POSITIVE STEADY STATES OF A DENSITY-DEPENDENT PREDATOR-PREY MODEL WITH DIFFUSION

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Abstract. In this paper, we investigate the rich dynamics of a diffusive Holling type-II predator-prey model with density-dependent death rate for the predator under homogeneous Neumann boundary condition. The value of this study lies in two-aspects. Mathematically, we show the stability of the constant positive steady state solution, the existence and nonexistence, the local and global structure of nonconstant positive steady state solutions. And biologically, we find that Turing instability is induced by the density-dependent death rate, and both the general stationary pattern and Turing pattern can be observed as a result of diffusion.

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1. Introduction. In this paper, we study the positive steady states of the following reaction-diffusion predator-prey model with prey-dependent Holling type-II functional response and density-dependent death rate for the predator:

\[
\begin{aligned}
N_t - d_1 \Delta N &= rN \left(1 - \frac{N}{K}\right) - \frac{cNP}{a + N}, & x \in \Omega, \ t > 0, \\
P_t - d_2 \Delta P &= sP \left(-q - \delta P + \frac{cN}{a + N}\right), & x \in \Omega, \ t > 0, \\
\frac{\partial N}{\partial \nu} &= \frac{\partial P}{\partial \nu} = 0, & x \in \partial \Omega, \ t > 0, \\
N(x, 0) &= N_0(x) \geq 0, \ P(x, 0) = P_0(x) \geq 0, & x \in \Omega,
\end{aligned}
\]

(1)

where \(N(x, t), P(x, t)\) represent population densities of prey and predator at time \(t\) and location \(x \in \Omega \subset \mathbb{R}^2\), respectively. \(\Omega\) is a bounded domain with smooth boundary \(\partial \Omega\) and \(\nu\) is the outward unit normal vector of the boundary \(\partial \Omega\). And \(\frac{cN}{a + N}\) describes functional response of the predator, which is Holling type-II functional response. All parameters \(r, c, a, q, s, K, \delta\) are positive. \(r\) is the intrinsic growth rate or biotic potential of the prey \(N\), \(c\) the rate of capture, \(a\) half saturation constant, \(q\) the death rate of the predator, \(s\) the feed concentration, \(\delta\) proportional to the density-dependent death rate and \(K\) the carrying capacity. The positive constants \(d_1\) and \(d_2\) are the diffusion coefficients of \(N(x, t)\) and \(P(x, t)\), respectively. \(\Delta\) is the Laplacian in two dimensional space, which describes the random moving.

In mathematical ecology, the classical predator-prey system, due independently to Lotka and Volterra in the 1920s, reflects only population changes due to predation in a situation where predator and prey densities are not spatially dependent, and the corresponding model is systems of ordinary differential equations (ODE). Interaction between predator and prey has been a central research theme in ecology over many decades [1, 2, 4, 12, 15, 28]. A wide variety of temporal predator-prey models have been investigated to help us understand the steady-state or oscillatory coexistence of both the species as well as the factors responsible for the system collapse through the extinction of one or both the species. Prey-dependant functional responses play an important role in dynamics of predator-prey models [1, 2, 17]. Gause type predator-prey models have been studied by many researchers [3, 13, 32, 18]. The Gause type predator-prey models with predator’s density-dependant functional response exhibit very rich dynamic behavior [17, 13].

But the ODE model does not take into account either the fact that population is usually not homogeneously distributed, or the fact that predators and preys naturally develop strategies for survival. Both of these considerations involve diffusion processes which can be quite intricate as different concentration levels of predators and preys cause different population movements [16, 37, 38, 11, 36, 31].

In [5], the authors established the following model with Allee effect (measured by the term \(\frac{m}{N + b}\)):

\[
\begin{aligned}
N_t - d_1 \Delta N &= rN \left(1 - \frac{N}{K} - \frac{m}{N + b}\right) - \frac{cNP}{a + N}, & x \in \Omega, \ t > 0, \\
P_t - d_2 \Delta P &= sP \left(-q + \frac{cN}{a + N}\right), & x \in \Omega, \ t > 0.
\end{aligned}
\]

(2)

and investigated the asymptotical stability of the positive equilibrium, and gave the conditions of the existence of the Hopf bifurcation. Furthermore, in [6], based on the results in [5], the authors investigated the effect of density-dependent death rate
on the dynamics of the following model:

\[
\begin{aligned}
N_t - d_1 \Delta N &= r N \left(1 - \frac{N}{K}\right) - \frac{m P}{a+N}, \quad x \in \Omega, \ t > 0, \\
N_t - d_2 \Delta P &= s P \left(-q - \delta P + \frac{c N}{a+N}\right), \quad x \in \Omega, \ t > 0.
\end{aligned}
\]

(3)

and found that the density-dependent death rate \(\delta\) in predator can induce Turing instability, and model (3) exhibits a diffusion-controlled formation growth of spots, stripes, and holes pattern replication via numerical simulations. Obviously, model (1) is the special case of \(m = 0\) of model (3) in [6].

And there naturally comes a question: does model (3) without Allee effect, i.e., model (1), exhibit Turing pattern replication? This is one of our main goals in this paper.

The other goal of this paper is to investigate the existence, nonexistence and structure of nonconstant positive steady-state solutions to problem (1), specifically, we will concentrate on the following steady state system

\[
\begin{aligned}
-d_1 \Delta N &= r N \left(1 - \frac{N}{K}\right) - \frac{m P}{a+N}, \quad x \in \Omega, \\
-d_2 \Delta P &= s P \left(-q - \delta P + \frac{c N}{a+N}\right), \quad x \in \Omega, \\
\frac{\partial N}{\partial \nu} = \frac{\partial P}{\partial \nu} = 0, \quad x \in \partial \Omega.
\end{aligned}
\]

(4)

The rest of this article is organized as follows: in Section 2, we discuss the stability of constant steady state solution and give the conditions of Turing instability. In Section 3, we investigate the nonexistence/existence of nonconstant positive steady states. In Section 4, we analyze the local and global structure of nonconstant positive solutions, and give the direction of the bifurcation.

2. Constant steady state and Turing instability. In this section, we mainly discuss the stability of constant steady state solution. For convenience, we denote

\[
\begin{aligned}
f(N, P) &= r N \left(1 - \frac{N}{K}\right) - \frac{m P}{a+N}, \\
g(N, P) &= s P \left(-q - \delta P + \frac{c N}{a+N}\right).
\end{aligned}
\]

Then (1) can be written as

\[
\begin{aligned}
N_t - d_1 \Delta N &= f(N, P), \quad x \in \Omega, \ t > 0, \\
P_t - d_2 \Delta P &= g(N, P), \quad x \in \Omega, \ t > 0, \\
\frac{\partial N}{\partial \nu} = \frac{\partial P}{\partial \nu} = 0, \quad x \in \partial \Omega, \ t > 0,
\end{aligned}
\]

(5)

Whereas the corresponding spatially homogeneous counterpart (i.e., \(d_1 = d_2 = 0\)) of problem (5) is as follows:

\[
\begin{aligned}
\frac{dN}{dt} &= f(N, P), \quad t > 0, \\
\frac{dP}{dt} &= g(N, P), \quad t > 0.
\end{aligned}
\]

(6)

The Turing instability refers to “diffusion driven instability”, i.e., the stability of the positive constant steady state \(E^*\) changing from stable for the ordinary differential equations (ODE) dynamics (6), to unstable, for the partial differential equations (PDE) dynamics (1) or (5).

