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Time Delay-Induced Instabilities and Hopf Bifurcations in General Reaction–Diffusion Systems

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Abstract The distribution of the roots of a second order transcendental polynomial is analyzed, and it is used for solving the purely imaginary eigenvalue of a transcendental characteristic equation with two transcendental terms. The results are applied to the stability and associated Hopf bifurcation of a constant equilibrium of a general reaction–diffusion system or a system of ordinary differential equations with delay effects. Examples from biochemical reaction and predator–prey models are analyzed using the new techniques.

Keywords Second order transcendental polynomial · Characteristic equation · Reaction–diffusion · Stability · Hopf bifurcation

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1 Introduction

Differential equation models have been used to describe the rate of change of quantities in the natural world. Such changes often do not respond immediately to the

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variation of the environment or the interacting species, but rather respond to the variations in the past. Hence time delays can often be incorporated into the model to make it more realistic. Since the pioneering effort of Hutchinson (1948), delay differential equations have been used in the models of population biology, medical treatment, molecular and cellular biology, chemical and biological pattern formation, engineering and control theory (Culshaw and Ruan 2000; Erneux 2009; Herz et al. 1996; Kolmanovskii and Myshkis 1999; May 1973; Murray 2002; Nelson and Perelson 2002; Perelson and Nelson 1999; Lee et al. 2010). The mathematical theory of the delay differential equations, or more generally functional differential equations, has been developed and documented (Diekmann et al. 1995; Erneux 2009; Hale and Lunel 1993; Kuang 1993; Smith 2011; Wu 1996).

Central to the theory of delay differential equations is the stability of an equilibrium under the effect of the time delay. The linear stability of an equilibrium is determined by the characteristic equation, whose roots are the eigenvalues of the corresponding linearized equation. In general for a delay differential equation in the form of

$$\dot{x}(t) = f\big(x(t), x(t-\tau_1), \dots, x(t-\tau_k)\big), \tag{1.1}$$

where $x \in \mathbb{R}^n$, $\tau_i > 0$ for $1 \le i \le k$, the characteristic equation takes the form

$$\det\left(\lambda I - A_0 - \sum_{j=1}^{m} A_j \mathrm{e}^{-\lambda\tau_j}\right) = 0, \tag{1.2}$$

where A_j $(0 \le j \le m)$ is an $n \times n$ constant matrix (Hale and Lunel 1993; Ruan 2001). However, due to the complexity of the analysis, most previous work only considers the cases of $n \le 3$ and $m \le 2$. For the case of $n = 1$ and $m \ge 2$ (scalar equations with two or more delays), the corresponding characteristic equation and associated stability/bifurcation problems have been studied in Bélair and Campbell (1994), Hale and Huang (1993), Li et al. (1999), Ruan and Wei (2003), and Wei and Yuan (2005). For the case of $n = 2$ and $m = 2$, some special cases of a planar system with two delays have been considered in Shayer and Campbell (2000), Song et al. (2007), and Wei and Ruan (1999). A special case with $m = 2$ and $n = 6$ was studied in Fan et al. (2010). The cases of $m = 1$ and $n \le 2$ were studied in Cooke and Grossman (1982). A third order equation with $n = 3$ and $m = 1$ was considered in Ruan and Wei (2001) and Song and Wei (2004). The analysis of distribution of the roots of (1.2) is based on that as the parameters vary, the sum of the order of the roots of (1.2) on the open right half plane can change only if a root appears on or crosses the imaginary axis, which was proved in Ruan and Wei (2003).

In general, most work has been about a characteristic equation with only one transcendental term, that is, an equation in the form of

$$P(\lambda) + \mathrm{e}^{-\lambda\tau} Q(\lambda) = 0, \tag{1.3}$$

where P and Q are polynomials of λ, and the degree of P is greater than that of Q. A characteristic equation in the form of (1.3) appears in many important applications.

For example, scalar equations with a single delay, planar systems with only one delay term, planar systems in the form of

$$\begin{cases}\dot{x}(t) = f(x(t), y(t-\tau_1)),\\ \dot{y}(t) = g(x(t-\tau_2), y(t)),\end{cases} \tag{1.4}$$

and planar systems in the form of

$$\begin{cases}\dot{x}(t) = f(x(t), y(t)) \pm k_1 g(x(t-\tau), y(t-\tau)),\\ \dot{y}(t) = h(x(t), y(t)) \pm k_2 g(x(t-\tau), y(t-\tau)).\end{cases} \tag{1.5}$$

Notice that (1.4) includes the case of Kolmogorov-type predator–prey systems with two delays (Ruan 2001, 2009), and (1.5) includes the cases of competitive, mutualistic, and predator–prey models with symmetric delayed interaction terms. A model of an autocatalytic chemical reaction is also in the form (1.5); for example, the well-known Schnakenberg model, Gray–Scott model, and Brusellator model (Murray 2002). On the other hand, for a system with two independent delays, the characteristic equation could have two transcendental terms:

$$P(\lambda) + \mathrm{e}^{-\lambda\tau_1} Q_1(\lambda) + \mathrm{e}^{-\lambda\tau_2} Q_2(\lambda) = 0, \tag{1.6}$$

where P, Q_1, Q_2 are polynomials of λ. In some cases, (1.6) can be dealt by fixing one delay and varying the other, or solving a relation between the two delays which produces the instability condition (see Bélair and Campbell 1994; Wei and Yuan 2005) and many others. In all the cases above, usually solving the parameter values for the purely imaginary eigenvalues $\pm \mathrm{i}\omega$ is reduced to a quadratic equation (or essentially a quadratic equation) of ω, hence the critical parameter values can be explicitly solved.

However, for a general planar system with just one delay in the form of

$$\begin{cases}\dot{x}(t) = f\big(x(t), y(t), x(t-\tau), y(t-\tau)\big),\\ \dot{y}(t) = g\big(x(t), y(t), x(t-\tau), y(t-\tau)\big),\end{cases} \tag{1.7}$$

the corresponding characteristic equation would contain a second order transcendental term so it takes the form

$$\lambda^2 + a\lambda + b + (c\lambda + d)\mathrm{e}^{-\lambda\tau} + h\mathrm{e}^{-2\lambda\tau} = 0. \tag{1.8}$$

For (1.8), the case of $c = d = 0$ or $h = 0$ has been analyzed by many authors for delayed differential equations (see e.g. Bodnar et al. 2011; Cooke and Grossman 1982; Hassard et al. 1981; Ruan 2001, 2009). Recently, the joint effect of delay and diffusion on population models and chemical reaction models have been studied extensively, and interesting phenomena, such as Turing instability, Hopf bifurcation, Turing–Hopf bifurcation, can occur. For example, spatially homogeneous periodic orbits or spatially nonhomogeneous periodic orbits can arise though Hopf bifurcation (Faria 2001; Hu and Li 2010; Zuo and Wei 2011); the relation between Turing instability and Hopf bifurcation was considered in Hadeler and Ruan (2007), and it was shown that a periodic oscillation can be achieved via increasing the delay or changing the diffusion rates; Hopf bifurcation of a model for which the characteristic equation depending on time delay was considered in Crauste et al. (2008); stability/instability in delayed chemical reaction models have been investigated in Dutta and Ray (2008), Ghosh (2011), Ghosh et al. (2010), and Sen et al. (2008). For most of these work, the corresponding characteristic equations also contain one transcendental term as they are in the form (1.8) but $c = d = 0$ or $h = 0$.

In this paper, we analyze the quadratic transcendental equation (1.8) with a more general assumption:

(A) At least one of c and d is not zero, and h is not zero.

Note that the case of $a = b = 0$ was analyzed in Hu et al. (2009). The characteristic equation around an equilibrium in many models takes the form in (1.8) with the assumption (A) (see for example Kyrychko et al. 2009; Lee et al. 2010; Sen et al. 2008). We will show the conditions under which the equilibrium is stable or unstable, and we will also discuss related bifurcation problems. Moreover we will consider the same questions for reaction–diffusion systems with delay. The main significance of our work is to provide a systematic way of analyzing the change of stability for the roots of characteristic equation in the form of (1.8), and a detailed step by step method is shown here for models from any applications. Also the new analysis for (1.8) can be applied to *any* planar system with one delay, no matter how the delay terms appearing in the two equations, which removes the special symmetry of delay terms in previous work on equations like (1.4) or (1.5).

Our main idea is to convert the problem of solving purely imaginary eigenvalues $\pm i\omega$ of (1.8) into an (essentially) quartic polynomial of ω, and then analyze the roots of quartic polynomial to obtain related results. Due to the nature of the quartic polynomial, the explicit form of ω and associated bifurcation values are not easy to obtain (contrast to the quadratic polynomial case). But we provide a complete route of analyzing the roots of the quartic characteristic equation, and conditions on the coefficients of characteristic equation or original linearized equations which lead to instability of equilibrium.

In Sect. 2, we analyze the roots of the transcendental polynomial in the form (1.8), and we apply the results in Sect. 2 to reaction–diffusion systems with delay in Sect. 3. We consider several specific examples in Sect. 4 to showcase our analysis. Some concluding remarks and suggestions of future work are given in Sect. 5.

This work is partly motivated by the recently proposed Gierer–Meinhardt system with gene expression time delays (see (4.8)) which was proposed in Lee et al. (2010). The delayed terms in the system do not appear symmetrically as in (1.5), hence the corresponding characteristic equation cannot be reduced to a quadratic algebraic equation as many other previously studied cases. This inspires the studies of a characteristic equation in the form of (1.8). In Sect. 4 we discuss the stability and Hopf bifurcations of the equilibrium in the Leslie–Gower predator–prey system (Chen et al. 2012), and Gierer–Meinhardt pattern formation systems with gene expression time delays (Lee et al. 2010).

We use $\mathbb{C}$, $\mathbb{R}$, $\mathbb{N}$ to denote the set of complex numbers, real numbers and natural numbers, respectively. We have $\mathbb{N}_0 = \mathbb{N} \cup \{0\}$, $\mathbb{R}^+ = \{x \in \mathbb{R} : x > 0\}$, and $\mathbb{C}^- = \{x = x_1 + ix_2 \in \mathbb{C} : x_1 < 0\}$.

2 A Second Order Transcendental Polynomial

In this section we consider the distribution of the roots of the second order transcendental polynomial equation (1.8) where the parameters a, b, c, d, h, and τ are real numbers and c, d, and h satisfy assumption (A). Throughout this section we fix a, b, c, d, h, and use τ as a parameter.

2.1 Solving the Transcendental Polynomial Equation

We look for parameter values so that the characteristic equation (1.8) has purely imaginary roots. If $\pm \mathrm{i}\omega$ $(\omega > 0)$ is a pair of roots of (1.8), then we have

$$-\omega^2 + a\omega\mathrm{i} + b + (c\omega\mathrm{i} + d)\mathrm{e}^{-\mathrm{i}\omega\tau} + h\mathrm{e}^{-2\mathrm{i}\omega\tau} = 0.$$

If $\frac{\omega\tau}{2} \neq \frac{\pi}{2} + j\pi$, $j \in \mathbb{Z}$, then let $\theta = \tan\frac{\omega\tau}{2}$, and we have $\mathrm{e}^{-\mathrm{i}\omega\tau} = \frac{1-\mathrm{i}\theta}{1+\mathrm{i}\theta}$. Separating the real and imaginary parts, we find that θ satisfies

$$\begin{cases} (\omega^2 - b + d - h)\theta^2 - 2a\omega\theta = \omega^2 - b - d - h, \\ (c\omega - a\omega)\theta^2 + (-2\omega^2 + 2b - 2h)\theta = -(a\omega + c\omega). \end{cases} \tag{2.1}$$

Denote

$$M = \begin{pmatrix} \omega^2 - b + d - h & -2a\omega & \omega^2 - b - d - h \\ (c-a)\omega & -2\omega^2 + 2b - 2h & -(c+a)\omega \end{pmatrix},$$

$$M_1 = \begin{pmatrix} \omega^2 - b + d - h & -2a\omega \\ (c-a)\omega & -2\omega^2 + 2b - 2h \end{pmatrix},$$

$$M_2 = \begin{pmatrix} \omega^2 - b - d - h & -2a\omega \\ -(c+a)\omega & -2\omega^2 + 2b - 2h \end{pmatrix},$$

and

$$M_3 = \begin{pmatrix} \omega^2 - b + d - h & \omega^2 - b - d - h \\ (c-a)\omega & -(c+a)\omega \end{pmatrix}.$$

We define

$$D(\omega) = \det(M_1), \qquad E(\omega) = \det(M_2), \quad \text{and} \quad F(\omega) = \det(M_3). \tag{2.2}$$

If $D(\omega) \neq 0$, then we can solve from (2.1) that

$$\theta^2 = \frac{E(\omega)}{D(\omega)}, \quad \theta = \frac{F(\omega)}{D(\omega)}, \tag{2.3}$$

and from (2.3), we find that ω satisfies

$$D(\omega)E(\omega) = F(\omega)^2. \tag{2.4}$$

If $D(\omega) = 0$, in order to make sure the solvability of (2.1) for θ, then we have

$$E(\omega) = F(\omega) = 0,$$

and hence ω satisfies (2.4) in this case as well. Simplifying (2.4), we conclude that ω satisfies a polynomial equation with degree 8:

$$\omega^8 + s_1\omega^6 + s_2\omega^4 + s_3\omega^2 + s_4 = 0, \tag{2.5}$$

where

$$\begin{aligned} s_1 &= 2a^2 - 4b - c^2, \\ s_2 &= 6b^2 - 2h^2 - 4ba^2 - d^2 + a^4 - a^2c^2 + 2c^2b + 2hc^2, \\ s_3 &= 2d^2b - a^2d^2 - 4b^3 + 2b^2a^2 - c^2b^2 - 2bc^2h \\ &\quad + 4acdh - 2d^2h + 4bh^2 - 2h^2a^2 - c^2h^2, \\ s_4 &= b^4 - d^2b^2 - 2b^2h^2 + 2bd^2h - d^2h^2 + h^4 = (b-h)^2\big[-d^2 + (b+h)^2\big], \end{aligned} \tag{2.6}$$

and ω^2 is a positive root of

$$z^4 + s_1z^3 + s_2z^2 + s_3z + s_4 = 0. \tag{2.7}$$

If $\omega\tau = \frac{\pi}{2} + j\pi$, $j \in \mathbb{Z}$, then $a = c$, $\omega^2 = b + h - d$, and hence $D(\omega) = F(\omega) = 0$. So ω^2 is still a positive root of (2.7). From the above analysis we have the following lemma:

Lemma 2.1 *If* $\pm i\omega$ $(\omega > 0)$ *is a pair of purely imaginary roots of* (1.8), *then* ω^2 *is a positive root of* (2.7) *where* s_i $(1 \le i \le 4)$ *are given in* (2.6).

The converse of Lemma 2.1 does not always hold. In the following three subsections, we shall examine under what conditions, the converse of Lemma 2.1 holds. That is, if (2.7) has a positive root ω^2, then (1.8) has a pair of purely imaginary roots.

