



Research article

Bifurcation structure of nonconstant positive steady states for a diffusive predator-prey model

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Abstract: In this paper, we make a detailed descriptions for the local and global bifurcation structure of nonconstant positive steady states of a modified Holling-Tanner predator-prey system under homogeneous Neumann boundary condition. We first give the stability of constant steady state solution to the model, and show that the system exhibits Turing instability. Second, we establish the local structure of the steady states bifurcating from double eigenvalues by the techniques of space decomposition and implicit function theorem. It is shown that under certain conditions, the local bifurcation can be extended to the global bifurcation.

Keywords: turing instability; nonconstant positive steady states; global bifurcation; neumann boundary condition

1. Introduction

Understanding the mechanisms by which patterns are created in the living system poses one of the most challenging problems in developmental biology [1], since the pioneer work of Turing [2]. Turing's revolutionary idea was that passive diffusion could interact with the chemical reaction in such a way that even if the reaction by itself has no symmetry-breaking capabilities, diffusion can destabilize the symmetry so that the system with diffusion can have them [3–6].

There has been considerable interest in investigating the pattern formation of population system by taking into account the effect of diffusion [7–24, 26–33]. These investigations have revealed that spatial inhomogeneities like the inhomogeneous distribution of nutrients as well as interactions on spatial scales like migration play an important role in specializing and stabilizing population levels.

In a recent analytic approach by Shi, Li and Lin [17], the following reaction-diffusion predator-prey

model is considered:

$$\begin{cases} u_t - d_1 u_{xx} = u(1 - u) - \frac{kuv}{a + u + mv}, & x \in (0, \pi), t > 0, \\ v_t - d_2 v_{xx} = v\left(\delta - \frac{\beta v}{u}\right), & x \in (0, \pi), t > 0, \\ u_x = 0, v_x = 0, & x = 0, \pi, t > 0, \\ u(x, 0) = u_0(x) \geq 0, v(x, 0) = v_0(x) \geq 0, & x \in (0, \pi), \end{cases} \quad (1.1)$$

where $u := u(x, t)$ and $v := v(x, t)$ represent the densities of the prey and predator, respectively. The parameter $k > 0$ is the maximum consumption rate, a a saturation constant, m a predator interference parameter ($m < 0$ the case where predators benefit from cofeeding [18]), δ the intrinsic growth rate of prey, and β the numbers of prey required to support one predator at equilibrium when v equals to u/β [34]. d_1, d_2 are the diffusion coefficients of u and v , respectively.

In [17], the authors show that, model (1.1) has a boundary steady state $(1, 0)$ which is unstable and a unique positive steady state

$$E^* = (u^*, v^*) = \left(\frac{\beta(1 - a) + \delta(m - k) + \sqrt{(a\beta - \beta - m\delta + k\delta)^2 + 4a\beta(\beta + m\delta)}}{2(\beta + m\delta)}, \frac{\delta}{\beta} u^* \right).$$

And the authors investigated the qualitative properties, including the global attractor, persistence property under the condition of $m > k$, local and global stability of E^* , and established the existence and nonexistence of nonconstant positive steady states of model (1.1). In this paper, we always assume that $m > k$.

And there naturally comes a question: What is the structure of nonconstant positive steady states of model (1.1)?

Thus we will investigate the steady state problem corresponding to model (1.1)

$$\begin{cases} -d_1 u_{xx} = u(1 - u) - \frac{kuv}{a + u + mv}, & x \in (0, \pi), \\ -d_2 v_{xx} = v\left(\delta - \frac{\beta v}{u}\right), & x \in (0, \pi), \\ u_x = v_x = 0, & x = 0, \pi. \end{cases} \quad (1.2)$$

It is our purpose in this paper to make a better description for the structure of the set of nonconstant positive steady states of model (1.1). The rest of this article is organized as follows: In Section 2, we prepare some preliminaries and give the Turing instability in details. In Section 3, we give the local and global bifurcation structure of nonconstant positive steady states.

2. Turing instability

It's well known that the *Turing instability* refers to “diffusion driven instability”, i.e., the stability of the positive equilibrium $E^* = (u^*, v^*)$ changing from stable for the ordinary differential equations (ODE) dynamics (i.e., $d_1 = d_2 = 0$ in model (1.1)), to unstable, for the partial differential equations (PDE) dynamics (1.1) [1, 14]. The occurrence of Turing pattern is caused by the existence of nonconstant positive steady states of model (1.1) as a result of diffusion. In this section, we mainly discuss Turing instability.

Before proceeding, we recall the following Neumann eigenvalue problem

$$\begin{cases} -\varphi_{xx} = \lambda\varphi, & x \in (0, \pi), \\ \varphi_x = 0, & x = 0, \pi. \end{cases} \quad (2.1)$$

It is well known that (2.1) has a sequence of simple eigenvalues and associated eigenfunctions are explicitly given by

$$\lambda_i = i^2, \quad \varphi_i(x) = \begin{cases} \frac{1}{\sqrt{\pi}}, & i = 0, \\ \sqrt{\frac{2}{\pi}} \cos ix, & i > 0, \end{cases}$$

where $i = 0, 1, 2, \dots$. Let $Y = C^2((0, \pi)) \times C^2((0, \pi))$ be the Hilbert space, and

$$X = \{(u, v) \mid u, v \in C^2((0, \pi)), u_x = v_x = 0, x = 0, \pi\}.$$

Let us first recall that the ODE model corresponding to the PDE model (1.1):

$$\begin{cases} \frac{du}{dt} = u(1-u) - \frac{kuv}{a+u+mv} := f(u, v), \\ \frac{dv}{dt} = v\left(\delta - \frac{\beta v}{u}\right) := g(u, v). \end{cases} \quad (2.2)$$

Following [17], the Jacobian of model (2.2) around $E^* = (u^*, v^*)$ is given by

$$J = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}, \quad (2.3)$$

where

$$\begin{aligned} a_{11} &= \frac{u^*(\beta(1-a) - (m\delta + 2\beta)u^*)}{(m\delta + \beta)u^* + a\beta}, & a_{12} &= -\frac{k\beta^2 u^*(a+u^*)}{(m\delta + \beta)u^* + a\beta}, \\ a_{21} &= \frac{\delta^2}{\beta}, & a_{22} &= -\delta. \end{aligned} \quad (2.4)$$

The characteristic equation of J is

$$\eta^2 - \text{Tr}(J)\eta + \det(J) = 0,$$

where

$$\begin{aligned} \text{Tr}(J) &= -\frac{\beta u^{*2} + \delta(\delta m + \beta + m - k)u^* + \alpha\beta(\delta + 1)}{(m\delta + \beta)u^* + a\beta}, \\ \det(J) &= \frac{\delta u^*((\delta m + \beta)(\beta(1+a) + \delta(m-k)u^* + a\beta) (\alpha\beta + \delta k + \delta m + \beta))}{((m\delta + \beta)u^* + a\beta)^2} > 0. \end{aligned} \quad (2.5)$$

It follows from the assumption $m > k$ that $\text{Tr}(J) < 0$. Thus the positive equilibrium E^* of the ODE model (2.2) is locally stable.

