

Spatiotemporal dynamics of a predator–prey model

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Abstract Spatial component of ecological interactions has been identified as an important factor in how ecological communities are shaped. In this paper, we consider a Holling–Tanner model with spatial diffusion. Choosing appropriate parameter values in parameter spaces, we obtain rich patterns, including spotted, black-eye, and labyrinthine patterns. The numerical results show that predator–prey system can exhibit complicated behavior.

Keywords Holling–Tanner · Spatial diffusion · Pattern formation

1 Introduction

A reaction–diffusion system can be described as the following equations:

$$\frac{\partial C}{\partial t} = F(C, \mu) + D\nabla^2 C, \quad (1)$$

where C is the concentration vector of reaction, μ represents the total control parameters, F stands for re-

sponse function vector, D denotes the diffusion coefficient matrix, ∇^2 represents Laplace operator. For a given problem, initial conditions and boundary conditions should be given. Usually, diffusion is considered as a spatial transmission way, which moves from high concentration to low concentration. This simple reaction–diffusion system (1) can produce multiply spatial patterns, which are induced by several mechanisms.

Turing showed that a system of coupled reaction–diffusion equations could give rise to spatial concentration patterns of a fixed characteristic length from an arbitrary initial configuration due to diffusion-driven instability by mathematical analysis [1]. The work by Turing belongs to the field of pattern formation, a sub-field of mathematical biology. Pattern formation in nonlinear complex systems is one of the central problems of the natural, social, and technological sciences. The occurrence of multiple steady states and transitions from one to another after critical fluctuations, the phenomena of excitability, oscillations, 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 [2–9].

There has been considerable interest to investigate the stability behavior of a system of interacting populations by taking into account the effect of self diffusion [10]. The term self-diffusion implies the movement of individuals from a higher to lower concentration region. The Holling–Tanner model has been

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vastly investigated in homogeneous systems, in particular, authors have focused in the study of the local and global stability of equilibria [11–13], Hopf bifurcation [11, 14, 15], limit cycles [16, 17], amongst others. However, the spatial dynamics behavior has been not well studied.

In this paper, we will consider the spatially extended reaction–diffusion system of the Holling–Tanner model. The paper is organized as follows. In Sect. 2, we obtain a Holling–Tanner model with self diffusion, and interpret the biological meaning of these parameters of the model. We analysis the model, and derive the condition of Turing-instability, with respect to these parameters in Sect. 3. In Sect. 4, by numerical simulations, we illustrate the emergence of different Turing patterns. Finally, some conclusions and discussions are given.

2 Model

The traditional Holling–Tanner predator–prey model has received great attention among theoretical and mathematical biologists [15, 18]. Here, we will focus our attention to the Holling–Tanner model in the following form:

$$\frac{dU}{d\tau} = r_1 U \left(1 - \frac{U}{K} \right) - \frac{qUV}{U+c}, \tag{2a}$$

$$\frac{dV}{d\tau} = r_2 V \left(1 - \frac{V}{\gamma U} \right), \tag{2b}$$

where U and V 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 γU 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, $qU/(U + c)$, is know as a Holling type-II predator response [11, 19, 20]. Parameter q is the maximum number of prey that can be eaten per predator per time and the parameter c is a saturation value; it corresponds to the number of prey to achieve one half the maximum rate q .

Following the method in [15], we apply the scaling below

$$u = \frac{U}{K}, \quad v = \frac{P}{\gamma K}, \quad r = \frac{r_2}{r_1}, \tag{3a}$$

$$a = \frac{q\gamma}{r_1}, \quad b = \frac{c}{K}, \quad t = r_1 \tau, \tag{3b}$$

and obtain the following equations containing dimensionless quantities:

$$\frac{du}{dt} = u(1 - u) - \frac{auv}{b + u}, \tag{4a}$$

$$\frac{dv}{dt} = rv \left(1 - \frac{v}{u} \right). \tag{4b}$$

The objective of this paper is to investigate the spatial pattern of system (4). Thus, the model we employ is as follows:

$$\frac{\partial u}{\partial t} = u(1 - u) - \frac{auv}{b + u} + d_1 \nabla^2 u, \tag{5a}$$

$$\frac{\partial v}{\partial t} = rv \left(1 - \frac{v}{u} \right) + d_2 \nabla^2 v, \tag{5b}$$

where $\nabla^2 = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$ is the usual Laplacian operator in 2-dimensional space and the variables u and v denote prey and predator densities, respectively. d_1, d_2 are the diffusion coefficients of prey and predator, respectively.

