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

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Abstract

Explaining coexistence in species-rich communities of primary producers (e.g., tropical trees, phytoplankton) remains a challenge for ecologists because of the likely competition for shared basal resources. Following Hutchinson's seminal suggestion, many theoreticians have tried to create diversity through a fluctuating environment, which impairs or slows down competitive exclusion. There are now several fluctuating-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

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could, by itself, ensure the coexistence of all species present at the beginning of our simulations. Realistic seasonal environments only aggravated that picture, as they decreased persistence relative to white noise. Our results suggest that combining different mechanisms for biodiversity maintenance into community models might be more fruitful than trying to find which explains best the observed diversity levels. Our results on community composition (formation of clumps, biomass distribution) in the different scenarios give further hints on how to empirically weight the influence of coexistence mechanisms.

1 Introduction

There has been a rich debate in theoretical ecology on how to reconcile niche and neutral perspectives on species coexistence (Gravel et al, 2006; Carmel et al, 2017). Under the neutral perspective, all species have equal birth and death rates and compete equally (for space) whilst under the niche perspective, birth and death rates can vary between species and various mechanisms contribute to increasing intraspecific over interspecific competition (Hubbell, 2001). But as it has been pointed out repeatedly, niche and neutral processes are not mutually exclusive, 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 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 (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. However, the findings of Scheffer and van Nes (2006) have been disputed due to hidden niches in the original model (Barabás et al, 2013). Hidden niches emerge through stronger intraspecific competition mediated by a an additional intraspecific predation-like term (Barabás et al, 2013). This makes coexistence in the Scheffer and van Nes model more similar to

that of the classical Lotka-Volterra model (Barabás et al, 2016), so that coexistence within clumps is not exactly neutral.

Still, the idea that niche and neutral assembly can mould communities stays potent (Vergnon 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 Barabás et al, 2012).

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

Because many phytoplankton species or genera respond in similar ways to temperature despite having different optimas (Moisan et al, 2002), we hypothesized that a large seasonal variation might not necessarily foster species coexistence. In fact, similar responses to seasonal fluctuations should lead to an increased synchrony of species abundances which, in turn, should theoretically mitigate the expected temporal partitioning. How seasonality affects coexistence (as opposed to a purely randomly fluctuating environment) is therefore a key feature of this paper. In particular, we contrast cases where the storage

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effect is present vs. absent, which conveniently maps to two different parameterizations of the forced Lotka-Volterra model. Moreover, we realized while running Scranton and Vasseur (2016)'s model that the overall diversity obtained at the end of the simulations was relatively low compared to what we usually observe in phytoplankton communities (several dozens to hundreds of species). We have therefore sought out which mechanisms would foster a truly species-rich community for extended periods of time.

In an empirical study combining phytoplankton community-level time series and multivariate autoregressive models (Barraquand et al, 2017), we found that despite a large influence of the environment (including temperature, irradiance, and other factors), intraspecific (or intragenus) competition wasmost likely the key driver of species coexistence. In other words, stabilizing niche differences had a large role to play in maintaining species diversity in coastal phytoplankton (Barraquand et al, 2017)

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

2 Methods

Models description

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

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

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

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

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

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

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

Name	Definition	Value (unit)
S	Number of species	60
N_i	Biomass density of the ith species	(kg/area)
τ	Temperature	K
$r_i(\tau)$	Growth rate of species i as a function of temperature	$\frac{kg}{kg*year}$
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	$15\frac{kg}{kg*year}$
τ_0	Reference temperature	293 K
$a_r(\tau_0)$	Growth rate at reference temperature	$386\frac{kg}{kg*year}$
E_r	Activation energy	0.467 eV
k	Boltzmann's constant	$8.6173324.10^{-5}$eV.K^{-1}
$f_i(\tau)$	Fraction of the maximum rate achieved for the ith 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	$10^{3.1}\frac{kg}{kg*year}$
τ_i^{opt}	Thermal optimum for growth of the ith species	K
θ	Scaling between white noise and seasonal signal	$[0,\sqrt{(2)}]$
ρ	Ratio of intra-to-intergroup competition strengths	(1;10)

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

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

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

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 $r_i(\tau)$ (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.

