Why seed banks can help maintaining the diversity of interacting phytoplankton species

Coralie Picoche & Frédéric Barraquand

Institute of Mathematics of Bordeaux, University of Bordeaux and CNRS, France

Abstract

Seed formation is part of the reproductive cycle, leading to the accumulation of resistance stages that can withstand harsh environmental conditions for long periods of time. At the community scale, multiple species with such long-lasting life stages can be more likely to coexist thanks to seeds' buffering effect. While the implications of this process for biodiversity have been studied in terrestrial plants, seed (or cyst) banks are usually neglected in phytoplankton multispecies dynamic models, in spite of widespread empirical evidence for such cyst banks. In this study, we build a meta-community model of interacting phytoplankton species with a cyst bank. The model is parameterized with empirically-driven growth rate functions and field-based interaction estimates, which include both facilitative and competitive interactions. Exchanges between compartments (coastal pelagic cells, coastal cysts on the seabed, and open ocean pelagic cells) are controlled by hydrodynamical parameters to which the sensitivity of the model is assessed. We consider two models, i.e., with and without a saturating effect of the interactions on the growth rates. Our results are consistent between models, and show that a cyst bank is necessary to maintain all species in the community over 30 years. Indeed, a fraction of the species are vulnerable to extinction at specific times within the year, but this process is buffered by their survival in the coastal cyst bank. We thus highlight the role of the cyst bank in the recurrent re-invasion of the coastal community, and of coastal environments in re-seeding oceanic regions. Moreover, the cyst bank enables populations to tolerate stronger interactions within the community as well as more severe changes in the environment, such as those predicted within a climate change context. This study therefore uncovers the potential importance of the phytoplanktonic cyst stage for diversity maintenance.

Keywords: phytoplankton; seed bank; dormancy; cyst; coexistence; facilitation

Introduction

How the high biodiversity of primary producers maintains is still an unresolved question for both experimental and theoretical ecology. Terrestrial plants and phytoplanktonic communities can present hundreds of species relying on similar resources, a situation where Gause's principle implies that a handful of species should outcompete the others. Some degree of niche differentiation, perhaps hidden to the human observer, is generally expected for coexistence to maintain (Chesson, 2000). However, a complex life-history structure can further increase the likelihood of coexistence (e.g. Moll & Brown, 2008; Fujiwara *et al.*, 2011), and so does the response of life history traits to variation in the environment (Chesson & Huntly, 1988; Huang *et al.*, 2016).

Analyses of coexistence in terrestrial plant communities sometimes take into account several life stages (e.g., Aikio *et al.*, 2002; Comita *et al.*, 2010; Chu & Adler, 2015) though many consider only a single life-stage (see, among others, Ellner, 1987; Levine & Rees, 2004; Martorell & Freckleton, 2014). When considering at least two stages, seeds/seedlings and adults, several mechanisms that can contribute to long-term coexistence in spatially and/or temporally fluctuating environment have been uncovered (Shmida & Ellner, 1984; Chu & Adler, 2015). The storage effect, a major paradigm in modern coexistence theory (Chesson, 2000, 2018), is one of them. It has first been defined by the presence of a long-lived life stage combined with temporal variation in recruitment from this stage that helps escape interspecific competition (Chesson, 1986). The storage effect has often been discussed in the presence of a seed bank (Aikio *et al.*, 2002; Angert *et al.*, 2009; Chu & Adler, 2015). However, the contribution of seeds to coexistence may be much larger than their potential contribution to the storage effect. The seed stage itself contrasts with other parts of the life cycle as organisms can enter a dormant phase which allows them to sustain harsh environmental conditions for long periods of time (Aikio *et al.*, 2002). Although this is favourable ground for a storage effect, a long-lived seed bank can help coexistence by other, simpler means. For instance, in the meta-community model of Wisnoski *et al.* (2019), when dormancy and dispersal are present

(without seed dispersal), local diversity increases in temporally fluctuating environments. In their model, adding a dormant stage could increase species diversity both at the local and regional scales. These results suggest that considering a seed stage in dynamical models can profoundly alter our understanding of population (Nguyen *et al.*, 2019) and community persistence (Jabot & Pottier, 2017; Manna *et al.*, 2017; Wisnoski *et al.*, 2019).

Although there is some awareness of the role of cryptic life stages in shaping terrestrial plant coexistence, the effect of such dormant life stages on aquatic plant communities, and more specifically that of phytoplanktonic algae, is often ignored. The classical view behind phytoplankton dynamics is that their blooms (peaks in abundances several orders of magnitude above their baseline level) are due to seasonal variation in light, temperature and nutrients, as well as hydrodynamic processes (Reynolds, 2006). In this mindset, differential responses to environmental signals ensure the coexistence of multiple species (Margalef, 1978; Smayda & Reynolds, 2001), while always assuming that vegetative cells are already present in the environment. Momentary disappearances of a species are viewed as sampling issues at low density. However, a complementary hypothesis suggests that resuspension and germination of phytoplanktonic resting cells, or cysts, is another major player allowing re-invasion from very low or locally zero population densities (Patrick, 1948; Marcus & Boero, 1998). This long-standing hypothesis is supported by recent reviews (Azanza *et al.*, 2018; Ellegaard & Ribeiro, 2018) which confirm that life history strategies including dormant cysts are widespread in phytoplankton. Cyst formation can either be part of the life cycle of phytoplankton species and result from sexual reproduction or be triggered by specific environmental conditions, leading to asexual resting stages (Ellegaard & Ribeiro, 2018). A variety of models have endeavoured to explain and predict amplitude, timing and/or spatial distribution of blooms by explicitly modeling multiple stages in the life cycle of a particular species, but without interactions with other organisms (see for example McGillicuddy *et al.*, 2005; Hense & Beckmann, 2006; Hellweger *et al.*, 2008; Yñiguez *et al.*, 2012). Two-to-four species (Yamamoto *et al.*, 2002; Estrada *et al.*, 2010; Lee *et al.*, 2018) models also exist, but they focus on explaining the

dynamics of a single cyst-forming species or group interacting mostly with vegetative-only groups. This state of affairs means that we currently have no clear understanding of how the cyst stage might help maintain biodiversity in species-rich communities. In the present paper, we demonstrate the potential role of cyst banks using a phytoplankton community dynamics model including a cyst bank.

