1 Unimodal effects of pigment richness on niche and fitness
2 differences explain species richness and ecosystem function
3 in light-limited phytoplankton communities

4 **Running title:** Trait richness effects on species richness

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19

20 Abstract

21 Trait diversity is traditionally seen as promoting species richness and
 22 ecosystem function. Species with dissimilar traits would partition avail-
 23 able resources, increasing niche differences, facilitating coexistence and
 24 increasing ecosystem function. Here we first show, using theory and
 25 simulations for light-limited phytoplankton, that combining photosyn-
 26 thetic pigments is indeed a necessary condition for coexistence and
 27 stimulates ecosystem function. However, pigment richness does mostly
 28 not permit the coexistence of more than two species, and increases pro-
 29 ductivity at most 60% compared to single-pigment communities. Sur-
 30 prisingly, combining all nine pigments known to date leads to a 2.5%
 31 probability that four species would coexist, illustrating that the co-
 32 existence of a high number of species along a continuous niche axis
 33 is constrained by limiting similarity. We explain these constraints by
 34 unimodal effects of pigment richness on niche and fitness differences,
 35 which jointly limit the positive effect of pigment on species richness.
 36 Empirical data and additional simulations suggest that pigment rich-
 37 ness effects can be stronger during transient dynamics but inevitably
 38 weaken with time, i.e. pigment richness effects on species richness and
 39 function are likely short-lived. Our results highlight the need to apply
 40 coexistence theory to understand the long-term effects of trait diversity
 41 on biodiversity and ecosystem function.

42 **keywords:** coexistence, ecosystem function, niche differences, phyto-
43 plankton, pigment, species richness, trait diversity

44 **Introduction**

45 Species richness is a main predictor of ecosystem function and stability
46 (Hector & Loreau 2001; Hooper *et al.* 2005 but see Spaak *et al.* 2017; Srivas-
47 tava & Vellend 2005). Communities with more species typically produce
48 more biomass and more stably do so than communities with few species
49 (Striebel *et al.*, 2009; Tilman, 1996; Hector & Loreau, 2001; Balvanera *et al.*,
50 2006). Thus, identifying the factors that sustain and limit the capacity
51 of species to coexist is an essential task, and probably one of the most
52 fundamental objectives in ecology (Chase & Leibold, 2003; Hubell, 2001;
53 Chesson *et al.*, 2001; Tilman, 1982).

54 In the past three decades of community ecology, traits have been con-
55 sidered a key ingredient to explain species coexistence (Mcgill *et al.*, 2006;
56 HilleRisLambers *et al.*, 2012). Traits determine both how species respond
57 to environmental variation and to the presence of other species (Chase &
58 Leibold, 2003) and it is generally accepted that trait diversity drives niche
59 differences, which act to stabilize coexistence (McKane *et al.*, 2002; May-
60 field & Levine, 2010). Indeed, when all species have identical traits, trait
61 diversity is zero and stable coexistence is not possible (Chesson, 2000;
62 Bell, 2000; Hubell, 2001). In addition, trait diversity allows coexisting

species to exploit a more diverse set of resources and do so more completely, optimising function.

Recent progress in coexistence theory has shown that trait diversity can have both positive and negative effects on biodiversity, including species richness. That is because, apart from increasing stabilizing niche differences, trait diversity can also increase fitness differences (HilleRis-Lambers *et al.*, 2012; Gallego *et al.*, 2019; Narwani *et al.*, 2013), which can act to disrupt coexistence when they overrule the stabilizing effects. Whether trait diversity supports or limits the number of species that can stably coexist, and thus biodiversity, is therefore unsure (Violle *et al.*, 2011; Best *et al.*, 2013; Levine & HilleRisLambers, 2009). Do species coexist because they are sufficiently different or because they are sufficiently similar?

