



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

Pablo Rodríguez-Sánchez ^{*1}, Egbert H. van Nes ^{†1}, and Marten Scheffer ^{‡1}

¹Department of Aquatic Ecology, Wageningen University, The Netherlands

May 1, 2018

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. We show that, the closer the competition is to neutrality, the higher ~~are~~ the chances of the system ~~to develop~~ chaotic behaviour. The competitive exclusion principle, based in equilibrium assumptions, is thus less likely to be applicable to neutral systems. As a result, these systems have ~~more chances~~ developing supersaturated coexistence than non neutral ones.

Keywords: population dynamics, coexistence, competition, neutral competition, biodiversity paradox, chaos.

Contents

1	Background	2
2	Methods	3
2.1	Model description	3
2.2	Parameterization	5
2.2.1	Competition parameter	7
2.3	Numerical experiment	7
3	Results	8
4	Discussion	8

^{*}pablo.rodriguezsanchez@wur.nl

[†]egbert.vannes@wur.nl

[‡]marten.scheffer@wur.nl

5 Acknowledgements	11
6 Appendix	12
6.1 Generalized multispecies predation models	12
6.1.1 General properties of predation models	12
6.1.2 Lotka-Volterra equations	13
6.1.3 Multispecies Lotka-Volterra equations	13
6.1.4 Rosenzweig-MacArthur model	14
6.1.5 Multispecies Rosenzweig-MacArthur model	14
6.1.6 Summary	15
6.2 Neutral competition and system degeneration	15
6.3 Extra figures	17
6.3.1 Competition matrix	17
6.3.2 Flow chart	18

TODOs

<input type="checkbox"/> Move section	3
<input type="checkbox"/> Rename feeding	5
<input type="checkbox"/> Check name	15
<input type="checkbox"/> Online appendix	20
<input type="checkbox"/> Past tense	20

1 Background

Fascination for 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 as there is a big mystery: why are there so many species?

The mystery comes into scene together with the competitive exclusion principle [1], sometimes referred to as Gause's law. This principle, which some authors trace back to Charles Darwin's *On the origin of the species* [2], is one of the classical keystones 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, complete exclusion rarely occurs in nature [3], being the huge biodiversity in rather homogeneous ecosystems such as pelagic environments a remarkable counterexample [4]. This contradiction is known as the biodiversity paradox. The paradox can be rephrased as *Why are there so many species if there are so few niches?*

Several hypotheses have been proposed  to explain the paradox. For instance, Hutchinson [5] suggests that the number of niches of species can be higher than expected at first sight due to a separation in time of competition. As an example he reports observations of two sympatric species of beetles competing for the same resource, but not simultaneously because of having different breeding seasons. In a later, influential paper [4], Hutchinson proposes the possibility that more species can coexist due to external, time-dependent

environmental changes, being seasonal factors an obvious example. If the characteristic times of these environmental changes are fast enough, the ecosystem is prevented to reach an equilibrium. A pioneering quantitative discussion about ecosystems subject to periodically driven external perturbations can be found in [3] and, more recently, in [6].

After the discovery of deterministic chaos [7], it has been shown that non-equilibrium ecosystems can arise as well under constant environmental conditions [8, 9]. More specifically, those ecosystems develop cyclic or chaotic dynamics instead of fixed points. Of course, chaotic dynamics can arise as well in seasonally changing environments in a food web (as, for instance the model with multiple predators studied in [10]).

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 [11].

A rather radical other explanation for high diversity is *Hubbell's neutral competition theory* [12]. Here it is assumed that similar species inside an ecological community have identical *per capita* rates of birth, death, reproduction, etc. In those models, the long term differences between species are a result of stochastic processes. Despite its counter-intuitive and controversial foundations, neutral models have been successfully applied to populations of rainforest trees [12]. Even more interesting, neutrality has been found to arise as a self-organized effect allowing higher coexistence in evolutionary models [13].

Most of the previously mentioned theories involve competition only, whereas in many ecosystems predation is also relevant. It is known from models that the inclusion of a multi-species predation trophic level increases the probability of chaos [10], and may thus contribute to increase the number of coexisting species. In the present paper we explore the links between the heterogeneity at the competition level of a two trophic levels model and the type of long term dynamics exhibited.

2 Methods

2.1 Model description

Pablo: Move most of this to the appendix

We focused our attention on 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.

The dynamics were modelled as a system of ordinary differential equations. We used the Rosenzweig-MacArthur predator-prey model [14] generalized to a higher number of species [15]. 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 compete indirectly by sharing the same food. The consumers eat all kind of prey, but find some of them more

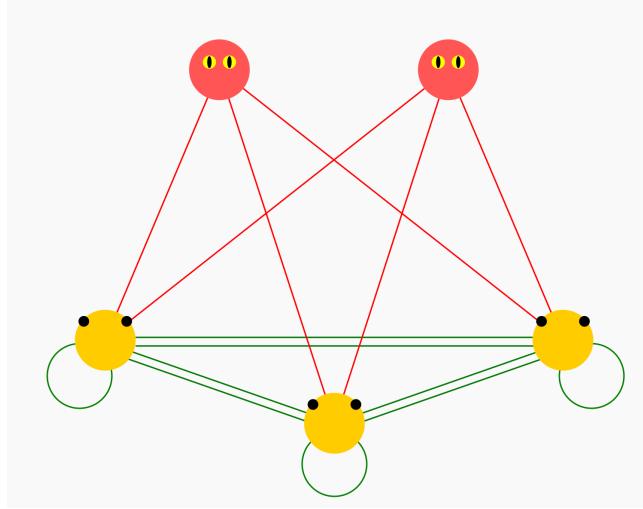


Figure 1: Example with 2 consumers and 3 prey. Each one of the red links represents a predation interaction (coded in the matrix of predator preference coefficients, S). Each green link represents a competition interaction (coded in the matrix of competition coefficients, A). The closed green loops are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

preferable than others. All these interactions are summarized in figure 1. The overall structure looks like:

