

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

Coralie Picoche¹, Alix Sauve¹, Frédéric Barraquand^{1,2}

May 12, 2018

¹Integrative and Theoretical Ecology Chair, Labex COTE, University of Bordeaux, ²Institute of Mathematics of Bordeaux, CNRS

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 (Scheffer and van Nes, 2006; Barabás et al, 2013; Vergnon et al, 2013) [we can add or replace this by refs Dom Gravel and Mutshinda+O’Hara here]. 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. But as it has been pointed out repeatedly (REFs Gravel and co.), niche and neutral processes are not mutually exclusive.

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 promote coexistence of multiple clumps through stronger net intraspecific competition (Chesson 2000), while within-clump coexistence occurs through neutral processes (Hubbell 2000, a new ref), 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. 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 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, and since then, several studies have searched for this ‘clumpy coexistence’ in

49 theoretical models,, most notably incorporating temporal variation (Scranton and Vasseur, 2016; Sakavara
50 et al, 2018). In these temporal-variation models, equal competitive strengths are combined with other
51 mechanisms like the storage effect that increase the possibility of coexistence (see also Barabás et al,
52 2012).

53 Here, we build on the work of Scranton and Vasseur (2016) to investigate the possibility of coexis-
54 tence through fluctuating environments (the so-called storage effect or temporal niche partitioning, that
55 are equivalent concepts for forced Lotka-Volterra models Barabás et al, 2012; Scranton and Vasseur,
56 2016). Our enthusiasm for the Scranton and Vasseur (2016) model stems from our interest in phyto-
57 plankton communities, that were the key inspiration for the thermal preferences curves in Scranton and
58 Vasseur (2016). Despite some interesting results, one key limitation of Scranton and Vasseur (2016)’s
59 model from the perspective of plankton ecology seemed to be the assumption of a randomly fluctuating
60 thermal environment. Temperature usually fluctuates seasonally, and random temporal variation only
61 add noise to a largely deterministic trend . Our present work can therefore be seen as an attempt to blend
62 Scranton and Vasseur (2016) with the periodic environments of Barabás et al (2012) into a mixture of
63 stochastic and deterministic environmental forces affecting Lotka-Volterra community dynamics.

64 Because many phytoplankton species or genera respond in similar ways to temperature despite having
65 different optimas [Insert REF here], we hypothesized that a large seasonal variation might not necessarily
66 foster species coexistence. In fact, an increased synchrony of species abundances should theoretically de-
67 crease their temporal partitioning. How seasonality affects coexistence (as opposed to a purely randomly
68 fluctuating environment) is therefore a key feature of this paper. In particular, we contrast cases where
69 the storage effect is present vs. absent, which elegantly maps to two different versions of the forced
70 Lotka-Volterra model (see Methods).

71 Moreover, we realized while running Scranton and Vasseur (2016)’s model that the overall diversity
72 obtained after 5000 years was relatively low compared to what we usually observe in phytoplankton com-
73 munities. In an empirical study combining phytoplankton community-level time series and multivariate
74 autoregressive models (REF), we found that despite a large influence of the environment (including tem-
75 perature, irradiance, and other factors), intraspecific (or intragenus) competition was rather large and
76 most likely the key driver of species coexistence. In other words, stabilizing niche differences had a large

77 role to play in maintaining species diversity in coastal phytoplankton (REF). Here, we therefore try to
 78 establish what are the relative contributions of the storage effect vs intraspecific density-dependence to
 79 coexistence in a phytoplankton-like theoretical community model.

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

83 2 Methods

84 *Models description*

85 The model described in Scranton and Vasseur (2016) is based on a variant of the Lotka-Volterra com-
 86 petition model. Fluctuations in the environment are introduced in the model by temperature-dependant
 87 growth rates (see eq. 1-2, all coefficients are defined in Tab. 1) so that species growth rates write:

