

# Stabilizing niche differences are still required to maintain species-rich communities in temporally variable 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-environments 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), 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 competition is symmetric), and we tuned the competition ratio based on empirical phytoplankton 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 (for space) 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). But as it has been pointed out repeatedly, niche and neutral processes are not mutually exclusive (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 niche and neutral community assembly may be simultaneously at work, creating several clumps of similar species along a single trait axis. Classical stabilizing niche differences 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. However, 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. But the idea that niche and neutral assembly can mould communities stays potent (Vernon et al, 2013), and since then, several studies have searched for this 'clumpy coexistence' in theoretical models, most notably 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 that increase the possibility of coexistence (see also Barabás et al, 2012).

Here, we build on the work of Scranton and Vasseur (2016) to investigate the possibility of coexistence through fluctuating environments (the so-called storage effect or temporal niche partitioning, that are equivalent concepts for forced Lotka-Volterra models, Barabás et al, 2012; Scranton and Vasseur, 2016). Our enthusiasm for the Scranton and Vasseur (2016) model stems from our interest in phytoplankton communities, that were the key inspiration for the thermal preferences curves in Scranton and Vasseur (2016). However, Scranton and Vasseur (2016) described temperature as a white noise, i.e. independent and identically distributed Gaussian random variates. This appeared to us as 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). Over short timescales, random temporal variation therefore 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, an increased synchrony of species abundances should theoretically decrease their 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 elegantly maps to two different versions of the forced Lotka-Volterra model (see Methods). Moreover, we realized while running Scranton and Vasseur (2016)'s model that the overall diversity obtained after 5000 years was relatively low compared to what we usually observe in phytoplankton communities. In an empirical study combining phytoplankton community-level time series and multivariate autoregressive models (Barraquand et al, 2017), we

found that despite a large influence of the environment (including temperature, irradiance, and other factors), intraspecific (or intragenus) competition was rather large and most likely the key driver of species coexistence. In other words, stabilizing niche differences had a large role to play in maintaining species diversity in coastal phytoplankton (Barraquand et al, 2017) Here, we therefore try to establish what are the relative contributions of the storage effect vs intraspecific density-dependence to coexistence 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, 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 a variant of the Lotka-Volterra competition model. Fluctuations in the environment are introduced in the model by temperature-dependant growth rates (see eq. 1-2, all coefficients are defined in Tab. 1) so that species growth rates can be expressed as:

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

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

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

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

Model parameters are detailed in Table 1, and we set their values to match the features of phytoplankton communities as in (Scranton and Vasseur, 2016). The niche of each species is defined by its thermal optimum  $\tau_i^{opt}$ . Thermal performance curves defined in eq. 3 are parameterized so that all species share

94 the same niche area (eq. 4), which sets a trade-off between maximum growth rates and 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	$\frac{\text{kg}}{\text{kg*year}}$
$\alpha_{ij}$	Strength of competition of species $j$ on species $i$	0.001 area/kg
$b_i$	Normalization of the thermal decay rate	
$m$	Mortality rate	$15 \frac{\text{kg}}{\text{kg*year}}$
$\tau_0$	Reference temperature	293 K
$a_r(\tau_0)$	Growth rate at reference temperature	$386 \frac{\text{kg}}{\text{kg*year}}$
$E_r$	Activation energy	0.467 eV
$k$	Boltzmann's constant	$8.6173324 \cdot 10^{-5} \text{eV.K}^{-1}$
$f_i(\tau)$	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	$10^{3.1} \frac{\text{kg}}{\text{kg*year}}$
$\tau_i^{\text{opt}}$	Thermal optimum for growth of the $i$ th species	K
$\theta$	Scaling between white noise to seasonal signal	$[0, \sqrt{(2)}]$
$\rho$	Ratio of intra-to-intergroup competition strengths	(1;10)

95 We kept the mean and standard deviation of the signal but included a lower-frequency component  
96 (eq.5). The ratio of low-to-high frequency depends on the variable  $\theta$ , enabling us to keep the same  
97 energy content in the forcing signal.

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

98 The upper limit for  $\theta$ ,  $\sqrt{2}$ , corresponds to a completely determinist model. We chose to keep the  
99 stochasticity in the signal and to model a plausible temperature signal with  $\theta = 1.3$  (see Fig. 1b).

100 The formulation of the forced Lotka-Volterra model of Scranton and Vasseur (2016) implies a storage  
101 effect, as the competition strengths covary positively with the growth rate value  $r_i(\tau)$  (Ellner et al, 2016).  
102 To test for the effect of an explicit storage effect in the model, we removed this assumption by using the  
103 mean value of a species' growth rate ( $\bar{r}_i$ ) to weight the interaction coefficients.

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

In eq. 6, competition strengths remain unaffected by the environmental conditions, in contrast to growth rates.

