



Replication / ecology

[Re] Biodiversity of plankton by species oscillations and chaos

Guillaume Doyen¹, Coralie Picoche^{1, }, and Frédéric Barraquand^{1, }¹Institut de Mathématiques de Bordeaux (UMR 5251), University of Bordeaux, CNRS, Bordeaux INP, Talence, FranceEdited by
(Editor)Received
XXXPublished
XXXDOI
—

1 Introduction

In the present article, we replicate the results of Huisman & Weissing 1999 *Biodiversity of plankton by species oscillations and chaos* [1], an attempt to resolve the paradox of the plankton [2] with a nonlinear ordinary differential equation model based on resource competition theory.

According to many mathematical models, the number of phytoplankton species in a single homogeneous medium cannot exceed the number of separate resources available [3, 4, 5] if the dynamics converge to a stable fixed point. However, it is very common to observe more species than easily identifiable resources in field conditions. This led Hutchinson to formulate the paradox of the plankton [2]. Using numerical simulations of their ODE model, Huisman & Weissing [1] showed that “supersaturated coexistence” is possible, where more consumer species than resource items coexist through oscillations or chaos, induced by the interactions between consumers and resources. We attempt here to check this finding.

In addition to the replication of the numerical results of Huisman and Weissing [1], in order to evaluate the sensitivity to the exact parameters used, we also present two novel numerical experiments inspired by follow-up articles, *Does “supersaturated coexistence” resolve the “paradox of the plankton”?* by Schippers et al. 2001 [6], and *Towards a solution of the plankton paradox: the importance of physiology and life history* by Huisman et al. 2001 [7]. These articles suggested that supersaturated coexistence might be difficult to obtain outside of the restricted parameter scenarios considered in the original article. Schippers et al. [6] assessed the sensitivity of diversity to parameter perturbations. They did so changing parameters for one species at a time, concluding that supersaturated coexistence was unlikely, while Huisman et al. [7] showed how some trade-offs can make parameter combinations favourable to coexistence emerge (although most of the scenarios they consider confirm the results of Schippers et al. [6]). Here, we further consider mild perturbations of intrinsic population growth rates of all species at once (though not necessarily in the same direction), a hypothesis which we deem coherent with whole-ecosystem perturbations. If supersaturated coexistence is a likely coexistence mechanism, small changes to population growth rates should not massively affect the number of coexisting species.

Copyright © 2023 G. Doyen, C. Picoche and F. Barraquand, released under a Creative Commons Attribution 4.0 International license.
Correspondence should be addressed to Frédéric Barraquand (frederic.barraquand@u-bordeaux.fr)
The authors have declared that no competing interests exist.
Code is available at https://github.com/fbarraquand/supersaturated_coexistence..

2 Model

We describe below the model of phytoplankton community dynamics of Huisman & Weissing [1]. Let N_i and R_j respectively be the population density of species i and concentration of resource j , $i \in \llbracket 1, n \rrbracket$ and $j \in \llbracket 1, k \rrbracket$ with n and k the number of different species and resources. The time derivatives of N_i and R_j are given by:

$$\frac{dN_i}{dt} = N_i(\mu_i(R_1, \dots, R_k) - m_i) \quad (1)$$

$$\frac{dR_j}{dt} = D(S_j - R_j) - \sum_{i=1}^n c_{ji}\mu_i(R_1, \dots, R_k)N_i \quad (2)$$

with parameters

m_i the mortality rate of species i

D the system's turnover rate

S_j the supply concentration of resource j

c_{ji} the content of resource j in species i

μ_i the growth rate of species i ,

defined using the Monod equation and Liebig's law of the minimum:

$$\mu_i(R_1, \dots, R_k) = \min_{j \in \llbracket 1, k \rrbracket} \left(\frac{r_i R_j}{K_{ji} + R_j} \right). \quad (3)$$

The growth rates are defined using:

r_i the maximum growth rate of species i

K_{ji} the half-saturation constant for resource j of species i .

In order to reproduce the results of Huisman & Weissing [1], the differential equations were integrated using the `deSolve` [8] package in its 1.32 version in R [9] 4.2.0, using the same parameter sets as in the original article.

Multiple simulations are performed and illustrated in the original article as well as here: In Figure 1 a) and b), 3 species are competing for 3 resources, in c), 6 species are competing for 3 resources (supersaturation) and in d), 9 species are competing for 3 resources (supersaturation again). In Figure 2, 5 species are competing for 3 resources. In Figure 3, 5 species are competing for 5 resources. In Figure 4, 12 species are competing for 5 resources. In Figure 2 and Figure 1 a), b) and for the bifurcation diagram of Figure 3, all of the species are introduced at the same time in the simulation. In Figure 4 and Figure 1 c), d), the species were introduced sequentially. Huisman et al. [1] have provided the starting times of each species introduction when needed, in addition to the parameters.

As Schippers et al. [6], we were wondering how and why the parameter sets were initially chosen, and if the results would remain the same for slightly different parameters. Several simulations were made in Schippers et al. [6] and Huisman et al.'s response [7], in order to evaluate how robust was supersaturated coexistence. In the same spirit, we carried out some new numerical experiments with a slightly different perspective.

We chose to focus on evaluating the robustness of the last simulation of Huisman & Weissing [1], displayed on Figure 4. We focused on perturbing the growth rate parameter, r_i , denoted as μ_{\max} in the follow-up articles [6, 7]. As changing only a single one of the n intrinsic growth rates r_i (as done earlier in the follow-up articles [6, 7]) appeared a little artificial to us, we chose to randomly perturb all of the n intrinsic growth rates r_i at once, as would typically do an ecosystem-wide perturbation that is not directly related to the modelled resources. Furthermore, it seems overall more realistic, as the literature supports the idea that growth rates may vary between species even in the absence of perturbations [10]. In a first numerical experiment, we considered the exact same invasion sequence as Huisman & Weissing [1]. In the second numerical experiment, we started with the full set of species at once.

