Journal of Dynamics and Differential Equations
https://doi.org/10.1007/s10884-021-10070-w

Hopf Bifurcation in a Delayed Population Model Over Patches with General Dispersion Matrix and Nonlocal Interactions

Dan Huang[1] · Shanshan Chen[2] · Xingfu Zou[3]

Received: 23 May 2021 / Revised: 10 August 2021 / Accepted: 16 August 2021

Abstract
In this paper, we consider a single species population model over patches with delay and nonlocal interactions, for which *no symmetry* for the dispersion (connection) matrix is assumed. We show that there exists a positive equilibrium when the dispersal rate is large. We also discuss the stability/instability of this positive equilibrium, establish the threshold dynamics and explore the associated Hopf bifurcation. Moreover, we demonstrate our theoretical results by a nonlocal logistic population model and by the Nicholson's blowflies model.

Keywords Hopf bifurcation · Patch structure · Delay · Asymmetric connection matrix

Mathematics Subject Classification 92D25 · 34K18 · 34K13 · 37N25

1 Introduction

The mutual effect of diffusion and time delay has been investigated extensively in continuous space settings by reaction-diffusion equation models. For example, for the following classical delayed logistic (Pearl-Verhulst) model

$$\frac{\partial u(x,t)}{\partial t} = d\Delta u + u(x,t)\left(m(x) - b(x)u(x,t-\tau)\right), \quad x \in \Omega, \quad t > 0, \tag{1.1}$$

the stability/instability of the positive steady state and the associated Hopf bifurcation were analyzed for the homogeneous Neumann boundary condition [7,18,20,32] and the homogeneuos Dirichlet boundary condition [2,3,13,15,22,23,28,29]. Here the intrinsic growth rate $m(x)$ can be spatially dependent and change sign, and $b(x) > 0$ represents the intraspecific competition. Considering the effect of nonlocal competition, Britton [1] improved model

✉ Shanshan Chen
chenss@hit.edu.cn

1 School of Mathematics, Harbin Institute of Technology Harbin, Heilongjiang 150001, People's Republic of China

2 Department of Mathematics, Harbin Institute of Technology Weihai, Shandong 264209, People's Republic of China

3 Department of Applied Mathematics, University of Western Ontario, London, ON N6A 5B7, Canada

Published online: 27 August 2021

(1.1) and proposed the following nonlocal model:

$$\frac{\partial u}{\partial t} = d\Delta u + u\left[1 + \alpha u - (1+\alpha) g * u\right], \quad x \in \Omega, \quad t > 0, \tag{1.2}$$

where αu denotes the local aggregation, and $g * u$ represents the intraspecific competition and has different forms, e.g. $g * u = \int_\Omega g(x, y)u(y, t - \tau)dy$ which represents a purely spatial average. For the unbounded domain, the existence of periodic traveling wave solutions was shown in [1], and we also refer to [5,9,10,12] and the references therein for the Hopf bifurcation of model (1.2) on the bounded domain. Another classical delayed single population model is the following Nicholson's blowflies model:

$$\frac{\partial u}{\partial t} = d\Delta u + p(x)u(x, t-\tau)e^{-a(x)u(x,t-\tau)} - \delta(x)u(x, t), \quad x \in \Omega, \ t > 0, \tag{1.3}$$

where $p(x) > 0$ is the maximum per capita egg production rate, $1/a(x) > 0$ is the size at which the population reproduces at its maximum rate, $\delta(x)$ is the per capita daily death rate. We refer to [30,31] and the references therein for the stability/instability of the positive steady state.

When the spatial environment is regarded as a discrete variable, the above mentioned models (1.1)-(1.3) have the associated patch forms. Actually, they are all included by the following general form:

$$\begin{cases} \dfrac{du_j}{dt} = d\displaystyle\sum_{k=1}^{n} \alpha_{jk}u_k + f_j\left(u_j, \sum_{k=1}^{n} \beta_{jk}u_k(t-\tau)\right), & t > 0, \quad j = 1, \dots, n, \\ \boldsymbol{u}(t) = \boldsymbol{\psi}(t) \geq \boldsymbol{0}, & t \in [-\tau, 0]. \end{cases} \tag{1.4}$$

where $n \geq 2$ is the number of patches, u_j represents the population density in patch j, and $\boldsymbol{u} = (u_1, \dots, u_n)^T$; $f_j(\cdot, \cdot)$ is the growth rate function; $d > 0$ is the dispersal rate of the population; and time delay $\tau \geq 0$ represents the maturation time of the population. Here $A := (\alpha_{jk})_{n\times n}$ is the connection matrix, where $\alpha_{jk}(j \neq k) \geq 0$ denotes the rate of movement from patch k to patch j, α_{jj} denotes the rate of leaving patch j, and $\alpha_{jj} = -\sum_{k\neq j} \alpha_{kj}$ for $j = 1, \dots, n$; and the matrix $B := (\beta_{jk})_{n\times n} \neq \boldsymbol{0}_{n\times n}$ represents the nonlocal effects if it is not a diagonal matrix.

If

$$f_j(x, y) = x(m_j - y), \quad j = 1, \dots, n, \tag{1.5}$$

and $B = \mathrm{diag}(b_j)$, then model (1.4) is a patch form of (1.1), and the stability of the positive equilibrium and the associated Hopf bifurcation were investigated in [4,16] when the connection matrix A is symmetric; if

$$f_j(x, y) = x(m_j + a_j x - (1 + a_j)y), \quad j = 1, \dots, n, \tag{1.6}$$

then model (1.4) is a patch form of (1.2), and the Hopf bifurcation was also considered in [14,17] when A and B are symmetric by virtue of the symmetric Hopf bifurcation theory [27]. The symmetric Hopf bifurcation theory was also used to analyze the Hopf bifurcation for coupled neural network models with some symmetric assumptions, see e.g. [11,34]. If

$$f_j(x, y) = p_j y e^{-a_j y} - \delta_j x, \quad j = 1, \dots, n, \tag{1.7}$$

and B is an identity matrix, then model (1.4) is a patch form of (1.3), the existence and global stability of the positive equilibrium was analyzed in [8], and there exists no results on Hopf bifurcations to our knowledge. Moreover, we remark that a delay induced Hopf bifurcations were also investigated in [25,33] for two or three patches with other forms of nonlocal delay.

A natural question is whether Hopf bifurcations can occur for model (1.4) when A and B are asymmetric. In this paper, we give an affirmative answer to this question for the case of a large dispersal rate d. Throughout the paper, we assume that:

(**H1**) The connection matrix $A := (\alpha_{jk})_{n\times n}$ is irreducible and quasi-positive.

Here we remark that real matrices with nonnegative off-diagonal elements are referred to as quasi-positive matrices (or respectively, essentially nonnegative matrices). Denote the spectral bound of A by

$$s(A) := \max\{\mathcal{R}e\mu : \mu \text{ is an eignvalue of } A\}. \tag{1.8}$$

It follows directly from the Perron-Frobenius theorem that, under assumption (**H1**), $s(A)$ is a simple eigenvalue of A with an eigenvector $\boldsymbol{\eta} \gg \mathbf{0}$, where

$$\boldsymbol{\eta} = (\eta_1, \ldots, \eta_n)^T, \quad \eta_j > 0 \text{ for all } j = 1, 2\ldots, n, \quad \text{and} \quad \sum_{j=1}^{n} \eta_j = 1. \tag{1.9}$$

Moreover, there exists no other eigenvalue with a nonnegative eigenvector. This, together with the fact that $\sum_{j=1}^{n} \alpha_{jk} = 0$ for $k = 1, \ldots, n$, implies $s(A) = 0$. We note that while a *symmetric* dispersion matrix A in **(H1)** may mimic random diffusion of the species, an *asymmetric* A could reflect advective movements of the species.

On the reaction part, based on the existing studies on various special cases of (1.4), we impose the following assumption:

(**H2**) For all $j = 1, \ldots, n$, $f_j(x, y) \in C^4(\mathbb{R} \times \mathbb{R}, \mathbb{R})$. Define

$$g(w) := \sum_{j=1}^{n} \frac{f_j(w\eta_j, w\sum_{k=1}^{n} \beta_{jk}\eta_k)}{w},$$

where $\boldsymbol{\eta} = (\eta_1, \ldots, \eta_n)^T$ is defined in (1.9), and then $g(w)$ is strictly decreasing in $w \in (0, \infty)$, and $M = \lim_{w\to 0} g(w)$ and $N = \lim_{w\to\infty} g(w)$ exist, where $0 < M < \infty$ and $-\infty \le N < 0$.

We would also like to point out that assumption **(H2)** can actually accommodate all those reaction terms in the aforementioned works (and most, if not all, in the literature). For example, assumption **(H2)** is satisfied for (1.5) when $\sum_{j=1}^{n} m_j\eta_j > 0$, and (1.6) and (1.7) are illustrated in Sect. 3. As will be seen in Sect. 2, **(H2)** will play a crucial role in guaranteeing the existence of a positive equilibrium for a large dispersal rate d.

To analyze the Hopf bifurcation for network or patch models, a common used assumption is that the dispersion matrix A is symmetric. Then the symmetric Hopf bifurcation theory or some other methods can be used, see [4,19,27] and references therein. In [4], we showed that the perturbation method in [2] can also be used for Hopf bifurcations of patch models. Here we do not assume symmetry for the dispersion matrix A, and it brings some more technical hurdles. We overcome these difficulties via constructing an equivalent system (see (2.26)) for the eigenvalue problem, which is different from [2,4].

Now, we denote the following notations. For $\mu \in \mathbb{C}$, we define the real and imaginary parts by $\mathcal{R}e\mu$ and $\mathcal{I}m\mu$, respectively. We denote complexification of a linear space Z to be $Z_{\mathbb{C}} := Z \oplus \mathrm{i}Z = \{x_1 + \mathrm{i}x_2 | x_1, x_2 \in Z\}$, and define the domain of a linear operator T by

$\mathscr{D}(T)$, the kernel of T by $\mathscr{N}(T)$, and the range of T by $\mathscr{R}(T)$. For the complex-valued space $\mathbb{C}^n$, we choose the standard inner product $\langle \boldsymbol{u}, \boldsymbol{v} \rangle = \sum_{j=1}^n \overline{u}_j v_j$, and for $\boldsymbol{u} \in \mathbb{C}^n$, we define

$$\|\boldsymbol{u}\|_\infty = \max_{j=1,\dots,n} |u_j|, \quad \|\boldsymbol{u}\|_2 = \left(\sum_{j=1}^n |u_j|^2 \right)^{1/2}. \tag{1.10}$$

The rest of the paper is organized as follows. In Sect. 2, we study the existence of the positive equilibrium $\boldsymbol{u}_d$ and the associated Hopf bifurcation when the dispersal rate d is sufficiently large. In Sect. 3, we apply the obtained theoretical results to a nonlocal logistic population model and a Nicholson's blowflies model, and also give some numerical simulations.

2 Positive Equilibrium and Hopf Bifurcation

In this section, we will consider the Hopf bifurcation of model (1.4) when the dispersal rate d is sufficiently large. Let $\lambda = 1/d$ throughout the paper, and consequently, the existence of a Hopf bifurcation for a large d is equivalent to that for a small λ.

2.1 Existence of Positive Equilibrium

In this subsection, we show the existence of the positive equilibrium $\boldsymbol{u}_d = (u_{d,1}, \dots, u_{d,n})^T$ (or equivalently $\boldsymbol{u}_\lambda$) of Eq. (1.4), and $\boldsymbol{u}_\lambda = (u_{\lambda,1}, \dots, u_{\lambda,n})^T$ satisfies

$$\sum_{k=1}^n \alpha_{jk} u_k + \lambda f_j \left(u_j, \sum_{k=1}^n \beta_{jk} u_k \right) = 0, \quad j = 1, \dots, n, \tag{2.1}$$

where $\lambda = 1/d$. It is well known that, for every $\boldsymbol{x} = (x_1, \dots, x_n)^T \in \mathbb{R}^n$,

$$\boldsymbol{y} = \boldsymbol{x} - \gamma \boldsymbol{\eta} \in X_1,$$

where $\boldsymbol{\eta}$ is as in (1.9), $\gamma = \sum_{j=1}^n x_j \in \mathbb{R}$ and

$$X_1 = \left\{ (x_1, \dots, x_n)^T \in \mathbb{R}^n : \sum_{j=1}^n x_j = 0 \right\}. \tag{2.2}$$

From assumption **(H2)**, we give the following result for further application.

Lemma 2.1 *Denote*

$$G(w) := \sum_{j=1}^n f_j \left(w\eta_j, w \sum_{k=1}^n \beta_{jk} \eta_k \right), \tag{2.3}$$

where $\boldsymbol{\eta} = (\eta_1, \dots, \eta_n)^T$ is defined in (1.9). Then $G(w) = 0$ has a unique positive solution $w = c_0$ and $G'(c_0) < 0$.

Proof Clearly, $G(w) = wg(w)$, where $g(w)$ is defined in **(H2)**. Since $g(w)$ is strictly decreasing, and

$$\lim_{w \to 0} g(w) \in (0, \infty) \quad \text{and} \quad \lim_{w \to \infty} g(w) \in [-\infty, 0),$$

we see that $g(w) = 0$ has a unique positive solution $w = c_0$, which implies that $G(w) = 0$ has a unique positive solution $w = c_0$. A direct computation yields

$$G'(c_0) = c_0 g'(c_0) < 0.$$

This complete the proof. □

Now we show the existence of the positive equilibrium $\boldsymbol{u}_\lambda$ near $\lambda = 0$.

