

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

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January 28, 2019

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Abstract

Explaining coexistence in species-rich communities of primary producers remains a challenge for ecologists because of the 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. There are now several fluctuating-environment models allowing coexistence, but they often produce only a dozen of coexisting species at best. Here, we investigate how to create even 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 competition ratio based on empirical analyses, in which self-regulation usually 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, by itself, ensure the coexistence of all species present at the beginning of our simulations. Realistic seasonal environments only aggravated that picture, as they decreased persistence relative to a random environment. Our results suggest that combining different mechanisms for biodiversity maintenance into community models might be more fruitful than trying to find which mechanism explains best the observed diversity levels. We additionally highlight that while trait-biomass distributions provide some clues regarding coexistence mechanisms, they cannot indicate by themselves which coexistence mechanisms are at play.

Number of words: 242

Keywords: coexistence; seasonality; competition; phytoplankton; Lotka-Volterra; storage effect

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. 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; 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 ~~such as~~from immigration sustain diversity (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 is the model of 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).

54 How seasonality affects coexistence, as opposed to a randomly fluctuating environment, is therefore
55 a key feature of this paper. Our present work can be seen as an attempt to blend Scranton and
56 Vasseur (2016)’s stochastic framework with the periodic environments of Barabás et al (2012), to
57 better represent the mixture of stochastic and deterministic environmental forces affecting phyto-
58 plankton community dynamics.

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

68 Niche models have often been opposed to the neutral theory (Hubbell, 2001), where disper-
69 sal and drift can ensure a transient coexistence of many species, ~~though~~^{but} several authors have
70 attempted to blend niche and neutral processes (Gravel et al, 2006; Scheffer and van Nes, 2006;
71 Carmel et al, 2017). An intriguing offshoot of these attempts is the concept of ‘clumpy coexistence’
72 (Scheffer and van Nes, 2006), whereby simultaneous influences of both niche and neutral processes
73 create several clumps of similar species along a single trait axis. Niche differences enable coexis-
74 tence of multiple clumps (Chesson, 2000) while within-clump coexistence occurs through neutral
75 processes. This ‘emergent neutrality’ within groups (Holt, 2006) has been proposed as a unifying
76 concept for niche and neutral theories (even though the neutrality of the original model has been
77 disputed due to hidden niches, Barabás et al, 2013). Since then, clumpy coexistence has been
78 shown to occur in theoretical models incorporating a temporally variable environment interacting
79 with a thermal preference trait axis (Scranton and Vasseur, 2016; Sakavara et al, 2018). The re-
80 lationship (or absence thereof) between biomass-trait distributions and coexistence mechanisms is
81 currently debated (D’Andrea and Ostling, 2016), although there are suggestions that clustering on

82 trait axes under competition may be a robust find (d'Andrea et al., 2018, 2019)(D'Andrea et al,
83 2018, 2019).

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

91 2 Methods

92 *Models description*

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

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

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

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

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

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

99 defined by its thermal optimum τ_i^{opt} . Thermal performance curves defined in Eq. 3 are parameter-
100 ized so that all species share the same niche area (Eq. 4), which sets a trade-off between maximum
101 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 with time and/or 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_{ij}	Strength of competition of species $j \rightarrow i$	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)

102 The original environmental forcing is a normally distributed variable centered on 293 K (20 $^{\circ}\text{C}$),
103 with a 5 K dispersion. Temperature varies from one day to the next, but is kept constant through-
104 out the day. At the monthly or annual temporal scale usually used in ecological studies, tempera-
105 ture could therefore be considered as a white noise (Vasseur and Yodzis, 2004). However, from a
106 mathematical viewpoint, the noise is slightly autocorrelated as the integration process goes below
107 the daily time step. We therefore use the expression ‘random noise’ to describe this forcing, as
108 opposed to the ‘seasonal noise’ described hereafter. To construct the seasonal noise, we add to the
109 random forcing signal a lower-frequency component, using a sinusoidal function with a period of
110 365 days (Eq. 5). We tune the ratio of low-to-high frequency with the variable θ so as to keep the

111 same energy content - i.e., equal total variance - in the forcing signal.

