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

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November 5, 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 based on empirical analyses, in which self-regulation usually dominates interspecific interactions. Although a strong self-regulation maintained more species (50%) than the storage effect (25%), we show that none of the two coexistence mechanisms considered could, by itself, ensure the coexistence of all species present at the beginning of our simulations. Realistic seasonal environments only aggravated that picture, as they decreased persistence relative to a random environment. Our results suggest that combining different mechanisms for biodiversity maintenance into community models might be more fruitful than trying to find which mechanism explains best the observed diversity levels. We additionally highlight that while trait-biomass distributions provide some clues regarding coexistence mechanisms, they cannot indicate by themselves which coexistence mechanisms are at play.

Number of words: 242

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

1 Introduction

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 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 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.

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

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

2 Methods

Models description

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

$$
\begin{aligned}
\frac{dN_i}{dt} &= r_i(\tau)N_i\left(1-\sum_{j=1}^{S}\alpha_{ij}N_j\right)-mN_i && (1)\\
r_i(\tau) &= a_r(\tau_0)e^{E_r\frac{(\tau-\tau_0)}{k\tau\tau_0}}f_i(\tau) && (2)\\
\text{where } f_i(\tau) &= \begin{cases} e^{-|\tau-\tau_i^{opt}|^3/b_i}, & \tau \leq \tau_i^{opt}\\ e^{-5|\tau-\tau_i^{opt}|^3/b_i}, & \tau > \tau_i^{opt}\end{cases} && (3)\\
\text{and} \quad b_i \text{ is defined by numerically solving} & \int r_i(\tau)d\tau = A && (4)
\end{aligned}
$$

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

Table 1: Parameter definitions and values for the model described in Eqs. 1-4. Parameter values are not specified when they vary 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 (°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	$8.6173324.10^{-5}$(eV.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)
$\tau_{\min}$	Minimum thermal optimum	288 (K)
$\tau_{\max}$	Maximum thermal optimum	298 (K)
A	Niche breadth	$10^{3.1}(\frac{\text{kg}}{\text{kg}\times\text{year}})$
τ_i^{opt}	Thermal optimum for growth of the ith species	(K)
θ	Scaling between random and seasonal noise	(0;1.3) (NA)
κ	Ratio of intra-to-interspecific competition strength	(1;10) (NA)

The original environmental forcing is a normally distributed variable centered on 293 K (20°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 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.

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

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

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

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

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

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

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

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

[1]The 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 $\kappa = 10$.

"equal competitive strengths" where intra- and interspecific competition strengths are equal.

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

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

Set-up

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

All simulations were run with Matlab's ode45 algorithm, an explicit Runge-Kutta (4,5) integration scheme with an absolute error tolerance of 10^{-8}, and relative error tolerance of 10^{-3}. The code is available in a GitHub repository[2] .

[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 left its maximum biomass, then as temperature decreases through the season, these species leave room for the growth of the low-temperature group.