Choosing d_2 as the bifurcation parameter, we have the following linearized operator of model (1.2) evaluated at E^* :

$$\mathcal{L}(d_2) = \begin{pmatrix} d_1 \frac{\partial^2}{\partial x^2} + a_{11} & a_{12} \\ a_{21} & d_2 \frac{\partial^2}{\partial x^2} + a_{22} \end{pmatrix}.$$

It is easy to see that the eigenvalues of $\mathcal{L}(d_2)$ are given by those of the following operator $\mathcal{L}_i(d_2)$ (see, e.g., [16, 17, 36]):

$$\mathcal{L}_i = \begin{pmatrix} -d_1 i^2 + a_{11} & a_{12} \\ a_{21} & -d_2 i^2 + a_{22} \end{pmatrix},$$

whose characteristic equation is

$$\xi^2 - \xi T_i + Q_i = 0, \quad i = 0, 1, 2, \dots$$

where

$$\begin{aligned} T_i &= -(d_1 + d_2)i^2 + \text{Tr}(J) < 0, \\ Q_i &= i^2(d_1 i^2 - a_{11}) \left(d_2 - \frac{d_1 \delta i^2 + \det(J)}{i^2(a_{11} - d_1 i^2)} \right). \end{aligned} \quad (2.6)$$

For simplicity, we define

$$\theta := (1 - a)\beta - (m\delta + 2\beta)u^*. \quad (2.7)$$

If $\theta > 0$ and

$$d_1 < a_{11}, \quad (2.8)$$

then what we define as $i_0 := i_0(k, a, m, \delta, \beta)$ is the largest positive integer such that $d_1 i^2 < a_{11}$ with $i \leq i_0$.

Clearly, if (2.8) is satisfied, then $1 \leq i_0 \leq \infty$. In this case, we denote

$$\bar{d}_2 = \min_{0 \leq i \leq i_0} d_2^i, \quad \text{where} \quad d_2^i := \frac{d_1 \delta i^2 + \det(J)}{i^2(a_{11} - d_1 i^2)}. \quad (2.9)$$

Therefore we can obtain the local stability of $E^* = (u^*, v^*)$ of model (1.1) as follows:

Theorem 2.1. *For model (1.1),*

(i) *If $\theta < 0$ holds, then E^* is locally asymptotically stable.*

(ii) *If $\theta > 0$, we have*

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

(ii-2) *If $d_1 \leq a_{11}$, $d_2 > \bar{d}_2$ hold, then E^* is Turing unstable.*

Example 2.2. As an example, we take the parameters in model (1.1) as:

$$a = 0.035, m = 0.05, k = 0.8, \beta = 1.5, \delta = 2, d_1 = 0.01$$

Easy to know there is a unique positive equilibrium $E^* = (u^*, v^*) = (0.16548, 0.22064)$. From Theorem 2.1, we can know that if $d_2 > \bar{d}_2 = 0.19$ holds, E^* is Turing unstable, and model (1.1) exhibits *Turing pattern*. In Figure 1, we show the numerical results of model (1.1) with different values of d_2 . Figure 1(a) shows Turing pattern with $d_2 = 0.21 > \bar{d}_2$, and one can see that the solutions of (1.1) are not dependent on time t but space x . In other words, model (1.1) in this case has nonconstant positive steady states as a result of diffusion. Figure 1(b) gives the stable behavior of model (1.1) with $d_2 = 0.15 < \bar{d}_2$.

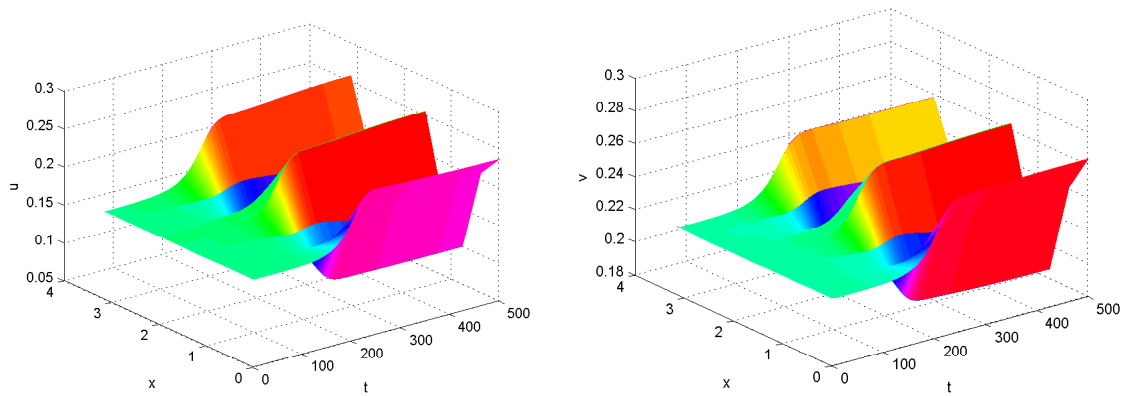
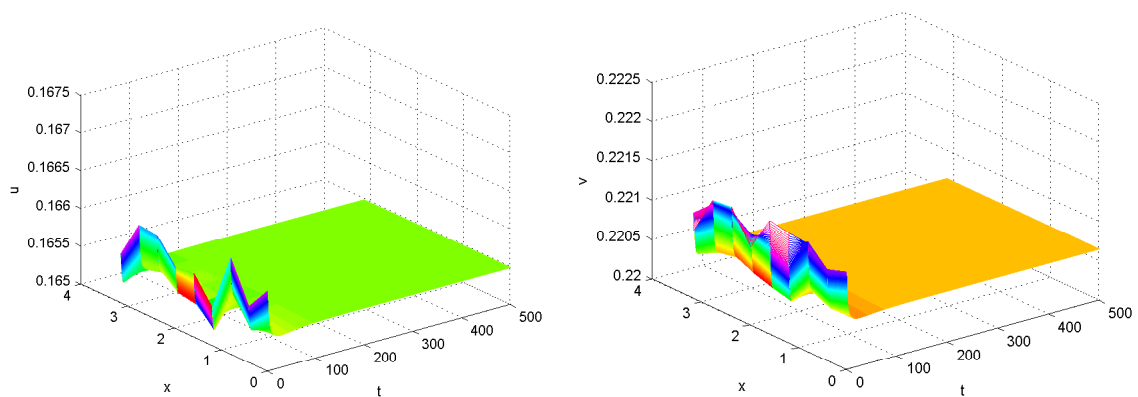
(a) Turing pattern with $d_2 = 0.21$ (b) Stable behavior with $d_2 = 0.15$

Figure 1. Numerical simulations of the long time behavior of solution $(u(x, t), v(x, t))$ of model (1.1) with different values of d_2 . (a) $d_2 = 0.21$; (b) $d_2 = 0.15$.

3. Bifurcation analysis

In this section, we will focus on the local and global bifurcation structure of the nonconstant positive steady states for model (1.2).

If $(u, v) = (u(x), v(x))$ is a positive solution to model (1.2), then it is proved in [17] and the maximum principle [35] that

$$1 - \frac{k}{m} < u(x) < 1, \quad \frac{\alpha}{\beta} \left(1 - \frac{k}{m}\right) < v(x) < \frac{\alpha}{\beta}, \quad x \in \Omega. \quad (3.1)$$

We translate (u^*, v^*) to the origin by the translation $(\tilde{u}, \tilde{v}) = (u - u^*, v - v^*)$. For convenience, we still denote \tilde{u}, \tilde{v} by u, v , respectively, and then we can obtain the following system

$$\begin{cases} -d_1 u_{xx} = (u + u^*)(1 - (u + u^*)) - \frac{k(u + u^*)(v + v^*)}{a + (u + u^*) + m(v + v^*)} =: f(u + u^*, v + v^*), & x \in (0, \pi), \\ -d_2 v_{xx} = (v + v^*) \left(\delta - \frac{\beta(v + v^*)}{(u + u^*)} \right) =: g(u + u^*, v + v^*), & x \in (0, \pi), \\ u_x = v_x = 0, & x = 0, \pi. \end{cases} \quad (3.2)$$

3.1. Local bifurcation

We study the local structure of nonconstant positive solutions for the new system (3.2). In brief, by regarding d_2 as bifurcation parameter, we verify the existence of positive solutions bifurcation from $(d_2, 0, 0)$. In this section, we assume that $\theta > 0$.