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

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

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

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

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

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 focused 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 $\left(\frac{1}{\alpha S}\right)$. Each simulation was run for 5000 years in 1-day intervals. When the density of a species dropped below 10^{-6} , it was considered extinct. For each combination of parameters (type of environmental signal, storage effect and stabilizing niche differences), we ran 100 simulations.

All simulations were run with Matlab’s ode45 algorithm, an explicit 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>, will be made public upon acceptance or at the reviewer’s request and stored in Zenodo

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.

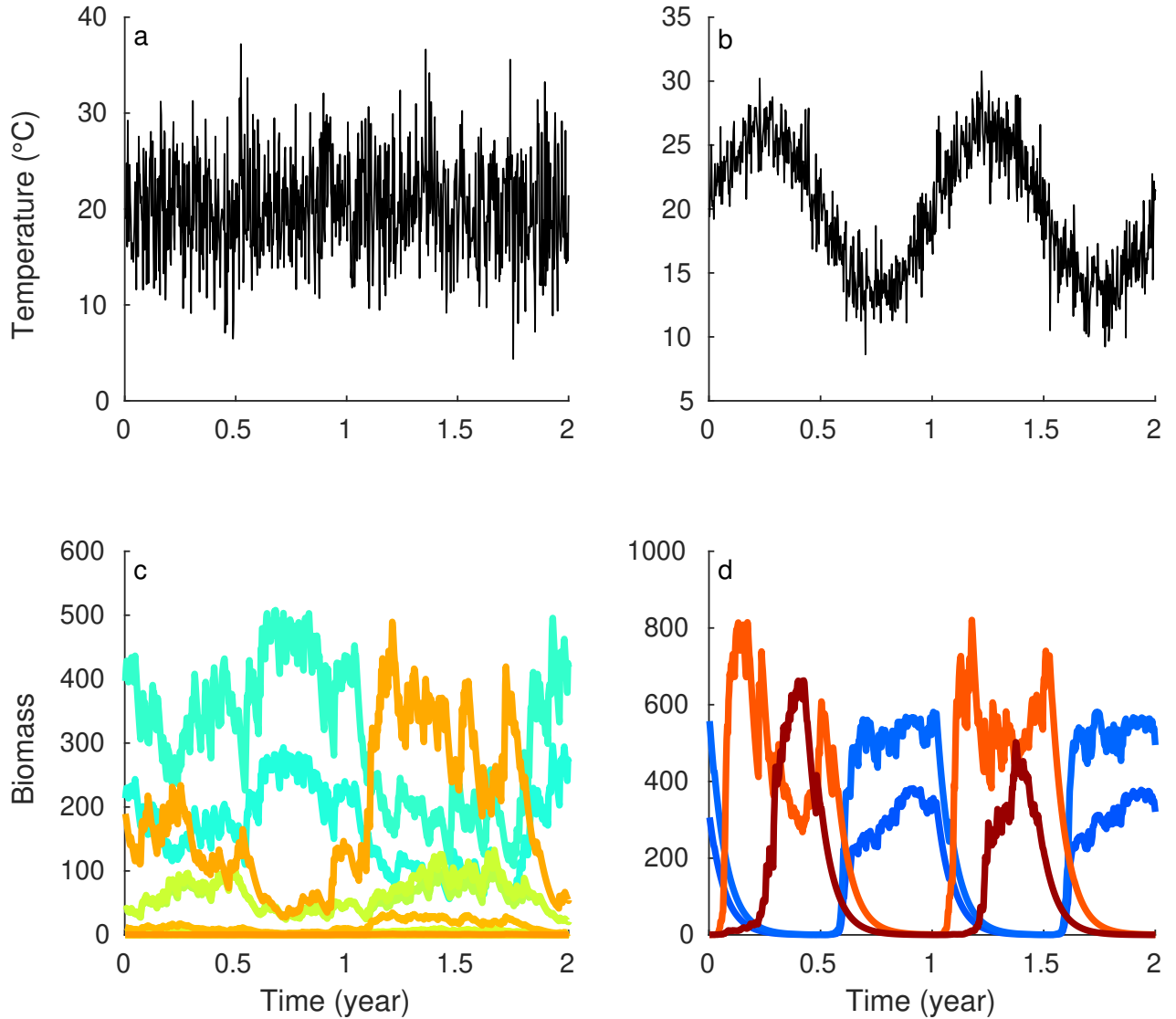


Figure 1: Time series of temperature (top; a-b) and extant species (bottom; c-d) for the 2 last years of a 5000-year simulation, with storage effect but no differences between intraspecific and interspecific competition strengths. The forcing temperature is either a random noise (a) or a seasonal noise (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.
179 When only the storage effect was present, the number of extant species varied between 8 and 20
180 (14.8 ± 2.4) with random noise, or 2 and 6 (4.1 ± 0.7) with a seasonal signal. On the other
181 hand, when only a strong self-regulation was present, the number of extant species nearly doubled,
182 varying between 20 and 32 (27.5 ± 2.4), or 12 and 15 (13.3 ± 0.6), with a random or a seasonal
