

How self-regulation, the storage effect and their interaction contribute to coexistence in stochastic and seasonal environments

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Abstract

Explaining coexistence in species-rich communities of primary producers remains a challenge for ecologists because of their likely competition for shared resources. Following Hutchinson's seminal suggestion, many theoreticians have tried to create diversity through a fluctuating environment, which impairs or slows down competitive exclusion. However, fluctuating-environment models often only produce a dozen of coexisting species at best. Here, we investigate how to create richer communities in fluctuating environments, using an empirically parameterized model. Building on the forced Lotka-Volterra model of Scranton and Vasseur (2016), inspired by phytoplankton communities, we have investigated the effect of two coexistence mechanisms, namely the storage effect and higher intra- than interspecific competition strengths (i.e., strong self-regulation). We tuned the intra/inter competition ratio based on empirical analyses, in which self-regulation dominates interspecific interactions. Although a strong self-regulation maintained more species (50%) than the storage effect (25%), we show that none of the two coexistence mechanisms considered could ensure the coexistence of all species alone. Realistic seasonal environments only aggravated that picture, as they decreased persistence relative to a random environment. However, strong self-regulation and the storage effect combined superadditively so that all species could persist with both mechanisms at work. Our results suggest that combining different coexistence mechanisms into community models might be more fruitful than trying to find which mechanism best explains diversity. We additionally highlight that while biomass-trait distributions provide some clues regarding coexistence mechanisms, they cannot indicate unequivocally which mechanisms are at play.

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1 Introduction

The continued maintenance of diversity in spite of widespread competition has long bewildered ecologists, especially for primary producers such as phytoplankton that share the same basic resources (Hutchinson, 1961). A solution for the ‘paradox of the plankton’ was proposed by Hutchinson: temporal variation of the environment. By making the identity of the fittest species change over time, temporal variation could render competitive exclusion less likely, which was confirmed by early experiments (Sommer, 1984). However, it has been shown later that inclusion of temporal variability *per se* in competition models is not sufficient for maintaining a realistic diversity (Chesson and Huntly, 1997; Fox, 2013). Additional mechanisms such as the storage effect (Chesson, 1994; Ellner et al, 2016) or a relative nonlinearity of competition (Armstrong and McGehee, 1980; Chesson, 2000; Descamps-Julien and Gonzalez, 2005; Jiang and Morin, 2007; Fox, 2013) need to be introduced for diversity to maintain. Moreover, richness rarely exceeds a handful to a dozen of species in model competitive communities in fluctuating environments, except when external inputs from immigration sustain diversity (e.g., Huisman et al, 2001; Jabot and Lohier, 2016). To our knowledge, the effect of temporal variability on persistence in competition models has mostly been examined in theoretical communities of 2 to 3 species (e.g., Chesson and Huntly, 1997; Litchman and Klausmeier, 2001; Li and Chesson, 2016; Miller and Klausmeier, 2017).

One of the richest modeled communities that we identified can be found in Scranton and Vasseur (2016), which is based on temperature variation and different thermal optima for each species (Moisan et al, 2002). In this model, the synchronizing effect of the environment and the storage effect can maintain 12 phytoplankton-like species on average. Scranton and Vasseur (2016) described daily temperature as a random noise, i.e., independent and identically distributed Gaussian random variates over time. However, under most latitudes, seasonality drives part of the environmental variation: over short timescales, random temporal variations often only add noise to a largely deterministic seasonal trend (Scheffer et al, 1997; Boyce et al, 2017; Barraquand et al, 2018).

Seasonal forcing of parameters can strongly affect the dynamics of model communities by synchronizing species to the seasonal signal or even promoting oscillations with lower frequency

(Rinaldi et al, 1993; Barabás et al, 2012; Miller and Klausmeier, 2017; Vesipa and Ridolfi, 2017). How seasonality affects coexistence, as opposed to a randomly fluctuating environment, is therefore a key feature of this paper. Our present work can be seen as an attempt to blend Scranton and Vasseur (2016)’s stochastic framework with the periodic environments of Barabás et al (2012), to better represent the mixture of stochastic and deterministic environmental forces affecting phytoplankton community dynamics.

What other key features of field communities should be considered when modeling phytoplankton? Strong self-regulation, with intraspecific competition much stronger than interspecific interactions, has been found to be widespread in terrestrial plant communities (Adler et al, 2018), animal communities (Mutshinda et al, 2009), and phytoplanktonic communities (Barraquand et al, 2018). We will therefore insert those niche differences, manifesting as strong self-regulation, into our models of phytoplankton competition. The interaction between environment variability and niche overlap was investigated by Abrams (1976) but his results did not extend to communities more diverse than 4 species; our objective is therefore to see how those mechanisms interact for species-rich communities.

Niche models have often been opposed to the neutral theory (Hubbell, 2001), where dispersal and drift can ensure a transient coexistence of many species, but several authors have attempted to blend niche and neutral processes (Gravel et al, 2006; Scheffer and van Nes, 2006; Carmel et al, 2017). An intriguing offshoot of these attempts is the concept of ‘clumpy coexistence’ (Scheffer and van Nes, 2006), whereby simultaneous influences of both niche and neutral processes create several clumps of similar species along a single trait axis. Niche differences enable coexistence of multiple clumps (Chesson, 2000) while within-clump coexistence occurs through neutral processes. This ‘emergent neutrality’ within groups (Holt, 2006) has been proposed as a unifying concept for niche and neutral theories (even though the neutrality of the original model has been disputed due to hidden niches, Barabás et al, 2013). Since then, clumpy coexistence has been shown to occur in theoretical models incorporating a temporally variable environment interacting with a thermal preference trait axis (Scranton and Vasseur, 2016; Sakavara et al, 2018). The relationship (or absence thereof) between biomass-trait distributions and coexistence mechanisms is currently

debated (D’Andrea and Ostling, 2016), although there are suggestions that clustering on trait axes under competition may be a robust find (D’Andrea et al, 2018, 2019).

Here, we try to establish what are the relative contributions to coexistence of the storage effect vs strong self-regulation, in a phytoplankton-like theoretical community model with a large number of species. This led us to cross combinations of seasonality vs randomness in the forcing signal, presence of the storage effect or not, and intra- vs interspecific competition intensity, in order to disentangle the contributions of these factors to biodiversity maintenance and their potential interactions. Alongside the resulting species richness, we also report which biomass-trait distribution can be expected under a given combination of processes leading to coexistence.

