

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

Coralie Picoche¹, Frédéric Barraquand^{1,2*}

1 University of Bordeaux, Integrative and Theoretical Ecology, LabEx COTE, Bât. B2 - Allée Geoffroy St-Hilaire, 33615 Pessac, France

2 CNRS, Institute of Mathematics of Bordeaux, 351 Cours de la Libération, 33405 Talence, France

* frederic.barraquand@u-bordeaux.fr

Abstract

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.

Author summary

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.

Introduction

How species or close genera can coexist together in spite of competition is one of the main puzzles of community ecology, especially for primary producers that seemingly share the same basic resources [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, 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.

32

Results

33

Interaction estimates

34

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 (S3 Fig). 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 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.

35

36

37

38

39

40

41

42

43

44

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.

45

46

47

48

49

50

51

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 S5 Fig. 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].

52

53

54

55

56

57

58

59

60

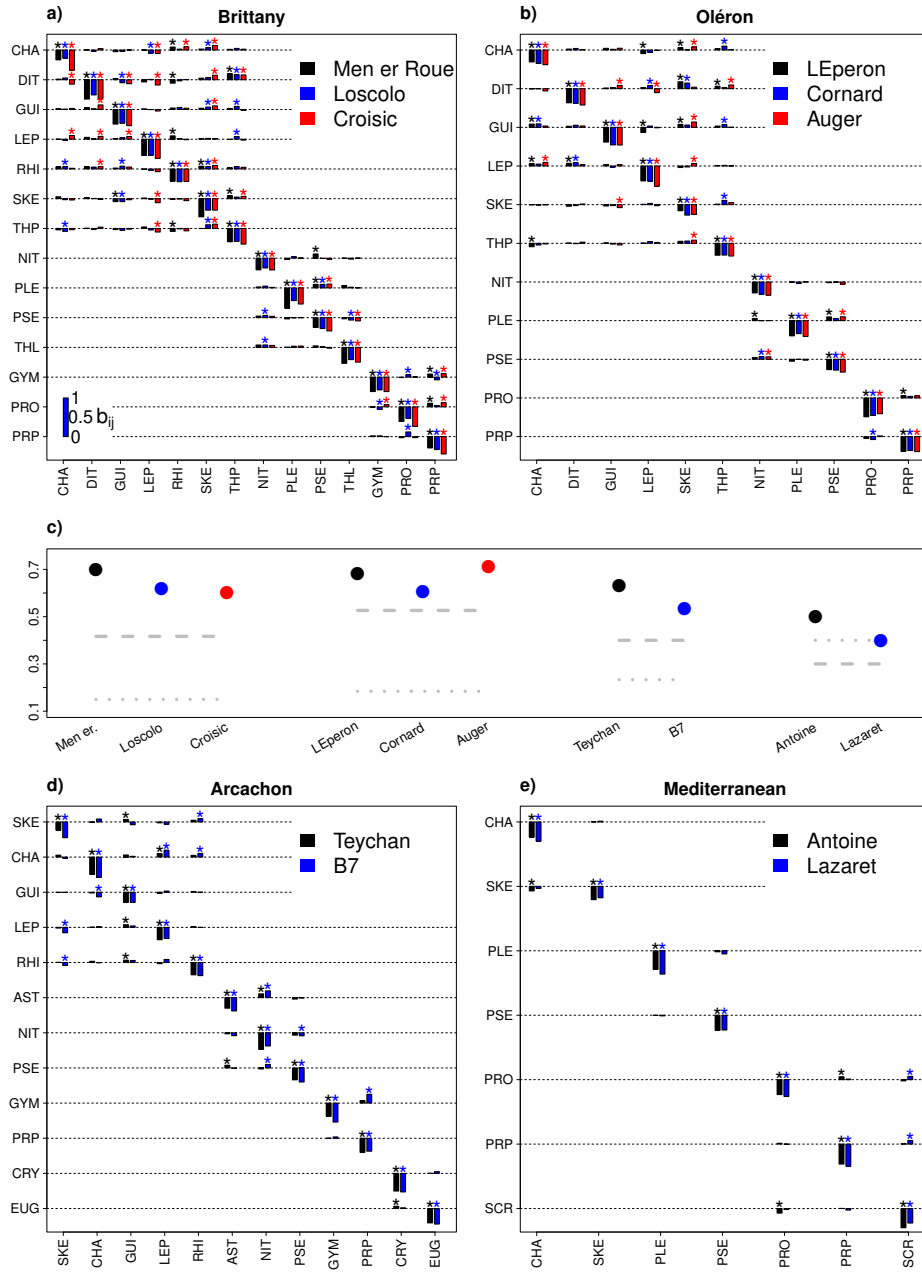


