

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 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.

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

1 Introduction

The continued maintenance of diversity in spite of widespread competition has bewildered ecologists, especially for primary producers such as phytoplankton that share the same basic resources (Hutchinson, 1961). The first solution that has been proposed for the 'paradox of the plankton' was the temporal variation of the environment. However, 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 relative nonlinearity of competition (Armstrong and R., 1980; Chesson, 2000; Descamps-Julien and Gonzalez, 2005; Fox, 2013) need to be introduced for diversity to maintain. Richness rarely exceeds a handful of species in this type of model, except when external inputs such as immigration maintain the dynamics (Jabot and Lohier, 2016). To our knowledge, the effect of temporal variability on persistence in competition models has mostly been tested in theoretical communities of 2 to 3 species (e.g., Chesson and Huntly, 1997; Litchman and Klausmeier, 2001; 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).

Seasonality can strongly affect the dynamics of communities (Rinaldi et al, 1993; 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

54 deterministic environmental forces affecting phytoplankton community dynamics.

55 Niche differences between species, leading to intraspecific interaction stronger than interspecific
56 interactions, has recently been confirmed as a key mechanism in terrestrial plant communities
57 (Adler et al, 2018), animal communities (Mutshinda et al, 2009), and phytoplanktonic communities
58 (Barraquand et al, 2018). The interaction between environment variability and niche overlap has
59 been investigated by Abrams (1976) but his results did not extend to communities more diverse
60 than 4 species.

61 Niche models have often been opposed to the neutral theory (Hubbell, 2001). An intriguing
62 offshoot of the niche vs neutrality debate is the concept of ‘clumpy coexistence’ (Scheffer and van
63 Nes, 2006), whereby simultaneous influences of both niche and neutral processes create several
64 clumps of similar species along a single trait axis. Niche differences enable coexistence of multiple
65 clumps (Chesson, 2000) while within-clumps coexistence occurs through neutral processes. This
66 ‘emergent neutrality’ within groups (Holt, 2006) has been proposed as a unifying concept for
67 niche and neutral theories even though the neutrality of such model has been disputed due to
68 hidden niches (Barabás et al, 2013). Since then, clumpy coexistence has appeared in theoretical
69 models incorporating temporal variations (Scranton and Vasseur, 2016; Sakavara et al, 2018). The
70 relationship (or absence thereof) between biomass-trait distributions and coexistence mechanisms
71 is currently debated (D’Andrea and Ostling, 2016).

72 Here, we therefore try to establish what are the relative contributions to coexistence of the
73 storage effect vs strong self-regulation, in a phytoplankton-like theoretical community model. We
74 consider both species richness and the emerging biomass-trait distributions. This led us to cross
75 different combinations of seasonality in the forcing signal, presence of the storage effect or not, and
76 intra- vs interspecific competition intensity, in order to disentangle the contributions of all these
77 factors to biodiversity maintenance.

78 ~~There has been a rich debate in theoretical ecology on how to reconcile niche and neutral~~
79 ~~perspectives on species coexistence (Gravel et al, 2006; Carmel et al, 2017). Under the neutral~~
80 ~~perspective, all species have equal birth and death rates and compete equally (since space is limited)~~
81 ~~whilst under the niche perspective, birth and death rates can vary between species and various~~

mechanisms contribute to increasing intraspecific over interspecific competition (Hubbell, 2001). However, as it has been pointed out repeatedly, niche and neutral processes are not mutually exclusive: they may actually act together to produce observed species coexistence (Gravel et al, 2006; Mutshin

An intriguing offshoot of the niche vs neutrality debate 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. Classical stabilizing niche differences (SNDs), such as a net intraspecific competition stronger than interspecific competition, enable coexistence of multiple clumps (Chesson, 2000), while within-clump coexistence occurs through neutral processes (Hubbell, 2001; Munoz and Huneman, 2016), as species that differ too little in their fitnesses cannot exclude themselves out on reasonable timeframes. Indeed, clumps on the trait axis eventually thin out in absence of immigration, but transient coexistence can last for extended periods of time. This ‘emergent neutrality’ within groups (Holt, 2006) has been proposed as a unifying concept for the niche and neutral theories. The findings of Scheffer and van Nes (2006) have been disputed due to hidden niches in the original model (Barabás et al, 2013). Hidden niches emerge through stronger intraspecific competition mediated by an additional predation-like term (Barabás et al, 2013). This makes coexistence in the Scheffer and van Nes model more similar to that of the classical Lotka-Volterra model (Barabás et al, 2016), so that coexistence within clumps is not exactly neutral. Still, the idea that niche and neutral assembly can mould communities stays potent (Haegeman and Loreau, 2011; Vergnon et al, 2013). Since then, several studies have suggested that ‘clumpy coexistence’ can occur in theoretical models, most notably models incorporating temporal variation (Scranton and Vasseur, 2016; Sakavara et al, 2018). In these temporal-variation models, equal competitive strengths are combined with other mechanisms like the storage effect (or temporal niche partitioning, that is an equivalent concept for forced Lotka-Volterra models, Barabás et al, 2012; Scranton and Vasseur, 2016). The storage effect increases the possibility of coexistence by making the interaction strength covary positively with a fluctuating environmental quality (see also Barabás et al, 2012).

