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Density-dependent effects on Turing patterns and steady state bifurcation in a Beddington–DeAngelis-type predator–prey model

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Abstract
In this paper, Turing patterns and steady state bifurcation of a diffusive Beddington–DeAngelis-type predator–prey model with density-dependent death rate for the predator are considered. We first investigate the stability and Turing instability of the unique positive equilibrium point for the model. Then the existence/nonexistence, the local/global structure of nonconstant positive steady state solutions, and the direction of the local bifurcation are established. Our results demonstrate that a Turing instability is induced by the density-dependent death rate under appropriate conditions, and both the general stationary pattern and Turing pattern can be observed as a result of diffusion. Moreover, some specific examples are presented to illustrate our analytical results.

MSC: 92D25; 35K57; 35B35

Keywords: Predator–prey model; Density-dependent; Turing instability; Bifurcation; Steady state

1 Introduction

Understanding the dynamical relationship between predator and prey is a central research subject in ecology, and one significant component of the predator–prey relationship is the predator's rate of feeding upon prey, i.e., the so-called functional response. Functional response is a double rate: It is the average number of prey killed per individual predator per unit of time. In general, the functional response can be classified into two types: Prey-dependent and predator-dependent. Prey dependence means that the functional response is only a function of the prey's density, while predator dependence means that the functional response is a function of both the prey's and the predator's densities. For the functional response functions, there are many types, such as the Holling family which are predominant in the literature [1].

Since 1959, the Holling II-type prey-dependent functional response has served as the basis for a very large literature on predator–prey theory [2]. However, the prey-dependent functional responses fail to describe the interference among predators, and have been facing challenges from the biology and physiology communities [3, 4]. Some biologists have argued that in many situations, especially when predators have to search for food (and therefore, have to share or compete for food), the functional response in a predator–prey model should be predator-dependent. There is much significant evidence to suggest that predator dependence in the functional response occurs quite frequently in laboratory and natural systems [5, 6]. Given that large numbers of experiments and observations suggest that predators do indeed interfere with one another's activities so as to result in competition effects and that prey alters its behavior under increased predator-threat, the models with predator-dependent functional response stand as reasonable alternatives to the models with prey-dependent functional response [2]. Starting from this argument and the traditional prey-dependent model, to describe mutual interference among predators, Beddington [7] and DeAngelis [8] proposed that an individual from a population of more than two predators not only allocates time in searching for and processing their prey but also takes time in encountering other predators. This result in the so-called Beddington–DeAngelis functional response $p(u,v) = \frac{mu}{a+u+bv}$. The Beddington–DeAngelis functional response is similar to the well-known Holling type II functional response, but it has an extra term bv in the denominator modelling mutual interference among predators, and it also has some similar qualitative features as the ratio-dependent form but avoids the singular behaviors of ratio-dependent models at low densities which have been the source of controversy.

We know the classical Beddington–DeAngelis-type predator–prey system which has received considerable attention [9–17] and takes the form

$$\begin{cases} \frac{du}{dt} = u(1-u) - \frac{muv}{a+u+bv}, \\ \frac{dv}{dt} = sv(-q + \frac{mu}{a+u+bv}). \end{cases} \tag{1}$$

A salient statistical evidence from nineteen predator–prey systems prove that Beddington–DeAngelis functional response provides better description of predator feeding over a range of predator–prey abundances [2]. In some cases, it performs even better than other functional responses. The most crucial finding of Skalski and Gilliam [2] was that predator dependence in the functional response is a nearly ubiquitous property of the published data sets. Cantrell and Cosner [10] have partially analyzed the dynamics of the system (1). Hwang [13] has solved the problem for the uniqueness of a limit cycle of the system (1). A detailed mathematical analysis of the dynamics for (1) with unlimited carrying capacity for prey population was presented in [14]. Further, Kartina [15] found that predator dependence is important at not only very high predator densities on per capita predation rate but also at low predator densities. In ecology, we should consider the predator density dependence, and we need to take into account realistic levels of predator dependence.

In this paper, we consider the following density-dependent Beddington–DeAngelis-type predator–prey model:

$$\begin{cases} \frac{du}{dt} = u(1-u) - \frac{muv}{a+u+bv}, \\ \frac{dv}{dt} = sv(-q - \delta v + \frac{mu}{a+u+bv}), \end{cases} \tag{2}$$

where u and v represent prey and predator densities, respectively. q is the death rate of the predator, s is the feed concentration and δ is the density-dependent death rate. Biologically speaking, the positive density-dependent death rate δ has depressing effect on the growth rate of the predator, i.e., causes the reduction in predator growth rate [16].

In [17], the authors studied the dynamics of (2). They proved the permanence, locally and globally asymptotic stability of the positive equilibrium for the model (2) by using stability theory of differential equations and Lyapunov functions. For the permanence, they showed that the density dependence for predator gives some negative effect, compared to the models without the density dependence. In addition, the authors compared results for the model with Beddington–DeAngelis functional response on permanence, locally and globally asymptotic stability to the system with Lotka–Volterra interaction or Holling type II functional response or ratio-dependent functional response.

When the densities of the prey and predator are spatially inhomogeneous in a bounded domain, and the prey and predator move randomly-described as Brownian random motion [18–20], we need consider the following reaction–diffusion model:

$$\begin{cases} u_t - d_1\triangle u = u(1-u) - \frac{muv}{a+u+bv}, & x\in\Omega, t>0,\\ v_t - d_2\triangle v = sv(-q-\delta v + \frac{mu}{a+u+bv}), & x\in\Omega, t>0,\\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0, & x\in\partial\Omega, t>0,\\ u(x,0)=u_0(x)\geq(\not\equiv)0, \qquad v(x,0)=v_0(x)\geq(\not\equiv)0, & x\in\Omega, \end{cases} \tag{3}$$

where Ω is a bounded domain with smooth boundary $\partial\Omega$ and ν is the outward unit normal vector of the boundary $\partial\Omega$. The positive constants d_1 and d_2 are the diffusion coefficients of $u(x,t)$ and $v(x,t)$, respectively. $\triangle$ is the Laplacian operator which describes the random moving.

In the case $b=0$, Huang et al. in [21] derived the conditions for the existence of nonconstant steady states of the model (3) with $\delta>0$. At the same time, they proved that the same system without the density-dependent death rate for the predators does not admit pattern formations. Hence, in the case $b>0$, a natural question is raised: Is the density-dependent death rate δ also a decisive factor inducing Turing instability in the model (3)? We will answer this problem in this paper.

To study the stationary patterns, we need consider the steady state problem associated with (3)

$$\begin{cases} -d_1\triangle u = u(1-u) - \frac{muv}{a+u+bv}, & x\in\Omega,\\ -d_2\triangle v = sv(-q-\delta v + \frac{mu}{a+u+bv}), & x\in\Omega,\\ \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0, & x\in\partial\Omega. \end{cases} \tag{4}$$

The rest of this paper is organized as follows: In Sect. 2, the stability and Turing instability of the positive equilibrium point (u^*,v^*) in (3) are discussed. In Sect. 3, we investigate the nonexistence/existence of nonconstant positive steady states. In Sect. 4, the local and global structure of nonconstant positive steady state are established, and the direction of the local bifurcation is given.

2 Stability and Turing instability of positive equilibrium point

In this section, we mainly discuss the stability and Turing instability of the positive equilibrium point of (3). For convenience, we denote

$$f(u,v) = u(1-u) - \frac{muv}{a+u+bv}, \qquad g(u,v) = sv\left(-q-\delta v + \frac{mu}{a+u+bv}\right).$$

Obviously, the model (2) has a trivial equilibrium point $E_0 = (0,0)$, a semitrivial equilibrium point $E_1 = (1,0)$ and at least one positive equilibrium point $E^* = (u^*, v^*)$ if

$$m > (a+1)q,$$

where

$$u^* = \frac{b\delta v^{*2} + (a\delta + bq)v^* + aq}{m - q - \delta v^*}$$

and v^* is the positive roots of polynomial equation

$$\begin{aligned}&\delta\big(b^2+\delta\big)v^3 + \big[(2ab+b-2m+2q)\delta + b^2 q\big]v^2 \\ &\quad + \big[\big(a^2+a\big)\delta + q^2 + (2ab+b-2m)q + m(m-b)\big]v + a\big[(a+1)q - m\big] = 0.\end{aligned} \tag{5}$$

To illustrate the uniqueness of the positive equilibrium point, we first give the following lemma.

Lemma 1 (Shengjins discriminant [22]) *For the equation $x^3 + Bx^2 + Cx + D = 0$, where $B, C, D \in \mathbf{R}$, denote $\mathbb{A} = B^2 - 3C$, $\mathbb{B} = BC - 9D$, $\mathbb{C} = C^2 - 3BD$ and $\Delta = \mathbb{B}^2 - 4\mathbb{A}\mathbb{C}$.*

(i) *The equation has three real roots if and only if $\Delta \le 0$.*
(ii) *The equation has one real root and a pair of conjugate complex roots if and only if $\Delta > 0$.*

For Eq. (5), corresponding to Lemma 1, let

$$\begin{aligned}&B := \big[(2ab+b-2m+2q)\delta + b^2 q\big]/\big[\delta\big(b^2+\delta\big)\big], \\ &D := a\big[(a+1)q - m\big]/\big[\delta\big(b^2+\delta\big)\big], \\ &C := \big[\big(a^2+a\big)\delta + q^2 + (2ab+b-2m)q + m(m-b)\big]/\big[\delta\big(b^2+\delta\big)\big],\end{aligned} \tag{6}$$

and

$$\mathbb{A} := B^2 - 3C, \qquad \mathbb{B} := BC - 9D, \qquad \mathbb{C} := C^2 - 3BD, \qquad \Delta := \mathbb{B}^2 - 4\mathbb{A}\mathbb{C}. \tag{7}$$

Then we can obtained the following conclusion.