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

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

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

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

88 Model parameters are detailed in Table 1, and we set their values to match the features of phytoplank-
 89 ton communities. The niche of each species is defined by its thermal optimum τ_i^{opt} . Thermal performance
 90 curves defined in eq. 3 are parameterized so that all species share the same niche area (eq. 4), which sets
 91 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)
τ	Temperature	K
$r_i(\tau)$	Growth rate of species i as a function of temperature	$\frac{\text{kg}}{\text{kg}^*\text{year}}$
α_{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	$15 \frac{\text{kg}}{\text{kg}^*\text{year}}$
τ_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	
μ_τ	Mean temperature	293 K
σ_τ	Standard deviation for temperature	5 K
τ_{\min}	Minimum thermal optimum	288K
τ_{\max}	Maximum thermal optimum	298 K
A	Niche breadth	$10^{3.1} \frac{\text{kg}}{\text{kg}^*\text{year}}$
τ_i^{opt}	Thermal optimum for growth of the i th species	K
θ	Scaling between white noise to seasonal signal	$[0, \sqrt{(2)}]$
ρ	Ratio of intra-to-intergroup competition strengths	(1;10)

Scranton and Vasseur (2016) described temperature as a white noise, i.e. independent and identically distributed Gaussian random variates (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 θ , 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 θ , $\sqrt{2}$, 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).

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.

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

104 In eq. 7, competition strengths remain unaffected by the environmental conditions, in contrast to
 105 growth rates.

106 Stabilizing niche differences are ensured by the addition of the coefficient ρ , which is the ratio of
 107 intra-to-intergroup competition strength. We can therefore re-write the interaction coefficients α_{ij} in eq.

108 8

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

109 where δ_{ij} is the Kronecker symbol, equal to 1 if $i = j$ and to 0 otherwise. The value of the parameter
 110 $\rho = 10$ was chosen from analyses of phytoplanktonic data (Barraquand et al, 2017).

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

115 Set-up

116 We repeat the 'Species sorting' experiment of Scranton and Vasseur (2016) so as to investigate on how
 117 synthetic phytoplankton communities structure under the various scenarios we described above. We
 118 focused on the dynamics of a community initialized with 60 species with thermal optima uniformly
 119 spaced along the interval [15°C, 25°C]. All species started with the same initial density ($\frac{1}{\alpha S}$). Each
 120 simulation was run for 5000 years in 1-day intervals. When the density of a species dropped below 10^{-6} ,
 121 it was considered extinct. For each combination of the parameters of the model (type of environmental

122 signal, storage effect and stabilizing niche differences), we ran 100 simulations.

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

125 **3 Results**

126 Typical dynamics of the community following Eq. 1 (the model of Scranton and Vasseur, 2016), with both
127 the environmental signals described in Eq. 5 (original choice of Scranton and Vasseur, 2016) and 6 (our
128 variant), are shown in Fig. 1. Forcing by a sinusoidal signal produces the strongly seasonally structured
129 dynamics that are typical of phytoplankton. Even though only 5 species can be seen in Fig. 1c), there
130 were 14 species still present at the end of the simulation forced by a white noise, with large disparities
131 in the range of variation of their biomasses. A third of the species kept a biomass above 10 kg/area
132 while 6 out of the 14 remained below the unit. All species in the white noise simulations were clustered
133 along a 3.2°C-range of thermal optima. No obvious temporal patterns (e.g., cycles) could be seen in the
134 communities forced by white noise. On the other hand, seasonal cycles were clear in the seasonally-
135 forced case of Fig. 1 d). Only 4 species coexisted at the end of the simulation with seasonal forcing,
136 gathered in two groups with large thermal optimum differences (5.7°C between the maximum thermal
137 optimum of the first group and the minimum thermal optimum of the second group). When temperatures
138 are high, the group with a higher thermal optima reach maximum biomass, then as temperature decreases
139 through the season, they leave room for the growth of the low-temperature group.

