

Strong self-regulation and widespread facilitative interactions in phytoplankton communities

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Complete List of Authors:	Picoche, Coralie; Université de Bordeaux, ITE group, Labex COTE Barraquand, Frederic; Universite de Bordeaux; CNRS, INSMI - Institut de Mathématiques de Bordeaux
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Strong self-regulation and widespread facilitative interactions in phytoplankton communities

Coralie Picoche^{1,2}, Frédéric Barraquand^{1,2*}

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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: Email: frederic.barraquand@u-bordeaux.fr

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-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 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 (on average, more than 50% of interactions were positive). 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 more abundant ones.
4. *Synthesis:* We demonstrate that strong niche differentiation, widespread facilitation between phytoplanktonic taxa and stabilizing covariances between interaction strengths should be common features of coexisting phytoplankton communities in the field. These are structural

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

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

1 Introduction

2 How species or close genera can coexist together in spite of competition is one of the main puzzles of
3 community ecology, especially for primary producers that seemingly share the same basic resources
4 (Hutchinson, 1961). Many theoretical studies of competition models have shown that competitive
5 exclusion is likely in those circumstances, unless mechanisms involving spatial or temporal variation
6 are at play (Armstrong & McGehee, 1976, 1980; Chesson & Huntly, 1997; Huisman & Weissing, 2001;
7 Li & Chesson, 2016; Chesson, 2018). Neutral theory, that assumes a non-equilibrium coexistence
8 maintained by dispersal and equal competitive abilities for all species (Hubbell 2001, though there
9 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,
12 niche rather than neutral processes may be paramount to explain coexistence, with intraspecific
13 competition dwarfing interspecific competition in most cases (Adler *et al.*, 2010, 2018b). Whether
14 these conclusions drawn mostly from studies of terrestrial plants apply to other ecosystems and taxa
15 is currently 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
17 large number of facilitative interactions (30%) and several reviews (Brooker *et al.*, 2008; McIntire
18 & Fajardo, 2014; Kinlock, 2019) have highlighted that facilitation may be much more widespread
19 than ecologists usually tend to think. Although some theoretical studies suggest that facilitative
20 interactions can be destabilizing (*sensu* resilience) and therefore undermine coexistence in Lotka-
21 Volterra models (Coyte *et al.*, 2015), multiple other modelling (Gross, 2008) and empirical (Brooker
22 *et al.*, 2008; Cavieres & Badano, 2009) studies have suggested that facilitative interactions can
23 to a large degree benefit coexistence, especially when multiple interaction types are considered
24 simultaneously (Mougi & Kondoh, 2012; García-Callejas *et al.*, 2018).

25 Here, we analyse a spatially replicated, long-term community-level dataset, consisting of ten
26 multivariate time series of phytoplankton abundance along the French coastline. We do so using
27 multivariate autoregressive (MAR) models, that allow to estimate interactions between genera.

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

38 Material and methods

39 Sampling methods

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

48 Abiotic variables (temperature, salinity) were measured directly from the boat during the sampling
49 process while water samples for biotic analyses were fixed with a Lugol's solution and examined later.
50 Phytoplankton cells above 20 μm were identified at the lowest possible taxonomic level and counted
51 with the Utermöhl method using an optical microscope (Utermöhl, 1958). Throughout the years
52 and sites, more than 600 taxa were identified at different taxonomic levels. We aggregated them at
53 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 S4.

58 For each region, the MAR(1) analysis focused on the most abundant and most frequently observed
 59 genera to avoid most of the gaps in the time series. When gaps did not exceed a month, missing
 60 values were linearly interpolated; remaining missing values were replaced by a random number
 61 between 0 and half of the lowest observed abundance (Hampton *et al.*, 2006). Time series are plotted
 62 in Fig. S2. 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
 74 \mathbf{e}_t is a $1 \times S$ noise vector, following a multivariate normal distribution with a variance-covariance
 75 matrix \mathbf{Q} . \mathbf{Q} is diagonal and we have previously showed that this parsimonious choice did not
 76 affect qualitatively the results (Barraquand *et al.*, 2018). We used the MARSS package (Holmes
 77 *et al.*, 2014) v3.9, in R v3.3.2 (Venables & Smith, 2013), to estimate parameters with a maximum

78 likelihood procedure.

79 Our previous analysis of the Arcachon region, for which more covariates 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).

84 They are therefore used to summarize the abiotic environment in the remainder of the article.

85 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 highlight how intra- and inter-taxon interaction strengths in a MAR(1) model map to their counterparts in a multispecies Beverton-Holt model, i.e., a discrete-time Lotka-Volterra model (Cushing *et al.*, 2004), in the Supporting Information.

100 In this study, the number of phytoplankton taxa (S) and the community composition vary
101 slightly between regions but sites share on average 67% of their taxa. In order to have comparable
102 models, we also keep the same 2 covariates, i.e., water temperature and salinity, that were measured
103 at all study sites. Therefore, the dimension of the dynamical system depends on the (square of
104 the) number of phytoplankton taxa we study, which ranges between 7 (Mediterranean Sea) and
105 14 (Brittany). The smallest system still requires 63 parameters to be estimated (49 for the 7×7

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

Analysis of interaction strengths

The interaction matrix obtained from MAR(1) analyses can be used to determine the stability of a discrete-time dynamical system ([Ives et al., 1999, 2003](#)). To investigate stability-complexity relationships, we compared the maximum modulus of the eigenvalues of the pennate/centric matrices for each site to network descriptors. The maximum modulus is analogous to the real part of the leading eigenvalue for continuous time models, and measures resilience while still accounting for some variability properties ([Ives et al., 1999](#)). However, because most theory on stability-complexity has been developed in continuous time (e.g., [Allesina & Tang, 2015](#)), we numerically checked that the maximum modulus of the eigenvalues in a discrete-time interaction matrix and its continuous-time model counterpart yield similar information in the Supporting Information. We then compared this resilience measure to complexity metrics, such as the interaction strength distribution (sign,

mean and variance) and weighted connectance (Bersier *et al.*, 2002). Weighted connectance is a measure of the proportion of realized links compared to all possible links, taking into account the shape of the flux distribution. This metric is adapted to weighted interaction matrices but cannot accommodate for both positive and negative coefficients: we therefore chose to 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. Interaction coefficient variance is multiplied by the number of taxa, according to theory (Allesina & Tang, 2015).

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 that can be expected on the growth rate of a taxon from the rest of the community (i.e., is the effect of others mostly positive or negative?), 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 S4. Authors usually reported only coefficients that were significant with a 5% significance level, 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. S9). We considered both; a detailed description of these different ways to compare intra- and inter-taxa interactions can be found in the Supporting Information.

159 Results

160 Interaction estimates

161 Using MAR(1) autoregressive models, we produced interaction matrices (Ives *et al.*, 2003; Hampton
162 *et al.*, 2013) – i.e., Jacobian community matrices on the logarithmic abundance scale (Ives *et al.*,
163 2003). Best-fitting models corresponded to a phylogenetically-structured interaction scenario, where
164 interactions only occurred between closely related genera (Fig. S3). This led to sparse, modular
165 matrices that have two main features. First, we observed a strong self-regulation for all sites (Fig. 1,
166 diagonal elements of all matrices), a feature that we had previously highlighted in a more detailed
167 analysis on one of the considered study regions (Barraquand *et al.*, 2018). The ratio of mean
168 intragenus to intergenus interaction coefficients varied between 6 and 10, not counting coefficients
169 set to 0 before the estimation process. When we included the zeroes in the interaction matrix in
170 the computation of the intra/inter mean interaction strength (see the Supporting Information for
171 details of that computation), the ratio rose to 21-43. Therefore, intragenus interactions were on
172 average one order of magnitude stronger than intergenus interactions.

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

180 We found that the percentage of true mutualism (+/+) was substantial: averaged over all sites,
181 32% of all interactions were (+/+) while only 12% of them were (-/-), see also Fig. S5. The sign
182 correspondence was not always maintained between regions: the only interaction that was non-zero
183 in the 10 sites (CHA/SKE) was mutualistic in Men er Roue only (Brittany) and mixed (+/-) in
184 all other sites. Within the same region, however, interactions measured in different sites tended to
185 keep the same sign. In the 3 sites of Oléron, for instance, there were 4 interactions which remained

