

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

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February 23, 2019

Abstract

The persistence of phytoplanktonic diversity in spite of competition for basic resources has long been a source of wonder and inspiration to ecologists. To sort out, among the many coexistence mechanisms suggested by theory and experiments, which ones actually maintain diversity in natural ecosystems, long-term field studies are paramount. Here, we analyze a large dataset of phytoplankton abundance time series, counted every two weeks over 20 years, at 10 sites along the French coastline. We estimate biotic interactions using dynamic, multispecies autoregressive models. We show that a strong self-regulation, with intraspecific competition strength an order of magnitude higher than interspecific, was present in all phytoplanktonic interaction networks. Furthermore, positive net effects between phytoplanktonic taxa constituted at least 40% of non-null interactions in all sites. Both strong self-regulation and widespread net facilitation should therefore be key features of coexistence mechanisms intending to explain phytoplankton diversity maintenance.

Introduction

How species or related genera can coexist together in spite of competition is one of the main puzzles of community ecology, especially for primary producers that seemingly share the same basic resources¹. Many theoretical studies of competition models have shown that competitive exclusion is likely in those circumstances^{2,3}, unless mechanisms involving spatial or temporal variation are at play^{4,5,6,7}. Neutral theory, that assumes a non-equilibrium coexistence maintained by dispersal and equal competitive abilities for all species⁸ (though there are exceptions^{9,10}) has been proposed as a solution to explain highly diverse communities^{8,11}.

However, the evidence gathered from terrestrial plant communities starts to suggest that, in fact, niche rather than neutral processes may be paramount to explain coexistence, with intraspecific competition dwarfing interspecific competition in most cases^{12,13}. Whether these conclusions drawn from studies of annual plants and forest trees apply to other ecosystems and taxa is currently little known (but see¹⁴).

Moreover, even within a single trophic level, competition may not be the rule: the meta-analysis by Adler et al.¹³

reported a large number of facilitative interactions (30%) and several reviews^{15,16} have highlighted 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 in Lotka-Volterra models¹⁷, multiple other modelling¹⁸ and empirical^{15,19} studies have suggested that facilitative interactions can to a large degree benefit coexistence, especially when multiple interaction types are considered simultaneously^{20,21}.

Here, we analyse a large multi-species dataset consisting of several multivariate long-term time series of phytoplankton dynamics along the French coastline, which we then analyze using multivariate autoregressive (MAR) time series models, allowing for interactions between genera. Although many ecological studies focus on interactions between species, competition has been shown experimentally to occur between different genera of phytoplankton^{22,23}. Because competition should - according to theory and experiments - occur between genera, and the genus level is for phytoplankton interaction studies a rather fine taxonomic scale (most phytoplankton interaction studies are restricted to interaction between different classes or even phyla^{24,25,26}, we study here interactions between different genera of phytoplankton, belong mostly to diatoms and dinoflagellates. To put our results into a more general context, we then compare our interaction strengths estimates to previously published interaction networks produced under the same statistical framework.

Results

MAR(1) estimates Using MAR(1) autoregressive models, we have produced interaction matrices - i.e., Jacobian community matrices on the logarithmic scale²⁴. Best-fitting models corresponded to a phylogenetically-structured interaction scenario, where interaction only occurred between closely related genera (Supplementary Fig. 3). This led to sparse, modular matrices that have two main features. First, we observe a strong self-regulation for all sites (Fig. 1, diagonal elements of all matrices), a feature that we have previously highlighted in a more detailed analysis on one of the considered study regions²⁷. The ratio of mean intragenus to intergenus interaction coefficients varied between 6 and 10, not counting coefficients set to 0 in the estimation process. If we include the zeroes in the interaction matrix in the computation of the intra/inter mean interaction strength, the ratio rises to between 21 and 43. Therefore, intragenus interactions are on average much stronger than intergenus interactions, approximately 10 to 20 times stronger.

Second, although the percentage of facilitative interactions seemed to vary among sites (between 40% and 71% of interactions in the selected models), facilitation remained predominant in 9 sites out of 10 (only Lazaret, in the Mediterranean Sea, has 60% negative interactions). Our observational setup being nested, with sites within regions, we can examine whether locally positive interactions remain positive in a regional context: the percentage of consistently positive interactions at the regional level varies between 30% and 53%, higher than the percentage of similarly defined negative interactions (between 15% and 40%), except for sites in the Mediterranean Sea.