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).

In addition to two types of environmental forcings (white noise,  $\theta = 0$ , and seasonal,  $\theta = 1.3$ ), 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).

$\frac{dN_i}{dt} + mN_i$	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

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## 116 Set-up

We repeat the 'Species sorting' experiment of Scranton and Vasseur (2016) so as to investigate on how synthetic phytoplankton communities structure under the various scenarios we described above. We focused on the dynamics of a community initialized with 60 species with thermal optima uniformly spaced along the interval  $[15^\circ\text{C}, 25^\circ\text{C}]$ . All species started 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 the parameters of the model (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  $10^{-8}$ .

### 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. ?? (original choice of Scranton and Vasseur, 2016) and 5 (our variant), are shown in Fig. 1. Forcing by a sinusoidal signal 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 while 6 out of the 14 remained below the unit. All species in the white noise simulations were clustered along a 3.2°C-range of thermal optima (Fig. 5). No obvious temporal patterns (e.g., cycles) could be seen in the communities forced by white noise. On the other hand, 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°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 a higher thermal optima reach maximum biomass, then as temperature decreases through the season, they leave room for the growth of the low-temperature group.

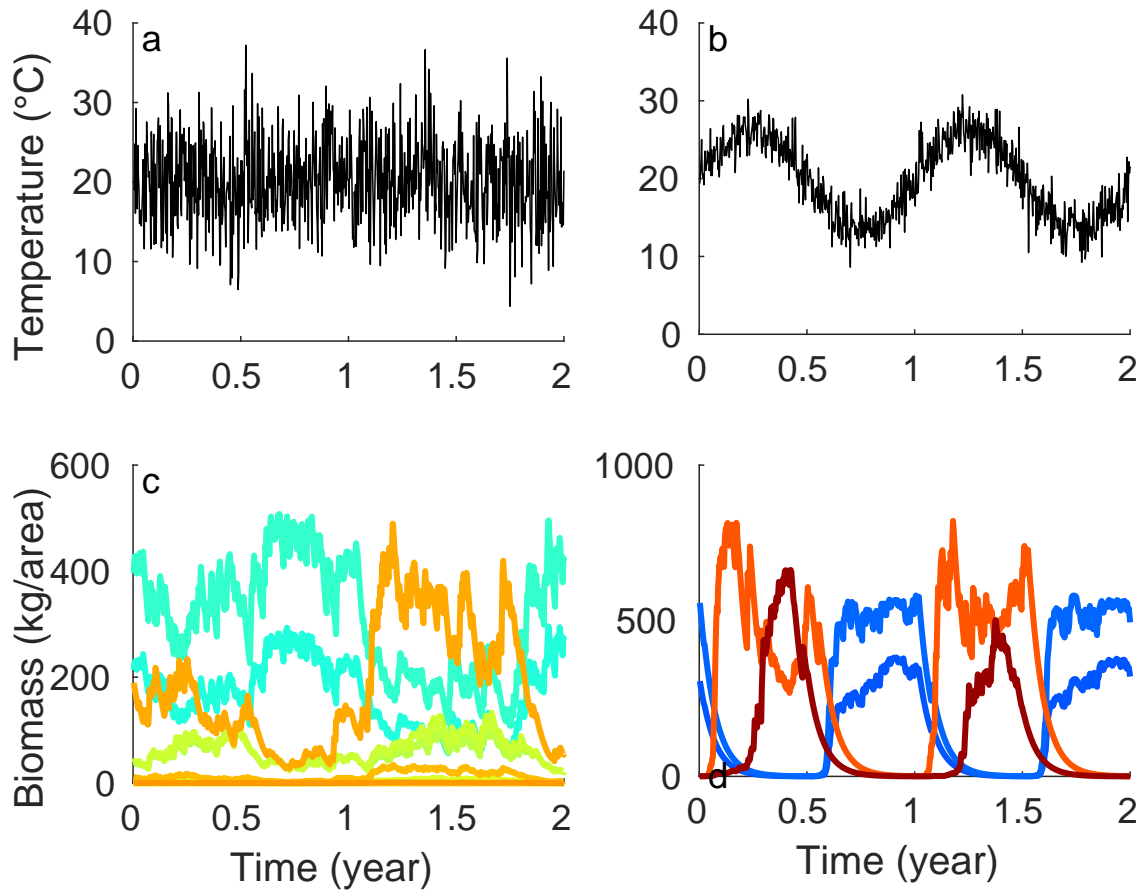


Figure 1: Times series of temperature (top) and extant species (bottom) for the 2 last years of a 5000 year simulation, with storage effect and no stabilizing niche differences. The forcing temperature is either a white noise (left) or a noisy seasonal signal (right). Line colors of species biomasses correspond to their thermal optima (from blue, corresponding to low thermal optima, to red, corresponding to high thermal optima. The whole range of the biomass distribution is shown on Fig. 3).

