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Spatial dynamics of a predator-prey system with cross diffusion

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ABSTRACT

In this paper, a spatial predator-prey model with self-defense mechanism that the prey species keep themselves away from the attack of the predator, which leads the existence of the cross diffusion in biological communities, is investigated. Conditions for cross diffusion induced Turing instability are obtained by mathematical analysis. By the numerical simulations, five types of patterns such as hot/cold spots, hot/cold spots-stripes and stripes patterns emerge. Our study suggests that the interactions of self and cross diffusion have great effects on the mechanism for the emergence of complex dynamics in biological systems.

1. Introduction

Originally proposed by Turing's study in chemistry, pattern formation in reaction-diffusion system is widely investigated in many fields, such as modern ecology and biology [1–6]. For spatial patterns, they can identify the exact distributions in both space and time of the populations and may provide some insights on the evolution rules of the individuals.

In particular, one typical example of the spatiotemporal model is predator-prey system. Spatial patterns are mainly used to understand the impacts of individual mobility on the stable and oscillatory states of species survival by using the reaction-diffusion equations, in which self diffusion stands for the random motions of species. Along this way, a lot of work has been done about spatial predator-prey model [7–12]. Holling–Tanner predator-prey spatiotemporal model [13,14] is one of the most famous predator-prey models. In line with ratio-dependent predator-prey model, another well-known proposal is Holling type III functional response [15], which is the most important and useful functional response in population dynamics. In this paper, we consider the following Holling–Tanner predator-prey spatial model with Holling type III functional response:

$$\begin{cases} \frac{\partial U}{\partial T} = rU\left(1-\frac{U}{K}\right) - \frac{mU^2V}{aU^2+1} + D_{11}\nabla^2 U, \ \ (\mathbf{x},t) \in \Omega \times (0,\infty), \\ \frac{\partial V}{\partial T} = \theta V\left(1-\frac{hV}{U}\right) + D_{22}\nabla^2 V, \ \ (\mathbf{x},t) \in \Omega \times (0,\infty), \\ \frac{\partial U(\mathbf{x},t)}{\partial n} = \frac{\partial V(\mathbf{x},t)}{\partial n} = 0, \ \ (\mathbf{x},t) \in \partial\Omega \times (0,\infty), \\ U(\mathbf{x},0) = U_0 > 0, \ \ \mathbf{x} \in \Omega, \\ V(\mathbf{x},0) = V_0 > 0, \ \ \mathbf{x} \in \Omega, \end{cases} \quad (1)$$

where $U(\mathbf{x}, T)$ and $V(\mathbf{x}, T)$ stand for prey and predator density respectively at $\mathbf{x} \in \Omega$ and at time T, Ω is a bounded domain with a Lipschitz boundary $\partial\Omega$. $\nabla^2 = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$ is the usual Laplacian operator in space $\Omega \in R^2$, which describes the random motion of both prey and predator. n is the outward unit normal vector on $\partial\Omega$. The zero-flux boundary condition indicates that no external input is imposed from outside. r, K, a, θ, m and h are all positive constants. r is the prey intrinsic growth rate and K the carrying capacity . m is capturing rate, a the half-saturation constant. θ is predator intrinsic growth rate, h the conversion rate of prey into predator biomass. D_{11} and D_{22} are the self diffusion coefficients for U and V respectively, which are nonnegative and describe the natural dispersive force of random motion of individuals.

However, the tendency of the prey species will keep away from the predator species in order not to be caught, which made the concentration levels of prey change [16,17]. At the same time, the movement of the predator is affected by the gradient of the concentration of the prey at the same location. This phenomenon is described by cross diffusion mathematically [18–25]. As a result, in the present paper, we aim to study the effect of the cross diffusion on spatiotemporal dynamics of a predator-prey model with Holling type III functional response. Consequently, we have the following model:

$$\begin{cases} \frac{\partial U}{\partial T} = rU\left(1-\frac{U}{K}\right) - \frac{mU^2V}{aU^2+1} + D_{11}\nabla^2 U + D_{12}\nabla^2 V, \ (\mathbf{x},t) \in \Omega\times(0,\infty), \\ \frac{\partial V}{\partial T} = \theta V\left(1-\frac{hV}{U}\right) + D_{21}\nabla^2 U + D_{22}\nabla^2 V, \ \ (\mathbf{x},t) \in \Omega\times(0,\infty), \\ \frac{\partial U(\mathbf{x},t)}{\partial n} = \frac{\partial V(\mathbf{x},t)}{\partial n} = 0, \ \ \mathbf{x} \in \partial\Omega\times(0,\infty), \\ U(\mathbf{x},0) = U_0 > 0, \ \ \mathbf{x} \in \Omega, \\ V(\mathbf{x},0) = V_0 > 0, \ \ \mathbf{x} \in \Omega, \end{cases} \quad (2)$$

