

1 Individual-level trait diversity predicts phytoplankton community 2 properties better than species richness or evenness

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25 Abstract

26 Understanding how microbial diversity influences ecosystem properties is of paramount
27 importance. Cellular traits – which determine responses to the abiotic and biotic environment -
28 may help us rigorously link them. However, our capacity to measure traits in natural communities
29 has thus far been limited. Here we compared the predictive power of trait richness (trait space
30 coverage), evenness (regularity in trait distribution) and divergence (prevalence of extreme
31 phenotypes) derived from individual-based measurements with two species-level metrics
32 (taxonomic richness and evenness) when modelling the productivity of natural phytoplankton
33 communities. Using phytoplankton data obtained from 28 lakes sampled at different spatial and
34 temporal scales, we found that the diversity in individual-level morpho-physiological traits
35 strongly improved our ability to predict community resource-use and biomass yield. Trait
36 evenness - the regularity in distribution of individual cells/colonies within the trait space - was
37 the strongest predictor, exhibiting a robust negative relationship across scales. Our study suggests
38 that quantifying individual microbial phenotypes in trait space may help us understand how to
39 link physiology to ecosystem-scale processes. Elucidating the mechanisms scaling individual-
40 level trait variation to microbial community dynamics could there improve our ability to forecast
41 changes in ecosystem properties across environmental gradients.

42 **List of abbreviations:** TD = trait diversity; TOP = *trait onion peeling* index of trait richness
43 (Fontana *et al.*, 2016); TED = *trait even distribution* index of trait evenness (Fontana *et al.*,
44 2016); FDis = *functional dispersion* index of trait divergence (Laliberté and Legendre, 2010);
45 SFC = scanning flow-cytometry; TP = total phosphorus; PAR = photosynthetic active radiation;
46 FWS = light forward scattering; SWS = light sideward scattering; RUE = resource use efficiency
47 (*sensu* Ptacnik *et al.*, 2008), calculated here as [biomass / TP].

48 **Introduction**

49 Functional traits can help illuminate the relationship between biodiversity and ecosystem
50 processes (e.g. Norberg *et al.*, 2001; Norberg, 2004; Hillebrand and Matthiessen, 2009; Reiss *et*
51 *al.*, 2009). Most research in this area has thus far largely focused on taxonomic or phylogenetic
52 richness as measures of biodiversity (see reviews by Cardinale *et al.*, 2011 and Krause *et al.*,
53 2014). However, the importance of relative species densities for ecological processes has been
54 neglected (Mulder *et al.*, 2004; Hillebrand *et al.*, 2008; Zhang *et al.*, 2012), as well as the
55 functional redundancy or diversity of organisms (including intraspecific variation) that may
56 partially decouple the number of species from the functions supported by a community (Chase
57 and Leibold, 2003).

58 Traits, which are often analysed in terms of species mean values, may be better defined as the
59 features of *individual* organisms' phenotypes that determine fitness and life history (McGill *et al.*
60 2006 ;Violle *et al.*, 2007). They influence ecological interactions and dynamics (e.g. Bolnick *et*
61 *al.*, 2011; de Bello *et al.*, 2011; Violle *et al.*, 2012) and have important consequences for
62 population demography and ecosystem processes (Norberg, 2004; McGill *et al.*, 2006; Cadotte *et*
63 *al.*, 2011). Empirical evidence for the importance of individual trait variation for ecosystem
64 properties is still lacking, despite the fact that intraspecific trait variance contributes significantly
65 to plant community functional responses to environmental change (Siefert and Ritchie, 2016;
66 Volf *et al.*, 2016). The importance of intraspecific variation for explaining community properties
67 has mostly been explored theoretically in ecology (Bolnick *et al.*, 2011; Albert *et al.*, 2012;
68 Violle *et al.*, 2012; De Laender *et al.*, 2014; Barabás and D'Andrea, 2016; Hart *et al.*, 2016). We
69 expect that, for example, changes in trait diversity (TD) should reflect natural selection
70 mechanisms, which affect processes at all scales of community and ecosystem organization

71 (Matthews *et al.*, 2011). Additionally, competition for resources, predation, environmental
72 change and rates of mutation and plasticity will all affect individual phenotypes and consequently
73 TD within and between taxa, which will in turn influence population demography, community
74 dynamics and ecosystem properties (Norberg *et al.*, 2001). The link between individual-level TD
75 and large-scale processes is underexplored in real communities, particularly in microorganisms
76 (Gsell *et al.*, 2013; Ackermann, 2015; Schreiber *et al.*, 2016).

