

## THE BIFURCATION ANALYSIS OF TURING PATTERN FORMATION INDUCED BY DELAY AND DIFFUSION IN THE SCHNAKENBERG SYSTEM

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**ABSTRACT.** A delayed reaction-diffusion Schnakenberg system with Neumann boundary conditions is considered in the context of long range biological self-organisation dynamics incorporating gene expression delays. We perform a detailed stability and Hopf bifurcation analysis and derive conditions for determining the direction of bifurcation and the stability of the bifurcating periodic solution. The delay-diffusion driven instability of the unique spatially homogeneous steady state solution and the diffusion-driven instability of the spatially homogeneous periodic solution are investigated, with limited simulations to support our theoretical analysis. These studies analytically demonstrate that the modelling of gene expression time delays in Turing systems can eliminate or disrupt the formation of a stationary heterogeneous pattern in the Schnakenberg system.

**1. Introduction.** A core question in developmental self-organisation concerns resolving the mechanisms by which long range spatial patterning emerges from an essentially homogeneous system. In 1952, Turing [42] suggested that interacting chemicals at a homogeneous steady state can be destabilized by diffusion, as explored via a system of two coupled reaction-diffusion equations. This class of instability is usually referred to as the Turing instability or the diffusively-driven instability. This concept has been confirmed in chemical systems [16, 33] but awaits validation in biological systems, though numerous studies are indicative [5, 18, 19, 20, 22, 23, 24, 34, 32, 39].

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Over the years, Turing’s idea has attracted the attention of a great number of investigators and has been explored theoretically. As well as being applied in biological pattern formation via morphogenic systems, Turing’s idea has extended substantial influence over several fields including chemistry, economics, and semiconductor physics. Nevertheless, in the context of developmental biology, further complications arise when considering the fact that signaling morphogens induce each other’s production via signaling pathways, which ultimately requires intracellular dynamics, including gene expression. This, in turn, requires DNA transcription and mRNA translation, which takes time. Empirical estimates for the magnitudes of transcriptional and translational timescales are estimated to be in the range of 10 minutes to several hours [21, 41]. Recently, the impact of this delayed feedback due to the process of gene expression for the resulting morphogenic dynamics and its temporal behaviour has been intensively explored for Turing systems by modelling studies pursued mostly via computational simulations ([15, 36, 37, 38]), with the observation that that delayed dynamics can critically influence the prospect of robust patterns.

In particular, incorporating gene expression time delays into Turing models is most relevant for the self-enhancement production of a morphogen. Firstly, protein production by a cell requires gene expression, as observed in the context of morphogens by in-situ hybridisation which records mRNA levels, as illustrated in developmental self-organisation via Nodal and Lefty gene products in zebrafish mesendodermal induction [32]. Secondly, the extra-cellular regulation of such processes by an extracellular protein such as a morphogen requires signal transduction from the extra-cellular environment to the intra-cellular compartment and, for self-regulation, this signalling is also driven by the morphogen itself. Thus for Turing’s mechanism in the context of cell biology, the extra-cellular morphogen binds a receptor on the cell membrane, consequently inducing a target gene expression [1], which results in the production of another new morphogen protein. Hence feedback delays appear in the production terms of the reaction kinetics, which are directly formulated via the law of kinetic mass action including time delays; in addition, the diffusion terms are unchanged since the delays are induced by intracellular dynamics, which is not coupled to the extracellular morphogen transport [15].

Furthermore, bound ligands, such as morphogens in the current context, have the potential to be endocytosed by cells and this mechanism is contemplated to be a means of regulation, by attenuating receptor signalling [40]. Thus, in addition to exploring reversible ligand binding (RLB) systems where the bound morphogen is released back into the extracellular environment, we also consider models where the bound ligand, here morphogen protein, is internalised via endocytosis. This results in an altered set of delayed kinetics, as detailed and derived by Seirin and Gaffney [36], and are referred to as ligand internalisation (LI) models below. In particular we will study both representations of morphogen signalling dynamics to assess the impact of delays on the behaviour of Turing systems, predominantly exploiting mathematical tools in distinct contrast to previous simulation based studies.

**1.1. Main Equations and Objectives.** Throughout this paper we consider Schnakenberg kinetics [27, 35], firstly in the context of a reference RLB (reversible ligand binding) delayed model, whereby morphogen-regulated-morphogen-production proceeds via signal transduction driven by the reversible binding of ligand to the cell surface. The detailed model derivation can be found elsewhere [36] and, in summary,

this model is given by

$$\begin{aligned}\frac{\partial u(x, t)}{\partial t} &= d_1 \frac{\partial^2}{\partial x^2} u(x, t) + a - u(x, t) + u^2(x, t - \tau) v(x, t - \tau), \\ \frac{\partial v(x, t)}{\partial t} &= d_2 \frac{\partial^2}{\partial x^2} v(x, t) + b - u^2(x, t - \tau) v(x, t - \tau).\end{aligned}\tag{1}$$

Here  $x \in \Omega \subset \mathbf{R}$  is a one dimensional open bounded domain,  $t > 0$  with the initial conditions and Neumann boundary conditions respectively given by

$$u(x, t) = \phi(x, t) \geq 0, \quad v(x, t) = \varphi(x, t) \geq 0, \quad x \in \Omega \cup \partial\Omega, \quad t \in [-\tau, 0] \tag{2}$$

$$\partial_x u(x, t) = \partial_x v(x, t) = 0 \text{ on } x \in \partial\Omega, \quad t \geq 0. \tag{3}$$

In particular,  $u(x, t)$  and  $v(x, t)$  are concentrations of the activator and the inhibitor at  $(x, t)$  respectively, and  $a, b, d_1, d_2, \tau$  are all positive constants.

We also consider an alternative delayed model, based on ligand internalisation, and denoted as the LI model, which assumes that interactions proceed via morphogen internalisation to the cell interior, prior to the induction of the required signal transduction and downstream gene expression. As derived in [36], the LI model is given by

$$\begin{aligned}\frac{\partial u(x, t)}{\partial t} &= d_1 \frac{\partial^2}{\partial x^2} u(x, t) + a - u(x, t) - 2u^2(x, t)v(x, t) + 3u^2(x, t - \tau)v(x, t - \tau), \\ \frac{\partial v(x, t)}{\partial t} &= d_2 \frac{\partial^2}{\partial x^2} v(x, t) + b - u^2(x, t)v(x, t),\end{aligned}\tag{4}$$

together with the initial conditions and boundary conditions of equations (2), (3).

The model systems (1) and (4) have been formulated based on the incorporation of morphogen-induced-morphogen production delays in the Schnakenberg system [27, 35],

$$\begin{aligned}\frac{\partial u}{\partial t} &= d_1 \frac{\partial^2}{\partial x^2} u + a - u + u^2 v, \\ \frac{\partial v}{\partial t} &= d_2 \frac{\partial^2}{\partial x^2} v + b - u^2 v,\end{aligned}\tag{5}$$

which is recovered by setting  $\tau = 0$  in the system (1) or (4). Clearly, all these systems, (1)-(5), have a unique positive constant equilibrium solution  $E_* = (u_*, v_*)$ , where

$$u_* = a + b, \quad v_* = \frac{b}{(a + b)^2}.\tag{6}$$

Reaction-diffusion systems including time delays have been explored in many papers [6, 7, 8, 9, 13, 14, 17, 25, 28, 30], but there has not been an investigation at the analytic level of how delays impact Schnakenberg Turing pattern formations. In particular, it is important to assess how delays influence the symmetry breaking dynamics from a homogenous steady state, as well as investigating the interaction of delay, kinetics and diffusion in self-organisation dynamics. Hence in studying the above delayed Schnakenberg systems, our first objective is to prove the existence (or absence) of spatially homogeneous and non-homogenous periodic solutions resulting from Hopf bifurcations, by using Hopf bifurcation theory, center manifold theory and normal form methods. With the help of analytical observations, we also confirm the presence of temporally periodic solutions of both spatially homogeneous and heterogeneous solutions via numerical simulations when relevant. Our

final objective is to show that the interplay of delay and diffusion can induce the instability of the homogeneous solution leading to a stable stationary pattern and also to highlight cases where such an instability is not present.

**1.2. Definitions and Notations.** For clarity, we define the following instability properties. A solution of the system (1) or (4) is *unstable via a diffusion driven instability* if and only if the solution is stable in the system (1) or (4) when  $d_1 = d_2 = 0$  but unstable for suitably chosen  $d_1, d_2 > 0$ . A solution of the system (1) or (4) is *unstable via a delay-diffusion driven instability* if and only if the solution is stable when both  $d_1 = d_2 = 0, \tau \geq 0$  and  $d_1, d_2 > 0, \tau = 0$  but unstable for suitably chosen  $d_1, d_2 > 0$  and  $\tau > 0$ . Trivially, the *delay-diffusion driven instability* is a special case of *diffusion driven instability*.

Throughout the paper, we denote by  $\mathbb{N}$  the set of all the positive integers, and  $\mathbb{N}_0 = \mathbb{N} \cup \{0\}$ . We respectively use FDEs and PFDEs to denote Functional Differential Equations (no diffusion but a delay is present) and Partial Functional Differential Equations (which possess both diffusion and delay terms).

The remaining parts of the paper are structured as follows. In Section 2, a detailed stability and Hopf bifurcation analysis for FDEs is presented. In section 3, we perform a stability and Hopf bifurcation analysis of PFDEs; in particular, we consider the delay-diffusion driven instability of the unique constant equilibrium solution and the diffusion-driven instability of the spatially homogeneous periodic solution of PFDEs. In section 4, the conclusions of the study are presented.

