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13 **Functional diversity supports the biomass-diversity humped-**
14 **back relationship in phytoplankton assemblages**

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27

28 **Summary**

29
30 1. Modelling the relationship between biomass and diversity in phytoplankton
31 assemblages provides new insights into the mechanisms responsible for the
32 coexistence of species, even in terrestrial ecosystems.

33
34 2. We tested the biomass-diversity relationship in lake phytoplankton along a wide
35 biomass gradient using functional species groups. We hypothesized that changes in
36 the taxonomic diversity of the phytoplankton along a biomass gradient are associated
37 with altered functional diversity.

38
39 3. For the analyses, in total 768 samples were collected from 30 oxbows, reservoirs
40 and lakes in the Hungarian Lowland Region and analysed between 1992 and 2002.
41

42 4. We found that the diversity and also the number of functional species groups
43 showed a humped-back curve similar to the species richness. The changes in
44 functional group composition act as a good proxy for phytoplankton species
45 responses. We found that the peak of the number of strategy groups and their Shannon
46 diversity was at a much lower biomass than that of species richness.

47

48 5. We revealed the fine-scale effects of increasing the dominance of respective species
49 or species groups with increasing biomass. This increase was well reflected by the
50 changes in the functional characteristics: first, the species evenness; then, the Shannon
51 diversity; and finally, the species richness started to decrease with increasing biomass.

52

53 6. Cyanoprokaryota were positively correlated with increasing biomass and negatively
54 with the increase in species richness; thus, the high increase both in their abundance
55 and biomass can be responsible for the abruptly decreasing part of the humped-back
56 curve.

57

58 7. We detected a humped-back curve between biomass and diversity, where the peak
59 compared to terrestrial plant communities tended to be towards high biomass scores,
60 that is, greater than 60% instead of the 20 to 60% of the biomass range typical for
61 terrestrial plant communities. Marked differences in the structural and dynamic
62 features of phytoplankton assemblages and terrestrial plant communities are likely
63 responsible for this difference.

64

65 **Key-words** algae, species richness, functional redundancy, ecological strategy,
66 unimodal curve, functional strategies, humpback model

67

68

69 **Introduction**

70

71 Species richness and biomass production in natural communities has been a focus of
72 interest for decades. One model that describes this relationship is the humped-back
73 model, proposed by Grime (1973) for terrestrial plant communities. According to this
74 model, a humped-back or unimodal relationship exists between the species richness
75 and biomass along a wide gradient of biomass (Graham & Duda 2011). At the
76 ascending part of the curve, species richness is increasing, likely because of the
77 increasing amount of nutrients, the decreasing rate of stress or by the facilitative
78 interactions between the constituting species (Michalet et al. 2006, Grime & Pierce
79 2012). In contrast, at the descending part of the curve at high biomass, the species
80 richness is decreasing because of the increasing dominance of a few, generally strong
81 competitor species that are favoured by an increase in nutrients, an increased rate of
82 disturbance or by other biotic interactions (Michalet et al. 2006, Kelemen et al. 2013;
83 Šímová, Li & Storch 2013; Skácelová & Lepš 2014). The highest species richness is
84 in the mentioned model at an intermediate level of biomass because of the
85 intermediate levels of stress and/or disturbance and biotic interactions (Michalet et al.
86 2006, Pierce 2014). In terrestrial herbaceous communities, high species richness at an
87 intermediate biomass is also associated with high variance in functional traits and a
88 high diversity of plant strategies (Cerabolini et al. 2014).

89

90 Modelling the relationship between biomass and species richness in phytoplankton
91 assemblages provides new insights into the mechanisms responsible for the
92 coexistence of species. The analogues and/or similarities between the phytoplankton
93 and terrestrial plant communities help with the elucidation of the dynamics and
94 mechanisms supporting diversity. Until now, the literature of the relationship of
95 species richness and biomass was dominated by papers reporting studies of terrestrial
96 plant communities (Mittelbach et al. 2001; Michalet et al. 2006; Graham & Duda
97 2011). The study of production and diversity in phytoplankton assemblages dates
98 back at least to the ground-breaking work of Hutchinson (1961), which was dedicated
99 to issues of competitive exclusion and coexistence. After Hutchinson's pioneering
100 work, only a few papers reported studies focusing on the biomass-richness gradients
101 in phytoplankton. However, more than two decades later, Brown (1981) emphasized
102 that this neglected aspect of ecology may hamper a better understanding of
103 community organisation and mechanisms governing the maintenance of diversity. In
104 the review by Waide et al. (1999), there were 3 papers, and in the most
105 comprehensive review, which was by Mittelbach (2001), there were 6 out of 171
106 papers focusing on the biomass-species richness relationship in phytoplankton
107 assemblages. In the last decade, the number of papers dealing with this topic increased
108 rapidly (for example Passy & Legendre 2006; Korhonen et al. 2011; Borics et al. 2012
109 and 2014; and Skácelová & Lepš 2014). Most of the papers revealed a humped-back
110 relationship between biomass (or production) and species richness of phytoplankton

111 assemblages from the local up to the regional scale (for example, Leibold 1999;
112 Dodson et al. 2000; Irigoien, Huisman & Harris 2004; Passy & Legendre 2006;
113 Spatharis et al. 2008); however, a functional analysis of this phenomenon for
114 phytoplankton is still lacking.

