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PAPER

Hopf bifurcations for a delayed discrete single population patch model in advective environments

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Abstract
In this paper, we consider a delayed discrete single population patch model in advective environments. The individuals are subject to both random and directed movements, and there is a net loss of individuals at the downstream end due to the flow into a lake. Choosing time delay as a bifurcation parameter, we show the existence of Hopf bifurcations for the model. In homogeneous non-advective environments, it is well known that the first Hopf bifurcation value is independent of the dispersal rate. In contrast, for homogeneous advective environments, the first Hopf bifurcation value depends on the dispersal rate. Moreover, we show that the first Hopf bifurcation value in advective environments is larger than that in non-advective environments if the dispersal rate is large or small, which suggests that directed movements of the individuals inhibit the occurrence of Hopf bifurcations.

1. Introduction

Time delays can induce periodic solutions through Hopf bifurcations, and this phenomenon can explain population oscillations in the natural world. Take the following n-patch single population model

$$\frac{du_j}{dt} = \sum_{k=1}^{n} L_{jk}u_k + u_j[a_j - b_ju_j(t-\tau)], \;\; j = 1, \cdots, n, \;\; t > 0 \tag{1.1}$$

for instance. Here, u_j denotes the population density in patch j, (L_{jk}) is the dispersion matrix, τ is the time delay and represents the maturation time, and a_j and b_j represent the intrinsic growth rate and intraspecific competition of the species in patch j, respectively. It was shown that time delay can induce Hopf bifurcations for model (1.1) when the dispersion matrix $(L_{jk}) = \epsilon(\hat{L}_{jk})$ with $0 < \epsilon \ll 1$ or $\epsilon \gg 1$ [8, 24]. Especially, if $n = 2$, delay-induced Hopf bifurcations can occur for a wider range of parameters [31].

The species in streams are subject to both random and directed movements. For example, the following Figure 1 represents stream to a lake, and the diffusive flux into and from the lake balances. Therefore, the flux into the lake at the downstream end is only the advective flux, and one can refer to [34, 35, 49] for more biological explanation. For the river network illustrated in Figure 1, the dispersion matrix (L_{jk}) in model (1.1) takes the following form:

$$(L_{jk}) = dD + qQ. \tag{1.2}$$

Here, d and q are the random diffusion rate and drift rate, respectively; and $D = (D_{ij})$ and $Q = (Q_{ij})$ represent the diffusion pattern and directed movement pattern of individuals, respectively, where

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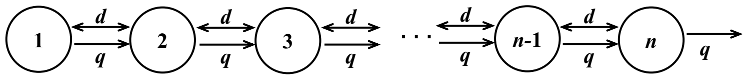

Figure 1. *A sample river network.*

$$D_{jk} = \begin{cases} 1, & j = k-1 \text{ or } j = k+1, \\ -2, & j = k = 2, \cdots, n-1, \\ -1, & j = k = 1, n, \\ 0, & \text{otherwise}, \end{cases} \tag{1.3}$$

and

$$Q_{jk} = \begin{cases} 1, & j = k+1, \\ -1, & j = k = 1, \cdots, n, \\ 0, & \text{otherwise}. \end{cases} \tag{1.4}$$

The population dynamics in streams have been studied extensively, and it can be modelled by discrete patch models or partial differential equations (PDE) models. It is well known that the stream flow takes individuals to the downstream locations, which is unfavourable for their persistence, see, for example, [35, 36, 45, 49] for PDE models. The directed drift is also a disadvantage for two competing species, and to win the competition, the species need a faster random movement rate to compensate the net loss induced by directed movements, see, for example, [3, 13, 35, 36, 53] for PDE models and, for example, [6, 22, 25, 26, 42] for discrete patch models. A natural question is:

(Q_1) Whether model (1.1) undergoes Hopf bifurcations with (L_{jk}) defined in (1.2) and how directed movements of individuals affect Hopf bifurcations?

We remark that d and q are normally not proportional, and consequently results in [8, 24] cannot apply to this type of dispersion matrix.

In this paper, we aim to answer question (Q_1) and consider the river network illustrated in Figure 1. To emphasise the effect of directed drift, we exclude the effect of spatial heterogeneity, and let $a_1 = \cdots = a_n = a$ and $b_1 = \cdots = b_n = b$ in model (1.1). Then model (1.1) is reduced to the following form:

$$\begin{cases} \dfrac{du_j}{dt} = \displaystyle\sum_{k=1}^{n} \left(dD_{jk} + qQ_{jk}\right) u_k + u_j \left(a - bu_j(t-\tau)\right), & t > 0, \ j = 1, \cdots, n, \\ \boldsymbol{u}(t) = \boldsymbol{\psi}(t) \geq 0, & t \in [-\tau, 0], \end{cases} \tag{1.5}$$

where $n \geq 2$ is the number of patches, d and q are the random diffusion rate and drift rate, respectively, $D = (D_{jk})$ and $Q = (Q_{jk})$ are defined in (1.3) and (1.4), respectively, and parameters $a, b, \tau > 0$ have the same meanings as the above model (1.1).

Our study is also motivated by some researches on reaction–diffusion models with time delay. One can refer to [1, 2, 9, 12, 19, 20, 23, 46, 50, 51] and [7, 11, 27, 30, 33, 38, 41, 47] for reaction–diffusion models without and with advection term, respectively. The following reaction–diffusion model with time delay

$$\begin{cases} u_t = \hat{d}u_{xx} - \hat{q}u_x + u\,(a - bu(t-\tau))\,, & x \in (0,l),\ t>0 \\ \hat{d}u_x(0,t) - \hat{q}u(0,t) = 0, & t>0 \\ \hat{d}u_x(l,t) - \hat{q}u(l,t) = -\beta\hat{q}u(l,t), & t>0 \\ u(x,t) = \psi(x,t) \geq 0, & x \in (0,l),\ t \in [-\tau,0] \end{cases} \tag{1.6}$$

models population dynamics in streams, where $\beta \geq 0$ represents the loss of individuals at the downstream end. Actually, model (1.5) can be viewed as a discrete version of model (1.6) with $\beta = 1$, which describes streams into a lake at the downstream end. Divide the interval $[0, l]$ into $n+1$ sub-intervals with equal length $\Delta x = l/(n+1)$, and denote the endpoints by $0, 1, \cdots, n+1$. Discretising the spatial variable of the first equation of (1.6) at endpoints $j = 1, \cdots, n$, we obtain the following equation:

$$\frac{du_j}{dt} = \hat{d}\frac{u_{j+1} - 2u_j + u_{j-1}}{(\Delta x)^2} - \hat{q}\frac{u_j - u_{j-1}}{\Delta x} + u_j(a - bu_j(t-\tau)),\ \ j = 1, \cdots, n, \tag{1.7}$$

where $u_j(t)$ is the population density at endpoint j. Let $d = \hat{d}/(\Delta x)^2$ and $q = \hat{q}/\Delta x$. Then we obtain (1.5) from (1.7) for $j = 2, \cdots, n-1$. At the upstream end, we discretise the no-flux boundary condition and obtain that

$$d(u_1 - u_0) - qu_0 = 0. \tag{1.8}$$

Plugging (1.8) into (1.7) with $j = 1$, we obtain (1.5) for $j = 1$. Similarly, discretising the boundary condition at the downstream end with $\beta = 1$, we have $u_n = u_{n+1}$. Plugging it into (1.7), we obtain (1.5) for $j = n$. The above discretisation for model (1.6) with $\tau = 0$ can be found in [10, 34], and here we include it for the sake of completeness.

For the non-advective case ($\hat{q} = 0$), model (1.6) admits a unique positive steady state $u = a/b$, and it was shown in [40, 52] that large delay can make such a constant steady state unstable and induce Hopf bifurcations. If $\hat{d}$ and $\hat{q}$ are proportional with $\hat{q} \neq 0$, delay-induced Hopf bifurcations can also be investigated. Letting $\tilde{u} = e^{-(\hat{q}/\hat{d})x}u$ and $\tilde{t} = dt$, model (1.6) can be transformed as follows:

$$\begin{cases} \tilde{u}_{\tilde{t}} = e^{-\lambda x}(e^{\lambda x}\tilde{u}_x)_x + r\tilde{u}\left(a - be^{\lambda x}\tilde{u}(\tilde{t} - \tilde{\tau})\right), & x \in (0,l),\ \tilde{t} > 0, \\ \tilde{u}_x(0,\tilde{t}) = 0, & \tilde{t} > 0, \\ \tilde{u}_x(l,\tilde{t}) = -\beta\lambda\tilde{u}, & \tilde{t} > 0, \end{cases} \tag{1.9}$$

where $\lambda = \hat{d}/\hat{q}$, $r = 1/\hat{d}$ and $\tilde{\tau} = \hat{d}\tau$. For the case of $\beta = 0$, it was shown in [11] that delay can induce Hopf bifurcations for model (1.9) if $r \ll 1$, which implies that delay-induced Hopf bifurcations can occur if $\hat{d}$ and $\hat{q}$ are proportional and both large for the original model (1.6). To our knowledge, the case that $\hat{d}$ and $\hat{q}$ are not proportional is also unknown for model (1.6). Our study on question (Q_1) also solves this problem in a discrete setting.

The main results of the paper are summarised as follows. It is well known that large delay can induce Hopf bifurcations for model (1.5) if the directed drift rate $q = 0$ (the non-advective case), and the first Hopf bifurcation value is $\tau_{non} = \pi/2a$, which is independent of the random diffusion rate d (Proposition 5.1). In contrast, if $q \neq 0$ (the advection case), the first Hopf bifurcation value τ_{adv} depends on d and is strictly monotone decreasing in $d \in (\hat{d}_3, \infty)$ with $\hat{d}_3 \gg 1$ (Proposition 5.2). Moreover, we show that $\tau_{adv} > \tau_{non}$ for $d \gg 1$ or $d \ll 1$ (Propositions 5.2 and 5.3), which suggests that directed movements of the individuals inhibit the occurrence of Hopf bifurcations. The comparison of Hopf bifurcation values between non-advective and advective cases is illustrated in Figure 2. Moreover, we obtain that the total population size is strictly increasing in $d \in [\delta, \infty)$ with $\delta \gg 1$ (Proposition 2.6 and remark 2.7).

For patch models in homogeneous non-advective environments, one can refer to [16–18] for the framework of Turing and Hopf bifurcations, see also [4, 15] for cross diffusion-induced Turing bifurcations and [5, 32, 39, 43, 44, 48] for delay-induced Hopf bifurcations. For homogeneous advective

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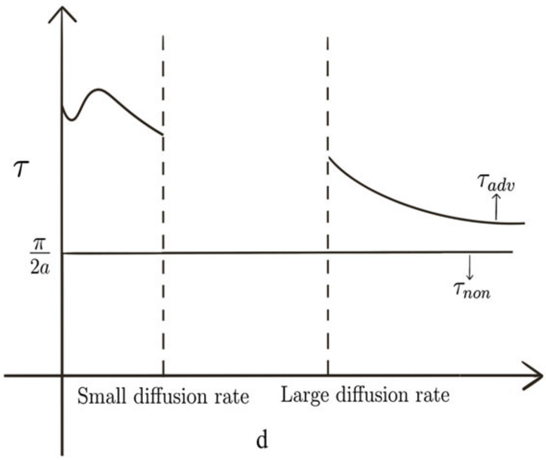

Figure 2. *The comparison of Hopf bifurcation values.*

environments, one cannot obtain the explicit expressions for the positive equilibria. This brings some difficulties in bifurcation analysis, and we overcome them by constructing equivalent eigenvalue problems in this paper.

The rest of the paper is organised as follows. In Section 2, we give some preliminaries and obtain some properties for the unique positive equilibrium $\boldsymbol{u}_d$ of model (1.5). In Section 3, we study the eigenvalue problem associated with the positive equilibrium $\boldsymbol{u}_d$ for three cases. In Section 4, we obtain the local dynamics and the existence of Hopf bifurcations for model (1.5). Finally, we show the effect of drift rate on Hopf bifurcation values and give some numerical simulations in Section 5.

2. Preliminary

We first list some notations for later use. Denote $\mathbf{1} = (1, \cdots, 1)^T$ and define the real and imaginary parts of $\mu \in \mathbb{C}$ by $\mathcal{R}e\mu$ and $\mathcal{I}m\mu$, respectively. For a space Z, we denote complexification of Z to be $Z_{\mathbb{C}} := \{x_1 + \mathrm{i}x_2 | x_1, x_2 \in Z\}$. For a linear operator T, we define the domain, the range and the kernel of T by $\mathscr{D}(T)$, $\mathscr{R}(T)$ 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 denote

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

For $\boldsymbol{u} = (u_1, \cdots, u_n)^T \in \mathbb{R}^n$, we write $\boldsymbol{u} \gg \mathbf{0}$ if $u_j > 0$ for all $j = 1, \cdots, n$. For an $n \times n$ real-valued matrix M, we denote the spectral bound of M by:

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

and the spectral radius of M by:

$$\rho(M) := \max\{|\mu| : \mu \text{ is an eigenvalue of } M\}.$$

An eigenvalue of M with a positive eigenvector is called the principal eigenvalue of M. A real-valued square matrix M with non-negative off-diagonal entries is referred to as the essentially non-negative matrix. If M is an irreducible essentially non-negative matrix, then there exists $c > 0$ such that $M + cI$ is an irreducible non-negative matrix. It follows from [28, Theorem 2.1] that

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(i) $\rho(M+cI)$ is positive and is an algebraically simple eigenvalue of $M+cI$ with a positive eigenvector.

(ii) $\rho(M+cI)$ is the unique eigenvalue with a non-negative eigenvector.

By (i), we have $s(M)+c=s(M+cI)=\rho(M+cI)$, and consequently, $s(M)$ is an algebraically simple eigenvalue of M with a positive eigenvector. By (ii), we see that $s(M)$ is the unique principal eigenvalue of M.

Consider the following eigenvalue problem:

$$\sum_{k=1}^{n} dD_{jk}\phi_k + \sum_{k=1}^{n} qQ_{jk}\phi_k + a\phi_j = \lambda\phi_j, \quad j=1,\cdots,n, \tag{2.1}$$

where (D_{jk}) and (Q_{jk}) are defined in (1.3) and (1.4), respectively. Since $dD+qQ+aI$ is an irreducible and essentially non-negative matrix, it follows that (2.1) admits a unique principal eigenvalue $\lambda_1(d,q)$ with

$$\lambda_1(d,q) = s\,(dD+qQ+aI)\,.$$

The global dynamics of model (1.5) for $\tau=0$ is determined by the sign of $\lambda_1(d,q)$ (see [14, 29, 37] for the proof).

Lemma 2.1. *Suppose that $\tau=0$. If $\lambda_1(d,q)\le 0$, then the trivial equilibrium $\mathbf{0}$ of model (1.5) is globally asymptotically stable; if $\lambda_1(d,q)>0$, then model (1.5) admits a unique positive equilibrium, which is globally asymptotically stable.*

For later use, we cite the following result from [10].

Lemma 2.2. *Let $\lambda_1(d,q)$ be the principal eigenvalue of (2.1). Then the following statements hold:*

(i) For fixed $d>0$, $\lambda_1(d,q)$ is strictly decreasing with respect to q in $[0,\infty)$, and there exists $q_d^*>0$ such that $\lambda_1(d,q_d^*)=0$, $\lambda_1(d,q)<0$ for $q>q_d^*$, and $\lambda_1(d,q)>0$ for $q<q_d^*$;

(ii) q_d^* is strictly increasing in $d\in(0,\infty)$ with $\lim_{d\to 0} q_d^*=a$ and $\lim_{d\to\infty} q_d^*=na$.

Here, we remark that Lemma 2.2 (i) follows from [10, Lemma 3.1 and Proposition 3.2 (i)], and Lemma 2.2 (ii) follows from [10, Lemma 3.7]. The following result is deduced directly from Lemma 2.2.

Lemma 2.3. *Let $\lambda_1(d,q)$ be the principal eigenvalue of (2.1). Then the following statements hold:*

(i) If $q\in(0,a]$, then $\lambda_1(d,q)>0$ for all $d>0$;

(ii) If $q\in(a,na)$, then there exists $d_q^*>0$ such that $\lambda_1(d_q^*,q)=0$, $\lambda_1(d,q)<0$ for $0<d<d_q^*$ and $\lambda_1(d,q)>0$ for $d>d_q^*$;

(iii) If $q\in[na,\infty)$, then $\lambda_1(d,q)<0$ for all $d>0$.

By Lemmas 2.1 and 2.3, we obtain the global dynamics of model (1.5) for $\tau=0$.

Proposition 2.4. *Suppose that $d,q,a,b>0$ and $\tau=0$. Then the following statements hold:*

(i) If $q\in(0,a]$, then model (1.5) admits a unique positive equilibrium $\boldsymbol{u}_d\gg\mathbf{0}$ for all $d>0$, which is globally asymptotically stable;

(ii) If $q\in(a,na)$, then the trivial equilibrium $\mathbf{0}$ of model (1.5) is globally asymptotically stable for $d\in(0,d_q^*]$; and for $d\in(d_q^*,\infty)$, model (1.5) admits a unique positive equilibrium $\boldsymbol{u}_d\gg\mathbf{0}$, which is globally asymptotically stable;

(iii) If $q\in[na,\infty)$, then the trivial equilibrium $\mathbf{0}$ of model (1.5) is globally asymptotically stable.

