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LOTKA-VOLTERRA DYNAMICS IN MODEL ECOSYSTEMS

Francesca Sofía Blanco Janer

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Thesis Supervisor's Name: Emilio Hernández-García

Co-Supervisor's Name (if applicable):

Abstract

This work explores different types of population dynamics and stability, and their implications for the coexistence of biological species, using the Generalized Lotka-Volterra model. On the one hand, an analysis of the model is carried out from a deterministic point of view. First, the simplest case that the model is able to describe, the logistic equation, is presented. Then, already established parameterizations are used to represent examples of different dynamics for systems of 3-4 species, and the stability analysis is performed for each of them. Then, the study focuses on systems whose parameters are unknown and are given by randomness, which leads to the need to present the stability criteria established by the Theory of Random Matrices. On the other hand, the model is analyzed from the point of view of stochastic methods. The objective here is to solve the case of a single species, i.e., the logistic equation, from a stochastic method. An analogy is made between the logistic growth and the Markovian process known as Birth-and-Death. Finally, it is solved by means of Gillespie's Algorithm. To conclude, once the two resolutions have been presented, a comparison of both is made.

Resum

Aquest treball explora diferents tipus de dinàmica i estabilitat de poblacions, així com les seves implicacions per a la coexistència de les espècies biològiques, utilitzant el model Lotka-Volterra Generalizat. D'una banda, es fa una anàlisi del model des d'un punt determinista. Primer, es presenta el cas més senzill que el model és capaç de descriure, l'equació logística. A continuació, s'utilitzen parametritzacions ja establertes per representar exemples de diferents dinàmiques per a sistemes de 3-4 espècies i es fa l'anàlisi de l'estabilitat per a cadascun. Després, l'estudi s'enfoca en sistemes amb paràmetres desconeguts, per tant, venen donats per l'aleatorietat, la qual cosa comporta la necessitat de presentar els criteris d'estabilitat establerts per la Teoria de les Matrius Aleatòries. D'altra banda, el model s'analitza des del punt de vista dels mètodes estocàstics. L'objectiu és resoldre el cas d'una espècie, és a dir, l'equació logística, a partir d'un mètode estocàstic. Es realitza una analogia entre el creixement logístic i el procés markovià conegut com a Birth-and-Death. Finalment, es resol mitjançant l'algorisme de Gillespie. Per concloure, una vegada presentades les dues resolucions es realitza la comparació entre ambdues.

Resumen

Este trabajo explora diferentes tipos de dinámica y la estabilidad de poblaciones, así como sus implicaciones para la coexistencia de las especies biológicas, utilizando el modelo Lotka-Volterra Generalizado. Por un lado, se realiza un análisis del modelo desde un punto determinista. Primero, se presenta el caso más sencillo que el modelo es capaz de describir, la ecuación logística. A continuación, se utilizan parametrizaciones ya establecidas para representar ejemplos de distintas dinámicas para sistemas de 3-4 especies y se realiza el análisis de la estabilidad para cada uno de ellos. Después, el estudio se enfoca en sistemas cuyos parámetros son desconocidos y vienen dados por la aleatoriedad, lo cual conlleva a la necesidad de presentar los criterios de estabilidad establecidos por la Teoría de las Matrices Aleatorias. Por otro lado, se analiza el modelo desde el punto de vista de los métodos estocásticos. El objetivo aquí es resolver el caso de una especie, es decir, la ecuación logística a partir de un método estocástico. Se realiza una analogía entre el crecimiento logístico y el proceso markoviano conocido como Birth-and-Death. Finalmente, se resuelve mediante el Algoritmo de Gillespie. Para concluir, una vez presentadas las dos resoluciones se realiza la comparación de ambas.

Contents

1   Introduction

The evolution of mankind has been linked from its beginnings to the study of ecosystems. An ecosystem is defined as a biological system made up of a community of living organisms and the physical environment in which they interact. The scientific community has always been dedicated to studying them in order to understand them and thus facilitate their development with the aim of reaching their maximum performance. Ecology is a branch of science that, like most, in its beginnings was purely observational in nature, but with the development of mathematical models this has changed. Experience showed that models made it possible to quantitatively describe simplified systems of reality, and this opened the way to new approaches.

There is a whole branch of physics oriented to the study of systems made up of a large number of elements, and this is statistical physics. Its objective is to link the macroscopic or collective properties of a system with the properties of its members. This connection is made using statistical mechanics as a mathematical tool, which, by means of probability theory, is capable of deducing the behavior of physical systems. Although in the beginnings of statistical physics the studies were oriented to the explanation of the macroscopic properties of matter in terms of its microscopic properties, nowadays the field of study has been extended to other situations that are far from the original idea of the parents of the theory (basically Boltzmann and Gibbs) [1]. The aim is to take advantage of experience in the methods of statistical physics to deduce the global behavior of a system made up of several relatively simple constituents, even if these simple systems are not described by the classical fundamental laws of physics. Among them is the object of study of this work, the coexistence between species within an ecosystem.

Within a single ecosystem inhabited by different species, the factors that determine the course of its life are more than the sum of the properties of its constituents. Moreover, for a realistic study of the system's behavior, the relationships between the constituents are more important than if only the constituents and their properties are taken into account. In other words, in an ecosystem there are many conditions that affect the growth of coexisting species, e.g., seasonal variation, habitat, food, sexual partner, etc. In all these examples, the time it takes to find the targets is a totally determining factor, and even the survival of the individual may depend on minimizing it. Individuals of the same species interact with each other, but also with those of other species, this interaction can have different levels of intensity. This type of systems composed of interwoven parts whose links create additional information due to interactions between elements are known as complex systems. In order to function properly, ecosystems must maintain adequate proportions between their constituent species, resources and others. The events that mainly govern ecosystems are stochastic in nature. A stochastic process is a mathematical concept used for the representation of random quantities that vary with time. Stochastic Processes allow to treat dynamic processes in which there is randomness.

For the study and development of complex systems, mathematical models have been created to simulate the system's evolution taking into account the connections between its constituents. This study will focus on the development of one of them, the *Generalized Lotka-Volterra* method. This model was introduced during the 1920s independently by the two scientists after whom it is named. Lotka was studying a specific chemical reaction, which exhibited perpetual oscillations in terms of the concentrations of reactants and products, when he developed a system of two equations that gave an answer to the behavior described above. Regarding Volterra, he reached the same conclusions while studying the demographic variation of piscivorous fishes during the WWI. The original model described the particular case of the *Predator-Prey*, which can be seen in the papers presented by each of them [2, 3]. The Generalized Lotka-Volterra equation is a simple model of population dynamics in which the factors of trophic interactions are included for a deeper analysis of coexistence, thus allowing a study of the dynamics and stability of com-

munities [4].

In Section 2 the *Generalized Lotka-Volterra* model is presented. The objective of this section is to carry out an in-depth analysis of the model. Taking into account the generality of the model, the aim is to establish criteria to help classify the systems in terms of stability. The models generality refers to the fact that this set of equations is capable of describing all types of dynamics, e.g., *Predator-Prey* (which is the most famous), mutualism or competition relationships. First, the simplest case, corresponding to a single species, is presented, and then the study focuses on more complex systems formed by several species. Considering that this model requires the knowledge of the parameters to represent concrete dynamics; the stability theory is presented. It allows to classify the system according to its feasibility and stability. Once the theory is presented, concrete examples of each possible dynamics are shown. Continuing with the study of stability, the concept of stability of random large communities is introduced. Finally, stability criteria are presented with the objective of classifying the stability of these systems.

Once the deterministic model has been developed, and taking into account that, as mentioned above, the processes governing ecosystems are stochastic in nature; Section 3 presents an analysis of the model based on stochastic processes. To approach the problem as realistically as possible, the dynamics of the system is described as a Markov process, i.e., the probability of each event is considered to depend only on the state of the previous event. Then, an analogy is made between the logistic equation of the *Generalized Lotka-Volterra* with the *Birth-Death Process*, which is a scheme in which each individual of the species can reproduce or die and each of these possibilities has an associated rate. Thus, the case is particularized so that it responds in the same way as the logistic equation. Finally, to simulate the system, the Gillespie's algorithm is presented with its parameters particularized.

To conclude, Section 4 presents the comparison between the two models developed during the study: the deterministic and the stochastic.

2   Generalized Lotka-Volterra Model

The Generalized Lotka-Volterra equations are a set of non-linear ordinary differential equations that for n populations are given as:

$$\frac{dx_i(t)}{dt} = x_i(t) \left(r_i + \sum_{j=1}^{n} a_{ij} x_j(t) \right), \quad i = 1, ..., N, \tag{1}$$

where x_i denotes the abundances of species i at time t. Regarding r_i, they are "intrinsic growth (or death) rates" hence r is the parameter in charge of measuring the variations of population i when grown alone at low density. Thus, positive values of r are attributed to producers because they are able to reproduce in the absence of any other species, and negative values to consumers, due to their incapacity to survive unless the appropriate other species are present. As for A, which is the matrix grouping the interaction coefficients, a_{ij}, it represents the relationships between the species. The interaction coefficients, a_{ij}, will be positive when the growth is benefited by the interaction and negative when it is detrimental. As a_{ij} represents the effect that species j has upon species i, it will be determinant on the type of relationship established between the species in the system. So that, a competitive interaction will be represented when a_{ij} and a_{ji} are both negative due to the negative effect that each species creates on the other species. In the event that a_{ij} is positive and a_{ji} is negative, species i is considered to be a predator on species j because it grows at j's expenses. When a_{ij} and a_{ji} are both positive the described interaction is mutualism, but it is not usually used due to the possibility of having an indefinite growth. As stated, the parameters r and A are the ones that determine the type of dynamics followed by the system [5]. The fact that it is referred to as Generalized is due to the capacity of this model to represent all the combinations of pairs of signs for both species.

