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Journal of Differential Equations 305 (2021) 242–269

Journal of Differential Equations

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Spatial movement with diffusion and memory-based self-diffusion and cross-diffusion ☆

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Received 17 July 2021; revised 8 October 2021; accepted 11 October 2021

Abstract

Spatial memory has been considered significant in animal movement modeling. In this paper, we formulate a two-species interaction model by incorporating both random walk and spatial memory-based walk in their movement. The spatial memory-based walk, described by a chemotactic-like term, is derived by a modified Fick's law involving a directed movement toward the gradient of the density distribution function at a past time. For the proposed model, local stability and bifurcations are studied at constant steady states. Unlike a classical reaction-diffusion equation, we show that the accumulation points of eigenvalues for the model will locate at a vertical line in the complex plane, which will make the model generate spatially inhomogeneous time-periodic patterns through Hopf bifurcation. As illustrations, we apply these results to competition and cooperative models with memory-based diffusion. For the competition model, it turns out that the outcomes are far more complicated than those of classic Lotka-Volterra reaction-diffusion models, due to the consideration of memory-based diffusion. In particular, the existence of periodic oscillations is proved under weak competition. Similar conclusions hold for the cooperative model.

Keywords: Competition model; Memory-based diffusion; Bifurcation

☆ Supported by US NSF DMS-1853598, NSFC Nos. 11871176, 12171118, Heilongjiang NSF No. LH2019A010, NSERC Discovery Grant RGPIN-2020-03911 and NSERC Accelerator Grant RGPAS-2020-00090.

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https://doi.org/10.1016/j.jde.2021.10.021

1. Introduction

Aside from Brownian motion, animal movement is commonly affected by other factors, such as the resource distribution, the spatial memory of animals or living environment [10]. To incorporate the memory effect in movement models of high-developed animals, the following model was proposed in [30]:

$$\frac{\partial u}{\partial t} = \widetilde{D_1}\Delta u + \widetilde{D_2}\nabla \cdot (u\nabla F(u(x, t-\tau))) + G(u), \tag{1.1}$$

for studying the movement of a single population with spatial memory. Here, $\widetilde{D_1}$ is the Fickian diffusion rate, $\widetilde{D_2}$ is the memory-based diffusion coefficient, τ represents the averaged memory period, F is a function showing the dependence of memory-based diffusion on the gradient of concentration at τ time unit before present time, and G describes the biological birth or death. The model outcomes reveal that memory-based diffusion may have great impact on the spatial distribution of the population. This model is also investigated in [29,32,35,36] by further considering the factors of maturation delay, nonlocal effect in reaction term, distributed memory delay, or distributed delays in both diffusion and reaction.

In this paper, we incorporate the memory-based diffusion to classic diffusive models for describing the interaction of two species. The model is formulated along the same line as in [30], by assuming the movements of two species (u_1-population of species 1, u_2-population of species 2) are both governed by the modified Fickian flux in the form of

$$\mathbf{J}_i(x,t) = -D_i\nabla u_i(x,t) - d_i u_i(x,t) F_i(\nabla u_1(x, t-\tau_i), \nabla u_2(x, t-\tau_i)), \quad i = 1, 2. \tag{1.2}$$

Again, $D_i > 0$, $d_i \in \mathbb{R}$ represent random diffusion and memory-based diffusion rates, respectively. The function F_i depends on the population gradients for both species at past time $t - \tau_i$. Combining the chemical/biological processes of the species, the density functions $u_i(x, t)$ satisfy the following reaction-diffusion equations:

$$\begin{aligned}\frac{\partial u_i}{\partial t}(x,t) = {} & D_i\Delta u_i(x,t) + d_i\nabla \cdot [u_i(x,t)F_i(\nabla u_1(x,t-\tau_i), \nabla u_2(x,t-\tau_i))] \\ & + G_i(u_1(x,t), u_2(x,t)),\end{aligned} \tag{1.3}$$

where G_i describes the chemical reaction or biological birth/death of species i. For simplicity, in the following we assume that

$$F_i = \alpha_i\nabla u_1(x, t-\tau_i) + \beta_i\nabla u_2(x, t-\tau_i),$$

where α_i, β_i describe the weights of the memorized two species distributions on the movement decision of species i, and the movement is confined to a smooth bounded region Ω in $\mathbb{R}^K$. Further, we assume the competing species have the same memory period, i.e. $\tau_1 = \tau_2 = \tau$. Then, we arrive at the following autonomous initial-boundary value problem by using the new notations $u = u_1$, $v = u_2$, $f(u, v) = G_1(u, v)$, $g(u, v) = G_2(u, v)$:

$$\begin{cases} \dfrac{\partial u}{\partial t} = D_1 \Delta u + D_{11} \nabla \cdot (u \nabla u_\tau) + D_{12} \nabla \cdot (u \nabla v_\tau) + f(u, v), & x \in \Omega,\ t > 0, \\ \dfrac{\partial v}{\partial t} = D_2 \Delta v + D_{21} \nabla \cdot (v \nabla u_\tau) + D_{22} \nabla \cdot (v \nabla v_\tau) + g(u, v), & x \in \Omega,\ t > 0, \\ \dfrac{\partial u}{\partial n} = 0, \quad \dfrac{\partial v}{\partial n} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,t) = \phi_1(x,t), \quad v(x,t) = \phi_2(x,t), & x \in \Omega,\ -\tau \le t \le 0, \end{cases} \tag{1.4}$$

where $u_\tau = u(x, t - \tau)$, $v_\tau = v(x, t - \tau)$

$$D_{11} = d_1\alpha_1, \quad D_{12} = d_1\beta_1, \quad D_{21} = d_2\alpha_2, \quad D_{22} = d_2\beta_2.$$

The initial functions of (1.4), still denoted by $\phi_i(x, t)$, satisfy

$$\phi_i(x,t) \in C^{2+\delta,\delta/2}(\overline{\Omega} \times [-\tau, 0]), \ \frac{\partial \phi_i}{\partial n}(x,t) = 0, \ (x,t) \in \partial\Omega \times [-\tau, 0], \tag{1.5}$$

for some $\delta \in (0, 1)$. When $\tau = 0$, the model (1.4) is the same as the dispersive movement model in continuous environment proposed in [33], hence (1.4) can also be viewed as an extension of the model in [33] with memory-based self-diffusion (terms with coefficients D_{ii} for $i = 1, 2$) and memory-based cross-diffusion (terms with coefficients D_{ij} for $i, j = 1, 2$ and $i \neq j$).

For (1.4), we mainly focus the impact of memory-based self-diffusion and cross-diffusion on its dynamics, by carrying out the stability and bifurcation analysis. To this end, we analyze the associated characteristic equations of steady states in the first place, particularly on the positive one, whose eigenvalues will determine the asymptotic stability of steady states as in [30]. Due to the Neumann boundary condition, the characteristic equations of (1.4) consist of a sequence of transcendental equations, and therefore, many techniques in the literature, such as [5,40,19,34], could be applied to deal with such problems. Similar to results for the single population model in [30], we prove that most eigenvalues of the characteristic equations for the positive steady state are also determined by a transcendental equation corresponding to a difference equation with continuous time. Another observation of the distribution of roots for characteristic equation is that: the eigenvalues derived from the n-th characteristic equation may locate at the right hand side of the ones for $(n-1)$-th equation, under a certain choice of parameters. Due to this fact, we show that the memory-based self-diffusion and cross-diffusion will indeed generate spatially inhomogeneous time-periodic patterns for the model through Hopf bifurcations. This phenomenon rarely occurs for classical reaction-diffusion equations.

As illustrations, we apply the above conclusions to diffusive competition and cooperative models with memory-based self-diffusion and cross-diffusion. Recall that, for the classic competitive and cooperative models, with the aid of the theory of monotone dynamical systems, one can easily show the global stability of the positive steady state in the weak competition (cooperation) regime. When memory-based diffusion is considered, we find that, the stability of semi-trivial equilibria depends on the choice of competition parameters α and β, as well as memory-based self-diffusion rates D_{11} and D_{22}; while the memory-based cross-diffusion rates D_{12} and D_{21} do not affect their stabilities. At the positive steady state, we show that either Turing or Hopf bifurcation will take place, provided that only one of the four memory-based diffusion rates is not equal to 0 (could be D_{12} or D_{21}), that is, only one species moves toward the gradient of density of the other species. This implies that the factors (diffusion rate or average memory period) of memory-based diffusion will drive these models to generate spatially inhomogeneous pattern, or spatially inhomogeneous time-periodic pattern. In addition, for the Hopf bifurcation analysis, we employ the algorithm for computing first Lyapunov coefficient for neutral equations in [37] to derive the explicit formula of first Lyapunov coefficients for the competition and cooperative models with memory-based diffusion. This makes Hopf bifurcation analysis more complete than our previous work on one-dimensional population model in [29], where the computation of first Lyapunov coefficient is not accomplished.

Mathematical models on competition between two species have long been studied, such as the classic Lotka-Volterra competition model (LV model) [4,16], the LV model with spatial heterogeneity [7,11–13,17,18,21], the LV model in the advective environment [1,25,41,42], the LV model with cross-diffusion and self-diffusion effect [23,24,26,33] and the LV model with nonlocal effect [27,31]. Among all these references, it appears that time-periodic pattern rarely occurs for competition models. Here we show that for the LV competition model with a memory-based cross-diffusion, increasing the average memory period τ will destabilize the constant coexistence state and generate spatially inhomogeneous time-periodic solutions via Hopf bifurcations. This means, if the species u is an aggressive competitor who tracks it opponent v by moving upward its past gradient, then the outcome of competition between two species can be a coexistence with time-periodic oscillations.

It is remarked that the memory-based cross-diffusion term, such as $D_{12}\nabla \cdot (u\nabla v_\tau)$, can be viewed as the chemotactic movement driven by the past gradient of v. For the classic chemotactic models (i.e., $\tau = 0$), there are a tremendous amount of studies, see survey articles [2,14,15] and references therein. Most of these works focused on the global existence or blow-up of solutions, and the global stability of the constant steady state, even though various spatial-temporal patterns were also observed. However, the time-periodic patterns were less investigated with few exceptions, such as [20] where the occurrence of Hopf bifurcations was proved for a Keller-Segel model with both attraction and repulsion effect of chemical, and [32], where Hopf bifurcation can induce time-periodic patterns in a memory-based diffusion model with spatial-temporal memory effect. Numerical simulations also show time-periodic patterns existing in basic Keller-Segel chemotactic models [8,28]. Our study here indicates that the time-periodic patterns are very likely to take place in models with memory-based cross-diffusion, which suggests this may also be the case if the time delay is taken into account for chemotaxis models.

This paper is organized as follows. In Section 2, the global existence of solution for (1.4) is proved, and the characteristic equation associated with steady states is analyzed, which turns to be closely related to a transcendental equation associated with a difference equation. In Sections 3 and 4, we apply the results in Section 2 to diffusive competition and cooperative models with memory-based cross-diffusion and self-diffusion, respectively. The main conclusions are summarized in Section 5, and in the Appendix, we compute the normal forms of the Hopf bifurcations for (1.4). Throughout the paper, $\mathbb{N}$ is the set of all positive integers, $\mathbb{N}_0 = \mathbb{N} \cup \{0\}$ is the set of all non-negative integers, and $\mathbb{Z}$ is the set of all integers.

2. Stability and bifurcation

In this section, we first prove the well-posedness of (1.4), and then study its local dynamics near steady states. Throughout this paper, we assume

(H0) $f(u, v) = uf_1(u, v)$ and $g(u, v) = vg_1(u, v)$ for some $f_1, g_1 \in C^1(\mathbb{R}^+)$, and there exist $M > 0$ such that $f_1(u, v) \le M$ and $g_1(u, v) \le M$ for all $u, v \in \mathbb{R}^+ := [0, \infty)$.

Theorem 2.1. *Suppose* **(H0)** *holds. Then* (1.4) *has a unique positive classical solution that exists for* $t \in (0, \infty)$ *if the initial values satisfy* (1.5).

