

A great title

March 21, 2020

Introduction

The high biodiversity of plant communities is still an unresolved question for both experimental and theoretical ecologists. Both terrestrial plants and phytoplanktonic communities can present hundreds of species which seem to consume the same resources. Earlier theoreticians have proposed that environmental fluctuations only [ref] could sustain coexistence but further research showed that this could not explain the order of magnitude of species richness [ref]. Other mechanisms such as niche differentiation [ref], demography [ref] and life history traits [ref] have completed environmental variation and stochasticity as other explanations.

Analyses of coexistence in terrestrial plant communities often take into account several life stages [refs]. Considering at least two stages, seeds/juveniles and adults, different models have uncovered mechanisms that might explain long-term coexistence. Examples of such mechanisms are the bet-hedging strategy, the storage effect and the Janzen-Connell effect. Bet-hedging is a long-term strategy relying on the creation of seeds which can remain dormant for a long period of time (over a year, often much longer). Dormant seeds can tolerate harsher years during which adults cannot maintain, but they also reduce part of the population that could germinate from one year to another (in case of an annual plant). The storage effect has first been defined by the presence of a long-lived life stage and temporal variation in recruitment from this long-lived life stage that helps escape interspecific competition (Chesson, 1986; Cáceres, 1997). This has been later generalized as a negative correlation between the effect of the environment and the effect of competition (Ellner *et al.*, 2016). In good environmental conditions, competition from other individuals is stronger as seeds might germinate at the same time. Finally, models and experiments suggest that adults can have a negative effect on seed survival, through the Janzen-Connell effect (Comita *et al.*, 2014). Therefore, neglecting explicit modeling of this life stage can modify the understanding we have of the dynamics of the populations (Nguyen *et al.*, 2019).

Even though different coexistence mechanisms have been unveiled through the use of several life stages and a focus on the youngest stage (seeds) for terrestrial plants, aquatic plants, and more specifically phytoplanktonic algae, have not been modeled with the same precision. Although ecologists have proposed for a long time that the blooms may initiate after the resuspension and germination of seeds (Patrick, 1948; Marcus & Boero, 1998), it is unusual to see an explicit model of such process. The classical view behind phytoplankton dynamics is that bloom formation is mostly seasonal, due to the variation in light and temperature, assuming that there are always enough cells in the environment to duplicate. However, a recent review suggests that there might be more complexity behind phytoplanktonic seeds/cysts (Ellegaard & Ribeiro, 2018).

Phytoplankton communities in coastal environments may benefit from seed banks even more than the oceanic communities [REF-find back], as the distance to the bottom is lower. Similarly to the seed bank approach, Smayda (2002) has proposed the term “pelagic seed bank” to characterize the contribution of the ocean to coastal communities. This has been noticed for dinoflagellate especially [[ref Dinophysis, check what we have on diatoms]]. We can

wonder, however, to which extent the seed banks can contribute to the biodiversity in the ocean, especially in the long term. Indeed, spores are able to germinate again after tens of years (McQuoid *et al.*, 2002; Ellegaard & Ribeiro, 2018) or even thousands of years (Sanyal *et al.*, 2018) of dormancy, which can play a huge role on biodiversity in both oceanic and coastal environments.

Here we build on the work by Shoemaker & Melbourne (2016); Wisnoski *et al.* (2019), and previous findings in Picoche & Barraquand (2019, 2020), to examine the effect on coexistence and feedbacks from the different compartments (ocean, coastal water column and bottom).

Methods

Model

The model developed by Shoemaker & Melbourne (2016) and Wisnoski *et al.* (2019) builds on a two-step discrete-time model. Parameters and state variables are defined in Table 1. First, coastal and oceanic cell numbers increase following Beverton-Holt (BH) dynamics (eq. 1). The BH formulation is classical for discrete-time models of terrestrial plants and includes both a species- and temperature-specific maximum achievable growth rates $r_i(T)$ and its modification by positive and negative interactions α_{ij} . During the same first step, the abundance of cells present at the bottom of the water column in coastal areas (hereafter called cysts) decreases with cyst mortality (m) and burial resulting from sedimentation (ζ).