Here, we build on the work of Scranton and Vasseur (2016) to investigate the possibility of

110 coexistence through species response to fluctuating environments. Our enthusiasm for the Seranton and Vasseur
 111 model stems from our interest in phytoplankton communities, that inspired their thermal preference
 112 curves modeling intrinsic growth rates. However, Seranton and Vasseur (2016) described daily
 113 temperature as a random noise, i.e., independent and identically distributed Gaussian random
 114 variates over time. This appeared to us a key assumption to relax. Under most latitudes,
 115 temperature is indeed a seasonal signal, and seasonal forcing can strongly affect the dynamics of the
 116 community considered (Vesipa and Ridolfi, 2017). Hence, over short timescales, random temporal
 117 variations often only add noise to a largely deterministic seasonal trend. Our present work can
 118 therefore be seen as an attempt to blend Seranton and Vasseur (2016)’s stochastic framework with
 119 the periodic environments of Barabás et al (2012), to better represent the mixture of stochastic
 120 and deterministic environmental forces affecting phytoplankton community dynamics.

121 Because many phytoplankton species or genera respond in similar ways to temperature despite
 122 having different optimas (Moisan et al, 2002), we hypothesized that a large seasonal variation
 123 might not necessarily foster species coexistence. In fact, similar responses to seasonal fluctuations
 124 should lead to an increased synchrony of species abundances which, in turn, should theoretically
 125 mitigate the expected temporal partitioning. How seasonality affects coexistence (as opposed to a
 126 purely randomly fluctuating environment) is therefore a key feature of this paper. In particular, we
 127 contrast cases where the storage effect is present vs absent, which conveniently maps to two different
 128 parameterizations of the forced Lotka-Volterra model. Moreover, the overall diversity obtained at
 129 the end of the simulations with Seranton and Vasseur (2016)’s model was relatively low compared
 130 to what we usually observe in phytoplankton communities (several dozens to hundreds of species).
 131 We have therefore sought out which mechanisms would foster a truly species-rich community for
 132 extended periods of time.

133 In an empirical study combining phytoplankton community-level time series and multivariate
 134 autoregressive models (Barraquand et al, 2018), we found that despite a large influence of the
 135 environment (including temperature, irradiance, and other factors), a strong intraspecific (or
 136 intragenus) competition, when compared to interspecific interaction coefficients, was most likely
 137 the key driver of species coexistence. In other words, strong self-regulation had a large role to play

138 in maintaining species diversity in coastal phytoplankton (Barraquand et al, 2018). These high
 139 intraspecific interaction strengths mirror those found in a number of terrestrial plant communities
 140 (Adler et al, 2018) and in animal communities (Mutshinda et al, 2009).

141 Here, we therefore try to establish what are the relative contributions to coexistence of the
 142 storage effect vs strong self-regulation, in a phytoplankton-like theoretical community model.
 143 This led us to cross different combinations of seasonality in the forcing signal, presence of the
 144 storage effect or not, and intra- vs interspecific competition intensity, in order to disentangle the
 145 contributions of all these factors to biodiversity maintenance.

146 2 Methods

147 *Models description*

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

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

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

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

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

152 Model parameters are detailed in Table 1, and we set their values to match the features of
 153 phytoplankton communities as in Scranton and Vasseur's work (2016). The niche of each species is
 154 defined by its thermal optimum τ_i^{opt} . Thermal performance curves defined in Eq. 3 are parameter-

155 ized so that all species share the same niche area (Eq. 4), which sets a trade-off between maximum
 156 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)

157 The original environmental forcing is a normally distributed variable centered on 293 K (20 $^{\circ}\text{C}$),
 158 with a 5 K dispersion. Temperature varies from one day to the next, but is kept constant through-
 159 out the day. At the monthly or annual temporal scale usually used in ecological studies, tempera-
 160 ture could therefore be considered as a white noise (Vasseur and Yodzis, 2004). However, from a
 161 mathematical viewpoint, the noise is slightly autocorrelated as the integration process goes below
 162 the daily time step. We therefore use the expression ‘random noise’ to describe this forcing, as
 163 opposed to the ‘seasonal noise’ described hereafter. To construct the seasonal noise, we add to the
 164 random forcing signal a lower-frequency component, using a sinusoidal function with a period of
 165 365 days (Eq. 5). We tune the ratio of low-to-high frequency with the variable θ so as to keep the
 166 same energy content - i.e., equal total variance - in the forcing signal.

