The role of noise in a predator–prey model with Allee effect

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Abstract The existence and implications of alternative stable states in ecological systems have been investigated extensively within deterministic models. However, it is known that natural systems are undeniably subject to random fluctuations, arising from either environmental variability or internal effects. Thus, in this paper, we study the role of noise on the pattern formation of a spatial predator–prey model with Allee effect. The obtained results show that the spatially extended system exhibits rich dynamic behavior. More specifically, the stationary pattern can be induced to be a stable target wave when the noise intensity is small. As the noise intensity is increased, patchy invasion emerges. These results indicate that the dynamic behavior of predator–prey models may be partly due to stochastic factors instead of deterministic factors, which may also help us to understand the effects arising from the undeniable susceptibility to random fluctuations of real ecosystems.

Keywords Predator–prey · Noise · Spatial pattern · Patchy invasion

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1 Introduction

Since the pioneering work of Turing [1], pattern formation in nonlinear complex systems has been one of the central problems of the natural, social, and technological sciences [2–4]. The occurrence of multiple steady states and transitions from one to another after critical fluctuations; the phenomena of excitability, oscillations, and waves; and the emergence of macroscopic order from microscopic interactions in various nonlinear, nonequilibrium systems in nature and society have been the subject of many theoretical and experimental studies [5]. In particular, spatial patterns are ubiquitous in nature; these patterns modify the temporal dynamics and stability properties of population densities at a range of spatial scales. Additionally, the spatial component of ecological interactions has been identified as an important factor in how ecological communities are shaped [6–8].

More recently, past investigations have revealed that spatial inhomogeneities like the inhomogeneous distribution of nutrients, as well as interactions on spatial scales like migration, can have an important impact on the dynamics of ecological populations [5, 9]. Holling emphasized the influence of noise in ecological dynamics and resilience [10]. The first source of noise is that there are inherent uncertainties in an ecological system such as varying rainfall or nutrient inputs. On the other hand, there are considerable anthropogenic disturbances that exacerbate the uncertainty in the way an ecosystem responds [11]. Apart from random fluctuations, there may be seasonal variations in various ecological parameters. Several studies consider the effects of seasonality [12, 13], for instance, on phytoplankton enrichment in lakes [13, 14].

Several groups have investigated the influence of noise in ecologically relevant models. The models they employed were ordinary differential equations [15–19] or partial differential equations with logistic growth [20–25]. However, it has been observed in the literature that the Allee effect [26–30], especially combined with diffusion of the spatial patterns, had been generally overlooked, despite its potential ecological reality and intrinsic theoretical interest. These structures may in fact correspond to the real world. For this reason, the main purpose of the present paper is to investigate the effect of noise on the spatial patterns of a predator–prey model with an Allee effect.

The paper is organized as follows. In Section 2, we give a predator–prey model with Allee effect. These parameters determine the dynamics of the system and we show, considering them taken from literature, that these parameters can be interpreted biologically. We also show the effect of noise by numerical simulations in Section 3. Finally, some discussion and conclusions are given.

2 The model

We investigate the two-dimensional spatial dynamics of a predator–prey system described by two partial differential equations of reaction-diffusion type. The system is considered in a homogeneous environment, which is as the following form [9, 31–35]:

$$\frac{\partial U}{\partial T} = F(U) - f(U, V) + D_1 \nabla^2 U, \quad (1a)$$

$$\frac{\partial V}{\partial T} = kf(U, V) - MV + D_2 \nabla^2 V, \quad (1b)$$

where $\nabla^2 = \partial^2/\partial X^2 + \partial^2/\partial Y^2$ is the usual Laplacian operator in two-dimensional space and D_1, D_2 are, respectively, prey and predator diffusion coefficients. Here, $U = U(X, Y, T)$ and $V = V(X, Y, T)$ stand for prey and predator density, respectively, at moment T and position (X, Y) . The function $F(U)$ describes the intrinsic prey growth, $f(U, V)$ describes predation, and the term MV stands for predator mortality.

To keep the model as simple as possible, we assume that the predator response is as follows:

$$f(U, V) = AUV, \quad (2)$$

where A is the predation rate, which corresponds to the classical Volterra scheme. Simple models, by their own nature, cannot incorporate many complex biological factors. However, they often provide useful insights to help our understanding of complex processes.

Assuming Allee dynamics for the prey population, its growth rate can be parameterized as follows [36, 37]:

$$F(U) = \frac{4wU(U - U_0)(K - U)}{(K - U_0)^2}, \quad (3)$$

where K is the prey-carrying capacity, w is the maximum per capita growth rate, and U_0 is the threshold ($U_0 < K$), so that, for $U < U_0$, the growth rate becomes negative. U_0 can be considered as a measure of the intensity of the Allee effect: the lower the value of U_0 , the less prominent is the Allee effect. For $U_0 = -1$, (3) is equivalent to the logistic population growth rate.

