

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 co-exist 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 metacommunity model of interacting phytoplankton species with a cyst bank. The model is parameterized with empirically-driven growth rates 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

1 Introduction

2 How the high biodiversity of primary producers maintains is still an unresolved question for both
3 experimental and theoretical ecology. Terrestrial plants and phytoplanktonic communities can
4 present hundreds of species relying on similar resources, a situation where Gause's principle implies
5 that a handful of species should outcompete the others. Some degree of niche differentiation,
6 perhaps hidden to the human observer, is generally expected for coexistence to maintain (Chesson,
7 2000). However, a complex life-history structure can further increase the likelihood of coexistence
8 (Loreau & Ebenhöf, 1994; Moll & Brown, 2008; Fujiwara *et al.*, 2011; Chu & Adler, 2015), and so
9 does the response of life history traits to variation in the environment (Chesson & Huntly, 1988;
10 Rees *et al.*, 2001; Huang *et al.*, 2016).

11 Analyses of coexistence in terrestrial plant communities sometimes take into account several life
12 stages (e.g., Aikio *et al.*, 2002; Comita *et al.*, 2010; Chu & Adler, 2015) though many consider only
13 a single life-stage (see, among others, Ellner, 1987; Levine & Rees, 2004; Martorell & Freckleton,
14 2014; Adler *et al.*, 2018). When considering at least two stages, seeds/seedlings and adults, several
15 mechanisms that can contribute to long-term coexistence in spatially and/or temporally fluctuating
16 environment have been uncovered (Shmida & Ellner, 1984; Chu & Adler, 2015). The storage effect,
17 a major paradigm in modern coexistence theory (Chesson, 2000, 2018), is one of them. It has
18 first been defined by the presence of a long-lived life stage combined with temporal variation in
19 recruitment from this stage that helps escape interspecific competition (Chesson, 1986; Cáceres,
20 1997; Ellner *et al.*, 2016). The storage effect has often been discussed in the presence of a seed
21 bank (Aikio *et al.*, 2002; Angert *et al.*, 2009; Chu & Adler, 2015). However, the contribution of
22 seeds to coexistence may be much larger than their potential contribution to the storage effect.
23 The seed stage itself contrasts with other parts of the life cycle as organisms can enter a dormant
24 phase which allows them to sustain harsh environmental conditions for long periods of time (Aikio
25 *et al.*, 2002). Although this is favourable ground for a storage effect, a long-lived seed bank can help
26 coexistence by other, simpler means. For instance, in the meta-community model of Wisnoski *et al.*
27 (2019), when dormancy and dispersal are present (without seed dispersal), local diversity increases
28 in temporally fluctuating environments. In their model, adding a dormant stage could increase

29 species diversity both at the local and regional scales. These results suggest that considering a seed
 30 stage in dynamical models can profoundly alter our understanding of population (Nguyen *et al.*,
 31 2019) and community persistence (Manna *et al.*, 2017; Wisnoski *et al.*, 2019).

32 Although there is some awareness of the role of cryptic life stages in shaping terrestrial plant coex-
 33 istence, the effect of such dormant life stages on aquatic plant communities, and more specifically
 34 that of phytoplanktonic algae, is often ignored. The classical view behind phytoplankton dynamics
 35 is that their blooms (peaks in abundances several orders of magnitude above their baseline level) are
 36 due to seasonal variation in light, temperature and nutrients, as well as hydrodynamics processes
 37 (Reynolds, 2006). In this mindset, differential responses to environmental signals ensure the coex-
 38 istence of multiple species (Margalef, 1978; Smayda & Reynolds, 2001), while always assuming that
 39 vegetative cells are already present in the environment. Momentary disappearances of a species
 40 are viewed as sampling issues at low density. However, a complementary hypothesis suggests that
 41 resuspension and germination of phytoplanktonic resting cells, or cysts (Patrick, 1948; Marcus &
 42 Boero, 1998), is another major player allowing re-invasion from very low or locally zero popula-
 43 tion densities. This long-standing hypothesis is supported by recent reviews (Azanza *et al.*, 2018;
 44 Ellegaard & Ribeiro, 2018) which confirm that life history strategies including dormant cysts are
 45 widespread in phytoplankton. [Cyst formation can either be part of the lifecycle of phytoplankton](#)
 46 [species and result from sexual reproduction or be triggered by specific environmental conditions](#)
 47 [leading to asexual resting stages \(Ellegaard & Ribeiro, 2018\).](#) A variety of models have endeav-
 48 oured to explain and predict amplitude, timing and/or spatial distribution of blooms by explicitly
 49 modeling multiple stages in the life cycle of a particular species, but without interactions with
 50 other organisms (see for example McGillicuddy *et al.*, 2005; Hense & Beckmann, 2006; Hellweger
 51 *et al.*, 2008; Yñiguez *et al.*, 2012). Two-to-four species (Estrada *et al.*, 2010; Yamamoto *et al.*,
 52 2002) models also exist, but they focus on explaining the dynamics of a single cyst-forming species
 53 interacting with vegetative-only groups. This state of affairs means that we currently have no
 54 clear understanding of how the cyst stage might help maintain biodiversity in species-rich commu-
 55 nities. In the present paper, we demonstrate the potential role of cyst banks using a phytoplankton
 56 community dynamics model including a cyst bank.

