Effect of time-varying cross-diffusivity in a two-species Lotka–Volterra competitive system

S. Raychaudhuri [a,*], D.K. Sinha [a], J. Chattopadhyay [b]

[a] Department of Applied Mathematics, University of Calcutta 92, A.P.C. Road, Calcutta – 700 009, India
[b] Embryology Research Unit Indian Statistical Institute 203, B.T. Road, Calcutta – 700 035, India

Received 7 June 1995; accepted 13 November 1995

Abstract

Cross-diffusion is necessary for achieving spatial pattern (patchiness) in a two-species Lotka–Volterra diffusive system. Cross-diffusive instability is less likely to occur with time varying than with constant cross-diffusivity.

Keywords: Spatial patterns; Diffusion; Temporal patterns; Lotka–Volterra models

1. Introduction

Reaction-diffusion systems have been proposed as mechanisms for biological pattern formation in embryological and ecological context. All such works are based on the pioneering work of Turing (1952). Segel and Jackson (1972) were the first to call attention to the fact that Turing's idea would be applicable in ecological situation also. They conjectured that the nature of the equations which describe chemical interaction does not seem fundamentally different from the nature of those which describe ecological interaction among the species. Again, the idea that dispersal could give rise to instabilities and hence to spatial pattern was due to a number of authors (see Okubo, 1980, for review).

Self-diffusion mechanisms form is the most widely studied class of models for ecological pattern formation and in these cases, the system parameters are usually treated as independent of time. The literature shows that in some situations self diffusion alone cannot generate or maintain spatial pattern (for example, see, McLaughlin and Roughgarden, 1992; Chattopadhyay et al., 1994) and hence, necessity for other mechanisms, for example, cross-diffusion arises. The idea of cross-diffusive instability has been examined by several authors (Gurtin, 1974; Okubo, 1980). Moreover, in real situations, diffusivities can vary in time and oceanic diffusion may serve as an example. Recently Okubo and Timm (1992) have taken into account these important phenomena in an ecological model by Levin and Segel (1976) for predator–prey planktonic species.

In this paper we have considered a two-species Lotka Volterra diffusive competitive system and observed that cross-diffusion is necessary for pattern forming instability. By considering the time-varying cross-diffusivity in this system we have observed that time-varying cross-diffusivities makes the system more stable in comparison with the constant cross-diffusivity.

2. The mathematical model

The reaction diffusion Lotka–Volterra two-species competition model can be written as

$$\left.\begin{aligned}\frac{\partial X_1}{\partial t}&=X_1(r_1-a_{11}X_1-a_{12}X_2)+D_{11}\frac{\partial^2 X_2}{\partial r^2}+\frac{\partial}{\partial r}\left\{D_{12}(X_1)\frac{\partial X_2}{\partial r}\right\}\\ \frac{\partial X_2}{\partial t}&=X_2(r_2-a_{21}X_1-a_{22}X_2)+D_{22}\frac{\partial^2 X_2}{\partial r^2}+\frac{\partial}{\partial r}\left\{D_{21}(X_2,t)\frac{\partial X_1}{\partial r}\right\}\end{aligned}\right] \quad (1)$$

with $r_i > 0$, $a_{ij} > 0$.

$X_1(r,t)$ and $X_2(r,t)$ denote population densities of two competing species at time t, r is the spatial co-ordinate, D_{11} and D_{22} are the constant self-diffusion coefficients of two competing species, $D_{12}(X_1)$ is the density-dependent cross-diffusion coefficient of X_1 and $D_{21}(X_2,t)$ is the density and time-dependent cross-diffusion coefficient of X_2 such that $D_{12}(X_1) \to 0$ as $X_1 \to 0$ and $D_{21}(X_2,t) \to 0$ as $X_2 \to 0$.

The system (Eq. 1) has to be analysed with the following initial and boundary conditions:

$$X_i(r,0) > 0 \quad (2)$$

$$\left.\frac{\partial X_i}{\partial r}\right|_{r=0}=0,\ \left.\frac{\partial X_i}{\partial r}\right|_{r=R}=0. \quad i=1,2 \quad (3)$$

The meaning of zero-flux boundary condition is that no external input is imposed from outside (Murray, 1990).