Proof. For $0 < t < \tau$, rewrite the equations in (1.4) as

$$\begin{aligned}\frac{\partial u}{\partial t} &= D_1 \Delta u + (D_{11}\nabla u_\tau + D_{12}\nabla v_\tau)\cdot\nabla u + (D_{11}\Delta u_\tau + D_{12}\Delta v_\tau)u + f(u,v),\\ \frac{\partial v}{\partial t} &= D_2 \Delta v + (D_{21}\nabla u_\tau + D_{22}\nabla v_\tau)\cdot\nabla v + (D_{21}\Delta u_\tau + D_{22}\Delta v_\tau)v + g(u,v).\end{aligned} \tag{2.1}$$

By letting $\bar{f} = (D_{11}\Delta u_\tau + D_{12}\Delta v_\tau)u + f(u,v)$ and $\bar{g} = (D_{21}\Delta u_\tau + D_{22}\Delta v_\tau)v + g(u,v)$ and noting (1.5) and **(H0)**, we can apply Theorem 4.2 in [39] to conclude that (2.1) possesses a unique classical solution for $t \in (0, T)$ with $T > 0$. Moreover since $f(u,v) \le Mu$ and $g(u,v) \le Mv$ for all $u, v \ge 0$ in **(H0)**, the solution can be extended to $t \in [0, \tau]$ and $u, v \in C^{2+\delta, 1+\delta/2}(\overline{\Omega} \times [0, \tau])$. From $f(u,v) = uf_1(u,v)$ and the comparison principle for parabolic equations, we have $u \ge 0$ for $t \in [0, \tau]$ from the first equation of (2.1), and $u > 0$ for $t \in [0, \tau]$ from the strong maximum principle. Similarly we have $v > 0$ for $t \in [0, \tau]$. Repeating the above proof for $t \in [\tau, 2\tau]$ and further for any $[k\tau, (k+1)\tau]$ with $k \ge 2$, we obtain the global existence of a unique classic solution for (1.4) if the initial values satisfy (1.5), and the solution (u, v) is positive for $t > 0$. $\square$

Now, assume that (1.4) admits a constant steady state $(\bar{u}, \bar{v})$ which is locally asymptotically stable with respect to the kinetic system $u_t = f(u,v)$, $v_t = g(u,v)$. That is,

(H1) $f(\bar{u}, \bar{v}) = g(\bar{u}, \bar{v}) = 0$, $f_u + g_v < 0$ and $f_u g_v - f_v g_u > 0$ at $(\bar{u}, \bar{v})$, where

$$f_u = \frac{\partial f}{\partial u}(\bar{u}, \bar{v}), \quad f_v = \frac{\partial f}{\partial v}(\bar{u}, \bar{v}), \quad g_u = \frac{\partial g}{\partial u}(\bar{u}, \bar{v}), \quad g_v = \frac{\partial g}{\partial v}(\bar{u}, \bar{v}).$$

We consider the stability of $(\bar{u}, \bar{v})$ with respect to the reaction-diffusion system with memory-induced movement (1.4). The linearization of (1.4) at $(\bar{u}, \bar{v})$ is given by

$$\begin{cases} \dfrac{\partial \varphi}{\partial t} = D_1 \Delta\varphi + D_{11}\bar{u}\Delta\varphi_\tau + D_{12}\bar{u}\Delta\psi_\tau + f_u\varphi + f_v\psi, & x \in \Omega,\ t > 0,\\ \dfrac{\partial \psi}{\partial t} = D_2 \Delta\psi + D_{21}\bar{v}\Delta\varphi_\tau + D_{22}\bar{v}\Delta\psi_\tau + g_u\varphi + g_v\psi, & x \in \Omega,\ t > 0,\\ \dfrac{\partial \varphi}{\partial n} = 0, \quad \dfrac{\partial \psi}{\partial n} = 0, & x \in \partial\Omega,\ t > 0. \end{cases} \tag{2.2}$$

Let $0 = \mu_0 < \mu_1 \le \mu_2 \le \cdots \le \mu_n \le \cdots \to \infty$ be the sequence of eigenvalues of the linear eigenvalue problem

$$\begin{cases} \Delta\phi + \mu\phi = 0, & x \in \Omega,\\ \dfrac{\partial \phi}{\partial n} = 0, & x \in \partial\Omega. \end{cases} \tag{2.3}$$

Denote

$$B_1 = \begin{pmatrix} D_1 & 0 \\ 0 & D_2 \end{pmatrix}, \quad B_2(\bar{u}, \bar{v}) = \begin{pmatrix} D_{11}\bar{u} & D_{12}\bar{u} \\ D_{21}\bar{v} & D_{22}\bar{v} \end{pmatrix}, \quad B_3(\bar{u}, \bar{v}) = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix}$$

and

$$\Pi_n(\lambda) = \lambda I + \mu_n B_1 + \mu_n e^{-\lambda\tau} B_2(\bar{u}, \bar{v}) - B_3(\bar{u}, \bar{v}).$$

The characteristic equations of (2.2) are the following sequence of transcendental equations

$$\det(\Pi_n(\lambda)) = 0, \quad n \in \mathbb{N}_0,$$

or equivalently,

$$E(n, \tau, \lambda) := \lambda^2 + a_n\lambda + b_n + (c_n\lambda + d_n)e^{-\lambda\tau} + h_n e^{-2\lambda\tau} = 0, \quad n \in \mathbb{N}_0, \tag{2.4}$$

where the coefficients, depending on n, are given by

$$\begin{aligned} &a_n = (D_1 + D_2)\mu_n - f_u - g_v, \;\; b_n = b\mu_n^2 - (D_1 g_v + D_2 f_u)\mu_n + f_u g_v - f_v g_u, \\ &d_n = d\mu_n^2 + (D_{21} f_v \bar{v} + D_{12} g_u \bar{u} - D_{11} g_v \bar{u} - D_{22} f_u \bar{v})\mu_n, \;\; c_n = c\mu_n, \quad h_n = h\mu_n^2, \end{aligned} \tag{2.5}$$

with

$$b = D_1 D_2, \;\; c = D_{11}\bar{u} + D_{22}\bar{v}, \;\; d = D_2 D_{11}\bar{u} + D_1 D_{22}\bar{v}, \;\; h = (D_{11}D_{22} - D_{12}D_{21})\bar{u}\bar{v}. \tag{2.6}$$

The spectral set of (2.2) is

$$\sigma_n(\tau) = \{\lambda \in \mathbb{C} : E(n, \tau, \lambda) = 0\}, \quad \sigma(\tau) = \bigcup_{n=0}^{\infty} \sigma_n(\tau), \qquad n \in \mathbb{N}_0. \tag{2.7}$$

The constant steady state $(\bar{u}, \bar{v})$ is linearly stable if $\sigma(\tau) \subseteq \mathbb{C}^- := \{\alpha + i\beta : \alpha < 0\}$, and it is unstable if there exists $n \in \mathbb{N}_0$ such that $\sigma_n(\tau) \cap \mathbb{C}^+ \neq \emptyset$.

From the assumption **(H1)**, the only two elements in $\sigma_0(\tau)$ have strictly negative real parts. But unlike the classic diffusive model (i.e. without memory-induced diffusion), the real parts of elements in $\sigma_n(\tau)$ will not always be negative for $n \geq 1$ large enough. This suggests that the memory-based diffusion might induce new dynamics of (1.4), even if the dynamics of the system without memory-based diffusion are relatively simple (such as the classic Lotka-Volterra competition model). To verify this, we first study the distribution of the roots of $E(n, \tau, \lambda) = 0$ for large n, which is closely related to the roots of a limiting equation

$$E_\infty(\tau, \lambda) := be^{\lambda\tau} + d + he^{-\lambda\tau} = 0. \tag{2.8}$$

In the following we discuss the roots of (2.8) in terms of $d, h \in \mathbb{R}$ and $b, \tau > 0$. Define

$$\sigma_\infty(\tau) = \{\lambda \in \mathbb{C} : E_\infty(\tau, \lambda) = 0\}.$$

Related results on that regard have also been considered in [5,19,34,40].

Proposition 2.2. *Assume that $d \geq 0$.*

(1) *When $h > 0$, if $d \le 2\sqrt{hb}$, then*

$$\sigma_\infty(\tau) = \left\{\rho^* \pm i\nu^* + i\frac{2k\pi}{\tau} \in \mathbb{C} : k \in \mathbb{Z}\right\}, \tag{2.9}$$

where

$$\rho^* := \frac{\ln(|h|/b)}{2\tau}, \quad \nu^* = \frac{\arccos(-d/(2\sqrt{hb}))}{\tau} \tag{2.10}$$

if $d > 2\sqrt{hb}$, then

$$\sigma_\infty(\tau) = \left\{\rho_1 + i\frac{(2k+1)\pi}{\tau} \in \mathbb{C} : k \in \mathbb{Z}\right\} \cup \left\{\rho_2 + i\frac{(2k+1)\pi}{\tau} \in \mathbb{C} : k \in \mathbb{Z}\right\}, \tag{2.11}$$

where $\rho_2 < \rho^* < \rho_1$ satisfying $be^{\rho_i\tau} + he^{-\rho_i\tau} = d$ for $i = 1, 2$.

(2) *When $h < 0$, then*

$$\sigma_\infty(\tau) = \left\{\rho_3 + i\frac{2k\pi}{\tau} \in \mathbb{C} : k \in \mathbb{Z}\right\} \cup \left\{\rho_4 + i\frac{(2k+1)\pi}{\tau} \in \mathbb{C} : k \in \mathbb{Z}\right\}, \tag{2.12}$$

where $\rho_3 < \rho^* < \rho_4$. Moreover, if $b + d + h > 0$ ($b + d + h < 0$), then $\rho_3 < 0$ ($\rho_3 > 0$); if $b - d + h > 0$ ($b - d + h < 0$), then $\rho_4 < 0$ ($\rho_4 > 0$).

Proof. Suppose that $\rho \pm i\nu$ are the roots of (2.8), then

$$\begin{aligned}(be^{\rho\tau} + he^{-\rho\tau})\cos\nu\tau + d = 0,\\ (be^{\rho\tau} - he^{-\rho\tau})\sin\nu\tau = 0.\end{aligned} \tag{2.13}$$

(1) Suppose that $h > 0$. Case I: $d < 2\sqrt{hb}$. If $\sin\nu\tau \ne 0$, it then follows from the second equation of (2.13) that $\rho = \rho^*$. Therefore, $\cos\nu\tau = \frac{-d}{2\sqrt{hb}} \in (-1, 0]$, which has infinitely many solutions of ν. If $\sin\nu\tau = 0$, then $\cos\nu\tau = 1$ or $\cos\nu\tau = -1$. When $\cos\nu\tau = 1$, the first equation of (2.13) turns into

$$be^{\rho\tau} + he^{-\rho\tau} + d = 0, \tag{2.14}$$

which has no solution for ρ since $b > 0$, $d \ge 0$ and $h > 0$. When $\cos\nu\tau = -1$, we have

$$-be^{\rho\tau} - he^{-\rho\tau} + d = 0. \tag{2.15}$$

But for any $\rho \in \mathbb{R}$, $be^{\rho\tau} + he^{-\rho\tau} \ge 2\sqrt{bh} > d$, therefore (2.15) has no solution for ρ. Accordingly, the roots of (2.8) are given by $\rho^* + i\nu$ with $\cos\nu\tau = \frac{-d}{2\sqrt{hb}}$. Case II: $d = 2\sqrt{hb}$. Along the same lines as above, we can conclude that $\rho^* + i\frac{(2k+1)\pi}{\tau}$, $k \in \mathbb{Z}$ are precisely all the roots for (2.8). Case III: $d > 2\sqrt{hb}$. In this case, if $\sin\nu\tau \ne 0$, then $\rho = \rho^*$ again and $\cos\nu\tau = \frac{-d}{2\sqrt{hb}}$ has no solution for ν. If $\sin\nu\tau = 0$ and $\cos\nu\tau = -1$, it then follows from $d > 2\sqrt{hb}$, (2.15) always has two real roots ρ_1, ρ_2 such that $\rho_2 < \rho^* < \rho_1$, which correspond to two sequences of complex roots $\rho_1 + i\frac{(2k+1)\pi}{\tau}$ and $\rho_2 + i\frac{(2k+1)\pi}{\tau}$, $k \in \mathbb{Z}$.