57 Phytoplankton communities in coastal environments may benefit from seed banks (hereafter called
58 cyst banks to be more consistent with the terminology in use for such species) even more than
59 the oceanic communities (see for example McGillicuddy *et al.*, 2005), as the distance to the sea
60 bottom is smaller, which favours recolonization from the sea bottom, something that is impossible
61 in the deep ocean. Moreover, ‘horizontal’ exchanges between oceanic and coastal pelagic phyto-
62 planktonic communities are usually observed. Smayda (2002) coined the term “pelagic seed bank”
63 to characterize the contribution of the ocean to coastal communities. This has been noticed for
64 dinoflagellates especially (Tester & Steidinger, 1997; Batifoulier *et al.*, 2013). Conversely, in many
65 other bloom-forming species, the nutrient-rich coastal areas might function as a reservoir for the
66 biodiversity in the ocean, given the more accessible cyst bank at the coast, especially in the long
67 run. Indeed, cysts are able to germinate again after dozens of years (McQuoid *et al.*, 2002; Elle-
68 gaard & Ribeiro, 2018) or even thousands of years (Sanyal *et al.*, 2018) of dormancy. Therefore,
69 we consider in this study three interlinked compartments: the coastal pelagic environment, the
70 seed (cyst) bank, and the pelagic open ocean. The coastal pelagic environment acts as a bridge
71 between the cyst bank and the open ocean.

72 Our model is parameterized from field data (growth and interaction rates), and includes biotic and
73 abiotic constraints (e.g., particle sinking). In our analyses, [we examine how cyst banks may influ-](#)
74 [ence the maintenance of biodiversity under changing biotic interactions or changing environmental](#)
75 [conditions.](#) ~~W~~We either add or remove the dormant compartment, which allows to pinpoint its
76 contribution to coexistence. We find that the presence of cysts prevents the extinction of several
77 species. Cyst banks also allow a community to maintain its richness even with strong disturbances
78 of its interaction network, unless facilitative interactions completely eclipse competitive interac-
79 tions. Changes in the environment, here represented by an increase in the mean temperature, can
80 also be buffered by cyst banks. Finally, we discuss the importance of this often ignored life stage in
81 phytoplanktonic demography and the information that would be required to further more accurate
82 modeling of cyst bank dynamics.

83 Methods

84 Models

85 Our models build atop recent models developed by Shoemaker & Melbourne (2016) and Wisnoski
 86 *et al.* (2019), although they diverge in several aspects developed below (e.g., possibility for facili-
 87 tative interactions). These discrete-time models are designed for metacommunities with multiple
 88 interacting populations. Any discrete-time model requires an ordering of events; in our models,
 89 these unfold as follows: first, populations grow or decline according to a Beverton-Holt (BH) mul-
 90 tispecies density-dependence (eqs. 1 and 3), and then, in a second step, exchanges occur between
 91 the different compartments or patches constituting the metacommunity (eq. 4).

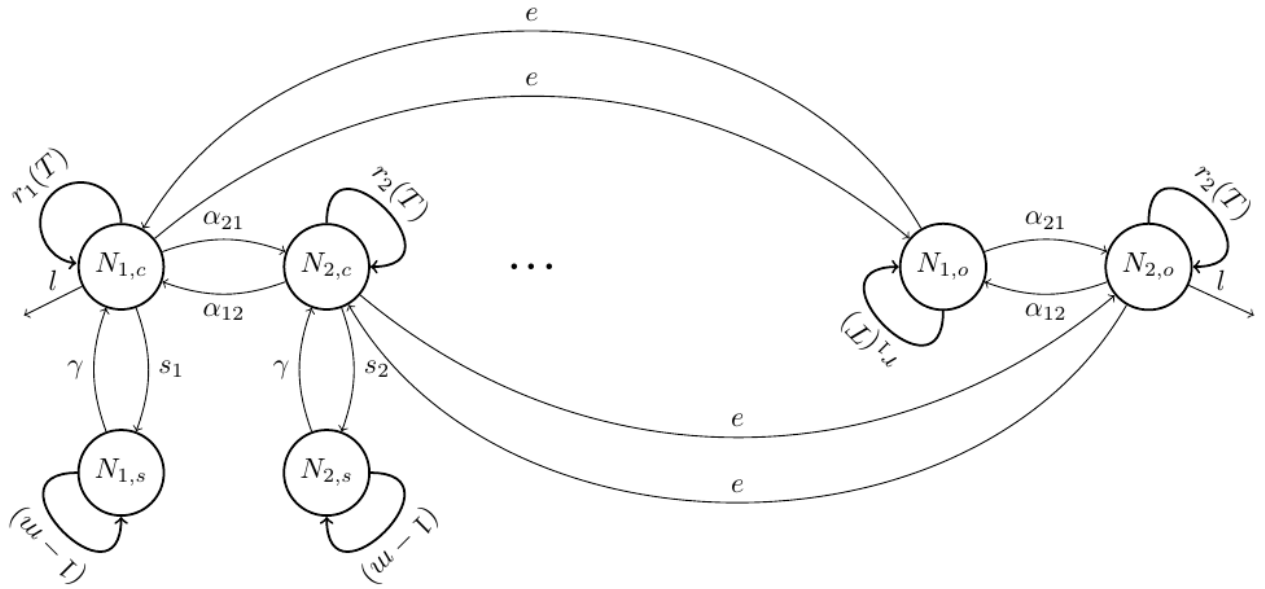


Figure 1: Conceptual model of the exchanges between compartments in the metacommunity (states and parameters are defined in Table 1)