77 Individual-level traits in microbial assemblages have become easier to measure due to recent
78 technological developments (Shade *et al.*, 2009; Pomati *et al.*, 2011; Fontana *et al.*, 2014; Krause
79 *et al.*, 2014). Indices that quantify community TD using individual-level data (thereby integrating
80 inter- and intraspecific trait variation) have also been recently tested and developed (Fontana *et*
81 *al.*, 2016). Hereafter, we refer to them as ‘individual-level TD indices’ because, despite
82 quantifying community properties, they are calculated using traits measured on individual
83 organisms. These indices jointly describe the three independent components of TD (richness,
84 evenness and divergence, respectively): the *trait onion peeling* (TOP; Fontana *et al.*, 2016) index
85 is the sum of all successive convex hulls’ areas touching the individuals of a community in
86 multidimensional trait space, the *trait even distribution* (TED; Fontana *et al.*, 2016) index is the
87 regularity in the distribution of individuals when compared to a perfectly even reference
88 distribution, and the *functional dispersion index* (FDis; Laliberté and Legendre, 2010) is the mean
89 distance of individuals to the centroid of trait distribution. The TOP index has been successfully
90 applied to high-throughput individual-level data to study the role of phenotypic variation over
91 time in the adaptation of microbial populations to environmental perturbations (Krismer *et al.*,
92 2016). It reflects changes in the trait space coverage, which may happen as a consequence of
93 environmental filtering both within and at the edges of trait distribution. TED is related to the
94 reciprocal distances between neighbor individuals in the trait space and is likely to reflect biotic

95 interactions (Fontana *et al.*, 2016). FDis distinguishes communities where individuals are closer
96 to the centroid of the multidimensional trait distribution from communities where extreme
97 phenotypes are found (Fontana *et al.*, 2016).

98 In this study we focus on natural phytoplankton communities, whose diversity and dynamics are
99 tightly linked to large-scale biogeochemical processes. These microorganisms form the basis of
100 aquatic food webs and are responsible for almost 50% of total global primary production (Field *et*
101 *al.*, 1998). The TD metrics described above have allowed us to explore the relative strength of
102 individual-level trait variation and taxonomic diversity metrics (species richness and evenness),
103 as predictors of important ecosystem properties - phytoplankton community biomass and
104 resource use efficiency.

105 We studied these ecosystem properties in 28 lakes from two European regions (Switzerland and
106 Danube Delta, Romania), sampled at different temporal and spatial scales (Table S1). We related
107 these properties to the TD and taxonomic diversity metrics, while accounting for variation in
108 water chemistry and physics. This heterogeneity across sites allowed us to sample environmental
109 responses in terms of individual-level TD change or turnover of species, and their effects on
110 community properties. We used microscopy for classification of algal species and scanning flow-
111 cytometry (SFC) to estimate total biovolume (hereafter biomass) and morphological and
112 physiological traits measured on individual cells/colonies (Table 1, more details in
113 Supplementary Table S2). We tested all combinations of species richness, evenness, TOP, TED
114 and FDis using linear mixed-effects model averaging to quantify and compare their predictive
115 ability on biomass and resource-use efficiency, while controlling for environmental variables.

116 We expected that the inclusion of individual-level TD would improve the variance explained by
117 statistical models predicting phytoplankton productivity. In our SFC data, we cannot distinguish

118 between inter- and intraspecific trait variation because we are unable to classify cells into species
119 groups. Therefore, our assessment of the importance of intraspecific trait variation is only
120 indirect: if interspecific trait variation is more important in influencing ecosystem properties,
121 models including TD indices should not improve on those that incorporate species richness and
122 evenness. However, if intraspecific trait variation plays an important role, standard biodiversity
123 metrics will be poorer predictors of ecosystem properties than TD indices.

124 **Materials and methods**

125 **Phytoplankton communities at three study sites**

126 To test relationships between biodiversity indices and ecosystem properties, we used monitoring
127 data from three different lake systems, covering a wide range of temporal and spatial scales. Lake
128 Greifensee, Lake Zurich and Danube Delta (with 26 lakes), in this order, represent a gradient of
129 increasing sampling time span (3 months, 7 months, 2 years), decreasing sampling frequency
130 (weekly, monthly, seasonally) and increasing spatial scale (6 depths from 1m to 8.5m, 11 depths
131 from 0m to 40m, 26 lakes in a geographical region). All datasets include microscopy data
132 (phytoplankton classification, enumeration and biomass calculation) obtained using the Utermöhl
133 method (Utermöhl, 1931), as well as phytoplankton morphological and physiological traits
134 acquired by SFC, in addition to physical and chemical water parameters. Supplementary Table S1
135 summarizes the characteristics of the three lake systems.

136 In lake Greifensee (Switzerland), monitoring data were collected from a single location at the
137 North end of the lake by an automated system that integrates physical, chemical (Idronaut,
138 Brugherio, Italy, www.idronaut.it) and biological analyses (Pomati *et al.*, 2011). From the 31st of
139 July to the 24th of October 2014, SFC measurements were collected every four hours from
140 samples collected at six different depths (1, 2.5, 4, 5.5, 7 and 8.5 m). Additional chemical
141 analyses and microscopy measurements (to obtain species diversity metrics) were performed on
142 water samples collected manually at the same location, depths and time (average time interval
143 between successive samples = 58.3 h, standard deviation = 67.7 h). Total phosphorus (TP) and
144 total nitrogen (TN) were measured using DIN Standards (German Institute for Standardization).
145 The sample size is 207 (36 time points x 6 depths, with some missing data points due to technical

146 problems). To examine the influences of limiting resources on TED, we used a multiple linear
147 regression (N = 195) with photosynthetic active radiation (PAR, from high-frequency profiles),
148 TP (both log-transformed) and their interaction as explanatory variables.