183 noise, respectively. Remarkably, when the storage effect and a strong self-regulation both affected
184 the community dynamics, all species persisted in the community: the number of species coexisting
185 with both mechanisms present is therefore greater than the sum of the species coexisting with either
186 mechanism alone. The two mechanisms therefore combine superadditively, as their interaction has
187 a positive effect on the richness of the community.

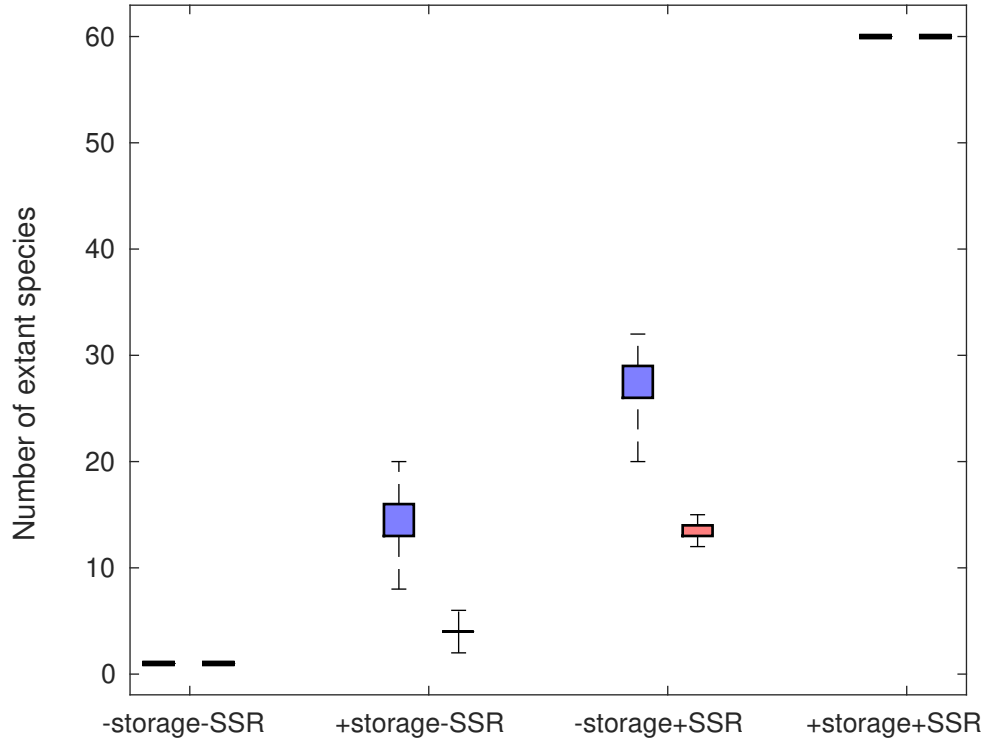


Figure 2: Number of species still present at the end of 100 simulations (5000 years each), initialized with 60 species, with a random forcing signal (blue) or a seasonal noise (red). The signs + or - storage refer to presence or absence of the storage effect, respectively; + / - SSR, presence or absence 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 storage effect and strong self-regulation were present, the 60 initial species coexisted
203 with small variations in biomasses for each species over the 100 simulations (mean CV=0.008
204 across simulations with either a random or a seasonal noise, Fig. 3b and d). The forcing signal
205 modified only the distribution of biomasses resulting in contrasted community structures despite
206 equal richness in both simulation types. With a random noise, the distribution was unimodal with
207 a maximum biomass reached for the second highest long-term average growth rate (corresponding
208 to a thermal optimum of 20.2°C). On the contrary, a seasonal signal led to a bimodal distribution
209 (centered on 17.0°C and 24.4°C), each corresponding to one season, with highest biomasses for
210 higher thermal optima (Fig. 3d). The minimum biomass was reached for the highest long-term
211 average growth rate at an intermediate temperature (20.4°C).