92 In this paper, individuals are phytoplanktonic cells that move between the upper layer of coastal
 93 water, its bottom layer where a cyst bank accumulates in the sediment, ~~and the ocean and the~~
 94 ~~oceanic zone surrounding the coastal water masses~~ (hereafter "the ocean"). Only oceanic and
 95 coastal pelagic cells are subject to BH-density dependence. Cysts are only affected by mortality
 96 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 this 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), which is also used in Shoemaker & Melbourne (2016) and Wisnoski *et al.* (2019). However, the rate of facilitative interactions, which we found to be rather high compared to common assumptions (Picoche & Barraquand, 2020), could destabilize the community. We subsequently define saturating interactions (model II, eq. 3) based on Qian & Akçay (2020) who showed that mutualist interactions could stabilize communities when saturation was included. ~~More specifically, i~~In our case, the first step of the model I can be written as

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

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

$$r_i(T) = E(T)f_i(T) \quad (2)$$

$$\text{where } E(T) = d \times 0.81e^{0.0631T_{\circ c}}$$

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

120 The metabolism part describes the maximum achievable intrinsic growth rate based on Bissinger
 121 *et al.* (2008), as an update of the formula by Eppley (1972) used by Scranton & Vasseur (2016).
 122 This maximum daily intrinsic growth rate is weighted by the daylength d as no growth occurs at
 123 night. The niche part $f_i(T)$ describes the decrease in growth rate due to the difference between the
 124 temperature in the environment and the taxon-specific thermal optimum $T_{K,i}^{opt}$, and is controlled
 125 by the species-specific thermal decay b_i , which depends on the niche width. Parameterisation is
 126 further detailed in Section S1 of the SI.

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

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

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

137 After growth and mortality processes occur, exchanges take place between the three compartments,
 138 which constitutes the second step of the model (eq. 4):

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

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
$T_{K/^{\circ}C}$	Temperature	NA ($K/^{\circ}C$)	Dynamic
$r_i(T)$	Growth rate of taxon i	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	0.5 (%)	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, taxon-specific (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	$\{0.1; \mathbf{0.3}; 0.5\}\beta(0.55, 1.25)$	Fixed
e	Exchange rate between ocean and coast	0; 0.4; 0.9	Fixed
l	Loss rate of pelagic phytoplanktonic cells	0.04; 0.1; $\mathbf{0.2}$	Fixed
m	Cyst mortality rate	$\mathbf{10}^{-5}$	Fixed
ζ	Cyst burial rate	$10^{-3}, \mathbf{10}^{-2}, 10^{-1}$	Fixed
γ	Germination \times Resuspension rate	$(10^{-3}, \mathbf{10}^{-2}, 10^{-1}) \times (10^{-5}, 10^{-3}, \mathbf{10}^{-1})$	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. $\beta(0.55, 1.25)$ indicates the Beta distribution with parameters 0.55 and 1.25. For γ , germination values for sensitivity analysis were multiplied by the reference value for resuspension, and conversely.

Each compartment (ocean, coast, cyst bank) contains 10^3 cells at the beginning of the simulation, and the dynamics are run for 30 years with a daily time step. We model the temperature input as a noisy sinusoidal signal with the same mean and variance as the empirical data set described below, i.e. the amplitude of the sinusoid is 12.4°C and the standard deviation of the noise SD is 0.25.

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)

148 considered a rate around 0.04 day^{-1} while a review by Sarthou *et al.* (2005) indicates a grazing
149 rate of the standing stock between 0.2 and 1.8 day^{-1} and an autolysis rate around between 0.005
150 and 0.24 day^{-1} (in the absence of nutrients, or because of viral charge). A maximum value of 0.2
151 is fixed for the model (see Section S3 of the SI for more details).

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

159 **Exchange rate** The exchange rate between the ocean and the coast depends on the shape and
160 location of the coast (estuary, cape, ...). ~~At our calibration site (see below), the renewal time ranges~~
161 ~~between 1 and 2.5 days (Ascione Kenov *et al.*, 2015), which corresponds to a daily exchange rate~~
162 ~~between 40 and 100 %~~ Our calibration site is located at an inlet linking the ocean and the coast.
163 The flow at the inlet leads to a renewal time of the coastal area water evaluated between 1 and
164 2.5 days (Ascione Kenov *et al.*, 2015), which corresponds to a daily exchange rate between 40 and
165 100 %.

