

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

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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. Here, we analyse a large dataset of phytoplankton abundance time series, counted every two weeks over 20 years, at 10 sites along the French coastline. We estimate biotic interactions using dynamic, multispecies autoregressive models. We show that a strong self-regulation, with competition strength within a genus an order of magnitude higher than between genera, was present in all phytoplanktonic interaction networks. Furthermore, the fraction of positive net effects between phytoplanktonic taxa was above 50% of non-zero interactions on average and at least 40% in all sites. Both strong self-regulation and widespread net facilitation should therefore be key features of coexistence mechanisms intending to explain phytoplankton diversity maintenance.

phytoplankton | coexistence | time series | niche theory | networks

How species or close genera can coexist together in spite of competition is one of the main puzzles of community ecology, especially for primary producers that seemingly share the same basic resources (1). Many theoretical studies of competition models have shown that competitive exclusion is likely in those circumstances (2, 3), unless mechanisms involving spatial or temporal variation are at play (4–7). Neutral theory, that assumes a non-equilibrium coexistence maintained by dispersal and equal competitive abilities for all species (8, 10), though there are exceptions, see (9, 10) has been proposed as a solution to explain highly diverse communities (8, 11).

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

Moreover, even within a single trophic level, competition may not be the rule: the meta-analysis by Adler et al. (13) reported a large number of facilitative interactions (30%) and several reviews (15, 16) have highlighted that facilitation may be much more widespread than ecologists usually tend to think. Although some theoretical studies suggest that facilitative interactions can be destabilizing (*sensu* resilience) and therefore undermine coexistence in Lotka-Volterra models (17), multiple other modelling (18) and empirical (15, 19) studies have suggested that facilitative interactions can to a large degree benefit coexistence, especially when multiple interaction types are considered simultaneously (20, 21).

Here, we study a large multi-species dataset consisting of several multivariate long-term time series of phytoplankton dynamics along the French coastline, which we then analyse using multivariate autoregressive (MAR) time series models, allowing for interactions between genera. Although many ecological studies focus on interactions between species, competition has been shown experimentally to occur between different genera of phytoplankton (22, 23). The genus level is also a rather fine taxonomic scale for phytoplankton interaction studies, as most studies are restricted to interaction between different classes or even phyla (24–26). Studying interactions between different genera of phytoplankton therefore both makes empirical sense in light of competition experiments and allows to estimate better-resolved networks. We focus here on genera that belong mostly to diatoms and dinoflagellates. To put our results into a more general context, we then compare our interaction strength estimates to previously published interaction networks produced under the same statistical framework, both in plankton and other empirical systems.

Results

Interaction estimates. Using MAR(1) autoregressive models, we have produced interaction matrices (24, 27) – i.e., Jacobian community matrices on the logarithmic scale (24). Best-fitting models corresponded to a phylogenetically-structured interaction scenario, where interaction only occurred between closely related genera (SI Appendix, Fig. S3). This led to sparse, modular matrices that have two main features. First, we observe a strong self-regulation for all sites (Fig. 1, diagonal elements of

Significance Statement

The continued coexistence of multiple species of phytoplankton in spite of likely competition is a long-standing puzzle of ecology, the so-called paradox of the plankton. Based on the long-time monitoring of 10 coastal study sites every two weeks over 20 years, we explore how biotic interactions shape the diversity of phytoplanktonic communities. We reveal that niche differentiation rather than neutral processes promotes coexistence. Moreover, although competition is often thought to dominate in phytoplanktonic systems, we show that a majority of interactions are in fact facilitative. We suggest that both strong niche differentiation and facilitation hold the key to the phytoplankton coexistence paradox.

C.P. and F.B. contributed equally to the project design. C.P. wrote the code for the analyses. F.B. and C.P. interpreted the results and wrote the manuscript.

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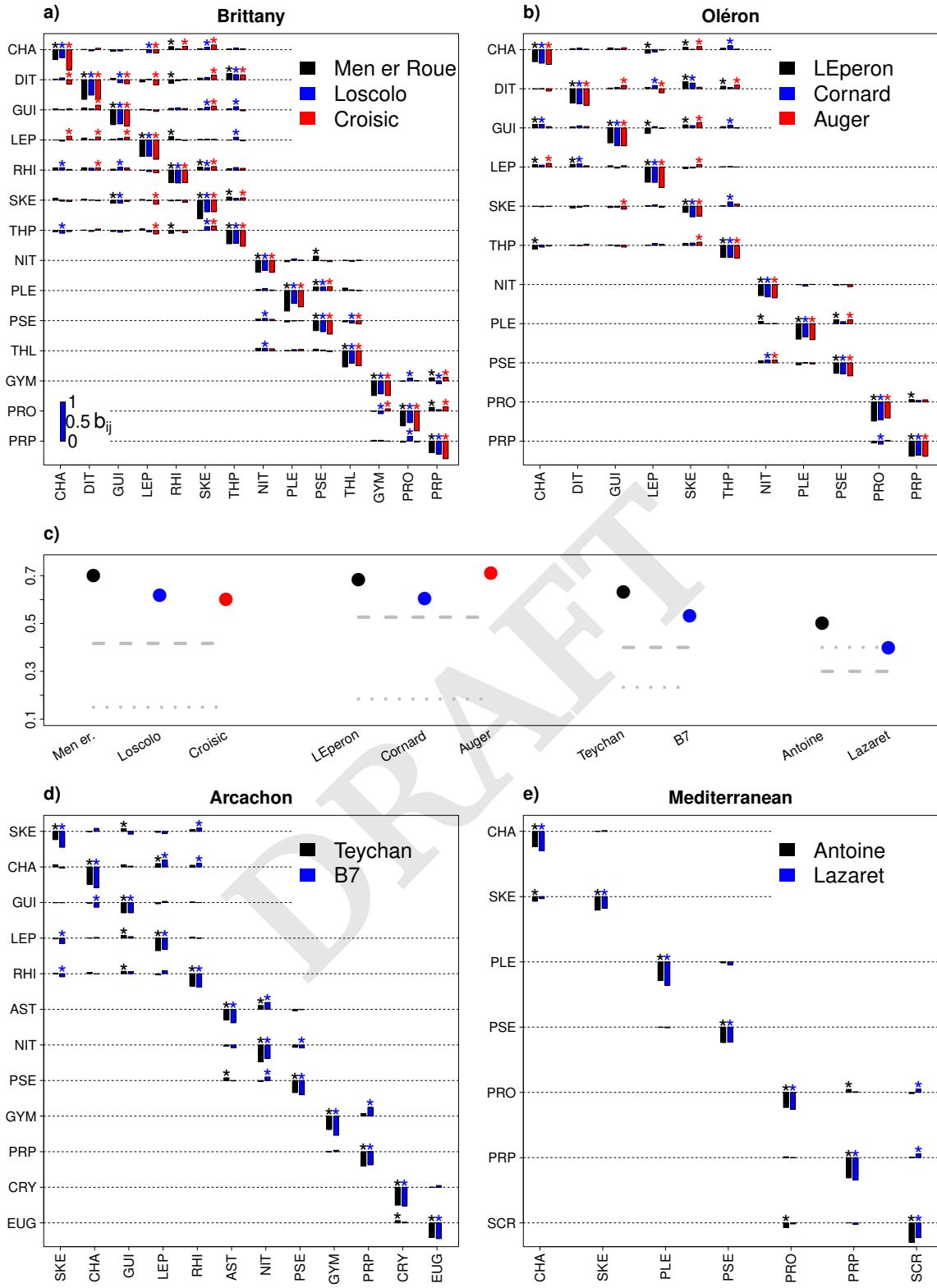


Fig. 1. Interaction matrices estimated in 10 sites along the French coastline. Four regions are distinguished: Brittany (a), Oléron (b), Arcachon (d) and the Mediterranean Sea (e). Only interactions between clades (pennate and centric diatoms, dinoflagellates, other planktonic taxa) are allowed, as this is the best fitting interaction scenario (SI Appendix, Fig. S3). Taxon j (in columns) has an effect illustrated by the bar height on taxon i 's growth rate (in rows). 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 SI Appendix, Table S2. The fraction of positive interactions in each matrix is given by points in c) while the dashed (resp., dotted) line represents the ratio of interactions remaining positive (resp., negative) for all sites of a given region.

