

1 Stabilizing niche differences are still required to maintain  
2 species-rich communities in temporally variable  
3 environments

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## Abstract

Explaining coexistence in species-rich communities of primary producers (e.g., tropical trees, phytoplankton) remains a challenge for ecologists because of the likely competition for shared basal 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 that allow coexistence, but they often produce only a dozen of coexisting species at best. Here, we investigate what it would take to create even richer communities in fluctuating environments using an empirically parameterized model. Building on the forced multi-species 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 stabilizing niche differences (SNDs). SNDs occur when intraspecific competition is stronger than interspecific (as opposed to neutral models where all coefficients are identical), and we tuned the competition ratio based on empirical data. Although SNDs maintained more species than the storage effect (50 % w.r.t 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 white noise. Our results suggest that combining different mechanisms for biodiversity maintenance into community models might be more fruitful than trying to find which explains best the observed diversity levels. Our results on community composition (formation of clumps, biomass distribution) in the different scenarios give further hints on how to empirically weight the influence of coexistence mechanisms.

# 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, and may actually act together to produce observed species coexistence (Gravel et al, 2006; Mutshinda et al, 2009; Götzenberger et al, 2012).

For instance, Scheffer and van Nes (2006) put forward the concept of 'clumpy coexistence', 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) enable coexistence of multiple clumps through stronger net intraspecific competition (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 (Vernon 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) that increases the possibility of coexistence by making the interaction strength covary positively with a fluctuating environment (see also

57 Barabás et al, 2012).

58 Here, we build on the work of Scranton and Vasseur (2016) to investigate the possibility of coexis-  
59 tence through species response to fluctuating environments. Our enthusiasm for the Scranton and Vasseur  
60 (2016) model stems from our interest in phytoplankton communities, that were the key inspiration for  
61 the thermal preference curves modeling intrinsic growth rates in Scranton and Vasseur (2016). However,  
62 Scranton and Vasseur (2016) described temperature as a white noise, i.e. independent and identically  
63 distributed Gaussian random variates over time. This appeared to us as a key assumption to relax. Un-  
64 der most latitudes, temperature is indeed a seasonal signal, and seasonal forcing can strongly affect the  
65 dynamics of the community considered (Vesipa and Ridolfi, 2017). Over short timescales, random tem-  
66 poral variations therefore often only add noise to a largely deterministic seasonal trend. Our present work  
67 can therefore be seen as an attempt to blend Scranton and Vasseur (2016)’s framework with the periodic  
68 environments of Barabás et al (2012), to better represent the mixture of stochastic and deterministic  
69 environmental forces affecting phytoplankton community dynamics.

70 Because many phytoplankton species or genera respond in similar ways to temperature despite hav-  
71 ing different optimas (Moisan et al, 2002), we hypothesized that a large seasonal variation might not  
72 necessarily foster species coexistence. In fact, similar responses to seasonal fluctuations should lead to  
73 an increased synchrony of species abundances which, in turn, should theoretically mitigate the expected  
74 temporal partitioning. How seasonality affects coexistence (as opposed to a purely randomly fluctuating  
75 environment) is therefore a key feature of this paper. In particular, we contrast cases where the storage  
76 effect is present vs. absent, which conveniently maps to two different parameterizations of the forced  
77 Lotka-Volterra model. Moreover, we realized while running Scranton and Vasseur (2016)’s model that  
78 the overall diversity obtained at the end of the simulations was relatively low compared to what we usu-  
79 ally observe in phytoplankton communities (several dozens to hundreds of species). We have therefore  
80 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 autore-  
82 gressive models (Barraquand et al, 2017), we found that despite a large influence of the environment  
83 (including temperature, irradiance, and other factors), intraspecific (or intragenus) competition was most  
84 likely the key driver of species coexistence. In other words, stabilizing niche differences had a large

85 role to play in maintaining species diversity in coastal phytoplankton (Barraquand et al, 2017). These  
 86 SNDs mirror those found in a number of terrestrial plant communities (Adler et al, 2018) and in animal  
 87 communities (Mutshinda et al, 2009).-

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

## 92 2 Methods

### 93 *Models description*

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

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

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

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

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

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

102 niche width.

