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**Riverine phytoplankton shifting along a lentic-lotic
continuum under hydrological, physiochemical conditions
and species dispersal**

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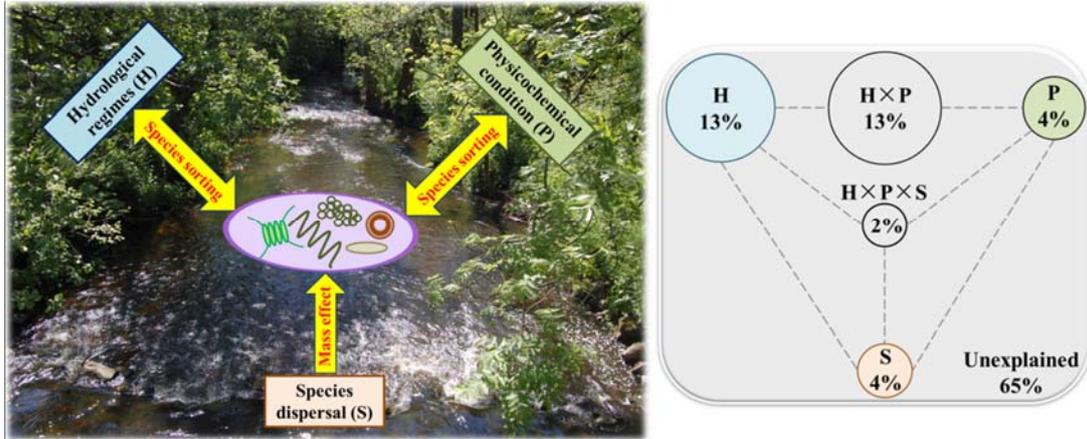
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19

20 **Graphical abstract**



21

22 **HIGHLIGHTS:**

- 23 • Phytoplankton community shows extremely high spatial and temporal variations.
- 24 • Lentic water body has significant effects on downstream phytoplankton
- 25 community.
- 26 • Flow regimes impact algal local composition and regional beta diversities.
- 27 • Hydrological and physiochemical factors contribute more than dispersal in study
- 28 area.

29

30 **ABSTRACT**

31 The importance of phytoplankton-based bio-assessment has been recently recognized
32 in lowland rivers which are affected by multi-environmental factors. However, some
33 basic questions remain unclear to date, such as: (i) spatial and temporal variations of
34 phytoplankton, (ii) the impact of upstream lakes on downstream community, (iii) the
35 main drivers for species composition or (iv) the regional biodiversity along a
36 lentic-lotic continuum. To answer these questions, we collected and analyzed the
37 fluvial phytoplankton communities along a lentic-lotic continuum from a German
38 lowland catchment, where a well-established ecohydrological modelling predicted
39 long-term discharges at each sampling site. Our results revealed very high spatial and
40 temporal variations of phytoplankton community. The changes of a lake on
41 downstream phytoplankton assemblages were significant, especially the nearest reach
42 after the lake. However, these influences varied along with seasons and limited in a
43 relatively short distance to the lake. Redundancy analysis and Mantel tests showed
44 that phytoplankton composition and dissimilarities along the lentic-lotic continuum
45 attributed more to local hydrological and physicochemical variables than species
46 dispersal, which confirmed the suitability of lowland phytoplankton-based
47 bioassessment. In addition, our findings highlighted the importance of flow regime in
48 shaping phytoplankton community composition and regional beta diversities. This
49 study emphasized the necessity to include the hydrological variables and their
50 relationship with phytoplankton community in future bio-monitoring investigations.

51 *Keywords:*
52 Riverine phytoplankton,
53 Hydrological regimes,
54 Physiochemical condition,
55 Species dispersal,
56 Lentic-lotic continuum,
57 Lowland river
58

59 **1. Introduction**

60 Multiple stressors resulting from intensive anthropogenic activities are affecting the
61 global water resources significantly (Hering et al., 2015). Generally they include flow
62 regime alteration, diffuse and point sources. For example, flow diversion due to dam
63 construction disrupts the river's natural connectivity and impedes the cycling of
64 organic matter, sediments and nutrients from upstream to downstream (Wu et al.,
65 2012). Flow conditions may determine the physical habitat conditions and directly or
66 indirectly affect many other physiochemical variables which are key factors
67 regulating ecological processes in aquatic ecosystems (Bhat et al., 2010). In addition,
68 river eutrophication, which is often associated with diffuse (agriculture) and point
69 source pollution (sewage), has exerted additional stressors for aquatic ecosystem
70 (Hilton et al., 2006). This pollution leads to increased costs of water treatment for
71 public supply (Pretty et al., 2003) as well as loss of biodiversity (Binzer et al., 2016).
72 Since human-mediated disturbances and their effects become a pressing focus, it is
73 essential to understand how the interaction between multiple stressors and their
74 impacts on water quantity and quality issues as well as aquatic organisms, because
75 these are fundamental for prioritizing global and regional conservation efforts and
76 achieving sustainability of freshwater resources (Piggott et al., 2012). However, the
77 combined effects of multiple, simultaneously operating stressors on a comprehensive
78 set of aquatic organisms, particularly for algal communities are still to be studied
79 (Lange et al., 2016).

80 Riverine phytoplanktons are valuable bio-indicator for assessing water quality in
81 aquatic systems since their irreplaceable role and sensitivity to multiple ecological
82 stressors (EU, 2013; Pasztaleniec and Poniewozik, 2010; Wu et al., 2014b; Zeng et al.,
83 2017). In lowland rivers, phytoplankton instead of benthic algae serves as an
84 important primary producer, due to the low hydraulic gradients and a strong
85 dominance of muddy, sandy substrates (Wu et al., 2011; 2014a). Although their
86 important roles as bio-indicator were recognized recently (Stevenson et al., 2010;
87 Thomas et al., 2016), the occurrence and distribution of phytoplankton in rivers are
88 still unclear. It was believed that there was no true riverine plankton and the pelagic
89 algae found in rivers which originate from either upstream lentic waterbodies or the
90 periphyton (Hötzel and Croome, 1999). However, recent studies (Centis et al., 2010;
91 Wu et al., 2011) argued that benthic diatom communities as the source of the riverine
92 pelagic algae might be too simplistic and that the long retention time in lowland rivers
93 allowed the reproduction of phytoplankton communities and development of
94 substantial populations *in situ*. Various sources could be initial reasons which lead to
95 various algae species composition along the river (Gillett et al., 2016). The effects of
96 upstream lake in the river system and the dynamics of the lentic-lotic linkage
97 ecosystem attracts ecologists' increasing attentions (Arp and Baker, 2007; Jones, 2010;
98 Ellis and Jones, 2013). Linkage lakes act as either sink or source for phytoplankton in
99 river systems (Bridgeman et al., 2012; Miller and McKnight, 2015). A eutrophic lake
100 in the upper stream may lead to serious problems in downstream river ecology.