Obviously, the ODE model (6) has the same constant steady states as the PDE model (5). And model (6) has a trivial steady state \(E_0 = (0,0)\), a semitrivial steady
state $E_1 = (K, 0)$. In addition, model (6) has at least one positive steady state $E^* = (N^*, P^*)$, where $P^* = \frac{1}{\delta(a + N^*)}((c - q)N^* - aq)$, and $N^*$ is the positive roots of polynomial equation

$$N^3 + (2a - K)N^2 + (a^2 + \frac{cK(c - q)}{r\delta} - 2aK)N - \left(a^2K + \frac{acqK}{r\delta}\right) = 0.$$  

(7)

Lemma 2.1. (Shengjins discriminant [10]) Let equation $x^3 + Bx^2 + Cx + D = 0$, where $B, C, D \in \mathbb{R}$. Assume $\Delta = B^2 - 3C, \mathbb{B} = BC - 9D, \mathbb{C} = C^2 - 3BD$ and $\Delta = \mathbb{B}^2 - 4\mathbb{A}\mathbb{C}$. Then

(i) The equation has three real roots if and only if $\Delta \leq 0$;

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

Lemma 2.2. (Descartes' rule of signs [9]) Let $A(X) = \sum_{i=0}^{n} a_iX^i$ be a polynomial of degree $n$ with real coefficients that has exactly $p$ positive real roots, counted with multiplicities. Let $v = \text{var}(a_0, \ldots, a_n)$ be the number of sign variations in its coefficient sequence. Then $v \geq p$ and $v \equiv p \pmod{2}$. If all roots of $A(X)$ are real, then $v = p$.

For equation (7), it follows from Lemma 2.1, set

$$B := 2a - K, \quad C := a^2 + \frac{cK(c - q)}{r\delta} - 2aK, \quad D := -\left(a^2K + \frac{acqK}{r\delta}\right).$$  

(8)

and

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

(9)

Theorem 2.3. (i) If $\Delta > 0$, then equation (7) has a unique positive solution.

(ii) If $\Delta \leq 0$, then

(ii-1) if $B \geq 0$ (i.e., $a \geq K/2$), equation (7) has a unique positive solution;

(ii-2) if $B < 0$ (i.e., $a < K/2$) and $C < 0$ (i.e., $a^2r\delta + cK(c - q) < 2ar\delta K$), equation (7) has a unique positive solution.

Proof. (i) If $\Delta > 0$, by Lemma 2.1, (7) has a unique positive roots. Notice that the constant term $D$ of the left hand of equation (7) is negative, hence equation (7) has a unique positive solution.

(ii) If $\Delta \leq 0$, applying Lemma 2.1 again, then (7) has three real roots,

(ii-1) if $a > K/2$, the signs of the coefficient $1, B, C, D$ of (7) may be $++--$ or $+-+-$, the signs change only one time in these two cases above. By Lemma 2.2, we can claim that (7) has a unique positive root. It’s easy to verify that the conclusion is correct in the case of $a = K/2$.

(ii-2) if $a < K/2$ and $a^2r\delta + cK(c - q) < 2ar\delta K$ hold, the signs of the coefficient $1, B, C, D$ of (7) is $+-+-$. Combined with Lemma 2.2, (7) has a unique positive root. The proof is complete.

Based on the results above, we can obtain that (6) or (5) has a unique positive steady state $E^* = (N^*, P^*)$.

Next, for simplicity, we will focus on the stability of the unique positive steady state $E^*$ for ODE model (6) and PDE model (5), respectively.
First, we consider the stability of $E^*$ for ODE model (6). By simple calculation, we can obtain the Jacobian matrix of (6) evaluated at $E^*$ is given by

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

where

$$a_{11} = \frac{cP^*N^*}{(a + N^*)^2} - \frac{rN^*}{K}, \quad a_{12} = -\frac{cN^*}{a + N^*} < 0, \quad a_{21} = \frac{acsP^*}{(a + N^*)^2} > 0, \quad a_{22} = -\delta sP^* < 0.$$  \hspace{1cm} (10)

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

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

where

$$Q = a_{11} + a_{22}, \quad P = a_{11}a_{22} - a_{12}a_{21}.$$  \hspace{1cm} (11)

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

**Theorem 2.4.** The constant steady state solution $E^*$ of ODE model (6) is locally asymptotically stable, if one of the following conditions holds:

(i) $a_{11} < 0$;

(ii) $a_{11} > 0$, $s > 1 - \frac{cP^*N^*}{\bar{\delta}P^*\left(\frac{cP^*N^*}{(a + N^*)^2} - \frac{rN^*}{K}\right)}$, and $\frac{ac^2}{(a + N^*)^3} - \delta\left(\frac{cP^*}{(a + N^*)^2} - \frac{r}{K}\right) > 0$.

Next, we consider the stability of $E^*$ for PDE model (5). Consider the eigenvalue problem

$$-\Delta \phi = \lambda \phi, \quad x \in \Omega, \quad \frac{\partial \phi}{\partial \nu} = 0, \quad x \in \partial \Omega. \hspace{1cm} (12)$$

Let $0 = \lambda_0 < \lambda_1 < \ldots$ be the sequence of eigenvalues for the elliptic operator $-\Delta$ subject to the Neumann boundary condition on $\Omega$, where $\lambda_i (i \geq 1)$ has multiplicity $m_i \geq 1$, whose corresponding normalized eigenfunctions are given by $\phi_{ij}$, where $j = 1, 2, \ldots, m_i$. This set of eigenfunctions form an orthogonal basis in $L^2(\Omega)$.

If $a_{11} > 0$ and $d_1\lambda_1 < a_{11}$, \hspace{1cm} (13)

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

Clearly, if (13) is satisfied, $1 \leq i_0 < \infty$. In this case, we let

$$\tilde{d}_2 = \min_{0 \leq i \leq i_0} d_2(E^*),$$

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

$$d_2(E^*) = \frac{a_{11}a_{22}\lambda_i - a_{11}a_{22} + a_{12}a_{21}}{\lambda_i(d_1\lambda_i - a_{11})}.$$  \hspace{1cm} (14)

Therefore we can obtain the stability of $E^*$ of PDE model (5) as follows:

**Theorem 2.5.** (i) If $a_{11} < 0$, $E^*$ is locally asymptotically stable.

(ii) If $a_{11} > 0$, assume that $s > 1 - \frac{cP^*N^*}{\bar{\delta}P^*\left(\frac{cP^*N^*}{(a + N^*)^2} - \frac{rN^*}{K}\right)}$, and $\frac{ac^2}{(a + N^*)^3} - \delta\left(\frac{cP^*}{(a + N^*)^2} - \frac{r}{K}\right) > 0$ hold, then

(ii-1) if $d_1\lambda_1 < a_{11}$ and $0 < \tilde{d}_2 < d_2$ hold, $E^*$ is locally asymptotically stable.
(ii-2) if $d_1 \lambda_1 < a_{11}$ and $d_2 > \tilde{d}_2$ hold, then $E^*$ is unstable, and hence Turing unstable.

**Proof.** Consider the linearization operator evaluated at $E^*$:

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

Suppose $\Phi = (\varphi, \psi) \in L$ is an eigenfunction of $L$ corresponding to an eigenvalue $\eta$, and we can obtain

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

write $\varphi = \sum_{0 \leq i \leq m, 1 \leq j \leq m_i} a_{ij} \phi_{ij}$, $\psi = \sum_{0 \leq i \leq m, 1 \leq j \leq m_i} b_{ij} \phi_{ij}$, then

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

where

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

Easy to know that $\eta$ is the eigenvalue of $L$ if and only if det $B_i = 0$, which leads to

$$\eta^2 + Q_i \eta + P_i = 0,$$

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 $P_i > 0$, which implies that $\text{Re}\{\eta_i\} < 0$ for all eigenvalues $\eta$. Therefore, the constant solution $E^*$ is locally asymptotically stable.

(ii) Moreover, if $s > \frac{1}{\delta P^*} \left( \frac{c P^* N^*}{(a + N^*)^2} - \frac{\sigma N^*}{K} \right) + \frac{ac^2}{(a + N^*)^3} - \delta \left( \frac{c P^*}{(a + N^*)^2} - \frac{\sigma}{K} \right) > 0$ holds, then we have $Q_i > 0$ and $d_1 a_{22} \lambda_i - a_{11} a_{22} + a_{12} a_{21} < 0$, and therefore,

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

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

One the other hand, if $i > i_0$, then $d_1 \lambda_i > a_{11}$. So, we have $P_i > 0$. The analysis yields the local asymptotical stability of $E^*$.

