

# Strong self-regulation and widespread facilitative interactions between groups of phytoplankton

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## Abstract

XXX

## Introduction

How species or related genera can coexist together in spite of likely competition is still one of the main puzzles of community ecology, especially for primary producers that seemingly share the same basic resources [REFS]. Many theoretical studies of competition models have shown that competitive exclusion is likely in those circumstances [REFs], unless some special mechanisms involving spatial or temporal variation are at play<sup>1,2,3</sup> [More refs?]. Neutral theory, that in its most basic formulation assumes equal competitive abilities [REFs] and non-equilibrium coexistence sustained by immigration from a larger pool (but see ref.<sup>4,5</sup>) has been proposed as a solution to explain highly diverse communities<sup>6</sup> [More refs?]. However, the evidence gathered from plant communities starts to suggest that, in fact, niche rather than neutral processes may be paramount, with intraspecific competition dwarfing interspecific competition in most cases<sup>7,8</sup>. Whether these conclusions apply to other systems is currently unknown.

Moreover, the meta-analysis by Adler et al.<sup>8</sup> reported a large number of facilitative interactions (30%) [I think, check] and reviews<sup>9</sup> [More refs] have highlighted that in fact that facilitation may be much more widespread than ecologists usually tend to think. Although some theoretical studies suggest that facilitative interactions can be destabilizing (sensu resilience) and therefore undermine coexistence<sup>10</sup>, many modelling studies<sup>11</sup> [More refs] have suggested that facilitative interactions can to a large degree benefit coexistence.

Here, we analyse a large dataset of several long-term time series of phytoplankton dynamics along the French coastline , using statistical time series models allowing for interactions between groups.

## Results and discussion

Using MAR(1) autoregressive models, we have produced interaction matrices – Jacobian community matrices on the logarithmic scale<sup>12</sup> – that have two main features. First, we observe a strong self-regulation for all sites (Fig. 1, diagonal elements of all matrices), a feat that we have highlighted on a previous, more detailed analysis on one of the considered study sites only<sup>13</sup>. Second, although the percentage of facilitative interactions seem to vary among sites [insert percentages here], we have found that it is substantial for all sites: contrary to our initial expectations, commensalism (the interactions are rarely two-way mutualism [check]) seems to be the rule rather than the exception.

