

Discussed with Egbert

# Neutral competition among prey promotes chaos in two-level food webs Draft

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## Abstract

Neutral competition can be interpreted as a limit case between dominant intraspecific competition and dominant interspecific competition. Using a numerical model of a two trophic levels ecosystem, the present paper explores the surroundings of this limit case, that is, weak non-neutral competition interactions. It is shown that, the closer the competition is to be neutral, the higher are the chances of the system to develop chaotic behaviour.

*Keywords:* population dynamics, competition models, neutral competition, biodiversity paradox, chaos.

Is there a better name?  
| contest/scramble?

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## 1 Background

The fascination by biodiversity is one of the main motivations for studying ecology. Even very young children feel the joy of learning about different species, so no prior knowledge of biology seems to be a requirement for being sensitive to the amazing variety of species. Scientific knowledge increases this sense of wonder even more. Like in a good mystery book, there is a big unknown behind biodiversity: we don't know how it is possible.

The mystery comes into scene together with the competitive exclusion principle [Hardin, 1960], sometimes referred to as Gause's law. This principle, which some authors trace back to Charles Darwin's *On the origin of the species* [Darwin, 1859], is one of the classical touchstones of ecology. The principle states that "*for each niche only one species will dominate in the long run, out-competing the rest*". Most competition models satisfy this principle, and it has been observed experimentally under laboratory conditions. On the other hand, most of the field observations seem to contradict the competitive exclusion principle, being the huge biodiversity in Earth its most noticeable counterexample. This contradiction is known as the biodiversity paradox. The paradox can be carelessly (but poetically) rephrased as *Why are there so many species?*

There are several alternative hypotheses for escaping the paradox. For instance, Hutchinson [Hutchinson, 1959] reports his observations on two sympatric species of beetles competing for the same resource, but not simultaneously because of having different breeding seasons. In a later, influential paper [Hutchinson, 1961], Hutchinson proposes the possibility of ecosystems to be driven by external, time-dependent environmental changes. If the characteristic times of this environmental changes are fast enough, the ecosystem is prevented to reach an equilibrium.

After the discovery of chaos [Lorenz, 1963], it has been shown that non-equilibrium ecosystems can arise as well under constant environmental conditions [Huisman and Weissing, 1999]. More specifically, those ecosystems develop cyclic or chaotic dynamics instead of equilibrium. Of course, chaotic dynamics can arise as well in non-constant environments [Dakos et al., 2009].

All the previous hypotheses refer to the time domain. Regarding the spatial dimension, the inhomogeneity of ecosystems, and the possibility of migration between them has been pointed out as another possible explanation of the paradox [Tilman, 1994].

} Keep? Enlarge?

Another hypotheses deserving attention are that of neutral competition, whose better known exponent is *Hubbell's neutral competition theory* [Hubbell, 2001]. In neutral models, similar species inside an ecological community are assumed to have identical per capita rates of birth, rate, reproduction, etc. In those models, the long term differences between species are a result of random events. Despite its counter-intuitive and controversial foundations, neutral models have been successfully applied to populations of rainforest trees.

In this paper we explore... (not much than ohint)

Balance  
Intro / Conclusions

In the present paper we show that there is a link between neutral competition and the type of long term dynamics exhibited. Using weakly non-neutral models, our simulations show that the likelihood of chaos increases with neutrality at the competitors' trophic level, having a clear maximum for purely neutral competition. Both neutral hypotheses and the classical non-equilibrium ones seem to not be independent.

Where mention code?

[EvN34][92]

## 2 Methods

### 2.1 Model description

We focused our attention in food webs with two trophic levels, one of consumers and another of prey (see figure 1). The consumers predate on the prey, and the prey populations compete among each other for a common resource.

