PAPER

Dynamics of a delayed population patch model with the dispersion matrix incorporating population loss

Dan Huang[1] and Shanshan Chen[2,*] (iD)

[1]School of Mathematics, Harbin Institute of Technology, Harbin, Heilongjiang, 150001, P.R. China and [2]Department of
Mathematics, Harbin Institute of Technology, Weihai, Shandong, 264209, P.R. China
*Correspondence author. Email: chenss@hit.edu.cn

Abstract

In this paper, we consider a general single population model with delay and patch structure, which could model
the population loss during the dispersal. It is shown that the model admits a unique positive equilibrium when
the dispersal rate is smaller than a critical value. The stability of the positive equilibrium and associated Hopf
bifurcation are investigated when the dispersal rate is small or near the critical value. Moreover, we show the effect
of network topology on Hopf bifurcation values for a delayed logistic population model.

1. Introduction

The population dynamics can be investigated via reaction–diffusion systems or discrete patch models
[1, 3]. For some biological species, time delays such as the maturation time and hunting time may
have important effect on the population dynamics, and it should be included in the modelling pro-
cess. Therefore, various reaction–diffusion models with time delay and delayed patch models have been
proposed to understand the interaction between biological species [30, 40].

For reaction–diffusion models with time delay, time delay-induced Hopf bifurcations and double
Hopf bifurcations were studied extensively. For example, one can refer to [16, 18, 20, 31, 33, 43] and
references therein for results on Hopf bifurcations of reaction–diffusion models with time delay under the
homogeneous Neumann boundary conditions, and see [13, 14] for results on double Hopf bifurcations.
For the case of the homogeneous Dirichlet boundary conditions, delay-induced Hopf bifurcations were
studied in [2, 10–12, 19, 21, 37, 38, 42] and references therein, and the bifurcating stable periodic
solutions through Hopf bifurcation are usually spatially heterogeneous. Moreover, spatial heterogeneity
was recently taken into consideration for reaction–diffusion models with time delay, and the associated
Hopf bifurcations were investigated in [6, 9, 22, 24, 26, 34].

There are also extensive results on bifurcations for delayed patch models. For the spatially homoge-
neous environments, one can refer to [4, 15, 17] and references therein for dispersal-induced Turing
bifurcations, and delay-induced Hopf bifurcations were also studied extensively, see, for example,
[5, 29, 32, 36, 39]. Considering the spatial heterogeneity, Liao and Lou [27] investigated the following
two-patch model, which models the growth of a single species:

$$\begin{cases} \dfrac{du_1}{dt} = d\left(\alpha_{11}u_1 + \alpha_{12}u_2\right) + \mu u_1\left[m_1 - u_1(t-r)\right], & t > 0, \\ \dfrac{du_2}{dt} = d\left(\alpha_{21}u_1 + \alpha_{22}u_2\right) + \mu u_2\left[m_2 - u_2(t-r)\right], & t > 0, \end{cases} \quad (1.1)$$
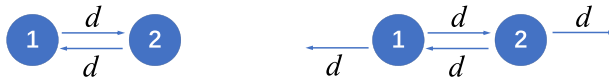
Figure 1. *The connection between two patches. (Left) Dispersion matrix (a); (right) dispersion matrix (b).*

where u_j denotes the population density in patch j and time t, d is the dispersal rate, μ is a scalar factor, r represents the maturation time and m_j is the intrinsic growth rate in patch j, which depends on patch j and represents the spatial heterogeneity. Dispersion matrix $A := (\alpha_{jk})_{2\times2}$ in [27] is chosen to be

$$(a)\, \alpha_{11} = \alpha_{22} = -1, \alpha_{12} = \alpha_{21} = 1, \text{ or } (b)\, \alpha_{11} = \alpha_{22} = -2, \alpha_{12} = \alpha_{21} = 1,$$

where $\alpha_{jk}(j \neq k) \geq 0$ denotes the rate of population movement from patch k to patch j, and $\alpha_{jj} < 0$ denotes the rate of population leaving patch j. Model (1.1) with dispersion matrix (a) (respectively, (b)) can be regarded as a discrete form of Hutchinson's model under the homogeneous Neumann (respectively, Dirichlet) boundary condition. For case (a), the dispersion matrix satisfies $-\alpha_{jj} = \sum_{k\neq j} \alpha_{kj}$ for $j = 1, 2$, which implies that the two-patch habitat is closed, and there is no population loss during the dispersal. For case (b), the dispersion matrix satisfies $-\alpha_{jj} > \sum_{k\neq j} \alpha_{kj}$, and the species has population loss at the boundary, see Figure 1.

A natural question is whether Hopf bifurcations can occur for model (1.1) when the number of patches is finite but arbitrary, and in such a case, the connection among patches may also be complex. One can also refer to [41, 45] for detailed discussions on complex connection among patches. In this paper, we aim to answer this question and consider the following patch model:

$$\begin{cases} \dfrac{du_j}{dt} = d \sum_{k=1}^{n} \alpha_{jk}u_k + u_j f_j \left(u_j, u_j(t-\tau)\right), & t > 0, \ j = 1, \cdots, n, \\ \boldsymbol{u}(t) = \boldsymbol{\psi}(t) \geq \boldsymbol{0}, & t \in [-\tau, 0]. \end{cases} \quad (1.2)$$

Here $\boldsymbol{u} = (u_1, \cdots, u_n)^T$, where u_j stands for the number of individuals in patch j, $n \geq 2$ is the number of patches, $f_j(\cdot, \cdot)$ is the growth rate *per* capita, $d > 0$ is the dispersal rate of the population and time delay $\tau \geq 0$ represents the maturation time of the population. Moreover, $A := (\alpha_{jk})_{n\times n}$ is the dispersion matrix, where $\alpha_{jk}(j \neq k) \geq 0$ denotes the rate of population movement from patch k to patch j, and $\alpha_{jj} \leq 0$ denotes the rate of population leaving patch j.

We remark that if there is no population loss during the dispersal ($-\alpha_{jj} = \sum_{k\neq j} \alpha_{kj}$ for $j = 1, \ldots, n$), Hopf bifurcation can occur when the dispersal rate is small, large or near some critical value, see [7, 23]. Therefore, in this paper, we consider model (1.2) when the species has population loss during the dispersal. That is, the following assumption holds:

(H0) $A := (\alpha_{jk})_{n\times n}$ is irreducible and essentially nonnegative; and $-\alpha_{jj} \geq \sum_{k\neq j} \alpha_{kj}$ for all $j = 1, \cdots, n$, and $-\alpha_{jj} > \sum_{k\neq j} \alpha_{kj}$ for some j.

Here, we remark that real matrices with nonnegative off-diagonal elements are referred as essentially nonnegative matrices. Throughout the paper, we also impose the following assumption:

(H1) For $j = 1, 2, \cdots, n$, $f_j(x, y) \in C^4(\mathbb{R} \times \mathbb{R}, \mathbb{R})$, $f_j(0, 0) = m_j > 0$ and $g_j'(x) < 0$ for $x > 0$ with $g_j(x) = f_j(x, x)$.

Here, m_j represents the intrinsic growth rate in patch j. The smooth condition that $f_j(x, y) \in C^4(\mathbb{R} \times \mathbb{R}, \mathbb{R})$ is used to determine the direction of the Hopf bifurcation and the stability of the bifurcating periodic solutions, and we do not include this part in the paper for simplicity. We remark that for the case of population loss, we need to modify the arguments in [7, 23] to derive *a priori* estimates for eigenvalue problem. Moreover, we show the effect of dispersal rate d and network topology on the Hopf bifurcation values for the logistic population model.

For simplicity, we give some notations here. For a matrix D, we denote the spectral bound of D by

$$s(D) := \max\{\mathcal{R}e\mu : \mu \text{ is an eigenvalue of } D\}.$$

For $\mu \in \mathbb{C}$, we denote the real and imaginary parts by $\mathcal{R}e\mu$ and $\mathcal{I}m\mu$, respectively. For a space Z, we denote complexification of Z to be $Z_{\mathbb{C}} := Z \oplus iZ = \{x_1 + ix_2 | x_1, x_2 \in Z\}$. For a linear operator T, we define the domain and the kernel of T by $\mathscr{D}(T)$ and $\mathscr{N}(T)$, respectively. For $\mathbb{C}^n$, we choose the inner product $\langle \boldsymbol{u}, \boldsymbol{v} \rangle = \sum_{j=1}^{n} \overline{u}_j v_j$ for $\boldsymbol{u}, \boldsymbol{v} \in \mathbb{C}^n$ and define the norm

$$\|\boldsymbol{u}\|_2 = \left(\sum_{j=1}^{n} |u_j|^2 \right)^{1/2}.$$

For $\boldsymbol{u} = (u_1, \cdots, u_n)^T \in \mathbb{R}^n$, we write $\boldsymbol{u} \gg \boldsymbol{0}$ if $u_j > 0$ for all $j = 1, \cdots, n$.

The rest of the paper is organised as follows. In Section 2, we give some preliminaries and show that model (1.2) admits a unique positive equilibrium $\boldsymbol{u}_d$ for $d \in (0, d_*)$. In Section 3, we show the existence of the Hopf bifurcation when $0 < d \ll 1$ and $0 < d_* - d \ll 1$, respectively. In Section 4, we apply the obtained theoretical results to a logistic population model, discuss the effect of network topology on Hopf bifurcation values and give some numerical simulations.

2. Some preliminaries

In this section, we cite some results on the properties of the spectrum bound $s(dA + \text{diag}(m_j))$ and the global dynamics of model (1.2) for $\tau = 0$. The first one is from [8].

Lemma 2.1. *Assume that* **(H0)** *holds, and denote* $s(d) := s(dA + \text{diag}(m_j))$. *Then* $s(d)$ *is strictly decreasing in* $d \in (0, \infty)$, $\lim_{d \to 0} s(d) = \max_{1 \le j \le n}\{m_j\}$, *and* $\lim_{d \to \infty} s(d) = -\infty$. *Moreover, there exists* $d_* > 0$ *such that* $s(d_*) = 0$, $s(d) > 0$ *for* $d \in (0, d_*)$ *and* $s(d) < 0$ *for* $d > d_*$.

This, combined with [8, 25, 28, 44], implies that:

Lemma 2.2. *Assume that* **(H0)**-**(H1)** *hold, and* $\tau = 0$. *Then the trivial equilibrium* $\boldsymbol{0} = (0, \cdots, 0)^T$ *of* (1.2) *is globally asymptotically stable for* $d \ge d_*$, *and for* $d < d_*$, *system* (1.2) *admits a unique positive equilibrium* $\boldsymbol{u}^d = \left(u_1^d, \cdots, u_n^d \right)^T \gg \boldsymbol{0}$, *which is globally asymptotically stable.*

It follows directly from the Perron–Frobenius theorem that $s(d_*A + \text{diag}(m_j))(=0)$ is a simple eigenvalue of $d_*A + \text{diag}(m_j)$ with corresponding eigenvector $\boldsymbol{\eta} \gg \boldsymbol{0}$ (or respectively, a simple eigenvalue of $d_*A^T + \text{diag}(m_j)$ with corresponding eigenvector $\boldsymbol{\varsigma} \gg \boldsymbol{0}$), where

$$\boldsymbol{\eta} = (\eta_1, \cdots, \eta_n)^T \text{ where } \eta_j > 0 \text{ for all } j = 1, 2, \cdots, n, \text{ and } \sum_{j=1}^{n} \eta_j = 1,$$

$$\boldsymbol{\varsigma} = (\varsigma_1, \cdots, \varsigma_n)^T, \text{ where } \varsigma_j > 0 \text{ for all } j = 1, 2, \cdots, n, \text{ and } \sum_{j=1}^{n} \varsigma_j = 1. \tag{2.1}$$

Then, we have the following decomposition:

$$\mathbb{R}^n = \text{span}\{\boldsymbol{\eta}\} \oplus X_1 = \text{span}\{\boldsymbol{\varsigma}\} \oplus \widetilde{X}_1, \tag{2.2}$$

where

$$X_1 := \{\boldsymbol{x} \in \mathbb{R}^n : \langle \boldsymbol{\varsigma}, \boldsymbol{x} \rangle = 0\} = \left\{ \left[d_*A + \text{diag}(m_j) \right] \boldsymbol{y} : \boldsymbol{y} \in \mathbb{R}^n \right\},$$
$$\widetilde{X}_1 := \{\boldsymbol{x} \in \mathbb{R}^n : \langle \boldsymbol{\eta}, \boldsymbol{x} \rangle = 0\} = \left\{ \left[d_*A^T + \text{diag}(m_j) \right] \boldsymbol{y} : \boldsymbol{y} \in \mathbb{R}^n \right\}. \tag{2.3}$$

To show the existence of Hopf bifurcation, we describe the profile of the unique positive equilibrium $\boldsymbol{u}^d$ as $d \to 0$ or $d \to d_*$. Clearly, $\boldsymbol{u}^d = (u_1^d, \cdots, u_n^d)^T$ satisfies

$$d \sum_{k=1}^{n} \alpha_{jk} u_k + u_j f_j \left(u_j, u_j\right) = 0, \quad j = 1, \cdots, n. \tag{2.4}$$

Lemma 2.3. *Assume that* **(H0)**-**(H1)** *hold. Let* $\boldsymbol{u}^d$ *be the unique positive equilibrium of* (1.2) *obtained in Lemma* 2.2 *for* $d \in (0, d_*)$, *and denote*

$$\tilde{a} := \sum_{j=1}^{n} a_j \eta_j^2 \varsigma_j, \quad \tilde{b} := \sum_{j=1}^{n} b_j \eta_j^2 \varsigma_j, \tag{2.5}$$

where $\boldsymbol{\eta} = (\eta_1, \cdots, \eta_n)^T$ *and* $\boldsymbol{\varsigma} = (\varsigma_1, \cdots, \varsigma_n)^T$ *are defined in* (2.1), *and*

$$a_j := \frac{\partial f_j(0, 0)}{\partial x}, \quad b_j := \frac{\partial f_j(0, 0)}{\partial y} \text{ for } j = 1, 2, \cdots, n. \tag{2.6}$$

Then the following statements hold.

(i) *Let* $\boldsymbol{u}^d = \left(u_1^0, \cdots, u_n^0\right)^T$ *for* $d = 0$, *where* u_j^0 *is the unique positive solution of* $f_j(x, x) = 0$ *for* $j = 1, \cdots, n$. *Then* $\boldsymbol{u}^d$ *is continuously differentiable for* $d \in [0, d_*)$.

(ii) *There exists a continuously differentiable mapping* $d \mapsto \left(\beta^d, \boldsymbol{\xi}^d\right)$ *from* $(0, d_*]$ *to* $\mathbb{R}^+ \times X_1$ *such that, for any* $d \in (0, d_*)$, *the unique positive equilibrium of* (1.2) *can be represented as the following form:*

$$\boldsymbol{u}^d = \beta^d (d_* - d) \left[\boldsymbol{\eta} + (d_* - d) \boldsymbol{\xi}^d\right]. \tag{2.7}$$

Moreover,

$$\beta^{d_*} = \frac{\sum_{j=1}^{n} m_j \eta_j \varsigma_j}{-d_* \left(\tilde{a} + \tilde{b}\right)} > 0, \tag{2.8}$$

and $\boldsymbol{\xi}^{d_*} = \left(\xi_1^{d_*}, \cdots, \xi_n^{d_*}\right)^T \in X_1$ *is the unique solution of the following equation:*

$$d_* \left(d_* \sum_{k=1}^{n} \alpha_{jk} \xi_k + m_j \xi_j\right) + \eta_j \left[m_j + d_* \beta^{d_*} \left(a_j + b_j\right) \eta_j\right] = 0, \quad j = 1, \cdots, n. \tag{2.9}$$

Proof. We first prove (*i*). It follows from assumption **(H1)** that $f_j(x, x) = 0$ admits a unique positive solution, denoted by u_j^0. Define

$$G(d, \boldsymbol{u}) = \begin{pmatrix} d \sum_{k=1}^{n} \alpha_{1k} u_k + u_1 f_1(u_1, u_1) \\ d \sum_{k=1}^{n} \alpha_{2k} u_k + u_2 f_2(u_2, u_2) \\ \vdots \\ d \sum_{k=1}^{n} \alpha_{nk} u_k + u_n f_n(u_n, u_n) \end{pmatrix}.$$

Clearly, $G\left(0, \boldsymbol{u}^0\right) = \boldsymbol{0}$ and $D_{\boldsymbol{u}} G\left(0, \boldsymbol{u}^0\right) = \text{diag}\left(u_j^0 \left(a_j^0 + b_j^0\right)\right)$, where $D_{\boldsymbol{u}} G\left(0, \boldsymbol{u}^0\right)$ is the Fréchet derivative of $G(d, \boldsymbol{u})$ with respect to $\boldsymbol{u}$ at $\left(0, \boldsymbol{u}^0\right)$, and

$$a_j^0 = \left.\frac{\partial f_j}{\partial x}\right|_{\left(u_j^0, u_j^0\right)}, \quad b_j^0 = \left.\frac{\partial f_j}{\partial y}\right|_{\left(u_j^0, u_j^0\right)}, \quad j = 1, \cdots, n. \tag{2.10}$$

By assumption **(H1)**, we see that

$$a_j^0 + b_j^0 < 0 \text{ for all } j = 1, \cdots, n, \tag{2.11}$$

which implies that $D_u G(0, \boldsymbol{u}^0)$ is invertible. It follows from the implicit function theorem that there exist $d_1 > 0$ and a continuously differentiable mapping

$$d \in [0, d_1] \mapsto \boldsymbol{u}(d) = (u_1(d), \cdots, u_n(d))^T \gg \boldsymbol{0}$$

such that $G(d, \boldsymbol{u}(d)) = \boldsymbol{0}$ and $\boldsymbol{u}(0) = \boldsymbol{u}^0$. Therefore, $\boldsymbol{u}^d = \boldsymbol{u}(d)$, and $\boldsymbol{u}^d$ is continuously differentiable for $d \in [0, d_1]$. Note that $G(d, \boldsymbol{u}^d) = \boldsymbol{0}$ for $d \in (0, d_*)$, and $\boldsymbol{u}^d$ is stable. Then, by the implicit function theorem, we obtain that $\boldsymbol{u}^d$ is continuously differentiable for $d \in (0, d_*)$. Here, we omit the proof for simplicity.

