

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

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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 a key feature of 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 purporting to explain phytoplankton diversity maintenance. [New proposition, as we repeat “key feature” and likely misuse the verb purport: Both strong self-regulation and widespread net facilitation are therefore central coexistence mechanisms to maintain phytoplankton diversity.]

Introduction

[V1]

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 resources¹. Many theoretical studies of competition models have shown that competitive exclusion is likely in those circumstances^{2,3}, unless some special mechanisms involving spatial or temporal variation are at play^{4,5,6,7}. Neutral theory, that in its most basic formulation assumes equal competitive abilities⁸ and non-equilibrium coexistence sustained by immigration from a larger pool (but see ref.^{9,10}) has been proposed as a solution to explain highly diverse communities^{8,11}.

-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^{12,13}.

Whether these conclusions apply to other systems is currently unknown.

Moreover, the meta-analysis by Adler et al.¹³ reported a large number of facilitative interactions (30%) and reviews^{14,15} 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 in Lotka-Volterra models¹⁶, multiple other modelling¹⁷ and empirical^{14,18} studies have suggested that facilitative interactions can to a large degree benefit coexistence, especially when multiple interaction types are considered simultaneously^{19,20}.

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 statistical time series models allowing for interactions between groups.

[V2]

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. This is the premise of the well-known ‘paradox of the plankton’¹, which has elicited numerous modeling and experimental studies on both marine and terrestrial communities for half a century^{21,22,7}. Many theoretical studies of competition models have shown that competitive exclusion is likely in those circumstances^{23,2,3}, unless some special mechanisms involving spatial or temporal variation are at play^{4,5,6,7}. Meanwhile, even in stable, controlled environment, experimental studies on phytoplankton have led to contradictory results: while some systems are dominated by only one species^{24,25}, other communities are able to maintain a certain level of diversity^{26,27}. The level of competition between persisting species in these experiments is still unclear.

Neutral theory, that in its most basic formulation assumes equal competitive abilities⁸ and non-equilibrium coexistence sustained by immigration from a larger pool (but see ref.^{9,10}) has been proposed as a solution to explain highly diverse communities^{8,11}. 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^{12,13}. The extent to which such conclusions can be generalized still needs to be quantified in other systems.

Nonetheless, the accurate quantification of interactions in field-based or in-vitro data can be hindered by other niche-derived hypothesis. One example of this is the frequency of positive interactions in competitive networks. On the one hand, some theoretical studies suggest that facilitative interactions can be destabilizing (sensu resilience) and therefore undermine coexistence in Lotka-Volterra models¹⁶, and some field-based analyses may discard them *a priori*^{28,29}. On the other hand, multiple¹⁷ and empirical^{14,18,15} studies have suggested that facilitative interactions can to a large degree benefit coexistence, especially when multiple interaction types are considered simultaneously^{19,20}. This has recently been confirmed by a meta-analysis by Adler et al.¹³, reporting about 30 % of facilitative interactions.

Here, we analyze the structure of 10 different phytoplanktonic interaction networks. We exploit a long-term, multi-species dataset covering most of the French coastline on which we apply multivariate auto-regressive (MAR) models. These statistical methods allow us to take into account both environmental variation and interaction between species and have already been thoroughly tested on this type of data^{28,30,31}. We confirm that intraspecific interactions are much stronger than interspecific interactions and generalize this hypothesis with other data from the same type of system. We also establish that facilitative interactions can dominate our networks. Finally, we consider the characteristic network structure and relations between interaction strengths to better inform coexistence theory.

Results and discussion

MAR(1) estimates Using MAR(1) autoregressive models, we have produced interaction matrices – i.e., Jacobian ~~community~~-matrices on the logarithmic scale²⁸, which correspond to a phylogenetic scenario that only allows interaction between close groups (Supplementary Fig. 2). This leads 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 highlighted in a previous, more detailed analysis on one of the considered study ~~sites~~regions only³¹. The ratio of mean intragroup effects to intergroup effects varies between 6 and 10, ignoring coefficients set to 0 in the estimation process. If we consider the whole interaction matrix, including coefficients set to 0 in the calculation of the mean effects, this ratio varies between 21 and 43.

