

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

Sampling

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

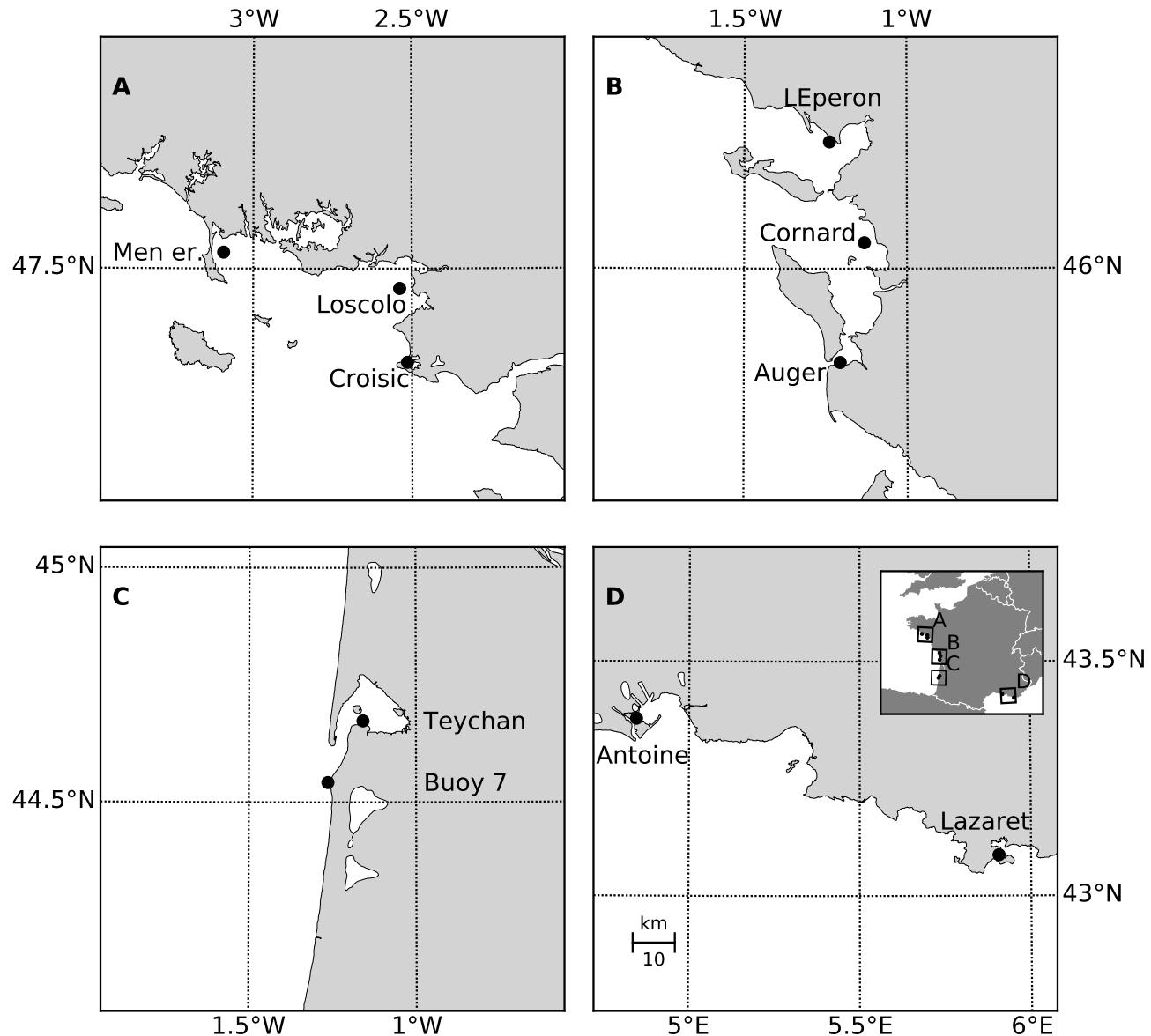


Figure S1: **Location of each study site in their region:** Brittany (A), Oléron (B), Arcachon (C) and the Mediterranean Sea (D). The common scale of the panels is given in the left corner of D.

