Seasonal dynamics of a community of competitors with thermal optimums in a fluctuating environment

April 10, 2018

1 Introduction

Scranton and Vasseur (2016) devised a model to investigate what maintains the diversity of competitors in a fluctuating environment. Their model is loosely based on the dynamics of phytoplankton, and corresponds for the most part to how we (and many others) think such dynamics can play out. For instance, nutrients do not necessarily have strong forcing effects but other abiotic drivers may impose a synchronous forcing, including most notably irradiance and temperature. Their model, which includes thermal preference curves, is also relatively simple in terms of parameterization, which attracted our interest.

Scranton and Vasseur (2016) have shown that

- "Lumpy" or "clumpy coexistence", with both stabilizing differences and equalizing differences between competitors, is possible here

- Stabilizing differences for coexistence occur here through a built-in storage effect ("We find that competitors with sufficiently different temperature niches coexist via temporal niche differentiation")

- Equalizing differences between similar competitors presumably maintain near-neutral dynamics within clumps, because the thermal curves of the various species are (i) similar enough and (ii) environmental variability forbids that a clump of competitors maintains itself in good conditions long enough that exclusion could occur.

- Near neutrality results in interspecific synchrony within the groups of similar competitors

This helps maintaining a "high diversity in competitive communities where synchrony is commonly observed".

We've been puzzled by several elements, largely inspired by our phytoplankton work (Barraquand et al. (2017)):

- The forcing signal, aka temperature, is strongly random (white noise) here, whilst it is rather seasonal. Would the same results hold in a seasonal environment, where similar species can potentially compete over a longer time period (because the season can be long compared to the timeframe of plankton generation).

- What's the role of the built-in storage effect there? Are coexistence and a fluctuating environment necessarily linked, as suggested by Barabás et al. (2012) who equate it with temporal niche differentiation?

- *[something we haven't tackled yet but could be useful later on]* Are the patterns of species synchrony in this model (and in seasonal variants thereof) similar to what we see in the field?

We have therefore aimed at reproducing the model and produce new variants to test these questions and better understand phytoplankton-like communities, that live in fairly seasonal environments.

2 Model

2.1 Introducing the Scranton-Vasseur model

The competition model described in Scranton and Vasseur (2016) is based on a variant of the Lotka-Volterra competition model, with growth depending on the temperature τ (see eq. 1-4, all coefficients are defined in Tab. 1)

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

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

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

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

In this model, temperature is a white noise (surprisingly, perhaps):

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

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	$8.6173324.10^{-5}\text{eV.K}^{-1}$
$f_i(\tau)$	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

Table 1: Coefficients used in Scranton and Vasseur (2016) model for large communities

2.2 Reproducing previous results

Before changing the model, we wanted to check that we obtained the same results as in (Scranton and Vasseur, 2016)[1].

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[1]We had to change the thermal optimum range from 283-303K in the text of the paper to 288-298K in order to obtain the same figures and results
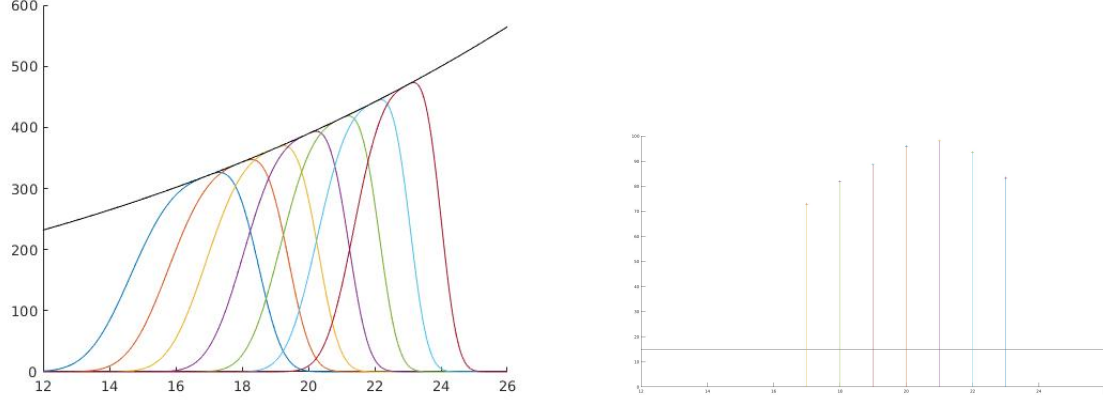
Figure 1: Thermal niches of seven species with thermal optima spaced regularly on the interval [17.5°C-22.5°C] (left) and long-term mean intrisic growth rates of species as a function of their thermal optima (right)

We can see the variability in growth rates according to thermal optima in a 7-species community on Fig. 1. Thermal niches are normalized so that all species have the same niche area.

2.2.1 Species dynamics

Species dynamics were explored in communities of 60 species. Their thermal optima are spaced regularly on the interval [15°C-25°C] and they are all initialized with density $\frac{1}{\alpha S}$. Dynamics are simulated for 5000 years with a daily updating of temperature conditions, i.e., the numerical integration is performed using time intervals lower than a day, but a day constitutes the baseline unit for recording the times series.

If the density of a species declines below 10^{-6}, the species is considered extinct.

In a first set of simulations, all species are subjected to the same temperature sequence (reflecting what is generally observed in the field). In a second set of simulations, the same temperature sequence is shuffled differently for every species in order to test for the effect of the environmental driver on species synchrony. We ran both simulations 20 times[2].