Now, we prove (*ii*). It follows from (2.2) that $\boldsymbol{u}^d$ can be represented as (2.7). Since $\boldsymbol{u}^d$ is continuously differentiable for $d \in (0, d_*)$, we see that β^d and $\boldsymbol{\xi}^d$ are also continuously differentiable for $d \in (0, d_*)$. Then, we will show that β^d and $\boldsymbol{\xi}^d$ are continuously differentiable for $d = d_*$.

It follows from (2.11) that

$$\tilde{a} + \tilde{b} < 0, \tag{2.12}$$

which implies that β^{d_*} is positive. Since

$$\sum_{j=1}^n m_j \eta_j \varsigma_j + d_* \beta^{d_*} \left(\tilde{a} + \tilde{b} \right) = 0,$$

we see that

$$\left(\eta_1 \left[m_1 + d_* \beta^{d_*}(a_1 + b_1)\eta_1 \right], \cdots, \eta_n \left[m_n + d_* \beta^{d_*}(a_n + b_n)\eta_n \right] \right)^T \in X_1,$$

and consequently $\boldsymbol{\xi}^{d_*} \in X_1$ is uniquely defined.

Multiplying (2.4) by d_*, we have

$$d \left[d_* \sum_{k=1}^n \alpha_{jk} u_k + m_j u_j \right] + (d_* - d)u_j m_j + d_* u_j \left[f_j \left(u_j, u_j \right) - m_j \right] = 0, \ j = 1, \cdots, n. \tag{2.13}$$

Substituting

$$\boldsymbol{u} = \beta(d_* - d) \left[\boldsymbol{\eta} + (d_* - d)\boldsymbol{\xi} \right]$$

into (2.13), where $\boldsymbol{\eta}$ is defined in (2.1) and $\boldsymbol{\xi} = (\xi_1, \cdots, \xi_n)^T \in X_1$, we see that $(\beta, \boldsymbol{\xi})$ satisfies, for all $j = 1, \cdots, n$,

$$p_j(d, \beta, \boldsymbol{\xi}) := d \left(d_* \sum_{k=1}^n \alpha_{jk} \xi_k + m_j \xi_j \right) + \left[\eta_j + (d_* - d)\xi_j \right] \left(m_j + d_* q_j(d, \beta, \boldsymbol{\xi}) \right) = 0,$$

where

$$q_j(d, \beta, \boldsymbol{\xi}) = \begin{cases} \dfrac{f_j \left(u_j, u_j \right) - m_j}{d_* - d}, & d \neq d_* \\[2mm] \beta \left(a_j + b_j \right) \eta_j, & d = d_* \end{cases} \tag{2.14}$$

with $u_j = \beta(d_* - d)[\eta_j + (d_* - d)\xi_j]$. Define $\boldsymbol{p}(d, \beta, \boldsymbol{\xi}) : \mathbb{R} \times \mathbb{R} \times X_1 \mapsto \mathbb{R}^n$ by

$$\boldsymbol{p}(d, \beta, \boldsymbol{\xi}) = (p_1(d, \beta, \boldsymbol{\xi}), \cdots, p_n(d, \beta, \boldsymbol{\xi}))^T.$$

Then $(d, \boldsymbol{u})$ solves (2.4) if and only if $\boldsymbol{p}(d, \beta, \boldsymbol{\xi}) = \boldsymbol{0}$ for $(\beta, \boldsymbol{\xi}) \in \mathbb{R} \times X_1$. Clearly, $\boldsymbol{p} \left(d_*, \beta^{d_*}, \boldsymbol{\xi}^{d_*} \right) = \boldsymbol{0}$, and the Fréchet derivative of $\boldsymbol{p}$ with respect to $(\beta, \boldsymbol{\xi})$ at $\left(d_*, \beta^{d_*}, \boldsymbol{\xi}^{d_*} \right)$ is

$$D_{(\beta,\xi)}\boldsymbol{p} \left(d_*, \beta^{d_*}, \boldsymbol{\xi}^{d_*} \right) [\epsilon, \boldsymbol{v}] = d_* \begin{pmatrix} d_* \sum_{k=1}^n \alpha_{1k} v_k + m_1 v_1 + (a_1 + b_1)\eta_1^2 \epsilon \\ d_* \sum_{k=1}^n \alpha_{2k} v_k + m_2 v_2 + (a_2 + b_2)\eta_2^2 \epsilon \\ \vdots \\ d_* \sum_{k=1}^n \alpha_{nk} v_k + m_n v_n + (a_n + b_n)\eta_n^2 \epsilon \end{pmatrix},$$

where $\epsilon \in \mathbb{R}$ and $\boldsymbol{v} = (v_1, \cdots, v_n)^T \in X_1$. Since $\tilde{a} + \tilde{b} < 0$ from (2.12), we see that $D_{(\beta,\xi)}\boldsymbol{p} \left(d_*, \beta^{d_*}, \boldsymbol{\xi}^{d_*} \right)$ is bijective from $\mathbb{R} \times X_1$ to $\mathbb{R}^n$. It follows from the implicit function theorem that there exist $d_1 < d_*$ and a

continuously differentiable mapping $d \in [d_1, d_*] \mapsto \left(\tilde{\beta}^d, \tilde{\boldsymbol{\xi}}^d\right) \in \mathbb{R} \times X_1$ such that $\boldsymbol{p}\left(d, \tilde{\beta}^d, \tilde{\boldsymbol{\xi}}^d\right) = \boldsymbol{0}$, and $\tilde{\beta}^d = \beta^{d_*}$ and $\tilde{\boldsymbol{\xi}}^d = \boldsymbol{\xi}^{d_*}$ for $d = d_*$. The uniqueness of the positive equilibrium of (1.2) implies that $\beta^d = \tilde{\beta}^d$ and $\boldsymbol{\xi}^d = \tilde{\boldsymbol{\xi}}^d$ for $d \in [d_1, d_*)$. Therefore, β^d and $\boldsymbol{\xi}^d$ are continuously differentiable for $d \in (0, d_*]$. $\square$

3. Stability and Hopf bifurcation

In this section, we consider the stability of the unique positive equilibrium $\boldsymbol{u}^d$ and show the existence/nonexistence of a Hopf bifurcation for model (1.2). Linearizing (1.2) at $\boldsymbol{u}^d$, we have

$$\frac{d\boldsymbol{v}}{dt} = dA\boldsymbol{v} + \text{diag}\left(f_j\left(u_j^d, u_j^d\right)\right)\boldsymbol{v} + \text{diag}\left(u_j^d a_j^d\right)\boldsymbol{v} + \text{diag}\left(u_j^d b_j^d\right)\boldsymbol{v}(t - \tau), \tag{3.1}$$

where

$$a_j^d = \left.\frac{\partial f_j}{\partial x}\right|_{(u_j^d, u_j^d)}, \quad b_j^d = \left.\frac{\partial f_j}{\partial y}\right|_{(u_j^d, u_j^d)}. \tag{3.2}$$

It follows from [40] that the solution semigroup of (3.1) has the infinitesimal generator $A_\tau(d)$ satisfying

$$A_\tau(d)\boldsymbol{\Psi} = \dot{\boldsymbol{\Psi}},$$

and the domain of $A_\tau(d)$ is

$$\mathscr{D}(A_\tau(d)) = \left\{\boldsymbol{\Psi} \in C_\mathbb{C} \cap C_\mathbb{C}^1 : \boldsymbol{\Psi}(0) \in \mathbb{C}^n, \dot{\boldsymbol{\Psi}}(0) = dA\boldsymbol{\Psi}(0) + \text{diag}\left(f_j(u_j^d, u_j^d)\right)\boldsymbol{\Psi}(0) \right.$$
$$\left. + \text{diag}(u_j^d a_j^d)\boldsymbol{\Psi}(0) + \text{diag}(u_j^d b_j^d)\boldsymbol{\Psi}(-\tau)\right\},$$

where $C_\mathbb{C} = C([-\tau, 0], \mathbb{C}^n)$ and $C_\mathbb{C}^1 = C^1([-\tau, 0], \mathbb{C}^n)$. Then, we see that $\mu \in \mathbb{C}$ is an eigenvalue of $A_\tau(d)$, if and only if there exists $\boldsymbol{\varphi} = (\varphi_1, \cdots, \varphi_n)^T (\neq \boldsymbol{0}) \in \mathbb{C}^n$ such that

$$\Delta(d, \mu, \tau)\boldsymbol{\varphi} := dA\boldsymbol{\varphi} + \text{diag}\left(f_j\left(u_j^d, u_j^d\right)\right)\boldsymbol{\varphi} + \text{diag}\left(u_j^d a_j^d\right)\boldsymbol{\varphi}$$
$$+ e^{-\mu\tau}\text{diag}\left(u_j^d b_j^d\right)\boldsymbol{\varphi} - \mu\boldsymbol{\varphi} = \boldsymbol{0}. \tag{3.3}$$

Here, the dispersion matrix A may be asymmetric, and the environment can also be spatially heterogeneous. Therefore, one cannot obtain the explicit expression of $\boldsymbol{u}^d$. By Lemma 2.3, we obtain the asymptotic profile of $\boldsymbol{u}^d$ as $d \to 0$ or $d \to d_*$. Then, the following discussion is divided into two cases: (I) $0 < d_* - d \ll 1$ and (II) $0 < d \ll 1$.

3.1. The case of $0 < d_* - d \ll 1$

In this section, we will consider the existence of a Hopf bifurcation for (1.2) with $0 < d_* - d \ll 1$. First, we obtain *a priori* estimates for solutions of (3.3).

Lemma 3.1. *Assume that* $(\mu_d, \tau_d, \boldsymbol{\psi}_d)$ *solves* (3.3) *for* $d \in (0, d_*)$, *where* $\mathcal{R}e\mu_d, \tau_d \geq 0$, *and* $\boldsymbol{\psi}_d = (\psi_{d,1}, \cdots, \psi_{d,n})^T (\neq \boldsymbol{0}) \in \mathbb{C}^n$. *Then there exists* $d_1 \in (0, d_*)$ *such that* $\left|\dfrac{\mu_d}{d_* - d}\right|$ *is bounded for* $d \in [d_1, d_*)$. *Moreover, ignoring a scalar factor,* $\boldsymbol{\psi}_d$ *can be represented as follows:*

$$\begin{cases} \boldsymbol{\psi}_d = r_d \boldsymbol{\eta} + \boldsymbol{w}_d, \, \boldsymbol{w}_d \in (X_1)_\mathbb{C}, \, r_d \geq 0, \\ \|\boldsymbol{\psi}_d\|_2^2 = \|\boldsymbol{\eta}\|_2^2, \end{cases} \tag{3.4}$$

where $\boldsymbol{\eta}$ *is defined in* (2.1), *and* $r_d, \boldsymbol{w}_d$ *and* $\boldsymbol{\psi}_d$ *satisfy*

$$\lim_{d \to d_*} r_d = 1, \quad \lim_{d \to d_*} \boldsymbol{w}_d = \boldsymbol{0}, \quad \lim_{d \to d_*} \boldsymbol{\psi}_d = \boldsymbol{\eta}.$$

Proof. We first show that $|\mu_d|$ is bounded for $d \in (0, d_*)$. Substituting $(\mu_d, \tau_d, \boldsymbol{\psi}_d)$ into (3.3), we have

$$d \sum_{k=1}^{n} \alpha_{jk}\psi_{d,k} + f_j\left(u_j^d, u_j^d\right)\psi_{d,j} + u_j^d a_j^d \psi_{d,j} + u_j^d b_j^d \psi_{d,j} e^{-\mu_d \tau_d} - \mu_d \psi_{d,j} = 0, \quad j = 1, \cdots, n. \tag{3.5}$$

Multiplying (3.5) by $\overline{\psi}_{d,j}$ and summing the result over all j yield

$$d \sum_{j=1}^{n} \sum_{k=1}^{n} \alpha_{jk}\overline{\psi}_{d,j}\psi_{d,k} + \sum_{j=1}^{n} f_j(u_j^d, u_j^d)|\psi_{d,j}|^2 + \sum_{j=1}^{n} u_j^d a_j^d |\psi_{d,j}|^2 + e^{-\mu_d \tau_d} \sum_{j=1}^{n} u_j^d b_j^d |\psi_{d,j}|^2 - \mu_d \sum_{j=1}^{n} |\psi_{d,j}|^2 = 0.$$

Since $\|\boldsymbol{\psi}_d\|_2^2 = \|\boldsymbol{\eta}\|_2^2$, we see that, for $d \in (0, d_*)$,

$$|\mu_d| \leq \max_{d \in [0,d_*], 1 \leq j \leq n} |f_j\left(u_j^d, u_j^d\right)| + \max_{d \in [0,d_*], 1 \leq j \leq n} |u_j^d a_j^d| + \max_{d \in [0,d_*], 1 \leq j \leq n} |u_j^d b_j^d| + n d_* \max_{1 \leq j,k \leq n} |\alpha_{jk}|,$$

which implies that $|\mu_d|$ is bounded for $d \in (0, d_*)$.

Clearly, ignoring a scalar factor, $\boldsymbol{\psi}_d$ can be represented as (3.4). Note from (3.4) that $\|\boldsymbol{\psi}_d\|_2^2 = \|\boldsymbol{\eta}\|_2^2$. Then, up to a subsequence, we can assume that

$$\lim_{d \to d_*} \mu_d = \gamma, \quad \lim_{d \to d_*} \boldsymbol{\psi}_d = \lim_{d \to d_*} (r_d \boldsymbol{\eta} + \boldsymbol{w}_d) = \boldsymbol{\psi}^* \tag{3.6}$$

with $\mathcal{R}e\gamma \geq 0$ and $\|\boldsymbol{\psi}^*\|_2^2 = \|\boldsymbol{\eta}\|_2^2$. This, combined with (3.3), implies that

$$(d_* A + \mathrm{diag}(m_j))\boldsymbol{\psi}^* - \gamma \boldsymbol{\psi}^* = \mathbf{0},$$

and consequently, γ is an eigenvalue of $d_* A + \mathrm{diag}(m_j)$. Then, by [35, Corollary 4.3.2], we have $\gamma = s(d_* A + \mathrm{diag}(m_j)) = 0$. This, combined with (3.4) and (3.6), implies that $\boldsymbol{\psi}^* = \boldsymbol{\eta}$, and consequently,

$$\lim_{d \to d_*} r_d = 1, \quad \lim_{d \to d_*} \boldsymbol{w}_d = \mathbf{0}. \tag{3.7}$$

Then multiplying (3.5) by d_*, we have

$$0 = d \left[d_* \sum_{k=1}^{n} \alpha_{jk}\psi_{d,k} + m_j \psi_{d,j}\right] + (d_* - d)m_j \psi_{d,j} + d_* \left[f_j\left(u_j^d, u_j^d\right) - m_j\right]\psi_{d,j}$$
$$+ d_* u_j^d a_j^d \psi_{d,j} + d_* u_j^d b_j^d \psi_{d,j} e^{-\mu_d \tau_d} - d_* \mu_d \psi_{d,j}, \quad j = 1, \cdots, n. \tag{3.8}$$

Plugging (2.7) and (3.4) into (3.8), we have, for $j = 1, \cdots, n$,

$$0 = d \left(d_* \sum_{k=1}^{n} \alpha_{jk} w_{d,k} + m_j w_{d,j}\right) + (d_* - d)\left[m_j + d_* q_j\left(d, \beta^d, \boldsymbol{\xi}^d\right)\right](r_d \eta_j + w_{d,j})$$
$$- d_* \mu_d (r_d \eta_j + w_{d,j}) + d_*(d_* - d)\beta^d \left(a_j^d + b_j^d e^{-\mu_d \tau_d}\right)\left[\eta_j + (d_* - d)\xi_j^d\right](r_d \eta_j + w_{d,j}), \tag{3.9}$$

where $q_j(d, \beta, \boldsymbol{\xi})$ is defined in (2.14). Note that $\boldsymbol{\varsigma}$ is the eigenvector of $d_* A^T + \mathrm{diag}(m_j)$ with respect to eigenvalue 0. This, combined with (2.3), implies that

$$\sum_{j=1}^{n} \left(d_* \sum_{k=1}^{n} \alpha_{jk} w_{d,k} + m_j w_{d,j}\right)\varsigma_j = 0, \quad \sum_{j=1}^{n} w_{d,j}\varsigma_j = 0.$$

Then multiplying (3.9) by ς_j and summing the result over all j yield

$$\frac{\mu_d}{d_* - d} = \frac{\beta^d \sum_{j=1}^{n} \varsigma_j \left(a_j^d + b_j^d e^{-\mu_d \tau_d}\right)(r_d \eta_j + w_{d,j})\left[\eta_j + (d_* - d)\xi_j^d\right]}{r_d \sum_{j=1}^{n} \eta_j \varsigma_j}$$
$$+ \frac{\sum_{j=1}^{n} \varsigma_j \left[m_j + d_* q_j\left(d, \beta^d, \boldsymbol{\xi}^d\right)\right](r_d \eta_j + w_{d,j})}{d_* r_d \sum_{j=1}^{n} \eta_j \varsigma_j}. \tag{3.10}$$

This, combined with (3.7), implies that there exists $d_1 \in (0, d_*)$ such that $\left|\dfrac{\mu_d}{d_* - d}\right|$ is bounded for $d \in [d_1, d_*)$. $\qquad\square$

By Lemma 3.1, we have the following result.

