

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

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October 16, 2018

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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. Our results on community composition (formation of clumps, biomass distribution) in the different scenarios give further hints about likely coexistence mechanisms at work.

**Number of words: 240**

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

# 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 a 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 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 of the storage effect vs  
90 strong self-regulation to coexistence ~~are~~ in a phytoplankton-like theoretical community model. This  
91 led us to cross different combinations of seasonality in the forcing signal, presence of the storage  
92 effect or not, and intra- vs interspecific competition, in order to disentangle the contributions of  
93 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  $\tau_i^{opt}$ . 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)
$\tau$	Temperature	(K)
$r_i(\tau)$	Growth rate of species $i$ as a function of temperature	$(\frac{\text{kg}}{\text{kg*year}})$
$\alpha_{ij}$	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	$15(\frac{\text{kg}}{\text{kg*year}})$
$\tau_0$	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)
$\mu_\tau$	Mean temperature	293 (K)
$\sigma_\tau$	Standard deviation for temperature	5 (K)
$\tau_{\min}$	Minimum thermal optimum	288 (K)
$\tau_{\max}$	Maximum thermal optimum	298 (K)
$A$	Niche breadth	$10^{3.1}(\frac{\text{kg}}{\text{kg*year}})$
$\tau_i^{\text{opt}}$	Thermal optimum for growth of the $i$ th species	(K)
$\theta$	Scaling between random and seasonal noise	$[0, \sqrt{(2)}]$ (NA)
$\kappa$	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. ~~This variable~~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 auto-correlated 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  $\theta$  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  $\theta$ ,  $\sqrt{2}$ , 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 on a given species exerted by species  $j$  on  $i$  is  
 121 the product of the temperature-related growth rate  $r_i(\tau)$  and the sum of product of competitive  
 122 strengths  $\alpha_{ij}$  exerted by other species an individual of species  $j$  with the abundance  $N_j$ . -Therefore,  
 123 net competition covaries positively with the growth rate values  $r_i(\tau)$  (Chesson, 1994; Ellner et al,  
 124 2016).~~---~~. To remove the assumption of an explicit storage effect, we created another version of  
 125 the model using the mean value of a species' growth rate ( $\bar{r}_i$ ) to weight the interaction coefficients  
 126 (see Table 2). The mean growth rate value was computed by first generating the temperature time  
 127 series and averaging all  $r_i$  over the corresponding sequences of  $\tau$  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  $\kappa$ , which is the ratio of intra-  
 131 to-intergroup competition strength. We can therefore re-write the interaction coefficients  $\alpha_{ij}$  in  
 132 Eq. 7

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

133 where  $\delta_{ij}$  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)  
 135 <sup>1</sup>. Hereafter, the phrase “strong self-regulation” characterizes dynamics where the intraspecific  
 136 competition strength is 10 times higher than the interspecific competition strength, as opposed

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<sup>1</sup>The values of non-zero interspecific competition coefficients reported in Fig. 5 of Barraquand et al (2018) are somewhat higher than here (and  $\kappa$  lower, closer to 4) because the best-fitting model actually set to zero some intergroup competition coefficients; using a model where all  $\alpha_{ij}$  are non-zero leads in contrast to  $\kappa = 10$ .



137 to the equal competitive strengths where intra- and interspecific competition strengths are equal.  
138 When we use the word “strong”, we therefore consider a “relatively stronger” self-regulation but do  
139 not wish to compare our interaction values to those used outside of our framework.

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

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

Table 2: Growth rate of species  $i$  in the four formulations of the model we present

144

## 145 Set-up

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

153 All simulations were ran with Matlab’s ode45 algorithm, an explicit Runge-Kutta (4,5) algo-  
154 rithm with an absolute error tolerance of  $10^{-8}$ , and relative error tolerance of  $10^{-3}$ . The code is  
155 available in a GitHub repository <sup>2</sup>.