Scranton and Vasseur (2016) chose a species-specific synchrony index based on Pearson's correlation coefficient ρ, weighted by the standard deviation of each competitor j, σ_j.[3]. Synchrony is calculated for the last 200 years of dynamics with a moving window of 5 years.

$$\zeta_i = \sum_{j=1, j \neq 1}^{S} \alpha_{ij} \sigma_j \rho_{i,j}$$

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[2]In contrast with Scranton and Vasseur (2016) who performed 100 simulations for each case. We chose to lower this number as simulations are quite time consuming -still working on it, BTW

[3]F/ This will be very interesting to look at this simulated data -later on - using the measure of Keitt, Loreau and co. BTW [!make sure we output time series of the simulations!] C: For now, I'm just keeping the 500 last years, as SV did, and for memory reasons. Do we really need longer TS?
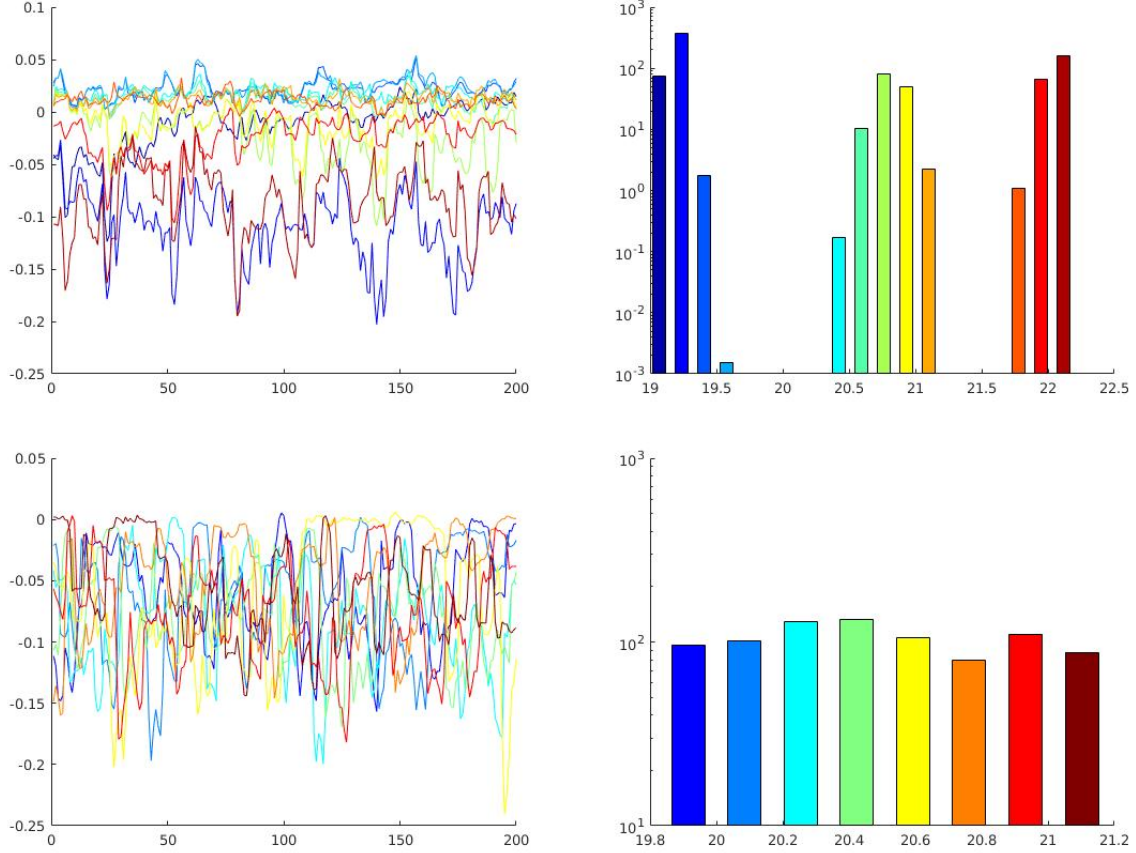
Figure 2: Synchrony of each species measured as the weighted correlations between species and its heterospecific competitors (left) and species density averaged over the last 200 years of dynamics, arranged on the x-axis by thermal optima. Temperature is the same for all species in the top-panel, temperatures are random in the bottom-panel. There were 60 species at the beginning of the simulation.

We can see the results for the two sets of simulations on Fig. 2. As described in the original paper, when the system is dominated by seasonal dynamics, species form three clumps within the [19-22]°C interval and show small or negative values of synchrony. When temperatures are different for every species, less species survive, with more homogeneous abundances and no patterns of synchrony.
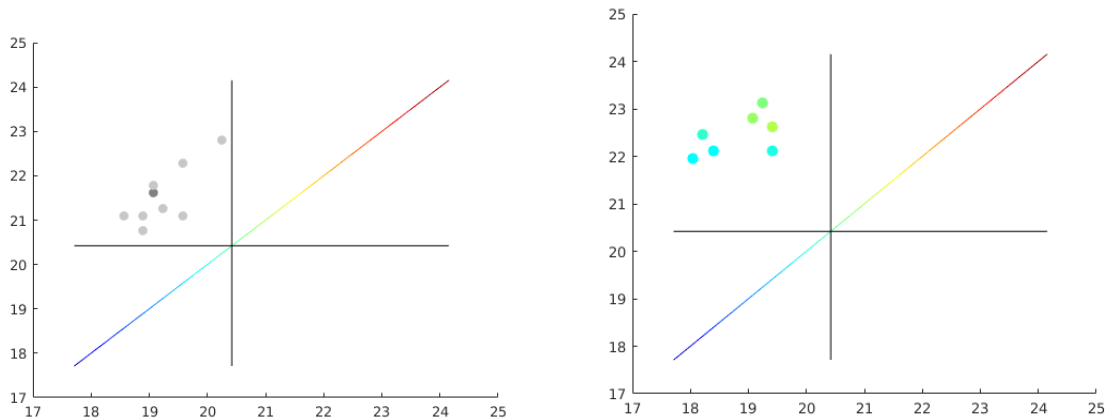
2.2.2 Community assembly

Figure 3: Species coexistence according to their thermal optimum for 2-species communities (left) and 3-species communities (right). Black lines indicate the thermal optimum of 20.42°C. On the left, the frequency of each pair is indicated by the intensity of the gray scale. On the right, the color corresponds to the thermal optimum of third species being present, while pairs correspond to extreme values of thermal optima.

