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# Dynamics and pattern formation in a diffusive predator–prey system with strong Allee effect in prey<sup>☆</sup>

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## ABSTRACT

The dynamics of a reaction–diffusion predator–prey system with strong Allee effect in the prey population is considered. Nonexistence of nonconstant positive steady state solutions are shown to identify the ranges of parameters of spatial pattern formation. Bifurcations of spatially homogeneous and nonhomogeneous periodic solutions as well as nonconstant steady state solutions are studied. These results show that the impact of the Allee effect essentially increases the system spatiotemporal complexity.

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## 1. Introduction

The understanding of patterns and mechanisms of spatial dispersal of interacting species is an issue of significant current interest in conservation biology and ecology, and biochemical reactions. Different species of chemical or living organisms compete and/or consume limited resource, and such competition and consumption also generate feedbacks in the complex network of biological

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species. The spatial dispersal makes the dynamics and behavior of the organisms even more complicated. A typical type of interaction is the one between a pair of predator and prey, or more generally, a pair of consumer and resource. Mathematical model of predator–prey type has played a major role in the studies of biological invasion of foreign species, epidemics spreading, extinction/spread of flame balls in combustion or autocatalytic chemical reaction. A variety of theoretical approaches has been developed and considerable progress has been made during the last three decades [5,8,11,26,30,35,44].

The spatiotemporal dynamics of a predator–prey system in a homogeneous environment can be described by a system of nonlinear parabolic partial differential equations (or reaction–diffusion equations) [26,33–35,40]:

$$\begin{aligned} \frac{\partial H(X, T)}{\partial T} &= D_1 \Delta H + F(H)H - G(H)P, \\ \frac{\partial P(X, T)}{\partial T} &= D_2 \Delta P + kG(H)P - M(P), \end{aligned} \tag{1.1}$$

where  $H(X, T)$  and  $P(X, T)$  are the densities of prey and predator at time  $T$  and position  $X$  respectively; here  $X \in \Omega_0 (\subseteq \mathbb{R}^n)$  is the spatial habitat of the two species; the Laplace operator  $\Delta$  describes the spatial dispersal with passive diffusion;  $D_1$  and  $D_2$  are the diffusion coefficients of species and  $k$  is the food utilization coefficient. The function  $F(H)$  describes the per capita growth rate of the prey,  $G(H)$  is the functional response of the predator, which corresponds to the saturation of their appetites and reproductive capacity, and  $M(P)$  stands for predator mortality.

The functions  $F(H)$ ,  $G(H)$  and  $M(P)$  can be of different types in various specific situations. Since the first differential equation model of predator–prey type Lotka–Volterra equation was formulated [27,52] in 1920s, a logistic type growth  $F(H)$  is usually assumed for the prey species in the models, while a linear mortality rate  $M(P)$  is assumed for the predator. Some conventional functional response functions  $G(H)$  include Holling types I, II, III and Ivlev type (see [17,24,43,53]). When  $F(H)$  is of a logistic growth, the dynamics of (1.1) has been considered in many articles, see for example [11,13, 19,25,28,60].

In recent years, Allee effect in the growth of a population has been studied extensively [9]. Allee effect is named after ecologist Warder C. Allee [2]. A strong Allee effect refers to the phenomenon that the population has a negative growth when the size of the population is below certain threshold value [3,47,50,53], while a weak Allee effect means that growth is positive and increasing when below a threshold [22,47,56].

By means of extensive computer simulations, Lewis and Karevia [26] used a scalar partial differential equation to model the population and they found that strong Allee effect may reduce the spread of invading organisms; Owen and Lewis [35] considered (1.1) and indicated that predation pressure can slow, stop or reverse a spatial invasion of prey; Morozov, Petrovskii and Li [32,33,39,40] showed that the dynamic of system (1.1) is remarkably rich and that its complexity increases with an increase of the prey maximum growth rate; Also in [33], a thorough study of the system (1.1) in connection to biological invasion is fulfilled and a detailed classification of possible patterns of species spread and even the spatiotemporal chaos are obtained. Note that most of these studies are numerical not analytical. There are very little mathematical analysis results for (1.1) with strong Allee effect in prey.

On the other hand, the authors [53,54] have recently completed a comprehensive study of a general ODE predator–prey system with strong Allee effect in prey. In [53] we considered a planar ODE system

$$\begin{cases} \frac{du}{dt} = g(u)(f(u) - v), \\ \frac{dv}{dt} = v(g(u) - d), \end{cases} \tag{1.2}$$

where  $g(u)$  is the predator functional response which an increasing function, and  $f(u)$  is a function with strong Allee effect character. We completely classified the global dynamics of (1.2) when  $f$  and  $g$  satisfy some mild conditions. In particular, we showed that the dynamics is mostly bistable with one stable state  $(0, 0)$  and the other one being an equilibrium, or a periodic orbit, or a loop of heteroclinic orbits for a threshold parameter value, and in the other case,  $(0, 0)$  is globally asymptotically stable.

In this paper, we rigorously consider the dynamics of the system (1.1) with the form considered in [32,33,40]. That is, we assume that the functional response is of Holling type II [17], and the predator mortality rate is linear:

$$G(H) = \frac{AH}{H + B}, \quad M(P) = MP,$$

where  $A$  describes the maximum predation rate,  $B$  is the self-saturation prey density and  $M$  is the per capita mortality rate; and the prey growth rate is given by the form in [26]:

$$F(H) = \frac{4\omega}{(K - H_0)^2} H(H - H_0)(K - H),$$

where  $K$  is the prey carrying capacity,  $\omega$  is the maximum per capita growth rate and  $H_0$  quantifies the intensity of the Allee effect so that it is strong with  $0 < H_0 < K$ .

With these choices of functions and using new dimensionless variables and parameters:

$$u = \frac{H}{K}, \quad v = \frac{P}{kK}, \quad \gamma = \frac{4\omega}{(K - H_0)^2}, \quad t = \frac{\gamma H_0 T}{K^2}, \quad l = \frac{AKk}{B}, \quad x = \sqrt{l}X,$$

we consider the following nondimensionalized form of reaction–diffusion model:

$$\begin{cases} \frac{\partial u}{\partial t} = d_1 \Delta u + u(1 - u) \left( \frac{u}{b} - 1 \right) - \frac{muv}{a + u}, & x \in \Omega, t > 0, \\ \frac{\partial v}{\partial t} = d_2 \Delta v - dv + \frac{muv}{a + u}, & x \in \Omega, t > 0, \\ \frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, & x \in \Omega, \end{cases} \quad (1.3)$$

where the new parameters are

$$d_1 = \frac{D_1 l K^2}{H_0 \gamma}, \quad d_2 = \frac{D_2 l K^2}{H_0 \gamma}, \quad m = \frac{AK^2 k}{\gamma H_0}, \quad d = \frac{MK^3 k l}{\gamma H_0}, \quad a = \frac{B}{K}, \quad b = \frac{H_0}{K}.$$

For the new parameters,  $d$  is the death rate of the predator,  $a$  measures the saturation effect [17] and  $m$  is the strength of the interaction. The Allee threshold is  $b = H_0/K < 1$  [3,51,56]: a strong Allee effect introduces a population threshold, and the population must surpass this threshold to grow. We consider an initial–boundary value problem over a smooth bounded spatial domain  $\Omega \subset \mathbb{R}^n$  for  $n \geq 1$ , and we impose a no-flux boundary condition so it is a closed ecosystem.

In this paper we prove the global existence of the solutions to (1.3), and in various situations, global asymptotical behavior of the solutions can be determined. In particular, we show that a large amount of predator initially will always drive both population into extinction, which is called *overexploitation* [51,53] and it is a character of predator–prey system with Allee effect. We also use energy estimates to obtain *a priori* bounds of the dynamic and steady state solutions, which also identifies the regions of parameters of nonexistence of nonconstant spatial patterns. While a precise description

of the global dynamics cannot be obtained as the case of ODE model in [53], we prove the basic dynamics of the system is still bistable, but the PDE system possesses more spatiotemporal patterns: nonconstant spatial patterns and time-periodic orbits, at least. We use stability analysis and bifurcation theory to show the existence of such nonconstant steady states and time-periodic orbits, which partially verifies the richness of the dynamics shown in [33,40].

Methods of analysis of reaction–diffusion systems have been developed since late 1970s (see for example, [1,5,8,36,49]). In this paper we apply some classical techniques like comparison methods, *a priori* estimates, and bifurcation theory. But there are several difficulties when using these methods to (1.3). One is the lack of comparison principle for the reaction–diffusion predator–prey systems, which is well known [11–13]. Here we have to use the comparison principle in a more creative way, often to some components or variations of the original system. Another difficulty is the lack of lower bound estimates of positive steady states, which is caused by the bistability of the system so that the system could have a large number of semi-trivial steady state solutions with  $v$ -component being zero. Without such lower bound, one is not able to use the powerful Leray–Schauder degree theory to prove the existence of nonconstant steady states as in [28,29,37,38,55]. Instead we use global bifurcation theory developed in [41,48] to obtain the existence of nonconstant steady state solutions with certain eigen-modes. We also prove the existence of spatially nonhomogenous time-periodic orbits following the method of [60]. We believe that the class of reaction–diffusion systems with bistable character such as (1.3) is an important one in the studies of mathematical biology and complex patterns, and this paper is only the first rigorous step toward a deeper understanding.

The rest of the paper are structured in the following way. In Section 2, we carry out the analysis of basic dynamics and the *a priori* bound of solutions of (1.3); In Section 3, we consider the stability of trivial steady state solutions and bifurcation of semi-trivial steady state solutions; In Section 4, we investigate the *a priori* estimates and nonexistence of the steady state solutions; In Section 5, we show the existence of steady state solutions and time-periodic orbits with a careful Hopf bifurcation and steady state bifurcation analysis. We end with concluding remarks in Section 6. We denote by  $\mathbb{N}$  the set of all the positive integers, and  $\mathbb{N}_0 = \mathbb{N} \cup \{0\}$ .

## 2. Basic dynamics and *a priori* bound

In this section, the existence of solution to the dynamical equation (1.3) is proved, and *a priori* bound of the solution is also established.

**Theorem 2.1.** *Suppose that  $d, m, a, d_1, d_2 > 0$ ,  $0 < b < 1$ , and  $\Omega \subset \mathbb{R}^n$  is a bounded domain with smooth boundary:*

- (a) *If  $u_0(x) \geq 0$ ,  $v_0(x) \geq 0$ , then (1.3) has a unique solution  $(u(x, t), v(x, t))$  such that  $u(x, t) > 0$ ,  $v(x, t) > 0$  for  $t \in (0, \infty)$  and  $x \in \overline{\Omega}$ ;*
- (b) *If  $u_0(x) \leq b$  and  $(u_0, v_0) \neq (b, 0)$ , then  $(u(x, t), v(x, t))$  tends to  $(0, 0)$  uniformly as  $t \rightarrow \infty$ ;*
- (c) *If  $d > \frac{m}{a+1}$ , then  $(u(x, t), v(x, t))$  tends to  $(u_S(x), 0)$  uniformly as  $t \rightarrow \infty$ , where  $u_S(x)$  is a non-negative solution of*

$$d_1 \Delta u + u(1 - u)(b^{-1}u - 1) = 0, \quad x \in \Omega, \quad \frac{\partial u}{\partial n} = 0, \quad x \in \partial\Omega; \quad (2.1)$$

- (d) *For any solution  $(u(x, t), v(x, t))$  of (1.3),*

$$\limsup_{t \rightarrow \infty} u(x, t) \leq 1, \quad \limsup_{t \rightarrow \infty} \int_{\Omega} v(x, t) dx \leq \left(1 + \frac{(1 - b)^2}{4db}\right) |\Omega|.$$

Moreover, for any  $d_{2*} > 0$ , there exists a positive constant  $C > 0$  independent of  $u_0, v_0, d_1$  but depends on  $d_{2*}$  only, such that for any  $x \in \overline{\Omega}$ ,

$$\limsup_{t \rightarrow \infty} v(x, t) \leq C,$$

for all  $d_2 \geq d_{2*}$ ; if  $d_1 = d_2$ , then for any  $x \in \overline{\Omega}$ ,

$$\limsup_{t \rightarrow \infty} v(x, t) \leq 1 + \frac{(1 - b)^2}{4db}.$$

**Proof.** 1. Define

$$M(u, v) = u(1 - u)(b^{-1}u - 1) - \frac{muv}{a + u}, \quad N(u, v) = -dv + \frac{muv}{a + u},$$

then  $M_v \leq 0$  and  $N_u \geq 0$  in  $\mathbb{R}_+^2 = \{u \geq 0, v \geq 0\}$  and (1.3) is a mixed quasi-monotone system (see [36,59]). Let  $(\underline{u}(x, t), \underline{v}(x, t)) = (0, 0)$  and  $(\bar{u}(x, t), \bar{v}(x, t)) = (u^*(t), v^*(t))$ , where  $(u^*(t), v^*(t))$  is the unique solution to

$$\begin{cases} \frac{du}{dt} = u(1 - u)(b^{-1}u - 1), \\ \frac{dv}{dt} = -dv + \frac{muv}{a + u}, \\ u(0) = u^*, \quad v(0) = v^*, \end{cases} \quad (2.2)$$

where  $u^* = \sup_{\overline{\Omega}} u_0(x)$  and  $v^* = \sup_{\overline{\Omega}} v_0(x)$ . Then  $(\underline{u}(x, t), \underline{v}(x, t)) = (0, 0)$  and  $(\bar{u}(x, t), \bar{v}(x, t)) = (u^*(t), v^*(t))$  are the lower-solution and upper-solution to (1.3), respectively, since

$$\begin{aligned} \frac{\partial \bar{u}(x, t)}{\partial t} - \Delta \bar{u}(x, t) - M(\bar{u}(x, t), \underline{v}(x, t)) &= 0 \\ &\geq 0 = \frac{\partial \underline{u}(x, t)}{\partial t} - \Delta \underline{u}(x, t) - M(\underline{u}(x, t), \bar{v}(x, t)), \end{aligned}$$

and

$$\begin{aligned} \frac{\partial \bar{v}(x, t)}{\partial t} - \Delta \bar{v}(x, t) - N(\bar{u}(x, t), \bar{v}(x, t)) &= -d\bar{v} + \frac{m\bar{u}\bar{v}}{a + \bar{u}} = 0 \\ &\geq 0 = \frac{\partial \underline{v}(x, t)}{\partial t} - \Delta \underline{v}(x, t) - N(\underline{u}(x, t), \underline{v}(x, t)), \end{aligned}$$

the boundary conditions are satisfied, and  $0 \leq u_0(x) \leq u^*$  and  $0 \leq v_0(x) \leq v^*$ . Here we use the definition of lower/upper-solution in Definition 8.1.2 in [36] or Definition 5.3.1 in [59]. Therefore Theorem 8.3.3 in [36] or Theorem 5.3.3 in [59] shows that (1.3) has a unique globally defined solution  $(u(x, t), v(x, t))$  which satisfies

$$0 \leq u(x, t) \leq u^*(t), \quad 0 \leq v(x, t) \leq v^*(t), \quad t \geq 0.$$

The strong maximum principle implies that  $u(x, t), v(x, t) > 0$  when  $t > 0$  for all  $x \in \overline{\Omega}$ . Moreover if  $u_0(x) \leq u^* < b$ , then apparently  $u^*(t) \rightarrow 0$  and consequently  $v^*(t) \rightarrow 0$  as  $t \rightarrow \infty$ . This completes the proof of parts (a) and (b).