Second, although the percentage of facilitative interactions seems to vary among sites (between 40% and 71% of interactions in the selected models), facilitation remains predominant in 9 sites out of 10 (Lazaret, in the Mediterranean Sea, has 60% negative interactions).~~we have found that the percentage of mutualism is substantial for all sites:—~~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%, which is ~~always~~ higher than the percentage of similarly defined negative interactions (between 15% and 40%), except for sites in the Mediterranean Sea.

When interactions are facilitative on both sides, we consider that they are mutualistic. We have found that the percentage of mutualism is substantial for all sites: there are on average 32% of all interactions which are beneficial for both interacting groups while only 12% of them are detrimental. Remaining interactions can either characterize competitive effects or commensalism. The sign correspondence is not maintained between regions: the only interaction that is common to the 10 sites (CHA/SKE) is mutualistic in Men er Roue only and mixed (+/-) in all other sites. At the region scale, however, interaction tends to keep their sign between sites. While the only consistency in negative interaction is the link between PSE and PLE in both Mediterranean Sea sites, mutualistic interactions hold in more sites. In the 3 sites of Marennes-Oléron, for instance, there were 4 interactions which remained positive on both sides (CHA/GUI, DIT/GUI, LEP/THP, SKE/THP), 3 of them being also mutualistic

94 in some of the Brittany sites. This contradicts previous observations that mutualistic interactions tend to be more
95 context-dependent than competitive interactions³² but, remarkably, this only concern a specific phytoplankton
96 group. Stable mutualistic interactions can only be found between centric diatoms. Other groups either compete
97 with each others or are commensalist.