Table 1: Parameter definition and values of the model described in Eq. 1-4

Name	Definition	Value (unit)
$S$	Number of species	60
$N_i$	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	$\frac{\text{kg}}{\text{kg}^*\text{year}}$
$\alpha_{ij}$	Strength of competition of species $j$ on species $i$	0.001 area/kg
$b_i$	Normalization of the thermal decay rate	
$m$	Mortality rate	$15 \frac{\text{kg}}{\text{kg}^*\text{year}}$
$\tau_0$	Reference temperature	293 K
$a_r(\tau_0)$	Growth rate at reference temperature	$386 \frac{\text{kg}}{\text{kg}^*\text{year}}$
$E_r$	Activation energy	0.467 eV
$k$	Boltzmann's constant	$8.6173324 \cdot 10^{-5} \text{eV.K}^{-1}$
$f_i(\tau)$	Fraction of the maximum rate achieved for the $i$ th species	
$\mu_\tau$	Mean temperature	293 K
$\sigma_\tau$	Standard deviation for temperature	5 K
$\tau_{\min}$	Minimum thermal optimum	288K
$\tau_{\max}$	Maximum thermal optimum	298 K
$A$	Niche breadth	$10^{3.1} \frac{\text{kg}}{\text{kg}^*\text{year}}$
$\tau_i^{\text{opt}}$	Thermal optimum for growth of the $i$ th species	K
$\theta$	Scaling between white noise and seasonal signal	$[0, \sqrt{(2)}]$
$\rho$	Ratio of intra-to-intergroup competition strengths	(1;10)

103 We kept the mean and standard deviation of the forcing signal but included a lower-frequency com-  
 104 ponent using a sinusoidal function with a period of 365 days (1 time unit being one day, Eq.5). We tune  
 105 the ratio of low-to-high frequency with the variable  $\theta$  so as to keep the same energy content - i.e., equal  
 106 total variance - in the forcing signal.

$$\tau(t) = \mu_\tau + \theta \sigma_\tau \sin\left(\frac{2\pi t}{365}\right) + \varepsilon_t, \text{ where } \varepsilon_t \sim \mathcal{N}(0, \sigma_\tau \sqrt{1 - \frac{\theta^2}{2}}) \quad (5)$$

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

111 The formulation of the forced Lotka-Volterra model of Scranton and Vasseur (2016) implies a storage

effect, as the competition strengths covary positively with the growth rate values  $r_i(\tau)$  (Chesson, 1994; Ellner et al, 2016). To test for the effect of an explicit storage effect in the model, we formulated a new version of this model, where we removed this assumption by using the mean value of a species' growth rate ( $\bar{r}_i$ ) to weight the interaction coefficients (see Table 2).

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

In this way, competition strengths remain unaffected by the environmental conditions, in contrast to growth rates (Eq. 6), while preserving the same average magnitude as in Eq. 1.

Stabilizing niche differences are ensured by the addition of the coefficient  $\rho$ , which is the ratio of intra-to-intergroup competition strength. We can therefore re-write the interaction coefficients  $\alpha_{ij}$  in Eq.

7

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

where  $\delta_{ij}$  is the Kronecker symbol, equal to 1 if  $i = j$  and to 0 otherwise. The value of the parameter  $\rho = 10$  was chosen from analyses of phytoplanktonic data (Barraquand et al, 2017) <sup>1</sup>.

In addition to two types of environmental forcings (white noise with  $\theta = 0$ , and seasonal forcing with  $\theta = 1.3$ ), we therefore compare the results for four formulations of the model: with and without an explicit storage effect (Eq. 1 and Eq. 6, respectively) ; with and without stabilizing niche differences ( $\rho = 10$  or  $\rho = 1$ , respectively). These are summed up in Table 2

$\frac{dN_i}{dt} + mN_i$	Storage effect	No storage effect
Stabilizing niche differences	$r_i(\tau) N_i \left( 1 - \sum_{j=1}^S \alpha (1 + 9\delta_{ij}) N_j \right)$	$N_i \left( r_i(\tau) - \sum_{j=1}^S \bar{r}_i \alpha (1 + 9\delta_{ij}) N_j \right)$
No stabilizing niche differences	$r_i(\tau) N_i \left( 1 - \sum_{j=1}^S \alpha N_j \right)$	$N_i \left( r_i(\tau) - \sum_{j=1}^S \bar{r}_i \alpha N_j \right)$

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

127

<sup>1</sup>The values of non-zero interspecific competition coefficients reported in Fig. 5 of Barraquand et al (2017) are somewhat higher than here (and  $\rho$  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  $\rho = 10$ .

## Set-up

We replicate the 'Species sorting' experiment of Scranton and Vasseur (2016) so as to investigate how the structure of synthetic phytoplankton communities varies under the different scenarios we described above. We focused on the dynamics of a community initialized with 60 species with thermal optima uniformly spaced along the interval  $[15^{\circ}\text{C}, 25^{\circ}\text{C}]$ , and with the same initial density  $(\frac{1}{\alpha\delta})$ . 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 ran with Matlab's ode45 algorithm, an explicit Runge-Kutta (4,5) algorithm with an absolute error tolerance of  $10^{-8}$ , and relative error tolerance  $10^{-3}$ .

