

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 on empirical data, 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: 240

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1 Introduction

There has been a rich debate in theoretical ecology on how to reconcile niche and neutral perspectives on species coexistence (Gravel et al, 2006; Carmel et al, 2017). Under the neutral perspective, all species have equal birth and death rates and compete equally (since space is limited) 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; Mutshinda et al, 2009; Götzenberger et al, 2012).

An intriguing offshoot of the niche vs neutrality debate is the concept of ‘clumpy coexistence’ (Scheffer and van Nes, 2006), whereby a simultaneous influence 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 stronger net intraspecific competition 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 intraspecific 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 (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 environment (see also Barabás et al, 2012).

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

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

81 In an empirical study combining phytoplankton community-level time series and multivariate
82 autoregressive models (Barraquand et al, 2018), we found that despite a large influence of the
83 environment (including temperature, irradiance, and other factors), a strong intraspecific (or in-
84 tragenus) competition, when compared to interspecific interaction coefficients, was most likely the
85 key driver of species coexistence. In other words, strong self-regulation had a large role to play
86 in maintaining species diversity in coastal phytoplankton (Barraquand et al, 2018). These high
87 intraspecific interaction strengths mirror those found in a number of terrestrial plant communities
88 (Adler et al, 2018) and in animal communities (Mutshinda et al, 2009).

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

94 **2 Methods**

95 *Models description*

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

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

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

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

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

100 Model parameters are detailed in Table 1, and we set their values to match the features of
 101 phytoplankton communities as in Scranton and Vasseur's work (2016). The niche of each species is
 102 defined by its thermal optimum τ_i^{opt} . Thermal performance curves defined in Eq. 3 are parameter-
 103 ized so that all species share the same niche area (Eq. 4), which sets a trade-off between maximum
 104 growth rates and niche width.

Table 1: Parameter definition and values of the model described in Eq. 1-4. Parameter values are not specified when they vary with time and/or the species considered.

Name	Definition	Value (unit)
S	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	$(\frac{\text{kg}}{\text{kg*year}})$
α_{ij}	Strength of competition of species j on species i	0.001 (area/kg)
b_i	Normalization of the thermal decay rate	(K^3)
m	Mortality rate	$15(\frac{\text{kg}}{\text{kg*year}})$
τ_0	Reference temperature	293 (K) / 20 ($^{\circ}\text{C}$)
$a_r(\tau_0)$	Growth rate at reference temperature	$386(\frac{\text{kg}}{\text{kg*year}})$
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	$10^{3.1}(\frac{\text{kg}}{\text{kg*year}})$
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-intergroup competition strengths	(1;10) (NA)

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

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

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

119 The formulation of the forced Lotka-Volterra model of Scranton and Vasseur (2016) implies
 120 a storage effect, as the net effect of competition exerted by species j on i is the product of the
 121 temperature-related growth rate $r_i(\tau)$ and the product of competitive strength α_{ij} exerted by
 122 species j with the abundance N_j . Therefore, net competition covaries positively with the growth
 123 rate values $r_i(\tau)$ (Chesson, 1994; Ellner et al, 2016). To remove the assumption of an explicit storage
 124 effect, we created another version of the model using the mean value of a species' growth rate (\bar{r}_i)
 125 to weight the interaction coefficients (see Table 2). The mean growth rate value was computed by
 126 first generating the temperature time series and averaging all r_i over the corresponding sequences
 127 of τ values.

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

128 In this way, net competition remains unaffected by the environmental conditions, in contrast
 129 to intrinsic growth rates (Eq. 6), while preserving the same average magnitude as in Eq. 1.

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

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

133 where δ_{ij} is the Kronecker symbol, equal to 1 if $i = j$ and to 0 otherwise. The value of the
 134 parameter $\kappa = 10$ was chosen from analyses of phytoplanktonic data (Barraquand et al, 2018)¹.
 135 Hereafter, the expression “strong self-regulation” characterizes dynamics where the intraspecific
 136 competition strength is 10 times higher than the interspecific competition strength, as opposed to

¹The values of non-zero interspecific competition coefficients reported in Fig. 5 of Barraquand et al (2018) are somewhat 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 $\kappa = 10$.