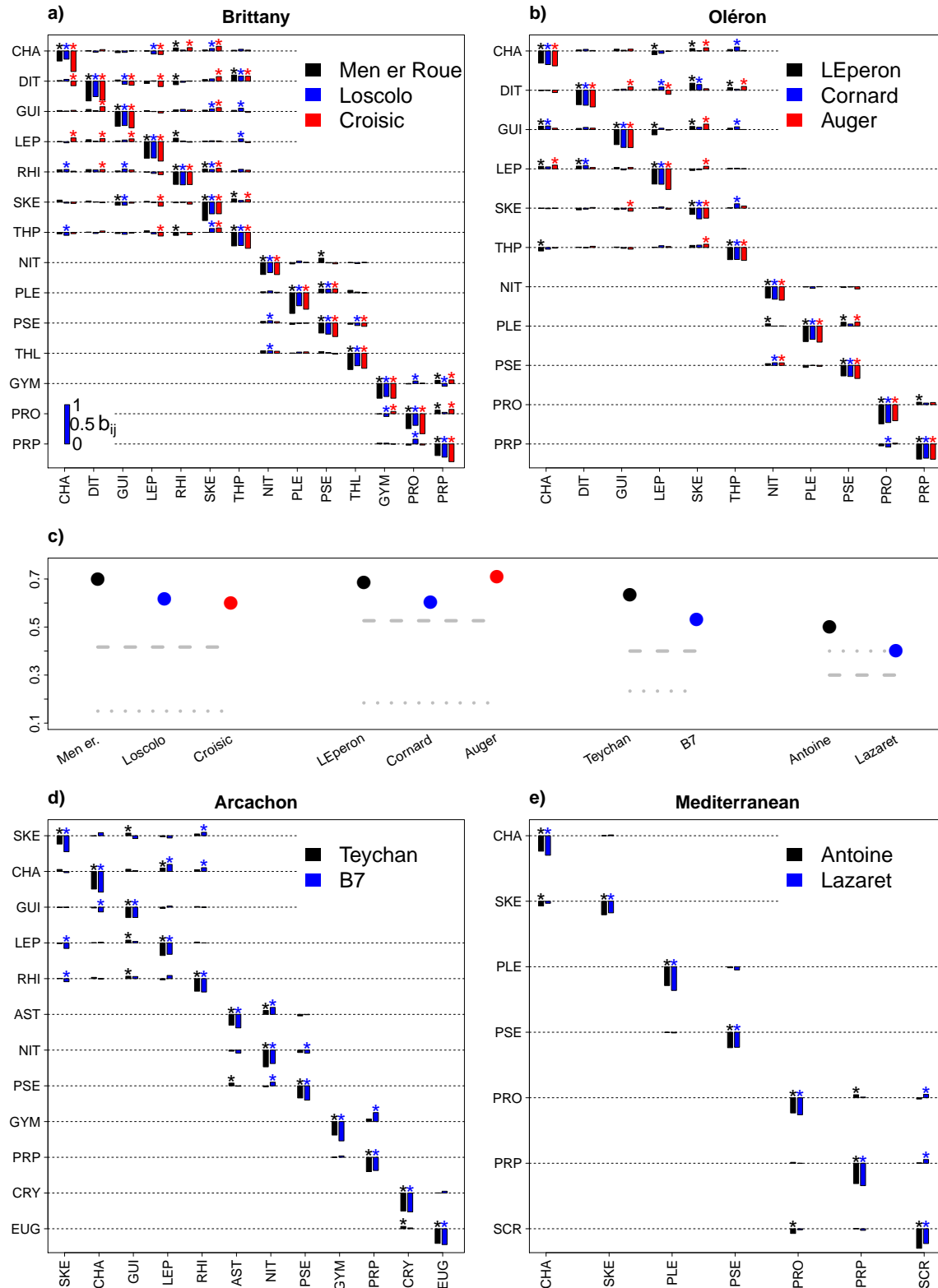


Figure 1: **Interaction matrices estimated in 10 sites along the French coastline.** Four regions are distinguished: Brittany (a), Marennes-Oléron (b), Arcachon (d) and the Mediterranean Sea (e). Only interactions between clades (pennate and centric diatoms, dinoflagellates, other planktonic taxa) are allowed, as this is the best fitting **modelscenario** (Supplementary Fig.2 in Supplementary Information). Taxon j (in columns) has an effect illustrated by the bar height on taxon i (in rows)'s growth rate. We present the log-scale **communityinteraction** 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 the Supplementary Information Table 1. 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

Interaction network analysis

We then asked whether the stability (resilience) of those all interaction matrices was not strongly affected by the percentage of mutualistic positive interactions or their connectivity properties (Fig. 22), as the maximum modulus of the interaction matrix eigenvalues remained between 0.65 and 0.80. Stability seemed to decrease with an increase in positive interactions but this was only observed for Mediterranean sites, which were also characterized by lower-dimension interaction matrices [and a different ecosystem, subjected to other hydrodynamics features]. There was also a slight increase in stability with the increase of weighted connectance, with a drop in eigenvalue modulus for weighted connectances between 0.09 and 0.1 [add here ref to complexity/stability in literature?]. -