With the help of a *a priori* estimate (3.1), let

$$X = \{(u, v) \in C^2(0, \pi) \times C^2(0, \pi) : u_x = v_x = 0, x = 0, \pi\}$$

and $Y = L^p(0, \pi) \times L^p(0, \pi)$. Define the map $F : (0, \infty) \times X \rightarrow Y$ by

$$F(d_2, u, v) = \begin{pmatrix} d_1 \frac{\partial^2 u}{\partial x^2} + f(u + u^*, v + v^*) \\ d_2 \frac{\partial^2 v}{\partial x^2} + g(u + u^*, v + v^*) \end{pmatrix}.$$

Then the solutions of the boundary problem (3.2) are exactly zero of the map $F(d_2, u, v)$. Note that $(0, 0)$ is the unique constant solution of (3.2), then we have $F(d_2, 0, 0) = 0$. The Fréchet derivative of $F(d_2, u, v)$ with respect to (u, v) at $(0, 0)$ can be given by

$$L_1(d_2) = F_{(u,v)}(d_2, 0, 0) = \begin{pmatrix} d_1 \frac{\partial^2}{\partial x^2} + a_{11} & a_{12} \\ a_{21} & d_2 \frac{\partial^2}{\partial x^2} + a_{22} \end{pmatrix},$$

where a_{11}, a_{12}, a_{21} and a_{22} are given in (2.4).

Theorem 3.1. *Let*

$$d_2 = d_2^j := \frac{d_1 \delta \lambda_j + \det(J)}{\lambda_j (a_{11} - d_1 \lambda_j)}, \quad \lambda_j = j^2 \text{ for } 1 \leq j \leq i_0. \quad (3.3)$$

(i) Suppose that $d_2^j \neq d_2^i$ for any integer $i \neq j$. Then $(d_2^j, 0, 0)$ is a bifurcation point of $F(d_2, u, v) = 0$. Moreover, there is a one-parameter family of non-trivial solutions $\Gamma_j(s) = (d_2(s), u(s), v(s))$ of $F(d_2, u, v) = 0$ for $|s|$ sufficiently small, where $d_2(s), u(s), v(s)$ are continuous functions, $(u(0), v(0)) = (0, 0)$, $d_2(0) = d_2^j$ and $u(s) = s\varphi_j + o(s)$, $v(s) = sb_j\varphi_j + o(s)$, $b_j = \frac{a_{11}-d_1\lambda_j}{a_{12}} > 0$. The zero set of $F(d_2, u, v)$ consists of two curves $(d_2, 0, 0)$ and $\Gamma_j(s)$ in a neighborhood of the bifurcation point $(d_2^j, 0, 0)$.

(ii) Suppose that there exists a positive integer $i (\neq j)$ such that $d_2^i = d_2^j \triangleq \hat{d}$. Let

$$b_i = \frac{a_{11} - d_1\lambda_i}{a_{12}}, \quad b_i^* = \frac{d_1\lambda_i - a_{11}}{a_{21}}, \quad \Phi_i = \begin{pmatrix} 1 \\ b_i \end{pmatrix} \varphi_i, \quad (3.4)$$

$$X_2 = \left\{ (u, v) \in Y : \int_0^\pi (u + b_i v) \varphi_i dx = \int_0^\pi (u + b_j v) \varphi_j dx = 0 \right\}. \quad (3.5)$$

If $\frac{1 + b_i^*}{1 + b_i b_i^*} \neq 0$, $\frac{1 + b_j^*}{1 + b_j b_j^*} \neq 0$ and $j = 2i$ (resp. $i = 2j$), then $(\hat{d}, 0, 0)$ is a bifurcation point of $F(d_2, u, v) = 0$. Moreover, there exists a curve of nonconstant solutions $(d_2(\omega), s(\omega)(\cos \omega \Phi_i + \sin \omega \Phi_j) + W(\omega))$ of $F(d_2, u, v) = 0$ for $|\omega - \omega_0|$ sufficiently small, where $d_2(\omega), s(\omega)$, and $W(\omega)$ are continuously differentiable functions with respect to ω , $W(\omega) \in X_2$ and satisfy $d_2(\omega_0) = \hat{d}$, $s(\omega_0) = 0$, $W(\omega_0) = 0$. Here ω_0 is any constant satisfying

$$\cos \omega_0 \neq 0 \text{ and } c_2 c_4 b_j \lambda_j \sin^2 \omega_0 \neq c_1 c_3 b_i \lambda_i \cos^2 \omega_0, \quad (3.6)$$

$$\text{(resp. } \sin \omega_0 \neq 0 \text{ and } c_2 c_5 b_j \lambda_j \sin^2 \omega_0 \neq c_1 c_6 b_i \lambda_i \cos^2 \omega_0), \quad (3.7)$$

where

$$c_1 = \frac{b_i^*}{1 + b_i b_i^*}, \quad c_2 = \frac{b_j^*}{1 + b_j b_j^*}, \quad c_3 = \sqrt{\frac{1}{2\pi} \frac{A_1 + B_1 b_j^*}{1 + b_j b_j^*}},$$

$$c_4 = \sqrt{\frac{1}{2\pi} \frac{A_2 + B_2 b_i^*}{1 + b_i b_i^*}}, \quad c_5 = \sqrt{\frac{1}{2\pi} \frac{A_3 + B_3 b_i^*}{1 + b_i b_i^*}}, \quad c_6 = \sqrt{\frac{1}{2\pi} \frac{A_2 + B_2 b_j^*}{1 + b_j b_j^*}},$$

and

$$A_1 = \left(-1 + \frac{kv^*(mv^* + a)}{(a + u^* + mv^*)^3} \right) - \frac{k(amv^* + 2mu^*v^* + a^2 + au^*)}{(a + u^* + mv^*)^3} b_i + \frac{ku^*m(a + u^*)}{(a + u^* + mv^*)^3} b_i^2,$$

$$A_2 = 2 \left(-1 + \frac{kv^*(mv^* + a)}{(a + u^* + mv^*)^3} \right) - \frac{k(amv^* + 2mu^*v^* + a^2 + au^*)}{(a + u^* + mv^*)^3} (b_i + b_j) + \frac{ku^*m(a + u^*)}{(a + u^* + mv^*)^3} b_i b_j,$$

$$A_3 = \left(-1 + \frac{kv^*(mv^* + a)}{(a + u^* + mv^*)^3} \right) - \frac{k(amv^* + 2mu^*v^* + a^2 + au^*)}{(a + u^* + mv^*)^3} b_j + \frac{ku^*m(a + u^*)}{(a + u^* + mv^*)^3} b_j^2,$$

$$B_1 = -\frac{\delta^2}{\beta u^*} + \frac{2\delta}{u^*} b_i - \frac{\beta}{u^*} b_i^2,$$

$$B_2 = -2\frac{\delta^2}{\beta u^*} + \frac{2\delta}{u^*} (b_i + b_j) - \frac{\beta}{u^*} b_i b_j,$$

$$B_3 = -\frac{\delta^2}{\beta u^*} + \frac{2\delta}{u^*} b_j - \frac{\beta}{u^*} b_j^2. \quad (3.8)$$

Proof. (i) By using the Crandall-Rabinowitz bifurcation theorem [37], we know that $(d_2^j; 0, 0)$ is a bifurcation point provided that:

- (a) the partial derivatives F_{d_2} , $F_{(u,v)}$, and $F_{d_2, (u,v)}$ exist and are continuous;
- (b) $\ker F_{(u,v)}(d_2^j, 0, 0)$ and $\text{codim Im}(F_{(u,v)}(d_2^j, 0, 0))$ are one-dimensional (here Im: image);
- (c) let $\ker F_{(u,v)}(d_2^j, 0, 0) = \text{span}\{\Phi_j\}$, then $F_{d_2, (u,v)}(d_2^j, 0, 0)\Phi_j \notin \text{Im}(F_{(u,v)}(d_2^j, 0, 0))$.