The model's aim is to describe the variation of the state of a set of elements, the abundances of the species studied, as time goes by. In other words, it is a dynamical system. Population dynamics is too complex a system to be fully described by current numerical models. This leads to questioning the validity of numerical resolutions. In order to study their viability, we proceed to examine the stability of the systems. Part of the system's behavior can be extracted from the fixed points (constant solution of a differential equation), therefore, it will be useful to analyze the stability of an equilibrium.

Dynamical systems are described mathematically in a state space, which in the present case is the non-negative orthant $\mathbb{R}^n_+ = \{\mathbf{x} = (x_1, ..., x_n) \in \mathbb{R}^n: x_i \geq 0 \text{ for } i = 1, ..., n\}$. Its boundary points are on $x_i = 0$, corresponding to the absence of species i. Assuming the system had no feasible equilibrium, the trajectories (solutions of the dynamical systems, derived by the numerical models) described by the species would reach $\mathbb{R}^n_+$'s boundary, what implies the extinction of the species [5, 4].

This section aims to show the more general characteristics of the dynamics of the Generalized Lotka-Volterra. To this end, at the beginning, the simplest case that the GLV is able to represent is described. This introduces, in the most fundamental way, the concepts of the Stability Theory. Then, once they have been established, it will be possible to continue with the development of the deterministic model. From that point, the study will focus on the simulation of more complex systems representing different dynamics, all of them obtained from already known parameterizations. Finally, as the fact of being able to simulate systems only if the parameters that define them are known gives a rather poor view of the problem, the problem will be analyzed from the perspective of Random Matrices. Then, some of the most characteristic criteria within the stability of large random systems will be developed.

2.1 Logistic Equation

The simplest situation that can be reproduced with this method is that of a single population, in which case the model goes on to describe the logistic equation [4]. This was introduced to the scientific scene by Verhulst, who proposed it as an improvement of the exponential growth model to describe the development of a population in a more realistic way since it describes the self-limitation of the growth of a species. In this case it is possible to determine the number of individuals in the species' population for any time by solving this particular case of the equation (1):

$$\frac{dx(t)}{dt} = x(t)(r + ax(t)). \tag{2}$$

Whose analytical solution is given by:

$$x(t) = \frac{rx_0 e^{rt}}{r - ax_0(e^{rt} - 1)}, \tag{3}$$

where x_0 is the initial number of individuals in the population. A comparison between the analytical and numerical solutions is presented below for the parameter values $a = -0.05$ and $r = 0.1$. As expected both results match perfectly.
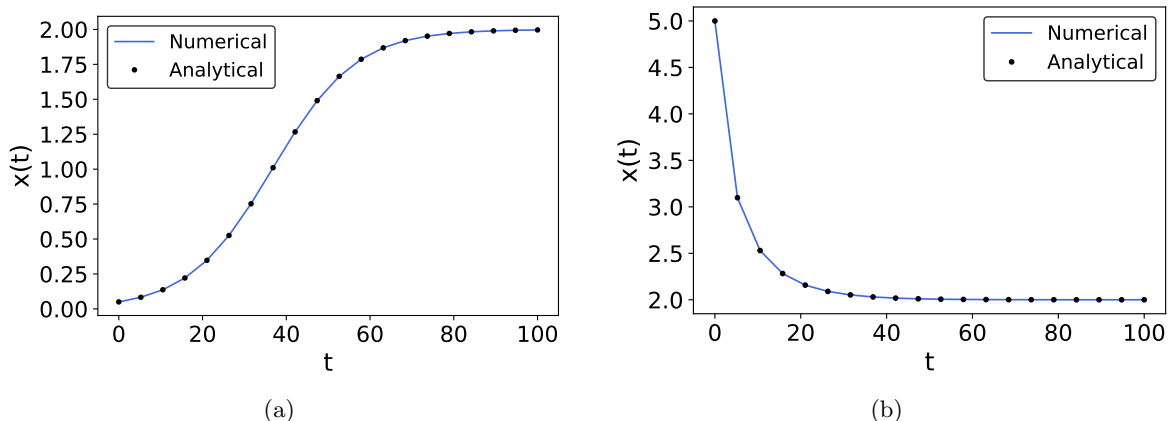

Figure 1: (a) Plotting of the Logistic Equation with an initial population below the saturation value. (b) Plotting of the Logistic Equation with an initial population above the saturation value.

As seen in the graphs, the function presents an exponential growth (or decline, case (b)) until it saturates and reaches equilibrium. This rest point is $x = -r/a$ and is found by setting $dx(t)/dt = 0$.

2.2 Multi-Species Dynamics

Returning to ecosystems, a species that inhabits an environment usually shares resources and space with others, so, if the most precise possible results are to be obtained, it is interesting to study the relationships between coexisting species. Then, in analogy with the case of one species, in the study of dynamical systems, an important element to take into consideration is the stability of the system as this will determine whether a species is able to survive over time. The characteristic of the systems that establishes the possibility of the existence of a fixed point (or equilibrium point) in which all species are present, is known as *Feasibility*. An equilibrium is referred to as "feasible" when the stationary points of (1) in which all species have non-zero abundances, i.e. the solution of $r_i + \sum_{j=1}^{n} a_{ij}x_j = 0$, is positive. Feasibility is one of the elements

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that limits the ability of species to co-exist, so when analyzing a system it is crucial to study its feasibility by checking the existence of a positive fixed point.

After observing the logistic equation's results, it is attainable to ask whether in the case of multi-species there will also be an equilibrium reached by the coexisting species. This is done by studying local stability, which will be described in the next section, where the Stability Theory is presented.

2.2.1   Stability Theory

In dynamical systems, Stability Theory, addresses the stability of their trajectories under small perturbations of initial conditions. During this section, two different types of stability will be developed. Global Stability, which means that the system reaches the equilibrium point from any possible starting point (i.e., there is no "nearby" condition). And Local Stability which is based on the idea of analyzing the behavior of a well-known trajectory after promoting a little disturbance on the initial condition. If the change that the system undergoes is negligible it is considered stable. Otherwise, when it departs from the known trajectory it is referred as unstable. In the following, the study will focus on Local Stability, i.e., the stability close to the fixed point of the system will be tested. Global Stability is presented in more depth in section 2.3.

In order to study the stability of a system, as mentioned above, the first thing to do is to check its feasibility, and for this purpose the fixed points of the system in which all the species have non-zero abundances must be calculated. Mathematically, the values of the abundances are arbitrary, but in ecological systems the interest is focused on strictly positive equilibria [5, 4]. Then, the point which satisfies this condition will be unique and will correspond to:

$$x^* = -A^{-1}r, \quad \text{with} \quad x_i^* > 0 \quad \forall i. \tag{4}$$

Once the feasibility is checked and the fixed point has been determined, it is natural to proceed with the study of their stability. Stability is of great importance in the study of dynamical systems, since the initial conditions, which determine the solutions of the ODEs, are not known with complete precision. This leads to the need to verify that the system does not undergo significant changes when there is a perturbation on the initial value.

Several criteria have been developed to determine whether a fixed point is stable or unstable. In general, the qualitative behavior of a trajectory (solution of the ODE) that has been perturbed can be analyzed by linearizing the system in its surrounding area. In particular, an ecological community can be considered as a system of nonlinear, autonomous ODEs:

$$\frac{dx_i(t)}{dt} = f_i(x(t)). \tag{5}$$

A given system might have multiple equilibrium points, which are defined as vectors of abundances such that:

$$\left. \frac{dx_i(t)}{dt} \right|_{x^*} = f_i(x^*) = 0 \quad \forall i. \tag{6}$$

Considering that the system proves to be stable, which means that under small perturbations the orbits do not suffer notorious changes, two situations can occur. The first one arises when the nearby orbit stays close to the given one indefinitely i.e. is stable in the Lyapunov sense; the second case takes places when the neighbouring one eventually converges to the given one, this is known as asymptotically stable. In the following only the second case will be considered.

