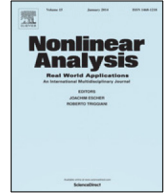




Contents lists available at ScienceDirect

## Nonlinear Analysis: Real World Applications

[www.elsevier.com/locate/nonrwa](http://www.elsevier.com/locate/nonrwa)


# Dynamics of an intraguild predation food web model with strong Allee effect in the basal prey


 Dingyong Bai<sup>a,b</sup>, Yun Kang<sup>c,d</sup>, Shigui Ruan<sup>e,\*</sup>, Lisha Wang<sup>f</sup>
<sup>a</sup> School of Mathematics and Information Science, Guangzhou University, Guangzhou 510006, PR China

<sup>b</sup> Center for Applied Mathematics, Guangzhou University, Guangzhou 510006, PR China

<sup>c</sup> Science and Mathematics Faculty, College of Integrative Sciences and Arts, Arizona State University, Mesa, AZ 85212, USA

<sup>d</sup> Simon A. Levin Mathematical, Computational, and Modeling Sciences Center, Arizona State University, Tempe, AZ 85281, USA

<sup>e</sup> Department of Mathematics, University of Miami, Coral Gables, FL 33146, USA

<sup>f</sup> Department of Mathematics, Nanjing University of Science and Technology, Nanjing 210094, PR China

## ARTICLE INFO

## Article history:

Received 6 May 2020

Received in revised form 19 August 2020

Accepted 21 August 2020

Available online xxxx

## Keywords:

Intraguild predation

Food web

Strong Allee effect

Hopf bifurcation curve

Multiple attractors

## ABSTRACT

Since intraguild predation (IGP) is a ubiquitous and important community module in nature and Allee effect has strong impact on population dynamics, in this paper we propose a three-species IGP food web model consisted of the IG predator, IG prey and basal prey, in which the basal prey follows a logistic growth with strong Allee effect. We investigate the local and global dynamics of the model with emphasis on the impact of strong Allee effect. First, positivity and boundedness of solutions are studied. Then existence and stability of the boundary and interior equilibria are presented and the Hopf bifurcation curve at an interior equilibrium is given. The existence of a Hopf bifurcation curve indicates that if competition between the IG prey and IG predator for the basal resource lies below the curve then the interior equilibrium remains stable, while if it lies above the curve then the interior equilibrium loses its stability. In order to explore the impact of Allee effect, the parameter space is classified into sixteen different regions and, in each region, the number of interior equilibria is determined and the corresponding bifurcation diagrams on the Allee threshold are given. The extinction parameter regions of at least one species and the necessary coexistence parameter regions of all three species are provided. In addition, we explore possible dynamical patterns, i.e., the existence of multiple attractors. By theoretical analysis and numerical simulations, we show that the model can have one (i.e. extinction of all species), two (i.e. bi-stability) or three (i.e. tri-stability) attractors. It is also found by simulations that when there exists a unique stable interior equilibrium, the model may generate multiple attracting periodic orbits and the coexistence of all three species is enhanced as the competition between the IG prey and IG predator for the basal resource is close to the Hopf bifurcation curve from below. Our results indicate that the intraguild predation food web model exhibits rich and complex dynamic behaviors and strong Allee effect in the basal prey increases the extinction risk of not only the basal prey but also the IG prey or/and IG predator.

© 2020 Elsevier Ltd. All rights reserved.

\* Corresponding author.

 E-mail addresses: [baidy@gzhu.edu.cn](mailto:baidy@gzhu.edu.cn) (D. Bai), [Yun.Kang@asu.edu](mailto:Yun.Kang@asu.edu) (Y. Kang), [ruan@math.miami.edu](mailto:ruan@math.miami.edu) (S. Ruan), [wls930@163.com](mailto:wls930@163.com) (L. Wang).

## 1. Introduction

Intraguild predation (IGP) is defined as the killing and eating of potential competitors and is a combination of predation and competition [1]. A simple example of an IGP food web is the tri-trophic community module including a predator population (IG predator) and its prey (IG prey) sharing a common resource. Since the IG predator feeds on different trophic levels (the IG prey and their common basal resource), and simultaneously competes with another species (its IG prey), it is a specific case of omnivory [2–5]. IGP is an important community module to understand the mechanism for persistence of complex food webs. Because of the ubiquity and importance of this interaction in nature, IGP has received considerable attention [6–10].

Various IGP models have been proposed and studied by many researchers. Holt and Polis [11] formed a three-species Lotka–Volterra type IGP model with Holling Type I functional response and showed that increase in the strength of intraguild predation could destabilize the positive equilibrium. Tanabe and Nambe [12] also considered an IGP model with the same functional response as in [11] and observed that intraguild predation might destabilize the system and induce chaos by numerical simulations. Hsu, Ruan, and Yang [2] considered a three-species food web model with Lotka–Volterra type interaction between populations, classified the parameter space into three categories containing eight cases, and demonstrated extinction results for five cases and verified uniform persistence for the other three cases. For more studies on the dynamics of IGP models, including ODE models, PDE models and delay models, we refer to [13–21] and the references therein.

In many studies of IGP models, see for example [2,3,11,12,14–16,18,19], the common prey of the IG predator and IG prey is assumed to follow the logistic growth. Although a logistic growth function can better depict individual population growth and has become extremely popular, but in real natural situation there are abundant evidences showing that, unlike the logistic growth, populations at low densities are influenced by positive relationship between the growth rate and the density of the population [22–27]. This biological phenomenon is known as *Allee effect* [23,25,27,28] and occurs when the species engages in social behavior such as cooperative hunting or group defense [22,23,29–32].

A simple model with Allee effect takes the form

$$\frac{dX}{dt} = rX(K - X)(X - K_0), \quad (1.1)$$

where  $r > 0$ ,  $K > 0$  and  $|K_0| < K$ . The term  $X - K_0$  is included as a modification of the logistic model. When  $0 < K_0 < K$ ,  $K_0$  is a threshold population level (called *Allee threshold*), below which the population declines to extinction while above which the population persists. In this case, Eq. (1.1) describes the *strong Allee effect* [33–37]. If  $K_0 \leq 0$ , Eq. (1.1) represents the *weak Allee effect* [38]. A population with weak Allee effect does not have a critical threshold. Allee effect can result in the increase of the likelihood of extinction. Recently, Allee effect has attracted much attention owing to its strong potential impact on population dynamics and there are several different ways to model strong Allee effect (e.g. see [33,34,39–47]).

In this paper, we consider a three-species intraguild predation food web model which includes a predator population (IG predator) and its prey (IG prey) sharing a common prey. It is assumed that the shared prey exhibits strong Allee effect which is formulated by following [33–37]. The IGP food web model is represented as follows:

$$\begin{aligned} \frac{dR}{dt} &= rR \left(1 - \frac{R}{K}\right) (R - K_0) - b_1 RP - b_2 RQ, \\ \frac{dP}{dt} &= P(e_1 b_1 R - b_3 Q - d_p), \\ \frac{dQ}{dt} &= Q(e_2 b_2 R + e_3 b_3 P - d_q), \end{aligned} \quad (1.2)$$

where  $R(t)$ ,  $P(t)$  and  $Q(t)$  denote the densities of the shared prey, IG prey and IG predator at time  $t$ , respectively. All parameters are positive.  $r$  and  $K$  are the intrinsic growth rate and carrying capacity of

the shared prey  $R$ , respectively;  $K_0$  is the Allee threshold satisfying  $0 < K_0 < K$ ;  $d_p$  and  $d_q$  are death rates of the IG prey  $P$  and IG predator  $Q$ , respectively;  $b_1$  and  $b_2$  are predation rates of species  $P$  and  $Q$  to the shared prey  $R$ , respectively;  $b_3$  is the predation rate of the IG predator  $Q$  to IG prey  $P$ ;  $e_1$  and  $e_2$  are conversion rates of resource consumption into reproduction for species  $P$  and  $Q$ , respectively;  $e_3$  is the conversion rate of the IG predator from the IG prey.

System (1.2) can be used to model many IGP food webs with strong Allee effect such as the predatory invertebrates–planktivorous fish–herbivorous zooplankton system, in which both predatory invertebrates and planktivorous fish feed on herbivorous zooplankton, while planktivorous fish also feeds on predatory invertebrates [48]. Sarnelle and Knapp [49] showed that the zooplankton suffers a strong Allee effect.

For mathematical simplification, we rewrite model (1.2) in a nondimensional form. Let  $x = \frac{R}{K}$ ,  $y = P$ ,  $z = Q$  and  $\tau = rKt$ . Then (1.2) takes the form

$$\begin{aligned} x' &= x(x - \theta)(1 - x) - \alpha xy - \beta xz, \\ y' &= \gamma_1 y(x - a_1 z - d_1), \\ z' &= \gamma_2 z(x + a_2 y - d_2), \end{aligned} \tag{1.3}$$

where  $\theta = \frac{K_0}{K}$ ,  $0 < \theta < 1$ , and  $\alpha = \frac{b_1}{rK}$ ,  $\beta = \frac{b_2}{rK}$ ,  $\gamma_i = \frac{e_i b_i}{r}$  ( $i = 1, 2$ ),  $a_1 = \frac{b_3}{e_1 b_1 K}$ ,  $a_2 = \frac{e_3 b_3}{e_2 b_2 K}$ ,  $d_1 = \frac{d_p}{e_1 b_1 K}$ ,  $d_2 = \frac{d_q}{e_2 b_2 K}$ .

We will provide detailed mathematical analysis of model (1.3) with related biological implications. The main purpose of this article is to investigate the following two questions: First, how does Allee effect affect the dynamics of intraguild predation? Second, in the presence of Allee effect on the shared prey, under what conditions will the shared prey, IG prey and IG predator coexist?

To answer these two questions, we first show the positive invariance and boundedness of model (1.3) in Section 2. In order to understand the dynamics of (1.3), in Section 3 we first discuss the local and global properties of subsystems of (1.3). Then in Section 4 we investigate the existence and local stability of boundary equilibria and interior equilibria as well as the existence of Hopf bifurcation. The extinction of at least one species of the basal prey  $x$ , IG prey  $y$  and IG predator  $z$  is also studied in Section 4. Our results indicate that Allee effect in the basal prey increases the extinction risk of not only the basal prey but also the IG prey or/and IG predator. In Section 5 we explore the impact of Allee effect on the dynamics of model (1.3) in detail. The parameter space of  $\lambda = (\alpha, \beta, a_1, a_2, d_1, d_2)$  is divided into sixteen different regions, and in each region the number of interior equilibria is determined and the corresponding bifurcation diagrams on the Allee threshold  $\theta$  are given. The extinction parameter regions of at least one species and the necessary coexistence parameter regions of all three species are obtained. In Section 6, we focus on the possible dynamical patterns, i.e., the existence of multiple attractors, and their biological implications. It is shown that model (1.3) can have one (i.e. extinction of all species), two (i.e. bi-stability) or three (i.e. tri-stability) attractors. We also find by simulations that the orbits which tend to the extinction state and the stable interior equilibrium may be attracted to some periodic orbits as  $(\gamma_1, \gamma_2)$  is close to the Hopf bifurcation curve from below, and thus multiple attracting periodic orbits are generated and the coexistence of all three species is enhanced. In Section 7, we briefly make a comparison between the dynamics of model (1.3) and the dynamics of the IGP model without Allee effect in the basal prey, and provide a summary of our results.

## 2. Positivity and boundedness

We define the state space of (1.3) as  $X = \{(x, y, z) \in \mathbb{R}_+^3\}$  with its interior defined as  $\mathring{X} = \{(x, y, z) \in \mathbb{R}_+^3 : xyz > 0\}$ .

### Theorem 2.1. (Positivity and Boundedness)

(i) Both  $X$  and  $\mathring{X}$  are positively invariant sets of system (1.3);

(ii) System (1.3) is uniformly ultimately bounded in  $X$ , and  $\limsup_{t \rightarrow \infty} x(t) \leq 1$ ,  $\limsup_{t \rightarrow \infty} y(t) \leq \frac{1}{\alpha} \left[ \frac{(1-\theta)^2}{4d_1} + \gamma_1 \right]$ .

**Proof.** (i). For  $x \geq 0, y \geq 0$  and  $z \geq 0$ , we have  $x'|_{x=0} = 0$ ,  $y'|_{y=0} = 0$ ,  $z'|_{z=0} = 0$ , which implies that  $x = 0, y = 0, z = 0$  are invariant manifolds, respectively. Due to the continuity of the system, we can conclude that system (1.3) is positively invariant in  $X$  and  $\dot{X}$ .

(ii). Choose any point  $(x, y, z) \in X$ . Since

$$x'|_{x=1} = -\alpha y - \beta z \leq 0, \quad x'|_{x>1} = x(x-\theta)(1-x) - \alpha xy - \beta xz \leq 0,$$

we have  $\limsup_{t \rightarrow \infty} x(t) \leq 1$ .

Define two functions by  $N = \gamma_1 x + \alpha y$  and  $W = \gamma_2 x + \frac{\beta \gamma_2 a_2}{\gamma_1 a_1} y + \beta z$ , then we have

$$\frac{dN}{dt} \leq \gamma_1 x(x-\theta)(1-x) - \alpha \gamma_1 d_1 y = h(x) - \gamma_1 d_1 N(t),$$

where  $h(x) = \gamma_1 x(x-\theta)(1-x) + \gamma_1^2 d_1 x$ , and

$$\begin{aligned} \frac{dW}{dt} &= \gamma_2 x(x-\theta)(1-x) - \alpha \gamma_2 xy + \frac{\beta \gamma_2 a_2}{a_1} y(x-d_1) - \beta \gamma_2 d_2 z \\ &= H(x, y) - \gamma_2 d_2 W(t), \end{aligned}$$

where

$$H(x, y) = \gamma_2 x(x-\theta)(1-x) - \alpha \gamma_2 xy + \frac{\beta \gamma_2 a_2}{a_1} y(x-d_1) + \gamma_2^2 d_2 \left( x + \frac{\beta a_2}{\gamma_1 a_1} y \right).$$

Since  $\lim_{t \rightarrow \infty} x(t) \leq 1$ , for any  $\epsilon > 0$  there exists  $T_1 > 0$  such that for  $t > T_1$ ,  $x(t) \leq 1 + \epsilon$ . Let  $L_\epsilon = \max_{0 \leq x \leq 1+\epsilon} h(x)$ . Thus, for  $t > T_1$ ,  $N'(t) \leq L_\epsilon - \gamma_1 d_1 N$ . This implies that

$$\limsup_{t \rightarrow \infty} N(t) = \limsup_{t \rightarrow \infty} (\gamma_1 x(t) + \alpha y(t)) \leq \frac{L}{\gamma_1 d_1},$$

where  $L = \max_{0 \leq x \leq 1} h(x)$ . Therefore,  $y(t)$  is uniformly ultimately bounded. Notice that

$$h(x) \leq \gamma_1 \left( \frac{(1-\theta)^2}{4} + \gamma_1 d_1 \right), \quad x \in [0, 1].$$

Thus, we have

$$\limsup_{t \rightarrow \infty} y(t) \leq \frac{1}{\alpha} \left[ \frac{(1-\theta)^2}{4d_1} + \gamma_1 \right].$$

Denote  $B = \frac{1}{\alpha} \left[ \frac{(1-\theta)^2}{4d_1} + \gamma_1 \right]$ . Then, there exists  $T_2 > T_1$  such that for  $t > T_2$ ,  $y(t) \leq B + \epsilon$ . Let

$$M_\epsilon = \max_{0 \leq x \leq 1+\epsilon, 0 \leq y \leq B+\epsilon} H(x, y).$$

Thus, for  $t > T_2$ ,  $W'(t) \leq M_\epsilon - \gamma_2 d_2 W$ . This implies that

$$\limsup_{t \rightarrow \infty} W(t) = \limsup_{t \rightarrow \infty} \left( \gamma_2 x + \frac{\beta \gamma_2 a_2}{\gamma_1 a_1} y + \beta z \right) \leq \frac{M}{\gamma_2 d_2},$$

where  $M = \max_{0 \leq x \leq 1, 0 \leq y \leq B} H(x, y)$ . Therefore,  $z(t)$  is also uniformly ultimately bounded. The proof is complete.  $\square$

**Remark 2.2.** Theorem 2.1 indicates that IGP model (1.3) with Allee effect in the basal prey has a compact global attractor  $\{(x, y, z) \in X : 0 \leq x \leq 1, 0 \leq y, z \leq B, B > 0\}$ .

**Table 1**  
The local stability of equilibria for subsystems.

Subsystems	Equilibria	Existence conditions	Stability conditions
<i>xy</i> -subsystem	$E_0^{xy}$	Always	Always L.A.S.
	$E_\theta^{xy}$	Always	Always unstable. Saddle if $\theta < d_1$ , source if $\theta > d_1$
	$E_1^{xy}$	Always	L.A.S. if $d_1 \geq 1$ , saddle if $d_1 < 1$
	$E^{xy}$	$\theta < d_1 < 1$	L.A.S. if $\frac{1}{2}(1 + \theta) < d_1 < 1$ , source if $\theta < d_1 < \frac{1}{2}(1 + \theta)$
<i>xz</i> -subsystem	$E_0^{xz}$	Always	Always L.A.S.
	$E_\theta^{xz}$	Always	Always unstable. Saddle if $\theta < d_2$ , source if $\theta > d_2$
	$E_1^{xz}$	Always	L.A.S. if $d_2 \geq 1$ , saddle if $d_2 < 1$
	$E^{xz}$	$\theta < d_2 < 1$	L.A.S. if $\frac{1}{2}(1 + \theta) < d_2 < 1$ , source if $\theta < d_2 < \frac{1}{2}(1 + \theta)$
<i>yz</i> -subsystem	$E_0^{yz}$	Always	L.A.S.

### 3. Dynamics of subsystems

In order to understand the dynamics of the full model (1.3), we first consider the dynamics of the following subsystems:

1. The *xy*-subsystem. The predator–prey model in the absence of the IG predator  $z$

$$x' = x(x - \theta)(1 - x) - \alpha xy, \quad y' = \gamma_1 y(x - d_1) \tag{3.1}$$

has three boundary equilibria  $E_0^{xy} := (0, 0)$ ,  $E_\theta^{xy} := (\theta, 0)$  and  $E_1^{xy} := (1, 0)$ , and an interior equilibrium  $E^{xy} := (d_1, \frac{1}{\alpha}(d_1 - \theta)(1 - d_1))$  if  $\theta < d_1 < 1$ .

2. The *xz*-subsystem. The predator–prey model in the absence of the IG prey  $y$

$$x' = x(x - \theta)(1 - x) - \beta xz, \quad z' = \gamma_2 z(x - d_2) \tag{3.2}$$

has three boundary equilibria  $E_0^{xz} := (0, 0)$ ,  $E_\theta^{xz} := (\theta, 0)$  and  $E_1^{xz} := (1, 0)$ , and an interior equilibrium  $E^{xz} := (d_2, \frac{1}{\beta}(d_2 - \theta)(1 - d_2))$  if  $\theta < d_2 < 1$ .

3. The *yz*-subsystem. The predator–prey model in the absence of the basal prey  $x$

$$y' = \gamma_1 y(-a_1 z - d_1), \quad z' = \gamma_2 z(a_2 y - d_2) \tag{3.3}$$

has a unique trivial equilibrium  $E_0^{yz} := (0, 0)$ .

From Theorem 2.1, we have the following result.

**Corollary 3.1.** Both subsystems (3.1) and (3.2) are positively invariant and uniformly ultimately bounded in  $\mathbb{R}_+^2$  with  $\limsup_{t \rightarrow \infty} x(t) \leq 1$ .

#### 3.1. Local dynamics of subsystems

The local stability of equilibria of subsystems (3.1)–(3.3) can be summarized as follows.

**Theorem 3.2.** The existence and local stability of equilibria of (3.1)–(3.3) are listed in Table 1. Moreover, the *xy*-subsystem (3.1) undergoes a Hopf-bifurcation at equilibrium  $E^{xy}$  with  $d_1 = \frac{1}{2}(1 + \theta)$  and the *xz*-subsystem (3.2) undergoes a Hopf-bifurcation at equilibrium  $E^{xz}$  with  $d_2 = \frac{1}{2}(1 + \theta)$ .

**Proof.** Since the *xy*-subsystem (3.1) and the *xz*-subsystem (3.2) have the same form, we only need to analyze the *xy*-subsystem (3.1). The local stability is determined by the eigenvalues  $\lambda_i (i = 1, 2)$  of the following Jacobian matrix  $J$  associated to subsystem (3.1), evaluated at equilibria

$$J|_E = \begin{pmatrix} (x - \theta)(1 - x) + x(1 - x) - x(x - \theta) - \alpha y & -\alpha x \\ \gamma_1 y & \gamma_1(x - d_1) \end{pmatrix}.$$

At  $E_0^{xy} = (0, 0)$ , we have eigenvalues  $\lambda_1 = -\theta < 0$ ,  $\lambda_2 = -\gamma_1 d_1 < 0$ , which imply that  $E_0^{xy}$  is always locally asymptotically stable.

At  $E_\theta^{xy} = (\theta, 0)$ , we get  $\lambda_1 = \theta(1 - \theta) > 0$  since  $0 < \theta < 1$  and  $\lambda_2 = \gamma_1(\theta - d_1)$ . Thus,  $E_\theta^{xy}$  is always unstable and is a saddle if  $\theta < d_1$  and a source if  $\theta > d_1$ .

At  $E_1^{xy} = (1, 0)$ , we get  $\lambda_1 = -(1 - \theta) < 0$ ,  $\lambda_2 = \gamma_1(1 - d_1)$ . Thus,  $E_1^{xy}$  is locally asymptotically stable if  $d_1 > 1$  and a saddle point if  $d_1 < 1$ .

If  $d_1 = 1$ , then  $E_1^{xy}$  is nonhyperbolic with eigenvalues  $\lambda_1 = -(1 - \theta) < 0$ ,  $\lambda_2 = 0$ . We use Center Manifold Theorem to determine the stability of subsystem (3.1) at  $E_1^{xy}$ . For that, consider

$$\Phi(y) = b_1 y^2 + b_2 y^3 + \text{higher order terms.}$$

By some simple calculation we can get  $\Phi(y) \equiv 0$ . Thus, the flow on the center manifold is given by  $\frac{dy}{dt} = -\gamma_1 d_1 y$ . Therefore, the boundary equilibrium  $E_1^{xy}$  is locally asymptotically stable if  $d_1 = 1$ .

At  $E^{xy} = (d_1, \frac{1}{\alpha}(d_1 - \theta)(1 - d_1))$  ( $\theta < d_1 < 1$ ), the characteristic equation is as follows

$$\det(\lambda I - J|_{E^{xy}}) = \lambda^2 - d_1(1 - 2d_1 + \theta)\lambda + \gamma_1 d_1(d_1 - \theta)(1 - d_1) = 0.$$

Clearly,  $\text{Re}\lambda_1$  and  $\text{Re}\lambda_2$  have the same sign since  $1 > d_1 > \theta$ . From  $\lambda_1 + \lambda_2 = d_1(1 - 2d_1 + \theta)$ , we can conclude that  $E^{xy}$  is locally asymptotically stable if  $\frac{1}{2}(1 + \theta) < d_1 < 1$ , while it is a source if  $\theta < d_1 < \frac{1}{2}(1 + \theta)$ .