In order to conduct the numerical experiments proposed earlier, the method used to plot the fourth Figure has been reused. The two experiments were conducted 500 times each, with as many different parameter sets: the r_i , originally all set to the value of 1, were drawn according to a truncated normal distribution. The mean was $\mu = 1$ and the variance was $\sigma = 0.1$, corresponding to $CV = 10\%$. The distribution was truncated using $\mu \pm 3\sigma$, in other words r_i values remain between 0.7 and 1.3 (and most values are much closer to 1). This range of values remains consistent, and even conservative, when compared to experimental values [10], where CVs can be larger. As we are trying to challenge the robustness of the replicated simulation, we do not change any other parameters: thus we only conduct the simulations for a duration of 10000 days, as the original simulations. However, in order to easily visualise how biodiversity changes over time, we also measure the number of extant species at the times used in the article to introduce new species, i.e. after 1,000, 3,000 and 5,000 days.

3 Results

3.1 Reproduction

We were able to replicate the four figures of Huisman & Weissing [1], presented below.

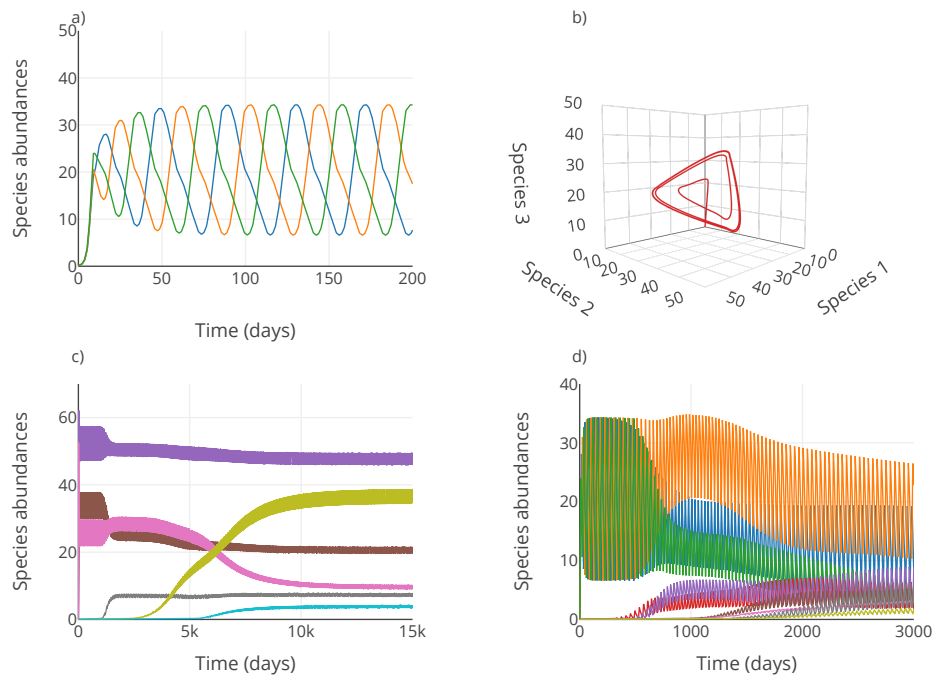


Figure 1. Oscillations on three resources. a), Time course of the abundances of three species competing for three resources. b), The corresponding limit cycle. c), Small-amplitude oscillations of six species on three resources. d), Large-amplitude oscillations of nine species on three resources.

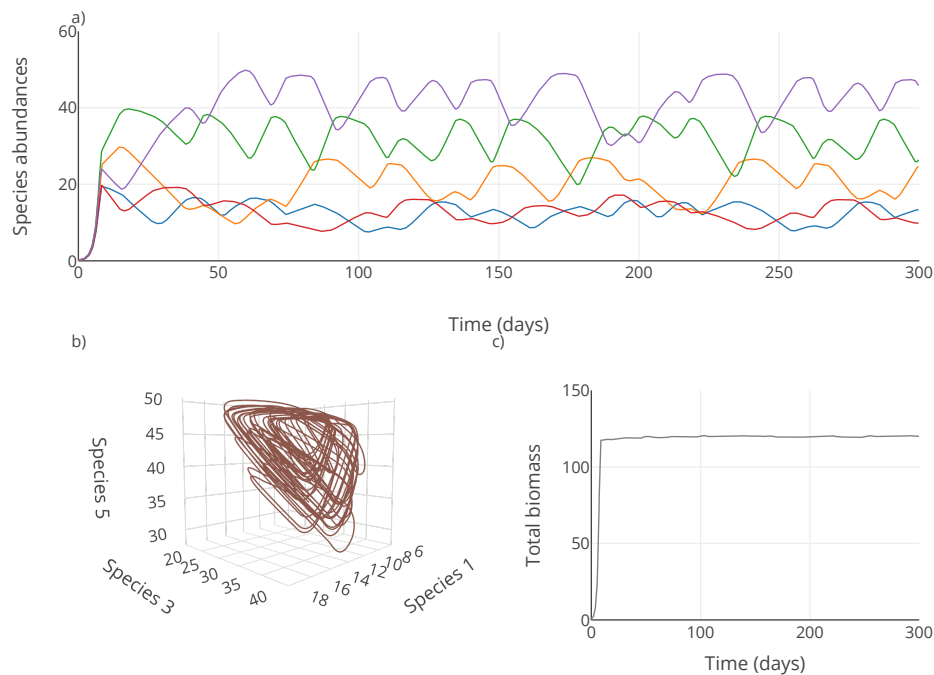


Figure 2. Chaos on five resources. a) Time course of the abundances of five species competing for five resources, b) The corresponding chaotic attractor. The trajectory is plotted for three of the five species, from the period from $t = 1, 000$ to $t = 2, 000$ days, c) Time course of total community biomass.