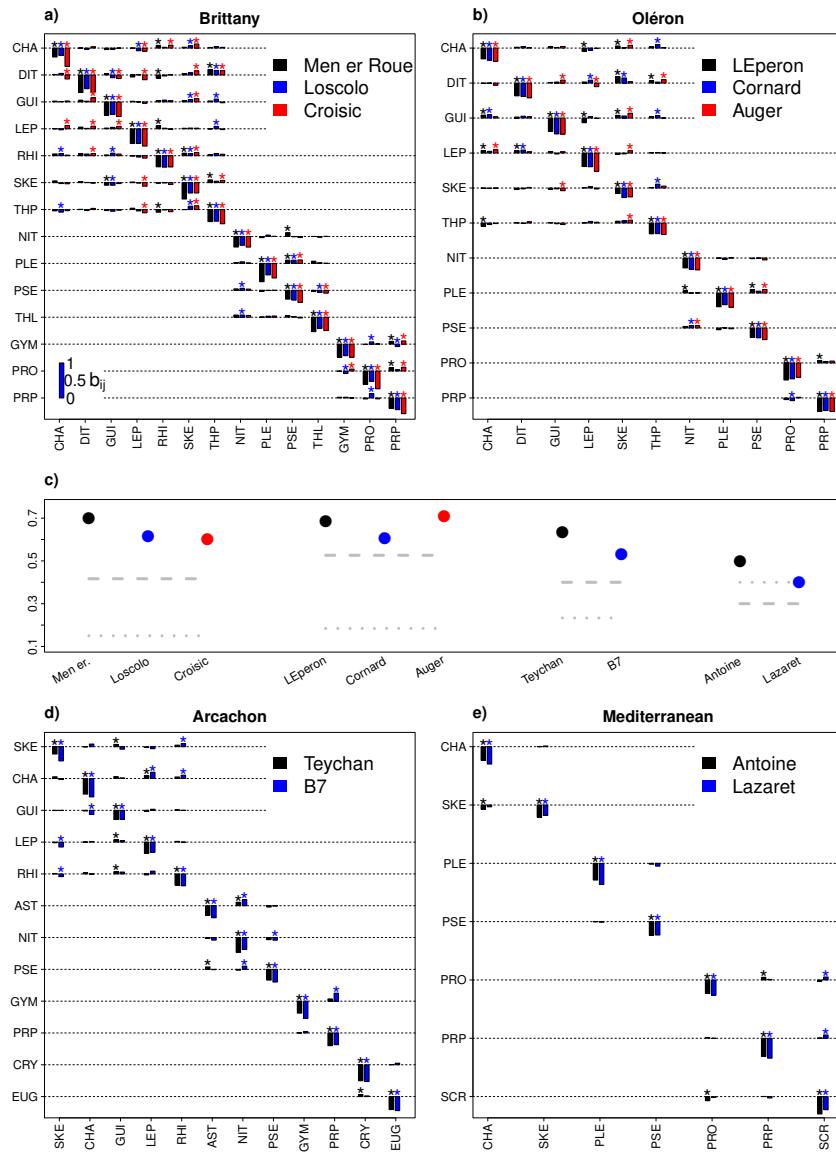


Figure 1: Interaction matrices estimated in 10 sites along the French coastline. Taxon j (in columns) has an effect on taxon i 's growth rate (in rows) proportional to the bar height, which corresponds to the $\mathbf{B} - \mathbf{I}$ matrix (community composition in Table S2, most parsimonious interaction scenario presented). The scale for the coefficient values is given at the bottom left of panel a). Coefficients significantly different from 0 ($\alpha = 5\%$) are marked by asterisks (*). 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.

positive for both taxa involved (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 in eigenvalue modulus for weighted connectances between 0.09 and 0.1. The maximum modulus of the interaction matrix eigenvalues remained between 0.65 and 0.80.

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

Aside from the trade-offs of Fig. 3, we found no remarkable patterns of covariation between matrix elements (Fig. S5) other than a mean-variance scaling of interaction coefficients (Fig. S6).

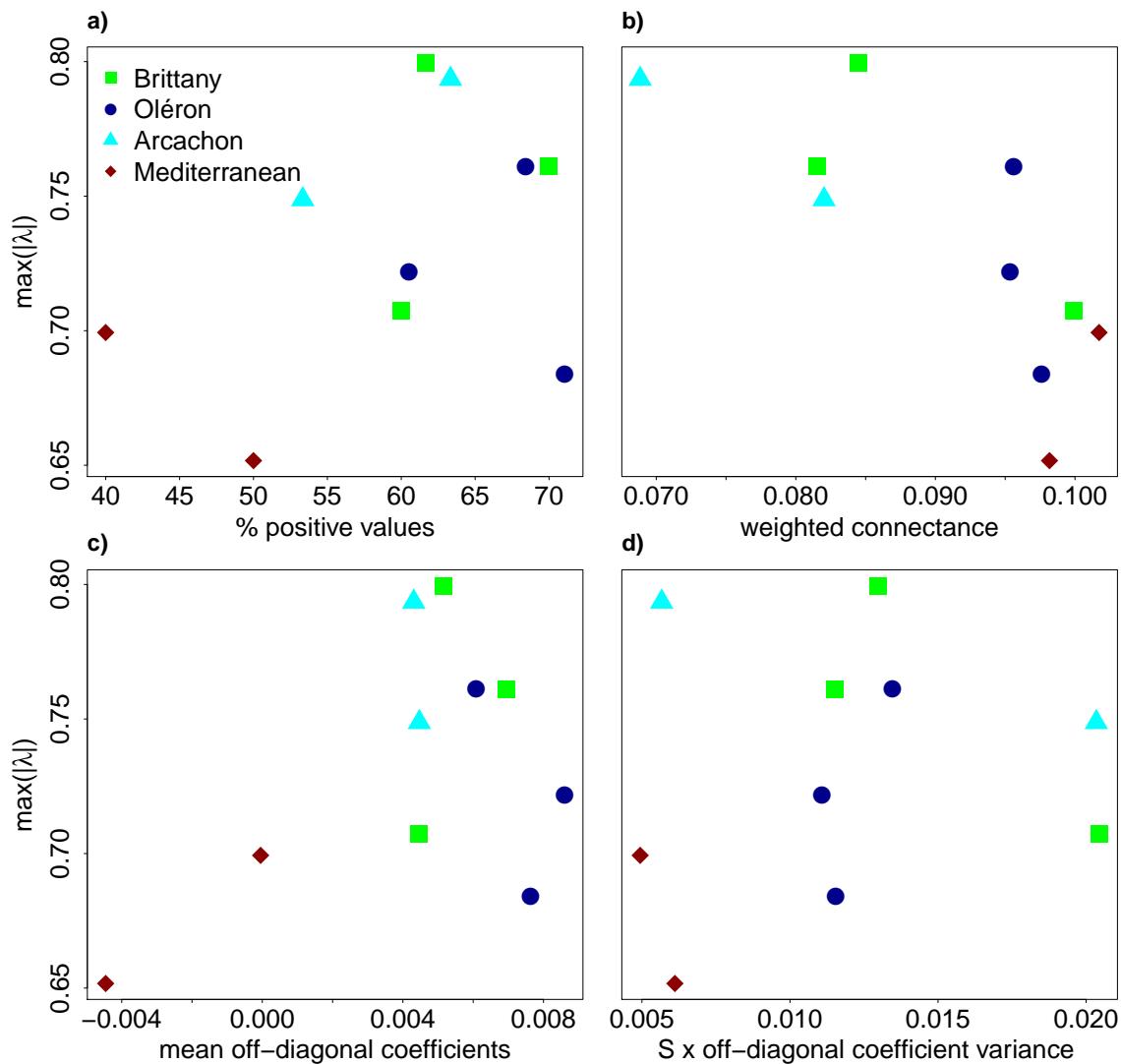


Figure 2: Relation between stability and complexity of the interaction networks. The maximum modulus of the eigenvalues of the interaction matrix \mathbf{B} indicates stability *sensu* resilience. Off-diagonal coefficient variance is multiplied by the dimension of the network, that is the number of species in the region. Each color or shape corresponds to a given region. The formula for weighted connectance is given in the Supporting Information.

211 Literature comparison

212 Finally, we sought to put these results in a broader context by compiling the intra vs inter group
 213 estimates of previous MAR(1) studies of long-term observational count data (listed in Table S4).

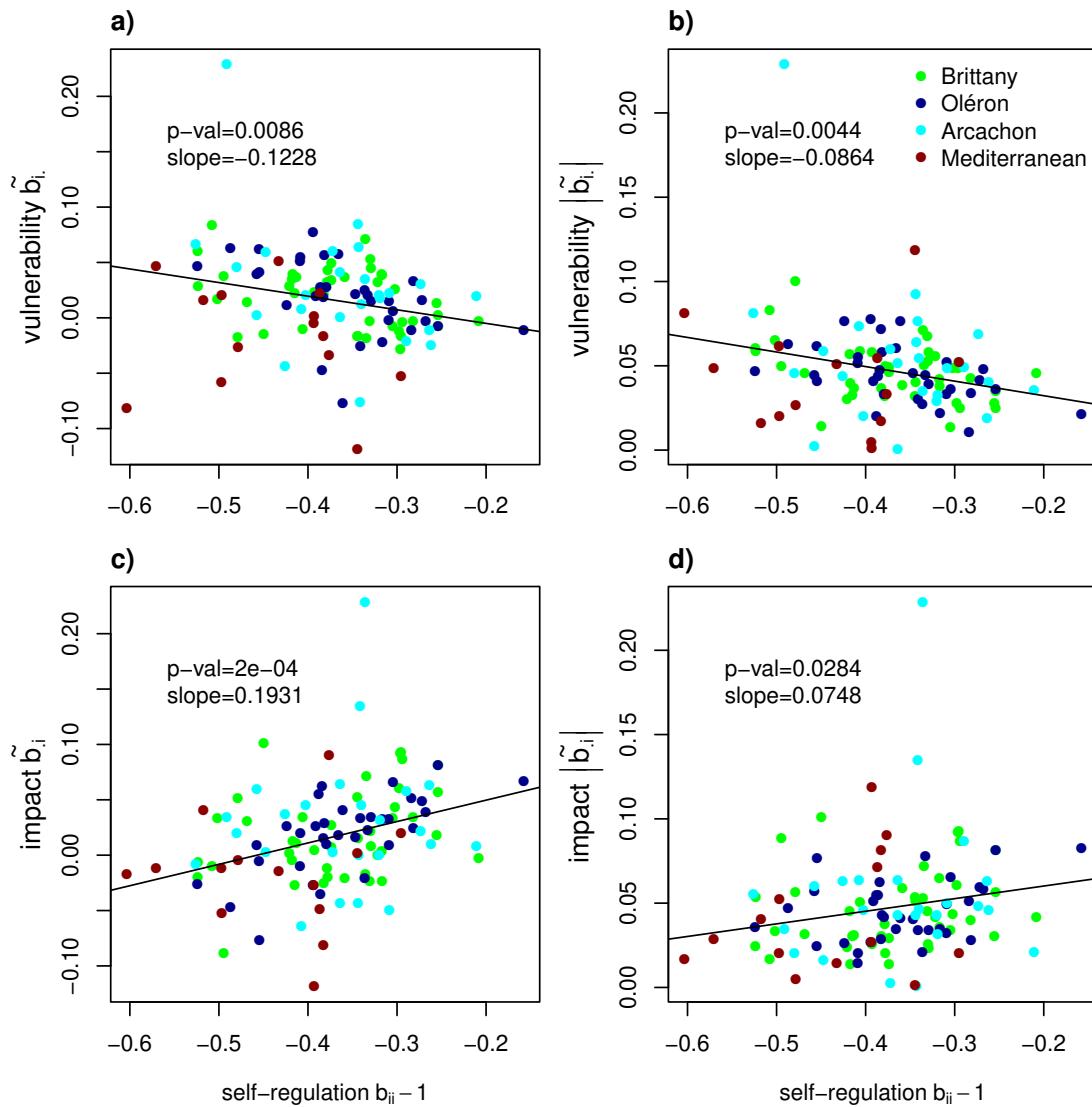


Figure 3: Relation between vulnerability/impact and self-regulation. Average vulnerability (effects of others on the focal taxon growth rate, a-b) and impact (effects of the focal taxon on others' growth rates, c-d), as well as self-regulation, are computed for untransformed (a-c) or absolute (b-d) values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