To model community assembly, Scranton and Vasseur (2016) iniate a community with only one species chosen at random from the previous 60 species pool, set its density to $\frac{1}{2\alpha}$ and run the simulation for 10,000 years, during which the community is subjected to invasion events. The time between invasions is exponentially distributed with a mean of 20 years and for every invasion event, a species is chosen at random from the species pool to be introduced at its extinction threshold (10^{-6}). Authors repeated this simulation 2000 times[4].

Considering the time required for each simulation (see section 8.), we only launched 20 simulations and checked if we had qualitatively the same results, that is a majority of simulations with only 2 or 3 extant species laying on opposite sides of the most fit species' thermal optimum, around 20.42°C (Species 33). We also reduced the range of explored species to those whose thermal optima were within ±2K) of the previously observed thermal limits.

In the 20 communities we obtained, half of them had 2 species and 7 had 3 species; remaining communities had 4 species. We confirmed that species laid on opposites sides of the thermal optimum, with the third species, when present, being part of the clump which can also include the fittest species in the first simulation. .

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[4]C : Dicussing with Fred and Alix, it appears that we could test for possible persistence before the invasion. By using the maximum growth rates and competition competitions, we could first calculate the feasibility of an equilibrium, as done by Maynard et al. (2018) in their invasion process. [FB Note: feasibility is the consecrated term in ecology for a strictly positive equilibrium; mathematicians would speak of an interior equilibrium point (which may actually be better)]

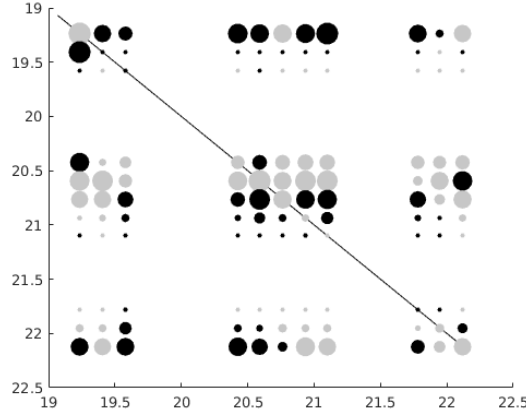### 2.2.3 Species removal and reintroduction

Figure 4: Effect of knocking out a species (on the y-axis) on the other species abundance (on the x-axis). The size of the circles is proportional to the absolute value of the difference between a simulation with a knocked-out species and a simulation without knocking out. Grey circle indicate negative difference (the abundance of the given species is higher when no knocking-out took place) while black circles indicate positive value (the knocking-out of ones species enable the other one to increase its abundance). The identity of the 11 species present at the beginning of the simulation is given by their thermal optima shown on the axes.

In this experiment, Scranton and Vasseur (2016) use a previous simulation of community dynamics to initialize their model and then knock out each species separately, then reintroduce it after 5000 years with a density of 10^{-5} (due to stochasticity, the same species is given 9 chances to invade the communitiy and observe the final abundances after 5000 more years.

We can see on Fig. 4 that our results are a bit different as the effect of a given clump is not restricted to its clump (effect of stochasticity?)

3 Implementing a seasonal variation of temperature

Description of the forcings We wanted to keep the same mean and variance of the forcing signal, and simply change the frequency content to include a seasonal component (low-frequency component). The underlying idea here is that the reaction of any dynamical/physical system forced by a signal depends on the energy content of the forcing (variance) so we'll do best to preserve the total variance of the forcing signal.

We propose the function[5][6]:

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

where $0 \leqslant \theta \leqslant \sqrt{2}$ indicates the relative proportion of variance due to the seasonal signal as opposed to white noise and σ_τ is the standard deviation of the white noise. When $\theta = 0$, we recover the original model (with all frequencies), whereas when $\theta = \sqrt{2}$, we have a seasonal-only signal (with only one frequency). It can be a way of measuring the impact of seasonality on the community dynamics[7].

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[5]We may also consider autocorrelated noise if the general shape of the power spectrum governs the results rather than the precise frequency content (just to keep this in mind)

[6]We could also consider using a real signal, such as the one with have in Arcachon

[7]Note this signal setup corresponds to a case where we want to compare the effect of the forcing in theoretical models. If we wanted to contrast, say, lab and field conditions we would change the energy content of the signal because the seasonal forcing in the field would increase the energy content.
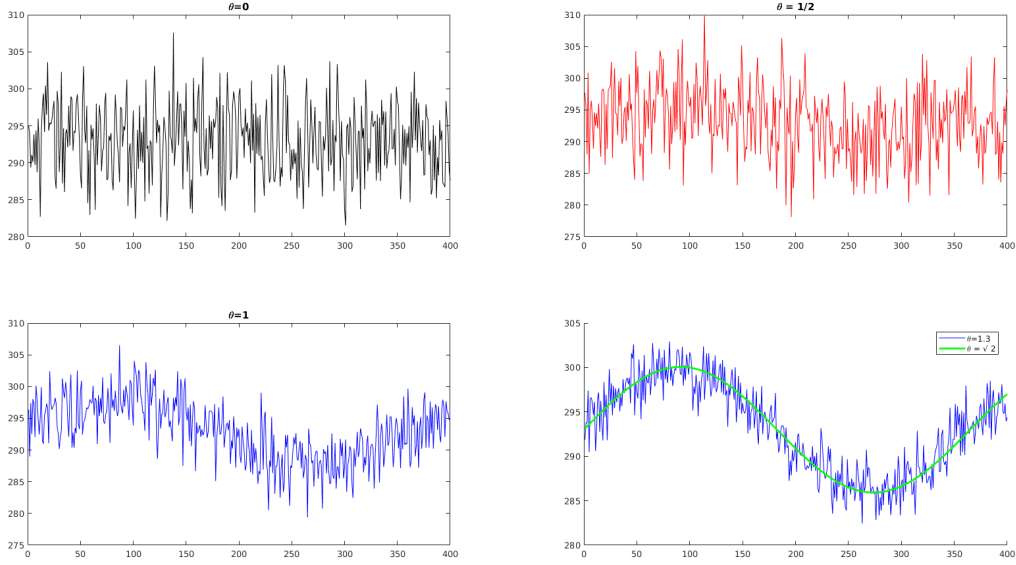
Figure 5: Comparison of temperatures with different values of θ

Simulation convergence First measures of stability can be taken from Sakavara et al. (2018) who use persistence, maximum biomass of each species and total biomass during a cycle as measures of convergence (but we should note that they have a deterministic model). A first visual check can therefore be useful. The coefficient of variation of the total biomass over one year can also be used (suggested by Fred).