149 In lake Zurich (Switzerland), monitoring data were collected from a single location in the centre
150 of the lake by the Zurich drinking water company (WVZ), which also performed microscopy and
151 chemical analyses as described in Pomati *et al.* (2012). Water was sampled at eleven different
152 depths (0, 1, 2.5, 5, 7.5, 10, 12.5, 15, 20, 30 and 40 m) from the 6th of May to the 2nd of
153 December 2009, with a time interval of one month. The same water samples were analysed with
154 SFC. The sample size is 82 (8 months x 11 depths, with some missing data points due to
155 technical problems).

156 Monitoring data were collected from 26 shallow lakes of the Danube Delta (Romania). These
157 lakes form a complex system in a region of hundreds of km² (Supplementary Table S1). From a
158 single location in each lake, an integrated sample over the water column was collected in spring,
159 summer and autumn of two following years (May, July and September 2013; May, July and
160 October 2014). The same water samples were used for microscopy and chemical analyses, as
161 well as SFC measurements. TP and TN were measured using standard colorimetric methods
162 (Tartari and Mosello, 1997). The sample size is 136 (6 months x 26 lakes, with some missing
163 data points due to technical problems).

164 **SFC measurements**

165 The scanning flow-cytometer Cytobuoy (Woerden, The Netherlands, www.cytobuoy.com) was
166 used for counting and characterising phytoplankton single cells and colonies (e.g. Dubelaar *et al.*,
167 2004; Pomati *et al.*, 2013; Fontana *et al.*, 2014). The present instrument contains two laser beams

168 (coherent solid-state sapphire, wavelengths 488 nm and 635 nm), but the samples from lake
169 Zurich were measured with a previous version of the instrument containing only one laser
170 (wavelength 488 nm). Light, both from forward scattering (FWS) and sideward scattering (SWS),
171 provides information on particle morphology. The fluorescence emitted by photosynthetic
172 pigments was measured by three different detectors referred to as red (668–734 nm range;
173 FL.Red from the 488 nm laser and FL.2.Red from the 635 nm laser), orange (601–668 nm range;
174 FL.Orange) and yellow (536–601 nm range; FL.Yellow). Cytobuoy measurements provide time-
175 resolved pulse signals, from which many descriptors of morphology, internal structure and
176 fluorescence profile of each particle were extracted. More details on the instrument can be found
177 elsewhere (Dubelaar *et al.*, 2004; Pomati *et al.*, 2011; Pomati *et al.*, 2013; Fontana *et al.*, 2014).

178 **Individual-level TD indices**

179 For all phytoplankton samples, we calculated the TD indices describing the three components of
180 TD defined in Mason *et al.* (2005): richness, evenness and divergence. We quantified these three
181 TD components using distinct indices: TOP, TED and FDis, respectively (Laliberté and
182 Legendre, 2010; Fontana *et al.*, 2016). These TD indices fulfil theoretical requirements that make
183 them suitable for application to individual-based measurements, when every organism constitutes
184 a unique combination of traits and therefore influences the TD (Fontana *et al.*, 2014). Thus, in the
185 present study we did not identify neither taxonomic nor functional groups in the SFC data, and
186 we calculated TD metrics without classifying particles (single cells represent the fundamental
187 unit in this study). These multivariate indices were calculated using seven Cytobuoy-derived
188 traits, selected on the basis of their ecological and physiological relevance for phytoplankton
189 (Table 1), and to avoid trait multicollinearity: length (maximum value between length by SWS
190 and length by FWS), average FWS, average FL.Red, average FL2.Red, average FL.Yellow, fill

191 factor FL.Red, ratio between average SWS and average FWS. Thanks to this *a priori* selection of
192 traits, there was no need for dimensionality reduction. In all datasets the absolute value of pair-
193 wise Pearson's correlation coefficients between the selected traits were below 0.7, which we
194 chose as the maximal acceptable limit to reduce collinearity issues (Dormann *et al.*, 2013).
195 Before calculating TD indices, the selected traits were standardized (mean = 0; standard deviation
196 = 1) so that each trait has equal weight (Petchey and Gaston, 2006). This was necessary because
197 the selected traits have different units and vary in value by orders of magnitude. Details about the
198 interpretation of the selected traits and their ecological relevance are reported in Supplementary
199 Table S2. These seven traits provide information on phytoplankton three-dimensional structure,
200 fluorescence properties, cell/colony size and distribution of pigments and other structures within
201 cells (Pomati *et al.*, 2013). Although they do not cover all relevant dimensions of traits space in
202 phytoplankton (e.g. life history, nutrient uptake kinetics and mixotrophy), these traits relate to
203 photosynthesis, resource acquisition (surface to volume ratio), reproduction and predator
204 avoidance (Litchman and Klausmeier, 2008; Pomati *et al.*, 2013; Table 1).

