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

Coralie Picoche [1], Alix Sauve[1], Frédéric Barraquand [1,2]

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1 Introduction

There has been a rich debate in theoretical ecology on how to reconcile niche and neutral perspectives (Scheffer and van Nes, 2006; Barabás et al, 2013; Vergnon et al, 2013) [we can add or replace this by refs Dom Gravel and others here].For instance, Scheffer and van Nes (2006) suggested that niche and neutrality can occur at the same time, with clumps of similar species on a trait axis. Coexistence between clumps is provided by classical stabilizing niche differences, while within-clump coexistence occur through neutral processes. Although eventually, in absence of immigration, clumps do thin out, transient coexistence can last for extended periods of time. However, the findings of Scheffer and van Nes (2006) have been disputed due to hidden niches in the original model (Barabás et al, 2013), that occur because of stronger intraspecific competition (as in the classical Lotka-Volterra model, (Barabás et al, 2016)). Since then, several studies have looked for this clumpy coexistence in theoretical models using other frameworks, most notably incorporating temporal variation (Scranton and Vasseur, 2016; Sakavara et al, 2018). In these models, equal competitive strengths are combined with other mechanisms like the storage effect that increase the possibility of coexistence (see also Barabás et al, 2012).

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

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

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

This multifaceted objectives 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.

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[1]Integrative and Theoretical Ecology Chair, Labex COTE, University of Bordeaux, [2]Institute of Mathematicsof Bordeaux, CNRS

2 Methods

Description

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

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

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

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

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

The coefficient values (Tab. 1) characterize a phytoplankton community. 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 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 (eq. 5).

$$\tau_t \sim N(\mu_\tau, \sigma_\tau) \tag{5}$$

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.

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

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).

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

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

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

Stabilizing niche differences are ensured by the addition of the coefficient ρ, which is the ratio of intra-to-intergroup competition strength. We can therefore re-write the interaction coefficients α_{ij} in eq. 8

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

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

Set-up

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

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

3 Results

Typical dynamics of the community following Eq. 1 with the environmental signals described in Eq. 5 and 6 are shown in Fig. 1. Even though only 5 species can be distinguished in Fig. 1c), there were 14 species still present at the end of the simulation forced by a white noise, with large disparities in the range of variation of their biomasses. A third of the species kept a biomass above 10 kg/area while 6 out of the 14 remained below the unit. All species were clustered along a 3.2°C-range of thermal optima. No pattern can be distinguished in their dynamics. On the other hand, cycles were clear in the seasonal example in Fig. 1 d). Only 4 species coexisted at the end of the simulation, 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, species with a higher thermal optima reached their maximum biomass, then left room for the growth of lower-temperature tolerant species.
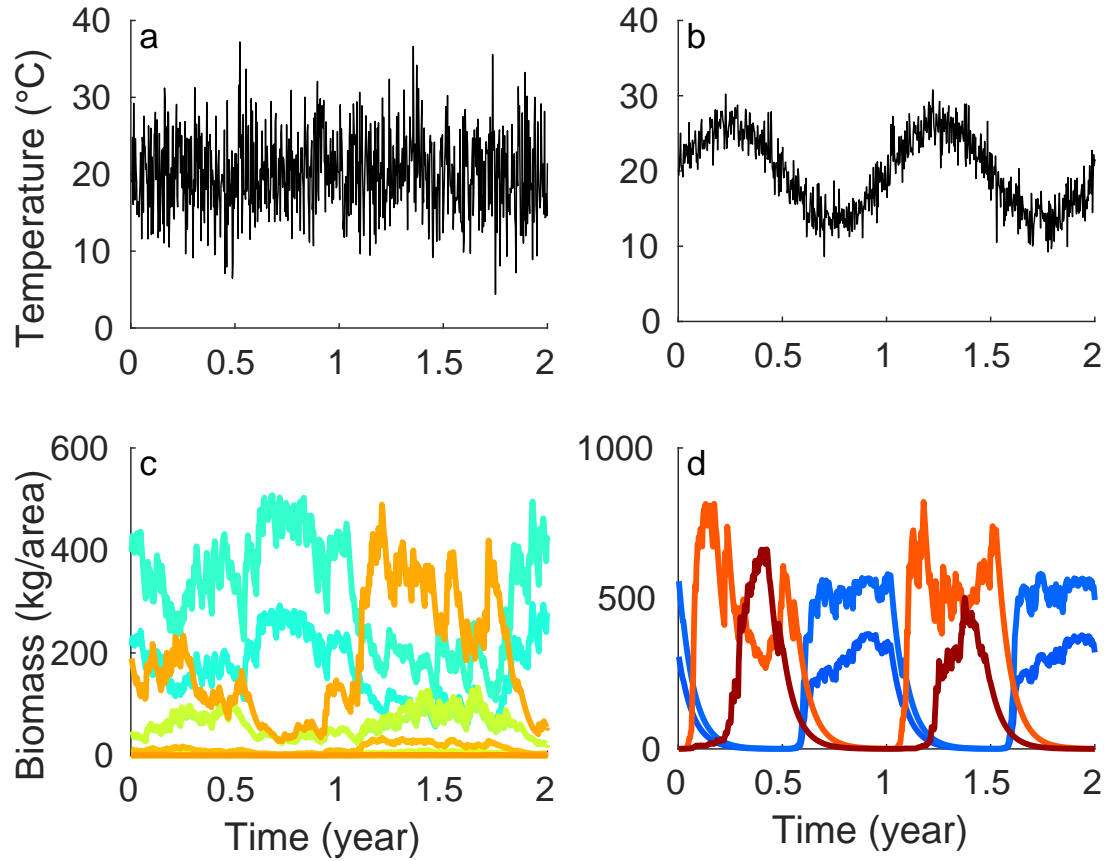
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[1] Running 100 right now