60 We have found that the percentage of true mutualism (+/+) is substantial: averaged over all sites, 32% of all
 61 interactions are (+/+) while only 12% of them are (-/-). The sign correspondence is not always maintained between
 62 French regions: the only interaction that is non-zero in the 10 sites (CHA/SKE) is mutualistic in Men er Roue only
 63 (Brittany) and mixed (+/-) at all other sites. Within the same region, however, interactions measured at different
 64 sites tend to keep the same sign. In the 3 sites of Marennes-Oléron, for instance, there were 4 interactions which
 65 remained positive on both sides (CHA/GUI, DIT/GUI, LEP/THP, SKE/THP), 3 of them being also mutualistic
 66 in some of the Brittany sites. This contradicts previous observations that mutualistic interactions tend to be
 67 more context-dependent than competitive interactions²⁸. Remarkably, mutualistic interactions that are consistent
 68 between sites can only be found between genera of centric diatoms. Interactions that are consistent at the regional
 69 level, for other phyla such as pennate diatoms or dinoflagellates, are always either competition/amensalism (- or
 70 +/-) or commensalism (0/+).

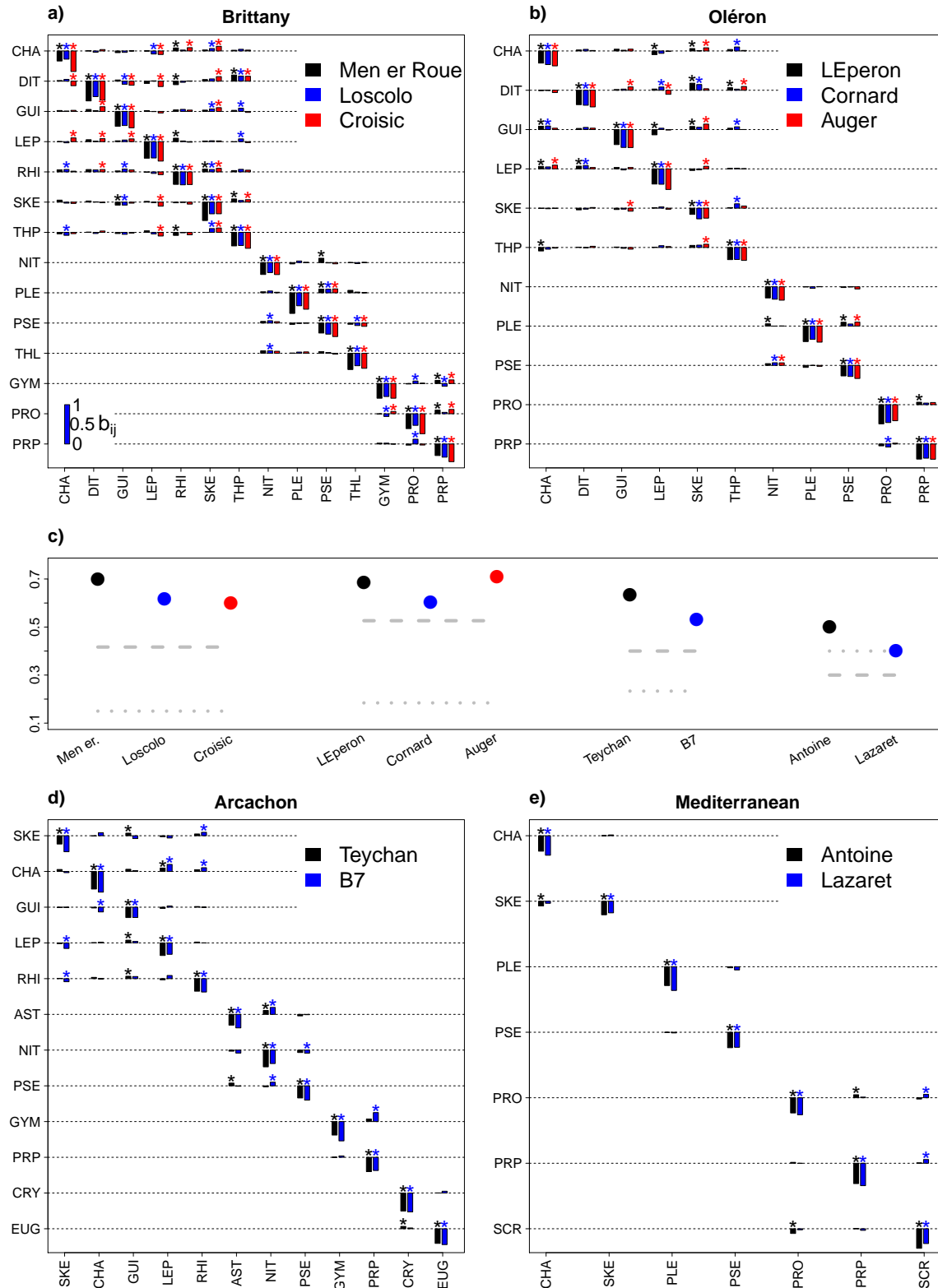


Figure 1: **Interaction matrices estimated in 10 sites along the French coastline.