166 **Cyst mortality and burial** Cyst loss is the result of cyst mortality m and burial by sedimenta-
167 tion ζ . Mortality values range between 10^{-5} and 10^{-4} per day (more details on the approximation
168 of mortality rates from McQuoid *et al.* 2002 are given in Section 3 of the SI). However, cyst burial
169 by sedimentation is the prevailing phenomenon. Indeed, once cysts have been buried, they are not
170 accessible for resuspension even if they could have germinated from an accessible location. Burial
171 depends on the hydrodynamics of the site, but also on biotic processes (i.e., bioturbation) and
172 anthropogenic disturbances such as fishing or leisure activities (e.g., jet skiing). This parameter is
173 thus heavily dependent on the environmental context and varies here between 0.001 and 0.1 per

174 day.

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

183 **Parameter calibration**

184 In addition to phenology parameters, whose estimation process is described in Section S1 of the SI,
185 the 49 non-zero interactions that form the community matrix of the model are calibrated from field
186 data (Picoche & Barraquand, 2020)¹. We used initial interaction estimates from a previous time
187 series modelling study (Picoche & Barraquand, 2020, see Section 2 of the SI for the equations).
188 These initial interaction estimates were then calibrated, to take into account the differences in
189 model structure and timescale between this study and Picoche & Barraquand (2020).

190 The calibration procedure consisted in launching 1000 simulations, each characterized by a specific
191 set of interaction coefficients. More precisely, for each simulation, an interaction coefficient (α_{ij} in
192 model I, H_{ij} in model II) has probability $\frac{1}{5}$ to keep its present value, being increased or decreased
193 by 10%, or being halved or doubled. The numbers of coastal pelagic cells (which are the ones
194 measured empirically) are then extracted over the last 2 years of the simulation, and compared to
195 observations using the following summary statistics:

- 196 • 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
197 the logarithm of the mean abundance of taxon i

¹We use this ref in the sentence just after, should we keep the two of them or remove this one or the following one?

- 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. ~~Models~~Parameter sets are then ranked according to their performance for each summary statistic, and ~~the set of interactions with the best rank for each summary statistics is selected~~ we selected the set of interactions optimizing the sum of the ranks corresponding to each summary statistics.

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 for 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 possible important

223 contribution of the benthic environment (Guarini *et al.*, 2004). We aim to approximate the pop-
224 ulation dynamics of the 11 most abundant and most frequent groups of genera (taxa) focusing
225 on the amplitude of fluctuations and their timing (phenology). The estimation of the parameters
226 characterizing each taxon (T_i^{opt} and b_i), is described in Section 1 of the SI. The interactions between
227 model taxa have already been inferred from a MAR model (Picoche & Barraquand, 2020). The
228 community matrix is characterized by a phylogeny-based modular structure which differentiates
229 between centric and pennate diatoms and dinoflagellates, a high level of facilitative interactions
230 ($\approx 70\%$) and a strong self-regulation.

231 Scenarii

232 The effect of the cyst bank on biodiversity and community dynamics can be evaluated through
233 the response to disturbance with and without the cyst compartment. Removing the cyst bank was
234 done by setting cyst mortality to 100%. We evaluated two main disturbances:

- 235 1. increase or decrease in interaction strength
- 236 2. temperature change, either in mean value or variability

237 In the first scenario, interaction strengths were multiplied or divided by a factor ranging between
238 1 and 10. In order to differentiate the effects of facilitative and competitive interactions on coex-
239 istence, only one type of interactions was subject to this change at a time. For each value of the
240 multiplicative factor, we therefore ran 4 simulations for each growth model: one where positive (re-
241 spectively, negative) interactions were multiplied by the factor and one where positive (respectively,
242 negative) interactions were divided by the same factor. Here, both intraspecific and interspecific
243 interactions were changed; we present in Section 5 of the SI additional simulations with a change
244 in interspecific interactions only.

245 In the second scenario, five different climate change scenarios were assessed. In the first three, the
246 average temperature was increased by 2, 5, or 7°C (Boucher *et al.*, 2020). In the next two, keeping
247 the reference average temperature, the total variance of the temperature, including seasonality and
248 noise, was either decreased or increased by 25%. ~~To acknowledge the stochasticity induced by the~~

249 ~~noise, the model was ran with five different temperature signals in each case.~~Each climate change
250 scenario was run 5 times to account for the intrinsic stochasticity of the temperature signal.

251 In both scenarios, simulations were ran for 30 years for both population growth models, with and
252 without a cyst compartment, and only the last 2 years were considered for evaluating effects of
253 change in parameters and in temperature.

254 Results

255 Phytoplankton dynamics

256 The classical Beverton-Holt (model I) and saturating interaction (model II) formulations of multi-
257 species dynamics both reproduced the main characteristics of observed phytoplankton dynamics.
258 They produced one or two blooms during the year and a range of abundances covering several
259 orders of magnitude, with the right timing of the blooms. At the Auger site that was used for
260 calibration, abundances increase in spring and can last over part of summer, or start a new bloom
261 in autumn, which is what we observed as well in the models. Annual mean abundance of the
262 various taxa was also well reproduced. That said, in some cases, abundances could be lower than
263 expected and the variation in abundances due to seasonality was underestimated (Fig. 2). In all
264 cases, saturating interactions led to higher abundances than mass-action interactions throughout
265 the year (Fig. S5).