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Clearly, $\boldsymbol{u}_d$ satisfies

$$\sum_{k=1}^{n} (dD_{jk} + qQ_{jk})u_k + u_j \left(a - bu_j\right) = 0, \quad j = 1, \cdots, n. \tag{2.2}$$

For simplicity, we first list some notations. Define

$$\mathcal{L} = (\mathcal{L}_{jk}) := d_q^* D + qQ + aI, \tag{2.3}$$

where d_q^* is defined in Lemma 2.3. It follow from Lemma 2.3 (ii) that 0 is the principal eigenvalue of $\mathcal{L}$ and a corresponding eigenvector is

$$\boldsymbol{\eta} = (\eta_1, \cdots, \eta_n)^T \gg 0 \text{ with } \sum_{i=1}^{n} \eta_i = 1. \tag{2.4}$$

Clearly, 0 is also the principal eigenvalue of $\mathcal{L}^T$ and a corresponding eigenvector is

$$\hat{\boldsymbol{\eta}} = (\hat{\eta}_1, \cdots, \hat{\eta}_n)^T \gg 0 \text{ with } \sum_{i=1}^{n} \hat{\eta}_i = 1. \tag{2.5}$$

Here, we remark that 0 is an algebraically simple eigenvalue of $\mathcal{L}$ and $\mathcal{L}^T$, and the corresponding eigenvector is unique up to multiplying by a scalar. Then, we have the following decompositions:

$$\mathbb{R}^n = \text{span}\{\boldsymbol{\eta}\} \oplus X_1 = \text{span}\{\mathbf{1}\} \oplus X_1, \tag{2.6}$$

where

$$X_1 := \left\{ (x_1, \cdots, x_n)^T \in \mathbb{R}^n : \sum_{i=1}^{n} \hat{\eta}_i x_i = 0 \right\}. \tag{2.7}$$

In fact, for any $\boldsymbol{y} = (y_1, \cdots, y_n)^T \in \mathbb{R}^n$, $\boldsymbol{y} = c_1\mathbf{1} + \boldsymbol{\xi}_1 = c_2\boldsymbol{\eta} + \boldsymbol{\xi}_2$, where

$$c_1 = \sum_{i=1}^{n} \hat{\eta}_i y_i, \quad \boldsymbol{\xi}_1 = \boldsymbol{y} - c_1\mathbf{1} \in X_1, \quad c_2 = \frac{\sum_{i=1}^{n} \hat{\eta}_i y_i}{\sum_{i=1}^{n} \eta_i \hat{\eta}_i}, \quad \boldsymbol{\xi}_2 = \boldsymbol{y} - c_2\boldsymbol{\eta} \in X_1.$$

Now, we explore further properties on the positive equilibrium $\boldsymbol{u}_d$.

Proposition 2.5. *Let $\boldsymbol{\eta}$, $\hat{\boldsymbol{\eta}}$ and X_1 be defined in (2.4), (2.5) and (2.7), respectively. Then the following statements hold:*

(i) For fixed $q \in (0, a)$, $\boldsymbol{u}_d$ is continuously differentiable with respect to $d \in [0, \infty)$, where $\boldsymbol{u}_d = \boldsymbol{u}_0$ for $d = 0$, and $\boldsymbol{u}_0$ is the unique solution of

$$\begin{cases} u_{0,1} = \dfrac{a-q}{b}, \quad qu_{0,j-1} = -u_{0,j}\left(a - q - bu_{0,j}\right) \text{ for } j = 2, \cdots, n, \\ u_{0,j} > 0 \text{ for } j = 1, \cdots, n. \end{cases} \tag{2.8}$$

Moreover,

$$u_{0,1} < \ldots < u_{0,n}; \tag{2.9}$$

(ii) For fixed $q \in (a, na)$, $\boldsymbol{u}_d$ can be represented as follows:

$$\boldsymbol{u}_d = (d - d_q^*)(\alpha_d\boldsymbol{\eta} + \boldsymbol{\xi}_d) \text{ for } d > d_q^*. \tag{2.10}$$

Here, $(\alpha_d, \boldsymbol{\xi}_d) \in \mathbb{R} \times X_1$ is continuously differentiable with respect to $d \in [d_q^*, \infty)$, and for $d = d_q^*$, $(\alpha_d, \boldsymbol{\xi}_d) = (\alpha^*, \boldsymbol{0})$ with

$$\alpha^* = \frac{\sum_{j,k=1}^{n} D_{jk}\eta_k\hat{\eta}_j}{b\sum_{j=1}^{n} \eta_j^2\hat{\eta}_j} > 0. \tag{2.11}$$

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Proof. (i) It follows from Proposition 2.4 that $\boldsymbol{u}_d$ is the unique positive equilibrium of (1.5), which is stable (non-degenerate). Therefore, by the implicit function theorem, we obtain that $\boldsymbol{u}_d$ is continuously differentiable for $d \in (0, \infty)$. Then we need to show that $\boldsymbol{u}_d$ is continuously differentiable for $d \in [0, d_1]$ with $0 < d_1 \ll 1$.

Define

$$\boldsymbol{H}(d, \boldsymbol{u}) = \begin{pmatrix} d \sum_{k=1}^{n} D_{1k} u_k - q u_1 + u_1 (a - b u_1) \\ d \sum_{k=1}^{n} D_{2k} u_k + q (u_1 - u_2) + u_2 (a - b u_2) \\ \vdots \\ d \sum_{k=1}^{n} D_{nk} u_k + q (u_{n-1} - u_n) + u_n (a - b u_n) \end{pmatrix}.$$

Clearly, $\boldsymbol{H}(0, \boldsymbol{u}_0) = \boldsymbol{0}$, where $\boldsymbol{u}_0$ is defined by (2.8). Let $D_{\boldsymbol{u}}\boldsymbol{H}(0, \boldsymbol{u}_0)$ be the Jacobian matrix of $\boldsymbol{H}(d, \boldsymbol{u})$ with respect to $\boldsymbol{u}$ at $(0, \boldsymbol{u}_0)$. A direct computation implies that $D_{\boldsymbol{u}}\boldsymbol{H}(0, \boldsymbol{u}_0) = (h_{j,k})$ with

$$h_{j,k} = \begin{cases} a - q - 2b u_{0,j} & j = k = 1, \cdots, n, \\ q, & j = k + 1, \\ 0, & \text{otherwise}. \end{cases}$$

By (2.8), we have $\dfrac{a-q}{b} = u_{0,1} < \ldots < u_{0,n}$, which implies that $D_{\boldsymbol{u}}\boldsymbol{H}(0, \boldsymbol{u}_0)$ is invertible. Then we see from the implicit function theorem that there exist $d_1 > 0$, and a continuously differentiable mapping

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

such that $\boldsymbol{H}(d, \boldsymbol{u}(d)) = 0$, $\boldsymbol{u}(d) \gg \boldsymbol{0}$, and $\boldsymbol{u}(0) = \boldsymbol{u}_0$. Therefore, $\boldsymbol{u}(d)$ is the positive equilibrium of model (1.5) for small d. This combined with Proposition 2.4 implies that $\boldsymbol{u}(d) = \boldsymbol{u}_d$. Consequently, $\boldsymbol{u}_d$ is continuously differentiable for $d \in [0, \infty)$.

(ii) Using similar arguments as in (i), we see that $\boldsymbol{u}_d$ is continuously differentiable for $d \in (d_q^*, \infty)$. By the first decomposition in (2.6), we see that $\boldsymbol{u}_d$ can be represented as in (2.10), where α_d and $\boldsymbol{\xi}_d$ are also continuously differentiable for $d \in (d_q^*, \infty)$. Then we need to show that α_d and $\boldsymbol{\xi}_d$ are also continuously differentiable for $d \in [d_q^*, \tilde{d}_1)$ with $0 < \tilde{d}_1 - d_q^* \ll 1$.

We first show that $\alpha^* > 0$. A direct computation yields

$$\sum_{j,k=1}^{n} D_{jk} \eta_k \hat{\eta}_j = \sum_{j=1}^{n-1} \left(\eta_{j+1} - \eta_j\right) \left(\hat{\eta}_j - \hat{\eta}_{j+1}\right). \tag{2.12}$$

Noticing that $\boldsymbol{\eta}$ (respectively, $\hat{\boldsymbol{\eta}}$) is an eigenvector of $\mathcal{L}$ (respectively, $\mathcal{L}^T$) corresponding to eigenvalue 0, we have

$$(d_q^* + q)(\eta_{n-1} - \eta_n) = -a\eta_n,$$
$$(d_q^* + q)(\eta_{j-1} - \eta_j) = -a\eta_j + d_q^*(\eta_j - \eta_{j+1}), \ \ j = 2, \cdots, n-1,$$

and

$$(d_q^* + q)(\hat{\eta}_2 - \hat{\eta}_1) = -a\hat{\eta}_1,$$
$$(d_q^* + q)(\hat{\eta}_{j+1} - \hat{\eta}_j) = -a\eta_j + d_q^*(\hat{\eta}_j - \hat{\eta}_{j-1}), \ \ j = 2, \cdots, n-1,$$

which implies that $\eta_1 < \eta_2 < \ldots < \eta_n$ and $\hat{\eta}_1 > \hat{\eta}_2 > \ldots > \hat{\eta}_n$. This combined with (2.11) and (2.12) yields $\alpha^* > 0$.

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By the definition of $\mathcal{L}$, we rewrite (2.2) as follows:

$$\sum_{k=1}^{n} \mathcal{L}_{jk} u_k + (d - d_q^*) \sum_{j=1}^{n} D_{jk} u_k - b u_j^2 = 0. \tag{2.13}$$

From the first decomposition in (2.6), we see that $\boldsymbol{u}$ in (2.13) can be represented as follows:

$$\boldsymbol{u} = (d - d_q^*)(\alpha \boldsymbol{\eta} + \boldsymbol{\xi}) \text{ for } d > d_q^*. \tag{2.14}$$

Plugging (2.14) into (2.13), we have

$$\sum_{k=1}^{n} \mathcal{L}_{jk} \xi_k + (d - d_q^*) \left[\sum_{j=1}^{n} D_{jk}(\alpha \eta_k + \xi_k) - b(\alpha \eta_j + \xi_j)^2 \right] = 0, \quad j = 1, \cdots, n. \tag{2.15}$$

Denoting the left side of (2.15) by y_j, we see from the second decomposition in (2.6) that

$$\boldsymbol{y} = (y_1, \cdots, y_n)^T = c\mathbf{1} + \boldsymbol{z} \text{ with } c = \sum_{j=1}^{n} \hat{\eta}_j y_j \text{ and } \boldsymbol{z} \in X_1.$$

Therefore, $\boldsymbol{y} = \mathbf{0}$ if and only if $c = 0$ and $\boldsymbol{z} = \mathbf{0}$. Since $\mathcal{L}\boldsymbol{\xi} \in X_1$, it follows that

$$c = (d - d_q^*) G_2 \text{ and } \boldsymbol{z} = \left(G_{1,1}, \cdots, G_{1,n} \right)^T,$$

where

$$G_{1,j}(d, \alpha, \boldsymbol{\xi}) = \sum_{k=1}^{n} \mathcal{L}_{jk} \xi_k + (d - d_q^*) \left[\sum_{j=1}^{n} D_{jk}(\alpha \eta_k + \xi_k) - b(\alpha \eta_j + \xi_j)^2 \right]$$
$$- (d - d_q^*) G_2(d, \alpha, \boldsymbol{\xi}), \quad j = 1, \cdots, n,$$
$$G_2(d, \alpha, \boldsymbol{\xi}) = \sum_{j=1}^{n} \hat{\eta}_j \left[\sum_{k=1}^{n} D_{jk}(\alpha \eta_k + \xi_k) - b(\alpha \eta_j + \xi_j)^2 \right].$$

Define $\boldsymbol{G}(d, \alpha, \boldsymbol{\xi}) : \mathbb{R}^2 \times X_1 \to X_1 \times \mathbb{R}$ by $\boldsymbol{G} := (G_{1,1}, \cdots, G_{1,n}, G_2)^T$. It follows that, for $d > d_q^*$, $\boldsymbol{u}$ (represented in (2.14)) is a solution of (2.13) if and only if $(\alpha, \boldsymbol{\xi}) \in \mathbb{R} \times X_1$ is a solution of $\boldsymbol{G}(d, \alpha, \boldsymbol{\xi}) = \mathbf{0}$.

Now we consider the equivalent problem $\boldsymbol{G}(d, \alpha, \boldsymbol{\xi}) = \mathbf{0}$. Clearly, $\boldsymbol{G}(d_q^*, \alpha^*, \mathbf{0}) = \mathbf{0}$. Let $\boldsymbol{T}\left(\check{\alpha}, \check{\boldsymbol{\xi}}\right) = (T_{1,1}, \cdots, T_{1,n}, T_2)^T : \mathbb{R} \times X_1 \mapsto X_1 \times \mathbb{R}$ be the Fréchet derivative of $\boldsymbol{G}$ with respect to $(\alpha, \boldsymbol{\xi})$ at $(d_q^*, \alpha^*, \mathbf{0})$. Then we compute that

$$T_{1,j}\left(\check{\alpha}, \check{\boldsymbol{\xi}}\right) = \sum_{k=1}^{n} \mathcal{L}_{jk} \check{\xi}_k, \; j = 1, \cdots, n,$$

$$T_2\left(\check{\alpha}, \check{\boldsymbol{\xi}}\right) = \sum_{j=1}^{n} \hat{\eta}_j \left(\sum_{k=1}^{n} D_{jk} \eta_k - 2b\alpha^* \eta_j^2 \right) \check{\alpha} + \sum_{j=1}^{n} \hat{\eta}_j \left(\sum_{k=1}^{n} D_{jk} \check{\xi}_k - 2b\alpha^* \eta_j \check{\xi}_j \right).$$

By (2.11), we see that $\boldsymbol{T}$ is a bijection from $\mathbb{R} \times X_1$ to $X_1 \times \mathbb{R}$. Then it follows from the implicit function theorem that there exists $\tilde{d}_1 > d_q^*$ and a continuously differentiable mapping $d \in \left[d_q^*, \tilde{d}_1\right] \mapsto \left(\tilde{\alpha}_d, \tilde{\boldsymbol{\xi}}_d\right) \in \mathbb{R} \times X_1$ such that $\boldsymbol{G}(d, \tilde{\alpha}_d, \tilde{\boldsymbol{\xi}}_d) = \mathbf{0}$, and $\tilde{\alpha}_d = \alpha^*$ and $\tilde{\boldsymbol{\xi}}_d = \mathbf{0}$ for $d = d_q^*$. It follows from Proposition 2.4 and Eq. (2.6) that the unique positive equilibrium $\boldsymbol{u}_d$ can be represented as (2.10) for $d > d_q^*$. Then we obtain that $\alpha_d = \tilde{\alpha}_d$, $\boldsymbol{\xi}_d = \tilde{\boldsymbol{\xi}}_d$ for $d \in \left(d_q^*, \tilde{d}_1\right]$. Therefore, α_d and $\boldsymbol{\xi}_d$ are continuously differentiable for $d \in \left[d_q^*, \infty\right)$ if we define $(\alpha_d, \boldsymbol{\xi}_d) = (\alpha^*, \mathbf{0})$ for $d = d_q^*$. □

Now, we consider the case $d \gg 1$. Clearly, $\boldsymbol{u}_d$ satisfies

$$\sum_{k=1}^{n} D_{jk}u_k + \lambda \left[q \sum_{k=1}^{n} Q_{jk}u_k + u_j \left(a - bu_j\right) \right] = 0, \ j = 1, \cdots, n \tag{2.16}$$

with $d = 1/\lambda$. To avoid confusion, we denote $\boldsymbol{u}_d$ by $\boldsymbol{u}^\lambda$ for the case $d \gg 1$. Then the properties of $\boldsymbol{u}_d$ for $d \gg 1$ is equivalent to $\boldsymbol{u}^\lambda$ for $0 < \lambda \ll 1$. Clearly, $s(D) = 0$ is the principal eigenvalue of D, and a corresponding eigenvector is

$$\boldsymbol{\varsigma} = (\varsigma_1, \cdots, \varsigma_n)^T \ \text{ with } \ \varsigma_j = \frac{1}{n} \ \text{ for all } j = 1, \cdots, n. \tag{2.17}$$

Define

$$\widetilde{X}_1 = \left\{ (x_1, \cdots, x_n)^T \in \mathbb{R}^n : \sum_{j=1}^{n} x_j = 0 \right\}, \tag{2.18}$$

and $\mathbb{R}^n$ also has the following decomposition:

$$\mathbb{R}^n = \text{span}\{\boldsymbol{\varsigma}\} \oplus \widetilde{X}_1. \tag{2.19}$$

Proposition 2.6. *Suppose that $q \in (0, na)$, let $\boldsymbol{u}^\lambda$ be the unique positive solution of (2.16), and define $\boldsymbol{u}^0 = (u_1^0, \cdots, u_1^0)^T$, where*

$$u_j^0 = \frac{na - q}{nb} \ \textit{for all } j = 1, \cdots, n.$$

Then the following statements hold:

(i) $\boldsymbol{u}^\lambda = \left(u_1^\lambda, u_2^\lambda, \cdots, u_n^\lambda\right)$ *is continuously differentiable for $\lambda \in [0, \lambda_q^*)$;*

(ii)

$$\sum_{j=1}^{n} \left(u_j^\lambda\right)' \big|_{\lambda=0} = -\frac{q^2(n+1)(n-1)}{6b} < 0, \tag{2.20}$$

and the total population size $\sum_{j=1}^n u_j^\lambda$ is strictly decreasing in $\lambda \in (0, \epsilon)$ with $\epsilon \ll 1$.

Here, $'$ is the derivative with respect to λ and

$$\lambda_q^* = \begin{cases} 1/d_q^*, & \textit{if } q \in (a, na) \\ \infty, & \textit{if } q \in (0, a] \end{cases}$$

with d_q^* defined in Proposition 2.5.