Lemma 2.2 *There exists $\lambda_1 > 0$ and a continuously differentiable mapping $\lambda \mapsto \boldsymbol{u}_\lambda$ from $[0, \lambda_1]$ to $\mathbb{R}^n$ such that $\boldsymbol{u}_\lambda$ is a positive solution of Eq. (2.1) for $\lambda \in (0, \lambda_1]$. Moreover, $\lim_{\lambda\to 0} \boldsymbol{u}_\lambda = \boldsymbol{u}_0 = \left(u_{0,1}, \ldots, u_{0,n}\right)^T$, where $\boldsymbol{u}_0 = c_0\boldsymbol{\eta}$, and c_0 and $\boldsymbol{\eta}$ are defined in Lemma 2.1 and Eq. (1.9), respectively.*

Proof Define $\boldsymbol{h} : \mathbb{R} \times \mathbb{R} \times X_1 \mapsto \mathbb{R}^n$ by

$$\boldsymbol{h}(\lambda, c, \boldsymbol{w}) = \left(h_1(\lambda, c, \boldsymbol{w}), \ldots, h_n(\lambda, c, \boldsymbol{w})\right)^T,$$

where

$$h_j(\lambda, c, \boldsymbol{w}) = \sum_{k=1}^{n} \alpha_{jk} w_k + \lambda f_j \left(c\eta_j + w_j, \sum_{k=1}^{n} \beta_{jk}(c\eta_k + w_k) \right) = 0 \ \text{ for } \ j = 1, \ldots, n.$$

Letting

$$\boldsymbol{u} = c\boldsymbol{\eta} + \boldsymbol{w}, \tag{2.4}$$

where $\boldsymbol{\eta}$ is defined in (1.9), $c \in \mathbb{R}$, $\boldsymbol{w} \in X_1$ and X_1 is defined in (2.2). Plugging (2.4) into (2.1), we see that $(\lambda, \boldsymbol{u})$ solves (2.1), where $\lambda > 0$ and $\boldsymbol{u} \in \mathbb{R}^n$, if and only if $\boldsymbol{h}(\lambda, c, \boldsymbol{w}) = \boldsymbol{0}$ is solvable for some value of $\lambda > 0$, $c \in \mathbb{R}$ and $\boldsymbol{w} \in X_1$.

Obviously, $\boldsymbol{h}(0, c, \boldsymbol{0}) = \boldsymbol{0}$ for all $c \in \mathbb{R}$. One can easily check that

$$D_{(\lambda,\boldsymbol{w})}\boldsymbol{h}(0, c, \boldsymbol{0})[\sigma, \boldsymbol{v}] = \begin{pmatrix} \sum_{k=1}^{n} \alpha_{1k} v_k + \sigma f_1 \left(c\eta_1, c\sum_{k=1}^{n} \beta_{1k}\eta_k\right) \\ \sum_{k=1}^{n} \alpha_{2k} v_k + \sigma f_2 \left(c\eta_2, c\sum_{k=1}^{n} \beta_{2k}\eta_k\right) \\ \vdots \\ \sum_{k=1}^{n} \alpha_{nk} v_k + \sigma f_n \left(c\eta_n, c\sum_{k=1}^{n} \beta_{nk}\eta_k\right) \end{pmatrix},$$

where $\boldsymbol{v} = (v_1, \ldots, v_n)^T \in X_1$ and $D_{(\lambda,\boldsymbol{w})}\boldsymbol{h}(0, c, \boldsymbol{0})$ is the Fréchet derivative of $\boldsymbol{h}(\lambda, c, \boldsymbol{w})$ with respect to $(\lambda, \boldsymbol{w})$ at $(0, c, \boldsymbol{0})$. It follows from Lemma 2.1 that

$$\begin{pmatrix} f_1 \left(c_0\eta_1, c_0\sum_{k=1}^{n} \beta_{1k}\eta_k\right) \\ f_2 \left(c_0\eta_2, c_0\sum_{k=1}^{n} \beta_{2k}\eta_k\right) \\ \vdots \\ f_n \left(c_0\eta_n, c_0\sum_{k=1}^{n} \beta_{nk}\eta_k\right) \end{pmatrix} \in X_1.$$

Then we see that there exists a unique $\boldsymbol{v}^* \in X_1$ such that

$$D_{(\lambda,\boldsymbol{w})}\boldsymbol{h}(0, c_0, \boldsymbol{0})[1, \boldsymbol{v}^*] = \boldsymbol{0},$$

which yields

$$\mathscr{N}\left(D_{(\lambda,\boldsymbol{w})}\boldsymbol{h}(0, c_0, \boldsymbol{0})\right) = \left\{\left(s, s\boldsymbol{v}^*\right) : s \in \mathbb{R}\right\}.$$

A direct computation shows that

$$D_c D_{(\lambda,\boldsymbol{w})}\boldsymbol{h}(0,c_0,\boldsymbol{0})[1,\boldsymbol{v}^*] = \begin{pmatrix} \eta_1 a_1^0 + \sum_{k=1}^n \beta_{1k}\eta_k b_1^0 \\ \eta_2 a_2^0 + \sum_{k=1}^n \beta_{2k}\eta_k b_2^0 \\ \vdots \\ \eta_n a_n^0 + \sum_{k=1}^n \beta_{nk}\eta_k b_n^0 \end{pmatrix},$$

where $D_c D_{(\lambda,\boldsymbol{w})}\boldsymbol{h}(0,c_0,\boldsymbol{0})$ is the Fréchet derivative of $D_{(\lambda,w)}\boldsymbol{h}(\lambda,c,\boldsymbol{w})$ with respect to c at $(0,c_0,\boldsymbol{0})$, and

$$a_j^0 = \frac{\partial f_j}{\partial x}\Big|_{(c_0\eta_j,\, c_0\sum_{k=1}^n \beta_{jk}\eta_k)}, \quad b_j^0 = \frac{\partial f_j}{\partial y}\Big|_{(c_0\eta_j,\, c_0\sum_{k=1}^n \beta_{jk}\eta_k)}, \quad j=1,\dots,n. \tag{2.5}$$

We claim that

$$D_c D_{(\lambda,\boldsymbol{w})}\boldsymbol{h}(0,c_0,\boldsymbol{0})\left[1,\boldsymbol{v}^*\right] \notin \mathscr{R}\left(D_{(\lambda,\boldsymbol{w})}\boldsymbol{h}(0,c_0,\boldsymbol{0})\right). \tag{2.6}$$

If it is not true, then there exists $(\hat{\sigma},\hat{\boldsymbol{v}})$ such that

$$\sum_{k=1}^n \alpha_{jk}\hat{v}_k + \hat{\sigma} f_j\left(c_0\eta_j, c_0\sum_{k=1}^n \beta_{jk}\eta_k\right) = \eta_j a_j^0 + \sum_{k=1}^n \beta_{jk}\eta_k b_j^0, \quad j=1,\dots,n.$$

This implies that

$$\begin{pmatrix} \eta_1 a_1^0 + \sum_{k=1}^n \beta_{1k}\eta_k b_1^0 \\ \eta_2 a_2^0 + \sum_{k=1}^n \beta_{2k}\eta_k b_2^0 \\ \vdots \\ \eta_n a_n^0 + \sum_{k=1}^n \beta_{nk}\eta_k b_n^0 \end{pmatrix} \in X_1,$$

which contradicts the fact in Lemma 2.1 that

$$G'(c_0) = \sum_{j=1}^n \eta_j a_j^0 + \sum_{j=1}^n\sum_{k=1}^n \beta_{jk}\eta_k b_j^0 < 0. \tag{2.7}$$

Therefore, (2.6) holds, and we see from the Crandall-Rabinowitz bifurcation theorem [6] that the solutions of $\boldsymbol{h}(\lambda,c,\boldsymbol{w})=0$ near $(0,c_0,\boldsymbol{0})$ defines a curve

$$\{(\lambda(s),c(s),\boldsymbol{w}(s)) : s\in(-\epsilon,\epsilon)\},$$

where $\lambda(s), c(s), \boldsymbol{w}(s)$ are smooth, $\lambda(0)=0$, $c(0)=c_0$, $\boldsymbol{w}(0)=\boldsymbol{0}$, $\boldsymbol{w}'(0)=\boldsymbol{v}^*$ and $\lambda'(0)=1$. Noticing that $\lambda'(0)=1>0$, we see that $\lambda(s)$ has a inverse function $s(\lambda)$ for a small s. Then there exists $\lambda_1>0$ such that (2.1) has a positive solution $\boldsymbol{u}_\lambda = c(s(\lambda))\boldsymbol{\eta} + \boldsymbol{w}(s(\lambda))$ for $\lambda\in(0,\lambda_1]$, and $\lim_{\lambda\to 0}\boldsymbol{u}_\lambda = \boldsymbol{u}_0$, where

$$\boldsymbol{u}_0 = c(s(0))\boldsymbol{\eta} + \boldsymbol{w}(s(0)) = c(0)\boldsymbol{\eta} + \boldsymbol{w}(0) = c_0\boldsymbol{\eta}.$$

This completes the proof. □

Note that $\lambda = 1/d$ throughout the paper. Then we have shown the existence of the positive equilibrium with respect to the parameter d, as stated in the following lemma.

Lemma 2.3 *Assume that $d\in[\hat{d},\infty)$, where $\hat{d}$ is sufficiently large. Then there exists a continuously differentiable mapping $d\mapsto \boldsymbol{u}_d$ from $[\hat{d},\infty)$ to $\mathbb{R}^n$ such that $\boldsymbol{u}_d$ is a positive equilibrium of model (1.4) for $d\in[\hat{d},\infty)$. Moreover, $\lim_{d\to\infty}\boldsymbol{u}_d = \boldsymbol{u}_0 = \left(u_{0,1},\dots,u_{0,n}\right)^T$, where $\boldsymbol{u}_0$ is defined in Lemma 2.2.*

2.2 The Eigenvalue Problem

In this subsection, we consider the eigenvalue problem associated with the positive equilibrium $\boldsymbol{u}_\lambda$ obtained in Lemma 2.2 (or equivalently, $\boldsymbol{u}_d$ obtained in Lemma 2.3). Linearizing system (1.4) at $\boldsymbol{u}_\lambda$, we have

$$\frac{d\boldsymbol{v}}{dt} = dA\boldsymbol{v} + \operatorname{diag}\left(a_j^\lambda\right)\boldsymbol{v} + \operatorname{diag}\left(b_j^\lambda\right)B\boldsymbol{v}(t-\tau), \tag{2.8}$$

where $d = 1/\lambda$, and

$$a_j^\lambda = \frac{\partial f_j}{\partial x}\Big|_{(u_{\lambda,j},\sum_{k=1}^n \beta_{jk}u_{\lambda,k})}, \quad b_j^\lambda = \frac{\partial f_j}{\partial y}\Big|_{(u_{\lambda,j},\sum_{k=1}^n \beta_{jk}u_{\lambda,k})}. \tag{2.9}$$

Then $a_j^\lambda = a_j^0$ and $b_j^\lambda = b_j^0$ for $\lambda = 0$, where a_j^0 and b_j^0 are defined in (2.5).

It follows from [26] that the solution semigroup of (2.8) has the infinitesimal generator $A_\tau(\lambda)$ satisfying

$$A_\tau(\lambda)\boldsymbol{\Psi} = \dot{\boldsymbol{\Psi}}, \tag{2.10}$$

with the domain

$$\begin{aligned}\mathscr{D}\left(A_\tau(\lambda)\right) = \Big\{&\boldsymbol{\Psi} \in C_{\mathbb{C}} \cap C_{\mathbb{C}}^1 : \boldsymbol{\Psi}(0) \in \mathbb{C}^n,\\ &\dot{\boldsymbol{\Psi}}(0) = dA\boldsymbol{\Psi}(0) + \operatorname{diag}\left(a_j^\lambda\right)\boldsymbol{\Psi}(0) + \operatorname{diag}\left(b_j^\lambda\right)B\boldsymbol{\Psi}(-\tau)\Big\},\end{aligned}$$

where $C_{\mathbb{C}} = C\left([-\tau,0],\mathbb{C}^n\right)$ and $C_{\mathbb{C}}^1 = C^1\left([-\tau,0],\mathbb{C}^n\right)$. Then, we see that $\mu \in \mathbb{C}$ is an eigenvalue of $A_\tau(\lambda)$, if and only if there exists $\boldsymbol{\psi} = (\psi_1,\ldots,\psi_n)^T\ (\neq \boldsymbol{0}) \in \mathbb{C}^n$ such that

$$\begin{aligned}\Delta(\lambda,\mu,\tau)\boldsymbol{\psi} :=& \left[A + \lambda\operatorname{diag}\left(a_j^\lambda\right) + \lambda e^{-\mu\tau}\operatorname{diag}\left(b_j^\lambda\right)B - \lambda\mu I\right]\boldsymbol{\psi}\\ =& A\boldsymbol{\psi} + \lambda\operatorname{diag}\left(a_j^\lambda\right)\boldsymbol{\psi} + \lambda e^{-\mu\tau}\operatorname{diag}\left(b_j^\lambda\right)B\boldsymbol{\psi} - \lambda\mu\boldsymbol{\psi} = \boldsymbol{0},\end{aligned} \tag{2.11}$$

where $\lambda = 1/d$.

Firstly, we obtain a *priori* estimates for solutions of Eq. (2.11), which is crucial for the analysis of the Hopf bifurcation.

Lemma 2.4 *Assume that $\left(\mu_\lambda,\tau_\lambda,\boldsymbol{\psi}_\lambda\right)$ solves Eq. (2.11) for $\lambda \in (0,\lambda_1]$, where λ_1 is defined in Lemma 2.2, $\mathcal{R}e\mu_\lambda, \tau_\lambda \geq 0$, and $\boldsymbol{\psi}_\lambda = (\psi_{\lambda,1},\ldots,\psi_{\lambda,n})^T (\neq \boldsymbol{0}) \in \mathbb{C}^n$ satisfies $\|\boldsymbol{\psi}_\lambda\|_2^2 = \|\boldsymbol{\eta}\|_2^2$. Then there exists $\hat{\lambda}_1 \in (0,\lambda_1]$ such that $|\mu_\lambda|$ is bounded for $\lambda \in (0,\hat{\lambda}_1]$.*

Proof Substituting $\left(\mu_\lambda,\tau_\lambda,\boldsymbol{\psi}_\lambda\right)$ into (2.11), we have

$$\sum_{k=1}^n \alpha_{jk}\psi_{\lambda,k} + \lambda a_j^\lambda\psi_{\lambda,j} + \lambda e^{-\mu_\lambda\tau_\lambda}b_j^\lambda\left(\sum_{k=1}^n \beta_{jk}\psi_{\lambda,k}\right) - \lambda\mu_\lambda\psi_{\lambda,j} = 0, \quad j = 1,\ldots,n. \tag{2.12}$$

Multiplying (2.12) by $\overline{\psi}_{\lambda,j}$ and summing these over all j yield

$$\begin{aligned}&\sum_{j=1}^n\sum_{k=1}^n \alpha_{jk}\overline{\psi}_{\lambda,j}\psi_{\lambda,k} + \lambda\sum_{j=1}^n a_j^\lambda|\psi_{\lambda,j}|^2 + \lambda e^{-\mu_\lambda\tau_\lambda}\sum_{j=1}^n\sum_{k=1}^n \beta_{jk}b_j^\lambda\overline{\psi}_{\lambda,j}\psi_{\lambda,k}\\ &-\lambda\mu_\lambda\sum_{j=1}^n|\psi_{\lambda,j}|^2 = 0.\end{aligned}$$

Note that $\|\boldsymbol{\psi}_\lambda\|_2^2 = \|\boldsymbol{\eta}\|_2^2$. Then for $\lambda \in (0, \lambda_1]$, we have

$$|\lambda\mu_\lambda| \le \lambda_1 \max_{\lambda\in[0,\lambda_1],1\le j\le n} |a_j^\lambda| + \lambda_1 n \max_{1\le j,k\le n} |\beta_{jk}| \max_{\lambda\in[0,\lambda_1],1\le j\le n} |b_j^\lambda| + n \max_{1\le j,k\le n} |\alpha_{jk}|,$$

which implies that $|\lambda\mu_\lambda|$ is bounded for $\lambda \in (0, \lambda_1]$.