<sup>2</sup><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 the environmental signals described in Eq. 1 (original choice of Scranton and Vasseur, 2016; Fig. 1a) and Eq. 5 (our variant, Fig. 1b), are shown in Fig. 1c and d. 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, produce a realistic standing biomasses; Reynolds, 2006) while 6 out of the 14 remained below the unit. All persisting species in the random noise simulations were clustered within a 3.2°C-range of thermal optima (see the biomass distribution as a function of the thermal optimum in Fig. A1 in the Supplementary Material). No obvious temporal patterns (e.g., cycles) could be seen in the communities 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.

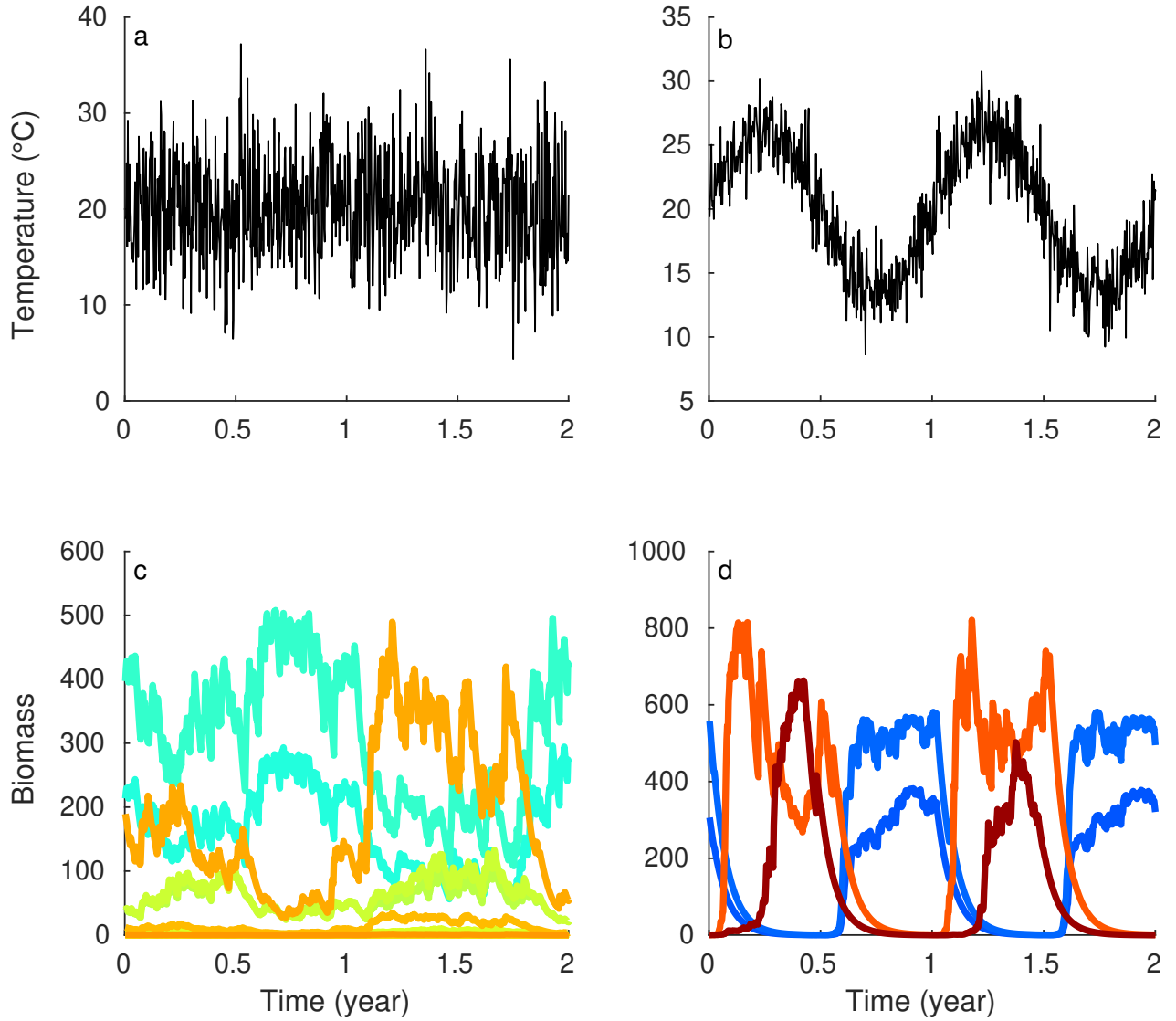


Figure 1: Time series of temperature (top; a-b) and extant species (bottom; c-d) for the 2 last years of a 5000-year simulation, with storage effect and no differences between intraspecific and interspecific competition strengths. The forcing temperature is either a random noise (a) or a seasonal noise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