2 Methods

Models

The model described in Scranton and Vasseur (2016) is based on the Lotka-Volterra competition model. Fluctuations in the environment are introduced in the model by temperature-dependent intrinsic growth rates (see Eq. 1-2, all coefficients are defined in Table 1) so that the community dynamics can be expressed as:

$$\frac{dN_i}{dt} = r_i(\tau)N_i \left(1 - \sum_{j=1}^S \alpha_{ij}N_j \right) - mN_i \quad (1)$$

$$r_i(\tau) = a_r(\tau_0)e^{E_r \frac{(\tau - \tau_0)}{k\tau\tau_0}} f_i(\tau) \quad (2)$$

$$\text{where } f_i(\tau) = \begin{cases} e^{-|\tau - \tau_i^{opt}|^3/b_i}, & \tau \leq \tau_i^{opt} \\ e^{-5|\tau - \tau_i^{opt}|^3/b_i}, & \tau > \tau_i^{opt} \end{cases} \quad (3)$$

$$\text{and } b_i \text{ is defined by numerically solving } \int r_i(\tau)d\tau = A \quad (4)$$

Model parameters are detailed in Table 1, and we set their values to match the features of phytoplankton communities as in Scranton and Vasseur’s work (2016). The niche of each species is

defined by its thermal optimum τ_i^{opt} . Thermal performance curves defined in Eq. 3 are parameterized so that all species share the same niche area (Eq. 4), which sets a trade-off between maximum growth rates and niche width.

Table 1: Parameter definitions and values for the model described in Eqs. 1-4. Parameter values are not specified when they vary over time and/or with the species considered.

Name	Definition	Value (unit)
S	Initial number of species	60 (NA)
N_i	Biomass density of the i^{th} species	(kg/area)
τ	Temperature	(K)
$r_i(\tau)$	Growth rate of species i as a function of temperature	$(\frac{\text{kg}}{\text{kg} \times \text{year}})$
α	Strength of competition	0.001 (area/kg)
b_i	Normalization constant for the thermal decay rate	(K^3)
m	Mortality rate	$15(\frac{\text{kg}}{\text{kg} \times \text{year}})$
τ_0	Reference temperature	293 (K) / 20 ($^{\circ}\text{C}$)
$a_r(\tau_0)$	Growth rate at reference temperature	$386(\frac{\text{kg}}{\text{kg} \times \text{year}})$
E_r	Activation energy	0.467 (eV)
k	Boltzmann's constant	$8.6173324 \cdot 10^{-5} (\text{eV} \cdot \text{K}^{-1})$
$f_i(\tau)$	Fraction of the maximum rate achieved for the i^{th} species	(NA)
μ_τ	Mean temperature	293 (K)
σ_τ	Standard deviation for temperature	5 (K)
τ_{\min}	Minimum thermal optimum	288 (K)
τ_{\max}	Maximum thermal optimum	298 (K)
A	Niche breadth	$10^{3.1}(\frac{\text{kg}}{\text{kg} \times \text{year}})$
τ_i^{opt}	Thermal optimum for growth of the i^{th} species	(K)
θ	Scaling between random and seasonal noise	(0;1.3) (NA)
κ	Ratio of intra-to-interspecific competition strength	(1;10) (NA)

The original environmental forcing is a normally distributed variable centered on 293 K (20 $^{\circ}\text{C}$), with a 5 K dispersion. Temperature varies from one day to the next, but is kept constant throughout the day. At and above the daily scale, temperature could therefore be considered as a white noise (Vasseur and Yodzis, 2004). However, from a mathematical viewpoint, the noise is slightly autocorrelated as the integration process goes below the daily time step. We therefore use the expression ‘random noise’ to describe this forcing, as opposed to the ‘seasonal noise’ described hereafter. To construct the seasonal noise, we add to the random forcing signal a lower-frequency component, using a sinusoidal function with a period of 365 days (Eq. 5). We tune the ratio of low-to-high frequency with the variable θ so as to keep the same energy content - i.e., equal total

110 variance - in the forcing signal.

$$\tau(t) = \mu_\tau + \theta\sigma_\tau \sin(2\pi t) + \epsilon_t, \text{ where } \epsilon_t \sim \mathcal{N}\left(0, \sigma_\tau \sqrt{1 - \frac{\theta^2}{2}}\right) \quad (5)$$

111 Note that the upper limit for θ , $\sqrt{2}$, corresponds to a completely deterministic model which we
 112 do not explore here (but see Zhao (1991) proving bounded coexistence). We choose to keep the
 113 stochasticity in the signal and to model a plausible temperature signal with $\theta = 1.3$ (illustrated in
 114 Fig. 1b) when considering a seasonal forcing of the dynamics.

115 The formulation of the forced Lotka-Volterra model of Scranton and Vasseur (2016) implies
 116 a storage effect, as the net effect of competition exerted by species j on i is the product of the
 117 temperature-related growth rate $r_i(\tau)$ and the competitive strength α_{ij} exerted by species j multi-
 118 plied by its abundance N_j . Therefore, total net competition ($\sum_{j=1}^S r_i(\tau)\alpha_{ij}N_j$) covaries positively
 119 with the growth rate values $r_i(\tau)$, which defines the storage effect (Chesson, 1994; Fox, 2013; Ellner
 120 et al, 2016). To remove the assumption of an explicit storage effect, we create another version of
 121 the model using the mean value of a species' growth rate (\bar{r}_i) to weight the interaction coefficients
 122 (see Eq. 6). The mean growth rate value is computed by first generating the temperature time
 123 series and then averaging all r_i over the corresponding sequences of τ values.

$$\frac{dN_i}{dt} = N_i \left(r_i(\tau) - \sum_{j=1}^S \bar{r}_i \alpha_{ij} N_j \right) - mN_i \quad (6)$$

124 Following Eq. 6, net competition remains unaffected by the environmental conditions, in con-
 125 trast to intrinsic growth rates, while preserving the same average magnitude of competition as in
 126 Eq. 1.