** Four regions are distinguished: Brittany (a), Marennes-Oléron (b), Arcachon (d) and the Mediterranean Sea (e). Only interactions between clades (pennate and centric diatoms, dinoflagellates, other planktonic taxa) are allowed, as this is the best fitting interaction scenario (Supplementary Fig.3). Taxon j (in columns) has an effect illustrated by the bar height on taxon i 's growth rate (in rows). We present the log-scale interaction matrix minus the identity matrix ($\mathbf{B} - \mathbf{I}$) because this compares unambiguously the effects of intra- and inter-group interactions on population growth rates. 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 composition of planktonic groups is given in Supplementary Table 2. The fraction of positive interactions in each matrix is given by points in c) while the dashed (resp., dotted) line represents the ratio of interactions remaining positive (resp., negative) for all sites of a

Interaction network analysis

The stability (*sensu* resilience²⁹) of all interaction matrices was not strongly affected by the percentage of positive interactions or their connectivity properties (Fig. 2). The maximum modulus of the interaction matrix eigenvalues remained between 0.65 and 0.80. There was also a slight increase in stability with weighted connectance, with a drop in eigenvalue modulus for weighted connectances between 0.09 and 0.1.

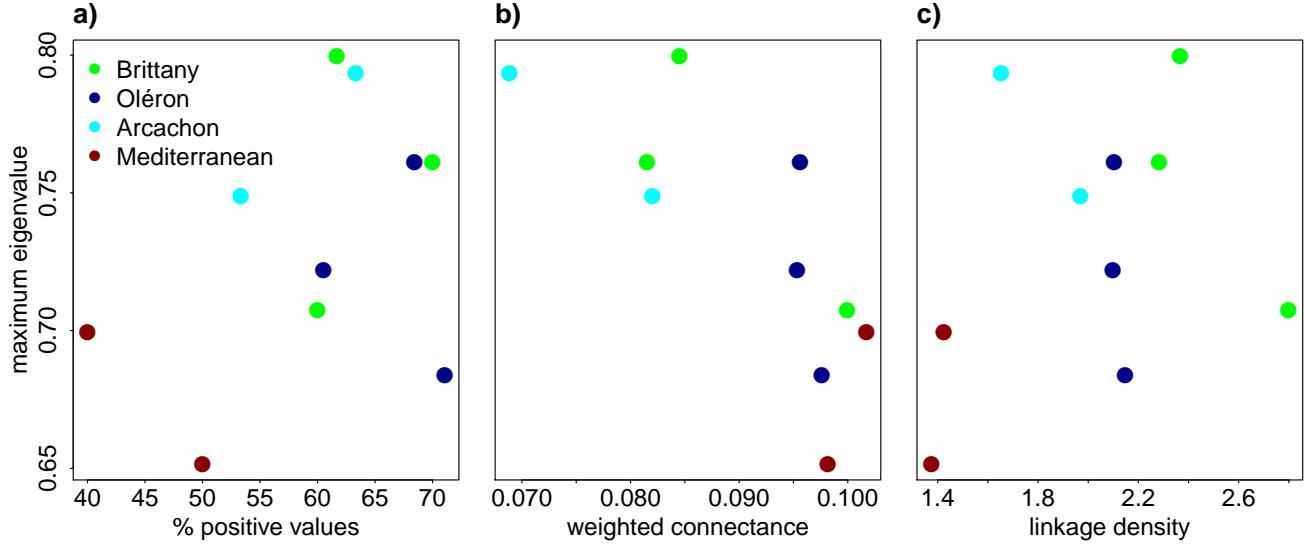


Figure 2: **Relation between stability and complexity of the interaction networks.** The maximum modulus of the interaction matrix \mathbf{B} eigenvalues indicates stability *sensu* resilience. Each point color corresponds to a given region. Metrics formula for weighted connectance and linkage density are given in Supplementary Information.