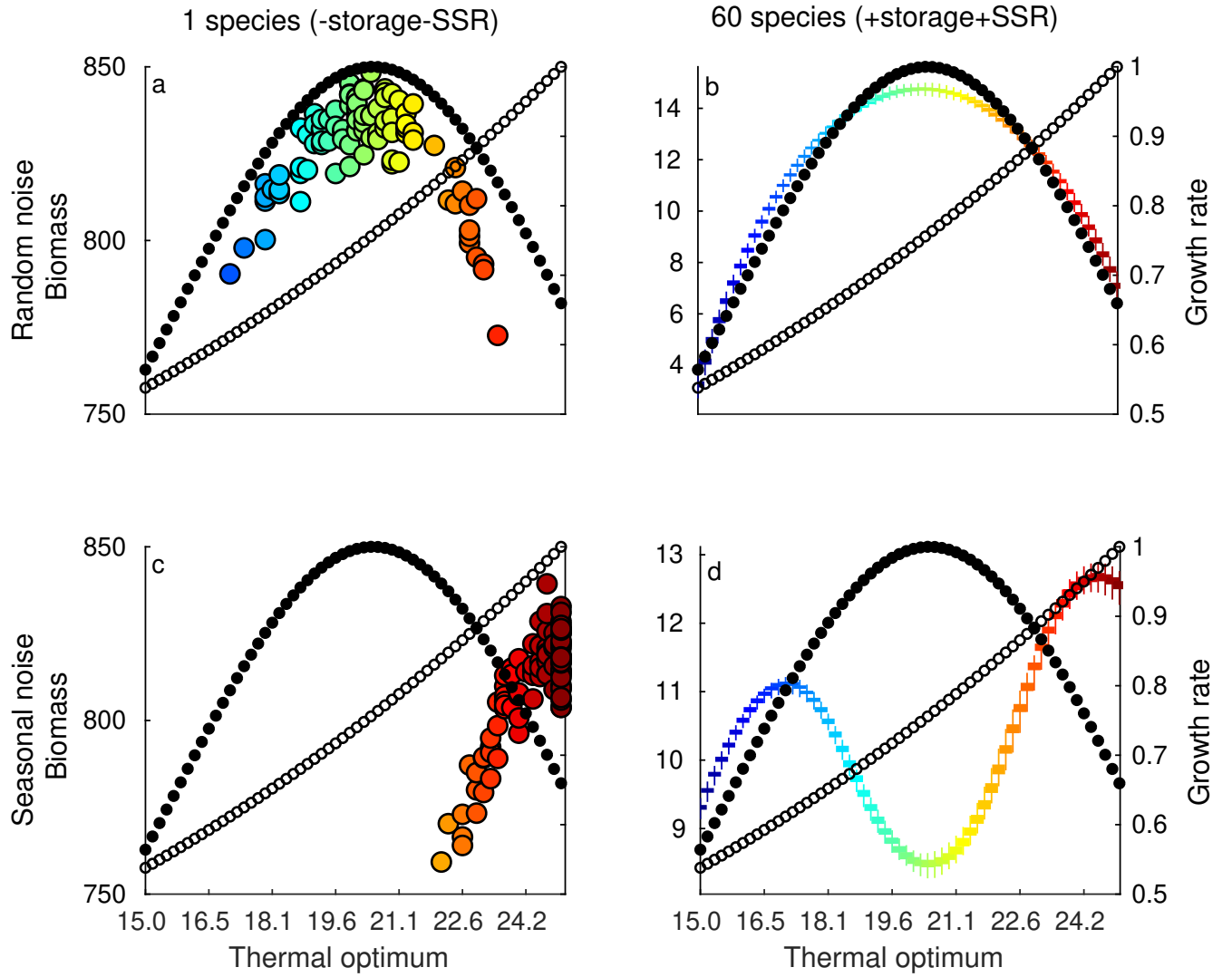


Figure 3: Mean biomass distribution over the last 200 years for 100 simulations, as a function of the species thermal optima. Here we consider the two stable-composition cases and two types of forcing signal. On the left column, simulations without storage effect nor strong self-regulation are presented. 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.

