Journal of Mathematics and Computer Science

Turing instability in two-patch predator-prey population dynamics

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Abstract

In this paper, a spatio-temporal model as systems of ODE which describe two-species Beddington-DeAngelis type predator-prey system living in a habitat of two identical patches linked by migration is investigated. It is assumed in the model that the per capita migration rate of each species is influenced not only by its own but also by the other one's density, i.e., there is cross diffusion present. We show that a standard (self-diffusion) system may be either stable or unstable, a cross-diffusion response can stabilize an unstable standard system and destabilize a stable standard system. For the diffusively stable model, numerical studies show that at a critical value of the bifurcation parameter the system undergoes a Turing bifurcation and the cross migration response is an important factor that should not be ignored when pattern emerges.

Keywords: Self-diffusion, cross-diffusion, diffusive instability, pattern formation.

2010 MSC: 35K57, 92B25, 93D20.

1. Introduction

The Turing bifurcation [7] is the basic bifurcation generating spatial pattern, wherein an equilibrium of a nonlinear system is asymptotically stable in the absence of diffusion but unstable in the presence of diffusion. This lies at the heart of almost all mathematical models for patterning in ecology, embryology, and elsewhere in biology and chemistry [1, 2]. Since the relation between the organisms and the space seems to be essential to stability of an ecological system, the effect of diffusion on the possibility of species coexistence in an ecological community has been an important subject in population biology [3–6].

To formulate a spatio-temporal model, one has to make some basic choices about space, time, and state variables. Each of them may be continuous or discrete [1]. One of the fundamental issues in spatial ecology is how explicit considerations of space alter the prediction of population models. Classical theories, such as diffusion-driven instability and meta-population dynamics which are developed via simple spatial population models, have profoundly increased our understanding of the issue. In this paper we scrutinize these theories by considering more complicated processes of spatial interaction of

populations. For this purpose we consider spatio-temporal models as systems of ODE which describe two-species Beddington-DeAngelis-type predator-prey system living in a habitat of two identical patches linked by migration, where the phenomenon of the Turing bifurcation occurs. It is assumed in the models that the migration rate of each species is influenced only by its own density (self-diffusion) or not only by its own but also by the other one's density (cross diffusion). We show that the equilibrium of a standard (self-diffusion) system may be either stable or unstable, a cross-diffusion response can stabilize an unstable equilibrium of standard system and destabilize a stable equilibrium of standard system. For the models we show that at a critical value of the bifurcation parameter the system undergoes a Turing bifurcation and numerical studies show that if the bifurcation parameter is increased through a critical value the spatially homogeneous equilibrium loses its stability and two new stable equilibria emerge. We conclude that the cross migration response is an important factor that should not be ignored when pattern emerges.

This paper is organized as follows. In Section 2 the model is built, in Section 3 the conditions for the Turing bifurcation are established with self-diffusion, in Section 4 the conditions for the Turing bifurcation are established with cross-diffusion (these are the main results of this paper) with an example to illustrate what can be expected, in Section 5 we summarize the main conclusions of the study.

2. The model

In this section, we consider a two-species Beddington-DeAngelis-type predator-prey system living in a habitat of two identical patches linked by migration.

Let $u_1(t,j)$:= density of prey in patch j at time t and $u_2(t,j)$:= density of predator in patch j at time t, $j = 1, 2$; $t \in R$. The interaction between two species is described as a system of differential equations as follows:

$$
\begin{aligned}
\dot{u}_1(t,1) &= r_1 u_1(t,1)(1 - \frac{u_1(t,1)}{K}) - \frac{\beta u_1(t,1)u_2(t,1)}{\alpha + u_1(t,1) + \gamma u_2(t,1)} \\
&\quad + d_1(\rho_1(u_2(t,2))u_1(t,2) - \rho_1(u_2(t,1))u_1(t,1)), \\
\dot{u}_2(t,1) &= -r_2 u_2(t,1) + \frac{\varepsilon \beta u_1(t,1)u_2(t,1)}{\alpha + u_1(t,1) + \gamma u_2(t,1)} + d_2(\rho_2(u_1(t,2))u_2(t,2) - \rho_2(u_1(t,1))u_2(t,1)), \\
\dot{u}_1(t,2) &= r_1 u_1(t,2)(1 - \frac{u_1(t,2)}{K}) - \frac{\beta u_1(t,2)u_2(t,2)}{\alpha + u_1(t,2) + \gamma u_2(t,2)} \\
&\quad + d_1(\rho_1(u_2(t,1))u_1(t,1) - \rho_1(u_2(t,2))u_1(t,2)), \\
\dot{u}_2(t,2) &= -r_2 u_2(t,2) + \frac{\varepsilon \beta u_1(t,2)u_2(t,2)}{\alpha + u_1(t,2) + \gamma u_2(t,2)} + d_2(\rho_2(u_1(t,1))u_2(t,1) - \rho_2(u_1(t,2))u_2(t,2)),
\end{aligned}
\tag{2.1}
$$