In order to minimize the number of parameters involved in the model system, it is extremely useful to write the system in nondimensionalized form. Although there is no unique method of doing this, it is often a good idea to relate the variables to some key relevant parameters. Thus, following Morozov et al. [35], and taking

$$u = \frac{U}{K}, v = \frac{V}{kK}, t = aT, \quad (4a)$$

$$x = X\sqrt{a/D_1}, y = Y\sqrt{a/D_1}, \quad (4b)$$

where $a = AkK/B$, we arrive at the following equations containing dimensionless quantities:

$$\frac{\partial u}{\partial t} = \gamma u(u - \beta)(1 - u) - uv + \nabla^2 u, \quad (5a)$$

$$\frac{\partial v}{\partial t} = uv - dv + \varepsilon \nabla^2 v, \quad (5b)$$

where $\nabla^2 = \partial^2/\partial x^2 + \partial^2/\partial y^2$. Equation 5 contains four dimensionless parameters (against eight in the original equations), i.e., $\gamma = 4wK/(Ak(K - U_0)^2)$, $\beta = U_0/K$, $d = M/a$, and $\varepsilon = D_1/D_2$. Thus, the behavior of dimensionless solutions u and v appears to depend on four dimensionless combinations of the original parameters rather than on each of them separately. From the biological point of view, we assume that all the parameters are positive constants.

Combining with the noise term, we have the SPDE system as follows:

$$\frac{\partial u}{\partial t} = \gamma u(u - \beta)(1 - u) - uv + \nabla^2 u, \quad (6a)$$

$$\frac{\partial v}{\partial t} = uv - dv + \eta(\mathbf{r}, t) + \varepsilon \nabla^2 v. \quad (6b)$$

In (6), the stochastic factors are taken into account in the term $\eta(\mathbf{r}, t)$, which is obtained from microscopic interactions in the space [38–41], where the typical white noise will emerge. Recently, colored noise and white noise have both been used in describing ecological evolution [42–44]. White noise is the limiting case of colored noise, so we consider the more general case of colored noise. In the present paper, we only consider the noise presented in one of the equations (6b). The noise term $\eta(\mathbf{r}, t)$ is introduced additively in space and time, which is the Ornstein–Uhlenbeck process [45] (see Appendix). The colored noise $\eta(\mathbf{r}, t)$, which is temporally correlated and white in space, satisfies

$$\langle \eta(\mathbf{r}, t) \eta(\mathbf{r}', t') \rangle = \frac{\phi}{\tau} \exp\left(-\frac{|t - t'|}{\tau}\right) \delta(\mathbf{r} - \mathbf{r}'), \quad (7)$$

where τ controls the temporal correlation, and ϕ measures the noise intensity.

To well understand the dynamics of the system given by (6), it is worth giving a brief account of the properties of the well-mixed, spatially homogeneous system (5) without diffusion terms. Thus, we firstly find the steady states as follows:

- (a) $E_0 = (0, 0)$, which corresponds to extinction of both the predator and prey
- (b) $E_1 = (\beta, 0)$ and $E_2 = (1, 0)$, which correspond to extinction of the predator
- (c) Interior equilibrium point $E^* = (u^*, v^*)$, which corresponds to coexistence of prey and predator and

$$u^* = d, \quad (8a)$$

$$v^* = \gamma(d - \beta)(1 - d). \quad (8b)$$

It is easy to show that u^* and v^* are positive under the condition

$$\beta < d < 1. \quad (9)$$

By using standard linear stability analysis, it can be readily seen that $E_0 = (0, 0)$ is always a stable node. The steady states $E_1 = (\beta, 0)$ and $E_2 = (1, 0)$ are either nodes or saddle points, depending on the relation between the parameters. However, under the condition $\beta < d < 1$, $E_1 = (\beta, 0)$ and $E_2 = (1, 0)$ are saddle points.

We compare the predator–prey system with logistic growth of prey and only three steady states, one of which corresponds to coexistence of the species. For the parameter values for which the coexistence state exists in the domain $u > 0, v > 0$, it can also be either a focus or a node, and the loss of its stability is followed by formation of a stable limit cycle. However, in this case, an important difference is that the limit cycle exists for all parameter values in the range where the coexistence state is unstable, and the spatiotemporal complexity of a predator–prey system is usually associated with its local oscillatory kinetics [46, 47].

