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Spatiotemporal patterns provoked by environmental variability in a predator–prey model

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ABSTRACT

The emergence of spatiotemporal patterns in the distribution of species is one of the most striking phenomena in ecology and nonlinear science. Since it is known that spatial inhomogeneities can significantly affect the dynamics of ecological populations, in the present paper we investigate the impact of environmental variability on the formation of patterns in a spatially extended predator–prey model. In particular, we utilize a predator–prey system with a Holling III functional response and introduce random spatial variations of the kinetic parameter signifying the intrinsic growth rate of the prey, reflecting the impact of a heterogeneous environment. Our results reveal that in the proximity of the Hopf bifurcation environmental variability is able to provoke pattern formation, whereby the coherence of the patterns exhibits a resonance-like dependence on the variability strength. Furthermore, we show that the phenomenon can only be observed if the spatial heterogeneities exhibit large enough regions with high growth rates of the prey. Our findings thus indicate that variability could be an essential pattern formation mechanism of the populations.

1. Introduction

Ecological communities constitute complex dynamical systems governed by interactions of individual organisms with each other and with the environment. Since the publication of the paradigmatic Lotka–Volterra equations researchers from various disciplines are devoting a great deal of attention to studies of population dynamics models. The main objective of those studies is to provide a comprehensive understanding of the co-evolution of competitory species and to determine the factors which govern the distribution of populations and the structure of communities. It is known that population densities of some species vary not only periodically over time, but also in spatial dispersion (Liu et al., 2008; Medvinsky et al., 2002; Sieber et al., 2010; Turchin, 2003), which is an important mechanism for the appearance of complex spatiotemporal dynamics in an ecosystem (Yoshida, 2005). Discovering how the population numbers are being changed and which mechanisms cause the observed patterns is a serious a challenge to researchers in the natural sciences. Mathematical modeling has turned out to be one of the most useful tools, whose main goal is not just limited to the improvement of the understanding of the mechanisms leading to complex spatiotemporal dynamics. Namely, theoretical studies may also provide valuable insight into the stability of ecosystems, for example in the context of human's interference into the environment (Malchow et al., 2008).

Predator–prey systems where spatial patterns form spontaneously, purely from the dynamics of the system, have led to the characterization of two basic types of symmetry-breaking bifurcations – Hopf and Turing bifurcation, which are responsible for the emergence of spatiotemporal patterns. Conditions for Hopf and Turing instabilities were derived in several studies (Baurmann et al., 2007; Wang et al., 2007; Yang et al., 2002). An important component of the predator–prey system is the predator's functional response, i.e. the prey consumption rate by an average single predator. In general, functional responses can be classified as prey dependent (Sun et al., 2010; Wang et al., 2008), predator dependent (Wang et al., 2007) or multi-species dependent (Abrams and Ginzburg, 2000). Furthermore, Wang et al. (2008) have shown that special initial conditions can affect the nature of emerging spatial patterns. Several studies gave emphasis to additional aspects of predator–prey dynamics, such as predator cannibalism (Sun et al., 2009b), the provision of alternative food to predators (Kar and Ghosh, 2012) or the role of the Allee effect (Allee, 1938; Dennis, 1989; Gyllenberg et al., 1999; Petrovskii et al., 2002). For instance, Wang et al. (2011a) have studied the impact of the Allee effect on the spatial structure and temporal dynamics of an epidemic invasion. Another interesting report was reported by Su and Hui (2011), who have studied the complex dynamics in eco-epidemiological

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systems and the impact of predation on the epidemic transmission in spatially structured prey populations.

In ecological systems, many stochastic factors can have a significant impact on dynamics of interacting species as well as on pattern formation of the populations (Malchow et al., 2002; Serizawa et al., 2009; Sieber et al., 2010). For example, it has been shown that noise can trigger regime shifts in an aquatic model (Serizawa et al., 2009) or prevent the onset of chaos in spatiotemporal population dynamics (Petrovskii et al., 2010). Remarkably thought, it is nowadays a well known fact that in certain nonlinear systems noise has organizing rather than disruptive effects. Perhaps the most prominent phenomena related to this apparently paradoxical fact are stochastic (Gammaitoni et al., 1998) and coherence resonance (Pikovsky and Kurths, 1997) and the occurrence of both has already been reported in various population dynamics models (Borgogno et al., 2012; Rozenfeld et al., 2001; Sieber et al., 2007). Of particular interest are the studies investigating the role of noise in systems with spatial degrees of freedom. The manifestation of noise-induced ordered phases, patterns and traveling waves have been witnessed in various physical, chemical, biological and artificial setups (for a comprehensive review see (Sagués et al., 2007)). Along these lines several groups devoted plenty of attention to the impact of noise in spatially extended ecologically relevant models (Li and Jin, 2012; Liu et al., 2008; Mobilia et al., 2007; Sun et al., 2009a; Wang et al., 2011b). Apart from random fluctuations, ecological parameters are exposed to seasonal variations such as changes in climate or photoperiods as well (Steffen et al., 1997). Accordingly, a lot of interest has been given to the analysis of a combined effect of noise and external periodic forcing. In particular, recent studies reveal that in this manner very complex spatiotemporal behavior can occur, such as resonant patterns or frequency-locking phenomena (Liu et al., 2008; Rao et al., 2009; Jiang et al., 2009; Sun et al., 2010).