Fig. 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).

The decrease in persistence due to seasonality observed in the first example was confirmed in all our simulations (Fig. 2). In cases where richness at the end of the simulation varied (namely, with storage effect, without stabilizing niche differences, and without storage, with stabilizing niche differences), seasonality reduced the number of extant species to, in average, 29% and 49% of its original value, respectively. A seasonal signal tended to constrain the system to a smaller persistence range. Neither the storage effect nor stabilizing niche differences alone could ensure the coexistence of all species at the end of the simulations. 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 11 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 14, with a white noise or a seasonal signal respectively. When storage effect and stabilizing niche differences both affected the dynamics, all species persisted in the community.
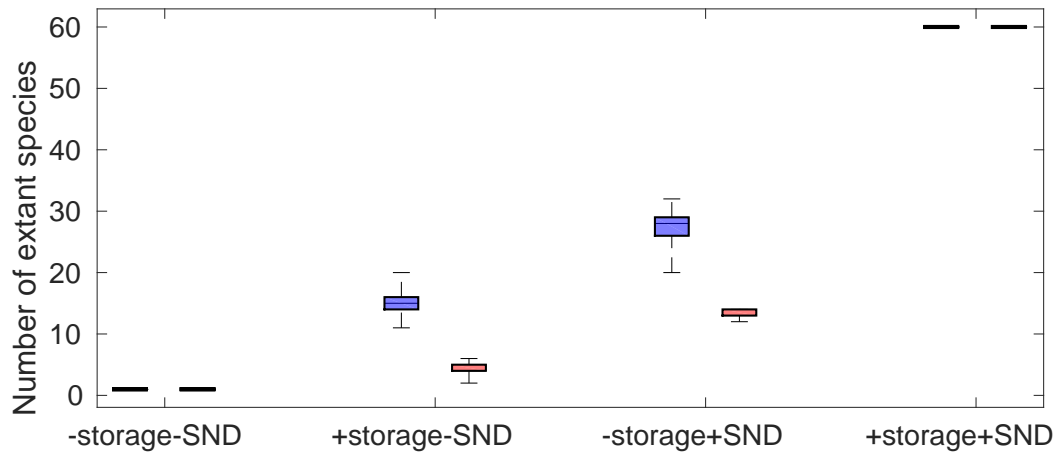
Fig. 2 Number of species still present at the end of 5000-year simulations, initialized with 60 species, with a white noise forcing signal (blue) or a noisy seasonal signal (red). For each model type (with and without Storage Effect, + / - storage, respectively; with and without Stabilizing Niche Differences, + / - SND, respectively), 50 simulations were launched. Community compositions are stable in the cases -storage-SND and +storage+SND (1 or 60 species are still present at the end of all simulations, respectively).

