Commented by Sebastian
07/13/XII/2016

great title because short, but could include how you conclude that
→ maybe add "in population models" or so..

Neutral competition promotes chaos

Draft

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Abstract

An increase in the neutrality of the competition at the prey's trophic level in a two-level food web rises the chances of chaotic behaviour in the long term.

mention model experiments

Keywords: population dynamics, competition models, chaos.

Contents

1 Introduction

The biodiversity paradox, that can be carelessly rephrased as *Why are there so many species?*, is one of the main problems in theoretical ecology. The paradox consists in the contradiction between the competitive exclusion principle and the observed biodiversity. ~~In the current state of the art,~~ there are several alternative hypotheses for dealing with this problem. Two of these hypotheses are: *a. Hubbell's neutral competition theory* [1] and *b. Ecosystems as non-equilibrium systems.* More references about the controversy are probably advisable here.

Hubbell's neutral competition theory, despite its counter-intuitive foundations, has been successfully applied to populations of rainforest trees. I don't see the relationship of Hubbell's theory with the biodiversity paradox.

can be shown (proof only exists in mathematics)

If ecosystems are proven to be non-equilibrium systems, the biodiversity paradox will be automatically solved. Despite the population of a particular species can vary greatly in time, the overall picture will contain a large mix of species at each and every time. From the mathematical point of view, non-equilibrium systems have cyclic or chaotic attractors associated with their dynamics. The analysis of ~~this~~ these attractors is a well known method, used often in physics and climate sciences.

very vague

more explanation needed. It sounds like a trivial truth to me that ecosystems are not in equilibrium..

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Is this seemingly probabilistic statement justified? Or is it rather a deterministic outcome of the particular model?

perfect as part of the abstract

Our simulations show that the likelihood of chaos in a competition model increases with neutrality at the competitors' trophic level, so both hypotheses are not completely independent. This should be at the end of the introduction?, or just a the conclusions section?

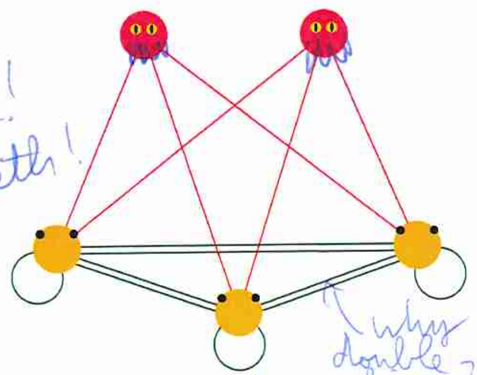
I agree.

A more detailed overview of the competing hypotheses and/or of another natural phenomena explained by chaos can be an interesting introduction.

2 Model description

We will use a generalized Rosenzweig-MacArthur predator-prey model [2, 3] with two trophic levels. It will be composed of n preys and N predators.

cool! could add dangerous teeth!



why double lines? if directional, add "→"

Figure 1: Example with 2 predators and 3 preys. Each one of the red links represents a palatability coefficient (coded in the matrix S). Each green link represents a competition coefficient (coded in matrix A). The closed green loops are related with carrying capacity (diagonal elements of A) interpreted here as intra-species competition.

We will use p_i for accounting the size of the population of prey i, and P_j for the population of predator j. When it is not explicitly stated, i will run from 1 to n, and j from 1 to N. The preys compete among themselves, and the predators don't. The preys' competition doesn't need to be necessarily symmetrical. The predators eat all kinds of ~~preys~~ prey (see figure 1), but find some of them preferable ~~than~~ to others.

The dynamics can be described as ~~a~~ an $n+N$ dimensional system of ordinary autonomous differential equations. The overall structure ~~looks like:~~ is

$$\begin{cases} \frac{d}{dt}(prey) = Growth - Predation + Immigration \\ \frac{d}{dt}(Pred) = Feeding - Death \end{cases}$$

The growth term is modelled as a multispecies logistic growth. The strength of the competition is given by A_{ik}. Those coefficients can be arranged as ~~a~~ an $n \times n$ matrix. So, for prey i, we have:

$$Growth_i = rp_i\left(1 - \frac{1}{K}\sum_{k=1}^{n} A_{ik} \cdot p_k\right) \qquad (1)$$

what is that?

