

Response to comments (2) – Strong self-regulation and widespread facilitative interactions in phytoplankton communities

Coralie Picoche and Frederic Barraquand

Associate Editor’s comments:

Both reviewers are satisfied with the revision. I recommend its publication after minor revision.

Dear Editor,

We thank both reviewers for their comments and for this opportunity to improve our manuscript. Hereafter, we answer (in blue) to the main remark regarding the comparison between continuous- and discrete-time models in the context of stability theory. Overall, we show that our results using interaction matrices in discrete-time are robust to considering mathematical equivalents of continuous-time matrices, as requested (and anticipated) by reviewer 1.

In addition to the changes described in response to the referee comments, we have taken this opportunity to improve the wording of certain sentences, l. 26-27, l. 96-99, l. 124-125, l. 234-235, l. 246-247, l. 255, and l. 368-371 in the main text. It also occurred to us that it was not always crystal clear on which set of interaction coefficients our reported metrics, such as intra/inter interaction strengths, were computed (i.e., coefficients that are all significantly different from zero vs coefficients including non-significant values, excluding coefficients set to zero before model fitting vs including such exactly-zero values, etc.). To provide the reader with an unambiguous map to all computations performed in this paper, we have added a section in the SI which explains unequivocally to which assumption on coefficients corresponds which reported figure in the main text.

We hope that the text is once again clearer, and now fit for publication in Journal of Ecology,

With our best regards,

Coralie Picoche & Frédéric Barraquand.

Reviewer: 1

I thank the Authors for thoroughly addressing all my previous points. I just wanted to briefly revisit the problem of the random matrix results. By all means, if the Authors still think that this is worthwhile including, then they should go ahead and do so. In that case though, I have one extra technical point to make.

Right now, the claim is that the discrete-time analogue of the matrix A is $B - I$ (where A is the continuous-time interaction matrix, B is the discrete time one, and I is the identity matrix). My understanding is slightly different. Let us start from the linearized system

$$\frac{dx(t)}{dt} = Ax(t),$$

where x is the state vector, t is time, and A is the interaction matrix. Solving this equation using the matrix exponential $\exp(A)$ (obtained by substituting A into the Taylor series of the exponential function), we get

$$x(t) = e^{At}x(0).$$

For one time step then,

$$x(t+1) = e^{A(t+1-t)}x(t) = e^A x(t),$$

so the discrete-time analogue of A is actually $B = \exp(A)$. From this, $A = \log(B)$, where we take the matrix logarithm of B . Now, if B is almost equal to the identity matrix, this indeed reduces to $A \approx B - I$ (by Taylor expanding the log function to first order near I). But this only holds in that special case.

We agree with the referee’s mathematics and are thankful for this meticulous analysis. That said, we believe that there are multiple ways to connect a discrete-time (log)linear model to the (potentially nonlinear) continuous-time process that it approximates:

- Make a linear continuous-time approximation, which is then integrated over time, as done by the referee.
- Integrate a continuous-time model over a time period, and then linearize it, as we do in “Connection to Lotka-Volterra dynamics”.

Indeed, the quality of the linear approximation used is ultimately dependent on the choice of the timescale (see Hampton & Schindler 2006). In our case where the time step is two weeks, the linear approximation is adequate as shown before. But there is no guarantee that the model would stay linear for very short intervals of time. Hence, it is not 100% clear that $A = \log(B)$ is intrinsically better than the crude approximation $A = B - I$ in all cases: this statement is somehow conditional to how well a linear continuous-time model approximates the true underlying continuous-time process.

But we agree with the referee that his suggestion makes excellent mathematical sense, and we do investigate below what would occur if we used $A = \log(B)$ as the equivalent continuous-time mathematical model.

