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Coexistence in species-rich communities still needs stabilizing niche differences in temporally variable environment

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1 Introduction

Unifying niche and neutral perspectives still under debate (Scheffer and van Nes, 2006; Barabás et al, 2013; Vergnon et al, 2013)

Influence of the seasonality on temporal niche partitioning (Barabás et al, 2012; Sakavara et al, 2018) + definition of the storage effect (Barabás et al, 2012; Ellner et al, 2016)

Focus SV model (Scranton and Vasseur, 2016)

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.

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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	$\frac{\text{kg}}{\text{kg*year}}$
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	$8.6173324.10^{-5}$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
$\tau_{\min}$	Minimum thermal optimum	288K
$\tau_{\max}$	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 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 our 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.

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

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 $\theta = 1.3$.

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.

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

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

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

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

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

Set-up

We focused on the dynamics of a community initialized with 60 species with thermal optima uniformly spaced along the interval [15°C, 25°C]. All species started with the same initial density $\left(\frac{1}{\alpha S}\right)$. Each simulation was run for 5000 years in 1-day intervals. When the density of a species drops below 10^{-6}, it is considered extinct. This 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

[We should have a figure where thermal optima for each species would be represented by its color as in SV. We can either represent growth rates as suggested by Fred, or maybe the mean biomass at the end of a simulation for storage effect+stabilizing niche differences, which would give an idea of the dome-shaped distribution of abundances (and we would have something to discuss it afterwards 2.]

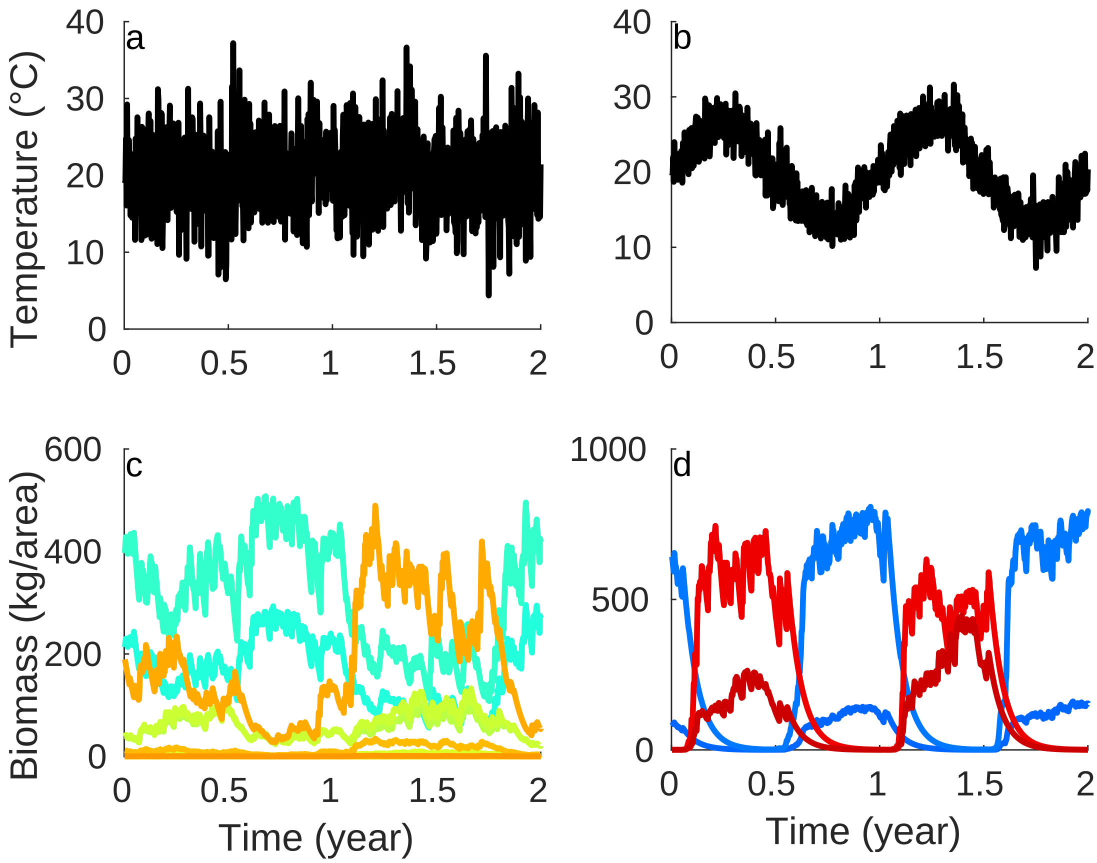


Fig. 1 Times series of temperature (top) and extant species (bottom) for the 2 last years of a 5000 year simulation. The forcing temperature is either a white noise (left) or a noisy season signal (right). Line colors of species biomasses correspond to their thermal optima.