137 “equal competitive strengths” where intra- and interspecific competition strengths are equal.

138 In addition to two types of environmental forcings (random noise with $\theta = 0$, and seasonal
139 noise with $\theta = 1.3$), we compare the results for four formulations of the model: with and without
140 an explicit storage effect (Eq. 1 and Eq. 6, respectively) ; with strong self-regulation or equal
141 intra- and inter-competition strength ($\kappa = 10$ or $\kappa = 1$, respectively). These are summed up in
142 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

143

144 Set-up

145 We replicate the ‘Species sorting’ experiment of Scranton and Vasseur (2016) so as to investigate
146 how the structure of synthetic phytoplankton communities varies under the different scenarios we
147 described above. We focused on the dynamics of a community initialized with 60 species with
148 thermal optima uniformly spaced along the interval $[15^\circ\text{C}, 25^\circ\text{C}]$, and with the same initial density
149 $\left(\frac{1}{\alpha S}\right)$. Each simulation was run for 5000 years in 1-day intervals. When the density of a species
150 dropped below 10^{-6} , it was considered extinct. For each combination of parameters (type of
151 environmental signal, storage effect and stabilizing niche differences), we ran 100 simulations.

152 All simulations were run with Matlab’s ode45 algorithm, an explicit Runge-Kutta (4,5) algo-
153 rithm with an absolute error tolerance of 10^{-8} , and relative error tolerance of 10^{-3} . The code is
154 available in a GitHub repository².

²<https://github.com/CoraliePicoche/Seasonality>, will be made public upon acceptance or at the reviewer’s request

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 variation 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 are high, the group with higher thermal optima reaches its maximum biomass, then as temperature decreases through the season, these species leave room for the growth of the low-temperature group.