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

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

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

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

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

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

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

185 where δ_{ij} is the Kronecker symbol, equal to 1 if $i = j$ and to 0 otherwise. The value of the
 186 parameter $\kappa = 10$ was chosen from analyses of phytoplanktonic data (Barraquand et al, 2018)¹.

¹~~The values of non-zero interspecific competition coefficients reported in Fig. 5 of Barraquand et al (2018) are~~

187 Hereafter, the expression “strong self-regulation” characterizes dynamics where the intraspecific
 188 competition strength is 10 times higher than the interspecific competition strength, as opposed to
 189 “equal competitive strengths” where intra- and interspecific competition strengths are equal.

190 In addition to two types of environmental forcings (random noise with $\theta = 0$, and seasonal
 191 noise with $\theta = 1.3$), we compare the results for four formulations of the model: with and without
 192 an explicit storage effect (Eq. 1 and Eq. 6, respectively); with strong self-regulation or equal intra-
 193 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

194

195 Set-up

196 We replicate the ‘Species sorting’ experiment of Scranton and Vasseur (2016) so as to investigate
 197 how the structure of synthetic phytoplankton communities varies under the different scenarios we
 198 described above. We focused on the dynamics of a community initialized with 60 species with
 199 thermal optima uniformly spaced along the interval $[15^\circ\text{C}, 25^\circ\text{C}]$, and with the same initial density
 200 $(\frac{1}{\alpha S})$. Each simulation was run for 5000 years in 1-day intervals. When the density of a species
 201 dropped below 10^{-6} , it was considered extinct. For each combination of parameters (type of
 202 environmental signal, storage effect and stabilizing niche differences), we ran 100 simulations.

203 All simulations were run with Matlab’s ode45 algorithm, an explicit Runge-Kutta (4,5) inte-
 204 gration scheme with an absolute error tolerance of 10^{-8} , and relative error tolerance of 10^{-3} . The
 205 code is available in a GitHub repository².

~~somehow higher than here (and κ lower, closer to 4) because the best-fitting model actually set to zero some
 intergroup competition coefficients; using a model where all α_{ij} are non-zero leads in contrast to $\kappa = 10$.~~

²<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 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.