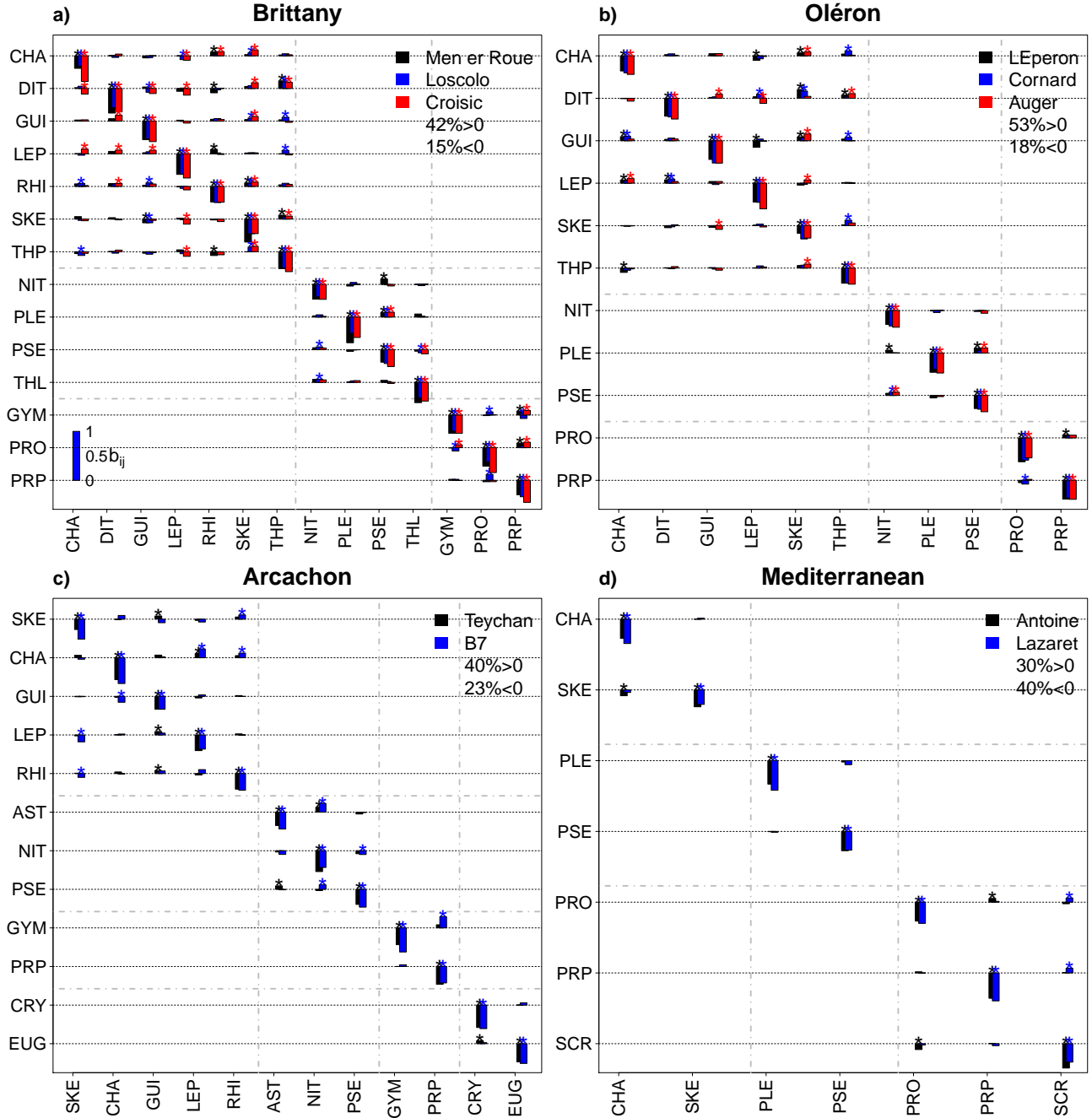


Figure 1: Interaction matrices in the 10 study sites, in 4 regions. Only interactions within clades (pennate and centric diatoms, dinoflagellates, other planktonic taxa) are allowed. The figure should be read as taxon  $i$  having effect  $e_{ji}$  on taxon  $j$ . The scale for the coefficient values is given at the bottom left of panel a). 95% significance of coefficients was determined by bootstrapping and is marked by asterisks (\*). The percentage of interactions keeping the same sign in each site for a given region is indicated in the legend. The identity matrix was subtracted to the interaction matrix ( $\mathbf{B}-\mathbf{I}$ ) in order to make effects on growth rates comparable. Composition of planktonic groups is given in the Supplementary Information.

