

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

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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 an ecosystem with two trophic levels, we explore the surroundings of this limit case, that is, weak non-neutral competition interactions. It is shown that, the closer the competition is to neutrality, the higher are the chances of the system to develop chaotic behaviour.

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

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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 life. 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*

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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. This means that time, and not only space, needs to be taken into account in the definition of ecological niche. 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 [Jos 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].

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, death, 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 the present paper we explore the links between neutral competition and the type of long term dynamics exhibited. Using competition models with different degrees of heterogeneity, our simulations show that the likelihood of ending up inside a chaotic attractor increases when heterogeneity at the competitors' trophic level is minimal. That is, that neutrality promotes chaos.

## 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 source of resources.

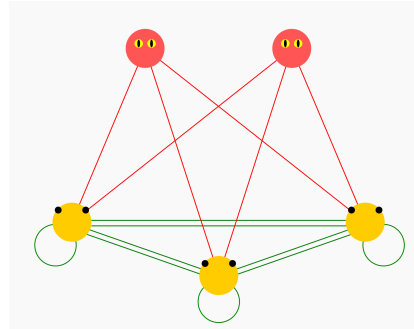


Figure 1: Example with 2 consumers and 3 prey. Each one of the red links represents a predation interaction (coded in the matrix of palatability coefficients,  $S$ ). Each green link represents a competition interaction (coded in the matrix of competition coefficients,  $A$ ). The closed green loops 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 the Rosenzweig-MacArthur predator-prey model [Rosenzweig and MacArthur, 1963] generalized to a higher number of species [van Nes and Scheffer, 2004]. Our model is composed of  $n_P$  prey species and  $n_C$  consumer species.  $P_i(t)$  was used for accounting the size of the population of prey  $i$  at time  $t$ , and  $C_j(t)$  for the population of consumer  $j$ . When it is not explicitly stated,  $i$  runs from 1 to  $n_P$ , and  $j$  from 1 to  $n_C$ . The prey compete directly among themselves, while the consumers don't interact directly. The prey competition is not necessarily symmetrical. The consumers eat all kind of prey (i.e.: they are generalists), but find some of them more preferable than others. All these interactions are summarized in figure 1. The overall structure looks like:

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

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  $n_P \times n_P$  matrix.~~ So, for prey  $i$ , we have:

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

The ~~palatability~~ of each prey species is given by  $S_{ij}$ . That is,  $S_{ij}$  represents the weight that consumer  $j$  gives to prey  $i$  in his *menu*. ~~Those coefficients can be arranged as an  $n_C \times n_P$  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  $j$ :


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

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:

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

$e$  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 prey species  $i$  as follows:

$$\text{Predation}_i = g \sum_{k=1}^{n_C} \left( \frac{S_{ki} P_i}{V_k} \right) C_k F_2(V_j; H) \quad (4)$$

Where the term inside the parentheses represents the relative ~~weight~~ of prey species  $i$  inside "the menu" of predator . It is interesting to note that the way the predation and feeding terms are defined satisfies the following property:

$$\sum_{j=1}^{n_C} \text{Feeding}_j = e \sum_{i=1}^{n_P} \text{Predation}_i \quad (5)$$

that is, all the deaths at the prey level are invested in the growth of consumers. For future clarity, it is a good idea to define the auxiliary function  $R_i$  as a summary of the effect of all consumers on prey  $i$ :

$$R_i(P, C) \equiv \sum_{k=1}^{n_C} \left( \frac{S_{ki} P_i}{V_k(P)} \right) C_k F_2(V_k(P); H) \quad (6)$$

Putting all together, the dynamical system reads:

$$\begin{cases} \dot{P}_i = rP_i \left( 1 - \frac{1}{K} \sum_{k=1}^{n_P} A_{ik} \cdot P_k \right) - gR_i(P, C) + f \\ \dot{C}_j = egC_j F_2(V_j(P); H) - lC_j \end{cases} \quad (7)$$

Depending on the parameters and the initial conditions, this system can give rise to three types of asymptotic behaviour, each of them corresponding to a different type of attractor. 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 ~~stabilizing nor~~ giving rise to periodicity (see figure 2).