²¹⁴ We found that the order of magnitude of intra/inter interaction strengths considered here is not
²¹⁵ particularly above those found for most planktonic systems to which MAR(1) models have been

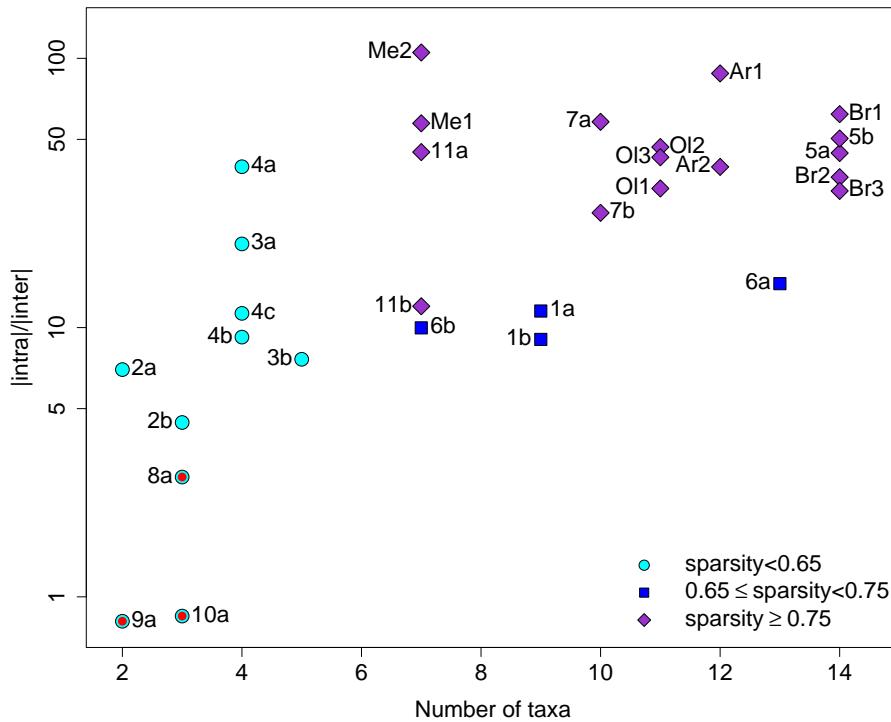


Figure 4: Ratio of intra- to inter-group interaction strength in Multivariate AutoRegressive (MAR) models. The reference for each study is given in Table S4. Codes beginning with letters correspond to the present study (Ar: Arcachon; Ol: Oléron; Br: Brittany; Me: Mediterranean Sea). The symbol color 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 5% level; Fig. S9 is the same figure taking into account only significant interactions)

fitted, considering that our systems are relatively high-dimensional and that the higher the number of taxa, the larger the intraspecific regulation (Barabás *et al.*, 2017). We included in Fig. 4 not only plankton studies but also a couple of vertebrate or insect studies on less diverse communities, where interactions are stronger, in order to provide lower bounds for the intra/inter ratio. The conclusion from this comparison seems to be that, unlike small communities that can be tight-knit, any diverse field system of competitors and facilitators has evolved large niche differences making intragroup competition much larger in magnitude than intergroup interactions.

223 Discussion

224 Strong self-regulation and facilitation

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

228 The intra/intertaxa interaction strength ratio (Levine & HilleRisLambers, 2009) that we found,
229 from 6–10 to above 20, depending on whether one includes interactions set to zero before the
230 estimation process, could appear very high in light of previous intra/interspecific competition
231 strength estimates of 4 to 5 by Adler *et al.* (2018b). Additional estimates using the unconstrained
232 interaction matrix yielded ratios between 8 and 11 depending on the site (Table S3 and Fig. S8 in
233 the Supporting Information), but weak intertaxa effects are likely to be inflated in the full model.
234 Therefore, a intra/inter ratio of 10 seems like a conservative estimate, twice that of Adler *et al.*
235 (2018b) who use a different model, i.e., a Lotka-Volterra competition model. We outline how to relate
236 a MAR(1) model to a discrete-time Lotka-Volterra equivalent in the Supporting Information; even
237 though there is a relationship between intra/inter ratios in both models, the relationship is not trivial
238 when abundances vary greatly between species. Hence, to some degree, intra/inter ratios can differ
239 between model frameworks or ways of measuring density-dependencies (e.g., a high measurement
240 error due to using proxies of densities for plants can result in bias in interaction coefficient estimates,
241 Detto *et al.*, 2019). However, a ratio intra/inter at least twice larger than the ones previously found
242 may call for other explanations. One could also argue that our high intra/inter ratio arises because
243 we consider the genus as our baseline taxonomic unit, rather than the species. It is logical that
244 niche differentiation increases as one gets up the phylogenetic tree, and that getting down to the
245 species level could slightly decrease that ratio (but see Narwani *et al.*, 2017, in which phylogenetic
246 closeness decreases competition strength). However, taxonomic resolution is unlikely to be the sole
247 explanation for the high intra/inter ratio of interaction strength found here, for two reasons. First,
248 phytoplankton species belonging to different genera are often found to compete in experiments
249 (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. We discuss below possible mechanistic interpretations.

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, resulting 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; de Ruiter & Gaedke, 2017). We believe this to be likely for the present study, given that the study regions (Arcachon, Oléron, Brittany, Mediterranean) have similar predators (zooplankton, e.g., Jamet *et al.*,

278 2001; Modéran *et al.*, 2010; Tortajada *et al.*, 2012) and parasites (viruses, e.g., Ory *et al.*, 2010;
279 fungi). Though natural enemies are good candidates to explain the observed niche differences and
280 emerging facilitation, one must bear in mind that other known drivers of phytoplankton dynamics
281 such as allelopathy (Felpeto *et al.*, 2018), auxotrophy (Tang *et al.*, 2010) or hydrodynamics (Lévy
282 *et al.*, 2018) can all, in theory, help create different niches and an emerging facilitation (see last
283 subsection of the Discussion). Finally, resources that are usually considered limiting for all species
284 might in fact not always be: Burson *et al.* (2018) show that phytoplanktonic taxa specialize on
285 different components of the light spectrum. This constitutes an example of fine-scale resource
286 partitioning of one resource, light, that all species and genera are usually thought to compete for.

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

289 There was no relation between the complexity of the communities (measured as either the weighted
290 connectance or the interaction coefficient variance) and their stability (measured by the largest
291 modulus of the eigenvalues, which quantifies the return time to a point equilibrium, i.e., resilience).
292 This result is conditional upon our model being a good approximate description of the system
293 (i.e., no multiyear limit cycles or chaotic attractors as the mapping between eigenvalues and actual
294 stability is distorted in that case, Certain *et al.*, 2018). However, we already showed on a subset of
295 this data that a fixed point in a MAR(1) model, perturbed by seasonality and abiotic variables, is an
296 accurate description of the system (Barraquand *et al.*, 2018). Therefore, we are confident that the
297 absence of complexity-resilience relationship found here is not a mere artefact of an inadequate model.
298 This absence of direct link between complexity and stability could be an actual feature of empirical
299 systems, as shown previously by Jacquet *et al.* (2016) using a different technique. This result seems to
300 contradict theory based on random matrices, especially for competitive and/or mutualistic networks
301 (Allesina & Tang, 2012). However, one must bear in mind that such result could also be generated
302 by the limited size of our networks, as random matrix theory relies on asymptotics (Allesina &
303 Tang, 2015). We should also mention that our interaction matrices (based on a discrete-time model)
304 are not strictly analogous to the ones used most frequently in theoretical ecology (continuous-time

model), though the spectral radius (largest modulus) is here tightly related to the real part of the lead eigenvalue in equivalent continuous-time models (see Supporting Information). Thus while the jury is still out regarding the absence of complexity-resilience relation found here, it may well be a genuine absence. In addition to 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), does not in fact have a major impact on our networks' resilience.

In addition to weighted connectance and interaction variance, indices at the genus level (vulnerability and impact) approximate the average effects exerted and sustained by any given taxa in the different study sites. While, at the network level, network structure (either complexity measures or the percentage of mutualistic interactions) did not affect resilience, 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's 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. A low self-regulation was also 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 relative rarity and self-regulation could explain the lesser impact of highly 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 the less common taxa to have large impacts. In contrast, it was more difficult to explain the relationship between self-regulation and vulnerability: a genus that is more self-regulated and less common 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.* 2019) for the network as a whole, because the taxa that are the more vulnerable

333 to other taxa's impacts are also those whose dynamics are intrinsically more buffered. By which
334 mechanisms this could happen is so far unclear and open to speculation. It could just be a "mass
335 effect": common taxa are in high enough numbers to deplete resources or change the environment in
336 ways that affect the less common ones, but the reverse is not true. As a final note on relationships
337 between interaction matrix coefficients, we caution that the trends evidenced are all relatively weak:
338 considerable stochasticity still dominates the distribution of interaction matrix coefficients.

339 **Ghosts of competition past and present**

340 Overall, the dominance of niche differentiation in observational plankton studies – based on our
341 analysis of the REPHY dataset and re-analysis of the MAR(1) literature – is similar to what has been
342 recently found in plant community studies (Volkov *et al.*, 2007; Adler *et al.*, 2018b) or empirically
343 parameterized food webs including horizontal diversity (Barabás *et al.*, 2017). Large niche differences
344 might be due to the ghost of competition past, i.e., competition has occurred in the past, leading to
345 strong selection and subsequent evolution, and then to progressive niche separation. In this scenario,
346 species have evolved niches that allow them not to compete or to interact only weakly (very strong
347 facilitative effects might be likewise destabilizing, Coyte *et al.*, 2015). The likely predator effects that
348 we highlighted above could be comprised within such niche differentiation *sensu largo*: specialized
349 predators can make strong conspecific density-dependence emerge (Bagchi *et al.*, 2014; Comita *et al.*,
350 2014), while switching generalists can also promote diversity (Vallina *et al.*, 2014). Both predators
351 and resources have often symmetrical effects and can therefore contribute almost equally to such
352 past niche differentiation (Chesson, 2018).