## 2. Dynamics of FDEs.

**2.1. RLB model.** To examine the dynamics of the homogeneous steady state  $E_* = (u_*, v_*)$  for the system (1), we first consider the following FDEs of the main equations (1):

$$\begin{aligned}\frac{du(t)}{dt} &= a - u(t) + u^2(t - \tau)v(t - \tau), \\ \frac{dv(t)}{dt} &= b - u^2(t - \tau)v(t - \tau).\end{aligned}\tag{7}$$

The linearized equations of the system (7) evaluated at  $(u_*, v_*)$  are given by

$$\begin{aligned}\frac{du(t)}{dt} &= -u(t) + 2u_*v_*u(t - \tau) + u_*^2v(t - \tau), \\ \frac{dv(t)}{dt} &= -2u_*v_*u(t - \tau) - u_*^2v(t - \tau),\end{aligned}$$

and thus the characteristic equation of system (2.1) is given by

$$D(\lambda, \tau) = \lambda^2 + \lambda + [(u_*^2 - 2u_*v_*)\lambda + u_*^2]e^{-\lambda\tau} = 0.\tag{8}$$

Since  $D(0, \tau) = u_*^2 \neq 0$ ,  $\lambda = 0$  can never be a root of (8), so that the Bogdanov-Takens singularity will never arise in system (7) for all  $\tau > 0$ .

Furthermore, the characteristic equation (8) is a special case of the following general second-degree transcendental polynomial equation

$$D(\lambda, \tau) := \lambda^2 + p\lambda + r + (s\lambda + q)e^{-\lambda\tau} = 0,\tag{9}$$

which has been extensively studied (see, for example, [2, 4, 29, 31]). In order to prove the existence of Hopf bifurcation at  $E_*$  with bifurcation parameter  $\tau$ , we use Lemma 2.1 below. To proceed, let  $\lambda = i\omega$ , with  $\omega > 0$ , be the prospective

pure imaginary eigenvalues of the characteristic equation (9). Then, the direct substitution of  $D(i\omega, \tau) = 0$  yields

$$\omega^4 - (s^2 - p^2 + 2r)\omega^2 + r^2 - q^2 = 0. \quad (10)$$

Then under the following conditions, Lemma 2.1 [29] holds.

- ( $\mathcal{R}_1$ )  $p + s > 0$ ;
- ( $\mathcal{R}_2$ )  $q + r > 0$ ;
- ( $\mathcal{R}_3$ )  $s^2 - p^2 + 2r < 0$  and  $r^2 - q^2 > 0$ ;
- ( $\mathcal{R}_4$ )  $r^2 - q^2 < 0$ .

**Lemma 2.1.** ([29]) *For the eigenvalue problem (9), we have:*

1. If ( $\mathcal{R}_1$ ), ( $\mathcal{R}_2$ ) and ( $\mathcal{R}_3$ ) hold, then all roots of (9) have negative real parts for all  $\tau \geq 0$ ;
2. If ( $\mathcal{R}_1$ ), ( $\mathcal{R}_2$ ) and ( $\mathcal{R}_4$ ) hold, then
  - (a) when  $\tau \in [0, \tau_0)$ , all roots of (9) have negative real parts; when  $\tau \in (\tau_0, \infty]$ , (9) has at least one root with positive real part;
  - (b) when  $\tau = \tau_j, j \in \mathbb{N}_0$ , (9) has a pair of purely imaginary roots  $\pm i\omega_0$ ,

where

$$\omega_0 = \frac{\sqrt{2}}{2} \left( s^2 - p^2 + 2r + \sqrt{(s^2 - p^2 + 2r)^2 - 4(r^2 - q^2)} \right)^{1/2}, \quad (11)$$

$$\tau_j = \frac{1}{\omega_0} \arccos \left( \frac{q(\omega_0^2 - r) - ps\omega_0^2}{s^2\omega_0^2 + q^2} \right) + \frac{2j\pi}{\omega_0}, \quad j \in \mathbb{N}_0. \quad (12)$$

Now we apply Lemma 2.1 to our problem. Firstly, from (8), we have

$$p = 1, \quad r = 0, \quad s = u_*^2 - 2u_*v_*, \quad q = u_*^2. \quad (13)$$

Note that ( $\mathcal{R}_2$ ) and ( $\mathcal{R}_4$ ) hold since  $q + r = u_*^2 > 0$  and  $r^2 - q^2 = -u_*^4 < 0$ . On the other hand, in order that ( $\mathcal{R}_1$ ) is satisfied, we need the following assumption

$$(\mathbf{H}_1) \quad u_*^2 - 2u_*v_* > -1.$$

Hence Lemma 2.1-2 holds given the condition ( $\mathbf{H}_1$ ), and in addition, substituting (13) into (11), we obtain

$$\omega_0 := \frac{\sqrt{2}}{2} \left( (u_*^2 - 2u_*v_*)^2 - 1 + \sqrt{((u_*^2 - 2u_*v_*)^2 - 1)^2 + 4u_*^4} \right)^{1/2}.$$

Substituting  $\omega_0$  into (12), we obtain that the Hopf bifurcation points are given by

$$\tau_j = \frac{1}{\omega_0} \left( \arccos \frac{2u_*v_*\omega_0^2}{(u_*^2 - 2u_*v_*)^2\omega_0^2 + u_*^4} + 2j\pi \right), \quad j \in \mathbb{N}_0. \quad (14)$$

In addition, the following lemma ensures that the  $\tau_j$  become the Hopf bifurcation points by use of Lemma 2.1-2(ii).

**Lemma 2.2.** *Suppose that  $\tau_j$ , with  $j \in \mathbb{N}_0$ , are defined as in (14). Then,*

$$\left. \frac{d\operatorname{Re}\lambda(\tau)}{d\tau} \right|_{\tau=\tau_j} > 0$$

where  $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$  is a root of  $D(\lambda, \tau) = 0$  in (8) near  $\tau = \tau_j$  satisfying  $\alpha(\tau_j) = 0$ ,  $\omega(\tau_j) = \omega_0$ .

*Proof.* Since the eigenvalue problem (9) is a special case of problem 4.1 of [2], we use Theorem 4.1 of [2] to prove this Lemma. Following [2], we define,

$$S_j(\tau) = \tau - \frac{\theta(\tau) + 2j\pi}{\omega(\tau)}.$$

Here in the context of our eigenvalue problem (9), we have,

$$\theta(\tau) \equiv \arccos \frac{2u_*v_*\omega_0^2}{(u_*^2 - 2u_*v_*)^2\omega_0^2 + u_*^4}, \quad \omega(\tau) \equiv \omega_0,$$

which implies that  $(\theta(\tau) + 2j\pi)/\omega(\tau) = \tau_j$ , independent of  $\tau$ . Then, by Theorem 4.1 in [2], we have,

$$\text{sign} \left\{ \frac{d\text{Re}\lambda(\tau)}{d\tau} \Big|_{\tau=\tau_j} \right\} = \text{sign} \left\{ \frac{d\text{Re}S_j(\tau)}{d\tau} \Big|_{\tau=\tau_j} \right\}.$$

This completes the proof of the lemma.  $\square$

Consequently, we obtain the following theorem directly from Lemma 2.1(2(b)) and Lemma 2.2.

**Theorem 2.3.** *Assume that  $(\mathbf{H}_1)$  holds and let  $\tau_j$  be defined as in (14). Then,*

1.  $(u_*, v_*)$  is asymptotically stable in system (7) for all  $\tau \in [0, \tau_0]$ , and unstable for all  $\tau > \tau_0$ .
2. At  $\tau = \tau_j$ ,  $j \in \mathbb{N}_0$ , system (7) undergoes a Hopf bifurcation near  $(u_*, v_*)$ .

In what follows, we investigate the stability of the periodic solutions and consider the bifurcation direction of the local Hopf bifurcation associated with Theorem 2.3.

Let  $\tilde{u}(t) = u(\tau t) - u_*$ , and  $\tilde{v}(t) = v(\tau t) - v_*$ . Then, system (7) can be reduced to the following equations

$$\begin{aligned} \frac{d\tilde{u}(t)}{dt} &= \tau [a - (u(t) + u_*) + (u(t-1) + u_*)^2(v(t-1) + v_*)], \\ \frac{d\tilde{v}(t)}{dt} &= \tau [b - (u(t-1) + u_*)^2(v(t-1) + v_*)], \end{aligned} \quad (15)$$

where we drop the tildes of  $u$  and  $v$  for the sake of simplicity if this is unambiguous. Let  $U = (u, v)^T$ . Then, system (15) is equivalent to the following abstract form in  $C([-1, 0], \mathbf{R}^2)$ :

$$U_t = L(\tau)U_t + F(U_t, \tau), \quad (16)$$

where

$$\begin{aligned} L(\tau)\phi &:= \tau \begin{pmatrix} -\phi_1(0) + 2u_*v_*\phi_1(-1) + u_*^2\phi_2(-1) \\ -2u_*v_*\phi_1(-1) - u_*^2\phi_2(-1) \end{pmatrix}, \\ F(\phi, \tau) &:= \tau \begin{pmatrix} \sum_{i+j \geq 2} \frac{1}{i!j!} f_{ij}^{(1)} \phi_1^i(-1) \phi_2^j(-1) \\ \sum_{i+j \geq 2} \frac{1}{i!j!} f_{ij}^{(2)} \phi_1^i(-1) \phi_2^j(-1) \end{pmatrix}, \end{aligned} \quad (17)$$

with  $\phi = (\phi_1, \phi_2)^T \in C([-1, 0], \mathbf{R}^2)$ ,  $f^{(1)} = a - u + u^2v$ ,  $f^{(2)} = b - u^2v$ , and,

$$f_{ij}^{(1)} = \frac{\partial^{i+j} f^{(1)}}{\partial x^i \partial y^j} \Big|_{(u_*, v_*)}, \quad \text{and,} \quad f_{ij}^{(2)} = \frac{\partial^{i+j} f^{(2)}}{\partial x^i \partial y^j} \Big|_{(u_*, v_*)}, \quad i, j \in \mathbb{N}_0. \quad (18)$$