Phytoplankton communities in coastal environments may benefit from seed banks (hereafter called cyst banks to be more consistent with the terminology in use for such species) even more than the oceanic communities (see for example McGillicuddy *et al.*, 2005), as the distance to the sea bottom is smaller, which favours recolonization from the sea bottom, something that is impossible in the deep ocean. Moreover, 'horizontal' exchanges between oceanic and coastal pelagic phytoplanktonic communities are usually observed. A flow from the ocean to coastal communities has been noticed for dinoflagellates especially (Tester & Steidinger, 1997; Batifoulier *et al.*, 2013). Conversely, in many other bloom-forming species, the nutrient-rich coastal areas might function as a reservoir for the biodiversity in the ocean, given the more accessible cyst bank at the coast, especially in the long run. Indeed, cysts are able to germinate again after dozens of years (McQuoid *et al.*, 2002; Ellegaard & Ribeiro, 2018) or even thousands of years (Sanyal *et al.*, 2018) of dormancy. Therefore, we consider in this study three interlinked compartements: the coastal pelagic environment, the seed (cyst) bank, and the pelagic open ocean. The coastal pelagic environment acts as a bridge between the cyst bank and the open ocean.

Our model is parameterized from field data (growth and interaction rates), and includes biotic and abiotic constraints (e.g., particle sinking). In our analyses, we examine how cyst banks may influence the maintenance of biodiversity, including under changing biotic interactions or changing environmental conditions. We either add or remove the dormant compartment, which allows to pinpoint its contribution to coexistence. We find that the presence of cysts prevents the extinction of several species. Cyst banks also allow a community to maintain its richness even with strong disturbances of its interaction network, unless facilitative in-

teractions completely eclipse competitive interactions. Changes in the environment, here represented by an increase in the mean temperature, can also be buffered by cyst banks. Finally, we discuss the importance of this often ignored life stage in phytoplanktonic demography and the information that would be required to further more accurate modeling of cyst bank dynamics.

Methods

Models

Our models (Fig. 1) build atop recent models developed by Shoemaker & Melbourne (2016) and Wisnoski *et al.* (2019), although they diverge in several aspects developed below (e.g., possibility for facilitative interactions). These discrete-time models are designed for meta-communities with multiple interacting populations. Any discrete-time model requires an ordering of events; in our models, these unfold as follows: first, populations grow or decline according to a Beverton-Holt (BH) multispecies density-dependence (eqs. 1 and 3), and then, in a second step, exchanges occur between the different compartments or patches constituting the metacommunity (eq. 4).
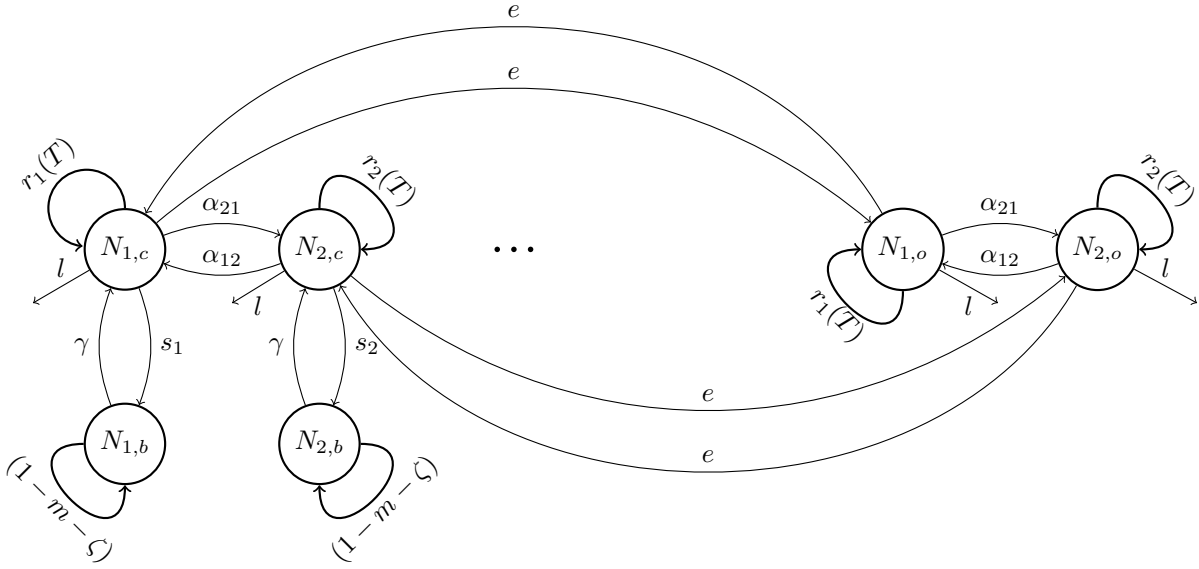
Figure 1: Structure of the model. Phytoplanktonic species (represented by circles) are present in the coast (subscript c), the ocean (o) and the cyst bank (b). Parameters governing demography, interactions between organisms and exchanges between compartments are defined in Table 1. Only two species are shown here for the sake of simplicity but 11 species are present in the model.

In this paper, individuals are phytoplanktonic cells that move between the upper layer of coastal water, its bottom layer where a cyst bank accumulates in the sediment, and the oceanic zone surrounding the coastal water masses (hereafter "the ocean"). Only oceanic and coastal pelagic cells are subject to BH-density dependence. Cysts are only affected by mortality m and burial due to sedimentation ζ. The different populations are field-inspired morphotypes accounting for the most frequent genera observed along the French coast (Picoche & Barraquand, 2020) and will hereafter be called taxa. Parameters and state variables are defined in Table 1.

The Beverton-Holt (BH) formulation of multispecies population dynamics, sometimes called Leslie-Gower (Cushing *et al.*, 2004), is a Lotka-Volterra competition equivalent for discrete-time models, and is often used to represent terrestrial plant population/community dynamics. In our implementation of the model, the maximum achievable growth rate is modified by both competitive and facilitative interactions, which translates into positive and negative

α_{ij} coefficients, respectively. We present two different interaction models. We first use the classical multispecies BH model (model I, eq. 1), also present in the original models of Shoemaker & Melbourne (2016) and Wisnoski *et al.* (2019). However, the high number of facilitative interactions characterizing the modeled phytoplankton community (Picoche & Barraquand, 2020) combined to the mass-action assumption could have very irrealistic destabilizing consequences, which have been likened to an "orgy of mutual benefaction" (May, 1981): populations grow to infinity because there is no saturation of beneficial effects when density increases. In model I, we therefore forbid the realized growth rate to go above the intrinsic growth rate (its theoretical limit), by setting a minimum value of 1 to the denominator of the BH formulation. We subsequently define saturating interactions, inspired by Qian & Akçay (2020), in our model II (eq. 3). Model II provides a more process-orientated solution to the issue of excessive mutual benefaction (but to the cost of added parameters). In our framework, the first step of model I can be written as

$$
\begin{cases}
N_{t',i,c} &= \frac{\exp(r_i(T))N_{t,i,c}}{1+\sum_j \alpha_{ij}N_{t,j,c}} - lN_{t,i,c} \\
N_{t',i,o} &= \frac{\exp(r_i(T))N_{t,i,o}}{1+\sum_j \alpha_{ij}N_{t,j,o}} - lN_{t,i,o} \\
N_{t',i,b} &= N_{t,i,b}(1-m-\zeta)
\end{cases}
\tag{1}
$$

where the intrinsic growth rate $r_i(T)$ is a taxon-specific function of the temperature (see eq. 2), the interaction coefficients α_{ij} are per capita effects of taxon j on taxon i, and the loss term l accounts for lethal processes such as natural mortality, predation or parasitism. First estimates of interaction coefficients are inferred from a previous study of coastal community dynamics with Multivariate AutoRegressive (MAR) models (Picoche & Barraquand, 2020). We later calibrate these coefficients for model I, since MAR models were applied at a different timescale.

