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

Coralie Picoche<sup>1</sup>, Frédéric Barraquand<sup>1,2\*</sup>

**1** University of Bordeaux, Integrative and Theoretical Ecology, LabEx COTE, Bât. B2 - Allée Geoffroy St-Hilaire, 33615 Pessac, France; coralie.picoche@u-bordeaux.fr

**2** CNRS, Institute of Mathematics of Bordeaux, 351 Cours de la Libération, 33405 Talence, France; frederic.barraquand@u-bordeaux.fr

\* corresponding author

## 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, multivariate 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-taxon 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 exclusion  
5 is likely in those circumstances (Armstrong & McGehee, 1980; Chesson, 2018), unless mechanisms  
6 involving spatial or temporal variation are at play (Armstrong & McGehee, 1976; Chesson & Huntly,  
7 1997; Huisman & Weissing, 2001; Li & Chesson, 2016). Neutral theory, that assumes a non-equilibrium  
8 coexistence maintained by dispersal and equal competitive abilities for all species (Hubbell 2001, though  
9 there are exceptions, see Volkov *et al.* 2003, 2007) has been proposed as a solution to explain highly  
10 diverse communities (Hubbell, 2001; Rosindell *et al.*, 2011).

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

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

24 Here, we analyse a spatially replicated, long-term community-level dataset, consisting of ten multi-  
25 variate time series of phytoplankton abundance along the French coastline. The time series are modelled  
26 using multivariate autoregressive (MAR) models, allowing for interactions between genera. Although  
27 many ecological studies focus on interactions between species, competition has been shown experimentally  
28 to occur between different genera of phytoplankton (Titman, 1976; Descamps-Julien & Gonzalez, 2005).  
29 The genus level is also a rather fine taxonomic scale for phytoplankton interaction studies, as most studies  
30 are restricted to interactions between different classes or even phyla (Ives *et al.*, 2003; Hampton *et al.*,  
31 2008; Griffiths *et al.*, 2015). Studying interactions between different genera of phytoplankton therefore

32 both makes empirical sense in light of competition experiments and allows to estimate better-resolved  
33 networks. We focus here on genera that belong mostly to diatoms and dinoflagellates. To put our  
34 results into a more general context, we then compare our interaction strength estimates to previously  
35 published interaction networks produced under the same statistical framework, both in plankton and  
36 other empirical systems.

## 37 Material and methods

### 38 Sampling methods

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

47 Abiotic variables (temperature, salinity) were measured directly from the boat during the sampling  
48 process while water samples for biotic analyses were fixed with a Lugol's solution and examined later.  
49 Phytoplankton cells above 20  $\mu\text{m}$  were identified at the lowest possible taxonomic level and counted  
50 with the Utermöhl method using an optical microscope ([Utermöhl, 1958](#)). Throughout the years and  
51 sites, more than 600 taxa were identified at different taxonomic levels. We aggregated them at the genus  
52 (or group of genera when not possible) level based on previous work (Table S2; [Hernández Fariñas et al.](#)  
53 [2015](#); [Barraquand et al. 2018](#)), except for cryptophytes and euglenophytes in Arcachon, which could not  
54 be identified below the family level. Although the taxonomic resolution used here may seem coarse in  
55 comparison to land plants, it is in fact more refined than 86% of the MAR(1) studies of phytoplankton  
56 listed in Table S3.

57 For each region, the MAR(1) analysis focused on the most abundant and most frequently observed  
58 genera to avoid most of the gaps in the time series. Time series are plotted in Fig. S2. When gaps did  
59 not exceed a month, missing values were linearly interpolated; remaining missing values were replaced by  
60 a random number between 0 and half of the lowest observed abundance ([Hampton et al., 2006](#)). We  
61 tested extensively this and other methods to deal with missing data in a previous publication on a subset

62 of this dataset (Barraquand *et al.*, 2018). All time series were scaled and centered before MAR analyses.

### 63 MAR(1) model

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

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

69 where  $\mathbf{n}_t$  is the  $1 \times S$  vector of log-abundance of phytoplankton taxa,  $\mathbf{B}$  is the  $S \times S$  community  
 70 (interaction) matrix,  $\mathbf{C}$  is the  $S \times V$  environment matrix describing the effects of  $V$  variables (stacked in  
 71 vector  $\mathbf{u}_{t+1}$ ) on growth rates, and  $\mathbf{e}_t$  is a  $1 \times S$  noise vector which covers both process and observation  
 72 error, following a multivariate normal distribution with a variance-covariance matrix  $\mathbf{Q}$ .  $\mathbf{Q}$  is diagonal  
 73 and we have previously showed that this parsimonious choice did not affect qualitatively the results  
 74 (Barraquand *et al.*, 2018). We used the MARSS package (Holmes *et al.*, 2014) v3.9, in R v3.3.2 (Venables  
 75 & Smith, 2013), to estimate parameters with a maximum likelihood procedure.

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

82 The analysis of real data in Barraquand *et al.* (2018) was complemented by that of simulated data  
 83 mimicking the study design, which confirmed the ability of MAR(1) models to infer biotic interactions and  
 84 abiotic forcings. There was no need to account for extra non-linearities to model relative nonlinearities  
 85 or a storage effect, as these were found to be non-existent (through threshold autoregressive models,  
 86 Barraquand *et al.*, 2018). Other aspects of the MAR(1) modelling are likewise quite robust: using two  
 87 abiotic variables (temperature and salinity) in this study rather than the full set used in Barraquand *et al.*  
 88 (2018) led to almost identical covariate effects and interaction estimates for the Arcachon study sites.  
 89 Even if some departures from the true data-generating model may not always be detectable through

90 MAR(1) diagnostics (e.g., residuals), simulation work has showed that MAR(1) models are in general  
91 robust to nonlinearities ([Certain et al., 2018](#)) if the inference focuses on interaction sign and order of  
92 magnitude of model coefficients, which is how these models are used here. For ease of interpretation of  
93 MAR(1) interaction coefficients, we also prove the correspondence between the magnitude of intra/inter  
94 interaction strength in a MAR(1) model and a multispecies Beverton-Holt model, i.e., a discrete-time  
95 Lotka-Volterra model ([Cushing et al., 2004](#)), in the Supporting Information.

96 In this study, the number of phytoplankton taxa ( $S$ ) and the community composition vary slightly  
97 between regions but sites share on average 67% of their taxa. In order to have comparable models, we  
98 also keep the same 2 covariates, i.e., water temperature and salinity, that were measured at all study  
99 sites. Therefore, the dimension of the dynamical system depends on the (square of the) number of  
100 phytoplankton taxa we study, which ranges between 7 (Mediterranean Sea) and 14 (Brittany). The  
101 smallest system still requires 63 parameters to be estimated if we consider all possible interactions  
102 between taxa. To reduce this dimensionality and remove unnecessary parameters, we compared different  
103 ‘interaction scenarios’ based on BIC (Fig S3), which proved to be satisfactory in our previous analyses  
104 of both real data and similar simulated datasets ([Barraquand et al., 2018](#), Appendix 2). The null  
105 interaction scenario assumed no interaction between groups of species (diagonal interaction matrix)  
106 and was compared to four other interaction scenarios. The first interaction scenario assumed that  
107 interactions could only occur between phylogenetically close organisms, i.e., within a class (groups  
108 were then diatoms, dinoflagellates, and other phytoplanktonic organisms) while the second interaction  
109 scenario further differentiated pennate and centric diatoms. The third interaction scenario considered the  
110 reverse hypothesis, that only unrelated organisms could interact (i.e., a diatom could only interact with  
111 a dinoflagellate or a cryptophyte, but not with another diatom), and the last interaction scenario did  
112 not constrain the interactions at all (full interaction matrix). The second interaction scenario, hereafter  
113 called the pennate-centric scenario, had the lowest BIC for all sites (Fig. S3). This parsimonious scenario  
114 was therefore chosen as the basis for further investigations of network structure.

## 115 Analysis of interaction strengths

116 The interaction matrix obtained from MAR(1) analyses can be used to determine the stability of a  
117 discrete-time dynamical system ([Ives et al., 2003](#)). We compared the maximum modulus of the eigenvalues  
118 of the pennate/centric matrices in each site, as a measure of resilience, to network metrics which could be  
119 related to complexity, such as weighted connectance and linkage density ([Bersier et al., 2002](#)). Weighted  
120 connectance is a measure of the proportion of realized links, taking into account the shape of the flux

121 distribution, while link density measures the average proportion and strength of interactions for a given  
122 taxon. These metrics are adapted to weighted interaction matrices but cannot accommodate for both  
123 positive and negative coefficients: we therefore chose to focus on the absolute values of these coefficients,  
124 which can be linked to their strength, irrespective of interaction sign.

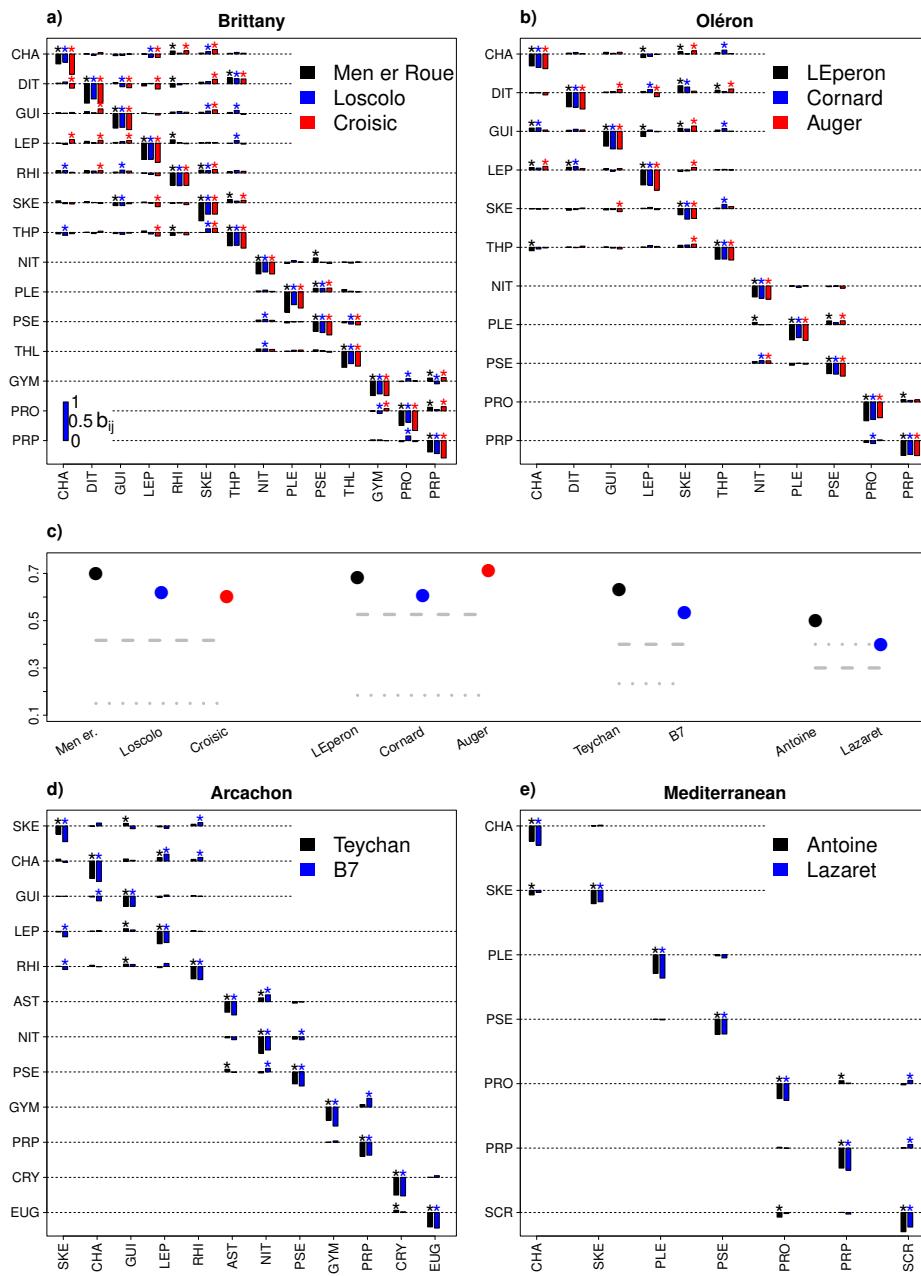
125 In addition to these network-level metrics, we also computed the average vulnerability (average effect  
126 of other taxa on a focal taxon, eq. S5) and impact (average effect of a focal taxon on other taxa, eq. S6)  
127 on both raw and absolute values of the coefficients, and compared these to the regulation a focal species  
128 exerted on itself. Raw values indicate the average effect (i.e., is the effect of others mostly positive or  
129 negative?) that can be expected on a taxon' growth rate from other planktonic taxa while absolute  
130 effects characterise the strength of all types of interactions on a taxon (i.e., is a taxon strongly affected  
131 by the others?).