The model run was first launched with $\theta = 1$ for 15000 years, which corresponds to three times the duration of the first simulation with noise-only forcing.Scranton and Vasseur (2016) seem to consider 5000 years as the necessary time to reach a stochastic process stable in distribution, but they don't justify it with convergence criteria, hence we topped up the time necessary due to long transients in most seasonal models (Vesipa and Ridolfi, 2017) [8]. A seasonal signal may also lead to a shorter burn-inthough - we will consider this later. However, with these parameters, we can see no clear sign of convergence on Fig. 6.
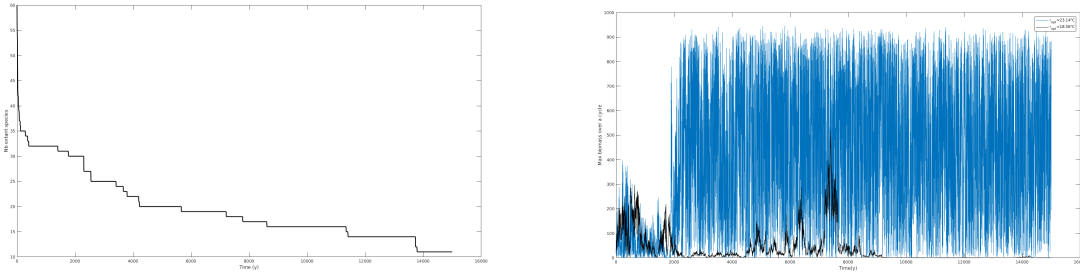

Figure 6: Number of extant species (left) and maximum biomass over a cycle for two species with extreme values of optimal temperature (right).

We also launched the same model with $\theta = \sqrt{2}$ to see if we could reach convergence when no noise can modify the dynamics. We can see on Fig. 7 that convergence is reached after 2000 time steps.

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[8]F: I think Alix will be able to add a REF on that later A: I would say Vesipa & Ridolfi 2017 in J. Theor. Biol. ("Impact of seasonal forcing on reactive ecological systems") which summerises cases of transient growth. C: This paper is only determinist, right?
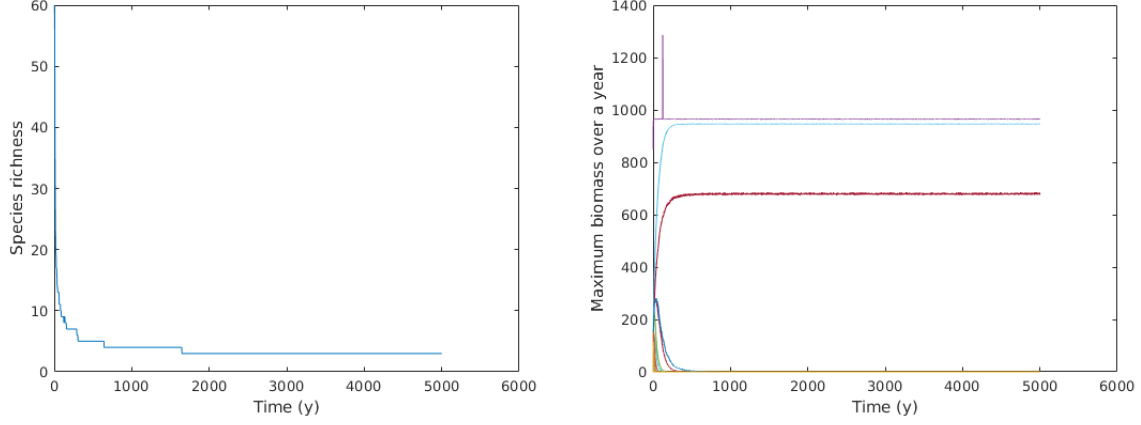
Figure 7: Number of extant species (left) and maximum biomass over a cycle, using a purely seasonal signal (right). Spikes in species dynamics can be found during the burn-in of the model run, such as the one shown in violet on the right-hand side of the panel.

In addition to these experiments, we launched a longer simulation for a model with $\theta = 0$ and realized the 5000 time steps used by Scranton and Vasseur (2016) might not be enough to be sure that we have reached a stable community (see species richness in Fig. 8). This duration might have been chosen as a trade-off between time for burn-in and computing time.
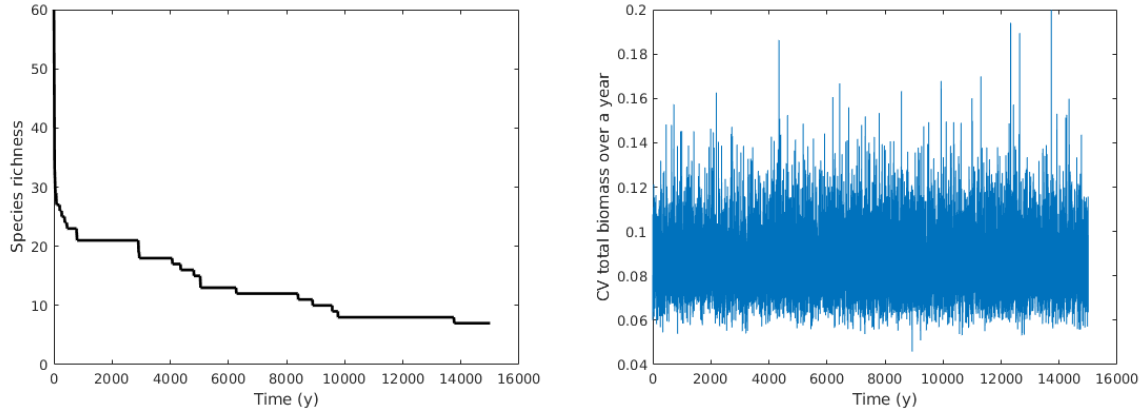