101 Lacustrine bloom-forming toxic Cyanobacteria (e.g. *Microcystis aeruginosa* Kützing)
102 can be transferred to the river downstream which heavily impacted downstream river
103 water quality (Jacoby and Kann, 2007; Yu et al., 2015). In this situation
104 phytoplankton are definitely influenced by multiple factors, including hydrological
105 regimes, physiochemical variables, and species dispersal during their floating
106 processes.

107 One of the primary goals of ecological surveys is to describe the temporal and spatial
108 distribution in relation to the abiotic factors. The relationships between aquatic
109 organism and abiotic factors have been studied for a long time (Hering et al., 2006;
110 Heathwaite, 2010; Mantyka - pringle et al., 2012). However, previous studies and
111 monitoring investigations primarily focused on local physiochemical variables,
112 especially on nutrients loading (Larson et al., 2007; Wang et al., 2016). The flow
113 alteration and geographic characteristics also affected the structure and function of
114 aquatic ecosystem (Lytle and Poff, 2004; Heino et al., 2015; Dong et al., 2016).
115 Nevertheless, most of the publications about flow-ecology relationship preferred to
116 prospect fish or invertebrate communities as targets (Stewart et al., 2014; Guse et al.,
117 2015b; Kiesel et al., 2015) rather than focus on riverine phytoplankton community
118 patterns.

119 In our research area, a lentic-lotic linkage lowland catchment, we are also facing this
120 similar situation: very few studies investigating the relationships between algae
121 community and abiotic factors. To find out the shaping factors, we examined fluvial

122 phytoplankton community patterns from different levels of biological aspects, which
123 were not only overall indexes, but also their spatiotemporal distribution in local and
124 regional scales. In this study we ascertained following questions:

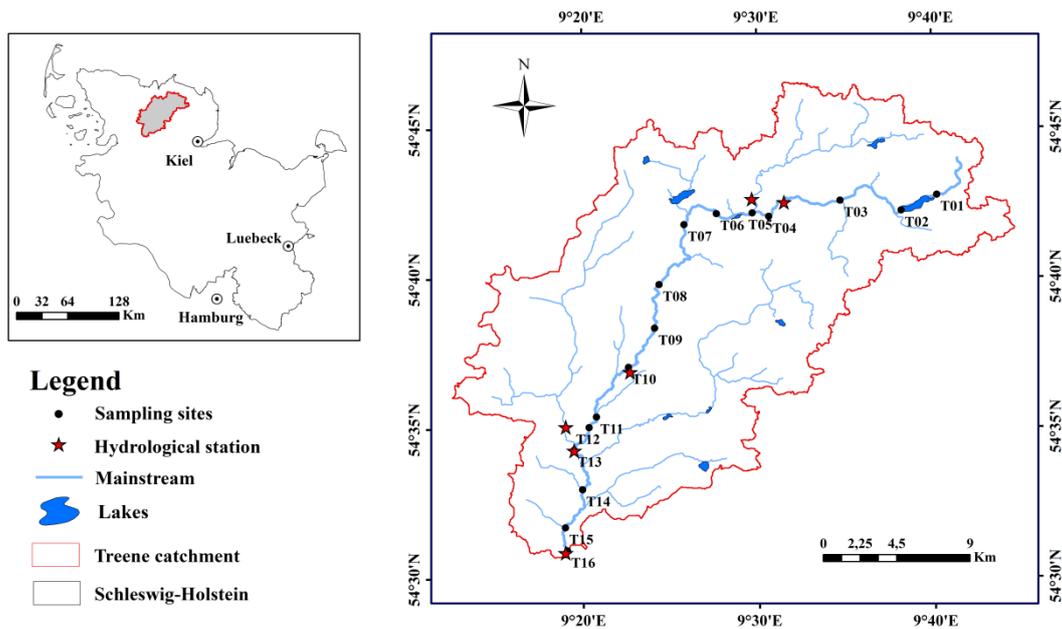
125 (1) How large is the influence of upstream lake in the lentic-lotic linkage system
126 among the spatiotemporal dynamics?

127 (2) Which of hydrological regimes, physiochemical variables and species dispersal
128 factors, is the key driving factor for shaping the lowland phytoplankton communities
129 at local and regional scale?

130 **2. Methods**

131 *2.1. Study area and field sampling*

132 River Treene catchment (481 km² at the catchment outlet Treia) is part of the lowland
133 area located in the State of Schleswig-Holstein in north Germany. Agriculture is the
134 dominant land use in the study area (80%), and this sand-bed river is naturally heavily
135 meandering with a small altitude gradient (elevations range from 2 to 80 m). The
136 Bondenau, as one of its original tributaries, contains a lake (Sueden See, 0.64 km²) in
137 the upstream. Our field samplings were conducted seasonally from December 2014 to
138 September 2015, and 16 sites (APPENDIX_1) along the mainstream were visited
139 each time. The sites were placed evenly under consideration of the lake and tributaries.
140 The number count along the longitudinal axis of rivers from the upstream to outlet is
141 T01-T16 (Fig. 1).



142

143 **Fig. 1** The 6 hydrological stations and 16 sampling sites of Treene catchment (right)
 144 in the Schleswig-Holstein State (left) of Germany.