132 Finally, we compared our results on the ratio between mean self-regulation (intrataxon interaction  
133 strength) and mean intertaxa interaction strength to other published studies based on a MAR(1) model.  
134 A list of references is given in Table S3. Authors usually reported only coefficients that were significant  
135 at the 95% significance threshold, thus ignoring potentially many weak effects. This implies that there  
136 are two ways of computing the mean intertaxa interactions, i.e., taking the mean value of all coefficients  
137 outside of the matrix diagonal, including zeroes (which decreases the estimated mean intertaxa interaction  
138 strength), and the mean value of statistically significant intertaxa coefficients only (which increases the  
139 estimated mean intertaxa interaction strength, Fig. S8). We considered both.

## 140 Results

### 141 Interaction estimates

142 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 abundance scale ([Ives et al., 2003](#)).  
143 Best-fitting models corresponded to a phylogenetically-structured interaction scenario, where interactions  
144 only occurred betwen closely related genera (Fig S3). This led to sparse, modular matrices that have  
145 two main features. First, we observe a strong self-regulation for all sites (Fig. 1, diagonal elements  
146 of all matrices), a feature that we have previously highlighted in a more detailed analysis on one of  
147 the considered study regions ([Barraquand et al., 2018](#)). The ratio of mean intragenus to intergenus  
148 interaction coefficients varies between 6 and 10, not counting coefficients set to 0 in the estimation  
149 process. If we include the zeroes in the interaction matrix in the computation of the intra/inter mean  
150



**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 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.

151 interaction strength, the ratio rises to 21-43. Therefore, intragenus interactions are on average much  
152 stronger than intergenus interactions, approximately 10 to 20 times stronger.

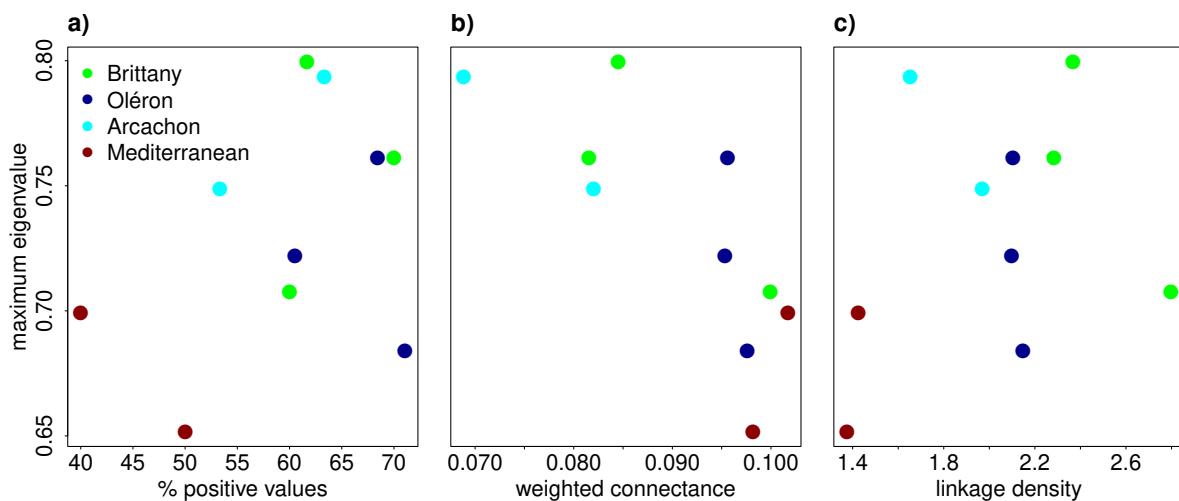
153 Second, although the percentage of facilitative interactions seemed to vary among sites (between 40%  
154 and 71% of interactions in the selected models), facilitation remained predominant in 9 sites out of 10  
155 (only Lazaret, in the Mediterranean Sea, has 60% negative interactions). Our observational setup being  
156 nested, with sites within regions, we can examine whether locally positive interactions remain positive  
157 in a regional context: the percentage of consistently positive interactions at the regional level varies  
158 between 30% and 53%, higher than the percentage of similarly defined negative interactions (between  
159 15% and 40%), except for sites in the Mediterranean Sea.

160 We have found that the percentage of true mutualism (+/+) is substantial: averaged over all sites, 32%  
161 of all interactions are (+/+) while only 12% of them are (-/-), see also Fig S5. The sign correspondence  
162 is not always maintained between French regions: the only interaction that is non-zero in the 10 sites  
163 (CHA/SKE) is mutualistic in Men er Roue only (Brittany) and mixed (+/-) at all other sites. Within  
164 the same region, however, interactions measured at different sites tend to keep the same sign. In the 3  
165 sites of Oléron, for instance, there were 4 interactions which remained positive on both sides (CHA/GUI,  
166 DIT/GUI, LEP/THP, SKE/THP), 3 of them being also mutualistic in some of the Brittany sites. This  
167 contradicts previous observations that mutualistic interactions tend to be more context-dependent than  
168 competitive interactions ([Chamberlain et al., 2014](#)).

## 169 Interaction network analysis

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

175 Given that a direct complexity-stability link was not obvious, we investigated whether the matrix  
176 coefficients had some particular structure that could help theoretical ecology to make better null models  
177 of joint community dynamics and interactions ([James et al., 2015](#)). We defined two scores, vulnerability  
178 (summed effect of others on the focal taxon growth rate, eq. S5) and impact (summed effect of the focal  
179 taxon onto other taxa's growth rates, eq. S6). Relations between inter- and intra-genus interactions  
180 emerged (Fig. 3): genera that were more self-regulating also had also a higher vulnerability score and a  
181 lower impact score. Those two influences are likely to trade-off: a high degree of self-regulation somehow



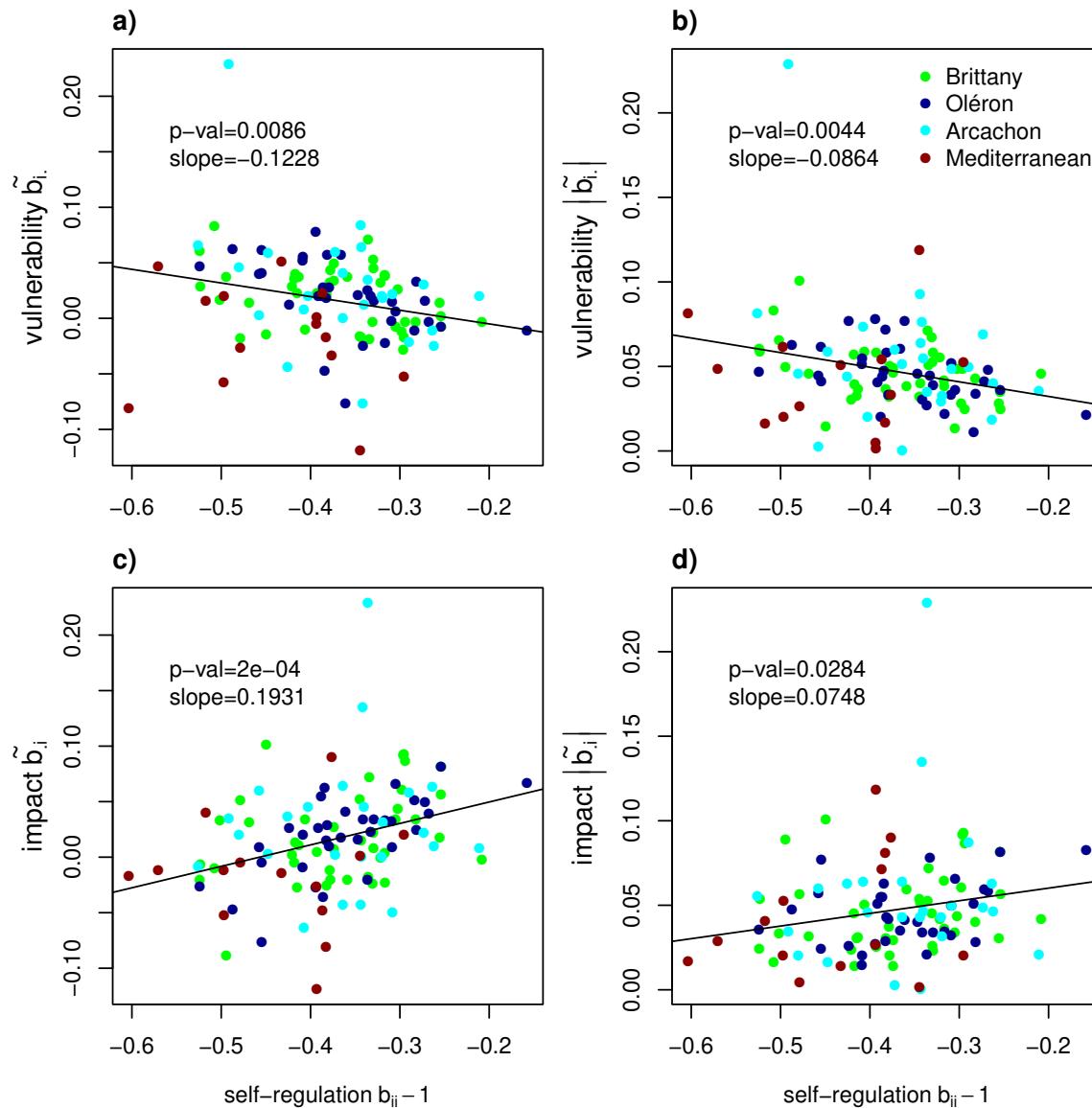
**Fig 2. Relation between stability and complexity of the interaction networks.** The maximum modulus of the interaction matrix  $\mathbf{B}$  eigenvalues indicates stability *sensu* resilience. Each color corresponds to a given region. Metrics formula for weighted connectance and linkage density are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

182 buffers outside influences. Taxa that were less self-regulating were also more likely to have a stronger  
 183 effect onto other taxa. As these genera tended to be more abundant (Fig S7), this could be mediated by  
 184 the average density of a genus. It is important to note, however, that these trends are weak and there is  
 185 therefore a considerable amount of randomness dominating the interaction matrix: many scenarios of  
 186 self-regulation vs limitation by others are therefore possible.

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

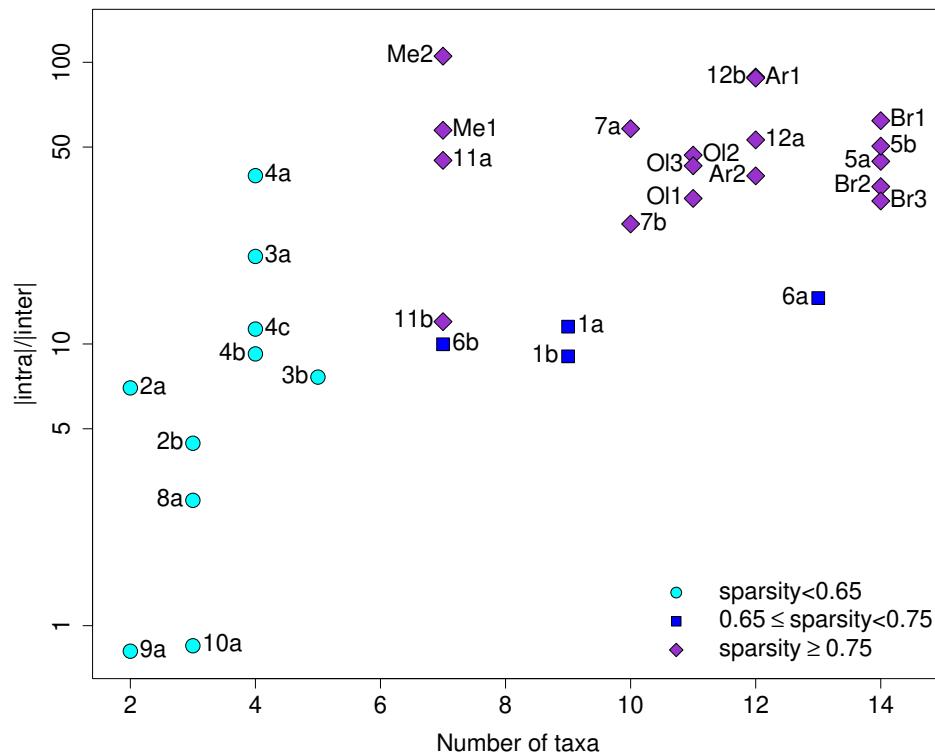
### 189 Literature comparison

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



**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.

<sup>199</sup> facilitators has evolved large niche differences making intragroup competition much larger in magnitude  
<sup>200</sup> than intergroup interactions.



