

An evolutionary theory model using Lotka–Volterra equations

Author: Adrià Garcés Ortiz.*

Facultat de Física, Universitat de Barcelona, Diagonal 645, 08028 Barcelona, Spain.

Advisor: M. del Carmen Miguel López

Abstract: Ecosystems, influenced by a large number of factors, are in constant evolution. Climate, seasonal changes and anthropogenic interactions, for example, can induce changes that play a fundamental role while studying an ecosystem’s stability. Evolution, on the other hand, is a fundamental feature of ecosystems’ dynamics, as the appearance of fitter species may drastically alter how species interact with each other, which, consequently, may induce relevant changes in the ecosystem’s composition and structure. We propose a simple evolutionary model using the generalized Lotka–Volterra equations, and compare analytical results in the steady state with results obtained by simulating a competitive two species system altered by the presence of a new evolved species.

I. INTRODUCTION

Understanding how an ecosystem stabilizes itself through time is not a trivial matter and still remains a major open research challenge. Studying this process could help us, among other things, to quantify the effects of invasive species in an already stable ecosystem, or to characterize the mechanisms used by some species to gain a dominant role in an ecosystem, thus deepening our current understanding of natural selection rules and the theory of evolution.

Many mathematical models have been proposed in order to explain an ecosystem’s dynamics [1, 2]. Some of these models are deterministic, others are stochastic or mixed. Deterministic models apply to systems in which no randomness is involved, so that future states depend only on the initial condition and can be certainly predicted. On the other hand, stochastic models apply to systems in which randomness is involved. The future states now follow a random probability distribution that may be analysed statistically. Future states cannot be precisely determined in this case. Mixed models are just a mix of both.

Complex networks have also been used with the aim of portraying the natural complexity of ecosystems due to the species’ interactions [2, 3]. Quantification of results in the shape of analysable data in real ecosystems is not an easy task to do. Although not easy, experiments have been carried out in order to verify mathematical and theoretical models of ecology [3, 4].

The Lotka–Volterra equations need a special mention, since they have been studied deeply in order to understand ecosystem dynamics [1–9]. These equations are said to have a linear functional response, since they assume that individuals of a given species reproduce or die in a linear way when interacting with another species of the ecosystem [5, 6].

The complexity and highly coupled interactions in an ecosystem make these models hard to solve analytically.

Thus, the numerical implementation is the usual approach. Throughout this project we attempt to study the effect of the introduction of a new species into an ecosystem in order to understand the relevant parameters for an evolutionary theory model, considering the introduced species as the evolved of a previous species already living in the ecosystem. With that purpose in mind, we make use of generalized Lotka–Volterra equations including intra-specific, self-regulating, interactions and stochastic inter-species interactions. Our report is organized as follows: In section II we introduce the Lotka–Volterra equations and explain their main terms and the parameters involved. In section III we present our evolution model and derive some analytical stationary results, while in section IV we make simulations for a two species ecosystem in order to illustrate our analytical results. We finally present our main conclusions.

II. THE LOTKA–VOLTERRA EQUATIONS

Lotka–Volterra equations have been used to study the basic predator–prey models, as well as mutualist and competitive environments. A generalized formulation can be made for n interacting species. In this case we have n coupled ordinary differential equations that read

$$\frac{dx_i}{dt} = x_i \left(r_i + \sum_{j=1}^n \alpha_{ij} x_j \right), \quad i = 1, \dots, n, \quad (1)$$

where $x_i(t)$ indicates the population abundance of the i -th species, $i = 1, 2, \dots, n$, at a given time t , r_i are the replication rates of each species, named growth rates for $r_i > 0$ and death rates for $r_i < 0$, and α_{ij} are the interaction coefficients. These α_{ij} make up a matrix known as interaction matrix, $A = (\alpha_{ij})$. The off-diagonal elements, α_{ij} for $i \neq j$, portray what is known as inter-specific interactions. They quantify the interaction between the j -th species and the i -th species. If $\alpha_{ij} > 0$, the existence of j benefits the growth of i (mutualist interaction), while if $\alpha_{ij} < 0$, it disfavors it (competitive interaction). The diagonal elements α_{ii} represent the intra-specific interactions. These need to be included when one considers same-species interactions,

