NONMONOTONIC BEHAVIOR OF SPATIOTEMPORAL PATTERN FORMATION IN A NOISY LOTKA–VOLTERRA SYSTEM*

A. Fiasconaro[†], D. Valenti and B. Spagnolo

INFM, Group of Interdisciplinary Physics and
Dipartimento di Fisica e Tecnologie Relative, Università di Palermo
Viale delle Scienze, 90128 Palermo, Italy

The noise-induced pattern formation in a population dynamical model of three interacting species in the coexistence regime is investigated. A coupled map lattice of Lotka–Volterra equations in the presence of multiplicative noise is used to analyze the spatiotemporal evolution. The spatial correlation of the species concentration as a function of time and of the noise intensity is investigated. A nonmonotonic behavior of the area of the patterns as a function of both noise intensity and evolution time is found.

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1. Introduction

The study of models of population dynamics is one of the topics that in the last few years has revealed large interest ranging from chaos to spatial organization, covering several branches of physics and different disciplines such as biology, theoretical ecology, oceanography and medicine. In particular the addition of noise in such mathematical models can be useful to describe the phenomenology in a realistic and relatively simple form. The introduction of noise in real systems gives rise to non trivial effects, modifying sometimes in an unexpected way the deterministic dynamics. Examples of noise induced phenomena are stochastic resonance [1,2], noise-enhanced stability [3], temporal oscillations and noise-induced pattern formation [4–6]. Biological complex systems can be modeled as open systems in which interactions between the components are nonlinear and a noisy interaction

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with the environment is present [7]. The dynamics of interacting biological species can be successfully described by means of a set of Lotka–Volterra equations with the addition of a multiplicative noise and a diffusive term to take into account spatial extension of the ecosystem. Recently it has been found that nonlinear interaction and the presence of multiplicative noise can give rise to pattern formation in population dynamics of spatially extended systems [8,9]. The model studied in this work concerns the ecosystem composed of three interacting species: two competing preys and one predator. The area of the patterns of maximum density has been quantitatively evaluated, finding a nonmonotonic behavior as a function of time and as a function of the noise intensity. The site correlation between the species concentration as a function of time and of the noise intensity is also investigated.

2. The model

The starting point of our study is the simple discrete set of generalized Lotka–Volterra equations describing a population of two preys and one predator. The dynamics of our spatially distributed system is therefore described by the following model of coupled map lattice (CML) [10]

$$x_{i,j}^{n+1} = \mu x_{i,j}^n (1 - \nu x_{i,j}^n - \beta^n y_{i,j}^n - \alpha z_{i,j}^n) + \sqrt{q} x_{i,j}^n X_{i,j}^n + D \sum_p (x_p^n - x_{i,j}^n),$$

$$y_{i,j}^{n+1} = \mu y_{i,j}^n (1 - \nu y_{i,j}^n - \beta^n x_{i,j}^n - \alpha z_{i,j}^n) + \sqrt{q} y_{i,j}^n Y_{i,j}^n + D \sum_p (y_p^n - y_{i,j}^n),$$

$$z_{i,j}^{n+1} = \mu_z z_{i,j}^n [-1 + \gamma(x_{i,j}^n + y_{i,j}^n)] + \sqrt{q} z_{i,j}^n Z_{i,j}^n + D \sum_p (z_p^n - z_{i,j}^n), \quad (2.1)$$

where $x_{i,j}^n$, $y_{i,j}^n$ and $z_{i,j}^n$ are respectively the densities of preys x, y and the predator z in the site (i,j) at the time step n. Here α and γ are the interaction parameters between preys and predator, X, Y and Z are the white Gaussian noise variables with

$$\langle X(t) \rangle = \langle Y(t) \rangle = \langle Z(t) \rangle = 0, \quad (2.2)$$