## 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	$d^{-1}$
$K$	Carrying capacity	1.00	$mg \ l^{-1}$
$g$	Predation rate	0.40	$d^{-1}$
$f$	Immigration rate	$10^{-5}$	$mg \ l^{-1} \ d^{-1}$
$e$	Assimilation efficiency	0.60	1
$H$	Half-saturation constant	2.00	$mg \ l^{-1}$
$l$	Loss rate	0.15	$d^{-1}$
$S$	$n_C \times n_P$ palatability matrix	$S_{ij} \sim (0, 1)$	1
$A$	$n_P \times n_P$ competition matrix	See section 2.2.1	1

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

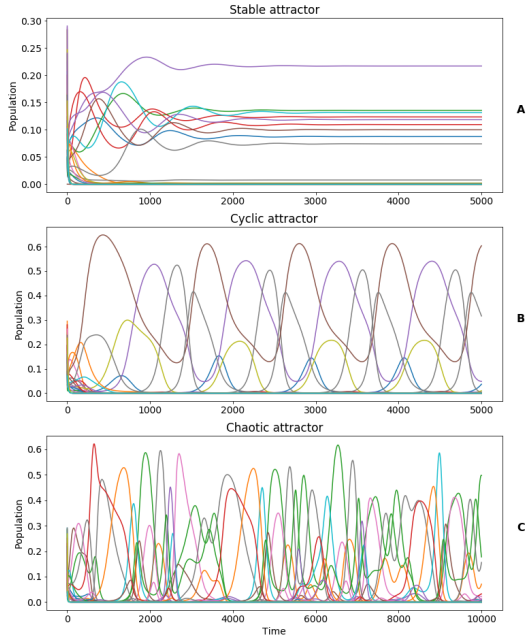


Figure 2: Our model generates time series of the population of each species. The time series can be classified in 3 types depending on their asymptotic behavior: *stable*, *periodic* and *chaotic*. In **figure A**, the system reaches a stable attractor after a transient time. In **figure B**, a periodic attractor, with an approximate period of 1000 days, is reached after the transient time. The system in **figure C** never reaches a stable nor a cyclic attractor, but a chaotic one.

### 2.2.1 Competition parameter

Our aim is to analyze the behavior of the system described in equation 7 for competition interactions differing in heterogeneity. In order to quantify heterogeneity and controlling how far from neutral the competition is, we introduce the competition parameter  $\epsilon$ . This dimensionless parameter allows 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 neither the intra nor the interspecific competition is dominant, represents neutral competition (see figure 4).

The numerical implementation of these ideas can be easily achieved by building a competition matrix whose non diagonal terms are perturbed by an additive random number  $W$ , whose size is controlled by  $\epsilon$  (see figure 4 and equation 8).

$$A_{ij}(\epsilon) = \begin{cases} 1 & : i = j \\ W(\epsilon) & : i \neq j \end{cases} \quad (8)$$

The random numbers  $W$  have been drawn from a uniform distribution<sup>1</sup> of width 0.2 centered in  $\epsilon$ . This parameterization allows us to travel continuously from strong dominant intraspecific to strong interspecific competition, meeting neutral competition at the border in between.

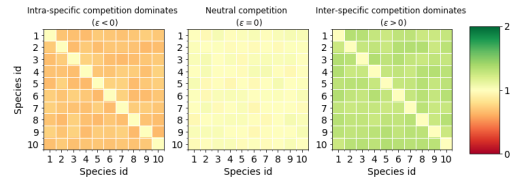


Figure 4: The competition matrix on the left is a clear case of dominant intraspecific competition. The central one represents a case of neutral competition. The matrix in the right panel shows a case of dominant interspecific competition. The difference between them is the relative size of the non-diagonal elements respective of the diagonal ones. This qualitative properties of the competition matrices is controlled by the parameter  $\epsilon$ .