Here, we theoretically investigate the effects of trait diversity (the number of different traits, i.e. trait richness) on the number of stably coexisting species, niche and fitness differences and ecosystem function (total biovolume). Our working hypothesis was that a greater trait richness would lead to higher species richness and function because it would increase niche differences more than fitness differences, corresponding to prevailing ideas on the effects of trait richness. We considered light limited phytoplankton communities as a globally relevant study system that drives most aquatic food-webs. (Field *et al.*, 2009; Irigoien *et al.*, 2004; Striebel *et al.*, 2012; Baggio *et al.*, 2018; Kulkarni & De Laender, 2017).

86 Competition for light in phytoplankton communities is a major process
87 explaining community composition throughout the world's aquatic habi-
88 tats (Goldman *et al.*, 1979; Langdon, 1988; Stomp *et al.*, 2007). Phytoplank-
89 ton communities in meso- and eutrophic lakes and oceans, where light is
90 the main limiting factor, produce approximately 30%-40% of the world's
91 annual primary production (Field *et al.*, 2009; Berger *et al.*, 2006; Boyd,
92 2002). In addition, competition for light is particularly suitable to test
93 our expectations because the light spectrum represents a continuous re-
94 source axis, which a high number of species could in principle be able to
95 partition.

96 The traits involved in competition for light are pigments and pho-
97 tosynthetic efficiency, i.e. the amount of biovolume gained per absorbed
98 photon (Huisman & Weissing, 1994; Stomp *et al.*, 2004). Differences of pig-
99 mentation phenotypes have been shown to facilitate coexistence among,
100 for example, cyanobacteria species (Stomp *et al.*, 2004, 2007). Pigment di-
101 versity is also expected to allow a more complete utilisation of the light
102 spectrum (Striebel *et al.*, 2009), thus promoting both species richness and
103 optimizing function. Photosynthetic efficiency alone cannot facilitate co-
104 existence, the reason for which we do not consider this trait further.

105 We start this paper by theoretically examining how pigment richness
106 determines the number of stably coexisting phytoplankton species and
107 ecosystem function (total biovolume). We do so by analysing a phyto-
108 plankton growth model that incorporates the partitioning of the light

spectrum among species with different pigments (Stomp *et al.*, 2004). We show that, when all species share one pigment, communities evolve to mono-dominance. When a community contains multiple of the main nine photosynthetically active pigments found in nature, up to four species co-exist based on light spectrum partitioning, but with low probability. We explain this result through unimodal effects of pigment richness on niche and fitness differences. Higher pigment richness also increases total bio-volume by approximately 60%.

Next, we compile data from the literature and find a much stronger positive effects of pigment trait richness on species richness and ecosystem function. We reconcile these data with additional model simulations, finding that the reported effects are likely short-lived (transient) phenomena. Our findings highlight that applying coexistence theory is needed to understand the mechanisms linking species richness to ecosystem functions on time scales relevant for natural systems.

Methods

Model description

We used a model proposed earlier by Stomp *et al.* (2004), which is equivalent to (Appendix S1):

$$\frac{dN_s}{dt} = \phi_s \int_{400}^{700} \frac{N_s k_s(\lambda)}{\text{abs}(\lambda)} \cdot I_{in}(\lambda) \left(1 - e^{-\text{abs}(\lambda)}\right) d\lambda - l N_s \quad (1)$$

Where N_s is the density of species s (in fl/ml), ϕ_s is the photosynthetic efficiency, $k_s(\lambda)$ is the absorption spectrum of species s , $\text{abs}(\lambda) = z_m \cdot (k_{BG}(\lambda) + \sum_{i=1}^n k_i(\lambda) N_i)$ is the sum of all absorbers (background and phytoplankton species), where k_{BG} is the background absorption, z_m is the mixing depth and n is the species richness, $I_{in}(\lambda)$ is the incoming light intensity and l is the loss rate. Note that we considered the loss rate not as a species-specific parameter but rather the dilution rate of the system. The integral is taken over the whole range of photosynthetic active radiation (400nm - 700nm).

$I_{in}(\lambda) \left(1 - e^{-\text{abs}(\lambda)}\right)$ can be thought of as the total amount of photons absorbed by the system and $\frac{N_s k_s(\lambda)}{\text{abs}(\lambda)}$ is the fraction of these photons that species s uses for its growth.