145 **2.2. Physiochemical and biological measurements**

146 At each site, water temperature (WT), pH, electric conductivity (EC), and dissolved
 147 oxygen (DO) of the surface water were measured *in situ* using Portable Meter (WTM
 148 Multi 340i and WTW Cond 330i, Germany). River width, water depth and flow
 149 velocity (FlowSens Single Axis Electromagnetic Flow Meter, Hydrometrie, Germany)
 150 were surveyed simultaneously. At the same time, water samples were collected for
 151 nutrients analysis. They were partially filtered through GF/F glass microfiber filter
 152 (Whatmann 1825-047) to remove and collect the total suspended substances. Both
 153 filtered and unfiltered samples were kept frozen at -20°C until measurements. The
 154 concentrations of total phosphorus (TP), phosphate-phosphorus ($\text{PO}_4\text{-P}$),

155 ammonium-nitrogen ($\text{NH}_4^+\text{-N}$), nitrate-nitrogen ($\text{NO}_3^-\text{-N}$), nitrite-nitrogen ($\text{NO}_2^-\text{-N}$),
156 chloride (Cl^-) and sulphate (SO_4^{2-}) were measured according to the standard DEV
157 (Deutsche Einheitsverfahren zur Wasser-, Abwasser- und Schlammuntersuchung)
158 methods. DIN is the sum of nitrite ($\text{NO}_2^-\text{-N}$), nitrate ($\text{NO}_3^-\text{-N}$) and ammonia ($\text{NH}_4^+\text{-N}$).
159 Nitrogen to phosphorus ratio (NPR) is the ratio of DIN and TP. Samples for
160 phytoplankton analysis were collected using a plankton net with a mesh size of 20 μm .
161 A known volume of water was filtered and fixed immediately by neutral lugol's
162 solution. Algae samples were concentrated to 25 mL for further processing after
163 natural sedimentation in the laboratory.

164 For the soft algae (non-diatom) identification, algae were counted with optical
165 microscope (Nikon Eclipse E200-LED, Germany) at 400X magnifications in a
166 Fuchs-Rosental chamber. The counting unit was individual (unicell) and at least 300
167 units were counted for each sample. Taxonomic identification of species was done
168 according to the introductions of Hu (2006) and Burchardt (2014). To identify
169 diatoms, permanent slides were prepared after oxidization (using 5 mL of 30%
170 hydrogen peroxide, H_2O_2 , and 0.5 mL of 1 M hydrochloric acid, HCl), and then 0.1
171 mL of the diatom-ethanol mix was transferred on a 24mm X 24mm cover slip. A drop
172 of Naphrax was used to mount the slides. Diatoms were identified with the optical
173 microscope (Nikon Eclipse E200-LED, Germany) with 1000X magnification under
174 oil immersion, based on the key books by Bey and Ector (2013), Hofmann (2011) and
175 Bak (2012). Algae densities were expressed as cells/L.

176 *2.3. Modeling and statistical analysis*

177 *2.3.1. Modeling discharge*

178 A semi-distributed hydrological model is required for this analysis. The
179 ecohydrological SWAT model (Soil and Water Assessment Tool, Arnold et al. 1998),
180 which is discretized in subbasins, was selected. The SWAT model provides outputs of
181 different hydrological variables for each subbasin in a daily resolution. In this model
182 application, the model discretization for the Treene catchment resulted into 108
183 subbasins. Due to the semi-distributed model type, separate subbasins were also
184 included for the major tributaries (Guse et al., 2014). This allows a consideration of
185 the spatial heterogeneity.

186 To ensure accurate model results within the entire catchment, six hydrological stations
187 were used in a multi-site calibration as shown in Fig. 1 (Guse et al., 2015a). The
188 modeling period consisted of a calibration (2001 to 2005) and a validation period
189 (2006 to 2016) for discharge. During the model validation, we only used five stations
190 due to an early termination of the measurements at one hydrological station in 2014.
191 The model performance was evaluated by using three performance measures
192 (Nash-Sutcliffe Efficiency, Percent Bias, RSR (root mean square error divided by
193 standard deviation)) (Guse et al. 2015a). The comparison of modeled and measured
194 discharge yielded a reliable performance for the six hydrological stations. Thus, the
195 results of this eco-hydrological model can be used for the consecutive analyses. Daily
196 model results were extracted for subbasins which includes one or more a sampling

197 point. For reason of consistency, each sampling point of this study was assigned to the
198 model results from the closest outlet of a subbasin outlet.

199 2.3.2. *Data processing and statistical analysis*

200 We classified the abiotic factors into three categories: hydrological regimes (H),
201 physiochemical condition (P), and species dispersal (S). They composed as three
202 explanatory gradients for biotic patterns.

203 Based on the modeled daily discharge time series from the SWAT model, we
204 calculated 57 hydrologic indices (APPENDIX_2) describing different aspects of the
205 flow regime (Olden and Poff, 2003), including the other two *in situ* parameters: depth
206 and velocity, which constituted the hydrological regimes group (H). The 14 local
207 physiochemical parameters (APPENDIX_3) measured from the sampling sites were
208 composed as physiochemical condition group (P). For species dispersal group (S),
209 except for the coordinates (X: Latitude, Y: Longitude), Moran's eigenvector maps
210 were used to generate species dispersal variables representing geographical positions
211 and dispersal across the rivers. This method is a powerful approach to detect spatial
212 structures of varying scale in response data and more flexible than other eigenvector
213 based approaches for irregular sampling design (Tang et al., 2013a). In brief, this
214 method proceeds as follows: i) a geographical distance matrix as Euclidean distance
215 between each pair of sampling sites was calculated using the *earth.dist* function in the
216 package *fossil* in R. ii) Principal Coordinates of Neighborhood Matrix (PCNM)

217 analysis based on the geographical distance were used to compute species dispersal
218 representing geographical positions through the *pcnm* function in R package *vegan*.
219 The generated eigenvectors were considered as spatial variables (i.e., PCNMs), which
220 could reflect unmeasured broadscale variation in the modern environment or historical
221 factors, e.g. natural dispersal-generated patterns demonstrating internal local-scale
222 dispersal dynamics or regional-scale migration history (Svenning et al., 2009).
223 PCNMs are ranked in descending order based on their eigenvalues and
224 simultaneously coded in ascending order (starting from 1), and PCNMs with large
225 eigenvalues and small code represent broad-scale spatial pattern, while the smaller
226 eigenvalues with large code represent fine-scale patterns. PCNMs are commonly used
227 to describe species dispersal processes (Curry and Baird, 2015). Usually, only
228 PCNMs with positive eigenvalues are retained as spatial explanatory variables (Tang
229 et al., 2013b). Among the 15 PCNMs generated, eigenvalues of PCNM component
230 1-10 were positive and thus 12 variables (including X, Y) were included in the species
231 dispersal group (S).

232 For testing the differences of phytoplankton community composition and structure
233 among the four seasons and 16 sites, multi-response permutation procedure (MRPP)
234 was used (function: *mrpp*; package: *vegan*). The null hypothesis was that there was no
235 difference among the groups in a Monte Carlo randomization procedure with 999
236 permutations. Classification and regression trees (CART) was used to find out the

237 relative important abiotic factors to a single biological index (function: *rpart*; package:
238 *party*).

