta\text{NTI} > 2$ ) and less (i.e., homogeneous selection;  $\beta\text{NTI} < -2$ )  
220 phylogenetic turnover than expected. If  $|\beta\text{NTI}| < 2$ ,  $RC_{\text{bray}} < -0.95$  and  $RC_{\text{bray}} > 0.95$ ,  
221 this represents the relative contributions of homogenizing dispersal and dispersal  
222 limitation, respectively. If  $|\beta\text{NTI}| < 2$  and  $|RC_{\text{bray}}| < 0.95$ , this indicates the  
223 influence of “undominated” assembly, which mostly comprises diversification,  
224 ecological drift, weak selection, and/or weak dispersal (Stegen et al., 2016; Huber et

225 [al., 2020](#)). The detailed algorithm for this is described in prior literature ([Stegen et al.,](#)  
226 [2016](#)). The neutral model analysis was employed to further reflect the contribution of  
227 astochastic process to the bacterioplankton community assembly by predicting the  
228 interconnection between species abundance distribution and species area ([Zhou and](#)  
229 [Ning, 2017](#)). In this model, the migration rate of “*m*” and model fitness of “*R*<sup>2</sup>” were  
230 calculated by applying the “stats4” and “hmisc” packages in R ([Sloan et al., 2006](#)).

231

### 232 **3. Results**

#### 233 **3.1. Abundance, composition, and diversity of bacterioplankton community** 234 **before and after dredging**

235 Significant decreases in the Chl- $\alpha$  content and abundance of bacterioplankton and  
236 cyanobacteria were found after dredging (Wilcoxon rank-sum test,  $p < 0.001$ ; [Fig. 1a](#)).  
237 The Chl- $\alpha$  content was strongly positively correlated with pH and DO, while  
238 noticeably negatively correlated with NH<sub>4</sub> before and after dredging ( $p < 0.05$  or  $p <$   
239  $0.01$ ) ([Table 1](#)). Linear regressions reflected significant correlations between Chl- $\alpha$   
240 content and cyanobacterial abundance before and after dredging ( $p < 0.001$ ), while no  
241 significant correlation was found between Chl- $\alpha$  content and bacterioplankton  
242 abundance ( $p > 0.05$ ) ([Fig. 1b](#)). This might suggest that the blooms in eutrophic  
243 Lake Nanhu were mainly dominated by cyanobacteria before and after dredging.

244 We identified 1528 OTUs from the retained 1,201,742 high-quality sequences at  
245 97% sequence similarity. The bacterioplankton communities shared 1026 OTUs  
246 before and after dredging ([Fig. S3](#)), and the OTUs were classified into 33 phyla.  
247 *Actinobacteria*, *Proteobacteria*, and *Bacteroidetes* dominated before and after

248 dredging, with total relative abundances higher than 85%. The relative abundances of  
249 *Proteobacteria* and *Bacteroidetes* significantly decreased after dredging (Wilcoxon  
250 rank-sum test,  $p < 0.05$ ). The NMDS plot reflected distinct differences in  
251 bacterioplankton community composition before and after dredging, and ANOSIM  
252 further confirmed that the difference was significant ( $R = 0.415$ ,  $p < 0.001$ ) (Fig. S3).  
253 The 16 physicochemical variables explained 62.95% and 53.57% of total variations in  
254 community composition before and after dredging, respectively (Fig. S4). According  
255 to the PERMANOVA results, N (e.g., TN and NH<sub>4</sub>) and P (e.g., AP and TP) exhibited  
256 significant effects on bacterioplankton community structure (Fig. S4). These results  
257 suggest that nutrient loss caused by dredging affected bacterioplankton community  
258 composition.