2.2 Non-degenerate Case

Suppose that (2.7) has a positive root ω^2 $(\omega > 0)$ and it is called non-degenerate if $D(\omega) \neq 0$, otherwise it is degenerate. For the non-degenerate case, we have the following simple result regarding the purely imaginary roots of (1.8):

Lemma 2.2 *If* (2.7) *has a positive root* ω_N^2 $(\omega_N > 0)$ *and* $D(\omega_N) \neq 0$, *then* (2.1) *has a unique real root* $\theta_N = \frac{F(\omega_N)}{D(\omega_N)}$ *when* $\omega = \omega_N$. *Hence* (1.8) *has a pair of purely imaginary roots* $\pm i\omega_N$ *when*

$$\tau = \tau_N^j = \frac{2\arctan\theta_N + 2j\pi}{\omega_N}, \quad j \in \mathbb{Z}. \tag{2.8}$$

Proof If $D(\omega_N) \neq 0$, then $\frac{E(\omega_N)}{D(\omega_N)} = (\frac{F(\omega_N)}{D(\omega_N)})^2$. Consequently (2.1) has a real root when $\omega = \omega_N$, and hence (1.8) has a pair of purely imaginary roots $\pm i\omega_N$ when $\tau = \tau_N^j$ is defined as in (2.8). □

We notice that if the root ω^2 of (2.7) and the root θ of (2.1) are solved, then the corresponding τ-value is always solved from the relation:

$$\tau = \tau^j = \frac{2\arctan\theta + 2j\pi}{\omega}, \quad j \in \mathbb{Z}, \tag{2.9}$$

since $\theta = \tan\frac{\omega\tau}{2}$. If τ is restricted to be positive (delay value), then $j \in \mathbb{N}$ or $j \in \mathbb{N} \cup \{0\}$ depending on θ. There will be one exception given in Lemma 2.5, which is a limit case in the sense that $\theta = \infty$, $\omega\tau = \pi$, and $\arctan\theta = \pi/2$.

The non-degeneracy condition $D(\omega) \neq 0$ is satisfied for generic parameter values. Indeed we can prove the following more specific result to guarantee the non-degeneracy:

Lemma 2.3 *Suppose that* (2.7) *has a positive root* ω^2 *for some* $\omega > 0$. *Assume that* $c \neq 0$, *and one of the following is satisfied*:

$$b + h \leq \frac{ad}{c}, \quad \textit{or} \tag{2.10}$$

$$\frac{d}{c}\left(2h - \frac{ad}{c}\right) - a\left(b + h - \frac{ad}{c}\right) \neq 0, \quad \textit{and} \quad a \neq c. \tag{2.11}$$

Then $D(\omega) \neq 0$.

Proof Assume that $c \neq 0$. If $D(\omega) = 0$, then $F(\omega) = 0$, which leads to

$$\omega^2 = b + h - \frac{ad}{c}. \tag{2.12}$$

If (2.10) is satisfied, then $\omega^2 \leq 0$, which is a contradiction to $\omega > 0$. If (2.11) is satisfied, then we substitute (2.12) into equation $D(\omega) = 0$, and we will have

$$(a - c)\left[\frac{d}{c}\left(2h - \frac{ad}{c}\right) - a\left(b + h - \frac{ad}{c}\right)\right] = 0,$$

which is a contradiction to (2.11). □

We remark that Lemma 2.3 is very useful in applications. For example, it will be used in each example in Sect. 4. Next we consider the case of $c = 0$:

Lemma 2.4 *Suppose that* (2.7) *has a positive root* ω^2 *for some* $\omega > 0$. *Assume that* $c = 0$, *and one of the following assumptions holds*:

$$a \neq 0, \quad \textit{or} \tag{2.13}$$

$$a = 0, \quad b + h - d \leq 0, \quad \textit{and} \quad b - h \leq 0. \tag{2.14}$$

Then $D(\omega) \neq 0$.

Table 1 Summary of non-degenerate case. Here ω_N^2 is a positive root of (2.7) such that $D(\omega_N) \neq 0$

c	Parameter condition	θ	Results
$c \neq 0$	$b+h \leq \frac{ad}{c}$	$\theta_N = \frac{F(\omega_N)}{D(\omega_N)}$	Lemma 2.3
	$\frac{d}{c}(2h-\frac{ad}{c}) - a(b+h-\frac{ad}{c}) \neq 0$ and $a \neq c$		Lemma 2.2
$c = 0$	$a \neq 0$	$\theta_N = \frac{F(\omega_N)}{D(\omega_N)}$	Lemma 2.4
	$a = 0$, $b+h-d \leq 0$, and $b-h \leq 0$		Lemma 2.2

Proof We assume that $c = 0$, and hence $d \neq 0$ from (A). If $D(\omega) = 0$, then $F(\omega) = 0$, which leads to $ad = 0$. If (2.13) is satisfied, then $ad \neq 0$, which is a contradiction to $ad = 0$. If (2.14) is satisfied, then we have

$$D(\omega) = \left[\omega^2 - (b+h-d)\right]\left(-2\omega^2 + 2b - 2h\right) \neq 0.$$

□

We summarize the results for the non-degenerate cases in Table 1 for the convenience of applications.

2.3 Degenerate Case when $c \neq 0$

From the proof of Lemma 2.3 we know that if $c \neq 0$, and (2.7) has a positive root ω^2 ($\omega > 0$) satisfying $D(\omega) = 0$, then we see that either

$$b + h - \frac{ad}{c} > 0, \quad \frac{d}{c}\left(2h - \frac{ad}{c}\right) - a\left(b + h - \frac{ad}{c}\right) \neq 0, \quad a = c, \tag{2.15}$$

or

$$b + h - \frac{ad}{c} > 0, \quad \frac{d}{c}\left(2h - \frac{ad}{c}\right) - a\left(b + h - \frac{ad}{c}\right) = 0. \tag{2.16}$$

For the case that the parameter a, b, c, d, and h satisfy (2.15) and (2.16), we have the following two results.

Lemma 2.5 *Assume that $c \neq 0$ and the parameters a, b, c, d, and h satisfy* (2.15). *Then* (2.7) *has a unique positive root,*

$$\omega_D^2 = b + h - \frac{ad}{c}, \quad \omega_D > 0, \tag{2.17}$$

satisfying $D(\omega_D) = 0$. Moreover, $\pm \mathrm{i}\omega_D$ is a pair of purely imaginary roots of (1.8) *when*

$$\tau = \tilde{\tau}_D^j = \frac{\pi + 2j\pi}{\omega_D}, \quad j \in \mathbb{Z}. \tag{2.18}$$

Proof We assume that $c \neq 0$ and the parameters a, b, c, d, and h satisfy (2.15). Then we obtain $D(\omega_D) = F(\omega_D) = 0$. Hence ω_D^2 is a positive root of (2.7). If we have another positive root ω^2 ($\omega > 0$) satisfying $D(\omega) = 0$, then ω satisfies $F(\omega) = 0$, which leads to

$$\omega^2 = \omega_D^2 = b + h - \frac{ad}{c} = b + h - d.$$

That is a contradiction. Hence (2.7) has a unique positive root ω_D^2 ($\omega_D > 0$) satisfying $D(\omega_D) = 0$. Substituting ω_D^2 into $E(\omega)$, it is easy to verify that $E(\omega_D) \neq 0$. So (2.1) has no roots when $\omega = \omega_D$. On the other hand, since $b + h - d > 0$ and $a = c$, from the above analysis we see that $\pm \mathrm{i}\omega_D$ are a pair of purely imaginary roots of (1.8) when $\tau = \tilde{\tau}_D^j$ is defined as in (2.18). □

Lemma 2.6 *Assume that $c \neq 0$ and the parameters a, b, c, d, and h satisfy* (2.16). *Then* (2.7) *has a unique positive root ω_D^2 defined as in* (2.17) *satisfying $D(\omega_D) = 0$. Moreover, we have the following.*

1. *If $a \neq c$, and $\frac{2ahd}{c} - d^2 \geq 0$, then* (2.1) *has exactly two real roots $\theta_{D,i}$ $(i = 1, 2)$*

$$\theta_{D,1} = \frac{a\omega_D + \sqrt{\frac{2ahd}{c} - d^2}}{\omega_D^2 - b + d - h}, \qquad \theta_{D,2} = \frac{a\omega_D - \sqrt{\frac{2ahd}{c} - d^2}}{\omega_D^2 - b + d - h}. \tag{2.19}$$

   Hence (1.8) *has a pair of purely imaginary roots $\pm \mathrm{i}\omega_D$ when*

$$\tau = \tau_{D,i}^j = \frac{2\arctan\theta_{D,i} + 2j\pi}{\omega_D}, \qquad j \in \mathbb{Z},\ i = 1, 2. \tag{2.20}$$

2. *If $a \neq c$, and $\frac{2ahd}{c} - d^2 < 0$, then $\pm \mathrm{i}\omega_D$ is not a pair of purely imaginary roots of* (1.8).
3. *If $a = c$, then* (2.1) *has exactly one real root*

$$\theta_D = -\frac{\omega_D^2 - b - d - h}{2a\omega_D}. \tag{2.21}$$

   Hence (1.8) *has a pair of purely imaginary roots $\pm \mathrm{i}\omega_D$ when*

$$\tau = \tau_D^j = \frac{2\arctan\theta_D + 2j\pi}{\omega_D}, \qquad j \in \mathbb{Z}, \tag{2.22}$$

   or when $\tau = \tilde{\tau}_D^j$ defined as in (2.18).

Proof We assume that $c \neq 0$ and the parameters a, b, c, d, and h satisfy (2.16).

If $a \neq c$, then we have $D(\omega_D) = F(\omega_D) = E(\omega_D) = 0$, and

$$\omega_D^2 - b + d - h = d\left(1 - \frac{a}{c}\right) \neq 0, \qquad (c - a)\omega_D \neq 0.$$

Table 2 Summary of the degenerate case and $c \neq 0$. In this case (2.7) has a unique degenerate root $\omega_D^2 = b + h - \frac{ad}{c}$ such that $D(\omega_D) = 0$. The case that $\theta = \infty$ is understood as $\arctan\theta = \pi/2$

Parameter condition		θ	Results
$b + h - \frac{ad}{c} > 0$, $a = c$, and $\frac{d}{c}(2h - \frac{ad}{c}) - a(b + h - \frac{ad}{c}) \neq 0$		∞	Lemma 2.5
$b + h - \frac{ad}{c} > 0$, and $\frac{d}{c}(2h - \frac{ad}{c}) - a(b + h - \frac{ad}{c}) = 0$	$\frac{2ahd}{c} - d^2 \geq 0$, and $a \neq c$	$\theta_{D,1} = \frac{a\omega_D + \sqrt{\frac{2ahd}{c} - d^2}}{\omega_D^2 - b + d - h}$ $\theta_{D,2} = \frac{a\omega_D - \sqrt{\frac{2ahd}{c} - d^2}}{\omega_D^2 - b + d - h}$	Lemma 2.6(1)
	$\frac{2ahd}{c} - d^2 < 0$, and $a \neq c$	None	Lemma 2.6(2)
	$a = c$	$\theta_D = -\frac{\omega_D^2 - b - d - h}{2a\omega_D}$ ∞	Lemma 2.6(3)

Hence ω_D^2 is a root of (2.7) satisfying $D(\omega_D) = 0$ and the rank of matrices M and M_1 are the same when $\omega = \omega_D$. If $\frac{2ahd}{c} - d^2 \geq 0$, then from (2.16), we find that the discriminant of the first equation of (2.1) is

$$\begin{aligned}
\Delta(\omega_D) &= 4a^2\omega_D^2 + 4\left(\omega_D^2 - b - h + d\right)\left(\omega_D^2 - b - h - d\right) \\
&= 4\left[a^2\left(b + h - \frac{ad}{c}\right) + \frac{a^2d^2}{c^2} - d^2\right] \\
&= 4\left(\frac{2ahd}{c} - d^2\right) \geq 0. \qquad (2.23)
\end{aligned}$$

So we easily find that the first equation of (2.1) has two real roots $\theta_{D,1}$ and $\theta_{D,2}$, defined as in (2.19), when $\omega = \omega_D$. Hence (1.8) has a pair of purely imaginary roots $\pm i\omega_D$ when $\tau = \tau_{D,i}^j$ $(i = 1,\ 2)$ defined as in (2.20). If $\frac{2ahd}{c} - d^2 < 0$, then $\Delta(\omega_D) < 0$. So (2.1) has no roots when $\omega = \omega_D$. Consequently, $\pm i\omega_D$ is not a pair of purely imaginary roots of (1.8).

If $a = c$, as that in the case of $a \neq c$, then the rank of matrices M and M_1 are the same when $\omega = \omega_D$. In this case $\omega_D^2 - b + d - h = (c - a)\omega_D = 0$, so (2.1) has only one real root θ_D defined as in (2.21) when $\omega = \omega_D$. Hence (1.8) has a pair of purely imaginary roots $\pm i\omega_D$ when $\tau = \tau_D^j$ defined as in (2.22). Since $a = c$ and $b + h - d > 0$, (1.8) also has a pair of purely imaginary roots $\pm i\omega_D$ when $\tau = \tilde{\tau}_D^j$ defined as in (2.18). □

The summary for the degenerate case and $c \neq 0$ is given in Table 2.

2.4 Degenerate Case when $c = 0$

If $c = 0$ then $d \neq 0$, since we always assume that the condition (A) is satisfied. From Lemma 2.4 we know that if (2.7) has a positive root ω^2 $(\omega > 0)$ satisfying $D(\omega) = 0$, then we have either

$$a=0, \quad \text{and} \quad b+h-d>0, \quad \text{or} \tag{2.24}$$

$$a=0, \quad \text{and} \quad b-h>0. \tag{2.25}$$

Similarly to Lemma 2.6, we arrive at the following results:

Lemma 2.7 *Assume that $c=0$, (2.25) is satisfied, and (2.24) is not satisfied. Then (2.7) has a unique positive root $\omega_{Z,1}^2=b-h$ ($\omega_{Z,1}>0$) satisfying $D(\omega_{Z,1})=0$.*

1. *If $2h+d>0$, then $\pm i\omega_{Z,1}$ is not a pair of purely imaginary roots of (1.8).*
2. *If $2h+d\le 0$, then (2.1) has two real roots*

$$\theta_{Z,1}^{+}=\sqrt{\frac{2h+d}{2h-d}}, \quad \text{and} \quad \theta_{Z,1}^{-}=-\sqrt{\frac{2h+d}{2h-d}}, \tag{2.26}$$

when $\omega=\omega_{Z,1}$. Hence (1.8) has a pair of purely imaginary roots $\pm i\omega_{Z,1}$ when

$$\tau=\tau_{Z,1}^{\pm,j}=\frac{2\arctan\theta_{Z,1}^{\pm}+2j\pi}{\omega_{Z,1}}, \quad j\in\mathbb{Z},\ i=1,2. \tag{2.27}$$

Proof Since $a=c=0$, $\omega_{Z,1}^2=b-h$, the second equation of (2.1) holds and the first equation of (2.1) becomes $(d-2h)\theta^2=-2h-d$. Since (2.25) is satisfied, and (2.24) is not satisfied, $d-2h>0$. Hence we obtain the desired conclusions. We remark that in this case $\omega_{Z,1}^2=b-h\neq b+h-d$, hence $\omega_{Z,1}\tau$ cannot be $\pi+2j\pi$ for $j\in\mathbb{Z}$. □

Lemma 2.8 *Assume that $c=0$, (2.24) is satisfied, and (2.25) is not satisfied. Then (2.7) has a unique positive root $\omega_{Z,2}^2=b-d+h$ ($\omega_{Z,2}>0$) satisfying $D(\omega_{Z,2})=0$. Moreover $\pm i\omega_{Z,2}$ is a pair of purely imaginary roots of (1.8) when*

$$\tau=\tilde{\tau}_{Z,2}^{j}=\frac{\pi+2j\pi}{\omega_{Z,2}}, \quad j\in\mathbb{Z}. \tag{2.28}$$

