Replication / ecology

[Re] Biodiversity of plankton by species oscillations and chaos

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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]. However it is very common to observe more species than easily identifiable resources in real-life 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.

In addition to the replication of the numerical results of Huisman and Weissing, we also present new numerical experiments inspired by two follow-up articles, "Does "supersaturated coexistence" resolve the "paradox of the plankton" ?" by Schippers et al. 2008[6], and "Towards a solution of the plankton paradox: the importance of physiology and life history" by Huisman et al. 2008[7]. These seemed to show that supersaturated coexistence might be difficult to obtain outside of the restricted parameter scenarios considered in the original article, but did not consider direct perturbation of intrinsic growth rates, as we do here.

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, $i \in [\![1, n]\!]$ and $j \in [\![1, k]\!]$ with n and k the number of different species and resources. The time derivatives of N_i and R_j are given by:

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

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

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 minimum:

$$\mu_i(R_1, ..., R_k) \;=\; \min_{j \in [\![1,k]\!]} \left(\frac{r_i R_j}{K_{ji} + R_j} \right). \tag{3}$$

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 (1999), the differential equations were integrated using the `deSolve` package in R [[CP: which versions of deSolve and R?]], 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 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 introductions when needed, in addition to the dynamical 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. paper[6] and Huisman et al.'s response[7], in order to evaluate how robust was supersaturated coexistence. In the same spirit, we carried out 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 perturbating the growth rate parameter, r_i, denoted as $\mu_{\max}$ 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 r_i at once, as would typically do an ecosystem-wide perturbation that is not directly related to the modelled resources. In a first numerical experiment, we considered the exact same invasion sequence as Huisman & Weissing[1]. In a second step, we started with the full set of species at once.