127 Strong self-regulation is ensured by the addition of the coefficient κ , which is the ratio of intra-
 128 to-interspecific competition strength. We can therefore re-write the interaction coefficients α_{ij} in
 129 Eq. 7

$$\alpha_{ij} = \alpha (1 + (\kappa - 1)\delta_{ij}) \quad (7)$$

130 where δ_{ij} is the Kronecker symbol, equal to 1 if $i = j$ and to 0 otherwise. The value of the

parameter $\kappa = 10$ was chosen from analyses of phytoplanktonic data (Barraquand et al, 2018). Hereafter, the expression “strong self-regulation” characterizes dynamics where the intraspecific competition strength is 10 times higher than the interspecific competition strength, as opposed to “equal competitive strengths” where intra- and interspecific competition strengths are equal.

In addition to two types of environmental forcings (random noise with $\theta = 0$, and seasonal noise with $\theta = 1.3$), we compare the results for four versions of the original model: with and without an explicit storage effect (Eq. 1 and Eq. 6, respectively); with strong self-regulation or equal intra- and inter-competition strength ($\kappa = 10$ or $\kappa = 1$, respectively). These are summed up in Table 2.

$\frac{1}{N_i} \frac{dN_i}{dt} + m_i$	Storage effect	No storage effect
Strong self-regulation ($\kappa = 10$)	$r_i(\tau) \left(1 - \sum_{j=1}^S \alpha (1 + 9\delta_{ij}) N_j \right)$	$r_i(\tau) - \sum_{j=1}^S \bar{r}_i \alpha (1 + 9\delta_{ij}) N_j$
Equal competitive strengths ($\kappa = 1$)	$r_i(\tau) \left(1 - \sum_{j=1}^S \alpha N_j \right)$	$r_i(\tau) - \sum_{j=1}^S \bar{r}_i \alpha N_j$

Table 2: Growth rate of species i in the four models

139

140 Set-up

We replicate the ‘Species sorting’ experiment of Scranton and Vasseur (2016) so as to investigate how the structure of synthetic phytoplankton communities varies under the different scenarios we described above. We focus on the dynamics of a community initialized with 60 species with thermal optima uniformly spaced along the interval $[15^\circ\text{C}, 25^\circ\text{C}]$, and with the same initial density ($\frac{1}{\alpha S}$). Each simulation is run for 5000 years in 1-day intervals. When the density of a species drops below 10^{-6} , it is considered extinct. For each combination of parameters (type of environmental signal, storage effect and self-regulation), we run 100 simulations.

All simulations are run with Matlab’s ode45 algorithm, an adaptive Runge-Kutta (4,5) integration scheme with an absolute error tolerance of 10^{-8} , and relative error tolerance of 10^{-3} . The code is available in a GitHub repository¹.

¹<https://github.com/CoraliePicoche/Seasonality>

3 Results

Typical dynamics of the community following Eq. 1 (the model of Scranton and Vasseur, 2016), with both a purely Gaussian noise (original choice of Scranton and Vasseur, 2016; Fig. 1a) and a seasonal noise described in Eq. 5 (our variant, Fig. 1b), are shown in Fig. 1c and d, respectively. A sinusoidal forcing produces the strongly seasonally structured dynamics that are typical of phytoplankton. Even though only 5 species can be seen in Fig. 1c, there were 14 species still present at the end of the simulation forced by a random noise, with large disparities in the range of their biomasses. A third of the species kept a biomass above 10 kg/area (setting area = 1 ha, with a depth of a few meters, produces a realistic standing biomasses; Reynolds, 2006) while 6 out of the 14 species biomasses remained below the unit. All persisting species in the random noise simulation were clustered within a 3.2°C-range of thermal optima (see the biomass distribution as a function of the thermal optimum in Electronic Supplementary Material, Fig. A1). No obvious temporal patterns (e.g., cycles) could be seen in the community forced by random noise. On the contrary, seasonal cycles were clear in the seasonally-forced case of Fig. 1d. Only 4 species coexisted at the end of the simulation with seasonal noise, gathered in two groups with large thermal optimum differences (5.7°C between the maximum thermal optimum of the first group and the minimum thermal optimum of the second group). When temperatures were high, the group with higher thermal optima reached its maximum biomass, then as temperature decreases through the season, these species leave room for the growth of the low-temperature group.