The model (5) needs to be analyzed with the initial populations

$$u(0) > 0, \quad v(0) > 0. \tag{6}$$

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

$$\frac{\partial u}{\partial n} \Big|_{(x,y)} = \frac{\partial v}{\partial n} \Big|_{(x,y)} = 0, \tag{7}$$

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

3 Bifurcation analysis of the system

We first consider a spatially homogeneous system and find the steady state as follows:

- (i) $E_1 = (1, 0)$, which is corresponding to extinction of the predator;
- (ii) positive equilibrium point $E^* = (u^*, v^*)$, which is corresponding to coexistence of prey and predator and

$$u^* = v^* = \frac{1 - a - b + \sqrt{(a + b - 1)^2 + 4b}}{2}. \tag{8}$$

From the biological point of view, we are interested to study the stability behavior of the interior equilibrium point E^* [21–24]. The Jacobian corresponding to this equilibrium point is that

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

where

$$a_{11} = 2(-1 + 4a - 2b - b^2 + ab - 5a^2 + 2a^3 + ab^2 + 3a^2b - M - bM + 3aM - abM - 2a^2M)/(-1 - a - b - M)^2, \tag{9}$$

$$a_{12} = \frac{a(-1 + a + b - M)}{1 - a + b + M}, \tag{10}$$

$$a_{21} = r, \tag{11}$$

$$a_{22} = -r, \tag{12}$$

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

To consider pattern formation for system (5), we need to look for the dispersion relation. Following [25], we will give the linear stability of system (5) following the standard route [26, 27]. We make the following substitute:

$$u = u^* + \bar{u}(\vec{r}, t), \tag{13}$$

and

$$v = v^* + \bar{v}(\vec{r}, t), \tag{14}$$

into (5) and assume $|\bar{u}| \ll u^*$, $|\bar{v}| \ll v^*$. Here, $\vec{r} = x$ (y) or $\vec{r} = (x, y)$, which is corresponding to the one- or two-dimension space. Then, in the linear approximation, we have

$$\frac{\partial \bar{u}}{\partial t} = a_{11}\bar{u} + a_{12}\bar{v} + D_u \nabla^2 \bar{u}, \tag{15a}$$

$$\frac{\partial \bar{v}}{\partial t} = a_{21}\bar{u} + a_{22}\bar{v} + D_v \nabla^2 \bar{v}. \tag{15b}$$

The initial conditions are assumed as that

$$\bar{u}|_{t=0} = f(\vec{r}) \tag{16}$$

and

$$\bar{v}|_{t=0} = g(\vec{r}), \tag{17}$$

where the functions $f(\vec{r})$ and $g(\vec{r})$ decay rapidly for $\vec{r} \rightarrow \pm\infty$. Following the standard approach, let us now perform a Laplace transformation of the linearized equations over the two independent variables \vec{r} and t . For \vec{r} , we use the so-called two-sided version of the transformation. The relations for the forward and backward transforms are

$$u_{sq} = \int_0^\infty e^{-st} dt \int_{-\infty}^{+\infty} \bar{u}(\vec{r}, t) e^{-q\vec{r}} d\vec{r} \tag{18}$$

and

$$\bar{u}(\vec{r}, t) = -\frac{1}{4\pi^2} \int_{\beta-i\infty}^{\beta+i\infty} e^{st} ds \int_{-i\infty}^{i\infty} u_{sq} e^{q\vec{r}} dq, \tag{19}$$

where s and q are complex variables. And s is the Laplace transform variable, q is the Fourier transform variable. That is to say that, $q = ik$ or (ik, il) corresponding to one- and two-dimensional space, and the wave numbers k and l are real number. In formula (18) for the backward transformation, the integration contour in the q -plane is the imaginary axis. In the s -plane, the contour is parallel to the imaginary axis and located to the right of all singularities of the integrand.