(2) Suppose that $h < 0$. When $\sin \nu\tau \neq 0$, from the second equation of (2.13), we have $be^{\rho\tau} = he^{-\rho\tau}$, which has no solution for ρ. When $\sin \nu\tau = 0$, we have $\cos \nu\tau = 1$ or $\cos \nu\tau = -1$. Denote $F(\rho) = be^{\rho\tau} + he^{-\rho\tau} + d$. Then $F(-\infty) = -\infty$, $F(+\infty) = +\infty$ and $F'(\rho) > 0$. If $\cos \nu\tau = 1$, it then follows that (2.14) always has a unique root for ρ, denoted by ρ_3. Furthermore, $\rho_3 < 0$ for $b + d + h > 0$, and $\rho_3 > 0$ for $b + d + h < 0$. From $F(\rho^*) = d > 0$, we know that $\rho_3 < \rho^*$. Similarly, if $\cos \nu\tau = -1$, (2.15) has a unique negative (or positive) root $\rho_4 > \rho^*$ for $b - d + h > 0$ (or $b - d + h < 0$). □

Corollary 2.3. *Assume that $d \geq 0$. Then,*

(1) *When $h > b$, (2.8) has infinitely many complex roots with positive real parts;*
(2) *When $0 < h < b$, if $b - d + h < 0$, then all the roots of (2.8) are in form (2.11) with $\rho_2 < \rho^* < 0 < \rho_1$; if $b - d + h > 0$, then all the roots of (2.8) have strictly negative real parts.*

Proof. (1) If $h > b$, then $\rho^* > 0$. It then follows from (1) of Proposition 2.2 that (2.8) always has a sequence of complex roots with positive real parts, no matter whether $d \leq 2\sqrt{hb}$ or $d > 2\sqrt{hb}$.

(2) If $h > 0$ and $b - d + h < 0$, then $d > b + h \geq 2\sqrt{bh}$. By (1) of Proposition 2.2 again, we know (2.8) has two sequence of complex roots $\rho_1 + i\frac{(2k+1)\pi}{\tau}$ and $\rho_2 + i\frac{(2k+1)\pi}{\tau}$, $k \in \mathbb{Z}$, with $\rho_2 < \rho^* < \rho_1$. Since $h < b$, we have $\rho_2 < \rho^* < 0$. Note that $b - d + h < 0$ if and only if $F(0) < 2d$. This implies $\rho_1 > 0$ as long as $b - d + h < 0$. On the other hand, if $b - d + h > 0$, then the real parts of the roots for (2.8) are either ρ^* or ρ_1, ρ_2 such that $\rho_2 < \rho^* < \rho_1$, depending on the value of d. Furthermore $\rho_1 < 0$ as $b + h > d$. □

By similar arguments as in Proposition 2.2 and Corollary 2.3, we have results on the roots of (2.8) when $d < 0$ as well.

Corollary 2.4. *Assume that $d < 0$. Then,*

(1) *When $h > b$, then (2.8) has infinitely many complex roots with positive real parts;*
(2) *When $0 < h < b$, if $b + d + h < 0$, then*

$$\sigma_\infty(\tau) = \left\{\rho_5 + i\frac{2k\pi}{\tau} \in \mathbb{C} : k \in \mathbb{Z}\right\} \cup \left\{\rho_6 + i\frac{2k\pi}{\tau} \in \mathbb{C} : k \in \mathbb{Z}\right\}, \tag{2.16}$$

with $\rho_6 < \rho^* < 0 < \rho_5$; if $b + d + h > 0$, then all the roots of (2.8) have strictly negative real parts.
(3) *When $h < 0$, then all the roots of (2.8) are in form (2.12). Moreover, if $b + d + h > 0$ ($b + d + h < 0$), then $\rho_3 < 0$ ($\rho_3 > 0$); if $b - d + h > 0$ ($b - d + h < 0$), then $\rho_4 < 0$ ($\rho_4 > 0$).*

From Corollaries 2.3 and 2.4, we have a complete classification of the set $\sigma_\infty(\tau)$ for fixed $\tau > 0$ with $d, h \in \mathbb{R}$ and $b > 0$, which completely determine the stability with to the limiting equation (2.8).

Proposition 2.5. *Assume that $\tau > 0$, and $d, h \in \mathbb{R}$, $b > 0$ satisfy*

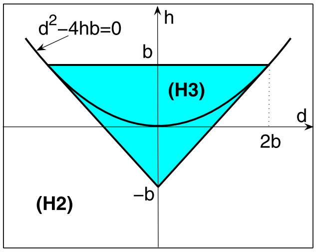

Fig. 1. The regions of (h, d), satisfying **(H2)** and **(H3)**, for fixed $b > 0$.

(H2) *$h > b$, or $h < b$ and $b + h - |d| < 0$,*

then (2.8) has infinitely many complex roots with positive real parts; on the other hand, when $d, h \in \mathbb{R}$, $b > 0$ satisfy

(H3) *$h < b$ and $b + h - |d| > 0$,*

then all the roots of (2.8) have strictly negative real parts.

The regions of (h, d) defined by **(H2)** and **(H3)** are shown in Fig. 1. Next we use the information of the limiting spectral set $\sigma_\infty(\tau)$ to determine the stability of $(\bar{u}, \bar{v})$ with respect to (2.4). From (2.9), (2.11), (2.12) and (2.16), the set $\sigma_\infty(\tau)$ must lie on one or two vertical lines in the complex plane. In order to study the relations of $\sigma_\infty(\tau)$ and $\sigma_n(\tau)$ for large n, we prove the following perturbation result based on the implicit function theorem.

Lemma 2.6. *Consider a function $\mathcal{F} : (-\delta, \delta) \times \mathbb{C} \to \mathbb{C}$ defined by*

$$\mathcal{F}(\epsilon, \lambda) = \epsilon^2\lambda^2 + (f_1\epsilon + f_2\epsilon^2)\lambda + b + (f_3\epsilon + f_4\epsilon^2) + (f_5\epsilon + f_6\epsilon\lambda + d)e^{-\lambda\tau} + he^{-2\lambda\tau}, \quad (2.17)$$

where $\delta, \tau > 0$, $b, d, h \in \mathbb{R}$ satisfying $d^2 - 4hb \neq 0$, and $f_i \in \mathbb{R}$ for $i = 1, 2, \cdots, 6$. Suppose that $\lambda_0 \in \mathbb{C}$ satisfies $\mathcal{F}(0, \lambda_0) = 0$. Then, there exists $\delta_1 \in (0, \delta)$ and an analytic function $\lambda : (-\delta_1, \delta_1) \to \mathbb{C}$ such that $\mathcal{F}(\epsilon, \lambda(\epsilon)) = 0$ and $\lambda(0) = \lambda_0$, and

$$\lambda(\epsilon) = \lambda_0 + \epsilon\frac{(\lambda_0 f_1 + f_3) + (\lambda_0 f_6 + f_5)e^{-\lambda_0\tau}}{\tau e^{-\lambda_0\tau}(d + 2he^{-\lambda_0\tau})} + o(\epsilon)$$

is the unique solution of $\mathcal{F}(\epsilon, \lambda) = 0$ near $\lambda = \lambda_0$.

Proof. Suppose that λ_0 is a root of $\mathcal{F}(0, \lambda_0) = 0$. Then $b + de^{-\lambda_0\tau} + he^{-2\lambda_0\tau} = 0$, and

$$\frac{\partial\mathcal{F}}{\partial\lambda}(0, \lambda_0) = -d\tau e^{-\lambda_0\tau} - 2h\tau e^{-2\lambda_0\tau} = \tau(2b + de^{-\lambda_0\tau}).$$

Assume that $2b + de^{-\lambda_0\tau} = 0$. Then $x = e^{-\lambda_0\tau}$ satisfies both $b + dx + hx^2 = 0$ and $2b + dx = 0$, which only occurs when $d^2 - 4hb = 0$. Hence when $d^2 - 4hb \neq 0$, we have $2b + de^{-\lambda_0\tau} \neq 0$ and $\frac{\partial\mathcal{F}}{\partial\lambda}(0, \lambda_0) \neq 0$. Then the conclusion is a direct consequence of the implicit function theorem. $\square$

We have the following relation between a root of $E_\infty(\tau,\lambda)=0$ and roots of $E(n,\tau,\lambda_n)=0$ with large n.

Corollary 2.7. *Suppose that $\tau>0$, $b,d,h\in\mathbb{R}$ satisfying $d^2-4hb\neq 0$, and λ_0 is a root of (2.8), i.e., $E_\infty(\tau,\lambda_0)=0$. Then there exist $N\in\mathbb{N}$ and $\{\lambda_n\}_{n\geq N}\subset\mathbb{C}$ such that*

$$E(n,\tau,\lambda_n)=0,\qquad \lim_{n\to\infty}\lambda_n=\lambda_0.$$

Proof. Define $\bar{E}(n,\tau,\lambda)=E(n,\tau,\lambda)/\mu_n^2$. Then, $\bar{E}(n,\tau,\lambda)=0$ if and only if $\mathcal{F}(\mu_n^{-1},\lambda)=0$, where $\mathcal{F}$ is defined in (2.17) with

$$\begin{aligned}
&f_1=D_1+D_2,\quad f_2=-f_u-g_v,\quad f_3=-D_1g_v-D_2f_u,\quad f_4=f_ug_v-f_vg_u,\\
&f_5=D_{21}f_v\bar{v}+D_{12}g_u\bar{u}-D_{11}g_v\bar{u}-D_{22}f_u\bar{v},\quad f_6=c.
\end{aligned}$$

Since $\mathcal{F}(0,\lambda)=E_\infty(\tau,\lambda)$, the result follows from Lemma 2.6 as $\lim_{n\to\infty}\mu_n^{-1}=0$. □

From Corollary 2.7, the elements with positive real parts in $\sigma_n(\tau)$ for large n on the complex plane are completely determined by the roots for (2.8). Combining Proposition 2.5 and Corollary 2.7, we have the following instability result for $(\bar{u},\bar{v})$ with respect to (1.4).

Theorem 2.8. *Assume that* **(H1)** *and* **(H2)** *are satisfied, and in addition $d^2-4hb\neq 0$, then the constant steady state $(\bar{u},\bar{v})$ is unstable with respect to (1.4) for any $\tau>0$.*

Proof. It follows from Proposition 2.5 that when **(H1)** and **(H2)** are satisfied, (2.8) has a complex root λ_0 with strictly positive real parts. Thus, by Corollary 2.7, we can conclude that $\sigma(\tau)$ possesses an infinite number of complex elements with strictly positive real parts, which implies the instability of $(\bar{u},\bar{v})$. □

We remark that the instability result in Theorem 2.8 requires a non-degeneracy condition $d^2-4hb\neq 0$ which holds generically. Fig. 1 shows the curve $d^2-4hb=0$ on the (h,d)-plane.

On the other hand, when **(H3)** holds, Proposition 2.5 implies that all roots of the limiting equation (2.8) have negative real parts, and hence from Corollary 2.7 all the elements in $\sigma_n(\tau)$ have strictly negative real parts for $n>N$. So $(\bar{u},\bar{v})$ could be stable in the parameter region defined by **(H3)**. In what follows, we examine how the stability of $(\bar{u},\bar{v})$ changes as the memory delay τ varies under the condition **(H3)**, especially when (2.4) have roots with purely imaginary part. Suppose that $\pm i\omega$, $\omega>0$, are a pair of purely imaginary roots of (2.4) for some $n\in\{1,2,\cdots,N\}$. Then

$$\begin{aligned}
b_n-\omega^2+d_n\cos\omega\tau+c_n\omega\sin\omega\tau+h_n\cos 2\omega\tau&=0,\\
a_n\omega-d_n\sin\omega\tau+c_n\omega\cos\omega\tau-h_n\sin 2\omega\tau&=0,
\end{aligned}\tag{2.18}$$

which implies

$$\begin{aligned}
(b_n-\omega^2+h_n)\cos\omega\tau-a_n\omega\sin\omega\tau+d_n&=0,\\
a_n\omega\cos\omega\tau+(b_n-\omega^2-h_n)\sin\omega\tau+c_n\omega&=0.
\end{aligned}$$

Therefore,

$$\begin{aligned} \cos\omega\tau &= -\frac{d_n(b_n-\omega^2-h_n)+a_nc_n\omega^2}{(b_n-\omega^2)^2-h_n^2+a_n^2\omega^2}, \\ \sin\omega\tau &= -\frac{c_n\omega(b_n-\omega^2+h_n)-a_nd_n\omega}{(b_n-\omega^2)^2-h_n^2+a_n^2\omega^2}. \end{aligned} \tag{2.19}$$

From (2.19), we know that ω satisfies the following equation

$$\begin{aligned} F_n(\omega) &:= [(b_n-\omega^2)^2-h_n^2+a_n^2\omega^2]^2-[d_n(b_n-\omega^2-h_n)+a_nc_n\omega^2]^2 \\ &\quad -[c_n\omega(b_n-\omega^2+h_n)-a_nd_n\omega]^2 \\ &= \omega^8+p_n\omega^6+q_n\omega^4+r_n\omega^2+s_n=0, \end{aligned} \tag{2.20}$$

where

$$\begin{aligned} p_n &= 2a_n^2-4b_n-c_n^2, \\ q_n &= 6b_n^2-2h_n^2-4a_n^2b_n-d_n^2+a_n^4-a_n^2c_n^2+2b_nc_n^2+2c_n^2h_n, \\ r_n &= 2b_nd_n^2-a_n^2d_n^2-4b_n^3+2a_n^2b_n^2-b_n^2c_n^2-2b_nc_n^2h_n \\ &\quad +4a_nc_nd_nh_n-2d_n^2h_n+4b_nh_n^2-2a_n^2h_n^2-c_n^2h_n^2, \\ s_n &= (b_n-h_n)^2[(b_n+h_n)^2-d_n^2], \end{aligned} \tag{2.21}$$

or equivalently, $z=\omega^2$ is a positive root of

$$G_n(z)=z^4+p_nz^3+q_nz^2+r_nz+s_n=0. \tag{2.22}$$

We remark that (2.20) derived here is the same as the one in [5], except that the coefficients now depend on n. We present it in a different way in order to deduce another transversality condition, which seems to be easier to check in geometric way, given by Theorem 2.9 below. If (2.20) has a positive root, say ω_n, for some n, then there exists a sequence of τ_n^j, $j=0,1,\cdots$, given by

$$\tau_n^j=\frac{1}{\omega_n}\left[\arctan\left(\frac{c_n\omega_n(b_n-\omega_n^2+h_n)-a_nd_n\omega_n}{d_n(b_n-\omega_n^2-h_n)+a_nc_n\omega_n^2}\right)+j\pi\right], \tag{2.23}$$

such that (2.4) has a purely imaginary root when $\tau=\tau_n^j$.