If  $d_1 = \frac{1}{2}(1 + \theta)$ , then the characteristic equation of  $E^{xy}$  has a pair of purely imaginary roots

$$\lambda_1 = i\sqrt{\gamma_1 d_1(d_1 - \theta)(1 - d_1)}, \quad \lambda_2 = -i\sqrt{\gamma_1 d_1(d_1 - \theta)(1 - d_1)}.$$

Let  $A = d_1(1 - 2d_1 + \theta)$ . Notice that

$$\left. \frac{dA}{d(d_1)} \right|_{d_1 = \frac{1}{2}(1+\theta)} = -(1 + \theta) < 0.$$

Thus, according to Theorem 3.1.3 in [50], we know that the subsystem (3.1) undergoes a Hopf-bifurcation at  $E^{xy}$  when  $d_1 = \frac{1}{2}(1 + \theta)$ .

The  $yz$ -subsystem has a unique trivial equilibrium  $E_0^{yz} = (0, 0)$ . The eigenvalues at  $E_0^{yz}$  are  $\lambda_1 = -\gamma_1 d_1 < 0$  and  $\lambda_2 = -\gamma_2 d_2 < 0$ . Hence,  $E_0^{yz}$  is locally asymptotically stable. The proof is complete.  $\square$

**Remark 3.3.** (1) Both the existence and local stability of boundary and interior equilibria of the  $xy$ -subsystem (3.1) ( $xz$ -subsystem (3.2)) are independent of  $\gamma_1$  ( $\gamma_2$ , respectively). (2) Theorem 3.2 suggests that the coexistence of the basal prey  $x$  and IG prey  $y$  (IG predator  $z$ ) at the equilibrium  $E^{xy}$  ( $E^{xz}$ ) of subsystem (3.1) ((3.2)) is determined by the Allee threshold  $\theta$  and the death rate of IG prey  $y$  (IG predator  $z$ ) since  $E^{xy}$  ( $E^{xz}$ ) is locally asymptotically stable if  $\frac{1}{2}(1 + \theta) < d_1 < 1$  ( $\frac{1}{2}(1 + \theta) < d_2 < 1$ , respectively).

### 3.2. Global features of subsystems

In this subsection, we focus on the global dynamics of both subsystems (3.1) and (3.2). First, we have the following theorem regarding the extinction of one or both species.

**Theorem 3.4.** (Extinction)

- (i) If  $d_1 \geq 1$ , then the population of the IG prey  $y$  in the  $xy$ -subsystem (3.1) goes extinct for any initial condition in  $\mathbb{R}_+^2$ . Similarly, if  $d_2 \geq 1$ , then the population of the IG predator  $z$  in the  $xz$ -subsystem (3.2) goes extinct for any initial condition in the interior of  $\mathbb{R}_+^2$ ;

- (ii) If  $d_1 \leq \theta$ , then the solution of the  $xy$ -subsystem (3.1) converges to  $(0, 0)$  for any initial condition in the interior of  $\mathbb{R}_+^2$ . Similarly, if  $d_2 \leq \theta$ , then the solution of the  $xz$ -subsystem (3.2) converges to  $(0, 0)$  for any initial condition in the interior of  $\mathbb{R}_+^2$ ;
- (iii) If  $x(0) \leq \theta$ , then all species in both subsystems (3.1) and (3.2) converge to  $(0, 0)$ ;
- (iv) In the absence of the basal prey  $x$ , both the IG prey and IG predator go extinct for any initial condition in  $\mathbb{R}_+^2$ .

**Proof.** We only need to prove the result for the  $xy$ -subsystem (3.1) and the  $yz$ -subsystem (3.3).

Let  $d_1 > 1$ . By  $\limsup_{t \rightarrow \infty} x(t) \leq 1$ , we have that for sufficiently small  $\epsilon > 0$  satisfying  $d_1 > 1 + \epsilon$ , there exists  $T_1 > 0$  such that for all  $t > T_1$ ,  $x(t) \leq 1 + \epsilon$ . Then by the second equation of the  $xy$ -subsystem (3.1), we have that

$$y' = \gamma_1 y(x - d_1) \leq \gamma_1 y(1 + \epsilon - d_1) \leq 0, \quad \forall t > T_1.$$

It follows that  $\lim_{t \rightarrow \infty} y(t) = 0$ .

If  $d_1 = 1$ , then according to Theorem 3.2, the  $xy$ -subsystem (3.1) only has three boundary equilibria  $E_u^{xy}$ ,  $u = 0, \theta, 1$ , where both  $E_0^{xy}$  and  $E_1^{xy}$  are locally asymptotically stable and  $E_\theta^{xy}$  is a saddle. Corollary 3.1 implies that the  $xy$ -subsystem (3.1) has a compact global attractor. Thus, from an application of Poincaré-Bendixson theorem [51] we conclude that  $\lim_{t \rightarrow \infty} y(t) = 0$  for any solution  $(x(t), y(t))$  of (3.1) initiated from the interior of  $\mathbb{R}_+^2$ .

If  $d_1 \leq \theta$ , then from Theorem 3.2, the  $xy$ -subsystem (3.1) only has three boundary equilibria  $E_u^{xy}$ ,  $u = 0, \theta, 1$ , where  $E_0^{xy}$  is locally asymptotically stable,  $E_\theta^{xy}$  is unstable, and  $E_1^{xy}$  is a saddle point. Thus, Corollary 3.1 and Poincaré-Bendixson theorem [51] imply that  $\lim_{t \rightarrow \infty} (x(t), y(t)) = (0, 0)$  for any solution  $(x(t), y(t))$  of (3.1) initiated from the interior of  $\mathbb{R}_+^2$ .

Assume  $x(0) \leq \theta$ . From the first equation of the  $xy$ -subsystem (3.1), we have

$$x'|_{x < \theta} \leq 0, \quad \text{and} \quad x'|_{x = \theta} \leq 0,$$

which implies that  $\lim_{t \rightarrow \infty} x(t) = 0$ . Thus, the second equation of (3.1) implies that  $\lim_{t \rightarrow \infty} y(t) = 0$ .

In the absence of the basal prey  $x$ , the  $yz$ -subsystem (3.3) has a unique equilibrium  $(0, 0)$  which is locally asymptotically stable. Theorem 2.1 implies that the  $yz$ -subsystem (3.3) has a compact global attractor. Thus, Poincaré-Bendixson theorem [51] implies that the solution of the  $yz$ -subsystem (3.3) converges to  $(0, 0)$  for any initial condition in  $\mathbb{R}_+^2$ . The proof is complete.  $\square$

**Remark 3.5.** The second part of Theorem 3.4 is about IG prey (IG predation)-driven extinction due to Allee effect of the basal prey population. The invasion or reproduction of the IG prey (IG predator) is excessive while the reproduction of the basal prey is not fast enough to sustain its own population. Thus, the excessive invasion or reproduction of the IG prey (IG predator) drives the population of basal prey to below its Allee threshold and eventually to zero, which consequently drives the population of the IG prey (IG predator, respectively) to extinction. The third and fourth statements of Theorem 3.4 indicate that in the absence of the basal prey, when the population density of the basal prey is below its Allee threshold, all species will be extinct.

Now, let  $\theta, \alpha, \gamma_1$  be fixed and  $d_1$  vary, we show the global dynamics of the  $xy$ -subsystem (3.1). The features of the  $xz$ -subsystem (3.2) are same to (3.1) and are omitted here. We refer to Sieber and Hilker [52], Wang et al. [37] and Kang et al. [53] for more details and numerical simulations.

- (i)  $d_1 \geq 1$ . This leads to the IG prey free dynamics with  $E_0^{xy} \cup E_1^{xy}$  as attractors.
- (ii)  $\frac{1}{2}(1 + \theta) < d_1 < 1$ . There is a transcritical bifurcation at  $d_1 = 1$ . When the value of  $d_1$  is decreased from 1,  $E_1^{xy}$  becomes unstable and a unique and locally asymptotically stable interior equilibrium  $E^{xy}$  appears.
- (iii)  $d_1 = \frac{1}{2}(1 + \theta)$ . A Hopf bifurcation occurs.
- (iv) There exists a threshold value  $d_1^* : \theta < d_1^* < \frac{1}{2}(1 + \theta)$  such that

- (a) when  $d_1^* < d_1 < \frac{1}{2}(1 + \theta)$ , there exists a unique limit cycle such that below the stable manifold of  $E_\theta^{xy}$  trajectories converge to the limit cycle and above the stable manifold of  $E_\theta^{xy}$  trajectories converge to the extinction equilibrium  $E_0^{xy}$ ;
- (b) when  $d_1 = d_1^*$ , the unique stable limit cycle disappears and a heteroclinic bifurcation occurs; i.e., there is a heteroclinic orbit connecting  $E_1^{xy}$  to  $E_\theta^{xy}$ . Outside the heteroclinic cycle, trajectories converge to  $E_0^{xy}$ , while inside the heteroclinic cycle trajectories converge towards the heteroclinic cycle;
- (c) when  $\theta < d_1 < d_1^*$ , the heteroclinic orbit is broken, which leads  $E_0^{xy}$  to be globally asymptotically stable and all species cannot coexist.
- (v)  $d_1 \leq \theta$ . The IG prey-driven extinction occurs and no interior equilibrium appears any more, all trajectories in the interior of  $\mathbb{R}_+^2$  converge to  $E_0^{xy}$ .

#### 4. Dynamics of the full IGP system

In this section, we study the dynamics of the full IGP system (1.3). First, we study the existence and stability of boundary equilibria of system (1.3).

##### 4.1. Boundary equilibria of the full IGP system

It is easy to check that system (1.3) has three axial equilibria:

$$E_0 = (0, 0, 0), \quad E_\theta = (\theta, 0, 0), \quad E_1 = (1, 0, 0),$$

and two planar equilibria:

$$E_2 = \left( d_2, 0, \frac{1}{\beta}(d_2 - \theta)(1 - d_2) \right) \quad \text{if } \theta < d_2 < 1,$$

$$E_3 = \left( d_1, \frac{1}{\alpha}(d_1 - \theta)(1 - d_1), 0 \right) \quad \text{if } \theta < d_1 < 1.$$

The existence and stability of these boundary equilibria can be summarized as the following theorem.

**Theorem 4.1.** (Existence and Stability of Boundary Equilibria) *Sufficient conditions for the existence and local stability of boundary equilibria for system (1.3) are summarized in Table 2.*

**Proof.** The Jacobian matrix  $J$  associated to system (1.3) is given by

$$J|_E = \begin{pmatrix} (x - \theta)(1 - x) + x(1 - x) - x(x - \theta) - \alpha y - \beta z & -\alpha x & -\beta x \\ \gamma_1 y & \gamma_1(x - a_1 z - d_1) & -\gamma_1 a_1 y \\ \gamma_2 z & \gamma_2 a_2 z & \gamma_2(x + a_2 y - d_2) \end{pmatrix}.$$

At  $E_0 = (0, 0, 0)$ , we have eigenvalues  $\lambda_1 = -\theta$ ,  $\lambda_2 = -\gamma_1 d_1$ ,  $\lambda_3 = -\gamma_2 d_2$ , which imply that  $E_0 = (0, 0, 0)$  is always locally asymptotically stable.

At  $E_\theta = (\theta, 0, 0)$ , we get  $\lambda_1 = \theta(1 - \theta) > 0$ ,  $\lambda_2 = \gamma_1(\theta - d_1)$  and  $\lambda_3 = \gamma_2(\theta - d_2)$ . Thus,  $E_\theta$  is always unstable and a source if  $d_1 < \theta$ ,  $d_2 < \theta$  and a saddle if at least one of  $d_1$  and  $d_2$  is larger than  $\theta$ .

At  $E_1 = (1, 0, 0)$ , we get  $\lambda_1 = -(1 - \theta) < 0$ ,  $\lambda_2 = \gamma_1(1 - d_1)$  and  $\lambda_3 = \gamma_2(1 - d_2)$ . Thus,  $E_1$  is locally asymptotically stable if  $d_1 > 1$ ,  $d_2 > 1$  while a saddle if at least one of  $d_1$  and  $d_2$  is less than 1.

At  $E_2 = \left( d_2, 0, \frac{1}{\beta}(d_2 - \theta)(1 - d_2) \right)$  ( $\theta < d_2 < 1$ ), the characteristic equation is given by

$$\left( \lambda - \gamma_1 \left( d_2 - d_1 - \frac{1}{\beta} a_1 (d_2 - \theta)(1 - d_2) \right) \right) (\lambda^2 - d_2(1 - 2d_2 + \theta)\lambda + \gamma_2 d_2 (d_2 - \theta)(1 - d_2)) = 0.$$



**Table 2**  
The boundary equilibria and their local stability for system (1.3).

Boundary equilibria	Existence conditions	Stability conditions
$E_0$	Always	Always L.A.S.
$E_\theta$	Always	Always unstable. Source if $0 < d_1, d_2 < \theta$ ; Saddle if at least one of $d_1$ and $d_2$ is larger than $\theta$ .
$E_1$	Always	L.A.S. if $d_1, d_2 > 1$ ; Saddle if at least one of $d_1$ and $d_2$ is less than 1.
$E_2$	$\theta < d_2 < 1$	L.A.S. if $d_1 > d_2 - \frac{\alpha_1}{\beta}(d_2 - \theta)(1 - d_2)$ and $\frac{1}{2}(1 + \theta) < d_2 < 1$ ; Source if $d_1 < d_2 - \frac{\alpha_1}{\beta}(d_2 - \theta)(1 - d_2)$ and $\theta < d_2 < \frac{1}{2}(1 + \theta)$ ; Saddle if either (1) $d_1 < d_2 - \frac{\alpha_1}{\beta}(d_2 - \theta)(1 - d_2), \frac{1}{2}(1 + \theta) < d_2 < 1$ or (2) $d_1 > d_2 - \frac{\alpha_1}{\beta}(d_2 - \theta)(1 - d_2), \theta < d_2 < \frac{1}{2}(1 + \theta)$ .
$E_3$	$\theta < d_1 < 1$	L.A.S. if $d_2 > d_1 + \frac{\alpha_2}{\alpha}(d_1 - \theta)(1 - d_1)$ and $\frac{1}{2}(1 + \theta) < d_1 < 1$ ; Source if $d_2 < d_1 + \frac{\alpha_2}{\alpha}(d_1 - \theta)(1 - d_1)$ and $\theta < d_1 < \frac{1}{2}(1 + \theta)$ ; Saddle if either (1) $d_2 < d_1 + \frac{\alpha_2}{\alpha}(d_1 - \theta)(1 - d_1), \frac{1}{2}(1 + \theta) < d_1 < 1$ or (2) $d_2 > d_1 + \frac{\alpha_2}{\alpha}(d_1 - \theta)(1 - d_1), \theta < d_1 < \frac{1}{2}(1 + \theta)$ .

Thus, we have  $\lambda_2 = \gamma_1 \left( d_2 - d_1 - \frac{1}{\beta} a_1 (d_2 - \theta)(1 - d_2) \right)$  and  $\lambda_1, \lambda_3$  are roots of the following equation:

$$\lambda^2 - d_2(1 - 2d_2 + \theta)\lambda + \gamma_2 d_2 (d_2 - \theta)(1 - d_2) = 0.$$

Notice that  $\theta < d_2 < 1$ , we know that  $E_2$  is locally asymptotically stable if  $d_1 > d_2 - \frac{1}{\beta} a_1 (d_2 - \theta)(1 - d_2)$  and  $\frac{1}{2}(1 + \theta) < d_2 < 1$ ;  $E_2$  is a saddle if either

$$\begin{cases} d_1 < d_2 - \frac{1}{\beta} a_1 (d_2 - \theta)(1 - d_2), \\ \frac{1}{2}(1 + \theta) < d_2 < 1, \end{cases} \quad \text{or} \quad \begin{cases} d_1 > d_2 - \frac{1}{\beta} a_1 (d_2 - \theta)(1 - d_2), \\ \theta < d_2 < \frac{1}{2}(1 + \theta), \end{cases}$$

and a source if  $d_1 < d_2 - \frac{1}{\beta} a_1 (d_2 - \theta)(1 - d_2)$  and  $\theta < d_2 < \frac{1}{2}(1 + \theta)$ .

At  $E_3 = (d_1, \frac{1}{\alpha}(d_1 - \theta)(1 - d_1), 0)$  ( $\theta < d_1 < 1$ ), the characteristic equation is given by

$$\left( \lambda - \gamma_2 \left( d_1 - d_2 + \frac{1}{\alpha} a_2 (d_1 - \theta)(1 - d_1) \right) \right) \left( \lambda^2 - d_1(1 - 2d_1 + \theta)\lambda + \gamma_1 d_1 (d_1 - \theta)(1 - d_1) \right) = 0.$$

Thus,  $E_3$  is locally asymptotically stable if  $d_2 > d_1 + \frac{1}{\alpha} a_2 (d_1 - \theta)(1 - d_1)$  and  $\frac{1}{2}(1 + \theta) < d_1 < 1$ ;  $E_3$  is a saddle if either

$$\begin{cases} d_2 < d_1 + \frac{1}{\alpha} a_2 (d_1 - \theta)(1 - d_1), \\ \frac{1}{2}(1 + \theta) < d_1 < 1, \end{cases} \quad \text{or} \quad \begin{cases} d_2 > d_1 + \frac{1}{\alpha} a_2 (d_1 - \theta)(1 - d_1), \\ \theta < d_1 < \frac{1}{2}(1 + \theta), \end{cases}$$

and a source if  $d_2 < d_1 + \frac{1}{\alpha} a_2 (d_1 - \theta)(1 - d_1)$  and  $\theta < d_1 < \frac{1}{2}(1 + \theta)$ . The proof is complete.  $\square$

**Remark 4.2.**

(1) According to [Theorem 4.1](#), both  $E_2$  and  $E_3$  are locally asymptotically stable in  $\mathbb{R}_+^3$  if

$$\begin{cases} \frac{1}{2}(1 + \theta) < d_1 < d_2 < 1, \\ \frac{a_1}{\beta} > \frac{d_2 - d_1}{(d_2 - \theta)(1 - d_2)}, \quad \frac{a_2}{\alpha} < \frac{d_2 - d_1}{(d_1 - \theta)(1 - d_1)}. \end{cases}$$

(2) By [Theorem 3.2](#) and the proof of [Theorem 4.1](#), if  $d_1 > d_2 - \frac{a_1}{\beta}(d_2 - \theta)(1 - d_2)$ ,  $\theta < d_2 < \frac{1}{2}(1 + \theta)$ , then  $E_2$  is a saddle in  $\mathbb{R}_+^3$ , but it is a source in the  $xz$ -plane and there exists  $d_2^* : \theta < d_2^* < \frac{1}{2}(1 + \theta)$  such that for  $d_2^* < d_2 < \frac{1}{2}(1 + \theta)$  there is a unique stable limit cycle surrounding  $E_2$ . Similarly, if  $d_2 > d_1 + \frac{a_2}{\alpha}(d_1 - \theta)(1 - d_1)$ ,  $\theta < d_1 < \frac{1}{2}(1 + \theta)$ , then  $E_3$  is a saddle in  $\mathbb{R}_+^3$ , but it is a source in the  $xy$ -plane, and there exists  $d_1^* : \theta < d_1^* < \frac{1}{2}(1 + \theta)$  such that for  $d_1^* < d_1 < \frac{1}{2}(1 + \theta)$  there is a unique stable limit cycle surrounding  $E_3$ .

(3) Both the existence and local stability of boundary equilibria of [\(1.3\)](#) are independent of  $(\gamma_1, \gamma_2)$ .

**4.2. Extinction**

By [Theorems 2.1, 3.2](#) and [3.4](#), we have the following result regarding the extinction of at least one species of the basal prey  $x$ , IG prey  $y$  and IG predator  $z$ .

**Theorem 4.3.** (Basic Global Features)

- (i) If  $d_1 \geq 1$ , then  $\lim_{t \rightarrow \infty} y(t) = 0$ . If, in addition,  $d_2 \geq 1$ , then  $\lim_{t \rightarrow \infty} \max\{y(t), z(t)\} = 0$ . While if  $d_1 \geq 1$  and  $d_2 \leq \theta$ , then  $\lim_{t \rightarrow \infty} (x(t), y(t), z(t)) = E_0$ ;
- (ii) If  $d_2 \geq 1 + \frac{a_2}{\alpha} \left[ \frac{(1-\theta)^2}{4d_1} + \gamma_1 \right]$ , then  $\lim_{t \rightarrow \infty} z(t) = 0$ . If, in addition,  $d_1 \leq \theta$ , then  $\lim_{t \rightarrow \infty} (x(t), y(t), z(t)) = E_0$ ;
- (iii) All trajectories of system [\(1.3\)](#) converge to  $E_0$  if  $x(0) \leq \theta$ .

**Proof.** (i) The fact that

$$\begin{aligned} x' &= x(x - \theta)(1 - x) - \alpha xy - \beta xz \leq x(x - \theta)(1 - x) - \alpha xy, \\ y' &= \gamma_1 y(x - a_1 z - d_1) \leq \gamma_1 y(x - d_1) \end{aligned}$$

implies that the dynamics of  $x$  and  $y$  of the full system [\(1.3\)](#) can be governed by the  $xy$ -subsystem [\(3.1\)](#). Therefore, by [Theorem 3.4](#),  $d_1 \geq 1$  implies  $\lim_{t \rightarrow \infty} y(t) = 0$  and the limiting system of [\(1.3\)](#) is the  $xz$ -subsystem [\(3.2\)](#). Thus, if in addition  $d_2 \geq 1$ , then

$$\lim_{t \rightarrow \infty} \max\{y(t), z(t)\} = 0.$$

Moreover, if in addition  $d_2 \leq \theta$ , then from [Theorem 3.2](#) we can conclude that the omega limit set of the  $xz$ -plane is  $E_0 \cup E_\theta \cup E_1$ . By [Theorem 2.1](#) and the condition  $d_1 \geq 1$  ([Theorem 3.4](#)), for any  $\epsilon > 0$ , all trajectories enter the compact set  $[0, 1] \times [0, \epsilon] \times [0, B]$  when time is large enough. Therefore, the conditions  $d_1 \geq 1$  and  $d_2 \leq \theta$  indicate that for any  $\epsilon > 0$ , all trajectories enter the compact set  $M = [0, 1] \times [0, \epsilon] \times [0, \epsilon]$  when time is large enough. Choose  $\epsilon > 0$  small enough, then the omega limit set of the interior of  $M$  is  $E_0$  since  $E_0$  is locally asymptotically stable and  $E_\theta, E_1$  are unstable according to [Theorem 3.2](#). Therefore, the conditions  $d_1 \geq 1$  and  $d_2 \leq \theta$  imply that  $\lim_{t \rightarrow \infty} (x(t), y(t), z(t)) = E_0$ .

(ii) By [Theorem 2.1](#), we have  $\limsup_{t \rightarrow \infty} x(t) \leq 1$  and  $\limsup_{t \rightarrow \infty} y(t) \leq \frac{1}{\alpha} \left[ \frac{(1-\theta)^2}{4d_1} + \gamma_1 \right]$ . This indicates that for any  $\epsilon > 0$  sufficiently small, there exists a time  $T > 0$  such that for all  $t > T$ ,

$$\frac{dz}{zdt} < \gamma_2 \left( 1 + \epsilon + \frac{a_2}{\alpha} \left[ \frac{(1-\theta)^2}{4d_1} + \gamma_1 + \epsilon \right] - d_2 \right).$$

It follows from the arbitrariness of  $\epsilon$  and the condition  $1 + \frac{a_2}{\alpha} \left[ \frac{(1-\theta)^2}{4d_1} + \gamma_1 \right] \leq d_2$  that  $\lim_{t \rightarrow \infty} z(t) = 0$ . The rest of this item can be shown by applying similar arguments as in the proof of (i).