We shall now investigate Eq. 1 with initial condition as in Eq. 2 and the zero flux boundary conditions as in Eq. 3. Note that when $X_1 = 0$ and $X_2 \neq 0$ for all r, $\partial X_1/\partial r = 0$. Similarly, when $X_2 = 0$ and $X_1 \neq 0$ for all r, $\partial X_2/\partial r = 0$.

As a special case, we assume that cross-diffusion coefficients are given by

$$\left.\begin{aligned}D_{12}(X_1)&=D'_{12}\left(\frac{X_1}{\epsilon_1+X_1}\right)\\ D_{21}(X_2,t)&=D'_{21}(t)\left(\frac{X_2}{\epsilon_2+X_2}\right)\end{aligned}\right\} \quad (4)$$

where ϵ_1 and ϵ_2 are very small so that

$$\left.\begin{aligned}D_{12}(X_1)&=D'_{12} &&\text{for } X_1 \gg \epsilon_1\\ D_{21}(X_2,t)&=D'_{21}(t) &&\text{for } X_2 \gg \epsilon_2\end{aligned}\right\} \quad (5)$$

We then restrict our analysis to the population domain given by

$$w=\{(X_1,X_2)\mid X_1 \gg \epsilon_1, \text{ and } X_2 \gg \epsilon_2\} \quad (6)$$

where we may consider the cross-diffusion coefficients as density independent. Then Eq. 1 corresponding to the region w is given by

$$\left.\begin{aligned}\frac{\partial X_1}{\partial t}&=X_1(r_1-a_{11}X_1-a_{12}X_2)+D_{11}\frac{\partial^2 X_1}{\partial r^2}+D'_{12}\frac{\partial^2 X_2}{\partial r^2}\\ \frac{\partial X_2}{\partial t}&=X_2(r_2-a_{21}X_1-a_{22}X_2)+D_{22}\frac{\partial^2 X_2}{\partial r^2}+D'_{21}(t)\frac{\partial^2 X_1}{\partial r^2}\end{aligned}\right\} \tag{7}$$

As we are mainly interested to investigate the behaviour of the system around the interior equilibrium point, so we shall put emphasis on (X_1^*, X_2^*), where X_1^* and X_2^* are the interior equilibrium, given by

$$X_1^* = \frac{r_1 a_{22} - r_2 a_{12}}{a_{11}a_{22} - a_{21}a_{12}} \tag{8}$$

and

$$X_2^* = \frac{r_2 a_{11} - r_1 a_{21}}{a_{11}a_{22} - a_{21}a_{12}} \tag{9}$$

Now, (X_1^*, X_2^*) are feasible if

$$\frac{a_{11}}{a_{21}} > \frac{r_1}{r_2} > \frac{a_{12}}{a_{22}} \tag{10}$$

or,

$$\frac{a_{11}}{a_{21}} < \frac{r_1}{r_2} < \frac{a_{12}}{a_{22}}. \tag{11}$$

The community matrix of Eq. 7 without diffusion with elements A_{ij} $(i,j = 1,2)$ evaluated at the equilibrium X_i^* is given by,

$$\begin{aligned}A_{11} &= -a_{11}X_1^* < 0\\ A_{12} &= -a_{12}X_1^* < 0\\ A_{21} &= -a_{21}X_2^* < 0\\ A_{22} &= -a_{22}X_2^* < 0.\end{aligned} \tag{12}$$

For local stability without diffusion, we require

$$A_{11} + A_{22} < 0 \tag{13}$$

i.e., $-a_{11}X_1^* - a_{22}X_2^* < 0$ which is obvious, and

$$A_{11}A_{22} > A_{12}A_{21} \tag{14}$$

i.e., $a_{11}a_{22} > a_{12}a_{21}$.

If $a_{11}a_{22} > a_{12}a_{21}$, the model is said to describe a tolerant competition. In case of severe competition the model without diffusion is locally unstable if it admits a positive equilibrium. Hence it can not achieve spatial pattern according to the Turing concept. So we shall only consider the case of Eq. 10.

