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Pattern formation induced by cross-diffusion in a predator–prey system*

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This paper considers the Holling–Tanner model for predator–prey with self and cross-diffusion. From the Turing theory, it is believed that there is no Turing pattern formation for the equal self-diffusion coefficients. However, combined with cross-diffusion, it shows that the system will exhibit spotted pattern by both mathematical analysis and numerical simulations. Furthermore, asynchrony of the predator and the prey in the space. The obtained results show that cross-diffusion plays an important role on the pattern formation of the predator–prey system.

Keywords: Holling–Tanner, cross-diffusion, pattern structures
PACC: 0290, 0565

1. Introduction

The dynamics of spontaneous spatial pattern formation, first introduced to biology by Turing[1] five decades ago, has recently been attracting attention in many subfields of biology to describe various phenomena. Non-equilibrium labyrinthine patterns are observed in chemical reaction–diffusion systems with a Turing instability[2−4] and in bistable reaction–diffusion systems.[5] Such dynamic patterns in a two dimensional space have recently been introduced into ecology.[6−8]

Recently, there has been considerable interest to investigate the stability behaviour of a system of interacting populations by taking into account the effect of self as well as cross-diffusion.[9] The term self-diffusion implies the movement of individuals from a higher to lower concentration region. Cross-diffusion expresses the population fluxes of one species due to the presence of the other species. The value of the cross-diffusion coefficient may be positive, negative or zero. The term positive cross-diffusion coefficient denotes the movement of the species in the direction of lower concentration of another species and negative cross-diffusion coefficient denotes that one species tends to diffuse in the direction of higher concentration of another species.[10]

Turing suggested that, when the self-diffusion coefficients are equal, there is no Turing pattern in the spatial model.[1] Then it is natural to ask whether Turing patterns emerge, when combined with cross-diffusion. To this end, we will investigate the pattern formation of a predator–prey model with self and cross-diffusion.

The paper is organized as follows. In Section 2, we obtain a Holling–Tanner model with self and cross-diffusion, and interpret the biological meaning of these parameters of the model. We analyse the model, and derive the condition of Turing-instability, with respect to these parameters in Section 3. By numerical simulations, we illustrate the emergence of spotted Turing patterns. Finally, some conclusions and discussions are given in Section 4.

2. Model

Since the traditional Holling–Tanner type predator–prey model received great attention among

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theoretical and mathematical biologists,[11−13] we will focus our attention here on the following form

$$\frac{\mathrm{d}n}{\mathrm{d}\tau} = r_1 n\left(1-\frac{n}{K}\right) - \frac{qnp}{n+c}, \tag{1a}$$

$$\frac{\mathrm{d}p}{\mathrm{d}\tau} = r_2 p(1-\frac{p}{\gamma n}), \tag{1b}$$

where n and p denote the prey and predator, respectively. The parameters r_1 and r_2 represent the intrinsic growth rate. The value K represents the carrying capacity of the prey and γn takes on the role of a prey-dependent carrying capacity for the predator. The parameter γ is a measure of the quality of the prey as food for the predator. The rate at which predators remove the prey, $qn/(n+c)$, is know as a Holling type-II predator response.[13−16] The parameter q is the maximum number of prey that can be eaten per predator per time. The parameter c is a saturation value which corresponds to the number of prey to achieve one half the maximum rate q.

Following the method in Ref.[11], with the scaling

$$N = \frac{n}{K}, \quad P = \frac{p}{\gamma K}, \quad r = \frac{r_2}{r_1}, \tag{2a}$$

$$a = \frac{q\gamma}{r_1}, \quad b = \frac{c}{K}, \quad t = r_1\tau, \tag{2b}$$

we arrive at the following equations containing dimensionless quantities:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = N(1-N) - \frac{aNP}{b+N}, \tag{3a}$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = rP\left(1-\frac{P}{N}\right). \tag{3b}$$