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

The growth term is modelled as a multispecies logistic growth. The strength of the competition between species i and k is given by the community matrix element A_{ik} . So, for prey i , we have:

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

A secondary source for prey's growth in our model will be a small constant immigration term f , representing immigration from neighboring areas. Additionally, the inclusion of this term avoids unrealistic long-stretched cycles with near extinctions [15].

The predator preference for each prey species is given by the matrix S . That is, the matrix element S_{ij} represents the relative proportion of prey i in consumer's j menu. We define an auxiliary vector V , whose elements V_j are calculated as a sum of the prey's populations weighted by the predator preference coefficients. Biologically, this represents the total composition of consumer j 's menu:

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

We hypothesized that the feeding term will be linear in C_j . The dependency on V_j happens through a Holling type II functional response with half saturation constant H in order to account for consumer satiation [16].

$$Feeding_j = egC_j \frac{V_j}{V_j + H} \quad (3)$$

Egbert: Feeding is confusing as the sum of predation should be the sum of the feeding. Possible new name: GrossGrowth (NetGrowth = GrossGrowth - Loss).

Pablo: being the sum up to assimilation constant maybe it is clearer to take the constant out of the equation.

Pablo: I'll do it after moving part of this section to the appendix.

e represents the assimilation efficiency of the predation. Thus, the effect of consumer j on all prey's populations is given by $Feeding_j/e$. Knowing this, we can sum the effect of all consumers in the prey species i as follows:

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

Where the term inside the parentheses represents the relative proportion of prey species i in the menu of predator k , and F_2 is a shorthand for the Holling type II functional form introduced before. It is interesting to note that the way the predation and feeding terms are defined satisfies the following property:

$$\sum_{j=1}^{n_C} Feeding_j = e \sum_{i=1}^{n_P} Predation_i \quad (5)$$

that is, all the deaths at the prey level are invested in the growth of consumers. We 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:

$$\begin{cases} \dot{P}_i = r P_i \left(1 - \frac{1}{K} \sum_{k=1}^{n_P} A_{ik} \cdot P_k \right) - g R_i(P, C) + f \\ \dot{C}_j = e g C_j F_2(V_j(P); H) - l C_j \end{cases} \quad (7)$$



2.2 Parameterization

We parameterized our model as a freshwater plankton system based on Dakos' model [10]. Dakos' model, focusing on plankton communities, uses as well a Rosenzweig-McArthur dynamic with two trophic levels (that of zooplankton

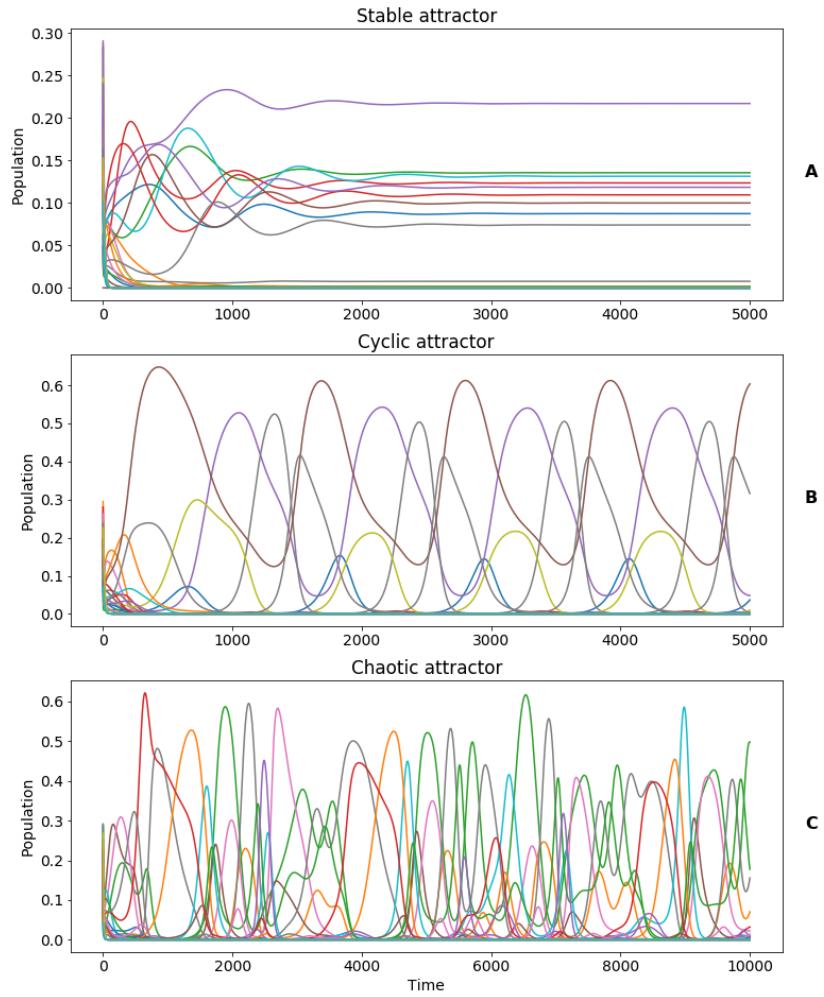


Figure 2: Our model generates time series of the population of each species. The time series can be classified in 3 qualitative types depending on their asymptotic behavior: *stable*, *periodic* and *chaotic*. In **figure A**, the system reaches a stable attractor after a transient time. In **figure 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.