141 The decrease in persistence due to seasonality observed in Fig. 1 was confirmed in all our simulations  
 142 (Fig. 2). In cases where final species richness varied from one simulation to another (namely, the two  
 143 middle cases in Fig. 2): with storage effect but without stabilizing niche differences, or without storage  
 144 effect but with stabilizing niche differences), seasonality reduced the number of extant species to, on  
 145 average, 27% and 48% of its original value, respectively (Fig. 2). A seasonal signal therefore led to a  
 146 much smaller average persistence. There was also less variance in persistence between seasonally forced  
 147 simulations when compared to white noise simulations.

148 Both the stabilizing niche differences and the storage effect have a marked effect on increasing per-  
 149 sistence. Without any of these coexistence mechanisms, only one species persisted at the end of the



simulation. When only the storage effect was present, the number of extant species varied between 8 and 20 with a white noise, or 2 and 6 with a seasonal signal. On the other hand, when only stabilizing niche differences were present, the number of extant species nearly doubled, varying between 20 and 32, or 12 and 15, with a white noise or a seasonal signal respectively. Remarkably, when the storage effect and stabilizing niche differences (SNDs) both affected the community dynamics, all species persisted in the community, while neither the storage nor SNDs were able in isolation to produce that result, for both white noise and seasonal forcing.

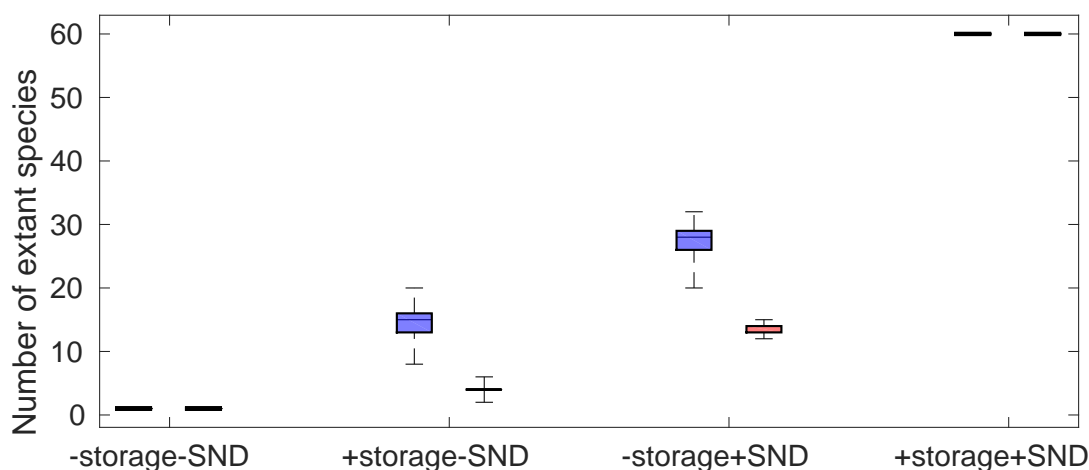


Figure 2: Number of species still present at the end of 5000-year simulations, initialized with 60 species, with a white noise forcing signal (blue) or a noisy seasonal signal (red). For each model type (with and without storage effect, + / - storage, respectively; with and without Stabilizing Niche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

When the richness of the community was stable (either 1 or 60 species at the end of the simulation, Fig. 3), there were still large differences in the structure of the community due to both stochasticity and the type of forcing (Fig. 3). Without storage effect and SNDs, a white noise forcing favoured species with intermediate thermal optima, with two thirds of the simulations ending with a species with a thermal optima between 18.9°C and 21.4°C (corresponding to 25% of the range of thermal optima present at the beginning of the simulation) and reaching a maximum average biomass in this range (Fig. 3 a). This distribution can be related to a selection for the highest long-term growth rates, averaged over time (see normalized growth rates in Fig. 4). On the contrary, seasonality tended to favour species with

165 larger maximum growth rates, with thermal optima above 22°C, their frequency of persistence and mean  
166 biomass increasing with the thermal optimum (Fig. 3). 38% of the simulations therefore ended with the  
167 species having the highest temperature optimum, 25°C.

168 When both coexistence mechanisms were present, the 60 initial species coexisted with small vari-  
169 ations in biomasses over the 50 simulations (mean CV=0.008 across simulations with either a white  
170 noise or a seasonal forcing signal, Fig. 3b and d). The forcing signal modified only the distribution  
171 of biomasses. With a white noise, the distribution was unimodal with a maximum biomass reached for  
172 the second best long-term average growth rate (corresponding to a thermal optimum of 20.2°C). On the  
173 contrary, a seasonal signal led to a bi-modal distribution (centered on 17.0°C and 24.4°C) with higher  
174 biomasses for higher thermal optima (Fig. 3 d). The minimum biomass was reached for the best long-  
175 term average growth rate (20.4°C), one species apart from the maximum biomass in the white noise case,  
176 thus there are quite broad changes in community composition even though the richness is equal for the  
177 two forcing signals. The two modes in the seasonal biomass distribution correspond to the two modes in  
178 the seasonal signal (winter and summer).

