

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

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## Abstract

1. The persistence of phytoplanktonic diversity in spite of competition for basic resources has long been a source of wonder and inspiration to ecologists. To sort out, among the many coexistence mechanisms suggested by theory and experiments, which ones actually maintain diversity in natural ecosystems, long-term field studies are paramount.
2. We analysed a large dataset of phytoplankton abundance time series using dynamic, 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 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 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. The time series are  
27 modelled using multivariate autoregressive (MAR) models, allowing for 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 counts 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).

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  $\mu\text{m}$  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 S3.

58 For each region, the MAR(1) analysis focused on the most abundant and most frequently observed  
 59 genera to avoid most of the gaps in the time series. Time series are plotted in Fig. S2. When gaps  
 60 did not exceed a month, missing values were linearly interpolated; remaining missing values were  
 61 replaced by a random number between 0 and half of the lowest observed abundance ([Hampton  
 62 \*et al.\*, 2006](#)). We tested extensively this and other methods to deal with missing data in a previous  
 63 publication on a subset of this dataset ([Barraquand \*et al.\*, 2018](#)). All time series were scaled and  
 64 centered before MAR analyses.

## 65 **MAR(1) model**

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

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

71 where  $\mathbf{n}_t$  is the  $1 \times S$  vector of log-abundance of phytoplankton taxa,  $\mathbf{B}$  is the  $S \times S$  community  
 72 (interaction) matrix,  $\mathbf{C}$  is the  $S \times V$  environment matrix describing the effects of  $V$  variables (stacked  
 73 in vector  $\mathbf{u}_{t+1}$ ) on growth rates, with  $V = 2$  in our case (temperature and salinity). The noise  $\mathbf{e}_t$   
 74 is a  $1 \times S$  noise vector which covers both process and observation error, following a multivariate  
 75 normal distribution with a variance-covariance matrix  $\mathbf{Q}$ .  $\mathbf{Q}$  is diagonal and we have previously  
 76 showed that this parsimonious choice did not affect qualitatively the results ([Barraquand \*et al.\*,  
 77 2018](#)). We used the MARSS package ([Holmes \*et al.\*, 2014](#)) v3.9, in R v3.3.2 ([Venables & Smith,](#)

78 2013), to estimate parameters with a maximum likelihood procedure.

79 Our previous analysis of the Arcachon region, for which more covariables were available (Bar-  
80 raquand *et al.*, 2018), revealed that hydrodynamics and hydrology had more influence on phyto-  
81 plankton dynamics than nutrients on the two-week timescale. Because temperature and salinity sum  
82 up seasonal changes in light as well as hydrology (salinity is inversely related to freshwater inflow),  
83 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  
86 data mimicking the study design, which confirmed the ability of MAR(1) models to infer biotic  
87 interactions and abiotic forcings. Fitting a more sophisticated model (threshold autoregressive  
88 model) did not reveal extra non-linearities or a storage effect in the Arcachon subset of the data  
89 (Barraquand *et al.*, 2018). Other aspects of the MAR(1) modelling are likewise quite robust: using  
90 two abiotic variables (temperature and salinity) in this study rather than the full set used in  
91 Barraquand *et al.* (2018) led to almost identical covariate effects and interaction estimates for the  
92 Arcachon study sites. Even if some departures from the true data-generating model may not always  
93 be detectable through MAR(1) diagnostics (e.g., residuals), the analysis of nonlinear simulations  
94 has showed that MAR(1) models are in general robust to nonlinearities if the inference focuses on  
95 interaction sign and order of magnitude of model coefficients (Certain *et al.*, 2018), which is how  
96 these models are used here. For ease of interpretation of MAR(1) interaction coefficients, we also  
97 prove the correspondence between the magnitude of intra/inter interaction strength in a MAR(1)  
98 model and a multispecies Beverton-Holt model, i.e., a discrete-time Lotka-Volterra model (Cushing  
99 *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  $7 \times 7$

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

## 122 **Analysis of interaction strengths**

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



133 of interaction sign. In contrast, mean and variance of the off-diagonal coefficients, which can affect  
134 the stability of a community (Allesina & Tang, 2015), are computed on raw values of the coefficients.