353 An intriguing new possibility, dubbed the "ghost of competition present" (Tuck *et al.*, 2018),
354 suggests by contrast that spatial distributions in relation to abiotic factors might have a large
355 impact on the interaction strengths inferred from temporal interaction models such as ours. Recent
356 combinations of model fitting and removal experiments have shown that model fitting usually
357 underestimates the effect of competitors that are uncovered by removal experiments (Tuck *et al.*,
358 2018; Adler *et al.*, 2018a). This could occur for instance if species are spatially segregated (at a small
359 scale) because each species only exists within a domain where it is relatively competitive (Pacala's

360 spatial segregation hypothesis, chapter 15 in [Pacala & Levin 1997](#)), while a focal species could
361 spread out if competitors were removed. This means that a species can be limited by competitors,
362 but act so as to minimize competition (a little like avoidance behaviour in animals) and maximize
363 opportunities for positive interactions, which implies that competition is in effect hard to detect
364 when all species are present. This mechanism would require some spatial segregation between
365 phytoplankton species at the scale of interactions, i.e., at the microscale. At the moment, while it
366 is known that fine-scale hydrodynamics generate inhomogeneities at the microscale ([Barton et al.](#),
367 [2014](#); [Breier et al., 2018](#)) it is yet quite unclear how they might affect multivariate spatial patterns
368 of species distributions (*sensu* [Bolker & Pacala 1999](#) or [Murrell & Law 2003](#)). Moreover, even with
369 some microscale spatial segregation between species, a “ghost of competition present” mechanism
370 might not work in phytoplankton as in terrestrial plants, because the turbulent, ever-changing
371 aquatic environment imposes additional constraints on the spatial distribution of organisms.

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379 Supporting Information

380 This article contains supporting information.

381 Authors' contributions

382 CP and FB contributed equally to the project design and the methodology. The computer code was
383 written by CP. The authors jointly interpreted the results and co-wrote the manuscript after an
384 early draft by FB.

385

386 **Data accessibility**

387 The REPHY dataset has already been published ([REPHY, 2017](#)) and all scripts for MAR models
388 and subsequent network analyses are available online in a GitHub repository (<https://github.com/CoraliePicoche/REPHY-littoral>).
389

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Supporting Information for Strong self-regulation and widespread facilitative interactions in phytoplankton communities – Picoche C. & Barraquand F.

Sampling

Study sites are shown on Fig. S1 and the characteristics of each site are given in Table S1; they are part of the REPHY monitoring network by Ifremer coastal laboratories (REPHY, 2017). The mean temperature in each site 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.

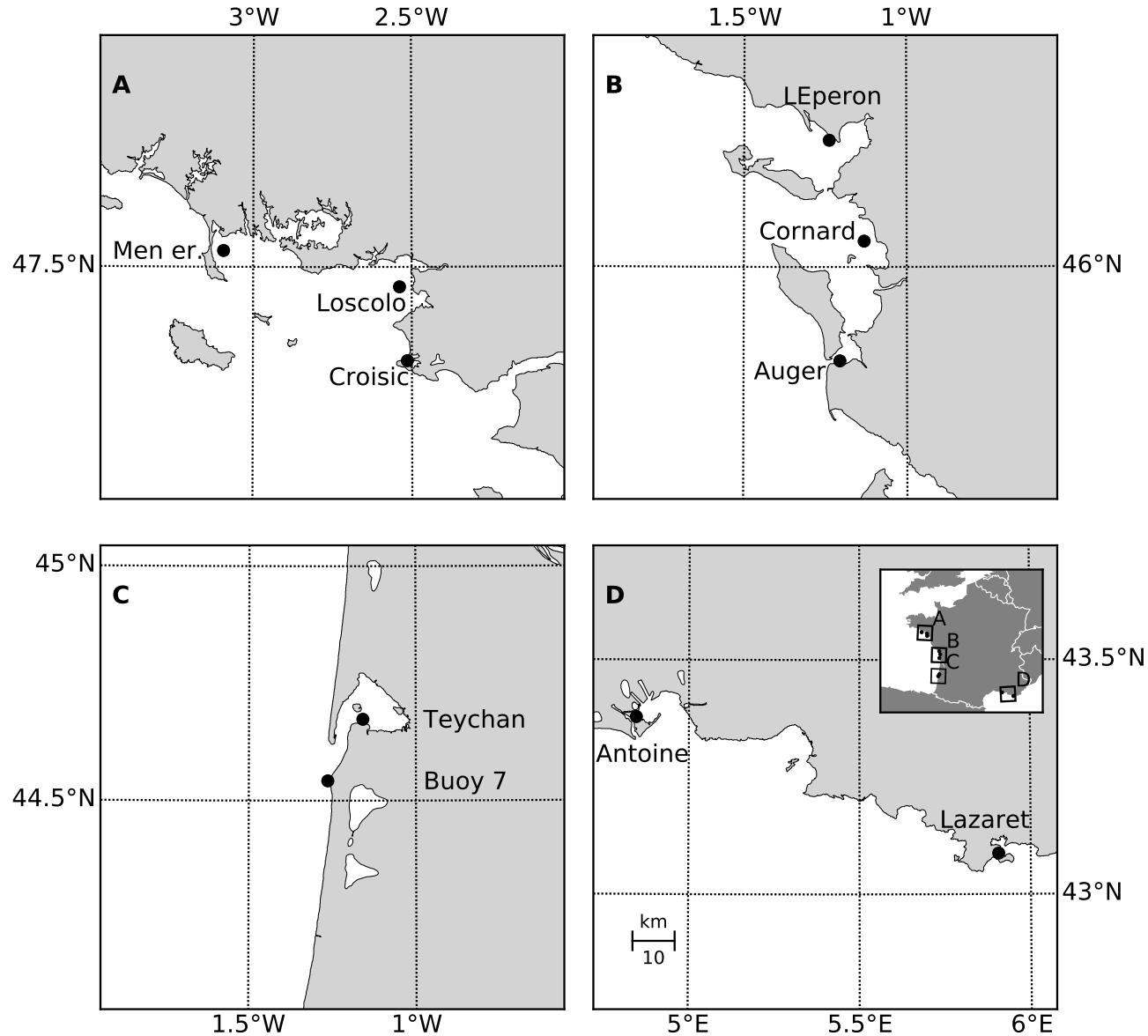


Figure S1: **Location of each study site in their region:** Brittany (A), Oléron (B), Arcachon (C) and the Mediterranean Sea (D). The common scale of the panels is given in the left corner of D.

At each site, water samples were collected below surface (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 μm , 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 the main text**, based on the work by Hernández Fariñas *et al.* (2015)

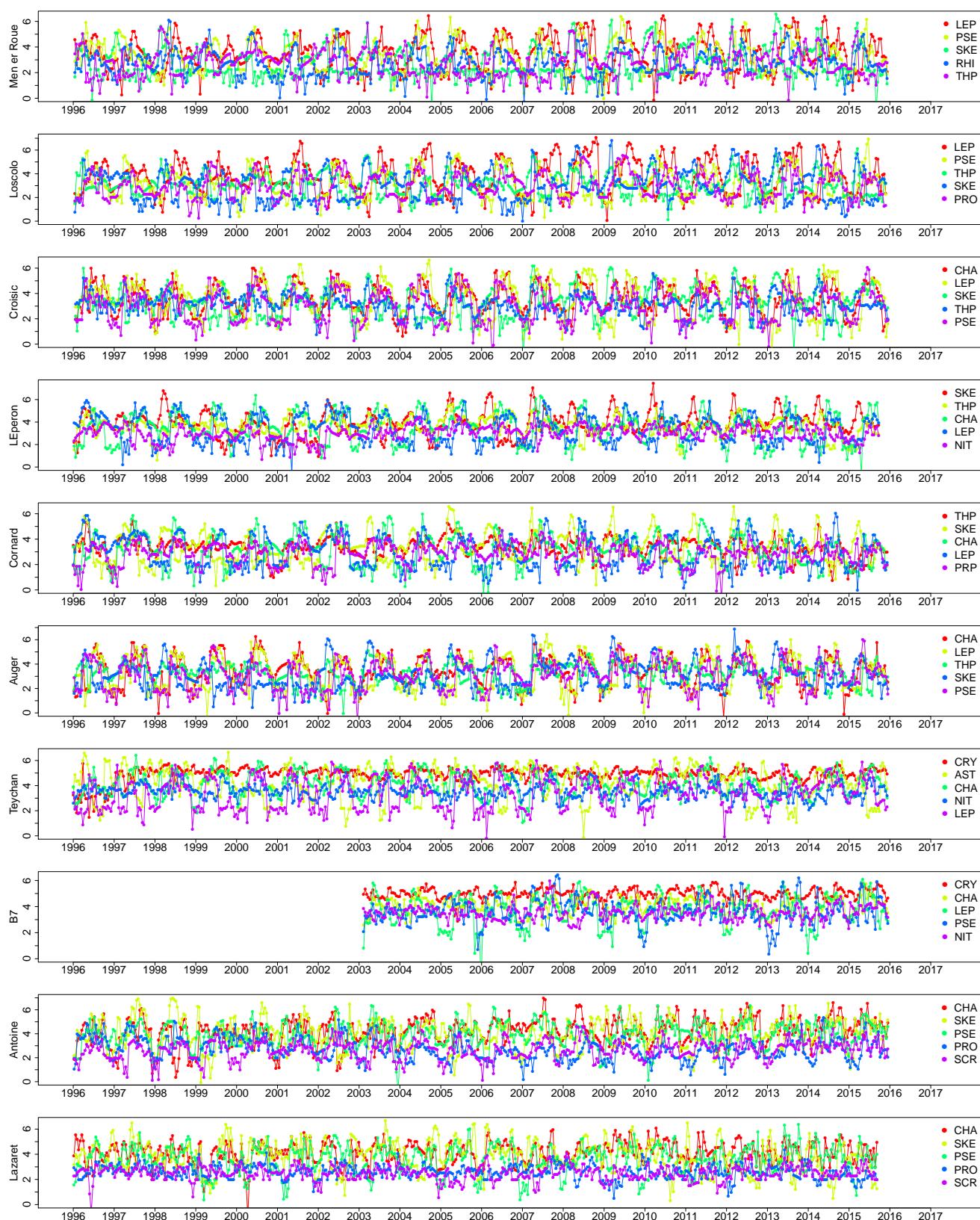


Figure S2: Time series of the 5 most abundant phytoplanktonic genera in each site.