It suffices to verify conditions (a)-(c) above. When $d_2 = d_2^j$, the operator $L_1(d_2)$ is given by

$$L_1(d_2^j) = F_{(u,v)}(d_2, 0, 0) = \begin{pmatrix} d_1 \frac{\partial^2}{\partial x^2} + a_{11} & a_{12} \\ a_{21} & d_2^j \frac{\partial^2}{\partial x^2} + a_{22} \end{pmatrix},$$

It is clear that the linear operators $F_{(u,v)}$, $F_{d_2, (u,v)}$ and F_{d_2} are continuous. The condition (a) is verified.

Suppose $\Phi_i = (\bar{\phi}, \bar{\psi})^\top \in \ker L_1$, and write $\bar{\phi} = \Sigma \bar{a}_i \varphi_i$, $\bar{\psi} = \Sigma \bar{b}_i \varphi_i$. Then

$$\sum_{i=0}^{\infty} \bar{B}_i \begin{pmatrix} \bar{a}_i \\ \bar{b}_i \end{pmatrix} \varphi_i = 0, \quad \text{where } \bar{B}_i = \begin{pmatrix} a_{11} - d_1 \lambda_i & a_{12} \\ a_{21} & a_{22} - d_2 \lambda_i \end{pmatrix}. \quad (3.9)$$

By a simple calculation, we have $\det \bar{B}_i \neq 0$, when $i \neq j$. Hence if and only if $i = j$,

$$\det \bar{B}_i = 0 \quad \Leftrightarrow \quad d_2 = d_2^i = \frac{d_1 \delta \lambda_i - \det(J)}{\lambda_i (a_{11} - d_1 \lambda_i)},$$

taking $d_2 = d_2^j$ implies that

$$\ker L_1 = \text{span}\{\Phi_j\}, \quad \Phi_j = \begin{pmatrix} 1 \\ b_j \end{pmatrix} \varphi_j.$$

Consider the adjoint operator

$$L_1^* = \begin{pmatrix} d_1 \frac{\partial^2}{\partial x^2} + a_{11} & a_{21} \\ a_{12} & d_2 \frac{\partial^2}{\partial x^2} + a_{22} \end{pmatrix}.$$

In the same way as above we obtain

$$\ker L_1^* = \text{span}\{\Phi_j^*\}, \quad \Phi_j^* = \begin{pmatrix} 1 \\ b_j^* \end{pmatrix} \varphi_j.$$

Since $\text{Im}(L_1) = \ker(L_1^*)^\perp$ (here $^\perp$: complementary set), thus

$$\text{codim}(\text{Im}(L_1)) = \dim(\ker(L_1^*)) = 1.$$

Condition (b) is also verified.

Finally, since

$$F_{(u,v)}(d_2^j, 0, 0)\Phi_j = \begin{pmatrix} 0 & 0 \\ 0 & \frac{\partial^2}{\partial x^2} \end{pmatrix} \Phi_j = \begin{pmatrix} 0 \\ -\lambda_j b_j \varphi_j \end{pmatrix},$$

and

$$\langle F_{d_2, (u, v)}(d_2^j, 0, 0)\Phi_j, \Phi_j^* \rangle_Y = \langle -\lambda_j b_j \varphi_j, b_j^* \varphi_j \rangle = -\lambda_j b_j b_j^* > 0.$$

We can see that $F_{d_2, (u, v)}(d_2^j, 0, 0)\Phi_j \notin \text{Im}(L_1)$, and so condition (c) is satisfied. The proof of (i) is completed.

(ii) Suppose that there exists a positive integer $i (\neq j)$ such that $d_2^i = d_2^j \triangleq \hat{d}$. Then

$$\ker L_1(\hat{d}) = \text{span}\{\Phi_i, \Phi_j\}, \quad \ker L_1^*(\hat{d}) = \text{span}\{\Phi_i^*, \Phi_j^*\}$$

and

$$\text{Im}(L_1(\hat{d})) = \left\{ (u, v) \in Y : \int_0^\pi (u + b_i^* v) \varphi_i dx = \int_0^\pi (u + b_j^* v) \varphi_j dx = 0 \right\},$$

which leads to $\text{codim Im}(L_1(\hat{d})) = \dim \ker L_1(\hat{d}) = 2$.

Clearly, the Crandall-Rabinowitz bifurcation theorem does not work in the situation since condition (b) in (i) is not satisfied. Now, we deal with this situation by the techniques of space decomposition and implicit function theorem.

To achieve our aim, we first make the following decomposition

$$X = X_1 \oplus X_2,$$

where $X_1 = \text{span}\{\Phi_i, \Phi_j\}$ and X_2 is defined in (3.5). We next look for the solution of $F(d_2, u, v)$ in the following form

$$(u, v) = s(\cos \omega \Phi_i + \sin \omega \Phi_j + W), \quad W = (W_1, W_2)^T \in X_2,$$

where $s, \omega \in \mathbb{R}$ are parameters. Define an operator P on Y by

$$P \begin{pmatrix} u \\ v \end{pmatrix} = \frac{1}{1 + b_i b_i^*} \int_0^\pi (u + b_i^* v) \varphi_i dx \Phi_i + \frac{1}{1 + b_j b_j^*} \int_0^\pi (u + b_j^* v) \varphi_j dx \Phi_j.$$

Then $\text{Im}(P) = \text{span}\{\Phi_i, \Phi_j\} = X_1 \subset Y$, $P^2 = P$. Hence, P is the projection from Y to $X_1 \subset Y$. Thus we decompose Y as $Y = Y_1 \oplus Y_2$ with $Y_1 := \text{Im}(P)$ and $Y_2 := \ker P = \text{Im}(L_1(\hat{d}))$.

Next, we rewrite the map $F : (0, \infty) \times X \rightarrow Y$ by

$$F(d_2, u, v) = L_1(d_2) \begin{pmatrix} u \\ v \end{pmatrix} + \begin{pmatrix} h_1 \\ h_2 \end{pmatrix},$$

where

$$h_1(u, v) = \left(\frac{kv^*(mv^* + a)}{(a + u^* + mv^*)^3} - 1 \right) u^2 - \frac{k(amv^* + 2mu^*v^* + a^2 + au^*)}{(a + u^* + mv^*)^3} uv + \frac{ku^*m(a + u^*)}{(a + u^* + mv^*)^3} v^2 + O(|u|^3, |u|^2|v|),$$

$$h_2(u, v) = -\frac{\delta^2}{\beta u^*} u^2 + \frac{2\delta}{u^*} uv - \frac{\beta}{u^*} v^2 + O(|u|^3, |u|^2|v|).$$

It is obvious that $F(\hat{d}, 0, 0) = 0$, and $F_{(u, v)}(\hat{d}, 0, 0) = L_1(\hat{d})$. In order to verify the existence of nonconstant positive solutions of (3.2), we only need to find the existence of nonconstant pair (u, v) satisfying $F(d_2, u, v) = 0$.

