

Stochastic dynamics and mean field approach in a system of three interacting species

Research Article

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Abstract:

The spatio-temporal dynamics of three interacting species, two preys and one predator, in the presence of two different kinds of noise sources is studied, by using Lotka-Volterra equations. A correlated dichotomous noise acts on the interaction parameter between the two preys, and a multiplicative white noise affects directly the dynamics of the three species. After analyzing the time behaviour of the three species in a single site, we consider a two-dimensional spatial domain, applying a mean field approach and obtaining the time behaviour of the first and second order moments for different multiplicative noise intensities. We find noise-induced oscillations of the three species with an anticorrelated behaviour of the two preys. Finally, we compare our results with those obtained by using a coupled map lattice (CML) model, finding a good qualitative agreement. However, some quantitative discrepancies appear, that can be explained as follows: i) different stationary values occur in the two approaches; ii) in the mean field formalism the interaction between sites is extended to the whole spatial domain, conversely in the CML model the species interaction is restricted to the nearest neighbors; iii) the dynamics of the CML model is faster since an unitary time step is considered.

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1. Introduction

Noise is not generally detrimental to biological systems but can be employed to generate genotypic, phenotypic, and behavioral diversity [1–4]. Real ecosystems are affected by the presence of noise sources which consist of random variability of environmental parameters, such as

temperature, food availability, general conditions which can favour or thwart the increase of some biological species. This randomly fluctuating behaviour can be modeled by Gaussian noise sources, which influence, through a multiplicative interaction, the system dynamics. Multiplicative noise often causes the appearance of fluctuating barriers or processes of anomalous diffusion and has been investigated in the context of population growth and extinction [1, 5–20]. In this paper we study the time evolution of three interacting species, two preys, x and y , and one predator, z . The interaction between the two preys is symmetric and it is given by the parameter β . We study

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the ecosystem dynamics, described by generalized Lotka-Volterra equations, in the presence of two different kinds of noise sources: (i) a dichotomous noise acting on the β parameter, (ii) three external sources, modeled as independent multiplicative Gaussian noises, which act directly on the three species. First we consider the deterministic dynamics of the system in a single site and we get the time behaviour of x , y and z , by analyzing the stability of the ecosystem with different constant values of the interaction parameter β , which correspond to a coexistence regime ($\beta_{down} < 1$) or to an exclusion regime ($\beta_{up} > 1$). Then we consider the interaction parameter β varying dichotomously between these two values. In this condition we study the time behaviour of the species concentrations x , y and z for different levels of the multiplicative noise intensity. We find noise-induced oscillations and strong anticorrelations between the preys. Afterwards we take into account the spatial version of our ecosystem, considering a two-dimensional domain formed by N sites and adding a diffusion term in the L-V equations. By using a mean field approach, we obtain the corresponding moment equations in Gaussian approximation. We find that, for β varying dichotomously, the 1st order moments of the three species concentrations are independent on the multiplicative noise intensity. On the other hand, the behavior of the 2nd order moments is strongly affected by the presence of external noise sources. In particular we find that the time behavior is anticorrelated for the species densities of the two preys, and correlated between the predator and the total density of the two preys. Finally we get the time behavior of the 1st and 2nd order moments using a coupled map lattice (CML) model [21] and we compare these results with those previously obtained within the mean field approach. In view of an application on real systems, the results obtained could be useful to explain experimental data, reproducing the behaviour of natural ecosystems [5–11, 22, 23].

2. The model

Time evolution of our system is given by a stochastic model consisting of generalized Lotka-Volterra equations with multiplicative noise terms, within the Ito scheme, and diffusive terms in a spatial lattice formed of N sites

$$\dot{x}_{i,j} = \lambda x_{i,j} (1 - \nu x_{i,j} - \beta y_{i,j} - \alpha z_{i,j}) + x_{i,j} \sqrt{\sigma_x} \xi_{i,j}^x + D (\langle x \rangle - x_{i,j}), \quad (1)$$

$$\dot{y}_{i,j} = \lambda y_{i,j} (1 - \nu y_{i,j} - \beta x_{i,j} - \alpha z_{i,j}) + y_{i,j} \sqrt{\sigma_y} \xi_{i,j}^y + D (\langle y \rangle - y_{i,j}), \quad (2)$$

$$\dot{z}_{i,j} = \lambda_z z_{i,j} [-1 + \nu (x_{i,j} + y_{i,j})] + z_{i,j} \sqrt{\sigma_z} \xi_{i,j}^z + D (\langle z \rangle - z_{i,j}), \quad (3)$$

where the dot indicates the time derivative. The variables $x_{i,j}$, $y_{i,j}$ and $z_{i,j}$ are functions of the time t , and denote the densities, respectively, of the two preys and the predator in the lattice site (i, j) . λ and λ_z are scale factors, ν is the saturation parameter for the two preys, D is the diffusion coefficient, and $\langle x \rangle$, $\langle y \rangle$, $\langle z \rangle$ indicate the spatial mean, performed on the whole lattice, of the three species densities. The coefficient β is the interaction parameter between the two preys. The coefficients α and γ account for the interaction between preys and predator. $\xi_{i,j}^x(t)$, $\xi_{i,j}^y(t)$, $\xi_{i,j}^z(t)$ are statistically independent Gaussian white noises with zero mean and unit variance, and they model the interaction between species and environment. Finally, σ_x , σ_y , σ_z are the intensities of the three sources of Gaussian white noise.

2.1. Single site dynamics

2.1.1. Stability analysis and dynamical regimes

Depending on the value of the interaction parameter, coexistence or exclusion regimes take place. In the absence both of multiplicative noise ($\sigma_x = \sigma_y = \sigma_z = 0$) and diffusion terms ($D = 0$), Eqs. (1)–(3) describe the deterministic dynamics of a single site ecosystem. In these conditions, for the generic site of lattice the stationary values of the three species densities are given by

$$x^{stat} = y^{stat} = \frac{1}{2\nu}, \quad (4)$$

$$z^{stat} = \frac{2\nu - (\beta + \nu)}{2\alpha\gamma}. \quad (5)$$

where the indices i, j were suppressed. From Eq. (4) one can see that the two prey densities have stationary values that are independent on the interaction parameter β . Conversely, the stationary value of the predator density (Eq. (5)) is connected with the value of β . This indicates that the interaction parameter between the two preys determines the coexistence or exclusion regimes for the whole system, affecting the stationary value z^{stat} . From Eq. (5) the survivance condition for the predator is $z^{stat} > 0$, which allows to get the coexistence condition for the three species as a function of β

$$\beta < 2\nu - \nu. \quad (6)$$

The inequality (6) indicates that the system is characterized by two stationary states, which become stable or unstable depending on the values that β , γ and ν take on.

In order to determine the conditions for which the stationary values given in Eqs. (4), (5) correspond to a point of stable equilibrium in the phase space, we perform a stability analysis for the deterministic dynamics in single site. Therefore, in Eqs. (1) - (3) we neglect the noise terms

and consider the generic site of lattice, suppressing the indices i, j . Afterwards, we obtain the equations for the variations δx , δy , δz around the stationary values x^{stat} , y^{stat} , z^{stat}

$$\delta \dot{x} = \lambda (1 - 2\nu x^{stat} - \beta y^{stat} - \alpha z^{stat}) \delta x - \lambda \beta x^{stat} \delta y - \lambda \alpha x^{stat} \delta z, \quad (7)$$

$$\delta \dot{y} = \lambda (1 - 2\nu y^{stat} - \beta x^{stat} - \alpha z^{stat}) \delta y - \lambda \beta y^{stat} \delta x - \lambda \alpha y^{stat} \delta z, \quad (8)$$

$$\delta \dot{z} = \lambda_z [-1 + \gamma (x^{stat} + y^{stat})] \delta z + \lambda_z \gamma z^{stat} \delta x + \lambda_z \gamma z^{stat} \delta y. \quad (9)$$

By considering the solutions

$$\delta x = \delta x^0 e^{kt}, \quad \delta y = \delta y^0 e^{kt}, \quad \delta z = \delta z^0 e^{kt}, \quad (10)$$

with k generic complex number and δx^0 , δy^0 , δz^0 initial variations around the stationary values, and replacing Eqs. (10) in Eqs. (7) - (9), we obtain the following linear system of algebraic equations

$$[\lambda (1 - 2\nu x^{stat} - \beta y^{stat} - \alpha z^{stat}) - k] \delta x^0 - \lambda \beta x^{stat} \delta y^0 - \lambda \alpha x^{stat} \delta z^0 = 0, \quad (11)$$

$$-\lambda \beta y^{stat} \delta x^0 + [\lambda (1 - 2\nu y^{stat} - \beta x^{stat} - \alpha z^{stat}) - k] \delta y^0 - \lambda \alpha y^{stat} \delta z^0 = 0, \quad (12)$$

$$\lambda_z \gamma z^{stat} \delta x^0 + \lambda_z \gamma z^{stat} \delta y^0 + \{\lambda_z [-1 + \gamma (x^{stat} + y^{stat})] - k\} \delta z^0 = 0. \quad (13)$$