2. From proof above, we obtain that  $u(x, t) \leq u^*(t)$  for all  $t > 0$ . From the ODE satisfied by  $u^*(t)$ , one can see that  $u^*(t) \rightarrow 0$  if  $u^* < b$  and  $u^*(t) \rightarrow 1$  if  $u^* > b$ . Thus for any  $\varepsilon > 0$ , there exists  $T_0 > 0$  such that  $u(x, t) \leq 1 + \varepsilon$  in  $[T_0, \infty) \times \overline{\Omega}$ .

If  $d > \frac{m}{a+1}$ , we choose  $\varepsilon > 0$  such that  $d \geq \frac{m(1+\varepsilon)}{a+1+\varepsilon}$ , then for  $t > T$ ,  $u(x, t) \leq 1 + \varepsilon$ . We use the comparison argument above again with  $u(T) = u^* \leq 1 + \varepsilon$ . Then the equation of  $v^*(t)$  implies that  $0 \leq v(x, t) \leq v^*(t) \rightarrow 0$  as  $t \rightarrow \infty$  uniformly for  $x \in \bar{\Omega}$ . The equation of  $u(x, t)$  is now asymptotically autonomous (see [7,21,31]), and its limit behavior is determined by the semiflow generated by the scalar parabolic equation:

$$\begin{cases} u_t = d_1 \Delta u + u(1-u)(b^{-1}u - 1), & x \in \Omega, t > 0, \\ \frac{\partial u}{\partial n} = 0, & x \in \partial\Omega. \end{cases} \tag{2.3}$$

It is well known that (2.3) is a gradient system, and every orbit of (2.3) converges to a steady state  $u_S$  [14]. Then from the theory of asymptotically autonomous dynamical systems, the solution  $(u(x, t), v(x, t))$  of (1.3) converges to  $(u_S, 0)$  as  $t \rightarrow \infty$ . This proves part (c).

3. For the estimate of  $v(x, t)$ , let  $\int_{\Omega} u(x, t) dx = U(t)$ ,  $\int_{\Omega} v(x, t) dx = V(t)$ , then

$$\frac{dU}{dt} = \int_{\Omega} u_t dx = \int_{\Omega} d_1 \Delta u dx + \int_{\Omega} \left[ u(1-u)(b^{-1}u - 1) - \frac{mu v}{a+u} \right] dx; \tag{2.4}$$

$$\frac{dV}{dt} = \int_{\Omega} v_t dx = \int_{\Omega} d_2 \Delta v dx - dV + \int_{\Omega} \frac{mu v}{a+u} dx. \tag{2.5}$$

Adding (2.4) and (2.5) and by virtue of the Neumann boundary condition, we obtain that

$$\begin{aligned} (U + V)_t &= -dV + \int_{\Omega} u(1-u)(b^{-1}u - 1) dx \\ &= -d(U + V) + dU + \int_{\Omega} u(1-u)(b^{-1}u - 1) dx \\ &\leq -d(U + V) + \left( d + \frac{(1-b)^2}{4b} \right) U. \end{aligned}$$

By using  $\limsup_{t \rightarrow \infty} u(x, t) \leq 1$  proved above, we have  $\limsup_{t \rightarrow \infty} U(t) \leq |\Omega|$ . Thus for small  $\varepsilon > 0$ , there exists  $T_1 > 0$  such that

$$(U + V)_t \leq -d(U + V) + \left( d + \frac{(1-b)^2}{4b} \right) (1 + \varepsilon) |\Omega|, \quad t > T_1. \tag{2.6}$$

An integration of (2.6) leads to, for  $T_2 > T_1$ ,

$$\int_{\Omega} v(x, t) dx = V(t) < U(t) + V(t) \leq \frac{1 + \varepsilon}{d} \left( d + \frac{(1-b)^2}{4b} \right) |\Omega| + \varepsilon, \quad t > T_2, \tag{2.7}$$

which implies that  $\limsup_{t \rightarrow \infty} \int_{\Omega} v(x, t) dx \leq (1 + \frac{(1-b)^2}{4db}) |\Omega|$ .

From (2.7), we know that any solution  $v(x, t)$  satisfies an  $L^1$  a priori estimate  $K_1 = (1 + \frac{(1-b)^2}{4db}) |\Omega|$  for large  $t > 0$ , which only depends on  $d, b$  and  $\Omega$ . Furthermore we can use the  $L^1$  bound to obtain an  $L^\infty$  bound  $K_2$  for large  $t > 0$  from Theorem 3.1 in [1] (see also [4]), where  $K_2$  depends on  $K_1$  and  $v_0$ .

Recall the proof of Lemma 4.7 in [4] (and also use the notation in that proof), when  $d_2 > d_{2*}$ , we can choose  $2d_{2*}/(2 - d + \frac{m}{a+1}) < \varepsilon_0 < 2d_2/(2 - d + \frac{m}{a+1})$ , then  $C_1$  depends on  $a, m, d, \Omega$  and  $d_{2*}$ . Therefore the  $L^\infty$  bound  $B^*$  only depends on  $C_1$  and  $K_1$ . Therefore, there exists  $C > 0$ , such that  $\limsup_{t \rightarrow \infty} v(x, t) \leq C$  with  $C$  independent of  $u_0, v_0, d_1, d_2$  but only on a lower bound of  $d_2$ .

4. If  $d_1 = d_2$ , we can add the two equations in (1.3) and obtain

$$\begin{cases} w_t - d_1 \Delta w = u(1 - u)(b^{-1}u - 1) - dv, & x \in \Omega, t > T, \\ \frac{\partial w}{\partial n} = 0, & x \in \partial\Omega, t > T, \\ w(x, T) = u(x, T) + v(x, T), & x \in \Omega, \end{cases}$$

where  $w(x, t) = u(x, t) + v(x, t)$ . Since when  $t > T$ ,  $u(x, t) \leq 1 + \varepsilon$ , then we have

$$\begin{aligned} u(1 - u)(b^{-1}u - 1) - dv &= u(1 - u)(b^{-1}u - 1) + du - dw \leq \left(\frac{(1 - b)^2}{4b} + d\right)u - dw \\ &\leq \left(\frac{(1 - b)^2}{4b} + d\right)(1 + \varepsilon) - dw, \end{aligned}$$

and for the equation

$$\begin{cases} \frac{\partial \phi}{\partial t} = d_1 \Delta \phi + \left(\frac{(1 - b)^2}{4b} + d\right)(1 + \varepsilon) - d\phi, & x \in \Omega, t > T, \\ \frac{\partial \phi}{\partial n} = 0, & x \in \partial\Omega, t > T, \end{cases} \tag{2.8}$$

it is well known that the solution  $\phi(x, t) \rightarrow d^{-1}(\frac{(1-b)^2}{4b} + d)(1 + \varepsilon)$  as  $t \rightarrow \infty$ , then the comparison argument shows that

$$\limsup_{t \rightarrow \infty} v(x, t) \leq \limsup_{t \rightarrow \infty} w(x, t) \leq d^{-1} \left(\frac{(1 - b)^2}{4b} + d\right)(1 + \varepsilon),$$

which implies the last part of (d).  $\square$

**Remark 2.2.**

1. The global existence and boundedness of the positive solution to (1.3) can also be obtained from a general result of Hollis, Martin and Pierre [18] (see Theorems 1 and 2). Here we show the detailed construction to obtain specific bounds for this particular model.
2. A discussion of the steady state solutions of (2.1) will be given in Section 3.2. In general, the dynamics of the parabolic equation corresponding to (2.1) is bistable with two locally stable steady states  $u = 0$  and  $u = 1$ , and there is a co-dimension one manifold  $M$  which separates the basins of attraction of the two locally stable steady states (see [20–22]). All other steady state solutions discussed in Section 3.2 are unstable.

The results on the dynamical behavior of (1.3) in Theorem 2.1 parts (b) and (c) also imply the following results on the steady state solutions of (1.3), which satisfy:



$$\begin{cases} -d_1 \Delta u = u(1-u)(b^{-1}u-1) - \frac{muv}{a+u}, & x \in \Omega, \\ -d_2 \Delta v = -dv + \frac{muv}{a+u}, & x \in \Omega, \\ \frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0, & x \in \partial\Omega. \end{cases} \quad (2.9)$$

**Corollary 2.3.** Suppose that  $d, m, a, d_1, d_2 > 0, 0 < b < 1$ , and  $\Omega$  is a bounded domain with smooth boundary. Let  $(u(x), v(x))$  be a non-negative solution of (2.9):

1. If  $u(x) \leq b$  for all  $x \in \bar{\Omega}$ , then  $(u(x), v(x))$  must be either  $(0, 0)$  or  $(b, 0)$ .
2. If  $d \geq \frac{m}{a+1}$ , then  $(u(x), v(x))$  must be in form of  $(u_S, 0)$ , which we call a semi-trivial solution.

**Proof.** From Theorem 2.1 parts (b) and (c), we only need to prove the case when  $d \geq m/(a+1)$ . From Theorem 2.1 part (d), then  $u(x) \leq 1$  and  $-d + \frac{mu(x)}{a+u(x)} \leq 0$ . By integrating the second equation of (2.9), we obtain

$$0 \leq d_2 \int_{\Omega} |\nabla v|^2 dx = \int_{\Omega} v^2 \left( -d + \frac{mu}{a+u} \right) dx \leq 0.$$

Hence  $v \equiv 0$  on  $\bar{\Omega}$ .  $\square$

For the ODE system corresponding to the kinetic system of (1.3), it is known that the predator invasion leads to the extinction of both species, this phenomenon is called *overexploitation* [51,53]. Mathematically it means for any given initial prey population, a large enough initial predator population will always lead to the extinction of both species, i.e. the convergence to the steady state  $(0, 0)$ . In the following result, we establish this result for the reaction–diffusion system (1.3).

**Theorem 2.4.** Suppose that  $d, m, a, d_1, d_2 > 0, 0 < b < 1$  are fixed. For a given initial value of the prey population  $u_0(x) \geq 0$ , there exists a constant  $v_0^*$  which depends on parameters and  $u_0(x)$ , such that when the initial predator population  $v_0(x) \geq v_0^*$ , then the corresponding solution  $(u(x, t), v(x, t))$  of (1.3) tends to  $(0, 0)$  uniformly for  $x \in \bar{\Omega}$  as  $t \rightarrow \infty$ .

**Proof.** For a fixed  $\varepsilon > 0$ , there exists  $T_1 > 0$  such that  $u(t, x) \leq 1 + \varepsilon$  for  $t > T_1$  from Theorem 2.1(d). Therefore  $u(x, t)$  satisfies

$$\begin{cases} u_t = d_1 \Delta u + b^{-1}u(1-u)(u-b) - \frac{muv}{a+u}, & x \in \Omega, t > T_1, \\ u(x, T_1) \leq 1 + \varepsilon. \end{cases}$$

Let  $v_1(x, t)$  be the solution to

$$\begin{cases} v_t = d_2 \Delta v - dv, & x \in \Omega, t > 0, \\ \frac{\partial v}{\partial n} = 0, & x \in \partial\Omega, t > 0, \\ v(x, 0) = v_0(x), & x \in \Omega. \end{cases} \quad (2.10)$$

Then  $v(x, t) \geq v_1(x, t)$  from the comparison principle of parabolic equation for any  $t > 0$ . Moreover, if  $v_0(x) \geq v_0^*$ , then  $v(x, t) \geq v_0^* e^{-d(T_1+T_2)}$  when  $t \in [0, T_1 + T_2]$  for some  $T_2 > 0$ .