By the Rieze Representation Theorem, there exists a  $2 \times 2$  matrix function  $\eta(\theta, \tau)$ , with  $\theta \in [-1, 0]$ , whose elements are of bounded variation such that, for any  $\phi \in C([-1, 0], \mathbf{R}^2)$ ,

$$L(\tau)(\phi) = \int_{-1}^0 d\eta(\theta, \tau) \phi(\theta).$$

Actually, we can choose

$$\eta(\theta, \tau) = \tau \begin{pmatrix} -1 & 0 \\ 0 & 0 \end{pmatrix} \delta(\theta) - \tau \begin{pmatrix} 2u_*v_* & u_*^2 \\ -2u_*v_* & -u_*^2 \end{pmatrix} \delta(\theta + 1),$$

where  $\delta(\theta)$  is the Heaviside function. We Taylor expand  $F(\phi, \tau)$  as

$$F(\phi, \tau) = \frac{1}{2!} F_2(\phi, \tau) + \frac{1}{3!} F_3(\phi, \tau) + \cdots + o(|\phi|^4),$$

where  $F_n(\phi, \tau)$  takes the form

$$\frac{1}{n!} F_n(\phi, \tau) := \tau \begin{pmatrix} \sum_{i+j=n} \frac{1}{i!j!} f_{ij}^{(1)} \phi_1^i(-1) \phi_2^j(-1) \\ \sum_{i+j=n} \frac{1}{i!j!} f_{ij}^{(2)} \phi_1^i(-1) \phi_2^j(-1) \end{pmatrix}. \quad (19)$$

We next introduce a new parameter  $\mu = \tau - \tau_j$ , and then system (16) can be rewritten as

$$\frac{dU}{dt} = L(\tau_j)U_t + F_0(U_t, \mu), \quad (20)$$

where  $F_0(\phi, \mu) = L(\mu)(\phi) + F(\phi, \mu + \tau_j)$ .

For  $\phi \in C^1([-1, 0], \mathbf{R}^2)$  and  $\psi \in C^1([0, 1], (\mathbf{R}^2)^*)$ , we define the following bilinear inner product

$$\langle \psi(s), \phi(\theta) \rangle = \psi(0)\phi(0) - \int_{-1}^0 \int_{\xi=0}^{\xi=\theta} \psi(\xi - \theta) d\eta(0, \theta) \phi(\xi) d\xi.$$

Let  $\mathcal{A}$  be the infinitesimal generator of  $\frac{dU}{dt} = L(\tau_j)U_t$ ,  $\mathcal{A}$  and  $\mathcal{A}^*$  are adjoint operators, and  $\pm i\rho_j$  ( $\rho_j := \tau_j \omega_0$ ) are eigenvalues of  $\mathcal{A}$  and  $\mathcal{A}^*$ . We let  $\Lambda = \{-i\rho_j, i\rho_j\}$ . Then, by applying the formal adjoint theory for functional differential equations in [11],  $C := C([-1, 0], \mathbf{R}^2)$  can be decomposed by  $\Lambda$  as  $C = P \oplus Q$ , where  $P$  is the generalized eigenspace associated with  $\Lambda$ , and its dimension is two. We extend the space  $C([-1, 0], \mathbf{R}^2)$  to  $C([-1, 0], \mathbb{C}^2)$ .

Let  $\Phi$  and  $\Psi$  be the bases for  $P$  and  $P^*$  associated with the eigenvalues  $\pm i\rho_j$  of the adjoint equations, respectively. Note that  $\dot{\Phi} = \Phi B$ , where  $B = \text{diag}(i\rho_j, -i\rho_j)$ . We choose

$$\begin{aligned} \Phi(\theta) &= (\phi_1(\theta), \phi_2(\theta)) = \begin{pmatrix} e^{i\rho_j \theta} p_1, & e^{-i\rho_j \theta} \overline{p_1} \\ e^{i\rho_j \theta} p_2, & e^{-i\rho_j \theta} \overline{p_2} \end{pmatrix}, \quad \theta \in [-1, 0], \\ \Psi(s) &= \begin{pmatrix} \psi_1(s) \\ \psi_2(s) \end{pmatrix} = \begin{pmatrix} e^{-i\rho_j s} q_1, & e^{-i\rho_j s} q_2 \\ e^{i\rho_j s} \overline{q_1}, & e^{i\rho_j s} \overline{q_2} \end{pmatrix}, \quad s \in [0, 1], \end{aligned}$$

where

$$p_1 = 1, \quad p_2 = \frac{1 - 2u_*v_*e^{-i\rho_j} + \omega_0 i}{u_*^2 e^{-i\rho_j}}, \quad q_1 = \frac{1}{N}, \quad q_2 = \frac{1 - 2u_*v_*e^{-i\rho_j} - \omega_0 i}{Nu_*^2 e^{-i\rho_j}},$$

with

$$N = 1 + \frac{(1 - 2u_*v_*e^{-i\rho_j})^2 + \omega_0^2}{u_*^4 e^{-2i\rho_j}} + \frac{\tau_j(1 + \omega_0 i)[(u_*^2 + 2u_*v_*)e^{-i\rho_j} + \omega_0 i - 1]}{u_*^2 e^{-i\rho_j}}.$$

Clearly,  $(\Psi, \Phi) = I$ , the  $2 \times 2$  identity.

As in [11], we enlarge the phase space  $C$  by introducing  $BC$ , denoted to be the space of the functions from  $[-1, 0]$  to  $\mathbb{C}^2$  which are uniformly continuous on  $[-1, 0)$  and which have a jump discontinuity at 0. The projection  $\varphi| \rightarrow \Phi(\Psi, \varphi)$  of  $C([-1, 0], \mathbb{C}^2)$  upon  $P$ , associated with the decomposition  $C([-1, 0], \mathbb{C}^2) = P \oplus Q$ , is now replaced by  $\pi : BC \rightarrow P$ , such that  $\pi(\varphi + X_0\alpha) = \Phi(\Psi, \varphi) + \Psi(0)\alpha$ . By using the decomposition  $U_t = \Phi z(t) + y_t$ ,  $z \in \mathbb{C}^2$ ,  $y_t \in Q^1$  (see [11, 12]), we decompose system (20) as,

$$\begin{cases} \dot{z} = Bz + \Psi(0)F_0(\Phi z + y, \mu), \\ \dot{y} = \mathcal{A}|_{Q^1}y + (I - \pi)X_0F_0(\Phi z + y, \mu), \end{cases}$$

with  $F_0$  defined in (20), and  $X_0 = X_0(\theta)$  is given by

$$X_0(\theta) = \begin{cases} I, \theta = 0; \\ 0, -1 \leq \theta < 0. \end{cases}$$

In reducing to normal form, as in [12], we need to consider the following term:

$$\Psi(0)F_0(\Phi z + y, \mu) = \frac{1}{2!}f_2^1(z, y, \mu) + \frac{1}{3!}f_3^1(z, y, \mu) + h.o.t., \quad (21)$$

where  $f_j^1(z, y, \mu)$ , with  $j = 1, 2$ , are the homogeneous polynomials in  $(z, y, \mu)$  of degree  $j$  with coefficients in  $\mathbb{C}^2$  and  $h.o.t$  denotes higher order terms. Then, in a finite dimensional locally invariant manifold tangent to the invariant subspace  $P$  of the linearized system (15) at  $z = 0$ ,  $\mu = 0$ , the normal form of system (15) is given by

$$\dot{z} = Bz + \frac{1}{2!}g_2^1(z, 0, \mu) + \frac{1}{3!}g_3^1(z, 0, \mu) + h.o.t., \quad (22)$$

where  $g_2^1$  and  $g_3^1$  are the second and the cubic terms in  $(z, \mu)$ . As in [11, 12], we define,

$$M_j^1(p)(z, \mu) = D_z p(z, \mu)Bz - Bp(z, \mu), j \geq 2.$$

Therefore, we have

$$\text{Ker}(M_2^1) = \text{span} \left\{ \begin{pmatrix} z_1\mu \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ z_2\mu \end{pmatrix} \right\}.$$

From (21), we have

$$f_2^1(z, y, \mu) = \Psi(0)[2L(\mu)(\Phi z + y) + F_2(\Phi z + y, \tau_j)],$$

with  $F_2$  defined precisely in (19). A direct calculation shows that

$$f_2^1(z, 0, \mu) = \begin{pmatrix} 2A_1z_1\mu + 2A_2z_2\mu + a_{20}z_1^2 + 2a_{11}z_1z_2 + a_{02}z_2^2 \\ 2\bar{A}_2z_1\mu + 2\bar{A}_1z_2\mu + \bar{a}_{02}z_1^2 + 2\bar{a}_{11}z_1z_2 + \bar{a}_{20}z_2^2 \end{pmatrix} \quad (23)$$

where

$$\begin{aligned} A_1 &= (2u_*v_* + u_*^2p_2)(q_1 - q_2)e^{-i\rho_j} - q_1, \quad A_2 = (2u_*v_* + u_*^2\bar{p}_2)(q_1 - q_2)e^{i\rho_j} - q_1, \\ a_{20} &= \tau_j(q_1 - q_2)(f_{20}^{(1)} + 2f_{11}^{(1)}p_2)e^{-2i\rho_j}, \quad a_{11} = \tau_j(q_1 - q_2)[f_{20}^{(1)} + f_{11}^{(1)}(p_2 + \bar{p}_2)], \\ a_{02} &= \tau_j(q_1 - q_2)[f_{20}^{(1)} + 2f_{11}^{(1)}\bar{p}_2]e^{2i\rho_j}. \end{aligned} \quad (24)$$

Since by [12], we have  $\frac{1}{2}g_2^1(z, 0, \mu) = \frac{1}{2}\text{Proj}_{\text{Ker}(M_2^1)}f_2^1(z, 0, \mu)$ , then,

$$\frac{1}{2}g_2^1(z, 0, \mu) = \begin{pmatrix} A_1z_1\mu \\ \bar{A}_1z_2\mu \end{pmatrix}. \quad (25)$$



Next, we need to consider the cubic terms  $g_3^1(z, 0, \mu)$ . Since we concentrate on the properties of the local Hopf bifurcation, we only need to calculate the coefficient of  $z_1^2 z_2$  instead of computing the coefficients of the terms  $o(|z|\mu^2)$  which are irrelevant for the Hopf bifurcation.

