## Self-organized Dynamic Predation-and-Migration model to simulate impacts of global change in food webs

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## **Abstract**

Advances in the development of a framework to simulate dynamics undergoing ecosystem networks are presented. In this research, we build networks of geographical spots (nodes). The links between them mimic routes allowing species to move around geographically. At each spot it takes place simultaneously the interacting dynamics between species lead by the architecture of a food web. We combine the dynamics of food-webs together with spreading due to pursuit and evasion along the geography. Besides, non-biotic interactions can be focused on by including migration restrictions displayed by the niche of each

#### 1 Introduction

Recent studies have found that at certain latitudes, both the speed and direction of climate change and shifts in the seasonal timing of temperatures are changing faster in the ocean than on land [1]. This difference is higher when compared to Polar regions. The Arctic Ocean and Antarctic Peninsula mean annual temperatures have increased 3 times more than the world average last 50 years, and those regions are considered to be regions of recent rapid regional warming [2]. Moreover, Arctic ice loss and warming and the instability of West Antarctic Ice Sheet are considered to be Tipping Elements in the Earth climate system [3].

Polar biota is particularly vulnerable to climate change [4]. Whereas the assessment of the impacts of climate change on ecosystems is often addressed through the evaluation of effects on individual species, responding by changing their ranges and phenology to track shifts in their thermal niche [5,6], individual species do not respond in isolation but their responses are dependent on the interactions with species at the same or adjacent trophic levels [7–9].

In this context, ecological network research provides a very compelling framework for addressing the complexity of species interactions with each other and the environment [10]. Over the last decades ecological networks has provided new ways to identify and quantify the overall consequences of direct and indirect effects of perturbations due to environmental changes [11,12].

Understanding the structure and dynamics of ecological networks has become critical for understanding the persistence and stability of ecosystems [13, 14]. Recent works

described topological properties [15] and the robustness of polar food webs to the extinction of species at different trophic levels following different sequences [16] and have revealed that those ecosystems can respond differently to the effects of global environmental changes. Such structural analyses are relatively fast and easy but their utility in capturing important information about functions and processes is often questioned [17]. Dynamical models in contrast provide essential information especially if one needs to understand changes in abundances, with the structure of the food web being almost constant [17].

#### 2 Materials and Methods

We have developed a simulation model that represents dynamics of predation and migration considering biological and geographical conditions defined by ecological networks. The biological conditions are the trophic relationships among species living in a same region, and the geographical conditions are the connectivity among different regions. This model can help to simulate how changes of environmental control mechanisms can affect those ecological relationships and to describe it we will use some descriptions as defined in Table 1.

We use a Monte Carlo (MC) approach to simulate the dynamics of predation and migration in an ecosystem for different timeline. Different patches are represented as nodes of a geographical neighborhood network and the connectivity of those patches are represented as edges of this network. At each patch there are individuals of different species. The trophic relationships among these species are represented by a directed network in which each node represents a species and each edge represents a trophic relationship between a pair of species in which the origin of the edge represents a prey species and its

target represents a predator species. This network is called food-web and it is the basis for running the predation dynamic simulation.

#### 2.1 Predation model

At each time of the MC simulation we leave all the individuals of each patch, pt, to be choosen by a Multinomial Distribution. So, the chosen individual ind can have three different behaviors: 1) it can die for natural reasons; 2) it can eat one individual among its prey; 3) if ind have eaten an individual among its prey, so it can give an offspring. If the individual is not a predator (is a basal species) the model assumes it has infinity food suply and the only possible behaviors are 1) and 2). For each time-step, this simulation is repeated for all individuals of each patch of the landscape. In Fig. 2 we show a fluxogram representing the running of the predation dynamic of the model.

The births will occur only if there is free space in the patch pt, that means, if the number of individuals alive at pt is lower than its carrying capacity (cc). Each time t one individual of species sp gives an offspring in a patch pt its number of individuals in this patch will be increased by 1; each time one individual of species sp dies naturally or by predation, its number of individuals will be decreased by 1.

