A generalized model for population dynamics where interactions change over time

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Abstract

Population dynamics has been modeled with differential equations since Malthus began their studies more than two hundred years ago. Conventional models always treat relations among species as static, denoting only their dependency for a fixed period of time, although it is well known that relations among species can, and in fact change over time. Here we propose a model for population dynamics that incorporates the evolution over time of the interactions among species. This model includes a wide range of interactions, from predator-prey to mutualistic relations, either obligate and facultative. The mechanism we describe allows the transition from one kind of relation among species to any other, according to some external parameters, fixed by the context. These transitions could avoid the extinction of one of the species, if it ends up depending too much of the environment or its relation with the other species.

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1. Introduction

Ecological models that describe the interaction among species or with their environment has being studied for a long time. The first models began by describing the interactions of one species with their environment were those of Fibonacci and Verhulst, also known as the exponential and logistic models. At the beginning of the twentieth century, Lotka and Volterra developed a set of equations that model the relation within two species, a predator and a prey. That model became a paradigm of this kind of relationship among two competitive entities, and it has been extrapolated to many other disciplines. Further attempts to incorporate the relations within two or more species were developed by May and Wrigth, although not necessarily through simpler mechanisms. García-Algarra et al.[1] proposed a logistic-mutualistic model that shows a more robust dynamic and also a direct biological interpretation of the terms involved. This model works specially by allowing a wide range of mutualistic behaviors. However, all models reproduce either mutualistic, antagonistic or even comensalistic behaviors, it has never been evaluated how relationships change through time. That is, there is no single model that explains or reflects the fact that a mutualistic relation may become antagonistic, or the other way around.

There is an enormous amount of cases where it is exactly the transition from one kind of relation among species, to the opposite one, in which relays the more interesting aspect of them. It happens either when the relation begins as mutualistic and becomes antagonistic, or when the relation begins as antagonistic and becomes mutualistic. This kind of relation transitions were mainly explored by Lynn Margulis [2–5] among her extensive bibliographic production.

One of the most representative examples of this transition, from an antagonistic relation among two species to a mutualistic relation, is the origin of the eukaryotic cell. The main idea behind this transition is that initially there were two big groups of bacteria: eubacterias and archaea. Both groups involved a great variety of types and sub-types of bacteria, but because of the horizontal transmission of genes among bacteria, they are usually considered to be one single species [4]. Unlike eubacteria, archaea maintained the energy production through fermentation, by directly ingesting complex molecules or any other bacteria they could find around them. In a world where such molecules, remanents from the violent Earth formation, were being consumed during hundreds of millions of years, new forms of energy were becoming a pressing need. The eubacterias came into play here when they developed other two additional forms to generate energy: the photosynthesis and the breathing of oxygen. While these new varieties were gaining ground, some mobile archaea, the spirochetes, found a particular use when they recklessly approached to certain heterotrophic archaea, the thermoplasmas. The proximity to them exposed the spirochetes to be swallowed, but as they achieved to grasp to their cell walls, they were able to use the great amount of organic residues disposed by the thermoplasmas. The association was unexpectedly useful for the last ones, because the frenetic movement of spirochetes gave them a movement that the slow heterotrophic archaea did not have. This symbiosis, that began as an antagonistic relationship to become soon a mutualistic one, advanced in an unexpected direction. The dependency among both types of bacteria became so strong that over million years, if it was not more time, the spirochetes learned to feed exclusively from thermoplasma waste and thus, they lost any capacity to live without them. After even more time, the spirochetes were assimilated within the thermoplasmas and the first eukaryotic cells were born.

Another example of this kind of relationship is when the eubacterias began to develop new forms to generate energy. The appearance of photosynthesis came hand in hand with the first globally ecological catastrophe: the generation of great volumes of oxygen that invaded the atmosphere. The oxygen was the starting point for other energy production mechanism, breathing. But breathing was lethal for the anaerobic archaea that ignite with oxygen. It has been proposed that an assimilation similar to that considered between spirochetes and thermoplasmas allowed new nucleated cells incorporating photosynthetic cyanobacterias and other, aerobic eubacterias, that would become plastids and mitochondria, respectively; although the assimilation of the first ones was later and it only occurred in those cells that previously had incorporated mitochondria and, therefore, who could survive in the new atmosphere.

There are several examples of antagonistic relationships that have resulted in mutualistic relationships. The platelminto *Convoluta roscoffensis* acquires during its larva stage, a great amount of *Tetraselmis* algae. Those who survive until the adult stage of the worm provide it food as a result of the photosynthesis they carry out, directly to its digestive system [6], without the risk of being digested. Likewise, Kwang W. Jeon reported in 1995 [7], a research developed during several years in the amebas *Amoeba proteus*, which developed a symbiotic relationship with a kind of bacteria (called *X-bacteria*) after some specimens of it resist to be digested. Strangely enough, the *X-bacteria* began to provide the amebas certain kind of protein. After that, the last ones became dependent on the first ones.

Another fascinating example is the case of the termites, usually divided in inferior and superior, according to their food habits and their capacity to process wood. Evidence [4] shows that this division happened when the inferior termites, whose digestive system is full of protists generating cellulase (the enzyme capable to degrade cellulose), were forced to adapt themselves to high humidity conditions. Under these conditions, the presence of fungi was very common and one way to avoid infection and colonization by the fungi was eating them before they reach the reproductive stage. There is some speculation that the relationship between these termites and the fungi reached such level of symbiosis, that the first ones completely lost all sign of protist life in their digestive systems. Because of the fungi they learned to cultivate, such dependency became unnecessary. The fungi (*termitomyces*) on their own became incapable to survive without the termites, which have made very difficult their cultivation by the mycologists. Tellera [8] refers to a very similar case for the *Attini* ants, which have a mutualistic relationship with the *Agaricaceae* and *Pterulaceae* fungi. In fact, there has been some debate about if these species evolve first their mutualistic relationship from an accidental commensalism or an incidental antagonism.

It is from these cases, which have happened and continue happening relatively frequent among different species, that we considered the possibility of extending an ecological model to consider the case in which the relationships among species change over time. In the following section we introduce the model that we have developed and then, in the following section, we present the simulations performed demonstrating the validity of our model, within the assumptions and restrictions that we consider. Finally, we present the conclusions and a brief indication about what will be necessary to make for extending and completing the current model.

2. Methodology

What we are going to develop here is a first approach to a model of population dynamics of two species, where it is possible that both of them modify their relationship over time. In other words, the species will be able to alternate between mutualism, antagonism and commensalism according of how the parameters are chosen.

