

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

Introduction

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

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

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

Here, we analyse a spatially replicated, long-term community-level dataset, consisting of ten multivariate time series of phytoplankton abundance along the French coastline. The time series are modelled using multivariate autoregressive (MAR) 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 interactions 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 and Table 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 μm 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 (Table S2; Hernández

54 [Fariñas *et al.* 2015](#); [Barraquand *et al.* 2018](#)), except for cryptophytes and euglenophytes in Arcachon,
 55 which could not be identified below the family level. Although the taxonomic resolution used here
 56 may seem coarse in comparison to land plants, it is in fact more refined than 86% of the MAR(1)
 57 studies 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. Time series are plotted in Fig. S2. When gaps
 60 did not exceed a month, missing values were linearly interpolated; remaining missing values were
 61 replaced by a random number between 0 and half of the lowest observed abundance ([Hampton
 62 *et al.*, 2006](#)). We tested extensively this and other methods to deal with missing data in a previous
 63 publication on a subset of this dataset ([Barraquand *et al.*, 2018](#)). All time series were scaled and
 64 centered before MAR analyses.

65 **MAR(1) model**

66 Multivariate autoregressive (MAR) models are used to determine the interspecific interactions and
 67 abiotic effects shaping a community’s dynamics ([Ives *et al.*, 2003](#)). MAR(1) models are based on a
 68 stochastic, discrete-time Gompertz equation which relates the log-abundance of each of the S taxa
 69 at time $t + 1$ to log-abundances of the whole community at time t , with possible interactions between
 70 taxa, and effects of V abiotic variables at time $t + 1$. These assumptions are encapsulated in eq. 1:

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

71 where \mathbf{n}_t is the $1 \times S$ vector of log-abundance of phytoplankton taxa, \mathbf{B} is the $S \times S$ community
 72 (interaction) matrix, \mathbf{C} is the $S \times V$ environment matrix describing the effects of V variables (stacked
 73 in vector \mathbf{u}_{t+1}) on growth rates, with $V = 2$ in our case (temperature and salinity). The noise \mathbf{e}_t
 74 is a $1 \times S$ noise vector which covers both process and observation error, following a multivariate
 75 normal distribution with a variance-covariance matrix \mathbf{Q} . \mathbf{Q} is diagonal and we have previously
 76 showed that this parsimonious choice did not affect qualitatively the results ([Barraquand *et al.*,
 77 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. . Fitting a more sophisticated model (threshold autoregressive model) did not reveal extra non-linearities or a storage effect in the Arcachon subset of the data (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), the analysis of nonlinear simulations has showed that MAR(1) models are in general robust to nonlinearities 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 7×7

106 interaction matrices and 14 for the 7×2 environment matrices) if we consider all possible interactions
 107 between taxa. To reduce this dimensionality and remove unnecessary parameters, we built different
 108 ‘interaction scenarios’ based on known phylogenetic information (as suggested in [Violle *et al.*, 2011](#);
 109 [Narwani *et al.*, 2017](#)). The null interaction scenario assumed no interaction between genera (diagonal
 110 interaction matrix) and was compared to four other interaction scenarios. The first interaction
 111 scenario assumed that interactions could only occur between phylogenetically close organisms, i.e.,
 112 within a class (groups were then diatoms, dinoflagellates, and other phytoplanktonic organisms)
 113 while the second interaction scenario further differentiated pennate and centric diatoms. The third
 114 interaction scenario considered the reverse hypothesis, that only unrelated organisms could interact
 115 (i.e., a diatom could only interact with a dinoflagellate or a cryptophyte, but not with another
 116 diatom), and the last interaction scenario did not constrain the interactions at all (full interaction
 117 matrix). We selected the best scenario by comparing BIC (Fig S3), which proved to be satisfactory
 118 in our previous analyses of both real data and similar simulated datasets ([Barraquand *et al.*, 2018](#),
 119 Appendix 2). The second interaction scenario, hereafter called the pennate-centric scenario, had the
 120 lowest BIC for all sites (Fig. S3). This parsimonious scenario was therefore chosen as the basis for
 121 further investigations of network structure.