Theorem 3.2. *Assume that* **(H0)-(H1)** *hold, and* $\tilde{a} - \tilde{b} < 0$, *where* $\tilde{a}$ *and* $\tilde{b}$ *are defined in* (2.5). *Then there exists* $d_2 \in [d_1, d_*)$, *such that*

$$\sigma\left(A_\tau(d)\right) \subset \{x + \mathrm{i}y : x, y \in \mathbb{R}, x < 0\} \text{ for } d \in [d_2, d_*) \text{ and } \tau \geq 0.$$

Proof. If the conclusion is not true, then there exists a positive sequence $\{d_l\}_{l=1}^\infty$ such that $\lim_{l \to \infty} d_l = d_*$, and, for $l \geq 1$, $\Delta(d_l, \mu, \tau)\boldsymbol{\psi} = 0$ is solvable for some value of $(\mu_{d_l}, \tau_{d_l}, \boldsymbol{\psi}_{d_l})$ with $\mathcal{R}e\mu_{d_l}, \mathcal{I}m\mu_{d_l} \geq 0, \tau_{d_l} \geq 0$ and $\boldsymbol{0} \neq \boldsymbol{\psi}_{d_l} \in \mathbb{C}^n$. Note from the proof of Lemma 3.1 that $\left\{\left|\frac{\mu_{d_l}}{d_* - d_l}\right|\right\}_{l=1}^\infty$ and $\{|\mu_{d_l}|\}_{l=1}^\infty$ are bounded. Then, we see that there exists a subsequence $\{d_{l_k}\}_{k=1}^\infty$ (we still use $\{d_l\}_{l=1}^\infty$ for convenience) such that

$$\lim_{l \to \infty} \frac{\mu_{d_l}}{d_* - d} = \mu^*, \ \lim_{l \to \infty} \left(e^{-\tau_{d_l}\left(\mathcal{R}e\mu_{d_l}\right)}, e^{-\mathrm{i}\tau_{d_l}\left(\mathcal{I}m\mu_{d_l}\right)}\right) = \left(\sigma^*, e^{-\mathrm{i}\theta^*}\right), \tag{3.11}$$

where

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

It follows from Lemma 3.1 that $\lim_{l \to \infty} r_{d_l} = 1$, $\lim_{l \to \infty} \boldsymbol{w}_{d_l} = \boldsymbol{0}$. By (2.7) and (3.2), we have $a_j^d = a_j$ and $b_j^d = b_j$ for $d = d_*$, where a_j and b_j are defined in (2.6). Then, substituting $d = d_l, \mu_d = \mu_{d_l}, r_d = r_{d_l}$ and $\boldsymbol{w}_d = \boldsymbol{w}_{d_l}$ into (3.10) and taking $l \to \infty$, we see from (2.14) and (3.11) that

$$\mu^* = \frac{\sum_{j=1}^n \eta_j\varsigma_j\left\{\left[m_j + d_*\beta^{d_*}\eta_j\left(a_j + b_j\right)\right] + d_*\beta^{d_*}\eta_j\left(a_j + b_j\sigma^*e^{-\mathrm{i}\theta^*}\right)\right\}}{d_*\sum_{j=1}^n \eta_j\varsigma_j}. \tag{3.12}$$

By (2.8), we have

$$\sum_{j=1}^n \eta_j\varsigma_j\left\{\left[m_j + d_*\beta^{d_*}\eta_j\left(a_j + b_j\right)\right]\right\} = 0.$$

This, combined with (2.5) and (3.12), yields

$$\begin{cases} \beta^{d_*}\left(\tilde{a} + \sigma^*\tilde{b}\cos\theta^*\right) = \mathcal{R}e\mu^*\sum_{j=1}^n \eta_j\varsigma_j \geq 0, \\ \mathcal{I}m\mu^*\sum_{j=1}^n \eta_j\varsigma_j + \beta^{d_*}\sigma^*\tilde{b}\sin\theta^* = 0. \end{cases} \tag{3.13}$$

It follows from **(H1)** (see also (2.12)) that $\tilde{a} + \tilde{b} < 0$. Then if $\tilde{a} - \tilde{b} < 0$, we have

$$\tilde{a} < \min\left\{\tilde{b}, -\tilde{b}\right\} \leq 0 \text{ and } -1 < -\frac{\tilde{b}}{\tilde{a}} < 1.$$

This, combined with the first equation of (3.13), yields

$$-\frac{\tilde{b}}{\tilde{a}}\sigma^*\cos\theta^* \geq 1,$$

which is a contradiction. This completes the proof. $\qquad\square$

From Theorem 3.2, we see that if $\tilde{a} - \tilde{b} < 0$, then the positive equilibrium $\boldsymbol{u}^d$ is locally asymptotically stable for $0 < d_* - d \ll 1$, and Hopf bifurcations cannot occur. Next, we show the existence of a Hopf bifurcation for $\tilde{a} - \tilde{b} > 0$. Clearly, $A_\tau(d)$ has a purely imaginary eigenvalue $\mu = \mathrm{i}\nu(\nu > 0)$ for some $\tau \geq 0$, if and only if

$$H(d, \nu, \theta, \boldsymbol{\varphi}) := dA\boldsymbol{\varphi} + \mathrm{diag}\left(f_j\left(u_j^d, u_j^d\right)\right)\boldsymbol{\varphi} + \mathrm{diag}\left(u_j^d a_j^d\right)\boldsymbol{\varphi}$$
$$+ e^{-\mathrm{i}\theta}\mathrm{diag}\left(u_j^d b_j^d\right)\boldsymbol{\varphi} - \mathrm{i}\nu\boldsymbol{\varphi} = \boldsymbol{0} \tag{3.14}$$

is solvable for some value of $\nu > 0, \theta \in [0, 2\pi)$ and $\boldsymbol{\varphi}(\neq \mathbf{0}) \in \mathbb{C}^n$. Ignoring a scalar factor, $\boldsymbol{\psi}(\neq \mathbf{0}) \in \mathbb{C}^n$ in (3.14) can be represented as follows:

$$\boldsymbol{\psi} = r\boldsymbol{\eta} + \boldsymbol{w}, \ \ \boldsymbol{w} \in (X_1)_{\mathbb{C}}, \ \ r \geq 0,$$

$$\|\boldsymbol{\psi}\|_2^2 = r^2 \|\boldsymbol{\eta}\|_2^2 + r \sum_{j=1}^{n} \eta_j \left(w_j + \overline{w}_j \right) + \|\boldsymbol{w}\|_2^2 = \|\boldsymbol{\eta}\|_2^2. \tag{3.15}$$

Then, we obtain an equivalent problem of (3.14) as follows.

Lemma 3.3. *Assume that* $d \in (0, d_*)$. *Then* $(\nu, \theta, \boldsymbol{\psi})$ *is a solution of (3.14), where* $\nu = (d_* - d)h > 0$, $\theta \in [0, 2\pi)$ *and* $\boldsymbol{\psi}$ *satisfies (3.15), if and only if* $(\boldsymbol{w}, r, h, \theta)$ *solves the following system:*

$$\begin{cases} F(\boldsymbol{w}, r, h, \theta, d) = (F_{1,1}, \cdots, F_{1,n}, F_2, F_3)^T = \mathbf{0}, \\ \boldsymbol{w} \in (X_1)_{\mathbb{C}}, \ r \geq 0, \ h > 0, \ \theta \in [0, 2\pi). \end{cases} \tag{3.16}$$

Here, $F(\boldsymbol{w}, r, h, \theta, d) : (X_1)_{\mathbb{C}} \times \mathbb{R}^4 \mapsto (X_1)_{\mathbb{C}} \times \mathbb{C} \times \mathbb{R}$ *is continuously differentiable, and*

$$\begin{cases} F_{1,j}(\boldsymbol{w}, r, h, \theta, d) := d \left(d_* \sum_{k=1}^{n} \alpha_{jk} w_k + m_j w_j \right) - (d_* - d) F_2(\boldsymbol{w}, r, h, \theta, d) \\ \qquad + (d_* - d) \left[m_j + d_* q_j \left(d, \beta^d, \boldsymbol{\xi}^d \right) - \mathrm{i} d_* h \right] \left(r \eta_j + w_j \right) \\ \qquad + d_*(d_* - d) \beta^d \left[\eta_j + (d_* - d) \xi_j^d \right] \left(a_j^d + b_j^d e^{-\mathrm{i}\theta} \right) \left(r \eta_j + w_j \right), \\ F_2(\boldsymbol{w}, r, h, \theta, d) := \sum_{j=1}^{n} \varsigma_j \left[m_j + d_* q_j \left(d, \beta^d, \boldsymbol{\xi}^d \right) - \mathrm{i} d_* h \right] \left(r \eta_j + w_j \right) \\ \qquad + \sum_{j=1}^{n} \varsigma_j d_* \beta^d [\eta_j + (d_* - d) \xi_j^d] \left(a_j^d + b_j^d e^{-\mathrm{i}\theta} \right) \left(r \eta_j + w_j \right), \\ F_3(\boldsymbol{w}, r, h, \theta, d) := (r^2 - 1) \|\boldsymbol{\eta}\|_2^2 + r \sum_{j=1}^{n} \eta_j \left(w_j + \overline{w}_j \right) + \|\boldsymbol{w}\|_2^2, \end{cases} \tag{3.17}$$

where $q_j(d, \beta, \boldsymbol{\xi})$ *and* a_j^d, b_j^d *are defined in (2.14) and (3.2), respectively.*

Proof. Multiplying (3.14) by d_*, we have

$$0 = d \left[d_* \sum_{k=1}^{n} \alpha_{jk} \varphi_k + m_j \varphi_j \right] + (d_* - d) m_j \varphi_j + d_* \left[f_j \left(u_j^d, u_j^d \right) - m_j \right] \varphi_j$$
$$+ d_* u_j^d a_j^d \varphi_j + d_* u_j^d b_j^d \varphi_j e^{-\mathrm{i}\theta} - \mathrm{i} d_* \nu \varphi_j, \quad j = 1, \cdots, n. \tag{3.18}$$

Then plugging (2.7), the first equation of (3.15), and $\nu = (d_* - d)h$ into (3.18), we have $\boldsymbol{y} = (y_1, \cdots, y_n)^T = \mathbf{0}$, where

$$y_j s := d \left(d_* \sum_{k=1}^{n} \alpha_{jk} w_k + m_j w_j \right)$$
$$+ (d_* - d) \left[m_j + d_* q_j \left(d, \beta^d, \boldsymbol{\xi}^d \right) - \mathrm{i} d_* h \right] \left(r \eta_j + w_j \right)$$
$$+ d_*(d_* - d) \beta^d \left[\eta_j + (d_* - d) \xi_j^d \right] \left(a_j^d + b_j^d e^{-\mathrm{i}\theta} \right) \left(r \eta_j + w_j \right). \tag{3.19}$$

Since

$$\mathbb{C}^n = \mathrm{span}\{\boldsymbol{\rho}\} \oplus (X_1)_{\mathbb{C}} \ \text{ with } \ \boldsymbol{\rho} = (1, \cdots, 1)^T,$$

we see that

$$\mathbf{y} = (d_* - d)F_2(\mathbf{w}, r, h, \theta, d)\boldsymbol{\rho} + \big(F_{1,1}(\mathbf{w}, r, h, \theta, d), \cdots, F_{1,n}(\mathbf{w}, r, h, \theta, d)\big)^T.$$

Therefore, $\mathbf{y} = \mathbf{0}$ if and only if $F_2(\mathbf{w}, r, h, \theta, d) = 0$ and $F_{1,j}(\mathbf{w}, r, h, \theta, d) = 0$ for all $j = 1, \cdots, n$. Clearly, the second equation of (3.15) is equivalent to $F_3(\mathbf{w}, r, h, \theta, d) = 0$. This completes the proof. $\qquad\square$

We first show that $F(\mathbf{w}, r, h, \theta, d) = \mathbf{0}$ has a unique solution for $d = d_*$.

Lemma 3.4. *Assume that* **(H0)**-**(H1)** *hold, and $\tilde{a} - \tilde{b} > 0$, where $\tilde{a}$ and $\tilde{b}$ are defined in (2.5). Then the following equation:*

$$\begin{cases} F(\mathbf{w}, r, h, \theta, d_*) = \mathbf{0} \\ \mathbf{w} \in (X_1)_{\mathbb{C}}, \ r \geq 0, \ h \geq 0, \ \theta \in [0, 2\pi] \end{cases} \tag{3.20}$$

has a unique solution $(\mathbf{w}_{d_*}, r_{d_*}, h_{d_*}, \theta_{d_*})$, where

$$\mathbf{w}_{d_*} = \mathbf{0}, \ \ r_{d_*} = 1, \ \ h_{d_*} = \frac{\beta^{d_*}\sqrt{\tilde{b}^2 - \tilde{a}^2}}{\sum_{j=1}^n \eta_j \varsigma_j}, \ \ \theta_{d_*} = \arccos\left(-\tilde{a}/\tilde{b}\right), \tag{3.21}$$

and β^{d_*} is defined in (2.8).

Proof. Set $F_1 = (F_{1,1}, \cdots, F_{1,n})^T$, and $F_1(\mathbf{w}, r, h, \theta, d_*) = \mathbf{0}$ if and only if $\mathbf{w} = \mathbf{w}_{d_*} = \mathbf{0}$. This, together with $F_3(\mathbf{w}, r, h, \theta, d_*) = 0$, implies $r = r_{d_*} = 1$. Note from (2.7) and (3.2) that $a_j^d = a_j$ and $b_j^d = b_j$ for $d = d_*$, where a_j and b_j are defined in (2.6). Then, substituting $\mathbf{w} = \mathbf{w}_{d_*}$ and $r = r_{d_*}$ into $F_2(\mathbf{w}, r, h, \theta, d_*) = 0$, we see from (2.5) and (2.8) that

$$d_*\beta^{d_*}\left(\tilde{a} + \tilde{b}e^{-\mathrm{i}\theta}\right) - \mathrm{i}d_*h \sum_{j=1}^n \eta_j \varsigma_j = 0, \tag{3.22}$$

which implies that

$$\begin{cases} \tilde{a} + \tilde{b}\cos\theta = 0, \\ \beta^{d_*}\tilde{b}\sin\theta + h\sum_{j=1}^n \eta_j \varsigma_j = 0. \end{cases} \tag{3.23}$$

It follows from **(H1)** (see also (2.12)) that $\tilde{a} + \tilde{b} < 0$. Then if $\tilde{a} - \tilde{b} > 0$, we have

$$\tilde{b} < \min\{\tilde{a}, -\tilde{a}\} \leq 0 \text{ and } -1 < -\tilde{a}/\tilde{b} < 1. \tag{3.24}$$

This, combined with (3.23), yields

$$\theta = \theta_{d_*} = \arccos\left(-\tilde{a}/\tilde{b}\right), \ \ h = h_{d_*} = \frac{\beta^{d_*}\sqrt{\tilde{b}^2 - \tilde{a}^2}}{\sum_{j=1}^n \eta_j \varsigma_j}.$$

This completes the proof. $\qquad\square$

Then we solve $F(\mathbf{w}, r, h, \theta, d) = \mathbf{0}$ for $0 < d_* - d \ll 1$.

Theorem 3.5. *Assume that* **(H0)**-**(H1)** *hold, and $\tilde{a} - \tilde{b} > 0$, where $\tilde{a}$ and $\tilde{b}$ are defined in (2.5). Then there exists $\tilde{d}_2$ ($0 < d_* - \tilde{d}_2 \ll 1$) and a continuously differentiable mapping $d \mapsto (\mathbf{w}_d, r_d, h_d, \theta_d)$ from $\left[\tilde{d}_2, d_*\right]$ to $(X_1)_{\mathbb{C}} \times \mathbb{R}^3$ such that $(\mathbf{w}_d, r_d, h_d, \theta_d)$ is the unique solution of the following problem:*

$$\begin{cases} F(\mathbf{w}, r, h, \theta, d) = \mathbf{0} \\ \mathbf{w} \in (X_1)_{\mathbb{C}}, \ r \geq 0, \ h > 0, \ \theta \in [0, 2\pi) \end{cases} \tag{3.25}$$

for $d \in \left[\tilde{d}_2, d_*\right)$.

Proof. Let $T(\boldsymbol{\chi}, \kappa, \epsilon, \vartheta) = (T_{1,1}, \cdots, T_{1,n}, T_2, T_3)^T : (X_1)_{\mathbb{C}} \times \mathbb{R}^3 \mapsto (X_1)_{\mathbb{C}} \times \mathbb{C} \times \mathbb{R}$ be the Fréchet derivative of $F(\boldsymbol{w}, r, h, \theta, d)$ with respect to $(\boldsymbol{w}, r, h, \theta)$ at $(\boldsymbol{w}_{d_*}, r_{d_*}, h_{d_*}, \theta_{d_*}, d_*)$. A direct computation yields

$$T_{1j}(\boldsymbol{\chi}, \kappa, \epsilon, \vartheta) = d_* \left(d_* \sum_{k=1}^{n} \alpha_{jk} \chi_k + m_j \chi_j \right), \; j = 1, \cdots, n,$$

$$T_2(\boldsymbol{\chi}, \kappa, \epsilon, \vartheta) = \sum_{j=1}^{n} \varsigma_j (\kappa \eta_j + \chi_j) \left\{ m_j + d_* \beta^{d_*} \left(a_j + b_j \right) \eta_j + d_* \beta^{d_*} (a_j + b_j e^{-i\theta_{d_*}}) \eta_j - i d_* h_{d_*} \right\}$$

$$- i\epsilon d_* \sum_{j=1}^{n} \varsigma_j \eta_j - i\vartheta d_* \beta^{d_*} \tilde{b} e^{-i\theta_{d_*}},$$

$$T_3(\boldsymbol{\chi}, \kappa, \epsilon, \vartheta) = \sum_{j=1}^{n} \eta_j \left(\chi_j + \overline{\chi}_j \right) + 2\kappa \|\boldsymbol{\eta}\|_2^2,$$

where we have used (2.5) and (2.14) to obtain T_2.