Since  $b^{-1}(1-u)(u-b) \leq \frac{(1-b)^2}{4b} \equiv M_1$  for all  $u \geq 0$ , and  $\frac{m}{a+u(x,t)} \geq \frac{m}{a+1+\varepsilon}$  for  $t > T_1$ , then  $u(x, t)$  satisfies that

$$\begin{cases} u_t \leq d_1 \Delta u + \left[ M_1 - \frac{m}{a+1+\varepsilon} v_0^* e^{-d(T_1+T_2)} \right] u, & x \in \Omega, T_1 < t < T_1 + T_2, \\ u(x, T_1) \leq 1 + \varepsilon. \end{cases}$$

Hence the comparison principle shows that for  $t \in [T_1, T_1 + T_2]$ , and  $x \in \bar{\Omega}$ ,

$$u(x, t) \leq (1 + \varepsilon) \exp \left[ \left( M_1 - \frac{m}{a+1+\varepsilon} v_0^* e^{-d(T_1+T_2)} \right) (t - T_1) \right].$$

Direct calculation implies that if we choose

$$v_0^* \geq e^{2dT_1} \left( \frac{1 + \varepsilon}{b} \right)^{d/M_1} \cdot \frac{2M_1(a+1+\varepsilon)}{m},$$

and

$$T_2 \geq T_1 + \frac{\ln(1 + \varepsilon) - \ln b}{M_1},$$

then

$$M_1 - \frac{m}{a+1+\varepsilon} v_0^* e^{-d(T_1+T_2)} \leq -M_1,$$

and for any  $x \in \bar{\Omega}$ ,

$$u(x, T_1 + T_2) \leq (1 + \varepsilon) \exp \left[ \left( M_1 - \frac{m}{a+1+\varepsilon} v_0^* e^{-d(T_1+T_2)} \right) (T_2 - T_1) \right] < b.$$

Therefore,  $(u(x, t), v(x, t))$  tends to  $(0, 0)$  for as  $t \rightarrow \infty$  from Theorem 2.1(b). Since  $\varepsilon$  is chosen arbitrarily, then it is clear that  $v_0^*$  depends only on the fixed parameters and  $T_1$  which depends on  $u_0(x)$ .  $\square$

Theorem 2.4 implies that  $(0, 0)$  is always a locally stable steady state with basin of attraction including all large  $v_0$  for a given  $u_0$ . Thus the system (1.3) is bistable (or multi-stable) if there is another locally stable steady state solution or periodic orbit.

### 3. Trivial and semi-trivial steady state solutions

#### 3.1. Constant steady state solutions

From Theorem 2.1 part (c), the dynamics of (1.3) is reduced to that of a scalar equation (2.1) if  $d > \frac{m}{a+1}$ . Therefore in the remaining part of the paper, we always assume that  $d \leq \frac{m}{a+1} < m$ . Under this assumption, (1.3) has the following non-negative constant steady state solutions:

- (1) the trivial solution  $(0, 0)$ ;
- (2) the semi-trivial solution in the absence of predator  $(1, 0)$  and  $(b, 0)$ ;
- (3) the unique positive constant solution  $(\lambda, v_\lambda)$ , where

$$\lambda = \frac{ad}{m-d}, \quad v_\lambda = \frac{(a+\lambda)(1-\lambda)(b^{-1}\lambda-1)}{m}.$$

The positive constant solution  $(\lambda, v_\lambda)$  exists if and only if  $b < \lambda < 1$ . In the following, we fix  $a, b$  and  $d$  and take  $\lambda$  as the bifurcation parameter (or equivalently  $m$  as a parameter). Since we assume that  $d \leq \frac{m}{a+1}$ , then we only consider  $0 < \lambda \leq 1$ . Theorem 2.1 part (c) and the analysis of the scalar equation (2.1) completely determine the dynamics of (1.3) for  $\lambda > 1$  and  $\lambda < 0$ .

Recall that  $-\Delta$  under Neumann boundary condition has eigenvalues  $0 = \mu_0 < \mu_1 \leq \mu_2 \leq \dots$  and  $\lim_{i \rightarrow \infty} \mu_i = \infty$ . Let  $S(\mu_i)$  be eigenspace corresponding to  $\mu_i$  with multiplicity  $m_i \geq 1$ . Let  $\phi_{ij}, 1 \leq j \leq m_i$ , be the normalized eigenfunctions corresponding to  $\mu_i$ . Then the set  $\{\phi_{ij}, i \geq 0, 1 \leq j \leq m_i\}$  forms a complete orthonormal basis in  $L^2(\Omega)$ .

The local stability of the constant steady state solutions can be analyzed as follows:

**Theorem 3.1.** *Suppose that  $d, m, a, d_1, d_2 > 0, 0 < b < 1$ , and  $\Omega$  is a bounded domain with smooth boundary. Then:*

- (a)  $(0, 0)$  is locally asymptotically stable for all  $\lambda > 0$ ;
- (b)  $(b, 0)$  is unstable for all  $\lambda > 0$ ;
- (c)  $(1, 0)$  is locally asymptotically stable for  $\lambda > 1$  and is unstable for  $\lambda < 1$ ;
- (d) If  $b < \lambda < 1$ , then  $(\lambda, v_\lambda)$  is locally asymptotically stable for  $\bar{\lambda} < \lambda < 1$  and is unstable  $b < \lambda < \bar{\lambda}$ , where  $\bar{\lambda}$  is given by

$$\bar{\lambda} = \frac{b + 1 - a + \sqrt{(b + 1 - a)^2 + 3(ab + a - b)}}{3}. \tag{3.1}$$

**Proof.** The linearization of (1.3) at a constant solution  $e^* = (u, v)$  can be expressed by

$$\begin{pmatrix} \phi_t \\ \psi_t \end{pmatrix} = L \begin{pmatrix} \phi \\ \psi \end{pmatrix} := D \begin{pmatrix} \Delta \phi \\ \Delta \psi \end{pmatrix} + J_{(u,v)} \begin{pmatrix} \phi \\ \psi \end{pmatrix} \tag{3.2}$$

with domain  $X = \{(\phi, \psi) \in H^2(\Omega) \times H^2(\Omega) : \frac{\partial \phi}{\partial n} = \frac{\partial \psi}{\partial n} = 0\}$ , where

$$D = \begin{pmatrix} d_1 & 0 \\ 0 & d_2 \end{pmatrix}, \quad J_{(u,v)} = \begin{pmatrix} A(u, v) & B(u, v) \\ C(u, v) & D(u, v) \end{pmatrix},$$

and

$$A(u, v) = -3b^{-1}u^2 + 2(1 + b^{-1})u - 1 - \frac{amv}{(a + u)^2}, \quad B(u, v) = -\frac{mu}{a + u},$$

$$C(u, v) = \frac{amv}{(a + u)^2}, \quad D(u, v) = -d + \frac{mu}{a + u}.$$

From Theorem 5.1.1 and Theorem 5.1.3 of [16], it is known that if all the eigenvalues of the operator  $L$  have negative real parts, then  $e^* = (u, v)$  is asymptotically stable; if there is an eigenvalue with positive real part, then  $e^* = (u, v)$  is unstable; if all the eigenvalues have non-positive real parts while some eigenvalues have zero real part, then the stability of  $e^* = (u, v)$  cannot be determined by the linearization.

Let  $X_{ij} = \{c \cdot \phi_{ij} : c \in \mathbb{R}^2\}$ , where  $\{\phi_{ij} : 1 \leq j \leq \dim[S(\mu_i)]\}$  is an orthonormal basis of  $S(\mu_i)$ . For  $i \geq 0$ , it can be observed that  $X = \bigoplus_{i=1}^{\infty} X_i$  and  $X_i = \bigoplus_{j=1}^{\dim[S(\mu_i)]} X_{ij}$  is invariant under the operator  $L$  and  $\sigma$  is an eigenvalue of  $L$  if and only if  $\sigma$  is an eigenvalue of the matrix  $J_i = -\mu_i D + J_{(u,v)}$  for some  $i \geq 0$ . So the stability is reduced to consider the characteristic equation

$$\det(\sigma I - J_i) = \sigma^2 - \text{trace } J_i \sigma + \det J_i, \tag{3.3}$$

with

$$\begin{aligned} \text{trace}(J_i) &= -\mu_i(d_1 + d_2) + A(u, v) + D(u, v), \\ \det(J_i) &= d_1 d_2 \mu_i^2 - (A(u, v)d_2 + D(u, v)d_1)\mu_i + \det J_{(u,v)}. \end{aligned}$$

1. If  $e^* = (0, 0)$ , then  $J_{(0,0)} = \begin{pmatrix} -1 & 0 \\ 0 & -d \end{pmatrix}$ , and

$$\begin{aligned} \text{trace}(J_i) &= -\mu_i(d_1 + d_2) - (d + 1) < 0, \\ \det(J_i) &= d_1 d_2 \mu_i^2 + (d_1 + d_2)\mu_i + d > 0. \end{aligned}$$

Thus  $(0, 0)$  is locally asymptotically stable.

2. If  $e^* = (b, 0)$ , then  $J_{(b,0)} = \begin{pmatrix} 1-b & -\frac{mb}{a+b} \\ 0 & -d+\frac{mb}{a+b} \end{pmatrix}$ . For  $i = 0$ , one of the eigenvalues is  $1 - b > 0$  so  $(b, 0)$  is unstable.

3. If  $e^* = (1, 0)$ , then  $J_{(1,0)} = \begin{pmatrix} 1-b^{-1} & -\frac{m}{a+1} \\ 0 & -d+\frac{m}{a+1} \end{pmatrix}$ :

(a) When  $\lambda = \frac{ad}{m-d} > 1$ , then  $-d + \frac{mb}{a+b} > 0$ , so for  $i \geq 0$ ,

$$\begin{aligned} \text{trace}(J_i) &= -\mu_i(d_1 + d_2) + (1 - b^{-1}) + \left(-d + \frac{m}{a+1}\right) < 0, \\ \det(J_i) &= d_1 d_2 \mu_i^2 + \left((b^{-1} - 1)d_2 + \left(d - \frac{m}{a+1}\right)d_1\right)\mu_i + (1 - b^{-1})\left(-d + \frac{m}{a+1}\right) > 0. \end{aligned}$$

Hence  $(1, 0)$  locally asymptotically stable.

(b) When  $\lambda \leq 1$ , then  $-d + \frac{m}{a+1} > 0$ . For  $i = 0$ ,  $\det(J_i) = (1 - b^{-1})\left(-d + \frac{m}{a+1}\right) < 0$ , which implies that (3.3) has at least one root with positive real part. Hence  $(1, 0)$  is an unstable steady state solution of (1.3).

4. If  $e^* = (\lambda, v_\lambda)$ , then  $J_{(\lambda, v_\lambda)} = \begin{pmatrix} A(\lambda) & B(\lambda) \\ C(\lambda) & 0 \end{pmatrix}$ , where

$$\begin{aligned} A(\lambda) &= (1 - 2\lambda)(b^{-1}\lambda - 1) + b^{-1}(\lambda - \lambda^2) - \frac{a(1 - \lambda)(b^{-1}\lambda - 1)}{a + \lambda}, \\ B(\lambda) &= -d, \quad C(\lambda) = \frac{a(1 - \lambda)(b^{-1}\lambda - 1)}{a + \lambda}, \end{aligned} \tag{3.4}$$

and we notice that  $\bar{\lambda} \in (b, 1)$  defined in (3.1) is the larger root of  $A(\lambda) = 0$ :

(a) When  $\bar{\lambda} < \lambda < 1$ , then  $A(\lambda) < 0$ , so for  $i \geq 0$ ,

$$\begin{aligned} \text{trace}(J_i) &= -\mu_i(d_1 + d_2) + A(\lambda) < 0, \\ \det(J_i) &= d_1 d_2 \mu_i^2 - A(\lambda)d_2 \mu_i - B(\lambda)C(\lambda) > 0. \end{aligned} \tag{3.5}$$

Hence  $(\lambda, v_\lambda)$  is a locally asymptotically stable steady state solution of (1.3).

(b) When  $b < \lambda < \bar{\lambda}$ , then  $A(\lambda) > 0$ . For  $i = 0$ ,

$$\text{trace}(J_i) = A(\lambda) > 0,$$

which implies that (3.3) has at least one root with positive real part. Hence  $(\lambda, v_\lambda)$  is an unstable steady state solution of (1.3).  $\square$

Theorem 3.1 shows that when  $\lambda > \bar{\lambda}$ , either  $(\lambda, v_\lambda)$  or  $(1, 0)$  is a locally asymptotically stable constant steady state hence the overall dynamics of (1.3) is bistable.

### 3.2. Nonconstant semi-trivial steady state solutions

Besides the constant steady state solutions, (1.3) can have steady state solutions in form of  $(u(x), 0)$ . In this case,  $u(x)$  satisfies

$$\begin{cases} d_1 \Delta u + u(1-u)(b^{-1}u - 1) = 0, & x \in \Omega, \\ \frac{\partial u}{\partial n} = 0, & x \in \partial\Omega. \end{cases} \quad (3.6)$$

The set of solutions to (3.6) is also of independent interest. To derive some *a priori* estimates for non-negative solutions of (3.6) and (2.9), we recall the following maximum principle [38]:

**Lemma 3.2.** *Let  $\Omega$  be a bounded Lipschitz domain in  $\mathbb{R}^n$ , and let  $g \in C(\bar{\Omega} \times \mathbb{R})$ . If  $z \in H^1(\Omega)$  is a weak solution of the inequalities*

$$\Delta z + g(x, z(x)) \geq 0 \quad \text{in } \Omega, \quad \frac{\partial z(x)}{\partial n} \leq 0 \quad \text{on } \partial\Omega,$$

and if there is a constant  $K$  such that  $g(x, z) < 0$  for  $z > K$ , then  $z \leq K$  a.e. in  $\Omega$ .