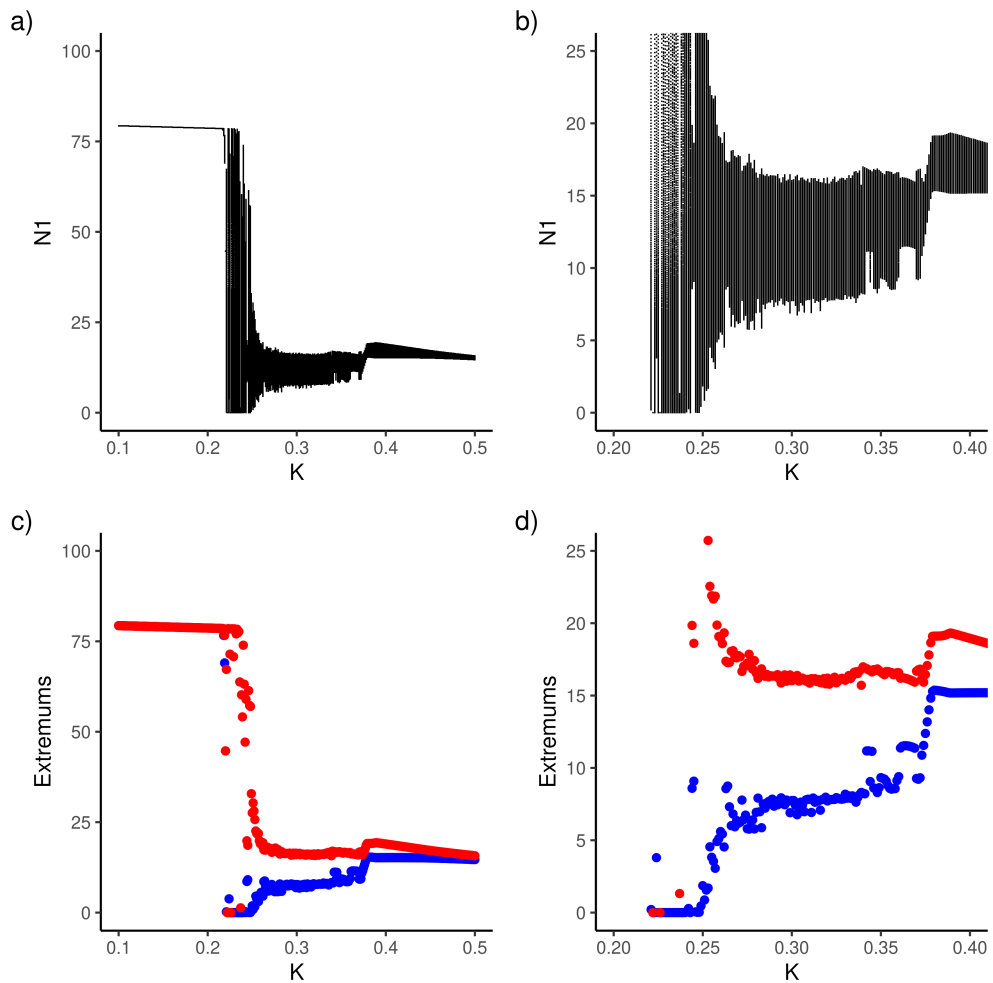


Figure 3. Bifurcation diagram, for five species competing for five resources. a) All of the values of species 1, plotted during the period from $t = 2,000$ to $t = 4,000$ days, as a function of the half-saturation constant K_{41} . Part of a) is magnified in b). c) show the local minima and maxima of species 1, plotted during the period from $t = 2,000$ to $t = 4,000$ days, as a function of the half-saturation constant K_{41} . Part of c) is magnified in d).

The bifurcation diagram 3 caption did not seem to correspond to the actual Figure, which seemed to display all of the points of the simulation between $t = 2,000$ and $t = 4,000$ rather than only the local extrema as the legend of the original article suggested. We have therefore chosen to draw those two options.

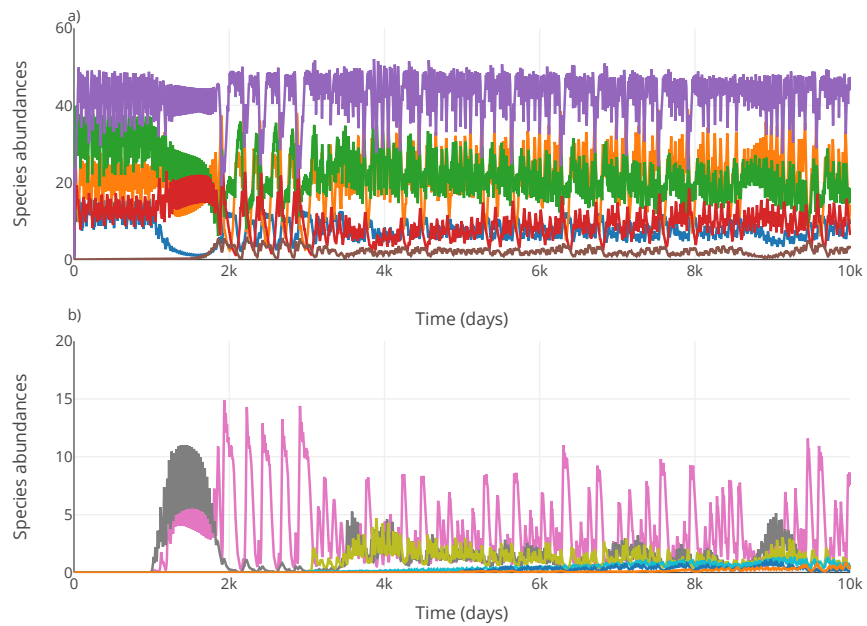


Figure 4. Competitive chaos and the coexistence of twelve species on five resources. a) abundances of species 1-6, b) abundances of species 7-12.

3.2 Additional numerical experiments

For the first numerical experiment, which introduces species sequentially as in the original simulation, the distribution of the number of extant species is displayed in Figure 5.