The intrinsic growth rate $r_i(T)$ is defined through a modified version of the formula used by Scranton & Vasseur (2016) (eq. 2), which classically decomposes $r_i(T)$ in two parts: the taxon-independent metabolism part $E(T)$ and the taxon-specific niche part $f_i(T)$:

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$$r_i(T) = E(T)f_i(T) \tag{2}$$

$$\text{where } E(T) = d \times 0.81 e^{0.0631(T-273.15)}$$

$$\text{and } f_i(T) = \begin{cases} \exp(-|T - T_i^{opt}|^3/b_i), & T \leq T_i^{opt} \\ \\ \exp(-5|T - T_i^{opt}|^3/b_i), & T > T_i^{opt}. \end{cases}$$

The metabolism part describes the maximum achievable intrinsic growth rate based on Bissinger *et al.* (2008). This maximum daily intrinsic growth rate is weighted by the daylength d as no growth occurs at night. The niche part $f_i(T)$ describes the decrease in growth rate due to the difference between the temperature in the environment and the taxon-specific thermal optimum T_i^{opt}, and is controlled by the species-specific thermal decay b_i, which depends on the niche width. Parameterisation is further detailed in Section S1 of the SI.

In model II, oceanic and coastal dynamics are governed by eq. 3.

$$N_{t',i,c/o} = \frac{\exp(r_i(T))N_{t,i,c/o}}{1 + \sum_{j \in \mathbb{C}} \frac{a_C N_{t,j,c/o}}{H_{ij} + N_{t,j,c/o}} + \sum_{j \in \mathbb{F}} \frac{a_F N_{t,j,c/o}}{H_{ij} + N_{t,j,c/o}}} - lN_{t,i,c/o} \tag{3}$$

where a_C and a_F are the maximum competition and facilitation strengths, respectively, with $\mathbb{C}$ and $\mathbb{F}$ the sets of competitors and facilitators of taxon i. We use here similar notations to Qian & Akçay (2020), but use different parameters that vary between species. Indeed, the half-saturation coefficients H_{ij} vary between species, as opposed to the maximum rates in Qian & Akçay (2020). It did not make sense biologically for H_{ij} to be fixed (e.g., in a resource competition context, different species are expected to feel resource limitations at different concentrations of nutrients and at different numbers of competitors). How to shift from MAR- to BH-interaction matrices in model I, and to use the parameter estimates of model I to specify parameters in model II is described in Section S2 of the SI.

After growth and mortality processes occur, exchanges take place between the three com-

150 partments, which constitutes the second step of the model (eq. 4):

$$
\begin{cases}
N_{t+1,i,c} & = \quad (1 - s_i - e)N_{t',i,c} + \gamma N_{t',i,b} + e N_{t',i,o} \\
N_{t+1,i,o} & = \qquad\quad (1 - s_i - e)N_{t',i,o} + e N_{t',i,c} \\
N_{t+1,i,b} & = \qquad\quad\quad (1 - \gamma)N_{t',i,b} + s_i N_{t',i,c}
\end{cases}
\tag{4}
$$

Parameter	Name	Value (unit)	Status
$N_{t,i,c/o/b}$	Abundance of taxon i at time t in the coast (c), ocean (o), or coastal bank (b)	NA (Number of cells)	Dynamic
T	Temperature	NA (K)	Dynamic
$r_i(T)$	Growth rate of taxon i	NA (day^{-1})	Dynamic
b_i	Thermal decay	Field-based, taxon-specific (K^3)	Calibrated
T_i^{opt}	Optimal temperature for taxon i	Field-based, taxon-specific (K)	Calibrated
d	Daylength	50 (%)	Fixed
α_{ij}	Interaction strength of taxon j on i in model I	Field-based, taxon-specific (Cells^{-1})	Calibrated
a_C/a_F	Maximum competitive/facilitative interaction strength in model II	Field-based (NA)	Calibrated
H_{ij}	Half-saturation for the interaction strength of taxon j on i in model II	Field-based, taxon-specific (Cells)	Calibrated
s_i	Sinking rate of taxon i cyst	$\{0.1; \mathbf{0.3}; 0.5\} \times \beta(0.55, 1.25)$ (day^{-1})	Fixed
e	Exchange rate between ocean and coast	$\{0; \mathbf{0.4}; 0.9\}$ (day^{-1})	Fixed
l	Loss rate of pelagic phytoplanktonic cells	$\{0.04; 0.1; \mathbf{0.2}\}$ (day^{-1})	Fixed
m	Cyst mortality rate	$\mathbf{10^{-5}}$ (day^{-1})	Fixed
ζ	Cyst burial rate	$\{10^{-3}, \mathbf{10^{-2}}, 10^{-1}\}$ (day^{-1})	Fixed
γ	Germination $\times$ Resuspension rate	$\{10^{-3}, \mathbf{10^{-2}}, 10^{-1}\} \times \{10^{-5}, 10^{-3}, \mathbf{10^{-1}}\}$ (day^{-1})	Fixed

Table 1: Definition of main state variables and model parameters. State variables and fluctuating parameters are indicated in the last column as "Dynamic". Parameters that are constant through time are either "Fixed" (directly obtained from literature) or "Calibrated" (obtained through model fitting, with initial values arising from previous studies at the study site). When a range of values is given, the bold numbers indicate the reference values while the others are used for sensitivity analysis. $\beta(0.55, 1.25)$ is the Beta distribution with parameters 0.55 and 1.25. For γ, germination values for sensivity analysis were multiplied by the reference value for resuspension, and conversely.

151 Each compartment (ocean, coast, cyst bank) contains 10^3 cells at the beginning of the simula-

152 tion, and the dynamics are run for 30 years with a daily time step. We model the temperature

153 input as a noisy sinusoidal signal with the same mean and variance as the empirical data set

154 described below: the amplitude of the sinusoid is 12.4°C and the standard deviation of the

155 noise is 0.25°C.

