

Noise induced phenomena in ecological models

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Abstract: Understanding population dynamics, and in particular, population cycles is one of the central issues in ecology. In this work we study noise induced phenomena in generalized Lotka-Volterra ecological models and we show how a stochastic model for population dynamics can give rise to periodic cyclic behaviour in the presence of intrinsic noise. We will show how the intrinsic noise in a prey-predator dynamics including intra-specific, or logistic auto-regulatory, interactions gives rise to a resonant frequency in the power spectrum characterizing the system evolution, but at the same time, we show that there are other types of interactions among species where a resonant frequency does not appear. Furthermore, we analyze the effects of random transport between different ecological patches or metapopulations and see that cyclic behaviours can appear, if a prey-predator dynamics is imposed, or disappear.

I. INTRODUCTION

Mathematicians and physicists have developed over the years many models for studying population dynamics. These models are usually dynamical models that describe the temporal evolution of individuals or their corresponding spatial-temporal density. In the context of ecosystem modeling population dynamics is challenging because of the large number of coexisting species, as well as the multiplicity of interactions between them. The most common interactions considered when modeling ecosystems are prey-predator, mutualistic and competitive interactions. The later ones indicate species that either help each other to survive or that compete for the same resources. Real ecosystems are complex networks where species can interact with each other in multiple ways. However, to better understand the evolution of an ecological system and the effects that the diverse interactions can have on its stability and diversity, it is convenient to focus the study of population dynamics on systems with a relatively low number of species.

One of the most well-known and simple models in population dynamics is the Lotka-Volterra model, a deterministic model that attempts to capture the behaviour of predator-prey systems [1]. Although this model describes a simple situation it has the advantage that can be easily generalized to populations of N species and accommodate the three main types of interactions already mentioned. Moreover, the prey-predator Lotka-Volterra model also has the peculiarity that gives rise to oscillatory dynamics and therefore to population cycles.

Understanding and explaining the causes for population cycles is a central issue in ecology [2]. There are many hypothesis on the subject but no clear answers. Some of the hypothesis used in this research area are the following: the presence of external cyclic effects, such as

climate, that are reflected in the animals' population; or genetic effects where it's proposed that the cyclic dynamics stem from the change in genetics, favouring the survival of animals with lower reproduction and/or survival rates when populations are dense, and higher reproduction and/or survival rates when populations are sparse. The Lotka-Volterra model suggests that cycles could result from predator-prey interactions. As this cyclic behaviour is also seen in equivalent systems such as host-pathogen or herbivore animals and plants.

However, the Lotka-Volterra equations without intra-specific or self-regulation terms don't give rise to stable cycles but to a center. Therefore the trajectories depend highly on the initial conditions and a small perturbation in the system can make them change, even reaching trajectories that cross the axis that will imply the extinction of one of the species [3]. As we know from observations, population cycles in nature are stable over time and space. Furthermore, when we add self-regulation terms into the model, which results in trajectories that collapse in an stable fixed point, the oscillations are lost. In order to regain the oscillations in the model, higher order terms need to be added to the deterministic Lotka-Volterra equations.

In this work we will study how we can recover the oscillations by simply considering the intrinsic stochasticity of the model. We will base our studies on a predator-prey model based on individual level interactions (ILM model) [4][5]. The deterministic Lotka-Volterra model doesn't take into account the intrinsic noise present in the system, like fluctuations due to the finite number of individuals in the system. The advantage of an stochastic model is that it allows us to study the noisy behaviour and compare it to the deterministic results. We will see how, in the prey-predator interaction, the fluctuations that arise from the ILM model are cyclic, indicating that population cycles can stem from the nature of the species interaction. Moreover, we will

also use the ILM model to study the fluctuations that appear in other types of interactions, mutualistic and competitive systems, along with systems with higher number of species N with different interaction patterns. Finally, we will examine how the oscillations of the system change when we consider the random transport of individuals between several metapopulations with different properties.

The structure of the report is the following: in Sec.II we go through the main properties of the Lotka-Volterra equations with and without the logistic term. In Sec.III we present the stochastic model and study the behaviour of prey-predator dynamics; and in Sec.IV we expand the stochastic model to describe other interaction patterns. In Sec.V we extend the stochastic model to study the behavior of some representative three species ecological chains to see whether some of our results can be generalized to higher number of species. Following the study of isolated systems, in Sec.VI we consider random transport between two metapopulations of similar or different composition. Finally, in Sec.VII we present our main conclusions.

II. DETERMINISTIC LOTKA-VOLTERRA EQUATIONS

The Lotka-Volterra model is a population model used to describe the evolution of ecological systems. The prey-predator model describes a system with a well-mixed environment where the prey, characterized by the density x , takes resources from it and gets eaten by the predator species whose density is given by y . A system of two non-linear equations describes the evolution of the population densities for this particular predator-prey interaction and has the form:

$$\begin{aligned} \frac{dx(t)}{dt} &= ax - bxy \\ \frac{dy(t)}{dt} &= cyx - dy, \end{aligned} \quad (1)$$

where a is the growth rate of the prey, b and c model the prey-predator interactions and d is the growth rate of the predator, that in this case is negative because we only consider the birth of predators when eating prey; in the same way we only consider the death of prey when being eaten by a predator.

As we see in Figure 1 the solution of the Lotka-Volterra model is a center; therefore, it gives rise to oscillations sustained in time for the population densities of prey and predator.

If now we add a self-regulatory term to the system, known as the logistic term, that controls that the population of the species so that they don't grow indefinitely,

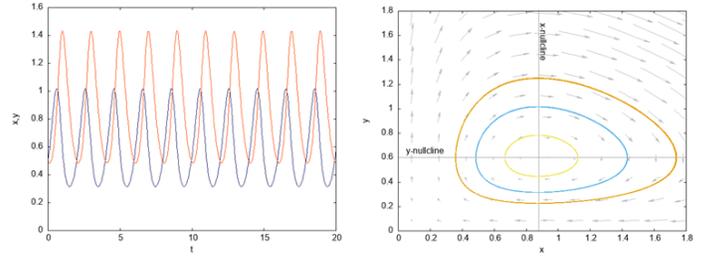


FIG. 1. Time evolution of prey, in blue, and predator, in red, for the Lotka-Volterra model (left). Phase plane of prey-predator model for three sets of initial conditions(right), the nullclines are represented in grey as are the velocity vectors. In both cases the parameters used are: $a=3.5$, $b=4.0$, $c=3.0$ and $d=5.0$

the resulting system of equations is:

$$\begin{aligned} \frac{dx(t)}{dt} &= x(a - by - x/K_1) \\ \frac{dy(t)}{dt} &= y(cx - d - y/K_2), \end{aligned} \quad (2)$$

where K_i are the carrying capacities, the parameters that control the population size for each independent species in stationary conditions.

Adding a logistic term to the equations to control population growth has, however, the effect of eliminating the sustained oscillations observed in the original model. Instead of a center the solution to the system of Eqs. (2) is a stable fixed point, as we can see in the phase plane of Figure 2.

The solution of the model without the logistic term suggests that the population cycles can be an effect of the prey-predator interaction. The addition of the logistic term seems to destroy the cyclic behaviour. In the following section we will attempt to regain the cycle by including the stochasticity that is inherent to this and similar interaction models.

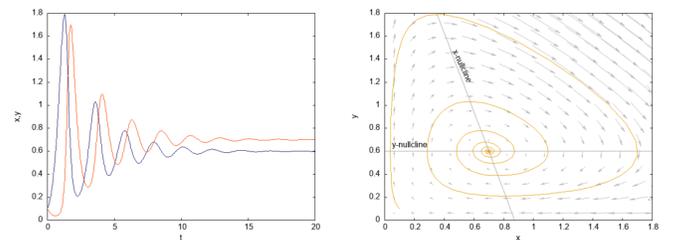


FIG. 2. Time evolution of prey, in blue, and predator, in red, for the Lotka-Volterra model with the logistic term (left). Phase plane of prey-predator model with the logistic term (right) the nullclines are represented in grey with the velocity vectors. In both cases the parameters used are: $a=3.5$, $b=4.0$, $c=3.0$, $d=5.0$ and $K_i = 3.0$ for $i=1,2$.

III. STOCHASTIC MODEL FOR PREY-PREDATOR INTERACTIONS

In this section we will present the stochastic model used to simulate predator-prey systems that can be extended to other types of interaction. It is a non-spatial model based on individual level interactions (ILM). By considering that each individual can partake in stochastic processes of birth, death and interaction with another individual we can derive a description of the system for a large but finite number of individuals that will be equivalent to the deterministic Lotka-Volterra [4][5].

The specific ILM we will study consist of two species A , the predator, and B , the prey. In a certain time t we will have n individuals of A and m of B . In order to control the growth we include empty space E such that the size of the system L is defined as $L = n + m + E$. Since this is a non-spatial model E doesn't represent physical space but are passive constituents of the system that indicate whether the number of individuals can keep growing or not. We allow only the birth process $BE \xrightarrow{b} BB$; death processes $A \xrightarrow{d_1} E$ and $B \xrightarrow{d_2} E$; and interaction processes $AB \xrightarrow{p_1} AA$ and $AB \xrightarrow{p_2} AE$, where b, d_1, d_2, p_1 and p_2 are parameters of the system that represent the probability of a certain event happening when two individuals interact. We allowed for two separate types of interactions: one where the predator simply kills or eats the prey, and one where the predator kills the prey and another predator is born. This differentiation allows for the birth of predators to be completely dependent on whether there are preys in the system and acts as a control for the maximum growth of the predator population, in an equivalent manner than the logistic term.