In order to get solutions different from the trivial ones, *i.e.* $\delta x^0 = \delta y^0 = \delta z^0 = 0$, after substituting for x^{stat} , y^{stat} and z^{stat} the expressions given in Eqs. (4), (5), we set to zero the determinant of the system (11) - (13), obtaining the corresponding eigenvalue equation

$$\begin{aligned} & -\lambda^2 \nu^2 k - 4\lambda \nu \gamma k^2 - 2\lambda^2 \nu \lambda_z \gamma + \lambda^2 \nu^2 \lambda_z - 4\gamma^2 k^3 - 4\gamma^2 \lambda \lambda_z k + 2\gamma \lambda \lambda_z \beta k + 2\gamma \lambda \lambda_z \nu k \\ & + \lambda^2 \beta^2 k + 2\lambda^2 \beta \lambda_z \gamma - \lambda^2 \beta^2 \lambda_z = 0, \end{aligned} \quad (14)$$

whose solutions are

$$k_1 = \frac{\lambda(\beta - \nu)}{2\gamma}, \quad (15)$$

$$k_2 = \frac{-\lambda(\beta + \nu) + \sqrt{\lambda^2 \nu^2 + 2\lambda^2 \nu \beta + \lambda^2 \beta^2 + 8\gamma \lambda \lambda_z \nu + 8\gamma \lambda \lambda_z \beta - 16\gamma^2 \lambda \lambda_z}}{4\gamma}, \quad (16)$$

$$k_3 = \frac{-\lambda(\beta + \nu) - \sqrt{\lambda^2 \nu^2 + 2\lambda^2 \nu \beta + \lambda^2 \beta^2 + 8\gamma \lambda \lambda_z \nu + 8\gamma \lambda \lambda_z \beta - 16\gamma^2 \lambda \lambda_z}}{4\gamma}. \quad (17)$$

Setting $\lambda = 3$, $\lambda_z = 0.06$, $\nu = 1$, $\alpha = 0.02$, $\gamma = 1$, we calculate the eigenvalues and the corresponding eigenvectors for two different values of the interaction parameter β

$$k_1^s = -2.9081, \quad k_2^s = -0.0900, \quad k_3^s = -0.0019 \quad (\beta = \beta_{down} = 0.94 < 1), \quad (18)$$

$$\begin{aligned} \mathbf{v}_1^s &= [-0.7071, -0.7071, 0.0438], \quad \mathbf{v}_2^s = [-0.7064, 0.7064, 0.9247 \cdot 10^{-10}], \\ \mathbf{v}_3^s &= [0.0103, 0.0103, -1.0017] \quad (\beta = \beta_{down} = 0.94 < 1), \end{aligned} \quad (19)$$

$$k_1^u = -3.0612, \quad k_2^u = 0.0600, \quad k_3^u = 0.0012 \quad (\beta = \beta_{up} = 1.04 > 1), \quad (20)$$

$$\begin{aligned} \mathbf{v}_1^u &= [-0.7071, -0.7071, -0.0277], & \mathbf{v}_2^u &= [0.7068, -0.7068, 0.1445 \cdot 10^{-9}], \\ \mathbf{v}_3^u &= [-0.0098, -0.0098, 1.0000] & (\beta = \beta_{down} = 1.04 > 1), \end{aligned} \quad (21)$$

where the apices "s" and "u" indicate stable and unstable equilibrium, respectively.

In fact, for $\beta = \beta_{down} = 0.94$, all the eigenvalues are negative (Eqs. (18)), what causes the corresponding equilibrium point, given by Eqs. (4), (5) for $\beta = \beta_{down}$, to be stable. Analogously, in the second set of eigenvalues (Eqs. (20)) k_2^u and k_3^u are positive, what determines the equilibrium point, given by Eqs. (4), (5) for $\beta = \beta_{up}$, to become unstable. This is clear obtaining the generic vector $[\delta x^s, \delta y^s, \delta z^s]$, whose components are the variations around the equilibrium point. We can express $[\delta x^s, \delta y^s, \delta z^s]$ as a function of the eigenvalues given in Eqs. (18) and the corresponding eigenvectors (Eqs. (19)). By this way we obtain

$$\begin{aligned} [\delta x^s, \delta y^s, \delta z^s] &= C_1 [-0.7071, -0.7071, 0.0438] e^{-2.9081t} \\ &+ C_2 [-0.7064, 0.7064, 0.9247 \cdot 10^{-10}] e^{-0.0900t} \\ &+ C_3 [0.0103, 0.0103, -1.0017] e^{-0.0019t}, \end{aligned} \quad (22)$$

where C_1, C_2, C_3 are generic real numbers. Since k_1, k_2 and k_3 take on negative values, $[\delta x^s, \delta y^s, \delta z^s]$ tends to zero for $t \rightarrow \infty$, this behaviour indicating stability. Analogously, for $\beta = \beta_{up} = 1.04$, we write $[\delta x^u, \delta y^u, \delta z^u]$ as a function of the eigenvalues given in Eqs. (20) and the corresponding eigenvectors (Eqs. (21)), obtaining

$$\begin{aligned} [\delta x^u, \delta y^u, \delta z^u] &= C_1 [-0.7071, -0.7071, -0.0277] e^{-3.0612t} \\ &+ C_2 [0.7068, -0.7068, 0.1445 \cdot 10^{-9}] e^{0.0600t} \\ &+ C_3 [-0.0098, -0.0098, 1.0000] e^{0.0012t}. \end{aligned} \quad (23)$$

Since k_2 and k_3 take on positive values, $[\delta x^u, \delta y^u, \delta z^u]$ diverges for $t \rightarrow \infty$, what indicates instability. In particular, when the condition (6) is satisfied, the stable state, obtained for $\beta = \beta_{down} = 0.94$, is represented by the coexistence of the three species. Otherwise, after a transient, the predator tends to disappear (inequality (6) doesn't hold anymore) and we get a system formed by two competing species, whose coexistence/exclusion conditions depend directly on the value of the parameter β [22, 24–31]. Therefore, the predator plays a regulatory role for the dynamics of the two preys, whose reciprocal behavior is mediated by the interaction parameter β through the presence of the species z . We calculate the numerical solutions for single site dynamics by integrating Eqs. (1) – (3). The parameter values are the same used in the stability analysis, that is $\lambda = 3, \lambda_z = 0.06$,

$\nu = 1, \alpha = 0.02, \gamma = 1$, with the two different values $\beta_{down} = 0.94$ and $\beta_{up} = 1.04$. The initial conditions are $x(0) = y(0) = 0.1, z(0) = 2.0$. The values of multiplicative noise intensity are the same for the three species, that is $\sigma = \sigma_x = \sigma_y = \sigma_z$. In Fig. 1 we show the time series of the three species in coexistence ($\beta = \beta_{down}$) and exclusion ($\beta = \beta_{up}$) regimes, for $\sigma = 0$ and $\sigma = 10^{-16}$. When the system is subject to deterministic dynamics, the coexistence regime causes, after a transient, the three species to reach the stationary values, $x^{stat} = y^{stat} = 0.5, z^{stat} = 1.5$, obtained from Eqs. (4) – (5) using $\nu = 1, \alpha = 0.02, \gamma = 1, \beta = \beta_{down} = 0.94$ (see Fig. 1a). We note that in the graph, as in panels b and c of the same figure, the densities of the two preys overlap, so that the time behaviour of species x (black line) is not visible.

These stationary values, according to the previous stability analysis (see Eq. (22)), correspond to a stable equilibrium point in the phase space. Conversely, taking $\beta = \beta_{up} = 1.04$ and using the same values for the other parameters, from Eqs. (4) – (5) we get $x^{stat} = y^{stat} = 0.5, z^{stat} = -1.0$. According to the previous stability analysis (see Eq. (23)), we observe that these stationary values correspond to an unstable equilibrium point in the phase space. This agrees with two aspects of the dynamics of this system: i) the predator density cannot maintain a negative value, so that it evolves towards a new value, that, in particular, is given by zero (in Fig. 1 we show the time series of the species for $\beta = \beta_{up} = 1.04$ observing the extinction of the species z); ii) one of the two preys cannot keep the equilibrium value 0.5, but has to evolve towards a different stationary value. In fact, after the species z vanishes, the system consists of two competing species, whose dynamics depends on the value of β . In particular, for the value of β considered, that is $\beta = \beta_{up} = 1.04$, after a transient, one of the two species (x and y) disappears (exclusion regime) [24, 29, 30]. We observe that in deterministic exclusion regime the predator tends very slowly to vanish, while the two prey densities reach the stationary values, remaining constant (Fig. 1b), even if this equilibrium point is unstable (see Eq. (23)). However, in the presence of a small level of multiplicative noise, the symmetry, due to the parameter values and initial conditions used in our simulations, is broken and one of the two preys prevails, displacing the other one (Fig. 1d), according to the results previously obtained [29, 30]. Finally we note that no significative modifications occur, with respect

to the deterministic case, when a small level of noise is present in coexistence regime (see Fig. 1c). This obviously depends on the fact that, for $\beta = \beta_{down}$, the system

occupies a stable equilibrium point (see Eq. (22)), which is maintained also in the presence of low levels of multiplicative noise.