3 Results

We were able to replicate the four figures of Huisman & Weissing[1], presented below.
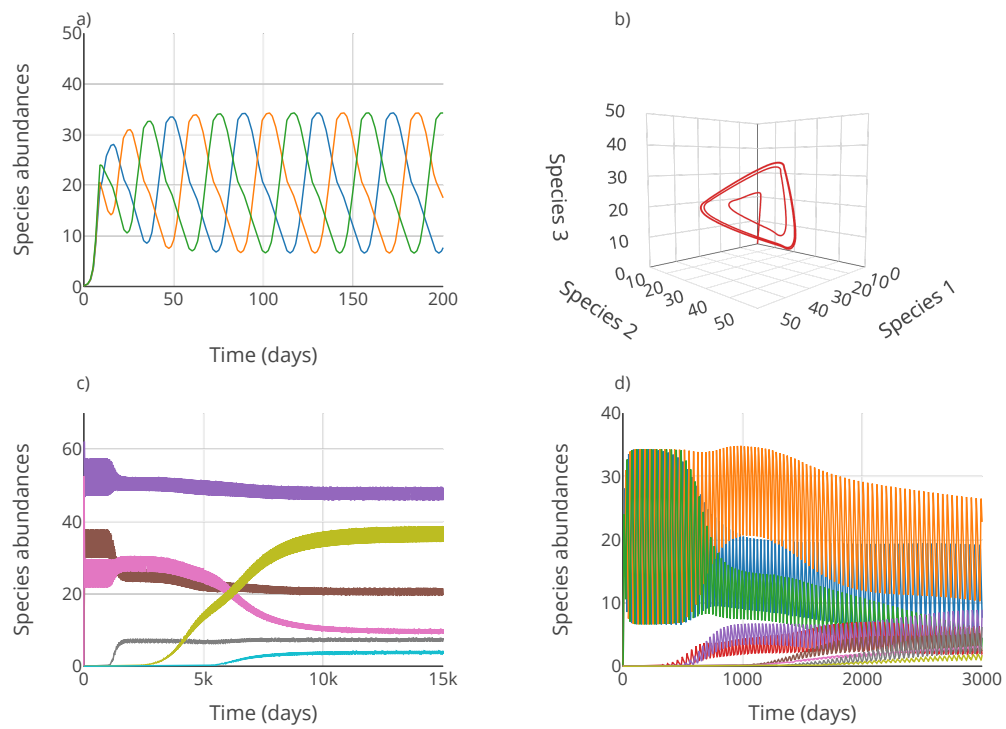
Figure 1. Oscillations on three resources. a), Time course of the abundances of three species competing for three resources. b), The corresponding limit cycle. c), Small-amplitude oscillations of six species on three resources. d), Large-amplitude oscillations of nine species on three resources.
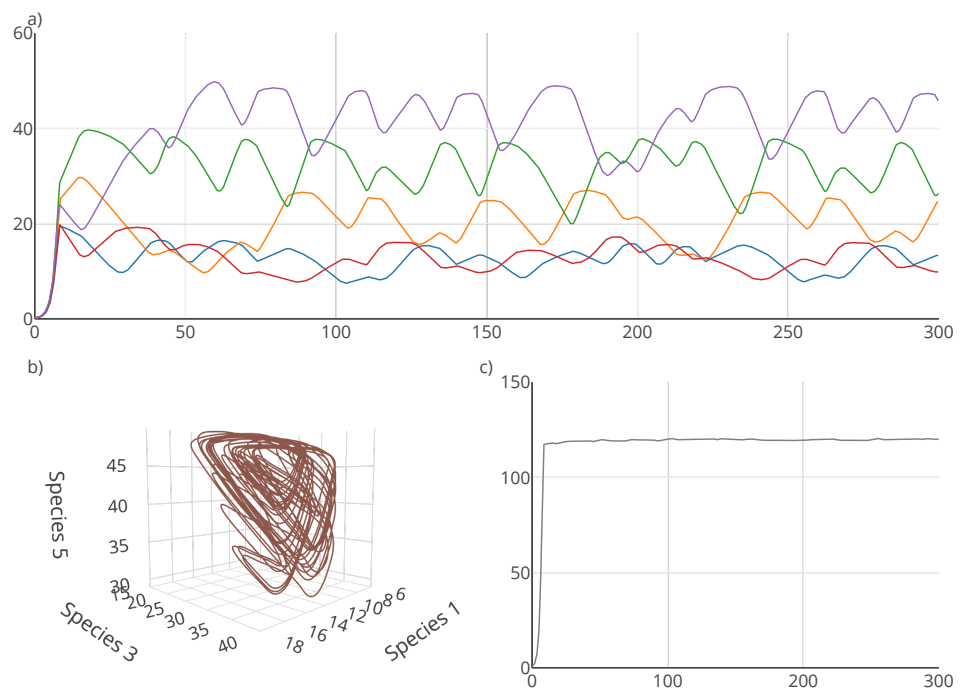
Figure 2. Chaos on five resources. a), Time course of the abundances of five species competing for five resources. b), The corresponding chaotic attractor. The trajectory is plotted for three of the five