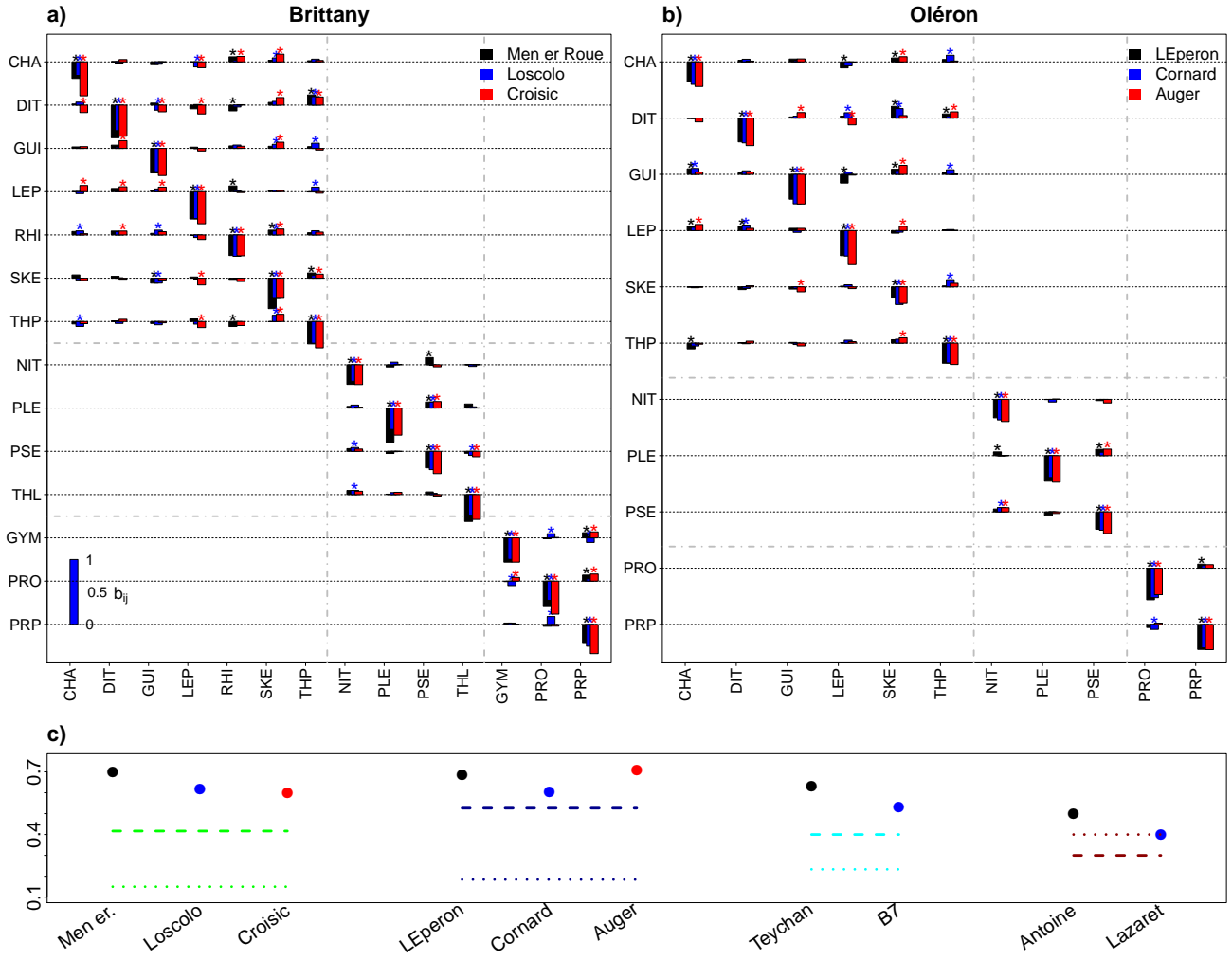


Figure 2: Interaction matrices estimated in Brittany (a) and in Marennes-Oléron (b). Only interactions between clades (pennate and centric diatoms, dinoflagellates, other planktonic taxa) are allowed. The figure should be read as taxon  $i$  having effect  $e_{ji}$  on taxon  $j$ . The scale for the coefficient values is given at the bottom left of panel a). 95% significance of coefficients was determined by bootstrapping and is marked by asterisks (\*). Other estimates for the 4 sites in Arcachon and the Mediterranean Sea can be found in the Supplementary Information. The identity matrix was subtracted to the interaction matrix ( $\mathbf{B}-\mathbf{I}$ ) in order to make effects on growth rates comparable. Composition of planktonic groups is given in the Supplementary Information. The ratio of positive interaction in each matrix is given by points in c) while the dashed (respectively, dotted) line represents to ratio of interactions remaining positive (respectively, negative) in all sites of a given region.

We then asked whether the stability (resilience) of those matrices was affected by the percentage of mutualistic interactions or their connectivity properties (Fig. 2).