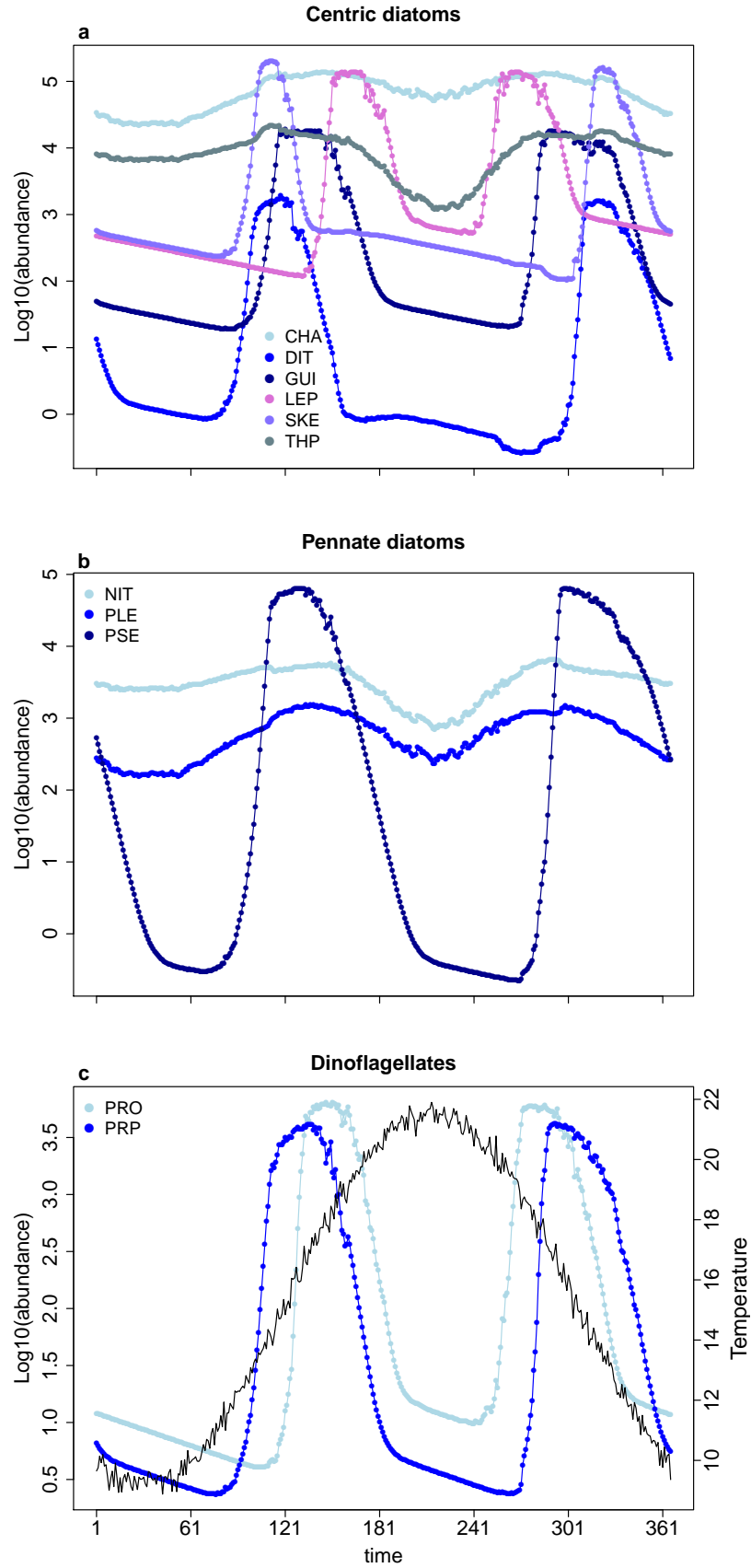


Figure 2: Simulated phytoplankton dynamics for a year in model I. Each panel corresponds to a cluster of interacting taxa.

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 m had the more impact of 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 the exchange rate set to 0), the final richness of the 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.