Fig 1. Interaction matrices estimated in 10 sites along the French coastline. Four regions are distinguished: Brittany (a), Oléron (b), Arcachon (d) and the Mediterranean Sea (e). Only interactions between clades (pennate and centric diatoms, dinoflagellates, other planktonic taxa) are allowed, as this is the best fitting interaction scenario (S3 Fig). 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 S2 Table. 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.

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.

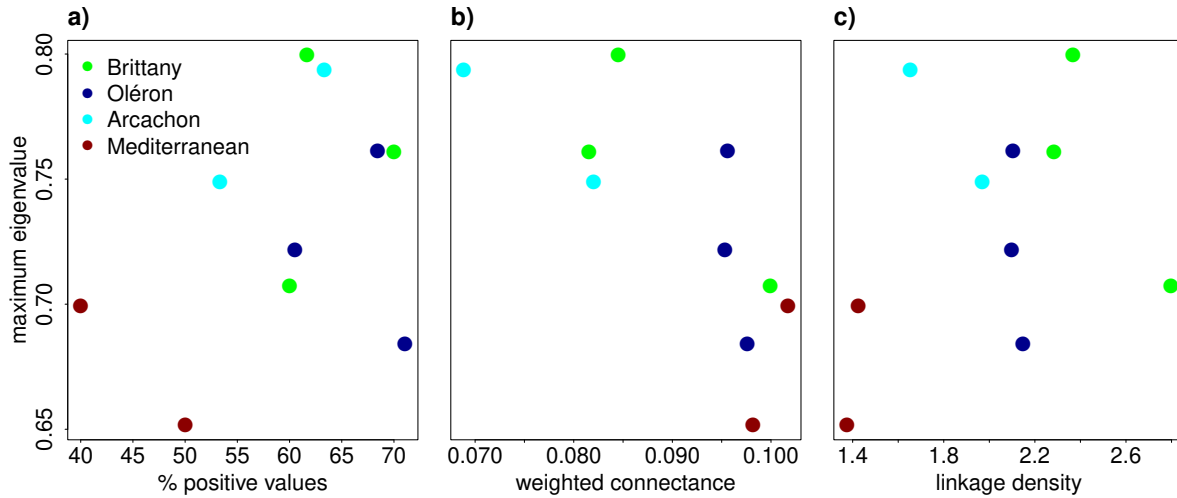


Fig 2. Relation between stability and complexity of the interaction networks. The maximum modulus of the interaction matrix \mathbf{B} eigenvalues indicates stability *sensu* resilience. Each point color corresponds to a given region. Metrics formula for weighted connectance and linkage density are given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

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, S5 Eq) and impact (summed effect of the focal species onto other species growth rates, S6 Eq). Relations between inter- and intra-genus interactions emerged (Fig. 3): genera that were more self-regulating also had also a higher vulnerability score and a lower impact score. Those two influences are likely to trade-off: a high degree of self-regulation somehow buffers 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 (S7 Fig), 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.