At each time-step we either pick two individuals from our system, with probability μ , or simply one, with probability $(1 - \mu)$. For example, the probability of picking a pair of type BE is:

$$BE = 2\mu \frac{m(L - n - m)}{L(L - 1)}, \quad (3)$$

where the two factor comes from the equivalence of the choices BE and EB , and we expressed E as a function of the other elements present in the system.

Once we have the interacting elements, we apply the different processes with the respective probability rates to compute the system's evolution. In order to simplify notation we will redefine the probability rates scaling them by L , for the processes that involve only one element, or $L(L - 1)$, for the ones that involve two. This particular scaling is chosen to obtain in a direct way a mean-field approximation with the desired L factors that allow us to compare with the corresponding deterministic results.

We will also factor the parameters μ and $(1 - \mu)$ in these rates. Since the value of μ cannot be adjusted from any real system attribute. In this way, all the parameters present in the microscopic model have a clear meaning in real systems. Therefore, the transition rates for this model, written as the probability of going from the state (n, m) to the state (n', m') as $T(n', m'|n, m)$, are:

$$\begin{aligned} T(n - 1, m|n, m) &= d_1 n \\ T(n, m + 1|n, m) &= 2b \frac{m(L - n - m)}{L} \\ T(n + 1, m - 1|n, m) &= 2p_1 \frac{nm}{L} \\ T(n, m - 1|n, m) &= 2p_2 \frac{nm}{L} + d_2 m \end{aligned} \quad (4)$$

Having found the transition rates that describe the stochastic processes we can write the master equation of the system as:

$$\begin{aligned} \frac{dP(n, m, t)}{dt} &= (\mathcal{E}_x - 1)T(n - 1, m|n, m)P(n, m, t) \\ &+ (\mathcal{E}_y^{-1} - 1)T(n, m + 1|n, m)P(n, m, t) \\ &+ (\mathcal{E}_y - 1)T(n, m - 1|n, m)P(n, m, t) \\ &+ (\mathcal{E}_x^{-1}\mathcal{E}_y - 1)T(n + 1, m - 1|n, m)P(n, m, t), \end{aligned} \quad (5)$$

where we define the step operator \mathcal{E} as $\mathcal{E}_x^{\pm 1}f(n, m, t) = f(n \pm 1, m, t)$ and $\mathcal{E}_y^{\pm 1}f(n, m, t) = f(n, m \pm 1, t)$.

The mean field approximation of the ILM will give us the mean value of n and m that we can divide by the size of the system to obtain the density of species, $f_1 = \langle n \rangle / L$ and $f_2 = \langle m \rangle / L$. We obtain the mean field by multiplying Eq. (10) by n or m , and summing over all possible values of n and m in both cases. Therefore, we will obtain two equations one for $\langle n \rangle$ and another for $\langle m \rangle$, that only depend on the mean values of the variables. Using the normalization property of the probability $\sum_{n, m} P(n, m, t) = 1$; and assuming that we are in the limit $L \rightarrow \infty$ we can make the replacements $\langle m^2 \rangle \rightarrow \langle m \rangle^2$ and $\langle nm \rangle \rightarrow \langle n \rangle \langle m \rangle$. We arrive to the mean field equations:

$$\begin{aligned} \frac{df_1}{dt} &= \gamma_1 f_1 f_2 - \mu f_1 \\ \frac{df_2}{dt} &= r f_2 \left(1 - \frac{f_2}{K}\right) - \gamma_2 f_2 f_1, \end{aligned} \quad (6)$$

with $\gamma_1 = 2p_1$, $\mu = d_1$, $r = 2b - d_2$, $K = 1 - \frac{d_2}{2b}$ and $\gamma_2 = 2[p_1 + p_2 + b]$.

We can identify these set of differential equations as a deterministic Lotka-Volterra model where f_1 is the predator density and f_2 the prey density. In this case only the prey have a logistic term, this is enough to

control the population growth of both species since in the individual model we imposed that predators cannot give birth without the presence of prey. As we know, this deterministic model doesn't present any cycle in the temporal evolution of any of the populations, i.e. in stationary conditions it reaches a stable fixed point characterized by:

$$f_1^s = \frac{(2bp_1 - bd_1 - p_1d_2)}{2p_1(p_1 + p_2 + b)}$$

$$f_2^s = \frac{d_1}{2p_1}$$

We will simulate the stochastic model using the Gillespie algorithm, which is a stochastic algorithm suited to simulate chemical reactions, where time is updated by sampling a time interval dt between two consecutive reactions in the system from an exponential distribution, and where we choose probabilistically the reaction that occurs after dt based on the rates of the all the possible reactions a_i [6]. Therefore, between the times computed by the algorithm, there is no change in the state system. For our model the transition rates will act as the rates a_i . This means that we will compute the time between two consecutive processes with an exponential weighed by the sum of the transition rates of all possible processes. And then we will choose the process i with a probability a_i , its transition rate.

The results of the simulation are represented in Figure 3. We can observe that each realization of the simulation exhibits a cyclic behaviour that is lost when taking the mean over multiple realizations. As we will check when studying the power spectrum of the system, this implies the existence of a characteristic frequency in which all replicas oscillate; however, there is a difference on the phases of oscillations such that they cancel out when taking the average behavior. As we expected, the mean of the stochastic model is almost indistinguishable from the deterministic model of Eq. (6).

To analyze the nature of the oscillations observed in the simulation we will study the power spectrum of the model. We can derive the theoretical power spectrum from the Langevin equations.

The Langevin equations can be obtained doing a linear transformation of the form $\frac{n}{L} = f_1 + \frac{x}{\sqrt{L}}$ and analogously for the prey $\frac{m}{L} = f_1 + \frac{y}{\sqrt{L}}$ to the master equation (10). The terms with leading order in L will give us the mean field approximation in Eq. (6) and the terms of the order $O\left(\frac{1}{\sqrt{L}}\right)$ give rise to the Langevin equations [7]:

$$\begin{aligned} \dot{x} &= a_{11}x + a_{12}y + \eta_1(t) \\ \dot{y} &= a_{21}x + a_{22}y + \eta_2(t), \end{aligned} \quad (7)$$

where the constants a_{ij} are the terms of the stability matrix. The matrix is given by $a_{11} = 0$, $a_{12} = 2p_1f_1^s$, $a_{21} = -2(p_1 + p_2 + b)f_2^s$ and $a_{22} = -2bf_2^s$.

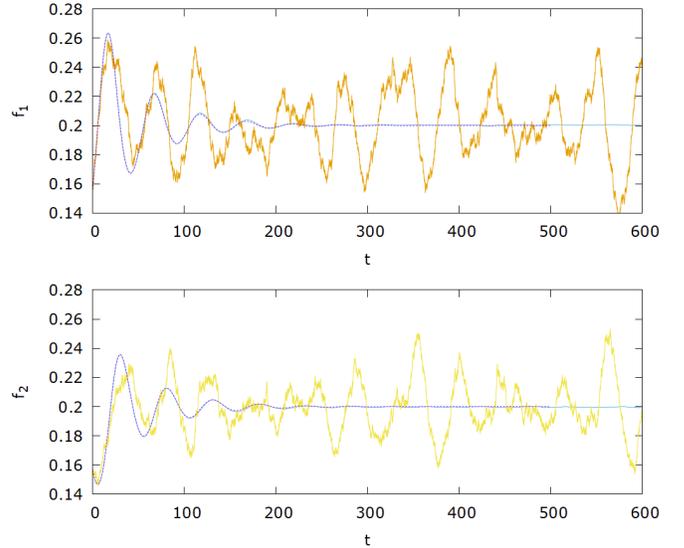


FIG. 3. Representation of the time evolution of predators (f_1), in orange, and preys (f_2), in yellow, for one realization of the ILM model for a two species predator-prey interaction. We also represented the mean values obtained after $M = 1000$ realizations of the stochastic model, blue line, and compare it with the deterministic model, dashed line. Here we show the results of simulations for a system of size $L = 3200$ with the parameters $b = 0.1$, $d_1 = 0.1$, $d_2 = 0.0$, $p_1 = 0.25$ and $p_2 = 0.05$.

The noise terms η_i that appear in the two Langevin equations are not decoupled from each other because we obtain the equations within a linear approximation framework. The characteristics of this linearization process affects the noise terms. In particular, the noise correlation matrix $\langle \eta_i(t)\eta_j(t') \rangle$ can be found doing the Van Kampen expansion of the master equation [7].

By writing the system in the form of Langevin equations we have gone from a discrete description of the system, in the variables n and m , to a continuous one, with the variables $x(t)$ and $y(t)$, valid for systems with large L [8]. From this description we can compute the Fourier transform and obtain the system of equations:

$$\begin{aligned} i\omega\tilde{x}(\omega) &= a_{11}\tilde{x}(\omega) + a_{12}\tilde{y}(\omega) + \eta_1(\omega) \\ i\omega\tilde{y}(\omega) &= a_{21}\tilde{x}(\omega) + a_{22}\tilde{y}(\omega) + \eta_2(\omega). \end{aligned} \quad (8)$$

By solving the system of equations and averaging over the square modulus of $\tilde{x}(\omega)$ we can obtain the power spectrum $P = \langle |\tilde{x}(\omega)|^2 \rangle$. We define the constants $b_{ij} = \langle \eta_i(\omega)\eta_j(\omega') \rangle$ as the correlations between the noise terms, since it is white noise it doesn't depend on the frequency. The expression of the power spectrum for the prey-predator system is:

$$P(\omega) = \frac{\alpha + \beta\omega^2}{(\omega^2 - \Omega^2)^2 + \Gamma^2\omega^2}, \quad (9)$$

where $\Omega_o^2 = a_{12}|a_{21}|$ and $\Gamma = |a_{22}|$ for both species. However, α and β have slightly different expressions for predator and prey. For example for the prey, $\alpha = b_{11}a_{21}^2$ and $\beta = b_{22}$.