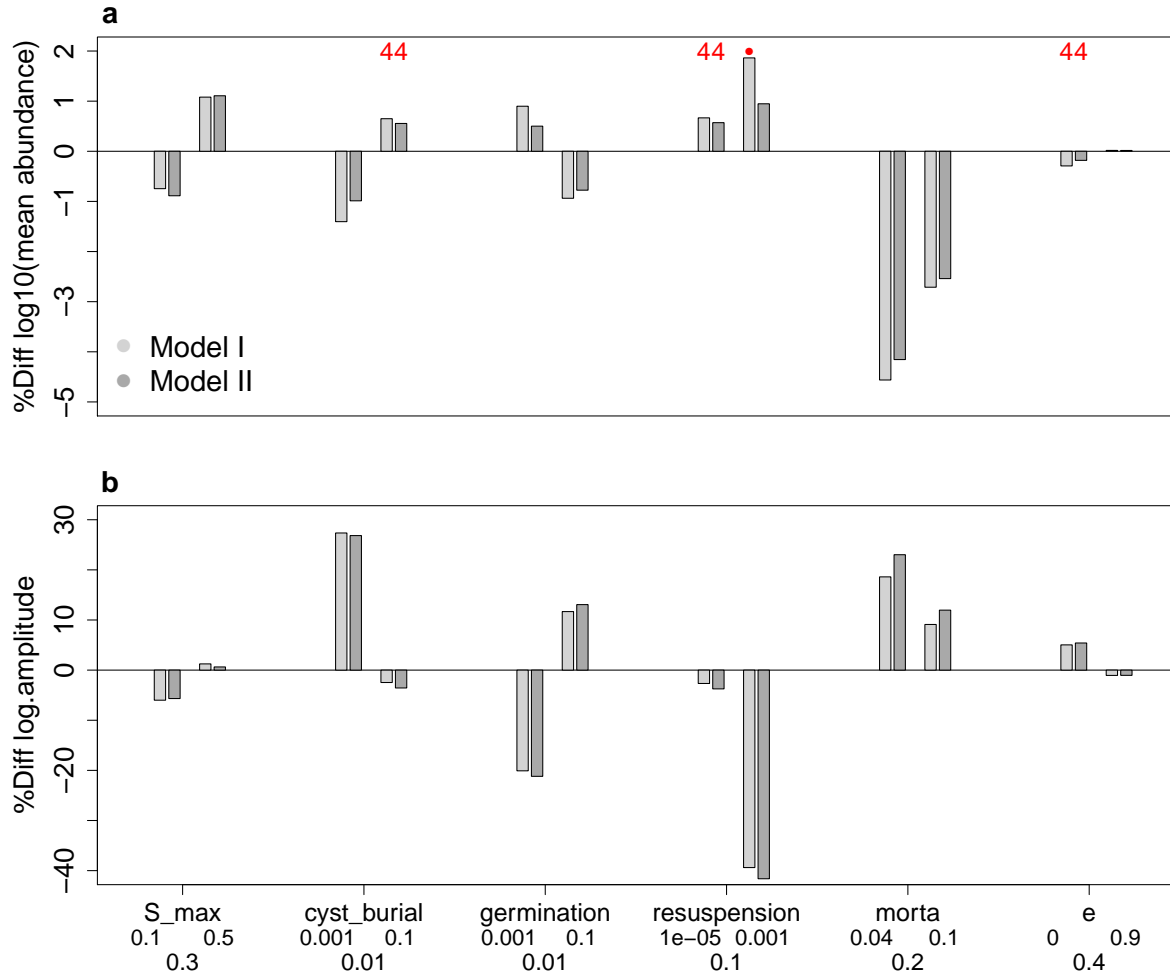


Figure 3: Sensitivity of the model to variation in parameters, measured as the difference between the reference simulation metric and the metric for the simulation including a change in parameter. The two metrics used were the average decimal log abundance (a) and the decimal logarithm of the ratio between maximum and minimum abundance (b) of the coastal phytoplanktonic community. 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 inside 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. Without any other disturbance to the system, this led to a decrease in taxon richness from 11

294 to 4 taxa at the end of the simulation (Fig. 4) while the total abundance of phytoplankton was
295 not strongly affected (around 10^5 in all cases). The inverse of the Simpson index (the second Hill
296 number) decreased from approximately 3 to 1, showing that the disappearance of the cyst bank
297 does not affect only the rarest species.

298 **Biotic effects**

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

312 The inverse of the Simpson index was also affected by the changes in interaction strengths, with
313 similar patterns to richness, as it was lowest for high facilitation or low competition. Presumably
314 some species reach very high growth rates in these scenarios, which then feed backs onto community
315 dynamics, generating lower diversity in the end.