### 2.2 Dispersal migration

The model allows the Dispersal Migration of individuals living in some patches pt to each patch in the neighborhood pt. The neighborhood is given by the topology of the neighborhood network, and here we are using a regular 2-dimensional toroidal lattice (see Fig. 1). Is assumed that, for each time step, each species in the landscape has a level of preference to each patch  $(Pf_t^{pt}(sp))$ , here defined as a value that quantifies how sp is

adapted to pt at that time step, considering the number of preys and predators of sp in that patch. The preference of a species sp to a patch pt in time t ( $Pf_t^{pt}(sp)$ ) is defined by the difference between the number of individuals of species preys and species predators of sp in that patch. The migration of a species sp from a patch pt to a neighborhood patch np will occur only if  $Pf_t^{np}(sp) > Pf_t^{pt}(sp)$ . The number of individuals of species sp that migrate is defined by the Mobility Probability (the number of individuals of species sp that can migrate, calculated as seen in Equation 2), and must respect the threshold imposed by the carrying capacity of the target patch  $(cc_t^{ns}(sp))$ .

$$Pf_t^{pt}(sp) = \left(\sum_{b \in H(sp)} \rho_t^{pt}(b) - \sum_{c \in P(sp)} \rho_t^{pt}(c)\right)$$

$$\tag{1}$$

$$mp_t^{sp}(pt, np) = \left(\lambda_t^{pt}(sp) * \frac{Pf_t^{pt}(sp) - Pf_t^{np}(sp)}{\sum_{k \in Neigh(pt)} Pf_t^{pt}(sp) - Pf_t^{k}(sp)}\right)$$
(2)

$$\lambda_t^{pt}(sp) = \frac{1}{2} * (1 - RE_t^{pt}(sp)) \tag{3}$$

Where  $RE_t^{pt}(sp)$  is the Reproductive Exitus, a measure of the number of new individuals of species sp in patch pt during the simulation of the time step t by calculating the ratio between the number of new individuals of sp in pt in the end of the simulation for time step t, given by births and by migrations, and the same amount in the beginning of the simulation for time step t.

#### 2.3 Species Parameters

The dynamic of the system depends on some parameters defined for the species and for the patch. The parameters of the predation model are: Birth Probability (BP); Death by Predation Probability (DPP); Natural Death Probability (NDP); Mobility Probability (MP). These probabilities are used to control the birth, the death caused by predation and by natural causes, and the number of individuals of a species that can migrate from a patch. Their values can be different for each species and patch at each time. The value of the probabilities for a species sp in a patch pt changes according to the density of individuals of all the species living in pt. This Self Organized Approach is based on a similar one used for a 2 species system proposed by [18], as follows:

$$N_{t+1}^{pt}(sp) = N_t^{pt}(sp) * \left(Births_t^{pt}(sp) - Deaths_t^{pt}(sp) - NaturalDeaths_t^{pt}(sp)\right)$$
(4)

Equation 4 just defines that the number of individuals of a species sp that live in a patch pt in a time step t+1 depends on the number of individuals of sp that lived in the same patch in the previous time step, and on the difference between the number of births and the number of deaths of sp in pt between time step t and t+1. The total numbers of Births and Deaths are calculated as follows:

- $Births_t^{pt}(sp)$ : It is inversely proportional to the proabability of sp to die naturally in this patch in this time step and directly proportional to the death probability of its prey and to its own Birth Probability (see equation 8 and table 1);
- $Deaths_t^{pt}(sp)$ : It is directly proportional to the proportion of predators of sp and of predators of its preys in pt, and to the Death by Predation Probability of sp in pt

(see equation 9 and 7 and table 1).