259 The taxonomic  $\alpha$ -diversity represented by the Shannon-Wiener index for the  
260 bacterioplankton was significantly higher before dredging than afterwards ( $p < 0.05$ ;  
261 Fig. 1a), suggesting bacterioplankton diversity loss caused by the dredging event. The  
262 phylogenetic  $\alpha$ -diversity represented by SES.MNTD was noticeably lower before  
263 dredging than afterwards, and were all less than zero and all at  $p < 0.001$  (Wilcoxon  
264 rank-sum test,  $p < 0.05$ ; Fig. 1a). Relatively more physicochemical factors (e.g., TP,  
265 AP, NH<sub>4</sub>, and NO<sub>3</sub>) had significant effects on taxonomic or phylogenetic  $\alpha$ -diversity  
266 before rather than after dredging (Table 1). Additionally, the taxonomic  $\alpha$ -diversity  
267 was significantly correlated with Chl- $\alpha$  before dredging ( $p < 0.05$ ), but was not after  
268 dredging ( $p > 0.05$ ) (Fig 1b). The phylogenetic  $\alpha$ -diversity was slightly correlated  
269 with Chl- $\alpha$  before rather than after dredging ( $p > 0.05$ ). These results indicate that the

270 bacterioplankton diversity contributed differently to the water trophic level before and  
271 after dredging.

272

### 273 **3.2. Environmental adaptation of bacterioplankton at taxonomic and** 274 **phylogenetic levels**

275 Both community distance (represented by Bray-Curtis dissimilarity) and  
276 phylogenetic distance (represented by  $\beta$ MNTD) of bacterioplankton were  
277 significantly correlated with physicochemical factor dissimilarity before and after  
278 dredging ( $p < 0.001$ ; Fig. S5, S6). Subsequently, we evaluated environmental  
279 adaptation of bacterioplankton at both taxonomic and phylogenetic levels (Fig. 2).

280 The bacterioplankton exhibited a broader range of environmental thresholds for  
281 almost all environmental factors before dredging than after dredging (Fig 2a).

282 Furthermore, the bacterioplankton showed stronger phylogenetic signals for almost all  
283 environmental parameters before dredging than after dredging based on Blomberg's  $K$   
284 statistic (Fig 2b) and Fritz-Purvis  $D$  test (Fig 2c). These results indicated that  
285 bacterioplankton taxa showed stronger environmental adaptation before rather than  
286 after dredging.

287

### 288 **3.3. Ecological processes and influence on bacterioplankton community assembly**

289 Based on the null model, dispersal limitation (47.7%) and variable selection  
290 (28.1%) contributed most to community assembly before dredging (Fig. 3a). However,  
291 “undominated” processes (51.0%) and dispersal limitation (41.8%) contributed most  
292 to community assembly after dredging. Homogenizing dispersal and homogeneous

293 selection contributed less to community assembly. Consequently, stochastic and  
294 differentiating processes dominated bacterioplankton community assembly, and both  
295 processes were higher before dredging than after dredging (Fig. 3a). The neutral  
296 community model revealed that the bacterioplankton community was more affected  
297 by neutral processes after dredging ( $m = 0.303$ ,  $R^2 = 0.731$ ) than before dredging ( $m =$   
298  $0.262$ ,  $R^2 = 0.717$ ) (Fig. 3b). These results revealed that dredging led to an increase in  
299 “undominated” processes probably via increasing ecological drift, which in turn  
300 increased stochasticity.

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

311 Subsequently, we used co-occurrence networks and function profiling to reflect  
312 outcomes of stochasticity-dominated assembly of bacterioplankton community (Fig.  
313 4). We observed relatively more nodes and edges before dredging (node = 644, edge =  
314 51,082) than after dredging (node = 528, edge = 12,508) (Fig. 4a; Table S1). The ratio