*E-mail: adria.garces@gmail.com

which happen in a non–favourable way, $\alpha_{ii} < 0$, as pictured in the logistic equation. The solutions of equation Eq. (1) are positive, $x_i(t) \geq 0$, and live in what we know as phase space Ω , $x_i(t) \in \Omega$. The phase space trajectories can be drawn by taking out the dynamical parameter t .

A point $\mathbf{x}^* = (x_1^*, x_2^*, \dots, x_n^*) \in \Omega$ such that $dx_i(t)/dt = 0$, $\forall i = 1, \dots, n$, or, samewise,

$$x_i^* \left(r_i + \sum_{j=1}^n \alpha_{ij} x_j^* \right) = 0, \quad i = 1, \dots, n. \quad (2)$$

is called fixed point or steady state, since it makes the dynamics freeze. The fixed points, or steady states, are known as equilibrium solutions of equation Eq. (1). The stability of a fixed point with respect to small perturbations can be studied by linearizing the equations around the fixed point as stated in the Hartman-Grobman theorem [6]. This is done by computing the Jacobian at the fixed point, $J(\mathbf{x}^*)$. The eigenvalues of $J(\mathbf{x}^*)$ characterize the stability of the fixed point. Fixed points, in this case, are also positive, $x_i^* \geq 0 \forall i$.

One can go further and study the behaviour of ecological models when parameters take randomly distributed values. This idea was pioneered by May [7]. In this particular case, randomly distributed interaction matrices A are useful to understand local stability in large ecological communities and have been of huge interest in recent studies [8]. The most usual approach is taking $\alpha_{ii} = -d$, $d > 0$, and sampling random interaction matrices in which the off–diagonal elements (with probability C) follow a normal distribution, $\alpha_{ij} \sim \mathcal{N}(\mu = 0, \sigma)$, with zero mean (and zero otherwise), thus mixing competitive and mutualistic interactions.

Sampling with normal distributions helps with analytical results, which otherwise are hard to deal with. In this case, May proved that for n large the probability of existence of stable attractors is close to zero when the complexity, $K = \sigma\sqrt{nC} > d$. This is useful to study the maximum size of ecological communities [6, 7].

For our evolutionary theory model, we use the generalized Lotka–Volterra equations. In order to do so, we consider a competitive ecosystem ($\alpha_{ij} < 0 \forall i, j$), and a species we shall name primitive, i.e. x_p with $1 \leq p \leq n$. This species is selected as one that does not play a *dominant* role in the ecosystem (weak species). We have to understand a *dominant* species as one that prospers with advantage with respect to weak or primitive ones. This means, in this context, that it has a smaller stable population density, and a rather small replication rate, $r_p < r_i$, $x_p^* < x_i^*$ for $i \neq p$. With the purpose of understanding evolution, we introduce a new, *evolved* species, i.e. x_e , into the system of equations and make the system evolve until its new steady state to study whether the evolved species adapts to the ecosystem or not. We consider x_e to be the evolved species from x_p , and so fitter to the new environment, and thus with $r_e > r_p$ and smaller autoregulation term, $|\tilde{\alpha}_{ee}| < |\alpha_{pp}|$. In the following, we compare analytical results in stationary con-

ditions with simulations made for the particular case of two competitive species, a weak and a dominant species, which face the introduction of a third, fitter version of the weak species. Since we use a competitive ecosystem, the growth of the species is always bounded by logistic growth terms, so we avoid possible divergences.