205 **Species-level biodiversity metrics**

206 We calculated species richness (number of species) and Pielou's evenness using microscopic
207 counts of the phytoplankton community in each sample. Effort was made to standardize the
208 counting method and taxonomic identification (at the species level) across all datasets. The same
209 sample preparation method was used (Utermöhl, 1931) and taxonomists exchanged knowledge
210 and information. Pielou's evenness was calculated based on the biovolume of each species
211 present, derived by multiplying the abundance data from microscopy by the best available
212 estimate of species-specific biovolume.

213 **Biomass calculation**

214 Biomass was defined as the sum of the biovolumes of all phytoplankton cells or colonies in the
215 samples, divided by the sample volume analysed. The biovolume of each single particle was
216 estimated assuming an ellipsoid shape with the formula [$\text{Biovolume}^2 = 0.0017 * \text{FWS.Total} -$
217 $0.013]$ (Foladori *et al.*, 2008; Pomati and Nizzetto, 2013). It is important to note that total FWS
218 was derived by SFC, but it is not one of the traits included in the calculation of the TD indices
219 (see above).

220 **Model selection and averaging**

221 We formulated linear mixed-effects models to explain variation in ecosystem properties. We
222 included all possible combinations of five explanatory variables as fixed effects: species richness,
223 Pielou's evenness and the three metrics of individual-level TD (TOP, TED and FDis). TD
224 estimates are not independent from taxonomy-based biodiversity measures. However, we found
225 these two groups of predictors to be only weakly correlated (a maximum Pearson's r of 0.50
226 across all datasets, between TED and Pielou's evenness in lake Zurich). In addition, we
227 accounted for temporal and spatial autocorrelation in abiotic (physics and chemistry) and biotic
228 environmental variables (e.g. grazers and parasites). First, we included the date of sampling as a
229 fixed effect, with a quadratic term. In the case of lake Greifensee (high temporal sampling
230 frequency), the exact time of sampling and the date were combined in a single variable. Second,
231 random intercepts were also included in all models to account for spatial ecosystem
232 heterogeneity: depth of sampling for lakes Greifensee and Zurich, and lake identity for the
233 shallow Danube Delta lakes. This approach resulted in a list of 32 models for each dataset. The

234 variance inflation factors (VIFs) of all variables of interest were lower than 4 in all models,
235 indicating that multicollinearity was not a problem.

236 We calculated marginal R^2 values (Nakagawa and Schielzeth 2013) to estimate the proportion of
237 variance explained by the fixed effects alone in each model. Models with delta AICc < 7 were
238 defined as the strongest set of models (Burnham and Anderson, 2002; Richards, 2005). These
239 were subsequently used for model averaging to minimize the dependence of the regression
240 coefficients on single models and to assess overall predictive power. Model selection and
241 averaging were performed using the *MuMin* R-package (R-Core-Team, 2013).

242 **Additional analyses**

243 We also performed all the above analyses using resource use efficiency (RUE, *sensu* Ptacnik *et al.*,
244 2008) as ecosystem property instead of biomass, which allowed us to study the predictive
245 power of biodiversity metrics on the ability of a community to take up limiting resources. We
246 defined RUE as the amount of standing phytoplankton biomass per unit of limiting resource
247 present (Ptacnik *et al.*, 2008). We used phytoplankton total biovolume (calculated with SFC data)
248 as a proxy for biomass and TP as the main limiting resource in temperate lakes (Ptacnik *et al.*,
249 2008), which in turn is a proxy for potential system productivity. Therefore, RUE was calculated
250 as [biomass / TP].

251 Additionally, we ran a full set of analyses including in all models the number of particles
252 measured by SFC as a fixed effect, in order to account for variation in biomass or RUE caused by
253 SFC sample size.

254 To examine the influence of phytoplankton limiting resources on TED, we used high-resolution
255 data from lake Greifensee including TD, PAR (from high-frequency profiles) and TP, the key

256 limiting factors for algal growth in freshwater environments (Ptacnik *et al.*, 2008). We performed
257 a multiple linear regression analysis with PAR, TP and their interaction as explanatory variables.

258 **Results**

259 The best models retained for model averaging explained more than 60% of the variance in
260 phytoplankton biomass, with a large proportion contributed by the biodiversity metrics (Fig. 1,
261 Table 2). Temporal structure in the data contributed variable amounts depending on the lake
262 system (Table 2). Note that marginal R^2 values represent the variance explained by the fixed
263 effects alone, and therefore do not include the variance attributable to spatial autocorrelation
264 (random factor). Models containing individual-level TD metrics improved predictions of
265 microbial biomass and RUE. Our results show a consistent negative correlation between TED
266 and community biomass across datasets. The other components of TD (richness and divergence),
267 after correcting for the number of cells/colonies, had a non-significant effect on ecosystem
268 properties (see Supplementary Information), except TOP in the lake Greifensee data where it had,
269 however, a weaker effect than TED (Supplementary Figures S2-S3).

270 Species richness was not a significant predictor of biomass. A positive relationship in the Danube
271 Delta lakes disappeared when the models accounted for the number of individuals measured by
272 SFC (see Supplementary Information), suggesting a sampling effect.

