

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

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Abstract

1. 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.
2. We analysed a large dataset of phytoplankton abundance time series using dynamic, multi-variate autoregressive models. Phytoplankton was counted and identified down to the genus level, every two weeks over twenty years, at ten sites along the French coastline. Multivariate autoregressive models allowed to estimate biotic interaction networks, while also accounting for abiotic variables that may drive part of the phytoplankton fluctuations. We then analysed the ratio of intra- to inter-taxa interactions (measuring self-regulation, itself a measure of niche differentiation), the frequency of negative vs positive interactions, and how stability metrics (both at the network and genus level) relate to the network complexity and genus self-regulation or abundance.
3. We showed that a strong self-regulation, with competition strength within a taxon (genus) an order of magnitude higher than between taxa, was present in all phytoplanktonic interaction networks. This much stronger intragenus competition suggests that niche differentiation - rather than neutrality - is commonplace in phytoplankton. Furthermore, interaction networks were dominated by positive net effects between phytoplanktonic taxa (above 50% of non-zero interactions on average). While network stability (*sensu* resilience) was unrelated to complexity measures, we unveiled links between self-regulation, intergenus interaction strengths and abundance. The less common taxa tend to be more strongly self-regulated and can therefore maintain in spite of competition with abundant ones.
4. *Synthesis*: We prove that strong niche differentiation, widespread facilitation between phytoplanktonic taxa and stabilizing covariances between interactions strengths should be common features of coexisting phytoplankton communities in the field. These are structural properties

that we can expect to emerge from plausible mechanistic models of phytoplankton communities. We discuss mechanisms, such as predation or restricted microscale movement, that are consistent with these findings, which paves the way for further research.

Keywords: phytoplankton; coexistence; facilitation; mutualism; niche theory; time series; networks

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, 1980;
7 Chesson & Huntly, 1997; Huisman & Weissing, 2001; Li & Chesson, 2016; Chesson, 2018). Neutral
8 theory, that assumes a non-equilibrium coexistence maintained by dispersal and equal competitive
9 abilities for all species (Hubbell 2001, though there are exceptions, see Volkov *et al.* 2003, 2007) has
10 been proposed as a solution to explain highly diverse communities (Hubbell, 2001; Rosindell *et al.*,
11 2011).

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

17 Moreover, competition may not be the rule: the meta-analysis by Adler *et al.* (2018b) reported a
18 large number of facilitative interactions (30%) and several reviews (Brooker *et al.*, 2008; McIntire
19 & Fajardo, 2014; Kinlock, 2019) have highlighted that facilitation may be much more widespread
20 than ecologists usually tend to think. Although some theoretical studies suggest that facilitative
21 interactions can be destabilizing (*sensu* resilience) and therefore undermine coexistence in Lotka-
22 Volterra models (Coyte *et al.*, 2015), multiple other modelling (Gross, 2008) and empirical (Brooker
23 *et al.*, 2008; Cavieres & Badano, 2009) studies have suggested that facilitative interactions can
24 to a large degree benefit coexistence, especially when multiple interaction types are considered
25 simultaneously (Mougi & Kondoh, 2012; García-Callejas *et al.*, 2018).

26 Here, we analyse a spatially replicated, long-term community-level dataset, consisting of ten
27 multivariate time series of phytoplankton abundance along the French coastline. The time series are

28 modelled using multivariate autoregressive (MAR) models, allowing for interactions between genera.
29 Although many ecological studies focus on interactions between species, competition has been shown
30 experimentally to occur between different genera of phytoplankton ([Titman, 1976](#); [Descamps-Julien
31 & Gonzalez, 2005](#)). The genus level is also a rather fine taxonomic scale for phytoplankton interaction
32 studies, as most studies are restricted to interactions between different classes or even phyla ([Ives
33 et al., 2003](#); [Hampton et al., 2008](#); [Griffiths et al., 2015](#)). Studying interactions between different
34 genera of phytoplankton therefore both makes empirical sense in light of competition experiments
35 and allows to estimate better-resolved networks. We focus here on genera that belong mostly to
36 diatoms and dinoflagellates. To put our results into a more general context, we then compare our
37 interaction strength estimates to previously published interaction networks produced under the
38 same statistical framework, both in plankton and other empirical systems.

39 Material and methods

40 Sampling methods

41 All phytoplankton counts were collected by Ifremer coastal laboratories as part of the National
42 Phytoplankton and Phycotoxin Monitoring Network ([REPHY, 2017](#)). Since 1987, this monitoring
43 program has required the sampling of 26 sites along the French coastline every 2 weeks within 2
44 hours of high tide to document both biotic (phytoplankton counts) and abiotic (water temperature,
45 salinity) variables. We focused on sites which had the longest time series. We also excluded time
46 series which had missing data for over 6 months or an average delay between sampling dates above
47 20 days. This reduced the number of study sites to 10 sites nested within 4 regions (Brittany, Oléron,
48 Arcachon and the Mediterranean Sea; Fig. S1 and Table S1).