239 To calculate the explanation of unique and interaction of abiotic gradients' effect on
240 local phytoplankton community variations, a variation partitioning canonical
241 redundancy analysis (partial RDA) was performed. For achieving a best performance,
242 the phytoplankton abundance matrix was Hellinger transformed (Legendre and
243 Gallagher, 2001; Legendre and Legendre, 2012). In the meanwhile, the three sets of
244 abiotic variables were tested significance, when using all variables in the model of
245 explaining variations of phytoplankton communities. Afterwards, a *forward selection*
246 (Blanchet, 2008) was proceeded to choose a parsimonious subset of explanatory
247 variables, and then modeled multivariate community structure (function: *cor*, *anova* -
248 package: *stats*; function: *rda*, *varpart* - package: *vegan*; function: *forward.sel* -
249 package: *adespatial*).

250 Shannon-Wiener Index based on algal density was used to assess the local
251 phytoplankton community diversity (alpha diversity) (Shannon, 2001). Furthermore,
252 Mantel test was applied to examine the phytoplankton communities' dissimilarity in
253 regional scale (beta-diversity) along distance matrices (Mantel, 1967). The biological
254 matrix was generated by Bray-Curtis similarity index based on phytoplankton relative
255 abundance data, since the index takes into account of the differences between species
256 and emphasizes dominant species. Distance matrices were calculated for hydrological
257 regimes (H), physiochemical condition (P), species dispersal (S), respectively by

258 Euclidean distances approach (function: *mantel*, *mantel.partial*, *vegdist*; package:
259 *adespatial*).

260 All analyses were performed with the R software (version 3.3.3, R Development Core
261 Team, 2017).

262 **3. Results**

263 *3.1. Environmental variations*

264 During the sampling period, the main environmental parameters varied widely both
265 seasonally and spatially (APPENDIX_3). The annual water temperature in the study
266 period is 10.8°C. The results show that the average value of pH and EC increased from
267 winter (December of 2014) to autumn (September of 2015), from 7.81 to 8.21, and
268 435.19 to 539.25 $\mu\text{s}/\text{cm}$, respectively. On the contrary, nitrogen compounds
269 (ammonium-nitrogen, nitrate-nitrogen, DIN) decreased, and showed the smallest
270 magnitude in autumn (0.05 mg/L, 8.70 mg/L and 8.76 mg/L, respectively). For the
271 hydrological variables, mean flow of river discharge decreased from winter to autumn,
272 and had a greater longitudinal variation in winter than in autumn in this study area.
273 For instance, the intraday discharge (H01) varies from 0.31 to 18.3 m^3/s with a
274 standard deviation (SD) of 5.68 in winter, while from 0.008 to 2.31 m^3/s with a SD of
275 0.77 in autumn. In addition, there are similar results from the frequency of flow
276 events. We also found high flood pulse count (H45) had more days in winter and
277 spring time. For example, high flood pulse count for 30 days (H45) have 8 days in

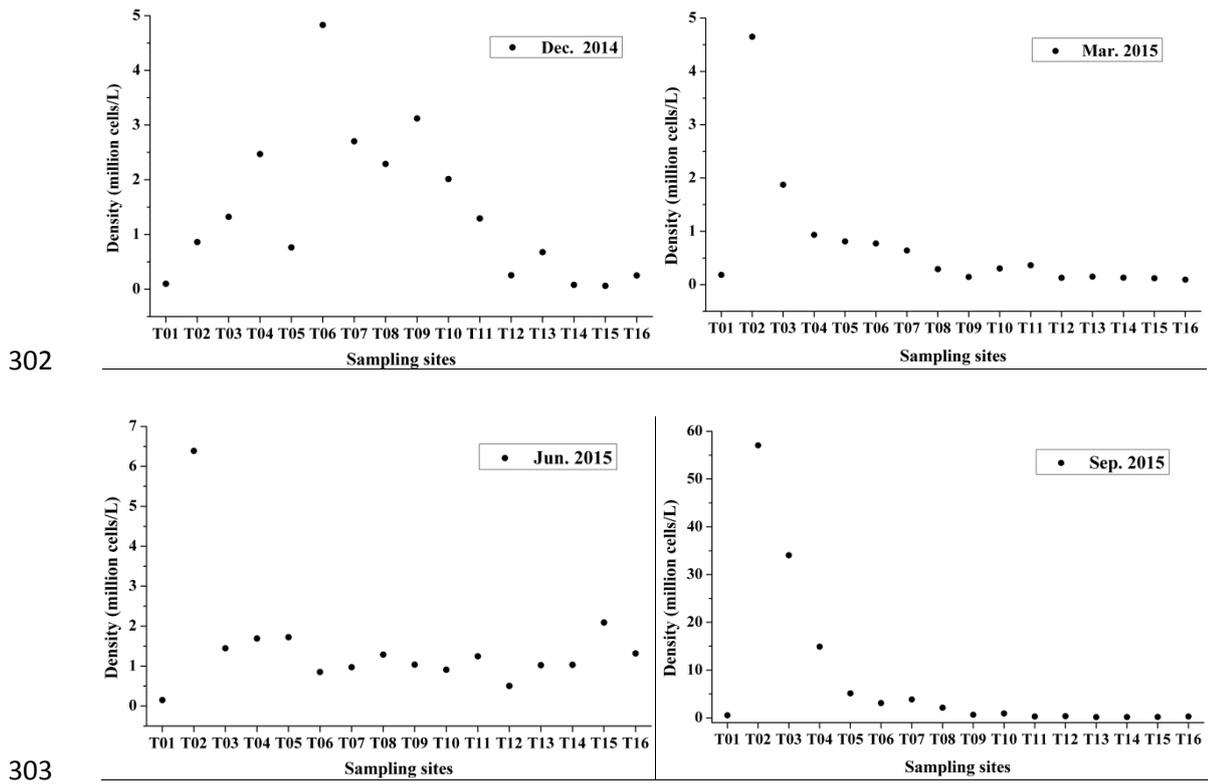
278 December 2014, 13 days in March 2015, while zero day in June and September of
279 2015.