Theorem 2.1 *Assume that*

$$(\mathbf{H_1}) \quad m > (a+1)q, \qquad \Delta > 0$$

hold, then Eq. (5) has a unique positive root, and (2) has a unique positive equilibrium point $E^* = (u^*, v^*)$.

Now we discuss the stability and instability of E^* for the ODE model (2) and PDE model (3), respectively. By simple calculation, we can see that the Jacobian matrix of (2) evaluated at E^* is given by

$$J\big(E^*\big) = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix},$$

where

$$a_{11} = \frac{mu^*v^*}{(bv^*+a+u^*)^2} - u^*, \qquad a_{12} = -\frac{mu^*(a+u^*)}{(bv^*+a+u^*)^2} < 0,$$
$$a_{21} = \frac{m(bv^*+a)}{(bv^*+a+u^*)^2} > 0, \qquad a_{22} = -sv^*\left(\delta + \frac{mbu^*}{(bv^*+a+u^*)^2}\right) < 0. \tag{8}$$

The characteristic equation of $J(E^*)$ is

$$\eta^2 - Q\eta + P = 0,$$

where

$$Q = a_{11} + a_{22}, \qquad P = a_{11}a_{22} - a_{12}a_{21}. \tag{9}$$

Obviously that E^* is locally asymptotically stable if $Q < 0$ and $P > 0$. Thus, we can obtain the following theorem.

Theorem 2.2 *Assume* $(\mathbf{H_1})$ *hold. For the model* (2), *the following statements are true.*

(i) *If* $mu^*v^* < (u^*+\delta sv^*)(bv^*+a+u^*)^2 + bsmu^*v^*$ *and*

$$(\mathbf{H_{21}}) \quad sv^*\left[m^2bu^*v^* + m(\delta v^* - bu^*)(bv^*+a+u^*)^2\right] < m^2(a+u^*)(a+bv^*) + \delta sv^*(bv^*+a+u^*)^4,$$

then equilibrium point E^* *is locally asymptotically stable.*

(ii) *If* $mu^*v^* > (u^*+\delta sv^*)(bv^*+a+u^*)^2 + bsmu^*v^*$ *or*

$$(\mathbf{H_{22}}) \quad sv^*\left[m^2bu^*v^* + m(\delta v^* - bu^*)(bv^*+a+u^*)^2\right] > m^2(a+u^*)(a+bv^*) + \delta sv^*(bv^*+a+u^*)^4,$$

then equilibrium point E^* *is unstable.*

To consider Turing instability of E^* for PDE model (3), we denote $0 = \lambda_0 < \lambda_1 < \cdots$, the sequence of eigenvalues for the problem

$$-\Delta\phi = \lambda\phi, \quad x \in \Omega, \qquad \frac{\partial\phi}{\partial\nu} = 0, \quad x \in \partial\Omega, \tag{10}$$

and λ_i $(i \geq 1)$ has multiplicity $m_i \geq 1$, whose corresponding normalized eigenfunctions are given by ϕ_{ij}, where $j = 1, 2, \ldots, m_i$. This set of eigenfunctions form an orthogonal basis in $L^2(\Omega)$.

If $a_{11} > 0$ and

$$d_1\lambda_1 < a_{11}, \tag{11}$$

then we define i_0 be the largest positive integer such that $d_1\lambda_i < a_{11}$.

Clearly, if (11) is satisfied, then $1 \le i_0 < \infty$. In this case, let

$$\bar{d}_2 = \min_{0 \le i \le i_0} d_2^i(E^*), \tag{12}$$

where $d_2^i(E^*)$ is given by

$$d_2^i(E^*) = \frac{d_1 a_{22}\lambda_i - a_{11}a_{22} + a_{12}a_{21}}{\lambda_i(d_1\lambda_i - a_{11})}. \tag{13}$$

Theorem 2.3 *Assume that* $(\mathbf{H_1})$ *holds. Then the following conclusions for the model* (3) *are true.*

(i) *If* $a_{11} < 0$, *then* E^* *is locally asymptotically stable.*

(ii) *Let* $a_{11} > 0$, $(\mathbf{H_{21}})$ *and* $mu^*v^* < (u^* + \delta sv^*)(bv^* + a + u^*)^2 + bsmu^*v^*$ *hold.*

 (ii-1) *If* $d_1\lambda_1 < a_{11}$ *and* $0 < d_2 < \bar{d}_2$, *then* E^* *is locally asymptotically stable.*

 (ii-2) *If* $d_1\lambda_1 < a_{11}$ *and* $d_2 > \bar{d}_2$, *then* E^* *is unstable, and hence in the model* (3) *Turing instability occurs.*

Proof Consider the linearization operator of (3) at E^*

$$L = \begin{pmatrix} d_1\triangle + a_{11} & a_{12} \\ a_{21} & d_2\triangle + a_{22} \end{pmatrix}.$$

Suppose that $\Phi = (\varphi, \psi) \in L^2(\Omega) \times L^2(\Omega)$ is an eigenfunction of L corresponding to an eigenvalue η, then

$$\bigl(d_1\triangle\varphi + (a_{11} - \eta)\varphi + a_{12}\psi, d_2\triangle\psi + (a_{22} - \eta)\psi + a_{21}\varphi\bigr) = (0,0).$$

Writing $\varphi = \sum_{0 \le i \le \infty, 1 \le j \le m_i} a_{ij}\phi_{ij}$, $\psi = \sum_{0 \le i \le \infty, 1 \le j \le m_i} b_{ij}\phi_{ij}$, then

$$\sum_{0 \le i \le \infty, 1 \le j \le m_i} B_i \begin{pmatrix} a_{ij} \\ b_{ij} \end{pmatrix} \phi_{ij} = 0,$$

where

$$B_i = \begin{pmatrix} a_{11} - d_1\lambda_i - \eta & a_{12} \\ a_{21} & a_{22} - d_2\lambda_i - \eta \end{pmatrix}.$$

We easily see that η is the eigenvalue of L if and only if $\det B_i = 0$ for some i, which leads to

$$\eta^2 + Q_i\eta + P_i = 0, \tag{14}$$

where

$$Q_i = (d_1 + d_2)\lambda_i - a_{11} - a_{22},$$
$$P_i = \lambda_i(d_1\lambda_i - a_{11})\left(d_2 - \frac{d_1 a_{22}\lambda_i - a_{11}a_{22} + a_{12}a_{21}}{\lambda_i(d_1\lambda_i - a_{11})}\right).$$

(i) If $a_{11} < 0$, then $Q_i > 0$ and $P_i > 0$ for all i, which implies that $\mathrm{Re}\{\eta_i\} < 0$ for all i, where η_i are the eigenvalues of (14). Therefore, the equilibrium point E^* is locally asymptotically stable.

(ii) If $(\mathbf{H_{21}})$ and $mu^*v^* < (u^* + \delta sv^*)(bv^* + a + u^*)^2 + bsmu^*v^*$ hold, then $Q_i > 0$ and $d_1a_{22}\lambda_i - a_{11}a_{22} + a_{12}a_{21} < 0$.

(ii-1) If $a_{11} > 0$, $d_1\lambda_1 < a_{11}$ and $0 < d_2 < \bar{d}_2$, then $d_1\lambda_i < a_{11}$ and $d_2 < d_2^i$ for all $i \in [1, i_0]$. Thus,

$$P_i = \lambda_i(d_1\lambda_i - a_{11})\left\{d_2 - \frac{d_1a_{22}\lambda_i - a_{11}a_{22} + a_{12}a_{21}}{\lambda_i(d_1\lambda_i - a_{11})}\right\} > 0.$$

On the other hand, if $i > i_0$, then $d_1\lambda_i > a_{11}$, and $P_i > 0$. The analysis yields the locally asymptotical stability of E^*.

(ii-2) If $a_{11} > 0$, $d_1\lambda_1 < a_{11}$ and $d_2 > \bar{d}_2$, then we may assume the minimum in (13) is attained at $j \in [1, i_0]$. Thus $d_2 > d_2^j$, which implies

$$P_j = \lambda_j(d_1\lambda_j - a_{11})\left\{d_2 - \frac{d_1a_{22}\lambda_j - a_{11}a_{22} + a_{12}a_{21}}{\lambda_j(d_1\lambda_j - a_{11})}\right\} < 0.$$

Hence, E^* is unstable in this case. The proof of Theorem 2.3 is complete. □

Example 2 We take the parameters in model (2) and (3) as

$$a = 0.1, \qquad b = 0.2, \qquad m = 0.6, \qquad s = 2, \qquad q = 0.25, \qquad \delta = 0.1.$$

It is easy to verify that there is a unique positive equilibrium point $E^*(u^*, v^*) = (0.22, 0.56)$.