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

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

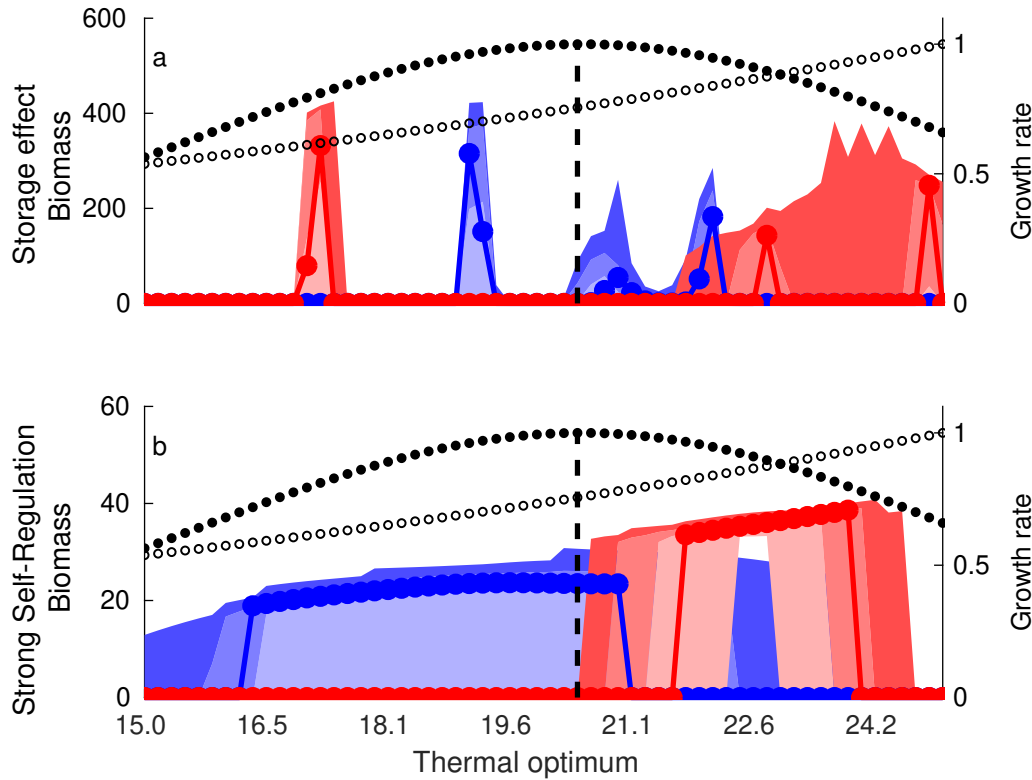


Figure 4: Mean biomass distribution over the last 200 years for 100 simulations, as a function of thermal optima, with storage effect and equal competitive strengths (a) and without storage effect, with strong self-regulation (b). The forcing signal is either a random (in blue) or a seasonal noise (in 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 (whose maximum is indicated by the dashed line) and maximum growth rates are shown as filled and open and circles, respectively, and indexed on the right y-axis.

4 Discussion

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

Before discussing the ecological interpretation of our results, we first recall some technical assumptions made in this study. All our simulations lasted for a fixed duration (5000 timesteps) as in Scranton and Vasseur (2016). ~~This means that~~ While short- and medium-term transients (a few years to hundreds of years) are completely negligible at the end of the time series, ~~but~~ very long transients can remain in this class of models (Hastings et al, 2018): ~~these are not mere artefacts but instead traduce the fact that some processes (e.g., exclusion of a species) can be really slow.~~ We realized that convergence ~~could be~~ was incomplete after 5000 years in some cases (e.g., random noise + storage effect + equal competitive strength). Such simulations would take up to 15 000 years to converge and the rate of convergence would slow over time, as can also be observed for similar models (Scheffer and van Nes, 2006). ~~We kept a fixed time integration window rather than waiting for convergence. From a technical standpoint, adding 10 000 years of numerical integration (or more) for the sake of reaching equilibrium is more challenging computationally, and~~ We could have considered longer time intervals, but comparison with the values reported by Scranton and Vasseur (2016) would then have been compromised. Another way to shorten the transients, suggested by a referee (GB), would be to vary the mortality parameter. This worked, and did not alter the conclusions (see Appendix B in Electronic Supplementary Material). Unfortunately, added variability also shifts the model further away from neutral dynamics, which renders comparisons difficult. ~~We checked this for robustness's sake and This did not alter the conclusions (see Appendix~~