In nature the tendency of the prey would be to keep away from predators and hence the escape velocity of the prey may be taken to be proportional to the dispersive velocity of the predators. Also, the tendency of predators would be to get closer to the prey and hence the chase velocity of predators may be considered to be proportional to the dispersive velocity of the prey.[10] The objective of this paper is to investigate the cross-diffusion influence on the system. Thus, the model which we employ is as follows:

$$\frac{\partial N}{\partial t} = N(1-N) - \frac{aNP}{b+N} + \nabla^2 N + d_{12}\nabla^2 P, \tag{4a}$$

$$\frac{\partial P}{\partial t} = rP\left(1-\frac{P}{N}\right) + d_{21}\nabla^2 N + \nabla^2 P, \tag{4b}$$

where $\nabla^2 = \dfrac{\partial^2}{\partial x^2} + \dfrac{\partial^2}{\partial y^2}$ is the usual Laplacian operator in 2-dimensional space and the variables N and P denote predator and prey densities, respectively. d_{12}, d_{21} are the cross-diffusion coefficients of predator and prey respectively.

The model (4) needs to be analysed with the initial populations

$$N(0) > 0, \ P(0) > 0.$$

We also assume that no external input is imposed from outside. Hence, the boundary conditions are taken as

$$\frac{\partial N}{\partial n}|_{(x,y)} = \frac{\partial P}{\partial n}|_{(x,y)} = 0, \tag{5}$$

where $(x, y) \in \partial\Omega$ and Ω is the spatial domain.

To study patterns of the cross-diffusion system given by Eq.(4), we must consider a spatially homogeneous system. So we first find the steady state as follows:

(i) $E_1 = (1, 0)$, which corresponds to extinction of the predator;

(ii) interior equilibrium point $E^* = (N^*, P^*)$, which corresponds to coexistence of prey and predator and

$$N^* = P^* = \frac{1-a-b+\sqrt{(a+b-1)^2+4b}}{2}. \tag{6}$$

From the biological point of view, we are interested to study the stability behaviour of the interior equilibrium point E^*. The Jacobian corresponding to this equilibrium point is

$$\boldsymbol{J} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix},$$

where

$$\begin{aligned} a_{11} = {} & 2(-1+4a-2b-b^2+ab-5a^2+2a^3 \\ & +ab^2+3a^2b-M-bM+3aM \\ & -abM-2a^2M)/(-1-a-b-M)^2, \end{aligned} \tag{7}$$

$$a_{12} = \frac{a(-1+a+b-M)}{1-a+b+M}, \tag{8}$$

$$a_{21} = r, \tag{9}$$

$$a_{22} = -r, \tag{10}$$

and $M = \sqrt{(a+b-1)^2+4b}$.

To find these conditions for Turing instabilities, first we notice that system requires a stable homogeneous state which implies a Jacobian with a positive

determinant and a negative trace.[1,17] That is to say that

$$a_{11} + a_{22} < 0, \tag{11a}$$
$$a_{11}a_{22} - a_{12}a_{21} > 0. \tag{11b}$$

Following the standard linear analysis of the reaction–diffusion equation,[18,19] we consider a perturbation near the steady state,

$$N(\boldsymbol{r}, t) = N^* + A(\boldsymbol{r}, t), \tag{12a}$$
$$P(\boldsymbol{r}, t) = P^* + B(\boldsymbol{r}, t), \tag{12b}$$

and we assume that

$$A(\boldsymbol{r}, t) = \alpha \exp(\lambda t) \exp(\mathrm{i}\boldsymbol{k} \cdot \boldsymbol{r}), \tag{13a}$$
$$B(\boldsymbol{r}, t) = \beta \exp(\lambda t) \exp(\mathrm{i}\boldsymbol{k} \cdot \boldsymbol{r}). \tag{13b}$$

Then we obtain the following relation by using the above expressions:

$$\lambda \begin{pmatrix} \alpha \\ \beta \end{pmatrix} = \begin{pmatrix} a_{11} - k^2 & a_{12} - d_{12}k^2 \\ a_{21} - d_{21}k^2 & a_{22} - k^2 \end{pmatrix} \begin{pmatrix} \alpha \\ \beta \end{pmatrix}. \tag{14}$$