**Fig 4. Ratio of intra- to inter-group interaction strength in Multivariate AutoRegressive (MAR) models.** The name of each study, corresponding to a code, 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). 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)

## 201 Discussion

### 202 Strong self-regulation and facilitation

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

206 The rather high intra/intertaxon interaction strength ratio (Levine & HilleRisLambers, 2009) that we  
 207 found, from 5 to 20, depending on how one counts the interactions set to zero in the estimation process,  
 208 could appear extremely high in light of previous intra/interspecific competition strength estimates of 4  
 209 to 5 by Adler *et al.* (2018b). Even though their model is a different one, i.e., Lotka-Volterra competition,  
 210 we prove in the Supporting Information that the intra/inter ratio should remain commensurate in a  
 211 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, 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 in phytoplankton compares to facilitation in terrestrial plants. We note that several authors using MAR(1) models previously forbade positive interactions within the same trophic level, so that the fraction of facilitative interactions in plankton cannot be computed from literature-derived MAR(1) estimates.

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

(Oléron, Brittany, Mediterranean) have similar predators to the Arcachon site (zooplankton, e.g., [Jamat et al., 2001](#); [Modérán et al., 2010](#); [Tortajada et al., 2012](#)) and parasites (viruses, e.g., [Ory et al., 2010](#); fungi). Though natural enemies are good candidates to explain the observed niche differences and emerging facilitation, one must bear in mind that other known drivers of phytoplankton dynamics such as allelopathy ([Felpeto et al., 2018](#)), auxotrophy ([Tang 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.

## 254 No complexity-stability relationship but connections between self-regulation 255 and intergroup interactions

256 There was no relation between the complexity of the communities (measured as either the weighted  
257 connectance or linkage density of the interaction matrices) and their stability, as measured by the  
258 dominant eigenvalue of the interaction matrix, which quantifies the return time to a point equilibrium  
259 (i.e., resilience). This result is conditional upon our model being a good approximate description of the  
260 system (i.e., no multiyear limit cycles or chaotic attractors as the mapping between eigenvalues and  
261 actual stability is distorted in that case, [Certain et al., 2018](#)). However, we already showed on a subset  
262 of this data that a fixed point in a MAR(1) model, perturbed by seasonality and abiotic variables, is  
263 an accurate description of the system ([Barraquand et al., 2018](#)). Therefore, we are confident that the  
264 absence of complexity-resilience relationship found here is genuine. This absence of direct link between  
265 complexity and stability could be an actual feature of empirical systems, as shown previously by [Jacquet](#)  
266 [et al. \(2016\)](#) using a different technique, even though it does contradict theory based on random matrices,  
267 especially for competitive and/or mutualistic networks ([Allesina & Tang, 2012](#)). We also found that  
268 the percentage of mutualistic interactions, that is thought to affect the stability of a network ([Mougi &](#)  
269 [Kondoh, 2012](#); [Coyte et al., 2015](#); [García-Callejas et al., 2018](#)), does not have a major impact on our  
270 networks' resilience.

271 In addition to weighted connectance, indices at the network-level (e.g., linkage density) and at the  
272 species or genus level (vulnerability and impact) approximate the average effects exerted and sustained  
273 by any given taxa in the different study sites. While, at the network level, network structure (either  
274 complexity measures or the percentage of mutualistic interactions) did not affect stability, a relation

emerged between self-regulation, necessary for coexistence, and genus-level indices. We found that the more a genus is self-regulated, the more it tends to be vulnerable to other genera impacts and the less it impacts other genera. We examined whether vulnerability and impact could be affected by phylogenetic correlations; they were not as on Fig. 3 points were not clustered according to genus, family or phylum. High self-regulation usually indicates large niche differences with the rest of the community, and it makes therefore sense that a species/genus whose needs strongly differ from the others only marginally impacts the resources of the other coexisting species. This is what we expect under strong niche partitioning. Furthermore, a low self-regulation was correlated with high average abundance, which echoes findings by Yenni *et al.* (2017) who demonstrated that rare species usually show stronger self-regulation. This correlation between rarity and self-regulation could also explain the lesser impact of high self-regulated species/genus: a taxon which dominates the community composition can have a major effect on the others, especially as they usually cover more space, while it is harder for rare, localised taxa to have large impacts. However, it was more difficult to explain the relationship between self-regulation and vulnerability: a genus that is more self-regulated and rarer was found here to be on average more vulnerable to other genera's increases in densities. Such relation implies greater stability (*sensu* resilience, Ives *et al.* 2003, and also invariability, Arnoldi *et al.* 2018) for the network as a whole, because the taxa that are the most vulnerable to other taxa's impacts are also those whose dynamics are intrinsically more buffered. By which mechanisms this could happen is so far unclear and open to speculation. It could be just a "mass effect": common taxa are in high enough numbers to deplete resources or change the environment in ways that affects the rarer ones, but the reverse is not true. We caution, however, that the relationships between vulnerability, impact and self-regulation that we evidenced are all relatively weak: considerable stochasticity still dominates the distribution of interaction matrix coefficients.

## 297 Ghosts of competition past and present

298 Overall, the dominance of niche differentiation in observational plankton studies – based on our analysis  
299 of the REPHY dataset and re-analysis of the MAR(1) literature – is similar to what has been recently  
300 found in plant community studies (Volkov *et al.*, 2007; Adler *et al.*, 2018b) or empirically parameterized  
301 food webs including horizontal diversity (Barabás *et al.*, 2017). Large niche differences might be due to  
302 the ghost of competition past, i.e., competition has occurred in the past, leading to strong selection and  
303 subsequent evolution, and then to progressive niche separation. In this scenario, species have evolved  
304 niches that allow them not to compete or to interact only weakly (very strong facilitative effects might be  
305 likewise destabilizing (Coyte *et al.*, 2015). The likely predator effects that we highlighted above could be

306 comprised within such niche differentiation *sensu largo*: specialized predators can make strong conspecific  
307 density-dependence emerge (Bagchi *et al.*, 2014; Comita *et al.*, 2014), while switching generalists can also  
308 promote diversity (Vallina *et al.*, 2014). Both predators and resources have often symmetrical effects  
309 and can therefore contribute almost equally to such past niche differentiation (Chesson, 2018).

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

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

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

335

336      **Data accessibility:** The REPHY dataset has already been published (REPHY, 2017) and all scripts  
337      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  
338      codes can be shared with referees should they wish to access them.  
339

## References

- Abrams, P., Holt, R. & Roth, J. (1998). Apparent competition or apparent mutualism? Shared predation when populations cycle. *Ecology*, 79, 201–212.
- Adler, P., Ellner, S. & Levine, J. (2010). Coexistence of perennial plants: an embarrassment of niches. *Ecology letters*, 13, 1019–1029.
- Adler, P., Kleinhesselink, A., Hooker, G., Taylor, J., Teller, B. & Ellner, S. (2018a). Weak interspecific interactions in a sagebrush steppe? Conflicting evidence from observations and experiments. *Ecology*, 99, 1621–1632.
- Adler, P., Smull, D., Beard, K., Choi, R., Furniss, T., Kulmatiski, A., Meiners, J., Tredennick, A. & Veblen, K. (2018b). Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecology Letters*, 21, 1319–1329.
- Allesina, S. & Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, 483, 205–208.
- Armstrong, R. & McGehee, R. (1976). Coexistence of species competing for shared resources. *Theoretical Population Biology*, 9, 317–328.
- Armstrong, R. & McGehee, R. (1980). Competitive exclusion. *The American Naturalist*, 115, 151–170.
- Arnoldi, J.F., Loreau, M. & Haegeman, B. (2018). The variability spectrum of ecological communities: How common and rare species shape stability patterns. *bioRxiv*.
- Bagchi, R., Gallery, R., Gripenberg, S., Gurr, S., Narayan, L., Addis, C., Freckleton, R. & Lewis, O. (2014). Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature*, 506, 85–88.
- Barabás, G., Michalska-Smith, M. & Allesina, S. (2017). Self-regulation and the stability of large ecological networks. *Nature Ecology & Evolution*, 1, 1870–1875.

- Barraquand, F., New, L., Redpath, S. & Matthiopoulos, J. (2015). Indirect effects of primary prey population dynamics on alternative prey. *Theoretical Population Biology*, 103, 44–59.
- Barraquand, F., Picoche, C., Maurer, D., Carassou, L. & Auby, I. (2018). Coastal phytoplankton community dynamics and coexistence driven by intragroup density-dependence, light and hydrodynamics. *Oikos*, 127, 1834–1852.
- Barton, A., Ward, B., Williams, R. & Follows, M. (2014). The impact of fine-scale turbulence on phytoplankton community structure: Phytoplankton and turbulence. *Limnology and Oceanography: Fluids and Environments*, 4, 34–49.
- Bersier, L.F., Banasek-Richter, C. & Cattin, M.F. (2002). Quantitative descriptors of food-web matrices. *Ecology*, 83, 2394.
- Bolker, B. & Pacala, S. (1999). Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *The American Naturalist*, 153, 575–602.
- Breier, R., Lalescu, C., Waas, D., Wilczek, M. & Mazza, M. (2018). Emergence of phytoplankton patchiness at small scales in mild turbulence. *Proceedings of the National Academy of Sciences*, 115, 12112–12117.
- Brooker, R., Maestre, F., Callaway, R., Lortie, C., Cavieres, L., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C., Saccone, P., Schiffers, K., Seifan, M., Touzard, B. & Michalet, R. (2008). Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, 96, 18–34.
- Burson, A., Stomp, M., Greenwell, E., Grosse, J. & Huisman, J. (2018). Competition for nutrients and light: testing advances in resource competition with a natural phytoplankton community. *Ecology*, 99, 1108–1118.
- Cavieres, L. & Badano, E. (2009). Do facilitative interactions increase species richness at the entire community level? *Journal of Ecology*, 97, 1181–1191.
- Certain, G., Barraquand, F. & Gårdmark, A. (2018). How do MAR(1) models cope with hidden nonlinearities in ecological dynamics? *Methods in Ecology and Evolution*, 9, 1975–1995.
- Chamberlain, S., Bronstein, J. & Rudgers, J. (2014). How context dependent are species interactions? *Ecology Letters*, 17, 881–890.

- Chesson, P. (2018). Updates on mechanisms of maintenance of species diversity. *Journal of Ecology*, 106, 1773–1794.
- Chesson, P. & Huntly, N. (1997). The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *The American Naturalist*, 150, 519–553.
- Comita, L., Queenborough, S., Murphy, S., Eck, J., Xu, K., Krishnadas, M., Beckman, N. & Zhu, Y. (2014). Testing predictions of the Janzen-Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *Journal of Ecology*, 102, 845–856.
- Coyte, K., Schlüter, J. & Foster, K. (2015). The ecology of the microbiome: Networks, competition, and stability. *Science*, 350, 663–666.
- Cushing, J., Leverage, S., Chitnis, N. & Henson, S.M. (2004). Some discrete competition models and the competitive exclusion principle. *Journal of Difference Equations and Applications*, 10, 1139–1151.
- Descamps-Julien, B. & Gonzalez, A. (2005). Stable coexistence in a fluctuating environment: an experimental demonstration. *Ecology*, 86, 2815–2824.
- Felpeto, A., Roy, S. & Vasconcelos, V. (2018). Allelopathy prevents competitive exclusion and promotes phytoplankton biodiversity. *Oikos*, 127, 85–98.
- García-Callejas, D., Molowny-Horas, R. & Araújo, M. (2018). The effect of multiple biotic interaction types on species persistence. *Ecology*, 99, 2327–2337.
- García-Callejas, D., Molowny-Horas, R. & Araújo, M. (2018). Multiple interactions networks: towards more realistic descriptions of the web of life. *Oikos*, 127, 5–22.
- Griffiths, J., Hajdu, S., Downing, A., Hjerne, O., Larsson, U. & Winder, M. (2015). Phytoplankton community interactions and environmental sensitivity in coastal and offshore habitats. *Oikos*, 125, 1134–1143.
- Gross, K. (2008). Positive interactions among competitors can produce species-rich communities. *Ecology Letters*, 11, 929–936.
- Hampton, S., Holmes, E., Scheef, L., Scheuerell, M., Katz, S., Pendleton, D. & Ward, E. (2013). Quantifying effects of abiotic and biotic drivers on community dynamics with multivariate autoregressive (MAR) models. *Ecology*, 94, 2663–2669.