Now, we show that T is a bijection and only need to show that T is an injective mapping. By (2.1)–(2.3), we see that $d_* A + \text{diag}(m_j)$ is a bijection from $(X_1)_{\mathbb{C}}$ to $(X_1)_{\mathbb{C}}$. Then if $T_{1j}(\boldsymbol{\chi}, \kappa, \epsilon, \vartheta) = \boldsymbol{0}$ for all $j = 1, \cdots, n$, we have $\boldsymbol{\chi} = \boldsymbol{0}$. Substituting $\boldsymbol{\chi} = \boldsymbol{0}$ into $T_3(\boldsymbol{\chi}, \kappa, \epsilon, \vartheta) = 0$, we have $\kappa = 0$. Then plugging $\boldsymbol{\chi} = \boldsymbol{0}$ and $\kappa = 0$ into $T_2(\boldsymbol{\chi}, \kappa, \epsilon, \vartheta) = \boldsymbol{0}$, we see from (3.21) that $\epsilon = \vartheta = 0$. Therefore, T is an injection. It follows from the implicit function theorem that there exists $\tilde{d}_2 \in [d_2, d_*)$ and a continuously differentiable mapping $d \mapsto (\boldsymbol{w}_d, r_d, h_d, \theta_d)$ from $[\tilde{d}_2, d_*]$ to $(X_1)_{\mathbb{C}} \times \mathbb{R}^3$ such that $(\boldsymbol{w}_d, r_d, h_d, \theta_d)$ satisfies (3.25).

Then, we prove the uniqueness of the solution of (3.25). Actually, we only need to verify that if $\left(\boldsymbol{w}^d, r^d, h^d, \theta^d \right)$ satisfies (3.25), then $\left(\boldsymbol{w}^d, r^d, h^d, \theta^d \right) \to \left(\boldsymbol{w}_{d_*}, r_{d_*}, h_{d_*}, \theta_{d_*} \right) = \left(\boldsymbol{0}, 1, h_{d_*}, \theta_{d_*} \right)$ as $d \to d_*$. It follows from Lemma 3.1 that h^d is bounded for $d \in [\tilde{d}_2, d_*)$. Then, up to a subsequence, we can assume that $\lim_{d \to d_*} \theta^d = \theta^{d_*}$ and $\lim_{d \to d_*} h^d = h^{d_*}$. It follows from Lemma 3.1 that $\lim_{d \to d_*} r^d = r_{d_*} = 1$, $\lim_{d \to d_*} \boldsymbol{w}^d = \boldsymbol{w}_{d_*} = \boldsymbol{0}$. Taking the limits of $F\left(\boldsymbol{w}^d, r^d, h^d, \theta^d, d \right) = \boldsymbol{0}$ as $d \to d_*$, we have

$$F\left(\boldsymbol{w}_{d_*}, r_{d_*}, h^{d_*}, \theta^{d_*}, d_* \right) = \boldsymbol{0}.$$

This, combined with Lemma 3.4, implies that $\theta^{d_*} = \theta_{d_*}$ and $h^{d_*} = h_{d_*}$, Therefore, $\left(\boldsymbol{w}^d, r^d, h^d, \theta^d \right) \to \left(\boldsymbol{w}_{d_*}, r_{d_*}, h_{d_*}, \theta_{d_*} \right)$ as $d \to d_*$. This completes the proof. $\square$

By Theorem 3.5, we obtain the following result.

Theorem 3.6. *Assume that* **(H0)-(H1)** *hold, and $\tilde{a} - \tilde{b} > 0$, where $\tilde{a}$ and $\tilde{b}$ are defined in (2.5). Then for each $d \in [\tilde{d}_2, d_*)$, where $0 < d_* - \tilde{d}_2 \ll 1$, the following equation:*

$$\begin{cases} \Delta(d, iv, \tau)\boldsymbol{\psi} = \boldsymbol{0} \\ v > 0, \; \tau \geq 0, \; \boldsymbol{\psi}(\neq \boldsymbol{0}) \in \mathbb{C}^n \end{cases}$$

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

$$v = v_d = (d_* - d)h_d, \; \boldsymbol{\psi} = c\boldsymbol{\psi}_d, \; \tau = \tau_{d,l} = \frac{\theta_d + 2l\pi}{v_d}, \; l = 0, 1, 2, \cdots, \tag{3.26}$$

where $\boldsymbol{\psi}_d = r_d \boldsymbol{\eta} + \boldsymbol{w}_d$, c is a nonzero constant, and $\boldsymbol{w}_d, r_d, \theta_d, h_d$ are defined in Theorem 3.5.

For further application, we consider the adjoint eigenvalue problem of (3.3). For $\boldsymbol{\psi}, \widetilde{\boldsymbol{\psi}} \in \mathbb{C}^n$, we have

$$\left\langle \widetilde{\boldsymbol{\psi}}, \Delta(d, iv_d, \tau_{d,l})\boldsymbol{\psi} \right\rangle = \left\langle \widetilde{\Delta}(d, iv_d, \tau_{d,l})\widetilde{\boldsymbol{\psi}}, \boldsymbol{\psi} \right\rangle,$$

where

$$\widetilde{\Delta}(d, iv_d, \tau_{d,l})\widetilde{\boldsymbol{\psi}} = dA^T \widetilde{\boldsymbol{\psi}} + \text{diag}\left(f_j \left(u_j^d, u_j^d \right) \right) \widetilde{\boldsymbol{\psi}} + \text{diag}\left(u_j^d a_j^d \right) \widetilde{\boldsymbol{\psi}}$$

$$+ \text{diag}\left(u_j^d b_j^d \right) \widetilde{\boldsymbol{\psi}} e^{iv_d \tau_{d,l}} + iv_d \widetilde{\boldsymbol{\psi}}. \tag{3.27}$$

Here, $\widetilde{\Delta}(d, iv_d, \tau_{d,l})$ is the conjugate transpose matrix of $\Delta(d, iv_d, \tau_{d,l})$. Clearly, 0 is also an eigenvalue of $\widetilde{\Delta}(d, iv_d, \tau_{d,l})$.

Proposition 3.7. *Let $\widetilde{\boldsymbol{\psi}}_d$ be the corresponding eigenvector of $\widetilde{\Delta}(d, \mathrm{i}\nu_d, \tau_{d,l})$ with respect to eigenvalue 0. Then, ignoring a scalar factor, $\widetilde{\boldsymbol{\psi}}_d$ can be represented as follows:*

$$\begin{cases} \widetilde{\boldsymbol{\psi}}_d = \widetilde{r}_d \boldsymbol{\varsigma} + \widetilde{w}_d, \ \widetilde{w}_d \in \left(\widetilde{X}_1\right)_{\mathbb{C}}, \ \widetilde{r}_d \geq 0, \\ \|\widetilde{\boldsymbol{\psi}}_d\|_2^2 = \|\boldsymbol{\varsigma}\|_2^2, \end{cases} \tag{3.28}$$

and satisfies

$$\lim_{d \to d_*} \widetilde{\boldsymbol{\psi}}_d = \boldsymbol{\varsigma}, \tag{3.29}$$

where $\boldsymbol{\varsigma}$ is defined in (2.1).

Proof. It follows from (3.28) that $\widetilde{\boldsymbol{\psi}}_d$ is bounded. Then, up to a subsequence, we can assume that $\lim_{d \to d_*} \widetilde{\boldsymbol{\psi}}_d = \widetilde{\boldsymbol{\psi}}^*$. Substituting $\widetilde{\boldsymbol{\psi}} = \widetilde{\boldsymbol{\psi}}_d$ into (3.27), and taking $d \to d_*$, we have

$$\left(d_* A^T + \mathrm{diag}(m_j)\right) \widetilde{\boldsymbol{\psi}}^* = \mathbf{0}, \tag{3.30}$$

Noticing that $(d_* A^T + \mathrm{diag}(m_j))\boldsymbol{\varsigma} = \mathbf{0}$, we see from (3.28) and (3.30) that $\widetilde{\boldsymbol{\psi}}^* = \boldsymbol{\varsigma}$. This completes the proof. $\qquad\square$

For simplicity, we will always assume $d \in [\tilde{d}_2, d_*)$ in the following Theorems 3.8–3.10, where $0 < d_* - \tilde{d}_2 \ll 1$. Actually, $\tilde{d}_2$ may be chosen bigger than the one in Theorem 3.5 since further perturbation arguments are used. Next, we show that $\mathrm{i}\nu_d$ (obtained in Theorem 3.6) is simple, and the transversality condition holds.

Theorem 3.8. *Assume that* **(H0)**-**(H1)** *hold, $\tilde{a} - \tilde{b} > 0$, and $d \in [\tilde{d}_2, d_*)$, where $0 < d_* - \tilde{d}_2 \ll 1$. Then $\mu = \mathrm{i}\nu_d$ is a simple eigenvalue of $A_{\tau_{d,l}}(d)$ for $l = 0, 1, 2, \cdots$.*

Proof. It follows from Theorem 3.6 that $\mathscr{N}[A_{\tau_{d,l}}(d) - \mathrm{i}\nu_d] = \mathrm{span}[e^{\mathrm{i}\nu_d\theta}\boldsymbol{\psi}_d]$, where $\theta \in [-\tau_{d,l}, 0]$ and $\boldsymbol{\psi}_d$ is defined in Theorem 3.6. Then, we show that

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

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

$$\left[A_{\tau_{d,l}}(d) - \mathrm{i}\nu_d\right]\boldsymbol{\phi} \in \mathscr{N}\left[A_{\tau_{d,l}}(d) - \mathrm{i}\nu_d\right] = \mathrm{span}\left[e^{\mathrm{i}\nu_d\theta}\boldsymbol{\psi}_d\right],$$

and consequently, there exists a constant γ such that

$$\left[A_{\tau_{d,l}}(d) - \mathrm{i}\nu_d\right]\boldsymbol{\phi} = \gamma e^{\mathrm{i}\nu_d\theta}\boldsymbol{\psi}_d,$$

which yields

$$\dot{\boldsymbol{\phi}}(\theta) = \mathrm{i}\nu_d\boldsymbol{\phi}(\theta) + \gamma e^{\mathrm{i}\nu_d\theta}\boldsymbol{\psi}_d, \quad \theta \in \left[-\tau_{d,l}, 0\right],$$

$$\dot{\boldsymbol{\phi}}(0) = dA\boldsymbol{\phi}(0) + \mathrm{diag}\big(f_j\big(u_j^d, u_j^d\big)\big)\boldsymbol{\phi}(0) + \mathrm{diag}\big(u_j^d a_j^d\big)\boldsymbol{\phi}(0) + \mathrm{diag}\big(u_j^d b_j^d\big)\boldsymbol{\phi}(-\tau_{d,l}). \tag{3.31}$$

By the first equation of equation (3.31), we obtain that

$$\boldsymbol{\phi}(\theta) = \boldsymbol{\phi}(0)e^{\mathrm{i}\nu_d\theta} + \gamma\theta e^{\mathrm{i}\nu_d\theta}\boldsymbol{\psi}_d,$$

$$\dot{\boldsymbol{\phi}}(0) = \mathrm{i}\nu_d\boldsymbol{\phi}(0) + \gamma\boldsymbol{\psi}_d. \tag{3.32}$$

This, together with the second equation of (3.31), yields

$$\begin{aligned} \Delta\left(d, \mathrm{i}\nu_d, \tau_{d,l}\right)\boldsymbol{\phi}(0) &= dA\boldsymbol{\phi}(0) + \mathrm{diag}\big(f_j\big(u_j^d, u_j^d\big)\big)\boldsymbol{\phi}(0) + \mathrm{diag}\big(u_j^d a_j^d\big)\boldsymbol{\phi}(0) \\ &\quad + e^{-\mathrm{i}\theta_d}\mathrm{diag}\big(u_j^d b_j^d\big)\boldsymbol{\phi}(0) - \mathrm{i}\nu_d\boldsymbol{\phi}(0) \\ &= \gamma\left(\boldsymbol{\psi}_d + \tau_{d,l}e^{-\mathrm{i}\theta_d}\mathrm{diag}\big(u_j^d b_j^d\big)\boldsymbol{\psi}_d\right). \end{aligned} \tag{3.33}$$

Multiplying both sides of (3.33) by $\left(\overline{\widetilde{\psi}}_{d,1}, \cdots, \overline{\widetilde{\psi}}_{d,n}\right)$ to the left, we have

$$
\begin{aligned}
0 &= \left\langle \widetilde{\Delta}\left(d, \mathrm{i}\nu_d, \tau_{d,l}\right) \widetilde{\psi}_d, \phi(0) \right\rangle = \left\langle \widetilde{\psi}_d, \Delta\left(d, \mathrm{i}\nu_d, \tau_{d,l}\right) \phi(0) \right\rangle \\
&= \gamma \left(\sum_{j=1}^n \overline{\widetilde{\psi}}_{d,j} \psi_{d,j} + \tau_{d,l} e^{-\mathrm{i}\theta_d} \sum_{j=1}^n u_j^d b_j^d \overline{\widetilde{\psi}}_{d,j} \psi_{d,j} \right).
\end{aligned}
$$

Define

$$
S_l(d) := \sum_{j=1}^n \overline{\widetilde{\psi}}_{d,j} \psi_{d,j} + \tau_{d,l} e^{-\mathrm{i}\theta_d} \sum_{j=1}^n u_j^d b_j^d \overline{\widetilde{\psi}}_{d,j} \psi_{d,j}. \tag{3.34}
$$

By Theorems 3.5, 3.6 and (3.29), we have $\psi_d \to \eta, \widetilde{\psi}_d \to \varsigma, \theta_d \to \theta_{d_*}, (d_* - d)\tau_{d,l} \to \frac{\theta_{d_*}+2l\pi}{h_{d_*}}$ and $b_j^d \to b_j$ for $j = 1, \cdots, n$ as $d \to d_*$, where θ_{d_*} and h_{d_*} are defined in (3.21). Then we see from (2.7) and (3.21) that

$$
\lim_{d \to d_*} S_l(d) = \sum_{j=1}^n \varsigma_j \eta_j \left[1 + \left(\theta_{d_*} + 2l\pi\right) \left(\frac{-\tilde{a}}{\sqrt{\tilde{b}^2 - \tilde{a}^2}} + \mathrm{i} \right) \right] \neq 0,
$$

which implies that $\gamma = 0$ for $d \in [\tilde{d}_2, d_*)$, where $0 < d_* - \tilde{d}_2 \ll 1$. Therefore, for any $l = 0, 1, 2, \cdots$,

$$
\mathcal{N}[A_{\tau_{d,l}}(d) - \mathrm{i}\nu_d]^j = \mathcal{N}[A_{\tau_{d,l}}(d) - \mathrm{i}\nu_d], \quad j = 2, 3, \cdots,
$$

and consequently, $\mathrm{i}\nu_d$ is a simple eigenvalue of $A_{\tau_{d,l}}(d)$ for $l = 0, 1, 2, \cdots$. $\qquad\square$

By Theorem 3.8, we see that $\mu = \mathrm{i}\nu_d$ is a simple eigenvalue of $A_{\tau_{d,l}}(d)$. Then, it follows from the implicit function theorem, for each $l = 0, 1, \cdots$, there exists a neighbourhood $O_l \times D_l \times H_l$ of $(\tau_{d,l}, \mathrm{i}\nu_d, \psi_d)$ and a continuously differentiable function $(\mu(\tau), \psi(\tau)): O_{q,l} \to D_{q,l} \times H_{q,l}$ such that $\mu(\tau_{d,l}) = \mathrm{i}\nu_d, \psi(\tau_{d,l}) = \psi_d$, and for each $\tau \in O_l$, the only eigenvalue of $A_\tau(d)$ in D_l is $\mu(\tau)$, and

$$
\begin{aligned}
\Delta(d, \mu(\tau), \tau)\psi(\tau) = {}& dA\psi(\tau) + \mathrm{diag}\big(f_j\left(u_j^d, u_j^d\right)\big) \psi(\tau) + \mathrm{diag}\big(u_j^d a_j^d\big) \psi(\tau) \\
& + e^{-\mu(\tau)\tau} \mathrm{diag}\big(u_j^d b_j^d\big) \psi(\tau) - \mu(\tau)\psi(\tau) = \mathbf{0}.
\end{aligned} \tag{3.35}
$$

Then, we prove that the following transversality condition holds.