49 Abiotic variables (temperature, salinity) were measured directly from the boat during the sampling
50 process while water samples for biotic analyses were fixed with a Lugol's solution and examined later.
51 Phytoplankton cells above 20 μm were identified at the lowest possible taxonomic level and counted
52 with the Utermöhl method using an optical microscope ([Utermöhl, 1958](#)). Throughout the years
53 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 (Table S2; [Hernández Fariñas *et al.* 2015](#); [Barraquand *et al.* 2018](#)), 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 Table S3.

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. Time series are plotted in Fig. S2. 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 abundance ([Hampton *et al.*, 2006](#)). We tested extensively this and other methods to deal with missing data in a previous publication on a subset of this dataset ([Barraquand *et al.*, 2018](#)). 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 effects shaping a community's dynamics ([Ives *et al.*, 2003](#)). MAR(1) models are based on a stochastic, discrete-time Gompertz equation which relates the log-abundance of each of the S taxa at time $t + 1$ to log-abundances of the whole community at time t , with possible interactions between taxa, and effects of V abiotic variables at time $t + 1$. These assumptions are encapsulated in 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 $1 \times S$ vector of log-abundance of phytoplankton taxa, \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 (stacked in vector \mathbf{u}_{t+1}) on growth rates, with $V=2$ in our case (temperature and salinity). and The noise \mathbf{e}_t is a $1 \times S$ noise vector which covers both process and observation error, following a multivariate normal distribution with a variance-covariance matrix \mathbf{Q} . \mathbf{Q} is diagonal and we have previously showed that this parsimonious choice did not affect qualitatively the results ([Barraquand *et al.*,](#)

2018). We used the MARSS package (Holmes *et al.*, 2014) v3.9, in R v3.3.2 (Venables & Smith, 2013), to estimate parameters with a maximum likelihood procedure.

Our previous analysis of the Arcachon region, for which more covariables were available (Barraquand *et al.*, 2018), revealed that hydrodynamics and hydrology had more influence on phytoplankton dynamics than nutrients on the two-week timescale. Because temperature and salinity sum up seasonal changes in light as well as hydrology (salinity is inversely related to freshwater inflow), these represent the two key drivers needed to account for abiotic influences (Scheef *et al.*, 2013). They are therefore used to summarize the abiotic environment in the remainder of the article.

The analysis of real data in Barraquand *et al.* (2018) was complemented by that of simulated data mimicking the study design, which confirmed the ability of MAR(1) models to infer biotic interactions and abiotic forcings. ~~There was no need to account for extra non-linearities to model relative nonlinearities or a storage effect, as these were found to be non-existent (through threshold autoregressive models, Barraquand *et al.*, 2018).~~ A different type of model Fitting a more sophisticated model (threshold autoregressive model) did not reveal extra non-linearities or a storage effect in ~~this~~ the Arcachon subset of the data ~~on a subset of the present dataset~~ (Barraquand *et al.*, 2018). Other aspects of the MAR(1) modelling are likewise quite robust: using two abiotic variables (temperature and salinity) in this study rather than the full set used in Barraquand *et al.* (2018) led to almost identical covariate effects and interaction estimates for the Arcachon study sites. Even if some departures from the true data-generating model may not always be detectable through MAR(1) diagnostics (e.g., residuals), ~~simulation work~~ analysis the analysis of nonlinear simulations has showed that MAR(1) models are in general robust to nonlinearities ~~(Certain *et al.*, 2018)~~ if the inference focuses on interaction sign and order of magnitude of model coefficients (Certain *et al.*, 2018), which is how these models are used here. For ease of interpretation of MAR(1) interaction coefficients, we also prove the correspondence between the magnitude of intra/inter interaction strength in a MAR(1) model and a multispecies Beverton-Holt model, i.e., a discrete-time Lotka-Volterra model (Cushing *et al.*, 2004), in the Supporting Information.

In this study, the number of phytoplankton taxa (S) and the community composition vary slightly between regions but sites share on average 67% of their taxa. In order to have comparable models, we

also keep the same 2 covariates, i.e., water temperature and salinity, that were measured at all study sites. Therefore, the dimension of the dynamical system depends on the (square of the) number of phytoplankton taxa we study, which ranges between 7 (Mediterranean Sea) and 14 (Brittany). The smallest system still requires 63 parameters to be estimated (49 for the 7x7 interaction matrices and 14 for the 7x2 environment matrices) if we consider all possible interactions between taxa. To reduce this dimensionality and remove unnecessary parameters, we compared built different ‘interaction scenarios’ with based on known phylogenetic grounds information (as suggested in Violle *et al.*, 2011; Narwani *et al.*, 2017). We chose a based on BIC model comparison selection of these scenarios (Fig S3), which proved to be satisfactory in our previous analyses of both real data and similar simulated datasets (Barraquand *et al.*, 2018, Appendix 2). The null interaction scenario assumed no interaction between groups of species genera (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). We selected the best scenario by comparing BIC (Fig S3), which proved to be satisfactory in our previous analyses of both real data and similar simulated datasets (Barraquand *et al.*, 2018, Appendix 2). The second interaction scenario, hereafter called the pennate-centric scenario, had the lowest BIC for all sites (Fig. S3). This parsimonious scenario was therefore 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 measure of resilience (similar to