122 **Analysis of interaction strengths**

123 The interaction matrix obtained from MAR(1) analyses can be used to determine the stability of a
 124 discrete-time dynamical system ([Ives *et al.*, 1999, 2003](#)). We compared the maximum modulus of the
 125 eigenvalues of the pennate/centric matrices in each site, to network descriptors such as the interaction
 126 strength distribution (sign, mean and variance) and weighted connectance ([Bersier *et al.*, 2002](#)). The
 127 maximum modulus is analogous to the real part of the leading eigenvalue for continuous time models
 128 and measures resilience while still accounting for some variability properties ([Ives *et al.*, 1999](#)).
 129 Weighted connectance is a measure of the proportion of realized links compared to all possible links,
 130 taking into account the shape of the flux distribution. This metric is adapted to weighted interaction
 131 matrices but cannot accommodate for both positive and negative coefficients: we therefore chose to
 132 focus 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 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 taxon 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 the observed ratio between mean self-regulation (intrataxon 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 set to 0. 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 strength, Fig. 4), or taking the mean value of statistically significant intertaxa coefficients only (which increases the estimated mean intertaxa interaction strength, Fig. S8). We considered both.

Results

Interaction estimates

Using MAR(1) autoregressive models, we produced interaction matrices (Ives *et al.*, 2003; Hampton *et al.*, 2013) – i.e., Jacobian community matrices on the logarithmic abundance scale (Ives *et al.*, 2003). Best-fitting models corresponded to a phylogenetically-structured interaction scenario, where interactions only occurred between closely related genera (Fig S3). This led to sparse, modular matrices that have two main features. First, we observed a strong self-regulation for all sites (Fig. 1,

diagonal elements of all matrices), a feature that we had 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 varied between 6 and 10, not counting coefficients set to 0 in the estimation process. When we included the zeroes in the interaction matrix in the computation of the intra/inter mean interaction strength, the ratio rised to 21-43. Therefore, intragenus interactions were on average one order of magnitude stronger than intergenus interactions.

Second, although the percentage of facilitative interactions varied 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 could examine whether locally positive interactions remain positive in a regional context: the percentage of consistently positive interactions at the regional level varied 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 found that the percentage of true mutualism (+/+) was substantial: averaged over all sites, 32% of all interactions were (+/+) while only 12% of them were (-/-), see also Fig S5. The sign correspondence was not always maintained between French regions: the only interaction that was non-zero in the 10 sites (CHA/SKE) was mutualistic in Men er Roue only (Brittany) and mixed (+/-) at all other sites. Within the same region, however, interactions measured at different sites tended 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 mutualistic in some of the Brittany sites. This contradicts previous observations that mutualistic interactions tend to be more context-dependent than competitive interactions (Chamberlain *et al.*, 2014).

Interaction network analysis

The stability (*sensu* resilience, Ives & Carpenter 2007) of all interaction matrices was not strongly affected by the percentage of positive interactions or the mean and variance of the intergenus interactions (Fig. 2). There was a slight increase in stability with weighted connectance, with a drop

186 in eigenvalue modulus for weighted connectances between 0.09 and 0.1. The maximum modulus of
187 the interaction matrix eigenvalues remained between 0.65 and 0.80.

188 Given that a direct complexity-stability (*sensu* resilience) link was not obvious, we investigated
189 whether the matrix coefficients had some particular structure that could help theoretical ecology to
190 make better null models of joint community dynamics and interactions (James *et al.*, 2015). We
191 defined two scores, vulnerability (summed effect of others on the focal taxon growth rate, eq. S5)
192 and impact (summed effect of the focal taxon onto other taxa's growth rates, eq. S6). Relations
193 between inter- and intra-genus interactions emerged (Fig. 3): genera that were more self-regulating
194 also had also a higher vulnerability score and a lower impact score. Those two influences are likely
195 to trade-off: a high degree of self-regulation somehow buffers the effect of outside influences on
196 population dynamics. Taxa that were less self-regulating were also more likely to have a stronger
197 effect onto other taxa. As these genera tended to be more abundant (Fig S7), this could be mediated
198 by the average density of a genus. It is important to note, however, that these trends are weak and
199 there is therefore a considerable amount of randomness dominating the interaction matrix: many
200 scenarios of self-regulation vs limitation by others are therefore possible.

201 Aside from the trade-offs of Fig. 3, we found no remarkable patterns of covariation between
202 matrix elements other than a mean-variance scaling of interaction coefficients (Fig S6).

