

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

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5 July 13, 2018

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Abstract

Explaining coexistence in species-rich communities of primary producers (e.g., tropical trees, phytoplankton) remains a challenge for ecologists because of the likely competition for shared basal resources. Following Hutchinson's seminal suggestion, many theoreticians have tried to create diversity through a fluctuating environment, which impairs or slows down competitive exclusion. There are now several fluctuating-environment models that allow coexistence, but they often produce only a dozen of coexisting species at best. Here, we investigate what it would take to create even richer communities in fluctuating environments using an empirically parameterized model. Building on the forced multi-species Lotka-Volterra model of Scranton and Vasseur (2016) inspired by phytoplankton communities, we have investigated the effect of two coexistence mechanisms, namely the storage effect and stabilizing niche differences (SNDs). SNDs occur when intraspecific competition is stronger than interspecific (as opposed to neutral models where all coefficients are identical), and we tuned the competition ratio based on empirical data. Although SNDs maintained more species than the storage effect (50 % w.r.t 25%), we show that none of the two coexistence mechanisms considered could, by itself, ensure the coexistence of all species present at the beginning of our simulations. Realistic seasonal environments only aggravated that picture, as they decreased persistence relative to white noise. Our results suggest that combining different mechanisms for biodiversity maintenance into community models might be more fruitful than trying to find which explains best the observed diversity levels. Our results on community composition (formation of clumps, biomass distribution) in the different scenarios give further hints on how to empirically weight the influence of coexistence mechanisms.

1 Introduction

There has been a rich debate in theoretical ecology on how to reconcile niche and neutral perspectives on species coexistence (Gravel et al, 2006; Carmel et al, 2017). Under the neutral perspective, all species have equal birth and death rates and compete equally (since space is limited) whilst under the niche perspective, birth and death rates can vary between species and various mechanisms contribute to increasing intraspecific over interspecific competition (Hubbell, 2001). However as it has been pointed out repeatedly, niche and neutral processes are not mutually exclusive, and may actually act together to produce observed species coexistence (Gravel et al, 2006; Mutshinda et al, 2009; Götzenberger et al, 2012).

For instance, Scheffer and van Nes (2006) put forward the concept of 'clumpy coexistence', whereby a simultaneous influence of both niche and neutral processes create several clumps of similar species along a single trait axis. Classical stabilizing niche differences (SNDs) enable coexistence of multiple clumps through stronger net intraspecific competition (Chesson, 2000), while within-clump coexistence occurs through neutral processes (Hubbell, 2001; Munoz and Huneman, 2016), as species that differ too little in their fitnesses cannot exclude themselves out on reasonable timeframes. Indeed, clumps on the trait axis eventually thin out in absence of immigration, but transient coexistence can last for extended periods of time. This 'emergent neutrality' within groups (Holt, 2006) has been proposed as a unifying concept for the niche and neutral theories. The findings of Scheffer and van Nes (2006) have been disputed due to hidden niches in the original model (Barabás et al, 2013). Hidden niches emerge through stronger intraspecific competition mediated by a an additional intraspecific predation-like term (Barabás et al, 2013). This makes coexistence in the Scheffer and van Nes model more similar to that of the classical Lotka-Volterra model (Barabás et al, 2016), so that coexistence within clumps is not exactly neutral. Still, the idea that niche and neutral assembly can mould communities stays potent (Vernon et al, 2013). Since then, several studies have suggested that 'clumpy coexistence' can occur in theoretical models, most notably models incorporating temporal variation (Scranton and Vasseur, 2016; Sakavara et al, 2018). In these temporal-variation models, equal competitive strengths are combined with other mechanisms like the storage effect (or temporal niche partitioning, that is an equivalent concept for forced Lotka-Volterra models, Barabás et al, 2012; Scranton and Vasseur, 2016) that increases the possibility of coexistence by making the interaction strength covary positively with a fluctuating environment (see also