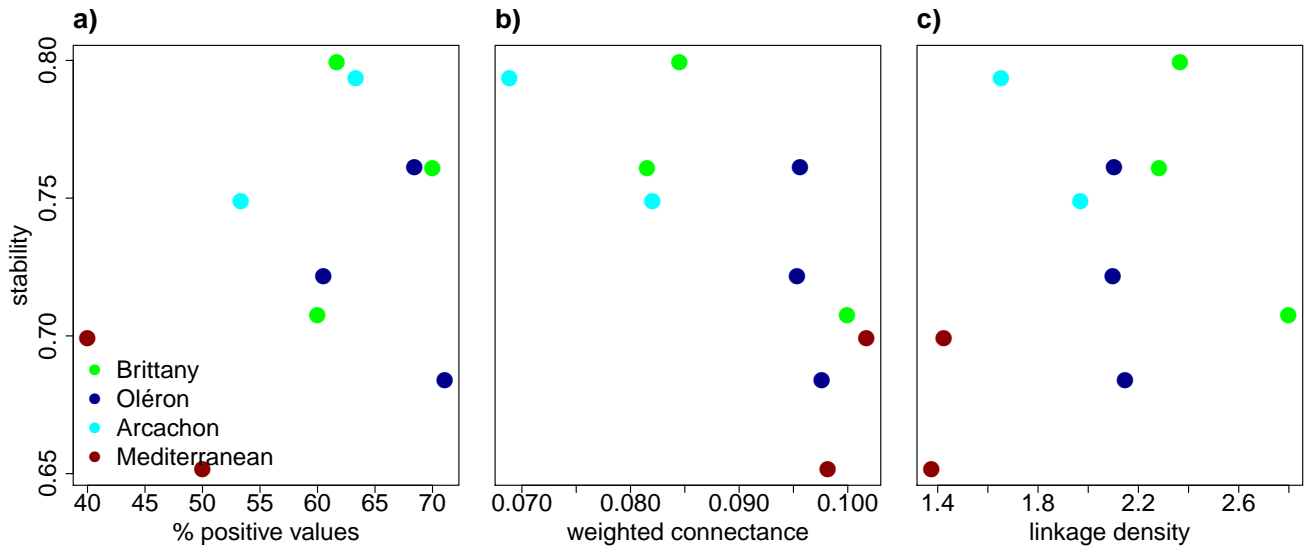


Figure 3: Stability (maximum eigenvalue of the community matrix  $\mathbf{B}$ ) as a function of network metrics in the 10 study sites. Each color corresponds to a given region. Metrics formula are given in the Methods.

More information than sign and the magnitude of interspecific / intergroup interactions can be gathered from interaction matrices. We investigated whether the matrix has some particular structure that could help theoretical ecology to make better null models of joint community dynamics and interactions<sup>14</sup>. We defined two scores, vulnerability (summed effect of others on the focal species growth rate) and generality (summed effect of the focal species onto other species growth rates). Species that were more self-regulating also had also a higher vulnerability score, and those two influences are likely to trade-off: a high degree of self-regulation somehow buffers outside influences. Species that were less self-regulating were also more likely to have a broad range of effects onto other species [to interpret this we may also need to check that they were more abundant, if so I would say that species varying broadly have a higher likelihood to generate effects in other species]. It is important to note, however, that these patterns are weak and there is therefore a considerable amount of randomness dominating the interaction matrix: many scenarios of self-regulation vs limitation by others are therefore possible.