Parameterization of the models

Literature-derived parameter values

Loss rate   The loss rate of vegetative cells can be attributed to natural mortality, predation or parasitism. This rate is quite variable in the literature: the model of Scranton & Vasseur (2016) considered a rate around 0.04 day^{-1} while a review by Sarthou *et al.* (2005) indicates a grazing rate of the standing stock between 0.2 and 1.8 day^{-1} and an autolysis rate around between 0.005 and 0.24 day^{-1} (in the absence of nutrients, or because of viral charge). A maximum value of 0.2 is fixed for the model (see Section 3 of the SI for more details).

Sinking rate   Phytoplanktonic particles have a higher density than water and cannot swim to prevent sinking (although they are able to regulate their buoyancy, Reynolds 2006). Sinking is mostly affected by hydrodynamics, but at the species-level, size, shape, density-regulation and colony-formation capabilities are key determinants of the particle flotation. In this model, the sinking rate of each taxon cysts is drawn from a Beta distribution with a mean value of 9%, and a maximum (S_max) around 30%, that is $s \backsim 0.3\beta(0.55, 1.25)$ (see Fig. S4), adapted from observations by Passow (1991) and Wiedmann *et al.* (2016).

Exchange rate   The exchange rate between the ocean and the coast depends on the shape and location of the coast (estuary, cape, ...). Our calibration site is located at an inlet. The flow at the inlet leads to a renewal time of the coastal area water evaluated between 1 and 2.5 days (Ascione Kenov *et al.*, 2015), which corresponds to a daily exchange rate between 40 and 100 %.

Cyst mortality and burial   Cyst loss is the result of cyst mortality m and burial by sedimentation ζ. Mortality values range between 10^{-5} and 10^{-4} per day (more details on the approximation of mortality rates from McQuoid *et al.* 2002 are given in Section 3 of the SI). However, cyst burial by sedimentation is the prevailing phenomenon. Indeed, once cysts have

been buried, they are not accessible for resuspension even if they could still 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 is thus heavily dependent on the environmental context and varies here between 0.001 and 0.1 per day.

Germination/resuspension Both resuspension and germination are needed for cysts to contribute to the vegetative pool in the water column (γ = resuspension×germination). Following McQuoid *et al.* (2002) and Agrawal (2009), we assume a temperature threshold: germination is triggered by temperatures going above 15℃. As actual rates of germination are not easily deduced from the literature, a set of credible values has been tested (1%, 0.1%, 0.01%). Similarly, resuspension values are seldom computed for phytoplanktonic cells, but models for inorganic particles can be used (see Section S3 of the SI for literature and details). In this paper, we explore values between 10^{-5} (stratified water column) to 0.1 (highly mixed environment).

Parameter calibration

In addition to phenology parameters, whose estimation process is described in Section S1 of the SI, the 49 non-zero interactions that form the community matrix of the model are calibrated from field data. We use initial interaction estimates from our previous time series modelling study (Picoche & Barraquand, 2020, see Section 3 of the SI for the equations). These initial interaction estimates are then calibrated, to take into account the differences in model structure and timescale between this study and Picoche & Barraquand (2020).

The calibration procedure consiste in lauching 1000 simulations, each characterized by a specific set of interaction coefficients. More precisely, for each simulation, an interaction coefficient (α_{ij} in model I, H_{ij} in model II) has probability $\frac{1}{5}$ to keep its present value, probability $\frac{1}{5}$ to increase by 10% , $\frac{1}{5}$ to decrease by 10%, $\frac{1}{5}$ to be halved and $\frac{1}{5}$ to be doubled.

The numbers of coastal pelagic cells (which are the ones measured empirically) are then extracted over the last 2 years of the simulation, and compared to observations using the following summary statistics:

- average abundance $f_1 = \sqrt{\frac{1}{S} \sum_i^S (\bar{n}_{i,obs} - \bar{n}_{i,sim})^2}$ where S is the number of taxa and $\bar{n}_i$ is the logarithm of the mean abundance of taxon i

- amplitude of the cycles $f_2 = \sqrt{\frac{1}{S} \sum_i^S [(\max(n_{i,obs}) - \min(n_{i,obs})) - (\max(n_{i,sim}) - \min(n_{i,sim}))]^2}$ where n_i is the logarithm of the abundance of taxon i.

- period of the bloom. The year is divided in 3 periods, i.e. summer, winter and the spring/autumn group (as taxa blooming in these periods can appear in either or both seasons). We give a score of 0 if the taxon blooms in the same period as its observed counterpart and 1 otherwise.

Simulations with taxon extinction (i.e., the taxon is absent for more than 6 months in a compartment) are discarded, as extinctions are not observed in the field data. Parameter sets are then ranked according to their performance for each summary statistic, and we select the set of interactions minimizing the sum of the ranks.

Sensitivity analysis   Certain parameters, which were evaluated from the literature, may be site- or model- specific. Some also vary over one order of magnitude in the literature, e.g. rates of sinking s, resuspension/germination γ, cyst mortality m and burial ζ, as well as the loss rate l. Parameter value sensitivity to these highly uncertain parameters needs to be investigated before drawing conclusions. The set of tested values for each parameter is given in Table 1. Variations in average abundances and amplitudes at the community and taxon levels for the last 2 years of simulations are the major model diagnostics.

Empirical dataset used for calibration

The modeled community is inspired by previously analysed field data (REPHY, 2017; Picoche & Barraquand, 2020). We use time series of phytoplanktonic abundances that have been monitored biweekly for 21 years in the Marennes-Oléron Bay, on the French Atlantic Coast (the Auger site analysed in Picoche & Barraquand, 2020). The Auger sampling site is characterized by a high phytoplanktonic biodiversity, even by regional standards, sustained by the joint influences of the Atlantic Ocean and terrestrial (nutrient) inputs from the Seudre River, with a possibly important contribution of the benthic environment (Guarini *et al.*, 2004). We aim to approximate the population dynamics of the 11 most abundant and most frequent groups of genera (hereafter taxa defined in Section 4 of the SI) focusing on the amplitude of fluctuations and their timing (phenology). The estimation of the parameters characterizing each taxon (T_i^{opt} and b_i), is described in Section 1 of the SI. The interactions between model taxa have already been inferred from a MAR model (Picoche & Barraquand, 2020). The community matrix is characterized by a phylogeny-based modular structure which differentiates between centric and pennate diatoms and dinoflagellates, a high level of facilitative interactions ($\approx 70\%$) and a strong self-regulation.