This choice was made because these webs are the simplest realization of a system where neutrality doesn't lead to mathematical degeneration (see 5). Degeneration is prevented by the non-neutral predation rates breaking the excess of symmetry provided by neutrality. *at prey's level*

i'll try to  
Keep the figure  
[EvN22]

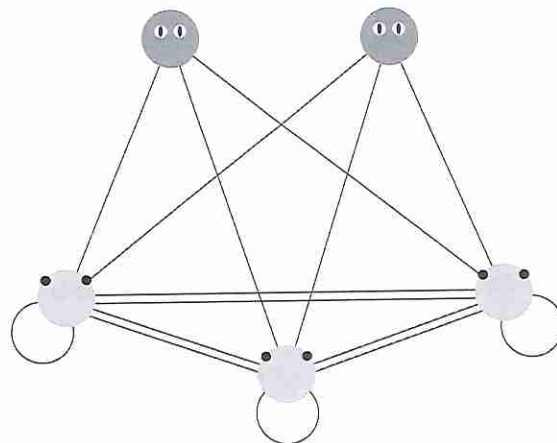


Figure 1: Example with 2 consumers and 3 prey. Each one of the red links represents a predation interaction (coded in the matrix of palatability coefficients,  $S$ ). Each green link represents a competition interaction (coded in the matrix of competition coefficients,  $A$ ). The closed green loops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

The dynamics were modelled as a system of ordinary differential equations. We used a generalized Rosenzweig-MacArthur predator-prey model [Rosenzweig and MacArthur, 1963, van Nes and Scheffer, 2004], composed of  $n$  prey and  $N$  consumers.  $P_i(t)$  was used for accounting the size of the population of prey  $i$

$n$  and  $N$ ?



at time  $t$ , and  $C_j(t)$  for the population of consumer  $j$ . When it is not explicitly stated,  $i$  runs from 1 to  $n$ , and  $j$  from 1 to  $N$ . The prey compete directly among themselves, while the consumers don't interact directly. The prey competition doesn't need to be necessarily symmetrical. The consumers eat all kind of prey (see figure 1), but find some of them preferable than others. All these interactions are summarized in 1. The overall structure looks like:

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

Keep didactic approach?

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

$$\text{Growth}_i = rP_i \left( 1 - \frac{1}{K} \sum_{k=1}^n A_{ik} \cdot P_k \right) \quad (1)$$

The palatability of each prey species is given by  $S_{ij}$ . Those coefficients can be arranged as an  $N \times n$  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 composition of the menu of consumer  $j$ :

Explain palatability

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

We hypothesized that the feeding term will be linear in  $C_j$ , and have a Holling type II functional response on  $V_j$  in order to account for consumer satiation:

$$\text{Feeding}_j = egC_j F_2(V_j; H) = egC_j \frac{V_j}{V_j + H} \quad (3)$$

$e$  represents the assimilation efficiency of the predation, that is, it regulates the biomass exchange between consumer and prey. Thus, the effect of consumer  $j$  on all prey's populations is given by  $\text{Feeding}_j/e$ . Knowing this, we can sum the effect of all consumers in the species  $i$  as follows:

$$\text{Predation}_i = gP_i \sum_{k=1}^N S_{ki} \cdot \frac{C_k}{V_k + H} \equiv gP_i R_i \quad (4)$$

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

$$R_i(C_1, \dots, C_N, V_k; S) \equiv \sum_{k=1}^N S_{ki} \cdot \frac{C_k}{V_k + H} \quad (5)$$

Putting all together, the dynamical system reads:

$$\begin{cases} \dot{P}_i = rP_i \left( 1 - \frac{1}{K} \sum_{k=1}^n A_{ik} \cdot P_k \right) - gP_i R_i + f \\ \dot{C}_j = egC_j \frac{V_j}{V_j + H} - lC_j \end{cases} \quad (6)$$

[EvN 25]

Depending on the parameters and the initial conditions, this system can give rise to three types of asymptotic behaviour, each of them corresponding with a different type of attractor (see figure 2). The easier one, corresponding to a stable point attractor, gives rise to a constant species composition. Cyclic attractors give rise to periodic behaviour in the species composition. Finally, chaotic attractors, make the species composition keep changing without stabilising nor giving rise to periodicity.