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

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

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

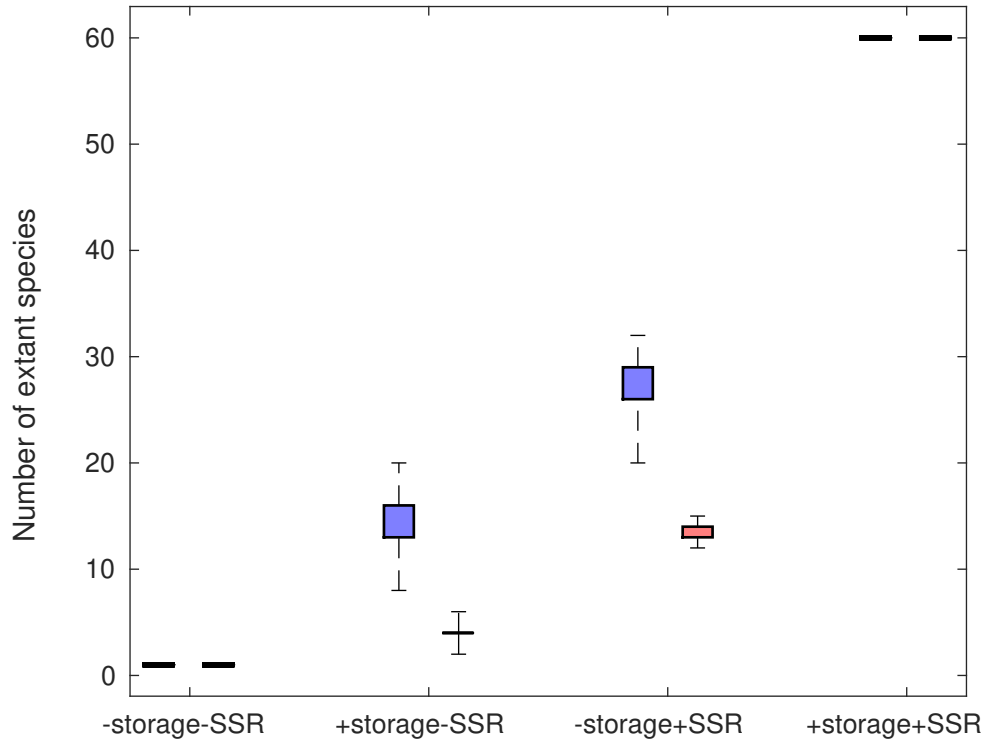


Figure 2: Number of species still present at the end of 100 simulations (5000 years each), initialized with 60 species, with a random ~~noise~~-forcing signal (blue) or a seasonal noise (red). The signs + or - storage refer to presence or absence of a storage effect, respectively; + / - SSR, presence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