115

116 The use of functional classifications based on various criteria (morphological,
117 physiological, or behavioural) has become common in ecological research. The
118 functional approach enables (i) the comparison of habitats with quite different species
119 compositions; (ii) the generation of generalisations about dynamic changes in
120 ecosystems caused by altered management, natural disturbance regimes or climate
121 change; (iii) the ease of use in assemblages with a high number of taxa; and (iv) in the
122 case of taxonomically problematic groups, easier classification than the taxonomic
123 approach (Grime et al. 2007, Grime & Pierce 2012, Salmaso et al. 2015). The
124 phytoplankton is a polyphyletic, extremely species-rich and morphologically variable
125 group consisting of photosynthetic prokaryotic and eukaryotic organisms (Salmaso et
126 al. 2015). In phytoplankton ecology, various functional classification systems have
127 been developed (functional groups: FG, morpho-functional groups: MFG,
128 morphologically based functional groups: MBFG) or adapted (C-S-R strategies) based
129 on morphological and functional traits. An excellent overview of the functional
130 classification systems was provided recently by Salmaso et al. (2015). Phytoplankton
131 can be classified using criteria ranging from purely morphological and structural
132 criteria (MBFG) to phenologically and functionally driven criteria (FG). While the
133 functional approaches are increasingly involved both in theoretical (Borics et al.
134 2012) and applied studies in studying phytoplankton assemblages (Várbíró et al.
135 2007; Borics et al. 2007; Stankovich et al. 2012; Abonyi et al. 2014), they have been
136 poorly used in analysing diversity-biomass relationships until now.

137

138 In our study, we tested the biomass-diversity relationship for lake phytoplankton
139 along a wide biomass gradient using functional species group analyses based on a
140 high number of samples. We hypothesised that changes in the taxonomic diversity of
141 phytoplankton along a biomass gradient are associated with similar changes in
142 functional diversity, as determined by various functional classification systems (FG,
143 MFG, MBFG and CSR). We specifically asked the following questions: (i) How are
144 the diverse phytoplankton strategies related to increasing biomass? (ii) Can the
145 decreasing diversity and richness of phytoplankton communities at high biomass be
146 associated with the decreasing diversity in phytoplankton strategies? (iii) How are the
147 relationships between biomass and species richness in phytoplankton assemblages
148 related to the relationship of these figures studied in terrestrial plant communities?

149

150 **Materials and methods**

151

152 *Phytoplankton data*

153

154 For the analyses, phytoplankton data stored in the Hungarian national water quality
155 monitoring system were used. Altogether, 768 samples were collected in 30 eutrophic
156 and hypertrophic oxbows, reservoirs and lakes in the Hungarian Lowland Region
157 between 1992 and 2002 (Appendix S1). Sampling was conducted for the entire year,
158 but more frequent sampling was done in the growing season from April to September
159 (543) than in the dormant one (225). Samples were collected from the photic layer
160 ($2.5 \times$ Secchi depth) of the deepest part of the lakes, integrating all the euphotic zone
161 into one sample. In shallow lakes ($Z_{\max} < 2$ m), the whole water column was
162 sampled. Phytoplankton samples were fixed with Lugol's solution in the field. A
163 minimum of 400 settled units (cells, filaments or colonies) was counted using
164 Utermöhl's standard settling procedure (Lund et al., 1958, Utermöhl et al. 1958).
165 Phytoplankton was identified to the species level. Specimens were identified and
166 counted by two co-working specialists (Borics G, T-Krasznai E). The biomass of the
167 phytoplankton was used as a proxy for production. Specific volumes, estimated by
168 appropriate geometric forms for each taxon, were used to count the bio-volume of the
169 phytoplankton taxa (Hillebrand, Dürselen & Kirschtel 1999). Phytoplankton biomass
170 was calculated from the average cell bio-volumes for each taxa, assuming a
171 phytoplankton specific gravity of 'one'. Water samples were kept at 4 °C until
172 laboratory processing. For a proportion of the samples, data were provided for the
173 total nitrogen (TN; 297 samples), total phosphorus (TP; 339), total suspended solids
174 (TSS; 351) and for the Secchi depth (97). Hungarian national guidelines were used to
175 collect the TN (summarised the amounts of the different nitrogen forms), TP
176 (measured by the acid molybdate method) and TSS data (measured by the gravimetric
177 method).

178

179 *Data analysis*

180

181 To facilitate study of their functional diversity, the species were assigned to
182 phytoplankton functional classifications: (i) CSR-strategy (Grime 1977 adapted by
183 Reynolds 1988, 2006); (ii) functional groups (FG, Reynolds et al. 2002; Padisák et al.
184 2009); (iii) morpho-functional groups (MFG) (Salmaso & Padisák 2007); and
185 (iv) morphologically based functional groups (MBFG) (Kruk et al. 2010). The
186 classification of all taxa was possible in FG, and with exception of species in codon V
187 (i.e., purple and green sulphur bacteria), classification into the CSR, MFG and MBFG
188 functional groups was possible (see Appendix S2A-D for a detailed explanation of the
189 functional classifications). Curves were fitted using the polynomial peak 'Lorentzian
190 3 parameter' and the 'Nonlinear four parameter Logistic Curve' (Fig. 1C) functions of
191 the graphic software SigmaPlot 12 (Systat Inc., Chicago, IL, USA). Spearman rank-
192 correlation was used to analyse the relationship between the available environmental

193 parameters and the biomass (Zar 1999). Canonical Correspondence Analysis (CCA)
194 was applied to explore the relationship between functional species groups, species
195 richness and biomass using CANOCO 4.5 program package (Lepš & Šmilauer 2003).
196 We calculated a CCA using the biomass-weighted species composition (main matrix)
197 and biomass-weighted functional groups, species richness and total biomass (as an
198 overlay). For all CCAs, we tested whether the detected pattern is significantly
199 different from random (Monte-Carlo permutation test; in the full model, the number
200 of permutations were set to 1,000). Species richness and the Shannon diversity were
201 used as measures of diversity (Zar 1999).