263 ~~B in Electronic Supplementary Material).~~ WeAll things considered, we therefore kept the 5000-year
264 time window for integration.

265 Another strong assumption pertains to competition coefficients. To allow for comparison with
266 Scranton and Vasseur (2016), we did not introduce variability in intraspecific competition strength
267 or interspecific competition strength. By contrast, data-based coefficients vary between species
268 (Barraquand et al, 2018), with a majority of weak interactions (as suggested in Wootton and
269 Emmerson, 2005) and more variance in intraspecific coefficients. Stump (2017) recently considered
270 the potential effects of competition coefficient variability (also called non-diffuse competition), as
271 did Kokkoris et al (2002); more variance in interspecific competition strength is usually detrimental
272 to coexistence (see Stump (2017) for a classification of the various effects). Setting the competition
273 coefficients using a multidimensional trait-based framework, like that of Ashby et al (2017), would
274 provide a natural development to the work presented here; it is in our opinion difficult to speculate
275 on those variance effects because both intra- and interspecific competition coefficient variances may
276 matter to community persistence.

277 Finally, our study is limited to communities whose species have fast population dynamics rela-
278 tive to the yearly timescale, like phytoplankton and likely other fast-living organisms, so that many
279 generations can occur in a year. Persistence in community with slower dynamics may be affected
280 differently by seasonality (Miller and Klausmeier, 2017). This especially true for species with gen-
281 erations that extend over multiple years. In models where trophic interactions are implemented,
282 seasonality has been shown to promote ~~(e.g.,~~ multiyear cycles and the existence of chaotic attrac-
283 tors; (Rinaldi et al, 1993; Taylor et al, 2013; Tyson and Lutscher, 2016). ~~Inter-annual variability,~~
284 ~~as opposed to intra-annual seasonality, can also emerge in the presence of an additional trophic~~
285 ~~level.~~ These rich dynamics of consumers may feed back into the lower trophic levels: Dakos et al
286 (2009) present a planktonic community with seasonally-entrained chaotic dynamics which may be
287 partly due to zooplanktonic predation. Predation probably entails additional niche differences,
288 possibly with an emerging self-regulation created by predation processes (Chesson, 2018), but it
289 seems unlikely that we would be able to generate such dynamics with the models presented in this
290 article. Additional nonlinearities would be needed.

291 With these assumptions in mind, we have found that first, temporally forced Lotka-Volterra
 292 dynamics cannot sustain any diversity with our phytoplankton-based set of parameters, unless the
 293 structure is geared to include either a storage effect or a strong self-regulation. Although this
 294 absence of diversity-enhancing effect of “pure” environmental variation has already been stated by
 295 other authors (Chesson and Huntly, 1997; Barabás et al, 2012; Fox, 2013; Scranton and Vasseur,
 296 2016), this is not always intuitive (Fox, 2013), so we feel compelled to stress it once more: temporal
 297 variation in growth rate alone cannot help coexistence within competitive communities. A nice
 298 point made by Scranton and Vasseur (2016) was that a built-in storage effect in a forced Lotka-
 299 Volterra model, parameterized for phytoplankton communities, could lead to a reasonable degree
 300 of coexistence. Our investigation reproduced these results, using the random noise considered by
 301 Scranton and Vasseur (2016). However, an arguably more lifelike noisy and seasonal temperature
 302 forcing considerably lessened the richness of the community after 5000 years, decreasing from
 303 15 to 4 species on average. Even imagining that groups represented here are genera or classes
 304 rather than species, this is a fairly low diversity for a phytoplankton-like community (see e.g.,
 305 Chapter 1 in Reynolds, 2006). This suggests that the storage effect may not, on its own, be
 306 sufficient to maintain species-rich communities (e.g., dozens to hundreds of species). We have
 307 therefore sought out whether a stronger self-regulation could maintain a higher diversity, using
 308 field-based intra- vs intergroup (species or genera) competition strength ratio (Barraquand et al,
 309 2018), where the intragroup density-dependence was estimated 10 times stronger. Implementing
 310 such strong self-regulation, in the forced Lotka-Volterra models that we considered, produced a
 311 higher level of diversity than the storage effect (almost double). Of course, the result is somehow
 312 contingent upon the strength of self-regulation. Our estimates are a little stronger than what was
 313 found in perennial plants (Adler et al, 2010), where interspecific competition was suggested 4 or 5
 314 times stronger than intraspecific. Still, the widespread effects of natural enemies in phytoplankton
 315 (zooplankton, parasites) may contribute to increase the strength of self-regulation (Barraquand
 316 et al, 2018; Chesson, 2018) relative to other systems, hence we believe that 10 times stronger
 317 intraspecific competition constitutes a reasonable order of magnitude.