Scenarii

The effect of the cyst bank on biodiversity and community dynamics can be evaluated through the response to disturbance with and without the cyst compartment. Cyst mortality is set to 100% to remove the cyst bank. We evaluate two main disturbances:

1. increase or decrease in interaction strength

2. temperature change, either in mean value or variability

In the first scenario, interaction strengths are multiplied or divided by a factor ranging between 1 and 10. In order to differentiate the effects of facilitative and competitive interactions

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on coexistence, we only vary only one type of interactions at a time. For each value of the multiplicative factor, we therefore run 4 simulations for each growth model: one where positive (respectively, negative) interactions are multiplied by the factor and one where positive (respectively, negative) interactions are divided by the same factor. Here, both intra and intertaxa interactions are modified; we present in Section 6 of the SI additional simulations with a change in intertaxa interactions only.

In the second scenario, five different climate change trajectories are assessed. In the first three, the average temperature is increased by 2, 5, or 7°C (Boucher *et al.*, 2020). In the next two, keeping the reference average temperature, the total variance of the temperature, including seasonality and noise, is either decreased or increased by 25%. Each climate change trajectory is run 5 times to account for the intrinsic stochasticity of the temperature signal. In both scenarios, simulations are run for 30 years for both population growth models, with and without a cyst compartment, and only the last 2 years are considered to evaluate effects of changes in parameters and in temperature.

Results

Phytoplankton dynamics

The classical mass-action (model I) and saturating interaction (model II) formulations of multispecies dynamics both reproduced the main characteristics of observed phytoplankton dynamics. They produced one or two blooms during the year and a range of abundances covering several orders of magnitude, with the right timing of the blooms. At the Auger site that was used for calibration, abundances increase in spring and can last over part of summer, or start a new bloom in autumn, which is what we observed as well in the models. Annual mean abundance of the various taxa was also well reproduced. That said, in some cases, abundances could be lower than expected and the variation in abundances due to seasonality

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was underestimated (Fig. 2). In all cases, saturating interactions led to higher abundances
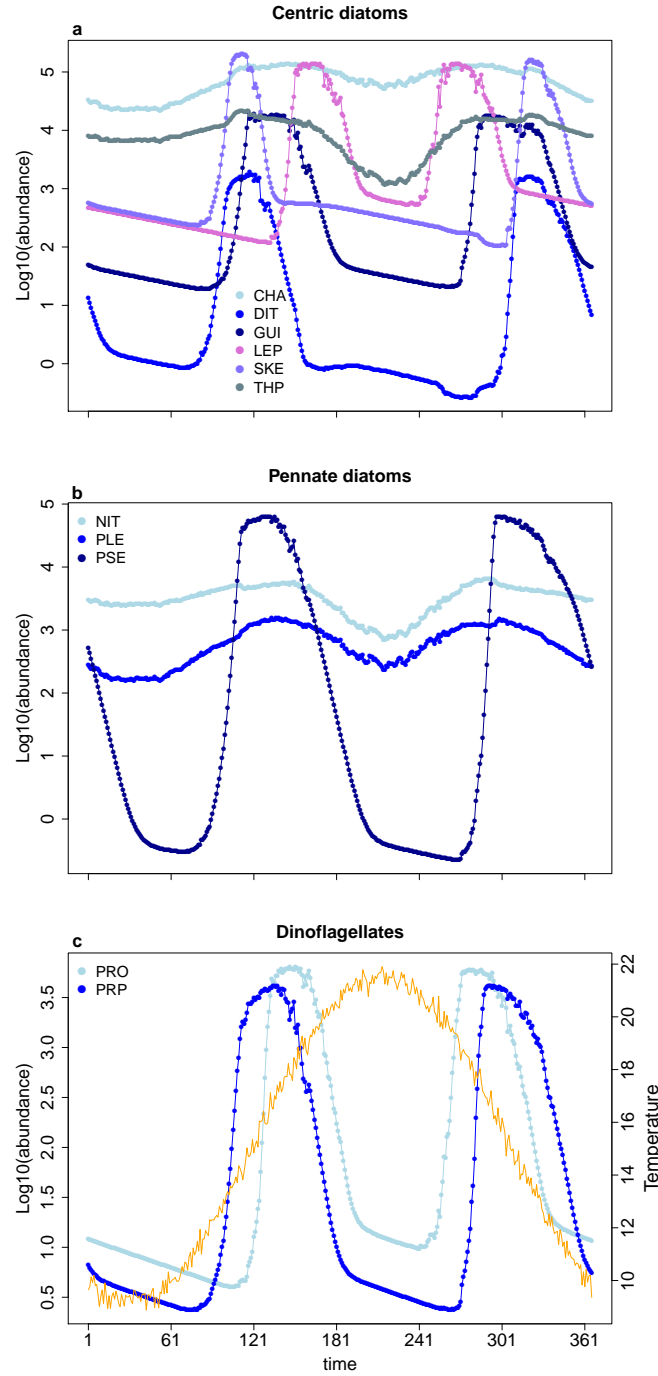than mass-action interactions throughout the year (Fig. S5).

Figure 2: Simulated phytoplankton dynamics for a year in model I. Each panel corresponds to a cluster of interacting taxa. The orange line in the third panel indicates the temperature.

Sensitivity to uncalibrated parameters

Total phytoplankton dynamics were not strongly affected by changes in the parameter values (Fig. 3). As values were varied in their plausible range, the average change in mean abundance on the coast between the reference simulation and the sensitivity simulations varied between -4.6 and 1.9% for model I and between -4.2 and 1.1% for model II, with similar deviations (same sign and magnitude) in the two models. The only parameter that led to a substantially different results between the two models was the resuspension parameter (leading to a different value of the parameter γ in Eq. 4) which, when decreased, led to an increase in abundance of approximately 1.9% in model I while it was only 0.9% in model II. In the two models, the decrease in mortality rate of vegetative cells l had the more impact on the final average abundance, leading to an increase in abundances. The exchange rate between the ocean and the coast had much less effect on the coastal average abundance.

On the other hand, the decimal logarithm of the maximum to minimum ratio of abundance (i.e., the order of magnitude of the range of abundances for each taxa) was more affected by changes in parameters and could vary by -39.4 to 18.6% in model I, and between -41.2% and 23% in model II. Results were qualitatively the same in the two models, with a decrease in cyst burial being the main driver of the decrease in amplitude, and a decrease in resuspension leading to an increase in amplitude.

In three cases (cyst burial rate set to 0.1, resuspension to 10^{-5} or exchange rate set to 0), the final richness of the oceanic community decreased from 11 to 4. Extant taxa were the same in all simulations (CHA, THP, NIT, PSE). When resuspension was set to 0.001, a taxon periodically disappeared from the ocean, to be subsequently re-seeded by the coastal population.