To analyze local stability, it is assumed that, given a system which is resting in its equilibria, when it is slightly perturbed its state is then found to be $\Delta x(0) = x(0) - x^*$. The Taylor expansion around x^* is then carried out:

$$f(\Delta x(0)) = f(x^*) + J|_{x^*}\,\Delta x(0) + ... \tag{7}$$

where J is the system's Jacobian matrix built as:

$$J_{ij} = \frac{\partial f_i(x)}{\partial x_j}. \tag{8}$$

Therefore, J turns out to be a matrix whose elements are functions of the densities of the populations, x. The "community matrix", M, turns out to be J evaluated at an equilibrium point x^*:

$$M = J|_{x^*} \tag{9}$$

Hence, even though every system has a unique Jacobian matrix, J, there will be as many community matrices as there are equilibrium points. The community matrix, M, exposes the effect of increasing the density of a species in front of any other species near the equilibria. Then, it is suitable to rewrite the differential equation depending on M:

$$\frac{d\Delta x(t)}{dt} \approx M\Delta x(t), \tag{10}$$

whose solution is:

$$\Delta x(t) = e^{Mt}\Delta x(0) = Qe^{\Lambda t}Q^{-1}\Delta x(0), \tag{11}$$

where Q is the matrix that contains the (unit) eigenvectors of the community matrix, and Λ is a diagonal matrix containing the eigenvalues of M. The eigenvalues of M are the ones that will determine the stability of the equilibria. The rule is that if all the eigenvalues have negative real part, then after being slightly perturbed the system will return to the equilibrium. Otherwise, if any of the eigenvalues has positive real part, the system will not return and will move away from its equilibria. Consequently, it is possible to establish a mathematical rule to determine the stability of an equilibrium. Depending on the sign of the "rightmost" eigenvalue of M, λ_1, the stability criteria will be:

$$Re(\lambda_1) \begin{cases} < 0 \longrightarrow x^* & \text{is stable,} \\ > 0 \longrightarrow x^* & \text{is unstable.} \end{cases}$$

In the former case, the GLV model, the Jacobian is computed as:

$$J_{ij} = \frac{\partial f_i}{\partial x_j} = a_{ij}x_i, \qquad \text{if} \quad i \neq j, \tag{12}$$

and

$$J_{ii} = \frac{\partial f_i}{\partial x_i} = r_i + \sum_j a_{ij}x_j + a_{ii}x_i. \tag{13}$$

Thus, the Jacobian evaluated at the equilibrium point is given by:

$$J_{ij}(x^*) = a_{ij}x_i^*, \quad \forall i,j. \tag{14}$$

2.2.2 Variety of Dynamics

Although for a single population the possible scenarios displayed by the General Lotka-Volterra model are: infinity growth, extinction, or asymptotically reaching an equilibrium point; this changes when more than two species are involved. Instability is not completely determinant for the permanence of the species. In the competitive GLV model limit cycles (closed trajectories in the phase-space that have the property that there is at least one other trajectory that arrives following a spiral into it, either when time tends to infinity or negative infinity) are a possibility for three or more species. In the circumstance of having four species, chaotic solutions may be produced [6]. Some examples of these types of dynamics are constructed and reproduced below.

An illustration of a system for which the equilibrium in which all species coexist is unfeasible can be shown with the parameterization:

$$r = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}, \qquad A = - \begin{pmatrix} 10 & 9 & 5 \\ 9 & 10 & 9 \\ 5 & 9 & 10 \end{pmatrix}.$$

As indicated above, the first step to follow during the study of the stability of a system is to check the feasibility. For the simulations, the programming language known as *Python* has been used, which has the library *NumPy* with the function *np.linalg.solve()*, which is the one used to apply (4). Then, for the given parameters the equilibrium points turn out to be:

$$x^* = \begin{pmatrix} -0.083 \\ 0.25 \\ -0.083 \end{pmatrix}.$$

It results that not all abundances have positive values, in fact, two of the three abundances calculated have a negative value. This means that the equilibrium in which all three species coexist is not feasible, since, from a biological point of view, it makes no sense for the equilibrium point of a species to be given by negative values. As mentioned above, negative abundances are not possible. This implies that what is expected to be seen in the simulation is that at least one of the three species that constitute the system will become extinct.

Regarding the parameters, A is symmetric which implies that its eigenvalues are real, thus the stability will be determined by the sign of its rightmost eigenvalue. The programming language used (*Python*) has the subroutine *np.linalg.eig()* which provides all the eigenvalues of the desired matrix. In addition, the *Python* has the function *.real* which extracts the real part of the eigenvalues. Therefore, to study the stability one simply uses these functions by particularizing them for each set of parameters.

In this particular case, the real part of the rightmost eigenvalue turns out to be positive $\left(\frac{-25+\sqrt{673}}{2} \right)$. Following the criteria established in the previous section, the coexistence would be unstable. But taking into account that the equilibrium is not feasible (i.e., the results show that there is no fixed point at which species coexist) their stability means nothing.
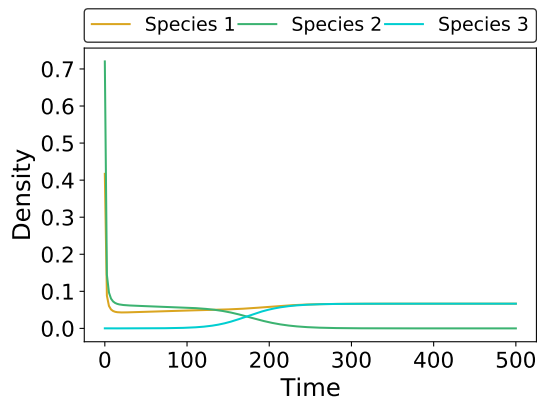
Figure 2: Competitive system without feasible equilibrium of three species.

As expected, according to the above description, it can be observed in Figure 2 that the *Species 2* is not able to coexist and finally gets extinct.

Then, it is interesting to present an example with a feasible equilibrium that is unstable. This is given by the following parameters:

$$r = \begin{pmatrix} 1 \\ 0.8 \\ 1.2 \end{pmatrix}, \qquad A = - \begin{pmatrix} 1 & 2 & 0.1 \\ 2 & 1 & 0.1 \\ 0.1 & 0.8 & 1 \end{pmatrix}.$$

The next step is to carry out a study of the system's feasibility, following the steps described above. Thus, it is obtained that the equilibrium points of each species are:

$$x^* = \begin{pmatrix} 0.162 \\ 0.362 \\ 1.148 \end{pmatrix}.$$

All the abundances turn to be positive, which implies that the equilibrium is feasible. Finally, it is necessary to analyze the system's stability. Then, following the same procedure as in the previous example, it turns out that the real part of the rightmost eigenvalue is positive, which means, according to the above theory, that the equilibrium is unstable. Therefore, one of the expected outcomes to see in the system's simulation is that at least one of the species becomes extinct. The results are presented below:
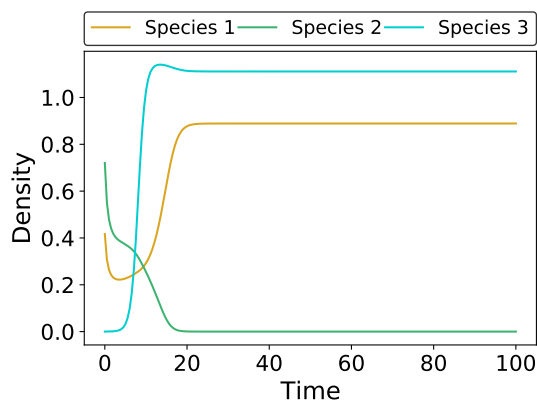

Figure 3: Competitive system with an unstable feasible equilibrium of three species.

Another example of dynamics described by the model is given by using the growth rates and the interaction matrix:

$$r = \begin{pmatrix} 10 \\ 10 \\ 10 \end{pmatrix}, \qquad A = -\begin{pmatrix} 10 & 7 & 12 \\ 15 & 10 & 8 \\ 7 & 11 & 10 \end{pmatrix}.$$

Following the same procedure as in the previous case, the fixed points of the system are calculated using the function of *Python*, *np.linalg.solve()*:

$$x^* = \begin{pmatrix} 0.166 \\ 0.365 \\ 0.482 \end{pmatrix}.$$

The results show that all abundances are positive, which, following the theory, implies that the equilibrium is feasible. In addition, with this parameterization the real part of the rightmost eigenvalue $(-2/301 \pm i\sqrt{1591}/301)$ turns to be negative, what implies that in this case the system is stable thus the coexistence is expected to be possible.
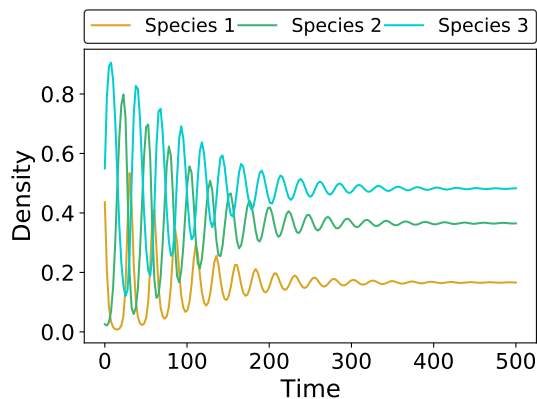

Figure 4: Competitive system with a stable feasible equilibrium of three species.

The simulations above show the expected dynamics. Since the equilibrium was feasible and stable, it was expected that the three coexisting species would survive and reach their equilibrium point. Indeed, the three trajectories initially fluctuate quite a lot, but then dampen until they reach equilibrium.

An example of a stable limit cycle can be represented using the parameterization:

$$r = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}, \qquad A = -\begin{pmatrix} 10 & 6 & 12 \\ 14 & 10 & 2 \\ 8 & 18 & 10 \end{pmatrix}.$$

Then, following the indicated procedure, the feasibility of the system is checked by calculating the equilibrium points corresponding to each species:

$$x^* = \begin{pmatrix} 0.057 \\ 0.014 \\ 0.029 \end{pmatrix}.$$

The abundances are positive, so the equilibrium is feasible. Regarding the system's stability, the real part of the rightmost eigenvalue is positive so the equilibrium is unstable.
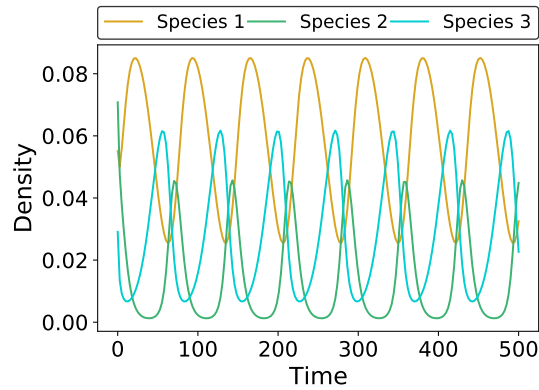
Figure 5: Competitive system with stable limit cycles of three species.