(ii-2) If $a_{11} > 0$, $d_1 \lambda_1 < a_{11}$ and $d_2 > \tilde{d}_2$, then we may assume the minimum in (15) is attained at $j \in [1, i_0]$. Thus $d_2 > \tilde{d}_2$, which implies

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

Hence, $E^*$ is unstable in this case.

The proof is complete. \hfill \Box

**Remark 1.** From Theorem 2.4 and 2.5, we can know that if $a_{11} > 0$, the stability of the constant equilibrium $E^*$ may change from stable, for the ODE dynamics (6), to unstable, for the PDE dynamics (5), whereas those of other constant equilibria are invariant.
Remark 2. Compare these results above with [5] and [6], we can conclude that Turing instability is not induced by Allee effect, but density-dependent death rate $\delta$.

Example 1. As an example, motivated by [6], we take the parameters in model (5) and (6) as:

$$s = 3, r = 1, K = 10, a = 1.5, c = 1, q = 0.35, \delta = 0.0425.$$ 

And easy to know that there is a unique constant positive steady state $E^* = (N^*, P^*) = (1.2369, 2.3984)$.

For the ODE model (6), from Theorem 2.4, easy to verify that $E^*$ is stable. For the PDE model (5) on one-dimensional space domain $(0, \pi)$, after fixing $d_1 = 0.015$, from Theorem 2.5, we can know that if $d_2 > d_2 = 0.4928$, $E^*$ is Turing unstable, and model (5) exhibits Turing pattern. In Fig. 1, we show the numerical results of model (5) with different values of $d_2$. Fig. 1(a) shows the numerical simulations of Turing instability in model (5) with $d_2 = 0.6 > d_2$. And Fig. 1(b) the numerical simulations of the stable coexistence equilibrium solution $(N(x, t), P(x, t))$ of model (5) with $d_2 = 0.25 < d_2$.

3. Nonconstant positive solutions. In this section, we study the steady state problem (4), and we establish the existence and nonexistence results of positive nonconstant solutions, and in these results, the diffusion coefficients $d_1$ and $d_2$ play an important role. The mathematical techniques to be employed are energy method and implicit function theorem, respectively. From now on, let $N(\lambda_i) \in H^1(\Omega)$ be the eigenspace. Unless otherwise specified, in the following section, we always require that $a_{11} > 0$ and

$$\frac{ac^2}{(a + N^*)^3} - \delta \left( \frac{cP^*}{(a + N^*)^2} - \frac{r}{K} \right) > 0$$ hold.

3.1. A priori estimate for positive solutions. In this subsection, we derive some priori estimates of upper and lower bounds for positive solutions to (4), and these estimates will become fundamental in yielding the existence and nonexistence results of positive nonconstant solutions to (4) in the forthcoming subsections.

Lemma 3.1. (Maximum Principle [22]) Suppose that $g \in C(\overline{\Omega} \times \mathbb{R})$.

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

$$\Delta w(x) + g(x, w(x)) \geq 0, \quad x \in \Omega, \quad \partial_{\nu} w \leq 0, \quad x \in \partial\Omega.$$ 

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

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

$$\Delta w(x) + g(x, w(x)) \leq 0, \quad x \in \Omega, \quad \partial_{\nu} w \geq 0, \quad x \in \partial\Omega.$$ 

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

Lemma 3.2. (Harnack inequality [21]) Assume that $c \in C(\overline{\Omega})$ and let $w \in C^2(\Omega) \cap C^1(\overline{\Omega})$ be a positive solution to $\Delta w(x) + c(x)w(x) = 0$ in $\Omega$ and $\frac{\partial w}{\partial \nu} = 0$ on $\partial\Omega$.

Then there exist a positive constant $C_\ast(\|c\|_\infty)$ such that

$$\max_{\Omega} w \leq C_\ast \min_{\Omega} w.$$ 

Similar to Theorem 3.4 in [6], we can obtain the upper and lower bounds of the solutions to model (4).
Figure 1. Numerical simulations of the long time behavior of solution \((N(x,t), P(x,t))\) of model (5) with different values of \(d_2\). (a) \(d_2 = 0.6\); (b) \(d_2 = 0.25\);

Theorem 3.3. Assume that \(q < \frac{(c-q)K}{a}\) holds, let \(\tilde{d}\) be an arbitrary positive number, there exists a positive constant \(C = C(r, s, \delta, a, c, K)\) such that if \(d_1, d_2 \geq \tilde{d}\), then any positive solution \((N(x), P(x))\) of model (4) satisfies

\[
C \leq N(x), P(x) \leq \max\left\{K, \frac{(c-q)K - aq}{\delta(a + K)}\right\}.
\]

(16)

3.2. Nonexistence of nonconstant positive steady state solutions. In this subsection, we will present several nonexistence results of nonconstant positive solutions to (4).

First, similar to Theorem 4.4 in [6], we apply energy method to establish results of the nonexistence of nonconstant positive solutions of (4). For convenience, we denote \(\Lambda = \Lambda(r, K, s, c, a, q, \delta)\).

Theorem 3.4. Let \(\lambda_1\) be the smallest positive eigenvalue of the operator \(-\triangle\) on \(\Omega\) with zero-flux boundary condition. Assume \(q < c - \frac{ac}{a + K}\) holds, let \(D_2 > \frac{s(c-q)}{\lambda_1}\).

Then there exists a positive \(D_1 = D_1(\Lambda, D_2)\) such that model (4) has no positive non-constant steady-state provided that \(d_1 \geq D_1, \ d_2 \geq D_2\).
Second, we apply the implicit function theorem method to establish results of the nonexistence of nonconstant positive solutions of (4). First of all, we show the following Lemma, which can be found in [8].

**Lemma 3.5.** ([8]) Let \((N, P)\) be the positive solution of (4). Then we have
\[
\lim_{d_1 \to \infty} (N, P) = (N^*, P^*) \quad \text{in} \quad [C^2(\bar{\Omega})]^2,
\]
where \((N^*, P^*)\) is the positive solution of (4).

**Theorem 3.6.** Let \(\Lambda\) and \(d_2\) be fixed positive constants. Then there exists a positive constant \(d_1\) such that, when \(d_1 \geq d_1\), (4) has no nonconstant positive solutions.

**Proof.** Define \(W^{2,2}_\nu(\Omega) = \{ N \in W^{2,2} : \frac{\partial N}{\partial \nu}|_{\partial \Omega} = 0 \}\) and \(W^{2,2}_{\nu,0}(\Omega) = W^{2,2}_\nu(\Omega) \cap L^2_0(\Omega)\), where \(L^2_0(\Omega) = \{ N \in L^2(\Omega) : \int_\Omega N \, dx = 0 \}\). Denote \(\rho = d_1^{-1}\) and decompose \(N = h + z\) with \(h \in \mathbb{R}^1\) and \(z \in W^{2,2}_{\nu,0}\). Let
\[
F(\rho, N, h, z) = \begin{pmatrix}
\Delta z + \rho r(h + z) \left( 1 - \frac{h + z}{K} \right) - \frac{c(h + z)P}{a + (h + z)} \\
\int_\Omega r(h + z) \left( 1 - \frac{h + z}{K} \right) - \frac{c(h + z)P}{a + (h + z)} \, dx \\
d_2 \Delta P + sP \left( -q - \delta P + \frac{c(h + z)}{a + (h + z)} \right)
\end{pmatrix},
\]
Then
\[
F : \mathbb{R}^1 \times W^{2,2}_{\nu,0}(\Omega) \times \mathbb{R}^1 \times W^{2,2}_\nu(\Omega) \to \mathbb{R}^1 \times L^2_0(\Omega) \times L^2(\Omega)
\]
is a well-defined mapping, and for any \(\rho > 0\), it is clear that the solutions \((N, P)\) of (4) satisfy \(F(\rho, h, z, P) = 0\).