Given that a direct complexity-stability link was not obvious, we investigated whether the matrix coefficients had some particular structure that could help theoretical ecology to make better null models of joint community dynamics and interactions³⁰. We defined two scores, vulnerability (summed effect of others on the focal species growth rate, Supplementary Eq. 5) and impact (summed effect of the focal species onto other species growth rates, Supplementary Eq. 6). Relations between inter- and intragroup interactions emerged (Fig. 3): species that were more self-regulating also had also a higher vulnerability score and a lower impact score. 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. As these species tended to be more abundant (Supplementary Fig. 6), they were more likely to affect other species. It is important to note, however, that these trends 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.

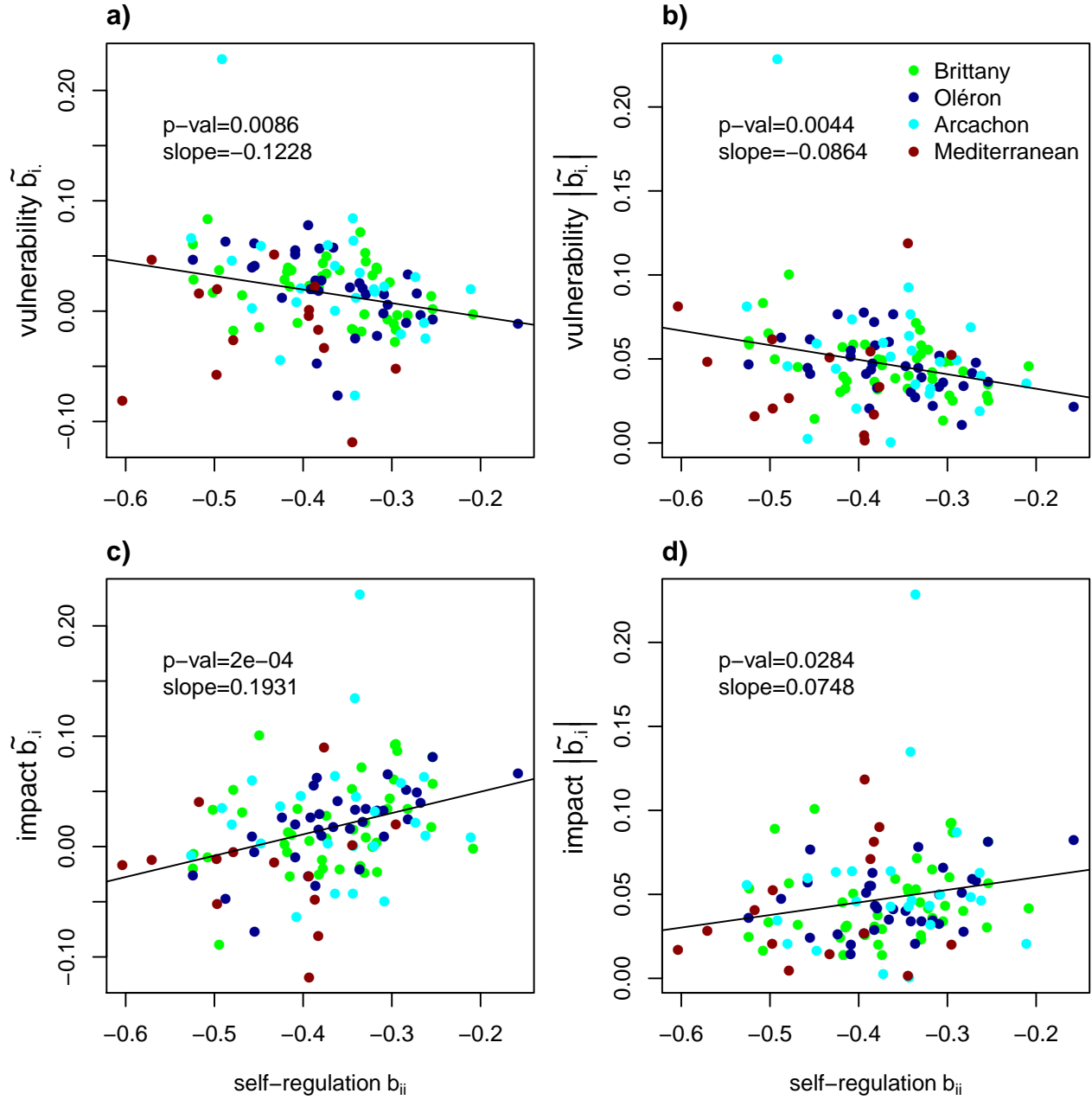


Figure 3: **Relation between vulnerability/impact and self-regulation.** Average vulnerability (effects of others onto the focal species growth rate, a-b) and impact (effects of the focal species unto other's growth rates, c-d), as well as self-regulation, are computed for untransformed (a-c) or absolute (b-d) values of the coefficients of the interaction matrix ($\mathbf{B} - \mathbf{I}$) for the 10 study sites. Each color corresponds to a given region (Supplementary Fig. 1). The p-value of the Pearson correlation between vulnerability (respectively impact) and self-regulation is given in the top left of each panel and the slope of the linear regression is given by the black line across scatter plots.

86 Aside from these trade-offs, some of which promote some stability (sensu invariability), we found no remarkable
87 patterns of covariation between matrix elements (other than a mean-variance scaling of interaction coefficients,
88 Supplementary Fig. 5).

89 **Literature comparison** Finally, we sought to put these results in a broader context by compiling the intra vs.
90 inter group estimates of previous MAR(1) studies of long-term observational count data (listed in Supplementary
91 Table 3). We found that the order of magnitude of intra/inter interaction strengths considered here is not particularly
92 above those found for most planktonic systems to which MAR(1) models have been fitted, considering that our
93 systems are relatively high-dimensional and that the higher the dimension, the larger the intraspecific regulation³¹.
94 We included in Fig. 4 not only plankton studies but also a couple of vertebrate or insect studies on less diverse
95 communities, where interactions are stronger. The conclusion from this comparison seems to be that any diverse
96 system of competitors and facilitators has evolved large niche differences making intragroup competition much larger
97 in magnitude than intergroup interactions.