3. Cross-diffusive instability

To examine the stability of the uniform steady state to spatial and temporal perturbations in the presence of self-diffusion and cross-diffusion terms we write

$$X_i(r,t) = X_i^* + x_i(r,t), \quad (i = 1,2) \tag{15}$$

where x_i are assumed to be small. Then the linearized version of Eq. 1 is

$$\frac{\partial x_1}{\partial t} = A_{11} x_1 + A_{12} x_2 + D_{11} \frac{\partial^2 x_1}{\partial r^2} + D'_{12} \frac{\partial^2 x_2}{\partial r^2} \tag{16}$$

and

$$\frac{\partial x_2}{\partial t} = A_{21} x_1 + A_{22} x_2 + D_{22} \frac{\partial^2 x_2}{\partial r^2} + D'_{21}(t) \frac{\partial^2 x_1}{\partial r^2}. \tag{17}$$

Now we consider the case without cross-diffusion, then Eq. 16 and Eq. 17 take the form

$$\frac{\partial x_1}{\partial t} = A_{11} x_1 + A_{12} x_2 + D_{11} \frac{\partial^2 x_1}{\partial r^2} \tag{18}$$

$$\frac{\partial x_2}{\partial t} = A_{21} x_1 + A_{22} x_2 + D_{22} \frac{\partial^2 x_2}{\partial r^2}. \tag{19}$$

Now we define the dimensionless time by $wt \equiv \tau$ $(w > 0)$, and we express the solution in the form

$$\begin{aligned} x_1 &= \phi_1(t) e^{ikr} \\ x_2 &= \phi_2(t) e^{ikr}. \end{aligned} \tag{20}$$

Then we obtain the equations for ϕ_i, as

$$\frac{d\phi_1}{d\tau} = \left(A_{11} - K^2 D_{11}\right) \phi_1 w^{-1} + A_{12} \phi_2 w^{-1} \tag{21}$$

$$\frac{d\phi_2}{d\tau} = A_{21} \phi_1 w^{-1} + \left(A_{22} - K^2 D_{22}\right) \phi_2 w^{-1}. \tag{22}$$

Eq. 21 and Eq. 22 can be written as

$$\frac{d\phi_1}{d\tau} = \hat{A}_{11} \phi_1 + \hat{A}_{12} \phi_2 \tag{23}$$

$$\frac{d\phi_2}{d\tau} = \hat{A}_{21} \phi_1 + \hat{A}_{22} \phi_2, \tag{24}$$

where

$$\begin{aligned} \hat{A}_{11} &= \left(A_{11} - K^2 D_{11}\right) w^{-1} \\ \hat{A}_{12} &= A_{12} w^{-1} \\ \hat{A}_{21} &= A_{21} w^{-1} \\ \hat{A}_{22} &= \left(A_{22} - K^2 D_{22}\right) w^{-1}. \end{aligned} \tag{25}$$

For the equilibrium to be stable without cross-diffusion ($D'_{12} = D'_{21} = 0$), we require,

$$\begin{aligned} &\hat{A}_{11} + \hat{A}_{22} < 0 \\ &\hat{A}_{11} \hat{A}_{22} > \hat{A}_{12} \hat{A}_{21}. \end{aligned} \tag{26}$$

Now

$$\hat{A}_{11} + \hat{A}_{22} = -\left(a_{11} X_1^* + a_{22} X_2^*\right) w^{-1} - K^2 w^{-1} \left(D_{11} + D_{22}\right) < 0,$$

while $\hat{A}_{11}\hat{A}_{22} > \hat{A}_{12}\hat{A}_{21}$ implies

$$(a_{11}a_{22} - a_{12}a_{21})X_1^*X_2^* + a_{11}K^2D_{22}X_1^* + a_{22}K^2D_{11}X_2^* + K^4D_{11}D_{22} > 0$$

which follows from Eq. 14.

Hence the Eq. 7 is locally stable without cross-diffusion. If we introduce cross-diffusion terms, then Eq. 21 and Eq. 22 take the form

$$\frac{d\phi_1}{d\tau} = (A_{11} - K^2D_{11})\phi_1 w^{-1} + (A_{12} - K^2D'_{12})\phi_2 w^{-1} \tag{27}$$

$$\frac{d\phi_2}{d\tau} = (A_{21} - K^2D'_{21}(\tau))\phi_1 w^{-1} + (A_{22} - K^2D_{22})\phi_2 w^{-1}. \tag{28}$$