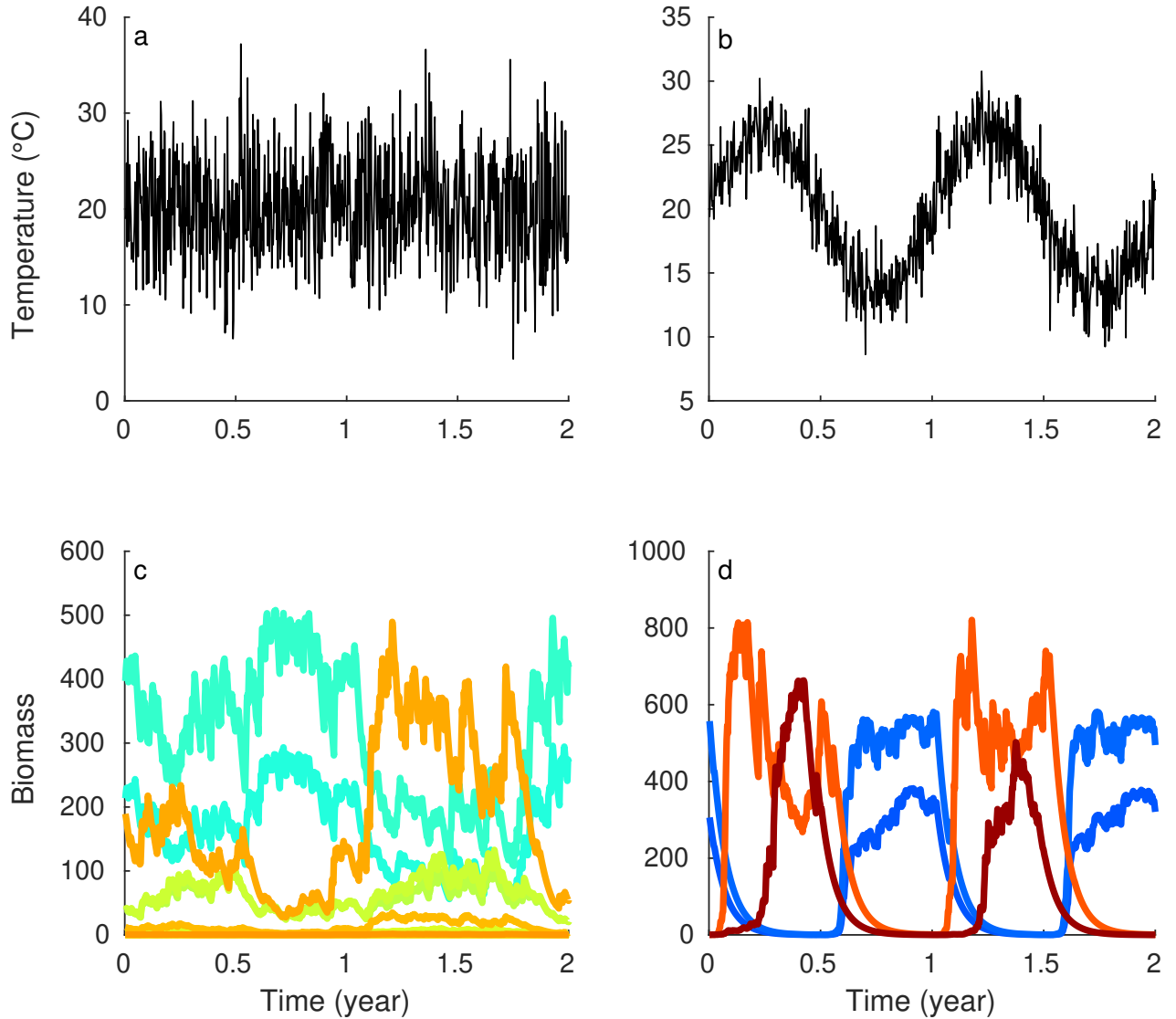


Figure 1: Time series of temperature (top; a-b) and extant species (bottom; c-d) for the 2 last years of a 5000-year simulation, with storage effect and no differences between intraspecific and interspecific competition strengths. The forcing temperature is either a random noise (a) or a seasonal noise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

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

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

181 Both a strong self-regulation and the storage effect markedly increased persistence. Without
 182 any of these coexistence mechanisms, only one species persisted at the end of the simulations.
 183 When only the storage effect was present, the number of extant species varied between 8 and 20
 184 (14.8 ± 2.4) with random noise, or 2 and 6 (4.1 ± 0.7) with a seasonal signal. On the other
 185 hand, when only a strong self-regulation was present, the number of extant species nearly doubled,
 186 varying between 20 and 32 (27.5 ± 2.4), or 12 and 15 (13.3 ± 0.6), with a random or a seasonal
 187 noise, respectively. Remarkably, when the storage effect and a strong self-regulation both affected
 188 the community dynamics, all species persisted in the community, while neither of these mechanisms
 189 was able to produce that result alone, for either random and seasonal noise.