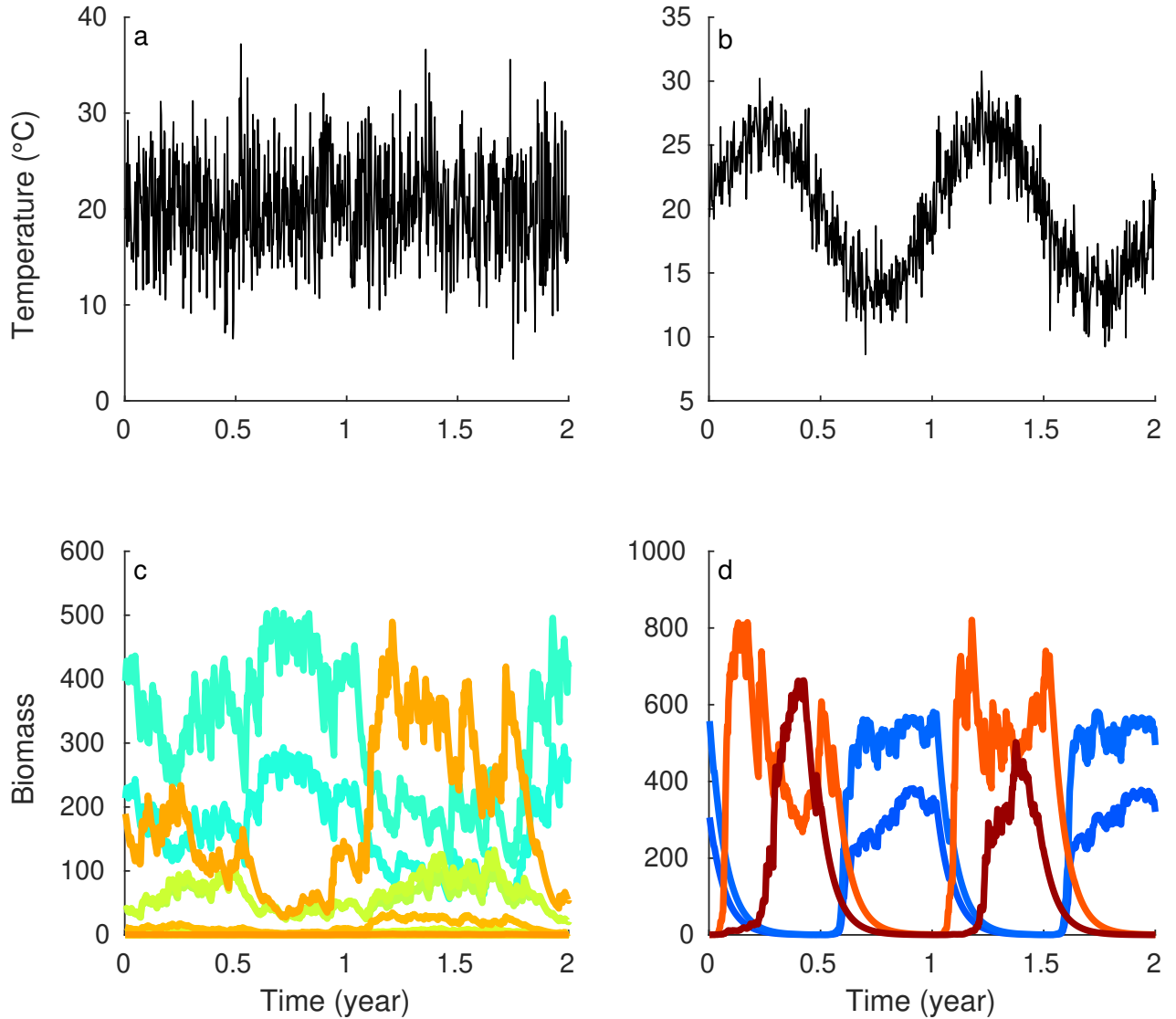


Figure 1: Time series of temperature (top; a-b) and extant species (bottom; c-d) for the 2 last years of a 5000-year simulation, with storage effect but no differences between intraspecific and interspecific competition strengths. The forcing temperature is either a random noise (a) or a seasonal noise (b), leading to community dynamics with more erratic fluctuations (c) vs seasonally structured fluctuations (d). Line colors of species biomasses correspond to their thermal optimum (from blue, corresponding to low thermal optimum, to red, corresponding to high thermal optimum).

170 The decrease in persistence due to seasonality observed in Fig. 1 was confirmed in all our
 171 simulations (Fig. 2). In cases where final species richness varied from one simulation to another
 172 (namely, the two middle cases in Fig. 2: with storage effect but without strong self-regulation, or
 173 without storage effect but with strong self-regulation), seasonality reduced the number of extant
 174 species to, on average, 27% and 48% of their original values, respectively (Fig. 2). A seasonal signal

175 therefore led to a much smaller average persistence. There was also less variance in persistence
176 between seasonally forced simulations compared to random noise simulations.

177 Both a strong self-regulation and the storage effect markedly increased persistence. Without
178 any of these coexistence mechanisms, only one species persisted at the end of the simulations. When
179 only the storage effect was present, the number of extant species varied between 8 and 20 ($14.8 \pm$
180 2.4) with random noise, or 2 and 6 (4.1 ± 0.7) with a seasonal signal. On the other hand, when
181 only a strong self-regulation was present, the number of extant species nearly doubled, varying
182 between 20 and 32 (27.5 ± 2.4), or 12 and 15 (13.3 ± 0.6), with a random or a seasonal noise,
183 respectively. Remarkably, when the storage effect and a strong self-regulation both affected the
184 community dynamics, all species persisted in the community: the number of species coexisting with
185 both mechanisms present is greater than the sum of the species coexisting with either mechanism
186 alone. The two mechanisms therefore combine superadditively, as their interaction has a positive
187 effect on the richness of the community.

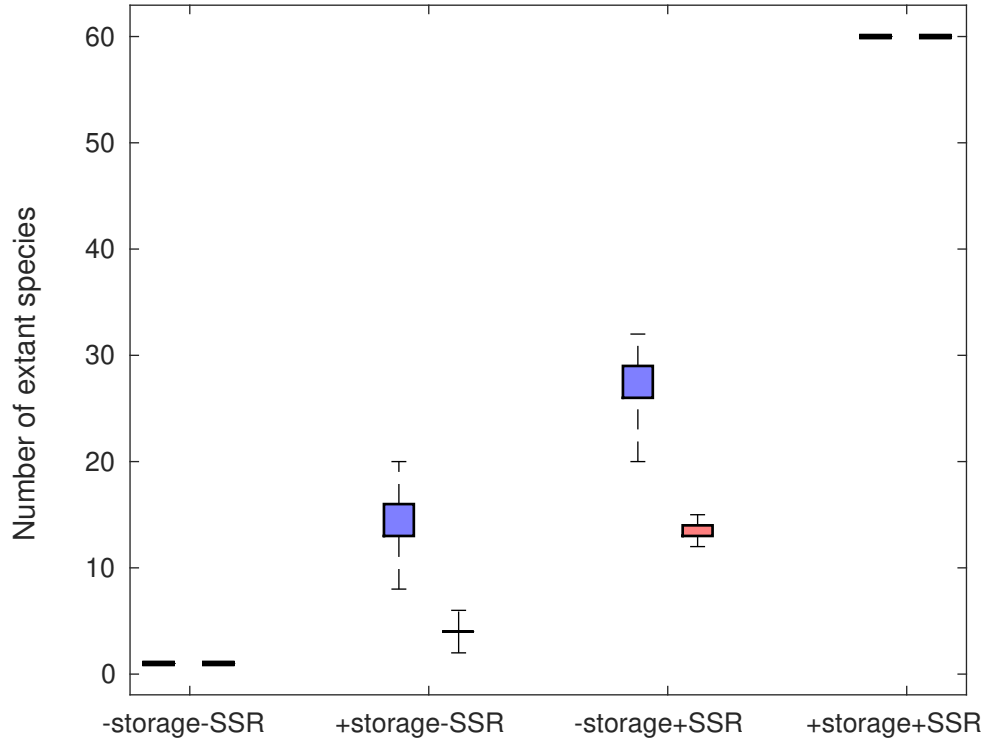


Figure 2: Number of species still present at the end of 100 simulations (5000 years each), initialized with 60 species, with a random (blue) or a seasonal forcing signal (red). The signs + or -storage refer to presence or absence of the storage effect, respectively; + / - SSR, presence or absence of Strong Self-Regulation, respectively. Community compositions are stable in the cases -storage-SSR and +storage+SSR, for which 1 or 60 species are still present at the end of all simulations, respectively. Due to low variance, the whiskers here represent min and max rather than 1.5 interquartile range.