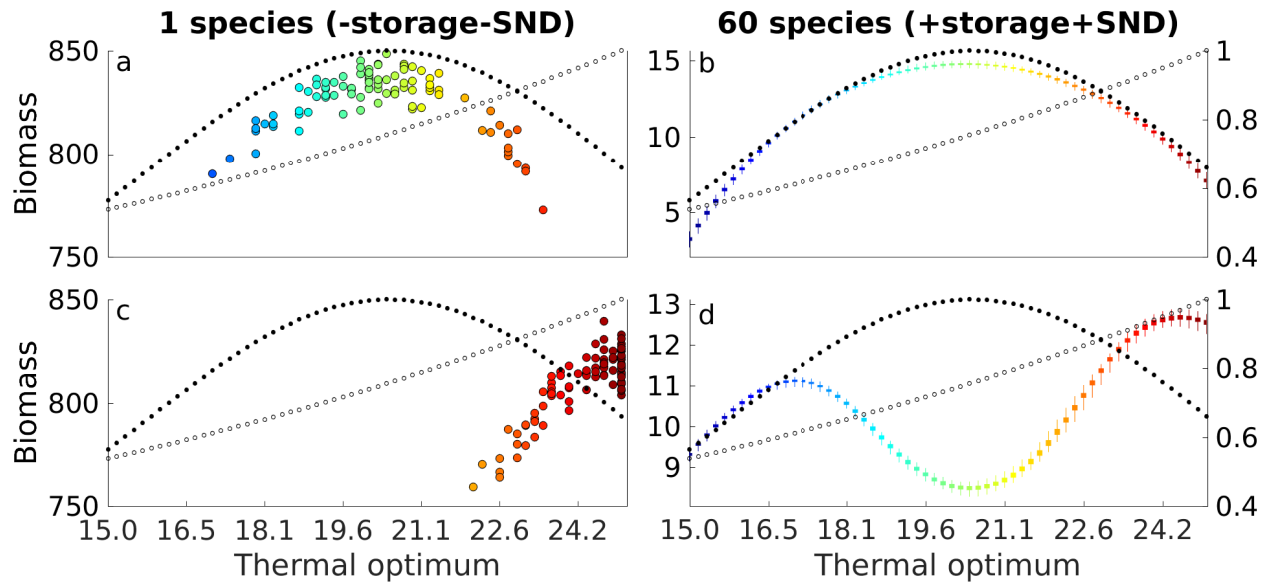


Figure 3: Mean biomass distribution over the last 200 years of 100 simulations, as a function of thermal optima, for the two stable-composition cases: without storage effect nor stabilizing niche differences (left, only one species is extant at the end of simulation, its mean value is represented by a dot for one simulation. There can be several dots for the same species, corresponding to multiple simulations ending with this species alone) and with storage effect and stabilizing niche differences (right, all species are present at the end of the simulation, their mean biomass is represented by boxplots of the mean value for 50 simulations). The forcing signal is either a white noise (top) or a seasonal signal (bottom). Each species is identified by its thermal optimum and its color code. Mean (filled circles) and maximum (open circles) growth rates for each species are indexed on the right axis [CP: Not sure about showing GR on this figure, though. I have another one without GR if necessary Fred: if you do this, you need to make it a yy-plot, with a right-hand y-axis labelled “Growth rate”].

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

183 The storage effect led to a multi-modal biomass distribution with respect to thermal optima. We  
 184 always observed 3 modes with a white noise and 3 modes in 95% of the seasonal simulations, Fig.  
 185 4a. With a white noise, extant species are grouped in rather similar clumps regarding species thermal  
 186 optimum (between 18.8°C and 22.2°C whereas clumps tended to be further apart in the seasonal case,  
 187 covering a total range of 7.7°C, with species grouping in the higher part of the thermal range, above 22°C.

188 On the other hand, stabilizing niche differences led to a quasi-uniform biomass distribution (Fig. 4  
 189 b). Species characterising communities forced by a white noise stayed in the lower range of temperatures

190 (in 96% of the simulations, the highest thermal optimum was 22.4°C) while they were filtered out in  
 191 communities subjected to a seasonal fluctuations of their environment, for which species with thermal  
 192 optima above 20.5°C persisted.