Fixing $\omega_0 \in \mathbb{R}$ for the time being, we define a nonlinear mapping

$$K(d_2, s, W; \omega) : \mathbb{R}^+ \times \mathbb{R} \times X_2 \times (\omega_0 - \delta, \omega_0 + \delta) \rightarrow Y$$

by

$$\begin{aligned} K(d_2, s, W; \omega) &= s^{-1} F(d_2, s(\cos \omega \Phi_i + \sin \omega \Phi_j + W)) \\ &= L_1(d_2)(\cos \omega \Phi_i + \sin \omega \Phi_j + W) + s^{-1} \begin{pmatrix} h_1 \\ h_2 \end{pmatrix} \\ &= L_1(d_2)(\cos \omega \Phi_i + \sin \omega \Phi_j + W) + s \begin{pmatrix} \tilde{h}_1 \\ \tilde{h}_2 \end{pmatrix}, \end{aligned}$$

where

$$\begin{aligned} \tilde{h}_1 &= \left(-1 + \frac{kv^*(mv^* + a)}{(a + u^* + mv^*)^3}\right)(\cos \omega \varphi_i + \sin \omega \varphi_j + W_1)^2 + \frac{ku^*m(a + u^*)}{(a + u^* + mv^*)^3}(b_i \cos \omega \varphi_i + b_j \sin \omega \varphi_j + W_2)^2 \\ &\quad - \frac{k(amv^* + 2mu^*v^* + a^2 + au^*)}{(a + u^* + mv^*)^3}(\cos \omega \varphi_i + \sin \omega \varphi_j + W_1)(b_i \cos \omega \varphi_i + b_j \sin \omega \varphi_j + W_2) + O(|s|), \\ \tilde{h}_2 &= -\frac{\delta^2}{\beta u^*}(\cos \omega \varphi_i + \sin \omega \varphi_j + W_1)^2 - \frac{\beta}{u^*}(b_i \cos \omega \varphi_i + b_j \sin \omega \varphi_j + W_2)^2 \\ &\quad + \frac{2\delta}{u^*}(\cos \omega \varphi_i + \sin \omega \varphi_j + W_1)(b_i \cos \omega \varphi_i + b_j \sin \omega \varphi_j + W_2) + O(|s|). \end{aligned}$$

It is clear that $K(\hat{d}, 0, 0; \omega_0) = 0$. By some calculations, we see that the Frechet derivative of $K(d_2, s, W; \omega)$ with respect to (d_2, s, W) at $(d_2, s, W; \omega) = (\hat{d}, 0, 0; \omega_0)$ is the liner mapping

$$\begin{aligned} K_{(d_2, s, W)}(\hat{d}, 0, 0; \omega_0)(d_2, s, W) &= L_1(\hat{d})W - d_2 b_i \cos \omega_0 \lambda_i \begin{pmatrix} 0 \\ \varphi_i \end{pmatrix} - d_2 b_j \sin \omega_0 \lambda_j \begin{pmatrix} 0 \\ \varphi_j \end{pmatrix} \\ &\quad + s \cos^2 \omega_0 \begin{pmatrix} A_1 \varphi_i^2 \\ B_1 \varphi_i^2 \end{pmatrix} + s \cos \omega_0 \sin \omega_0 \begin{pmatrix} A_2 \varphi_i \varphi_j \\ B_2 \varphi_i \varphi_j \end{pmatrix} + s \sin^2 \omega_0 \begin{pmatrix} A_3 \varphi_j^2 \\ B_3 \varphi_j^2 \end{pmatrix}, \end{aligned}$$

where A_k and B_k ($k = 1, 2, 3$) are given in (3.8).

We then show that

$$K_{(d_2, s, W)}(\hat{d}, 0, 0; \omega_0) : \mathbb{R}^+ \times \mathbb{R} \times X_2 \rightarrow Y$$

is an isomorphism. To this end, we rewrite

$$K_{(d_2, s, W)}(\hat{d}, 0, 0; \omega_0)(d_2, s, W) = \Upsilon_1 + \Upsilon_2,$$

where $\Upsilon_1 \in Y_1$, $\Upsilon_2 \in Y_2$, and we decompose

$$\begin{pmatrix} 0 \\ \varphi_i \end{pmatrix} = c_1 \Phi_i + \begin{pmatrix} u_1 \\ v_1 \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} 0 \\ \varphi_j \end{pmatrix} = c_2 \Phi_j + \begin{pmatrix} u_2 \\ v_2 \end{pmatrix},$$

where

$$c_1 = \frac{b_i^*}{1 + b_i b_i^*} \neq 0, \quad \begin{pmatrix} u_1 \\ v_1 \end{pmatrix} = \begin{pmatrix} -c_1 \\ 1 - c_1 b_i \end{pmatrix} \varphi_i;$$

$$c_2 = \frac{b_j^*}{1 + b_j b_j^*} \neq 0, \quad \begin{pmatrix} u_2 \\ v_2 \end{pmatrix} = \begin{pmatrix} -c_2 \\ 1 - c_2 b_j \end{pmatrix} \varphi_j.$$

Furthermore, we can easily check that

$$\begin{pmatrix} u_1 \\ v_1 \end{pmatrix}, \quad \begin{pmatrix} u_2 \\ v_2 \end{pmatrix} \in Y_2.$$

In the next moment, we shall divide our discussion into two cases $j = 2i$ and $i = 2j$.

Case 1: $j = 2i$. In this case, a simple calculation yields

$$\int_0^\pi \varphi_i^2 \varphi_j = \sqrt{\frac{1}{2\pi}}, \quad \int_0^\pi \varphi_j^2 \varphi_i = 0 \quad \text{and} \quad \int_0^\pi \varphi_i^3 = \int_0^\pi \varphi_j^3 = 0.$$

Then, it is clear that

$$\begin{pmatrix} A_3 \varphi_j^2 \\ B_3 \varphi_j^2 \end{pmatrix} \in Y_2.$$

We decompose

$$\begin{pmatrix} A_1 \varphi_i^2 \\ B_1 \varphi_i^2 \end{pmatrix} = c_3 \Phi_j + \begin{pmatrix} u_3 \\ v_3 \end{pmatrix} \quad \text{and} \quad \begin{pmatrix} A_2 \varphi_i \varphi_j \\ B_2 \varphi_i \varphi_j \end{pmatrix} = c_4 \Phi_i + \begin{pmatrix} u_3 \\ v_3 \end{pmatrix},$$

where

$$c_3 = \frac{A_1 + B_1 b_j^*}{1 + b_j b_j^*} \int_0^\pi \varphi_i^2 \varphi_j dx = \sqrt{\frac{1}{2\pi}} \frac{A_1 + B_1 b_j^*}{1 + b_j b_j^*}, \quad \begin{pmatrix} u_3 \\ v_3 \end{pmatrix} = \begin{pmatrix} A_1 \varphi_i^2 - c_3 \varphi_j \\ B_1 \varphi_i^2 - c_3 b_j \varphi_j \end{pmatrix} \in Y_2,$$

$$c_4 = \frac{A_2 + B_2 b_i^*}{1 + b_i b_i^*} \int_0^\pi \varphi_i^2 \varphi_j dx = \sqrt{\frac{1}{2\pi}} \frac{A_2 + B_2 b_i^*}{1 + b_i b_i^*}, \quad \begin{pmatrix} u_4 \\ v_4 \end{pmatrix} = \begin{pmatrix} A_2 \varphi_i \varphi_j - c_4 \varphi_i \\ B_2 \varphi_i \varphi_j - c_4 b_i \varphi_i \end{pmatrix} \in Y_2.$$