(iii) If  $x(0) \leq \theta$ , similar to the proof of Theorem 3.4, we have  $\lim_{t \rightarrow \infty} (x(t), y(t)) = 0$ . Thus, the third equation of (1.3) implies  $\lim_{t \rightarrow \infty} z(t) = 0$ . Therefore, all trajectories of system (1.3) converge to  $E_0$ . The proof is complete.  $\square$

**Remark 4.4.** Theorem 4.3 implies the following statements:

(1) The high death rate(s) of the IG prey or/and IG predator lead(s) to the extinction of the IG prey or/and IG predator.

(2) If  $d_1 \geq 1$  and  $d_2 \leq \theta$  (or  $d_2 \geq 1 + \frac{a_2}{\alpha} \left[ \frac{(1-\theta)^2}{4d_1} + \gamma_1 \right]$  and  $d_1 \leq \theta$ ), then the IG predator (or IG prey, respectively)-driven extinction occurs due to Allee effect of the basal prey population, and all species will be extinct. Therefore, Allee effect in the basal prey increases the extinction risk of not only the basal prey but also both IG prey and predator, even if the initial population density of the basal prey is abundant.

(3) The initial population of the basal prey plays an important role in the persistence of  $x$  or  $y$  or  $z$  due to Allee effect in the basal prey. If the population density of the basal prey is low, then all species will be extinct.

### 4.3. Interior equilibrium

In this subsection, we explore sufficient conditions for the existence of the interior equilibria and their stability for system (1.3).

The interior equilibria of system (1.3) are determined by the following equations:

$$\begin{cases} (x - \theta)(1 - x) - \alpha y - \beta z = 0, \\ x - a_1 z - d_1 = 0, \\ x + a_2 y - d_2 = 0. \end{cases}$$

Thus,  $(x^*, y^*, z^*)$  is an interior equilibrium of system (1.3) if and only if  $x^*$  is a positive root of the following quadratic equation

$$f(x) := x^2 - \left( 1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} \right) x + \theta + \frac{d_2 \alpha}{a_2} - \frac{d_1 \beta}{a_1} = 0, \tag{4.1}$$

and

$$y^* = \frac{1}{a_2}(d_2 - x^*) > 0, \quad z^* = \frac{1}{a_1}(x^* - d_1) > 0. \tag{4.2}$$

Let

$$\Delta = \left( 1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} \right)^2 - 4 \left( \theta + \frac{d_2 \alpha}{a_2} - \frac{d_1 \beta}{a_1} \right). \tag{4.3}$$

If  $\Delta < 0$ , then the quadratic equation (4.1) has no root, and hence system (1.3) has no interior equilibrium.

If  $\Delta \geq 0$ , then the quadratic equation (4.1) has two real roots  $x_1^*$  and  $x_2^*$  ( $x_1^* \leq x_2^*$ ):

$$x_1^* = \frac{1}{2} \left( 1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} - \sqrt{\Delta} \right), \quad x_2^* = \frac{1}{2} \left( 1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} + \sqrt{\Delta} \right). \tag{4.4}$$

Clearly,  $x_1^* \leq \frac{1}{2} \left( 1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} \right) \leq x_2^*$ . Let

$$y_i^* = \frac{1}{a_2}(d_2 - x_i^*), \quad z_i^* = \frac{1}{a_1}(x_i^* - d_1), \quad i = 1, 2.$$

If  $\Delta > 0$ , then the number of interior equilibria is determined by the relative locations of  $x_1^*, x_2^*$  and  $d_1, d_2$ :

- No interior equilibrium if (1)  $d_1, d_2 \leq x_1^*$ , or (2)  $d_1, d_2 \geq x_2^*$ , or (3)  $x_1^* \leq d_1, d_2 \leq x_2^*$ ;
- A unique interior equilibrium  $E_1^* = (x_1^*, y_1^*, z_1^*)$  if  $d_1 < x_1^* < d_2 \leq x_2^*$ ;

- Two interior equilibria  $E_1^* = (x_1^*, y_1^*, z_1^*)$  and  $E_2^* = (x_2^*, y_2^*, z_2^*)$  if  $d_1 < x_1^* \leq x_2^* < d_2$ ;
- A unique interior equilibrium  $E_2^* = (x_2^*, y_2^*, z_2^*)$  if  $x_1^* \leq d_1 < x_2^* < d_2$ .

Based on the above analysis and the [Theorem 4.3](#), we obtain the following sufficient conditions for which system [\(1.3\)](#) has no interior equilibrium.

**Theorem 4.5.** (No Interior Equilibrium) *System [\(1.3\)](#) has no interior equilibrium if one of the following conditions is satisfied:*

- (i)  $d_1 \geq 1$ ;
- (ii)  $d_2 \geq 1 + \frac{a_2}{\alpha} \left[ \frac{(1-\theta)^2}{4d_1} + \gamma_1 \right]$ ;
- (iii)  $d_2 \geq d_1$ ;
- (iv)  $\Delta = \left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)^2 - 4\left(\theta + \frac{d_2\alpha}{a_2} - \frac{d_1\beta}{a_1}\right) < 0$ ;
- (v)  $\Delta = \left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)^2 - 4\left(\theta + \frac{d_2\alpha}{a_2} - \frac{d_1\beta}{a_1}\right) \geq 0$  and one of the following conditions holds: (1)  $d_1, d_2 \leq x_1^*$ , (2)  $d_1, d_2 \geq x_2^*$ , (3)  $x_1^* \leq d_1, d_2 \leq x_2^*$ .

Now, we state the existence and local stability of the interior equilibria for system [\(1.3\)](#).

**Theorem 4.6.** (Existence and Local Stability of Interior Equilibria)

- (i) If  $\Delta > 0, d_1 < x_1^* < d_2 \leq x_2^*$ , then system [\(1.3\)](#) has a unique interior equilibrium  $E_1^* = (x_1^*, y_1^*, z_1^*)$ .
- (ii) If  $\Delta > 0, d_1 < x_1^* < x_2^* < d_2$ , then system [\(1.3\)](#) has two interior equilibria  $E_1^* = (x_1^*, y_1^*, z_1^*)$  and  $E_2^* = (x_2^*, y_2^*, z_2^*)$ .
- (iii) If  $\Delta > 0, x_1^* \leq d_1 < x_2^* < d_2$ , then system [\(1.3\)](#) has a unique interior equilibrium  $E_2^* = (x_2^*, y_2^*, z_2^*)$ .

Moreover, if  $E_1^*$  exists then it is always unstable; and if  $E_2^*$  exists then it is locally asymptotically stable if and only if  $x_2^* > \frac{1}{2}(1 + \theta)$  and  $\rho > 0$ . In addition, if  $x_2^* > \frac{1}{2}(1 + \theta)$  then system [\(1.3\)](#) undergoes a Hopf bifurcation at  $E_2^*$  when  $\rho = 0$ . Here,

$$\rho = x_2^*(2x_2^* - (1 + \theta))(\gamma_1\alpha y_2^* + \gamma_2\beta z_2^*) + \left(\frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)\gamma_1\gamma_2 a_1 a_2 y_2^* z_2^*. \quad (4.5)$$

**Proof.** The existence of the interior equilibria can be directly obtained. At  $E_i^* (i = 1, 2)$ , the Jacobian matrix  $J|_{E_i^*}$  associated to system [\(1.3\)](#) is given as follows:

$$J|_{E_i^*} = \begin{pmatrix} x^*(1 - x^*) - x^*(x^* - \theta) & -\alpha x^* & -\beta x^* \\ \gamma_1 y^* & 0 & -\gamma_1 a_1 y^* \\ \gamma_2 z^* & \gamma_2 a_2 z^* & 0 \end{pmatrix},$$

which yields the characteristic equation  $F(\lambda) = \lambda^3 + \tau_1\lambda^2 + \tau_2\lambda + \tau_3 = 0$ , where

$$\begin{aligned} \tau_1 &= x_i^*(2x_i^* - (1 + \theta)), \\ \tau_2 &= \gamma_1\alpha x_i^* y_i^* + \gamma_2\beta x_i^* z_i^* + \gamma_1\gamma_2 a_1 a_2 y_i^* z_i^*, \\ \tau_3 &= \gamma_1\gamma_2 a_1 a_2 \left(2x_i^* - \left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)\right) x_i^* y_i^* z_i^*, \quad i = 1, 2. \end{aligned}$$

Note  $\tau_2 > 0$ . At  $E_1^*$ , since  $x_1^* < \frac{1}{2}\left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)$ , we know  $\tau_3 < 0$ . Therefore,  $F(\lambda) = 0$  has at least one positive real root and hence  $E_1^*$  is always unstable.

At  $E_2^*$ , since  $x_2^* > \frac{1}{2} \left( 1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} \right)$ , we know  $\tau_3 > 0$ . Let

$$\begin{aligned} \Delta_1 &= \tau_1 = x_2^*(2x_2^* - (1 + \theta)), \\ \Delta_2 &= \begin{vmatrix} \tau_1 & \tau_3 \\ 1 & \tau_2 \end{vmatrix} = x_2^* \left( x_2^*(2x_2^* - (1 + \theta))(\gamma_1 \alpha y_2^* + \gamma_2 \beta z_2^*) + \left( \frac{\alpha}{a_2} - \frac{\beta}{a_1} \right) \gamma_1 \gamma_2 a_1 a_2 y_2^* z_2^* \right) = x_2^* \rho, \\ \Delta_3 &= \begin{vmatrix} \tau_1 & \tau_3 & 0 \\ 1 & \tau_2 & 0 \\ 0 & \tau_1 & \tau_3 \end{vmatrix} = \tau_3 \Delta_2. \end{aligned}$$

From Routh–Hurwitz criterion,  $E_2^*$  is locally asymptotically stable if and only if  $x_2^* > \frac{1}{2}(1 + \theta)$  and  $\rho > 0$ .

Assume  $x_2^* > \frac{1}{2}(1 + \theta)$ . We will use  $\rho$  as the bifurcation parameter. It is easy to see that  $\rho = \frac{1}{x_2^*}(\tau_1 \tau_2 - \tau_3)$ . The characteristic equation in the eigenvalues of  $E_2^*$  can be rewritten as follows:

$$\lambda^3 + \tau_1 \lambda^2 + \frac{1}{\tau_1}(x_2^* \rho + \tau_3) \lambda + \tau_3 = 0.$$

In the case  $\rho = 0$ , we have  $(\lambda + \tau_1) \left( \lambda^2 + \frac{\tau_3}{\tau_1} \right) = 0$ , which gives one negative root  $\lambda_1 = -\tau_1 = -x_2^*(2x_2^* - (1 + \theta))$  since  $x_2^* > \frac{1}{2}(1 + \theta)$ , and a pair of purely imaginary roots  $\lambda_{2,3} = \pm i \sqrt{\frac{\tau_3}{\tau_1}}$ . If  $\rho > 0$ , then we have  $\Delta_2 > 0$ , so all eigenvalues have negative real parts and  $E_2^*$  is stable. If  $\rho < 0$ , then we have  $\Delta_2 < 0$ , so  $\lambda_{2,3}$  have positive real parts and  $E_2^*$  is unstable.

If  $\rho \neq 0$ , let the eigenvalues be denoted  $\lambda = p(\rho) + q(\rho)i$  with  $p(0) = 0$  and  $q(0) = \sqrt{\frac{\tau_3}{\tau_1}} > 0$ . To show a Hopf bifurcation occurs, we need to show  $\frac{dp(\rho)}{d\rho} \Big|_{\rho=0} = p'(0) \neq 0$ . Implicitly differentiating the characteristic equation with respect to  $\rho$ , we get

$$3\lambda^2 \lambda' + 2\tau_1 \lambda \lambda' + \frac{x_2^*}{\tau_1} \lambda + \frac{1}{\tau_1}(x_2^* \rho + \tau_3) \lambda' = 0.$$

Evaluating it at  $\rho = 0$ , we have

$$\left( 3\lambda^2 + 2\tau_1 \lambda + \frac{\tau_3}{\tau_1} \right) \lambda' + \frac{x_2^*}{\tau_1} \lambda = 0.$$

Since  $\lambda(0) = q(0)i$ ,  $\lambda^2(0) = -q^2(0) = -\frac{\tau_3}{\tau_1}$  and  $\lambda'(0) = p'(0) + q'(0)i$ , we obtain

$$-\frac{2\tau_3}{\tau_1} p'(0) - 2\sqrt{\tau_1 \tau_3} q'(0) + i \left[ 2\sqrt{\tau_1 \tau_3} p'(0) - \frac{2\tau_3}{\tau_1} q'(0) + \frac{x_2^*}{\tau_1} \sqrt{\frac{\tau_3}{\tau_1}} \right] = 0.$$

Setting the real and imaginary terms of the equation above equal to 0, respectively, we get

$$\begin{bmatrix} \frac{\tau_3}{\tau_1} & \sqrt{\tau_1 \tau_3} \\ -\sqrt{\tau_1 \tau_3} & \frac{\tau_3}{\tau_1} \end{bmatrix} \begin{bmatrix} p'(0) \\ q'(0) \end{bmatrix} = \begin{bmatrix} 0 \\ \frac{x_2^*}{2\tau_1} \sqrt{\frac{\tau_3}{\tau_1}} \end{bmatrix}.$$

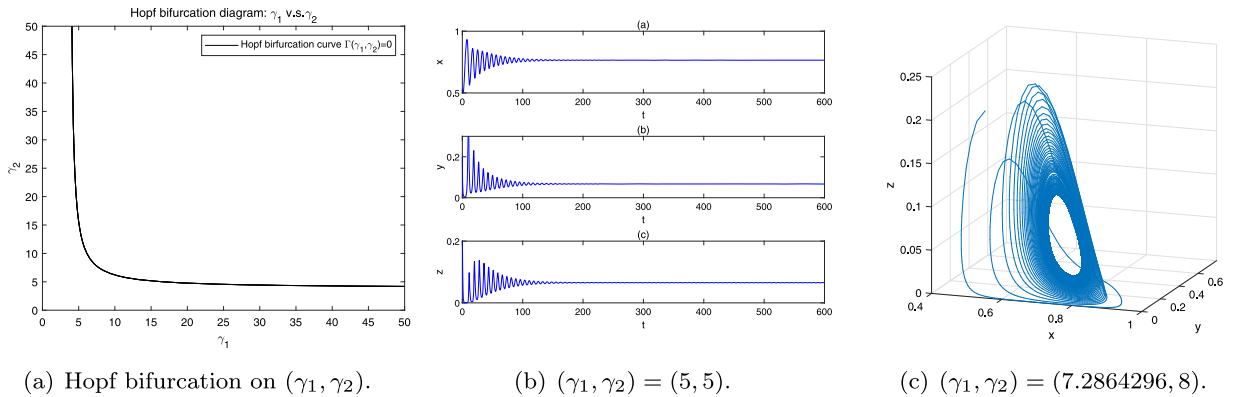
Thus,  $p'(0) = -\frac{x_2^* \tau_1}{2(\tau_1^3 + \tau_3)} < 0$ . The proof is complete.  $\square$

From (4.5),  $\frac{\alpha}{\beta} - \frac{a_2}{a_1} < 0$  is necessary for the occurrence of Hopf bifurcation. It is easy to see that if  $x_2^* > \frac{1}{2}(1 + \theta)$  then  $\rho = 0$  is equivalent to  $\Gamma(\gamma_1, \gamma_2) = 0$ , where  $\Gamma(\gamma_1, \gamma_2)$  is given by

$$\Gamma(\gamma_1, \gamma_2) = \frac{1}{\gamma_1} \frac{\beta}{y_2^*} + \frac{1}{\gamma_2} \frac{\alpha}{z_2^*} - \frac{a_2 \beta - a_1 \alpha}{x_2^*(2x_2^* - (1 + \theta))}. \tag{4.6}$$

Thus, we directly have the following result.

**Corollary 4.7.** *If the interior equilibrium  $E_2^*$  exists and  $x_2^* > \frac{1}{2}(1 + \theta)$ , then  $E_2^*$  is locally asymptotically stable if and only if the pair of parameters  $(\gamma_1, \gamma_2)$  satisfies  $\Gamma(\gamma_1, \gamma_2) > 0$ ; while system (1.3) undergoes a Hopf bifurcation at  $E_2^*$  on the curve  $\Gamma(\gamma_1, \gamma_2) = 0$ .*



**Fig. 1.** Parameter values:  $\theta = 0.2, d_1 = 0.7, d_2 = 0.9, \alpha = \beta = a_1 = 1, a_2 = 2$ . System (1.3) has a unique interior equilibrium  $E_2^* = (0.7653, 0.0673, 0.0653)$ . (a) The Hopf bifurcation curve on the  $(\gamma_1, \gamma_2)$ -plane. (b) When  $(\gamma_1, \gamma_2) = (5, 5)$ ,  $E_2^*$  is locally asymptotically stable. (c) When  $(\gamma_1, \gamma_2) = (7.2864296, 8)$ , which lies on the bifurcation curve  $\Gamma(\gamma_1, \gamma_2) = 0$ ,  $E_2^*$  loses its stability and a limit cycle is born due to the Hopf bifurcation. In both (b) and (c), the initial value is chosen as  $(0.5, 0.2, 0.2)$ .

**Remark 4.8.** Theorem 4.6 and Corollary 4.7 indicate the following implications:

(1) System (1.3) has at most two interior equilibria  $E_1^*$  and  $E_2^*$ . The existence of both  $E_1^*$  and  $E_2^*$  depends on Allee effect and is independent of the pair of parameters  $(\gamma_1, \gamma_2)$ .  $E_1^*$  is always unstable while the stability of  $E_2^*$  depends on Allee threshold  $\theta$ .

(2) Assuming  $E_2^*$  exists and  $x_2^* > \frac{1}{2}(1 + \theta)$ . From (4.6), if the ratio of the attack rates on the basal prey of IG prey to IG predator is not less than the conversion rate of IG predator from IG prey (i.e.,  $\frac{\alpha}{\beta} - \frac{a_2}{a_1} \geq 0$ ), then  $E_2^*$  is stable for all  $(\gamma_1, \gamma_2)$ . However, if  $\frac{\alpha}{\beta} - \frac{a_2}{a_1} < 0$ , then  $(\gamma_1, \gamma_2)$  determines the stability of  $E_2^*$ . The Hopf bifurcation curve  $\Gamma(\gamma_1, \gamma_2) = 0$  depicts the relationship between competition levels of the IG prey and IG predator for the basal resource. If the competition of IG prey and IG predator for the basal resource lies below the critical curve  $\Gamma(\gamma_1, \gamma_2) = 0$ , then  $E_2^*$  remains stable, while above it  $E_2^*$  loses its stability.

(3) For example, take  $\theta = 0.2, d_1 = 0.7, d_2 = 0.9, \alpha = \beta = a_1 = 1, a_2 = 2$ , then system (1.3) has a unique interior equilibrium  $E_2^* = (0.7653, 0.0673, 0.0653)$ . Clearly,  $x_2^* > \frac{1}{2}(1 + \theta)$  and  $\frac{\alpha}{\beta} - \frac{a_2}{a_1} < 0$ . If we choose  $\gamma_1 = \gamma_2 = 5$ , then  $\Gamma(\gamma_1, \gamma_2) = 2.08 > 0$  and  $E_2^*$  is locally asymptotically stable according to Theorem 4.6 (see Fig. 1(a) and (b)). However, if we choose  $(\gamma_1, \gamma_2) = (7.2864296, 8)$ , which lies on the Hopf bifurcation curve  $\Gamma(\gamma_1, \gamma_2) = 0$ , then  $E_2^*$  loses its stability and system (1.3) has periodically oscillating solutions (see Fig. 1(c)).

From Theorems 4.5 and 4.6, the number of interior equilibria can be described by the signs of  $f(d_1), f(d_2)$  and  $f\left(\frac{1}{2}\left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)\right)$ , and the relative locations of  $d_1, d_2$  and  $\frac{1}{2}\left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)$ .

**Corollary 4.9.** Let  $0 < d_1 < d_2, d_1 < 1$ .

(i) If one of the following conditions is satisfied, then system (1.3) has no interior equilibrium:

- (a)  $f\left(\frac{1}{2}\left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)\right) > 0$ ;
- (b)  $f(d_1) < 0, f(d_2) < 0$ ;
- (c)  $f(d_1) > 0, f(d_2) > 0, f\left(\frac{1}{2}\left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)\right) < 0$  and  $f'(d_1)f'(d_2) > 0$  (i.e., either  $d_1 < d_2 < \frac{1}{2}\left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)$  or  $d_2 > d_1 > \frac{1}{2}\left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)$ ).

(ii) If  $f(d_1) > 0, f(d_2) < 0$ , then system (1.3) has a unique interior equilibrium  $E_1^* = (x_1^*, y_1^*, z_1^*)$  satisfying  $d_1 < x_1^* < d_2 < x_2^*$ .

- (iii) If  $f(d_1) < 0, f(d_2) > 0$ , then system (1.3) has a unique interior equilibrium  $E_2^* = (x_2^*, y_2^*, z_2^*)$  satisfying  $x_1^* < d_1 < x_2^* < d_2$ .
- (iv) If  $f(d_1) > 0, f(d_2) > 0$ ,  $f\left(\frac{1}{2}\left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)\right) < 0$  and  $d_1 < \frac{1}{2}\left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right) < d_2$  (i.e.,  $f'(d_1) f'(d_2) < 0$ ), then system (1.3) has two interior equilibria  $E_1^* = (x_1^*, y_1^*, z_1^*)$  and  $E_2^* = (x_2^*, y_2^*, z_2^*)$  satisfying  $d_1 < x_1^* < x_2^* < d_2$ .

Moreover, if  $E_1^*$  exists then it is always unstable; and if  $E_2^*$  exists then it is locally asymptotically stable if and only if  $x_2^* > \frac{1}{2}(1 + \theta)$  and  $\Gamma(\gamma_1, \gamma_2) > 0$ , where  $\Gamma(\gamma_1, \gamma_2)$  is defined in (4.6).

Denote  $\Delta(d_1, d_2) = \left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)^2 - 4\left(\theta + \frac{d_2\alpha}{a_2} - \frac{d_1\beta}{a_1}\right)$ . The following lemma can be easily verified.

**Lemma 4.10.** Let  $0 < d_1 < d_2, d_1 < 1$ .

- (i)  $f\left(\frac{1}{2}\left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)\right) > 0$  is equivalent to  $\Delta(d_1, d_2) < 0$ ;
- (ii)  $f(d_1) > 0$  is equivalent to  $d_2 > d_1 + \frac{a_2}{\alpha}(d_1 - \theta)(1 - d_1)$ ;
- (iii)  $f(d_2) > 0$  is equivalent to  $d_1 < d_2 - \frac{a_1}{\beta}(d_2 - \theta)(1 - d_2)$ .

Thus, Corollary 4.9 can be restated as follows.

