

# 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).

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

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

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

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

The coefficient values (Tab. 1) characterize a phytoplankton community. The niche of each species is defined by its thermal optimum  $\tau_i^{opt}$ . 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 $i$ th species	(kg/area)
$\tau$	Temperature	K
$r_i(\tau)$	Growth rate of species $i$ as a function of temperature	$\frac{\text{kg}}{\text{kg*year}}$
$\alpha_{ij}$	Strength of competition of species $j$ on species $i$	0.001 area/kg
$b_i$	Normalization of the thermal decay rate	
$m$	Mortality rate	$15 \frac{\text{kg}}{\text{kg*year}}$
$\tau_0$	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	
$\mu_\tau$	Mean temperature	293 K
$\sigma_\tau$	Standard deviation for temperature	5 K
$\tau_{\min}$	Minimum thermal optimum	288K
$\tau_{\max}$	Maximum thermal optimum	298 K
$A$	Niche breadth	$10^{3.1} \frac{\text{kg}}{\text{kg*year}}$
$\tau_i^{\text{opt}}$	Thermal optimum for growth of the $i$ th species	K
$\theta$	Scaling between white noise to seasonal signal	$[0, \sqrt{2}]$
$\rho$	Ratio of intra-to-intergroup competition strengths	(1;10)

Scranton and Vasseur (2016) described temperature as a white noise (eq. 5).

$$\tau_t \sim N(\mu_\tau, \sigma_\tau) \quad (5)$$

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  $\theta$ , enabling us to keep the same energy content in the forcing signal.

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

The upper limit for  $\theta$ ,  $\sqrt{2}$ , 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.

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

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  $\rho$ , which is the ratio of intra-to-intergroup competition strength. We can therefore re-write the interaction coefficients  $\alpha_{ij}$  in eq. 8

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

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  $[15^\circ\text{C}, 25^\circ\text{C}]$ . All species started 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 drops below  $10^{-6}$ , it is considered extinct. This corresponds to the first experiment, so called

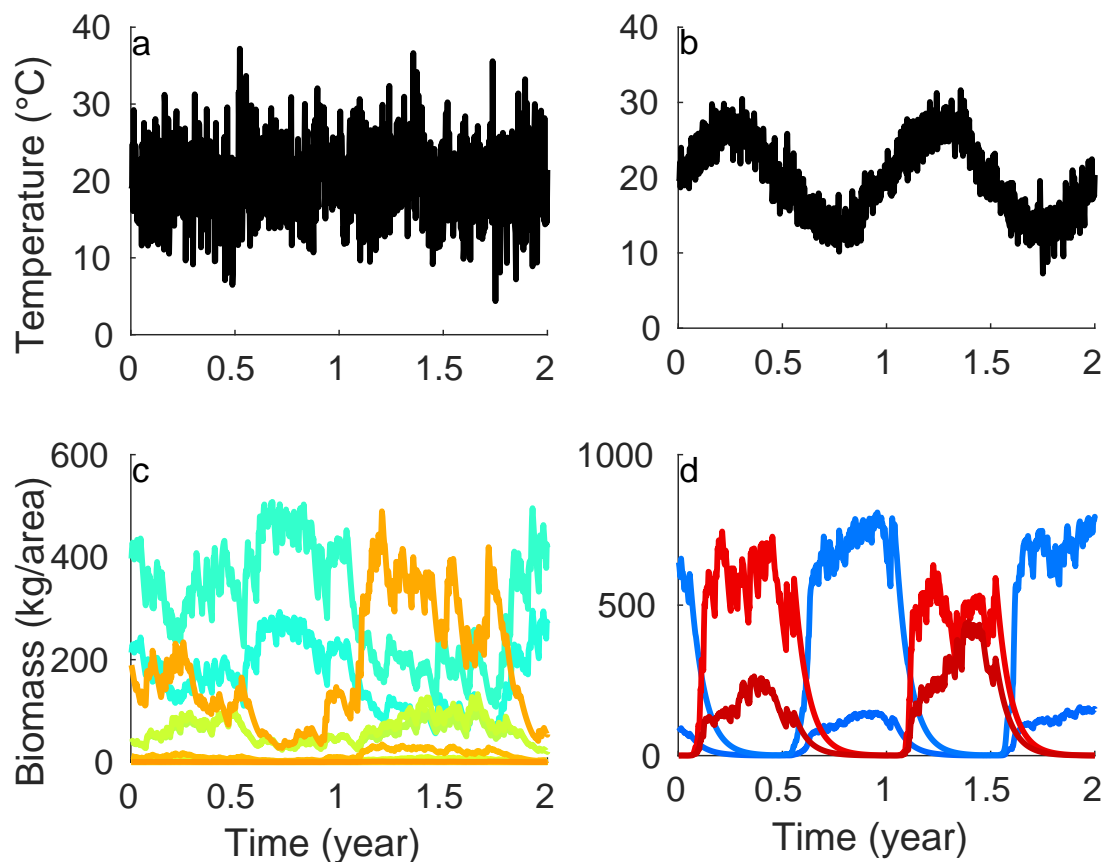
'Species sorting', in Scranton and Vasseur (2016). For each combination of the parameters of the model (type of environmental signal, storage effect and stabilizing niche differences), we ran 50<sup>1</sup> simulations.