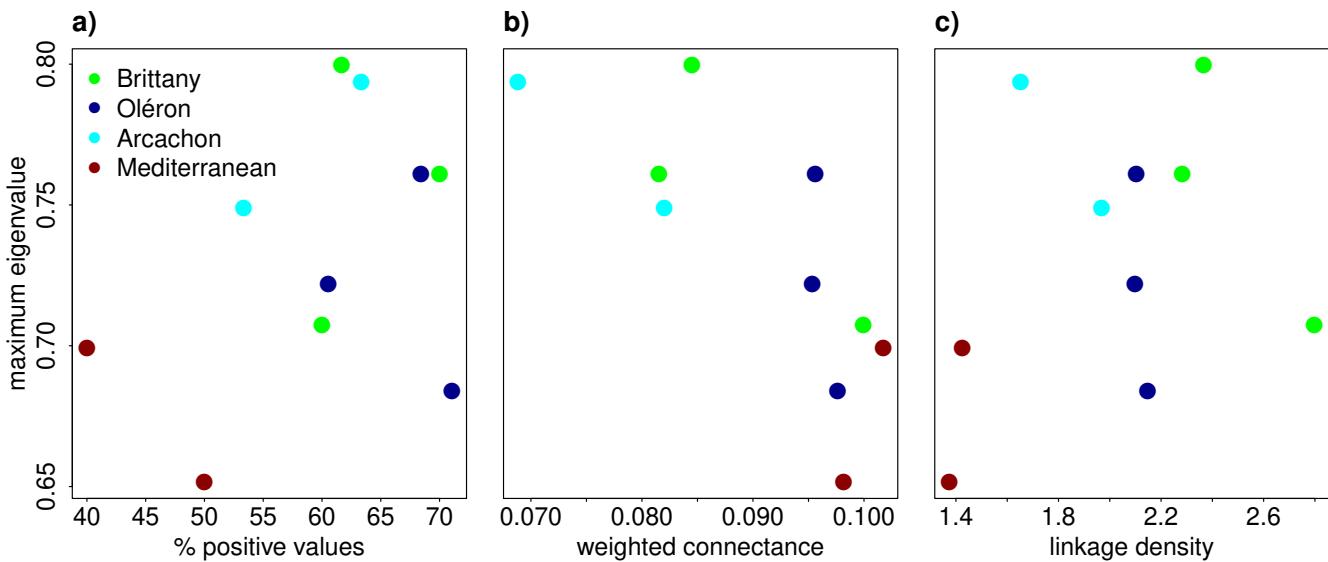


Fig. 2. Relation between stability and complexity of the interaction networks. The maximum modulus of the interaction matrix \mathbf{B} eigenvalues indicates stability *sensu* resilience. Each point color corresponds to a given region. Metrics formula for weighted connectance and linkage density are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

all matrices), a feature that we have previously highlighted in a more detailed analysis on one of the considered study regions (28). The ratio of mean intragenus to intergenus interaction coefficients varies between 6 and 10, not counting coefficients set to 0 in the estimation process. If we include the zeroes in the interaction matrix in the computation of the intra/inter mean interaction strength, the ratio rises to 21-43. Therefore, intragenus interactions are on average much stronger than intergenus interactions, approximately 10 to 20 times stronger.

Second, although the percentage of facilitative interactions seemed to vary 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 can examine whether locally positive interactions remain positive in a regional context: the percentage of consistently positive interactions at the regional level varies 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 have found that the percentage of true mutualism (+/+) is substantial: averaged over all sites, 32% of all interactions are (+/+) while only 12% of them are (-/-), see also SI Appendix, Fig. S5. The sign correspondence is not always maintained between French regions: the only interaction that is non-zero in the 10 sites (CHA/SKE) is mutualistic in Men er Roue only (Brittany) and mixed (+/-) at all other sites. Within the same region, however, interactions measured at different sites tend to keep the same sign. In the 3 sites of Oléron, for instance, there were 4 interactions which remained positive on both sides (CHA/GUI, DIT/GUI, LEP/THP, SKE/THP), 3 of them being also mutualistic in some of the Brittany sites. This contradicts previous observations that mutualistic interactions tend to be more context-dependent than competitive interactions (29).

Interaction network analysis. The stability (*sensu* resilience, 30) of all interaction matrices was not strongly affected by the percentage of positive interactions or their connectivity properties (Fig. 2). The maximum modulus of the interaction matrix eigenvalues remained between 0.65 and 0.80. There was also a slight increase in stability with weighted connectance, with a drop in eigenvalue modulus for weighted connectances between 0.09 and 0.1.

Given that a direct complexity-stability 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 (31). We defined two scores, vulnerability (summed effect of others on the focal species growth rate, SI Appendix, Eq. S5) and impact (summed effect of the focal species onto other species growth rates, SI Appendix, Eq. S6). Relations between inter- and intra-genus interactions emerged (Fig. 3): genera that were more self-regulating also had 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 outside influences. Taxa that were less self-regulating were also more likely to have a broad range of effects onto other taxa. As these genera tended to be more abundant (SI Appendix, Fig. S7), they were more likely to affect other genera. 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 these trade-offs, some of which promote some stability (*sensu* invariability, 32), we found no remarkable patterns of covariation between matrix elements (other than a mean-variance scaling of interaction coefficients, SI Appendix Fig. S6).

Literature comparison. Finally, we sought to put these results in a broader context by compiling the intra vs inter group estimates of previous MAR(1) studies of long-term observational count data (listed in SI Appendix Table S3). We found that

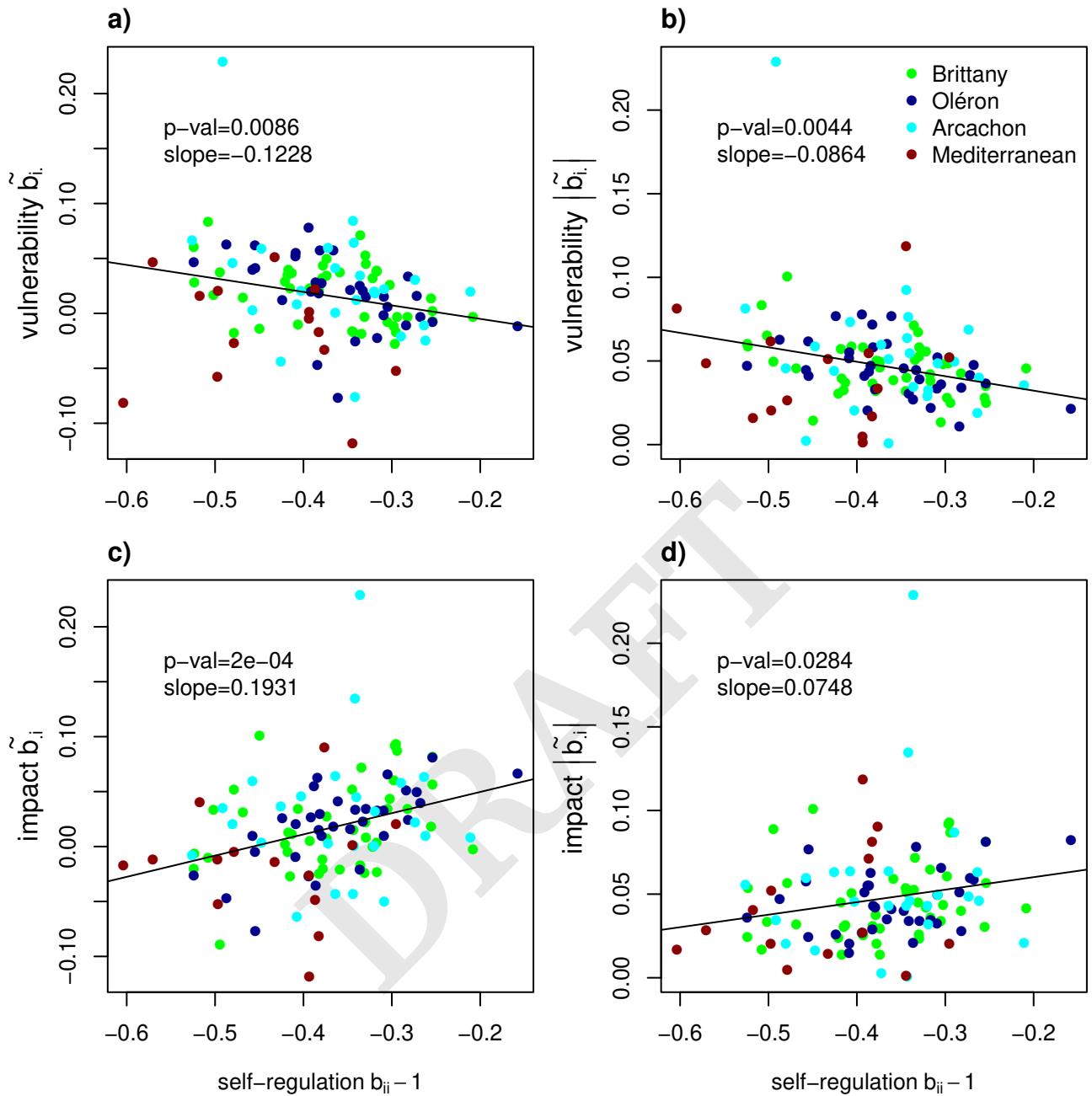


Fig. 3. Relation between vulnerability/impact and self-regulation. Average vulnerability (effects of others on the focal taxon growth rate, a-b) and impact (effects of the focal taxon on others' growth rates, c-d), as well as self-regulation, are computed for untransformed (a-c) or absolute (b-d) values of the coefficients of the interaction matrix ($\mathbf{B} - \mathbf{I}$) for the 10 study sites. Each color corresponds to a given region (SI Appendix, Fig. S1). The p-value of the Pearson correlation between vulnerability (respectively impact) and self-regulation is given in the top left of each panel and the slope of the linear regression is given by the black line across scatter plots.

the order of magnitude of intra/inter interaction strengths considered here is not particularly above those found for most planktonic systems to which MAR(1) models have been fitted, considering that our systems are relatively high-dimensional and that the higher the number of taxa, the larger the intraspecific regulation (33). 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. The conclusion from this comparison seems to be that, unlike small

communities that can be tight-knit, any diverse system of competitors and facilitators has evolved large niche differences making intragroup competition much larger in magnitude than intergroup interactions.