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

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

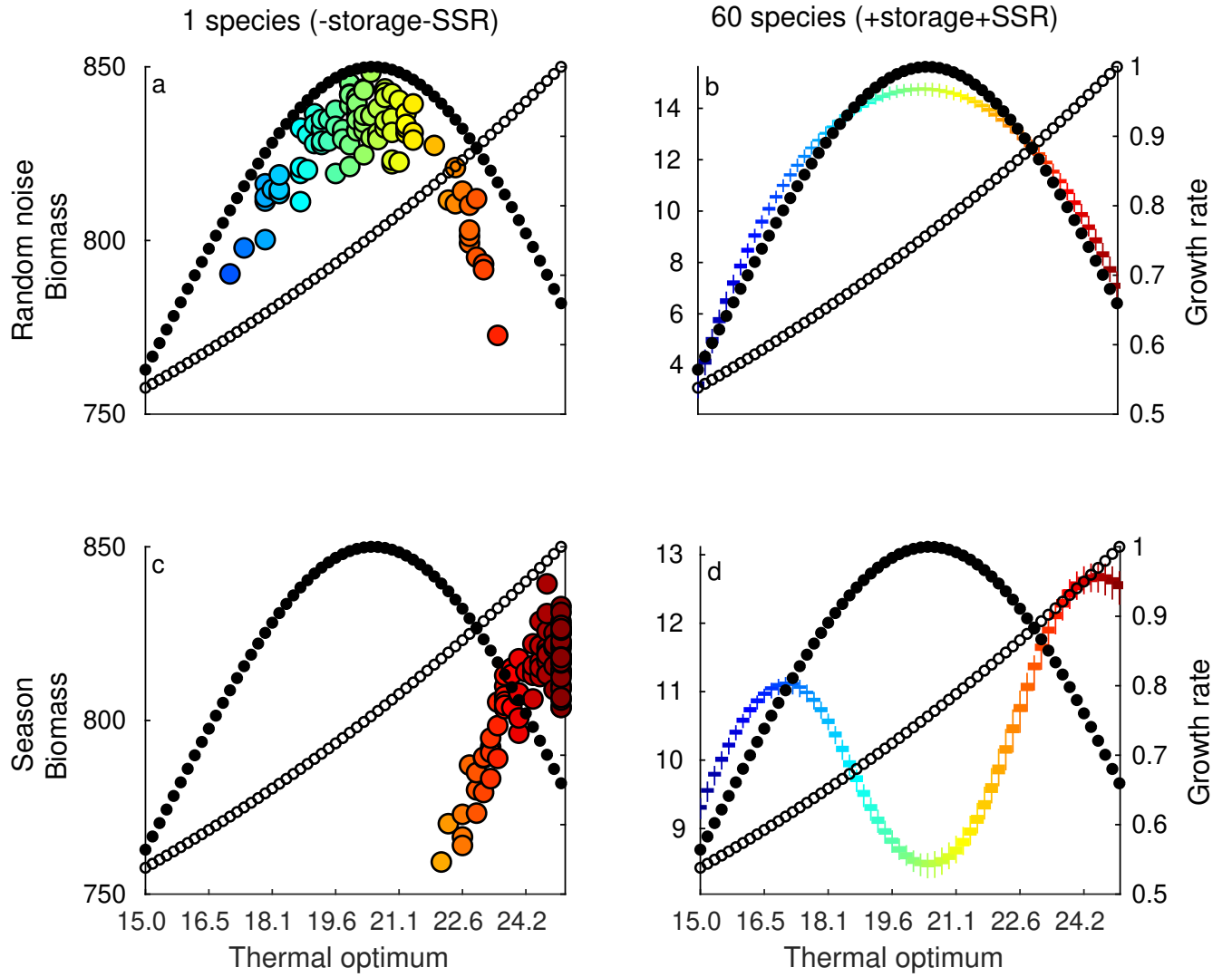


Figure 3: Mean biomass distribution over the last 200 years for 100 simulations, as a function of the species thermal optima. Here we consider the two stable-composition cases and two types of forcing signal. On the left column, simulations without storage effect nor strong self-regulation are presented.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

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

different shapes. Indeed, the storage effect 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 are grouped in rather similar clumps regarding species thermal optima (between 18.8°C and 22.2°C) whereas ~~elumps~~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 characterising communities forced by a random noise stayed in the lower range of temperatures (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 rates since the autocorrelated temperatures enabled them to achieve this highest growth rate for a longer period of time than a random noise would have.