## 2.2 Parameterization

For the parameterization of our model we used [Dakos et al., 2009] as a reference. Dakos' model, focusing on plankton communities, uses as well a Rosenzweig-McArthur dynamic with two trophic levels (that of zooplankton and phytoplankton). Unlike Dakos, who uses periodic, time-dependent parameters, our parameters will be constant.

| Symbol | Interpretation                   | Value                | Units                |
|--------|----------------------------------|----------------------|----------------------|
| $r$    | Growth rate                      | 0.50                 | $d^{-1}$             |
| $g$    | Predation rate                   | 0.40                 | $d^{-1}$             |
| $l$    | Loss rate                        | 0.15                 | $d^{-1}$             |
| $K$    | Carrying capacity                | 1.00                 | $mg\ l^{-1}$         |
| $H$    | Half-saturation constant         | 2.00                 | $mg\ l^{-1}$         |
| $f$    | Immigration rate                 | $10^{-5}$            | $mg\ l^{-1}\ d^{-1}$ |
| $e$    | Assimilation efficiency          | 0.60                 | 1                    |
| $S$    | $N \times n$ palatability matrix | $S_{ij} \sim (0, 1)$ | 1                    |
| $A$    | $n \times n$ competition matrix  | See section 2.3      | 1                    |

Figure 3: Values and meanings of the parameters used in our numerical experiment

## 2.3 Competition parameter

Our aim is to analyse the behaviour of the system described in equation 6 for competition interactions differing in neutrality. But, how can an interaction be more or less neutral? In order to quantify neutrality and controlling the *flavour* of the competition, we introduce the competition parameter  $\epsilon$ . This dimensionless parameter will allow us to vary continuously from interactions where intraspecific competition is stronger than interspecific (for  $\epsilon < 0$ ) to the opposite case (for  $\epsilon > 0$ ). The border between both cases (i.e.  $\epsilon = 0$ ), where none of the intra nor interspecific competition is dominant, represents neutral competition (see figure 4). The higher the absolute value of  $\epsilon$ , the less neutral our model is.

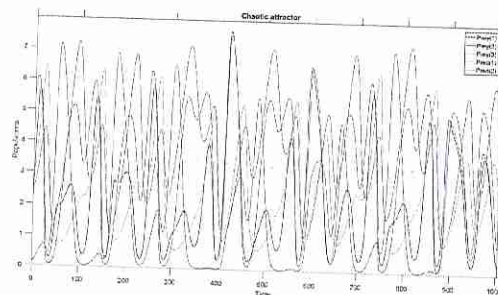
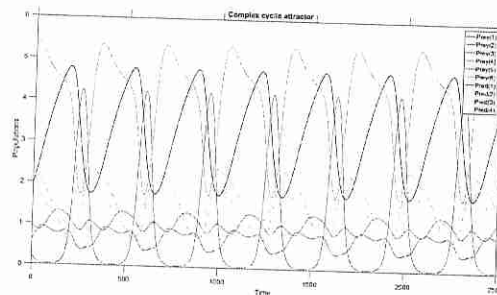
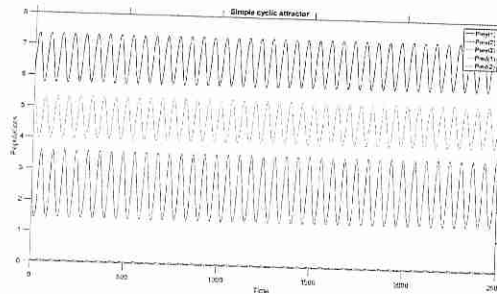
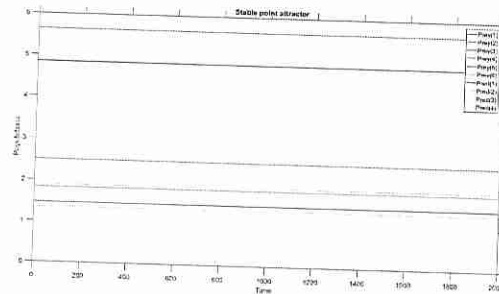
The numerical implementation of these ideas can be easily achieved by building a competition matrix like this:

$$A(\epsilon) = A_0 + \epsilon \cdot W \quad (7)$$

Read more about  
parameter choice?

Try to save space

Make more compact figure



Add attractors?

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

| Re-do figure?

Where  $A_0$  is a purely 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).

| Parameter value     | Dominant competition | Example of competition matrix   |
|---------------------|----------------------|---|
| $-1 < \epsilon < 0$ | Intraspecific        | $A = \begin{bmatrix} 1 & .2 & .3 \\ .3 & 1 & .4 \\ .5 & .4 & 1 \end{bmatrix}$       |
| $\epsilon = 0$      | None (neutral)       | $A = \begin{bmatrix} 1 & 1 & 1 \\ 1 & 1 & 1 \\ 1 & 1 & 1 \end{bmatrix}$             |
| $\epsilon > 0$      | Interspecific        | $A = \begin{bmatrix} 1 & 1.7 & 1.6 \\ 1.9 & 1 & 1.5 \\ 1.8 & 1.6 & 1 \end{bmatrix}$ |

Figure 4: Effect of the competition parameter on the competition matrix

By choosing  $-1$  as a lower limit for  $\epsilon$  we exclude the possibility of negative numbers in the competition matrix. This coefficients of *negative competition* can be understood as a simple approach to mutualism, and we wanted to focus only in classical competition.

## 2.4 Detection of chaos

Dynamical systems with chaotic attractors are extremely sensitive to initial conditions. Two trajectories whose initial conditions are slightly different will diverge exponentially if they lie in the basin of a chaotic attractor. The rate of divergence is quantified by the Lyapunov exponent [Strogatz, 1994].

Our procedure for classifying the attractors as chaotic or non-chaotic was based in the analysis of Lyapunov exponents. More specifically, this is the procedure we've followed:

1. Run the simulation for a sufficient time, in order to guarantee that a trajectory is on an attractor
2. Use the run in step 1 as a starting point for a second, shorter run on the attractor (mention parameters shortly)
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

## 2.5 Numerical experiment

Our main target is to estimate the probability of finding a chaotic attractor under different intensities of neutrality. Due to the complexity of the system,

Jump too abrupt

Appendix?



we face the problem as a numerical simulation<sup>1</sup>. As well, and for the sake of reproducibility, we provide a *GitHub* link to the scripts used. Discuss with Egbert and Marten about which code repository use

Sweeping for different values of  $\epsilon$ , we use the following procedure to estimate the probability of a chaotic attractor:

1. Use the competition parameter  $\epsilon$  to draw a competition matrix  $A$  (as described in section 2.3). Notice that this matrix is being drawn from a probability distribution function (PDF), so it will change in every run
2. Draw the rest of parameters and initial conditions from the values described in [Dakos et al., 2009]. Those which are defined as ranges will be taken as uniform PDFs. Notice that those parameters taken from a PDF will change in every run
3. Determine numerically if the attractor generated by this conditions is chaotic or not (see section 2.4)
4. Go back to step (2)  $R$  times

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

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<sup>1</sup>The present analysis were performed using GRIND for MATLAB. It's freely available at <http://www.sparcs-center.org/grind.html>

I'll try to  
keep it  
[EVN39]