$$\begin{cases} N_{t+h,i,c/o} &= \frac{e^{r_i(T)} N_{t,i,c/o}}{1 + \sum_j \alpha_{ij,c/o} N_{t,j,c/o}} - l N_{t,i,c/o} \\ N_{t+h,i,b} &= N_{t,i,b} (1 - m - \zeta) \end{cases} \quad (1)$$

Second, exchanges take place between the three compartments (eq. 2).

$$\begin{cases} N_{t+1,i,c} &= N_{t+h,i,c} (1 - s_i - e) + \gamma N_{t+h,i,b} + e N_{t+h,i,o} \\ N_{t+1,i,o} &= N_{t+h,i,o} (1 - s_i - e) + e N_{t+h,i,c} \\ N_{t+1,i,b} &= N_{t+h,i,b} (1 - \gamma) + s_i N_{t+h,i,c} \end{cases} \quad (2)$$

Param	Name	Value (unit)
$N_{t,i,c/o/b}$	Abundances of species i at time t in the coast (c) or ocean (o) water column, or in the benthos (b)	NA (Number of cells)
T	temperature	NA (K)
$r_i(T)$	growth rate of species i	NA
b_i	Normalization constant for the thermal decay rate	(K^3)
τ_0	Reference temperature	293 (K) / 20 ($^{\circ}C$) (Scranton & Vasseur, 2016)
$a_r(\tau_0)$	Growth rate at reference temperature	386 ($\frac{kg}{kg \times year}$) (Scranton & Vasseur, 2016)
E_r	Activation energy	0.467 (eV) (Scranton & Vasseur, 2016)
k	Boltzmann's constant	8.6173324.10 $^{-5}$ (eV.K $^{-1}$) (Scranton & Vasseur, 2016)
A_i	Niche area	15 [arbitrary], maybe species-dependent
l	loss of vegetative phytoplankton (predation, mortality...)	0.04 (Scranton & Vasseur, 2016)
$f_i(T)$	Fraction of the maximum rate achieved for the i^{th} species	(NA)
T_{min}	Minimum thermal optimum	0
T_{max}	Maximum thermal optimum	30 (approximate of the range in Edwards <i>et al.</i> (2016))
T_i^{opt}	Optimal temperature for species i	Adapted from Picoche & Barraquand (2020)
$\alpha_{ij,c/o}$	interaction strength of species j on i	Adapted from Picoche & Barraquand (2020)
k_{co}	conversion coefficient from coastal to oceanic interactions	1.5 [arbitrary]
m	cyst mortality	$\approx 10^{-4}/10^{-5}$ (McQuoid <i>et al.</i> , 2002)
ζ	cyst burial	{0.01 ; 0.1 ; 0.3} [arbitrary]
s_i	sinking rate of species i in a coastal environment	{0.1; 0.3; 0.5} β (0.55, 1.25) (Passow, 1991)
e	exchange rate between ocean and coast	{0.4 ; 0.6 ; 1} (Ascione Kenov <i>et al.</i> , 2015)
γ	germination + resuspension rate of species	{0.1; 0.01; 0.001} * {10 $^{-5}$; 0.1} [arbitrary]
g	gain in growth rate	0.2 [this study, based on Edwards <i>et al.</i> (2016)]

Table 1: Definition of variable states and parameters. Fixed values or distributions are from the literature. When a set or a range of values is given, the sensitivity of the model related to changes in parameters has been assessed.

More precisely, in eq. 1, the coefficients α_{ij} , i.e. the strength of the effect of species j on species i for all i and j , are inferred from a previous work on real data with a Multivariate AutoRegressive (MAR) model (Picoche & Barraquand, 2020). The shift from MAR to BH- matrices of interactions is described in SI. The change in growth rate $r_i(T)$ is based on the formula by Scranton & Vasseur (2016) (eq. 3).