~~the real part of the leading eigenvalue for continuous time model),~~ to network ~~metries~~ descriptors
~~which could be related to complexity,~~ such as the interaction strength distribution (sign, mean
 and variance) and weighted connectance ~~and linkage density~~ (Bersier *et al.*, 2002). The maximum
 modulus is analogous to the real part of the leading eigenvalue for continuous time models and
 measures resilience while still accounting for some variability properties (Ives *et al.*, 1999). Weighted
 connectance is a measure of the proportion of realized links compared to all possible links, taking into
 account the shape of the flux distribution, ~~while link density measures the average proportion and~~
~~strength of interactions for a given taxon.~~ These ~~These~~ metrics ~~are~~ ~~is~~ 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,~~ on interaction
 strength only (absolute values of the coefficients), irrespective of interaction sign. In contrast, mean
 and variance of the off-diagonal coefficients, which can affect the stability of a community (Allesina
 & Tang, 2015), are computed on raw values of the coefficients.

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. ~~Vulnerability and impact can~~
~~be related to in-strength and out-strength in the meta-analysis of Kinlock (2019).~~ We then ~~and~~
 compared these to the regulation a focal species exerted on itself. Raw values indicate the average
 effect (i.e., is the effect of others mostly positive or negative?) that can be expected on the growth
 rate of a taxon² growth rate from other planktonic taxa while absolute effects characterise the
 strength of all types of interactions on a taxon (i.e., is a taxon strongly affected by the others?).

Finally, we compared ~~our results on the~~ the observed ratio between mean self-regulation (in-
 trataxon interaction strength) and mean intertaxa interaction strength to other published studies
 based on a MAR(1) model. A list of references is given in Table S3. Authors usually reported only
 coefficients that were significant at the 95% significance threshold, thus ignoring potentially many
 weak effects, ~~which we had to~~ ~~re set to 0 by default.~~ ~~This implies that t~~ There are therefore two ways
 of computing the mean intertaxa interactions, i.e., taking the mean value of all coefficients outside
 of the matrix diagonal, including zeroes (which decreases the estimated mean intertaxa interaction

161 strength, Fig. 4), ~~and~~ taking the mean value of statistically significant intertaxa coefficients only
162 (which increases the estimated mean intertaxa interaction strength, Fig. S8). We considered both.

163 Results

164 Interaction estimates

165 Using MAR(1) autoregressive models, we ~~have~~ produced interaction matrices (Ives *et al.*, 2003;
166 Hampton *et al.*, 2013) – i.e., Jacobian community matrices on the logarithmic abundance scale
167 (Ives *et al.*, 2003). Best-fitting models corresponded to a phylogenetically-structured interaction
168 scenario, where interactions only occurred between closely related genera (Fig S3). This led to sparse,
169 modular matrices that have two main features. First, we observed a strong self-regulation for all
170 sites (Fig. 1, diagonal elements of all matrices), a feature that we ~~have~~ previously highlighted in a
171 more detailed analysis on one of the considered study regions (Barraquand *et al.*, 2018). The ratio
172 of mean intragenus to intergenus interaction coefficients varies between 6 and 10, not counting
173 coefficients set to 0 in the estimation process. ~~If~~ When we included the zeroes in the interaction
174 matrix in the computation of the intra/inter mean interaction strength, the ratio rises to 21-43.
175 Therefore, intragenus interactions ~~are~~ were on average ~~much stronger~~ one order of magnitude stronger
176 than intergenus interactions, ~~approximately 10 to 20 times stronger~~.

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

185 We ~~have~~ found that the percentage of true mutualism (+/+) ~~was~~ is substantial: averaged over all
186 sites, 32% of all interactions ~~are~~ were (+/+) while only 12% of them ~~are~~ were (-/-), see also Fig S5.

187 The sign correspondence ~~was~~ is not always maintained between French regions: the only interaction
 188 that ~~was~~ is non-zero in the 10 sites (CHA/SKE) ~~was~~ is mutualistic in Men er Roue only (Brittany)
 189 and mixed (+/-) at all other sites. Within the same region, however, interactions measured at
 190 different sites tended to keep the same sign. In the 3 sites of Oléron, for instance, there were 4
 191 interactions which remained positive on both sides (CHA/GUI, DIT/GUI, LEP/THP, SKE/THP), 3
 192 of them being also mutualistic in some of the Brittany sites. This contradicts previous observations
 193 that mutualistic interactions tend to be more context-dependent than competitive interactions
 194 (Chamberlain *et al.*, 2014).