$$Births_t^{pt}(sp) = \left( \left( 1 - NDP_t^{pt}(sp) \right) * \left( \sum_{b \in H(sp)} \rho_t^{pt}(b) DPP_t^{pt}(b) \right) * \left( BP_t^{pt}(sp) \right) \right)$$
 (5)

$$Deaths_t^{pt}(sp) = \left( \left( \sum_{c \in P(sp)} \left( \rho_t^{pt}(c) * (1 - NDP_t^{pt}(c)) \frac{\rho_t^{pt}(sp)}{\sum_{d \in H(c)} (\rho_t^{pt}(d))} \right) \right) \right)$$
 (6)

$$NaturalDeaths_t^{pt}(sp) = \left(NDP_t^{pt}(sp)\right) \tag{7}$$

Where H(sp) is the set of species that are prey of species sp; P(sp) is the set of species that are predator of species sp;  $\rho_t^{pt}(sp)$  is the abundance of species sp in patch pt at time t;  $BP_t^{pt}(sp)$ ,  $DPP_t^{pt}(sp)$ , and  $NDP_t^{pt}(sp)$  are the Birth Probability, the Death by Predation Probability, and the Natural Death Probability of species sp in patch pt at time-step t, respectively (see Table 1). These probabilities are calculated for each iteration of the model, depending on the abundance of species of different trophic levels at the same patch sp is located, as follows:

- Birth Probability is directly proportional to the availability of space and resources and to the safety of sp in pt at time t (see Equation 8);
- Death by Predation Probability is directly proportional to the intra-specific competition and the privation of resources for species sp in pt at time t, and also inversely proportional to the abundance of predators of sp in pt at time t, the so called

surpriseeffect: it means that the more predators of species sp a patch pt has, the more ready for the danger sp will be (see Equation 9);

• Natural Death Probability is directly proportional to the intra-specific competition and the privation of resources for species sp in pt at time t (see Equation 10).

$$BP_t^{pt}(sp) = \left( \left( space_t^{pt}(sp) \right) * \left( resources_t^{pt}(sp) \right) * \left( safety_t^{pt}(sp) \right) \right)$$
 (8)

$$DPP_t^{pt}(sp) = \left( \left( intracomp_t^{pt}(sp) \right) * \left( privation_t^{pt}(sp) \right) * \left( surprise_t^{pt}(sp) \right) \right)$$
(9)

$$NDP_t^{pt}(sp) = \left( \left( intracomp_t^{pt}(sp) \right) * \left( privation_t^{pt}(sp) \right) \right)$$
(10)

Where:

$$space_t^{pt}(sp) = \left(1 - \left(\rho_t^{pt}(sp)\right)\right) \tag{11}$$

$$resources_t^{pt}(sp) = \left(\sum_{b \in H(sp)} \left( \left( \rho_t^{pt}(b) \right) * \left( \sum_{c \in P(b)} \left( 1 - \rho_t^{pt}(c) \right) \right) \right) \right)$$
(12)

$$safety_t^{pt}(sp) = \left(1 - \left(\sum_{c \in P(sp)} \rho_t^{pt}(c)\right)\right)$$
(13)

$$intracomp_t^{pt}(sp) = \left(\rho_t^{pt}(sp)\right)$$
 (14)

$$privation_t^{pt}(sp) = \left(\sum_{b \in H(sp)} \left( \left(1 - \rho_t^{pt}(b)\right) * \left(\sum_{c \in P(b)} \rho_t^{pt}(c)\right) \right) \right)$$
(15)

$$surprise_t^{pt}(sp) = \left(1 - \left(\sum_{c \in P(sp)} \rho_t^{pt}(c)\right)\right)$$
(16)

#### 2.4 Patches Parameters

Each patch of the model have only one parameter that is also self-organized depending on the abundance of the species that live in that patch: the carrying capacity  $(cc_t^{pt})$ . Here we define carrying capacity of a species sp in a patch pt at a time t as the maximum number of individuals of sp that can be alive at patch pt simultaneously. We calculate it as a function directly proportional to the availability of resources for species sp in patch pt at time t, as follows:

$$cc_t^{pt}(sp) = \left(\sum_{b \in H(sp)} \frac{\rho_t^{pt}(b)}{\sum_{c \in P(b)} \rho(c)}\right)$$
(17)

#### 2.5 Disturbing the system

The model allows the simulation of disturbances in the food webs by increasing or decreasing the species and/or the patches parameters from a certain time step of the simulation. This feature allows the study of how natural and anthropogenic changes in the environmental conditions can affect the stability of the biodiversity. To input these disturbances to the model is necessary to edit a text file according to the setting parameters described at Table 2.