**Corollary 4.11.** Let  $0 < d_1 < d_2, d_1 < 1$ .

- (i) If one of the following conditions is satisfied, then system (1.3) has no interior equilibrium.
  - (a)  $\Delta(d_1, d_2) < 0$ ;
  - (b)  $d_2 < d_1 + \frac{a_2}{\alpha}(d_1 - \theta)(1 - d_2), d_1 > d_2 - \frac{a_1}{\beta}(d_2 - \theta)(1 - d_2)$ ;
  - (c)  $d_2 > d_1 + \frac{a_2}{\alpha}(d_1 - \theta)(1 - d_2), d_1 < d_2 - \frac{a_1}{\beta}(d_2 - \theta)(1 - d_2), \Delta(d_1, d_2) > 0$ , and  $f'(d_1)f'(d_2) > 0$ .
- (ii) If  $d_2 > d_1 + \frac{a_2}{\alpha}(d_1 - \theta)(1 - d_2)$  and  $d_1 > d_2 - \frac{a_1}{\beta}(d_2 - \theta)(1 - d_2)$ , then system (1.3) has a unique interior equilibrium  $E_1^* = (x_1^*, y_1^*, z_1^*)$  satisfying  $d_1 < x_1^* < d_2 < x_2^*$ .
- (iii) If  $d_2 < d_1 + \frac{a_2}{\alpha}(d_1 - \theta)(1 - d_2)$  and  $d_1 < d_2 - \frac{a_1}{\beta}(d_2 - \theta)(1 - d_2)$ , then system (1.3) has a unique interior equilibrium  $E_2^* = (x_2^*, y_2^*, z_2^*)$  satisfying  $x_1^* < d_1 < x_2^* < d_2$ .
- (iv) If  $d_2 > d_1 + \frac{a_2}{\alpha}(d_1 - \theta)(1 - d_2), d_1 < d_2 - \frac{a_1}{\beta}(d_2 - \theta)(1 - d_2), \Delta(d_1, d_2) > 0$ , and  $f'(d_1)f'(d_2) < 0$ , then system (1.3) has two interior equilibria  $E_1^* = (x_1^*, y_1^*, z_1^*)$  and  $E_2^* = (x_2^*, y_2^*, z_2^*)$  satisfying  $d_1 < x_1^* < x_2^* < d_2$ .

Moreover, if  $E_1^*$  exists then it is always unstable; and if  $E_2^*$  exists then it is locally asymptotically stable if and only if  $x_2^* > \frac{1}{2}(1 + \theta)$  and  $\Gamma(\gamma_1, \gamma_2) > 0$ , where  $\Gamma(\gamma_1, \gamma_2)$  is defined in (4.6).

The above result shows the impact of  $(d_1, d_2)$  on the dynamics of system (1.3). See Fig. 2, in which we take  $\theta = 0.12, \alpha = 0.42, \beta = 0.88, a_1 = 1.5, a_2 = 1.1, \gamma_1 = \gamma_2 = 1$  and regard  $(d_1, d_2)$  as the bifurcation parameters.

**Remark 4.12.** Theorem 4.6 and Corollary 4.11, combined with Fig. 2, indicate the following implications:

(1) If  $E_1$  is locally asymptotically stable, then system (1.3) has no interior equilibrium and both  $E_2$  and  $E_3$  do not exist (see Fig. 2).

(2) If  $E_2$  is locally asymptotically stable, then system (1.3) has at most one interior equilibrium  $E_1^*$  which is unstable if it exists (see Fig. 2). This implies that the IG-prey goes extinct. In fact, since  $E_2$  is locally asymptotically stable, we know from Theorem 4.1 that

$$\frac{1}{2}(1 + \theta) < d_2 < 1, \quad d_1 > d_2 - \frac{a_1}{\beta}(d_2 - \theta)(1 - d_2),$$

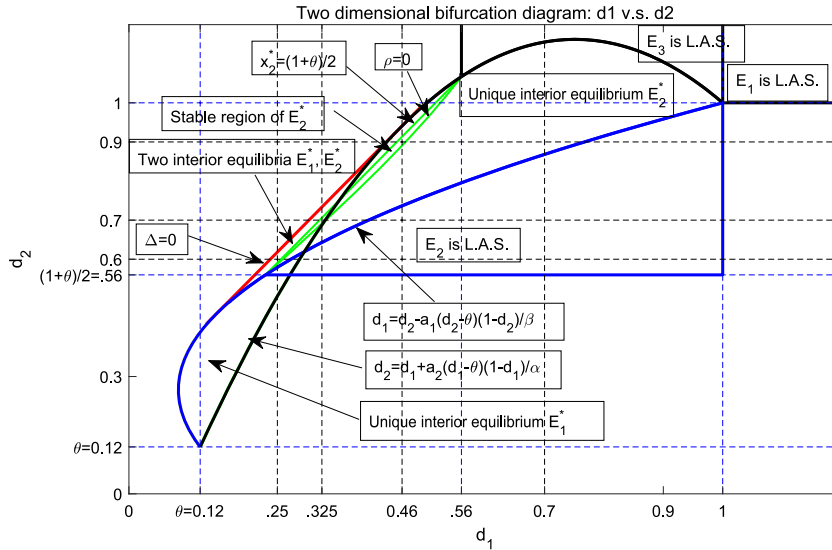


Fig. 2. Two-dimensional bifurcation diagram on the  $(d_1, d_2)$ -plane. Here  $\theta = 0.12, \alpha = 0.42, \beta = 0.88, a_1 = 1.5, a_2 = 1.1, \gamma_1 = \gamma_2 = 1$ .

which imply that  $f(d_2) < 0$ , where  $f(x)$  is defined by (4.1). Therefore, system (1.3) has at most one interior equilibrium  $E_1^*$  which is unstable if it exists by Theorem 4.6.

(3) If  $E_3$  is locally asymptotically stable, then from Theorem 4.1 we know that  $\frac{1}{2}(1 + \theta) < d_1 < 1$  and  $d_2 > d_1 + \frac{a_2}{\alpha}(d_1 - \theta)(1 - d_1)$ . It follows that  $f(d_1) > 0$  and system (1.3) may have no, one or two interior equilibria. More precisely, (a) if  $\frac{1}{2}(1 + \theta) < d_1 < 1$  and either  $\Delta < 0$  or  $f(d_1) > 0, f(d_2) > 0, f'(d_1)f'(d_2) > 0$ , then system (1.3) has no interior equilibrium; (b) if  $\frac{1}{2}(1 + \theta) < d_1 < 1$  and  $f(d_1) > 0 > f(d_2)$ , then system (1.3) has a unique interior equilibrium  $E_1^*$  which is unstable; (c) if  $\frac{1}{2}(1 + \theta) < d_1 < 1, \Delta > 0$  and  $f(d_1) > 0, f(d_2) > 0, f'(d_1)f'(d_2) < 0$ , then system (1.3) has two interior equilibria  $E_1^*$  and  $E_2^*$ . In this case,  $E_2^*$  must be locally asymptotically stable. In fact,  $E_3$  is locally asymptotically stable and  $E_1^*$  and  $E_2^*$  exist, we have

$$d_2 > x_2^* > \frac{1}{2} \left( 1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} \right) > x^* > d_1 > \frac{1}{2}(1 + \theta),$$

which implies that  $\frac{\alpha}{\beta} - \frac{a_2}{a_1} > 0$ , and hence  $\rho > 0$ . Therefore,  $E_2^*$  is locally asymptotically stable by Theorem 4.6. For example, we take parameters  $\theta = 0.1, d_1 = 0.7, d_2 = 0.95, a_1 = 4, a_2 = 1.35, \alpha = \beta = \gamma_1 = \gamma_2 = 1$ , then system (1.3) has two interior equilibria:

$$E_1^* = (0.7328, 0.1609, 0.0082), \quad E_2^* = (0.8579, 0.0682, 0.0395).$$

Clearly,  $0.55 = \frac{1}{2}(1 + \theta) < 0.7 = d_1 < 1$  and  $0.95 = d_2 > d_1 + \frac{a_2}{\alpha}(d_1 - \theta)(1 - d_1) = 0.943$ . By Theorem 4.1,  $E_3 = (0.7, 0.18, 0)$  is locally asymptotically stable. Since  $\frac{\alpha}{a_2} - \frac{\beta}{a_1} = 0.4907 > 0$ ,  $E_2^*$  is locally asymptotically stable by Theorem 4.6 (see Fig. 14).

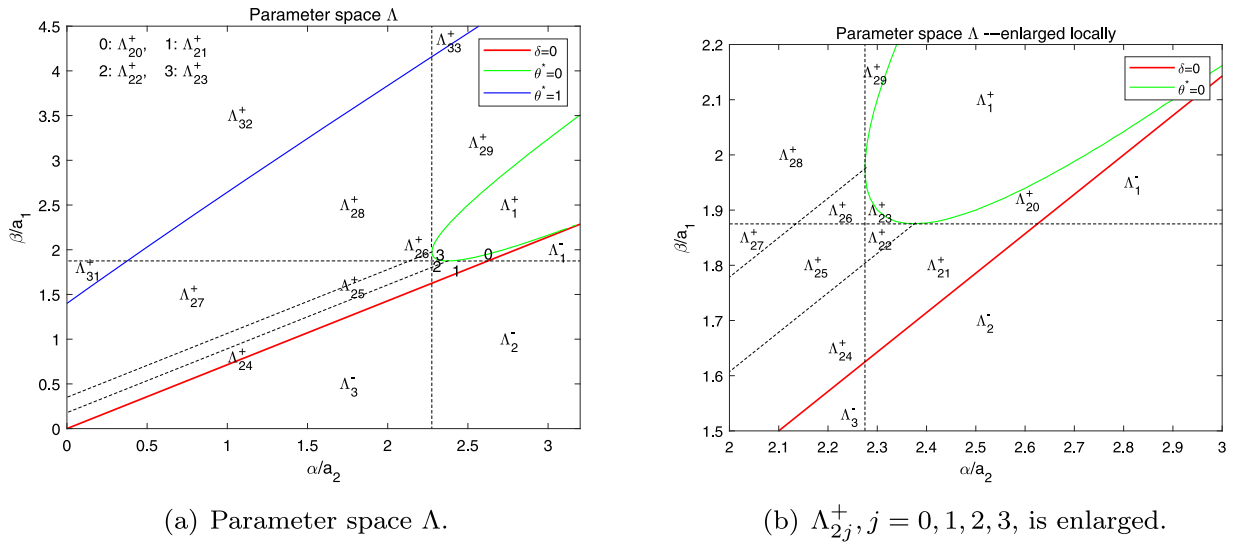
(4) From the above two last items, we see that if both  $E_2$  and  $E_3$  are locally asymptotically stable, then system (1.3) has a unique interior equilibrium  $E_1^*$ , which is unstable.

### 5. The impact of Allee effect

In this section, we focus on the impact of  $\theta$  on the dynamics of system (1.3). The discriminant  $\Delta$  defined by (4.3) of the quadratic polynomial  $f(x)$  in (4.1) is a function of  $\theta$ . We rewrite it as follows:

$$\Delta(\theta) = \theta^2 - 2 \left( 1 + \frac{\beta}{a_1} - \frac{\alpha}{a_2} \right) \theta + \left( 1 + \frac{\alpha}{a_2} - \frac{\beta}{a_1} \right)^2 - 4 \left( \frac{d_2 \alpha}{a_2} - \frac{d_1 \beta}{a_1} \right). \tag{5.1}$$





**Fig. 3.** (a) The parameter space  $\Lambda : \Lambda = \Lambda^- \cup \Lambda^+$ ,  $\Lambda^- = \bigsqcup_{j=1}^3 \Lambda_j^-$ ,  $\Lambda^+ = \bigsqcup_{j=1}^3 \Lambda_j^+$ ,  $\Lambda_2^+ = \bigsqcup_{j=0}^9 \Lambda_{2j}^+$ ,  $\Lambda_3^+ = \bigsqcup_{j=1}^3 \Lambda_{3j}^+$ . (b) The locally enlarged diagram for  $\Lambda_{2j}^+$ ,  $j = 0, 1, 2, 3$ . Here,  $d_1 = 0.65, d_2 = 0.75$ .

$\Delta(\theta) = 0$  has the discriminant

$$\delta = 16 \left( (1 - d_1) \frac{\beta}{a_1} - (1 - d_2) \frac{\alpha}{a_2} \right). \tag{5.2}$$

Denote  $\lambda = (\alpha, \beta, a_1, a_2, d_1, d_2)$ . Define the parameter space

$$\Lambda = \{ \lambda \in \mathbb{R}_+^6 : \alpha\beta a_1 a_2 > 0, 0 < d_1 < d_2, d_1 < 1 \}.$$

By the sign of  $\delta$ , we divide  $\Lambda$  into two regions (see Fig. 3):

$$\begin{aligned} \Lambda^- &= \left\{ \lambda \in \mathbb{R}_+^6 : \alpha\beta a_1 a_2 > 0, 0 < d_1 < d_2, d_1 < 1, (1 - d_1) \frac{\beta}{a_1} - (1 - d_2) \frac{\alpha}{a_2} \leq 0 \right\}, \\ \Lambda^+ &= \left\{ \lambda \in \mathbb{R}_+^6 : \alpha\beta a_1 a_2 > 0, 0 < d_1 < d_2, d_1 < 1, (1 - d_1) \frac{\beta}{a_1} - (1 - d_2) \frac{\alpha}{a_2} > 0 \right\}. \end{aligned}$$

The following statements are clear.

(1) If  $\lambda = (\alpha, \beta, a_1, a_2, d_1, d_2) \in \Lambda^-$ , then for each  $\theta \in \mathbb{R}$ ,  $\Delta(\theta) \geq 0$  and  $f(x)$  has two real roots  $x_1^* \leq x_2^*$  given by (4.4).

(2) If  $\lambda \in \Lambda^+$ , then  $\Delta(\theta) = 0$  has two different real roots  $\theta^* < \theta^{**}$  given by

$$\begin{aligned} \theta^* &= 1 + \frac{\beta}{a_1} - \frac{\alpha}{a_2} - \frac{\sqrt{\delta}}{2} = 1 + \frac{\beta}{a_1} - \frac{\alpha}{a_2} - 2\sqrt{(1 - d_1) \frac{\beta}{a_1} - (1 - d_2) \frac{\alpha}{a_2}}, \\ \theta^{**} &= 1 + \frac{\beta}{a_1} - \frac{\alpha}{a_2} + \frac{\sqrt{\delta}}{2} = 1 + \frac{\beta}{a_1} - \frac{\alpha}{a_2} + 2\sqrt{(1 - d_1) \frac{\beta}{a_1} - (1 - d_2) \frac{\alpha}{a_2}}. \end{aligned} \tag{5.3}$$

For  $\theta \in \mathbb{R} : \theta \leq \theta^*$  or  $\theta \geq \theta^{**}$ ,  $\Delta(\theta) \geq 0$  and  $f(x)$  has two real roots  $x_1^* \leq x_2^*$  (at  $\theta = \theta^*, \theta^{**}$ ,  $x_1^* = x_2^*$ ), while for  $\theta^* < \theta < \theta^{**}$ ,  $\Delta(\theta) < 0$  and  $f(x)$  has no real root.

The real roots of  $f(x) = 0$  can be regarded as functions of  $\theta$ . We rewrite  $x_1^*$  and  $x_2^*$  as follows:

$$x_{1,2}^*(\theta) = \frac{1}{2} \left( 1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} \pm \sqrt{\Delta(\theta)} \right), \tag{5.4}$$

where  $\Delta(\theta)$  is defined by (5.1). At  $\theta = 0, 1$ ,

$$\begin{aligned} x_{1,2}^*(0) &= \frac{1}{2} \left( 1 + \frac{\alpha}{a_2} - \frac{\beta}{a_1} \pm \sqrt{\left(1 + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)^2 - 4 \left(\frac{d_2\alpha}{a_2} - \frac{d_1\beta}{a_1}\right)} \right), \\ x_{1,2}^*(1) &= \frac{1}{2} \left( 2 + \frac{\alpha}{a_2} - \frac{\beta}{a_1} \pm \sqrt{\left(2 + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)^2 - 4 \left(1 + \frac{d_2\alpha}{a_2} - \frac{d_1\beta}{a_1}\right)} \right). \end{aligned} \quad (5.5)$$

In order to explore the impact of  $\theta$  on the dynamics of system (1.3), we consider the following two cases: (i)  $\lambda \in \Lambda^-$ , (ii)  $\lambda \in \Lambda^+$ .

### 5.1. The case $\lambda \in \Lambda^-$

**Lemma 5.1.** *Let  $\lambda \in \Lambda^-$ ,  $x_1^* = x_1^*(\theta)$  and  $x_2^* = x_2^*(\theta)$  be two different real roots of  $f(x) = 0$  for  $\theta \in (0, 1)$ . We have the following statements:*

- (i)  $x_2^*(\theta) \geq 1$  for all  $\theta \in (0, 1)$ , which indicates that system (1.3) has at most one unstable interior equilibrium  $E_1^*(x_1^*, y_1^*, z_1^*)$ ;
- (ii)  $x_1^*(\theta) \leq 1$  for all  $\theta \in (0, 1)$ ,  $x_1^*(0) > 0$  and  $x_1^*(1) > d_2$ ;
- (iii)  $x_1^*(\theta)$  is strictly increasing and concave on  $(0, 1)$ .

**Proof.**  $\lambda \in \Lambda^-$  implies  $0 < d_1 < d_2 < 1$  and  $\frac{d_2\alpha}{a_2} - \frac{d_1\beta}{a_1} \leq \frac{\alpha}{a_2} - \frac{\beta}{a_1}$ . Thus,

$$\Delta(\theta) \geq \left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)^2 - 4 \left(\theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right) = \left(1 - \left(\theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)\right)^2.$$

Then, for  $\theta \in (0, 1)$ , we have that if  $\theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} \leq 1$ ,

$$\begin{aligned} x_1^*(\theta) &= \frac{1}{2} \left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} - \sqrt{\Delta(\theta)}\right) \leq \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} \leq 1, \\ x_2^*(\theta) &= \frac{1}{2} \left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} + \sqrt{\Delta(\theta)}\right) \geq 1, \end{aligned}$$

and that if  $\theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} > 1$ ,  $x_1^*(\theta) < 1$ ,  $x_2^*(\theta) > \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} > 1$ .

By a direct computation, we get

$$\frac{d}{d\theta} x_1^*(\theta) = \frac{1}{\sqrt{\Delta(\theta)}} (1 - x_1^*(\theta)), \quad \frac{d^2}{d\theta^2} x_1^*(\theta) = \frac{2}{(\Delta(\theta))^{\frac{3}{2}}} (x_1^*(\theta) - 1)(x_2^*(\theta) - 1).$$

Therefore,  $x_1^*(\theta)$  is strictly increasing and concave on  $(0, 1)$ .

Since  $\frac{1-d_2}{1-d_1} \frac{\alpha}{a_2} - \frac{\beta}{a_1} \geq 0$ , we get  $\frac{\alpha}{a_2} - \frac{\beta}{a_1} > 0$ . Thus,

$$\frac{d_2\alpha}{a_2} - \frac{d_1\beta}{a_1} = d_1 \left(\frac{d_2}{d_1} \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right) > d_1 \left(\frac{\alpha}{a_2} - \frac{\beta}{a_1}\right) > 0.$$

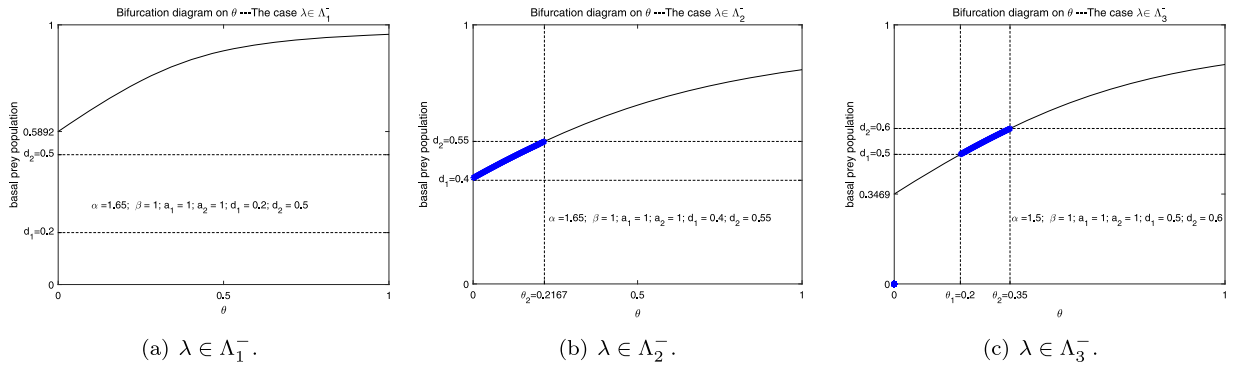
Therefore,  $x_1^*(0) > 0$ .

If  $x_1^*(1) \leq d_2$ , then by a direct computation, we have that  $(d_2 - d_1) \frac{\beta}{a_1} \leq -(1 - d_2)^2 < 0$ , which is impossible. Therefore,  $x_1^*(1) > d_2$ . The proof is complete.  $\square$

By Lemma 5.1, we divide  $\Lambda^-$  into three different regions

$$\begin{aligned} \Lambda_1^- &= \{\lambda \in \Lambda^- : d_1 < d_2 \leq x_1^*(0)\}, & \Lambda_2^- &= \{\lambda \in \Lambda^- : d_1 \leq x_1^*(0) < d_2\}, \\ \Lambda_3^- &= \{\lambda \in \Lambda^- : x_1^*(0) < d_1 < d_2\}. \end{aligned}$$

It is clear that  $\Lambda^- = \Lambda_1^- \cup \Lambda_2^- \cup \Lambda_3^-$  (see Fig. 3).



**Fig. 4.** Bifurcation diagrams on  $\theta$  in the case  $\lambda \in \Lambda^-$ . Here,  $\gamma_1 = 1, \gamma_2 = 1$ . Blue segment shows the interior equilibrium  $E_1^*$ . (a)  $\lambda \in \Lambda_1^-$  and no interior equilibrium for all  $\theta \in (0, 1)$ ; (b)  $\lambda \in \Lambda_2^-$  and there is a unique unstable interior equilibrium  $E_1^*$  for  $\theta \in (0, \theta_2)$ , and no interior equilibrium for  $\theta \in [\theta_2, 1)$ ,  $\theta_2 = 0.2167$ ; (c) There is no interior equilibrium for  $\theta \in (0, \theta_1] \cup [\theta_2, 1)$  and a unique unstable interior equilibrium  $E_1^*$  for  $\theta \in (\theta_1, \theta_2)$ ,  $\theta_1 = 0.2, \theta_2 = 0.35$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

We also have the following lemma.

**Lemma 5.2.**

- (i) If there exists  $\theta \in \mathbb{R}$ , denoted by  $\theta_1$ , such that  $d_1 = x_1^*(\theta)$  or  $d_1 = x_2^*(\theta)$ , then  $\theta_1 = d_1 - \frac{\alpha}{a_2} \frac{d_2 - d_1}{1 - d_1}$ .
- (ii) If there exists  $\theta \in \mathbb{R}$ , denoted by  $\theta_2$ , such that  $d_2 = x_1^*(\theta)$  or  $d_2 = x_2^*(\theta)$ , then  $\theta_2 = d_2 - \frac{\beta}{a_1} \frac{d_2 - d_1}{1 - d_2}$ .

Now, by Theorems 4.5 and 4.6 and Lemmas 5.1 and 5.2, for the case  $\lambda \in \Lambda^-$ , we show the impact of Allee threshold  $\theta$  on the dynamics of system (1.3) as follows.

**Theorem 5.3.** Let  $\lambda \in \Lambda^-$ ,  $x_1^* = x_1^*(\theta)$  and  $x_2^* = x_2^*(\theta)$  be two different real roots of  $f(x) = 0$  for  $\theta \in (0, 1)$ .  $\theta_1$  and  $\theta_2$  are given in Lemma 5.2.

- (i) If  $\lambda \in \Lambda_1^-$ , then system (1.3) has no interior equilibrium for all  $\theta \in (0, 1)$  (see Fig. 4(a)).
- (ii) If  $\lambda \in \Lambda_2^-$ , then system (1.3) has a unique unstable interior equilibrium  $E_1^*(x_1^*, y_1^*, z_1^*)$  for  $\theta \in (0, \theta_2)$ , while no interior equilibrium for  $\theta \in [\theta_2, 1)$  (see Fig. 4(b)).
- (iii) If  $\lambda \in \Lambda_3^-$ , then system (1.3) has no interior equilibrium for  $\theta \in (0, \theta_1] \cup [\theta_2, 1)$ , while it has a unique unstable interior equilibrium  $E_1^*(x_1^*, y_1^*, z_1^*)$  for  $\theta \in (\theta_1, \theta_2)$  (see Fig. 4(c)).