273 The different lake systems showed some idiosyncratic patterns, but the main results were
274 consistent. In lake Greifensee, TED was the strongest predictor of biomass, while TOP was the
275 second (Table 2, Figure 1a). Species richness, Pielou's evenness and FDis were non-significant
276 predictors of biomass (Figure 1a). In Lake Zurich, Pielou's evenness was the strongest predictor
277 of biomass, while TED was the second (Table 2, Figure 1b). Species richness, TOP and FDis
278 were non-significant predictors of biomass (Figure 1b). In the Danube Delta lakes, TOP was the
279 strongest predictor of biomass, while TED and species richness were the second and third,

280 respectively (Table 2, Figure 1c). Pielou's evenness and FDis were non-significant predictors of
281 biomass (Figure 1c).

282 Identical analyses using RUE instead of biomass as the ecosystem property of interest yielded
283 almost identical patterns as those presented in Figure 1 (see Supplementary Information).

284 Including in all models the number of individuals measured by SFC as a fixed effect, in order to
285 correct for potential biases associated with the fact that some biodiversity metrics, especially
286 TOP (Fontana *et al.*, 2016), are increasing functions of sampled abundance, also did not change
287 the results (see Supplementary Information). These additional steps had the effect of reducing the
288 predictive strength of species richness and TOP, when analysing both biomass and RUE in the
289 Danube Delta lakes (Supplementary Figures S2c and S3c). TED was however the strongest
290 predictor of ecosystem properties (Supplementary Figures S2d and S3d) under all analytical
291 conditions.

292 A multiple linear regression to test the influence of the main limiting resources on TED revealed
293 a negative, significant effect of PAR and TP ($p = 0.03$ and $p < 0.001$, respectively; $R^2 = 0.25$).

294 TED was highest under limitation by both light and nutrients, with a marginal effect ($p = 0.07$) of
295 their interaction (Figure 2).

296 **Discussion**

297 This study demonstrates that individual-level trait metrics may help link biodiversity in natural
298 microbial communities to essential ecosystem properties. In particular, we found that TED
299 (regularity in the distribution of individual phenotypes in trait space) was the most important
300 predictor of community productivity. Previous studies have explored the correlation between TD
301 measures and ecosystem properties in macro and microorganisms, but trait evenness has rarely
302 emerged as being important (Tilman *et al.*, 1997; Mouillot *et al.*, 2011; Bílá *et al.*, 2014). Gagic
303 *et al.* (2015) found contrasting effects of trait evenness, while Santos *et al.* (2014) showed a
304 negative correlation between trait evenness and phytoplankton productivity, consistent with our
305 results. These differences are probably due to the fact that the tested relationships are dependent
306 on environmental heterogeneity (Norberg *et al.*, 2001; Hodapp *et al.*, 2016). It has to be noted,
307 however, that the concept of trait evenness used in previous studies is radically different from the
308 one employed here, where regularities in trait distances among individuals represent the unit of
309 measure. Previous studies calculated TD using species-level data, disregarding the individual-
310 level trait differences that we find to be the most important predictors.

311 Individual-level trait evenness, as characterised by TED, is also conceptually different from
312 species evenness, since, by measuring the distances of individual organisms in multidimensional
313 trait space, it does not include any information about relative abundances (Supplementary Figure
314 S4; Fontana *et al.*, 2016). To understand the negative correlation between TED and community
315 biomass in our data, it is necessary to refer to environmental effects on both, although they
316 cannot be fully disentangled given the correlative nature of our analyses. Our interpretation of the
317 negative relationship between TED and total biomass is that resource scarcity indirectly affected
318 both in opposite ways - decreasing total community biomass and increasing TED (Figure 2). The

319 pattern that we observed may be explained by plasticity or selection for particular phenotypic
320 characters under conditions of resource limitation. This may induce individual microbes to be
321 more evenly spaced in a multidimensional landscape defined by their functional traits (thereby
322 minimising the overlap of “individual niches”). Our analyses confirmed that low levels of both
323 light and nutrients maximized TED values in microbial communities (Figure 2).

324 We believe that resource limitation constrained the total productivity of the phytoplankton
325 communities in our study, inducing individual phenotypes to spread more evenly along trait axes
326 (to better exploit available resources), leading to the negative correlation between TED and
327 community biomass. This interpretation does not contradict the expected outcomes of
328 competition under resource limitation, which leads to the dominance (at the population level) of
329 the species with the highest affinity for resources (Tilman, 1982). Variation in TED signals
330 individual organisms converging around certain trait combinations (low TED) or spreading more
331 regularly among trait space (Fig. S4); this happens as a consequence of co-occurring
332 physiological and ecological processes. While both acclimation and competitive dominance could
333 explain the above patterns, the fact that individual-level TD dominates the predictive power of
334 our statistical models relative to species-based metrics (considered here as proxies of trait change
335 due to taxa turnover) suggests that variation in TED may be explainable mainly by physiological
336 responses at the single-cell level or genetic variation within species.