Proof Since $a=c=0$, $\omega_{Z,2}^2=b+h-d$, the first equation of (2.1) becomes $0=-2d$ when $\omega=\omega_{Z,2}$. Since $d\neq 0$ from (A), the first equation of (2.1) is not satisfied. So (2.1) has no real roots when $\omega=\omega_{Z,2}$. However, in this case $\omega_{Z,2}^2=b+h-d$ and $a=c$, so we see that $\pm i\omega_{Z,2}$ are a pair of purely imaginary roots of (1.8) when $\tau=\tilde{\tau}_{Z,2}^{j}$ defined as in (2.28). □

Lemma 2.9 *Assume that $c=0$, and (2.24) and (2.25) are both satisfied. Then (2.7) has exactly two positive roots $\omega_{Z,1}^2=b-h$, $\omega_{Z,2}^2=b+h-d$, where $\omega_{Z,i}>0$, satisfying $D(\omega_{Z,i})=0$ for $i=1,2$.*

1. *If $2h=d$, $\pm i\omega_{Z,1}=\pm i\omega_{Z,2}$ are a pair of purely imaginary roots of (1.8) when $\tau=\tilde{\tau}_{Z,2}^{j}$ defined as in (2.28).*
2. *If $2h\neq d$ and $4h^2-d<0$, then $\pm i\omega_{Z,1}$ are not purely imaginary roots of (1.8) and $\pm i\omega_{Z,2}$ are a pair of purely imaginary roots of (1.8) when $\tau=\tilde{\tau}_{Z,2}^{j}$ defined as in (2.28).*

Table 3 Summary of the degenerate case and $c=0$. In this case (2.7) may have two degenerate roots $\omega_{Z,i}^2$ $(i=1,2)$ such that $D(\omega_{Z,i})=0$. The case that $\theta=\infty$ is understood as $\arctan\theta=\pi/2$

Parameter condition		ω^2	θ	Results
$a=0, b-h>0$ and $b+h-d\le 0$	$2h+d>0$	$\omega_{Z,1}=b-h$	None	Lemma 2.7(1)
	$2h+d\le 0$		$\theta_{Z,1}^+=\sqrt{\frac{2h+d}{2h-d}}$ $\theta_{Z,1}^-=-\sqrt{\frac{2h+d}{2h-d}}$	Lemma 2.7(2)
$a=0, b-h\le 0$, and $b+h-d>0$		$\omega_{Z,2}=b-d+h$	∞	Lemma 2.8
$a=0, b-h>0$ and $b+h-d>0$	$2h=d$	$\omega_{Z,1}=\omega_{Z,2}$ $=b-h$	∞	Lemma 2.9(1)
	$2h\ne d$, and $4h^2<d$	$\omega_{Z,1}=b-h$	None	Lemma 2.9(2)
		$\omega_{Z,2}=b-d+h$	∞	
	$2h\ne d$, and $4h^2\ge d$	$\omega_{Z,1}=b-h$	$\theta_{Z,1}^+=\sqrt{\frac{2h+d}{2h-d}}$ $\theta_{Z,1}^-=-\sqrt{\frac{2h+d}{2h-d}}$	Lemma 2.9(3)
		$\omega_{Z,2}=b-d+h$	∞	

3. *If* $2h\ne d$ *and* $4h^2-d\ge 0$, *then* (1.8) *has a pair of purely imaginary roots* $\pm i\omega_{Z,1}$ *when* $\tau=\tau_{Z,1}^{\pm,j}$ *defined as in* (2.27), *and also a pair of purely imaginary roots* $\pm i\omega_{Z,2}$ *when* $\tau=\tilde\tau_{Z,2}^j$ *defined as in* (2.28).

Proof It can be proved that if $b-d+h>0$, and $b-h>0$, then $\omega_{Z,1}^2=b-h$, $\omega_{Z,2}^2=b+h-d$ $(\omega_{Z,i}>0)$ satisfying $D(\omega_{Z,i})=0$ for $i=1,\ 2$.

If $2h=d$, then we have $b-d+h=b-h$. Consequently, the second equation of (2.1) hold, and the first equation of (2.1) becomes $0=-2d$, when $\omega=\omega_{Z,1}=\omega_{Z,2}$. So (2.1) has no real roots when $\omega=\omega_{Z,1}=\omega_{Z,2}$. However, in this case $\omega_{Z,1}^2=\omega_{Z,2}^2=b+h-d$ and $a=c$, so we find that $\pm i\omega_{Z,2}$ are a pair of purely imaginary roots of (1.8) when $\tau=\tilde\tau_{Z,2}^j$ defined as in (2.28).

In the case of $2h\ne d$, when $\omega=\omega_{Z,2}$, the first equation of (2.1) becomes $0=2d$. Since $d\ne 0$, (2.1) has no real roots when $\omega=\omega_{Z,2}$. When $\omega=\omega_{Z,1}$, the second equation of (2.1) holds, and the first of (2.1) become $(2h-d)\theta^2=2h+d$. So if $4h^2-d^2<0$, (2.1) has no real roots when $\omega=\omega_{Z,1}$. If $4h^2-d^2\ge 0$, then (2.1) has two real roots $\theta_{Z,1}^{\pm}$ defined as (2.26) when $\omega=\omega_{Z,1}$, and consequently, (1.8) has a pair of purely imaginary roots $\pm i\omega_{Z,1}$ when $\tau=\tau_{Z,2}^{\pm,j}$ defined as in (2.27). However, in this case $\omega_{Z,2}^2=b+h-d$ and $a=c$, so we see that $\pm i\omega_{Z,2}$ are a pair of purely imaginary roots of (1.8) when $\tau=\tilde\tau_{Z,2}^j$ defined as in (2.28). □

Table 3 summarizes the results of the degenerate case and $c=0$.

2.5 Transversality Condition

If (2.7) has a positive root ω^2 $(\omega>0)$, and (2.1) has a real root θ with this ω, then we know that when $\tau=\tau^j=\frac{2\arctan\theta+2j\pi}{\omega}$, $j\in\mathbb{Z}$, (1.8) has a pair of purely imaginary roots $\pm i\omega$. Here we allow θ to take the value ∞ as in the last three subsections in the sense that $\arctan\theta = \pi/2$ in the definition of τ^j. Since we are interested in possible Hopf bifurcation (for the nonlinear equation which generates the linearized equation (1.8)) at $\tau = \tau^j$, we examine the transversality condition of the pair of complex roots of (1.8) moving across the imaginary axis.

In the following result, we show that under what transversality condition, a curve of simple root $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$ exists and moves across the imaginary axis transversally at $\tau = \tau^j$:

Lemma 2.10 *Suppose that (2.7) has a positive root ω^2 ($\omega > 0$), (2.1) has a real root θ with this ω, and $\tau = \tau^j$ ($j \in \mathbb{Z}$) is defined as in (2.9).*

1. *For $\theta \in (-\infty, \infty)$, define*

$$\mathcal{G}(\omega,\theta) = \big[d\big(1+\theta^2\big) + 2h\big(1-\theta^2\big)\big]\cdot\big[2\omega\big(1-\theta^2\big) + 2a\theta\big] \\ - \big[c\omega\big(1+\theta^2\big) - 4h\theta\big]\cdot\big[a\big(1-\theta^2\big) - 4\omega\theta + c\big(1+\theta^2\big)\big]. \quad (2.29)$$

If $\mathcal{G}(\omega,\theta) \neq 0$, then $i\omega$ is a simple root of (1.8) for $\tau = \tau^j$ and there exists $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$ which is the unique root of (1.8) for $\tau \in (\tau^j - \epsilon, \tau^j + \epsilon)$ for some small $\epsilon > 0$ satisfying $\alpha(\tau^j) = 0$ and $\omega(\tau^j) = \omega$. Moreover,

$$\frac{\mathrm{d}\mathcal{R}e\{\lambda(\tau)\}}{\mathrm{d}\tau}\bigg|_{\tau=\tau^j} = \frac{\mathrm{d}\alpha(\tau)}{\mathrm{d}\tau}\bigg|_{\tau=\tau^j} > 0, \quad j \in \mathbb{Z}, \quad \textit{when } \mathcal{G}(\omega,\theta) > 0; \\ \frac{\mathrm{d}\mathcal{R}e\{\lambda(\tau)\}}{\mathrm{d}\tau}\bigg|_{\tau=\tau^j} = \frac{\mathrm{d}\alpha(\tau)}{\mathrm{d}\tau}\bigg|_{\tau=\tau^j} < 0, \quad j \in \mathbb{Z}, \quad \textit{when } \mathcal{G}(\omega,\theta) < 0. \quad (2.30)$$

2. *For $\theta = \infty$ (in the sense that* $\arctan\theta = \pi/2$), *if $2h - d \neq 0$, then the conclusions in part 1 hold.*

Proof Denote

$$M(\lambda,\tau) = \lambda^2 + a\lambda + b + (c\lambda + d)e^{-\lambda\tau} + he^{-2\lambda\tau}.$$

Then we have

$$\frac{\partial M}{\partial\lambda}(\lambda,\tau) = e^{-\lambda\tau}P(\lambda,\tau), \quad \text{and} \quad \frac{\partial M}{\partial\tau}(\lambda,\tau) = -\lambda e^{-\lambda\tau}Q(\lambda,\tau),$$

where

$$P(\lambda,\tau) = (2\lambda + a)e^{\lambda\tau} + c - (c\lambda + d)\tau - 2h\tau e^{-\lambda\tau},$$

and

$$Q(\lambda,\tau) = c\lambda + d + 2he^{-\lambda\tau}.$$

For $\theta \in (-\infty, +\infty)$, substituting $\lambda = i\omega$, $\tau = \tau^j$, and $\theta = \tan\frac{\omega\tau^j}{2}$ into $P(\lambda,\tau)$ and $Q(\lambda,\tau)$, we have

$$\begin{aligned}&(1+\theta^2)P(\mathrm{i}\omega,\tau^j)\\&\quad=a(1-\theta^2)-4\omega\theta+c(1+\theta^2)-\tau^j d(1+\theta^2)-2h\tau^j(1-\theta^2)\\&\qquad+\mathrm{i}[2\omega(1-\theta^2)+2a\theta-c\omega\tau^j(1+\theta^2)+4h\tau^j\theta],\end{aligned}$$

and

$$(1+\theta^2)Q(\mathrm{i}\omega,\tau^j)=d(1+\theta^2)+2h(1-\theta^2)+\mathrm{i}(c\omega(1+\theta^2)-4h\theta).$$

Hence

$$\begin{aligned}&\mathcal{I}m\{(1+\theta^2)^2P(\mathrm{i}\omega,\tau^j)\overline{Q(\mathrm{i}\omega,\tau^j)}\}\\&\quad=[d(1+\theta^2)+2h(1-\theta^2)]\cdot[2\omega(1-\theta^2)+2a\theta-c\omega\tau^j(1+\theta^2)+4h\tau^j\theta]\\&\qquad-[c\omega(1+\theta^2)-4h\theta]\cdot[a(1-\theta^2)-4\omega\theta+c(1+\theta^2)]\\&\qquad-[c\omega(1+\theta^2)-4h\theta]\cdot[-\tau^j d(1+\theta^2)-2h\tau^j(1-\theta^2)]\\&\quad=[d(1+\theta^2)+2h(1-\theta^2)]\cdot[2\omega(1-\theta^2)+2a\theta]\\&\qquad-[c\omega(1+\theta^2)-4h\theta]\cdot[a(1-\theta^2)-4\omega\theta+c(1+\theta^2)]\\&\quad=\mathcal{G}(\omega,\theta).\end{aligned}$$

Since

$$\frac{\partial M}{\partial\lambda}(\mathrm{i}\omega,\tau^j)=P(\mathrm{i}\omega,\tau^j)\mathrm{e}^{-\mathrm{i}\omega\tau^j},$$

when $\mathcal{G}(\omega,\theta)\neq 0$, we have $\frac{\partial M}{\partial\lambda}(\mathrm{i}\omega,\tau^j)\neq 0$. From the implicit function theorem, we find that $\mathrm{i}\omega$ is simple and there exists $\lambda(\tau)=\alpha(\tau)+\mathrm{i}\omega(\tau)$ which is the unique root of (1.8) for $\tau\in(\tau^j-\epsilon,\tau^j+\epsilon)$ for some small $\epsilon>0$ satisfying $\alpha(\tau^j)=0$ and $\omega(\tau^j)=\omega$. Substituting $\lambda(\tau)$ into (1.8) and taking the derivatives with respect to τ yields

$$P(\lambda,\tau)\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}=\lambda Q(\lambda,\tau),$$

and

$$\begin{aligned}&\left.\frac{\mathrm{d}\mathcal{R}e\{\lambda(\tau)\}}{\mathrm{d}\tau}\right|_{\tau=\tau^j}>0,\quad j\in\mathbb{Z},\quad\text{when } \mathcal{G}(\omega,\theta)>0;\\&\left.\frac{\mathrm{d}\mathcal{R}e\{\lambda(\tau)\}}{\mathrm{d}\tau}\right|_{\tau=\tau^j}<0,\quad j\in\mathbb{Z},\quad\text{when } \mathcal{G}(\omega,\theta)<0.\end{aligned}$$

Hence the case when $\theta\neq\infty$ is obtained.

If $\theta=\infty$, then $a=c$ and $b+h-d>0$, and (1.8) has a pair of purely imaginary root $\pm\mathrm{i}\omega=\pm\mathrm{i}\sqrt{b+h-d}$ when $\tau^j=\frac{\pi+2j\pi}{\omega}$. In this case,

$$\mathcal{I}m\{P(\mathrm{i}\omega,\tau^j)\overline{Q(\mathrm{i}\omega,\tau^j)}\}=2\omega(2h-d),$$

hence we obtain the desired result in this case. □

2.6 Roots of Quartic Polynomials

We have shown that finding purely imaginary roots of (1.8) is equivalent to finding real positive roots of the quartic polynomial equation (2.7). In this subsection, we will analyze when the quartic polynomial equation (2.7) has positive real roots. Here we follow the method in Li and Wei (2005). We denote

$$h(z) = z^4 + s_1 z^3 + s_2 z^2 + s_3 z + s_4,$$

where s_i $(1 \le i \le 4)$ are defined as in (2.6). Set

$$h'(z) = 4z^3 + 3s_1 z^2 + 2s_2 z + s_3 = 0. \tag{2.31}$$

Let $y = z + \frac{3s_1}{4}$, then (2.31) becomes

$$y^3 + p_1 y + q_1 = 0, \tag{2.32}$$

where

$$p_1 = \frac{s_2}{2} - \frac{3s_1^2}{16}, \qquad q_1 = \frac{s_1^3}{32} - \frac{s_1 s_2}{8} + s_3.$$

Define

$$\begin{aligned}
D &= \left(\frac{q_1}{2}\right)^3 + \left(\frac{p_1}{3}\right)^3, \qquad \sigma = \frac{-1+\sqrt{3}\mathrm{i}}{2}, \\
y_1 &= \sqrt[3]{-\frac{q_1}{2} + \sqrt{D}} + \sqrt[3]{-\frac{q_1}{2} - \sqrt{D}}, \\
y_2 &= \sqrt[3]{-\frac{q_1}{2} + \sqrt{D}}\sigma + \sqrt[3]{-\frac{q_1}{2} - \sqrt{D}}\sigma^2, \\
y_3 &= \sqrt[3]{-\frac{q_1}{2} + \sqrt{D}}\sigma^2 + \sqrt[3]{-\frac{q_1}{2} - \sqrt{D}}\sigma, \\
z_i &= y_i - \frac{3s_1}{4}, \quad i = 1, 2, 3.
\end{aligned} \tag{2.33}$$

From Li and Wei (2005, Lemma 2.2), we have the following lemma regarding the real positive roots of (2.7).