Then we claim that $\lim_{\lambda\to 0} |\lambda\mu_\lambda| = 0$. Note that $\|\boldsymbol{\psi}_\lambda\|_2^2 = \|\boldsymbol{\eta}\|_2^2$. We see that if the claim is not true, then there exists a sequence $\{\lambda_l\}_{l=1}^\infty$ and a constant $\kappa \ne 0$ such that $\lim_{l\to\infty} \lambda_l = 0$, $\lim_{l\to\infty} \lambda_l\mu_{\lambda_l} = \kappa$ with $\mathcal{R}e\kappa \ge 0$, and $\lim_{l\to\infty} \boldsymbol{\psi}_{\lambda_l} = \boldsymbol{\psi}_*$ with $\|\boldsymbol{\psi}_*\|_2^2 = \|\boldsymbol{\eta}\|_2^2$. Then it follows from (2.11) that

$$A\boldsymbol{\psi}_* - \kappa\boldsymbol{\psi}_* = \mathbf{0},$$

which implies that $\kappa(\ne s(A))$ is an eigenvalue of A. If follows from [21, Corollary 4.3.2] that $\mathcal{R}e\kappa < 0$, which is a contradiction. Therefore, $\lim_{\lambda\to 0} |\lambda\mu_\lambda| = 0$.

Finally, we show there exists $\hat{\lambda}_1 \in (0, \lambda_1]$ such that $|\mu_\lambda|$ is bounded for $\lambda \in (0, \hat{\lambda}_1)$. If it is not true, then there exists a sequence, which we still denote by $\{\lambda_l\}_{l=1}^\infty$, such that $\lim_{l\to\infty} \lambda_l = 0$, and $\lim_{l\to\infty} |\mu_{\lambda_l}| = \infty$. Ignoring a scalar factor, $\boldsymbol{\psi}_{\lambda_l}$ can be represented as

$$\boldsymbol{\psi}_{\lambda_l} = r_{\lambda_l}\boldsymbol{\eta} + \boldsymbol{w}_{\lambda_l}, \ \ \boldsymbol{w}_{\lambda_l} \in (X_1)_{\mathbb{C}}\,, \ \ r_{\lambda_l} \ge 0, \tag{2.13}$$

where X_1 is defined in (2.2). Plugging (2.13) into (2.12), we have, for $j = 1, \ldots, n$,

$$\begin{aligned} &\sum_{k=1}^n \alpha_{jk} w_{\lambda_l,k} + \lambda_l a_j^{\lambda_l}(r_{\lambda_l}\eta_j + w_{\lambda_l,j}) + \lambda_l b_j^{\lambda_l} \sum_{k=1}^n \beta_{jk}(r_{\lambda_l}\eta_k + w_{\lambda_l,k})e^{-\mu_{\lambda_l}\tau_{\lambda_l}} \\ &\quad -\lambda_l\mu_{\lambda_l}(r_{\lambda_l}\eta_j + w_{\lambda_l,j}) = 0. \end{aligned} \tag{2.14}$$

Summing (2.14) over all j yields

$$\mu_{\lambda_l} r_{\lambda_l} = \sum_{j=1}^n \left[a_j^{\lambda_l}(r_{\lambda_l}\eta_j + w_{\lambda_l,j}) + b_j^{\lambda_l} \sum_{k=1}^n \beta_{jk}(r_{\lambda_l}\eta_k + w_{\lambda_l,k})e^{-\mu_{\lambda_l}\tau_{\lambda_l}} \right]. \tag{2.15}$$

Noticing that $\|\boldsymbol{\psi}_\lambda\|_2^2 = \|\boldsymbol{\eta}\|_2^2$, we see that there exists a subsequence $\left\{\lambda_{l_q}\right\}_{q=1}^\infty$ (we still use $\{\lambda_l\}_{l=1}^\infty$ for convenience) and $\boldsymbol{\psi}^* = (\psi_1^*, \ldots, \psi_n^*) \in \mathbb{C}^n(\|\boldsymbol{\psi}^*\|_2^2 = \|\boldsymbol{\eta}\|_2^2)$ such that

$$\lim_{l\to\infty} \boldsymbol{\psi}_{\lambda_l} = \lim_{l\to\infty} \left(r_{\lambda_l}\boldsymbol{\eta} + \boldsymbol{w}_{\lambda_l}\right) = \boldsymbol{\psi}^*. \tag{2.16}$$

Since $\lim_{\lambda\to 0} |\lambda\mu_\lambda| = 0$, taking the limit of (2.14) as $l \to \infty$, we see that $A\boldsymbol{\psi}^* = \mathbf{0}$. This, combined with the fact that $\|\boldsymbol{\psi}^*\|_2^2 = \|\boldsymbol{\eta}\|_2^2$, implies that $\boldsymbol{\psi}^* = \kappa_1\boldsymbol{\eta}$ with $|\kappa_1| = 1$. It follows from (2.16) that

$$\lim_{l\to\infty} \sum_{j=1}^n \left(r_{\lambda_l}\eta_j + w_{\lambda_l,j}\right) = \lim_{l\to\infty} r_{\lambda_l} = \sum_{j=1}^n \psi_j^* = \kappa_1, \tag{2.17}$$

which yields $\kappa_1 \ge 0$, and consequently $\kappa_1 = 1$. Therefore,

$$\lim_{l\to\infty} r_{\lambda_l} = 1, \quad \lim_{l\to\infty} \boldsymbol{w}_{\lambda_l} = \mathbf{0}. \tag{2.18}$$

This, combined with (2.15), implies that $\{|\mu_{\lambda_l}|\}_{l=1}^\infty$ is bounded, which is a contradiction. This completes the proof. $\square$

From Lemma 2.4, we have the following result.

Theorem 2.5 *Let*

$$\widetilde{r}_1 = \sum_{j=1}^{n} a_j^0 \eta_j \quad \textit{and} \quad \widetilde{r}_2 = \sum_{j=1}^{n} \sum_{k=1}^{n} \beta_{jk} b_j^0 \eta_k, \tag{2.19}$$

where a_j^0 and b_j^0 are defined in (2.5), and assume that $\widetilde{r}_1 - \widetilde{r}_2 < 0$. Then there exists $\lambda_2 > 0$, where λ_2 is sufficiently small, such that

$$\sigma\left(A_\tau(\lambda)\right) \subset \{x + \mathrm{i}y : x, y \in \mathbb{R}, x < 0\} \ \textit{for} \ \lambda \in (0, \lambda_2] \ \textit{and} \ \tau \geq 0.$$

Proof If the conclusion is not true, then there exists a positive sequence $\{\lambda_l\}_{l=1}^{\infty}$ such that $\lim_{l\to\infty} \lambda_l = 0$, and, for $l \geq 1$, $\Delta(\lambda_l, \mu, \tau)\,\boldsymbol{\psi} = 0$ is solvable for some value of $\left(\mu_{\lambda_l}, \tau_{\lambda_l}, \boldsymbol{\psi}_{\lambda_l}\right)$ with $\mathcal{R}e\mu_{\lambda_l}, \mathcal{I}m\mu_{\lambda_l} \geq 0$, $\tau_{\lambda_l} \geq 0$ and $\mathbf{0} \neq \boldsymbol{\psi}_{\lambda_l} \in \mathbb{C}^n$. Noticing that $\{|\mu_{\lambda_l}|\}_{l=1}^{\infty}$ is bounded from Lemma 2.4, we see that there exists a subsequence $\left\{\lambda_{l_q}\right\}_{q=1}^{\infty}$ (we still use $\{\lambda_l\}_{l=1}^{\infty}$ for convenience) such that $\lim_{l\to\infty} \mu_{\lambda_l} = \mu^*$, and

$$\lim_{l\to\infty} \left(e^{-\tau_{\lambda_l}(\mathcal{R}e\mu_{\lambda_l})}, e^{-\mathrm{i}\tau_{\lambda_l}(\mathcal{I}m\mu_{\lambda_l})}\right) = \left(\sigma^*, e^{-\mathrm{i}\theta^*}\right),$$

where

$$\sigma^* \in [0, 1], \quad \theta^* \in [0, 2\pi), \quad \mu^* \in \mathbb{C}\left(\mathcal{R}e\mu^*, \mathcal{I}m\mu^* \geq 0\right). \tag{2.20}$$

As is proved in Lemma 2.4 (see the proof between (2.13) and (2.18)), $\boldsymbol{\psi}_{\lambda_l}$ can be represented as

$$\begin{aligned} &\boldsymbol{\psi}_{\lambda_l} = r_{\lambda_l}\boldsymbol{\eta} + \boldsymbol{w}_{\lambda_l}, \quad \boldsymbol{w}_{\lambda_l} \in (X_1)_{\mathbb{C}}, \quad r_{\lambda_l} \geq 0, \\ &\|\boldsymbol{\psi}_{\lambda_l}\|_2^2 = r_{\lambda_l}^2 \|\boldsymbol{\eta}\|_2^2 + r_{\lambda_l} \sum_{j=1}^{n} \eta_j (w_{\lambda_l, j} + \overline{w}_{\lambda_l, j}) + \|\boldsymbol{w}_{\lambda_l}\|_2^2 = \|\boldsymbol{\eta}\|_2^2, \end{aligned} \tag{2.21}$$

where $\{r_{\lambda_l}\}_{l=1}^{\infty}$ and $\{\boldsymbol{w}_{\lambda_l}\}_{l=1}^{\infty}$ satisfy

$$\lim_{l\to\infty} r_{\lambda_l} = 1, \quad \lim_{l\to\infty} \boldsymbol{w}_{\lambda_l} = \mathbf{0},$$

and (2.15) holds. Taking the limits of (2.15) on the both sides as $l \to \infty$, we have

$$\sum_{j=1}^{n} \left(a_j^0 \eta_j + \sigma^* b_j^0 \sum_{k=1}^{n} \beta_{jk} \eta_k e^{-\mathrm{i}\theta^*} \right) = \mu^*,$$

which implies that

$$\begin{cases} \widetilde{r}_1 + \sigma^* \widetilde{r}_2 \cos\theta^* = \mathcal{R}e\mu^*, \\ \mathcal{I}m\mu^* + \sigma^* \widetilde{r}_2 \sin\theta^* = 0. \end{cases} \tag{2.22}$$

In fact, it follows from Lemma 2.1 and (2.7) that

$$G'(c_0) = \widetilde{r}_1 + \widetilde{r}_2 < 0. \tag{2.23}$$

Noticing that $\widetilde{r}_1 - \widetilde{r}_2 < 0$, we have

$$\widetilde{r}_1 < \min\{\widetilde{r}_2, -\widetilde{r}_2\} \leq 0 \text{ and } -1 < -\widetilde{r}_2/\widetilde{r}_1 < 1.$$

Then, we see from the first equation of (2.22) that

$$-\frac{\widetilde{r}_2}{\widetilde{r}_1} \cos\theta^* \sigma^* \geq 1,$$

which is a contradiction. $\square$

From Theorem 2.5, we see that if $\widetilde{r}_1 - \widetilde{r}_2 < 0$, then all the eigenvalues of $A_\tau(\lambda)$ have negative real parts for $\lambda \in (0, \lambda_2]$, where λ_2 is sufficiently small. In the following, we show that Hopf bifurcations can occur in the case $\widetilde{r}_1 - \widetilde{r}_2 > 0$. Clearly, $A_\tau(\lambda)$ has a purely imaginary eigenvalue $\mu = \mathrm{i}\nu(\nu > 0)$ for some $\tau \geq 0$, if and only if

$$A\boldsymbol{\psi} + \lambda \operatorname{diag}\left(a_j^\lambda\right)\boldsymbol{\psi} + \lambda \operatorname{diag}\left(b_j^\lambda\right) B\boldsymbol{\psi} e^{-\mathrm{i}\theta} - \mathrm{i}\lambda\nu\boldsymbol{\psi} = \mathbf{0} \tag{2.24}$$

is solvable for some value of $\nu > 0$, $\theta \in [0, 2\pi)$ and $\boldsymbol{\psi}(\neq \mathbf{0}) \in \mathbb{C}^n$. Ignoring a scalar factor, $\boldsymbol{\psi}(\neq \mathbf{0}) \in \mathbb{C}^n$ in (2.24) can be represented as

$$\begin{aligned} &\boldsymbol{\psi} = r\boldsymbol{\eta} + \boldsymbol{w}, \quad \boldsymbol{w} \in (X_1)_{\mathbb{C}}, \quad r \geq 0, \\ &\|\boldsymbol{\psi}\|_2^2 = r^2\|\boldsymbol{\eta}\|_2^2 + r\sum_{j=1}^n \eta_j(w_j + \overline{w}_j) + \|\boldsymbol{w}\|_2^2 = \|\boldsymbol{\eta}\|_2^2. \end{aligned} \tag{2.25}$$