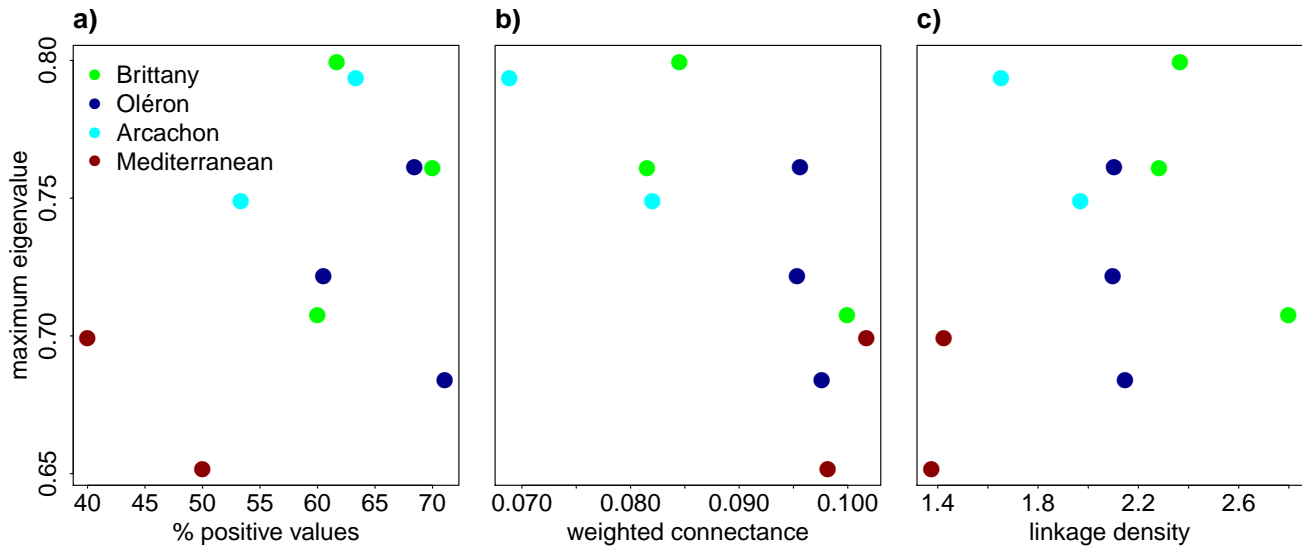


Figure 2: **Relation between stability and complexity of the interaction networks.** The maximum modulus of the community interaction matrix B -eigenvalues indicates stability *sensu* resilience. Each point color corresponds to a given region. Metrics formula for weighted connectance and linkage density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

More information than sign and the magnitude of interspecific / intergroup interactions can be gathered from interaction matrices. 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 interactions³³. We defined two scores, vulnerability (summed effect of others on the focal species growth rate, Supplementary Eq. ??) and generality impact (summed effect of the focal species onto other species growth rates, Supplementary Eq. ??). 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. -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. As these species tended to be more abundant (Supplementary Fig. ??), they were more likely to affect 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.-