Figure 8: Number of extant species (left) and coefficient of variation of the whole biomass over a year (right), using a white noise as temperature input.
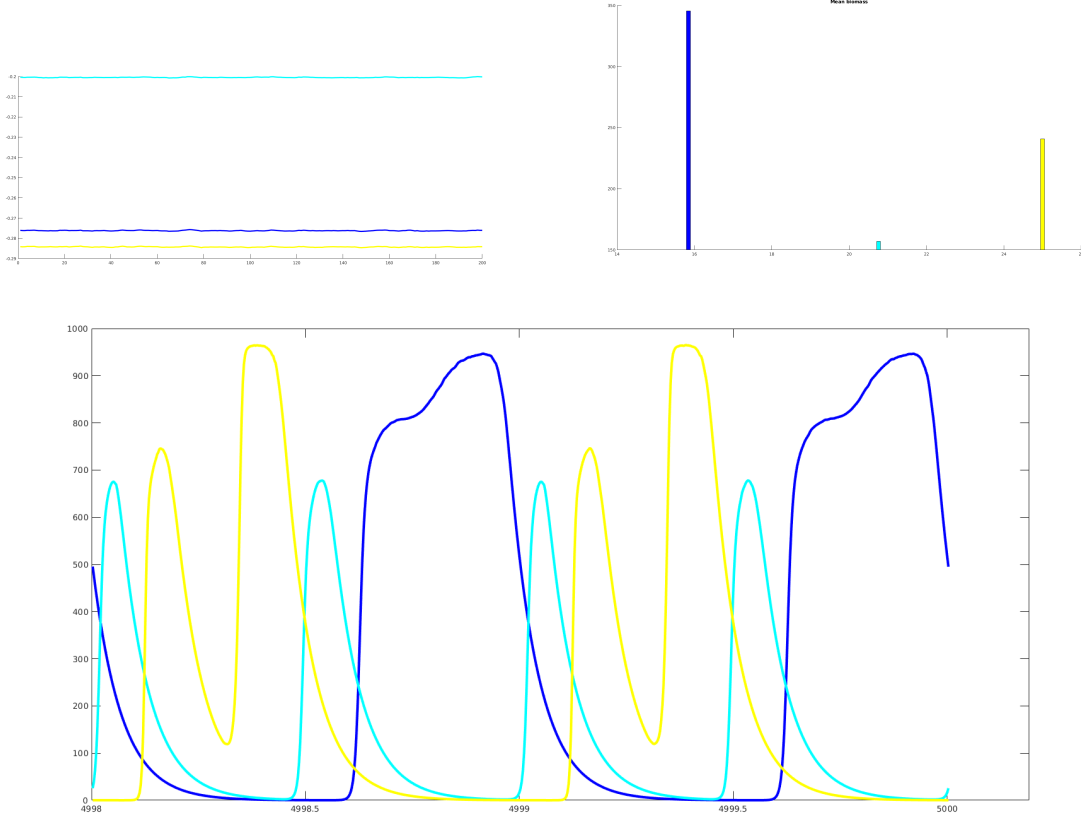
Figure 9: Synchrony of each species measured as the weighted correlations between species and its heterospecific competitors (left) and species density averaged over the last 200 years of dynamics, arranged on the x-axis by thermal optima. The dynamics of the three extant species for the last two years of simulation is shown at the bottom of the figure. Temperature is a purely seasonal signal. There were 60 species at the beginning of the simulation.

Dynamics of a model with a purely seasonal signal Using a purely seasonal temperature ($\theta = \sqrt{2}$), we can see that only three species survive at the end of the simulation, with extrema of optimal temperatures (15.8°C and 25.0°C, corresponding to indices 6 and 60 in the increasing range of optimal temperatures) and an average optima (20.8°C, corresponding to index 35). The average species has the lowest average biomass.

4   Discussion of the SV16 model and possible variants

A few words about the storage effect The concept of storage effect emerged in the 1980's (Chesson and Warner, 1981; Warner and Chesson, 1985; Chesson and Huntly, 1988) and is classically described as the temporal partioning of the niche, encouraging coexistence. It requires three main features: (1) species-specific responses to the environmental variability, (2) density-dependent covariance between environment and competition and (3) buffered population growth. If we define the instantaneous growth rate $\gamma_i(t) = \frac{1}{N_i(t)} \frac{dN_i(t)}{dt} = K_i(E_i(t), C_i(t))$where K_i is the kernel for species i, written as a function of E_i, a set of environment-dependent parameters for species i and $C_i, C_i(t) = c_i(E_j(t), N_j(t) \forall j)$[9], the competition experienced by species i, which is itself a function of populations and environment (Ellner et al., 2016). Conditions for coexistence in a fluctuating environment are then met when $\frac{\partial^2 \gamma}{\partial E \partial C} < 0$. Barabás et al. (2012)generalized this definition in the case of periodic environments. Shifting from analyzing the *possibility* of coexistence to its *likelihood*, they define the set of environmental conditions in which coexistence is possible as a volume whose form can change with species similarity (in the equilibrium theory, this volume shrinks with increasing similarity). They define a community matrix $a_{ij}(t) = \boldsymbol{S}_i(t)\boldsymbol{I}_j(t) = \frac{\partial r_i(t)}{\partial \boldsymbol{R}(t)} \frac{\partial \boldsymbol{R}(t)}{\partial n_j(t)} n_j(t)$