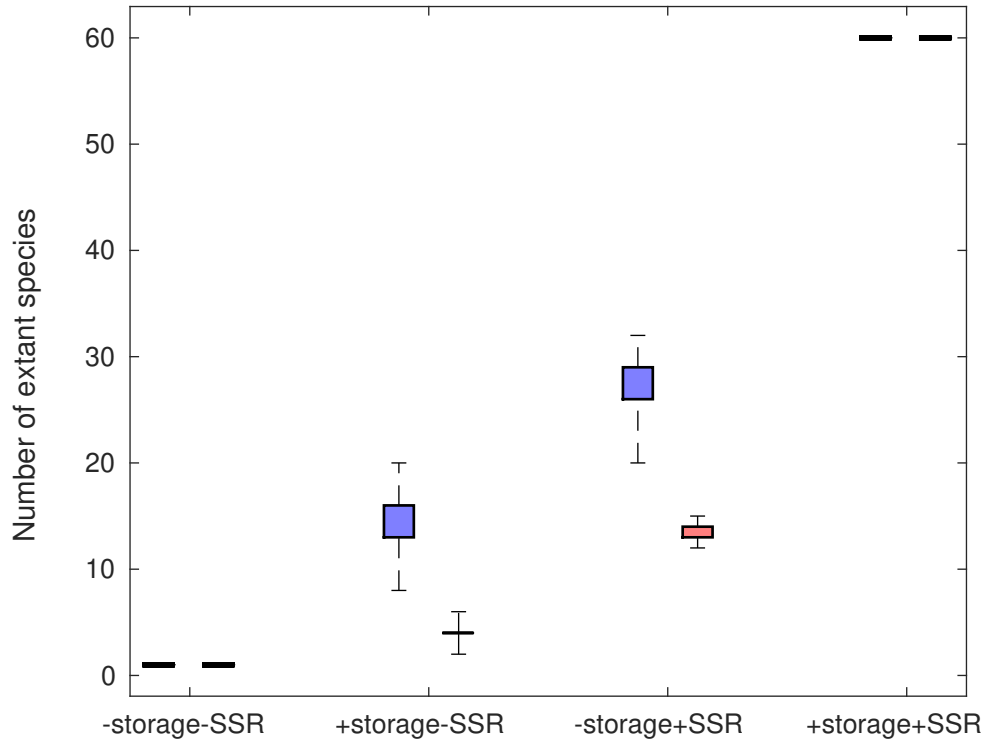


Figure 2: Number of species still present at the end of 100 simulations (5000 years each), initialized with 60 species, with a random forcing signal (blue) or a seasonal noise (red). The signs + or - storage refer to presence or absence of the storage effect, respectively; + / - SSR, presence or absence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

190 The trait-biomass distribution of the community was affected by the type of forcing even
 191 when the richness of the community was stable (Fig. 3). Without storage effect nor strong self-
 192 regulation, there was only one species left at the end of the simulations. A random noise favored
 193 species with intermediate thermal optima: the final species had a thermal optimum between 18.9°C
 194 and 21.4°C (only a fourth of the initial range of thermal optima) for two simulations out of three
 195 and the maximum final biomasses over 100 simulations was reached in this range (Fig. 3a). This
 196 distribution may indicate a selection for the highest long-term growth rates, averaged over time (see
 197 scaled growth rates in Fig. 3). Seasonality with no coexistence mechanisms also led to a single
 198 final species but, in this case, the species always had a higher maximum growth rate (thermal
 199 optimum above 22°C). Species with a higher thermal optimum were more likely to persist and to
 200 reach a higher biomass at the end of the simulation. 38% of the simulations therefore ended with
 201 the species having the highest temperature optimum, 25°C. The shift in trait distribution towards
 202 higher maximum growth rates with a seasonal noise vs higher average growth rates with a random
 203 noise was consistent for all model types considered.