[1] Later, 100 ?

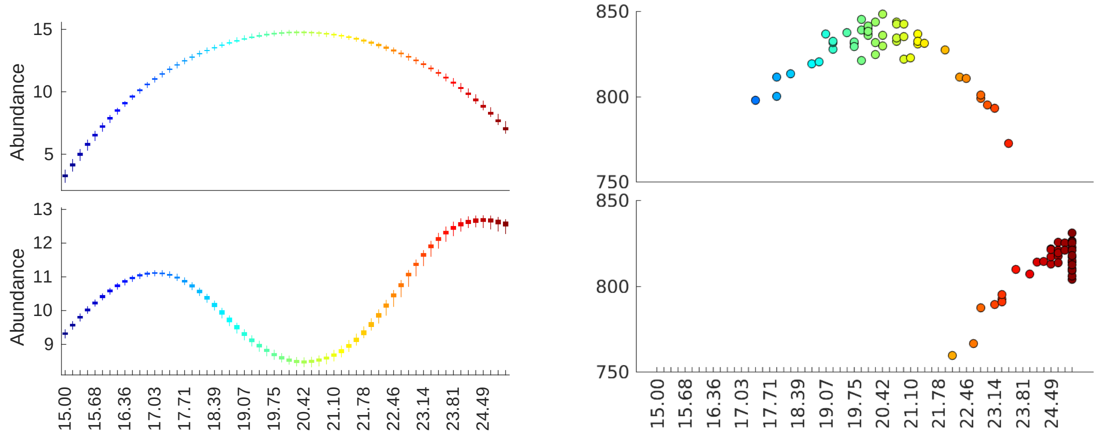
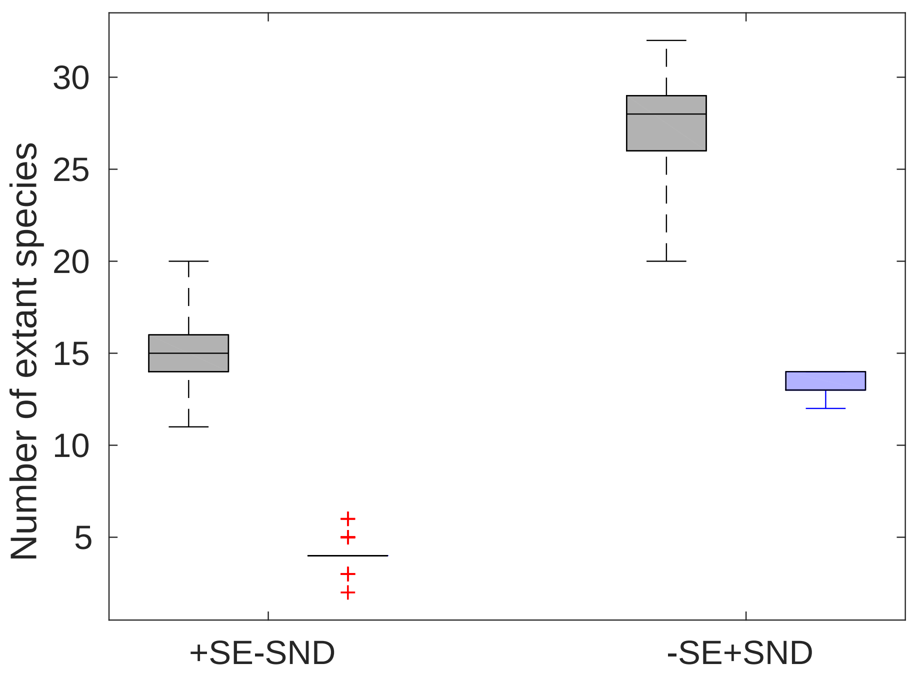


Fig. 2 Mean biomass over the last 200 years of simulation for the two stable cases : with storage effect and stabilizing niche differences (left, all species are always present at the end of the simulation, their mean biomass is represented by boxplots of the mean value for 50 simulations) and without storage effect nor stabilizing niche differences (right, 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). Temperature is either a white noise (top) or a seasonal signal (bottom). Each species is identified by its thermal optimum and its color code.



White noise	Storage effect	No storage effect	Season+White noise	Storage effect	No storage effect
Stabilizing niche differences	60	28 [25-29]	Stabilizing niche differences	60	13 [12-14]
No stabilizing niche differences	14.5 [11-19]	1	No stabilizing niche differences	4 [3-6]	1

Table 2 Median value [min-max] for the first ten simulations [Will be replaced -?- by corresponding boxplots. In grey, white noise. In blue, season]

4 Discussion

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