135 In addition to these network-level metrics, we also computed the average vulnerability (average  
136 effect of other taxa on a focal taxon, eq. S5) and impact (average effect of a focal taxon on other  
137 taxa, eq. S6) on both raw and absolute values of the coefficients. Vulnerability and impact can be  
138 related to in-strength and out-strength in the meta-analysis of Kinlock (2019). We then compared  
139 these to the regulation a focal species exerted on itself. Raw values indicate the average effect that  
140 can be expected on the growth rate of a taxon from the rest of the community (i.e., is the effect of  
141 others mostly positive or negative?), while absolute effects characterise the strength of all types of  
142 interactions on a taxon (i.e., is a taxon strongly affected by the others?).

143 Finally, we compared the observed ratio between mean self-regulation (intrataxon interaction  
144 strength) and mean intertaxa interaction strength to other published studies based on a MAR(1)  
145 model. A list of references is given in Table S3. Authors usually reported only coefficients that were  
146 significant at the 95% significance threshold, thus ignoring potentially many weak effects, which we  
147 had to set to 0. There are therefore two ways of computing the mean intertaxa interactions, i.e.,  
148 taking the mean value of all coefficients outside of the matrix diagonal, including zeroes (which  
149 decreases the estimated mean intertaxa interaction strength, Fig. 4), or taking the mean value of  
150 statistically significant intertaxa coefficients only (which increases the estimated mean intertaxa  
151 interaction strength, Fig. S8). We considered both.

## 152 Results

### 153 Interaction estimates

154 Using MAR(1) autoregressive models, we produced interaction matrices (Ives *et al.*, 2003; Hampton  
155 *et al.*, 2013) – i.e., Jacobian community matrices on the logarithmic abundance scale (Ives *et al.*,  
156 2003). Best-fitting models corresponded to a phylogenetically-structured interaction scenario, where  
157 interactions only occurred between closely related genera (Fig S3). This led to sparse, modular  
158 matrices that have two main features. First, we observed a strong self-regulation for all sites (Fig. 1,

