

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

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## 1 Introduction

There has been a rich debate in theoretical ecology on how to reconcile niche and neutral perspectives (Scheffer and van Nes, 2006; Barabás et al, 2013; Vergnon et al, 2013) [we can add or replace this by refs Dom Gravel and others here]. For instance, Scheffer and van Nes (2006) suggested that niche and neutrality can occur at the same time, with clumps of similar species on a trait axis. Coexistence between clumps is provided by classical stabilizing niche differences, while within-clump coexistence occur through neutral processes. Although eventually, in absence of immigration, clumps do thin out, transient coexistence can last for extended periods of time. However, the findings of Scheffer and van Nes (2006) have been disputed due to hidden niches in the original model (Barabás et al, 2013), that occur because of stronger intraspecific competition (as in the classical Lotka-Volterra model, (Barabás et al, 2016)). Since then, several studies have looked for this clumpy coexistence in theoretical models using other frameworks, most notably incorporating temporal variation (Scranton and Vasseur, 2016;

20 Sakavara et al, 2018). In these models, equal competitive strengths are combined with other mechanisms  
21 like the storage effect that increase the possibility of coexistence (see also Barabás et al, 2012).

22 Here, we build on the work of Scranton and Vasseur (2016) to investigate the possibility of coexis-  
23 tence through fluctuating environments (the so-called storage effect or temporal niche partitioning, that  
24 seem equivalent for forced Lotka-Volterra models, (Barabás et al, 2012; Scranton and Vasseur, 2016).  
25 Our enthusiasm for the model stems from phytoplankton communities, a key inspiration for the thermal  
26 preferences curves in Scranton and Vasseur (2016) . Despite some interesting results, one key limitation  
27 of Scranton and Vasseur (2016)’s model from the perspective of plankton ecology seemed to be the as-  
28 sumption of a randomly fluctuating thermal environment. Temperature usually fluctuates seasonally, and  
29 random temporal variation only add noise to a largely deterministic trend . Our present work can therefore  
30 be seen as an attempt to blend Scranton and Vasseur (2016) with the periodic environments of Barabás  
31 et al (2012) into a mixture of stochastic and deterministic environmental forces affecting Lotka-Volterra  
32 community dynamics.

33 Because many phytoplankton species or genera respond in similar ways to temperature despite having  
34 different optimas, we hypothesized that a large seasonal variation might not necessarily affect coexistence  
35 in a positive way. In fact, an increased synchrony could theoretical decrease the temporal partitioning  
36 between the species. How seasonality affects coexistence (as opposed to a purely randomly fluctuating  
37 environment) is therefore a key feature of this paper. In particular, we contrast cases where the storage  
38 effect is present vs. absent, which elegantly maps to two different versions of the forced Lotka-Volterra  
39 model (see Methods).

40 Moreover, we realized while running Scranton and Vasseur (2016)’s model that the overall diversity  
41 obtained after 5000 years was relatively low compared to what we usually observe in phytoplankton com-  
42 munities. In an empirical study combining phytoplankton community-level time series and multivariate  
43 autoregressive models (REF), we found that despite a large influence of the environment (including tem-  
44 perature, irradiance, and other factors), intraspecific (or intragenus) competition was rather large and  
45 most likely the main reason for coexistence; in other words, stabilizing niche differences had a large  
46 role to play in maintaining species diversity in coastal phytoplankton (REF). Here, we therefore try to  
47 establish what are the relative contributions of the storage effect vs intraspecific density-dependence to

48 coexistence in a phytoplankton-like theoretical community model.

49 This multifaceted objectives led us to cross different combinations of seasonality in the forcing signal,  
 50 presence of the storage effect or not, and intra- vs interspecific competition, in order to disentangle the  
 51 contributions of all these factors to biodiversity maintenance.

## 52 **2 Methods**

### 53 *Description*

54 The model described in Scranton and Vasseur (2016) is based on a variant of the Lotka-Volterra com-  
 55 petition model. Fluctuations in the environment are introduced in the model by temperature-dependant  
 56 growth rates (see eq. 1-2, all coefficients are defined in Tab. 1).