Proposition 2.9. *Let $\lambda(\tau)=\alpha(\tau)+i\omega(\tau)$ be a root of (2.4) for $\tau\in(\tau_n^j-\varepsilon,\tau_n^j+\varepsilon)$ and $\varepsilon>0$, such that $\alpha(\tau_n^j)=0$ and $\omega(\tau_n^j)=\omega_n$. Then,*

$$Sign\alpha'(\tau_n^j)=Sign[G_n'(z)/H_n(z)]|_{z=\omega_n^2} \tag{2.24}$$

where $G_n(z)$ is defined in (2.22) and

$$H_n(z)=z^2+(a_n^2-2b_n)z+b_n^2-h_n^2. \tag{2.25}$$

Proof. By the Implicit Function Theorem, we have

$$\begin{aligned}\frac{d\tau}{d\lambda} &= -\frac{2\lambda + a_n + c_n e^{-\lambda\tau} - \tau(c_n\lambda + d_n)e^{-\lambda\tau} - 2\tau h_n e^{-2\lambda\tau}}{-\lambda(c_n\lambda + d_n)e^{-\lambda\tau} - 2\lambda h_n e^{-2\lambda\tau}} \\ &= \frac{(2\lambda + a_n)e^{\lambda\tau} + c_n}{\lambda(c_n\lambda + d_n) + 2\lambda h_n e^{-\lambda\tau}} - \frac{\tau}{\lambda}.\end{aligned}$$

From (2.18) and (2.19), we get

$$\begin{aligned}\mathrm{Sign}\alpha'(\tau_n^j) &= \mathrm{Sign}\left(\mathrm{Re}\frac{d\tau}{d\lambda}\right)|_{\lambda=i\omega_n,\tau=\tau_n^j} \\ &= \mathrm{Sign}[(a_n\cos\omega\tau - 2\omega\sin\omega\tau + c_n)(2\omega h_n\sin\omega\tau - c_n\omega^2) \\ &\quad + (a_n\sin\omega\tau + 2\omega\cos\omega\tau)(\omega d_n + 2\omega h_n\cos\omega\tau)]|_{\omega=\omega_n,\tau=\tau_n^j} \\ &= \mathrm{Sign}[2a_nh_n\omega\sin 2\omega\tau + 4h_n\omega^2\cos 2\omega\tau + \omega^2(2d_n - a_nc_n)\cos\omega\tau \\ &\quad - c_n^2\omega^2 + \omega(2c_n\omega^2 + 2h_nc_n + a_nd_n)\sin\omega\tau]|_{\omega=\omega_n,\tau=\tau_n^j} \\ &= \mathrm{Sign}[(2a_n^2 - 4b_n + 4\omega^2 - c_n^2)\omega^2 + \omega^2(a_nc_n - 2d_n)\cos\omega\tau \\ &\quad - \omega(2c_n\omega^2 - 2h_nc_n + a_nd_n)\sin\omega\tau]|_{\omega=\omega_n,\tau=\tau_n^j} \\ &= \mathrm{Sign}\frac{\omega^2(4\omega^6 + 3p_n\omega^4 + 2q_n\omega^2 + r_n)}{\omega^4 + (a_n^2 - 2b_n)\omega^2 + b_n^2 - h_n^2}|_{\omega=\omega_n} \\ &= \mathrm{Sign}[G_n'(z)/H_n(z)]|_{z=\omega_n^2},\end{aligned}$$

where $H_n(z)$ is given by (2.25). □

From Proposition 2.9, we arrive at the following result on Hopf bifurcations for (1.4) when the time delay τ in the memory-based diffusion changes.

Theorem 2.10. *Assume that* **(H1)** *and* **(H3)** *hold. If there exists* $1 \le n \le N$ *such that* (2.20) *admits a positive root* $\omega_n > 0$, $\alpha'(\tau_n^j) \ne 0$ *and* $c_1(0) \ne 0$, *then* (1.4) *undergoes a Hopf bifurcation at* τ_n^j, $j = 0, 1, \cdots$, *which generates a spatially inhomogeneous periodic solution near the bifurcation point.*

We remark that the procedure for computing the first Lyapunov coefficient $c_1(0)$ can follow from the one for partial neutral functional differential equations [37]. However, it is rather complicated when all of the memory-based diffusions in (1.4) are considered, and lots of symbolic manipulations are required which leads to a long expression of $c_1(0)$. Hence the general case calculation is omitted here, but it will be done for examples in next section under some particular choices of memory-based diffusions.

It is expected from Theorem 2.10 that the bifurcating spatially inhomogeneous periodic solution is stable at $\bar{\tau} := \min\{\tau_n^0, 1 \le n \le N\}$, as long as $(\bar{u}, \bar{v})$ is locally asymptotically stable for $\tau = 0$. In this case, more assumptions are required to ensure the local stability of $(\bar{u}, \bar{v})$ when $\tau = 0$, as suggested in [38]. For $\tau = 0$, (2.4) becomes

$$\lambda^2+(a_n+c_n)\lambda+(b_n+d_n+h_n)=0. \tag{2.26}$$

Assume

(H4) $D_1+D_2+c\ge 0$ and $D_{21}f_v\bar{v}+D_{12}g_u\bar{u}-D_{11}g_v\bar{u}-D_{22}f_u\bar{v}-D_1g_v-D_2f_u\ge 0$.

It then follows from **(H1)**, **(H3)** and **(H4)** that $a_n+c_n>0$ and $b_n+d_n+h_n>0$ for all $n\in\mathbb{N}$, and all the roots of (2.26) have negative real parts for any n. This, together with Theorem 2.10 implies the following conclusion.

Corollary 2.11. *Assume that* **(H1)**, **(H3)** *and* **(H4)** *hold.*

(1) *If* (2.20) *has no positive root for any $n\in\mathbb{N}$, then $(\bar{u},\bar{v})$ is linearly stable for all $\tau\ge 0$;*
(2) *If there exists $1\le n\le N$ such that* (2.20) *admits a positive root $\omega_n>0$, then $(\bar{u},\bar{v})$ is linearly stable for $\tau\in[0,\bar{\tau})$; Furthermore, if $\alpha'(\bar{\tau})\ne 0$ and $c_1(0)\ne 0$, then there exists a periodic solution for $\tau>\bar{\tau}$ ($\tau<\bar{\tau}$ resp.), bifurcated from $(\bar{u},\bar{v})$ through a Hopf bifurcation, provided that Sign$(\alpha'(\bar{\tau})/c_1(0))<0$ (Sign$(\alpha'(\bar{\tau})/c_1(0))>0$ resp.). In addition, if $c_1(0)<0$ ($c_1(0)>0$ resp.), then the bifurcating periodic solution is stable (unstable resp.).*

3. Lotka-Volterra competition model

In this section, we apply results in Section 2 to the following diffusive Lotka-Volterra competition model with memory-based self-diffusion and cross-diffusion:

$$\begin{cases} \dfrac{\partial u}{\partial t}=D_1\Delta u+D_{11}\nabla\cdot(u\nabla u_r)+D_{12}\nabla\cdot(u\nabla v_r)+u(1-u-\alpha v), & x\in\partial\Omega,\ t>0,\\ \dfrac{\partial v}{\partial t}=D_2\Delta v+D_{21}\nabla\cdot(v\nabla u_r)+D_{22}\nabla\cdot(v\nabla v_r)+\gamma v(1-v-\beta u), & x\in\partial\Omega,\ t>0,\\ \dfrac{\partial u}{\partial n}=0,\quad \dfrac{\partial v}{\partial n}=0, & x\in\partial\Omega,\ t>0,\\ u(x,t)=\phi_1(x,t),\quad v(x,t)=\phi_2(x,t), & x\in\Omega,\ -\tau\le t\le 0. \end{cases} \tag{3.1}$$

Here $\alpha,\beta,\gamma>0$. It is easy to see that **(H0)** is satisfied, then from Theorem 2.1, a unique positive classical solution of (3.1) exists globally.

The kinetic system associated with (3.1) is

$$\begin{cases} u'=u(1-u-\alpha v),\\ v'=\gamma v(1-v-\beta u). \end{cases} \tag{3.2}$$

It is well-known that (3.2) has three equilibria $E_0=(0,0)$, $E_1=(1,0)$ and $E_2=(0,1)$, and E_0 is always unstable. The stabilities of E_1 and E_2 are determined by the competition coefficients α and β, respectively, that is, E_1 is stable (unstable) when $\beta>1$ ($\beta<1$), and E_2 is stable (unstable) when $\alpha>1$ ($\alpha<1$). Moreover, under the weak competition condition ($\alpha,\beta<1$), it is known that (3.2) has a coexistence equilibrium $E^*=(u^*,v^*)$, which is globally asymptotically stable. Here, $u^*=\dfrac{1-\alpha}{1-\alpha\beta}<1$ and $v^*=\dfrac{1-\beta}{1-\alpha\beta}<1$. Without the memory-based diffusion ($D_{ij}=0$ for $i,j=1,2$), (3.1) becomes the classical reaction-diffusion Lotka-Volterra competition model, and it is well known [3] that the asymptotic dynamical behavior of (3.1) is almost the same as the one of (3.2). This implies the diffusion terms have essentially no other effects than smoothing and averaging.

Now, we investigate the effect of memory-based diffusion on the dynamics of (3.1). Suppose that $(\bar{u}, \bar{v})$ is a constant steady state for (3.1). Then,

$$f_u = 1 - 2\bar{u} - \alpha\bar{v}, \quad f_v = -\alpha\bar{u}, \quad g_u = -\gamma\beta\bar{v}, \quad g_v = \gamma(1 - 2\bar{v} - \beta\bar{u}). \tag{3.3}$$

The stability of boundary steady states E_0, E_1 and E_2 can be easily obtained.

Proposition 3.1. *Assume that $D_1, D_2 > 0$, $D_{ij} \in \mathbb{R}$ $(i, j = 1, 2)$, and $\alpha, \beta, \gamma > 0$. Then for* (3.1)*,*

(1) *$E_0 = (0, 0)$ is unstable;*
(2) *If $\beta > 1$ and $|D_{11}| < D_1$, then $E_1 = (1, 0)$ is locally asymptotically stable;*
(3) *If $\alpha > 1$ and $|D_{22}| < D_2$, then $E_2 = (0, 1)$ is locally asymptotically stable.*

Proof. Using (3.3), it is easy to check that (2.4) with $\bar{u} = \bar{v} = 0$, $n = 0$ has two positive eigenvalues 1 and r, which implies E_0 is always unstable. At E_1, (2.4) reduces to

$$[\lambda + D_1\mu_n + D_{11}\mu_n e^{-\lambda r} + 1][\lambda + D_2\mu_n - \gamma(1-\beta)] = 0, \quad n \in \mathbb{N}_0.$$

Consider

$$\lambda + D_1\mu_n + D_{11}\mu_n e^{-\lambda r} + 1 = 0 \tag{3.4}$$

It follows from [30, Corollary 3.9] that all the roots of (3.4) have strictly negative real parts when $|D_{11}| < D_1$. On the other hand, the root of $\lambda + D_2\mu_n - \gamma(1-\beta) = 0$ is $\lambda = -D_2\mu_n + \gamma(1-\beta)$, which is negative for all $n \in \mathbb{N}_0$ if $\beta > 1$. This proves the local stability of E_1 in (2). The stability of E_2 can be shown by a similar argument. $\square$

Remark 3.2. If $|D_{11}| > D_1$, it is also known from [30, Corollary 3.9] that there are infinitely many roots of (3.4) concentrated on the vertical line $\{z \in \mathbb{C} : \mathrm{Re}(z) = \ln(|D_{11}|/D_1)\}$ in the complex plane, and hence E_1 is always unstable. This, together with Proposition 3.1, indicates that the linear stability of boundary steady state E_1 (or E_2) depends not only on the competition coefficient β (or α), but also on the memory-based self-diffusion rate D_{11} (or D_{22}) of itself, and the memory-based cross-diffusion rates D_{12} and D_{21} do not affect the stabilities of E_1 and E_2.