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

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

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

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).

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	$r_i(\tau)N_i\left(1 - \sum_{j=1}^{S}\alpha\left(1+9\delta_{ij}\right)N_j\right)$	$N_i\left(r_i(\tau) - \sum_{j=1}^{S}\bar{r}_i\alpha\left(1+9\delta_{ij}\right)N_j\right)$
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°C, 25°C], and with the same initial density $\left(\frac{1}{\alpha S}\right)$. Each simulation was run for 5000 years in 1-day intervals. When the density of a species dropped below 10^{-6}, it was considered extinct. For each combination of 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) and Eq. 5 (our variant), are shown in Fig. 1. 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

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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 species in the white noise simulations were clustered along 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 reach its maximum biomass, then as temperature decreases through the season, they leave room for the growth of the low-temperature group.
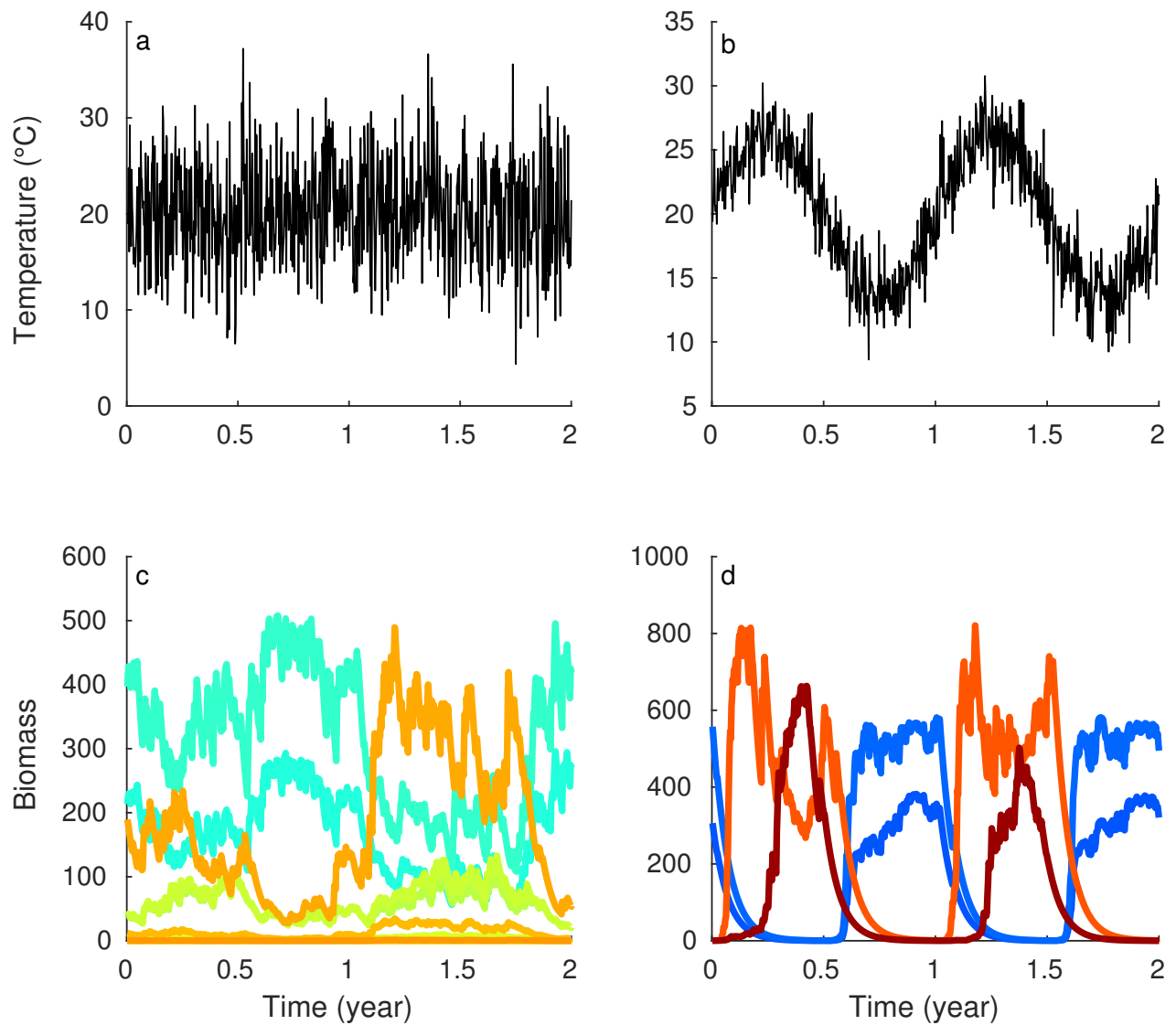
Figure 1: Time series of temperature (top) and extant species (bottom) for the 2 last years of a 5000 year simulation, with storage effect and no stabilizing niche differences. The forcing temperature is either a white noise (left) or a noisy seasonal signal (right). Line colors of species biomasses correspond to their thermal optima (from blue, corresponding to low thermal optima, to red, corresponding to high thermal optima. .