Let \(\Psi\) be the Fréchet derivative of \(F\) at \((0, N^*, 0, P^*)\) with respect to \((h, z, P)\), a direct computation yields
\[
\Psi(h, z, P) = \begin{pmatrix}
\Delta z \\
\int_\Omega (a_{11}(h + z) + a_{12}P) \, dx \\
d_2 \Delta P + a_{21}(h + z) + a_{22}P
\end{pmatrix},
\]
where \(a_{ij}\) is given in (10).

We claim that \(\Psi\) is an isomorphism operator. Assume that \(\Psi(h, z, P) = (0, 0, 0)\), then \(z = 0\). From the equation of \(P\), it follows that \(\int_\Omega P \, dx = -\frac{a_{21}}{a_{22}} h|\Omega|\). Substitute these results into the integral equations \(\int_\Omega (a_{11}(h + z) + a_{12}P) \, dx\) and we can obtain
\[
\left( -\frac{a_{12}a_{21}}{a_{22}} + a_{11} \right) h = 0.
\]
This is equivalent to \(\det\{J(E^*)\} h = 0\), considering the fact \(\det\{J(E^*)\} > 0\), therefore \(h = 0\), which implies that \((h, z, P) = (0, 0, 0)\) and \(\Psi\) is injection.

On the other hand, for a given \(h_1 \in L^2_0(\Omega)\), the problem
\[
-\Delta N = h_1 \quad \text{in} \quad \Omega, \quad N \in W^{2,2}_{\nu,0}(\Omega)
\]
has a unique solution. By using \(\det\{J(E^*)\} > 0\) again, one can also check that \(\Psi\) is also surjective. Consequently, \(\Psi^{-1}\) exists and is a bounded linear operator.

To complete the proof of this Theorem, we note that, by an implicit function theorem, there is a constant \(\sigma\) such that, for all \(0 < \rho < \sigma\), in a small neighborhood
of \((N^*, 0, P^*)\), the equation \(F(\rho, h, z, P)\) has a unique solution, which must be \((N^*, 0, P^*)\). Correspondingly, when \(d_1\) is large, in a small neighborhood of \((N^*, P^*)\), the problem (4) has only the constant solution \((N^*, P^*)\). This fact, combined with Lemma 3.5, concludes the proof. \(\square\)

**Remark 3.** The results in this subsection demonstrate such a phenomenon: when all diffusion coefficients are large, no patterns exist (c.f., Theorem 3.4); or even if only one diffusion coefficient is large, the patterns do not exist (c.f., Theorem 3.6), which implies that the diffusion is helpful to create nonconstant positive steady-states solutions to the predator-prey model (1). That is, these results show more delicate dependence on the diffusion coefficients for the predator-prey system.

### 3.3. Existence of nonconstant positive solutions

Let \(X = [H^1(\Omega)]^2, \{\phi_{ij}; j = 1, \cdots, dimN(\lambda_i)\}\) be an orthonormal basis of \(N(\lambda_i)\), and let

\[
X_{ij} = \{c\Phi_{ij} : c \in \mathbb{R}^2\}, \quad X_i = \bigoplus_{j=1}^{dimN(\lambda_i)} X_{ij}, \quad X = \bigoplus_{i=1}^{\infty} X_i.
\]

Let \(\Phi(E) = (d_1N, d_2P)^T, G = (f, g)^T\), where \(f\) and \(g\) are given in Section 2. Then the stationary problem of (4) can be written as

\[
-\Delta \Phi(E) = G(E), \quad x \in \Omega; \quad \frac{\partial E}{\partial \nu} = 0, \quad x \in \partial \Omega.
\]  \(\text{(17)}\)

In this subsection, we study the linearization of (17) at \(E^*\) and then proceed to calculate the fixed point index of \(E^*\) when it is an isolated solution.

Define

\[
Y = \{(N, P)^T \in [C^1(\Omega)]^2 | \frac{\partial N}{\partial \nu} = \frac{\partial P}{\partial \nu} = 0, \quad x \in \partial \Omega\},
\]

\[
Y^+ = \{E \in Y : N, P > 0 \text{ on } \Omega\},
\]

and, for \(C > 0\),

\[
B(C) = \{E \in Y : C^{-1} < N, P < C \text{ on } \Omega\}.
\]

Since the determinant of \(\Phi_E(E)\) is a positive for all nonnegative \(E, \Phi^{-1}_E(E)\) exists and \(\det\{\Phi^{-1}_E(E)\}\) is positive. Hence, \(E\) is a positive solution to (17) if and only if

\[
F(E) := E - (I - \Delta)^{-1}\{\Phi^{-1}_E(E)G(E) + E\} = 0 \quad \text{in } Y^+,
\]

where \((I - \Delta)^{-1}\) is the inverse of \(I - \Delta\) under the homogeneous Neumann boundary conditions. As \(F(\cdot)\) is a compact perturbation of the identity operator, for any \(B = B(C)\), the Leray-Schauder degree \(\text{deg}(F(\cdot), 0, B)\) is well defined if \(F(E) \neq 0\) on \(\partial B\).

Further, we note that \(D_E F(E^*) = I - (I - \Delta)^{-1}\{\Phi^{-1}_E(E^*)G_E(E^*) + I\}\) and recall that, if \(D_E F(E^*)\) is invertible, the fixed point index of \(F\) at \(E^*\) is well defined and

\[
\text{index}(F(\cdot), E^*) = (-1)^\gamma,
\]

where \(\gamma\) is the sum of the algebraic multiplicities of all the negative eigenvalues of \(D_E F(E^*)\).

Since the eigenvalues of \(D_E F(E^*)\) and their algebraic multiplicities are the same regardless of whether we consider an operator in \(X\) or in \(Y\), a straightforward calculation shows that, for each integer \(i \geq 0\) and each integer \(0 \leq j \leq \dim N(\lambda_i), X_{ij}\) is invariant under \(D_E F(E^*)\). Moreover, \(\lambda\) is an eigenvalue of \(D_E F(E^*)\) if and only if, for some \(i \geq 0\), it is an eigenvalue of the matrix

\[
B_i := I - \frac{1}{1 + \lambda_i}[\Phi^{-1}G_E(E^*) + I] = \frac{1}{1 + \lambda_i}[\lambda_i - \Phi^{-1}_E(E^*)G_E(E^*)].
\]

Thus, \(D_E F(E^*)\) is invertible if and only if the matrix \(B_i\) is nonsingular for all \(i \geq 0\).
Let $\lambda$ be an eigenvalue of $D_EF(E^*)$. We now calculate its algebraic multiplicity, which we denote by $\sigma(\lambda)$. Write
\[ H(\lambda) = H(E^*; \lambda) := \det \{ \lambda I - \Phi_E^{-1}G_E(E^*) \} = \det \{ (\lambda - \lambda_i)I + (1 + \lambda_i)B_i \}, \quad (18) \]
and we can see that \[ \frac{(\lambda_i - \lambda)}{(1 + \lambda_i)} \]
is an eigenvalue of $B_i$ if and only if $H(\lambda) = 0$.
Moreover, if $H(\lambda_i) \neq 0$, then the number of negative eigenvalues of $B_i$ is odd if and only if $H(\lambda_i) < 0$. Therefore,
\[ \sigma(\lambda) = \sum_{i \geq 0, H(\lambda_i) < 0} \dim N(\lambda_i). \]

As a consequence, we have the following Lemma.

**Lemma 3.7.** ([26]) Suppose that, for all $i \geq 0$, $H(\lambda_i) \neq 0$. Then
\[ \text{index}(F(\cdot), E^*) = (-1)^{\gamma}, \text{ where } \gamma = \sum_{i \geq 0, H(\lambda_i) < 0} \dim N(\lambda_i). \]

To facilitate our computation of $\text{index}(F(\cdot), E^*)$, we need to determine the sign of $H(\lambda_i)$. In particular, we will concentrate on the dependence of $H(\lambda_i)$ on $d_2$. At this point, we note that $H(\lambda) = \det \{ \Phi_E^{-1}(E^*) \} \det \{ \Phi(E^*) - G_E(E^*) \}$. Since we have already established that $\det \{ \Phi_E^{-1}(E^*) \}$ is positive, we will need only to consider $\det \{ \Phi(E^*) - G_E(E^*) \}$.