For $0 < \alpha, \beta < 1$, we consider the stability of the constant coexistence state E^*. At E^*, $f_u + g_v = -(u^* + \gamma v^*) < 0$ and $f_u g_v - f_v g_u = \gamma u^* v^*(1 - \alpha\beta) > 0$, so **(H1)** is satisfied and $\sigma_0(\tau) \subseteq \mathbb{C}^-$. For $\sigma_n(\tau)$ for $n \in \mathbb{N}$, we notice that the coefficients in (2.5) become

$$\begin{aligned} a_n &= (D_1 + D_2)\mu_n + u^* + \gamma v^* > 0, \\ b_n &= b\mu_n^2 + (D_2 u^* + D_1\gamma v^*)\mu_n + \gamma(1-\alpha\beta)u^* v^* > 0, \\ d_n &= d\mu_n^2 + (\gamma D_{11} + D_{22} - \alpha D_{21} - \gamma\beta D_{12})u^* v^* \mu_n. \end{aligned} \tag{3.5}$$

In general the distribution of the elements in $\sigma_n(\tau)$ is rather complicated. In the remaining part, we shall study (3.1) for the following two special cases:

(D1) $D_{12} = D_{21} = D_{22} = 0$ and $D_{11} \neq 0$.
(D2) $D_{11} = D_{22} = D_{21} = 0$ and $D_{12} \neq 0$.

The effect of memory-based self-diffusion rate D_{11} and memory-based cross-diffusion rate D_{12} are shown in the following results.

Theorem 3.3. *Assume that $0 < \alpha, \beta < 1$ and* **(D1)** *holds. Then the constant coexistence steady state (u^*, v^*) is linearly stable provided that $|D_{11}|u^* < D_1$, and it is unstable if $|D_{11}|u^* > D_1$.*

Proof. For $D_{12} = D_{21} = D_{22} = 0$, we have

$$d_n = D_2 D_{11} u^* \mu_n^2 + \gamma D_{11} u^* v^* \mu_n, \quad c_n = D_{11} u^* \mu_n, \quad h_n = 0,$$

and in (2.21), we have

$$p_n = 2(a_n^2 - 2b_n) - c_n^2 > 0, \qquad q_n = (a_n^2 - 2b_n)(a_n^2 - 2b_n - c_n^2) + (2b_n^2 - d_n^2),$$
$$r_n = (a_n^2 - 2b_n)(2b_n^2 - d_n^2) - b_n^2 c_n^2, \qquad s_n = b_n^2(b_n^2 - d_n^2).$$

If $|D_{11}|u^* < D_1$, then **(H4)** holds and we further have

$$b_n + d_n > 0, \;\; b_n - d_n > 0, \;\; a_n^2 - 2b_n - c_n^2 > 0,$$

and **(H3)** is also satisfied. This, together with $a_n^2 - 2b_n > 0$, implies that

$$r_n = (a_n^2 - 2b_n)(b_n^2 - d_n^2) + (a_n^2 - 2b_n)b_n^2 - b_n^2 c_n^2 > b_n^2(a_n^2 - 2b_n - c_n^2) > 0.$$

Accordingly $G_n(z) = 0$ has no positive roots for z whenever $|D_{11}|u^* < D_1$, and thus (u^*, v^*) is locally asymptotically stable from Corollary 2.11. On the other hand, if $|D_{11}|u^* > D_1$, **(H2)** is also satisfied, it follows from Theorem 2.8 that (u^*, v^*) is unstable in the sense that the associated characteristic equation (2.4) has infinitely many complex roots with positive real parts. □

If we assume $D_{11} = D_{12} = D_{21} = 0$ and $D_{22} \neq 0$, then analogous results as Theorem 3.3 on the stability of (u^*, v^*) hold in terms of D_{22}. Under the condition **(D2)**, we have $c = d = h = c_n = h_n = 0$ and $d_n = -\gamma\beta D_{12} u^* v^* \mu_n$. Therefore, $h < b$ and $b + h - |d| > 0$, i.e., **(H3)** is satisfied. In addition, (2.4) reduces to

$$\lambda^2 + a_n \lambda + b_n + d_n e^{-\lambda r} = 0, \tag{3.6}$$

where a_n, b_n are given by (3.5). First, we show that (u^*, v^*) loses its stability if D_{12} is positive and D_{12} increases, and steady state bifurcations occur when D_{12} increases. In this case, (3.1) possesses non-constant steady state solutions.

Theorem 3.4. *Assume that* $0 < \alpha, \beta < 1$, *and* **(D2)** *holds. Then* (3.1) *undergoes a mode-n steady state bifurcation near* (u^*, v^*) *at* $D_{12} = D_{12}^n > 0$ *for* $n \in \mathbb{N}$ *given that* μ_n *is a simple eigenvalue of* (2.3)*, where*

$$D_{12}^n = \frac{b\mu_n^2 + (D_2u^* + D_1\gamma v^*)\mu_n + \gamma(1-\alpha\beta)u^*v^*}{\gamma\beta u^*v^*\mu_n}, \quad n \in \mathbb{N}. \tag{3.7}$$

Precisely, near (D_{12}^n, u^*, v^*), (3.1) *has a line of trivial steady state solutions* $\Gamma_0 = \{(D_{12}, u^*, v^*) : D_{12} > 0\}$ *and a family of nontrivial solutions bifurcating from* Γ_0 *at* $D_{12} = D_{12}^n$*:*

$$\Gamma_n = \left\{\left(D_{12}^n(s), u_n(s,x), v_n(s,x)\right) : -\delta < s < \delta\right\},$$

where $\delta > 0$, $A_1, A_2 \in \mathbb{R}$, $u_n(s,x) = u^* + A_1 s\phi_n(x) + sg_{1n}(s,x)$, $v_n(s,x) = v^* + A_2 s\phi_n(x) + sg_{2n}(s,x)$ *and* $D_{12}^n(s)$, $g_{in}(s,\cdot)$ $(i = 1, 2)$ *are smooth functions defined for* $s \in (-\delta, \delta)$ *such that* $D_{12}^n(0) = D_{12}^n$, *and* $g_{in}(0,\cdot) = 0$*; and there are no other steady state solutions of* (3.1) *than the ones on* Γ_0 *and* Γ_n *near* $(D_{12}, u, v) = (D_{12}^n, u^*, v^*)$.

Proof. Recall that b_n is independent of D_{12}. For $1 \le n \le N$, $b_n + d_n = 0$ when $D_{12} = D_{12}^n$, which implies $\lambda = 0$ is a root of (3.6). Suppose that $\lambda(D_{12})$ is the root of (3.6) such that $\lambda(D_{12}^n) = 0$. Then

$$\left.\frac{d\lambda(D_{12})}{dD_{12}}\right|_{D_{12}=D_{12}^n} = \frac{\gamma\beta u^*v^*\mu_n}{a_n + r\gamma\beta D_{12}^n u^*v^*\mu_n} > 0.$$

Then one can apply the bifurcation from simple eigenvalue theorem [6, Theorem 1.7] to conclude that spatially nonhomogeneous steady state solutions of (3.1) bifurcate from (u^*, v^*) at $D_{12} = D_{12}^n$. Details of bifurcation proof are omitted here, see for example, the proof of Theorem 3 in [32]. □

The generation of spatial patterns in Theorem 3.4 with large positive cross-diffusion is known, see for example [26]. Next we show that under the condition **(D2)**, the constant coexistence steady state (u^*, v^*) could lose its stability for negative D_{12} through Hopf bifurcations, when the time delay r increases.

Lemma 3.5. *Assume that* $0 < \alpha, \beta < 1$, *and* **(D2)** *holds. If* $D_{12} < 0$ *such that* $b_n < d_n$ *for some* $n \ge 1$, *then* (3.6) *with such n has a pair of purely imaginary roots* $\pm i\omega_n$ *when*

$$r = r_n^j := \begin{cases} \dfrac{1}{\omega_n}\left[\arccos\dfrac{d_n(z_n - b_n)}{(b_n - z_n)^2 + a_n^2 z_n} + 2j\pi\right], & a_n^2 b_n - d_n^2 > 0, \\ \dfrac{1}{\omega_n}\left[\arcsin\dfrac{a_n d_n \omega_n}{(b_n - z_n)^2 + a_n^2 z_n} + 2j\pi\right], & a_n^2 b_n - d_n^2 < 0, \end{cases} \quad j = 0, 1, \cdots. \tag{3.8}$$

Furthermore $Sign\alpha'(r_n^j) > 0$, *where* $\alpha(r_n^j)$ *is defined in Theorem* 2.9.

Proof. Note that

$$p_n = 2(a_n^2 - 2b_n), \quad q_n = (a_n^2 - 2b_n)^2 + (2b_n^2 - d_n^2),$$
$$r_n = (a_n^2 - 2b_n)(2b_n^2 - d_n^2), \quad s_n = b_n^2[b_n^2 - d_n^2].$$

Then $G_n(z)$ defined in (2.22) can be expressed as

$$G_n(z) = f_1(z) + b_n^2(b_n^2 - d_n^2),$$

with

$$f_1(z) = z[z + (a_n^2 - 2b_n)][z^2 + (a_n^2 - 2b_n)z + (2b_n^2 - d_n^2)].$$

It can be verified that

$$a_n^2 - 4b_n = [(D_1 - D_2)\mu_n + (u^* - \gamma v^*)]^2 + 4\gamma\alpha\beta u^* v^* > 0.$$

If $b_n < d_n$ for some $n \geq 1$, then $(a_n^2 - 2b_n)^2 - (2b_n^2 - d_n^2) > 0$ for such n. Thus $f_1(z)$ is increasing for $z \geq 0$, and consequently $G_n(z) = 0$ has a unique positive root, denoted by z_n. Note that

$$G_n(b_n) = a_n^2 b_n (a_n^2 b_n - d_n^2).$$

It then follows that $z_n < b_n$ ($z_n > b_n$ resp.) if and only if $a_n^2 b_n - d_n^2 > 0$ ($a_n^2 b_n - d_n^2 < 0$ resp.). Let $\omega_n = \sqrt{z_n}$. From (2.19), we have

$$\cos\omega_n r = \frac{d_n(z_n - b_n)}{(b_n - z_n)^2 + a_n^2 z_n}, \quad \sin\omega_n r = \frac{a_n d_n \omega_n}{(b_n - z_n)^2 + a_n^2 z_n} > 0.$$

Furthermore, if $a_n^2 b_n - d_n^2 > 0$ ($a_n^2 b_n - d_n^2 < 0$ resp.), then $\cos\omega_n r < 0$ ($\cos\omega_n r > 0$ resp.). This gives the critical values r_n^j, given by (3.8), for (3.6) having a pair of purely imaginary roots.

In order to check the transversality condition, we first compute

$$\begin{aligned} G_n'(z_n) &= 4z_n^3 + 6(a_n^2 - 2b_n)z_n^2 + 2[(a_n^2 - 2b_n)^2 + (2b_n^2 - d_n^2)]z_n + (a_n^2 - 2b_n)(2b_n^2 - d_n^2) \\ &= [z_n^2 + (a_n^2 - 2b_n)z_n + (2b_n^2 - d_n^2)][4z_n + 2(a_n^2 - 2b_n)] \\ &\quad - 2(2b_n^2 - d_n^2)z_n - (a_n^2 - 2b_n)(2b_n^2 - d_n^2). \end{aligned}$$

If $b_n < d_n < \sqrt{2}b_n$, then $G_n'(z_n) > 0$. If $d_n > \sqrt{2}b_n$, it follows from $z_n^2 + (a_n^2 - 2b_n)z_n + (2b_n^2 - d_n^2) > 0$ for $z_n > 0$ that

$$G_n'(z_n) > 2z_n^2 + 3(a_n^2 - 2b_n)z_n + (a_n^2 - 2b_n)^2 > 0.$$

Thus, $\text{Sign}\alpha'(r_n^j) > 0$ follows directly from the fact that $H_n(z) > 0$ for any $z > 0$. □

Under **(D2)**, it is straightforward that **(H4)** is also satisfied for $D_{12} < 0$. Therefore, we can arrive at the following Hopf bifurcation theorem for (3.1) from Corollary 2.11 and Lemma 3.5.