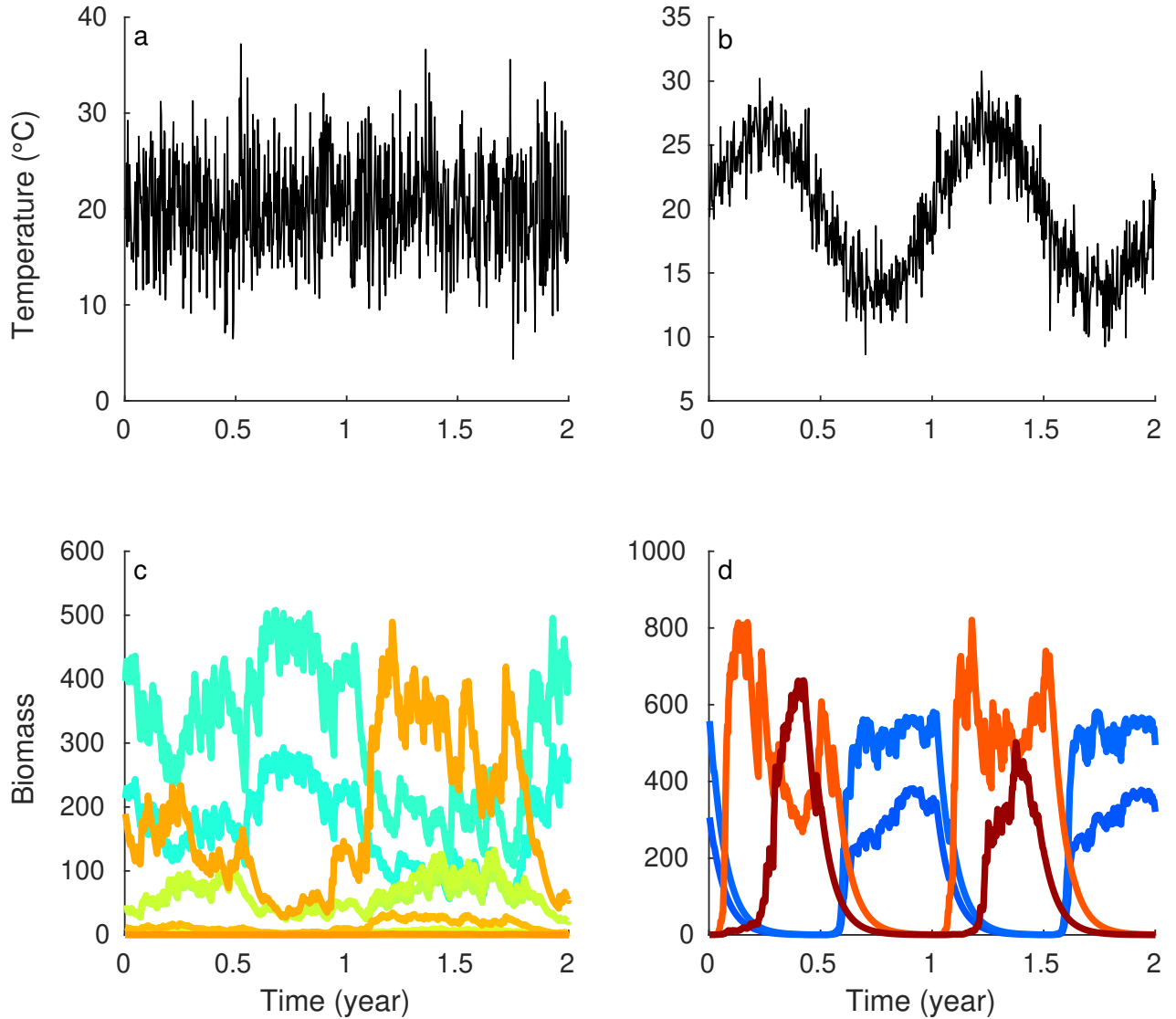


Figure 1: Time series of temperature (top; a-b) and extant species (bottom; c-d) for the 2 last years of a 5000-year simulation, with storage effect but no differences between intraspecific and interspecific competition strengths. The forcing temperature is either a random noise (a) or a seasonal noise (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).

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

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

232 Both a strong self-regulation and the storage effect markedly increased persistence. Without
233 any of these coexistence mechanisms, only one species persisted at the end of the simulations.
234 When only the storage effect was present, the number of extant species varied between 8 and 20
235 (14.8 ± 2.4) with random noise, or 2 and 6 (4.1 ± 0.7) with a seasonal signal. On the other
236 hand, when only a strong self-regulation was present, the number of extant species nearly doubled,
237 varying between 20 and 32 (27.5 ± 2.4), or 12 and 15 (13.3 ± 0.6), with a random or a seasonal
238 noise, respectively. Remarkably, when the storage effect and a strong self-regulation both affected
239 the community dynamics, all species persisted in the community: the number of species coexisting
240 with both mechanisms present is therefore greater than the sum of the species coexisting with either
241 mechanism alone. The two mechanisms therefore combine superadditively, as their interaction has
242 a positive effect on the richness of the community. ; while neither of these mechanisms was able
243 to produce that result alone, for either random and seasonal noise.

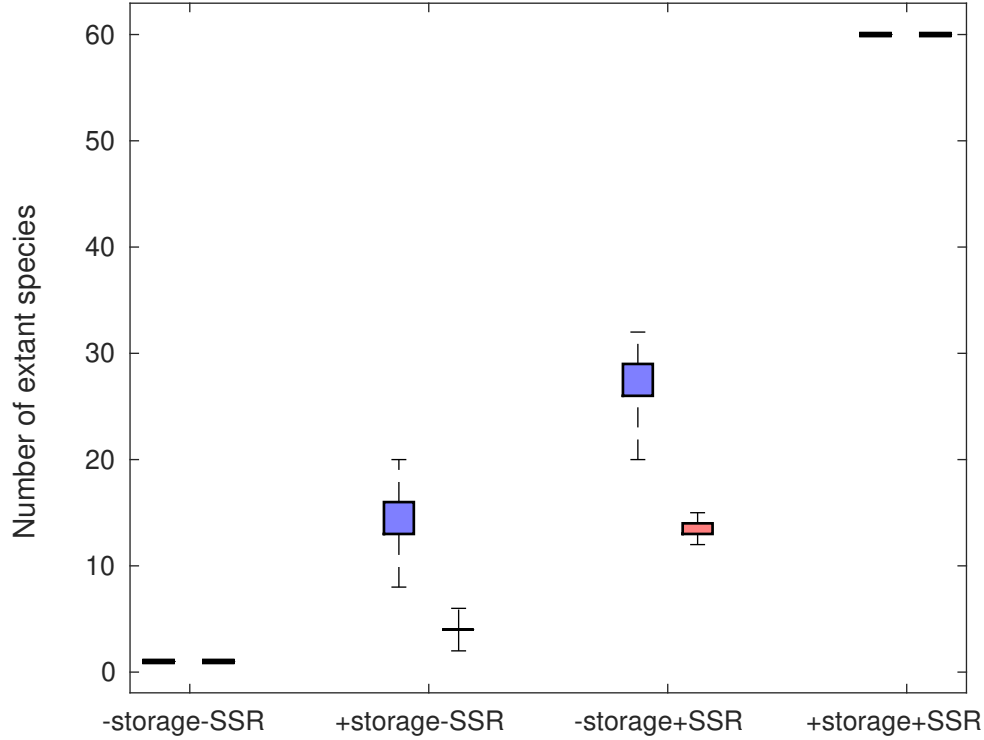


Figure 2: Number of species still present at the end of 100 simulations (5000 years each), initialized with 60 species, with a random forcing signal (blue) or a seasonal noise (red). The signs + or - storage refer to presence or absence of the storage effect, respectively; + / - SSR, presence or absence 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.