Discussion

Strong self-regulation and facilitation. We found very large niche differences between genera, translating into much higher intragenus than intergenus effects on growth rates (i.e., strong

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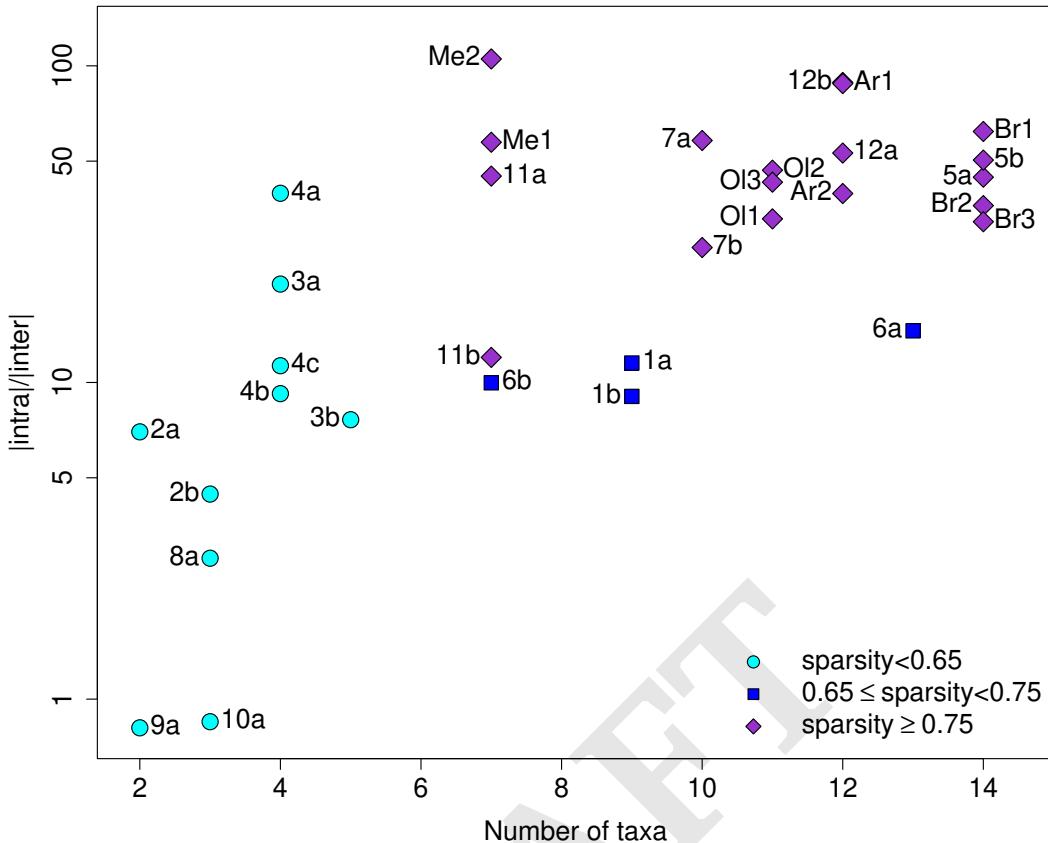


Fig. 4. Ratio of intra- to inter-group interaction strength in Multivariate AutoRegressive (MAR) models in the ecological literature as a function of the number of species they include. The name of each studies, corresponding to each code, is given in SI Appendix, Table S3. Codes beginning with letters correspond to the present study. The symbol color and shape correspond to the sparsity of the interaction matrix (e.g., the proportion of null interactions in the matrix). Intergroup interactions were set to 0 when they were not specified in the articles (in most cases, articles removed non-significant interactions at the 95% threshold).

self-regulation), together with a high degree of facilitative net interactions.

The rather high intra/intertaxon interaction strength ratio (34) that we found, from 5 to 20, depending on how one counts the interactions set to zero in the estimation process, could appear extremely high in light of previous intra/interspecific competition strength estimates of 4 to 5 by Adler et al. (13). Even though their model is a different one, i.e., Lotka-Volterra competition, we prove in the SI Appendix that the intra/inter ratio should remain commensurate. The difference in the intra/inter ratio that we found should therefore lie elsewhere, which requires some explanation. First, one could argue that such high intra/inter ratio arises because we consider the genus as our baseline taxonomic unit, rather than the species. Although it is logical that niche differentiation increases as one gets up the phylogenetic tree, and that getting down to the species level could slightly decrease that ratio, there are two arguments suggesting that the niche differences found here extend to the species level. First, species belonging to the various genera considered here are often found to compete in experiments (22, 23, 35). There is therefore a massive difference between niches in the lab and in the field (28). Second, the only other study that managed to provide MAR(1) estimates down to the species level for phytoplankton, that of Huber and Gaedke (36), provides an intra/interspecific strength ratio similar to ours (point 7a in Fig. 4). Strong self-regulation

seems therefore a genuine feature of field phytoplanktonic communities.

Another main finding of our study is the large frequency of positive interactions, with 30% truly mutualistic (+/+) interactions and between 40 and 70% facilitative effects. This again can be compared to the meta-analysis by Adler et al. (13) who also found facilitative interactions, but a little less than here ($\approx 30\%$). However, Adler et al. (13)'s review contains many experiments while the plant literature is replete with field examples of facilitation (15, 16), so that plant facilitation could be higher in the field. At the moment, it is therefore unknown how the predominance of facilitative interactions that we found in phytoplankton compares to facilitation in terrestrial plants. We note that several authors using MAR(1) models previously forbade positive interactions within the same trophic level, so that the fraction of facilitative interactions in plankton cannot be computed from literature-derived MAR(1) estimates.

The large niche differences and facilitative interactions that arise when considering a single trophic level are an emergent property, arising from hidden effects of resources or predator partitioning/sharing (3). In our previous publication investigating in detail the Arcachon study sites (28), we have argued that for phytoplankton, the strong intragroup density-dependence could arise from effects of natural enemies (28, 37). Natural enemies could also very well create apparent mutu-

alism between prey species (38–40). We believe this to be likely true for the present study as well, given that the new study regions (Oléron, Brittany, Mediterranean) have similar predators to the Arcachon site (zooplankton 41–43) and parasites (viruses 44, 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 (45), auxotrophy (46) or hydrodynamics (47) 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: the changes in phytoplankton absorption spectrum documented by Burson et al. (48) constitute an example of fine-scale resource partitioning of one resource, light, that is usually believed to be limiting for all species and genera.

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 linkage density of the interaction matrices) and their stability, as measured by the dominant eigenvalue of the interaction matrix, which measures the return time to a point equilibrium. 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, 49), but we 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 (28). Therefore, we are confident that the absence of complexity-resilience found here is genuine. This absence of direct link between complexity and stability could be an actual feature of empirical systems, as shown previously by Jacquet et al. (50) using a different technique, even though it does contradict previous results on random matrices, especially for competitive and/or mutualistic networks (51). We also found that the percentage of mutualistic interactions, that is thought to affect the stability of the network (17, 20, 52), does not have a major impact on the network's resilience.

In addition to weighted connectance, indices at the network-level (e.g., linkage density) and at the species or genus level (vulnerability and impact) approximate the average effects exerted and sustained by any given taxa in the different study sites. While, at the network level, network structure (either complexity measures or the percentage of mutualistic interactions) did not affect stability, a relation emerged between self-regulation, necessary for coexistence, and genus-level indices. We found that the more a genus is self-regulated, the more it tends to be vulnerable to other genera impacts and the less it impacts other genera. 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. Furthermore, a low self-regulation was correlated with high average abundance, which echoes findings by Yenni et al. (53) who found that rare species usually show stronger self-regulation. This correlation between rarity and self-regulation could explain the lesser impact effect of high self-regulated species/genus: a species which dominates the community composition can have

a major effect on the others, especially as they usually cover more space, while it is harder for rare, localised species to have large impacts. However, it was more difficult to explain the relationship between self-regulation and vulnerability: a genus that is more self-regulated and rarer was found here to be on average more vulnerable to other genera's increases in densities. Such relation implies greater stability (*sensu* resilience) for the network as a whole, because the taxa that are the most vulnerable to other taxa's impacts are also those whose dynamics are intrinsically more buffered. By which mechanisms this could happen is so far unclear and open to speculation. We caution, however, that the relationships between vulnerability, impact and self-regulation that we evidenced are all relatively weak: considerable stochasticity 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 (10, 13) or empirical food webs including horizontal diversity (33). Large niche differences might be due to the ghost of the competition past, i.e., competition has occurred in the past, leading to strong selection and subsequent evolution leading to progressive niche separation. In this scenario, species have evolved niches that allow them not to compete or to interact only weakly (very strong facilitative effects might be likewise destabilizing, 17). The likely predator effects that we highlighted above could be comprised within such niche differentiation *sensu largo*: specialized predators can make strong conspecific density-dependence emerge (54, 55), while switching generalists can also promote diversity (56). Both predators and resources have often symmetrical effects and can therefore contribute almost equally to such past niche differentiation (3).

An intriguing new possibility, dubbed the “ghost of competition present” (57), suggests by contrast that spatial distributions in relation to abiotic factors might have a large impact on the interaction strengths inferred from temporal interaction models such as ours. Recent combinations of model fitting and removal experiments have shown that the model fitting usually underestimates the effect of competitors that are uncovered by removal experiments (57, 58). This could occur for instance if species are spatially segregated (at a small scale) because each species only exists within a domain where it is relatively competitive (Pacala's spatial segregation hypothesis (59)), while a focal species could spread out if competitors were removed. This means that a species can be limited by competitors, but act so as to minimize competition (a little like avoidance behaviour in animals), which implies that competition is in effect hard to detect when all species are present. This would require spatial segregation between phytoplankton species at the scale of interactions, i.e., at the microscale. At the moment, it is known that turbulence generates inhomogeneities at the microscale (60, 61) but it is quite unclear how this affects multivariate spatial patterns of species distributions (*sensu* Bolker and Pacala, 62, or Murrell and Law, 63). Moreover, even if turbulence generates spatial structure with segregation between species, it is not quite clear that the “ghost of competition present” mechanism could work for plankton, because turbulence rather than organism movement dictates where the phytoplankton patches can or

cannot appear.