195 Interaction network analysis

196 The stability (*sensu* resilience, Ives & Carpenter 2007) of all interaction matrices was not strongly
 197 affected by the percentage of positive interactions or the mean and variance of the intergenus
 198 ~~interactions or their connectivity properties~~ (Fig. 2). There was a slight increase in stability with
 199 weighted connectance, with a drop in eigenvalue modulus for weighted connectances between 0.09 and
 200 0.1. The maximum modulus of the interaction matrix eigenvalues remained between 0.65 and 0.80.
 201 ~~There was also a slight increase in stability with weighted connectance, with a drop in eigenvalue~~
 202 ~~modulus for weighted connectances between 0.09 and 0.1.~~

203 Given that a direct complexity-stability (*sensu* resilience) link was not obvious, we investigated
 204 whether the matrix coefficients had some particular structure that could help theoretical ecology to
 205 make better null models of joint community dynamics and interactions (James *et al.*, 2015). We
 206 defined two scores, vulnerability (summed effect of others on the focal taxon growth rate, eq. S5) and
 207 impact (summed effect of the focal taxon onto other taxa's growth rates, eq. S6). Relations between
 208 inter- and intra-genus interactions emerged (Fig. 3): genera that were more self-regulating also had
 209 also a higher vulnerability score and a lower impact score. Those two influences are likely to trade-off:
 210 a high degree of self-regulation somehow buffers outside influences. ~~[[Not sure about that! In the~~
 211 ~~sentence before, we say that more selfregulation also means higher vulnerability]]~~ Taxa that were
 212 less self-regulating were also more likely to have a stronger effect onto other taxa. As these genera
 213 tended to be more abundant (Fig S7), this could be mediated by the average density of a genus. 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.

Aside from the trade-offs of Fig. 3, we found no remarkable patterns of covariation between matrix elements other than a 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, in order to provide lower bounds for the intra/inter ratio. The conclusion from this comparison seems to be that, unlike small communities that can be tight-knit, any diverse field 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 Supporting Information that the intra/inter ratio should remain commensurate in a MAR(1) model. 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. ~~Although~~ It is logical that niche differentiation increases as one gets up the phylogenetic tree, and that getting down to the species level could slightly decrease that ratio (but see [Narwani *et al.*, 2017](#), in which phylogenetic closeness decreases competition strength). However, there are two arguments suggesting that the niche differences found here extend to the species level. First, phytoplankton species belonging to different genera are often found to compete in experiments ([Titman, 1976](#); [Tilman *et al.*, 1982](#); [Descamps-Julien & Gonzalez, 2005](#)). In the field-based dataset studied here, the same genera that are considered in experiments are found not to compete (or only weakly), hence there must be some niche differentiation occurring in the field but not in the lab. Second, the only other study that managed to provide MAR(1) estimates down to the species level for phytoplankton, that of [Huber & Gaedke \(2006\)](#), provides an intra/interspecific strength ratio similar to ours (point 7a in Fig. 4). Strong self-regulation seems therefore a genuine feature of field phytoplanktonic communities.

Another main finding of our study is the large frequency of positive interactions, with 30% truly mutualistic (+/+) interactions and between 40 and 70% facilitative effects. Although a seasonal environment can generate some positive covariation between taxa, those effects have already been filtered out by the inclusion of our 2 abiotic covariates (Fig. S4). The facilitative effects shown here are therefore residual effects, once abiotic trends are accounted for. Between 40 and 70% facilitation can be compared to the meta-analysis by [Adler *et al.* \(2018b\)](#) who also found facilitative interactions, but less than here ($\approx 30\%$). However, [Adler *et al.* \(2018b\)](#)'s review contains many experiments while the plant literature is replete with field examples of facilitation ([Brooker *et al.*, 2008](#); [McIntire & Fajardo, 2014](#)), so that plant facilitation could be higher in the field. At the moment, it is therefore unknown how the predominance of facilitative interactions that we found

266 in phytoplankton compares to facilitation in terrestrial plants. We note that several authors using
267 MAR(1) models previously forbade positive interactions within the same trophic level, so that the
268 fraction of facilitative interactions in plankton cannot be computed from literature-derived MAR(1)
269 estimates.

