

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

## Regulation and facilitation in phytoplankton

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**Data accessibility:** The REPHY dataset has already been published ([REPHY, 2017](#)) and all scripts for MAR and subsequent network analyses are available online in a GitHub repository (<https://github.com/CoraliePicoche/REPHY-littoral>). This repository will be made public upon acceptance and codes can be shared with referees should they wish to access them.

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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 analyse 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 competition strength within a genus an order of magnitude higher than between genera, 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.

# 1 Introduction

2 How species or close genera can coexist together in spite of competition is one of the main puzzles of  
3 community ecology, especially for primary producers that seemingly share the same basic resources  
4 ([Hutchinson, 1961](#)). Many theoretical studies of competition models have shown that competitive  
5 exclusion is likely in those circumstances ([Armstrong & McGehee, 1980](#); [Chesson, 2018](#)), unless  
6 mechanisms involving spatial or temporal variation are at play ([Armstrong & McGehee, 1976](#);  
7 [Chesson & Huntly, 1997](#); [Huisman & Weissing, 2001](#); [Li & Chesson, 2016](#)). Neutral theory, that  
8 assumes a non-equilibrium coexistence maintained by dispersal and equal competitive abilities for all  
9 species ([Hubbell 2001](#), though there are exceptions, see [Volkov \*et al.\* 2003, 2007](#)) has been proposed  
10 as a solution to explain highly diverse communities ([Hubbell, 2001](#); [Rosindell \*et al.\*, 2011](#)).

11 However, the evidence gathered from terrestrial plant communities starts to suggest that, in fact,  
12 niche rather than neutral processes may be paramount to explain coexistence, with intraspecific  
13 competition dwarfing interspecific competition in most cases ([Adler \*et al.\*, 2010, 2018b](#)). Whether  
14 these conclusions drawn from studies of annual plants and forest trees apply to other ecosystems  
15 and taxa is currently little known (but see [Mutshinda \*et al.\* 2009](#)).

16 Moreover, even within a single trophic level, competition may not be the rule: the meta-analysis  
17 by [Adler \*et al.\* \(2018b\)](#) reported a large number of facilitative interactions (30%) and several reviews  
18 ([Brooker \*et al.\*, 2008](#); [McIntire & Fajardo, 2014](#)) have highlighted that facilitation may be much more  
19 widespread than ecologists usually tend to think. Although some theoretical studies suggest that  
20 facilitative interactions can be destabilizing (*sensu* resilience) and therefore undermine coexistence  
21 in Lotka-Volterra models ([Coyte \*et al.\*, 2015](#)), multiple other modelling ([Gross, 2008](#)) and empirical  
22 ([Brooker \*et al.\*, 2008](#); [Cavieres & Badano, 2009](#)) studies have suggested that facilitative interactions  
23 can to a large degree benefit coexistence, especially when multiple interaction types are considered  
24 simultaneously ([Mougi & Kondoh, 2012](#); [García-Callejas \*et al.\*, 2018](#)).

25 Here, we study a large multi-species dataset consisting of several multivariate long-term time series  
26 of phytoplankton dynamics along the French coastline, which we then analyse using multivariate  
27 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 (Titman, 1976; Descamps-Julien & Gonzalez, 2005). The genus level is also a rather fine taxonomic scale for phytoplankton interaction studies, as most studies are restricted to interaction between different classes or even phyla (Ives *et al.*, 2003; Hampton *et al.*, 2008; Griffiths *et al.*, 2015). Studying interactions between different genera of phytoplankton therefore both makes empirical sense in light of competition experiments and allows to estimate better-resolved networks. We focus here on genera that belong mostly to diatoms and dinoflagellates. To put our results into a more general context, we then compare our interaction strength estimates to previously published interaction networks produced under the same statistical framework, both in plankton and other empirical systems.

## Material and methods

### Sampling methods

All phytoplankton counts were collected by Ifremer coastal laboratories as part of the National Phytoplankton and Phycotoxin Monitoring Network (REPHY, 2017). Since 1987, this monitoring program has required the sampling of 26 sites along the French coastline every 2 weeks within 2 hours of high tide to document both biotic (phytoplankton counts) and abiotic (water temperature, salinity) variables. We focused on sites which had the longest 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, Oléron, Arcachon and the Mediterranean Sea; Fig. S1).

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  $\mu\text{m}$  were identified at the lowest possible taxonomic level and counted with the Utermöhl method using an optical microscope (Utermöhl, 1958). 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 (Hernández Fariñas

54 *et al.*, 2015; Barraquand *et al.*, 2018), except for cryptophytes and euglenophytes in Arcachon, which  
 55 could not be identified below the family level. Although the taxonomic resolution used here may  
 56 seem coarse in comparison to land plants, it is in fact more refined than 86% of the MAR(1) studies  
 57 of phytoplankton listed in Table S3.