<sup>1</sup>Other distributions have been tried, leading to the same qualitative results.

## 2.3 Numerical experiment

Our target is to estimate the probability of reaching a chaotic attractor under different degrees of heterogeneity. In order to achieve this, we'll simulate several ecosystems with different initial conditions and relative predation intensities, but sharing the same competition parameter. We consider thus that those ecosystems share a qualitative property: the same degree of heterogeneity.

Numerical methods are used to integrate the equation 7. As a result, we obtain time series as the ones in figure 2. Using the Gottwald-Melbourne [CITE] test<sup>2</sup>, we classify each individual simulation as *chaotic* or *non-chaotic*. The ratio of attractors found to be chaotic can be used to estimate the probability of ecosystems of a given degree of heterogeneity developing chaotic asymptotic behavior.

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.

For the sake of reproducibility, we provide a *GitHub* link to the analysis scripts used [DON'T FORGET TO ACTUALLY PROVIDE IT].

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

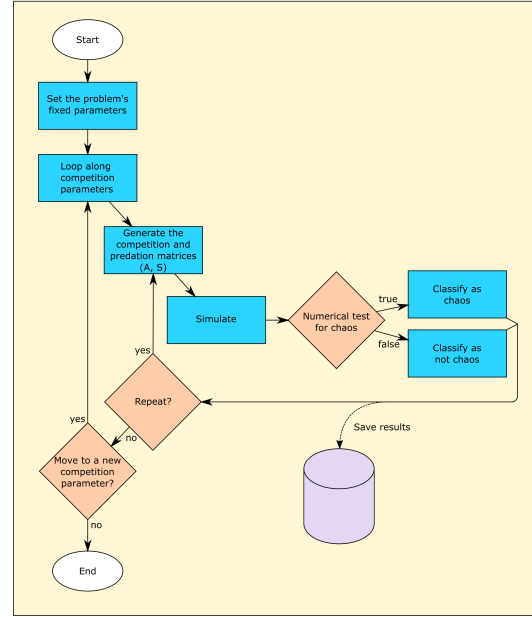


Figure 5: Flow chart describing the numerical experiment

## 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.

There's another local maximum for  $\epsilon = -1$ . This means that ~~strong intraspecific interaction~~ also promote chaos [COBERT MENTIONED IT THIS IS REASONABLE, BUT A CITATION WILL BE NEEDED HERE].

The probability of chaos has a local minimum between  $\epsilon = -1$  and  $\epsilon = 0$ , whose exact position differs between experiments. We interpret this result as a consequence of the two previous effects: assuming continuity, there should be necessarily at least one minimum between two maxima<sup>3</sup>.

The overall likelihood of chaos, which can be interpreted as the area under the curve, increases

<sup>2</sup>We also applied the maximum Lyapunov exponent test, together with visual inspection, finding the same qualitative results.

<sup>3</sup>This is a direct consequence of applying Bolzano's theorem to the first derivative. Intuitively: there should be at least one valley between two mountains

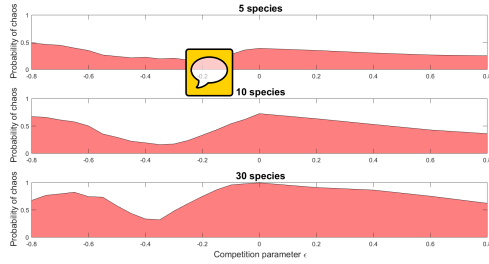


Figure 6: Results for a low, medium and high dimensional system. Notice how the probability of chaos has a local maximum around  $\epsilon = 0$ . The overall probability of chaos, understood as the area under the curve, grows with the system size. The local maximum stays at  $\epsilon = 0$  even for systems with a big amount of species.

with the size of the food web (see figure 6). This effect should not be surprising: the more dimensions the phase space has, the easier is to fulfill the requirements of the complex geometry of a chaotic attractor<sup>4</sup>. Even in those higher dimensional cases, a maximum is still happening at the neutral competition case.