III. INVASIVE DYNAMICS AND EVOLUTION

Consider an ecosystem made up of n –interacting species, governed by the Lotka–Volterra equations introduced in Sec. II. Let A be the interaction matrix associated to this ecosystem, which for practical purposes we shall name Ω from now on. For our competitive system, we will consider a symmetrical interaction, $\alpha_{ij} = \alpha_{ji}$. Let $\mathbf{r} = (r_1, \dots, r_n)^T$ be the reproduction rates of each species. Thus, the ecosystem’s dynamics is governed by

$$\left(\frac{dx_i}{dt} \right)_{\Omega} = x_i \left(r_i + \sum_{j=1}^n \alpha_{ij} x_j \right), \quad i = 1, 2, \dots, n. \quad (3)$$

where α_{ij} are the elements of the interaction matrix $(A)_{ij} = \alpha_{ij}$, and the subindex Ω denotes the equation governs the evolution of x_i in the ecosystem Ω . Let x_p , with $1 \leq p \leq n$, be the primitive species which will later on be replaced, or not, by its evolved analogue.

Once the ecosystem has reached the steady state, $\{x_1^*, x_2^*, \dots, x_p^*, \dots, x_n^*\} \in \Omega$, and since we have taken the primitive species x_p as non–dominant, we will have $x_p^* < x_j^*$ for a certain $j \neq p$. At this point, we introduce the evolved species, x_e , to the ecosystem Ω . We shall call this new ecosystem, the one including x_e , $\tilde{\Omega}$. The introduction of x_e to the new ecosystem plays a relevant role. Now we have a set of $n + 1$ coupled differential equations. This means the reproduction rate vector \mathbf{r}' is $n + 1$ dimensional, and the interaction matrix A' is $(n + 1) \times (n + 1)$ dimensional.

One can make a few assumptions on what values \mathbf{r}' and A' take. If we consider the ecosystem Ω is abundant in resources, one may acknowledge that the reproduction rates of the species living in Ω may not be altered by the introduction of x_e into the system. Thus, $\mathbf{r}' = (r_1, r_2, \dots, r_p, \dots, r_n, r_e)^T$, where r_e is the reproduction of the evolved species, $r_e > r_p$, and the remaining r_i ones, $i \neq e$, are the ones we had in Ω .

For the new interaction matrix, A' , one may assume that the interactions between species of the old ecosystem Ω do not change with the introduction of x_e , as done in [5]. A new interaction arises when x_e is introduced, the interaction of x_i with x_e , $\forall i \neq e$. Thus, the new interaction matrix shall be

$$A' = \left(\begin{array}{ccc|c} & & & \tilde{\alpha}_{1e} \\ & & & \vdots \\ & & & \tilde{\alpha}_{ne} \\ \hline \tilde{\alpha}_{e1} & \dots & \tilde{\alpha}_{en} & \tilde{\alpha}_{ee} \end{array} \right), \quad (4)$$

where A is the interaction matrix of the old ecosystem, $A = (\alpha_{ij})$. The dynamics of the $\tilde{\Omega}$ ecosystem will be described by

$$\left(\frac{dx_i}{dt}\right)_{\tilde{\Omega}} = x_i \left(r_i + \sum_{x_j \in \tilde{\Omega}} (A')_{ij} x_j \right). \quad (5)$$

Note that Eq. (5) is analogous to Eq. (3). However, the last one runs over all the species living in $\tilde{\Omega}$.

Given the dynamical evolution portrayed by Eq. (5), we study how the new steady state, including x_e , looks like. More specifically, we will focus on the steady states $x_p^*, x_e^* \in \tilde{\Omega}$. The new steady state for x_p and x_e will be given by the system of equations

$$\left(\frac{dx_p}{dt}\right)_{\tilde{\Omega}} \Big|_{x_p^*} = 0, \quad \left(\frac{dx_e}{dt}\right)_{\tilde{\Omega}} \Big|_{x_e^*} = 0, \quad (6)$$

which can be rewritten, using Eq. (5), as

$$\left\{ \begin{array}{l} x_p^* \left(r_p + \alpha_{pp} x_p^* + \tilde{\alpha}_{pe} x_e^* + \sum_{j \neq p, e} \alpha_{pj} x_j \right) = 0 \quad (7a) \\ x_e^* \left(r_e + \tilde{\alpha}_{ee} x_e^* + \tilde{\alpha}_{ep} x_p^* + \sum_{j \neq p, e} \tilde{\alpha}_{ej} x_j \right) = 0 \quad (7b) \end{array} \right. \quad (7)$$

The solutions to this system can be a set of zero and non-zero values for x_p^* and x_e^* , depending on the interaction matrix elements, the densities x_j , $j \neq p, e$ and \mathbf{r}' .