**Proof.** We only show the proof of (iii). Let  $\lambda \in \Lambda_3^-$ . From Lemma 5.1, we know that system (1.3) has at most one unstable interior equilibrium  $E_1^*(x_1^*, y_1^*, z_1^*)$ , and  $x_1^*(0) < d_1 < d_2 < x_1^*(1)$ . Also, from Lemma 5.1, we know that  $x_1^*(\theta)$  is strictly increasing and concave on  $(0, 1)$ . Thus, there exists a unique  $\theta_1 \in (0, 1)$  such that  $d_1 = x_1^*(\theta)$ . Also, there exists a unique  $\theta_2 \in (0, 1)$  such that  $d_2 = x_1^*(\theta)$ . By Lemma 5.2,  $\theta_1 = d_1 - \frac{\alpha}{a_2} \frac{d_2 - d_1}{1 - d_1}$ ,  $\theta_2 = d_2 - \frac{\beta}{a_1} \frac{d_2 - d_1}{1 - d_2}$ .

Clearly,  $\theta_1 < \theta_2$ . By the monotonic property of  $x_1^*(\theta)$ , we have that if  $\theta \in (0, \theta_1]$ , then  $d_1 \geq x_1^*(\theta)$ . If  $\theta \in [\theta_2, 1)$ , then  $d_2 \leq x_1^*(\theta)$ . Therefore, by Theorem 4.5, system (1.3) has no interior equilibrium for  $\theta \in (0, \theta_1] \cup [\theta_2, 1)$ . If  $\theta \in (\theta_1, \theta_2)$ , then  $d_1 < x_1^*(\theta) < d_2$ , and hence system (1.3) has a unique unstable interior equilibrium  $E_1^*(x_1^*, y_1^*, z_1^*)$  by Theorem 4.6.  $\square$

### 5.2. The case $\lambda \in \Lambda^+$

Now let  $\lambda \in \Lambda^+$ . In this case the equation  $\Delta(\theta) = 0$  has two real roots  $\theta^* < \theta^{**}$  given by (5.3). If  $\theta \leq \theta^*$  or  $\theta \geq \theta^{**}$ , then  $\Delta(\theta) \geq 0$  and  $f(x) = 0$  has two real roots  $x_1^* \leq x_2^*$ , which is given by (4.4), and has no real root if  $\theta^* < \theta < \theta^{**}$ .

We divide  $\Lambda^+$  into three regions (see Fig. 3)

$$\Lambda_1^+ = \{\lambda \in \Lambda^+ : \theta^* \leq 0\}, \quad \Lambda_2^+ = \{\lambda \in \Lambda^+ : 0 < \theta^* < 1\}, \quad \Lambda_3^+ = \{\lambda \in \Lambda^+ : \theta^* \geq 1\}.$$

If  $\lambda \in \Lambda_1^+$ , we have the following result, which implies that system (1.3) has no interior equilibrium for all  $\theta \in (0, 1)$ .

**Theorem 5.4.** *Let  $\lambda \in \Lambda^+$ ,  $\theta^*$  and  $\theta^{**}$  be two real roots of  $\Delta(\theta) = 0$  given by (5.3). Let  $x_1^* = x_1^*(\theta)$  and  $x_2^* = x_2^*(\theta)$  be two real roots of  $f(x) = 0$  for  $\theta \in \mathbb{R} : \theta \leq \theta^*$  or  $\theta \geq \theta^{**}$ .*

- (i) *If  $\theta \geq \theta^{**}$ ,  $\theta \in \mathbb{R}_+$ , then  $x_1^*(\theta) > 1$ ;*
- (ii) *If  $\theta^* < 1$ , then for  $\theta \in (\theta^*, 1)$ , system (1.3) has no interior equilibrium. Especially, if  $\lambda \in \Lambda_1^+$ , then for all  $\theta \in (0, 1)$ , system (1.3) has no interior equilibrium.*

**Proof.** By  $\theta \geq \theta^{**}$ , we have  $\theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} \geq 1$ . Since  $(1 - d_1)\frac{\beta}{a_1} - (1 - d_2)\frac{\alpha}{a_2} > 0$  is equivalent to  $\frac{d_2\alpha}{a_2} - \frac{d_1\beta}{a_1} > \frac{\alpha}{a_2} - \frac{\beta}{a_1}$ , we have

$$\Delta(\theta) < \left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)^2 - 4\left(\theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right) = \left(1 - \left(\theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)\right)^2.$$

Thus,  $x_1^* = \frac{1}{2}\left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} - \sqrt{\Delta}\right) > 1$ . The second result is clear since  $f(x) = 0$  has no real root if  $\theta^* < \theta < \theta^{**}$  and  $x_1^*(\theta) > 1$  for  $\theta \in \mathbb{R}_+ : \theta \geq \theta^{**}$ .  $\square$

We consider the case  $\lambda \in \Lambda_2^+$ . First, we have the following lemma.

**Lemma 5.5.** *Let  $\lambda \in \Lambda^+$  and  $\theta^* > 0$ . Let  $x_1^*(\theta)$  and  $x_2^*(\theta)$  be two real roots of  $f(x) = 0$  for  $\theta \in (0, \theta^*)$ . Then  $x_1^*(\theta)$  and  $x_2^*(\theta)$  have the following properties:*

- (i)  *$x_1^*(\theta) < x_2^*(\theta) < 1$  in  $(0, \theta^*)$ . In particular,  $x_2^*(0) < 1$ ;*
- (ii)  *$x_1^*(\theta)$  is strictly increasing and convex on  $(0, \theta^*)$ ;*
- (iii)  *$x_2^*(\theta)$  is strictly decreasing and concave on  $(0, \theta^*)$ ;*
- (iv) *At  $\theta = \theta^*$ ,  $x_1^*(\theta) = x_2^*(\theta) = 1 - \frac{\sqrt{\delta}}{4}$ , where  $\delta$  is given in (5.2).*

**Proof.** It is clear that  $x_1^*(\theta) = x_2^*(\theta) = 1 - \frac{\sqrt{\delta}}{4}$  at  $\theta = \theta^*$ . Similar to the proof of Theorem 5.4(i), we can show that  $x_1^*(\theta) < x_2^*(\theta) < 1$ ,  $\theta \in (0, \theta^*)$ . In fact, by  $\theta \leq \theta^*$ , we have  $\theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} < 1$ . Since  $(1 - d_1)\frac{\beta}{a_1} - (1 - d_2)\frac{\alpha}{a_2} > 0$  is equivalent to  $\frac{d_2\alpha}{a_2} - \frac{d_1\beta}{a_1} > \frac{\alpha}{a_2} - \frac{\beta}{a_1}$ , we have  $\Delta(\theta) < \left(1 - \left(\theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)\right)^2$ . Thus,

$$x_1^*(\theta) < x_2^*(\theta) = \frac{1}{2}\left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} + \sqrt{\Delta(\theta)}\right) < 1.$$

By a direct computation, we get

$$\begin{aligned} \frac{d}{d\theta}x_1^*(\theta) &= \frac{1}{\sqrt{\Delta(\theta)}}(1 - x_1^*(\theta)), & \frac{d}{d\theta}x_2^*(\theta) &= \frac{1}{\sqrt{\Delta(\theta)}}(x_2^*(\theta) - 1), \\ \frac{d^2}{d\theta^2}x_1^*(\theta) &= \frac{2}{(\Delta(\theta))^{\frac{3}{2}}}(x_1^*(\theta) - 1)(x_2^*(\theta) - 1), & \frac{d^2}{d\theta^2}x_2^*(\theta) &= \frac{2}{(\Delta(\theta))^{\frac{3}{2}}}(1 - x_1^*(\theta))(x_2^*(\theta) - 1). \end{aligned}$$

Therefore,  $x_1^*(\theta)$  is strictly increasing and convex on  $(0, \theta^*)$ , and  $x_2^*(\theta)$  is strictly decreasing and concave on  $(0, \theta^*)$ .  $\square$

By Lemma 5.5, we divide  $\Lambda_2^+$  into the following ten different regions by the relative positions of  $x_1^*(0), x_2^*(0), 1 - \frac{\sqrt{\delta}}{4}, d_1$  and  $d_2$  (see Fig. 3).

$$\begin{aligned} \Lambda_{20}^+ &= \left\{ \lambda \in \Lambda_2^+ : d_1 < d_2 \leq x_1^*(0) < 1 - \frac{\sqrt{\delta}}{4} \right\}, \\ \Lambda_{21}^+ &= \left\{ \lambda \in \Lambda_2^+ : d_1 \leq x_1^*(0) < d_2 \leq 1 - \frac{\sqrt{\delta}}{4} \right\}, \\ \Lambda_{22}^+ &= \left\{ \lambda \in \Lambda_2^+ : d_1 \leq x_1^*(0) < 1 - \frac{\sqrt{\delta}}{4} < d_2 < x_2^*(0) \right\}, \\ \Lambda_{23}^+ &= \left\{ \lambda \in \Lambda_2^+ : d_1 \leq x_1^*(0) < 1 - \frac{\sqrt{\delta}}{4} < x_2^*(0) \leq d_2 \right\}, \\ \Lambda_{24}^+ &= \left\{ \lambda \in \Lambda_2^+ : x_1^*(0) < d_1 < d_2 \leq 1 - \frac{\sqrt{\delta}}{4} \right\}, \\ \Lambda_{25}^+ &= \left\{ \lambda \in \Lambda_2^+ : x_1^*(0) < d_1 < 1 - \frac{\sqrt{\delta}}{4} < d_2 < x_2^*(0) \right\}, \\ \Lambda_{26}^+ &= \left\{ \lambda \in \Lambda_2^+ : x_1^*(0) < d_1 < 1 - \frac{\sqrt{\delta}}{4} < x_2^*(0) \leq d_2 \right\}, \\ \Lambda_{27}^+ &= \left\{ \lambda \in \Lambda_2^+ : 1 - \frac{\sqrt{\delta}}{4} \leq d_1 < d_2 < x_2^*(0) \right\}, \\ \Lambda_{28}^+ &= \left\{ \lambda \in \Lambda_2^+ : 1 - \frac{\sqrt{\delta}}{4} \leq d_1 < x_2^*(0) \leq d_2 \right\}, \\ \Lambda_{29}^+ &= \left\{ \lambda \in \Lambda_2^+ : d_2 > d_1 \geq x_2^*(0) > 1 - \frac{\sqrt{\delta}}{4} \right\}. \end{aligned}$$

Now, by Theorems 4.5 and 4.6 and Lemmas 5.2 and 5.5, for the case  $\lambda \in \Lambda_2^+$  we show the impact of Allee threshold  $\theta$  on the dynamics of system (1.3) as follows.

**Theorem 5.6.** *Let  $\lambda \in \Lambda_2^+$ ,  $x_1^*(\theta)$  and  $x_2^*(\theta)$  be two real roots of  $f(x) = 0$  for  $\theta \in (0, \theta^*)$ ,  $\theta_1$  and  $\theta_2$  be given in Lemma 5.2.*

- (i) *If  $\lambda \in \Lambda_{20}^+$ , then for all  $\theta \in (0, 1)$ , system (1.3) has no interior equilibrium (see Fig. 5(a)).*
- (ii) *If  $\lambda \in \Lambda_{21}^+$ , then system (1.3) has a unique interior equilibrium  $E_1^*(x_1^*, y_1^*, z_1^*)$  for  $\theta \in (0, \theta_2)$ , and no interior equilibrium for  $\theta \in [\theta_2, 1)$  (see Fig. 5(b)).*
- (iii) *If  $\lambda \in \Lambda_{22}^+$ , then system (1.3) has a unique interior equilibrium  $E_1^*(x_1^*, y_1^*, z_1^*)$  for  $\theta \in (0, \theta_2]$ , two interior equilibria  $E_1^*(x_1^*, y_1^*, z_1^*)$  and  $E_2^*(x_2^*, y_2^*, z_2^*)$  for  $\theta \in (\theta_2, \theta^*)$ , and no interior equilibrium for  $\theta \in (\theta^*, 1)$  (see Fig. 5(c)).*
- (iv) *If  $\lambda \in \Lambda_{23}^+$ , then system (1.3) has two interior equilibria  $E_1^*(x_1^*, y_1^*, z_1^*)$  and  $E_2^*(x_2^*, y_2^*, z_2^*)$  for  $\theta \in (0, \theta^*)$ , and no interior equilibrium for  $\theta \in (\theta^*, 1)$  (see Fig. 5(d)).*
- (v) *If  $\lambda \in \Lambda_{24}^+$ , then system (1.3) has no interior equilibrium for  $\theta \in (0, \theta_1] \cup [\theta_2, 1)$ , and a unique interior equilibrium  $E_1^*(x_1^*, y_1^*, z_1^*)$  for  $\theta \in (\theta_1, \theta_2)$  (see Fig. 5(e)).*
- (vi) *Let  $\lambda \in \Lambda_{25}^+$ .*
  - (a) *If  $\theta_1 > \theta_2$ , then system (1.3) has no interior equilibrium for  $\theta \in (0, \theta_2] \cup (\theta^*, 1)$ , a unique interior equilibrium  $E_2^*(x_2^*, y_2^*, z_2^*)$  for  $\theta \in (\theta_2, \theta_1]$ , two interior equilibria  $E_1^*(x_1^*, y_1^*, z_1^*)$  and  $E_2^*(x_2^*, y_2^*, z_2^*)$  for  $\theta \in (\theta_1, \theta^*)$  (see Fig. 5(f));*
  - (b) *If  $\theta_1 < \theta_2$ , then system (1.3) has no interior equilibrium for  $\theta \in (0, \theta_1] \cup (\theta^*, 1)$ , a unique interior equilibrium  $E_1^*(x_1^*, y_1^*, z_1^*)$  for  $\theta \in (\theta_1, \theta_2]$ , two interior equilibria  $E_1^*(x_1^*, y_1^*, z_1^*)$  and  $E_2^*(x_2^*, y_2^*, z_2^*)$  for  $\theta \in (\theta_2, \theta^*)$  (see Fig. 5(g));*
  - (c) *If  $\theta_1 = \theta_2$ , then system (1.3) has no interior equilibrium for  $\theta \in (0, \theta_1] \cup (\theta^*, 1)$ , and two interior equilibria  $E_1^*(x_1^*, y_1^*, z_1^*)$  and  $E_2^*(x_2^*, y_2^*, z_2^*)$  for  $\theta \in (\theta_1, \theta^*)$  (see Fig. 5(h)).*
- (vii) *If  $\lambda \in \Lambda_{26}^+$ , then system (1.3) has a unique interior equilibrium  $E_2^*(x_2^*, y_2^*, z_2^*)$  for  $\theta \in (0, \theta_1]$ , two interior equilibria  $E_1^*(x_1^*, y_1^*, z_1^*)$  and  $E_2^*(x_2^*, y_2^*, z_2^*)$  for  $\theta \in (\theta_1, \theta^*)$ , and no interior equilibrium for  $\theta \in (\theta^*, 1)$  (see Fig. 5(i)).*

(viii) If  $\lambda \in \Lambda_{27}^+$ , then system (1.3) has no interior equilibrium for  $\theta \in (0, \theta_2] \cup [\theta_1, 1)$ , and a unique interior equilibrium  $E_2^*(x_2^*, y_2^*, z_2^*)$  for  $\theta \in (\theta_2, \theta_1)$  (see Fig. 5(j)).

(ix) If  $\lambda \in \Lambda_{28}^+$ , then system (1.3) has a unique interior equilibrium  $E_2^*(x_2^*, y_2^*, z_2^*)$  for  $\theta \in (0, \theta_1)$ , and no interior equilibrium for  $\theta \in [\theta_1, 1)$  (see Fig. 5(k)).

(x) If  $\lambda \in \Lambda_{29}^+$ , then for all  $\theta \in (0, 1)$ , system (1.3) has no interior equilibrium (see Fig. 5(l)).

Moreover, if  $E_1^*$  exists then it is always unstable; if  $E_2^*$  exists then it is locally asymptotically stable if and only if  $x_2^* > \frac{1}{2}(1 + \theta)$  and  $\Gamma(\gamma_1, \gamma_2) > 0$ ; and system (1.3) undergoes a Hopf bifurcation at  $E_2^*$  on the curve  $\Gamma(\gamma_1, \gamma_2) = 0$ , where  $\Gamma(\gamma_1, \gamma_2)$  is defined in (4.6).

**Proof.** We only show the proof of the case (vi-a)  $\lambda \in \Lambda_{25}^+$  and  $\theta_1 > \theta_2$ . Since  $\lambda \in \Lambda_{25}^+$ , we have  $0 < \theta^* < 1$  and

$$x_1^*(0) < d_1 < 1 - \frac{\sqrt{\delta}}{4} < d_2 < x_2^*(0) < 1.$$

By Lemma 5.5, we know that on  $(0, \theta^*)$ ,  $x_1^*(\theta)$  is strictly increasing and convex, while  $x_2^*(\theta)$  is strictly decreasing and concave. At  $\theta = \theta^*$ ,  $x_1^*(\theta)$  and  $x_2^*(\theta)$  intersect each other, i.e.,  $1 - \frac{\sqrt{\delta}}{4} = x_1^*(\theta^*) = x_2^*(\theta^*)$ . Thus, there exists a unique  $\theta_1 \in (0, \theta^*)$  such that  $d_1 = x_1^*(\theta_1)$ . Also, there exists a unique  $\theta_2 \in (0, \theta^*)$  such that  $d_2 = x_2^*(\theta_2)$ . By Lemma 5.2,  $\theta_1 = d_1 - \frac{\alpha}{a_2} \frac{d_2 - d_1}{1 - d_1}$ ,  $\theta_2 = d_2 - \frac{\beta}{a_1} \frac{d_2 - d_1}{1 - d_2}$ .

Since  $\theta_1 > \theta_2$ , by the monotonic properties of  $x_1^*(\theta)$  and  $x_2^*(\theta)$ , we have that

- if  $\theta \in (0, \theta_2]$ , then  $x_1^*(\theta) \leq d_1 < d_2$  and  $x_2^*(\theta) \geq d_2 > d_1$ . By Theorem 4.5, system (1.3) has no interior equilibrium;
- if  $\theta \in (\theta^*, 1)$ , then by Theorem 5.4 system (1.3) has no interior equilibrium;
- if  $\theta \in (\theta_2, \theta_1]$ , then  $x_1^*(\theta) \leq d_1 < x_2^*(\theta) < d_2$ . By Theorem 4.6, system (1.3) has a unique interior equilibrium  $E_2^*(x_2^*, y_2^*, z_2^*)$ ;
- if  $\theta \in (\theta_1, \theta^*)$ , then  $d_1 < x_1^*(\theta) \leq x_2^*(\theta) < d_2$ . By Theorem 4.6, system (1.3) has two interior equilibria  $E_1^*(x_1^*, y_1^*, z_1^*)$  and  $E_2^*(x_2^*, y_2^*, z_2^*)$ .

By Theorem 4.6, if  $E_1^*$  exists then it is always unstable; if  $E_2^*$  exists then it is locally asymptotically stable if and only if  $x_2^* > \frac{1}{2}(1 + \theta)$  and  $\Gamma(\gamma_1, \gamma_2) > 0$ ; and the model undergoes a Hopf bifurcation at  $E_2^*$  on the curve  $\Gamma(\gamma_1, \gamma_2) = 0$ . The proof is complete.  $\square$

For the case  $\lambda \in \Lambda_3^+$ , we first have the following lemma.

**Lemma 5.7.** Let  $\lambda \in \Lambda_3^+$ , i.e.,  $\theta^* \geq 1$ ,  $x_1^*(\theta)$  and  $x_2^*(\theta)$  be two real roots of  $f(x) = 0$  for  $\theta \in (0, \theta^*)$ . Then  $x_1^*(0) < 0$  and  $d_2 > d_1 > x_2^*(1)$ .

By Lemmas 5.5 and 5.7, we divide the parameter space  $\Lambda_3^+$  into the following three different regions (see Fig. 3).

$$\begin{aligned} \Lambda_{31}^+ &= \{ \lambda \in \Lambda_3^+ : 0 < d_1 < d_2 < x_2^*(0) \}, \quad \Lambda_{32}^+ = \{ \lambda \in \Lambda_3^+ : 0 < d_1 < x_2^*(0) \leq d_2 \}, \\ \Lambda_{33}^+ &= \{ \lambda \in \Lambda_3^+ : d_2 > d_1 \geq x_2^*(0) \}. \end{aligned}$$

Thus, we have the following result.

**Theorem 5.8.** Let  $\lambda \in \Lambda_3^+$ , i.e.,  $\theta^* \geq 1$ ,  $x_1^*(\theta)$  and  $x_2^*(\theta)$  be two real roots of  $f(x) = 0$  for  $\theta \in (0, \theta^*)$ .

- (i) If  $\lambda \in \Lambda_{31}^+$ , then system (1.3) has no interior equilibrium for  $\theta \in (0, \theta_2] \cup [\theta_1, 1)$ , and a unique interior equilibrium  $E_2^*(x_2^*, y_2^*, z_2^*)$  for  $\theta \in (\theta_2, \theta_1)$  (see Fig. 6(a)).
- (ii) If  $\lambda \in \Lambda_{32}^+$ , then system (1.3) has a unique interior equilibrium  $E_2^*(x_2^*, y_2^*, z_2^*)$  for  $\theta \in (0, \theta_1)$ , and no interior equilibrium for  $\theta \in [\theta_1, 1)$  (see Fig. 6(b)).
- (iii) If  $\lambda \in \Lambda_{33}^+$ , then for all  $\theta \in (0, 1)$ , system (1.3) has no interior equilibrium (see Fig. 6(c)).

Moreover, if  $E_2^*$  exists then it is locally asymptotically stable if and only if  $x_2^* > \frac{1}{2}(1 + \theta)$  and  $\Gamma(\gamma_1, \gamma_2) > 0$ ; and system (1.3) undergoes a Hopf bifurcation at  $E_2^*$  on the curve  $\Gamma(\gamma_1, \gamma_2) = 0$ , where  $\Gamma(\gamma_1, \gamma_2)$  is given by (4.6).

**Remark 5.9.** For convenience, denote  $L(\lambda) = (1 - d_1)\frac{\beta}{a_1} - (1 - d_2)\frac{\alpha}{a_2}$ . The following statements are easy to check:

- (1)  $x_1^*(0) - d_2 > 0(= 0)$  is equivalent to  $d_2 - \frac{\beta}{a_1} \frac{d_2 - d_1}{1 - d_2} < 0(= 0, \text{ resp.})$ ;
- (2)  $x_1^*(0) - d_1 > 0(= 0)$  is equivalent to  $d_1 - \frac{\alpha}{a_2} \frac{d_2 - d_1}{1 - d_1} < 0(= 0, \text{ resp.})$ ;
- (3)  $x_2^*(0) - d_2 > 0(= 0)$  is equivalent to  $\frac{\beta}{a_1} - \frac{d_2(1 - d_2)}{d_2 - d_1} < 0(= 0, \text{ resp.})$ ;
- (4)  $x_2^*(0) - d_1 > 0(= 0)$  is equivalent to  $\frac{\alpha}{a_2} - \frac{d_1(1 - d_1)}{d_2 - d_1} < 0(= 0, \text{ resp.})$ ;
- (5)  $1 - \frac{\sqrt{\delta}}{4} - d_2 > 0(= 0)$  is equivalent to  $L(\lambda) - (1 - d_2)^2 < 0(= 0, \text{ resp.})$ ;
- (6)  $1 - \frac{\sqrt{\delta}}{4} - d_1 > 0(= 0)$  is equivalent to  $L(\lambda) - (1 - d_1)^2 < 0(= 0, \text{ resp.})$ .