203 Literature comparison

204 Finally, we sought to put these results in a broader context by compiling the intra vs inter group
205 estimates of previous MAR(1) studies of long-term observational count data (listed in Table S3).
206 We found that the order of magnitude of intra/inter interaction strengths considered here is not
207 particularly above those found for most planktonic systems to which MAR(1) models have been
208 fitted, considering that our systems are relatively high-dimensional and that the higher the number
209 of taxa, the larger the intraspecific regulation (Barabás *et al.*, 2017). We included in Fig. 4 not only
210 plankton studies but also a couple of vertebrate or insect studies on less diverse communities, where
211 interactions are stronger, in order to provide lower bounds for the intra/inter ratio. The conclusion
212 from this comparison seems to be that, unlike small communities that can be tight-knit, any diverse

213 field system of competitors and facilitators has evolved large niche differences making intragroup
214 competition much larger in magnitude than intergroup interactions.

215 Discussion

216 Strong self-regulation and facilitation

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

220 The rather high intra/intertaxa interaction strength ratio ([Levine & HilleRisLambers, 2009](#))
221 that we found, from 5 to 20, depending on how one counts the interactions set to zero in the
222 estimation process, could appear extremely high in light of previous intra/interspecific competition
223 strength estimates of 4 to 5 by [Adler *et al.* \(2018b\)](#). Even though their model is a different one,
224 i.e., Lotka-Volterra competition, we prove in the Supporting Information that the intra/inter ratio
225 should remain commensurate in a MAR(1) model. The difference in the intra/inter ratio that we
226 found should therefore lie elsewhere, which requires some explanation. One could argue that such
227 high intra/inter ratio arises because we consider the genus as our baseline taxonomic unit, rather
228 than the species. It is logical that niche differentiation increases as one gets up the phylogenetic
229 tree, and that getting down to the species level could slightly decrease that ratio (but see [Narwani
230 *et al.*, 2017](#), in which phylogenetic closeness decreases competition strength). However, there are
231 two arguments suggesting that the niche differences found here extend to the species level. First,
232 phytoplankton species belonging to different genera are often found to compete in experiments
233 ([Titman, 1976](#); [Tilman *et al.*, 1982](#); [Descamps-Julien & Gonzalez, 2005](#)). In the field-based dataset
234 studied here, the same genera that are considered in experiments are found not to compete (or only
235 weakly), hence there must be some niche differentiation occurring in the field but not in the lab.
236 Second, the only other study that managed to provide MAR(1) estimates down to the species level
237 for phytoplankton, that of [Huber & Gaedke \(2006\)](#), provides an intra/interspecific strength ratio
238 similar to ours (point 7a in Fig. 4). Strong self-regulation seems therefore a genuine feature of field

239 phytoplanktonic communities.

240 Another main finding of our study is the large frequency of positive interactions, with 30% truly
241 mutualistic (+/+) interactions and between 40 and 70% facilitative effects. Although a seasonal
242 environment can generate some positive covariation between taxa, those effects have already been
243 filtered out by the inclusion of our 2 abiotic covariates (Fig. S4). The facilitative effects shown
244 here are therefore residual effects, once abiotic trends are accounted for. Between 40 and 70%
245 facilitation can be compared to the meta-analysis by [Adler *et al.* \(2018b\)](#) who also found facilitative
246 interactions, but less than here ($\approx 30\%$). However, [Adler *et al.* \(2018b\)](#)'s review contains many
247 experiments while the plant literature is replete with field examples of facilitation ([Brooker *et al.*,
248 2008](#); [McIntire & Fajardo, 2014](#)), so that plant facilitation could be higher in the field. At the
249 moment, it is therefore unknown how the predominance of facilitative interactions that we found
250 in phytoplankton compares to facilitation in terrestrial plants. We note that several authors using
251 MAR(1) models previously forbade positive interactions within the same trophic level, so that the
252 fraction of facilitative interactions in plankton cannot be computed from literature-derived MAR(1)
253 estimates.