$$\langle X(t)X(t+\tau) \rangle = \langle Y(t)Y(t+\tau) \rangle = \langle Z(t)Z(t+\tau) \rangle = \delta(\tau), \quad (2.3)$$

$$\langle X(t)Y(t') \rangle = \langle X(t)Z(t') \rangle = \langle Y(t)Z(t') \rangle = 0 \quad \forall \, t, t', \quad (2.4)$$

q is the noise intensity, D is the diffusion coefficient, μ and μ_z are scale factors. $\sum_p$ indicates the sum over the four nearest neighbors in the map lattice. The multiplicative noise in the above equations models the interaction between the species and the environment. The boundary conditions have been established in such a way that no interaction is present out of

lattice. This means that for the four corner sites we have only two interactions and for the other 4×98 line-confined sites the number of interactions is three.

We analyze the transient dynamics of the system with a time varying interaction parameter $\beta(t)$ between the two preys

$$\beta(t) = 1 + \varepsilon + \eta \cos(\omega t), \tag{2.5}$$

due to the environment temperature. Here $\eta = 0.2$, $\omega = \pi 10^{-3}$ and $\varepsilon = -0.1$. The interaction parameter $\beta(t)$ oscillates around the critical value $\beta_c = 1$ in such a way that the dynamical regime of Lotka–Volterra model for two competing species changes from coexistence of the two preys ($\beta < 1$) to exclusion of one of them ($\beta > 1$) [11]. The parameters used in our simulations are $\mu = 2$; $\nu = 1$; $\alpha = 0.03$; $\mu_z = 0.02$; $\gamma = 205$ and $D = 0.1$. The noise intensity q varies between 10^{-12} and 10^{-2}. With this choice of parameters the interspecies competition among the two prey populations is stronger compared to the intraspecies competition (preys-predator), and, therefore, both prey populations can stably coexist in the presence of the predator [11].

By considering the influence of noise and spatial diffusion, we analyze the noise-induced pattern formation. Specifically the time evolution of the area of the patterns and the correlation r over the grid between two species, as a function of the noise intensity, are analyzed. The quantitative calculations of the site correlation between a couple of species in the lattice have been done using the following formula

$$r^n = \frac{\sum_{i,j}^{N}(w_{i,j}^n - \bar{w}^n)(k_{i,j}^n - \bar{k}^n)}{\left[\sum_{i,j}^{N}(w_{i,j}^n - \bar{w}^n)^2 \sum_{i,j}^{N}(k_{i,j}^n - \bar{k}^n)^2\right]^{1/2}}, \tag{2.6}$$

where N is the number of sites in the grid, the symbols w^n, k^n represent one of the three species x, y, z, and $\bar{w}^n, \bar{k}^n$ represent the mean values of the concentration of the species in all the lattice at the step n. From the definition (2.6) it follows

$$-1 \le r^n \le 1. \tag{2.7}$$

We calculate the correlation between the two preys and between preys and predator.

3. Results and comments

The bidimensional spatial grid considered is composed by 100×100 sites in (x, y) plane. The calculations have been done for various noise intensities and at different steps of the iteration process. To quantify our analysis we

consider only the maximum patterns, defined as the ensemble of adjoining sites in the lattice for which the density of the species belongs to the interval $[3/4\,\mathrm{max}, \mathrm{max}]$, where max is the absolute maximum of density in the specific grid. For each spatial distribution, in a temporal step and for a given noise intensity value, the following quantities have been evaluated referring to the maximum pattern (MP): mean area of the various MPs found in the lattice and spatial correlation r between two preys, and between preys and predator.