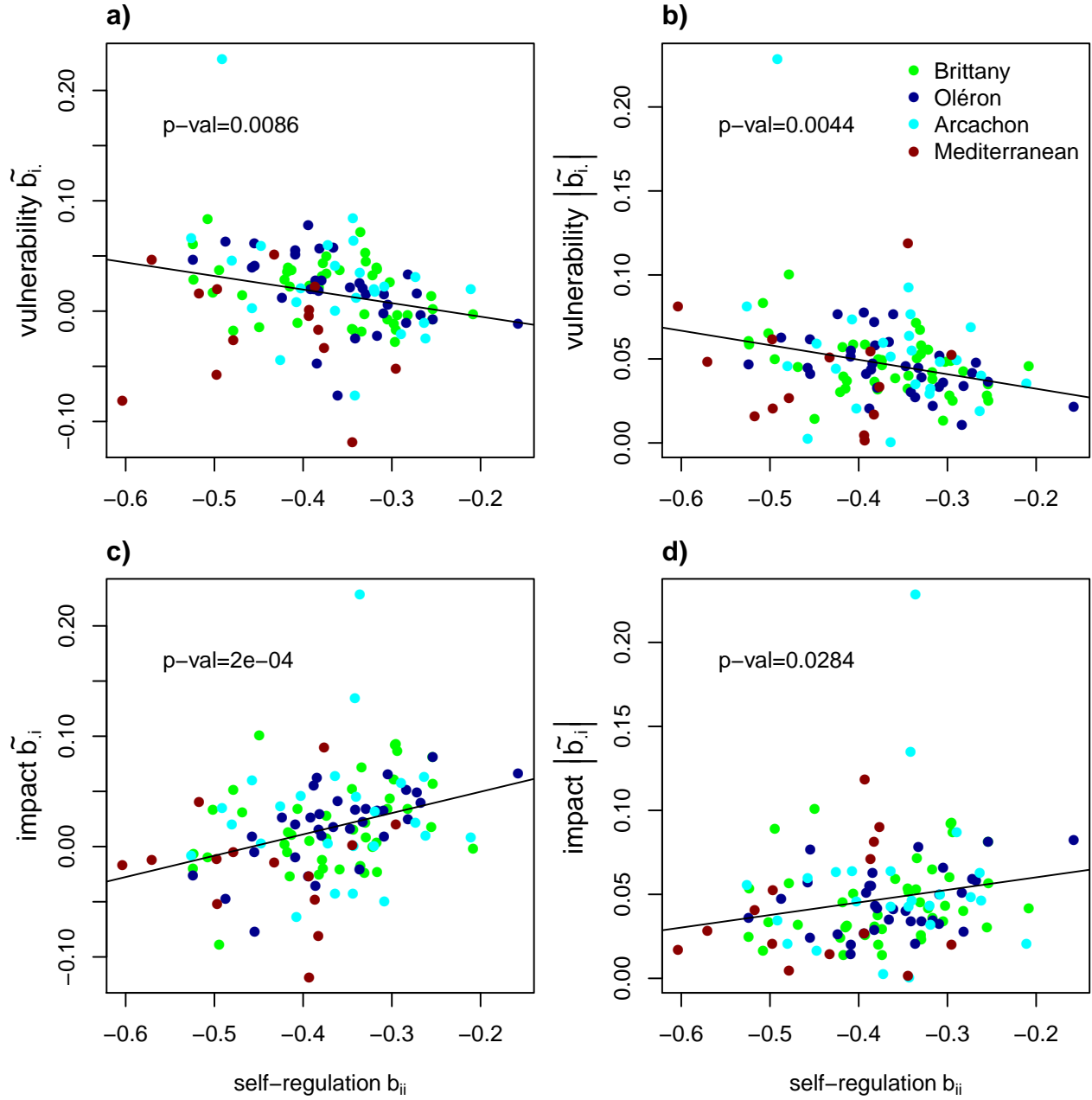


Figure 3: **Relation between vulnerability/generalityimpact and self-regulation.** Average vulnerability (effects of others onto the focal species growth rate, a-b) and **generalityimpact** (effects of the focal species unto other's growth rates, c-d), as well as self-regulation, are computed for untransformed (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. 1see map in SI). The p-value of the Pearson correlation between vulnerability (respectively **generalityimpact**) 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.

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 Supplementary Fig. 4SI-XXX-Fig.-XXX). A main finding of our study seems therefore to be the presence of very

large niche differences between the species/genera, translating into much higher intragroup than intergroup effects on growth rates, together with a high degree of facilitative net interactions. In our previous publication investigating in detail the Arcachon study sites³¹, we have argued that those large niche differences, with strong intra-group density-dependence could arise from predation effects. ~~that~~Predation effects could also very well create apparent mutualism between prey species ~~[REFs -- from previous paper]~~^{34,35,36} ~~and strong intragroup density-dependence [REFs]~~. This is still very much likely here given ~~our~~the new study regions (Oléron, Brittany, Mediterranean) added for this study could have similar predators (zooplankton^{37,38,39}), parasites (viruses⁴⁰, fungi~~[REFs]~~), or even competitors⁴¹, though there are other ~~possibilities~~possible drivers of phytoplankton dynamics such as allelopathy⁴², auxotrophy⁴³ or hydrodynamics⁴⁴. ~~The~~ multidimensionality of the niche⁴⁵ and the fine partitioning of the same set of resources between species having slightly different needs²⁷ can also explain the niche differences leading to coexistence.

Literature comparison 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 of long-term observational count data (~~detailed~~listed in Supplementary ~~Appendix~~Table XXX3 in SI). We ~~have~~found that the order of magnitude of intra/inter interaction strengths considered here is not particularly ~~below~~above those found for most planktonic systems to which MAR(1) models have been fitted. We included in Fig. 44 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 has evolved large niche differences making intragroup competition much larger in magnitude than intergroup interactions.-