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

Both the stabilizing niche differences and the storage effect have a marked effect on increasing persistence. Without any of these coexistence mechanisms, only one species persisted at the end of the simulations. When only the storage effect was present, the number of extant species varied between 8 and 20 (14.8 ± 2.4) with a white noise, or 2 and 6 (4.1 ± 0.7) 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 (27.5 ± 2.4), or 12 and 15 (13.3 ± 0.6), with a white noise or a seasonal signal respectively. Remarkably, when the storage effect and SNDs both affected the community dynamics, all species persisted in the community, while neither of these mechanisms was able to produce that result alone, for either white noise and seasonal forcing.
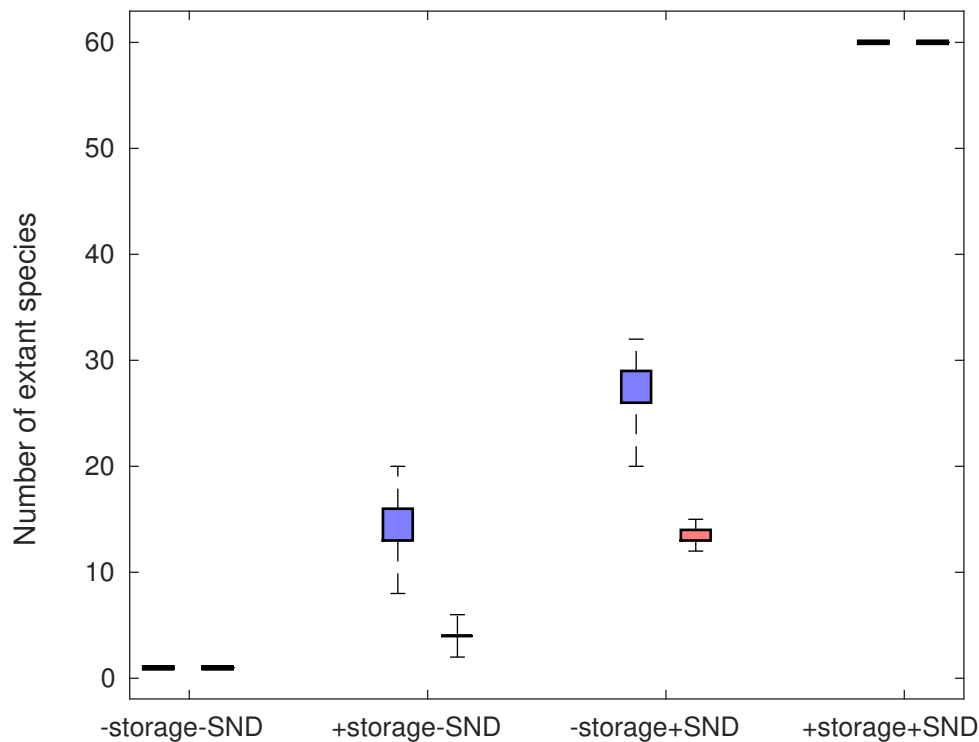