3.1. Deterministic analysis

In the absence of noise and with constant interaction parameter β we obtain: *(i)* for $\varepsilon < 0$ $(\beta < 1)$ a coexistence regime of the two preys characterized in the lattice by a strong correlation between them with the predator lightly anti-correlated with the two preys; *(ii)* for $\varepsilon > 0$ $(\beta > 1)$ wide exclusion zones in the lattice (see Fig. 1), characterized by a strong anti-correlation between preys. In Fig. 1 we report the spatial configuration of the species after long time evolution. We chose Gaussian initial distribution with mean value $\bar{x}_0 = \bar{y}_0 = \bar{z}_0 = 0.25$ and variance $\sigma_0 = 0.1$.
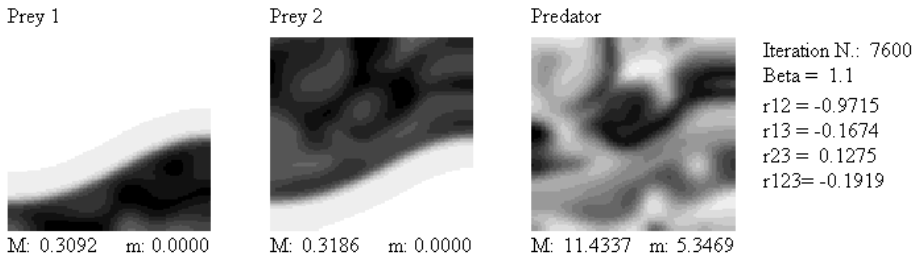

Fig. 1. Spatial configuration of the species obtained after long time evolution in noiseless dynamics and in the exclusion regime between preys. The parameter set is: $\varepsilon = 0.1, \beta = 1.1, \eta = 0, q = 0, D = 0.1, \mu = 2, \nu = 1, \alpha = 0.03, \mu_z = 0.02, \gamma = 205$. The initial conditions are random with a Gaussian distribution, with mean values $\bar{x}(0) = \bar{y}(0) = \bar{z}(0) = 0.25$ and variance $\sigma_0 = 0.1$. Here r_{12}, r_{13}, r_{23} and r_{123} are respectively the site correlations between: *(i)* preys, *(ii)* prey 1 and predator, *(iii)* prey 2 and predator, and *(iv)* predator and both preys.

By considering the periodic variation of the interaction parameter $\beta(t)$, we obtain for $\varepsilon = 0$, after a transient anti-correlated behavior between preys, a coexistence regime with strong correlation between preys that evolves towards an homogeneous spatial distribution of all three species. For $\varepsilon > 0$ we find an oscillating behavior of the site correlation coefficient from coexistence regime between preys, corresponding to strong correlation, to an exclusion regime, corresponding to strong anticorrelation. This last behavior is

prevalent. The oscillating frequency coincides with that of the β-parameter. When $\varepsilon < 0$, the two preys, after an initial transient, remain strongly correlated for all the time, in spite of the fact that the parameter $\beta(t)$ takes values greater than 1 during the periodical evolution. This situation corresponds to a coexistence regime between preys. In Fig. 2 we report the behavior of the site correlation parameter r as a function of time for three values of the parameter $\varepsilon = -0.1, 0, 0.1$.

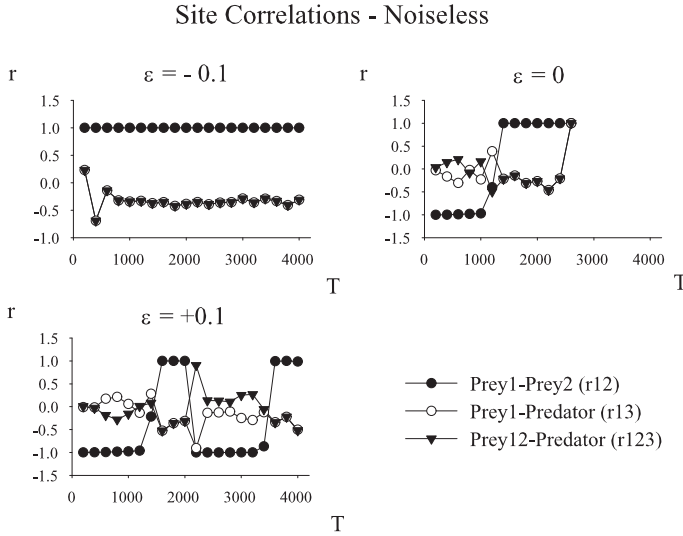Site Correlations - Noiseless

Fig. 2. Site correlation parameter r in noiseless dynamics as a function of time for different values of the parameter $\varepsilon : -0.1, 0., +0.1$. Here $\eta = 0.2$. The values of the other parameters are the same used for Fig. 1.