When the richness of the community was stable (either 1 or 60 species at the end of the simulation, in the absence or presence of coexistence mechanisms), there were still differences in the structure of the community due to both stochasticity and type of forcing (Fig. 3). Without coexistence mechanisms, a white noise forcing favoured species whose thermal optima lied between 17.4°C and 24.3°C, 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 the maximization of the long-term averaged growth rates (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 biomass increasing with the thermal optimum. 46% of the simulations 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 50 simulations (mean CV=0.01 with either a white noise or a seasonal signal, Fig. 3b and d). The forcing signal modified the distribution of biomasses. With a white noise, the distribution was unimodal with a maximum biomass reached for the best average growth rate (corresponding to a thermal optimum of 22.4°C). On the contrary, a seasonal signal led to a bi-modal distribution (centered on 17.4°C and 24.4°C) with higher biomasses for higher thermal optima. The minimum biomass was reached for a thermal optimum of 22.4°C, corresponding to the maximum biomass in the white noise case. The two modes in the biomass distribution correspond to the two modes in the seasonal signal.
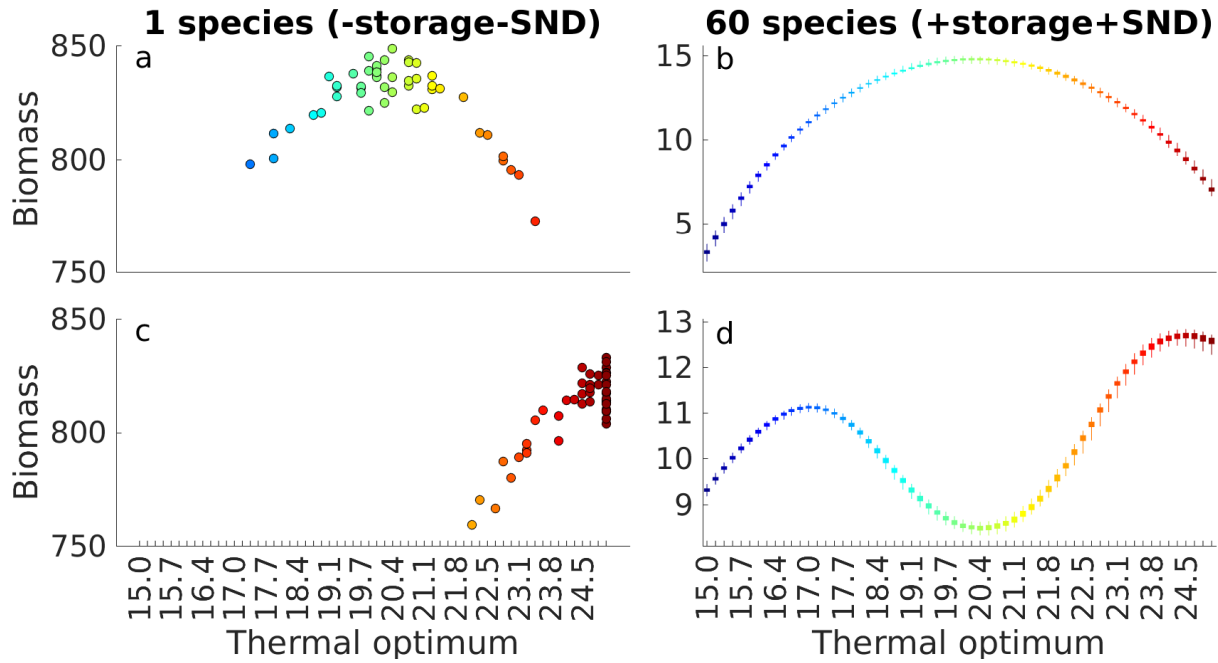
Fig. 3 Mean biomass distribution over the last 200 years of 50 simulations, as a function of thermal optima, for the two stable-composition cases: without storage effect nor stabilizing niche differences (left, only one species is extant at the end of simulation, its mean value is represented by a dot for one simulation. There can be several dots for the same species, corresponding to multiple simulations ending with this species alone) and with storage effect and stabilizing niche differences (right, all species are present at the end of the simulation, their mean biomass is represented by boxplots of the mean value for 50 simulations). The forcing signal is either a white noise (top) or a seasonal signal (bottom). Each species is identified by its thermal optimum and its color code.