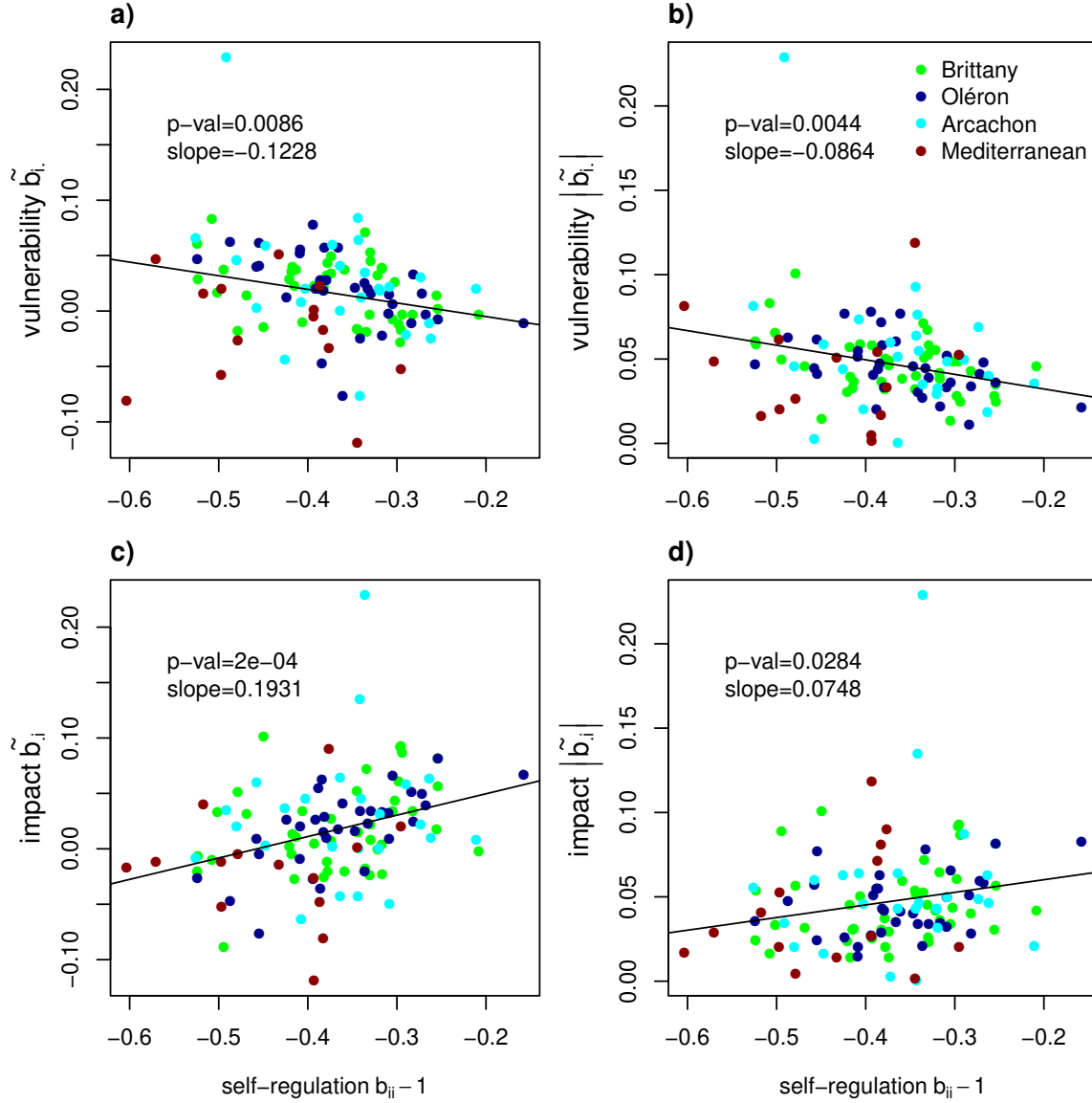


Fig 3. Relation between vulnerability/impact and self-regulation. Average vulnerability (effects of others on the focal taxon growth rate, a-b) and impact (effects of the focal taxon on others' growth rates, c-d), as well as self-regulation, are computed for untransformed (a-c) or absolute (b-d) values of the coefficients of the interaction matrix ($\mathbf{B} - \mathbf{I}$) for the 10 study sites. Each color corresponds to a given region (S1 Fig). 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.

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, S6 Fig).

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 S3 Table). We found that 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.