$$\begin{aligned}
r_i(T) &= a_r(\tau_0) e^{E_r \frac{(T-\tau_0)}{kT\tau_0}} f_i(T) + g \\
\text{where } f_i(T) &= \begin{cases} e^{-|T-T_i^{opt}|^3/b_i}, & T \leq T_i^{opt} \\ e^{-5|T-T_i^{opt}|^3/b_i}, & T > T_i^{opt} \end{cases} \\
\text{and } b_i &\text{ is defined by numerically solving } \int r_i(\tau) d\tau = A_i
\end{aligned} \tag{3}$$

Two modifications were made on the formula by Scranton & Vasseur (2016). Species roughly divide between generalists and specialists, with more or less tolerance to variations in the temperature. Generalists have a larger niche width than specialists, which can be roughly translated by a larger A_i ¹. Field-based estimation of the niche area A_i is described below. However, apart from a radical and unrealistic change in A_i value, the resulting growth rate decreases very rapidly with the distance from T_i^{opt} , leading to values close to 0 for temperatures in which phytoplankton can normally grow. The meta-analysis by Edwards *et al.* (2016) allows to correct the growth rate for temperature outside the range, at least qualitatively, with a gain g in the final growth rate (see a comparison of the original and final versions of the growth rates in SI, Fig. S4).

Finally, the temperature at each time step is a repetition of the temperatures observed over 20 yers in our example dataset.

Each compartment (ocean, coast, seed bank) contains 10^3 cells at the beginning of the simulation, which is run for 10000 time steps.

Parameterisation

Data set example

Blabla on REPHY, Auger in Marennes Oléron, Fig of exact position in SI

Parameter values

Phenology In eq. 4, the growth rate is mainly defined by two parameters: the thermal optimum T_i^{opt} and the niche area A_i , which drive the phenology of the genus. Each year, the dynamics of these organisms is characterized by a blooming period and a lower concentration during the rest of the year. The bloom can be triggered by a combination of nutrient and light input, as well as a sufficient temperature. All parameters being more or less dependent on seasonality, it is reasonable to restrain this study to the effect of temperature.

We base estimates of T_{opt}^i and A_i on field observations. For each genus and each year, the beginning of the bloom is defined by the date at which the abundance exceed the median abundance over the year. The optimal temperature is the temperature at this date. The duration of the bloom is the number of days between the beginning and the date where abundance fall below the median value. Generalists are characterized by one long bloom in the year or

¹I should actually check how height and width vary with A_i , this is an area, not a width. Maybe I should actually change b_i and not care about A_i

several blooms (over 4²) corresponding to various temperatures. Specialists tend to appear only once or twice in the year and to favour lower temperatures. A genus is therefore defined as a generalist if it meets to two criteria.

- a bloom lasts over 100 days in at least 10 years out of the 20 covered by the time series
- the standard deviation of the temperatures at the beginning of the blooms is over the median of the standard deviation of all genera.

With these values in mind, we can define two range of values for the niche width (5-10 for specialists, 12-17 for the generalists and then order the species in these ranges, $sd(mean_y(T_{i,y})) > sd(mean_y(T_{j,y})) \Rightarrow A_i > A_j$.

The thermal optimum T_i^{opt} is defined as the mean minimum value of the temperature at the beginning bloom over 20 years.

Exchange rate The exchanges between the ocean and the coast depend on the shape and location of the estuary. In Marennes-Oléron and more specifically in Auger, the renewal time is very short, between 1 and 2.5 days (Ascione Kenov *et al.*, 2015), which corresponds to a daily rate of [40-100] %.

Cyst mortality and burial Cyst loss is a composite of cyst mortality and inaccessibility. McQuoid *et al.* (2002) provide species-specific values of mean and maximum depths at which cysts can still germinate. Corresponding mortality values range between 10^{-5} and 10^{-4} (more details on the approximation of mortality rate are given SI). However, cyst burial³ might be a prevailing phenomenon in driving phytoplanktonic dynamics. Once cysts have been buried, they are not accessible for resuspension even if they could germinate. Burial depends on the hydrodynamics of the site, but also on biotic processes (i.e., bioturbation) and anthropogenic disturbances such as fishing or leisure activities (e.g., jet skiing). This parameter thus heavily dependent on the environmental context we wish to describe.