Materials and Methods

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327 **Sampling methods.** All phytoplankton counts were collected by Ifremer coastal laboratories as part of the National Phytoplankton and
328 Phycotoxin Monitoring Network (REPHY, 64). Since 1987, this
329 monitoring program has required the sampling of 26 sites along
330 the French coastline every 2 weeks within 2 hours of high tide to
331 document both biotic (phytoplankton counts) and abiotic (water
332 temperature, salinity) variables. We focused on sites which had the
333 longest time series. We also excluded time series which had missing
334 data for over 6 months or an average delay between sampling
335 dates above 20 days. This reduced the number of study sites to 10
336 sites nested within 4 regions (Brittany, Oléron, Arcachon and the
337 Mediterranean Sea; SI Appendix, Fig. S1).

338 Abiotic variables (temperature, salinity) were measured directly
339 from the boat during the sampling process while water samples for
340 biotic analyses were fixed with a Lugol's solution and examined
341 later. Phytoplankton cells above 20 μm were identified at the lowest
342 possible taxonomic level and counted with the Utermöhl method
343 using an optical microscope (65). Throughout the years and sites,
344 more than 600 taxa were identified at different taxonomic levels. We
345 aggregated them at the genus (or group of genera when not possible)
346 level based on previous work (28, 66), except for cryptophytes and
347 euglenophytes in Arcachon, which could not be identified below the
348 family level. Although the taxonomic resolution used here may seem
349 coarse in comparison to land plants, it is in fact more refined than
350 86% of the MAR(1) studies of phytoplankton listed in SI Appendix,
351 Table S3.

352 For each region, the MAR(1) analysis focused on the most
353 abundant and most frequently observed genera to avoid most of
354 the gaps in the time series. When gaps did not exceed a month,
355 missing values were linearly interpolated; remaining missing values
356 were replaced by a random number between 0 and half of the lowest
357 observed abundance (67). We tested extensively this and other
358 methods to deal with missing data in a previous publication on a
359 subset of this dataset (28). All time series were scaled and centered
360 before MAR analyses. All scripts for MAR and subsequent network
361 analyses are available online in a GitHub repository*.

362 **MAR(1) model.** Multivariate autoregressive (MAR) models are used
363 to determine the interspecific interactions and abiotic effects shaping
364 a community's dynamics (24). MAR(1) models are based
365 on a stochastic, discrete-time Gompertz model which relates log-
366 abundance of S species at time $t+1$ to interactions with the rest of
367 the community at time t , and effects of V abiotic variables at time
368 $t+1$, following eq. 1.

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

369 where \mathbf{n}_t is the $1 \times S$ log abundance vector of abundance of phyto-
370 plankton groups, \mathbf{B} is the $S \times S$ community (interaction) matrix, \mathbf{C}
371 is the $S \times V$ environment matrix describing the effects of V variables
372 (stacked in vector \mathbf{u}_{t+1}) on species growth rates, and \mathbf{e}_t is a $1 \times S$
373 noise vector which covers both process and observation error, following
374 a multivariate normal distribution with a variance-covariance
375 matrix \mathbf{Q} . \mathbf{Q} is diagonal and we have previously showed that this
376 parsimonious choice did not affect qualitatively the results (28).

377 We used the MARSS package (68) v3.9, in R v3.3.2 (69), to
378 estimate parameters with a maximum likelihood procedure.

379 We have previously published a detailed analysis of one of the
380 dataset (Arcachon) for which more covariates were available (28),
381 including nutrients and hydrodynamics variables. We found that
382 hydrodynamics variables were more influential than nutrients; nu-
383 trient dynamics contributed little to phytoplankton dynamics on
384 the two-week timescale. Because temperature and salinity sum
385 up seasonal changes in light as well as hydrology (salinity is in-
386 versely related to freshwater inflow), these represent the two key
387 drivers needed to account for abiotic influences (70). The analysis
388 of real data in Barraquand et al. (28) was complemented by that

391 of phytoplankton-like simulated data, which confirmed the ability
392 of MAR(1) models to infer biotic interactions and abiotic forcings
393 (e.g., no need for extra non-linearities to model the storage effect,
394 which was found to be nearly non-existent, as in previous analyses
395 of plant data for which strong-self regulation was observed, 12, 71).
396 Furthermore, using two abiotic variables (temperature and salinity)
397 in this study rather than the full set used in Barraquand et al. (28)
398 led to almost identical estimates to the ones obtained previously
399 (28). We are therefore confident that the MAR(1) models presented
400 here are robust to small changes in model specification. In general,
401 MAR(1) models tend to be fairly robust to small deviations of the
402 underlying (non-linear) data-generating model, provided that one
403 asks mainly order of magnitude of coefficients values (rather than
404 precise point estimates) and sign of interaction coefficients (49),
405 which is how these models are used here. For ease of interpretation
406 of those coefficients, we also prove the correspondance between
407 the magnitude of intra/inter interaction strength in a MAR(1)
408 model and a multispecies Beverton-Holt model, i.e., a discrete-time
409 Lotka-Volterra model, in the SI Appendix.

410 In this study, the number of phytoplankton groups, S , varies
411 between regions but we keep the same 2 covariates, i.e. water
412 temperature and salinity, that were measured at all study sites.
413 Therefore, the dimension of the dynamical system only depends
414 on the (square of the) number of phytoplankton groups we study,
415 which ranges between 7 (Mediterranean Sea) and 14 (Brittany).
416 The smallest system still requires 70 parameters to be estimated if
417 we consider all possible interactions between species. To reduce this
418 dimensionality and remove unnecessary parameters, we compared
419 different 'interaction scenarios' based on BIC (SI Appendix Fig. S3),
420 which proved to be satisfactory in our previous analyses of both
421 real data and similar simulated datasets (28). The null interaction
422 scenario assumed no interaction between groups of species
423 (diagonal interaction matrix) and was compared to four other interaction
424 scenarios. The first interaction scenario assumed that interactions
425 could only occur between phylogenetically close organisms,
426 i.e., within a class (groups were then diatoms, dinoflagellates,
427 and other phytoplanktonic organisms) while the second interaction
428 scenario further differentiated pennate and centric diatoms. The
429 third interaction scenario considered the reverse hypothesis, that
430 only unrelated organisms could interact (i.e., a diatom could only
431 interact with a dinoflagellate or a cryptophyte, but not with another
432 diatom), and the last interaction scenario did not constrain the
433 interactions at all (full interaction matrix). The second interaction
434 scenario, hereafter called the pennate-centric scenario, had the
435 lowest BIC for all sites and was therefore the most parsimonious,
436 and was chosen as the basis for further investigations of network
437 structure.

438 **Analysis of interaction strengths.** The interaction matrix obtained
439 from MAR(1) analyses can be used to determine the stability of a
440 discrete-time dynamical system (24). We compared the maximum
441 modulus of the eigenvalues of the pennate/centric matrices in each
442 site, as a proxy of stability, to network metrics which could be
443 related to complexity, such as weighted connectance and linkage
444 density (61). Weighted connectance is a measure of the proportion of
445 realized links, taking into account the shape of the flux distribution,
446 while link density measures the average proportion and strength
447 of interactions for a given species. These metrics are adapted
448 to weighted interaction matrices but cannot accomodate for both
449 positive and negative coefficients: we therefore chose to focus on
450 the absolute values of these coefficients, which can be linked to their
451 strength, irrespective of interaction sign.

452 In addition to these network-level metrics, we also computed the
453 average vulnerability (average effect of other taxa on a focal taxon,
454 SI Appendix, Eq. S5) and impact (average effect of a focal taxon on
455 other taxa, SI Appendix Eq. S6) on both raw and absolute values
456 of the coefficients, and compared these to the regulation a focal
457 species exerted on itself. Raw values indicate the average effect (i.e.,
458 is the effect mostly positive or negative?) that can be expected on
459 a species' growth rate from other planktonic species while absolute
460 effects characterise the strength of all types of interactions on a
461 species (i.e., is a species strongly affected by the others?). We
462 examined whether vulnerability and impact could be affected by
463 phylogenetic correlations; they were not as on Fig. 3 points were
464 not clustered according to genus, family or phylum.

*<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.

Finally, we compared our results on the ratio between mean self-regulation/intraspecific interaction strength and mean interspecific interaction strength to other published studies based on a MAR(1) model. A list of references is given in SI Appendix, Table S3. Authors usually reported only coefficients that were significant at the 95% significance threshold, thus ignoring potentially many weak effects. For mean intergroup interactions, we therefore computed both the mean value of all coefficients outside of the matrix diagonal, including zeroes (Fig. 4, which decreases the mean intergroup interaction strength), and the mean value of statistically significant intergroup coefficients only (SI Appendix, Fig. S8, which increases the mean intergroup interaction strength). We should mention two potential biases associated with this comparison across the published literature: low-dimensional matrices tended to be more complete (less sparse) than high-dimensional matrices, as these small interaction matrices were used to study known interaction phenomena (observed predation between organisms, for instance). Conversely, the number of parameters to estimate increases as the square of the number of interacting groups, 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 (SI Appendix, Fig. S9). A second caveat is that while we informed our model selection by phylogeny (see above), several authors have reduced the number of estimated parameters by an automated procedure, usually based on the comparison of 100 randomly chosen interaction matrices by BIC (24). The latter choice may 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, which should be less sensitive to the model selection method and therefore make comparisons across studies possible.

Supporting Information (SI).

This article contains supporting information.

1. Hutchinson G (1961) The paradox of the plankton. *The American Naturalist* 95(882):137–145.
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Supplementary Information for Strong self-regulation and widespread facilitative interactions between genera of phytoplankton - Picoche C. & Barraquand F.