## 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. 1-a) and Eq. 5 (our variant, Fig. 1-b), are shown in Fig. 1-c 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 white 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 white noise simulations were clustered within a  $3.2^{\circ}\text{C}$ -range of thermal optima (see the biomass distribution as a function of the thermal optimum in Fig. A.1 in the Supplementary Material). No obvious temporal patterns (e.g., cycles) could be seen in the communities forced by white noise. On the contrary, seasonal cycles were clear in the seasonally-forced case of Fig. 1-d). Only 4 species coexisted at the end of the simulation with seasonal forcing, gathered in two groups with large thermal optimum differences ( $5.7^{\circ}\text{C}$  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



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

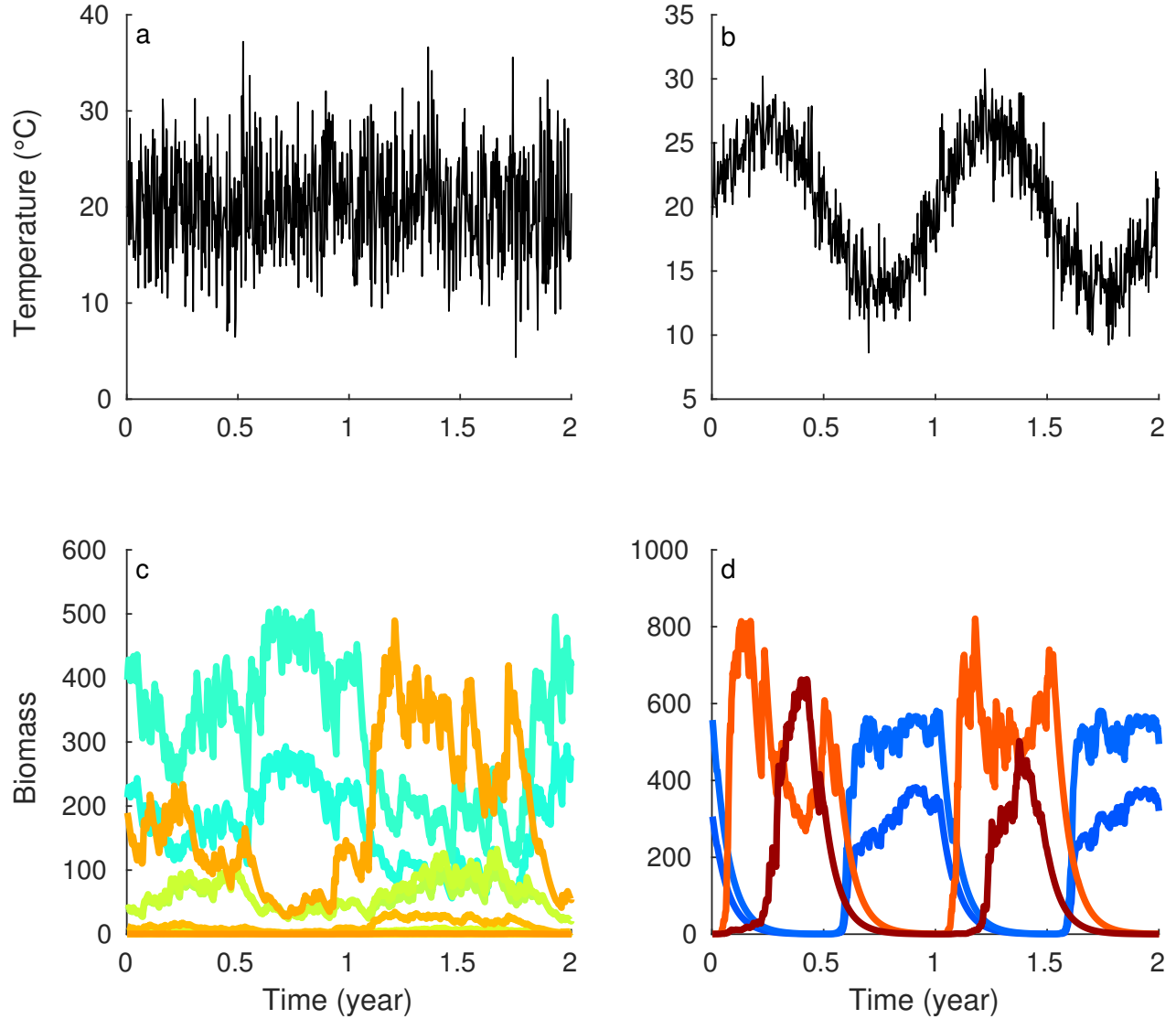


Figure 1: Time series of temperature (top; a-b) and extant species (bottom; c-d) for the 2 last years of a 5000 years simulation, with storage effect and no stabilizing niche differences. The forcing temperature is either a white noise (left a) or a noisy seasonal signal (right b), leading to community dynamics with more erratic fluctuations (d) 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).