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

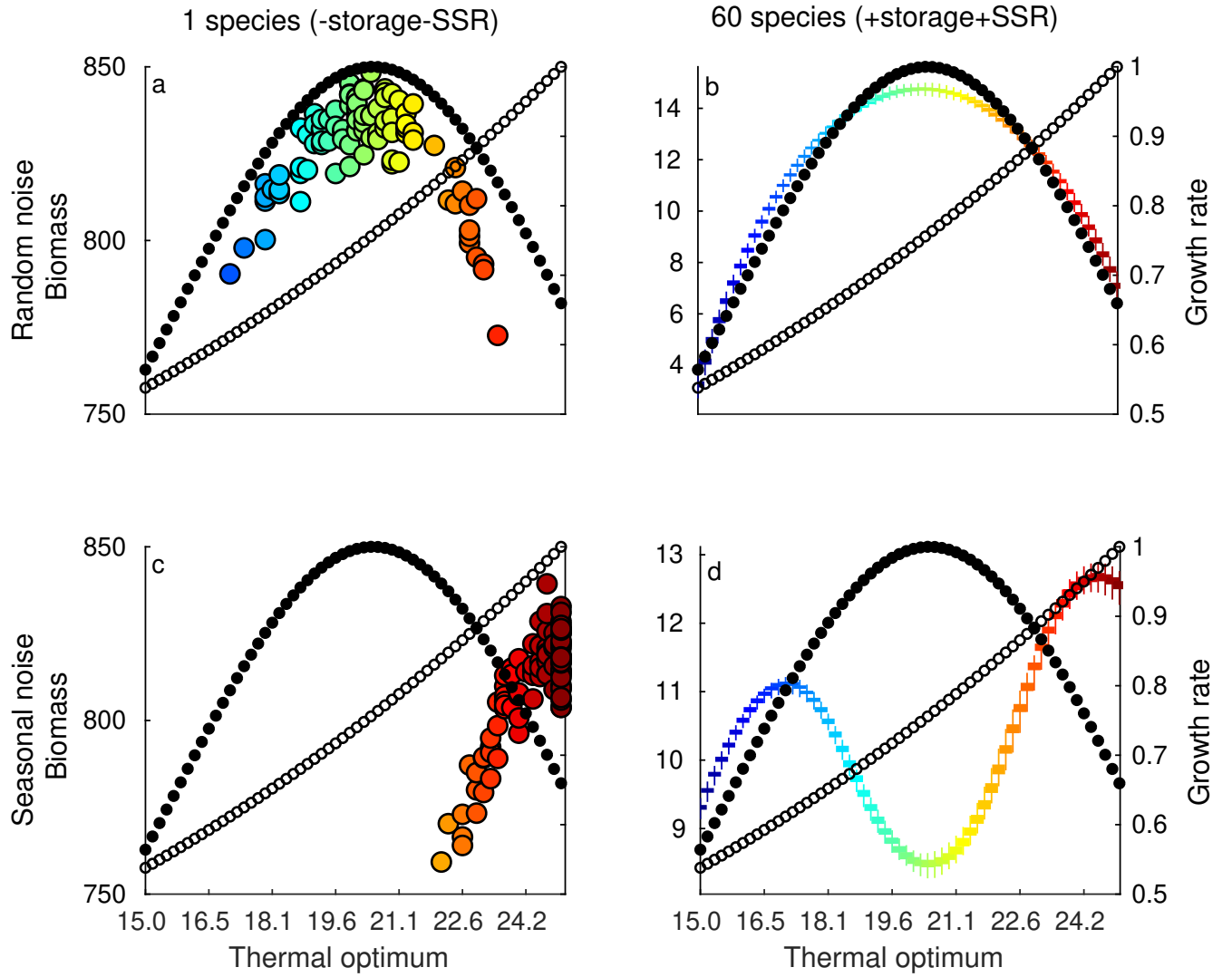


Figure 3: Mean biomass distribution over the last 200 years for 100 simulations, as a function of the species thermal optima. Here we consider the two stable-composition cases and two types of forcing signal. On the left column, simulations without storage effect nor strong self-regulation are presented.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

214 In cases where the richness of the community varied, the overall shape (multimodal vs unimodal)
 215 of the marginal distribution of extant species with respect to the trait axis were similar for both
 216 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.