Lemma 2.11 *Consider* (2.7), *where* s_i $(1 \le i \le 4)$ *are defined as in* (2.6), *and* D *and* z_i $(1 \le i \le 3)$ *is defined as in* (2.33). *Then* (2.7) *has at least one positive root if and only if one of the following conditions is satisfied*:

(R_1) $b \ne h$ *and* $(b+h-d)(b+h+d) < 0$.
(R_2) $b = h$ *or* $(b+h-d)(b+h+d) \ge 0$, $D \ge 0$, $z_1 > 0$, *and* $h(z_1) < 0$.
(R_3) $b = h$ *or* $(b+h-d)(b+h+d) \ge 0$, $D < 0$, *there exists at least one* $z^* \in \{z_1, z_2, z_3\}$, *such that* $z^* > 0$ *and* $h(z^*) \le 0$.

A characteristic equation of form (1.8) often arises from the linearized equation at an equilibrium of a delayed differential equation/system or at a constant equilibrium of a delayed reaction–diffusion equation/system, and the parameter τ represents the delay effect. Usually we are concerned with the delay effect on the stability of the equilibrium. Here we assume that the equilibrium is locally asymptotically stable when $\tau = 0$. That is, all the roots of (1.8) with $\tau = 0$ have negative real parts. We assume that

(H_1) $a + c > 0$.
(H_2) $b + d + h > 0$.

As τ increases from 0 to ∞, the stability of the equilibrium changes either when (1.8) has a zero root or a pair of purely imaginary roots. However, a zero root of (1.8) is not possible from (H_2), thus only purely imaginary roots is possible for some $\tau > 0$. Here we fix a set of parameters $\{a, b, c, d, h\}$, and we denote the set of all positive roots of (2.7) by $\mathcal{D}$, which has at most 4 elements. For each $\omega_i^2 \in \mathcal{D}$, (2.1) may have one or two real roots $\theta_{k,i}$ (as mentioned earlier, we allow that $\theta_{k,i} = \infty$ in the sense that $\arctan \theta_{k,i} = \pi/2$), then from the analysis given in Sects. 2.2–2.4, if we define

$$\tau_{k,i}^j = \begin{cases} \frac{2 \arctan \theta_{k,i} + 2j\pi}{\omega_i}, \ j \in \mathbb{N}_0, & \text{if } \theta_{k,i} \geq 0; \\ \frac{2 \arctan \theta_{k,i} + 2(j+1)\pi}{\omega_i}, \ j \in \mathbb{N}_0, & \text{if } \theta_{k,i} < 0, \end{cases} \tag{2.34}$$

then (2.7) has a pair of purely imaginary roots $\mathrm{i}\omega_i$ when and only when $\tau = \tau_{k,i}^j$. It is apparent that $\tau_{k,i}^j$ is strictly increasing in j, hence $\tau_{k,i}^0 = \min_{j \geq 0} \tau_{k,i}^j$. From the analysis in Sects. 2.2–2.4, the index set for i has at most four elements, and the one for k at most has two. We define $\tau_{k,i}^j = \infty$ if the ith root of (2.7) is not positive, or $\theta_{k,i}$ does not exist. Then we can define the smallest τ so that the stability will change:

$$\tau_* = \tau_{k_0,i_0}^0 = \min\{\tau_{k,i}^0 : i = 1, 2, 3, 4, k = 1, 2\}, \qquad \theta_* = \theta_{k_0} \quad \text{and} \quad \omega_* = \omega_{k_0}. \tag{2.35}$$

Then the following stability criterion can easily be established:

Lemma 2.12 *Let $a, b, c, d, h \in \mathbb{R}$. Assume that (H_1) and (H_2) hold and τ_*, θ_* and ω_* are defined as in (2.35).*

1. *If none of the conditions (R_1)–(R_3) in Lemma 2.11 is satisfied, then all the roots of (1.8) have negative real parts for all $\tau \geq 0$.*
2. *If one of the conditions (R_1)–(R_3) in Lemma 2.3 is satisfied, then (2.7) has at least one positive root; all the roots of (1.8) have negative real parts when $\tau \in [0, \tau_*)$. Moreover, if $\tau_* < \infty$, $\mathcal{G}(\theta_*, \omega_*) \neq 0$, and $\tau_{k,i}^0 \neq \tau_*$ for $k \neq k_0$ and $i \neq i_0$, then when $\tau = \tau_*$, all the roots of (1.8) have negative real parts except a pair of simple purely imaginary roots $\pm\mathrm{i}\omega_*$, and for $\tau \in (\tau_*, \tau_* + \epsilon)$ with some small $\epsilon > 0$, (1.8) has exactly one pair of conjugate complex roots with positive real parts.*

Finally we prove a result about the *nonexistence* of positive roots of (1.8).

Proposition 2.13 *Suppose that* $a, b > 0$ *and* $a^2 - 2b > 0$, *then there exists* $\delta > 0$ *such that when* $\max\{|c|, |d|, |h|\} < \delta$, *all roots of* (1.8) *have negative real parts for all* $\tau \geq 0$.

Proof We notice that when $c = d = h = 0$, then $s_1 = 2(a^2 - 2b)$, $s_2 = (a - 2b)^2 + 2b^2$, $s_3 = 2b^2(a^2 - 2b)$, and $s_4 = b^4$. Thus (2.7) becomes $(z^2 + (a^2 - 2b)z + b^2)^2 = 0$. Hence if $a^2 - 2b > 0$ and $c = d = h = 0$, then (2.7) has no positive roots and (1.8) has no purely imaginary roots. Also, since $c = d = h = 0$, $a + c = a > 0$ and $b + d + h = b > 0$. Then a perturbation argument yields the stated result. □

2.7 Summary

The results in this section provide a route of determining the purely imaginary roots of the characteristic equation (1.8) and the corresponding delay value τ. While there are many different cases that have been considered here, the following result is convenient to apply.

Theorem 2.14 *Suppose that* $a, b, c, d, h \in \mathbb{R}$ *satisfy*

(i) $c \neq 0$ *and* $h \neq 0$.
(ii) $b \neq h$ *and* $d^2 > (b + h)^2$.
(iii) $b + h \leq \frac{ad}{c}$ *or* $(\frac{d}{c}(2h - \frac{ad}{c}) - a(b + h - \frac{ad}{c})) \cdot (a - c) \neq 0$.

Recall that $D(\omega)$, $F(\omega)$ *are defined as in* (2.2). *Then we have the following.*

1. *The quartic equation* (2.7) *has a positive root* ω_N^2 *for some* $\omega_N > 0$ *satisfying* $D(\omega_N) \neq 0$.
2. *Let*
$$\theta_N = \frac{F(\omega_N)}{D(\omega_N)}, \quad \text{and} \quad \tau = \tau_N^j = \frac{2\arctan\theta_N + 2j\pi}{\omega_N},$$
where $j \in \mathbb{Z}$. *Then the characteristic equation* (1.8) *has a pair of purely imaginary eigenvalues* $\pm \mathrm{i}\omega_N$ *when* $\tau = \tau_N^j$.
3. *Let* $\mathcal{G}(\omega, \theta)$ *be defined as in* (2.29). *If* $\mathcal{G}(\omega_N, \theta_N) \neq 0$, *then* $\mathrm{i}\omega_N$ *is a simple root of* (1.8) *for* $\tau = \tau_N^j$ *and there exists* $\lambda(\tau) = \alpha(\tau) + \mathrm{i}\omega(\tau)$ *which is the unique root of* (1.8) *for* τ *near* τ_N^j *satisfying* $\alpha(\tau_N^j) = 0$, $\omega(\tau_N^j) = \omega_N$, *and* $\alpha'(\tau_N^j) \neq 0$.

Moreover, if $a, b, c, d, h \in \mathbb{R}$ *also satisfy*

(iv) $a + c > 0$ *and* $b + d + h > 0$,

then there exists $\tau_* > 0$ *defined in* (2.35) *such that when* $\tau \in [0, \tau_*)$, *all the roots of* (1.8) *have negative real parts*; *if* $\mathcal{G}(\theta_*, \omega_*) \neq 0$, *then when* $\tau = \tau_*$, *all the roots of* (1.8) *have non-positive real parts but* (1.8) *has at least one pair of simple purely imaginary roots* $\pm \mathrm{i}\omega_0$, *and for* $\tau \in (\tau_*, \tau_* + \epsilon)$ *with some small* $\epsilon > 0$, (1.8) *has at least one pair of conjugate complex roots with positive real parts.*

We remark that all the conditions (i), (ii), and (iii) except $d^2 > (b + h)^2$ hold for all parameter values except a zero measure set. Combining with the condition (iv) we have the following observation for the appearance of roots of (1.8) with positive real parts for $\tau > 0$.

Corollary 2.15 *Define a subset in the parameter space*

$$P = \{(a, b, c, d, h) \in \mathbb{R}^5 : a + c > 0,\ b + d + h > 0,\ b - d + h < 0\}. \tag{2.36}$$

Then for almost every $(a, b, c, d, h) \in P$, *there exists* $\tau_* > 0$ *such that when* $\tau \in [0, \tau_*)$, *all the roots of* (1.8) *have negative real parts*; *when* $\tau = \tau_*$, (1.8) *has at least one pair of simple purely imaginary roots* $\pm i\omega_*$, *and for* $\tau \in (\tau_*, \tau_* + \epsilon)$ *with some small* $\epsilon > 0$, (1.8) *has at least one pair of conjugate complex roots with positive real parts*.

Since the condition (iv) is necessary for the stability when $\tau = 0$, Corollary 2.15 shows that $b - d + h < 0$ is almost sufficient for the instability when τ is large. Although Corollary 2.15 shows that the parameter values in P is most likely to induce instability, we shall be cautious that parameter values outside of P may also lead to instability by using other results in Sect. 2. On the other hand, the physically realistic parameters may always fall in the zero measure set in P where Theorem 2.14 is not readily applicable, then again application of other results in Sect. 2 may be needed. In Sect. 3, we will give more explanation of these conditions in terms of the reaction kinetics of the model.

Usually it is difficult to obtain the exact number of the positive roots for (2.7). We also should be cautious that the system may regain the stability for $\tau > \tau_*$. Since (2.7) may have more than one positive roots, stability switches and double Hopf bifurcation are both possible. We do not pursue these issues in this paper but leave them to further investigation.

3 Stability in Delayed Reaction–Diffusion Systems

3.1 General Framework

We consider a reaction–diffusion system with two variables and a simultaneous delay $\tau \geq 0$ in the following form:

$$\begin{cases} \dfrac{\partial u}{\partial t} = D_1 \Delta u + f(u, v, u_\tau, v_\tau), & x \in \Omega,\ t > 0, \\ \dfrac{\partial v}{\partial t} = D_2 \Delta v + g(u, v, u_\tau, v_\tau), & x \in \Omega,\ t > 0, \\ \dfrac{\partial u(x,t)}{\partial \nu} = \dfrac{\partial v(x,t)}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,t) = \phi_1(x,t) \geq 0, v(x,t) = \phi_2(x,t) \geq 0, & x \in \Omega,\ t \in [-\tau, 0], \end{cases} \tag{3.1}$$

where $u = u(x,t)$, $v = v(x,t)$, $u_\tau = u(x, t-\tau)$, and $v_\tau = v(x, t-\tau)$, Ω is a bounded connected domain in $\mathbb{R}^n$ $(n \geq 1)$ with smooth boundary $\partial\Omega$, Δ is the Laplace operator in $\mathbb{R}^n$, and $\partial w/\partial\nu$ is the outer normal derivative of $w = u, v$. Hence the system is a closed one as a no-flux boundary condition is imposed for both u and v. The functions $f(u,v,w,z)$ and $g(u,v,w,z)$ are continuously differentiable in $\mathbb{R}^4$. We assume that there exist $u^*>0$ and $v^*>0$ such that

$$f\big(u^*,v^*,u^*,v^*\big)=0,\qquad g\big(u^*,v^*,u^*,v^*\big)=0.$$

Then (u^*,v^*) is a constant positive equilibrium of system (3.1). Linearizing system (3.1) at (u^*,v^*), for $U_t\in\mathcal{C}=C([-\tau,0],C(\overline{\Omega},\mathbb{R}^2))$, we have

$$\frac{\mathrm{d}U(t)}{\mathrm{d}t}=D\Delta U(t)+L(U_t), \tag{3.2}$$

where

$$U(t)=\begin{pmatrix}\phi(t)\\ \psi(t)\end{pmatrix},\qquad D=\begin{pmatrix}D_1 & 0\\ 0 & D_2\end{pmatrix}, \tag{3.3}$$

and

$$L\begin{pmatrix}\phi_t\\ \psi_t\end{pmatrix}=L_1\begin{pmatrix}\phi(t)\\ \psi(t)\end{pmatrix}+L_2\begin{pmatrix}\phi(t-\tau)\\ \psi(t-\tau)\end{pmatrix}, \tag{3.4}$$

where L_1, L_2 are the Jacobian matrices

$$L_1=\begin{pmatrix}f_u & f_v\\ g_u & g_v\end{pmatrix},\qquad L_2=\begin{pmatrix}f_w & f_z\\ g_w & g_z\end{pmatrix}, \tag{3.5}$$

and

$$f_\alpha=\frac{\partial f}{\partial\alpha}\big(u^*,v^*,u^*,v^*\big),\quad \text{for } \alpha=u,v,w,z;$$
$$g_\alpha=\frac{\partial g}{\partial\alpha}\big(u^*,v^*,u^*,v^*\big),\quad \text{for } \alpha=u,v,w,z.$$

From Wu (1996), the corresponding integral equation of (3.2) is

$$U(t)=T(t)U(0)+\int_0^t T(t-s)L(U_s)\,\mathrm{d}s, \tag{3.6}$$

where $T(t)$ is a strongly continuous semigroup of linear operator in $C(\overline{\Omega},\mathbb{R}^2)$ with the infinitesimal generator $D\Delta$. $\lambda\in\mathbb{C}$ is a characteristic value of (3.6) if there exists $y\in\mathrm{Dom}(D\Delta)\setminus\{0\}$ such that

$$D\Delta y-\lambda y+L\big(\mathrm{e}^{\lambda\cdot}y\big)=0, \tag{3.7}$$

where

$$\big(\mathrm{e}^{\lambda\cdot}\big)(\theta)=\mathrm{e}^{\lambda\theta}y,\quad \theta\in[-\tau,0].$$

For simplicity we assume that all eigenvalues μ_n ($n\in\mathbb{N}_0$) of $-\Delta$ with Neumann boundary condition are simple, and the corresponding eigenfunction are $\gamma_n(x)$,

$n \in \mathbb{N}_0$. By using the Fourier expansion in (3.7),

$$y = \sum_{n=0}^{\infty} \gamma_n(x) \begin{pmatrix} p_n \\ q_n \end{pmatrix},$$

where $p_n, \ q_n \in \mathbb{C}$, we find that for a fixed $n \in \mathbb{N}_0$, the characteristic equation of system (3.1) is

$$\det \begin{pmatrix} \lambda + D_1\mu_n - f_u - f_w \mathrm{e}^{-\lambda\tau} & -f_v - f_z \mathrm{e}^{-\lambda\tau} \\ -g_u - g_w \mathrm{e}^{-\lambda\tau} & \lambda + D_2\mu_n - g_v - g_z \mathrm{e}^{-\lambda\tau} \end{pmatrix} = 0.$$