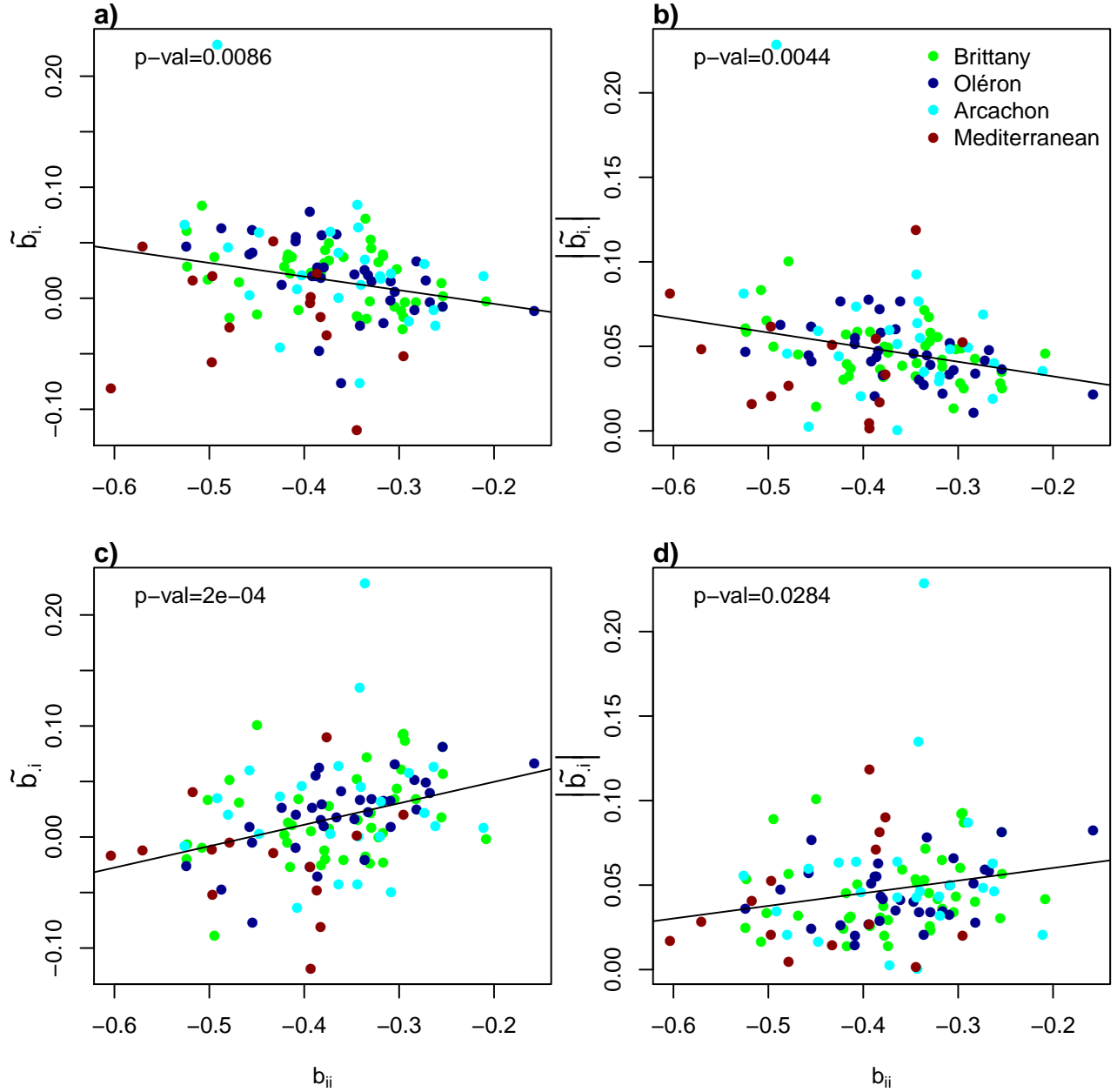


Figure 4: Average vulnerability (a-b) and generality (c-d), computed on raw values (a-c) or absolute values (b-d) of the community matrix coefficients for 10 different sites, as a function of self-regulation, for a pennate-centric interaction matrix, ignoring the coefficients which were forced to 0 in the estimation process. Each color corresponds to a given region. The p-value of the Pearson correlation between vulnerability (respectively generality) and self-regulation is given in the top left of each panel.

Aside from these trade-offs, some of which promote some stability (sensu invariability), we found no remarkable patterns of covariation between matrix elements (other than a mean-variance scaling of interaction coefficients, see SI XXX Fig. XXX). The big finding of our study seems really to be the presence of very large niche differences between the species, translating into a much higher intragroup competition, together with a high degree of facilitative net interactions. In our previous publication [REF], we have argued that those could arise from predation effects that

could well create apparent mutualism between prey species and strong intragroup density-dependence [REFs]. This is still very much likely here given our new study regions (Oléron, Brittany, Mediterranean) could have similar predators, though there are other possibilities.