58 For each region, the MAR(1) analysis focused on the most abundant and most frequently observed  
 59 genera to avoid most of the gaps in the time series. When gaps did not exceed a month, missing  
 60 values were linearly interpolated; remaining missing values were replaced by a random number  
 61 between 0 and half of the lowest observed abundance (Hampton *et al.*, 2006). We tested extensively  
 62 this and other methods to deal with missing data in a previous publication on a subset of this  
 63 dataset (Barraquand *et al.*, 2018). All time series were scaled and centered before MAR analyses.

## 64 **MAR(1) model**

65 Multivariate autoregressive (MAR) models are used to determine the interspecific interactions and  
 66 abiotic effects shaping a community’s dynamics (Ives *et al.*, 2003). MAR(1) models are based on a  
 67 stochastic, discrete-time Gompertz model which relates log-abundance of  $S$  species at time  $t + 1$   
 68 to interactions with the rest of the community at time  $t$ , and effects of  $V$  abiotic variables at time  
 69  $t + 1$ , following eq. 1.

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

70 where  $\mathbf{n}_t$  is the  $1 \times S$  vector of log-abundance of phytoplankton groups,  $\mathbf{B}$  is the  $S \times S$  community  
 71 (interaction) matrix,  $\mathbf{C}$  is the  $S \times V$  environment matrix describing the effects of  $V$  variables (stacked  
 72 in vector  $\mathbf{u}_{t+1}$ ) on species growth rates, and  $\mathbf{e}_t$  is a  $1 \times S$  noise vector which covers both process and  
 73 observation error, following a multivariate normal distribution with a variance-covariance matrix  
 74  $\mathbf{Q}$ .  $\mathbf{Q}$  is diagonal and we have previously showed that this parsimonious choice did not affect  
 75 qualitatively the results (Barraquand *et al.*, 2018).

76 We used the MARSS package (Holmes *et al.*, 2014) v3.9, in R v3.3.2 (Venables & Smith, 2013),  
 77 to estimate parameters with a maximum likelihood procedure.

78 We have previously published a detailed analysis of one of the dataset (Arcachon) for which more  
 79 covariables were available (Barraquand *et al.*, 2018), including nutrients and hydrodynamics variables.  
 80 We found that hydrodynamics variables were more influential than nutrients; nutrient dynamics  
 81 contributed little to phytoplankton dynamics on the two-week timescale. Because temperature  
 82 and salinity sum up seasonal changes in light as well as hydrology (salinity is inversely related to  
 83 freshwater inflow), these represent the two key drivers needed to account for abiotic influences  
 84 (Scheef *et al.*, 2013). The analysis of real data in Barraquand *et al.* (2018) was complemented by that  
 85 of phytoplankton-like simulated data, which confirmed the ability of MAR(1) models to infer biotic  
 86 interactions and abiotic forcings (e.g., no need for extra non-linearities to model the storage effect,  
 87 which was found to be nearly non-existent, as in previous analyses of plant data for which strong-self  
 88 regulation was observed (Adler *et al.*, 2010; Ellner *et al.*, 2016). Furthermore, using two abiotic  
 89 variables (temperature and salinity) in this study rather than the full set used in Barraquand *et al.*  
 90 (2018) led to almost identical estimates to the ones obtained previously (Barraquand *et al.*, 2018).  
 91 We are therefore confident that the MAR(1) models presented here are robust to small changes in  
 92 model specification. In general, MAR(1) models tend to be fairly robust to small deviations of the  
 93 underlying (non-linear) data-generating model, provided that one asks mainly order of magnitude of  
 94 coefficients values (rather than precise point estimates) and sign of interaction coefficients (Certain  
 95 *et al.*, 2018), which is how these models are used here. For ease of interpretation of those coefficients,  
 96 we also prove the correspondance between the magnitude of intra/inter interaction strength in a  
 97 MAR(1) model and a multispecies Beverton-Holt model, i.e., a discrete-time Lotka-Volterra model,  
 98 in the Supplementary Information.

99 In this study, the number of phytoplankton groups,  $S$ , varies between regions but we keep  
 100 the same 2 covariates, i.e. water temperature and salinity, that were measured at all study sites.  
 101 Therefore, the dimension of the dynamical system only depends on the (square of the) number of  
 102 phytoplankton groups we study, which ranges between 7 (Mediterranean Sea) and 14 (Brittany). The  
 103 smallest system still requires 70 parameters to be estimated if we consider all possible interactions  
 104 between species. To reduce this dimensionality and remove unnecessary parameters, we compared  
 105 different ‘interaction scenarios’ based on BIC (Fig S3), which proved to be satisfactory in our

previous analyses of both real data and similar simulated datasets (Barraquand *et al.*, 2018). The null interaction scenario assumed no interaction between groups of species (diagonal interaction matrix) and was compared to four other interaction scenarios. The first interaction scenario assumed that interactions could only occur between phylogenetically close organisms, i.e., within a class (groups were then diatoms, dinoflagellates, and other phytoplanktonic organisms) while the second interaction scenario further differentiated pennate and centric diatoms. The third interaction scenario considered the reverse 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 interaction scenario did not constrain the interactions at all (full interaction matrix). The second interaction scenario, hereafter called the pennate-centric scenario, had the lowest BIC for all sites and was therefore the most parsimonious, and was chosen as the basis for further investigations of network structure.