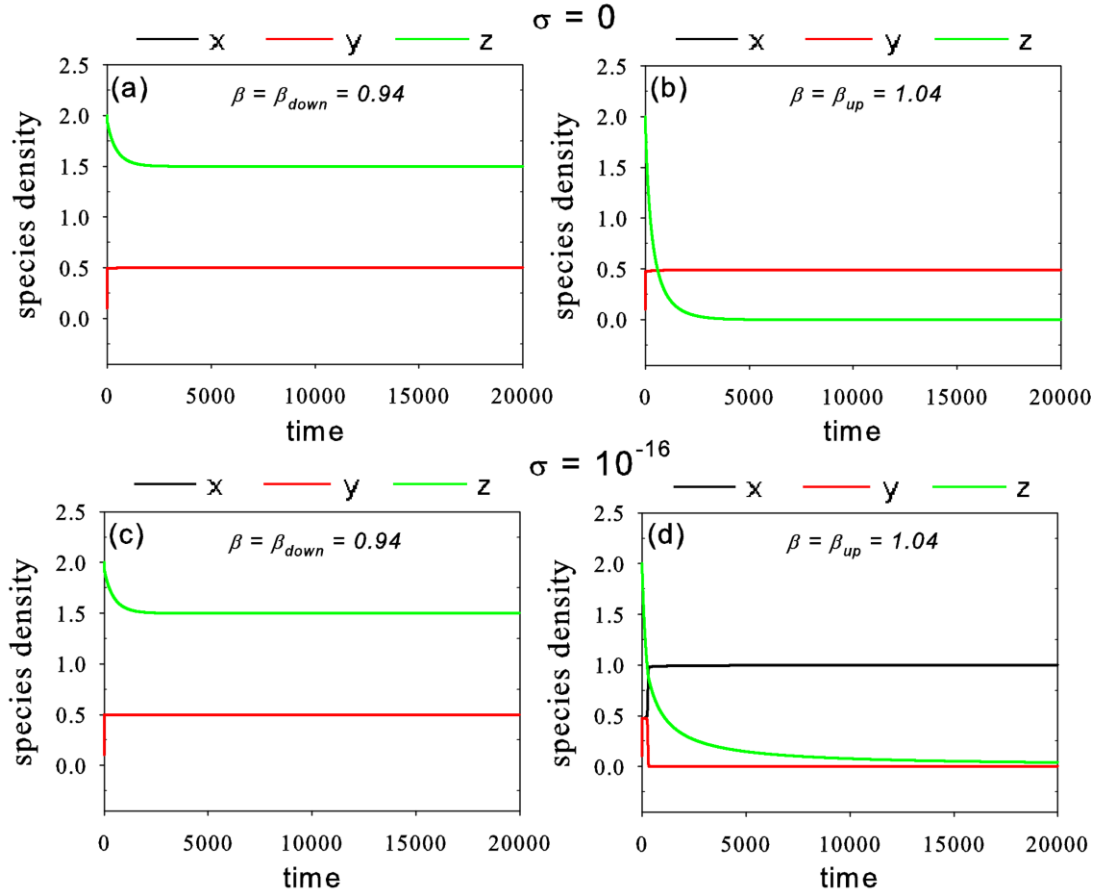


Figure 1. Time evolution of the three species. Deterministic dynamics in (a) coexistence and (b) exclusion regime. Stochastic dynamics, for $\sigma = 10^{-16}$ in (c) coexistence and (d) exclusion regime. Values of the parameters and initial conditions are $\lambda = 3$, $\lambda_z = 0.06$, $\nu = 1$, $\alpha = 0.02$, $\gamma = 1$, $x(0) = y(0) = 0.1$, $z(0) = 2.0$.

However, environmental perturbations, due to the presence both of deterministic and random fluctuations of biological and physical variables, such as the temperature, affect the dynamics of the species. These external forces can modify the behaviour of the populations, either introducing multiplicative noise sources which act directly on the species or affecting the dynamics of the interaction parameter β . In fact, the environmental variations can cause the system dynamics to change between coexistence ($\beta < 2\gamma - \nu$) and exclusion ($\beta > 2\gamma - \nu$) regimes. This dynamical behavior can be described by considering

that the interaction parameter $\beta(t)$ is a stochastic process driven by a dichotomous noise, whose jump rate is given by

$$\chi(t) = \begin{cases} 0, & \Delta t \leq \tau_d, \\ \chi_0 (1 + A |\cos \omega t|), & \Delta t > \tau_d. \end{cases} \quad (24)$$

where Δt is the time interval between two consecutive switches, and τ_d is the delay between two jumps, that is the time interval after a switch, before another jump can occur. In Eq. (24), A and ω are respectively amplitude

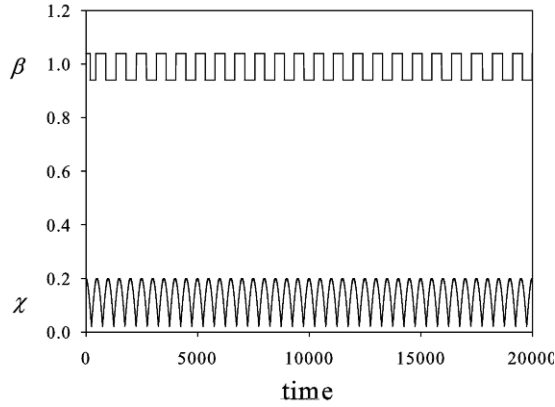


Figure 2. Time evolution of the interaction parameter $\beta(t)$ with initial value $\beta(0) = 1.04$ and delay time $\tau_d = 435$. The interaction parameter $\beta(t)$ switches quasi-periodically between $\beta_{down} = 0.94$ and $\beta_{up} = 1.04$. The values of the other parameters are $A = 9.0$, $\omega/(2\pi) = 10^{-3}$, $\chi_0 = 2 \cdot 10^{-2}$.

and angular frequency of the periodic term, and χ_0 is the jump rate in the absence of periodic term. This causes $\beta(t)$ to jump between two values, $\beta_{down} < 2\gamma - \nu$ and $\beta_{up} > 2\gamma - \nu$. According to the condition (6), these values determine the two possible dynamical regimes (coexistence or exclusion) of the deterministic Lotka-Volterra's model for three interacting species. For given values of the parameters A , ω and χ_0 the switching time between the two levels of $\beta(t)$ depends on τ_d . Applying a procedure analogous to that followed for the two-species case [24], we set $A = 9.0$, $\omega/(2\pi) = 10^{-3}$, $\chi_0 = 2 \cdot 10^{-2}$, obtaining the time series of $\beta(t)$ for $\tau_d = 435$, with $\beta_{down} = 0.94$ and $\beta_{up} = 1.04$. The results, shown in Fig. 2, indicate the presence of a synchronization between the jumps and the periodicity of the rate $\chi(t)$. For a system formed by two competing species this causes a quasi-periodical time behavior of the two populations, which can be considered as a signature of the stochastic resonance phenomenon [32–35] in population dynamics [25–31]. Therefore we fix the delay at the value $\tau_D = 435$, which determines an oscillating dynamical regime. In these conditions, $\beta(t)$ switches quasi-periodically between β_{down} and β_{up} (see Fig. 2), causing the system to be alternatively subject to the coexistence and exclusion regimes.

2.1.2. Time behaviour of the species in a single site

In this section we analyze the time behaviour of three interacting species in a single site of the lattice. From

Eqs. (1)–(3), by setting $D = 0$ we get

$$\dot{x} = \lambda x(1 - \nu x - \beta y - \alpha z) + x\sqrt{\sigma_x}\xi_x(t), \quad (25)$$

$$\dot{y} = \lambda y(1 - \nu y - \beta x - \alpha z) + y\sqrt{\sigma_y}\xi_y(t), \quad (26)$$

$$\dot{z} = \lambda_z z(-1 + \gamma x + \gamma y) + z\sqrt{\sigma_z}\xi_z(t), \quad (27)$$

where the indices i, j where suppressed.

By choosing $\beta(0) = 1.04$ and $\tau_d = 435$, we obtain for $\beta(t)$ the time behaviour shown in Fig. 2. We analyze the time evolution of the species densities by numerical simulation of Eqs. (25)–(27). The time series of x , y and z are obtained for different values of the multiplicative noise intensity, namely $\sigma = 0, 10^{-12}, 10^{-6}, 10^{-3}$. The values of the other parameters are the same used in the previous section, that is $\lambda = 3$, $\lambda_z = 0.06$, $\nu = 1$, $\alpha = 0.02$, $\gamma = 1$, $\beta_{down} = 0.94$, $\beta_{up} = 1.04$. The initial values of the species densities are $x(0) = y(0) = 0.1$, $z(0) = 2.0$. In Fig. 3, where the results are reported, the time series of $x(t)$, $y(t)$ (preys) and $z(t)$ (predator) show correlated behaviour in the absence of noise (panel a). Here, the densities of the two preys overlap and the time series of species x (black line) is not visible.