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. However, in order to be as comprehensive as possible, we also present results for the full/unconstrained matrix in a section below (“Comparison with a full interaction matrix”).

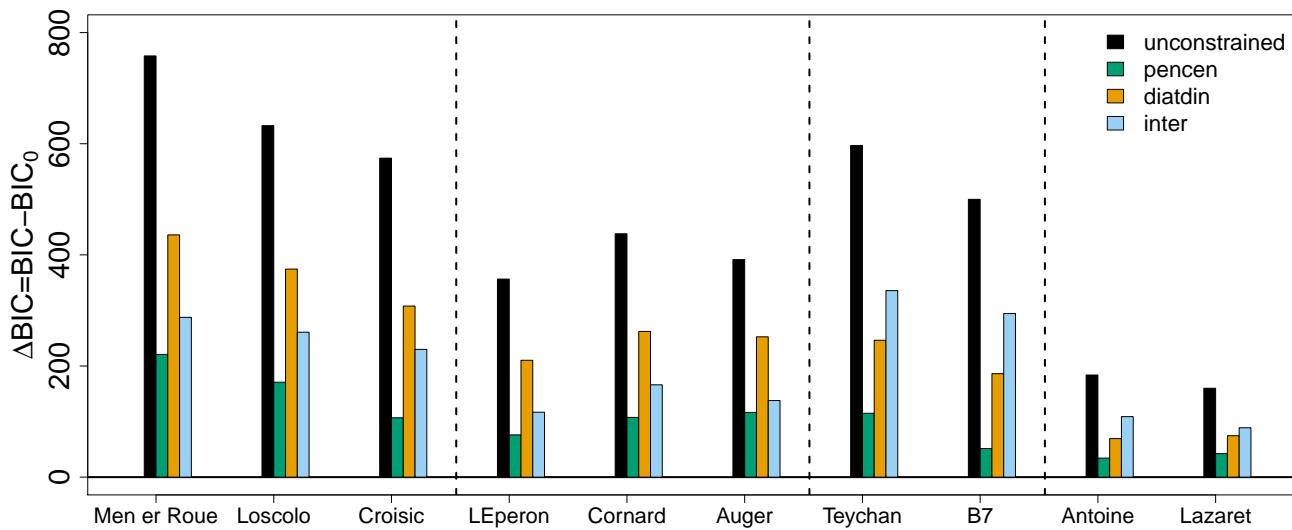


Figure S3: **Comparison of the BIC of different interaction scenarios**, compared to the null scenario (diagonal interaction matrix, allowing only intragroup interactions), for 10 sites in 4 different regions, separated by dashed lines (Brittany, Oléron, Arcachon and the Mediterranean Sea). Different 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 data structures (length of the times series) 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 in order 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 is 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 5% level 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.

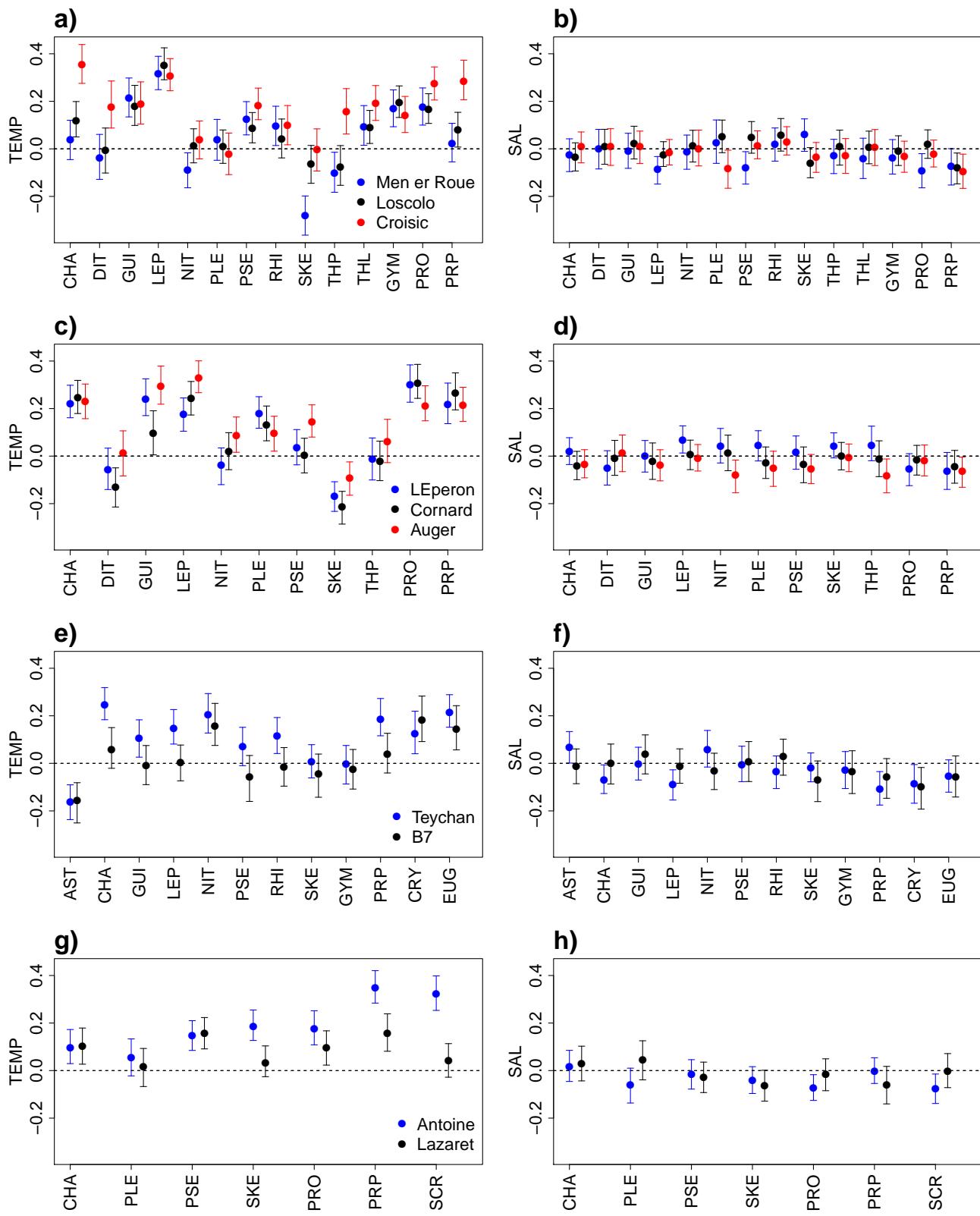


Figure S4: Effect of environmental variables (temperature, TEMP or salinity, SAL) on phytoplankton genera in Brittany (a, b), Oléron (c, d), Arcachon (e, f) and in the Mediterranean Sea (g, h). Each color corresponds to a different site. Error bars correspond to the 95% confidence interval around the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

Network analysis

Computation of intra/inter-taxa interaction strength ratios from interaction coefficients

We present in the main text ratios between intra and inter-taxon interaction strength, $\kappa = \frac{\text{mean}|b_{ii}|}{\text{mean}|b_{ij, j \neq i}|}$, in several places. These are computed from three sets of interspecific interaction coefficients:

- b_{ij}^* , coefficients significantly different from 0 at the 5% level
- $b_{ij}^{\bar{*}}$, coefficients not significantly different from 0
- b_{ij}^0 , coefficients set to 0 before the estimation process.

Some coefficients are indeed set to 0 before the estimation process, in order to reduce the dimensionality of the system (see section above). There are therefore different estimates of κ , depending on the set of b_{ij} chosen for the denominator.

- $\{b_{ij}\} = \{b_{ij}^*\} \cup \{b_{ij}^{\bar{*}}\}$, leading to an observed ratio κ between 6 and 10.
- $\{b_{ij}\} = \{b_{ij}^*\} \cup \{b_{ij}^{\bar{*}}\} \cup \{b_{ij}^0\}$, leading to a ratio κ between 21 and 43.
- $\{b_{ij}\} = \{b_{ij}^*\} \cup \{b_{ij}^{\bar{*}}\} \cup \{b_{ij}^0\}$ where $b_{ij}^{\bar{*}} := 0$ for comparisons with literature-based MAR(1) coefficients, as results in the literature rarely differentiate between non-significant coefficients and coefficients that were set to 0 beforehand. This corresponds to Fig. 4 in the main text.
- $\{b_{ij}\} = \{b_{ij}^*\}$, illustrated in Fig. S9.

Unless otherwise stated, all analyses presented in the main text and below are based on $\{b_{ij}\} = \{b_{ij}^*\} \cup \{b_{ij}^{\bar{*}}\}$.