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

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

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

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

Phytoplankton dynamics

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

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

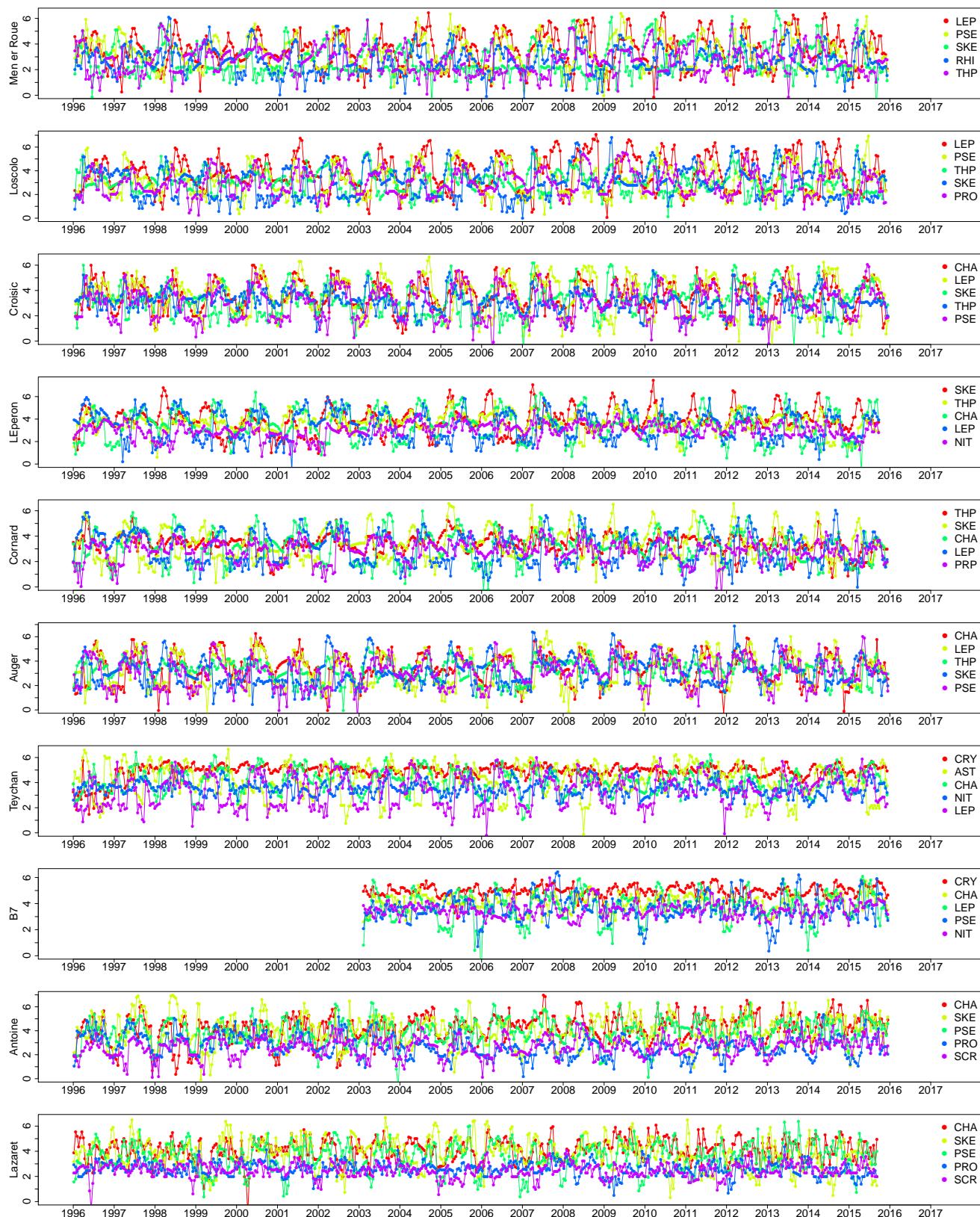


Figure S2: Time series of the 5 most abundant phytoplanktonic genera in each site.