where $r_1 > 0$ and $r_2 > 0$ are the intrinsic growth rate and intrinsic mortality of the respective species, ε is the conversion rate, K is the carrying capacity for the prey, β, $\alpha > 0$ are the maximum consumption rate and the saturation constant of predator respectively, the constant γ a predator interference parameter, ad $\gamma < 0$ is the case where predators benefit from cofeeding. $d_i > 0$ ($i = 1, 2$) are the diffusion coefficients and $\rho_1 \in C^1$ is a positive increasing function of u_2, the density of the predator, $\rho_1' > 0$ and $\rho_2 \in C^1$ is a positive decreasing function of u_1 the density of the prey, $\rho_2' < 0$. The idea is that the dependence of the diffusion coefficient on the density of the other species reflects the inclination of a prey (or an activator) to leave from a certain patch because of the danger (or the inhibition) and the tendency of a predator (or the inhibition) to stay at a certain patch because of the abundance of prey (or an activator) (see [2, 7]). The functions ρ_i model the cross-diffusion effect. We say that the cross diffusion is strong if $\left| \rho'_{iu_k} \right|$ ($i \neq k$) is large. If by varying a parameter, $\left| \rho'_{iu_k} \right|$ ($i \neq k$) is increasing, then we say that the cross diffusion effect is increasing. If $\rho_i = 1$, $i = 1, 2$, then we have mere "self-diffusion".

First we consider the kinetic system without migration, i.e., $d_1 = d_2 = 0$:

$$\dot{u}_1(t,1) = r_1 u_1(t,1)(1 - \frac{u_1(t,1)}{K}) - \frac{\beta u_1(t,1)u_2(t,1)}{\alpha + u_1(t,1) + \gamma u_2(t,1)},$$

$$\dot{u}_2(t,1) = -r_2 u_2(t,1) + \frac{\varepsilon \beta u_1(t,1)u_2(t,1)}{\alpha + u_1(t,1) + \gamma u_2(t,1)},$$

$$\dot{u}_1(t,2) = r_1 u_1(t,2)(1 - \frac{u_1(t,2)}{K}) - \frac{\beta u_1(t,2)u_2(t,2)}{\alpha + u_1(t,2) + \gamma u_2(t,2)},$$

$$\dot{u}_2(t,2) = -r_2 u_2(t,2) + \frac{\varepsilon \beta u_1(t,2)u_2(t,2)}{\alpha + u_1(t,2) + \gamma u_2(t,2)}.$$

(2.2)

In particular, we will focus on the existence of equilibria and their local stability. This information will be crucial in the next section where we study the effect of the diffusion parameters on the stability of the steady states. System (2.2) is made up by two identical uncoupled systems, in which has a positive equilibrium

$$(u_1(t,1), u_2(t,1), u_1(t,2), u_2(t,2)) \equiv (\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2),$$

where

$$\overline{u}_1 = \frac{1}{2r_1\gamma\varepsilon}[K(r_1\gamma\varepsilon - \varepsilon\beta + r_2) + \sqrt{K^2(r\varepsilon\gamma - \varepsilon\beta + r_2)^2 + 4r_1K\gamma\varepsilon r_2\alpha}], \quad \overline{u}_2 = \frac{(\beta\varepsilon - r_2)\overline{u}_1}{\gamma r_2} - \frac{\alpha}{\gamma}.$$