Interaction types

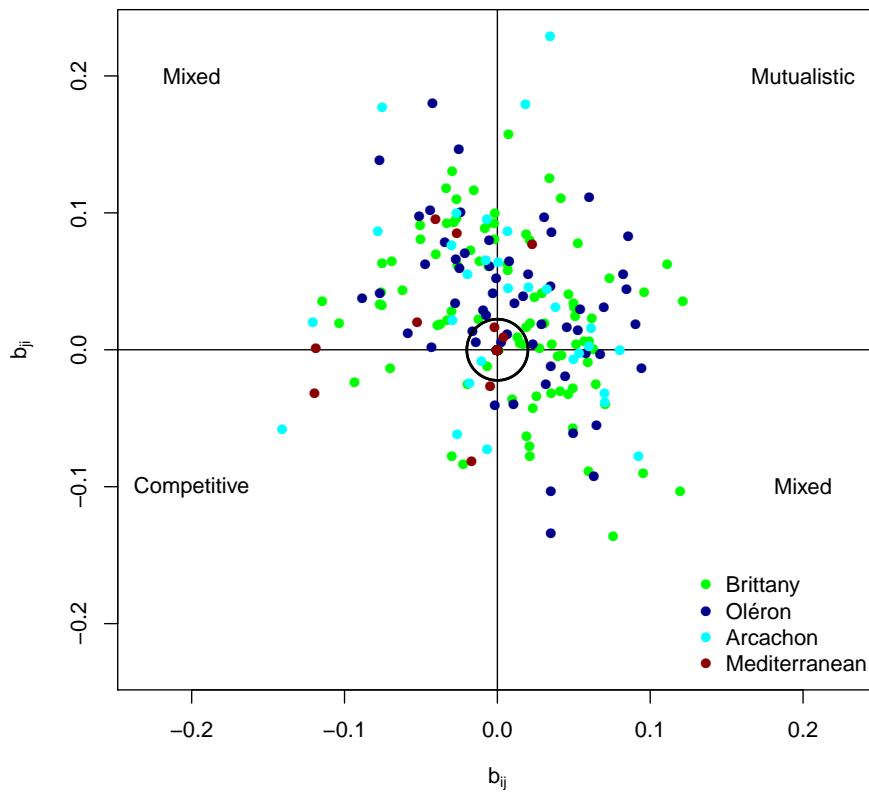


Figure S5: Pairs of coefficients for each study site. The effect of species i on j is given as a function of the effect of species j on species i . The black circle indicates the first quartile of the interaction values, under which we can assume that the effect is weak or null. Below this limit, $(+/+)$,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

Metrics

We characterised each interaction network with 3 quantitative descriptors: the mean and variance of the intra- and intergenus coefficients (i.e., on and off the matrix diagonal) and the weighted connectance of $\mathbf{B}-\mathbf{I}$. The mean of absolute values of intragenus coefficients was approximately 8 times higher than the mean of the absolute values of the effect of intergenus interactions. The intragenus interactions' variance was about 4 times higher than the variance of intergenus interactions (Fig. S6).

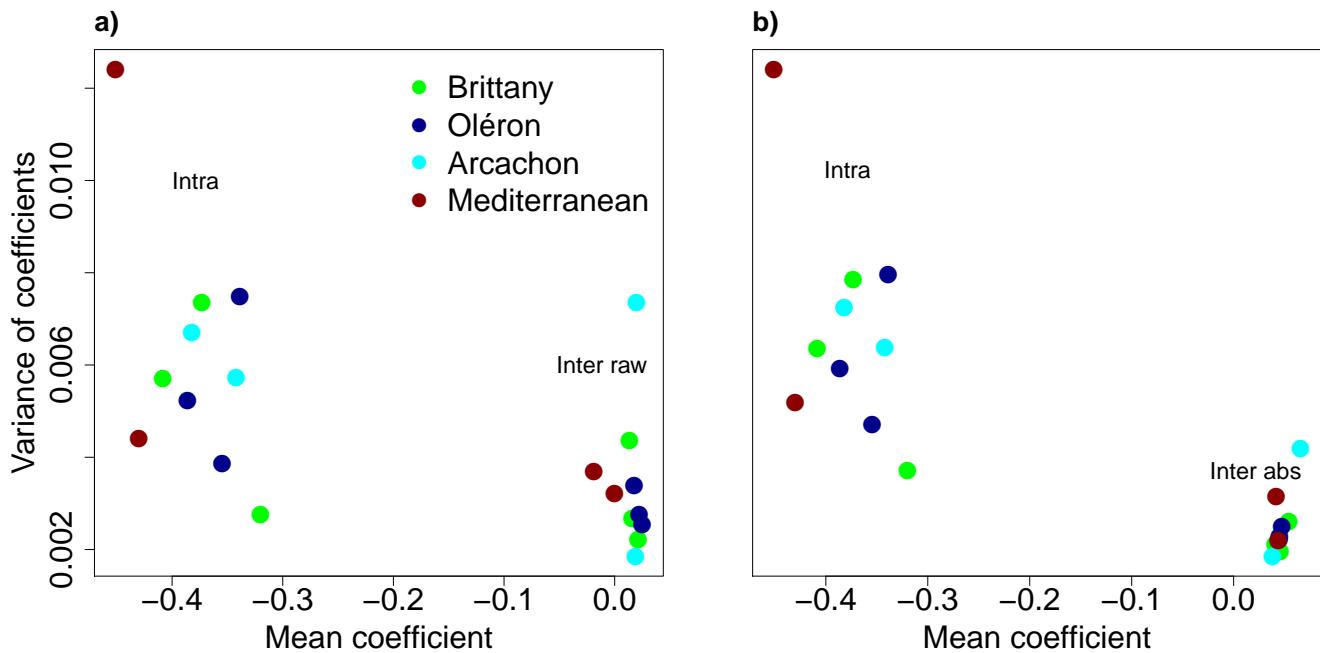


Figure S6: Relation between mean and variance of the intra- and intergenus interaction coefficients. The variance of the coefficients in the interaction matrix ($\mathbf{B}-\mathbf{I}$) increases with the mean, for 10 sites in 4 regions, with a model allowing interactions only within clads (within centric 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). We did not take the absolute value of intragroup coefficients since they were all negative.

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).

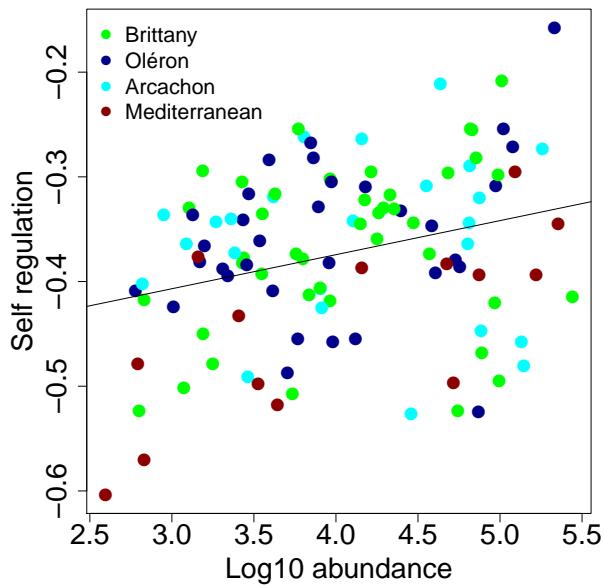


Figure S7: Relation between abundance and self-regulation (intragenus interaction coefficients). Mean abundance is computed for each genus in each site and intragenus interaction strengths are the diagonal coefficients of the interaction matrix ($\mathbf{B}-\mathbf{I}$).

Weighted connectance is described in Bersier *et al.* (2002). It is based on 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 ($\mathbf{B-I}$), $b_{\cdot k} = \sum_{i=1}^S b_{ki}$ 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 ($\mathbf{B-I}$).

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 this network-level metric, 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 .

Comparison with a full interaction matrix

We checked that, by choosing the model with the lowest BIC, we did not miss interactions which would have changed our conclusions. To do so, we examined the full (unconstrained) model results for all study sites. We present those results below (Fig. S8 and Table S3).

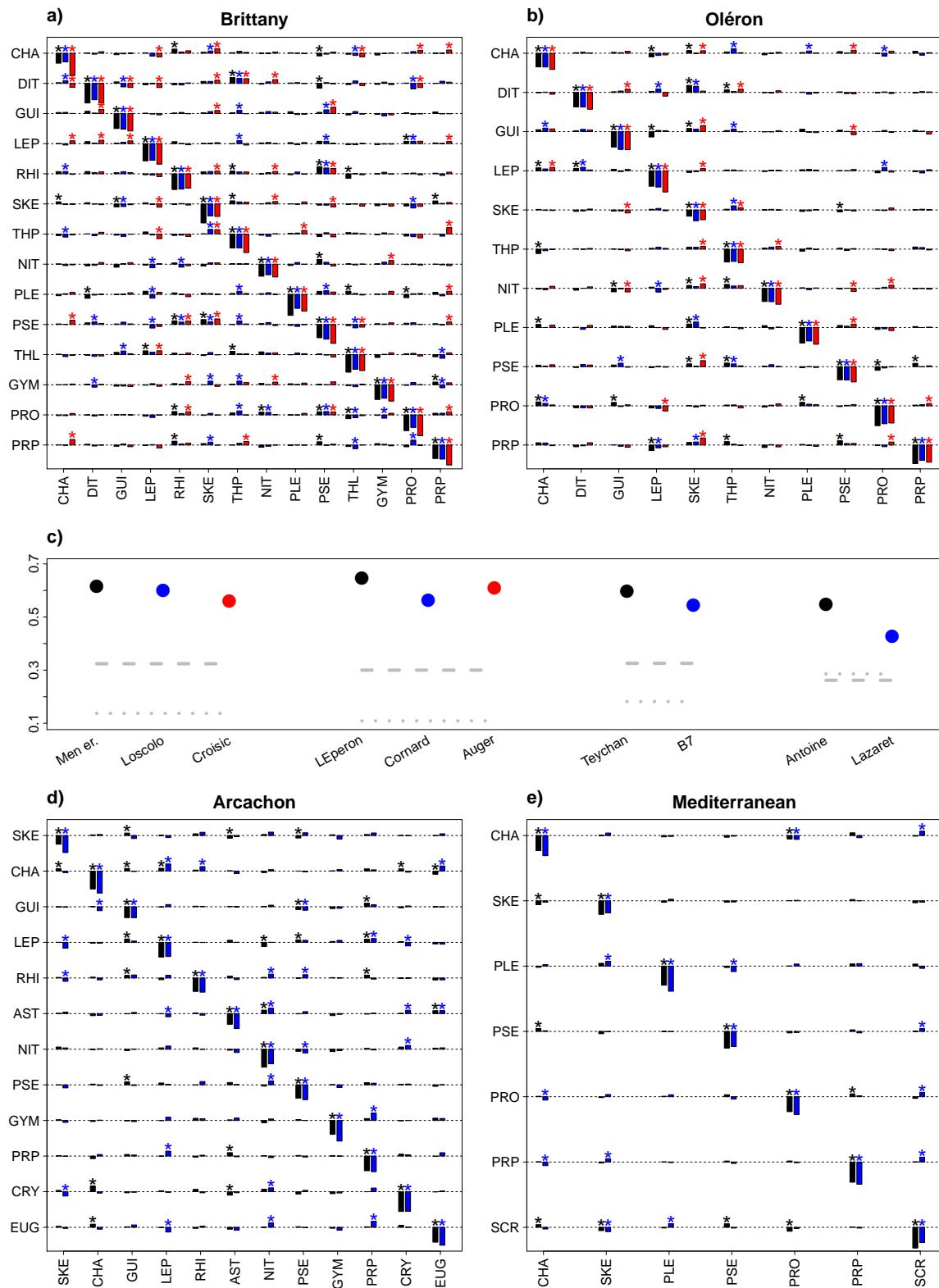


Figure S8: Interaction matrices estimated in 10 sites along the French coastline. Four regions are distinguished: Brittany (a), Oléron (b), Arcachon (d) and the Mediterranean Sea (e). There is no constraint on the structure (modularity) of the interaction matrices. The fraction of positive interactions 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.