254 The large niche differences and facilitative interactions that arise when considering a single
255 trophic level are an emergent property, resulting from hidden effects of resource or predator
256 partitioning/sharing ([Chesson, 2018](#)). In our previous publication investigating in detail the
257 Arcachon study sites ([Barraquand *et al.*, 2018](#)), we have argued that for phytoplankton, the strong
258 intragroup density-dependence could arise from effects of natural enemies ([Haydon, 1994](#)). Natural
259 enemies could also very well create apparent mutualism between prey species ([Abrams *et al.*, 1998](#);
260 [Barraquand *et al.*, 2015](#); [de Ruiter & Gaedke, 2017](#)). We believe this to be likely for the present study,
261 given that the study regions (Arcachon, Oléron, Brittany, Mediterranean) have similar predators
262 (zooplankton, e.g., [Jamet *et al.*, 2001](#); [Modéran *et al.*, 2010](#); [Tortajada *et al.*, 2012](#)) and parasites
263 (viruses, e.g., [Ory *et al.*, 2010](#); fungi). Though natural enemies are good candidates to explain
264 the observed niche differences and emerging facilitation, one must bear in mind that other known
265 drivers of phytoplankton dynamics such as allelopathy ([Felpeto *et al.*, 2018](#)), auxotrophy ([Tang
266 *et al.*, 2010](#)) or hydrodynamics ([Lévy *et al.*, 2018](#)) can all, in theory, help create different niches

and an emerging facilitation (see last subsection of the Discussion). Finally, resources that are usually considered limiting for all species might in fact not always be: [Burson *et al.* \(2018\)](#) show that phytoplanktonic taxa specialize on different components of the light spectrum. This constitutes an example of fine-scale resource partitioning of 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 of the interaction matrices) and their stability (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 not an artefact of a wrong model. 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. This result seems to contradict theory based on random matrices, especially for competitive and/or mutualistic networks ([Allesina & Tang, 2012](#)). However, this could also be linked to the limited size of our networks, as random matrix theory relies on asymptotics ([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). Thus the jury is still out regarding the absence of complexity-resilience relation, though it ~~might~~ may well be a genuine absence. In addition to ~~connectance~~ complexity metrics, we also found that the percentage of mutualistic interactions, that is thought to affect the stability of a network, ~~either~~ positively or negatively ([Mougi & Kondoh, 2012](#); [Coyte *et al.*, 2015](#); [García-Callejas *et al.*, 2018](#)),

294 does not [in fact](#) have a major impact on our networks' resilience.-

295 In addition to weighted connectance and interaction variance, indices at the species or genus
296 level (vulnerability and impact) approximate the average effects exerted and sustained by any given
297 taxa in the different study sites. While, at the network level, network structure (either complexity
298 measures or the percentage of mutualistic interactions) did not affect resilience, a relation emerged
299 between self-regulation, necessary for coexistence, and genus-level indices. We found that the more
300 a genus is self-regulated, the more it tends to be vulnerable to other genera impacts and the less
301 it impacts other genera. We examined whether vulnerability and impact could be affected by
302 phylogenetic correlations; they were not, as on Fig. 3, points were not clustered according to genus,
303 family or phylum. High self-regulation usually indicates large niche differences with the rest of the
304 community, and it makes therefore sense that a species/genus whose needs strongly differ from
305 the others only marginally impacts the resources of the other coexisting species. This is what we
306 expect under strong niche partitioning. Furthermore, a low self-regulation was correlated with high
307 average abundance, which echoes findings by [Yenni et al. \(2017\)](#) who demonstrated that rare species
308 usually show stronger self-regulation. This correlation between relative rarity and self-regulation
309 could also explain the lesser impact of highly self-regulated species/genus: a taxon which dominates
310 the community composition can have a major effect on the others, especially as they usually cover
311 more space, while it is harder for the least common taxa to have large impacts. However, it was
312 more difficult to explain the relationship between self-regulation and vulnerability: a genus that
313 is more self-regulated and less common was found here to be on average more vulnerable to other
314 genera's increases in densities. Such relation implies greater stability (*sensu* resilience, [Ives et al.](#)
315 [2003](#), and also invariability, [Arnoldi et al. 2019](#)) for the network as a whole, because the taxa that
316 are the more vulnerable to other taxa's impacts are also those whose dynamics are intrinsically
317 more buffered. By which mechanisms this could happen is so far unclear and open to speculation.
318 It could be just a "mass effect": common taxa are in high enough numbers to deplete resources
319 or change the environment in ways that affects the less common ones, but the reverse is not true.
320 We caution, however, that the relationships between vulnerability, impact and self-regulation that
321 we evidenced are all relatively weak: considerable stochasticity still dominates the distribution of

322 interaction matrix coefficients.