Next we compute that cubic terms  $g_3^1(z, 0, \mu)$ . We note that

$$g_3^1(z, 0, \mu) \in \text{Ker}(M_3^1) = \text{span} \left\{ \begin{pmatrix} z_1^2 z_2 \\ 0 \end{pmatrix}, \begin{pmatrix} z_1 \mu^2 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ z_1 z_2^2 \end{pmatrix}, \begin{pmatrix} 0 \\ z_2 \mu^2 \end{pmatrix} \right\}.$$

Then, we have

$$\frac{1}{3!} g_3^1(z, 0, \mu) = \frac{1}{3!} \text{Proj}_{\text{Ker}(M_3^1)} \bar{f}_3^1(z, 0, \mu) = \frac{1}{3!} \text{Proj}_{\mathcal{M}} \bar{f}_3^1(z, 0, 0) + o(|z|\mu^2),$$

where

$$\mathcal{M} := \text{span} \left\{ \begin{pmatrix} z_1^2 z_2 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ z_1 z_2^2 \end{pmatrix} \right\},$$

and,

$$\bar{f}_3^1(z, 0, 0) = f_3^1(z, 0, 0) + \frac{3}{2} [(D_z f_2^1) U_2^1 - (D_z U_2^1) g_2^1] \big|_{(z, 0, 0)} + \frac{3}{2} [(D_y f_2^1) h] \big|_{(z, 0, 0)}, \quad (26)$$

which are the third order terms of the equation, obtained after computing the second order terms of the normal form. Here,  $U_2^1(z, 0)$  is the solution of the equation

$$M_2^1 U_2^1(z, 0) = P_{I,2}^1 f_2^1(z, 0, 0),$$

and  $h = (h^1, h^2)$  is a second order homogeneous polynomial in  $(z_1, z_2, \mu)$  with coefficients in  $Q^1$ . Since  $g_2^1(z, 0, 0) = (0, 0)^T$  by (25), we have,

$$\bar{f}_3^1(z, 0, 0) = f_3^1(z, 0, 0) + \frac{3}{2} [(D_z f_2^1) U_2^1] \big|_{(z, 0, 0)} + \frac{3}{2} [(D_y f_2^1) h] \big|_{(z, 0, 0)}. \quad (27)$$

Next, following [43], we compute  $\frac{1}{3!} g_3^1(z, 0, \mu)$  step by step:

**Step 1:** We compute  $f_3^1(z, 0, 0)$  and  $\frac{1}{3!} \text{Proj}_{\text{Ker}(M_3^1)} f_3^1(z, 0, 0)$ . From (21), we have

$$f_3^1(z, 0, 0) = \begin{pmatrix} a_{30} z_1^3 + 3a_{21} z_1^2 z_2 + 3a_{12} z_1 z_2^2 + a_{03} z_2^3 \\ \bar{a}_{03} z_1^3 + 3\bar{a}_{12} z_1^2 z_2 + 3\bar{a}_{21} z_1 z_2^2 + \bar{a}_{30} z_2^3 \end{pmatrix},$$

where

$$\begin{aligned} a_{30} &= 3\tau_j(q_1 - q_2)p_2 f_{21}^{(1)} e^{-3i\rho_j}, \quad a_{21} = \tau_j(q_1 - q_2)(\bar{p}_2 + 2p_2) f_{21}^{(1)} e^{-i\rho_j}, \\ a_{12} &= \tau_j(q_1 - q_2)(2\bar{p}_2 + p_2) f_{21}^{(1)} e^{i\rho_j}, \quad a_{03} = 3\tau_j(q_1 - q_2)\bar{p}_2 f_{21}^{(1)} e^{3i\rho_j}, \end{aligned} \quad (28)$$

from which we have

$$\text{Proj}_{\text{Ker}(M_3^1)} f_3^1(z, 0, 0) = \begin{pmatrix} 3a_{21} z_1^2 z_2 \\ 3\bar{a}_{21} z_1 z_2^2 \end{pmatrix}.$$

**Step 2:** We then calculate  $U_2^1(z, 0)$  and  $\text{Proj}_{\mathcal{M}} [(D_z f_2^1) U_2^1] \big|_{(z, 0, 0)}$ . Following [12], we take

$$U_2^1(z, 0) = (M_2^1)^{-1} P_{I,2}^1 f_2^1(z, 0, 0),$$

by which, the equation  $M_2^1 U_2^1(z, 0) = f_2^1(z, 0, 0)$  can be written via the following partial differential equations:

$$\begin{aligned} z_1 \frac{\partial u_1}{\partial z_1} - z_2 \frac{\partial u_1}{\partial z_2} - u_1 &= \frac{1}{i\rho_j} (a_{20} z_1^2 + 2a_{11} z_1 z_2 + a_{02} z_2^2), \\ z_1 \frac{\partial u_2}{\partial z_1} - z_2 \frac{\partial u_2}{\partial z_2} + u_2 &= \frac{1}{i\rho_j} (\bar{a}_{02} z_1^2 + 2\bar{a}_{11} z_1 z_2 + \bar{a}_{20} z_2^2). \end{aligned}$$

from which one can obtain that

$$U_2^1(z, 0) = \frac{1}{i\rho_j} \begin{pmatrix} a_{20}z_1^2 - 2a_{11}z_1z_2 - a_{02}z_2^2/3 \\ \bar{a}_{02}z_1^2 - 2\bar{a}_{11}z_1z_2 - \bar{a}_{20}z_2^2/3 \end{pmatrix}. \quad (29)$$

Thus, from (23) and (29), we have

$$\text{Proj}_{\mathcal{M}}[(D_z f_2^1)U_2^1]|_{(z,0,0)} = \frac{2}{i\rho_j} \begin{pmatrix} (\frac{1}{3}|a_{02}|^3 + 2|a_{11}|^2 - a_{11}a_{20})z_1^2z_2 \\ -(\frac{1}{3}|a_{02}|^3 + 2|a_{11}|^2 - \bar{a}_{11}\bar{a}_{20})z_1z_2^2 \end{pmatrix}.$$

**Step 3:** Finally, we calculate  $h(z, \mu)$  and  $\text{Proj}_{\mathcal{M}}[(D_y f_2^1)h(z, 0)]$ . Let

$$h = h(z_1, z_2, \mu) = h_{110}z_1z_2 + h_{101}z_1\mu + h_{011}z_2\mu + h_{200}z_1^2 + h_{020}z_2^2 + h_{002}\mu^2,$$

where  $h = (h_1, h_2)^T$ . Following [12], it follows that  $h = h(z_1, z_2, \mu)$  is the unique solution in  $V_2^3(Q^1)$  of

$$(M_2^2)h(z, \mu) = (I - \pi)X_0[2L(\mu)(\Phi z) + F_2(\Phi x, \tau_j)].$$

By the definition of  $M_2^2h$ , we have

$$\begin{aligned} M_2^2h(z, \mu) &= D_z h(z, \mu)Bz - A_{Q_1}h(z, \mu) \\ &= D_z h(z, \mu)Bz - \dot{h}(z, \mu) - X_0[L(\tau_j)h(z, \mu) - \dot{h}(z, \mu)(0)] \\ &= (I - \pi)X_0[2L(\mu)(\Phi z) + F_2(\Phi x, \tau_j)], \end{aligned}$$

where  $\dot{h}(z, \mu)$  stands for the derivative of  $h$  with respect to  $\theta$ , and  $h = h(z, 0)(\theta)$  solves the following equations:

$$\begin{aligned} \dot{h}(z, 0) - D_z h(z, 0)Bz &= \Phi\Psi(0)F_2(\phi z, \tau_j), \\ \dot{h}(z, 0)(0) - L(\tau_j)h &= F_2(\phi z, \tau_j). \end{aligned} \quad (30)$$

One can directly check that

$$f_2^1(z, y, 0) = \Psi(0)F_2(\phi z + y, \tau_j) = \tau_j(f_{20}^{(1)}t_1^2 + 2f_{11}^{(1)}t_1t_2) \begin{pmatrix} q_1 - q_2 \\ \bar{q}_1 - \bar{q}_2 \end{pmatrix},$$

where  $t_1 = z_1e^{-i\rho_j} + z_2e^{i\rho_j} + y_1(-1)$  and  $t_2 = p_2z_1e^{-i\rho_j} + \bar{p}_2z_2e^{i\rho_j} + y_2(-1)$ .

Then, it follows that

$$[(D_y f_2^1)h]|_{(z,0,0)} = \tau_j(s_1h^1(-1) + s_2h^2(-1)) \begin{pmatrix} q_1 - q_2 \\ \bar{q}_1 - \bar{q}_2 \end{pmatrix},$$

where

$$s_1 = 2f_{20}^{(1)}(z_1e^{i\rho_j} + z_2e^{-i\rho_j}) + 2f_{11}^{(1)}(p_2z_1e^{-i\rho_j} + \bar{p}_2z_2e^{i\rho_j}), s_2 = 2f_{11}^{(1)}(z_1e^{i\rho_j} + z_2e^{-i\rho_j}).$$

Then, we have

$$\text{Proj}_{\mathcal{M}}[(D_y f_2^1)h]|_{(z,0,0)} = \begin{pmatrix} 2c_3z_1^2z_2 \\ 2\bar{c}_3z_1z_2^2 \end{pmatrix},$$

where

$$\begin{aligned} c_3 &= 2\tau_j(q_1 - q_2)[f_{20}^{(1)}e^{i\rho_j}h_{110}^{(1)}(-1) + f_{20}^{(1)}e^{-i\rho_j}h_{200}^{(1)}(-1) + f_{11}^{(1)}p_2e^{-i\rho_j}h_{110}^{(1)}(-1) \\ &\quad + f_{11}^{(1)}\bar{p}_2e^{i\rho_j}h_{200}^{(1)}(-1) + f_{11}^{(1)}e^{i\rho_j}h_{110}^{(2)}(-1) + f_{11}^{(1)}e^{-i\rho_j}h_{200}^{(2)}(-1)]. \end{aligned} \quad (31)$$

In order to compute  $c_3$ , we need to calculate  $h_{110}(\theta)$  and  $h_{200}(\theta)$ . From (23) and (30), it follows that,  $h_{110} = (h_{110}^1, h_{110}^2)^T$  is the solution of,

$$\dot{h}_{110}(\theta) = (\Phi_1, \Phi_2) \begin{pmatrix} 2a_{11} \\ 2\bar{a}_{11} \end{pmatrix}, \quad \dot{h}_{110}(0) - L(\tau_j)h_{110} = \tau_j \begin{pmatrix} a_1 \\ -a_1 \end{pmatrix},$$

where  $a_1 = f_{20}^{(1)} + 2f_{11}^{(1)}(p_2 + \bar{p}_2)$ . Furthermore,  $h_{200} = (h_{200}^1, h_{200}^2)^T$  is the solution of,

$$\dot{h}_{200} - 2i\rho_j h_{200} = (\Phi_1, \Phi_2) \begin{pmatrix} a_{20} \\ \bar{a}_{02} \end{pmatrix}, \quad \dot{h}_{200}(0) - L(\tau_j)h_{200} = \tau_j \begin{pmatrix} a_2 \\ -a_2 \end{pmatrix},$$

where  $a_2 = (f_{20}^{(1)} + 2f_{11}^{(1)}p_2)e^{-2i\rho_j}$ .