Sinking rate Phytoplanktonic particles have a higher density than water and are not able to prevent sinking (although see [ref on Reynolds to show that actually, even diatoms seem to control this]). The sinking rate of vegetative cells depends mostly on their size and shape, which can be affected by their capacity to form colonies. Sinking is also affected by hydrodynamics: more turbulence and eddies can retain the cells at the top of the water column while laboratory conditions in still water specifically measure parameters that affect particle settling. In field conditions (Gotland Basin in central Baltic Sea), Passow (1991) measured a large variability in sinking rates, even within the same genus (e.g., between 1 and 30% for *Chaetoceros* spp.). However, a pattern could be distinguished, with a small number of genera that sanked more than the rest of the community. The mean rate for *Chaetoceros* and *Thalassiosira* was around 10% while it was around 1% for the other species. Sinking rate values around 10% are consistent with the loss rate values in Kowe *et al.* (1998) in a river and Wiedmann *et al.* (2016) in an estuary (mouth of Adventfjorden).

An arbitrary beta distribution was selected, with mean value close to the one observed in both papers (between 9 and 10), and a maximum around 30%, that is $s \sim \beta(0.55, 1.25) * 0.3$.

However, it should be noted that the sinking rate measured in these two articles represent the sinking of all cells. In our model, it should represent the exchange of live cells between the coast and the seed bank, or a loss of cells in the ocean. Our sinking rate might therefore need to be decreased to avoid modeling dead cells already taken into account in the loss term.

²CHECK THAT

³Find a better way to call it than burial

Germination/resuspension Germination and resuspension might be difficult to differentiate as they are finally gathered in only one parameter ($\gamma = \text{resuspension} * \text{germination}$).

The germination process has been studied a lot. From McQuoid *et al.* (2002), we can only assume that there is a temperature threshold for germination. The existence of a thermal threshold is confirmed by the review by Agrawal (2009). Eilertsen *et al.* (1995) also present an effect of photoperiodicity but this can be mingled with seasonal variation in temperature. In this model, germination is triggered by temperatures going above 15°C. As rates are not easily deduced from the literature, arbitrary values are fixed (1%, 0.1%, 0.01%) and the effect of their variation on the simulations is assessed. Germination can be 1%, 0.1%, 0.01%.

Resuspension values are seldom devoted to phytoplanktonic cells, but models for other particles such as sediments can be used. Rates vary from one publication to another: in Fransz & Verhagen (1985) in a coastal area, resuspension rate of sediments is evaluated around $5.10^{-5} \text{ day}^{-1}$ in winter and decreases in summer, with a link between resuspension/sinking and light extinction coefficient. In Kowe *et al.* (1998), the resuspension rate of diatoms is evaluated around $1.9.10^{-5} \text{ day}^{-1}$. In Le Pape *et al.* (1999), resuspension rate of sediments and dead diatoms is 0.002 day^{-1} . In this paper, we explore values between 10^{-5} (stratified water column) to 0.1 (highly mixed environment).

Mortality Mortality value is defined according to Scranton & Vasseur (2016). It could however be turned into a delayed, density-dependent mortality to take into account phenomena such as predation (simplest form: $m_i N_{t-\tau, i, o/c}$ where τ is the necessary lag between phytoplanktonic growth and predator response [look for ref, Reynolds not helpful here]).

Finally, it should be noted that cyst burial, sinking rate and resuspension are all dependent on the hydrodynamics of the place and are therefore, at least in biological terms, not identifiable.

Parameter calibration

Maynard *et al.* (2019) recently applied quadratic programming (Bazaraa *et al.*, 2013) to ecological data, which improved the calibration of certain parameters and led to more realistic simulations. Even though we could directly use the values obtained in the literature and in previous studies (Picoche & Barraquand, 2020), the switch from a fifteen-day MAR model to a daily BH-model and the high uncertainty for all parameters due to the use of proxies, values in the literature and high variability in phytoplanktonic genera on their own, are motivations to calibrate the model more precisely. Following the example of Maynard *et al.* (2019) with the package `limSolve` in R [ref, version], we intend⁴ to apply quadratic programming to our interaction matrices. Contrary to them, we do not broaden the calibration process to growth rates as these are not fixed values in a linear model⁵.