The Jacobian matrix of the system (2.2) linearized at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is

$$J_k = \begin{pmatrix} \Phi_1 & -\Phi_2 & 0 & 0 \\ \Phi_3 & -\Phi_4 & 0 & 0 \\ 0 & 0 & \Phi_1 & -\Phi_2 \\ 0 & 0 & \Phi_3 & -\Phi_4 \end{pmatrix},$$

where

$$\Phi_1 = -\frac{r_1\overline{u}_1}{K} + r_1(1 - \frac{\overline{u}_1}{K}) - \frac{\beta\overline{u}_2}{\alpha + \overline{u}_1 + \gamma\overline{u}_2} + \frac{\beta\overline{u}_1\overline{u}_2}{(\alpha + \overline{u}_1 + \gamma\overline{u}_2)^2},$$

$$\Phi_2 = \frac{\beta\gamma\overline{u}_1\overline{u}_2}{(\alpha + \overline{u}_1 + \gamma\overline{u}_2)^2} - \frac{\beta\overline{u}_1}{\alpha + \overline{u}_1 + \gamma\overline{u}_2},$$

$$\Phi_3 = \frac{\varepsilon\beta\overline{u}_2}{\alpha + \overline{u}_1 + \gamma\overline{u}_2} + \frac{\varepsilon\beta\overline{u}_1\overline{u}_2}{(\alpha + \overline{u}_1 + \gamma\overline{u}_2)^2},$$

$$\Phi_4 = r_2 - \frac{\varepsilon\beta\gamma\overline{u}_1\overline{u}_2}{(\alpha + \overline{u}_1 + \gamma\overline{u}_2)^2} - \frac{\varepsilon\beta\overline{u}_2}{\alpha + \overline{u}_1 + \gamma\overline{u}_2}.$$

The characteristic polynomial is

$$D_4(\lambda) = (D_2(\lambda))^2, \quad D_2(\lambda) = \lambda^2 + \lambda(\Phi_4 - \Phi_1) + \Phi_2\Phi_3 - \Phi_1\Phi4.$$

Assume that

$$\Phi_4 - \Phi_1 > 0 \text{ and } \Phi_2\Phi_3 - \Phi_1\Phi_4 > 0,$$

(2.3)

then the coexistence equilibrium point $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is linearly asymptotically stable.

3. The effects of a self-diffusion response

In this section, we treat a two-species model in a habitat of two identical patches linked by migration in which the migration rate of each species is influenced only by its own density, i.e., there is no response to

the density of the other one. The interaction is described as a system of differential equations as follows:

$$\dot{u}_1(t,1) = r_1 u_1(t,1)(1 - \frac{u_1(t,1)}{K}) - \frac{\beta u_1(t,1)u_2(t,1)}{\alpha + u_1(t,1) + \gamma u_2(t,1)} + d_1(u_1(t,2) - u_1(t,1)),$$

$$\dot{u}_2(t,1) = -r_2 u_2(t,1) + \frac{\varepsilon\beta u_1(t,1)u_2(t,1)}{\alpha + u_1(t,1) + \gamma u_2(t,1)} + d_2(u_2(t,2) - u_2(t,1)),$$

$$\dot{u}_1(t,2) = r_1 u_1(t,2)(1 - \frac{u_1(t,2)}{K}) - \frac{\beta u_1(t,2)u_2(t,2)}{\alpha + u_1(t,2) + \gamma u_2(t,2)} + d_1(u_1(t,1) - u_1(t,2)),$$

$$\dot{u}_2(t,2) = -r_2 u_2(t,2) + \frac{\varepsilon\beta u_1(t,2)u_2(t,2)}{\alpha + u_1(t,2) + \gamma u_2(t,2)} + d_2(u_2(t,1) - u_2(t,2)),$$

The Jacobian matrix of the system with self-diffusion at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ can be written as:

$$J_{Self} = \begin{pmatrix} \Phi_1 - d_1 & -\Phi_2 & d_1 & 0 \\ \Phi_3 & -\Phi_4 - d_2 & 0 & d_2 \\ d_1 & 0 & \Phi_1 - d_1 & -\Phi_2 \\ 0 & d_2 & \Phi_3 & -\Phi_4 - d_2 \end{pmatrix}.$$

The characteristic polynomial is

$$D_{Self} = D_2(\lambda)(\lambda^2 + \lambda(\Phi_4 - \Phi_1 + 2(d_1 + d_2)) + \Phi_2\Phi_3 - \Phi_1\Phi_4 + 2d_1\Phi_4 - 2d_2(\Phi_1 - 2d_1)).$$

We know that $D_2(\lambda)$ has two roots with negative real parts. By (2.3), clearly, $\Phi_4 - \Phi_1 + 2(d_1 + d_2) > 0$. The other polynomial will have a negative and a positive root if the constant term is negative. By the properties of the model and conditions (2.3) the first three terms are positive. Suppose that the parameters have been chosen so that

$$\Phi_1 - 2d_1 > 0. \tag{3.1}$$

If we have achieved this we may increase d_2 and the constant term becomes negative. The calculations lead to the following Theorem.