From this expression we can infer that there will be a resonant frequency $\omega_o = \sqrt{\Omega^2 - \Gamma^2/2}$ when the value in the square root is real. This stochastic system behaves as a damped oscillator with natural frequency Ω_o^2 and a damping term represented by Γ . Additionally, it's important to notice that the resonance is achieved through the noise in the system, there is no external noise in the model. This could indicate that the resonance, and therefore the cyclic behaviour, is inherent to the system as the Lotka-Volterra model suggested. In Figure 4, we represent the power spectrum of our simulations. There is a clear pick corresponding to the theoretical resonant frequency, as the simulation is in accordance with the theoretical expression of Eq.(12).

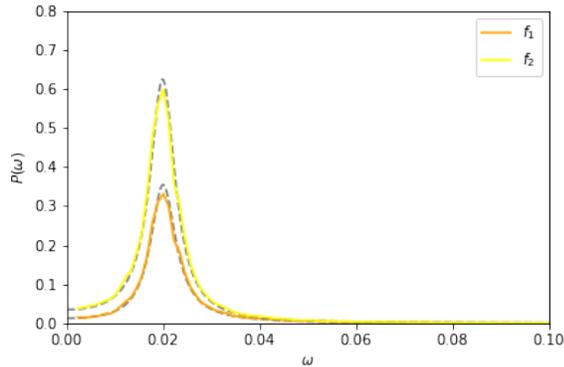


FIG. 4. Representation of the power spectrum for the predators f_1 and preys f_2 as a mean of $M = 500$ realizations of the ILM model. We represent the theoretical expression found in Eq. (12) as a dashed line. We made the simulations for a system of size $L = 3200$ with the parameters $b = 0.1$, $d_1 = 0.1$, $d_2 = 0.0$, $p_1 = 0.25$ and $p_2 = 0.05$.

An important characteristic of stochastic systems is that the size of the system needs to be large enough to avoid a variable reaching zero because of fluctuations. Doing a comparison with systems of diverse sizes, as is done in Figure 5, we confirm that the mean values of the simulations done with small systems ($L = 50$ or 100) go towards zero instead of following the deterministic model. It's interesting to notice that the relative fluctuations also decrease with the size of the system, however, that doesn't affect the resonant frequency characteristic of the system. The increase of relative fluctuations is

what can make species go extinct simply because of the finite size of a real ecological system.

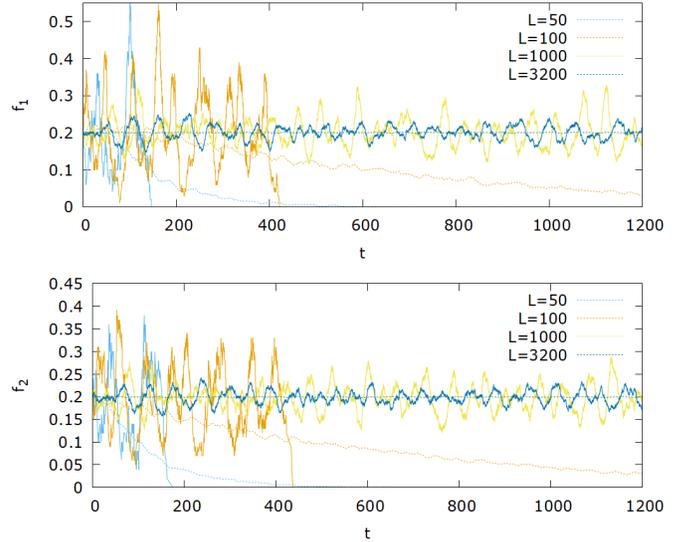


FIG. 5. Representation of the mean of $M = 1000$ realizations of the ILM as well as the time evolution of one realization for the sizes of the system $L = 50, 100, 1000, 3200$.

IV. GENERALIZED STOCHASTIC MODEL AND INTERACTION PATTERNS

A similar model, based on individual level interactions (ILM), can also be used to model mutualistic and competitive interactions between species. Following a similar process than in the previous section, we determine which individual processes can take place considering a system of two species A with a number of individuals n and B with m individuals. Then we proceed to write the transition rates and the corresponding master equation. In both cases, mutualistic and competitive, we will allow for birth and death processes of both species. To model the competition between two species we include a process that results in the death of one of the species when the two meet: $AB \xrightarrow{c_1} AE$ and $AB \xrightarrow{c_2} BE$. In the mutualistic interaction both species help each other survive, therefore when the two species meet, provided there is empty space in the system, another individual will be born: $ABE \xrightarrow{m_1} ABA$ and $ABE \xrightarrow{m_2} ABB$. The corresponding transition rates are shown in Table I.

The master equation for both systems, with the corre-

TABLE I. Table with the transition rates for the competitive and mutualistic interactions of two species systems. The number of individuals of the species are the variable n and m , in a system of size L . The rates are: birth rates b_i , death rates d_i , competitive interaction c_i and mutualistic interaction m_i .

Competitive	Mutualistic
$T(n+1, m n, m) = 2b_1 \frac{n}{L}(L_1 - n)$	$T(n+1, m n, m) = 2b_1 \frac{n}{L}(L_1 - n) + 6m_1 \frac{nm}{L(L-1)}(L_1 - n)$
$T(n-1, m n, m) = d_1 n + 2c_2 \frac{nm}{L}$	$T(n-1, m n, m) = d_1 n$
$T(n, m+1 n, m) = 2b_2 \frac{m}{L}(L_2 - m)$	$T(n, m+1 n, m) = 2b_2 \frac{m}{L}(L_2 - m) + 6m_2 \frac{nm}{L(L-1)}(L_2 - m)$
$T(n, m-1 n, m) = d_2 m + 2c_1 \frac{nm}{L}$	$T(n, m-1 n, m) = d_2 m$

sponding transition rates, is:

$$\begin{aligned} \frac{dP(n, m, t)}{dt} = & (\mathcal{E}_x^{-1} - 1)T(n+1, m|n, m)P(n, m, t) \\ & + (\mathcal{E}_x - 1)T(n-1, m|n, m)P(n, m, t) \\ & + (\mathcal{E}_y^{-1} - 1)T(n, m+1|n, m)P(n, m, t) \\ & + (\mathcal{E}_y - 1)T(n, m-1|n, m)P(n, m, t), \end{aligned} \quad (10)$$

where \mathcal{E} is the step operator already defined.

By doing the mean field approximation in the same manner than in the previous section we find the deterministic equation for the competitive system:

$$\begin{aligned} \frac{df_1}{dt} &= f_1((2b_1 l_1 - d_1) - 2b_1 f_1 - 2c_2 f_2) \\ \frac{df_2}{dt} &= f_2((2b_2 l_2 - d_2) - 2b_2 f_2 - 2c_1 f_1), \end{aligned} \quad (11)$$

where f_1 and f_2 are defined as: $f_1 = \langle n \rangle / L$ and $f_2 = \langle m \rangle / L$. The parameters in the set of equations are defined in Table I with $l_i = L_i / L$. To find stable solutions for competitive interactions the parameters that appear in the Eq. (13) need to verify certain restrictions [3]. In order for the rates to verify the conditions of stability we need to decouple the available empty space for the two species. Therefore, instead of $E = L - n - m$ each specie will have their empty space defined as $E_1 = L_1 - n$ or $E_2 = L_2 - m$. Therefore the only contribution of one species to the other comes from the competitive interaction.

The results of the simulation of the competitive system are shown in Figure 6. The simulation for the mean field stochastic model and the corresponding deterministic model coincide. However, the fluctuations for each realization of the ILM do not have the same cyclic behaviour than in the prey-predator case. Now we will study the power spectrum of the system to see if we can identify a resonant frequency.

The transformation of the master equation to the Langevin equations results in the same set of equations than Eq. (7). However, in this case the expression of the power spectrum we arrive at is not the same due to the term in the stability matrix a_{11} not being equal to zero.

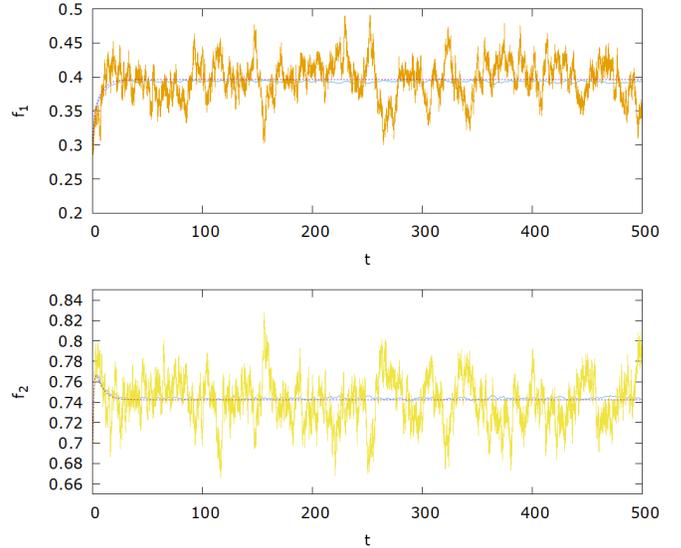


FIG. 6. Representation of the time evolution of f_1 and f_2 for one realization of the ILM for the competitive model. We also represent the mean over $M = 1000$ realizations of the stochastic model, blue line, and compare it with the deterministic model, dashed line. We made the simulations for a system of size $L = 1000$ with the parameters $b = 0.5$, $d_1 = 0.01$, $d_2 = 0.02$, $p_1 = 0.3$ and $p_2 = 0.4$.