Sensitivity analysis As mentioned above, several parameters are highly variable and the effect of a change in parameter values need to be evaluated. The sinking, resuspension/germination and burial rates are the parameters to evaluate. The range of probable values for each parameter, and more specifically the set of values to be tested, is given in Table 1. The main diagnostics are the final mean abundance, amplitude and timing of the bloom (peak in abundance) for each genus.

For each combination of values, the diagnostics are performed on the last year of the simulation and the variability of these diagnostics with respect to each parameter is determined, as well as the best fit to real data.

Scenarios

Maintenance of biodiversity by exchanges between compartments can be gauged with two main scenarios.

⁴I use this term because I am really not sure this is what we want to keep. I need to know how this method can be applied to cycles.

⁵However, it just occurred to me that, using a mean temperature, we may be able to retrieve b_i

1. removing such seed bank (by setting seed mortality/burial to 1)
2. changing the exchanges between the coast and the ocean ($e=0$)

Final richness and average abundance/biomass productivity (to link with ecosystem functions) can be diagnostics. We can make 2 a-priori hypotheses. First, removing the seed bank would increase the sensitivity to competition, i.e. decrease the maximum sustainable interspecific competition strength, and decrease the resilience of the community confronted to changes in the environment. (Fig. 1).⁶

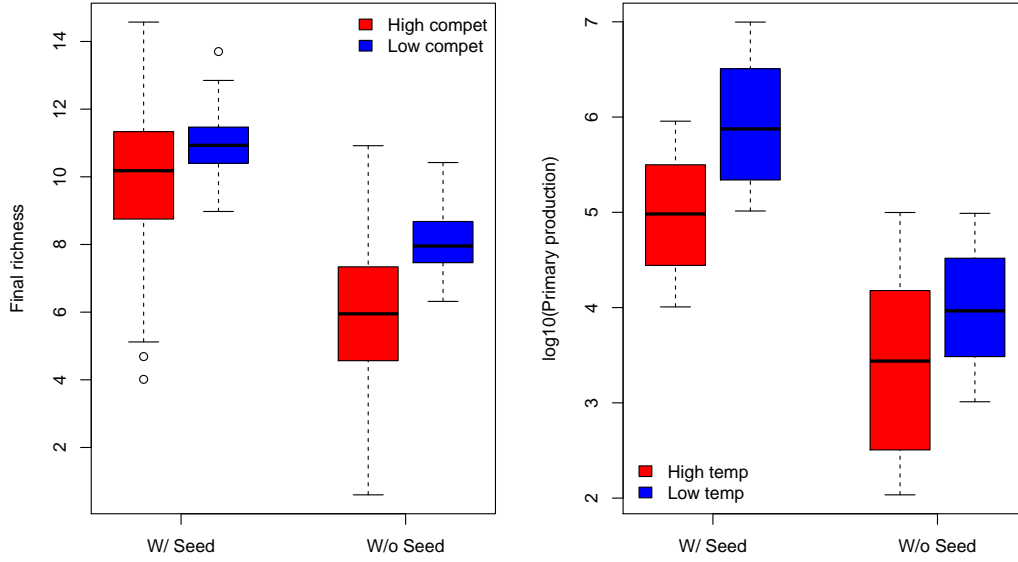


Figure 1: Expected changes in tolerance (stable richness) to interspecific competition and increase in temperature with and without seed banks

Second, reducing the exchange with the ocean might end up depleting the ocean biomass and richness as it loses species by sinking but cannot regain them thanks to coastal production. Fig. 2 gives a more precise view of the possible interactions of seed mortality and exchange between the coast and the ocean.