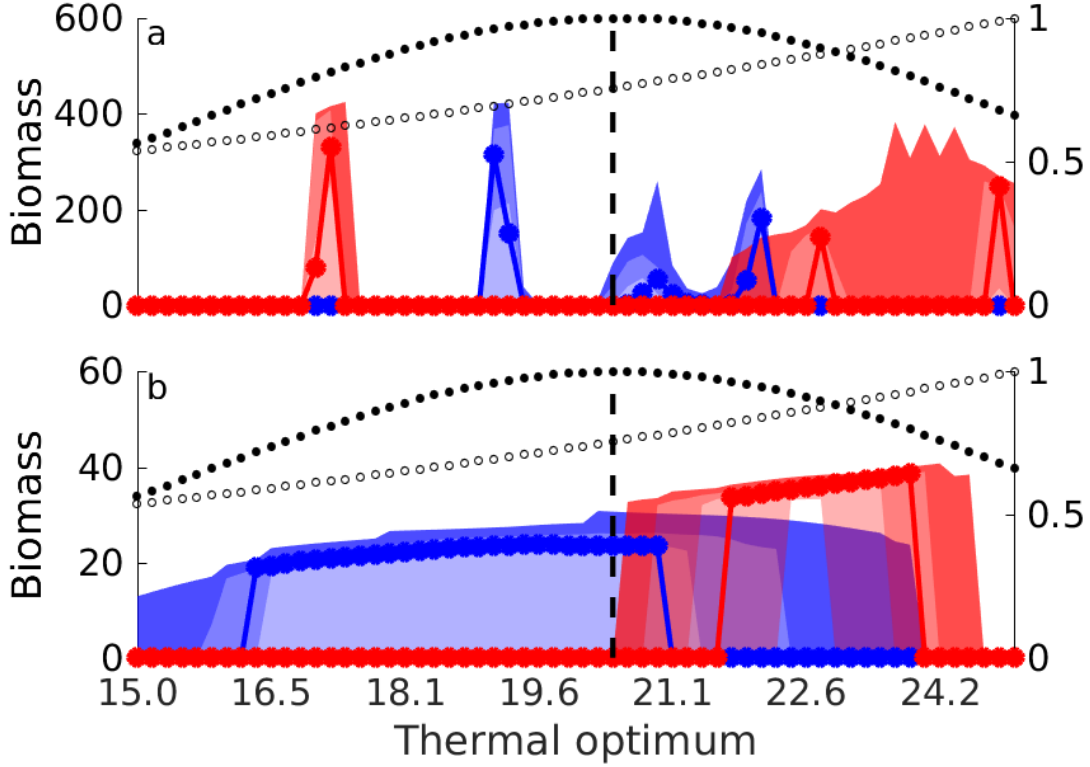


Figure 4: Mean biomass distribution over the last 200 years of 100 simulations, as a function of thermal optima, with storage effect and no stabilizing niche differences (top) and without storage effect, with stabilizing niche differences (bottom). The forcing signal is either a white noise (blue) or a seasonal signal (red). Shades of the same colour corresponds to the 50th, 90th and 100th percentiles of the distributions while coloured lines correspond to one representative simulation. Scaled average (whose optimum is indicated by the dashed line) and maximum growth rates are shown as filled and open and circles, respectively, and indexed on the left y-axis. [F: Add a right-handed y-axis labelled “Growth rates”]

## 193 4 Discussion

194 We have simulated competitive Lotka-Volterra dynamics forced by a fluctuating environment (e.g., tem-  
 195 perature fluctuations) under a range of scenarios allowing more or less coexistence. Two coexistence  
 196 mechanisms, the storage effect and stabilizing niches differences, could be either present or absent, which  
 197 led to four scenarios. These four scenarios were crossed with two possibilities for the forcing signal, a

198 white noise and a stochastic yet seasonal signal, both with equal temporal variance. Our investigation  
199 therefore built on the model of Scranton and Vasseur (2016), which included a white noise forcing and a  
200 storage effect, but considered seven additional combinations of mechanisms. This was motivated by our  
201 wish to include two observed features of phytoplankton dynamics: seasonal cycles (Winder and Cloern,  
202 2010) and stabilizing niche differences (Barraquand et al, 2017).

203 We have found that first, forced Lotka-Volterra dynamics cannot sustain any diversity with our  
204 phytoplankton-based set of parameters, unless the structure is geared to include either a storage effect  
205 or SNDs. Although this absence of diversity-enhancing effect of “pure” environmental variation has al-  
206 ready been stated by other authors (Barabás et al, 2012; Fox, 2013; Scranton and Vasseur, 2016), this is  
207 not always intuitive (Fox, 2013), so we feel compelled to stress it once more: temporal variation in growth  
208 rate alone cannot help coexistence within competitive communities. A nice point made by Scranton and  
209 Vasseur (2016) was that a built-in storage effect in a forced Lotka-Volterra model, parameterised for phy-  
210 toplankton communities, could lead to some degree of coexistence. Our investigation reproduced these  
211 results, using the white noise forcing considered by Scranton and Vasseur (2016), but an arguably more  
212 realistic seasonal forcing by temperature (thinking of phytoplankton) considerably lessened the number  
213 of species coexisting after 5000 timesteps, decreasing from 15 on average to 4 on average. Even imagin-  
214 ing that groups represented here are genera or classes rather than species, this is a fairly low diversity for  
215 a phytoplankton-like community (Reynolds, 2006) .