57 Barabás et al, 2012).

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

70 Because many phytoplankton species or genera respond in similar ways to temperature despite hav-
71 ing different optimas (Moisan et al, 2002), we hypothesized that a large seasonal variation might not
72 necessarily foster species coexistence. In fact, similar responses to seasonal fluctuations should lead to
73 an increased synchrony of species abundances which, in turn, should theoretically mitigate the expected
74 temporal partitioning. How seasonality affects coexistence (as opposed to a purely randomly fluctuating
75 environment) is therefore a key feature of this paper. In particular, we contrast cases where the storage
76 effect is present vs. absent, which conveniently maps to two different parameterizations of the forced
77 Lotka-Volterra model. Moreover, we realized while running Scranton and Vasseur (2016)’s model that
78 the overall diversity obtained at the end of the simulations was relatively low compared to what we usu-
79 ally observe in phytoplankton communities (several dozens to hundreds of species). We have therefore
80 sought out which mechanisms would foster a truly species-rich community for extended periods of time.

81 In an empirical study combining phytoplankton community-level time series and multivariate autore-
82 gressive models (Barraquand et al, 2017), we found that despite a large influence of the environment
83 (including temperature, irradiance, and other factors), intraspecific (or intragenus) competition was most
84 likely the key driver of species coexistence. In other words, stabilizing niche differences had a large role

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

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

92 2 Methods

93 *Models description*

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

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

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

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

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

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

102 niche width.

Table 1: Parameter definition and values of the model described in eEq. 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 | $\frac{\text{kg}}{\text{kg*year}}$ |
| 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 | $15 \frac{\text{kg}}{\text{kg*year}}$ |
| τ_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 | |
| 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 | $10^{3.1} \frac{\text{kg}}{\text{kg*year}}$ |
| τ_i^{opt} | Thermal optimum for growth of the i th species | K |
| θ | Scaling between white noise and seasonal signal | $[0, \sqrt{(2)}]$ |
| ρ | Ratio of intra-to-intergroup competition strengths | (1;10) |

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

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

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

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

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

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

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

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

7

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

where δ_{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). The values reported in Barraquand et al (2017) are higher because some intergroup competition coefficients were set to 0 in the best model.

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

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

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

Set-up

We replicate the 'Species sorting' experiment of Scranton and Vasseur (2016) so as to investigate how the structure of synthetic phytoplankton communities varies under the different scenarios we described above. We focused on the dynamics of a community initialized with 60 species with thermal optima uniformly spaced along the interval $[15^{\circ}\text{C}, 25^{\circ}\text{C}]$, and with the same initial density $(\frac{1}{\alpha S})$. 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. For each combination of parameters (type of environmental signal, storage effect and stabilizing niche differences), we ran 100 simulations.

All simulations were ran with Matlab's ode45 algorithm, an explicit Runge-Kutta (4,5) algorithm with an absolute error tolerance of 10^{-8} , and relative error tolerance 10^{-3} .

3 Results

Typical dynamics of the community following Eq. 1 (the model of Scranton and Vasseur, 2016), with both the environmental signals described in Eq. 1 (original choice of Scranton and Vasseur, 2016 ; Fig. 1 a) and Eq. 5 (our variant, Fig. 1 b), are shown in Fig. 1 c and d. A sinusoidal forcing produces the strongly seasonally structured dynamics that are typical of phytoplankton. Even though only 5 species can be seen in Fig. 1c), there were 14 species still present at the end of the simulation forced by a white noise, with large disparities in the range of variation of their biomasses. A third of the species kept a biomass above 10 kg/area (area=ha with a depth of a few meters produce a realistic standing biomasses Reynolds, 2006) while 6 out of the 14 remained below the unit. All persisting species in the white noise simulations were clustered within a 3.2°C -range of thermal optima (see the biomass distribution as a function of the thermal optimum in Fig. A.1 in the Supplementary Material). No obvious temporal patterns (e.g., cycles) could be seen in the communities forced by white noise. On the contrary, seasonal cycles were clear in the seasonally-forced case of Fig. 1 d). Only 4 species coexisted at the end of the simulation with seasonal forcing, gathered in two groups with large thermal optimum differences (5.7°C between the maximum thermal optimum of the first group and the minimum thermal optimum of the second group). When temperatures are high, the group with higher thermal optima reaches its maximum