3.2. Noise effects

To analyze the effect of the noise we focus on the interesting dynamical regime characterized, in absence of noise, by coexistence between preys in all the period of β, *i.e.* with $\varepsilon < 0$. The noise triggers the oscillating behavior of the site correlation r giving rise to periodical alternation of coexistence and exclusion regime. Even a very small amount of noise is able to destroy the coexistence regime periodically as we can see from Fig. 3, where the correlation parameter r as a function of time is reported. Noise is also responsible for a nonmonotonic behavior of the area of spatial patterns, which repeats periodically in time. In Fig. 4 we report a nonmonotonic behavior of the area of the maximum pattern as a function of noise intensity. A maximum of the area of maximum patterns is visible for the preys at $q = 10^{-9}$ and for the predator at $q = 10^{-8}$. The same behavior is present in the following time
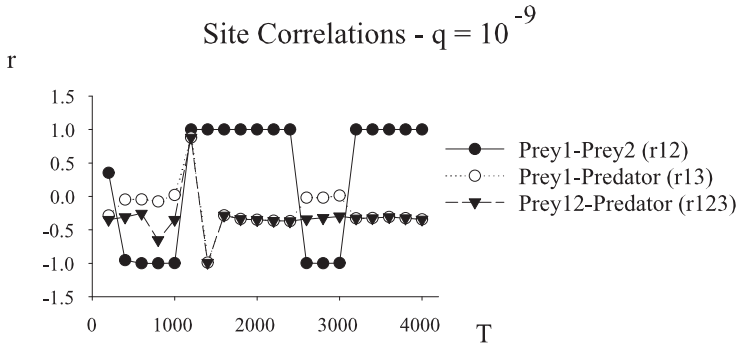
Site Correlations - q = 10^{-9}

r

Fig. 3. Site correlation parameter as a function of time. Here $\varepsilon = -0.1, \eta = 0.2$ and the noise intensity is $q = 10^{-9}$. The values of the other parameters are the same used for Fig. 1. The initial spatial distribution is homogeneous and equal for all species, i.e. $x_{ij}^{\text{init}} = y_{ij}^{\text{init}} = z_{ij}^{\text{init}} = 0.25$ for all sites (i, j).
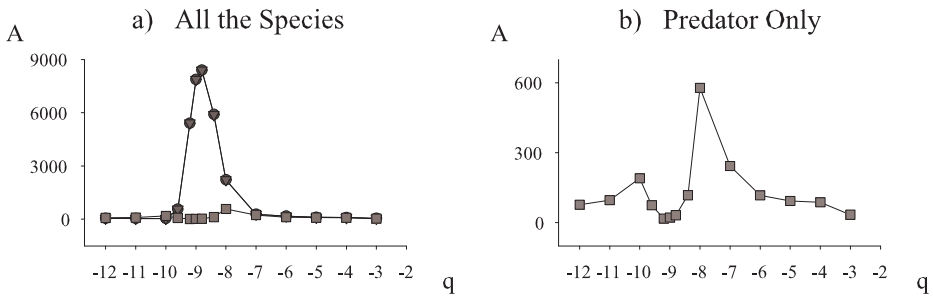

Fig. 4. Semi-Log plot of the mean area of the maximum patterns for all species as a function of noise intensity, at iteration step 1400. Here circles and triangles are related to preys, squares to predator. The values of the other parameters and the homogeneous initial distribution are the same used in Fig. 3.