⁶Note on the variability

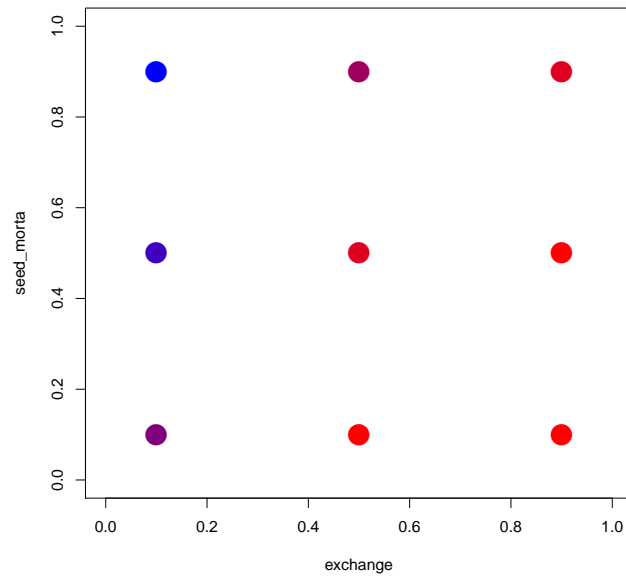


Figure 2: Expected changes in community richness in the ocean for different values of seed mortality/burial (=access to the seed compartment) and exchange with the ocean. Point color indicates richness, from low (blue) to high (red).

Discussion

Supplementary Information

Sinking rate distribution

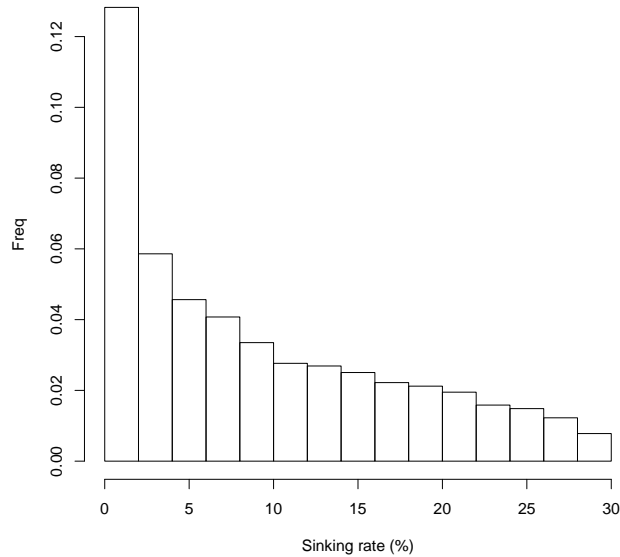


Figure 3: Possible distribution of sinking rates

Growth rate

Phytoplanktonic growth rates are highly variable, in situ or in experimental conditions. As an example of such variability appears in Balzano *et al.* (2011). For ten strains of one genus only (*Skeletonema*), and in the same experimental conditions, Balzano *et al.* (2011) have been able to detect growth rates between 0.5 and 1.25 day^{-1} , which corresponds more generally to the values found in the literature (between 0.2 and 1.78 for diatoms in Reynolds (2006), even reaching 3 in the meta-analysis of 308 experiments by Edwards *et al.* (2015); this can be much lower for dinoflagellates). These growth rates are maximum, fixed values for isolated species in laboratory conditions. Most of the time, they correspond to fixed temperature conditions, or to only a small set of values. These observations therefore cannot accomodate realistic, seasonal environment.

In this context, Bissinger *et al.* (2008) based their study on a seminal work by Eppley (1972) to compute the maximum possible growth rate depending on the temperature. The relationship between temperature and growth rate, evaluated on a large database, is then $r(T) = 0.81e^{0.0631T}$, with T in $^{\circ}\text{C}$. This represents the daily growth rate under a continuous irradiance and can therefore be at least halved because mean daylight is around 12 hours. In this case, growth rates vary between 0.5 and 1.9 , in line with previous observations. However, these values only illustrate a maximum, exponential growth which cannot be realistic for species which actually show different niche temperatures.