By the decomposition of Y , we have

$$\Upsilon_1 = (-d_2 c_1 b_i \lambda_i \cos \omega_0 + s c_4 \sin \omega_0 \cos \omega_0) \Phi_i + (-d_2 c_2 b_j \lambda_j \sin \omega_0 + s c_3 \cos^2 \omega_0) \Phi_j,$$

$$\begin{aligned} \Upsilon_2 = & L_1(\hat{d})W - d_2 b_i \lambda_i \cos \omega_0 \begin{pmatrix} u_1 \\ v_1 \end{pmatrix} - d_2 b_j \lambda_j \sin \omega_0 \begin{pmatrix} u_2 \\ v_2 \end{pmatrix} + s \cos^2 \omega_0 \begin{pmatrix} u_3 \\ v_3 \end{pmatrix} \\ & + s \cos \omega_0 \sin \omega_0 \begin{pmatrix} u_4 \\ v_4 \end{pmatrix} + s \sin^2 \omega_0 \begin{pmatrix} A_3 \varphi_j^2 \\ B_3 \varphi_j^2 \end{pmatrix}. \end{aligned}$$

Let $K_{(d_2, s, W)}(\hat{d}, 0, 0; \omega_0)(d_2, s, W) = 0$, then we get $\Upsilon_1 = 0$ and $\Upsilon_2 = 0$. Since ω_0 satisfies (3.6) when $j = 2i$, we obtain $d_2 = 0$ and $s = 0$ from $\Upsilon_1 = 0$. Embedding them into $\Upsilon_2 = 0$, we have $W = 0$. This shows that $K_{(d_2, s, W)}(\hat{d}, 0, 0; \omega_0)$ is injective.

We now prove that $K_{(d_2, s, W)}(\hat{d}, 0, 0; \omega_0)$ is surjective. For any $(u, v) \in Y$, we need to find $(d_2, s, W) \in \mathbb{R}^+ \times \mathbb{R} \times X_2$ such that

$$K_{(d_2, s, W)}(\hat{d}, 0, 0; \omega_0)(d_2, s, W) = \begin{pmatrix} u \\ v \end{pmatrix}. \quad (3.10)$$

By the decomposition of Y , there exist $\alpha, \beta \in \mathbb{R}$ and $(\bar{u}, \bar{v}) \in Y_2$ such that

$$\begin{pmatrix} u \\ v \end{pmatrix} = \alpha \Phi_i + \beta \Phi_j + \begin{pmatrix} \bar{u} \\ \bar{v} \end{pmatrix}.$$

Substituting it into (3.10), we obtain

$$\begin{cases} -d_2 c_1 b_i \lambda_i \cos \omega_0 + s c_4 \sin \omega_0 \cos \omega_0 = \alpha, \\ -d_2 c_2 b_j \lambda_j \sin \omega_0 + s c_3 \cos^2 \omega_0 = \beta, \\ L_1(\hat{d})W - d_2 b_i \lambda_i \cos \omega_0 \begin{pmatrix} u_1 \\ v_1 \end{pmatrix} - d_2 b_j \lambda_j \sin \omega_0 \begin{pmatrix} u_2 \\ v_2 \end{pmatrix} + s \cos^2 \omega_0 \begin{pmatrix} u_3 \\ v_3 \end{pmatrix} \\ + s \cos \omega_0 \sin \omega_0 \begin{pmatrix} u_4 \\ v_4 \end{pmatrix} + s \sin^2 \omega_0 \begin{pmatrix} A_3 \varphi_j^2 \\ B_3 \varphi_j^2 \end{pmatrix} = \begin{pmatrix} \bar{u} \\ \bar{v} \end{pmatrix}. \end{cases} \quad (3.11)$$

By (3.6), we obtain

$$d_2 = \tilde{d}_2 := \frac{\beta c_4 \sin \omega_0 - \alpha c_3 \cos \omega_0}{c_1 c_3 b_i \lambda_i \cos^2 \omega_0 - c_2 c_4 b_j \lambda_j \sin^2 \omega_0},$$

$$s = \tilde{s} := \frac{\alpha c_2 b_j \lambda_j \sin \omega_0 - \beta c_1 b_i \lambda_i \cos \omega_0}{c_2 c_4 b_j \lambda_j \sin^2 \omega_0 \cos \omega_0 - c_1 c_3 b_i \lambda_i \cos^3 \omega_0}.$$

Note that $L_1(\hat{d})$ is an isomorphism from X_2 to Y_2 , and we get

$$W = L_1^{-1}(\hat{d}) \begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix},$$

by embedding $d_2 = \tilde{d}_2$ and $s = \tilde{s}$ into the third equation of (3.11), where

$$\begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix} = \begin{pmatrix} \bar{u} \\ \bar{v} \end{pmatrix} + \tilde{d}_2 b_i \lambda_i \cos \omega_0 \begin{pmatrix} u_1 \\ v_1 \end{pmatrix} + \tilde{d}_2 b_j \lambda_j \sin \omega_0 \begin{pmatrix} u_2 \\ v_2 \end{pmatrix} - \tilde{s} \cos^2 \omega_0 \begin{pmatrix} u_3 \\ v_3 \end{pmatrix} \\ - \tilde{s} \cos \omega_0 \sin \omega_0 \begin{pmatrix} u_4 \\ v_4 \end{pmatrix} - \tilde{s} \sin^2 \omega_0 \begin{pmatrix} A_3 \varphi_j^2 \\ B_3 \varphi_j^2 \end{pmatrix}.$$

Then

$$(d_2, s, W) = \left(\tilde{d}_2, \tilde{s}, L_1^{-1}(\hat{d}) \begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix} \right)$$

is the solution of (3.10), which implies $K_{(d_2, s, W)}(\hat{d}, 0, 0; \omega_0)$ is surjective.

Applying the implicit function theorem to

$$K(d_2, s, W; \omega) = 0, \quad (3.12)$$

we can know that there is a curve of nonconstant solutions $(d_2(\omega), s(\omega), W(\omega))$ of (3.12) in small neighborhood of ω_0 , where ω_0 satisfies (3.6), $d_2(\omega)$, $s(\omega)$ and $W(\omega)$ are continuously differentiable functions and satisfy $d_2(\omega_0) = \hat{d}$, $s(\omega_0) = 0$, $W(\omega_0) = 0$. Therefore, $(d_2(\omega), s(\omega)(\cos \omega \Phi_i + \sin \omega \Phi_j) + W(\omega))$ are nonconstant solutions of $F(d_2, (u, v)) = 0$.

Case 2: $i = 2j$. A simple calculation yields

$$\int_0^\pi \varphi_i^2 \varphi_j = 0, \quad \int_0^\pi \varphi_j^2 \varphi_i = \sqrt{\frac{1}{2\pi}} \text{ and } \int_0^\pi \varphi_i^3 = \int_0^\pi \varphi_j^3 = 0.$$

Then

$$\begin{pmatrix} A_1 \varphi_i^2 \\ B_1 \varphi_i^2 \end{pmatrix} \in Y_2.$$

We decompose

$$\begin{pmatrix} A_3 \varphi_j^2 \\ B_3 \varphi_j^2 \end{pmatrix} = c_5 \Phi_i + \begin{pmatrix} u_5 \\ v_5 \end{pmatrix} \text{ and } \begin{pmatrix} A_2 \varphi_i \varphi_j \\ B_2 \varphi_i \varphi_j \end{pmatrix} = c_6 \Phi_j + \begin{pmatrix} u_6 \\ v_6 \end{pmatrix},$$

where

$$c_5 = \frac{A_3 + B_3 b_i^*}{1 + b_i b_i^*} \int_0^\pi \varphi_i \varphi_j^2 dx = \sqrt{\frac{1}{2\pi}} \frac{A_3 + B_3 b_i^*}{1 + b_i b_i^*}, \quad \begin{pmatrix} u_5 \\ v_5 \end{pmatrix} = \begin{pmatrix} A_3 \varphi_j^2 - c_5 \varphi_i \\ B_3 \varphi_j^2 - c_5 b_i \varphi_i \end{pmatrix} \in Y_2;$$

$$c_6 = \frac{A_2 + B_2 b_j^*}{1 + b_j b_j^*} \int_0^\pi \varphi_i \varphi_j^2 dx = \sqrt{\frac{1}{2\pi}} \frac{A_2 + B_2 b_j^*}{1 + b_j b_j^*}, \quad \begin{pmatrix} u_6 \\ v_6 \end{pmatrix} = \begin{pmatrix} A_2 \varphi_i \varphi_j - c_6 \varphi_j \\ B_2 \varphi_i \varphi_j - c_6 b_j \varphi_j \end{pmatrix} \in Y_2.$$