After this transformation, the kinetic equations read

$$(s - a_{11} - d_1q^2)u_{sq} - a_{12}v_{sq} = F(q) \tag{20}$$

and

$$(s - a_{22} - d_2q^2)v_{sq} - a_{21}u_{sq} = G(q), \tag{21}$$

where $F(q)$ and $G(q)$ are the transforms of $f(\vec{r})$ and $g(\vec{r})$. To reveal the presence of an instability and disclose its character, it is sufficient to consider one variable. The temporal growth of the perturbations can now be found by inverting the Laplace transforms, which follows directly after factorizing the denominator. By solving the linear equations (20) and (21) we find u_{sq} and then use the backward transformation (19) to obtain the following formal solution:

$$\begin{aligned} \bar{u}(\vec{r}, t) = & -\frac{1}{4\pi^2} \int_{\beta-i\infty}^{\beta+i\infty} e^{st} ds \\ & \times \int_{-i\infty}^{i\infty} \frac{(s - a_{22} - d_2q^2)F(q) + a_{12}G(q)}{D(s, q)} \\ & \times e^{q\vec{r}} dq. \end{aligned} \tag{22}$$

Then we obtain the denominator

$$\begin{aligned} D(s, q) = & (s - a_{22} - d_2q^2)(s - a_{11} - d_1q^2) \\ & - a_{12}a_{21}. \end{aligned} \tag{23}$$

Hence, the dispersion equation is that

$$(s - a_{22} - d_2q^2)(s - a_{11} - d_1q^2) - a_{12}a_{21} = 0. \tag{24}$$

A symmetry breaking occurs when a homogeneous steady state solution of the system (5) is linearly stable to perturbations in the absence of the diffusion and advection terms but linearly unstable to small spatial perturbations in the presence of diffusion and advection. The condition for instability is that (24) has a root s with positive real part. We find the roots from that

$$s = \frac{\alpha(q^2) + \sqrt{[\alpha(q^2)]^2 - 4\beta(q^2)}}{2}, \tag{25}$$

where

$$\alpha(q^2) = (d_1 + d_2)q^2 + (a_{11} + a_{22}), \quad (26a)$$

$$\beta(q^2) = d_1 d_2 q^4 + (a_{11} + a_{22})q^2 + a_{11} a_{22} - a_{12} a_{21}. \quad (26b)$$

The condition for a spatial mode q (in one- or two-dimensional space) to be unstable and thus grow into a pattern is that $\text{Re}(s) > 0$. To well see the dispersion relation, we set that $a = 0.75$, $b = 0.25$, $r = 0.015$, $d_1 = 0.2$, and vary d_2 . Figure 1 depicts the range of the values of q for some constant values, and the small perturbation may bring about an instability with time. From Fig. 1, we can see that the spatial pattern can occur due to the positive real parts of s .

4 Pattern structures

In order to solve differential equations by computers, one has to let the space and time be discrete. The two-dimensional space is solved in a discrete domain with $M \times N$ lattice sites and the spacing between the lattice points is defined by Δh . For $\Delta h \rightarrow 0$ the differences approach the derivatives. The time evolution is also discrete and the time step is Δt . In the present paper, we set $\Delta h = 1$, $\Delta t = 0.001$ and $M = N = 500$.

In the simulations, different types of dynamics are observed and we have found that the distributions of predator and prey are always of the same type. As a

result, we can restrict our analysis of pattern formation to one distribution (in this paper, we show the distribution of prey, for instance). Figure 2 shows the evolution of the spatial pattern of prey, with small random perturbation of the stationary solution u^* and v^* . And the values of the parameters are that $a = 0.75$,