species, from the period from $t = 1,000$ to $t = 2,000$ days. c), Time course of total community biomass.
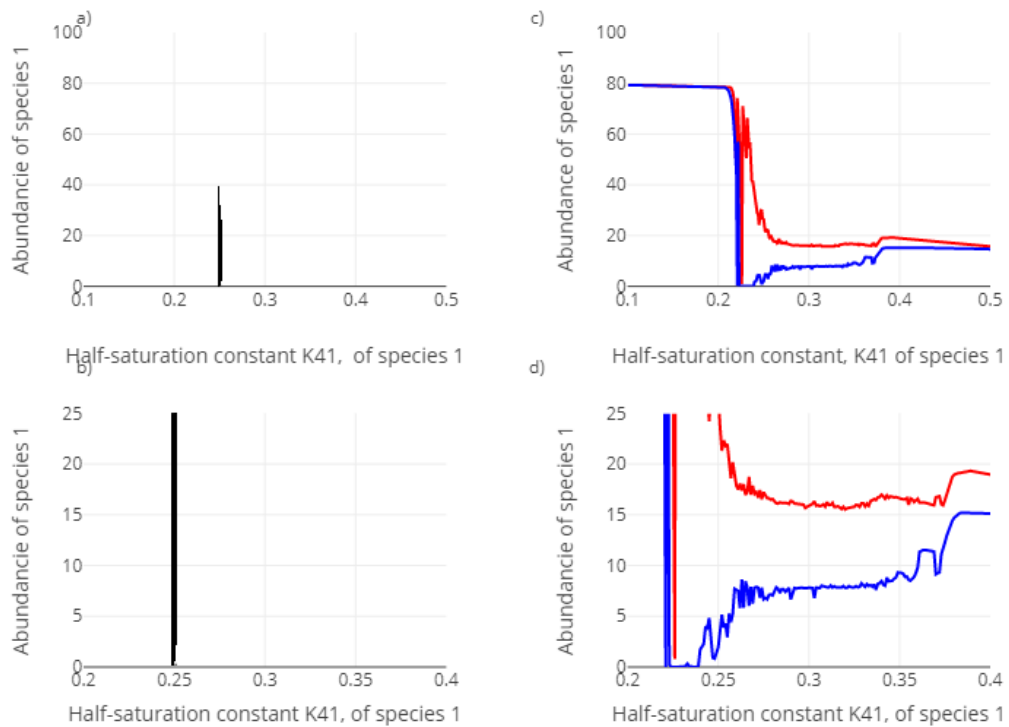
Figure 3. Bifurcation diagram, for five species competing for five resources. a) Show all of the values of species 1, plotted during the period from t=2,000 to t=4,000 days, as a function of the half-saturation constant K_{41}. Part of a) is magnified in b). c) show the local minima and maxima of species 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 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 that only the local extrema.
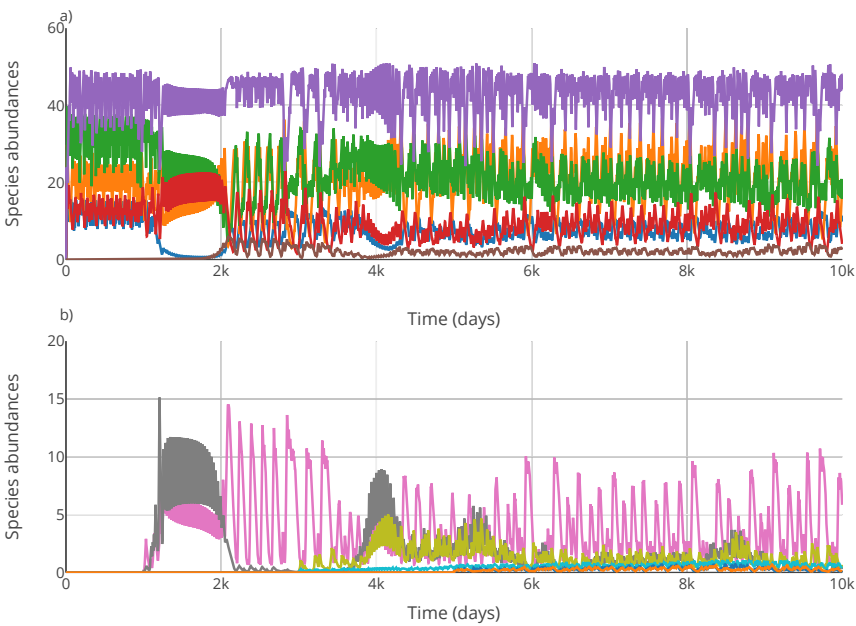We have therefore chosen to draw those two options.