270 The large niche differences and facilitative interactions that arise when considering a single
271 trophic level are an emergent property, ~~arising~~resulting from hidden effects of resource or predator
272 partitioning/sharing (Chesson, 2018). In our previous publication investigating in detail the Arcachon
273 study sites (Barraquand *et al.*, 2018), we have argued that for phytoplankton, the strong intragroup
274 density-dependence could arise from effects of natural enemies (Haydon, 1994). Natural enemies could
275 also very well create apparent mutualism between prey species (Abrams *et al.*, 1998; Barraquand
276 *et al.*, 2015; de Ruiter & Gaedke, 2017). We believe this to be likely ~~true~~ for the present study ~~as~~
277 ~~well~~, given that the ~~new~~ study regions (Arcachon, Oléron, Brittany, Mediterranean) have similar
278 predators ~~to the Arcachon site~~ (zooplankton, e.g., Jamet *et al.*, 2001; Modéran *et al.*, 2010; Tortajada
279 *et al.*, 2012) and parasites (viruses, e.g., Ory *et al.*, 2010; fungi)[[As we have not proven that there is
280 apparent facilitation due to predation, even though we suspect it, in Barraquand *et al.* 2018, I don't
281 think we can write the sentence this way. It suggested that we did find this mechanism in Arcachon.]].
282 Though natural enemies are good candidates to explain the observed niche differences and emerging
283 facilitation, one must bear in mind that other known drivers of phytoplankton dynamics such as
284 allelopathy (Felpeto *et al.*, 2018), auxotrophy (Tang *et al.*, 2010) or hydrodynamics (Lévy *et al.*,
285 2018) can all, in theory, help create different niches and an emerging facilitation (see last subsection
286 of the Discussion). Finally, resources that are usually considered limiting for all species might in
287 fact not always be: Burson *et al.* (2018) show that phytoplanktonic taxa specialize on different
288 components of the light spectrum. This constitutes an example of fine-scale resource partitioning of
289 one resource, light, that all species and genera are usually thought to compete for.

No complexity-stability relationship but connections between self-regulation and intergroup interactions

There was no relation between the complexity of the communities (measured as either the weighted connectance or the interaction coefficient variance or linkage density of the interaction matrices) and their stability, (as measured by the dominant eigenvalue of the interaction matrix, which quantifies the return time to a point equilibrium, (i.e., resilience). This result is conditional upon our model being a good approximate description of the system (i.e., no multiyear limit cycles or chaotic attractors as the mapping between eigenvalues and actual stability is distorted in that case, *Certain et al.*, 2018). However, we already showed on a subset of this data that a fixed point in a MAR(1) model, perturbed by seasonality and abiotic variables, is an accurate description of the system (*Barraquand et al.*, 2018). Therefore, we are confident that the absence of complexity-resilience relationship found here is genuine. This absence of direct link between complexity and stability could be an actual feature of empirical systems, as shown previously by *Jacquet et al.* (2016) using a different technique, even though it does contradict theory based on random matrices, especially for competitive and/or mutualistic networks (*Allesina & Tang*, 2012). This result does contradict theory based on random matrices especially for competitive and/or mutualistic networks (*Allesina & Tang*, 2012). While this might be linked to the limited size of our networks (*Allesina & Tang*, 2015), we should also mention that our interaction matrices (discrete-time model) are not strictly analogous to the ones used in classical random matrix theory (continuous-time model). But it could be that our networks are too small for relationships based on random matrix theory to be apparent (*Allesina and Tang* 2015). In addition to connectance, we also found that the percentage of mutualistic interactions, that is thought to affect the stability of a network (*Mougi & Kondoh*, 2012; *Coyte et al.*, 2015; *García-Callejas et al.*, 2018), does not have a major impact on our networks' resilience.

In addition to weighted connectance, indices at the network-level (e.g., linkage density) and at the species or genus level (vulnerability and impact) approximate the average effects exerted and sustained by any given taxa in the different study sites. While, at the network level, network

317 structure (either complexity ~~measures~~proxy or the percentage of mutualistic interactions) did not
 318 affect stability, a relation emerged between self-regulation, necessary for coexistence, and genus-level
 319 indices. We found that the more a genus is self-regulated, the more it tends to be vulnerable to
 320 other genera impacts and the less it impacts other genera. We examined whether vulnerability and
 321 impact could be affected by phylogenetic correlations; theyre were notne, as on Fig. 3, points were
 322 not clustered according to genus, family or phylum. High self-regulation usually indicates large
 323 niche differences with the rest of the community, and it makes therefore sense that a species/genus
 324 whose needs strongly differ from the others only marginally impacts the resources of the other
 325 coexisting species. This is what we expect under strong niche partitioning. Furthermore, a low
 326 self-regulation was correlated with high average abundance, which echoes findings by Yenni *et al.*
 327 (2017) who demonstrated that rare species usually show stronger self-regulation. This correlation
 328 between relative rarity and self-regulation could also explain the lesser impact of highly self-regulated
 329 species/genus: a taxon which dominates the community composition can have a major effect on
 330 the others, especially as they usually cover more space, while it is harder for ~~rare, localised~~the least
 331 common taxa to have large impacts. However, it was more difficult to explain the relationship
 332 between self-regulation and vulnerability: a genus that is more self-regulated and ~~rarer~~less common
 333 was found here to be on average more vulnerable to other genera’s increases in densities. Such
 334 relation implies greater stability (*sensu* resilience, Ives *et al.* 2003, and also invariability, Arnoldi
 335 *et al.* 2019) for the network as a whole, because the taxa that are the morest vulnerable to other
 336 taxa’s impacts are also those whose dynamics are intrinsically more buffered. By which mechanisms
 337 this could happen is so far unclear and open to speculation. It could be just a “mass effect”:
 338 common taxa are in high enough numbers to deplete resources or change the environment in ways
 339 that affects the ~~rarer~~less common ones, but the reverse is not true. We caution, however, that the
 340 relationships between vulnerability, impact and self-regulation that we evidenced are all relatively
 341 weak: considerable stochasticity still dominates the distribution of interaction matrix coefficients.