Analyses and simulations

We used equation 1 to examine how trait (pigment) richness affects species richness and ecosystem function. We first theoretically analysed the maximum number of species that can stably coexist based on a predefined number of pigments.

Next, we ran simulations to determine the actual number of species and level of ecosystem function corresponding to a given pigment rich-

ness. To do so first, we collected 15 algal pigmentation types from the literature representing the major pigmentations of marine and freshwater phytoplankton (Six *et al.*, 2007; Van Den Hoek *et al.*, 1995) (Appendix S2). Then, we randomly assembled 400'000 communities composed of a random number of species (1 to 15). In every community, every species was randomly assigned a pigmentation type. The absorption spectrum of a species is defined as the sum of its pigments:

$$k_s(\lambda) = \sum_p \alpha_{s,p} k_p(\lambda) \quad (2)$$

Where k_s is the absorption spectrum of the species, k_p is the absorption spectrum of the pigment and $\alpha_{s,p}$ is the concentration of pigment p in species s . The identity of the pigments present in a species is given by its pigmentation type. The absorption spectra of the pigments ($k_p(\lambda)$) were taken from the literature (Bricaud *et al.*, 2004; Six *et al.*, 2007). Fig. 1 B,C shows an example for two pigmentation types. The total absorption of each species was kept constant ($\int_{400}^{700} k_s(\lambda) d\lambda = 2 \cdot 10^{-7} cm^{-1} fl^{-1}$), to avoid species with more pigments absorbing more light. Furthermore, we varied the photosynthetic efficiency ($1.0 \cdot 10^6 \frac{fl}{\mu mol photons} \leq \phi_s \leq 3.0 \cdot 10^6 \frac{fl}{\mu mol photons}$) (Langdon, 1988), the dilution rate ($0.003 h^{-1} \leq l \leq 0.015 h^{-1}$) (Stomp *et al.*, 2004; Striebel *et al.*, 2009) and the incoming light intensity ($20 \mu mol photons m^{-2} s^{-1} \leq I_{tot} \leq 200 \mu mol photons m^{-2} s^{-1}$) (Stomp *et al.*, 2004; Striebel *et al.*, 2009). We assumed that the background absorp-

tion is negligible ($k_{BG} \approx 0$, Appendix 3 for simulation with non-zero background absorption).

For every community we measured species richness, pigment richness and ecosystem function over time. To measure species richness and pigment richness we assumed that species with relative densities below 0.01% are extinct. Changing this threshold to 1% or 0.0001% did not change our results. The ecosystem function we considered was total biovolume ($EF = \sum_{i=1}^n N_i$). The ecosystem function was measured in communities with intensity of incoming light fixed at $40\mu\text{mol photons } m^{-2}s^{-1}$. Again, changing this value to $20\mu\text{mol photons } m^{-2}s^{-1}$ or $80\mu\text{mol photons } m^{-2}s^{-1}$ did not qualitatively alter the results.

For each community at equilibrium we computed the niche and fitness differences ($\mathcal{N}_i$ and $\mathcal{F}_i$) of the persisting species, using the definition Spaak & De Laender (2020). Technically, Spaak & De Laender (2020) define $\mathcal{N}_i$ based a species i 's growth rate under various conditions, including its invasion growth rate (i.e. its growth rate when seeded in a community of other species) and its intrinsic niche growth rate (i.e. at low density in absence of competitors). As the difference between the invasion and intrinsic growth rate gets larger, $\mathcal{N}_i$ will approach zero, which indicates strong species interactions. In the current context, we expect this to correspond to the case where species have identical pigmentation, and thus compete maximally for light. Conversely, as the difference between the invasion and intrinsic growth rate gets smaller, $\mathcal{N}_i$ will approach one,

181 which indicates weak species interactions. We expect this to correspond
 182 to the case where species differ markedly in pigmentation. Spaak & De
 183 Laender (2020) define $\mathcal{F}_i$ as the growth rate of species i in absence of
 184 niche differences, scaled by the intrinsic growth rate of species i . In that
 185 case, the species with the highest scaled growth rate has the largest fit-
 186 ness difference. Because these definitions do not lead to closed forms of
 187 $\mathcal{N}_i$ and $\mathcal{F}_i$, we computed $\mathcal{N}_i$ and $\mathcal{F}_i$ numerically.