Sampling

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

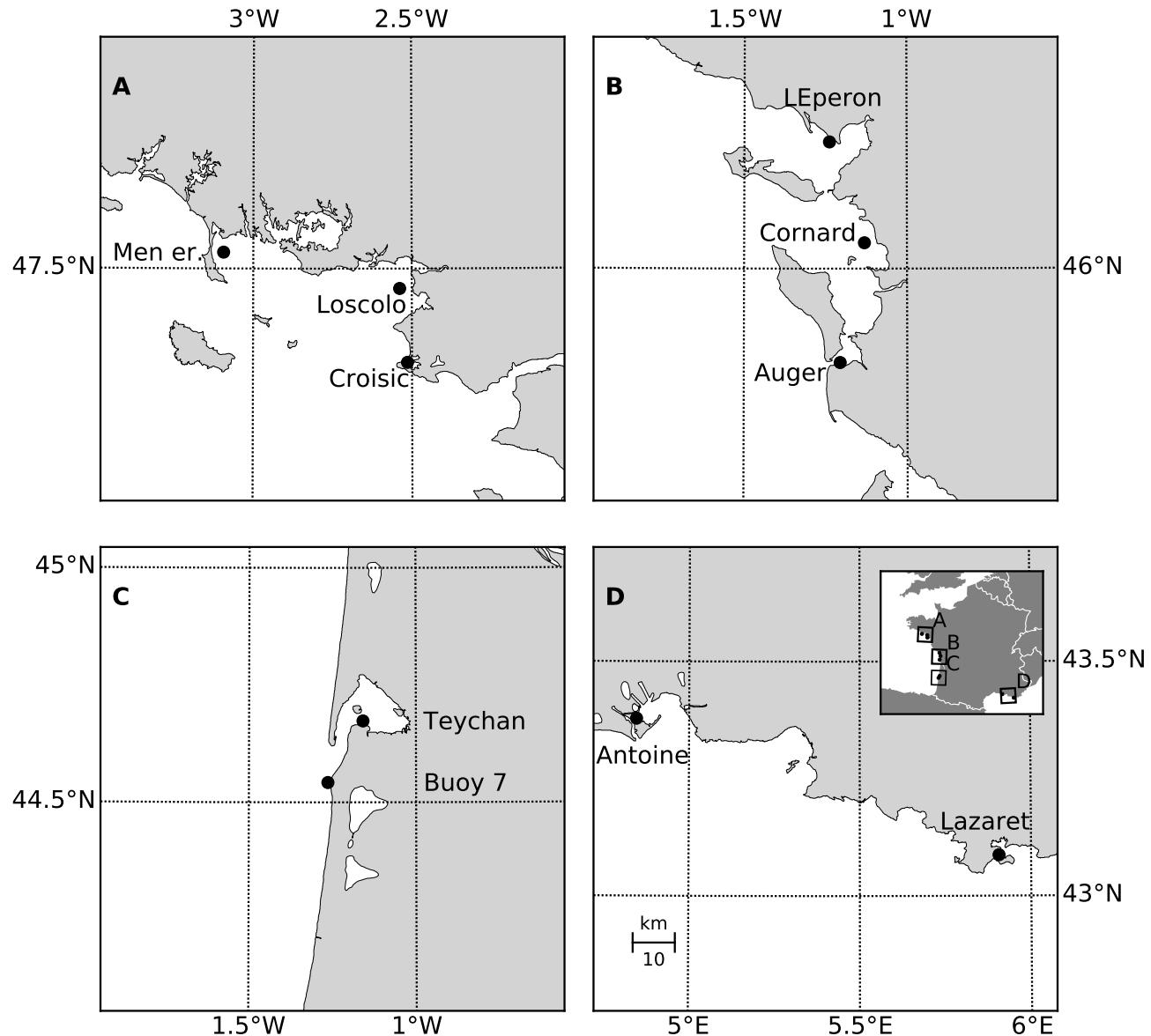


Figure S1: **Location of each study site in their region:** Brittany (A), Oléron (B), Arcachon (C) and the Mediterranean Sea (D). The common scale of the panels is given in the left corner of D.

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

microphytoplankton fraction [1]. 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. Or in other words, the volume sampled is approximately 1000 body sizes to the power three. We therefore consider samples to be representative of local community competition, if not of the spatial structure of the community.

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

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

Phytoplankton dynamics

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

Table S2: **Name and composition of the phytoplanktonic groups used in main text**, based on the work by Hernández-Fariñas et al. [2]

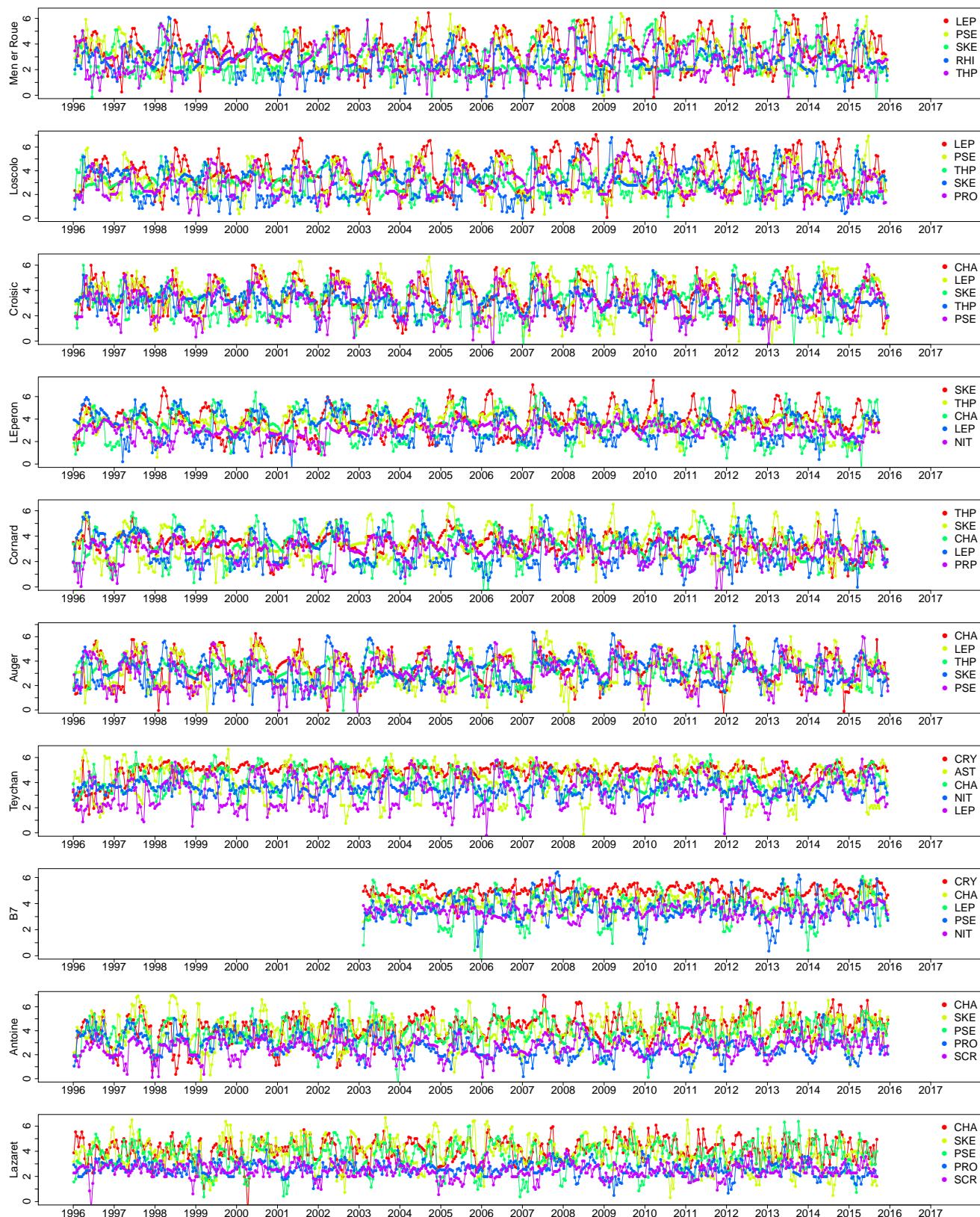


Figure S2: Time series of the 5 most abundant phytoplanktonic genera in each site.

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 was similar for most sites (Fig. S3). Based on these results, we considered the model selection to be quite robust, and focused on the pennate-centric scenario to analyze interaction matrices, as this scenario corresponded to the best fitted models that still allowed interactions between groups.