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

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

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

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

57 The coefficient values (Tab. 1) characterize a phytoplankton community. The niche of each species is  
 58 defined by its thermal optimum  $\tau_i^{opt}$ . Thermal performance curves defined in eq. 3 are parameterized so  
 59 that all species share the same niche area (eq. 4), which sets a trade-off between maximum growth rates  
 60 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	$\frac{\text{kg}}{\text{kg}^*\text{year}}$
$\alpha_{ij}$	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 to seasonal signal	$[0, \sqrt{(2)}]$
$\rho$	Ratio of intra-to-intergroup competition strengths	(1;10)

Scranton and Vasseur (2016) described temperature as a white noise (eq. 5).

$$\tau_t \sim N(\mu_\tau, \sigma_\tau) \quad (5)$$

Under most latitudes, however, temperature is a seasonal signal, which can affect the dynamics of the community considered (Vesipa and Ridolfi, 2017). We kept the mean and standard deviation of the signal but included a lower-frequency component (eq.6). The ratio of low-to-high frequency depends on the variable  $\theta$ , enabling us to keep the same energy content in the forcing signal.

$$\tau(t) = \mu_\tau + \theta \sigma_\tau \sin\left(\frac{2\pi t}{365}\right) + \varepsilon_t, \text{ where } \varepsilon_t \sim \mathcal{N}(0, \sigma_\tau \sqrt{1 - \frac{\theta^2}{2}}) \quad (6)$$

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

The formulation of Lotka-Volterra according to Scranton and Vasseur (2016) implies a storage effect,

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

$$\frac{dN_i}{dt} = N_i \left( r_i(\tau) - \sum_{j=1}^S \bar{r}_i \alpha_{ij} N_j \right) - mN_i \quad (7)$$

In eq. 7, competition strengths depend on the species considered, but not on the environmental conditions which affect 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. 8

$$\alpha_{ij} = \alpha (1 + (\rho - 1) \delta_{ij}) \quad (8)$$

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 2 types of environmental forcings (white noise,  $\theta = 0$ , and seasonal,  $\theta = 1.3$ ), we therefore compare the results for 4 formulations of the model: with and without an explicit storage effect (eq. 1 and eq. 7, respectively) ; with and without stabilizing niche differences ( $\rho = 10$  or  $\rho = 1$ , respectively).

## Set-up

We focused on the dynamics of a community initialized with 60 species with thermal optima uniformly spaced along the interval [15°C, 25°C]. All species started with the same initial density ( $\frac{1}{\alpha S}$ ). 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. This framework corresponds to the first experiment, so called 'Species sorting', in Scranton and Vasseur (2016). For each combination of the parameters of the model (type of environmental signal, storage effect and stabilizing niche differences), we ran 50<sup>1</sup> simulations.

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<sup>1</sup>Running 100 right now

90 All simulations were ran with Matlab's ode45 algorithm, an explicit Runge-Kutta (4,5) algorithm  
91 with an absolute error tolerance of  $10^{-8}$ .

## 92 **3 Results**

93 Typical dynamics of the community following Eq. 1 (the model of Scranton and Vasseur, 2016), with  
94 both the environmental signals described in Eq. 5 (original choice of Scranton and Vasseur, 2016) and  
95 6 (our variant), are shown in Fig. 1. Forcing by a seasonal signal produces the strongly seasonally  
96 structured dynamics that are typical of phytoplankton. Even though only 5 species can be seen in Fig.  
97 1c), there were 14 species still present at the end of the simulation forced by a white noise, with large  
98 disparities in the range of variation of their biomasses. A third of the species kept a biomass above 10  
99 kg/area while 6 out of the 14 remained below the unit. All species in the white noise simulations were  
100 clustered along a 3.2°C-range of thermal optima. No obvious temporal patterns (e.g., cycles) could be  
101 seen in On the other hand, seasonal cycles were clear in the seasonally-forced case of Fig. 1 d). Only 4  
102 species coexisted at the end of the simulation with seasonal forcing, gathered in two groups with large  
103 thermal optimum differences (5.7°C between the maximum thermal optimum of the first group and the  
104 minimum thermal optimum of the second group). When temperatures are high, species with a higher  
105 thermal optima reached maximum biomass, then left room for the growth of lower-temperature tolerant  
106 species.