	signif outside	positive	ratio intra/inter	ratio in/out block	transfo sign
Men er Roue	0.09	0.57	11.06	3.03	0.04
Loscolo	0.14	0.56	8.42	2.65	0.07
Croisic	0.13	0.52	10.15	2.89	0.09
LEperon	0.13	0.59	8.78	2.75	0.04
Cornard	0.08	0.51	10.32	3.64	0.06
Auger	0.07	0.55	9.66	3.10	0.06
Antoine	0.10	0.47	11.18	5.21	0.00
Lazaret	0.18	0.37	8.67	4.30	0.00
Teychan	0.11	0.55	10.46	3.68	0.14
B7	0.11	0.50	8.29	3.59	0.14

Table S3: Descriptors of coefficients in unconstrained interaction matrices and comparison to best-fitting pennate-centric structures: ratio of coefficients significantly different from 0 outside of the pennate-centric blocks vs total number of coefficients in the unconstrained matrix, proportion of positive interactions in the unconstrained matrix, ratio of mean intragroup interaction strength and mean intergroup interaction strength in the unconstrained matrix, ratio of mean interaction strength inside the pennate-centric modules vs outside the pennate-centric modules in the unconstrained matrix and proportion of interactions changing sign between the two structures.

Thus, even if we chose to select the full interaction model, there would be no difference in our main conclusions: intragenus interactions are much stronger than intergenus interactions and positive interactions are still the rule. There is at most 18% of interactions significantly different from zero outside of the pennate and centric blocks and those interactions are on average 3.5 times lower than the interactions inside the pennate and centric blocks (Table S3).

MAR references and analysis

We present here the MAR references we used to compare the effects of intra- and intergroup interactions (Table S4, Fig. S9). We add information on the biome and taxa used in the study as they tend to be linked to the estimated parameters (Fig. S10). 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). In fact, we add a handful of predator-prey systems (in red) mainly to give a scale to the plot. 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. S10). 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 hundreds of randomly chosen interaction matrices by AIC (Ives *et al.*, 1999). 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. S9, mean interaction strengths were computed as the mean absolute value of the set of coefficients which were deemed significant at the 5% level in the **B-I** matrix (see the “Computation of intra/inter-taxon ratios” section above for details).

Code	Ref	Dimension	Type of organisms	Taxonomic level	System	T
1a	Ives <i>et al.</i> (1999), CLS	9	Zooplankton	Species and functional groups	Lake	100
1b	Ives <i>et al.</i> (1999), TLS	9	Zooplankton	Species and functional groups	Lake	100
2a	Klug <i>et al.</i> (2000)	2	Phytoplankton	Phylum	Lake	100
2b	Klug <i>et al.</i> (2000)	3	Zooplankton	Species	Lake	50
3a	Klug & Cottingham (2001)	4	Functional groups of plankton	NA	Lake	300
3b	Klug & Cottingham (2001)	5	Taxonomic groups of plankton	Phylum/division	Lake	300
4a	Ives <i>et al.</i> (2003)	4	Plankton	Zooplankton v. phytoplankton, size classes	Lake	100
4b	Ives <i>et al.</i> (2003)	4	Plankton	Zooplankton v. phytoplankton, size classes	Lake with high planktivory	100
4c	Ives <i>et al.</i> (2003)	4	Plankton	Zooplankton v. phytoplankton, size classes	Lake with low planktivory	100
5a	Hampton & Schindler (2006)	14	Plankton	Phylum (phytoplankton), genus (zooplankton)	Lake	300
5b	Hampton & Schindler (2006)	14	Plankton, growing season	Phylum (phytoplankton), genus (zooplankton)	Lake	200
6a	Hampton <i>et al.</i> (2006)	13	Plankton	Phylum (phytoplankton), genus (zooplankton)	Lake	400
6b	Hampton <i>et al.</i> (2006)	7	Simpler web, plankton	Phylum (phytoplankton), genus (zooplankton)	Lake	400
7a	Huber & Gaedke (2006)	10	Ciliates	Genus and species	Lake	300
7b	Huber & Gaedke (2006)	10	Phytoplankton	Genus and species	Lake	300
8a	Yamamura <i>et al.</i> (2006)	3	Insects	Terrestrial	50	
9a	Vik <i>et al.</i> (2008)	2	Lynx/Hare	Terrestrial	100	
10a	Lindegren <i>et al.</i> (2009)	3	Fish	Baltic Sea	30	
11a	Griffiths <i>et al.</i> (2015)	7	Phytoplankton	Coastal site	1000	
11b	Griffiths <i>et al.</i> (2015)	7	Phytoplankton	Offshore site	700	

Table S4: Studies used when comparing |intra|/|inter| ratios in Fig. 4 in main text. T is the approximate number of sampling dates in each time series.

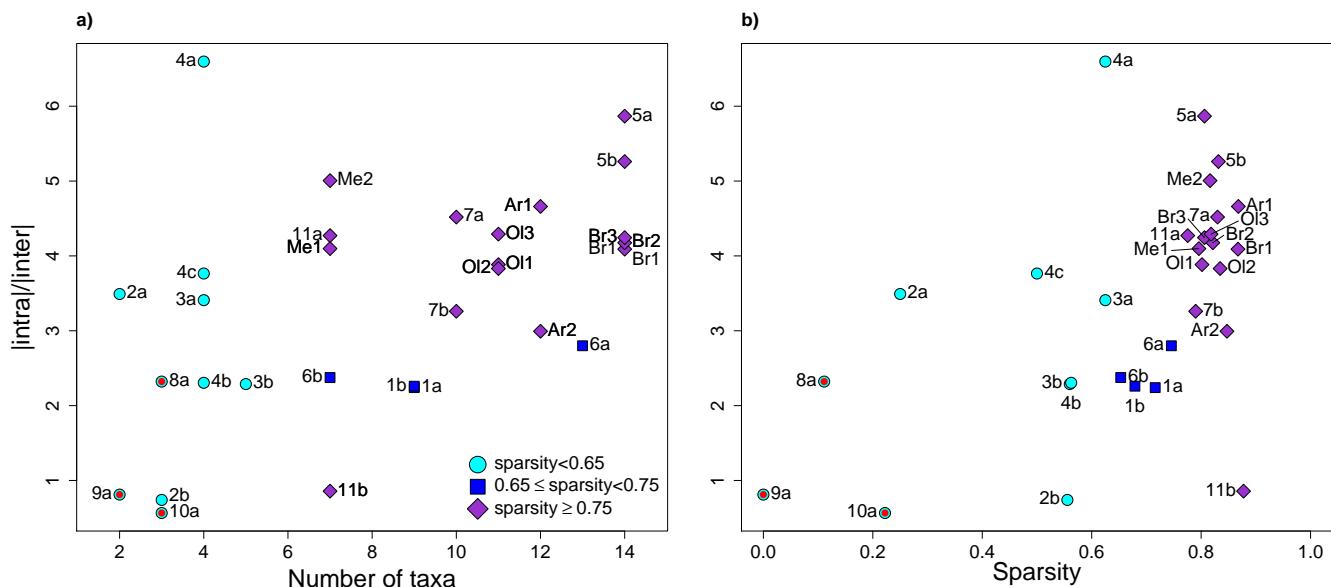


Figure S9: **Ratio of intra-to-intergroup interaction strength in MAR(1) studies.** Only significant values are taken into account and missing values in the matrix are not considered (e.g., not replaced by 0 as they are in the main text). The color and shape of each point are a function of the sparsity 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. Red dots correspond to terrestrial and/or low dimension, predator-prey systems, giving a lower bound for the intra/inter ratio. Corresponding studies are described in Table S4.

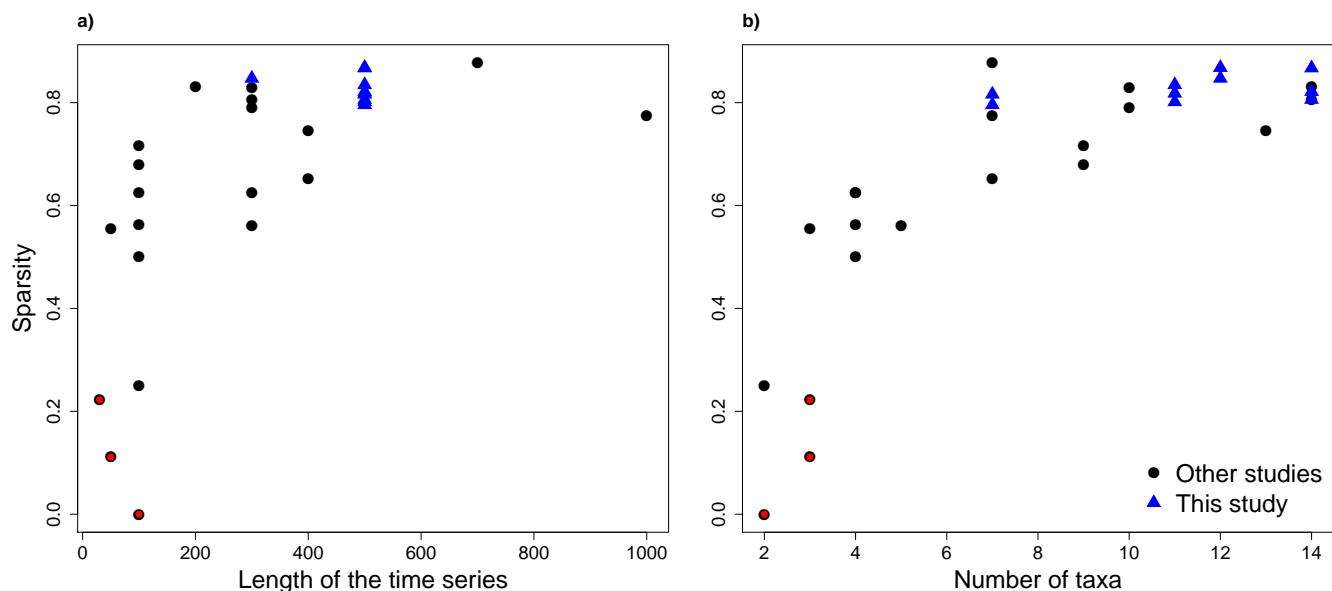


Figure S10: **Relation between interaction sparsity and study design** in studies described in Table S4. Red dots correspond to terrestrial and/or low dimension, predator-prey systems, giving a lower bound for the intra/inter ratio. Blue triangles correspond to the present study.