~~and phytoplankton).~~ Unlike Dakos, who uses seasonally changing parameters, our parameters were constant (see table 1).

Symbol	Interpretation	Value	Units
r	Maximum 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	$n_C \times n_P$ predator preference matrix	$S_{ij} \sim (0, 1)$	1
A	$n_P \times n_P$ competition matrix	See section 2.2.1	1

Table 1: Values and meanings of the parameters used in our numerical experiment

2.2.1 Competition parameter

In order to control how far from  the competition is, we introduce the competition parameter ϵ . 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 7 in Appendix).

~~The numerical implementation of these ideas can be easily achieved by building a competition matrix whose diagonal terms are identically 1, and whose non-diagonal terms are drawn from a uniform probability distribution centered at $1 + \epsilon$ and with a given width (here we chose $w = 0.2$).~~

This parameterization allows us to travel continuously from strong dominant intraspecific ($\epsilon < 0$) to strong interspecific competition ($\epsilon > 0$), meeting neutral competition at the border in between (i.e., at $\epsilon = 0$).

2.3 Numerical experiment

Depending on the parameters and the initial conditions, the system described in equation 7 can give rise to three types of asymptotic behavior, each of them roughly corresponding to a different type of attractor (see figure 2). The easier one, corresponding to a stable point attractor, generates a constant species composition. Limit cycle (and limit tori) attractors give rise to periodically (or quasiperiodically) changing species composition. Last but not least, we'll refer as chaotic to attractors not fitting in any of the previous categories.

Our target is to estimate the probability of reaching one of such chaotic attractors under different assumptions about intraspecific competition. In order to achieve this, we simulated several ecosystems with ~~different initial conditions and relative predation intensities~~, but ~~sharing~~ the same competition parameter.

Numerical methods are used to integrate  equation 7. A first stabilizing run of 2000 days is generated in order to get closer to the attractor. Simulating for 5000 more days, we obtain time series as the ones in figure 2.

In the exploratory phase of this research three parallel approaches to chaos detection were followed: Lyapunov exponents estimation [17], Gottwald-Melbourne $0\text{-}1$ test [18] and visual inspection. Despite differences in the exact probabilities, the three of them led us to the same qualitative conclusions. We found the results of the Gottwald-Melbourne test most consistent with visual inspection. We called chaotic all those time series complicated enough to trigger the Gottwald-Melbourne test. Using this approach, we classified each individual simulation as *chaotic* or *non-chaotic*. Our numerical experiment was repeated 200 times for each competition parameter. 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.

Additionally, the experiment was 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 used¹. For further information  please refer to the *read me* file and/or to the Appendix.

3 Results

Plotting the probability of chaos against the competition parameter (see figures 3), 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. This result remains true for systems with different amount of species (figures 3 and 4).

The overall likelihood of s, which can be interpreted as the area under the curve in figure 3, 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 fulfill the requirements of the complex geometry of a chaotic attractor [17]. 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. Even in those higher dimensional cases, there is still a clear maximum at neutral competition.

There's another local maximum for $\epsilon = -1$. This means that weak competition coupling, in our model, also promotes chaos.

Between both local maxima there is obviously a local minimum whose exact position differed between experiments.

4 Discussion

The asymptotic dynamics of our model are affected by how strong intraspecific  competition compared to interspecific competition is. We find particularly interesting the fact that the closer to neutrality the competition in our food web is, the higher are the chances of developing chaotic behaviour. This suggests that in a system with predation, near-neutrality at the competition level may increase the probability of complex dynamics if the species are not equally prone

¹<https://github.com/PabRod/Chaos-and-neutrality>

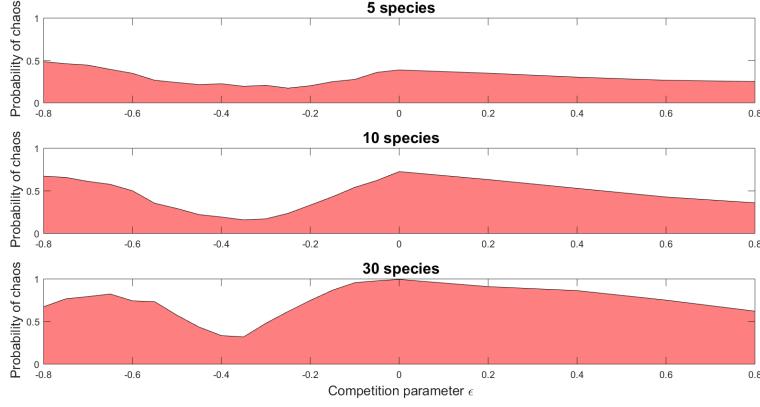


Figure 3: Results for a low, medium and high dimensional system. Notice how the probability of chaos has a local maximum around $\epsilon = 0$. The overall probability of chaos, understood as the area under the curve, grows with the system size. The local maximum stays at $\epsilon = 0$ even for systems with a big amount of species.