Eq. 27 and Eq. 28 can be written as

$$\frac{d\phi_1}{d\tau} = \bar{A}_{11}\phi_1 + \bar{A}_{12}\phi_2 \tag{29}$$

$$\frac{d\phi_2}{d\tau} = \bar{A}_{21}\phi_1 + \bar{A}_{22}\phi_2 \tag{30}$$

where

$$\begin{aligned} \bar{A}_{11} &= (A_{11} - K^2D_{11})w^{-1} \\ \bar{A}_{12} &= (A_{12} - K^2D'_{12})w^{-1} \\ \bar{A}_{21} &= (A_{21} - K^2D'_{21})w^{-1} \\ \bar{A}_{22} &= (A_{22} - K^2D_{22})w^{-1}. \end{aligned} \tag{31}$$

In order to investigate cross-diffusive instability with time-varying D'_{21}, we now specify D'_{21}, in the form

$$D'_{21}(\tau) = D'_{12}(a + b\sin\tau) > 0 \tag{32}$$

$$\text{with } a > 1, \quad a > |b|. \tag{33}$$

Then Eq. 29 and Eq. 30 can be written as

$$\frac{d\phi_1}{d\tau} = \bar{\bar{A}}_{11}\phi_1 + \bar{\bar{A}}_{12}\phi_2 \tag{34}$$

$$\frac{d\phi_2}{d\tau} = \bar{\bar{A}}_{21}\phi_1 + \bar{\bar{A}}_{22}\phi_2, \tag{35}$$

where

$$\bar{\bar{A}}_{11} = \bar{A}_{11},\ \bar{\bar{A}}_{12} = \bar{A}_{12},\ \bar{\bar{A}}_{22} = \bar{A}_{22}$$

but

$$\bar{\bar{A}}_{21} = -(a_{21}X_2^* + K^2aD_{12})w^{-1} - k^2w^{-1}D'_{12}b\sin\tau = \bar{\bar{A}}_{21}^* - k^2w^{-1}D'_{12}b\sin\tau. \tag{36}$$

The amplitude Eq. 34 and Eq. 35 will be used to find the stability of system Eq. 16 and Eq. 17.

As a reference state we take a case of b = 0, i.e., constant $\bar{\bar{A}}_{21}$. If $\bar{\bar{A}}_{21}$ is constant, cross-diffusive instability sets in when at least one of the following conditions is violated subject to Eq. 26.

$$\bar{\bar{A}}_{11} + \bar{\bar{A}}_{22} < 0 \tag{37}$$

and

$$\bar{\bar{A}}_{11}\bar{\bar{A}}_{22}-\bar{\bar{A}}_{12}\bar{\bar{A}}_{21}^{*}>0 \tag{38}$$

Note that Eq. 37 is met when Eq. 26 holds. Hence only violation of Eq. 38 will give rise to instability.

Reversal of the inequality yields,

$$H(K^2)=\bar{\bar{A}}_{11}\bar{\bar{A}}_{22}-\bar{\bar{A}}_{12}\bar{\bar{A}}_{21}^{*}<0$$

i.e.,

$$H(K^2)=K^4\left(D_{11}D_{22}-aD_{12}'^2\right)-K^2\left(A_{22}D_{11}+A_{11}D_{22}-D_{12}'A_{21}-aD_{12}'A_{21}\right)+A_{11}A_{22}-A_{12}A_{21}<0.$$

The minimum of $H(K^2)$ occurs at $K^2=K_m^2$ where

$$K_m^2=\frac{\left(A_{22}D_{11}+A_{11}D_{22}-D_{12}'A_{21}-aD_{12}'A_{12}\right)}{2\left(D_{11}D_{22}-aD_{12}'^2\right)}>0. \tag{39}$$

Hence,

$$A_{22}D_{11}+A_{11}D_{22}-A_{21}D_{12}-aD_{12}A_{12}>0$$

and

$$D_{11}D_{22}-aD_{12}^2>0\ \left(\text{As } H(K^2) \text{ is minimum at } K^2=K_m^2\right) \tag{40}$$

A sufficient criterion for instability is that $H(K_m^2)$ is negative. This condition, in combination with Eq. 14 and Eq. 39, leads to the following criterion for cross-diffusive instability:

$$A_{22}D_{11}+A_{11}D_{22}-A_{21}D_{12}-aD_{12}A_{12}>2\left(D_{11}D_{22}-aD_{12}^2\right)^{1/2}\left(A_{11}A_{22}-A_{12}A_{21}\right)^{1/2}>0. \tag{41}$$

The critical value of a, i.e., a_{cr}, for the instability is obtained when the first inequality of Eq. 41 becomes an equality.