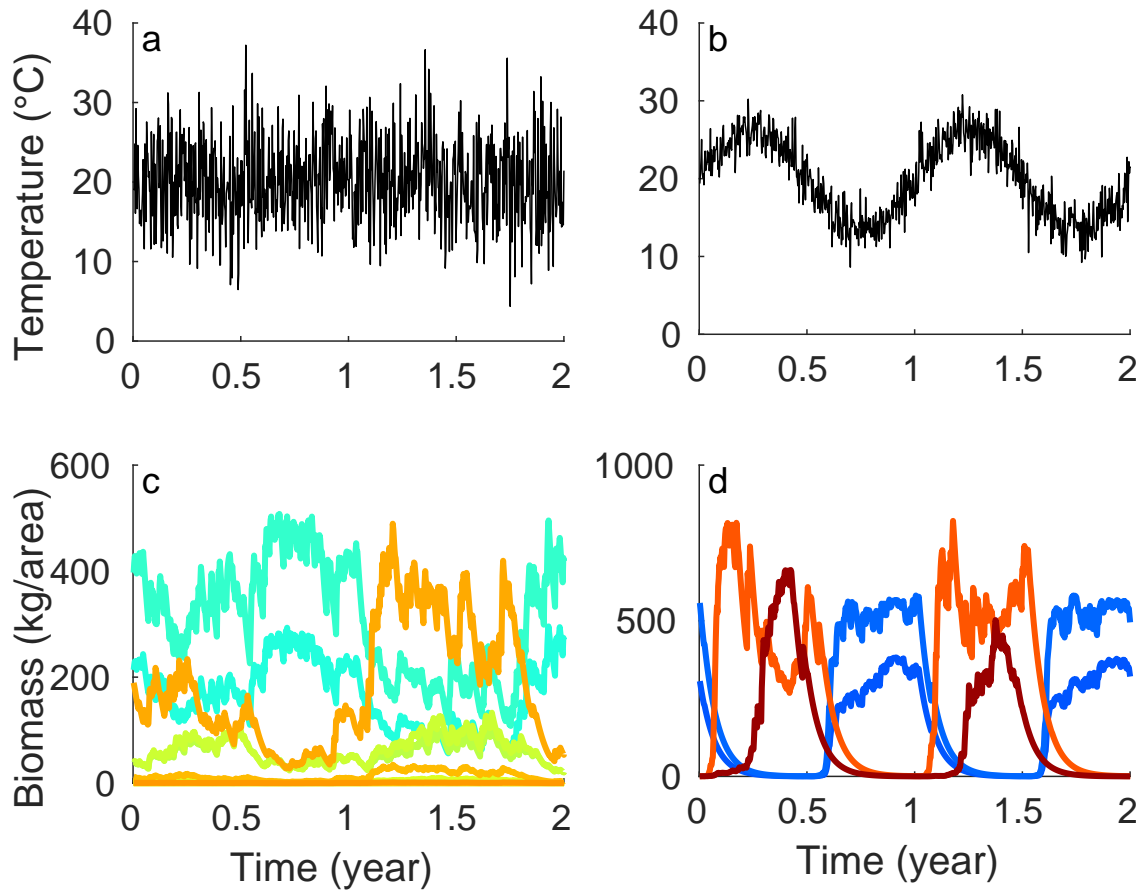


Figure 1: Times series of temperature (top) and extant species (bottom) for the 2 last years of a 5000 year simulation, with storage effect and no stabilizing niche differences. The forcing temperature is either a white noise (left) or a noisy seasonal signal (right). Line colors of species biomasses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

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

147 Both the stabilizing niche differences and the storage effect have a marked effect on increasing per-
 148 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.