I am mentioning this because relating certain metrics to $\max|\lambda|$ (like SV , as in Figure 2d) will only connect to existing literature well if $A \approx B - I$ holds. The reason is that SV has been related to continuous-time stability, not discrete-time, and the Authors’ system is discrete time. However, as long as $A \approx B - I$, it is indeed true that any effect making B more stable will also make A more stable. The difference between discrete- and continuous-time formulations therefore disappears. But $A \approx B - I$ is not true generally. For instance, consider the example below, with a matrix whose offdiagonal entries are skewed towards mutualisms:

```
set.seed(1) ## set random seed for reproducibility; feel free to change this
S <- 500 ## number of species
mu <- 0.2 ## mean of offdiagonal coefficients
sigma <- 1 ## standard deviation of offdiagonal coefficients
d <- -100 ## diagonal of matrix
A <- matrixnorm(S*S, mu, sigma), S, S) ## generate random matrix
diag(A) <- d ## set its diagonal entries to d
eA <- eigen(A)$values ## obtain eigenvalues
plot(eA) ## plot the spectrum
## add analytical predictions of the dominant (largest modulus) and leading (largest
## real part) eigenvalues to the plot, based on random matrix theory
## (e.g., Barabás et al 2016 Am Nat, Appendix B4.2)
points(c(d - mu - sqrt(S * sigma^2) + 0i, S * mu + d + 0i), col="red", pch=3)
```

In this example, the leading eigenvalue (the one with maximum real part) is small, while the dominant eigenvalue (the one with maximum modulus) is large. Here, if we e.g. change ‘mu’ from 0.2 to 0, this will have a large effect on the leading eigenvalue, but a negligible effect on the dominant one.

Long story short: in general, the effects that will result in stability in discrete time (small dominant eigenvalue) are different from those resulting in stability in continuous time (small leading eigenvalue). The only time they coincide is when B is almost the identity, because then $A \approx B - I$. Now, the Authors’ matrices happen to be diagonally dominated, so there is good reason to think that $A \approx B - I$ is a fine approximation. However, it would be important to perform a quick calculation to make sure

- e.g., by comparing $B - I$ and $\log(B)$.

We are very grateful for this thorough analysis. In the manuscript, we present the dominant eigenvalue of B , which is the usual metric of resilience for this type of model (Ives *et al.*, 1999, 2003). As highlighted by the referee, the relationship between the dominant eigenvalue of B , $\max(|\lambda_B|)$ and complexity properties should be mediated by the continuous-time resilience equivalent $\max(\text{Re}(\lambda_A))$, where A is either $B - I$ or $\log(B)$. We therefore decompose the relationship into two panels: $\max(|\lambda_B|) = f(\max(\text{Re}(\lambda_A)))$ (Fig. 1 a) and $\max(\text{Re}(\lambda_A)) = f(SV)$ (Fig. 1 b).