188 The trait-biomass distribution of the community was affected by the type of forcing even
189 when the richness of the community was stable (Fig. 3). Without storage effect nor strong self-
190 regulation, there was only one species left at the end of the simulations. A random noise favored
191 species with intermediate thermal optima: the final species had a thermal optimum between 18.9°C
192 and 21.4°C (only a fourth of the initial range of thermal optima) for two simulations out of three
193 and the maximum final biomasses over 100 simulations was reached in this range (Fig. 3a). This
194 distribution may indicate a selection for the highest long-term growth rates, averaged over time (see
195 scaled growth rates in Fig. 3). Seasonality with no coexistence mechanisms also led to a single
196 final species but, in this case, the species always had a higher maximum growth rate (thermal
197 optimum above 22°C). Species with a higher thermal optimum were more likely to persist and to

198 reach a higher biomass at the end of the simulation. 38% of the simulations therefore ended with
199 the species having the highest temperature optimum, 25°C. The shift in trait distribution towards
200 higher maximum growth rates with a seasonal noise vs higher average growth rates with a random
201 noise was consistent for all model types considered.

202 When both the storage effect and strong self-regulation were present, the 60 initial species
203 coexist with almost no variation in their respective biomasses from one simulation to the next
204 (mean CV across simulations is 0.008, averaged across species, Fig. 3b and d). The forcing signal
205 modified only the distribution of biomasses, resulting in contrasted community structures despite
206 equal richness. With a random noise, the distribution was unimodal. On the contrary, a seasonal
207 signal led to a bimodal distribution (centered on 17.0°C and 24.4°C), each corresponding to one
208 season, with highest biomasses for higher thermal optima (Fig. 3d). The minimum biomass was
209 reached for the highest long-term average growth rate at an intermediate temperature (20.4°C).

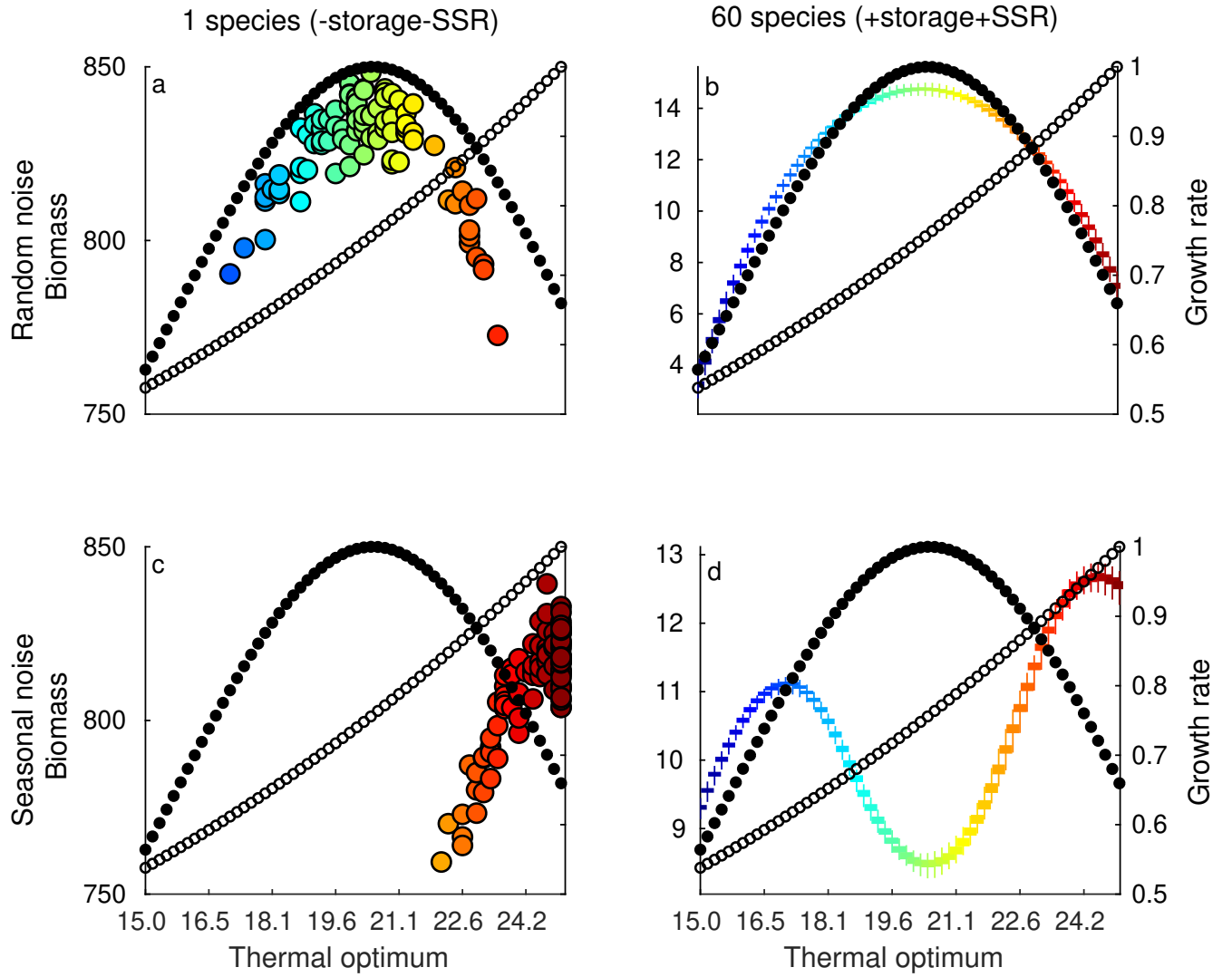


Figure 3: Mean biomass distribution over the last 200 years for 100 simulations, as a function of the species thermal optima. Here we consider the two stable-composition cases and two types of forcing signal. On the left column, simulations without storage effect nor strong self-regulation are presented. Only one species is present at the end of the simulations and its mean value is represented by one large colored circle per simulation. There can be several circles for the same species, corresponding to multiple simulations ending with this species alone. On the right column, simulations with storage effect and strong self-regulation are represented. All species are present at the end of the simulations and small boxplots present the variation in the temporal average of biomass with a given trait, for 100 simulations. The forcing signal is either a random (top) or a seasonal noise (bottom). Each species is identified by its thermal optimum through its color code. Scaled (divided by maximum) average and maximum growth rates are shown as small filled and open circles, respectively, and are indexed on the right y-axis.