Theorem 3.9. *Assume that* **(H0)-(H1)** *hold,* $\tilde{a} - \tilde{b} > 0$, *and* $d \in [\tilde{d}_2, d_*)$, *where* $0 < d_* - \tilde{d}_2 \ll 1$. *Then*

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

Proof. Differentiating equation (3.35) with respect to τ at $\tau = \tau_{d,l}$, we have

$$
\begin{aligned}
-\frac{d\mu\left(\tau_{d,l}\right)}{d\tau} \left(\tau_{d,l} \mathrm{diag}\big(u_j^d b_j^d\big) \psi_d e^{-\mathrm{i}\theta_d} + \psi_d \right) + \Delta\left(d, \mathrm{i}\nu_d, \tau_{d,l}\right) \frac{\psi\left(\tau_{d,l}\right)}{d\tau} \\
- \mathrm{i}\nu_d \mathrm{diag}\big(u_j^d b_j^d\big) \psi_d e^{-\mathrm{i}\theta_d} = \mathbf{0}.
\end{aligned} \tag{3.36}
$$

Clearly,

$$
\left\langle \widetilde{\psi}_d, \Delta\left(d, \mathrm{i}\nu_d, \tau_{d,l}\right) \frac{d\psi\left(\tau_{d,l}\right)}{d\tau} \right\rangle = \left\langle \widetilde{\Delta}\left(d, \mathrm{i}\nu_d, \tau_{d,l}\right) \widetilde{\psi}_d, \frac{d\psi\left(\tau_{d,l}\right)}{d\tau} \right\rangle = 0.
$$

Then, multiplying both sides of equation (3.36) by $(\overline{\widetilde{\psi}}_{d,1}, \cdots, \overline{\widetilde{\psi}}_{d,n})$ to the left, we have

$$
\begin{aligned}
\frac{d\mu\left(\tau_{d,l}\right)}{d\tau} &= \frac{-\mathrm{i}\nu_d \sum_{j=1}^{n} u_j^d b_j^d \overline{\widetilde{\psi}}_{d,j} \psi_{d,j} e^{-\mathrm{i}\theta_d}}{\sum_{j=1}^{n} \overline{\widetilde{\psi}}_{d,j} \psi_{d,j} + \tau_{d,l} \sum_{j=1}^{n} u_j^d b_j^d \overline{\widetilde{\psi}}_{d,j} \psi_{d,j} e^{-\mathrm{i}\theta_d}} \\
&= \frac{1}{|S_l(d)|^2} \left[-\mathrm{i}\nu_d e^{-\mathrm{i}\theta_d} \left(\sum_{j=1}^{n} \widetilde{\psi}_{d,j} \overline{\psi}_{d,j} \right) \sum_{j=1}^{n} u_j^d b_j^d \overline{\widetilde{\psi}}_{d,j} \psi_{d,j} \right. \\
&\quad \left. -\mathrm{i}\nu_d \tau_{d,l} \left(\sum_{j=1}^{n} u_j^d b_j^d \overline{\widetilde{\psi}}_{d,j} \psi_{d,j} \right) \left(\sum_{j=1}^{n} u_j^d b_j^d \widetilde{\psi}_{d,j} \overline{\psi}_{d,j} \right) \right].
\end{aligned}
$$

It follows from Theorems 3.5, 3.6 and (3.29) that $\boldsymbol{\psi}_d \to \boldsymbol{\eta}$, $\widetilde{\boldsymbol{\psi}}_d \to \boldsymbol{\varsigma}$, $\theta_d \to \theta_{d_*}$, $\frac{\nu_d}{d_* - d} = h_d \to h_{d_*}$ and $b_j^d \to b_j$ for $j = 1, \cdots, n$ as $d \to d_*$, where θ_{d_*} and h_{d_*} are defined in (3.21). Then we see that

$$
\lim_{d \to d_*} \frac{1}{(d_* - d)^2} \frac{d\mathcal{R}e\left[\mu\left(\tau_{d,l}\right)\right]}{d\tau} = \frac{\left(\beta^{d_*}\right)^2 \left(\tilde{b}^2 - \tilde{a}^2\right)}{\lim_{d \to d_*} |S_l(d)|^2} > 0,
$$

where we have used (3.24) in the last step. This completes the proof. $\qquad \square$

By Theorems 3.6, 3.8 and 3.9, we obtain the main result for this subsection.

Theorem 3.10. *Assume that* **(H0)-(H1)** *hold and* $d \in [\tilde{d}_2, d_*)$, *where* $0 < d_* - \tilde{d}_2 \ll 1$. *Let* $\boldsymbol{u}^d$ *be the positive equilibrium of model (1.2) obtained in Lemma 2.2. Then the following statements hold.*

(i) *If* $\tilde{a} - \tilde{b} < 0$, *where* $\tilde{a}$ *and* $\tilde{b}$ *are defined in (2.5), then* $\boldsymbol{u}^d$ *is locally asymptotically stable for* $\tau \in [0, \infty)$.

(ii) *If* $\tilde{a} - \tilde{b} > 0$, *then there exists* $\tau_{d,0} > 0$ *such that* $\boldsymbol{u}^d$ *of (1.2) is locally asymptotically stable for* $\tau \in [0, \tau_{d,0})$, *and unstable for* $\tau \in (\tau_{d,0}, \infty)$. *Moreover, when* $\tau = \tau_{d,0}$, *system (1.2) undergoes a Hopf bifurcation at* $\boldsymbol{u}^d$.

3.2. The case of $0 < d \ll 1$

In this section, we will consider the case of $0 < d \ll 1$. First, we give *a priori* estimates for solutions of (3.3).

Lemma 3.11. *Assume that* $\left(\mu^d, \tau^d, \boldsymbol{\varphi}^d\right)$ *solves (3.3), where* $\mathcal{R}e\mu^d, \tau^d \geq 0$, *and* $\boldsymbol{\varphi}^d = \left(\varphi_1^d, \cdots, \varphi_n^d\right)^T (\neq \boldsymbol{0}) \in \mathbb{C}^n$. *Then for any* $\tilde{d} > 0$, $|\mu^d|$ *is bounded for* $d \in (0, \tilde{d}]$.

Proof. Without loss of generality, we assume that $\|\boldsymbol{\varphi}^d\|_2^2 = 1$. Substituting $\left(\mu^d, \tau^d, \boldsymbol{\varphi}^d\right)$ into (3.3) and multiplying both sides of (3.3) by $(\overline{\varphi_1^d}, \cdots, \overline{\varphi_n^d})$ to the left, we obtain that

$$
\begin{aligned}
\left(\overline{\varphi_1^d}, \cdots, \overline{\varphi_n^d}\right) &\left[dA\boldsymbol{\varphi}^d + \mathrm{diag}(f_j\left(u_j^d, u_j^d\right)) \boldsymbol{\varphi}^d + \mathrm{diag}\left(u_j^d a_j^d\right) \boldsymbol{\varphi}^d \right. \\
&\left. + e^{-\mu^d \tau^d} \mathrm{diag}\left(u_j^d b_j^d\right) \boldsymbol{\varphi}^d - \mu^d \boldsymbol{\varphi}^d \right] = 0.
\end{aligned}
$$

Then, for $d \in (0, \tilde{d}]$, we have

$$
\left|\mu^d\right| \leq \max_{d \in [0,\tilde{d}], 1 \leq j \leq n} |f_j\left(u_j^d, u_j^d\right)| + \max_{d \in [0,\tilde{d}], 1 \leq j \leq n} |u_j^d a_j^d| + \max_{d \in [0,\tilde{d}], 1 \leq j \leq n} |u_j^d b_j^d| + \tilde{d}n \max_{1 \leq j,k \leq n} |\alpha_{jk}|,
$$

and consequently, $|\mu^d|$ is bounded for $d \in (0, \tilde{d}]$. $\qquad \square$

Using similar arguments as in the proof of Theorem 3.2, we can obtain the following result, and here we omit the proof for simplicity.

Theorem 3.12. *Assume that* **(H0)-(H1)** *hold, and* $a_j^0 - b_j^0 < 0$ *for all* $j = 1, \cdots, n$, *where* a_j^0 *and* b_j^0 *are defined in (2.10). Then there exists* $\hat{d}_1 \in (0, d_*]$, *such that*

$$\sigma\left(A_\tau(d)\right) \subset \{x + \mathrm{i}y : x, y \in \mathbb{R}, x < 0\} \text{ for } d \in (0, \hat{d}_1] \text{ and } \tau \geq 0.$$

It follows from Theorem 3.12 that if $a_j^0 - b_j^0 < 0$ for all $j = 1, \cdots, n$, then Hopf bifurcations cannot occur for $0 < d \ll 1$. Then we define

$$\mathcal{M} = \left\{ j \in 1, \cdots, n : a_j^0 - b_j^0 > 0 \right\}, \tag{3.37}$$

and show that Hopf bifurcations can occur when $\mathcal{M} \neq \emptyset$. For simplicity, we impose the following assumption:

(H2) $a_j^0 - b_j^0 > 0$ for $j = 1, \cdots, p$, and $a_j^0 - b_j^0 < 0$ for $j = p + 1, \cdots, n$, where $1 \leq p \leq n$.

In fact, if the patches are independent of each other ($d = 0$), we have

$$u_j' = u_j f_j\left(u_j, u_j(t - \tau)\right), \ t > 0, \ j = 1, \cdots, n. \tag{3.38}$$

A direct computation implies the following result.

Lemma 3.13. *Assume that* **(H1)-(H2)** *hold. Then for each* $1 \leq j \leq n$, *model (3.38) admits a unique positive equilibrium* u_j^0, *where* u_j^0 *(defined in Lemma 2.3) is the unique positive solution of* $f_j(x, x) = 0$. *Moreover, the following statements hold.*

(i) *For each* $1 \leq j \leq p$, *the unique positive equilibrium* u_j^0 *of model (3.38) is locally asymptotically stable when* $\tau \in [0, \tau_j^0)$, *and unstable when* $\tau \in (\tau_j^0, \infty)$. *Moreover, when* $\tau = \tau_j^0$, *model (3.38) undergoes a Hopf bifurcation, where*

$$\tau_j^0 = \frac{\theta_j^0}{v_j^0} \text{ with } \theta_j^0 = \arccos\left(-a_j^0/b_j^0\right) \in (0, \pi) \text{ and } v_j^0 = u_j^0 \sqrt{\left(b_j^0\right)^2 - \left(a_j^0\right)^2} > 0. \tag{3.39}$$

(ii) *For each* $p + 1 \leq j \leq n$, *the unique positive equilibrium* u_j^0 *of model (3.38) is locally asymptotically stable for* $\tau \geq 0$.

Now, we consider the solution of (3.14) for $d = 0$.

Lemma 3.14. *Assume that* **(H1)-(H2)** *hold,* $d = 0$, *and*

$$\left(v_j^0, \theta_j^0\right) \neq \left(v_k^0, \theta_k^0\right) \text{ for any } j \neq k \text{ and } 1 \leq j, k \leq p, \tag{3.40}$$

where θ_j^0 *and* v_j^0 *are defined in (3.39) for* $j = 1, \cdots, p$. *Then*

$$\left\{(v, \theta) : v \geq 0, \ \theta \in [0, 2\pi], \ \mathcal{S}^0(v, \theta) \neq \{\mathbf{0}\}\right\} = \left\{\left(v_q^0, \theta_q^0\right)\right\}_{q=1}^p, \tag{3.41}$$

where $\left(v_q^0, \theta_q^0\right) \in (0, \infty) \times (0, \pi)$, *and*

$$\mathcal{S}^0(v, \theta) := \{\boldsymbol{\varphi} : H(0, v, \theta, \boldsymbol{\varphi}) = \mathbf{0}\}$$

with $H(d, v, \theta, \boldsymbol{\varphi})$ *defined in (3.14). Moreover, denoting* $\mathcal{S}_q = \mathcal{S}^0\left(v_q^0, \theta_q^0\right)$ *for any* $q = 1, \cdots, p$, *we have* $\mathcal{S}_q = \left\{c\boldsymbol{\varphi}_q^0 : c \in \mathbb{C}\right\}$, *where* $\boldsymbol{\varphi}_q^0 = \left(\varphi_{q,1}^0, \cdots, \varphi_{q,n}^0\right)$, $\varphi_{q,q}^0 = 1$ *and* $\varphi_{q,j}^0 = 0$ *for* $j \neq q$.

Proof. It follows from Lemma 2.3 that u_j^0 satisfies $f_j\left(u_j^0, u_j^0\right) = 0$ for $j = 1, \cdots, n$. Therefore, if there exists $\boldsymbol{\varphi} \neq \mathbf{0}$ such that $H(0, v, \theta, \boldsymbol{\varphi}) = \mathbf{0}$, then

$$\prod_{i=1}^n \left(u_j^0 a_j^0 + u_j^0 b_j^0 e^{-\mathrm{i}\theta} - \mathrm{i}v\right) = 0,$$

and consequently, for $j = 1, \cdots, n$,

$$\begin{cases} a_j^0 + b_j^0 \cos \theta = 0, \\ u_j^0 b_j^0 \sin \theta + \nu = 0. \end{cases}$$

It follows from **(H1)** and **(H2)** that $a_j^0 + b_j^0 < 0$ for $j = 1, \cdots, n$ and $a_j^0 - b_j^0 > 0$ for $j = 1, \cdots, p$. Then, for $j = 1, \cdots, p$,

$$b_j^0 < \min \left\{ a_j^0, -a_j^0 \right\} \le 0 \text{ and } -1 < -a_j^0/b_j^0 < 1, \tag{3.42}$$

which leads to $\nu = \nu_q^0$, $\theta = \theta_q^0$ for $q = 1, \cdots, p$, where ν_q^0 and θ_q^0 are defined in (3.39). Since $(\nu_j^0, \theta_j^0) \ne (\nu_k^0, \theta_k^0)$ for any $j \ne k$ and $1 \le j, k \le p$, it follows that $\mathcal{S}_q^0 = \{ c\boldsymbol{\varphi}_q^0 : c \in \mathbb{C} \}$. This completes the proof. $\square$

Remark 3.15. We remark that if

$$\frac{\theta_j^0}{\nu_j^0} \ne \frac{\theta_k^0}{\nu_k^0} \text{ for any } j \ne k \text{ and } 1 \le j, k \le p, \tag{3.43}$$

then (3.40) in Lemma 3.14 hold. By Lemma 3.13, we see that (3.43) implies that the first Hopf bifurcation values of model (3.38) for $1 \le j \le p$ are not identical. That is, the first Hopf bifurcation values of each isolated patch j for $1 \le j \le p$ are not identical.

Then we consider the solution of (3.14) for $0 < d \ll 1$.

Lemma 3.16. *Assume that* **(H0)**-**(H2)** *and (3.40) hold, and* $d \in (0, \tilde{d})$ *with* $0 < \tilde{d} \ll 1$. *Then there exists* p *pairs of* $\left(\nu_q^d, \theta_q^d \right) \in (0, \infty) \times (0, \pi)$ *such that*

$$\left\{ (\nu, \theta) : \nu \ge 0, \ \theta \in [0, 2\pi), \ \mathcal{S}^d(\nu, \theta) \ne \{\boldsymbol{0}\} \right\} = \left\{ \left(\nu_q^d, \theta_q^d \right) \right\}_{q=1}^p, \tag{3.44}$$

where

$$\mathcal{S}^d(\nu, \theta) := \{ \boldsymbol{\varphi} : H(d, \nu, \theta, \boldsymbol{\varphi}) = \boldsymbol{0} \}$$

with $H(d, \nu, \theta, \boldsymbol{\varphi})$ *defined in (3.14). Moreover, denoting* $\mathcal{S}_q^d = S^d \left(\nu_q^d, \theta_q^d \right)$ *for any* $q = 1, \cdots, p$, *we have* $\mathcal{S}_q^d = \left\{ c\boldsymbol{\varphi}_q^d : c \in \mathbb{C} \right\}$, *and*

$$\lim_{d \to 0} \nu_q^d = \nu_q^0 = u_q^0 \sqrt{\left(b_q^0 \right)^2 - \left(a_q^0 \right)^2}, \ \lim_{d \to 0} \theta_q^d = \theta_q^0 = \arccos \left(-a_q^0/b_q^0 \right) \text{ and } \lim_{d \to 0} \boldsymbol{\varphi}_q^d = \boldsymbol{\varphi}_q^0,$$

where ν_q^0, θ_q^0 *and* $\boldsymbol{\varphi}_q^0$ *are defined in Lemma 3.14.*

Proof. First, we show the existence. Here, we will only show the existence of (ν_1^d, θ_1^d), and the others could be obtained similarly. Let

$$Y_1 := \{ \boldsymbol{x} = (x_1, \cdots, x_n)^T \in \mathbb{C}^n : x_1 = 0 \},$$

and consequently $\mathbb{C}^n = \text{span}\{\boldsymbol{\varphi}_1^0\} \oplus Y_1$. Let

$$H_1 \left(d, \nu, \theta, \boldsymbol{\xi}_1 \right) := H \left(d, \nu, \theta, \boldsymbol{\varphi}_1^0 + \boldsymbol{\xi}_1 \right) : \mathbb{R}^3 \times Y_1 \to \mathbb{C}^n.$$

Clearly, we have $H_1 \left(0, \nu_1^0, \theta_1^0, \boldsymbol{0} \right) = \boldsymbol{0}$, and the Fréchet derivative of H_1 with respect to $(\nu, \theta, \boldsymbol{\xi}_1)$ at $\left(0, \nu_1^0, \theta_1^0, \boldsymbol{0} \right)$ is

$$D_{(\nu, \theta, \boldsymbol{\xi}_1)} H_1 \left(0, \nu_1^0, \theta_1^0, \boldsymbol{0} \right) [\vartheta, \epsilon, \boldsymbol{\chi}] = \begin{pmatrix} -\mathrm{i} e^{-\mathrm{i}\theta_1^0} b_1^0 u_1^0 \epsilon - \mathrm{i}\vartheta \\ \left(a_2^0 u_2^0 + b_2^0 u_2^0 e^{-\mathrm{i}\theta_1^0} - \mathrm{i}\nu_1^0 \right) \chi_2 \\ \vdots \\ \left(a_n^0 u_n^0 + b_n^0 u_n^0 e^{-\mathrm{i}\theta_1^0} - \mathrm{i}\nu_1^0 \right) \chi_n \end{pmatrix},$$

where $\vartheta, \epsilon \in \mathbb{R}$ and $\boldsymbol{\chi} = (\chi_1, \cdots, \chi_n) \in Y_1$. Note from (3.40) that $D_{(\nu,\theta,\boldsymbol{\xi})}H_1\left(0, \nu_1^0, \theta_1^0, \mathbf{0}\right)$ is a bijection. Then from the implicit function theorem, there exists a constant $\delta > 0$, a neighbourhood N_1 of $\left(\nu_1^0, \theta_1^0, \mathbf{0}\right)$ and a continuously differentiable function

$$\left(\nu_1^d, \theta_1^d, \boldsymbol{\xi}_1^d\right) : [0, \delta) \mapsto N_1$$

such that for any $d \in [0, \delta)$, the unique solution of $H_1(d, \nu, \theta, \boldsymbol{\xi}_1) = \mathbf{0}$ in the neighbourhood N_1 is $\left(\nu_1^d, \theta_1^d, \boldsymbol{\xi}_1^d\right)$. Letting $\boldsymbol{\varphi}_1^d = \boldsymbol{\varphi}_1^0 + \boldsymbol{\xi}_1^d$, we see that

$$\text{span}\left(\boldsymbol{\varphi}_1^d\right) \subset \mathcal{S}_1^d \text{ for any } d \in [0, \delta). \tag{3.45}$$

Since the dimension of $\mathcal{S}_1^d$ is upper semicontinuous, then there exists $\delta_1 < \delta$ such that $\dim \mathcal{S}_1^d \le 1$ for any $d \in [0, \delta_1)$. This, together with (3.45), implies that $\mathcal{S}_1^d = \{c\boldsymbol{\varphi}_1^d : c \in \mathbb{C}\}$. By (3.39), we see that $\left(\nu_q^0, \theta_q^0\right) \in (0, \infty) \times (0, 2\pi)$, which yields $\left(\nu_q^d, \theta_q^d\right) \in (0, \infty) \times (0, 2\pi)$ for $0 < d \ll 1$. This completes the part of existence.