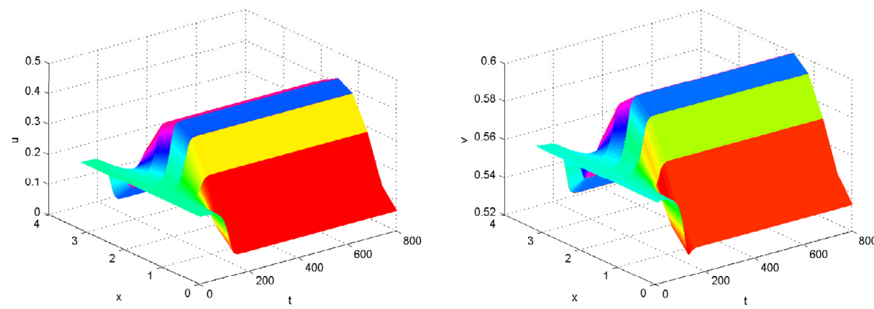
For the ODE model (2), from Theorem 2.2, we can verify that E^* is stable. For the PDE model (3) in one-dimensional interval $(0, \pi)$, after fixing $d_1 = 0.015$, from Theorem 2.3, we know that if $d_2 > \bar{d}_2 = 0.31$, then E^* is Turing unstable, and model (3) exhibits Turing pattern. In Fig. 1, we show the numerical results of model (3) with different values for d_2. Figure 1(a) shows the numerical simulations of Turing instability in model (3) with $d_2 = 0.75 > \bar{d}_2$. And Fig. 1(b) is for the numerical simulations of the stable positive equilibrium point of model (3) with $d_2 = 0.20 < \bar{d}_2$. From Fig. 2 we can observe the Turing patterns for the different values of d_2. One can see that the model exhibits pattern formation, including a cold spots pattern in Fig. 2(a) and a spot–stripe pattern in Fig. 2(b).

3 Nonexistence/existence of nonconstant positive steady state

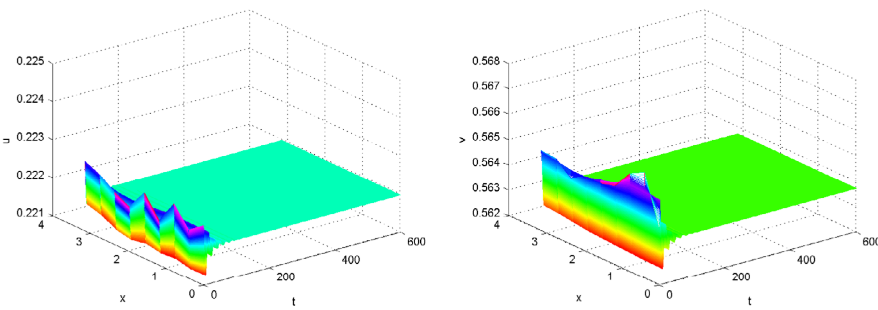
In this section, we consider the nonexistence/existence of nonconstant positive steady states of (4).

Let $N(\lambda_i)$ be the eigenspace corresponding to λ_i in $H^1(\Omega)$. Let $X = [H^1(\Omega)]^2$, $\{\phi_{ij}; j = 1, \ldots, \dim N(\lambda_i)\}$ be an orthonormal basis of $N(\lambda_i)$, and $X_{ij} = \{c\Phi_{ij} : c \in R^2\}$. Then we decompose X as

$$X = \bigoplus_{i=1}^{\infty} X_i, \qquad X_i = \bigoplus_{j=1}^{\dim N(\lambda_i)} X_{ij}.$$

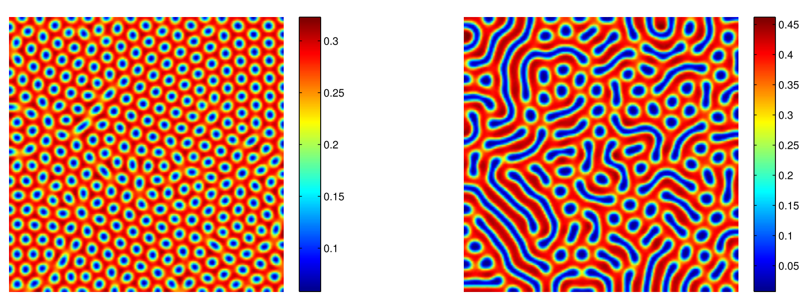


(a) Turing instability with $d_2 = 0.75$



(b) Stable behavior with $d_2 = 0.2$

Figure 1 Numerical simulations of the long time behavior of solution $(u(x,t), v(x,t))$ of model (3) with different values of d_2. (**a**) $d_2 = 0.75$; (**b**) $d_2 = 0.20$



(a) $d_2 = 0.35$ (b) $d_2 = 1$

Figure 2 Turing pattern with different values of d_2. (**a**) Cold spots pattern with $d_2 = 0.35$; (**b**) spot-stripe pattern with $d_2 = 1$

3.1 A priori estimates for positive steady states

In this subsection, by using the maximum principle, we establish a priori estimates of positive steady state for (4).

Lemma 3 (*Maximum principle* [23]) *Suppose that* $g \in C(\overline{\Omega} \times \mathbb{R})$.

(i) *Assume that* $w \in C^2(\Omega) \cap C^1(\overline{\Omega})$, *and*

$$\triangle w(x) + g\big(x, w(x)\big) \geq 0, \quad x \in \Omega, \qquad \frac{\partial w}{\partial \nu} \leq 0, \quad x \in \partial\Omega.$$

If $w(x_0) = \max_{\overline{\Omega}} w$, *then* $g(x_0, w(x_0)) \geq 0$.

(ii) *Assume that* $w \in C^2(\Omega) \cap C^1(\overline{\Omega})$, *and*

$$\triangle w(x) + g\big(x, w(x)\big) \leq 0, \quad x \in \Omega, \qquad \frac{\partial w}{\partial \nu} \geq 0, \quad x \in \partial\Omega.$$

If $w(x_0) = \min_{\overline{\Omega}} w$, *then* $g(x_0, w(x_0)) \leq 0$.

Theorem 3.1 *Assume* $m > (a+1)q$. *Let* $(u(x), v(x))$ *be a positive solution of* (4). *If*

$$a\delta(a+1) > \max\big\{m\big(m-(a+1)q\big), m^2 + aq - m\big\},$$

then $(u(x), v(x))$ *satisfies*

$$1 - \frac{m\alpha}{a} \leq u(x) \leq 1, \qquad \frac{1}{\delta}\left(\frac{m(a-m\alpha)}{a^2 + a + (a-m)\alpha} - q\right) \leq v(x) \leq \alpha,$$

where $\alpha = \frac{m-(a+1)q}{\delta(a+1)}$.

Proof A direct application of Lemma 3 to (4) yields $u(x) \leq 1$ and $v(x) \leq \alpha$. To obtain the lower bound for $u(x)$ and $v(x)$, we let

$$u(x_0) = \min_{\bar{\Omega}} u(x), \qquad v(y_0) = \min_{\bar{\Omega}} v(x), \qquad v(y_1) = \max_{\bar{\Omega}} v(x).$$

By virtue of Lemma 3, we have

$$1 - u(x_0) - \frac{m\alpha}{a} \leq 1 - u(x_0) - \frac{mv(x_0)}{a + u(x_0) + bv(x_0)} \leq 0.$$

Since $a\delta(a+1) > m(m-(a+1)q)$, $1 - \frac{m\alpha}{a} > 0$ and $u(x_0) \geq 1 - \frac{m\alpha}{a}$.

Notice that

$$-q - \delta v(y_0) + \frac{mu(x_0)}{a + u(x_0) + bv(y_1)} \leq -q - \delta v(y_0) + \frac{mu(x_0)}{a + u(x_0) + bv(y_0)} \leq 0,$$

we have $v(y_0) \geq \frac{1}{\delta}(\frac{m(a-m\alpha)}{a(a+1+\alpha)-m\alpha} - q)$. The proof is complete. □

3.2 Nonexistence of nonconstant positive steady state

In this subsection, we apply the energy method to prove the nonexistence of the nonconstant positive steady state to (4). For convenience, let $\Gamma = \Gamma(m, a, b, s, q, \delta)$ be the set of parameters m, a, b, s, q, and δ.

Theorem 3.2 *Assume* $m > q$. *Let* λ_1 *be the smallest positive eigenvalue of the operator* $-\triangle$ *on* Ω *with zero-flux boundary condition and* d_2^* *be a fixed positive constant satisfying* $d_2^* > \frac{s(m-q)}{\lambda_1}$. *Then there exists a positive* $d_1^* = d_1^*(\Gamma, d_2^*)$ *such that model* (4) *has no nonconstant positive steady state provided that* $d_1 \geq d_1^*$, $d_2 \geq d_2^*$.