188 Literature data

189 We searched the literature for experimental data describing the effects
 190 of pigment richness on species richness and ecosystem function. We
 191 used the search term (phytoplankton OR algae) AND ("pigment rich-
 192 ness" OR "pigment diversity") AND ("ecosystem function" OR biodiver-
 193 sity) using the search engines scopus and google scholar. Additionally,
 194 we screened all papers cited by or citing as such identified papers. We
 195 identified four datasets (two representing field samples from freshwa-
 196 ter lakes and two representing experiments with freshwater and marine
 197 phytoplankton respectively). The two field data sets represent different
 198 sampling locations in one lake (Fietz & Nicklisch, 2004) and from multiple
 199 lakes (Striebel, personal communications), respectively. The experimental
 200 dataset of Estrada *et al.* (2004) represents phytoplankton diversity in solar
 201 salterns with salinity ranging from 4% to 22.4%. We excluded salinities
 202 above 22.4%, as they do not resemble marine ecosystems (Estrada *et al.*,

203 2004). Striebel *et al.* (2009) assembled 1 to 10 species of freshwater phy-
 204 toplankton and measured pigment richness and ecosystem function after
 205 14 days. Pigment richness was measured using high-performance liquid
 206 chromatography in all datasets. The datasets contain more pigments, as
 207 they include the pigments used for photo protection. For every dataset,
 208 we linearly regressed the log transformed species richness and log trans-
 209 formed biovolume against pigment richness, and compared it with the
 210 theoretical results.

211 The empirical data we found differs in two aspects from our simu-
 212 lated data. First, our simulated data represent long-term effects of pig-
 213 ment richness on species richness and function under steady environ-
 214 mental conditions and it is not sure if the empirical data likewise rep-
 215 resent such long-term effects. The field communities will have been ex-
 216 posed to environmental fluctuations and the experimental communities
 217 were observed during relatively short-term experiments (8-14 days). Sec-
 218 ond, the empirical data contain photosynthetic pigments as well as non-
 219 photosynthetic pigments, typically used for photoprotection. We there-
 220 fore repeated our simulations, breaking them off after 10 days, hence
 221 simulating the time window typically adopted by experiments. We also
 222 included six non-photosynthetic active pigments, that absorb light, but
 223 do not contribute to growth (Bricaud *et al.*, 2004). Specifically we changed
 224 $\text{abs}(\lambda) = z_m \cdot (k_{BG}(\lambda) + \sum_i (k_i(\lambda) + k_i^p(\lambda))N_i)$ from equation 1, where
 225 $k_i^p(\lambda)$ is the combined absorption spectra of the photo protective pig-

ments. $k_i^p(\lambda)$ was generated similar to $k_i(\lambda)$.

Results

Effects of pigment richness on coexistence

We found that one can decompose the growth rate of a species as:

$$\frac{1}{N_s} \frac{dN_s}{dt} = \phi_s \sum_p \alpha_{s,p} \Psi_p(N) - l \quad (3)$$

$$\Psi_p(N) = \int_{400}^{700} \frac{k_p(\lambda)}{\text{abs}(\lambda)} \cdot I_{in}(\lambda) \left(1 - e^{-\text{abs}(\lambda)}\right) d\lambda \quad (4)$$

Where $\Psi_p(N)$ is the amount of light absorbed by pigment p . Stable and feasible coexistence, i.e. all species have non-zero equilibrium densities, would impose $\frac{dN_s}{dt} = 0$ for all the species s . This yields a linear equation in the variables $\Psi_p(N)$. This equation can only have a solution if the number of species is at most equal to the number of pigments in the community. This finding proves the fact that species richness is limited by pigment richness for constant incoming light intensity (Mészéna *et al.*, 2006).