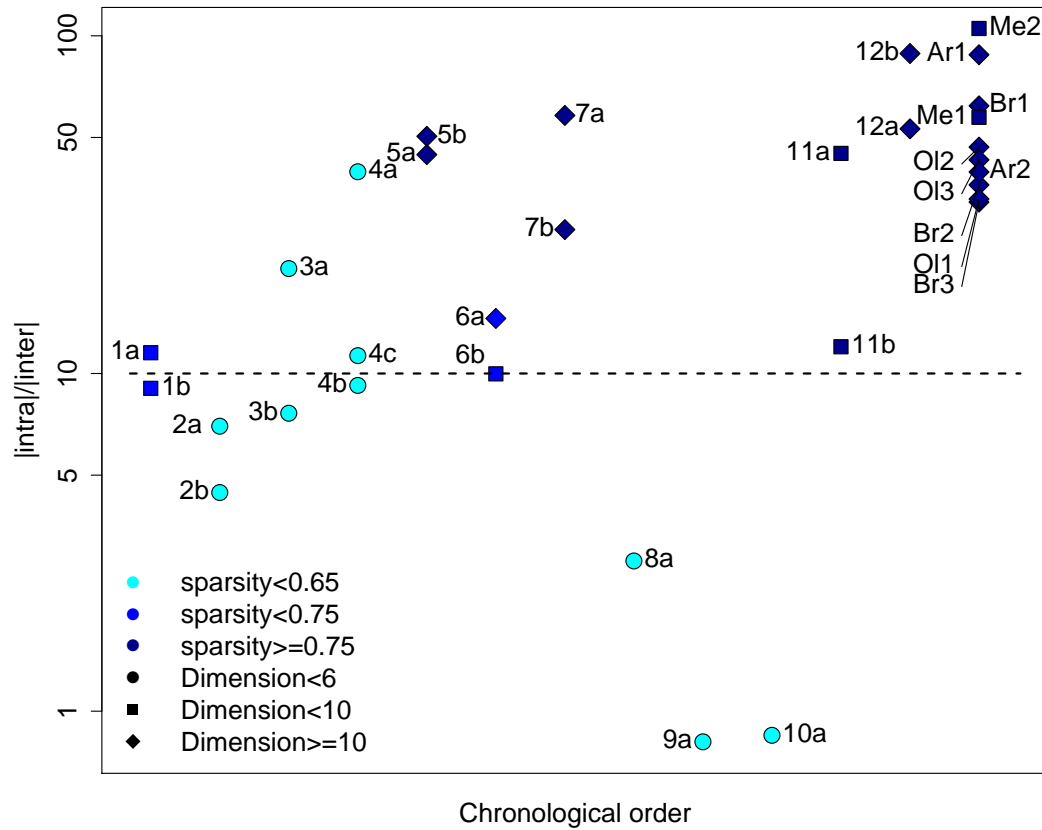


Figure 4: **Ratio of intra- to inter-group interaction strength in Multivariate AutoRegressive (MAR) models in the ecological literature.** The name of each studies, corresponding to each code, is given in the Supplementary Information Table 3. The symbol color corresponds to the sparsity of the community 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, because they were not deemed significant at the 95% threshold). Last column corresponds to the present study.-

Niche differences This 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 competitive effects⁴⁶. 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 destabilizing¹⁶). 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^{47,48} [Janzen-Connell REFs], while switching generalists can also promote diversity⁴⁹. 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” present⁵⁰, 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^{50,51}. 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^{52,53} but it is quite unclear how this affects multiple interacting species and which multivariate spatial patterns (as in ref.⁵⁴) 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

~~Data collection~~Sampling methods

All phytoplankton counts were collected as part of the National Phytoplankton and Phycotoxin Monitoring Network (REPHY⁵⁵). 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 that had been sampled at least 10 years after 1996, when methods were standardized among sites. We also excluded time series which had missing data for over 6 months or an average delay between sampling dates above ~~more than~~ 20 days, ~~on average, between sampling dates~~. This reduced the number of study sites to 10 sites nested within 4 regions (Brittany, Marennes-Oléron, Arcachon and the Mediterranean Sea; ~~a map is shown in the Supplementary Information~~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 microscope⁵⁶. 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^{57,31}, 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 XX75% of the MAR(1) studies of phytoplankton listed in Table XX in the SI~~Supplementary Table 3 [86% if not taking Barraquand 2018 into account].-

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;

184 remaining missing values were replaced by a random number between 0 and half of the lowest observed abundance⁵⁸.
 185 We tested extensively this and other methods to deal with missing data in a previous publication on a subset of
 186 this dataset³¹. All time series were scaled and centered before MAR analyses. -

187 MAR(1) model

188 Multivariate autoregressive (MAR) models are used to determine the interspecific interactions and abiotic variables
 189 shaping a community's dynamics²⁸. They are based on a stochastic, discrete-time Gompertz model which relates
 190 log-abundance of S species at time $t + 1$ to interactions with the rest of the community at time t , and effects of V
 191 abiotic variables at time $t + 1$, following eq. 1.