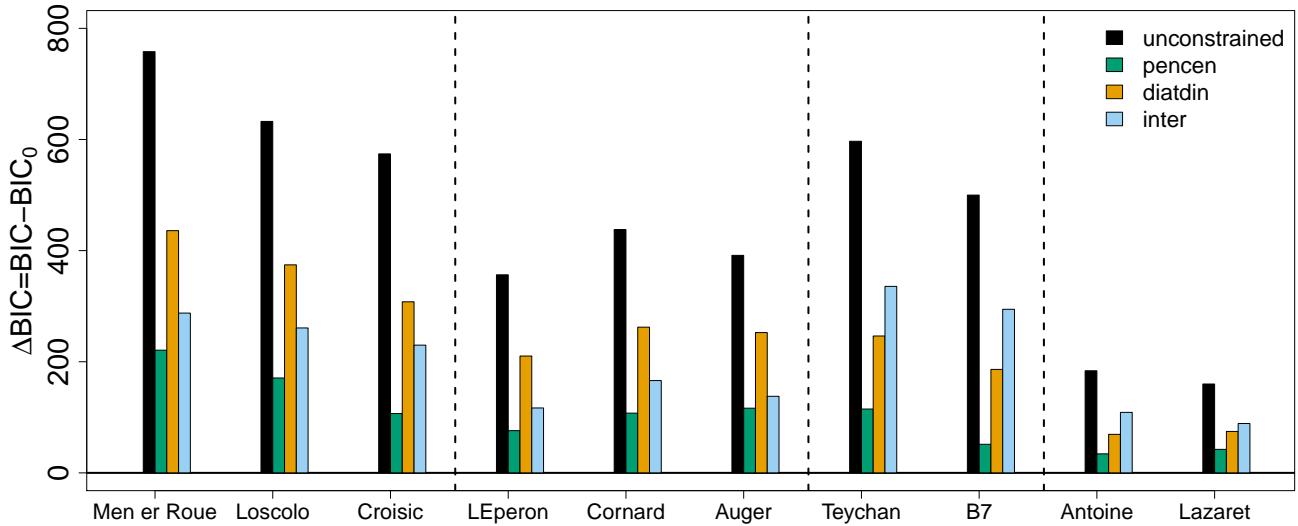


Figure S3: **Comparison of the BIC of different interaction scenarios**, compared to the null scenario (diagonal interaction matrix, allowing only intragroup interactions), for 10 sites in 4 different regions, separated by dashed lines (Brittany, Oléron, Arcachon and the Mediterranean Sea). Different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

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

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

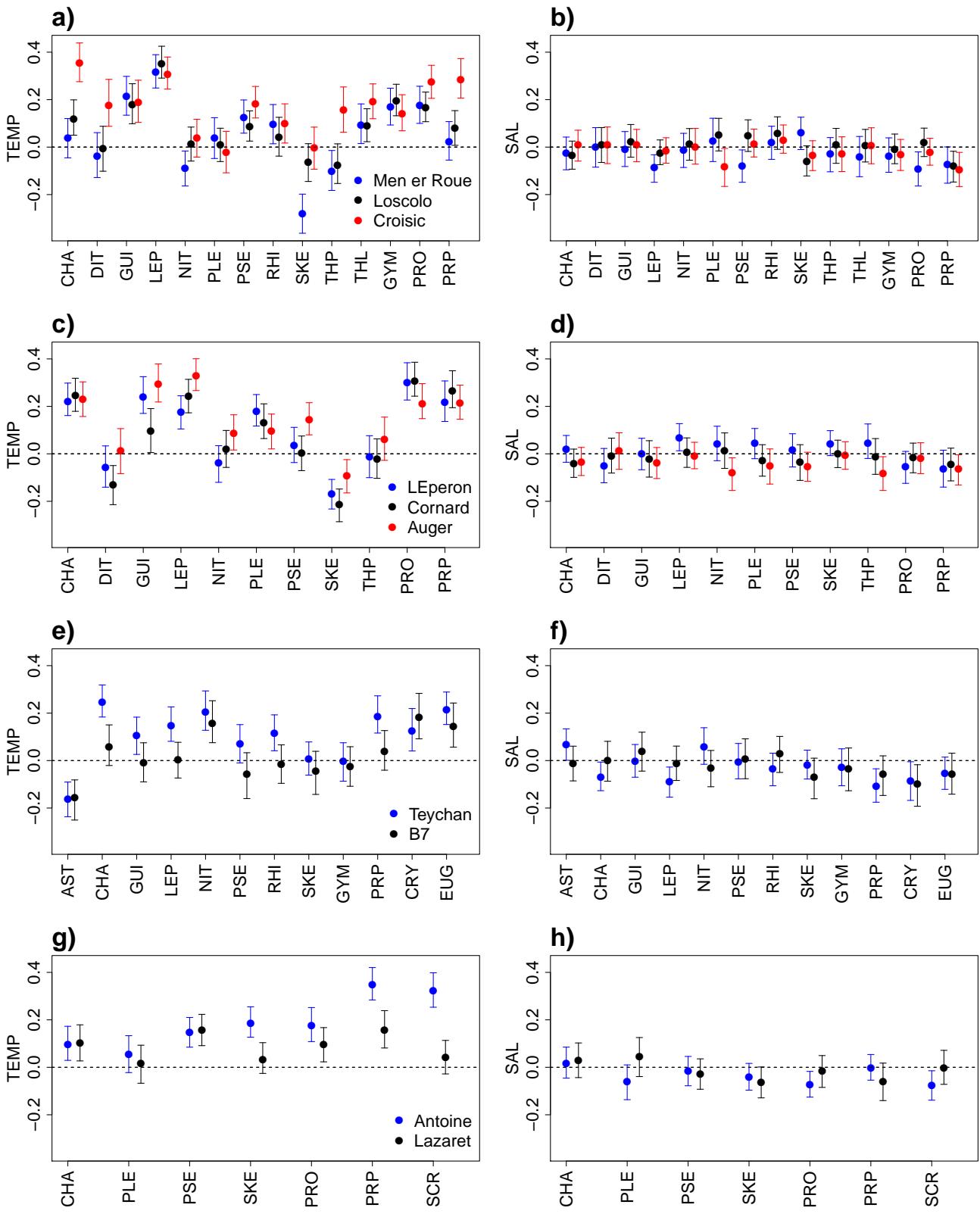


Figure S4: Effect of environmental variables (temperature, TEMP or salinity, SAL) on phytoplankton genera in Brittany (a, b), Oléron (c, d), Arcachon (e, f) and in the Mediterranean Sea (g, h). Each color corresponds to a different site. Error bars correspond to the 95% confidence interval around the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

Network analysis

Interaction types

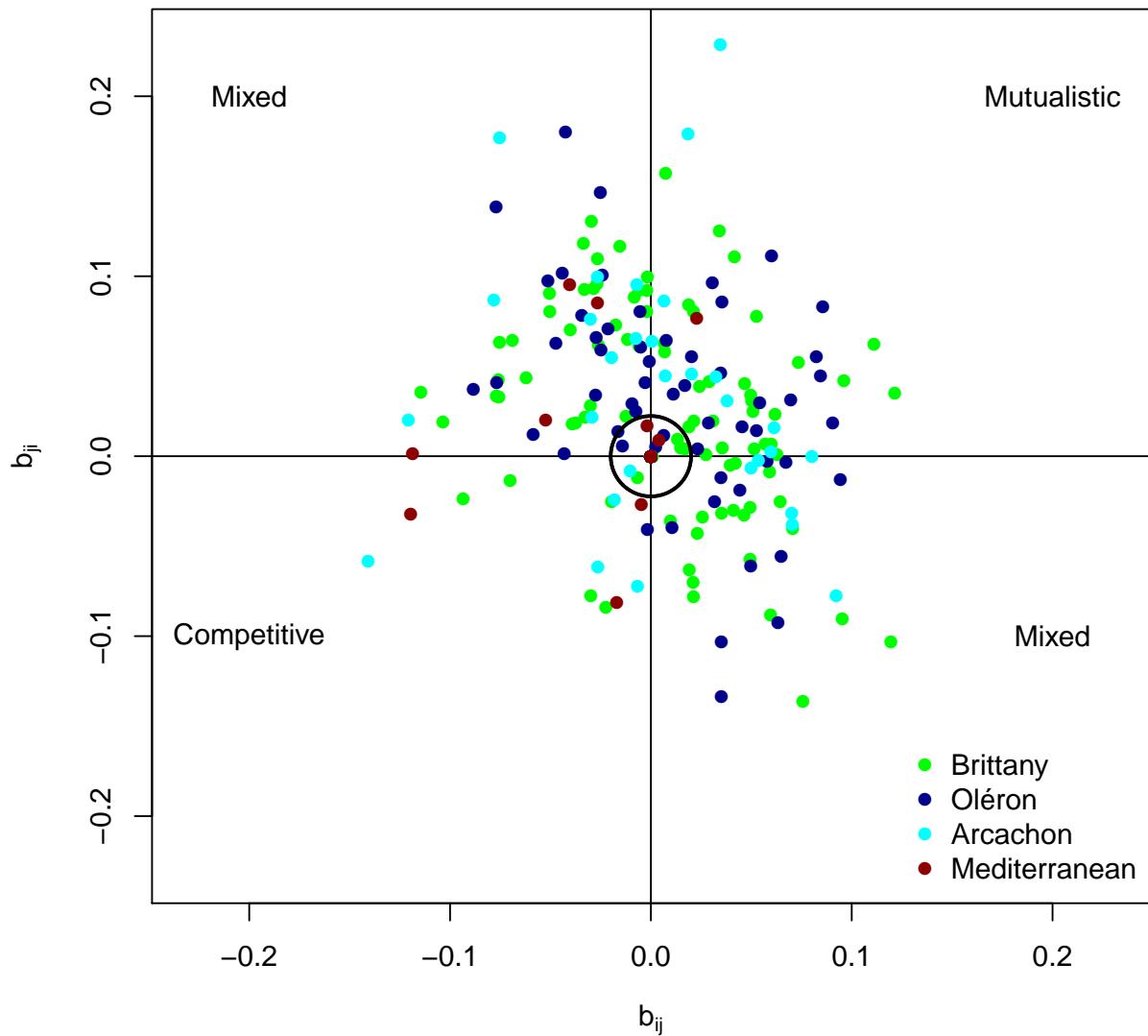


Figure S5: Pairs of coefficients for each study site. The effect of species i on j is given as a function of the effect of species j on species i . The black circle indicates the first quartile of the interaction values, under which we can assume that the effect is weak or null. Below this limit, $(+/+)$,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