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

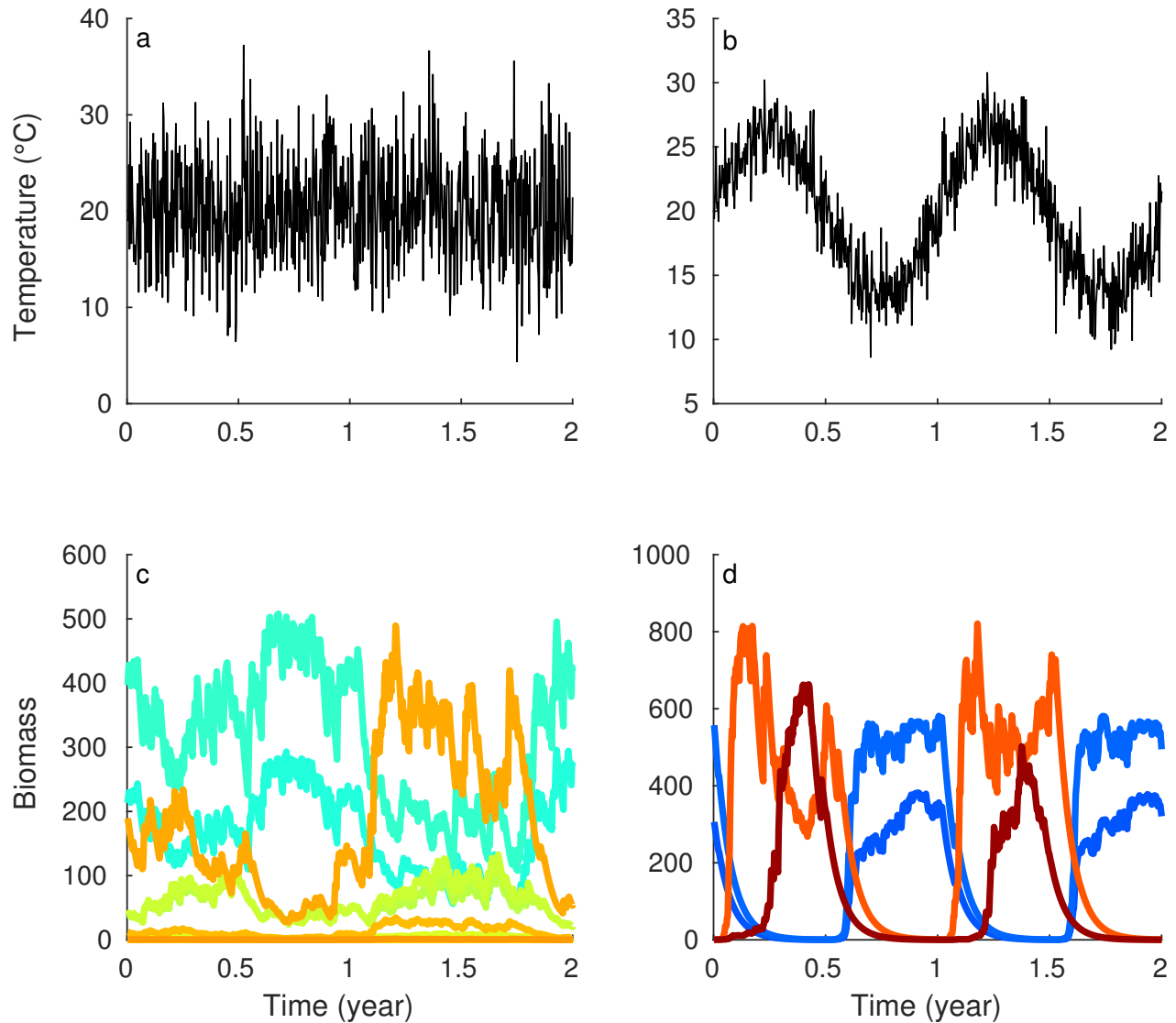


Figure 1: Time series of temperature (top) and extant species (bottom) for the 2 last years of a 5000 year simulation, with storage effect and no stabilizing niche differences. The forcing temperature is either a white noise (left) or a noisy seasonal signal (right). Line colors of species biomasses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