A. Coexistence of primitive and evolved species

Let the steady state $\{x_1^*, \dots, x_p^*, \dots, x_n^*, x_e^*\} \in \tilde{\Omega}$, be a set of zero and non-zero values. The coexistence of the primitive and the evolved species implies that their population densities in the steady state are greater than zero, $x_p^*, x_e^* > 0$. Plugging this into Eqs. (7) manifests that the terms in brackets must be zero. Thus, the non-linear system of equations becomes a linear one. If we now subtract the in-bracket terms and assume (for practical and formal purposes) $\alpha_{pp} = \tilde{\alpha}_{pe} = \tilde{\alpha}_{ep}$, we get

$$x_e^* = -\frac{1}{\alpha_{pp} - \tilde{\alpha}_{ee}} \left[r_p - r_e + \sum_{j \neq p, e} (\alpha_{pj} - \tilde{\alpha}_{ej}) x_j^* \right]. \quad (8)$$

We will use this approximation along the model. Imposing that $x_e^* > 0$, the condition

$$r_p - r_e + \sum_{j \neq p, e} (\alpha_{pj} - \tilde{\alpha}_{ej}) x_j^* > 0, \quad (9)$$

must be fulfilled, since $|\tilde{\alpha}_{ee}| < |\alpha_{pp}|$. In the same direc-

tion, one can find x_p^* , to obtain

$$x_p^* = -\frac{1}{\alpha_{pp}(\tilde{\alpha}_{ee} - \alpha_{pp})} \left[\tilde{\alpha}_{ee} r_p - \alpha_{pp} r_e + \sum_{j \neq p, e} (\tilde{\alpha}_{ee} \alpha_{pj} - \alpha_{pp} \tilde{\alpha}_{ej}) x_j^* \right], \quad (10)$$

from which the condition

$$\tilde{\alpha}_{ee} r_p - \alpha_{pp} r_e + \sum_{j \neq p, e} (\tilde{\alpha}_{ee} \alpha_{pj} - \alpha_{pp} \tilde{\alpha}_{ej}) x_j^* > 0 \quad (11)$$

must be fulfilled. The coexistence of x_p and x_e relies on these two strong boundaries, which get harder as we consider that the steady states x_j^* do depend on the interaction matrix and the reproduction rates, $x_j^* = x_j^*(A', \mathbf{r}')$, $\forall j \neq p, e$.

B. Extinction of the primitive species

Another possible solution of the system of equations Eqs. (7) is the extinction of the primitive species and the incorporation of the evolved one, so that $x_p^* = 0$, $x_e^* > 0$. Solving Eqs. (7) for this case returns as with

$$x_e^* = -\frac{1}{\tilde{\alpha}_{ee}} \left[r_e + \sum_{j \neq p, e} \tilde{\alpha}_{ej} x_j^* \right]. \quad (12)$$

Note that if $x_j^* = 0$ for all $j \neq p, e$, we get the steady state of a logistic equation, $x_e^* = -r_e/\tilde{\alpha}_{ee}$. Imposing $x_e^* > 0$ this time, we get

$$\sum_{j \neq p, e} |\tilde{\alpha}_{ej}| x_j^* < r_e, \quad (13)$$

since the interaction matrix elements are strictly negative for our competitive system ($|\cdot|$ denotes the absolute value). Condition (13) is easily fulfilled when the competition between the evolved species and the environment excluding the primitive one, $|\tilde{\alpha}_{ej}|$, $j \neq p, e$, is relatively small, when r_e is big enough, and/or when the ecosystem is not strongly populated with biodiversity, i.e. when not many terms x_j^* contribute to the sum. In this case, we say x_e has incorporated itself to the ecosystem. Not fulfilling the condition, i.e. strong competition with relatively small r_e and strong biodiversity, would benefit x_p , which would jump out of extinction.

