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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 α -diversities of the bacterioplankton exhibited a higher contribution
40 to the water trophic level, as represented by chlorophyl α 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 α -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 α (Chl- α) 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 (β 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). β -nearest taxon index (β NTI)
216 and null model-based Bray-Curtis-based Raup-Crick (RC_{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*²” 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- α content and abundance of bacterioplankton and
236 cyanobacteria were found after dredging (Wilcoxon rank-sum test, $p < 0.001$; [Fig. 1a](#)).
237 The Chl- α content was strongly positively correlated with pH and DO, while
238 noticeably negatively correlated with NH₄ before and after dredging ($p < 0.05$ or $p <$
239 0.01) ([Table 1](#)). Linear regressions reflected significant correlations between Chl- α
240 content and cyanobacterial abundance before and after dredging ($p < 0.001$), while no
241 significant correlation was found between Chl- α 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 NH₄) 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 α -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 α -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, NH₄, and NO₃) had significant effects on taxonomic or phylogenetic α -diversity
266 before rather than after dredging (Table 1). Additionally, the taxonomic α -diversity
267 was significantly correlated with Chl- α before dredging ($p < 0.05$), but was not after
268 dredging ($p > 0.05$) (Fig 1b). The phylogenetic α -diversity was slightly correlated
269 with Chl- α 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 β 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 β NTI compared to other environmental factors before
303 and after dredging (Table 1). Additionally, β 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, β 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 β 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 β NTI and changes in Chl- α 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 χ^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 χ^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 α -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 α -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 α -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, β 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, bacterioplankton 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 α -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 β 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).