280 3.2. *Temporal and longitudinal variation of phytoplankton community* 281 *patterns*

282 According to our four seasonal samplings in 16 sites from the River Treene, 334 algae
283 species were identified belonging to seven families. The number of species assigned to
284 Bacillariophyta, Cyanobacteria, and Chlorophyta were 217, 32 and 59 respectively.
285 The dominant species switched along the longitudinal direction and across seasons
286 (APPENDIX_4). The site T01 is located at the most upstream part of Treene River
287 and was mainly dominated by *Navicula lanceolata* Ehrenberg and *Melosira varians* C.
288 Agardh. The site T02 is close to T01 (~1.7 km downstream) with a lake in between,
289 the dominant species shifted dramatically to *Microcystis*. At the sites afterwards
290 (T03-T16), dominant species changed back to *Navicula lanceolata* Ehrenberg and
291 *Melosira varians* C. Agardh. In addition, *Microcystis aeruginosa* Kützing remain in
292 species composition, while their percentage decreased generally along the lentic-lotic
293 continuum. The differences between T01 and the sites after the lake (e.g., T02-T16)
294 can be explained by the lake in-between.

295 In different seasons, the species densities and diversities also showed a great variation
296 (Fig. 2 & Fig. 3). The average algal densities in Dec. 2014, Mar. 2015, Jun. 2015, Sep.
297 2015 were 1.44 millions cells/L, 0.72 million cells/L, 1.48 million cells/L and 7.74

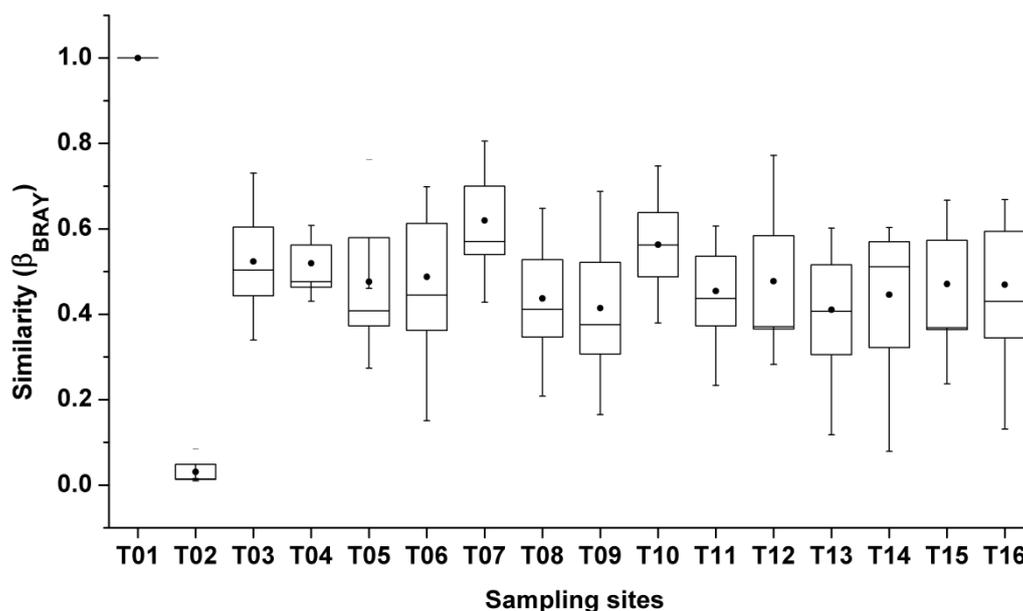
298 million cells/L, respectively, while Shannon-Wiener Index were 2.43, 2.70, 2.38 and
 299 2.34, respectively. Generally, species densities downstream of the lake increased
 300 significantly compared with T01, and afterwards showed a clear decline trend (from
 301 T02 to T16) (except for Dec., 2014), particularly for Mar. and Sep., 2015 (Fig. 2).



304 **Fig. 2** Longitudinal variation of phytoplankton communities' density from up- (T01)
 305 to downstream site (T16) at different sampling seasons (Dec. 2014, Mar. 2015, Jun.
 306 2015, Sep. 2015) in the Treene catchment.

307 Based on the Bray-Curtis similarities, we compared all the sites with T01, the site
 308 without lake impact, and we found that the similarities at T02 declined significantly
 309 and afterwards (T03-T15) stayed steady with high values without significant change.
 310 Furthermore, based on the MRPP results, which compared the community

311 composition between T01 and the other 15 sites, in four times sampling, only T01 and
 312 T02 have significant dissimilarity ($A=0.1475$, $p=0.036$ based on MRPP), while the
 313 differences between T01 and other 14 sites (T03-T16) were nonsignificant
 314 respectively ($p>0.05$, based on MRPP). Thus, we could conclude that the impact of
 315 the lake at downstream sites was constrained to T02 and other sites were less affected.
 316 On the other hand, we also found that the phytoplankton community species
 317 composition and abundance in four seasons showed a significantly difference
 318 ($A=0.1519$, $p=0.001$ based on MRPP) demonstrating a significant temporal dynamic.



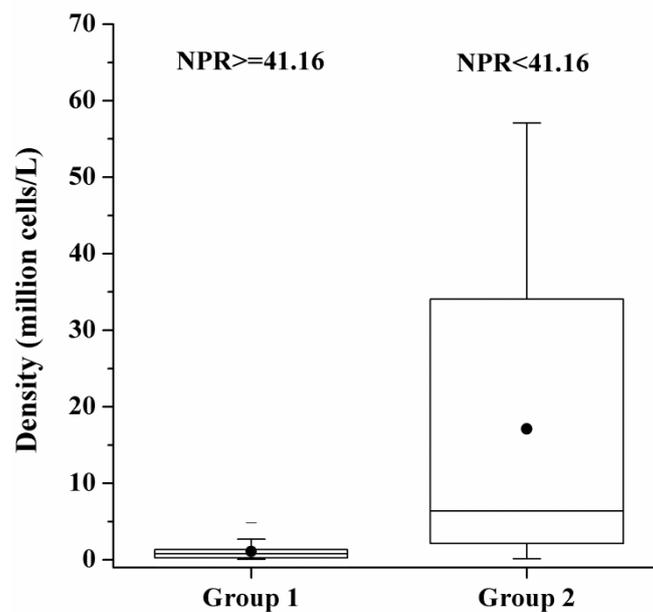
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320 **Fig. 3** Phytoplankton community similarity in the main stream of River Treene (the
 321 similarity calculation for all sites are compared with T01).