C. Failure of the evolved species

If the evolved species disappears in the steady state, i.e. $x_e^* = 0$, we say it has failed to incorporate itself into the ecosystem. The steady state is governed by the dynamics portrayed in Eq. (5),

$$x_i^* \left(r_i + \sum_{x_j \in \tilde{\Omega}} (A')_{ij} x_j^* \right) = 0, \quad i = 1, \dots, n, e. \quad (14)$$

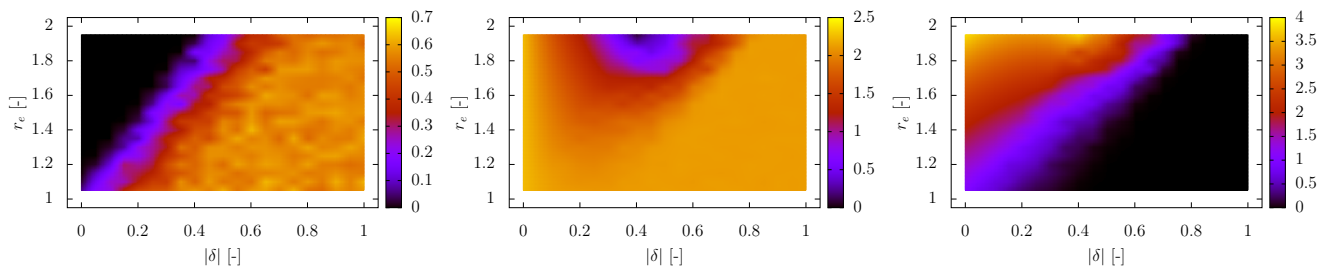


FIG. 1: Heatmaps of the average steady state abundance for each species in the space of parameters (δ, r_e) . Left: Weak species. Middle: Dominant species. Right: Evolved species.

Imposing $x_e^* = 0$, the terms of the sum including the interaction between x_i and x_e vanish, and since A' has the shape portrayed in equation Eq. (4), for $i, j = 1, \dots, n$, we have $(A')_{ij} = (A)_{ij} = \alpha_{ij}$. Thus, the last one becomes

$$x_i^* \left(r_i + \sum_{j=1}^n \alpha_{ij} x_j^* \right) = 0, \quad i = 1, \dots, n, \quad (15)$$

which is actually the system of equations for the steady state of the ecosystem Ω , governed by equation Eq. (3). Hence, the failure of x_e to introduce itself to the ecosystem leaves unaltered the steady state of the old one, $\{x_1^*, \dots, x_n^*\} \in \Omega$. Once reached the steady state in Ω , the introduction of x_e , if it fails, alters the population densities just for them to travel back to their original steady state. Thus, the new steady state cannot depend on r_e or $\tilde{\alpha}_{ej}$.

IV. SIMULATION OF TWO SPECIES ECOSYSTEMS

To analyze the formal stationary results derived in Sec. III, we numerically integrate the equations for a two species ecosystem using a simple Euler method. We let the system evolve until it reaches its steady state, and then introduce the *evolved* species.

With this aim, we first generate a symmetric, random interaction matrix A for our two species ecosystem, taking $\alpha_{ii} = -1/r_i$, so that only the competitive term is a randomly distributed variable, which follows a uniform distribution between 0 and -1 , $\alpha_{ij} \sim U(0, -1)$.