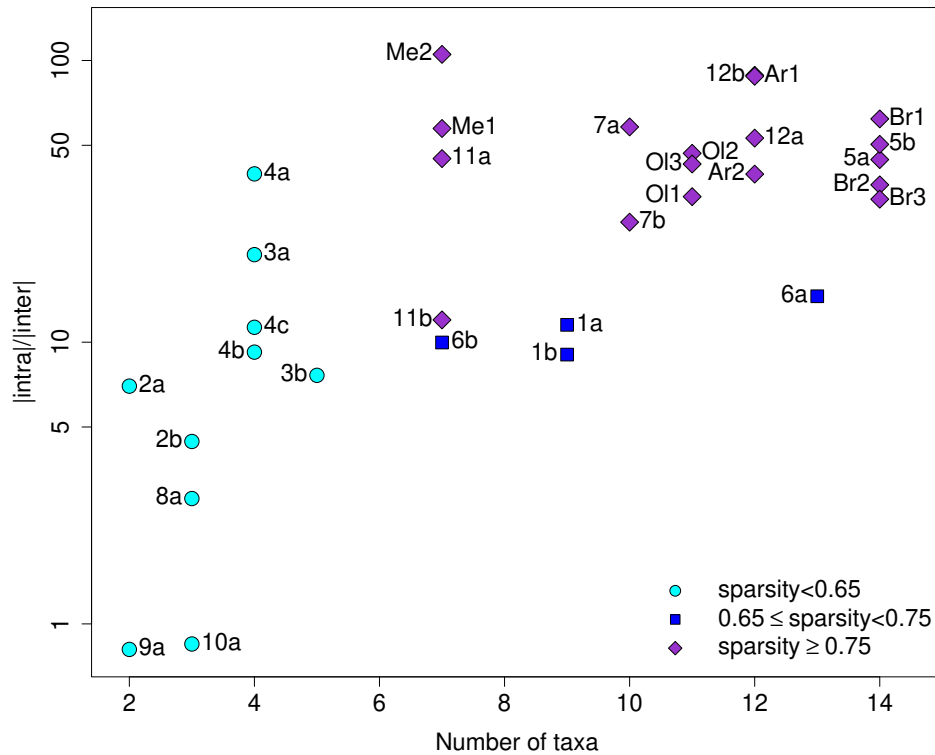


Fig 4. Ratio of intra- to inter-group interaction strength in Multivariate AutoRegressive (MAR) models in the ecological literature as a function of the number of species they include. The name of each studies, corresponding to each code, is given in S3 Table. Codes beginning with letters correspond 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).

Discussion

93

Strong self-regulation and facilitation

94

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.

95
96
97

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 Text 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.

98
99
100
101
102
103
104
105
106
107
108
109
110
111
112

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.

113
114
115
116
117
118
119
120
121

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].

122
123

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 mutualism 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

Sampling methods

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

Abiotic variables (temperature, salinity) were measured directly from the boat during the sampling process while water samples for biotic analyses were fixed with a Lugol’s solution and examined later. Phytoplankton cells above 20 μm were identified at the lowest possible taxonomic level and counted with the Utermöhl method using an optical microscope [65]. Throughout the years and sites, more than 600 taxa were identified at different taxonomic levels. We aggregated them at the genus (or group of genera

when not possible) level based on previous work [28,66], except for cryptophytes and euglenophytes in Arcachon, which could not be identified below the family level. Although the taxonomic resolution used here may seem coarse in comparison to land plants, it is in fact more refined than 86% of the MAR(1) studies of phytoplankton listed in S3 Table.

For each region, the MAR(1) analysis focused on the most abundant and most frequently observed genera to avoid most of the gaps in the time series. When gaps did not exceed a month, missing values were linearly interpolated; remaining missing values were replaced by a random number between 0 and half of the lowest observed abundance [67]. We tested extensively this and other methods to deal with missing data in a previous publication on a subset of this dataset [28]. All time series were scaled and centered before MAR analyses. All scripts for MAR and subsequent network analyses are available online in a GitHub repository¹.

MAR(1) model

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

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

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

We used the MARSS package [68] v3.9, in R v3.3.2 [69], to estimate parameters with a maximum likelihood procedure.