322 3.3. *Driving factors for phytoplankton communities*

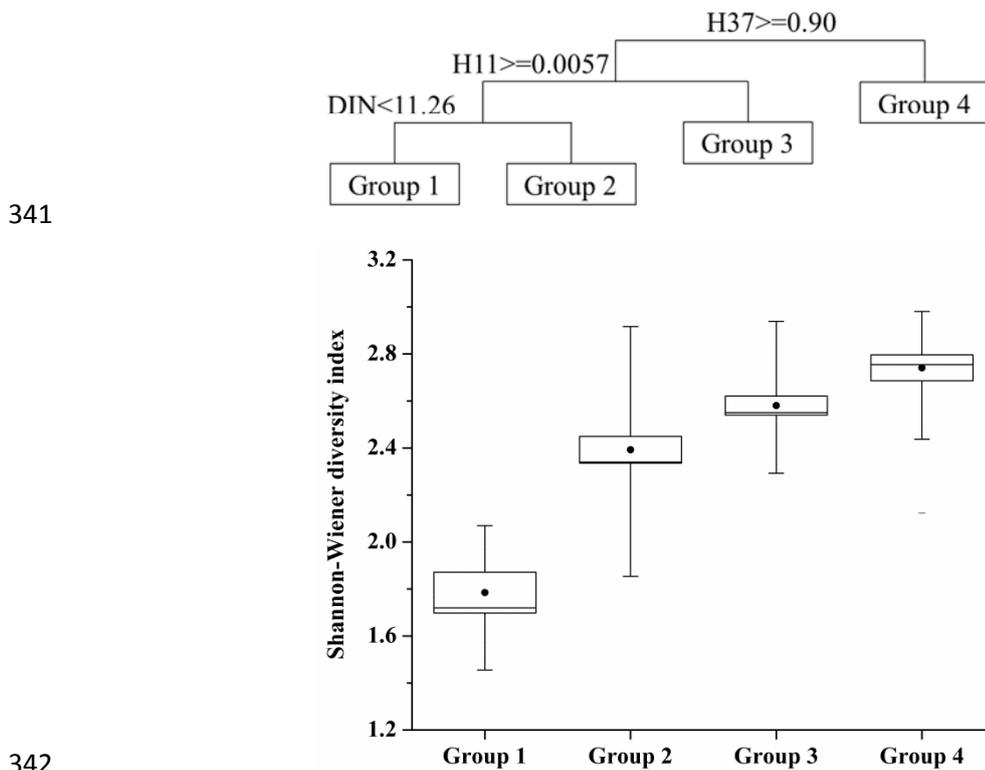
323 3.3.1. *Driving factors for phytoplankton density*

324 With CART, the NPR was selected as the most important key factor for
325 phytoplankton density during the one year seasonal investigation, and the threshold
326 value was 41.16 (Fig. 4). Samples were separated into two groups. The mean density
327 was 1.10 million cells/L in Group 1 with $\text{NPR} \geq 41.16$, while, Group 2, with $\text{NPR} <$
328 41.16, were made up of larger density samples (the average value is 17.1 million
329 cells/L) with a high portion of Cyanobacteria. On the other side, phytoplankton
330 diversity gradients were classified into four groups by three potential abiotic factors:
331 skewness of 30 days (H37), variability flows of 3 days (H11), and dissolved inorganic
332 nitrogen (DIN). Their thresholds were 0.9, 0.006, 11.26, respectively (Fig. 5). Sites in
333 Group 4 shared the characteristic of $\text{H37} < 0.9$. Compared with the others, the Group
334 4 has the highest diversity, and samples came all from spring (campaign on March
335 2015). However, Group 1 with least diversity, has been shaped by less nitrogen
336 concentration and higher flow alteration.



337

338 **Fig. 4** Partition the variation of phytoplankton density by classification and regression
 339 tree (NPR represent for nitrogen to phosphorus ratio. NPR separate phytoplankton
 340 communities in two groups based on the magnification of density)

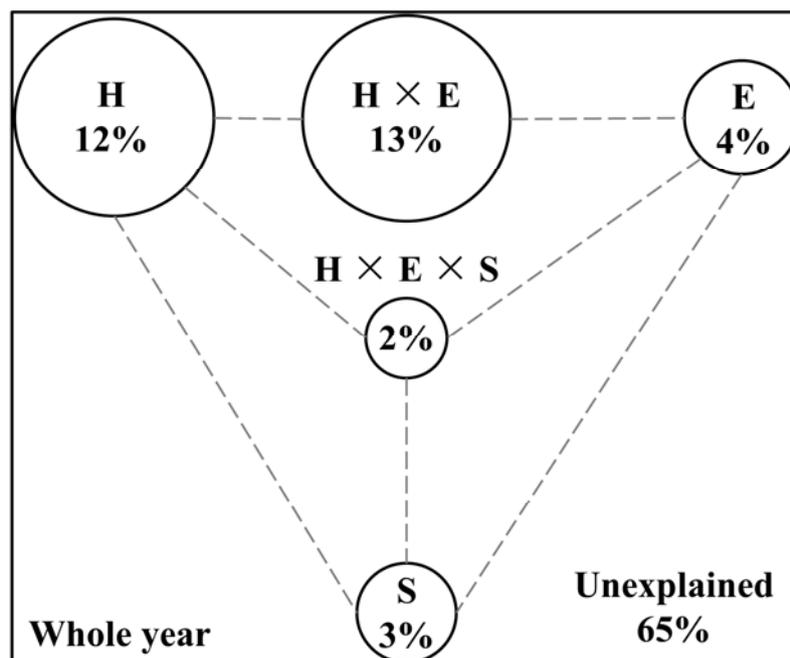


343 **Fig. 5** Partition the variation of phytoplankton diversity by classification and
 344 regression tree (H37 represents skewness of 30 days, H11 represents variability flows
 345 of 3 days, DIN represents dissolved inorganic nitrogen. Shannon-Wiener diversity
 346 index were used for evaluating phytoplankton diversity variation)

347 *3.3.2. The importance of explanatory variables on local phytoplankton community*

348 When we consider the whole year, there are four hydrological (H) variables (i.e.,
 349 mean flows of 30 days, skewness of 30 days, high flood pulse count for 30 days, and

350 the rate of change in flow events from 30 days), and six physiochemical (P) variables
 351 (i.e., WT, Cond, PO₄⁻-P, NH₄⁺-N, NO₃⁻-N, NO₂⁻-N) were selected by *forward*
 352 *selection*. The variance partitioning analysis (Fig. 6) showed that 12% of the total
 353 variation in the phytoplankton data could be explained by pure hydrological variables,
 354 which was much higher than that by pure physiochemical variables (4%). Whereas,
 355 the interaction between hydrologic indices and physiochemical property influenced
 356 the variation of phytoplankton and explained 13%, also stands a relatively important
 357 part. Species dispersal factors explained only 3%. Interaction of the three factors (H×
 358 P×S) was 2.2%, and a total of 65% variation was still left unexplained.