156 The decrease in persistence due to seasonality observed in Fig. 1 was confirmed in all our simulations  
 157 (Fig. 2). In cases where final species richness varied from one simulation to another (namely, the two  
 158 middle cases in Fig. 2: with storage effect but without stabilizing niche differences, or without storage  
 159 effect but with stabilizing niche differences), seasonality reduced the number of extant species to, on

160 average, 27% and 48% of ~~their~~its original values, respectively (Fig. 2). A seasonal signal therefore led  
161 to a much smaller average persistence. There was also less variance in persistence between seasonally  
162 forced simulations when compared to white noise simulations.

163 Both the stabilizing niche differences and the storage effect markedly increased persistence. Without  
164 any of these coexistence mechanisms, only one species persisted at the end of the simulations. When only  
165 the storage effect was present, the number of extant species varied between 8 and 20 ( $14.8 \pm 2.4$ ) with a  
166 white noise, or 2 and 6 ( $4.1 \pm 0.7$ ) with a seasonal signal. On the other hand, when only stabilizing niche  
167 differences were present, the number of extant species nearly doubled, varying between 20 and 32 ( $27.5$   
168  $\pm 2.4$ ), or 12 and 15 ( $13.3 \pm 0.6$ ), with a white noise or a seasonal signal, respectively. Remarkably,  
169 when the storage effect and SNDs both affected the community dynamics, all species persisted in the  
170 community, while neither of these mechanisms was able to produce that result alone, for either white  
171 noise and seasonal forcing.

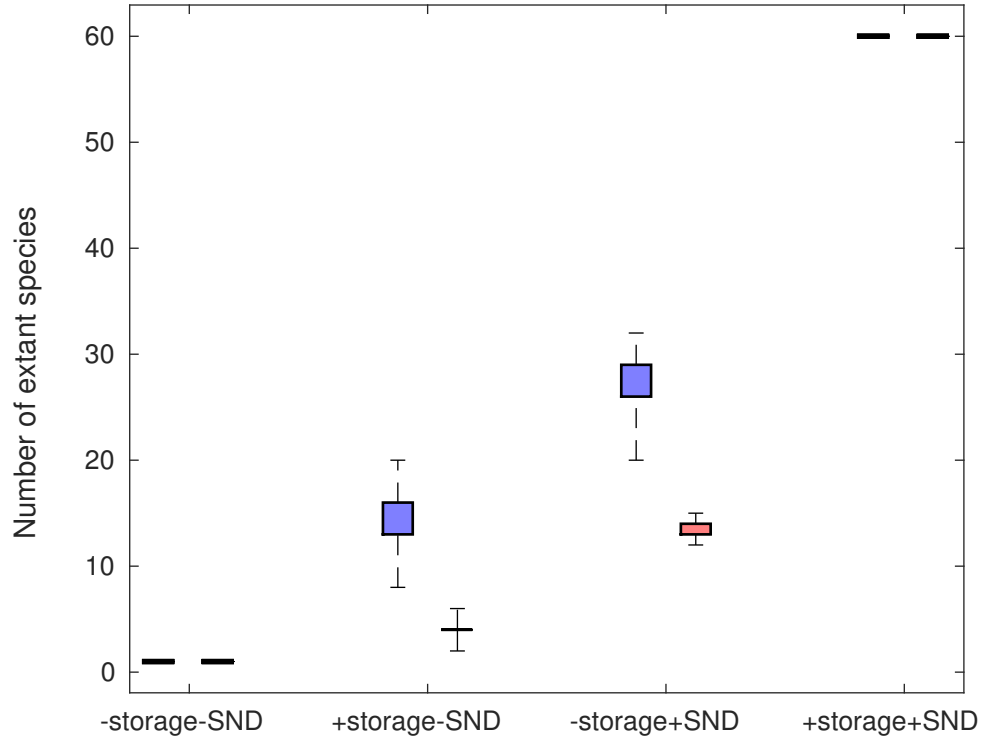


Figure 2: Number of species still present at the end of 100 5000-year simulations (5000 years each), initialized with 60 species, with a white noise forcing signal (blue) or a noisy seasonal signal (red). For each model type (with and without storage effect, The signs + or - storage refer to presence or absence of a storage effect, respectively; + / - SND, with and without presence or absence of Stabilizing Niche Differences, + / - SND, respectively). Community compositions are stable in the cases -storage-SND and +storage+SND (, for which 1 or 60 species are still present at the end of all simulations, respectively).