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

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 400 times each, with as many different parameter sets: the r_i 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 between 0.7 and 1.3.

For the first numerical experiment, introducing species one after the other as in the original simulation, the following statistics, displaying the frequencies (expressed in %) of the number of species present at the end of the simulation could be obtained: (A species has been considered present if $N_i > 0.001$ at the end of the simulation)

	0 species	1 species	2 species	3 species	4 species	5 species	6 species
Probability	0.00	13.68	26.56	35.01	11.27	8.85	4.02

	7 species	8 species	9 species	10 species	11 species	12 species	Supersaturated
Probability	0.60	0.00	0.00	0.00	0.00	0.00	4.63

This simulation shows that the persistence of five species and more is very unlikely, and supersaturated coexistence may be present for a limited domain of parameter space.

The pattern of extinction and its interaction with the sequential introduction of species [[CP: What do you mean?]] is shown in the Figure 5. Note that the subfigure 1) represents the original results with $r_i = 1 \, \forall i$.
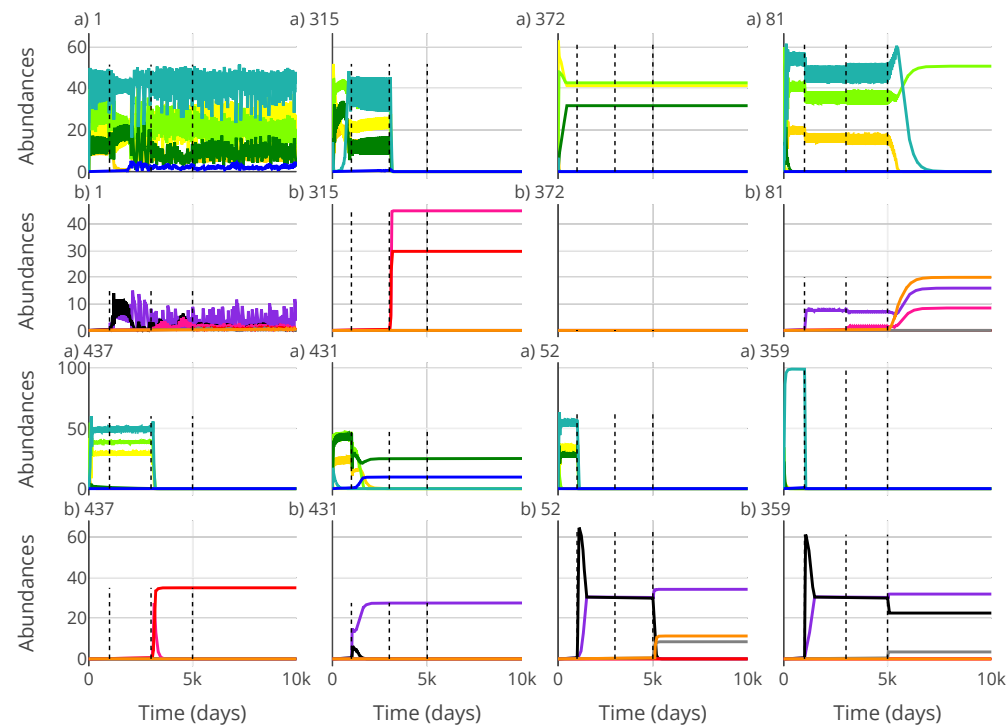
Figure 5. Visualisation of 8 different simulations of competitive chaos and coexistence of 12 species on five ressources, following the Figure 4 method except that each species has a different maximum growth rate r_i. Except for the first one, the simulations illustrated were randomly picked among the 500 of the experience. a), The abundances of species 1-6 ; b), the abundances of species 7-12.

We observe contrasted stationary endpoints, possibly with some oscillations or chaos during the invasion process. As shown in Figure**??**, however, most species do not persist.

It is also noticable that the 5 species on 5 ressources (before the first invasion at $t = 1,000$) is sometimes already unstable.

For the second experiment, introducing all species at the same time, the following statistics could be obtained, displaying the frequencies (expressed in %) of the number of species present at the end of the simulation : (A species has been considered present if $N_i > 0.001$ at the end of the simulation)

	0 species	1 species	2 species	3 species	4 species	5 species	6 species
Probability	0.00	36.40	41.40	5.00	10.00	6.00	1.20

	7 species	8 species	9 species	10 species	11 species	12 species	Supersaturated
Probability	0.00	0.00	0.00	0.00	0.00	0.00	1.20

This simulation shows that the subsistance of five species and more is very unlikely and the supersaturated coexistance very rare in the parameter space.