315 of positive to negative edges was relatively low before (ratio = 3.38) than after  
316 dredging (ratio = 8.06) (Table S1), suggesting relatively less conflicting interactions  
317 between bacterioplankton after dredging. The core nodes in each network module  
318 were affiliated with *Bacteroidetes*, *Cyanobacteria*, *Firmicutes*, *Planctomycetes*, and  
319 *Proteobacteria* before dredging (Table S2), and were affiliated with *Actinobacteria*,  
320 *Bacteroidetes*, *Chloroflexi*, and *Proteobacteria* after dredging (Table S3). The core  
321 microorganisms represented by core nodes showed differing correlations with  
322 physicochemical variables (Table S2, S3). These results demonstrated that comparable  
323 divergence in bacterioplankton interactions before and after dredging. According  
324 to function profiling results, 8608 functions at KEGG pathway level 3 were detected  
325 before and after dredging, and these shared 8504 functions (Fig. S9). Among these,  
326 5632 functions showed higher functional redundancy before dredging, while 1108  
327 functions exhibited higher functional redundancies after dredging (Fig. S9). More  
328 unique functions were found after dredging, such as cytokinin dehydrogenase (EC:  
329 1.5.99.12), creatinine deaminase (EC: 3.5.4.21), and c-di-GMP phosphodiesterase  
330 (EC: 3.1.4.52). At KEGG pathway level 2, some functions (e.g., amino acid  
331 metabolism, carbohydrate metabolism, lipid metabolism, and environmental  
332 adaptation) were significantly higher before dredging than after dredging (Fig. 4b).  
333 These results suggested that a general functional decrease in the bacterioplankton  
334 community and a gain of some unique functions occurred after dredging. According  
335 to the PERMANOVA results, sediment TP showed significantly higher effects on  
336 bacterioplankton community function compared to other physicochemical factors



337 before and after dredging (Fig. S10). This implies that the phosphorus resource is the  
338 determinant affecting bacterioplankton community function.

339 Finally, we quantitatively estimated effects of bacterioplankton community  
340 assembly on community function and water trophic level before and after dredging  
341 (Fig 5). A more significant correlation was found between  $\beta$ NTI and the functional  
342 redundancy index after dredging ( $R^2 = 0.11$ ,  $p < 0.001$ ) than before dredging ( $R^2 =$   
343  $0.04$ ,  $p < 0.001$ ) (Fig. 5a), suggesting bacterioplankton community function was more  
344 affected by community assembly after dredging. We also found a significant  
345 correlation between  $\beta$ NTI and changes in Chl- $\alpha$  content before dredging ( $R^2 = 0.10$ ,  $p$   
346  $< 0.001$ ) rather than after dredging ( $R^2 = 0.012$ ,  $p > 0.05$ ) (Fig. 5b). This suggested  
347 that dredging disturbance might reduce the effects of bacterioplankton community  
348 assembly on water trophic level.

349

### 350 **3.4. Relationships between trophic level, environmental factors, diversity and** 351 **function of bacterioplankton**

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

360 6a). In contrast, physicochemical factors showed limited direct or indirect effects on  
361 water trophic level after dredging ( $p > 0.05$ ; Fig. 6b, 6d). The model also exhibited a  
362 good fit to the data, as indicated by the non-significant  $\chi^2$  test ( $N = 18$ ,  $\chi^2 = 0.75$ , d.f.  
363  $= 1$ ,  $p = 0.387$ ; Fig. 6b). Bacterioplankton community function showed significant  
364 positive effects on both taxonomic and phylogenetic diversities, while phylogenetic  
365 diversity exhibited limited effects on the water trophic level before and after dredging  
366 ( $p < 0.01$ ; Fig. 6a, 6b). Direct effects of physicochemical factors, community function,  
367 taxonomic diversity, and phylogenetic diversity on water trophic level were stronger  
368 than indirect effects of corresponding components (Fig. 6c, 6d). These results  
369 suggested that water trophic level, environmental factors, taxonomic diversity,  
370 phylogenetic diversity, and community function were more closely connected before  
371 dredging than after dredging.

372

#### 373 **4. Discussion**

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

383 to environmental change. Unexpectedly, we found distinct shifts in diversity,  
384 composition, interactions, function, environmental adaptation, and ecological  
385 assembly processes of the bacterioplankton community after dredging.