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

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

When both storage effect and strong self-regulation were present, the 60 initial species coexisted with small variations in biomasses for each species over the 100 simulations (mean CV=0.008 across simulations with either a random or a seasonal noise, Fig. 3b and d). The forcing signal modified only the distribution of biomasses resulting in contrasted community structures despite equal richness in both simulation types. With a random noise, the distribution was unimodal with a maximum biomass reached for the second highest long-term average growth rate (corresponding to a thermal optimum of 20.2°C). On the contrary, a seasonal signal led to a bimodal distribution (centered on 17.0°C and 24.4°C), each corresponding to one season, with highest biomasses for higher thermal optima (Fig. 3d). The minimum biomass was reached for the highest long-term average growth rate at an intermediate temperature (20.4°C).

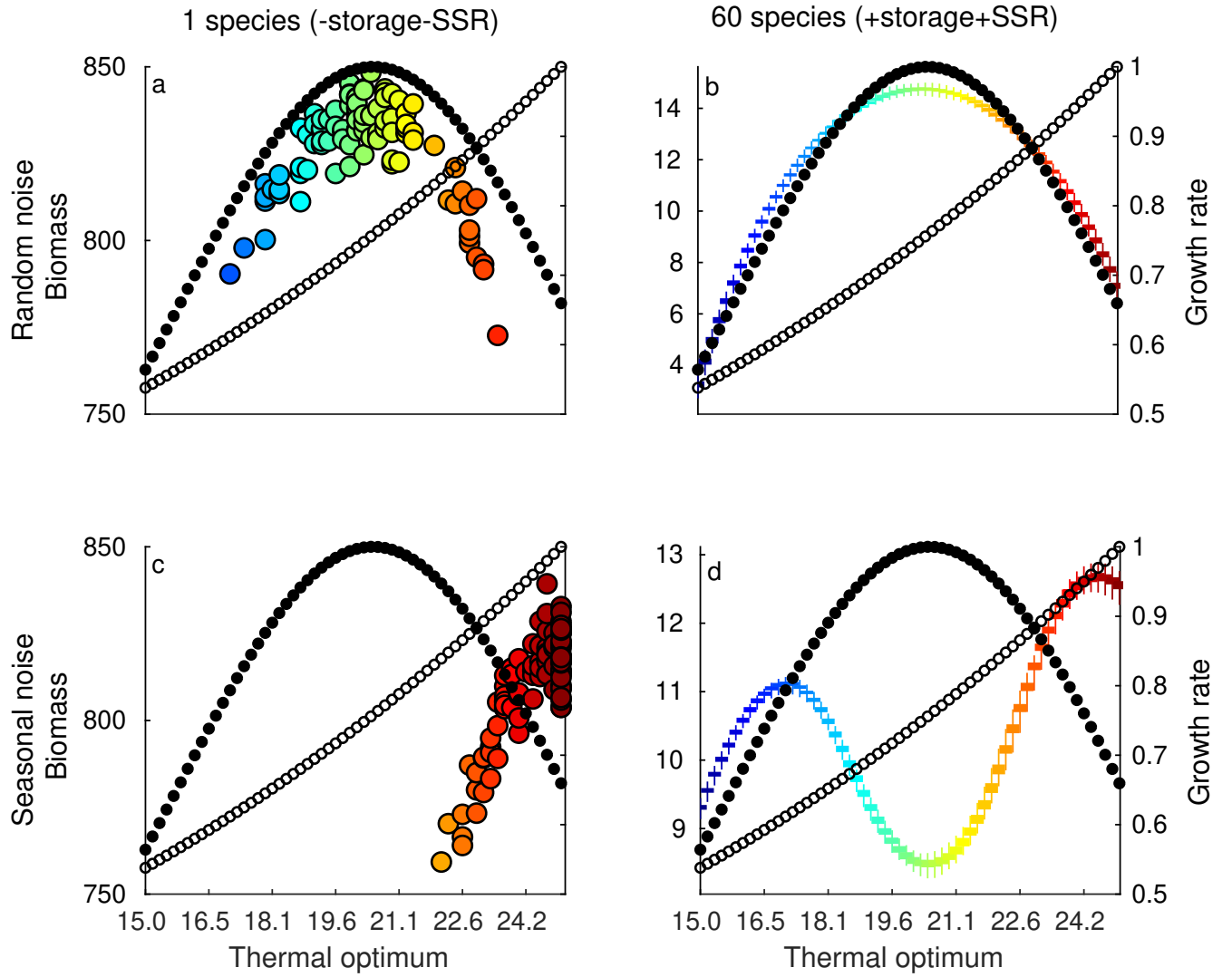


Figure 3: Mean biomass distribution over the last 200 years for 100 simulations, as a function of the species thermal optima. Here we consider the two stable-composition cases and two types of forcing signal. On the left column, simulations without storage effect nor strong self-regulation are presented.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

268 In cases where the richness of the community varied, the overall shape (multimodal vs unimodal)
 269 of the marginal distribution of extant species with respect to the trait axis were similar for both
 270 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 the 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.