Theorem 3.1. *If* (2.3) *and* (3.1) *hold and if*

$$d_2 > d_{2crit} = \frac{(\Phi_2\Phi_3 - \Phi_1\Phi_4 + 2d_1\Phi_4)}{2(\Phi_1 - 2d_1)},$$

then Turing instability occurs.

Remark 3.2. If the corresponding conditions hold and the parameters have been chosen so that

$$\Phi_1 - 2d_1 < 0, \tag{3.2}$$

then self-diffusion never destabilizes the equilibrium $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ which is asymptotically stable for the kinetic system, i.e., the equilibrium $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is diffusively stable for all values of d_2.

We apply our analytical approach to the following example and we are looking for conditions which imply Turing instability with self diffusion.

Example 3.3. We choose $r_1 = 0.5$, $r_2 = 0.25$, $\alpha = 0.6$, $\beta = 0.6$, $\gamma = 0.4$, $\epsilon = 1$, $K = 2.6$, $d_1 = 0.004$. The unique positive equilibrium is $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2) = (0.72812, 1.0484, 0.72812, 1.0484)$. We see that it is asymptotically stable for the kinetic system (2.2).

We consider d_2 as a bifurcation parameter. In this case at $d_{2crit} \cong 10.11330832$, we have four eigenvalues $\lambda_i(i = 1, 2, 3, 4)$ such that $\text{Re}\,\lambda_i < 0, (i = 1, 2, 3)$ and $\lambda_4 = 0$.

If $d_2 < d_{2crit} \Rightarrow \text{Re}\,\lambda_i < 0, (i = 1, 2, 3, 4)$, then $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is asymptotically stable.

If $d_2 > d_{2crit} \Rightarrow \text{Re}\,\lambda_i < 0, (i = 1, 2, 3)$ and $\lambda_4 > 0$, then $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is unstable.

Thus as d_2 is increased through $d_2 = d_{2crit}$ the spatially homogeneous equilibrium loses its stability. Numerical calculations show that two new spatially non-constant equilibria emerge (see Figure 1) and these equilibria are asymptotically stable; so that this is a pitchfork bifurcation.
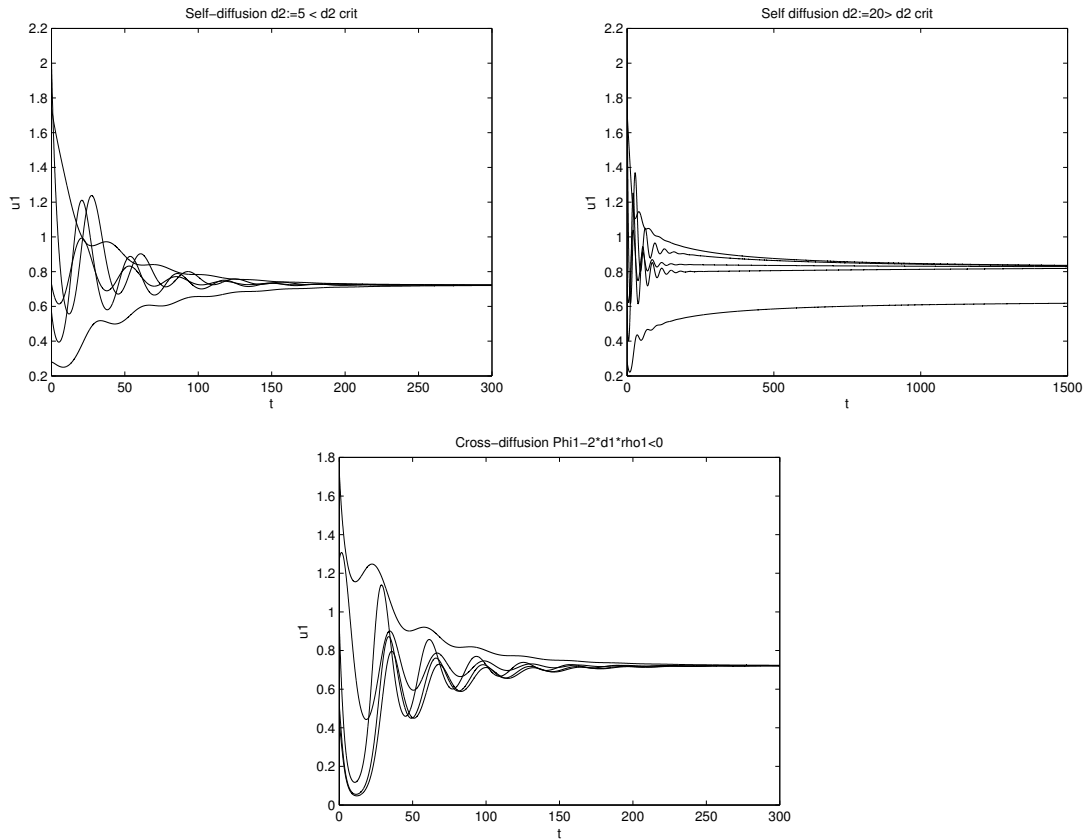
Figure 1: Graphs of the coordinate $u_1(t, 1)$ of five solutions of the Example corresponding to the respective initial conditions (3.7281, 1.0484, 0.5281, 3.484), (1.7281, 0.0484, 1.2812, 1.4841), (2.0281, 3.8401, 0.92812,1.0484), (5.5728, 2.0484, 0.4281, 2.0484), (0.2812, 1.0484, 1.7281, 1.0484) (Figure produced by applying Matlab).