## Analysis of interaction strengths

The interaction matrix obtained from MAR(1) analyses can be used to determine the stability of a discrete-time dynamical system (Ives *et al.*, 2003). 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 density (Breier *et al.*, 2018). 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, Eq S5) and impact (average effect of a focal taxon on other taxa, Eq S6) 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



133 positive or negative?) that can be expected on a species' growth rate from other planktonic species  
134 while absolute effects characterise the strength of all types of interactions on a species (i.e., is a  
135 species strongly affected by the others?). ~~We examined whether vulnerability and impact could be~~  
136 ~~affected by phylogenetic correlations; they were not as on Fig. 3 points were not clustered according~~  
137 ~~to genus, family or phylum.~~

138 Finally, we compared our results on the ratio between mean self-regulation/intraspecific in-  
139 teraction strength and mean interspecific interaction strength to other published studies based  
140 on a MAR(1) model. A list of references is given in Table S3. Authors usually reported only  
141 coefficients that were significant at the 95% significance threshold, thus ignoring potentially many  
142 weak effects. For mean intergroup interactions, we therefore computed both the mean value of  
143 all coefficients outside of the matrix diagonal, including zeroes (Fig. 4, which decreases the mean  
144 intergroup interaction strength), and the mean value of statistically significant intergroup coefficients  
145 only (Fig S8, which increases the mean intergroup interaction strength). We should mention two  
146 potential biases associated with this comparison across the published literature: low-dimensional  
147 matrices tended to be more complete (less sparse) than high-dimensional matrices, as these small  
148 interaction matrices were used to study known interaction phenomena (observed predation between  
149 organisms, for instance). Conversely, the number of parameters to estimate increases as the square  
150 of the number of interacting groups, leading most authors to reduce this set before the estimation  
151 process for large interaction matrices. There is therefore a positive correlation between sparsity  
152 and dimensionality (Fig S9). A second caveat is that while we informed our model selection by  
153 phylogeny (see above), several authors have reduced the number of estimated parameters by an  
154 automated procedure, usually based on the comparison of 100 randomly chosen interaction matrices  
155 by BIC ([Ives et al., 2003](#)). The latter choice may bias high non-zero interactions in the literature.  
156 This is why we decided to present in the main text intra/inter ratios including interspecific (or  
157 intergroup) coefficients set to zero, which should be less sensitive to the model selection method and  
158 therefore make comparisons across studies possible.

## Results

### Interaction estimates

Using MAR(1) autoregressive models, we have produced interaction matrices (Ives *et al.*, 2003; Hampton *et al.*, 2013) – i.e., Jacobian community matrices on the logarithmic scale (Ives *et al.*, 2003). Best-fitting models corresponded to a phylogenetically-structured interaction scenario, where interaction only occurred between closely related genera (Fig S3). 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 regions (Barraquand *et al.*, 2018). The ratio of mean intragenus to intergenus interaction coefficients varies 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 21-43. 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.

We have found that the percentage of true mutualism (+/+) is substantial: averaged over all sites, 32% of all interactions are (+/+) while only 12% of them are (-/-), see also Fig S5. The sign correspondence is not always maintained between French regions: the only interaction that is non-zero in the 10 sites (CHA/SKE) is mutualistic in Men er Roue only (Brittany) and mixed (+/-) at all other sites. Within the same region, however, interactions measured at different sites tend to keep the same sign. In the 3 sites of 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

186 mutualistic in some of the Brittany sites. This contradicts previous observations that mutualistic  
187 interactions tend to be more context-dependent than competitive interactions (Chamberlain *et al.*,  
188 2014).

## 189 Interaction network analysis

190 The stability (*sensu* resilience, Ives & Carpenter 2007) of all interaction matrices was not strongly  
191 affected by the percentage of positive interactions or their connectivity properties (Fig. 2). The  
192 maximum modulus of the interaction matrix eigenvalues remained between 0.65 and 0.80. There  
193 was also a slight increase in stability with weighted connectance, with a drop in eigenvalue modulus  
194 for weighted connectances between 0.09 and 0.1.

195 Given that a direct complexity-stability link was not obvious, we investigated whether the matrix  
196 coefficients had some particular structure that could help theoretical ecology to make better null  
197 models of joint community dynamics and interactions (James *et al.*, 2015). We defined two scores,  
198 vulnerability (~~summed effect of others on the focal species growth rate, Eq S5~~) and impact (~~summed~~  
199 ~~effect of the focal species onto other species growth rates, Eq S6~~). Relations between inter- and  
200 intra-genus interactions emerged (Fig. 3): genera that were more self-regulating also had also a  
201 higher vulnerability score and a lower impact score. Those two influences are likely to trade-off: a  
202 high degree of self-regulation somehow buffers outside influences. Taxa that were less self-regulating  
203 were also more likely to have a broad range of effects onto other taxa. As these genera tended to  
204 be more abundant (Fig S7), they were more likely to affect other genera. It is important to note,  
205 however, that these trends are weak and there is therefore a considerable amount of randomness  
206 dominating the interaction matrix: many scenarios of self-regulation vs limitation by others are  
207 therefore possible.