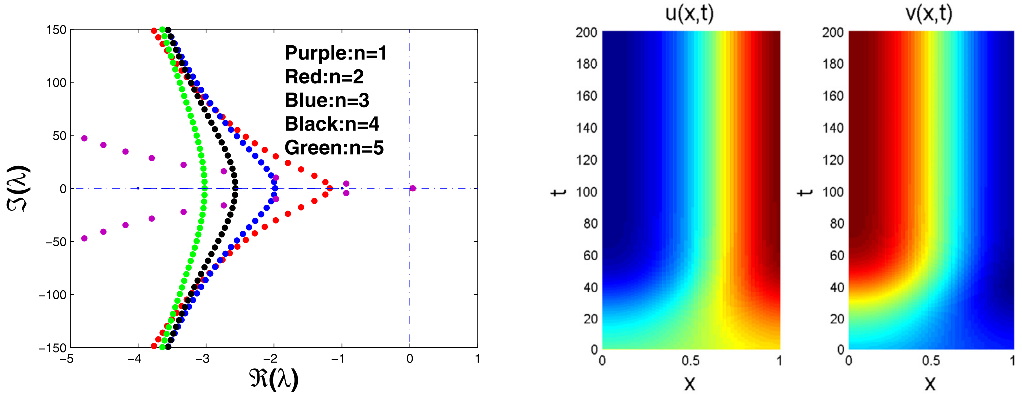

Fig. 2. Left: The roots of (3.6) with $n = 1, 2, 3, 4, 5$ and parameters given by (3.9), in Example 3.8. The figure is plotted with the aid of a Matlab package DDE-BIFTOOL [9]. Right: A solution of (3.1) tends to a spatially inhomogeneous steady state. Here parameters are as in (3.9), $D_{12} = 8.5 > 0$ and $r = 1$. (For interpretation of the colors in the figures, the reader is referred to the web version of this article.)

Theorem 3.6. *Assume that $0 < \alpha, \beta < 1$, and* **(D2)** *holds. Suppose that $D_{12} < 0$ is fixed such that $b_n < d_n$ for some $1 \le n \le N$. Then, (u^*, v^*) is linearly stable for $r \in [0, \bar{r})$, where $\bar{r} := \min\{r_n^0, 1 \le n \le N\}$. If $c_1(0) < 0$ ($c_1(0) > 0$ resp.), then there exists a stable (unstable resp.) spatially inhomogeneous periodic solution of (3.1) for $r > \bar{r}$ ($r < \bar{r}$ resp.), bifurcated from (u^*, v^*) through Hopf bifurcation, where r_n^j is given by (3.8) and the first Lyapunov coefficient $c_1(0)$ at the Hopf bifurcation point is given in the Appendix.*

Remark 3.7.

(1) In the condition **(D2)**, one can also substitute $D_{21} = 0$ and $D_{12} \neq 0$ by $D_{21} \neq 0$ and $D_{12} = 0$, and similar steady state bifurcations for $D_{21} > 0$ and Hopf bifurcations for $D_{21} < 0$ and $\tau > 0$ can be obtained.

(2) Note that the necessary condition $b_n < d_n$ for instability and Hopf bifurcations can be expanded as

$$0 > b_n - d_n = D_1 D_2 \mu_n^2 + (D_2 u^* + D_1 \gamma v^* + \beta\gamma D_{12} u^* v^*)\mu_n + \gamma(1 - \alpha\beta)u^* v^*.$$

Hence it is necessary that $D_{12} < -(D_2 u^* + D_1 \gamma v^*)/(\beta\gamma u^* v^*)$ so that the result of Theorem 3.6 holds.

Example 3.8. Suppose $D_{11} = D_{21} = D_{22} = 0$, and let

$$\Omega = (0, 1), \ D_1 = 1, \ \ D_2 = 0.1, \ \alpha = \beta = 0.5, \ \gamma = 1. \tag{3.9}$$

Then, $\mu_n = (n\pi)^2$. If $D_{12} > 0$, it then follows from (3.7) that $D_{12}^1 \approx 7.9833$, $D_{12}^2 \approx 21.1033, \cdots$. Therefore, $D_{12}^* = 7.9833$. Set $D_{12} = 8.5$ and $r = 1$. From Theorem 3.4, we can conclude that there is a positive root of (3.6) for $n = 1$, and all the roots of (3.6) with $n \ge 2$ have strictly negative real parts, see Fig. 2 (Left) for numerical illustrations. Moreover, a stable spatially in-

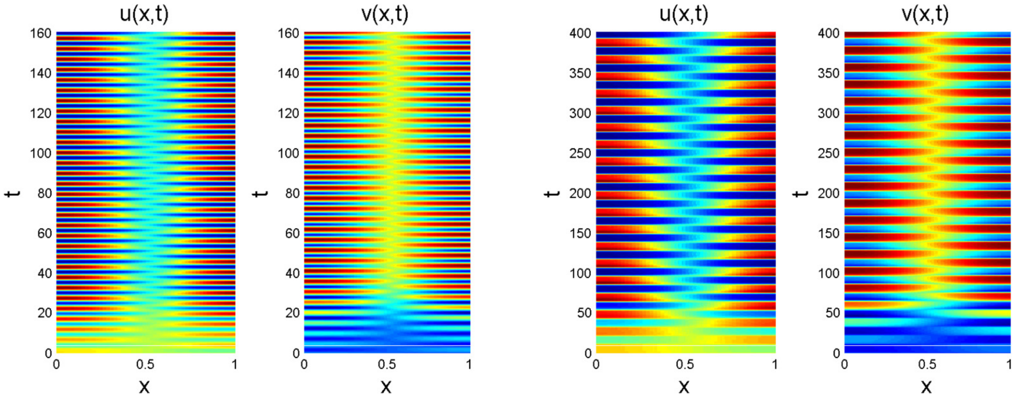

Fig. 3. Periodic solutions of (3.1) for $r = 2.5 > r_1^0$ (left) and $r = 10$ (right). Here parameters are as in (3.9), and $D_{12} = -12$.

homogeneous steady state could be observed, see Fig. 2 (Right). Note that $D_{12} > 0$ means that the species u stays away from locations with high density of its competitor v. Therefore the two species do not distribute uniformly in the habitat, and the two species u and v achieve a segregated steady state.

On the other hand if we choose $D_{12} = -12$, then only when $n = 1$, $G_n(z) = 0$ has a unique root $z_1 \approx 3.3497$. This implies $\omega_1 \approx 1.8302$. In addition, it can be also verified that $a_1^2 b_1 - d_1^2 > 0$. Therefore, by (2.23), we have $\bar{r} = r_1^0 \approx 1.1638$. From Lemma 3.5, we can conclude that a pair of conjugate complex roots of (2.4) cross the imaginary axis, as r passes through r_1^0. Furthermore, it can be computed (using the method in the Appendix) that $\text{Sign}\alpha'(r_1^0) > 0$ and $c_1(0) \approx -1.6488$. It then follows from Theorem 3.6 that there exists a stable spatially inhomogeneous time-periodic solution for $r > \bar{r} = r_1^0$, see Fig. 3. For $D_{12} < 0$, the species u moves up along the gradient of its competitor v, and the memory-based diffusion plays a key role on the oscillatory dynamics. As seen in Fig. 3, spatiotemporal oscillations could take place, as the memory delay crosses a critical value. In addition, the period also increases when r becomes large.

From Theorems 3.3, 3.4 and 3.6, we can see both the memory-induced self-diffusion and the memory-induced cross-diffusion could destabilize the constant steady state (u^*, v^*) of the diffusive Lotka-Volterra competition system (3.1) in the weak competition regime, but in a very different way. With a repulsive memory-induced diffusion cross-diffusion ($D_{12} > 0$), the system reaches a spatially inhomogeneous steady state that the two species coexist in segregated state (Fig. 2). On the other hand, an attractive memory-induced diffusion cross-diffusion ($D_{12} < 0$ and $\tau > 0$ large) produces a spatially inhomogeneous time-periodic solution (Fig. 3). These spatial and spatiotemporal patterns are generated through Turing and Hopf bifurcations respectively. For the memory-induced self-diffusion ($D_{11} \neq 0$), when $|D_{11}|$ exceeds a critical value D_1/u^*, infinitely many complex roots will cross the imaginary axis as τ increases, so that (u^*, v^*) becomes unstable, see Fig. 4 (left). However, the dynamics of (3.1) is still unclear in this situation. In Fig. 4 (right), we numerically found the “checkerboard” pattern for large D_{11}, which has already been observed in [30] for a scalar population model with memory-induced self-diffusion.

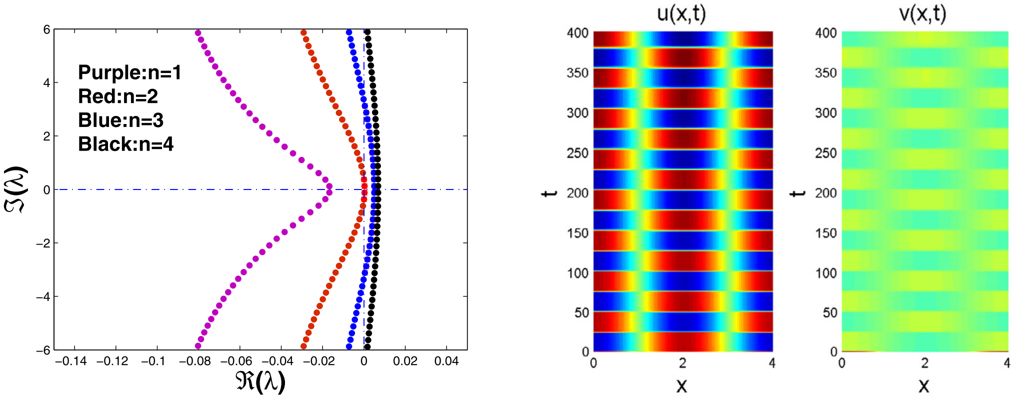

Fig. 4. The roots of (3.6) with $n = 1, 2, 3, 4$ (left), and periodic pattern of (3.1) (right). Here $D_1 = D_2 = 1$, $D_{12} = D_{21} = D_{22} = 0$, $\alpha = \beta = 0.5$, $\gamma = 1$, $r = 25$, and $D_{11} = 1.9 > 1/u^*$.

4. Lotka-Volterra cooperative model

In this section, we apply results in Section 2 to the following diffusive Lotka-Volterra cooperative model with memory-based self-diffusion and cross-diffusion:

$$\begin{cases} \dfrac{\partial u}{\partial t} = D_1 \Delta u + D_{11} \nabla \cdot (u \nabla u_r) + D_{12} \nabla \cdot (u \nabla v_r) + u(1 - u + \alpha v), & x \in \partial\Omega,\ t > 0, \\ \dfrac{\partial v}{\partial t} = D_2 \Delta v + D_{21} \nabla \cdot (v \nabla u_r) + D_{22} \nabla \cdot (v \nabla v_r) + \gamma v(1 - v + \beta u), & x \in \partial\Omega,\ t > 0, \\ \dfrac{\partial u}{\partial n} = 0, \quad \dfrac{\partial v}{\partial n} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,t) = \phi_1(x,t), \quad v(x,t) = \phi_2(x,t), & x \in \Omega,\ -\tau \le t \le 0. \end{cases} \tag{4.1}$$

Here, the notations are the same as the ones in (3.1) except $\alpha, \beta > 0$ are the cooperative coefficients. The dynamic behavior of (4.1) without self-diffusion and cross-diffusion was considered in [22]. For (4.1), there always exist three equilibria $E_0 = (0, 0)$, $E_1 = (1, 0)$ and $E_2 = (0, 1)$, and if $\alpha\beta < 1$, there is a positive steady state $E^* = (u^*, v^*)$ with $u^* = \dfrac{1+\alpha}{1-\alpha\beta}$ and $v^* = \dfrac{1+\beta}{1-\alpha\beta}$. For the boundary steady states, we can prove that they are all unstable for any choice of parameters, since $\sigma_0(r)$ always consists of $\gamma(1 + \beta) > 0$. For example, at E_1, the characteristic equation is

$$[\lambda + D_1\mu_n + D_{11}\mu_n e^{-\lambda r} + 1][\lambda + D_2\mu_n - \gamma(1 + \beta)] = 0, \quad n \in \mathbb{N}_0.$$

Obviously, $\gamma(1 + \beta) \in \sigma_0(r)$, so it is unstable.