The three trajectories fluctuate maintaining the same cycle; while the *Species 1* is the one who reaches the maximum of abundance the *Species 2* is the one who goes to the minimum of abundance but still none of the three is extinguished. And even though they do not stagnate at a fixed point, all three are able to survive following the observed cycle.

A sample of a chaotic solution for a system of four species can be represented by using the growth rates, and the interaction matrix:

$$r = \begin{pmatrix} 1.00 \\ 0.72 \\ 1.53 \\ 1.27 \end{pmatrix}, \qquad A = - \begin{pmatrix} 1.0000 & 1.0900 & 1.5200 & 0.0000 \\ 0.0000 & 0.7200 & 0.3168 & 0.9792 \\ 3.5649 & 0.0000 & 1.5300 & 0.7191 \\ 1.5367 & 0.6477 & 0.4445 & 1.2700 \end{pmatrix}.$$

The feasibility is checked by calculating:

$$x^* = \begin{pmatrix} 0.301 \\ 0.459 \\ 0.131 \\ 0.356 \end{pmatrix}.$$

This implies that the equilibrium is feasible, but the analysis of the eigenvalues determines that the equilibrium is unstable. The dynamics is shown below.
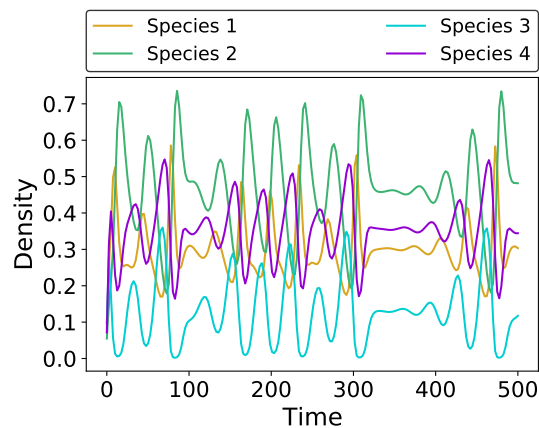

Figure 6: Chaotic dynamics shown by the Generalized Lotka-Volterra model in a four species system.

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As has been previously said, in this particular case, the coexistence equilibrium is unstable, which may lead to the conclusion that the species will not be able to survive. Instead, what is observed is that the species are able to coexist on a chaotic system. This is a clear example of a natural system which operates out-of-equilibrium, and still achieves the persistence of the species by more complex dynamics.

2.3   Global Stability

So far, the concept of Local Stability has been developed by studying each trajectory separately. But, as anticipated above, there is the concept of Global Stability, which implies that in the system there are no unbounded trajectories even if they start far from the origin. By definition, the concept of Global Stability is more complex than Local Stability, so it is reasonable for its demonstration to be more complex as well.

There is a property of matrices, based in the Lyapunov Stability, useful to prove Global Stability. This is based on the assumption of the existence of a positive diagonal matrix ,"C", such that $CA + A^t C$ is negative definite i.e. it just has negative eigenvalues which are real due to the symmetry of the matrix. This implies that matrix A is Lyapunov-Diagonally stable, which means that A is stable and any diagonal positive matrix "D" combined with it as DA is stable too. Note that the community matrix of the GLV equation (14) is of the form DA, with D being the diagonal matrix with x^* in the diagonal. Thus, this condition of 'Lyapunov-diagonal stability' allows to asses the stability of the system GLV by looking only at the matrix A, independently of r. Then, considering a Lyapunov Diagonally-stable matrix, A, and the existence of a feasible equilibrium, x^*, it is possible to prove that all trajectories starting at a non-negative density will converge to the equilibrium [4].

A couple of examples with random initial conditions are presented below. The parameterization for this is:

$$r = \begin{pmatrix} 1 \\ 1 \end{pmatrix}, \qquad A = - \begin{pmatrix} -1 & 3/2 \\ -1/2 & -1 \end{pmatrix}.$$

As in the previous examples, the first step in the stability study is to check the feasibility of the equilibrium. For this particular parameterization the fixed points are:

$$x^* = \begin{pmatrix} 1.43 \\ 0.29 \end{pmatrix}.$$

Implying that the equilibrium is feasible. Therefore, as the conditions for a system to be globally stable are that a feasible equilibrium, x^*, has to exist, and that matrix A has to be Lyapunov Diagonally-stable. Then, having proved the existence of x^* it only remains to show that A is Lyapunov Diagonally-stable. Which can be done by proving that $A + A^T$ has only negative eigenvalues. This is achieved by using the aforementioned *np.linalg.eig()*. Thus, the eigenvalues are -1 and -3, therefore, both are negative and it is confirmed that A is Lyapunov Diagonally-stable.
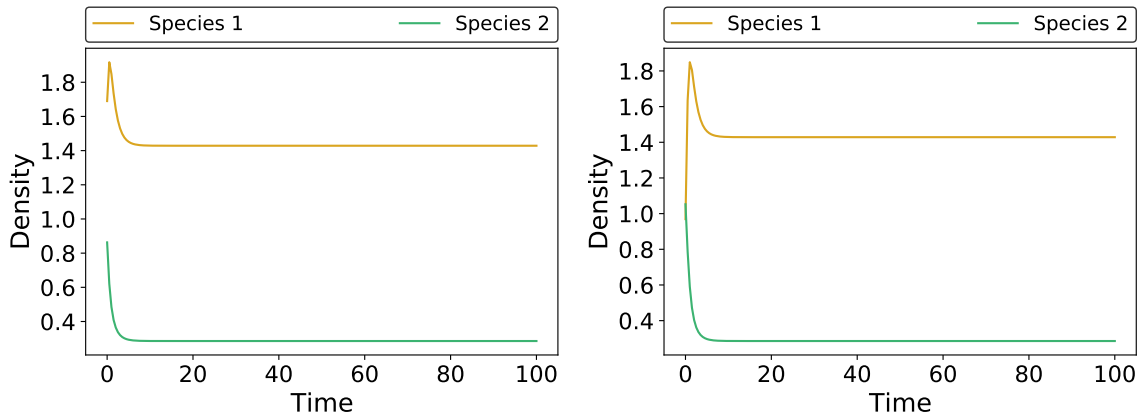
Figure 7: Two samples of global stability. The system reaches the same equilibrium even having different initial conditions.

The results show that the system reaches equilibrium regardless of the initial conditions.

2.4 Stability of Large Random Communities

It has been shown in the previous sections that for an equilibrium to be stable, the eigenvalues of the community matrix must have negative real part. This implies that to characterize an equilibrium it is necessary to specify the growth rates, r, and the matrix of interactions, A. Therefore, if one intends to study a system composed of many individuals this is especially impractical, since one would have to describe matrices of n and n^2 values. Hence, it is of interest to investigate the limit in which many species are in the community [4].

Robert May investigated the transition from stability to instability in a large complex system with the aim of clarifying the relation between stability and complexity in ecological systems with many interacting species [7]. May attempted to describe a system in which there were many species by means of the Random Matrix Theory (RMT), whose idea is to analyze the properties of large matrices built from specific random distributions [8]. He was inspired by Wigner's work on symmetric matrices.

2.4.1 Circular Law

The pioneer in this field was Wigner, who described a matrix $S \times S$, A, such that its diagonal is 0. Next, the upper triangle of the matrix is given values from a probability distribution with mean 0, variance σ^2, and all moments finite. And finally, each element of the lower triangle, A_{ij}, is equated to A_{ji} hence making the matrix symmetric. This kind of matrices are called *Wigner matrices*. Then, taking into account that the matrix $A/\sqrt{S\sigma^2}$ is symmetrical, its eigenvalues are real. It finally turns out that their empirical spectral distribution, for large S, follows the *Wigner semicircle distribution* [8].

May, inspired by Wigner's work, decided to take the study beyond symmetrical matrices. He designed an algorithm to construct a non-symmetric community matrix. At the present time, the most general statement of the Circular Law goes as follows. Take an $S \times S$ matrix, M, whose entries are independent and identically distributed (i.i.d.) random variables with mean zero and variance one. Then, the empirical spectral distribution (i.e., the distribution putting $1/S$ probability mass on each eigenvalue) of $M/\sqrt{S}$ converges to the uniform distribution on the unit disk as $S \to \infty$ [9, 10]. The statement does not specify anything about the coefficients distribution due to "universality".

In a GLV system the elements on the diagonal of the community matrix, $M_{ii} = A_{ii}x_i^*$, are influenced by self-regulation, and those outside the diagonal, $M_{ij} = A_{ij}x_i^*$, are responsible for representing the effect of species j on the equilibrium of species i. Then, for this system the algorithm consists in constructing the matrix by setting its elements with a certain probability. In ecology the systems are usually slightly connected, thus most of the community matrix's elements are zero. By setting $M_{ij} = 0$ with probability $1 - C$, where C corresponds to the proportion of established connections and is known as the system's "connectance", it is possible to create a "zero-inflated" distribution. The probability C corresponds to the rest of M_{ij} which are given by a distribution with mean 0 and variance σ^2. The diagonal elements are set to $-d$ in order to model self-regulation [4]. At last, the built matrix corresponds to an $n \times n$ non-symmetric matrix with independent and identically distributed entries.