With all parameters, except the sinking rate, an increase in mean abundance was linked to a decrease in amplitude.
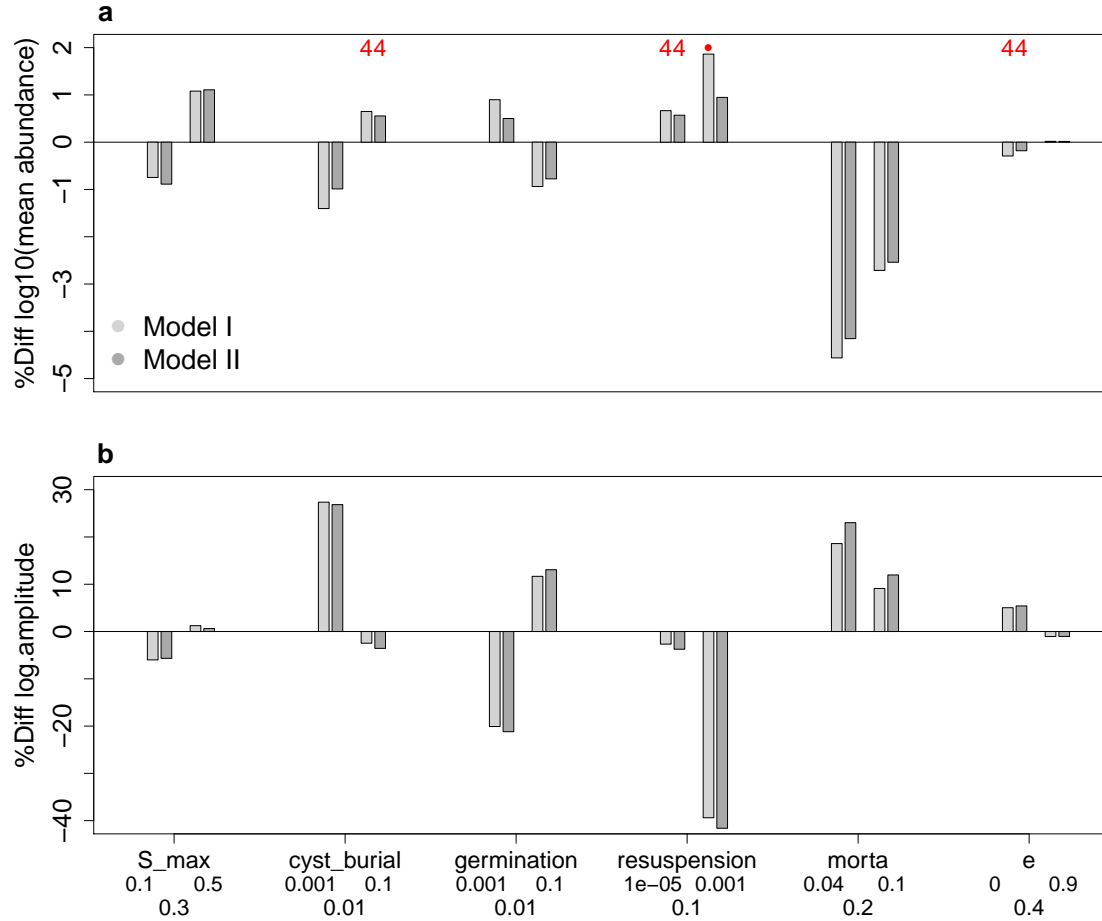
Figure 3: Sensitivity of the model to variation in parameters, measured as the difference between the reference simulation metric and the metric for the simulation including a change in parameter. The two metrics used were the average decimal log abundance (a) and the decimal logarithm of the ratio between maximum and minimum abundance (b) of the coastal phytoplanktonic community. S_max is the maximum sinking rate of cysts and morta is the mortality of vegetative cells l. Values used in the sensitivity analysis are in the second row of the x-axis while values used in the reference simulation are shown in the third row. Note that the reference value is not necessarily within the range of values used in the sensitivity analysis (e.g. mortality rates in the sensitivity analysis are both below the value used in other simulations). Numbers in red are the final number of taxa in the ocean and dots correspond to simulations in which at least one taxon reached 0 at one point but did not disappear.

Scenarios of environmental change

Two scenarios were designed to test the buffering effect of the cyst bank against disruption. In both cases, it consisted in removing the cyst bank by setting cyst mortality to 100% per day.

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Without any other disturbance to the system, this led to a decrease in taxon richness from 11 to 4 taxa at the end of the simulation (Fig. 4) while the total abundance of phytoplankton was not strongly affected (around 10^5 in all cases). The inverse of the Simpson index (the second Hill number) decreased from approximately 3 to 1, showing that the disappearance of the cyst bank did not affect only the rarest species.

Biotic effects

Our first hypothesis was that the absence of the cyst bank would cause the community to be more affected by a higher competition strength. Counter-intuitively, our results (Fig. 4) showed that an increase in competition strength only had negative effects with model I, and for high competition values (6 times the reference ones at least), shifting from 4 taxa to 3 taxa in the oceanic compartment of a community without cyst bank. By contrast, an increase in competition strength did not affect the richness of a community with a cyst bank. On the contrary, a decrease in competition (from a factor 0.5 and lower) or an increase in facilitation (starting from a factor 2 and higher) led to much smaller communities in model II in the absence of a cyst bank, sometimes with a complete competitive exclusion. Richness was lowest when competition was divided by 6 or when facilitation was multiplied by 8 in model II. The same pattern (richness stability with model I, sensitivity to a decrease in competition or an increase in facilitation with model II) was observed in a community with a cyst bank, but for larger disturbances. Competition indeed had to be at least divided by 6 or facilitation, to be multiplied by 7 for richness to decrease to 9 taxa.