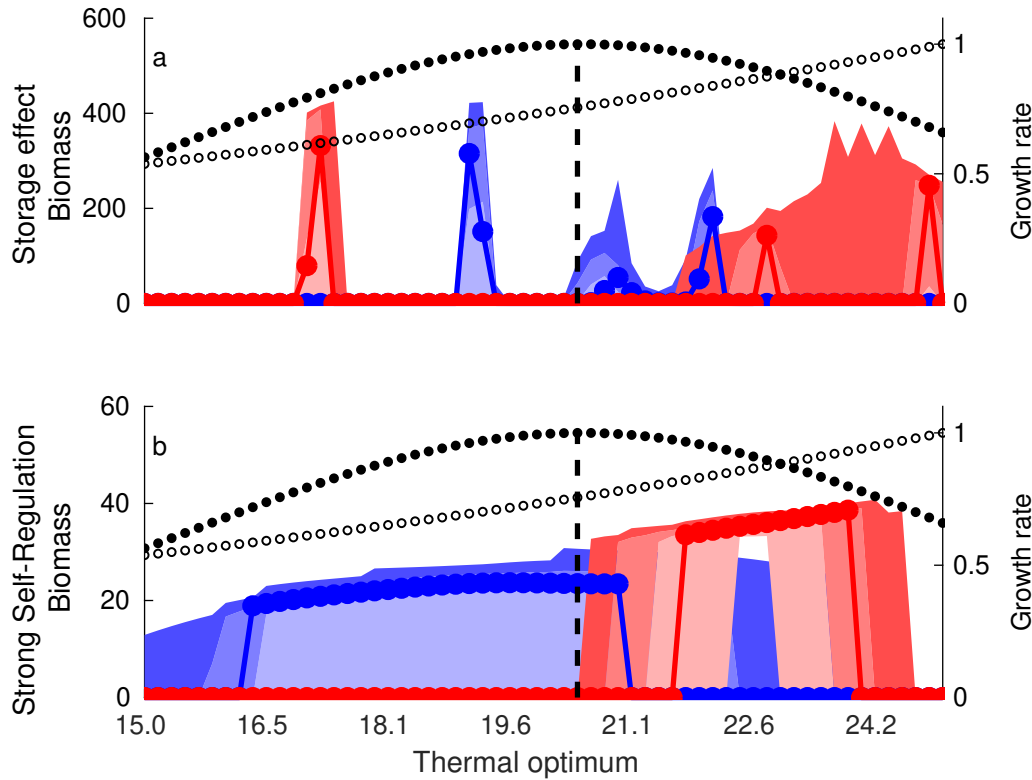


Figure 4: Mean biomass distribution over the last 200 years for 100 simulations, as a function of thermal optima, with storage effect and equal competitive strengths (a) and without storage effect, with strong self-regulation (b). The forcing signal is either a random (in blue) or a seasonal noise (in 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 ~~relied upon the~~ lasted a fixed period of time (5000 timesteps) ~~for numerical integration that were also used~~ as was also the case ~~by~~ 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. We realized that convergence could ~~in some cases~~ be incomplete after 5000 years ~~in some cases~~ (e.g., random noise + storage effect + equal competitive strength). ~~These would not even be stabilized well after 10 000 years, t~~Such simulations ~~hey~~ would take up to  $\sim 15\,000$  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 for the sake of reaching the equilibrium would have been very computationally challenging, and comparison with the values reported by Scranton and Vasseur (2016) would have been compromised. From an ecological standpoint, waiting for full convergence when there are extremely long transients (Hastings et al, 2018) ~~(Hastings et al, 2018)~~ is also quite artificial: there is no reason to believe that very long transients (i.e., one that maintains for thousands of year) has any less ecological reality than an attractor that is deemed stable because convergence has been reached. Speed of convergence is therefore an issue to judge

266 whether transients should be considered or excluded, and very long yet fixed time window for  
267 integration allows advantageously to compare mechanisms for which speed of convergence might  
268 differ.