Plugging (2.25) into (2.24), we see that $(\nu, \theta, \boldsymbol{\psi})$ is a solution of (2.24), where $\nu > 0$, $\theta \in [0, 2\pi)$ and $\boldsymbol{\psi} \in \mathbb{C}^n(\|\boldsymbol{\psi}\|_2^2 = \|\boldsymbol{\eta}\|_2^2)$, if and only if the following system:

$$\begin{cases} F_{1,j}(\boldsymbol{w}, r, \nu, \theta, \lambda) \\ \quad := \displaystyle\sum_{k=1}^n \alpha_{jk} w_k + \lambda\left[a_j^\lambda(r\eta_j + w_j) + b_j^\lambda \sum_{k=1}^n \beta_{jk}(r\eta_k + w_k)e^{-\mathrm{i}\theta} - \mathrm{i}\nu(r\eta_j + w_j)\right] \\ \quad - \dfrac{\lambda}{n}\displaystyle\sum_{j=1}^n\left[a_j^\lambda(r\eta_j + w_j) + b_j^\lambda\sum_{k=1}^n \beta_{jk}(r\eta_k + w_k)e^{-\mathrm{i}\theta} - \mathrm{i}\nu(r\eta_j + w_j)\right] = 0, \;\; j = 1, \ldots, n \\ F_2(\boldsymbol{w}, r, \nu, \theta, \lambda) := \displaystyle\sum_{j=1}^n\left[a_j^\lambda(r\eta_j + w_j) + b_j^\lambda\sum_{k=1}^n \beta_{jk}(r\eta_k + w_k)e^{-\mathrm{i}\theta} - \mathrm{i}\nu(r\eta_j + w_j)\right] = 0 \\ F_3(\boldsymbol{w}, r, \nu, \theta, \lambda) := (r^2 - 1)\|\boldsymbol{\eta}\|_2^2 + r\displaystyle\sum_{k=1}^n \eta_k(w_k + \overline{w}_k) + \|\boldsymbol{w}\|_2^2 = 0 \end{cases} \tag{2.26}$$

is solvable for some value of $\boldsymbol{w} = (w_1, \ldots, w_n)^T \in (X_1)_{\mathbb{C}}$, $\nu > 0$, $r \geq 0$ and $\theta \in [0, 2\pi)$. Set $\boldsymbol{F}_1 = (F_{1,1}, \ldots, F_{1,n})^T$, and define $\boldsymbol{F} : (X_1)_{\mathbb{C}} \times \mathbb{R}^4 \mapsto (X_1)_{\mathbb{C}} \times \mathbb{C} \times \mathbb{R}$ by $\boldsymbol{F} = (F_{1,1}, \ldots, F_{1,n}, F_2, F_3)^T$.

We first obtain that $\boldsymbol{F}(\boldsymbol{w}, r, \nu, \theta, \lambda) = 0$ has a unique solution for $\lambda = 0$.

Lemma 2.6 *Assume that $\widetilde{r}_1 - \widetilde{r}_2 > 0$, where $\widetilde{r}_1$ and $\widetilde{r}_2$ are defined in (2.19). Then the following equation*

$$\begin{cases} \boldsymbol{F}(\boldsymbol{w}, r, \nu, \theta, 0) = \mathbf{0} \\ \boldsymbol{w} \in (X_1)_{\mathbb{C}}, \;\; r \geq 0, \;\; \nu \geq 0, \;\; \theta \in [0, 2\pi] \end{cases} \tag{2.27}$$

has a unique solution $(\boldsymbol{w}_0, r_0, \nu_0, \theta_0)$, where

$$\boldsymbol{w}_0 = \mathbf{0}, \quad r_0 = 1, \quad \theta_0 = \arccos\left(-\widetilde{r}_1/\widetilde{r}_2\right), \quad \nu_0 = \sqrt{\widetilde{r}_2^2 - \widetilde{r}_1^2}. \tag{2.28}$$

Proof From (2.26), we see that $\boldsymbol{F}_1(\boldsymbol{w}, r, \nu, \theta, 0) = \mathbf{0}$ if and only if $\boldsymbol{w} = \boldsymbol{w}_0 = 0$. This, combined with $F_3(\boldsymbol{w}, r, \nu, \theta, 0) = 0$, implies that $r = r_0 = 1$.

Substituting $\boldsymbol{w} = \boldsymbol{w}_0$ and $r = r_0$ into $F_2(\boldsymbol{w}, r, \nu, \theta, 0) = 0$, we have

$$\sum_{j=1}^n\left[a_j^0\eta_j + b_j^0\sum_{k=1}^n \beta_{jk}\eta_k e^{-\mathrm{i}\theta} - \mathrm{i}\nu\eta_j\right] = 0. \tag{2.29}$$

Then (2.29) has a solution (θ, ν), where $\theta \in [0, 2\pi]$, $\nu \geq 0$, if and only if

$$\begin{cases} \widetilde{r}_1 + \widetilde{r}_2 \cos\theta = 0, \\ \nu + \widetilde{r}_2 \sin\theta = 0, \end{cases} \tag{2.30}$$

where $\widetilde{r}_1$ and $\widetilde{r}_2$ are defined in (2.19).

Since $\widetilde{r}_1 - \widetilde{r}_2 > 0$ and $\widetilde{r}_1 + \widetilde{r}_2 < 0$ from (2.23), we have

$$\widetilde{r}_2 < \min\{\widetilde{r}_1, -\widetilde{r}_1\} \leq 0 \text{ and } -1 < -\widetilde{r}_1/\widetilde{r}_2 < 1.$$

This, combined with (2.30), implies

$$\theta = \theta_0 = \arccos\left(-\widetilde{r}_1/\widetilde{r}_2\right), \quad \nu = \nu_0 = \sqrt{\widetilde{r}_2^2 - \widetilde{r}_1^2}.$$

This completes the proof. □

Now, we solve $\boldsymbol{F} = \mathbf{0}$ for a small λ.

Theorem 2.7 *Assume that* $\widetilde{r}_1 - \widetilde{r}_2 > 0$ *and* $\lambda \in (0, \lambda_2]$, *where* λ_2 *is sufficiently small. Then there exists a continuously differentiable mapping* $\lambda \mapsto (\boldsymbol{w}_\lambda, r_\lambda, \nu_\lambda, \theta_\lambda)$ *from* $[0, \lambda_2]$ *to* $(X_1)_{\mathbb{C}} \times \mathbb{R}^3$ *such that* $(\boldsymbol{w}_\lambda, r_\lambda, \nu_\lambda, \theta_\lambda)$ *is the unique solution of the following problem*

$$\begin{cases} \boldsymbol{F}(\boldsymbol{w}, r, \nu, \theta, \lambda) = \mathbf{0} \\ \boldsymbol{w} \in (X_1)_{\mathbb{C}}, \ r \geq 0, \ \nu > 0, \ \theta \in [0, 2\pi) \end{cases} \tag{2.31}$$

for $\lambda \in (0, \lambda_2]$.

Proof Let $\boldsymbol{T}(\boldsymbol{\chi}, \kappa, \epsilon, \vartheta) = (T_{1,1}, \ldots, T_{1,n}, T_2, T_3)^T : (X_1)_{\mathbb{C}} \times \mathbb{R}^3 \mapsto (X_1)_{\mathbb{C}} \times \mathbb{C} \times \mathbb{R}$ be the Fréchet derivative of $\boldsymbol{F}$ with respect to $(\boldsymbol{w}, r, \nu, \theta)$ at $(\boldsymbol{w}_0, r_0, \nu_0, \theta_0, 0)$. Thus, we have

$$\begin{aligned} \boldsymbol{T}_1(\boldsymbol{\chi}, \kappa, \epsilon, \vartheta) &= \left(\sum_{j=1}^n \alpha_{1j}\chi_j, \ldots, \sum_{j=1}^n \alpha_{nj}\chi_j\right)^T, \\ T_2(\boldsymbol{\chi}, \kappa, \epsilon, \vartheta) &= \sum_{j=1}^n a_j^0 \chi_j + e^{-\mathrm{i}\theta_0} \sum_{j=1}^n \sum_{k=1}^n \beta_{jk} b_j^0 \chi_k - \mathrm{i}\nu_0 \sum_{j=1}^n \chi_j - \mathrm{i}\epsilon - \mathrm{i}\widetilde{r}_2 e^{-\mathrm{i}\theta_0}\vartheta, \\ T_3(\boldsymbol{\chi}, \kappa, \epsilon, \vartheta) &= \sum_{j=1}^n \eta_j(\chi_j + \overline{\chi}_j) + 2\kappa \|\boldsymbol{\eta}\|_2^2, \end{aligned} \tag{2.32}$$

where $\boldsymbol{\chi} = (\chi_1, \ldots, \chi_n)^T \in (X_1)_{\mathbb{C}}$. A direct computation implies that $\boldsymbol{T}$ is a bijection from $(X_1)_{\mathbb{C}} \times \mathbb{R}^3$ to $(X_1)_{\mathbb{C}} \times \mathbb{C} \times \mathbb{R}$. It follows from the implicit function theorem that there exists $\lambda_2 > 0$ and a continuously differentiable mapping $\lambda \mapsto (\boldsymbol{w}_\lambda, r_\lambda, \nu_\lambda, \theta_\lambda)$ from $[0, \lambda_2]$ to $(X_1)_{\mathbb{C}} \times \mathbb{R}^3$ such that $(\boldsymbol{w}_\lambda, r_\lambda, \nu_\lambda, \theta_\lambda)$ satisfies (2.31).

Next, we prove the uniqueness of the solution of (2.31). Actually, we only need to verify that if $(\boldsymbol{w}^\lambda, r^\lambda, \nu^\lambda, \theta^\lambda)$ satisfies (2.31), then $\left(\boldsymbol{w}^\lambda, r^\lambda, \nu^\lambda, \theta^\lambda\right) \to (\boldsymbol{w}_0, r_0, \nu_0, \theta_0) = (\mathbf{0}, 1, \nu_0, \theta_0)$ as $\lambda \to 0$. Note that $\theta_\lambda \in [0, 2\pi]$, and $|\nu_\lambda|$ is also bounded for $\lambda \in (0, \hat{\lambda}_1]$ from Lemma 2.4. Then we see that, for any sequence $\{\lambda_l\}_{l=1}^\infty$ satisfying $\lim_{l\to\infty} \lambda_l = 0$, there exists a subsequence $\left\{\lambda_{l_q}\right\}_{q=1}^\infty$ (we still use $\{\lambda_l\}_{l=1}^\infty$ for convenience), $\theta^0 \in [0, 2\pi]$ and

$\nu^0 \geq 0$ such that $\lim_{l\to\infty} \theta^{\lambda_l} = \theta^0$ and $\lim_{l\to\infty} \nu^{\lambda_l} = \nu^0$. As is proved in Lemma 2.4 (see the proof between (2.13) and (2.18)), we see that

$$\lim_{l\to\infty} r^{\lambda_l} = r_0 = 1, \quad \lim_{l\to\infty} \boldsymbol{w}^{\lambda_l} = \boldsymbol{w}_0 = \boldsymbol{0}.$$

Taking the limits of $F_2(\boldsymbol{w}^{\lambda_l}, r^{\lambda_l}, \nu^{\lambda_l}, \theta^{\lambda_l}, \lambda_l) = 0$ in (2.26) as $l \to \infty$, we have

$$\sum_{j=1}^{n} \left[a_j^0 \eta_j + b_j^0 \sum_{k=1}^{n} \beta_{jk} \eta_k e^{-\mathrm{i}\theta^0} - \mathrm{i}\nu^0 \eta_j \right] = 0,$$

which yields $\theta^0 = \theta_0$ and $\nu^0 = \nu_0$, Therefore, $\left(\boldsymbol{w}^\lambda, r^\lambda, \nu^\lambda, \theta^\lambda\right) \to (\boldsymbol{w}_0, r_0, \nu_0, \theta_0)$ as $\lambda \to 0$. This completes the proof. □

The following result is derived directly from Theorem 2.7.

Theorem 2.8 *Assume that* $\widetilde{r}_1 - \widetilde{r}_2 > 0$ *and* $\lambda \in (0, \lambda_2]$, *where* λ_2 *is sufficiently small. Then the following equation*

$$\begin{cases} \Delta(\lambda, \mathrm{i}\nu, \tau)\boldsymbol{\psi} = \boldsymbol{0} \\ \nu > 0, \ \ \tau \geq 0, \ \ \boldsymbol{\psi}(\neq \boldsymbol{0}) \in \mathbb{C}^n \end{cases}$$

has a solution $(\nu, \tau, \boldsymbol{\psi})$, *if and only if*

$$\nu = \nu_\lambda, \ \ \boldsymbol{\psi} = \kappa \boldsymbol{\psi}_\lambda, \ \ \tau = \tau_{\lambda,l} = \frac{\theta_\lambda + 2l\pi}{\nu_\lambda}, \quad l = 0, 1, 2, \cdots, \tag{2.33}$$

where $\boldsymbol{\psi}_\lambda = r_\lambda \boldsymbol{\eta} + \boldsymbol{w}_\lambda$, κ *is a nonzero constant, and* $\boldsymbol{w}_\lambda, r_\lambda, \theta_\lambda, \nu_\lambda$ *are defined in Theorem 2.7.*

At the end of this subsection, we consider the adjoint eigenvalue problem of (2.11), which is used in the next subsection for Hopf bifurcation analysis. For $\boldsymbol{\psi}, \widetilde{\boldsymbol{\psi}} \in \mathbb{C}^n$, we have

$$\langle \widetilde{\boldsymbol{\psi}}, \Delta(\lambda, \mathrm{i}\nu, \tau)\boldsymbol{\psi} \rangle = \langle \widetilde{\Delta}(\lambda, \mathrm{i}\nu, \tau)\widetilde{\boldsymbol{\psi}}, \boldsymbol{\psi} \rangle, \tag{2.34}$$

where

$$\widetilde{\Delta}(\lambda, \mathrm{i}\nu, \tau) = A^T + \lambda \operatorname{diag}\left(a_j^\lambda\right) + \lambda B^T \operatorname{diag}(b_j^\lambda) e^{\mathrm{i}\nu\tau} + \mathrm{i}\lambda\nu,$$
$$\widetilde{\Delta}(\lambda, \mathrm{i}\nu, \tau)\widetilde{\boldsymbol{\psi}} = A^T \widetilde{\boldsymbol{\psi}} + \lambda \operatorname{diag}\left(a_j^\lambda\right) \widetilde{\boldsymbol{\psi}} + \lambda B^T \operatorname{diag}(b_j^\lambda)\widetilde{\boldsymbol{\psi}} e^{\mathrm{i}\nu\tau} + \mathrm{i}\lambda\nu\widetilde{\boldsymbol{\psi}}.$$

Here $\widetilde{\Delta}(\lambda, \mathrm{i}\nu, \tau)$ is the conjugate transpose of $\Delta(\lambda, \mathrm{i}\nu, \tau)$. Similar to the study of (2.24), we can conclude that if the corresponding adjoint equation

$$A^T \widetilde{\boldsymbol{\psi}} + \lambda \operatorname{diag}\left(a_j^\lambda\right) \widetilde{\boldsymbol{\psi}} + \lambda B^T \operatorname{diag}(b_j^\lambda)\widetilde{\boldsymbol{\psi}} e^{\mathrm{i}\widetilde{\theta}} + \mathrm{i}\lambda\widetilde{\nu}\widetilde{\boldsymbol{\psi}} = \boldsymbol{0}, \quad \widetilde{\boldsymbol{\psi}}(\neq \boldsymbol{0}) \in \mathbb{C}^n \tag{2.35}$$

is solvable for some value of $\widetilde{\nu} > 0, \widetilde{\theta} \in [0, 2\pi)$, then

$$\widetilde{\Delta}\left(\lambda, \mathrm{i}\widetilde{\nu}, \widetilde{\tau}_l\right) \widetilde{\boldsymbol{\psi}} = 0, \quad \text{where} \quad \widetilde{\tau}_l = \frac{\widetilde{\theta} + 2l\pi}{\widetilde{\nu}}, \quad l = 0, 1, 2, \cdots.$$

Similar to Theorem 2.7, we can show that there is a unique solution $(\widetilde{\nu}, \widetilde{\theta}, \widetilde{\boldsymbol{\psi}})$ of (2.35) with $\widetilde{\boldsymbol{\psi}}(\neq \boldsymbol{0}) \in \mathbb{C}^n$ when λ is small.