208 Aside from these trade-offs, some of which promote some stability (*sensu* invariability, Arnoldi  
209 *et al.* 2018), we found no remarkable patterns of covariation between matrix elements (other than a  
210 mean-variance scaling of interaction coefficients, Fig S6).

## Literature comparison

~~Finally, we 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 (listed in Table S3), we found that the order of magnitude of intra/inter interaction strengths considered here is not particularly above those found for most planktonic systems to which MAR(1) models have been fitted, considering that our systems are relatively high-dimensional and that the higher the number of taxa, the larger the intraspecific regulation (Barabás *et al.*, 2017). We included in Fig. 4 not only plankton studies but also a couple of vertebrate or insect studies on less diverse communities, where interactions are stronger. The conclusion from this comparison seems to be that, unlike small communities that can be tight-knit, any diverse system of competitors and facilitators has evolved large niche differences making intragroup competition much larger in magnitude than intergroup interactions.

## Discussion

### Strong self-regulation and facilitation

We found very large niche differences between genera, translating into much higher intragenus than intergenus effects on growth rates (i.e., strong self-regulation), together with a high degree of facilitative net interactions.

The rather high intra/intertaxon interaction strength ratio (Levine & HilleRisLambers, 2009) that we found, from 5 to 20, depending on how one counts the interactions set to zero in the estimation process, could appear extremely high in light of previous intra/interspecific competition strength estimates of 4 to 5 by Adler *et al.* (2018b). Even though their model is a different one, i.e., Lotka-Volterra competition, we prove in the Supplementary Information that the intra/inter ratio should remain commensurate. The difference in the intra/inter ratio that we found should therefore lie elsewhere, which requires some explanation. First, one could argue that such high intra/inter ratio arises because we consider the genus as our baseline taxonomic unit, rather than the species.

236 Although it is logical that niche differentiation increases as one gets up the phylogenetic tree, and  
 237 that getting down to the species level could slightly decrease that ratio, there are two arguments  
 238 suggesting that the niche differences found here extend to the species level. First, species belonging  
 239 to the various genera considered here are often found to compete in experiments (Titman, 1976;  
 240 Tilman *et al.*, 1982; Descamps-Julien & Gonzalez, 2005). There is therefore a massive difference  
 241 between niches in the lab and in the field (Barraquand *et al.*, 2018). Second, the only other study  
 242 that managed to provide MAR(1) estimates down to the species level for phytoplankton, that  
 243 of Huber & Gaedke (2006), provides an intra/interspecific strength ratio similar to ours (point  
 244 7a in Fig. 4). Strong self-regulation seems therefore a genuine feature of field phytoplanktonic  
 245 communities.

246 Another main finding of our study is the large frequency of positive interactions, with 30% truly  
 247 mutualistic (+/+) interactions and between 40 and 70% facilitative effects. This again can be  
 248 compared to the meta-analysis by Adler *et al.* (2018b) who also found facilitative interactions, but a  
 249 little less than here ( $\approx 30\%$ ). However, Adler *et al.* (2018b)’s review contains many experiments while  
 250 the plant literature is replete with field examples of facilitation (Brooker *et al.*, 2008; McIntire &  
 251 Fajardo, 2014), so that plant facilitation could be higher in the field. At the moment, it is therefore  
 252 unknown how the predominance of facilitative interactions that we found in phytoplankton compares  
 253 to facilitation in terrestrial plants. We note that several authors using MAR(1) models previously  
 254 forbade positive interactions within the same trophic level, so that the fraction of facilitative  
 255 interactions in plankton cannot be computed from literature-derived MAR(1) estimates.

256 The large niche differences and facilitative interactions that arise when considering a single  
 257 trophic level are an emergent property, arising from hidden effects of resources or predator parti-  
 258 tioning/sharing (Chesson, 2018). In our previous publication investigating in detail the Arcachon  
 259 study sites (Barraquand *et al.*, 2018), we have argued that for phytoplankton, the strong intragroup  
 260 density-dependence could arise from effects of natural enemies (Haydon, 1994; Barraquand *et al.*,  
 261 2018). Natural enemies could also very well create apparent mutualism between prey species (Abrams  
 262 *et al.*, 1998; Barraquand *et al.*, 2015; de Ruiter & Gaedke, 2017). We believe this to be likely true  
 263 for the present study as well, given that the new study regions (Oléron, Brittany, Mediterranean)