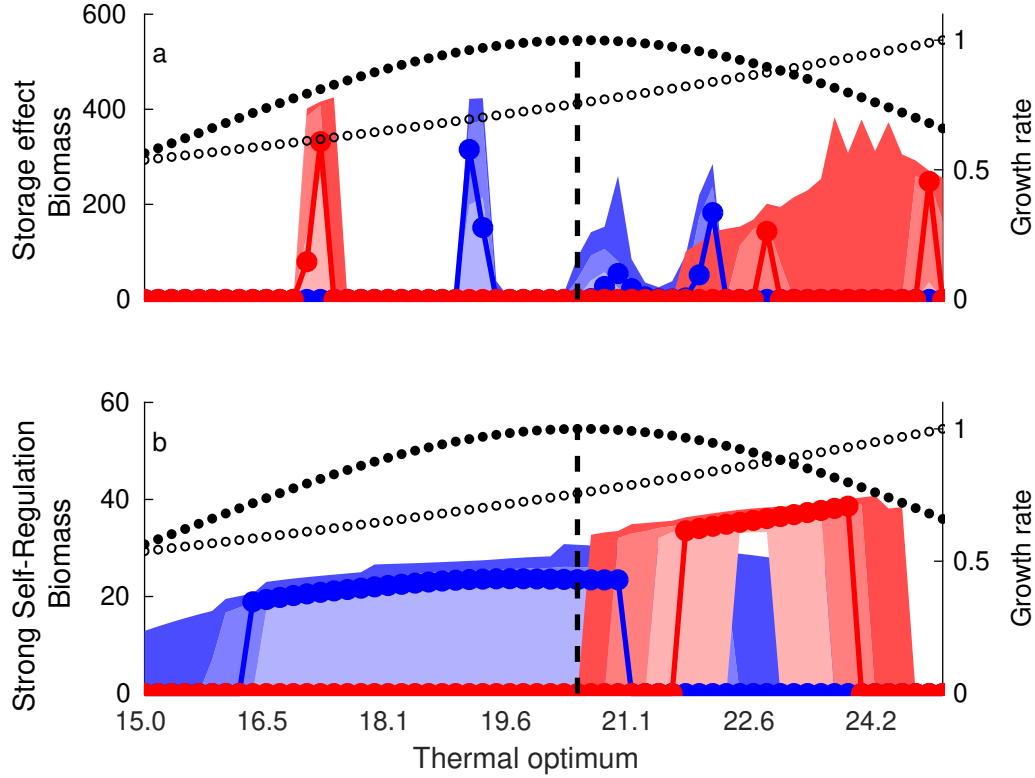


Figure 4: Mean biomass distribution over the last 200 years for 100 simulations, as a function of thermal optima, with storage effect and equal competitive strengths (a) and without storage effect, with strong self-regulation (b). The forcing signal is either a random (in blue) or a seasonal noise (in 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.

237 Our investigation therefore built on the model of Scranton and Vasseur (2016), which included a
 238 random forcing and a storage effect, but considered seven additional combinations of mechanisms.
 239 This was motivated by our wish to include two observed features of phytoplankton dynamics:
 240 seasonal cycles (Winder and Cloern, 2010) and strong self-regulation (Chesson, 2000; Adler et al,
 241 2010; Barraquand et al, 2018). Many mechanisms can lead to intraspecific competition being
 242 stronger than interspecific competition: nonlinearities in the functional forms of competition or
 243 mutualism that contribute to increasing self-regulation (Kawatsu and Kondoh, 2018), or predation
 244 as well as parasitism (see e.g., the generalist predators in Haydon, 1994). Strong self-regulation
 245 seems nonetheless an ubiquitous feature in competition networks of primary producers (Adler et al,
 246 2018), and perhaps even more general networks (Barabás et al, 2017).

247 Before discussing the ecological interpretation of our results, we first recall some technical
 248 assumptions made in this study. All our simulations lasted for a fixed duration (5000 timesteps) as
 249 in Scranton and Vasseur (2016). This means that short- and medium-term transients (a few years
 250 to hundreds of years) are completely negligible at the end of the time series, but very long transients
 251 can remain. We realized that convergence could be incomplete after 5000 years in some cases (e.g.,
 252 random noise + storage effect + equal competitive strength). Such simulations would take up to 15
 253 000 years to converge and the rate of convergence would slow over time, as can also be observed for
 254 similar models (Scheffer and van Nes, 2006). We kept a fixed time integration window rather than
 255 waiting for convergence for both technical and ecological reasons. From a technical standpoint,
 256 adding 10 000 years of numerical integration (or more) for the sake of reaching equilibrium would
 257 have been very computationally challenging, and comparison with the values reported by Scranton
 258 and Vasseur (2016) would have been compromised. From an ecological standpoint, waiting for full
 259 convergence when there are extremely long transients (Hastings et al, 2018) is also quite artificial:
 260 there is no reason to believe that very long transients (i.e., transients that maintains for thousands
 261 of years) has any less ecological reality than an attractor that is deemed stable because convergence
 262 has been reached. Speed of convergence is therefore an issue to judge whether transients should be
 263 considered or excluded, and very long yet fixed time window for integration allows advantageously
 264 to compare mechanisms for which speed of convergence might differ.