In cases where the richness of the community varied, distributions of extant species were similar for the two types of forcings but differed according to the type of coexistence mechanism taken into account (Fig. 4). The storage effect led to a multi-modal distribution (always 3 modes with a white noise and in 94% of the seasonal simulations, Fig. 4a). With a white noise, extant species always had a thermal optimum between 18.8°C and 22.2°C whereas clumps tend to be further apart in the seasonal case, covering a total range of 8°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 distribution (Fig. 4 b). Species subject to a white noise lay in the lower range of temperatures (in 96% of the time, the highest thermal optimum was 22.8°C) whereas species subject to a seasonal signal were favored by temperatures above 20.5°C.
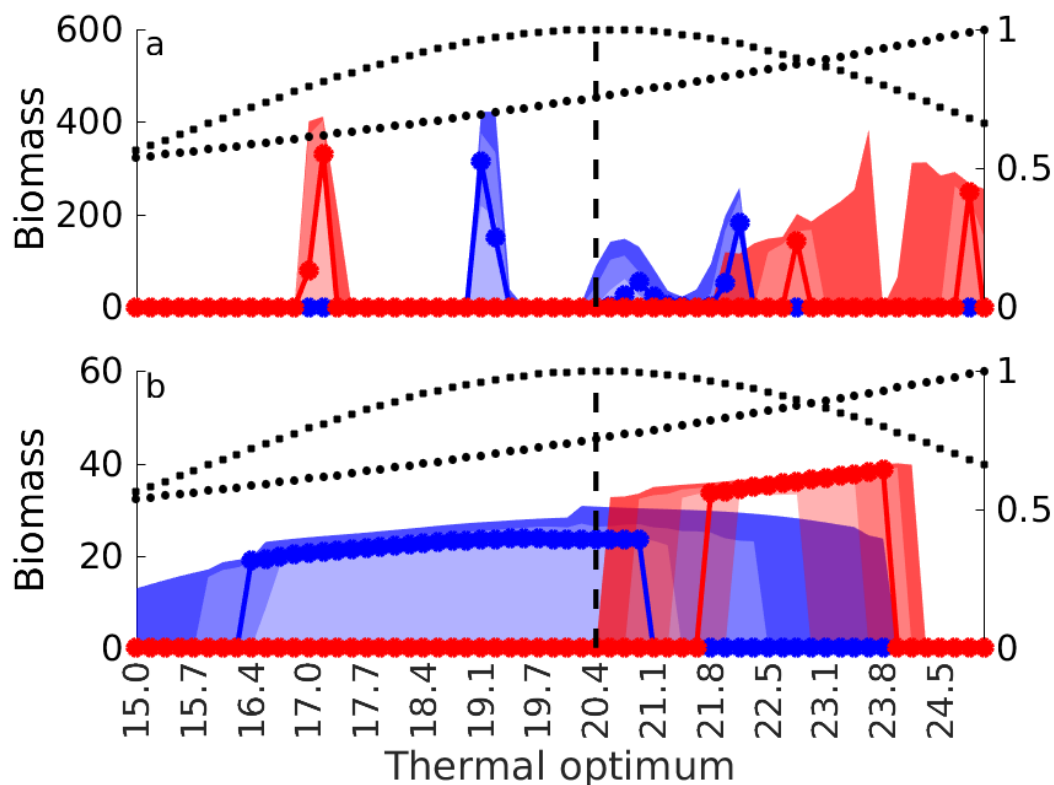
Fig. 4 Mean biomass distribution over the last 200 years of 50 simulations, as a function of thermal optima, with storage effect and no stabilizing niche differences (top) and without storage effect, with stabilizing niche differences (bottom). The forcing signal is either a white noise (blue) or a seasonal signal (red). Shades of the same colour corresponds to the 50th, 90th and 100th percentiles of the distributions while coloured lines correspond to one representative simulation. Scaled average (whose optimum is indicated by the dotted line) and maximum growth rates are shown as squares and circles, respectively, and indexed on the left y-axis.