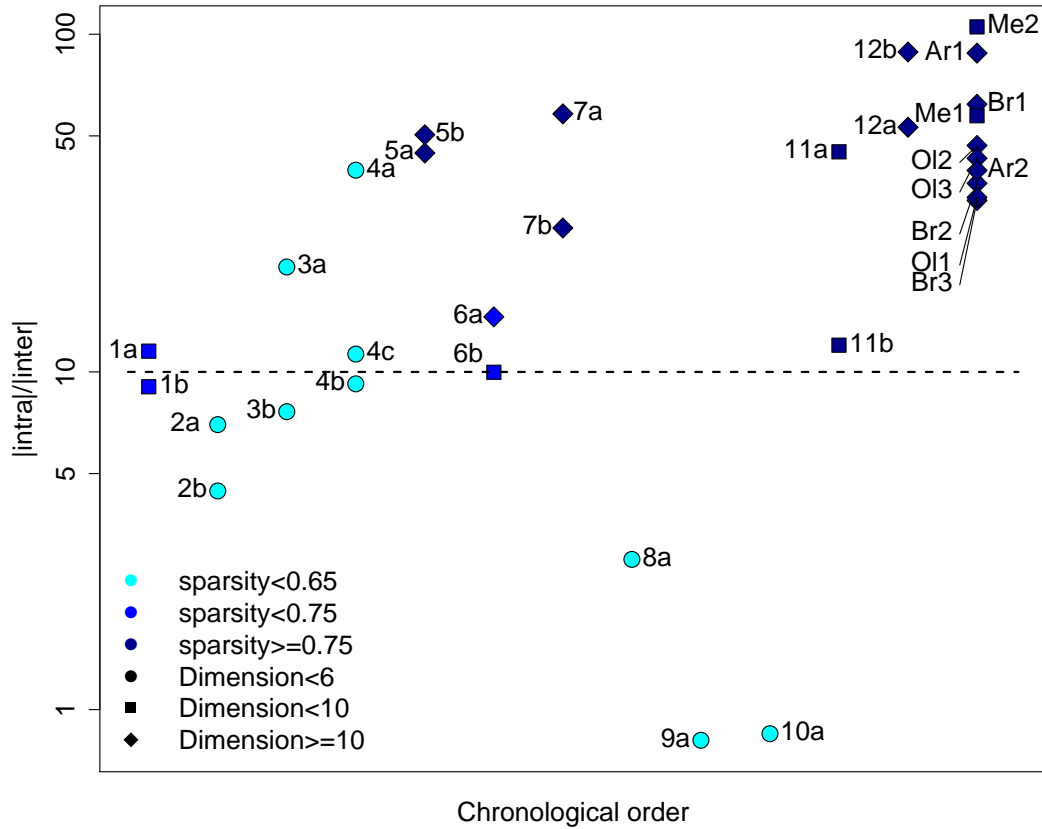


Figure 4: **Ratio of intra- to inter-group interaction strength in Multivariate AutoRegressive (MAR) models in the ecological literature.** The name of each studies, corresponding to each code, is given in Supplementary Table 3. The symbol color corresponds to the sparsity of the interaction matrix (e.g., the proportion of null interactions in the matrix) and the symbol shape corresponds to the number of species taken into account. Intergroup interactions were set to 0 when they were not specified in the articles (in most cases, articles removed non-significant interactions at the 95% threshold). Last column corresponds to the present study.

98 Discussion

99 We found very large niche differences between genera, [[as measured by the intra/intergenus interaction strength
100 ratio³²]], translating into much higher intragenus than intergenus effects on growth rates, together with a high degree
101 of facilitative net interactions. This is in spite of competition being demonstrated in the lab and in experiments
102 between those genera^{22,33,23}..

103 Strong self-regulation such as the one found in our study can be explained by many mechanisms which can
104 act together to create high net effects of density-dependence. In our previous publication investigating in detail
105 the Arcachon study sites²⁷, we have argued that those large niche differences, with strong intragroup density-
106 dependence could arise from predation effects^{34,27}. Predation effects could also very well create apparent mutualism
107 between prey species^{35,36,37}. This is still very much likely here given the new study regions (Oléron, Brittany,
108 Mediterranean) added for this study could have similar predators (zooplankton^{38,39,40}), parasites (viruses⁴¹, fungi),
109 or even competitors such as macrophytes⁴², though there are other possible drivers of phytoplankton dynamics such
110 as allelopathy⁴³, auxotrophy⁴⁴ or hydrodynamics⁴⁵. The multidimensionality of the niche⁴⁶ could also help explain
111 the large niche differences leading to coexistence. Finally, resources that are usually considered limiting for all
112 species might in fact not always be: the changes in phytoplankton absorption spectrum documented by Burson et
113 al.⁴⁷ is an example of fine-scale resource partitioning.

114 **No complexity-stability relationship** There was no relation between the complexity of the communities (mea-
115 sured as either the weighted connectance or linkage density of the interaction matrices) and their stability. Such