For all $\boldsymbol{x} = (x_1, \ldots, x_n)^T \in \mathbb{R}^n$,

$$\boldsymbol{x} = \widetilde{\gamma}(1, 1, \ldots, 1)^T + \widetilde{\boldsymbol{y}},$$

where

$$\widetilde{\gamma}=\sum_{j=1}^{n}\eta_j x_j\in\mathbb{R}\ \text{ and }\ \widetilde{\boldsymbol{y}}\in\widetilde{X}_1=\left\{(x_1,\ldots,x_n)^T\in\mathbb{R}^n:\sum_{j=1}^{n}\eta_j x_j=0\right\}.$$

Ignoring a scalar factor, we see that $\widetilde{\boldsymbol{\psi}}$ in (2.35) can be represented as

$$\begin{aligned}&\widetilde{\boldsymbol{\psi}}=\widetilde{r}(1,1,\ldots,1)^T+\widetilde{\boldsymbol{w}},\quad \widetilde{\boldsymbol{w}}\in\left(\widetilde{X}_1\right)_{\mathbb{C}},\quad \widetilde{r}\geq 0\\ &\|\widetilde{\boldsymbol{\psi}}\|_2^2=\widetilde{r}^2 n+\widetilde{r}\sum_{j=1}^{n}(\widetilde{w}_j+\overline{\widetilde{w}_j})+\|\widetilde{\boldsymbol{w}}\|_2^2=n.\end{aligned}\tag{2.36}$$

Plugging (2.36) into Eq. (2.35), we obtain that the following system is equivalent to (2.35),

$$\begin{cases}\widetilde{F}_{1,j}(\widetilde{\boldsymbol{w}},\widetilde{r},\widetilde{\nu},\widetilde{\theta},\lambda):=\displaystyle\sum_{k=1}^{n}\alpha_{kj}\widetilde{w}_k+\lambda\left[a_j^\lambda(\widetilde{r}+\widetilde{w}_j)+\sum_{k=1}^{n}\beta_{kj}b_k^\lambda(\widetilde{r}+\widetilde{w}_k)e^{\mathrm{i}\widetilde{\theta}}+\mathrm{i}\widetilde{\nu}(\widetilde{r}+\widetilde{w}_j)\right]\\ \qquad -\lambda\displaystyle\sum_{j=1}^{n}\eta_j\left[a_j^\lambda(\widetilde{r}+\widetilde{w}_j)+\sum_{k=1}^{n}\beta_{kj}b_k^\lambda(\widetilde{r}+\widetilde{w}_k)e^{\mathrm{i}\widetilde{\theta}}+\mathrm{i}\widetilde{\nu}(\widetilde{r}+\widetilde{w}_j)\right]=0,\\ \widetilde{F}_2(\widetilde{\boldsymbol{w}},\widetilde{r},\widetilde{\nu},\widetilde{\theta},\lambda):=\displaystyle\sum_{j=1}^{n}\eta_j\left[a_j^\lambda(\widetilde{r}+\widetilde{w}_j)+\sum_{k=1}^{n}\beta_{kj}b_k^\lambda(\widetilde{r}+\widetilde{w}_k)e^{\mathrm{i}\widetilde{\theta}}+\mathrm{i}\widetilde{\nu}(\widetilde{r}+\widetilde{w}_j)\right]=0,\\ \widetilde{F}_3(\widetilde{\boldsymbol{w}},\widetilde{r},\widetilde{\nu},\widetilde{\theta},\lambda):=(\widetilde{r}^2-1)n+\widetilde{r}\displaystyle\sum_{j=1}^{n}(\widetilde{w}_j+\overline{\widetilde{w}_j})+\|\widetilde{\boldsymbol{w}}\|_2^2=0,\end{cases}\tag{2.37}$$

where $\widetilde{\boldsymbol{w}}=(\widetilde{w}_1,\ldots,\widetilde{w}_n)^T\in\left(\widetilde{X}_1\right)_{\mathbb{C}},\widetilde{\nu}>0,\widetilde{r}\geq 0$ and $\widetilde{\theta}\in[0,2\pi)$. Set $\widetilde{\boldsymbol{F}}_1=(\widetilde{F}_{1,1},\ldots,\widetilde{F}_{1,n})^T$, and define $\widetilde{\boldsymbol{F}}:(\widetilde{X}_1)_{\mathbb{C}}\times\mathbb{R}^4\mapsto(\widetilde{X}_1)_{\mathbb{C}}\times\mathbb{C}\times\mathbb{R}$ by

$$\widetilde{\boldsymbol{F}}=(\widetilde{F}_{1,1},\ldots,\widetilde{F}_{1,n},\widetilde{F}_2,\widetilde{F}_3)^T.$$

A direct calculation implies that

$$\widetilde{\boldsymbol{F}}(\widetilde{\boldsymbol{w}}_0,\widetilde{r}_0,\widetilde{\nu}_0,\widetilde{\theta}_0,0)=\boldsymbol{0},$$

where

$$\widetilde{\boldsymbol{w}}_0=\boldsymbol{0},\ \ \widetilde{r}_0=1,\ \ \widetilde{\theta}_0=\arccos\left(-\widetilde{r}_1/\widetilde{r}_2\right),\ \ \widetilde{\nu}_0=\sqrt{\widetilde{r}_2^2-\widetilde{r}_1^2},\tag{2.38}$$

and $\widetilde{r}_1$ and $\widetilde{r}_2$ are defined in (2.19).

Therefore, we obtain the following result similar to Theorem 2.7 and Theorem 2.8, and here we omit the proof.

Theorem 2.9 *Assume that $\widetilde{r}_1-\widetilde{r}_2>0$ and $\lambda\in[0,\lambda_2)$, where λ_2 is sufficiently small. Then the following two statements hold.*

(*i*) *There exists a continuously differentiable mapping $\lambda\mapsto(\widetilde{\boldsymbol{w}}_\lambda,\widetilde{r}_\lambda,\widetilde{\nu}_\lambda,\widetilde{\theta}_\lambda)$ from $[0,\lambda_2]$ to $(\widetilde{X}_1)_{\mathbb{C}}\times\mathbb{R}^3$ such that $\widetilde{\boldsymbol{F}}(\widetilde{\boldsymbol{w}}_\lambda,\widetilde{r}_\lambda,\widetilde{\nu}_\lambda,\widetilde{\theta}_\lambda,\lambda)=\boldsymbol{0}$. Moreover, for $\lambda\in[0,\lambda_2]$, $(\widetilde{\boldsymbol{w}}_\lambda,\widetilde{r}_\lambda,\widetilde{\nu}_\lambda,\widetilde{\theta}_\lambda)$ is the unique solution of the following problem*

$$\begin{cases}\widetilde{\boldsymbol{F}}(\widetilde{\boldsymbol{w}},\widetilde{r},\widetilde{\nu},\widetilde{\theta},\lambda)=\boldsymbol{0},\\ \widetilde{\boldsymbol{w}}\in(X_1)_{\mathbb{C}},\ \widetilde{r}\geq 0,\ \widetilde{\nu}>0,\ \widetilde{\theta}\in[0,2\pi).\end{cases}$$

(*ii*) *For each* $\lambda \in (0, \lambda_2]$, *the following equation*

$$\begin{cases} \widetilde{\Delta}(\lambda, \mathrm{i}\widetilde{\nu}, \widetilde{\tau})\widetilde{\boldsymbol{\psi}} = \mathbf{0} \\ \widetilde{\nu} > 0,\ \ \widetilde{\tau} \geq 0,\ \ \widetilde{\boldsymbol{\psi}}(\neq \mathbf{0}) \in \mathbb{C}^n \end{cases}$$

has a solution $(\widetilde{\nu}, \widetilde{\tau}, \widetilde{\boldsymbol{\psi}})$, *if and only if*

$$\widetilde{\nu} = \widetilde{\nu}_\lambda,\ \ \widetilde{\boldsymbol{\psi}} = \widetilde{\kappa}\widetilde{\boldsymbol{\psi}}_\lambda,\ \ \widetilde{\tau} = \widetilde{\tau}_{\lambda,l} = \frac{\widetilde{\theta}_\lambda + 2l\pi}{\widetilde{\nu}_\lambda},\quad l = 0, 1, 2, \cdots,$$

where $\widetilde{\boldsymbol{\psi}}_\lambda = \widetilde{r}_\lambda(1, 1, \ldots, 1)^T + \widetilde{\boldsymbol{w}}_\lambda$, $\widetilde{\kappa}$ *is a nonzero constant, and* $\widetilde{\boldsymbol{w}}_\lambda, \widetilde{r}_\lambda, \widetilde{\theta}_\lambda, \widetilde{\nu}_\lambda$ *are defined in* (*i*).

Remark 2.10 It follows from Theorem 2.8 that 0 is an eigenvalue of $\Delta\left(\lambda, \mathrm{i}\nu_\lambda, \tau_{\lambda,l}\right)$, where ν_λ and $\tau_{\lambda,l}$ are also defined in Theorem 2.8. Noticing that $\widetilde{\Delta}(\lambda, \mathrm{i}\nu, \tau)$ is the conjugate transpose of $\Delta(\lambda, \mathrm{i}\nu, \tau)$, we see that 0 is also an eigenvalue of $\widetilde{\Delta}(\lambda, \mathrm{i}\nu, \tau)$. From the uniqueness of $\left(\widetilde{\nu}_\lambda, \widetilde{\theta}_\lambda\right)$ in Theorem 2.9, we obtain that $\nu_\lambda = \widetilde{\nu}_\lambda$ and $\theta_\lambda = \widetilde{\theta}_\lambda$, and consequently $\widetilde{\tau}_{\lambda,l} = \tau_{\lambda,l}$. We remark that the corresponding eigenfunction $\boldsymbol{\psi}_\lambda$ of $\Delta\left(\lambda, \mathrm{i}\nu_\lambda, \tau_{\lambda,l}\right)$ with respect to eigenvalue 0 is possibly different from $\widetilde{\boldsymbol{\psi}}_\lambda$ for $\widetilde{\Delta}\left(\lambda, \mathrm{i}\nu_\lambda, \tau_{\lambda,l}\right)$.

2.3 Stability and Hopf Bifurcation

In this subsection, we first consider the stability of the positive equilibrium $\boldsymbol{u}_d$ (or equivalently, $\boldsymbol{u}_\lambda$) of model (1.4) when $\tau = 0$. Note that we denote $\lambda = 1/d$ throughout the paper, and then the stability/instability of $\boldsymbol{u}_d$ for a large d is equivalent to that of $\boldsymbol{u}_\lambda$ for a small λ.

Theorem 2.11 *Assume that* $d \in [\hat{d}, \infty)$, *where* $\hat{d}$ *is sufficiently large. Then the positive equilibrium* $\boldsymbol{u}_d$ *of model (1.4) (obtained in Lemma 2.3) is locally asymptotically stable when* $\tau = 0$.