269 With these assumptions in mind, we have found that first, temporally forced Lotka-Volterra  
270 dynamics cannot sustain any diversity with our phytoplankton-based set of parameters, unless the  
271 structure is geared to include either a storage effect or a strong self-regulation. Although this  
272 absence of diversity-enhancing effect of “pure” environmental variation has already been stated  
273 by other authors (Barabás et al, 2012; Fox, 2013; Scranton and Vasseur, 2016), this is not always  
274 intuitive (Fox, 2013), so we feel compelled to stress it once more: temporal variation in growth rate  
275 alone cannot help coexistence within competitive communities. A nice point made by Scranton and  
276 Vasseur (2016) was that a built-in storage effect in a forced Lotka-Volterra model, parameterized  
277 for phytoplankton communities, could lead to some degree of coexistence. Our investigation repro-  
278 duced these results, using the random noise considered by Scranton and Vasseur (2016). However,  
279 an arguably more lifelike noisy and seasonal temperature forcing considerably lessened the richness  
280 of the community after 5000 years, decreasing from 15 to 4 species on average. Even imagining  
281 that groups represented here are genera or classes rather than species, this is a fairly low diversity  
282 for a phytoplankton-like community (see Chapter 1 in Reynolds, 2006). This suggests that the  
283 storage effect may not, on its own, be sufficient to maintain species-rich communities (e.g., dozens  
284 to hundreds of species). We have therefore sought out whether a stronger self-regulation could  
285 maintain a higher diversity, using field-based intra- vs intergroup (species or genera) competition  
286 strength ratio (Barraquand et al, 2018), where the intragroup density-dependence was chosen 10  
287 times stronger. Implementing such strong self-regulation in the forced Lotka-Volterra models that  
288 we considered, it produced a higher level of diversity than the storage effect (almost double).  
289 Of course, the result is somehow contingent upon the strength of self-regulation. Our estimates  
290 are a little stronger than what was found in perennial plants (Adler et al, 2010), where inter-  
291 specific competition was suggested 4 or 5 times stronger than intraspecific. Still, the widespread  
292 effects of natural enemies in phytoplankton (zooplankton, parasites) may contribute to increase  
293 the strength of self-regulation (Huber and Gaedke, 2006; Barraquand et al, 2018) relative to other

294 systems, hence we believe that 10 times stronger intraspecific competition constitutes a reasonable  
295 order of magnitude.

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

309 Our results may appear at odds with recent proposals that seasonal forcing in itself would help  
310 maintain diversity (Sakavara et al, 2018). However, we compared the effect of seasonal forcing  
311 to that of other forcing signals while controlling for total variance. Thus, the contrast between  
312 our results and those of Sakavara et al (2018) may be due to the role of forcing variance over  
313 time (we compare scenarios under a constant total variance). Overall, while seasonality may be  
314 slightly better than no forcing at all in maintaining diversity, seasonal forcing of parameters does  
315 not improve coexistence: diversity within clumps is lower when seasonality is included.

316 In addition to community diversity, the biomass-trait relationship also varied from one sim-  
317 ulation to another. Some regularities did emerge across simulations though. The storage effect  
318 begot several clumps along the trait space (as observed by Scranton and Vasseur, 2016). The  
319 seasonality that we added to the temperature signal led to more distant clumps on the trait axis  
320 (as said above, less species per clump). Conversely, strong self-regulatory mechanisms alone led to  
321 relatively uniform biomass distributions, with species forming a single large cluster, which covers a

322 fraction of the initial trait space. Therefore, the shape of the distribution was affected by the coex-  
 323 istence mechanism at work while the average trait value was modified by the type of environmental  
 324 forcing, even though the mean value of the environmental signal did not change. The biomass-trait  
 325 distributions therefore constitute clues to interpret community dynamics (D’Andrea and Ostling,  
 326 2016; Loranger et al, 2018), although we certainly recommend to interpret them with caution to  
 327 avoid over-generalization. The identification of multiple modes in biomass-trait relationships and  
 328 SADs is relatively recent (Dornelas and Connolly, 2008; Matthews et al, 2014) and is a rare pat-  
 329 tern in theoretical models (McGill et al, 2007). Barabás et al (2013) convincingly argued that  
 330 multimodality could arise from the demographic stochasticity of a single model run (with either  
 331 self-regulation or neutrality, but without the clumpy coexistence emerging from a storage effect).  
 332 However, our results are based on many model runs, for which either the storage effect alone or  
 333 a storage effect + strong self-regulation in a seasonal context consistently produced multimodal  
 334 distributions, while simulations without the storage effect always led to a single cluster along the  
 335 trait axis. Our suggestion for empirical studies is as follows: if only one spatial location is observed,  
 336 caution in interpreting multiple clumps on the trait axis is of course required, as Barabás et al  
 337 (2013) highlighted. However, with several locations - or in a theoretical context - one could average  
 338 across locations to reproduce similar graphs to the ones produced here. Clumps in the trait axis  
 339 when averaged across model runs/locations are therefore a signature of the storage effect for the  
 340 cases that we considered in the article. Of course, other mechanisms that we did not include in  
 341 our models may produce similar patterns (Rael et al, 2018). Still, clustering on the trait axis, in  
 342 scenarios where the environment fluctuates strongly in time, suggests that storage effects could be  
 343 at work.