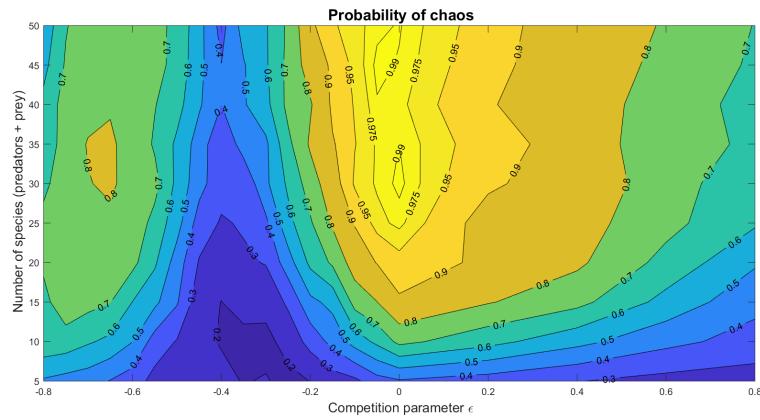


Figure 4: Contour map showing the probability of chaos for various competition parameters (horizontal axis) and number of species (vertical axis). The consumers' population is fixed as $2/3$ of the prey's population. Notice that chaotic attractors appear more easily (i.e., for smaller systems) the closer is the competition to neutral (i.e., $\epsilon = 0$).

to predation. Provided the competitive exclusion principle rests on the assumption of equilibrium, near-neutrality reduces the chances of the principle to be applicable, improving the chance for a higher number of coexisting species. Additionally, this observation suggests that the hypothesis of non-equilibrium and Hubbell's hypothesis of neutrality are not completely independent. Our model shows another local maximum for the probability of chaos for weak competition coupling. We consider this a reasonable result, as predation is known to be the main driver of chaos in this kind of models [15].

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 and saturation in the simplest possible ways. The choice of a two-level model may seem 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 a predator level, chaos will never develop in a model with neutral competition. The reason for this is that 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 just to one differential equation, that of the total population (see section 6.2 for details). Using the Poincaré-Bendixson theorem, it can be proven that chaos autonomous systems with less than 3 dimensions cannot exhibit chaos [17].

Even in the absence of neutral competition, it is known that the presence of chaos or cycles instead of fixed points depends crucially on predation and heterogeneity [18]. This predation effects can be interpreted as a type of response diversity [19], so including them provides additional realism to the model.

Both the competition and predation parameters were drawn from probability distributions. The interactions in our system can be interpreted as a weighted network with a high connectivity. Trophic networks studied in nature tend to show modular structure with various clusters [20]. The present model restricts its attention on one of those modules, neglecting possible interactions with others.

It is known that the asymptotic behaviour of this kind of systems can be very sensitive to the parameters choice. In particular, introducing correlations between parameters can greatly modify the probabilities of chaotic attractors to be reached (see for instance [21], in response to the letter [22]). In the present paper we didn't introduce any correlation, i.e., all our random parameters were drawn independently from the others. Studying the effect of different physiological scenarios (in the sense of [21], that is, constraints between the parameters) on the probabilities of chaos could be a continuation to this paper.

Due to the large amount of simulations made, we had to rely in automatic methods for detecting chaos. Numerical detection of chaos has fundamental limitations. All of them can be boiled down to the fact that, in general, numerical methods cannot distinguish robustly between long, complicated transients and genuine chaos. We think that our approach to chaos detection, despite being open to improvement, suffices to hold the biological conclusions.

The paradox of biodiversity is a tremendously complex scientific problem. With these model exercises we definitely do not claim to have solved it, but we show that predation in combination with neutral competition may increase the probability of chaos, and thereby increase the number of coexisting species.

5 Acknowledgements

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

6 Appendix

6.1 Generalized multispecies predation models

6.1.1 General properties of predation models

Most predation models based on differential equations follow a structure like this:

$$\begin{cases} \dot{P} = Growth(P) - Predation(P, C) \\ \dot{C} = -Loss(C) + GrossGrowth(P, C) \end{cases} \quad (8)$$

where P represents the biomass of the prey population, and C the biomass of the consumer/predator population. The functional dependences have been explicitly written in order to remark the fact that the coupling of the system happens via the *Predation* and *GrossGrowth* terms.

~~It is important to note that, in models like this, all deaths at the prey's level are due to predation. This can be understood as all deaths being invested into consumer's growth. In order of this effect to be true, a restriction must be applied to the functional forms of Predation and GrossGrowth.~~

$$GrossGrowth(P, C) = e \cdot Predation(P, C) \quad (9)$$

where e represents the efficiency of the energy transfer process. Equation 9, when plugged into 8, yields:

$$e\dot{P} + \dot{C} = e \cdot Growth(P) - Loss(C) \quad (10)$$

Equation 10 allows us to think of our system as an open system from the point of view of thermodynamics, with *Growth* being the only source of the system, and *Loss* the only sink (see figure 5). All the energy exchange due to predation stays inside the system, so predation can be considered a closed subsystem.