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

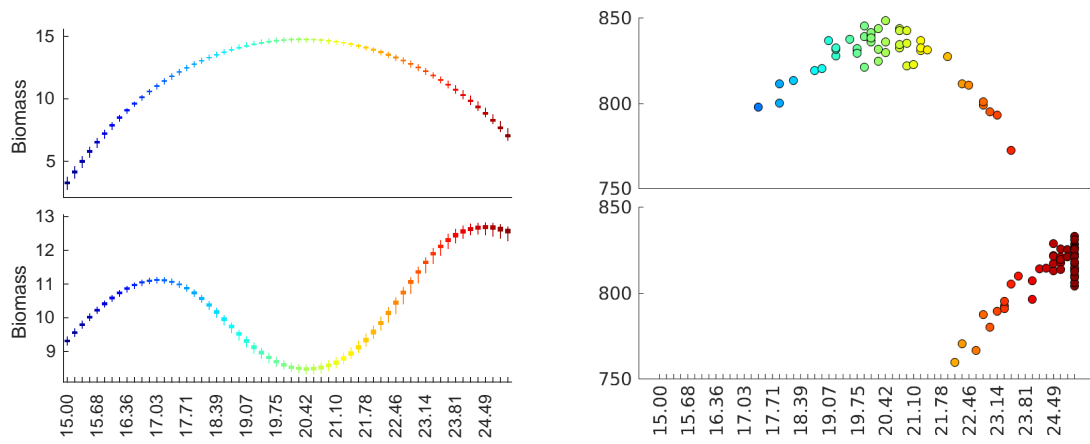
Summary of main results so far :

- Stabilizing niche differences are more important than storage effect to maintain biodiversity
- Storage effect without stabilizing niche differences lead to multimodal abundance distribution (which is quite stable : always 3 modes. **Why ?**) whereas no storage effect with stabilizing niche differences lead to a unimodal, more even distribution (in line with previous point, not sure that's really a result).
- Seasonality tends to decrease the total number of extant species when compared to white noise (small fitness differences for longer: species are driven to extinction whereas they can recover before crashing with a white noise).
- 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.

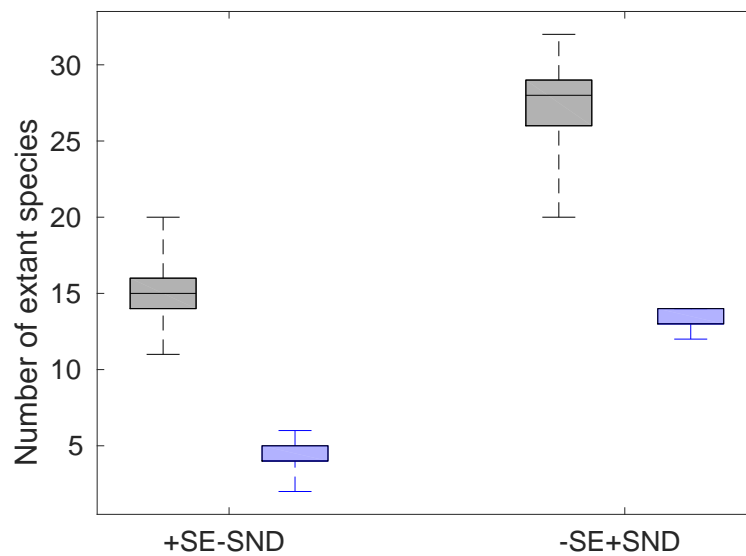


**Fig. 1** Times series of temperature (top) and extant species (bottom) for the 2 last years of a 5000 year simulation. The forcing temperature is either a white noise (left) or a noisy season signal (right). Line colors of species biomasses correspond to their thermal optima.