202

203 **Results**

204 We analysed 768 phytoplankton samples. Altogether, 896 phytoplankton taxa were
205 found in the samples; the highest number of species in a sample was 73. Altogether,
206 797 taxa were identified at the species level (89%), 98 taxa at the genus level and 1
207 taxon at the order level (Centrales). The biomass ranged six orders of magnitude from
208 3.79×10^{-4} to 640.46 mg L⁻¹. The biomass correlated positively with the amount of TP
209 and TSS (Spearman rank-correlation, $p < 0.001$, $R = 0.216$ and $p < 0.001$, $R = 0.184$,
210 respectively), and negatively with the Secchi depth ($p = 0.009$, $R = -0.264$). No
211 significant correlation was found between the biomass and the TN ($p = 0.356$,
212 $R = 0.054$).

213

214 We detected an asymmetric humped-back curve between biomass and species
215 richness, where the peak of the curve tended to be towards rather high biomass scores
216 (17.76 mg L⁻¹, Tab. 1, Fig. 1A). Also, a similar curve was detected for the Shannon
217 diversity (Tab. 1, Fig. 1B). A sharp decline in both species richness and Shannon
218 diversity was typical at a relatively high biomass (75.1% and 59.9% of the whole
219 range of biomass, respectively, Fig. 1A-C). We found that the evenness, in contrast to
220 species richness and diversity, did not display a humped-back curve. The evenness
221 remained more or less constant until 1.08 mg/L biomass, and then, a continuous
222 decrease was detected (Fig. 1C). Similarly, a hump-shaped curve was detected for
223 samples collected in the growing and dormant season (not reported in the paper); thus,
224 we worked with pooled datasets. Lower species numbers were typical in the dormant
225 season (up to a maximum of 63 taxa) compared to the growing season (up to 73
226 species).

227

228 The relationship between the diversity of functional groups (FG, MFG, MBFG and
229 CSR) and biomass could also be described by a hump-shaped curve. The maxima and
230 the shape of the curves were very similar regardless of the type of the functional
231 classification. The peaks of the curves were at lower biomass scores than the peaks of
232 the biomass-species richness curves (Fig. 2A-D, Tab. 1). Diversity of the functional
233 groups showed a significantly positive correlation with each other ($p < 0.001$; R scores
234 ranged between 0.86 and 0.95), which is also indicated by the very similar shape of
235 the curves in Fig. 2A-D.

236

237 The relationship between the number of functional groups and the biomass was
238 possible to analyse in the case of the two functional classifications containing the
239 highest number of groups (FG and MFG, 30 and 29 groups, respectively, Appendix
240 S2). The number of the functional groups also showed a humped-back curve, but the
241 maxima of the curves were at an intermediate position between that of the Shannon
242 diversity curves (both overall and functional classifications) and species richness
243 along the biomass gradient (Fig. 1 and Fig. 3, Tab. 1).

244

245 For the FG overlay, the Monte-Carlo permutation test was significant for the first
246 (eigenvalue = 0.820, $F = 13.012$, $p = 0.049$) and for all canonical axes (Trace = 9.869,
247 $F = 6.081$, $p = 0.001$). For the MFG overlay, the Monte-Carlo permutation test was
248 significant both for the first (eigenvalue = 0.816, $F = 12.967$, $p = 0.0015$) and all
249 canonical axes (Trace = 9.324, $F = 5.853$, $p = 0.001$). For the CSR overlay, the
250 Monte-Carlo permutation test was significant for the first (eigenvalue = 0.752, $F =$
251 12.326 , $p = 0.007$) and for all canonical axes (Trace = 2.70, $F = 6.595$, $p = 0.001$). For
252 the MBFG overlay, the Monte-Carlo permutation test was significant for the first
253 (eigenvalue = 0.762, $F = 12.453$, $p = 0.004$) and for all canonical axes (Trace = 3.519,
254 $F = 6.793$, $p = 0.001$). In the CCA, most species of Chlorococcales (FG: J; MFG: 11a,
255 MBFG: IV) and the shade-tolerant and moderately shade-tolerant cyanoprokaryotes
256 (e.g., planktic Oscillatoriales - FG: S1, MFG: 5a, MBFG: III-IV; Nostocales -
257 characteristic species *Cylindrospermopsis raciborskii* - FG: SN, MFG: 5e, MBFG: III,
258 in CSR both S strategists) showed a relatively high positive correlation with
259 increasing biomass. The cyanoprokaryotes were also negatively correlated with the
260 species richness (Tab. 2). In contrast, the biomass of some species groups requiring
261 clear (oligotrophic) water and sensitive to the increase in pH (centric diatoms, FG: A),
262 or characteristic of small- and medium-sized eutrophic waters and sensitive to the
263 onset of stratification (mostly centric diatoms, FG: C) tended to increase with the
264 increase in species richness. The biomass of stratification-tolerant medium- to large-
265 sized flagellates (Dinophytes, FG: L₀, MFG: 1b, MBFG: V), or stratification-sensitive
266 small flagellates (Chrysophytes and Haptophytes, MFG: 2a), pennate diatoms and
267 conjugatophytes (FG: P; MFG: 9a) was also increased with the increase in species
268 richness (Tab 2).