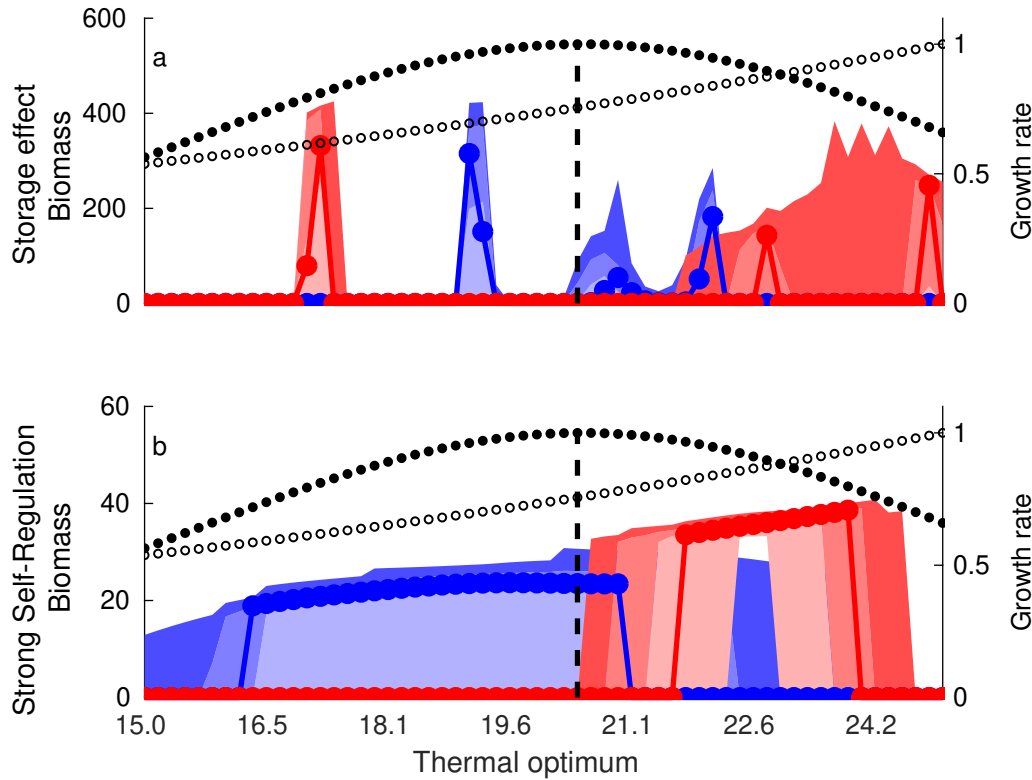


Figure 4: Mean biomass distribution over the last 200 years for 100 simulations, as a function of thermal optima, with storage effect and equal competitive strengths (a) and without storage effect, with strong self-regulation (b). The forcing signal is either a random (in blue) or a seasonal noise (in 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 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 [and can still reveal part of the community functioning Hastings et al \(2018\)](#). We realized that convergence could be 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 ~~for both technical and ecological reasons~~. From a technical standpoint, adding 10 000 years of numerical integration (or more) for the sake of reaching equilibrium would have been very challenging computationally, and comparison with the values reported by Scranton and Vasseur (2016) would have been compromised. [Another way to shorten the transients in the case developed by Scranton and Vasseur \(2016\) would be to vary the mortality parameter, shifting the model further away from neutral dynamics. This did not alter the conclusions \(see Appendix B in Supplementary Material\). Speed of convergence therefore depends on the mechanisms considered. As we wanted to focus on the storage effect and the self-regulation while keeping all other things equal, we did not change the time window for integration.](#) ~~From an ecological standpoint, waiting~~

319 for full convergence when there are extremely long transients (Hastings et al, 2018) is also quite
320 artificial: there is no reason to believe that very long transients (i.e., transients that maintains
321 for thousands of years) have any less ecological reality than an attractor that is deemed stable.
322 Speed of convergence is therefore an issue to judge whether transients should be considered or
323 excluded, and a very long yet fixed time window for integration allows advantageously to compare
324 all mechanisms.—