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where D_{12}, D_{21} are the cross diffusion coefficients of predator and prey respectively, which are either positive, negative, or zero. In this paper, we assume $D_{12} > 0$ and $D_{21} < 0$, which means that prey species tend to orient towards lower concentration of the predator species, and the predator species tend to move towards the higher concentration of the prey species.

This paper is organized as follows. In Section 2, we derive the conditions for the existence of positive equilibrium in the absence of both self diffusion and cross diffusion. In Section 3, we analyze the model (2) and obtain the condition for emerging patterns. In Section 4, we illustrate spatial patterns by performing a series of numerical simulation. Finally, some conclusions and discussions are given in Section 5.

2. Analysis of positive equilibrium

In order to minimize the number of parameters involved in model (2), we choose the scaling $u = \frac{U}{K}, v = \frac{mKV}{r}, t = rT,$ then model (2) becomes

$$\begin{cases} \frac{\partial u}{\partial t} = u(1-u) - \frac{u^2 v}{\epsilon u^2+1} + d_{11}\nabla^2 u + d_{12}\nabla^2 v, \ \ (\mathbf{x}, t) \in \Omega \times (0, \infty), \\ \frac{\partial v}{\partial t} = v\eta\left(1 - \frac{\gamma v}{u}\right) + d_{21}\nabla^2 u + d_{22}\nabla^2 v, \ \ (\mathbf{x}, t) \in \Omega \times (0, \infty), \\ \frac{\partial u(\mathbf{x},t)}{\partial n} = \frac{\partial v(\mathbf{x},t)}{\partial n} = 0, \ \ (\mathbf{x}, t) \in \partial\Omega \times (0, \infty), \\ u(\mathbf{x}, 0) = u_0 > 0, \ \ \mathbf{x} \in \Omega, \\ v(\mathbf{x}, 0) = v_0 > 0, \ \ \mathbf{x} \in \Omega, \end{cases} \tag{3}$$

where

$$\epsilon = aK^2, \quad \eta = \frac{\theta}{r}, \quad \gamma = \frac{hr}{mK^2},$$

$$d_{11} = \frac{KD_{11}}{r}, \quad d_{12} = \frac{rD_{12}}{m^2K^3}, \quad d_{21} = \frac{mK^3D_{21}}{r^2}, \quad d_{22} = \frac{D_{22}}{mK}.$$

We need to analyze the stability criteria of model (3) without diffusion. The corresponding model is

$$\begin{cases} \frac{du}{dt} = u(1-u) - \frac{u^2 v}{\epsilon u^2+1} := f(u, v), \\ \frac{dv}{dt} = v\eta\left(1 - \frac{\gamma v}{u}\right) := g(u, v). \end{cases} \tag{4}$$

Obviously, system (4) has equilibrium $E_0 = (1, 0)$, which corresponds to extinction of the predator. From the biological point of view, we are interested in the interior equilibria points, which are the positive solutions of the following cubic polynomial equations of system (4):

$$u(1-u) = \frac{u^2 v}{\epsilon u^2 + 1}, \tag{5}$$

$$v\eta\left(1 - \frac{\gamma v}{u}\right) = 0. \tag{6}$$

Let the second equality in (5) replace the v of the first equality in (6)

$$H(u) := u^3 + C_2u^2 + C_1u + C_0 = 0. \tag{7}$$

And $C_2 = \frac{1}{\gamma\epsilon} - 1, C_1 = \frac{1}{\epsilon}$ and $C_0 = -\frac{1}{\epsilon} < 0$. The number of real roots of F in the interval $I_0 = (0, 1)$ determines the number of equilibria in (4). What is more, $H'(u) = 3u^2 + 2C_2u + C_1$ has the following roots:

$$S_{\pm} = \frac{\gamma\epsilon - 1 \pm \sqrt{T_1}}{3\epsilon\gamma}, \tag{8}$$

and

$$T_1 = (\gamma\epsilon - 1)^2 - 3\epsilon\gamma^2 \geq 0. \tag{9}$$

The discriminant of the cubic polynomial H is given by

$$T_2 = \left(\frac{L}{2}\right)^2 + \left(\frac{K}{3}\right)^3, \tag{10}$$

where $K = C_1 - C_2^2/3$ and $L = (2C_2^3 - 9C_1C_2 + 27C_0)/27$.

We are interested in the positive equilibrium state $E^* = (u^*, v^*)$. Let $E^*(u^*, v^*)$ be any equilibrium of system (4), where $v^* = \frac{u^*}{\gamma}$. The Jacobian matrix of system (4) at $E^*(u^*, v^*)$ takes the following form

$$J = \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix}_{(u^*, v^*)} \triangleq \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix}$$
$$= \begin{pmatrix} \frac{-2\epsilon(u^*)^3 - 1 + \epsilon(u^*)^2}{\epsilon(u^*)^2+1} & \frac{-(u^*)^2}{\epsilon(u^*)^2+1} \\ \frac{\eta}{\gamma} & -\eta \end{pmatrix}. \tag{11}$$

and the trace and determinant of matrix J are given by

$$\mathrm{tr}(J) = \frac{-2\epsilon(u^*)^3 + \epsilon(u^*)^2 - 1}{\epsilon(u^*)^2 + 1} - \eta \triangleq f_u + g_v, \tag{12}$$

$$\det(J) = \frac{\eta u^*}{\epsilon(u^*)^2 + 1} F'(u^*) \triangleq f_u g_v - f_v g_u. \tag{13}$$

The conditions to ensure the positive equilibrium state $E^* = (u^*, v^*)$ to be stable are that:

$$\mathrm{tr}(J) < 0, \tag{14}$$

$$\det(J) > 0. \tag{15}$$

3. Turing instability analysis of model (3)

In this section, we will find the conditions for Turing instability of model (3). For the sake of convenience, let $E^*(u^*, v^*)$ be anyone of the interior steady equilibrium. The characteristic polynomial at $E^*(u^*, v^*)$ is

$$|\lambda E - J_k| = 0, \tag{16}$$

where J_k is given by

$$J_k = \begin{pmatrix} f_u - d_{11}k^2 & f_v - d_{12}k^2 \\ g_u - d_{21}k^2 & g_v - d_{22}k^2 \end{pmatrix}, \tag{17}$$

where k is a wavenumber and we obtain that the eigenvalue is the root of the following equation

$$\lambda^2 + A_k\lambda + B_k = 0, \tag{18}$$

where

$$A_k = (d_{11} + d_{22})k^2 - (f_u + g_v), \tag{19}$$

$$B_k = (d_{11}d_{22} - d_{12}d_{21})k^4 - (d_{22}f_u + d_{11}g_v - d_{12}g_u - d_{21}f_v) + f_u g_v - f_v g_u. \tag{20}$$

Therefore, the solution of (18) is given by

$$\lambda_k = \frac{-A_k \pm \sqrt{A_k^2 - 4B_k}}{2}. \tag{21}$$

Apart from a stable homogeneous state with the condition that $\det(J_k)$ is positive and $\mathrm{tr}(J_k)$ is negative, the condition for unstable steady state to heterogeneous perturbations leading to Turing patterns is that the real part of the eigenvalue, $Re(\lambda_k)$, has to be bigger than zero. Obviously, A_k is positive, so the condition reduces to that B_k is negative for some value of k. That is

$$d_{22}f_u + d_{11}g_v - d_{12}g_u - d_{21}f_v > 0, \tag{22}$$

and

$$(d_{22}f_u + d_{11}g_v - d_{12}g_u - d_{21}f_v)^2 - 4(d_{11}d_{22} - d_{12}d_{21})(f_u g_v - f_v g_u) > 0. \tag{23}$$

Finally, we can get the condition of diffusion induced instability. In other words, if (14), (13), (22) and (23) are satisfied, then we can obtain the Turing patterns of model (3).