210 In cases where the richness of the community varied, the overall shape (multimodal vs unimodal)
 211 of the marginal distribution of extant species with respect to the trait axis were similar for both
 212 types of environmental forcings (Fig. 4). By contrast, the type of coexistence mechanism generated

213 different shapes. Indeed, the storage effect (when acting alone) led to a multimodal biomass
 214 distribution with respect to thermal optima. We always observed 3 modes with a random noise
 215 and 3 modes in 95% of the seasonal simulations (Fig. 4a). With a random noise, extant species
 216 were grouped in rather similar clumps regarding species thermal optima (between 18.8°C and
 217 22.2°C) whereas species tended to be further apart in the seasonal case, covering a total range of
 218 7.7°C, with species grouping in the higher part of the thermal range, above 22°C. On the other
 219 hand, strong self-regulation led to a quasi-uniform biomass distribution (Fig. 4 b). Species in
 220 communities forced by a random noise stayed in the lower range of thermal optima (in 96% of the
 221 simulations, the highest thermal optimum was 22.4°C, see Fig. A2 in Electronic Supplementary
 222 Material) while they were filtered out in communities subjected to a seasonal fluctuation of their
 223 environment, for which species with thermal optima above 20.5°C persisted. As before (Fig. 3
 224 c,d), seasonality promoted species with a higher maximum growth rate, since the autocorrelated
 225 temperatures enabled them to achieve this highest growth rate for a longer period of time than a
 226 random noise would have.

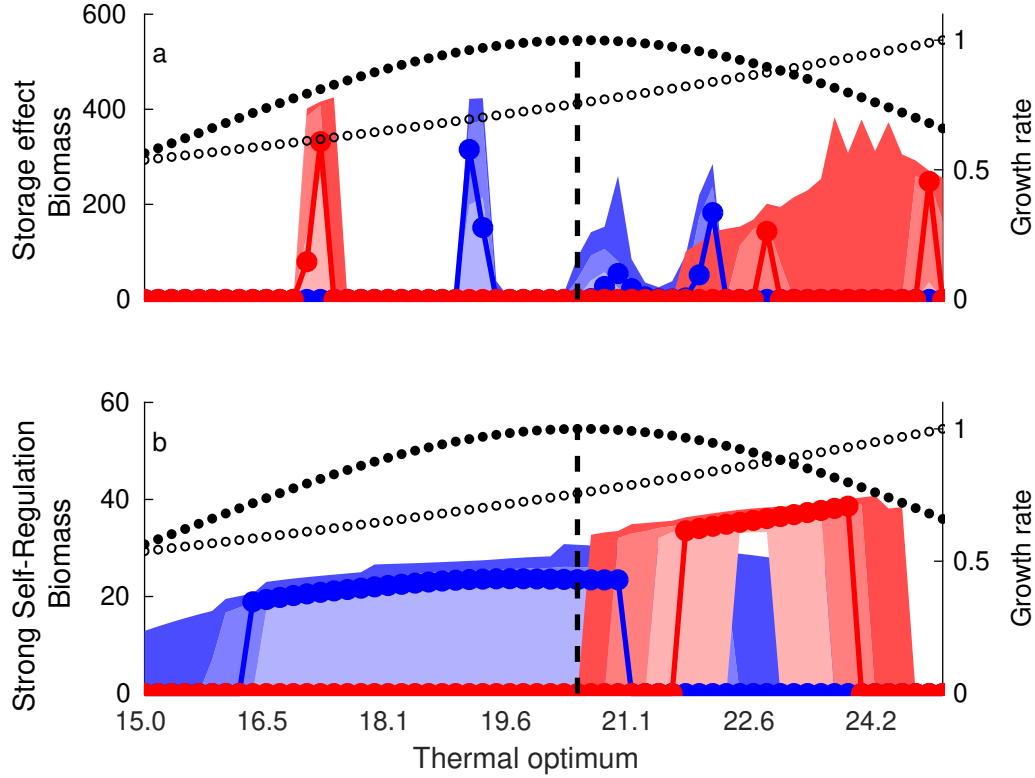


Figure 4: Mean biomass distribution over the last 200 years for 100 simulations, as a function of thermal optima, (a) with storage effect and equal competitive strengths and (b) without storage effect, with strong self-regulation. The forcing signal is either a random (in blue) or a seasonal noise (in red). Shades of the same color correspond to the 50th, 90th and 100th percentiles of the distributions while colored lines correspond to one representative simulation. Scaled (divided by maximum) average and maximum growth rates are shown as filled and open circles, respectively, and indexed on the right y-axis. The maximum average growth rate is indicated by the dashed line.

4 Discussion

We have simulated competitive Lotka-Volterra dynamics forced by a fluctuating temperature under a range of scenarios allowing more or less coexistence. Two coexistence mechanisms, the storage effect and strong self-regulation (i.e., intraspecific competition much stronger than interspecific competition), could be either present or absent, which led to four scenarios. These four scenarios were crossed with two possibilities for the forcing signal, a random noise (mostly white) and a stochastic yet seasonal signal, both with equal temporal variance. Our investigation therefore

234 built on the model of Scranton and Vasseur (2016), which included a random forcing signal and a
 235 storage effect, but considered seven additional combinations of mechanisms. This was motivated
 236 by our wish to include two observed features of phytoplankton dynamics: seasonal cycles (Winder
 237 and Cloern, 2010; Boyce et al, 2017) and strong self-regulation (Chesson, 2000; Adler et al, 2010;
 238 Barraquand et al, 2018). Many mechanisms can lead to intraspecific competition being stronger
 239 than interspecific competition: nonlinearities in the functional forms of competition or mutualism
 240 that contribute to increasing self-regulation (Kawatsu and Kondoh, 2018), or predation as well as
 241 parasitism (see e.g., the generalist predators in Haydon, 1994). Strong self-regulation seems an
 242 ubiquitous feature in competition networks of primary producers (Adler et al, 2018), and perhaps
 243 even more general networks (Barabás et al, 2017).