For the semi-trivial solutions, we have the following result:

**Theorem 3.3.** *Suppose that  $d_1 > 0$  and  $0 < b < 1$ ,  $\Omega$  is a bounded domain with smooth boundary, and  $\mu_m$  are the eigenvalues of  $-\Delta$  under Neumann boundary condition on  $\Omega$ :*

- (a) *All nontrivial solutions of (3.6) satisfy  $0 < u(x) < 1$ .*
- (b) *Let  $d_{1*} = \frac{2(b+1)}{b\mu_1}$ . Then for  $d_1 > d_{1*}$ , the only non-negative solutions to (3.6) are  $u = 0$ ,  $u = b$  or  $u = 1$ .*
- (c) *Let  $D_m = \frac{1-b}{\mu_m}$  with  $m \geq 1$ , then  $d_1 = D_m$  is a bifurcation point for (3.6), where a continuum  $\Sigma_m$  of positive nontrivial solutions of (3.6) bifurcates from  $u = b$ .*
- (d) *If  $\mu_m$  has odd algebraic multiplicity, then either the projection of  $\Sigma_m$  to  $d_1$ -axis  $\text{Proj } \Sigma_m \supset (0, D_m)$ , or  $\Sigma_m$  contains another bifurcation point  $(D_k, b)$ ; Moreover if  $\mu_m$  is a simple eigenvalue, then  $\Sigma_m$  is a curve near the bifurcation point  $(D_m, b)$ .*

**Proof.** (a) This can be easily derived from Lemma 3.2 and strong maximum principle.

(b) Let  $u(x)$  be a non-negative solution of (3.6). Denote  $\bar{u} = |\Omega|^{-1} \int_{\Omega} u(x) dx \geq 0$  and  $f(u) = u(1-u)(b^{-1}u - 1)$ . Then

$$\int_{\Omega} (u - \bar{u}) dx = 0.$$

Multiplying the equation in (3.6) by  $u - \bar{u}$  and from part (a), we get

$$\begin{aligned}
 d_1 \int_{\Omega} |\nabla(u - \bar{u})|^2 dx &= \int_{\Omega} (u - \bar{u}) f(u) dx \\
 &= \int_{\Omega} (u - \bar{u})(f(u) - f(\bar{u})) dx \\
 &= \frac{1}{b} \int_{\Omega} (u - \bar{u})^2 (-(u^2 + u\bar{u} + \bar{u}^2) + (b + 1)(u + \bar{u}) - b) dx \\
 &\leq \frac{1}{b} \int_{\Omega} (u - \bar{u})^2 (b + 1)(u + \bar{u}) dx \\
 &\leq \frac{2(b + 1)}{b} \int_{\Omega} (u - \bar{u})^2 dx.
 \end{aligned} \tag{3.7}$$

Then with the Poincaré inequality:

$$\mu_1 \int_{\Omega} (u - \bar{u})^2 dx \leq \int_{\Omega} |\nabla(u - \bar{u})|^2 dx,$$

we find that

$$d_1 \mu_1 \int_{\Omega} (u - \bar{u})^2 dx \leq \int_{\Omega} \frac{2(b + 1)}{b} (u - \bar{u})^2 dx,$$

which implies that  $d_1 \leq \frac{2(b+1)}{b\mu_1}$  unless  $u - \bar{u} \equiv 0$ .

(c) Rewrite (3.6) as

$$\begin{cases} \Delta u + pf(u) = 0, & x \in \Omega, \\ \frac{\partial u}{\partial n} = 0, & x \in \partial\Omega, \end{cases} \tag{3.8}$$

with  $p = d_1^{-1}$  and we will take  $p$  as the parameter in the following. Define  $F(p, u) = \Delta u + pf(u)$ ,  $u \in Y = \{v \in C^{2,\alpha}(\bar{\Omega}) : \partial v / \partial n = 0 \text{ on } \partial\Omega\}$ . Notice that  $(p, u) = (p, b)$  is a solution to the equation for any  $p \in \mathbb{R}$ . The partial derivative  $F_u(p, b) = \Delta + pf'(b) : Y \rightarrow C^\alpha(\bar{\Omega})$  is a Fredholm operator with index zero from Proposition 2.2 in [45]. It is clear that  $F_u(p, b)$  is not invertible if and only if  $pf'(b) = \mu_m$ , equivalent to  $d_1 = f'(b)/\mu_m = (1 - b)/\mu_m$ , for  $m \geq 1$ . We can apply Theorem 11.4 in [42] (since  $F(p, u)$  is a potential operator) to conclude that  $d_1 = D_m \equiv f'(b)/\mu_m$  is a bifurcation point for (3.6) where a continuum  $\Sigma_m$  of nontrivial solutions of (3.6) bifurcates from  $u = b$ . Near  $(d_1, u) = (D_m, b)$ , the solutions on  $\Sigma_m$  are clearly positive as they are perturbation of  $u = b$ . Since  $\Sigma_m$  is a connected component of the solution set of (3.6), then all nontrivial solutions on  $\Sigma_m$  are positive.

(d) If  $\mu_m$  has odd algebraic multiplicity, then we define  $\tilde{\Sigma}_m = \{(p, u) : p = d_1^{-1}, (d_1, u) \in \Sigma_m\}$ . We can apply the celebrated Rabinowitz global bifurcation theorem [41] to conclude that  $\tilde{\Sigma}_m$  is unbounded or  $\tilde{\Sigma}_m$  contains another bifurcation point  $(D_k^{-1}, b)$ . From part (a), all solutions are bounded, and from part (b), there is no nontrivial solutions for  $d_1$  large, thus  $\tilde{\Sigma}_m$  being unbounded implies that its projection to  $p$ -axis contains  $(D_m^{-1}, \infty)$ . Hence either the projection of  $\Sigma_m$  to  $d_1$ -axis  $\text{Proj } \Sigma_m \supset (0, D_m)$ , or  $\Sigma_m$  contains another bifurcation point  $(D_k, b)$ .

If  $\mu_m$  is a simple eigenvalue, then  $N(F_u(D_m, b)) = \text{span}\{w_0\}$ , which is one-dimensional and  $R(F_u(D_m, b)) = \{v \in C^\alpha(\bar{\Omega}) : \int_{\Omega} w_0 v dx = 0\}$ , which is codimension one. Finally,  $F_{pu}(D_m, b)[w_0] =$

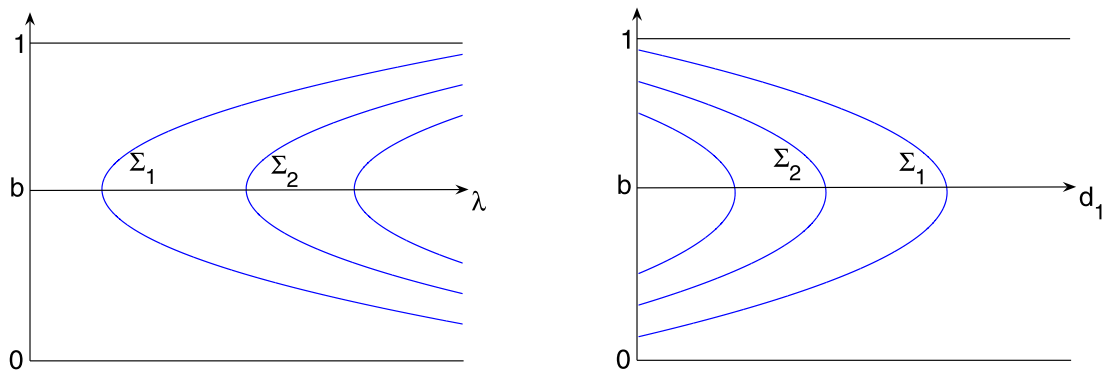


Fig. 1. Solution set of (3.9).

$f'(b)w_0 \notin R(F_u(D_m, b))$  since  $\int_{\Omega} f'(b)w_0^2 dx > 0$ . Therefore near bifurcation point  $\Sigma_m$  is a curve, which follows from Theorem 1.7 of [10] or result in [48].  $\square$

When the spatial dimension  $n = 1$ , a much clearer picture of the global bifurcation of positive solutions to (3.6) can be obtained.

**Theorem 3.4.** Consider

$$d_1 u'' + u(1 - u)(b^{-1}u - 1) = 0, \quad x \in (-R, R), \quad u'(-R) = u'(R) = 0. \quad (3.9)$$

Then  $\Sigma_m = \{(d_1, u_m^{\pm}(d_1, x)) : 0 < d_1 < D_m\}$ ,  $u_m^{\pm}(d_1, \cdot) - b$  changes sign exactly  $m$  times in  $(-R, R)$ ,  $u_m^+(d_1, -R) > b$  and  $u_m^-(d_1, -R) < b$ . In particular, (3.9) has exactly  $2m$  nontrivial positive solutions if  $D_{m+1} < d_1 < D_m$ , and all of them are unstable. In fact here  $D_m = 4(1 - b)R^2 / (m\pi)^2$ .

**Proof.** The result follows from Proposition 2.1, Theorem 2.2, Theorem 2.5 and Theorem 2.7 in [46], since we can verify that  $f(u) = u(1 - u)(b^{-1}u - 1)$  satisfies (f1)–(f5) with  $m = 0$ ,  $M = 1$  and (2.35) in [46]. The monotonicity of  $\Sigma_m$  is also proved in [57]. Note that (f2) in [46] is not necessary, but only for definiteness, see remark on p. 3126 of [46]. A pitchfork bifurcation occurs at each  $(D_m, b)$  for  $\Sigma_m$ , see Fig. 1 for illustration. Note that we exclude the case of  $\mu_0 = 0$ . In fact here a crossing-curve bifurcation does occur, but the solution branch is a trivial one  $\{(p, u) = (0, u) : u \in \mathbb{R}\}$ .  $\square$

Now we state the results for the semi-trivial solutions of (1.3):

**Corollary 3.5.** Suppose that  $d, m, a, d_1, d_2 > 0$ ,  $0 < b < 1$ , and  $\Omega$  is a bounded domain with smooth boundary:

1. If  $(u(x), 0)$  is a solution of (2.9), and  $u(x)$  is not constant, then  $0 < u(x) < 1$  for  $x \in \Omega$  and  $d_1$  satisfies  $d_1 < d_{1*} = \frac{2(b+1)}{b\mu_1}$ .
2.  $d_1 = D_m = (1 - b) / \mu_m$  is a bifurcation point for (2.9), where a continuum  $\hat{\Sigma}_m = \Sigma_m \times \{0\}$  of semi-trivial solutions of (2.9) bifurcates from  $(u, v) = (b, 0)$ , and  $\Sigma_m$  is defined in Theorem 3.3.
3. If  $\mu_m$  has odd algebraic multiplicity, then either the projection of  $\hat{\Sigma}_m$  to  $d_1$ -axis  $\text{Proj } \hat{\Sigma}_m \supset (0, D_m)$ , or  $\hat{\Sigma}_m$  contains another bifurcation point  $(D_k, b, 0)$ ; Moreover if  $\mu_m$  is a simple eigenvalue, then  $\hat{\Sigma}_m$  is a curve near the bifurcation point  $(D_m, b, 0)$ .
4. If  $n = 1$  and  $\Omega = (-R, R)$ ,  $D_{m+1} < d_1 < D_m$ , then (1.3) has exactly  $2m + 2$  non-negative semi-trivial solutions when  $\lambda \in (0, b] \cup [1, \infty)$ , and exactly  $2m + 3$  such solutions when  $\lambda \in (b, 1)$ ; These solutions are the ones described in Theorem 3.4 and the constant ones  $(b, 0)$ ,  $(1, 0)$ .

In the case of  $n = 1$ , Corollary 3.5 completely classifies all semi-trivial solutions of (2.9). For spatial dimension  $n = 1$ , (3.9) is often referred as Chafee–Infante equation [6] for the special case of  $b = 1/2$ ,

which is the balanced case. Here all results for (3.6) are for higher-dimensional domains and  $b \in (0, 1)$  (balanced and unbalanced cases, see [46]).

#### 4. A priori estimates and nonexistence of solutions

In this section we discuss the nonexistence of nonconstant positive solutions of (2.9) for certain parameter ranges. First we have the following *a priori* estimate for any non-negative solutions for (2.9), using similar argument as the proof of Theorem 2.1 part (c) with  $d_1 = d_2$ .

**Lemma 4.1.** *Suppose that  $(u(x), v(x))$  is a non-negative solution of (2.9). Then either  $(u, v)$  is a semi-trivial solution in form of  $(u(x), 0)$  where  $u$  satisfies (3.6), or for  $x \in \bar{\Omega}$ ,  $(u(x), v(x))$  satisfies*

$$0 < u(x) < 1, \quad \text{and} \quad 0 < v(x) < C^* = \frac{(1-b)^2}{4bd} + \frac{d_1}{d_2}, \quad (4.1)$$

where  $d, d_1, d_2, a, m > 0$  and  $0 < b < 1$ .

**Proof.** Let  $(u(x), v(x))$  be a non-negative solution of (2.9). If there exists  $x_0 \in \bar{\Omega}$  such that  $v(x_0) = 0$ , then  $v(x) \equiv 0$  from the strong maximum principle and  $u(x)$  satisfies (3.6). Similarly if  $u(x_0) = 0$  for some  $x_0 \in \Omega$ , we also have  $u(x) \equiv 0$  which also implies  $v \equiv 0$ . Otherwise  $u(x) > 0$  and  $v(x) > 0$  for  $x \in \bar{\Omega}$ .

From Lemma 3.2,  $u(x) \leq 1$  and from the strong maximum principle,  $u(x) < 1$  for all  $x \in \bar{\Omega}$ . By adding the two equations in (2.9), we have

$$\begin{aligned} -(d_1 \Delta u + d_2 \Delta v) &= u(1-u)(b^{-1}u-1) - dv \\ &= u \left( (1-u)(b^{-1}u-1) + \frac{dd_1}{d_2} \right) - \frac{d}{d_2} (d_1 u + d_2 v) \\ &\leq \left( \frac{(1-b)^2}{4b} + \frac{dd_1}{d_2} \right) - \frac{d}{d_2} (d_1 u + d_2 v). \end{aligned}$$

Then the maximum principle implies that

$$d_1 u + d_2 v < \frac{1}{d} \left( \frac{(1-b)^2 d_2}{4b} + dd_1 \right),$$

which implies the desired estimate.  $\square$

Now we can show the nonexistence of positive steady state solutions when the diffusion coefficients  $d_1$  and  $d_2$  are large.