We can generalize this basic structure to multispecies, two trophic levels systems. First, we'll go back to equation 8 and just add more rows, being specially careful with the variables if the functional relations:

$$\begin{cases} \dot{P}_i = Growth_i(P) - Predation_i(P, C) & : i = 1..n_P \\ \dot{C}_j = -Loss_j(C_j) + GrossGrowth_j(P, C_j) & : j = 1..n_C \end{cases} \quad (11)$$

where now i runs from 1 to the number of prey n_P and j from 1 to the number of consumers n_C . Here, we've used P_i to denote the population of the prey labeled by i , and P for the vector containing all prey populations. Notice that, while the *Growth* term can involve competition (and thus, depends on the whole vector P), the *Loss* term for species j depends only in the population of that species (i.e.: C_j), regardless of the rest.

Requiring once again our predation to be fully invested in consumer's growth, we find the following generalization of equation 9:

$$\sum_{j=1}^{n_C} GrossGrowth_j(P, C_j) = \sum_{i=1}^{n_P} e_i \cdot Predation_i(P, C) \quad (12)$$

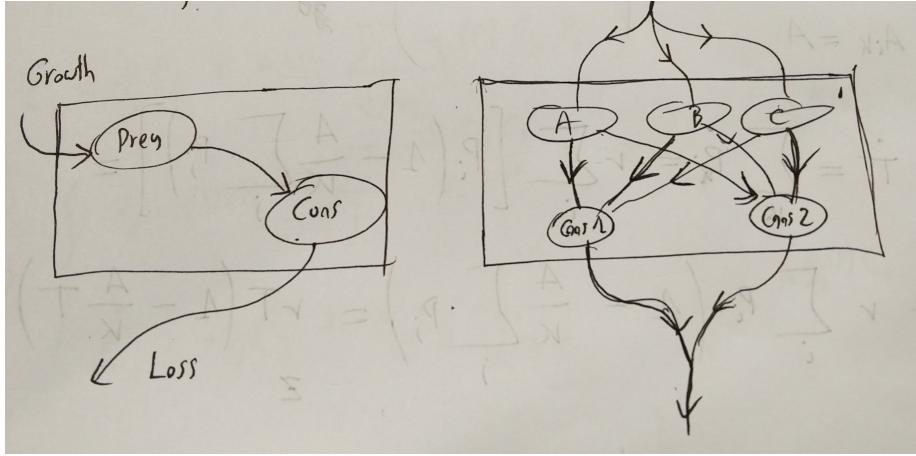


Figure 5: Plot showing the energy flow for a two species and a multispecies system.

Using 12 and 11, it is easy to prove that the multispecies generalization of 10 is:

$$\sum_{i=1}^{n_P} e_i \dot{P}_i + \sum_{j=1}^{n_C} \dot{C}_j = \sum_{i=1}^{n_P} e_i \cdot Growth_i(P) - \sum_{j=1}^{n_C} Loss_j(C_j) \quad (13)$$

The intuitive interpretation is, again, that the sinks and sources of energy in our systems are the total *Loss* and *Growth*.

It is difficult to overestimate the importance of restriction 12 (or equivalently, 13). We need it to build realistic functional forms for the coupling terms. Being the coupled terms those related with predation, those terms are the very core of this models.

6.1.2 Lotka-Volterra equations

The most basic model of predation is the Lotka-Volterra system of equations:

$$\begin{cases} \dot{P} = rP - gPC \\ \dot{C} = -lC + egCP \end{cases} \quad (14)$$

Where r represents the growth rate of the prey, g the grazing rate of the predator against the prey, l the loss rate of the predator and e the efficiency conversion factor.

It is trivial to prove that the Lotka-Volterra model satisfies the requirements shown in subsection 6.1.1.

6.1.3 Multispecies Lotka-Volterra equations

Lotka-Volterra equations can be generalized to a model with multiple species by noting that each prey will be affected by all consumers, and each consumer

will be affected by all prey. In order to code the strength of this interactions, we introduce the matrix S , whose element S_{ji} gives the strength of the coupling of consumer j and prey i . As a consequence: for prey dynamics, this matrix is scanned row-wise, while for predators it is scanned column-wise. The generalized system looks like:

$$\begin{cases} \dot{P}_i = r_i P_i - P_i \sum_{j=1}^{n_C} g_j S_{ji} C_j & : i = 1..n_P \\ \dot{C}_j = -l_j C_j + g_j e_j C_j \sum_{i=1}^{n_P} S_{ji} P_i & : j = 1..n_C \end{cases} \quad (15)$$

The fulfillment of condition 12 is again easily proven.

In this model, all terms can grow without boundaries. This is not only unrealistic, but also creates some problems from the sole point of view of mathematical stability.

6.1.4 Rosenzweig-MacArthur model

The Rosenzweig-MacArthur predator-prey model improves the previous model by adding boundaries to the terms' dependency on the prey population. This is achieved by encapsulating P inside saturating functions. In particular, the growth rate r now depends on P , and the grazing rate g in the coupling terms is now a function of P (see equation 16 and compare it with 14).

$$\begin{cases} \dot{P} = r(P)P - g(P)PC \\ \dot{C} = -lC + eg(P)CP \end{cases} \quad (16)$$

Once again, condition 9 is trivially fulfilled independently of the functional form of $r(P)$ and $g(P)$. If those both functions are chosen appropriately, we avoid unbounded effects. Typically a logistic growth form is chosen for $r(P)$, that is, $r(P) = r_0 \left(1 - \frac{P}{K}\right)$, and a Holling type II functional form for the grazing $g(P)$, that is, $g(P) = \frac{g_0}{P+H}$. After making this choices, our system takes its classical form:

$$\begin{cases} \dot{P} = rP \left(1 - \frac{P}{K}\right) - gC \frac{P}{P+H} \\ \dot{C} = -lC + egC \frac{P}{P+H} \end{cases} \quad (17)$$