For the constant coexistence steady state E^*, the conclusion is slightly different from Theorems 3.4 and 3.6. When $1 - \alpha\beta > 0$, the coefficient d_n of the characteristic equation associated with E^* is given by

$$d_n = d\mu_n^2 + (\gamma D_{11} + D_{22} + \alpha D_{21} + \gamma\beta D_{12})u^*v^*\mu_n > 0, \tag{4.2}$$

while a_n, b_n are the same as the ones in (3.5), and c_n, h_n are still given by (2.5) (since they are independent of reaction terms). Furthermore, under the condition **(D2)**, we have $d_n = \gamma\beta D_{12}u^*v^*\mu_n$. Therefore, using the similar argument for discussing competition model in previous section, we can also get the Turing and Hopf bifurcations for (4.1) as follows.

Theorem 4.1. *Assume that* $1-\alpha\beta > 0$, *and* **(D2)** *holds.*

(1) *If* $D_{12} < 0$, (4.1) *undergoes a mode-n steady state bifurcation near* (u^*, v^*) *at* $D_{12} = D_{12}^n < 0$ *for* $n \in \mathbb{N}$, *given that* μ_n *is a simple eigenvalue of* (2.3), *where*

$$D_{12}^n = \frac{b\mu_n^2 + (D_2u^* + D_1\gamma v^*)\mu_n + \gamma(1-\alpha\beta)u^*v^*}{-\gamma\beta u^*v^*\mu_n}. \tag{4.3}$$

(2) *Suppose* $D_{12} > 0$ *is fixed such that* $b_n < d_n$ *for some* $n \geq 1$. *Then,* (u^*, v^*) *is linearly stable for* $r \in [0, \bar{r})$, *where* $\bar{r} := \min\{r_n^0, 1 \leq n \leq N\}$, *and* r_n^j *is given by* (3.8) *in which* d_n *is replaced by* (4.2). *If* $c_1(0) < 0$ ($c_1(0) > 0$ *resp.*), *then there exists a stable (unstable resp.) spatially inhomogeneous periodic solution of* (4.1) *for* $r > \bar{r}$ ($r < \bar{r}$ *resp.*). *Here, the first Lyapunov coefficient* $c_1(0)$ *can be also derived, by simply replacing* α *with* $-\alpha$ *in all the formula from* (6.1) *to* (6.17) *in the Appendix.*

Notice that the conditions for occurrence of Turing and Hopf bifurcations for the cooperative system (4.1) are opposite to the ones for competition model. That is, for cooperative system, an attractive memory-based cross-diffusion ($D_{12} < 0$) generates spatially inhomogeneous steady states through Turing bifurcations, while a repulsive memory-based cross-diffusion ($D_{12} > 0$) yields spatially inhomogeneous time-periodic solutions through Hopf bifurcations. This is biologically reasonable since competition and mutualism are opposite biological process, and therefore the memory-based movement with different directions, with all the other factors unchanged, should play the same role on their dynamics.

Example 4.2. Suppose the parameters of (4.1) are given in Example 3.8. If $D_{12} < 0$, it then follows from (4.3) that $D_{12}^* \approx -1.7455$. Set $D_{12} = -2$ and $r = 1$. From (1) of Theorem 4.1, we can conclude that there is a positive root of (3.6) for $n = 1$, and all the roots of (3.6) with $n \geq 2$ have strictly negative real parts. Moreover, a stable spatially inhomogeneous steady state could be observed, see Fig. 5. However, the steady state is not segregated for u and v as in the competition model (3.1). If we choose $D_{12} = 2.5$, then only when $n = 1$, $G_n(z) = 0$ has a unique root $z_1 \approx 7.8189$. Again, it can be verified that $a_1^2b_1 - d_1^2 > 0$. Therefore, by (2.23), we have $\bar{r} = r_1^0 \approx 0.7657$. In addition, $c_1(0) \approx -0.4166$. It then follows from (2) of Theorem 4.1 that a stable spatially inhomogeneous time-periodic solution will be bifurcated from E^*, when r crosses r_1^0, see Fig. 6.

5. Conclusion

In this paper, we proposed a memory-based diffusive model for two interactive species, by using a modified Fick's law involving a direct movement toward the gradient of the density function at a past time. The stability of constant steady states is extensively studied, by examining the impact of memory-based self-diffusion and cross-diffusion. For a positive constant steady state, it is revealed that eigenvalues of the linearized system accumulate to one or two vertical lines in the

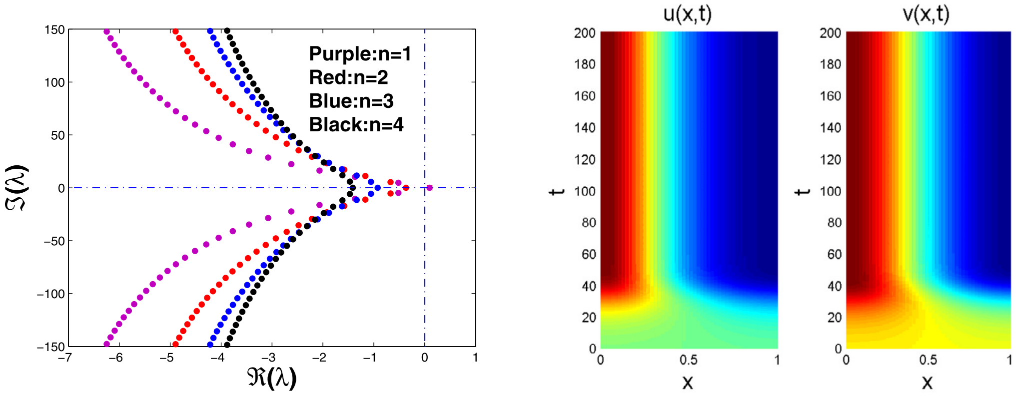

Fig. 5. Left: The characteristic roots of (4.1) at E^*. Right: A solution of (4.1) tends to a spatially inhomogeneous steady state. All parameters are given in Example 3.8 except that $D_{12} = -2$.

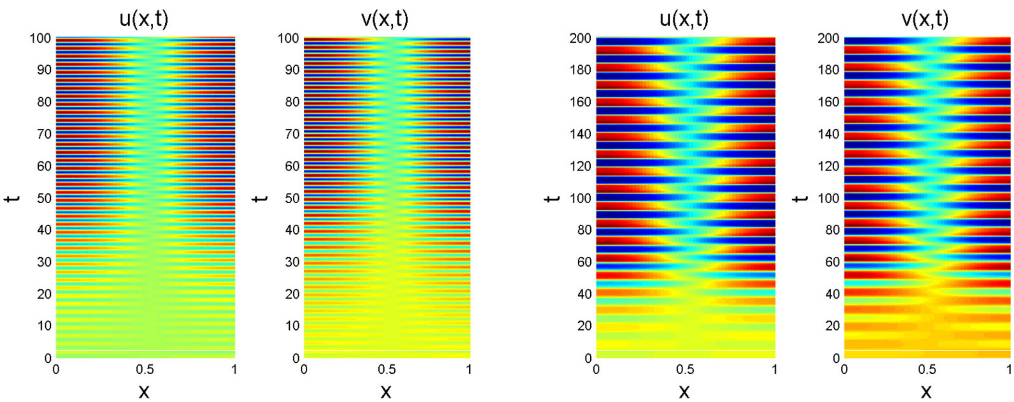

Fig. 6. Periodic solutions of (4.1) for $r = 0.9 > r_1^0$ (left) and $r = 5$ (right). Here, $D_{12} = 2.5$ and other parameters are as in Example 3.8.

complex plane, which is determined by a transcendental equation corresponding to a difference equation. This is similar to the distribution of eigenvalues for partial neutral functional difference equation, since the “difference structures” are all involved in these two types of equations, which play a key role on their dynamics. It is expected that such distribution of eigenvalues is also valid for n-species reaction-diffusion systems with memory-based self-diffusion and cross-diffusion.

The spectral set $\sigma(\tau)$ of the linearized equation of two-variable reaction-diffusion systems with memory-based self-diffusion and cross-diffusion is completely determined in a general setting. It is shown that $\sigma(\tau)$ is the union of $\sigma_n(\tau)$ for $n = 0, 1, 2, \cdots$ and each $\sigma(\tau)$ depends on the n-th eigenvalue λ_n of Laplacian operator. For scalar reaction-diffusion model with memory-based diffusion, it was found that the curve $\sigma_n(\tau)$ is always on the left hand side of complex plane of $\sigma_{n-1}(\tau)$. But for the two-variable reaction-diffusion systems with memory-based self-diffusion and cross-diffusion, different $\sigma_n(\tau)$ curves can interweave in some situations. As a result, a pair of complex eigenvalues in the set $\sigma_n(\tau)$ for some $n \geq 1$ may cross the imaginary axis of complex plane when the average memory period τ increases, with all other eigenvalues having strictly negative real parts. In this case, a stable spatially inhomogeneous time-periodic solution could be generated through Hopf bifurcation. This shows that time-periodic spatial-temporal patterns can be generated in two-variable reaction-diffusion systems with memory-based self-diffusion and cross-diffusion, but it cannot happen for scalar reaction-diffusion model with memory-based diffusion.

Diffusive Lotka-Volterra competition and cooperation models memory-based self-diffusion and cross-diffusion are studied as examples of the above general instability principle, for some particular choice of memory-based diffusion rates. For the competition model in the weak competition regime, if u is a timid competitor who moves away from the past of its competitor v (i.e., $D_{12} > 0$), then the constant coexistence steady state will be destabilized and a spatially inhomogeneous steady state pattern appears through Turing type bifurcation, as the memory-based diffusion rate D_{12} increases; on the other hand if u is an aggressive competitor who moves towards the past of its competitor v (i.e., $D_{12} < 0$), then Hopf bifurcation occurs at the constant coexistence steady state when the memory period τ increases. After computing the first Lyapunov coefficient in the normal form, a stable spatially inhomogeneous time-periodic solution appears when the memory period τ is larger than a critical value. This indicates the memory-based cross-diffusion indeed alters the dynamics of classic Lotka-Volterra competition model in different ways from those in the literature. For the cooperative model, there is a similar scenario, with the conditions being reversed from the ones for the competition model.

6. Appendix

Here we compute the Hopf bifurcation properties in Theorem 3.6 for $D_{12} < 0$, following the algorithm in [37]. Let $\Omega = (0, l)$. Then, $\mu_n = \left(\frac{n\pi}{l}\right)^2$ and $\phi_n(x) = \cos \nu_n x$ with $\nu_n = \sqrt{\mu_n}$ are the solution of eigenvalue problem (2.3). Suppose that $\pm i\omega_n$ are the roots of (2.4) for some fixed $n \ge 1$ when $r = r_n^j$, $j = 0, 1, \cdots$, that is, the infinitesimal generator A_U of the linearized equation (2.2) has a pair of purely imaginary roots. Then, $\pm i\omega_n$ are also the eigenvalues of the formal adjoint operator A_U^*. Furthermore, the eigenfunctions of A_U and A_U^* with respect to $\pm i\omega_n$ are given by

$$\Phi(\theta) = (e^{i\omega_n\theta}\phi_n(x)u_0, e^{-i\omega_n\theta}\phi_n(x)\bar{u}_0), \quad \Psi(s) = \begin{pmatrix} ce^{-i\omega_n s}\phi_n(x)v_0 \\ \bar{c}e^{i\omega_n s}\phi_n(x)\bar{v}_0 \end{pmatrix},$$

where u_0 and v_0 are nonzero solutions of $\Pi_n(i\omega_n)u_0 = 0$ and $v_0\Pi_n(i\omega_n) = 0$ respectively, given by

$$u_0 = \left(1, -\frac{\gamma\beta v^*}{i\omega_n + D_2\mu_n + \gamma v^*}\right)^T =: (1, c_1)^T,$$
$$v_0 = \left(1, -\frac{i\omega_n + D_1\mu_n + u^*}{\gamma\beta v^*}\right) =: (1, c_2).$$

If we choose c as

$$c = \frac{2}{l[(1 + c_2c_1) - \mu_n r_n^j D_{12}u^* c_1 e^{-i\omega_n r_n^j}]},$$

then, $(\Psi, \Phi) = I$, where

$$(\alpha,\varphi)=\langle\alpha(0),\varphi(0)\rangle+\int_{-\tau}^{0}\langle\alpha(\xi+\tau),\Delta\Lambda_2\varphi(\xi)\rangle d\xi,\quad \Lambda_2=\begin{pmatrix}0 & D_{12}u^*\\ 0 & 0\end{pmatrix}.$$