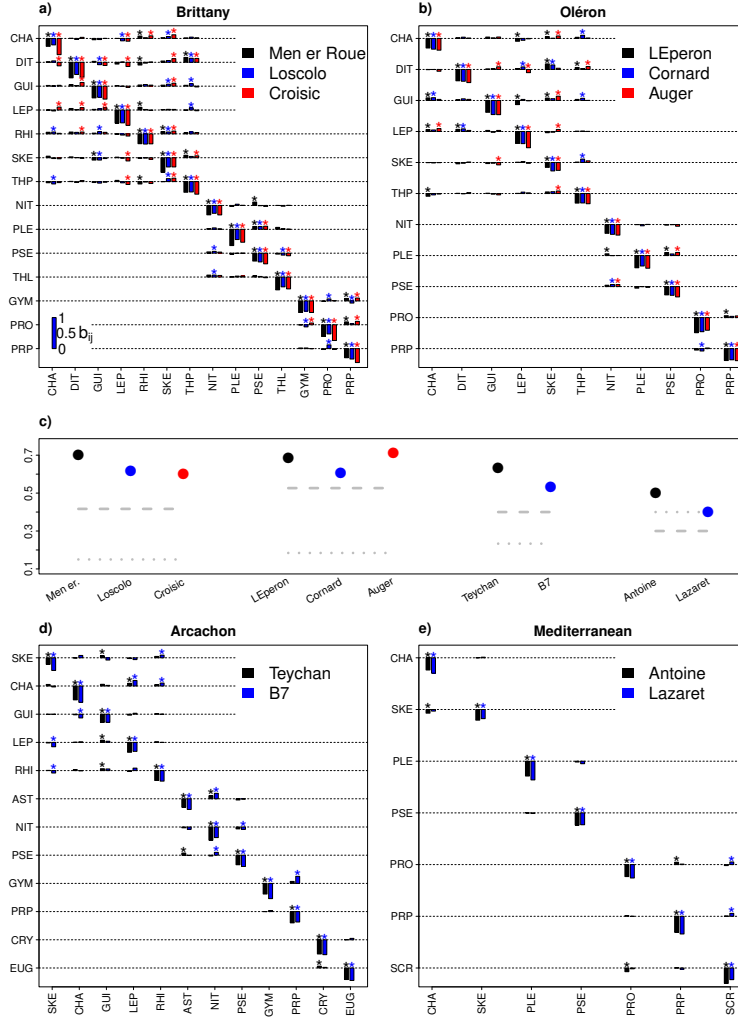


Figure 1: **Interaction matrices estimated in 10 sites along the French coastline.** Four regions are distinguished: Brittany (a), Oléron (b), Arcachon (d) and the Mediterranean Sea (e). Only interactions within a clade (pennate and centric diatoms, dinoflagellates, other planktonic taxa) are allowed,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

diagonal elements of all matrices), a feature that we had previously highlighted in a more detailed analysis on one of the considered study regions (Barraquand *et al.*, 2018). The ratio of mean intragenus to intergenus interaction coefficients varied between 6 and 10, not counting coefficients set to 0 in the estimation process. When we included the zeroes in the interaction matrix in the computation of the intra/inter mean interaction strength, the ratio rised to 21-43. Therefore, intragenus interactions were on average one order of magnitude stronger than intergenus interactions.