Proof Let (u, v) be a positive solution of (4) and denote

$$\bar{u} = \frac{1}{|\Omega|}\int_\Omega u\,dx \quad \text{and} \quad \bar{v} = \frac{1}{|\Omega|}\int_\Omega v\,dx.$$

Then multiplying the first equation of model (4) by $(u-\bar{u})$, integrating over Ω and from Theorem 3.1, we have

$$\begin{aligned} d_1 \int_\Omega \left|\nabla(u-\bar{u})\right|^2 dx &= \int_\Omega (u-\bar{u})^2 \left(1-(u+\bar{u}) - \frac{m\bar{v}(a+bv)}{(a+u+bv)(a+\bar{u}+b\bar{v})}\right) dx \\ &\quad - \int_\Omega \frac{m\bar{u}(a+u)}{(a+u+bv)(a+\bar{u}+b\bar{v})}(u-\bar{u})(v-\bar{v})\, dx \\ &\le \int_\Omega (u-\bar{u})^2 + m\int_\Omega |u-\bar{u}||v-\bar{v}|\, dx, \end{aligned}$$

in a similar manner, multiplying the second equation in model (4) by $(v-\bar{v})$, we have

$$\begin{aligned} d_2 \int_\Omega \left|\nabla(v-\bar{v})\right|^2 dx &= \int_\Omega s(v-\bar{v})^2 \left(-q-\delta(v+\bar{v}) + \frac{m\bar{u}(a+u)}{(a+u+bv)(a+\bar{u}+b\bar{v})}\right) dx \\ &\quad + \int_\Omega \frac{m\bar{v}(a+bv)}{(a+u+bv)(a+\bar{u}+b\bar{v})}(u-\bar{u})(v-\bar{v})\, dx \\ &\le s(m-q)\int_\Omega (v-\bar{v})^2\, dx + \frac{m}{b}\int_\Omega |u-\bar{u}||v-\bar{v}|\, dx. \end{aligned}$$

It follows from the above and the ϵ-Young inequality that

$$\begin{aligned} & d_1 \int_\Omega \left|\nabla(u-\bar{u})\right|^2 dx + d_2 \int_\Omega \left|\nabla(v-\bar{v})\right|^2 dx \\ &\quad \le \int_\Omega \left((u-\bar{u})^2 + s(m-q)(v-\bar{v})^2\right) dx + 2L\int_\Omega |u-\bar{u}||v-\bar{v}|\, dx \\ &\quad \le \int_\Omega \left(\left(1+\frac{L}{\epsilon}\right)(u-\bar{u})^2 + \left(s(m-q)+\epsilon L\right)(v-\bar{v})^2\right) dx \end{aligned}$$

for $L := \frac{(b+1)m}{2b}$ and an arbitrary positive constant ϵ. It follows from the well-known Poincaré inequality that

$$\begin{aligned} & d_1 \int_\Omega \left|\nabla(u-\bar{u})\right|^2 dx + d_2 \int_\Omega \left|\nabla(v-\bar{v})\right|^2 dx \\ &\quad \le \frac{1}{\lambda_1}\left(\left(1+\frac{L}{\epsilon}\right)\int_\Omega \left|\nabla(u-\bar{u})\right|^2 dx + \left(s(m-q)+\epsilon L\right)\int_\Omega \left|\nabla(v-\bar{v})\right|^2 dx\right). \end{aligned}$$

Since $d_2^*\lambda_1 > s(m-q)$, from the assumption, we can choose a sufficiently small ϵ such that

$$d_2^*\lambda_1 \ge s(m-q) + \epsilon L.$$

Finally, by taking $d_1^* := \frac{1}{\lambda_1}(1+\frac{L}{\epsilon})$, one can conclude that $u=\bar{u}$ and $v=\bar{v}$, which asserts our results. □

3.3 Existence of nonconstant positive steady state

In this subsection, by using the Leray–Schauder degree theory, we discuss the existence of nonconstant positive steady state to (4) when the diffusion coefficients d_1 and d_2 vary while the parameters in Γ keep fixed.

For simplicity, define $F = (f, g)^\top$, where f and g are given in Sect. 2. Then the stationary problem of (4) can be written as

$$\begin{cases} -\triangle E = D^{-1}F(E), & x \in \Omega, \\ \frac{\partial E}{\partial \nu} = 0, & x \in \partial\Omega, \end{cases} \tag{15}$$

where $D = \operatorname{diag}(d_1, d_2)$. Therefore, E solves (15) if and only if it satisfies

$$\widehat{f}(d_1, d_2; E) := E - (I - \Delta)^{-1}\{D^{-1}F(E) + E\} = 0 \quad \text{on } X, \tag{16}$$

where $(I - \Delta)^{-1}$ represents the inverse of $I - \Delta$ with homogeneous Neumann boundary condition.

A straightforward computation reveals

$$D_E\widehat{f}(d_1, d_2; E^*) = I - (I - \Delta)^{-1}(D^{-1}J(E^*) + I).$$

For each X_i, λ is an eigenvalue of $D_E\widehat{f}(d_1, d_2; E^*)$ on X_i if and only if $\lambda(1 + \lambda_i)$ is an eigenvalue of the following matrix:

$$M_i := \lambda_i I - D^{-1}J(E^*) = \begin{pmatrix} \lambda_i - d_1^{-1}a_{11} & -d_1^{-1}a_{12} \\ -d_2^{-1}a_{21} & \lambda_i - d_2^{-1}a_{22} \end{pmatrix}.$$

Clearly,

$$\det M_i = d_1^{-1}d_2^{-1}\left[d_1d_2\lambda_i^2 - (d_1a_{22} + d_2a_{11})\lambda_i + a_{11}a_{22} - a_{12}a_{21}\right],$$

and $\operatorname{tr} M_i = 2\lambda_i - d_1^{-1}a_{11} - d_2^{-1}a_{22}$. Define

$$\widehat{g}(d_1, d_2; \lambda) = d_1d_2\lambda^2 - (d_1a_{22} + d_2a_{11})\lambda + a_{11}a_{22} - a_{12}a_{21}.$$

Then $\widehat{g}(d_1, d_2; \lambda) = d_1d_2 \det M_i$. If

$$|d_1a_{22} + d_2a_{11}| > 2\sqrt{d_1d_2(a_{11}a_{22} - a_{12}a_{21})}, \tag{17}$$

then $\widehat{g}(d_1, d_2; \lambda) = 0$ has two real roots:

$$\lambda_- = \frac{d_2a_{11} + d_1a_{22} - \sqrt{(d_2a_{11} + d_1a_{22})^2 - 4d_1d_2(a_{11}a_{22} - a_{12}a_{21})}}{2d_1d_2},$$
$$\lambda_+ = \frac{d_2a_{11} + d_1a_{22} + \sqrt{(d_2a_{11} + d_1a_{22})^2 - 4d_1d_2(a_{11}a_{22} - a_{12}a_{21})}}{2d_1d_2}.$$

Set

$$A = A(d_1, d_2) = \{\lambda : \lambda \geq 0, \lambda_-(d_1, d_2) < \lambda < \lambda_+(d_1, d_2)\},$$
$$S_p = \{\lambda_0, \lambda_1, \lambda_2, \ldots\},$$

and let $m(\lambda_i)$ be multiplicity of λ_i. In order to calculate the index of $\widehat{f}(d_1, d_2; \cdot)$ at E^*, we need the following lemma.

Lemma 4 ([24]) *Suppose* $\widehat{g}(d_1,d_2;\lambda_i) \neq 0$ *for all* $\lambda_i \in S_p$. *Then*

$$\operatorname{index}\big(\widehat{f}(d_1,d_2;\cdot),E^*\big) = (-1)^{\sigma},$$

where

$$\sigma = \begin{cases} \sum_{\lambda_i\in A\cap S_p} m(\lambda_i), & \text{if } A\cap S_p \neq \varnothing, \\ 0, & \text{if } A\cap S_p = \varnothing. \end{cases}$$

In particular, if $\widehat{g}(d_1,d_2;\lambda_i) > 0$ *for all* $\lambda_i \geq 0$, *then* $\sigma = 0$.

By determining the range of λ for which $\widehat{g}(d_1,d_2;\lambda) < 0$, we have the existence of nonconstant steady state to (4).

Theorem 3.3 *Let* d_1, Γ *be fixed and* $(\mathbf{H_1})$, $(\mathbf{H_{21}})$, $a_{11} > 0$ *hold. If* $\frac{a_{11}}{d_1} \in (\lambda_k,\lambda_{k+1})$ *for some* $k \geq 1$, *and* $\sigma_k = \sum_{i=1}^{k} m(\lambda_i)$ *is odd, then there exists a positive constant* d^* *such that model* (4) *has at least one nonconstant positive steady state for all* $d_2 \geq d^*$.

Proof Notice that if d_2 is large enough, then (17) and $\lambda_+(d_1,d_2) > \lambda_-(d_1,d_2) > 0$ hold. Furthermore,

$$\lim_{d_2\to\infty} \lambda_+(d_1,d_2) = \frac{a_{11}}{d_1}, \qquad \lim_{d_2\to\infty} \lambda_-(d_1,d_2) = 0.$$

As $\frac{a_{11}}{d_1} \in (\lambda_k,\lambda_{k+1})$, there exists $d_0 \gg 1$ such that

$$\lambda_+(d_1,d_2) \in (\lambda_k,\lambda_{k+1}), \qquad 0 < \lambda_-(d_1,d_2) < \lambda_1 \quad \text{for all } d_2 \geq d_0. \tag{18}$$

From Theorem 3.2, we know that there exists $\tilde{d} > d_0$ such that (4) with $d_1 = \tilde{d}$ and $d_2 \geq \tilde{d}$ has no nonconstant positive steady state. Let $\tilde{d} > 0$ be large enough such that $\frac{a_{11}}{d_1} < \lambda_1$. Then there exists $d^* > \tilde{d}$ such that

$$0 < \lambda_-(d_1,d_2) < \lambda_+(d_1,d_2) < \lambda_1 \quad \text{for all } d_2 \geq d^*. \tag{19}$$

Now we prove that, for any $d_2 \geq d^*$, (4) has at least one nonconstant positive steady state. By way of contradiction, assume that the assertion is not true for some $d_2^* \geq d^*$. By using the homotopy argument, we can derive a contradiction in the sequel.