Ghosts of competition past and present

Overall, the dominance of niche differentiation in observational plankton studies – based on our analysis of the REPHY dataset and re-analysis of the MAR(1) literature – is similar to what has been recently found in plant community studies (Volkov *et al.*, 2007; Adler *et al.*, 2018b) or empirically parameterized food webs including horizontal diversity (Barabás *et al.*, 2017). Large niche differences might be due to the ghost of competition past, i.e., competition has occurred in the past, leading to strong selection and subsequent evolution, and then to progressive niche separation. In this scenario, species have evolved niches that allow them not to compete or to interact only weakly (very strong facilitative effects might be likewise destabilizing, Coyte *et al.*, 2015). 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 (Bagchi *et al.*, 2014; Comita *et al.*, 2014), while switching generalists can also promote diversity (Vallina *et al.*, 2014). Both predators and resources have often symmetrical effects and can therefore contribute almost equally to such past niche differentiation (Chesson, 2018).

An intriguing new possibility, dubbed the “ghost of competition present” (Tuck *et al.*, 2018), suggests by contrast that spatial distributions in relation to abiotic factors might have a large impact on the interaction strengths inferred from temporal interaction models such as ours. Recent combinations of model fitting and removal experiments have shown that the model fitting usually underestimates the effect of competitors that are uncovered by removal experiments (Tuck *et al.*, 2018; Adler *et al.*, 2018a). 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 (Pacala’s spatial segregation hypothesis Pacala & Levin 1997), 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) and maximize opportunities for positive interactions, which implies that competition is in effect hard to detect when all species are present. This would require spatial 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 (Barton *et al.*, 2014; Breier *et al.*, 2018) but it is quite unclear how this affects multivariate spatial patterns of species distributions (*sensu* Bolker & Pacala 1999, or Murrell & Law 2003). Moreover, 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 phytoplankton, because turbulence rather than organism movement dictates where the phytoplankton patches can or cannot appear.

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Supporting Information: This article contains supporting information.

Authors’ contributions: CP and FB contributed equally to the project design. CP wrote the code for the analyses. FB and CP interpreted the results and wrote the manuscript.

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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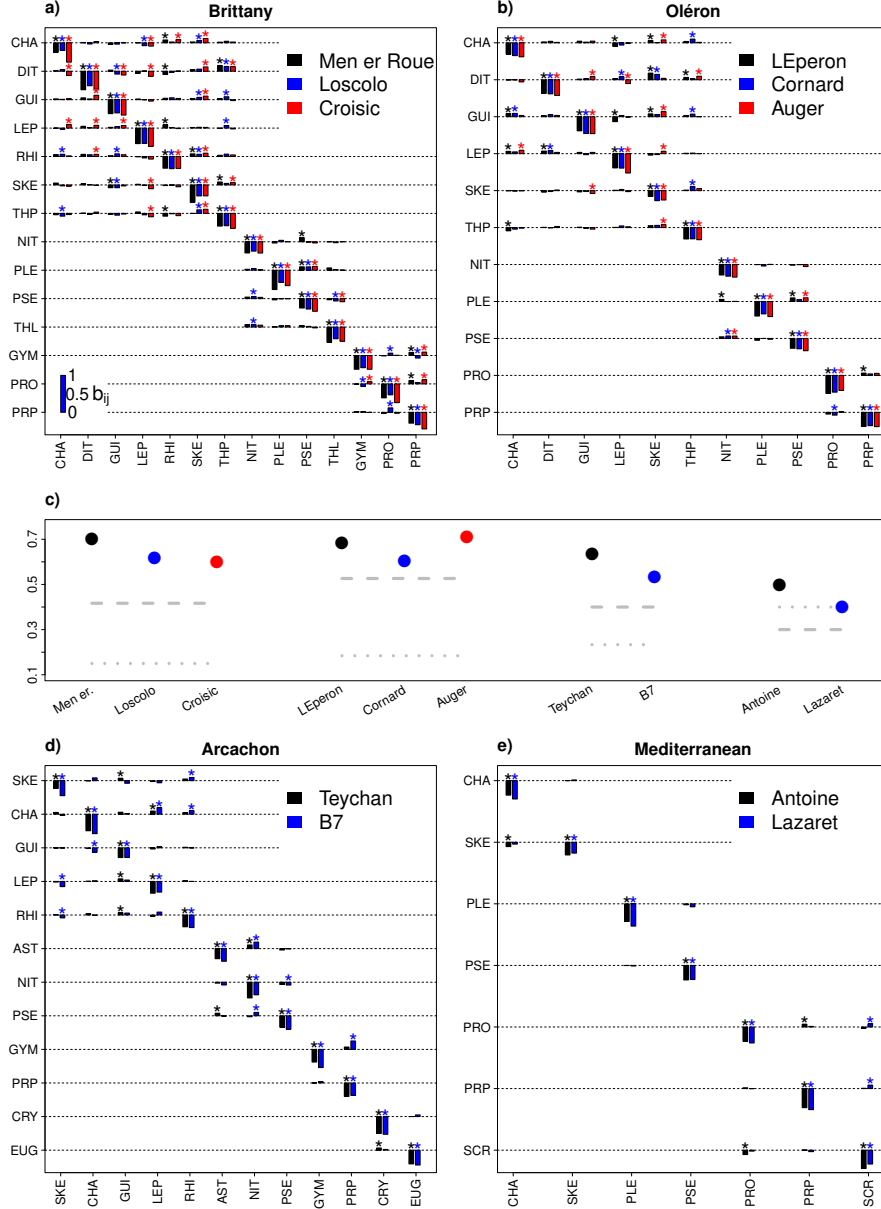