6.1.5 Multispecies Rosenzweig-MacArthur model

Noticing the similarities between equations 14 and 16, the latter can be generalized in the same fashion as we did to obtain 15, yielding:

$$\begin{cases} \dot{P}_i = r_i(P)P_i - P_i \sum_{j=1}^{n_C} g_j(P)S_{ji}C_j & : i = 1..n_P \\ \dot{C}_j = -l_j C_j + g_j(P)e_j C_j \sum_{i=1}^{n_P} S_{ji}P_i & : j = 1..n_C \end{cases} \quad (18)$$

Written like this, it is easy to see that the condition 12 is fulfilled.

Regarding the proper functional forms of $r_i(P)$ and $g_j(P)$, our growth term has to take into account both the inter and intraspecific competition. This can be easily modelled by choosing:

$$r_i(P) = r_i \left(1 - \sum_{k=1}^{n_P} A_{ik} P_k \right) \quad (19)$$

We hypothesize that the grazing rates corresponding to predator j , that is, $g_j(P)$, follow a Holling type II functional response dependent on the total consumption of prey by predator j , that is: $V_j(P) = \sum_{i=1}^{n_P} S_{ji} P_i$

$$g_j(P) = \frac{g_j}{V_j + H_j} = \frac{g_j}{\sum_{i=1}^{n_P} S_{ji} P_i + H_j} \quad (20)$$

6.1.6 Summary

	Two species	Multispecies
Lotka-Volterra	$\begin{cases} \dot{P}_i = r_i P_i - g_i P_i C \\ \dot{C} = -l C + e g_i P_i C \end{cases}$	$\begin{cases} \dot{P}_i = r_i P_i - P_i \sum_{j=1}^{n_C} g_j S_{ji} C_j \\ \dot{C}_j = -l_j C_j + g_j e_j C_j \sum_{i=1}^{n_P} S_{ji} P_i \end{cases}$
Rosenzweig-MacArthur	$\begin{cases} \dot{P}_i = r_i(P) P_i - g_i(P) P_i C \\ \dot{C} = -l C + e g_i(P) C P \end{cases}$	$\begin{cases} \dot{P}_i = r_i(P) P_i - P_i \sum_{j=1}^{n_C} g_j(P) S_{ji} C_j \\ \dot{C}_j = -l_j C_j + g_j(P) e_j C_j \sum_{i=1}^{n_P} S_{ji} P_i \end{cases}$

Table 2: Summary table with the different types of predation models studied. Written this way, the parallelisms are obvious. In multispecies models, the index i runs from 1 to n_P , and j from 1 to n_C . The functional forms of $r_i(P)$ and $g_j(P)$ are given in equations 19 and 20

6.2 Neutral competition and system degeneration

Pablo: Check degeneration is the correct word

If we drop everything but the competition part of our dynamics (see equation 7), we will find a system of n_P equations like the following:

$$\dot{P}_i = r P_i \left(1 - \frac{1}{K} \sum_{k=1}^{n_P} A_{ik} \cdot P_k \right) \quad (21)$$

In order to model a neutral competition, we should use the same competition coefficient for each interaction between species. That is, take $A_{ik} = A$ for all i and k . Equation 21 then becomes:

$$\dot{P}_i = r P_i \left(1 - \frac{A}{K} \sum_{k=1}^{n_P} P_k \right) \quad (22)$$

From equation 22 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 (see figure 6).

This problem can be solved noticing that, in a competition-only system, the effect of neutrality is to fade out the differences between species. Being this the case, the labels i distinguishing them become meaningless. It is a natural idea

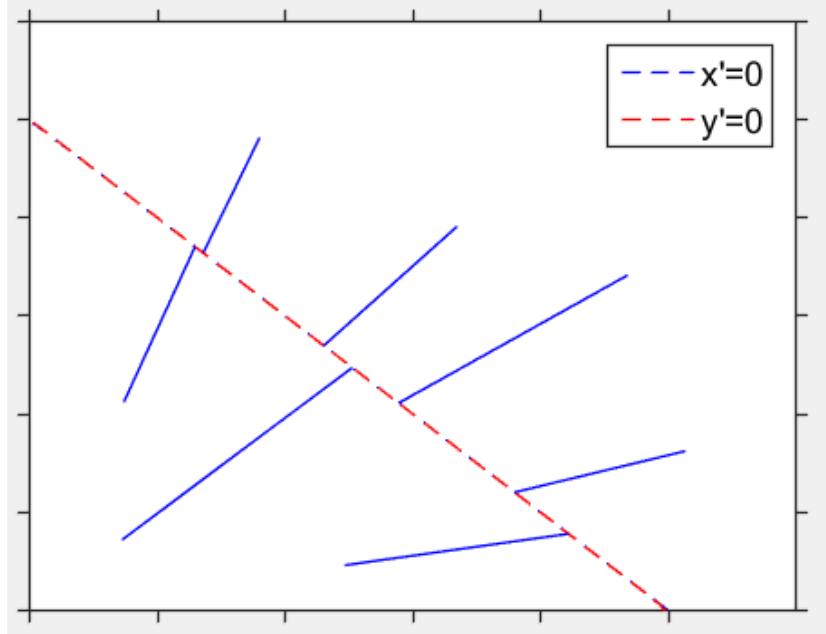


Figure 6: Example with 2 prey under neutral competition. Both nullclines coincide point to point, giving rise to a higher dimensional equilibrium manifold (in this case, a straight line)

to sum up all the biomasses of competing species into a new variable, that of total population of (now indistinguishable) species, defined by:

$$T(t) = \sum_{i=1}^{n_P} P_i(t) \quad (23)$$

In agreement with the biological intuition, manipulating 23 and 22 it can be proved (see eq. 24), that the total population biomass will follow the same differential equation as the individual species abundances (i.e., equation 22).