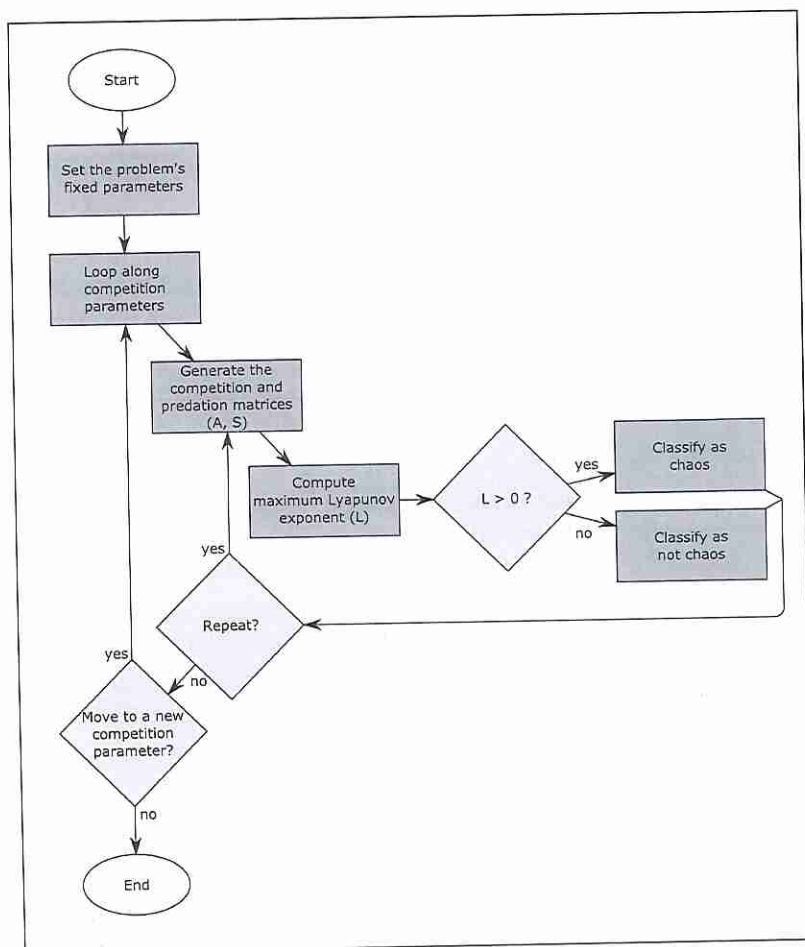


Figure 5: Flow chart describing the numerical experiment

The outcome of the numerical experiment described above is a list of  $R$  maximum Lyapunov exponents per value of  $\epsilon$ . This list can be used to estimate the probability of chaos for each value of  $\epsilon$  via the classical frequentist interpretation of probability, that is, as the ratio of attractors found to be chaotic.

(can be removed)

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

This numerical experiment can be repeated for food webs of different sizes. In our simulations, we kept a ratio of 2:3 for the number of species at the consumer and the prey level.

### 3 Results

Plotting the probability of chaos against the competition parameter (see figures 6 and 7), we observe a clear maximum around  $\epsilon = 0$ . That is, for neutral competition at the prey's trophic level, the likelihood of chaotic behaviour is higher than for dominant inter or intraspecific competition. From the biological point of view, we show that neutrality and non-equilibrium dynamics are not completely independent. Maybe this can be a first step to reconcile both views.

The probability of chaos when intraspecific competition is dominant has a valley between  $\epsilon = -1$  and  $\epsilon = 0$ . We interpret this result as the overlap of two effects. On the one hand, as we have shown, weak dominant interspecific competition is less prone to chaos than neutral competition. On the other, strong interspecific competition increases the likelihood of chaos again. Assuming continuity, there has to be necessarily at least one minimum between both cases by virtue of Rolle's theorem [Simmons, 1996].

The overall likelihood of chaos increases with the size of the food web. This effect should not be surprising: the more dimensions the phase space has, the easier is to develop the complex geometry of a chaotic attractor. Intuitively, we can understand this as increasing the available room for the formation of the attractor. Even in those higher dimensional cases, a maximum is still happening at the neutral competition case.