Fig 1. Interaction matrices estimated in 10 sites along the French coastline. Four regions are distinguished: Brittany (a), Oléron (b), Arcachon (d) and the Mediterranean Sea (e). Only interactions within a clade (pennate and centric diatoms, dinoflagellates, other planktonic taxa) are allowed, as this is the best fitting interaction scenario (Fig S3). Taxon j (in columns) has an effect on taxon i 's growth rate (in rows) illustrated by proportional to the bar height. 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.

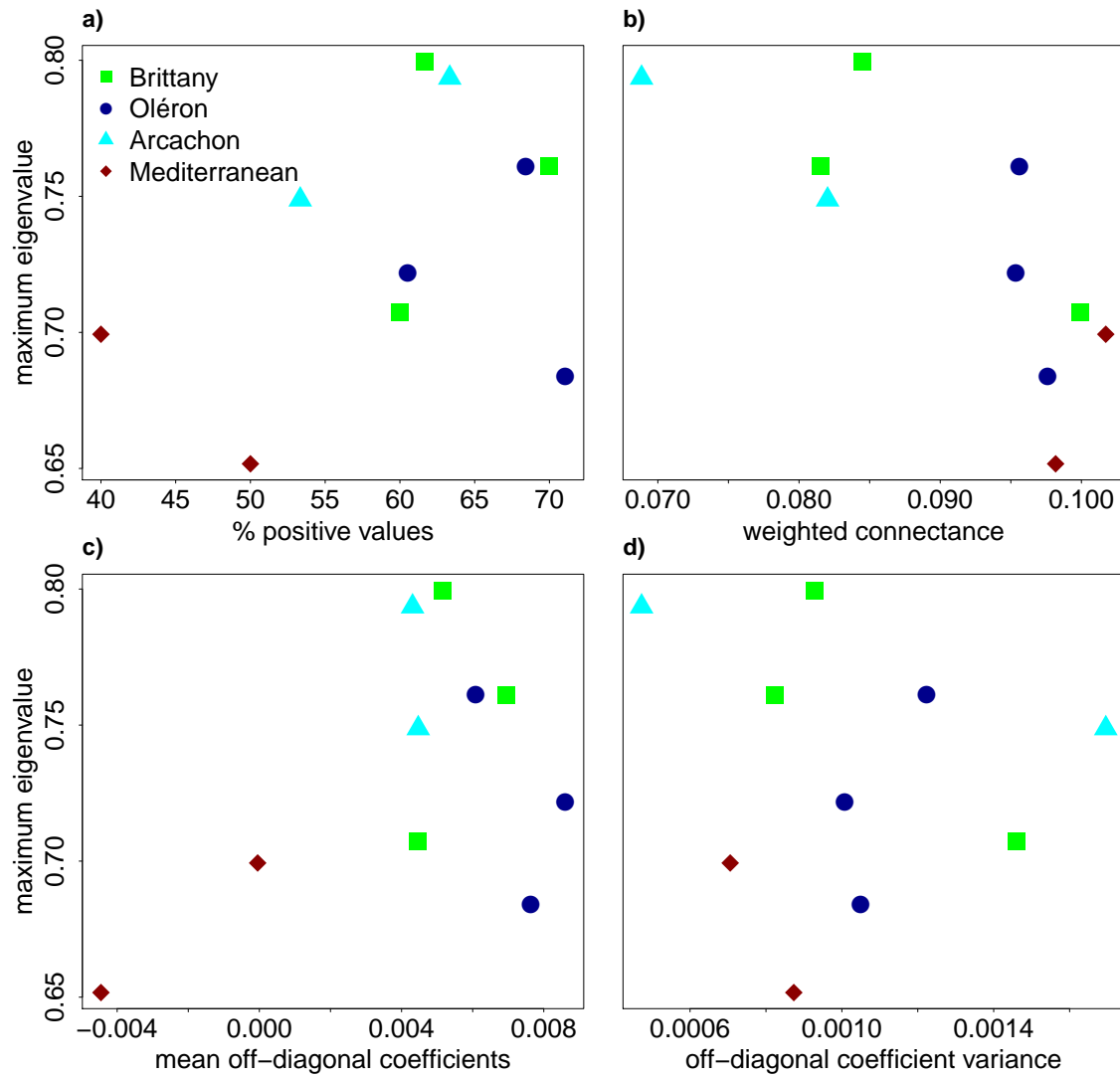


Fig 2. Relation between stability and complexity of the interaction networks. The maximum modulus of the interaction matrix \mathbf{B} eigenvalues indicates stability *sensu* resilience. Each color-and-shape corresponds to a given region. Metrics formula for weighted connectance and linkage density are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