MAR(1) models

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

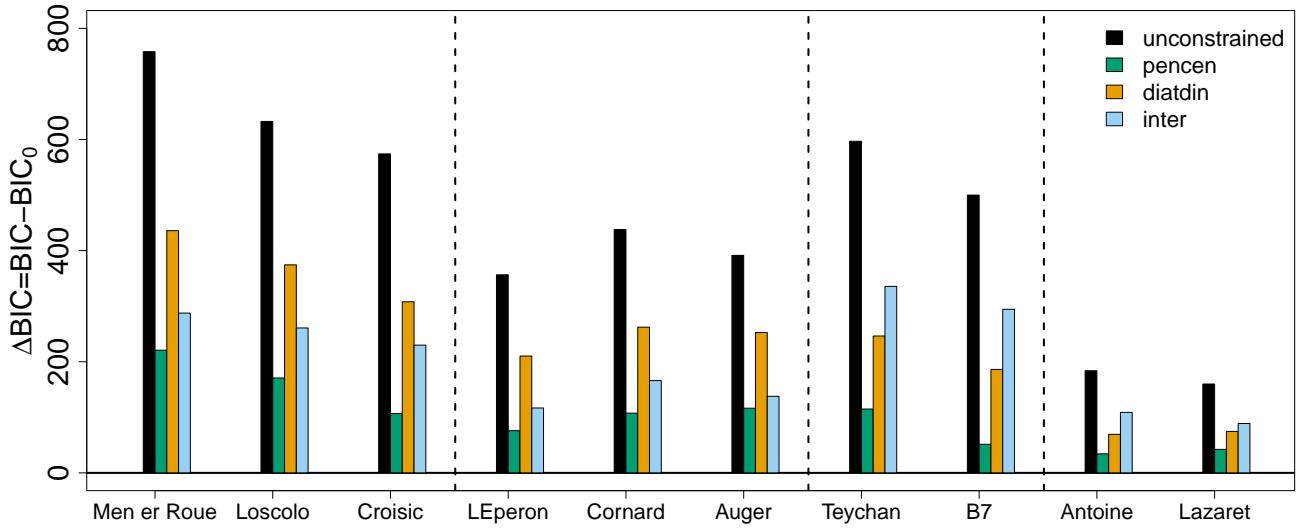


Figure S3: **Comparison of the BIC of different interaction scenarios**, compared to the null scenario (diagonal interaction matrix, allowing only intragroup interactions), for 10 sites in 4 different regions, separated by dashed lines (Brittany, Oléron, Arcachon and the Mediterranean Sea). Different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

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

In addition to the coefficients of the interaction matrix, MAR(1) models allowed us to estimate the effect of environmental variables. The regression coefficients reveal abiotic effects such as phenology (temperature, related to insolation) or responses to hydrological changes such as salinity variation (Fig. S4). Overall, temperature tended to have more effect on phytoplankton dynamics than salinity, which 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