To begin with, we will start with the mutualistic logistic model developed by Garcia-Algarra [1] whose system of differential equations is given, in the case of having two populations, by:

$$\begin{aligned} \dot{X}[t] &= X[t]\{r_1 + b_{12}Y[t] - (\alpha_1 + c_1 b_{12} Y[t])X[t]\} \\ \dot{Y}[t] &= Y[t]\{r_2 + b_{21}X[t] - (\alpha_2 + c_2 b_{21} X[t])Y[t]\} \end{aligned} \tag{1}$$

Where population of species 1 is represented by the $X[t]$ function and the population of species 2 by the $Y[t]$ function. To prove that from this model we can obtain the three types of relationships among species, we use to the following table:

Table 1: Possible interactions within the logistic mutualistic model according to the signs of its parameters. It is ultimately the interaction between one species to their environment or to the other species which determines the type of relationships among them.

Parameter	**Valor**	**Relationship**
r_i	$+$	Species i gets its resources from their environment
r_i	$-$	Species i can not depend only of its environment
b_{ij}	$+$	Species i benefits from species j
b_{ij}	$-$	Species i is harmed from the presence of species j

From the possibilities described in the table, it is clear that when two species have mutual benefit, we have a mutualistic regime. In that case, both $b_{ij}, b_{ji} > 0$. When a species benefits from the other, but the last one harms from the first one, we have an antagonistic regime. For example, if $b_{ij} > 0, b_{ji} < 0$, we are in an interaction of type "species i predates/parasitizes species j". The commensalistic regime happens provided that one of the species benefits from the other, but being the last one unaffected by this benefit. That corresponds to the case $b_{ij} > 0, b_{ji} = 0$ which, because it is a trivial case (dynamically speaking) in which one of the interactions is cancelled, we will not consider.

Since it is possible to generate mutualistic and antagonistic regimes from changing the signs in the parameters of (1) what we present is a model that allows performing those changes, but independently to population dynamics. This responds to the goal of determining a parallel and controlled evolution of these parameters, out of the equations that describe the populations. If this function is demonstrable, that is, if we achieve the parameters to change from outside, according to what is needed, it only remains to justify how these changes happen. With that, our system will be a valid model for describing the transitions among the regimes that describe interactions among species.

2.1. The model

The simplest model that reflects what we have proposed to extend the mutualistic logistic model is as follows. We define:

$$\begin{aligned} r_1[t] &= r_x[t] - \tilde{r}_1 \\ r_2[t] &= r_y[t] - \tilde{r}_2 \\ b_{12}[t] &= b_x[t] - \tilde{b}_{12} \\ b_{21}[t] &= b_y[t] - \tilde{b}_{21} \end{aligned} \tag{2}$$

In this way, we are including a minimum change in the original model, but that allow us making the changes of sign discussed. This model has been adapted from a system proposed by Strogatz in [9] although for a different aim, but reproducing the same dynamics. Then, our model remains reformulated as follows:

$$\begin{aligned}\dot{X}[t] &= X[t]\{(r_x[t]-\tilde{r}_1)+(b_x[t]-\tilde{b}_{12})Y[t]\\ &\quad -(\alpha_1+c_1(b_x[t]-\tilde{b}_{12})Y[t])X[t]\}\\ \dot{Y}[t] &= Y[t]\{(r_y[t]-\tilde{r}_2)+(b_y[t]-\tilde{b}_{21})X[t]\\ &\quad -(\alpha_2+c_2(b_y[t]-\tilde{b}_{21})X[t])Y[t]\}\end{aligned} \tag{3}$$

And the new parameters that we have included will according to the following relationships:

$$\begin{aligned}\dot{r}_x[t] &= r_x[t](a_x-d_xr_x[t]-e_xb_x[t])\\ \dot{b}_x[t] &= b_x[t](f_x-g_xb_x[t]-h_xr_x[t])\end{aligned} \tag{4}$$

$$\begin{aligned}\dot{r}_y[t] &= r_y[t](a_y-d_yr_y[t]-e_yb_y[t])\\ \dot{b}_y[t] &= b_y[t](f_y-g_yb_y[t]-h_yr_y[t])\end{aligned} \tag{5}$$

$$\begin{aligned}\tilde{r}_1,\tilde{r}_2,\tilde{b}_{12},\tilde{b}_{21} &> 0\\ a_x,d_x,e_x,f_x,g_x,h_x &> 0\\ a_y,d_y,e_y,f_y,g_y,h_y &> 0\end{aligned} \tag{6}$$

Once the model is established, the following we show the linear stability analysis (LSA). Thus, we will be able to predict how they work and what dynamics appear among the populations. We have three simultaneous systems in their evolution, but independent from each other. Consequently, our LSA will be formed by three parts, the one that corresponds to the evolution of populations 1 and 2, given from (3), the one that corresponds to the evolution of $r_x[t]$ and $b_x[t]$ parameters, corresponding to species 1 and is given by the (4), and finally the one that corresponds to the evolution of $r_y[t]$ and $b_y[t]$ parameters belonging to species 2 and is given by the(5). As the evolutions of parameters (equations (4) and (5)) are solved independently of each other, we will be able to make a LSA for each pair of them. The system of differential equations of populations (3) will depend on the parameters, but it can be noted that their behavior will not be different from what we know about this system, provided that we consider what is developed from table 1.

The idea of proposing this model is that it allows the parameters to be able to adopt positive or negative values, from the temporary evolution of thetime dependent terms. Here, we can have a great amount of combinations for parameters. As will be seen further on the LSA, this system has three types of fixed points: the cancellation of both parameters, the cancellation of one of them and the presence of the other, and the coexistence of both. These combinations will be valid for parameters of species 1 and 2. For simplicity and without any alteration in the results, we will determine that species 2 always has its parameters in partial cancellation status: if $r_2 > 0, b_{21} < 0$ and if $r_2 < 0, b_{21} > 0$. Under this assumption, we will consider now the case where $r_x[t], b_x[t]$ are also cancelled in a limited way, which will give us the possibilities described in table 2. In case the parameters are not cancelled, they will converge to a stable fixed value that will be indicated as $r_{x0}, r_{y0}, b_{x0}, b_{y0}$ and will be positive in all the cases.

Table 2: Possible interactions according to the dependent values that parameters can adopt. These parameters determine the evolution of both species if we suppose that they are mutually exclusive. Here we consider that $r_{x0}, r_{y0}, b_{x0}, b_{y0} > \tilde{r}_1, \tilde{r}_2, \tilde{b}_{12}, \tilde{b}_{21}$. $r_{x0}, r_{y0}, b_{x0}, b_{0y}$ represent the fixed stable values to which the parameters converge in case they do not cancelle each other. It is importante to note that the whole first column represent only one condition.