172 When the richness of the community was stable (either 1 or 60 species at the end of the simulation,  
 173 Fig. 3), there were still large differences in the structure of the community with respect to temperature,  
 174 due to both stochasticity and the type of forcing (Fig. 3). Without storage effect nor SNDs, a white noise  
 175 forcing favoured species with intermediate thermal optima, with two thirds of the simulations ending  
 176 with a species with a thermal optimum between 18.9°C and 21.4°C (corresponding to only one fourth of  
 177 the range of thermal optima present at the beginning of the simulation) and reaching a maximum average  
 178 biomass in this range (Fig. 3 a). This distribution can be related to a selection for the highest long-term  
 179 growth rates, averaged over time (see scaled growth rates in Fig.3). On the contrary, seasonality tended  
 180 to favor species with larger maximum growth rates (thermal optima above 22°C). Species with a higher  
 181 thermal optima are more likely to persist and to reach a higher biomass at the end of the simulation. 38%  
 182 of the simulations therefore ended with the species having the highest temperature optimum, 25°C.

183 When both coexistence mechanisms were present, the 60 initial species coexisted with small varia-  
184 tions in biomasses for each species over the 100 simulations (mean CV=0.008 across simulations with  
185 either a white noise or a seasonal forcing signal, Fig. 3b and d). The forcing signal modified only the  
186 distribution of biomasses resulting in contrasted community structures despite equal richness in both  
187 simulation types. With a white noise, the distribution was unimodal with a maximum biomass reached  
188 for the second best long-term average growth rate (corresponding to a thermal optimum of 20.2°C). On  
189 the contrary, a seasonal signal led to a bi-modal distribution (centered on 17.0°C and 24.4°C), each cor-  
190 responding to one season, with highest biomasses for higher thermal optima (Fig. 3 d). The minimum  
191 biomass was reached for the best long-term average growth rate at an intermediate temperature (20.4°C),  
192 one species apart from the maximum biomass in the white noise case