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[9]In Ellner et al. (2016), there is a subtlety between N_i and n_i (measure and state of the population of species i, respectively), which I am not considering here

where r_i is the growth rate of species i, a function of the lof of the population densities n_j and $\boldsymbol{R}$, a vector of environmental/regulating conditions depending the instantaneous values of the population densities. The first vector $\boldsymbol{S}_i(t)$ is the sensitivity niche vector, ie the sensitivity of the population to changes in the environment. Species similarity leads to a small sensitivity volume. The second vector $\boldsymbol{I}_j(t)$ is the impact niche vector, ie the impact of a change in population densities on the regulation factors, which can buffer the growth of the population. This factor is only implicit in Chesson's formalism. Provided the periodicity of the environment remains constant and the dynamics of the environment variables are fast compared to population dynamics, they confirm that the product of the volumes spanned by the temporal sensitivity and impact vectors is the proper measure for robustness. This formulation does not rely on the small-fluctuation approach, contrary to Chesson's formalism.

HERE, I'd like to add the different formulations of the LV model by Ellner and Barabas, comparing to ours.

We noticed that the formulation of LV according to Scranton and Vasseur (2016) implies a storage effect.

Indeed, it can also be written as :

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

This means that growth rates and strengths of competitive interactions covary positively. This assumption is usual in recent works using Lotka-Volterra competitive models in seasonal environments; it can be found under different forms in Barabás et al. (2012) and Kremer and Klausmeier (2017).

The SV16 model actually contrasts with the derivation of competition in a chemostat, given in Appendix A of Scranton and Vasseur (2016). Assuming a single shared resource in chemostat framework, and a fast resource dynamics so that an quasi-steady-state approximation is possible, the consumer community dynamics can be written as:

$$\frac{dN_i}{dt} = a_iR_{in}N_i - DN_i - \sum_{j=1}^{S} c_jN_iN_j$$

or

$$\frac{dN_i}{dt} = N_i(a_iR_{in} - D - \sum_{j=1}^{S} c_jN_j)$$

where a_iR_{in} is the per capita rate of consumption related to the resource inflow R_{in} (this is under the assumption of a linear functional response of consumers), D is the dilution rate of the chemostat, and c_j is a multiplicative coefficient for the losses of resources due to species j consumption.

If we extend this case to a fluctuating resource supply R_{in} (assuming a separation of timescales between nutrient and consumer dynamics), the quantity that would be seasonally varying is $R_{in}(\tau)$:

$$\frac{dN_i}{dt} = a_iR_{in}(\tau)N_i - DN_i - \sum_{j=1}^{S} c_jN_iN_j$$

In this case, competition and growth do not covary. Such a model is built on the hypothesis that changes in effective competition only depend on species densities which respond to the temporal forcing embedded in the intrinsic growth rates. This also seems to be the case in Sakavara et al. (2018) who considered only seasonal forcing in resources' abundances (at least, growth rates and resources do not covary explicitly). However, Sakavara et al. (2018) consider a mechanistic model of competition with two resources shared by many consumers so any comparison is for now tentative. Indeed, they explicit the dynamics of resources which only the growth rates embed some seasonal variability.

We should therefore check if the persistence and dynamics of the species are affected by the deletion of an explicit storage effect in the LV model. We want to check if we still observe clumps and a few remaining species when the temporal partitioning of the niche, due to the storage effect, is removed from the model.

'Naive' simulations   The most straightforward way of removing the forcing on growth rates is to use exactly the same model and set of parameters as LV, re-writing eq. 1 as

$$\frac{dN_i}{dt} = N_i \left(r_i(\tau) - \sum_{j=1}^{S} \alpha N_j \right) - mN_i \tag{6}$$

We launched 10 simulations. All of them ended with only one species, whose index felt between 32 and 35 with 50% of them being the 33rd species (with thermal optima being 20.42°C, which corresponds to the highest growth rate observed in (Scranton and Vasseur, 2016) and in our simulations (Fig. 10).

We then weigthed the competion coefficients to follow eq. 7

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

where $\bar{r}_i(\tau)$ is the mean value of growth rate over the simulation. In this case, a species is more sensitive to competition when it has a higher growth rate, but we keep the same coefficients within and between groups.
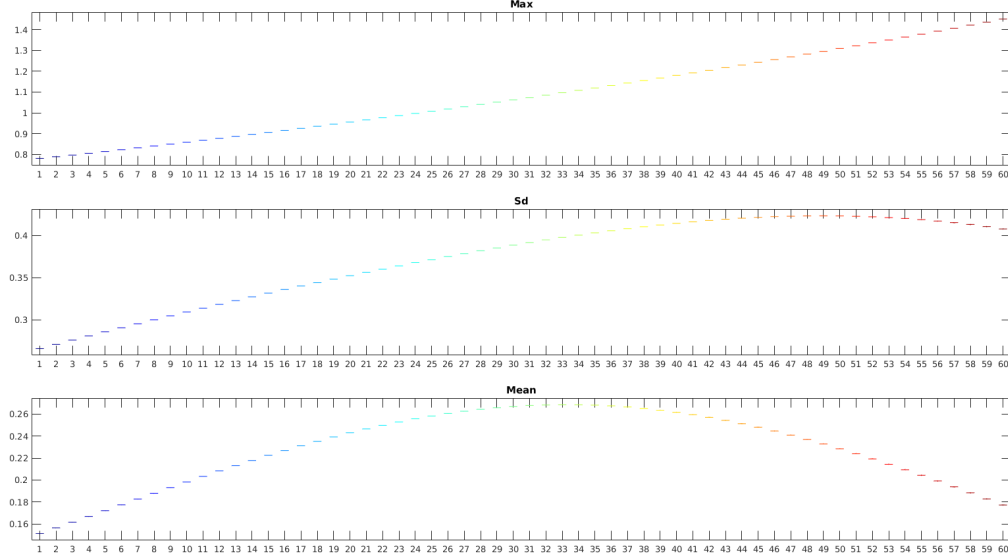

Figure 10: Boxplots of growth rate maximum values, standard deviation and mean value over 10 different simulations for 60 species in the standard SV model. Boxplots are seen as simple lines in the plot because values are similar for a given species .