Proof. (i) By Proposition 2.5, we see that $\boldsymbol{u}^\lambda$ is continuously differentiable for $\lambda \in (0, \lambda_q^*)$. Then we need to show that $\boldsymbol{u}^\lambda$ is continuously differentiable for $\lambda \in [0, \tilde{\lambda}_1)$ with $0 < \tilde{\lambda}_1 \ll 1$. From the decomposition in (2.19), we see that $\boldsymbol{u} = (u_1, \cdots, u_n)^T$ in (2.16) can be represented as follows:

$$\boldsymbol{u} = r\boldsymbol{\varsigma} + \boldsymbol{v} \ \text{ with } \ r = \sum_{j=1}^{n} u_j \in \mathbb{R} \ \text{ and } \ \boldsymbol{v} \in \widetilde{X}_1. \tag{2.21}$$

Plugging (2.21) into (2.16), we have

$$\sum_{k=1}^{n} D_{jk}v_k + \lambda \left[q \sum_{k=1}^{n} Q_{jk}\left(r\varsigma_k + v_k\right) + \left(r\varsigma_j + v_j\right)\left(a - b\left(r\varsigma_j + v_j\right)\right) \right] = 0 \tag{2.22}$$

for $j = 1, \cdots, n$. Denoting the left side of (2.22) by $\widetilde{y}_j$, we see from (2.19) that

$$\widetilde{\boldsymbol{y}} = (\widetilde{y}_1, \cdots, \widetilde{y}_n)^T = \widetilde{c}\boldsymbol{\varsigma} + \widetilde{z} \ \text{ with } \ \widetilde{c} = \sum_{j=1}^{n} y_j \ \text{ and } \ \widetilde{z} \in \widetilde{X}_1.$$

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Therefore, $\widetilde{\boldsymbol{y}}=\mathbf{0}$ if and only if $\widetilde{c}=0$ and $\widetilde{\boldsymbol{z}}=\mathbf{0}$. This combined with (2.22) implies that

$$\widetilde{c}=\lambda\widetilde{G}_2 \text{ and } \widetilde{\boldsymbol{z}}=\left(\widetilde{G}_{1,1},\ldots,\widetilde{G}_{1,n}\right)^T,$$

where

$$\begin{aligned}\widetilde{G}_{1,j}(\lambda,r,\boldsymbol{v})&=\sum_{k=1}^{n}D_{jk}v_k+\lambda\left[q\sum_{k=1}^{n}Q_{jk}\left(r\varsigma_k+v_k\right)+a\left(r\varsigma_j+v_j\right)-b\left(r\varsigma_j+v_j\right)^2\right]\\&-\frac{\lambda}{n}\widetilde{G}_2(\lambda,r,\boldsymbol{v}),\quad j=1,\cdots,n,\\\widetilde{G}_2(\lambda,r,\boldsymbol{v})&=\sum_{j=1}^{n}\left[q\sum_{k=1}^{n}Q_{jk}\left(r\varsigma_k+v_k\right)+a\left(r\varsigma_j+v_j\right)-b\left(r\varsigma_j+v_j\right)^2\right].\end{aligned}$$

Define $\widetilde{\boldsymbol{G}}(\lambda,r,\boldsymbol{v}):\mathbb{R}^2\times\widetilde{X}_1\to\widetilde{X}_1\times\mathbb{R}$ by $\widetilde{\boldsymbol{G}}:=(\widetilde{G}_{1,1},\cdots,\widetilde{G}_{1,n},G_2)^T$. It follows that, for $\lambda\in[0,\lambda_q^*)$, $\boldsymbol{u}$ (represented in (2.21)) is a solution of (2.16) if and only if $(r,\boldsymbol{v})\in\mathbb{R}\times\widetilde{X}_1$ is a solution of $\widetilde{\boldsymbol{G}}(\lambda,r,\boldsymbol{v})=\mathbf{0}$. Then using similar arguments as in the proof of Proposition 2.5, we can show that there exists $\tilde{\lambda}_1>0$ and a continuously differentiable mapping $\lambda\in\left[0,\tilde{\lambda}_1\right]\mapsto\left(r^\lambda,\boldsymbol{v}^\lambda\right)\in\mathbb{R}\times\widetilde{X}_1$ such that

$$\left(r^0,\boldsymbol{v}^0\right)=\left(\frac{na-q}{b},\mathbf{0}\right) \text{ and } \widetilde{\boldsymbol{G}}(\lambda,r^\lambda,\boldsymbol{v}^\lambda)=\mathbf{0} \text{ for } \lambda\in[0,\tilde{\lambda}_1]. \tag{2.23}$$

This combined with (2.21) implies that, for $\lambda\in(0,\tilde{\lambda}_1)$,

$$\boldsymbol{u}^\lambda=r^\lambda\boldsymbol{\varsigma}+\boldsymbol{v}^\lambda \text{ with } r^\lambda=\sum_{j=1}^{n}u_j^\lambda \text{ and } \boldsymbol{v}^\lambda\in\widetilde{X}_1. \tag{2.24}$$

Therefore, $\boldsymbol{u}^\lambda$ is continuously differentiable for $\lambda\in[0,\tilde{\lambda}_1]$ if we defined $\boldsymbol{u}^0=r^0\boldsymbol{\varsigma}$.

(ii) Now we compute $\sum_{j=1}^{n}\left(u_j^\lambda\right)'\big|_{\lambda=0}$. Differentiating (2.23) with respect to λ at $\lambda=0$ and noticing that $\boldsymbol{v}^0=\mathbf{0}$, we have

$$\begin{aligned}&\sum_{k=1}^{n}D_{jk}(v_k^\lambda)'\big|_{\lambda=0}+q\sum_{k=1}^{n}Q_{jk}r^0\varsigma_k+ar^0\varsigma_j-b\left(r^0\varsigma_j\right)^2-\frac{1}{n}\widetilde{G}_2(0,r^0,\boldsymbol{v}^0)=0,\\&q\sum_{j=1}^{n}\sum_{k=1}^{n}Q_{jk}\left[(r^\lambda)'\varsigma_k+(v_k^\lambda)'\right]\big|_{\lambda=0}+\sum_{j=1}^{n}\left[a-2b\left(r^0\varsigma_j+v_j^0\right)\right]\left[(r^\lambda)'\varsigma_j+(v_j^\lambda)'\right]\big|_{\lambda=0}=0.\end{aligned}$$

Noting that $r^0=\frac{na-q}{b}$, $(\boldsymbol{v}^\lambda)'\in\widetilde{X}_1$ and $\widetilde{G}_2(0,r^0,\boldsymbol{v}^0)=0$, we have

$$\begin{cases}\displaystyle\sum_{k=1}^{n}D_{1k}(v_k^\lambda)'\big|_{\lambda=0}-\frac{na-q}{nb}\cdot q+\frac{na-q}{nb}\cdot\frac{q}{n}=0,\\\displaystyle\sum_{k=1}^{n}D_{jk}(v_k^\lambda)'\big|_{\lambda=0}+\frac{na-q}{nb}\cdot\frac{q}{n}=0,\ j=2,\cdots,n,\\\displaystyle\left(-a+\frac{q}{n}\right)(r^\lambda)'\big|_{\lambda=0}-q(v_n^\lambda)'\big|_{\lambda=0}=0.\end{cases}$$

By a tedious computation (see Proposition 5.4 in the appendix), we obtain that

$$(v_n^\lambda)'\big|_{\lambda=0}=\frac{q(na-q)(n+1)(n-1)}{6nb},\quad (r^\lambda)'\big|_{\lambda=0}=-\frac{q^2(n+1)(n-1)}{6b}.$$

This, combined with (2.24), implies that

$$\sum_{j=1}^{n}(u_j^\lambda)'\big|_{\lambda=0}=(r^\lambda)'\big|_{\lambda=0}=-\frac{q^2(n+1)(n-1)}{6b}.$$

This completes the proof. □

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Remark 2.7. *Note that $\lambda = 1/d$. Then the total population size $\sum_{j=1}^{n} u_{d,j}$ for (2.2) is strictly increasing in $d \in [\delta, \infty)$ with $\delta \gg 1$.*

3. Eigenvalue problem

Linearising model (1.5) at $\boldsymbol{u}_d$, we have

$$\frac{d\boldsymbol{v}}{dt} = dD\boldsymbol{v} + qQ\boldsymbol{v} + \operatorname{diag}\left(a - bu_{d,j}\right)\boldsymbol{v} - \operatorname{diag}\left(bu_{d,j}\right)\boldsymbol{v}(t-\tau). \tag{3.1}$$

It follows from [21, Chapter 7] that the infinitesimal generator $A_\tau(d)$ of the solution semigroup of (3.1) is defined by:

$$A_\tau(d)\boldsymbol{\Psi} = \dot{\boldsymbol{\Psi}} \tag{3.2}$$

with the domain

$$\begin{aligned}\mathscr{D}(A_\tau(d)) = \Big\{ & \boldsymbol{\Psi} \in C^1([-\tau, 0], \mathbb{C}^n) : \dot{\boldsymbol{\Psi}}(0) = dD\boldsymbol{\Psi}(0) + qQ\boldsymbol{\Psi}(0) \\ & + \operatorname{diag}\left(a - bu_{d,j}\right)\boldsymbol{\Psi}(0) - \operatorname{diag}\left(bu_{d,j}\right)\boldsymbol{\Psi}(-\tau)\Big\}.\end{aligned} \tag{3.3}$$

Then $\mu \in \sigma_p(A_\tau(d))$ (resp., μ is an eigenvalue of $A_\tau(d)$) if and only if there exists $\boldsymbol{\psi} = (\psi_1, \cdots, \psi_n)^T(\neq \mathbf{0}) \in \mathbb{C}^n$ such that $\triangle(d, \mu, \tau)\boldsymbol{\psi} = 0$, where matrix

$$\triangle(d, \mu, \tau) := dD + qQ + \operatorname{diag}\left(a - bu_{d,j}\right) - e^{-\mu\tau}\operatorname{diag}\left(bu_{d,j}\right) - \mu I. \tag{3.4}$$

To determine the distribution of the eigenvalues of $A_\tau(d)$, one need to consider whether

$$\sigma_p(A_\tau(d)) \cap \{x + \mathrm{i}y : x = 0\} \neq \emptyset.$$

By Proposition 2.4, we have

$$0 \notin \sigma_p(A_\tau(d)) \text{ for all } \tau \geq 0,$$

$$\sigma_p(A_\tau(d)) \subset \{x + \mathrm{i}y : x < 0\} \text{ for } \tau = 0.$$

In fact, if $0 \in \sigma_p(A_{\tau_0}(d))$ for some $\tau_0 \geq 0$, then 0 is an eigenvalue of matrix

$$dD + qQ + \operatorname{diag}\left(a - 2bu_{d,j}\right),$$

which contradicts Proposition 2.4. By (3.4), we see that $\mathrm{i}\nu(\nu > 0) \in \sigma_p(A_\tau(d))$ for some $\tau > 0$ if and only if

$$\begin{cases} \mathcal{M}(d, \nu, \theta)\boldsymbol{\psi} = \mathbf{0} \\ \nu > 0, \quad \theta \in [0, 2\pi), \quad \boldsymbol{\psi}(\neq \mathbf{0}) \in \mathbb{C}^n \end{cases} \tag{3.5}$$

admits a solution $(\nu, \theta, \boldsymbol{\psi})$, where matrix

$$\mathcal{M}(d, \nu, \theta) = dD + qQ + \operatorname{diag}\left(a - bu_{d,j}\right) - e^{-\mathrm{i}\theta}\operatorname{diag}\left(bu_{d,j}\right) - \mathrm{i}\nu I. \tag{3.6}$$

It follows from Proposition 2.5 that the properties of $\boldsymbol{u}_d$ are different for the following three cases (see Figure 3):

Case I: $q \in (a, na)$ and $0 < d - d_q^* \ll 1$;

Case II: $q \in (0, a)$ and $0 < d \ll 1$;

Case III: $q \in (0, na)$ and $d \gg 1$.

Therefore, the following analysis on eigenvalue problem (3.5) is divided into three cases.

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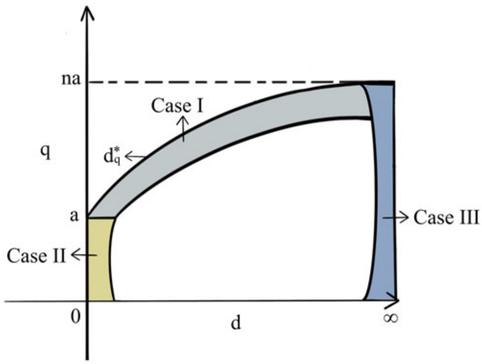

Figure 3. *Diagram for parameter ranges of Cases I–III.*

3.1. A priori estimates

In this subsection, we give *a priori* estimates for solutions of (3.5).

Lemma 3.1. *Let $(\nu^d, \theta^d, \boldsymbol{\psi}^d)$ be a solution of (3.5). Then the following statements hold:*

(i) *For fixed $q \in (a, na)$, $\left|\frac{\nu^d}{d - d_q^*}\right|$ is bounded for $d \in (d_q^*, \tilde{d}_1]$ with $0 < \tilde{d}_1 - d_q^* \ll 1$;*

(ii) *For fixed $q \in (0, a)$, $|\nu^d|$ is bounded for $d \in (0, \tilde{d}_2)$ with $0 < \tilde{d}_2 \ll 1$;*

(iii) *For fixed $q \in (0, na)$, $|\nu^d|$ is bounded for $d \in (\tilde{d}_3, \infty)$ with $\tilde{d}_3 \gg 1$.*

Proof. We only prove (i), and (ii)–(iii) can be proved similarly. Define matrix $\varrho := (\varrho_{jk})$ with

$$\varrho_{jk} = \begin{cases} \left(\dfrac{d}{d+q}\right)^{j-1}, & j = k = 1, \cdots, n, \\ 0, & \text{otherwise}. \end{cases}$$

Substituting $(\nu, \theta, \boldsymbol{\psi}) = (\nu^d, \theta^d, \boldsymbol{\psi}^d)$ into (3.5), and multiplying both sides of (3.5) by $\left(\overline{\psi_1^d}, \overline{\psi_2^d}, \ldots, \overline{\psi_n^d}\right) \varrho$ to the left, we have

$$\mathcal{S} + \sum_{k=1}^{n} \left[(a - bu_{d,k}) - e^{-\mathrm{i}\theta^d} bu_{d,k} - \mathrm{i}\nu^d \right] \left(\frac{d}{d+q}\right)^{k-1} |\psi_k^d|^2 = 0, \tag{3.7}$$

where

$$\mathcal{S} := \left(\overline{\psi_1^d}, \overline{\psi_2^d}, \cdots, \overline{\psi_n^d}\right) \varrho (dD + qQ) \boldsymbol{\psi}^d.$$

Since $\varrho(dD + qQ)$ is symmetric, we see that $\mathcal{S} \in \mathbb{R}$. This combined with (3.7) yields

$$\nu^d \sum_{k=1}^{n} \left(\frac{d}{d+q}\right)^{k-1} |\psi_k^d|^2 = \left(\sin \theta^d\right) \sum_{k=1}^{n} bu_{d,k} \left(\frac{d}{d+q}\right)^{k-1} |\psi_k^d|^2. \tag{3.8}$$

By Proposition 2.5 (ii), we see that there exists $M > 0$ such that $\dfrac{\|\boldsymbol{u}_d\|_\infty}{d - d_q^*} < M$ for $d \in (d_q^*, \tilde{d}_1]$ with $0 < \tilde{d}_1 - d_q^* \ll 1$. This combined with (3.8) implies that

$$\left|\frac{\nu^d}{d - d_q^*}\right| \le bM \text{ for } d \in (d_q^*, \tilde{d}_1].$$

This completes the proof. □

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3.2. Case I

For this case, the positive equilibrium $\boldsymbol{u}_d$ can be represented as (2.10). Plugging (2.10) into (3.5), we rewrite the eigenvalue problem (3.5) as follows:

$$\begin{cases} \sum_{k=1}^n \mathcal{L}_{jk}\psi_k + (d-d_q^*)f_j(\boldsymbol{\psi},\theta,d) - \mathrm{i}\nu\psi_j = 0, \quad j=1,\cdots,n, \\ \nu>0, \quad \theta\in[0,2\pi), \quad \boldsymbol{\psi}(\neq\mathbf{0})\in\mathbb{C}^n, \end{cases} \tag{3.9}$$

where $\mathcal{L}$ is defined in (2.3), and

$$f_j(\boldsymbol{\psi},\theta,d) = \sum_{k=1}^n D_{jk}\psi_k - b(\alpha_d\eta_j+\xi_{d,j})\psi_j - e^{-\mathrm{i}\theta}b\left(\alpha_d\eta_j+\xi_{d,j}\right)\psi_j \tag{3.10}$$

with α_d and $\boldsymbol{\xi}_d$ defined in (2.10). By (2.6), we see that, ignoring a scalar factor, $\boldsymbol{\psi}(\neq\mathbf{0})\in\mathbb{C}^n$ in (3.9) can be represented as follows:

$$\begin{cases} \boldsymbol{\psi} = \beta\boldsymbol{\eta} + \boldsymbol{z} \text{ with } \boldsymbol{z}\in(X_1)_{\mathbb{C}}, \quad \beta\ge 0, \\ \|\boldsymbol{\psi}\|_2^2 = \beta^2\|\boldsymbol{\eta}\|_2^2 + \beta\sum_{j=1}^n \eta_i(z_i+\overline{z_i}) + \|\boldsymbol{z}\|_2^2 = \|\boldsymbol{\eta}\|_2^2, \end{cases} \tag{3.11}$$

where $\boldsymbol{\eta}$ is defined in (2.4). Then we obtain an equivalent problem of (3.9) in the following.