Finally, we have sought to put these results in a broader context by compiling the intra vs. inter group estimates of previous MAR(1) studies (detailed in Appendix XXX). We have found that the order of magnitude of intra/inter interaction strengths considered here ( $\approx 10$ ) not particularly below those found for most planktonic systems. We include in Fig. 4 not only plankton studies but also a couple of vertebrate or insect studies on smaller (less diverse) communities where interactions are stronger. The conclusion from this comparison seems to be that any diverse system of competitors and facilitators seem to have evolved large niche differences making intragroup competition much higher than intergroup interactions.

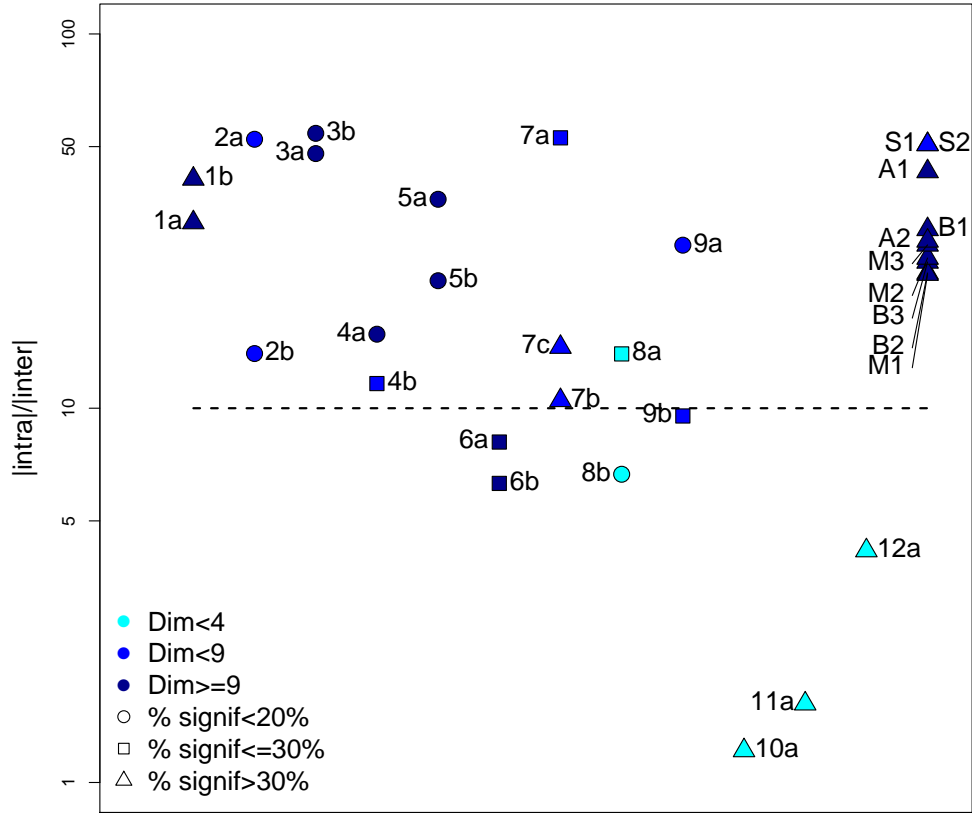


Figure 5: Ratio, on the log scale, of intra to intergroup interaction strengths for MAR(1) studies (corresponding articles are given in SI). The colour of each point corresponds to the number of species in the interaction matrix and its shape corresponds to the proportion of significant interactions. Intergroup interactions were set to 0 when they were not given in the studies (most of the time, because they were not deemed significant at the 95% threshold). Last column corresponds to the present study.