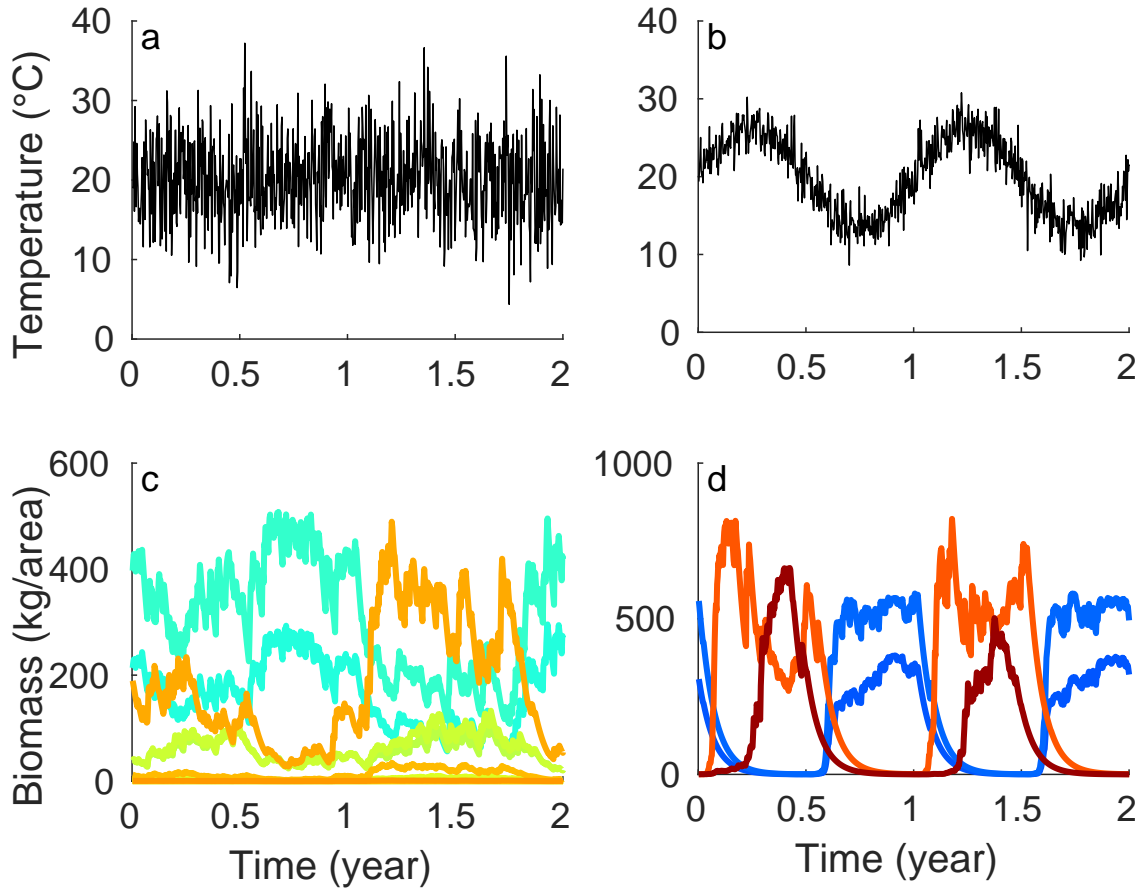


Figure 1: Times series of temperature (top) and extant species (bottom) for the 2 last years of a 5000 year simulation, with storage effect and no stabilizing niche differences. The forcing temperature is either a white noise (left) or a noisy seasonal signal (right). Line colors of species biomasses 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).

107 The decrease in persistence due to seasonality observed in Fig. 1 was confirmed in all our simulations  
 108 (Fig. 2). In cases where richness at the end of the simulation varied (namely, with storage effect but with-  
 109 out stabilizing niche differences, or without storage but with stabilizing niche differences), seasonality  
 110 reduced the number of extant species to, in average, 29% and 49% of its original value, respectively (Fig.  
 111 2). A seasonal signal therefore led to a smaller persistence range.