In the presence of noise intensity an anticorrelated oscillating behaviour of $x(t)$ and $y(t)$ appears (see panels (b)–(d)). Moreover we note that, for all the values of multiplicative noise intensity, the two prey densities oscillate, with the frequency of the external driving force, around the stationary values, $x^{stat} = y^{stat} = 0.5$. We observe that the predator density show an oscillating behaviour, with the same frequency, around a value much smaller than $z^{stat} = 1.5$. However, the oscillations of $z(t)$ are characterized by a larger amplitude with respect to $x(t)$ and $y(t)$. This behaviour is connected with the different effect that the alternating regime (exclusion/coexistence) produces on preys and predator. In fact, the quasi-periodical behaviour of $\beta(t)$ affects directly the dynamics of the predator (see Eq. (5)), causing a decrease of the mean value of z during the exclusion regime. Conversely, in coexistence regime the two preys maintain a constant value (see Eq. (4)) going towards an anticorrelated regime for $\beta(t) = \beta_{up}$. In this last condition the two preys are subject to a pure competitive dynamics, recovering the behaviour observed in a system of two competing species [29, 30].

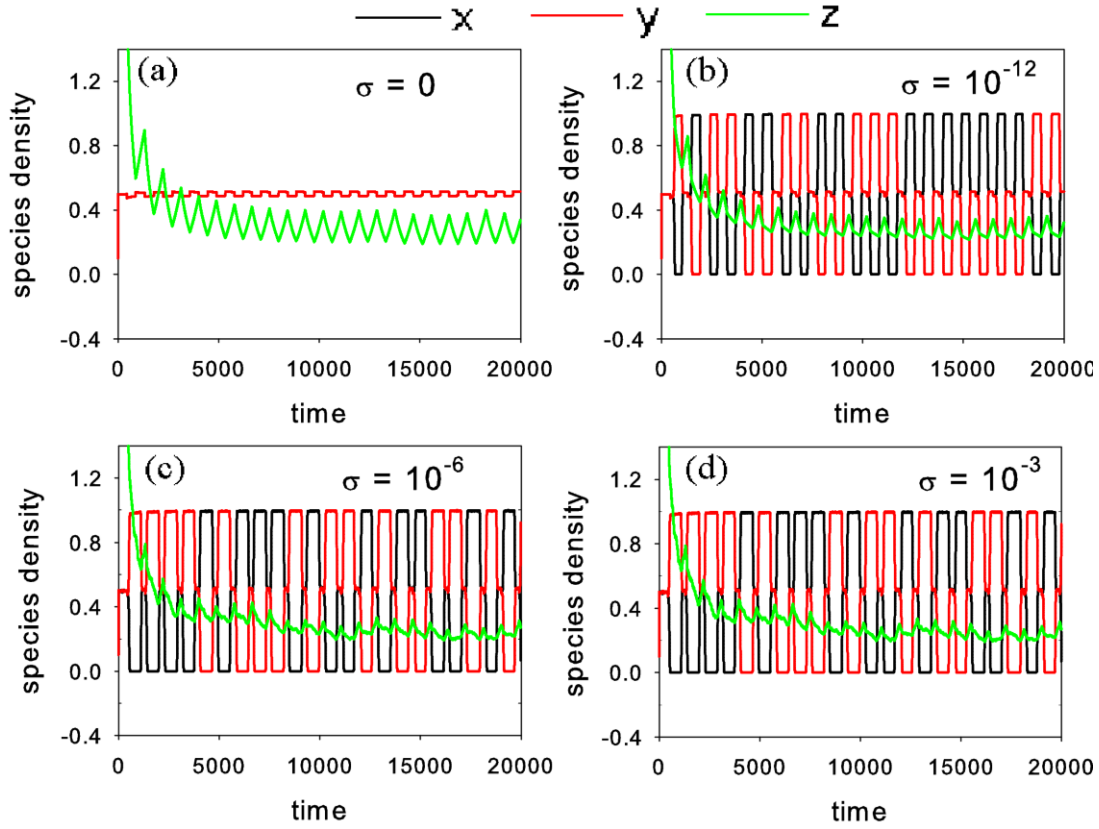


Figure 3. Time evolution of the three species densities in a single site of the lattice. The values of the multiplicative noise intensity are: (a) $\sigma = 0$, (b) $\sigma = 10^{-12}$, (c) $\sigma = 10^{-6}$, (d) $\sigma = 10^{-3}$. Here $\lambda = 3$, $\lambda_z = 0.06$, $\nu = 1$, $\alpha = 0.02$, $\gamma = 1$. The values of the other parameters are the same of Fig. 2. The initial values of the species densities are $x(0) = y(0) = 0.1$, $z(0) = 2.0$. The time series of $x(t)$, $y(t)$ (preys) and $z(t)$ (predator) show a correlated behaviour in the absence of noise (panel a). In the presence of the noise (panels (b)-(d)) an anticorrelated behaviour of $x(t)$ and $y(t)$ appears.

2.2. Spatially extended system: mean field approach

In this section we analyze the time behaviour of three interacting species in a spatially extended system by using a mean field approach. The system dynamics is described by Eqs. (1)–(3) in the presence of the diffusive term ($D \neq 0$). In order to use a mean field approach we derive the moment equations for this system. Assuming $N \rightarrow \infty$, we write Eqs. (1)–(3) in a mean field form

$$\dot{x} = f_x(x, y, z) + \sqrt{\sigma_x} g_x(x) \xi^x(t) + D(\langle x \rangle - x), \quad (28)$$

$$\dot{y} = f_y(x, y, z) + \sqrt{\sigma_y} g_y(y) \xi^y(t) + D(\langle y \rangle - y), \quad (29)$$

$$\dot{z} = f_z(x, y, z) + \sqrt{\sigma_z} g_z(z) \xi^z(t) + D(\langle z \rangle - z), \quad (30)$$

where $\langle x \rangle$, $\langle y \rangle$ and $\langle z \rangle$ are average values on the spatial lattice considered (ensemble averages in the thermody-

namic limit) and we set $f_x(x, y, z) = \lambda x(1 - \nu x - \beta y - \alpha z)$, $g_x(x) = x$, $f_y(x, y, z) = \lambda y(1 - \nu y - \beta x - \alpha z)$, $g_y(y) = y$, $f_z(x, y, z) = \lambda_z z[-1 + \gamma(x + y)]$, $g_z(z) = z$. By site averaging Eqs. (28)–(30), we obtain

$$\begin{aligned} \langle \dot{x} \rangle &= \langle f_x(x, y, z) \rangle, \\ \langle \dot{y} \rangle &= \langle f_y(x, y, z) \rangle, \\ \langle \dot{z} \rangle &= \langle f_z(x, y, z) \rangle. \end{aligned} \quad (31)$$

By expanding the functions $f_x(x, y, z)$, $g_x(x)$, $f_y(x, y, z)$, $g_y(y)$, $f_z(x, y, z)$, $g_z(z)$ around the 1st order moments $\langle x(t) \rangle$, $\langle y(t) \rangle$ and $\langle z(t) \rangle$, we get an infinite set of simultaneous ordinary differential equations for all the moments [36]. To truncate this set we apply a Gaussian approximation, for which the cumulants above the 2nd order vanish. Therefore we obtain

$$\langle \dot{x} \rangle = \lambda \langle x \rangle (1 - \nu \langle x \rangle - \beta \langle y \rangle - \alpha \langle z \rangle) - \lambda (\nu \mu_{200} + \beta \mu_{110} + \alpha \mu_{101}), \quad (32)$$

$$\langle \dot{y} \rangle = \lambda \langle y \rangle (1 - \nu \langle y \rangle - \beta \langle x \rangle - \alpha \langle z \rangle) - \lambda (\nu \mu_{020} + \beta \mu_{110} + \alpha \mu_{011}), \quad (33)$$

$$\langle \dot{z} \rangle = \lambda_z \langle z \rangle (-1 + \nu \langle x \rangle + \nu \langle y \rangle) + \lambda_z \nu (\mu_{101} + \mu_{011}), \quad (34)$$

$$\begin{aligned} \dot{\mu}_{200} &= 2\lambda (1 - 2\nu \langle x \rangle - \beta \langle y \rangle - \alpha \langle z \rangle) \mu_{200} \\ &\quad - 2\lambda \langle x \rangle (\beta \mu_{110} + \alpha \mu_{101}) + 2\sigma_x (\mu_{200} + \langle x \rangle^2) - 2D\mu_{200}, \end{aligned} \quad (35)$$

$$\begin{aligned} \dot{\mu}_{020} &= 2\lambda (1 - 2\nu \langle y \rangle - \beta \langle x \rangle - \alpha \langle z \rangle) \mu_{020} \\ &\quad - 2\lambda \langle y \rangle (\beta \mu_{110} + \alpha \mu_{011}) + 2\sigma_y (\mu_{020} + \langle y \rangle^2) - 2D\mu_{020}, \end{aligned} \quad (36)$$