The form of the power spectrum is:

$$P(\omega) = \frac{\alpha + \beta\omega^2}{(\omega^2 - \Omega^2)^2 + \Gamma^2\omega^2 + C}, \quad (12)$$

where $\Omega_o^2 = a_{12}a_{21}$, $\Gamma^2 = a_{22}^2 + a_{11}^2$ and $C = a_{22}^2 a_{11}^2 - 2a_{22}a_{11}a_{12}a_{21}$. Once again, α and β are slightly different expressions for both species. The appearance of a constant in the denominator changes the behaviour of the resonant frequency. There aren't resonant frequencies in the system compatible with the existence of a positive solution for both species. Instead, as seen in Figure 7 the power spectrum attains a maximum value at $\omega = 0$ that decays towards zero. After an initial exponentially fast decay, an interesting scale-free power law decay after $\omega \sim 0.2$, compatible with a $1/f$ noise spectrum. This type of power spectrum has been widely observed in many different research areas, from physics to language and economics and even in music, but despite its ubiquity its theoretical

explanation remains as an open challenge to science.

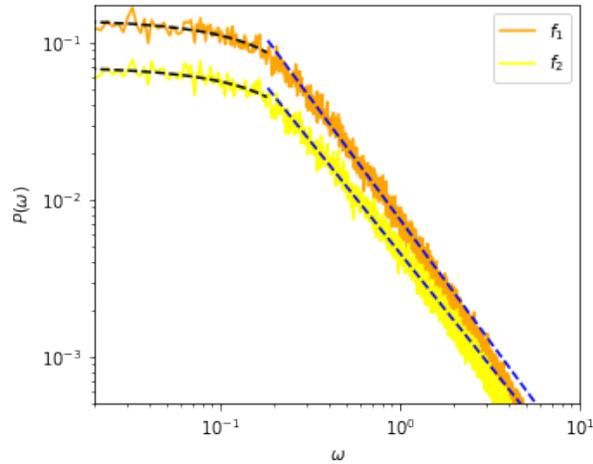


FIG. 7. Representation of the power spectrum f_1 and f_2 of the competitive system as a mean of $M = 500$ realizations of the ILM in a logarithmic scale. We made the simulations with the same parameters used in Figure 6. In black we represented the fit to the exponential decay and in blue the fit to the power law decay.

The mutualistic system described in terms of birth and death processes gives rise to a deterministic equation with a different functional form, with non-linear terms of higher order (cubic terms):

$$\begin{aligned} \frac{df_1}{dt} &= f_1 ((2b_1 - d_1) - 2b_1 f_1 + 6m_1 f_2 (1 - f_1)) \\ \frac{df_2}{dt} &= f_2 ((2b_2 d_2) - 2b_2 f_2 + 6m_2 f_1 (1 - f_2)) \end{aligned} \quad (13)$$

When simulating the stochastic model we obtain the results shown in Figure 8. The fluctuations in this system aren't oscillatory as the prey-predator model, they seem to have a similar behaviour to the competitive system. As can be seen from Figure 9, the power spectrum of this system has the same behaviour as the competitive one. There is a maximum of the power-spectrum at $\omega = 0$ that decays towards zero as a power law, therefore once again we observe a typical scale-free decay compatible with a $1/f$ noise spectrum.

V. STOCHASTIC MODEL FOR THREE SPECIES ECOLOGICAL CHAINS

In this section we will extend and adapt our stochastic model to simulate three species ecological chains in order to examine whether the addition of complexity and diversity into the system changes its characteristic oscillatory behaviour. We will study three cases: two cyclic

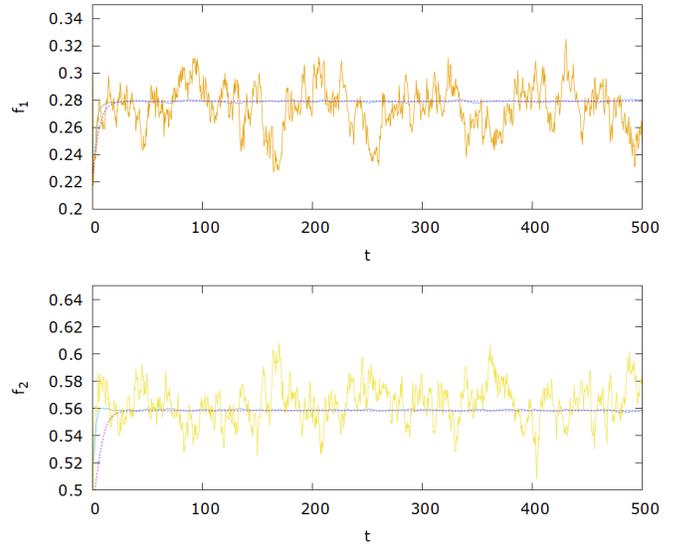


FIG. 8. Representation of the time evolution of f_1 and f_2 for one realization of the ILM for the mutualistic model. We also represent the mean over $M = 1000$ realizations of the stochastic model, blue line. We made the simulations for a system of size $L = 1000$ with the parameters $b = 0.1$, $d = 0.1$ and $m_1 = m_2 = 0.25$.

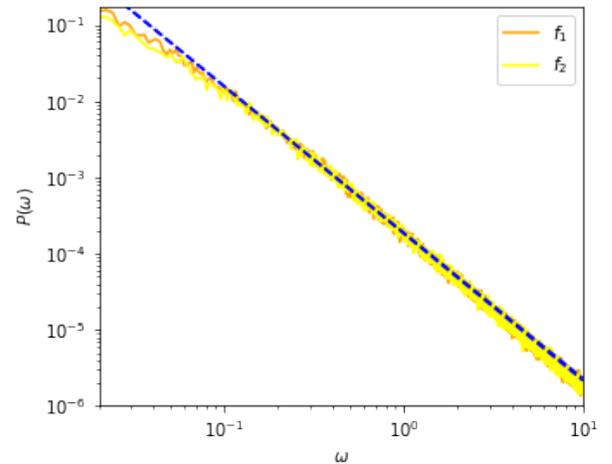


FIG. 9. Representation of the power spectrum for f_1 and f_2 as a mean of $M = 100$ realizations of the ILM mutualistic model in a logarithmic scale. We made the simulations with the same parameters used in Figure 8. In blue we represent the fit to a power law.

chain models, one with predator-prey interactions and another with mutualistic interactions, and finally an open predator-prey trophic chain. We choose these three systems because they represent typical interaction patterns observed experimentally that can be modeled with Lotka-Volterra type equations. Moreover, as we will see in the following pages, these three species systems also present different temporal evolution patterns: either an oscillatory

tory stationary state with a characteristic frequency, an exponentially or a power-law decaying power spectrum without a characteristic frequency.

A. Cyclic prey-predator food chain

In this cyclic model all three species act at the same time as prey and predator, the interactions between them can be seen in Figure 10. The three species in the system are completely equivalent. We will differentiate the three species by the rates of the processes that occur in the dynamics.

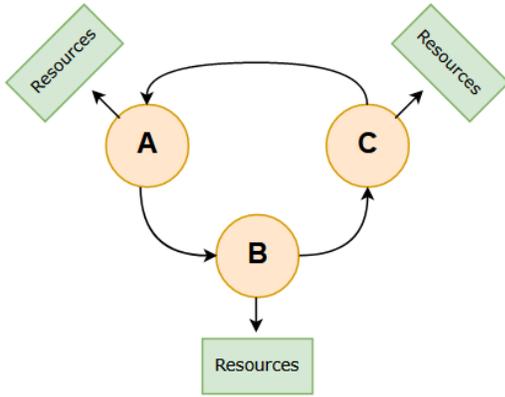


FIG. 10. Schematic representation of the cyclic system. The arrows go from the predator towards the prey. The resources indicate the resources available for the preys.