We obtain from Eq.(14) that the eigenvalue is the root of the following equation:

$$\lambda^2 + \alpha(k^2)\lambda + \beta(k^2) = 0, \tag{15}$$

where

$$\alpha(k^2) = 2k^2 - (a_{11} + a_{22}), \tag{16a}$$
$$\beta(k^2) = (1 - d_{12}d_{21})k^4 - (a_{11} + a_{22} - d_{12}a_{21} - d_{21}a_{12})k^2 + a_{11}a_{22} - a_{12}a_{21}. \tag{16b}$$

For unstable steady states subjected to heterogeneous perturbations which lead to Turing patterns, the real part of the eigenvalue, $\mathrm{Re}(\lambda(k^2))$, has to be greater than zero. However, since $\alpha(k^2)$ is always greater than zero, it is required that $\beta(k^2)$ is negative for some values of k. Therefore, the solution of Eq.(15) for $k > 0$ reduces to

$$\lambda(k^2) = \frac{-\alpha(k^2) + \sqrt{(\alpha(k^2))^2 - 4\beta(k^2)}}{2}. \tag{17}$$

For the reason that $\beta(k^2)$ needs to be negative for some values of k, from Eq.(16b) and $1 - d_{12}d_{21} > 0$ we find that

$$a_{11} + a_{22} - d_{12}a_{21} - d_{21}a_{12} > 0 \tag{18}$$

must be satisfied. Finally, the k interval of possible values is determined by the zeros of $\beta(k^2)$. In this case we obtain real and positive k values if the following condition is satisfied:

$$(a_{11}+a_{22}-d_{12}a_{21}-d_{21}a_{12})^2 - 4 \det D \det J > 0, \tag{19}$$

where

$$\det D = 1 - d_{12}d_{21}.$$

From the above analysis, we know that Turing pattern are observed if Eqs.(11), (18) and (19) hold.

3. Pattern formation

In the following, we will show the pattern by a finite difference method. To solve differential equations by computers, one has to discretize the space and time of the problem. In practice the continuous problem defined by the reaction–diffusion system in two dimension is solved in a discrete domain with $M \times N$ lattice sites. The spacing between the lattice points is defined by the lattice constant Δh. In the discrete system the Laplacian describing diffusion is calculated by using finite differences, i.e., the derivatives are approximated by differences over Δh. For $\Delta h \to 0$ the differences approach the derivatives. The time evolution is also discrete, i.e., the time goes in steps of Δt.[20] We set $\Delta h = 2$, $\Delta t = 0.05$ and $M = N = 200$. Note that when Δh, Δt are further decreased, the dynamics does not change any more.

Figure 1 shows the evolution of the spatial pattern of prey, with small random perturbation of the stationary solution N^* and P^*. And the values of the parameters are that $a = 0.75$, $b = 0.25$, $r = 0.004$, $d_{12} = -0.08$ and $d_{21} = 0.8$. After irregular transient pattern, we can see that the regular spotted patterns with the same radius prevail over the whole domain finally, and the dynamics of the system does not undergo any further changes.