216 We have therefore sought out whether stabilizing niche differences (SNDs) could produce a higher  
217 diversity maintenance, using field-based intra- vs inter-group (species or genera) competition coefficient  
218 ratio (Barraquand et al, 2017), where the intra-group density-dependence is approximately 10 times  
219 stronger. On their own, SNDs produced a higher level of diversity than the storage effect (almost double  
220 for white noise).

221 However, the seasonal forcing still considerably reduced diversity when SNDs were considered, es-  
222 pecially the “neutral” kind of diversity, i.e., diversity within clumps of similar traits. This diversity  
223 reduction occurs because within a season, the signal autocorrelation gives long, contiguous chunks of  
224 time to the best competitor to exclude its less adapted heterospecifics, while white noise contains also  
225 very low forcing signal frequencies that make thermal optima shift more frequently, and thereby forbid

226 such competitive exclusion. In a seasonal setting, even though a species has the best long-term averaged  
227 growth rate, it can disappear as a result of a strong competition from both low- and high-temperature tol-  
228 erant species, with and without storage effect. Our results are therefore at odds with recent proposals that  
229 seasonal forcing in itself would help maintain diversity (Sakavara et al, 2018), at least not when seasonal  
230 forcing is compared to other forcing signals of equal variance. Seasonality may be slightly better than  
231 no forcing at all in maintaining diversity, but on its own, seasonal forcing of parameters combined to a  
232 storage effect does little to improve coexistence and it does not really help to maintain diversity within  
233 clumps here.

234 In our previous empirical study of coastal phytoplankton dynamics (Barraquand et al, 2017), we  
235 have not found any storage effect (which certainly does not mean that it could not be observed in other  
236 systems). Given the results on species richness and composition presented here, we are skeptical that  
237 even if it was present, the storage effect alone could help explaining phytoplankton diversity. This is all  
238 the more likely that SNDs seem fairly strong when estimated from phytoplankton time series (Barraquand  
239 et al, 2017). However, our results suggest that in phytoplankton-like seasonal environments, even though  
240 empirically-based SNDs produce more diversity than the storage effect when considered in isolation,  
241 the storage effect can help diversity maintenance when combined to other mechanisms. Indeed, the  
242 combination storage effect + SNDs is non-additive: the cases where both SNDs and the storage effect  
243 were present showed more diversity than generated by any mechanism on its own.

244 This suggests the very exciting idea that multiple coexistence mechanisms might combine superad-  
245 ditively, thus helping us to better understand the astounding diversity of primary producers. This logic  
246 could, in principle, be extended to mechanisms that we have not considered here (e.g., spatial struc-  
247 ture, specialized natural enemies, that could be as important here for plankton as they are for tropical  
248 trees Bagchi et al; Comita et al; Stump and Chesson; Barraquand et al). Previous research has however  
249 demonstrated that generalist seed predation could weaken the storage effect (Kuang and Chesson, 2009,  
250 2010) thus different mechanisms might not always combine superadditively as we found here. That  
251 said, other models have shown that pathogens could enhance the storage effect (Mordecai, 2015) or that  
252 equalizing mechanisms due to optimally foraging predators are not greatly affected by environmental  
253 variation (Stump and Chesson, 2017). 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 and SNDs or 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 TPB 2003). Numerous studies (Bolker and Pacala Am Nat 2000, Murrell and Law Ecology 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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## 341 A Supplementary Material