#### 4 ~~Conclusions~~

Discussion Go back to the paradox

#### 5 Appendix

##### 5.1 Neutral competition

If we drop everything but the competition part of our dynamics (see equation 6), we will find a system of equations  $n$  like the following:

$$\dot{P}_i = P_i \left( 1 - \sum_{k=1}^n A_{ik} \cdot P_k \right) \quad (9)$$

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:

$$\dot{P}_i = P_i \left( 1 - A \sum_{k=1}^n P_k \right) \quad (10)$$

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 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

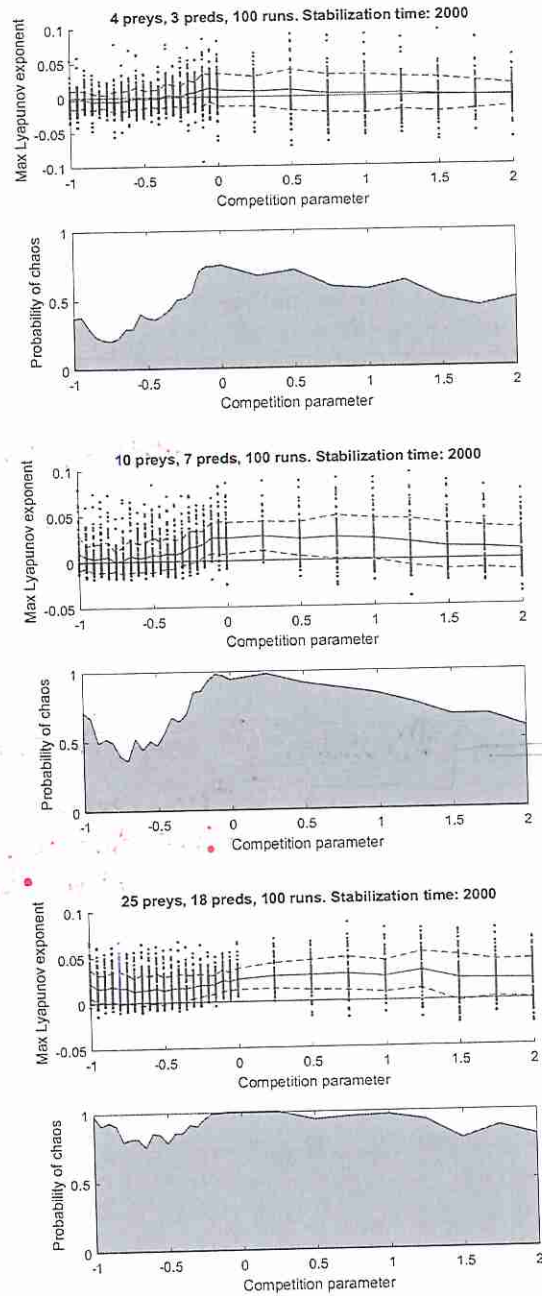
$\epsilon$  seems to be a really important parameter

Balance:  
Results  $\leftrightarrow$  Discussion

[ENV41]

Critical review of the model  
- Don't focus on network architecture  
- What if predators are generalists?

Some brainstorming



Local maxima related  
to symmetry

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 lower. The lower row represents the estimated probability of chaotic behaviour