Proof Note that $\lambda = 1/d$. To the contrary, there exists a positive sequence $\{\lambda_l\}_{l=1}^\infty$ such that $\lim_{l\to\infty} \lambda_l = 0$, and, for $l \geq 1$, the corresponding eigenvalue problem

$$A\boldsymbol{\psi} + \lambda_l \operatorname{diag}\left(a_j^{\lambda_l}\right)\boldsymbol{\psi} + \lambda_l \operatorname{diag}\left(b_j^{\lambda_l}\right)B\boldsymbol{\psi} = \lambda_l\mu\boldsymbol{\psi} \tag{2.39}$$

has an eigenvalue μ_{λ_l} with $\mathcal{R}e\mu_{\lambda_l} \geq 0$, where $a_j^{\lambda_l}$ and $b_j^{\lambda_l}$ are defined in (2.9). Ignoring a scalar factor, the associated eigenfunction $\boldsymbol{\psi}_{\lambda_l}$ can be represented as

$$\begin{aligned} &\boldsymbol{\psi}_{\lambda_l} = r_{\lambda_l}\boldsymbol{\eta} + \boldsymbol{w}_{\lambda_l},\ \ \boldsymbol{w}_{\lambda_l} \in (X_1)_{\mathbb{C}},\ \ r_{\lambda_l} \geq 0, \\ &\|\boldsymbol{\psi}_{\lambda_l}\|_2^2 = r_{\lambda_l}^2\|\boldsymbol{\eta}\|_2^2 + r_{\lambda_l}\sum_{j=1}^n \eta_j(w_{\lambda_l,j} + \overline{w}_{\lambda_l,j}) + \|\boldsymbol{w}_{\lambda_l}\|_2^2 = \|\boldsymbol{\eta}\|_2^2, \end{aligned} \tag{2.40}$$

Noticing that $\{|\mu_{\lambda_l}|\}_{l=1}^\infty$ is bounded from Lemma 2.4, we see that there exists a subsequence $\left\{\lambda_{l_q}\right\}_{q=1}^\infty$ (we still use $\{\lambda_l\}_{l=1}^\infty$ for convenience) such that $\lim_{l\to\infty}\mu_{\lambda_l} = \mu^*$ with $\mathcal{R}e\mu^* \geq 0$. As in the proof of Lemma 2.4 (see the proof between (2.13) and (2.18)), we have

$$\mu_{\lambda_l}r_{\lambda_l} = \sum_{j=1}^n\left[a_j^{\lambda_l}(r_{\lambda_l}\eta_j + w_{\lambda_l,j}) + b_j^{\lambda_l}\sum_{k=1}^n\beta_{jk}(r_{\lambda_l}\eta_k + w_{\lambda_l,k})\right], \tag{2.41}$$

and

$$\lim_{l\to\infty} r_{\lambda_l} = 1,\quad \lim_{l\to\infty}\boldsymbol{w}_{\lambda_l} = \mathbf{0}.$$

Taking the limits of (2.41) on the both sides as $l \to \infty$, we have

$$\sum_{j=1}^{n} \left(a_j^0 \eta_j + b_j^0 \sum_{k=1}^{n} \beta_{jk} \eta_k \right) = \mu^*.$$

It follows from (2.7) and (2.19) that

$$\mu^* = \widetilde{r}_1 + \widetilde{r}_2 < 0,$$

which contradicts the fact that $\mathcal{R}e\mu^* \geq 0$. This completes the proof. □

In the following, we will prove that $\mathrm{i}\nu_\lambda$ (obtained in Theorem 2.8) is simple, and the transversality condition holds.

Lemma 2.12 *Assume that $\widetilde{r}_1 - \widetilde{r}_2 > 0$ and $\lambda \in (0, \lambda_2]$, where λ_2 is sufficiently small. Let*

$$S_l(\lambda) := \sum_{j=1}^{n} \overline{\widetilde{\psi}_{\lambda,j}} \psi_{\lambda,j} + \tau_{\lambda,l} e^{-\mathrm{i}\theta_\lambda} \sum_{j=1}^{n} \sum_{k=1}^{n} \beta_{jk} \overline{\widetilde{\psi}_{\lambda,j}} \psi_{\lambda,k} b_j^\lambda, \tag{2.42}$$

where $\widetilde{\boldsymbol{\psi}}_\lambda$, $\boldsymbol{\psi}_\lambda$, $\tau_{\lambda,l}$ and θ_λ are defined in Theorems 2.8 and 2.9, respectively. Then $\lim_{\lambda \to 0} S_l(\lambda) \neq 0$ *for $l = 0, 1, 2, \cdots$.*

Proof From Theorems 2.7-2.9, we obtain that $b_j^\lambda \to b_j^0$, $\theta_\lambda \to \theta_0$, $\tau_{\lambda,l} \to \dfrac{(\theta_0 + 2l\pi)}{\nu_0}$, $\boldsymbol{\psi}_\lambda \to \boldsymbol{\eta}$ and $\widetilde{\boldsymbol{\psi}}_\lambda \to (1, \ldots, 1)^T$ as $\lambda \to 0$, where θ_0 and ν_0 are defined in (2.28). This, combined with (2.30), implies that

$$\begin{aligned}
\lim_{\lambda \to 0} S_l(\lambda) &= \sum_{j=1}^{n} \eta_j + \frac{(\theta_0 + 2l\pi)}{\nu_0} e^{-\mathrm{i}\theta_0} \left(\sum_{j=1}^{n} \sum_{k=1}^{n} \beta_{jk} b_j^0 \eta_k \right), \\
&= 1 + \frac{(\theta_0 + 2l\pi)}{\nu_0} e^{-\mathrm{i}\theta_0} \widetilde{r}_2 \\
&= 1 + (\theta_0 + 2l\pi) \left(-\frac{\widetilde{r}_1}{\sqrt{\widetilde{r}_2^2 - \widetilde{r}_1^2}} + \mathrm{i} \right) \neq 0.
\end{aligned} \tag{2.43}$$

This completes the proof. □

Theorem 2.13 *Assume that $\widetilde{r}_1 - \widetilde{r}_2 > 0$ and $\lambda \in (0, \lambda_2]$, where λ_2 is sufficiently small. Then $\mu = \mathrm{i}\nu_\lambda$ is a simple eigenvalue of $A_{\tau_{\lambda,l}}(\lambda)$ for $l = 0, 1, 2, \cdots$.*

Proof Firstly, from Theorem 2.8, we have $\mathscr{N}\left[A_{\tau_{\lambda,l}}(\lambda) - \mathrm{i}\nu_\lambda\right] = \mathrm{Span}\left[e^{\mathrm{i}\nu_\lambda\theta}\boldsymbol{\psi}_\lambda\right]$, where $\theta \in [-\tau_{\lambda,l}, 0]$ and $\boldsymbol{\psi}_\lambda$ is defined in Theorem 2.8. Then, we show that

$$\mathscr{N}\left[A_{\tau_{\lambda,l}}(\lambda) - \mathrm{i}\nu_\lambda\right]^2 = \mathscr{N}\left[A_{\tau_{\lambda,l}}(\lambda) - \mathrm{i}\nu_\lambda\right].$$

If $\boldsymbol{\phi} \in \mathscr{N}\left[A_{\tau_{\lambda,l}}(\lambda) - \mathrm{i}\nu_\lambda\right]^2$, then

$$\left[A_{\tau_{\lambda,l}}(\lambda) - \mathrm{i}\nu_\lambda\right]\boldsymbol{\phi} \in \mathscr{N}\left[A_{\tau_{\lambda,l}}(\lambda) - \mathrm{i}\nu_\lambda\right] = \mathrm{Span}\left[e^{\mathrm{i}\nu_\lambda\theta}\boldsymbol{\psi}_\lambda\right],$$

and consequently, there is a constant κ such that

$$\left[A_{\tau_{\lambda,l}}(\lambda) - \mathrm{i}\nu_\lambda\right]\boldsymbol{\phi} = \kappa e^{\mathrm{i}\nu_\lambda\theta}\boldsymbol{\psi}_\lambda,$$

which yields

$$\begin{aligned} \dot{\boldsymbol{\phi}}(\theta) &= \mathrm{i}\nu_\lambda \boldsymbol{\phi}(\theta) + \kappa e^{\mathrm{i}\nu_\lambda \theta} \boldsymbol{\psi}_\lambda, \quad \theta \in \left[-\tau_{\lambda,l}, 0\right], \\ \dot{\boldsymbol{\phi}}(0) &= dA\boldsymbol{\phi}(0) + \operatorname{diag}\left(a_j^\lambda\right) \boldsymbol{\phi}(0) + \operatorname{diag}(b_j^\lambda) B \boldsymbol{\phi}(-\tau_{\lambda,l}). \end{aligned} \tag{2.44}$$

From the first equation of Eq. (2.44), we deduce that

$$\begin{aligned} \boldsymbol{\phi}(\theta) &= \boldsymbol{\phi}(0) e^{\mathrm{i}\nu_\lambda \theta} + \kappa \theta e^{\mathrm{i}\nu_\lambda \theta} \boldsymbol{\psi}_\lambda, \\ \dot{\boldsymbol{\phi}}(0) &= \mathrm{i}\nu_\lambda \boldsymbol{\phi}(0) + \kappa \boldsymbol{\psi}_\lambda. \end{aligned} \tag{2.45}$$

Then, Eqs. (2.44) and (2.45) imply that

$$\begin{aligned} d\Delta\left(\lambda, \mathrm{i}\nu_\lambda, \tau_{\lambda,l}\right) \boldsymbol{\phi}(0) =& dA\boldsymbol{\phi}(0) + \operatorname{diag}\left(a_j^\lambda\right) \boldsymbol{\phi}(0) + \operatorname{diag}(b_j^\lambda) B \boldsymbol{\phi}(0) e^{-\mathrm{i}\theta_\lambda} - \mathrm{i}\nu_\lambda \boldsymbol{\phi}(0) \\ =& \kappa \left(\boldsymbol{\psi}_\lambda + \tau_{\lambda,l} e^{-\mathrm{i}\theta_\lambda} \operatorname{diag}(b_j^\lambda) B \boldsymbol{\psi}_\lambda \right). \end{aligned} \tag{2.46}$$

It follows from Remark 2.10 that $d\widetilde{\Delta}\left(\lambda, \mathrm{i}\widetilde{\nu}_\lambda, \widetilde{\tau}_{\lambda,l}\right) \widetilde{\boldsymbol{\psi}}_\lambda = d\widetilde{\Delta}\left(\lambda, \mathrm{i}\nu_\lambda, \tau_{\lambda,l}\right) \widetilde{\boldsymbol{\psi}}_\lambda = \mathbf{0}$. Then, multiplying (2.46) by $(\overline{\widetilde{\psi}_{\lambda,1}}, \ldots, \overline{\widetilde{\psi}_{\lambda,n}})$, we have

$$\begin{aligned} 0 &= \left\langle d\widetilde{\Delta}\left(\lambda, \mathrm{i}\nu_\lambda, \tau_{\lambda,l}\right) \widetilde{\boldsymbol{\psi}}_\lambda, \boldsymbol{\phi}(0) \right\rangle = \left\langle \widetilde{\boldsymbol{\psi}}_\lambda, d\Delta\left(\lambda, \mathrm{i}\nu_\lambda, \tau_{\lambda,l}\right) \boldsymbol{\phi}(0) \right\rangle \\ &= \kappa \left(\sum_{j=1}^n \overline{\widetilde{\psi}_{\lambda,j}} \psi_{\lambda,j} + \tau_{\lambda,l} e^{-\mathrm{i}\theta_{\lambda,l}} \sum_{j=1}^n \sum_{k=1}^n \beta_{jk} \overline{\widetilde{\psi}_{\lambda,j}} \psi_{\lambda,k} b_j^\lambda \right) = \kappa S_l(\lambda). \end{aligned}$$

As a consequence of Lemma 2.12, we get $\kappa = 0$ for $\lambda \in (0, \lambda_2]$, where λ_2 is sufficiently small. This leads to $\boldsymbol{\phi} \in \mathscr{N}\left[A_{\tau_{\lambda,l}}(\lambda) - \mathrm{i}\nu_\lambda\right]$, and consequently, $\lambda = \mathrm{i}\nu_\lambda$ is a simple eigenvalue of $A_{\tau_{\lambda,l}}$ for $l = 0, 1, 2, \cdots$. □

Note that $\mu = \mathrm{i}\nu_\lambda$ is a simple eigenvalue of $A_{\tau_{\lambda,l}}$, and by using the implicit function theorem we can show that there exists a neighborhood $O_n \times D_n \times H_n$ of $\left(\tau_{\lambda,l}, \mathrm{i}\nu_\lambda, \boldsymbol{\psi}_\lambda\right)$ and a continuously differentiable function $(\mu(\tau), \boldsymbol{\psi}(\tau)) : O_n \to D_n \times H_n$ such that for each $\tau \in O_n$, the only eigenvalue of $A_\tau(\lambda)$ in D_n is $\mu(\tau)$, and

$$\begin{aligned} & d\Delta(\lambda, \mu(\tau), \tau)\boldsymbol{\psi}(\tau) \\ & := dA\boldsymbol{\psi}(\tau) + \operatorname{diag}\left(a_j^\lambda\right) \boldsymbol{\psi}(\tau) + \operatorname{diag}(b_j^\lambda) B \boldsymbol{\psi}(\tau) e^{-\mu(\tau)\tau} - \mu(\tau)\boldsymbol{\psi}(\tau) = \mathbf{0}, \end{aligned} \tag{2.47}$$

where $\mu\left(\tau_{\lambda,l}\right) = \mathrm{i}\nu_\lambda$ and $\boldsymbol{\psi}\left(\tau_{\lambda,l}\right) = \boldsymbol{\psi}_\lambda$. Then, we show that the following transversality condition holds.