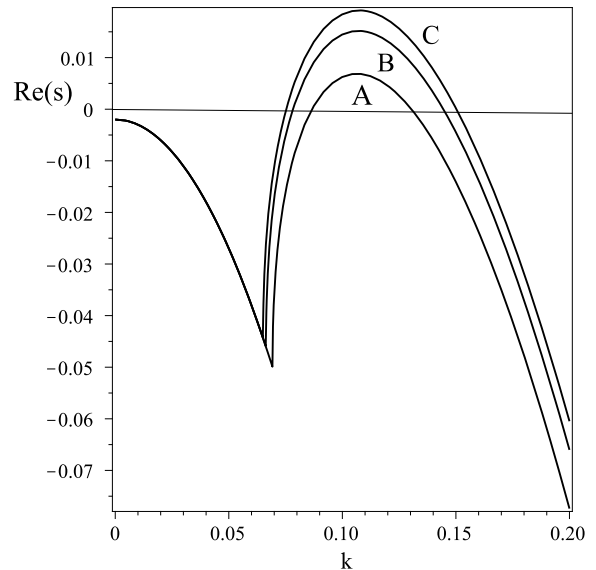


Fig. 1 An illustration of the dispersion relation from the (25) and the parameter values are in the text. A: $d_2 = 1.2$; B: $d_2 = 3$; C: $d_2 = 10$. For other parameters' values, see text. Here, k is wavenumber

Fig. 2 (Color online) Snapshots of contour pictures of the time evolution of the prey, u , at different instants with $d_2 = 1.2$. For other parameters' values, see text. (a) 10 iterations; (b) 10,000 iterations; (c) 15,000 iterations; (d) 100,000 iterations

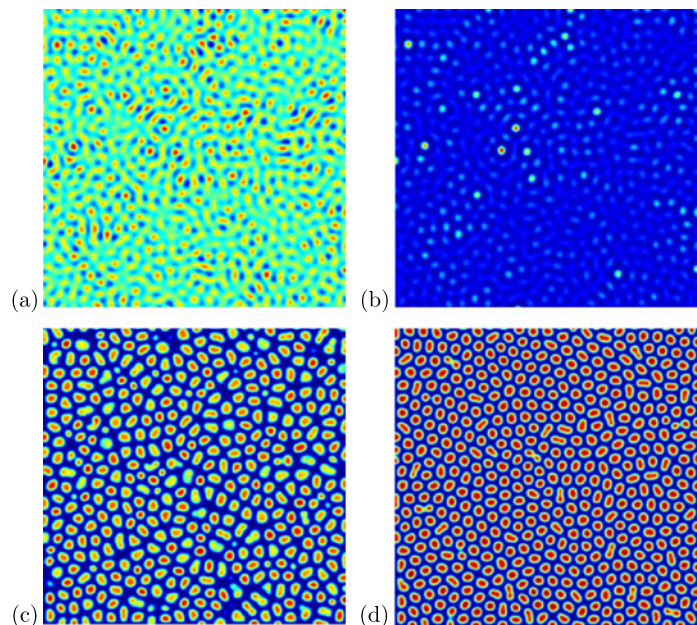


Fig. 3 (Color online) Snapshots of contour pictures of the time evolution of the prey, u , at different instants with $d_2 = 3$. For other parameters' values, see text. **(a)** 10 iterations; **(b)** 10,000 iterations; **(c)** 15,000 iterations; **(d)** 100,000 iterations

