# 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]**

April 27, 2018

## 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.

[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 $\tau_i^{opt}$. 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.

**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 | $\frac{kg}{kg*year}$ |
| $\alpha_{ij}$ | Strength of competition of species $j$ on species $i$ | 0.001 area/kg |
| $b_i$ | Normalization of the thermal decay rate | |
| $m$ | Mortality rate | $15\frac{kg}{kg*year}$ |
| $\tau_0$ | 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 $i$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 | $10^{3.1}\frac{kg}{kg*year}$ |
| $\tau_i^{opt}$ | 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).

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

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

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

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.

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

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

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

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

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.
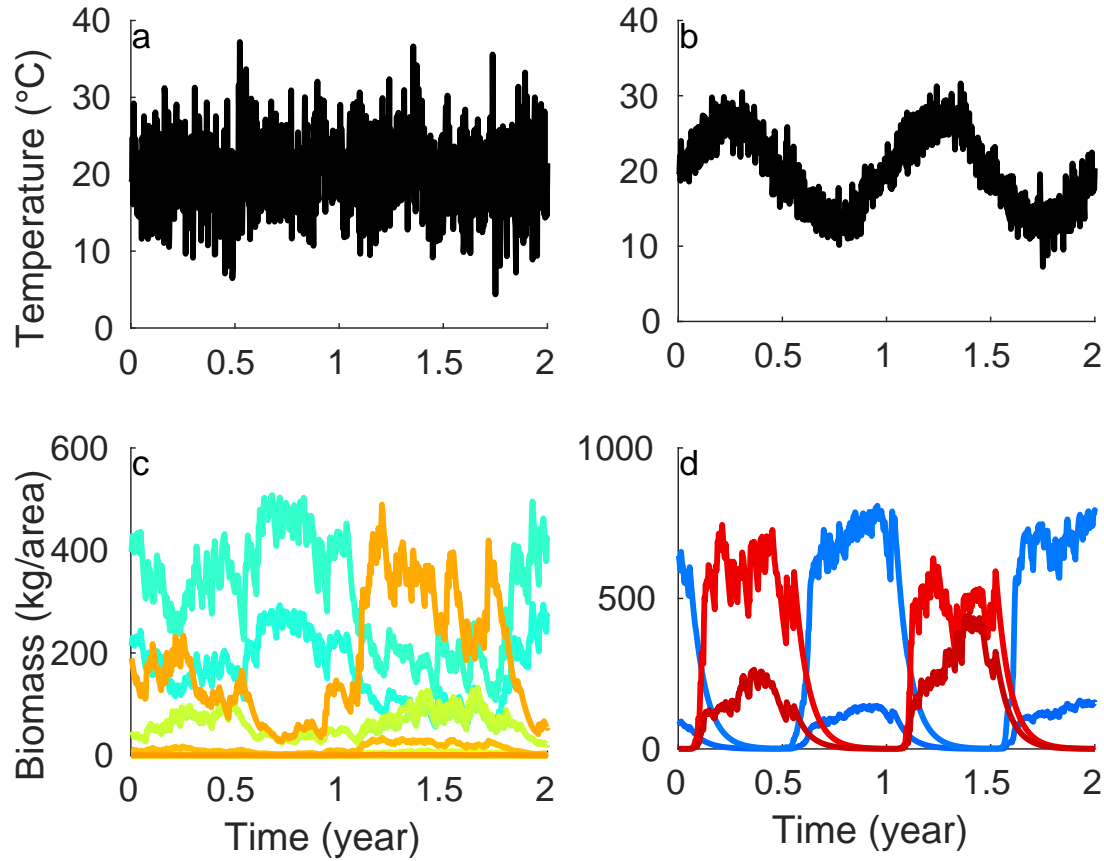
---

[1] Later, 100 ?