Solving for  $h_{110}(\theta)$  and  $h_{200}(\theta)$ , we have

$$\begin{aligned} h_{110}(\theta) &= \frac{2}{i\rho_j}(a_{11}e^{i\rho_j\theta}(1, p_2)^T - \bar{a}_{11}e^{-i\rho_j\theta}(1, \bar{p}_2)^T) + c_1, \\ h_{200}(\theta) &= -\frac{1}{i\rho_j}(a_{20}e^{i\rho_j\theta}(1, p_2)^T + \frac{1}{3}\bar{a}_{02}e^{-i\rho_j\theta}(1, \bar{p}_2)^T) + e^{2i\rho_j\theta}c_2, \end{aligned} \quad (32)$$

where  $c_1 = (c_1^{(1)}, c_1^{(2)})^T$ ,  $c_2 = (c_2^{(1)}, c_2^{(2)})^T$ , and,

$$\begin{aligned} c_1^{(1)} &= -\frac{2}{i\rho_j}(a_{11} - \bar{a}_{11}) - \frac{2}{\tau_k}[a_{11}(1 + p_2) + \bar{a}_{11}(1 + \bar{p}_2)], \\ c_1^{(2)} &= -\frac{2}{\tau_j u_*^2}(a_{11}p_2 + \bar{a}_{11}\bar{p}_2) - \frac{2}{i\rho_j}(e^{-i\rho_j}a_{11}p_2 - e^{i\rho_j}\bar{a}_{11}\bar{p}_2) \\ &\quad - \frac{1}{i\rho_j u_*^2}[4u_*v_*(e^{-i\rho_j}a_{11} - e^{i\rho_j}\bar{a}_{11}) + i\rho_j(2u_*v_*c_1^{(1)} + a_1)], \end{aligned}$$

and  $c_2^{(1)}, c_2^{(2)}$  solve the following equations,

$$\begin{pmatrix} 2i\rho_j h_{200}^{(1)}(0) + a_{20} + \bar{a}_{02} \\ 2i\rho_j h_{200}^{(2)}(0) + a_{20}p_2 + \bar{a}_{02}\bar{p}_2 \end{pmatrix} = \tau_j \begin{pmatrix} -h_{200}^{(1)}(0) + 2u_*v_*h_{200}^{(1)}(-1) + u_*^2h_{200}^{(2)}(-1) + a_2 \\ -2u_*v_*h_{200}^{(1)}(-1) - u_*^2h_{200}^{(2)}(-1) - a_2 \end{pmatrix}, \quad (33)$$

with  $h_{200}^{(1)}(\theta)$  and  $h_{200}^{(2)}(\theta)$  the components of  $h_{200}(\theta)$  defined in (32).

Now we are in position to obtain

$$\frac{1}{3!}g_3^1(x, 0, 0) = \begin{pmatrix} A_3 z_1^2 z_2 \\ A_3 z_1 z_2^2 \end{pmatrix}, \quad (34)$$

$$A_3 = \frac{1}{2i\rho_j} \left( \frac{1}{3}|a_{02}|^2 + 2|a_{11}|^2 - a_{11}a_{20} \right) + \frac{1}{2}(a_{21} + c_3). \quad (35)$$

By (25) and (34), the normal form (22) now has the form of,

$$\dot{z} = Bz + \begin{pmatrix} \frac{A_1 z_1 \mu}{A_1 z_2 \mu} \end{pmatrix} + \begin{pmatrix} \frac{A_3 z_1^2 z_2}{A_3 z_1 z_2^2} \end{pmatrix} + o(|z|\mu^2 + |z|^4). \quad (36)$$

Then the normal form (36) relative to  $P$  can be written in real coordinates  $(x, y)$  through the change of variables  $z_1 = x - iy$ ,  $z_2 = x + iy$ . With the subsequent use of polar coordinates  $(r, \xi)$ ,  $x = r \cos \xi$ ,  $y = r \sin \xi$ , the normal form becomes

$$\begin{cases} \dot{r} = c_1 \mu r + c_2 r^3 + o(\mu^2 r + |(r, \mu)^4|), \\ \dot{\xi} = -\rho_j + |(r, \mu)|. \end{cases}$$

where  $c_1 = \text{Re}\{A_1\}$  and  $c_2 = \text{Re}\{A_3\}$ .

From [3], it follows that, the sign of  $c_1 c_2$  determines the direction of the bifurcation and the sign of  $c_2$  determines the stability of the nontrivial periodic solution bifurcating from Hopf bifurcation on the center manifold.

So far, we have the following theorem for the local properties of the Hopf bifurcation we obtained in Theorem 2.3.

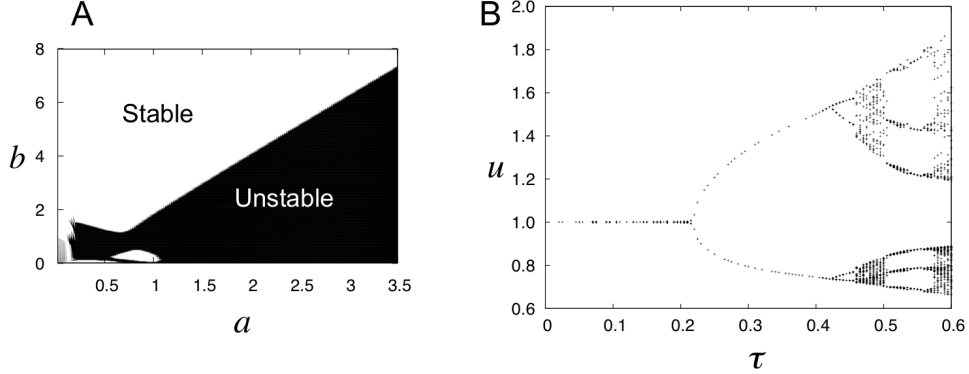


FIGURE 1. **A:** The parameter space of  $(a, b)$  which satisfies Theorem 2.4. In the white region, we will have a stable periodic solution for the FDEs. **B:** A bifurcation diagram for  $\tau$  for the FDEs. This has been plotted using the value of  $u(t)$  at which  $v(t) = v_*$ . The parameter values  $(a, b) = (0.1, 0.9)$  have been chosen and the system exhibits the first Hopf bifurcation at approximately  $\tau_0 = 0.2171$ . For  $\tau \in [0, \tau_0)$ ,  $E_* = (1.0, 0.9)$  is always asymptotically stable, bifurcating first at  $\tau_0$  then exhibiting subsequent bifurcations with frequency doubling prior to chaotic dynamics.

**Theorem 2.4.** Suppose that  $(H_1)$  holds and let  $\tau_j$  be defined as in (14). Define  $c_1 = \text{Re}\{A_1\}$  and  $c_2 = \text{Re}\{A_3\}$ , with  $A_1$  and  $A_3$  defined as in (24) and (35) respectively. If  $c_1 \neq 0$ , then system (7) exhibits a generic Hopf bifurcation near  $(u_*, v_*)$  when  $\tau = \tau_j$ . Moreover,

1. If  $c_1 < 0$  ( $> 0$ , respectively), there exists a unique nontrivial periodic orbit  $(u(t), v(t)) = (p_1(t), p_2(t))$  with the period close to  $2\pi/\omega_0$  near  $(u_*, v_*)$  when  $\tau > \tau_j$  ( $\tau < \tau_j$  respectively) and no nontrivial periodic orbit for  $\tau < \tau_j$  ( $\tau > \tau_j$  respectively);
2. At  $\tau = \tau_0$ , the nontrivial periodic orbit  $(p_1(t), p_2(t))$  is orbitally stable if  $c_2 < 0$  and unstable if  $c_2 > 0$ ; Here  $c_2$  is evaluated by setting  $A_3 = A_3|_{\rho_j = \rho_0}$ .
3. At  $\tau = \tau_j$ , with  $j \geq 1$ , the nontrivial periodic orbit  $(p_1(t), p_2(t))$  is unstable since at  $\tau = \tau_j$ , the eigenvalue problem (9) has at least one root with positive real part.

**Remark 1.** In order to confirm the existence of parameter space satisfying Theorem 2.4, we show the result numerically in Figure 1.