We select the random interaction matrix A such that the achieved steady state consists of two non-negative values, $x_w^*, x_d^* > 0$ that verify $x_w^* < x_d^*$ when we fix $r_p = 1$ and $r_d = 1.5$. We can identify the weak species x_w as the primitive one, and x_d as the dominant. We let them evolve from their initial condition up until they reach their steady state and then introduce the evolved species x_e with reproduction rate $r_e \in (1, 2)$. In order to generate the new interaction matrix, we take into account the assumptions made in Sec. III. Thus the new interaction matrix becomes

$$A' = \begin{pmatrix} w & b & w \\ b & d & \delta \\ w & \delta & e \end{pmatrix},$$

where $w = -1/r_w$, $d = -1/r_d$, $e = -1/r_e$ and b is randomly distributed. Note that the parameter δ corresponds to the terms $\tilde{\alpha}_{ej}$, $j \neq p, e$. Here, we consider $\delta \in [-1, 0]$. We let the new system evolve until it reaches a new stationary regime and report the average behaviour after 75 realizations of the dynamics for each value of the model parameters r_e and δ .

Heatmaps in Fig. 1 show the averaged steady state abundances of x_w , x_d and x_e for different values of δ and r_e . We can see the survival of x_w is granted for strong enough competition $|\delta|$ as r_e gets bigger. The condition relaxes when r_e is fairly small. Oppositely, x_w goes extinct for small $|\delta|$ when r_e is small, and the condition relaxes as r_e gets bigger, going extinct for a wider range of $|\delta|$, just as mentioned in Sec. III B. Fluctuations in the weak species steady state abundance are very apparent in this case. Moreover, one can see that at the extinction transition boundary, there is a linear relationship between r_e and $|\delta|$. On the other hand, we can see that fluctuations in the steady state abundance of the dominant species x_d for big $|\delta|$ and r_e are much smaller. We shall also emphasize that for $r_e < r_d$ it seems to be almost constant, whereas for $r_e > r_d$ the steady state starts to decrease. Particularly we can see how it decreases as r_e gets higher and, surprisingly, when $|\delta| \sim 0.5$ and $r_e \sim 2$, the dominant species can even go extinct. This tells us the introduction of x_e cannot only replace x_w , but also make other, more dominant, species go extinct. Finally, we can see how the survival of x_e is granted, as mentioned in Sec. III B, for small competition $|\delta|$, and the condition relaxes as r_e gets bigger. The failure of x_e , as we can see takes a wide range of values. The extinction transition boundary again seems to imply a linear relation between the two parameters. However, another transition can be appreciated which seems to be linear for small $|\delta|$, and ends up curving itself. The bright spot in Fig. 1 (right) corresponds to a peak of the population density x_e around $(r_e \sim 2, |\delta| \sim 0.5)$. This tells us that the x_e is responsible for the relevant decrease of the former dominant species' abundance, replacing it in its dominant role in this range of parameter values.

As mentioned in Sec. II, we can also see that the growth of every species involved is limited by its corresponding logistic term, $\langle x_i^* \rangle \leq -r_i / \alpha_{ii} = r_i^2$. Likewise, note that for our parameter range, we can't see the si-

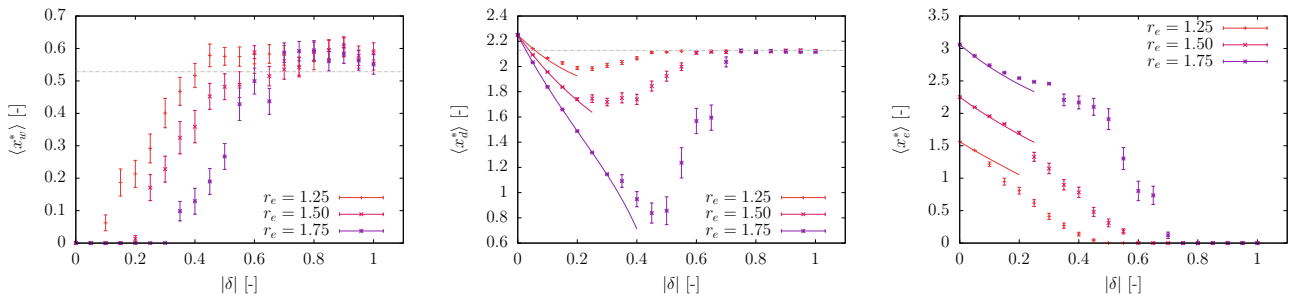


FIG. 2: Average steady state abundance for each species in the space of parameters (δ, r_e) . Left: Weak species. Middle: Dominant species. Right: Evolved species.

multaneous extinction and failure of both x_w and x_e . Between the extinction of x_w and the failure of x_e we can see a transition region that exhibits large fluctuations. Indeed, in this region, some repetitions take us to extinction of x_w , while the others to the failure of x_e , hence the fluctuations on the average steady state.