- Hampton, S., Izmest'eva, L., Moore, M., Katz, S., Dennis, B. & Silow, E. (2008). Sixty years of environmental change in the world's largest freshwater lake - Lake Baikal, Siberia. *Global Change Biology*, 14, 1947–1958.
- Hampton, S., Scheuerell, M. & Schindler, D. (2006). Coalescence in the lake washington story: Interaction strengths in a planktonic food web. *Limnology and Oceanography*, 51, 2042–2051.
- Haydon, D. (1994). Pivotal assumptions determining the relationship between stability and complexity: an analytical synthesis of the stability-complexity debate. *The American Naturalist*, 144, 14–29.
- Hernández Fariñas, T., Bacher, C., Soudant, D., Belin, C. & Barillé, L. (2015). Assessing phytoplankton realized niches using a French national phytoplankton monitoring network. *Estuarine, Coastal and Shelf Science*, 159, 15–27.
- Holmes, E.E., Ward, E.J. & Scheuerell, M.D. (2014). Analysis of multivariate time-series using the MARSS package. *User guide: <http://cran.r-project.org/web/packages/MARSS/vignettes/UserGuide.pdf>*.
- Hubbell, S. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press.
- Huber, V. & Gaedke, U. (2006). The role of predation for seasonal variability patterns among phytoplankton and ciliates. *Oikos*, 114, 265–276.
- Huisman, J. & Weissing, F. (2001). Biological conditions for oscillations and chaos generated by multispecies competition. *Ecology*, 82, 2682–2695.
- Hutchinson, G. (1961). The paradox of the plankton. *The American Naturalist*, 95, 137–145.
- Ives, A.R. & Carpenter, S.R. (2007). Stability and diversity of ecosystems. *Science*, 317, 58–62.
- Ives, A.R., Dennis, B., Cottingham, K.L. & Carpenter, S.R. (2003). Estimating community stability and ecological interactions from time-series data. *Ecological monographs*, 73, 301–330.
- Jacquet, C., Moritz, C., Morissette, L., Legagneux, P., Massol, F., Archambault, P. & Gravel, D. (2016). No complexity-stability relationship in empirical ecosystems. *Nature Communications*, 7.
- James, A., Plank, M., Rossberg, A., Beecham, J., Emmerson, M. & Pitchford, J. (2015). Constructing random matrices to represent real ecosystems. *The American Naturalist*, 185, 680–692.

- Jamet, J.L., Boge, G., Richard, S., Geneys, C. & Jamet, D. (2001). The zooplankton community in bays of Toulon area (northwest Mediterranean Sea, France). *Hydrobiologia*, 557, 155–165.
- Levine, J. & HilleRisLambers, J. (2009). The importance of niches for the maintenance of species diversity. *Nature*, 461, 254–257.
- Lévy, M., Franks, P. & Smith, K. (2018). The role of submesoscale currents in structuring marine ecosystems. *Nature Communications*, 9, 4758.
- Li, L. & Chesson, P. (2016). The effects of dynamical rates on species coexistence in a variable environment: the paradox of the plankton revisited. *The American Naturalist*, 188, E46–E58.
- McIntire, E. & Fajardo, A. (2014). Facilitation as a ubiquitous driver of biodiversity. *New Phytologist*, 201, 403–416.
- Modéran, J., Bouvais, P., David, V., Le Noc, S., Simon-Bouhet, B., Niquil, N., Miramand, P. & Fichet, D. (2010). Zooplankton community structure in a highly turbid environment (Charente estuary, France): Spatio-temporal patterns and environmental control. *Estuarine, Coastal and Shelf Science*, 88, 219–232.
- Mougi, A. & Kondoh, M. (2012). Diversity of interaction types and ecological community stability. *Science*, 337, 349–351.
- Murrell, D. & Law, R. (2003). Heteromyopia and the spatial coexistence of similar competitors. *Ecology Letters*, 6, 48–59.
- Mutshinda, C.M., O'Hara, R.B. & Woiwod, I.P. (2009). What drives community dynamics? *Proceedings of the Royal Society B: Biological Sciences*, 276, 2923–2929.
- Ory, P., Hartmann, H., Jude, F., Dupuy, C., Del Amo, Y., Catala, P., Mornet, F., Huet, V., Jan, B., Vincent, D., Sautour, B. & Montanié, H. (2010). Pelagic food web patterns: do they modulate virus and nanoflagellate effects on picoplankton during the phytoplankton spring bloom? Effects of viruses and nanoflagellates on picoplankton. *Environmental Microbiology*, pp. 2755–2772.
- Pacala, S. & Levin, S. (1997). *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, NJ.
- REPHY (2017). *REPHY dataset - French Observation and Monitoring program for Phytoplankton and Hydrology in coastal waters. 1987-2016 Metropolitan data*. <https://www.seanoe.org/data/00361/47248/>.

- Rosindell, J., Hubbell, S. & Etienne, R. (2011). The unified neutral theory of biodiversity and biogeography at age ten. *Trends in ecology & evolution*, 26, 340.
- de Ruiter, P. & Gaedke, U. (2017). Emergent facilitation promotes biological diversity in pelagic food webs. *Food Webs*, 10, 15–21.
- Scheef, L., Hampton, S. & Izmest'eva, L. (2013). Inferring plankton community structure from marine and freshwater long-term data using multivariate autoregressive models. *Limnology and Oceanography: Methods*, 11, 475–484.
- Tang, Y.Z., Koch, F. & Gobler, C.J. (2010). Most harmful algal bloom species are vitamin B1 and B12 auxotrophs. *Proceedings of the National Academy of Sciences*, 107, 20756–20761.
- Tilman, D., Kilham, S. & Kilham, P. (1982). Phytoplankton community ecology: the role of limiting nutrients. *Annual Review of Ecology and Systematics*, 13, 349–372.
- Titman, D. (1976). Ecological competition between algae: experimental confirmation of resource-based competition theory. *Science*, 192, 463–465.
- Tortajada, S., Niquil, N., Blanchet, H., Grami, B., Montanié, H., David, V., Glé, C., Saint-Béat, B., Johnson, G., Marquis, E., Del Amo, Y., Dubois, S., Vincent, D., Dupuy, C., Jude, F., Hartmann, H. & Sautour, B. (2012). Network analysis of the planktonic food web during the spring bloom in a semi enclosed lagoon (Arcachon, SW France). *Acta Oecologica*, 40, 40–50.
- Tuck, S., Porter, J., Rees, M. & Turnbull, L. (2018). Strong responses from weakly interacting species. *Ecology Letters*, 21, 1845–1852.
- Utermöhl, H. (1958). Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitt. int. Ver. theor. angew. Limnol.*, 9.
- Vallina, S., Ward, B., Dutkiewicz, S. & Follows, M. (2014). Maximal feeding with active prey-switching: A kill-the-winner functional response and its effect on global diversity and biogeography. *Progress in Oceanography*, 120, 93–109.
- Venables, W.N. & Smith, D.M. (2013). the R Core Team. *An Introduction to R. Notes on R: A Programming Environment for Data Analysis and Graphics*. URL: [ran. r-project. org/doc/manuals/r-release/R-intro. pdf](http://cran.r-project.org/doc/manuals/r-release/R-intro.pdf).

Volkov, I., Banavar, J., Hubbell, S. & Maritan, A. (2003). Neutral theory and relative species abundance in ecology. *Nature*, 424, 1035–1037.

Volkov, I., Banavar, J., Hubbell, S. & Maritan, A. (2007). Patterns of relative species abundance in rainforests and coral reefs. *Nature*, 450, 45–49.

Yenni, G., Adler, P. & Ernest, S.K.M. (2017). Do persistent rare species experience stronger negative frequency dependence than common species? Asymmetric NFD and persistent rare species. *Global Ecology and Biogeography*, 26, 513–523.

**Supporting Information for Strong self-regulation and widespread facilitative interactions between genera of phytoplankton – Picoche C. & Barraquand F.**

## Sampling

Study sites are shown on Fig. S1 and the characteristics of each site are given in Table S1. The mean temperature in each region mostly depended on its latitude, reflecting the climate of the region, while salinity in one site could be considered as a proxy for evaporation and terrestrial inputs from rivers.

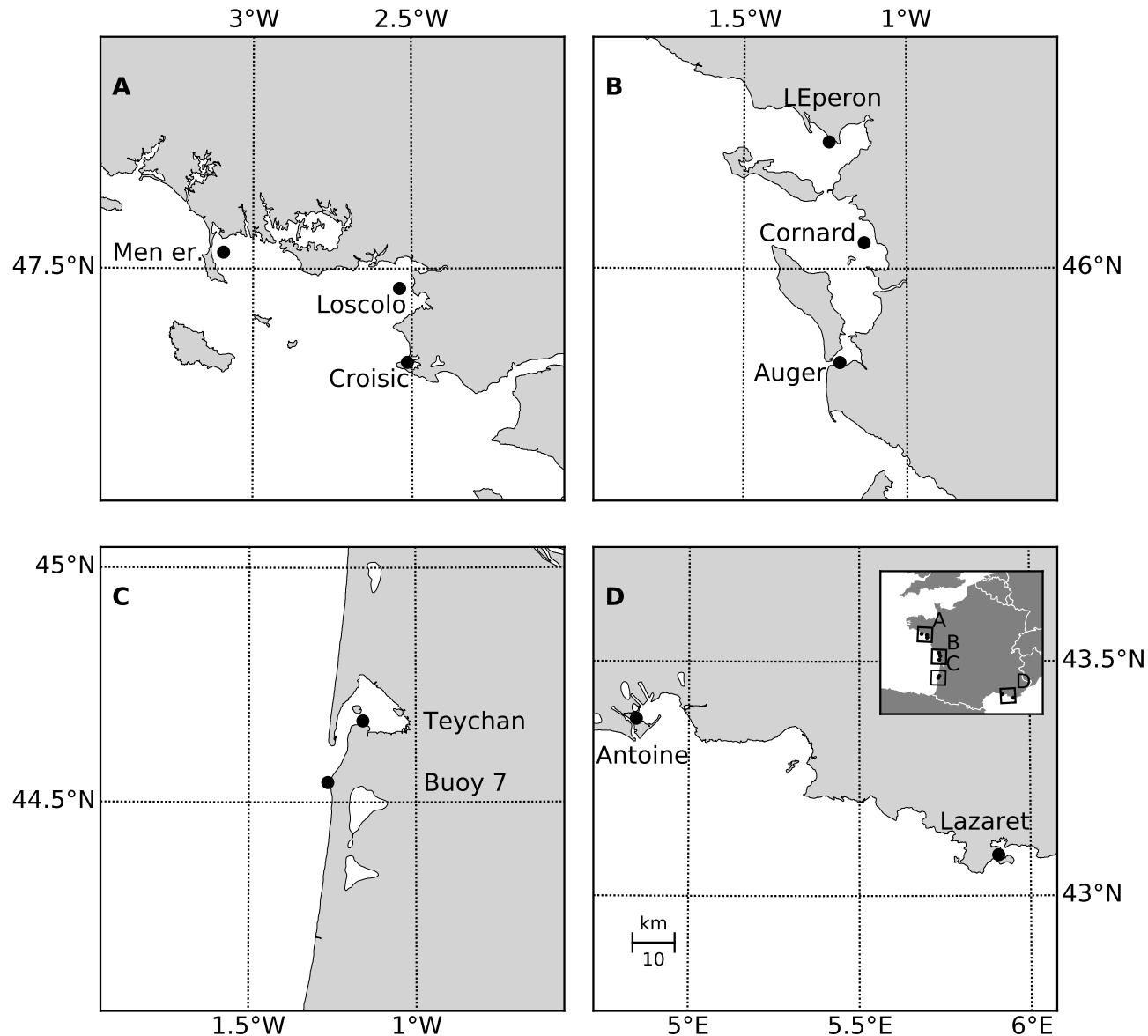


Figure S1: **Location of each study site in their region:** Brittany (A), Oléron (B), Arcachon (C) and the Mediterranean Sea (D). The common scale of the panels is given in the left corner of D.