A straightforward computation gives
\[ H_1(\lambda) := \det \{ \lambda \Phi_E(E^*) - G_E(E^*) \} = d_1d_2\lambda^2 - (a_{11}d_2 + a_{22}d_1)\lambda + \det G_E(E^*). \quad (19) \]
Since we always assume $a_{11} > 0$ and \[ \frac{ac^2}{(a + N^*)^3} - \delta \left( \frac{cP^*}{(a + N^*)^2} - \frac{r}{K} \right) > 0 \]
holds in this section, hence, if $d_1$ is small enough and $d_2$ is large such that $a_{11}d_2 + a_{22}d_1 > 0$ and
\[ (a_{11}d_2 + a_{22}d_1)^2 - 4d_1d_2 \det G_E(E^*) > 0, \]
then two roots $\tilde{\lambda}_1(d_2)$, $\tilde{\lambda}_2(d_2)$ of the equation $H_1(\lambda) = 0$ are all real and satisfy
\[ \lim_{d_2 \to \infty} \tilde{\lambda}_1(d_2) = 0, \text{ and } \lim_{d_2 \to \infty} \tilde{\lambda}_2(d_2) = \frac{a_{11}}{d_1} := \bar{\lambda} > 0. \quad (20) \]

Now we state our main results in this subsection.

**Theorem 3.8.** Let $d_1$, $\Lambda$ be fixed and $a_{11} > 0$, \[ \frac{ac^2}{(a + N^*)^3} - \delta \left( \frac{cP^*}{(a + N^*)^2} - \frac{r}{K} \right) > 0 \]
and (20) holds. If $\bar{\lambda} \in (\lambda_n, \lambda_{n+1})$ for some $n \geq 1$ and $\sum_{i=1}^{n} \dim N(\lambda_i)$ is odd, then there exists a positive constant $\hat{d}_2$ such that, for $d_2 \geq \hat{d}_2$, model (4) has at least one constant positive solution.

**Proof.** The proof, which is by contradiction, is based on the homotopy invariance of the topological degree. Suppose on the contrary that the assertion is not true for some $d_2 = \hat{d}_2 \geq \hat{d}_2$. In what follows we fix $d_2 = \hat{d}_2$.

From Theorem 3.4, we know that there exists $\hat{d}_1, \hat{d}_2$ such that model (4) with $d_1 \geq \hat{d}_1$ and $d_2 \geq \hat{d}_2$ has no positive non-constant solution. For $t \in [0, 1]$, define $\Phi(t; E) = (d_1N, \lfloor td_2 + (1 - t)d_2 \rfloor P)^\top$, and consider the problem
\[
\begin{cases}
-\Delta \Phi(t; E) = G(E), & x \in \Omega, \\
\frac{\partial E}{\partial \nu} = 0, & x \in \partial \Omega.
\end{cases}
\] (21)
Then $E$ is a positive nonconstant solution of (4) if and only if it is such a solution of (21) for $t = 1$. It is obvious that $E^*$ is the unique constant positive solution of (21) for any $0 \leq t \leq 1$. For any $0 \leq t \leq 1$, $E$ is a positive solution of (21) if and only if

$$F(t; E) := E - (I - \triangle)^{-1}\{\Phi_E^{-1}(t; E)G(E) + E\} = 0$$

in $Y^+$. It is obvious that $F(1; E) = F(E)$. Theorem 3.6 shows that $E^*$ is the only solution of $F(0; E) = 0$ in $Y^+$. By a direct computation, $D_E F(t; E^*) = I - (I - \triangle)^{-1}\{\Phi_E^{-1}(t; E^*)G_E(E^*) + I\}$. In particular

$$D_E F(0; E^*) = I - (I - \triangle)^{-1}\{D^{-1}G_E(E^*) + I\}$$

and

$$D_E F(1; E^*) = I - (I - \triangle)^{-1}\{\Phi_E^{-1}G_E(E^*) + I\} = D_E F(E^*),$$

where $D = \text{diag}(d_1, d_2)$. From (18) and (19), we get

$$\begin{cases}
H(\lambda_0) = H(0) > 0, \\
H(\lambda_i) < 0, & 1 \leq i \leq n, \\
H(\lambda_i) > 0, & i \geq n + 1,
\end{cases}$$

where, zero is not an eigenvalue of the matrix $\lambda E - \Phi_E^{-1}(E^*)G_E(E^*)$ for all $i \geq 0$. Applying Lemma 3.7, we have

$$\gamma = \sum_{i \geq 0, H(\lambda_i) < 0} \dim N(\lambda_i) = \sum_{i=1}^n \dim N(\lambda_i),$$

which is odd, and

$$\text{index}(F(1; \cdot), E^*) = (-1)^\gamma = -1.$$  \hspace{1cm} (22)

In addition, since $\det\{G_E(E^*)\} > 0$ and $\lim_{i \to \infty} \lambda_i = \infty$, we can choose $\hat{d}_2$ to be so large that $H_1(\lambda) > 0$, then by Lemma 3.7, we have

$$\text{index}(F(1; \cdot), E^*) = (-1)^0 = 1.$$  \hspace{1cm} (23)

Now, by Theorem 3.3, there exists a positive constant $C$ such that, for all $0 \leq t \leq 1$, the positive solution of (4) satisfies $1/C < N, P < C$. Therefore, $F(t; E) \neq 0$ on $\partial B(C)$ for all $0 \leq t \leq 1$. By the homotopy invariance of the topological degree,

$$\deg(F(1; \cdot), 0, B(C)) = \deg(F(0; \cdot), 0, B(C)).$$  \hspace{1cm} (24)

On the other hand, by our supposition, both equations $F(1; E) = 0$ and $F(0; E) = 0$ have only the positive solution $E^*$ in $B(C)$, and hence, by (22) and (23),

$$\deg(F(0; \cdot), 0, B(C)) = \text{index}(F(0; \cdot), E^*) = (-1)^0 = 1,$$

and

$$\deg(F(1; \cdot), 0, B(C)) = \text{index}(F(1; \cdot), E^*) = -1.$$  \hspace{1cm}

This contradicts (24), and the proof is complete. \hfill \Box

**Remark 4.** Theorem 3.8 shows that, if the parameters are properly chosen, both the general stationary pattern and more interesting Turing pattern can arise as a result of diffusion. About Turing pattern formation of model (1), refer to [6].

4. **Structure of nonconstant positive solutions.** Let $Y = C(\bar{\Omega}) \times C(\bar{\Omega})$, $X = \{(N, P) \mid N, P \in C^2(\bar{\Omega}), \, \frac{\partial N}{\partial \nu} = \frac{\partial P}{\partial \nu} = 0, \, x \in \partial \Omega\}$. 

4.1. Local structure of nonconstant positive solutions. In this subsection, we study the local structure of nonconstant positive solutions for model (4). In brief, by regarding $d_2$ as the bifurcation parameter, we verify the existence of positive solutions bifurcating from $(d_2, 0)$. The Crandall-Rabinowitz bifurcation theorem in [7] will be applied to obtain bifurcations from simple eigenvalues.

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

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

where $f, g$ are given in Section 2. Then the solutions of boundary value problem (4) are exactly zero. With $E^* = (N^*, P^*)$, we have

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

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

**Theorem 4.1.** Suppose $j$ is a positive integer such that $d_1 \lambda_j < a_{11}$ and $d_2^k \neq d_2^l > 0$ for any integer $k \neq l$. Then $(d_2^*, E^*)$ 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 $\Gamma_j(s) = (d_2(s), N(s), P(s))$ of the problem (1.3) for $|s|$ sufficiently small, where $d_2(s), N(s), P(s)$ are continuous functions, $d_2(0) = d_2^*$ and

$$N(s) = N^* + s\phi_j + o(s), \quad P(s) = P^* + sb_j \phi_j + o(s), \quad b_j = \left(\frac{d_1 \lambda_j - a_{11}}{a_{12}}\right) > 0.$$

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

**Proof.** It suffices to verify conditions (a)-(c) as follows [7],

(a) the partial derivatives $F_{d_2}, F_E$, and $F_{d_2}E$ exist and are continuous,
(b) $\ker F_E(\tau, E^*)$ and $Y/R(F_E(\tau, E^*))$ are one-dimensional,
(c) let $\ker F_E(\tau, E^*) = \text{span}\{\Phi\}$, then $F_{d_2}E(\tau, E^*)\Phi \notin R(F_E(\tau, E^*))$.