Figure 2: Number of species still present at the end of 5000-year simulations, initialized with 60 species, with a white noise forcing signal (blue) or a noisy seasonal signal (red). For each model type (with and without storage effect, + / - storage, respectively; with and without Stabilizing Niche 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 nor SNDs, a white noise forcing favoured species with intermediate thermal optima, with two thirds of the simulations ending with a species with a thermal optima between 18.9°C and 21.4°C (corresponding to only one fourth of the range of thermal optima present at the beginning of the simulation) and reaching a maximum average biomass in this range (Fig. 3 a). This distribution can be related to a selection for the highest long-term growth rates, averaged over time (see scaled growth rates in Fig.3). On the contrary, seasonality tended to favor species with larger maximum growth rates (thermal optima above 22°C). Species with a higher thermal optima are more likely to persist and to reach a higher biomass at the end of the simulation. 38% of the simulations therefore ended with the species having the highest temperature optimum, 25°C.

When both coexistence mechanisms were present, the 60 initial species coexisted with small variations in biomasses over the 100 simulations (mean CV=0.008 across simulations with either a white noise or a seasonal forcing signal, Fig. 3b and d). The forcing signal modified only the distribution of biomasses resulting in contrasted community structures despite equal richness in both simulation types. With a white noise, the distribution was unimodal with a maximum biomass reached for the second best long-term average growth rate (corresponding to a thermal optimum of 20.2°C). On the contrary, a seasonal signal led to a bi-modal distribution (centered on 17.0°C and 24.4°C), each corresponding to one season, with highest biomasses for higher thermal optima (Fig. 3 d). The minimum biomass was reached for the best long-term average growth rate at an intermediate temperature (20.4°C), one species apart from the maximum biomass in the white noise case
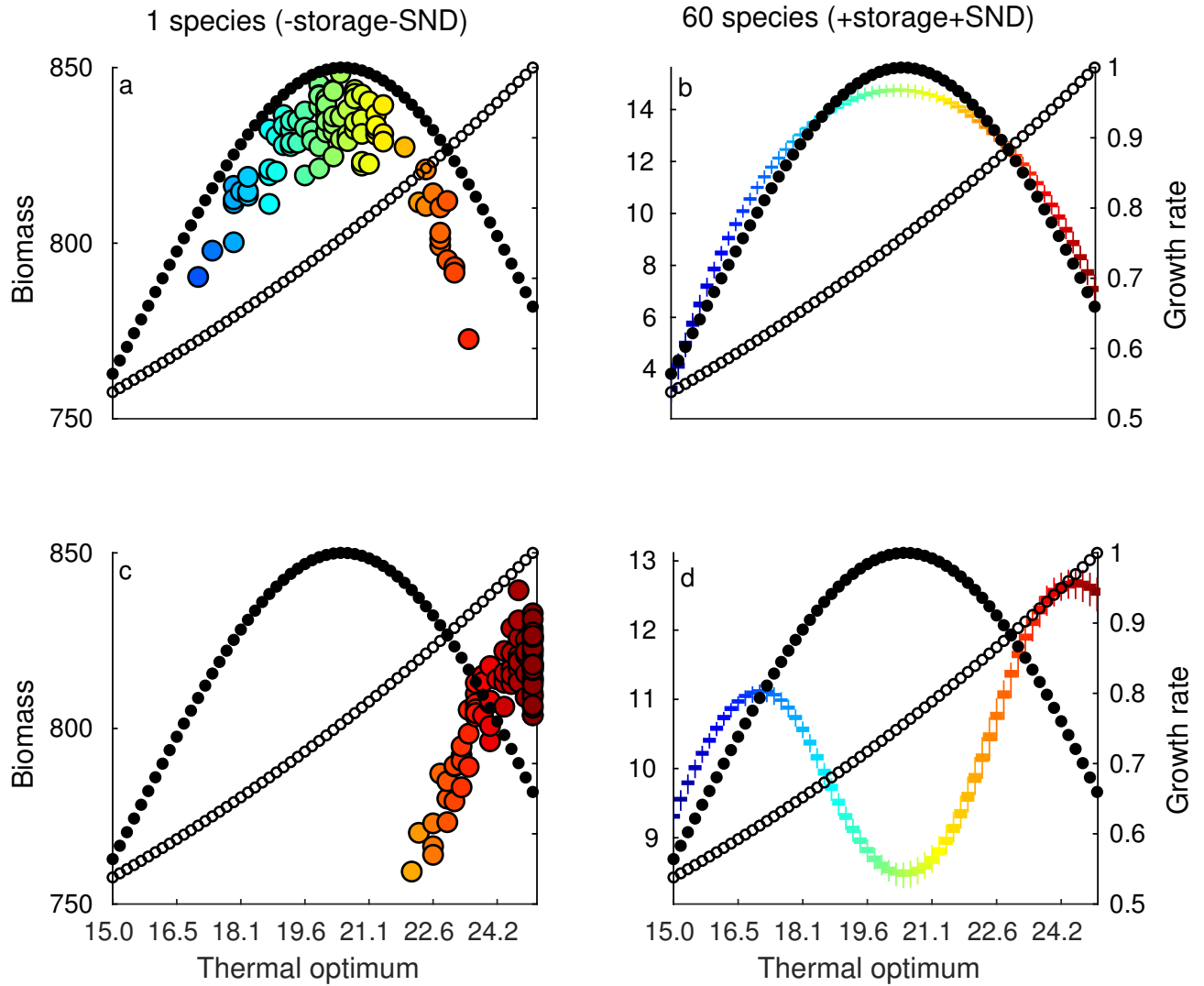
Figure 3: Mean biomass distribution over the last 200 years of 100 simulations, as a function of thermal optima, for the two stable-composition cases: without storage effect nor stabilizing niche differences (left, only one species is extant at the end of simulation, its mean value is represented by 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, the mean biomass of each speciesis represented by boxplots of the mean value 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 average and maximum growth rates are shown as filled and open and circles, respectively, and indexed on the right y-axis. Fred: if you do this, you need to make it a yy-plot, with a right-hand y-axis labelled "Growth rate" Done].