While the mean of the non-diagonal elements of M_{ij} sampled from the "zero inflated" distribution is zero, their variance turns out to be $C\sigma^2$. As a consequence, the non-diagonal entries of $M/\sqrt{C\sigma^2}$ have $\sigma^2 = 1$. Thus, eigenvalues of M for large n fill uniformly a circle of radius $\sigma\sqrt{nC}$. Since the presence of the same value $-d$ in all the diagonal positions shifts all the eigenvalues by this amount, the circle is centered at the value $-d$ on the real axis. Therefore, May's criterion establishes that in order to ensure stability the diagonal has to be reasonably negative [8, 4]:

$$\sigma\sqrt{nC} < d.$$

As a demonstration of the previous statements, the plotting of the eigenvalues of two matrices built with different distributions and the parameterization: $n = 1000$, $C = 0.5$, $\sigma^2 = 1$ and $d = 10$, is shown below. The eigenvalues are obtained using the aforementioned $np.linalg.eig()$ function. The results from Figure 8 are the numerical demonstration of the property of universality.

The Figure 8 also shows in purple the plotting of $-d + \sigma\sqrt{nC}$ which, as expected, approximately coincides with the location of the rightmost eigenvalue. It is worth noting that for large n when the circle crosses the coordinate origin, indicated in the Figure 8 by a yellow line, part of the eigenvalues turn to be non-negative which determines the equilibrium's non-stability.
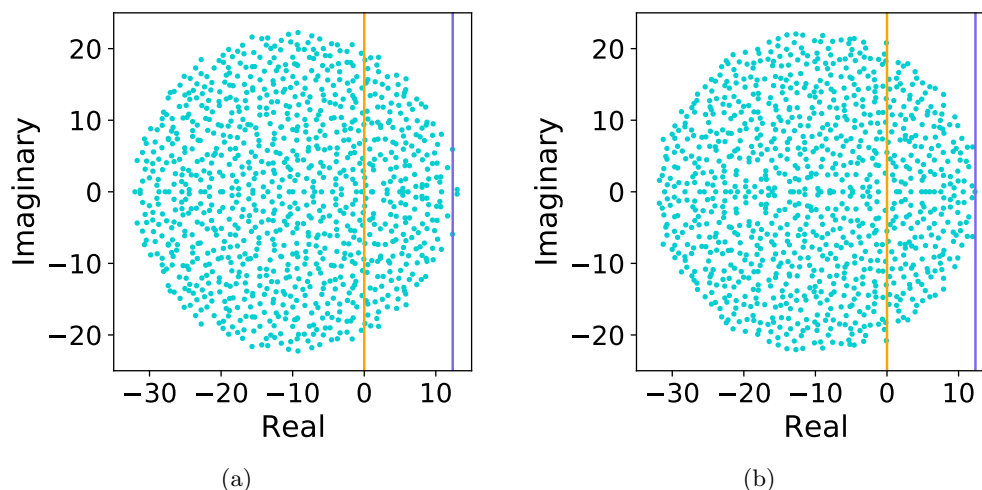

Figure 8: (a) Plotting of the eigenvalues of May's random community matrix for entries sampled from a normal distribution. (b) Plotting of the eigenvalues of May's random community matrix for entries sampled from a uniform distribution. The location of $-d + \sigma\sqrt{nC}$ is shown in both figures by a purple line. The coordinate origin is shown as a yellow line.

2.4.2 Elliptic Law

The ecological networks are a representation of the biotic interactions in an ecological community, they are used to describe and compare the structures of real ecosystems. When modelling them, the species are considered as nodes whose links are pairwise interactions, in these cases the coefficients M_{ij} depend on M_{ji}. In the Circular Law it was assumed that both are independent, a generalization of this law to the case where both coefficients are sampled from a bivariate distribution is the Elliptic Law, which is stated as follows. Take M, an $n \times n$ matrix whose coefficients from outside the diagonal are independently sampled in pairs from a bivariate distribution with zero marginal means, unit marginal variances, and correlation ρ, and the diagonal elements are zero. Subsequently, as $n \longrightarrow \infty$ the eigenvalue distribution of $M/\sqrt{n}$ converges to the uniform distribution on an ellipse centered at the origin of the coordinates system with horizontal and vertical semi-axis $1 \pm \rho$ [11, 8]. In this case, for a community matrix with $-d$ in the diagonal, connectance C and correlation ρ between M_{ij} and M_{ji}, the stability criterion becomes:

$$\sqrt{nC\sigma^2}(1 + \rho) < d.$$

It should be noted that when $\rho = 0$ the Circular Law is recovered. The plotting of two matrices built by sampling the coefficients in pairs from a bivariate normal distribution are shown below. The parameterization used is $n = 1000$, $C = 0.5$, $\sigma^2 = 1$, $d = 10$ and $\rho = \pm 0.4$. The plotting of $-d + \sqrt{nC\sigma^2}(1 + \rho)$ is presented at the following figures as a green line and, as expected, it is approximately the value of the rightmost eigenvalue.
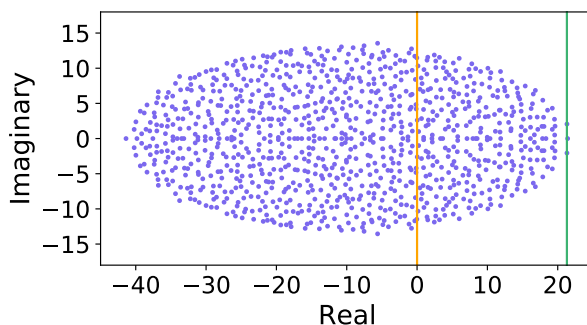

Figure 9: Plotting of the eigenvalues of matrix M, which coefficients are set from a bivariate distribution and positive correlation, $\rho = 0.4$. The location of $-d + \sigma\sqrt{nC}(1 + \rho)$ is shown in both figures by a green line. The coordinate origin is shown as a yellow line.

The system with positive correlations is described as a horizontally stretched ellipse, comparing it with the case of a vertically stretched ellipse also centered at $d = -10$, shown below in Figure 10, it is trivial to note that the amount of eigenvalues falling on the positive part of the real number axis is larger, and therefore, it is more difficult to stabilize. In both figures it has been plotted in yellow the line that crosses the coordinates origin to get a more visual picture of how many positive eigenvalues there are, and therefore also to get an idea of the degree of instability of the system.
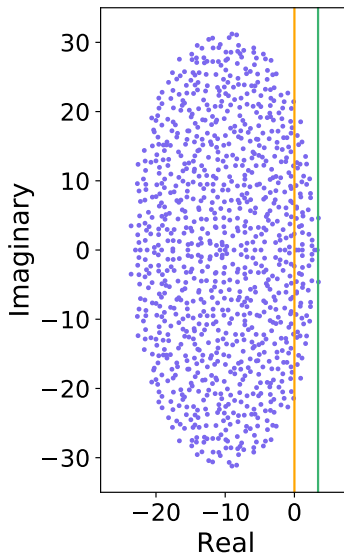
Figure 10: Plotting of the real part of the eigenvalues of matrix M, which coefficients are set from a bivariate distribution and negative correlation, $\rho = -0.4$. The location of $-d + \sigma\sqrt{nC}(1 + \rho)$ is shown in both figures by a green line. The coordinate origin is shown as a yellow line.

As can be seen in Figure 10, the system with negative correlation corresponds to a vertical-stretched ellipse, which makes it easier to stabilize. As it happened in the symmetric case, the elliptic law is universal, i.e., any bi-variate distribution with identical marginal variances and correlation will imply that the eigenvalues are distributed in the same ellipse.

Therefore, the results obtained show that for values of $\rho > 0$ the systems are more unstable than those represented by values of $\rho < 0$. Thus, it can be interpreted that the case in which ρ is positive corresponds to a competitive relationship between species, since this type of dynamics usually leads to the extinction of one of the rival species, and the case in which ρ is negative can be interpreted as a Predator-Prey relationship which corresponds to a system that usually represents stable cycles.

The study on stability has shown that what is expected when considering a large ecological community ($n \to \infty$ with d fixed) is that it is unstable, which, considering the examples of dynamics exposed during the previous section, normally leads to the extinction of some or all of the coexisting species.

3 Generalized Lotka-Volterra Model: Stochastic Approach

There are two fundamental approaches to the mathematical modelling of the Lotka-Volterra set of differential equations: the deterministic models which have been described in the previous sections; and stochastic simulations. A stochastic process can be defined as a mathematical concept, belonging to probability theory, which is used for the representation of time-varying random quantities or to characterize a succession of random variables that evolve as a function of another variable (usually time). Each of these random variables has its own probability distribution function, and may or may not be correlated with each other. Thus, it can be established that each variable or set of variables subject to random influences or effects constitutes a stochastic process. In the present work, stochastic processes serve as a useful tool for dealing with dynamic processes governed by certain randomness.

One way of interpreting stochastic processes is to consider that multiple probabilistic simulations are performed, one for each time instant, and the final trajectory of the system will depend on the product of each simulation. Consequently, to determine the position of the system in the phase space, it is not enough to know the condition of the system at the initial instant, but, to fully determine the final state, it is necessary to know the result of all the probabilistic simulations performed between the initial and the final moment. This is due to the probabilistic nature acquired by the trajectories [12].