323 Ghosts of competition past and present

324 Overall, the dominance of niche differentiation in observational plankton studies – based on our
325 analysis of the REPHY dataset and re-analysis of the MAR(1) literature – is similar to what has been
326 recently found in plant community studies (Volkov *et al.*, 2007; Adler *et al.*, 2018b) or empirically
327 parameterized food webs including horizontal diversity (Barabás *et al.*, 2017). Large niche differences
328 might be due to the ghost of competition past, i.e., competition has occurred in the past, leading to
329 strong selection and subsequent evolution, and then to progressive niche separation. In this scenario,
330 species have evolved niches that allow them not to compete or to interact only weakly (very strong
331 facilitative effects might be likewise destabilizing, Coyte *et al.*, 2015). The likely predator effects that
332 we highlighted above could be comprised within such niche differentiation *sensu largo*: specialized
333 predators can make strong conspecific density-dependence emerge (Bagchi *et al.*, 2014; Comita *et al.*,
334 2014), while switching generalists can also promote diversity (Vallina *et al.*, 2014). Both predators
335 and resources have often symmetrical effects and can therefore contribute almost equally to such
336 past niche differentiation (Chesson, 2018).

337 An intriguing new possibility, dubbed the “ghost of competition present” (Tuck *et al.*, 2018),
338 suggests by contrast that spatial distributions in relation to abiotic factors might have a large
339 impact on the interaction strengths inferred from temporal interaction models such as ours. Recent
340 combinations of model fitting and removal experiments have shown that the model fitting usually
341 underestimates the effect of competitors that are uncovered by removal experiments (Tuck *et al.*,
342 2018; Adler *et al.*, 2018a). This could occur for instance if species are spatially segregated (at a
343 small scale) because each species only exists within a domain where it is relatively competitive
344 (Pacala’s spatial segregation hypothesis Pacala & Levin 1997), while a focal species could spread
345 out if competitors were removed. This means that a species can be limited by competitors, but
346 act so as to minimize competition (a little like avoidance behaviour in animals) and maximize
347 opportunities for positive interactions, which implies that competition is in effect hard to detect
348 when all species are present. This would require spatial segregation between phytoplankton species

349 at the scale of interactions, i.e., at the microscale. At the moment, it is known that the fine-scale
350 hydrodynamics generate inhomogeneities at the microscale (Barton *et al.*, 2014; Breier *et al.*, 2018)
351 but it is quite unclear how this affects multivariate spatial patterns of species distributions (*sensu*
352 Bolker & Pacala 1999, or Murrell & Law 2003). Moreover, even if microscale hydrodynamics
353 generates spatial structure with segregation between species, it is not clear either that the “ghost
354 of competition present” mechanism could work for phytoplankton, because turbulence rather than
355 organism movement dictates where the phytoplankton patches can or cannot appear.

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361 **Supporting Information:** This article contains supporting information.

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

364

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

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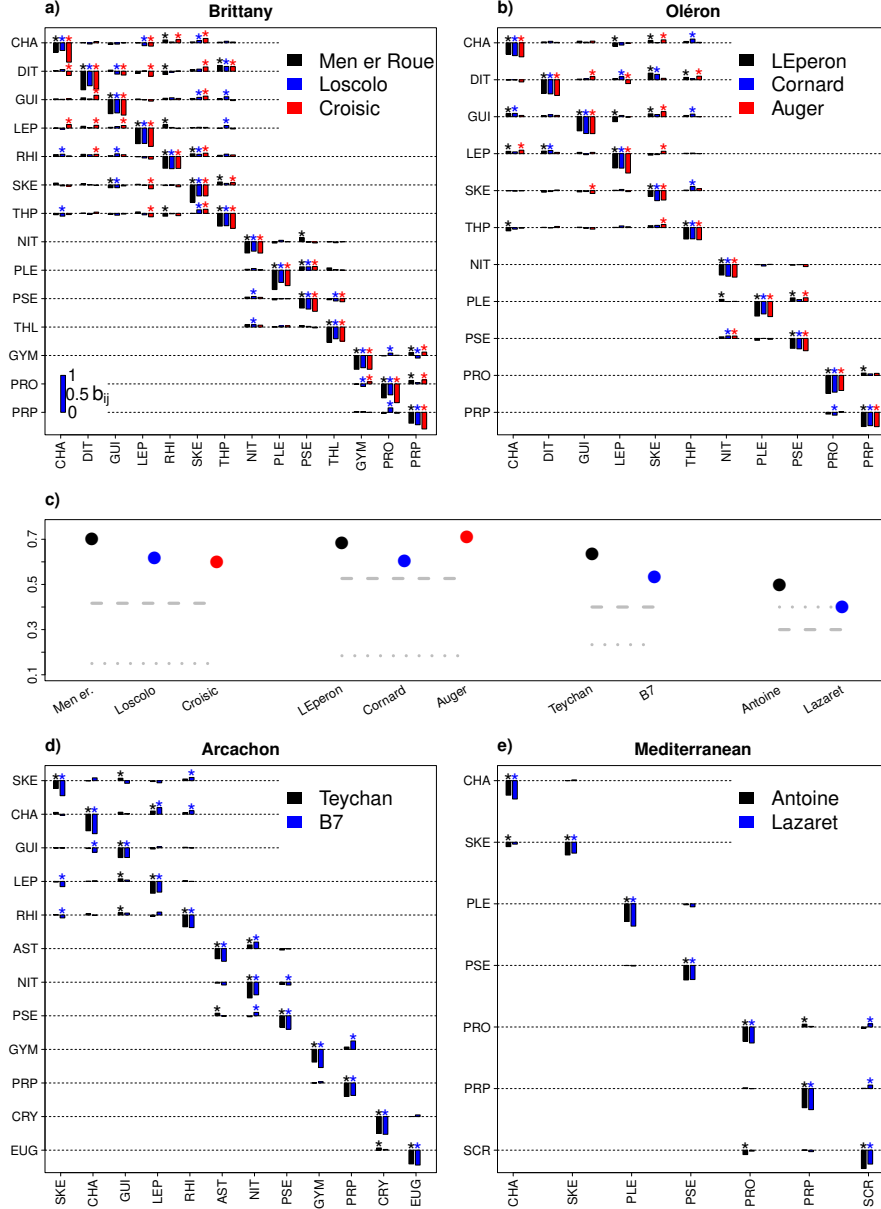