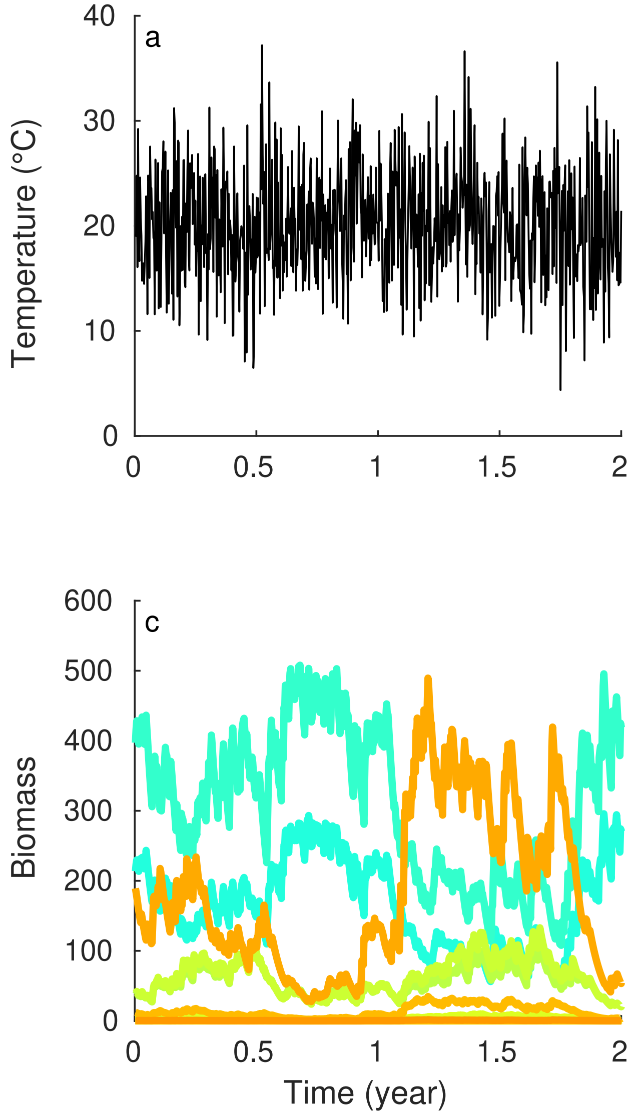

Figure 1: Time series of temperature (top; a-b) and extant species (bottom; c-d) for the 2 last years of a 5000-year simulation, with storage effect but no differences between intraspecific and interspecific competition strengths. The forcing temperature is either a random noise (a) or a seasonal noise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

The decrease in persistence due to seasonality observed in Fig. 1 was confirmed in all our simulations (Fig. 2). In cases where final species richness varied from one simulation to another (namely, the two middle cases in Fig. 2: with storage effect but without strong self-regulation, or without storage effect but with strong self-regulation), seasonality reduced the number of extant species to, on average, 27% and 48% of their original values, respectively (Fig. 2). A seasonal signal therefore led to a much smaller average persistence. There was also less variance in persistence between seasonally forced simulations compared to random noise simulations.

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

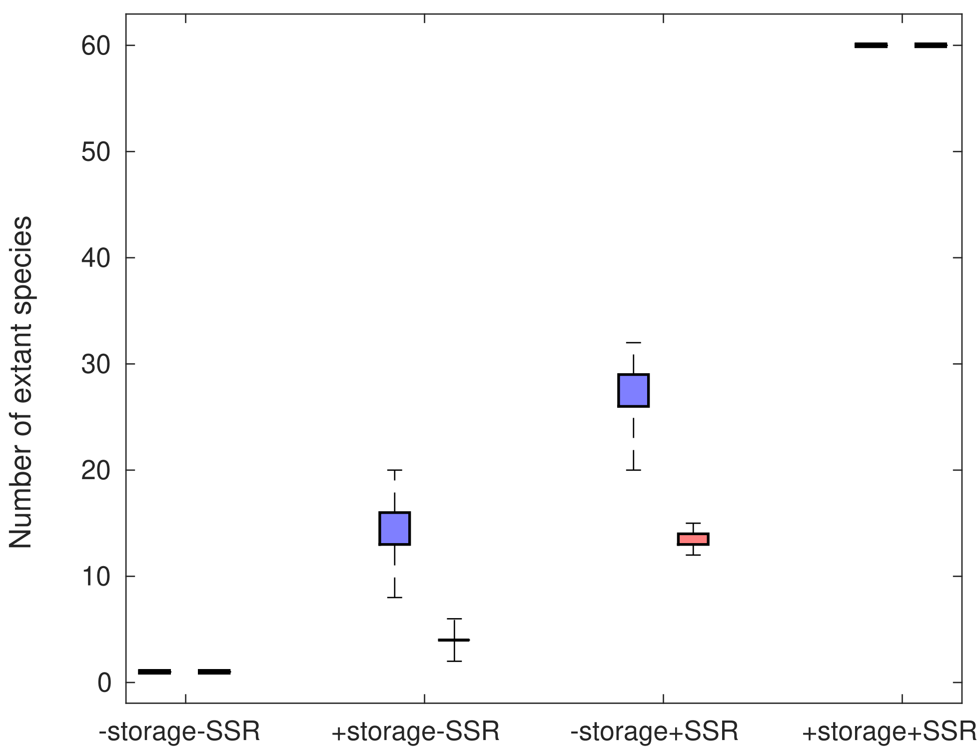

Figure 2: Number of species still present at the end of 100 simulations (5000 years each), initialized with 60 species, with a random forcing signal (blue) or a seasonal noise (red). The signs + or - storage refer to presence or absence of the storage effect, respectively; + / - SSR, presence or absence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