Lemma 3.2. *Assume that $d>d_q^*$ and $q\in(a,na)$. Then $(\boldsymbol{\psi},\nu,\theta)$ solves (3.9), where $\boldsymbol{\psi}$ is defined in (3.11) and $\nu=(d-d_q^*)\varpi$, if and only if $(\beta,\varpi,\theta,\boldsymbol{z})$ solves*

$$\begin{cases} \boldsymbol{F}(\beta,\varpi,\theta,\boldsymbol{z},d)=0, \\ \beta\ge 0, \ \varpi>0, \ \theta\in[0,2\pi), \ \boldsymbol{z}\in(X_1)_{\mathbb{C}}. \end{cases} \tag{3.12}$$

Here

$$\boldsymbol{F}(\beta,\varpi,\theta,\boldsymbol{z},d) = (F_{1,1},\cdots,F_{1,n},F_2,F_3)^T$$

is a continuously differentiable mapping from $\mathbb{R}^3\times(X_1)_{\mathbb{C}}\times[d_q^*,\infty]$ to $(X_1)_{\mathbb{C}}\times\mathbb{C}\times\mathbb{R}$, and

$$\begin{cases} F_{1,j} := \sum_{k=1}^n \mathcal{L}_{jk}z_k \\ +(d-d_q^*)\left[f_j(\beta\boldsymbol{\eta}+\boldsymbol{z},\theta,d) - i\varpi\left(\beta\eta_j+z_j\right) - F_2(\beta,\varpi,\theta,\boldsymbol{z},d)\right], \ j=1,\cdots,n, \\ F_2 := \sum_{j=1}^n \hat{\eta}_j\left[f_j(\beta\boldsymbol{\eta}+\boldsymbol{z},\theta,d) - i\varpi\left(\beta\eta_j+z_j\right)\right], \\ F_3 := (\beta^2-1)\|\boldsymbol{\eta}\|_2^2 + \beta\sum_{i=j}^n \eta_j(z_j+\overline{z}_j) + \|\boldsymbol{z}\|_2^2, \end{cases} \tag{3.13}$$

where f_j $(j=1,\cdots,n)$ are defined in (3.10).

Proof. Clearly, $F_3=0$ is equivalent to second equation of (3.11). Substituting (3.11) and $\nu=(d-d_q^*)\varpi$ into (3.9), we see that

$$\sum_{k=1}^n \mathcal{L}_{jk}z_k + (d-d_q^*)\left[f_j(\beta\boldsymbol{\eta}+\boldsymbol{z},\theta,d) - \mathrm{i}\varpi\left(\beta\eta_j+z_j\right)\right] = 0, \quad j=1,\cdots,n. \tag{3.14}$$

Denote the left side of (3.14) by y_j and let $\boldsymbol{y}=(y_1,\cdots,y_n)^T$. Using similar arguments as in the proof of Proposition 2.5 (ii), we see that $\boldsymbol{y}=\mathbf{0}$ if and only $F_2=0$ and $F_{1,j}=0$ for all $j=1,\cdots,n$. This completes the proof. □

We first show that the equivalent problem (3.12) has a unique solution for $d=d_q^*$.

Lemma 3.3. *The following equation*

$$\begin{cases} \boldsymbol{F}(\beta,\varpi,\theta,\boldsymbol{z},d_q^*)=\boldsymbol{0} \\ \beta\ge 0, \ \varpi\ge 0, \ \theta\in[0,2\pi], \ \boldsymbol{z}\in(X_1)_{\mathbb{C}} \end{cases}$$

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has a unique solution $(\beta^*, \varpi^*, \theta^*, z^*)$. *Here*

$$z^* = \mathbf{0},\ \ \beta^* = 1,\ \ \varpi^* = \frac{\sum_{j,k=1}^n D_{jk}\eta_k\hat{\eta}_j}{\sum_{j=1}^n \eta_j\hat{\eta}_j} > 0,\ \ \theta^* = \frac{\pi}{2}.$$

Proof. Clearly,

$$F_{1,j}(\beta, \varpi, \theta, z, d_q^*) = 0 \text{ for all } j = 1, \cdots, n$$

if and only if $z = z^* = \mathbf{0}$. Substituting $z = \mathbf{0}$ into $F_3(\beta, \varpi, \theta, z, d_q^*) = 0$, we have $\beta = \beta^* = 1$. Then plugging $z = \mathbf{0}$ and $\beta = 1$ into $F_2(\beta, \varpi, \theta, z, d_q^*) = 0$, we have

$$\sum_{j=1}^n \hat{\eta}_j \left[f_j(\boldsymbol{\eta}, \theta, d_q^*) - \mathrm{i}\varpi\eta_j\right] = 0, \tag{3.15}$$

where f_j $(j = 1, \cdots, n)$ are defined in (3.10). By Proposition 2.5 (ii), we have

$$f_j(\boldsymbol{\eta}, \theta, d_q^*) = \sum_{k=1}^n D_{jk}\eta_k - b\alpha^*\eta_j^2 - e^{-\mathrm{i}\theta} b\alpha^*\eta_j^2,$$

where α^* is defined in (2.11). Then we see from (3.15) that

$$\sum_{j,k=1}^n D_{jk}\eta_k\hat{\eta}_j - \sum_{j=1}^n b\alpha^*\hat{\eta}_j\eta_j^2 - e^{-\mathrm{i}\theta} b\alpha^* \sum_{j=1}^n \hat{\eta}_j\eta_j^2 - \mathrm{i}\varpi \sum_{j=1}^n \eta_j\hat{\eta}_j = 0.$$

This combined with (2.11) yields

$$\varpi = \varpi^* = \frac{\sum_{j,k=1}^n D_{jk}\eta_k\hat{\eta}_j}{\sum_{j=1}^n \eta_j\hat{\eta}_j} > 0,\ \ \theta = \theta^* = \frac{\pi}{2}.$$

This completes the proof. □

Then we solve the equivalent problem (3.12) for $0 < d - d_q^* \ll 1$.

Lemma 3.4. *Assume that* $d > d_q^*$ *and* $q \in (a, na)$. *Then there exists* $\tilde{d}_1$ *with* $0 < \tilde{d}_1 - d_q^* \ll 1$ *and a continuously differentiable mapping* $d \mapsto (\beta_d, \varpi_d, \theta_d, z_d)$ *from* $[d_q^*, \tilde{d}_1]$ *to* $\mathbb{R}^3 \times (X_1)_{\mathbb{C}}$ *such that* $(\beta_d, \varpi_d, \theta_d, z_d)$ *is the unique solution of the following problem:*

$$\begin{cases} \boldsymbol{F}(\beta, \varpi, \theta, z, d) = \mathbf{0} \\ \beta \geq 0,\ \varpi > 0,\ \theta \in [0, 2\pi),\ z \in (X_1)_{\mathbb{C}} \end{cases} \tag{3.16}$$

for $d \in \left(d_q^*, \tilde{d}_1\right]$.

Proof. Let $\boldsymbol{P}\left(\check{\beta}, \check{\varpi}, \check{\theta}, \check{z}\right) = (P_{1,1}, \cdots, P_{1,n}, P_2, P_3)^T : \mathbb{R}^3 \times (X_1)_{\mathbb{C}} \mapsto (X_1)_{\mathbb{C}} \times \mathbb{C} \times \mathbb{R}$ be the Fréchet derivative of $\boldsymbol{F}$ with respect to $(\beta, \varpi, \theta, z)$ at $\left(\beta^*, \varpi^*, \theta^*, z^*, d_q^*\right)$. It follows from (3.12) and (3.13) that

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$$P_{1,j}\left(\check{\beta},\check{\varpi},\check{\theta},\check{z}\right)=\sum_{k=1}^{n}\mathcal{L}_{jk}\check{z}_k,\ \ j=1,\cdots,n,$$

$$P_2\left(\check{\beta},\check{\varpi},\check{\theta},\check{z}\right)=\sum_{j=1}^{n}\hat{\eta}_j\left(\sum_{k=1}^{n}D_{jk}\check{z}_k-b\alpha^*\eta_j\check{z}_j+\mathrm{i}b\alpha^*\eta_j\check{z}_j-\mathrm{i}\varpi^*\check{z}_j+b\alpha^*\eta_j^2\check{\theta}-\mathrm{i}\eta_j\check{\varpi}\right)$$

$$+\sum_{j=1}^{n}\hat{\eta}_j(\mathrm{i}b\alpha^*\eta_j^2\check{\beta}-\mathrm{i}\varpi^*\eta_j\check{\beta}),$$

$$P_3\left(\check{\beta},\check{\varpi},\check{\theta},\check{z}\right)=2\|\eta\|_2^2\check{\beta}+\sum_{j=1}^{n}\eta_j\left(\check{z}_j+\overline{\check{z}_j}\right),$$

where we have used (2.11) to obtain P_2. A direct computation implies that $\boldsymbol{P}$ is a bijection from $\mathbb{R}^3\times(X_1)_{\mathbb{C}}$ to $(X_1)_{\mathbb{C}}\times\mathbb{C}\times\mathbb{R}$. It follows from the implicit function theorem that there exists $\hat{d}>d_q^*$ and a continuously differentiable mapping $d\mapsto(\beta_d,\varpi_d,\theta_d,z_d)$ from $\left[d_q^*,\hat{d}\right]$ to $\mathbb{R}^3\times(X_1)_{\mathbb{C}}$ such that $(\beta_d,\varpi_d,\theta_d,z_d)$ solves (3.16).

Then we prove the uniqueness for $d\in[d_q^*,\tilde{d}_1]$ with $0<\tilde{d}_1-d_q^*\ll 1$. We only need to verify that if $\left(\beta^d,\varpi^d,\theta^d,z^d\right)$ satisfies (3.16), then $\lim_{d\to d_q^*}\left(\beta^d,\varpi^d,\theta^d,z^d\right)=(\beta^*,\varpi^*,\theta^*,z^*)$, where $(\beta^*,\varpi^*,\theta^*,z^*)$ is defined in Lemma 3.3. Since

$$F_3\left(\beta^d,\varpi^d,\theta^d,z^d,d\right)=0,$$

we have

$$\|\beta^d\boldsymbol{\eta}+z^d\|_2^2=\|\boldsymbol{\eta}\|_2^2. \tag{3.17}$$

Note from Lemma 3.1 (i) that ϖ^d is bounded for $d\in\left[d_q^*,\tilde{d}_1\right]$. This combined with (3.17) and the first equation of (3.13) implies that $\lim\limits_{d\to d_q^*}\mathcal{L}z=\boldsymbol{0}$, and consequently, $\lim\limits_{d\to d_q^*}z^d=z^*=\boldsymbol{0}$. By the third equation of (3.13), we obtain that $\lim\limits_{d\to d_q^*}\beta^d=\beta^*=1$. Then, it follows from the second equation of (3.13) that $\lim\limits_{d\to d_q^*}\theta^d=\theta^*$ and $\lim\limits_{d\to d_q^*}\varpi^d=\varpi^*$. This completes the proof. □

By Lemma 3.4, we obtain the following result.

Theorem 3.5. *Assume that $q\in(a,na)$. Then for $d\in\left(d_q^*,\tilde{d}_1\right]$ with $0<\tilde{d}_1-d_q^*\ll 1$, $(\nu,\tau,\boldsymbol{\psi})$ satisfies the following equation:*

$$\begin{cases}\Delta(d,\mathrm{i}\nu,\tau)\boldsymbol{\psi}=\boldsymbol{0}\\ \nu>0,\ \ \tau\geq 0,\ \ \boldsymbol{\psi}(\neq\boldsymbol{0})\in\mathbb{C}^n\end{cases} \tag{3.18}$$

if and only if

$$\nu=\nu_d=(d-d_q^*)\varpi_d,\ \ \boldsymbol{\psi}=c_1\boldsymbol{\psi}_d,\ \ \tau=\tau_{d,l}=\frac{\theta_d+2l\pi}{\nu_d},\ \ l=0,1,2,\cdots,$$

where $\boldsymbol{\psi}_d=\beta_d\boldsymbol{\eta}+z_d$, $c_1\in\mathbb{C}$ is a non-zero constant, and β_d, ϖ_d, θ_d and z_d are defined in Lemma 3.4.

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3.3. *Case II*

For this case, the positive equilibrium $\boldsymbol{u}_d$ is continuously differentiable for $d \in [0, \infty)$. We first solve the eigenvalue problem (3.5) for $d = 0$.

Lemma 3.6. *Let $\mathcal{M}(d, \nu, \theta)$ be defined in (3.6), and let*

$$Ker(\mathcal{M}(0, \nu, \theta)) := \{\boldsymbol{\psi} \in \mathbb{C}^n : \mathcal{M}(0, \nu, \theta)\boldsymbol{\psi} = \boldsymbol{0}\}.$$

Assume that $q \in (0, a)$. Then

$$\{(\nu, \theta) : \nu \geq 0,\ \theta \in [0, 2\pi],\ Ker(\mathcal{M}(0, \nu, \theta)) \neq \{\boldsymbol{0}\}\} = \left\{(\nu_p^0, \theta_p^0)\right\}_{p=1}^n, \tag{3.19}$$

where

$$\theta_p^0 = \arccos \frac{a - q - bu_{0,p}}{bu_{0,p}}, \quad \nu_p^0 = \sqrt{\left(bu_{0,p}\right)^2 - \left(a - q - bu_{0,p}\right)^2} \tag{3.20}$$

with

$$\frac{\pi}{2} = \theta_1^0 < \ldots < \theta_n^0 < \pi, \quad a - q = \nu_1^0 < \ldots < \nu_n^0. \tag{3.21}$$

Moreover, for each $p = 1, 2, \cdots, n$, $Ker(\mathcal{M}(0, \nu_p^0, \theta_p^0)) = \left\{c\boldsymbol{\psi}_p^0 : c \in \mathbb{C}\right\}$, where $\boldsymbol{\psi}_p^0 = \left(\psi_{p,1}^0, \cdots, \psi_{p,n}^0\right)^T$, and

$$\begin{aligned} &\psi_{p,j}^0 = 0 \text{ for } 1 \leq j \leq p-1, \quad \psi_{p,p}^0 = 1, \\ &\psi_{p,j}^0 = (-1)^{j-p} \prod_{k=p+1}^{j} \frac{q}{h_k(\theta_p^0, \nu_p^0)} \text{ for } p+1 \leq j \leq n \end{aligned} \tag{3.22}$$

with

$$h_k(\theta, \nu) = \left(a - q - bu_{0,k}\right) - bu_{0,k}e^{-i\theta} - i\nu, \quad k = 1, \cdots, n. \tag{3.23}$$

Proof. Clearly, $\det[M(d, \nu, \theta)] = \prod_{p=1}^n h_p(\theta, \nu)$. For each $p = 1, \cdots, n$, we compute that

$$\begin{cases} h_p(\theta, \nu) = 0 \\ \theta \in [0, 2\pi], \quad \nu \geq 0 \end{cases}$$

admits a unique solution (ν_p^0, θ_p^0), which yields (3.19) holds. By (2.8) and (2.9), we see that (3.21) holds, and consequently, $h_k(\theta_p^0, \nu_p^0) \neq 0$ for $k \neq p$, which implies that $\boldsymbol{\psi}_p^0$ is well defined for $p = 1, \cdots, n$. A direct computation implies that $\text{Ker}(\mathcal{M}(0, \nu_p^0, \theta_p^0)) = \left\{c\boldsymbol{\psi}_p^0 : c \in \mathbb{C}\right\}$ for $p = 1, \cdots, n$. This completes the proof. □

The following result explores further properties of (ν_p^0, θ_p^0) $(p = 1, \cdots, n)$.

Lemma 3.7. *Assume that $q \in (0, a)$, and let (ν_p^0, θ_p^0) $(p = 1, \cdots, n)$ be defined in (3.20). Then the following statements hold:*

(i) $\dfrac{\theta_1^0}{\nu_1^0} > \dfrac{\theta_2^0}{\nu_2^0} > \ldots > \dfrac{\theta_n^0}{\nu_n^0}$;

(ii) For all $p = 1, \cdots, n$, $\dfrac{\theta_p^0}{\nu_p^0}$ is strictly monotone increasing in $q \in (0, a)$ and satisfies $\lim_{q \to 0} \dfrac{\theta_p^0}{\nu_p^0} = \dfrac{\pi}{2a}$.

Proof. By (3.20), we have

$$\frac{\theta_p^0}{\nu_p^0} = \frac{\arccos \dfrac{a - q - bu_{0,p}}{bu_{0,p}}}{\sqrt{\left(bu_{0,p}\right)^2 - \left(a - q - bu_{0,p}\right)^2}}, \quad p = 1, \cdots, n, \tag{3.24}$$

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where $u_{0,p} \geq (a-q)/b$ is defined in (2.8) and depends on q for $p = 1, \cdots, n$. Then we denote $u_{0,p}$ by $u_{0,p}(q)$ throughout the proof. We define an auxiliary function

$$f_1(q,x) = \frac{\arccos \dfrac{a-q-bx}{bx}}{\sqrt{(bx)^2 - (a-q-bx)^2}} \quad \text{with } x \geq \frac{a-q}{b},$$

and consequently,

$$\frac{\theta_p^0}{\nu_p^0} = f_1\left(q, u_{0,p}(q)\right) \quad \text{for } p = 1, \cdots, n. \tag{3.25}$$

Let

$$A_1 = \arccos \frac{a-q-bx}{bx} \quad \text{and} \quad B_1 = \sqrt{(bx)^2 - (a-q-bx)^2}.$$

Noticing that $q \in (0,a)$, we compute that, for $x \geq \dfrac{a-q}{b}$,

$$\frac{\partial A_1}{\partial x} = \frac{a-q}{x\sqrt{(bx)^2 - (a-q-bx)^2}} > 0, \quad \frac{\partial B_1}{\partial x} = \frac{b\,(a-q)}{\sqrt{(bx)^2 - (a-q-bx)^2}} > 0,$$

$$\frac{\partial A_1}{\partial q} = \frac{1}{\sqrt{(bx)^2 - (a-q-bx)^2}} > 0, \quad \frac{\partial B_1}{\partial q} = \frac{a-q-bx}{\sqrt{(bx)^2 - (a-q-bx)^2}} \leq 0,$$

which yields

$$\frac{\partial f_1}{\partial q} = \frac{1}{B_1^2}\left(B_1 \frac{\partial A_1}{\partial q} - A_1 \frac{\partial B_1}{\partial q}\right) > 0 \text{ for } x \geq \frac{a-q}{b}. \tag{3.26}$$

By $x \geq (a-q)/b$ and $q \in (0,a)$ again, we have

$$0 < \frac{\sqrt{(bx)^2 - (a-q-bx)^2}}{bx} \leq 1 \quad \text{and} \quad \arccos \frac{a-q-bx}{bx} \geq \frac{\pi}{2},$$

which yields

$$\begin{aligned} \frac{\partial f_1}{\partial x} &= \frac{1}{B_1^2}\left(B_1 \frac{\partial A_1}{\partial x} - A_1 \frac{\partial B_1}{\partial x}\right) \\ &= \frac{b(a-q)}{B_1^3}\left[\frac{\sqrt{(bx)^2 - (a-q-bx)^2}}{bx} - \arccos \frac{a-q-bx}{bx}\right] < 0 \end{aligned} \tag{3.27}$$

for $x \geq (a-q)/b$.