116 result must be considered with caution as it may be partly explained by the use of a MAR(1) model, which pro-
117 vides a fixed point even in the presence of other types of attractors (e.g., limit cycles)⁴⁸. However, the absence
118 of direct link between complexity and stability could be an actual feature of empirical systems⁴⁹, even though it
119 does contradict previous results on random matrices, especially for competitive and/or mutualistic networks⁵⁰. In
120 particular, the role of mutualistic interactions in stabilizing communities is still debated: while it does not strongly
121 alter the stability of the communities we examined, an increase in the number of positive interactions can either
122 maximize the persistence of a network²¹ or narrow the range of richness and connectance values allowing for a stable
123 community⁵⁰.

124 In addition to weighted connectance, indices at the network-level (vulnerability and generality, encapsulated in
125 the linkage density) and at the species-level ([vulnerability] and impact) approximate the average effects exerted
126 and sustained by any given species in the different study sites. While, at the network level, linkage density did
127 not affect stability, a relation emerged between self-regulation, necessary for coexistence, and species-level indices.
128 The more a species is self-regulated, the more it tends to be vulnerable to other species and the less it impacts
129 other species. Indeed, self-regulation indicates large niche differences: a species whose needs strongly differ from
130 the others only marginally impacts the resources of the other coexisting species. Furthermore, a low self-regulation

is correlated with strong average abundance: a species which dominate the community composition can have a major effect on the others, just by a mechanistic increase in the probability of direct and indirect interactions. To our knowledge, relations between different types of interactions (competitive, commensalist and mutualistic), and frequency-dependence, has not been fully explored up to now (but see⁵¹). Usually, interactions are only competitive and the intensity of self-regulation may be fixed for all species in the community. In this case, stability in the community is ensured by a correlation between the intensity of self-regulation and the variance of the interspecific interactions⁵². This relation still needs to be extended to asymmetric matrices with high abundance variation to be fully applied to empirical systems such as ours.