264 have similar predators to the Arcachon site (zooplankton, [Jamet \*et al.\* 2001](#); [Modéran \*et al.\* 2010](#);  
 265 [Tortajada \*et al.\* 2012](#), e.g.) and parasites (viruses, [Ory \*et al.\* 2010](#), e.g., fungi). Though natural  
 266 enemies are good candidates to explain the observed niche differences and emerging facilitation, one  
 267 must bear in mind that other known drivers of phytoplankton dynamics such as allelopathy ([Felpeto  
 268 \*et al.\*, 2018](#)), auxotrophy ([Tang \*et al.\*, 2010](#)) or hydrodynamics ([Lévy \*et al.\*, 2018](#)) can all, in theory,  
 269 help create different niches and an emerging facilitation (see last subsection of the Discussion).  
 270 Finally, resources that are usually considered limiting for all species might in fact not always be:  
 271 the changes in phytoplankton absorption spectrum documented by [Burson \*et al.\* \(2018\)](#) constitute  
 272 an example of fine-scale resource partitioning of one resource, light, that is usually believed to be  
 273 limiting for all species and genera.

## 274 **No complexity-stability relationship but connections between self-regulation** 275 **and intergroup interactions**

276 There was no relation between the complexity of the communities (measured as either the weighted  
 277 connectance or linkage density of the interaction matrices) and their stability, as measured by the  
 278 dominant eigenvalue of the interaction matrix, which measures the return time to a point equilibrium.  
 279 This result is conditional upon our model being a good approximate description of the system  
 280 (i.e., no multiyear limit cycles or chaotic attractors as the mapping between eigenvalues and actual  
 281 stability is distorted in that case ([Certain \*et al.\*, 2018](#)) but we showed on a subset of this data that  
 282 a fixed point in a MAR(1) model, perturbed by seasonality and abiotic variables, is an accurate  
 283 description of the system ([Barraquand \*et al.\*, 2018](#)). Therefore, we are confident that the absence  
 284 of complexity-resilience found here is genuine. This absence of direct link between complexity and  
 285 stability could be an actual feature of empirical systems, as shown previously by [Jacquet \*et al.\* \(2016\)](#)  
 286 using a different technique, even though it does contradict previous results on random matrices,  
 287 especially for competitive and/or mutualistic networks ([Allesina & Tang, 2012](#)). We also found  
 288 that the percentage of mutualistic interactions, that is thought to affect the stability of the network  
 289 ([Mougi & Kondoh, 2012](#); [Coyte \*et al.\*, 2015](#); [García-Callejas \*et al.\*, 2018](#)), does not have a major  
 290 impact on the network's resilience.

291 In addition to weighted connectance, indices at the network-level (e.g., linkage density) and  
 292 at the species or genus level (vulnerability and impact) approximate the average effects exerted  
 293 and sustained by any given taxa in the different study sites. While, at the network level, network  
 294 structure (either complexity measures or the percentage of mutualistic interactions) did not affect  
 295 stability, a relation emerged between self-regulation, necessary for coexistence, and genus-level  
 296 indices. We found that the more a genus is self-regulated, the more it tends to be vulnerable to other  
 297 genera impacts and the less it impacts other genera. High self-regulation usually indicates large  
 298 niche differences with the rest of the community, and it makes therefore sense that a species/genus  
 299 whose needs strongly differ from the others only marginally impacts the resources of the other  
 300 coexisting species. Furthermore, a low self-regulation was correlated with high average abundance,  
 301 which echoes findings by [Yenni \*et al.\* \(2017\)](#) who found that rare species usually show stronger  
 302 self-regulation. This correlation between rarity and self-regulation could explain the lesser impact  
 303 effect of high self-regulated species/genus: a species which dominates the community composition  
 304 can have a major effect on the others, especially as they usually cover more space, while it is harder  
 305 for rare, localised species to have large impacts. However, it was more difficult to explain the  
 306 relationship between self-regulation and vulnerability: a genus that is more self-regulated and rarer  
 307 was found here to be on average more vulnerable to other genera's increases in densities. Such  
 308 relation implies greater stability (*sensu* resilience) for the network as a whole, because the taxa that  
 309 are the most vulnerable to other taxa's impacts are also those whose dynamics are intrinsically more  
 310 buffered. By which mechanisms this could happen is so far unclear and open to speculation. We  
 311 caution, however, that the relationships between vulnerability, impact and self-regulation that we  
 312 evidenced are all relatively weak: considerable stochasticity dominates the distribution of interaction  
 313 matrix coefficients.

## 314 **Ghosts of competition past and present**

315 Overall, the dominance of niche differentiation in observational plankton studies – based on our  
 316 analysis of the REPHY dataset and re-analysis of the MAR(1) literature – is similar to what has  
 317 been recently found in plant community studies ([Volkov \*et al.\*, 2007](#); [Adler \*et al.\*, 2018b](#)) or empirical

318 food webs including horizontal diversity (Barabás *et al.*, 2017). Large niche differences might be  
 319 due to the ghost of the competition past, i.e., competition has occurred in the past, leading to  
 320 strong selection and subsequent evolution leading to progressive niche separation. In this scenario,  
 321 species have evolved niches that allow them not to compete or to interact only weakly (very strong  
 322 facilitative effects might be likewise destabilizing (Coyte *et al.*, 2015). The likely predator effects that  
 323 we highlighted above could be comprised within such niche differentiation *sensu largo*: specialized  
 324 predators can make strong conspecific density-dependence emerge (Bagchi *et al.*, 2014; Comita *et al.*,  
 325 2014), while switching generalists can also promote diversity (Vallina *et al.*, 2014). Both predators  
 326 and resources have often symmetrical effects and can therefore contribute almost equally to such  
 327 past niche differentiation (Chesson, 2018).