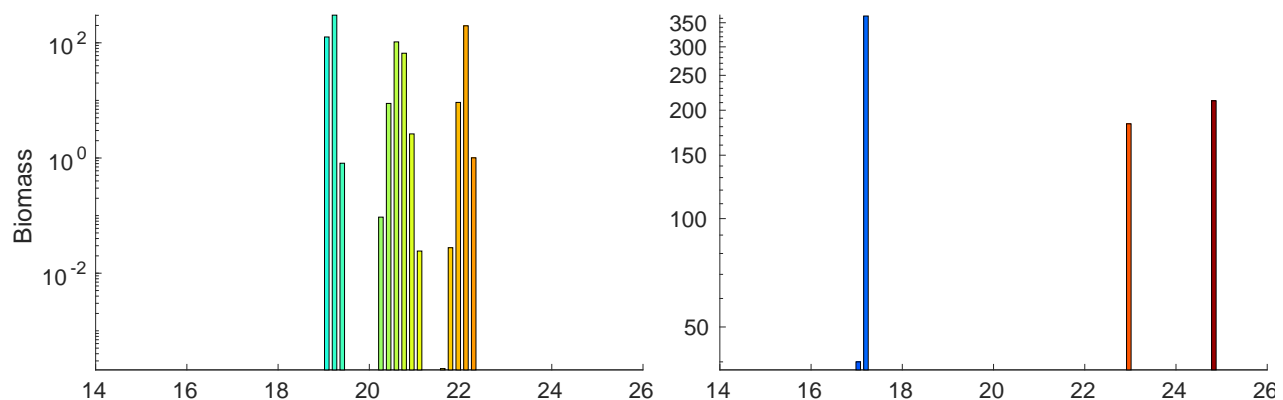


Figure 5: Mean biomasses over the last 200 years of 5000-year simulations as a function of the thermal optimum defining each species, for a white noise (left) or a seasonal signal (right) with storage effect and no stabilizing niche differences. This simulation is the one described in Fig. 1.

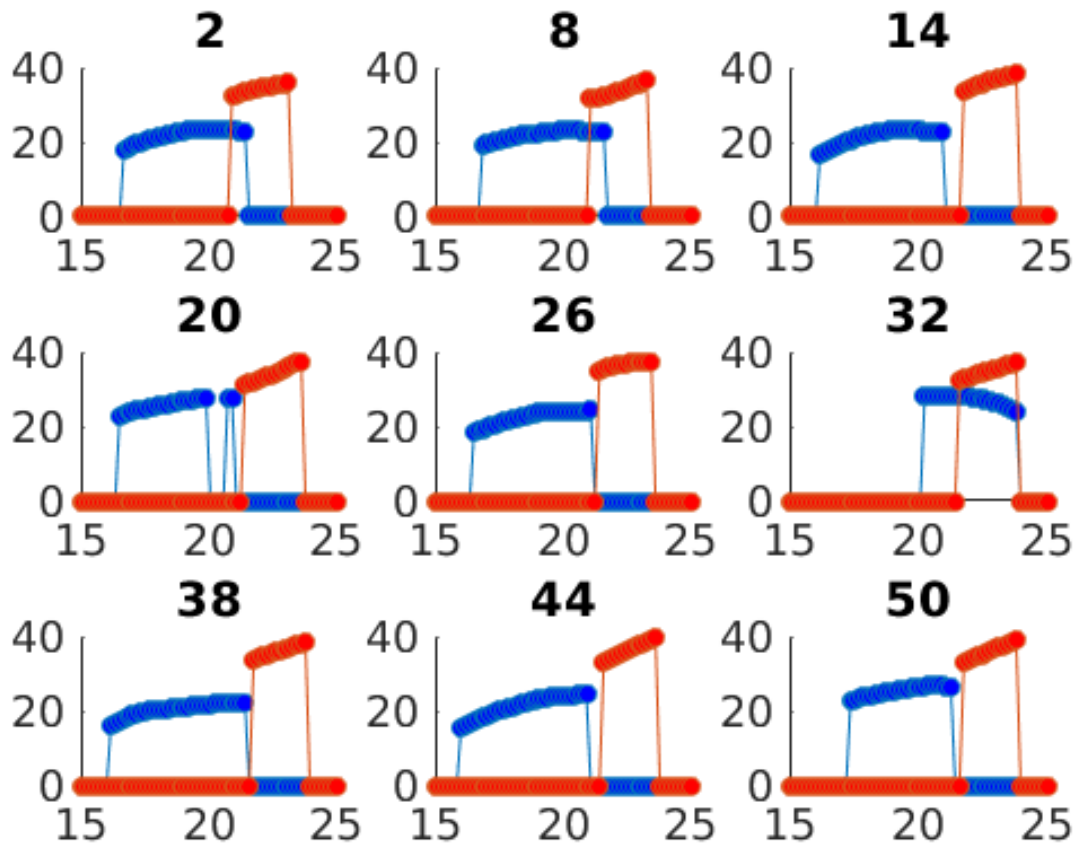


Figure 6: Mean biomass distribution over the last 200 years of 9 representative simulations, as a function of thermal optima, without storage effect with stabilizing niche differences, in which temperature is either a seasonal signal (red) or a white noise (blue). The distribution induced by a white noise overlaps the one obtained with a seasonal signal in only 2 simulations out of 50.

NOTE: figures below are here for discussion between us. I am not sure we should keep them in the paper. I think this illustrates an issue (?) in the model: when I removed the storage effect, I must have changed the total carrying capacity of the environment. Should we correct it? **Note from Fred: there is clear underyielding which can be confirmed by field data (Schmidtke et al, 2010)**

I also computed the evenness, not as an explanation but as a further exploration of the community.