In Fig. 2 we also represent the average steady state of each species as a function of δ , for certain values of r_e , as well as its standard deviation. As shown in Fig. 1, we see that in order for x_w to survive, $|\delta|$, i.e. the competition between the evolved and the dominant species, needs to be stronger as r_e grows. Then its population density seems to increase in the linear way we already mentioned before, to reach a stable steady state, that, apparently does not depend on r_e nor on δ , as mentioned in III C. Likewise, when x_e fails to introduce itself for large enough $|\delta|$, the steady state abundance x_d^* does not depend on r_e , nor on δ . The dashed lines (left and middle) represent the theoretical average steady state and have been calculated using results from Sec. III C. The adjusted theoretical curves for small $|\delta|$ values have also been obtained from the results of Sec. III B, for the extinction of the primitive species, x_w , in this case. Theoretical curves have also been calculated in this case for x_e . Here we can see there is a little bump for $r_e = 1.75$, and around $|\delta| \sim 0.5$. As discussed above, this behaviour signals the extinction of the original dominant species at large enough values of r_e .

V. CONCLUSIONS

Following previous work on synthetic biological communities and invasion dynamics [5], we have implemented a model to study the evolution and coexistence of primi-

tive and evolved species in a competitive ecosystem. We have determined the conditions under which (i) both species coexist, (ii) the weaker species extinguishes or (iii) the evolved species fails to incorporate itself, as a function of the relevant parameters characterizing the ecosystem interactions. Strong biodiversity seems to disfavour the inclusion of new species into the ecosystem, as reported in [9], and stochasticity plays a major role on the steady state abundances giving rise to important fluctuations. We have also seen how our formal results describe the behavior of a two species ecosystem that faces the introduction of an evolved species, giving us accurate estimations of the regions corresponding to the extinction of x_w and the failure of x_e as a function of the model parameters r_e and δ .

In conclusion, our model, relying on a few assumptions, is able to reproduce the rich variety of behaviors observed in diverse ecological communities, and is able to give rise to extinction and integration failure phenomena reported in real invasive dynamics. Future work could be done with the aim of studying the influence of the size of the community in order to extract more information from our analytical results, and to characterize more deeply the transition between extinction and failure.

Acknowledgments

I would like to thank Dra. M. del Carmen Miguel López for the suggestions, help and guidance throughout this work. I would also like to thank Ot Garcés, David March and Kader Morkoç for their contributions and support. And lastly, I would like to thank my family for the unconditional support.

-
- [1] V. Gertsev and V. Gertseva, *Ecological Modelling* **178**, 329 (2004).
 - [2] G. Greenbaum, O. Hoffman, O. Shalev, and Y. R. Zelnik, *Israel Journal of Ecology and Evolution* **61**, 67 (2015).
 - [3] J. Bascompte, *Basic and Applied Ecology* **8**, 485 (2007).
 - [4] G. Losapio, J. Bascompte, *et al.*, *Ecology* **102**, e03243.
 - [5] V. Maull and R. Solé, (2021), 10.1101/2021.07.05.451200.
 - [6] M. Taberner, “Coexistence of species in complex ecological communities,” TFG, U. de Barcelona (2021).
 - [7] R. M. May, *Nature* **238**, 413 (1972).
 - [8] B. Goh and L. Jennings, *Ecological Modelling* **3**, 63 (1977).
 - [9] T. J. Case, *Proceedings of the National Academy of Sciences* **87**, 9610 (1990).