This dominance of niche differentiation is similar to what has been found in plant community studies<sup>5,8</sup>, and might be due to the ghost of the competition past, i.e., selection and evolution leading to progressive niche separation. Species have evolved niches that allow them not to compete or to interact only weakly (very strong facilitative

effects might be likewise destabilizing [je crois qu’il y a des refs sur les effets non-monotone des interactions +, je rechercherai]. The predator effects that we highlighted above can be comprised within such niche differentiation sensu largo: specialized predators can make strong conspecific density-dependence emerge [REFs], while switching generalists can also promote diversity [REFs, same from Oikos]. Both predators and resources have often symmetrical effects and can contribute to niche differentiation<sup>15</sup>

An intriguing new possibility, dubbed the “ghost of competition” present<sup>16</sup>, suggests that spatial patterns in relation to abiotic factors might have a large impact on the patterns inferred from interaction models. Recent combinations of model fitting and removal experiments have shown that the model fitting usually underestimate the effect of competitors that are uncovered by removal experiments<sup>16,17</sup>. This could occur for instance if species are spatially segregated (at a small scale) because each species only exists within a domain where it is relatively competitive, while a focal species could spread out if competitors were removed. This means that a species can be limited by competitors, but act so as to minimize competition (a little like avoidance behaviour in animals) so that competition is in effect hard to detect when all species are present. This would require some fine-scale segregation between phytoplankton species at the scale of interactions, i.e., at the microscale. At the moment, it is known that turbulence generates inhomogeneities at the microscale<sup>18,19</sup> but it is quite unclear how this affects multiple interacting species and which multivariate spatial patterns (as in ref.<sup>20</sup>) could be expected. Also, even if turbulence generates spatial structure with segregation between species, it is not quite clear that the “ghost of competition present” mechanism could work for plankton, where the turbulence may somehow dictates where the plankton patches can or cannot appear.

## Methods<sup>1</sup>

The methods used in this study have previously been applied at a smaller (regional) scale and have been described extensively in ref.<sup>13</sup> and Appendices. Here, we give a summary of these methods and refer readers to the previous study for further details and justification.

### Data collection

All data were collected as part of the National Phytoplankton and Phycotoxin Monitoring Network (REPHY<sup>21</sup>). This monitoring program requires sites along the French coastline to be sampled every 2 weeks within 2 hours of high tide since 1987 to determine both biotic (phytoplankton counts) and abiotic (water temperature, salinity) parameters. Phytoplankton cells above 20  $\mu\text{m}$  were identified as precisely as possible and counted with the Utermöhl method<sup>22</sup> using an optical microscope. Throughout the years, more than 600 taxa were identified at different taxonomic levels. We aggregated them at the genus, or group of genera, level based on previous work<sup>23</sup>, except for cryptophytes and

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<sup>1</sup>Only 1000 words for this awkward, badly written, draft: we can still triple the length



euglenophytes in Arcachon, which could not be identified below the family level.

The completeness of the time series depended on the accessibility of each study site. We selected 10 sites in 4 regions (Brittany, Marennes-Oléron, Arcachon and the Mediterranean Sea, a map is shown in the Supplementary Information) based on their compliance with the sampling design. For each species, the frequency of observations depended on local commonness and identification difficulty. For each region, we focused on the most abundant and most frequently observed species and we chose to restrain our analyses to the years after 1995, in which an important taxonomy training took place. When gaps did not exceed a month, missing values were linearly interpolated and remaining missing values were replaced by a random number between 0 and half of the lowest observed abundance<sup>24</sup>.

## MAR(1) model

Multivariate autoregressive (MAR) models are often used to determine the interspecific interactions and abiotic parameters shaping a community<sup>12</sup>. They are based on a stochastic, discrete-time Gompertz model which relates log-abundance of  $S$  species at time  $t+1$  to interactions with the rest of the community at time  $t$ , and effects of  $V$  abiotic variables at time  $t+1$ , following eq. 1.

$$\mathbf{n}_{t+1} = \mathbf{B}\mathbf{n}_t + \mathbf{C}\mathbf{u}_{t+1} + \mathbf{e}_t, \mathbf{e}_t \sim \mathcal{N}_S(0, \mathbf{Q}) \quad (1)$$

where  $\mathbf{n}_t$  is the  $1 \times S$  log abundance vector of abundance of phytoplankton groups,  $\mathbf{B}$  is the  $S \times S$  community (interaction) matrix,  $\mathbf{C}$  is the  $S \times V$  environment matrix describing the effects of  $V$  variables  $\mathbf{u}_{t+1}$  on species growth, and  $\mathbf{e}_t$  is a  $1 \times S$  noise vector which covers both process and observation error, following a multivariate normal distribution with a variance-covariance matrix  $\mathbf{Q}$ .  $\mathbf{Q}$  is diagonal and we have previously showed that this parsimonious choice did not affect qualitative results<sup>13</sup>.