**Theorem 4.2.** *For any fixed  $m, a, d > 0$  and  $0 < b < 1$ , there exists  $d^* = d^*(m, a, b, d, \Omega)$  such that if  $\min\{d_1, d_2\} > d^*$ , then the only non-negative solutions to (2.9) are  $(0, 0)$ ,  $(b, 0)$ ,  $(1, 0)$  and  $(\lambda, v_\lambda)$ .*

**Proof.** Let  $(u, v)$  be a non-negative solution of (2.9), and denote  $\bar{u} = |\Omega|^{-1} \int_\Omega u \, dx$ ,  $\bar{v} = |\Omega|^{-1} \int_\Omega v \, dx$ . Then

$$\int_\Omega (u - \bar{u}) \, dx = \int_\Omega (v - \bar{v}) \, dx = 0. \quad (4.2)$$



Multiplying the first equation in (2.9) by  $u - \bar{u}$  and applying Lemma 4.1, we get

$$\begin{aligned}
 & d_1 \int_{\Omega} |\nabla(u - \bar{u})|^2 dx \\
 &= \int_{\Omega} (u - \bar{u})u(1 - u)(b^{-1}u - 1) dx - \int_{\Omega} \frac{mu v(u - \bar{u})}{a + u} dx \\
 &= \int_{\Omega} (u - \bar{u})u(1 - u)(b^{-1}u - 1) dx - \int_{\Omega} \frac{mv(u - \bar{u})^2}{a + u} dx - \int_{\Omega} \frac{mv\bar{u}(u - \bar{u})}{a + u} dx \\
 &\leq \frac{2(b + 1)}{b} \int_{\Omega} (u - \bar{u})^2 dx + \int_{\Omega} \frac{-mv\bar{u}(u - \bar{u})}{a + u} dx.
 \end{aligned} \tag{4.3}$$

In a similar manner, we multiply the second equation in (2.9) by  $v - \bar{v}$  to have

$$\begin{aligned}
 d_2 \int_{\Omega} |\nabla(v - \bar{v})|^2 dx &= \int_{\Omega} \left(-d + \frac{mu}{a + u}\right) (v - \bar{v})^2 dx + \int_{\Omega} \left(-d + \frac{mu}{a + u}\right) \bar{v}(v - \bar{v}) dx \\
 &= \int_{\Omega} \left(-d + \frac{mu}{a + u}\right) (v - \bar{v})^2 dx + \int_{\Omega} \frac{mu\bar{v}}{a + u} (v - \bar{v}) dx \\
 &\leq \int_{\Omega} \left(-d + \frac{m}{a + 1}\right) (v - \bar{v})^2 dx + \int_{\Omega} \frac{mu\bar{v}}{a + u} (v - \bar{v}) dx.
 \end{aligned} \tag{4.4}$$

Furthermore, adding the two equations in (2.9) and integrating over  $\Omega$ , we get

$$\int_{\Omega} (-d_1 \Delta u - d_2 \Delta v) dx = \int_{\Omega} [u(1 - u)(b^{-1}u - 1) - dv] dx, \tag{4.5}$$

then the Neumann boundary conditions lead to

$$d \int_{\Omega} v dx = \int_{\Omega} u(1 - u)(b^{-1}u - 1) dx \leq \frac{|\Omega|}{4b}. \tag{4.6}$$

Here we use the fact that  $|u(1 - u)| \leq 1/4$  and  $|b^{-1}u - 1| \leq b^{-1}$  for  $0 \leq u \leq 1$  (we know that  $0 \leq u(x) \leq 1$  from Theorem 2.1). Thus

$$\bar{v} = \frac{1}{|\Omega|} \int_{\Omega} v dx \leq \frac{1}{4bd}. \tag{4.7}$$

From (4.7) and (4.2), we have

$$\begin{aligned}
 \int_{\Omega} \frac{mu\bar{v}}{a + u} (v - \bar{v}) dx &= \int_{\Omega} \frac{mu\bar{v}}{a + u} (v - \bar{v}) dx - \int_{\Omega} \frac{m\bar{u}\bar{v}}{a + \bar{u}} (v - \bar{v}) dx \\
 &= \int_{\Omega} \frac{am\bar{v}(v - \bar{v})}{(a + u)(a + \bar{u})} (u - \bar{u}) dx
 \end{aligned}$$

$$\begin{aligned} &\leq \frac{m}{4abd} \int_{\Omega} |u - \bar{u}| |v - \bar{v}| dx \\ &\leq \frac{m}{8abd} \int_{\Omega} (u - \bar{u})^2 dx + \frac{m}{8abd} \int_{\Omega} (v - \bar{v})^2 dx, \end{aligned} \tag{4.8}$$

and similarly

$$\begin{aligned} \int_{\Omega} \frac{-mv\bar{u}}{a+u} (u - \bar{u}) dx &= \int_{\Omega} m\bar{u} \left( \frac{\bar{v}}{a+\bar{u}} - \frac{v}{a+u} \right) (u - \bar{u}) dx \\ &= \int_{\Omega} \frac{m\bar{u}(u - \bar{u})}{(a+u)(a+\bar{u})} [\bar{v}(u - \bar{u}) + (a + \bar{u})(\bar{v} - v)] dx \\ &\leq \frac{m}{4abd} \int_{\Omega} (u - \bar{u})^2 dx + \frac{m}{a} \int_{\Omega} |u - \bar{u}| |v - \bar{v}| dx \\ &\leq \frac{m}{4abd} \int_{\Omega} (u - \bar{u})^2 dx + \frac{m}{2a} \int_{\Omega} (u - \bar{u})^2 dx + \frac{m}{2a} \int_{\Omega} (v - \bar{v})^2 dx. \end{aligned} \tag{4.9}$$

From (4.3), (4.4), (4.8) and (4.9) and the Poincaré inequality, we obtain that

$$\begin{aligned} &d_2 \int_{\Omega} |\nabla(v - \bar{v})|^2 dx + d_1 \int_{\Omega} |\nabla(u - \bar{u})|^2 dx \\ &\leq \frac{1}{\mu_1} \left( A \int_{\Omega} |\nabla(v - \bar{v})|^2 dx + B \int_{\Omega} |\nabla(u - \bar{u})|^2 dx \right), \end{aligned}$$

where

$$A = -d + \frac{m}{a+1} + \frac{m}{2a} \left( 1 + \frac{1}{4bd} \right), \quad B = \frac{2(b+1)}{b} + \frac{m}{2a} \left( 1 + \frac{3}{4bd} \right).$$

This shows that if

$$\min\{d_1, d_2\} > \frac{1}{\mu_1} \max\{A, B\},$$

then

$$\nabla(u - \bar{u}) = \nabla(v - \bar{v}) = 0,$$

and  $(u, v)$  must be a constant solution.  $\square$

**Remark 4.3.**

1. One can make an apparent comparison of the results of Theorem 4.2 and Theorem 3.3(b) (or Corollary 3.5(a)) to see that

$$d^* = \frac{1}{\mu_1} \max\{A, B\} \geq \frac{B}{\mu_1} > \frac{2(b+1)}{b\mu_1} = d_{1*}.$$

Note that Theorem 4.2 holds for any fixed  $a, b, m, d$  or equivalently any  $\lambda > 0$ .

2. An earlier result in [8] implies the nonexistence of spatial nonhomogeneous patterns for general reaction–diffusion systems when the diffusion coefficients are large. Our results here are more specific to the model (1.3).

**5. Bifurcation analysis and existence of steady states**

*5.1. Determination of bifurcation points*

To prove the existence of nonconstant steady state solutions and periodic solutions of (1.3), we further analyze the stability/instability of the constant coexistence steady state  $(\lambda, v_\lambda)$ . Recall from Section 3.1, the precise stability information of  $(\lambda, v_\lambda)$  is determined by the trace and determinant of  $J_i$  ( $i \geq 0$ ), which are defined in (3.5) with  $A(\lambda)$ ,  $B(\lambda)$  and  $C(\lambda)$  defined in (3.4).

For that purpose, we define

$$\begin{aligned} T(\lambda, p) &= -p(d_1 + d_2) + A(\lambda), \\ D(\lambda, p) &= d_1d_2p^2 - d_2A(\lambda)p - B(\lambda)C(\lambda). \end{aligned} \tag{5.1}$$

We call the set  $\{(\lambda, p) \in \mathbb{R}_+^2: T(\lambda, p) = 0\}$  to be the Hopf bifurcation curve, and the set  $\{(\lambda, p) \in \mathbb{R}_+^2: D(\lambda, p) = 0\}$  to be the steady state bifurcation curve. The studies in [23,60] show that the geometric properties of the Hopf and steady state bifurcation curves play important role in the bifurcation analysis of (1.3).

First for the Hopf bifurcation curve, we notice that  $T(\lambda, p) = 0$  is equivalent to  $p = A(\lambda)/(d_1 + d_2)$ . Recall from Section 3.1,

$$A(\lambda) = \frac{\lambda}{b(a + \lambda)} (-3\lambda^2 + 2(b + 1 - a)\lambda + a(1 + b) - b).$$

The following lemma characterizes the profile of the function  $A(\lambda)$ , and its proof is straightforward calculation thus omitted:

**Lemma 5.1.** *Suppose that  $a > 0, 0 < b < 1$ , then there exist  $0 < \lambda^* < \bar{\lambda} < 1$  such that:*

- (a) *If  $a(1 + b) - b \geq 0$ , then  $A(\lambda) > 0$  in  $(0, \bar{\lambda})$  and  $A(0) = A(\bar{\lambda}) = 0$ ;*
- (b) *If  $a(1 + b) - b < 0$ , then there exists  $\lambda_c \in (0, \lambda^*)$  such that  $A(\lambda) < 0$  in  $(0, \lambda_c)$ ;  $A(\lambda) > 0$  in  $(\lambda_c, \bar{\lambda})$  and  $A(0) = A(\lambda_c) = A(\bar{\lambda}) = 0$ ;*
- (c) *For either case,  $A'(\lambda) > 0$  in  $(\max\{0, \lambda_c\}, \lambda^*)$ ;  $A'(\lambda) < 0$  in  $(\lambda^*, \bar{\lambda})$ ;  $A'(\lambda^*) = 0$  and  $A(\lambda)$  attains its maximum  $M^*$  at  $\lambda^*$  for  $\lambda \in [0, 1]$ . Moreover  $M^*$  satisfies*

$$1 - b = A(b) \leq M^* \leq \frac{(b^2 + 1 - b + a(1 + b) + a^2)}{3b(a + 1)}.$$

Secondly for the steady state bifurcation curve  $D(\lambda, p) = 0$ , we notice that it is equivalent to  $\tilde{D}(\lambda, p) \equiv (a + \lambda)D(\lambda, p) = 0$  for  $\lambda \geq 0$ . For fixed  $p$ ,  $\tilde{D}$  is a degree 3 polynomial of  $\lambda$ , and for fixed  $\lambda$ , it is quadratic in  $p$ . Indeed we can solve  $p$  from  $D(p, \lambda) = 0$ ,

$$p = p_{\pm}(\lambda) := \frac{d_2 A(\lambda) \pm \sqrt{d_2^2 A^2(\lambda) + 4d_1 d_2 B(\lambda) C(\lambda)}}{2d_1 d_2}. \tag{5.2}$$

One can also see that the function  $D(p, \lambda)$  has no critical points in the first quadrant, hence the set  $\{(\lambda, p) \in \mathbb{R}_+^2 : D(\lambda, p) = 0\}$  must be a bounded connected smooth curve.

Let  $S(\lambda) = d_2^2 A^2(\lambda) + 4d_1 d_2 B(\lambda) C(\lambda)$ . There exists a unique root of  $S(\lambda) = 0$  denoted by  $\lambda^s$ , and  $p_{\pm}(\lambda)$  exists only for  $\lambda \leq \lambda^s$ . It is easy to verify that

$$S(b) = d_2^2 A^2(b) > 0 \quad \text{and} \quad S(\bar{\lambda}) = 4d_1 d_2 B(\bar{\lambda}) C(\bar{\lambda}) < 0,$$

so  $\lambda^s \in (b, \bar{\lambda})$ . We can summarize the properties of  $p_{\pm}(\lambda)$  as follows:

**Lemma 5.2.** *Let  $p_{\pm}(\lambda)$  be the functions defined in (5.2). Then there exists a  $\lambda^s \in (b, \bar{\lambda})$  such that  $p_+(\lambda)$  exists for  $\lambda \in [0, \lambda^s]$ , and  $p_-(\lambda)$  exists for  $\lambda \in [b, \lambda^s]$ . Moreover*

$$\lim_{\lambda \rightarrow \lambda^s} p_+(\lambda) = \lim_{\lambda \rightarrow \lambda^s} p_-(\lambda) = \frac{A(\lambda^s)}{2d_1},$$

and

$$p_+(0) = \sqrt{\frac{d}{d_1 d_2}}, \quad p_-(b) = 0.$$

Hence the steady state bifurcation curve  $\{D(\lambda, p) = 0 : p \geq 0, \lambda \geq 0\}$  is a smooth curve connecting  $(\lambda, p) = (0, \sqrt{\frac{d}{d_1 d_2}})$ ,  $(\lambda, p) = (\lambda^s, \frac{A(\lambda^s)}{2d_1})$  and  $(\lambda, p) = (b, 0)$ . Moreover,  $p_+(\lambda)$  attains its maximum value  $M^{**}$  at  $\lambda^{**} \in [b, \lambda^s]$  thus the steady state bifurcation curve exists only for  $p \in [0, M^{**}]$ , and  $M^{**}$  can be estimated as

$$\frac{1-b}{d_1} = p_+(b) \leq M^{**} \leq \frac{M^*}{d_1} \leq \frac{b^2 + 1 - b + a(1+b) + a^2}{3d_1 b(a+1)}.$$

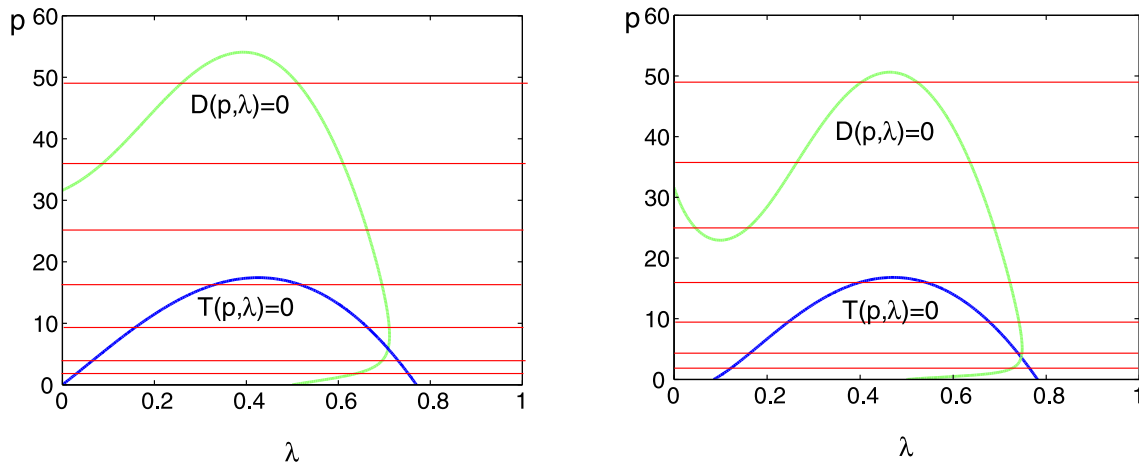
Figs. 2 and 3 show several possible graphs of the Hopf and steady state bifurcation curves. From Theorem 3.1, the constant coexistence equilibrium  $(\lambda, v_\lambda)$  is locally stable for  $\lambda \in (\bar{\lambda}, 1)$ . Hence possible bifurcation from  $(\lambda, v_\lambda)$  can only occur for  $\lambda \in (b, \bar{\lambda})$ . We prove a monotonicity result of  $p_{\pm}(\lambda)$  for  $\lambda \in (b, \lambda^s)$ .