Theorem 2.14 *Assume that* $\widetilde{r}_1 - \widetilde{r}_2 > 0$ *and* $\lambda \in (0, \lambda_2]$, *where* λ_2 *is sufficiently small. Then*

$$\frac{d\mathcal{R}e\left[\mu\left(\tau_{\lambda,l}\right)\right]}{d\tau} > 0, \quad l = 0, 1, 2, \cdots.$$

Proof Differentiating Eq. (2.47) with respect to τ at $\tau = \tau_{\lambda,l}$, we obtain

$$\begin{aligned} & -\frac{d\mu\left(\tau_{\lambda,l}\right)}{d\tau} \left(\tau_{\lambda,l} \operatorname{diag}(b_j^\lambda) B \boldsymbol{\psi}_\lambda e^{-\mathrm{i}\theta_\lambda} + \boldsymbol{\psi}_\lambda \right) \\ & + d\Delta\left(\lambda, \mathrm{i}\nu_\lambda, \tau_{\lambda,l}\right) \frac{d\boldsymbol{\psi}\left(\tau_{\lambda,l}\right)}{d\tau} - \mathrm{i}\nu_\lambda \operatorname{diag}(b_j^\lambda) B \boldsymbol{\psi}_\lambda e^{-\mathrm{i}\theta_\lambda} = \mathbf{0}. \end{aligned} \tag{2.48}$$

Note that

$$\left\langle \widetilde{\boldsymbol{\psi}}_\lambda, d\Delta\left(\lambda, \mathrm{i}\nu_\lambda, \tau_{\lambda,l}\right) \frac{d\boldsymbol{\psi}\left(\tau_{\lambda,l}\right)}{d\tau} \right\rangle = \left\langle d\widetilde{\Delta}\left(d, \mathrm{i}\nu_\lambda, \tau_{\lambda,l}\right) \widetilde{\boldsymbol{\psi}}_\lambda, \frac{d\boldsymbol{\psi}\left(\tau_{\lambda,l}\right)}{d\tau} \right\rangle = 0. \tag{2.49}$$

Then, multiplying Eq. (2.48) by $(\overline{\widetilde{\psi}_{\lambda,1}}, \ldots, \overline{\widetilde{\psi}_{\lambda,n}})$, we have

$$\begin{aligned} \frac{d\mu\left(\tau_{\lambda,l}\right)}{d\tau} &= \frac{-\mathrm{i}\nu_\lambda \sum_{j=1}^n \sum_{k=1}^n \beta_{jk} \overline{\widetilde{\psi}_{\lambda,j}} \psi_{\lambda,k} b_j^\lambda e^{-\mathrm{i}\theta_\lambda}}{\sum_{j=1}^n \overline{\widetilde{\psi}_{\lambda,j}} \psi_{\lambda,j} + \tau_{\lambda,l} \sum_{j=1}^n \sum_{k=1}^n \beta_{jk} \overline{\widetilde{\psi}_{\lambda,j}} \psi_{\lambda,k} b_j^\lambda e^{-\mathrm{i}\theta_\lambda}} \\ &= \frac{1}{|S_l(\lambda)|^2} \left[-\mathrm{i}\nu_\lambda e^{-\mathrm{i}\theta_\lambda} \left(\sum_{j=1}^n \widetilde{\psi}_{\lambda,j} \overline{\psi_{\lambda,j}} \right) \sum_{j=1}^n \sum_{k=1}^n \beta_{jk} \overline{\widetilde{\psi}_{\lambda,j}} \psi_{\lambda,k} b_j^\lambda \right. \\ &\quad \left. -\mathrm{i}\nu_\lambda \tau_{\lambda,l} \left| \sum_{j=1}^n \sum_{k=1}^n \beta_{jk} \overline{\widetilde{\psi}_{\lambda,j}} \psi_{\lambda,k} b_j^\lambda \right|^2 \right]. \end{aligned} \tag{2.50}$$

It follows from Theorems 2.7-2.9 that $b_j^\lambda \to b_j^0$, $\theta_\lambda \to \theta_0$, $\tau_{\lambda,l} \to \dfrac{(\theta_0 + 2l\pi)}{\nu_0}$, $\boldsymbol{\psi}_\lambda \to \boldsymbol{\eta}$ and $\widetilde{\boldsymbol{\psi}}_\lambda \to (1, \ldots, 1)^T$ as $\lambda \to 0$, where θ_0 and ν_0 are defined in (2.28). Then we see from (2.30) that

$$\lim_{\lambda \to 0} \frac{d\mathcal{R}e\left[\mu\left(\tau_{\lambda,l}\right)\right]}{d\tau} = \frac{\nu_0^2}{\lim_{\lambda\to 0} |S_l(\lambda)|^2} = \frac{\widetilde{r}_2^2 - \widetilde{r}_1^2}{\lim_{\lambda\to 0} |S_l(\lambda)|^2} > 0.$$

This completes the proof. □

Note that $\lambda = 1/d$ throughout the paper. Then, from Theorems 2.5, 2.8, 2.11, 2.13 and 2.14, we have the following result on the threshold dynamics of model (1.4).

Theorem 2.15 *Assume that $d > \hat{d}$, where $\hat{d}$ is sufficiently large. Let $\boldsymbol{u}_d$ be the positive equilibrium of model (1.4) obtained in Lemma 2.3. Then the following statements hold.*

- (i) *If $\widetilde{r}_1 - \widetilde{r}_2 < 0$, where $\widetilde{r}_1$ and $\widetilde{r}_2$ are defined in (2.19), then the positive equilibrium $\boldsymbol{u}_d$ is locally asymptotically stable for $\tau \in [0, \infty)$.*
- (ii) *If $\widetilde{r}_1 - \widetilde{r}_2 > 0$, then there exists $\tau_0^d > 0$ such that the positive equilibrium $\boldsymbol{u}_d$ of (1.4) is locally asymptotically stable when $\tau \in \left[0, \tau_0^d\right)$, and unstable when $\tau \in \left(\tau_0^d, \infty\right)$. Moreover, when $\tau = \tau_0^d$, system (1.4) undergoes a Hopf bifurcation at $\boldsymbol{u}_d$.*

3 Applications

In this section, we apply the obtained results in Sect. 2 to two concrete examples and give some numerical simulations to illustrate the theoretical results.

3.1 Example I

In this subsection, we consider model (1.4), where the nonlinearities $f_j(u, v)$ is defined in (1.6):

$$\begin{cases} \dfrac{du_j}{dt} = d\displaystyle\sum_{k=1}^{n} \alpha_{jk} u_k + u_j \left[m_j - a_j u_j - (1-a_j) \displaystyle\sum_{k=1}^{n} \beta_{jk} u_k(t-\tau) \right], & t > 0,\ j = 1, \ldots, n, \\ \boldsymbol{u}(t) = \boldsymbol{\psi}(t) \geq \boldsymbol{0}, & t \in [-\tau, 0], \end{cases} \tag{3.1}$$

where the connection matrix $(\alpha_{jk})_{n\times n}$ is irreducible and quasi-positive (or respectively, essentially nonnegative). Here for simplicity, we assume that $a_j > 0$ for $j = 1, \ldots, n$, which implies that the local aggregation has negative effect. If

$$\sum_{j=1}^{n} \sum_{k=1}^{n} (1-a_j)\beta_{jk}\eta_j\eta_k + \sum_{j=1}^{n} a_j\eta_j^2 > 0 \text{ and } \sum_{j=1}^{n} m_j\eta_j > 0, \tag{3.2}$$

then

$$g(w) = \sum_{j=1}^{n} \frac{f_j(w\eta_j, w\sum_{k=1}^{n}\beta_{jk}\eta_k)}{w} = \sum_{j=1}^{n} \eta_j \left[m_j - a_j w\eta_j - (1-a_j)w \sum_{k=1}^{n} \beta_{jk}\eta_k \right]$$

is strictly decreasing in $w \in (0, \infty)$, and

$$M = \lim_{w\to 0} g(w) = \sum_{j=1}^{n} m_j\eta_j > 0, \quad N = \lim_{w\to\infty} g(w) = -\infty.$$

Therefore, assumptions **(H1)** and **(H2)** are satisfied. Then, from Lemma 2.3 and Theorem 2.15, we have the following result.

Proposition 3.1 *Assume that $(\alpha_{jk})_{n\times n}$ is irreducible and quasi-positive, (3.2) holds, and $d > \hat{d}$, where $\hat{d}$ is sufficiently large. Then there exists a positive equilibrium $\boldsymbol{u}_d$ of (3.1) satisfying $\lim_{d\to\infty} \boldsymbol{u}_d = c_0\boldsymbol{\eta}$, where $\boldsymbol{\eta}$ is defined in (1.9) and*

$$c_0 = \frac{\sum_{j=1}^{n} m_j\eta_j}{\sum_{j=1}^{n}\sum_{k=1}^{n}(1-a_j)\beta_{jk}\eta_j\eta_k + \sum_{j=1}^{n} a_j\eta_j^2} > 0.$$

Moreover, the following two statements hold.

(i) If

$$\widetilde{r}_1 - \widetilde{r}_2 = \sum_{j=1}^{n} m_j\eta_j - 2c_0 \sum_{j=1}^{n} a_j\eta_j^2 < 0,$$

then the positive equilibrium $\boldsymbol{u}_d$ is locally asymptotically stable for $\tau \in [0, \infty)$.

(ii) If

$$\widetilde{r}_1 - \widetilde{r}_2 = \sum_{j=1}^{n} m_j\eta_j - 2c_0 \sum_{j=1}^{n} a_j\eta_j^2 > 0,$$

then there exists $\tau_0^d > 0$ such that the positive equilibrium $\boldsymbol{u}_d$ of (3.1) is locally asymptotically stable when $\tau \in \left[0, \tau_0^d\right)$, and unstable when $\tau \in \left(\tau_0^d, \infty\right)$. Moreover, when $\tau = \tau_0^d$, system (3.1) undergoes a Hopf bifurcation at $\boldsymbol{u}_d$.

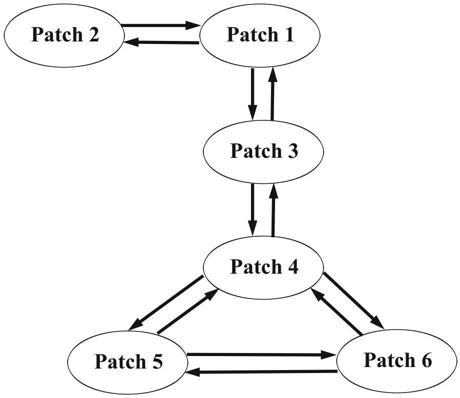

Fig. 1 A sample water network

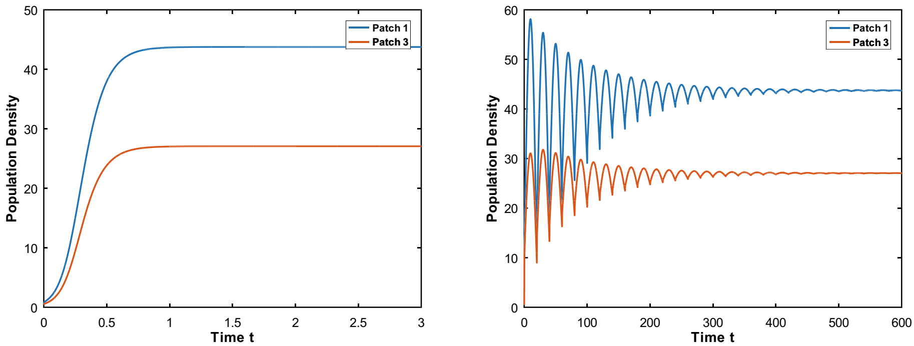

Fig. 2 The case $\widetilde{r}_1 - \widetilde{r}_2 < 0$. Here we only plot two patches for simplicity, $d = 7$, $(a_1, \ldots, a_6) = (1.68, 0.84, 1.12, 0.56, 1.40, 0.84)$, and $\widetilde{r}_1 - \widetilde{r}_2 = -39.956$. (Left): $\tau = 0.01$; (Right): $\tau = 20$

Now we give some numerical simulations to support our theoretical results for model (3.1). We consider the communities in a landscape, connected by a water network, see Fig. 1, and more explanation for this network can be found in [24].

Then we choose the asymmetric connection matrix $A = (\alpha_{jk})$, $B = (\beta_{jk})$ and (m_j) as follows:

$$A = \begin{pmatrix} -3 & 1 & 1 & 0 & 0 & 0 \\ 2 & -1 & 0 & 0 & 0 & 0 \\ 1 & 0 & -4 & 2 & 0 & 0 \\ 0 & 0 & 3 & -9 & 1 & 2 \\ 0 & 0 & 0 & 4 & -5 & 1 \\ 0 & 0 & 0 & 3 & 4 & -3 \end{pmatrix}, \quad B = \begin{pmatrix} 2 & 2 & 2 & 0 & 0 & 0 \\ 4 & 2 & 0 & 0 & 0 & 0 \\ 2 & 0 & 2 & 4 & 0 & 0 \\ 0 & 0 & 6 & 2 & 2 & 4 \\ 0 & 0 & 0 & 8 & 2 & 2 \\ 0 & 0 & 0 & 6 & 8 & 2 \end{pmatrix}, \tag{3.3}$$

and

$$(m_1, \ldots, m_6) = (35, 15, 30, -15, 10, 15). \tag{3.4}$$

It follows from Proposition 3.1 that when $\widetilde{r}_1 - \widetilde{r}_2 < 0$, the positive equilibrium is locally asymptotically stable for all $\tau \geq 0$. Here we numerically illustrate this phenomenon for a large and a small delay, and show that the solution converges to the positive equilibrium, see Fig. 2.

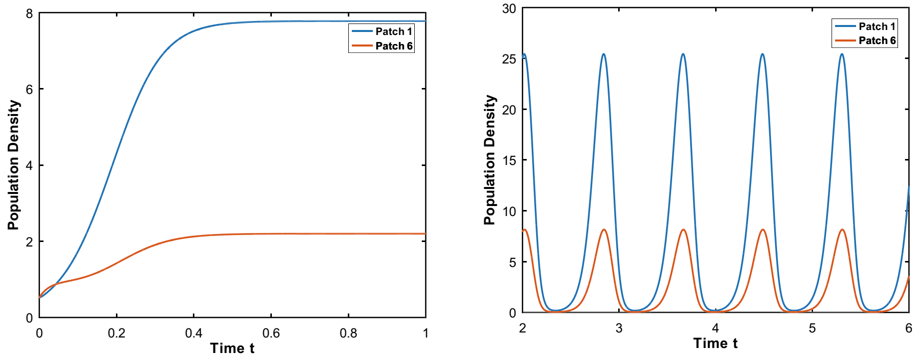

Fig. 3 The case $\widetilde{r}_1 - \widetilde{r}_2 > 0$. Here we only plot two patches for simplicity, $d = 7$, $(a_1, \dots, a_6) = (0.2, 0.2, 0.4, 0.2, 0.1, 0.3)$, and $\widetilde{r}_1 - \widetilde{r}_2 = 16.472$. (Left): $\tau = 0.01$; (Right): $\tau = 0.2$

Moreover, we also numerically show that a large delay τ can make the positive equilibrium unstable through a Hopf bifurcation, and the solution converges to a positive periodic solution when $\widetilde{r}_1 - \widetilde{r}_2 > 0$, see Fig. 3.

3.2 Example II

Now, we consider model (1.4), where the nonlinearities $f_j(u, v)$ is defined in (1.7):

$$\begin{cases} \dfrac{du_j}{dt} = d \displaystyle\sum_{k=1}^{n} \alpha_{jk} u_k + p_j u_j(t-\tau) e^{-a_j u_j(t-\tau)} - \delta_j u_j, & t > 0,\ j = 1, \dots, n, \\ \boldsymbol{u}(t) = \boldsymbol{\psi}(t) \geq 0, & t \in [-\tau, 0], \end{cases} \tag{3.5}$$

where $p_j, \delta_j, a_j > 0$ for $j = 1, \dots, n$, and the connection matrix $(\alpha_{jk})_{n\times n}$ is irreducible and quasi-positive. If

$$\sum_{j=1}^{n} p_j \eta_j > \sum_{j=1}^{n} \delta_j \eta_j, \tag{3.6}$$

then

$$g(w) = \sum_{j=1}^{n} \frac{f_j(w\eta_j, w\eta_j)}{w} = \sum_{j=1}^{n} \left(p_j \eta_j e^{-a_j w \eta_j} - \delta_j \eta_j \right)$$

is strictly decreasing in $w \in (0, \infty)$, and

$$M = \lim_{w\to 0} g(w) = \sum_{j=1}^{n} (p_j \eta_j - \delta_j \eta_j) > 0, \quad N = \lim_{w\to\infty} g(w) = -\sum_{j=1}^{n} \delta_j \eta_j < 0.$$

Therefore, assumptions **(H1)** and **(H2)** are satisfied.