5   Effect of competitive interactions

When growth rates do no affect the values of competition coefficients , we can consider different parameterization of the competition coefficients:

1. competition strengths are based on the niche model (Ashby et al. (2017)). The general formulation of the strength of competition exerted by species j on species i is $\alpha_{ij} = \frac{\int U_i(\mathbf{z}) U_j(\mathbf{z}) d\mathbf{z}}{\int U_i(\mathbf{z})^2 d\mathbf{z}}$ where $U_i(\mathbf{z})$ is the resource utilization function of the (potentially multidimensional) resource $\mathbf{z}$ for species i. A first step would be to use $U_i(\mathbf{z}) = r_i(\tau)$.

2. competition strengths are fixed, as in SV16, but with a difference between inter and intra-species competition [10]. In this case, $\alpha_{ii} = \rho \alpha_{ij}$ with $|\rho| > 1$ A first step would be to use $\rho = 10$ or $\rho = 4$ and $\forall i, \forall j, i \neq j, \alpha_{ij} = \alpha = 0.001$. The two values of $|\rho|$ are taken from estimated values in Barraquand et al. (2017), taking all coefficients into account or only the ones significantly different from 0, respectively.

3. competition strengths are chosen as $\alpha_{ij} \sim N(\frac{1}{\rho}\alpha_{ii}, \sigma_\alpha)$, with $\sigma_\alpha = \alpha \bar{\sigma}_r$ where $\bar{\sigma}_r$ is the median value of the standard deviation of $r_i(\tau)$ over all species i. We see on Fig. 10 that standard deviation varies with the species. The median value is 0.39 ($\sigma_\alpha = 0.0039$). We can keep $\rho = 10$ [11] and $\forall i, \alpha_{ii} = \rho \alpha = 0.01$.

We first considered the second case, where intra-group coefficients of interactions are ten-fold higher than inter-group coefficients. We used these values directly in the first model (ie., growth rates do affect competition coefficients). Fig. 11 is representative of the 10 simulations we launched. The coefficient of variation of the total biomass over a

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[10]We have to elaborate on the fact that models such as SV or Barabas, which do not differentiate coefficient values for the two types of interactions, are less likely to be stable than the ones with higher intra-species competition.

[11]Or $\rho = 4$?

year remains around 0.5 and the total number of extant species is the same at the beginning and at the end of the simulations.
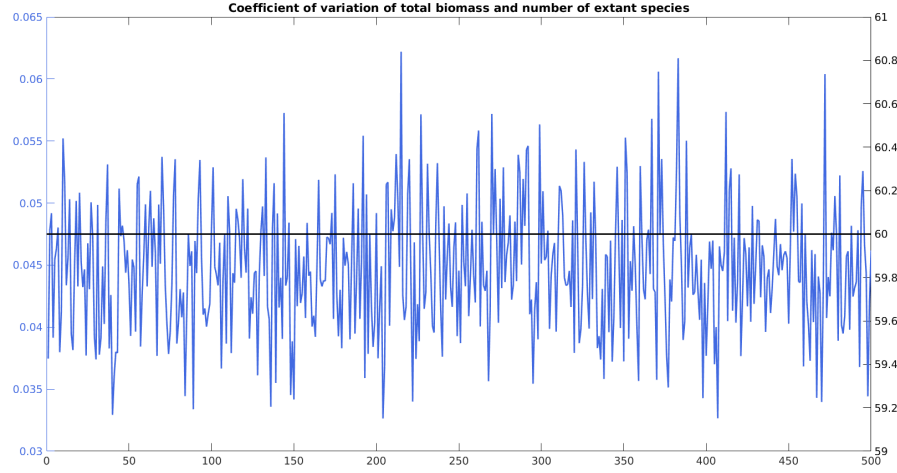

Figure 11: Convergence criteria for a simulation where intra-group coefficients are 10-fold higher than inter-group coefficients

We can see on Fig. 12 that species tend to synchronize according to their thermal optima, with absolute values remaining low when compared with previous simulations with the same interaction coefficients. Results are similar for all simulations: synchrony values remain between -0.01 and 0.01 and mean biomass does not exceed 10 for any species, but does not fall below 2. The most striking features of these simulations is the persistence of all species, with lower average biomass and no clumps formed. It seems that increasing the competition within groups lead to a more even and diverse community.
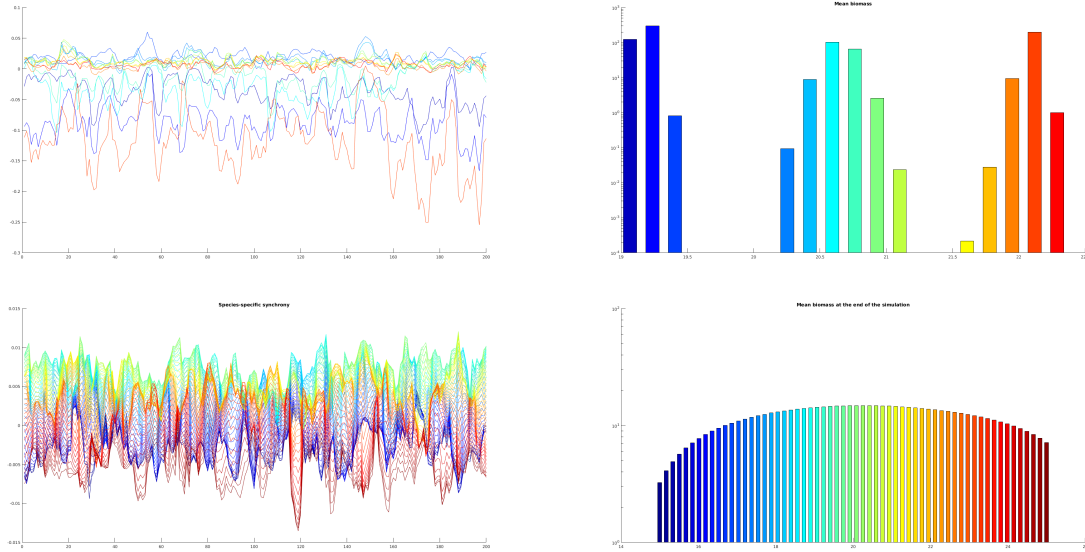