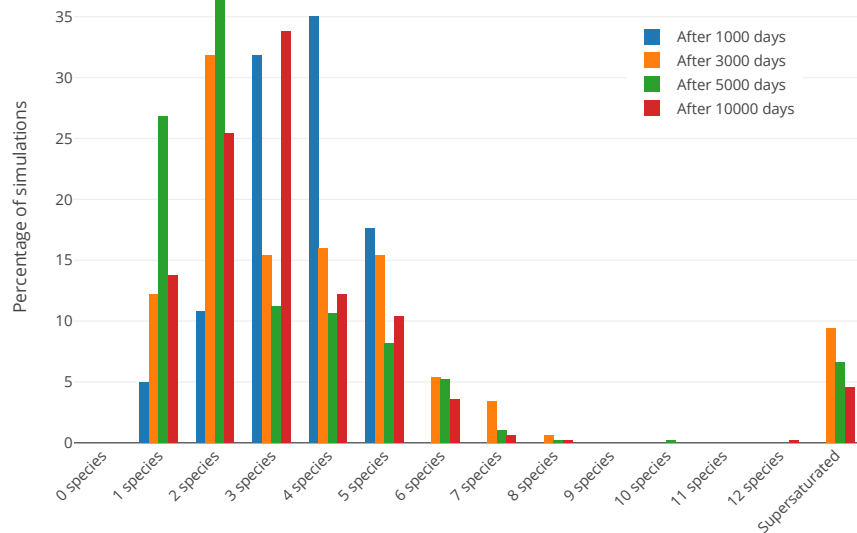


Figure 5. Percentages of simulations with x species present, or with observable supersaturated coexistence, at different times of the simulation for the first experiment. 500 simulations have been run in total and a species has been considered present if $N_i > 0.001$.

These percentages show that the persistence of five species or more is very unlikely, and that supersaturated coexistence may be present in a limited domain of parameter space.

Community dynamics for the first experiment, with possible extinctions, are shown by Figure 6. Note that panel 1 represents the original simulation with $r_i = 1 \forall i$, while r_i randomly varies between species for all other panels.

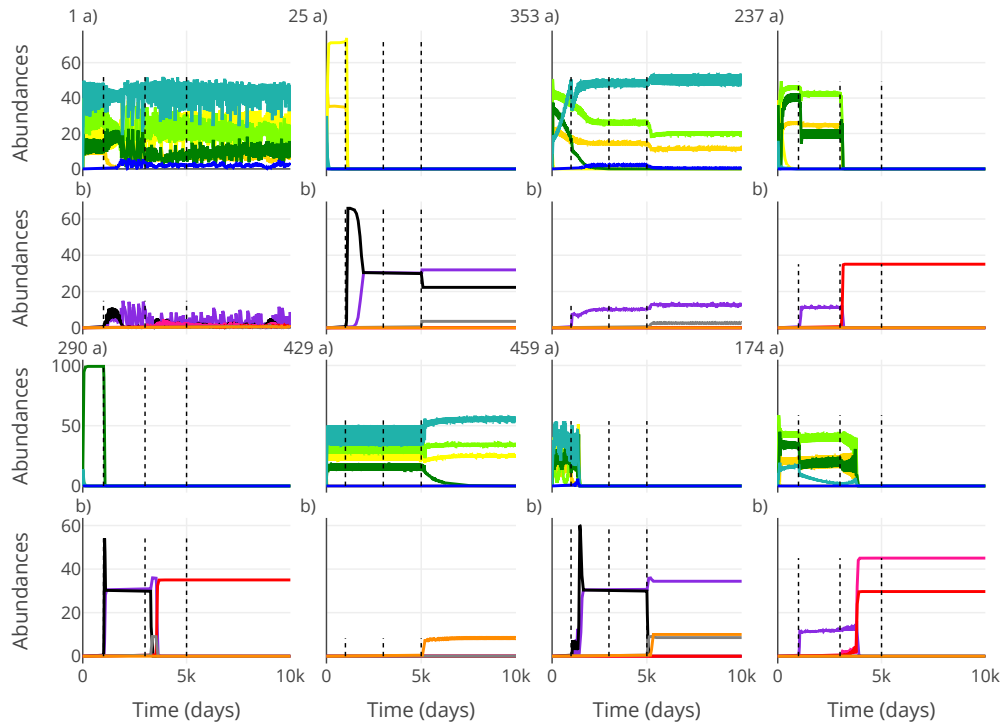


Figure 6. Visualisation of eight different simulations of twelve species on five resources. It is identical to Figure 4 except that intrinsic growth rates r_i are randomly varied. Except for the first panel (original Figure 4), the simulations chosen were randomly picked among the 500 constituting the numerical experiment. Each couple of subplots is labelled with the number of the corresponding simulation. a) abundances of species 1-6, b) abundances of species 7-12. Dashed vertical lines represent the introduction of new species.

We observe contrasted stationary endpoints, possibly with some oscillations or chaos during the invasion process. As shown in Figure 6, however, most species do not persist. For the second experiment, introducing all species at once, the percentage of experiments with x species present at different times of the simulation is displayed in Figure 7.

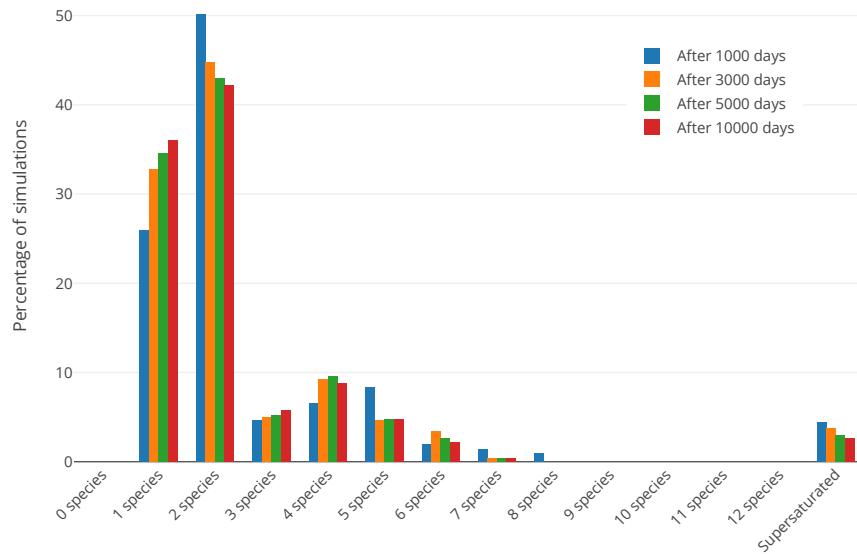


Figure 7. Percentage of simulations with x species present, or with observable supersaturated co-existence, at different times of the simulation for the second experiment. 500 simulations have been run in total and a species has been considered present if $N_i > 0.001$.