Hence, we have

$$\Upsilon_1 = (-d_2 c_1 b_i \lambda_i \cos \omega_0 + s c_5 \sin^2 \omega_0) \Phi_i + (-d_2 c_2 b_j \lambda_j \sin \omega_0 + s c_6 \sin \omega_0 \cos \omega_0) \Phi_j,$$

$$\Upsilon_2 = L_1(\hat{d})W - d_2 b_i \lambda_i \cos \omega_0 \begin{pmatrix} u_1 \\ v_1 \end{pmatrix} - d_2 b_j \lambda_j \sin \omega_0 \begin{pmatrix} u_2 \\ v_2 \end{pmatrix} + s \cos^2 \omega_0 \begin{pmatrix} A_1 \varphi_i^2 \\ B_1 \varphi_i^2 \end{pmatrix}$$

$$+ s \cos \omega_0 \sin \omega_0 \begin{pmatrix} u_6 \\ v_6 \end{pmatrix} + s \sin^2 \omega_0 \begin{pmatrix} u_5 \\ v_5 \end{pmatrix}.$$

As in **Case 1** above, if ω_0 satisfies (3.7), then $K_{(d_2, s, W)}(\hat{d}, 0, 0; \omega_0)$ is an isomorphism from $\mathbb{R}^+ \times \mathbb{R} \times X_2$ to Y . By the implicit function theorem, we finish the proof of this case. Thus the whole proof is completed. \square

Remark 3.2. In Theorem 3.1 (ii), the existence of nonconstant positive solution of (3.2) is showed. Indeed, we derive many curves of nonconstant solutions because ω_0 is not unique and can be chosen only to satisfy (3.6) or (3.7). Moreover, due to $b_i \neq b_j$, it is impossible that both A_k and $B_k, k = 1, 2, 3$, are simultaneously equal to zero, which implies that there must exists ω_0 satisfying the condition (3.6) above. Similarly, we can check that there must exists ω_0 satisfying the condition (3.7) above.

3.2. Global bifurcation

Theorem 3.1 provides no information of the bifurcation curve Γ_j far from the equilibrium. In order to understand its global structure, a further study is therefore necessary.

We first introduce the standard abstract bifurcation theorem from [37] for readers' convenience. Let X be a Banach space and let $T : \mathbb{R} \times X \rightarrow X$ be a compact, continuously differentiable operator such that $T(a, 0) = 0$. Assume that T can be written as

$$T(a, U) = K(a)U + W(a, U), \quad (3.13)$$

where $K(a)$ is a linear compact operator and the Fréchet derivative $W_U(a, 0) = 0$. Regarding a as a bifurcation parameter, we will undertake a global bifurcation analysis for the equation

$$U = T(a, U). \quad (3.14)$$

We suppose that $\mathbb{I} - K : X \rightarrow X$ is a bijection. Then the Leray-Schauder degree

$$\deg(\mathbb{I} - K, \hat{B}, 0) = (-1)^p,$$

where \hat{B} is a ball centered at 0 in X and p is the sum of the algebraic multiplicities of the eigenvalues of K that are larger than 1. If x_0 is an isolated fixed point of the operator T and B is a ball centered at x_0 such that x_0 is the unique fixed point of T in B , the index of T at x_0 is defined as

$$\text{index}(T, x_0) = \deg(\mathbb{I} - T, B, x_0).$$

Moreover, if x_0 is a fixed point of T and $I - T^*(x_0)$ is invertible, then x_0 is an isolated fixed point of T and

$$\text{index}(T, x_0) = \deg(\mathbb{I} - T, B, x_0) = \deg(\mathbb{I} - T^*(x_0), \hat{B}, 0),$$

where B and \hat{B} are sufficiently small.

We now state the result on the global bifurcation for the operator T defined by (3.14).

Lemma 3.3. [37, Theorem 1.3] *Let a_0 be such that $\mathbb{I} - K(a)$ is invertible if $0 < |a - a_0| < \epsilon$ for $\epsilon > 0$. Assume that $\text{index}(T(a, \cdot), 0)$ is constant on $(a_0 - \epsilon, a_0)$ and on $(a_0, a_0 + \epsilon)$; moreover, if $a_0 - \epsilon < a_1 < a_0 < a_2 < a_0 + \epsilon$, then $\text{index}(T(a_1, \cdot), 0) = \text{index}(T(a_2, \cdot), 0)$. Then there exists a continuum C in the $a - U$ plane of solutions of (3.14) such that one of the following alternatives is true*

- (i) C joins $(a_0, 0)$ to $(\hat{a}, 0)$ where $\mathbb{I} - K(\hat{a})$ is not invertible;
- (ii) C joins $(a_0, 0)$ to ∞ in $\mathbb{R} \times X$.

Theorem 3.4. *Under the same assumptions as in Theorem 3.1, the projection of the bifurcation curve Γ_j is 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 model (1.2) possesses at least one non-constant positive solution, where $\bar{d}_2 = \min_{0 \leq i \leq i_0} d_2^i$.*

Proof. First, we rewrite model (1.2) in a form that the standard global bifurcation theory can be more conveniently applied.

Let $\tilde{u} = u - u^*$, $\tilde{v} = v - v^*$, then (1.2) is transformed into

$$\begin{cases} -d_1 \tilde{u}_{xx} = a_{11} \tilde{u} + a_{12} \tilde{v} + h_1(\tilde{u}, \tilde{v}), \\ -d_2 \tilde{v}_{xx} = a_{21} \tilde{u} + a_{22} \tilde{v} + h_2(\tilde{u}, \tilde{v}), \end{cases} \quad (3.15)$$

where $h_1(\tilde{u}, \tilde{v}), h_2(\tilde{u}, \tilde{v})$ are higher-order terms of \tilde{u} and \tilde{v} . The constant steady state (u^*, v^*) of (1.2) shifts to $(0, 0)$ of this new system.

Let $G_1 : h \rightarrow \omega$ denote the Green operator for the boundary value problem

$$a_{11}\omega - d_1\omega_{xx} = h \quad \text{in } (0, \pi), \quad \omega_x = 0 \quad \text{on } 0, \pi,$$

and $G_2 : h \rightarrow \omega$ the Green operator for

$$a_{22}\omega - d_2\omega_{xx} = h \quad \text{in } (0, \pi), \quad \omega_x = 0 \quad \text{on } 0, \pi,$$

where $a_{11} > 0$ and $a_{22} < 0$. Put $\tilde{U} = (\tilde{u}, \tilde{v})$,

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

and

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

Recall that

$$X = \{(u, v) \mid u, v \in C^2(0, \pi), u_x = v_x = 0, x = 0, \pi\}.$$

Then the boundary value problem (3.15) can be interpreted as the equation

$$\tilde{U} = K(d_2)\tilde{U} + H(\tilde{U}) \text{ in } X. \quad (3.16)$$

Note that $K(d_2)$ is a compact linear operator on X for any given $d_2 > 0$, $H(\tilde{U}) = o(|\tilde{U}|)$ for \tilde{U} near zero uniformly on closed d_2 sub-intervals of $(0, \infty)$, and is a compact operator on X 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 3.1 it is seen that $\ker(K(d_2^j) - I) = \ker L_1 = \text{span}\{\Phi_j\}$, 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 hull space $\cup_{i=1}^{\infty} \ker(K - I)^i$, 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 [36], where K^* is the adjoint of K .