112 Both the stabilizing niche differences and the storage effect have a marked effect on increasing per-  
 113 sistence. Without any of these coexistence mechanisms, only one species persisted at the end of the  
 114 simulation. When only the storage effect was present, the number of extant species varied between 11  
 115 and 20 with a white noise, or 2 and 6 with a seasonal signal. On the other hand, when only stabilizing

116 niche differences were present, the number of extant species nearly doubled, varying between 20 and 32,  
 117 or 12 and 14, with a white noise or a seasonal signal respectively. Remarkably, when the storage effect  
 118 and stabilizing niche differences (SNDs) both affected the community dynamics, all species persisted in  
 119 the community, while neither the storage nor SNDs were able in isolation to produce that result, for both  
 120 white noise and seasonal forcing.

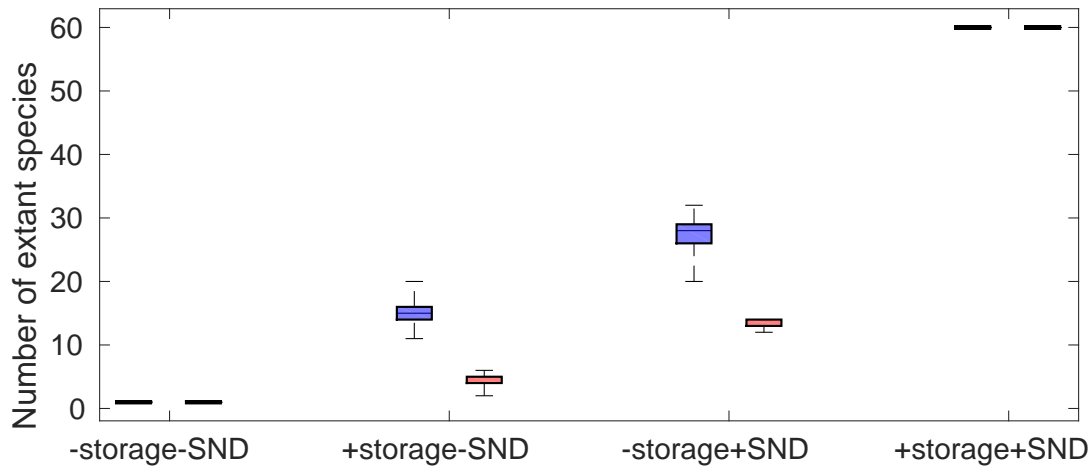


Figure 2: Number of species still present at the end of 5000-year simulations, initialized with 60 species, with a white noise forcing signal (blue) or a noisy seasonal signal (red). For each model type (with and without Storage Effect, + / - storage, respectively; with and without Stabilizing Niche Differences, + / - SND, respectively), 50 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).

121 When the richness of the community was stable (either 1 or 60 species at the end of the simulation,  
 122 Fig. 3), there were still large differences in the structure of the community due to both stochasticity and  
 123 the type of forcing (Fig. 3). Without storage effect and SNDs, a white noise forcing favoured species  
 124 whose thermal optima lied between 17.4°C and 24.3°C, with 66% of the simulations ending with a  
 125 species with a thermal optima between 19.1°C and 21.1°C and reaching a maximum average biomass in  
 126 this range (Fig. 3 a). This distribution can be related a selection for the highest the long-term growth  
 127 rates, averaged over time (see normalized growth rates in Fig. 4). On the contrary, seasonality tended  
 128 to favour species with larger maximum growth rates, with thermal optima above 22°C, their frequency  
 129 of persistence and mean biomass increasing with the thermal optimum (Fig. 3). 46% of the simulations  
 130 therefore ended with the species having the highest temperature optimum, 25°C.