steps within the first period of the interaction parameter: 600, 800, 1200, 1400. But at time steps $600, 800$ the preys are highly anticorrelated with site correlation parameter $r_{12} = -1$, while at time steps $1200, 1400$ the preys are highly correlated with $r_{12} = 1$. The formation of spatial patterns appear only when the preys are highly correlated, while large patches with clusterization of preys appear when they are anticorrelated. This means that the coexistence regime between preys corresponds to the appearance of spatial patterns, while the exclusion regime corresponds to clusterization of preys. The noise-induced pattern formation relative to the iteration 1400 is visible in Fig. 5, where we report five patterns of the preys and the predator for the following values of noise intensity: $q = 10^{-11}, 10^{-9}, 10^{-8}, 10^{-4}, 10^{-2}$. The
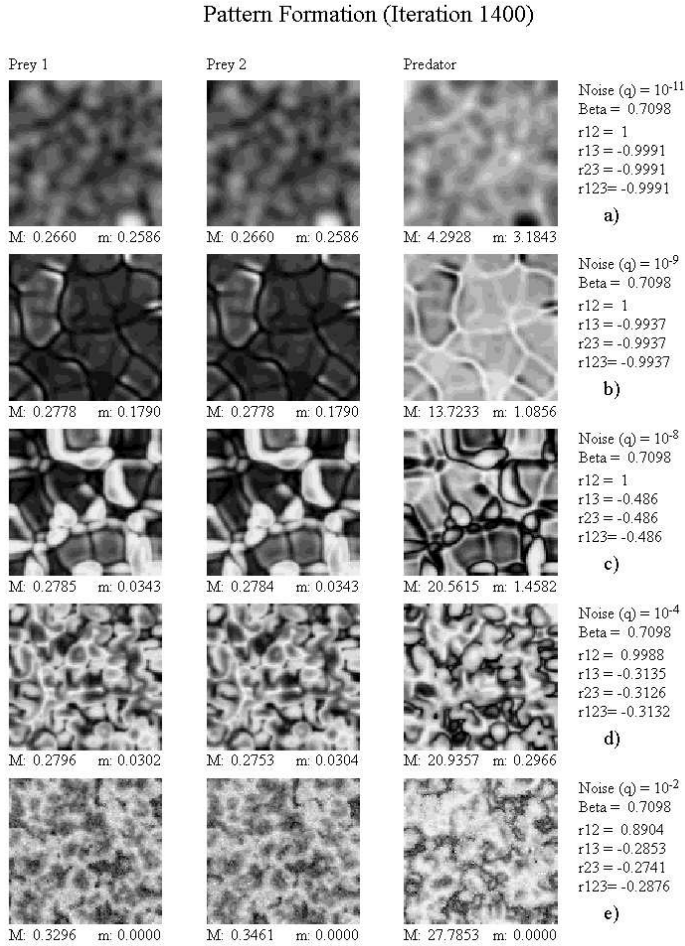
Pattern Formation (Iteration 1400)

Fig. 5. Spatial Pattern formation for preys and predator, at time iteration 1400 and for the following values of the noise intensity: $q = 10^{-11}, 10^{-9}, 10^{-8}, 10^{-4}, 10^{-2}$. The values of the other parameters and the homogeneous initial distribution are the same used in Fig. 3. The parameters $r_{12}, r_{13}, r_{23}, r_{123}$ have the same meaning of Fig. 1.