Note that

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

where $a_{11}, a_{12}, a_{21}$ and $a_{22}$ are given in (10). It is clear that the linear operators $F_E, F_{d_2}E$ and $F_{d_2}$ are continuous, and condition (a) is verified.

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

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

where

$$\tilde{B}_i = \begin{pmatrix} a_{11} - d_1 \lambda_i & a_{12} \\ a_{21} & a_{22} - d_2^* \lambda_i \end{pmatrix}.$$  \hfill (25)

Since

$$\det \tilde{B}_i = 0 \iff d_2 = d_2^*(E^*) = \frac{d_1 a_{22} \lambda_i - a_{11} a_{22} + a_{12} a_{21}}{\lambda_i (d_1 \lambda_i - a_{11})},$$

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

$$\Phi_1 = (1, b_j)^\top \phi_j, \quad b_j = \frac{d_1 \lambda_j - a_{11}}{a_{12}} > 0,$$
$\phi_j$ is the eigenfunction of $-\Delta$. Consider the adjoint operator

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

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

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

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

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

Condition (b) is also verified.

Finally, since

$$F_{d_2}(d_j^2, E^*)\Phi_1 = \begin{pmatrix} 0 & 0 \\ 0 & \Delta \end{pmatrix} \Phi_1 = \begin{pmatrix} 0 \\ -\lambda_j b_j \phi_j \end{pmatrix},$$ 

we find $F_{d_2}(d_j^2, E^*)\Phi_1 \notin R(L_1)$, and so condition (c) is satisfied. The proof is completed. \hfill \square

4.1.1. Direction of the bifurcation solutions. In this subsection, we investigate the direction of the bifurcation solutions of model (4) in the one-dimensional space domain. In the 1D interval $\Omega = (0, \pi)$, it is well known that the operator $-\Delta$ with no-flux boundary conditions has eigenvalues and eigenfunctions as follows:

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

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

$$\begin{cases} 
-d_1 N'' = r(N + N^*) - \frac{r(N + N^*)^2}{K} - \frac{c(N + N^*)(P + P^*)}{a + (N + N^*)}, \quad x \in (0, \pi), \\
-d_2 P'' = s(P + P^*)(-q - \delta(P + P^*) + \frac{c(N + N^*)}{a + (N + N^*)}), \quad x \in (0, \pi).
\end{cases} \tag{26}$$

Let

$$H = r(N + N^*) - \frac{r(N + N^*)^2}{K} - \frac{c(N + N^*)(P + P^*)}{a + (N + N^*)},$$

$$G = s(P + P^*)(-q - \delta(P + P^*) + \frac{c(N + N^*)}{a + (N + N^*)}).$$

Then a straightforward calculation yields
\[ H_N(0, 0) = r - \frac{2rN^*}{K} - \frac{acP^*}{(a + N^*)^2}, \quad G_N(0, 0) = \frac{acsP^*}{(a + N^*)^2}, \]
\[ H_P(0, 0) = -\frac{cN^*}{a + N^*}, \quad G_P(0, 0) = -\delta s P^*, \]
\[ H_{NN}(0, 0) = -\frac{2r}{K} + \frac{2acP^*}{(a + N^*)^3}, \quad G_{NN}(0, 0) = -\frac{2acsP^*}{(a + N^*)^4}, \]
\[ H_{NP}(0, 0) = -\frac{2ac}{(a + N^*)^3}, \quad G_{NP}(0, 0) = -\frac{2acs}{(a + N^*)^3}, \]
\[ H_{PP}(0, 0) = 0, \quad G_{PP}(0, 0) = -2\delta s, \]
\[ H_{NNP}(0, 0) = -\frac{6acP^*}{(a + N^*)^4}, \quad G_{NNP}(0, 0) = -\frac{6acsP^*}{(a + N^*)^4}, \]
\[ H_{NPP}(0, 0) = 0, \quad G_{NPP}(0, 0) = 0, \]
\[ H_{PPP}(0, 0) = 0, \quad G_{PPP}(0, 0) = 0. \]

Denote \( E = (N, P) \). We rewrite the map \( F : \mathbb{R}^+ \times X \rightarrow Y \) by
\[
F(d_2, E) = \left( \begin{array}{c} d_2 N'' + H(N, P) \\ d_2 P'' + G(N, P) \end{array} \right).
\]
By Theorem 4.1, we see that \( \dim \ker F_E(d_2^*, (0, 0)) = \text{codim} R(F_E(d_2, (0, 0))) = 1 \) and \( \ker F_E(d_2^*, (0, 0)) = \text{span}\{\Phi_1\} \). Hence, we can decompose \( X \) and \( Y \) as
\[
X = \ker F_E(d_2^*, (0, 0)) \oplus Z \quad \text{and} \quad Y = R(F_E(d_2^*, (0, 0))) \oplus Z',
\]
where \( Z \) is the complement of \( \ker F_E(d_2^*, (0, 0)) \) in \( X \) and \( Z' \) is the complement of \( R(F_E(d_2^*, (0, 0))) \) in \( Y \). Due to \( \text{codim} R(F_E(d_2^*, (0, 0))) = 1 \), there exists \( T \in Y^* \) such that
\[
R(F_E(d_2, (0, 0))) = \{ (\xi, \zeta) \in Y : \langle T, (\xi, \zeta) \rangle = 0 \},
\]
where \( Y^* := \text{span}\{\Phi_1^*\} \). Moreover, \( \Phi_1^* \) satisfies \( F_E(d_2^*, (0, 0))\Phi_1^* = 0 \) by Theorem 4.1. Hence, we can define
\[
\langle T, (\xi, \zeta) \rangle = \langle \Phi_1^*, (\xi, \zeta) \rangle = \int_{\Omega} \xi \phi_j dx + \int_{\Omega} b_j^* \zeta \phi_j dx.
\]
By \( F_{d_2 E}(d_2^*, (0, 0))\Phi_1 \not\in R(F_E(d_2^*, (0, 0))) \) derived in Theorem 4.1, we find that
\[
\left\langle F_{d_2 E}(d_2^*, (0, 0))\Phi_1, \Phi_1^* \right\rangle \neq 0.
\]
From [29], we can know that
\[
d_2^*(0) = \frac{\left\langle F_{EE}(d_2^*, (0, 0))\Phi_1^2, \Phi_1^* \right\rangle}{2 \left\langle F_{d_2 E}(d_2^*, (0, 0))\Phi_1, \Phi_1^* \right\rangle}.
\]
By some calculations, we obtain
\[
\left\langle F_{EE}(d_2^*, (0, 0))\Phi_1^2, \Phi_1^* \right\rangle = (g_j + h_j b_j^*) \int_0^\pi \phi_j^3 dx = 0
\]
and
\[
\left\langle F_{d_2 E}(d_2^*, (0, 0))\Phi_1, \Phi_1^* \right\rangle = \int_0^\pi b_j^* \phi_j (b_j \phi_j)^\nu dx = -j^2 b_j b_j^*,
\]
where
\[ g_j = H_{NN}(0, 0) + 2H_{NP}(0, 0)b_j + H_{PP}(0, 0)b_j^2, \]
\[ h_j = G_{NN}(0, 0) + 2G_{NP}(0, 0)b_j + G_{PP}(0, 0)b_j^2. \]

Hence, \( d''_j(0) = 0 \).