**Lemma 5.3.** *Let  $\lambda^*$  be the maximum point of  $A(\lambda)$  as defined in Lemma 5.1. If  $b \geq \lambda^*$ , then  $p_+(\lambda)$  is decreasing and  $p_-(\lambda)$  is increasing for  $b < \lambda < \lambda^s$ . Moreover, if  $-4b^3 + (2 - 7a)b^2 + 3a(1 - a)b + a^2 \leq 0$  or  $b \geq 1/2$ , then  $b \geq \lambda^*$  holds.*

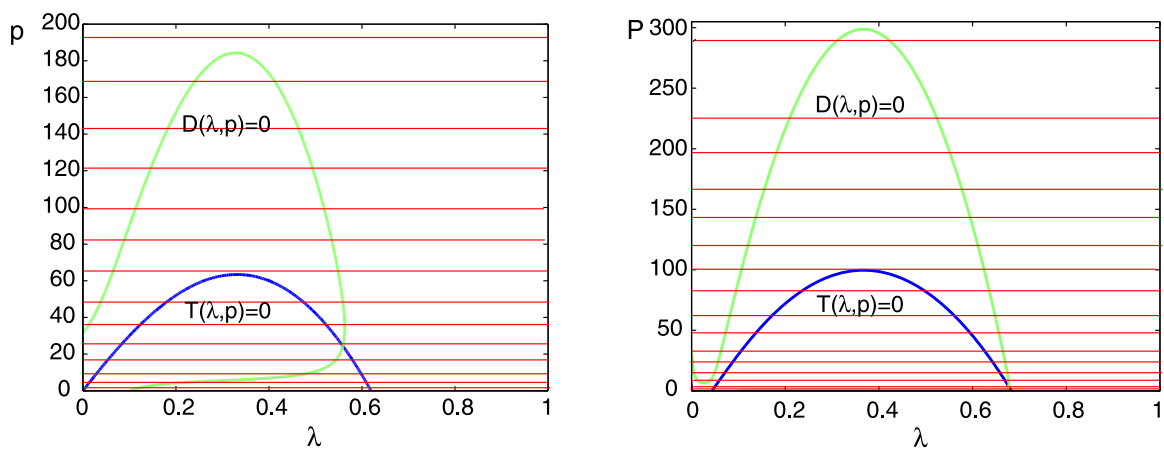
**Proof.** Since

$$A(\lambda) = \frac{\lambda}{b(a + \lambda)} (-3\lambda^2 + 2(b + 1 - a)\lambda + a(1 + b) - b),$$

$$A'(\lambda) = \frac{1}{b(a + \lambda)^2} [-6\lambda^3 + (2(1 + b) - 11a)\lambda^2 + 4a(1 + b - a)\lambda + a^2(1 + b) - ab],$$



**Fig. 2.** The graphs of  $T(\lambda, p) = 0$  and  $D(\lambda, p) = 0$ . Here  $b = 0.5$ ,  $d_1 = 0.01$ ,  $d_2 = 0.02$  and  $d = 0.2$ ; (left):  $a = 0.8$ ; (right):  $a = 0.2$ . In both cases  $b \geq \lambda^*$ . The horizontal lines are  $p = i^2$  for  $i \in \mathbb{N}$ .



**Fig. 3.** The graphs of  $T(\lambda, p) = 0$  and  $D(\lambda, p) = 0$ . Here  $b = 0.1$ ,  $d_1 = 0.01$ ,  $d_2 = 0.02$  and  $d = 0.2$ ; (left):  $a = 0.8$ ; (right):  $a = 0.01$ . In both cases  $b < \lambda^*$ . The horizontal lines are  $p = i^2$  for  $i \in \mathbb{N}$ .

we have

$$A'(b) = \frac{1}{b(a+b)^2} [-4b^3 + (2-7a)b^2 + 3a(1-a)b + a^2].$$

Differentiating  $D(p, \lambda) = 0$  with respect with  $\lambda$ , we obtain that

$$2d_1d_2p(\lambda)p'(\lambda) - d_2A'(\lambda)p(\lambda) - d_2A(\lambda)p'(\lambda) - B(\lambda)C'(\lambda) = 0.$$

Thus,  $p'(\lambda) = \frac{B(\lambda)C'(\lambda) + d_2A'(\lambda)p(\lambda)}{d_2(2d_1p(\lambda) - A(\lambda))}$ . While (5.2) implies that  $d_2(2d_1p_+(\lambda) - A(\lambda)) > 0$  and  $d_2(2d_1p_-(\lambda) - A(\lambda)) < 0$  for  $\lambda \in (b, \lambda^s)$ . Now we determine the sign of  $B(\lambda)C'(\lambda) + d_2A'(\lambda)p_{\pm}(\lambda)$ .

Recall that

$$A(\lambda) = \frac{\lambda}{b(a+\lambda)} (-3\lambda^2 + 2(b+1-a)\lambda + a(1+b) - b),$$

$$C(\lambda) = \frac{a(1-\lambda)(\lambda-b)}{b(a+\lambda)}, \quad C'(\lambda) = \frac{a(-\lambda^2 - 2a\lambda + a + (1+a)b)}{b(a+\lambda)^2},$$

then the unique positive critical point of  $C(\lambda)$  is  $\tilde{\lambda} = \sqrt{a^2 + a(1+b)} + b - a$ . While  $C'(\tilde{\lambda}) = 0$  implies that

$$\begin{aligned} A(\tilde{\lambda}) &= \frac{\tilde{\lambda}}{b(a + \tilde{\lambda})} (-3\tilde{\lambda}^2 + 2(b + 1 - a)\tilde{\lambda} + a(1 + b) - b) \\ &= \frac{\tilde{\lambda}}{b(a + \tilde{\lambda})} (-(1 + b + 2a)\tilde{\lambda} + 2b + a(1 + b)) \\ &= \frac{\tilde{\lambda}}{b(a + \tilde{\lambda})} (-(1 + b + 2a)\sqrt{a^2 + a(1 + b)} + b + 2a^2 + 2b + 2a(1 + b)). \end{aligned}$$

Since

$$\begin{aligned} &(2a^2 + 2b + 2a(1 + b))^2 - (1 + b + 2a)^2(a^2 + a(1 + b) + b) \\ &= (a^2 + a(1 + b) + b)[4a^2 + 4a(1 + b) + 4b - (1 + b + 2a)^2] \\ &= -(a^2 + a(1 + b) + b)(1 - b)^2 < 0, \end{aligned}$$

then  $A(\tilde{\lambda}) < 0$ , which shows that  $\lambda^s < \bar{\lambda} < \tilde{\lambda}$ . Thus,  $C'(\lambda) > 0$  for  $\lambda \in (b, \lambda^s)$ . If  $b \geq \lambda^*$ ,  $A'(\lambda) \leq 0$  for  $b < \lambda < \lambda^s$ . Thus  $B(\lambda)C'(\lambda) + d_2A'(\lambda)p_{\pm}(\lambda) < 0$  and  $p'_+(\lambda) < 0$ ,  $p'_-(\lambda) > 0$  for  $\lambda \in (b, \lambda^s)$ .

A direct condition to ensure  $A'(b) \leq 0$  (or  $b \geq \lambda^*$ ) is that  $-4b^3 + (2 - 7a)b^2 + 3a(1 - a)b + a^2 \leq 0$ . If  $b \geq 1/2$ , then

$$\begin{aligned} &-4b^3 + (2 - 7a)b^2 + 3a(1 - a)b + a^2 \\ &= b[(2b + 3a)(-2b + 1 - a) + ab] + a^2 = b(2b + 3a)(-2b + 1 - a) + ab^2 + a^2 \\ &= b(2b + 3a)(-2b + 1 - a) + a(b^2 + a) < b(2b + 3a)(-2b + 1 - a) + a(b + a) \\ &< b(2b + 3a)(-2b + 1 - a) + a\left(b + \frac{3a}{2}\right) = \left(b + \frac{3a}{2}\right)[2b(-2b + 1 - a) + a] \\ &= \left(b + \frac{3a}{2}\right)[-4b^2 + 2b - 2ab + a] = \left(b + \frac{3a}{2}\right)(2b + a)(1 - 2b) \leq 0. \end{aligned}$$

Therefore, when  $-4b^3 + (2 - 7a)b^2 + 3a(1 - a)b + a^2 \leq 0$  or  $b \geq 1/2$ ,  $A'(b) \leq 0$  thus  $b \geq \lambda^*$ .  $\square$

### 5.2. Steady state bifurcation

In this subsection we will identify bifurcation points  $\lambda^S$  along the branch of the constant steady states  $\{(\lambda, \lambda, v_\lambda) : b < \lambda < \bar{\lambda}\}$  where nonconstant steady state solutions bifurcate from.

In this subsection and also Section 5.3, we assume that all eigenvalues  $\mu_i$  of  $-\Delta$  in  $H^1(\Omega)$  are simple, and denote corresponding eigenfunction by  $\phi_i(x)$ . Note that this assumption always holds when  $n = 1$  for domain  $\Omega = (0, \ell\pi)$  that for  $i \in \mathbb{N}_0$ ,

$$\mu_i = \frac{i^2}{\ell^2}, \quad \text{and} \quad \phi_i(x) = \cos(ix/\ell);$$

and it also holds for a generic class of domains in higher dimensions.

Recall from Theorem 3.1, the linearization operator at  $(\lambda, v_\lambda)$  for (1.3) is

$$L(\lambda) \equiv \begin{pmatrix} d_1 \Delta + A(\lambda) & B(\lambda) \\ C(\lambda) & d_2 \Delta \end{pmatrix}. \tag{5.3}$$

Let

$$\begin{pmatrix} \psi \\ \varphi \end{pmatrix} = \sum_{i=0}^{\infty} \begin{pmatrix} a_i \\ b_i \end{pmatrix} \phi_i(x)$$

be an eigenfunction for  $L(\lambda)$  with eigenvalue  $\eta(\lambda)$  such that  $L(\lambda)(\psi, \varphi)^T = \eta(\lambda)(\psi, \varphi)^T$ . Then it is easy to show that for any  $i \in \mathbb{N}_0$ , such that  $L_i(\lambda)(a_i, b_i)^T = \eta(\lambda)(a_i, b_i)^T$ , where

$$L_i(\lambda) := \begin{pmatrix} A(\lambda) - d_1 \mu_i & B(\lambda) \\ C(\lambda) & -d_2 \mu_i \end{pmatrix}. \tag{5.4}$$

The characteristic equation of  $L_i(\lambda)$  is given by

$$\xi^2 - T_i \xi + D_i = 0, \quad i = 0, 1, 2, \dots, \tag{5.5}$$

where

$$\begin{cases} T_i(\lambda) = A(\lambda) - (d_1 + d_2)\mu_i, \\ D_i(\lambda) = -B(\lambda)C(\lambda) - d_2 A(\lambda)\mu_i + d_1 d_2 \mu_i^2. \end{cases} \tag{5.6}$$

From [60], we know that a steady state bifurcation point  $\lambda^S$  satisfies the condition:

(H2) there exists  $i \in \mathbb{N}_0$  such that

$$D_i(\lambda^S) = 0, \quad T_i(\lambda^S) \neq 0, \quad \text{and} \quad D_j(\lambda^S) \neq 0, \quad T_j(\lambda^S) \neq 0 \quad \text{for } j \neq i;$$

and

$$\frac{d}{d\lambda} D_i(\lambda^S) \neq 0.$$

Apparently  $D_0(\lambda) \neq 0$  for any  $b < \lambda < 1$ , hence we only consider  $i \in \mathbb{N}$  and determine the set

$$\Omega_2 := \{\lambda \in (b, \lambda^S): \text{for some } i \in \mathbb{N}, \text{ (H2) is satisfied}\}, \tag{5.7}$$

when a set of parameters  $(a, b, m, d, d_1, d_2)$  are given.

From Lemma 5.2, if  $\mu_i = p > M^{**}$ , then there is no  $\lambda \in (b, \lambda^S]$  such that  $D_i(\lambda) = 0$ . But for any  $\mu_i \leq M^{**}$ , there exists  $\lambda_i^S$  such that  $D(\lambda_i^S, \mu_i) = D_i(\lambda_i^S) = 0$  and these  $\lambda_i^S$  are potential steady state bifurcation points. Note that from Section 5.1, for each given  $i \in \mathbb{N}$ , there are at most three  $\lambda$ 's such that  $D(\lambda, \mu_i) = 0$ . And if the parameters are chosen so that  $b \geq \lambda^*$  (see Lemma 5.3) holds, then for each  $i \in \mathbb{N}$  so that  $\mu_i < M^{**}$ , there exists a unique  $\lambda_i^S \in (b, \lambda^S)$  such that  $D(\lambda_i^S, \mu_i) = 0$ , that is, there is at most one bifurcation point  $\lambda_i^S$  corresponding to the eigenmode associated with  $\mu_i$ .