That is, each characteristic value λ is a root of an equation

$$K(\lambda, \tau, n) \equiv \lambda^2 + a_n\lambda + b_n + (c_n\lambda + d_n)\mathrm{e}^{-\lambda\tau} + h_n \mathrm{e}^{-2\lambda\tau} = 0, \quad n \in \mathbb{N}_0, \tag{3.8}$$

where

$$\begin{aligned} a_n =&(D_1 + D_2)\mu_n - (f_u + g_v), \\ b_n =&D_1 D_2 \mu_n^2 - (D_1 g_v + D_2 f_u)\mu_n + f_u g_v - f_v g_u, \\ c_n =&- (f_w + g_z), \\ d_n =&- (D_1 g_z + D_2 f_w)\mu_n + (f_u g_z - f_z g_u) + (f_w g_v - f_v g_w), \\ h_n =&f_w g_z - f_z g_w. \end{aligned} \tag{3.9}$$

We define the spectrum set for a fixed $\tau \in \overline{\mathbb{R}^+}$ and $n \in \mathbb{N}_0$ by

$$S_{\tau,n} = \{\lambda \in \mathbb{C} : K(\lambda, \tau, n) = 0\},$$

and for a fixed $\tau \in \overline{\mathbb{R}^+}$,

$$S_\tau = \bigcup_{n \in \mathbb{N}_0} S_{\tau,n}.$$

Then the equilibrium (u^*, v^*) is stable with respect to system (3.1) for a given $\tau \geq 0$ if

$$S_\tau \subseteq \mathbb{C}^- \equiv \{x + \mathrm{i}y : x, y \in \mathbb{R}, x < 0\}.$$

Indeed, a hierarchy of stability can be defined through $S_{\tau,n}$. We say that (u^*, v^*) is stable with respect to ODE (Ordinary Differential Equation) if $S_{0,0} \subseteq \mathbb{C}^-$; it is stable with respect to DDE (Delay Differential Equation) for $\tau > 0$ if $S_{\tau,0} \subseteq \mathbb{C}^-$; it is stable with respect to PDE (Partial Differential Equation) if $S_0 \subseteq \mathbb{C}^-$; and it is stable with respect to DPDE (Delay Partial Differential Equation) for $\tau > 0$ if $S_\tau \subseteq \mathbb{C}^-$. Similarly, (u^*, v^*) is stable in mode n with respect to PDE if $S_{0,n} \subseteq \mathbb{C}^-$; and it is stable in mode n with respect to DPDE if $S_{\tau,n} \subseteq \mathbb{C}^-$. Apparently the stabilities defined above satisfy the relations shown in Fig. 1, and the converse may not hold.

Various instability mechanisms can be explored under the framework described above. For example, a Turing instability arises when (u^*, v^*) is stable for ODE, but

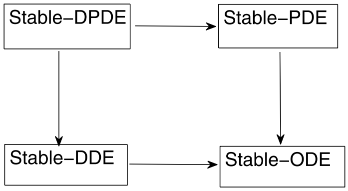

Fig. 1 Stability relations. Here "→" means "implies"

not for PDE. In this paper we focus on the delay-induced instability, hence in the following we assume that (u^*, v^*) is stable for PDE, and we consider the stability of (u^*, v^*) for the DDE and DPDE by analyzing the distribution of characteristic roots of (3.8) by using the method developed in Sect. 2. Here For $n \in \mathbb{N}_0$, (2.7) becomes

$$z^4 + s_1^n z^3 + s_2^n z^2 + s_3^n z + s_4^n = 0, \tag{3.10}$$

where

$$\begin{aligned} s_1^n &= -4b_n + 2a_n^2 - c_n^2, \\ s_2^n &= 6b_n^2 - 2h_n^2 - 4b_n a_n^2 - d_n^2 + a_n^4 - a_n^2 c_n^2 + 2c_n^2 b_n + 2h_n c_n^2, \\ s_3^n &= -a_n^2 d_n^2 - 4b_n^3 + 2d_n^2 b_n + 2b_n^2 a_n^2 - c_n^2 b_n^2 - 2b_n c_n^2 h_n \\ &\quad + 4a_n c_n d_n h_n - 2d_n^2 h_n + 4b_n h_n^2 - 2h_n^2 a_n^2 - c_n^2 h_n^2, \\ s_4^n &= (b_n - h_n)^2 \big[-d_n^2 + (b_n + h_n)^2\big], \end{aligned} \tag{3.11}$$

and a_n, b_n, c_n, d_n, h_n are defined as in (3.9).

3.2 Non-diffusive Case

For simplicity, we consider the system without spatial and diffusion effect in this subsection. Thus we consider the stability of an equilibrium (u^*, v^*) of a system

$$\begin{cases} u_t = f(u, v, u_\tau, v_\tau), & t > 0, \\ v_t = g(u, v, u_\tau, v_\tau), & t > 0, \\ u(t) = \phi_1(t) \ge 0, v(t) = \phi_2(t) \ge 0, & t \in [-\tau, 0], \end{cases} \tag{3.12}$$

where $u = u(t)$, $v = v(t)$, $u_\tau = u(t-\tau)$, and $v_\tau = v(t-\tau)$. Then the more general framework for the stability/instability in Sect. 3.1 is also valid for (3.12). In particular, the coefficients defined in (3.9) and (3.11) are simplified by $\mu_n = 0$. In this case, the coefficients a_0, b_0, c_0, d_0, h_0 are completely determined by the Jacobian matrices L_1 and L_2:

$$\begin{aligned} &a_0 = -\mathrm{Tr}(L_1), \qquad b_0 = \mathrm{Det}(L_1), \qquad c_0 = -\mathrm{Tr}(L_2), \\ &d_0 = \frac{1}{2}\big[\mathrm{Det}(L_1 + L_2) - \mathrm{Det}(L_1 - L_2)\big], \qquad h_0 = \mathrm{Det}(L_2). \end{aligned} \tag{3.13}$$

Now we can state a general delay-induced instability result based on Theorem 2.14:

Theorem 3.1 *Suppose that $f, g \in C^1(\mathbb{R}^4)$, and (u^*, v^*) is an equilibrium of (3.12). Let L_1 and L_2 be the Jacobian matrices defined as in (3.5). Assume that*

$$\mathrm{Tr}(L_2) \neq 0, \quad \mathrm{Tr}(L_2) \neq \mathrm{Tr}(L_1), \quad \mathrm{Det}(L_2) \neq 0, \quad \mathrm{Det}(L_2) \neq \mathrm{Det}(L_1), \tag{3.14}$$

and for a_0, b_0, c_0, d_0, h_0 defined in (3.13), we have

$$b_0 + h_0 \leq \frac{a_0 d_0}{c_0} \quad \text{or} \quad \frac{d_0}{c_0}\left(2h_0 - \frac{a_0 d_0}{c_0}\right) - a_0\left(b_0 + h_0 - \frac{a_0 d_0}{c_0}\right) \neq 0. \tag{3.15}$$

If L_1 and L_2 satisfy

$$\mathrm{Tr}(L_1 + L_2) < 0, \quad \mathrm{Det}(L_1 + L_2) > 0, \quad \text{and} \quad \mathrm{Det}(L_1 - L_2) < 0, \tag{3.16}$$

then there exists $\tau_0 > 0$, the equilibrium (u^*, v^*) is stable for (3.12) when $0 \leq \tau < \tau_0$, and when $\tau = \tau_0$, the associated characteristic equation has a pair of purely imaginary root $\pm i\omega_0$ with $\theta = \theta_0$. If $\mathcal{G}(\omega_0, \theta_0) \neq 0$, then (u^*, v^*) is unstable when $\tau \in (\tau_0, \tau_0 + \epsilon)$ for $\epsilon > 0$ and small, and if moreover $\pm ik\omega_0$ ($k \in \mathbb{N}$ and $k \neq 1$) is not the eigenvalues, then a Hopf bifurcation for (3.12) occurs at $\tau = \tau_0$.

Similarly Corollary 2.15 implies the following observation:

Corollary 3.2 *Suppose that f, g, (u^*, v^*), L_1, and L_2 are the same as in Theorem 3.1. Let $M_{2\times 2}$ be the set of all real-valued 2×2 matrices, and let $\mathcal{M}_1$ be a subset of $(M_{2\times 2})^2$ consisting of all matrix pairs (L_1, L_2) satisfying (3.16). Then for almost every $(L_1, L_2) \in \mathcal{M}_1$, the conclusions in Theorem 3.1 hold.*

Notice that the first two conditions in (3.16) are necessary for the local stability of (u^*, v^*) when $\tau = 0$, hence the condition $\mathrm{Det}(L_1 - L_2) < 0$ is "almost" sufficient for the instability: the condition (3.14) is to avoid the degeneracy caused by the similarity of L_1 and L_2, and the condition (3.15) is to guarantee the non-degeneracy of purely imaginary root of the characteristic equation. We also notice that $\mathrm{Det}(L_2) \neq 0$ is necessary for $h_0 \neq 0$. When $h_0 = 0$, the purely imaginary roots of the characteristic equation (3.8) can be reduced to a simpler quadratic equation instead of a quartic equation which we consider here.

To conclude our discussion here, we mention the following result based on Proposition 2.13, which shows that if the delay effect is small, then it will not affect the stability of the equilibrium.

Proposition 3.3 *Suppose that f, g, (u^*, v^*), L_1, and L_2 are same as in Theorem 3.1. If L_1 satisfies*

$$\mathrm{Tr}(L_1) < 0, \quad \mathrm{Det}(L_1) > 0, \quad \left[\mathrm{Tr}(L_1)\right]^2 - 2\mathrm{Det}(L_1) > 0, \tag{3.17}$$

and $\|L_2\|_M < \delta$ for some $\delta > 0$, where $\|\cdot\|_M$ is the matrix norm, then the equilibrium (u^*, v^*) is stable for (3.12) and any $\tau \geq 0$.

3.3 Diffusive Case

For a fixed eigen-mode n, a discussion parallel to the one in Sect. 3.2 can be carried out by using a_n, b_n, c_n, d_n, h_n defined as in (3.9) with a fixed $\mu_n > 0$. Hence we can obtain an instability and Hopf bifurcation theorem similar to Theorem 3.1 as follows.

Theorem 3.4 *Suppose that $f, g, (u^*, v^*), L_1$, and L_2 are the same as in Theorem 3.1, D_1, D_2 are the diffusion coefficients, and μ_n is a simple eigenvalue of $-\Delta$ with Neumann boundary condition for $n \in \mathbb{N}_0$. Assume that*

$$\begin{aligned} &\mathrm{Tr}(L_2) \neq 0, \quad \mathrm{Tr}(L_2) \neq \mathrm{Tr}(L_1) - (D_1 + D_2)\mu_n, \\ &\mathrm{Det}(L_2) \neq 0, \quad \mathrm{Det}(L_2) \neq \mathrm{Det}(L_1) - (D_1 g_v + D_2 f_u)\mu_n + D_1 D_2 \mu_n^2, \end{aligned} \tag{3.18}$$

and for a_n, b_n, c_n, d_n, h_n defined in (3.9), we have

$$b_n + h_n \le \frac{a_n d_n}{c_n} \quad \text{or} \quad \frac{d_n}{c_n}\left(2h_n - \frac{a_n d_n}{c_n}\right) - a_n\left(b_n + h_n - \frac{a_n d_n}{c_n}\right) \neq 0. \tag{3.19}$$

If (D_1, D_2), L_1, and L_2 satisfy

$$\begin{aligned} &\mathrm{Tr}(L_1 + L_2) < (D_1 + D_2)\mu_n, \\ &\mathrm{Det}(L_1 + L_2) > \big[D_1(g_v + g_z) + D_2(f_u + f_w)\big]\mu_n - D_1 D_2 \mu_n^2, \quad \text{and} \\ &\mathrm{Det}(L_1 - L_2) < \big[D_1(g_v - g_z) + D_2(f_u - f_w)\big]\mu_n - D_1 D_2 \mu_n^2, \end{aligned} \tag{3.20}$$

then there exists $\tau_n > 0$, the equilibrium (u^*, v^*) is stable in mode n for (3.1) when $0 \le \tau < \tau_n$, and when $\tau = \tau_0$, the associated characteristic equation has a pair of purely imaginary root $\pm \mathrm{i}\omega_0$ with $\theta = \theta_0$. If $\mathcal{G}(\omega_0, \theta_0) \neq 0$, then (u^*, v^*) is unstable when $\tau \in (\tau_0, \tau_0 + \epsilon)$ for $\epsilon > 0$ and small, and if moreover $\pm \mathrm{i}k\omega_0$ ($k \in \mathbb{N}$ and $k \neq 1$) is not the eigenvalues, then a Hopf bifurcation for (3.12) occurs at $\tau = \tau_0$, and the bifurcating periodic orbits have the spatial profile of $\gamma_n(x)$.

Recall that s_i^n ($i = 1, 2, 3, 4$) are the coefficients of quartic characteristic equation (3.10) defined in (3.11). Observe that $\lim_{n\to\infty} s_1^n = \lim_{n\to\infty} s_3^n = \lim_{n\to\infty} s_4^n = +\infty$, and

$$\lim_{n\to\infty} \big[s_1^n s_2^n s_3^n - \big(s_3^n\big)^2 - \big(s_1^n\big)^2 s_4^n\big] = +\infty.$$

Then from the Routh–Hurwitz stability criterion, there exists $N_0 \ge 0$ such that (3.10) has no positive roots for $n > N_0$. Hence the instability/Hopf bifurcation described in Theorem 3.4 is only possible for a finite number of eigen-modes $0 \le n \le N_0$.

From the definition in Sect. 3.1, if the equilibrium (u^*, v^*) is stable in mode n with respect to (3.1) for all $n \in \mathbb{N}_0$, then it is stable with respect to (3.1). On the other hand, the instability for any mode n implies the instability with respect to (3.1). When the instability is possible for multiple eigen-modes with the bifurcation value τ_n for mode n, one can define $\tau_* = \min\{\tau_n : 0 \le n \le N_0\}$ as the minimal bifurcation value, where the equilibrium (u^*, v^*) first loses the stability as the delay τ increases (see Lemma 2.12).

It is clear that if the equilibrium (u^*, v^*) is unstable with respect to (3.12) for $\tau > 0$, then it is also unstable with respect to (3.1) for the same $\tau > 0$. However, it is not clear whether the minimal bifurcation value τ_* is always identical to τ_0, or in some cases, the equilibrium (u^*, v^*) is stable with respect to (3.12) for all $\tau \geq 0$ but it is unstable in some mode n ($n \geq 1$) for (3.1). Some examples of Hopf bifurcations as in Theorems 3.1 and 3.4 will be shown in Sect. 4, and in these examples, $\tau_* = \tau_0$ holds, and the bifurcating periodic orbits are spatially homogeneous.