Metrics

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

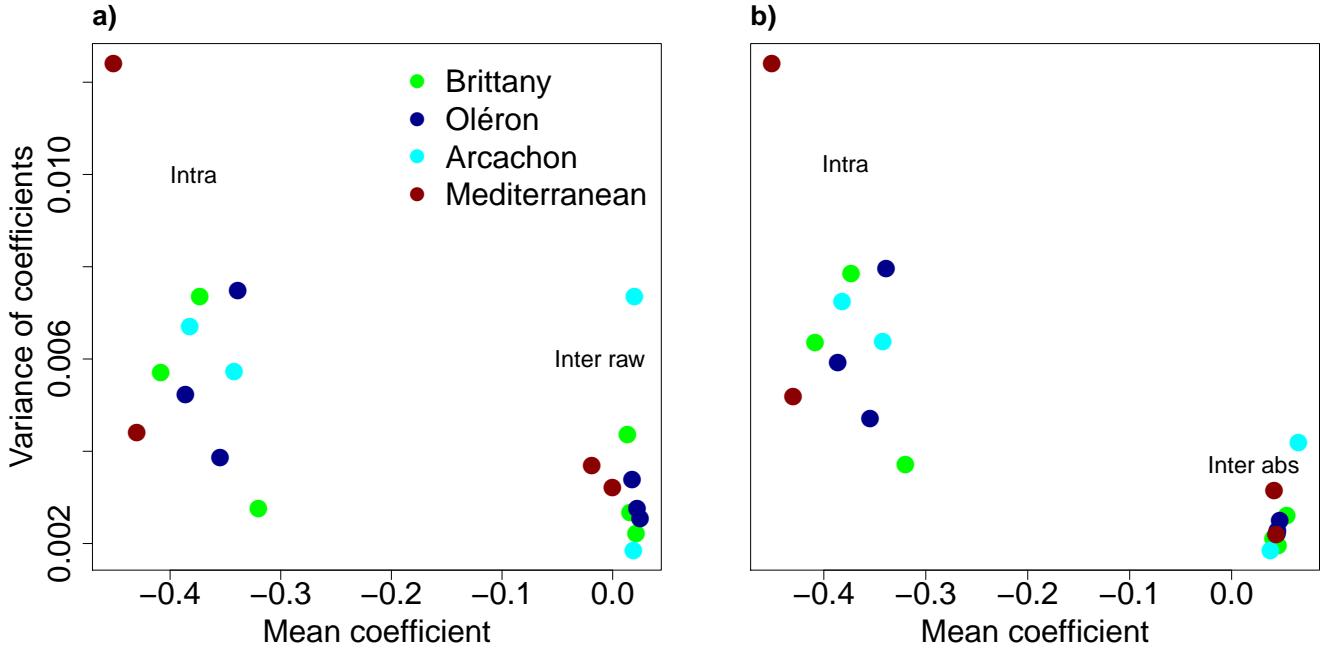


Figure S6: Relation between mean and variance of the intra- and intergenus interaction coefficients. The variance of the coefficients in the interaction matrix ($\mathbf{B} - \mathbf{I}$) increases with the mean, for 10 sites in 4 regions, with a model allowing interactions only within clads (within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

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

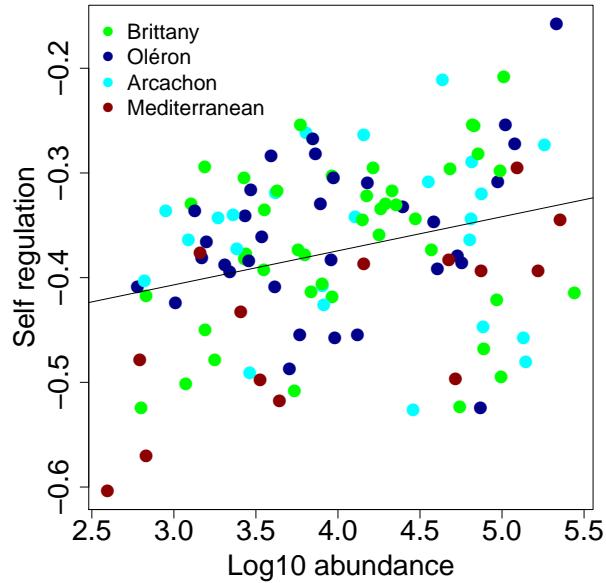


Figure S7: Relation between abundance and self-regulation (intragenus interaction coefficients). Mean abundance is computed for each genus in each site in 4 regions and intragenus interaction strengths are the diagonal coefficients of the interaction matrix ($\mathbf{B} - \mathbf{I}$).

Linkage density and weighted connectance were described in Bersier et al. [3]. Linkage density can be defined as the average of vulnerability and generality in the network. More precisely, diversity measures of the interactions

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

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

$$H_{P,k} = - \sum_{i=1}^S \frac{b_{ki}}{b_{k\cdot}} \log_2 \left(\frac{b_{ki}}{b_{k\cdot}} \right) \quad (2)$$

where b_{ik} is a coefficient of the interaction matrix $(\mathbf{B}-\mathbf{I})$, $b_{\cdot k} = \sum_{i=1}^S b_{ki}$ is the sum of all coefficients over row k and S is the number of species in the network. These indices are then averaged for the whole network as the linkage density LD (eq. 3).

$$LD = \frac{1}{2} \left(\sum_{k=1}^S \frac{b_{\cdot k}}{b_{\cdot\cdot}} 2^{H_{N,k}} + \sum_{k=1}^S \frac{b_{k\cdot}}{b_{\cdot\cdot}} 2^{H_{P,k}} \right) \quad (3)$$

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

Weighted connectance C is then defined as:

$$C = \frac{LD}{S} \quad (4)$$

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

In addition to these network-level metrics, we also considered metrics for each phytoplanktonic group. We measured both its vulnerability (mean strength of the interactions that are applied to a group, eq. 5) and its impact (mean strength of the interactions the group applied to other groups, eq. 6) in each network.

$$v_k = \frac{1}{\mathbf{1}_{b_{ki} \neq 0}} \sum_{i=1}^S b_{ki} \quad (5)$$

$$e_k = \frac{1}{\mathbf{1}_{b_{ik} \neq 0}} \sum_{i=1}^S b_{ik} \quad (6)$$

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

MAR references and analysis

We present here the MAR references we used to compare the effects of intra- and intergroup interactions (Table S3, Fig. S8). We add information on the biome and taxa used in the study as they tend to be linked to the estimated parameters (Fig. S9). Mean interaction strengths were computed as the mean absolute value of the coefficients which were deemed significant at the 95% threshold in the $(\mathbf{B}-\mathbf{I})$ matrix. The average value was either computed over the whole matrix (missing values in the matrix, or values which were not significant, were replaced by 0's, see Fig. 4 in the main text) or over the set of non-null coefficient only (Fig. S8).

Code	Ref	Dimension	Type of organisms	Taxonomic level	System	T
1a	[4], CLS	9	Zooplankton	Species and functional groups	Lake	100
1b	[4], TLS	9	Zooplankton	Species and functional groups	Lake	100
2a	[5]	2	Phytoplankton	Phylum	Lake	100
2b	[5]	3	Zooplankton	Species	Lake	50
3a	[6]	4	Functional groups of plankton	NA	Lake	300
3b	[6]	5	Taxonomic groups of plankton	Phylum/division	Lake	300
4a	[7]	4	Plankton	Zooplankton v. phytoplankton, size classes	Lake	100
4b	[7]	4	Plankton	Zooplankton v. phytoplankton, size classes	Lake with high planktivory	100
4c	[7]	4	Plankton	Zooplankton v. phytoplankton, size classes	Lake with low planktivory	100
5a	[8]	14	Plankton	Phylum (phytoplankton), genus (zooplankton)	Lake	300
5b	[8]	14	Plankton, growing season	Phylum (phytoplankton), genus (zooplankton)	Lake	200
6a	[9]	13	Plankton	Phylum (phytoplankton), genus (zooplankton)	Lake	400
6b	[9]	7	Simpler web, plankton	Phylum (phytoplankton), genus (zooplankton)	Lake	400
7a	[10]	10	Ciliates	Genus and species	Lake	300
7b	[10]	10	Phytoplankton	Genus and species	Lake	300
8a	[11]	3	Insects	Species	Terrestrial	50
9a	[12]	2	Lynx/Hare	Species	Terrestrial	100
10a	[13]	3	Fish	Species	Baltic Sea	30
11a	[14]	7	Phytoplankton	Phylum	Coastal site	1000
11b	[14]	7	Phytoplankton	Phylum	Offshore site	700
12a	[15]	12	Phytoplankton	Genus	Outside a bay	300
12b	[15]	12	Phytoplankton	Genus	Inside a bay	500