On the other hand, it is possible that for some  $\lambda \in (b, \lambda^S)$  and some  $i \neq j$ , we have

$$\mu_j = p_-(\lambda), \quad \text{and} \quad \mu_i = p_+(\lambda). \tag{5.8}$$

Then for this  $\lambda$ , 0 is not a simple eigenvalue of  $L(\lambda)$  and we shall not consider bifurcations at such points. However from an argument in [60], for  $n = 1$  and  $\Omega = (0, \ell\pi)$ , there are only countably many  $\ell$ , such that (5.8) occurs for some  $i \neq j$ . For general bounded domains in  $\mathbb{R}^n$ , one can also show that (5.8) does not occur for generic domains.

Next we verify  $\frac{dD_i}{d\lambda}(\lambda_i^S) \neq 0$  if  $b \geq \lambda^*$  and  $\lambda_i^S \neq \lambda^S$ . Indeed one has  $D'_i(\lambda) = -B(\lambda)C(\lambda) - d_2\mu_i A'(\lambda)$ , and from the proof of Lemma 5.3,

$$p'_\pm(\lambda) = \frac{B(\lambda)C'(\lambda) + d_2A'(\lambda)p_\pm(\lambda)}{d_2(2d_1p_\pm(\lambda) - A(\lambda))}.$$

Therefore from Lemma 5.3,  $\frac{dD_i}{d\lambda}(\lambda_i^S) \neq 0$  if  $b \geq \lambda^*$  and  $\lambda_i^S \neq \lambda^S$ .

Summarizing the above discussion and using a general bifurcation theorem [57], we obtain the main result of this section on the global bifurcation of steady state solutions:

**Theorem 5.4.** *Suppose that  $a, d, d_1, d_2 > 0$  and  $0 < b < 1$  are fixed. Let  $\Omega$  be a bounded smooth domain so that its spectral set  $S = \{\mu_i\}$  satisfy that:*

[S1] *All eigenvalues  $\mu_i$  are simple for  $i \geq 0$ ;*

[S2] *There exists  $k \in \mathbb{N}$  such that  $0 = \mu_0 < \mu_1 < \dots < \mu_k < M^{**} < \mu_{k+1}$ , where  $M^{**}$  is a constant depending on  $a, b, d, d_1, d_2$  which is defined in Lemma 5.3,*

*and we also assume that  $b \geq \lambda^*$ , then for each  $1 \leq i \leq k$ , there exists a unique  $\lambda_i^S \in (b, \bar{\lambda})$  such that  $D(\lambda_i^S, \mu_i) = 0$ . If in addition, we assume*

$$\lambda_i^S \neq \lambda_j^S, \quad \text{for any } 1 \leq i \neq j \leq k, \quad \text{and} \quad \lambda_i^S \neq \lambda^S, \quad \text{for any } 1 \leq i \leq k, \quad (5.9)$$

then:

1. *There is a smooth curve  $\Gamma_i$  of positive solutions of (2.9) bifurcating from  $(\lambda, u, v) = (\lambda_i^S, \lambda_i^S, v_{\lambda_i^S})$ , with  $\Gamma_i$  contained in a global branch  $\mathcal{C}_i$  of positive nontrivial solutions of (2.9);*
2. *Near  $(\lambda, u, v) = (\lambda_i^S, \lambda_i^S, v_{\lambda_i^S})$ ,  $\Gamma_i = \{(\lambda_i(s), u_i(s), v_i(s)) : s \in (-\epsilon, \epsilon)\}$ , where  $u_i(s) = \lambda_i^S + sa_i\phi_i(x) + s\psi_{1,i}(s)$ ,  $v_i(s) = \lambda_i^S + sb_i\phi_i(x) + s\psi_{2,i}(s)$  for some  $C^\infty$  smooth functions  $\lambda_i, \psi_{1,i}, \psi_{2,i}$  such that  $\lambda_i(0) = \lambda_i^S$  and  $\psi_{1,i}(0) = \psi_{2,i}(0) = 0$ ; Here  $(a_i, b_i)$  satisfies*

$$L(\lambda_i^S)[(a_i, b_i)^\top \phi_i(x)] = (0, 0)^\top.$$

3. *Either  $\bar{\mathcal{C}}_i$  contains another  $(\lambda_j^S, \lambda_j^S, v_{\lambda_j^S})$  for  $j \neq i$  and  $1 \leq j \leq k$ , or the projection of  $\bar{\mathcal{C}}_i$  onto  $\lambda$ -axis contains the interval  $(0, \lambda_i^S)$ , or  $\bar{\mathcal{C}}_i$  contains a solution in form  $(\lambda, u_S, 0)$  for  $0 < \lambda \leq 1$  and  $u_S > 0$ .*

**Proof.** The existence and uniqueness of  $\lambda_i^S$  follows from discussions above. Then the local bifurcation result follows from Theorem 3.2 in [60], and it is an application of a more general result Theorem 4.3 in [48].

For the global bifurcation, we apply Theorem 4.3 in [48]. After the change of variables:

$$w_1 = u - \lambda, \quad w_2 = v - v_\lambda, \quad m = \frac{d(a + \lambda)}{\lambda}, \quad v_\lambda = \frac{\lambda(1 - \lambda)(b^{-1}\lambda - 1)}{d},$$

we define a nonlinear equation:



$$F\left(\lambda, \begin{pmatrix} w_1 \\ w_2 \end{pmatrix}\right) = \begin{pmatrix} d_1 \Delta w_1 + (\lambda + w_1)(1 - \lambda - w_1)(b^{-1}(\lambda + w_1) - 1) - \frac{d(a+\lambda)(\lambda+w_1)(v_\lambda+w_2)}{\lambda(a+\lambda+w_1)} \\ d_2 \Delta w_2 - d(v_\lambda + w_2) + \frac{d(a+\lambda)(\lambda+w_1)(v_\lambda+w_2)}{\lambda(a+\lambda+w_1)} \end{pmatrix},$$

with domain

$$V = \left\{ \left( \lambda, \begin{pmatrix} w_1 \\ w_2 \end{pmatrix} \right) : 0 < \lambda < 1, w_1, w_2 \in X \text{ and } w_1 + \lambda \geq 0, w_2 + v_\lambda \geq 0 \right\}.$$

Then  $\{(\lambda, 0, 0) : 0 < \lambda < 1\}$  is a line of trivial solutions for  $F = 0$  and Theorem 4.3 in [48] can be applied to each continuum  $C_i$  bifurcated from  $(\lambda_i^S, 0, 0)$ . For each continuum  $C_i$ , either  $\bar{C}_i$  contains another  $(\lambda_j^S, 0, 0)$  or  $C_i$  is not compact. Here we do not make a distinction between the solutions of (2.9) and the ones of  $F = 0$  as they are essentially same, hence we use  $C_i$  for solution continuum for both equations.

From Lemma 4.1, every solution  $(u, v)$  of (2.9) is bounded in  $L^\infty$ , then it is also bounded in  $X$  from  $L^p$  estimates and Schauder estimates. Therefore, if  $C_i$  is not compact, then  $\bar{C}_i$  contains a boundary point  $(\tilde{\lambda}, \tilde{w}_1, \tilde{w}_2)$ :

- (a) If  $\tilde{\lambda} = 0$ , then the projection of  $\bar{C}_i$  onto  $\lambda$ -axis contains  $(0, \lambda_i^S)$ ;
- (b) If  $\tilde{\lambda} = 1$ , then Corollary 2.3 implies that  $(\tilde{\lambda} + \tilde{w}_1, v_{\tilde{\lambda}} + \tilde{w}_2) = (u_S, 0)$  is a semi-trivial solution;
- (c) If  $0 < \tilde{\lambda} < 1$ , then there exists  $x_0 \in \bar{\Omega}$  such that  $(\tilde{w}_1 + \tilde{\lambda})(x_0) = 0$  or  $(\tilde{w}_2 + v_{\tilde{\lambda}})(x_0) = 0$  since  $\tilde{w}_1$  and  $\tilde{w}_2$  are bounded from Lemma 4.1. The strong maximum principle implies that  $(\tilde{w}_1 + \tilde{\lambda})(x) \equiv 0$  or  $(\tilde{w}_2 + v_{\tilde{\lambda}})(x) \equiv 0$  for all  $x \in \Omega$ . If  $v \equiv 0$ , then  $(\tilde{\lambda}, u, v)$  is a solution in form  $(\tilde{\lambda}, u_S, 0)$ . If  $u \equiv 0$ , then  $v \equiv 0$  from maximum principle. But  $(u, v) = (0, 0)$  is not a bifurcation point from Theorem 3.1, hence  $u \equiv 0$  is not possible. Therefore  $(\tilde{w}_1 + \tilde{\lambda}, \tilde{w}_2 + v_{\tilde{\lambda}})$  must be in a form of  $(u_S, 0)$ .  $\square$

Due to the bistable structure, the system (1.3) possesses a large number of semi-trivial steady state solutions as shown in Corollary 3.5 for small  $d_1 > 0$ . These semi-trivial steady states make the bifurcation structure of the set of positive steady state solutions more complicated. It is unclear whether a branch of positive steady states can connect to a semi-trivial steady state here.

### 5.3. Hopf bifurcations

In this subsection, we analyze the properties of Hopf bifurcations for (1.3), and we will show the existence of spatial-dependent and independent periodic solutions of system (1.3).

To identify Hopf bifurcation values  $\lambda^H$ , we recall the following necessary and sufficient condition from [15,60]:  $T_i(\lambda)$  and  $D_i(\lambda)$  defined in (5.6).

(H1) There exists  $i \in \mathbb{N}_0$  such that

$$T_i(\lambda_0) = 0, \quad D_i(\lambda_0) > 0 \quad \text{and} \quad T_j(\lambda_0) \neq 0, \quad D_j(\lambda_0) \neq 0 \quad \text{for } j \neq i; \quad (5.10)$$

and for the unique pair of complex eigenvalues near the imaginary axis  $\alpha(\lambda) \pm i\omega(\lambda)$ ,

$$\alpha'(\lambda_0) \neq 0, \quad \text{and} \quad \omega(\lambda_0) > 0. \quad (5.11)$$

From (5.6),  $T_i(\lambda) < 0$  and  $D_i(\lambda) > 0$  for all  $i \in \mathbb{N}_0$  and  $\lambda \in (\bar{\lambda}, 1)$ , which implies that the trivial steady state  $(\lambda, v_\lambda)$  is locally asymptotically stable. Hence any potential Hopf bifurcation point  $\lambda^H$  must be in the interval  $(b, \bar{\lambda}]$ . In the following we assume that  $a, d, d_1, d_2 > 0$  and  $0 < b < 1$  are fixed.

First  $\lambda_0^H = \bar{\lambda}$  is always a Hopf bifurcation point since  $T_0(\lambda_0^H) = A(\lambda_0^H) = 0$  and  $T_j(\lambda_0^H) = -(d_1 + d_2)\mu_j^2 < 0$  for any  $j \geq 1$ ; and

$$D_i(\lambda_0^H) = -B(\lambda_0^H)C(\lambda_0^H) + d_1d_2\mu_j^2 > 0$$

for any  $j \in \mathbb{N}_0$ . This corresponds to the Hopf bifurcation of spatially homogeneous periodic orbits which have been known from the studies of Section 3 in [53]. Apparently  $\lambda_0^H$  is also the unique value  $\lambda$  for the Hopf bifurcation of spatially homogeneous periodic orbits from the uniqueness result of limit cycle in [53].

Hence in the following we search for spatially nonhomogeneous Hopf bifurcation for  $i \geq 1$  in (H1). Notice that  $A(b) > 0, A(\lambda_0^H) = 0$  and  $A(\lambda) > 0$  in  $(b, \lambda_0^H)$ . Similar to Theorem 5.4, we assume that  $b \geq \lambda_*$ , but we will comment on the case of  $b < \lambda_*$  at the end of this section. Again we assume that [S1] holds, i.e. all eigenvalues  $\mu_i$  are simple.

If  $b \geq \lambda_*$ , then clearly  $A(\lambda)$  is strictly decreasing for  $\lambda \in (b, \bar{\lambda})$  from Lemma 5.1. We define  $\lambda_i^H$  to be the unique solution of  $A(\lambda) = (d_1 + d_2)\mu_i$  satisfying  $b < \lambda < \bar{\lambda}$ . These points satisfy

$$b < \lambda_m^H < \lambda_{m-1}^H < \dots < \lambda_1^H < \lambda_0^H,$$

where  $m$  is the largest integer so that  $\mu_m < M^*/(d_1 + d_2)$ , and  $M^*$  is defined in Lemma 5.1. Clearly  $T_i(\lambda_i^H) = 0$  and  $T_j(\lambda_i^H) \neq 0$  for any  $j \neq i$ . The condition  $D_i(\lambda_i^H) > 0$  does not hold for all  $i$  satisfying  $1 \leq i \leq m$ . Geometrically  $D_i(\lambda_i^H) = D(\lambda_i^H, \mu_i) > 0$  is equivalent to that the point  $(\lambda_i^H, \mu_i)$  is in the exterior of the curve  $D(\lambda, p) = 0$  (see Figs. 2 and 3). From the monotonicity properties proved in Lemma 5.3, the curves  $D(\lambda, p) = 0$  and  $T(\lambda, p)$  have a unique intersection point  $(\lambda^b, p^b)$  for  $\lambda \in (b, \bar{\lambda})$  and  $p > 0$ . Hence  $D_i(\lambda_i^H) > 0$  if  $\lambda_i^H > \lambda^b$  while  $D_i(\lambda_i^H) < 0$  if  $\lambda_i^H < \lambda^b$ . Finally  $D_j(\lambda_i^H) \neq 0$  if  $\lambda_i^H \neq \lambda_j^S$  for  $1 \leq j \leq k$ , that is, a Hopf bifurcation point and a steady state bifurcation point do not overlap.