Fixing $d_2 = d_2^*$, for $t \in [0,1]$, we define

$$D(t) = \begin{pmatrix} td_1 + (1-t)\tilde{d} & 0 \\ 0 & td_2 + (1-t)d^* \end{pmatrix},$$

and consider the following problem:

$$\begin{cases} -\triangle E = D^{-1}(t)F(E), & x \in \Omega, \\ \frac{\partial E}{\partial \nu} = 0, & x \in \partial\Omega. \end{cases} \tag{20}$$

Notice that E is a nonconstant positive steady state of (4) if and only if it solves (20) with $t = 1$. Evidently, E^* is the unique constant positive steady state of (20). For any $t \in [0,1]$, E is a nonconstant positive steady state of (20) if and only if it is a solution of the following problem:

$$h(E;t) = E - (I - \Delta)^{-1}\left\{D^{-1}(t)F(E) + E\right\} = 0 \quad \text{on } X. \tag{21}$$

Form the above discussion, we know that (21) has no nonconstant positive steady state when $t = 0$, and there is no such solution for $t = 1$ at $d_2 = d_2^*$. Clearly, $h(E;1) = \widehat{f}(d_1, d_2; E)$, $h(E;0) = \widehat{f}(\tilde{d}, d^*; E)$ and

$$D_E\widehat{f}\left(d_1, d_2; E^*\right) = I - (I - \Delta)^{-1}\left(D^{-1}J\left(E^*\right) + I\right),$$
$$D_E\widehat{f}\left(\tilde{d}, d^*; E^*\right) = I - (I - \Delta)^{-1}\left(\widetilde{D}^{-1}J\left(E^*\right) + I\right).$$

Here, $\widehat{f}(\cdot,\cdot;\cdot)$ is as given in (16) and $\widetilde{D} = \operatorname{diag}(\tilde{d}, d^*)$. Form (18) and (19), we have $A(d_1, d_2) \cap S_p = \{\lambda_1, \lambda_2, \ldots, \lambda_k\}$ and $A(\tilde{d}, d^*) \cap S_p = \varnothing$. Since σ_k is odd, Lemma 4 yields

$$h\left((\cdot;1), E^*\right) = \left(\widehat{f}(d_1, d_2; \cdot), E^*\right) = (-1)^{\sigma_k} = -1,$$
$$h\left((\cdot;0), E^*\right) = \left(\widehat{f}\left(\tilde{d}, d^*; \cdot\right), E^*\right) = (-1)^0 = 1.$$

From Theorem 3.2, there exist positive constants $\underline{C} = \underline{C}(\tilde{d}, d_1, d^*, d_2^*, \Gamma)$ and $\overline{C} = \overline{C}(\tilde{d}, d^*, \Gamma)$ such that the positive solutions of (21) satisfy $\underline{C} < u(x), v(x) < \overline{C}$ on $\overline{\Omega}$ for all $t \in [0,1]$.

Define $\Sigma = \{E \in X : \underline{C} < u(x), v(x) < \overline{C}, x \in \overline{\Omega}\}$. Then $h(E;t) \neq 0$ for all $E \in \partial\Sigma$ and $t \in [0,1]$. By virtue of the homotopy invariance of the Leray–Schauder degree, we have

$$\deg\left(h(\cdot;0), \Sigma, 0\right) = \deg\left(h(\cdot;1), \Sigma, 0\right). \tag{22}$$

Note that both equations $h(E;0) = 0$ and $h(E;1) = 1$ have the unique positive solution E^* in Σ, and we obtain

$$\deg\left(h(\cdot;0), \Sigma, 0\right) = \left(h(\cdot;0), E^*\right) = 1,$$
$$\deg\left(h(\cdot;1), \Sigma, 0\right) = \left(h(\cdot;1), E^*\right) = -1,$$

which contradicts (22). The proof is complete. □

4 Structure of nonconstant positive steady state

Let $Y = C(\bar{\Omega}) \times C(\bar{\Omega})$, $X = \{(u,v) | u, v \in C^2(\bar{\Omega}), \frac{\partial u}{\partial \nu} = \frac{\partial v}{\partial \nu} = 0, x \in \partial\Omega\}$.

4.1 Local structure and direction of nonconstant positive steady state

In this subsection, we first study the local structure of nonconstant positive steady state for model (4). In brief, by regarding d_2 as the bifurcation parameter, we verify the existence of positive steady state bifurcating from (d_2, E^*). The Crandall–Rabinowitz bifurcation theorem in [25] will be applied to obtain bifurcations.

Define the map $F : (0,\infty) \times X \to Y$ by

$$F(d_2, E) = (d_1 \triangle u + f, d_2 \triangle v + g)^\top, \quad E = (u, v),$$

where f, g are given in Sect. 2. Then the solutions of boundary value problem (4) are exactly zeros of F. With $E^* = (u^*, v^*)$, we have

$$F(d_2, E^*) = 0, \quad \text{for all } d_2 > 0.$$

If there is a number $d_2 > 0$ such that every neighborhood of (d_2, E^*) contains zero of F in $(0, \infty) \times X$ not lying on the curve (d_2, E^*), then we say that (d_2, E^*) is a bifurcation point of the equation $F = 0$ with respect to this curve.

Theorem 4.1 *Let* $(\mathbf{H_1})$, $(\mathbf{H_{21}})$ *and* $a_{11} > 0$ *hold. Suppose that* j *is a positive integer such that* $d_1\lambda_j < a_{11}$ *and* $d_2^k \neq d_2^j > 0$ *for any integer* $k \neq j$. *Then* (d_2^j, E^*) *is a bifurcation point of* $F(d_2, E) = 0$ *with respect to the curve* (d_2, E^*). *There is a one-parameter family of non-trivial solution* $\Gamma_j(s) = (d_2(s), u(s), v(s))$ *of the problem* (4) *for* $|s|$ *sufficiently small, where* $d_2(s)$, $u(s)$, $v(s)$ *are continuous functions,* $d_2(0) = d_2^j$ *and*

$$u(s) = u^* + s\phi_j + o(s), \qquad v(s) = v^* + sb_j\phi_j + o(s), \qquad b_j = \frac{(d_1\lambda_j - a_{11})}{a_{12}} > 0.$$

The zero set of F *consists of two curves* (d_2, E^*) *and* $\Gamma_j(s)$ *in a neighborhood of the bifurcation point* (d_2^j, E^*).

Proof It suffices to verify conditions (a)–(c) as follows [25]:

(a) The partial derivatives F_{d_2}, F_E, and F_{d_2E} exist and are continuous.

(b) $\ker F_E(d_2^j, E^*)$ and $Y/R(F_E(d_2^j, E^*))$ are one-dimensional.

(c) Let $\ker F_E(d_2^j, E^*) = \operatorname{span}\{\Phi\}$, then $F_{d_2E}(d_2^j, E^*)\Phi \notin R(F_E(d_2^j, E^*))$.

Note that

$$L_1 = F_E(d_2^j, E^*) = \begin{pmatrix} d_1\Delta + a_{11} & a_{12} \\ a_{21} & d_2^j\Delta + a_{22} \end{pmatrix},$$

where a_{11}, a_{12}, a_{21} and a_{22} are given in (8). It is clear that the linear operators F_E, F_{d_2E} and F_{d_2} are continuous, and condition (a) is verified.

Suppose $\Phi = (\bar{\varphi}, \bar{\psi})^\top \in \ker L_1$, and write $\bar{\varphi} = \sum_{0\le i\le\infty, 1\le j\le m_i} \bar{a}_{ij}\phi_{ij}$, $\bar{\psi} = \sum_{0\le i\le\infty, 1\le j\le m_i} \bar{b}_{ij} \times \phi_{ij}$. Then

$$\sum_{0\le i<\infty, 1\le j\le m_i} \bar{B}_i \begin{pmatrix} \bar{a}_{ij} \\ \bar{b}_{ij} \end{pmatrix} \phi_{ij} = 0,$$

where

$$\bar{B}_i = \begin{pmatrix} a_{11} - d_1\lambda_i & a_{12} \\ a_{21} & a_{22} - d_2^j\lambda_i \end{pmatrix}. \tag{23}$$

Since

$$\det \bar{B}_i = 0 \quad \Leftrightarrow \quad d_2^j = d_2^i(E^*) = \frac{d_1 a_{22}\lambda_i - a_{11}a_{22} + a_{12}a_{21}}{\lambda_i(d_1\lambda_i - a_{11})},$$

taking $d_2 = d_2^j$ implies that $\ker L_1 = \operatorname{span}\{\Phi_1\}$, where

$$\Phi_1 = (1, b_j)^\top \phi_j, \quad b_j = \frac{d_1\lambda_j - a_{11}}{a_{12}} > 0,$$

ϕ_j is the eigenfunction of $-\triangle$. Consider the adjoint operator

$$L_1^* = \begin{pmatrix} d_1\Delta + a_{11} & a_{21} \\ a_{12} & d_2^j\Delta + a_{22} \end{pmatrix}.$$

In the same way as above we obtain $\ker L_1^* = \operatorname{span}\{\Phi_1^*\}$, where

$$\Phi_1^* = \left(1, b_j^*\right)^\top \phi_j, \quad b_j^* = \frac{d_1\lambda_j - a_{11}}{a_{21}} < 0.$$

By the Fredholm alternative theorem, we have $R(L_1) = \ker(L_1^*)^\perp$, thus

$$\operatorname{codim}\bigl(R(L_1)\bigr) = \dim\bigl(\ker\bigl(L_1^*\bigr)\bigr) = 1.$$

Condition (b) is also verified.