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

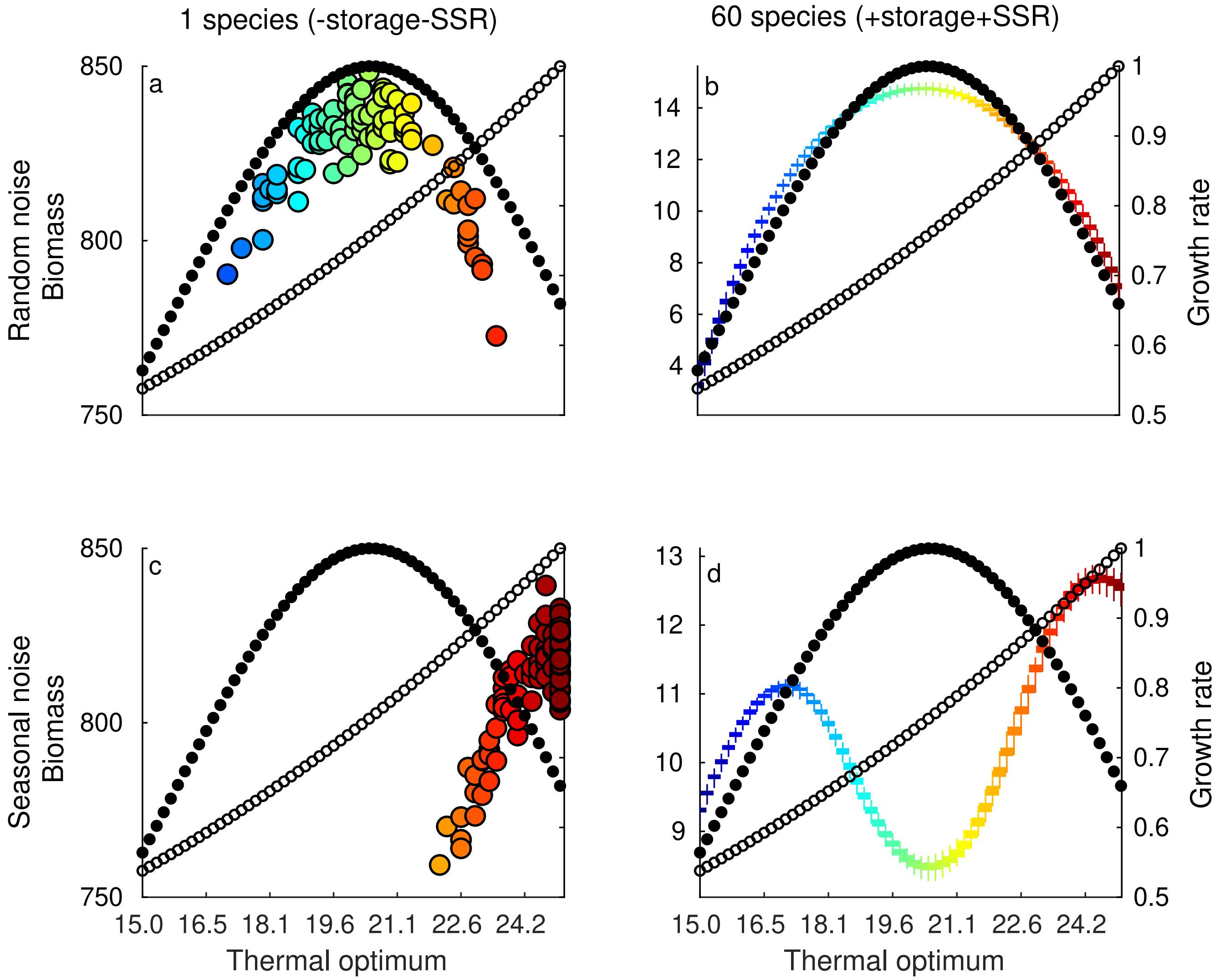

Figure 3: Mean biomass distribution over the last 200 years for 100 simulations, as a function of the species thermal optima. Here we consider the two stable-composition cases and two types of forcing signal. On the left column, simulations without storage effect nor strong self-regulation are presented.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

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

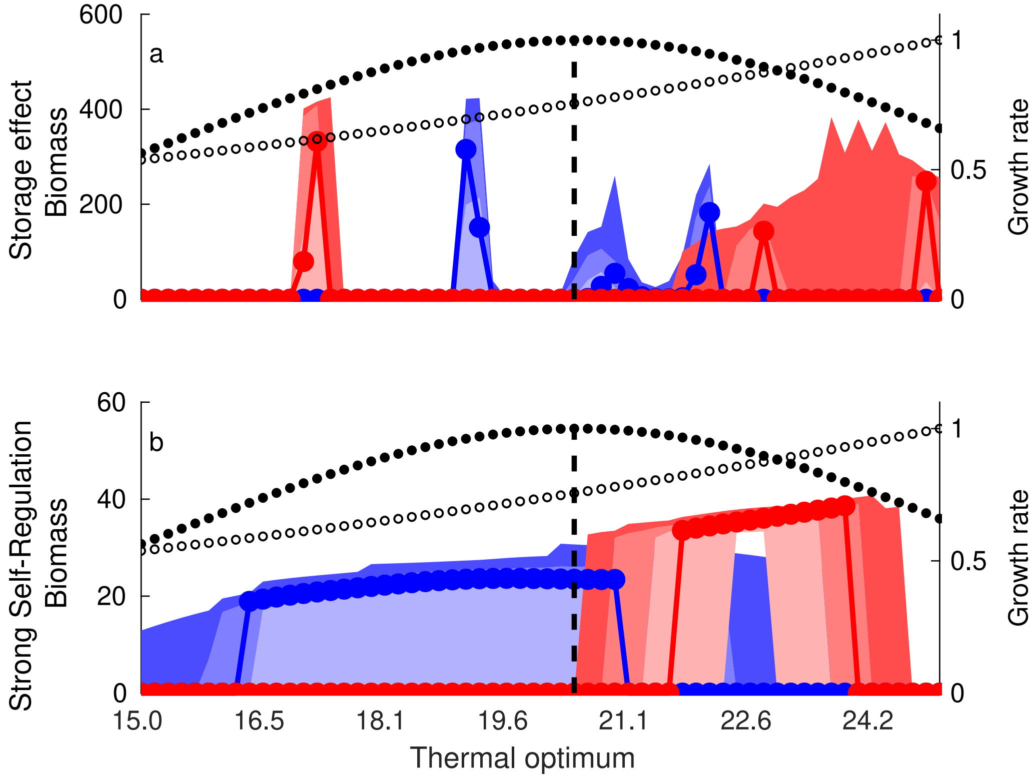

Figure 4: Mean biomass distribution over the last 200 years for 100 simulations, as a function of thermal optima, with storage effect and equal competitive strengths (a) and without storage effect, with strong self-regulation (b). The forcing signal is either a random (in blue) or a seasonal noise (in 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. 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. From an ecological standpoint, waiting for full convergence when there are extremely long transients (Hastings et al, 2018) is also quite artificial: there is no reason to believe that very long transients (i.e., transients that maintains for thousands of years) have any less ecological reality than an attractor that is deemed stable. Speed of convergence is therefore an issue to judge whether transients should be considered or excluded, and a very long yet fixed time window for integration allows advantageously to compare all mechanisms.