The pattern of extinction an its interaction with the introduction of all of the species at the same time is descirbed in following Figure 6, note that the subfigure 1) represent the original results with $r_i = 1 \; \forall i$:
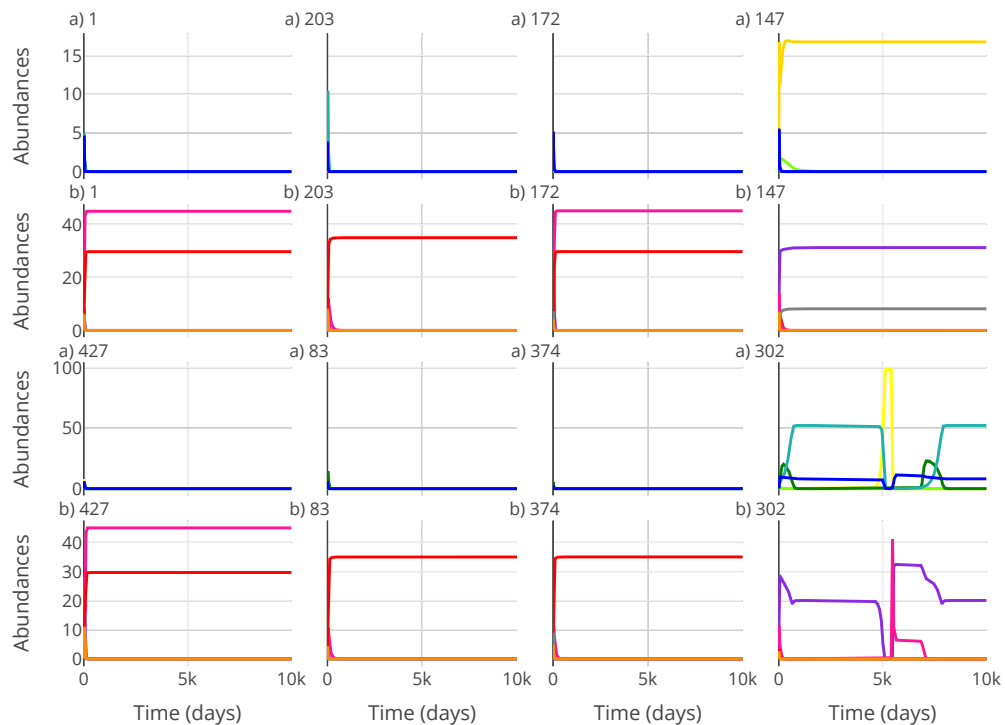
Figure 6. Visualisation of 8 different simulations of competitive chaos and coexistance of 12 species on five ressources, following the Figure 4 method exept that r_i was randomly for each of the species and all species were introduced at the same time. Except the first one, the simulations illustrated were randomly picked among the 500 of the experience. a),The abundances of species 1-6; b). the abundances of species 7-12.

As for the first experiment we observed either stationnary endpoints or oscillation but with even less persistent species as shown in Figure**??**.

4 Discussion

We were able to successfully replicate the Figures of the original paper.

There are minor differences in species dynamics in Figure 4, which are arguably due to differences in numerical integration during the resolution.

The experiments showed that slightly changing the values of the r_i parameter almost always prevents the coexistence of 12 species on five ressources and mostly prevents a supersaturated coexistence. This is true when introducing species sequentially as in the original paper as well as all at once.

Those results corroborate the results of Schippers et al.[6], who showed that supersaturated coexistence using chaos or oscillations are really unlikely in parameter space and requires a really precise -in addition to being uncommon- parameterization. Our results are therefore consistent with their conclusion that the claim of solving the paradox of plankton might be premature.
[[CP: Our final sentence, while not wrong, is strong: we may want to at least acknowledge the responses of Huisman et al. 2008, at least by saying that they have showed complementary ways of maintaining more species, e.g., with trade-offs.]]

References

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