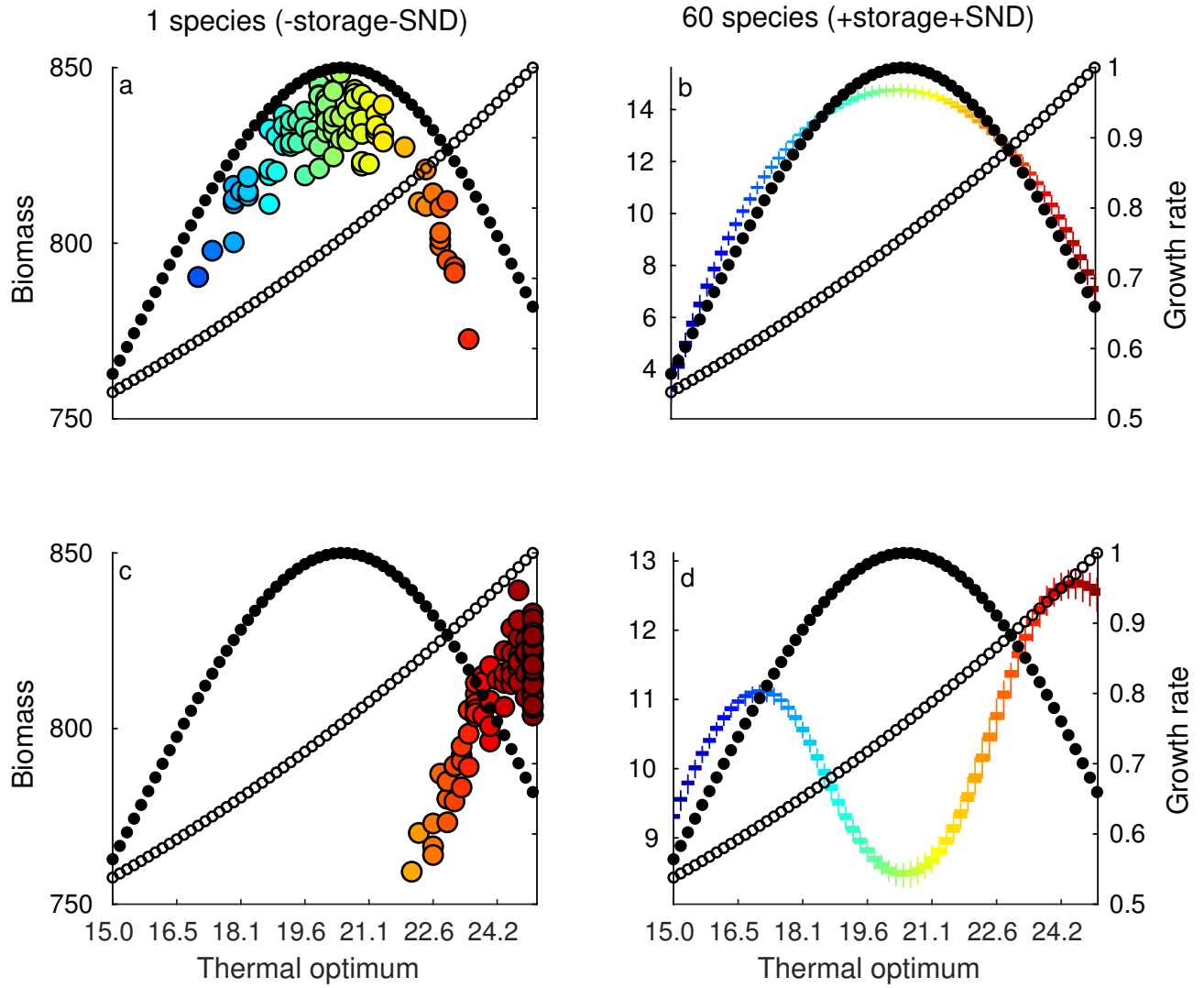


Figure 3: Mean biomass distribution over the last 200 years for 100 simulations, as a function of the species thermal optima. For Here we consider the two stable-composition cases and two types of forcing signal. On the left column, simulations without storage effect nor stabilizing niche differences are represented. Only one species is present at the end of the simulations and its mean value is represented by one point per simulation. There can be several dots for the same species, corresponding to multiple simulations ending with this species alone. On the right column, simulations with storage effect and stabilizing niche differences are represented. All species are present at the end of the simulations and boxplots correspond present the variation to the mean biomass of each species for in the temporal average of biomass with a given trait, for 100 simulations. The forcing signal is either a white noise (top) or a seasonal signal (bottom). Each species is identified by its thermal optimum and through its color code. Scaled (divided by maximum) average and maximum growth rates are shown as filled and open circles, respectively, and are indexed on the right y-axis.

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

196 shapes. Indeed, the storage effect led to a multimodal biomass distribution with respect to thermal optima.  
197 We always observed 3 modes with a white noise and 3 modes in 95% of the seasonal simulations, Fig. 4a.  
198 With a white noise, extant species are grouped in rather similar clumps regarding species thermal optima  
199 (between 18.8°C and 22.2°C whereas clumps tended to be further apart in the seasonal case, covering a  
200 total range of 7.7°C, with species grouping in the higher part of the thermal range, above 22°C. On the  
201 other hand, stabilizing niche differences led to a quasi-uniform biomass distribution (Fig. 4 b). Species  
202 characterising communities forced by a white noise stayed in the lower range of temperatures (in 96% of  
203 the simulations, the highest thermal optimum was 22.4°C, see Fig. A.2 in the Supplementary Material)  
204 while they were filtered out in communities subjected to a seasonal fluctuations of their environment, for  
205 which species with thermal optima above 20.5°C persisted.