These new analytical results show that the number of pigments puts an upper bound on the number of coexisting species, but how many coexisting species can we on average expect at a given number of pigments? While equation 3 will always have a solution, this solution might not be ecologically possible. For example, all pigments should have a positive

241 contribution to growth ($\Psi_p(N) > 0$). In addition, pigments in nature
 242 often share peaks: Many pigments have maxima in the blue part of the
 243 spectrum ($400nm - 450nm$) such that the different $\Psi_p(N)$ are not inde-
 244 pendent functions (Fig. 1 and Stomp *et al.* (2007)).

245 Our simulations of species richness at various combinations of pig-
 246 ment richness and photosynthetic efficiencies show that the number of
 247 coexisting species is often lower than the number of pigments. Initial
 248 pigment richness increased average species richness from 1 to 2.2 (Fig. 2).
 249 When all pigments are present (initial pigment richness = 9), at most 4
 250 species can coexist, but with low probability ($\approx 2.5\%$). We repeated the
 251 analysis with several alternative assumptions on initial species richness
 252 (ranging from 1-25), the included pigments (including carotenoids with
 253 photo-protective purposes), the absorption spectrum of the pigments, the
 254 presence of pigments in species, the absorption spectrum of the back-
 255 ground and the incoming light spectrum (see appendix 3). We also ran
 256 simulations in which absorption spectra of pigments were randomly
 257 generated and pigments were randomly distributed to species. All of
 258 these simulations lead to the same main conclusion: pigment richness is
 259 essential to allow coexistence but does mostly not allow the coexistence
 260 of more than two species in light limited phytoplankton communities.

261 We identified three reasons for this result, all related to how pigment
 262 richness affect niche ($\mathcal{N}_i$) and fitness differences (FD_i). First, pigment
 263 richness had a unimodal effect on $\mathcal{N}_i$ (Fig. 3 A). At low pigment richness,

264 pigment richness increases $\mathcal{N}_i$, as it increases the probability species will
 265 be coloured differently, which stimulates light partitioning. As pigment
 266 richness increases, however, species tend to contain an increasing number
 267 of pigments, blurring differences in pigmentation, which reduces $\mathcal{N}_i$. Sec-
 268 ond, pigment richness does not only affect $\mathcal{N}_i$, which benefits coexistence,
 269 but also increases differences among species' $\mathcal{F}_i$, which hampers coexis-
 270 tence. Intermediate pigment richness lead to clear competitive dominant
 271 (high $\mathcal{F}_i$) and subordinate (low $\mathcal{F}_i$) species (Fig 3 B). Communities with
 272 intermediate pigment richness will contain species with many pigments,
 273 that absorb most wavelengths and have high fitness, and species with
 274 few pigments, that absorb only part of the wavelength and have low fit-
 275 ness. The difference in these fitnesses leads to large $\mathcal{F}_i$, both positive and
 276 negative. As pigment richness increases all species become generalists
 277 and have high fitness, therefore $\mathcal{F}_i$ are closer to zero. Third, $\mathcal{N}_i$ and $\mathcal{F}_i$
 278 were located close to the origin of the $\mathcal{N}_i$ and $\mathcal{F}_i$ plane (Fig. 3 C), show-
 279 ing that different pigmentation types only offered limited opportunity
 280 for differentiation among species. This is explained by all pigmentation
 281 types containing chlorophyll a, which makes pigmentation more similar
 282 (Appendix S2, Van Den Hoek *et al.* (1995)), and different pigments having
 283 similar absorption spectra (Stomp *et al.*, 2007). Again, repetition of the
 284 simulations with altered parameters led to the same results, niche and
 285 fitness differences are located close to the origin in the $\mathcal{N}_i$ and $\mathcal{F}_i$ plane
 286 (Appendix 3).

Contrary to our theoretical results, the compiled empirical data did suggest a strong positive effect of pigment richness on species richness (Fietz & Nicklisch, 2004; Estrada *et al.*, 2004; Striebel *et al.*, 2009). However, our model analyses and simulations represent the long-term outcome of species interactions in stable environmental conditions, while the empirical data describe experiments performed on much shorter time scales (approximately 10 days) and natural communities with unknown environmental conditions. Thus, the empirical data potentially describe communities that are in a transient state, heading towards lower levels of species richness. Our additional model simulations of short-term effects of pigment richness on species richness indeed suggest time scale to be an important explanation for the difference between our model results and the empirical data. These simulations showed that effects of initial pigment richness on species richness are indeed initially strong, but become weaker over time: pigment richness promoted short-term species richness (Fig. 4A).