The palatability of each prey species is given by S_{ij}. Those coefficients can be arranged as a $N \times n$ matrix. Being a multispecies model, we can define the auxiliary variable V_j as a sum of the prey's populations weighted by the palatability coefficients. Biologically, this represents the overall composition of the "menu" of predator j:

$$V_j \equiv \sum_{k=1}^{n} S_{jk} \cdot p_k \qquad (2)$$

We hypothesize that the feeding term will be linear in P_j, and have a Holling type II functional response on V_j in order to account for predator satiation:

$$Feeding_j = egP_jF_2(V_j;\, H) = egP_j\frac{V_j}{V_j + H} \qquad (3)$$

e represents the assimilation efficiency of the predation, that is, it regulates the biomass exchange between predator and prey. Thus, the effect of predator j on all prey's populations is given by $Feeding_j/e$. Knowing this, we can sum the effect of all predators in the species i as follows:

$$Predation_i = gp_i\sum_{k=1}^{N} S_{ki} \cdot \frac{P_k}{V_k + H} \equiv gp_iR_i \qquad (4)$$

Where for convenience, we have defined the auxiliary function R_i as a summary of this effect of all predators on prey i:

$$R_i(P_1, ..., P_N, V_k;\ S) \equiv \sum_{k=1}^{N} S_{ki} \cdot \frac{P_k}{V_k + H} \qquad (5)$$

Putting all together, the dynamical system reads:

$$\begin{cases} \dot{p}_i = rp_i\left(1 - \frac{1}{K}\sum_{k=1}^{n} A_{ik} \cdot p_k\right) - gp_iR_i + f \\ \dot{P}_j = egP_j\frac{V_j}{V_j+H} - lP_j \end{cases} \qquad (6)$$

Depending on the parameters and the initial conditions, this system can give rise to four types of behaviour ~~on the long term~~, each of them corresponding ~~with~~ to a different type of attractor (see figure 2). The ~~easier~~ simplest one, corresponding to a stable point attractor, gives rise to a constant species composition in the system. Cyclic attractors, that can be subclassified as simple or complex, give rise to periodic behaviour in the species composition. Finally, chaotic attractors, makes the species composition keep evolving without stabilising nor giving rise to periodicity.

asymptotic ?

?

harmonic vs non-harm. ?

or quasi-periodic ?

is associated with

2.1 Parameterization

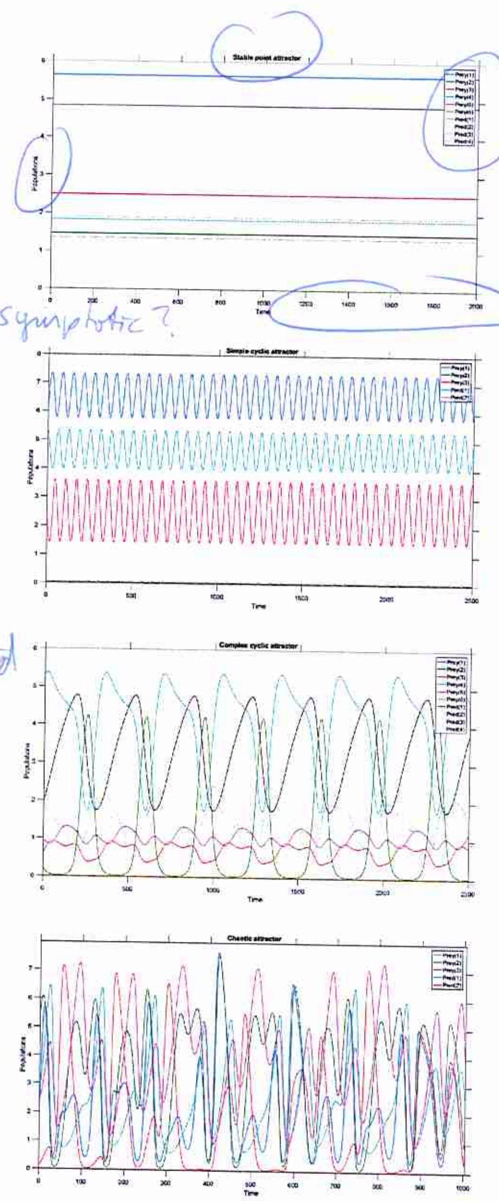
Taking [4] as reference, we will use the following values for our parameters:

Symbol	Interpretation	Value	Dimensions
r	Growth rate	0.5	T^{-1}
g	Predation rate	0.4	T^{-1}
l	Loss rate	0.15	T^{-1}
K	Carrying capacity	1	M
H	Half-saturation biomass	2	M
f	Immigration rate	10^{-5}	$M \cdot T^{-1}$
e	Assimilation efficiency	0.6	1
S	$N \times n$ palatability matrix	$S_{ij} \sim (0,1)$	1
A	$n \times n$ competition matrix	See section 3.1	1

Table 1

~~Figure 3~~: Values and meanings of the parameters used

As explained in section 6.2, this system allows parameter reduction.



very tiny

Figure 2: Time series of the species composition. First figure shows an stable attractor. The second one, a simple cyclic attractor. The third corresponds to a complex cyclic attractor. The last one shows a chaotic attractor

3 Methodology

Our aim is to analyse the behaviour of the system described in equation 6 for ~~increasingly more~~ neutral competition interactions. In order to accomplish this, we define in section 3.1 a *competition*

an increasing number of ...

parameter (ϵ), a single parameter that controls the overall neutrality of the competition interaction.

For different values of neutrality (i.e., of ϵ), we'll estimate the probability of the system developing a chaotic attractor (see section 3.4).

Due to the complexity of the system, we have faced the problem as a numerical simulation (see sections 3.2 and 3.3). As well, and for the sake of reproducibility, we provide a *GitHub* link to the scripts used for analysis. Discuss with Egbert and Marten about which code repository use

great!

3.1 Competition parameter

In order to control ~~easily~~ the neutrality of the competition, we introduce the competition parameter ϵ. This dimensionless parameter will allow us to vary continuously from interactions where intra-specific competition ~~is stronger that inter-specific (for $\epsilon < 0$) to the opposite case (for $\epsilon > 0$)~~. The border between both cases (i.e. $\epsilon = 0$) represents neutral competition (see figure 4).

dominates to a regime where ... dominates.

In order to accomplish this, we build our competition matrix using:

$$A(\epsilon) = A_0 + \epsilon \cdot W \tag{7}$$

Where A_0 is a totally neutral competition matrix (i.e., all its elements equal 1) and W is a random matrix whose non-diagonal elements have been drawn from a uniform distribution bounded to the interval $[0, 1]$, and whose diagonal elements are zero. This way, we make sure that the diagonal elements of A are 1 in all cases (see figure 4).

very important! explain reasoning.

Parameter value	Stronger competition	Example of competition matrix
$\epsilon < 0$	Intra-specific	$A = \begin{bmatrix} 1 & .2 & .3 \\ .3 & 1 & .4 \\ .5 & .4 & 1 \end{bmatrix}$
$\epsilon = 0$	Neutral	$A = \begin{bmatrix} 1 & 1 & 1 \\ 1 & 1 & 1 \\ 1 & 1 & 1 \end{bmatrix}$
$\epsilon > 0$	Inter-specific	$A = \begin{bmatrix} 1 & 1.7 & 1.6 \\ 1.9 & 1 & 1.5 \\ 1.8 & 1.6 & 1 \end{bmatrix}$

Figure 4: Effect of the competition parameter on the competition matrix. Notice that the diagonal elements are always 1

3.2 Software

All the subsequent analysis were performed using our software package GRIND for MATLAB[1]

Publish code and add link

3.3 Numerical experiment

How is 'probability' meant here?