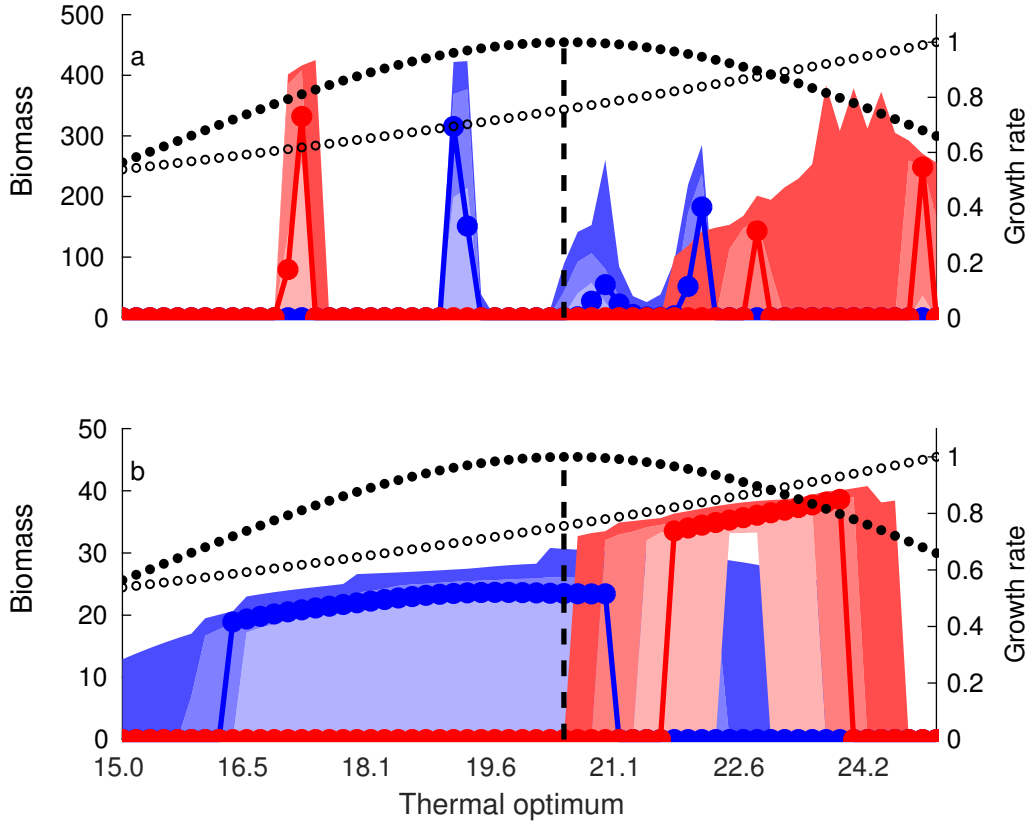


Figure 4: Mean biomass distribution over the last 200 years for 100 simulations, as a function of thermal optima, with storage effect and no stabilizing niche differences (a) and without storage effect, with stabilizing niche differences (b). The forcing signal is either a white noise (in blue) or a seasonal signal (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 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 stabilizing niches differences, could be either present or absent, which led to four scenarios. These four scenarios were crossed with two possibilities for the forcing signal, a white noise 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 white noise forcing and a

213 storage effect, but considered seven additional combinations of mechanisms. This was motivated by our  
214 wish to include two observed features of phytoplankton dynamics: seasonal cycles (Winder and Cloern,  
215 2010) and stabilizing niche differences (Chesson, 2000; Barraquand et al, 2017).

216 We have found that first, temporally forced Lotka-Volterra dynamics cannot sustain any diversity with  
217 our phytoplankton-based set of parameters, unless the structure is geared to include either a storage effect  
218 or SNDs. Although this absence of diversity-enhancing effect of “pure” environmental variation has  
219 already been stated by other authors (Barabás et al, 2012; Fox, 2013; Scranton and Vasseur, 2016), this is  
220 not always intuitive (Fox, 2013), so we feel compelled to stress it once more: temporal variation in growth  
221 rate alone cannot help coexistence within competitive communities. A nice point made by Scranton and  
222 Vasseur (2016) was that a built-in storage effect in a forced Lotka-Volterra model, parameterized for  
223 phytoplankton communities, could lead to some degree of coexistence. Our investigation reproduced  
224 these results, using the white noise forcing considered by Scranton and Vasseur (2016), but an arguably  
225 more realistic seasonal forcing by temperature considerably lessened the richness of the community after  
226 5000 years, decreasing from 15 to 4 species on average. Even imagining that groups represented here are  
227 genera or classes rather than species, this is a fairly low diversity for a phytoplankton-like community  
228 (see Chapter 1 in Reynolds, 2006).

229 We have therefore sought out whether stabilizing niche differences could maintain a higher diversity,  
230 using field-based intra- vs intergroup (species or genera) competition strength ratio (Barraquand et al,  
231 2017), where the intragroup density-dependence was chosen approximately 10 times stronger. On their  
232 own, SNDs produced a higher level of diversity than the storage effect (almost double for white noise),  
233 which not only aligns with our results on phytoplankton but also with results on perennial plants (Adler  
234 et al, 2010).

235 However, the seasonal forcing still considerably reduced diversity when SNDs were considered, es-  
236 pecially the “neutral” kind of diversity, i.e., diversity within clumps of similar traits. This diversity  
237 reduction occurs because within a season, the signal autocorrelation gives long, contiguous time intervals  
238 to the best competitor to exclude its less adapted heterospecifics. In contrast, a white noise generates  
239 large temperature shifts more frequently, and thereby forbid such competitive exclusion. In a seasonal  
240 setting, a species has the highest long-term averaged growth rate may not be the best competitor and can



241 disappear as a result of a strong competition from both low- and high-temperature tolerant species, with  
242 and without storage effect.

243 Our results may appear at odds with recent proposals that seasonal forcing in itself would help main-  
244 tain diversity (Sakavara et al, 2018). However, we compared the effect of seasonal forcing to that of  
245 other forcing signals while controlling total variance. Thus, the contrast between our results and those  
246 of Sakavara et al (2018) may be due to the role of forcing variance over time. Overall, seasonality  
247 may be slightly better than no forcing at all in maintaining diversity, but on its own, seasonal forcing of  
248 parameters does little to improve coexistence and it does not really foster diversity within clumps here.