At each site, water samples were collected between 0 and 1m depth in a Niskin bottle, from which 10mL were taken for phytoplanktonic counts. We focus on phytoplanktonic taxa between 20 and 200  $\mu\text{m}$ , the so-called

microphytoplankton fraction (Reynolds, 2006). The scaling between the volume sampled and the size of individual organisms means that approximately up to 1000 cells could be lined up (in a thought experiment) along one single dimension of an equivalent cubic sample. In other words, the volume sampled is approximately 1000 body sizes to the power three. We therefore consider samples to be representative of local community competition, if not of the spatial structure of the community.

Name of site	Location	Region	N. samples	Temperature (°C)	Salinity (g/L)
Men Er Roue	47°32' N / 3°5' W	Brittany	503	14.4 +/- 3.7	33.5 +/- 1.9
Loscolo	47°27' N / 2°32' W	Brittany	463	14.9 +/- 4.0	32.0 +/- 3.0
Croisic	47°18' N / 2°30' W	Brittany	500	14.7 +/- 3.9	31.8 +/- 3.1
L'Eperon	46°16' N / 1°14' W	Oléron	460	15.3 +/- 4.8	32.1 +/- 3.2
Cornard	46°3' N / 1°7' W	Oléron	491	15.6 +/- 4.8	32.7 +/- 2.4
Auger	45°47' N / 1°12' W	Oléron	524	15.4 +/- 4.4	32.7 +/- 1.8
Buoy 7	44°32' N / 1°15' W	Arcachon	311	15.2 +/- 3.8	34.7 +/- 0.7
Teychan	44°40' N / 1°9' W	Arcachon	494	15.5 +/- 4.6	32.5 +/- 1.9
Antoine	43°22' N / 4°50' E	Mediterranean Sea	539	16.8 +/- 5.1	32.3 +/- 3.9
Lazaret	43°5' N / 5°54' E	Mediterranean Sea	512	17.4 +/- 4.2	35.9 +/- 2.4

Table S1: **Summary of the study site characteristics**, including the mean and standard deviation of the two main environmental parameters (temperature and salinity).

## Phytoplankton dynamics

Code	Taxa
AST	<i>Asterionella+Asterionellopsis+Asteroplanus</i>
CHA	<i>Chaetoceros</i>
CRY	<i>Cryptophytes</i>
DIT	<i>Ditylum</i>
EUG	<i>Euglenophytes</i>
GUI	<i>Guinardia</i>
GYM	<i>Gymnodinium+Gyrodinium</i>
LEP	<i>Leptocylindrus</i>
NIT	<i>Nitzschia+Hantzschia</i>
PLE	<i>Pleurosigma+Gyrosigma</i>
PRO	<i>Prorocentrum</i>
PRP	<i>Protoperidinium+Archaeoperidinium+Peridinium</i>
PSE	<i>Pseudo-nitzschia</i>
RHI	<i>Rhizosolenia+Neocalyptrella</i>
SCR	<i>Scrippsiella+Ensicalifera+Pentapharsodinium+Bysmatrum</i>
SKE	<i>Skeletonema</i>
THL	<i>Thalassionema+Lioloma</i>
THP	<i>Thalassiosira+Porosira</i>

Table S2: **Name and composition of the phytoplanktonic groups used in main text**, based on the work by Hernández Fariñas *et al.* (2015)

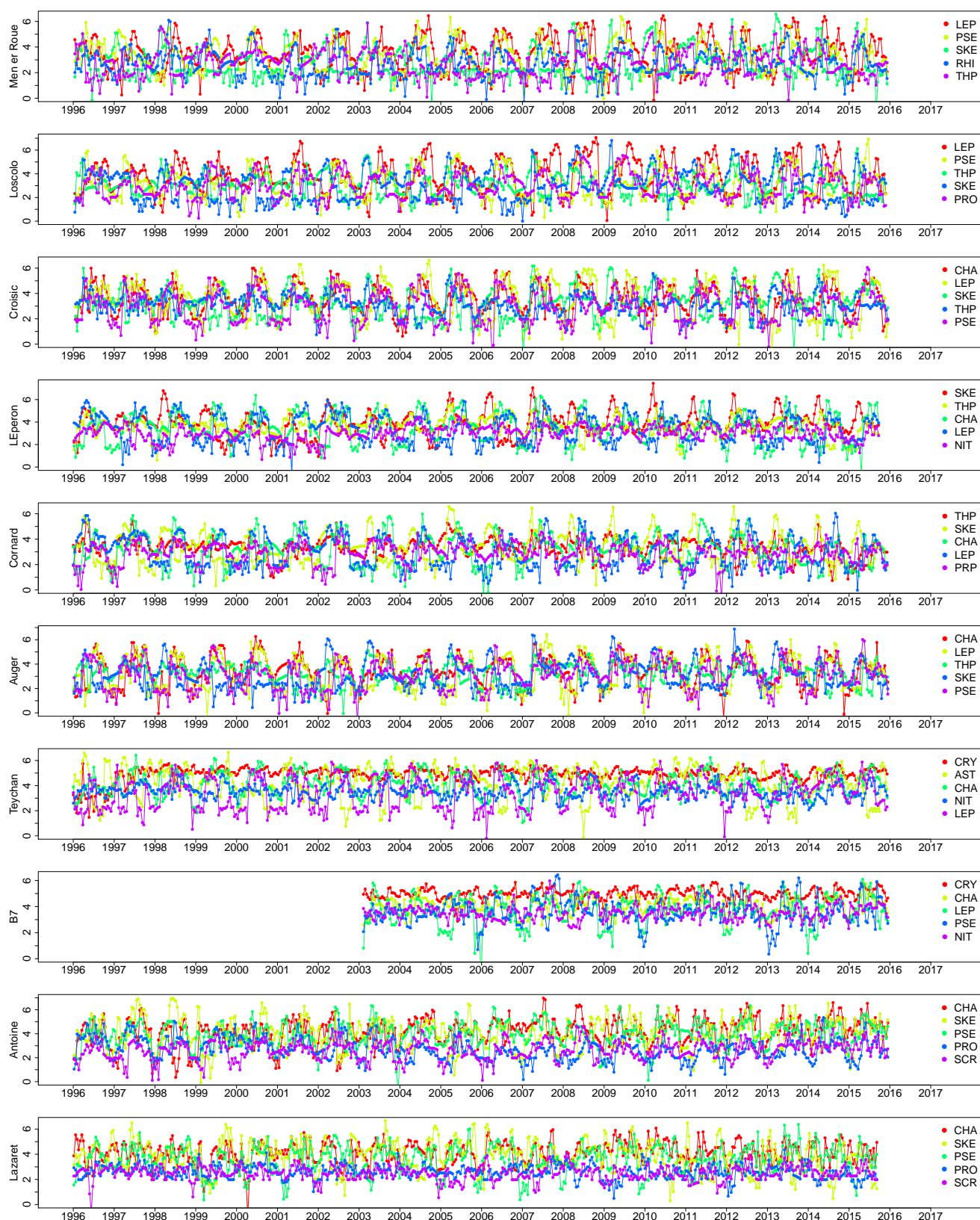
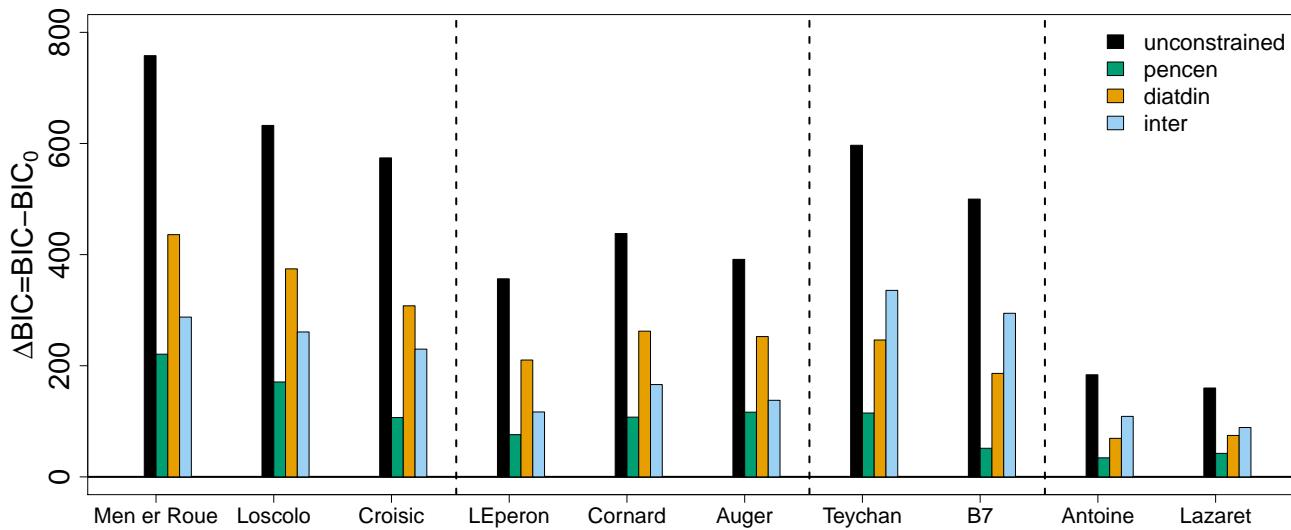


Figure S2: Time series of the 5 most abundant phytoplanktonic genera in each site.

## MAR(1) models

We selected the most parsimonious interaction matrices using BIC. Not only the best-ranking model, but also the overall ranking of interaction scenarios were similar for most sites (Fig. S3). Based on these results, we considered the model selection to be quite robust, and focused on the pennate-centric scenario to analyze interaction matrices, as this scenario corresponded to the best fitted models that still allowed interactions between groups.



**Figure S3: Comparison of the BIC of different interaction scenarios**, compared to the null scenario (diagonal interaction matrix, allowing only intragroup interactions), for 10 sites in 4 different regions, separated by dashed lines (Brittany, Oléron, Arcachon and the Mediterranean Sea). Different interaction matrices may allow interactions between all taxa (unconstrained), only interactions within pennate diatoms, centric diatoms, dinoflagellates, or other phytoplanktonic taxa (pencent), only interactions within diatoms, dinoflagellates or other taxa (diatdin), or only interactions between taxa belonging to these different groups (inter). As model structures (length of the times series taken into account) are different between sites and regions, groups of bars should not be compared.

We inspected the Hessian matrices (i.e., Hessians of the negative log-likelihood which is the observed Fisher Information Matrix) for interaction parameters, which was important to check that results presented in Fig. 3 of the main text could not be due to statistical constraints. Correlation matrices (derived from the Hessian matrices) showed that the mean absolute value of the correlation was 0.02 (hence on average there were no correlations), few of those were noticeable (75% were below 0.1 in only 1 site, even lower in the 9 other sites) and even the very few large ones were never above 0.5 in absolute value.

In addition to the coefficients of the interaction matrix, MAR(1) models allowed us to estimate the effect of environmental variables. The regression coefficients reveal abiotic effects such as phenology (temperature, related to insolation) or responses to hydrological changes such as salinity variation (Fig. S4). Overall, temperature tended to have more effect on phytoplankton dynamics than salinity, which was logical since it integrates seasonal variation in received solar energy. The absolute effect of temperature was on average 3.5 times higher than salinity effects and temperature coefficients were significant at the 95% threshold for 68% of all estimates, as opposed to 16% for salinity effects. Temperature had a positive effect in 80% of the cases while salinity had a negative effect for 66% of all estimates. The sign of significant temperature effects on a given species remained the same between regions, except for SKE, which was negatively affected by temperature in Brittany and Oléron but positively affected by temperature in the Mediterranean Sea.