### 3 Results and Discussion

The model we built can simulate predation and migration dynamics considering geographical and biological parameters. Our propose is to use it to understand how the Global Changes and Global Warm can affect the structure of ecological systems, such as food chains and mutualistic relationships. The trivial way to study it is to run the model with real data and change the relationships according to the predicted changes given by scientists from IPCC and other research groups. Any difference in the running can be related with the predicted changes in ecosystems and help to understand the range of global changes and the robustness of an ecosystem against those global changes.

We have created an artificial ecosystem with a hope geographical overlapping. We considered that a good simulation should be one that could maintain individuals of all species alive for a long time and generate the hope geographical overlapping. A good

simulation is represented by the species and sites parameters (BP, DPP, NDP, MP, CC) and our first challenge was to find those good parameters.

Using the Self Organized Approach to evaluate the species parameters we have obtained a simulation that has individuals of all species alive for a long time and have generated the hope Geographical Overlapping Network. The figures 2, 3, 4 and 5 shows the evolution of bp, dp, mp and ndp during a simulation with 1000 Monte Carlo time steps considering the food web shown in figure 1. We can see that the values of all parameters change during the simulation and converge to a range of values.

#### 3.1 Self-organized steady-state

Aparently, the use of a Self Organized Approach to calculate the species parameters allow the model to reach co-existence of all species in the food webs (see Figs. 3,4,5,6).

We simulate Predation and Migration of species in a landscape.

We have developed a predation-and-migration model in which Birth, Death and Migration probabilities of each species are defined automatically during run time, depending only on the availability of resources for the each species of the food web (the amount of resources of a species is given by the number of individuals of its preys; Basal species have infinite resources).

Birth Probabilities (BP), Death by Predation Probabilities (DPP), Natural Death Probabilities (NDP), Mobility Probabilities (MP), and Carrying Capacity (CC) for each species are automatically calculated depending only on the number of individuals of each species and its preys and predators.

By expressing the parameters that govern the dynamics as functions of densities, apparently, we introduce correlations between BP, DPP, NDP, MP, CC. As a result of that, the system self-organizes towards steady state, independent of the initial number of

individuals of each species.

In Figs. 3 and 4 we present the results for a simulation of predation dynamic within a landscape with 10x10 patches, each patch with a food web with individuals of 9 different species. These individuals have trophic relationships represented here by a the food web showed in Fig. 4, in which the dots represent the species, the arrows represent the predation relationships between each pair of species (the species represented by the target of an arrow eats the species represented by the origin of this arrow). Three species of this food web are top predators and 6 are basal species. Fig. 3 shows the average number of individuals of each species after 30 realizations, with 1000 interacitons each, with maximum 1000 individuals for each species. Green, Yellow and Red lines represent the basal species (there are 6 lines in different colors derived from these 3 basic colors); Blue (two lines in different blue colors) and Black lines represent the top species. So, starting with the same number of individuals, the model self-organizes the densities of each species forcing top species to have less individuals than basal species, maintaining the coexistence.

In Figs. 5 and 6 we present another simulation of predation dynamic within the same landscape, but for a toy food web with 30 species. Fig. 5 shows the average number of individuals of each species after 50 realizations with 1000 interactions each, with maximum 1000 individuals for each species at the beginning of the simulation. Again, starting with the same number of individuals, the model self-organizes the densities of each species forcing top species to have less individuals than basal species, maintaining the coexistence. We can see that after 1000 interactions some species have more than the initial 1000 individuals and other species have less individuals. Again, the basal species have more individuals and the top one have less.

#### 3.2 Space of parameters

We have compared the different values of the probabilities for species in different trophic levels. For the same food web with 30 species we showed before.