4. The effects of a cross-diffusion response

For model (2.1) with cross-diffusion response (i.e., $\frac{\partial \rho_i(u)}{\partial u_j} \neq 0, i \neq j$) we see that $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is also a spatially homogeneous equilibrium of the system with cross-diffusion.

The Jacobian matrix of the system with cross-diffusion at $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ can be written as:

$$J_{cross} = \begin{pmatrix} \Phi_1 - d_1\rho_1 & -\Phi_2 - d_1\rho_1'\overline{u}_1 & d_1\rho_1 & d_1\rho_1'\overline{u}_1 \\ \Phi_3 - d_2\rho_2'\overline{u}_2 & -\Phi_4 - d_2\rho_2 & d_2\rho_2'\overline{u}_2 & d_2\rho_2 \\ d_1\rho_1 & d_1\rho_1'\overline{u}_1 & \Phi_1 - d_1\rho_1 & -\Phi_2 - d_1\rho_1'\overline{u}_1 \\ d_2\rho_2'\overline{u}_2 & d_2\rho_2 & \Phi_3 - d_2\rho_2'\overline{u}_2 & -\Phi_4 - d_2\rho_2 \end{pmatrix},$$

where ρ_1 and ρ_1' are to be taken at $\overline{u}_2$ and ρ_2, ρ_2' at $\overline{u}_1$.

Theorem 4.1. *Under condition* (2.3), *if*

$$\Phi_1 - 2d_1\rho_1 > 0 \tag{4.1}$$

and $\rho_2(\overline{u}_1)$ is sufficiently large, then Turing instability occurs.

Proof.

$$\det(J_D - \lambda I) = \begin{vmatrix} \Phi_1 - d_1\rho_1 - \lambda & -\Phi_2 - d_1\rho_1'\overline{u}_1 & d_1\rho_1 & d_1\rho_1'\overline{u}_1 \\ \Phi_3 - d_2\rho_2'\overline{u}_2 & -\Phi_4 - d_2\rho_2 - \lambda & d_2\rho_2'\overline{u}_2 & d_2\rho_2 \\ d_1\rho_1 & d_1\rho_1'\overline{u}_1 & \Phi_1 - d_1\rho_1 - \lambda & -\Phi_2 - d_1\rho_1'\overline{u}_1 \\ d_2\rho_2'\overline{u}_2 & d_2\rho_2 & \Phi_3 - d_2\rho_2'\overline{u}_2 & -\Phi_4 - d_2\rho_2 - \lambda \end{vmatrix}.$$