As before, a species has been considered present if $N_i > 0.001$ at the end of the simulation. The second experiment shows that persistence of five species or more is very unlikely when introducing all species at once (even more so than when introducing species sequentially), and that supersaturated coexistence is consequently very rare in this configuration.

Community dynamics for the second experiment, with possible extinctions, are described in the following Figure 8. Note that the subfigure 1 represents the original results with $r_i = 1 \forall i$, while r_i randomly varies as described in the methods for all other panels.

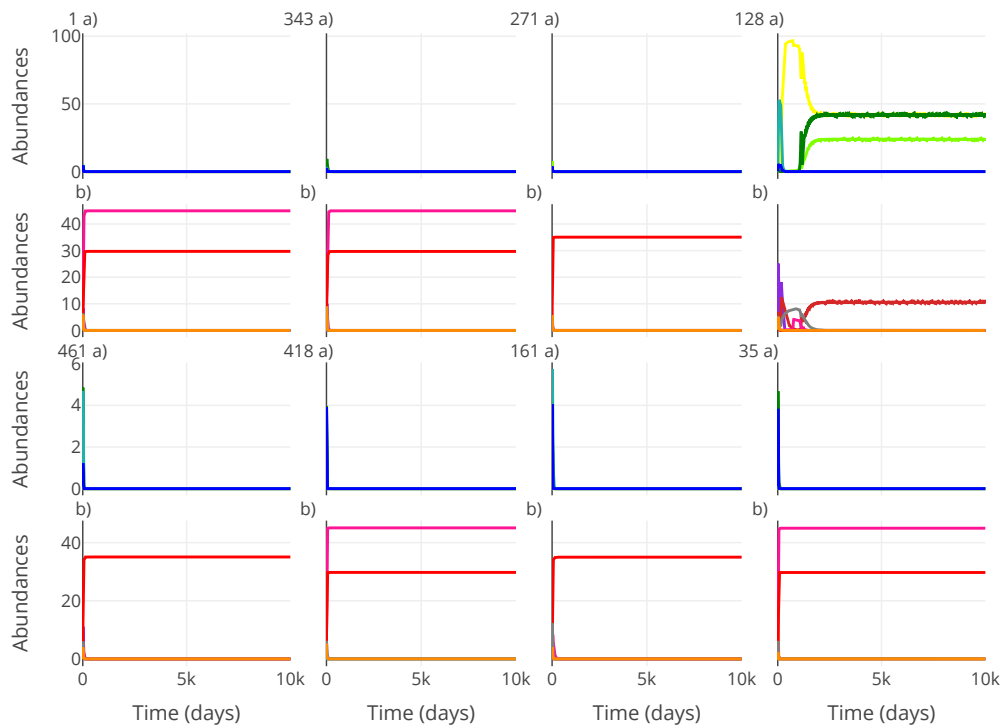


Figure 8. Visualisation of eight different simulations of twelve species on five resources, following the Figure 4 method except that r_i was randomly drawn for each of the species and all species were introduced at once. Except for the first panel (original parameters), the simulations illustrated were randomly picked among the 500 of the numerical experiment. Each couple of sub-plots is labelled with the number of the corresponding simulation. a) abundances of species 1-6, b) abundances of species 7-12.

As for the first experiment, we mostly observed either fixed (non-oscillatory) stationary endpoints or oscillations (Figure 8), but with even less persistent species than for the first experiment.

4 Discussion

We were able to successfully replicate the figures of the original paper. There are only minor differences in species dynamics in Figure 4, which are arguably due to differences in numerical integration.

However, the additional numerical experiments showed that slightly changing the values of the r_i parameters within a realistic range of values [10] almost always prevents the coexistence of twelve species on five resources and mostly prevents supersaturated coexistence in general. This is true when introducing species sequentially as in the original paper, as well as all at once.

Our results corroborate those of Schippers et al. [6], who showed that supersaturated coexistence through chaos or oscillations requires particular sets of parameter values, which are not robust to small perturbations. Our results, using a slightly different kind of perturbation, are therefore consistent with their conclusion that supersaturated coexistence is unlikely to solve the paradox of the plankton. Additionally, there are other reasons (mixing, spatial structure) not considered here, which could render supersaturated coexistence unlikely [11].

5 Appendix

We present below additional time series for random parameter sets and for the two numerical experiments. This is meant to help the reader to gain a better view of the dynamical behaviors for these two numerical experiments. The legends are identical to those of Figures 6 and 8.