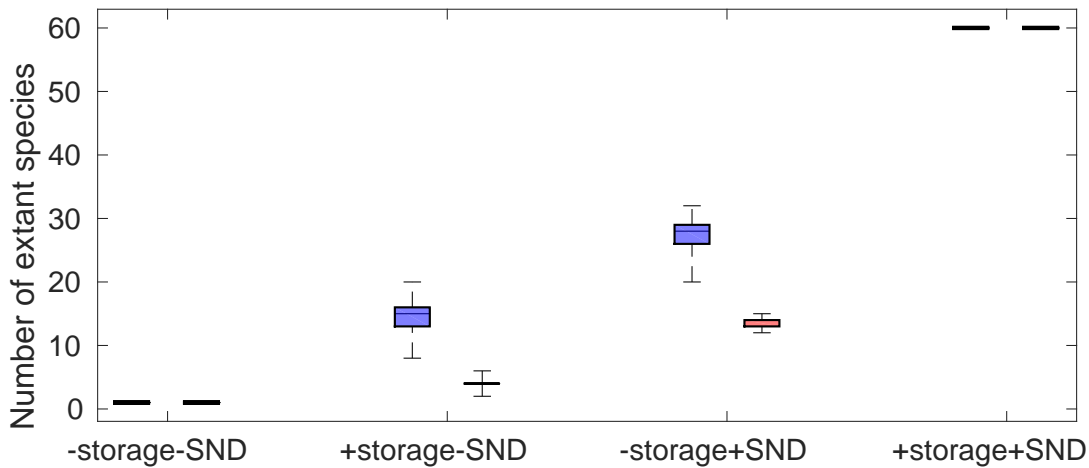


Figure 2: Number of species still present at the end of 5000-year simulations, initialized with 60 species, with a white noise forcing signal (blue) or a noisy seasonal signal (red). For each model type (with and without storage effect, + / - storage, respectively; with and without Stabilizing Niche 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 66% of the simulations ending with a species with a thermal optima between 19.1°C and 21.1°C 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 larger maximum growth rates, with thermal optima above 22°C, their frequency of persistence and mean

164 biomass increasing with the thermal optimum (Fig. 3). 46% of the simulations therefore ended with the
 165 species having the highest temperature optimum, 25°C.

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

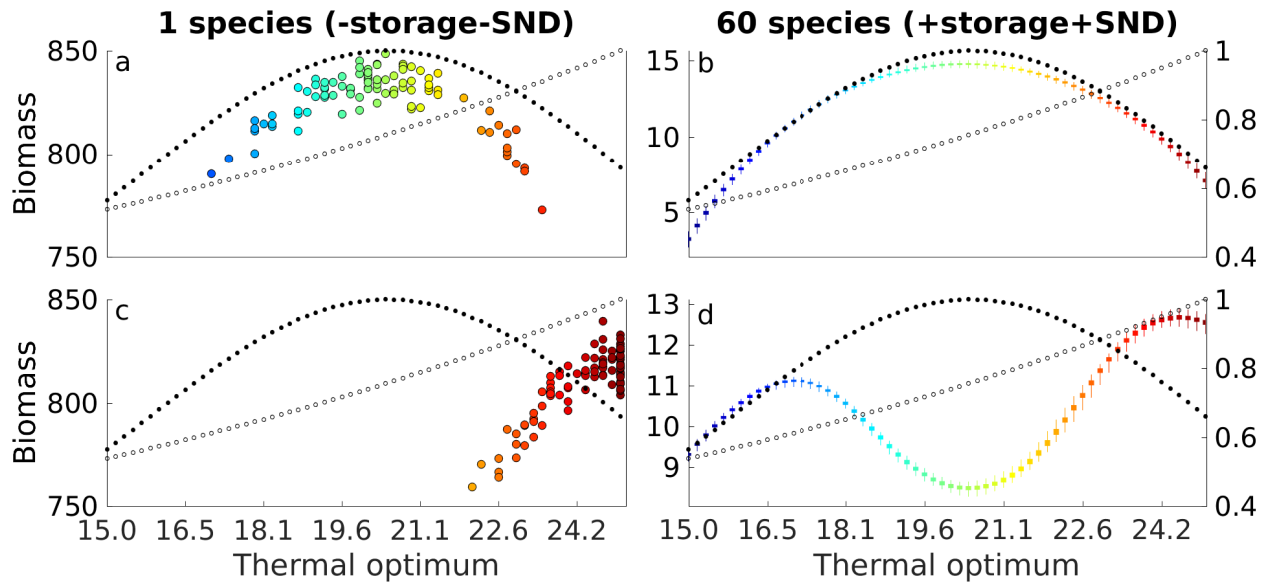


Figure 3: Mean biomass distribution over the last 200 years of 100 simulations, as a function of thermal optima, for the two stable-composition cases: without storage effect nor stabilizing niche differences (left, only one species is extant at the end of simulation, its mean value is represented by 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 index on the right axis [CP: Not sure about showing GR on this figure, though].