131 When both coexistence mechanisms were present, the 60 initial species coexisted with small varia-  
 132 tions in biomasses over the 50 simulations (mean CV=0.01 across simulations with either a white noise or  
 133 a seasonal forcing signal, Fig. 3b and d). The forcing signal modified only the distribution of biomasses.  
 134 With a white noise, the distribution was unimodal with a maximum biomass reached for the best long-  
 135 term average growth rate (corresponding to a thermal optimum of 22.4°C). On the contrary, a seasonal  
 136 signal led to a bi-modal distribution (centered on 17.4°C and 24.4°C) with higher biomasses for higher  
 137 thermal optima Fig. 3 d. The minimum biomass was reached for a thermal optimum of 22.4°C, corre-  
 138 sponding to the maximum biomass in the white noise case, thus there are quite broad changes in com-  
 139 munity composition even though the richness is equal for the two forcing signals. The two modes in the  
 140 seasonal biomass distribution correspond to the two modes in the seasonal signal.

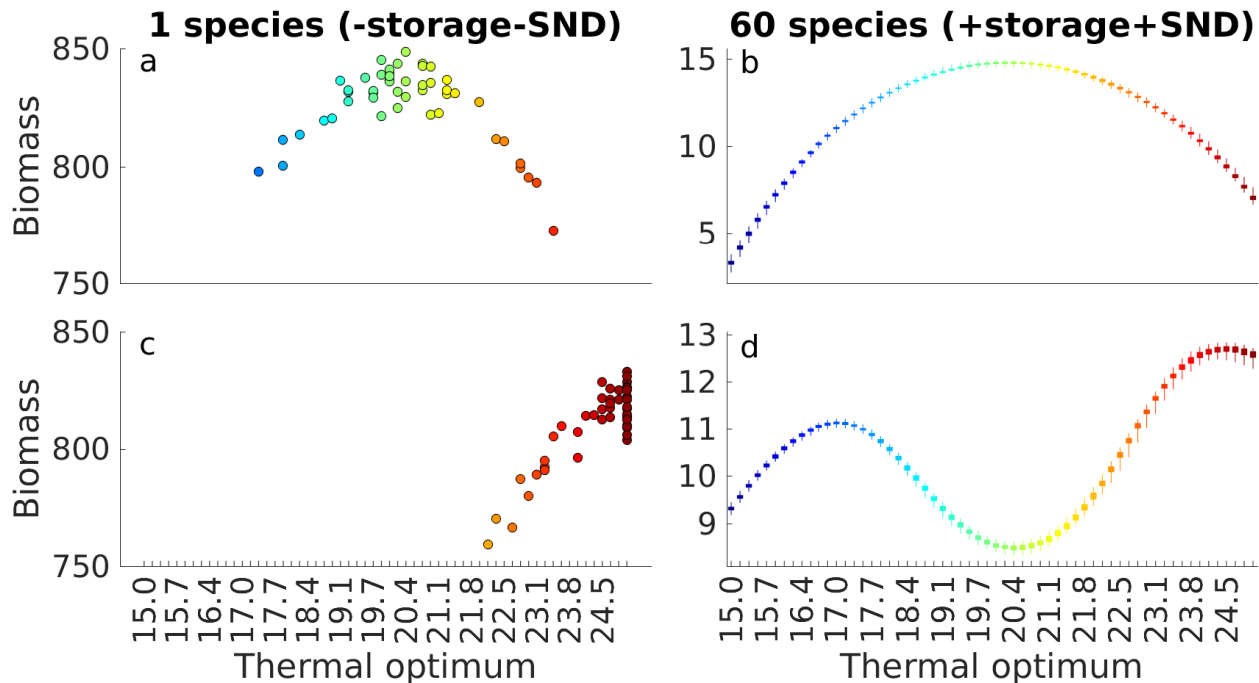


Figure 3: Mean biomass distribution over the last 200 years of 50 simulations, as a function of thermal optima, for the two stable-composition cases: without storage effect nor stabilizing niche differences (left, only one species is extant at the end of simulation, its mean value is represented by a 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.

141 In cases where the richness of the community varied, distributions of extant species were similar for

142 the two types of forcings but differed according to the type of coexistence mechanism taken into account  
143 (Fig. 4).