328 An intriguing new possibility, dubbed the “ghost of competition present” (Tuck *et al.*, 2018),  
 329 suggests by contrast that spatial distributions in relation to abiotic factors might have a large  
 330 impact on the interaction strengths inferred from temporal interaction models such as ours. Recent  
 331 combinations of model fitting and removal experiments have shown that the model fitting usually  
 332 underestimates the effect of competitors that are uncovered by removal experiments (Tuck *et al.*,  
 333 2018; Adler *et al.*, 2018a). This could occur for instance if species are spatially segregated (at a  
 334 small scale) because each species only exists within a domain where it is relatively competitive  
 335 (Pacala’s spatial segregation hypothesis Pacala & Levin 1997), while a focal species could spread  
 336 out if competitors were removed. This means that a species can be limited by competitors, but act  
 337 so as to minimize competition (a little like avoidance behaviour in animals), which implies that  
 338 competition is in effect hard to detect when all species are present. This would require spatial  
 339 segregation between phytoplankton species at the scale of interactions, i.e., at the microscale. At  
 340 the moment, it is known that turbulence generates inhomogeneities at the microscale (Barton *et al.*,  
 341 2014; Breier *et al.*, 2018) but it is quite unclear how this affects multivariate spatial patterns of  
 342 species distributions (*sensu* Bolker & Pacala 1999, or Murrell & Law 2003). Moreover, even if  
 343 turbulence generates spatial structure with segregation between species, it is not quite clear that  
 344 the “ghost of competition present” mechanism could work for plankton, because turbulence rather  
 345 than organism movement dictates where the phytoplankton patches can or cannot appear.



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## Supporting Information

This article contains supporting information.