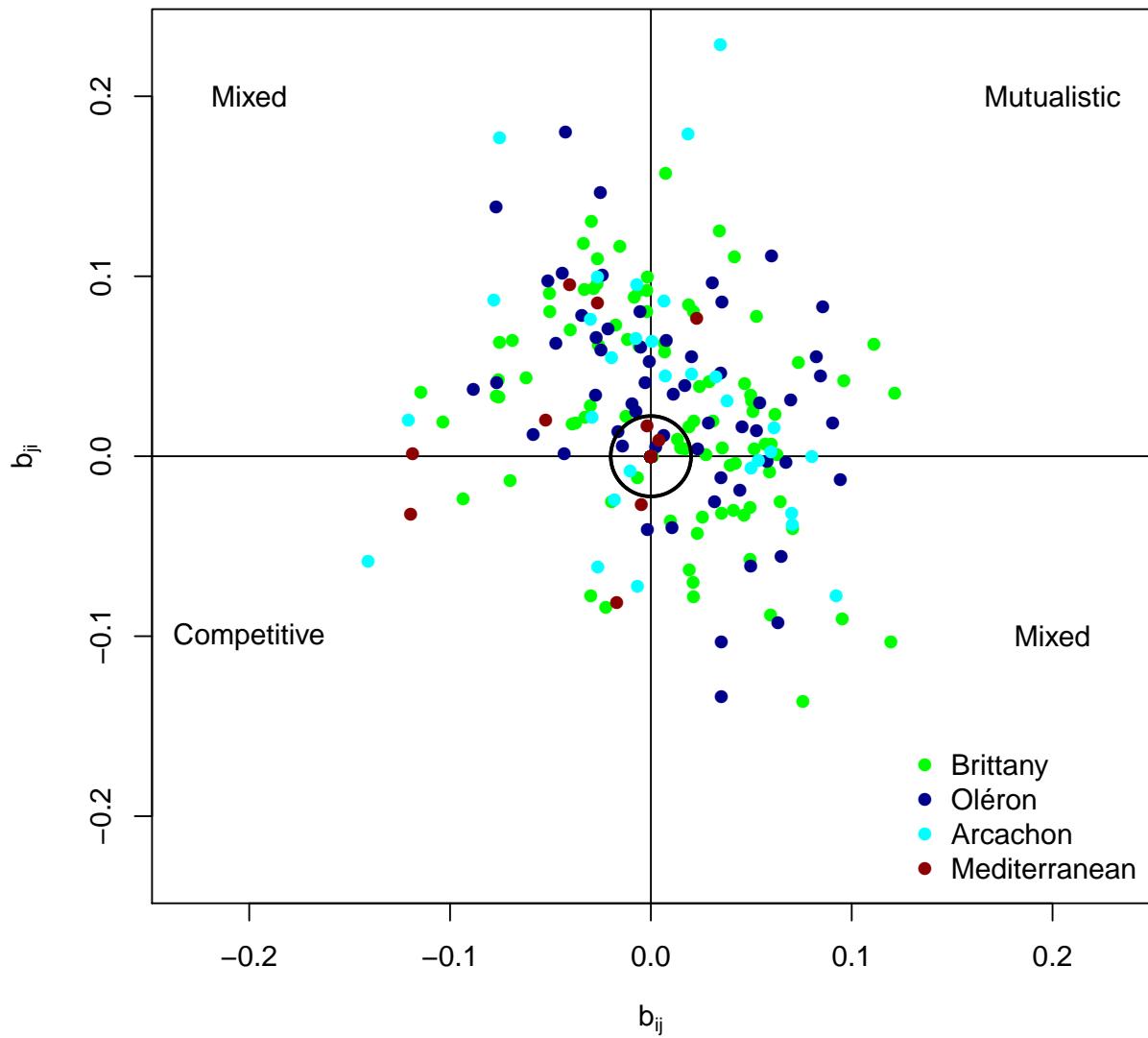


Figure S5: **Pairs of coefficients for each study site.** The effect of species i on j is given as a function of the effect of species j on species i . The black circle indicates the first quartile of the interaction values, under which we can assume that the effect is weak or null. Below this limit, $(+/+)$, $(+/-)$ 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 variance 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).