Now we prove (i). By Proposition 2.5, we have $u_{0,1} < \cdots < u_{0,n}$. This combined with (3.25) and (3.27) implies that (i) holds. Then we consider (ii). We first show that $u_{0,p}'(q) < 0$ for $q > 0$ and $p = 1, \cdots, n$. Here, $'$ is the derivative with respect to q. Differentiating (2.8) with respect to q yields

$$\begin{cases} u'_{0,1} = -\dfrac{1}{b}, \\ qu'_{0,j-1} + \left(u_{0,j-1} - u_{0,j}\right) = -u'_{0,j}\left(a - q - 2bu_{0,j}\right) \text{ for } j = 2, \cdots, n. \end{cases}$$

This combined with the fact that

$$u_{0,n} > \cdots > u_{0,1} \geq \frac{a-q}{b},$$

yields $u_{0,p}'(q) < 0$ for $q > 0$ and $p = 1, \cdots, n$. Then, by (3.25)–(3.27), we obtain that, for each $p = 1, \cdots, n$,

$$\left(\frac{\theta_p^0}{\nu_p^0}\right)' = \left[f_1(q, u_{0,p}(q))\right]' = \left.\frac{\partial f_1(q,x)}{\partial q}\right|_{x=u_{0,p}(q)} + \left.\frac{\partial f_1(q,x)}{\partial x}\right|_{x=u_{0,p}(q)} \cdot \frac{\partial u_{0,p}(q)}{\partial q} > 0,$$

where $'$ is the derivative with respect to q. Note that $\lim_{q\to 0} u_{0,p}(q) = a/b$ for $p = 1, \cdots, n$. Then, by (3.24), we have $\lim_{q\to 0} \frac{\theta_p^0}{\nu_p^0} = \frac{\pi}{2a}$ for $p = 1, \cdots, n$. This completes the proof. □

Then we consider the solutions of (3.5) for $d \neq 0$.

Lemma 3.8. *Let $\mathcal{M}(d, \nu, \theta)$ be defined in (3.6), and let*

$$Ker(\mathcal{M}(d, \nu, \theta)) := \{\boldsymbol{\psi} \in \mathbb{C}^n : \mathcal{M}(d, \nu, \theta)\boldsymbol{\psi} = \boldsymbol{0}\}.$$

Then there exists $\tilde{d}_2 > 0$ such that, for $d \in (0, \tilde{d}_2]$,

$$W := \{(\nu, \theta) : \nu > 0,\ \theta \in [0, 2\pi),\ Ker(\mathcal{M}(d, \nu, \theta)) \neq \{\boldsymbol{0}\}\} = \left\{(\nu_p^d, \theta_p^d)\right\}_{p=1}^n, \tag{3.28}$$

where $(\nu_p^d, \theta_p^d) \in (0, \infty) \times (0, \pi)$ for each $p = 1, \cdots, n$. Moreover, for each $p = 1, \cdots, n$,

$$Ker(\mathcal{M}(d, \nu_p^d, \theta_p^d)) = \left\{c\boldsymbol{\psi}_p^d : c \in \mathbb{C}\right\}, \tag{3.29}$$

where $(\nu_p^d, \theta_p^d, \boldsymbol{\psi}_p^d)$ satisfies $\lim_{d\to 0} (\nu_p^d, \theta_p^d, \boldsymbol{\psi}_p^d) = \left(\nu_p^0, \theta_p^0, \boldsymbol{\psi}_p^0\right)$, and $\left(\nu_p^0, \theta_p^0, \boldsymbol{\psi}_p^0\right)$ is defined in Lemma 3.6.

Proof. Step 1. We show the existence of $\left\{(\nu_p^d, \theta_p^d)\right\}_{p=1}^n$ such that $\left\{(\nu_p^d, \theta_p^d)\right\}_{p=1}^n \subset W$.

We only consider the existence of (ν_2^d, θ_2^d), and $\{(\nu_p^d, \theta_p^d)\}_{p\neq 2}$ can be obtained similarly. Letting $\mathcal{M}^H(d, \nu, \theta)$ be the conjugate transpose of $\mathcal{M}(d, \nu, \theta)$, we compute that

$$\text{Ker}\left(\mathcal{M}^H(0, \nu_2^0, \theta_2^0)\right) := \{\boldsymbol{\psi} \in \mathbb{C}^n : \mathcal{M}^H(0, \nu_2^0, \theta_2^0)\boldsymbol{\psi} = \boldsymbol{0}\} = \left\{c\boldsymbol{\varphi}_2^0 : c \in \mathbb{C}\right\},$$

where $\boldsymbol{\varphi}_2^0 = \left(\varphi_{2,1}^0, \cdots, \varphi_{2,n}^0\right)^T$ with

$$\varphi_{2,1}^0 = -\frac{q}{\overline{h}_1\left(\theta_2^0, \nu_2^0\right)},\quad \varphi_{2,2}^0 = 1,\quad \varphi_{2,k}^0 = 0 \text{ for } k = 3, \cdots, n, \tag{3.30}$$

and $\overline{h}_1\left(\theta_2^0, \nu_2^0\right)$ is the conjugate of $h_1\left(\theta_2^0, \nu_2^0\right)$. By Lemma 3.6, we see that

$$\text{Ker}(\mathcal{M}(0, \nu_2^0, \theta_2^0)) = \left\{c\boldsymbol{\psi}_2^0 : c \in \mathbb{C}\right\}.$$

By (3.22) and (3.30), we see that

$$\langle \boldsymbol{\varphi}_2^0, \boldsymbol{\psi}_2^0\rangle = 1, \tag{3.31}$$

and consequently

$$\mathbb{C}^n = \text{Ker}(\mathcal{M}(0, \nu_2^0, \theta_2^0)) \oplus Z, \tag{3.32}$$

where

$$Z := \left\{\boldsymbol{z} = (z_1, \cdots, z_n)^T \in \mathbb{C}^n : \langle \boldsymbol{\varphi}_2^0, \boldsymbol{z}\rangle = 0\right\}.$$

Then by (3.30), (3.31) and (3.32), we see that, for any $\boldsymbol{y} \in \mathbb{C}^n$,

$$\boldsymbol{y} = \widehat{c}\boldsymbol{\psi}_2^0 + \boldsymbol{z} \text{ with } \widehat{c} = \langle \boldsymbol{\varphi}_2^0, \boldsymbol{y}\rangle = \overline{\varphi}_{2,1}^0 y_1 + y_2 \text{ and } \boldsymbol{z} \in Z, \tag{3.33}$$

where $\overline{\varphi}_{2,1}^0$ is the conjugate of $\varphi_{2,1}^0$.

Let

$$\boldsymbol{H}(d, \nu, \theta, \boldsymbol{z}) = (H_1, \cdots, H_n)^T := \mathcal{M}(d, \nu, \theta)\left(\boldsymbol{\psi}_2^0 + \boldsymbol{z}\right) : \mathbb{R}^3 \times Z \to \mathbb{C}^n, \tag{3.34}$$

where matrix $\mathcal{M}(d, \nu, \theta)$ is defined in (3.6). By Lemma 3.6, we have $\boldsymbol{H}\left(0, \nu_2^0, \theta_2^0, \boldsymbol{0}\right) = \boldsymbol{0}$, and then we solve $\boldsymbol{H}(d, \nu, \theta, \boldsymbol{z}) = \boldsymbol{0}$ for $d \neq 0$. By (3.32) and (3.33), we see that $\boldsymbol{H}(d, \nu, \theta, \boldsymbol{z}) = \boldsymbol{0}$ if and only if $\widetilde{\boldsymbol{H}}(d, \nu, \theta, \boldsymbol{z}) = \boldsymbol{0}$, where

$$\widetilde{\boldsymbol{H}}(d, \nu, \theta, \boldsymbol{0}) = (\widetilde{H}_0, \widetilde{H}_{1,1}, \cdots, \widetilde{H}_{1,n})^T : \mathbb{R}^3 \times Z \to \mathbb{C} \times Z,$$

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and

$$\widetilde{H}_0\left(d,\nu,\theta,z\right)=\langle\boldsymbol{\varphi}_2^0,\boldsymbol{H}\left(d,\nu,\theta,z\right)\rangle=\overline{\varphi_{2,1}^0}H_1\left(d,\nu,\theta,z\right)+H_2\left(d,\nu,\theta,z\right),$$
$$\widetilde{H}_{1,j}\left(d,\nu,\theta,z\right)=H_j\left(d,\nu,\theta,z\right)-\widetilde{H}_0\left(d,\nu,\theta,z\right)\psi_{2,j}^0,\ \ j=1,\cdots,n. \tag{3.35}$$

Let

$$\boldsymbol{P}\left(\check{\nu},\check{\theta},\check{z}\right)=\left(P_0,P_{1,1},\cdots,P_{1,n}\right)^T:\mathbb{R}^2\times Z\to\mathbb{C}\times Z$$

be the Fréchet derivative of $\widetilde{\boldsymbol{H}}$ with respect to (ν,θ,z) at $\left(0,\nu_2^0,\theta_2^0,\mathbf{0}\right)$. By (3.23) and the first equation of (3.35), we have

$$\begin{aligned}P_0\left(\check{\nu},\check{\theta},\check{z}\right)=&(\overline{\varphi}_{2,1}^0h_1(\theta_2^0,\nu_2^0)+q)\check{z}_1+\mathrm{i}e^{-\mathrm{i}\theta_2^0}bu_{0,2}\check{\theta}-\mathrm{i}\check{\nu}\\=&\mathrm{i}e^{-\mathrm{i}\theta_2^0}bu_{0,2}\check{\theta}-\mathrm{i}\check{\nu},\end{aligned}$$

where we have used (3.30) in the last step. By (3.23) and the second equation of (3.35), we have

$$\begin{aligned}&\left(P_{1,1},\cdots,P_{1,n}\right)^T\left(\check{\nu},\check{\theta},\check{z}\right)\\=&\mathcal{M}(0,\theta_2^0,\nu_2^0)\check{z}\\&+\left(0,0,\left(\mathrm{i}e^{-\mathrm{i}\theta_2^0}bu_{0,3}\check{\theta}-\mathrm{i}e^{-\mathrm{i}\theta_2^0}bu_{0,2}\check{\theta}\right)\psi_{2,3}^0,\cdots,\left(\mathrm{i}e^{-\mathrm{i}\theta_2^0}bu_{0,n}\check{\theta}-\mathrm{i}e^{-\mathrm{i}\theta_2^0}bu_{0,2}\check{\theta}\right)\psi_{2,n}^0\right)^T.\end{aligned}$$

Since $\mathcal{M}(0,\theta_2^0,\nu_2^0)$ is a bijection from Z to Z, it follows that $\boldsymbol{P}$ is a bijection. Then we see from the implicit function theorem that there exists a constant $\tilde{d}>0$, a neighbourhood N_2 of $\left(\nu_2^0,\theta_2^0,\mathbf{0}\right)$ and a continuously differentiable function:

$$\left(\nu_2^d,\theta_2^d,z_2^d\right):[0,\tilde{d})\mapsto N_2$$

such that for any $d\in[0,\tilde{d})$, $\left(\nu_2^d,\theta_2^d,z_2^d\right)$ is the unique solution of $\widetilde{\boldsymbol{H}}\left(d,\nu,\theta,z\right)=\mathbf{0}$ in N_2. Therefore, $\left(\nu_2^d,\theta_2^d,z_2^d\right)$ is also the unique solution of $\boldsymbol{H}\left(d,\nu,\theta,z\right)=\mathbf{0}$ in N_2 for $d\in[0,\tilde{d})$. This combined with (3.34) implies that

$$\operatorname{span}(\boldsymbol{\psi}_2^d)\subset\operatorname{Ker}(\mathcal{M}(d,\nu_2^d,\theta_2^d))\ \text{ for }\ d\in[0,\tilde{d}), \tag{3.36}$$

where $\boldsymbol{\psi}_2^d=\boldsymbol{\psi}_2^0+z_2^d$. Note that the rank of $\mathcal{M}(d,\nu_2^d,\theta_2^d)$ is $n-1$. This combined with (3.36) implies that (3.29) holds. Therefore, we show the existence of (ν_2^d,θ_2^d). Moreover, $\lim_{d\to0}(\nu_2^d,\theta_2^d,\boldsymbol{\psi}_2^d)=\left(\nu_2^0,\theta_2^0,\boldsymbol{\psi}_2^0\right)$. This combined with (3.21) implies that $(\nu_2^d,\theta_2^d)\in(0,\infty)\times(0,\pi)$.

Step 2. We show that there exists $\tilde{d}_2$ such that (3.28) holds for $d\in(0,\tilde{d}_2]$.

If it is not true, then there exist sequences $\left\{d_j\right\}_{j=1}^\infty$ and $\left\{\left(\nu^{d_j},\theta^{d_j},\boldsymbol{\psi}^{d_j}\right)\right\}_{j=1}^\infty$ such that $\lim_{j\to\infty}d_j=0$, and for each j,

$$\left(\nu^{d_j},\theta^{d_j}\right)\notin\left\{\left(\nu_p^{d_j},\theta_p^{d_j}\right)\right\}_{p=1}^n,\ \ \|\boldsymbol{\psi}^{d_j}\|_2=1,\ \ \nu^{d_j}>0,\ \ \theta^{d_j}\in[0,2\pi),$$

and

$$\mathcal{M}\left(d_j,\nu^{d_j},\theta^{d_j}\right)\boldsymbol{\psi}^{d_j}=\mathbf{0}. \tag{3.37}$$

It follows from Lemma 3.1 (ii) that ν^{d_j} is bounded. Then, up to a subsequence, we have

$$\lim_{j\to\infty}\theta^{d_j}=\theta^*,\ \ \lim_{j\to\infty}\nu^{d_j}=\nu^*,\ \ \lim_{j\to\infty}\boldsymbol{\psi}^{d_j}=\boldsymbol{\psi}^*$$

with $\theta^*\in[0,2\pi]$, $\nu^*\geq0$ and $\|\boldsymbol{\psi}^*\|_2=1$. Taking $j\to\infty$ on both sides of (3.37), we have $\mathcal{M}\left(0,\nu^*,\theta^*\right)\boldsymbol{\psi}^*=\mathbf{0}$. This combined with Lemma 3.6 implies that there exists $1\leq p_0\leq n$ and a constant $c_{p_0}\neq0$ such that $\nu^*=\nu_{p_0}^0$ and $\theta^*=\theta_{p_0}^0$, $\boldsymbol{\psi}^*=c_{p_0}\boldsymbol{\psi}_{p_0}^0$. Without loss of generality, we assume that

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$p_0 = 2$. Then, for sufficiently large j,

$$\left(\nu^{d_j}, \theta^{d_j}, \frac{1}{c_2}\boldsymbol{\psi}^{d_j} - \boldsymbol{\psi}_2^0\right) \in N_2,$$

where N_2 (defined in step 1) is a neighbourhood of $\left(\nu_2^0, \theta_2^0, \mathbf{0}\right)$. By (3.34) and (3.37), we see that

$$\boldsymbol{H}\left(d_j, \nu^{d_j}, \theta^{d_j}, \frac{1}{c_2}\boldsymbol{\psi}^{d_j} - \boldsymbol{\psi}_2^0\right) = \mathbf{0}.$$

Note from the proof of step 1 that $\left(\nu_2^d, \theta_2^d, z_2^d\right)$ is the unique solution of $\boldsymbol{H}(d, \nu, \theta, z) = \mathbf{0}$ in N_2 for $d \in [0, \tilde{d})$. This implies that, for sufficiently large j,

$$\left(\nu^{d_j}, \theta^{d_j}\right) = \left(\nu_2^{d_j}, \theta_2^{d_j}\right),$$

which is a contradiction. Therefore, (3.28) holds. □

By Lemmas 3.7 and 3.8, we obtain the following result.