Figure 12: Synchrony of each species measured as the weighted correlations between species and its heterospecific competitors (left) and species density averaged over the last 200 years of dynamics (right), arranged on the x-axis by thermal optima. Intra-group competition strength is 10 times higher than inter-group competition strength at the bottom whereas all interaction strenghts are the same at the top. Both simulations at the top and bottom share the same environmental forcing.

6 Simulation plan

We therefore have 4 limit cases: with and without storage effect, and with a purely seasonal or purely noisy signal.

Type of environmental signal	Forced GR and Forced Competition	Forced GR
White noise (all frequency components)	Scranton and Vasseur (2016) [OK]	LV with random growth rates
Seasonal signal (one low-frequency component)	Barabás et al. (2012) [OK]	Classic seasonal competitive LV

Table 2: Preliminary simulation setup (limit cases) [we'll add mixtures later, Alix and I have refs to add on the classic seasonal LV I think, we'll need to dig this up]

Results found so far are summarized in the following rank abundance curves (RAC).
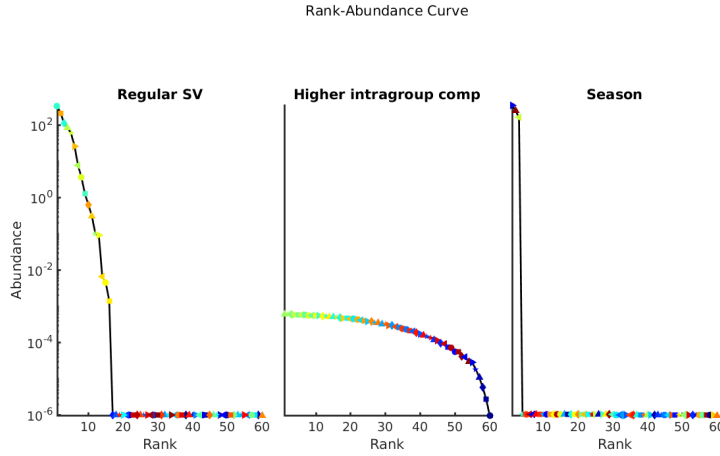

Figure 13: Rank abundance curves for a given environmental forcing and different coefficients of interactions (left), or a seasonal signal only (right). Marker colors correspond to each species' thermal optimum.

For future work: the number of species could be increased to make the proportion of extant species more relevant. In this case, if we don't want to increase the niche overlap, and therefore the competition, we should decrease A, the niche breadth. This would mean that we have more specialist species. We could also allow species to have different A so as to consider communities with various distributions of niche breadths and see the effect on persistence.

7 Ecological remarks

8 Notes on the algorithm

The model is integrated with ode45 in Matlab, a Runge-Kuntta 4th/5th order algorithm[12] One of the first issues we encountered was the time needed for each simulation. With usual algorithm settings (absolute tolerance set 10^{-9} and relative tolerance, to 10^{-8}), imposing no negative value for species abundance[13], a regular simulation as described in Sec. 2.2.1 takes about 35 minutes to run. Even increasing the tolerance levels to absolute tolerance

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[12] We should acknowledge the fact that we're trying to keep the same algorithm -and programming language- for all experiments with the model but Scranton and Vasseur (2016) use a multistep algorithm in Python/Fortran for 'regular' species dynamics, also called species sorting, a Runge-Kutta method in Fortran for community assembly and only mention Python for species removal - probably the multistep algorithm mentioned previously.

[13] This option is costly (the simulation is about 35% longer) but necessary, steps can still be too large and lead to high negative abundances

10^{-8} and relative tolerance to 10^{-3}only reduces the computation time to about 20 minutes (and final results can differ by about 10% in abundance).

When timing the code, the program shows

Function	Total time	Self time	%Time
Main	2823	309	11%
ode45	2370	494	17%
NonNegative option	1793	563	20%
ode integration (actual function to integrate)	1230	1230	43%
b computation	141	1	0.03%
Growth rate computation (also used for b)	137	137	5%
ntrp45 (ode45 related)	82	82	3%

Table 3: Time spent in the most important functions of the code. We used comm assembly to check if the interruption in the integration was time consuming.

In the ode integration function, 50% of the time is required only to load growth data ; 14% for the competition computation and 12% for the final computation : growth + competition. Initializing temperature and maximum growth rates in the main program is therefore time expensive but I don't really see how to do it differently if we want to save stochastic temperatures ; and I'm not sure computing maxium possible growth rates for each time step would be more effective. Should be tried, though[14].

We could also save b computation for once and load it, but this means we decide once and for all which species we use (and reduce the range considered by S&V, and/or increase the precision in the right range to increase the total number of species).

Scranton and Vasseur (2016) use 5000 time steps as the necessary time for the model to stabilize. However, we can expect the model to stabilize more quickly with seasonality (this will be a necessary check before lauching simulations).

In addition to the time cost, species invasion or removal requires the introduction of discontinuities in the dynamics of the community. This can be done in 3 ways using Matlab: using the event function (but events do not depend on the dynamics of the community, so are not really appropriate for this), integrating on segments of the total time span, stopping for every species addition or deletion (our choice, until now), or introducing the species for a given time without stopping the simulation (which would require the model to test each time step and compare it to the invasion or removal time sequence set in the main program: this is too expensive for what we want).

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[14]Tried: time spent on SV16 integration was 50% higher. My first implementation was the best one so far.

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