Implications for ecosystem function

Our simulations show that ecosystem function in communities with high pigment richness is up to 60% higher than in communities with low pigment richness (total biomass, Fig. 4B). This increase of ecosystem function is mainly due to selection effect and not complementarity (Appendix 4). Complementarity is low, because light partitioning allows only lim-

309 ited niche differentiation. As found for species richness, the compiled
310 empirical data did suggest a stronger positive effect (larger slope) of pig-
311 ment richness on ecosystem function (Striebel *et al.*, 2009; Estrada *et al.*,
312 2004; Fietz & Nicklisch, 2004) (Fig. 4). Again, we additionally simulated
313 short-term effects of pigment richness on ecosystem function (Fig. 4B,
314 light green) and found a stronger effect of pigment richness on ecosystem
315 function than for communities at equilibrium (dark green). The effects of
316 initial pigment richness on function are initially strong but dampen with
317 time.

318 Discussion

319 In the past decade, ecology has evolved towards trait based approaches,
320 as species interactions are governed through species traits and not through
321 species identities (Litchman & Klausmeier, 2008; McGill *et al.*, 2006; Degen
322 *et al.*, 2018). Trait based approaches have been used to explain species
323 richness (Violle *et al.*, 2011; Best *et al.*, 2013), coexistence mechanisms such
324 as niche and fitness differences (Kraft *et al.*, 2015; Narwani *et al.*, 2013;
325 Gallego *et al.*, 2019), and ecosystem function (Gross *et al.*, 2017; Degen
326 *et al.*, 2018). Here we investigated the effect of pigment richness on all
327 these key properties of ecological communities using a mechanistic com-
328 munity model describing light limited phytoplankton. We found that
329 pigment richness increases species richness from one to two species on

average (Fig. 2), has a unimodal effect on niche and fitness differences,
and increases ecosystem function by about 60%.

Effects of pigment richness on species richness

Light has traditionally been considered as one resource until Stomp *et al.* (2004) showed that different wavelengths allow niche partitioning along the light spectrum, supporting coexistence. Our results confirm that this additional trait axis, representing pigmentation phenotypes, indeed allows introducing niche differences that allow coexistence of multiple species that would not have been possible if a single pigment would have been present (Stomp *et al.*, 2004, 2007; Passarge *et al.*, 2006; Huisman & Weissing, 1994). However, our results also show that this mechanism alone cannot explain robust coexistence of many more species than two.

One important reason is the fact that pigments not only stimulate niche differences, but they also create competitive dominant and subordinate species, leading to large fitness differences, as they determine the total amount of absorbed photons ($\int_{400}^{700} k_p(\lambda) I_{in}(\lambda) d\lambda$). This result illustrates the effect of limiting similarity and the widespread occurrence of competitive exclusion despite trait differences (Meszéna *et al.*, 2006; Barabás *et al.*, 2012). While the light spectrum represents a continuous resource axis, along which an infinite number of species could specialise and persist, species that harvest too similar light colours will lead to the exclusion of the least fit. The fact that traits influence both niche and

352 fitness differences has been pointed out for other traits in other systems
 353 as well (Mayfield & Levine, 2010). For example, Kraft *et al.* (2015) found
 354 that phenology of annual plants did not only promote niche differences
 355 but also inflated fitness differences. Gallego *et al.* (2019) found that a
 356 single trait, phytoplankton size, increases both niche and fitness differ-
 357 ences. However, larger size differences between species does not promote
 358 coexistence.