3 Results

In this section, we explore the model (5) in detail, via numerical integration. In the numerical simulations, zero-flux boundary conditions are used and the time step is $\Delta t = 0.05$ time units. The spatial step is $\Delta x = \Delta y = 1$ length units and the grid sizes in the simulations are $m \times n$ (here, $m = n = 100$). The Fourier transform method is used for the deterministic part of (5). On the discrete square lattices, the stochastic partial differential equation (6) is integrated numerically by applying the Euler method. Several different discrete methods (simple Euler, Runge–Kutta, and Fourier transform) were checked, and the results indicate that the Fourier transform accurately approximates solutions of (5). On the other hand, the Fourier method offers a speed advantage over other numerical methods. We find that, on a PC, the Fourier method runs about three to four times faster than the Euler integration using the same time step and spatial step. The code is implemented in Matlab and the `fft2`, `fftshift`, `ifft2`, and `ifftshift` functions were used for the main numerical integration.

Although the noisy fluctuations may sometimes cause the density of the populations to be less than zero, it will lead the reaction-diffusion system to exhibit a cutoff effect at low densities when the species extinction is taken into account explicitly [48]. According to the spatially extended model (5), at each position in space, whenever the population densities fall below a certain prescribed value ξ , they are set to zero or a sufficiently small positive constant [48, 49]. From the biological point of view, in this paper, we set them equal to 10^{-6} when the variables become negative. Note that we are not much concerned here with the exact value of ξ , for the reason that an attempt to estimate the exact value would hardly make any ecological sense in terms of the very schematic model (5). To compare with the numerical results under the different cases, we used the same initial conditions that are randomly perturbed (the perturbations are space independent) by the coexistence state, except when explicitly stated.

Biological invasion usually starts with a local introduction of exotic species; thus, relevant initial conditions for system (6) should be described by functions of compact support when the density of one or both species at the initial moment of time is non-zero only inside a certain domain. The shape of the domain and the profiles of the population densities can be different in different cases [50]. In order to study the effect of noise on the biological invasion in the model (6), the initial distribution of species was taken as follows: $u(x, y, 0) = U_0$, if $x_1 < x < x_2$ and $y_1 < y < y_2$, otherwise, $u(x, y, 0) = 0$; $v(x, y, 0) = V_0$, if $x_3 < x < x_4$ and $y_3 < y < y_4$, otherwise, $v(x, y, 0) = 0$.

Equation 6, with the initial conditions stated above was solved numerically by finite differences. In order to avoid numerical artifacts, we checked the sensitivity of the results to the choice of the time and spatial steps, and their values have been chosen sufficiently small. Also, some of the results were reproduced by means of using a more advanced alternate directions scheme. Both numerical schemes are standard; hence, we do not describe them here [37]. It is well known that, in the case where population growth is affected by the strong Allee effect, not every species introduction leads to successful invasion [36, 50, 51]. There exists a minimum viable population size so that invasion success can only be guaranteed when the initially invaded area and the initial population density of the alien species are not too small. Correspondingly, since, in this paper, we are primarily concerned with the dynamics of species spread, in our numerical simulations, parameters U_0 and V_0 have always been chosen sufficiently large [50].

Figure 1 shows the evolution of the spatial pattern of prey at $t = 0, 20, 50, 100, 250$, and 450, without noise, for the parameter set: $\gamma = 5$, $\beta = 0.3$, $d = 0.5$, and $\varepsilon = 1$. We

Fig. 1 (Color online) Typical spatial pattern diagram of the prey density in two-dimensional space for the model (5) without noise. Parameter values: $\gamma = 5$, $\beta = 0.3$, $d = 0.5$, and $\varepsilon = 1$. **A** $t = 0$, **B** $t = 20$, **C** $t = 50$, **D** $t = 100$, **E** $t = 250$, **F** $t = 450$. Predator density exhibits similar properties

Fig. 2 (Color online) Typical spatial pattern diagram of the prey density in two-dimensional space for the model (6) with $\phi = 0.001$ and $\tau = 5$. Parameter values: $\gamma = 5$, $\beta = 0.3$, $d = 0.5$, and $\varepsilon = 1$. **A** $t = 0$, **B** $t = 20$, **C** $t = 50$, **D** $t = 150$, **E** $t = 200$, **F** $t = 300$. Predator density exhibits similar properties

Fig. 3 (Color online) Typical spatial pattern diagram of the prey density in two-dimensional space for the model (6) with $\phi = 0.01$ and $\tau = 5$. Parameter values: $\gamma = 5$, $\beta = 0.3$, $d = 0.5$, and $\varepsilon = 1$. **A** $t = 0$, **B** $t = 20$, **C** $t = 50$, **D** $t = 100$, **E** $t = 150$, **F** $t = 300$. Predator density exhibits similar properties

choose the initial conditions as $x_1 = x_3 = y_1 = y_3 = 25$, $x_2 = x_4 = y_2 = y_4 = 75$, $U_0 = 1$, and $V_0 = 0.1$. From this figure, one can see that the initial distribution leads to the formation of a square pattern. As time is increased, we observed traveling circular waves, and the radii of the circles became smaller with time. However, the patterns do not undergo any essential changes (cf. Fig. 1E–F). This type of system dynamics is somewhat paradoxical from an ecological point of view because successful species spread still leads to invasion failure.