318 However, such strong self-regulation was still insufficient to maintain the whole community

diversity (60 species) by itself, especially when the seasonal forcing (always decreasing species richness) was considered. The diversity within clumps of similar values of thermal optima was considerably decreased once seasonality was implemented. This diversity reduction occurs because within a season, the signal autocorrelation gives long, contiguous time intervals to the best competitor to exclude its less adapted competitors. This makes the results likely to hold not only for seasonal environments, but more generally for autocorrelated ones above the daily scale, i.e., “red” noise. In contrast, the random noise scenario – which can be considered white noise above the daily temporal scales – generates large temperature shifts more frequently, and thereby forbids such competitive exclusion. In a seasonal setting, a species with the highest long-term (arithmetically) averaged growth rate may not be the best competitor, and can disappear as a result of a strong competition from both low- and high-temperature tolerant species. This holds with or without a storage effect.

Our results may appear at odds with recent proposals that seasonal forcing in itself would help maintain diversity (Sakavara et al, 2018). However, we compared the effect of seasonal forcing to that of other forcing signals while controlling for total variance. Thus, the contrast between our results and those of Sakavara et al (2018) may be due to the role of forcing variance over time—(we compare scenarios under a constant total variance, much like what is done when examining the effect of noise color on population and community dynamics (Ruokolainen et al, 2009)). Overall, Thinking in terms of signal spectrum, while seasonality may maintain slightly more diversity than no forcing at all if a storage effect is present, the reddening of the environmental noise due to such seasonality does not necessarily improve reduces coexistence. This increase in autocorrelation, despite keeping the same strength in the forcing signal, can either increase or decrease biomass fluctuations and synchrony, depending on species intrinsic growth rates, which can in turn destabilize a community (Ruokolainen et al, 2009).—This result may be contingent upon the correlated positive responses of the species growth rate to increases in the environmental variable (Ruokolainen et al, 2009, and references therein).

In addition to community diversity, the biomass-trait relationship also varied from one simulation to another. Some regularities did emerge across simulations though. The biomass-trait relationship