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

180 The storage effect led to a multi-modal biomass distribution with respect to thermal optima. We
181 always observed 3 modes with a white noise and 3 modes in 94% of the seasonal simulations, Fig.
182 4a. With a white noise, extant species are grouped in rather similar clumps regarding species thermal
183 optimum (between 18.8°C and 22.2°C whereas clumps tended to be further apart in the seasonal case,
184 covering a total range of 8°C, with species grouping in the higher part of the thermal range, above 22°C.

185 On the other hand, stabilizing niche differences led to a quasi-uniform biomass distribution (Fig. 4
186 b). Species characterising communities forced by a white noise stayed in the lower range of temperatures
187 (96% of the simulations, the highest thermal optimum was 22.8°C) while they were filtered out in com-
188 munities subjected to a seasonal fluctuations of their environment, for which species with thermal optima
189 above 20.5°C persisted.

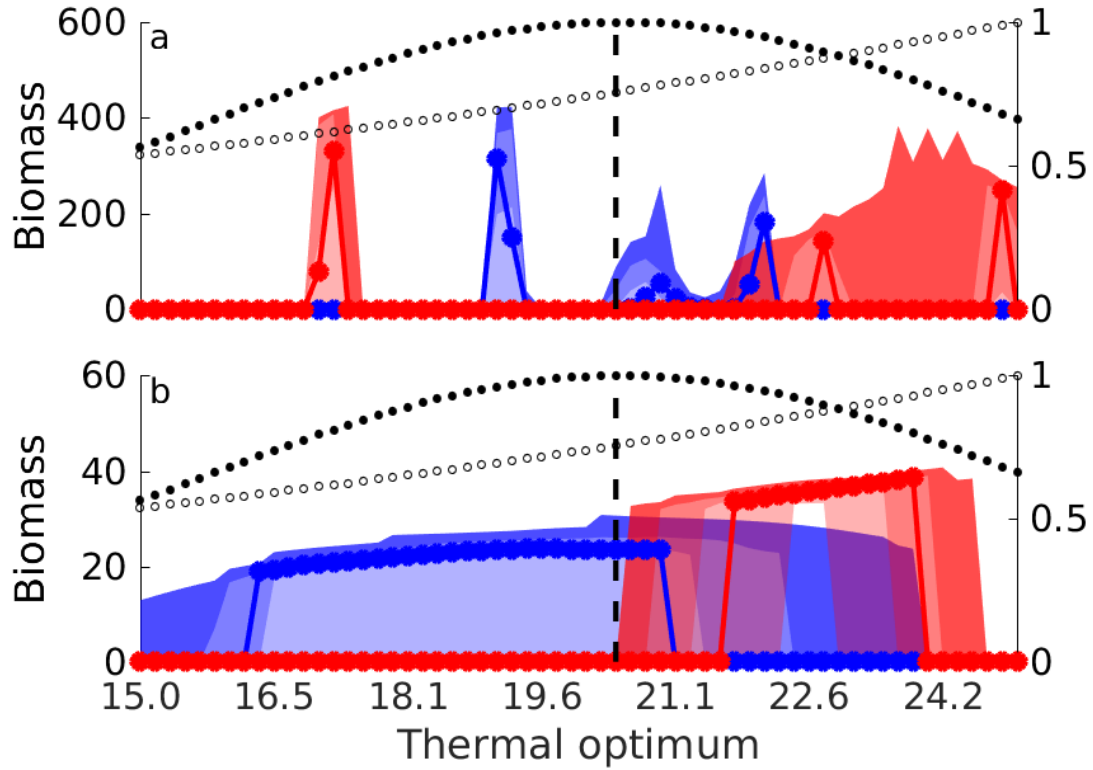


Figure 4: Mean biomass distribution over the last 200 years of 100 simulations, as a function of thermal optima, with storage effect and no stabilizing niche differences (top) and without storage effect, with stabilizing niche differences (bottom). The forcing signal is either a white noise (blue) or 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.