Ghosts of competition past and present The dominance of niche differentiation in observational plankton studies is similar to what has been recently found in plant community studies^{10,13} or empirical food webs including horizontal diversity³¹. Large niche differences might be due to the ghost of the competition past, i.e., competition has occurred in the past, leading to strong selection and subsequent 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 destabilizing¹⁷). The likely predator effects that we highlighted above could be comprised within such niche differentiation *sensu largo*: specialized predators can make strong conspecific density-dependence emerge^{53,54}, while switching generalists can also promote diversity⁵⁵. Both predators and resources have often symmetrical effects and can therefore contribute almost equally to niche differentiation³

An intriguing new possibility, dubbed the “ghost of competition present”⁵⁶, 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^{56,57}. 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^{58,59} but it is quite unclear how this affects multivariate spatial patterns of species distributions (*sensu* Bolker and Pacala⁶⁰ or Murrell and Law⁶¹). 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, because turbulence rather than organism movement may somehow dictates where the plankton patches can or cannot appear.

Methods

Sampling methods

All phytoplankton counts were collected as part of the National Phytoplankton and Phycotoxin Monitoring Network (REPHY⁶²). Since 1987, this monitoring program has required 26 sites along the French coastline to be sampled every 2 weeks within 2 hours of high tide to determine both biotic (phytoplankton counts) and abiotic (water temperature, salinity) parameters. We focused on sites which had the longest and most recent time series. We also excluded time series which had missing data for over 6 months or an average delay between sampling dates above 20 days. This reduced the number of study sites to 10 sites nested within 4 regions (Brittany, Marennes-Oléron, Arcachon and the Mediterranean Sea; Supplementary Fig. 1).

Abiotic variables (temperature, salinity) were measured directly from the boat during the sampling process while water samples for biotic analyses were fixed with a Lugol's solution and examined later. Phytoplankton cells above 20 μm were identified at the lowest possible taxonomic level and counted with the Utermöhl method using an optical microscope⁶³. Throughout the years and sites, more than 600 taxa were identified at different taxonomic levels. We aggregated them at the genus (or group of genera when not possible), level based on previous work^{64,27}, except for cryptophytes and euglenophytes in Arcachon, which could not be identified below the family level. Although the taxonomic resolution used here may seem coarse in comparison to land plants, it is in fact more refined than 86% of the MAR(1) studies of phytoplankton listed in Supplementary Table 3.

For each region, the MAR(1) analysis focused on the most abundant and most frequently observed genera to avoid most of the gaps in the time series. When gaps did not exceed a month, missing values were linearly interpolated; remaining missing values were replaced by a random number between 0 and half of the lowest observed abundance⁶⁵. We tested extensively this and other methods to deal with missing data in a previous publication on a subset of this dataset²⁷. All time series were scaled and centered before MAR analyses.

MAR(1) model

Multivariate autoregressive (MAR) models are used to determine the interspecific interactions and abiotic variables shaping a community's dynamics²⁴. 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,

191 and \mathbf{e}_t is a $1 \times S$ noise vector which covers both process and observation error, following a multivariate normal distri-
192 bution with a variance-covariance matrix \mathbf{Q} . \mathbf{Q} is diagonal and we have previously showed that this parsimonious
193 choice did not affect qualitatively the results²⁷.