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

192 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
 193 (interaction) matrix, \mathbf{C} is the $S \times V$ environment matrix describing the effects of V variables \mathbf{u}_{t+1} on species growth,
 194 and \mathbf{e}_t is a $1 \times S$ noise vector which covers both process and observation error, following a multivariate normal distri-
 195 bution with a variance-covariance matrix \mathbf{Q} . \mathbf{Q} is diagonal and we have previously showed that this parsimonious
 196 choice did not affect qualitative results³¹.

197 We used the MARSS package⁵⁹, in R, to estimate parameters with a maximum likelihood procedure.

198 We have previously published a very detailed analysis of one of the dataset (Arcachon) for which more covariables
 199 were available³¹. The analysis of real data was complemented by that of simulated data for a plankton time series
 200 set-up and confirmed the ability of the technique to infer biotic interactions and abiotic forcing. This analysis
 201 revealed that the MAR(1) approach was satisfactory (i.e., no need for extra non-linearities to model the storage
 202 effect, which was found to be weak as in previous analyses of plant data for which strong-self regulation was
 203 observed^{12,60}). Furthermore, using two abiotic variables in this study rather than the full set of used in Barraquand
 204 et al.³¹ led to almost identical estimates to the ones obtained previously in Arcachon³¹. We are therefore confident
 205 that the MAR(1) models presented here are appropriate models and robust. In general, MAR(1) models tend to be
 206 fairly robust to small deviations of the underlying data-generating model, provided that one asks mainly order of
 207 magnitude of coefficients values (rather than very precise estimates) and sign of interaction coefficients⁶¹.

208 In this study, the number of phytoplankton groups, S , varies between regions but we keep the same 2 covariates,
 209 i.e. water temperature and salinity, that could be measured for all study sites. Therefore, the dimension of the
 210 dynamical system only depends on the (square of the) number of phytoplankton groups we study, which ranges be-
 211 tween 7 (Mediterranean Sea) and 14 (Brittany). The smallest system still requires 70 parameters to be estimated if
 212 we consider all possible interactions between species. To reduce this dimensionality and remove unnecessary param-
 213 eters, we compared different 'interaction scenarios' based on BIC. The null model scenario assumed no interaction

between groups of species (diagonal interaction matrix) and was compared to four other **modelscenarios**. The first **modelscenario** 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 **modelscenario** further differentiated pennate and centric diatoms. The third **modelscenario** 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 **modelscenario** did not constrain the interactions at all (full interaction matrix). Based on **convergentcongruent** results **forin** all sites (**see-Supplementary InformationFig. 2**), we further investigated the second **modelscenario**, hereafter called the pennate-centric **modelscenario**.

Analysis of interaction strengths

The **communityinteraction** matrix obtained from MAR(1) analyses can be used to determine the stability of a discrete-time dynamical system²⁸. 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 density⁵³. 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 accomodate 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, **Supplementary Eq. ??**) and **generalityimpact** (average effect of a focal taxon on other taxa, **Supplementary Eq. ??**) 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 the MAR model. A list of references is given in **the Supplementary InformationSupplementary Table 3**. Authors usually reported only coefficients that were significant at the 95% threshold, ignoring weak effects. We therefore computed the mean interspecific interactions as either the mean value of significant coefficients only (**see-Supplementary InformationFig. 5**), or the mean value of all coefficients outside of the matrix diagonal, replacing missing values by 0 (**Fig. 4**). We should nevertheless mention two biases in this comparison: low-dimension matrices tended to be more complete (less sparse) than high-dimension matrices as these small **communityinteraction** matrices were used to study known interaction phenomena (observed predation between organisms, for instance). There is therefore a positive correlation between sparsity and dimensionality (**see-Supplementary Fig.6I**). 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. While we based our model choice on phylogeny (see above), the typical method used by authors to reduce the number of estimated parameters was -an automated procedure, usually based on the comparison of 100 randomly chosen interaction matrices, optimizing BIC²⁸. [This means that, even for high-dimension matrices, we are not comparing exactly the same interaction models.]

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