$$\begin{aligned} \dot{\mu}_{002} &= 2\lambda_z (-1 + \nu \langle x \rangle + \nu \langle y \rangle) \mu_{002} \\ &\quad + 2\lambda_z \nu \langle z \rangle (\mu_{101} + \mu_{011}) + 2\sigma_z (\mu_{002} + \langle z \rangle^2) - 2D\mu_{002}, \end{aligned} \quad (37)$$

$$\begin{aligned} \dot{\mu}_{110} &= \lambda [2 - 2\nu (\langle x \rangle + \langle y \rangle) - \beta (\langle x \rangle + \langle y \rangle) - 2\alpha \langle z \rangle] \mu_{110} \\ &\quad - \lambda \beta (\langle x \rangle \mu_{020} + \langle y \rangle \mu_{200}) - \lambda \alpha (\langle x \rangle \mu_{011} + \langle y \rangle \mu_{101}) - 2D\mu_{110}, \end{aligned} \quad (38)$$

$$\begin{aligned} \dot{\mu}_{101} &= \lambda (1 - 2\nu \langle x \rangle - \beta \langle y \rangle - \alpha \langle z \rangle) \mu_{101} + \lambda_z (-1 + \nu \langle x \rangle + \nu \langle y \rangle) \mu_{101} \\ &\quad - \lambda \langle x \rangle (\alpha \mu_{002} + \beta \mu_{011}) + \lambda_z \nu \langle z \rangle (\mu_{110} + \mu_{200}) - 2D\mu_{101}, \end{aligned} \quad (39)$$

$$\begin{aligned} \dot{\mu}_{011} &= \lambda (1 - 2\nu \langle y \rangle - \beta \langle x \rangle - \alpha \langle z \rangle) \mu_{011} + \lambda_z (-1 + \nu \langle x \rangle + \nu \langle y \rangle) \mu_{011} \\ &\quad - \lambda \langle y \rangle (\alpha \mu_{002} + \beta \mu_{101}) + \lambda_z \nu \langle z \rangle (\mu_{110} + \mu_{020}) - 2D\mu_{011}, \end{aligned} \quad (40)$$

where μ_{200} , μ_{020} , μ_{002} , μ_{110} , μ_{101} , μ_{011} are the 2^{nd} order central moments defined on the lattice

$$\begin{aligned} \mu_{200}(t) &= \langle x^2 \rangle - \langle x \rangle^2, \\ \mu_{020}(t) &= \langle y^2 \rangle - \langle y \rangle^2, \\ \mu_{002}(t) &= \langle z^2 \rangle - \langle z \rangle^2, \\ \mu_{110}(t) &= \langle xy \rangle - \langle x \rangle \langle y \rangle, \\ \mu_{101}(t) &= \langle xz \rangle - \langle x \rangle \langle z \rangle, \\ \mu_{011}(t) &= \langle yz \rangle - \langle y \rangle \langle z \rangle. \end{aligned} \quad (41)$$

In order to get the dynamics of the three species we analyze the time evolution of the 1^{st} and 2^{nd} order moments according to Eqs. (32)–(40). As initial conditions we consider each species uniformly distributed on the spatial domain, that is we set $\langle x(0) \rangle = \langle y(0) \rangle = 0.1$, $\langle z(0) \rangle = 2.0$, $\mu_{200}(0) = \mu_{020}(0) = \mu_{002}(0) = \mu_{110}(0) = \mu_{101}(0) = \mu_{011}(0) = 0$. Therefore, from Eqs. (32)–(40) we get, in the deterministic case, the stationary values for $\langle x \rangle$, $\langle y \rangle$ and $\langle z \rangle$, in the coexistence regime.

$$\begin{aligned} \langle x \rangle^{stat} &= \langle y \rangle^{stat} = \frac{1}{2\nu}, \\ \langle z \rangle^{stat} &= \frac{2\nu - (\beta_{down} + \nu)}{2\alpha\nu}. \end{aligned} \quad (42)$$

Using for the parameters the same values of the single site analysis, we obtain

$$\begin{aligned} \langle x \rangle^{stat} &= \langle y \rangle^{stat} = 0.5, \\ \langle z \rangle^{stat} &= 1.5. \end{aligned} \quad (43)$$

We also fix the delay time at the same value, $\tau_d = 435$, used in the single site case. Finally, by numerical integration of Eqs. (32)–(40), setting $D = 10^{-1}$, we get the time series of the 1^{st} and 2^{nd} order moments for the following values of multiplicative noise intensity $\sigma = 0, 10^{-12}, 10^{-6}, 10^{-3}$. The results are reported in Figs. 4, 5. Here we note that, after a transient, the mean values of the two prey densities (see panels a and d of Figs. 4, 5) oscillate around the stationary values. The oscillations are connected with the presence of two stable equilibrium points. For $\beta = \beta_{down} < 1$ the stable equilibrium is given by the contemporary presence of the three species (coexistence regime). Conversely, for $\beta = \beta_{up} > 1$ the system goes towards a new equilibrium point, with the predator tending to disappear (exclusion regime). In the presence of a dynamical regime (the system switches periodically from coexistence to exclusion), we observe the appearance of correlated oscillations in the time series of $\langle x(t) \rangle$, $\langle y(t) \rangle$ and $\langle z(t) \rangle$. In particular, we note that $\langle z(t) \rangle$ is subject to oscillations occurring around a value much smaller than

the stationary one ($\langle z \rangle^{stat} = 1.5$) and characterized by a larger amplitude with respect to $\langle x(t) \rangle$ and $\langle y(t) \rangle$. This

behaviour is analogous to that observed in the case of single site dynamics.

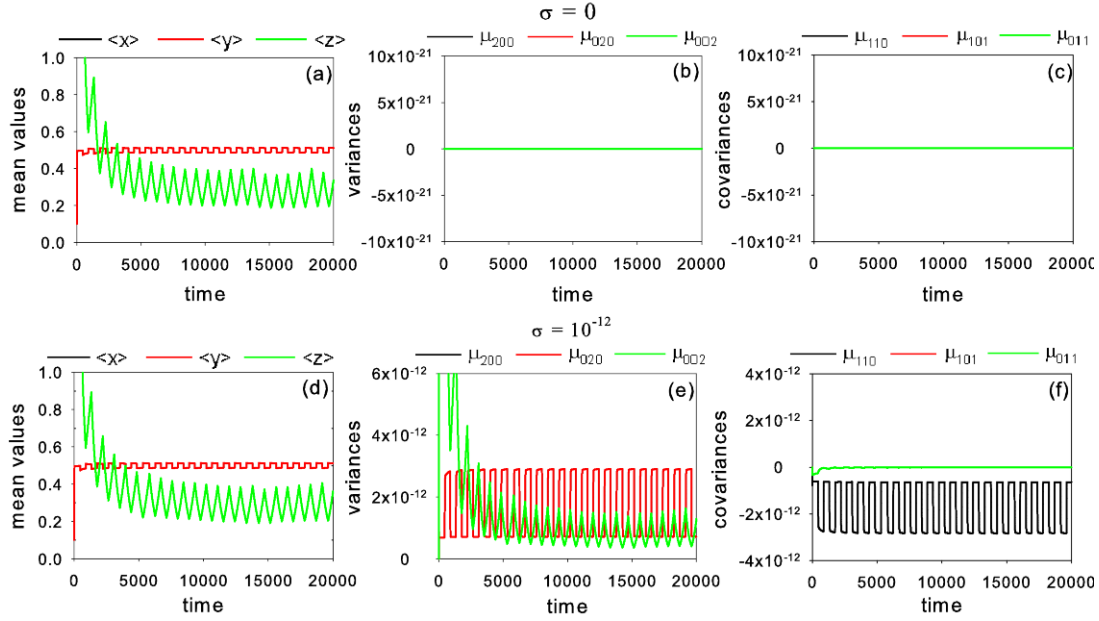


Figure 4. Time evolution of the 1^{st} and 2^{nd} order moments in the mean field approach. The values of the multiplicative noise intensity are: $\sigma = 0, 10^{-12}$ from top to bottom. In the absence of noise the time series of $\langle x(t) \rangle$, $\langle y(t) \rangle$ (panel a), μ_{200} , μ_{020} , μ_{002} (panel b) and μ_{110} , μ_{101} , μ_{011} (panel c) are completely overlapped. The predator (mean value of species z) shows a behaviour correlated with those of both preys (mean values of species x and y). For $\sigma = 10^{-12}$, no changes are observed in the behaviour of the mean values (panel d), the variances of the two preys oscillate overlapping each other and a correlation is observed with the variance of the species z (panel e), the covariance of the two preys, μ_{110} , oscillates taking on only negative values (the two preys are anticorrelated each other), while μ_{101} and μ_{011} are always zero (panel f). The initial values of the moments are $\langle x(0) \rangle = \langle y(0) \rangle = 0.1$, $\langle z(0) \rangle = 2.0$, $\mu_{200}(0) = \mu_{020}(0) = \mu_{002}(0) = \mu_{110}(0) = \mu_{101}(0) = \mu_{011}(0) = 0$. The diffusion coefficient is $D = 10^{-1}$. The values of the other parameters are the same used in Fig. 3.