Apparently, in a steady state, the lower species' trophic level, the higher species' birth probability. Independently of the initial number of individuals of each species, the system evolves towards a state in which there are more individuals of species at lower trophic levels than species at higher trophic levels.

In Fig. 8 we show the frequency of Birth Probability of species in a food web with 30 species. In Fig. 7 we show the trophic levels of each species of the same food web. Comparing both plots we see that species that are at lower trophic levels have higher values of Birth Probability (species 4,5,6,7,8,9,14,16,22,23,24,25,26,27 have *BP* between 0.9 and 1; 10,13,15 have *BP* between 0.8 and 0.9; and species 17 and 18 have Bp between 0.7 and 0.8).

### 3.3 Aspects regarding the Metabolic Theory of ocology

According to the allometric scaling laws published by [19] and [20], a relation between the number of individuals in a system and the birth probabilities of those individuals can be identified.

We have compared the different values of the number of individuals (N) and the Birth Probabilities (BP) of all the species of a 30 species food web in all the patches of a landscape with 10x10 patches. Observing the relationship of N and BP in a exponential regression  $N \approx BP^{\alpha}$  we got the following distribution of values for  $\alpha$  for all 100 patches (see Figure 9).

Sites whose value of  $\alpha$  is 1 present unstable dynamic of individuals (Figs. 10a, 10b).

Sites whose value of  $\alpha$  is 3 present stable dynamic of individuals (Figs. 11a, 11b). If we compare the results of [19] and [20] for the allometric scaling laws we can see that they have obtained the same value 3 for the relationship between N and BP, as explained in equations 18,19, and 20. So, apparently there is a relation between a steady state achievement and the assessed  $N \approx BP^{\alpha}$  in the patches of the landscape.

$$N \sim M^{-\frac{3}{4}}$$
 (18)

$$N \sim B^3 \tag{19}$$

$$B \sim M^{-\frac{1}{4}} \tag{20}$$

### 3.4 Adding perturbations to the system

The model allows the forcing of perturbations in the system by changing the abundance of individuals of species at different trophic levels in a given time step of the simulation. So we can simulate the indirect effects of global changes in an ecosystem by increasing or decreasing the abundance of species, or by simulating extinction or invasion of species in different trophic levels. Below we show some results of disturbances simulated for a toy 7 species food web (see Fig. 12).

According to Table 2, it is possible to change the abundance of a species at certain time

step and certain patch by defining a multiplier for the number of individuals in the system. If this multiplier is higher than 1, that means there is an increase in the abundance of the species. If it is between 0 and 1 it means there is a decrease in the abundance.

As an example, we simulated the increase in the abundance of a basal species (*species*6), in the toy 7 species food web. Increasing the abundance of species 6 causes in the increase of abundance of species 5 (see Fig. 13), that would have more availability of resources (more individuals of its prey species) to feed.

It also causes indirectly effects in other species. For example, there would be an increase of abundance of species 7 because species 5 will have more prey individuals of species 6 to feed, and so 7 will share its predator with more individuals. Also, species 2 would have more individuals of its prey (5) to feed, and it would so increase the abundance of species 4, as it would share its predator with more individuals (see Fig. 13). Last, it also causes in the increase of abundance of species 3, for the same reason: species 1 would have more individuals of its prey (2) and 3 would share its predator with more individuals.

As another example, we simulated the invasion of an intermediate species in the system from the time 50. We suggested the invasion of a called *species 8* that would be located at an intermediate trophic level in the food web, as shown by Fig. 14. As the invasive species would be a new predator of species 4, its abundance would decrease (see Fig. 15).

As a consequence of the decrease of species 4, species 2 would decrease its abundance too because of the less availability of individuals of species 2 prey. So, there would be a small increase in the abundance of species 5, that is prey of species 2 and consequently a decrease in the abundance of its prey, species 6 and species 7.

These small toy examples show how complex can be the behavior of an ecosystem under pressure and disturbances and how useful this framework could be to help to understand the effects of global environmental changes in ecosystems, especially in the most vulnerable to global changes like Arctic and Antarctic ones.