325 Another assumption pertains to competition coefficients. To allow for comparison with Scran-
326 ton and Vasseur (2016), we did not introduce variability in intraspecific competition strength
327 or interspecific competition strength. By contrast, data-based coefficients vary between species
328 (Barraquand et al, 2018), with a majority of weak interactions (as suggested in Wootton and Em-
329 merson, 2005) and more variance in intraspecific coefficients. Stump (2017) recently considered the
330 potential effects of competition coefficient variability (also called non-diffuse competition), as did
331 Kokkoris et al (2002); more variance in interspecific competition strength is usually detrimental to
332 coexistence (see Stump (2017) for a classification of the various effects). Setting the competition
333 coefficients using a multidimensional trait-based framework, like that of Ashby et al (2017), would
334 provide a natural development to the work presented here; it is in our opinion difficult to speculate
335 on those variance effects because both intra- and interspecific competition coefficient variances may
336 matter to community persistence.—

337 Finally, our study is limited to communities whose species have fast population dynamics
338 relative to the yearly timescale, like phytoplankton and likely other fast-living organisms, so that
339 many generations can occur in a year. Different effects of seasonality may occur in species that
340 have slower life histories or with generations that extend over multiple years (e.g., multiyear cycles
341 and chaotic attractors, Rinaldi et al 1993; Taylor et al 2013; Tyson and Lutscher 2016). Persistence
342 may be affected differently by seasonality in such cases with slower community dynamics (Miller
343 and Klausmeier, 2017).—

344 With these assumptions in mind, we have found that first, temporally forced Lotka-Volterra
345 dynamics cannot sustain any diversity with our phytoplankton-based set of parameters, unless the
346 structure is geared to include either a storage effect or a strong self-regulation. Although this

347 absence of diversity-enhancing effect of “pure” environmental variation has already been stated by
 348 other authors (Chesson and Huntly, 1997; Barabás et al, 2012; Fox, 2013; Scranton and Vasseur,
 349 2016), this is not always intuitive (Fox, 2013), so we feel compelled to stress it once more: tem-
 350 poral variation in growth rate alone cannot help coexistence within competitive communities. A
 351 nice point made by Scranton and Vasseur (2016) was that a built-in storage effect in a forced
 352 Lotka-Volterra model, parameterized for phytoplankton communities, could lead to some degree
 353 of coexistence. Our investigation reproduced these results, using the random noise considered by
 354 Scranton and Vasseur (2016). However, an arguably more lifelike noisy and seasonal temperature
 355 forcing considerably lessened the richness of the community after 5000 years, decreasing from 15
 356 to 4 species on average. Even imagining that groups represented here are genera or classes rather
 357 than species, this is a fairly low diversity for a phytoplankton-like community (see e.g., Chapter
 358 1 in Reynolds, 2006). This suggests that the storage effect may not, on its own, be sufficient
 359 to maintain species-rich communities (e.g., dozens to hundreds of species). We have therefore
 360 sought out whether a stronger self-regulation could maintain a higher diversity, using field-based
 361 intra- vs intergroup (species or genera) competition strength ratio (Barraquand et al, 2018), where
 362 the intragroup density-dependence was estimated 10 times stronger. Implementing such strong
 363 self-regulation, in the forced Lotka-Volterra models that we considered, produced a higher level of
 364 diversity than the storage effect (almost double). Of course, the result is somehow contingent upon
 365 the strength of self-regulation. Our estimates are a little stronger than what was found in perennial
 366 plants (Adler et al, 2010), where interspecific competition was suggested 4 or 5 times stronger than
 367 intraspecific. Still, the widespread effects of natural enemies in phytoplankton (zooplankton, para-
 368 sites) may contribute to increase the strength of self-regulation (Barraquand et al, 2018; Chesson,
 369 2018) relative to other systems, hence we believe that 10 times stronger intraspecific competition
 370 constitutes a reasonable order of magnitude.

371 However, such strong self-regulation was still insufficient to maintain the whole community
 372 diversity (60 species) by itself, especially when the seasonal forcing (always decreasing species
 373 richness) was considered. The diversity within clumps of similar values of thermal optima was
 374 considerably decreased once seasonality was implemented. This diversity reduction occurs because

375 within a season, the signal autocorrelation gives long, contiguous time intervals to the best com-
376 petitor to exclude its less adapted competitors. This makes the results likely to hold not only for
377 seasonal environments, but more generally for autocorrelated ones above the daily scale, i.e., “red”
378 noise. In contrast, the random noise scenario – which can be considered white noise above the
379 daily temporal scales – generates large temperature shifts more frequently, and thereby forbids such
380 competitive exclusion. In a seasonal setting, a species with the highest long-term (arithmetically)
381 averaged growth rate may not be the best competitor, and can disappear as a result of a strong
382 competition from both low- and high-temperature tolerant species. This holds with or without a
383 storage effect.