337 Light limitation can induce changes in the distribution of individual phytoplankton fluorescence
338 traits because both the absolute and relative intracellular abundance of different pigments can be
339 regulated, thereby changing absorbance across the light spectrum. This has been previously
340 shown in the cyanobacterium *Tolypothrix tenuis*, in which algal cells regulated the relative
341 amounts of different pigments to fill gaps in the prevailing light spectrum that were not already

342 exploited by competitors (Stomp *et al.*, 2004). And in plant communities, intraspecific trait
343 variability is influenced by light acquisition traits of neighbour individuals (Le Bagousse-Pinguet
344 *et al.*, 2015). These studies showed that a complementary effect caused by the differential use of
345 light is not always a consequence of increased taxa richness (as in Striebel *et al.* 2009a; Striebel
346 *et al.* 2009b), but is in principle possible at the intraspecific level. Light represents a spectrum of
347 wavelengths, being a potentially infinite set of resources that can be exploited by photosynthetic
348 organisms able to regulate pigment composition (Stomp *et al.*, 2007a; Stomp *et al.*, 2007b; Stomp
349 *et al.*, 2008).

350 The relationship between TP and TED is more difficult to interpret since many phytoplankton
351 traits might be involved in optimising phosphorus uptake rate and use (Litchman and Klausmeier,
352 2008; Table 1). In this context, cell size represents a key trait, which reflects different nutrient
353 acquisition strategies by determining surface to volume ratio (Litchman and Klausmeier, 2008).
354 The fact that patterns observed for RUE are very similar to those of biomass (see Supplementary
355 Information) suggests, however, that the TP-TED relationship might be less important than the
356 PAR-TED relationship. If the relationship between ecosystem properties and TED was driven by
357 limiting TP, then it would have disappeared when biomass was corrected for TP (that is,
358 considering RUE), which was not the case.

359 In our data, species richness, which represents the most commonly used metric in studies
360 correlating biodiversity with ecosystem properties (Cardinale *et al.*, 2011), did not show a strong
361 relationship with biomass. Interestingly, species richness showed no clear correlation with TD
362 metrics across our datasets (maximum absolute value of Pearson's r was 0.40). Our results seem
363 to contradict previous studies (e.g. Hector *et al.*, 1999; Cardinale *et al.*, 2011) and the common
364 assumption of a positive correlation between species richness and primary production. However,

365 non-significant as well as negative correlations have been already reported previously (Cardinale
366 *et al.*, 2011). One possible reason for the lack of importance of species richness in our study is
367 that we focused on natural communities shaped by natural selection gradients, whereas studies
368 correlating biodiversity with ecosystem properties typically deal with communities assembled
369 randomly from a species pool (Hooper *et al.*, 2005; Krause *et al.*, 2014). Natural communities are
370 the result of assembly processes over abiotic and biotic gradients and their species composition
371 reflects the adaptation to a specific environment. In this context, phenotypic composition might
372 play a more important role compared to the number of species present. However, Ptacnik *et al.*
373 (2008) found a significant positive relationship between genus richness and RUE in natural algal
374 communities. These authors investigated a very large spatial (almost continental) and temporal
375 scale (over several years), whereas our largest scale is regional (Danube Delta) with a generally
376 shorter temporal frequency. This suggests that the scale of analysis might also be important when
377 considering the relative importance of biodiversity metrics in explaining ecosystem processes
378 (Farnsworth, 1998; Cadotte *et al.*, 2011; Chalmandrier *et al.*, 2017).

379 The importance of species evenness for ecosystem properties has been intensively tested in the
380 last few years using experimental, observational and modelling approaches, with partially
381 contradictory results (positive effect of evenness through niche partitioning vs. dominance of
382 high productive species). Most studies have focussed on grassland and forest communities (e.g.
383 Mulder *et al.*, 2004; Zhang *et al.*, 2012; Orwin *et al.*, 2014; Dooley *et al.*, 2015), but some
384 microbial communities have also been investigated (Filstrup *et al.*, 2014; Powell *et al.*, 2015). In
385 this study, species evenness emerged as important only in lake Zurich (Figure 1), where it was
386 the strongest predictor of biomass. This result likely reflects the specific characteristics of this
387 lake's phytoplankton community: in the last few decades, the ecosystem has been dominated by a
388 single cyanobacterial species (*Planktothrix rubescens*) that accounts for approximately 40% of

389 the total annual phytoplankton biomass (Posch *et al.*, 2012). Variation in species evenness is
390 principally driven by growth of this cyanobacterium, which causes fluctuations in community
391 biomass (blooms). This is consistent with patterns observed in many other lakes (Filstrup *et al.*,
392 2014).

393 Ecosystem processes depend upon guilds of interacting organisms and their aggregated responses
394 to their immediate environment. Theoretically, individual-level trait variation is important to
395 maintain ecosystem processes only in a spatially or temporally heterogeneous environment
396 (under constant environmental conditions the fittest phenotype would eventually prevail)
397 (Norberg *et al.*, 2001; Norberg, 2004; Hodapp *et al.*, 2016). The importance of individual-level
398 TD in our analyses suggests that 1) there is significant environmental heterogeneity in the studied
399 aquatic ecosystems, which may lead to the emergence and maintenance of trait diversity
400 (Ackermann, 2015; Stark *et al.*, 2017), and 2) this heterogeneity (characterised by our TD
401 indices) is important to understand and predict ecosystem processes. Since TD can characterise
402 phenotypic variation among individual organisms, aggregating physiological (plastic) responses
403 of phenotypes, evolution of populations and ecological turnover of species, it has been long
404 hypothesised to perform better than species-level metrics in explaining ecosystem properties
405 (Norberg *et al.*, 2001; Petchey and Gaston, 2006; Fontana *et al.*, 2014; Fontana *et al.*, 2016).
406 Despite variation between systems, including TD metrics in statistical or mechanistic models
407 explaining phytoplankton productivity may allow us to improve our predictive power over a
408 range of environmental gradients. The relationship between trait evenness and both environment
409 and ecosystem properties deserves further investigation, both theoretical and empirical.
410 Experimental work can help disentangle the mechanisms (physiology/evolution) that determine
411 variation in the regularity of algal phenotypes in trait space, its dependency on environmental
412 conditions and its importance for ecological interactions.