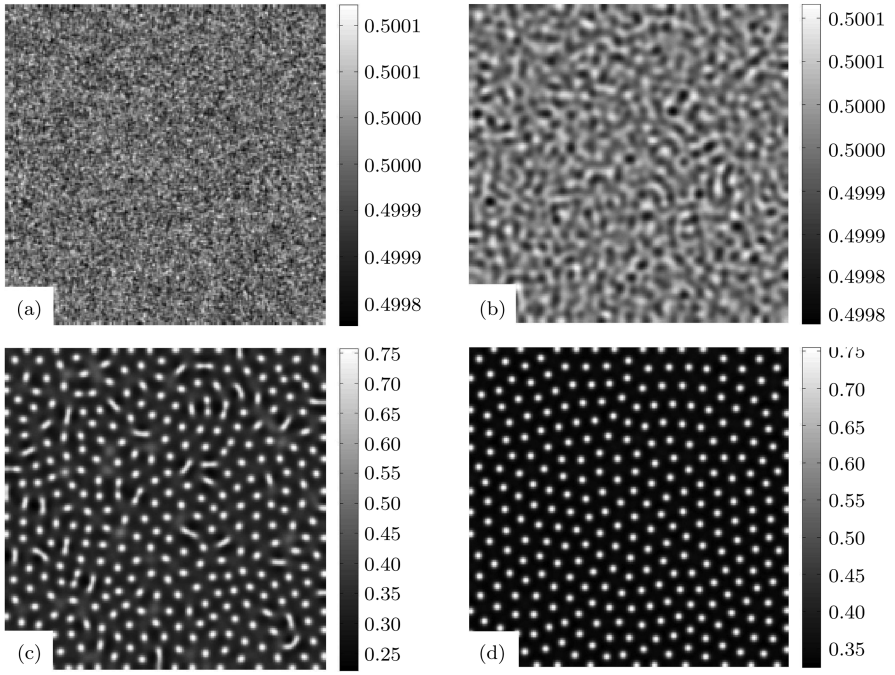


Fig.1. Snapshots of contour pictures of the time evolution of the N at different instants. (A): 0 iteration; (B): 2000 iterations; (C): 15000 iterations; (D): 100000 iterations.

In order to well see the evolution, we show space-time plots in Fig.2. The method of space–time plots is that let y be a constant (here, $y = 100$, the centre line of each snapshots), choose the line $y = 100$, from each pattern snapshots and pile these lines in-time-order. The space–time plots show the evolution process of the prey N throughout time t and space x.

We show that the prey and the predator are in asynchrony at different time in Fig.3. The presence, absence or degree of synchronization can be an important part of the function or malfunction of a biological system. This is because asynchrony enhances the global persistence even when there are local extinctions.[21]

In Fig.4, we include the dispersion relation to depict the spatiotemporal pattern. From it, we can see that, if $r > r_c$ ($r_c \approx 0.0166$), there is no Turing patterns.

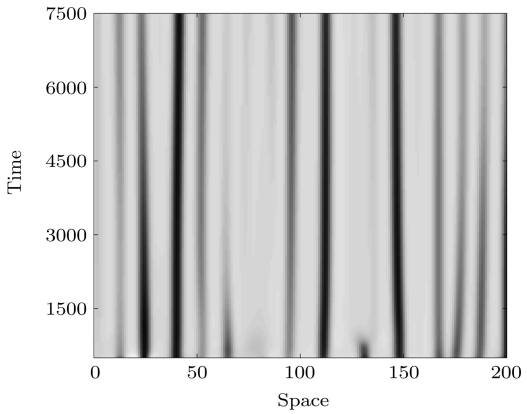


Fig.2. Space–time plots of N corresponding to the case Fig.1.

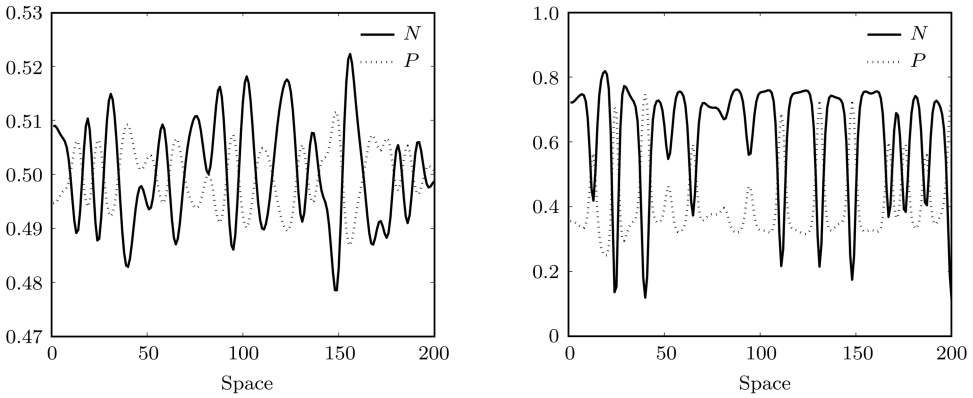


Fig.3. Asynchrony of the prey and the predator at $t = 250$ (the left one) and $t = 500$ (the right one). Here, N denotes the density of the prey and P denotes the density of the predator.