This model presents two major features that facilitates such study: 1) it needs only a few parameters to run: the trophic relationships among the species of the studied ecosystem, defined by a food web; and the connections among the patches of the landscape.

2) it allows the addition of disturbance in the abundance of the species (decrease of abundance, increase of abundance), and/or in the structure of the food web (extinction of species, invasion of species) or in the structure of the landscape (loss of habitat, change of connectivity). It thus represents a crucial framework to study effects of climate change in ecosystems, especially those most affected like Arctic and Antarctic ones.

Next step of this research would be to use this framework to simulate observed and predicted changes in keystone species in polar ecosystems using real food web data.

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Key: Brose2007

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## **Tables**

Table 1. Variables of the predation model.

Variables	Meaning
H(sp)	Set of species that are prey of species $sp$
P(sp)	Set of species that are predator of species $sp$
$\rho_t^{pt}(sp)$	Abundance of species $sp$ in patch $pt$ at time $t$
$BP_t^{pt}(sp)$	Birth Probability of species $sp$ in patch $pt$ at time-step $t$
$DPP_t^{pt}(sp)$	Death by Predation Probability of species $sp$ in patch $pt$ at time-step $t$
$NDP_t^{pt}(sp)$	Natural Death Probability of species $sp$ in patch $pt$ at time-step $t$

Table 2. Description of the parameters to set disturbance in the system.

Parameters	Meaning
$\mathbf{ts}$	time step when the disturbance should be simulated
$\operatorname{pt}$	index of patch which parameters will be changed (index starting by 0)
$\mathbf{sp}$	index of the species which parameters will be changed (index starting by 0)
bp	value to be multiplied by the birth probability of species $sp$ at patch $pt$
dpp	value to be multiplied by the death predator probability of species $sp$ at patch $pt$
ndp	value to be multiplied by the natural death probability of species $sp$ at patch $pt$
mp	value to be multiplied by the mobility probability of species $sp$ at patch $pt$
cc	value to be multiplied by the carrying capacity of species $sp$ at patch $pt$
nind	value to be multiplied by the number of individuals of species $sp$ at patch $pt$
inv	invasion (or speciation) of the species

# Figure Legends

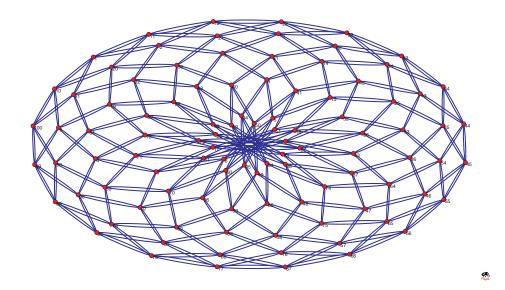


Figure 1. 10x10 Regular 2-dimensional toroidal lattice.

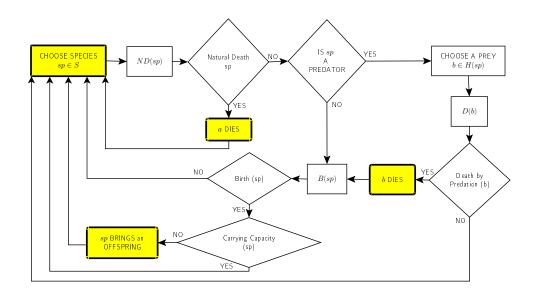


Figure 2. Fluxogram of the predation-prey model.

#### Individuals in Time in a food web with 9 species

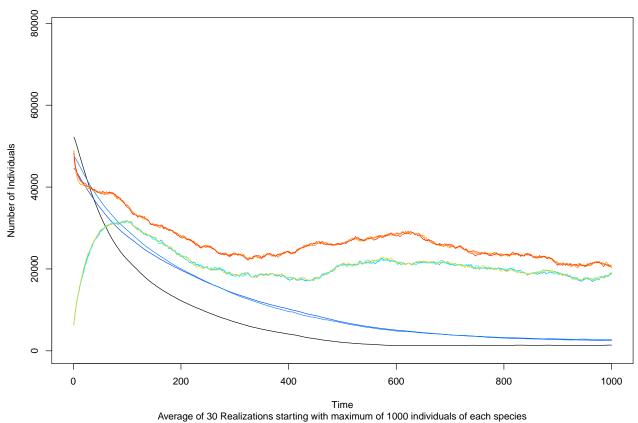


Figure 3. Average individuals in Time after 30 realizations with a 9 species food web.