Similarly to the predator-prey system seen in a previous section, we allow for certain processes to occur; birth processes in this case the three species can give birth dependent on the resources available to them, therefore there are three possible interactions: $AR_1 \xrightarrow{b_1} AA$, $BR_2 \xrightarrow{b_2} BB$ and $CR_3 \xrightarrow{b_3} CC$; death processes $A \xrightarrow{d_1} E$, $B \xrightarrow{d_2} E$ and $C \xrightarrow{d_3} E$; and interaction processes, for the three species: $AB \xrightarrow{p_1} AA$ and $AB \xrightarrow{p_2} AE$, $BC \xrightarrow{p_3} BB$ and $BC \xrightarrow{p_4} BE$, $CA \xrightarrow{p_5} CC$ and $CA \xrightarrow{p_6} CE$. Once again the parameters b_i , d_i and p_i indicate the probability of the correspondent reaction happening when two individuals interact. Analogously to the prey-predator model we can write the transition probabilities as:

$$\begin{aligned}
 T(n+1, m, q | n, m, q) &= 2b_1 \frac{n}{L} (R_1 - n) \\
 T(n-1, m, q | n, m, q) &= d_1 n + 2p_6 \frac{nq}{L} \\
 T(n, m+1, q | n, m, q) &= 2b_2 \frac{m}{L} (R_2 - m) \\
 T(n, m-1, q | n, m, q) &= d_2 m + 2p_2 \frac{mn}{L} \\
 T(n, m, q+1 | n, m, q) &= 2b_3 \frac{q}{L} (R_3 - q) \\
 T(n, m, q-1 | n, m, q) &= d_3 q + 2p_4 \frac{qm}{L} \\
 T(n+1, m-1, q | n, m, q) &= 2p_1 \frac{mn}{L} \\
 T(n, m+1, q-1 | n, m, q) &= 2p_3 \frac{qm}{L} \\
 T(n-1, m, q+1 | n, m, q) &= 2p_5 \frac{nq}{L}
 \end{aligned} \tag{14}$$

If we write the master equation and take the mean field approximation, the resulting equations for $f_1 = \langle n \rangle / L$, $f_2 = \langle m \rangle / L$ and $f_3 = \langle q \rangle / L$ are:

$$\begin{aligned}
 \frac{df_1}{dt} &= f_1 ((2b_1 r_1 - d_1) - 2b_1 f_1 + 2p_1 f_2 - 2(p_5 + p_6) f_3) \\
 \frac{df_2}{dt} &= f_2 ((2b_2 r_2 - d_2) - 2b_2 f_2 + 2p_3 f_3 - 2(p_1 + p_2) f_1) \\
 \frac{df_3}{dt} &= f_3 ((2b_3 r_3 - d_3) - 2b_3 f_3 + 2p_5 f_1 - 2(p_3 + p_4) f_2),
 \end{aligned} \tag{15}$$

where $r_i = \frac{R_i}{L}$ for $i = 1, 2, 3$. For simplicity we will impose that all species have the same growth $a_i = (2b_i r_i - d_i)$ and carrying capacity $k_i = 2b_i$, therefore we will take all the birth and death rates to be equal and equal to b and d respectively; and all the species will have access to the same amount of resources R .

The possible solutions of the set of equations (15) have a richer behaviour than the simple prey-predator model discussed before, as they have different types of solutions depending on the parameter values [9]. In the following discussion we will limit ourselves to parameters that allow for the coexistence of the three species since the extinction of one species will give solutions equivalent to the two species case we already studied. One solution is presented in Figure 11. Once again each realization has a cyclic behaviour that vanishes when taking the mean. Furthermore, the mean is equivalent to the deterministic set of equations (15).

Proceeding in the same manner than for the two species case we compute the power spectrum. For the case of prey-predator in a system with equivalent species, we find a power spectrum with the same characteristics as the previously studied case with this

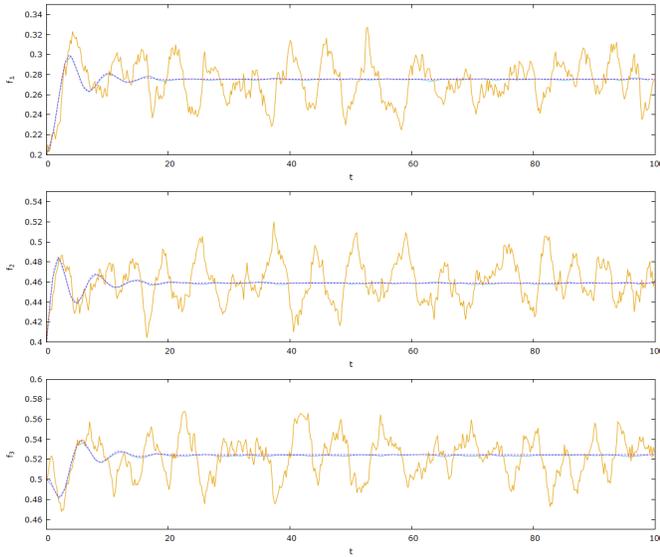


FIG. 11. Representation of the time evolution of f_1 , f_2 and f_3 for one realization of the ILM cyclic prey-predator model. In blue we represent the mean over $M = 1000$ realizations of the stochastic model, which we compare with the deterministic model, dashed line. We made the simulations for a system of size $L = 3200$ with the parameters $r = 1$, $b = 0.5$, $d = 0.2$, $p_1 = 0.7$, $p_2 = 0.4$, $p_3 = 0.6$, $p_4 = 0.8$ and $p_5 = p_6 = 0.7$.

type of interactions, a resonant frequency that results in a characteristic peak of the power spectrum. The resonant frequency is the same for all three species, the only difference in the power spectrum is the height of this characteristic peak.

B. Cyclic mutualistic chain

After verifying the existence of a resonant frequency for the prey-predator model with three coexisting species, we will look into interactions between species of a different nature. We will do so using the same interaction diagram shown in Figure 10 but with mutualistic interactions. Meaning that two members of an interacting species will help each other survive.

The processes involved in this type of interaction are once again birth and death processes, $AR_1 \xrightarrow{b} AA$ and $A \xrightarrow{d} E$ for the three species. To simplify the casuistics of this scenario we will also consider all birth (b) and death (d) rates the same. The mutualistic interactions are modeled in the same way that the two species case. The reactions are written as $ABR \xrightarrow{p_1} ABB$, $BCR \xrightarrow{p_2} BCC$ and $CAR \xrightarrow{p_3} CAA$. Notice that we write R for the three processes, however in this case the three species have the same amount of resources and they are not competing for them, as we can see in Figure 10. The

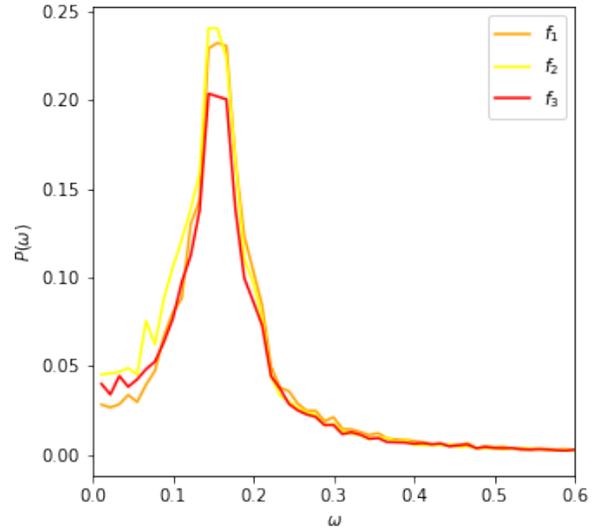


FIG. 12. Representation of the power spectrum for the three species as a mean of $M = 100$ realizations of the ILM cyclic prey-predator model. We made the simulations with the same parameters as in Fig. 11.

transition rates are stated in Table II.

From the transition rates we can derive the master equation and take the mean field and obtain the equivalent deterministic set of equations.

$$\begin{aligned} \frac{df_1}{dt} &= f_1 ((2b - d)(r - f_1) + 6p_3 f_3 (r - f_1)) \\ \frac{df_2}{dt} &= f_2 ((2b - d)(r - f_2) + 6p_1 f_1 (r - f_2)) \\ \frac{df_3}{dt} &= f_3 ((2b - d)(r - f_3) + 6p_2 f_2 (r - f_3)), \end{aligned} \quad (16)$$

with $r = \frac{R}{L}$, and the variables correspond to $f_1 = \langle n \rangle / L$, $f_2 = \langle m \rangle / L$ and $f_3 = \langle q \rangle / L$.

From these equations we can simulate the system with the stochastic and deterministic models and compare them. In Figure 13, we see that this system also has a similar behaviour to the two species case. The species populations don't appear to have a clear cycles; although it will be studied with the power spectrum. When we compute the power spectrum of this system, in Figure 14, we realize that the fluctuations around the mean in Figure 13 don't have any characteristic frequency. Instead, their temporal correlations exhibit, after an initial exponentially fast decay, an interesting scale-free power law decay after $\omega \sim 1$, compatible with a $1/f$ noise spectrum. This type of power spectrum has already been observed in the competitive case for two species. The three curves collapse into one because species are all equivalent (they share the same parameters) in this

TABLE II. Table with the transition rates for the mutualistic chain and the open food chain interactions of three species systems. The number of individuals of the species are the variable n , m and q , in a system of size L . The rates are: birth rates b_i , death rates d_i and interactions between species p_i . The parameter R represents the resources available to each specie.