359

360 **Fig. 6** Contribution of abiotic factors to local phytoplankton community (H represents
 361 hydrological variables, P represents physiochemical variables, S represents species
 362 dispersal.)

363 3.3.3. *Driving factors for regional phytoplankton communities*

364 Mantel tests showed that the relative importance of multiple factors to phytoplankton
365 dissimilarities (Bray-Curtis index) varied among seasons (Table 1). Based on the
366 entire year data, phytoplankton dissimilarities increased positively with only
367 physiochemical distance. Regarding to each season, the driving factors for the beta
368 diversities (i.e., dissimilarities) were different (Table 1). For example, phytoplankton
369 dissimilarities were decayed along hydrological and physiochemical distances
370 together by the samples in Dec. 2014 and Mar. 2015. Based on the summer data (Jun.
371 2015), the effects of both hydrological distances and species dispersal distance on
372 community dissimilarities were significant. In addition, the relationship between
373 dissimilarity and hydrological distance were stronger than that between dissimilarity
374 and species dispersal distance. In September, we found three of them weakly
375 correlated to local diversity changing.

376

377 **Table 1**

378 Results of Mantel tests for the correlation between phytoplankton community
379 dissimilarities (Bray-Curtis index) and hydrological (H), physiochemical (P) and
380 species dispersal (S) distances. Significance was expressed as * $p < 0.05$, ** $p < 0.01$,
381 *** $p < 0.001$.

Index	H	P	S
Entire year	0.049	0.240***	0.030
Dec. 2014	0.281*	0.298*	-0.064
Mar. 2015	0.511***	0.423**	0.182
Jun. 2015	0.412**	0.218	0.256*
Sep. 2015	-0.017	0.050	0.119

382 **4. Discussion**

383 In this study, phytoplankton compositions and their metacommunities were shown to
384 be excellent responders to both hydrological and physicochemical conditions.
385 Moreover, the impact from species dispersal factors only delineated from geographic
386 distinction, also slightly contributed to the biotic variations.

387 *4.1. Hydrological factors*

388 Hydrological variables have been identified as important factors in shaping riverine
389 phytoplankton community in our study lowland river. The characteristics of flow
390 alteration during a long period of time were detected as key hydrological driving
391 factors for algal communities, specifically, monthly skewness and variability of the
392 flows. In contrast to instant status, these monthly hydrological alterations influenced
393 water temperature, oxygen level, light intensity as well as nutrient availability in
394 water bodies (Richter et al., 1998, Mitrovic et al., 2011; Paerl et al., 2011), which

395 reflecting the dynamic living condition of riverine phytoplankton community. A study
396 in tropical streams detected that the combination of stream velocity and water depth
397 plays a vital role in structuring diatom communities (Bere et al., 2016). Similarly,
398 water depth was also found to be the most crucial factor for diatoms local species
399 richness in subarctic streams, while the elevation significantly correlated with
400 community dissimilarity (Teittinen et al., 2016). In Poyang Lake (China), Li et al.
401 (2016) found water level as the main controlling factor that controlled the
402 phytoplankton seasonal variability, which actually reflected changes of water quality.
403 Besides the hydrological factors themselves, there was more studies paid attention to
404 combined impacts. For example, low flow attributed to increased irradiance and water
405 temperature were conducive to sustaining cyanobacterial bloom over weeks (Ha et al.,
406 1999). Additionally, low flow reduced velocities, and hence, higher water residence
407 time and nutrients concentration enhanced potential toxic algal blooms and reduced
408 dissolved oxygen levels (Whitehead, 2009). In contrast, riverine bloom was retarded
409 by flow velocities above 0.03-0.05 m/s (Mitrovic et al., 2011). A model studied on
410 benthic algae in New Zealand stream suggested that hydrologic regime and nutrient
411 concentration interacted to shape patterns of biotic composition, and thus algal
412 biomass was strongly dependent on nutrient supply when frequent floods decreased
413 primary consumer biomass (Riseng et al., 2004). The results support that the
414 hydrological indicators, separated (themselves) or combined with other environmental
415 factors, stand as key influential factors, which similar to other studies in this research

416 area. However, different biotic taxonomic assemblages reflect different preference to
417 flow regimes.

418 Recently, Kiesel et al. (2017) improved hydrological model to explore benthic
419 invertebrates' response, based on hydrological condition in the Treene catchment.

420 Guse et al. (2015b) predicted the impact of stressors on Treene River's biota,
421 exemplarily for fishes focusing on hydraulic habitat and macroinvertebrates focusing

422 more on water quality (nitrate). Hydrological indices describing various aspects of the
423 flow regime can be selected to best match the particular ecological processes in local-

424 or regional scale analyses. For example, duration high flow event correlated best with
425 the abundance of individual benthic stream invertebrates (Kakouei et al., 2017).

426 Predictability of flows (annual skewness of the flow) has been linked with mobility
427 and colonizing ability of fish, while variability of pulse frequency with species

428 richness (Puckridge et al., 1998). The timing of flow events impacts on spawning
429 success, and high flows in spring would positively result in high red shiner density,

430 due to their unique life-history strategies (Mims and Olden, 2012). Therefore,
431 different flow alteration was associated with a variety of ecological responses (Poff

432 and Zimmerman, 2010). A key implication of our findings for freshwater
433 management is that long-term bio-monitoring campaigns should include hydrological

434 variables.

435 4.2. *Physicochemical factors*

436 For ascertaining the influences from physicochemical factors, we found that NPR is a
437 key driver for phytoplankton density (Fig. 2). This is a reasonable result, since the
438 research catchment is located in a rural area, where agriculture stands as the main
439 portion (80%) of land use pattern (Guse et al., 2015a). It has been reported that
440 agriculture and point sources in this watershed were the major contributor for nitrate
441 and ammonium, which has been noticed being the main factor affecting water quality
442 in the stream water (Schmalz et al., 2015). With regard to phytoplankton densities,
443 our samples were separated into two groups by CART. The samples with low NPR
444 have high species densities and high percentage of Cyanobacteria. This is specifically
445 the case for *Microcystis* which is known as a sign of nutrients enrichment in the water
446 body. Along the longitudinal direction, dominant species always changed from
447 lacustrine species (Cyanobacteria) to fluvial species (Bacillariophyta). This shift was
448 in accordance with Yu et al. (2015) and Gillett et al. (2016) and illustrated the impact
449 of lakes on downstream sites in different catchments. For example, Yu et al. (2016)
450 observed in Tanglan River that the toxic *Microcystis* from Dianchi Lake dominated at
451 the upper reaches, but replaced by Chlorococcales green algae and centric diatoms in
452 the lower reach. Gillett et al. (2016) found that the headwater of Klamath River was
453 dominated by planktonic blooming toxic Cyanobacteria resulting in generally low
454 NPR. This condition promoted the development of N-fixing benthic diatoms with
455 cyanobacterial endosymbionts from family Epithemiaceae. This trend followed a wide
456 acknowledged pattern from previous studies in lakes with high NPR in oligotrophic

457 status, while low NPR in eutrophic status (Downing and McCauley, 1992; Xu et al.,
458 2010). Studies also found that low NPR was corresponded to *Microcystis* bloom
459 (Smith, 1983; Xie et al., 2003; Orihel et al., 2015).