269

270 **Discussion**

271

272 *Biomass and species composition*

273

274 The humped-back is the most commonly observed relationship between biomass and
275 diversity from the local to regional scale (Waide et al. 1999; Mittelbach et al. 2001;
276 Michalet et al. 2006). This phenomenon might be especially true for aquatic
277 ecosystems (Stomp et al. 2011, Korhonen et al. 2011). We detected a humped-back
278 relationship between the biomass and diversity of the phytoplankton assemblages,

279 well in line with the findings of Stomp et al. (2011) and Skácelová & Lepš (2014) for
280 oligotrophic lakes. We emphasize, however, in line with Borics et al. (2014), that the
281 formation of a humped-back curve is strongly habitat and/or trophic-state dependent.
282 The peak of species richness detected in our study for eutrophic/hypertrophic water
283 bodies was at a much higher biomass than found by Skácelová & Lepš (2014) in
284 oligotrophic lakes (in the latter at 10^7 - $10^8 \mu\text{m}^3 \text{mL}^{-1}$ - which corresponds with 10^{-2} - 10^{-1}
285 mg L^{-1} ; compared to the 17.76 mg L^{-1} found in this study). We should also stress
286 that in the mentioned study, the peak was also at rather high biomass scores compared
287 to the studied range of the biomass.

288

289 We could reveal the fine-scale effects of increasing dominance of respective species
290 or species groups with increasing biomass. This was likely responsible for the
291 formation of the decreasing part of the humped-back curve. This increase was well
292 displayed by the changes of functional characteristics in Fig. 1. First, the species
293 evenness; then, the Shannon diversity; and finally, the species richness started to
294 decrease with increasing biomass. The species evenness remained almost constant to a
295 biomass of 1.08 mg L^{-1} , then a continuous decrease was detected with increasing
296 biomass. The Shannon diversity had a peak at 2.00 mg L^{-1} , whereas the species
297 richness had its peak at 17.76 mg L^{-1} in our study (Tab. 1). Skácelová & Lepš (2014)
298 assumed that the first sign of the increasing dominance of a competitor species is the
299 decrease in evenness, which was clearly demonstrated in our study. Hillebrand et al.
300 (2008) also demonstrated that evenness and the performance of the dominant species
301 are strongly related ecosystem functions. The decrease of evenness in many cases
302 signals the increasing dominance of a respective species very early before the
303 increased dominance leads to the decline of important functions or leads to the
304 decrease of species richness (Hillebrand et al. 2008).

305

306 At least one order of magnitude increase in biomass between the start of the abrupt
307 evenness and the species richness peak; thereafter, the species richness tended to
308 decrease rapidly. Therefore, in phytoplankton assemblages, a relatively high threshold
309 of species richness exists. That is, the disappearance of a respective species or
310 functional group is only feasible at a relatively high biomass. This threshold was also
311 supported by studies where, without having samples with extremely high biomass, a
312 positive linear relationship was found between biomass and diversity in
313 phytoplankton assemblages (Eloranta 1993; Agard et al. 1996; Korhonen et al. 2011).

314

315 *Biomass, species richness and phytoplankton strategies*

316

317 Some studies have observed that the relationship between biodiversity and production
318 in relation to ecosystem functioning is strongly determined by the functional
319 characteristics of the constituent species (Cadotte et al. 2011; Grime & Pierce 2012;
320 Hooper et al. 2012). Phytoplankton is an extremely species-rich, morphologically
321 variable and polyphyletic group, consisting of both photosynthetic prokaryotic and
322 eukaryotic organisms (Salmaso et al. 2015). Thus, during its evolution, well-

323 developed resource and niche partitioning developed and is expressed very well in the
324 distinct morphological, physiological and ecological attributes of the phytoplankton.
325 This high diversity is well displayed by the analysed phytoplankton functional
326 classifications. In our study, we found that the diversity and also the number of
327 functional species groups showed a humped-back curve (the analysis of the latter was
328 only feasible in the cases of FG and MFG groups, see Fig. 3), similar to the species
329 richness curve, which indicates that changes in the functional group composition can
330 act as a good proxy for phytoplankton species responses. The shape of the curve and
331 the position of the peak were quite similar for all studied functional classifications,
332 which underscore the robustness of the detected humped-back relationship. On
333 analysing the peaks of the Shannon diversity curves of the different classifications, we
334 found that the peaks of all functional classifications were at quite similar biomass
335 scores compared to the species diversity curve (Tab. 1). However, when we analysed
336 the number of categories in relation to the species richness, we found that the peak for
337 the number of strategy groups was at a lower biomass than the species richness
338 (Tab. 1 and Fig. 3). Notably, these results show that, despite the generally high
339 functional redundancy in phytoplankton assemblages, the functional redundancy
340 increased in some other functional groups (i.e., species richness of the respective
341 group increased), which provided a relatively high threshold for the species richness.
342 This was also well supported by the CCA results, where the biomass of the
343 stratification-tolerant medium- to large-sized flagellates, stratification-sensitive small
344 flagellates, pennate diatoms and conjugatophytes increased with the increase in
345 species richness.

346

347 In contrast, the Cyanoprokaryota groups (FG: S₁ and S_N) were positively correlated
348 with increasing biomass and negatively with the increase in species richness; thus, the
349 high increase both in their abundance and biomass can be considered responsible for
350 the abruptly decreasing part of the humped-back curve. These results are well in line
351 with the findings in phytoplankton assemblages that high biomass is often linked with
352 water blooms caused by a single (Borics et al. 2000) or limited number of species of
353 the above-mentioned species groups (Naselli-Flores et al. 2003; Borics et al. 2012).
354 Dominance of these species at high biomass can be explained by (i) the selective
355 grazing of the zooplankton (Watson et al. 1992; Leibold 1999; Dodson et al. 2000);
356 (ii) the increased competition for light and extreme abiotic conditions in highly
357 eutrophic lakes, both of which favour Cyanoprokaryota with high (even self-) shading
358 tolerance and low oxygen concentrations, especially in the night (Dodson et al. 2000;
359 Carey et al. 2012); (iii) high water temperature as one of the most important factors
360 regulating the life-cycle of phytoplankton (Litchman et al. 2010); and (iv) allelopathic
361 effects (Inderjit & Dakshini 1994; Legrand et al. 2003; Leflaive & Ten-Hage 2007;
362 Bácsi et al. 2013).