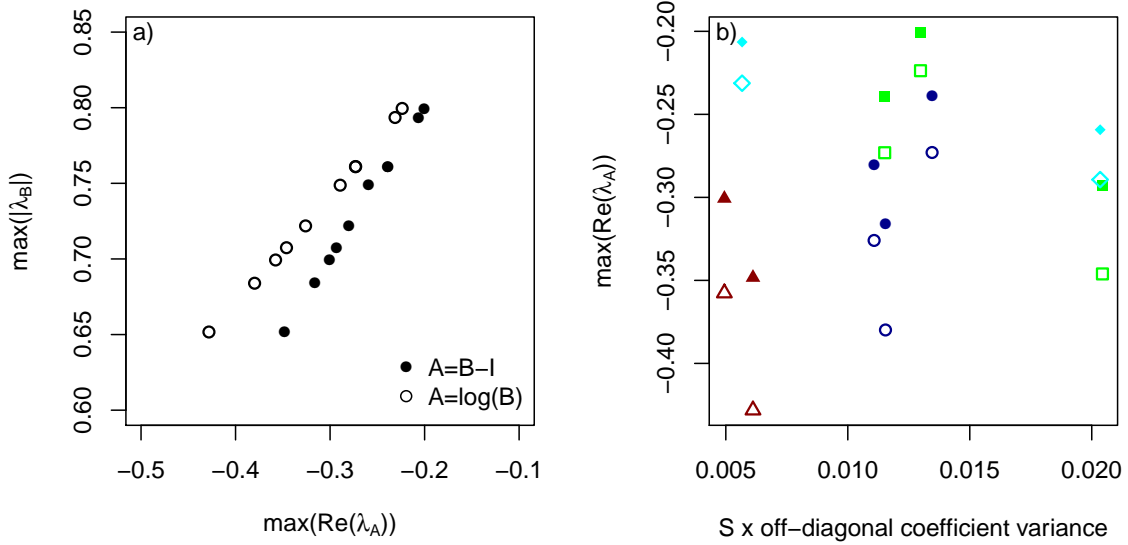


Figure 1: Relation between the modulus of the dominant eigenvalue for B (discrete time, on the y-axis) and real part of the lead eigenvalue for $A = B - I$ and $\log(B)$ (continuous time, on the x-axis) in (a); relation between $\max(\text{Re}(\lambda_A))$ and an index of complexity, that is the variance of the off-diagonal coefficients weighted by the number of species in each community in (b).

In our case, we see that:

- real parts of the lead eigenvalues of A are similar for $A = B - I$ and $A = \log(B)$ (the difference is around 0.04 for values between -0.45 and -0.2, Fig. 1 a), as guessed by the referee.
- the modulus of the dominant eigenvalue of B is strongly correlated to the real part of the lead eigenvalues of $A = B - I$ and $A = \log(B)$ (> 0.99 in both cases).
- there is still an absence of relation of $\max(\text{Re}(\lambda_A))$ with SV , for both $A = B - I$ and $A = \log(B)$.

Given that $\max(|\lambda_B|)$ correlates to $\max(\text{Re}(\lambda_A))$, irrespective of whether $A = B - I$ or $A = \log(B)$, and that $\max(\text{Re}(\lambda_A))$ does not show any relation to SV , we show that our conclusions concerning the lack of relation between resilience and complexity still hold and are consistent with a continuous-time model formulation.

The section “Connection to continuous-time stability” containing the figure and explanations given above has been added right before the section “Connection to Lotka-Volterra dynamics” of the SI.

In light of this, I also feel that the last section of the Authors’ supplement (“Connection to Lotka-Volterra dynamics”) is not really necessary - and it was somewhat hand-waivy to begin with. Instead, it could simply be argued that $B - I$ is indeed almost equal to $\log(B)$ (in case it is true).

As we highlight above, linearizing an integrated model is another way to obtain a discrete-time linear approximation. Moreover, this section of the Appendix relating the Beverton-Holt competition model to the linear MAR model is mostly directed at helping plant community ecologists understanding better our model framework. Indeed, the Beverton-Holt competition model prevails in this field. We

thus think that it makes it easier for the readership of Journal of Ecology to see how the models that we use in this paper connect to the ones that they have potentially used previously or often read about.

We now refer to this section of the SI l. 96-99 in the main text, explaining that its main purpose is to connect to Beverton-Holt competition, and then interpret more carefully the map between MAR(1) and Beverton-Holt models in the Discussion l. 235-242, acknowledging explicitly the potential difficulties in comparing the two frameworks (the SI adds some more refined computation of ratios of *averaged* interaction strengths).

But I emphasize that these are just minutia whose purpose is to make the manuscript even better than it currently is. Otherwise, I am very much satisfied with the paper and strongly recommend its publication.

Sincerely,
Gyuri Barabas

We would like to thank the referee for his kind and encouraging words, and for the chance to improve once more the analysis of our data.

Reviewer: 2

I thank the authors for their answers and modifications. Bérangère Péquin

Thank you for your second reading.

References

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- Ives, A., Gross, K. & Klug, J. (1999). Stability and Variability in Competitive Communities. *Science*, 286, 542–544.
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