194 We used the MARSS package⁶⁶ v3.9, in R v3.3.2⁶⁷, to estimate parameters with a maximum likelihood procedure.

195 We have previously published a detailed analysis of one of the dataset (Arcachon) for which more covariables
196 were available²⁷. Covariables included nutrients and hydrodynamics variables, and the latter were found more
197 influential; nutrient dynamics contributed little to phytoplankton dynamics on the two-weeks timescale. Because
198 temperature and salinity sum up seasonal changes in light as well as hydrology (salinity is inversely related to
199 freshwater inflow), these represent the two key drivers needed to account for abiotic influences. The analysis of real
200 data in Barraquand et al.²⁷ was complemented by that of phytoplankton-like simulated data, which confirmed the
201 ability of MAR(1) models to infer biotic interactions and abiotic forcing (e.g., no need for extra non-linearities to
202 model the storage effect, which was found to be nearly non-existent, as in previous analyses of plant data for which
203 strong-self regulation was observed^{12,68}). Furthermore, using two abiotic variables (temperature and salinity) in this
204 study rather than the full set of used in Barraquand et al.²⁷ led to almost identical estimates to the ones obtained
205 previously²⁷. We are therefore confident that the MAR(1) models presented here are robust to small changes in
206 model specification. In general, MAR(1) models tend to be fairly robust to small deviations of the underlying
207 (non-linear) data-generating model, provided that one asks mainly order of magnitude of coefficients values (rather
208 than precise estimates) and sign of interaction coefficients⁴⁸, which is how these are models are used here.

209 In this study, the number of phytoplankton groups, S , varies between regions but we keep the same 2 covariates,
210 i.e. water temperature and salinity, that could be measured for all study sites. Therefore, the dimension of the
211 dynamical system only depends on the (square of the) number of phytoplankton groups we study, which ranges
212 between 7 (Mediterranean Sea) and 14 (Brittany). The smallest system still requires 70 parameters to be estimated
213 if we consider all possible interactions between species. To reduce this dimensionality and remove unnecessary
214 parameters, we compared different ‘interaction scenarios’ based on BIC. The null interaction scenario assumed no
215 interaction between groups of species (diagonal interaction matrix) and was compared to four other interaction
216 scenarios. The first interaction scenario assumed that interactions could only occur between phylogenetically close
217 organisms, i.e., within a class (namely, diatoms, dinoflagellates, and other phytoplanktonic organisms) while the
218 second interaction scenario further differentiated pennate and centric diatoms. The third interaction scenario
219 considered the inverse hypothesis, that only unrelated organisms could interact (i.e., a diatom could only interact
220 with a dinoflagellate or a cryptophyte, but not with another diatom), and the last interaction scenario did not
221 constrain the interactions at all (full interaction matrix). The second interaction scenario, hereafter called the
222 pennate-centric scenario, had the lowest BIC for all sites and was therefore the most accurate while still parsimonious:
223 we chose to further investigate the corresponding networks.

Analysis of interaction strengths

The interaction matrix obtained from MAR(1) analyses can be used to determine the stability of a discrete-time dynamical system²⁴. We compared the maximum modulus of the eigenvalues of the pennate/centric matrices in each site, as a proxy of stability, to network metrics which could be related to complexity, such as weighted connectance and linkage density⁵⁹. 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 matrices 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, irrespective of interaction sign.

In addition to these network-level metrics, we also computed the average vulnerability (average effect of other taxa on a focal taxon, Supplementary Eq. 5) and impact (average effect of a focal taxon on other taxa, Supplementary Eq. 6) on both raw and absolute values of the coefficients, and compared these to the regulation a focal species exerted on itself. Raw values indicate the average effect (i.e., is the effect mostly positive or negative?) that can be expected on a species' growth rate from other planktonic species while absolute effects characterize the strength of all types of interactions on a species (i.e., is a species strongly affected by the others?).

Finally, we compared our results on self regulation/intraspecific interactions v. interspecific interactions to other published studies based on a MAR model. A list of references is given in Supplementary Table 3. Authors usually reported only coefficients that were significant at the 95% threshold, ignoring potentially many weak effects. We therefore computed both the mean value of all coefficients outside of the matrix diagonal, replacing missing values by 0 (Fig. 4, which decreases the mean intergroup interaction strength), and the mean value of statistically significant coefficients only (Supplementary Fig. 7, which increases the mean intergroup interaction strength). We should mention two potential biases associated with this comparison: low-dimensional matrices tended to be more complete (less sparse) than high-dimensional matrices, as these small interaction matrices were used to study known interaction phenomena (observed predation between organisms, for instance). There is therefore a positive correlation between sparsity and dimensionality (Supplementary Fig.8). The number of parameters to estimate increase as the square of the number of interacting groups, leading authors to reduce this set before the estimation process. A second caveat is that while we informed our model selection by phylogeny (see above), several authors have reduced the number of estimated parameters by an automated procedure, usually based on the comparison of 100 randomly chosen interaction matrices, optimizing BIC²⁴.

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