Scranton & Vasseur (2016) designed an equation that distinguished different niches based on optimal temperature.

$$\begin{aligned}
r_i(T) &= a_r(\tau_0) e^{E_r \frac{(T-\tau_0)}{kT\tau_0}} f_i(T) \\
\text{where } f_i(T) &= \begin{cases} e^{-|T-T_i^{opt}|^3/b_i}, & T \leq T_i^{opt} \\ e^{-5|T-T_i^{opt}|^3/b_i}, & T > T_i^{opt} \end{cases} \\
\text{and } b_i &\text{ is defined by numerically solving } \int r_i(\tau) d\tau = A
\end{aligned} \tag{4}$$

However, the niches described by this growth function are too narrow, corresponding to values close to 0 for temperatures in which phytoplankton can normally grow. The meta-analysis by Edwards *et al.* (2016) allows to correct, at least qualitatively the growth rates obtained with Scranton & Vasseur (2016).

By increasing the niche area in Scranton & Vasseur (2016) as well as directly increasing the final growth rate by 0.25, thermal niches seem closer to other values in the literature (Fig. 4).

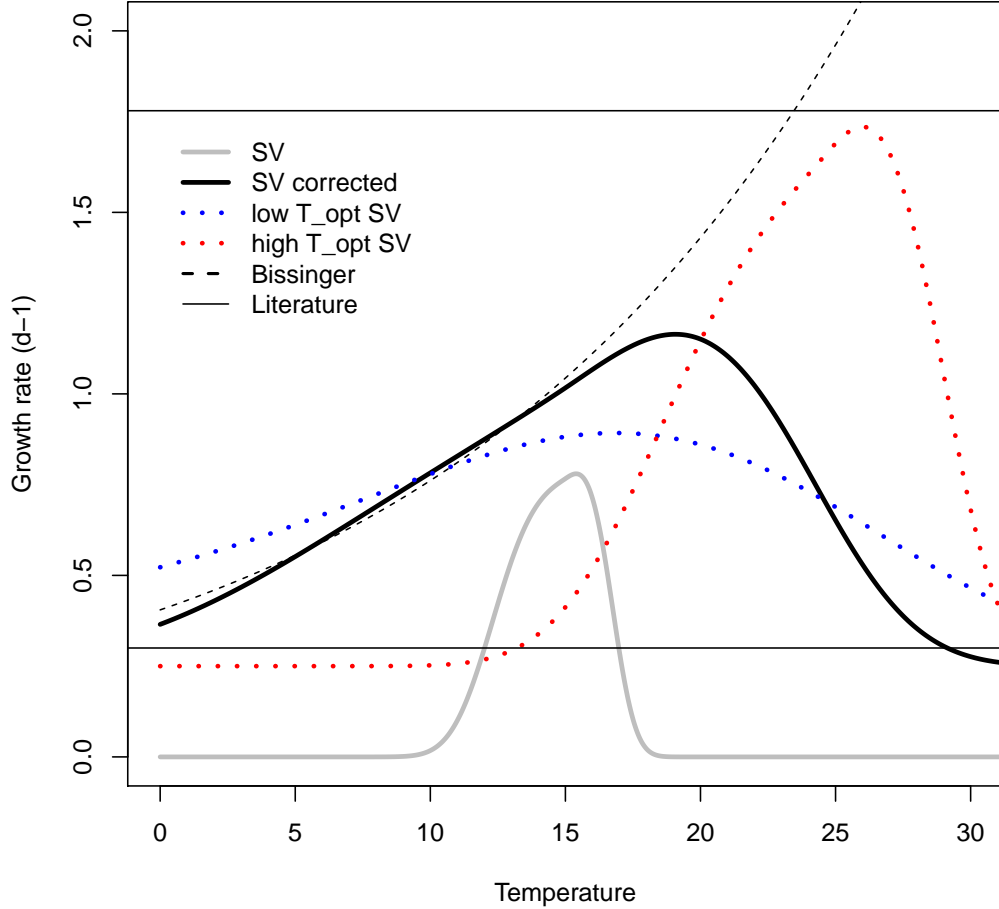


Figure 4: Comparison of growth rate formula

Community matrix: correspondence between Multivariate Autoregressive and Beverton-Holt models

Certain *et al.* (2018) showed that MAR and Beverton-Holt interaction coefficients, respectively b_{ij} and α_{ij} , could map once abundances at equilibrium N_i^* are defined.