The inverse of the Simpson index was also affected by the changes in interaction strengths, with similar patterns to richness, as it was lowest for high facilitation or low competition. Presumably some species reach very high growth rates in these scenarios, which then feeds back onto community dynamics, generating lower diversity in the end.
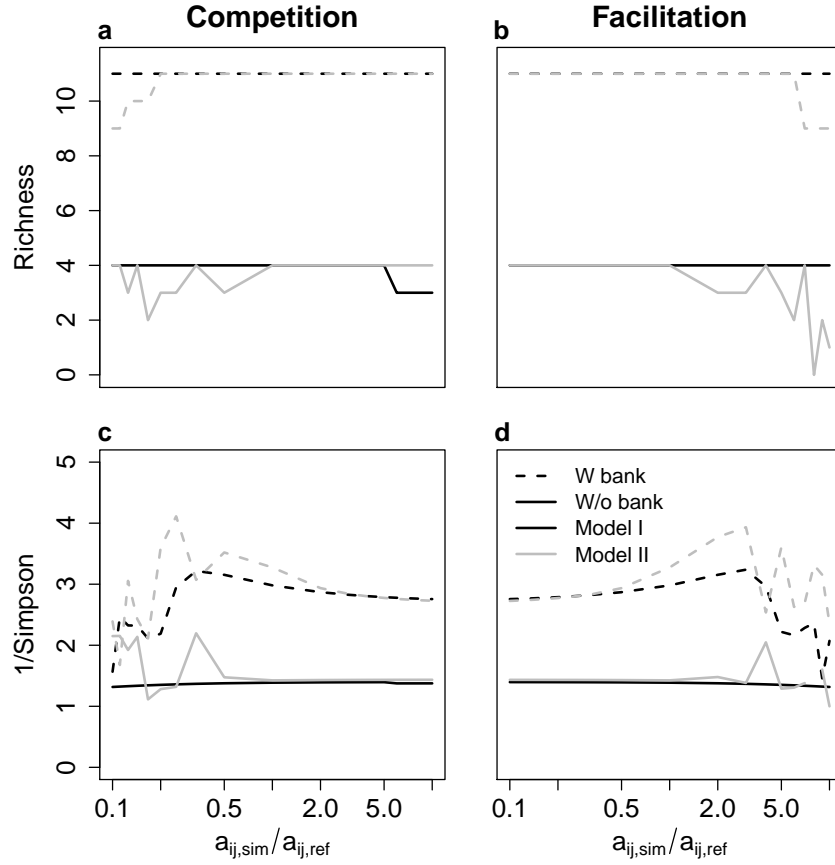
Figure 4: Measures of biodiversity in the ocean at the end of the simulation: a-b) richness and c-d) inverse of the Simpson index, with (dashed line) and without (solid line) a cyst bank, as a function of the strength of competition and facilitation with a classical Beverton-Holt (black lines) or a saturating interaction (grey lines) formulation. The x-axis shows the factor by which each interaction was multiplied (note the logarithmic scale).

Taxa which disappear were always the same and were characterized by a lower minimum abundance, a higher amplitude of fluctuations and a small niche (Fig. 5). In contrast, their interactions were not qualitatively different from the other taxa.
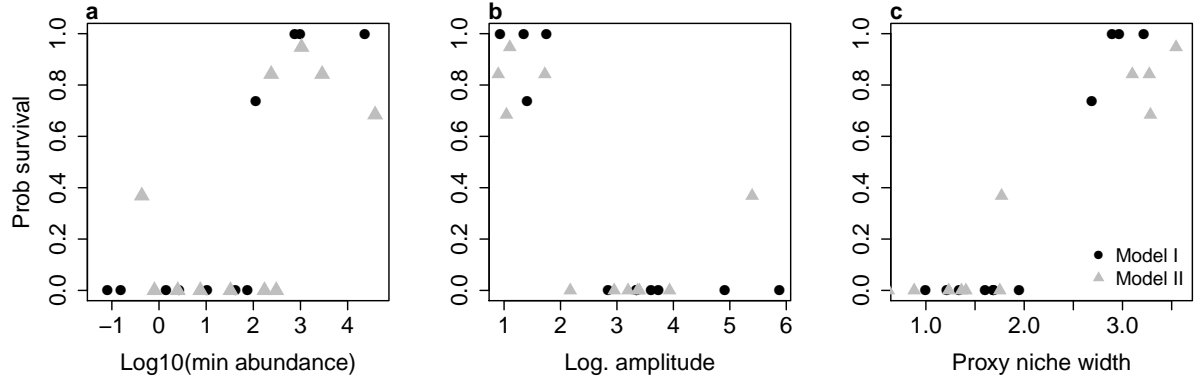
Figure 5: Probability of survival of taxa when competition increases in the absence of a cyst bank, as a function of their dynamics characteristics (minimum abundance, logarithm of amplitude and niche width) in the reference parameter set.

Abiotic effects Our second hypothesis was that the absence of a cyst bank would reduce the ability of a community to withstand changes in its abiotic environment, here represented by variation in the temperature. This was true for both models (Fig. 6), as the communities without a cyst bank could not maintain their richness with an increase in temperature above 2°C, as opposed to communities with a cyst bank, which could only be affected by a 7°C increase (scenario SSP5 8.5, Boucher *et al.* 2020). In all cases however, the total abundances were not strongly affected. Indeed, the total abundance of a community is driven by a small number of numerically dominant taxa, which did not disappear. High total abundances tended to correspond to the abundance of only one or two taxa. Model II consistenly led to higher abundances, as was already the case in the reference simulations.

The variance of the temperature did not affect richness nor total abundance of communities with a cyst bank. This was also true without a cyst bank. The presence of the cyst bank did increase total abundance though.
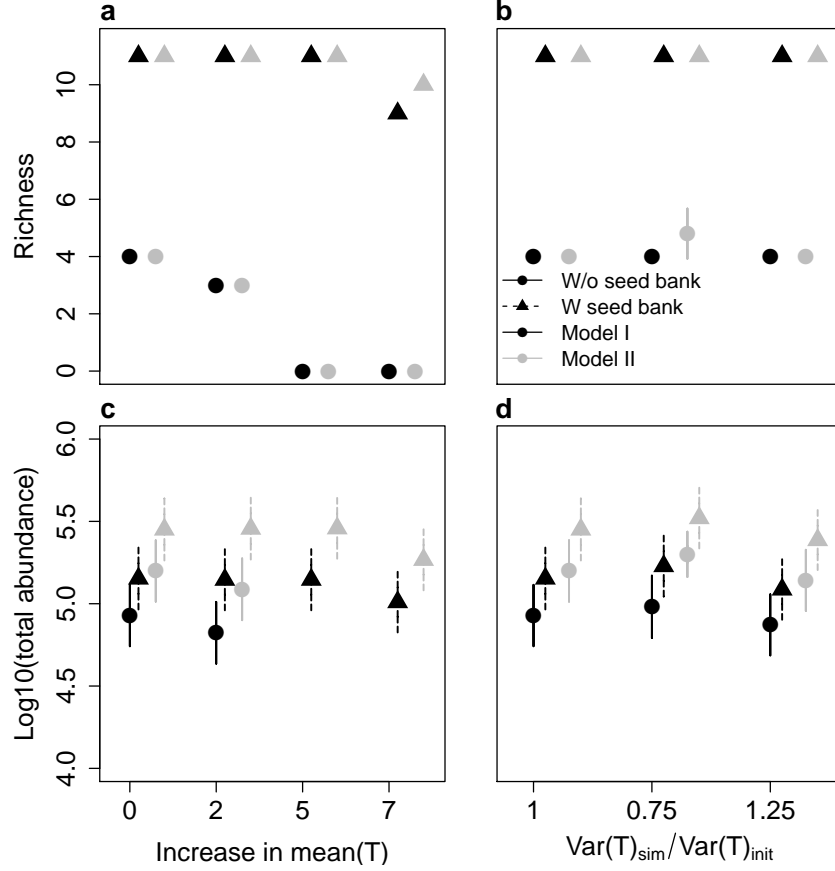
Figure 6: Variation in richness and total abundance with and without a cyst bank as a function of the mean (left) and variance (right) of the temperature with a mass-action (black line, model I) or a saturating interaction (grey line, model II) formulation.