## 4 Discussion

The asymptotic dynamics of our model are affected by the degree of heterogeneity of the competition. Particularly, the closer to neutrality our system is, the higher are the chances of developing chaotic behaviour. From the biological point of view, and going back to the hypotheses about biodiversity mentioned in section 1, this observation suggests that the hypothesis of non-equilibrium and Hubbell's hypothesis of neutrality<sup>5</sup> are not completely independent. Maybe this can be a first step to reconcile both views.

In the spirit of mathematical modelling, we chose the simplest realization required for the effects to be observed. We didn't use Allee effect, nor noise, and the functional form of each term has been chosen to account for satiation in the simplest possible way. The choice of a two-level model may seem

<sup>4</sup>We can understand this intuitively as increasing the available room for the trajectories to pack closer and closer without ever crossing each other nor collapsing to a point.

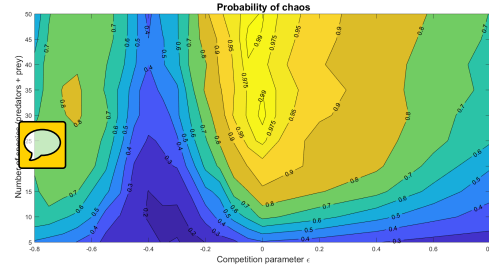


Figure 7: Contour map showing the probability of chaos for various competition parameters (horizontal axis) and prey populations (vertical axis). The consumers' population is fixed as  $2/3$  of the prey's population, in order to control the overall size of the system with a single parameter. Notice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

in contradiction with the pursue of simplicity, but actually it is a fundamental requirement for the effect under research to take place. In the absence of predation, chaos will never develop<sup>5</sup>.

We used the simplest predation network, that is, one with random predation coefficients. The predators can be considered generalists. A straightforward continuation of this paper could be studying the effect of the type of predation (generalist, specialist, neutral), controlling with a single parameter the flavour of the predation matrix  $S$ .

Numerical detection of chaos has fundamental limitations. Can be boiled down to the fact that, in general, numerical methods cannot distinguish robustly between long transients and genuine chaos. In the present paper three parallel approaches were followed: Lyapunov exponents estimation, Gottwald-Melbourne  $\neq$  test and visual inspection. Despite differences in the exact probabilities, the three of them lead us to the same qualitative conclusions. We think that our approach to chaos detection, despite being open to improvement, suf-

<sup>5</sup>If all interactions become equally strong, the differences among species at the same trophic level fade out. This makes labeling each species meaningless, and thus the prey-only system can be reduced to one differential equation, that of the total population. It can be proven that chaos cannot be developed in autonomous systems with less than 3 dimensions. For details, see Poincaré-Bendixson theorem.

fices to hold the biological conclusions.

Interestingly enough, a relatively small number of iterations suffices to generate a remarkably clear maximum in the probability of chaos for neutral competition. The position of this maximum is independent of the number of interacting species. This suggests that the parameter  $\epsilon$ , originally motivated by numerical convenience, may have a biological interpretation by itself. It will be interesting to reverse-engineer this parameter given a set of community matrices validated by experimental or field observations.

It may be worth noting that the position of both the maxima we've found (i.e.:  $\epsilon = -1$  and  $\epsilon = 0$ ) have something in common: the community matrix  $A$  at those values of the parameter is very symmetric in both cases. It will be interesting to develop a similar method that, instead of varying neutrality, varies the less restrictive property of symmetry.

Additionally, we are implicitly assuming without a proof that chaotic ecosystems are fitter than non-chaotic ones. A possible continuation of this research may be the setting of two independent ecosystems, one of them chaotic and the other one non-chaotic, and allow them to interact at some point of time (simulating an invasion), in order to assess how much of each of the original ecosystems survives to this traumatic event.



## 5 Acknowledgements

The preliminary analysis of this model were performed using GRIND for Matlab (<http://www.sparcs-center.org/grind>). Additionally, we thank Jelle Lever, Moussa N'Dour and Sebastian Bathiany for their useful comments and suggestions.

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