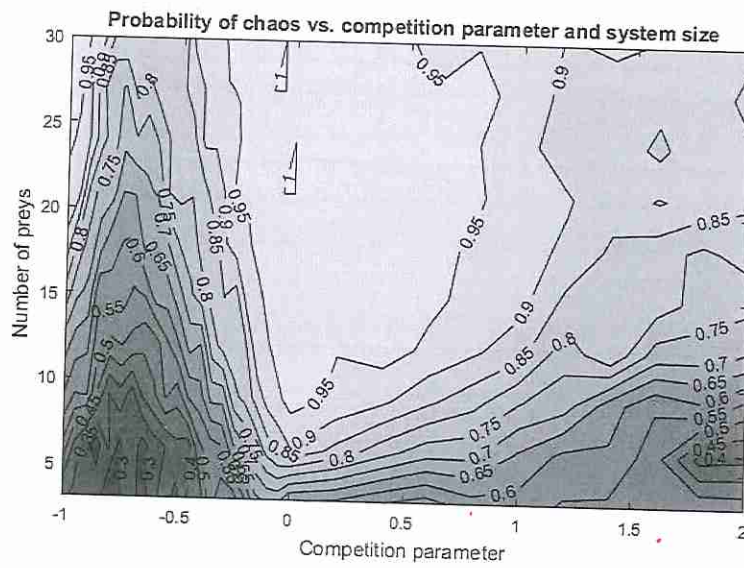


Figure 7: Contour map showing the probability of chaos for various competition parameters (horizontal axis) and prey populations (vertical axis). The consumers' population is fixed as  $2/3$  of the prey's population, in order to control the overall size of the system with a single parameter. Notice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

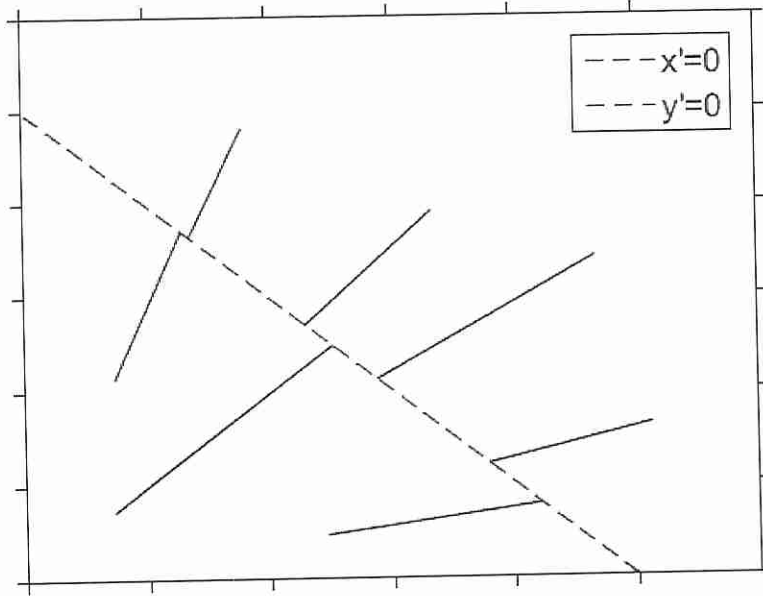


Figure 8: Example with 2 prey under neutral competition. Both nullclines coincide point to point, giving rise to a higher dimensional equilibrium manifold (in this case, a straight line)

species. Being this the case, the labels  $i$  distinguishing them become pointless. It is a good idea to sum up all the competing species into a new variable, that of total population of (now indistinguishable) species, defined by:

$$T(t) = \sum_{i=1}^n P_i(t) \quad (11)$$

It can be 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. This collapses the  $n$  dimensions of our original problem to a single one.

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

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 Acknowledgements

We thank Jelle Lever, for his useful comments and suggestions, and Sebastian Bathiany for the proofreading and suggestions.

## 7 To do

- 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 [van Nes and Scheffer, 2004], "*symmetry in competition strongly promotes multiplicity of attractors*"

No competition as a form of neutrality

Interpretation of probabilities? Are chaotic ecosystems fitter?

Details of numerics? Balance description - scripts

What should be done next?

- Mutualism ( $\epsilon < -1$ ?)
- Neutrality in predation

- Symmetry Read again Self-organized similarity

- Estimators of  $\epsilon$

Patches and diffusion?  
O-D model?

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