244 Before discussing the ecological interpretation of our results, we first recall some technical
 245 assumptions made in this study. All our simulations lasted for a fixed duration (5000 timesteps)
 246 as in Scranton and Vasseur (2016). While short- and medium-term transients (a few years to
 247 hundreds of years) are completely negligible at the end of the time series, very long transients can
 248 remain in this class of models (Scheffer and van Nes, 2006; Hastings et al, 2018): these are not
 249 mere artefacts but instead traduce the fact that some processes (e.g., exclusion of a species) can
 250 be really slow. We realized that convergence was incomplete after 5000 years in some cases (e.g.,
 251 random noise + storage effect + equal competitive strength). Such simulations would take up to 15
 252 000 years to converge and the rate of convergence would slow over time. We could have considered
 253 longer time intervals, but comparison with the values reported by Scranton and Vasseur (2016)
 254 would then have been compromised. Another way to shorten the transients, suggested by a referee
 255 (GB), is to vary the mortality parameter. This did not alter the conclusions (see Appendix B in
 256 Electronic Supplementary Material). Unfortunately, added variability also shifts the model further
 257 away from neutral dynamics (when intra and interspecific competition strengths are equal), which
 258 renders comparisons difficult. All things considered, we therefore kept the 5000-year time window
 259 for integration.

260 Another strong assumption pertains to competition coefficients. To allow for comparison with
 261 Scranton and Vasseur (2016), we did not introduce variability in intraspecific competition strength

262 or interspecific competition strength. By contrast, data-based coefficients vary between species
 263 (Barraquand et al, 2018), with a majority of weak interactions (as suggested in Wootton and
 264 Emmerson, 2005) and more variance in intraspecific coefficients. Stump (2017) recently considered
 265 the potential effects of competition coefficient variability (also called non-diffuse competition), as
 266 did Kokkoris et al (2002); more variance in interspecific competition strength is usually detrimental
 267 to coexistence for an equal amount of self-regulation (see Stump (2017) for a classification of
 268 the various effects). Setting the competition coefficients using a multidimensional trait-based
 269 framework, like that of Ashby et al (2017), would provide a natural development to the work
 270 presented here; it is in our opinion difficult to speculate on those variance effects because both
 271 intra- and interspecific competition coefficient variances may matter to community persistence.

272 Finally, our study is limited to communities whose species have fast population dynamics rel-
 273 ative to the yearly timescale, like phytoplankton and likely other fast-living organisms, so that
 274 many generations can occur in a year. Persistence in community with slower dynamics may be
 275 affected differently by seasonality (Miller and Klausmeier, 2017). This especially true for species
 276 with generations that extend over multiple years. In models where trophic interactions are im-
 277 plemented, seasonality has been shown to promote multiyear cycles and the existence of chaotic
 278 attractors (Rinaldi et al, 1993; Taylor et al, 2013; Tyson and Lutscher, 2016). These rich dynamics
 279 of consumers may feed back into the lower trophic levels: Dakos et al (2009) present a planktonic
 280 community with seasonally-entrained chaotic dynamics which may be partly due to zooplanktonic
 281 predation. Predation probably entails additional niche differences, possibly with an emerging self-
 282 regulation created by predation processes (Chesson, 2018), but it seems unlikely that we would be
 283 able to generate such dynamics with the models presented in this article. Additional nonlinearities
 284 would be needed to create intrinsically variable and chaotic dynamics.

285 With these assumptions in mind, we have found that first, temporally forced Lotka-Volterra
 286 dynamics cannot sustain any diversity with our phytoplankton-based set of parameters, unless the
 287 structure is geared to include either a storage effect or a strong self-regulation. Although this
 288 absence of diversity-enhancing effect of “pure” environmental variation has already been stated by
 289 other authors (Chesson and Huntly, 1997; Barabás et al, 2012; Fox, 2013; Scranton and Vasseur,

290 2016), this is not always intuitive (Fox, 2013), so we feel compelled to stress it once more: temporal
291 variation in growth rate alone cannot help coexistence within competitive communities. A nice
292 point made by Scranton and Vasseur (2016) was that a built-in storage effect in a forced Lotka-
293 Volterra model, parameterized for phytoplankton communities, could lead to a reasonable degree
294 of coexistence. Our investigation reproduced these results, using the random noise considered by
295 Scranton and Vasseur (2016). However, an arguably more lifelike noisy and seasonal temperature
296 forcing considerably lessened the richness of the community after 5000 years, decreasing from
297 15 to 4 species on average. Even imagining that groups represented here are genera or classes
298 rather than species, this is a fairly low diversity for a phytoplankton-like community (see e.g.,
299 Chapter 1 in Reynolds, 2006). This suggests that the storage effect may not, on its own, be
300 sufficient to maintain species-rich communities (e.g., dozens to hundreds of species). We have
301 therefore sought out whether a stronger self-regulation could maintain a higher diversity, using
302 field-based intra- vs intergroup (species or genera) competition strength ratio (Barraquand et al,
303 2018), where the intragroup density-dependence was estimated 10 times stronger. Implementing
304 such strong self-regulation, in the forced Lotka-Volterra models that we considered, produced a
305 higher level of diversity than the storage effect (almost double). Of course, the result is somehow
306 contingent upon the strength of self-regulation. Our estimates are a little stronger than what was
307 found in perennial plants (Adler et al, 2010), where interspecific competition was suggested 4 or 5
308 times stronger than intraspecific. Still, the widespread effects of natural enemies in phytoplankton
309 (zooplankton, parasites) may contribute to an increase in the self-regulation strength (Barraquand
310 et al, 2018; Chesson, 2018) relative to other systems, hence we believe that 10 times stronger
311 intraspecific competition constitutes a reasonable order of magnitude.

312 However, such strong self-regulation was still insufficient to maintain the whole community
313 diversity (60 species) by itself, especially when the seasonal forcing was considered (always de-
314 creasing species richness). The diversity within clumps of similar values of thermal optima was
315 considerably decreased once seasonality was implemented. This diversity reduction occurs because
316 within a season, the signal autocorrelation gives long, contiguous time intervals to the best com-
317 petitor to exclude its less adapted competitors. This makes the results likely to hold not only for

318 seasonal environments, but more generally for autocorrelated ones above the daily scale, i.e., “red”
319 noise. In contrast, the random noise scenario – which can be considered white noise above the
320 daily temporal scale – generates large temperature shifts more frequently, and thereby forbids such
321 competitive exclusion. In a seasonal setting, a species with the highest long-term (arithmetically)
322 averaged growth rate may not be the best competitor, and can disappear as a result of a strong
323 competition from both low- and high-temperature tolerant species. This holds with or without a
324 storage effect.