We used the MARSS package<sup>25</sup>, in R, to estimate parameters with a previously described maximum likelihood procedure<sup>13</sup>.

We have previously published a very detailed analysis of one of the dataset (Arcachon). The analysis of real data was complemented by that of simulated data for a plankton time series set-up and confirmed the ability of the technique to infer biotic interactions and abiotic forcing<sup>13</sup>. This analysis revealed that the MAR(1) approach was satisfactory (i.e., no need for extra non-linearities to model the storage effect, which was found to be weak as in previous analyses of plant data for which strong-self regulation was observed<sup>7,26</sup>). We are therefore confident that the MAR(1) models presented here are appropriate models. In general, MAR(1) models tend to be fairly robust to small deviations of the underlying data-generating model, provided that one asks mainly order of magnitude of coefficients values (rather than very precise estimates) and sign of interaction coefficients<sup>27</sup>. [for ease of interpretation we also present the connexion between MAR(1) model coefficients and a Beverton-Holt model in SI XX [see also ref.<sup>27</sup>]]

In this study, the number of phytoplankton groups,  $S$ , varies between region but we keep the same 2 covariates,

i.e. water temperature and salinity. Therefore, the dimension of the equation system only depends on the number of groups we study, which ranges between 7 (Mediterranean Sea) and 14 (Brittany). The smallest system still requires 70 parameters to be estimated if we consider all possible interactions between species. Before analyzing these parameters, we wondered if such over-parameterization was necessary and compared different 'interaction scenarios' based on BIC. Our null model assumed no interaction between groups of species (diagonal interaction matrix) and was compared to four other models. The first model assumed that interactions could only occur between phylogenetically close organisms, i.e., within a class (namely, diatoms, dinoflagellates, and other phytoplanktonic organisms) while the second model further differentiated pennate and centric diatoms, The third model considered the inverse hypothesis that only unrelated organisms could interact (i.e., a diatom could only interact with a dinoflagellate or a cryptophyte, but not with another diatom), and the last model did not constrain the interactions at all (full interaction matrix). Based on convergent results in all sites (see Supplementary Information), we further investigated the second model, hereafter called the pennate-centric model.

## Interaction matrix analysis

The community matrix obtained from MAR(1) analyses can be used to determine the stability of a system<sup>12</sup>. We compared the maximum modulus of the eigenvalues of the pennate/centric matrices in each site, as a proxy of stability, to complexity-related metrics such as weighted connectance and linkage density<sup>19</sup>. Weighted connectance is a measure of the proportion of realized links, taking into account the shape of the flux distribution, while link density measures the average proportion and strength of interactions for a given species. These metrics are adapted to weighted interaction matrix but cannot accommodate for both positive and negative coefficients: we therefore chose to focus on the absolute values of these coefficients, which can be linked to their strength even though we do not necessarily know the kind of interaction it describes.

In addition to these network-level metrics, we also computed the average vulnerability (average effect of other taxa on a focal taxon) and generality (average effect of a focal taxon on other taxa) and compared these to the regulation a focal species exerted on itself.

Finally, we compared our results on self regulation v. interspecific interactions to results found in the literature with the same analyses. A list of the references is given in the Supplementary Information. Most of the time, authors only report significant coefficients and ignore weak effects. We therefore computed the mean interspecific interactions as either the mean value of significant coefficients only (see Supplementary Information), or the mean value of all coefficients outside of the matrix diagonal, replacing missing values by 0 (Fig. 5).

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