359 Despite the extensive parameter range considered and the use of re-
 360 alistic pigmentation phenotypes, our analysis is a simplification of real-
 361 ity. In more complicated models, including additional factors, the effect
 362 of trait richness on species richness may be stronger. A first factor is
 363 individual-specific pigmentation. That is, the absorption spectrum of the
 364 same pigment may be different in different individuals from the same
 365 species, representing subtle but potentially important sources of inter-
 366 and intraspecific variation (Bricaud *et al.*, 2004; Six *et al.*, 2007; Bricaud
 367 *et al.*, 1995). Intraspecific variation of resource uptake traits can promote
 368 coexistence. For example, Hausch *et al.* (2018) recently showed that mod-
 369 erate intraspecific variation of bean weevils feeding on lentils and adzuki
 370 increased the resistance against invasion and invasion ability, thus pro-
 371 moting stable coexistence. However, theoretical results on annual plants
 372 obtained by Hart *et al.* (2016) suggest that initial intraspecific trait varia-
 373 tion may also hamper coexistence. A second factor embodies trade-offs
 374 among traits. For example, species with less competitive pigmentation

could have higher photosynthetic efficiencies, similar to larger phytoplankton species often having higher maximum growth rates (Langdon, 1988; Edwards *et al.*, 2015; Lavallée & Pick, 2002). Our assumption that all trait combinations were equally probable is therefore clearly a simplification of reality. A third factor is photoinhibition, which could facilitate coexistence, as it could turn our linear response of growth to light intensity into a non-linear response (Huisman & Weissing, 1994; Gerla *et al.*, 2011; Stomp *et al.*, 2007). This would introduce the potential for relative nonlinearities, which can contribute to temporal niche differentiation in case of external light intensity fluctuations (Litchman & Klausmeier, 2001). Litchman and Klausmeier showed that relative nonlinearities can sustain coexistence of light-limited phytoplankton communities (Litchman & Klausmeier, 2001). Another way in which light intensity fluctuations could affect coexistence is through storage effects (Chesson, 2003). However, only one of the three conditions required for the storage effects are met. Indeed, in our system, environmental conditions do covary with competition, however, the response of all species is similar to these covariances and population growth is additive in environment and competition. By including a dormant stage, which is not sensitive to environmental fluctuations, Tredennick *et al.* (2017) showed that the storage effect leads to coexistence in a simple resource competition model. Including different phytoplankton life stages could serve as dormant stages in this model as well, and possibly promote a positive effect of pigment richness

398 on species richness through storage effects.

399 **Implications for ecosystem function**

400 Our model showed that pigment richness positively affected ecosystem
 401 function (Fig. 4). However, coexistence requirements often caused the
 402 exclusion of many species in communities with high initial trait richness.
 403 This led to levels of ecosystem function that are comparable to that of
 404 communities with lower initial trait richness in which all species persist.
 405 This mechanism reduces the positive effect of trait richness on ecosystem
 406 function. Therefore, our results show how the effects of trait richness
 407 on ecosystem function can be limited on time scales that are sufficiently
 408 long for community dynamics to emerge. The limited long-term positive
 409 effect of trait richness on ecosystem function we find is due to the selec-
 410 tion effect. Our results show that higher initial trait richness increases the
 411 probability of having a highly productive species present in the commu-
 412 nity (Appendix S5). At the same time, complementarity is small in light
 413 limited phytoplankton communities (Appendix 4). Cadotte (2017) have
 414 found that complementarity was most prominent in species and trait-rich
 415 plant communities.

416 Positive effects of trait richness on species richness and ecosystem
 417 function have been found in many different study systems. For example,
 418 diversity of feeding traits in herbivorous marine amphipods increased co-
 419 existence (Best *et al.*, 2013), mouth size differences facilitated coexistence

of two bacterivorous ciliates (Violle *et al.*, 2011), and phylogenetic diversity, species richness and average productivity were all found to correlate positively in savanna grasslands (Cadotte *et al.*, 2009).

However, many of these studies share two features that may lead to higher trait diversity effects on function than we report on here. First, these experiments often are too short to observe competitive exclusion, and so species can contribute to function before they go extinct. Our results also show that it can take many generations to observe competitive exclusion, over 200 generations in our system, which is longer than most long term experiments. Similarly long times to competitive exclusion have been found for phytoplankton species competing for two limiting resources (Sakavara *et al.*, 2017). Second, available experimental studies often consider communities with relatively few species. Our results show that the trait richness effect on species richness and function is most pronounced when trait richness, and therefore species richness, is relatively low (between 2 and 7 pigments).