363

364 *Humped-shaped relationships in phytoplankton and terrestrial plant communities*

365

366 We found for phytoplankton assemblages, similarly to most findings in terrestrial
367 plant communities, that the biomass-species richness relationship showed a humped-
368 back curve, where the peak of the humped-back was at an intermediate biomass
369 (Fig. 1). Similar results were also reported for lake (Dodson et al. 2000; Stomp et al.
370 2011; Skácelová & Lepš 2014) and marine phytoplankton (Irigoinen et al. 2004;
371 Vallina et al. 2014). Interestingly, compared to the hump-shaped curves detected in
372 the terrestrial plant communities (see for example Kelemen et al. 2013; Pierce 2014;
373 or Cerabolini et al. 2014), the maxima of the humped-back curves in the
374 phytoplankton assemblages were at rather high scores within the studied range of the
375 biomass (Stomp et al. 2011; Borics et al. 2014; Skácelová & Lepš 2014 and in our
376 study). The peaks of the humped-back curves were typically situated at 20-60% of the
377 studied range of the biomass in the terrestrial plant communities (Cornwell & Grubb
378 2003), whereas, they were regularly higher than 60% of the biomass for
379 phytoplankton (in Irigoinen et al. 2004; Skácelová & Lepš 2014 and also in the
380 present study). The highly asymmetrical shape of the curve (a long ascending part and
381 a quite short and sharp descending part) detected in the phytoplankton assemblages in
382 most studies (See for example Stomp et al. 2011, Irigoinen et al. 2004, Skácelová &
383 Lepš 2014 and in the present study) can be explained with the marked differences in
384 the structural and dynamic features of the terrestrial plant communities and
385 phytoplankton assemblages as listed below and explained in detail:

386

387 (i) The species coexistence in terrestrial plant communities is spatially more strictly
388 coordinated than in phytoplankton assemblages. This was also supported by
389 succession studies in which it was found that the species turnover rapidly decreases if
390 the lifetimes of the constituent organisms increase (Lepš et al. 1982; Török et al.
391 2008) and the community species composition becomes relatively stable. Several
392 theories explain the species coexistence in phytoplankton assemblages. These theories
393 date back to Hutchinson (1961), who argued that the coexistence of a high number of
394 species is supported by the finding that the formation of a single equilibrium state is
395 unlikely in phytoplankton assemblages and the lack of spatially coordinated structure
396 and patterns between species prevents a formation of spatially stable interactions that
397 generally support competitive exclusion (i.e., by rapid fluctuations in weather and
398 nutrient availability, Scheffer et al. 2003). We can see a high fluctuation in species
399 richness in our dataset along the whole studied biomass gradient, and this fluctuation
400 is rather typical for all studied production-species richness relationships in
401 phytoplankton assemblages (e.g., Irigoinen et al. 2004; Ptacnik et al. 2008; Skácelová
402 & Lepš 2014) - even in those few studies where no humped-back curve was detected
403 (Korhonen et al 2011). The most likely explanation of this could be the presence of
404 multiple alternative semi-stable states of phytoplankton assemblages that are mediated
405 by rather random patterns of dispersal events, nutrient loads and biotic interactions (as
406 also suggested by Chase 2010; Korhonen et al. 2011; and Skácelová & Lepš 2014).
407 The neutral theory of species assembly (in the sense of Hubbel 2008) is also a likely
408 explanation of the highly positioned peak. This theory states that, in spite of the
409 relatively limited number of self-organised functional groups of species in a

410 respective habitat, a theoretically unlimited number of equivalent species exist within
411 the groups, which can coexist neutrally (Jamil et al. 2014) or replace each other (in
412 sense of functional redundancy) in a rather patchy abiotic and biotic environment.
413 This latter theory was also supported by our findings. For example, we detected the
414 loss of some functional groups prior to the decrease in species richness (i.e., the
415 decrease in richness by the loss of some groups was likely compensated by the
416 increase in species richness in the remaining functional groups resulting in a high
417 functional redundancy). These facts could potentially explain the high diversity and
418 richness detected at rather high biomass scores in the phytoplankton assemblages.

419

420 (ii) Most terrestrial plant communities are characterised by perennial sessile
421 organisms, with the exception of the initial stage of the development (i.e., initial stage
422 of succession characterised by pioneers or short-lived ruderals), or highly stressed
423 communities (i.e., some semi-deserts and deserts or hyper-saline vegetation). During
424 succession, the immigrating perennial species stabilise both the spatial and the
425 temporal community structure. Thus, high species richness in terrestrial plant
426 communities is often dependent on frequent anthropogenic or abiotic/biotic
427 disturbance events (Pierce 2014).

428

429 (iii) Finally, in terrestrial plant communities, the development of a humped-back
430 relationship between diversity and biomass also was found to be regulated by the
431 accumulation of dead plant material (litter), as demonstrated by Kelemen et al. (2013).
432 Such an accumulation is generally not an issue in phytoplankton assemblages.

433

434 *Conclusions*

435

436 We noted that functional diversity reflects the changes detected in species diversity in
437 phytoplankton assemblages, similarly to the findings of studies in terrestrial
438 vegetation. The similar shape of the diversity-productivity relationship and the
439 positions of the peaks in the functional and species diversity suggest that decreased
440 species diversity is strongly linked with the declining variability in the functional
441 strategies. We demonstrated that when considering the biomass/diversity
442 relationships, remarkable differences exist between the terrestrial vegetation and
443 phytoplankton assemblages. Thus, to give a unified explanation of species coexistence
444 and to explain the relationship between functional and species diversity, not only a
445 multi-taxa approach but the joint study and evaluation of terrestrial and aquatic
446 systems should be involved. Our findings also suggest that the contribution of the
447 underlying mechanisms responsible for the observed patterns might be different.
448 When applying a functional approach, considerable simplification can be made, but an
449 understanding of the fundamental processes responsible for species coexistence and a
450 unified explanation require a joint study and evaluation of these structurally highly
451 different systems. We stress the importance of using a functional approach for
452 understanding aquatic systems, and the proliferation of this approach will generate

453 further prospects for understanding biomass-diversity relationships and the
454 organization of aquatic ecosystems.