Mutualistic chain	Open Food Chain
$T(n+1, m, q n, m, q) = 2b\frac{n}{L}(R-n) + 6p_3\frac{nq}{L(L-1)}$	$T(n+1, m, q n, m, q) = 2b\frac{n}{L}(R-n)$
$T(n-1, m, q n, m, q) = dn$	$T(n-1, m, q n, m, q) = d_1n + 2p_1\frac{nm}{L}$
$T(n, m+1, q n, m, q) = 2b\frac{m}{L}(R-m) + 6p_1\frac{mn}{L(L-1)}$	$T(n, m-1, q n, m, q) = d_2m + c_1\frac{mq}{L} + 2p_3\frac{mq}{L}$
$T(n, m-1, q n, m, q) = dm$	$T(n, m, q-1 n, m, q) = d_3q + c_2\frac{qq}{L}$
$T(n, m, q+1 n, m, q) = 2b\frac{q}{L}(R-q) + 6p_2\frac{qm}{L(L-1)}$	$T(n-1, m+1, q n, m, q) = 2p_2\frac{nm}{L}$
$T(n, m, q-1 n, m, q) = dq$	$T(n, m-1, q+1 n, m, q) = 2p_4\frac{mq}{L}$

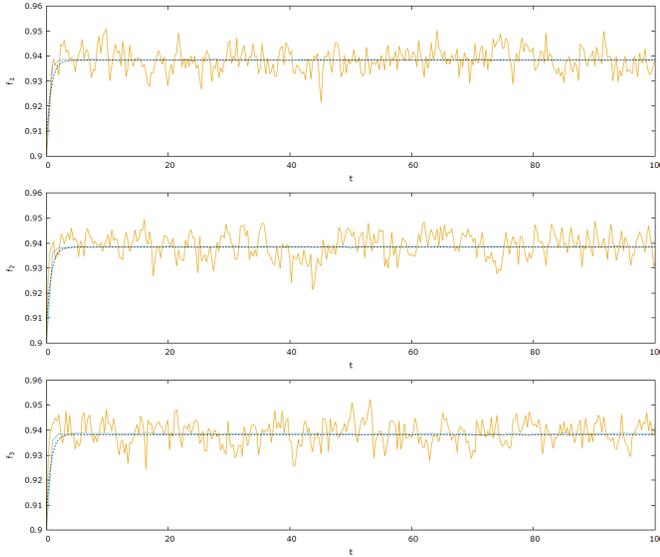


FIG. 13. Representation of the time evolution of f_1 , f_2 and f_3 for one realization of the ILM mutualistic model. In blue we represent the mean over $M = 1000$ realizations of the stochastic model that is compared with the deterministic model, dashed line. We made the simulations for a system of size $L = 3200$ with the parameters $r = 1$, $b = 0.5$, $d = 0.2$, $p_1 = 0.1$, $p_2 = 0.8$ and $p_3 = 0.4$.

system.

C. Open food chain system

Until now the examples of three interacting species considered have all the same interactive structure, that's why now we will consider an open food chain where there's no equivalence between all the species involved. As the diagram of Figure 15 illustrates, the species are a food chain where the predator C eats B , that acts as both prey and predator, that eats the prey A .

As in the first case studied, the interactions of the system are prey-predator type interactions. However due to the open structure of the chain, each species

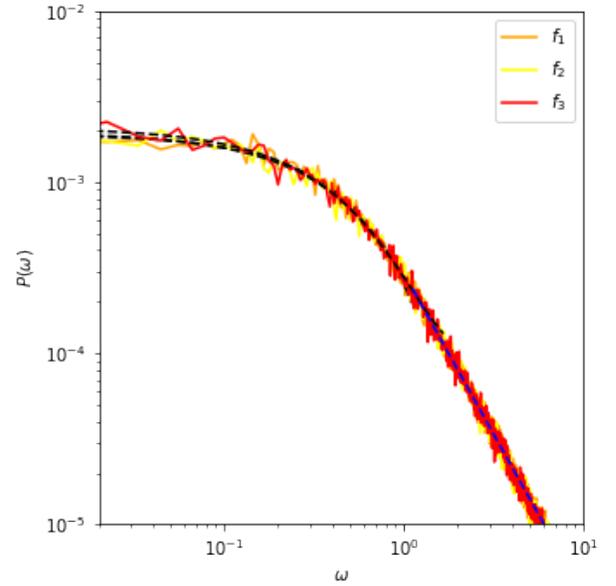


FIG. 14. Representation of the power spectrum for the three species as a mean of $M = 50$ realizations of the ILM mutualistic model in a double-logarithmic scale. We made the simulations with the same parameters as in Figure 13. In black we represented the fit of the exponential decay of the frequencies around zero. In blue we show the scale-free behaviour obtained for frequencies higher than $\omega = 1$.

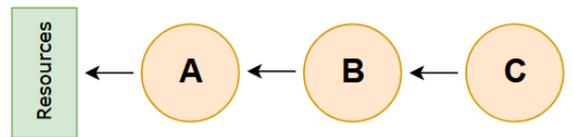


FIG. 15. Schematic representation of the chain system. The arrows go from the predator towards the prey. The resources indicate the food available for the prey.

will have different interactions. The species A has birth processes $AR \xrightarrow{b} AA$, death $A \xrightarrow{d_1} E$ and the prey-predator interactions we already considered before:

$BA \xrightarrow{p_1} BE$ and $BA \xrightarrow{p_2} BB$. The species B has the same interactions with A we have just described, but acts as the prey of C as $CB \xrightarrow{p_3} CE$ and $CB \xrightarrow{p_4} CC$. We include a death process $B \xrightarrow{d_2} E$ and, in order to include an explicit population control, we also include a competitive interaction of the species with itself $BB \xrightarrow{c_1} BE$. The specie C acts as a predator and also has the death and competitive processes: $C \xrightarrow{d_3} E$ and $CC \xrightarrow{c_2} CE$. The addition of the competitive process is done to be able to explicitly control the carrying capacities of each species. The transition rates for these processes can be found in Table II.

Finally, from the transition rates we derive the master equation and the mean field approximation as:

$$\begin{aligned}
 \frac{df_1}{dt} &= f_1 ((2br - d_1) - 2bf_1 - 2(p_1 + p_2) f_2) \\
 \frac{df_2}{dt} &= f_2 (-d_2 - c_1 f_2 - 2(p_3 + p_4) f_3 + 2p_2 f_1) \\
 \frac{df_3}{dt} &= f_3 (-d_3 - c_2 f_3 + 2p_4 f_2),
 \end{aligned} \quad (17)$$

with $r = \frac{R}{L}$, and the variables correspond to $f_1 = \langle n \rangle / L$, $f_2 = \langle m \rangle / L$ and $f_3 = \langle q \rangle / L$. To reduce the number of independent parameters, we impose that the carrying capacity of all the species is equal, $k = 2b = c_1 = c_2$ and that the death rates for the predators are also the same, i.e. $d_2 = d_3 = d$.

This system is once again based in prey-predator interactions however it lacks the equivalence between species. The power spectrum of the system has a peak at zero frequency. The peak is larger for the species A that acts purely as prey. Although we can identify a secondary peak at finite frequencies, in this case this peak seems to overlap with a continuously decaying spectrum over an intermediate range of frequencies. The decay after the second peak corresponds once again to a power law.

VI. STOCHASTIC TRANSPORT OF INDIVIDUALS BETWEEN METAPOPULATIONS

Until now we dedicated ourselves to study simple ecosystems with two or three species for various interactions and organization hierarchies. We found that these systems present different stochastic behaviours: some prey-predator structures have cyclic population densities given by a resonant frequencies while other interactions and topologies don't. Now we will consider each of this ecosystems as a metapopulation that can be in contact with another one, and therefore allow transport of species from one population to the other. Or in other words, we allow random transport or stochastic diffusion between two ecosystems originally disconnected and located in different patches. Our objective is to understand what are the effects of this new interaction, represented by

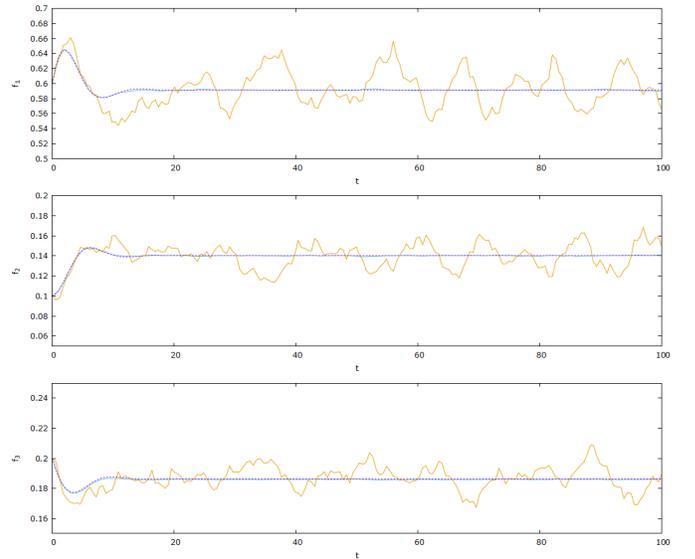


FIG. 16. Representation of the time evolution of f_1 , f_2 and f_3 for one realization of the ILM open food chain model. In blue we represent the mean over $M = 1000$ realizations of the stochastic model, which is compared with the deterministic model (dashed line). We made the simulations for a system of size $L = 3200$ with the parameters $r = 1$, $b = 0.5$, $d_1 = 0.01$, $d = 0.1$, $c_1 = c_2 = 1.0$, $p_1 = 0.8$, $p_2 = 0.5$, $p_3 = 0.7$ and $p_4 = 0.6$.

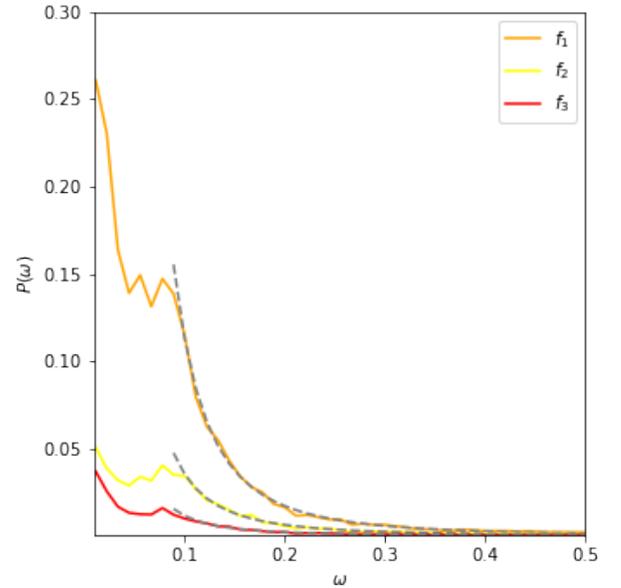


FIG. 17. Representation of the power spectrum for the three species as a mean of $M = 100$ realizations of the ILM for the open food chain system. We made the simulations with the same parameters as in Figure 16. In grey we represented the fit to a power law for the final decay.

this random transport of individuals between ecosystems with different characteristics, in the evolution of the

species. In particular, according to our previous analysis we will emphasize phenomena that imply the modification, appearance or disappearance of cyclic behaviours.