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

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

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

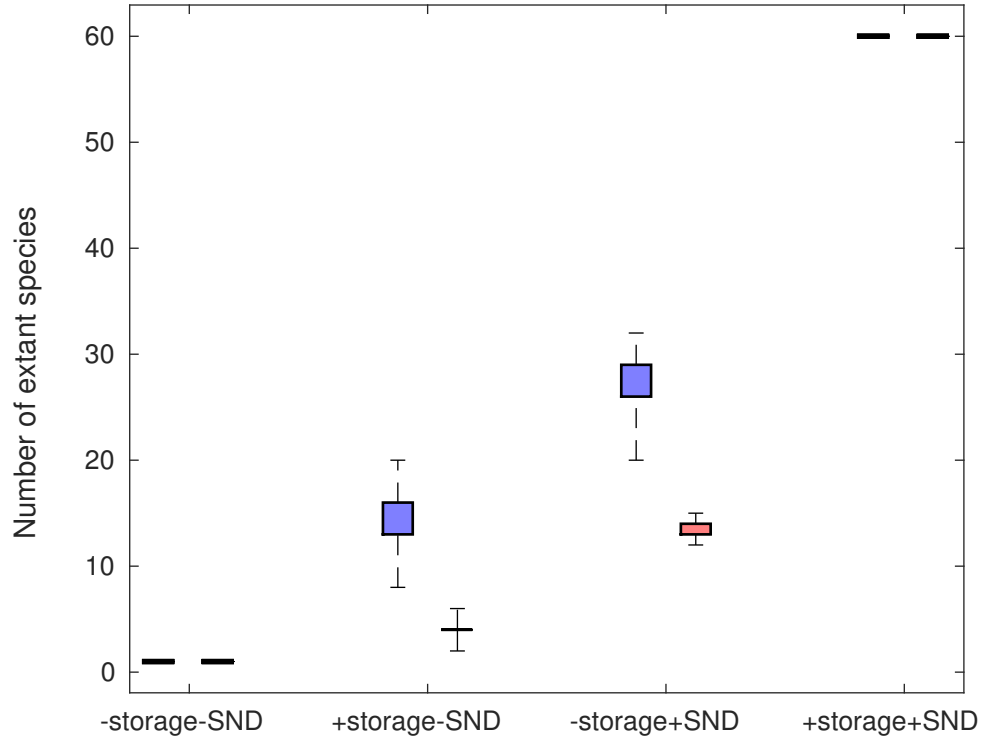


Figure 2: Number of species still present at the end of 5000-year simulations, initialized with 60 species, with a white noise forcing signal (blue) or a noisy seasonal signal (red). For each model type (with and without storage effect, + / - storage, respectively; with and without Stabilizing Niche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