Summarizing our analysis above and applying Theorem 2.1 in [60], we obtain the following results on the Hopf bifurcations:

**Theorem 5.5.** *Suppose that  $a, d, d_1, d_2 > 0$  and  $0 < b < 1$  are fixed. Let  $\Omega$  be a bounded smooth domain so that its spectral set  $S = \{\mu_i\}$  satisfies that [S1], and*

[S3] *There exists  $m \in \mathbb{N}$  such that  $0 = \mu_0 < \mu_1 < \dots < \mu_m < \frac{M^*}{d_1+d_2} < \mu_{m+1}$ , where  $M^*$  is a constant depending on  $a, b$  which is defined in Lemma 5.1,*

and we also assume that  $b \geq \lambda^*$ , then for each  $1 \leq i \leq m$ , there exists a unique  $\lambda_i^H \in (b, \bar{\lambda})$  such that  $T(\lambda_i^H, \mu_i) = 0$ , and there exist  $h \in \mathbb{N}$  and  $h \leq m$  such that for  $1 \leq i \leq h, D(\lambda_i^H, \mu_i) > 0$ . If in addition, we assume for  $1 \leq i \leq h$ ,

$$\lambda_i^H \neq \lambda_j^S, \quad \text{for any } 1 \leq j \leq k, \tag{5.12}$$

where  $\lambda_j^S$  ( $1 \leq j \leq k$ ) are defined in Theorem 5.4, then for each  $0 \leq i \leq h$ ,

1. (1.3) undergoes a Hopf bifurcation at  $\lambda = \lambda_j^H$ ; there is a smooth curve  $\Lambda_i$  of positive periodic orbits of (1.3) bifurcating from  $(\lambda, u, v) = (\lambda_i^H, \lambda_i^H, v_{\lambda_i^H})$ , with  $\Lambda_i$  contained in a global branch  $\mathcal{P}_i$  of positive nontrivial periodic orbits of (1.3).
2. The bifurcating periodic orbits from  $\lambda = \lambda_0^H$  are spatially homogeneous, which coincide with the periodic orbits of the corresponding ODE system (see [53]); the Hopf bifurcation at  $\lambda = \lambda_0^H$  is supercritical and backward; the bifurcating spatially homogeneous periodic orbits are locally asymptotically stable near  $\lambda = \lambda_0^H$ .
3. The bifurcating periodic orbits from  $\lambda = \lambda_i^H$  with  $1 \leq i \leq h$  are spatially nonhomogeneous; near bifurcation point, they are in a form of

$$(\lambda, u, v) = (\lambda_i^H + o(s), \lambda_i^H + se_i \cos(\omega(\lambda_i^H)t)\phi_i(x) + o(s), v_{\lambda_i^H} + sf_i \cos(\omega(\lambda_i^H)t)\phi_i(x) + o(s)),$$

for  $s \in (0, \delta)$ , where  $\omega(\lambda_i^H) = \sqrt{D_i(\lambda_i^H)}$  is the corresponding time frequency,  $\phi_i(x)$  is the corresponding spatial eigenfunction, and  $(e_i, f_i)$  is a corresponding eigenvector.

4. The global branch of spatially homogenous periodic orbits  $\mathcal{P}_0$  is a curve parameterized by  $\lambda \in (\lambda^\sharp, \bar{\lambda})$  from results in [53]; the spatially homogeneous periodic orbit is unique for each  $\lambda \in (\lambda^\sharp, \bar{\lambda})$ , and the period of the closed orbits approaches to  $\infty$  as  $\lambda \rightarrow (\lambda^\sharp)^-$ , that is, the cycle converges to a loop of heteroclinic orbits, which exists only when  $\lambda = \lambda^\sharp$ .
5. For  $1 \leq i \leq h$ , the global branch of spatially nonhomogeneous periodic orbits  $\mathcal{P}_i$  satisfies: either  $\bar{\mathcal{P}}_i$  contains another bifurcation point  $(\lambda, u, v) = (\lambda_j^H, \lambda_j^H, v_{\lambda_j^H})$  for  $1 \leq j \leq h$  and  $j \neq i$ , or  $\bar{\mathcal{P}}_i$  contains a spatially homogenous periodic orbit on  $\mathcal{P}_0$ , or the projection of  $\bar{\mathcal{P}}_i$  onto  $\lambda$ -axis contains the interval  $(0, \lambda_i^H)$  or  $(\lambda_i^H, 1)$ , or there exists  $\hat{\lambda} \in (0, 1)$  such that there exists a sequence of spatially nonhomogeneous periodic orbits  $(\lambda_l, u_l, v_l) \in \mathcal{P}_i$  such that  $\lambda_l \rightarrow \hat{\lambda}$  and the time period of  $(\lambda_l, u_l, v_l)$  tends to  $\infty$  as  $l \rightarrow \infty$ .

**Proof.** The local bifurcation results in parts 1 and 3 follow from discussions in this section and Theorem 2.1 in [60], and parts 2 and 4 follow from [53] as any solutions of the ODE model are spatially homogenous solutions of (1.3). The stability assertion in part 2 can be obtained in a similar way as [60] and the calculation in [53]. For the global bifurcation results, we use the one in Section 6.5 in [58] for the abstract setting. Indeed to obtain the four alternatives stated here, we have to use a more general version of global bifurcation theorem restricted to the positive cone in the function space, which is similar to the corresponding result in [48] for steady state solutions. Note that from Theorem 2.1, we know that all periodic orbits are uniformly bounded for  $\lambda \in [0, 1]$ .  $\square$

**Remark 5.6.**

1. Notice that Theorem 5.5 does not exclude a secondary bifurcation of spatial nonhomogeneous periodic orbits from the branch of spatially homogenous periodic orbits  $\mathcal{P}_0$ . It is known from [53] that all spatially homogenous periodic orbits on  $\mathcal{P}_0$  are locally asymptotically stable with respect to the ODE dynamics (which also implies the stability for PDE dynamics when  $d_1 = d_2$ ), but it is not known that whether the stability still hold for PDE dynamics for general diffusion coefficients  $d_1 \neq d_2$ .
2. The conditions [S2] in Theorem 5.4 and [S3] in Theorem 5.5 are compatible, as we have shown in Lemma 5.1 and Lemma 5.2. Hence the steady state bifurcation points  $\lambda_i^S$  ( $1 \leq i \leq k$ ) and the Hopf bifurcation points  $\lambda_i^H$  ( $0 \leq i \leq h$ ) could appear in an intertwining order (see example below). However the number  $k$  of steady state bifurcation in Theorem 5.4 and the number  $m$  or  $h$  in Theorem 5.5 are in general different, as clearly shown in Figs. 2 and 3. In all cases of Figs. 2 and 3, the relation  $k > m > h$  holds.
3. For a given eigen-mode  $\phi_i(x)$ , if  $\lambda_i^S$  and  $\lambda_i^H$  both exist, and the simplicity conditions (5.9) and (5.12) are both satisfied, then a steady state bifurcation always occurs at  $\lambda = \lambda_i^S$  with eigen-mode  $\phi_i$ , but a Hopf bifurcation with eigen-mode  $\phi_i$  occurs only if  $\lambda_i^S < \lambda_i^H$ .
4. In both Theorem 5.4 and Theorem 5.5, we assume that  $b \geq \lambda^*$ . Note that from Lemma 5.3,  $b > \lambda^*$  holds if  $b \geq 1/2$  or  $a$  and  $b$  satisfy a more complicated algebraic condition. Fig. 2 shows the bifurcation points in this case. However the condition  $b \geq \lambda^*$  is not necessary for the occurrence of steady state or Hopf bifurcations. If  $b < \lambda^*$  (see Fig. 3), then the curves  $D(\lambda, p) = 0$  and  $T(\lambda, p) = 0$  are not monotone with respect to  $\lambda$ , which implies even more bifurcation points. See Example 5.8 below.

To visualize the cascade of steady state or Hopf bifurcations, we consider two numerical examples. In both examples, we assume the spatial dimension  $n = 1$  and  $\Omega = (0, \pi)$ .

**Example 5.7.** We use the parameter values in Fig. 2 (left). Notice that the horizontal lines in Fig. 2 (left) are  $p = \mu_i = i^2$  (the eigenvalues of  $\Delta$  for  $\Omega = (0, \pi)$ ). Then the largest number  $k$  in [S2] of Theorem 5.4 so that a steady state bifurcation can occur is  $k = 7$ . On the other hand, the

largest number  $m$  in [S3] of Theorem 5.5 so that a Hopf bifurcation can occur is  $m = 4$ . But for the 4 intersection points of  $T(\lambda, p) = 0$  and  $p = \mu_i$ , only two of them are outside of the curve  $D(\lambda, p) = 0$ , so the number  $h$  in Theorem 5.5 is  $h = 2$ . Therefore there exist 3 Hopf bifurcation points and 7 steady state bifurcation points. The occurrence of bifurcations is in the order of

$$\begin{aligned} \lambda_0^H \approx 0.7698 > \lambda_1^H \approx 0.7601 > \lambda_2^H \approx 0.7292 > \lambda_3^S \approx 0.7135 > \lambda_2^S \approx 0.6985 > \lambda_4^S \approx 0.6983 \\ > \lambda_5^S \approx 0.6660 > \lambda_6^S \approx 0.6131 > \lambda_1^S \approx 0.5847 > \lambda_7^S \approx 0.5126 > b = 0.5. \end{aligned}$$

Here none of these bifurcation points overlap with each other, which assures the simplicity of eigenvalue with zero real part. One can also find that the heteroclinic bifurcation point is  $\lambda^\# \approx 0.7670$ , which is between the first two Hopf bifurcation points. Hence a spatially homogeneous periodic orbit only exists for  $\lambda^\# \approx 0.7670 < \lambda < 0.7698 \approx \lambda_0^H$ .

**Example 5.8.** We use the parameter values in Fig. 3 (left). Then similar to Example 5.8, we have  $k = 13$ ,  $m = 7$  and  $h = 4$  respectively. There are 5 Hopf bifurcation points for the eigen-mode  $0 \leq i \leq 4$ . For  $1 \leq i \leq 9$ , there is a single steady state bifurcation point  $\lambda_i^S$ , but for  $10 \leq i \leq 13$ , there are 2 steady state bifurcation points (which we call  $\lambda_{i,\pm}^S$ ) for each eigen-mode  $i$ . Hence totally there are 17 steady state bifurcation points. The occurrence of bifurcations is in the order of

$$\begin{aligned} \lambda_0^H \approx 0.6196 > \lambda_1^H \approx 0.6174 > \lambda_2^H \approx 0.6106 > \lambda_3^H \approx 0.5990 > \lambda_4^H \approx 0.5817 > \lambda_6^S \approx 0.5630 \\ > \lambda_5^S \approx 0.5595 > \lambda_7^S \approx 0.5589 > \lambda_8^S \approx 0.5497 > \lambda_4^S \approx 0.5409 > \lambda_9^S \approx 0.5362 \\ > \lambda_{10,+}^S \approx 0.5181 > \lambda_{11,+}^S \approx 0.4943 > \lambda_3^S \approx 0.4724 > \lambda_{12,+}^S \approx 0.4621 \\ > \lambda_{13,+}^S \approx 0.4117 > \lambda_{13,-}^S \approx 0.2415 > \lambda_2^S \approx 0.1894 > \lambda_{12,-}^S \approx 0.1847 \\ > \lambda_{11,-}^S \approx 0.1455 > \lambda_{10,-}^S \approx 0.1142 > \lambda_1^S \approx 0.1127 > b = 0.1. \end{aligned}$$

Note that here the heteroclinic bifurcation point  $\lambda^\# \approx 0.6123$ , which is between  $\lambda_1^H$  and  $\lambda_2^H$ .

Examples 5.7 and 5.8 demonstrate the richness of spatial and spatiotemporal patterns for  $\lambda$  between  $\lambda = b$  (system threshold value) and  $\lambda = \bar{\lambda}$  (primary Hopf bifurcation point).

## 6. Conclusions

Reaction–diffusion predator–prey models with strong Allee effect in prey such as (1.3) have been proposed in [35,39,40], and numerical simulation have shown that the system (1.3) is capable to generate complicated spatiotemporal dynamics. In this paper we rigorously prove some general behavior of the dynamical equation (1.3): for  $\lambda > 1$ , the predator is destined to go extinct (Theorem 2.1(c)); and for large predator initial values, both predator and prey go extinct (Theorem 2.4). The latter result confirms the overexploitation phenomenon still exists with the addition of the diffusion. With strong Allee effect in prey, extinction for both species is always a locally stable equilibrium. But for  $\lambda$  over the threshold value  $b$ , there always exist some other spatiotemporal patterns (steady state or oscillatory ones) (Theorems 5.4 and 5.5). These patterns are usually unstable, and they may lie on a threshold manifold which separates the basin of attraction of the extinction equilibrium and all other persistent orbits. The threshold manifold may also contain a large number of semi-trivial prey-only steady state solutions (Corollary 3.5).

Compared with the ODE dynamics classified in [53], the PDE dynamics shown here is still coarse. It would be interesting to know whether a global separatrix for the bistable dynamics exists. In ODE dynamics, the separatrix is simply the stable manifold of the threshold equilibrium  $(b, 0)$ . Our analysis does show that for the parameter range that the ODE system possesses a limit cycle, the corresponding PDE could have more patterned solutions (Theorems 5.4, 5.5 and Examples 5.7, 5.8). Comparison

with the ODE dynamics also suggests a conjecture that when  $\lambda \leq b$ , the extinction equilibrium is globally asymptotic stable. In general, it is useful to know conditions on initial conditions for the populations to persist, and the existence of large amplitude patterned steady state or oscillatory solutions far away from bifurcation points is also not known.

Our analysis here can also be generalized to diffusive predator–prey system with strong Allee effect like (1.1) but with more general functional responses and growth rates (see [53] for such functions). Bifurcation structure in higher-dimensional domains can also be more complex than the ones shown in Examples 5.7 and 5.8.

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