We have previously published a detailed analysis of one of the dataset (Arcachon) for which more covariables were available [28], including nutrients and hydrodynamics variables. We found that hydrodynamics variables were more influential than nutrients; nutrient dynamics contributed little to

¹<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.

phytoplankton dynamics on the two-week timescale. Because temperature and salinity sum up seasonal changes in light as well as hydrology (salinity is inversely related to freshwater inflow), these represent the two key drivers needed to account for abiotic influences [70]. The analysis of real data in Barraquand et al. [28] was complemented by that of phytoplankton-like simulated data, which confirmed the ability of MAR(1) models to infer biotic interactions and abiotic forcings (e.g., no need for extra non-linearities to model the storage effect, which was found to be nearly non-existent, as in previous analyses of plant data for which strong-self regulation was observed, 12, 71). Furthermore, using two abiotic variables (temperature and salinity) in this study rather than the full set used in Barraquand et al. [28] led to almost identical estimates to the ones obtained previously [28]. We are therefore confident that the MAR(1) models presented here are robust to small changes in model specification. In general, MAR(1) models tend to be fairly robust to small deviations of the underlying (non-linear) data-generating model, provided that one asks mainly order of magnitude of coefficients values (rather than precise point estimates) and sign of interaction coefficients [49], which is how these models are used here. For ease of interpretation of those coefficients, we also prove the correspondance between the magnitude of intra/inter interaction strength in a MAR(1) model and a multispecies Beverton-Holt model, i.e., a discrete-time Lotka-Volterra model, in the SI Text.

In this study, the number of phytoplankton groups, S , varies between regions but we keep the same 2 covariates, i.e. water temperature and salinity, that were measured at all study sites. Therefore, the dimension of the dynamical system only depends on the (square of the) number of phytoplankton groups we study, which ranges between 7 (Mediterranean Sea) and 14 (Brittany). The smallest system still requires 70 parameters to be estimated if we consider all possible interactions between species. To reduce this dimensionality and remove unnecessary parameters, we compared different ‘interaction scenarios’ based on BIC (S3 Fig), which proved to be satisfactory in our previous analyses of both real data and similar simulated datasets [28]. The null interaction scenario assumed no interaction between groups of species (diagonal interaction matrix) and was compared to four other interaction scenarios. The first interaction scenario assumed that interactions could only occur between phylogenetically close organisms, i.e., within a class (groups were then diatoms, dinoflagellates, and other phytoplanktonic organisms) while the second interaction scenario further differentiated pennate and centric diatoms. The third interaction scenario considered the reverse hypothesis, that only unrelated organisms could interact (i.e., a diatom could only interact with a dinoflagellate or a cryptophyte, but not with another diatom), and the last interaction scenario did not constrain the interactions at all (full interaction matrix). The second interaction scenario, hereafter called the pennate-centric scenario, had the lowest BIC for all sites and

was therefore the most parsimonious, and was chosen as the basis for further investigations of network structure.

Analysis of interaction strengths

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

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

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 S3 Table. 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 (S8 Fig, 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 (S9 Fig). 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.

Acknowledgments

This study was only made possible by the dedication of all members of the REPHY program [64] by
Ifremer, providing invaluable data through years of fieldwork. We are grateful to David Murrell for his
careful reading and suggestions, and to Peter Adler for helpful exchanges. This study was supported by
the French ANR through LabEx COTE (ANR-10-LABX-45).

Supporting Information (SI)

This article contains supporting information.

References

1. Hutchinson GE. The paradox of the plankton. *The American Naturalist*. 1961;95(882):137–145.
2. Armstrong RA, McGehee R. Competitive exclusion. *The American Naturalist*. 1980;115(2):151–170.
3. Chesson P. Updates on mechanisms of maintenance of species diversity. *Journal of Ecology*. 2018;106(5):1773–1794.
4. Armstrong RA, McGehee R. Coexistence of species competing for shared resources. *Theoretical Population Biology*. 1976;9(3):317–328.
5. Chesson P, Huntly N. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *The American Naturalist*. 1997;150(5):519–553.