4 Applications

4.1 Leslie–Gower Predator–Prey System with Delays

In this subsection we apply the result in Sect. 2 to the following Leslie–Gower system with delays:

$$\begin{cases} \dfrac{\mathrm{d}u(t)}{\mathrm{d}t} = u(t)\big(p - \alpha u(t) - \beta v(t-\tau)\big), & t > 0, \\ \dfrac{\mathrm{d}v(t)}{\mathrm{d}t} = \mu v(t)\left(1 - \dfrac{v(t-\tau)}{u(t-\tau)}\right), & t > 0, \end{cases} \tag{4.1}$$

where p, α, β, and μ are positive, and $\tau \geq 0$ reflects the delay effect. In the predation process, the predation of predator in the earlier times will decrease the rate of the prey population at a later times, and simultaneously, consumption of preys in earlier times will increase the predator population in a later time. The delay in the second equation shows the simultaneous effect of the prey and predator in the past on the per capita rate of predator $v(t)$. Similar simultaneous effect on the predator has analyzed extensively (see e.g. Beretta and Kuang 1998; Song et al. 2009, etc.). For example, Beretta and Kuang (1998) investigated the following delayed Holling–Tanner predator–prey model:

$$\begin{cases} \dfrac{\mathrm{d}x(t)}{\mathrm{d}t} = ax(t)\big(1 - x(t)/K\big) - cv\big(x(t)\big)y(t), & t > 0, \\ \dfrac{\mathrm{d}y(t)}{\mathrm{d}t} = dy(t)\big(1 - fy(t-\tau)/x(t-\tau)\big), & t > 0, \end{cases}$$

and Song et al. (2009) studied the following delayed Leslie–Gower model:

$$\begin{cases} \dfrac{\mathrm{d}x(t)}{\mathrm{d}t} = ax(t)\big(1 - x(t)/K\big) - cx(t)y(t), & t > 0, \\ \dfrac{\mathrm{d}y(t)}{\mathrm{d}t} = dy(t)\big(1 - fy(t-\tau)/x(t-\tau)\big), & t > 0. \end{cases}$$

Apart from the simultaneous delay effect of the prey and predator on the per capita rate of predator $v(t)$, we also consider the delay effect on the prey $u(t)$, and hence we arrive at the model (4.1).

System (4.1) has a unique positive equilibrium

$$\big(u^*, v^*\big) = \left(\frac{p}{\alpha+\beta}, \frac{p}{\alpha+\beta}\right), \tag{4.2}$$

and the Jacobian matrices at (u^*, v^*) are given by

$$L_1 = \begin{pmatrix} -\frac{\alpha p}{\alpha+\beta} & 0 \\ 0 & 0 \end{pmatrix}, \qquad L_2 = \begin{pmatrix} 0 & -\frac{\beta p}{\alpha+\beta} \\ \mu & -\mu \end{pmatrix}.$$

Hence the characteristic equation of system (4.1) is in the same form as (1.8) with

$$a = \frac{\alpha p}{\alpha+\beta}, \qquad b = 0, \qquad c = \mu, \qquad d = \frac{\mu\alpha p}{\alpha+\beta}, \qquad h = \frac{\mu\beta p}{\alpha+\beta}. \tag{4.3}$$

Since $a + c > 0$ and $b + d + h > 0$ hold for any parameter $\alpha, \beta, p, \mu > 0$, (u^*, v^*) is always locally asymptotically stable when $\tau = 0$.

If $\alpha > \beta$, then $d^2 > (b+h)^2$, and from Lemma 2.11, (2.7) has at least one positive root, which is a necessary condition that can induce the Hopf bifurcation. Indeed we can apply Theorem 2.14 to obtain the following result.

Theorem 4.1 *Assume that $\alpha > \beta > 0$, and $p, \mu > 0$. Then there exists a $\tau_* \in (0, \infty)$, such that the unique positive equilibrium (u_*, v_*) of system (4.1) is locally asymptotically stable when $0 \le \tau < \tau_*$, and when $\tau = \tau_*$, the associated characteristic equation has a pair of purely imaginary roots $\pm i\omega_*$. Moreover, if $\mathcal{G}(\theta_*, \omega_*) \neq 0$ (defined as in (2.29)) and $\pm ik\omega_*$ ($k \in \mathbb{N}$ and $k \neq 1$) is not the root of (1.8), then system (4.1) undergoes a Hopf bifurcation at (u_*, v_*) when $\tau = \tau_*$ it is unstable when $\tau \in (\tau_*, \tau_* + \epsilon)$ for $\epsilon > 0$ and small.*

Proof To apply Theorem 2.14, we observe that condition (i) is satisfied here. Since $\alpha > \beta$, condition (ii) in Theorem 2.14 is also satisfied. From (4.3), we also see that condition (iii) is satisfied if

$$\mu \neq \frac{\alpha^2 p}{(\alpha+\beta)\beta} \quad \text{and} \quad \mu \neq \frac{\alpha p}{\alpha+\beta}, \quad \text{or} \quad \mu \le \frac{\alpha^2 p}{(\alpha+\beta)\beta}, \tag{4.4}$$

which indeed covers all possible μ. Hence the conclusions in the theorem are obtained from Theorem 2.14. □

It is interesting to compare this theorem with a result in Chen et al. (2012), in which a similar system is considered:

$$\begin{cases} \dfrac{\partial u(x,t)}{\partial t} - d_1 \Delta u(x,t) = u(x,t)\big(p - \alpha u(x,t) - \beta v(x, t-\tau_1)\big), & x \in \Omega,\ t > 0, \\ \dfrac{\partial v(x,t)}{\partial t} - d_2 \Delta v(x,t) = \mu v(x,t)\left(1 - \dfrac{v(x,t)}{u(x,t-\tau_2)}\right), & x \in \Omega,\ t > 0, \\ \dfrac{\partial u(x,t)}{\partial \nu} = \dfrac{\partial v(x,t)}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ u(x,t) = u_0(x,t) > 0, & x \in \Omega,\ t \in [-\tau_2, 0]. \\ v(x,t) = v_0(x,t) > 0, & x \in \Omega,\ t \in [-\tau_1, 0], \end{cases} \tag{4.5}$$

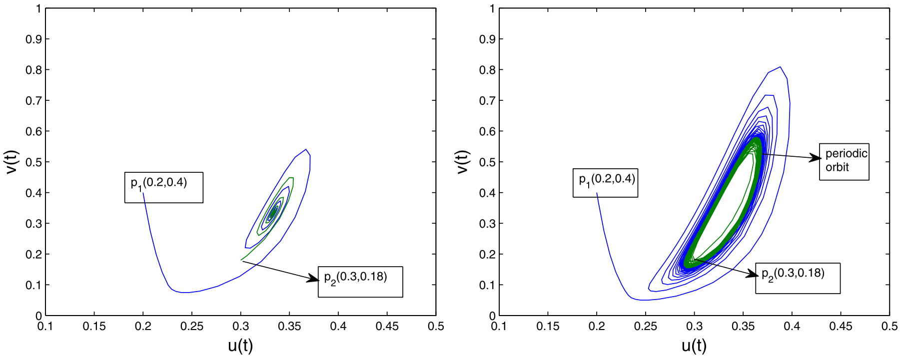

Fig. 2 Phase portraits for system (4.1) with initial conditions $P_1 = (0.2, 0.4)$ and $P_2 = (0.3, 0.18)$. Here $p = 0.5$, $\alpha = 1$, $\beta = 0.5$, $\mu = 1$. (*Left*) $\tau = 1.4$; (*right*) $\tau = 1.8$

where the two delays show the inter-specific interactions on the predator–prey system (see Ruan 2009). Here the increasing of the predator just depends on the prey in the past. Similar inter-specific interactions have been analyzed by many researchers (see e.g. Faria 2001). For system (4.5), it was shown that when $\alpha > \beta$, the positive equilibrium (u^*, v^*) is globally asymptotically stable for any $\tau_1, \tau_2 \geq 0$. The results in this paper show that the simultaneous delay effect can destabilize the positive equilibrium (u^*, v^*) and induce the oscillatory phenomenon through Hopf bifurcation. The methods in Sect. 2 can be used to numerically calculate the bifurcation values of (4.1). Here we choose $p = \beta = 0.5$, $\alpha = 1$, and $\mu = 1$; then

$$\begin{aligned} &a = 1/3, \quad b = 0, \quad c = 1, \quad d = 1/3, \quad h = 1/6, \\ &s_1 \approx -0.7778, \quad s_2 \approx 0.0679; \quad s_3 \approx -0.0093, \quad s_4 \approx -0.0023. \end{aligned} \tag{4.6}$$

By using Lemma 2.3, (2.7) has a non-degenerate positive real root $\omega^2 \approx 0.7068$, (1.8) has a pair of purely imaginary roots $\pm i\omega \approx \pm 0.8408i$, and the Hopf bifurcation values are given by $\tau^j \approx 1.748 + \frac{2j\pi}{0.8408}$ for $j \in \mathbb{N}_0$. In particular $\tau^0 \approx 1.748$. The transversality condition (positive value) at $\tau = \tau^j$ can also be verified by using (2.29) and the above values of θ and ω.

In Fig. 2, one can see that the positive equilibrium $(u^*, v^*) = (1/3, 1/3)$ of system (4.1) is locally asymptotically stable when $\tau \in [0, \tau^0)$, and when $\tau > \tau^0$, (u^*, v^*) is unstable and a limit cycle emerges. A bifurcation diagram showing the amplitude of the limit cycle versus the delay τ is plotted in Fig. 3.

4.2 Gierer–Meinhardt System with Delays

In this subsection we apply the results in previous sections to the following Gierer–Meinhardt system with the gene expression time delays which is proposed in Lee et

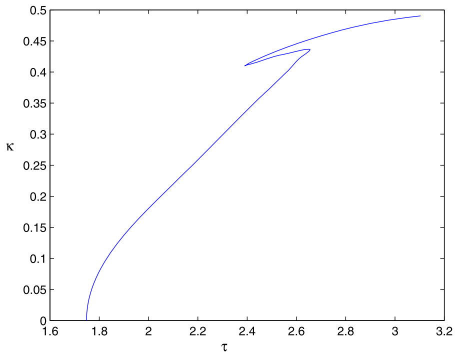

Fig. 3 Hopf bifurcation branch for (4.1) starting from $\tau^0 \approx 1.748$ on the (τ,κ)-plane, where $\kappa = \max u(t) - \min u(t)$. Hence the direction of the Hopf bifurcation is forward and the bifurcating periodic orbit is stable. Here $p = 0.5$, $\alpha = 1$, $\beta = 0.5$, and $\mu = 1$

al. (2010):

$$\begin{cases} \dfrac{\partial U}{\partial t} = D_1 \dfrac{\partial^2 U}{\partial x^2} + k_1 - k_2 U(x,t) + k_3 \dfrac{U^2(x,t-\tau)}{V(x,t-\tau)}, \\ \dfrac{\partial V}{\partial t} = D_2 \dfrac{\partial^2 V}{\partial x^2} + k_4 U^2(x,t-\tau) - k_5 V(x,t), \end{cases} \tag{4.7}$$

where k_i $(1 \le i \le 5)$ are positive constants which represent the feeding rate, the production rates, and the decay rates of the morphogens, and $\tau \ge 0$ represents the effect of the gene expression time delay. Here we shall consider a nondimensionalized version with spatial dimension $n = 1$ and the spatial domain $\Omega = (0,\pi)$ of the following form:

$$\begin{cases} \dfrac{\partial u(x,t)}{\partial t} = \epsilon^2 D \dfrac{\partial^2 u(x,t)}{\partial x^2} + \gamma\left(p - qu(x,t) + \dfrac{u^2(x,t-\tau)}{v(x,t-\tau)}\right), & x \in (0,\pi),\ t > 0, \\ \dfrac{\partial v(x,t)}{\partial t} = D \dfrac{\partial^2 v(x,t)}{\partial x^2} + \gamma\big(u^2(x,t-\tau) - v(x,t)\big), & x \in (0,\pi),\ t > 0, \\ \dfrac{\partial u(0,t)}{\partial x} = \dfrac{\partial u(\pi,t)}{\partial x} = \dfrac{\partial v(0,t)}{\partial x} = \dfrac{\partial v(\pi,t)}{\partial x} = 0, & t > 0, \\ u(x,t) = \phi_1(x,t) \ge 0, v(x,t) = \phi_2(x,t) \ge 0, & x \in (0,\pi),\ t \in [-\tau, 0], \end{cases} \tag{4.8}$$

where $D, \epsilon, p, q, \gamma$, and τ are positive parameters. System (4.8) has a unique positive equilibrium

$$\left(u^*, v^*\right) = \left(\frac{p+1}{q}, \left(\frac{p+1}{q}\right)^2\right). \tag{4.9}$$

For $n \in \mathbb{N}_0$, the eigenvalues of $-\Delta$ in $(0,\pi)$ with Neumann boundary conditions are $\mu_n = n^2$ with the corresponding eigenfunction $\cos nx$, and the Jacobian matrices at (u^*, v^*) are

$$L_1 = \begin{pmatrix} -\gamma q & 0 \\ 0 & -\gamma \end{pmatrix}, \qquad L_2 = \begin{pmatrix} \frac{2q\gamma}{p+1} & -\frac{q^2\gamma}{(p+1)^2} \\ \frac{2(p+1)\gamma}{q} & 0 \end{pmatrix}.$$

Hence we have

$$
\begin{aligned}
a_n &= (\epsilon^2+1)Dn^2+\gamma(q+1), \qquad b_n = (\epsilon^2 Dn^2+\gamma q)(Dn^2+\gamma),\\
c_n &= -\frac{2q\gamma}{p+1}, \qquad d_n = -(Dn^2+\gamma)\frac{2q\gamma}{p+1}, \qquad h_n = \frac{2q\gamma^2}{p+1}.
\end{aligned}
\tag{4.10}
$$

We first analyze system (4.8) without the diffusion effect, that is,

$$
\begin{cases}
\dfrac{du}{dt} = \gamma\left(p - qu(t) + \dfrac{u^2(t-\tau)}{v(t-\tau)}\right)\\
\dfrac{dv}{dt} = \gamma\left(u^2(t-\tau) - v(t)\right).
\end{cases}
\tag{4.11}
$$

The characteristic equation of (u^*, v^*) with respect to (4.11) is

$$
\lambda^2 + \gamma(q+1)\lambda + \gamma^2 q + \frac{2q\gamma}{p+1}\left[-(\lambda+\gamma)e^{-\lambda\tau} + \gamma e^{-2\lambda\tau}\right] = 0. \tag{4.12}
$$

Lemma 4.2 *Assume that* $p, q, \gamma > 0$. *If* $p > \frac{q-1}{q+1}$, *then the positive equilibrium* (u^*, v^*) *of system* (4.11) *is local asymptotically stable when* $\tau = 0$.

Proof When $\tau = 0$, the characteristic equation (4.12) is reduced to

$$
\lambda^2 + \gamma\left(q + 1 - \frac{2q}{p+1}\right)\lambda + \gamma^2 q = 0, \tag{4.13}
$$

then the result easily follows. □

By using Proposition 2.13, we have

Proposition 4.3 *For any* $q, \gamma > 0$, *there exist* $p_0(q) > 0$ *such that for any* $p > p_0(q)$, *the positive equilibrium* (u^*, v^*) *of system* (4.11) *is locally asymptotically stable for any* $\tau \ge 0$.

From Lemma 4.2 and Proposition 4.3, a delay-induced instability could occur for $\frac{q-1}{q+1} < p < p_0(q)$. For p in that range, if (2.7) has a positive root, then one can use the machineries in Sect. 2 to determine the nature of the Hopf bifurcation. It is easy to see that $d_0^2 \le (b_0 + h_0)^2$ here, hence one cannot apply Theorem 2.14 or the condition (R_1) in Lemma 2.11. The conditions (R_2) and (R_3) are more difficult to apply due to the complexity of the cubic/quartic equation. Analytically we can prove the following result regarding the positive roots of (2.7).