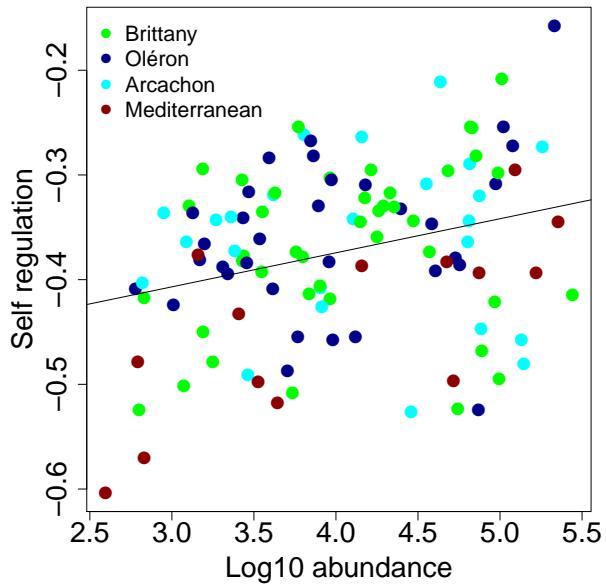


Figure S7: **Relation between abundance and self-regulation** (intragenus interaction coefficients). Mean abundance is computed for each genus in each site in 4 regions and intragenus interaction strengths are the diagonal coefficients of the interaction matrix ($\mathbf{B}-\mathbf{I}$).

Weighted connectance is described in Bersier *et al.* (2002). It is based on the average of vulnerability and generality in the network. More precisely, diversity measures of the interactions from ($H_{P,k}$) and to ($H_{N,k}$) the

phytoplanktonic group k can be computed as:

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

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

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

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

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

Weighted connectance C is then defined as:

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

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

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

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

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

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

MAR references and analysis

We present here the MAR references we used to compare the effects of intra- and intergroup interactions (Table S3, Fig. S8). We add information on the biome and taxa used in the study as they tend to be linked to the estimated parameters (Fig. S9). We should mention two potential biases associated with this comparison across the published literature. First, low-dimensional matrices tended to be more complete (less sparse) than high-dimensional matrices, as these small interaction matrices were used to study known interaction phenomena (observed predation between organisms, for instance). Conversely, the number of parameters to estimate increases as the square of the number of interacting taxa, leading most authors to reduce this set before the estimation process for large interaction matrices. There is therefore a positive correlation between sparsity and dimensionality (Fig S9). A second caveat is that while we informed our model selection by phylogeny, several authors have instead reduced the number of estimated parameters by an automated procedure, usually based on the comparison of hundreds of randomly chosen interaction matrices by AIC (Ives *et al.*, 1999). The latter choice is likely to bias high non-zero interactions in the literature. This is why we decided to present in the main text intra/inter ratios including interspecific (or intergroup) coefficients set to zero (see Fig. 4 in the main text), which should be less sensitive to the model selection method and therefore make comparisons across studies possible. In Fig. S8, mean interaction strengths were computed as the mean absolute value of only the set of coefficients which were deemed significant at the 95% threshold in the ($\mathbf{B}-\mathbf{I}$) matrix.