Finally, since

$$F_{d_2E}\bigl(d_2^j, E^*\bigr)\Phi_1 = \begin{pmatrix} 0 & 0 \\ 0 & \Delta \end{pmatrix}\Phi_1 = \begin{pmatrix} 0 \\ -\lambda_j b_j \phi_j \end{pmatrix}$$

and

$$\bigl\langle F_{d_2E}\bigl(d_2^j, E^*\bigr)\Phi_1, \Phi_1^*\bigr\rangle_Y = \bigl\langle -\lambda_j b_j \phi_j, b_j^*\phi_j\bigr\rangle_{L^2} = -\lambda_j b_j b_j^* > 0,$$

we find $F_{d_2E}(d_2^j, E^*)\Phi_1 \notin R(L_1)$, and so condition (c) is satisfied. The proof is completed. □

We investigate the direction of the steady state bifurcation of model (4) in the one-dimensional interval $\Omega = (0,\pi)$. It is well known that the operator $-\triangle$ with no-flux boundary conditions has eigenvalues and eigenfunctions as follows:

$$\lambda_0 = 0, \qquad \phi_0(x) = \sqrt{\frac{1}{\pi}}; \qquad \lambda_j = j^2, \qquad \phi_j(x) = \sqrt{\frac{2}{\pi}}\cos jx$$

for $j = 1, 2, 3, \ldots$. We translate (u^*, v^*) to the origin by the translation $(\bar{u}, \bar{v}) = (u - u^*, v - v^*)$. For convenience, we will denote $\bar{u}$, $\bar{v}$ by u, v, respectively. Then we can obtain the following system:

$$\begin{cases} -d_1u'' = (u + u^*) - (u + u^*)^2 - \frac{m(u+u^*)(v+v^*)}{a+(u+u^*)+b(v+v^*)}, & x \in (0,\pi), \\ -d_2v'' = s(v + v^*)(-q - \delta(v + v^*) + \frac{m(u+u^*)(v+v^*)}{a+(u+u^*)+b(v+v^*)}), & x \in (0,\pi). \end{cases} \tag{24}$$

Let

$$H = \bigl(u + u^*\bigr) - \bigl(u + u^*\bigr)^2 - \frac{m(u + u^*)(v + v^*)}{a + (u + u^*) + b(v + v^*)},$$

$$G = s\bigl(v + v^*\bigr)\left(-q - \delta\bigl(v + v^*\bigr) + \frac{m(u + u^*)(v + v^*)}{a + (u + u^*) + b(v + v^*)}\right).$$

Then a straightforward calculation yields

$$
\begin{aligned}
&H_u(0,0) = 1 - 2u^* - \frac{mv^*(bv^*+a)}{(bv^*+a+u^*)^2}, \qquad G_u(0,0) = \frac{smv^*(bv^*+a)}{(bv^*+a+u^*)^2},\\
&H_v(0,0) = -\frac{mv^*(bv^*+a)}{(bv^*+a+u^*)^2}, \qquad G_v(0,0) = sv\left(-\delta - \frac{mbu^*}{(bv^*+a+u^*)^2}\right),\\
&H_{uu}(0,0) = -2 + \frac{2mv^*(bv^*+a)}{(bv^*+a+u^*)^3}, \qquad G_{uu}(0,0) = -\frac{2smv^*(bv^*+a)}{(bv^*+a+u^*)^3},\\
&H_{uv}(0,0) = -\frac{m(a^2+(bv^*+u^*)a+2bu^*v^*)}{(bv^*+a+u^*)^3},\\
&G_{uv}(0,0) = \frac{sm(abv^*+2bu^*v^*+a^2+au^*)}{(bv^*+a+u^*)^3},\\
&H_{vv}(0,0) = \frac{2mbu^*(a+u^*)}{(bv^*+a+u^*)^3}, \qquad G_{vv}(0,0) = -\frac{2s((bv^*+a+u^*)^3\delta + mbu^*(a+u^*))}{(bv^*+a+u^*)^3},\\
&H_{uuu}(0,0) = -\frac{6mv^*(bv^*+a)}{(bv^*+a+u^*)^4}, \qquad G_{uuu}(0,0) = \frac{6smv^*(bv^*+a)}{(bv^*+a+u^*)^4},\\
&H_{uuv}(0,0) = \frac{2m(-b^2v^{*2}+2bu^*v^*+a^2+au^*)}{(bv^*+a+u^*)^4},\\
&G_{uuv}(0,0) = -\frac{2sm(-b^2v^{*2}+2bu^*v^*+a^2+au^*)}{(bv^*+a+u^*)^4},\\
&H_{uvv}(0,0) = \frac{2mb(abv^*+2bu^*v^*+a^2-u^{*2})}{(bv^*+a+u^*)^4},\\
&G_{uvv}(0,0) = -\frac{2smb(abv^*+2bu^*v^*+a^2-u^{*2})}{(bv^*+a+u^*)^4},\\
&H_{vvv}(0,0) = -\frac{6mb^2u^*(a+u^*)}{(bv^*+a+u^*)^4}, \qquad G_{vvv}(0,0) = \frac{6smb^2u^*(a+u^*)}{(bv^*+a+u^*)^4}.
\end{aligned}
$$

Denote $E = (u,v)$, then we rewrite the map $F : \mathbb{R}^+ \times X \to Y$ by

$$
F(d_2,E) = \begin{pmatrix} d_1u'' + H(u,v) \\ d_2v'' + G(u,v) \end{pmatrix}.
$$

By Theorem 4.1, we see that $\dim\ker F_E(d_2^j,(0,0)) = \operatorname{codim} R(F_E(d_2^j,(0,0))) = 1$ and $\ker F_E(d_2^j,(0,0)) = \operatorname{span}\{\Phi_1\}$. Hence, we can decompose X and Y as

$$
X = \ker F_E\big(d_2^j,(0,0)\big) \oplus Z \quad \text{and} \quad Y = R\big(F_E\big(d_2^j,(0,0)\big)\big) \oplus Z',
$$

where Z is the complement of $\ker F_E(d_2^j,(0,0))$ in X and Z' is the complement of $R(F_E(d_2^j,(0,0)))$ in Y. Due to $\operatorname{codim} R(F_E(d_2^j,(0,0))) = 1$, there exists $T \in Y^*$ such that

$$
R\big(F_E\big(d_2^j,(0,0)\big)\big) = \big\{(\xi,\zeta) \in Y : \big\langle T,(\xi,\zeta)\big\rangle = 0\big\},
$$

where $Y^* := \operatorname{span}\{\Phi_1^*\}$. Moreover, Φ_1^* satisfies $F_E(d_2^j,(0,0))\Phi_1^* = 0$ by Theorem 4.1. Hence, we can define

$$
\big\langle T,(\xi,\zeta)\big\rangle = \big\langle \Phi_1^*,(\xi,\zeta)\big\rangle = \int_\Omega \xi\phi_j\,dx + \int_\Omega b_j^*\zeta\phi_j\,dx.
$$

By $F_{d_2E}(d_2^j,(0,0))\Phi_1 \notin R(F_E(d_2^j,(0,0)))$ derived in Theorem 4.1, we find that

$$\langle F_{d_2E}(d_2^j,(0,0))\Phi_1,\Phi_1^*\rangle \neq 0.$$

From [26], we can know that

$$d_2'(0) = -\frac{\langle F_{EE}(d_2^j,(0,0))\Phi_1^2,\Phi_1^*\rangle}{2\langle F_{d_2E}(d_2^j,(0,0))\Phi_1,\Phi_1^*\rangle}.$$

By some calculations, we have

$$\langle F_{EE}(d_2^j,(0,0))\Phi_1^2,\Phi_1^*\rangle = (g_j + h_j b_j^*)\int_0^\pi \phi_j^3\,dx = 0$$

and

$$\langle F_{d_2E}(d_2^j,(0,0))\Phi_1,\Phi_1^*\rangle = \int_0^\pi b_j^*\phi_j(b_j\phi_j)''\,dx = -j^2 b_j b_j^*,$$

where

$$g_j = H_{uu}(0,0) + 2H_{uv}(0,0)b_j + H_{vv}(0,0)b_j^2,$$
$$h_j = G_{uu}(0,0) + 2G_{uv}(0,0)b_j + G_{vv}(0,0)b_j^2.$$

Hence, $d_2'(0) = 0$.

Note that $\langle F_{EE}(d_2^j,(0,0))\Phi_1^2,\Phi_1^*\rangle = 0$ implies

$$F_{EE}(d_2^j,(0,0))\Phi_1^2 \in R(F_E(d_2^j,(0,0))).$$

From [26], we see that the bifurcation is supercritical (resp. subcritical) if

$$d''(0) = -\frac{\langle F_{EEE}(d_2^j,(0,0))\Phi_1^3,\Phi_1^*\rangle + 3\langle F_{EE}(d_2^j,(0,0))\Phi_1\theta,\Phi_1^*\rangle}{3\langle F_{d_2E}(d_2^j,(0,0))\Phi_1,\Phi_1^*\rangle} > 0 \quad (\text{resp. } < 0),$$

where θ is the solution of the following problem:

$$F_{EE}(d_2^j,(0,0))\Phi_1^2 + F_E(d_2^j,(0,0))\theta = 0.$$

Let $\theta = (\theta_1,\theta_2)$. Then θ satisfies

$$\begin{cases} d_1\theta_1'' + H_u(0,0)\theta_1 + H_v(0,0)\theta_2 = -g_j\phi_j^2, \\ d_2^j\theta_2'' + G_u(0,0)\theta_1 + G_v(0,0)\theta_2 = -h_j\phi_j^2, \\ \theta_i'(0,t) = \theta_i'(\pi,t) = 0, \quad i = 1,2. \end{cases} \tag{25}$$