We will start by allowing transport between systems with the same interactions but with different characteristics between the metapopulations. Later we will generalize it to metapopulations where the species involved have different interactions between them. However, the first step is to implement the transport of individuals in the ILM model. Since it is a probabilistic model where we allow for certain processes to occur the diffusion between two patches or metapopulations can be thought of as a random walk process. In other words, there will be an additional process characterized by a certain probability for individuals to jump from one patch to another one.

In our Gillespie algorithm this simply translates into the addition of a diffusive transition rate a_μ . The probability of an individual from a patch p to diffuse to another ecosystem will be proportional to the sum of all the individuals in the patch, accounting for all species N , by a certain diffusion parameter D :

$$a_\mu = D \sum_{i=1}^N n_i^p \quad (18)$$

Therefore, diffusion will be accounted like all the other processes that can take place in the ecosystem. At each time step we will choose which process takes place while having a certain probability per patch of an individual diffusing. Based upon the number of individuals per species we will choose which individual will diffuse and to which patch. An important aspect of this process is that when individuals change from one patch to another they carry with them the interaction parameters from their original patch. Consequently, two individuals from the same species that come from two patches will not interact with their environment in exactly the same way. For example, if a predator of the patch p has a rate p_1 of eating prey when it diffuses to another patch it will continue eating prey with the same rate p_1 , independently of the eating rate of predators in the destination patch. Despite natural systems tend to evolve on the long time regime to adapt to its new environment, here we want to address the impact of the random transport of species in a shorter time scales than those involved in adaptation or evolution processes.

A. Random transport among prey-predator metapopulations

To begin, we considered the most simple case of two populations where each metapopulation consist of a simple two-species prey-predator dynamics with slightly

different characteristics, for example for the prey in one population can have a higher birth or death rate; or for the predators can have higher probability of eating the prey when they interact. This simple case will allow us to see how our model behaves when a better adapted or dominant species comes to an ecosystem with other individuals of the same species. The situation is the equivalent in real systems to a new invasive species arriving to an ecosystem due to external factors. Therefore, we expect the invasive species to dominate the native one at short times but, as happens in real ecosystems, to find a region of parameters where the native species stabilizes before it goes extinct.

In our simulations, we find that the dominant species always imposes its characteristic dynamics in both patches. We also observe the total extinction of the species with the less dominant traits, showing that the species with better survival characteristics will monopolize the resources and lead the other group to extinction. An example of this phenomenon is shown in Figure 18 where we can appreciate how a prey f_2 with a higher birth rate survives in both patches while the prey with the lower one goes extinct. For the prey it is equivalent to rise the birth rate than to decrease the death rate. For the predators we can decrease the death rate or increase the prey-predator interaction which is completely equivalent to the predators birth rate.

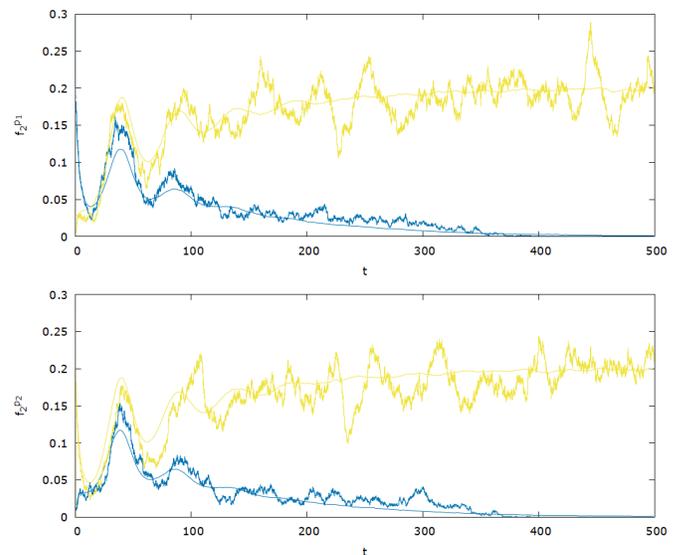


FIG. 18. Representation of the time evolution of f_2 , the prey, for two patches p_1 above and p_2 below. In blue is represented the individuals that have the characteristics of patch 1 and in yellow of patch 2. We represented the mean over $M = 100$ realizations of the stochastic model and the evolution for one realization. We made the simulations for a system of size $L = 1000$ in each patch with the parameters $p_1 = 0, 25$, $p_2 = 0.05$, $d_1 = 0.1$, $d_2 = 0$ and $b_1 = 0.1$ in patch 1 and $b_1 = 0.11$ in patch 2.

We would like to point out that the extinctions observed could be produced because of the simplicity of the original ecosystem we are considering. On the other hand, one could speculate that the existence of more complex ecological patches, both at the level of structure and biodiversity, could help accommodating the arrival of new more evolved species without triggering extinctions, at least in some region of the relevant parameter space.

Consequently, we followed our study by considering the circular prey-predator model, its scheme can be seen in Figure 10, to add complexity to each metapopulation. We observed the same behaviour than in the simple prey-predator system when improving the fitness of a given species in one of the patches subject to random transport. The three species ecological chain is still a simple ecosystem if we compare it to ecological networks therefore our results can still be explained by the lack of complexity. However, this system also allows the possibility of accounting for changes in the environment of each metapopulation, i.e. in the amount of available resources at each patch. We found that when increasing the accessible resources to one of the species there is additional interesting behaviour. In Figure 19 we represented the evolution of the system when putting in contact two metapopulations where the species A of the first patch has more resources than in the second.

When implementing this scheme we can observe that the number of individuals in the metapopulation with more resources increases in respect to the one they would have if no transport was allowed. Furthermore, the expected stationary solution for the population with less resources decreases from the expected one. In Figure 19 we compared the solutions for two values of the diffusive rate D and we can see how the increase of transport between patches expands the effect. Additionally, when analysing the power spectrum, in Figure 22 we find that the cycles of the two patches don't synchronize their characteristic frequency. On the contrary, the peak separations grow with the value of D . The patch with more resources has faster cycles while the other one slows down. These pieces of evidence indicate that the transport between populations with different resources acts as a rich club where the differences are expanded in favour of the one who had more to begin with. We only show here the power spectrum of one of the three species because they are equivalent.

B. Transportation between metapopulations with mutualistic and competitive dynamics

In the previous section we restrained ourselves to the discussion of prey-predator dynamics. Another interesting approach is the study of transport between

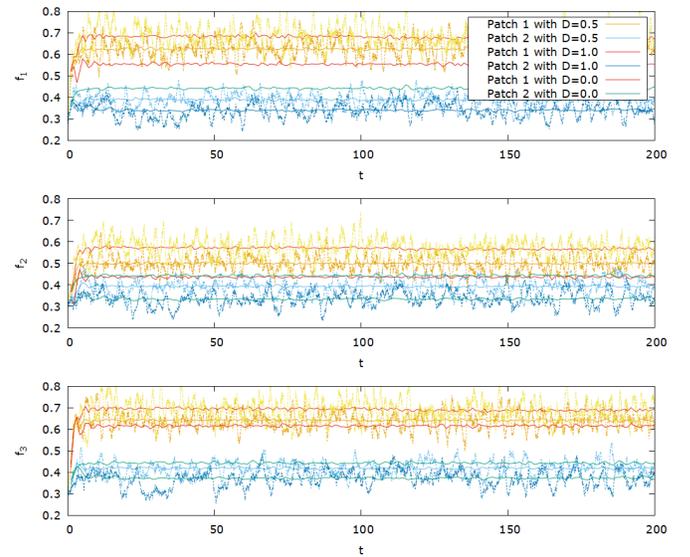


FIG. 19. Representation of the time evolution of f_1 , f_2 and f_3 for three values of the diffusive transport parameter $D = 0, 0.5, 1$. We show the values for the two patches considered. The solid line shows the mean values for the three D . The dashed line represents the evolution of one realization of the ILM model. We made the simulations for a system where each patch has a size $L = 1000$ with the parameters $b = 0.5$, $d = 0.2$, $p_1 = p_3 = p_5 = 0.7$, $p_2 = p_4 = p_6 = 0.4$, $p_3 = 0.7$ and $r_2 = r_3 = 1.0$. For the patch 1 $r_1 = 1.5$ and for the patch 2 $r_1 = 1.0$.