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

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

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

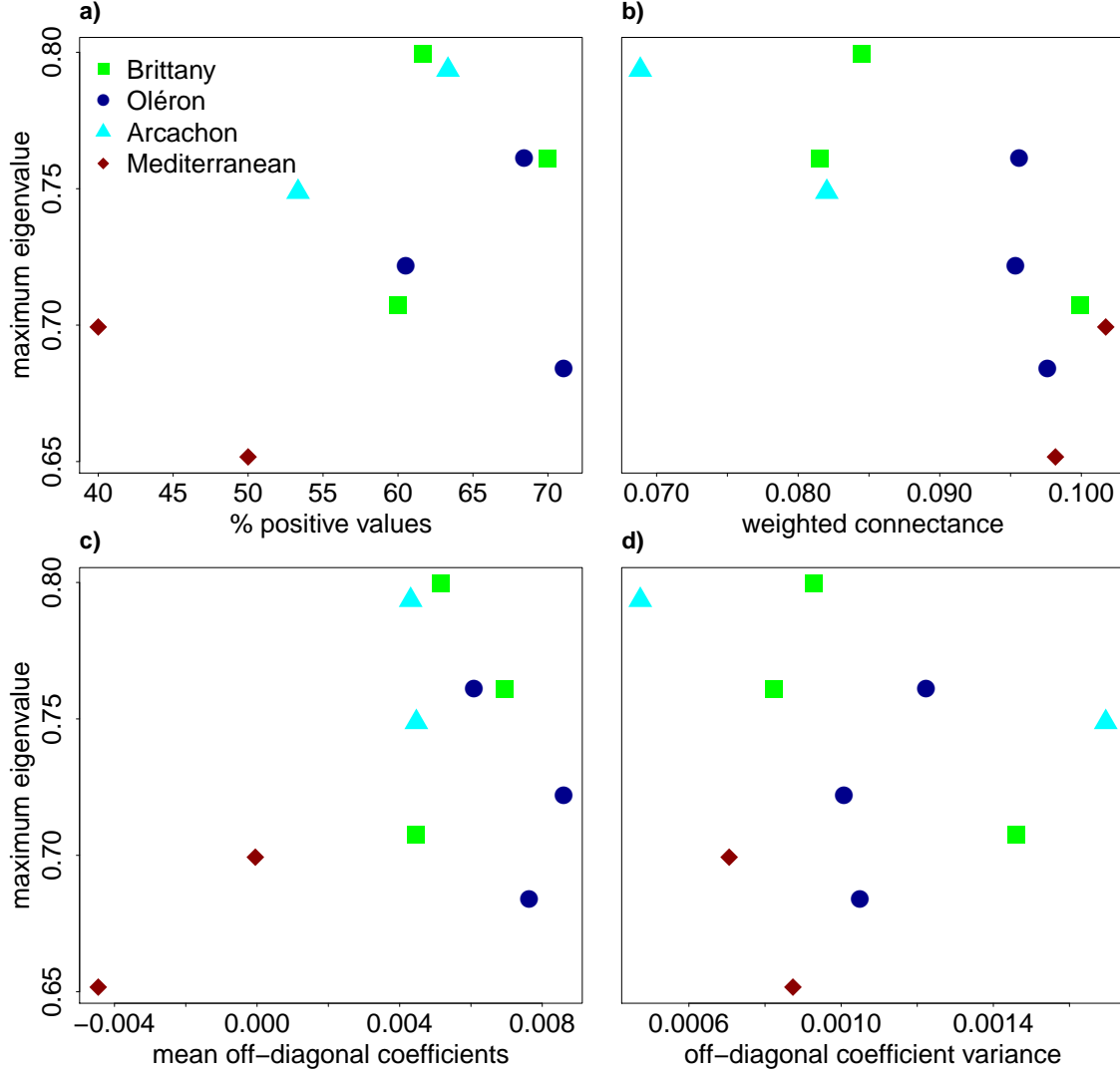


Figure 2: **Relation between stability and complexity of the interaction networks.** The maximum modulus of the eigenvalues of the interaction matrix  $\mathbf{B}$  indicates stability *sensu* resilience. Each color or shape corresponds to a given region. The formula for weighted connectance is given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