Fig 1. Interaction matrices estimated in 10 sites along the French coastline. Four regions are distinguished: Brittany (a), Oléron (b), Arcachon (d) and the Mediterranean Sea (e). Only interactions within a clade (pennate and centric diatoms, dinoflagellates, other planktonic taxa) are allowed, as this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

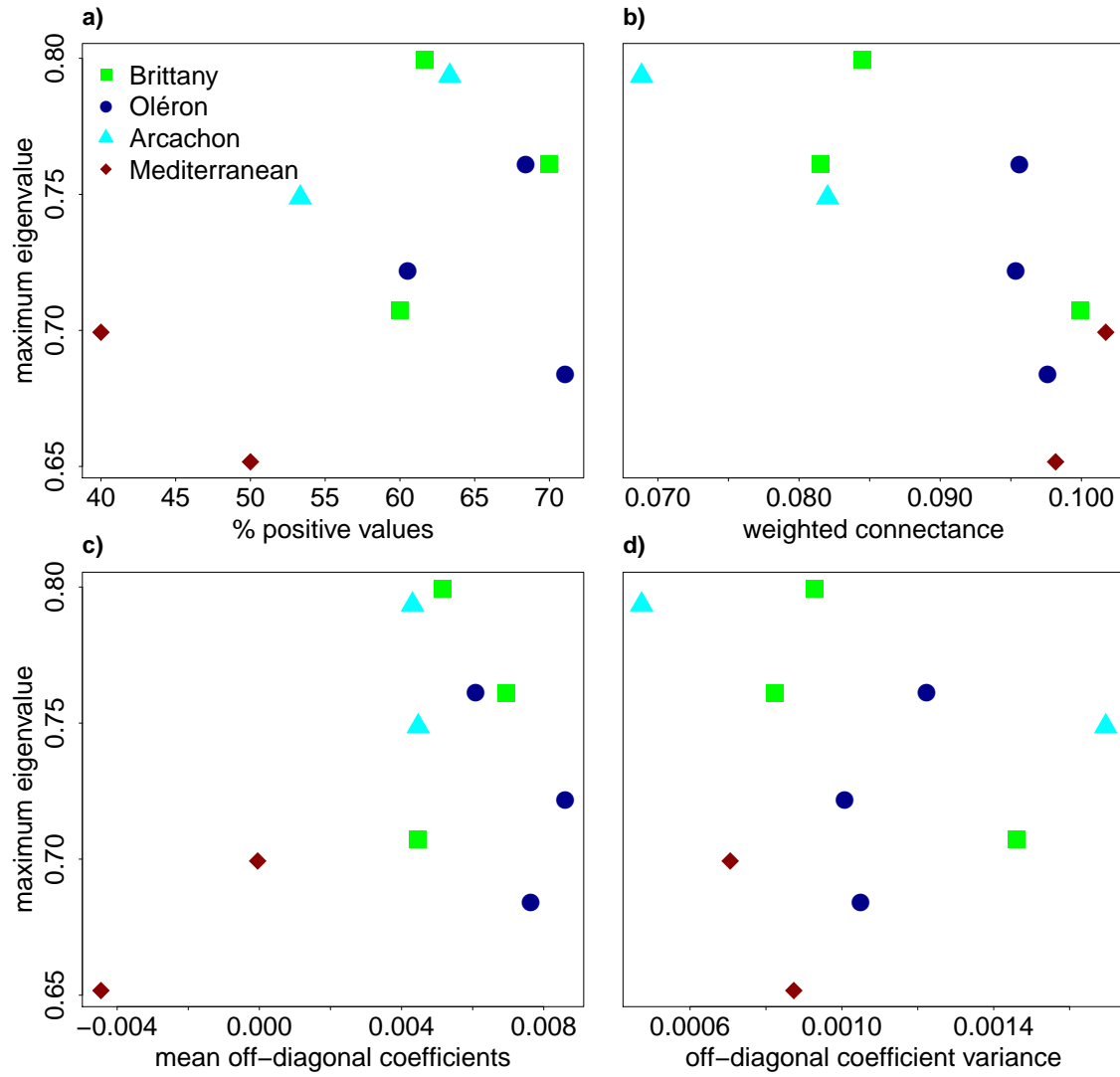


Fig 2. Relation between stability and complexity of the interaction networks. The maximum modulus of the interaction matrix \mathbf{B} eigenvalues indicates stability *sensu* resilience. Each color or shape corresponds to a given region. The formula for weighted connectance is given in the Supporting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