In the absence of noise (top of Fig. 4), the time series of $\langle x(t) \rangle$, $\langle y(t) \rangle$ and $\langle z(t) \rangle$ (panel a), $\mu_{200}(t)$, $\mu_{020}(t)$, $\mu_{002}(t)$ (panel b) and $\mu_{110}(t)$, $\mu_{101}(t)$, $\mu_{011}(t)$ (panel c) are completely overlapped and each species maintains a homogeneous distribution over the lattice, that is all the 2^{nd} order moments remain equal to zero. In particular we observe that in panels a, d of Fig. 4 and Fig. 5 the time behavior of prey x (black line) is not visible, because of the overlap with the time series of prey y . In panels b, c of Fig. 4 the 2^{nd} order moments of all the three species overlap and the only green line is visible. For $\sigma = 10^{-12}$ (bottom of Fig. 4) no changes are observed in the behaviour of the mean values (see panel d), and the variances of the three species show correlated oscillations (panel e). In panel f, μ_{110} oscillates taking on only negative values. This indicates that the spatial distributions in the lattice will be characterized by the presence of regions where species x or species y prevails. The two preys will be distributed

therefore in non-overlapping spatial patterns. This picture is in agreement with previous results obtained with a different model [37]. Conversely, μ_{101} and μ_{011} are always zero (see panel f of Fig. 4). This behaviour indicates that the predator is uncorrelated with the density of each prey: the species z tends to occupy indifferently the sites where x or y prevails (see the time behaviour of μ_{002} in panel e of Fig. 4), but is correlated with the total prey density (a global increase of food availability improves the life conditions of the predator). This explains why the variance of the predator shows small oscillations. On the other hand, when exclusion regime takes place, the two preys tend to occupy different sites, "spreading out" in the spatial domain and causing an increase of their variances (see panel e of Fig. 4) with a stronger anticorrelation (see the behaviour of μ_{110} in panel f of Fig. 4). Finally we note that the amplitude of the oscillations both of all variances and covariances μ_{110} increases as a function of the noise inten-

sity. This dependency is connected with pattern formation in the spatial distributions of the three species [37], what suggests the presence of a phase transition phenomenon. In particular the oscillations of the second order moments have the same order of magnitude of σ (see panels b, c, e, f, in Figs. 4, 5). In fact, for higher levels of multiplicative

noise ($\sigma = 10^{-6}, 10^{-3}$) the amplitude of the oscillations increases and the periodical anticorrelated behaviour between the two preys becomes more evident. Conversely, no modifications appear in the time series of the mean values as a function of the multiplicative noise intensity (see panels a, d in Figs. 4, 5).

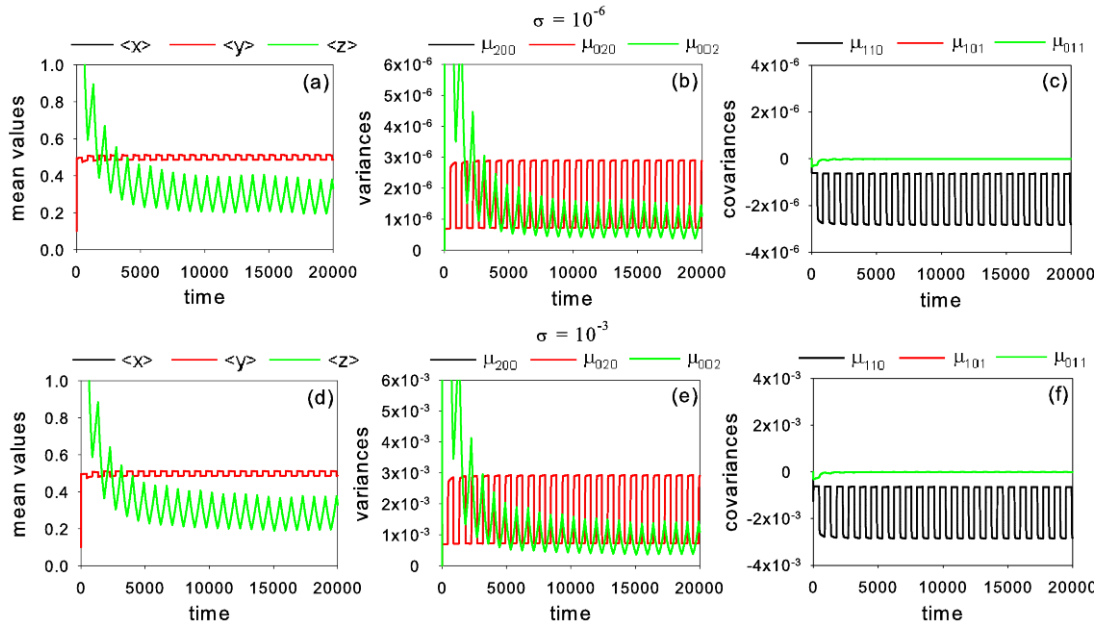


Figure 5. Time evolution of the 1st and 2nd order moments. The values of the multiplicative noise intensity are: 10^{-6} , 10^{-3} from top to bottom. No changes are observed in the time behaviour of $\langle x \rangle = \langle y \rangle = \langle z \rangle$ (see panels a and d) for both values of the noise intensity. An increase in the amplitude of oscillations, as a function of the noise intensity, appears both in the variances of the three species, μ_{200} , μ_{020} , μ_{002} (see panels b and e), and in the covariance of the two preys, μ_{110} (see panels c and f). The values both of initial conditions and parameters are the same used in Fig. 4.

Even if it is related to a very different mechanism, this behavior is similar to the stochastic resonance effect produced in population dynamics, when the interaction parameter is subjected to an oscillating bistable potential in the presence of additive noise [29–31]. We note that in the absence of external noise ($\sigma = 0$) both populations coexist and the species densities oscillate in phase around their stationary value [29, 30]. This occurs identically in each site of the spatial lattice (single site dynamics). The behavior of the mean values reproduces this situation. For $\sigma \neq 0$, in the single site dynamics we observe anticorrelated oscillations of x and y (preys). By site averaging these noise-induced oscillations (see Ref. [29, 30]) we recover the average behavior obtained in the absence of noise. This spatial auto-averaging effect explains why the 1st order moment behavior is independent on the external

noise intensity, while the 2nd order moments give information on “spreading” and anticorrelation of the species densities in the spatial domain.

3. Coupled map lattice model

In this section we adopt a different approach to analyze the dynamics of the three species on the square lattice defined in Section 2. We consider the time evolution of our system by using a coupled map lattice (CML) model [21]. In this formalism both correlated and anticorrelated spatial patterns of the three interacting species have been found [37]. Here we calculate the moments by using the CML model. By this approach, the dynamics of the spatial distributions of the three species is given by the following

equations

$$x_{i,j}^{(n+1)} = \lambda x_{i,j}^{(n)} \left(1 - \nu x_{i,j}^{(n)} - \beta^{(n)} y_{i,j}^{(n)} - \alpha z_{i,j}^{(n)} \right) + \sqrt{\sigma_x} x_{i,j}^{(n)} \xi_{i,j}^{x(n)} + D \sum_{\rho} \left(x_{\rho}^{(n)} - x_{i,j}^{(n)} \right), \quad (44)$$

$$y_{i,j}^{(n+1)} = \lambda y_{i,j}^{(n)} \left(1 - \nu y_{i,j}^{(n)} - \beta^{(n)} x_{i,j}^{(n)} - \alpha z_{i,j}^{(n)} \right) + \sqrt{\sigma_y} y_{i,j}^{(n)} \xi_{i,j}^{y(n)} + D \sum_{\rho} \left(y_{\rho}^{(n)} - y_{i,j}^{(n)} \right), \quad (45)$$

$$z_{i,j}^{(n+1)} = \lambda z_{i,j}^{(n)} \left(-1 + \gamma x_{i,j}^{(n)} + \gamma y_{i,j}^{(n)} \right) + \sqrt{\sigma_z} z_{i,j}^{(n)} \xi_{i,j}^{z(n)} + D \sum_{\rho} \left(z_{\rho}^{(n)} - z_{i,j}^{(n)} \right), \quad (46)$$

where $x_{i,j}^{(n)}$, $y_{i,j}^{(n)}$ and $z_{i,j}^{(n)}$ denote respectively the densities of prey x , prey y and predator z in the site (i, j) at the time step n . According to the notation used for the mean field approach, λ , λ_z , ν , β , α , γ and D represent the same quantities defined in Section 2. $\xi_{i,j}^{x(n)}$, $\xi_{i,j}^{y(n)}$, $\xi_{i,j}^{z(n)}$ are independent Gaussian white noise sources with zero mean and unit variance. The interaction parameter $\beta^{(n)}$ corresponds to the value of $\beta(t)$ taken at the time step n , according to Eq. (24). Here \sum_{ρ} indicates the sum over the four nearest neighbours.