265 Another assumption pertains to competition coefficients. To allow for comparison of our results
 266 with Scranton and Vasseur (2016), we took intra- and interspecific competition coefficients that
 267 were identical between species, i.e., there was no variance in α_{ii} and no variance in α_{ij} for $i \neq j$. By
 268 contrast, data-based coefficients vary to some degree (Barraquand et al, 2018), with a majority of
 269 weak interactions (as suggested in Wootton and Emmerson (2005)) and more variance in intraspe-
 270 cific coefficients. Stump (2017) recently considered the potential effects of competition coefficient
 271 variability (also called non-diffuse competition), as did Kokkoris et al (2002); more variance in
 272 interspecific competition strength is usually detrimental to coexistence (see Stump (2017) for a
 273 classification of the various effects). Setting the coefficients using a multidimensional trait-based
 274 framework, like that of Ashby et al (2017), would provide a natural development to the work pre-
 275 sented here; it is in our opinion difficult to speculate on those variance effects because both intra-
 276 and interspecific competition coefficient variances may matter to community persistence.

277 With these assumptions in mind, we have found that first, temporally forced Lotka-Volterra
 278 dynamics cannot sustain any diversity with our phytoplankton-based set of parameters, unless the
 279 structure is geared to include either a storage effect or a strong self-regulation. Although this
 280 absence of diversity-enhancing effect of “pure” environmental variation has already been stated
 281 by other authors (Barabás et al, 2012; Fox, 2013; Scranton and Vasseur, 2016), this is not always
 282 intuitive (Fox, 2013), so we feel compelled to stress it once more: temporal variation in growth rate
 283 alone cannot help coexistence within competitive communities. A nice point made by Scranton and
 284 Vasseur (2016) was that a built-in storage effect in a forced Lotka-Volterra model, parameterized
 285 for phytoplankton communities, could lead to some degree of coexistence. Our investigation repro-
 286 duced these results, using the random noise considered by Scranton and Vasseur (2016). However,
 287 an arguably more lifelike noisy and seasonal temperature forcing considerably lessened the richness
 288 of the community after 5000 years, decreasing from 15 to 4 species on average. Even imagining
 289 that groups represented here are genera or classes rather than species, this is a fairly low diversity
 290 for a phytoplankton-like community (see Chapter 1 in Reynolds, 2006). This suggests that the
 291 storage effect may not, on its own, be sufficient to maintain species-rich communities (e.g., dozens
 292 to hundreds of species). We have therefore sought out whether a stronger self-regulation could

293 maintain a higher diversity, using field-based intra- vs intergroup (species or genera) competition
 294 strength ratio (Barraquand et al, 2018), where the intragroup density-dependence was chosen 10
 295 times stronger. Implementing such strong self-regulation, in the forced Lotka-Volterra models
 296 that we considered, produced a higher level of diversity than the storage effect (almost double).
 297 Of course, the result is somehow contingent upon the strength of self-regulation. Our estimates
 298 are a little stronger than what was found in perennial plants (Adler et al, 2010), where inter-
 299 specific competition was suggested 4 or 5 times stronger than intraspecific. Still, the widespread
 300 effects of natural enemies in phytoplankton (zooplankton, parasites) may contribute to increase
 301 the strength of self-regulation (Huber and Gaedke, 2006; Barraquand et al, 2018) relative to other
 302 systems, hence we believe that 10 times stronger intraspecific competition constitutes a reasonable
 303 order of magnitude.