413 **Conflict of Interest**

414 The authors declare no conflict of interest.

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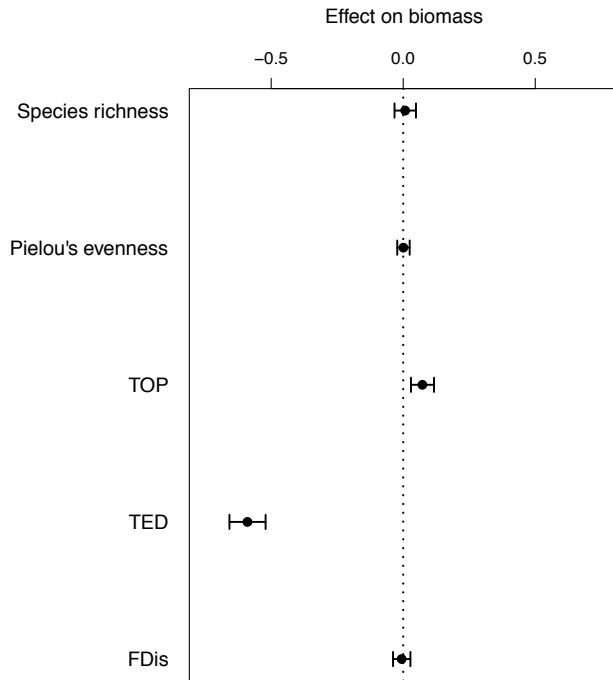
609 **Figure legends**

610 **Figure 1** Effect sizes of biodiversity metrics on biomass. TED is the strongest predictor of
611 biomass among the five biodiversity metrics. Values are standardized model-averaged regression
612 coefficients with 95% confidence intervals, derived from models accounting for temporal and
613 spatial heterogeneity.

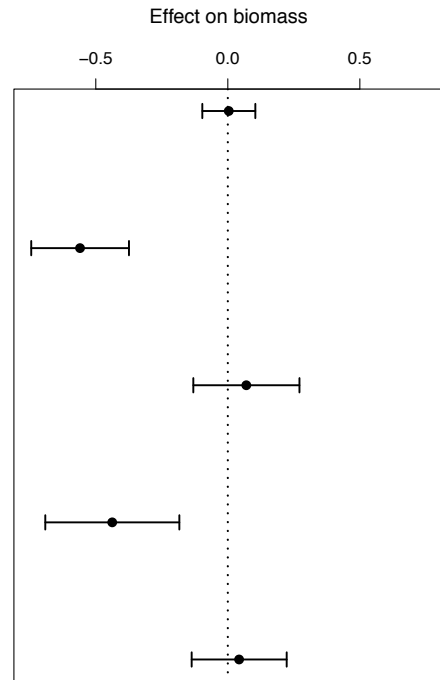
614 **Figure 2** Relationship between phytoplankton limiting resources and TED. Individual-level trait
615 evenness (TED) increases with decrease in photosynthetic active radiation and total phosphorus
616 in lake Greifensee (N = 195). The grey surface represents the fitted linear model relating TED to
617 $\log(\text{PAR})$, $\log(\text{TP})$ and their interaction.

618

(a) Lake Greifensee



(b) Lake Zurich



(c) Danube Delta lakes

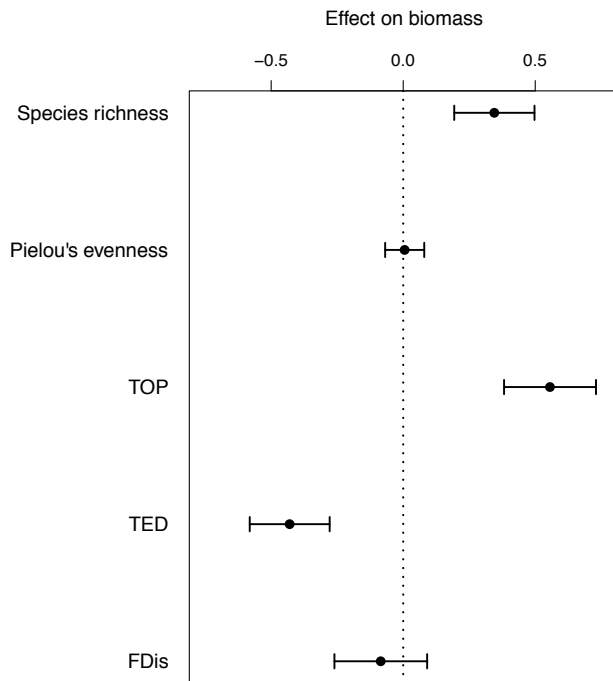


Fig. 1.