344 In our previous empirical study of coastal phytoplankton dynamics (Barraquand et al, 2018),  
 345 we did not find any storage effect (which does not mean that it could not be observed in other  
 346 planktonic systems). Given the consequences of the storage effect for species richness and compo-  
 347 sition presented here, we are skeptical that the storage effect could by itself help explaining  
 348 phytoplankton diversity. However, our results suggest that in phytoplankton-like seasonal envi-  
 349 ronments, even though empirically-based self-regulation produce much more diversity than the

350 storage effect when considered in isolation, the storage effect can help diversity maintenance when  
351 combined to other mechanisms. Indeed, the combination storage effect + strong self-regulation is  
352 non-additive: the cases where both self-regulation and the storage effect were present showed more  
353 diversity than generated by any mechanism on its own.

354 The above results suggest the very exciting idea that multiple coexistence mechanisms might  
355 combine superadditively, thus helping us to better understand the astounding diversity of primary  
356 producers. This logic could, in principle, be extended to mechanisms that we have not consid-  
357 ered here (e.g., spatial structure, specialized natural enemies, that could be as important here for  
358 plankton as they are for tropical trees, see Bagchi et al, 2014; Comita et al, 2014; Barraquand  
359 et al, 2018). Previous research has however demonstrated that generalist seed predation could  
360 weaken the storage effect (Kuang and Chesson, 2009, 2010) thus different mechanisms might not  
361 always combine superadditively as we found here. That said, superadditivity has been found in  
362 some cases, i.e., pathogens could enhance the storage effect (Mordecai, 2015). Better explaining  
363 plant or microbial diversity would then not be about selecting the best unique mechanism suscep-  
364 tible to explain the observed diversity, but rather better combining those mechanisms together.  
365 [Stump \(2017\) has defined a model that reveals two types of storage effect and expects competition](#)  
366 [strength to vary with phylogenetic similarities: such general model shows at least three ensuing](#)  
367 [effects which can affect coexistence at the same time \(central niche effect, common competitor](#)  
368 [effect and community redistribution effect\).](#) This may obviously be an annoyance for those who  
369 like to sharpen Occam’s razor, but it clearly holds opportunities for theoreticians wishing to in-  
370 vestigate synergies between coexistence mechanisms in highly diverse communities. Aside from  
371 the synergies between predator diversity-enhancing effects, strong self-regulation through various  
372 means and storage effects (on the temporal axis), one obvious follow-up of this research would be  
373 interactions with spatial structure. Spatial structure occurs both endogeneously, through spatially  
374 restricted movements and interactions, and exogeneously, through spatial variation in environmen-  
375 tal covariates (Bolker, 2003). Numerous studies (e.g., Bolker and Pacala, 1999; Murrell and Law,  
376 2002) have shown that spatially restricted movements and interactions - very small-scale spatial  
377 structure - can help coexistence, which we believe would be especially important for phytoplankton

378 since many species form colonies (Reynolds, 2006; see discussion in Barraquand et al, 2018). More-  
379 over, although temperature is usually relatively spatially homogeneous over space, other drivers  
380 (e.g., rainfall, pH in terrestrial ecosystems; salinity in aquatic ones) may exhibit spatial variation  
381 which is a main factor for coexistence (Snyder, 2008). The odds that different (resource) niches,  
382 natural enemies, spatial limits to competition and temporal niche partitioning all interact to pro-  
383 mote the very high-dimensional coexistence observed in the field seem much higher than for any  
384 of those mechanisms alone. Whether the diversity-enhancing effects of these mechanisms combine  
385 sub-additively (as in Kuang and Chesson, 2010) or super-additively like here is therefore worthy  
386 of further research.

## 387 Acknowledgements

388 We thank Alix Sauve for thoughtful comments and some bibliographic references, as well as  
389 Gyuriörgy Barabás and an anonymous referee for feedback. This study was supported by the  
390 French ANR through LabEx COTE (ANR-10-LABX-45).

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