Discussion

Using a meta-community model which accounts for exchanges between the ocean and the coast, as well as movements between the top and the bottom of the coastal water column, we were able to show that a specific life stage, the seed – or cyst – stage, can help maintain biodiversity. This dormant stage was integrated to a phytoplanktonic community dynamics model, which was parameterized based on literature and field-based phenology and interaction strength estimates. The model was then calibrated on phytoplankton community time series. Our model was able to simulate realistic community dynamics (both mean abundances and temporal patterns), while including the effects of both positive and negative interactions

on community dynamics. When removing the cyst bank, biodiversity decreased drastically. This was true for the reference parameter values, as well as when species interaction strengths and environmental fluctuation levels where altered, in which cases the cyst bank's buffering influence disappeared. The total abundance of the community decreased as well. Moreover, when faced with a biotic or abiotic "press" perturbation, communities where species could divert part of their population to a dormant stage were less prone to species loss and could maintain their biomass through the years. These results were consistent for the two interaction models that we considered, with and without saturation in interaction strengths. Our results therefore demonstrate the major potential role of phytoplanktonic cyst banks in maintaining biodiversity. These results align with the findings of previous theoretical studies, that have put forward similar effects of dormant stages in other taxa, such as plants (Levine & Rees, 2004), invertebrates (Wisnoski *et al.*, 2019) or (smaller) microbes (Jones & Lennon, 2010).

The effect of the cyst bank is, of course, contingent upon a long dormancy of the cyst stage. Dormancy has long been observed in field and experimental data, including for phytoplanktonic organisms (Eilertsen & Wyatt, 2000). It has been theorized to be an important and neglected process in the wider microbiology literature (Locey, 2010; Jones & Lennon, 2010). Processes behind diversity maintenance by the seed stage include the storage effect (Facelli *et al.*, 2005; Angert *et al.*, 2009; Bonis *et al.*, 1995) but are not limited to it. This is because a long dormancy alone can allow future recolonization of a community where counts of pelagic cells alone would suggest that some species have gone extinct. This colonization-in-time may of course combine with present recolonization from other spatial areas (Shmida & Ellner, 1984). In our case, our focus on phytoplankton led us to assume that organisms moved between the coast and the ocean, which were largely synchronous environments. Spatial recolonization was therefore less important than temporal recolonization; the relative importance of the two processes may vary depending on the organisms and their environment.

The specificities of phytoplankton cysts, that usually fall to the ocean bottom in coastal

areas, led us to assume that only the "vegetative" stage (here, the classic pelagic form of planktonic cells) disperse. In some other metacommunity models with dormant seed banks (e.g. Wisnoski *et al.*, 2019), the dormant stage can disperse as well. This would be true for most plants too (and perhaps some phytoplankters in situations where they are transported by animals). However, the restriction about which stage can move did not change the general conclusion: the combination of spatial dispersal and dormancy through seed banks greatly helps biodiversity maintenance. In our study, this main result was also robust to changes in exchange parameters and mean interaction values in the community.

The various species present in the community had different survival probabilities in the absence of a seed bank. Some species could persist without a cyst bank while others could not (which confirms conclusions from Hellweger *et al.* 2008 for single species). Other species periodically disappeared from the community in the open ocean, while being able to reinvade the coast which connected to the cyst bank. This suggests that some species may be locally transient: they are filtered out from certain patches, but can reinvade more or less periodically the environment (Guittar *et al.*, 2020). Certain species characteristics could explain species extinction, whether definitive or only temporary: higher amplitudes of population variation were typically associated with extinctions. We identified, by studying realised population growth rates (Fig. S7 in SI), that a smaller niche width (i.e., being a specialist) or being strongly affected by species interactions can explain rapid extinction without a cyst bank.

Despite the evidence for seed bank effects that we and others uncovered, phytoplanktonic community models designed to explain biodiversity usually avoid modelling seed/cyst banks. In our view, this may decrease the possibility of spontaneous re-colonization at the coast (at very low densities initially), which can then spill to the open ocean by progressive dispersal by the currents. If the goal of a community-level model is very short-term prediction (days, weeks), this recolonization can probably be neglected. However, over multiple years, ignoring cryptic stages allowing recolonization could strongly bias our view of long-term coexistence. Long-term phytoplankton coexistence modelling (over multiple decades or more) likely re-

quires that we take into account cysts, whose influence may become only more important as the timescale increases, due to the very long possible dormancies that have been evidenced (Ellegaard & Ribeiro, 2018; Sanyal *et al.*, 2018). When modelling different stages of the life cycle in a detailed manner – as done here – is impractical, the recolonization could perhaps be simplified to a stochastic immigration term (as done in Stock *et al.* 2005 in a single-species context). This suggestion certainly extends to models of (terrestrial) plant community dynamics.

More research on dormant stages may be needed to parameterize truly predictive mechanistic phytoplankton models with multiple life stages, in particular to inform parameters such as the sinking rate of resting cells, as well as burial and resuspension parameters. These parameters are all linked to hydrodynamics (Yamamoto *et al.*, 2002; Yñiguez *et al.*, 2012) and may locally vary. Sinking rates show an interesting conflict between short- and long-term survival: in coastal areas, a fraction of sinking cells contribute to the cyst bank, increasing the odds of species long-term survival at the cost of short-term individual cell survival. But high sinking rates are essentially "wasted" in the open ocean – whether different sinking rates can be selected, to some degree, by such different environments could be quite revealing. How cells get up rather than down in water column might be as interesting but more difficult to study. The likely idiosyncratic nature of recolonization by cysts – due to the contingency on local hydrodynamics – means that experimentation might be the only manner in which the frequency of reinvasion can be assessed. Currently, one of the only parameters measured in the field is the rate of survival of the cells found in the sediment (Montresor *et al.*, 2013; Solow *et al.*, 2014). While very important, this parameter is a necessary not sufficient condition for reinvasion of the population at future times. We need more information about the abilities of cysts buried in the sediment to come up to the pelagic zone, which is required for recolonization to actually occur. Many factors may contribute: bottom currents, benthic animals, ... We therefore encourage both experiments and field observations to follow actual seed trajectories, in order to help us understand this cryptic part of the diversity maintenance

process.

Acknowledgements

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