3.1. Stationary states for the CML model

Applying a procedure analogous to that used for Eqs. (1)–(3), we consider Eqs. (44)–(46) in the absence both of noise sources and diffusion terms ($D = 0$). In this conditions, for $x_{i,j}^{(n+1)} = x_{i,j}^{(n)}$, $y_{i,j}^{(n+1)} = y_{i,j}^{(n)}$, $z_{i,j}^{(n+1)} = z_{i,j}^{(n)}$, we obtain the stationary values of the three species densities for the generic site

$$x_{CML}^{stat} = y_{CML}^{stat} = \frac{1}{2\gamma} \left[\frac{\lambda_z + 1}{\lambda_z} \right], \quad (47)$$

$$z_{CML}^{stat} = \frac{2\gamma \left[\frac{\lambda-1}{\lambda} \right] - (\beta + \nu) \left[\frac{\lambda_z+1}{\lambda_z} \right]}{2\alpha\gamma}, \quad (48)$$

where the indices i, j were suppressed. As in the approach based on the use of differential equations, the stationary values of the two prey densities are independent on the interaction parameter β , which is responsible for the two different dynamical regimes, coexistence or exclusion, and affects the dynamics of the whole system through its action on the stationary value z_{CML}^{stat} . The existence condition for the predator

$$z_{CML}^{stat} = \frac{2\gamma \left[\frac{\lambda-1}{\lambda} \right] - (\beta + \nu) \left[\frac{\lambda_z+1}{\lambda_z} \right]}{2\alpha\gamma} > 0 \quad (49)$$

allows to get the following inequality for the interaction parameter β

$$\beta < 2\gamma \left[\frac{\frac{\lambda-1}{\lambda}}{\frac{\lambda_z+1}{\lambda_z}} \right] - \nu. \quad (50)$$

The inequality (50) indicates that, according to the analysis performed in Section 2.1, the CML model is characterized by two stationary states that become stable or unstable depending on the values of the parameters. Comparing the inequalities (6) and (50), we note that in the CML model the coexistence condition and the regulatory role, played by the predator on the dynamics of the two preys, depend also on the scale factors λ and λ_z .

3.2. Time series in the CML model

In view of a comparison between mean field approach and CML model, we define the 1st and 2nd order moments on the discrete lattice, at the time step n . The mean values, $\langle x \rangle^{(n)}$, $\langle y \rangle^{(n)}$, $\langle z \rangle^{(n)}$, given by

$$\langle u \rangle^{(n)} = \frac{\sum_{i,j} u_{i,j}^{(n)}}{N}, \quad (u = x, y, z) \quad (51)$$

represent the 1st order moments. The variances $var_x^{(n)}$, $var_y^{(n)}$, $var_z^{(n)}$ defined as

$$var_u^{(n)} = \frac{\sum_{i,j} \left(u_{i,j}^{(n)} - \langle u \rangle^{(n)} \right)^2}{N}, \quad (u = x, y, z), \quad (52)$$

and the covariances

$$cov_{uw}^{(n)} = \frac{\sum_{i,j} \left(u_{i,j}^{(n)} - \langle u \rangle^{(n)} \right) \left(w_{i,j}^{(n)} - \langle w \rangle^{(n)} \right)}{N}, \quad (u, w = x, y, z; \quad u \neq w) \quad (53)$$

are the 2nd order central moments.

In order to get $\beta = 1$ as critical value for the coexistence/exclusion regimes, we choose for all parameters, except γ , the same values of Section 2. In fact, by setting $\lambda = 3$, $\lambda_z = 0.06$, $\nu = 1$, $\alpha = 0.02$, $\gamma = 26.5$ in Eqs. (49), (50), we obtain, for $\beta < 1$, survivance of the species z and, as a consequence, coexistence of the three species. Conversely, for $\beta > 1$, we get the exclusion regime. Therefore, the value $\gamma = 26.5$ allows to obtain the coexistence/exclusion dynamical regime for the same time behaviour of $\beta(t)$ used in the moment approach (see Eq. (24) and Fig. 2).

Finally, by using this set of parameter values in Eqs. (47), (48), we calculate the stationary values for the

densities of the two preys and predator in the coexistence regime ($\beta = \beta_{down} = 0.94$)

$$\begin{aligned}\langle x \rangle_{CML}^{stat} &= \langle y \rangle_{CML}^{stat} = 0.3, \\ \langle z \rangle_{CML}^{stat} &= 1.0.\end{aligned}\quad (54)$$

We note that these values are close to those obtained in the mean field approach (see Eqs. (43)). The CML model can be considered as a time discrete version of the Lotka-Volterra system, with time step $\Delta t = 1$. For the numerical integration of Eqs. (32)–(40) we used $dt = 10^{-3}$, which is a suitable value to obtain convergence of the solution. Obviously, with these values of Δt and dt , the dynamics of the CML model results to be faster with respect to that obtained within the moment formalism. In particular, for $\beta = \beta_{up} > 1$, using the same parameter values of the mean field approach, the exclusion regime causes the species z to vanish in one time step ($\Delta t = 1$). This implies that, when the system is subject to the dynamical regime discussed in Section 2.1, the predator disappears. This behaviour disagrees with the results found by using the moment equations (see Section 2.2).

In particular, we calculated the solutions of Eqs. (44) – (46) in the coexistence/exclusion dynamical regime for values of the diffusion coefficient progressively decreasing, i.e. $D = 10^{-1}$, 10^{-2} , 10^{-3} , and we found exclusion of species z .

In order to remove this discrepancy between CML model and mean field approach, in the discrete time equations we use a much smaller value for the diffusion constant, namely $D = 10^{-4}$, that allows to obtain a slowdown of the diffusion dynamics and, as a consequence, the survival of the predator in the coexistence/exclusion dynamical regime. In order to get the time behaviour of the 1st and 2nd order moments within the scheme of the CML model, we consider a square lattice with $N = 100 \times 100$, using for $\beta(t)$ the time behaviour given in Fig. 2. Afterwards, at each time step n we calculate, from Eqs. (44), (45), (46), the new values of $x_{i,j}^{(n)}$, $y_{i,j}^{(n)}$, $z_{i,j}^{(n)}$, and the moments according to Eqs. (51), (52), (53). By iterating this procedure, we obtain the time series shown in Figs. 6, 7.

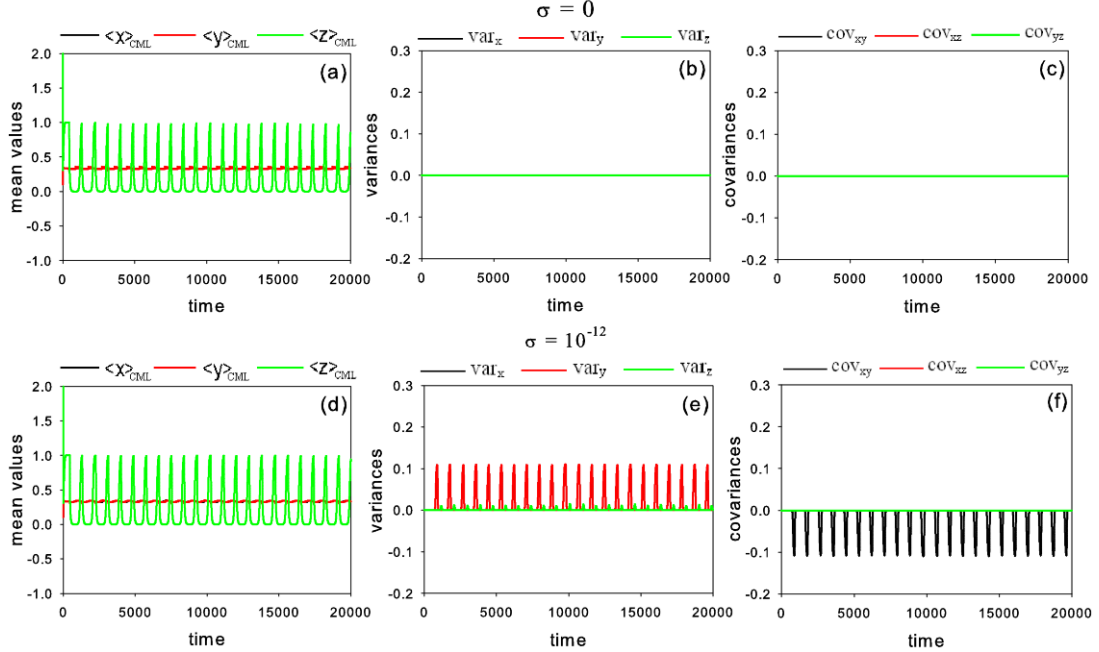


Figure 6. In panels (a), (b) and (c) we show, respectively, the mean values, $\langle x \rangle^{(n)}$, $\langle y \rangle^{(n)}$, $\langle z \rangle^{(n)}$, the variances, $var_x^{(n)}$, $var_y^{(n)}$, $var_z^{(n)}$, and the covariances, $cov_{xy}^{(n)}$, $cov_{yz}^{(n)}$, $cov_{xy}^{(n)}$ for $\sigma = 0$. The same quantities are shown in panels (d), (e) and (f) for $\sigma = 10^{-12}$. The time series are obtained within the formalism of the CML model (see Eqs. (44), (45), (46)). The diffusion coefficient is $D = 10^{-4}$, and $\gamma = 26.5$. The initial values of the species concentrations are $x_{i,j}^{(0)} = y_{i,j}^{(0)} = 0.1$, $z_{i,j}^{(0)} = 2.0$ for all the sites (i, j) . The values of the other parameters are the same of Fig. 4: $\lambda = 3$, $\lambda_z = 0.06$, $\nu = 1$, $\alpha = 0.02$.