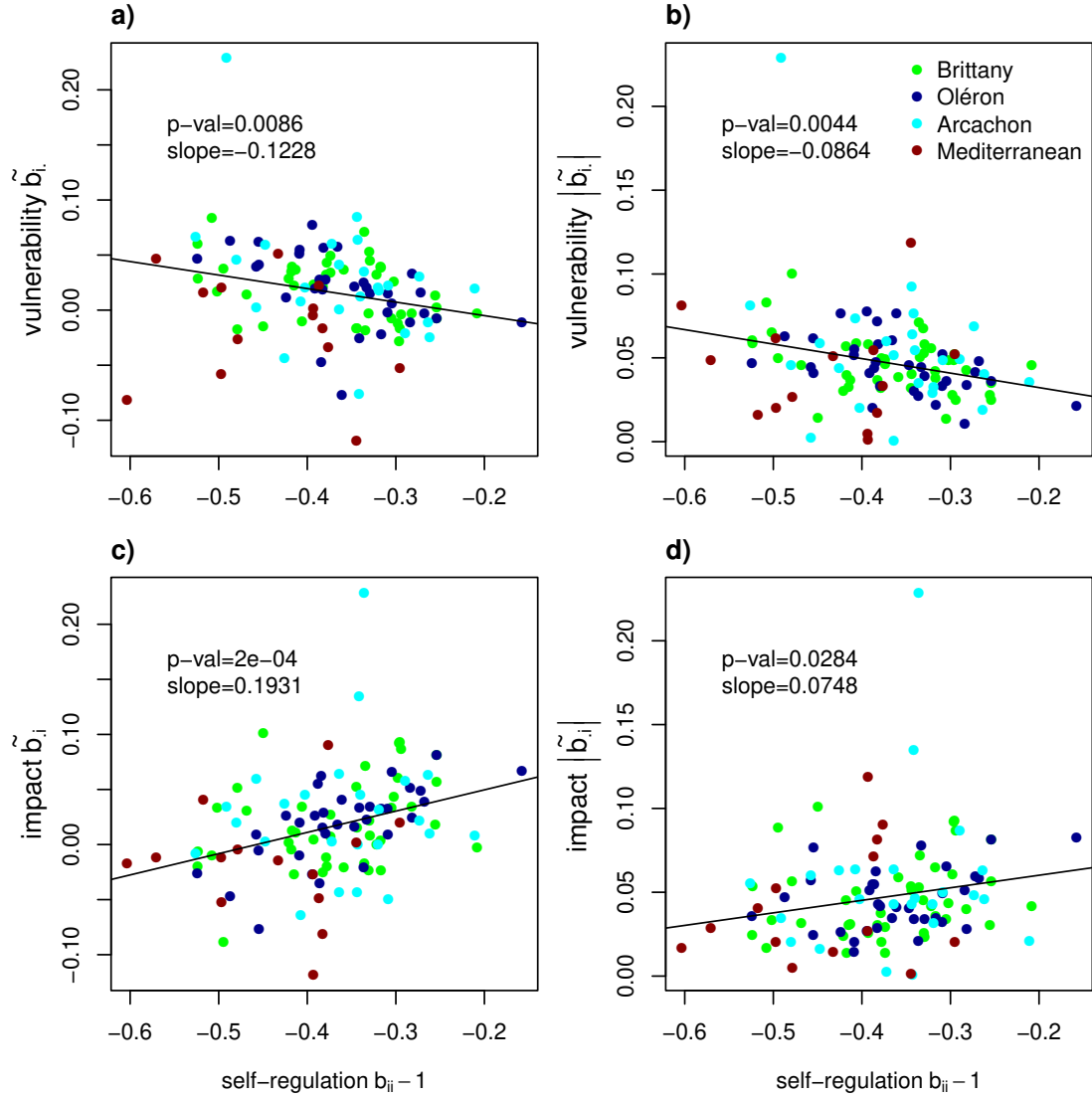


Figure 3: **Relation between vulnerability/impact and self-regulation.** Average vulnerability (effects of others on the focal taxon growth rate, a-b) and impact (effects of the focal taxon on others' growth rates, c-d), as well as self-regulation, are computed for untransformed (a-c) or absolute (b-d)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

188 Given that a direct complexity-stability (*sensu* resilience) link was not obvious, we investigated  
 189 whether the matrix coefficients had some particular structure that could help theoretical ecology to

190 make better null models of joint community dynamics and interactions (James *et al.*, 2015). We  
 191 defined two scores, vulnerability (summed effect of others on the focal taxon growth rate, eq. S5)  
 192 and impact (summed effect of the focal taxon onto other taxa’s growth rates, eq. S6). Relations  
 193 between inter- and intra-genus interactions emerged (Fig. 3): genera that were more self-regulating  
 194 also had also a higher vulnerability score and a lower impact score. Those two influences are likely  
 195 to trade-off: a high degree of self-regulation somehow buffers the effect of outside influences on  
 196 population dynamics. Taxa that were less self-regulating were also more likely to have a stronger  
 197 effect onto other taxa. As these genera tended to be more abundant (Fig S7), this could be mediated  
 198 by the average density of a genus. It is important to note, however, that these trends are weak and  
 199 there is therefore a considerable amount of randomness dominating the interaction matrix: many  
 200 scenarios of self-regulation vs limitation by others are therefore possible.