144 The storage effect led to a multi-modal biomass distribution with respect to thermal optima. We  
145 always observed 3 modes with a white noise and 3 modes in 94% of the seasonal simulations, Fig. 4a.  
146 With a white noise, extant species always had a thermal optimum between 18.8°C and 22.2°C whereas  
147 clumps tended to be further apart in the seasonal case, covering a total range of 8°C, with species grouping  
148 in the higher part of the thermal range, above 22°C.

149 On the other hand, stabilizing niche differences led to a quasi-uniform biomass distribution (Fig. 4  
150 b). Species subjected to a white noise stayed in the lower range of temperatures (96% of the simulations,  
151 the highest thermal optimum was 22.8°C) whereas species subjected to a seasonal signal were observed  
152 temperatures above 20.5°C.

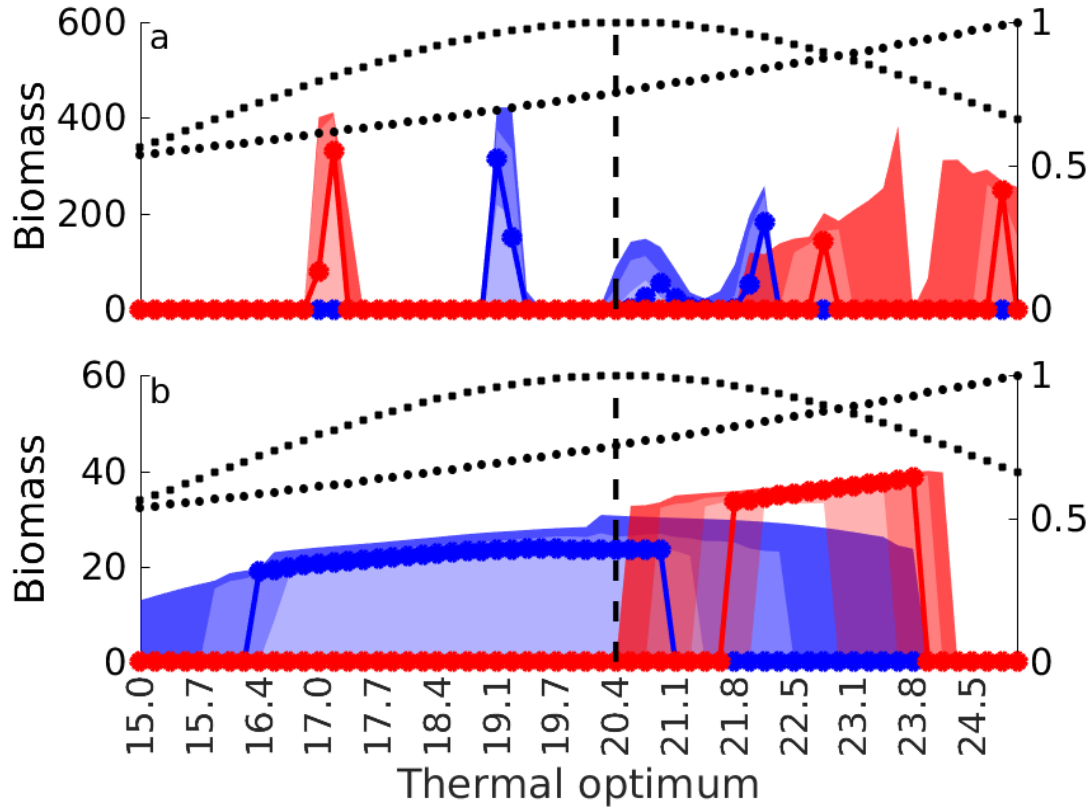


Figure 4: Mean biomass distribution over the last 200 years of 50 simulations, as a function of thermal optima, with storage effect and no stabilizing niche differences (top) and without storage effect, with stabilizing niche differences (bottom). The forcing signal is either a white noise (blue) or 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 dotted line) and maximum growth rates are shown as squares and circles, respectively, and indexed on the left y-axis.

## 4 Discussion

[F: I left Coralie's remarks that I hadn't tackled below, so we don't lose them, but I tried to quickstart the discussion!]