Now we show that (3.44) holds. If it is not true, then there exist sequences $\{d_j\}_{j=1}^\infty$ and $\{(\nu^{d_j}, \theta^{d_j}, \boldsymbol{\varphi}^{d_j})\}_{j=1}^\infty$ such that $\lim_{j\to\infty} d_j = 0$, and for each $j = 1, 2, \cdots, (\nu^{d_j}, \theta^{d_j}) \ne (\nu_q^{d_j}, \theta_q^{d_j})(q = 1, \cdots, p)$, $\|\boldsymbol{\varphi}^{d_j}\|_2 = 1$, $\nu^{d_j} > 0$, $\theta^{d_j} \in [0, 2\pi)$, and

$$H\left(d_j, \nu^{d_j}, \theta^{d_j}, \boldsymbol{\varphi}^{d_j}\right) = \mathbf{0}.$$

By Lemma 3.11, we see that $\{\nu^{d_j}\}$ is bounded. Using similar arguments as in the proof of [7, Lemma 3.4], we show that there exists $1 \le q_0 \le p$ such that $(\nu^{d_j}, \theta^{d_j}) = (\nu_{q_0}^{d_j}, \theta_{q_0}^{d_j})$ for sufficiently large j. This is a contradiction. Therefore, (3.44) holds. □

From Lemma 3.16, we obtain the following result.

Theorem 3.17. *Assume that* **(H0)**-**(H2)** *and (3.40) hold, and* $d \in (0, \tilde{d})$, *where* $0 < \tilde{d} \ll 1$. *Then* $(\nu, \tau, \boldsymbol{\varphi})$ *solves*

$$\begin{cases} \Delta(d, \mathrm{i}\nu, \tau)\boldsymbol{\varphi} = \mathbf{0}, \\ \nu > 0, \ \tau \ge 0, \ \boldsymbol{\varphi}(\ne \mathbf{0}) \in \mathbb{C}^n, \end{cases}$$

if and only if there exists $1 \le q \le p$ *such that*

$$\nu = \nu_q^d, \ \boldsymbol{\varphi} = c\boldsymbol{\varphi}_q^d, \ \tau = \tau_{q,l}^d = \frac{\theta_q^d + 2l\pi}{\nu_q^d}, \ l = 0, 1, 2, \cdots, \tag{3.46}$$

where ν_q^d, θ_q^d, *and* $\boldsymbol{\varphi}_q^d$ *are defined in Lemma 3.16.*

Then we show that the purely imaginary eigenvalue is simple.

Theorem 3.18. *Assume that* **(H0)**-**(H2)** *and (3.40) hold. Then, for each* $d \in (0, \tilde{d})$, *where* $0 < \tilde{d} \ll 1$, $\mu = \mathrm{i}\nu_q^d$ *is a simple eigenvalue of* $A_{\tau_{q,l}^d}(d)$ *for* $q = 1, \cdots, p$ *and* $l = 0, 1, 2, \cdots$.

Proof. It follows from Theorem 3.17 that

$$\mathscr{N}\left[A_{\tau_{q,l}^d}(d) - \mathrm{i}\nu_q^d\right] = \text{span}\left[e^{\mathrm{i}\nu_q^d\theta}\boldsymbol{\varphi}_q^d\right],$$

where $\theta \in [-\tau_{q,l}^d, 0]$, and $\boldsymbol{\varphi}_q^d$ is defined in Theorem 3.17. Then, we will show that

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

If $\boldsymbol{\phi} \in \mathscr{N}[A_{\tau_{q,l}^d}(d) - \mathrm{i}\nu_q^d]^2$, then

$$\left[A_{\tau_{q,l}^d}(d) - \mathrm{i}\nu_q^d\right]\boldsymbol{\phi} \in \mathscr{N}\left[A_{\tau_{q,l}^d}(d) - \mathrm{i}\nu_q^d\right] = \text{span}\left[e^{\mathrm{i}\nu_q^d\theta}\boldsymbol{\varphi}_q^d\right],$$

and consequently, there exists a constant γ such that

$$\left[A_{\tau_{q,l}^d}(d) - \mathrm{i}\nu_q^d\right]\boldsymbol{\phi} = \gamma e^{\mathrm{i}\nu_q^d\theta}\boldsymbol{\varphi}_q^d,$$

which yields

$$
\begin{aligned}
\dot{\boldsymbol{\phi}}(\theta) =&\, \mathrm{i}v_q^d \boldsymbol{\phi}(\theta) + \gamma\, e^{\mathrm{i}v_q^d\theta}\boldsymbol{\varphi}_q^d, \quad \theta \in \big[-\tau_{q,l}^d, 0\big], \\
\dot{\boldsymbol{\phi}}(0) =&\, dA\boldsymbol{\phi}(0) + \mathrm{diag}\big(f_j\big(u_j^d, u_j^d\big)\big)\boldsymbol{\phi}(0) + \mathrm{diag}\big(u_j^d a_j^d\big)\boldsymbol{\phi}(0) \\
&\, + \mathrm{diag}\big(u_j^d b_j^d\big)\boldsymbol{\phi}\big(-\tau_{q,l}^d\big).
\end{aligned}
\tag{3.47}
$$

From the first equation of equation (3.47), we have

$$
\begin{aligned}
\boldsymbol{\phi}(\theta) &= \boldsymbol{\phi}(0)e^{\mathrm{i}v_q^d\theta} + \gamma\theta e^{\mathrm{i}v_q^d\theta}\boldsymbol{\varphi}_q^d, \\
\dot{\boldsymbol{\phi}}(0) &= \mathrm{i}v_q^d\boldsymbol{\phi}(0) + \gamma\boldsymbol{\varphi}_q^d.
\end{aligned}
\tag{3.48}
$$

Then it follows from equations (3.47) and (3.48) that

$$
\begin{aligned}
\Delta\big(d, \mathrm{i}v_q^d, \tau_{q,l}^d\big)\boldsymbol{\phi}(0) =&\, dA\boldsymbol{\phi}(0) + \mathrm{diag}\big(f_j\big(u_j^d, u_j^d\big)\big)\boldsymbol{\phi}(0) + \mathrm{diag}\big(u_j^d a_j^d\big)\boldsymbol{\phi}(0) \\
&\, + e^{-\mathrm{i}\theta_q^d}\mathrm{diag}\big(u_j^d b_j^d\big)\boldsymbol{\phi}(0) - \mathrm{i}v_q^d\boldsymbol{\phi}(0) \\
=&\, \gamma\left(\boldsymbol{\varphi}_q^d + \tau_{q,l}^d e^{-\mathrm{i}\theta_q^d}\mathrm{diag}\big(u_j^d b_j^d\big)\boldsymbol{\varphi}_q^d\right).
\end{aligned}
\tag{3.49}
$$

Let $\widetilde{\Delta}\big(d, \mathrm{i}v_q^d, \tau_{q,l}^d\big)$ be the conjugate transpose matrix of $\Delta(d, \mathrm{i}v_q^d, \tau_{q,l}^d)$, and let $\widetilde{\boldsymbol{\varphi}}_q^d = \big(\widetilde{\varphi}_{q,1}^d, \cdots, \widetilde{\varphi}_{q,n}^d\big)^T$ be the the corresponding eigenvector of $\widetilde{\Delta}\big(d, \mathrm{i}v_q^d, \tau_{q,l}^d\big)$ with respect to eigenvalue 0. Then, using similar arguments as in the proof of Proposition 3.7, we see that, ignoring a scalar factor, $\widetilde{\boldsymbol{\varphi}}_q^d$ satisfies

$$
\lim_{d\to 0}\widetilde{\boldsymbol{\varphi}}_q^d = \boldsymbol{\varphi}_q^0,
\tag{3.50}
$$

where $\boldsymbol{\varphi}_q^0$ is defined in Lemma 3.14. Multiplying both sides of (3.49) by $(\overline{\widetilde{\varphi}}_{q,1}^d, \cdots, \overline{\widetilde{\varphi}}_{q,n}^d)$ to the left, we have

$$
\begin{aligned}
0 &= \big\langle \widetilde{\Delta}\big(d, \mathrm{i}v_q^d, \tau_{q,l}^d\big)\widetilde{\boldsymbol{\varphi}}_q^d, \boldsymbol{\phi}(0)\big\rangle = \big\langle \widetilde{\boldsymbol{\varphi}}_q^d, \Delta\big(d, \mathrm{i}v_q^d, \tau_{q,l}^d\big)\boldsymbol{\phi}(0)\big\rangle \\
&= \gamma\left(\sum_{j=1}^{n}\overline{\widetilde{\varphi}}_{q,j}^d\varphi_{q,j}^d + \tau_{q,l}^d e^{-\mathrm{i}\theta_q^d}\sum_{j=1}^{n}u_j^d b_j^d\overline{\widetilde{\varphi}}_{q,j}^d\varphi_{q,j}^d\right) := \gamma S_q(d).
\end{aligned}
$$

It follows from Lemma 3.16, Theorem 3.17 and equation (3.50) that

$$
\lim_{d\to 0} S_q(d) \neq 0.
$$

which implies that $\gamma = 0$ for $d \in (0, \tilde{d})$, where $0 < \tilde{d} \ll 1$, and consequently, $\mathrm{i}v_q^d$ is a simple eigenvalue of $A_{\tau_{q,l}^d}(d)$ for $q = 1, \cdots, p$ and $l = 0, 1, 2, \cdots$. $\qquad\square$

By Theorem 3.18 and the implicit function theorem, we see that, for each $q = 1, \cdots, p$ and $l = 0, 1, 2, \cdots$, there exists a neighbourhood $O_{q,l} \times D_{q,l} \times H_{q,l}$ of $\big(\tau_{q,l}^d, \mathrm{i}v_q^d, \boldsymbol{\varphi}_q^d\big)$ and a continuously differentiable function $(\mu(\tau), \boldsymbol{\varphi}(\tau)): O_{q,l} \to D_{q,l} \times H_{q,l}$ such that $\mu\big(\tau_{q,l}^d\big) = \mathrm{i}v_q^d$, $\boldsymbol{\varphi}\big(\tau_{q,l}^d\big) = \boldsymbol{\varphi}_q^d$, and for each $\tau \in O_{q,l}$, the only eigenvalue of $A_\tau(d)$ in $D_{q,l}$ is $\mu(\tau)$, and

$$
\begin{aligned}
\Delta(d, \mu(\tau), \tau)\boldsymbol{\varphi}(\tau) =&\, dA\boldsymbol{\varphi}(\tau) + \mathrm{diag}\big(f_j\big(u_j^d, u_j^d\big)\big)\boldsymbol{\varphi}(\tau) + \mathrm{diag}\big(u_j^d a_j^d\big)\boldsymbol{\varphi}(\tau) \\
&\, + e^{-\mu(\tau)\tau}\mathrm{diag}\big(u_j^d b_j^d\big)\boldsymbol{\varphi}(\tau) - \mu(\tau)\boldsymbol{\varphi}(\tau) = \mathbf{0}.
\end{aligned}
\tag{3.51}
$$

Then, using similar arguments as Theorem 3.9, we obtain the following transversality condition.

Theorem 3.19. *Assume that* **(H0)**-**(H2)** *and (3.40) hold. Then*

$$
\frac{d\mathcal{R}e\big[\mu\big(\tau_{q,l}^d\big)\big]}{d\tau} > 0, \ \ q = 1, \cdots, p, \ \ l = 0, 1, 2, \cdots.
$$

By Theorems 3.12 and 3.17–3.19, we obtain the following result.

Theorem 3.20. *Assume that* **(H0)**-**(H1)** *hold, and* $d \in (0, \tilde{d})$, *where* $0 < \tilde{d} \ll 1$. *Let* $\boldsymbol{u}^d$ *be the unique positive equilibrium obtained in Lemma 2.2. Then the following statements hold.*

(i) *If* $a_j^0 - b_j^0 < 0$ *for all* $j = 1, \cdots, n$, *then* $\boldsymbol{u}^d$ *is locally asymptotically stable for* $\tau \in [0, \infty)$

(ii) *If* **(H2)** *and (3.43) holds, then* $\boldsymbol{u}^d$ *is locally asymptotically stable for* $\tau \in \left[0, \tau_{\hat{q},0}^d\right)$, *and unstable for* $\tau \in \left(\tau_{\hat{q},0}^d, \infty\right)$, *where* $\tau_{\hat{q},0}^d = \min_{1 \leq q \leq p} \tau_{q,0}^d$. *Moreover, when* $\tau = \tau_{\hat{q},0}^d$, *system (1.2) undergoes a Hopf bifurcation.*

4. An example

In this section, we apply the obtained results in Section 3 to a concrete example and discuss the effect of network topology on Hopf bifurcations. Choose the growth rate *per* capita as follows:

$$f_j(u_j, u_j(t - \tau)) = m_j - \hat{a}_j u_j(t) - \hat{b}_j u_j(t - \tau) \text{ for } j = 1, \cdots, n.$$

Then model (1.2) takes the following form:

$$
\begin{cases}
\dfrac{du_j}{dt} = d \sum_{k=1}^{n} \alpha_{jk} u_k + u_j \left(m_j - \hat{a}_j u_j(t) - \hat{b}_j u_j(t - \tau) \right), & t > 0, \ j = 1, \cdots, n, \\
\boldsymbol{u}(t) = \boldsymbol{\psi}(t) \geq \boldsymbol{0}, & t \in [-\tau, 0],
\end{cases}
\tag{4.1}
$$

where (α_{jk}) satisfies assumption **(H0)**, m_j represents the intrinsic growth rate in patch j and $\hat{a}_j, \hat{b}_j > 0$ represent the instantaneous and delayed dependence of the growth rate in patch j, respectively. Clearly, assumption **(H1)** holds. We remark that the continuous space version of model (4.1) with spatially homogeneous environments has been investigated in [38].

4.1. Stability and Hopf bifurcations

For case (I) $(0 < d_* - d \ll 1)$, the quantities $\tilde{a}$ and $\tilde{b}$ take the following form:

$$\tilde{a} = -\sum_{j=1}^{n} \hat{a}_j \eta_j^2 \varsigma_j, \quad \tilde{b} = -\sum_{j=1}^{n} \hat{b}_j \eta_j^2 \varsigma_j, \tag{4.2}$$

where $\boldsymbol{\eta}$ and $\boldsymbol{\varsigma}$ are defined in (2.1). Then, by Theorem 3.10, we obtain the following result.

Proposition 4.1. *Let* $\boldsymbol{u}^d$ *be the unique positive equilibrium of (4.1) obtained in Lemma 2.2 for* $d \in (0, d_*)$. *Then, for* $d \in [\tilde{d}_2, d_*)$ *with* $0 < d_* - \tilde{d}_2 \ll 1$, *the following statements hold.*

(i) *If* $\sum_{j=1}^{n} \left(\hat{a}_j - \hat{b}_j \right) \eta_j^2 \varsigma_j > 0$, *then* $\boldsymbol{u}^d$ *of model (4.1) is locally asymptotically stable for* $\tau \in [0, \infty)$.

(ii) *If* $\sum_{j=1}^{n} \left(\hat{a}_j - \hat{b}_j \right) \eta_j^2 \varsigma_j < 0$, *then* $\boldsymbol{u}^d$ *is locally asymptotically stable for* $\tau \in [0, \tau_{d,0})$, *and unstable for* $\tau \in (\tau_{d,0}, \infty)$, *where* $\tau_{d,0}$ *is defined in Theorem 3.6. Moreover, when* $\tau = \tau_{d,0}$, *system (4.1) undergoes a Hopf bifurcation at* $\boldsymbol{u}^d$.

Now we consider case (II) $((0 < d \ll 1)$. The quantities for this case take the following form:

$$a_j^0 = -\hat{a}_j, \ \ b_j^0 = -\hat{b}_j, \ \ v_j^0 = \frac{m_j \sqrt{\left(\hat{b}_j \right)^2 - \left(\hat{a}_j \right)^2}}{\hat{a}_j + \hat{b}_j}, \ \ \theta_j^0 = \arccos\left(-\frac{\hat{a}_j}{\hat{b}_j} \right). \tag{4.3}$$

Moreover, **(H2)** is reduced as follows:

(H̃2) $\hat{a}_j - \hat{b}_j < 0$ for $j = 1, \cdots, p$, and $\hat{a}_j - \hat{b}_j > 0$ for $j = p + 1, \cdots, n$, where $1 \leq p \leq n$.

Then, by Theorem 3.20, we have the following result.