304 However, such strong self-regulation was still insufficient to maintain the whole community
 305 diversity (60 species) by itself, especially when the seasonal forcing (always decreasing species
 306 richness) was considered. The diversity within clumps of similar values of growth rates was consid-
 307 erably decreased once seasonality was implemented. This diversity reduction occurs because within
 308 a season, the signal autocorrelation gives long, contiguous time intervals to the best competitor to
 309 exclude its less adapted heterospecifics. This makes the results likely to hold not only for seasonal
 310 environments, but more generally for autocorrelated ones, i.e., “red” noise. This could be relevant
 311 for species whose population dynamics occur at timescales largely above one year. In contrast, the
 312 random noise – which can be considered white noise above the daily temporal scales – generates
 313 large temperature shifts more frequently, and thereby forbids such competitive exclusion. In a
 314 seasonal setting, a species with the highest long-term (arithmetically) averaged growth rate may
 315 not be the best competitor, and can disappear as a result of a strong competition from both low-
 316 and high-temperature tolerant species. This holds with or without a storage effect.

317 Our results may appear at odds with recent proposals that seasonal forcing in itself would help
 318 maintain diversity (Sakavara et al, 2018). However, we compared the effect of seasonal forcing
 319 to that of other forcing signals while controlling for total variance. Thus, the contrast between
 320 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). Overall, while seasonality may be slightly better than no forcing at all in maintaining diversity, seasonal forcing of parameters does not improve coexistence: diversity within clumps is lower when seasonality is included, when compared to whiter noise.

In addition to community diversity, the biomass-trait relationship also varied from one simulation to another. Some regularities did emerge across simulations though. The storage effect begot several clumps along the trait space (as observed by Scranton and Vasseur, 2016). The seasonality that we added to the temperature signal led to more distant clumps on the trait axis (as said above, less species per clump). Conversely, strong self-regulatory mechanisms alone led to relatively uniform biomass distributions, with species forming a single large cluster, which covers a fraction of the initial trait space. Therefore, the shape of the distribution was affected by the coexistence mechanism at work while the average trait value was modified by the type of environmental forcing, even though the mean value of the environmental signal did not change. The biomass-trait distributions therefore 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 relationships 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 obfuscate these patterns – typically strong self-regulation weakens the clustering on the trait axis. 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 (which 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 environments, 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, 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). 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 (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

377 opportunities for theoreticians wishing to investigate synergies between coexistence mechanisms
 378 in highly diverse communities. Aside from the synergies between predator diversity-enhancing ef-
 379 fects, strong self-regulation through various means and storage effects (on the temporal axis), one
 380 obvious follow-up of this research would be interactions with spatial structure. Spatial structure
 381 occurs both endogeneously, through spatially restricted movements and interactions, and exoge-
 382 neously, through spatial variation in environmental covariates (Bolker, 2003). Numerous studies
 383 (e.g., Bolker and Pacala, 1999; Murrell and Law, 2002) have shown that spatially restricted move-
 384 ments and interactions - very small-scale spatial structure - can help coexistence, which we believe
 385 would be especially important for phytoplankton since many species form colonies (Reynolds, 2006;
 386 see discussion in Barraquand et al, 2018). Moreover, although temperature is usually relatively
 387 spatially homogeneous over space, other drivers (e.g., rainfall, pH in terrestrial ecosystems; salin-
 388 ity in aquatic ones) may exhibit spatial variation which is a main factor for coexistence (Snyder,
 389 2008). The odds that different (resource) niches, natural enemies, spatial limits to competition and
 390 temporal niche partitioning all interact to promote the very high-dimensional coexistence observed
 391 in the field seem much higher than for any of those mechanisms alone. Whether the diversity-
 392 enhancing effects of these mechanisms combine subadditively (as in Kuang and Chesson, 2010) or
 393 superadditively like here is therefore worthy of further research.

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