**2.2. LI model.** To examine the dynamics of the homogeneous steady state  $E_* = (u_*, v_*)$  for the system (4), we now consider the following FDEs of the main equations (4):

$$\begin{aligned} \frac{du(t)}{dt} &= a - u(t) - 2u^2(t)v(t) + 3u^2(t-\tau)v(t-\tau), \\ \frac{dv(t)}{dt} &= b - u^2(t)v(t). \end{aligned} \tag{37}$$

The linearized system of (37) at  $E_*$  is simply given by

$$\begin{aligned}\frac{du(t)}{dt} &= -u(t) - 4u_*v_*u(t) + 6u_*v_*u(t-\tau) - 2u_*^2v(t) + 3u_*^2v(t-\tau), \\ \frac{dv(t)}{dt} &= -2u_*v_*u(t) - u_*^2v(t),\end{aligned}$$

and thus the characteristic equation is

$$D(\lambda, \tau) := \lambda^2 + p\lambda + r + (s\lambda + q)e^{-\lambda\tau} = 0,$$

where

$$p = u_*^2 + 4u_*v_* + 1, \quad r = u_*^2, \quad s = -6u_*v_*, \quad q = 0. \quad (38)$$

**Theorem 2.5.** Assume that  $(H_1)$  and

$$(H_3) \quad u_*^2 + 2u_*v_* < 1$$

hold. Then  $E_*$  is always asymptotically stable for all  $\tau \geq 0$  so that there is never a Hopf bifurcation in system (37).

*Proof.* By (38), we have

$$p + s = u_*^2 - 2u_*v_* + 1, \quad r + q = u_*^2, \quad r^2 - q^2 = u_*^4,$$

and

$$s^2 - p^2 + 2r = 8u_*v_*(2u_*v_* - u_*^2 - 1) + (2u_*v_* - u_*^2)(2u_*v_* + u_*^2) - 1.$$

Under  $(H_1)$  and  $(H_3)$ , we have  $s^2 - p^2 + 2r < 0 + 2u_*v_* + u_*^2 - 1 < 0$ . Thus, according to Lemma 2.1 (1), it follows that  $E_*$  is always asymptotically stable for all  $\tau \geq 0$ , so that there is never a Hopf bifurcation in system (37).  $\square$

### 3. Dynamics of PFDEs.

**3.1. RLB model.** In this section, we consider the dynamics of the main system (1). By the scaling of  $x \rightarrow x/|\Omega|$ ,  $d = d_2/|\Omega|^2$  and  $\varepsilon = d_1/d_2$ , the system (1) is rewritten as follows:

$$\begin{cases} \frac{\partial}{\partial t}u(x, t) = \varepsilon d \frac{\partial^2}{\partial x^2}u(x, t) + a - u(x, t) + u^2(x, t - \tau)v(x, t - \tau), & x \in (0, 1), \quad t > 0 \\ \frac{\partial}{\partial t}v(x, t) = d \frac{\partial^2}{\partial x^2}v(x, t) + b - u^2(x, t - \tau)v(x, t - \tau), & x \in (0, 1), \quad t > 0 \\ u_x(x, t) = v_x(x, t) = 0 & \text{at } x = 0, 1, \quad t \geq 0 \\ u(x, t) = \phi(x, t) \geq 0, v(x, t) = \varphi(x, t) \geq 0, & (x, t) \in [0, 1] \times [-\tau, 0]. \end{cases} \quad (39)$$

Below, we state the main results on the stability and Hopf bifurcation at  $E_* = (u_*, v_*)$  for system (39). First, we linearize (39) about  $(u_*, v_*)$ , which gives:

$$\begin{cases} u_t(x, t) = \varepsilon d u_{xx}(x, t) - u(x, t) + 2u_*v_*u(t - \tau) + u_*^2v(t - \tau), & x \in (0, 1), \quad t > 0, \\ v_t(x, t) = d v_{xx}(x, t) - 2u_*v_*u(t - \tau) + u_*^2v(t - \tau), & x \in (0, 1), \quad t > 0, \\ u_x(x, t) = v_x(x, t) = 0, & \text{at } x = 0, 1, \quad t \geq 0, \\ u(x, t) = \phi(x, t) - u_*, v(x, t) = \varphi(x, t) - v_*, & (x, t) \in [0, 1] \times [-\tau, 0]. \end{cases} \quad (40)$$

From direct calculation, by using a Fourier expansion and substituting  $(u(x, t), v(x, t))^t = \exp(\lambda t) \cos(k\pi x)(c_1, c_2)^t$ ,  $(k \in \mathbb{N})$  into the linearized system (40), we obtain the characteristic equation

$$D_k(\lambda, \tau) := \lambda^2 + p_k \lambda + r_k + (s_k \lambda + q_k)e^{-\lambda \tau} = 0, \quad k \in \mathbb{N}_0 \quad (41)$$

where

$$\begin{aligned} p_k &= (\varepsilon + 1)dk^2\pi^2 + 1, \quad r_k = \varepsilon d^2(k^2\pi^2)^2 + dk^2\pi^2, \\ s_k &= u_*^2 - 2u_*v_*, \quad q_k = (\varepsilon u_*^2 - 2u_*v_*)dk^2\pi^2 + u_*^2. \end{aligned} \quad (42)$$

Now, given the conditions specified below we prove that a stability of  $E_*$  and the existence of a Hopf bifurcation due to delay-dynamics.

**Theorem 3.1.** *Assume that*

$$(\mathbf{H}_2) \quad |u_*^2 - 2u_*v_*| < 1.$$

*Then, we have the following results.*

(1): *If  $0 < \varepsilon < 1$  and*

$$d > \frac{1}{(1 - \varepsilon)\pi^2}, \quad (43)$$

*then both the Turing instability and Turing bifurcation do not occur for all  $\tau \geq 0$ , whilst the Hopf bifurcation can only occur with  $\tau = \tau_j$ , where the latter is precisely defined in (14).*

(2): *If  $\varepsilon \geq 1$  and*

$$0 < d < d_k = \frac{\sqrt{1 + \varepsilon u_*^2} - 1}{\varepsilon \pi^2 k^2} \text{ for some fixed } k \in \mathbb{N},$$

*then  $E_*$  is asymptotically stable for all  $\tau \in [0, \tau_{inf})$ , and unstable for all  $\tau > \tau_{inf}$  where*

$$\tau_{inf} = \inf_{k \geq 0, j \geq 0} \{\tau_j^k\},$$

*and*

$$\tau_j^k := \frac{1}{\omega_k} \arccos \left( \frac{q_k(\omega_k^2 - r_k) - p_k s_k \omega_k^2}{s_k^2 \omega_k^2 + q_k^2} \right) + \frac{2j\pi}{\omega_k}, \quad j \in \mathbb{N}_0 \quad (44)$$

$$\omega_k := \frac{1}{\sqrt{2}} (s_k^2 - p_k^2 + 2r_k + \sqrt{(s_k^2 - p_k^2 + 2r_k)^2 - 4(r_k^2 - q_k^2)})^{1/2}, \quad k \in \mathbb{N}_0. \quad (45)$$

*Furthermore, the system (39) undergoes a Hopf bifurcation around  $E_*$  at  $\tau = \tau_j^k$ .*

*Proof.* For the proof, we mainly use Lemma 2.1. Firstly, under  $(\mathbf{H}_2)$ , we have

$$p_k + s_k = (\varepsilon + 1)dk^2\pi^2 + u_*^2 - 2u_*v_* + 1 > 0$$

and

$$s_k^2 - p_k^2 + 2r_k = -[(\varepsilon^2 + 1)d^2(k^2\pi^2)^2 + 2\varepsilon dk^2\pi^2] + (u_*^2 - 2u_*v_*)^2 - 1 < 0.$$

On the one hand, from  $(\mathbf{H}_2)$ , we have  $-2u_*v_* > -u_*^2 - 1$  and thus

$$\begin{aligned} r_k + q_k &= \varepsilon d^2(k^2\pi^2)^2 + (\varepsilon u_*^2 - 2u_*v_* + 1)dk^2\pi^2 + u_*^2 \\ &\geq \varepsilon d^2(k^2\pi^2)^2 + (\varepsilon u_*^2 - 1 - u_*^2 + 1)dk^2\pi^2 + u_*^2 \\ &= \varepsilon d^2(k^2\pi^2)^2 + \{(\varepsilon - 1)dk^2\pi^2 + 1\}u_*^2. \end{aligned}$$

Clearly,  $r_k + q_k > 0$  for either  $\varepsilon \geq 1$ , or

$$0 < \varepsilon < 1 \text{ and } d \geq \frac{1}{(1 - \varepsilon)\pi^2}. \quad (46)$$

Since now we know the sign of  $r_k + q_k$ , it will be sufficient to determine the sign of  $r_k - q_k$  in order to specify the sign of  $r_k^2 - q_k^2$ . From  $(\mathbf{H}_2)$ , we have  $2u_*v_* > u_*^2 - 1$  and thus

$$\begin{aligned} r_k - q_k &= \varepsilon d^2 (k^2 \pi^2)^2 - (\varepsilon u_*^2 - 2u_*v_* - 1)dk^2 \pi^2 - u_*^2 \\ &> \varepsilon d^2 (k^2 \pi^2)^2 - (\varepsilon u_*^2 + 1 - u_*^2 - 1)dk^2 \pi^2 - u_*^2 \\ &= \varepsilon d^2 (k^2 \pi^2)^2 + \{(1 - \varepsilon)dk^2 \pi^2 - 1\}u_*^2. \end{aligned}$$

Thus, given (46), we have  $r_k - q_k > 0$  for  $k \geq 1$ , so that  $(\mathcal{R}_3)$  is satisfied. Note that the condition (46) is not dependent on  $k$ . Hence from Lemma 2.1(1), all roots of the characteristic equation (41) have negative real parts for all  $k (\geq 1)$  and all  $\tau \geq 0$ , so that both the Turing instability and Hopf bifurcation do not occur. However, when  $k = 0$ , according to Theorem 2.3, system (39) will undergo a Hopf bifurcation at  $\tau = \tau_j$  near  $(u_*, v_*)$ .