The corresponding critical wave number K_c for the first perturbations to grow is found by evaluating K_m from Eq. 39.

We now return to the amplitude equations Eq. 34 and Eq. 35 with Eq. 36 and will examine the problem of time-varying cross-diffusive instability. We are interested to see whether the cross-diffusive instability can occur more likely or less likely in the system with variable cross-diffusivities, in comparison to the reference system with constant cross-diffusivities.

We apply the Floquet theory (see Okubo and Timm, 1992) to second-order differential equations. From Eq. 34 and Eq. 35 we get,

$$\frac{d^2\phi_1}{d\tau^2}-\left(\bar{\bar{A}}_{11}+\bar{\bar{A}}_{22}\right)\frac{d\phi_1}{d\tau}+\left[\bar{\bar{A}}_{11}\bar{\bar{A}}_{22}-\bar{\bar{A}}_{12}\bar{\bar{A}}_{21}(\tau)\right]\phi_1=0. \tag{42}$$

The transformation:

$$\psi_1=\exp\left[-\frac{1}{2}\left(\bar{\bar{A}}_{11}+\bar{\bar{A}}_{22}\right)\tau\right]\phi_1$$

leads Eq. 42 to the equation for ψ_1,

$$\frac{d^2\psi_1}{d\tau^2}+Q(\tau)\psi_1=0 \tag{43}$$

where

$$Q(\tau) = -\frac{1}{4}\left(\bar{\bar{A}}_{11} + \bar{\bar{A}}_{22}\right)^2 + \left\{\bar{\bar{A}}_{11}\bar{\bar{A}}_{22} - \bar{\bar{A}}_{12}\bar{\bar{A}}_{21}(\tau)\right\}. \tag{44}$$

It will be seen that Eq. 43 is the standard form of Hill's equation.

To this end, substitution of $\bar{\bar{A}}_{11}$, $\bar{\bar{A}}_{22}$, $\bar{\bar{A}}_{12}$, $\bar{\bar{A}}_{21}(\tau)$ in Eq. 44 results in

$$Q(\tau) = \delta + \epsilon \sin\tau. \tag{45}$$

Where

$$\delta = -\frac{1}{4w^2}\left[a_{11}X_1^* + a_{22}X_2^* + K^2D_{11} + K^2D_{22}\right]^2 + \left(a_{11}X_1^* + K^2D_{11}\right)\left(a_{22}X_2^* + K^2D_{22}\right)w^{-2}$$
$$-\left(a_{21}X_1^* + K^2D'_{12}\right)\left(a_{21}X_2^* + K^2aD'_{12}\right)w^{-2} \tag{46}$$

and

$$\epsilon = -\left(a_{12}X_1^* + K^2D'_{12}\right)K^2D'_{12}bw^{-1} \tag{47}$$

(where X_1^* and X_2^* are given by Eq. 10 and Eq. 11). Then Eq. 43 takes the form

$$\frac{d^2\psi_1}{d\tau^2} + (\delta + \epsilon\sin\tau)\psi_1 = 0. \tag{48}$$

We can write,

$$\phi_1 = \exp\left\{\frac{1}{2}\left(\bar{\bar{A}}_{11} + \bar{\bar{A}}_{22}\right)\tau\right\}\psi_1$$
or
$$\phi_1 = \exp\left\{\frac{1}{2w}\left(a_{11}X_1^* + a_{22}X_2^* + K^2D_{11} + K^2D_{22}\right)\tau\right\}\psi_1 \tag{49}$$

where ψ_1 is the solution of Eq. 42.

Now we shall carry out stability analysis of the system in the vicinity of the critical value a_{cr} for small b, to see the effect of varying diffusivity on the system stability.

When the amplitude b of variability in D'_{21} is small, it can be shown that the solutions of Eq. 34 and Eq. 35 are asymptotically stable under the condition that the reference state, i.e., $b = 0$, is marginally stable. To this end, we first set $a = a_{cr}$ and $K_m = K_c$ for marginal stability in the reference state and analyze the linear stability of the system when a small variation in D'_{21} is introduced. In this case Eq. 43 is reduced to

$$\frac{d^2\psi_1}{d\tau^2} + (\delta + \epsilon\sin\tau)\psi_1 = 0 \tag{50}$$

where

$$\delta = -\frac{1}{4}\left(\bar{\bar{A}}_{11} + \bar{\bar{A}}_{22}\right)^2$$
$$\left[\text{for critical value } \bar{\bar{A}}_{11}\bar{\bar{A}}_{22} - \bar{\bar{A}}_{12}\bar{\bar{A}}_{21}^* = 0\right] \tag{51}$$

and

$$\epsilon = \bar{\bar{A}}_{12}K_c^2D_{12}bw^{-2}. \tag{52}$$

Let

$$\psi_1 = \exp(\mu\tau) \sum_r a_r \exp(r\tau i), \tag{53}$$

where the sum runs from $-\alpha$ to α.