Note that \( \langle F_{EE}(d'_2, (0, 0))\Phi_2^2, \Phi_1^2 \rangle = 0 \) implies
\[ F_{EE}(d'_2, (0, 0))\Phi_2^2 \in R(F_{EE}(d'_2, (0, 0))). \]

From [29], we can obtain that the bifurcation is supercritical (resp. subcritical) if
\[ d''(0) = -\frac{\langle F_{EEE}(d'_2, (0, 0))\Phi_1^3, \Phi_1^1 \rangle + 3\langle F_{EE}(d'_2, (0, 0))\Phi_1^2, \Phi_1^1 \rangle}{3\langle F_{d_2E}(d'_2, (0, 0))\Phi_1, \Phi_1^1 \rangle} > 0(< 0), \]
where \( \theta \) is the solution of the following problem
\[ F_{EE}(d'_2, (0, 0))\Phi_1^2 + F_E(d'_2, (0, 0))\theta = 0. \]

Let \( \theta = (\theta_1, \theta_2) \). Then \( \theta \) satisfies
\[
\begin{aligned}
&\frac{d_1}{d_2^2}\theta'_1 + H_N(0, 0)\theta_1 + H_P(0, 0)\theta_2 = -g_j\phi_j^2, \\
&\frac{d_2}{d_2^2}\theta'_2 + G_N(0, 0)\theta_1 + G_P(0, 0)\theta_2 = -h_j\phi_j^2, \\
&\theta'_1(0, t) = \theta'_2(\pi, t) = 0, \ i = 1, 2. \tag{27}
\end{aligned}
\]

By direct calculation, we obtain
\[ \langle F_{EEE}(d'_2, (0, 0))\Phi_1^3, \Phi_1^1 \rangle = (m_j + n_j b_j^*) \int_0^\pi \phi_j^4 dx = \frac{3}{2\pi} (m_j + n_j b_j^*), \]
where
\[ m_j = H_{NNN}(0, 0) + 3b_j H_{NPP}(0, 0) + 3b_j^2 H_{PPP}(0, 0) + b_j^3 H_{PPP}(0, 0), \]
\[ n_j = G_{NNN}(0, 0) + 3b_j G_{NPP}(0, 0) + 3b_j^2 G_{PPP}(0, 0) + b_j^3 G_{PPP}(0, 0), \]
and \( b_j, b_j^* \) are given in subsection 4.1. Hence
\[ \langle F_{EEE}(d'_2, (0, 0))\Phi_1^3, \Phi_1^1 \rangle = \frac{3}{2\pi} (3b_j(b_j^* G_{NPP}(0, 0) + H_{NNN}(0, 0)) + b_j^* G_{NNN}(0, 0) + \tilde{H}_{NNN}(0, 0)). \]

In addition, a straightforward calculation yields
\[ \langle F_{EE}(d'_2, (0, 0))\Phi_1^2, \Phi_1^1 \rangle = C_1 \int_0^\pi \theta_1\phi_j^2 dx + C_2 \int_0^\pi \theta_2\phi_j^2 dx, \]
where
\[ C_1 = H_{NN}(0, 0) + b_j H_{NP}(0, 0) + b_j^* G_{NN}(0, 0) + b_j b_j^* G_{NP}(0, 0), \]
\[ C_2 = H_{NP}(0, 0) + b_j H_{PP}(0, 0) + b_j^* G_{NP}(0, 0) + b_j b_j^* G_{PP}(0, 0). \]

To complete our calculation, we now compute
\[ \int_0^\pi \theta_1\phi_j^2 dx \text{ and } \int_0^\pi \theta_2\phi_j^2 dx. \]
Multiplying (27) by \( \phi_j^2 \) and integrating by parts, we derive

\[ \begin{align*}
&d_1 \int_0^\pi \phi_j^2 \theta_1'' dx + H_N(0,0) \int_0^\pi \phi_j^2 \theta_1 dx + H_P(0,0) \int_0^\pi \phi_j^2 \theta_2 dx \\
&= -g_j \int_0^\pi \phi_j^2 dx, \\
&d_2 \int_0^\pi \phi_j^2 \theta_2'' dx + G_N(0,0) \int_0^\pi \phi_j^2 \theta_1 dx + G_P(0,0) \int_0^\pi \phi_j^2 \theta_2 dx \\
&= -h_j \int_0^\pi \phi_j^2 dx, \\
\end{align*} \tag{28} \]

where

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

Integrating (27) by parts yields

\[ \gamma_1 := \int_0^\pi \theta_1 dx = \frac{(h_j H_P(0,0) - g_j G_P(0,0))}{(H_N(0,0) G_P(0,0) - H_P(0,0) G_N(0,0))}, \]

\[ \gamma_2 := \int_0^\pi \theta_2 dx = \frac{(g_j G_N(0,0) - h_j H_N(0,0))}{(H_N(0,0) G_P(0,0) - H_P(0,0) G_N(0,0))}. \]

It follows from (28) that

\[ \begin{align*}
(h_N(0,0) - 4d_1 j^2) \int_0^\pi \phi_j^2 \theta_1 dx + H_P(0,0) \int_0^\pi \phi_j^2 \theta_2 dx &= -\frac{3g_j}{2\pi} \gamma_1 - \frac{4}{\pi} d_1 \gamma_1 j^2, \\
(G_P(0,0) - 4d_2 j^2) \int_0^\pi \phi_j^2 \theta_2 dx + G_N(0,0) \int_0^\pi \phi_j^2 \theta_1 dx &= -\frac{3h_j}{2\pi} \gamma_2 - \frac{4}{\pi} d_2 \gamma_2 j^2. \\
\end{align*} \]

Thus,

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

where

\[ A_1 := (-\frac{3}{2\pi} g_j - \frac{4}{\pi} d_1 \gamma_1 j^2)(G_P(0,0) - 4d_2 j^2) + H_P(0,0)(\frac{3}{2\pi} h_j + \frac{4}{\pi} d_2 \gamma_2 j^2), \]

\[ A_2 := (-\frac{3}{2\pi} h_j - \frac{4}{\pi} d_2 \gamma_2 j^2)(H_N(0,0) - 4d_1 j^2) + G_N(0,0)(\frac{3}{2\pi} g_j + \frac{4}{\pi} d_1 \gamma_1 j^2), \]

\[ B := (H_N(0,0) - 4d_1 j^2)(G_P(0,0) - 4d_2 j^2) - H_P(0,0) G_N(0,0). \]

Consequently, we obtain

\[ d_2''(0) = \frac{C}{2\pi j^2 b_j b_j^*} \tag{29} \]

where

\[ C := 3b_j(b_j^* G_{NPP}(0,0) + H_{NNP}(0,0)) + b_j^* G_{NNN}(0,0) + H_{NNN}(0,0) \]

\[ + 2\pi (C_1 L_1 + C_2 L_2). \]

From the analysis above, we obtain the following results:

**Theorem 4.2.** Under the same hypothesis of Theorem 4.1, there exists a smooth bifurcation branch from \((d_2'(0), 0)\). Furthermore, the bifurcation is supercritical (resp. subcritical) provided that \(d_2''(0) > 0(< 0)\), where \(d_2''(0)\) is given by (29).
4.2. Global structure of nonconstant positive solutions. Theorem 4.1 provides no information of the bifurcating curve \( \Gamma_j \) far from the equilibrium. A further study is therefore necessary in order to understand its global bifurcation. We will prove that \( \Gamma_j \) is unbounded, using the global bifurcation theory of Rabinowitz and the Leray-Schauder degree for compact operators.

Let \( H_1 = C_B^1(\bar{\Omega}) \times C_B^1(\bar{\Omega}), \) \( C_B^1(\bar{\Omega}) = \{ N, P \in C^1(\bar{\Omega}) | \frac{\partial N}{\partial \nu} |_{\partial \Omega} = \frac{\partial P}{\partial \nu} |_{\partial \Omega} = 0 \} \), we have the following Theorem.

**Theorem 4.3.** Under the same assumption of Theorem 4.1, the projection of the bifurcation curve \( \Gamma_j \) on the \( d_2 \)-axis contains \( (d_2^j, \infty) \).