In the Lotka-Volterra model there are occasions when deterministic models are not as realistic as one might expect. In these occasions it can be considered that the demography of the species that inhabit the ecosystem under study is described by stochastic processes, therefore, it is interesting to study the model from the approach of stochastic numerical methods. The dynamics of the system can be considered as a Markov process, that is, a stochastic process for which the probability of each event depends only on the state of the previous event.

Finally, once the identification of the type of stochastic process governing the system has been made, the election of the resolution method can be performed. Then, in this section the Lotka-Volterra model for a single species will be considered as a kind of *Birth-and-Death* process, which is a Markov process (i.e., a stochastic event will correspond to each time instant). The case to be studied is that in which there are only three possibilities for each individual at each particular time instant: that the individual reproduces, which implies that the total number of individuals of the species is increased by one unit, or, on the contrary, the individual dies, which means that the total number of individuals of the species is decreased by one. Finally the individual can continue unchanged after that time instant.

The purpose of this section is to present a stochastic resolution of the model in order to take into account the random nature of the demography. To this end, a specific resolution method, the Gillespie algorithm, will be presented and particularized for the analysis of the aforementioned *Birth-and-Death* process.

3.1 Birth and Death Process

For this part of the study the interest is in describing a stochastic model that works as the microscopic analogue of the logistic equation, which, as has been aforementioned, is the simplest form of the Lotka-Volterra model.

It is worth mentioning that, when introducing the logistic equation, (2), x was used as a variable whose meaning depended on the units used. In the current case, to link with the stochastic model, it will be set as the number of individuals in the population. Therefore, it is

16

renamed as N leaving equation (2) as follows:

$$\frac{dN(t)}{dt} = N(t)(r + aN(t)). \tag{15}$$

Then, the stochastic model considered to simulate the single species case is the *Birth-and-Death Process*. This scheme is an example of the use of a master equation in the context of population dynamics. The master equations are differential equations that are used to describe the probabilities' evolution for Markov processes for systems that jump between states in continuous time. Their use is emphasized whenever the number of possible states is discrete; in the current case the possible states are $N = 1, 2, 3, ...$ [12].

The aforementioned *Birth-and-Death Process* describes how each individual can reproduce, giving rise to another one with a rate of b_0, or, on the contrary, die with a rate of $(d_0 + aN)$. Then, in this process the number of individuals in a species can change in the next two different ways at each time interval, $[t, t + dt)$:

$$\begin{cases} N \longrightarrow N + 1 & \text{with a global rate of } Nb_0, \\ N \longrightarrow N - 1 & \text{with a global rate of } N(d_0 + gN), \end{cases}$$

where N represents the number of individuals in the current state and b_0 is the birth rate. Finally, it is worth mentioning that the death rate is chosen so as to have linear growth, $(d_0 + gN)$. It is established this way because the death must gain importance as the number of individuals increases, in order to obtain a logistic behavior.

Regarding the process' master equation, it is useful to compute the stochastic mean and quantify the stochastic fluctuations. To write it, it is necessary to determine the total probability: $P(N; t + dt)$. There are three contributions to $P(N; t + dt)$, according to the event that took place in the time-step, $[t, t + dt)$. The first corresponds to the case in which during the time interval there are N individuals and they neither reproduce nor die; this probability is given by the product of the probability to not disappear, $(1 - N(d_0 + gN)dt)$, and the probability to not reproduce, $(1 - Nb_0dt)$. The second is the case in which there are $(N + 1)$ individuals at time t and the event is death, here the probability is $(N + 1)(d_0 + g(N + 1))dt$. Finally, the last possible event occurs when there are $(N - 1)$ individuals and the event that takes place is the reproduction, the probability for this situation is given by $(N - 1)b_0dt$. The combination of these probabilities when $dt \to 0$ results in the next expression for the *Birth-and-Death Process*' master equation :

$$\frac{\partial p(N; t)}{\partial t} = -N(b_0 + d_0 + gN)p(N; t) + (N+1)(d_0 + g(N+1))p(N+1; t) + (N-1)b_0p(N-1; t). \tag{16}$$

The analytical treatment of master equations presents several difficulties, this leads to the need to resort the numerical simulations of the underlying stochastic process [12]. In this project the system will be described by the Gillespie Algorithm.

3.2   Gillespie Algorithm

The Gillespie Algorithm consists in a extraordinarily simple and effective implementation of the numerical algorithm to simulate a stochastic process and its associated master equation [12]. The stochastic process consists in a series of jumps in which the system composed by N particles changes to $N - 1$ or $N + 1$ particles. To keep this section more general, let's consider the case in which we can have jumps between a state of N particles to a state of M particles, being the corresponding jump rate (probability of change per unit of time) called $\omega_{N \to M}$.

To simulate the system there are some general steps that need to be performed. It is assumed that, at the initial time, t_0, the system is in the state with N_0 particles. The first step is to compute the rate of escape from the initial state to any other state $M \neq N_0$. This is given by $W_{N_0} = \sum_{M \neq N_0} \omega_{N_0 \to M}$. Then, the time interval between the current jump and the next one, $t_{N_0 \to N_1}$, is a random exponentially distributed variable with mean $W_{N_0}^{-1}$. This can be generated as follows:

$$t_{N_0 \to N_1} = \frac{-\ln u_0}{W_{N_0}}, \tag{17}$$

where u_0 represents a random number uniformly distributed in the interval (0,1).

The time of the next jump is given by: $t_1 = t_0 + t_{N_0 \to N_1}$, and therefore, it remains to determine the state to which it will jump to. Recalling that $\omega_{N \to M} dt$ represents the probability of jumping from state N to state M in the time interval $(t, t + dt)$, $W_N dt$ is the probability attributed to jumping to any state during that same time interval [12]. Thus, the probability of reaching state $M \neq N_0$ knowing that there has been a jump, $p_{N_0 \to M}$, is given by:

$$p_{N_0 \to M} = \frac{\omega_{N_0 \to M}}{W_{N_0}}. \tag{18}$$

In the present case, in which the jumps can only increase or decrease by one the number of particles, there are only two possibilities for M in (18): $N_0 + 1$ and $N_0 - 1$ and, using the expression for the birth and death rates, (18) becomes:

$$p_{N_0 \to N_0 + 1} = \frac{N_0 b_0}{N_0 b_0 + N_0 (d_0 + g N_0)} \ , \quad p_{N_0 \to N_0 - 1} = 1 - p_{N_0 \to N_0 + 1}. \tag{19}$$

To implement the sampling with this probability, another uniformly distributed random number within the interval $(0, 1)$, v_0, is generated and used to establish the condition that an event has occurred. So that for each time interval the number of individuals will vary according to:

$$N(t_1 + dt) = \begin{cases} N(t_1) + 1 & \text{if } v_0 < p_{N_0 \to M}, \\ N(t_1) - 1 & \text{if } v_0 \geq p_{N_0 \to M}. \end{cases}$$

The algorithm is then implemented, and iterations are carried out until it reaches the maximum time established.

3.3   Method Application

Finally, the Gillespie algorithm will be particularized for the given parameters. But first, it is necessary to select the parameters of the equation so that the average variation of the number of individuals, which is given by:

$$\frac{d\langle N \rangle}{dt} = \langle b_0 N - N d_0 - g N^2 \rangle = (b_0 - d_0)\langle N \rangle - g \langle N^2 \rangle, \tag{20}$$

behaves like the logistic equation, (15). On the one hand, although they are not exactly equal, for cases where the fluctuations are small one can make the approximation:

$$\langle N^2 \rangle \approx \langle N \rangle^2,$$

so that equation (20) is left as:

$$\frac{d\langle N \rangle}{dt} = \langle N \rangle (b_0 - d_0 - g\langle N \rangle), \tag{21}$$

which turns to be like equation (15) identifying N with the average $\langle N \rangle$, and the parameters $r = b_0 - d_0$ and $g = -a$.

Therefore, it has been shown that there are stochastic models that give rise to the logistic equation itself. These are all models where the value of the $(b_0 - d_0)$ term would give an approximation to the same value of r.

Now it is a matter of choosing some combination to perform the simulations. On average, almost all of them behave in the same way (as long as the fluctuations are small), but as far as fluctuations (e.g. variance) are concerned they are generally larger the larger b_0 and d_0 are.

A possible and simple choice is to define $d_0 = 0$, so the birth and death global rates turn to be:

$$\begin{cases} N \longrightarrow N + 1 & \text{with a global rate of } rN, \\ N \longrightarrow N - 1 & \text{with a global rate of } -aN^2. \end{cases}$$

Note that it is required that $r > 0$ and $a < 0$ to keep positivity of the rates.

Then, all that remains is to apply Gillespie's algorithm using the parameters that have just been established.

Once the algorithm has been implemented, following the above described steps, all that remains is to decide the simulation parameters. Then, a maximum time of $t_{\max} = 100$ is set, as it is considered sufficient time for the dynamics of the system to have developed. Additionally, the number of simulations has been established to be 1000 because it is a quantity that allows a satisfactory degree of accuracy to be maintained without the computational load being too high.

To extract as much information as possible from the implemented program, the intention has been to make simulations for different values of the algorithm's parameters. Then, in order to illustrate the algorithm's performance in describing the trajectories, some of them have been plotted. It has been established that 10 simulations should be plotted instead of all 1000, because if all of the simulations were to be shown, the results would be visually less clear. In addition, it has been decided to represent as well the analytical solution of the logistic equation to indicate the location of the fixed point of the equation, and thus facilitate the analysis of the results.