initial spatial distribution is homogeneous and equal for all species, that is $x_{ij}^{\text{init}} = y_{ij}^{\text{init}} = z_{ij}^{\text{init}} = 0.25$ for all sites (i, j). A spatial structure emerges with increasing noise intensity. At very low noise intensity, with respect to the value of the diffusion coefficient D, the spatial distribution appears almost homogeneous without any particular structure (see Fig. 5(a)). Increasing the multiplicative noise intensity, the symmetric dynamical evolution of the

two preys in each site of the lattice is destroyed, so oscillations in population density produce an exclusion regime of one of two preys [2]. This time evolution scenario corresponds to the appearance of spatial patterns due to different spatial density in each site. This spatial pattern disappears for sufficiently large noise intensity, producing a random spatial inhomogeneity (see Fig. 5(e)). As a final investigation we analyze the behavior of the area of the patterns as a function of time. We observe a nonmonotonic behavior of the area of MPs as a function of time for all values of the noise intensity investigated. Particularly for noise intensity values greater than $q = 10^{-7}$ this nonmonotonic behavior becomes periodical in time with the same period of $\beta(t)$, as shown in Fig. 6 for $q = 10^{-4}$. We note that this
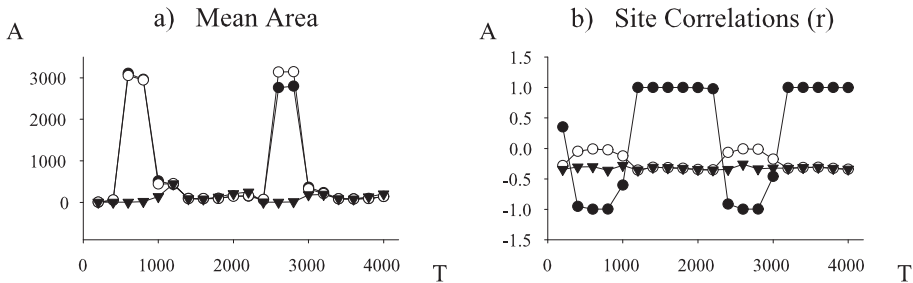

Fig. 6. Mean area of maximum pattern of the three species and relative sites correlations between preys and between preys and predator as a function of time. Here $q = 10^{-4}$. (a): black and white circles are related to preys, triangles to predator; (b) site correlation r_{12} (black circles), r_{13} (white circles), and r_{123} (triangles). The values of the other parameters and the homogeneous initial distribution are the same used in Fig. 3.

nonmonotonic behavior does not mean that a spatial pattern appears, like that of Fig. 5(b), but that a big clusterization of preys may occur, as shown in Fig. 7. In this figure in fact we report the spatial configuration obtained for a noise intensity value $q = 10^{-4}$, which corresponds to the maximum of the behavior of the mean area of MPs of preys as a function of time shown in Fig. 6(a). We see that this maximum corresponds to large patches of preys in the lattice investigated. The various quantities, such as pattern area and correlation parameter, have been averaged over 200 realizations, obtaining the mean values shown in the figures 3, 4 and 6. The effects induced by the interaction between the species and the environment, modeled by the multiplicative noise, can be summarized as: *(i)* to break the symmetry of the coexistence regime between the preys, producing an alternation with the exclusion regime; *(ii)* to trigger the oscillating behavior of the site correlation coefficient; *(iii)* to produce a nonmonotonic behavior of the pattern area as a function of the noise intensity with an appearance of spatial patterns.

Fig. 7. Spatial configuration of one prey obtained for $q = 10^{-4}$, at iteration step 800, corresponding to the maximum value of the mean area for preys reported in Fig. 6. The values of the other parameters and the homogeneous initial distribution are the same used in Fig. 3.

4. Conclusions

The noise-induced pattern formation in a lattice of three interacting species, described by Lotka–Volterra generalized equations, has been investigated. We find nonmonotonic behavior of the mean area of the maximum patterns as a function of noise intensity. The same behavior we find for the area of the patterns as a function of evolution time. The noise changes the dynamical regime of the species, breaking the symmetry of the coexistence regime. Besides the noise produces spatial patterns and temporal oscillations of the site correlation parameter defined on the lattice. We finally note that our simple model of an ecosystem of interacting species could be useful to interpret the experimental data of population dynamics strongly affected by the noise [12].

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