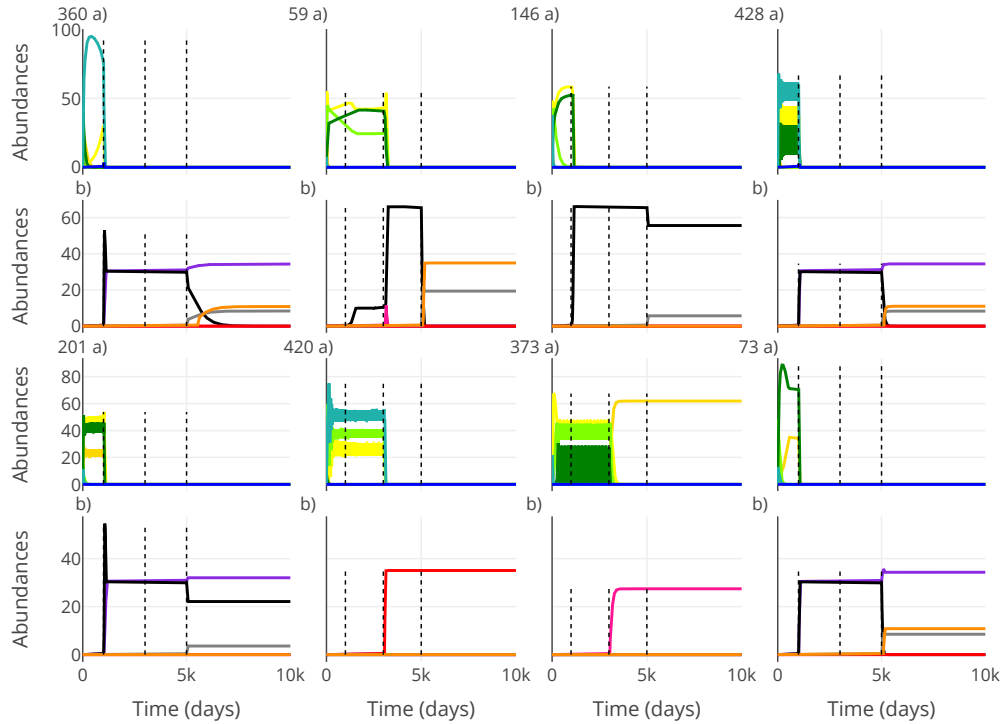


Figure 9. Visualisation of eight other different simulations of twelve species on five resources. It is identical to Figure 4 except that intrinsic growth rates r_i are randomly varied, and complements Figure 6. The simulations chosen were randomly picked among the 500 constituting the first numerical experiment. Each couple of subplots is labelled with the number of the corresponding simulation. a) abundances of species 1-6, b) abundances of species 7-12. Dashed vertical lines represent the introduction of new species.

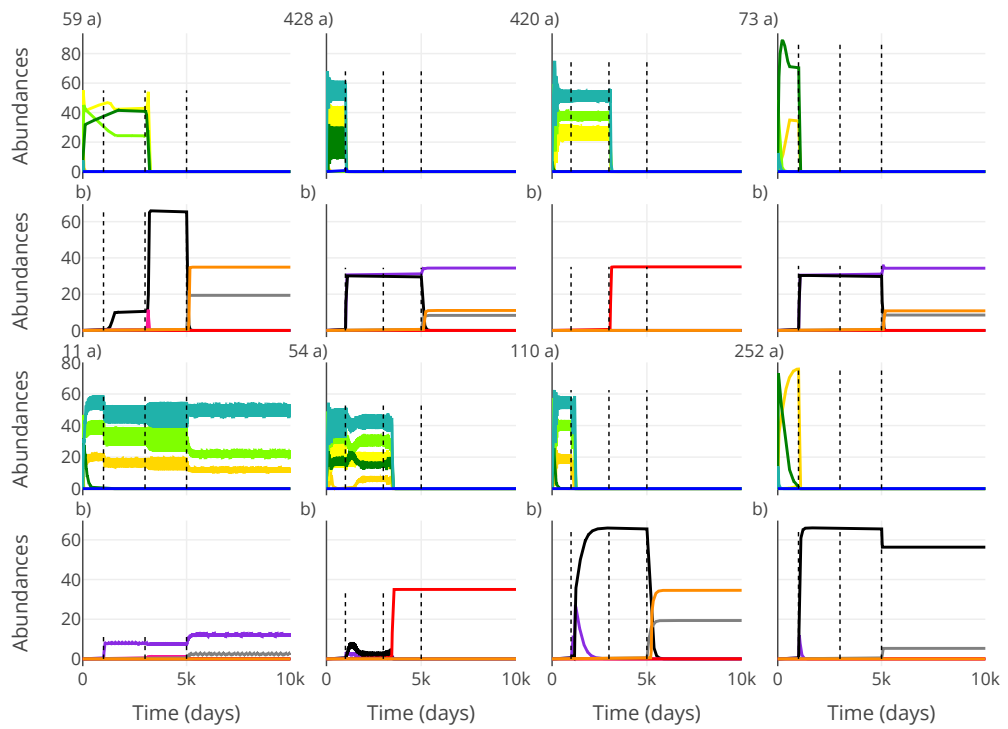


Figure 10. Visualisation of eight other different simulations of twelve species on five resources. It is identical to Figure 4 except that intrinsic growth rates r_i are randomly varied, and complements Figure 6. The simulations chosen were randomly picked among the 500 constituting the first numerical experiment. Each couple of subplots is labelled with the number of the corresponding simulation. a) abundances of species 1-6, b) abundances of species 7-12. Dashed vertical lines represent the introduction of new species.