$$\dot{T} = \sum_{i=1}^{n_P} \dot{P}_i = r \sum_{i=1}^{n_P} P_i \left(1 - \frac{A}{K} \sum_{k=1}^{n_P} P_k \right) = rT \left(1 - \frac{A}{K} T \right) \quad (24)$$

Additionally, this result shows that we are actually working with a one-dimensional system, being the apparent n_P dimensions of our original problem an artifact due to a wrong choice of state variables. 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.

6.3 Extra figures

6.3.1 Competition matrix

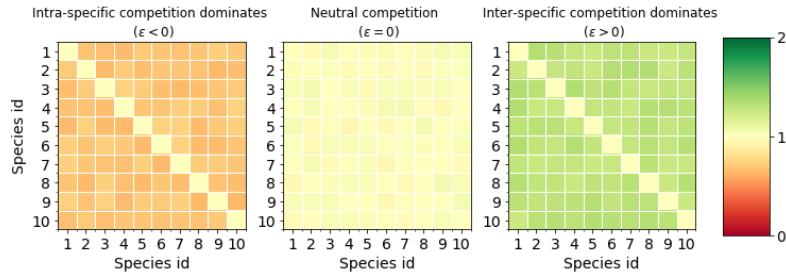


Figure 7: The competition matrix on the left is a clear case of dominant intraspecific competition. The central one represents a case of neutral competition. The matrix in the right panel shows a case of dominant interspecific competition. The difference between them is the relative size of the non-diagonal elements respective of the diagonal ones. This qualitative property of the competition matrices is controlled by the parameter ϵ .

6.3.2 Flow chart

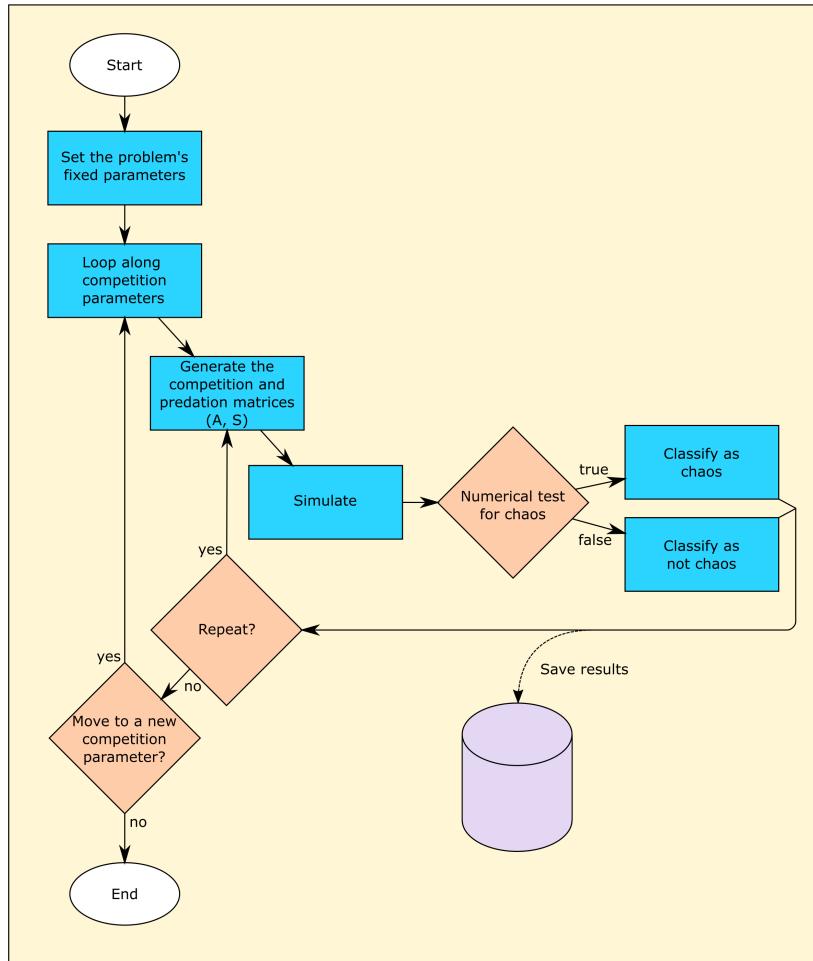


Figure 8: Flow chart describing the numerical experiment. The source code is available at <https://github.com/PabRod/Chaos-and-neutrality>.