As mentioned above, the expected result is that the larger the r the smaller the relative fluctuations, so that the approximation $\langle N^2 \rangle \approx \langle N \rangle^2$ becomes better and then the stochastic simulation becomes more similar to the deterministic dynamics. In Figure 11 four simulations for a fixed value of $a = -0.01$, and the values $r = 0.20, 0.45, 0.70, 0.95$, and an initial condition of $N_0 = 1$ are presented. As predicted, the results show that as the value of r increases the intensity of the relative fluctuations decreases considerably.
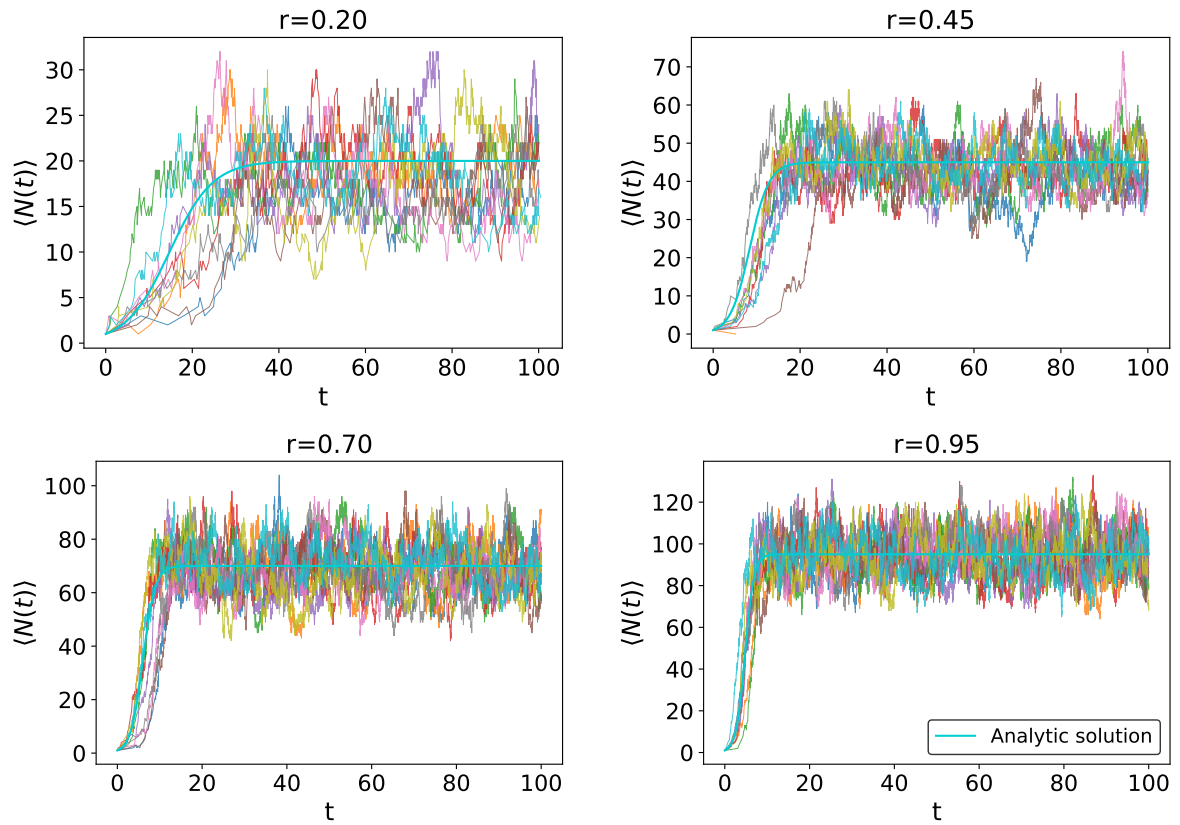
Figure 11: Four simulations showing 10 trajectories out of 1000 performed for the representation of the stochastic process corresponding to each of the four values of r represented. The analytical solution is shown in all the plots, although the legend is included only in the fourth one. The initial condition is $N_0 = 1$.

4   Comparison between Stochastic and Deterministic Resolution

When attempting to describe real systems by means of mathematical models, the objective is to formulate equations that reflect the perception obtained through observation of reality, and that are therefore capable of describing the dynamics of the system under study. There are several ways of analyzing these systems. On the one hand, there is the deterministic resolution, which has been developed in Section 2. It is based on a mathematical model that provides the state of a system at a certain time provided that the state it was in at the previous time is known. On the other hand, there is the stochastic resolution, which is presented in Section 3. Stochastic models are those models in which the prediction of the evolution of the system can only be made in terms of probabilities.

Then, in the previous sections the Generalized Lotka-Volterra model has been approached from the deterministic and stochastic standpoints. Therefore, in this last part of the project, taking into account that most of the events that govern ecosystems are stochastic in nature, it is interesting to compare the data obtained with the deterministic solution with the stochastic results obtained with Gillespie's algorithm.

So far it has been proven that, for the Lotka-Volterra model to represent the desired dynamics, the parameters that make up the model must be exactly known. Consequently, if the aim is to study the dynamics of realistic systems, in which demography is governed mainly by stochastic processes (i.e., it is represented by random magnitudes that vary with time), it is of interest to approach the problem from a stochastic standpoint.

In order to compare the deterministic results with the stochastic ones, the average of the 1000 trajectories performed with Gillespie's algorithm for each of the values of r has been plotted. In Gillespie's algorithm each time step is random, this complicates the calculation of the average of the trajectories, since it is difficult to take the same interval for each one. For this reason, considering that M is the number of trajectories performed, when they are all computed the time is discretized in K bins with width $h = t_{\max}/K$. With this procedure, all the trajectories are discretized in time in the same way. Then, the value of the trajectory corresponding to each bin is computed by performing weighted averages of the different values that $N(t)$ takes in each bin. This is given by:

$$x(k) = \frac{1}{h}\left(\sum_{i=i_{\min}}^{i_{\max}-1} n(t_i)(t_{i+1} - t_i) + n(t_{i_{\max}})(t_k + h - t_{i_{\max}}) + n(t_{i_{\min}-1})(t_{i_{\min}} - t_k)\right), \quad k = 1, ..., K,$$

(22)

where the index i denotes the different values of t included in each bin, and $t_k = kh$. The sum is done only when $i_{\max} \geq i_{\min}$. Then, the average is computed as:

$$\langle n(t_k)\rangle = \frac{1}{M}\sum_{j=1}^{M} x_j(k), \quad k = 1, ..., K. \tag{23}$$

From these equations, the average of each bin is obtained, which allows to plot the average of the trajectories calculated with the algorithm as a function of time. The parameters have been set to be $K = 500$ and $t_{\max} = 100$, which implies that $h = 0.2$. This is a valid value since it does not involve too many points in the plots, but at the same time it does not lose accuracy since it is satisfied that $\langle t_{i+1} - t_i\rangle \ll h$.

Four comparisons between the deterministic results and the stochastic approach for four different values of r are presented below. As a representation of the deterministic solution, the

analytical solution of the logistic equation already calculated in Section 2 is shown in each figure, and as concerns the stochastic solution, the average of the stochastic simulations is presented, calculated as described above. Then, in Figure 12 the same values of r as in the previous section have been plotted in order to complete the information from the simulations in Figure 11. In conclusion, as anticipated in the previous section, the simulations show that as the value of the parameter r increases, the results obtained using Gillespie's Algorithm become more similar to the deterministic model. The initial condition used in both models is $N_0 = 1$ and the parameter $a = -0.01$.
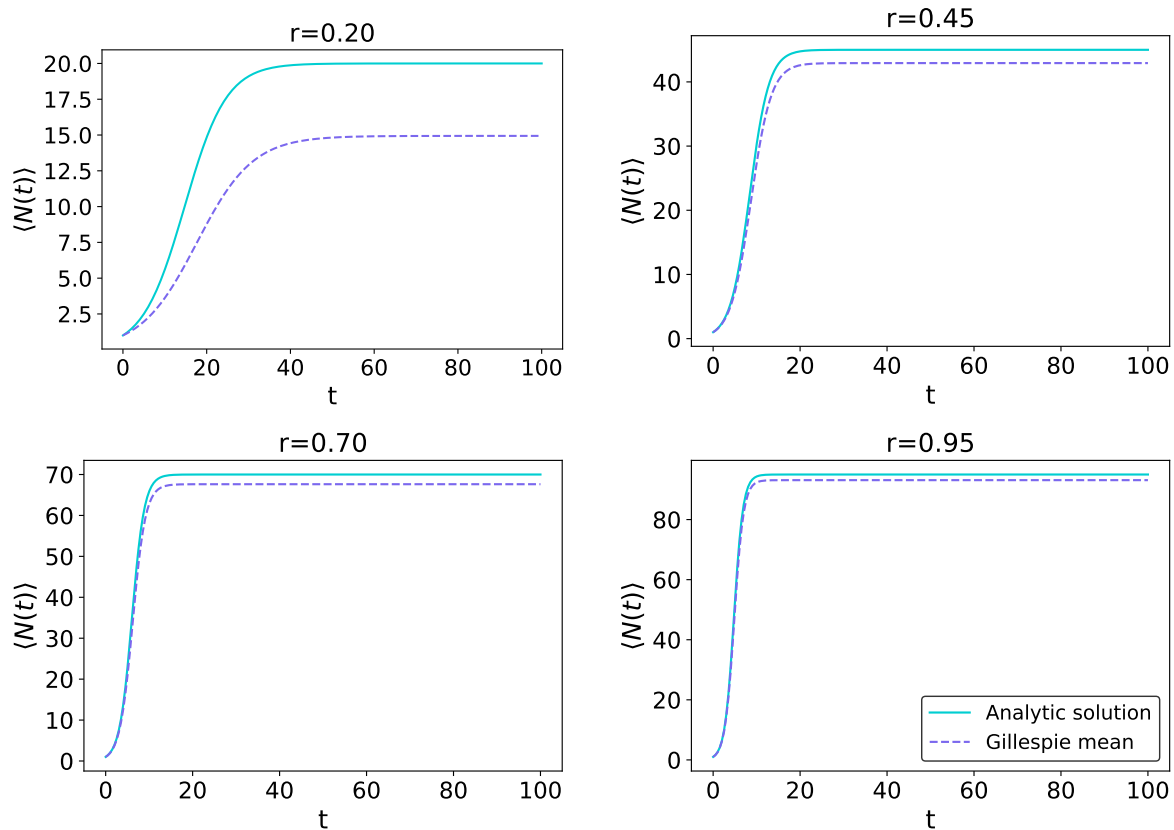