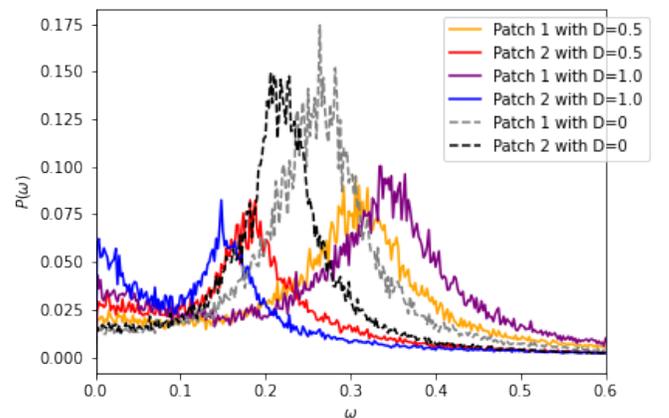


FIG. 20. Representation of the power spectrum for f_1 as a mean of $M = 100$ realizations of the ILM. We made the simulations with the same parameters as in Figure 22. It is shown the values for both patches and the three values of the diffusion parameter.

metapopulations with different dynamics. The interest stems from the diversity of oscillatory behaviour; allowing for the appearance or disappearance of cyclic behaviour. As we mentioned, cyclic behaviour is of special interest in ecology. With the presented stochastic model we have given an explanation of the behaviour

being found in prey-predator dynamics and with this study we want to explore if it can be expanded to prey-predator dynamics that are in contact with other dynamics that, on their own, do not exhibit cyclic behaviour.

We will focus on systems with two metapopulations, one with a prey-predator dynamics and another one with either a mutualistic or competitive interactions, each one consisting of two species. This means that only one metapopulation will have a cyclic behaviour in the absence of transport. Despite these restrictions, there is a wide variety of possible interactions between the species of different patches as well as the total number of different species. In this section, we will limit the discussion to systems where there is one common species in both patches, the prey in the prey-predator dynamics, and both species in the competitive/mutualistic dynamics act as prey in the presence of a predator. The interactions of the species in the absence of random transport have already been described. In the first patch there is a predator A and a prey B , in the second one there are two preys B and C that have either a competitive or mutualistic interaction. When there is transport, we allow the predator to eat both types of prey B and C . The predator reacts equally to the species B no matter their patch of origin.

With this set of rules there is a wide range of behaviours that can occur depending on the type of interaction and the values of the different parameters. It is particularly important the relation between the prey-predator rates and the competitive or mutualistic rates. If the former are larger, or even equal, they will dominate the behaviour, they will transfer the predator-prey dynamics to the other patch. On the other hand, if they are smaller the competitive/mutualistic interactions will dominate. The latter means that the oscillations characteristic of the predator-prey interactions can be lost. Therefore, with this scheme we can achieve both the appearance and disappearance of cyclic behaviour depending on the relation of the rates of both dynamics.

We will discuss the most interesting case that is the appearance of cycles. As an example, in Figure 21, we present the case of prey-predator dynamics coupled with competitive dynamics. When analysing the behaviour of the stationary solution there is a slight decrease in the number of prey and predator from the expected value in the prey-predator dynamics without transport. In the competitive dynamics there is a large decrease in the number of individuals explained by the sudden appearance of a predator. The decrease of the expected values in the prey-predator species can be explained by the empty space restrictions we imposed in the model. It is finally important to notice that both patches seem to arrive at the same stationary solution, which leads to believe that there may be a sincronization between the

two patches. We will corroborate this by looking at the power spectrum.

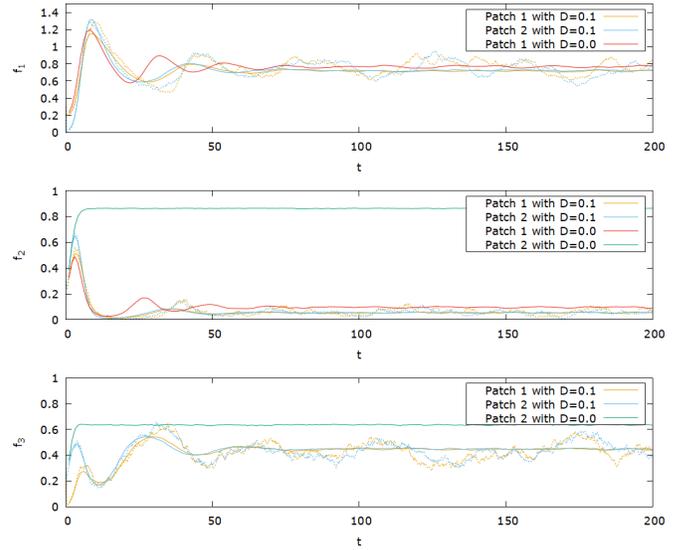


FIG. 21. Representation of the time evolution of the three species f_1 , f_2 and f_3 for the two patches. With $D = 0.1$ all species can be found in both patches. With $D = 0$, f_1 and f_3 can only be found in patches 1 and 2, respectively; f_2 can be found in both. In a solid line are shown the mean values for the three species. In a dashed line the evolution of one realization of the ILM. We made the simulations for a system where each patch has a size $L = 1000$ with the parameters $r = 1$, $b = 0.5$, $d_1 = 0.1$, $d_2 = 0.01$, $d_3 = 0.02$, $p_1 = 0.5$, $p_2 = p_4 = 0.05$, $p_3 = 0.3$, $c_1 = 0.1$ and $c_2 = 0.2$.

Studying the power spectrum corresponding to the different cases we see different behaviours. As we already mentioned, these differences depend on the relationship between the rates of the prey-predator interactions and the rates of the mutual or competitive interactions. If the prey-predator dynamics are imposed, all the species of the system start to oscillate with a resonant frequency. However, if the mutualistic/competitive dynamics are more relevant or predominate, the resonant frequency is lost for the entire system. In Figure 22 we represent the power spectrum that corresponds to the example we represent in Fig. 21. We compare the frequencies we find when there is no transport between the metapopulations and the ones appearing when we allow transport. The prey-predator dynamics now have a resonant frequency that decreases from the expected one. The competitive dynamics develop a cyclic behaviour with a resonant frequency that completely differs from the isolated case. Moreover, both metapopulations synchronize their oscillatory dynamics and have an indistinguishable power spectra. The resonant frequency of the three species also synchronize, as we saw for the studied cases of prey-predator interactions, i.e. the resonant frequency is the same for all the species.

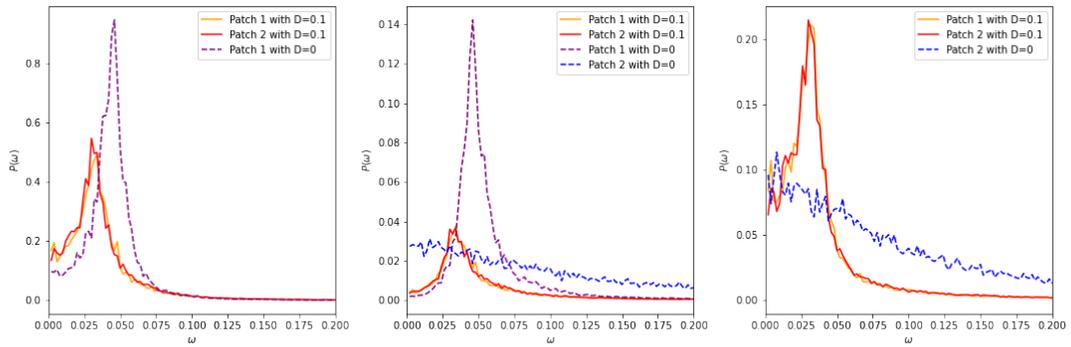


FIG. 22. Representation of the power spectrum for f_1 , f_2 and f_3 , from left to right, as a mean of $M = 100$ realizations of the ILM model. We made the simulations with the same parameters as in Figure 21. It shows the power spectrum with and without diffusion.

VII. CONCLUSIONS

In this work we have studied the appearance of population cycles in Lotka-Volterra like ecological systems due to intrinsic noise. The cycles appear in prey-predators dynamics for two species as well as for three species closed chains when species are all equivalent. In systems with other interactions commonly found in nature, such as mutualistic and competitive, we do not observe oscillatory behaviour in the population dynamics since the theoretical analysis of the stochastic model equations does not show a power spectrum behavior characterized by a resonant frequency. Therefore, the presence of cycles observed in nature between prey-predator systems could be a result of the intrinsic noise characteristic of these systems.

When looking at the ecosystems as metapopulations that can be put in contact with each other, for instance, allowing random diffusive transport, we observe a wide range of interesting phenomenology. One of the most interesting cases is the desynchronization of two metapopulations that contain species with the same characteristics but that can access to different amounts of resources in each metapopulation. In this situation the transport increases the population and the oscillation frequency in the patch where there are more resources in detriment to the other one. Another interesting observation is the imposition of cyclic behaviour in a system where initially there wasn't any. We have seen that we can achieve this by putting in contact one metapopulation with prey-predator dynamics with another one with competitive or mutualistic dynamics.

We can generalize this work by augmenting either the number of interacting species or the interacting number and topology of metapopulations. However, the generalization will imply a larger number of cases and parameters to explore, and therefore a probabilistic approach in terms of stochastic interaction parameters will be more appropriate to describe such systems. Several works in the literature are already using stochastic interaction matrices to determine the relation between species, see for example [10] and references therein. Another future perspective of this project is experimenting with systems that follow the processes we described to see if the results coincide with the theory and the numerical simulations. We could do it by means of robot swarms, where individual robots can interact with each other following a given set of rules. This set up will follow exactly the same processes that we considered in a controlled environment and would allow us to confirm our main findings in this work. Finally we would like to mention that extensions of this work can be quite useful for developing research objectives that help achieving some of the sustainable development goals (SDGs) which are an urgent call for action by all countries, as it can be used to understand and try to improve the preservation of biodiversity in ecosystems.

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