Connection to continuous-time models

The relation between complexity and stability in community models has been debated for decades in theoretical circles (May, 1972; Allesina & Tang, 2015). In theoretical ecology, random matrix theory has been mostly applied to continuous-time interaction models (Allesina & Tang 2015, but see Cohen & Newman 1984). Here, we intend to connect our statistical discrete-time models to the continuous-time models of stability theory. The discrete-time log-linear model writes $\mathbf{x}_{t+1} = \mathbf{B}\mathbf{x}_t$ in the main text. This model can only approximate continuous-time, possibly non-linear dynamics. There are at least two ways to relate discrete-time models to continuous-time dynamics.

The first approach is to linearize continuous-time dynamics ($d\mathbf{x} = \mathbf{A}\mathbf{x}dt$ where \mathbf{A} is the continuous-time community matrix) and integrate the system over time. In this case, the map from one time-step to the other can be written $\mathbf{x}_{t+1} = e^{\mathbf{A}}\mathbf{x}_t$. The discrete-time equivalent of the community matrix \mathbf{A} is then $\log(\mathbf{B})$ where $e^{\mathbf{A}}$ is a matrix exponential and $\log(\mathbf{B})$ the reciprocal of $e^{\mathbf{A}}$ with \mathbf{B} defined as above.

The second approach is to first integrate a continuous-time model over a time-step and then linearize the system. In this case, the equivalent matrix $\mathbf{A} = \mathbf{B} - \mathbf{I}$ because it describes the effects of densities on population growth rates (by contrast \mathbf{B} describes effects of log-densities at time t to log-densities at time $t + 1$). The second approach is illustrated in more detail in the next section of the Supporting Information.

Moreover, the measure of resilience differs in discrete- and continuous-time models. In discrete-time models, and therefore in this study, resilience is measured as the maximum modulus of the eigenvalues of the community matrix ($\max(|\lambda_B|)$), through the dominant eigenvalue of \mathbf{B} . In continuous-time models, resilience is linked to the maximum real part of the eigenvalues ($\max(\text{Re}(\lambda_A))$), *i.e.*, the real part of the leading eigenvalue of \mathbf{A} . There is therefore a link to be made between these metrics. We present in Fig. S11 the relationship between resilience metrics $\max(|\lambda_B|)$ and $\max(\text{Re}(\lambda_A))$ to make sure that our results in discrete-time are consistent with continuous-time theory.

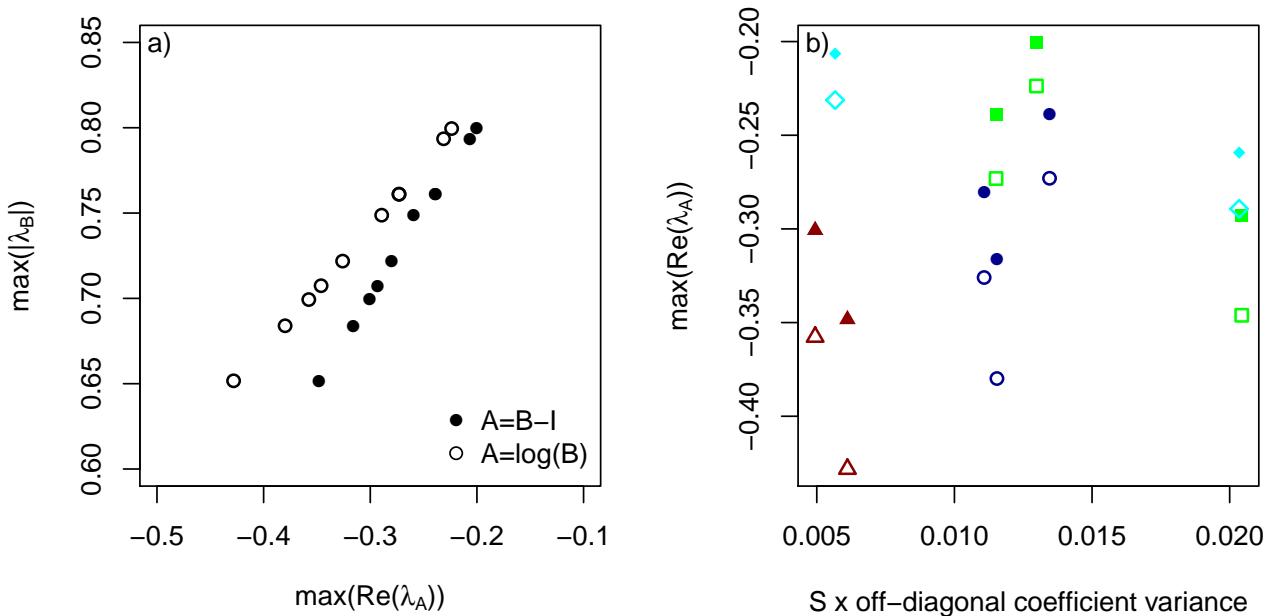


Figure S11: Relationship between discrete-time stability metrics and their continuous-time equivalents in (a); relationship between $\max(\text{Re}(\lambda_A))$ and an index of complexity, that is the variance of the off-diagonal coefficients weighted by the number of species in each community in (b).

We see in Fig. S11 that:

- leading eigenvalues of \mathbf{A} are similar for $\mathbf{A} = \mathbf{B} - \mathbf{I}$ and $\mathbf{A} = \log(\mathbf{B})$ (the difference in real parts is around 0.04 for values between -0.45 and -0.2). Hence, $\mathbf{B} - \mathbf{I}$ is a simpler approximation of \mathbf{A} (Fig S11 a),
- the modulus of the dominant eigenvalue of \mathbf{B} is strongly correlated to the real part of leading eigenvalue of $\mathbf{A} = \mathbf{B} - \mathbf{I}$ and $\mathbf{A} = \log(\mathbf{B})$ (> 0.99 in both cases), which means that our results are compatible with continuous-time theory (Fig S11 a)

- there is no apparent relationship between the continuous-time equivalent metric for stability/resilience and complexity (the latter being measured as the number of species times the variance of the intertaxa interaction coefficients) (Fig S11 b).

The link between stability and complexity that we study here is therefore of a similar nature to that studied in continuous-time stability theory, and the relation between stability and complexity was found to be non-existent using both discrete-time metrics and equivalent metrics mimicking continuous-time. The absence of relationship between complexity and stability *sensu* resilience therefore appears to be genuine.

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 $S \geq 3$, 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 α_{ij} is the effect of species j on species i . Here, we show how the interaction strengths α_{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

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

The same reasoning can actually be applied with S 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

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

However, in the main text, we use the ratio $\kappa = \frac{|(J - I)_{ii}|}{|(J - I)_{ij}|}$, with average quantities in the numerator and the denominator. To build a relationship between k and κ , we denote $b_{ij} = (J - I)_{ij}$, $N_T = \sum_{i=1}^S N_i$. In this simple diffuse competition case, all b_{ij} have the same negative sign. Therefore,

$$\begin{aligned} \kappa &= \frac{\overline{b}_{ii}}{\overline{b}_{ij}} \\ \text{where } \overline{b}_{ii} &= \frac{1}{n} \sum_{i=1}^S b_{ii} \\ \text{and } \overline{b}_{ij} &= \frac{1}{n(n-1)} \sum_{i=1}^S \sum_{j=1, j \neq i}^S b_{ij}. \end{aligned} \quad (\text{S21})$$

Using eq. S20, we obtain

$$\begin{aligned}
\overline{b_{ij}} &= \frac{1}{kS(S-1)} \sum_{i=1}^S \sum_{j=1, j \neq i}^S b_{ii} \frac{N_j}{N_i} \\
&= \frac{1}{kS(S-1)} \sum_{i=1}^S \frac{b_{ii}}{N_i} \left(\left(\sum_{j=1}^S N_j \right) - N_i \right) \\
&= \frac{1}{kS(S-1)} \sum_{i=1}^S \frac{b_{ii}}{N_i} (N_T - N_i) \\
&= \frac{1}{k(S-1)} \left(\frac{1}{S} \sum_{i=1}^S b_{ii} \frac{N_T}{N_i} - \frac{1}{S} \sum_{i=1}^S b_{ii} \right) \\
&= \frac{1}{k(S-1)} \left(\frac{1}{S} \sum_{i=1}^S b_{ii} \frac{N_T}{N_i} - \overline{b_{ii}} \right).
\end{aligned} \tag{S22}$$

Coupling eq. S21 and S22, this leads to

$$\frac{\overline{b_{ij}}}{\overline{b_{ii}}} = \frac{1}{\kappa} = \frac{1}{k(S-1)} \left(\frac{1}{S} \sum_{i=1}^S \frac{b_{ii}}{\overline{b_{ii}}} \frac{N_T}{N_i} - 1 \right). \tag{S23}$$

Thus, even in the simple case of diffuse competition, the ratio intra/inter might change to some degree between MAR(1) and BH competition, as a function of relative abundances. For even communities, the mapping between Lotka-Volterra and MAR(1) interaction strength ratios is good; the combined effect of variance in self-regulation strength and realistic levels of community unevenness may change this. Also, diffuse competition is a simplification: mapping such interaction strength ratios in the general many-species case is a non-trivial endeavour, and further deviations between the two frameworks could be expected (see Certain *et al.*, 2018, for the two-species case).

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