Substituting Eq. 53 into Eq. 48 and comparing the terms of $\exp(r\tau i)$, with r being fixed, we obtain

$$\{(\mu + ri)^2 + \delta\} a_r - \frac{i\epsilon}{2}(a_{r-1} - a_{r+1}) = 0. \tag{54}$$

Now, let

$$(\mu + ri)^2 + \delta = \delta - (r - i\mu)^2 \equiv \phi_r \tag{55}$$

assume $\phi_r \neq 0$, i.e., $\delta \neq (r - i\mu)^2$. Then Eq. 50 becomes,

$$a_r - \frac{i\epsilon}{2}\phi_r^{-1}(a_{r-1} - a_{r+1}) = 0, \quad -\alpha < r < \alpha. \tag{56}$$

Giving r the values $-\alpha, \ldots, -1, 0, 1, \ldots, +\alpha$ in succession, we obtain the following set of equations:

$$Ba = 0. \tag{57}$$

In Eq. 57. B is an infinite matrix, the rows of which consist of only three elements, i.e., $b_{r,-1} = -(i\epsilon/2)\phi_r^{-1}$ (diagonal element), and $b_{r,+1} = (i\epsilon/2)\phi_r^{-1}$ ($r = -\alpha, \ldots, -1, 0, 1, \ldots, +\alpha$), and a is an infinite column vector, the elements of which are a_r ($r = -\alpha, \ldots, -1, 0, 1, \ldots, +\alpha$). For Eq. 57 to be satisfied by a non-zero column vector a, we require that the following determinant of the matrix vanish,

$$\Delta(i\mu) = \begin{vmatrix} b_{r-1,-1} & \begin{bmatrix} 1 & b_{r-1,+1} & \\ b_{r,-1} & 1 & b_{r,+1} \\ & b_{r+1,-1} & 1 \end{bmatrix} & 0 \\ 0 & & b_{r+1,+1} \end{vmatrix} = 0. \tag{58}$$

This results in (see Okubo and Timm, 1992):

$$\sin^2\left(\frac{1}{2} i\mu\pi\right) = \Delta(0)\sin^2\left(\frac{1}{2}\pi\delta^{1/2}\right). \tag{59}$$

If ϵ is sufficiently small, we have:

$$\Delta(0) \cong 1 - \frac{\epsilon^2}{2}\{\delta(\delta - 1)\}^{-1}. \tag{60}$$

Eq. 60 results from Eq. 58 using $\phi_r = \delta - r^2$ (see the part of the determinant which is in square brackets).

$$\sin^2\left(\frac{1}{2} i\mu\pi\right) \cong \left[1 - \frac{\epsilon^2}{2}\{\delta(\delta - 1)\}^{-1}\right]\sin^2\left(\frac{1}{2}\pi\delta^{1/2}\right) \tag{61}$$

or

$$\sin\left(\frac{1}{2} i\mu\pi\right) \cong \left[1 - \frac{\epsilon^2}{2}\{\delta(\delta - 1)\}^{-1}\right]^{1/2}\sin\left(\frac{1}{2}\pi\delta^{1/2}\right) \tag{62}$$

Since $\delta < 0$, Eq. 62 becomes [using Eq. 45 for $Q(\tau)$]:

$$\sinh\left(\frac{1}{2}\mu\pi\right) \equiv \left\{1 - \frac{\epsilon^2}{2}(|\delta(\delta-1)|)^{-1}\right\}^{1/2} \sinh\left(\frac{1}{2}\pi|\delta|^{1/2}\right) \tag{63}$$

$$\therefore \mu < |\delta|^{1/2} = \left\{\frac{1}{4}\left(\bar{\bar{A}}_{11} + \bar{\bar{A}}_{22}\right)^2\right\}^{1/2} = \frac{1}{2}|\bar{\bar{A}}_{11} + \bar{\bar{A}}_{22}|. \tag{64}$$