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

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

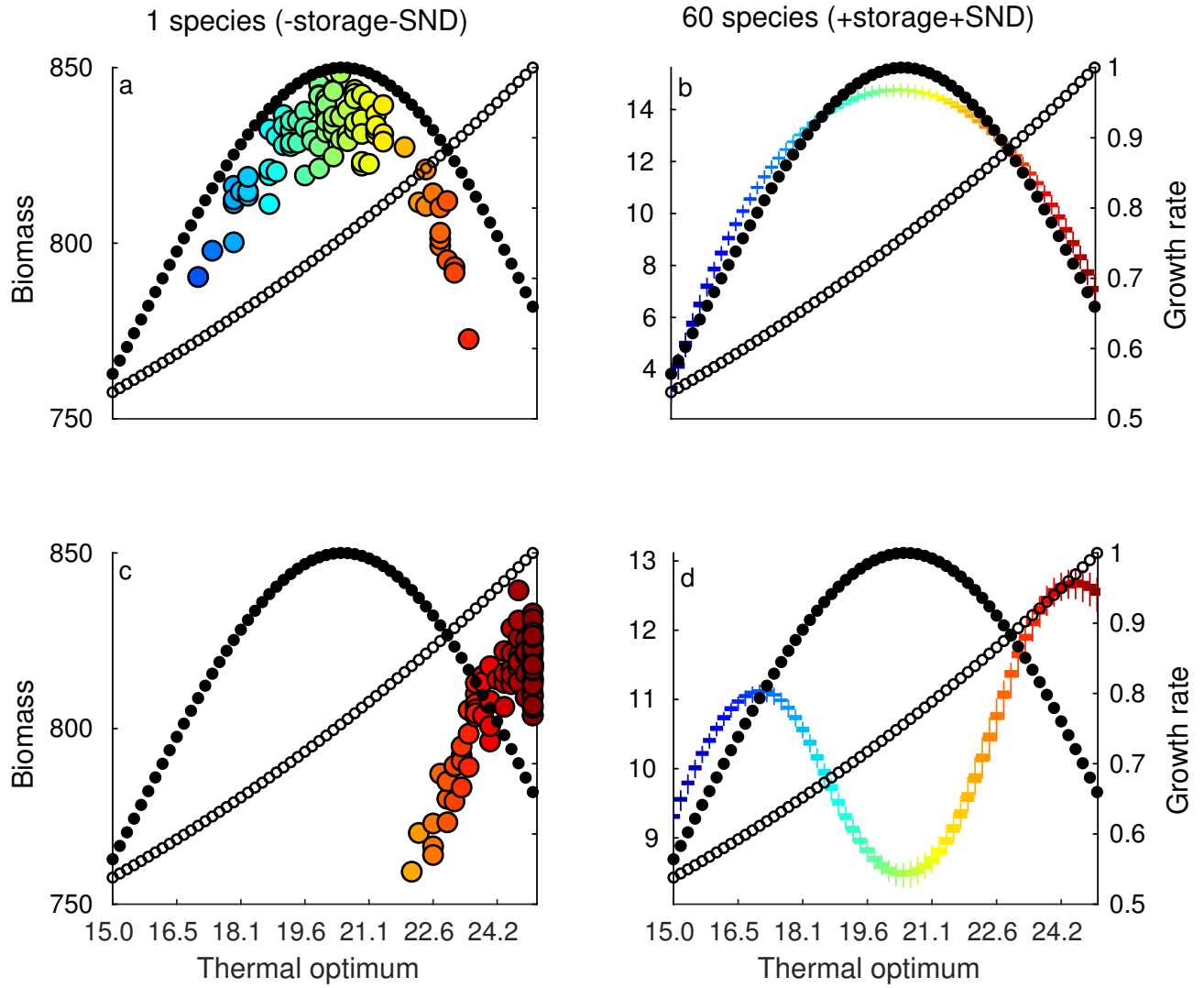


Figure 3: Mean biomass distribution over the last 200 years for 100 simulations, as a function of thermal optima, for the two stable-composition cases and two types of forcing signal. On the left, simulations without storage effect nor stabilizing niche differences are represented. Only one species is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

195 In cases where the richness of the community varied, the overall shape (multimodal vs. unimodal)
 196 of the marginal distribution of extant species with respect to the trait axis were similar for both types
 197 of environmental forcings (Fig. 4). By contrast, the type of coexistence mechanism generated different
 198 shapes. Indeed, the storage effect led to a multimodal biomass distribution with respect to thermal optima.