Code	Ref	Dimension	Type of organisms	Taxonomic level	System	T
1a	Ives <i>et al.</i> (1999), CLS	9	Zooplankton	Species and functional groups	Lake	100
1b	Ives <i>et al.</i> (1999), TLS	9	Zooplankton	Species and functional groups	Lake	100
2a	Klug <i>et al.</i> (2000)	2	Phytoplankton	Phylum	Lake	100
2b	Klug <i>et al.</i> (2000)	3	Zooplankton	Species	Lake	50
3a	Klug & Cottingham (2001)	4	Functional groups of plankton	NA	Lake	300
3b	Klug & Cottingham (2001)	5	Taxonomic groups of plankton	Phylum/division	Lake	300
4a	Ives <i>et al.</i> (2003)	4	Plankton	Zooplankton v. phytoplankton, size classes	Lake	100
4b	Ives <i>et al.</i> (2003)	4	Plankton	Zooplankton v. phytoplankton, size classes	Lake with high planktivory	100
4c	Ives <i>et al.</i> (2003)	4	Plankton	Zooplankton v. phytoplankton, size classes	Lake with low planktivory	100
5a	Hampton & Schindler (2006)	14	Plankton	Phylum (phytoplankton), genus (zooplankton)	Lake	300
5b	Hampton & Schindler (2006)	14	Plankton, growing season	Phylum (phytoplankton), genus (zooplankton)	Lake	200
6a	Hampton <i>et al.</i> (2006)	13	Plankton	Phylum (phytoplankton), genus (zooplankton)	Lake	400
6b	Hampton <i>et al.</i> (2006)	7	Simpler web, plankton	Phylum (phytoplankton), genus (zooplankton)	Lake	400
7a	Huber & Gaedke (2006)	10	Ciliates	Genus and species	Lake	300
7b	Huber & Gaedke (2006)	10	Phytoplankton	Genus and species	Lake	300
8a	Yamamura <i>et al.</i> (2006)	3	Insects	Species	Terrestrial	50
9a	Vik <i>et al.</i> (2008)	2	Lynx/Hare	Species	Terrestrial	100
10a	Lindegren <i>et al.</i> (2009)	3	Fish	Species	Baltic Sea	30
11a	Griffiths <i>et al.</i> (2015)	7	Phytoplankton	Phylum	Coastal site	1000
11b	Griffiths <i>et al.</i> (2015)	7	Phytoplankton	Phylum	Offshore site	700
12a	Barraquand <i>et al.</i> (2018)	12	Phytoplankton	Genus	Outside a bay	300
12b	Barraquand <i>et al.</i> (2018)	12	Phytoplankton	Genus	Inside a bay	500