Condition	r_1	r_2	b_{12}	b_{21}	**Relationship among species 1 and 2**
$r_{x0} > \tilde{r}_1$ $r_{y0} > \tilde{r}_2$ $b_{x0} > \tilde{b}_{12}$ $b_{y0} > \tilde{b}_{21}$	$+$	$+$	$-$	$-$	Competition for resources
	$+$	$-$	$-$	$+$	Prey/Predator
	$-$	$+$	$+$	$-$	Predator/Prey
	$-$	$-$	$+$	$+$	Obligate mutualism

It is interesting to note that this combination of parameters is the one that offers the greatest variety of relationships among species. The terminology for relationships has been chosen according to what is offered by the literature: an unidirectional dependency between one species and the other reflects a predation-prey model, while the mutual dependency just refers to the mandatory mutualism. Finally, a sufficient dependency on the environment, but under an antagonistic relationship, refers to the competition among species for the same resources.

Other sets of parameters can exist if we permute any of the relationships between $r_{x0}, r_{y0}, b_{x0}, b_{y0}$ and $\tilde{r}_1, \tilde{r}_2, \tilde{b}_{12}, \tilde{b}_{21}$. These changes can be seen in table 3 and they alter the relationship of one species to the other, but in a way they do not offer a new interesting behavior. The two results: the unequal competition and the *extinctuos* parasitoidism end inevitably in the extinction of some species. For example, if r_1 is always negative, this will indicate that species 1 is not capable to survive only from environment resources, in such a way that either it will need the mutualism with species 2 or it will have to predate it. Otherwise, it will be condemned to disappear. On the other hand, if it always keeps a relationship with species 2 that harms it, it may only be subjected to the competition or predation interaction: both requiring $r_1 > 0$. Otherwise, it will also disappear.

It is interesting to note which the limitations that exist in the evolution of relationships among two species from these boxes are . This is significant, because if a species always have its r_0 means that it is incapable to handle it by itself with the resources of the environment and it is forced to establish a relationship with other species, being or not beneficial for the other.

The extreme cases where r_1 and r_2 are negative, only offers a new scenario where all the parameters are negative and species extinguish very quickly. The same applies if b_{12} and b_{21} are always negative. Any behavior different from those already reviewed only causes the inevitable death of some species. These cases will not be relevant for us so we will not consider them later.

In case the parameters of a species coexist, this will only introduce the possibility that one of the species does not depend on the other, allowing two new behaviors to appear, the optional mutualism and predation. This is shown in table 4.

Table 3: Possible interactions according to the dependent values that parameters can adopt. These parameters determine the evolution of both species if we suppose that they are mutually exclusive. Here we consider that $r_{x0} < \tilde{r}_1$ and $b_{x0} < \tilde{b}_{12}$. In both cases we consider that $r_{y0}, b_{y0} > \tilde{r}_2, \tilde{b}_{21}$. $r_{x0}, r_{y0}, b_{x0}, b_{0y}$ represent the fixed stable values to which the parameters converge in case they do not cancelle each other. It is importante to note that the whole first column represent only one condition.

Condition	r_1	r_2	b_{12}	b_{21}	**Relationship among species 1 and 2**
$r_{x0} < \tilde{r}_1$ $r_{x0} > \tilde{r}_2$ $b_{x0} > \tilde{b}_{12}$ $b_{y0} > \tilde{b}_{21}$	$-$	$+$	$-$	$-$	Unbalanced competition
	$-$	$-$	$-$	$+$	*Extinctuos* parasitoidism
	$-$	$+$	$+$	$-$	Predator/Prey
	$-$	$-$	$+$	$+$	Obligate mutualism
Condition	r_1	r_2	b_{12}	b_{21}	**Relationship among species 1 and 2**
$r_{x0} > \tilde{r}_1$ $r_{y0} > \tilde{r}_2$ $b_{x0} < \tilde{b}_{12}$ $b_{y0} > \tilde{b}_{21}$	$+$	$+$	$-$	$-$	Competition
	$+$	$-$	$-$	$+$	Prey/Predator
	$-$	$+$	$-$	$-$	Unbalanced competition
	$-$	$-$	$-$	$+$	*Extinctuos* parasitoidism

Table 4: Possible interactions according to the dependent values that parameters can adopt. These parameters determine the evolution of both species if we suppose that parameters within the same species can coexist, but parameters for the other goes on partial cancellation. $r_{x0}, r_{y0}, b_{x0}, b_{0y}$ represent the fixed stable values to which the parameters converge in case they do not cancelle each other. It is importante to note that the whole first column represent only one condition.

Condition	r_1	r_2	b_{12}	b_{21}	**Relationship among species 1 and 2**
$r_{x0} > \tilde{r}_1$ $r_{y0} > \tilde{r}_2$ $b_{x0} > \tilde{b}_{12}$ $b_{y0} > \tilde{b}_{21}$	$+$	$+$	$+$	$-$	Optative predation/Prey
	$+$	$-$	$+$	$+$	Optative/obligate mutualism
	$-$	$+$	$-$	$-$	Unbalanced competition
	$-$	$-$	$-$	$+$	*Extinctuos* parasitoidism

In this last case, what we have is that it is indifferent for the species whose parameters coexist what will happen with the other. Either the second one takes advantage of the relationship or it harms from it.

As both systems of parameters are structurally symmetrical, the LSA for the equations (4) and (5) will be equivalent. In that sense, the solution of one of them will allow us to understan what would happen with the other and, therefore, we will only focus on the development of one of them and we will see what happens in all the regimes for their fixed points, the total cancellation, the partial cancellations or the coexistence.

2.2. LSA for parameters $r_x[t]$ and $b_x[t]$

For convenience, we will omit the subscript x in the coefficients, to not overextend the notation. Then, the system of equations would be as follows:

$$\begin{aligned} \dot{r}[t] &= r[t](a - dr[t] - eb[t]) \\ \dot{b}[t] &= b[t](f - gb[t] - hr[t]) \end{aligned} \tag{7}$$

The system of differential equations given by (7) has, namely, four fixed points $\{r_0, b_0\}$, which can be easily obtained when $\dot{r}[t] = 0, \dot{b}[t] = 0$ is cleared:

Complete cancellation

$$\{r_0, b_0\} = \{0, 0\} \tag{8}$$

Partial cancellations

$$\{r_0, b_0\} = \left\{0, \frac{f}{g}\right\}, \left\{\frac{a}{d}, 0\right\} \tag{9}$$

Coexistence

$$\{r_0, b_0\} = \left\{\frac{df - ha}{dg - eh}, \frac{ag - ef}{dg - eh}\right\} \tag{10}$$

As we are considering that each term is relevant in the dynamics that is being explored, none of the parameters a, d, e, f, g, h will be 0 and all will be positive. Furthermore, we will discuss the case where $dg = eh$ later. The Jacobean matrix of this system is given by

$$\begin{bmatrix} \frac{\partial \dot{r}}{\partial r} & \frac{\partial \dot{r}}{\partial b} \\ \frac{\partial \dot{b}}{\partial r} & \frac{\partial \dot{b}}{\partial b} \end{bmatrix} = \begin{bmatrix} a - 2dr_0 - eb_0 & -er_0 \\ -hb_0 & f - 2gr_0 - hr_0 \end{bmatrix} \tag{11}$$