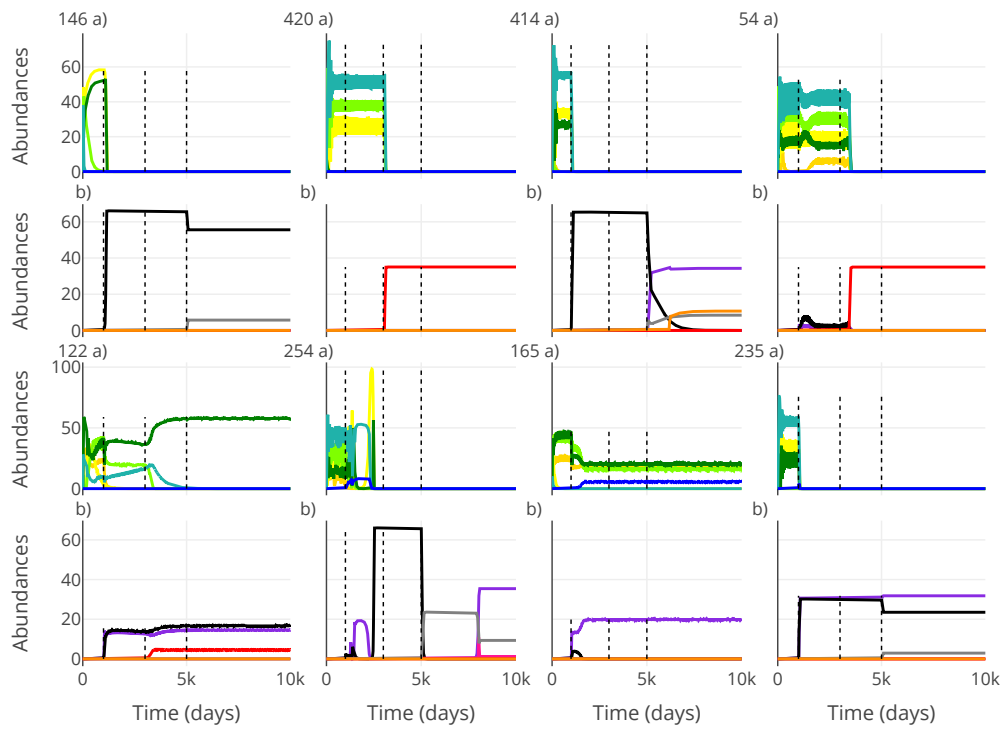


Figure 11. Visualisation of eight other different simulations of twelve species on five resources. It is identical to Figure 4 except that intrinsic growth rates r_i are randomly varied, and complements Figure 6. The simulations chosen were randomly picked among the 500 constituting the first numerical experiment. Each couple of subplots is labelled with the number of the corresponding simulation. a) abundances of species 1-6, b) abundances of species 7-12. Dashed vertical lines represent the introduction of new species.

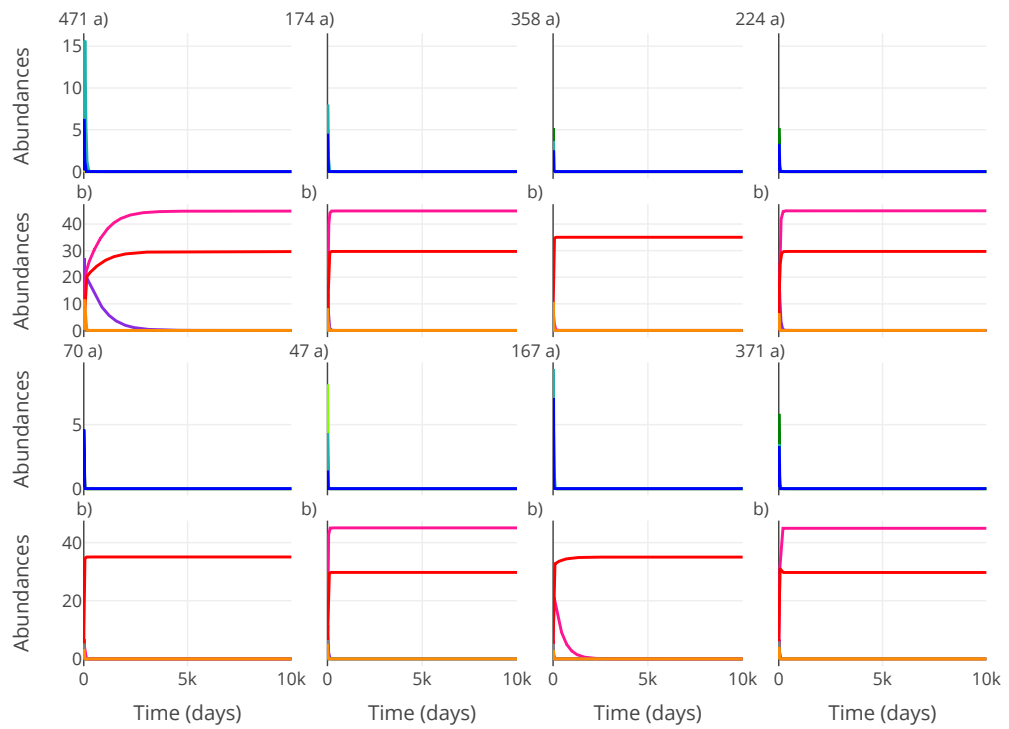


Figure 12. Visualisation of eight other different simulations of twelve species on five resources, following Figure 4, except that r_i are randomly drawn for each of the species, and all species were introduced at once (complements Figure 8). The simulations shown were randomly picked among the 500 of the numerical experiment. Each couple of subplots is labelled with the number of the corresponding simulation. a) abundances of species 1-6, b) abundances of species 7-12.

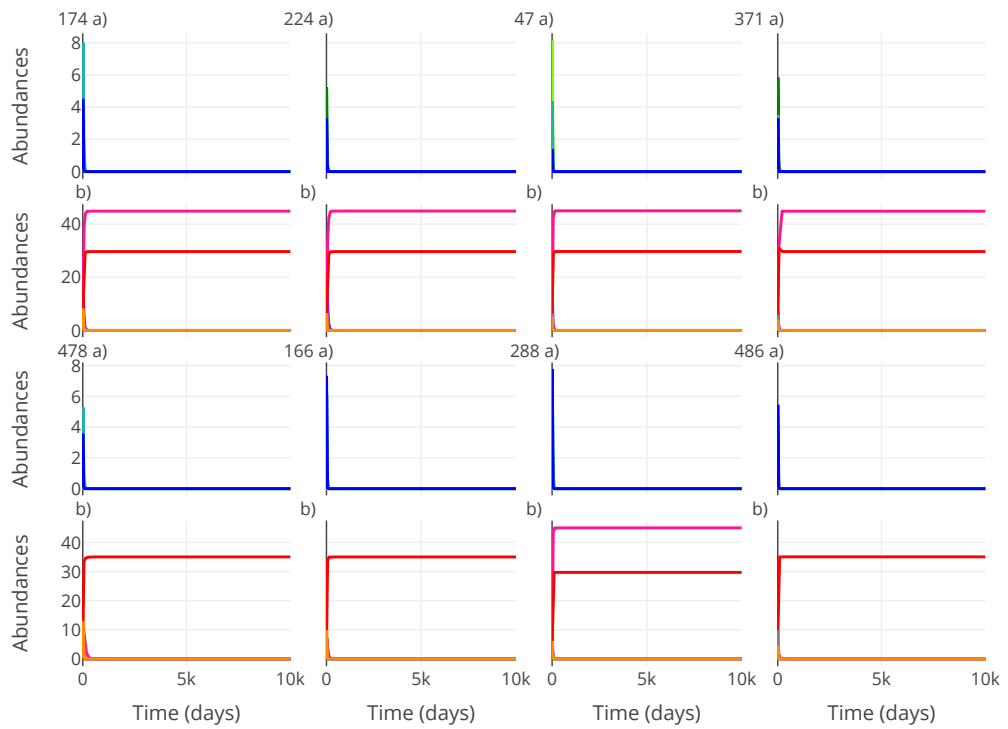


Figure 13. Visualisation of eight other different simulations of twelve species on five resources, following Figure 4, except that r_i are randomly drawn for each of the species, and all species were introduced at once (complements Figure 8). The simulations shown were randomly picked among the 500 of the numerical experiment. Each couple of subplots is labelled with the number of the corresponding simulation. a) abundances of species 1-6, b) abundances of species 7-12.