References

- [1] Hardin G. The Competitive Exclusion Principle. *Science*. 1960;131(3409).
- [2] Darwin C. *On The Origin of Species by Means of Natural Selection, or Preservation of Favoured Races in the Struggle for Life*. London: John Murray; 1859.
- [3] Huston M. A general hypothesis of species diversity. *The American Naturalist*. 1979;113(1):81–101. Available from: <http://www.jstor.org/stable/2459944>.
- [4] Hutchinson GE. The Paradox of the Plankton. *The American Naturalist*. 1961 may;95(882):137–145. Available from: <http://www.journals.uchicago.edu/doi/10.1086/282171>.
- [5] Hutchinson GE. Homage to Santa Rosalia or Why Are There So Many Kinds of Animals? *The American Naturalist*. 1959 may;93(870):145–159. Available from: <http://www.journals.uchicago.edu/doi/10.1086/282070>.
- [6] Sakavara A, Tsirtsis G, Roelke DL, Mancy R, Spatharis S. Lumpy species coexistence arises robustly in fluctuating resource environments. *Proceedings of the National Academy of Sciences of the United States of America*. 2018 jan;115(4):738–743. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/29263095> <http://www.ncbi.nlm.nih.gov/articlerender.fcgi?artid=PMC5789903>.
- [7] Lorenz EN. Deterministic Nonperiodic Flow. *Journal of the Atmospheric Sciences*. 1963 mar;20(2):130–141. Available from: [http://journals.ametsoc.org/doi/abs/10.1175/1520-0469%281963%29020%3C0130%3ADNF%3E2.0.CO%3B2](http://journals.ametsoc.org/doi/abs/10.1175/1520-0469\%281963\%29020\%3C0130\%3ADNF\%3E2.0.CO\%3B2).
- [8] May RM. Biological Populations with Nonoverlapping Generations: Stable Points, Stable Cycles, and Chaos. *Science*. 1974 nov;186(4164):645–647. Available from: <http://www.sciencemag.org/cgi/doi/10.1126/science.186.4164.645>.
- [9] Huisman J, Weissing FJ. Biodiversity of plankton by species oscillations and chaos. *Nature*. 1999 nov;402(6760):407–410. Available from: <http://www.nature.com/articles/46540>.
- [10] Dakos V, Beninca E, van Nes EH, Philippart CJM, Scheffer M, Huisman J. Interannual variability in species composition explained as seasonally entrained chaos. *Proceedings of the Royal Society B: Biological Sciences*. 2009 aug;276(1669):2871–2880. Available from: <http://rspb.royalsocietypublishing.org/cgi/doi/10.1098/rspb.2009.0584>.
- [11] Tilman D. Competition and Biodiversity in Spatially Structured Habitats. *Ecology*. 1994 jan;75(1):2–16. Available from: <http://doi.wiley.com/10.2307/1939377>.
- [12] Hubbell SP. The Unified Neutral Theory of Biodiversity and Biogeography. *Biological Conservation*. 2003 apr;110(2):305. Available from: <http://linkinghub.elsevier.com/retrieve/pii/S0006320702002288>.

- [13] Scheffer M, van Nes EH. Self-organized similarity, the evolutionary emergence of groups of similar species. *Proceedings of the National Academy of Sciences of the United States of America*. 2006;103(16):6230–6235.
- [14] Rosenzweig ML, MacArthur RH. Graphical Representation and Stability Conditions of Predator-Prey Interactions. *The American Naturalist*. 1963 jul;97(895):209–223. Available from: <http://www.journals.uchicago.edu/doi/10.1086/282272>.
- [15] van Nes EH, Scheffer M. Large Species Shifts Triggered by Small Forces. *The American Naturalist*. 2004 aug;164(2):255–266. Available from: <http://www.journals.uchicago.edu/doi/10.1086/422204>.
- [16] Edelstein-Keshet L. Mathematical Models in Biology. Society for Industrial and Applied Mathematics; 2005. Available from: <http://epubs.siam.org/doi/10.1137/1.9780898719147>.
- [17] Strogatz SH. Nonlinear Dynamics And Chaos: With Applications To Physics, Biology, Chemistry And Engineering; 1994.
- [18] Gottwald GA, Melbourne I. On the Implementation of the 0-1 Test for Chaos. *SIAM Journal on Applied Dynamical Systems*. 2009 jan;8(1):129–145. Available from: <https://arxiv.org/pdf/0906.1418.pdf><http://epubs.siam.org/doi/10.1137/080718851>.
- [19] Yachi S, Loreau M. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America*. 1999 feb;96(4):1463–8. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/9990046><http://www.ncbi.nlm.nih.gov/articlerender.fcgi?artid=PMC15485>.
- [20] Thebault E, Fontaine C. Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks. *Science*. 2010 aug;329(5993):853–856. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/20705861>.
- [21] Huisman J, Johansson AM, Folmer EO, Weissing FJ. Towards a solution of the plankton paradox: the importance of physiology and life history. *Ecology Letters*. 2001 sep;4(5):408–411. Available from: <http://doi.wiley.com/10.1046/j.1461-0248.2001.00256.x>.
- [22] Schippers P, Verschoor AM, Vos M, Mooij WM. Does "supersaturated coexistence" resolve the "paradox of the plankton"? *Ecology Letters*. 2001 sep;4(5):404–407. Available from: <http://doi.wiley.com/10.1046/j.1461-0248.2001.00239.x>.

Decide how to split the information into main paper + appendix. **Egbert:** I think you need to make an appendix explaining the relation between Lyapunov and the other indices. Maybe some additional figures (if you have them?) In the results section you should refer to those extra results.

Double check the use of past tense along all the paper