So, the evaluation of the fixed points is simply replacing them and calculates the matrix eigenvalues. For the total cancellation we have that a stable fixed point corresponds to:

$$\begin{bmatrix} a & 0 \\ 0 & f \end{bmatrix} \rightarrow \begin{matrix} \lambda_1 = a \\ \lambda_2 = f \end{matrix} \tag{12}$$

For the partial cancellations we have that it corresponds to points depending on certain conditions. In a case it is:

$$\begin{bmatrix} a - \dfrac{ef}{g} & 0 \\ -\dfrac{hf}{g} & -f \end{bmatrix} \rightarrow \begin{matrix} \lambda_1 = a - \dfrac{ef}{g} \\ \lambda_2 = -f \end{matrix} \tag{13}$$

$$\text{which corresponds to a fixed point:} \begin{cases} \text{stable} & \text{if } a < \dfrac{ef}{g} \\ \text{degenerate} & \text{if } a = \dfrac{ef}{g} \\ \text{saddle point} & \text{if } a > \dfrac{ef}{g} \end{cases} \tag{14}$$

And, on the other hand, we have:

$$\begin{bmatrix} -a & -\dfrac{ea}{d} \\ 0 & f - \dfrac{ha}{d} \end{bmatrix} \rightarrow \begin{matrix} \lambda_1 = -a \\ \lambda_2 = f - \dfrac{ha}{d} \end{matrix} \tag{15}$$

$$\text{which corresponds to a fixed point:} \begin{cases} \text{stable} & \text{if } f < \dfrac{ha}{d} \\ \text{degenerate} & \text{if } f = \dfrac{ha}{d} \\ \text{saddle point} & \text{if } f > \dfrac{ha}{d} \end{cases} \tag{16}$$

Here the fixed point is called *degenerate* when it is between the limit of a stable point and a saddle point. Degeneration is only a reference to the fact that stability is reached along a whole straight line in the phase space around which the other paths of stability are extended. For coexistence, as it is the most tedious case, we will make the development in some detail and appealing to the corresponding justified assumptions.

Case 1: $f = a, h = e, g = d$

$$\begin{bmatrix} -\dfrac{ad}{e+d} & -\dfrac{ae}{e+d} \\ -\dfrac{ae}{e+d} & -\dfrac{ad}{e+d} \end{bmatrix} \rightarrow \begin{matrix} \lambda_1 = -a \\ \lambda_2 = \dfrac{a(e-d)}{e+d} \end{matrix} \tag{17}$$

Here again we see that we have a dilemma. If $e > d$ we have simply obtained a saddle point. If $e < d$, we rather have a stable point. And if $e = d$, we have again the same type of degenerated stability now.

Case 2: $f = a, h = e, g = d + \epsilon$, considering $\epsilon \ll d, e$

$$\begin{bmatrix} -\dfrac{a(e-d)(d-\epsilon)}{e^2 - d^2 - d\epsilon} & -\dfrac{ae(e-d)}{e^2 - d^2 - d\epsilon} \\ -\dfrac{ae(e-d-\epsilon)}{e^2 - d^2 - d\epsilon} & -\dfrac{a(e-de\epsilon)(d+2\epsilon)}{e^2 - d^2 - d\epsilon} \end{bmatrix} \tag{18}$$

In this case, the analysis needs to be more analyzed thoroughly due to the amount of terms involved. Thus, if we subtract the trace T and the determinant D, we would have:

$$
\begin{aligned}
T &= (\frac{a}{e^2-d^2-d\epsilon})(2d^2-2d(e-\epsilon)-e\epsilon) \\
D &= -(\frac{a}{e^2-d^2-d\epsilon})^2(e-d)(e^3+d^3 \\
&\quad -d^2(d-2\epsilon)-e^2\epsilon-d(e^2+e\epsilon))
\end{aligned}
\tag{19}
$$

Here, we will be interested in conditions that make $T = 0, D = 0$ and $T^2 = 4D$, since the eigenvalues can be written like:

$$
\lambda_{1,2} = \frac{T \pm \sqrt{T^2-4D}}{2} \tag{20}
$$

Let's see what alternative we do have for these cases.

1. $D = 0$

This happens as long as $d = e$, or either $d+\epsilon = \sqrt{e(e-\epsilon)}$. And this gives $\lambda_1 = 0$ and $\lambda_2 = T$, from which the determination of it is a degenerate fixed pointor a stable one depends upon whether $T > 0$ or $T < 0$.

Now, $T = 0$ as long as $2d+\epsilon = 2e$ and in this case, both eigenvalues are 0. On the other hand, we have that $e < \frac{2d(d+\epsilon)}{2d+\epsilon}$, so then $T > 0$ and the fixed point would be degenerate and unstable. But, if $e > \frac{2d(d+\epsilon)}{2d+\epsilon}$, then $T < 0$ and we have instead a degenerate but stable fixed point.

2. $D > 0$

Which happens as long as $d > e$, or either $d+\epsilon > \sqrt{e(e-\epsilon)}$. For this case, the evaluation if $T^2 < 4D$ would allow us to determine if the eigenvalues are imaginary, but provided that this condition can never hold under our assumptions, this possibility is overruled. On the other hand, $T^2 = 4D$ only if we have that $2d+\epsilon = 2e$, but if $2d+\epsilon < 2e$ we always have that $T^2 > 4D$.

This allow us to focus again on the conditions that give $T = 0$, because $T > \sqrt{T^2-4D}$, as long as $D > 0$. And we already see that $T = 0$ as long as $2d+\epsilon = 2e$ and, in that case, $\lambda_1 = \lambda_2 = 0$ again. On the other hand, we have that $e < \frac{2d(d+\epsilon)}{2d+\epsilon}$, $T > 0$ and $\lambda_1 > \lambda_2 > 0$ which means that the fixed point would be unstable. Finally, if $e > \frac{2d(d+\epsilon)}{2d+\epsilon}$, then $T < 0$ and this would make $\lambda_1 < \lambda_2 < 0$, which means that the fixed point would be stable instead.

3. $D < 0$

This can only happens when $d+\epsilon < \sqrt{e(e-\epsilon)}$. For this case, the condition that $T^2 - 4D > 0$ holds always, which means that the roots are real, but also that $T < \sqrt{T^2-4D}$. Here we don't need to analyze anything else, because the relation between the eigenvalues with the trace and the determinant ensures that one eigenvalue is going to be positive, while the other remains negative. This garantees that our fixed point is goint to be a saddle point.