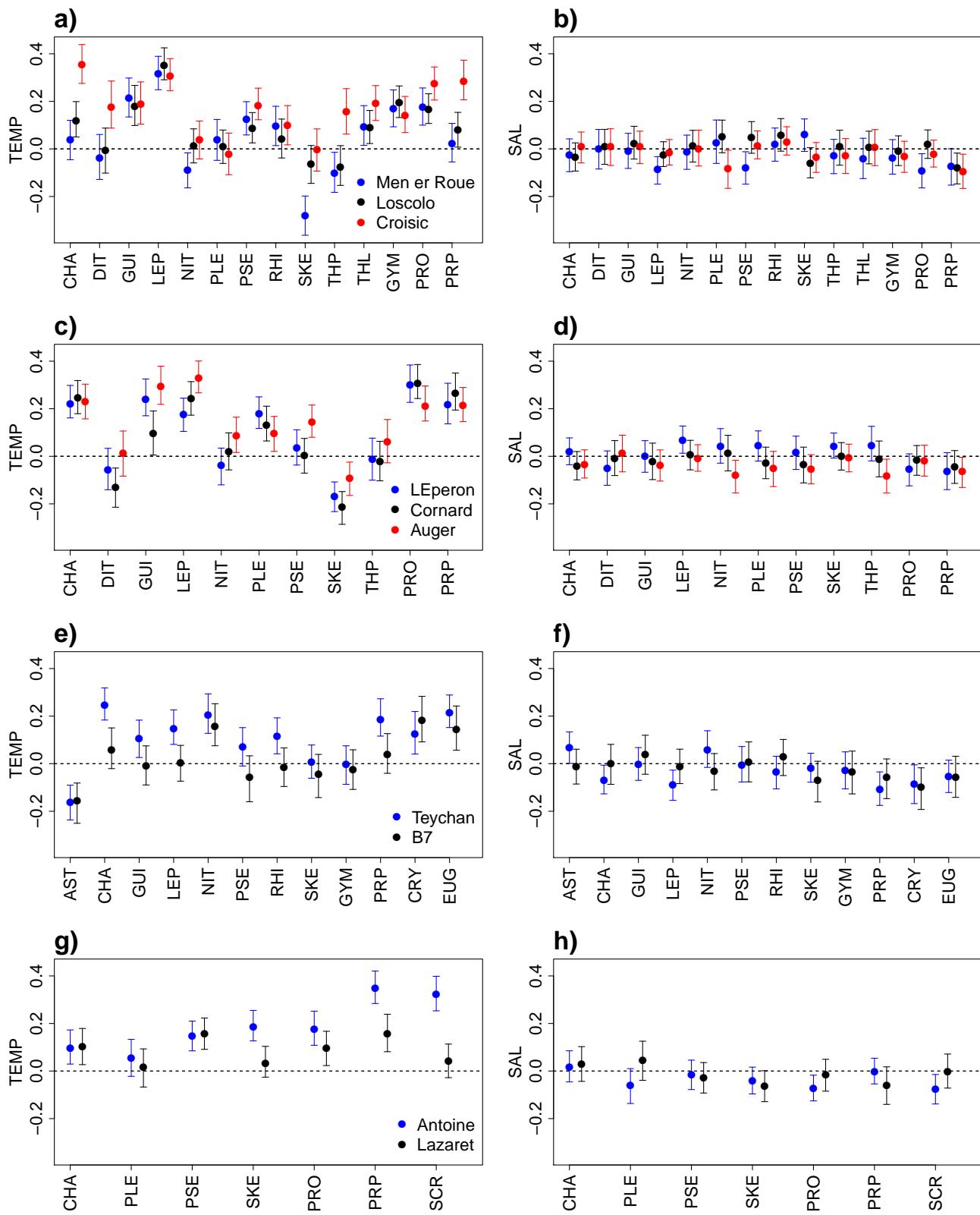
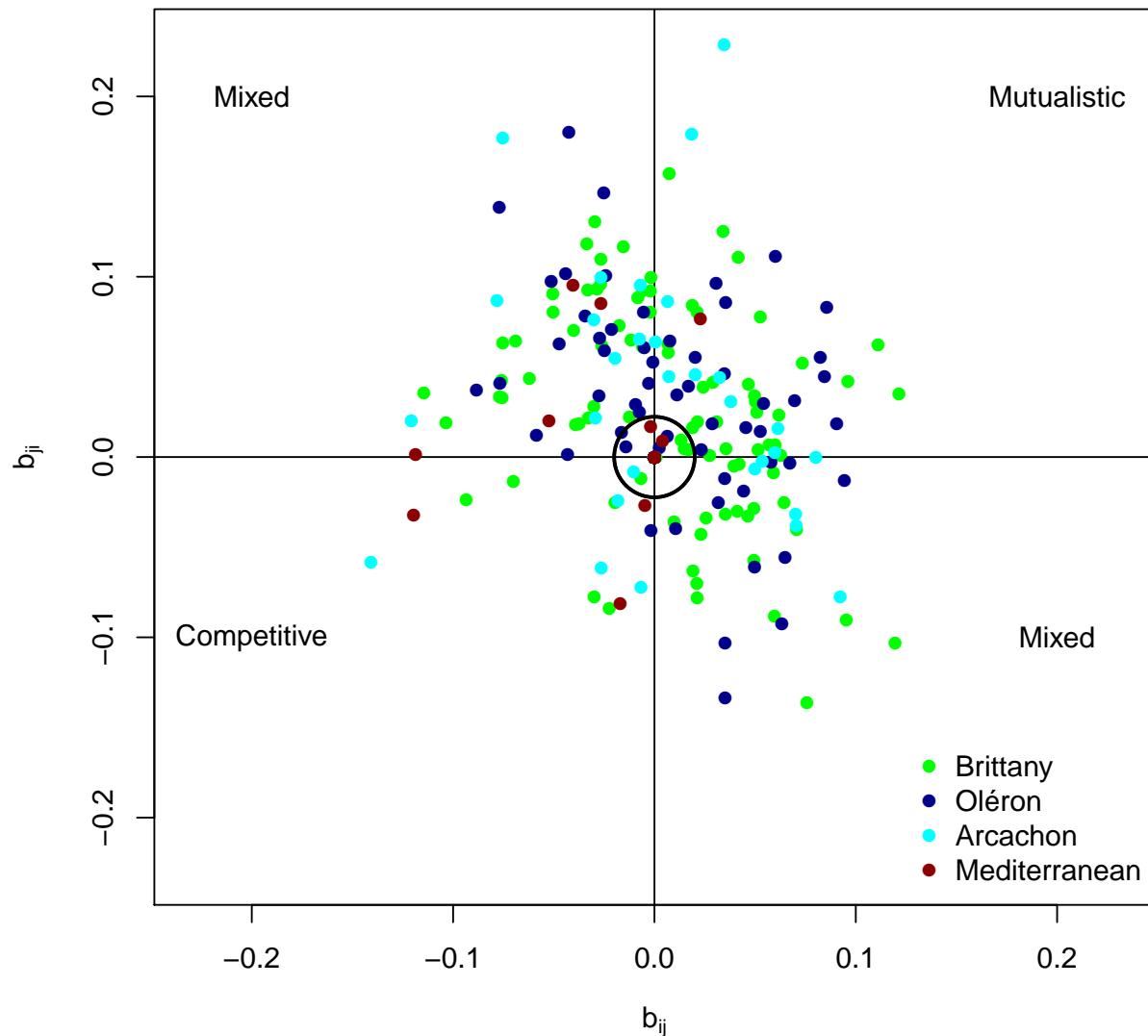


Figure S4: Effect of environmental variables (temperature, TEMP or salinity, SAL) on phytoplankton genera in Brittany (a, b), Oléron (c, d), Arcachon (e, f) and in the Mediterranean Sea (g, h). Each color corresponds to a different site. Error bars correspond to the 95% confidence interval around the estimated coefficient. All variables were normalized before estimation.

## Network analysis

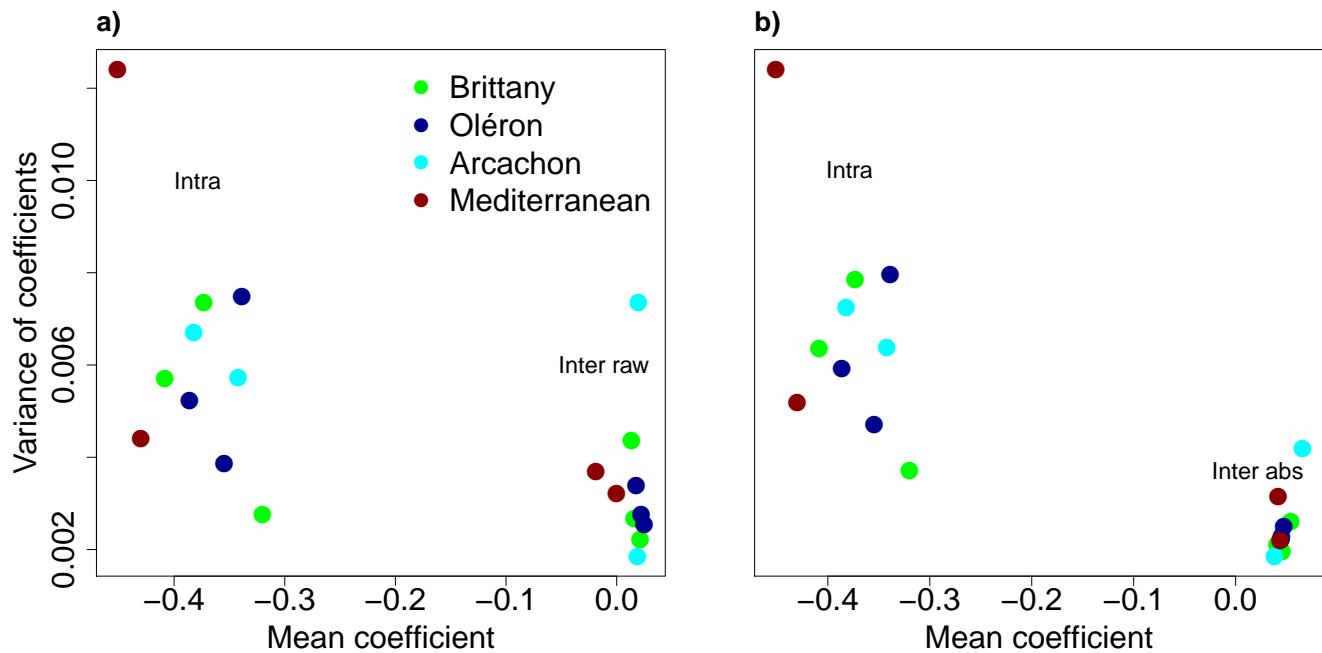
### Interaction types



**Figure S5: Pairs of coefficients for each study site.** The effect of species  $i$  on  $j$  is given as a function of the effect of species  $j$  on species  $i$ . The black circle indicates the first quartile of the interaction values, under which we can assume that the effect is weak or null. Below this limit,  $(+/+)$ ,  $(+/-)$  or  $(-/+)$  interactions can translate into commensalism or amensalism. Above, they can be respectively mutualistic or mixed  $(+/-)$  links.

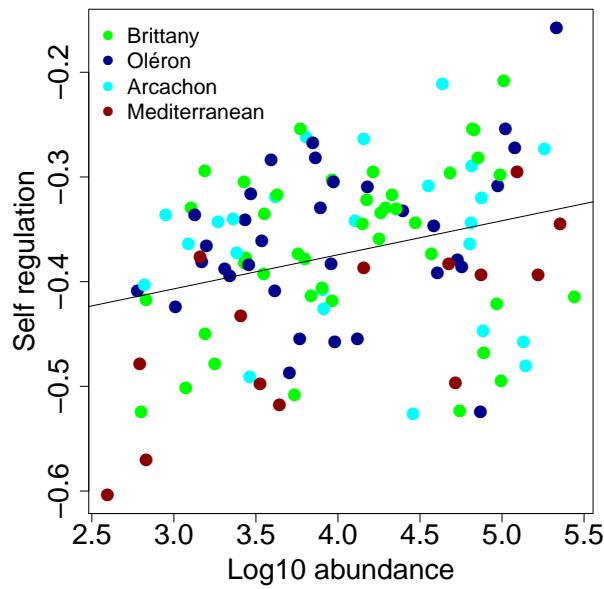
### Metrics

We characterised each interaction network with 4 quantitative descriptors: the mean and variance of the intra- and intergenus coefficients (i.e., on and off the matrix diagonal) and the linkage density and weighted connectance of **B-I**. Absolute values of intragenus coefficients were approximately 8 times higher than the absolute effects of intergenus interactions while the intragenus interaction's deviation was about 4 times higher (Fig. S6).