249 In addition to community diversity, the ~~species-abundance-distribution (SAD)~~ biomass-trait relation-  
250 ship also varied from one ~~set of~~ simulation to another. Some regularities did emerge across simulations  
251 though. The storage effect begot several clumps along the trait space, with seasonality leading to more  
252 distant clumps. Conversely, SNDs alone led to uniform distributions, with species forming a single cluster  
253 along a fraction of the initial trait space. The identifi~~cat~~ion of multiples modes in biomass-trait rela-  
254 tionships and SADs is relatively recent (Dornelas and Connolly, 2008; Matthews et al, 2014) and is a rare  
255 pattern in theoretical models (McGill et al, 2007). ~~While~~ Barabás et al (2013) convincingly argued that  
256 multimodality could~~an~~ arise from ~~artificial model formulation or~~ the demographic stochasticity of a sin-  
257 gle model run (with SNDs or neutrality, but without clumpy coexistence), ~~without underlying ecological~~  
258 ~~processes, we note that this does not hold for our results.~~ However, our results are based on many model  
259 runs, ~~since~~ for which either the storage effect alone, or a storage effect ~~and~~ +SNDs in a seasonal context  
260 ~~both~~ ~~consiste~~ntly produced multimodal distributions, while other sets of simulations always led to a  
261 single cluster along the trait axis. If only one spatial location is observed, caution is of course required  
262 as Barabás et al (2013) highlighted. However, with several locations - or in a theoretical context - one  
263 could average across locations to reproduce similar graphs to the ones produced here. Clumps in the trait  
264 axis when averaged across repeats is a feature that we found to emerge only through the combination of  
265 a fluctuating environment and a storage effect. Of course, biomass clustering on the environmental trait  
266 axis may not always indicate a storage effect in real-world ecosystems, as other mechanisms that we did  
267 not include in our model may produce similar patterns. Still, clustering on the trait axis may suggest to  
268 look more closely for potential storage effects at work. ~~This might indicate that multimodality is indeed~~

269 dependent on the community and ecological setting considered, which would explain the different results  
270 obtained until now on empirical SADs.

271 In our previous empirical study of coastal phytoplankton dynamics (Barraquand et al, 2017), we  
272 have not found any storage effect (which certainly does not mean that it could not be observed in other  
273 systems). Given the results on species richness and composition presented here, we are skeptical that even  
274 if it was present, the storage effect alone could help explaining phytoplankton diversity. However, our  
275 results suggest that in phytoplankton-like seasonal environments, even though empirically-based SNDs  
276 produce more diversity than the storage effect when considered in isolation, the storage effect can help  
277 diversity maintenance when combined to other mechanisms. Indeed, the combination storage effect  
278 + SNDs is non-additive: the cases where both SNDs and the storage effect were present showed more  
279 diversity than generated by any mechanism on its own.

280 The above results suggest the very exciting idea that multiple coexistence mechanisms might com-  
281 bine superadditively, thus helping us to better understand the astounding diversity of primary producers.  
282 This logic could, in principle, be extended to mechanisms that we have not considered here (e.g., spatial  
283 structure, specialized natural enemies, that could be as important here for plankton as they are for tropical  
284 trees, see Bagchi et al, 2014; Comita et al, 2014; Stump and Chesson, 2015; Barraquand et al, 2017). Pre-  
285 vious research has however demonstrated that generalist seed predation could weaken the storage effect  
286 (Kuang and Chesson, 2009, 2010) thus different mechanisms might not always combine superadditively  
287 as we found here. That said, superadditivity has been found in some cases, i.e., pathogens could enhance  
288 the storage effect (Mordecai, 2015). Better explaining plant or microbial diversity would then not be  
289 about selecting the best unique mechanism susceptible to explain the observed diversity, but rather bet-  
290 ter combining those mechanisms together. This may obviously be an annoyance for those who like to  
291 sharpen Occam's razor, but it clearly holds opportunities for theoreticians wishing to investigate syner-  
292 gies between coexistence mechanisms in highly diverse communities. Aside from the synergies between  
293 predator diversity-enhancing effects and SNDs or storage effects (on the temporal axis), one obvious  
294 follow-up of this research would be interactions with spatial structure. Spatial structure occurs both en-  
295 dogeneously, through spatially restricted movements and interactions, and exogeneously, through spatial  
296 variation in environmental covariates Bolker (2003). Numerous studies (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, 2017). 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 sub-additively (as in Kuang and Chesson, 2010) or super-additively like here is therefore worthy of further research.

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