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

## 203 Literature comparison

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

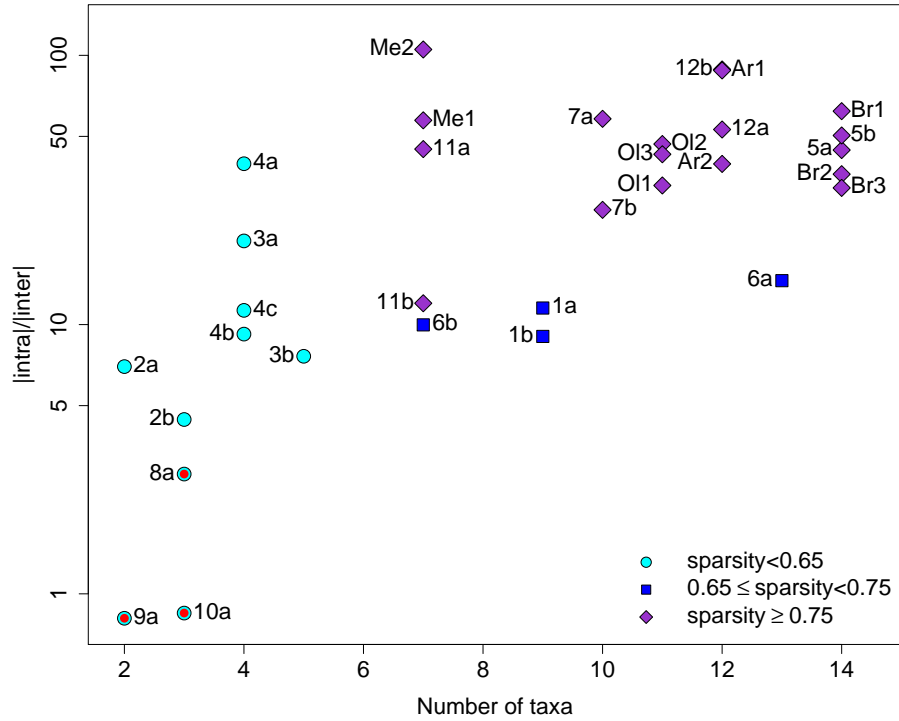


Figure 4: **Ratio of intra- to inter-group interaction strength in Multivariate AutoRegressive (MAR) models.** The reference for each study is given in Table S3. Codes beginning with letters correspond to the present study (Ar: Arcachon; Ol: Oléron; Br: Brittany; Me: Mediterranean Sea). The symbol color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

## Discussion

### Strong self-regulation and facilitation

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

The rather high intra/intertaxa interaction strength ratio (Levine & HilleRisLambers, 2009)

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

240 Another main finding of our study is the large frequency of positive interactions, with 30% truly  
 241 mutualistic (+/+) interactions and between 40 and 70% facilitative effects. Although a seasonal  
 242 environment can generate some positive covariation between taxa, those effects have already been  
 243 filtered out by the inclusion of our 2 abiotic covariates (Fig. S4). The facilitative effects shown  
 244 here are therefore residual effects, once abiotic trends are accounted for. Between 40 and 70%  
 245 facilitation can be compared to the meta-analysis by [Adler \*et al.\* \(2018b\)](#) who also found facilitative  
 246 interactions, but less than here ( $\approx 30\%$ ). However, [Adler \*et al.\* \(2018b\)](#)'s review contains many  
 247 experiments while the plant literature is replete with field examples of facilitation ([Brooker \*et al.\*,  
 248 2008](#); [McIntire & Fajardo, 2014](#)), so that plant facilitation could be higher in the field. At the



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; Barraquand *et al.*, 2015; 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.*, 2001; Modéran *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.

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

There was no relation between the complexity of the communities (measured as either the weighted connectance or the interaction coefficient variance of the interaction matrices) and their stability

(measured by the dominant eigenvalue of the interaction matrix, which quantifies the return time to a point equilibrium, i.e., resilience). This result is conditional upon our model being a good approximate description of the system (i.e., no multiyear limit cycles or chaotic attractors as the mapping between eigenvalues and actual stability is distorted in that case, [Certain \*et al.\*, 2018](#)). However, we already showed on a subset of this data that a fixed point in a MAR(1) model, perturbed by seasonality and abiotic variables, is an accurate description of the system ([Barraquand \*et al.\*, 2018](#)). Therefore, we are confident that the absence of complexity-resilience relationship found here is not an artefact of a wrong model. This absence of direct link between complexity and stability could be an actual feature of empirical systems, as shown previously by [Jacquet \*et al.\* \(2016\)](#) using a different technique. This result seems to contradict theory based on random matrices, especially for competitive and/or mutualistic networks ([Allesina & Tang, 2012](#)). However, this could also be linked to the limited size of our networks, as random matrix theory relies on asymptotics ([Allesina & Tang, 2015](#)). We should also mention that our interaction matrices (discrete-time model) are not strictly analogous to the ones used in classical random matrix theory (continuous-time model). Thus the jury is still out regarding the absence of complexity-resilience relation, though it 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 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 relative rarity and self-regulation could also 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 least common 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 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 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 less common 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.

## Ghosts of competition past and present

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

331 facilitative effects might be likewise destabilizing, [Coyte et al., 2015](#)). The likely predator effects that  
 332 we highlighted above could be comprised within such niche differentiation *sensu largo*: specialized  
 333 predators can make strong conspecific density-dependence emerge ([Bagchi et al., 2014](#); [Comita et al.,](#)  
 334 [2014](#)), while switching generalists can also promote diversity ([Vallina et al., 2014](#)). Both predators  
 335 and resources have often symmetrical effects and can therefore contribute almost equally to such  
 336 past niche differentiation ([Chesson, 2018](#)).

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

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

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

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