Remembering the transformation between ψ_1 and ϕ_1 (see after Eq. 42):

$$\phi_1 = \exp\left\{-\frac{1}{2}|\bar{\bar{A}}_{11} + \bar{\bar{A}}_{22}|\tau\right\}\psi_1 \text{ (at } a = a_{cr}) \ \tau \to \alpha. \tag{65}$$

From Eq. 53 and Eq. 62 we have:

$$\phi_1 = \exp\left\{\left(\mu - \frac{1}{2}|\bar{\bar{A}}_{11} + \bar{\bar{A}}_{22}|\right)\tau\right\} \sum_r a_r \exp(r\tau i). \tag{66}$$

Since

$$\sum_r a_r \exp(r\tau i) \le \sum_r |a_r \exp(r\tau i)| \le \sum_r |a_r|. \tag{67}$$

the behaviour of ϕ_1 as $\tau \to \infty$ depends upon

$$\exp\left\{\left(\mu - \frac{1}{2}|\bar{\bar{A}}_{11} + \bar{\bar{A}}_{22}|\right)\tau\right\}$$

and from Eq. 64 we conclude that the solutions of the system are asymptotically stable (since $\phi_1 \to 0$) for $a = a_{cr}$ and small b. In other words, variable cross-diffusivity tends to make the system more stable in comparison to constant cross-diffusivity as long as the variability of cross-diffusivity remains small.

4. Discussion

In this paper we have considered a two-species Lotka–Volterra diffusive competitive system and studied the dynamical behaviour of the system in the following cases:

1. when diffusion parameters are independent of time;
2. when one of the cross-diffusion coefficient is time dependent.

It has been observed that in the case of severe competition the system is locally unstable without diffusion, so the system does not undergo pattern forming instability in the Turing sense. In the case of tolerant competition, the system is locally stable in the absence of diffusion and hence its spatial pattern can be achieved. But we have observed that in this case also the system is locally stable in the presence of self-diffusion. Hence we may conclude that self-diffusion is not sufficient for pattern forming instability in this particular system. But in the presence of positive cross-diffusion, i.e., where one species tends to diffuse in the direction of lower concentration of another species, it is possible that variation of the parameter will bring about or breakdown the uniform steady state and form the spatial pattern for a certain well-defined critical wave number.

Another investigated feature is the time-varying cross-diffusivity. We have shown that time variation in the second species tends to stabilize the competitive system. It has been also observed that in general stabilizing tendency increases with the amplitude of time-varying cross-diffusivity of the second species.

Throughout the entire analysis we have only considered a population domain (Eq. 6) defining the lower bound of the populations X_1 and X_2 and considered D_{12} and D_{21}, the two cross-diffusion coefficients, to be constant in this domain. It would be interesting to extend this study outside this domain where D_{12} and D_{21} are strictly density dependent.

References

Chattopadhyay, J., Tapaswi, P.K., Datta, D. and Chattopadhyay, D., 1994. Formation of a dissipative structure: a nonlinear analysis. Ecol. Model., 73: 205–214.

Gurtin, M.E., 1974. Some mathematical models for population dynamics that lead to segregation. Q.J. Appl. Math., 32: 1–8.

Levin, S.A. and Segel, L.A., 1976. Hypothesis for origin of planktonic patchiness. Nature, 259: 659.

McLaughlin, J.F. and Roughgarden, J., 1992. Predation across spatial scales in heterogeneous environments. Theor. Popul. Biol., 41: 277–299.

Murray, J.D., 1990. Discussion: Turing's theory of morphogensis – its influence on modelling biological pattern and form, Bull. Math. Biol., 52: 119–152.

Okubo, A., 1980. Diffusion and Ecological Problems: Mathematical Models. Biomathematics, Vol. 10, Springer, Berlin.

Okubo, A. and Timm, U., 1992. Diffusion-driven instability in a predator–prey system with time-varying diffusivities. J. Math. Biol., 30: 307–320.

Segel, L.A. and Jackson. J.L., 1972. Dissipative structure: an ecological example. J. Theor. Biol., 37: 545–559.

Turing, A.M., 1952. The chemical basis of morphogenesis. Trans. R. Soc. Lond., B237: 37–72.