By direct calculation, we obtain

$$\langle F_{EEE}(d_2^j,(0,0))\Phi_1^3,\Phi_1^*\rangle = (m_j + n_j b_j^*)\int_0^\pi \phi_j^4\,dx = \frac{3}{2\pi}(m_j + n_j b_j^*),$$

where

$$m_j = H_{uuu}(0,0) + 3b_j H_{uuv}(0,0) + 3b_j^2 H_{uvv}(0,0) + b_j^3 H_{vvv}(0,0),$$
$$n_j = G_{uuu}(0,0) + 3b_j G_{uuv}(0,0) + 3b_j^2 G_{uvv}(0,0) + b_j^3 G_{vvv}(0,0),$$

and b_j, b_j^* are given in Sect. 4.1. Hence,

$$\begin{aligned}
&\bigl\langle F_{EEE}\bigl(d_2^j,(0,0)\bigr)\Phi_1^3, \Phi_1^*\bigr\rangle \\
&\quad = \frac{3}{2\pi}\bigl(3b_j\bigl[b_j^* G_{uuv}(0,0) + H_{uuv}(0,0)\bigr] + 3b_j^2\bigl[H_{uvv}(0,0) + b_j^* G_{uvv}(0,0)\bigr] \\
&\qquad + b_j^3\bigl[H_{vvv}(0,0) + b_j^* G_{vvv}(0,0)\bigr] + b_j^* G_{uuu}(0,0) + H_{uuu}(0,0)\bigr)
\end{aligned}$$

and

$$\bigl\langle F_{EE}(d_2^j,(0,0)\Phi_1\theta, \Phi_1^*\bigr\rangle = C_1\int_0^\pi \theta_1\phi_j^2\,dx + C_2\int_0^\pi \theta_2\phi_j^2\,dx,$$

where

$$C_1 = H_{uu}(0,0) + b_j H_{uv}(0,0) + b_j^* G_{uu}(0,0) + b_j b_j^* G_{uv}(0,0),$$
$$C_2 = H_{uv}(0,0) + b_j H_{vv}(0,0) + b_j^* G_{uv}(0,0) + b_j b_j^* G_{vv}(0,0).$$

We now compute

$$\int_0^\pi \theta_1\phi_j^2\,dx \quad\text{and}\quad \int_0^\pi \theta_2\phi_j^2\,dx.$$

Multiplying (25) by ϕ_j^2 and integrating by parts, we derive

$$\begin{cases} d_1\int_0^\pi \phi_j^2\theta_1''\,dx + H_u(0,0)\int_0^\pi \phi_j^2\theta_1\,dx + H_v(0,0)\int_0^\pi \phi_j^2\theta_2\,dx = -g_j\int_0^\pi \phi_j^4\,dx, \\ d_2^j\int_0^\pi \phi_j^2\theta_2''\,dx + G_u(0,0)\int_0^\pi \phi_j^2\theta_1\,dx + G_v(0,0)\int_0^\pi \phi_j^2\theta_2\,dx = -h_j\int_0^\pi \phi_j^4\,dx, \end{cases} \tag{26}$$

where

$$\int_0^\pi \phi_j^2\theta_i''\,dx = \frac{4}{\pi}j^2\int_0^\pi \theta_i\bigl(1-2\cos^2 jx\bigr)\,dx, \quad i=1,2.$$

Integrating (25) by parts yields

$$\gamma_1 := \int_0^\pi \theta_1\,dx = \frac{(h_j H_v(0,0) - g_j G_v(0,0))}{(H_u(0,0)G_v(0,0) - H_v(0,0)G_u(0,0))},$$
$$\gamma_2 := \int_0^\pi \theta_2\,dx = \frac{(g_j G_u(0,0) - h_j H_u(0,0))}{(H_u(0,0)G_v(0,0) - H_v(0,0)G_u(0,0))}.$$

It follows from (26) that

$$\begin{cases} (H_u(0,0) - 4d_1 j^2)\int_0^\pi \phi_j^2\theta_1\,dx + H_v(0,0)\int_0^\pi \phi_j^2\theta_2\,dx = -\frac{3g_j}{2\pi} - \frac{4}{\pi}d_1\gamma_1 j^2, \\ (G_v(0,0) - 4d_2^j j^2)\int_0^\pi \phi_j^2\theta_2\,dx + G_u(0,0)\int_0^\pi \phi_j^2\theta_1\,dx = -\frac{3h_j}{2\pi} - \frac{4}{\pi}d_2^j\gamma_2 j^2. \end{cases}$$

Thus,

$$L_1 := \int_0^\pi \theta_1 \phi_j^2\,dx = \frac{A_1}{B}, \qquad L_2 := \int_0^\pi \theta_2 \phi_j^2\,dx = \frac{A_2}{B},$$

where

$$\begin{aligned} A_1 &:= \left(-\frac{3}{2\pi} g_j - \frac{4}{\pi} d_1 \gamma_1 j^2\right)\left(G_v(0,0) - 4d_2^j j^2\right) + H_v(0,0)\left(\frac{3}{2\pi} h_j + \frac{4}{\pi} d_2^j \gamma_2 j^2\right), \\ A_2 &:= \left(-\frac{3}{2\pi} h_j - \frac{4}{\pi} d_2^j \gamma_2 j^2\right)\left(H_u(0,0) - 4d_1 j^2\right) + G_u(0,0)\left(\frac{3}{2\pi} g_j + \frac{4}{\pi} d_1 \gamma_1 j^2\right), \\ B &:= \left(H_u(0,0) - 4d_1 j^2\right)\left(G_v(0,0) - 4d_2^j j^2\right) - H_v(0,0) G_u(0,0). \end{aligned}$$

Consequently, we have

$$d_2''(0) = \frac{C}{2\pi j^2 b_j b_j^*}, \tag{27}$$

where

$$\begin{aligned} C &:= 3b_j\left[b_j^* G_{uuv}(0,0) + H_{uuv}(0,0)\right] + 3b_j^2\left[H_{uvv}(0,0) + b_j^* G_{uvv}(0,0)\right] \\ &\quad + b_j^3\left[H_{vvv}(0,0) + b_j^* G_{vvv}(0,0)\right] + b_j^* G_{uuu}(0,0) + H_{uuu}(0,0) + 2\pi(C_1 L_1 + C_2 L_2). \end{aligned}$$

From the analysis above, we obtain the following results.

Theorem 4.2 *Under the same hypothesis as Theorem 4.1, there exists a smooth bifurcation branch from* $(d_2^j, (0,0))$. *Furthermore, the bifurcation is supercritical (resp. subcritical) provided that* $d_2''(0) > 0$ (< 0), *where* $d_2''(0)$ *is given by* (27).

4.2 Global structure of nonconstant positive steady state

Theorem 4.1 provides no information of the bifurcating curve Γ_j far from the equilibrium point. A further study is therefore necessary in order to understand its global bifurcation. In the one-dimensional interval $\Omega = (0,\pi)$, by using the global bifurcation theory of Rabinowitz and the Leray–Schauder degree for compact operates, we prove that Γ_j is unbounded.

Theorem 4.3 *Under the same hypothesis as Theorem 4.1, the projection of the bifurcation curve* Γ_j *on the* d_2*-axis contains* (d_2^j, ∞).

If $d_2 > \bar{d}_2$ *and* $d_2 \neq d_2^k$ *for any integer* $k > 0$, *then the problem* (4) *possesses at least one nonconstant positive steady state.*

Proof Let $\tilde{u} = u - u^*$, $\tilde{v} = v - v^*$. Then (4) is transformed into

$$\begin{cases} -d_1 \tilde{u}'' = a_{11}\tilde{u} + a_{12}\tilde{v} + h_1(\tilde{u},\tilde{v}), \\ -d_2 \tilde{v}'' = a_{21}\tilde{u} + a_{22}\tilde{v} + h_2(\tilde{v},\tilde{v}), \end{cases} \tag{28}$$

where $h_1(\tilde{u},\tilde{v})$, $h_2(\tilde{u},\tilde{v})$ are higher-order terms of $\tilde{u}$ and $\tilde{v}$. The equilibrium point (u^*,v^*) of (4) shifts to $(0,0)$ of this new system. Let

$$G_1 = \left(-d_1\frac{\partial^2}{\partial x^2} + a_{11}\right)^{-1}, \qquad G_2 = \left(-d_2\frac{\partial^2}{\partial x^2} - a_{22}\right)^{-1}.$$

Then (28) is transformed into

$$\tilde{u} = G_1(2a_{11}\tilde{u}) + G_1(a_{12}\tilde{v}) + G_1\big(h_1(\tilde{u},\tilde{v})\big), \qquad \tilde{v} = G_2(a_{21}\tilde{v}) + G_2\big(h_2(\tilde{u},\tilde{v})\big).$$

Put $\tilde{E} = (\tilde{u},\tilde{v})$, $K(d_2)\tilde{E} = (2a_{11}G_1(\tilde{u}) + a_{12}G_1(\tilde{v}), a_{21}G_2(\tilde{u}))$ and

$$H(\tilde{E}) = \big(G_1\big(h_1(\tilde{u},\tilde{v})\big), G_2\big(h_2(\tilde{u},\tilde{v})\big)\big).$$

Recall that

$$U = \big\{(u,v) : u,v \in C^2\big([0,\pi]\big), u' = v' = 0 \text{ at } x = 0,\pi\big\}.$$

Then the boundary value problem (4) can be interpreted as the equation

$$\tilde{E} = K(d_2)\tilde{E} + H(\tilde{E}) \quad \text{in } E. \tag{29}$$

Note that $K(d_2)$ is a compact linear operator on U for any given $d_2 > 0$ and $H(\tilde{E}) = o(|\tilde{E}|)$ for $\tilde{E}$ near zero uniformly on closed d_2 sub-intervals of $(0,\infty)$, and $H(\tilde{E})$ is a compact operator on U as well.