Thus,  $A_1^-, A_2^-$  and  $A_3^-$  can be rewritten equivalently as the following forms:

$$A_1^- = \left\{ \lambda \in A^- : \frac{\beta}{a_1} \geq \frac{d_2(1 - d_2)}{d_2 - d_1} \right\}, \quad A_2^- = \left\{ \lambda \in A^- : \frac{\beta}{a_1} < \frac{d_2(1 - d_2)}{d_2 - d_1}, \frac{\alpha}{a_2} \geq \frac{d_1(1 - d_1)}{d_2 - d_1} \right\},$$

$$A_3^- = \left\{ \lambda \in A^- : \frac{\alpha}{a_2} < \frac{d_1(1 - d_1)}{d_2 - d_1} \right\}.$$

$A_{2j}^+, j = 0, 1, \dots, 9$ , can be rewritten equivalently as the following forms:

$$A_{20}^+ = \left\{ \lambda \in A_2^+ : \frac{\beta}{a_1} > \frac{d_2(1 - d_2)}{d_2 - d_1}, L(\lambda) < (1 - d_2)^2 \right\},$$

$$A_{21}^+ = \left\{ \lambda \in A_2^+ : \frac{\alpha}{a_2} \geq \frac{d_1(1 - d_1)}{d_2 - d_1}, \frac{\beta}{a_1} < \frac{d_2(1 - d_2)}{d_2 - d_1}, L(\lambda) \leq (1 - d_2)^2 \right\},$$

$$A_{22}^+ = \left\{ \lambda \in A_2^+ : \frac{\alpha}{a_2} \geq \frac{d_1(1 - d_1)}{d_2 - d_1}, \frac{\beta}{a_1} < \frac{d_2(1 - d_2)}{d_2 - d_1}, L(\lambda) > (1 - d_2)^2 \right\},$$

$$A_{23}^+ = \left\{ \lambda \in A_2^+ : \frac{\alpha}{a_2} \geq \frac{d_1(1 - d_1)}{d_2 - d_1}, \frac{\beta}{a_1} \geq \frac{d_2(1 - d_2)}{d_2 - d_1}, (1 - d_2)^2 < L(\lambda) < (1 - d_1)^2 \right\},$$

$$A_{24}^+ = \left\{ \lambda \in A_2^+ : \frac{\alpha}{a_2} < \frac{d_1(1 - d_1)}{d_2 - d_1}, L(\lambda) \leq (1 - d_2)^2 \right\},$$

$$A_{25}^+ = \left\{ \lambda \in A_2^+ : \frac{\alpha}{a_2} < \frac{d_1(1 - d_1)}{d_2 - d_1}, \frac{\beta}{a_1} < \frac{d_2(1 - d_2)}{d_2 - d_1}, (1 - d_2)^2 < L(\lambda) < (1 - d_1)^2 \right\},$$

$$A_{26}^+ = \left\{ \lambda \in A_2^+ : \frac{\alpha}{a_2} < \frac{d_1(1 - d_1)}{d_2 - d_1}, \frac{\beta}{a_1} > \frac{d_2(1 - d_2)}{d_2 - d_1}, L(\lambda) < (1 - d_1)^2 \right\},$$

$$A_{27}^+ = \left\{ \lambda \in A_2^+ : \frac{\beta}{a_1} < \frac{d_2(1 - d_2)}{d_2 - d_1}, L(\lambda) \geq (1 - d_1)^2 \right\},$$

$$A_{28}^+ = \left\{ \lambda \in A_2^+ : \frac{\alpha}{a_2} < \frac{d_1(1 - d_1)}{d_2 - d_1}, \frac{\beta}{a_1} \geq \frac{d_2(1 - d_2)}{d_2 - d_1}, L(\lambda) \geq (1 - d_1)^2 \right\},$$

$$A_{29}^+ = \left\{ \lambda \in A_2^+ : \frac{\alpha}{a_2} \geq \frac{d_1(1 - d_1)}{d_2 - d_1}, L(\lambda) > (1 - d_1)^2 \right\},$$

and  $A_{3j}^+, j = 1, 2, 3$ , can be rewritten as the follows:

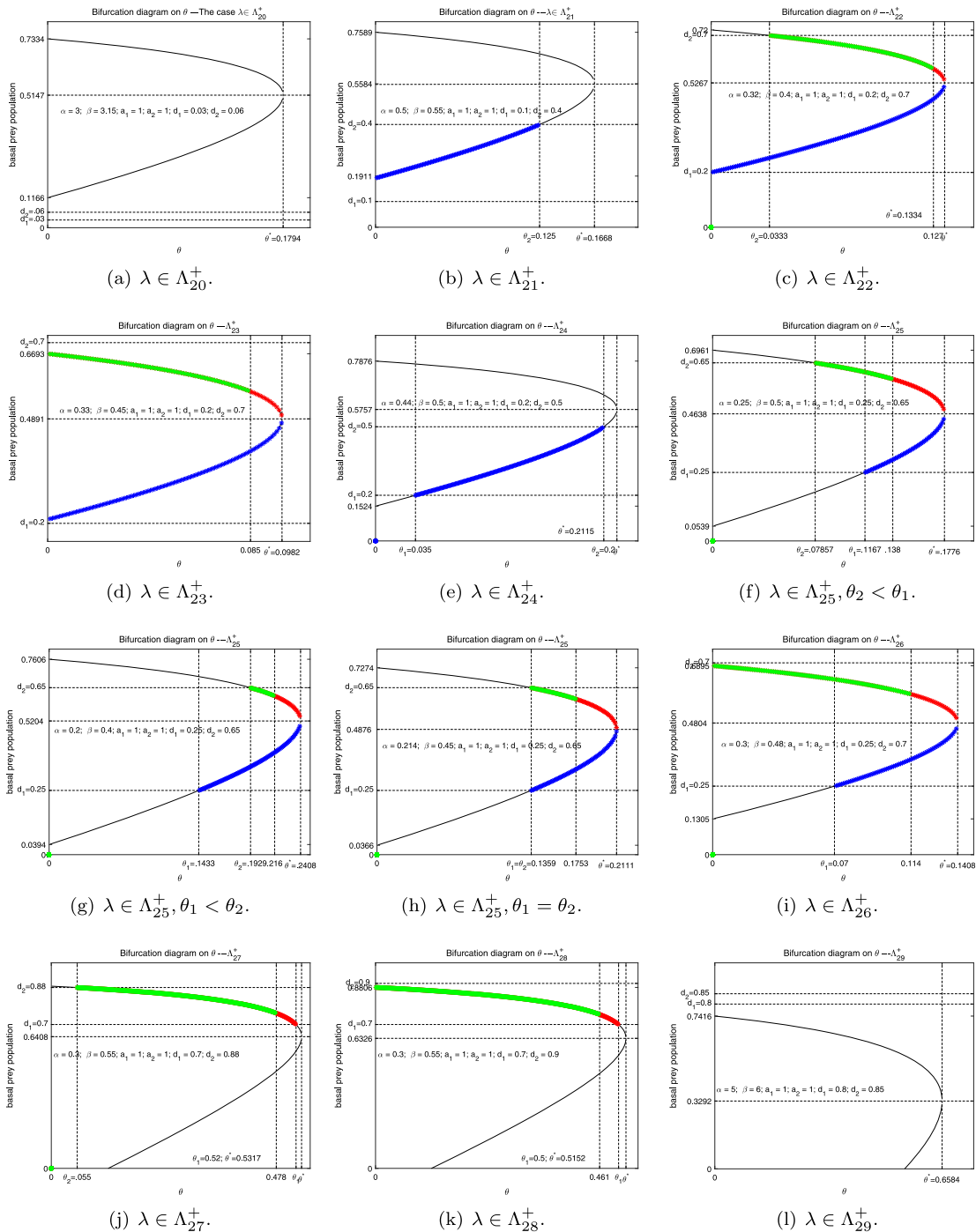
$$A_{31}^+ = \left\{ \lambda \in A_3^+ : \frac{\beta}{a_1} < \frac{d_2(1 - d_2)}{d_2 - d_1} \right\}, \quad A_{32}^+ = \left\{ \lambda \in A_3^+ : \frac{\beta}{a_1} \geq \frac{d_2(1 - d_2)}{d_2 - d_1}, \frac{\alpha}{a_2} < \frac{d_1(1 - d_1)}{d_2 - d_1} \right\},$$

$$A_{33}^+ = \left\{ \lambda \in A_3^+ : \frac{\alpha}{a_2} \geq \frac{d_1(1 - d_1)}{d_2 - d_1} \right\}.$$

We summarize Theorems 5.3, 5.6 and 5.8 as follows:

**Theorem 5.10.**

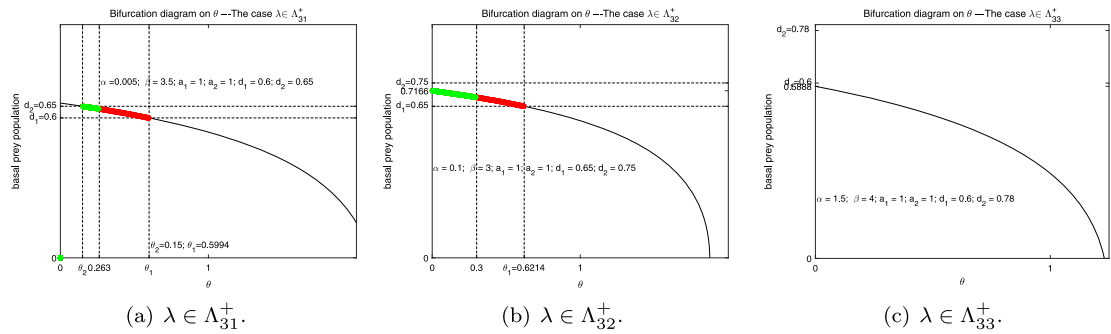
- (i) If  $\lambda \in A_1^- \cup A_1^+ \cup A_{20}^+ \cup A_{29}^+ \cup A_{33}^+$ , then for all  $\theta \in (0, 1)$ , system (1.3) has no coexistence equilibrium.
- (ii) If  $\lambda \in A_2^- \cup A_3^- \cup A_{21}^+ \cup A_{22}^+ \cup A_{24}^+$ , then for  $\theta \in (0, 1)$ , system (1.3) has at most one interior equilibrium  $E_1^*(x_1^*, y_1^*, z_1^*)$  which is always unstable if it exists.



**Fig. 5.** Bifurcations on  $\theta$  in the case  $\lambda \in \Lambda_2^+$ , i.e.,  $0 < \theta^* < 1$ . Here,  $\gamma_1 = 1, \gamma_2 = 1$ . Blue curve represents the interior equilibrium  $E_1^*$  which is unstable, green and red curves represent the interior equilibrium  $E_2^*$  where green means local asymptotical stability and red means instability. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(iii) If  $\lambda \in \Lambda_{23}^+ \cup \Lambda_{25}^+ \cup \Lambda_{26}^+ \cup \Lambda_{27}^+ \cup \Lambda_{28}^+$ , then system (1.3) may have the coexistence equilibrium  $E_2^*(x_2^*, y_2^*, z_2^*)$ , which depends on the value of  $\theta$  in  $(0, 1)$ . The stability of  $E_2^*$  is dependent on  $(\gamma_1, \gamma_2)$ ,  $E_2^*$  is locally asymptotically stable if and only if  $x_2^* > \frac{1}{2}(1 + \theta)$  and  $\Gamma(\gamma_1, \gamma_2) > 0$ .





**Fig. 6.** Bifurcation diagrams on  $\theta$  in the case  $\lambda \in \Lambda_3^+$ , i.e.,  $\theta^* \geq 1$ . Here,  $\gamma_1 = 1, \gamma_2 = 1$ . Green and red segments represent the interior equilibrium  $E_2^*$  where green means local asymptotical stability and red means instability. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

**Remark 5.11.** Theorems 5.3, 5.6, 5.8 and 5.10 demonstrate that system (1.3) has rich and complex dynamical behaviors due to Allee effect in the basal prey. Theorem 5.10 also implies the following statements:

- (1) The first two statements of Theorem 5.10 give the parameters regions of  $\lambda$ , in which the extinction of one of the species  $x, y$  and  $z$  may occur for all  $\theta \in (0, 1)$ .
- (2) The third statement of Theorem 5.10 indicates that  $\lambda \in \Lambda_{23}^+ \cup \Lambda_{25}^+ \cup \Lambda_{26}^+ \cup \Lambda_{27}^+ \cup \Lambda_{28}^+$  is necessary for the coexistence of all three species  $x, y$  and  $z$ .

## 6. Multiple attractors

In this section, we focus on possible dynamical patterns, i.e., the existence of multiple attractors, for system (1.3). Based on our previous analysis, system (1.3) can have one (i.e. extinction of all species), two (i.e. bi-stability) or three (i.e. tri-stability) attractors.

### 6.1. Extinction of all species

From Theorems 4.1 and 4.3, we know that the strong Allee effect in the basal prey may cause the extinction of all species.

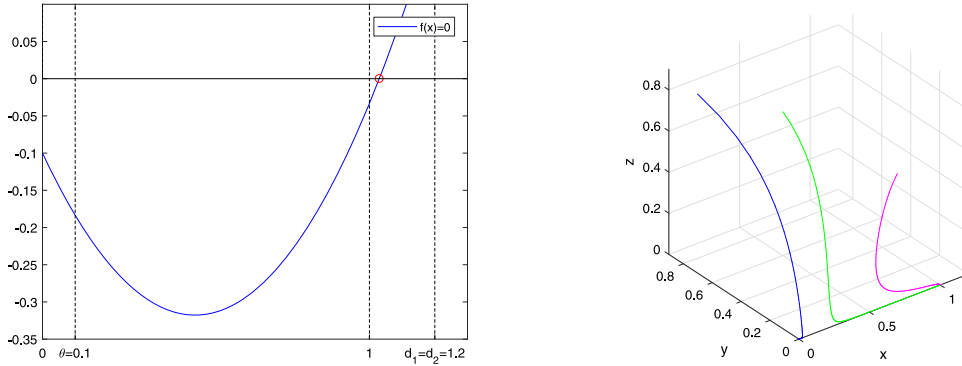
(a) From Theorem 4.3, we know that if the initial population density of the basal prey is below its Allee threshold, i.e.,  $x(0) \leq \theta$ , then the extinction of all species  $x, y$  and  $z$  occurs.

(b) According to Theorem 4.1, the extinction state  $E_0$  is always an attractor due to the strong Allee effect in the basal prey  $x$ . In addition, Theorem 4.3 implies that  $E_0$  is a global attractor if  $d_1 \geq 1, d_2 \leq \theta$  or  $d_1 \leq \theta, d_2 \geq 1 + \frac{\alpha_2}{\alpha} \left[ \frac{(1-\theta)^2}{4d_1} + \gamma_1 \right]$ . This indicates that IG predator (IG prey)-driven extinction due to the strong Allee effect in the basal prey population combined with the high natural death rate of IG prey (IG predator, respectively) leads to the extinction of all species.

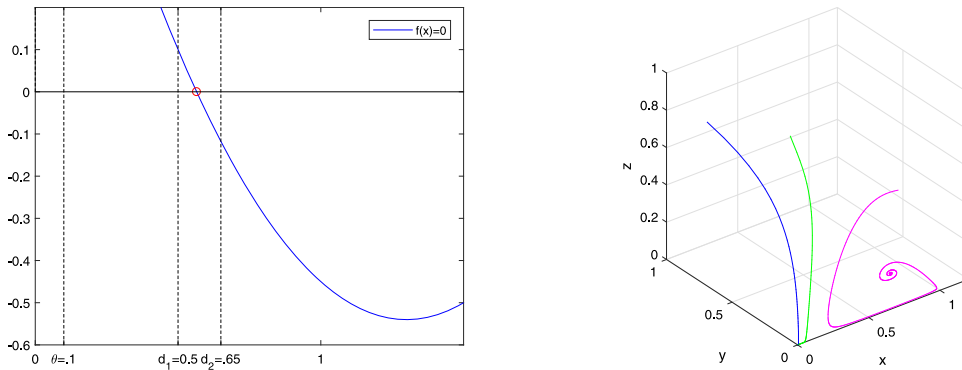
### 6.2. Bi-stability

System (1.3) may have two attractors: one is  $E_0$  and the other one is: (1)  $E_1$  (Fig. 7); (2)  $E_2$  (Fig. 8); (3)  $E_3$  (Fig. 9); (4) the stable interior equilibrium  $E_2^*$  (Fig. 10); (5) the unique stable limit cycle surrounding  $E_2$  in the  $xz$ -plane (Fig. 11); (6) the unique stable limit cycle surrounding  $E_3$  in the  $xy$ -plane (Fig. 12); (7) the stable limit cycle in  $\text{int}\mathbb{R}_+^3$  (Fig. 1).

(a) System (1.3) has two attractors  $E_0 \cup E_1$  if  $d_1 \geq 1, d_2 \geq 1$  (see Fig. 7). In this case, both  $E_0$  and  $E_1$  are locally asymptotically stable and  $E_2$  and  $E_3$  do not exist by Theorem 4.1, and system (1.3) has no interior



**Fig. 7.** Bi-stability:  $E_0 \cup E_1$ . Parameters:  $\theta = 0.1, d_1 = d_2 = 1.2, a_1 = 1.5, a_2 = 1, \alpha = 0.5, \beta = \gamma_1 = \gamma_2 = 1$ . System (1.3) has no interior equilibrium since  $d_1, d_2 > x_2^*$  (see the left figure) and no  $E_2$  and  $E_3$  since  $d_1 > 1, d_2 > 1$ . Therefore, system (1.3) has two attractors  $E_0 \cup E_1$  (see the right figure). The initial values are chosen as  $(0.1, 0.8, 0.8), (0.5, 0.6, 0.7)$  and  $(0.8, 0.1, 0.55)$ . The blue orbit starting from  $(0.1, 0.8, 0.8)$  tends to  $E_0$ , the orbits initiating at  $(0.5, 0.6, 0.7)$  (the green curve) and  $(0.8, 0.1, 0.55)$  (the red curve) tend to  $E_1$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

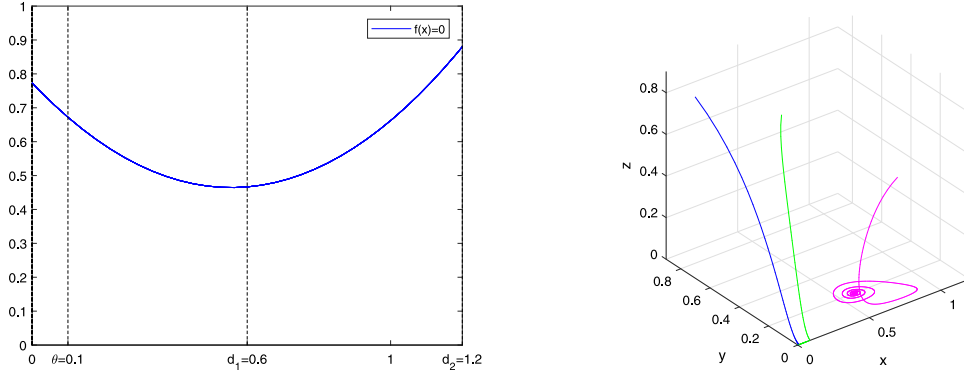


**Fig. 8.** Bi-stability:  $E_0 \cup E_2$ . Parameters:  $\theta = 0.1, d_1 = 0.5, d_2 = 0.65, a_1 = 2, a_2 = 0.5, \alpha = \beta = \gamma_1 = \gamma_2 = 1$ . The left figure indicates that  $d_1 < x_1^* < d_2 < x_2^*$  and hence system (1.3) has a unique unstable interior equilibrium  $E_1^*$ .  $E_3$  exists but is unstable,  $E_2$  is locally asymptotically stable. Therefore, system (1.3) has two attractors  $E_0 \cup E_2$  (see the right figure). The initial values are same as in Fig. 7. The trajectories initiating at  $(0.1, 0.8, 0.8)$  (the blue curve) and  $(0.5, 0.6, 0.7)$  (the green curve) tend to  $E_0$ . The trajectory initiating at  $(0.8, 0.1, 0.55)$  (the red curve) tends to  $E_2$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

equilibrium by Theorem 4.5. This indicates that the high natural death rates of IG prey and IG predator make the basal prey to possibly survive.

(b) System (1.3) has two attractors  $E_0 \cup E_2$  if  $\frac{1}{2}(1 + \theta) < d_2 < 1, d_1 > d_2 - \frac{\alpha_1}{\beta}(d_2 - \theta)(1 - d_2)$ , which implies that  $E_2$  exists and is locally asymptotically stable by Theorem 4.1 and system (1.3) has at most one unstable interior equilibrium  $E_1^*$  by Corollary 4.11, and one of conditions is satisfied:

- $d_1 \leq \theta$ . In this case, system (1.3) has no  $E_3$ . This indicates that the IG prey-driven extinction combined with the high ratio of attack rates of IG predator on IG prey to the basal prey such that  $\frac{\alpha_1}{\beta} > \frac{d_2 - d_1}{(d_2 - \theta)(1 - d_2)}$  with  $\frac{1}{2}(1 + \theta) < d_2 < 1$  leads to the extinction of IG prey and the possible survival of IG predator.
- $d_1 \geq 1$ . In this case, system (1.3) has no interior equilibrium by Theorem 4.5 and no  $E_3$  by Theorem 4.1. This indicates that the high natural death rate of IG prey combined with the high ratio of attack rates of IG predator on IG prey to basal prey such that  $\frac{\alpha_1}{\beta} > \frac{d_2 - d_1}{(d_2 - \theta)(1 - d_2)}$  with  $\frac{1}{2}(1 + \theta) < d_2 < 1$  leads to the extinction of IG prey and the possible survival of IG predator.
- $\theta < d_1 < 1, d_2 < d_1 + \frac{\alpha_2}{\alpha}(d_1 - \theta)(1 - d_1)$ . In this case, system (1.3) has no interior equilibrium by Corollary 4.11.  $E_3$  exists but is unstable by Theorem 4.1. This indicates that both the high ratio of the attack rates of IG predator on IG prey to basal prey and the high ratio of the predation rate of



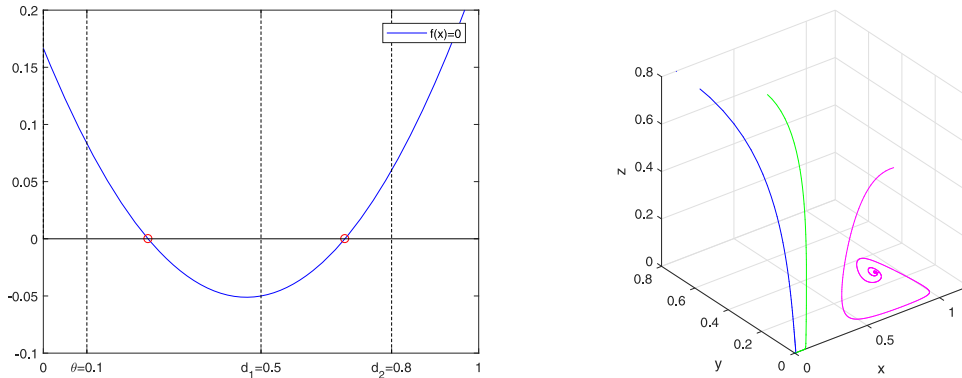
**Fig. 9.** Bi-stability:  $E_0 \cup E_3$ . Parameters:  $\theta = 0.1, d_1 = 0.6, d_2 = 1.2, a_1 = 1, a_2 = 0.9, \alpha = 1, \beta = 1.1, \gamma_1 = \gamma_2 = 1$ . System (1.3) has no interior equilibrium (see the left figure) and no  $E_2$ .  $E_3$  exists and is locally asymptotically stable. Therefore, system (1.3) has two attractors  $E_0 \cup E_3$  (see the right figure). The initial values are same as in Fig. 7. The orbits initiating at  $(0.1, 0.8, 0.8)$  (the blue curve) and  $(0.5, 0.6, 0.7)$  (the green curve) tend to  $E_0$ . The orbit initiating at  $(0.8, 0.1, 0.55)$  (the red curve) tends to  $E_3$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

IG predator on IG prey to the attack rate of IG prey on basal prey such that  $\frac{a_1}{\beta} > \frac{d_2 - d_1}{(d_2 - \theta)(1 - d_2)}$  and  $\frac{a_2}{\alpha} > \frac{d_2 - d_1}{(d_1 - \theta)(1 - d_1)}$  with  $\frac{1}{2}(1 + \theta) < d_2 < 1, \theta < d_1 < 1$  lead to the extinction of IG prey and the possible survival of IG predator.