Proposition 4.2. *Let $\boldsymbol{u}^d$ be the unique positive equilibrium of (1.2) obtained in Lemma 2.2 for $d \in (0, d_*)$. Then, for $d \in (0, \tilde{d})$ with $0 < \tilde{d} \ll 1$, the following statements hold.*

(i)   *If $\hat{a}_j - \hat{b}_j > 0$ for all $j = 1, \cdots, n$, then $\boldsymbol{u}^d$ is locally asymptotically stable for $\tau \in [0, \infty)$.*

(ii) *If $(\tilde{\mathbf{H}}2)$ holds and $\dfrac{\theta_j^0}{\nu_j^0} \neq \dfrac{\theta_k^0}{\nu_k^0}$ for any $j \neq k$ and $1 \leq j, k \leq p$, then $\boldsymbol{u}^d$ is locally asymptotically stable for $\tau \in \left[0, \tau_{\hat{q},0}^d\right)$, and unstable for $\tau \in \left(\tau_{\hat{q},0}^d, \infty\right)$, where $\tau_{\hat{q},0}^d$ is defined in Theorem 3.20. Moreover, when $\tau = \tau_{\hat{q},0}^d$, system (1.2) undergoes a Hopf bifurcation at $\boldsymbol{u}^d$.*

Remark 4.3. We remark that Proposition 4.2 (ii) also holds if $(\tilde{\mathbf{H}}2)$ is replaced by the following assumption:

$(\tilde{\mathbf{A}}2)$ $\{\hat{a}_j - \hat{b}_j\}_{j=1}^n$ changes sign and $\hat{a}_j - \hat{b}_j \neq 0$ for all $j = 1, \cdots, n$.

The proof is similar, and here we omit the details for simplicity.

4.2. The effect of network topologies

In this subsection, we discuss the effect of network topologies on Hopf bifurcations values for $0 < d \ll 1$. Since the computation is tedious, we only consider a special case for simplicity. Letting $\hat{a}_j = 0$ and $\hat{b}_j = 1$ for $j = 1, \cdots, n$, model (4.1) is reduced to the following system:

$$\begin{cases} \dfrac{du_j}{dt} = d \sum_{k=1}^n \alpha_{jk} u_k + u_j \left(m_j - u_j(t - \tau)\right), & t > 0, \ j = 1, \cdots, n, \\ \boldsymbol{u}(t) = \boldsymbol{\psi}(t) \geq \boldsymbol{0}, & t \in [-\tau, 0], \end{cases} \tag{4.4}$$

where (α_{jk}) satisfies assumption **(H0)**, and $m_j > 0$ for $j = 1, \cdots, n$. Clearly, **(H1)-(H2)** hold. By Proposition 4.2 (ii) and a direct computation, we see that, if

$$m_j \neq m_k \ \text{for any} \ j \neq k, \tag{4.5}$$

then model (4.4) undergoes a Hopf bifurcation for $0 < d \ll 1$ with the first Hopf bifurcation value $\tau = \tau_{\hat{q},0}^d$, where $\hat{q}$ satisfies $m_{\hat{q}} = \max\limits_{1 \leq j \leq n} m_j$. By Lemma 3.16 and Theorem 3.17, we see that

$$\tau_{\hat{q},0}^d = \frac{\theta_{\hat{q}}^d}{\nu_{\hat{q}}^d} \quad \text{and} \quad \lim_{d \to 0} \tau_{\hat{q},0}^d = \frac{\pi}{2 m_{\hat{q}}}. \tag{4.6}$$

Therefore, to obtain the effect of network topologies, we need to compute the first derivative of $\tau_{\hat{q},0}^d$ with respect to d in the following.

Proposition 4.4. *Let $\tau_{\hat{q},0}^d$ be defined in (4.6), where $\hat{q}$ satisfies $m_{\hat{q}} = \max_{1 \leq j \leq n} m_j$. Then*

$$\left(\tau_{\hat{q},0}^d\right)' \big|_{d=0} = \frac{\mathcal{T}(A)}{m_{\hat{q}}^2}, \tag{4.7}$$

where

$$\mathcal{T}(A) := -\frac{\pi}{2} \alpha_{\hat{q}\hat{q}} + \left(1 - \frac{\pi}{2}\right) \frac{1}{m_{\hat{q}}} \sum_{k \neq \hat{q}} \alpha_{\hat{q}k} m_k. \tag{4.8}$$

Proof. By (4.6), we have

$$\left(\tau_{\hat{q},0}^d\right)' = \left(\frac{\theta_{\hat{q}}^d}{v_{\hat{q}}^d}\right)' = \frac{\left(\theta_{\hat{q}}^d\right)' v_{\hat{q}}^d - \theta_{\hat{q}}^d \left(v_{\hat{q}}^d\right)'}{\left(v_{\hat{q}}^d\right)^2}, \tag{4.9}$$

where $'$ is the derivative with respect to d. Substituting $v = v_{\hat{q}}^d$, $\theta = \theta_{\hat{q}}^d$ and $\boldsymbol{\varphi} = \boldsymbol{\varphi}_{\hat{q}}^d$ into (3.14), we have

$$dA\boldsymbol{\varphi}_{\hat{q}}^d + \operatorname{diag}\left(m_j - u_j^d\right)\boldsymbol{\varphi}_{\hat{q}}^d - e^{-i\theta_{\hat{q}}^d}\operatorname{diag}\left(u_j^d\right)\boldsymbol{\varphi}_{\hat{q}}^d - iv_{\hat{q}}^d\boldsymbol{\varphi}_{\hat{q}}^d = \mathbf{0}. \tag{4.10}$$

Differentiating (4.10) with respect to d, we have

$$-\Delta\left(d, iv_{\hat{q}}^d, \tau_{\hat{q},0}^d\right)\left(\boldsymbol{\varphi}_{\hat{q}}^d\right)' = A\boldsymbol{\varphi}_{\hat{q}}^d - \operatorname{diag}\left((u_j^d)'\right)\boldsymbol{\varphi}_{\hat{q}}^d + i\left(\theta_{\hat{q}}^d\right)' e^{-i\theta_{\hat{q}}^d}\operatorname{diag}\left(u_j^d\right)\boldsymbol{\varphi}_{\hat{q}}^d$$
$$- e^{-i\theta_{\hat{q}}^d}\operatorname{diag}\left((u_j^d)'\right)\boldsymbol{\varphi}_{\hat{q}}^d - i\left(v_{\hat{q}}^d\right)'\boldsymbol{\varphi}_{\hat{q}}^d, \tag{4.11}$$

where $\Delta(d, \mu, \tau)$ is defined in (3.3). Let $\widetilde{\boldsymbol{\varphi}}_{\hat{q}}^d = \left(\widetilde{\varphi}_{\hat{q},1}^d, \cdots, \widetilde{\varphi}_{\hat{q},n}^d\right)^T$ be the corresponding eigenvector of $\widetilde{\Delta}(d, iv_{\hat{q}}^d, \tau_{\hat{q},0}^d)$ with respect to eigenvalue 0, where $\widetilde{\Delta}\left(d, iv_{\hat{q}}^d, \tau_{\hat{q},0}^d\right)$ is the conjugate transpose matrix of $\Delta\left(d, iv_{\hat{q}}^d, \tau_{\hat{q},0}^d\right)$. Using similar arguments as in the proof of Proposition 3.7, we see that, ignoring a scalar factor, $\widetilde{\boldsymbol{\varphi}}_{\hat{q}}^d$ satisfies

$$\lim_{d\to 0}\widetilde{\boldsymbol{\varphi}}_{\hat{q}}^d = \boldsymbol{\varphi}_{\hat{q}}^0, \tag{4.12}$$

where $\boldsymbol{\varphi}_q^0$ is defined in Lemma 3.14. Note that

$$0 = \left\langle\widetilde{\Delta}\left(d, iv_{\hat{q}}^d, \tau_{\hat{q},0}^d\right)\widetilde{\boldsymbol{\varphi}}_{\hat{q}}^d, \left(\boldsymbol{\varphi}_{\hat{q}}^d\right)'\right\rangle = \left\langle\widetilde{\boldsymbol{\varphi}}_{\hat{q}}^d, \Delta\left(d, iv_{\hat{q}}^d, \tau_{\hat{q},0}^d\right)\left(\boldsymbol{\varphi}_{\hat{q}}^d\right)'\right\rangle.$$

Then, multiplying both sides of (4.11) by $(\overline{\widetilde{\varphi}}_{\hat{q},1}^d, \cdots, \overline{\widetilde{\varphi}}_{\hat{q},n}^d)$ to the left, we have

$$0 = -\left\langle\widetilde{\boldsymbol{\varphi}}_{\hat{q}}^d, \Delta\left(d, iv_{\hat{q}}^d, \tau_{\hat{q},0}^d\right)\left(\boldsymbol{\varphi}_{\hat{q}}^d\right)'\right\rangle$$
$$= \left\langle\widetilde{\boldsymbol{\varphi}}_{\hat{q}}^d, A\boldsymbol{\varphi}_{\hat{q}}^d\right\rangle - \left\langle\widetilde{\boldsymbol{\varphi}}_{\hat{q}}^d, \operatorname{diag}\left((u_j^d)'\right)\boldsymbol{\varphi}_{\hat{q}}^d\right\rangle + i\left(\theta_{\hat{q}}^d\right)' e^{-i\theta_{\hat{q}}^d}\left\langle\widetilde{\boldsymbol{\varphi}}_{\hat{q}}^d, \operatorname{diag}\left(u_j^d\right)\boldsymbol{\varphi}_{\hat{q}}^d\right\rangle$$
$$- e^{-i\theta_{\hat{q}}^d}\left\langle\widetilde{\boldsymbol{\varphi}}_{\hat{q}}^d, \operatorname{diag}\left((u_j^d)'\right)\boldsymbol{\varphi}_{\hat{q}}^d\right\rangle - i\left(v_{\hat{q}}^d\right)'\left\langle\widetilde{\boldsymbol{\varphi}}_{\hat{q}}^d, \boldsymbol{\varphi}_{\hat{q}}^d\right\rangle. \tag{4.13}$$

It follows from Lemma 2.3 that $\boldsymbol{u}^d$ is continuously differentiable for $d \in [0, d_*)$, if we define $u_j^0 = m_j$ for $j = 1, \cdots, n$. A direct computation yields

$$\left(u_j^d\right)'\big|_{d=0} = \frac{1}{m_j}\sum_{k=1}^n \alpha_{jk}m_k. \tag{4.14}$$

By (4.12) and Lemma 3.16, we have

$$\boldsymbol{\varphi}_{\hat{q}}^d, \widetilde{\boldsymbol{\varphi}}_{\hat{q}}^d \to \boldsymbol{\varphi}_{\hat{q}}^0, \ v_{\hat{q}}^d \to m_{\hat{q}}, \text{and } \theta_{\hat{q}}^d \to \theta_{\hat{q}}^0 = \frac{\pi}{2} \text{ as } d \to 0, \tag{4.15}$$

where $\boldsymbol{\varphi}_{\hat{q}}^0$ satisfies $\varphi_{\hat{q},\hat{q}}^0 = 1$ and $\varphi_{\hat{q},k}^0 = 0$ for $k \neq \hat{q}$. This, combined with (4.13) and (4.14), implies that

$$\left(\theta_{\hat{q}}^d\right)'\big|_{d=0} = \frac{1}{m_{\hat{q}}^2}\sum_{k\neq\hat{q}}\alpha_{\hat{q}k}m_k \text{ and } \left(v_{\hat{q}}^d\right)'\big|_{d=0} = \frac{1}{m_{\hat{q}}}\sum_{k=1}^n\alpha_{\hat{q}k}m_k. \tag{4.16}$$

Substituting (4.16) into (4.9), we obtain that (4.7) holds. This completes the proof. $\qquad\square$

Therefore, for $0 < d \ll 1$ and a given dispersal matrix A, we obtain from (4.6) and (4.7) that

$$\tau_{\hat{q},0}^d = \frac{\pi}{2m_{\hat{q}}} + \frac{d}{m_{\hat{q}}^2}\mathcal{T}(A) + \mathcal{O}(d^2), \tag{4.17}$$
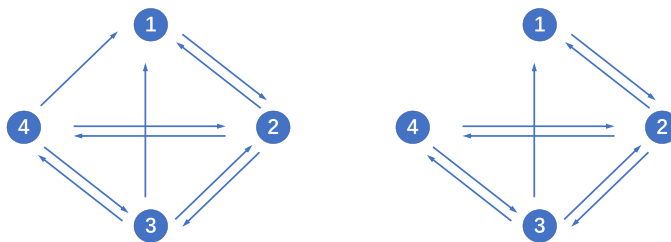
where $\mathcal{T}(A)$ is defined in (4.8).

Figure 2. *Two different network topologies. (Left): $A = A_1$; (right): $A = A_2$.*

Then, by Proposition 4.4, we obtain the effect of network topologies as follows.

Proposition 4.5. *Let $\tau_{\hat{q},0}^d(A_i)$ be the first Hopf bifurcation of model (4.4) for $A = A_i$, where $A_i = \left(\alpha_{jk}^{(i)}\right)$ ($i = 1, 2$) satisfies (**H0**). If $\mathcal{T}(A_1) > \mathcal{T}(A_2)$, then there is $\hat{d} > 0$, depending on A_1 and A_2, such that $\tau_{\hat{q},0}^d(A_1) > \tau_{\hat{q},0}^d(A_2)$ for $d \in (0, \hat{d}]$.*

Remark 4.6. We remark that if $\alpha_{\hat{q}k}^{(1)} < \alpha_{\hat{q}k}^{(2)}$ for all $k = 1, \cdots, n$, then $\mathcal{T}(A_1) > \mathcal{T}(A_2)$.

By Proposition 4.4, we can also show the monotonicity of $\tau_{\hat{q},0}^d$ for $0 < d \ll 1$.

Proposition 4.7. *Let $\tau_{\hat{q},0}^d$ be the first Hopf bifurcation of model (4.4), where $\hat{q}$ satisfies $m_{\hat{q}} = \max_{1 \leq j \leq n} m_j$. Then the following statements hold.*

 (i) *If $\mathcal{T}(A) > 0$, then $(\tau_{\hat{q},0}^d)' > 0$ for $0 < d \ll 1$.*
 (ii) *If $\mathcal{T}(A) < 0$, then $(\tau_{\hat{q},0}^d)' < 0$ for $0 < d \ll 1$.*

Therefore, network topologies also affect the monotonicity of $\tau_{\hat{q},0}^d$ for $0 < d \ll 1$.

4.3. Numerical simulations

Now, we give some numerical simulations to illustrate our theoretical results for model (4.4). Let $n = 4$ and $(m_j) = (7.5, 7, 6.5, 6)$ and choose the following two dispersal matrices:

$$A_1 = \left(\alpha_{jk}^{(1)}\right) = \begin{pmatrix} -1 & 0.2 & 0.5 & 0.6 \\ 0.5 & -1.2 & 0.2 & 0.1 \\ 0 & 0.1 & -0.9 & 0.1 \\ 0 & 0.1 & 0.2 & -1.2 \end{pmatrix},$$

and

$$A_2 = \left(\alpha_{jk}^{(2)}\right) = \begin{pmatrix} -2 & 0.2 & 0.5 & 0 \\ 0.5 & -1.2 & 0.2 & 0.1 \\ 0 & 0.1 & -0.9 & 0.1 \\ 0 & 0.1 & 0.2 & -1.2 \end{pmatrix}.$$

Then, corresponding network topologies with respect to A_1 and A_2 are different, see Figure 2.

We first choose $A = A_1$ and numerically show that delay τ can induce a Hopf bifurcation, and periodic solutions can occur when $0 < d \ll 1$ or $0 < d_* - d \leq 1$, see Figure 3.