In Fig. 2, the spatial pattern of the prey with noise ($\phi = 0.001$ and $\tau = 5$) is shown. The initial conditions and the parameter values are the same as in Fig. 1. It is easy to see that noise can induce the regular rings to be irregular. Moreover, as the time becomes large enough, a target wave-like pattern is formed (cf. Fig. 2E–F). From the biological point of view, the noise can lead a successful invasion and form target waves of high population density.

As the noise intensity is further increased, there is a drastic influence on the pattern formation, which is illustrated in Fig. 3 with ($\phi = 0.01$ and $\tau = 5$). Figure 3 shows the evolution of the spatial pattern of prey at $t = 0, 20, 50, 100, 150$, and 300 . Also, it shares the same initial condition and the parameter values with Fig. 1. Although, at the beginning of the invasion, a square pattern is formed, see Fig. 3B, at later stages, the front breaks into pieces (Fig. 3C–E). Further spreading of the populations takes place via the irregular dynamics of separate patches. In the course of time, the patches move, merge, disappear, and produce new patches (cf. Fig. 3F). In other words, the noise can make possible patchy invasion in a predator–prey system.

4 Discussion and conclusion

In this paper, a series of numerical simulations reveals that a certain amount of noise is sufficient to drive the system (5) dynamically from one type of pattern to another. More specifically, the noise can induce the regular circle pattern to be a target wave-like pattern. Furthermore, for a larger noise intensity, patchy invasion of the population can occur.

It should be noted that, in our model simulations, we have considered random fluctuations in one of the parameters for each of the models. In nature, however, all the parameters can show temporal and spatial variations: indeed, some can be both stochastic and show significant seasonal variations [14, 50, 52–55]. The intrinsic rate γ is one such parameter that can show both seasonal variations and noise. We have found that including noise (or seasonality) and spatial variations in the parameter, γ , in the model induces proportional changes (oscillations) in the density of the prey but has no impact on the density of the predator. Moreover, the question of two or more varying environments influencing the ecosystem is very important in the context of predator–prey interactions. We hope that our efforts will provide a good starting point for the analysis of more detailed models to understand the interplay fluctuations in ecological systems.

From the standpoint of prospective ecological applications, it seems interesting to reveal the correlation between the intrinsic patterns, i.e., patterns arising due to trophic interactions such as those considered above, and the forced patterns induced by the inhomogeneity of the environment or noise. However, in the oceanic ecological systems, the biological processes among the species are in a fluid environment, such as turbulent flow or chaotic advection. Recently, a few authors have considered the mixing of the flow and diffusion processes using a well-known standard model of chaotic advection [56–61] in excitable media; in particular, Reigada et al. [62] found that plankton blooms can also be induced by turbulent

flow. This issue, however, should be given a more careful investigation and will become a subject of a separate study.

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Appendix: More detail about noise term $\eta(\mathbf{r}, t)$

The Ornstein–Uhlenbeck process obeys the following stochastic partial differential equation:

$$\frac{\partial \eta(\mathbf{r}, t)}{\partial t} = -\frac{1}{\tau} \eta(\mathbf{r}, t) + \frac{1}{\tau} \xi(\mathbf{r}, t), \quad (10)$$

where $\xi(\mathbf{r}, t)$ is a Gaussian white noise with zero mean and correlation,

$$\langle \xi(\mathbf{r}, t) \rangle = 0, \quad (11a)$$

$$\langle \xi(\mathbf{r}, t) \xi(\mathbf{r}', t') \rangle = 2\varepsilon \delta(\mathbf{r} - \mathbf{r}') \delta(t - t'). \quad (11b)$$

As a result, the colored noise $\eta(\mathbf{r}, t)$, which is temporally correlated and white in space, satisfies

$$\langle \eta(\mathbf{r}, t) \eta(\mathbf{r}', t') \rangle = \frac{\varepsilon}{\tau} \exp\left(-\frac{|t - t'|}{\tau}\right) \delta(\mathbf{r} - \mathbf{r}'), \quad (12)$$

where τ controls the temporal correlation, and ε measures the noise intensity.

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