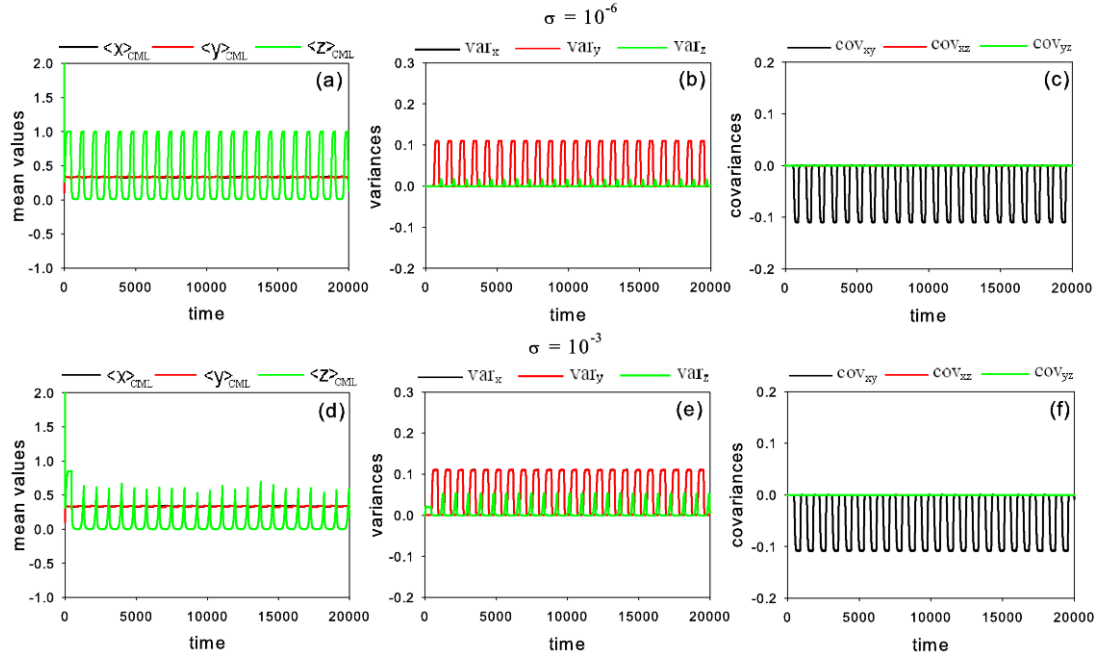


Figure 7. In panels (a), (b) and (c) we show, respectively, the mean values, $\langle x \rangle^{(n)}$, $\langle y \rangle^{(n)}$, $\langle z \rangle^{(n)}$, the variances, $var_x^{(n)}$, $var_y^{(n)}$, $var_z^{(n)}$, and the covariances, $cov_{xy}^{(n)}$, $cov_{yz}^{(n)}$, $cov_{xz}^{(n)}$ for $\sigma = 10^{-6}$. The same quantities are shown in panels (d), (e) and (f) for $\sigma = 10^{-3}$. The time series are obtained within the formalism of the CML model (see Eqs. (44), (45), (46)). The values of the other parameters and the initial conditions are the same of Fig. 6.

Since the interaction among sites is limited to the nearest neighbors (each site only interacts with other four ones), we expect that for a square lattice the results do not depend significantly on the size of the spatial domain, when the condition $N \gg 4$ is satisfied. An increase of the system size should delay the very short transient of the system dynamics towards the stationary behaviour shown in Figs. 6, 7, recovering the longer transient behaviour found in the mean field approach (see Figs. 4, 5).

The 1st and 2nd order moments calculated within the formalism of the CML model can be compared with the same quantities obtained in the mean field approach (see Figs. 4, 5). We note that the two set of time series are in a good qualitative agreement.

According to the results obtained in the formalism of the moment equations, the mean values of the three species show time oscillations, whose amplitude is larger for the predator (panels a, d of Figs. 6, 7). In the absence of noise, the 2nd order moments remain equal to zero (see panels b, c of Fig. 6), recovering the conditions of homogeneous distributions obtained for $\sigma = 0$ in the mean field approach (see panels b, c of Fig. 4). In the presence

of multiplicative noise, no modifications occur in the time series of the 1st order moments (see left side panels in Figs. 6, 7). However, for $\sigma \neq 0$ a symmetry breaking is introduced, with non-vanishing oscillating variances that are connected with inhomogeneous distributions of the three species. For higher levels of the noise intensity, the amplitude of the oscillations remains constant in the time series of var_x , var_y and var_z (see panels b, e of Figs. 6, 7). These results show some difference with those obtained in the formalism of moment equations, where higher noise intensities cause the oscillation amplitudes of μ_{200} , μ_{020} and μ_{002} to become larger (see panels b, e of Figs. 4, 5). Finally, we find that for $\sigma \neq 0$, temporal oscillations also appear in the time series of cov_{xy} . This agrees with the results of the mean field approach, revealing the presence of an anticorrelated dynamics between the two preys. On the other hand, cov_{xz} and cov_{yz} remain equal to zero also in the presence of multiplicative noise. This behaviour, in agreement with that obtained in the mean field formalism, indicates that the spatial distribution of the predator is uncorrelated with those of each prey considered separately, but depends on the total density of preys. The

comparison between the two approaches shows that the mean values $\langle x \rangle^{(n)}$, $\langle y \rangle^{(n)}$, $\langle z \rangle^{(n)}$ and those obtained within the formalism of the moment equations oscillate around different values. Moreover, the amplitudes of the oscillations in the 2nd order moments appear significantly larger in the CML model. This discrepancies can be explained recalling that: i) in the two approaches the stationary values are different (see Eqs. (42) and Eqs. (47)–(48)); ii) in the mean field formalism the interaction between sites is extended to the whole spatial domain, conversely in the CML model the species interaction is restricted to the nearest neighbors; iii) the dynamics of the CML model is faster since an unitary time step ($\Delta t = 1$) is taken, instead of the time step $dt = 10^{-3}$ used in the moment equations.

4. Conclusions

We report a study on the stochastic dynamics of an ecosystem with three interacting species (two preys and one predator), described by generalized Lotka-Volterra equations. After considering the single site dynamics of the ecosystem, we consider a spatially extended domain (two-dimensional lattice) by introducing diffusive terms to take into account the interaction of each site with all the other ones. The study is performed by a mean field approach, in the formalism of the moment equations. The system is affected by the presence of two noise sources, namely a multiplicative white noise and a correlated dichotomous noise. The role of the correlated dichotomous noise is to control the dynamical regime of the ecosystem (see Fig. 2), while the multiplicative noise is responsible for the anticorrelated behavior of the species concentrations. The mean field approach in Gaussian approximation enables us to obtain the time series of the 1st and 2nd order moments. We compare the results obtained within the mean field approach with the time series calculated by a coupled map lattice (CML) model. The agreement is quite good, even if some discrepancies are present, due to the discrete nature of the CML model and the limited extension of the diffusive interaction (nearest neighbors) among different sites of the coupled map lattice. Our theoretical results could explain the time evolution of populations in real ecosystems whose dynamics is strictly dependent on random fluctuations, always present in natural environment [23, 38, 39]. In particular, the time series of real data for vole and lemming populations revealed the presence both of cycles and random fluctuations, and the question is “whether a key feature of the cycle... is best understood in terms of highly nonlinear interactions with modest influence of environmental stochasticity or weakly nonlinear interactions with strong stochastic forcing” (see

in Ref. [7]). Detailed studies on the time series of the feral Soay sheep of the St. Kilda archipelago have been performed, reproducing the time behaviour of the sheep distributions by using an autoregressive model which involves nonlinearity, periodic climate variations and environmental noise [40]. The introduction of stochastic terms, into a system of Lotka-Volterra equations for two competing species, allowed to reproduce both the spatial distributions of benthic foraminifera in marine environment [41] and the time behaviour of the concentration of a bacterium, *Listeria monocytogenes*, in a food product [42], finding a good agreement with experimental data. Finally, we note that connections between random fluctuations of environmental variables and amplitude of oscillations in the population abundances were found in time series of planktonic foraminifera [43]. The model presented in this paper is the two-dimensional version of nonlinear stochastic models previously investigated. The application of a mean field approach makes direct to analyze the spatial distributions in terms of mean concentrations and corresponding variances and covariances (2nd order moments). The knowledge of the 2nd order moments and their relations with the amplitude of random fluctuations could be the key to explain spatial distributions of biological species, and to account the pattern formations appearing both in theoretical studies [22, 37] and in real ecosystems, such as fish populations in marine environment [23, 44, 45]. This analysis, performed on ecosystems consisting of three species, will be the subject of a forthcoming paper.

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