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

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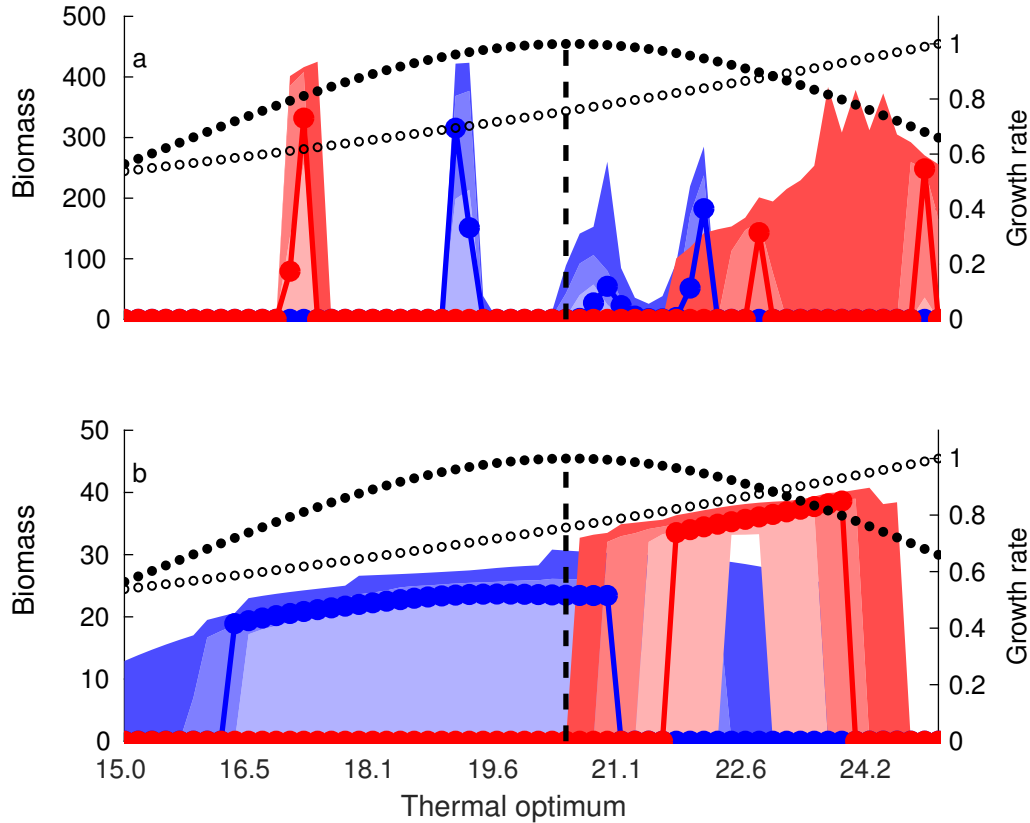