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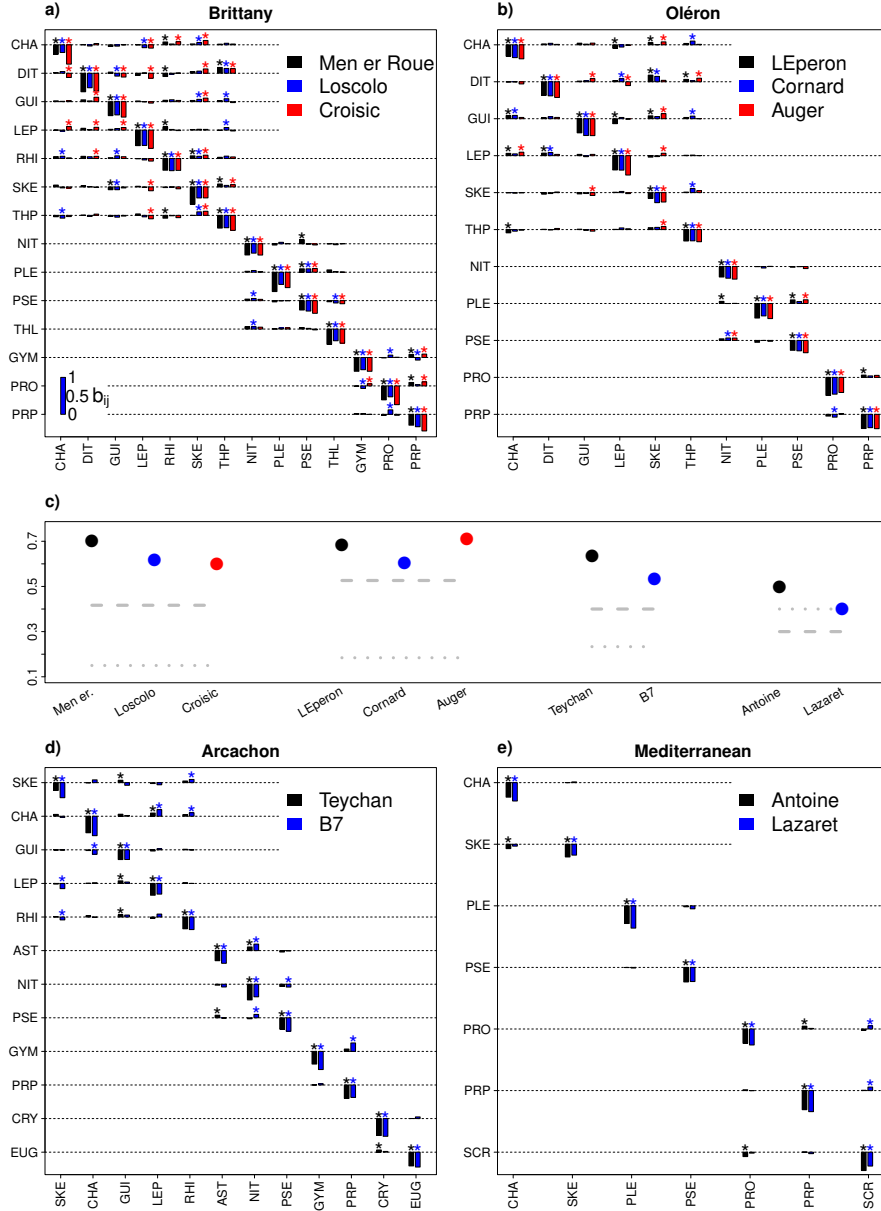
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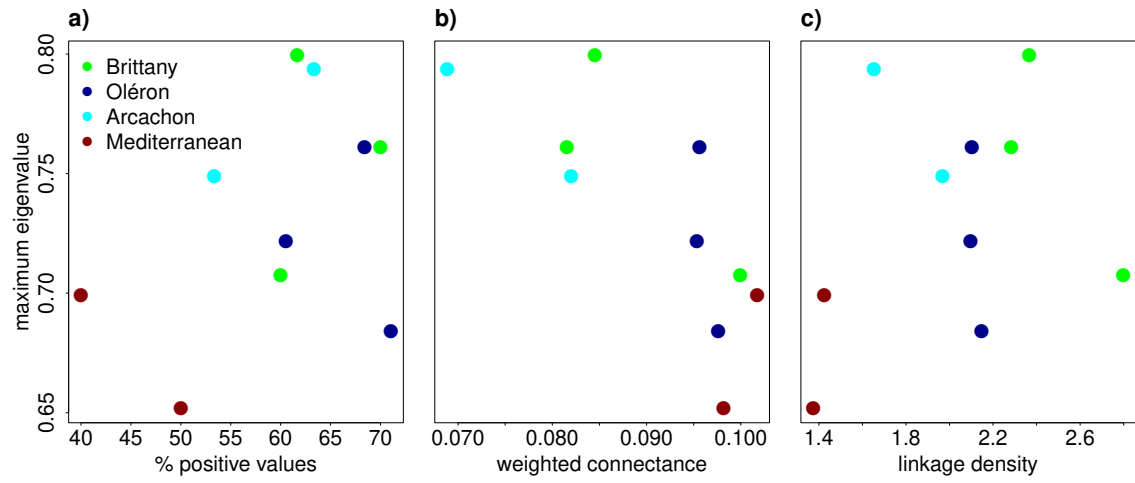
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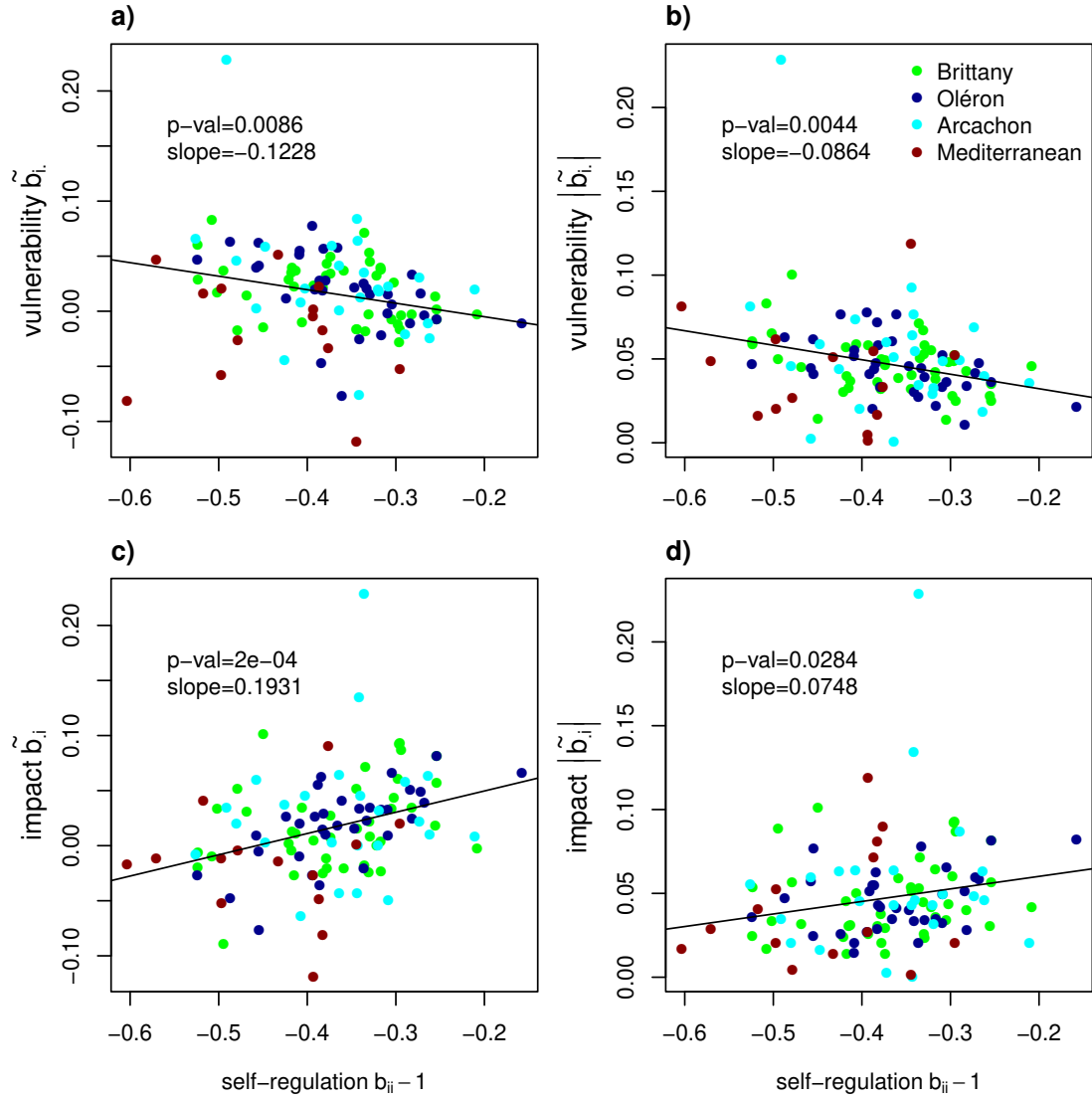