455

456

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461 15/1/KONV-2015-0001 programs.

462

463 **Data Accessibility**

464 The geo-coordinates of the sampled lakes and reservoirs and the detailed groups of
465 functional classifications of phytoplankton can be found in the supporting
466 information.

467

468 **Supporting Information**

469 Appendix S1 Sampled lakes and reservoirs

470 Appendix S2 A-D Phytoplankton strategies

471

472 **References**

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697 **Tab. 1** Maxima of the regression curves displayed in Fig. 1-3. Notations: Biomass
698 B% = location of the peak along the biomass gradient (expressed in the percentage of
699 the whole gradient). *= biomass-weighted. For evenness, the 'break-down' point is
700 reported. Functional groups: FG (Reynolds, 2002 and Padisák et al. 2009), Morpho-
701 functional groups: MFG (Salmaso & Padisák 2007), Morphologically based
702 functional groups: MBFG (Kruk et al. 2010), C-S-R-strategy types: CSR (based on
703 Reynolds 1988, 2006). For the detailed explanation of the classifications, see
704 Supporting Information S1A-D.
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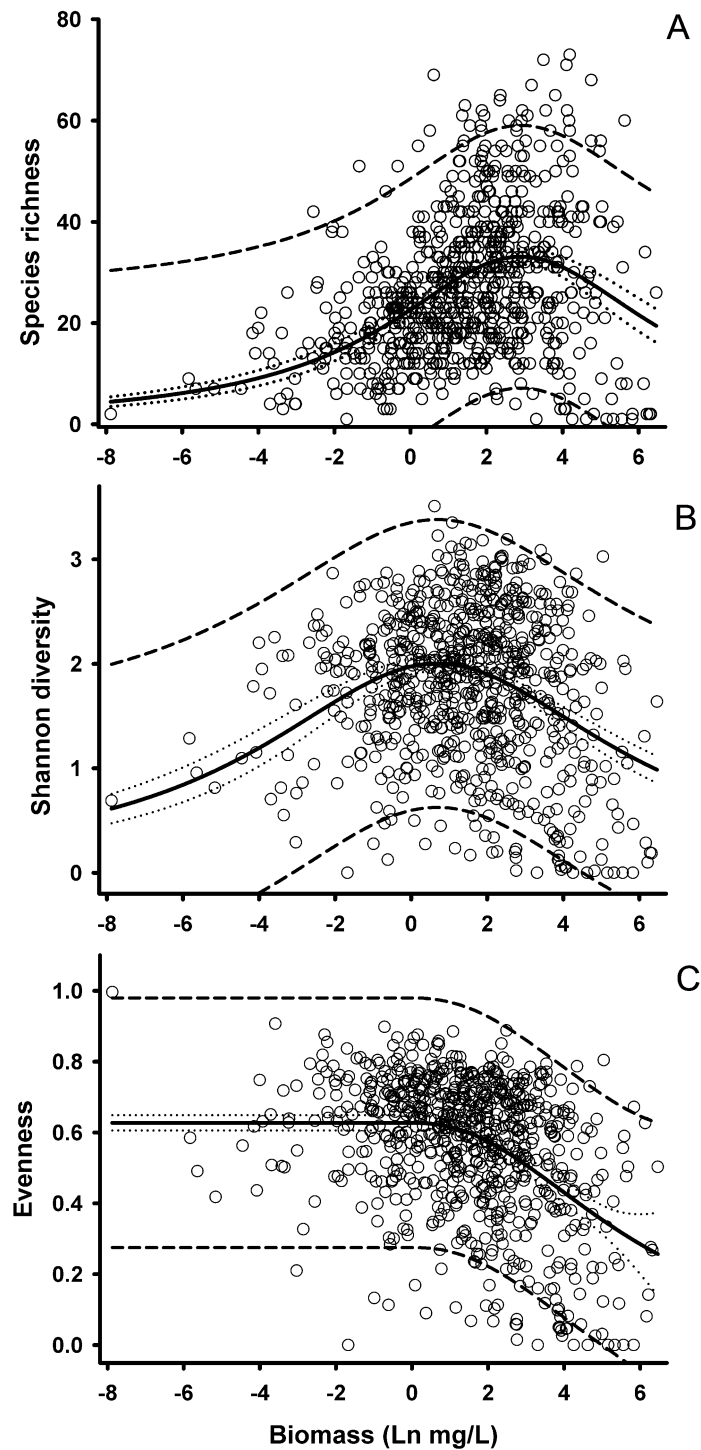
| Characteristic | Maximum | Biomass (mg L⁻¹) | B% |
|-----------------------------|----------------|------------------------------------|-----------|
| Species composition | | | |
| Number of species | 33.11 | 17.76 | 75.1 |
| Shannon diversity* | 2.003 | 2.00 | 59.9 |
| Evenness* (Shannon) | 0.627 | 1.08 | 55.6 |
| Functional richness | | | |
| Number of FG groups | 12.968 | 10.73 | 71.6 |
| Number of MFG groups | 13.485 | 12.00 | 72.4 |
| Functional diversity | | | |
| Shannon FG* | 1.458 | 2.36 | 61.1 |
| Shannon MFG* | 1.498 | 2.30 | 60.9 |
| Shannon MBFG* | 0.911 | 3.60 | 64.0 |
| Shannon CSR* | 0.997 | 2.11 | 60.3 |