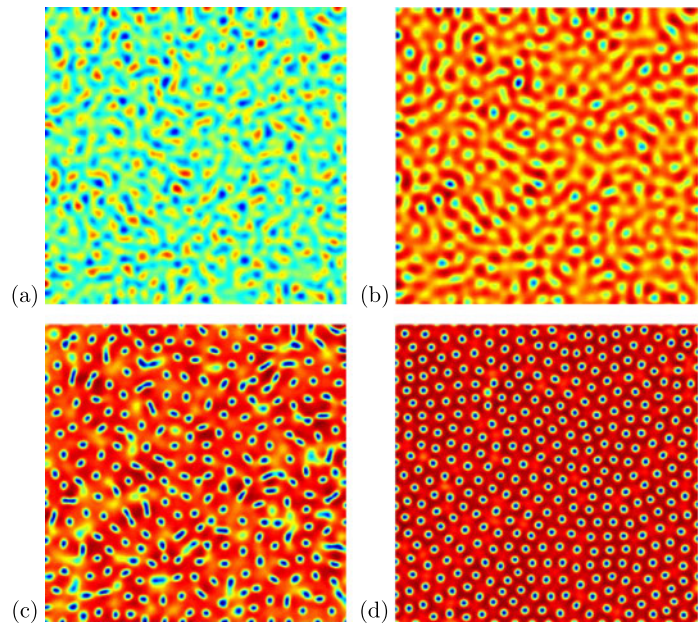
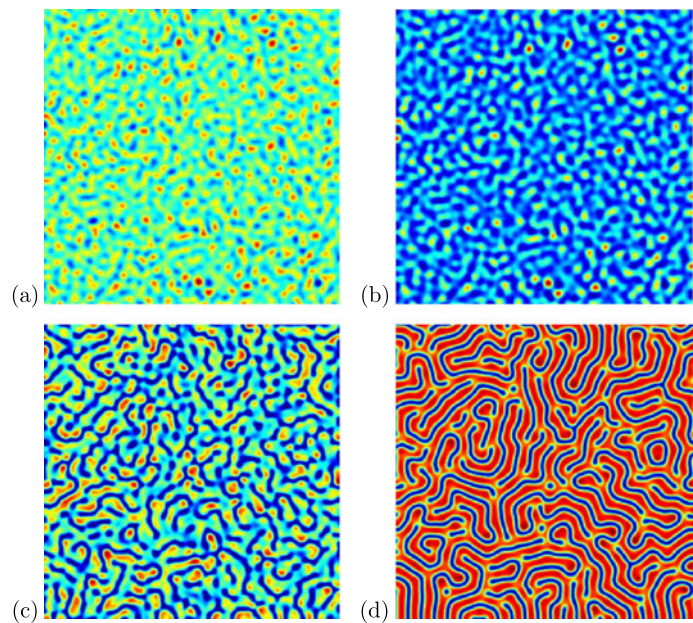


Fig. 4 (Color online) Snapshots of contour pictures of the time evolution of the prey, u , at different instants with $d_2 = 10$. For other parameters' values, see text. **(a)** 10 iterations; **(b)** 10,000 iterations; **(c)** 15,000 iterations; **(d)** 100,000 iterations



$b = 0.25$, $r = 0.015$, $d_1 = 0.2$, and $d_2 = 1.2$. 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.

The parameter values of Figs. 3–4 are in the domain of Turing space. All of the figures show the evolution of the spatial pattern of the 10, 10,000, 15,000

and 100,000 iterations, with small random perturbation of the stationary solution u^* and v^* of the spatially homogeneous systems. From Fig. 3, we can see that the regular black-eye patterns prevail over the whole domain finally, and the dynamics of the system does not undergo any further changes. Figure 4 shows that stationary labyrinthine patterns emerge in the distribution of the population density and prevail over the

whole domain. Although the dynamics of the system starts from the same initial condition as previous cases, there is an essential difference for the spatially extended model which can be seen from the three figures (cf. Figs. 2–4).

5 Discussion and conclusion

In this paper, we have investigated a Holling–Tanner model with spatial diffusion. By linear stability and bifurcation analysis, we present the dispersion relation diagrams. Numerical simulations show that the predator–prey model has rich dynamical behavior, such as spotted, black-eye, and labyrinthine patterns. The results show that the model with diffusion is more complicated than the model without it, which reveal that modeling by reaction–diffusion equations is an appropriate tool for investigating fundamental mechanisms.

Amplitude equations can be used to describe slow modulations in space and time of a reaction–diffusion system and their general forms can be derived from standard techniques of symmetry-breaking bifurcations [28–31]. In the future work, we will give the analysis of pattern selection of system (5) in detail.

Although more work is needed, in principle, it seems that diffusion is able to generate many different kinds of spatiotemporal patterns. For such reasons, we can predict that diffusion can be considered as an important mechanism for the appearance of complex spatiotemporal dynamics in ecology models. Moreover, migration is also an important motion of the populations [32], which needs further investigation.

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