386

#### 387 **4.1. Smaller contributions of bacterioplankton diversity to the water trophic level** 388 **after dredging**

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

396

#### 397 **4.2. Weaker environmental adaptation of bacterioplankton after dredging**

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

406 Environmental breadth and phylogenetic signal analyses are useful to reflect  
407 microbial environmental adaptation (Jiao and Lu, 2020; Wan et al., 2021a). For  
408 instance, a previous study reported that *Proteobacteria*, *Actinobacteria* and  
409 *Cyanobacteria* are regarded as indicator taxa in wastewater treatment plants by  
410 applying TITAN analysis (Romero et al., 2019). Abundant bacteria and/or fungi  
411 exhibit stronger phylogenetic signals than corresponding rare taxa (Jiao and Lu, 2020;  
412 Wan et al., 2021a, 2021b). Microbial functional traits for ecological preferences rely  
413 on the evolutionary history of the species (Morrissey et al., 2019). For instance,  
414 bacterial functional traits in four forest soils in North America were mainly  
415 determined by evolutionary history and less affected by environmental filtering (e.g.,  
416 vegetation type, precipitation, and temperature) (Morrissey et al., 2019). Species are  
417 not randomly distributed along the tree of life due to phylogenetic conservatism  
418 (Martiny et al., 2015), and the tree of life can provide information about evolutionary  
419 diversification, speciation and extinction rates (Stadler and Bokma, 2013). However,  
420 the stronger phylogenetic signals of bacterioplankton before dredging than afterwards  
421 might not be due to the shift in evolutionary history, since evolutionary diversification,  
422 speciation and extinction are strongly correlated with long-term environmental change  
423 (Lu et al., 2019). The stronger phylogenetic signals of bacterioplankton for functional  
424 traits before dredging might be via two pathways: (i) dredging-caused nutrient loss  
425 which in turn affected bacterioplankton community composition, and (ii) microbial  
426 ecological drift caused by removing sediment. It has been reported that exchanges of  
427 microorganisms and nutrients occurs between water and the sediment surface (Liao

428 [et al., 2020](#); [Wan et al., 2020](#)). Additionally, microbial responses to different  
429 environmental variables are phylogenetically conserved at different taxonomic levels  
430 ([Martiny et al., 2015](#)). For instance, in *Acidobacteria*, pH preference is reported to be  
431 deeply phylogenetically conserved at the phylum level, while in *Cyanobacteria* and  
432 *Actinobacteria*, temperature preference appears to be shallowly conserved at the  
433 species level ([Martiny et al., 2015](#)). In the present study, bacterioplankton showed  
434 stronger phylogenetic signals before rather than after dredging which might suggest  
435 that the bacterioplankton exhibit more phylogenetic niche conservatism ([Bennett et al.,](#)  
436 [2010](#)). This is similar to the results that showed that bacterioplankton exhibited closer  
437 phylogenetic clustering before dredging than after dredging. Additionally, the  
438 disturbance events of dredging can lead to an unstable ecosystem, which in turn could  
439 affect the bacterioplanktonic resistance to environmental change and the resilience to  
440 return to the original state or reach a new stable state ([Pimm, 1984](#); [Zhang et al.,](#)  
441 [2017](#)). The significant change in bacterioplankton community composition might  
442 reflect that the bacterioplankton did not possess strong resistance to disturbance, and  
443 could not recover to the initial stable state after dredging. These findings might also  
444 explain why higher contributions of taxonomic and phylogenetic  $\alpha$ -diversities to the  
445 water trophic level occur before dredging than after dredging.