6. Huisman J, Weissing FJ. Biological conditions for oscillations and chaos generated by multispecies competition. *Ecology*. 2001;82(10):2682–2695.
7. Li L, Chesson P. The effects of dynamical rates on species coexistence in a variable environment: the paradox of the plankton revisited. *The American Naturalist*. 2016;188(2):E46–E58.
8. Hubbell SP. The unified neutral theory of biodiversity and biogeography. Princeton University Press; 2001.
9. Volkov I, Banavar JR, Hubbell SP, Maritan A. Neutral theory and relative species abundance in ecology. *Nature*. 2003;424:1035–1037.
10. Volkov I, Banavar JR, Hubbell SP, Maritan A. Patterns of relative species abundance in rainforests and coral reefs. *Nature*. 2007;450(7166):45–49.
11. Rosindell J, Hubbell S, Etienne R. The unified neutral theory of biodiversity and biogeography at age ten. *Trends in ecology & evolution*. 2011;26(7):340.
12. Adler PB, Ellner SP, Levine JM. Coexistence of perennial plants: an embarrassment of niches. *Ecology letters*. 2010;13(8):1019–1029.
13. Adler PB, Smull D, Beard KH, Choi RT, Furniss T, Kulmatiski A, et al. Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecology Letters*. 2018;21(9):1319–1329.
14. Mutshinda CM, O’Hara RB, Woiwod IP. What drives community dynamics? *Proceedings of the Royal Society B: Biological Sciences*. 2009;276(1669):2923–2929.
15. Brooker RW, Maestre FT, Callaway RM, Lortie CL, Cavieres LA, Kunstler G, et al. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*. 2008;96(1):18–34.
16. McIntire EJB, Fajardo A. Facilitation as a ubiquitous driver of biodiversity. *New Phytologist*. 2014;201(2):403–416.
17. Coyte KZ, Schluter J, Foster KR. The ecology of the microbiome: Networks, competition, and stability. *Science*. 2015;350(6261):663–666.
18. Gross K. Positive interactions among competitors can produce species-rich communities. *Ecology Letters*. 2008;11(9):929–936.

19. Cavieres LA, Badano EI. Do facilitative interactions increase species richness at the entire community level? *Journal of Ecology*. 2009;97(6):1181–1191.
20. Mougi A, Kondoh M. Diversity of interaction types and ecological community stability. *Science*. 2012;337(6092):349–351.
21. García-Callejas D, Molowny-Horas R, Araújo MB. The effect of multiple biotic interaction types on species persistence. *Ecology*. 2018;99(10):2327–2337.
22. Titman D. Ecological competition between algae: experimental confirmation of resource-based competition theory. *Science*. 1976;192(4238):463–465.
23. Descamps-Julien B, Gonzalez A. Stable coexistence in a fluctuating environment: an experimental demonstration. *Ecology*. 2005;86(10):2815–2824.
24. Ives AR, Dennis B, Cottingham KL, Carpenter SR. Estimating community stability and ecological interactions from time-series data. *Ecological monographs*. 2003;73(2):301–330.
25. Hampton SE, Izmet'Eva LR, Moore MV, Katz SL, Dennis B, Silow EA. Sixty years of environmental change in the world's largest freshwater lake - Lake Baikal, Siberia. *Global Change Biology*. 2008;14(8):1947–1958.
26. Griffiths JR, Hajdu S, Downing AS, Hjerne O, Larsson U, Winder M. Phytoplankton community interactions and environmental sensitivity in coastal and offshore habitats. *Oikos*. 2015;125(8):1134–1143.
27. Hampton SE, Holmes EE, Scheef LP, Scheuerell MD, Katz SL, Pendleton DE, et al. Quantifying effects of abiotic and biotic drivers on community dynamics with multivariate autoregressive (MAR) models. *Ecology*. 2013;94(12):2663–2669.
28. Barraquand F, Picoche C, Maurer D, Carassou L, Auby I. Coastal phytoplankton community dynamics and coexistence driven by intragroup density-dependence, light and hydrodynamics. *Oikos*. 2018;127(12):1834–1852.
29. Chamberlain SA, Bronstein JL, Rudgers JA. How context dependent are species interactions? *Ecology Letters*. 2014;17(7):881–890.
30. Ives AR, Carpenter SR. Stability and diversity of ecosystems. *Science*. 2007;317(5834):58–62.