Theorem 3.9. *Suppose that $q \in (0, a)$. Then for $d \in (0, \tilde{d}_2]$ with $0 < \tilde{d}_2 \ll 1$, $(\nu, \tau, \boldsymbol{\psi})$ solves (3.18) if and only if there exists $1 \le p \le n$ such that*

$$\nu = \nu_p^d, \quad \boldsymbol{\psi} = c_2\boldsymbol{\psi}_p^d, \quad \tau = \tau_{p,l}^d = \frac{\theta_p^d + 2l\pi}{\nu_p^d}, \quad l = 0, 1, 2, \cdots,$$

where $c_2 \in \mathbb{C}$ is a non-zero constant, and $\left(\nu_p^d, \theta_p^d, \boldsymbol{\psi}_p^d\right)$ is defined in Lemma 3.8. Moreover,

$$\tau_{1,0}^d > \tau_{2,0}^d > \cdots > \tau_{n,0}^d. \tag{3.38}$$

Proof. We only need to show that (3.38) holds, and other conclusions are direct results of Lemma 3.8. By Lemma 3.7 (i), we have

$$\lim_{d\to 0} \tau_{1,0}^d > \lim_{d\to 0} \tau_{2,0}^d > \cdots > \lim_{d\to 0} \tau_{n,0}^d, \tag{3.39}$$

which implies that (3.38) holds for $d \in (0, \tilde{d}_2]$ with $0 < \tilde{d}_2 \ll 1$. This completes the proof. □

3.4. Case III

For this case, we also need to find the equivalent problem of (3.5). Throughout this subsection, we let $\lambda = 1/d$ and denote $\boldsymbol{u}_d$ by $\boldsymbol{u}^\lambda$. Then we rewrite (3.5) as follows:

$$\begin{cases} D\boldsymbol{\psi} + \lambda\left[qQ + \operatorname{diag}\left(a - bu_j^\lambda\right) - e^{-\mathrm{i}\theta}\operatorname{diag}\left(bu_j^\lambda\right) - \mathrm{i}\nu I\right]\boldsymbol{\psi} = \mathbf{0}, \\ \nu > 0, \quad \theta \in [0, 2\pi), \quad \boldsymbol{\psi}(\neq \mathbf{0}) \in \mathbb{C}^n. \end{cases} \tag{3.40}$$

By (2.17) and (2.18), we see that

$$\mathbb{C}^n = \operatorname{span}\{\boldsymbol{\varsigma}\} \oplus (\widetilde{X}_1)_{\mathbb{C}},$$

where $\boldsymbol{\varsigma}$ and $\widetilde{X}_1$ are defined in (2.17) and (2.18), respectively. Ignoring a scalar factor, $\boldsymbol{\psi}(\neq \mathbf{0}) \in \mathbb{C}^n$ in (3.40) can be represented as follows:

$$\begin{cases} \boldsymbol{\psi} = \gamma\boldsymbol{\varsigma} + z, \quad z \in (\widetilde{X}_1)_{\mathbb{C}}, \quad \gamma \ge 0, \\ \|\boldsymbol{\psi}\|_2^2 = \gamma^2\|\boldsymbol{\varsigma}\|_2^2 + \|z\|_2^2 = \|\boldsymbol{\varsigma}\|_2^2. \end{cases} \tag{3.41}$$

Then we obtain the equivalent problem of (3.40) in the following.

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Lemma 3.10. *Assume that* $\lambda \in (0, \lambda_q^*)$ *and* $q \in (0, na)$*. Then* $(\boldsymbol{\psi}, \nu, \theta)$ *solves (3.40), where* $\boldsymbol{\psi}$ *is defined in (3.41), if and only if* (γ, ν, θ, z) *solves*

$$\begin{cases} \widetilde{\boldsymbol{F}}(\gamma, \nu, \theta, \boldsymbol{z}, \lambda) = \boldsymbol{0}, \\ \gamma \geq 0, \ \nu > 0, \ \theta \in [0, 2\pi), \ \boldsymbol{z} \in (\widetilde{X}_1)_{\mathbb{C}}. \end{cases} \tag{3.42}$$

Here

$$\widetilde{\boldsymbol{F}}(\gamma, \nu, \theta, \boldsymbol{z}, \lambda) = (\widetilde{F}_{1,1}, \cdots, \widetilde{F}_{1,n}, \widetilde{F}_2, \widetilde{F}_3)^T$$

is a continuously differentiable mapping from $\mathbb{R}^3 \times (\widetilde{X}_1)_{\mathbb{C}} \times [0, \lambda_q^*)$ *to* $(\widetilde{X}_1)_{\mathbb{C}} \times \mathbb{C} \times \mathbb{R}$*, and*

$$\begin{cases} \widetilde{F}_{1,j}(\gamma, \nu, \theta, \boldsymbol{z}, \lambda) := \sum_{k=1}^n D_{jk} z_k + \lambda \left[g_j(\gamma \boldsymbol{\varsigma} + \boldsymbol{z}, \theta) - i\nu \left(\gamma \varsigma_j + z_j \right) - \frac{1}{n} \widetilde{F}_2(\gamma, \nu, \theta, \boldsymbol{z}, \lambda) \right], \\ \widetilde{F}_2(\gamma, \nu, \theta, \boldsymbol{z}, \lambda) := \sum_{j=1}^n \left[g_j(\gamma \boldsymbol{\varsigma} + \boldsymbol{z}, \theta) - i\nu \left(\gamma \varsigma_j + z_j \right) \right], \\ \widetilde{F}_3(\gamma, \nu, \theta, \boldsymbol{z}, \lambda) := (\gamma^2 - 1) \|\boldsymbol{\varsigma}\|_2^2 + \|\boldsymbol{z}\|_2^2, \end{cases} \tag{3.43}$$

where

$$g_j(\gamma \boldsymbol{\varsigma} + \boldsymbol{z}, \theta) = q \sum_{k=1}^n Q_{jk} \left(\gamma \varsigma_k + z_k \right) + (a - b u_j^\lambda) \left(\gamma \varsigma_j + z_j \right) - e^{-i\theta} b u_j^\lambda \left(\gamma \varsigma_j + z_j \right).$$

Proof. Plugging (3.41) into (3.40), we see that

$$\sum_{k=1}^n D_{jk} z_k + \lambda \left[g_j(\gamma \boldsymbol{\varsigma} + \boldsymbol{z}, \theta) - \mathrm{i}\nu \left(\gamma \varsigma_j + z_j \right) \right] = 0, \quad j = 1, \cdots, n. \tag{3.44}$$

Denote the left side of (3.44) by $\tilde{y}_j$ and let $\tilde{\boldsymbol{y}} = (\tilde{y}_1, \cdots, \tilde{y}_n)^T$. Using similar arguments as in the proof of Proposition 2.5 (ii), we see that $\tilde{\boldsymbol{y}} = \boldsymbol{0}$ if and only $\widetilde{F}_2 = 0$ and $\widetilde{F}_{1,j} = 0$ for all $j = 1, \cdots, n$. This completes the proof. □

We first solve the equivalent problem $\widetilde{\boldsymbol{F}}(\gamma, \nu, \theta, \boldsymbol{z}, \lambda) = \boldsymbol{0}$ for $\lambda = 0$.

Lemma 3.11. *The following equation*

$$\begin{cases} \widetilde{\boldsymbol{F}}(\gamma, \nu, \theta, \boldsymbol{z}, 0) = \boldsymbol{0} \\ \gamma \geq 0, \ \nu \geq 0, \ \theta \in [0, 2\pi], \ \boldsymbol{z} \in (\widetilde{X}_1)_{\mathbb{C}} \end{cases}$$

has a unique solution $(\gamma_*, \nu_*, \theta_*, \boldsymbol{z}_*)$*, where*

$$\boldsymbol{z}_* = \boldsymbol{0}, \ \ \gamma_* = 1, \ \ \nu_* = a - \frac{q}{n}, \ \ \theta_* = \frac{\pi}{2}.$$

Proof. Clearly,

$$\left(\widetilde{F}_{1,1}(\gamma, \nu, \theta, \boldsymbol{z}, 0), \cdots, \widetilde{F}_{1,n}(\gamma, \nu, \theta, \boldsymbol{z}, 0) \right) = \boldsymbol{0},$$

if and only if $\boldsymbol{z} = \boldsymbol{z}_* = \boldsymbol{0}$. Plugging $\boldsymbol{z} = \boldsymbol{0}$ into $\widetilde{F}_3(\gamma, \nu, \theta, \boldsymbol{z}, 0) = 0$, we have $\gamma = \gamma_* = 1$. Note from Proposition 2.6 that $u_j^0 = \dfrac{na - q}{nb}$ for $j = 1, \cdots, n$. Then plugging $\boldsymbol{z} = \boldsymbol{0}$ and $\gamma = 1$ into $\widetilde{F}_2(\gamma, \nu, \theta, \boldsymbol{z}, 0) = 0$, we have

$$\sum_{j=1}^n \left[q \sum_{k=1}^n Q_{jk} \varsigma_k + \frac{q}{n} \varsigma_j - e^{-\mathrm{i}\theta} \varsigma_j \frac{na - q}{n} \right] - \mathrm{i}\nu = 0,$$

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which yields

$$\nu = \nu_* = a - \frac{q}{n}, \ \ \theta = \theta_* = \frac{\pi}{2}.$$

This completes the proof. □

Now we solve $\widetilde{\boldsymbol{F}}(\gamma, \nu, \theta, z, \lambda) = \boldsymbol{0}$ for $0 < \lambda \ll 1$.

Lemma 3.12. *There exists $\tilde{\lambda}$ with $0 < \tilde{\lambda} \ll 1$ and a continuously differentiable mapping $\lambda \mapsto (\gamma^\lambda, \nu^\lambda, \theta^\lambda, z^\lambda)$ from $[0, \tilde{\lambda}]$ to $\mathbb{R}^3 \times (\widetilde{X}_1)_{\mathbb{C}}$ such that $(\gamma^\lambda, \nu^\lambda, \theta^\lambda, z^\lambda)$ is the unique solution of the following problem:*

$$\begin{cases} \widetilde{\boldsymbol{F}}(\gamma, \nu, \theta, z, \lambda) = \boldsymbol{0} \\ \gamma \geq 0, \ \ \nu > 0, \ \ \theta \in [0, 2\pi), \ z \in (\widetilde{X}_1)_{\mathbb{C}} \end{cases} \tag{3.45}$$

for $\lambda \in [0, \tilde{\lambda}]$.

Proof. Let $\widetilde{\boldsymbol{P}}\left(\check{\gamma}, \check{\nu}, \check{\theta}, \check{z}\right) = \left(\widetilde{P}_{1,1}, \cdots, \widetilde{P}_{1,n}, \widetilde{P}_2, \widetilde{P}_3\right)^T : \mathbb{R}^3 \times (\widetilde{X}_1)_{\mathbb{C}} \to (\widetilde{X}_1)_{\mathbb{C}} \times \mathbb{C} \times \mathbb{R}$ be the Fréchet derivative of $\widetilde{\boldsymbol{F}}$ with respect to (γ, ν, θ, z) at $(\gamma_*, \nu_*, \theta_*, z_*, 0)$. Then we compute that

$$\begin{aligned} \widetilde{P}_{1,j}\left(\check{\gamma}, \check{\nu}, \check{\theta}, \check{z}\right) &= \sum_{k=1}^{n} D_{jk}\check{z}_k, \\ \widetilde{P}_2\left(\check{\gamma}, \check{\nu}, \check{\theta}, \check{z}\right) &= -q\check{z}_n + \left(a - \frac{q}{n}\right)\check{\theta} - \mathrm{i}\check{\nu}, \\ \widetilde{P}_3\left(\check{\gamma}, \check{\nu}, \check{\theta}, \check{z}\right) &= 2\|\boldsymbol{\varsigma}\|_2^2\check{\gamma}, \end{aligned}$$

where we have used $\sum_{j=1}^{n} \check{z}_j = 0$ to obtain $\widetilde{P}_2$. Clearly, $\widetilde{\boldsymbol{P}}$ is a bijection from $\mathbb{R}^3 \times (\widetilde{X}_1)_{\mathbb{C}}$ to $\mathbb{R} \times \mathbb{C} \times (\widetilde{X}_1)_{\mathbb{C}}$. It follows from the implicit function theorem that there exists $\tilde{\lambda} > 0$ with $0 < \tilde{\lambda} \ll 1$ and a continuously differentiable mapping $\lambda \mapsto (\gamma^\lambda, \nu^\lambda, \theta^\lambda, z^\lambda)$ from $[0, \tilde{\lambda}]$ to $\mathbb{R}^3 \times (\widetilde{X}_1)_{\mathbb{C}}$ such that $(\gamma^\lambda, \nu^\lambda, \theta^\lambda, z^\lambda)$ satisfies (3.45).

Then we prove the uniqueness of the solution of (3.45). Actually, we only need to verify that if $(\gamma_\lambda, \nu_\lambda, \theta_\lambda, z_\lambda)$ satisfies (3.45), then $\lim_{\lambda \to 0} (\gamma_\lambda, \nu_\lambda, \theta_\lambda, z_\lambda) = (\gamma_*, \nu_*, \theta_*, z_*)$. Since $\widetilde{F}_3(\gamma_\lambda, \nu_\lambda, \theta_\lambda, z_\lambda, \lambda) = 0$, we see that

$$\|\gamma_\lambda \boldsymbol{\varsigma} + z_\lambda\|_2^2 = \|\boldsymbol{\varsigma}\|_2^2, \tag{3.46}$$

which implies that γ_λ is bounded for $\lambda \in (0, \tilde{\lambda})$. Note from Lemma 3.1 (iii) that ν_λ is bounded for $\lambda \in (0, \tilde{\lambda}]$. This combined with (3.46) and the first equation of (3.43) implies that $\lim_{\lambda \to 0} Dz_\lambda = \boldsymbol{0}$, and consequently, $\lim_{\lambda \to 0} z_\lambda = \boldsymbol{0}$. By the third equation of (3.43), we obtain that $\lim_{\lambda \to 0} \gamma_\lambda = 1$. Then, it follows the second equation of (3.43) that $\lim_{\lambda \to 0} \theta_\lambda = \theta_*$ and $\lim_{\lambda \to 0} \nu_\lambda = \nu_*$. Therefore, $(\beta_\lambda, \nu_\lambda, \theta_\lambda, z_\lambda) \to (\gamma_*, \nu_*, \theta_*, z_*)$ as $\lambda \to 0$. This completes the proof. □

By Lemma 3.12, we obtain the following result.

Theorem 3.13. *Assume that $q \in (0, na)$ and let $\lambda = 1/d$. Then for $d \in \left[\tilde{d}_3, \infty\right)$ with $\tilde{d}_3 \gg 1$, $(\nu, \tau, \boldsymbol{\psi})$ satisfies (3.18) if and only if*

$$\nu = \nu^\lambda, \ \ \boldsymbol{\psi} = c_3\boldsymbol{\psi}^\lambda, \ \ \tau = \tau_l^\lambda = \frac{\theta^\lambda + 2l\pi}{\nu_\lambda}, \ \ l = 0, 1, 2, \cdots,$$

where $\boldsymbol{\psi}^\lambda = \gamma^\lambda \boldsymbol{\varsigma} + z^\lambda$, $c_3 \in \mathbb{C}$ is a non-zero constant, and $(\gamma^\lambda, \nu^\lambda, \theta^\lambda, z^\lambda)$ is defined in Lemma 3.12.

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4. Local dynamics

In this section, we obtain the local dynamics of model (1.5) and show the existence of Hopf bifurcations. We first show that the purely imaginary eigenvalues obtained in Theorems 3.5, 3.9 and 3.13 are simple.

Lemma 4.1. *Let $\lambda = 1/d$, and define*

$$(\widehat{\tau}_*, \widehat{\nu}_*) = \begin{cases} (\tau_{d,l}, \nu_d), & \text{if } a < q < na \text{ and } d \in (d_q^*, \tilde{d}_1] \\ (\tau_{p,l}^d, \nu_p^d), & \text{if } 0 < q < a \text{ and } d \in (0, \tilde{d}_2] \\ (\tau_l^\lambda, \nu^\lambda), & \text{if } 0 < q < na \text{ and } d \in [\tilde{d}_3, \infty) \end{cases}$$

with $p = 1, \cdots, n$ and $l = 1, 2, \cdots$, where $(\tau_{d,l}, \nu_d, \tilde{d}_1)$, $(\tau_{p,l}^d, \nu_p^d, \tilde{d}_2)$ and $(\tau_l^\lambda, \nu^\lambda, \tilde{d}_3)$ are defined in Theorems 3.5, 3.9 and 3.13, respectively. Then, $\mu = \mathrm{i}\widehat{\nu}_*$ is an algebraically simple eigenvalue of $A_{\widehat{\tau}_*}(d)$.

Proof. For simplicity, we only consider the case that $0 < q < a$ and $d \in (0, \tilde{d}_2]$, and other cases can be proved similarly. For this case, $\widehat{\tau}_* = \tau_{p,l}^d$ and $\widehat{\nu}_* = \nu_p^d$ with $l = 0, 1, \cdots$ and $p = 1, \cdots, n$. It from Theorem 3.9 that $\mathscr{N}\left[A_{\tau_{p,l}^d}(d) - \mathrm{i}\nu_p^d\right] = \text{span}\left[e^{\mathrm{i}\nu_p^d\theta}\boldsymbol{\psi}_p^d\right]$, where $\theta \in [-\tau_{p,l}^d, 0]$ and $\boldsymbol{\psi}_p^d$ is defined in Theorem 3.9. Now we show that

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

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

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

and consequently, there is a constant σ such that

$$\left[A_{\tau_{p,l}^d}(d) - \mathrm{i}\nu_p^d\right]\boldsymbol{\phi} = \sigma e^{\mathrm{i}\nu_p^d\theta}\boldsymbol{\psi}_p^d.$$

This together with (3.2) and (3.3) yields

$$\begin{aligned} \dot{\boldsymbol{\phi}}(\theta) &= \mathrm{i}\nu_p^d\boldsymbol{\phi}(\theta) + \sigma e^{\mathrm{i}\nu_p^d\theta}\boldsymbol{\psi}_p^d, \quad \theta \in \left[-\tau_{p,l}^d, 0\right], \\ \dot{\boldsymbol{\phi}}(0) &= dD\boldsymbol{\phi}(0) + qQ\boldsymbol{\phi}(0) + \text{diag}\left(a - bu_{d,j}\right)\boldsymbol{\phi}(0) - \text{diag}\left(bu_{d,j}\right)\boldsymbol{\phi}(-\tau_{p,l}^d). \end{aligned} \tag{4.1}$$

By the first equation of (4.1), we have

$$\begin{aligned} \boldsymbol{\phi}(\theta) &= \boldsymbol{\phi}(0)e^{\mathrm{i}\nu_p^d\theta} + \sigma\theta e^{\mathrm{i}\nu_p^d\theta}\boldsymbol{\psi}_p^d, \\ \dot{\boldsymbol{\phi}}(0) &= \mathrm{i}\nu_p^d\boldsymbol{\phi}(0) + \sigma\boldsymbol{\psi}_p^d. \end{aligned} \tag{4.2}$$

Note from Theorem 3.9 that $e^{-\mathrm{i}\tau_{p,l}^d\nu_p^d} = e^{-\mathrm{i}\theta_p^d}$ with θ_p^d defined in Lemma 3.8. Then, substituting (4.2) into the second equation of (4.1), we have

$$\mathcal{M}\left(d, \theta_p^d, \nu_p^d\right)\boldsymbol{\phi}(0) = \sigma\left(\boldsymbol{\psi}_p^d - \tau_{p,l}^d e^{-\mathrm{i}\theta_p^d}\text{diag}\left(bu_{d,j}\right)\boldsymbol{\psi}_p^d\right), \tag{4.3}$$

where $\mathcal{M}(d, \nu, \theta)$ is defined in (3.6).