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707

708 **Tab. 2** Correlation matrix of the total biomass, species richness and respective
709 functional groups calculated by a CCA ordination based on the biomass-weighted
710 species composition (main matrix) and biomass-weighted functional groups, species
711 richness and total biomass (overlay). High correlation scores were marked with
712 **boldface** ($|R| \geq 0.2$). Notations: Biomass = Total biomass, SR = species richness.
713 Functional groups: FG (Reynolds, 2002 and Padisák et al. 2009), Morpho-functional
714 groups: MFG (Salmaso & Padisák 2007), Morphologically based functional groups:
715 MBFG (Kruk et al. 2010), C-S-R-strategy types: CSR (based on Reynolds 1988,
716 2006). For detailed explanation of the classifications, see Supporting Information S1.
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| | Biomass | SR | | Biomass | SR | | Biomass | SR |
|-----------------------|----------------|----------------|------------|----------------|----------------|------------|----------------|----------------|
| | FG | | | MFG | | | CSR | |
| A | -0.0857 | 0.2320 | 1a | -0.0543 | 0.0355 | C | 0.1604 | 0.0804 |
| B | 0.0063 | 0.0241 | 1b | 0.0001 | 0.4449 | CS | 0.2476 | 0.0943 |
| C | -0.0446 | 0.2131 | 1c | 0.1654 | -0.0444 | CSR | 0.1445 | 0.0541 |
| D | -0.0846 | 0.1361 | 2a | -0.0235 | 0.2121 | R | 0.2711 | -0.0299 |
| E | -0.0727 | 0.0770 | 2b | 0.1589 | 0.0299 | S | 0.7298 | -0.6358 |
| F | -0.0337 | 0.0960 | 2c | 0.0481 | 0.0641 | | | |
| G | -0.0599 | 0.0131 | 2d | -0.1993 | 0.1459 | | | |
| | | | | | | | MBFG | |
| H1 | 0.0540 | -0.0121 | 3a | -0.0523 | 0.0710 | I | 0.0110 | 0.0988 |
| J | 0.2503 | 0.0927 | 3b | -0.0612 | 0.0129 | II | -0.0702 | 0.0859 |
| K | 0.0213 | 0.0775 | 4 | -0.0671 | 0.0653 | III | 0.6938 | -0.6799 |
| L_M | -0.0402 | 0.0626 | 5a | 0.4411 | -0.4059 | IV | 0.3266 | 0.0875 |
| L_O | 0.1350 | 0.2737 | 5b | 0.0335 | 0.1345 | V | 0.1622 | 0.2358 |
| M | 0.0339 | 0.1341 | 5c | 0.0120 | 0.0804 | VI | 0.0031 | 0.1872 |
| MP | 0.1348 | -0.0692 | 5d | 0.0378 | 0.0872 | VII | 0.0194 | 0.1760 |
| P | 0.0315 | 0.2191 | 5e | 0.6942 | -0.6821 | | | |
| Q | -0.0071 | 0.0043 | 6a | -0.0473 | 0.1808 | | | |
| S1 | 0.4177 | -0.3436 | 6b | 0.0308 | 0.0954 | | | |
| S2 | -0.0513 | 0.0067 | 7a | -0.0378 | 0.1780 | | | |
| S_N | 0.6799 | -0.6727 | 7b | -0.0538 | 0.0454 | | | |
| T | 0.0989 | 0.0822 | 8a | 0.0028 | 0.0761 | | | |
| U | -0.0192 | 0.0581 | 8b | 0.0848 | 0.1637 | | | |
| V | -0.0347 | 0.1450 | 9a | -0.0667 | 0.2759 | | | |
| W1 | 0.1642 | -0.0368 | 9b | -0.0440 | 0.1373 | | | |
| W2 | -0.0031 | 0.0346 | 9d | -0.0138 | 0.0322 | | | |
| W_S | -0.0580 | 0.0071 | 10a | 0.0989 | 0.0823 | | | |
| X1 | 0.1638 | 0.0373 | 10b | -0.0434 | 0.0807 | | | |
| X2 | -0.0727 | 0.0849 | 11a | 0.2975 | 0.0933 | | | |
| X3 | -0.0177 | -0.0053 | 11b | -0.0513 | 0.0840 | | | |
| Y | -0.1580 | 0.1345 | 11c | -0.0386 | 0.1438 | | | |
| Y_{Ph} | 0.0511 | 0.1309 | | | | | | |