4 Discussion

Summary of main results so far :

– Stabilizing niche differences can sustain more diversity than the storage effect.
– Storage effect without stabilizing niche differences leads to a stable multimodal abundance distribution. It is unclear whether this regularity is a by-product of limiting similarities for our parameter values. Conversely, no storage effect with stabilizing niche differences leasd to an even distribution (in line with previous point and may be discussed with the help of Barabás et al (2013)).
– Seasonality decreases the total number of extant species when compared to white noise. The autocorrelation 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.

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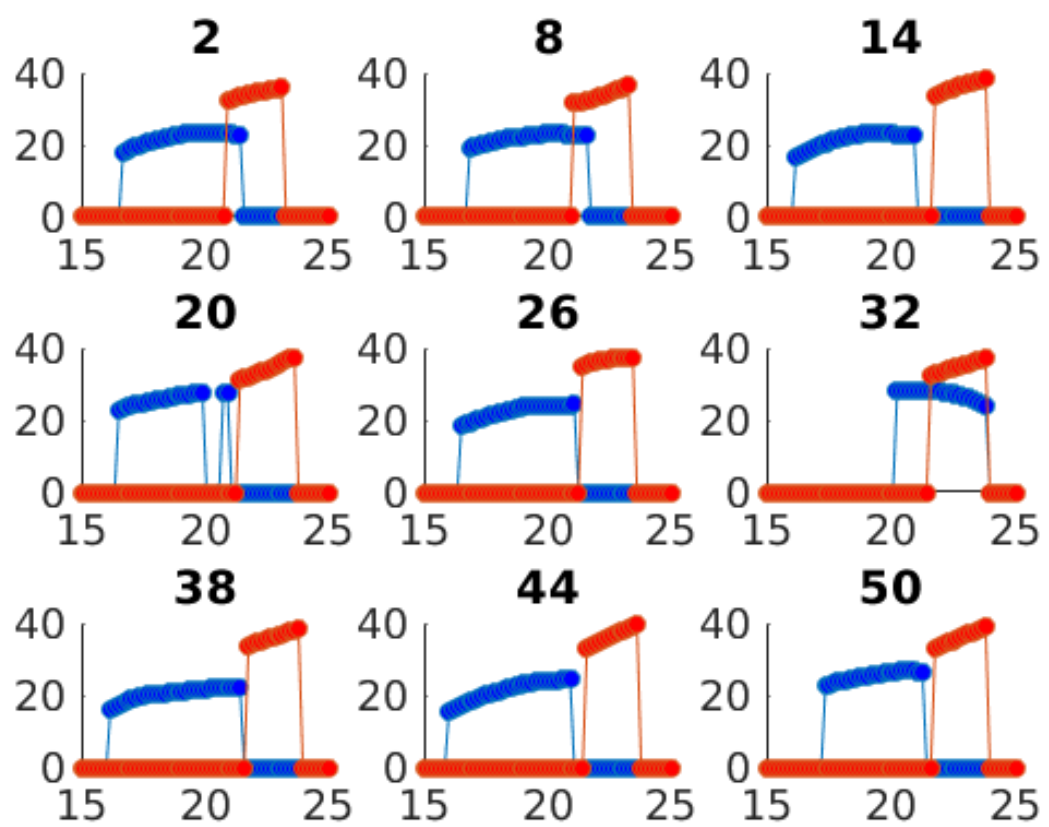
A Supplementary Material

Fig. 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 effect	No storage effect
Stabilizing niche differences	60	28 [20-32]	Stabilizing niche differences	60	13 [12-14]
No stabilizing niche differences	15 [11-20]	1	No stabilizing niche differences	4 [2-6]	1

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