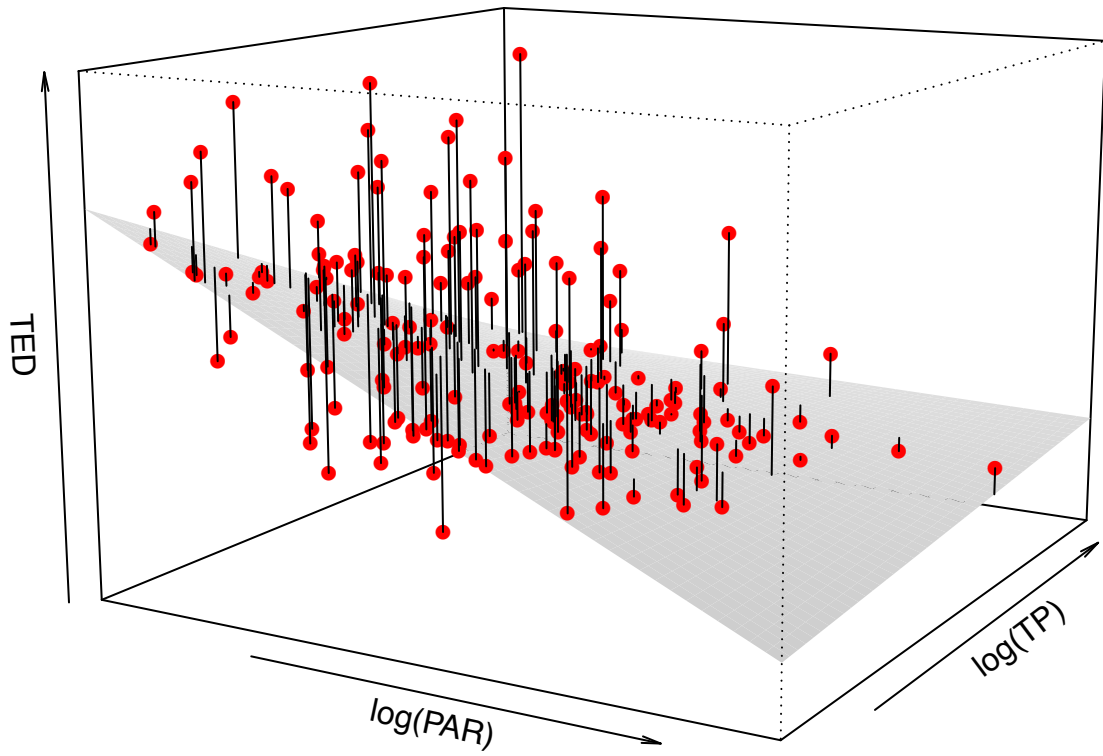


Fig. 2.

Table 1 Ecological relevance of the measured phytoplankton traits. List of the seven traits used for calculating trait diversity indices (Litchman and Klausmeier, 2008; Pomati *et al.*, 2013).

Measure	Ecological importance
Length of the particle	Reproduction, resource acquisition, predator avoidance
Frontal shape of the particle	Resource acquisition
Fluorescence of chlorophyll-a	Resource acquisition
Fluorescence of phycoerythrin*	Resource acquisition
Fluorescence of accessory and decaying pigments	Resource acquisition
Evenness in the distribution of pigments within cell/colony	Resource acquisition
Cell rugosity / internal structure / gas vesicles / thylacoids	Resource acquisition, predator avoidance

* For Lake Zurich data (only 1 laser), this measure is missing.

Table 2 Summary of the results with biomass as response variable. The estimates of the five explanatory variables (with 95% confidence intervals) represent standardized model-averaged regression coefficients. Values in bold are significant at the $p < 0.05$ level.

	Greifensee (N=207)	Lake Zurich (N=82)	Danube delta lakes (N=136)
Number of models used for model averaging (out of 32)	8	8	4
Sum of weights	98.8%	99.5%	>99.9%
Species richness estimate [95% CI]	0.008 [-0.033, 0.048]	0.004 [-0.097, 0.104]	0.345 [0.193, 0.497]
Pielou's evenness estimate [95% CI]	0.001 [-0.023, 0.024]	-0.559 [-0.744, -0.374]	0.006 [-0.068, 0.080]
TOP estimate [95% CI]	0.073 [0.029, 0.117]	0.070 [-0.131, 0.271]	0.556 [0.382, 0.730]
TED estimate [95% CI]	-0.590 [-0.658, -0.521]	-0.437 [-0.691, -0.184]	-0.430 [-0.581, -0.278]
FDis estimate [95% CI]	-0.006 [-0.039, 0.027]	0.043 [-0.137, 0.223]	-0.085 [-0.260, 0.091]
Mean R^2 (null model*)	0.65 (0.02)	0.63 (0.24)	0.65 (0.17)

* accounting for temporal and spatial heterogeneity.