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 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

199 therefore built on the model of Scranton and Vasseur (2016), which included 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 unless the struc-
204 ture is geared to include a storage effect or SNDs. Although this has already been stated by other authors
205 (Barabás et al, 2012; Fox, 2013; Scranton and Vasseur, 2016), this is not always intuitive (Fox, 2013), so
206 we feel compelled to stress it once more: temporal variation in growth rate alone cannot help coexistence
207 within competitive communities. A nice point made by Scranton and Vasseur (2016) was that a built-in
208 storage effect in the forced Lotka-Volterra dynamics could lead to some degree of coexistence. Our in-
209 vestigation reproduced these results, using the white noise forcing considered by Scranton and Vasseur
210 (2016), but an arguably more realistic seasonal forcing by temperature (thinking of phytoplankton) will
211 considerably lessen the number of species coexisting after 5000 timesteps, decreasing from 15 on average
212 to 4 on average. Even imagining that groups represented here are genera or classes rather than species,
213 this is a fairly low diversity for a phytoplankton-like community (REF Reynolds?).

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

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

227 compared to other forcing signals of equal variance.

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

238 This suggests the very exciting idea that multiple coexistence mechanisms might combine superad-
239 ditively, thus helping us to better understand the astounding diversity of primary producers. This logic
240 could, in principle, be extended to mechanisms that we have not considered here (e.g., spatial structure,
241 specialized natural enemies, that could be as important here for plankton as they are for tropical trees
242 [a few refs on Janzen Connell effects in trees]). Better explaining plant or microbial diversity would
243 then not be about selecting the best unique mechanism susceptible to explain the observed diversity, but
244 rather better combining those mechanisms together. This may obviously be an annoyance for those who
245 like to sharpen Occam's razor, but it clearly holds opportunities for theoreticians wishing to investigate
246 synergies between coexistence mechanisms in highly diverse communities.

247

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

- 249 •
- 250 • Storage effect without stabilizing niche differences leads to a stable multimodal abundance distri-
251 bution. It is unclear whether this regularity is a by-product of limiting similarities for our parameter
252 values. Conversely, no storage effect with stabilizing niche differences lead to an even distribution
253 (in line with previous point and may be discussed with the help of Barabás et al (2013)).
- 254 • Seasonality decreases the total number of extant species when compared to white noise. The au-

tocorrelation in the seasonal signal drives species to extinction as similar species compete for a 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...]

References

- Barabás G, Meszéna G, Ostling A (2012) Community robustness and limiting similarity in periodic environments. *Theoretical Ecology* 5(2):265–282, doi:10.1007/s12080-011-0127-z
- Barabás G, D'Andrea R, Rael R, Meszéna G, Ostling A (2013) Emergent neutrality or hidden niches? *Oikos* 122(11):1565–1572, doi:10.1111/j.1600-0706.2013.00298.x
- Barabás G, Michalska-Smith MJ, Allesina S (2016) The Effect of Intra- and Interspecific Competition on Coexistence in Multispecies Communities. *The American Naturalist* pp 000–000, doi:10.1086/686901
- Barraquand F, Picoche C, Maurer D, Carassou L, Auby I (2017) Weak interactions between groups and physical drivers of community dynamics in coastal phytoplankton. *bioRxiv* doi:10.1101/171264
- Ellner SP, Snyder RE, Adler PB (2016) How to quantify the temporal storage effect using simulations instead of math. *Ecology Letters* doi:10.1111/ele.12672

- 279 Fox JW (2013) The intermediate disturbance hypothesis should be abandoned. *Trends in Ecology &*
280 *Evolution* 28(2):86–92, doi:10.1016/j.tree.2012.08.014
- 281 Sakavara A, Tsirtsis G, Roelke DL, Mancy R, Spatharis S (2018) Lumpy species coexistence arises
282 robustly in fluctuating resource environments. *Proceedings of the National Academy of Sciences*
283 115(4):738–743, doi:10.1073/pnas.1705944115
- 284 Scheffer M, van Nes EH (2006) Self-organized similarity, the evolutionary emergence of groups of simi-
285 lar species. *Proceedings of the National Academy of Sciences* 103(16):6230–6235
- 286 Scranton K, Vasseur DA (2016) Coexistence and emergent neutrality generate synchrony among com-
287 petitors in fluctuating environments. *Theoretical Ecology* doi:10.1007/s12080-016-0294-z
- 288 Vergnon R, van Nes EH, Scheffer M (2013) Interpretation and predictions of the Emergent neutrality
289 model: a reply to Barab s et al. *Oikos* 122(11):1573–1575, doi:10.1111/j.1600-0706.2013.00790.x
- 290 Vesipa R, Ridolfi L (2017) Impact of seasonal forcing on reactive ecological systems. *Journal of Theo-*
291 *retical Biology* 419:23–35, doi:10.1016/j.jtbi.2017.01.036
- 292 Winder M, Cloern JE (2010) The annual cycles of phytoplankton biomass. *Philosophical Transactions of*
293 *the Royal Society B: Biological Sciences* 365(1555):3215–3226, doi:10.1098/rstb.2010.0125