The objective is to estimate the probability of a chaotic attractor being reached as a function of the competition parameter (ϵ) controlling neutrality. In order to accomplish this task, we designed the following numerical experiment. It consists on repeating the following steps R times for each of the competition parameters drawn from the range $[-1, 2]$:

1. Use the competition parameter ϵ to generate a competition matrix A (as described in section 3.1)

2. Draw the rest of parameters and initial conditions from the ranges described in [4], taken as uniform PDFs

3. Determine numerically if the attractor generated by this conditions is chaotic or not (see section 3.4), and store the value of the maximum Lyapunov exponent

4. Go back to step (2) R times

For those more familiar with flow charts, figure 5 can be illuminating.

[1] Freely available at `http://www.sparcs-center.org/grind.html`

You seem to vary only one degree of freedom. What about the other parameters? Still confused about that... Would be cool to scan the whole parameter space.

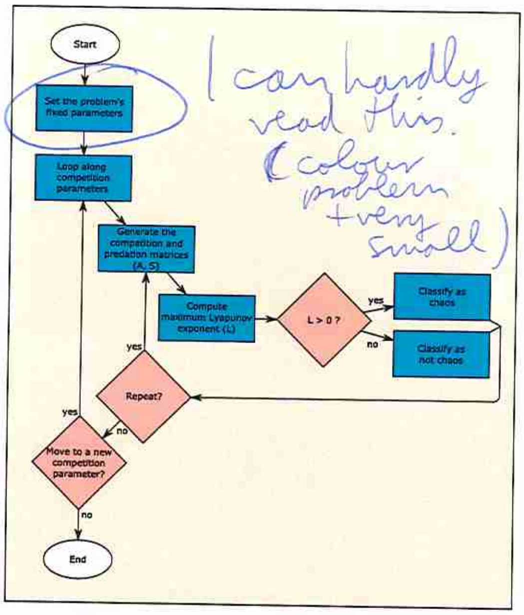


Figure 5: Flow chart describing the numerical experiment

nice!

The outcome of the numerical experiment described above is a list of R maximum Lyapunov exponents per value of ϵ. This list can be used to estimate the probability of chaos for each value of ϵ (see section 3.4).

This numerical experiment can be repeated for a different number of preys and predators (n and N). Choose a fixed predator-prey ratio, keep it, and mention it here

3.4 Detection of chaos

The procedure for classifying the attractors as chaotic or not is based ~~in~~ on the analysis of Lyapunov exponents (see figure 5 and reference [5]). More specifically, the procedure will be the following (see figure 5):

1. Run the simulation for a sufficient time ~~enough~~, in order to guarantee that an attractor has been reached traj. is on attr.
2. Use the run in step 1 as a starting point for a second, shorter run ~~inside~~ on the attractor
3. Use the run in step 2 to compute ~~numerically~~ the principal Lyapunov exponent
   - If it's positive, classify the attractor as chaotic
   - If it's negative, classify the attractor as non-chaotic

Big warning here: our method for detecting chaos sometimes gives false positives for complex cycles

The probability of chaos can be estimated via the classical bayesian B interpretation of probability, that is:

$$P(Chaos) \approx \frac{\#_{chaos}}{\#_{total}} \quad (8)$$

?! this looks frequentist to me, not Bayesian...

4 Results

Plotting the probability of chaos against the competition parameter (see figures 6 and 7), we observe a clear maximum in the probability of chaos around $\epsilon = 0$, that is, for neutral competition at the prey's trophic level. The overall likelihood of chaos increases with dimensionality, but a maximum is still clearly appreciable for the neutral case.

5 Conclusions

The fact that the overall likelihood of chaos increases with the amount of competing species, or equivalently, the system's dimensionality, is quite reasonable. Intuitively, we can understand this as increasing the available room for the formation of a complex chaotic attractor in the phase space.

Much more interesting and counterintuitive is the fact that neutrality, being a simplifying assumption (cf. section 6.1), increases the likelihood of chaos, and therefore the complexity of the ~~problem~~. system

From the biological point of view, we show that the hypotheses mentioned at the introductory section 1 are not completely independent. Maybe this can be a first step to reconcile both views. cool.

Could mention that apparently ϵ is much more important than the other parameters, otherwise Monte Carlo approach would not converge after so few realisations ?!