On the other hand, from  $(\mathbf{H}_2)$ , we also have  $2u_*v_* < 1 + u_*^2$  and thus

$$\begin{aligned} r_k - q_k &= \varepsilon d^2 (k^2 \pi^2)^2 - (\varepsilon u_*^2 - 2u_*v_* - 1)dk^2 \pi^2 - u_*^2 \\ &< \varepsilon d^2 (k^2 \pi^2)^2 - (\varepsilon u_*^2 - u_*^2 - 2)dk^2 \pi^2 - u_*^2 \\ &= (1 - \varepsilon)u_*^2 dk^2 \pi^2 + \varepsilon d^2 k^4 \pi^4 + 2dk^2 \pi^2 - u_*^2 \\ &= (1 - \varepsilon)u_*^2 dk^2 \pi^2 + (\varepsilon k^2 \pi^2 d + 1 + \sqrt{1 + \varepsilon u_*^2})(\varepsilon k^2 \pi^2 d + 1 - \sqrt{1 + \varepsilon u_*^2}). \end{aligned}$$

Thus we have  $r_k - q_k < 0$  when  $d < (-1 + \sqrt{1 + \varepsilon u_*^2})/(\varepsilon k^2 \pi^2)$  for some given  $k > 0$  and  $\varepsilon \geq 1$ . Note here that in fact,  $r_k - q_k < 0$  for any  $d \geq 0$  when  $k = 0$ . This condition satisfies  $(\mathcal{R}_4)$ , so that we complete the proof for (2) from Lemma 2.1(2) and Lemma 2.2.  $\square$

From the proof of Theorem 3.1 (1), we know that the stability of  $E_*$  is determined by the sign of the real eigenvalue of mode  $k = 0$ , which in fact corresponds to the FDE case. Thus we have only a Hopf bifurcation at  $E_*$  for some large  $\tau$ , and a homogeneous periodic solution under the given conditions. A simulation example is shown in Figure 2A. Further note that our simulation observations also suggest that when  $d \ll 1$  with  $\varepsilon < 1$ , we still have a homogeneous periodic solution though an asymmetric periodic solution appears initially as shown in Figure 2B.

In the following corollary, we consider the case of  $\tau_{inf} = \tau_0$  so that there does not exist a diffusion-driven Hopf bifurcation around  $E_*$ .

**Corollary 1.** *(When  $\tau_{inf} = \tau_0$ , there is no diffusively driven Hopf bifurcation.) Suppose that  $u_* = 2v_*$  holds. Then, for  $\varepsilon$  sufficiently close to 1, we have  $\tau_{inf} = \tau_0$  so that there does not exist a Hopf bifurcation induced by diffusion around  $E_*$  for all  $\tau > 0$ .*

*Proof.* By  $u_* = 2v_*$ , it follows that  $(\mathbf{H}_2)$  holds. Now we shall show that  $\tau_{inf} = \tau_0$ . First let us consider the special case when  $\varepsilon = 1$ , and then consider the small perturbation of  $\varepsilon = 1$ . At  $\varepsilon = 1$ , we have,

$$p_k = 2dk^2 \pi^2 + 1, r_k = d^2 (k^2 \pi^2)^2 + dk^2 \pi^2, s_k \equiv 0, q_k \equiv u_*^2, \text{ and } p_k^2 - 4r_k = 1. \quad (47)$$

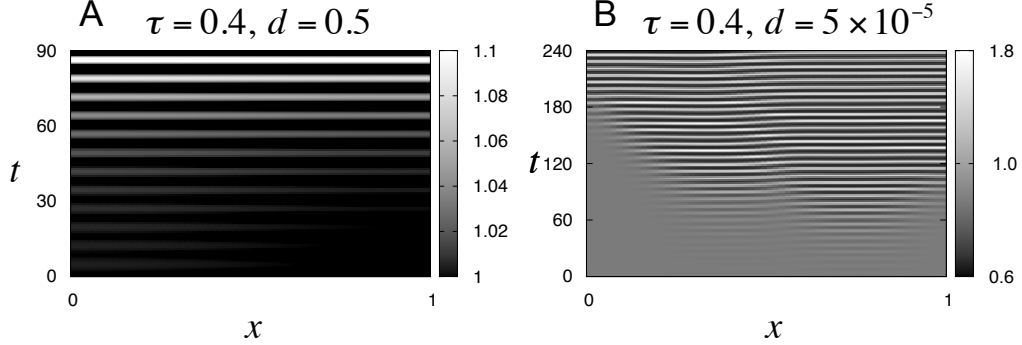


FIGURE 2. A homogeneous periodic solution for  $u$  with  $0 < \varepsilon < 1$ . The parameter values for the simulations are given by  $a = 0.1, b = 0.9, \varepsilon = 0.1$ . A: A plot of  $u$  for  $d = 0.5$ , when equation (43) is satisfied. B: A plot of  $u$  for  $d = 5 \times 10^{-5}$ , when equation (43) is not satisfied.

For  $k \geq 1$ , we rewrite  $r_k^2 - q_k^2$  as:

$$r_k^2 - q_k^2 = (r_k + q_k)(d^2(k^2\pi^2)^2 + dk^2\pi^2 - u_*^2) = (r_k + q_k)(d\pi^2k^2 - d_-)(d\pi^2k^2 - d_+),$$

where

$$d_- := \frac{1 - \sqrt{4u_*^2 + 1}}{2} < 0, \quad d_+ := \frac{1 + \sqrt{4u_*^2 + 1}}{2} > 0.$$

Let  $k_0 \in \mathbb{N}$ , be such that  $d\pi^2(k_0 - 1)^2 - d_+ < 0$  but  $d\pi^2k_0^2 - d_+ > 0$ .

Substituting (47) into (45), we have, for  $k \in [0, k_0), j \in \mathbb{N}_0$ ,

$$\begin{aligned} 2\omega_k^2 &= \sqrt{(2dk^2\pi^2 + 1)^2 + 4u_*^4} - (2d^2(k^2\pi^2)^2 + 2dk^2\pi^2 + 1) \\ 2(\omega_k^2 - r_k) &= \sqrt{(2dk^2\pi^2 + 1)^2 + 4u_*^4} - (2dk^2\pi^2 + 1)^2. \end{aligned} \quad (48)$$

Motivated by [7], we define

$$x := \sqrt{(2dk^2\pi^2 + 1)^2 + 4u_*^4}; \quad (49)$$

clearly,  $x \geq \sqrt{4u_*^4 + 1}$ . Solving  $dk^2\pi^2$  from (49) and substituting it into (48), we can obtain,

$$\omega_k^2 = (-x^2 + 2x + 4u_*^4 - 1)/4, \quad \omega_k^2 - r_k = (-x^2 + x + 4u_*^4)/2. \quad (50)$$

Substituting (50) into (44), we have, for  $k \in [0, k_0), j \in \mathbb{N}_0$ ,

$$\tau_j^k|_{\varepsilon=1} = \rho(x) := \frac{2 \arccos((-x^2 + x + 4u_*^4)/(2u_*^2) + 2j\pi)}{\sqrt{-x^2 + 2x + 4u_*^4 - 1}}, \quad (51)$$

which is well defined when  $\sqrt{4u_*^4 + 1} \leq x < 1 + 2u_*^2$ . It is easy to verify that for any  $\sqrt{4u_*^4 + 1} \leq x_1 < x_2 < 1 + 2u_*^2$ , we have  $\rho(x_1) < \rho(x_2)$ . Thus, for fixed  $j \in \mathbb{N}_0$ , we have

$$\tau_j^{k+1} > \tau_j^k, \quad \text{with } k = 0, 1, \dots, k_0 - 1. \quad (52)$$

Thus, we have  $\tau_0 = \tau_{inf}$ . By the definition of  $\tau_j^k$  in (44),  $\tau_j^k$  is continuously dependent on the parameter  $\varepsilon$ . Thus, we can conclude that,  $\tau_{inf} = \tau_0$  still holds even for  $\varepsilon$  sufficiently close to 1.  $\square$



**Remark 2.**

1. From the result of Theorem 3.1(1), there are no spatial patterns around  $E_*$  for large  $d$  given  $(\mathbf{H}_2)$  and  $\varepsilon < 1$ . This result also implies that if diffusion is sufficiently large (or if the spatial length is sufficiently small), Turing patterns never occur even for large delays.
2. If  $q_k + r_k < 0$ , that is  $\mathcal{R}_2$  fails, and  $(\mathbf{H}_1)$  holds, then  $E_*$  is always stable for the system (7) $_{\tau=0}$  but unstable for any  $(d, \varepsilon)$  with the system (39) $_{\tau=0}$ . Thus we have both possibility of a Turing instability and Hopf bifurcation for the system (39) $_{\tau>0}$  within the parameter space  $q_k + r_k < 0$ . In fact, the numerical results of [37] show that the both cases actually occur. In the case that (39) $_{\tau=0}$  has a Hopf bifurcation, we still have a Hopf bifurcation for  $E_*$  in the system (39) $_{\tau>0}$  in accordance with [4].
3. If  $\tau_{inf} < \tau_0$  holds, then the instability of homogeneous steady state  $E_*$  for  $\tau \in (\tau_{inf}, \tau_0)$  is induced by a joint influence of both diffusion and delay and we have a delay-diffusion driven instability. If either  $\tau = 0$  or  $d = 0$ ,  $E_*$  is always asymptotically stable.
4. In the case of  $\tau = 0$ ,  $E_*$  is asymptotically stable for any  $d$  and  $\varepsilon$  in system (39) given the conditions  $(\mathbf{H}_2)$  and either  $\varepsilon \geq 1$  or the condition (46). Thus the diffusion driven instability never occurs without delays under these conditions, and we cannot expect a Turing pattern, that is a non-constant stationary solution, induced by the destabilization of symmetric breaking by diffusion effects around  $E_*$ . From Theorem 3.1, we also know that Turing patterns do not occur for all  $\tau$  when  $\varepsilon < 1$  given a sufficiently large diffusion coefficient. This implies that even though the two diffusion coefficients have different scales, pattern formation will fail on small spatial length scales.
5. Let us consider the case of  $0 < \varepsilon < 1$  and  $d < 1/(1 - \varepsilon)\pi^2$  given the condition  $(\mathbf{H}_2)$ . In fact, this parameter space includes both regions of the Turing space and non-Turing space when  $\tau = 0$ . When the diffusion rate is in the Turing space, we have observed the Turing instability failure with a large delay (see [37]). In contrast, we may have symmetric breaking triggered by the interplay of diffusion and delay, in the alternative case.