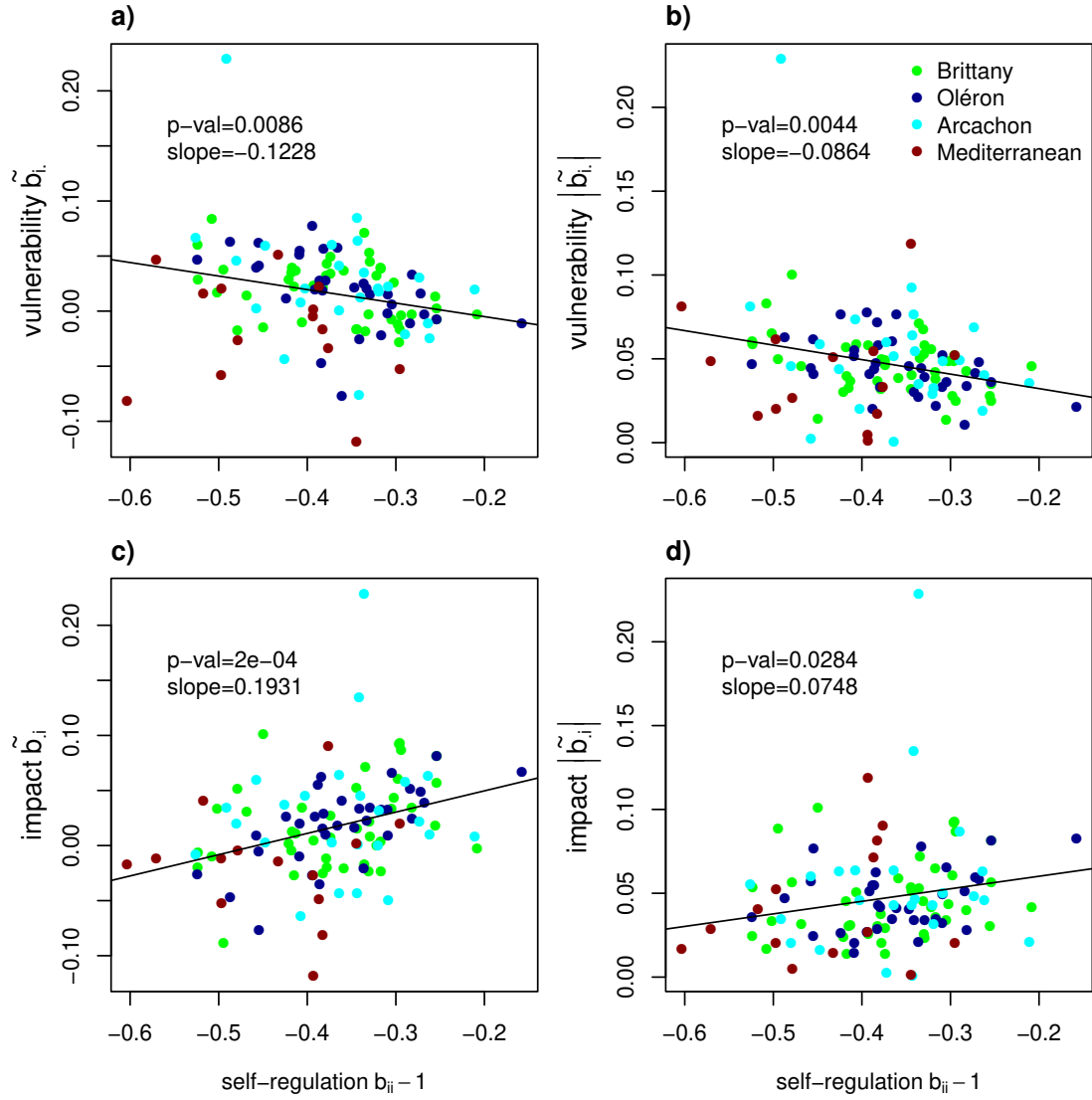


Fig 3. Relation between vulnerability/impact and self-regulation. Average vulnerability (effects of others on the focal taxon growth rate, a-b) and impact (effects of the focal taxon on others' growth rates, c-d), as well as self-regulation, are computed for untransformed (a-c) or absolute (b-d) values 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). Linear regressions are shown as black lines.