Using the properties of determinant we get

$$\begin{vmatrix} \Phi_1 - \lambda & -\Phi_2 & d_1\rho_1 & d_1\rho'_1\overline{u}_1 \\ \Phi_3 & -\Phi_4 - \lambda & d_2\rho'_2\overline{u}_2 & d_2\rho_2 \\ 0 & 0 & \Phi_1 - 2d_1\rho_1 - \lambda & -\Phi_2 - 2d_1\rho'_1\overline{u}_1 \\ 0 & 0 & \Phi_3 - 2d_2\rho'_2\overline{u}_2 & -\Phi_4 - 2d_2\rho_2 - \lambda \end{vmatrix}$$

$$= D_2(\lambda)\{\lambda^2 + \lambda[\Phi_4 - \Phi_1 + 2(d_1\rho_1 + d_2\rho_2)] + \Phi_2\Phi_3 - \Phi_1\Phi_4$$
$$+ 2d_1\Phi_4\rho_1 - 2d_2\rho_2(\Phi_1 - 2d_1\rho_1) + 2d_1\overline{u}_1\Phi_3\rho'_1 - 2d_2\rho'_2\overline{u}_2(\Phi_2 + 2d_1\rho'_1\overline{u}_1)\}.$$

We know that $D_2(\lambda)$ has two roots with negative real parts. By (2.3), clearly, $\Phi_4 - \Phi_1 + 2(d_1\rho_1 + d_2\rho_2) > 0$. The other polynomial will have a negative and a positive root if its constant term is negative. This can be achieved if $\rho_2(\overline{u}_1)$ is increased. □

Remark 4.2. If (3.2) holds and there is no cross-diffusion then the equilibrium remains stable for any $d_2 > 0$. Still, (4.1) may hold, i.e., in this case only the cross-diffusion effect may destabilize the equilibrium.

Remark 4.3. If the parameters have been chosen so that

$$\Phi_1 - 2d_1 > 0 \text{ and } \Phi_1 - 2d_1\rho_1 < 0,$$

then the equilibrium $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ remains asymptotically stable for any $d_2 > 0$ and $\rho_2 > 0$ in the cross-diffusion case while, as we have seen, it will undergo a Turing bifurcation in the absence of cross-diffusion.

We apply our analytical approach to the following example of migration function and we are looking for conditions which imply Turing instability with cross-diffusion.

Example 4.4. We choose

$$\rho_1(u_2) = \frac{m_1 u_2}{1 + u_2}, \quad \rho_2(u_1) = m_2 \exp(\frac{-u_1}{m_2}), \ m_1, \ m_2 > 0.$$

If $r_1 = 0.5$, $r_2 = 0.25$, $\alpha = 0.6$, $\beta = 0.6$, $\gamma = 0.4$, $\epsilon = 1$, $K = 2.6$, then the unique positive equilibrium is $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2) = (.728122, 1.04842, .728122, 1.04842)$. We see that this point is asymptotically stable with respect to the kinetic system (2.2).

If $d_2 = 8$ (Resp. 12), then $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is asymptotically stable (Resp. unstable).

For the cross-diffusion system we consider m_2 as a bifurcation parameter. In this case at $d_1 = 1$, $d_2 = 1$, $m_1 = 0.001$, and $m_{2crit} \cong 34.62$, we have four eigenvalues $\lambda_i(i = 1, 2, 3, 4)$ such that $\text{Re}\,\lambda_i < 0, (i = 1, 2, 3)$ and $\lambda_4 = 0$.

If $m_2 < m_{2crit} \Rightarrow \text{Re}\,\lambda_i < 0$ $(i = 1, 2, 3, 4)$, $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is asymptotically stable .

If $m_2 > m_{2crit} \Rightarrow \text{Re}\,\lambda_i < 0$ $(i = 1, 2, 3)$ and $\lambda_4 > 0$, $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is unstable.

If $d_1 = 0.004$, $d_2 = 11$, and $m_1 = 10$, then $(\overline{u}_1, \overline{u}_2, \overline{u}_1, \overline{u}_2)$ is asymptotically stable for all m_2.

In this example $\left|\rho'_{2u_1}(u_1, u_2)\right| = \exp(-\frac{u_1}{m_2})$. As we see, if m_2 is increased for fixed u_1, this derivative is increasing, i.e., the cross-diffusion effect is increasing and the spatially homogeneous equilibrium loses its stability. Numerical calculations show that two new spatially non-constant equilibria emerge (see Figure 2), and these equilibria are asymptotically stable; so that this is a pitchfork bifurcation.