We have simulated competitive Lotka-Volterra dynamics forced by an external signal (temperature) under a range of scenarios allowing more or less coexistence. Two coexistence mechanisms, the storage effect and stabilizing niches differences, could be 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 seasonal signal, with equal temporal variance. Our investigation therefore built on the model of Scran-

ton and Vasseur (2016), which included white noise forcing and a storage effect, but also considered more diverse ecological scenarios. This was motivated by our desire to include two observed features of phytoplankton dynamics: seasonal cycles (REF) and stabilizing niche differences (Barraquand et al, 2017).

We have found that first, forced Lotka-Volterra dynamics cannot sustain any diversity unless the structure is geared to include a storage effect. Although this has already been stated by other authors (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. A nice point made by Scranton and Vasseur (2016) was that a built-in storage effect in the forced Lotka-Volterra dynamics could lead to some degree of coexistence. Our investigation confirms this to be true for the white noise scenario considered by Scranton and Vasseur (2016), but an arguably more realistic seasonal forcing by temperature (in the case of phytoplankton) will considerably lessen the number of species coexisting after 5000 timesteps from around 15 to 4. Even imagining that groups represented here are genera or classes rather than species, this is a fairly low diversity.

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

However, the seasonal forcing still considerably reduced diversity when SNDs were considered, especially the “neutral” kind, diversity within clumps of similar traits. This occurs because within a season, the signal autocorrelation gives to the best competitor has a longer time to exclude its less adapted heterospecifics, while white noise also contains very low forcing signal frequencies that forbid such competitive exclusion. In this situation, even though a species has the best long-term averaged growth rate, it can disappear as a result of a strong competition from both low- and high-temperature tolerant species, with and without storage effect. Our results are therefore at odds with recent proposals that seasonal forcing would help maintain diversity (Sakavara et al, 2018), at least not when seasonal forcing is compared to other forcing signals.

190 In our previous empirical study of coastal phytoplankton dynamics (Barraquand et al, 2017), we  
191 have not found any storage effect (which certainly does not mean that it could not be observed in other  
192 plankton-like systems). Given the results presented here, we are skeptical that temporal niche partitioning  
193 through the storage effect could, on its own, help explaining the phytoplankton diversity, especially given  
194 that stabilizing niche differences seem fairly strong when estimated from phytoplankton time series.  
195 However, our results suggest that in phytoplankton-like seasonal environments, even though empirically-  
196 based stabilizing niche differences produce more diversity than the storage effect, the combination storage  
197 effect + SNDs is non-additive: the cases where both SNDs and the storage effect were present showed more  
198 diversity than generated by any mechanism on its own.

199 This suggests the very exciting possibility that coexistence mechanisms might combine superaddi-  
200 tively in general, thus helping us to better understand the astounding diversity of primary producers. The  
201 same logic could, in principle, be extended to mechanisms that we have not considered here (e.g., spatial  
202 structure, specialized natural enemies, that could be as important here for plankton as they are for tropical  
203 trees [a few refs on Janzen Connell effects in trees]). Better explaining plant or microbial diversity would  
204 then not be about selecting the best unique mechanism susceptible to explain the observed diversity, but  
205 rather better combining those mechanisms together. This may obviously be an annoyance for those who  
206 like to sharpen Occam's razor, but it clearly holds opportunities for theoreticians wishing to investigate  
207 synergies between coexistence mechanisms.

208

209 **[Other points not tackled so far] :**

- 210 •
- 211 • Storage effect without stabilizing niche differences leads to a stable multimodal abundance distri-  
212 bution. It is unclear whether this regularity is a by-product of limiting similarities for our parameter  
213 values. Conversely, no storage effect with stabilizing niche differences lead to an even distribution  
214 (in line with previous point and may be discussed with the help of Barabás et al (2013)).
- 215 • Seasonality decreases the total number of extant species when compared to white noise. The au-  
216 tocorrelation in the seasonal signal drives species to extinction as similar species compete for a  
217 longer time: temporal niche partitioning leads to larger differences in clumps. In this situation,

even though a species has the best long-term averaged growth rates, it can disappear as a result of a strong competition from both low- and high-temperature tolerant species, with and without storage effect.