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

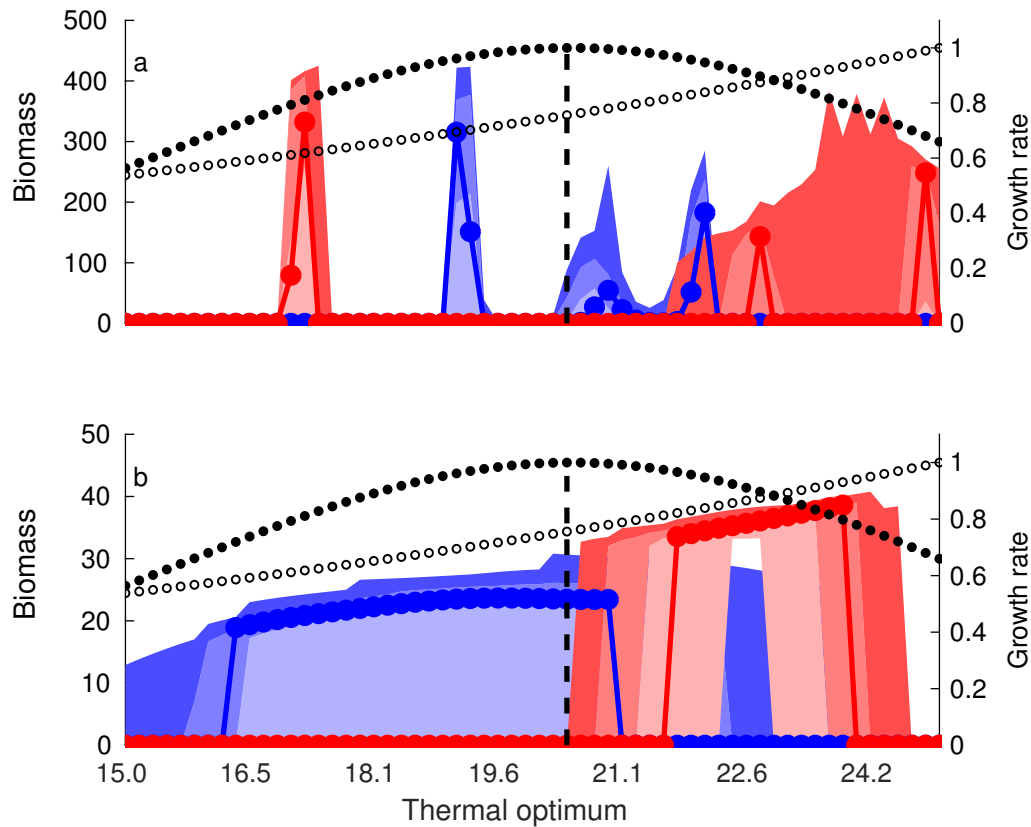


Figure 4: Mean biomass distribution over the last 200 years for 100 simulations, as a function of thermal optima, with storage effect and no stabilizing niche differences (a) and without storage effect, with stabilizing niche differences (b). The forcing signal is either a white noise (in blue) or a seasonal signal (in red). Shades of the same color correspond to the 50th, 90th and 100th percentiles of the distributions while colored lines correspond to one representative simulation. Scaled (divided by maximum) average (whose maximum is indicated by the dashed line) and maximum growth rates are shown as filled and open circles, respectively, and indexed on the right y-axis.

4 Discussion

We have simulated competitive Lotka-Volterra dynamics forced by a fluctuating environment (e.g., temperature fluctuations) under a range of scenarios allowing more or less coexistence. Two coexistence mechanisms, the storage effect and stabilizing niches differences, could be either present or absent, which led to four scenarios. These four scenarios were crossed with two possibilities for the forcing signal, a white noise and a stochastic yet seasonal signal, both with equal temporal variance. Our investigation therefore built on the model of Scranton and Vasseur (2016), which included a white noise forcing and a storage effect, but considered seven additional combinations of mechanisms. This was motivated by our wish to include two observed features of phytoplankton dynamics: seasonal cycles (Winder and Cloern, 2010) and stabilizing niche differences (Chesson, 2000; Barraquand et al, 2017).

We have found that first, temporally forced Lotka-Volterra dynamics cannot sustain any diversity with our phytoplankton-based set of parameters, unless the structure is geared to include either a storage effect or SNDs. Although this absence of diversity-enhancing effect of “pure” environmental variation 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 within competitive communities. A nice point made by Scranton and Vasseur (2016) was that a built-in storage effect in a forced Lotka-Volterra model, parameterized for phytoplankton communities, could lead to some degree of coexistence. Our investigation reproduced these results, using the white noise forcing considered by Scranton and Vasseur (2016), but an arguably more realistic seasonal forcing by temperature considerably lessened the richness of the community after 5000 years, decreasing from 15 to 4 species on average. Even imagining that groups represented here are genera or classes rather than species, this is a fairly low diversity for a phytoplankton-like community (see Chapter 1 in Reynolds, 2006).

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

et al, 2010).

However, the seasonal forcing still considerably reduced diversity when SNDs were considered, especially the “neutral” kind of diversity, i.e., diversity within clumps of similar traits. This diversity reduction occurs because within a season, the signal autocorrelation gives long, contiguous time intervals to the best competitor to exclude its less adapted heterospecifics. In contrast, a white noise generates large temperature shifts more frequently, and thereby forbid such competitive exclusion. In a seasonal setting, a species has the highest long-term averaged growth rate may not be the best competitor and can disappear as a result of a strong competition from both low- and high-temperature tolerant species, with and without storage effect.