Then, we discuss the effects of network topologies. Clearly, $\hat{q} = 1$ and $\mathcal{T}(A_1) > \mathcal{T}(A_2)$, where $\mathcal{T}(A)$ is defined in (4.8). This, combined with Proposition 4.4, implies that $\tau_{1,0}^d(A_1) > \tau_{1,0}^d(A_2)$. To confirm this, we fix $\tau_1(=0.2144)$ and numerically show that the positive equilibrium of model (4.4) is stable with $A = A_1$, while model (4.4) admits a positive periodic solution with $A = A_2$, see Figure 4. Therefore, $\tau_{1,0}^d(A_1) > \tau_{1,0}^d(A_2)$.
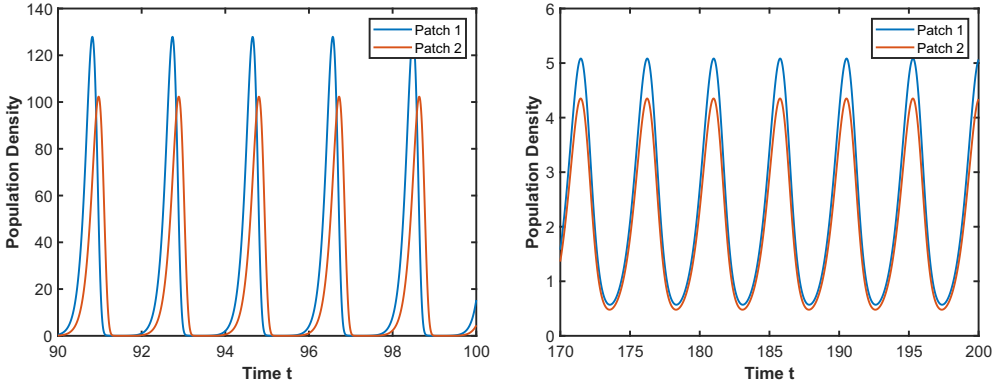
Figure 3. *Periodic solutions induced by a Hopf bifurcation for model (4.4) with $A = A_1$. (Left) The small dispersal case: $d = 0.3$ and $\tau = 0.5$. (Right) The large dispersal case: $d = 10$ and $\tau = 1.2$.*
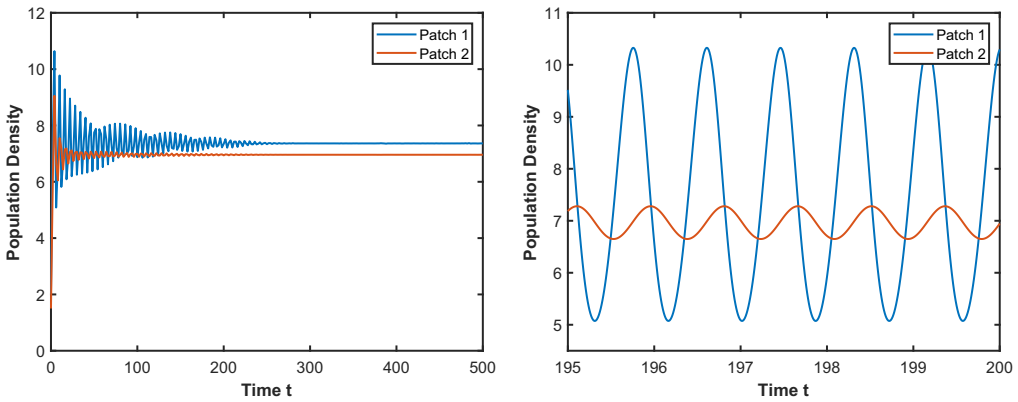

Figure 4. *The effect of network topologies. We only plot two patches for simplicity. Here $\tau_1 = 0.2144$. (Left): $A = A_1$; (right): $A = A_2$.*

Moreover, an interesting question is whether Hopf bifurcation can occur when d is intermediate. It is a challenge if $n \geq 3$. For the two-patch model, one can compute the Hopf bifurcation value $\tau_{\hat{q},0}^d$ for $d \in (0, d_*)$, see [27] with a symmetric dispersal matrix. Now we consider the asymmetric case. Let $(m_1, m_2) = (1, 2)$ and choose the following two dispersal matrices:

$$A_3 = \begin{pmatrix} -2 & 1 \\ 0.9 & -1 \end{pmatrix}, \quad A_4 = \begin{pmatrix} -20 & 1 \\ 15 & -1 \end{pmatrix}.$$

For $A = A_i$ with $i = 3, 4$, we numerically obtain a Hopf bifurcation curve $\tau_{\hat{q},0}^d(A_i)$, respectively. Here $\lim_{d \to 0} \tau_{\hat{q},0}^d(A_i) = \pi/4$ and $\lim_{d \to d_*^{(i)}} \tau_{\hat{q},0}^d(A_i) = \infty$ with $d_*^{(i)}$ satisfies $s(d_*^{(i)} A_i + \mathrm{diag}(m_j)) = 0$ for $i = 3, 4$. By Proposition 4.7, we see that network topologies also affect the monotonicity of $\tau_{\hat{q},0}^d$ for $0 < d \ll 1$. As is shown in Figure 5, $\tau_{\hat{q},0}^d(A_3)$ is monotone increasing for $0 < d \ll 1$ with $\mathcal{T}(A_3) = 1.3139 > 0$, and $\tau_{\hat{q},0}^d(A_4)$ is monotone decreasing for $0 < d \ll 1$ with $\mathcal{T}(A_4) = -2.7102 < 0$.

5. Discussion

Due to the limits of the method, we only show the existence of a Hopf bifurcation for two cases: (I) $0 < d_* - d \ll 1$ and (II) $0 < d \ll 1$.
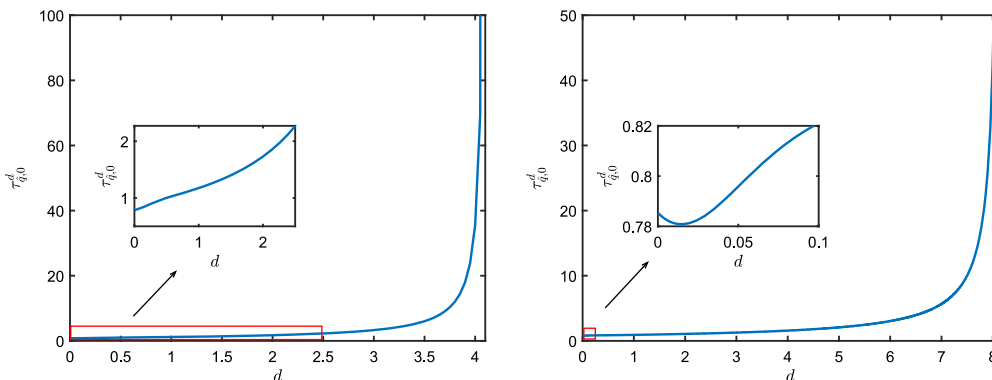
Figure 5. *The Hopf bifurcation curve. (Left): $A = A_3$; (right): $A = A_4$.*

For case (I), $\tilde{a} - \tilde{b}$ is critical to determine the existence of a Hopf bifurcation. We remark that $\tilde{a}$ and $\tilde{b}$ are usually negative (see model (4.1) for example), where $-\tilde{a} > 0$ and $-\tilde{b} > 0$ represent the instantaneous and delayed dependence of the growth rate, respectively. Therefore, $\tilde{a} - \tilde{b} < 0$ means that the instantaneous term is dominant, and consequently, delay-induced Hopf bifurcations cannot occur; $\tilde{a} - \tilde{b} > 0$ means that the delay term is dominant, and consequently, delay-induced Hopf bifurcations can occur. By (2.7), we conjecture that $\boldsymbol{v}(t)$ in (3.1) can be represented as follows:

$$\boldsymbol{v}(t) = (d_* - d)\left[c(t)\boldsymbol{\eta} + (d_* - d)\boldsymbol{z}(t)\right], \quad \text{where } c(t) \in \mathbb{R} \text{ and } \boldsymbol{z}(t) \in X_1. \tag{5.1}$$

Substituting (2.7) into (3.1), we rewrite (3.1) as follows:

$$
\begin{aligned}
\boldsymbol{v}'(t) = {}& \left[\frac{d}{d_*}\left(d_* A + \mathrm{diag}(m_j)\right)\right]\boldsymbol{v}(t) + (d_* - d)\mathrm{diag}\left(\frac{m_j}{d_*} + q_j\left(d, \beta^d, \boldsymbol{\xi}^d\right)\right)\boldsymbol{v}(t) \\
& + (d_* - d)\mathrm{diag}\left(a_j^d \beta^d \left(\eta_j + (d_* - d)\xi_j^d\right)\right)\boldsymbol{v}(t) \\
& + (d_* - d)\mathrm{diag}\left(b_j^d \beta^d \left(\eta_j + (d_* - d)\xi_j^d\right)\right)\boldsymbol{v}(t - \tau),
\end{aligned}
\tag{5.2}
$$

where $q_j(d, \beta, \boldsymbol{\xi})$ and a_j^d, b_j^d are defined in (2.14) and (3.2), respectively. Note that $a_j^d = a_j$ and $b_j^d = b_j$ for $d = d_*$, where a_j and b_j are defined in (2.6). Then, plugging (5.1) into (5.2) and removing higher order terms $\mathcal{O}(d_* - d)^2$, we see that $c(t)$ satisfies

$$c'(t)\eta_j = \left(\frac{m_j}{d_*} + q_j\left(d_*, \beta^{d_*}, \boldsymbol{\xi}^{d_*}\right)\right)\eta_j c(t) + \beta^{d_*} a_j \eta_j^2 c(t) + \beta^{d_*} b_j \eta_j^2 c(t - \tau), \quad j = 1, 2, \cdots, \tag{5.3}$$

where $q_j\left(d_*, \beta^{d_*}, \boldsymbol{\xi}^{d_*}\right) = \beta^{d_*}\left(a_j + b_j\right)\eta_j$ by (2.14). Multiplying (5.3) by ς_j and summing these over all j, we see that

$$
\begin{aligned}
c'(t)\sum_{j=1}^{n}\varsigma_j\eta_j &= \left[\frac{1}{d_*}\sum_{j=1}^{n}m_j\varsigma_j\eta_j + \beta^{d_*}\left(\tilde{a} + \tilde{b}\right)\right]c(t) + \beta^{d_*}\tilde{a}c(t) + \beta^{d_*}\tilde{b}c(t - \tau) \\
&= \beta^{d_*}\tilde{a}c(t) + \beta^{d_*}\tilde{b}c(t - \tau),
\end{aligned}
\tag{5.4}
$$

where we have used (2.8) in the first step. Therefore, removing higher order terms $\mathcal{O}(d_* - d)^2$, the linearized system (3.1) can be approximated by (5.4). This also explains why $\tilde{a} - \tilde{b}$ is crucial for the existence of a Hopf bifurcation.

For case (II), we also show the existence of a Hopf bifurcation and discuss the effect of network topology on Hopf bifurcation values for a concrete model. Our method can only apply to the case of spatial heterogeneity, since it is based on the fact that $\mathcal{S}_q$ is one dimensional (see Lemma 3.16). For example, we need to impose assumption (4.5) on model (4.4) to guarantee the existence of a Hopf bifurcation. The case of spatial homogeneity awaits further investigation.

Conflict of interest. There are no conflicts of interest.

References

[1] Busenberg, S. & Huang, W. (1996) Stability and Hopf bifurcation for a population delay model with diffusion effects. *J. Differ. Equations* **124** (1), 80–107.

[2] Cantrell, R. S. & Cosner, C. (2003) *Spatial Ecology Via Reaction-diffusion Equations*, John Wiley & Sons, Ltd., Chichester, Wiley Series in Mathematical and Computational Biology.

[3] Chang, L., Duan, M., Sun, G. & Jin, Z. (2020) Cross-diffusion-induced patterns in an SIR epidemic model on complex networks. *Chaos* **30** (1), 013147.

[4] Chang, L., Liu, C., Sun, G., Wang, Z. & Jin, Z. (2019) Delay-induced patterns in a predator-prey model on complex networks with diffusion. *New J. Phys.* **21** (7), 073035.

[5] Chen, S., Lou, Y. & Wei, J. (2018) Hopf bifurcation in a delayed reaction-diffusion-advection population model. *J. Differ. Equations* **264** (8), 5333–5359.

[6] Chen, S., Shen, Z. & Wei, J. Hopf bifurcation in a delayed single population model with patch structure. *to appear in J. Dynam. Differ. Equations*. DOI: 10.1007/s10884-021-09946-8.

[7] Chen, S. & Shi, J. (2012) Stability and Hopf bifurcation in a diffusive logistic population model with nonlocal delay effect. *J. Differ. Equations* **253** (12), 3440–3470.

[8] Chen, S., Shi, J., Shuai, Z. & Wu, Y. (2019) Two novel proofs of spectral monotonicity of perturbed essentially nonnegative matrices with applications in population dynamics. *SIAM J. Appl. Math.* **82** (2), 654–676.

[9] Chen, S., Wei, J. & Zhang, X. (2020) Bifurcation analysis for a delayed diffusive logistic population model in the advective heterogeneous environment. *J. Dyn. Differ. Equations* **32** (2), 823–847.

[10] Chen, S. & Yu, J. (2016) Stability analysis of a reaction-diffusion equation with spatiotemporal delay and Dirichlet boundary condition. *J. Dyn. Differ. Equations* **28** (3-4), 857–866.

[11] Chen, S. & Yu, J. (2016) Stability and bifurcations in a nonlocal delayed reaction-diffusion population model. *J. Differ. Equations* **260** (1), 218–240.

[12] Du, Y., Niu, B., Guo, Y. & Li, J. (2019) Double Hopf bifurcation induces coexistence of periodic oscillations in a diffusive Ginzburg-Landau model. *Phys. Lett. A* **383** (7), 630–639.

[13] Du, Y., Niu, B., Guo, Y. & Wei, J. (2020) Double Hopf bifurcation in delayed reaction-diffusion systems. *J. Dyn. Differ. Equations* **32** (1), 313–358.

[14] Duan, M., Chang, L. & Jin, Z. (2019) Turing patterns of an SI epidemic model with cross-diffusion on complex networks. *Physica A* **533,** 122023.

[15] Faria, T. (2000) Normal forms and Hopf bifurcation for partial differential equations with delays. *Trans. Am. Math. Soc.* **352** (5), 2217–2238.

[16] Fernandes, L. D. & de Aguiar, M. A. M. (2019) Turing patterns and apparent competition in predator-prey food webs on networks. *Phys. Rev. E* **86** (5), 056203.

[17] Gourley, S. A. & So, J. W.-H. (2002) Dynamics of a food-limited population model incorporating nonlocal delays on a finite domain. *J. Math. Biol.* **44** (1), 49–78.

[18] Guo, S. & Yan, S. (2016) Hopf bifurcation in a diffusive Lotka-Volterra type system with nonlocal delay effect. *J. Differ. Equations* **260** (1), 781–817.

[19] Hadeler, K. P. & Ruan, S. (2007) Interaction of diffusion and delay. *Discrete Contin. Dyn. Syst. Ser. B* **8** (1), 95–105.

[20] Hu, R. & Yuan, Y. (2011) Spatially nonhomogeneous equilibrium in a reaction-diffusion system with distributed delay. *J. Differ. Equations* **250** (6), 2779–2806.

[21] Huang, D. & Chen, S. (2021) The stability and Hopf bifurcation of the diffusive Nicholson's blowflies model in spatially heterogeneous environment. *Z. Angew. Math. Phys.* **72** (1), 41.

[22] Huang, D., Chen, S. & Zou, X. (2021) Hopf bifurcation in a delayed population model over patches with general dispersion matrix and nonlocal interactions. *submitted*. DOI: 10.1007/s10884-021-10070-w.

[23] Jin, Z. & Yuan, R. (2021) Hopf bifurcation in a reaction-diffusion-advection equation with nonlocal delay effect. *J. Differ. Equations* **271,** 533–562.

[24] Li, M. Y. & Shuai, Z. (2010) Global-stability problem for coupled systems of differential equations on networks. *J. Differ. Equations* **248** (1), 1–20.

[25] Li, Z. & Dai, B. (2021) Stability and Hopf bifurcation analysis in a Lotka-Volterra competition- diffusion-advection model with time delay effect. *Nonlinearity* **34** (5), 3271–3313.

[26] Liao, K.-L. & Lou, Y. (2014) The effect of time delay in a two-patch model with random dispersal. *Bull. Math. Biol.* **76** (2), 335–376.

[27] Lu, Z. Y. & Takeuchi, Y. (1993) Global asymptotic behavior in single-species discrete diffusion systems. *J. Math. Biol.* **32** (1), 67–77.

[28] Madras, N., Wu, J. & Zou, X. (1996) *Local-nonlocal interaction and spatial-temporal patterns in single species population over a patchy environment. Canad. Appl. Math. Quart.* **4** (1), 109–134.

[29] Magal, P. & Ruan, S. (2018) *Theory and Applications of Abstract semilinear Cauchy Problems, with a Foreword by Glenn Webb*, Vol. 201, Springer, Cham.

[30] Morita, Y. (1984) Destabilization of periodic solutions arising in delay-diffusion systems in several space dimensions. *Japan J. Appl. Math.* **1** (1), 39–65.

[31] Okubo, A. & Levin, S. A. (2001) *Diffusion and Ecological Problems: Modern Perspectives*, Springer. Springer New York, New York.

[32] Petit, J., Asllani, M., Fanelli, D., Lauwens, B. & Carletti, T. (2016) Pattern formation in a two-component reaction-diffusion system with delayed processes on a network. *Physica A* **462,** 230–249.

[33] Shi, H.-B., Ruan, S., Su, Y. & Zhang, J.-F. (2015) Spatiotemporal dynamics of a diffusive Leslie-Gower predator-prey model with ratio-dependent functional response. *Int. J. Bifur. Chaos Appl. Sci. Eng.* **25** (5), 16.

[34] Shi, Q., Shi, J. & Song, Y. (2019) Hopf bifurcation and pattern formation in a delayed diffusive logistic model with spatial heterogeneity. *Discrete Contin. Dyn. Syst. Ser. B* **24** (2), 467–486.

[35] Smith, H. L. (1995) *Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems*, Ams Ebooks Program, vol. 41, American Mathematical Society, Providence, RI.

[36] So, J. W.-H., Wu, J. & Zou, X. (2001) Structured population on two patches: modeling dispersal and delay. *J. Math. Biol.* **43** (1), 37–51.

[37] Su, Y., Wei, J. & Shi, J. (2009) Hopf bifurcations in a reaction-diffusion population model with delay effect. *J. Differ. Equations* **247** (4), 1156–1184.

[38] Su, Y., Wei, J. & Shi, J. (2012) Hopf bifurcation in a diffusive logistic equation with mixed delayed and instantaneous density dependence. *J. Dyn. Differ. Equations* **24** (4), 897–925.

[39] Tian, C. & Ruan, S. (2019) Pattern formation and synchronism in an allelopathic plankton model with delay in a network. *SIAM J. Appl. Dyn. Syst.* **18** (1), 531–557.

[40] Wu, J. (1996) *Theory and Applications of Partial Functional-Differential Equations*, Vol. 119, Springer-Verlag, New York.

[41] Xiao, Y., Zhou, Y. & Tang, S. (2011) Modelling disease spread in dispersal networks at two levels. *Math. Med. Biol.* **28** (3), 227–244.

[42] Yan, X.-P. & Li, W.-T. (2010) Stability of bifurcating periodic solutions in a delayed reaction-diffusion population model. *Nonlinearity* **23** (6), 1413–1431.

[43] Yoshida, K. (1982) The Hopf bifurcation and its stability for semilinear diffusion equations with time delay arising in ecology. *Hiroshima Math. J.* **12** (2), 321–348.

[44] Zhao, X.-Q. (2017) Dynamical Systems in Population Biology, *CMS Books in Mathematics/Ouvrages de Mathématiques de LA SMC*. 2nd ed., Springer, Cham.

[45] Zhu, H., Yan, X. & Jin, Z. (2021) Creative idea diffusion model in the multiplex network with consideration of multiple channels. *Commun. Nonlinear Sci. Numer. Simul.* **97,** 105734.