According to all of this, we can see that there are two cases: either the partial cancellations are stable fixed points and the coexistence is a saddle point, or the partial cancellations are saddle points and the coexistence is a stable fixed point. In both cases, the total cancellation is an unstable fixed point.

Case 1: stable partial cancellations and coexistence as saddle point

You can see in this case that the general trend of the system will be to run towards some cancellation, leaving the other parameter to exist. Here we can then have two cases:
$r \to 0, b \to b_0$, donde $b_0 > \tilde{b}_{12}$, de modo que $b_{12} > 0$ y $r_1 < 0$
$r \to r_0, b \to 0$, donde $r_0 > \tilde{r}_1$, de modo que $r_1 > 0$ y $b_{12} < 0$

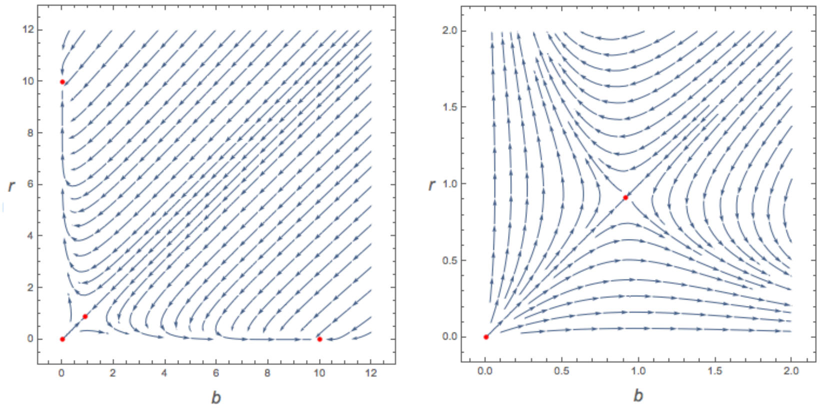

Figure 1: Diagram that shows the dynamics that can be obtained when the partial cancellations are stable fixed points and the coexistence is a saddle point. In the left figure we present the diagram with the four fixed points, while at the right figure we do a zoom to the region that the unstable and saddle points are. Here we use the following conditions $a = 1, f = 1, e = 1, h = 1, d = 0.1, g = 0.1$

This case is graphically explored in Figure 2, which shows the flow diagram of dynamics and the four fixed points. The idea in this graph is to be able to appreciate the transition through them.

Case 2: stable coexistence and partial cancellations as saddle points

Here, the trend of the system will be always to run towards the coexistence that will be located, according to the equation (10) in:

$$\{r_0, b_0\} = \left\{ \frac{df - ha}{dg - eh}, \frac{ag - ef}{dg - eh} \right\}$$

Thus, we have then obtained the possibilities established in the first part of the text, in which either the parameters coexist, or they are cancelled each other. It is interesting to note here that although the coexistence of the parameters allows relationships among species that we can catalogue as optional to appear,

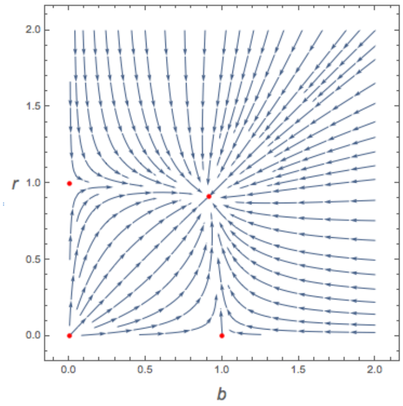

Figure 2: Diagram that shows the dynamics that can be obtained when the partial cancellations are saddle points and the coexistence is a stable fixed point. Here we use the following conditions $a = 1, f = 1, e = 0.1, h = 0.1, d = 1, g = 1$

in mutualism and in predation, these will be originated from establishing the parameters of one of the species in a stable point. This behavior is not important to us here because it is equivalent to set the parameters of the equation of species to fixed values; what we would be obtaining will be exactly the stability of the parameters around those values. In that sense, what is interesting will be to explore the partial cancellation of parameters, because that allows us to modify the relationship of one species with the other and it offers us, in turn, the most interesting development of behaviors.

As we have seen, we can have the partial cancellations for species 1 or when $r_x \to \frac{a}{d}$, or when $b_x \to \frac{f}{g}$, being equivalent for species 2, with their own ry and by parameters. In both cases, we will have to consider that $a < \frac{ef}{g}$ and $f < \frac{ha}{d}$, will be conditions for these points be stable.

It should be mention that we left pending discussing the condition $dg = eh$. This case has a particular interest to the extent that it would tend our fixed point towards infinity in the coexistence regime. This happens because such difference is in the denominator of equation (10) and this result can be extended if the form of the equation (7) is explored. That $dg = eh$ means that the compensatory terms for both parameters are equivalent to each other: d and g multiply the part of r [t] and b [t] that subtracts itself, while e subtracts $b[t]$ to $r[t]$ and h does the opposite thing. This type of condition is beyond our interest because it places the developments as the dominant part of the evolution of parameters and what we rather need here is that there must be a tangible influence among these, instead of cancelling such influence. On the other hand, the mathematical indeterminacy that indicates the case $dg = eh$ is pertinent only when the coexistence of parameters occurs, and we have just demonstrated that regime will not be useful in our model.

2.3. The simulation

2.3.1. Dynamical system of populations $X[t]$ and $Y[t]$

Numerical Poisson simulations have been performed to obtain the antagonism-mutualism and mutualism-antagonism transitions. The Poisson simulations are especially useful when dealing with population models since in each time step the algorithm varies discreetly the number of individuals and stochastic fluctuations are naturally introduced [10].

When the average frequency of occurrence λ of an event is well-known, the Poisson distribution gives the probability that a certain number of events happens during a fixed period of time 3. For example, figure 5 shows the distribution of the number of hurricanes per year in the USA superimposed to a Poisson distribution in which the average frequency of occurrence is 5.25 hurricanes per year.

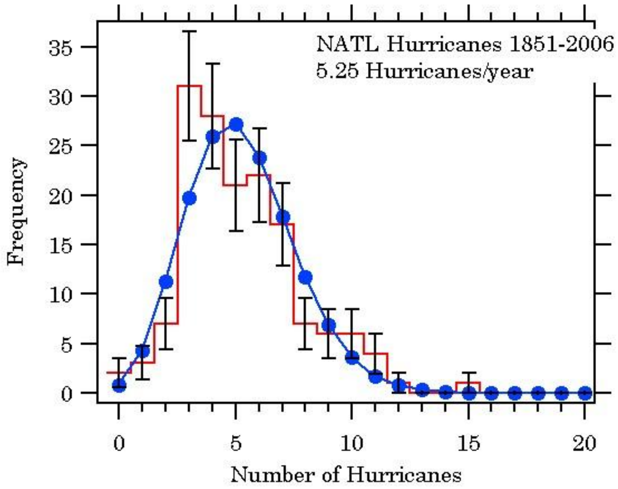

Figure 3: Probability distribution of the number of hurricanes per year within the US [**?**].