325 Our results may appear at odds with recent proposals that seasonal forcing in itself would help
326 maintain diversity (Sakavara et al, 2018). However, we compared the effect of seasonal forcing to
327 that of other forcing signals while controlling for total variance. Thus, the contrast between our
328 results and those of Sakavara et al (2018) may be due to the role of forcing variance over time: we
329 compare scenarios under a constant total variance, much like what is done when examining the
330 effect of noise color on population and community dynamics (Jiang and Morin, 2007; Ruokolainen
331 et al, 2009). Thinking in terms of signal spectrum, while seasonality may maintain slightly more
332 diversity than no forcing at all if a storage effect is present, the reddening of the environmental noise
333 due to such seasonality reduces coexistence. This result may be contingent upon the correlated
334 positive responses of the species growth rate to increases in the environmental variable (Ruokolainen
335 et al, 2009, and references therein).

336 The biomass-trait relationship was affected more marginally by the type of forcing signal.
337 The storage effect alone begot several clumps along the trait space (as observed by Scranton and
338 Vasseur, 2016). The seasonality that we added to the temperature signal led to more distant clumps
339 on the trait axis, with less species per clump. Conversely, strong self-regulatory mechanisms alone
340 led to relatively uniform biomass distributions, with species forming a single large cluster, which
341 covered a fraction of the initial trait space. Therefore, the shape of the distribution was mostly
342 affected by the coexistence mechanism at work while the average trait value was modified by
343 the type of environmental forcing, even though the mean value of the environmental signal did
344 not change. However, when both strong-self regulation and the storage effect were at play, the
345 biomass-trait distribution could either be unimodal or multimodal depending on the type of noise

346 driving the community dynamics (random or seasonal, respectively). This implies that the mere
347 observation of multimodality in a thermal preference trait-biomass distribution is not a proof of a
348 storage effect, or conversely, the proof of the influence of a seasonal environment.

349 The identification of multiple modes in biomass-trait distributions is relatively recent (Segura
350 et al, 2013; Loranger et al, 2018; D’Andrea et al, 2018, 2019), so we recommend to interpret
351 them with caution to avoid over-generalization. Barabás et al (2013) convincingly argued that
352 multimodality could arise from the demographic stochasticity of a single model run. However, with
353 several locations - or in a theoretical context as done here - one could average across locations.
354 Other mechanisms that we did not include in our models may produce similar clustered patterns
355 (Rael et al, 2018) or obfuscate clusters altogether: typically, strong self-regulation weakens the
356 clustering on the trait axis. Moreover, one should note that the occurrence of clustering is very
357 sensitive to the shape of the competition kernel: small differences in shape can shift the distribution
358 towards either clustered or uniform (Pigolotti et al, 2010). Finally, we recall that we focus on a
359 trait (thermal optimum) which clearly interacts with the environment: clustering may emerge on
360 another trait axis, such as size, which typically affects the competition coefficient, without having
361 any relationship to the storage effect (Segura et al, 2011, 2013; D’Andrea et al, 2018, 2019). We
362 therefore view clustering on the thermal preference trait axis as an interesting clue suggesting to
363 look for a storage effect, rather than any definite proof that the storage effect is at work.

364 In our previous empirical study of phytoplankton dynamics (Barraquand et al, 2018), we did
365 not find any storage effect. This does not mean that it could not be observed in other planktonic
366 systems: we studied a coastal ecosystem and focused a specific fraction of phytoplankton: relatively
367 large diatoms and dinoflagellates. However, given the consequences of the storage effect for species
368 richness and composition presented here, we are skeptical that the storage effect could, by itself,
369 fully explain phytoplankton diversity at any location. Our results suggest that in phytoplankton-
370 like seasonal environments, empirically-tuned self-regulation produces much more diversity than
371 the storage effect, when both are considered in isolation. The storage effect may therefore help
372 phytoplankton diversity maintenance, but only when combined to other mechanisms. This is all
373 the more likely that in our models, the combination storage effect + strong self-regulation is non-

additive: the cases where both self-regulation and the storage effect were present showed more diversity than generated by any mechanism on its own.

The above results suggest the very exciting idea that multiple coexistence mechanisms might combine superadditively to determine the richness of the community, thus helping us to better understand the astounding diversity of primary producers. This logic could, in principle, be extended to mechanisms that we have not considered here (e.g., spatial structure, specialized natural enemies, that could be as important here for plankton as they are for tropical trees, see Bagchi et al, 2014; Comita et al, 2014; Barraquand et al, 2018). Superadditivity, i.e. the positive effect of interactions between mechanisms can be measured either on community diversity, as we did here, or on the invasion growth rates (Ellner et al, 2019). Using the latter metric, previous research has however demonstrated that generalist seed predation could weaken the storage effect (Kuang and Chesson, 2009, 2010) thus different mechanisms might not always combine superadditively as we found here. That said, superadditivity has been found in some cases, i.e., pathogens could enhance the storage effect and broaden the conditions in which species could coexist (Mordecai, 2015). Better explaining plant or microbial diversity would then not be about selecting the best unique mechanism susceptible to explain the observed diversity, but rather better combining those mechanisms together. This may obviously be an annoyance for those who like to sharpen Occam's razor, but it clearly holds opportunities for theoreticians wishing to investigate synergies between coexistence mechanisms in highly diverse communities. Aside from the synergies between predator diversity-enhancing effects, strong self-regulation through various means and the storage effect (on the temporal axis), one obvious follow-up of this research would be interactions with spatial structure. Spatial structure occurs both endogeneously, through spatially restricted movements and interactions, and exogeneously, through spatial variation in environmental covariates (Bolker, 2003). Numerous studies (e.g., Bolker and Pacala, 1999; Murrell and Law, 2002) have shown that spatially restricted movements and interactions - very small-scale spatial structure - can help coexistence, which we believe would be especially important for phytoplankton since many species form colonies (Reynolds, 2006; see discussion in Barraquand et al, 2018). Moreover, although temperature is usually relatively spatially homogeneous over space, other drivers (e.g., rainfall, pH

in terrestrial ecosystems; salinity in aquatic ones) may exhibit spatial variation which is a main factor for coexistence (Snyder, 2008). The odds that different (resource) niches, natural enemies, spatial limits to competition and temporal niche partitioning all interact to promote the very high-dimensional coexistence observed in the field seem much higher than for any of those mechanisms alone. Whether the diversity-enhancing effects of these mechanisms combine subadditively (as in Kuang and Chesson, 2010) or superadditively like here is therefore worthy of further research.

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