Figure 4: Mean biomass distribution over the last 200 years of 100 simulations, as a function of thermal optima, with storage effect and no stabilizing niche differences (top) and without storage effect, with stabilizing niche differences (bottom). The forcing signal is either a white noise (blue) or a seasonal signal (red). Shades of the same color correspond to the 50th, 90th and 100th percentiles of the distributions while colored 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 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 (Barraquand et al, 2017).

We have found that first, 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 15to 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 (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 is 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).

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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, while a white noise generates large temperature shifts more frequently, and thereby forbid such competitive exclusion. In a seasonal setting, 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 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 our previous empirical study of coastal phytoplankton dynamics (Barraquand et al, 2017), we have not found any storage effect (which certainly does not mean that it could not be observed in other systems). Given the results on species richness and composition presented here, we are skeptical that even if it was present, the storage effect alone could help explaining phytoplankton diversity. This is all the more likely that SNDs seem fairly strong when estimated from phytoplankton time series (Barraquand et al, 2017). However, our results suggest that in phytoplankton-like seasonal environments, even though empirically-based SNDs produce more diversity than the storage effect when considered in isolation, the storage effect can help diversity maintenance when combined to other mechanisms. Indeed, the combination storage effect + SNDs is non-additive: the cases were both SNDs and the storage effect were present showed more diversity than generated by any mechanism on its own.

The above results suggest the very exciting idea that multiple coexistence mechanisms might combine superadditively, thus helping us to better understand the astounding diversity of primary producers. This logic could, in principle, be extended to mechanisms that we have not considered here (e.g., spatial structure, specialized natural enemies, that could be as important here for plankton as they are for tropical trees, see Bagchi et al, 2014; Comita et al, 2014; Stump and Chesson, 2015; Barraquand et al,

2017). Previous research has however demonstrated that generalist seed predation could weaken the storage effect (Kuang and Chesson, 2009, 2010) thus different mechanisms might not always combine superadditively as we found here. That said, other models have shown that pathogens could enhance the storage effect (Mordecai, 2015) or that equalizing mechanisms due to optimally foraging predators are not greatly affected by environmental variation (Stump and Chesson, 2017). Better explaining plant or microbial diversity would then not be about selecting the best unique mechanism susceptible to explain the observed diversity, but rather better combining those mechanisms together. This may obviously be an annoyance for those who like to sharpen Occam's razor, but it clearly holds opportunities for theoreticians wishing to investigate synergies between coexistence mechanisms in highly diverse communities. Aside from the synergies between predator diversity-enhancing effects and SNDs or storage effects (on the temporal axis), one obvious follow-up of this research would be interactions with spatial structure. Spatial structure occurs both endogeneously, through spatially restricted movements and interactions, and exogeneously, through spatial variation in environmental covariates Bolker (2003) . Numerous studies ((Bolker and Pacala, 1999; Murrell and Law, 2002),) have shown that spatially restricted movements and interactions - very small-scale spatial structure - can help coexistence, which we believe would be especially important for phytoplankton since many species form colonies (Reynolds, 2006; see discussion in Barraquand et al, 2017). Moreover, although temperature is usually relatively spatially homogeneous over space, other drivers (e.g., rainfall, pH in terrestrial ecosystems; salinity in aquatic ones) may exhibit spatial variation which is a main factor for coexistence (Snyder, 2008). The odds that different (resource) niches, natural enemies, spatial limits to competition and temporal niche partitioning all interact to promote the very high-dimensional coexistence observed in the field seem much higher than for any of those mechanisms alone. Whether the diversity-enhancing effects of these mechanisms combine sub-additively (as in Kuang and Chesson, 2010) or super-additively like here is therefore worthy of further research.

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