5. Conclusions

In the present article our interest is to study spatio-temporal models as systems of ODE which describe two-species Beddington-DeAngelis-type predator-prey system living in a habitat of two identical patches linked by migration. It is assumed in the models that the migration rate of each species is influenced only by its own density (self-diffusion) or not only by its own but also by the other one's density (cross

diffusion). We show that the equilibrium of a standard (self-diffusion) system may be either stable or unstable, a cross-diffusion response can stabilize an unstable equilibrium of standard system and destabilize a stable equilibrium of standard system and the cross migration response is an important factor that should not be ignored when pattern emerges, also as m_2 is increased through $m_2 = m_{2crit}$ the spatially homogeneous equilibrium loses its stability and two new stable equilibria emerge.
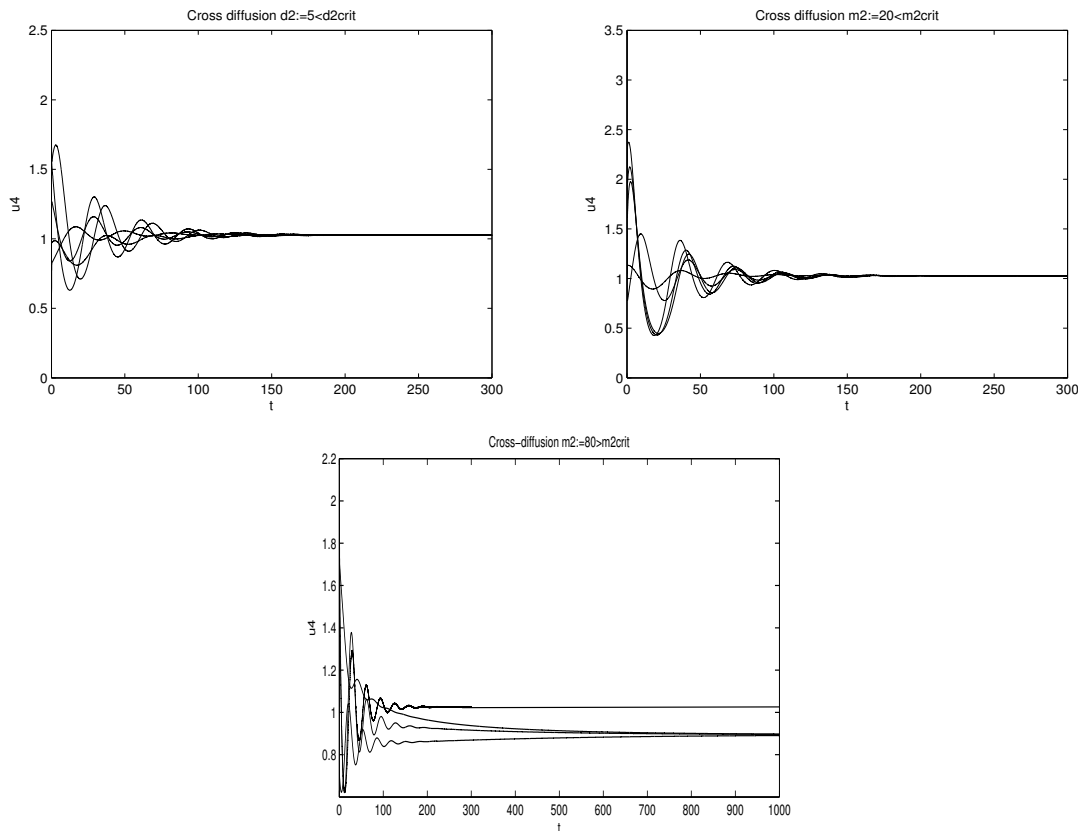

Figure 2: Graphs of the coordinate $u_4(t, 1)$ of five solutions of the Example corresponding to the respective initial conditions (3.7281, 1.0484, 0.5281, 3.484), (1.7281, 0.0484, 1.2812, 1.4841), (2.0281, 3.8401, 0.92812,1.0484), (5.5728, 2.0484, 0.4281, 2.0484), (0.2812, 1.0484, 1.7281, 1.0484) (Figure produced by applying Matlab).

Acknowledgment

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