347 was affected more marginally by the type of forcing signal. The storage effect alone begot several
 348 clumps along the trait space (as observed by Scranton and Vasseur, 2016). The seasonality that
 349 we added to the temperature signal led to more distant clumps on the trait axis, with less species
 350 per clump. Conversely, strong self-regulatory mechanisms alone led to relatively uniform biomass
 351 distributions, with species forming a single large cluster, which covers a fraction of the initial trait
 352 space. Therefore, the shape of the distribution was mostly affected by the coexistence mechanism
 353 at work while the average trait value was modified by the type of environmental forcing, even
 354 though the mean value of the environmental signal did not change. However, when both strong-
 355 self regulation and the storage effect were at play, the biomass-trait distribution could either be
 356 unimodal or multimodal depending on the type of noise (random or seasonal, respectively) driving
 357 the community dynamics. This implies that the mere observation of multimodality in a thermal
 358 preference trait-biomass distribution is not a proof of a storage effect, or conversely, the proof of
 359 the influence of a seasonal environment. The biomass-trait distributions constitute clues to inter-
 360 pret community dynamics (D’Andrea and Ostling, 2016; Loranger et al, 2018) but they seem to
 361 provide no clear-cut answers. The identification of multiple modes in these distributions is also a
 362 relatively recent feature in models and data (Segura et al, 2013; D’Andrea et al, 2018, 2019) and,
 363 so we recommend to interpret them with caution to avoid over-generalization. Barabás et al (2013)
 364 convincingly argued that multimodality could arise from the demographic stochasticity of a single
 365 model run (with either self-regulation or neutrality, but without the clumpy coexistence emerging
 366 from a storage effect). However, our results are based on many model runs, for which either the
 367 storage effect alone or a storage effect + strong self-regulation in a seasonal context consistently
 368 produced multimodal distributions, while simulations without the storage effect always led to a
 369 single cluster along the trait axis. Our suggestion for empirical studies is as follows: if only one
 370 spatial location is observed, caution in interpreting multiple clumps on the trait axis is of course
 371 required, as Barabás et al (2013) highlighted. However, with several locations - or in a theoretical
 372 context - one could average across locations. Clumps in the thermal preference trait axis when
 373 averaged across model runs/locations may therefore be a “storage effect clue”, for the cases that we
 374 considered in the article. Of course, other mechanisms that we did not include in our models may

375 produce similar clustered patterns (Rael et al, 2018) or obfuscate ~~these patterns~~ clusters altogether
 376 ~~—~~: typically, strong self-regulation weakens the clustering on the trait axis. Moreover, one should
 377 note that the occurrence of clustering is very sensitive to the shape of the competition kernel:
 378 small differences in shape can shift the distribution towards either clustered or uniform (Pigolotti
 379 et al, 2010). ~~Moreover,~~ Finally, we recall that we focus on a trait (thermal optimum) which clearly
 380 interacts with the environment: clustering may emerge on another trait axis, such as size, which
 381 typically affects the competition coefficient, without having any relationship to the storage effect
 382 (Segura et al, 2011, 2013; D’Andrea et al, 2018, 2019). We therefore view clustering on the thermal
 383 preference trait axis as an interesting clue suggesting to look for a storage effect, rather than any
 384 definite proof that the storage effect is at work.

385 In our previous empirical study of ~~coastal~~ phytoplankton dynamics (Barraquand et al, 2018),
 386 we did not find any storage effect. This, ~~however,~~ does not mean that it could not be observed
 387 in other planktonic systems: we studied a coastal ecosystem and focused a specific fraction of
 388 phytoplankton: relatively large diatoms and dinoflagellates. However, ~~g~~Given the consequences of
 389 the storage effect for species richness and composition presented here, we are skeptical that the
 390 storage effect could, by itself, ~~help explaining~~ fully explain phytoplankton diversity at any location.
 391 ~~However,~~ ~~o~~Our results suggest that in phytoplankton-like seasonal environments, ~~even though~~
 392 empirically-tuned self-regulation produces much more diversity than the storage effect, when both
 393 are considered in isolation. ~~T~~The storage effect ~~can~~ may therefore help phytoplankton diversity
 394 maintenance, but only when combined to other mechanisms. ~~Indeed,~~ This is all the more likely
 395 that in our models, the combination storage effect + strong self-regulation is non-additive: the
 396 cases where both self-regulation and the storage effect were present showed more diversity than
 397 generated by any mechanism on its own.

398 The above results suggest the very exciting idea that multiple coexistence mechanisms might
 399 combine superadditively to determine the richness of the community, thus helping us to better
 400 understand the astounding diversity of primary producers. This logic could, in principle, be ex-
 401 tended to mechanisms that we have not considered here (e.g., spatial structure, specialized natural
 402 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). The effect of interacting mechanisms can be measured either on community diversity, as we did here, or on processes rates directly, e.g. the invasion growth rates. 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 storage effects (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.

430 Acknowledgements

431 We thank Alix Sauve for thoughtful comments and some bibliographic references. We are very
432 grateful to György Barabás and an anonymous referee for their constructive feedback. This study
433 was supported by the French ANR through LabEx COTE (ANR-10-LABX-45).

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