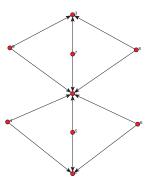


Figure 4. 9 species food web - Each node represents a species and each line between two nodes represents a trophic relationship between the species represented by these nodes. The source of the line is a the prey and the target of the line is a predator species. In this food web there are 6 basal species (species without any prey: species 4, 5, 6, 7, 8, 9) and 3 top predator species (species without any predator: species 1, 2, and 3).

#### Individuals in Time in a food web with 30 species

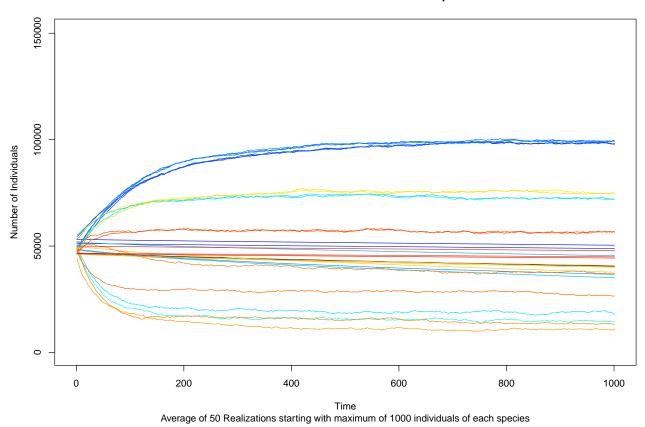


Figure 5. Average individuals in Time after 50 realizations with a 30 species food web.

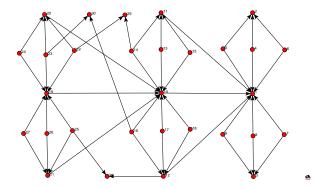


Figure 6. 30 species food web - Each node represents a species and each line between two nodes represents a trophic relationship between the species represented by these nodes. The source of the line is a the prey and the target of the line is a predator species. In this food web there are 18 basal species (species without any prey: species 4-9, 13-18, 22-27) and 6 top predator species (species without any predator: species 1-3, 28-30).

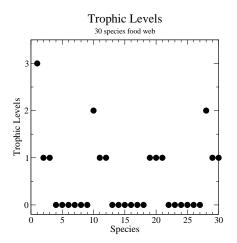


Figure 7. Distribution of trophic levels of each species of a 30 species food web - X-axis represent the identification of the species of the food web, and the Y-axis represent the trophic level this species is at the trophic network. Most of the species in the food web are at lower trophic levels (18 basal species), the highest trophic level is 3.

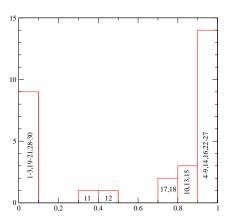


Figure 8. Distribution of Birth probabilities in a landscape 10x10 after running 1000 iterations in predation-prey model for a 30 species food web - X-axis represent the posible values of Birth Probability (between 0 and 1) and Y-axis represent the number of species that has an specific Birth Probability. Inside the bars of the plot are written the identification of the species of the 30-species food web described in Fig. 6. Species with lower values of Birth Probability are those that are at higher trophic levels in the food web (species 1-3; 19-21; 28-30). Species with higher values of Birth Probability are those that are at lower trophic levels in the food web (species 4-9; 14; 16; 22-27).