Let $\mathcal{M}^H(d, \nu, \theta)$ be the conjugate transpose of $\mathcal{M}(d, \nu, \theta)$. Using similar arguments as in the proof of Lemma 3.8, we obtain that for $d \in (0, \tilde{d}_2]$,

$$\left\{\boldsymbol{\varphi} \in \mathbb{C}^n : \mathcal{M}^H(d, \nu_p^d, \theta_p^d)\boldsymbol{\varphi} = \mathbf{0}\right\} = \{c\boldsymbol{\varphi}_p^d : c \in \mathbb{C}\},$$

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and $\lim_{d\to 0}\boldsymbol{\varphi}_p^d=\boldsymbol{\varphi}_p^0$. Here, $\boldsymbol{\varphi}_p^0=\left(\varphi_{p,1}^0,\cdots,\varphi_{p,n}^0\right)^T$ satisfies

$$\varphi_{p,j}^0=0 \text{ for } p+1\le j\le n,\ \ \varphi_{p,p}^0=1,$$

$$\varphi_{p,j}^0=(-1)^{p-j}\prod_{k=j}^{p-1}\frac{q}{\overline{h}_k(\theta_p^0,\nu_p^0)} \text{ for } 1\le j\le p-1,$$

where $\overline{h}_k\left(\theta_p^0,\nu_p^0\right)$ is the conjugate of $h_k\left(\theta_p^0,\nu_p^0\right)$, and $h_k(\theta,\nu)$ is defined in (3.23). One can also refer to (3.30) for $p=2$. Then by (4.3), we have

$$\begin{aligned}0=&\left\langle\mathcal{M}^H\left(d,\theta_p^d,\nu_p^d\right)\boldsymbol{\varphi}_p^d,\boldsymbol{\phi}(0)\right\rangle=\left\langle\boldsymbol{\varphi}_p^d,\mathcal{M}\left(d,\theta_p^d,\nu_p^d\right)\boldsymbol{\phi}(0)\right\rangle\\=&\sigma\left[\langle\boldsymbol{\varphi}_p^d,\boldsymbol{\psi}_p^d\rangle-\langle\boldsymbol{\varphi}^d,\tau_{p,l}^de^{-i\theta_p^d}\operatorname{diag}\left(bu_{d,j}\right)\boldsymbol{\psi}_p^d\rangle\right]\\=&\sigma\left[\sum_{j=1}^n\overline{\varphi}_{p,j}^d\psi_{p,j}^d-\tau_{p,l}^de^{-i\theta_p^d}\sum_{j=1}^n bu_{d,j}\overline{\varphi}_{p,j}^d\psi_{p,j}^d\right]=\sigma S_{p,l}(d).\end{aligned}$$

where

$$S_{p,l}(d):=\sum_{j=1}^n\overline{\varphi}_{p,j}^d\psi_{p,j}^d-\tau_{p,l}^de^{-i\theta_p^d}\sum_{j=1}^n bu_{d,j}\overline{\varphi}_{p,j}^d\psi_{p,j}^d \text{ for } p=1,\cdots,n \text{ and } l=0,1,\cdots.$$

By Lemmas 3.6, 3.8 and Theorem 3.9, we obtain that

$$\lim_{d\to 0}S_{p,l}(d)=1-\frac{\theta_p^0+2l\pi}{\nu_p^0}bu_{0,p}\cos\theta_p^0+i\frac{\theta_p^0+2l\pi}{\nu_p^0}bu_{0,p}\sin\theta_p^0\ne 0,$$

which implies $\sigma=0$. Therefore, for any $l=1,2,\cdots$,

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

and consequently, $i\nu_p^d$ is a simple eigenvalue of $A_{\tau_{p,l}^d}$ for $l=0,1,2,\cdots$. □

It follows from Lemma 4.1 that $\mu=i\widehat{\nu}_*$ is an algebraically simple eigenvalue of $A_{\widehat{\tau}_*}$. Then, by the implicit function theorem, we see that there exists a neighbourhood $\widehat{O}_*\times\widehat{D}_*\times\widehat{H}_*$ of $\left(\widehat{\tau}_*,i\widehat{\nu}_*,\widehat{\boldsymbol{\psi}}_*\right)$ and a continuously differentiable function $(\mu(\tau),\boldsymbol{\psi}(\tau)):\widehat{O}_*\to\widehat{D}_*\times\widehat{H}_*$ such that $\mu(\widehat{\tau}_*)=i\widehat{\nu}_*$, $\boldsymbol{\psi}(\widehat{\tau}_*)=\widehat{\boldsymbol{\psi}}_*$, and for $\tau\in\widehat{O}_*$,

$$\begin{aligned}\Delta(d,\mu(\tau),\tau)\boldsymbol{\psi}(\tau)=&dD\boldsymbol{\psi}(\tau)+qQ\boldsymbol{\psi}(\tau)+\operatorname{diag}\left(a-bu_{d,j}\right)\boldsymbol{\psi}(\tau)\\&-e^{-\mu(\tau)\tau}\operatorname{diag}\left(bu_{d,j}\right)\boldsymbol{\psi}(\tau)-\mu(\tau)\boldsymbol{\psi}(\tau)=\mathbf{0}.\end{aligned}\tag{4.4}$$

Here

$$\widehat{\boldsymbol{\psi}}_*=\begin{cases}\psi_d, & \text{if } a<q<na \text{ and } d\in(d_q^*,\tilde{d}_1]\\ \psi_p^d, & \text{if } 0<q<a \text{ and } d\in(0,\tilde{d}_2]\\ \psi^\lambda, & \text{if } 0<q<na \text{ and } d\in[\tilde{d}_3,\infty)\end{cases}$$

with $\lambda=1/d$ and $p=1,\cdots,n$, where $(\psi_d,\tilde{d}_1)$, $(\psi_p^d,\tilde{d}_2)$ and $(\psi^\lambda,\tilde{d}_3)$ are defined in Theorems 3.5, 3.9 and 3.13, respectively. By a direct calculation, we obtain the following transversality condition.

Lemma 4.2. *Let $\widehat{\tau}_*$ be defined in Lemma 4.1. Then*

$$\frac{d\mathcal{R}e\left[\mu\left(\widehat{\tau}_*\right)\right]}{d\tau}>0.$$

Proof. Similar to Lemma 4.1, we only consider the case that $0<q<a$ and $d\in(0,\tilde{d}_2]$, and other cases can be proved similarly. For this case, $\widehat{\tau}_*=\tau_{p,l}^d$, $\widehat{\nu}_*=\nu_p^d$ and $\widehat{\boldsymbol{\psi}}_*=\boldsymbol{\psi}_p^d$ with $p=1,\cdots,n$ and $l=0,1,\cdots$.

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Differentiating (4.4) with respect to τ at $\tau = \tau^d_{p,l}$, we have

$$\begin{aligned}&\frac{d\mu\left(\tau^d_{p,l}\right)}{d\tau}\left[-\boldsymbol{\psi}^d_p + \tau^d_{p,l}e^{-\mathrm{i}\theta^d_p}\operatorname{diag}\left(bu_{d,j}\right)\boldsymbol{\psi}^d_p\right]\\ &+\mathcal{M}\left(d,\theta^d_p,\nu^d_p\right)\frac{d\boldsymbol{\psi}\left(\tau^d_{p,l}\right)}{d\tau} + \mathrm{i}\nu^d_p e^{-\mathrm{i}\theta^d_p}\operatorname{diag}\left(bu_{d,j}\right)\boldsymbol{\psi}^d_p = \mathbf{0},\end{aligned} \tag{4.5}$$

where $\mathcal{M}(d,\nu,\theta)$ is defined in (3.6). Note that, for $l = 0, 1, \cdots$,

$$0 = \left\langle \mathcal{M}^H\left(d,\theta^d_p,\nu^d_p\right)\boldsymbol{\varphi}^d_p, \frac{d\boldsymbol{\psi}\left(\tau^d_{p,l}\right)}{d\tau}\right\rangle = \left\langle \boldsymbol{\varphi}^d_p, \mathcal{M}\left(d,\theta^d_p,\nu^d_p\right)\frac{d\boldsymbol{\psi}\left(\tau^d_{p,l}\right)}{d\tau}\right\rangle,$$

where $\mathcal{M}^H(d,\nu,\theta)$ and $\boldsymbol{\varphi}^d_p$ are defined in the proof of Lemma 4.1. This combined with (4.5) implies that

$$\begin{aligned}\frac{d\mu\left(\tau^d_{p,l}\right)}{d\tau} = \frac{1}{|S_l(d)|^2}&\left[\mathrm{i}\nu^d_p e^{-\mathrm{i}\theta^d_p}\left(\sum_{j=1}^n bu_{d,j}\overline{\varphi}^d_{p,j}\psi^d_{p,j}\right)\left(\sum_{j=1}^n \varphi^d_{p,j}\overline{\psi}^d_{p,j}\right)\right.\\ &\left.-\mathrm{i}\nu^d_p\tau^d_{p,l}\left(\sum_{j=1}^n bu_{d,j}\varphi^d_{p,j}\overline{\psi}^d_{p,j}\right)\left(\sum_{j=1}^n bu_{d,j}\overline{\varphi}^d_{p,j}\psi^d_{p,j}\right)\right].\end{aligned}$$

By Lemmas 3.6 and 3.8 and Theorem 3.9, we obtain that

$$\lim_{d\to 0}\frac{d\mathcal{R}e\left[\mu\left(\tau^d_{p,l}\right)\right]}{d\tau} > 0.$$

This completes the proof. □

By Theorems 3.5, 3.9 and 3.13 and Lemmas 4.1 and 4.2, we obtain the following result.

Theorem 4.3. *Let $\boldsymbol{u}_d$ be the unique positive equilibrium of model (1.5) obtained in Proposition 2.4. Then the following statements hold:*

(i) For $q \in (a, na)$ and $d \in (d^*_q, \tilde{d}_1]$ with $0 < \tilde{d}_1 - d^*_q \ll 1$, $\boldsymbol{u}_d$ is locally asymptotically stable for $\tau \in [0, \tau_{d,0})$ and unstable for $\tau \in (\tau_{d,0}, \infty)$. Moreover, model (1.5) undergoes a Hopf bifurcation when $\tau = \tau_{d,0}$.

(ii) For $q \in (0, a)$ and $d \in (0, \tilde{d}_2]$ with $0 < \tilde{d}_2 \ll 1$, $\boldsymbol{u}_d$ is locally asymptotically stable for $\tau \in [0, \tau^d_{n,0})$ and unstable for $\tau \in (\tau^d_{n,0}, \infty)$. Moreover, model (1.5) undergoes a Hopf bifurcation when $\tau = \tau^d_{n,0}$.

(iii) For $q \in (0, na)$ and $d \in [\tilde{d}_3, \infty)$ with $\tilde{d}_3 \gg 1$, $\boldsymbol{u}_d$ is locally asymptotically stable for $\tau \in [0, \tau^\lambda_0)$ and unstable for $\tau \in (\tau^\lambda_0, \infty)$ with $\lambda = 1/d$. Moreover, model (1.5) undergoes a Hopf bifurcation when $\tau = \tau^\lambda_0$.

Here $\tau_{d,0}$, $\tau^d_{n,0}$ and $\tau = \tau^\lambda_0$ are defined in Theorems 3.5, 3.9 and 3.13, respectively.

5. The effect of drift rate and numerical simulations

In this section, we show the effect of drift rate and give some numerical simulations. Throughout this section, we define the minimum Hopf bifurcation value by the first Hopf bifurcation value.

If the directed drift rate $q = 0$ (non-advective case), then model (1.5) admits a unique positive equilibrium $\boldsymbol{u}_d = (a/b, \cdots, a/b)^T$ for all $d > 0$. By the framework of [43, 48], we can show the existence of a Hopf bifurcation as follows. Here, we omit the proof.

Proposition 5.1. *Let $q = 0$. Then the first Hopf bifurcation value of model (1.5) is $\tau_{non} = \pi/2a$. Moreover, the unique positive equilibrium $\boldsymbol{u}_d$ of model (1.5) is stable for $\tau < \tau_{non}$ and unstable for $\tau > \tau_{non}$, and model (1.5) undergoes a Hopf bifurcation when $\tau = \tau_{non}$.*

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Therefore, the first Hopf bifurcation value τ_{non} for $q=0$ is independent of the random diffusion rate d. By Theorems 3.5, 3.9, 3.13 and 4.3, we see that the first Hopf bifurcation value τ_{adv} depends on the diffusion rate d for $q\neq 0$. Actually, we show that it can be strictly monotone decreasing in d when d is large.

Proposition 5.2. *Assume that $q\in(0,na)$, and let $\lambda=1/d$. Then, for $d\in[\tilde{d}_3,\infty)$ with $\tilde{d}_3\gg 1$, the first Hopf bifurcation value of model (1.5) is $\tau_{adv}=\tau_0^\lambda$, where τ_0^λ and $\tilde{d}_3$ are defined in Theorem 3.13. Moreover, the following statements hold:*

(i)

$$\left(\tau_0^\lambda\right)'\big|_{\lambda=0}=\frac{\pi q^2(n+1)(n-1)}{12(na-q)^2}>0, \tag{5.1}$$

where $'$ is the derivative with respect to λ;

(ii) There exists $\hat{d}_3>\tilde{d}_3$ such that $\tau_{adv}>\tau_{non}$ for $d\in[\hat{d}_3,\infty)$, and τ_{adv} is strictly monotone decreasing in $d\in[\hat{d}_3,\infty)$.

Proof. By Theorems 3.13 and 4.3, we see that for $d\in[\tilde{d}_3,\infty)$ with $\tilde{d}_3\gg 1$, the first Hopf bifurcation value of model (1.5) is $\tau_{adv}=\tau_0^\lambda$. We first show that (i) holds. Note from Lemmas 3.11 and 3.12 that $\left(\gamma^\lambda,\nu^\lambda,\theta^\lambda,z^\lambda\right)$ is the unique solution of (3.42) and $\left(\gamma^0,\nu^0,\theta^0,z^0\right)=\left(1,a-\frac{q}{n},\frac{\pi}{2},\mathbf{0}\right)$. Differentiating the first equation of (3.42) with respect to λ at $\lambda=0$ and noticing that $z^0=\mathbf{0}$, we have

$$\begin{aligned}
0=&\sum_{k=1}^n D_{jk}(z_k^\lambda)'\big|_{\lambda=0}+q\sum_{k=1}^n Q_{jk}\gamma^0\varsigma_k+\left(a-bu_j^0\right)\gamma^0\varsigma_j-e^{-\mathrm{i}\theta^0}bu_j^0\gamma^0\varsigma_j\\
&-\mathrm{i}\nu^0\gamma^0\varsigma_j-\frac{1}{n}\widetilde{F}_2\left(\gamma^0,\nu^0,\theta^0,z^0,0\right),\\
0=&\,q\sum_{j=1}^n\sum_{k=1}^n Q_{jk}\left[(\gamma^\lambda)'\varsigma_k+(z_k^\lambda)'\right]\big|_{\lambda=0}-\sum_{j=1}^n\left(bu_j^\lambda\right)'\big|_{\lambda=0}\gamma^0\varsigma_j\\
&+\sum_{j=1}^n\left[(a-bu_j^0)-e^{-\mathrm{i}\theta^0}bu_j^0-\mathrm{i}\nu^0\right]\left[(\gamma^\lambda)'\varsigma_j+(z_j^\lambda)'\right]\big|_{\lambda=0}\\
&+\sum_{j=1}^n\left[\left(\theta^\lambda\right)'\big|_{\lambda=0}bu_j^0-e^{-\mathrm{i}\theta^0}\left(bu_j^\lambda\right)'\big|_{\lambda=0}-\mathrm{i}\left(\nu^\lambda\right)'\big|_{\lambda=0}\right]\gamma^0\varsigma_j,\\
0=&\,2\gamma^0\left(\gamma^\lambda\right)'\big|_{\lambda=0}\|\boldsymbol{\varsigma}\|_2^2.
\end{aligned} \tag{5.2}$$

By the third equation of (5.2), we have $\left(\gamma^\lambda\right)'\big|_{\lambda=0}=0$. Then plugging $\left(\gamma^\lambda\right)'\big|_{\lambda=0}=0$ into the first and second equations of (5.2), and noticing that $\left(\gamma^0,\nu^0,\theta^0\right)=\left(1,a-\frac{q}{n},\frac{\pi}{2}\right)$, $z'\in(\widetilde{X}_1)_{\mathbb{C}}$ and $\widetilde{F}_2\left(\gamma^0,\nu^0,\theta^0,z^0,0\right)=0$, we have

$$\begin{cases}
\displaystyle\sum_{j=1}^n D_{1k}(z_k^\lambda)'\big|_{\lambda=0}-\frac{q}{n}+\frac{q}{n}\cdot\frac{1}{n}=0,\\
\displaystyle\sum_{j=1}^n D_{jk}(z_k^\lambda)'\big|_{\lambda=0}+\frac{q}{n}\cdot\frac{1}{n}=0,\ \ j=2,\cdots,n,\\
\displaystyle\left[-q(z_n^\lambda)'-\frac{1}{n}\sum_{j=1}^n\left(bu_j^\lambda\right)'+\left(a-\frac{q}{n}\right)\left(\theta^\lambda\right)'+\mathrm{i}\frac{1}{n}\sum_{j=1}^n\left(bu_j^\lambda\right)'-\mathrm{i}\left(\nu^\lambda\right)'\right]\Bigg|_{\lambda=0}=0.
\end{cases}$$

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This combined with (2.20) and Proposition 5.4 in the appendix implies that

$$(z_n^\lambda)'\big|_{\lambda=0} = \frac{q(n+1)(n-1)}{6n}, \quad (\nu^\lambda)'\big|_{\lambda=0} = -\frac{q^2(n+1)(n-1)}{6n}, \quad (\theta^\lambda)'\big|_{\lambda=0} = 0.$$

Then, by Theorem 3.13, we have

$$(\tau_0^\lambda)'\big|_{\lambda=0} = \left(\frac{\theta^\lambda}{\nu^\lambda}\right)'\bigg|_{\lambda=0} = \frac{\pi q^2 n(n+1)(n-1)}{12(na-q)^2}.$$

Now we consider (ii). By Lemmas 3.11, 3.12 and Theorem 3.13, we see that

$$\lim_{\lambda\to 0}\tau_{adv} = \lim_{\lambda\to 0}\tau_0^\lambda = \frac{\pi}{2(a-\frac{q}{n})} > \tau_{non}.$$

This, combined with (i), implies that (ii) holds. This completes the proof. □

Then we consider the case of small diffusion rate.