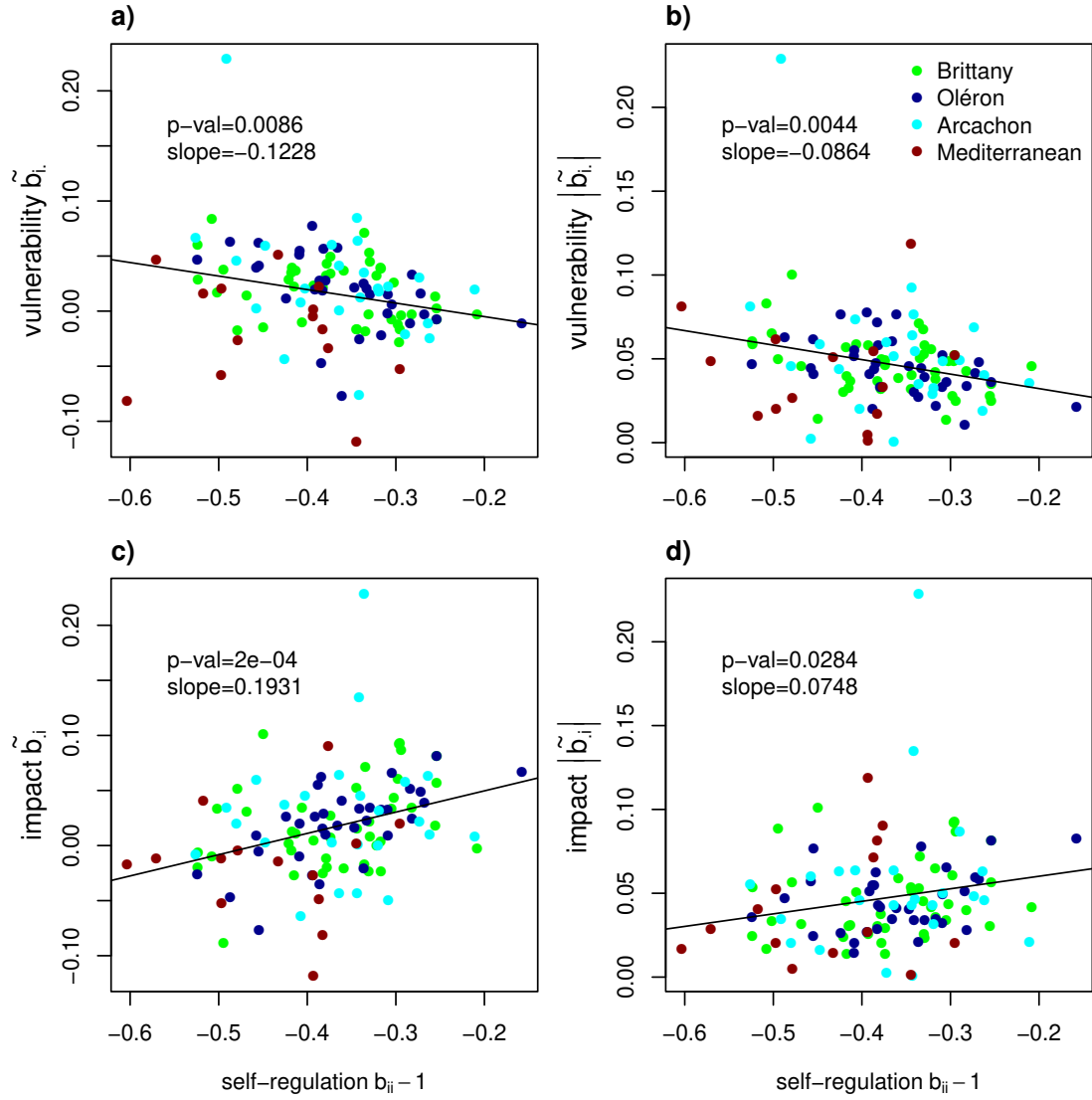


Fig 3. Relation between vulnerability/impact and self-regulation. Average vulnerability (effects of others on the focal taxon growth rate, a-b) and impact (effects of the focal taxon on others' growth rates, c-d), as well as self-regulation, are computed for untransformed (a-c) or absolute (b-d) values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

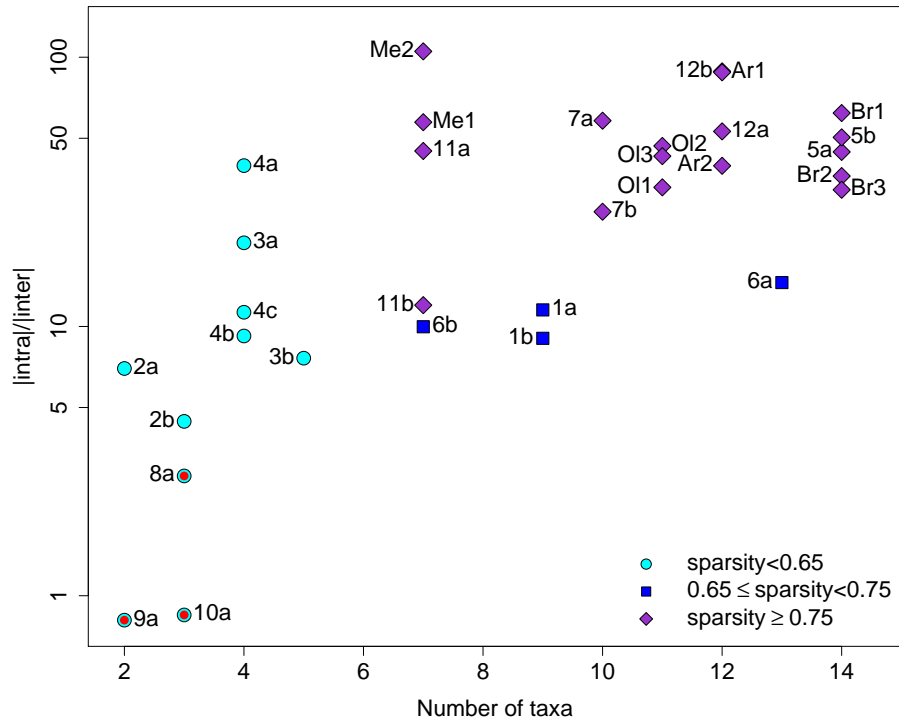


Fig 4. Ratio of intra- to inter-group interaction strength in Multivariate AutoRegressive (MAR) models. The reference for each study is given in Table S3. Codes beginning with letters correspond to the present study (Ar: Arcachon; Ol: Oléron; Br: Brittany; Me: Mediterranean Sea). The symbol color and shape correspond to the sparsity of the interaction matrix (e.g., the proportion of null interactions in the matrix). Red dots correspond to terrestrial and/or low dimension predator-prey systems, giving a lower bound for the intra/inter ratio. Intergroup interactions were set to 0 when they were not specified in the articles (in most cases, authors removed non-significant interactions at the 95% threshold; Fig. S8 is the same figure taking into account only significant interactions)