**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.
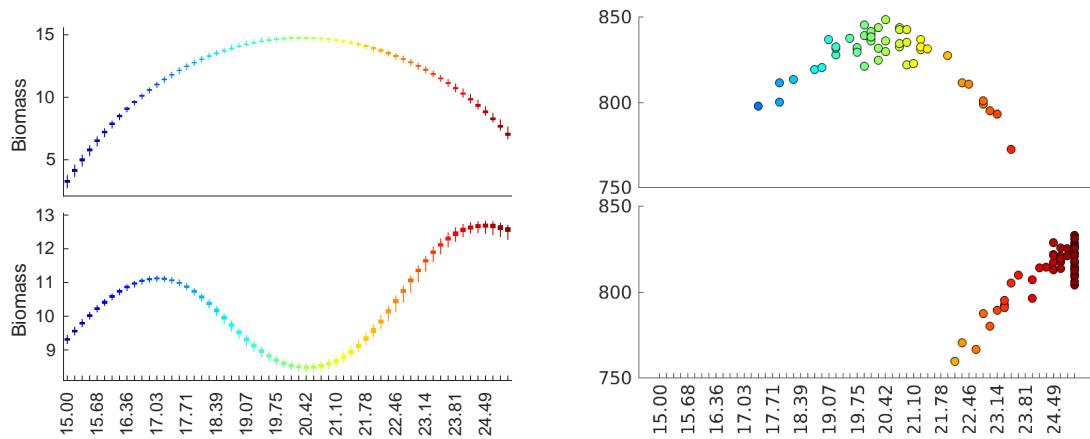


**Fig. 2** Mean biomass over the last 200 years of simulation for the two stable cases : with storage effect and stabilizing niche differences (left, all species are always present at the end of the simulation, their mean biomass is represented by boxplots of the mean value for 50 simulations) and without 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.
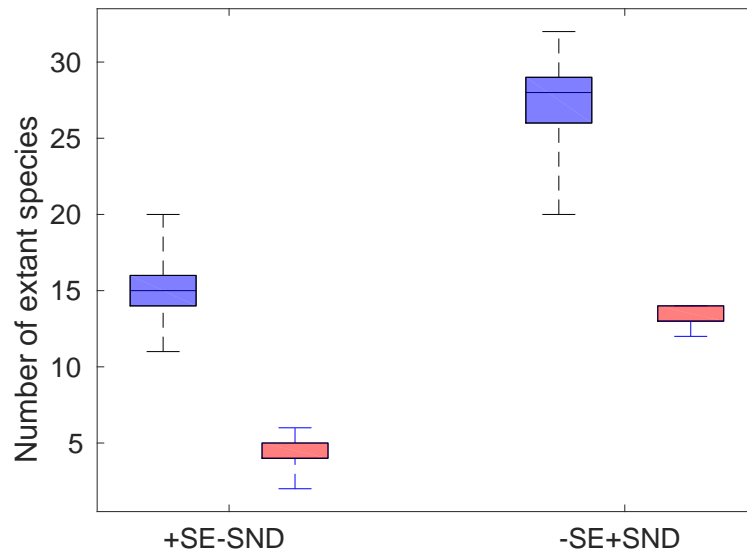
| White noise | Storage effect | No storage effect | Season+White noise | Storage effect | No storage effect |
|---|---|---|---|---|---|
| Stabilizing niche differences | 60 | 28 [20-32] | Stabilizing niche differences | 60 | 13 [12-14] |
| No stabilizing niche differences | 15 [11-20] | 1 | No stabilizing 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 blue, white noise. In red, season. +SE-SND=Storage effect, no stabilizing niche differences. -SE+SND=No storage effect, with stabilizing niche difference]
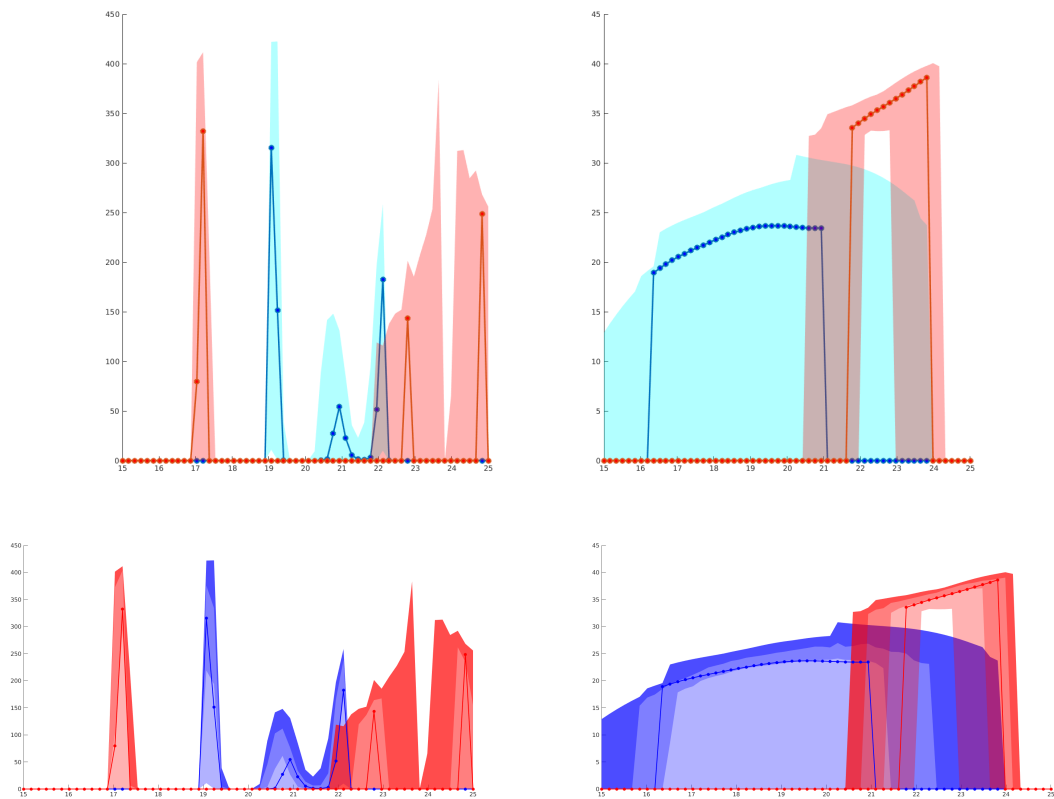