$$\begin{cases} b_{ii} - 1 = \frac{-\alpha_{ii}N_i^*}{1+\sum_l \alpha_{il}N_l^*} \\ b_{ij, i \neq j} = \frac{-\alpha_{ij}N_j^*}{1+\sum_l \alpha_{il}N_l^*} \end{cases}$$

Let's define $f_A(i) = \sum_l \alpha_{il}N_l^*$.

$$b_{ij}(1 + f_A(i)) = -\alpha_{ij}N_j^*$$

We then sum on columns (on j).

$$\begin{aligned} \sum_j [b_{ij}(1 + f_A(i))] &= -f_A(i) \\ \Leftrightarrow -f_A(i)(1 + \sum_j b_{ij}) &= \sum_j b_{ij} \\ \Leftrightarrow f_A(i) &= -\frac{\sum_j b_{ij}}{(1 + \sum_j b_{ij})} \\ \Leftrightarrow \alpha_{ij} &= -\frac{1}{N_j^*} b_{ij} \left(1 - \frac{\sum_j b_{ij}}{1 + \sum_j b_{ij}}\right) \\ \Leftrightarrow \alpha_{ij} &= -\frac{1}{N_j^*} \frac{b_{ij}}{1 + \sum_j b_{ij}} \end{aligned}$$

This gives an exact correspondance between α_{ij} and b_{ij} .

Quadratic programming

Even though we could directly use the values obtained previously, the switch to another model with a different timestep and the strong uncertainty for all parameters, among other factors of variability, are motivations to calibrate the model more precisely. Maynard *et al.* (2019) have already shown that an additional calibration of parameter could lead to more realistic simulations. Followin their example, we use quadratic programming (Bazaraa *et al.*, 2013), applied to interaction matrices and growth rates.

The quadratic programming algorithm aims at finding \mathbf{x} that minimizes $\|\mathbf{C}\mathbf{x} - \mathbf{d}\|^2$ under the constraints $\mathbf{E}\mathbf{x} = \mathbf{f}$ and $\mathbf{G}\mathbf{x} \geq \mathbf{h}$.

Here, $\mathbf{C} = \mathbf{I}$, $\mathbf{d} = [\text{vec}(\mathbf{A}^T) \wedge \mathbf{r}']$ where \mathbf{A} is the interaction matrix, $\mathbf{r}' = -(\mathbf{e}^{\mathbf{r}} - \mathbf{1})$ is the vector of growth rates, \mathbf{E} is built so that we verify the equality $\mathbf{A}\mathbf{N}^* + \mathbf{r}' = 0$ where \mathbf{N}^* is the vectore of abundance at equilibrium (more precisely, here, average abundance values over the whole time series), and \mathbf{G}, \mathbf{h} so that $\mathbf{r} > 0$ (genera have a positive growth rate when taken in isolation) and $\forall i, a_{ii} > 0$ (negative density-dependence, individuals from the same genus compete with each other).

NOTE: This may not be useful as only the mean growth rate can be used to adjust the model (due to its dependence on the temperature), and the calibration of the interaction matrix tends to lead to a stable community, that is not able to represent the yearly cycles due to seasonality.

Mortality in the sediment

McQuoid *et al.* (2002) present maximum and mean depth at which germination of diatoms and dinoflagellates occurred in sediments. They also present sediment datation according to depth. Depth can therefore be related to maximum and mean age of phytoplankton before death.

Assuming m is the probability of mortality, m follows a geometric law, i.e., m is the probability distribution of the number of days needed for a phytoplankton spore to die. The expectancy for the life duration (the number of days without dying) is $\frac{1}{m} \Leftrightarrow m = \frac{1}{L_{mean}}$ where L_{mean} is the average life duration.

Another way to look at the process is that life expectancy L follows the distribution $p(L > l) = e^{-ml}$. With maximum values, we can arbitrarily choose that for these values $p(L > l_{max}) = 0.05$. In this, $m = -\frac{\ln(p(L > l_{max}))}{l_{max}}$.

In both cases, $m \propto 10^{-4} \text{d}^{-1}$.

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