Effects of trait diversity on ecosystem function of grasslands have been found to intensify with time (Reich *et al.*, 2012). This temporal intensification has been explained by reciprocal feedbacks between community composition and environmental conditions such as on soil nitrogen availability (Reich *et al.*, 2012). Our results show that, in absence of such feedbacks and when given enough time, effects of biodiversity on ecosystem function can actually weaken with time. That is, packing a more

443 diverse set of species into our model system, light-limited phytoplank-
 444 ton, caused benefits for ecosystem function that were short-lived. These
 445 findings highlight the need to account for coexistence requirements when
 446 estimating the long-term benefits of biodiversity for ecosystem function
 447 (De Laender *et al.*, 2016; Bannar-Martin *et al.*, 2018).

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459 **Data accessibility statement** In case of acceptance we will put all code
 460 to perform this study on our git repository. No new experimental or field
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Figure 1: In vivo absorption spectra of all considered pigments (A) and two examples (B: Cyanobacteria type 1, C: Cyanobacteria type 3) showing how absorption spectra (black) can be decomposed into different pigments (Eq. 2). The two species in B and C can coexist under white light, as the Cyanobacteria type 1 is a superior absorber in the red light (620-700 nm), while the Cyanobacteria type 3 species is a better absorber in the blue-green light (450-550 nm).

Figure 2: Final species richness depends only weakly on the initial number of pigments. Colours denote the probability associated with these species richness levels. Blue dots show the average of the final species richness.

Figure 3: A: Pigment richness has a unimodal effect on $\mathcal{N}_i$. Initially multiple pigments allow niche differentiation by the use of different wavelength. However, this positive effect of pigment richness on species richness is limited to few pigments (up to about 4 pigments) and generates only small $\mathcal{N}_i$ compared to empirical measurements in phytoplankton (Narwani *et al.*, 2013; Gallego *et al.*, 2019). At higher pigment richness the species tend to be more generalists and absorb multiple wavelengths, which reduces pigment richness. Shown are the 5, 25, 50, 75 and 95 percentiles of $\mathcal{N}_i$ of all persisting species from all simulated communities. B: Similarly, pigment richness affects $\mathcal{F}_i$. Communities with intermediate pigment richness are composed of species with many pigments, that have high fitness, and species with few pigments, that have low fitness, leading to both, strong negative and positive $\mathcal{F}_i$. The species with strong negative $\mathcal{F}_i$ are most vulnerable to exclusion. Communities with low or high pigment richness are composed of species with few or many pigments, respectively. The species from these communities tend to have similar fitness, which leads to weak $\mathcal{F}_i$. C: Two-dimensional histogram of $\mathcal{N}_i$ and $\mathcal{F}_i$ for all species in all communities³⁵, independent of their pigment richness. Most species have both $\mathcal{N}_i$ and $\mathcal{F}_i$ close to 0. Shown are the 25, 50, 75, 95 and 99 percentiles of the distribution, e.g. 25% of the species have $\mathcal{N}_i$ and $\mathcal{F}_i$ within the yellow area. Species below the red-line have a positive invasion growth rate, i.e. they are assumed to persist.

Figure 4: Empirical effect of initial pigment richness on species richness (A) and ecosystem function (biovolume B). A: Effects of pigment richness on species richness is initially strong (light green line), but weakens as the communities approach equilibrium densities (dark green line). Similarly, empirical data report a positive effect of pigment richness on species richness. This positive effect is stronger in experimental datasets (dark blue and red) than in natural communities (light blue and orange), presumably because natural communities are closer to equilibrium densities than short term experiments. B: The same observations hold true for the effects of pigment richness on ecosystem function, these are initially strong (slope of light green: 0.101 ± 0.012), but weaken over time (slope of dark green: 0.063 ± 0.007). Dashed lines indicate, that slope did not significantly differ from 0 (i.e. $p > 0.05$).