A Supplementary Material

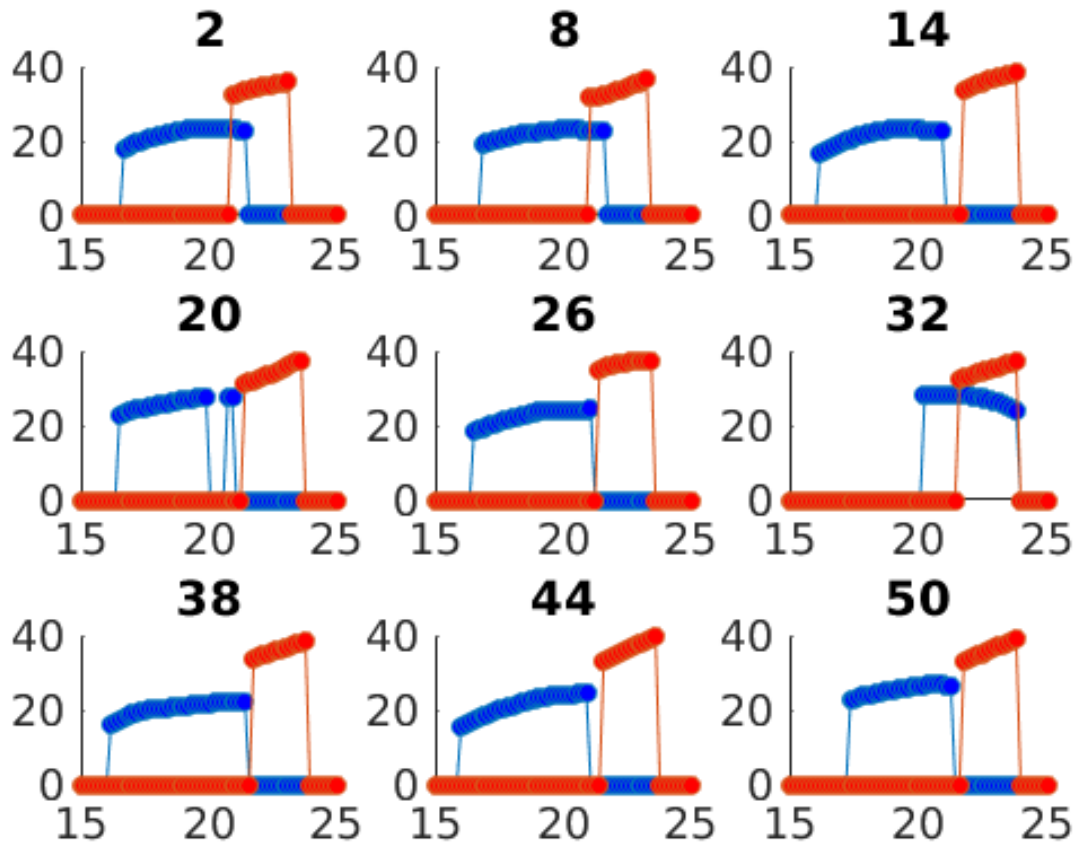


Figure 5: Mean biomass distribution over the last 200 years of 9 representative simulations, as a function of thermal optima, without storage effect with stabilizing niche differences, in which temperature is either a seasonal signal (red) or a white noise (blue). The distribution induced by a white 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 [8-20]	1	No stabilizing niche differences	4 [2-6]

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