When this type of simulation is implemented in a population model, the average frequency of occurrence is the net flow of individuals at any moment. If the model describes the change in population X, like a differential equation of the type $\frac{dX}{dt} = f(X)$, this variation can be simulated through a Poisson distribution with the following equation in differences:

$$x(t + \Delta t) = x(t) + Po[\lambda = \Delta t \cdot f(x)] \tag{21}$$

In addition, this method allows arbitrarily to vary the temporary step (and therefore the timescales) in a simple way through parameter t. In our case, the formulation of the model for the simulation is expressed as follows:

$$\begin{aligned}
X[t+\Delta t]=X+\text{sign}\Big\{&[(r_x-\tilde{r}_1)+10^{-3}(b_x-\tilde{b}_{12})Y]X-[\alpha_1+c_1 10^{-3}(b_x-\tilde{b}_{12})Y]X^2\Big\}\cdot\\
&Po\Big\{\Delta t\cdot\text{abs}\{[(r_x-\tilde{r}_1)+10^{-3}(b_x-b_{\tilde{1}2})Y]X-[\alpha_1+c_1 10^{-3}(b_x-b_{\tilde{1}2})Y]X^2\}\Big\}\\
Y[t+\Delta t]=Y+\text{sign}\Big\{&[(r_y-\tilde{r}_2)+10^{-3}(b_y-\tilde{b}_{21})X]Y-[\alpha_2+c_2 10^{-3}(b_x-\tilde{b}_{21})X]Y^2\Big\}\cdot\\
&Po\Big\{\Delta t\cdot\text{abs}\{[(r_y-\tilde{r}_2)+10^{-3}(b_y-\tilde{b}_{21})X]Y-[\alpha_2+c_2 10^{-3}(b_x-\tilde{b}_{21})X]Y^2\}\Big\}
\end{aligned}$$

Where functions "sign" and "abs" are used to resolve the fact that the Poisson distribution only admits positive average frequencies of occurrence. X and Y shall be understood here as $X[t]$ and $Y[t]$, notation that has been avoided due to clarity. The 10^{-3} are included to scale the parameters b_i, since the values of r_i and those of b_i come from the evolution of the dynamical system of parameters $(i = x, y)$.

2.3.2. Dynamical system of $r_i[t]$ and $b_i[t]$ parameters

The simulation of dynamical system of parameters has become something more complicated, since there shall be the impossibility, in this case, of turning to a Poisson simulation: the parameters are continuous values and their variation must be continuous.

In order to solve these problems, the Poisson simulation has been chosen to be adapted to a continuous system turning to the Gaussian distribution, taking the average and the traditional deviation equal to the instantaneous variation. Thus, the formulation of the variation of the parameters will be as follows:

$$\begin{aligned} r[t+\Delta t] =& r + \mathrm{Gauss}\{\mu = \Delta t \cdot r(a - dr - eb), \sigma = \mathrm{abs}[\Delta t \cdot r(a - dr - eb)]\} \\ b[t+\Delta t] =& b + \mathrm{Gauss}\{\mu = \Delta t \cdot b(f - gb - hr), \sigma = \mathrm{abs}[\Delta t \cdot b(f - gb - hr)]\} \end{aligned}$$

Where μ and σ are, respectively, the mean and the standard deviation. In the same way that in the equations of the evolution of populations, r must be read as $r[t]$ and b as $b[t]$.

3. Results

Two transitions have been simulated: those from antagonism to mutualism and from mutualism to antagonism. The same set of parameters has been used for both (tables 5 and 6), varying only the initial conditions for the dynamical system of parameters. The transitions have been simulated introducing an abrupt external change in the value of parameters b and r of one of the populations, in such a way that the system of the parameters of that population is stabilized in a new fixed point.

Table 5: Parameters set for the dynamical system of parameters

	a	d	e	f	g	h
X	1	1/2	1	1	1/9	1
Y	1	1/2	1	1	1/10	1

Table 6: Parameters set for the dynamical system of populations

	I.C.	$\tilde{r}$	$\tilde{b}$	α	c
X	400	1	4	0,0001	0,001
Y	400	1	5	0,0001	0,001

For the antagonism-mutualism transition, we have begun with the following initial conditions for the system of parameters:

$$\{r_{xo}, b_{xo}\} = \{2, 1\}$$
$$\{r_{yo}, b_{yo}\} = \{1, 9\}$$

In such a way the parameters change in the fixed point:

$$\{r_x, b_x\} = \{2, 0\}$$
$$\{r_y, b_y\} = \{0, 10\}$$

Resulting the parameters effective:

$$\{(r_x - \tilde{r}_1), 10^{-3}(b_x - \tilde{b}_{12})\} = \{1, -4 \cdot 10^{-3}\}$$
$$\{(r_y - \tilde{r}_2), 10^{-3}(b_y - \tilde{b}_{21})\} = \{-1, 5 \cdot 10^{-3}\}$$

At iteration $t = 30000$, b_x is suddenly changed to 3, pushing the system X to the attraction basin of the other stable fixed point:

$$\{r_x, b_x\} = \{0, 9\}$$

And causing the effective parameters of population X to become:

$$\{(r_x - \tilde{r}_1), 10^{-3}(b_x - \widetilde{b_{12}})\} = \{-1, 5 \cdot 10^{-3}\}$$

Figure 4 shows the evolution of two dynamical systems of parameters in their phase spaces.

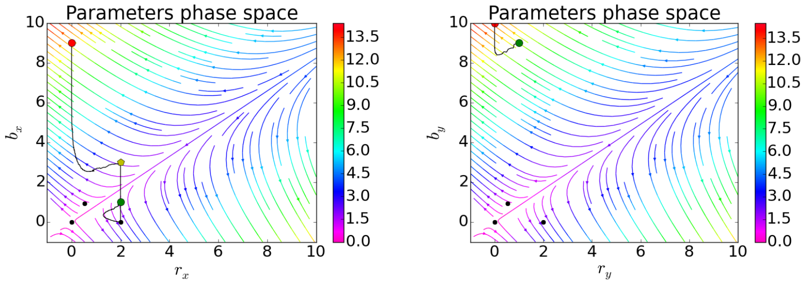

Figure 4: Transition from antagonism to mutualism: evolution of the populations across the phase spaces. The green dot corresponds to the initial conditions; the yellow pentagon is the point in which the external alteration is done and the red dot is the final point of the evolution.

The variation in the parameters of the dynamical system of the populations causes a change in its phase space, which goes from an antagonistic phase space to a mutualistic one; each one with its own fixed points. Figure 5 shows how a transition among fixed points happens when the phase space changes.