<sup>1</sup> Later, 100 ?

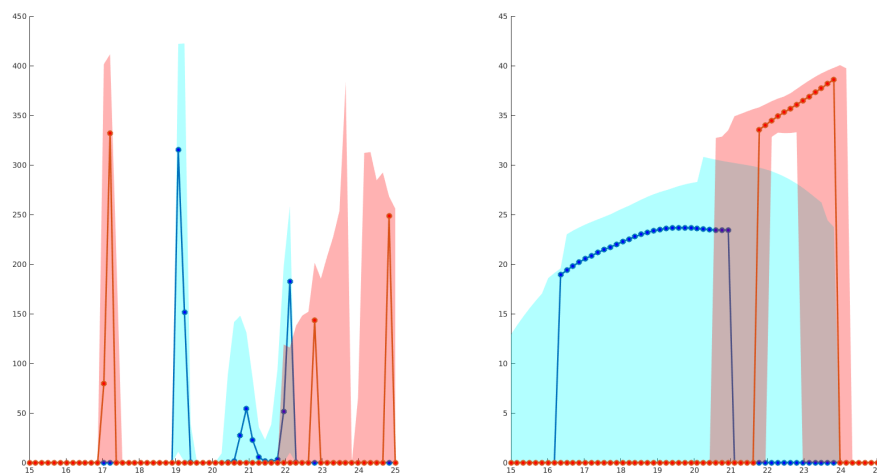


**Fig. 2** Mean biomass over the last 200 years of simulation for the two stable cases : with storage effect and stabilizing niche differences (left, all species are always present at the end of the simulation, their mean biomass is represented by boxplots of the mean value for 50 simulations) and without 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 [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** Median value [min-max] for 50 simulations per combination of parameters [Will we keep the boxplots? In grey, white noise. In blue, season. +SE-SND=Storage effect, no stabilizing niche differences. -SE+SND=No storage effect, with stabilizing niche difference]



**Fig. 3** [Preliminary, still searching for a better graph] Biomass distribution of species, ranked by their thermal optimum, with storage effect without stabilizing niche differences (left) and no storage effect with stabilizing niche differences (right). Shaded area corresponds to the range of values for 50 simulations, lines correspond to a typical simulation. Temperature is either a white noise (blue) or a seasonal signal (red)

## 4 Discussion

### References

- Barabás G, Meszéna G, Ostling A (2012) Community robustness and limiting similarity in periodic environments. *Theoretical Ecology* 5(2):265–282, doi:10.1007/s12080-011-0127-z
- Barabás G, D’Andrea R, Rael R, Meszéna G, Ostling A (2013) Emergent neutrality or hidden niches? *Oikos* 122(11):1565–1572, doi:10.1111/j.1600-0706.2013.00298.x
- Barraquand F, Picoche C, Maurer D, Carassou L, Auby I (2017) Weak interactions between groups and physical drivers of community dynamics in coastal phytoplankton. *bioRxiv* doi:10.1101/171264
- Ellner SP, Snyder RE, Adler PB (2016) How to quantify the temporal storage effect using simulations instead of math. *Ecology Letters* doi:10.1111/ele.12672
- Sakavara A, Tsirtsis G, Roelke DL, Mancy R, Spatharis S (2018) Lumpy species coexistence arises robustly in fluctuating resource environments. *Proceedings of the National Academy of Sciences* 115(4):738–743, doi:10.1073/pnas.1705944115
- Scheffer M, van Nes EH (2006) Self-organized similarity, the evolutionary emergence of groups of similar species. *Proceedings of the National Academy of Sciences* 103(16):6230–6235
- Scranton K, Vasseur DA (2016) Coexistence and emergent neutrality generate synchrony among competitors in fluctuating environments. *Theoretical Ecology* doi:10.1007/s12080-016-0294-z
- Vernon R, van Nes EH, Scheffer M (2013) Interpretation and predictions of the Emergent neutrality model: a reply to Barabás et al. *Oikos* 122(11):1573–1575, doi:10.1111/j.1600-0706.2013.00790.x
- Vesipa R, Ridolfi L (2017) Impact of seasonal forcing on reactive ecological systems. *Journal of Theoretical Biology* 419:23–35, doi:10.1016/j.jtbi.2017.01.036