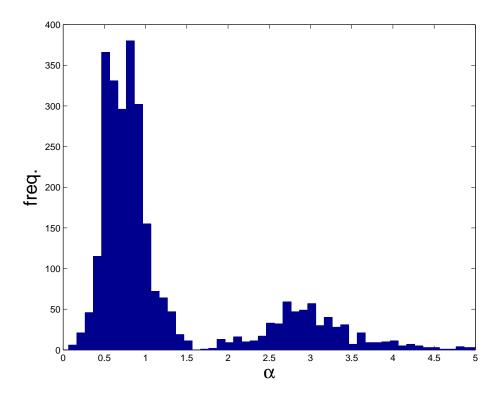


Figure 9. Distribution of values of  $\alpha$  -  $\alpha$  is given by the relation between Number of individuals and Birth Probabilities for each patch in the landscape of a simulation with a 30 species food web. The distribution of the values of  $\alpha$  calculated for each patch of the landscape shows a bimodal distribution with a peak around 1 and another peak around 3.

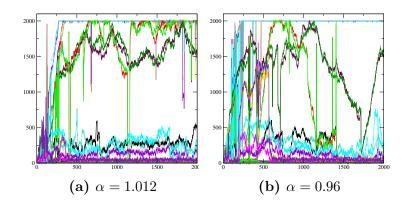


Figure 10. Number of individuals of species of a 30 species food web along the running of 2000 iterations of predation dynamic. The values of  $\alpha$  calculated for these patches are 1.012 and 0.96.

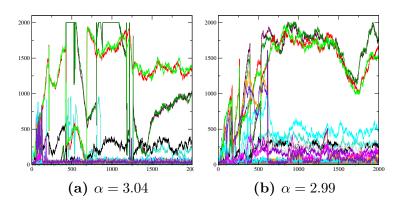


Figure 11. Number of individuals of species of a 30 species food web along the running of 2000 iterations of predation dynamic. The values of  $\alpha$  calculated for these patches are 3.04 and 2.99.

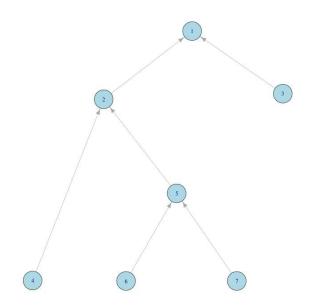


Figure 12. 7 species food web - Each node represents a species and each line between two nodes represents a trophic relationship between the species represented by these nodes. The source of the line is a the prey and the target of the line is a predator species. In this food web there are 3 basal species (species without any prey: species 4-7) and 1 top predator species (species without any predator: species 1).

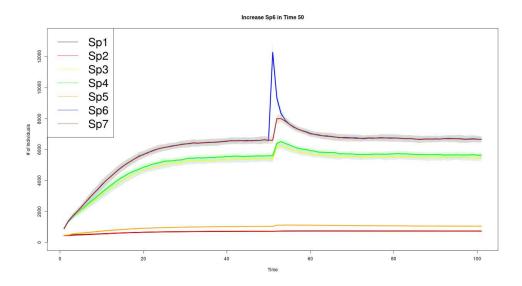


Figure 13. Effects of the Increase of abundance of a basal species in the system at time step 50.

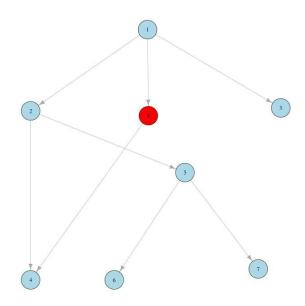


Figure 14. 7 species food web with the invasion of a new intermediate species (red dot).

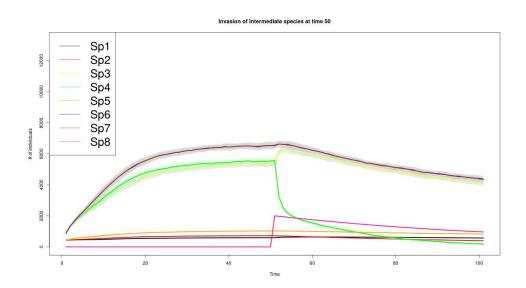


Figure 15. Effects of the Invasion of an intermediate species to the system at time step 50.