Proposition 5.3. *Assume that $q\in(0,a)$. Then, for $d\in(0,\tilde d_2]$ with $\tilde d_2 \ll 1$, the first Hopf bifurcation value of model (1.5) is $\tau_{adv}=\tau_{n,0}^d$, where $\tau_{n,0}^d$ and $\tilde d_2$ are defined in Theorem 3.9. Moreover, there exists $\hat d_2\in(0,\tilde d_2]$ such that $\tau_{adv}>\tau_{non}$ for $d\in(0,\hat d_2]$.*

Proof. By Theorems 3.9 and 4.3, we see that the first Hopf bifurcation value is $\tau_{adv}=\tau_{n,0}^d$, and

$$\lim_{d\to 0}\tau_{adv} = \lim_{d\to 0}\tau_{n,0}^d = \frac{\theta_n^0}{\nu_n^0}. \tag{5.3}$$

By Lemma 3.7 (ii), we see that $\dfrac{\theta_n^0}{\nu_n^0} > \dfrac{\pi}{2a}$. This, combined with (5.3), implies that there exists $\hat d_2\in(0,\tilde d_2]$ such that $\tau_{adv}>\tau_{non}$ for $d\in(0,\hat d_2]$. □

It follows from Propositions 5.2 and 5.3 that the first Hopf bifurcation value in advective environments is larger than that in non-advective environments if $d\gg 1$ or $d\ll 1$, see Figure 2. This result suggests that directed movements of the individuals inhibit the occurrence of Hopf bifurcation.

Now we give some numerical simulations. We choose three patches, that is, $n=3$, and set $a=1$ and $b=1$. Then we can numerically compute the first Hopf bifurcation τ_{adv} for a wider range of parameters. For the case $q\in(0,a)$, we prove that large delay can also induce Hopf bifurcations for model (1.5) if $0<d\ll 1$ or $d\gg 1$ (Theorem 4.3 (ii) and (iii)). Then we compute that there exist three families of Hopf bifurcation curves $\left\{\tau_{j,l}^d\right\}_{l=1}^\infty$ $(j=1,2,3)$. For simplicity, we only plot the first one for each family $\left\{\tau_{j,l}^d\right\}_{l=1}^\infty$ $(j=1,2,3)$ in Figure 4.

Then $\tau_{adv}=\min_{1\le j\le 3}\tau_{j,0}^d$, and it exists for $d\in(0,\infty)$, which implies that delay-induced Hopf bifurcation may occur for $d\in(0,\infty)$. Actually, we choose $d=0.06, 1.5, 20, 150$ and numerically show that there exist periodic solutions; see Figure 5.

For the case $q\in(a,na)$, we prove that large delay can induce Hopf bifurcations for model (1.5) if $0<d-d_q^*\ll 1$ or $d\gg 1$ (Theorem 4.3 (i) and (iii)). In Figure 6, we plot τ_{adv} for this case, and it exists for $d\in(d_q^*,\infty)$, which implies that delay-induced Hopf bifurcation may occur for $d\in(d_q^*,\infty)$.

By Figures 4 and 6, we conjecture that τ_{adv} change monotonicity once with respect to d. In fact, by Proposition 5.2, τ_{adv} is decreasing in d when d is sufficiently large. Moreover, in Propositions 5.2 and 5.3, we show that $\tau_{adv}>\tau_{non}$, which suggests that directed movements of the individuals inhibit the occurrence of Hopf bifurcation. To illustrate this phenomenon, we fix $\tau=1.6$, $d=1.14$ and choose the same initial values for $q=0$ and $q=2$. As is shown in Figure 7, periodic oscillations disappear for $q\neq 0$.

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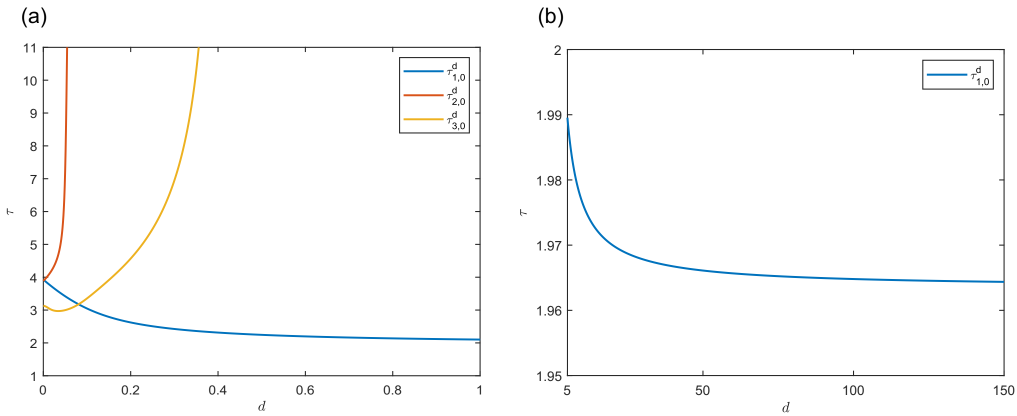

Figure 4. *The relation between Hopf bifurcation values and dispersal rate d for the case* $q \in (0, a)$ *with* $a = 1$, $b = 1$ *and* $q = 0.6$. *(a)* $d \in (0, 1]$; *(b)* $d \in [5, 150]$.

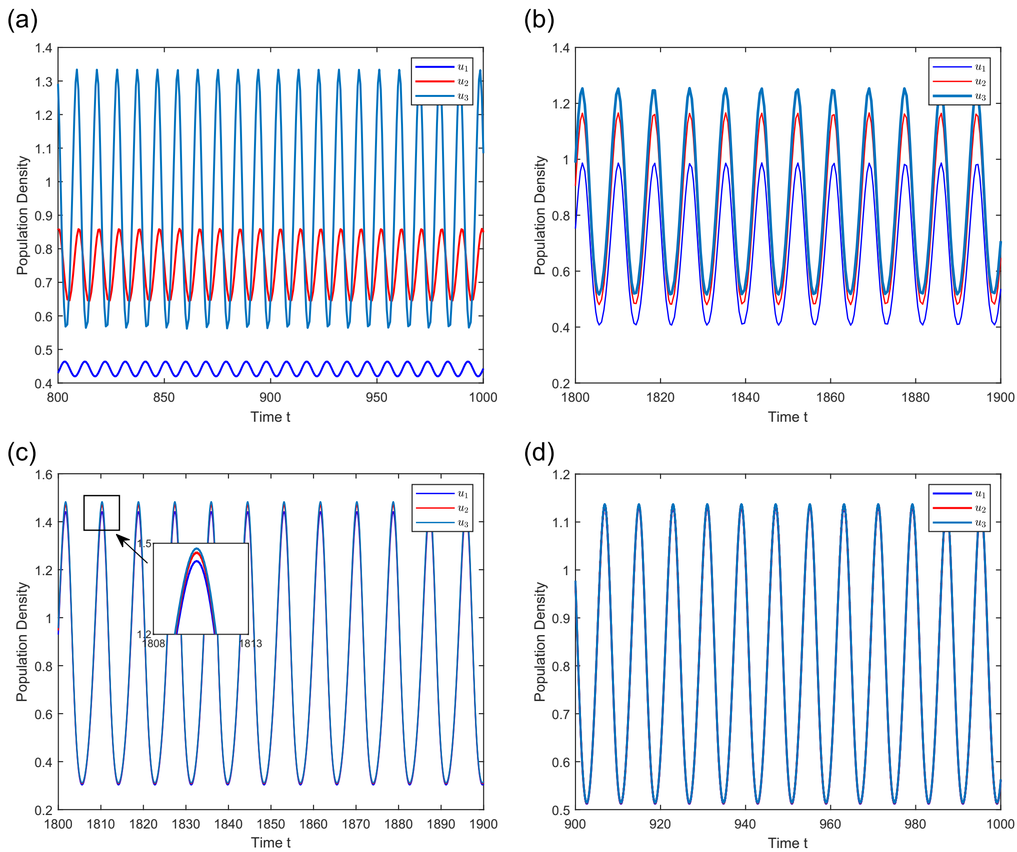

Figure 5. *Periodic solutions induced by a Hopf bifurcation with* $a = 1$, $b = 1$ *and* $q = 0.6$. *(a)* $d = 0.06$ *and* $\tau = 3.1$; *(b)* $d = 1.5$ *and* $\tau = 2.1$; *(c)* $d = 20$ *and* $\tau = 2.1$; *(d)* $d = 150$ *and* $\tau = 2.0$.

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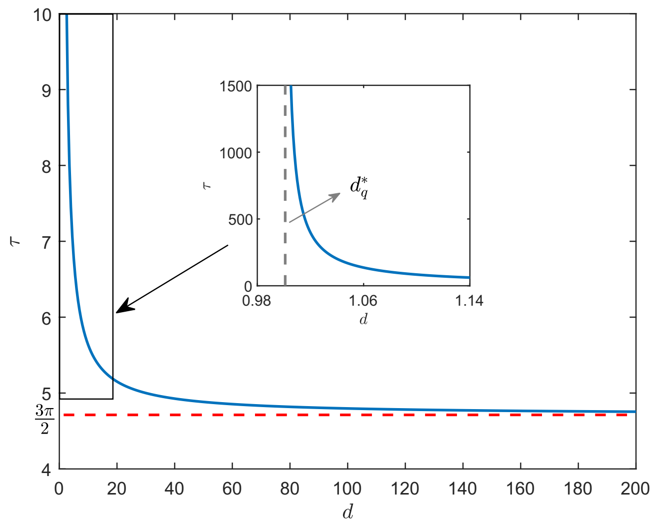

Figure 6. *The relation between Hopf bifurcation value and dispersal rate d for the case $q \in (a, na)$ with $a = 1$, $b = 1$ and $q = 2$.*

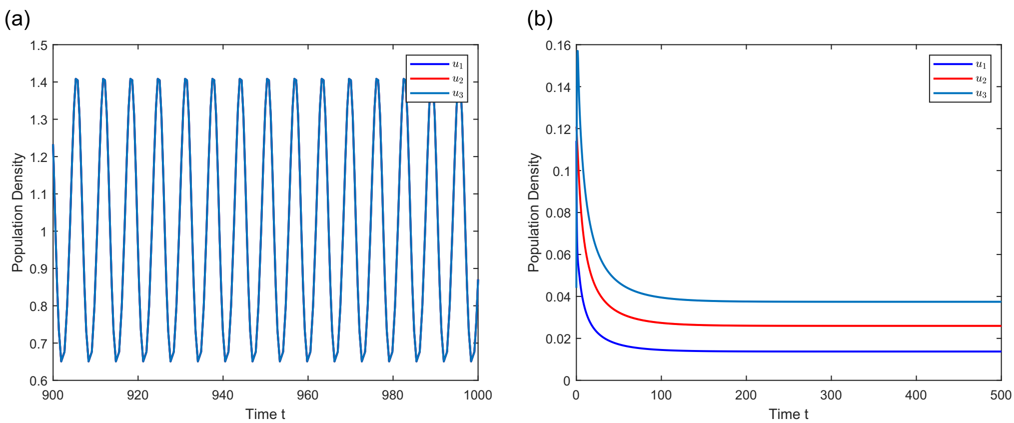

Figure 7. *Directed drift rate q inhibit the occurrence of Hopf bifurcation. Here, $a = 1$, $b = 1$, $d = 1.14$ and $\tau = 1.6$. (a) $q = 0$; (b) $q = 2$.*

We remark that model (1.5) is a discrete form of model (1.6), where D_{jk} is defined in (1.3) and

$$Q_{jk} = \begin{cases} 1, & j = k + 1, \\ -1, & j = k = 1, \cdots, n - 1, \\ -\beta, & j = k = n, \\ 0, & \text{otherwise}. \end{cases} \tag{5.4}$$

In this paper, we consider the case $\beta = 1$, and it is natural to ask whether β (the population loss rate at the downstream end) affects Hopf bifurcations. Then we consider this problem from the point view of numerical simulations and choose

$$n = 3 \text{ (three patches)}, \quad a = 1, \quad b = 1, \quad q = 0.6, \quad d = 2.$$

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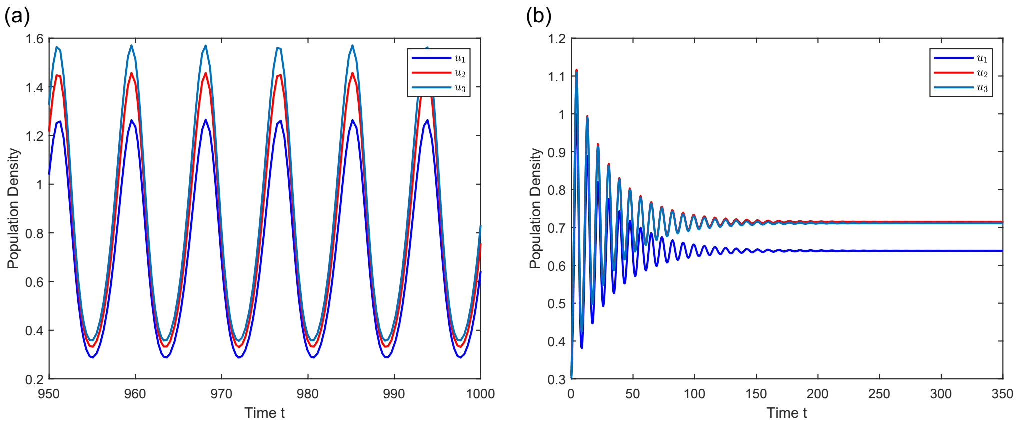

Figure 8. *The effect of β on the dynamics of model (1.5) with D_{jk} and Q_{jk} defined in (1.3) and (5.4), respectively. (a) $\beta = 0.9$, $\tau = 2.1$; (b) $\beta = 1.5$, $\tau = 2.1$.*

If $\beta = 1$, we compute that $\tau_{adv} \approx 2.03$. Then set $\tau = 2.1$, we show that there also exists periodic solutions for $\beta = 0.9$, and periodic oscillations disappear for $\beta = 1.5$, see Figure 8. Then, we conjecture that if the positive equilibrium of (1.5) exists, the minimum Hopf bifurcation value for the case $\beta > 1$ (resp. $\beta < 1$) is larger (resp. smaller) than that for the case $\beta = 1$.

Ethical standards. Not applicable.

Competing interests. The authors declare that they have no conflict of interest.

Author contributions. All authors contributed to the study conception and design. SC developed the idea for the study. The manuscript was written by LW, SZ and SC, and LW and SZ prepared Figures 1–7. All authors read and approved the final manuscript.

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Appendix

In the appendix, we show the following result by linear algebraic techniques.

Proposition 5.4. *Let $D = (D_{jk})$ with D_{jk} defined in (1.3), and let $\widetilde{X}_1$ be defined in (2.18). Assume that $D\boldsymbol{y} = \boldsymbol{a}$ with $\boldsymbol{a}, \boldsymbol{y} \in \widetilde{X}_1$. Then*

$$y_n = \frac{1}{n}\sum_{k=1}^{n-1} k\left(\sum_{j=1}^{k} a_j\right). \tag{5.5}$$

Especially, if $a_2 = \cdots = a_n$, then

$$y_n = \frac{n(n-1)}{2}a_1 + \frac{(n-2)(n-1)n}{3}a_2 \tag{5.6}$$

Proof. Since $D\boldsymbol{y} = \boldsymbol{a}$ and $\boldsymbol{y} \in \widetilde{X}_1$, we have

$$-y_1 + y_2 = a_1, \tag{5.7a}$$

$$y_{j-1} - 2y_j + y_{j+1} = a_j, \;\; j = 2, \cdots, n-1, \tag{5.7b}$$

and

$$\sum_{j=1}^{n} y_j = 0. \tag{5.8}$$

Summing the first k equations in (5.7), we find

$$-y_k + y_{k+1} = \sum_{j=1}^{k} a_j, \;\; k = 1, \cdots, n-1. \tag{5.9}$$

Multiplying (5.9) by k and summing these over all k yields

$$-\sum_{j=1}^{n-1} y_j + (n-1)y_n = \sum_{k=1}^{n-1} k\left(\sum_{j=1}^{k} a_j\right).$$

This combined with (5.8) implies that (5.5) holds.

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Now we consider (5.6). A direct computation yields

$$y_n = \left(\sum_{j=1}^{n-1} j\right) a_1 + \left(\sum_{j=1}^{n-2} j(j+1)\right) a_2$$
$$= \frac{n(n-1)}{2} a_1 + \frac{(n-2)(n-1)n}{3} a_2,$$

where we have used $\sum_{j=1}^{n} j(j+1) = \frac{n(n+1)(n+2)}{3}$ in the last step. This completes the proof. □

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