In order to apply Rabinowitz's global bifurcation theorem, we first verify that 1 is an eigenvalue of $K(d_2^j)$ of algebraic multiplicity one. From the argument in the proof of Theorem 4.1 it is seen that $\ker(K(d_2^j) - I) = \ker L_1 = \operatorname{span}\{\Phi_1\}$, so 1 is indeed an eigenvalue of $K = K(d_2^j)$, and $\dim\ker(K - I) = 1$. As the algebraic multiplicity of the eigenvalue 1 is the dimension of the generalized null space $\bigcup_{i=1}^{\infty}\ker(K - I)^i$, we need to verify that $\ker(K - I) = \ker(K - I)^2$, or $\ker(K - I) \cap R(K - I) = 0$.

We now compute $\ker(K^* - I)$ following the calculation in [27], where K^* is the adjoint of K. Let $(\hat{\varphi},\hat{\psi}) \in \ker(K^* - I)$. Then

$$2a_{11}G_1(\hat{\varphi}) + a_{21}G_2(\hat{\psi}) = \hat{\varphi}, \qquad a_{12}G_1(\hat{\varphi}) = \hat{\psi}.$$

By the definition of G_1 and G_2 we obtain

$$-d_2^j a_{12}\hat{\varphi}'' = f_{\hat{\varphi}}\hat{\varphi} + f_{\hat{\psi}}\hat{\psi}, \qquad -d_1\hat{\psi}'' = a_{12}\hat{\varphi} - a_{11}\hat{\psi},$$

where

$$f_{\hat{\varphi}} = \frac{2d_2^j a_{11}a_{12}}{d_1} + a_{12}a_{22}, \qquad f_{\hat{\psi}} = a_{12}a_{21} - 2\left(a_{11}a_{22} + \frac{d_2^j a_{11}^2}{d_1}\right).$$

Write $\hat{\varphi} = \sum_{0\le i\le\infty,1\le j\le m_i}\hat{a}_{ij}\phi_{ij}$, $\hat{\psi} = \sum_{0\le i\le\infty,1\le j\le m_i}\hat{b}_{ij}\phi_{ij}$. Then

$$\sum_{0\le i\le\infty,1\le j\le m_i}\hat{B}_i\begin{pmatrix}\hat{a}_{ij}\\ \hat{b}_{ij}\end{pmatrix}\phi_{ij} = 0,$$

where

$$\hat{B}_i = \begin{pmatrix} -d_2^j a_{12}\lambda_i + f_{\hat{\varphi}} & f_{\hat{\psi}} \\ a_{12} & -d_1\lambda_i - a_{11} \end{pmatrix}.$$

By a straightforward calculation one can check that $\det \hat{B}_i = a_{12} \det \bar{B}_i$, where $\bar{B}_i$ is given in (23) by replacing d_2 with d_2^j. Thus $\det \bar{B}_i = 0$ only for $i = j$, and $\ker(K^* - I) = \operatorname{span}\{\hat{\Phi}\}$, where $\hat{\Phi} = (\frac{d_1\lambda_i + a_{11}}{a_{12}}, 1)^\top \phi_j$. Since $(\Phi_1, \hat{\Phi})_Y = \frac{2d_1\lambda_j}{a_{12}} \neq 0$, $\Phi_1 \notin (\ker(K^* - I))^\perp = R((K - I))$, so $\ker(K - I) \cap R(K - I) = 0$ and the eigenvalue 1 has algebraic multiplicity one.

If $0 < d_2 \neq d_2^j$ is in a small neighborhood of d_2^j, then the linear operator $I - K(d_2) : U \to U$ is a bijection and 0 is an isolated solution of (29) for this fixed d_2. The index of this isolated zero of $I - K(d_2) - H$ is given by

$$\operatorname{index}\bigl(I - K(d_2) - H, (d_2, 0)\bigr) = \deg\bigl(I - K(d_2), B, 0\bigr) = (-1)^p,$$

where B is a sufficiently small ball with center at 0, and p is the sum of the algebraic multiplicities of the eigenvalues of $K(d_2)$ which are larger than 1. For our bifurcation analysis, it is also necessary to verify that this index changes as d_2 crosses d_2^j, that is, for $\epsilon > 0$ sufficiently small,

$$\operatorname{index}\bigl(I - K\bigl(d_2^j - \epsilon\bigr) - H, \bigl(d_2^j - \epsilon, 0\bigr)\bigr) \neq \operatorname{index}\bigl(I - K\bigl(d_2^j + \epsilon\bigr) - H, \bigl(d_2^j + \epsilon, 0\bigr)\bigr). \tag{30}$$

Indeed, if μ is an eigenvalue of $K(d_2)$ with an eigenfunction $(\tilde{\varphi}, \tilde{\psi})$, then

$$2a_{11}G_1(\tilde{\varphi}) + a_{12}G_1(\tilde{\psi}) = \mu\tilde{\varphi}, \qquad a_{21}G_2(\tilde{\varphi}) = \mu\tilde{\psi}.$$

By the definition of G_1, G_2 and

$$\tilde{\varphi} = \sum_{0\le i\le\infty, 1\le j\le m_i} \tilde{a}_{ij}\phi_{ij}, \tilde{\psi} = \sum_{0\le i\le\infty, 1\le j\le m_i} \tilde{b}_{ij}\phi_{ij},$$

we have

$$\sum_{0\le i\le\infty, 1\le j\le m_i} \tilde{B}_i \begin{pmatrix} \tilde{a}_{ij} \\ \tilde{b}_{ij} \end{pmatrix} \phi_{ij} = 0,$$

where

$$\tilde{B}_i = \begin{pmatrix} (2-\mu)a_{11} - d_1\lambda_i\mu & a_{12} \\ a_{21} & (a_{22} - d_2\lambda_i)\mu \end{pmatrix}.$$

Thus the set of eigenvalues of $K(d_2)$ consists of all μ that solve the characteristic equation

$$\mu^2 - \frac{2a_{11}}{d_1\lambda_i + a_{11}}\mu - \frac{a_{12}a_{21}}{(d_2\lambda_i - a_{22})(d_1\lambda_i + a_{11})} = 0. \tag{31}$$

In particular, for $d_2 = d_2^j$, if $\mu = 1$ is a root of (31), then a simple calculation leads to $d_2^j = d_2^i$, and $j = i$ by the assumption. For $i = j$ in (31), we let $\mu_1(d_2^j)$, $\mu_2(d_2^j)$ denote the two roots.

First we find that

$$\mu_1\left(d_2^j\right) = 1 \quad \text{and} \quad \mu_2\left(d_2^j\right) = \frac{a_{11} - d_1\lambda_j}{a_{11} + d_1\lambda_j} < 1.$$

Now for d_2 close to d_2^j, the root of (31) is given by

$$\mu_1(d_2) = \frac{a_{11} + \sqrt{a_{11}^2 + \frac{a_{12}a_{21}(d_1\lambda_i + a_{11})}{d_2\lambda_i - a_{22}}}}{(d_1\lambda_i + a_{11})}, \qquad \mu_2(d_2) < 1.$$

And $\mu_2(d_2)$ is an increasing function of d_2, there is a small $\epsilon > 0$ such that

$$\mu_1\left(d_2^j + \epsilon\right) > 1, \qquad \mu_1\left(d_2^j - \epsilon\right) < 1.$$

Consequently, $K(d_2^j + \epsilon)$ has exactly one more eigenvalues that are larger than 1 than $K(d_2^j - \epsilon)$ does, and by a similar argument to above we can show this eigenvalue has algebraic multiplicity one. This verifies (30).

With the help of (30), we can use the argument in [25] to conclude that Γ_j either meets infinity in $R \times U$ or meets $(d_2^k, 0)$ for some $k \neq j$, $d_2^k > 0$. We now show that the first alternative must occur, following the idea of [28] and [29]. Indeed, if Γ_j is bounded, then it is compact, and Γ_j meets some other bifurcation points. Let k be such that Γ_j meets $(d_2^k, 0)$, but not $(d_2^i, 0)$ for any $i > k$. Consider the problem (4) on the interval $(0, \pi)$ subject to the boundary condition

$$u' = v' \quad \text{at } x = 0, \pi. \tag{32}$$

We first note that if $\bar{E}$ solves (4) and (32), then one can construct a solution E of (4) by a reflective and periodic extension: Let $x_n = n\pi$, $n = 0, 1, \ldots, k$, and define

$$E(x) = \begin{cases} \bar{E}(x - x_{2n}) & \text{if } x_{2n} \leq x \leq x_{2n+1}, \\ \bar{E}(x_{2n+2} - x) & \text{if } x_{2n+1} \leq x \leq x_{2n+2}. \end{cases}$$

It is easy see that $(d_2^k, 0)$ is also a bifurcation point of the problem (4) and (32). Let Λ_k denote the bifurcation branch of this new problem that meets infinity or meets $(d_2^k, 0)$, then use the same argument above it is clear that it either meets infinity or meets $(d_2^{k'}, 0)$ for some $k' > k$. If the second case occurs, then by the above extension one sees that Γ_j meets $(d_2^{k'}, 0)$, which violates the definition of k, hence Λ_k meets infinity, and then by the extension again Γ_j meets infinity too. It then follows that the projection of Γ_j on the d_2 interval must be unbounded, since the solutions u, v are bounded by constants independent of d_2. It also follows from the a priori estimates that any solutions on the curve Γ_j must be positive. And the proof is complete. □

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