Let $(\hat{\phi}, \hat{\psi}) \in \ker(K^* - I)$, then

$$2a_{11}G_1(\hat{\phi}) + a_{22}G_2(\hat{\psi}) = \hat{\phi}, \quad a_{12}G_1(\hat{\phi}) = \hat{\psi}.$$

By the definition of G_1 and G_2 we obtain

$$-d_2^j a_{12} \frac{\partial^2}{\partial x^2} \hat{\phi} = f_{\hat{\phi}} \hat{\phi} + f_{\hat{\psi}} \hat{\psi}, \quad -d_1 \frac{\partial^2}{\partial x^2} \hat{\psi} = a_{12} \hat{\phi} - a_{11} \hat{\psi},$$

where

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

Let $\hat{\phi} = \sum_{i=0}^{\infty} \hat{a}_i \varphi_i$, $\hat{\psi} = \sum_{i=0}^{\infty} \hat{b}_i \varphi_i$, then

$$\sum_{i=0}^{\infty} \hat{B}_i \begin{pmatrix} \hat{a}_i \\ \hat{b}_i \end{pmatrix} \varphi_i = 0, \quad \text{where } \hat{B}_i = \begin{pmatrix} -d_2^j a_{12} \lambda_i + f_{\hat{\phi}} & f_{\hat{\psi}} \\ a_{12} & -d_1 \lambda_i - a_{11} \end{pmatrix}.$$

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 (3.9) (replacing d_2 there by d_2^j). Thus $\det \bar{B}_i = 0$ only for $i = j$, and $\ker(K^* - I) = \text{span}\{\hat{\Phi}_j\}$, where $\hat{\Phi}_j = (d_1 \lambda_j + a_{11}, 1)^T \varphi_j$. This shows that $\Phi_j \notin (\ker(K^* - I))^{\perp} = R(K - I)$, 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 $I - K(d_2) : X \rightarrow X$ is a bijection and 0 is an isolated solution of (3.15) for this fixed d_2 . The index of this isolated zero of $I - K(d_2) - H$ is given by

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

where B is a sufficiently small ball center at 0, and p is the sum of the algebraic multiplicities of the eigenvalues of $K(d_2)$ larger than 1.

For our bifurcation analysis, it is also necessary to show that this index changes as d_2 crosses d_2^j , that is, for $\epsilon > 0$ sufficiently small, we need to verify

$$\text{index}(I - K(d_2^j - \epsilon) - H, (d_2^j - \epsilon, 0)) \neq \text{index}(I - K(d_2^j + \epsilon) - H, (d_2^j + \epsilon, 0)). \quad (3.17)$$

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

$$-d_1\mu\hat{\phi}_{xx} = (2 - \mu)a_{11}\hat{\phi} + a_{12}\hat{\psi}, \quad -d_2\mu\hat{\psi}_{xx} = a_{21}\hat{\phi} + a_{22}\mu\hat{\psi}.$$

By using the Fourier cosine series $\hat{\phi} = \sum \hat{a}_i \varphi_i$ and $\hat{\psi} = \sum \hat{b}_i \varphi_i$, we have

$$\sum_{i=0}^{\infty} \tilde{B}_i \begin{pmatrix} \hat{a}_i \\ \hat{b}_i \end{pmatrix} \varphi_i = 0, \quad \text{where } \tilde{B}_i = \begin{pmatrix} (2 - \mu)a_{11} - d_1\lambda_i\mu & a_{12} \\ a_{21} & (a_{22} - d_2\lambda_i)\mu \end{pmatrix}.$$

Thus the set of eigenvalues of $K(d_2)$ consists of all μ which implies the following characteristic equation

$$(d_1\lambda_i + a_{11})\mu^2 - 2a_{11}\mu - \frac{a_{12}a_{21}}{d_2\lambda_i - a_{22}} = 0, \quad (3.18)$$

where the integer i runs from zero to ∞ . In particular, for $d_2 = d_2^j$, if $\mu = 1$ is a root of (3.18), then a simple calculation leads to $d_2^j = d_2^i$, and so $j = i$ by the assumption. Therefore, without counting the eigenvalues corresponding to $i \neq j$ in (3.18), $K(d_2)$ has the same number of eigenvalues greater than 1 for all d_2 close to d_2^j , and they have the same multiplicities. On the other hand, for $i = j$ in (3.18), we let $\mu(d_2), \tilde{\mu}(d_2)$ denote the two roots of (3.18). By a straightforward calculation, we find that

$$\mu(d_2^j) = 1 \quad \text{and} \quad \tilde{\mu}(d_2^j) = \frac{a_{11} - d_1\lambda_i}{a_{11} + d_1\lambda_i} < 1.$$

Now for d_2 close to d_2^j , we obtain $\tilde{\mu}(d_2^j) < 1$. As the constant term $-a_{12}a_{21}/d_2\lambda_i - a_{22}$ in (3.18) is a decreasing function of d_2 , there exists

$$\mu(d_2^j + \epsilon) > 1, \quad \mu(d_2^j - \epsilon) < 1.$$

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 above we can show this eigenvalue has algebraic multiplicity one. This verifies (3.17).

Therefore, we apply Theorem 1.3 in [37] to conclude that Γ_j either

- (1) meets infinity in $\mathbb{R} \times X$, or
- (2) meets $(d_2^k, (u^*, v^*))$ for some $k \neq j, d_2^k > 0$.

We show that Γ_j must extend to infinity in $\mathbb{R} \times X$ by the idea of Nishiura [38] and Takagi [39]. Thus, the theorem is verified. \square

Remark 3.5. Theorem 3.4 shows that there is a smooth curve Γ_j of positive solutions of model (1.2) bifurcating from (d_2^j, u^*, v^*) , with Γ_j contained in a global branch of the positive solutions of (1.2).

4. Discussion and conclusion

In this paper, based on the results in [17], we make a detailed descriptions for the local (c.f., Theorem 3.1) and global (c.f., Theorem 3.4) bifurcation structure of nonconstant positive steady states of a modified Holling-Tanner predator-prey system under homogeneous Neumann boundary condition. These theorems and the results in [17] can give a profile of the solutions of model (1.1). The results are beneficial to population persistence control, that is, we must do our best to regulate the parameters in the special range to avoid population extinction.

It is should be noted that our results are based on 1-dimensional space. And in the N -dimensional space, $N \geq 2$, we can also obtain a local bifurcation result, which is an analogue of Theorem 3.1. But the global bifurcation (Theorem 3.4) is only established in the square domain. For instance, in the special 2-D case with $(0, L) \times (0, L)$. In this special case, the Neumann eigenvalue problem has eigen-pairs

$$\lambda_{mn} = \frac{(m^2 + n^2)\pi^2}{L^2}, \quad \varphi_{mn}(x, y) = \cos \frac{m\pi x}{L} \cos \frac{n\pi y}{L}, \quad m, n \in \mathbb{N}^+.$$

Each eigenvalue gives rise to bifurcation point d_2^{mn} , with λ_j being replaced by λ_{mn} in (3.3). We mention that though the boundary of the square is not smooth, the Neumann boundary condition has to be interpreted in the weak fashion via first Green's identity in the standard way [40].

Acknowledgments

This research was supported by the National Science Foundation of China (11601179, 61672013 and 61772017) and Huaian Key Laboratory for Infectious Diseases Control and Prevention (HAP201704), Huaian, Jiangsu Province, China.

Conflict of interest

The authors declare that they have no competing interests.

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