31. James A, Plank MJ, Rossberg AG, Beecham J, Emmerson M, Pitchford JW. Constructing random matrices to represent real ecosystems. *The American Naturalist*. 2015;185(5):680–692.
32. Arnoldi JF, Loreau M, Haegeman B. The variability spectrum of ecological communities: How common and rare species shape stability patterns. *bioRxiv*. 2018;.
33. Barabás G, Michalska-Smith MJ, Allesina S. Self-regulation and the stability of large ecological networks. *Nature Ecology & Evolution*. 2017;1(12):1870–1875.
34. Levine JM, HilleRisLambers J. The importance of niches for the maintenance of species diversity. *Nature*. 2009;461(7261):254–257.
35. Tilman D, Kilham SS, Kilham P. Phytoplankton community ecology: the role of limiting nutrients. *Annual Review of Ecology and Systematics*. 1982;13:349–372.
36. Huber V, Gaedke U. The role of predation for seasonal variability patterns among phytoplankton and ciliates. *Oikos*. 2006;114(2):265–276.
37. Haydon D. Pivotal assumptions determining the relationship between stability and complexity: an analytical synthesis of the stability-complexity debate. *The American Naturalist*. 1994;144(1):14–29.
38. Abrams PA, Holt RD, Roth JD. Apparent competition or apparent mutualism? Shared predation when populations cycle. *Ecology*. 1998;79(1):201–212.
39. Barraquand F, New LF, Redpath S, Matthiopoulos J. Indirect effects of primary prey population dynamics on alternative prey. *Theoretical Population Biology*. 2015;103:44–59.
40. de Ruiter PC, Gaedke U. Emergent facilitation promotes biological diversity in pelagic food webs. *Food Webs*. 2017;10:15–21.
41. Jamet JL, Boge G, Richard S, Geneys C, Jamet D. The zooplankton community in bays of Toulon area (northwest Mediterranean Sea, France). *Hydrobiologia*. 2001;557:155–165.
42. Modéran J, Bouvais P, David V, Le Noc S, Simon-Bouhet B, Niquil N, et al. Zooplankton community structure in a highly turbid environment (Charente estuary, France): Spatio-temporal patterns and environmental control. *Estuarine, Coastal and Shelf Science*. 2010;88(2):219–232.
43. Tortajada S, Niquil N, Blanchet H, Grami B, Montanié H, David V, et al. Network analysis of the planktonic food web during the spring bloom in a semi enclosed lagoon (Arcachon, SW France). *Acta Oecologica*. 2012;40:40–50.

44. Ory P, Hartmann HJ, Jude F, Dupuy C, Del Amo Y, Catala P, et al. Pelagic food web patterns: do they modulate virus and nanoflagellate effects on picoplankton during the phytoplankton spring bloom? Effects of viruses and nanoflagellates on picoplankton. *Environmental Microbiology*. 2010; p. 2755–2772.
45. Felpeto AB, Roy S, Vasconcelos VM. Allelopathy prevents competitive exclusion and promotes phytoplankton biodiversity. *Oikos*. 2018;127(1):85–98.
46. Tang YZ, Koch F, Gobler CJ. Most harmful algal bloom species are vitamin B1 and B12 auxotrophs. *Proceedings of the National Academy of Sciences*. 2010;107(48):20756–20761.
47. Lévy M, Franks PJS, Smith KS. The role of submesoscale currents in structuring marine ecosystems. *Nature Communications*. 2018;9(1):4758.
48. Burson A, Stomp M, Greenwell E, Grosse J, Huisman J. Competition for nutrients and light: testing advances in resource competition with a natural phytoplankton community. *Ecology*. 2018;99(5):1108–1118.
49. Certain G, Barraquand F, Gårdmark A. How do MAR(1) models cope with hidden nonlinearities in ecological dynamics? *Methods in Ecology and Evolution*. 2018;9(9):1975–1995.
50. Jacquet C, Moritz C, Morissette L, Legagneux P, Massol F, Archambault P, et al. No complexity-stability relationship in empirical ecosystems. *Nature Communications*. 2016;7(1).
51. Allesina S, Tang S. Stability criteria for complex ecosystems. *Nature*. 2012;483(7388):205–208.
52. García-Callejas D, Molowny-Horas R, Araújo MB. Multiple interactions networks: towards more realistic descriptions of the web of life. *Oikos*. 2018;127(1):5–22.
53. Yenni G, Adler PB, Ernest SKM. Do persistent rare species experience stronger negative frequency dependence than common species? Asymmetric NFD and persistent rare species. *Global Ecology and Biogeography*. 2017;26(5):513–523.
54. Bagchi R, Gallery RE, Gripenberg S, Gurr SJ, Narayan L, Addis CE, et al. Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature*. 2014;506(7486):85–88.
55. Comita LS, Queenborough SA, Murphy SJ, Eck JL, Xu K, Krishnadas M, et al. Testing predictions of the Janzen-Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *Journal of Ecology*. 2014;102(4):845–856.