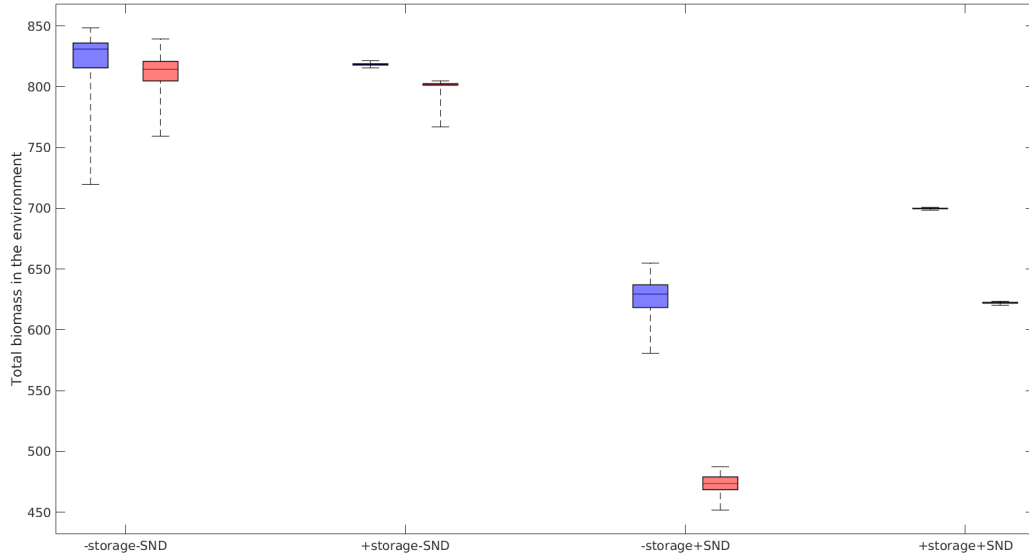


Figure 7: Sum of the average biomasses of all species for the last 200 years of a 5000-year simulation, initialized with 60 species with total initial biomass  $10^3$ , with a white noise forcing signal (blue) or a noisy seasonal signal (red). For each model type (with and without storage effect, + / - storage, respectively; with and without Stabilizing Niche Differences, + / - SND, respectively), 100 simulations were launched.

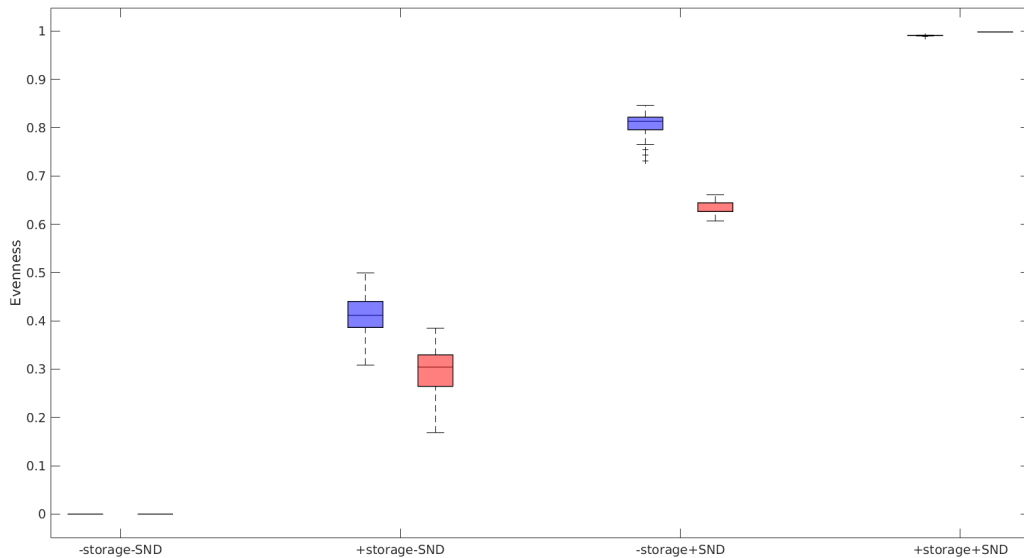


Figure 8: Normalized species evenness of the community, initialized with 60 species with total initial biomass  $10^3$ , with a white noise forcing signal (blue) or a noisy seasonal signal (red). For each model type (with and without storage effect, + / - storage, respectively; with and without Stabilizing Niche Differences, + / - SND, respectively), 100 simulations were launched.

White noise	Storage effect	No storage effect	Season+White noise	Storage ef
Stabilizing niche differences	60	28 [20-32]	Stabilizing niche differences	60
No stabilizing niche differences	15 [8-20]	1	No stabilizing niche differences	4 [2-6]

Table 3: Table corresponding to Fig. 2. Which one to choose?