It is important to emphasize that the antagonistic fixed point needs to be in the basin of survival of the mutualistic system [1], otherwise the change in parameters leads to the extinction of both species.

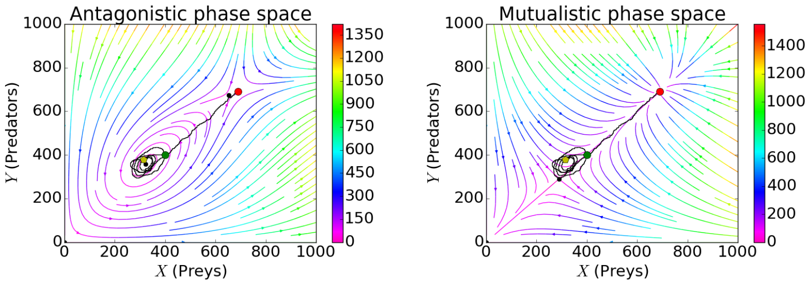

Figure 5: Transition from antagonism to mutualism: evolution of the populations across the phase spaces, both mutualist (left) and antagonist (right). The green dot corresponds to the initial conditions; the yellow pentagon is the point in which the external alteration is done and the red dot is the final point of the evolution.

The temporary evolution of populations and of effective value of parameters is shown in figure 6, where you can see how the evolution of the system of parameters stabilizes much more quickly than the one of populations. It can be interesting to play with this speed of change and to study how it conditions the evolution of populations.

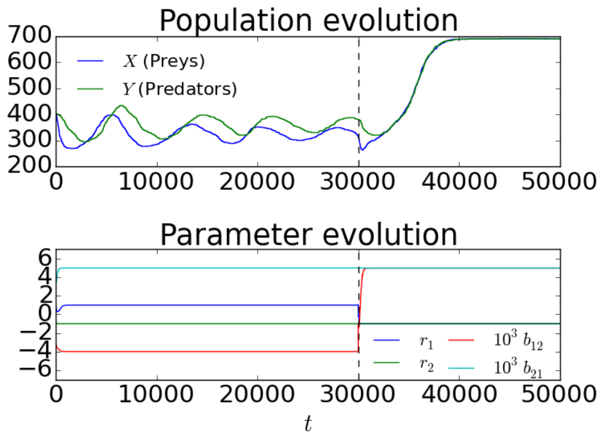

Figure 6: Transition form antagonism to mutualism: temporal evolution of the populations and the efective parameters.

For mutualism-antagonism transition, the initial conditions of the dynamical system of parameters are the following:

$$\{r_{xo}, b_{xo}\} = \{1, 4\}$$
$$\{r_{yo}, b_{yo}\} = \{1, 9\}$$

Which move them to the next fixed point:

$$\{r_x, b_x\} = \{0, 9\}$$
$$\{r_y, b_y\} = \{0, 10\}$$

So, the effective values of parameters are:

$$\{(r_x - \tilde{r}_1), 10^{-3}(b_x - \tilde{b}_{12})\} = \{-1, 5 \cdot 10^{-3}\}$$
$$\{(r_y - \tilde{r}_2), 10^{-3}(b_y - \tilde{b}_{21})\} = \{-1, 5 \cdot 10^{-3}\}$$

In this case, the external alteration (also in iteration $t = 30000$) of parameters is made in r and in b, because it is very difficult to reach the attraction basin of the other fixed point in another way. The values given are $b_x = 1$, $r_x = 3$, with which the system X becomes stabilized in the new fixed point:

$$\{r_x, b_x\} = \{2, 0\}$$

And the effective values of the corresponding parameters become:

$$\{(r_x - \tilde{r}_1), 10^{-3}(b_x - \tilde{b}_{12})\} = \{1, -4 \cdot 10^{-3}\}$$

Figure 7 shows the evolution of parameters during the mutualism-antagonism transition.

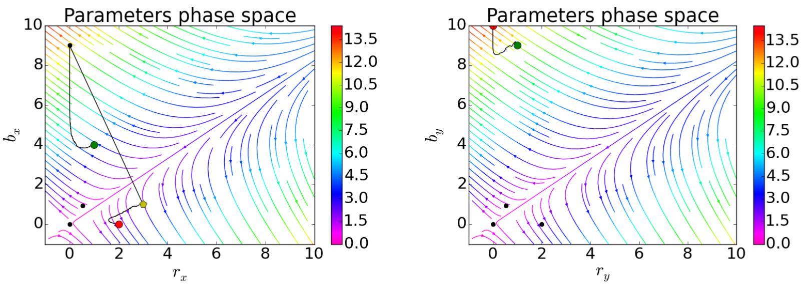

Figure 7: Transition from mutualism to antagonism: evolution of the populations across the phase spaces. The green dot corresponds to the initial conditions; the yellow pentagon is the point in which the external alteration is done and the red dot is the final point of the evolution.

Here you can see how the external intervention in parameters is significantly stronger than in antagonism-mutualism transition. This is necessary because the fixed point in which the system initially stabilized is much further away from the attraction basin than from its counterpart. From these results it could be inferred that, in nature, the type of existing relationships now among the different species is the one that live in a more stable attractor against external influences. In this case, the external influence causes the dynamical system of populations change from mutualistic to antagonistic one.

The populations will evolve first in a mutualistic phase space to become an antagonistic one after alteration of parameters (see figure 8).

The temporary evolution of populations and parameters are shown in figure 11.

3.1. Discussion and interpretation of results

In order to support that it is valid to introduce those disturbances, it will be necessary to remember that parameters are moving in equations which are

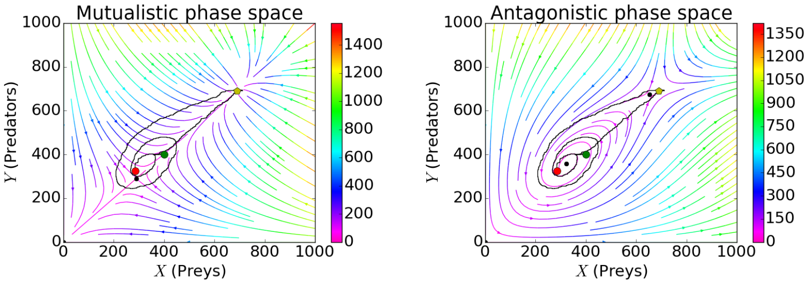

Figure 8: Transition from mutualism to antagonism: evolution of the populations across the phase spaces, both mutualist (left) and antagonist (right). The green dot corresponds to the initial conditions; the yellow pentagon is the point in which the external alteration is done and the red dot is the final point of the evolution.