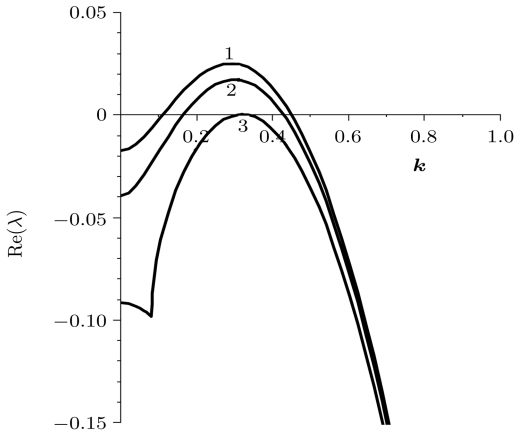


Fig.4. Dispersion relation for the system (1). curve 1: $r = 0.004$; curve 2: $r = 0.008$; curve 3: $r = 0.0166$. And the other parameters are the same as in Fig.1.

To gain some insights to the patterns, we compute the power spectra of the simulation patterns (Fig.1(d)) using the two-dimension Fourier transform in Fig.5. For $r = 0.004$, we find that the figure has two modes with different wave-numbers. The spatial frequency and direction of any component in the power spectrum are given in the length and direction, respectively, of a vector from the origin to the point on the circle. The magnitude is depicted by a grey scale or colour scale, but the units are dimensionless values related to the total darkness of the original images. In Fig.5, short wavelength, represented by a large circle, corresponds to Turing structures; longer wavelength, represented by a small white circle, corresponds to travelling and/or standing waves.

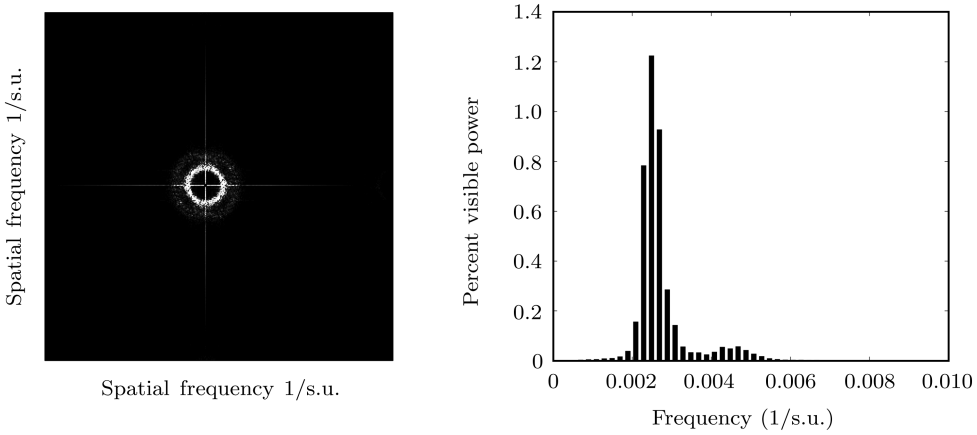


Fig.5. Spatial Fourier transformation for the system (1) with $r = 0.004$ at 100000 iterations.

4. Discussion and conclusion

In summary, we have investigated a Holling–Tanner model with self and cross-diffusion. We show that, when the self diffusion coefficients are equal, Turing pattern can emerge due to cross-diffusion in the present paper. The finding well enriches the finding of the pattern formation in predator–prey model.

In the present paper, we vary d_{21} and keep $a = 0.75$, $b = 0.25$, $d_{12} = -0.08$ and $d_{21} = 0.8$. By a series of numerical simulations, we find that only spotted patterns with the same radius are obtained. Ecological speaking, cross-diffusion may have effect on the distribution of the species, i.e., may lead the species to be isolated. In Ref.[22], for a predator–prey system with Michaelis–Menten type functional response, only self-diffusion is considered. However, they gained the spottedness which is not in the same wavelength. Our results are different from them.

Although more works are needed, in principle, it seems that cross-diffusion is able to generate many different kinds of spatiotemporal patterns. For such reason, we can predict that the interaction of self and cross-diffusion can be considered as an important mechanism for the appearance of complex spatiotemporal dynamics in ecology models.

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