**Fig. 3** [Alternative, maybe less is more, actually] [TOP description] Biomass distribution of species, ranked by their thermal optimum, with storage effect without stabilizing niche differences (left) and no storage effect with stabilizing niche differences (right). Shadowed area corresponds to the range of values for 50 simulations[TOP ; for Bottom line, shades correspond to the 50th, 90th and 100th percentile], lines correspond to a typical simulation. Temperature is either a white noise (blue) or a seasonal signal (red)[Bottom description]
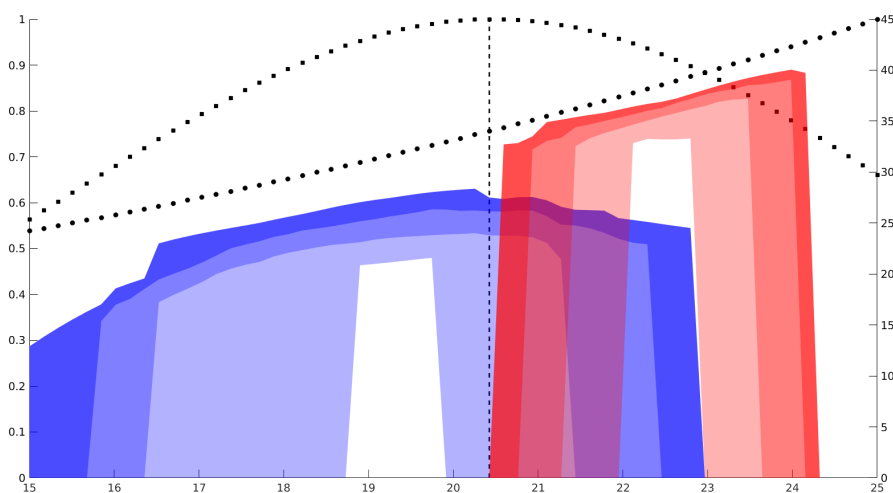
**Fig. 4** Mean (squares) and maximum (circles) growth rates values, depending on the thermal optimum of each species. Values are scaled by their maximum. The maximum of mean growth rates is indicated by a dotted line. Biomass distribution for a white noise (blue) or a seasonal signal (red) without storage effect with stabilizing niche differences are indexed on the left y-axis. Different shades correspond to the 50th, 90th and 100th percentile. For the sake of clarity, two simulations were withdrawn from the distribution as they had a different behaviour. They are shown in Fig. 5
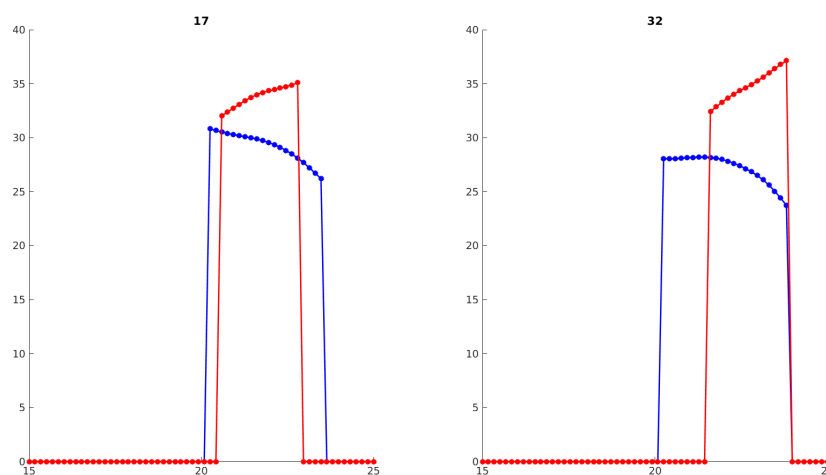
## 4 Discussion



**Fig. 5** Mean distribution of species at the end of a simulation without storage effect with stabilizing niche differences, for the only 2 cases in which seasonal (red) and white noise (blue) dsitributions overlapped

## 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

Barabás G, Michalska-Smith MJ, Allesina S (2016) The Effect of Intra- and Interspecific Competition on Coexistence in Multispecies Communities. The American Naturalist pp 000–000, doi:10.1086/686901

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

Vergnon R, van Nes EH, Scheffer M (2013) Interpretation and predictions of the Emergent neutrality model: a reply to BarabÃ¡s 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