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

In addition to community diversity, the species abundance distribution (SAD) also varied from one set of simulation to another. The storage effect begot several clumps along the trait space, with seasonality leading to more distant clumps. Conversely, SNDs alone led to uniform distributions, with species forming a single cluster along a fraction of the initial trait space. The identification of multiples modes in SAD is relatively recent (Dornelas and Connolly, 2008; Matthews et al, 2014) and is a rare pattern in theoretical models (McGill et al, 2007). While Barabás et al (2013) argue that multimodality can arise from artificial model formulation or demographic stochasticity, without underlying ecological processes, we note that this does not hold for our results, since storage effect alone, or storage effect and SNDs in a seasonal context both consistently produced multimodal distribution, while other sets of simulations always led to a single cluster along the trait axis. This might indicate that multimodality is indeed dependent on the community and ecological setting considered, which would explain the different results obtained until now on empirical SADs.

In our previous empirical study of coastal phytoplankton dynamics (Barraquand et al, 2017), we

264 have not found any storage effect (which certainly does not mean that it could not be observed in other
265 systems). Given the results on species richness and composition presented here, we are skeptical that even
266 if it was present, the storage effect alone could help explaining phytoplankton diversity. However, our
267 results suggest that in phytoplankton-like seasonal environments, even though empirically-based SNDs
268 produce more diversity than the storage effect when considered in isolation, the storage effect can help
269 diversity maintenance when combined to other mechanisms. Indeed, the combination storage effect
270 + SNDs is non-additive: the cases where both SNDs and the storage effect were present showed more
271 diversity than generated by any mechanism on its own.

272 The above results suggest the very exciting idea that multiple coexistence mechanisms might com-
273 bine superadditively, thus helping us to better understand the astounding diversity of primary producers.
274 This logic could, in principle, be extended to mechanisms that we have not considered here (e.g., spatial
275 structure, specialized natural enemies, that could be as important here for plankton as they are for tropical
276 trees, see Bagchi et al, 2014; Comita et al, 2014; Stump and Chesson, 2015; Barraquand et al, 2017). Pre-
277 vious research has however demonstrated that generalist seed predation could weaken the storage effect
278 (Kuang and Chesson, 2009, 2010) thus different mechanisms might not always combine superadditively
279 as we found here. That said, superadditivity has been found in some cases, i.e. pathogens could enhance
280 the storage effect (Mordecai, 2015) . Better explaining plant or microbial diversity would then not be
281 about selecting the best unique mechanism susceptible to explain the observed diversity, but rather bet-
282 ter combining those mechanisms together. This may obviously be an annoyance for those who like to
283 sharpen Occam's razor, but it clearly holds opportunities for theoreticians wishing to investigate syner-
284 gies between coexistence mechanisms in highly diverse communities. Aside from the synergies between
285 predator diversity-enhancing effects and SNDs or storage effects (on the temporal axis), one obvious
286 follow-up of this research would be interactions with spatial structure. Spatial structure occurs both en-
287 dogeneously, through spatially restricted movements and interactions, and exogeneously, through spatial
288 variation in environmental covariates Bolker (2003). Numerous studies (Bolker and Pacala, 1999; Murrell
289 and Law, 2002), have shown that spatially restricted movements and interactions - very small-scale spa-
290 tial structure - can help coexistence, which we believe would be especially important for phytoplankton
291 since many species form colonies (Reynolds, 2006; see discussion in Barraquand et al, 2017). Moreover,

292 although temperature is usually relatively spatially homogeneous over space, other drivers (e.g., rainfall,
293 pH in terrestrial ecosystems; salinity in aquatic ones) may exhibit spatial variation which is a main fac-
294 tor for coexistence (Snyder, 2008). The odds that different (resource) niches, natural enemies, spatial
295 limits to competition and temporal niche partitioning all interact to promote the very high-dimensional
296 coexistence observed in the field seem much higher than for any of those mechanisms alone. Whether
297 the diversity-enhancing effects of these mechanisms combine sub-additively (as in Kuang and Chesson,
298 2010) or super-additively like here is therefore worthy of further research.

299 Acknowledgements

300 We thank Alix Sauve for numerous thoughtful comments and references.

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