**Proof.** Let \( \bar{N} = N - N^* \), \( \bar{P} = P - P^* \). Then (4) is transformed into

\[
\begin{aligned}
-d_1 \Delta \bar{N} &= a_{11} \bar{N} + a_{12} \bar{P} + h_1(\bar{N}, \bar{P}), \\
-d_2 \Delta \bar{P} &= a_{21} \bar{N} + a_{22} \bar{P} + h_2(\bar{N}, \bar{P}),
\end{aligned}
\]  

(30)

where \( h_1(\bar{N}, \bar{P}), \ h_2(\bar{N}, \bar{P}) \) are higher-order terms of \( \bar{N} \) and \( \bar{P} \). The constant steady state \((N^*, P^*)\) of (4) shifts to \((0, 0)\) of this new system. Let

\[
G_1 = (-d_1 \Delta + a_{11})^{-1}, \ G_2 = (-d_2 \Delta - a_{22})^{-1}.
\]

Then (30) is transformed into

\[
\bar{N} = G_1(2a_{11} \bar{N}) + G_1(a_{12} \bar{P}) + G_1(h_1(\bar{N}, \bar{P})), \ \bar{P} = G_2(a_{21} \bar{N}) + G_2(h_2(\bar{N}, \bar{P})).
\]

Put \( \tilde{E} = (\bar{N}, \bar{P}) \),

\[
K(d_2) \tilde{E} = (2a_{11} G_1(\bar{N}) + a_{12} G_1(\bar{P}), a_{21} G_2(\bar{N})),
\]

and

\[
H(\tilde{E}) = (G_1(h_1(\bar{N}, \bar{P})), \ G_2(h_2(\bar{N}, \bar{P})).
\]

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

\[
\tilde{E} = K(d_2) \tilde{E} + H(\tilde{E}), \text{ in } H_1. \quad (31)
\]

Note that \( K(d_2) \) is a compact linear operator on \( H_1 \) for any given \( d_2 > 0, H(\tilde{E}) = o(|\tilde{E}|) \) for \( \tilde{E} \) near zero uniformly on closed \( d_2 \) sub-intervals of \((0, \infty)\), and is a compact operator on \( H_1 \) 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 \( \ker(K(d_2^j) - 1) = \ker L_1 = \text{span}\{\Phi_1\} \), so 1 is indeed an eigenvalue of \( K = K(d_2^j) \), and \( \text{dim} \ker(K - I) = 1 \). 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 [23], where \( K^* \) is the adjoint of \( K \). Let \((\hat{\varphi}, \hat{\psi}) \in \ker(K^* - I)\). Then

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

By the definition of \( G_1 \) and \( G_2 \) we obtain

\[
-d_2^j a_{12} \Delta \hat{\varphi} = f_{\varphi} \hat{\varphi} + f_{\psi} \hat{\psi}, \ -d_1 \Delta \hat{\psi} = a_{12} \hat{\varphi} - a_{11} \hat{\psi},
\]

where

\[
f_{\varphi} = \frac{2d_1^2 a_{11} a_{12}}{d_1} + a_{12} a_{22}, \ f_{\psi} = a_{12} a_{21} - 2(a_{11} a_{22} + \frac{d_2^j a_{11}^2}{d_1}).
\]
Write \( \hat{\varphi} = \sum_{0 \leq i, j \leq m} \hat{a}_{ij} \phi_{ij} \), \( \hat{\psi} = \sum_{0 \leq i, j \leq m} \hat{b}_{ij} \phi_{ij} \). Then
\[
\sum_{0 \leq i, j \leq m} \hat{B}_i \left( \begin{array}{c} \hat{a}_{ij} \\ \hat{b}_{ij} \end{array} \right) \phi_{ij} = 0,
\]
where
\[
\hat{B}_i = \begin{pmatrix} -d_2^2 a_{12} \lambda_i + f \hat{\varphi} /a_{12} & f \hat{\psi} \\ -d_1 \lambda_i - a_{11} \end{pmatrix}.
\]

By a straightforward calculation one can check that \( \det \hat{B}_i = a_{12} \det \tilde{B}_i \), where \( \tilde{B}_i \) is given in (25) by replacing \( d_2 \) with \( d_2^2 \). Thus \( \tilde{B}_i = 0 \) only for \( i = j \), and \( \ker(K^* - I) = \text{span}\{\Phi\} \), where \( \Phi = (\frac{d_1 \lambda_i + a_{11}}{a_{12}}, 1)^\top \phi_j \). 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 \( 0 < d_2 \neq d_2^2 \) is in a small neighborhood of \( d_2^2 \), then the linear operator \( I - K(d_2) : H_1 \rightarrow H_1 \) is a bijection and 0 is an isolated solution of (31) for this fixed \( d_2 \). The index of this isolated zero of \( I - K(d_2) - H \) is given by
\[
\text{index}(I - K(d_2) - H, (d_2, 0)) = \deg(I - K(d_2), B, 0) = (-1)^p,
\]
where \( B \) is a sufficiently small ball center at 0, and \( p \) is the sum of the algebraic multiplicities of the eigenvalues of \( K(d_2) \) that are > 1. For our bifurcation analysis, it is also necessary to verify that this index changes as \( d_2 \) crosses \( d_2^2 \), that is, for \( \epsilon > 0 \) sufficiently small,
\[
\text{index}(I - K(d_2^2 - \epsilon) - H, (d_2^2 - \epsilon, 0)) \neq \text{index}(I - K(d_2^2 + \epsilon) - H, (d_2^2 + \epsilon, 0)).
\]

Indeed, if \( \mu \) is an eigenvalue of \( K(d_2) \) with an eigenfunction \( (\hat{\varphi}, \hat{\psi}) \), then
\[
2a_{11} G_1(\hat{\varphi}) + a_{12} G_1(\hat{\psi}) = \mu \hat{\varphi}, \ a_{21} G_2(\hat{\varphi}) = \mu \hat{\psi}.
\]

By the definition of \( G_1, G_2 \) and \( \hat{\varphi} = \sum_{0 \leq i, j \leq m} \hat{a}_{ij} \phi_{ij}, \hat{\psi} = \sum_{0 \leq i, j \leq m} \hat{b}_{ij} \phi_{ij} \), we have
\[
\sum_{0 \leq i, j \leq m} \tilde{B}_i \left( \begin{array}{c} \hat{a}_{ij} \\ \hat{b}_{ij} \end{array} \right) \phi_{ij} = 0,
\]
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 \( \mu \)'s that solve the characteristic equation
\[
\mu^2 - \frac{2a_{11}}{d_1 \lambda_i + a_{11}} - \mu - \frac{a_{12} a_{21}}{(d_2 \lambda_i - a_{22})(d_1 \lambda_i + a_{11})} = 0.
\]

For \( d_2 = d_2^2 \) in particular, if \( \mu = 1 \) is a root of (33), then a simple calculation leads to \( d_2^2 = d_2 \), and \( j = i \) by the assumption. For \( i = j \) in (33), we let \( \mu_1(d_2^2) \), \( \mu_2(d_2^2) \) denote the two roots. First we find that
\[
\mu_1(d_2^2) = 1 \text{ and } \mu_2(d_2^2) = \frac{a_{11} - d_1 \lambda_j}{a_{11} + d_1 \lambda_j} < 1.
\]

Now for \( d_2 \) close to \( d_2^2 \), the root of (33) is given by
\[
\mu_1(d_2) = \frac{a_{11} + \sqrt{a_{11}^2 + \frac{a_{12} a_{21} (d_1 \lambda_i + a_{11})}{(d_1 \lambda_i + a_{11}) - a_{22}}}}{(d_1 \lambda_i + a_{11})}, \ \mu_2(d_2) < 1.
\]
And $\mu_2(d_2)$ is an increasing function of $d_2$, there is a small $\epsilon > 0$ such that

$$
\mu_1(d_2^2 + \epsilon) > 1, \quad \mu_1(d_2^2 - \epsilon) < 1.
$$

Consequently, $K(d_2^2 + \epsilon)$ has exactly one more eigenvalues that are larger than 1 than $K(d_2^2 - \epsilon)$ does, and by a similar argument above we can show this eigenvalue has algebraic multiplicity one. This verifies (32). And the proof is complete. □

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