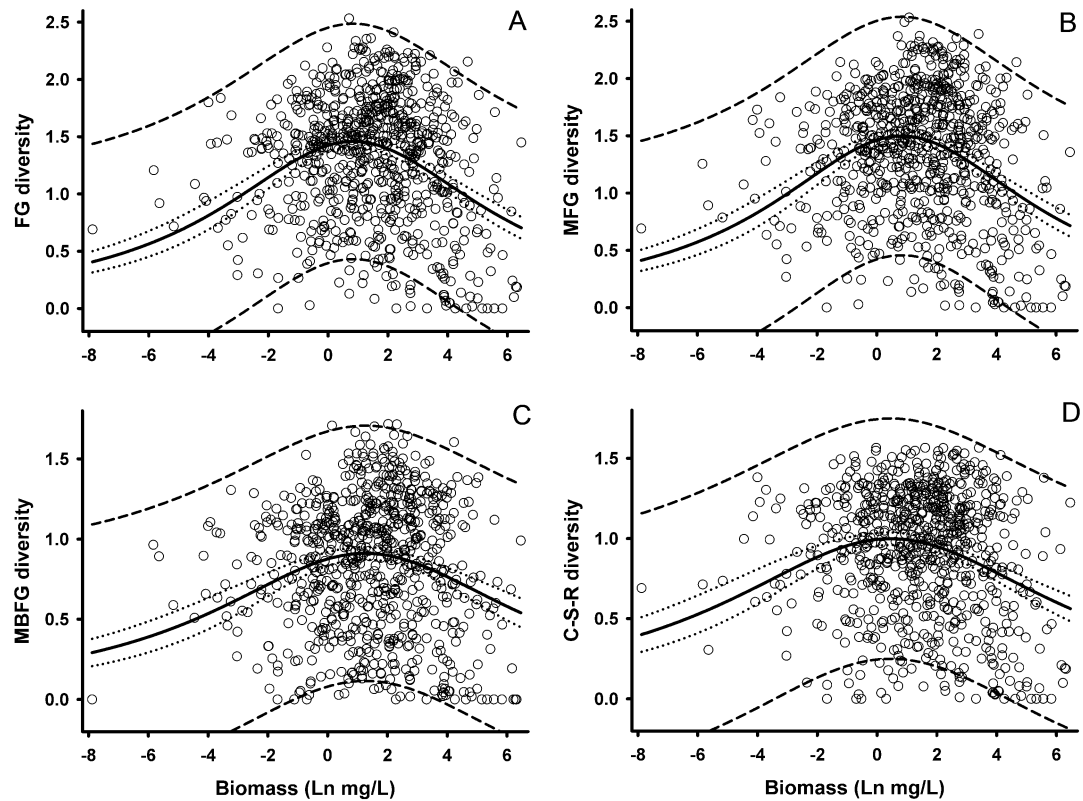
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720 **Fig. 1** Relationship between the biomass and species richness (A), Shannon diversity
 721 (B) and evenness (C). Shannon diversity and evenness was calculated using biomass-
 722 weighted species lists. Curves were fitted using the polynomial peak 'Lorentzian 3
 723 parameter' (A and B) and the 'Nonlinear four parameter Logistic Curve' (C) functions
 724 of the graphic software SigmaPlot 12 (Systat Inc., Chicago, IL, USA). The *R* and *p*
 725 values for the fittings were A: 0.41 and <0.001, B: 0.33 and <0.001, and C: 0.42 and
 726 <0.001, respectively. Solid lines represent fitted curves; dotted lines, 95% confidence
 727 bands; and dashed lines, 95% prediction bands.

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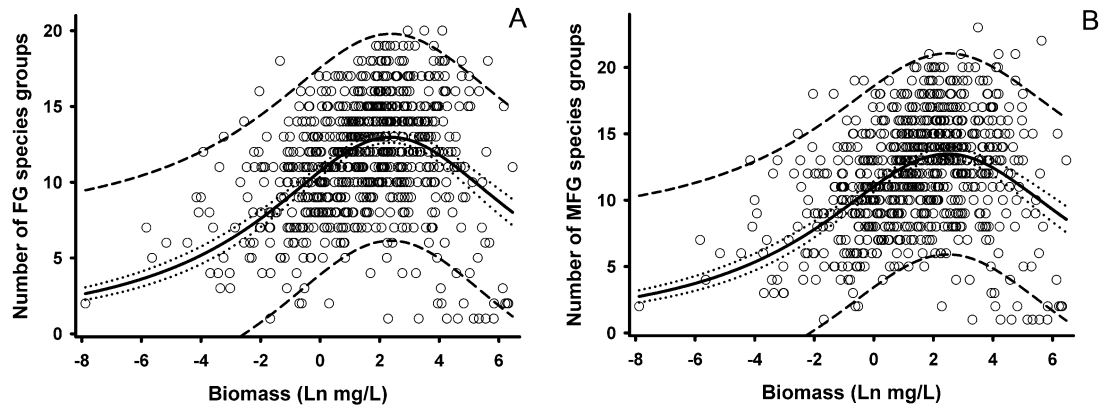


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730

731 **Fig. 2** Relationship between the biomass and the diversity of biomass-weighted
 732 phytoplankton functional classifications: FG (A), MFG (B), MBFG (C), and CSR (D).
 733 Functional groups: FG (Reynolds, 2002 and Padisák et al. 2009), Morpho-functional
 734 groups: MFG (Salmaso & Padisák 2007), Morphologically based functional groups:
 735 MBFG (Kruk et al. 2010), C-S-R-strategy types: CSR (based on Reynolds 1988,
 736 2006). For detailed explanation of the classifications, see Supporting Information S1.
 737 Curves were fitted using the polynomial peak ‘Lorentzian 3 parameter’ function of the
 738 graphic software SigmaPlot 12 (Systat Inc., Chicago, IL, USA). The *R* and *p* values
 739 for the fittings were A: 0.32 and <0.001, B: 0.33 and <0.001, and C: 0.21 and <0.001,
 740 D: 0.25 and <0.001, respectively. Other notations see Fig 1.

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Fig. 3 The relationship between biomass and the number of functional species groups. Only the two classifications with a high number of groups (FG: 30, MFG: 29) were considered for this analysis. Functional groups: FG (Reynolds, 2002 and Padisák et al. 2009), Morpho-functional groups: MFG (Salmaso & Padisák 2007). For detailed explanation of the classifications, see Supporting Information S1. Curves were fitted using the polynomial peak ‘Lorentzian 3 parameter’ function of the graphic software SigmaPlot 12 (Systat Inc., Chicago, IL, USA). The R and p values for the fittings were A: 0.44 and <0.001 , B: 0.42 and <0.001 , respectively. For other notations see Fig. 1.