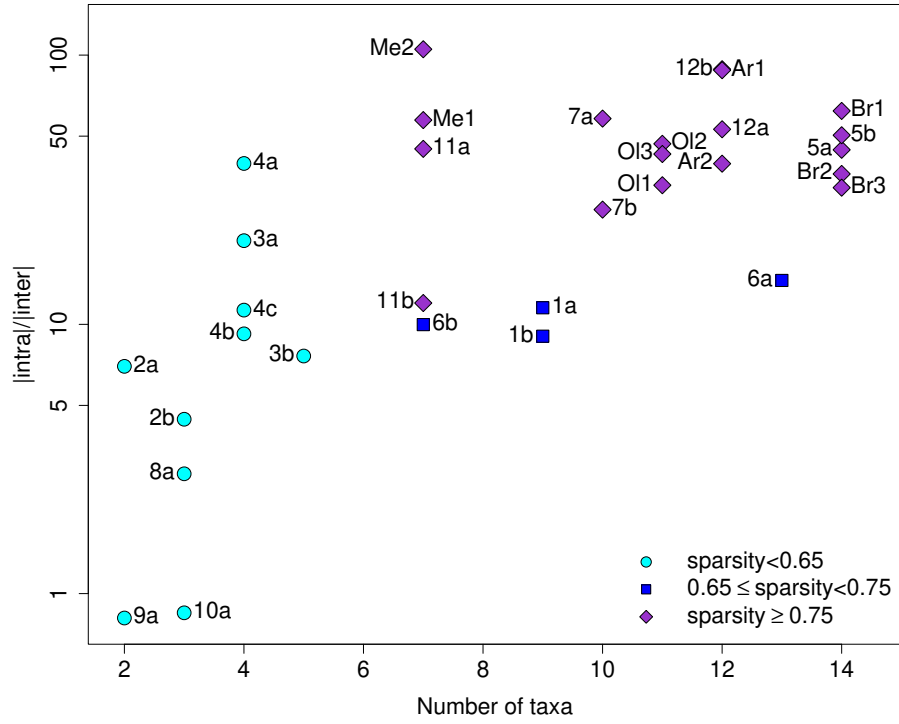
**Fig 1. Interaction matrices estimated in 10 sites along the French coastline.** Four regions are distinguished: Brittany (a), Oléron (b), Arcachon (d) and the Mediterranean Sea (e). Only interactions between clades (pennate and centric diatoms, dinoflagellates, other planktonic taxa) are allowed, as this is the best fitting interaction scenario (Fig S3). Taxon  $j$  (in columns) has an effect illustrated by the bar height on taxon  $i$ 's growth rate (in rows). We present the interaction matrix minus the identity matrix ( $\mathbf{B} - \mathbf{I}$ ) because this compares unambiguously intra- and intergenera interactions. The scale for the coefficient values is given at the bottom left of panel a). 95% significance of coefficients is marked by asterisks (\*). The community composition is given in Table S2. 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 given region.



**Fig 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 the Supplementary Information.



**Fig 3. Relation between vulnerability/impact and self-regulation.** Average vulnerability (effects of others on the focal taxon growth rate, a-b) and impact (effects of the focal taxon on others' 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 (Fig S1). 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.



**Fig 4. Ratio of intra- to inter-group interaction strength in Multivariate AutoRegressive (MAR) models in the ecological literature as a function of the number of species they include.** The name of each studies, corresponding to each code, is given in Table S3. Codes beginning with letters correspond to the present study. The symbol color and shape correspond to the sparsity of the interaction matrix (e.g., the proportion of null interactions in the matrix). 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).