Spatial heterogeneity of the environment has long been recognized as a very important issue in ecological dynamics (Griffin et al., 2009; Lander et al., 2009). It has been shown that the spatial structure affects the stability of an ecosystem (Poggiale et al., 2008), enhance the species fitness (Dobramysl and Täuber, 2008), or even contribute to species diversity (Griffin et al., 2009). Noteworthy, it has been shown that pattern formation in spatially extended nonlinear systems can also be provoked by spatial variability, i.e. static disorder. Till today, the phenomenon has been observed in a net of subexcitable oscillators (Glatt et al., 2007), in an ensemble of diffusively coupled cells (Sailer et al., 2006; Gosak, 2009) and in excitable neuronal networks (Sun and Lu, 2010). In all those studies the most coherent patterns were attained for intermediate values of parametric variability, thereby signifying the diversity-induced resonance phenomenon (Tessone et al., 2006). In the present article we aim to extend the concept of variability-induced pattern formation to a spatially extended predator prey model. We introduce random spatial variations in reaction rates that describe the population kinetics, which can be interpreted as direct environmental influences on the species reproduction rate, such as local variations of pollution, available resources, temperature, habitat landscape, etc. (Medvinsky et al., 2002). Our findings reveal that intermediate levels environmental variability can induce coherent traveling waves on the spatial domain in a resonant way. We additionally examine the relation between the characteristics of environmental variability and its ability to provoke spatiotemporal patterns.

2. Mathematical model

The prey-predator spatial dynamics of prey (z) and predator (y) populations is studied by using the nondimensional mathematical model determined by theoretical framework of Sun et al. (2010). We focus on a predator–prey system with prey dependent Holling III functional response (Chaudhuri, 1988). Elements are coupled by diffusion, and modeled in two spatial dimensions by reaction–diffusion equations. The spatially extended model is written as:

$$\frac{dz_{i,j}}{d\tau} = \alpha_{i,j} z_{i,j} - z_{i,j}^2 - \beta \frac{z_{i,j}^2 y_{i,j}}{1+z_{i,j}^2} + D_1 \nabla^2 z_{i,j}, \qquad (1a)$$

$$\frac{dy_{i,j}}{d\tau} = \gamma \frac{z_{i,j}^2 y_{i,j}}{1+z_{i,j}^2} - \mu y_{i,j} + D_2 \nabla^2 y_{i,j}. \qquad (1b)$$

The Laplacian operator is integrated into the numerical scheme via a five-point finite-difference formula (Barkley, 1991). D_1 and D_2 are the diffusion coefficients of phytoplankton and zooplankton, respectively. The term $\alpha_{i,j} z_{i,j}$ in Eq. (1a) introduces the impact of the variability of the natural environment. In particular, $\alpha_{i,j}$ is related to the intrinsic growth rate of the phytoplankton we assume that values of the parameter $\alpha_{i,j}$ are defined as follows:

$$\alpha_{i,j} = \alpha_0 + \sigma \eta_{i,j} - \langle \eta_{i,j} \rangle, \qquad (2)$$

where α_0 is the value of $\alpha_{i,j}$ when $\sigma = 0$. (Under there conditions all subjects are just below the Hopf bifurcation). σ defines the intensity of environmental fluctuations and $\eta_{i,j}$ are correlated random numbers accorded with 2-dimensional Perlin noise (Perlin, 1985). Perlin noise is the sum of several interpolated noise functions with various frequencies (b) and amplitudes ($1/a$). The generation of each noise function was based on $m \times m$ random numbers arranged on a square lattice, cubic interpolation between them and selected values of b^i and $1/a^i$, where i is the ith noise function being added. We subtract the term $\langle \eta_{i,j} \rangle$ in Eq. (2), in order to achieve that on average $\alpha_{i,j}$ is always below the Hopf bifurcation ($\langle \alpha \rangle = \alpha_0$). The generated spatial patterns are smooth and hence provide a pertinent description of the environmental variability, where sharp transitions and discontinuities are not expected.

Typical two dimensional spatial distributions of $\alpha_{i,j}$ are obtained for three different values of m are shown in Fig. 1. We can observe that the parameter m determinates the size of the patches with high or low growth rate of the prey. In particular, as m is increased, the size of the patches decreases. When $m \to L$, the spatial variations of $\alpha_{i,j}$ can be regarded as quenched uncorrelated random variables.

In our numerical simulations we employed zero-flux boundary conditions with a system size of $L \times L$ space units, time step $\Delta\tau = 0.01$ and space step $\Delta x = \Delta y = 1$. The parameters used throughout the whole study were: $\beta = 1.25$, $\gamma = 0.8$, $\eta = 0.5$, $D_1 = 0.05$, $D_2 = 1$, $L = 400$ and $m = 12$, unless stated otherwise. The system is integrated initially from the homogeneous state signifying the interior equilibrium point $(z_{i,j}^*, y_{i,j}^*)$, where (Sun et al., 2010)

$$z_{i,j}^* = \frac{\sqrt{\mu(\gamma-\mu)}}{\gamma-\mu}, \qquad (3a)$$

$$y_{i,j}^* = \frac{\gamma(\alpha - z_{i,j}^*)}{\beta z_{i,j}^* (\gamma-\mu)}. \qquad (3b)$$

Furthermore, by the analysis of the emergent spatial patterns a long enough transient time has been considered in order to ensure that the system is in its final dynamical state. In particular, the quantification of the spatial dynamics took place between $5000 < t \leq 10{,}000$.

3. Results

Hopf instability for individual oscillators occurs and spatially homogeneous oscillation comes up, when the parameter α is above this critical value $\alpha_H \approx 6.45$ (Sun et al., 2010). We want to achieve