Lemma 4.4 *Suppose that* $\gamma > 0$, $q > 0$, *and* $q \ne 1$. *Then there exists* $\epsilon = \epsilon(q) > 0$ *such that* (2.7) *corresponding to* (u^*, v^*) *of system* (4.11) *has two positive roots when* $0 < |p-1| < \epsilon(q)$, *and it has one positive root when* $p = 1$.

Proof One can calculate that for (u^*, v^*) of system (4.11), from (4.10) with $n = 0$,

$$\begin{aligned} s_1 &= 2\gamma^2\left(q^2 + 1 - \frac{2q^2}{(p+1)^2}\right), \\ s_2 &= \gamma^4\left(q^4 + 4q^2 + 1 + \frac{16q^3}{(p+1)^3} - \frac{4q^2(q^2+4)}{(p+1)^2}\right), \\ s_3 &= 2\gamma^6 q^2\left(q^2 + 1 + \frac{8q^2+8q}{(p+1)^3} - \frac{8q^2+6}{(p+1)^2} - \frac{8q^2}{(p+1)^4}\right), \\ s_4 &= \gamma^8 q^4 \frac{(p-1)^2(p+5)}{(p+1)^3}. \end{aligned} \tag{4.14}$$

In particular when $p = 1$, these coefficients are simplified to

$$s_1 = \gamma^2(q^2+2), \qquad s_2 = \gamma^4(2q^3+1), \qquad s_3 = -\gamma^6 q^2(q-1)^2, \qquad s_4 = 0.$$

Hence (2.7) in this case becomes

$$z \cdot \left[z^3 + \gamma^2(q^2+2)z^2 + \gamma^4(2q^3+1)z - \gamma^6 q^2(q-1)^2\right] = 0.$$

It is easy to see that the polynomial $h_1(z) = z^3 + \gamma^2(q^2+2)z^2 + \gamma^4(2q^3+1)z - \gamma^6 q^2(q-1)^2$ has one positive real root for any $q > 0$ and $q \neq 1$ as $h_1(0) < 0$, h_1 is strictly increasing and $h_1(z) \to \infty$ as $z \to \infty$. For $h(z) = z^4 + s_1 z^3 + s_2 z^2 + s_3 z + s_4$ with s_i defined in (4.14), $h(0) = s_4 > 0$ for any $p \neq 1$ and $q > 0$. Then a perturbation argument yields two positive roots of $h(z) = 0$ for $p \neq 1$ but close to $p = 1$. □

Lemma 4.4 shows that for an open subset in (p, q) parameter plane, (2.7) has two positive roots. On the other hand, one can see that when $(p, q) = (1, 1)$, then it does not have any positive roots.

To demonstrate the delay-induced instability, we choose $p = 0.2$, $q = 0.8$, and $\gamma = 1$, and we use the method in Sects. 2 and 3 to find bifurcation values. In this case, the positive equilibrium is $(u^*, v^*) = (1.5, 2.25)$ and we can compute that

$$\begin{aligned} &a = 1.8, \qquad b = 0.8, \qquad c \approx -1.3333, \qquad d \approx -1.3333, \qquad h \approx 1.3333, \\ &s_1 \approx 1.5022, \qquad s_2 \approx 0.4615, \qquad s_3 \approx -2.4124, \qquad s_4 \approx 0.7886. \end{aligned} \tag{4.15}$$

So the parameters satisfy (2.11), and from Lemma 2.3, any positive real root of (2.7) is non-degenerate, and then (1.8) has a pair of purely imaginary roots $\pm i\omega_+$ when $\tau = \tau^j$ defined as in (2.8).

From numerical root finding, (2.7) has two positive real roots $\omega_1^2 \approx 0.4194$ and $\omega_2^2 \approx 0.6441$, thus $\omega_1 \approx 0.6476$ and $\omega_2 \approx 0.8026$. Hence when $\tau = \tau_1^j \approx 0.4243 + \frac{2j\pi}{0.6476}$, $j = 0, 1, 2, \ldots$, (1.8) has a pair of purely imaginary roots $\pm i\omega_1 \approx \pm 0.6476i$; and when $\tau = \tau_2^j \approx 5.7817 + \frac{2j\pi}{0.8026}$, $j = 0, 1, 2, \ldots$, (1.8) has a pair of purely imaginary roots $\pm i\omega_2 \approx \pm 0.8026i$. The transversality condition (positive value) is satisfied at all bifurcation points.

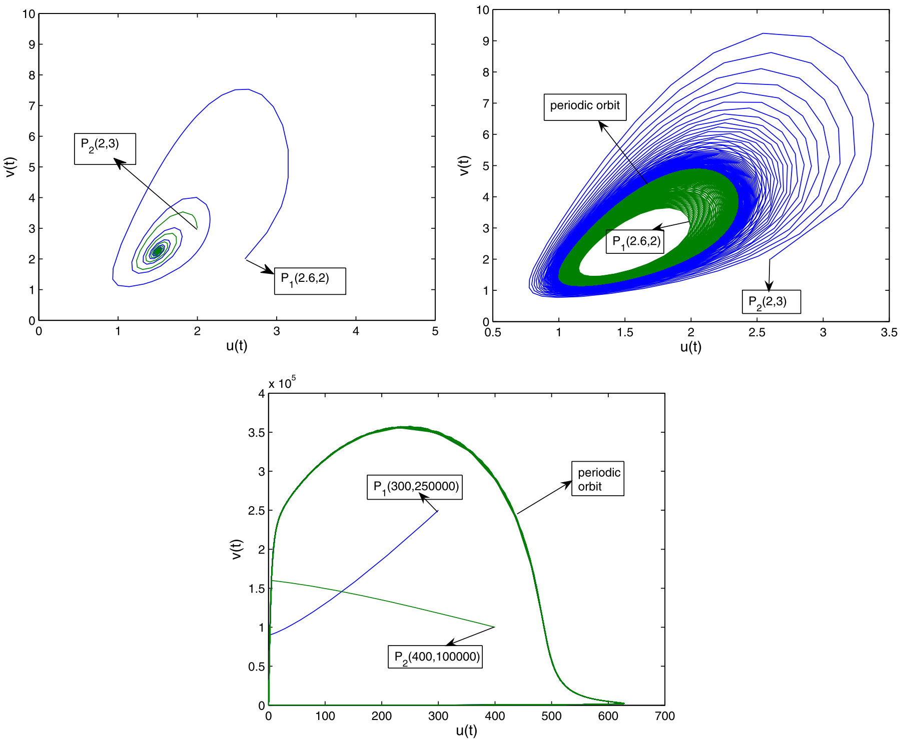

Fig. 4 Phase portraits and bifurcation diagram for system (4.11). Here $p = 0.2$, $q = 0.8$, $\gamma = 1$. (*Upper left*) Solution orbits for $\tau = 0.2$, initial conditions $P_1 = (2.6, 2)$ and $P_2 = (2, 3)$; (*upper right*) solution orbits for $\tau = 0.43$, initial conditions $P_1 = (2.6, 2)$ and $P_2 = (2, 3)$; (*lower*) solution orbits for $\tau = 6$, initial conditions $P_1 = (300, 250\,000)$ and $P_2 = (400, 100\,000)$

In particular $\tau_1^0 \approx 0.4243$ is the first Hopf bifurcation point, so that system (4.11) is locally asymptotically stable when $\tau \in [0, \tau_1^0)$, and when $\tau > \tau_1^0$, $(u^*, v^*) = (1.5, 2.25)$ becomes unstable and a periodic orbit becomes the attractor. In Fig. 4 (upper panel), solution trajectories for $\tau < \tau_1^0$ and $\tau > \tau_1^0$ are plotted. When the time delay τ increases, the size of the limit cycle grows sharply. In Fig. 4 (lower panel), the limit cycle profile with $\tau = 6$ is plotted, and for this case, a spiky pulse shape with large peak value is achieved by both $u(t)$ and $v(t)$ (see Fig. 5). From the bifurcation diagram (Fig. 6), which shows the amplitude of oscillation, one can observe that the amplitude of oscillation in u-direction increases almost linearly with τ with slope 100, and the amplitude of oscillation in v-direction is about the square of the amplitude of oscillation in u-direction. Indeed the peak of $v(t)$ appears to be achieved τ time units after the peak of $u(t)$ (see Fig. 5); hence from the equation of $v(t)$, $\max v(t) = v(t_0) \approx u^2(t_0 - \tau) = \max u^2(t)$.

Next we consider system (4.8) with the effect of diffusion. A similar analysis can be done parallel to that of (4.11). Here we will only consider the numerical case of $p = 0.2$, $q = 0.8$, and $\gamma = 1$ again, and let $\epsilon^2 = 0.1$, $D = 0.3$. Then (3.10) has no positive real roots for $n \geq 2$, and (3.10) has two positive real roots $\omega_{1,1}^2 \approx 0.09274$ and

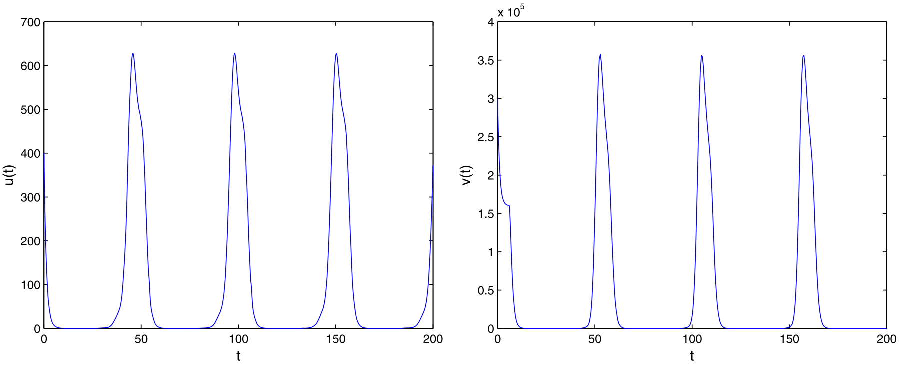

Fig. 5 Solution curves of (4.11) when $p = 0.2$, $q = 0.8$, $\gamma = 1$, $\tau = 6$. (*Left*) $u(t)$; (*right*) $v(t)$

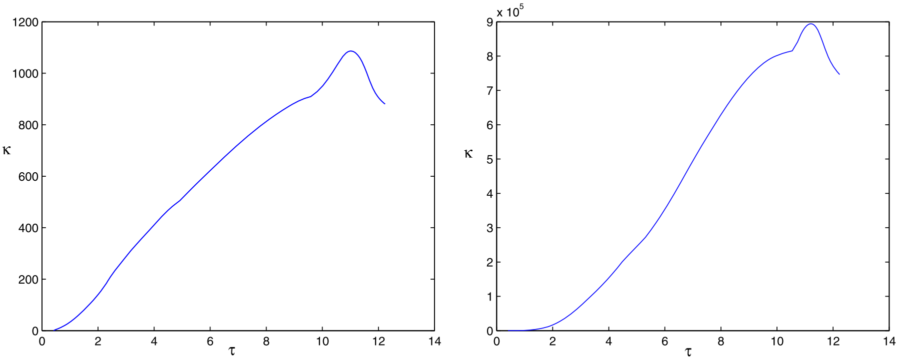

Fig. 6 Bifurcation diagram for system (4.11) with $p = 0.2$, $q = 0.8$, $\gamma = 1$. The curve is the Hopf bifurcation branch of (4.11) starting from $\tau_1^0 \approx 0.4243$ on the (τ, κ)-plane, where $\kappa = \max u(t) - \min u(t)$ (*left*); and $\kappa = \max v(t) - \min v(t)$ (*right*). Hence the direction of the Hopf bifurcation is forward and the bifurcating periodic orbit is stable

$\omega_{2,1}^2 \approx 0.493$ for $n = 1$. Hence there are two additional bifurcation sequences: $\tau = \tau_{1,1}^j \approx 1.6247 + \frac{2j\pi}{0.3045}$, $j = 0, 1, 2, \ldots$, (3.8) with $n = 1$ has purely imaginary roots $\pm \mathrm{i}\omega_{1,1} \approx \pm 0.3045\mathrm{i}$; and $\tau = \tau_{2,1}^j \approx 6.8979 + \frac{2j\pi}{0.7021}$, $j = 0, 1, 2, \cdots$, (3.8) with $n = 1$ has purely imaginary roots $\pm \mathrm{i}\omega_{2,1} \approx \pm 0.7021\mathrm{i}$. Again the transversality condition (positive value) is satisfied at these bifurcation points.

Together with the bifurcation points with $n = 0$, the delayed reaction–diffusion system (4.8) has four sequences of Hopf bifurcation points. But comparing the numerical values, we still have the smallest Hopf bifurcation value

$$\tau_* = \min\{\tau_{1,0}^0 = \tau_1^0, \tau_{2,0}^0 = \tau_2^0, \tau_{1,1}^0, \tau_{2,1}^0\}.$$

Hence the positive equilibrium $(u^*, v^*) = (1.5, 2.25)$ of system (4.8) is still locally asymptotically stable when $\tau \in [0, \tau_*)$; and when $\tau > \tau_*$, it becomes unstable and a spatially homogeneous periodic orbit becomes stable (see Figs. 7 and 8).

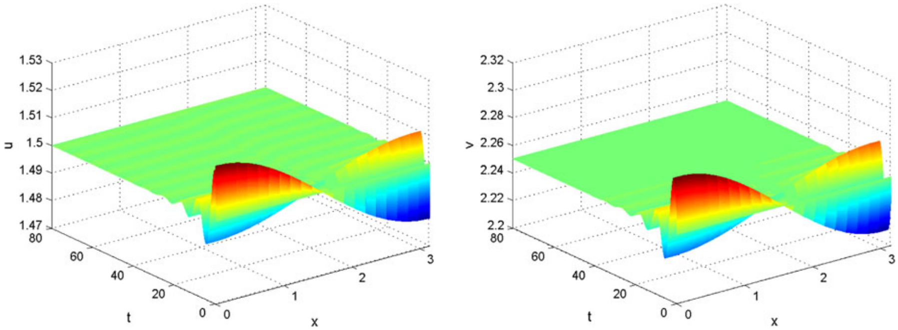

Fig. 7 Convergence to constant equilibrium for system (4.8) with $\tau = 0.2 < \tau_0^1$. Here $p = 0.2$, $q = 0.8$, and $\gamma = 1$, $\epsilon^2 = 0.1$, $D = 0.3$, and the initial value is $(u^* + 0.1t\cos x, v^* + 0.1t\cos x)$, $(x, t) \in [0, \pi] \times [-0.2, 0]$

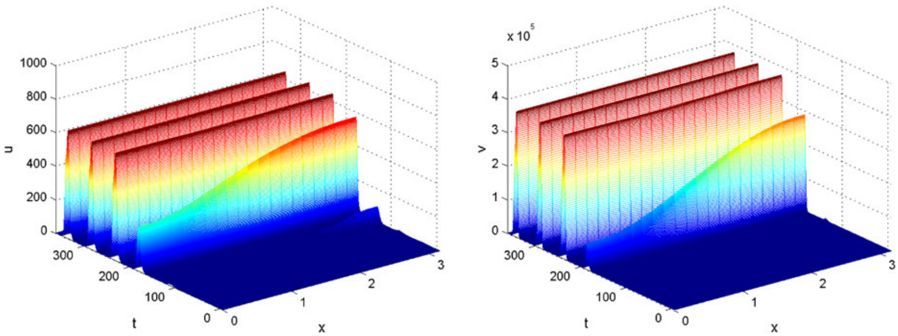

Fig. 8 Convergence to a spatially homogeneous periodic orbit for system (4.8) with $\tau = 6 > \tau_0^1$. Here $p = 0.2$, $q = 0.8$, and $\gamma = 1$, $\epsilon^2 = 0.1$, $D = 0.3$, and the initial value is $(u^* + 0.1t\cos x, v^* + 0.1t\cos x)$, $(x, t) \in [0, \pi] \times [-6, 0]$