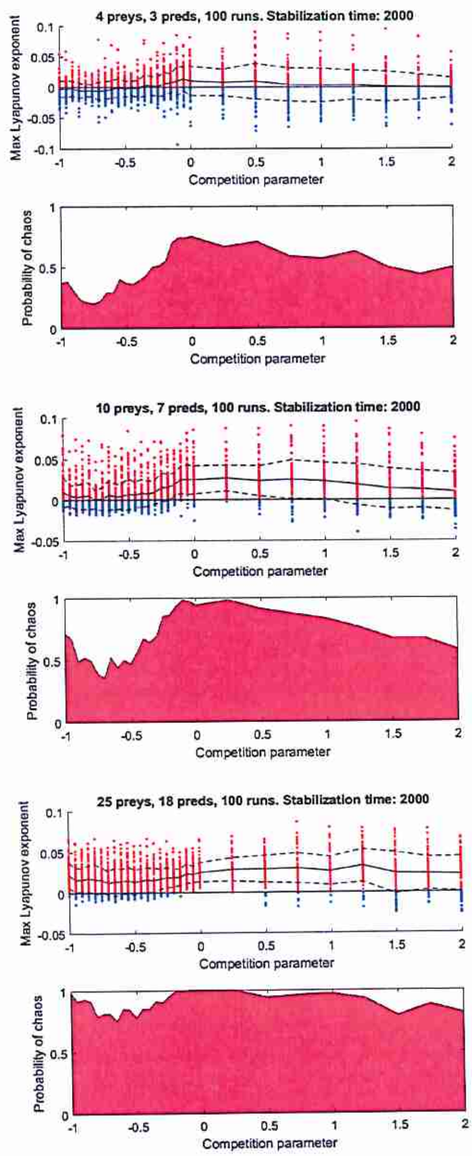


Figure 6: Results for a low, medium and high dimensional system. The upper row represents the measured Lyapunov exponents, coloured in red if larger than zero, and in blue if smaller. The lower row represents the estimated probability of chaotic behaviour

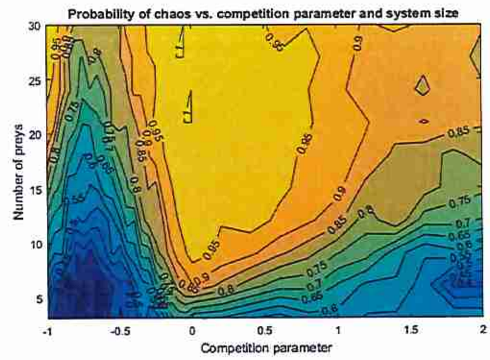


Figure 7: Contour map showing the probability of chaos for various competition parameters (horizontal axis) and prey populations (vertical axis). The predators' population is fixed as 2/3 of the prey's population, in order to control the overall size of the system with a single parameter. Notice that chaotic attractors appear more easily (i.e., for smaller systems) if the competition is neutral (i.e., $\epsilon = 0$)

Go deeper into the biological interpretation of the conclusion

~~6~~ Appendix A

~~6.1~~ A1 Neutral competition

If we drop everything but the competition part of our dynamics (see equation 13), we will find a system of equations n like the following:

$$\dot{p}_i = p_i \left(1 - \sum_{k=1}^{n} A_{ik} \cdot p_k \right) \tag{9}$$

In order to model a neutral competition, we should use the same competition coefficient for each species. That is, take $A_{ik} = A$ for all i and k, so:

$$\dot{p}_i = p_i \left(1 - A \sum_{k=1}^{n} p_k \right) \tag{10}$$

From equation 10 we see that all species have exactly the same dynamical equation. This will make the nullclines to coincide at all points, so the

Why the asymmetry in the chosen range of ϵ and in the results?

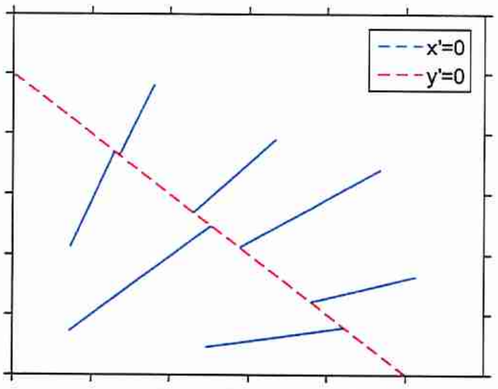


Figure 8: Example with 2 prey under neutral competition. Both nullclines coincide point to point, giving rise to a higher dimensional equilibirium manifold (in this case, a straight line)

equilibrium points will degenerate to equilibrium manifolds.