446

### 447 **4.3. Stochasticity community assembly after dredging**

448 Before dredging, both stochastic and deterministic processes had a relatively  
449 large influences on community assembly. These results differ from the findings of  
450 homogeneous selection referring to deterministic processes dominating

451 bacterioplankton community assembly in Lake Donghu across four seasons (Yan et al.,  
452 2017) and in coastal waters in the East China Sea across three seasons (i.e., spring,  
453 summer, and autumn) (Wang et al., 2020). A microbial community tends to be a  
454 stochasticity-dominated assembly in nutrient-rich conditions, and inclines to be a  
455 deterministic-dominated assembly in nutrient-poor conditions (Chase, 2010). After  
456 dredging, the relative contribution of “undominated” processes to bacterioplankton  
457 community assembly increased, which is similar to a report describing that  
458 “undominated” processes show a greater contribution to bacterioplankton community  
459 assembly in a flood-occurring period than in a dry season (Huber et al., 2020). These  
460 findings indicate that both anthropogenic (i.e., dredging) and natural (i.e., flood)  
461 disturbances increase microbial ecological drift.

462 Before and after dredging,  $\beta$ NTI values of bacterioplankton community were  
463 more strongly correlated with sediment total phosphorus than other environmental  
464 variables. The decisive role of sediment total phosphorus in affecting community  
465 assembly might be partially due to the high phosphorus demand for living organisms  
466 (Canfield et al., 2020). Sediment total phosphorus is an important phosphorus source  
467 for bacterioplankton growth via release from sediment (Taylor et al., 2018). Because  
468 the phosphorus cycle is coupled with carbon and nitrogen cycles (Canfield et al.,  
469 2020), sediment organic carbon and organic nitrogen might also affect stochastic and  
470 deterministic processes. We will investigate the effects of multiple environmental  
471 variables on bacterioplankton community assembly in differing aquatic ecosystems in  
472 future research.

473

#### 474 **4.4. Less conflicting interactions and weaker functions after dredging**

475 Ecological community assembly processes determine microbial interaction  
476 patterns and functions (Xun et al., 2019; Jiao et al., 2020; Wan et al., 2021c).  
477 Bacterioplankton community functions decreased after dredging and sediment total  
478 phosphorus was essential for community functions. Phosphorus limitation affected  
479 bacterioplankton community function in our and other studies (Yeh et al., 2020),  
480 which might be partially due to phosphorus effects on bacterioplankton community  
481 assembly. Co-occurrence networks showed that edges and nodes decreased after  
482 dredging, which is a similar finding for a flood-occurring river ecosystem in Paraná  
483 (Huber et al., 2020). The bacterioplankton community presented less conflicting  
484 interactions (mainly competition and predation) after dredging, which might be  
485 partially due to nutrient loss in water-sediment ecosystems. Sediments are important  
486 nutrient pool (Liu et al., 2016; Wan et al., 2020), and dredging-caused nutrient loss  
487 affects bacterioplankton growth, which in turn affects their abundance (Zhang et al.,  
488 2017). In addition, dredging can cause microbial ecological drift, which in turn affects  
489 the exchange of bacteria between water and sediment (Liao et al., 2020), thereby  
490 influencing bacterioplankton community stability and interactions. It is worth noting  
491 that the core bacterioplankton changed in the network module after dredging, which  
492 might lead to a community functional shift. For example, the phylum *Chloroflexi*,  
493 reported to be responsible for production of cobalamin (a microbial growth factor)  
494 (Mehrshad et al., 2018), was found to be one of the core nodes in the network module  
495 after dredging. Consequently, bactererioplankton function generally decreased after

496 dredging, although more unique functions were gained after dredging. From the  
497 perspective of water quality improvement, dredging should be performed promptly  
498 and efficiently to decouple bacterioplankton from their growth environment.

499

## 500 **5. Conclusions**

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

514

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519



520 **Conflict of interest**

521 The authors declare that they have no conflicts of interest.

522

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683



684 **Table 1** Pearson correlations between physicochemical factors and Chl-a content, taxonomic diversity (Shannon-Wiener index), and  
 685 phylogenetic diversity (SES.MNTD index), and Mantel's correlation between changes in physicochemical factors and phylogenetic turnover  
 686 represented by  $\beta$ NTI.

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

687 Note: The abbreviations of environmental factors are defined in Section 2. Asterisks represent significant level (\*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p$   
 688  $< 0.001$ ).