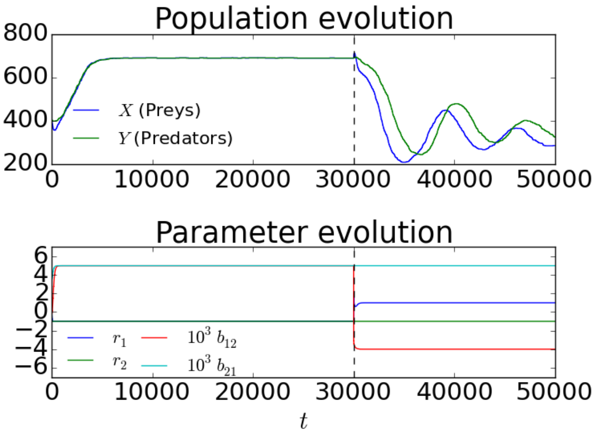

Figure 9: Transition form mutualism to antagonism: temporal evolution of the populations and the efective parameters.

parallel to the evolution of populations. Our proposal has been to make them independent because we consider that these parameters refer to the relationships of the species to their environment and among themselves, independently of the populations. These relationships can be then subject to changes that, either arise from external elements, or simply they are governed by a different temporary scale. If certain environmental conditions that before were beneficial $r_i > 0$ change (oxygen appears in the atmosphere, or a source of food begins to disappear), the relationships a species with its environment, reflected through the parameter r_i must also change, because it becomes negative. The survival of this species will be then conditioned to that its single other possible source of resources, that in our bipartite model is the other species. Then, the former species is forced to establish a beneficial relationship with the latter and, in account of that, b_{ij} changes from negative to positive. The reverse transition is identically interpretable. This interpretation already allows illustrating one of the phenomena explained in the introduction: the appearance of mitochondria and plastids in the eukaryotic cells.

However, this model has a more deep interpretation yet. The need of dependance on another source of resources, in the absence of the previous one is quite understandable. But the possibility of quit out from a source of resources, or totally replace it from depending on a new relationship is less obvious. Another possible interpretation that allows the transition from antagonism to mutualism is the appearance of the endosymbiosis and the consequent symbiogenesis. One can think that the change of predominance between r_i and b_{ij} is totally timeless, that is, they happen simultaneously. That allows us to interpret the causes of change in the reverse way to the one explained in the previous paragraph: it must be r_i the one that change from positive to negative because of the fact that b_{ij} changes from negative to positive. This type of transitions has also happened in the history of the first cells: it is the mechanism presented in the introduction that, in principle, explains the formation of eukaryotic cells. As explained above, the formation of the nucleus seems to be consequence of the association of certain species of spirochetes with archaea, photoautotrophic and heterotrophic ones. The association, probably accidental, would have originated since the slow archaea would dispose enough organic material to keep the spirochetes nearby. This proximity could caused later that the last ones began to join and to move the archaea, which would have been beneficial for both species: the archaea would have access to more opportunities of resources, either other predation bacteria or complex molecules (and that will be the mutualistic benefit these would obtain) and, in turn, a greater feeding of archaea would provide more waste to the spirochetes. Over time, its specialization would have excluded the dependency of the resources on the environment and the spirochetes would finish inevitably tied to the archaea.

That the evolution of parameters does not depend on populations is an assumption that we have established as a premise. This does not mean that an *ad hoc* model for some specific evolutionary process that requires and/or justifies taking that idea within the model, cannot be constructed. The equations of parameters are simple enough as to admit the presence of a population-dependant term. The analysis for that, however, although could start from what is presented here, would have to be elaborated again almost from the beginning.

4. Conclusions

In this paper, we develop a generalized model of the evolution of populations where the type of interaction among them can be changed within it. We introduce a mechanism by which transitions among the different types of interaction may be made, which on the other hand, has slightly limited the variety of possible biological interactions. Although the most relevant ones (predation/parasitism and mutualism) have been kept, adding also the competition for resources. This mechanism consists of a dynamical system independent from the populations, but which make vary the parameters of them. When a transition is caused, an external intervention in the dynamical system of parameters is performed causing a change of fixed point.

We also present a detailed linear stability analysis and a set of initial parameters and conditions that allows simulating antagonism-mutualism and mutualism-antagonism transitions avoiding the extinction of the involved species. We perform some numerical Poisson simulations in which the capacity of the model to reproduce these transitions can be demonstrated.

It will be extremely interesting to introduce a source of noise in the dynamical system of parameters so that the leaps among the two basins of attraction can be naturally given by stochastic variations, making the model develops in an autonomous way between the mutualistic and the antagonistic phase. A possible approach to attack this line of work will be to play with the value of the traditional deviation in the random number generator with Gaussian distribution that is used to make the parameters evolve.

The next step in the study of this proposed model could be to analyze bipartite networks of more than two species. Since the model allows for this, these networks would include relations of multiple types, being able to simulate a reasonably ecosystem close to reality. In addition, transitions among relationships could be introduced, although this company leads to the difficulty of finding a set of parameters in which, during the antagonistic phases, the populations do not fall within the basin of extinction. And maybe it will be also possible to find a way to identify what type of antagonistic relationships has the potentiality to revert its relationship and become a mutualistic one and which from the last ones, if they completely separate from the rest of the ecosystem, will have the possibility of merging and generating new species.

References

[1] García-Algarra, J., Galeano, J., Pastor, J. M., Iriondo, J. M., and Ramasco, J.J. (2014) Rethinking the logistic approach for population dynamics of mutualistic interactions. *Journal of Theoretical Biology*, **363**, 332-343.

[2] Margulis,L., and Dolan, M. F. (2002) *Early Life - Evolution on the Pre-Cambrian Earth*, Sudbury, MA: Jones and Bartlett Publishers.

[3] Margulis,L., and Sagan, D. (1997) *Microcosmos - Four Billion Years of Microbial Evolution* , Berkeley, CA: University of California Press.

[4] Margulis,L., and Sagan, D. (2002) *Acquiring Genomes: A Theory of the Origin of Species*, New York, NY: Basic Books.

[5] Margulis,L., and Sagan, D. (1995) *What is Life?*, Berkeley, CA: University of California Press.

[6] Keeble, F. (2012) *Plant-animals A study on symbiosis*, Cambridge: Cambridge University Press.

[7] Jeon, K. W. (1995) Bacterial endosymbiosis in amoebae. *Trends in Cell Biology*, **5**, 127-140. Cambridge: Cambridge University Press.

[8] Tellería, M. T. (2011) *¿Qué sabemos de? Los hongos.* Madrid: CSIC.

[9] Strogatz, S. H. (2015) *Nonlinear Dynamics and Chaos - With Applications to Physics, Biology, Chemistry, and Engineering.* Philadelphia, PA: Westview Press.

[10] Gustaffson, L and Sternad, M. (2007) Bringing consistency to simulation of population models - Poisson Simulation as a bridge between micro and macro simulation. *Mathematical Biosciences*, **209**, 361-385.