460 Both total density and cyanobacterial density decreased gradually in September from
461 sites T02 to T05 (with a distance of 6 km). As a typical lacustrine species, *Microcystis*
462 *spp.* was coming from the lake in the upstream. Despite the contribution of decreasing
463 concentration of nitrogen, the concentration of phosphorus in those sites was
464 relatively higher than the others, which also implied the possibility to high
465 phytoplankton density. These results were similar to Wu et al. (2014), which were not
466 surprising since major nutrients, such as nitrogen and phosphorus, were primary
467 elements for algae growing. Increased nutrient concentrations can potentially
468 stimulate algal growth and hence enhance gross primary production and ecosystem
469 respiration in aquatic ecosystems (Ye et al., 2016). On the other hand, nutrient remain
470 low concentration may due to rapid uptake by algae as well (Jirsa et al., 2013).
471 Similar to the lake-river system, reservoir-river systems are also facing a dominance
472 of toxic algae, which exported from the reservoir. *Microcystis* cells can withstand
473 passage through hydroelectric installations and transport over distance on the
474 downstream (Otten et al., 2015). Studies in a dammed lowland river in Poland also
475 observed summer-autumn dominance of toxic Cyanobacteria. They concluded that
476 higher rate of flushing induced a more rapid species dispersal, while low water level
477 led to an increase in phytoplankton population (Grabowska and Mazur-Marzec, 2016).

478 In addition, among the local variables, water temperature, conductivity as well as
479 nutrients were selected in RDA as significantly correlated to phytoplankton
480 composition, which was in agreement with an earlier report within this study area
481 (Wu et al., 2011). Our results from Mantel tests were consistent with Soininen et al.
482 (2016), and suggested that local environment was highly important for phytoplankton
483 at larger (regional) scale as well. These findings further emphasized the suitability of
484 lowland phytoplankton as bio-indicator for local habitat changes since they were more
485 affected by local environment rather than spatial effects as indicated by species
486 dispersal variables (Table 1). Nevertheless, as for phytoplankton based
487 bio-monitoring and bio-assessment, the impacts of upstream lake or reservoir should
488 be paid more attentions, which also remains a need to identify in the future studies
489 how far the lake might affect the downstream phytoplankton community in different
490 seasons.

491 *4.3. Species dispersal*

492 Species dispersal has a weak relationship with phytoplankton in both RDA analyses
493 and Mantel tests in our study area, considering of the whole year. This was
494 inconsistent with the research of Dong et al. (2016) in high mountain stream, which
495 concluded that directional processes and dispersal had prevailing effect on algae
496 metacommunity structuring rather than local physiochemical factors. However, the
497 Treene watershed is characterized by lower hydraulic gradients (Kiesel et al., 2010;
498 Pfannerstill et al., 2014), low altitude gradient (elevations range from 2 to 80 m), and

499 relatively smaller geographic location scale (with a size of 481 km²). Besides, as a
500 typical rural area, agricultural streams reduce retention time due to the alteration of
501 stream channels, which result in a low percentage of nutrient removal. Nevertheless,
502 in a large scale river basin, the phytoplankton composition and functional groups can
503 only be significantly explained by environment, not dispersal processes (Huszar et al.,
504 2015). On the other hand, species dispersal mechanisms imposed by the dendritic
505 structure stream networks can be evident at very small spatial extents (Göthe et al.,
506 2013). The River Treene has several tributaries in the catchment. The tributaries stand
507 with different landscape and scale, which lead to distinctive species composition and
508 abundance as well. In this study, we focused only on the mainstream of the river,
509 while following investigation will progress the species dispersal mechanisms by the
510 whole watershed scale.

511 The unexplained variation of phytoplankton community remained still very high (65%,
512 Fig. 6). Despite the three factors discussed above, some quite vital elements are not
513 included here due to some limitations. For example, light availability (Kirk, 1994),
514 dissolved reactive silica (Tavernini et al., 2011) as well as grazing from both
515 planktonic grazer (Kang et al., 2015) and benthic invertebrate filter-feeder (Rossetti et
516 al., 2009). The contribution of those components varies along the river continuum and
517 through the year. In many cases, the impacts of one are dependent on another. Water
518 discharge itself may produce changes on the physiochemical condition, and thus
519 affecting phytoplankton communities (Descy, 1993). An observation illustrated that

520 land use and lake use also potential drivers of phytoplankton biomass dynamics
521 (Borics et al., 2013). Therefore, either directly or indirectly factors, there are far more
522 potential contributors related to the riverine algal assemblages worth much concern.

523 **5. Conclusions**

524 In this study, the impact of hydrological regimes, physiochemical condition and
525 species dispersal on riverine phytoplankton along a lentic-lotic continuum was
526 analysed. The main outcomes are:

527 (1) Phytoplankton community in a lentic-lotic continuum catchment showed very high
528 spatial and temporal variations.

529 (2) The impacts of upper lake on downstream phytoplankton assemblages were
530 significant, especially for the first site (T02) after the lake. However, these effects
531 varied along with seasons and remained only to a relatively short distance in our
532 research area.

533 (3) RDA and Mantel tests showed that phytoplankton composition and dissimilarities
534 along the lentic-lotic continuum were shaped more by local hydrological and
535 physiochemical variables than species dispersal factors, which confirmed the
536 suitability of lowland phytoplankton-based bioassessment. However, upstream lake
537 impacts should be taken into consideration in future biomonitoring campaigns.

538 (4) The flow regime has been proved as a key driver for local phytoplankton
539 community patterns and regional beta diversity, although its relative importance
540 showed seasonal variations. Further examination on the flow alteration in a finer
541 resolution will gain a deeper understanding of the roles of hydrological condition in
542 structuring phytoplankton communities.

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