**3.2. LI model.** In what follows, we show that the LI system, (4), has neither a Hopf bifurcation nor a Turing bifurcation for any  $\tau \geq 0$ . The rescaled LI system is given by

$$\begin{cases} \frac{\partial}{\partial t} u(x, t) = \varepsilon d \frac{\partial^2}{\partial x^2} u(x, t) + a - u(x, t) \\ \quad - 2u^2(x, t)v(x, t) + 3u^2(x, t - \tau)v(x, t - \tau), & x \in (0, 1), t > 0 \\ \frac{\partial}{\partial t} v(x, t) = d \frac{\partial^2}{\partial x^2} v(x, t) + b - u^2(x, t)v(x, t), & x \in (0, 1), t > 0 \\ u_x(x, t) = v_x(x, t) = 0 & \text{at } x = 0, 1, t \geq 0 \\ u(x, t) = \phi(x, t) \geq 0, v(x, t) = \varphi(x, t) \geq 0, & (x, t) \in [0, 1] \times [-\tau, 0]. \end{cases} \quad (53)$$

The linearized system of (53) at  $E_*$  is simply given by

$$\begin{cases} u_t(x, t) = \varepsilon du_{xx}(x, t) - u(x, t) - 4u_*v_*u(x, t) \\ \quad + 6u_*v_*u(x, t - \tau) - 2u_*^2v(x, t) + 3u_*^2v(x, t - \tau), & x \in (0, 1), t > 0, \\ v_t(x, t) = dv_{xx}(x, t) - 2u_*v_*u(x, t) - u_*^2v(x, t), & x \in (0, 1), t > 0, \\ u_x(x, t) = v_x(x, t) = 0, & \text{at } x = 0, 1, t \geq 0, \\ u(x, t) = \phi(x, t) - u_*, v(x, t) = \varphi(x, t) - v_*, & (x, t) \in [0, 1] \times [-\tau, 0], \end{cases} \quad (54)$$

and thus the characteristic equation (41) is

$$\begin{aligned} p_k &= (\varepsilon + 1)d\pi^2k^2 + u_*^2 + 4u_*v_* + 1, \\ r_k &= (d\pi^2k^2 + u_*^2)(\varepsilon\pi^2k^2 + 4u_*v_* + 1) - 4u_*^3v_*, \\ s_k &= -6u_*v_*, \quad q_k = -6u_*v_*d\pi^2k^2. \end{aligned}$$

We have the following theorem which holds for all  $\varepsilon(\geq 0)$  and  $d(\geq 0)$ .

**Theorem 3.2.** Assume that  $(\mathbf{H}_1)$  and

$$(\mathbf{H}_3) \quad u_*^2 + 2u_*v_* < 1.$$

Then  $E_*$  is always asymptotically stable for all  $\tau \geq 0$  so that there is never a Turing bifurcation nor a Hopf bifurcation for the PFDEs (53).

*Proof.* We use Lemma 2.1(1) for the proof. Firstly, from  $(\mathbf{H}_1)$ , we obtain

$$(\mathcal{R}_1) \quad p_k + s_k = (\varepsilon + 1)d\pi^2k^2 + u_*^2 - 2u_*v_* + 1 > 0,$$

and from  $(\mathbf{H}_3)$ ,

$$\begin{aligned} (\mathcal{R}_2) \quad r_k + q_k &= \varepsilon d(\pi^2k^2)^2 + (1 - 2u_*v_*)d\pi^2k^2 + u_*^2\varepsilon\pi^2k^2 + u_*^2 \\ &\geq \varepsilon d(\pi^2k^2)^2 + u_*^2d\pi^2k^2 + u_*^2\varepsilon\pi^2k^2 + u_*^2 > 0. \end{aligned}$$

Since  $r_k - q_k = \varepsilon d(\pi^2k^2)^2 + (10u_*v_* + 1)d\pi^2k^2 + u_*^2 + u_*^2\varepsilon\pi^2k^2 > 0$ , we easily obtain  $r_k^2 - q_k^2 = (r_k + q_k)(r_k - q_k) > 0$ . Now if we show  $s_k^2 - p_k^2 + 2r_k < 0$ , then the proof is completed.

$$\begin{aligned} s_k^2 - p_k^2 + 2r_k &= 36u_*^2v_*^2 + 2\{(d\pi^2k^2 + u_*^2)(\varepsilon\pi^2k^2 + 4u_*v_* + 1) - 4u_*^3v_*\} \\ &\quad - (d\pi^2k^2 + u_*^2)^2 - (\varepsilon\pi^2k^2 + 4u_*v_* + 1)^2 - 2(d\pi^2k^2 + u_*^2)(\varepsilon\pi^2k^2 + 4u_*v_* + 1) \\ &= 36u_*^2v_*^2 - 8u_*^3v_* - (d\pi^2k^2 + u_*^2)^2 - (\varepsilon\pi^2k^2 + 4u_*v_* + 1)^2 \\ &= 20u_*^2v_*^2 - 8u_*^3v_* - u_*^4 - 8u_*v_* - 1 - d\pi^2k^2\{\varepsilon^2d\pi^2k^2 + d\pi^2k^2 + 2u_*^2 + 8u_*v_* + 2\} \\ &\leq (16u_*^2v_*^2 - 8u_*^3v_* - 8u_*v_*) + (4u_*^2v_*^2 - u_*^4) - 1 \\ &= 8u_*v_*(2u_*v_* - u_*^2 - 1) + (2u_*v_* - u_*^2)(2u_*v_* + u_*^2) - 1 \\ &< 0 + 2u_*v_* + u_*^2 - 1 \end{aligned} \quad (55)$$

$$< 0. \quad (56)$$

Here, the first term of (55) is from  $(\mathbf{H}_1)$ , the second term is from  $(\mathbf{H}_3)$ , and the final inequality, (56), is from  $(\mathbf{H}_3)$ . Thus the condition,  $(\mathcal{R}_3)$ , is satisfied. Note that all the above calculations hold for all  $\varepsilon(\geq 0)$  and  $d(\geq 0)$ , or  $k \geq 0$ . Hence, all roots of the characteristic equation, (41), have negative real parts for all  $\tau \geq 0$  and  $k \geq 0$  from Lemma 2.1, so that  $E_*$  is always asymptotically stable.  $\square$

**Remark 3.**

1. If  $(\mathbf{H}_1)$  and  $(\mathbf{H}_3)$  hold, then  $(\mathbf{H}_2)$  holds. Thus we have the same conclusion, Theorem 3.1, under  $(\mathbf{H}_1)$  and  $(\mathbf{H}_3)$ .
2. Theorem 3.2 implies that there does not exist a Hopf bifurcation about  $E_*$  for the parameter space which is not included in Turing instability space when  $\tau = 0$ . Further, in [15], it has been shown that there is never a Hopf bifurcation at a point where the Turing instability occurs. Thus we conjecture that a Hopf bifurcation never occurs for all  $\tau$  in LI PFDEs.
3. Note that the above results holds within the parameter space where the Turing instability does not occur in the absence of delay, with  $\tau = 0$  regardless of  $d$  and  $\varepsilon$ , because  $r_k + p_k > 0$ .

4. **Concluding Remarks.** By using bifurcation theory, normal form methods and center manifold theory, we performed a detailed stability and Hopf bifurcation analysis for the delayed reaction diffusion system associated with Schnakenberg kinetics, given the inclusion of gene expression delays for morphogen-induced-morphogen production. The results further allow an analytical basis for understanding how delayed biological self organization models behave and the parameter space for when bifurcations occur.

In particular, for ligand internalization models where morphogens binding to a cell are internalised, the analysis demonstrates the absence of bifurcations, and thus no spatial organisation, emerges in the system dynamics. Hence, in generality, extensive ligand internalization appears to antagonize the induction of pattern formation in the context of gene-expression delayed Schnakenberg representations of the Turing instability.

In contrast, for reversible ligand binding models, the existence of spatially homogeneous and non-homogeneous periodic solutions was proved and temporally periodic solutions of both spatially homogeneous and heterogeneous solutions were confirmed by numerical simulations. In particular, a Turing instability can occur but for a sufficiently large delay, a Hopf instability can also be excited, leading to oscillations. Thus, spatial patterning without oscillations requires parameter fine tuning, in that the kinetic scales have to be tuned relative the delay size.

Furthermore, this analytical study provides analytical-level insight into the resulting Turing space of parameters; for instance it especially emphasises that the emergence of a Hopf bifurcation and thus oscillations with increasing delay is general for Schnakenberg kinetics with reversible ligand binding. Similarly, it demonstrates that extensive ligand internalisation antagonizes biological patterning in extensive generality for Schnakenberg models of the Turing instability. In particular, such observations are not restricted to a few parameter sets, a necessary limitation of simulation studies.

However, of course, the observation that the formation of heterogeneous steady patterning in the Schnakenberg model of the Turing instability is often inhibited by gene expression time delays does not necessarily entail that one should not expect to see a Turing instability in biological systems. Indeed, and in contrast, the empirical evidence is indicative of such an instability [5, 18, 19, 20, 22, 23, 24, 34, 32, 39], even if molecular level details remain to be confirmed. Firstly, it may be that different kinetics are more robust to the inclusion of gene expression time-delays, motivating our future analytical studies of gene-expression delays for other models used to represent the Turing instability, such as the Gierer-Meinhardt system. More generally, the observations of this paper do not apply for the prospect of a generalized Turing

instability resulting from more than two interacting morphogens plus a host of other prospective biological complexities. Indeed it is of curious interest that Turing did not immediately restrict his prospective mechanism to just two interacting chemical species in his original paper [42], whilst the observed tendency for two species models to fail to exhibit the Turing instability given gene expression time delays indicates that Turing’s generality may yet prove important. Hence, the prospects of how gene expression time delays may impact on, or be compensated by, larger prospective biological self-organisation systems is still very much an uncharted area for theoretical study, both in terms of simulation and analysis, even though such systems are experimentally reported, at least to a limited extent, as illustrated with feather and hair patterning [10, 26].

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