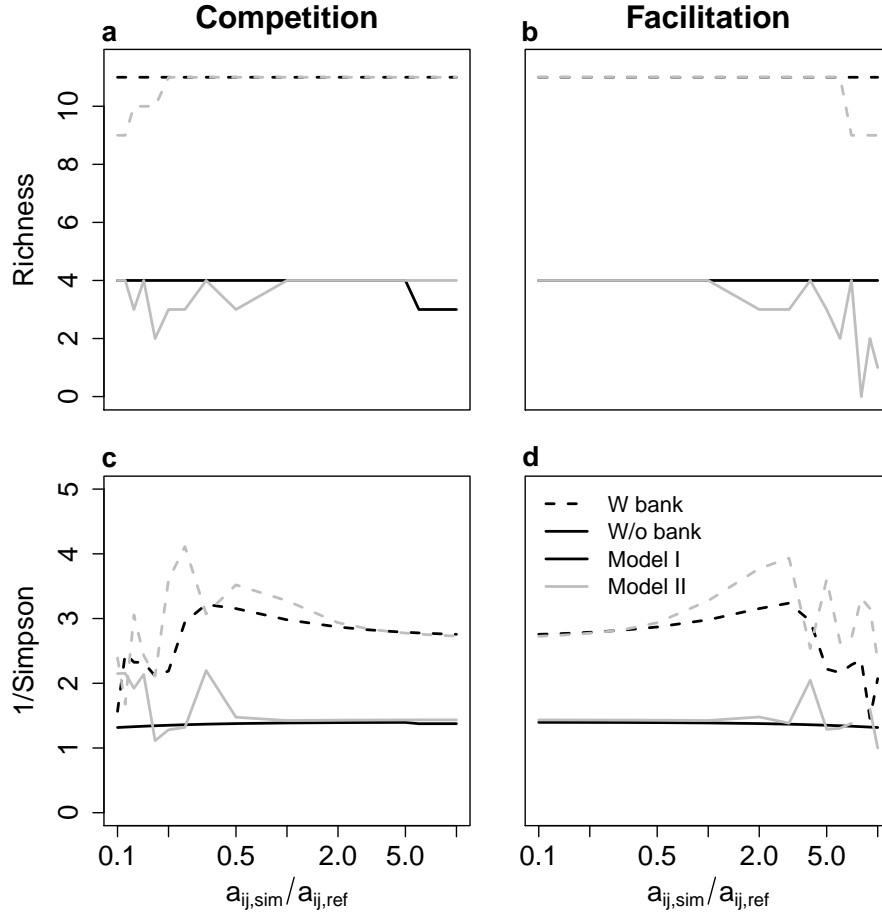


Figure 4: Measures of biodiversity in the ocean at the end of the simulation: a-b) richness and c-d) inverse of the Simpson index, with (dashed line) and without (solid line) a cyst bank, as a function of the strength of competition and facilitation with a classical Beverton-Holt (black lines) or a saturating interaction (grey lines) formulation. The x-axis shows the factor by which each interaction was multiplied (note the logarithmic scale).

316 Taxa which disappear were always the same and were characterized by a lower minimum abun-
 317 dance, a higher amplitude of fluctuations and a small niche (Fig. 5). In contrast, their interactions
 318 were not qualitatively different from the other taxa.

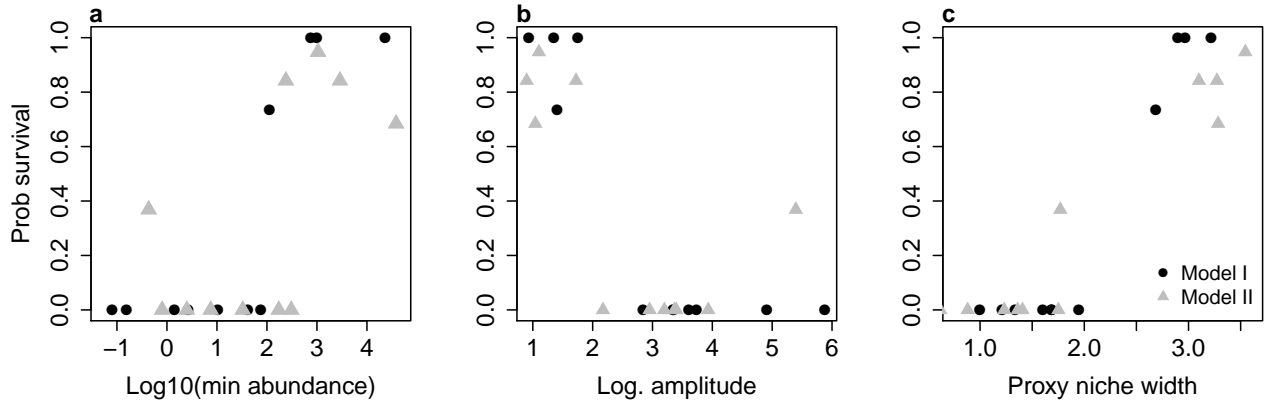


Figure 5: Probability of survival of taxa when competition increases in the absence of a cyst bank, as a function of their dynamics characteristics (minimum abundance, logarithm of amplitude and niche width) in the reference parameter set.

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 (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). 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 consistently 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 is also true without a cyst bank. The presence of the cyst bank did increase total abundance though.