**Figure S6: Relation between mean and variance of the intra- and intergenus interaction coefficients.** The variance of the coefficients in the interaction matrix ( $\mathbf{B}-\mathbf{I}$ ) increases with the mean, for 10 sites in 4 regions, with a model allowing interactions only within clads (within centric or pennate diatoms, dinoflagellates, or other taxa). The mean-variance relation was either computed with raw values of intergroup interactions (a) or absolute values of the intergroup coefficients (b). Intragroup coefficients were not modified.

The intragenus interaction strength could be related to the mean abundance of each genus as the most self-regulated genera were also the least abundant (Fig. S7).



**Figure S7: Relation between abundance and self-regulation** (intragenus interaction coefficients). Mean abundance is computed for each genus in each site in 4 regions and intragenus interaction strengths are the diagonal coefficients of the interaction matrix ( $\mathbf{B}-\mathbf{I}$ ).

Linkage density and weighted connectance were described in Bersier *et al.* (2002). Linkage density can be defined as the average of vulnerability and generality in the network. More precisely, diversity measures of the interactions

from  $(H_{P,k})$  and to  $(H_{N,k})$  the phytoplanktonic group  $k$  can be computed as:

$$H_{N,k} = - \sum_{i=1}^S \frac{b_{ik}}{b_{\cdot k}} \log_2 \left( \frac{b_{ik}}{b_{\cdot k}} \right) \quad (\text{S1})$$

$$H_{P,k} = - \sum_{i=1}^S \frac{b_{ki}}{b_{k\cdot}} \log_2 \left( \frac{b_{ki}}{b_{k\cdot}} \right) \quad (\text{S2})$$

where  $b_{ik}$  is a coefficient of the interaction matrix  $(\mathbf{B}-\mathbf{I})$ ,  $b_{\cdot k} = \sum_{i=1}^S b_{ki}$  is the sum of all coefficients over row  $k$  and  $S$  is the number of species in the network. These indices are then averaged for the whole network as the linkage density  $LD$  (eq. S3).

$$LD = \frac{1}{2} \left( \sum_{k=1}^S \frac{b_{\cdot k}}{b_{\cdot\cdot}} 2^{H_{N,k}} + \sum_{k=1}^S \frac{b_{k\cdot}}{b_{\cdot\cdot}} 2^{H_{P,k}} \right) \quad (\text{S3})$$

where  $b_{\cdot\cdot} = \sum_{j=1}^S \sum_{i=1}^S b_{ji}$  is the sum of all coefficients of the interaction matrix  $(\mathbf{B}-\mathbf{I})$ .

Weighted connectance  $C$  is then defined as:

$$C = \frac{LD}{S} \quad (\text{S4})$$

Contrary to linkage density, weighted connectance accounts for the dimension of the interaction matrix and can be used to compare network in different regions, with different dimensions.

In addition to these network-level metrics, we also considered metrics for each phytoplanktonic group. We measured both its vulnerability (mean strength of the interactions that are applied to a group, eq. S5) and its impact (mean strength of the interactions the group applies to other groups, eq. S6) in each network.

$$v_k = \frac{1}{\mathbf{1}_{b_{ki} \neq 0}} \sum_{i=1}^S b_{ki} \quad (\text{S5})$$

$$e_k = \frac{1}{\mathbf{1}_{b_{ik} \neq 0}} \sum_{i=1}^S b_{ik} \quad (\text{S6})$$

where  $\mathbf{1}_{b_{ki} \neq 0}$  is the number of interactions which are different from 0 in row  $k$ .

## MAR references and analysis

We present here the MAR references we used to compare the effects of intra- and intergroup interactions (Table S3, Fig. S8). We add information on the biome and taxa used in the study as they tend to be linked to the estimated parameters (Fig. S9). We should mention two potential biases associated with this comparison across the published literature. First, low-dimensional matrices tended to be more complete (less sparse) than high-dimensional matrices, as these small interaction matrices were used to study known interaction phenomena (observed predation between organisms, for instance). Conversely, the number of parameters to estimate increases as the square of the number of interacting taxa, leading most authors to reduce this set before the estimation process for large interaction matrices. There is therefore a positive correlation between sparsity and dimensionality (Fig S9). A second caveat is that while we informed our model selection by phylogeny, several authors have instead reduced the number of estimated parameters by an automated procedure, usually based on the comparison of 100 randomly chosen interaction matrices by BIC (Ives *et al.*, 2003). The latter choice is likely to bias high non-zero interactions in the literature. This is why we decided to present in the main text intra/inter ratios including interspecific (or intergroup) coefficients set to zero (see Fig. 4 in the main text), which should be less sensitive to the model selection method and therefore make comparisons across studies possible. In Fig. S8, mean interaction strengths were computed as the mean absolute value of only the set of coefficients which were deemed significant at the 95% threshold in the  $(\mathbf{B}-\mathbf{I})$  matrix.

Code	Ref	Dimension	Type of organisms	Taxonomic level	System
1a	Ives <i>et al.</i> (1999), CLS	9	Zooplankton	Species and functional groups	Lake
1b	Ives <i>et al.</i> (1999), TLS	9	Zooplankton	Species and functional groups	Lake
2a	Klug <i>et al.</i> (2000)	2	Phytoplankton	Phylum	Lake
2b	Klug <i>et al.</i> (2000)	3	Zooplankton	Species	Lake
3a	Klug & Cottingham (2001)	4	Functional groups of plankton	NA	Lake
3b	Klug & Cottingham (2001)	5	Taxonomic groups of plankton	Phylum/division	Lake
4a	Ives <i>et al.</i> (2003)	4	Plankton	Zooplankton v. phytoplankton, size classes	Lake
4b	Ives <i>et al.</i> (2003)	4	Plankton	Zooplankton v. phytoplankton, size classes	Lake
4c	Ives <i>et al.</i> (2003)	4	Plankton	Zooplankton v. phytoplankton, size classes	Lake
5a	Hampton & Schindler (2006)	14	Plankton	Phylum (phytoplankton), genus (zooplankton)	Lake with high planktivory
5b	Hampton & Schindler (2006)	14	Plankton, growing season	Phylum (phytoplankton), genus (zooplankton)	Lake with low planktivory
6a	Hampton <i>et al.</i> (2006)	13	Plankton	Phylum (phytoplankton), genus (zooplankton)	Lake
6b	Hampton <i>et al.</i> (2006)	7	Simpler web, plankton	Phylum (phytoplankton), genus (zooplankton)	Lake
7a	Huber & Gaedke (2006)	10	Ciliates	Genus and species	Lake
7b	Huber & Gaedke (2006)	10	Phytoplankton	Genus and species	Lake
8a	Yamamura <i>et al.</i> (2006)	3	Insects	Species	Terrestrial
9a	Vik <i>et al.</i> (2008)	2	Lynx/Hare	Species	Terrestrial
10a	Lindgren <i>et al.</i> (2009)	3	Fish	Species	Baltic Sea
11a	Griffiths <i>et al.</i> (2015)	7	Phytoplankton	Phylum	Coastal site
11b	Griffiths <i>et al.</i> (2015)	7	Phytoplankton	Phylum	Offshore site
12a	Barraquand <i>et al.</i> (2018)	12	Phytoplankton	Genus	Outside a bay
12b	Barraquand <i>et al.</i> (2018)	12	Phytoplankton	Genus	Inside a bay

Table S3: Studies used when comparing  $|\text{intra}|/|\text{inter}|$  ratios in Fig. 4 in main text and Fig. S8. T is the approximate number of sampling dates in each time series.

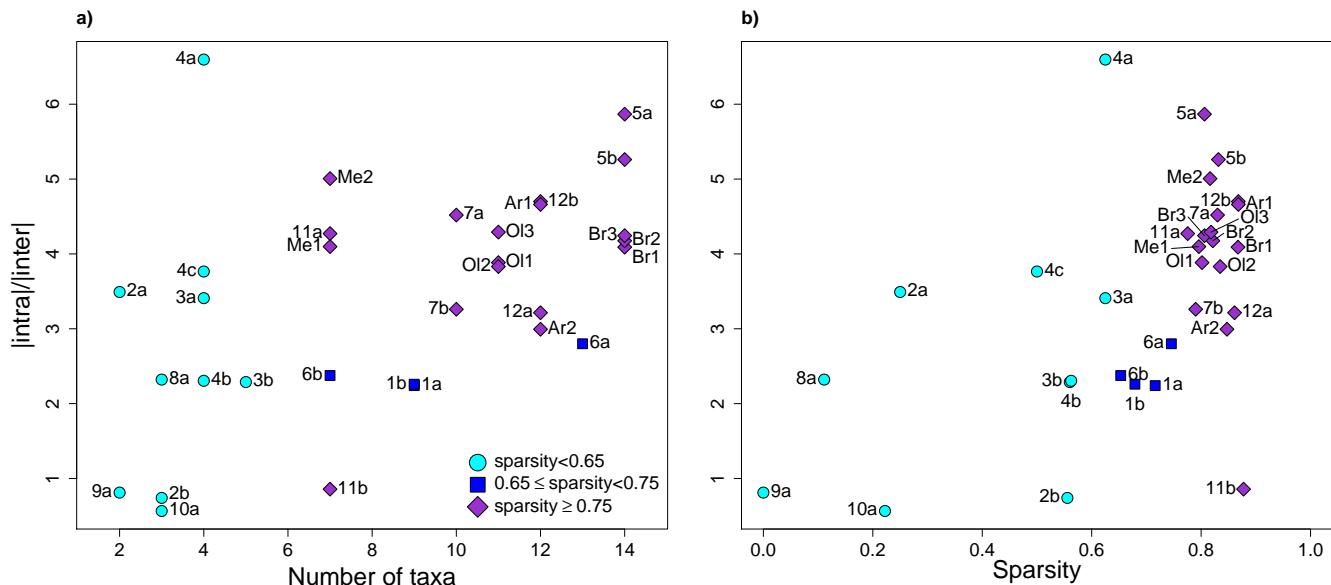


Figure S8: **Ratio of intra-to-intergroup interaction strength in MAR(1) studies.** Only significant values are taken into account and missing values in the matrix are not considered (e.g., not replaced by 0 as they are in the main text). The color and shape of each point are a function of the sparsity of the interaction matrix  $\mathbf{B} - \mathbf{I}$  and the relation between the ratio and the sparsity of the matrix is given in the right panel. Corresponding studies are described in Table S3.

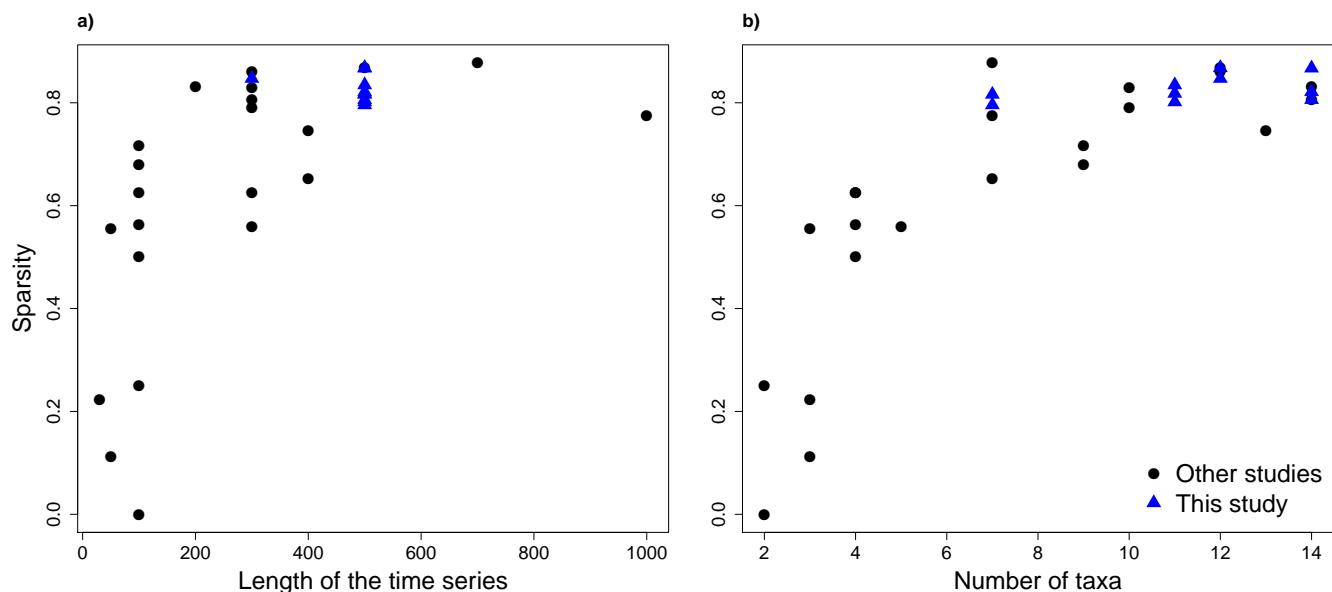


Figure S9: **Relation between interaction sparsity and study design** in studies described in Table S3. Blue triangles correspond to the present study.