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

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

With these assumptions in mind, we have found that first, temporally forced Lotka-Volterra dynamics cannot sustain any diversity with our phytoplankton-based set of parameters, unless the structure is geared to include either a storage effect or a strong self-regulation. Although this absence of diversity-enhancing effect of "pure" environmental variation has already been stated by other authors (Chesson and Huntly, 1997; Barabás et al, 2012; Fox, 2013; Scranton and Vasseur, 2016), this is not always intuitive (Fox, 2013), so we feel compelled to stress it once more: temporal variation in growth rate alone cannot help coexistence within competitive communities. A nice point made by Scranton and Vasseur (2016) was that a built-in storage effect in a forced Lotka-Volterra model, parameterized for phytoplankton communities, could lead to some degree of coexistence. Our investigation reproduced these results, using the random noise considered by

Scranton and Vasseur (2016). However, an arguably more lifelike noisy and seasonal temperature forcing considerably lessened the richness of the community after 5000 years, decreasing from 15 to 4 species on average. Even imagining that groups represented here are genera or classes rather than species, this is a fairly low diversity for a phytoplankton-like community (see e.g., Chapter 1 in Reynolds, 2006). This suggests that the storage effect may not, on its own, be sufficient to maintain species-rich communities (e.g., dozens to hundreds of species). We have therefore sought out whether a stronger self-regulation could maintain a higher diversity, using field-based intra- vs intergroup (species or genera) competition strength ratio (Barraquand et al, 2018), where the intragroup density-dependence was estimated 10 times stronger. Implementing such strong self-regulation, in the forced Lotka-Volterra models that we considered, produced a higher level of diversity than the storage effect (almost double). Of course, the result is somehow contingent upon the strength of self-regulation. Our estimates are a little stronger than what was found in perennial plants (Adler et al, 2010), where interspecific competition was suggested 4 or 5 times stronger than intraspecific. Still, the widespread effects of natural enemies in phytoplankton (zooplankton, parasites) may contribute to increase the strength of self-regulation (Barraquand et al, 2018; Chesson, 2018) relative to other systems, hence we believe that 10 times stronger intraspecific competition constitutes a reasonable order of magnitude.

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

Our results may appear at odds with recent proposals that seasonal forcing in itself would help maintain diversity (Sakavara et al, 2018). However, we compared the effect of seasonal forcing to that of other forcing signals while controlling for total variance. Thus, the contrast between our results and those of Sakavara et al (2018) may be due to the role of forcing variance over time (we compare scenarios under a constant total variance). Overall, while seasonality may be slightly better than no forcing at all in maintaining diversity if a storage effect is present, seasonal forcing of parameters does not improve coexistence when compared to white 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, with 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. 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 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 were 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 opportunities for theoreticians wishing to investigate synergies between coexistence mechanisms in highly diverse communities. Aside from the synergies between predator diversity-enhancing effects, strong self-regulation through various means and storage effects (on the temporal axis), one obvious follow-up of this research would be interactions with spatial structure. Spatial structure occurs both endogeneously, through spatially restricted movements and interactions, and exogeneously, through spatial variation in environmental covariates (Bolker, 2003). Numerous studies (e.g., Bolker and Pacala, 1999; Murrell and Law, 2002) have shown that spatially restricted movements and interactions - very small-scale spatial structure - can help coexistence, which we believe would be especially important for phytoplankton since many species form colonies (Reynolds, 2006; see discussion in Barraquand et al, 2018). Moreover, although temperature is usually relatively spatially homogeneous over space, other drivers (e.g., rainfall, pH in terrestrial ecosystems; salinity in aquatic ones) may exhibit spatial variation which is a main factor for coexistence (Snyder, 2008). The odds that different (resource) niches, natural enemies, spatial limits to competition and temporal niche partitioning all interact to promote the very high-dimensional coexistence observed in the field seem much higher than for any of those mechanisms alone. Whether the diversity-enhancing effects of these mechanisms combine subadditively (as in Kuang and Chesson, 2010) or superadditively like here is therefore worthy of further research.

Acknowledgements

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

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