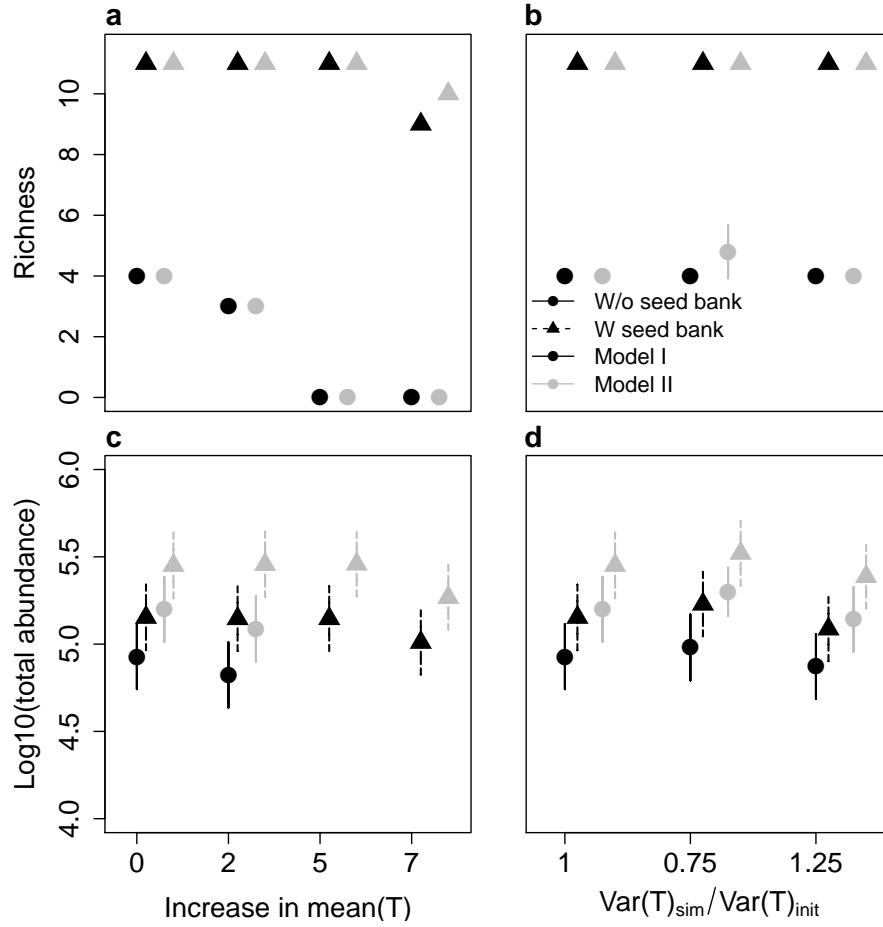


Figure 6: Variation in richness and total abundance with and without a cyst bank as a function of the mean and variance of the temperature with a classical Beverton-Holt (left) or a saturating interaction (right) formulation.

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,

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

351 The effect of the cyst bank is, of course, contingent upon a long dormancy of the cyst stage.
352 Dormancy has long been observed in field and experimental data, including for phytoplanktonic
353 organisms (Eilertsen & Wyatt, 2000). It has been theorized to be an important and neglected
354 process in the wider microbiology literature (Locey, 2010; Lennon & Jones, 2011; Wisnoski &
355 Lennon, 2020). Processes behind diversity maintenance by the seed stage include the storage
356 effect (Bonis *et al.*, 1995; Facelli *et al.*, 2005; Angert *et al.*, 2009) but are not limited to it. This
357 is because a long dormancy alone can allow future recolonization of a community where counts of
358 pelagic cells alone would suggest that some species have gone extinct. This colonization-in-time
359 may of course combine with present recolonization from other spatial areas (Shmida & Ellner,
360 1984). In our case, our focus on phytoplankton led us to assume that organisms moved between
361 the coast and the ocean, which were largely synchronous environments. Spatial recolonization was
362 therefore less important than temporal recolonization; the relative importance of the two processes
363 may vary depending on the organisms and their environment.

364 The specificities of phytoplankton cysts, that usually fall to the ocean bottom in coastal areas,
365 led us to assume that only the “vegetative” stage (here, the classic pelagic form of planktonic
366 cells) disperse. In some other metacommunity models with dormant seed banks (e.g. Wisnoski
367 *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 affect 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 re-colonization can probably be neglected. However, over multiple years, ignoring cryptic stages allowing re-colonization could strongly bias our view of long-term coexistence. Long-term phytoplankton coexistence modelling (over multiple decades or more) likely requires 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). 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

396 *et al.* 2005, who do this in a single-species context). This suggestion certainly extends to models
397 of (terrestrial) plant community dynamics.

398 More research on dormant stages may be needed to parameterize truly predictive mechanistic
399 phytoplankton models with multiple life stages, in particular to inform parameters such as the
400 sinking rate of resting cells, as well as burial and resuspension parameters. These parameters are
401 all linked to hydrodynamics (Yamamoto *et al.*, 2002; Yamamoto & Seike, 2003; Yñiguez *et al.*, 2012)
402 and may locally vary. Sinking rates are especially worthy of interest as they have opposed effects
403 on community dynamics in different compartments. In coastal areas, sinking cells contribute to the
404 cyst bank, increasing species long-term survival and buffering ability, while sinking cells are lost in
405 the ocean. Different coast/ocean mixing rates or resuspension rates may therefore lead to diverging
406 effects of sinking on community diversity and stability. In the opposite direction, the potential
407 idiosyncratic nature of recolonization by cysts – due to the contingency on local hydrodynamics –
408 means that experimentation might be the only manner in which the frequency of reinvasion can be
409 assessed. Currently, one of the only parameters measured is the rate of survival of the cells found
410 in the sediment (Montresor *et al.*, 2013; Solow *et al.*, 2014). While very important, this parameter
411 is a necessary not sufficient condition for re-invasion of the population at future times. We need
412 more information about the abilities of cysts buried in the sediment to come up to the pelagic zone,
413 which is required for recolonization to actually occur. We therefore encourage both experiments
414 and field observation to follow actual seed trajectories, in order to help us understanding this
415 cryptic part of the diversity maintenance process.

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