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

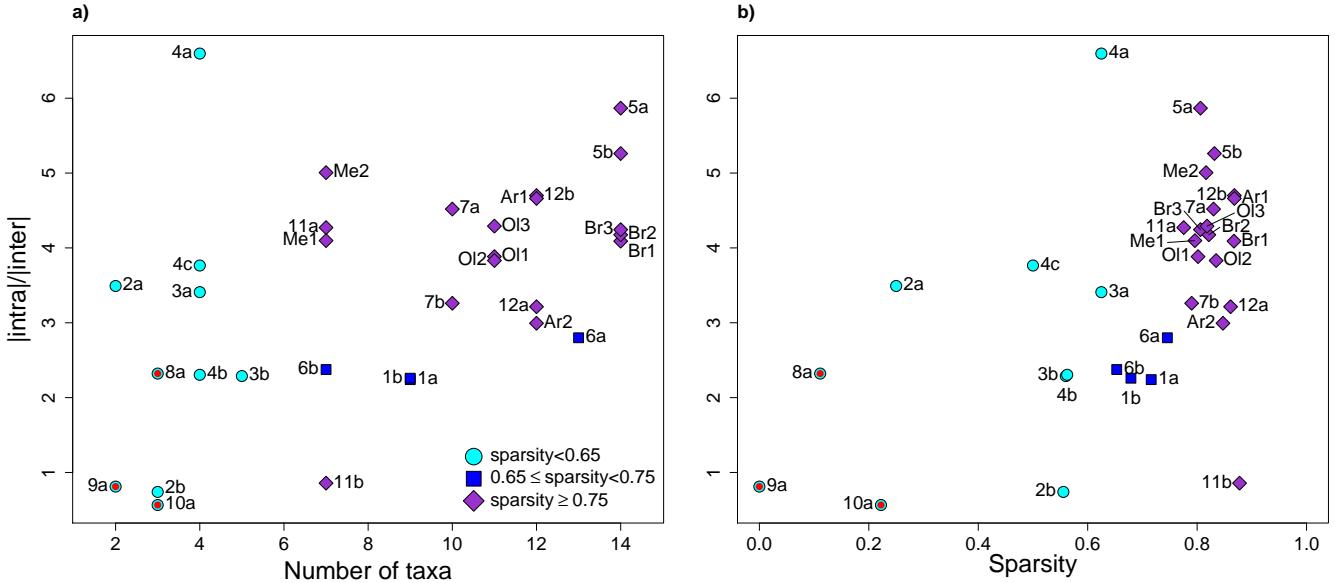


Figure S8: **Ratio of intra-to-intergroup interaction strength in MAR(1) studies.** Only significant values are taken into account and missing values in the matrix are not considered (e.g., not replaced by 0 as they are in the main text). The color and shape of each point are a function of the sparsity 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. Red dots correspond to terrestrial and/or low dimension, predator-prey systems, giving a lower bound for the intra/inter ratio. Corresponding studies are described in Table S3.

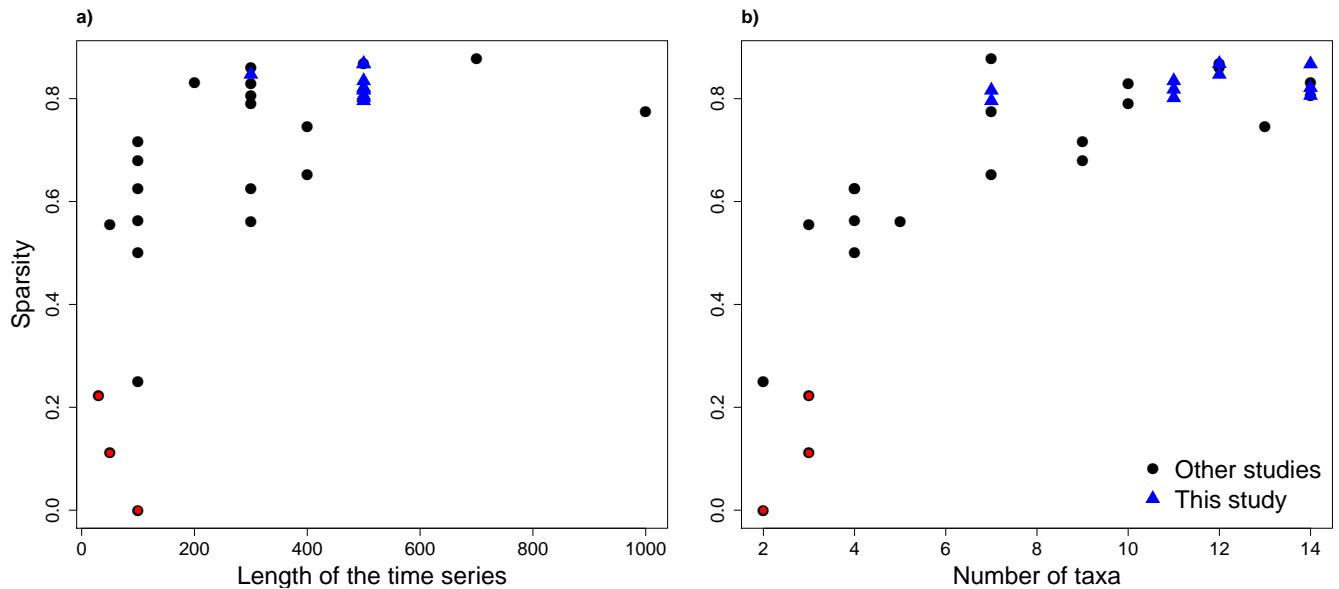


Figure S9: **Relation between interaction sparsity and study design** in studies described in Table S3. Red dots correspond to terrestrial and/or low dimension, predator-prey systems, giving a lower bound for the intra/inter ratio. Blue triangles correspond to the present study.

Connection to Lotka-Volterra competition dynamics

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

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

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

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

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

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

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

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

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

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

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

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

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

For this demonstration, we consider diffuse competition, that is

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

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

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

and

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

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

By symmetry, we can also write

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

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

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

and

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

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

References

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

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