56. Vallina SM, Ward BA, Dutkiewicz S, Follows M. Maximal feeding with active prey-switching: A kill-the-winner functional response and its effect on global diversity and biogeography. *Progress in Oceanography*. 2014;120:93–109.
57. Tuck SL, Porter J, Rees M, Turnbull LA. Strong responses from weakly interacting species. *Ecology Letters*. 2018;21(12):1845–1852.
58. Adler PB, Kleinhesselink A, Hooker G, Taylor JB, Teller B, Ellner SP. Weak interspecific interactions in a sagebrush steppe? Conflicting evidence from observations and experiments. *Ecology*. 2018;99(7):1621–1632.
59. Pacala SW, Levin SA. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, NJ; 1997.
60. Barton AD, Ward BA, Williams RG, Follows MJ. The impact of fine-scale turbulence on phytoplankton community structure: Phytoplankton and turbulence. *Limnology and Oceanography: Fluids and Environments*. 2014;4(1):34–49.
61. Breier RE, Lalescu CC, Waas D, Wilczek M, Mazza MG. Emergence of phytoplankton patchiness at small scales in mild turbulence. *Proceedings of the National Academy of Sciences*. 2018;115(48):12112–12117.
62. Bolker BM, Pacala SW. Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *The American Naturalist*. 1999;153(6):575–602.
63. Murrell DJ, Law R. Heteromyopia and the spatial coexistence of similar competitors. *Ecology Letters*. 2003;6(1):48–59.
64. Observation RF, program for Phytoplankton M, in coastal waters H. REPHY dataset - French Observation and Monitoring program for Phytoplankton and Hydrology in coastal waters. 1987-2016 Metropolitan data.; 2017.
65. Utermöhl H. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitt int Ver theor angew Limnol*. 1958;9.
66. Hernández Fariñas T, Bacher C, Soudant D, Belin C, Barillé L. Assessing phytoplankton realized niches using a French national phytoplankton monitoring network. *Estuarine, Coastal and Shelf Science*. 2015;159:15–27.

67. Hampton SE, Scheuerell MD, Schindler DE. Coalescence in the lake washington story: Interaction strengths in a planktonic food web. *Limnology and Oceanography*. 2006;51(5):2042–2051.
68. Holmes EE, Ward EJ, Scheuerell MD. Analysis of multivariate time-series using the MARSS package. User guide: <http://cran.r-project.org/web/packages/MARSS/vignettes/UserGuide.pdf>. 2014;.
69. Venables WN, Smith DM. the R Core Team. An Introduction to R Notes on R: A Programming Environment for Data Analysis and Graphics URL: [ran.r-project.org/doc/manuals/r-release/R-intro.pdf](http://cran.r-project.org/doc/manuals/r-release/R-intro.pdf). 2013;.
70. Scheef LP, Hampton SE, Izmet'eva LR. Inferring plankton community structure from marine and freshwater long-term data using multivariate autoregressive models. *Limnology and Oceanography: Methods*. 2013;11:475–484.
71. Ellner SP, Snyder RE, Adler PB. How to quantify the temporal storage effect using simulations instead of math. *Ecology Letters*. 2016;19(11):1333–1342.