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

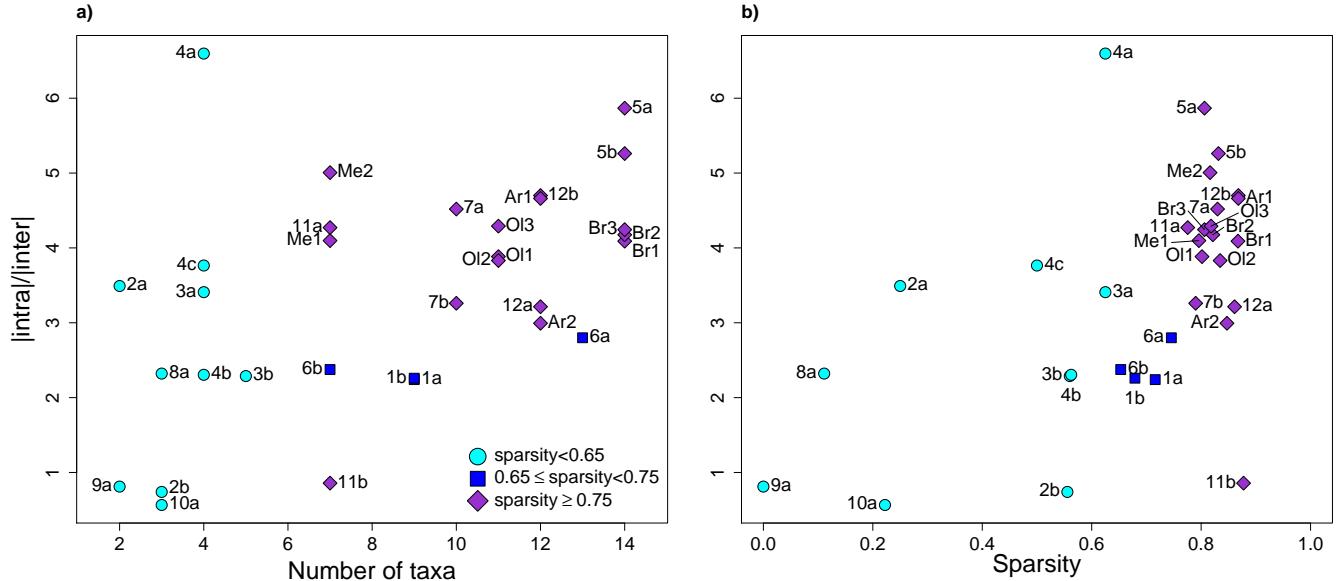


Figure S8: **Ratio of intra-to-intergroup interaction strength in MAR(1) studies.** Only significant values are taken into account and missing values in the matrix are not considered (e.g., not replaced by 0 as they are in the main text). The color and shape of each point are a function of the sparsity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

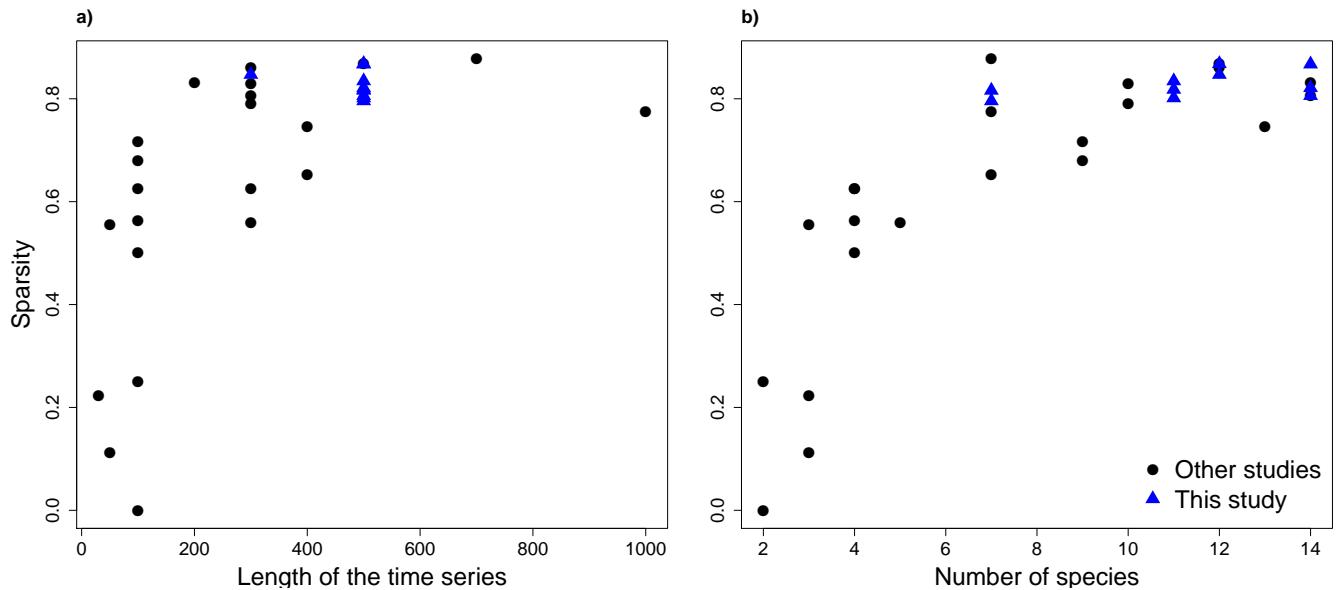


Figure S9: **Relation between interaction sparsity and study design** in studies described in Table S3. Blue triangles correspond to the present study.

Connection to Lotka-Volterra competition dynamics

The Beverton-Holt multispecies competition model, whose variants are widely used for modelling plant community dynamics [16, 17], is the closest discrete time equivalent to the continuous-time Lotka-Volterra model [18] (although the mapping is not perfect for $n \geq 3$) [19]. The Beverton-Holt multispecies competition model writes

$$N_{i,t+1} = \frac{e^{r_i} N_{i,t}}{1 + \sum_j \alpha_{ij} N_{j,t}} \quad (7)$$

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.

$$\begin{cases} R_1 = \alpha_{11}N_1 + \alpha_{12}N_2 \\ R_2 = \alpha_{21}N_1 + \alpha_{22}N_2 \end{cases}, \text{with} \quad \begin{cases} R_1 = e^{r_1} - 1 \\ R_2 = e^{r_2} - 1 \end{cases} \quad (8)$$

$$\Leftrightarrow \begin{cases} \alpha_{21}R_1 = \alpha_{21}\alpha_{11}N_1 + \alpha_{21}\alpha_{12}N_2 \\ \alpha_{11}R_2 = \alpha_{11}\alpha_{21}N_1 + \alpha_{11}\alpha_{22}N_2 \end{cases} \quad (9)$$

$$\Leftrightarrow \begin{cases} N_1 = \frac{\alpha_{12}R_2 - \alpha_{22}R_1}{\alpha_{12}\alpha_{21} - \alpha_{22}\alpha_{11}} \\ N_2 = \frac{\alpha_{21}R_1 - \alpha_{11}R_2}{\alpha_{12}\alpha_{21} - \alpha_{22}\alpha_{11}} \end{cases} \quad (10)$$

Setting $n = \log(N)$, eq. 7 is equivalent to

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

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 $Y = \ln(1 + \alpha_{21}N_1 + \alpha_{22}N_2)$.

$$J = \begin{pmatrix} 1 - \frac{\partial X}{\partial n_1} & -\frac{\partial X}{\partial n_2} \\ -\frac{\partial Y}{\partial n_1} & 1 - \frac{\partial Y}{\partial n_2} \end{pmatrix} \quad (12)$$

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

$$J - I = \begin{pmatrix} -\frac{\alpha_{11}N_1}{1 + \alpha_{11}N_1 + \alpha_{12}N_2} & -\frac{\alpha_{12}N_2}{1 + \alpha_{11}N_1 + \alpha_{12}N_2} \\ -\frac{\alpha_{21}N_1}{1 + \alpha_{21}N_1 + \alpha_{22}N_2} & -\frac{\alpha_{22}N_2}{1 + \alpha_{21}N_1 + \alpha_{22}N_2} \end{pmatrix} \quad (13)$$

For this demonstration, we consider diffuse competition, that is

$$\begin{cases} \alpha_{ii} = k\alpha \\ \alpha_{ij} = \alpha, \forall i \neq j \end{cases} \quad (14)$$

If we combine eq. 10 and eq. 14, we have

$$\begin{cases} N_1 = \frac{\alpha R_2 - k\alpha R_1}{\alpha^2 - k^2\alpha^2} \\ N_2 = \frac{\alpha R_1 - k\alpha R_2}{\alpha^2 - k^2\alpha^2} \end{cases} \quad (15)$$

and

$$J - I = \begin{pmatrix} -\frac{k\alpha N_1}{1 + k\alpha N_1 + \alpha N_2} & -\frac{\alpha N_2}{1 + k\alpha N_1 + \alpha N_2} \\ -\frac{\alpha N_1}{1 + \alpha N_1 + k\alpha N_2} & -\frac{k\alpha N_2}{1 + \alpha N_1 + k\alpha N_2} \end{pmatrix} \quad (16)$$

$$\Rightarrow \begin{cases} (J - I)_{11} = \frac{-\frac{k}{1-k^2}(R_2 - kR_1)}{1 + \frac{k}{1-k^2}(R_2 - kR_1) + \frac{1}{1-k^2}(R_1 - kR_2)} \\ (J - I)_{12} = \frac{-\frac{1}{1-k^2}(R_1 - kR_2)}{1 + \frac{k}{1-k^2}(R_2 - kR_1) + \frac{1}{1-k^2}(R_1 - kR_2)} \end{cases} \Rightarrow (J - I)_{11} = k \frac{R_2 - kR_1}{R_1 - kR_2} (J - I)_{12} \quad (17)$$

By symmetry, we can also write

$$(J - I)_{22} = k \frac{R_1 - k R_2}{R_2 - k R_1} (J - I)_{21} \quad (18)$$

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

$$\begin{aligned} (J - I)_{ii} &= \frac{-\alpha_{ii} N_i}{1 + \sum_j \alpha_{ij} N_j} \\ &= \frac{-k\alpha N_i}{1 + k\alpha N_i + \sum_{j,j \neq i} \alpha N_j} \end{aligned} \quad (19)$$

and

$$\begin{aligned} (J - I)_{ij} &= \frac{-\alpha_{ij} N_j}{1 + \sum_l \alpha_{il} N_l} \\ &= \frac{-\alpha N_j}{1 + k\alpha N_i + \sum_{l,l \neq i} \alpha N_l} \\ &= (J - I)_{ii} \frac{\alpha N_j}{k\alpha N_i} \\ &= \frac{1}{k} (J - I)_{ii} \frac{N_j}{N_i} \end{aligned} \quad (20)$$

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

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