4.3 Gierer–Meinhardt System with Saturation and Delays

In this subsection we apply the results in previous sections to the following Gierer–Meinhardt system with saturation and the gene expression time delays which is proposed in Lee et al. (2010):

$$
\begin{cases}
\dfrac{\partial u}{\partial t} = \epsilon^2 D \dfrac{\partial^2 u}{\partial x^2} + \gamma\left(p - qu(x,t) + \dfrac{u^2(x,t-\tau)}{(1+\kappa u^2(x,t-\tau))v(x,t-\tau)}\right), \\
\quad x \in (0,\pi),\ t > 0, \\
\dfrac{\partial v}{\partial t} = D\dfrac{\partial^2 v}{\partial x^2} + \gamma\left(u^2(x,t-\tau) - v(x,t)\right), \quad x \in (0,\pi),\ t > 0, \\
\dfrac{\partial u(0,t)}{\partial x} = \dfrac{\partial u(\pi,t)}{\partial x} = \dfrac{\partial v(0,t)}{\partial x} = \dfrac{\partial v(\pi,t)}{\partial x} = 0, \quad t > 0, \\
u(x,t) = \phi_1(x,t) \ge 0, v(x,t) = \phi_2(x,t) \ge 0, \quad x \in (0,\pi),\ t \in [-\tau, 0],
\end{cases}
\tag{4.16}
$$

where D, ϵ, p, q, γ, κ, and τ are positive parameters. Apparently the system (4.16) becomes (4.8) if $\kappa = 0$. System (4.16) has a unique positive equilibrium (u_*, v_*) satisfying

$$qu_* - p = \frac{1}{1+\kappa u_*^2}, \quad \text{and} \quad v_* = u_*^2. \tag{4.17}$$

For $n \in \mathbb{N}_0$, the eigenvalues of $-\Delta$ in $(0,\pi)$ with Neumann boundary conditions are $\mu_n = n^2$ with the corresponding eigenfunction $\cos nx$, and the Jacobian matrices at (u^*, v^*) are

$$L_1 = \begin{pmatrix} -\gamma q & 0 \\ 0 & -\gamma \end{pmatrix}, \qquad L_2 = \begin{pmatrix} \frac{2\gamma}{(1+\kappa u_*^2)^2 u_*} & -\frac{\gamma}{(1+\kappa u_*^2)u_*^2} \\ 2\gamma u_* & 0 \end{pmatrix}.$$

Hence we have

$$\begin{aligned} a_n &= (\epsilon^2+1)Dn^2 + \gamma(q+1), \qquad b_n = (\epsilon^2 Dn^2 + \gamma q)(Dn^2+\gamma), \\ c_n &= -\frac{2\gamma}{(1+\kappa u_*^2)^2 u_*}, \qquad d_n = -\frac{2\gamma(Dn^2+\gamma)}{(1+\kappa u_*^2)^2 u_*}, \qquad h_n = \frac{2\gamma^2}{(1+\kappa u_*^2)u_*}, \end{aligned} \tag{4.18}$$

and s_i^n $(1 \le i \le 4)$ can be defined as in (3.11). For each $n \in \mathbb{N}$,

$$\lim_{\kappa\to\infty} s_1^n = \lim_{\kappa\to\infty} s_3^n = \lim_{\kappa\to\infty} s_4^n = +\infty, \quad \text{and}$$
$$\lim_{\kappa\to\infty} \left(s_1^n s_2^n s_3^n - (s_3^n)^2 - (s_1^n)^2 s_4^n\right) = +\infty.$$

Then from the Routh–Hurwitz Criterion, we know that for sufficiently large $\kappa > 0$, the unique positive equilibrium (u_*, v_*) of system (4.16) is locally asymptotically stable. In Chen and Shi (2012), we prove that for sufficiently large $\kappa > 0$, (u_*, v_*) is globally attractive with respect to (4.16). Hence for sufficiently large $\kappa > 0$, (u_*, v_*) is globally asymptotically stable, and a delay-induced instability can only occur for $0 < \kappa < \kappa_0(p,q,\gamma)$ for some constant $\kappa_0(p,q,\gamma)$.

To focus on the effect of saturation, here we still choose $p = 0.2$, $q = 0.8$, $\gamma = 1$, $\epsilon^2 = 0.1$, and $D = 0.3$ as in Sect. 4.2, and we choose $\kappa = 0.8$. For $n \ge 2$, (3.10) has no positive roots, and hence (3.8) for $n \ge 2$ has no purely imaginary roots.

For $n = 0$, we can compute

$$\begin{aligned} &a_0 = 1.8, \quad b_0 = 0.8, \quad c_0 \approx -0.6791, \quad d_0 \approx -0.6791, \quad h_0 \approx 1.1858, \\ &s_1^0 \approx 2.8188, \quad s_2^0 \approx 1.0334, \quad s_3^0 \approx -2.2445, \quad s_4^0 \approx 0.5184. \end{aligned} \tag{4.19}$$

Then (3.10) for $n = 0$ has two positive real roots $\omega_{1,0}^2 \approx 0.4247$ and $\omega_{2,0}^2 \approx 0.3373$. This gives the corresponding bifurcation frequencies and delay values:

$$\omega_{1,0} \approx 0.5808, \qquad \tau_{1,0}^j \approx 1.1146 + \frac{2j\pi}{0.5808};$$
$$\omega_{2,0} \approx 0.6516, \qquad \tau_{2,0}^j \approx 6.7929 + \frac{2j\pi}{0.6516}.$$

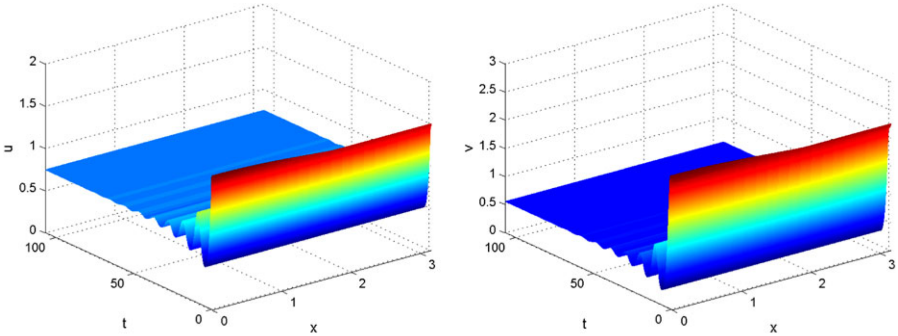

Fig. 9 Convergence to constant equilibrium for system (4.16) with $\tau = 0.8 < \tau_* \approx 1.1146$. Here $p = 0.2$, $q = 0.8$, and $\gamma = 1$, $\kappa = 0.8$, $\epsilon^2 = 0.1$, $D = 0.3$, $(u^*, v^*) \approx (0.9658, 0.9328)$, and the initial values are $P_1 = (u(t), v(t)) = (1.5 + 0.1t\cos x, 2.25 + t\cos x)$, $(x, t) \in [0, \pi] \times [-0.8, 0]$

Similarly for $n = 1$, we can compute

$$\begin{aligned} &a_1 \approx 2.1300, \quad b_1 \approx 1.0790, \quad c_1 \approx -0.6791, \quad d_1 \approx -0.8828, \\ &h_1 \approx 1.1858, \\ &s_1^1 \approx 4.2966, \quad s_2^1 \approx 4.3925, \quad s_3^1 \approx -1.1622, \quad s_4^1 \approx 0.0497. \end{aligned} \tag{4.20}$$

Then (3.10) for $n = 1$ has two positive real roots $\omega_{1,1}^2 \approx 0.0547$ and $\omega_{2,1}^2 \approx 0.1686$, which gives the corresponding bifurcation frequencies and delay values:

$$\begin{aligned} \omega_{1,1} &\approx 0.2339, \qquad \tau_{1,1}^j \approx 4.0666 + \frac{2j\pi}{0.2339}; \\ \omega_{2,1} &\approx 0.4106, \qquad \tau_{2,1}^j \approx 11.4849 + \frac{2j\pi}{0.4106}. \end{aligned}$$

Hence similar to the delayed Gierer–Meinhardt system (4.8), the delayed Gierer–Meinhardt system with saturation (4.16) also has four sequences of Hopf bifurcation points. Again similar to the case of (4.8), we still have

$$\tau_{1,0}^0 = \min\{\tau_{1,0}^0, \tau_{2,0}^0, \tau_{1,1}^0, \tau_{2,1}^0\}.$$

That is, the smallest Hopf bifurcation value τ_* arises for $n = 0$, and the constant equilibrium loses the stability to a spatially homogeneous limit cycle. It is unclear whether the smallest Hopf bifurcation value τ_* always occurs for $n = 0$, but it is true for both (4.8) and (4.16).

On the other hand, the smallest Hopf bifurcation value $\tau_* \approx 1.1146$ for (4.16) is larger than the one for (4.8) ($\tau_* \approx 0.4243$). This shows that the saturation effect will increase the threshold delay value τ_* where the constant equilibrium loses the stability.

Figures 9 and 10 shows the dynamical behavior of system (4.16) when $\tau < \tau_*$ and $\tau > \tau_*$, respectively, which is similar to those for (4.8). On the other hand, the result in Chen and Shi (2012) shows that when κ is sufficiently large (in this case $\kappa = 20$), (u^*, v^*) of system (4.8) is globally asymptotically stable (see Fig. 11).

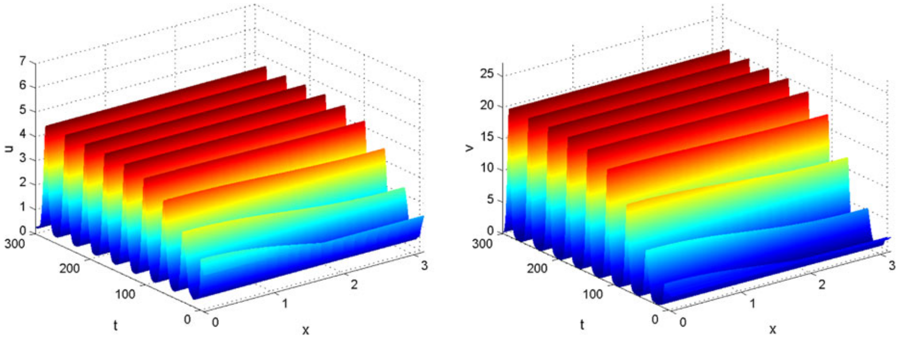

Fig. 10 Convergence to spatially homogeneous periodic orbit for system (4.16) with $\tau = 6 > \tau_* \approx 1.1146$. Here $p = 0.2$, $q = 0.8$, and $\gamma = 1$, $\kappa = 0.8$, $\epsilon^2 = 0.1$, $D = 0.3$, $(u^*, v^*) \approx (0.9658, 0.9328)$, and the initial values are $P_1 = (u(t), v(t)) = (1.5 + 0.1t\cos x, 2.25 + 0.1t\cos x)$, $(x, t) \in [0, \pi] \times [-6, 0]$

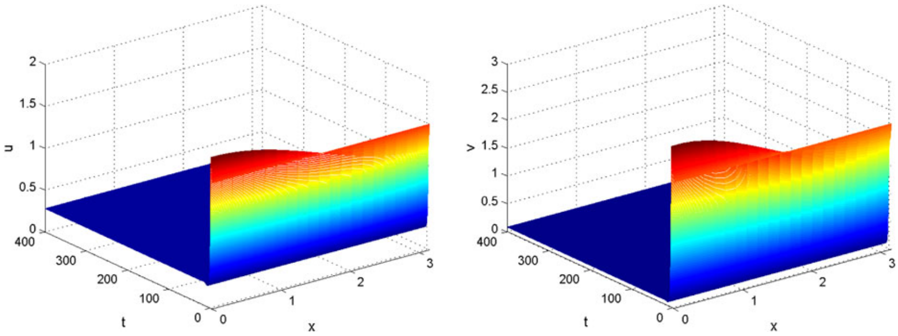

Fig. 11 Convergence to constant equilibrium for system (4.16) with $\tau = 3$ and large κ. Here $p = 0.2$, $q = 0.8$, and $\gamma = 1$, $\kappa = 20$, $\epsilon^2 = 0.1$, $D = 0.3$, $(u_*, v_*) \approx (0.4766, 0.2266)$, and the initial values are $P_1 = (u(t), v(t)) = (1.5 + 0.1t\cos x, 2.25 + 0.1t\cos x)$, $(x, t) \in [0, \pi] \times [-3, 0]$

The aim of Lee et al. (2010) was to assess whether gene expression time delays induce radically different spatial-temporal patterns. The numerical simulations in Lee et al. (2010) showed that time-periodic spatial-temporal behavior occurs for system (4.8) (see Fig. 5(C, F) and Fig. 6(F) in Lee et al. 2010). In Lee et al. (2010), Seirin Lee, Gaffney, and Monk also showed that time-periodic spatial-temporal behavior occurs for system (4.16) (see Fig. 7(E, F) in Lee et al. 2010). In this paper, we provide detailed stability and Hopf bifurcation analysis, which can explain the occurrence of such time-periodic spatial-temporal behavior (also see the simulation Fig. 8 for system (4.8) and Fig. 10 for system (4.16)). We rigorously prove the occurrence of Hopf bifurcations for a large parameter set and our algorithm can be used to calculate the exact bifurcation points where oscillatory patterns start to emerge.

5 Conclusions

The stability of an equilibrium in a delayed system is usually difficult to determine if there is more than one transcendental term in the characteristic equation (see e.g. Ruan and Wei 2003; Lee et al. 2010; Sen et al. 2008). A systematic approach to solve the purely imaginary roots of a second order transcendental polynomial is provided here to consider the stability of an equilibrium in a planar system with a simultaneous delay or a constant equilibrium of a planar reaction–diffusion system with a simultaneous delay. For such a simultaneous delay, the approach presented here is the most general by far to our knowledge and it can be readily applied or adapted to various different forms.

Our approach is easy to apply to a specific model from application as the coefficients in the transcendental polynomial depend only on the linearization of the system, and a complete set of conditions on the coefficients leading to instability are proved. Such conditions are easy to verify and numerical algorithms of finding bifurcation values are given, so the sequence of Hopf bifurcation points can be explicitly calculated (see Sects. 2 and 3). Here we demonstrate our methods on the Leslie–Gower predator–prey system with delays and the Gierer–Meinhardt system with gene expression delays (see Sect. 4). We believe that our methods have opened the door to stability analysis of a wider class of problems from applications.

On the other hand, the present work also motivates more questions and open problems. Our work here is still a special case of the characteristic equation with two delays (in our case, the two delays are τ and 2τ), and a complete analysis for the case of two arbitrary delays is still out of reach. Our general analysis for delayed reaction–diffusion systems shows that the equilibrium loses its stability at a lowest delay value $\tau_* > 0$. In all our examples, τ_* is identical to τ_0, where spatially homogeneous periodic orbits bifurcate from the equilibrium. The possibility of equilibrium first loses stability to spatially nonhomogeneous periodic orbits remains an open problem. Our analysis also focuses only on one of the positive roots of the characteristic equations. Global bifurcation such as stability switches and higher co-dimensional bifurcations such as double Hopf bifurcations or Turing–Hopf bifurcations all await future investigation.

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