- $\theta < d_1 < \frac{1}{2}(1 + \theta), d_2 > d_1 + \frac{a_2}{\alpha}(d_1 - \theta)(1 - d_1)$ . In this case, system (1.3) has a unique unstable interior equilibrium  $E_1^*$  by Corollary 4.11.  $E_3$  exists but is unstable by Theorem 4.1. This indicates that the high ratio of the attack rates of IG predator on IG prey to basal prey and the low ratio of the predation rate of IG predator on IG prey to the attack rate of IG prey on basal prey such that  $\frac{a_1}{\beta} > \frac{d_2 - d_1}{(d_2 - \theta)(1 - d_2)}$  and  $\frac{a_2}{\alpha} < \frac{d_2 - d_1}{(d_1 - \theta)(1 - d_1)}$  with  $\theta < d_1 < \frac{1}{2}(1 + \theta) < d_2 < 1$  lead to the extinction of IG prey and the possible survival of IG predator.
- As an example, take parameters:  $\theta = 0.1, d_1 = 0.5, d_2 = 0.65, a_1 = 2, a_2 = 0.5, \alpha = \beta = \gamma_1 = \gamma_2 = 1$ . System (1.3) has a unique unstable interior equilibrium  $E_1^*$  by Theorem 4.6 (see Fig. 8). By Theorem 4.1,  $E_3(0.5, 0.2, 0)$  exists but is unstable,  $E_2(0.65, 0, 0.1925)$  is locally asymptotically stable. Therefore, system (1.3) has two attractors  $E_0 \cup E_2$  (see Fig. 8).

(c) System (1.3) has two attractors  $E_0 \cup E_3$  if  $\frac{1}{2}(1 + \theta) < d_1 < 1, d_2 > d_1 + \frac{a_2}{\alpha}(d_1 - \theta)(1 - d_1)$ , which implies that  $E_3$  exists and is locally asymptotically stable by Theorem 4.1, and one of the following conditions is satisfied:

- $d_2 \geq 1$ . In this case, system (1.3) has at most one unstable interior equilibrium  $E_1^*$  by Corollary 4.11 and no  $E_2$  by Theorem 4.1. This indicates that the high natural death rate of IG predator combined with the low ratio of the predation rate of IG predator on IG prey to the attack rate of IG prey on the basal prey such that  $\frac{a_2}{\alpha} < \frac{d_2 - d_1}{(d_1 - \theta)(1 - d_1)}$  with  $\frac{1}{2}(1 + \theta) < d_1 < 1$  leads to the extinction of IG predator and the possible survival of IG prey.
- $d_2 < 1, d_1 < d_2 - \frac{a_1}{\beta}(d_2 - \theta)(1 - d_2), \left(2d_1 - \left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)\right) \left(2d_2 - \left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right)\right) > 0$ . In this case, system (1.3) has no interior equilibrium by Corollary 4.11, and  $E_2$  exists but is unstable by Theorem 4.1. This indicates that both the low ratio of the attack rates of IG predator on IG prey to the basal prey and the low ratio of the predation rate of IG predator on IG prey to the attack rate of IG prey on the basal prey such that  $\frac{a_1}{\beta} < \frac{d_2 - d_1}{(d_2 - \theta)(1 - d_2)}$  and  $\frac{a_2}{\alpha} < \frac{d_2 - d_1}{(d_1 - \theta)(1 - d_1)}$  with  $\frac{1}{2}(1 + \theta) < d_1 < d_2 < 1$  and either  $1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} < 2d_1$  or  $1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} > 2d_2$  lead to the extinction of IG predator and the possible survival of IG prey.
- As an example, take parameters  $\theta = 0.1, d_1 = 0.6, d_2 = 1.2, a_1 = 1, a_2 = 0.9, \alpha = 1, \beta = 1.1, \gamma_1 = \gamma_2 = 1$ . System (1.3) has no interior equilibrium by Theorem 4.6 (see Fig. 9). By Theorem 4.1,  $E_2$  does not



**Fig. 10.** Bi-stability:  $E_0 \cup E_2^*$ . Parameters:  $\theta = 0.1, d_1 = 0.5, d_2 = 0.8, a_1 = 1.5, a_2 = 1, \alpha = 0.5, \beta = 1, \gamma_1 = \gamma_2 = 1$ . System (1.3) has a unique interior equilibrium  $E_2^*$  (see left figure) which is locally asymptotically stable.  $E_2$  and  $E_3$  exist but both are unstable. Therefore, system (1.3) has two attractors  $E_0 \cup E_2^*$  (see the right figure). The initial values are same as in Fig. 7. The trajectories initiating at  $(0.1, 0.8, 0.8)$  (the blue curve) and  $(0.5, 0.6, 0.7)$  (the green curve) tend to  $E_0$ , the trajectory initiating at  $(0.8, 0.1, 0.55)$  (the red curve) tends to  $E_2^*$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

exist,  $E_3(0.6, 0.2, 0)$  exists and is locally asymptotically stable. Therefore, system (1.3) has two attractors  $E_0 \cup E_3$  (see Fig. 9).

(d) System (1.3) has two attractors  $E_0 \cup E_2^*$  if one of the following conditions is satisfied:

- $d_1 < d_2, d_1 < d_2 - \frac{a_1}{\beta}(d_2 - \theta)(1 - d_2), d_2 < d_1 + \frac{a_2}{\alpha}(d_1 - \theta)(1 - d_1)$  and  $\frac{\alpha}{a_2} - \frac{\beta}{a_1} + \sqrt{\Delta} > 0$  with

$$\frac{\alpha}{a_2} - \frac{\beta}{a_1} > -\frac{x_2^*(2x_2^* - (1 + \theta))(\gamma_1\alpha y_2^* + \gamma_2\beta z_2^*)}{\gamma_1\gamma_2 a_1 a_2 y_2^* z_2^*}. \tag{6.1}$$

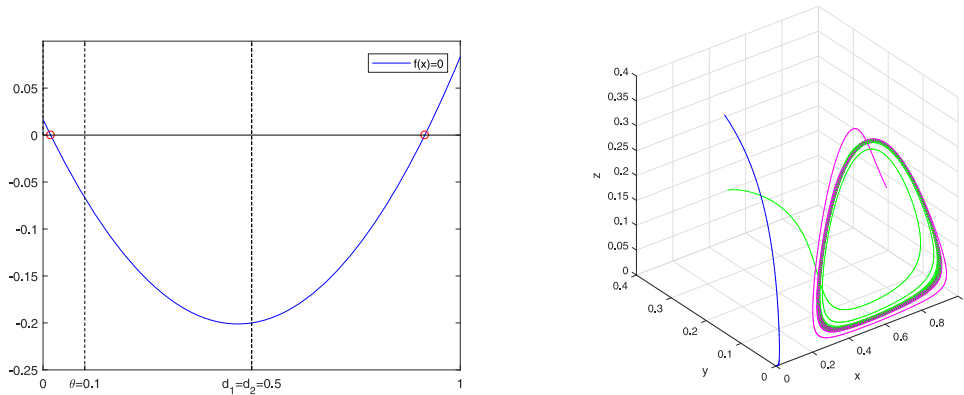
In this case, system (1.3) has a unique stable interior equilibrium  $E_2^*$ .  $E_2$  and  $E_3$  exist possibly but both are unstable. All species may survive.

- $\theta < d_1 < \frac{1}{2}(1 + \theta), d_1 < \frac{1}{2}\left(1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1}\right) < d_2, d_1 < d_2 - \frac{a_1}{\beta}(d_2 - \theta)(1 - d_2), d_2 > d_1 + \frac{a_2}{\alpha}(d_1 - \theta)(1 - d_1)$  and  $\frac{\alpha}{a_2} - \frac{\beta}{a_1} + \sqrt{\Delta} > 0$  with (6.1) holds. In this case, system (1.3) has two interior equilibria  $E_1^*$  which is unstable and  $E_2^*$  which is locally asymptotically stable.  $E_3$  exists and  $E_2$  possibly exists but both are unstable. All species may survive.
- As an example, take the parameters as in Fig. 1:  $\theta = 0.2, d_1 = 0.7, d_2 = 0.9, \alpha = \beta = a_1 = 1, a_2 = 2$ . By Theorem 4.6 and Fig. 1, system (1.3) has a unique interior equilibrium  $E_2^*$ . Both  $E_2(0.9, 0, 0.07)$  and  $E_3(0.7, 0.15, 0)$  exist but are unstable. Take  $\gamma_1 = \gamma_2 = 5$ , then  $E_2^*$  is locally asymptotically stable (see Fig. 1(b)). Therefore, system (1.3) has two attractors  $E_0 \cup E_2^*$ . We also give another example (see Fig. 10) to show that system (1.3) has two attractors  $E_0 \cup E_2^*$ .

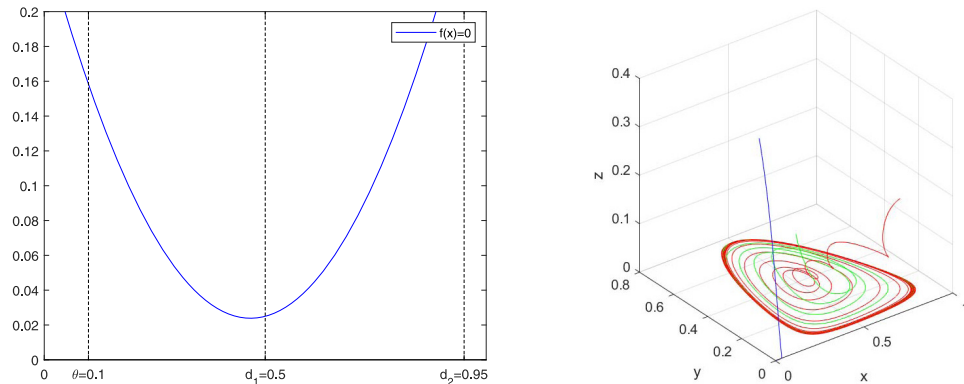
(e) The case that the other attractor is a limit cycle: (1) the stable limit cycle surrounding  $E_2$  in the  $xz$ -plane (Fig. 11); (2) the stable limit cycle surrounding  $E_3$  in the  $xy$ -plane (Fig. 12); (3) the stable limit cycle in  $\text{int}\mathbb{R}_+^3$  (see Fig. 1(c)).

### 6.3. Tri-stability

System (1.3) may have three attractors: one is  $E_0$ , the other two are: (1)  $E_2$  and  $E_3$  (see Fig. 13); (2)  $E_3$  and the stable interior equilibrium  $E_2^*$  (see Fig. 14); (3)  $E_2$  and the stable limit cycle surrounding  $E_3$  which locates in the  $xy$ -plane (see Fig. 15); (4) the stable interior equilibrium  $E_2^*$  and the stable limit cycle surrounding  $E_3$  which locates in the  $xy$ -plane (see Fig. 16); (5) the stable limit cycle surrounding  $E_2$



**Fig. 11.** Bi-stability:  $E_0$  and the stable limit cycle surrounding  $E_2$  in the  $xz$ -plane. We take  $d_1 = d_2 = 0.5$  and keep other parameters unchange in Fig. 10. System (1.3) has no interior equilibrium (see the left figure).  $E_3$  is a source in the  $xz$ -plane and there exists a unique stable limit cycle surrounding  $E_2$ . Initial values:  $(0.1, 0.2, 0.4)$ ,  $(0.5, 0.4, 0.1)$ ,  $(0.8, 0.1, 0.2)$ . The trajectory initiating at  $(0.1, 0.2, 0.4)$  (the blue curve) tends to  $E_0$ . The trajectories initiating at  $(0.5, 0.4, 0.1)$  (the green curve) and  $(0.8, 0.1, 0.2)$  (the red curve) tend to the stable limit cycle surrounding  $E_2$  in the  $xz$ -plane (see the right figure). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

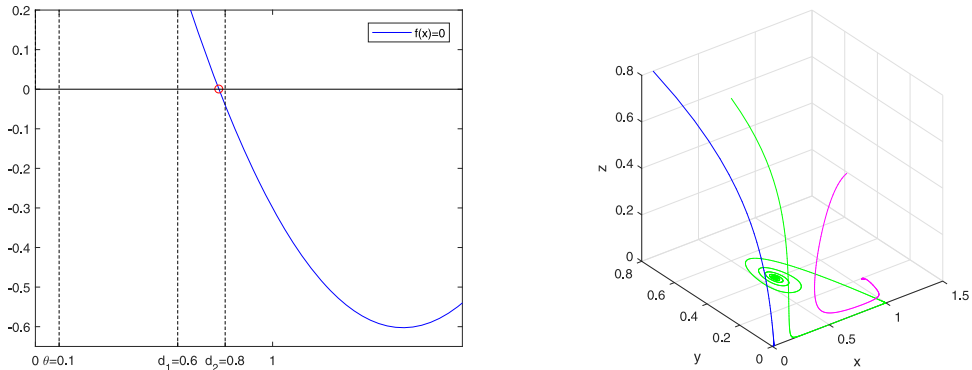


**Fig. 12.** Bi-stability:  $E_0$  and the stable limit cycle surrounding  $E_3$  in the  $xy$ -plane. We take  $d_1 = 0.5, d_2 = 0.95$  and keep other parameters unchange in Fig. 10. System (1.3) has no interior equilibrium (see the left figure).  $E_2$  is a saddle and has no stable manifold in  $\text{int}\mathbb{R}_+^3$ .  $E_3$  is a saddle in  $\mathbb{R}_+^3$  but a source in the  $xy$ -plane and there exists a unique stable limit cycle surrounding  $E_3$ . Initial values are same as in Fig. 11. The trajectory initiating at  $(0.1, 0.2, 0.4)$  (the blue curve) tends to  $E_0$ . The trajectories initiating at  $(0.5, 0.4, 0.1)$  (the green curve) and  $(0.8, 0.1, 0.2)$  (the red curve) tend to the stable limit cycle surrounding  $E_3$  in the  $xy$ -plane. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

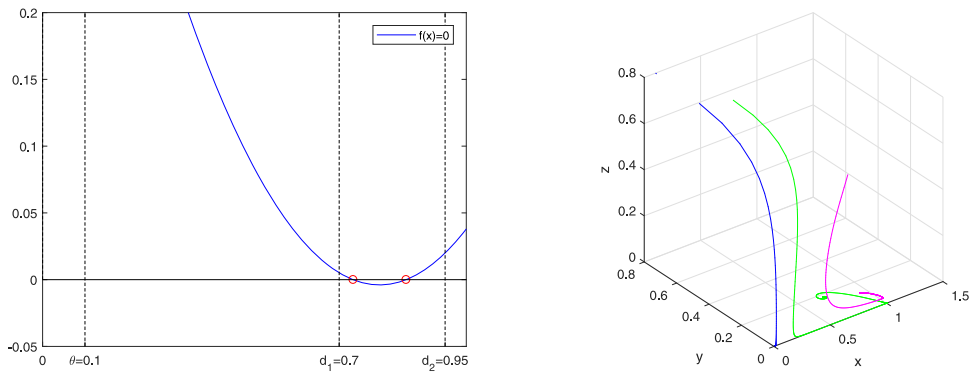
which locates in the  $xz$ -plane and the stable limit cycle surrounding  $E_3$  which locates in the  $xy$ -plane (see Fig. 17).

(a) System (1.3) has three attractors  $E_0 \cup E_2 \cup E_3$  if  $\frac{1}{2}(1+\theta) < d_1 < d_2 < 1, d_1 > d_2 - \frac{a_1}{\beta}(d_2 - \theta)(1 - d_2), d_2 > d_1 + \frac{a_2}{\alpha}(d_1 - \theta)(1 - d_1)$ . In this case, system (1.3) has a unique unstable interior equilibrium  $E_1^*$ . This implies that different initial values lead IG prey or IG predator to extinction. For example, we take parameters  $\theta = 0.1, d_1 = 0.6, d_2 = 0.8, a_1 = 2, a_2 = 0.2, \alpha = 0.5, \beta = 1, \gamma_1 = \gamma_2 = 1$ . By Theorem 4.6, system (1.3) has a unique unstable interior equilibrium  $E_1^*$  (see Fig. 13). By Theorem 4.1, both  $E_2(0.8, 0, 0.21)$  and  $E_3(0.6, 0.4, 0)$  exist and are stable. Therefore, system (1.3) has three attractors  $E_0 \cup E_2 \cup E_3$  (see Fig. 13).

(b) System (1.3) has three attractors  $E_0 \cup E_3 \cup E_2^*$  if  $\frac{1}{2}(1 + \theta) < d_1 < 1, d_1 < \frac{1}{2} \left( 1 + \theta + \frac{\alpha}{a_2} - \frac{\beta}{a_1} \right) < d_2, d_1 < d_2 - \frac{a_1}{\beta}(d_2 - \theta)(1 - d_2), d_2 > d_1 + \frac{a_2}{\alpha}(d_1 - \theta)(1 - d_1)$ , and  $\frac{\alpha}{a_2} - \frac{\beta}{a_1} + \sqrt{\Delta} > 0$  with (6.1) holds. In this case, system (1.3) has another unstable interior equilibrium  $E_1^*$ .  $E_2$  exists possibly but is unstable. This implies that different initial values lead to the survival of IG prey or all species. For example, we take parameters  $\theta = 0.1, d_1 = 0.7, d_2 = 0.95, a_1 = 4, a_2 = 1.35, \alpha = \beta = \gamma_1 = \gamma_2 = 1$ . By Theorem 4.6, system (1.3) has two



**Fig. 13.** Tri-stability:  $E_0 \cup E_2 \cup E_3$ . Parameters:  $\theta = 0.1, d_1 = 0.6, d_2 = 0.8, a_1 = 2, a_2 = 0.2, \alpha = 0.5, \beta = 1, \gamma_1 = \gamma_2 = 1$ . System (1.3) has a unique unstable interior equilibrium  $E_1^*$  (see the left figure). Both  $E_2$  and  $E_3$  exist and are stable. Initial values are same as in Fig. 7. The blue orbit starting from  $(0.1, 0.8, 0.8)$  tends to  $E_0$ , the green orbit starting from  $(0.5, 0.6, 0.7)$  tends to  $E_3$ , and the red orbit starting from  $(0.8, 0.1, 0.55)$  tends to  $E_2$  (see the right figure). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



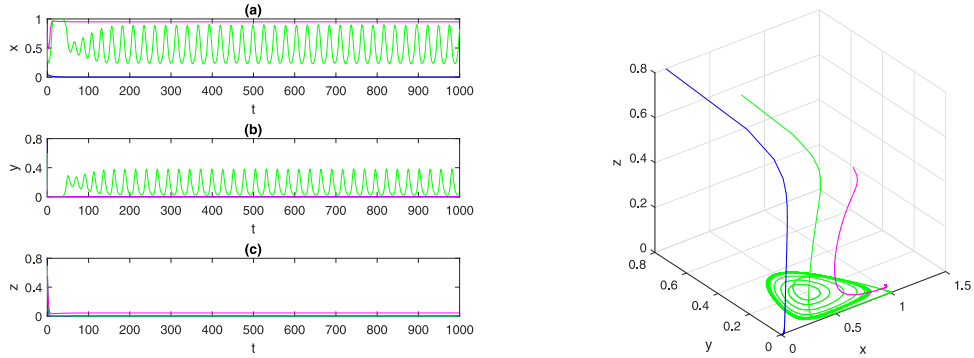
**Fig. 14.** Tri-stability:  $E_0 \cup E_3 \cup E_2^*$ . Parameters:  $\theta = 0.1, d_1 = 0.7, d_2 = 0.95, a_1 = 4, a_2 = 1.35, \alpha = \beta = \gamma_1 = \gamma_2 = 1$ . System (1.3) has two interior equilibria:  $E_1^* = (0.7328, 0.1609, 0.0082), E_2^* = (0.8579, 0.0682, 0.0395)$  (the left figure).  $E_1^*$  is unstable, and  $E_2^*$  is stable.  $E_2$  is unstable while  $E_3$  is stable. Therefore, system (1.3) has three attractors  $E_0 \cup E_3 \cup E_2^*$  (the right figure). Initial values are same as in Fig. 7. The blue orbit starting from  $(0.1, 0.8, 0.8)$  tends to  $E_0$ , the green orbit starting from  $(0.5, 0.6, 0.7)$  tends to  $E_3$ , and the red orbit starting from  $(0.8, 0.1, 0.55)$  tends to the interior equilibrium  $E_2^*$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

interior equilibria:  $E_1^*$  which is unstable, and  $E_2^*$  which is stable. By Theorem 4.1,  $E_2 = (0.95, 0, 0.0425)$  is unstable while  $E_3 = (0.7, 0.18, 0)$  is stable. Therefore, system (1.3) has three attractors  $E_0 \cup E_3 \cup E_2^*$  (see Fig. 14).

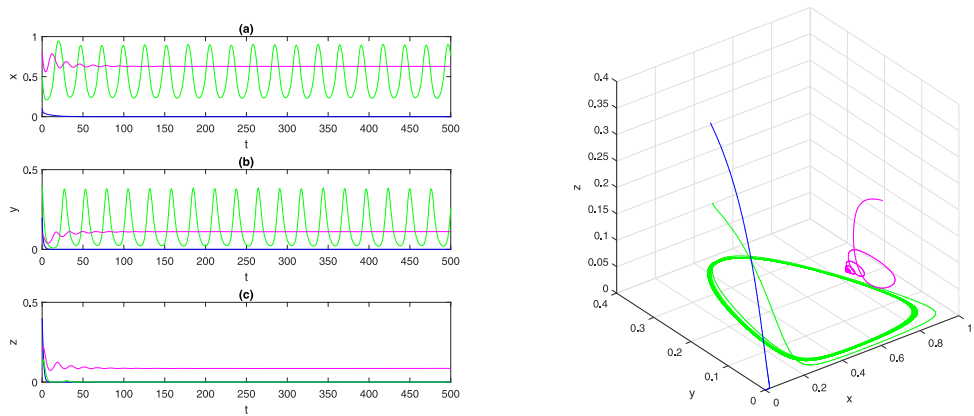
(c) By numerical simulations, we know that system (1.3) possibly has three attractors: one is  $E_0$ , the other two are: (1)  $E_2$  and the stable limit cycle surrounding  $E_3$  which locates in the  $xy$ -plane (see Fig. 15); (2) the stable interior equilibrium  $E_2^*$  and the stable limit cycle surrounding  $E_3$  which locates in the  $xy$ -plane (see Fig. 16); (3) the stable limit cycle surrounding  $E_2$  which locates in the  $xz$ -plane and the stable limit cycle surrounding  $E_3$  which locates in the  $xy$ -plane (see Fig. 17).