Now, let

$$F_2=2\begin{pmatrix}D_{12}\nabla u\nabla v(t-r)+D_{12}u\Delta v(t-r)-u(u+\alpha v)\\ -\gamma v(v+\beta u)\end{pmatrix}. \tag{6.1}$$

Substituting $\begin{pmatrix}u_t(\theta)\\ v_t(\theta)\end{pmatrix}=\Phi(\theta)\begin{pmatrix}x_1\\ x_2\end{pmatrix}+\begin{pmatrix}y_1\\ y_2\end{pmatrix}$ into (6.1), we have

$$f_2=f_{20}x_1^2+f_{11}x_1x_2+f_{02}x_2^2+(D_{1y}F_2)yx_1+(D_{2y}F_2)yx_2, \tag{6.2}$$

where $f_{20}=(f_{20}^1,f_{20}^2)^T$, $f_{11}=(f_{11}^1,f_{11}^2)^T$, $f_{02}=(f_{02}^1,f_{02}^2)^T$, $(D_{1y}F_2)y=((D_{1y}^1F_2)y,(D_{1y}^2F_2)y)^T$, $(D_{2y}F_2)y=((D_{2y}^1F_2)y,(D_{2y}^2F_2)y)^T$ with

$$\begin{aligned}&f_{20}^1=f_{201}^1\cos 2\nu_n x+f_{202}^1,\qquad f_{20}^2=f_{201}^2\cos 2\nu_n x+f_{202}^2,\\ &f_{11}^1=f_{111}^1\cos 2\nu_n x+f_{112}^1,\qquad f_{11}^2=f_{111}^2\cos 2\nu_n x+f_{112}^2,\\ &f_{02}^1=\bar f_{20}^1,\qquad f_{02}^2=\bar f_{20}^2,\end{aligned} \tag{6.3}$$

and

$$\begin{aligned}&f_{201}^1=-\left[2D_{12}\mu_n c_1e^{-i\omega_n r_n^j}+(1+\alpha c_1)\right],\qquad f_{202}^1=-(1+\alpha c_1),\\ &f_{201}^2=-\gamma c_1(c_1+\beta),\qquad f_{202}^2=f_{201}^2,\\ &f_{111}^1=-\left[2D_{12}\mu_n(c_1e^{-i\omega_n r_n^j}+\bar c_1e^{i\omega_n r_n^j})+(2+\alpha(c_1+\bar c_1))\right],\qquad f_{112}^1=-[2+\alpha(c_1+\bar c_1)],\\ &f_{111}^2=-\gamma[2|c_1|^2+\beta(c_1+\bar c_1)],\qquad f_{112}^2=f_{111}^2.\end{aligned}$$

Moreover,

$$\begin{aligned}(D_{1y}^1F_2)y&=2D_{12}\left[e^{-i\omega_n r_n^j}c_1(\nabla\phi_n\nabla y_1(0)+\Delta\phi_n y_1(0))+(\nabla\phi_n\nabla y_2(-r_n^j)+\phi_n\Delta y_2(-r_n^j))\right]\\ &\quad-2\phi_n[(2+\alpha c_1)y_1(0)+\alpha y_2(0)],\\ (D_{2y}^1F_2)y&=2D_{12}\left[e^{i\omega_n r_n^j}\bar c_1(\nabla\phi_n\nabla y_1(0)+\Delta\phi_n y_1(0))+(\nabla\phi_n\nabla y_2(-r_n^j)+\phi_n\Delta y_2(-r_n^j))\right]\\ &\quad-2\phi_n[(2+\alpha\bar c_1)y_1(0)+\alpha y_2(0)],\\ (D_{1y}^2F_2)y&=-2\gamma\phi_n[\beta c_1y_1(0)+(2c_1+\beta)y_2(0)],\\ (D_{2y}^2F_2)y&=-2\gamma\phi_n[\beta\bar c_1y_1(0)+(2\bar c_1+\beta)y_2(0)].\end{aligned} \tag{6.4}$$

Let

$$\frac{1}{2}\langle \psi_1(0), f_2 \rangle = \frac{1}{2} g_{20} x_1^2 + g_{11} x_1 x_2 + \frac{1}{2} g_{02} x_2^2 + \frac{1}{2} g_{21} x_1^2 x_2 + \cdots . \tag{6.5}$$

Note that

$$\int_0^l \phi_n(x) dx = \int_0^l \phi_n^3(x) dx = 0, \tag{6.6}$$

for $n \geq 1$. It then follows from (6.2), (6.3), (6.5) and (6.6) that

$$g_{20} = \langle \psi_1(0), f_{20} \rangle = 0, \quad g_{11} = \frac{1}{2}\langle \psi_1(0), f_{11} \rangle = 0, \quad g_{02} = \langle \psi_1(0), f_{02} \rangle = 0. \tag{6.7}$$

In addition, suppose that

$$y = (y_1, y_2)^T = \frac{1}{2} w_{20}(\theta) x_1^2 + w_{11}(\theta) x_1 x_2 + \frac{1}{2} w_{02}(\theta) x_2^2,$$

where $w_{20} = (w_{20}^1, w_{20}^2)^T$, $w_{11} = (w_{11}^1, w_{11}^2)^T$ and $w_{02} = (w_{02}^1, w_{02}^2)^T$. Then, from (6.4) and (6.5), we have

$$g_{21} = \langle \psi_1(0), (D_{1y} F_2) w_{11} \rangle + \frac{1}{2}\langle \psi_1(0), (D_{2y} F_2) w_{20} \rangle, \tag{6.8}$$

where $(D_{1y} F_2) w_{11}$ and $(D_{2y} F_2) w_{20}$ can be defined by (6.4). Thus,

$$g_{21} = \int_0^l G_{21} dx, \tag{6.9}$$

where

$$\begin{aligned} G_{21} = 2c \Big\{ &\phi_n D_{12} \Big[e^{-i\omega_n r_n^j} c_1 (\nabla \phi_n \nabla w_{11}^1(0) + \Delta \phi_n w_{11}^1(0)) + (\nabla \phi_n \nabla w_{11}^2(-r_n^j) \\ &+ \phi_n \Delta w_{11}^2(-r_n^j)) \Big] - (2 + \alpha c_1 + c_1 c_2 \gamma \beta) \phi_n^2 w_{11}^1(0) - [\alpha + c_2 \gamma (2c_1 + \beta)] \phi_n^2 w_{11}^2(0) \Big\} \\ &+ c \Big\{ \phi_n D_{12} \Big[e^{i\omega_n r_n^j} \bar{c}_1 (\nabla \phi_n \nabla w_{20}^1(0) + \Delta \phi_n w_{20}^1(0)) + (\nabla \phi_n \nabla w_{20}^2(-r_n^j) \\ &+ \phi_n \Delta w_{20}^2(-r_n^j)) \Big] - (2 + \alpha \bar{c}_1 + \bar{c}_1 c_2 \gamma \beta) \phi_n^2 w_{20}^1(0) - [\alpha + c_2 \gamma (2\bar{c}_1 + \beta)] \phi_n^2 w_{20}^2(0) \Big\} . \end{aligned} \tag{6.10}$$

In order to compute g_{21}, it remains to compute $w_{20}(\theta)$ and $w_{11}(\theta)$. It is known from [37] and (6.7) that

$$\begin{aligned} w_{20}(\theta) &= e^{2i\omega_n\theta}E_1 - \frac{g_{20}}{i\omega_n}e^{i\omega_n\theta}u_0 - \frac{\bar{g}_{02}}{3i\omega_n}e^{-i\omega_n\theta}\bar{u}_0 = e^{2i\omega_n\theta}E_1, \\ w_{11}(\theta) &= E_2 + \frac{g_{11}}{i\omega_n}e^{i\omega_n\theta}u_0 - \frac{\bar{g}_{11}}{i\omega_n}e^{-i\omega_n\theta}\bar{u}_0 = E_2, \end{aligned} \tag{6.11}$$

and $E_1 = (E_1^1, E_1^2)^T$, $E_2 = (E_2^1, E_2^2)^T$ are determined by

$$\begin{aligned} 2i\omega_n E_1 - \Delta D(e^{2i\omega_n\theta}E_1) - L(e^{2i\omega_n\theta}E_1) &= f_{20}, \\ -\Delta D(E_2) - L(E_2) &= \frac{1}{2}f_{11}, \end{aligned} \tag{6.12}$$

subject to Neumann boundary condition on $(0, l)$. From the linear equation (2.2), (6.12) is equivalent to

$$\begin{aligned} 2i\omega E_1 - M_1\Delta E_1 - M_3E_1 &= f_{20}, \\ -M_2\Delta E_2 - M_3E_2 &= \frac{1}{2}f_{11}, \end{aligned} \tag{6.13}$$

where

$$M_1 = \begin{pmatrix} D_1 & D_{12}u^* e^{-2i\omega_n r_n^j} \\ 0 & D_2 \end{pmatrix}, \quad M_2 = \begin{pmatrix} D_1 & D_{12}u^* \\ 0 & D_2 \end{pmatrix},$$
$$M_3 = \begin{pmatrix} -u^* & -\alpha u^* \\ -\gamma\beta v^* & -\gamma v^* \end{pmatrix}.$$

By solving (6.13) subject to Neumann boundary condition on $(0, l)$, we obtain

$$E_1 = E_{11}\cos 2\nu_n x + E_{12}, \qquad E_2 = E_{21}\cos 2\nu_n x + E_{22}, \tag{6.14}$$

and E_{11}, E_{12}, E_{21}, E_{22} are determined by the following linear algebraic equations

$$\begin{aligned} &(2i\omega_n I + 4\mu_n M_1 - M_3)E_{11} = f_{201}, \quad (2i\omega_n I - M_3)E_{12} = f_{202}, \\ &(4\mu_n M_2 - M_3)E_{21} = \frac{1}{2}f_{111}, \quad -M_3E_{22} = \frac{1}{2}f_{112}, \end{aligned} \tag{6.15}$$

respectively. Denote $E_{11} = (E_{11}^1, E_{11}^2)^T$, $E_{12} = (E_{12}^1, E_{12}^2)^T$, $E_{21} = (E_{21}^1, E_{21}^2)^T$ and $E_{22} = (E_{22}^1, E_{22}^2)^T$. Then,

$$\begin{aligned} w_{20}^1(\theta) &= E_{11}^1 \cos 2\nu_n x e^{2i\omega_n\theta} + E_{12}^1 e^{2i\omega_n\theta}, \\ w_{20}^2(\theta) &= E_{11}^2 \cos 2\nu_n x e^{2i\omega_n\theta} + E_{12}^2 e^{2i\omega_n\theta}, \\ w_{11}^1(\theta) &= E_{21}^1 \cos 2\nu_n x + E_{22}^1, \\ w_{11}^2(\theta) &= E_{21}^2 \cos 2\nu_n x + E_{22}^2. \end{aligned} \tag{6.16}$$

Note that

$$\int_0^l \cos^2 \nu_n x dx = \frac{l}{2}, \quad \int_0^l \sin \nu_n x \cos \nu_n x \sin 2\nu_n x dx = \int_0^l \cos^2 \nu_n x \cos 2\nu_n x dx = \frac{l}{4}.$$

This, together with (6.6) and (6.16), can simplify (6.9) as

$$\begin{aligned} g_{21} = \frac{1}{4} lc \Big\{ & D_{12}\mu_n \Big[2e^{-i\omega_n r_n^j} c_1(E_{21}^1 - 2E_{22}^1) + e^{i\omega_n r_n^j} \bar{c}_1(E_{11}^1 - 2E_{12}^1) - 4E_{21}^2 - 2E_{11}^2 e^{-2i\omega_n r_n^j} \Big] \\ & - [2(2 + \alpha c_1 + c_1 c_2 \gamma\beta)(E_{21}^1 + 2E_{22}^1) + (2 + \alpha\bar{c}_1 + \bar{c}_1 c_2 \gamma\beta)(E_{11}^1 + 2E_{12}^1)] \\ & - [2(\alpha + c_2\gamma(2c_1 + \beta))(E_{21}^2 + 2E_{22}^2) + (\alpha + c_2\gamma(2\bar{c}_1 + \beta))(E_{11}^2 + 2E_{12}^2)] \Big\}, \end{aligned} \tag{6.17}$$

and the first Lyapunov coefficient $c_1(0)$ now reads $c_1(0) = \frac{1}{2}\mathrm{Re}(g_{21})$.

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