Then from Lemma 2.2 and Theorem 2.15, we have the following result.

Proposition 3.2 *Assume that the positive parameters $p_j, \delta_j, a_j (j = 1, \dots, n)$ satisfy (3.6), $(\alpha_{jk})_{n\times n}$ is irreducible and quasi-positive, and $d > \hat{d}$, where $\hat{d}$ is sufficiently large. Then*

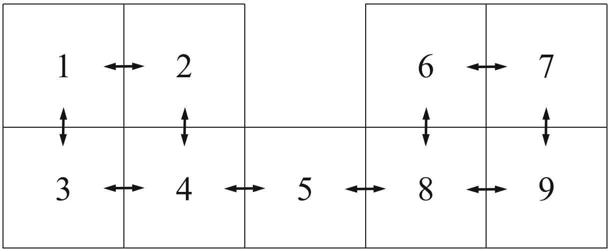

Fig. 4 Network schematic of two 2 × 2 grids, connected by a single " bridge" patch

there exists a positive equilibrium $\boldsymbol{u}_d$ *of (3.5) satisfying* $\lim_{d\to\infty} \boldsymbol{u}_d = c_0\boldsymbol{\eta}$, *where* $\boldsymbol{\eta}$ *is defined in (1.9), and* c_0 *satisfies*

$$\sum_{j=1}^{n} p_j \eta_j e^{-c_0 a_j \eta_j} = \sum_{j=1}^{n} \delta_j \eta_j. \tag{3.7}$$

Moreover, the following two statements hold.

(i) *If*

$$\widetilde{r}_1 - \widetilde{r}_2 = -2\sum_{j=1}^{n} \delta_j \eta_j + c_0 \sum_{j=1}^{n} a_j p_j \eta_j^2 e^{-c_0 a_j \eta_j} < 0,$$

then the positive equilibrium $\boldsymbol{u}_d$ *is locally asymptotically stable for* $\tau \in [0, \infty)$.

(ii) *If*

$$\widetilde{r}_1 - \widetilde{r}_2 = -2\sum_{j=1}^{n} \delta_j \eta_j + c_0 \sum_{j=1}^{n} a_j p_j \eta_j^2 e^{-c_0 a_j \eta_j} > 0,$$

then exists $\tau_0^d > 0$ *such that the positive equilibrium* $\boldsymbol{u}_d$ *of (3.5) is locally asymptotically stable when* $\tau \in \left[0, \tau_0^d\right)$, *and unstable when* $\tau \in \left(\tau_0^d, \infty\right)$. *Moreover, when* $\tau = \tau_0^d$, *system (3.5) undergoes a Hopf bifurcation at* $\boldsymbol{u}_d$.

Finally, we give some numerical simulations to demonstrate our theoretical results for model (3.5). Here we consider a network of two 2 × 2 grids, connected by a single " bridge" patch, see Fig. 4.

Then we choose the asymmetric connection matrix $A = (\alpha_{jk})$ and (a_j) as follows:

$$\begin{aligned}
&\alpha_{12} = \alpha_{13} = \alpha_{24} = \alpha_{31} = \alpha_{42} = \alpha_{45} = a_{58} = 1,\\
&\alpha_{67} = \alpha_{68} = \alpha_{76} = \alpha_{86} = \alpha_{89} = \alpha_{98} = 1,\\
&\alpha_{21} = \alpha_{34} = \alpha_{85} = \alpha_{97} = 2, \quad \alpha_{43} = \alpha_{79} = 3,\\
&\alpha_{54} = 4, \quad \text{other} \ \ \alpha_{jk}(j \neq k) = 0,\\
&(a_1, \ldots, a_9) = (2, 2, 2, 2, 2, 2, 2, 2, 2).
\end{aligned}$$

For the case $\widetilde{r}_1 - \widetilde{r}_2 < 0$, we also choose a large and a small delay to numerically show that the positive equilibrium is stable for all $\tau \geq 0$, see Fig. 5.

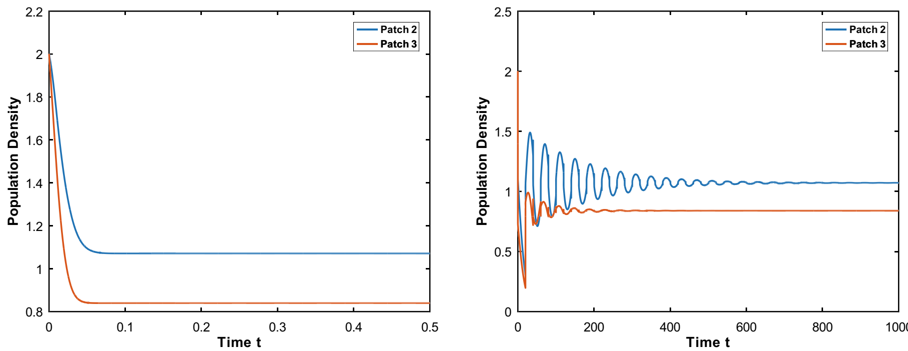

Fig. 5 The case $\widetilde{r}_1 - \widetilde{r}_2 < 0$. Here we only plot two patches for simplicity, $d = 5$, $(p_1, \dots, p_9) = (210, 214.2, 218.4, 222.6, 226.8, 231, 235.2, 239.4, 243.6)$, $(\delta_1, \dots, \delta_9) = (20.8, 23.4, 26, 28.6, 31.2, 33.8, 36.4, 39, 41.6)$, and $\widetilde{r}_1 - \widetilde{r}_2 = -0.51011$. (Left): $\tau = 0.01$; (Right): $\tau = 20$

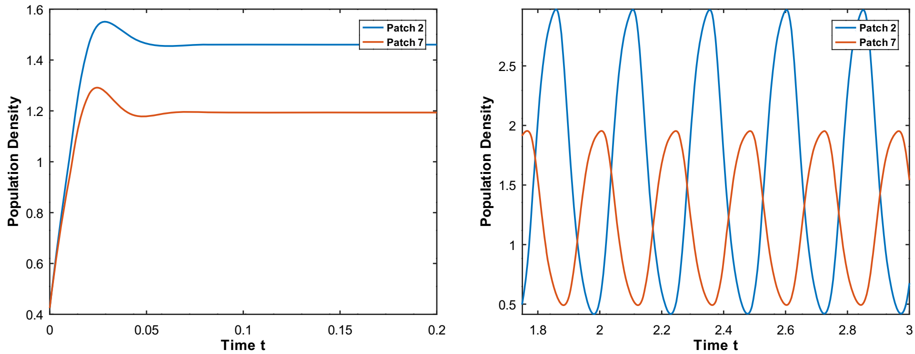

Fig. 6 The case $\widetilde{r}_1 - \widetilde{r}_2 > 0$. Here we only plot two patches for simplicity, $d = 5$, $(p_1, \dots, p_9) = (450, 459, 468, 477, 486, 495, 504, 513, 522)$, $(\delta_1, \dots, \delta_9)$ is the same as that in Fig. 5, and $\widetilde{r}_1 - \widetilde{r}_2 = 23.269$. (Left): $\tau = 0.01$; (Right): $\tau = 0.1$

Moreover, for $\widetilde{r}_1 - \widetilde{r}_2 > 0$, we numerically show that a large delay τ can make the positive equilibrium unstable through a Hopf bifurcation, and the solution converges to a positive periodic solution, see Fig. 6.

Funding This research is supported by the National Natural Science Foundation of China (Nos. 12171117, 11771109) and Shandong Provincial Natural Science Foundation of China (No. ZR2020YQ01).

References

1. Britton, N.F.: Spatial structures and periodic travelling waves in an integro-differential reaction-diffusion population model. SIAM J. Appl. Math. **50**(6), 1663–1688 (1990)
2. Busenberg, S., Huang, W.: Stability and Hopf bifurcation for a population delay model with diffusion effects. J. Differ. Equ. **124**(1), 80–107 (1996)
3. Chen, S., Lou, Y., Wei, J.: Hopf bifurcation in a delayed reaction-diffusion-advection population model. J. Differ. Equ. **264**(8), 5333–5359 (2018)
4. Chen, S., Shen, Z., Wei, J.: Hopf bifurcation in a delayed single population model with patch structure. J. Dyn. Differ. Equ. (2021). https://doi.org/10.1007/s10884-021-09946-8
5. Chen, S., Shi, J.: Stability and Hopf bifurcation in a diffusive logistic population model with nonlocal delay effect. J. Differ. Equ. **253**(12), 3440–3470 (2012)

6. Crandall, M.G., Rabinowitz, P.H.: Bifurcation from simple eigenvalues. J. Func. Anal. **8**, 321–340 (1971)
7. Faria, T.: Normal forms and Hopf bifurcation for partial differential equations with delays. Trans. Amer. Math. Soc. **352**(5), 2217–2238 (2000)
8. Faria, T., Röst, G.: Persistence, permanence and global stability for an n-dimensional Nicholson system. J. Dyn. Differ. Equ. **26**(3), 723–744 (2014)
9. Guo, S.: Stability and bifurcation in a reaction-diffusion model with nonlocal delay effect. J. Differ. Equ. **259**(4), 1409–1448 (2015)
10. Guo, S.: Spatio-temporal patterns in a diffusive model with non-local delay effect. IMA J. Appl. Math. **82**(4), 864–908 (2017)
11. Guo, S., Huang, L.: Hopf bifurcating periodic orbits in a ring of neurons with delays. Phys. D **183**(1–2), 19–44 (2003)
12. Guo, S., Yan, S.: Hopf bifurcation in a diffusive Lotka-Volterra type system with nonlocal delay effect. J. Differ. Equ. **260**(1), 781–817 (2016)
13. Hu, R., Yuan, Y.: Spatially nonhomogeneous equilibrium in a reaction-diffusion system with distributed delay. J. Differ. Equ. **250**(6), 2779–2806 (2011)
14. He, X., Wu, J., Zou, X.: Dynamics of single species populations over a patchy environment. In *Advanced topics in biomathematics (Hangzhou, 1997)*, pages 63–77. World Sci. Publ., River Edge, NJ, (1998)
15. Jin, Z., Yuan, R.: Hopf bifurcation in a reaction-diffusion-advection equation with nonlocal delay effect. J. Differ. Equ. **271**, 533–562 (2021)
16. Liao, K.-L., Lou, Y.: The effect of time delay in a two-patch model with random dispersal. Bull. Math. Biol. **76**(2), 335–376 (2014)
17. Madras, N., Wu, J., Zou, X.: Local-nonlocal interaction and spatial-temporal patterns in single species population over a patchy environment. Canad. Appl. Math. Quart. **4**(1), 109–134 (1996)
18. Memory, M.C.: Bifurcation and asymptotic behavior of solutions of a delay-differential equation with diffusion. SIAM J. Math. Anal. **20**(3), 533–546 (1989)
19. Tian, C., Ruan, S.: Pattern Formation and Synchronism in an Allelopathic Plankton Model with Delay in a Network. SIAM J. Appl. Dyn. Syst. **18**(1), 531–557 (2019)
20. Shi, Q., Shi, J., Song, Y.: Hopf bifurcation and pattern formation in a delayed diffusive logistic model with spatial heterogeneity. Discrete Contin. Dyn. Syst. Ser. B **24**(2), 467–486 (2019)
21. Smith, H.L.: Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems. AMS, Providence (1995)
22. Su, Y., Wei, J., Shi, J.: Hopf bifurcations in a reaction-diffusion population model with delay effect. J. Differ. Equ. **247**(4), 1156–1184 (2009)
23. Su, Y., Wei, J., Shi, J.: Hopf bifurcation in a diffusive logistic equation with mixed delayed and instantaneous density dependence. J. Dyn. Differ. Equ. **24**(4), 897–925 (2012)
24. Tien, J.H., Shuai, Z., Eisenberg, M.C., van den Driessche, P.: Disease invasion on community networks with environmental pathogen movement. J. Math. Biol. **70**(5), 1065–1092 (2015)
25. Weng, P., Xiao, C., Zou, X.: Rich dynamics in a non-local population model over three patches. Nonlinear Dyn. **59**(1–2), 161–172 (2010)
26. Wu, J.: Theory and applications of partial functional-differential equations. Applied Mathematical Sciences, vol. 119. Springer-Verlag, New York (1996)
27. Wu, J.: Symmetric functional-differential equations and neural networks with memory. Trans. Amer. Math. Soc. **350**(12), 4799–4838 (1998)
28. Yan, X.-P., Li, W.-T.: Stability of bifurcating periodic solutions in a delayed reaction-diffusion population model. Nonlinearity **23**(6), 1413–1431 (2010)
29. Yan, X.-P., Li, W.-T.: Stability and Hopf bifurcations for a delayed diffusion system in population dynamics. Discrete Contin. Dyn. Syst. Ser. B **17**(1), 367–399 (2012)
30. Yang, Y., So, J.W.-H., Dynamics for the diffusive Nicholson's blowflies equation. Number Added II, pp. 333–352, : Dynamical systems and differential equations, Vol, p. 1996. MO, II (Springfield) (1998)
31. Yi, T., Zou, X.: Global attractivity of the diffusive Nicholson blowflies equation with Neumann boundary condition: a non-monotone case. J. Differ. Equ. **245**(11), 3376–3388 (2008)
32. Yoshida, K.: The Hopf bifurcation and its stability for semilinear diffusion equations with time delay arising in ecology. Hiroshima Math. J. **12**(2), 321–348 (1982)
33. Yu, C., Wei, J., Zou, X.: Bifurcation analysis in an age-structured model of a single species living in two identical patches. Appl. Math. Model. **34**(4), 1068–1077 (2010)
34. Zhang, C., Zheng, B., Wang, L.: Multiple Hopf bifurcations of symmetric BAM neural network model with delay. Appl. Math. Lett. **22**(4), 616–622 (2009)