Figure 12: Four simulations comparing the mean of 1000 trajectories performed with the *Gillespie Algorithm* and the deterministic solution. The legend is included only in the fourth figure but is common to all of them. The initial condition used in both models is $N_0 = 1$.

To make these conclusions more visual, the same comparisons will be presented below, but for extreme values of the parameter r. Figure 13 shows the difference in accuracy of the algorithm according to the value used for r. In the case where r is very close to 0, the mean of the trajectories deviates a lot from the analytical solution of the logistic equation. It can be clearly observed how, from the first instants of the simulation, the number of individuals of the species does not manage to increase, stagnating at the same value, which does not correspond to the fixed point. In contrast, it is observed that the results corresponding to a high value of r are almost perfectly adapted to the analytical solution.
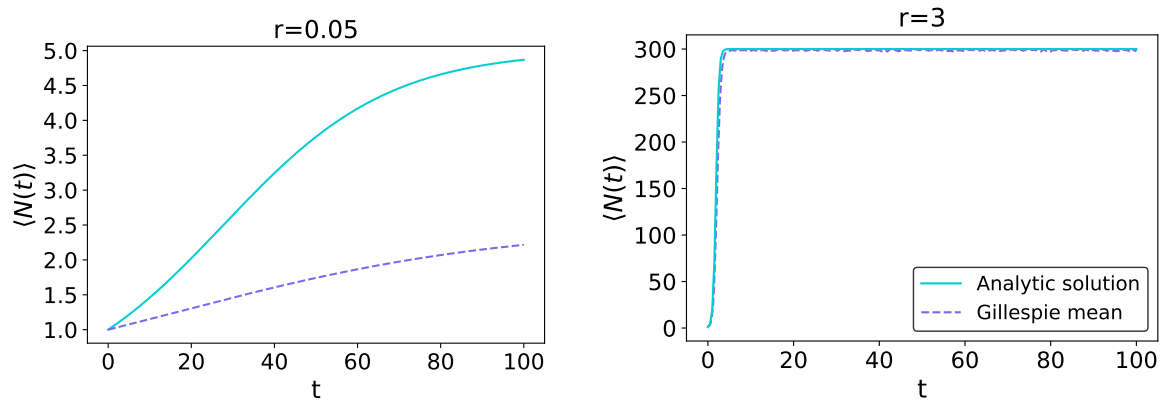
Figure 13: Two simulations comparing the mean of 1000 trajectories performed with the *Gillespie Algorithm* and the deterministic solution. The legend is included only in the second figure but is common to both of them. The initial condition used in both models is $N_0 = 1$.

A useful method to analyze the behavior of the algorithm is to create a comparative graph between the deterministic value of the logistic equation and that obtained by averaging the times of the average trajectory already in the asymptotic state, i.e., the values belonging to the time range $[60, 90]$, for different values of the growth rate, r. Therefore, in order to make a graph that clearly represents the obtained results, several simulations have been carried out for different values of r, all of them within a range of values between 0 and 1. The behavior of the stochastic simulations is thus visible, since it has been found that for high values of r the stochastic results are practically the same as the deterministic ones, and what is of interest to see now is the behavior of the algorithm for small values of r. The comparison has been plotted in Figure 14.
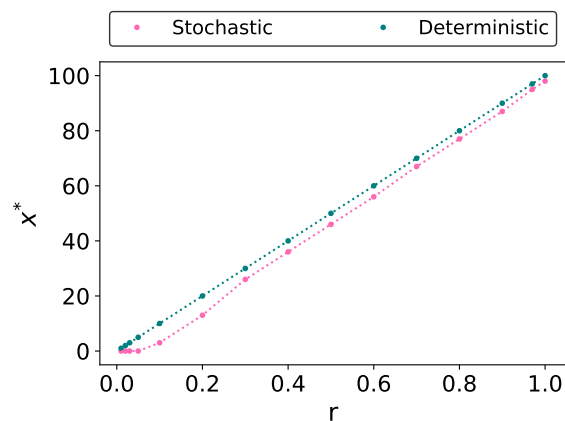

Figure 14: The figure compares, for different values of r, the long-time average population given by the *Gillespie Algorithm* with the deterministic long-time population given by the logistic equation, $x^* = -r/a$ $(a = -0.01)$.

As expected, the results show that Gillespie's algorithm responds in the same manner as the deterministic model above a certain value of r below which the results differ increasingly. Moreover, the differences between the two methods are visible from the start. This is due, among other reasons, to the fact that some of the stochastic simulations will eventually become extinct. Then, what happens for small values of r is that as this value decreases, the fewer the individuals in the species, and therefore, the easier it is for stochastic trajectories to end in extinction.

5 Conclusions

In general terms, this work has focused on the analysis of the dynamics described by the Generalized Lotka-Volterra in model ecosystems. This model, although quite simple, is capable of describing population dynamics, taking into consideration the factors of trophic interaction between species; thus making the results more realistic. The analysis has been carried out from two different perspectives: from the deterministic point of view, i.e., the description of the state of the system at a certain time based on prior knowledge of its state at a previous time, and considering demographic fluctuations by means of a stochastic method.

The deterministic model has been developed starting from the logistic equation. The solution of this equation has been analyzed, and one of the most important concepts in this work, the fixed point of the system, has been presented for the first time. It has been proved that the solution of this equation presents an exponential growth (or decrease) until the dynamics is fully developed, which is when the function reaches its fixed point. These results alone are not significantly representative, but they serve to establish the basis for the subsequent analysis, and highlight the importance of the study of the systems' stability. Thus, once the theory of stability has been presented, the need arises to test the validity of its statements. Existing parameterizations have been used to perform the stability analysis of the systems described by these parameters. In the description of biological models, the concept of feasibility has been presented, which establishes whether, given certain parameters, the fixed point in which all species coexist will be biologically feasible or not.

Once the concept of Local Stability has been exploited, the Global Stability analysis proceeds. Where it has been verified, by means of an existing parameterization, that the results of the Global Stability analysis of a system have no unbounded trajectories, and that they are independent from the initial conditions imposed. So far, specific parameterizations have been used for the description of known systems. But this is not viable in systems composed of many species, therefore, the stability criteria established by the random matrix theory are presented. On the one hand, there is the Circular law, which is defined in section 2.4.1. Two matrices have been constructed using two different distributions for the assignment of values of the matrix entries. And it has been proved that the eigenvalues of this matrices form a disk whose center is given by the value of the diagonal of the matrix and, in addition, universality has been proved. The same occurs in the case of the elliptic law, where it has also been proven that the stability of the system depends strongly on the correlation parameter, so that when this is negative, the probability that the system is stable increases considerably. Then, the conclusion drawn in this section is that a large ecological community will almost invariably be unstable, which possibly leads to extinctions.

Regarding the resolution by stochastic methods, an analogy has been made between the logistic equation and the Birth-and-Death process. The resolution of this process has been carried out by implementing Gillespie's Algorithm. Thus, by performing 1000 trajectories of the process, for a fixed value of the parameter a and various values of r, it has been verified that, indeed, the analogy was well defined, i.e., the mean of the trajectories behaves like the logistic equation.

Finally, once the processes have been presented and analyzed, the results are compared. The deterministic solution and the average of the trajectories performed by Gillespie's Algorithm, once the system dynamics had been developed and the system had stabilized at its fixed point, have been plotted. These plots show that the fixed point of the stochastic mean is lower than that of the deterministic solution. This is mainly due to the fact that in the stochastic model there are more extinctions because of fluctuations in species abundances. In addition, it has

been confirmed that the higher the value of r the more the results of both methods assimilate. Finally, as a corroboration of these ideas, a plot of the value of the fixed point, x^*, as a function of r has been drawn comparing the deterministic values with the stochastic ones. In this it has been found that the stochastic solutions die out more frequently as r decreases.

As future work, it would be good to extend the study to new situations. For example, instead of considering an ecosystem in which species are in the ecosystem from the beginning, analyze ecosystems in which, as time goes by, species are added. Furthermore, with respect to the stochastic approach, it would be interesting to extend the range of species studied to more than one, thus being able to simulate the interaction between species.

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