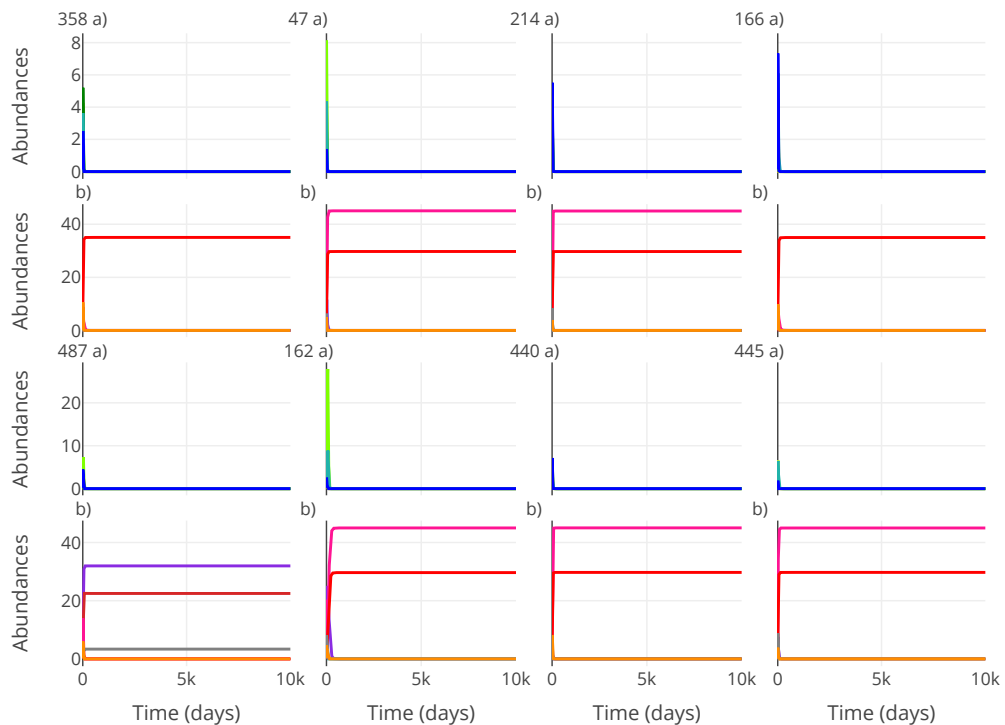


Figure 14. Visualisation of eight other different simulations of twelve species on five resources, following Figure 4, except that r_i are randomly drawn for each of the species, and all species were introduced at once (complements Figure 8). The simulations shown were randomly picked among the 500 of the numerical experiment. Each couple of subplots is labelled with the number of the corresponding simulation. a) abundances of species 1-6, b) abundances of species 7-12.

References

1. J. Huisman and F. Weissing. "Biodiversity of plankton by species oscillations and chaos." In: **Nature** 402 (1999), pp. 309–309. doi: <https://doi.org/10.1038/46540>.
2. G. Hutchinson. "The Paradox of the Plankton." In: **The American Naturalist** 95.882 (1961). doi: <https://doi.org/10.1086/282171>.
3. G. Hardin. "The Competitive Exclusion Principle." In: **Science** 131.3409 (1960), pp. 1292–1297. doi: <https://doi.org/10.1126/science.131.3409.1292>.
4. O. M. Phillips. "The Equilibrium and Stability of Simple Marine Biological Systems. I. Primary Nutrient Consumers." In: **The American Naturalist** 107.953 (1973). doi: <https://doi.org/10.1086/283553>.
5. R. A. Armstrong and R. McGehee. "Competitive Exclusion." In: **The American Naturalist** 115.2 (1980). doi: <https://doi.org/10.1086/282818>.
6. P. Schippers, A. M. Verschoor, M. Vos, and W. M. Mooij. "Does "supersaturated coexistence" resolve the "paradox of the plankton"?" In: **Ecology Letters** 4.6 (2001), pp. 404–407. doi: <https://doi.org/10.1046/j.1461-0248.2001.00239.x>.
7. J. Huisman, A. M. Johansson, E. O. Folmer, and F. J. Weissing. "Towards a solution of the plankton paradox: the importance of physiology and life history." In: **Ecology Letters** 4.5 (2001), pp. 408–411. doi: <https://doi.org/10.1046/j.1461-0248.2001.00256.x>.
8. Karlne Soetaert, Thomas Petzoldt, and R. Woodrow Setzer. "Solving Differential Equations in R: Package deSolve." In: **Journal of Statistical Software** 33.9 (2010), pp. 1–25. doi: [10.18637/jss.v033.i09](https://doi.org/10.18637/jss.v033.i09).
9. R Core Team. **R: A Language and Environment for Statistical Computing**. R Foundation for Statistical Computing. Vienna, Austria, 2023. URL: <https://www.R-project.org/>.
10. E. L. Kyle F. Edwards Christopher A. Klausmeier. "Nutrient utilization traits of phytoplankton." In: **Ecology** 96.8 (2015), pp. 2311–2311. doi: <https://doi.org/10.1890/14-2252.1>.

11. D. L. Roelke and P. M. Eldridge. "Mixing of supersaturated assemblages and the precipitous loss of species." In: **The American Naturalist** 171.2 (2008), pp. 162–175. doi: <https://doi.org/10.1086/524955>.