## Connection to Lotka-Volterra competition dynamics

The Beverton-Holt multispecies competition model, whose variants are widely used for modelling plant community dynamics (Levine & HilleRisLambers, 2009; Kraft *et al.*, 2015), is the closest discrete time equivalent to the continuous-time Lotka-Volterra model (see Cushing *et al.* 2004 although the mapping is not perfect for  $n \geq 3$ , Roeger & Allen 2004). The Beverton-Holt multispecies competition model writes

$$N_{i,t+1} = \frac{e^{r_i} N_{i,t}}{1 + \sum_j \alpha_{ij} N_{j,t}} \quad (\text{S7})$$

where  $N_{i,t}$  is the abundance of species  $i$  at time  $t$ ,  $r_i$  is its growth rate and  $\alpha_{ij}$  is the effect of species  $j$  on species  $i$ . Here, we show how the interaction strengths  $\alpha_{ij}$  map to those of the MAR(1) models used in the main text.

We start with a 2 species model for simplicity, and we note the equilibrium values of species 1 and 2 as  $N_1$  and  $N_2$  (without time subscript). We re-write the model at equilibrium.

$$\begin{cases} R_1 = \alpha_{11}N_1 + \alpha_{12}N_2 \\ R_2 = \alpha_{21}N_1 + \alpha_{22}N_2 \end{cases}, \text{with} \quad \begin{cases} R_1 = e^{r_1} - 1 \\ R_2 = e^{r_2} - 1 \end{cases} \quad (\text{S8})$$

$$\Leftrightarrow \begin{cases} \alpha_{21}R_1 = \alpha_{21}\alpha_{11}N_1 + \alpha_{21}\alpha_{12}N_2 \\ \alpha_{11}R_2 = \alpha_{11}\alpha_{21}N_1 + \alpha_{11}\alpha_{22}N_2 \end{cases} \quad (\text{S9})$$

$$\Leftrightarrow \begin{cases} N_1 = \frac{\alpha_{12}R_2 - \alpha_{22}R_1}{\alpha_{12}\alpha_{21} - \alpha_{22}\alpha_{11}} \\ N_2 = \frac{\alpha_{21}R_1 - \alpha_{11}R_2}{\alpha_{12}\alpha_{21} - \alpha_{22}\alpha_{11}} \end{cases} \quad (\text{S10})$$

Setting  $n = \log(N)$ , eq. S7 is equivalent to

$$\begin{cases} n_{1,t+1} = r_1 + n_{1,t} - \ln(1 + \alpha_{11}N_{1,t} + \alpha_{12}N_{2,t}) \\ n_{2,t+1} = r_2 + n_{2,t} - \ln(1 + \alpha_{21}N_{1,t} + \alpha_{22}N_{2,t}) \end{cases} \quad (\text{S11})$$

We want to compute  $J$ , the log-scale Jacobian matrix of the model. Let us note  $X = \ln(1 + \alpha_{11}N_1 + \alpha_{12}N_2)$  and  $Y = \ln(1 + \alpha_{21}N_1 + \alpha_{22}N_2)$ .

$$J = \begin{pmatrix} 1 - \frac{\partial X}{\partial n_1} & -\frac{\partial X}{\partial n_2} \\ -\frac{\partial Y}{\partial n_1} & 1 - \frac{\partial Y}{\partial n_2} \end{pmatrix} \quad (\text{S12})$$

We have  $\frac{\partial X}{\partial n_1} = \frac{\partial X}{\partial N_1} \frac{\partial N_1}{\partial n_1} = \frac{\alpha_{11}}{1 + \alpha_{11}N_1 + \alpha_{12}N_2} e^{n_1} = \frac{\alpha_{11}}{1 + \alpha_{11}N_1 + \alpha_{12}N_2} N_1$ , which leads to

$$J - I = \begin{pmatrix} -\frac{\alpha_{11}N_1}{1 + \alpha_{11}N_1 + \alpha_{12}N_2} & -\frac{\alpha_{12}N_2}{1 + \alpha_{11}N_1 + \alpha_{12}N_2} \\ -\frac{\alpha_{21}N_1}{1 + \alpha_{21}N_1 + \alpha_{22}N_2} & -\frac{\alpha_{22}N_2}{1 + \alpha_{21}N_1 + \alpha_{22}N_2} \end{pmatrix} \quad (\text{S13})$$

For this demonstration, we consider diffuse competition, that is

$$\begin{cases} \alpha_{ii} = k\alpha \\ \alpha_{ij} = \alpha, \forall i \neq j \end{cases} \quad (\text{S14})$$

If we combine eq. S10 and eq. S14, we have

$$\begin{cases} N_1 = \frac{\alpha R_2 - k\alpha R_1}{\alpha^2 - k^2\alpha^2} \\ N_2 = \frac{\alpha R_1 - k\alpha R_2}{\alpha^2 - k^2\alpha^2} \end{cases} \quad (\text{S15})$$

and

$$J - I = \begin{pmatrix} -\frac{k\alpha N_1}{1 + k\alpha N_1 + \alpha N_2} & -\frac{\alpha N_2}{1 + k\alpha N_1 + \alpha N_2} \\ -\frac{\alpha N_1}{1 + \alpha N_1 + k\alpha N_2} & -\frac{k\alpha N_2}{1 + \alpha N_1 + k\alpha N_2} \end{pmatrix} \quad (\text{S16})$$

$$\Rightarrow \begin{cases} (J - I)_{11} = \frac{-\frac{k}{1-k^2}(R_2 - kR_1)}{1 + \frac{k}{1-k^2}(R_2 - kR_1) + \frac{1}{1-k^2}(R_1 - kR_2)} \\ (J - I)_{12} = \frac{-\frac{1}{1-k^2}(R_1 - kR_2)}{1 + \frac{k}{1-k^2}(R_2 - kR_1) + \frac{1}{1-k^2}(R_1 - kR_2)} \end{cases} \Rightarrow (J - I)_{11} = k \frac{R_2 - kR_1}{R_1 - kR_2} (J - I)_{12} \quad (\text{S17})$$

By symmetry, we can also write

$$(J - I)_{22} = k \frac{R_1 - kR_2}{R_2 - kR_1} (J - I)_{21} \quad (\text{S18})$$

Therefore, unless the growth rates and the resulting abundances differ over several orders of magnitude, the strength of the competition ratio  $k$  should be roughly comparable between MAR(1) and Lotka-Volterra or Beverton-Holt models. The same reasoning can actually be applied with  $n$  species as the Jacobian has a similar form.

$$\begin{aligned} (J - I)_{ii} &= \frac{-\alpha_{ii}N_i}{1 + \sum_j \alpha_{ij}N_j} \\ &= \frac{-k\alpha N_i}{1 + k\alpha N_i + \sum_{j,j \neq i} \alpha N_j} \end{aligned} \quad (\text{S19})$$

and

$$\begin{aligned} (J - I)_{ij} &= \frac{-\alpha_{ij}N_j}{1 + \sum_l \alpha_{il}N_l} \\ &= \frac{-\alpha N_j}{1 + k\alpha N_i + \sum_{l,l \neq i} \alpha N_l} \\ &= (J - I)_{ii} \frac{\alpha N_j}{k\alpha N_i} \\ &= \frac{1}{k} (J - I)_{ii} \frac{N_j}{N_i} \end{aligned} \quad (\text{S20})$$

Therefore, as long as the intrinsic growth rates and the resulting equilibrium abundances do not differ too much, the order of magnitude of competition should be the same in MAR(1), Lotka-Volterra and multispecies Beverton-Holt models.

## References

- Barraquand, F., Picoche, C., Maurer, D., Carassou, L. & Auby, I. (2018). Coastal phytoplankton community dynamics and coexistence driven by intragroup density-dependence, light and hydrodynamics. *Oikos*, 127, 1834–1852.
- Bersier, L.F., Banasek-Richter, C. & Cattin, M.F. (2002). Quantitative descriptors of food-web matrices. *Ecology*, 83, 2394.
- Cushing, J., Leverage, S., Chitnis, N. & Henson, S.M. (2004). Some discrete competition models and the competitive exclusion principle. *Journal of Difference Equations and Applications*, 10, 1139–1151.
- Griffiths, J., Hajdu, S., Downing, A., Hjerne, O., Larsson, U. & Winder, M. (2015). Phytoplankton community interactions and environmental sensitivity in coastal and offshore habitats. *Oikos*, 125, 1134–1143.
- Hampton, S., Scheuerell, M. & Schindler, D. (2006). Coalescence in the lake washington story: Interaction strengths in a planktonic food web. *Limnology and Oceanography*, 51, 2042–2051.
- Hampton, S. & Schindler, D. (2006). Empirical evaluation of observation scale effects in community time series. *Oikos*, 113, 424–439.
- Hernández Fariñas, T., Bacher, C., Soudant, D., Belin, C. & Barillé, L. (2015). Assessing phytoplankton realized niches using a French national phytoplankton monitoring network. *Estuarine, Coastal and Shelf Science*, 159, 15–27.
- Huber, V. & Gaedke, U. (2006). The role of predation for seasonal variability patterns among phytoplankton and ciliates. *Oikos*, 114, 265–276.
- Ives, A., Carpenter, S. & Dennis, B. (1999). Community interaction webs and zooplankton responses to planktivory manipulations. *Ecology*, 80, 1405–1421.
- Ives, A.R., Dennis, B., Cottingham, K.L. & Carpenter, S.R. (2003). Estimating community stability and ecological interactions from time-series data. *Ecological monographs*, 73, 301–330.

- Klug, J. & Cottingham, K. (2001). Interactions among environmental drivers: Community responses to changing nutrients and dissolved organic carbon. *Ecology*, 82, 3390–3403.
- Klug, J., Fischer, J., Ives, A. & Dennis, B. (2000). Compensatory dynamics in planktonic community responses to pH perturbations. *Ecology*, 81, 387–398.
- Kraft, N., Godoy, O. & Levine, J. (2015). Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences*, 112, 797–802.
- Levine, J. & HilleRisLambers, J. (2009). The importance of niches for the maintenance of species diversity. *Nature*, 461, 254–257.
- Lindgren, M., Möllmann, C., Nielsen, A. & Stenseth, N. (2009). Preventing the collapse of the Baltic cod stock through an ecosystem-based management approach. *Proceedings of the National Academy of Sciences*, 106, 14722–14727.
- Reynolds, C.S. (2006). *The ecology of phytoplankton*. Cambridge University Press.
- Roeger, L.I.W. & Allen, L. (2004). Discrete May-Leonard competition models I. *Journal of Difference Equations and Applications*, 10, 77–98.
- Vik, J., Brinch, C., Boutin, S. & Stenseth, N. (2008). Interlinking hare and lynx dynamics using a century's worth of annual data. *Population Ecology*, 50, 267–274.
- Yamamura, K., Yokozawa, M., Nishimori, M., Ueda, Y. & Yokosuka, T. (2006). How to analyze long-term insect population dynamics under climate change: 50-year data of three insect pests in paddy fields. *Population Ecology*, 48, 31–48.