- In the absence of storage effect, seasonality tends to favor maximum growth rates even though it also leads to higher competition whereas white noise tends to favor balanced growth rates and competition.
- [Would it be correct to say that one of the model limitation is that all species are equally affected by the forcing? We could hypothesize (or couldn't we) that some of the rare species might be less affected by the seasonal cycles and more by white noise – or is this completely off? Cf. my comment in the email. That said I think I've seen some papers saying that rare species were *more* strongly self-regulated not less...]

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## A Supplementary Material

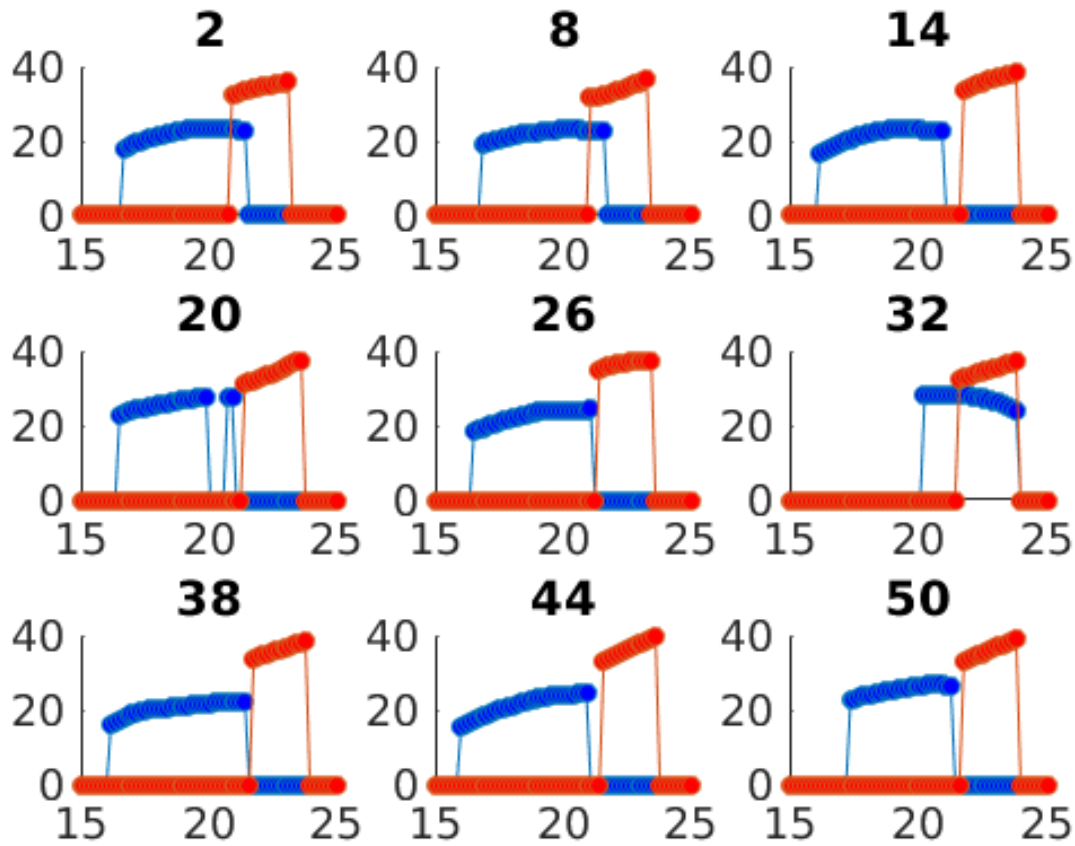


Figure 5: Mean biomass distribution over the last 200 years of 9 representative simulations, as a function of thermal optima, without storage effect with stabilizing niche differences, in which temperature is either a seasonal signal (red) or a white noise (blue). The distribution induced by a white noise overlaps the one obtained with a seasonal signal in only 2 simulations out of 50.

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 [11-20]	1	No stabilizing niche differences	4 [2-6]

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