This problem can be solved more easily noticing that, from the sole point of view of competition, the effect of neutrality is to fade out the differences between species, so the labels i distinguishing them become pointless. It is a good idea to sum up all the competing species into a single variable, ~~that~~ ~~of~~ the total population of (indistinguishable) species, defined by:

$$T(t) = \sum_{i=1}^{n} p_i(t) \tag{11}$$

It can be easily shown using equation 10 that, as expected from the biological intuition, the dynamics of this new variable will follow the same differential equation as the individual species abundances:

$$\dot{T}(t) = \sum_{i=1}^{n} \dot{p}_i(t) = T(1 - AT) \tag{12}$$

? In our model, the predation interaction breaks this excess of symmetry, so we can still work with neutral competition as long as the predation is not neutral without facing problems of system degeneration.

6.2 Parameter reduction

The dynamical system 6 has $n^2 + n \cdot N + 7$ parameters. Choosing appropriate units and parameter combinations, this number can be reduced by 3:

- By choosing an appropriate time scale ($\tau = rt$) we can get rid of r
- K can be absorbed into A_{ij} $\left(\frac{A_{ij}}{K} \to A_{ij}\right)$
- H can be absorbed into S_{ij} $\left(\frac{S_{ij}}{H} \to S_{ij}\right)$

So, finally we have:

$$\begin{cases} \dot{p}_i = p_i \left(1 - \sum_{k=1}^{n} A_{ik} \cdot p_k\right) - g p_i R_i + f \\ \dot{P}_j = egP_j \frac{V_j}{V_j + 1} - lP_j \end{cases} \tag{13}$$

wouldn't it make sense to use this for the experiments?

with the $n^2 + n \cdot N + 4$ external parameters, namely:

Parameter	Cardinal	Interpretation
A_{ij}	n^2	Competition between species i and j^2
S_{ij}	$n \cdot N$	Palatability of the prey i for predator j
g	1	Effect of predation on prey
e	1	Predators' efficiency
f	1	Prey's immigration flow
l	1	Predators' death rate

Table A1
~~Figure 9~~: Parameters left after reduction

compare to Table 1 would be nice

6.3 Algorithm used

The following pseudocode algorithm describes the whole procedure:

?
not so useful in paper. reader can get code in GitHub anyway. Fig 5 is great.

Algorithm 1 Pseudocode for the algorithm used

```
procedure NUMERICAL EXPERIMENT IN PSEUDOCODE

experiment design parameters:
    R ← Number of repetitions

biological parameters:
    n ← Prey's population
    N ← Predator's population
    g ← Effect of predation on prey
    e ← Predator's efficiency
    f ← Prey's immigration flow
    l ← Predator's death rate

loop:
    for ε in [−1, 2] do
        Draw a competition matrix A
        Draw a predation matrix S
        Draw random initial conditions
        for i in R do
            Compute dynamics
            Store maximum Lyapunov exponent λ

results:
    Return the lists (ε_i, λ_i1, ..., λ_iR)
```

"symmetry in competition strongly promotes multiplicity of attractors"

7 Acknowledgements

We thank Jelle Lever for his useful comments and suggestions.

8 To do

- More biolog. background info.
- Send more details to the appendix?
- ~~Remove or improve the pseudocode algorithm~~
- Clean and publish analysis code in *GitHub*

Further ideas, for this or future papers:

- Neutrality in predation
- Study symmetric competition with a parameter that controls symmetry
- Neutrality increases symmetry as well. May this be related with the fact that, as said in [3],

How relevant is the model used?
what do the calculated probabilities mean / tell us about reality?
What is the structural error of the model?
Would other models give a different result?
What should be done next to confirm/refute the hypothesis?

References

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List of Figures

not needed