384 Our results may appear at odds with recent proposals that seasonal forcing in itself would help
385 maintain diversity (Sakavara et al, 2018). However, we compared the effect of seasonal forcing to
386 that of other forcing signals while controlling for total variance. Thus, the contrast between our
387 results and those of Sakavara et al (2018) may be due to the role of forcing variance over time
388 (we compare scenarios under a constant total variance). Overall, while seasonality may be slightly
389 better than no forcing at all in maintaining diversity if a storage effect is present, seasonal forcing
390 of parameters does not improve coexistence when compared to white noise.

391 In addition to community diversity, the biomass-trait relationship also varied from one sim-
392 ulation to another. Some regularities did emerge across simulations though. The storage effect
393 alone-begot several clumps along the trait space (as observed by Scranton and Vasseur, 2016). The
394 seasonality that we added to the temperature signal led to more distant clumps on the trait axis,
395 with less species per clump. Conversely, strong self-regulatory mechanisms alone led to relatively
396 uniform biomass distributions, with species forming a single large cluster, which covers a fraction
397 of the initial trait space. –Therefore, the shape of the distribution was mostly-affected by the
398 coexistence mechanism at work while the average trait value was modified by the type of environ-
399 mental forcing, even though the mean value of the environmental signal did not change. However,
400 when both mechanisms were at play, the biomass-trait distribution could either be unimodal or
401 multimodal depending on the type of noise, random or seasonal, driving the community dynamics.
402 This implies that the mere observation of multimodality is not a proof of the storage effect acting

on its own, or conversely, the proof of the influence of a seasonal environment. The biomass-trait
 distributions ~~therefore indeed~~ constitute clues to interpret community dynamics (D’Andrea and
 Ostling, 2016; Loranger et al, 2018), although we certainly recommend to interpret them with
 caution to avoid over-generalization. The identification of multiple modes in biomass-trait rela-
 tionships and SADs is relatively recent (Dornelas and Connolly, 2008; Matthews et al, 2014) and
 is a rare pattern in theoretical models (McGill et al, 2007). Barabás et al (2013) convincingly
 argued that multimodality could arise from the demographic stochasticity of a single model run
 (with either self-regulation or neutrality, but without the clumpy coexistence emerging from a
 storage effect). However, our results are based on many model runs, for which either the storage
 effect alone or a storage effect + strong self-regulation in a seasonal context consistently produced
 multimodal distributions, while simulations without the storage effect always led to a single cluster
 along the trait axis. Our suggestion for empirical studies is as follows: if only one spatial location is
 observed, caution in interpreting multiple clumps on the trait axis is of course required, as Barabás
 et al (2013) highlighted. However, with several locations - or in a theoretical context - one could
 average across locations to reproduce similar graphs to the ones produced here. Clumps in the trait
 axis when averaged across model runs/locations are therefore a signature of a coexistence induced
 by the storage effect, for the cases that we considered in the article. Of course, other mechanisms
 that we did not include in our models may produce similar patterns (Rael et al, 2018) or obfus-
 cate these patterns – typically strong self-regulation weakens the clustering on the trait axis, ~~or,~~
~~on the contrary, the competition kernel may induce the same clumps (Pigoletti et al, 2010).~~—We
 therefore view clustering on the trait axis (when averaged over several samples) as an interesting
 clue suggesting to look for a storage effect, rather than any definite proof that the storage effect is
 at work.—

In our previous empirical study of coastal phytoplankton dynamics (Barraquand et al, 2018),
 we did not find any storage effect. This, however, does not mean that it could not be observed
 in other planktonic systems. Given the consequences of the storage effect for species richness and
 composition presented here, we are skeptical that the storage effect could by itself help explaining
 phytoplankton diversity. However, our results suggest that in phytoplankton-like seasonal envi-

ronments, even though empirically-based self-regulation produce much more diversity than the storage effect when considered in isolation, the storage effect can help diversity maintenance when combined to other mechanisms. Indeed, 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 affect 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). The effect of interacting mechanism can be measured either on community diversity, as we did here, or on other processes of the community such as the growth rates of species when rare. 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 co-

459 existence, which we believe would be especially important for phytoplankton since many species
 460 form colonies (Reynolds, 2006; see discussion in Barraquand et al, 2018). Moreover, although
 461 temperature is usually relatively spatially homogeneous over space, other drivers (e.g., rainfall, pH
 462 in terrestrial ecosystems; salinity in aquatic ones) may exhibit spatial variation which is a main
 463 factor for coexistence (Snyder, 2008). The odds that different (resource) niches, natural enemies,
 464 spatial limits to competition and temporal niche partitioning all interact to promote the very high-
 465 dimensional coexistence observed in the field seem much higher than for any of those mechanisms
 466 alone. Whether the diversity-enhancing effects of these mechanisms combine subadditively (as in
 467 Kuang and Chesson, 2010) or superadditively like here is therefore worthy of further research.-

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