#### 6.4. Multiple attracting periodic orbits

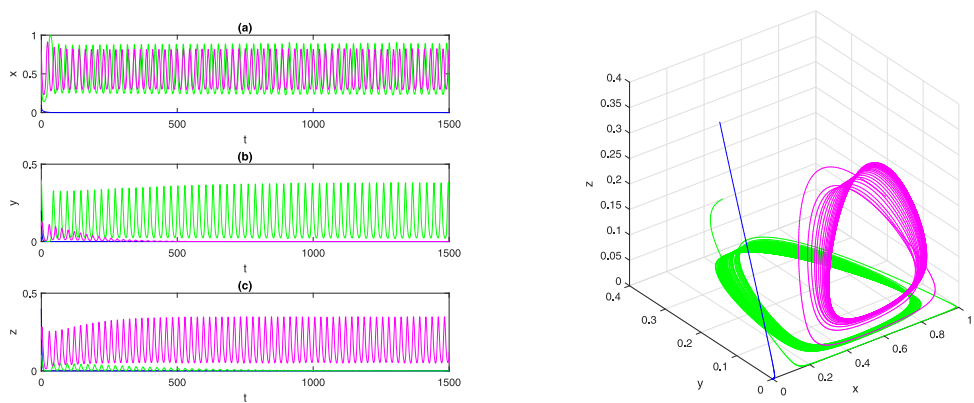
When system (1.3) has a unique locally asymptotically stable interior equilibrium  $E_2^*$ , the orbits tend to the extinction state  $E_0$  and the stable interior equilibrium  $E_2^*$  may be attracted to some periodic orbits as the pair of parameters  $(\gamma_1, \gamma_2)$  varies from the stable region to the unstable region. Even though we are not able to prove it analytically, we can perform simulations to confirm this phenomenon. Taking parameters



**Fig. 15.** Tri-stability:  $E_0 \cup E_2$  and the stable limit cycle surrounding  $E_3$  which locates in the  $xy$ -plane. Parameters:  $\theta = 0.1, d_1 = 0.5, d_2 = 0.95, a_1 = 13, a_2 = 1, \alpha = \beta = \gamma_1 = \gamma_2 = 2$ . Initial values are same as in Fig. 7. The blue orbit starting from  $(0.1, 0.8, 0.8)$  tends to  $E_0$ , the green orbit starting from  $(0.5, 0.6, 0.7)$  tends to the stable limit cycle surrounding  $E_3$  which locates in the  $xy$ -plane, and the red orbit starting from  $(0.8, 0.1, 0.55)$  tends to  $E_2$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



**Fig. 16.** Tri-stability:  $E_0$  and the stable interior equilibrium  $E_2^*$  and the stable limit cycle surrounding  $E_3$  which locates in the  $xy$ -plane. Parameters:  $\theta = 0.1, d_1 = 0.5, d_2 = 0.85, a_1 = 1.5, a_2 = 2, \alpha = \beta = \gamma_1 = \gamma_2 = 1$ . Initial values:  $(0.1, 0.2, 0.4), (0.5, 0.4, 0.1), (0.8, 0.1, 0.2)$ . The blue orbit starting from  $(0.1, 0.2, 0.4)$  tends to  $E_0$ , the green orbit starting from  $(0.5, 0.4, 0.1)$  tends to the stable limit cycle surrounding  $E_3$  which locates in the  $xy$ -plane, and the red orbit starting from  $(0.8, 0.1, 0.2)$  tends to the stable interior equilibrium  $E_2^*$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



**Fig. 17.** Tri-stability:  $E_0$  and the stable limit cycle surrounding  $E_2$  which locates in the  $xz$ -plane and the stable limit cycle surrounding  $E_3$  which locates in the  $xy$ -plane. Parameters:  $\theta = 0.1, d_1 = 0.5, d_2 = 0.52, a_1 = 0.18, a_2 = 0.11, \alpha = \beta = \gamma_1 = \gamma_2 = 1$ . Initial values are same as in Fig. 16. The blue orbit starting from  $(0.1, 0.2, 0.4)$  tends to  $E_0$ , the green orbit starting from  $(0.5, 0.4, 0.1)$  tends to the stable limit cycle surrounding  $E_3$  which locates in the  $xy$ -plane, and the red orbit starting from  $(0.8, 0.1, 0.2)$  tends to the stable limit cycle surrounding  $E_2$  which locates in the  $xz$ -plane. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

$\theta = 0.1, d_1 = 0.65, d_2 = 1.5, a_1 = 1.5, a_2 = 5, \alpha = 0.5, \beta = 1$ , system (1.3) has a unique interior equilibrium  $E_2^* = (0.7711, 0.1458, 0.0807)$  (see Fig. 18(a)). In addition, the boundary equilibrium  $E_2$  does not exist, and  $E_3$  exists but is unstable. Let  $\gamma_2 = 1$  be fixed. It is easy to check that  $\Gamma(\gamma_1, \gamma_2) = 0$  when  $\gamma_1 = 1.0938542$ ,  $\Gamma(\gamma_1, \gamma_2) > 0$  and  $E_2^*$  is locally asymptotically stable when  $\gamma_1 < 1.0938542$ , while unstable when  $\gamma_1 > 1.0938542$ .

(a) Take  $\gamma_1 = 0.2$ . From Fig. 18(b) we see that  $E_2^*$  is locally asymptotically stable. From Fig. 18(c) it can be seen that both the orbits initiated from  $(0.3, 0.1, 0.45)$  (blue orbit) and  $(0.3, 0.28, 0.8)$  (green orbit) tend to the extinction state  $E_0$ , and the red orbit initiated from  $(0.8, 0.2, 0.1)$  tends to the stable interior equilibrium  $E_2^*$ . Thus,  $E_0 \cup E_2^*$  are two attractors of system (1.3).

(b) Take  $\gamma_1 = 0.8$ . Then  $E_2^*$  is still locally asymptotically stable. From Fig. 18(d), we can see that the orbits initiated from  $(0.3, 0.28, 0.8)$  (green orbit) and  $(0.8, 0.2, 0.1)$  (red orbit) still tend  $E_0$  and  $E_2^*$ , respectively. However, the orbit initiated from  $(0.3, 0.1, 0.45)$  (blue orbit), which tended to  $E_0$  when  $\gamma_1 = 0.2$ , now is attracted to a periodic orbit. In this case, in addition to the two attractors  $E_0 \cup E_2^*$ , system (1.3) has another attracting periodic orbit (see Fig. 18(d)).

(c) Take  $\gamma_1 = 1$ . Then  $E_2^*$  is still locally asymptotically stable. In fact, the eigenvalues at  $E_2^*$  are  $\lambda_1 = -0.33525695, \lambda_{2,3} = -0.0028533322 \pm 0.45254531i$ . From Fig. 18(e), we can see that the orbit initiated from  $(0.3, 0.1, 0.45)$  (blue orbit) still tends to a periodic orbit. However, the orbit initiated from  $(0.3, 0.28, 0.8)$  (green orbit), which tended to  $E_0$  when  $\gamma_1 = 0.2$  and  $\gamma_1 = 0.8$ , now is attracted to another periodic orbit. In addition, the orbit initiated from  $(0.8, 0.2, 0.1)$  (red orbit), which tended to  $E_2^*$  when  $\gamma_1 = 0.2$  and  $\gamma_1 = 0.8$ , now is also attracted to a periodic orbit. Therefore, in this case, in addition to the two attractors  $E_0 \cup E_2^*$ , system (1.3) has three attracting periodic orbits (see Fig. 18(e)).

(d) When  $(\gamma_1, \gamma_2) = (1.0938542, 1)$ , i.e.,  $(\gamma_1, \gamma_2)$  lies on the Hopf bifurcation curve  $\Gamma(\gamma_1, \gamma_2) = 0$ ,  $E_2^*$  loses its stability and all orbits initiated from  $(0.3, 0.1, 0.45)$  (blue orbit),  $(0.3, 0.28, 0.8)$  (green orbit) and  $(0.8, 0.2, 0.1)$  (red orbit) are attracted to some periodic orbits (see Fig. 18(f)).

From these numerical simulations we know that with the increase of  $\gamma_1$  ( $\gamma_1 < 1.0938542$ ), multiple attracting periodic orbits may appear. This indicates that as  $(\gamma_1, \gamma_2)$  is close to the Hopf bifurcation curve  $\Gamma(\gamma_1, \gamma_2) = 0$  from the stable region  $\Gamma(\gamma_1, \gamma_2) > 0$ , the possibility of survival of all three species may increase, meanwhile the basin of attraction of the coexistence equilibrium  $E_2^*$  decreases until it loses its stability.

## 7. Discussion

In this paper, we proposed a three-species intraguild predation food web model (1.3) which includes the IG predator, IG prey and basal prey. The shared prey follows the logistic growth with strong Allee effect. We investigated the local and global dynamics of the system with emphasis on the impact of strong Allee effect.

For the following three-species Lotka–Volterra intraguild predation food web model without Allee effect in the shared prey

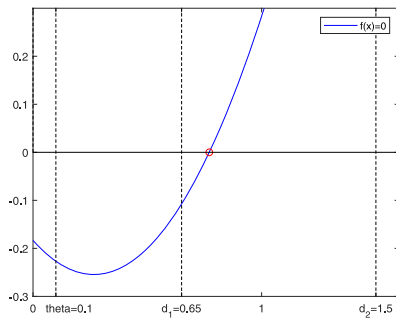
$$\begin{aligned} x' &= x(1-x) - \alpha xy - \beta xz, \\ y' &= \gamma_1 y(x - a_1 z - d_1), \\ z' &= \gamma_2 z(x + a_2 y - d_2), \end{aligned} \quad (7.1)$$

we know that it has four boundary equilibria:  $E_0 = (0, 0, 0)$ ,  $E_1 = (1, 0, 0)$ ,  $E_2 = (d_2, 0, \frac{1}{\beta}(1-d_2))$  and  $E_3 = (d_1, \frac{1}{\alpha}(1-d_1), 0)$ , and at most one positive equilibrium  $E^* = (x^*, y^*, z^*)$ , where

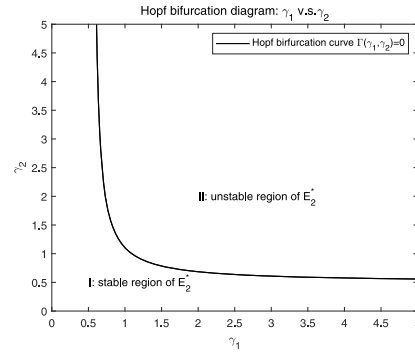
$$x^* = \frac{a_1 a_2 + \beta a_2 d_1 - \alpha a_1 d_2}{a_1 a_2 + \beta a_2 - \alpha a_1}, \quad y^* = \frac{1}{a_2}(d_2 - x^*), \quad z^* = \frac{1}{a_1}(x^* - d_1).$$

For the detailed dynamic analysis of IGP models of Lotka–Volterra type, we refer to [2,11,12,54] for some references.

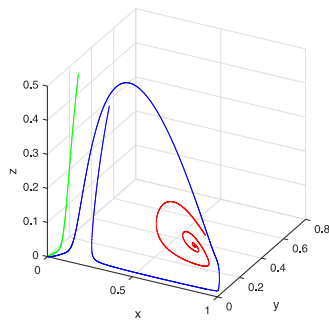




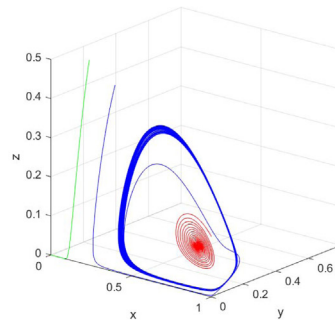
(a) unique interior equilibrium  $E_2^*$ .



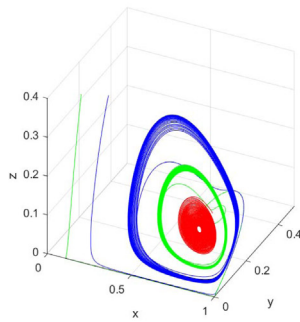
(b) Hopf bifurcation on  $(\gamma_1, \gamma_2)$ .



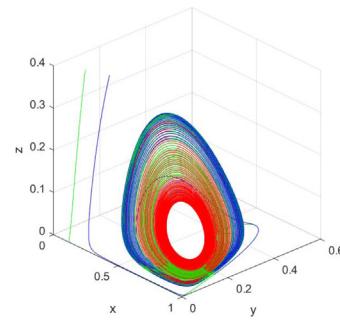
(c)  $\gamma_1 = 0.2, \gamma_2 = 1$ .



(d)  $\gamma_1 = 0.8, \gamma_2 = 1$ .



(e)  $\gamma_1 = \gamma_2 = 1$ .



(f)  $\gamma_1 = 1.0938542, \gamma_2 = 1$ .

**Fig. 18.** Parameters:  $\theta = 0.1, d_1 = 0.65, d_2 = 1.5, a_1 = 1.5, a_2 = 0.5, \alpha = 0.5, \beta = 1$ . Except the two attractors  $E_0 \cup E_2^*$ , system (1.3) may exist in other attracting periodic orbits as  $\gamma_1$  ( $\gamma_1 < 1.0938542$ ) increases with fixed  $\gamma_2 = 1$ . (a) System (1.3) has a unique interior equilibrium  $E_2^* = (0.7711, 0.1458, 0.0807)$ . (b) Hopf bifurcation on  $(\gamma_1, \gamma_2)$ . If  $\gamma_1 < 1.0938542$ ,  $E_2^*$  is local asymptotically stable. (c)  $\gamma_1 = 0.2$ , the red orbit which initiated from  $(0.8, 0.2, 0.1)$  tends to  $E_2^*$ , the blue and green orbits initiated from  $(0.3, 0.1, 0.45)$  and  $(0.3, 0.28, 0.8)$ , respectively, tend to the extinction state  $E_0$ . (d)  $\gamma_1 = 0.8$ , the red and green orbits which initiated from  $(0.8, 0.2, 0.1)$  and  $(0.3, 0.28, 0.8)$  still tend to  $E_2^*$  and  $E_0$ , respectively, while the blue orbit initiated from  $(0.3, 0.1, 0.45)$  tends to a periodic solution. (e)  $\gamma_1 = 1$ , all the orbits initiated from  $(0.3, 0.28, 0.8)$  (green orbit),  $(0.3, 0.1, 0.45)$  (blue orbit) and  $(0.8, 0.2, 0.1)$  (green orbit), tend to different periodic solutions, respectively. (f)  $\gamma_1 = 1.0938542$ , i.e.,  $(\gamma_1, \gamma_2)$  lies on the Hopf bifurcation curve  $\Gamma(\gamma_1, \gamma_2) = 0$ ,  $E_2^*$  loses its stability and all the orbits initiated from  $(0.3, 0.1, 0.45)$  (blue orbit),  $(0.3, 0.28, 0.8)$  (green orbit) and  $(0.8, 0.2, 0.1)$  (red orbit) are attracted to some periodic orbits. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Comparing the dynamics of model (1.3) (with Allee effect in the basal prey) to the dynamics of (7.1) (no Allee effect in the basal prey), we see that model (1.3) may have two resource-alone states  $E_\theta$  and  $E_1$  and two coexistence equilibria  $E_1^*$  and  $E_2^*$ , where  $E_\theta$  and  $E_1^*$  arise due to Allee effect in the basal resource.

For model (7.1),  $E_0$  is always unstable while it is stable for model (1.3). Strong Allee effect in the basal prey makes the initial conditions play an extreme important role in the survive of all three species, and increases the extinction risk of not only the basal resource but also the IG prey or/and IG predator. Due to the nonlinearity introduced by Allee effect, the existence and stability of boundary equilibria  $E_2, E_3$  and positive equilibrium  $E_2^*$  all are dependent on the Allee threshold  $\theta$ . Differing from model (7.1), model (1.3) has multiple tri-stability and multiple attracting periodic orbits. Therefore, the proposed model (1.3) with strong Allee effect in the basal prey exhibits much richer and more complex dynamic behaviors than (7.1).

The dynamic behaviors of model (1.3) obtained in this paper by theoretical analysis and numerical simulations can be summarized as follows:

(a) [Theorem 4.1](#) indicates that the extinction state  $E_0$  is always an attractor due to Allee effect in the basal prey  $x$ . [Theorem 4.3](#) indicates that strong Allee effect in the basal prey makes initial conditions very important for the survival of the basal prey as well as the IG prey and IG predator. If the initial population density of the basal prey is below its Allee threshold, i.e.,  $x(0) \leq \theta$ , then the extinction of all species  $x, y$  and  $z$  occurs. [Theorem 4.3](#) also implies that IG predator (IG prey)-driven extinction due to strong Allee effect of the basal prey population combined with the high natural death rate of IG prey (IG predator, respectively) leads to the extinction of all species. Therefore, strong Allee effect in the basal prey increases the extinction risk of not only the basal prey but also the IG prey or/and predator. This partially answers the first question listed in [Section 1](#).

(b) The existence and stability of the boundary and interior equilibria were presented in [Theorem 4.6](#). Model (1.3) has at most two interior equilibria  $E_1^*$  and  $E_2^*$ , in which  $E_1^*$  is always unstable. The existence of  $E_1^*$  and  $E_2^*$  and the stability of  $E_1^*$  are independent of  $(\gamma_1, \gamma_2)$ . However, if  $E_2^*$  exists, then its stability can be determined by  $(\gamma_1, \gamma_2)$ . The Hopf bifurcation curve  $\Gamma(\gamma_1, \gamma_2) = 0$  at  $E_2^*$  on  $(\gamma_1, \gamma_2)$ , which depicts the relationship between competition levels of the IG prey and IG predator for the basal resource, is given in [Corollary 4.7](#). If the competition between the IG prey and IG predator for basal resource lies below the critical curve  $\Gamma(\gamma_1, \gamma_2) = 0$ , then  $E_2^*$  remains stable, while above it  $E_2^*$  loses its stability. This partially answers the second question posed in [Section 1](#).

(c) In order to explore the impact of Allee effect, the parameter space of  $\lambda = (\alpha, \beta, a_1, a_2, d_1, d_2)$  was completely classified into sixteen different regions, and in each region the number of interior equilibria was presented as  $\theta$  varies in  $(0, 1)$ , and the corresponding bifurcation diagrams on the Allee threshold  $\theta$  were shown. See [Theorems 5.3, 5.4, 5.6 and 5.8](#) in [Section 5](#). Based on these theorems, we inductively gave the possible extinction parameter regions of at least one species and the necessary coexistence parameter regions of all three species in [Theorem 5.10](#). This may answer the two questions posed in [Section 1](#).

(d) Model (1.3) exhibits rich and complex dynamic behaviors due to Allee effect in the basal prey  $x$ . In [Section 6](#), we provided the possible dynamical patterns, i.e., the existence of multiple attractors, for model (1.3). By theoretical analysis and numerical simulations, we showed that system (1.3) can have one (i.e. extinction of all species), two (i.e. bi-stability) or three (i.e. tri-stability) attractors. This may answer the first question listed in [Section 1](#).

(e) In [Section 6](#) we also found by simulations that when there exists a unique stable interior equilibrium  $E_2^*$ , the orbits which tended to the extinction state  $E_0$  may be attracted to some periodic orbits as  $(\gamma_1, \gamma_2)$  gets closer to the Hopf bifurcation curve  $\Gamma(\gamma_1, \gamma_2) = 0$  from the stable region  $\Gamma(\gamma_1, \gamma_2) > 0$ , meanwhile the basin of attraction of the coexistence equilibrium  $E_2^*$  decreases until it loses its stability since the orbits which tended to  $E_2^*$  also may be attracted to some periodic orbits. Thus, multiple attracting periodic orbits are generated and the coexistence of all three species is enhanced as the competition between the IG prey and IG predator for the basal resource is close to the Hopf bifurcation curve from below. This also may answer the second question listed in [Section 1](#).

Our study provided useful insights on how Allee effect affects the coexistence and extinction of intraguild predation species. By numerical simulations, we found in [Section 6](#) that system (1.3) may have multiple

attracting periodic orbits but we were unable to provide a theoretical proof. Seasonal effects are important for the persistence and extinction of species. For future modeling study, it is meaningful to explore the impact of Allee effect in the nonautonomous version of model (1.3).

## Acknowledgments

The authors are very grateful to the referees for their helpful comments. The research of D. Bai was partially supported by NSF of China (11771104). The research of Y. Kang was supported by NSF, PR China (DMS-1313312, DMS-1716802, IOS/DMS-1558127) and the James S. McDonnell Foundation 21st Century Science Initiative in Studying Complex Systems Scholar Award, USA (220020472). The research of S. Ruan was supported by NSF, PR China (DMS-1853622).

## References

- [1] G.A. Polis, C.A. Myers, R.D. Holt, The ecology and evolution of intraguild predation: potential competitors that eat each other, *Annu. Rev. Ecol. Syst.* 20 (1989) 297–330.
- [2] S.-B. Hsu, S. Ruan, T.-H. Yang, Analysis of three species Lotka–Volterra food web models with omnivory, *J. Math. Anal. Appl.* 426 (2015) 659–687.
- [3] Y. Kang, L. Wedekin, Dynamics of a intraguild predation model with generalist or specialist predator, *J. Math. Biol.* 67 (2013) 1227–1259.
- [4] S.L. Pimm, J.H. Lawton, Feeding on more than one trophic level, *Nature* 275 (1978) 542–544.
- [5] S. Ruan, Persistence and coexistence in zooplankton-phytoplankton-nutrient models with instantaneous nutrient recycling, *J. Math. Biol.* 31 (1993) 633–654.
- [6] T.L. Anderson, R.D. Semlitsch, High intraguild predator density induces thinning effects on and increases temporal overlap with prey populations, *Popul. Ecol.* 56 (2014) 265–273.
- [7] M. Arim, P.A. Marquet, Intraguild predation: a widespread interaction related to species biology, *Ecol. Lett.* 7 (2004) 557–564.
- [8] J.A. Collera, F.M.G. Magpantay, Dynamics of a stage structured intraguild predation model, in: D. Kilgour, H. Kunze, R. Makarov, R. Melnik, X. Wang (Eds.), *Recent Advances in Mathematical and Statistical Methods, AMMCS 2017*, in: Springer Proceedings in Mathematics and Statistics, vol. 259, 2018, pp. 327–337.
- [9] G.A. Polis, Complex trophic interactions in deserts: an empirical critique of food-web theory, *Am. Nat.* 138 (1991) 123–155.
- [10] G.A. Polis, D.R. Strong, Food web complexity and community dynamics, *Am. Nat.* 147 (1996) 813–846.
- [11] R.D. Holt, G.A. Polis, A theoretical framework for intraguild predation, *Am. Nat.* 149 (1997) 745–764.
- [12] K. Tanabe, T. Namba, Omnivory creates chaos in simple food web models, *Ecology* 86 (2005) 3411–3414.
- [13] R. Han, B. Dai, Y. Chen, Pattern formation in a diffusive intraguild predation model with nonlocal interaction effects, *AIP Adv.* 9 (2019) 035046, <http://dx.doi.org/10.1063/1.5084948>.
- [14] S.-B. Hsu, S. Ruan, T.-H. Yang, On the dynamics of two-consumers-one-resource competing systems with Beddington–DeAngelis functional response, *Discrete Contin. Dyn. Syst. Ser. B* 18 (2013) 2331–2353.
- [15] M.R. Leung, A symmetric intraguild predation model for the invasion lionfish and native grouper, *Commun. Math. Biol. Neurosci.* 2015 (2015) 24.
- [16] J.F.T. Rabago, J.A. Collera, Hopf bifurcation in a delayed intraguild predation model, *Southeast Asian Bull. Math.* 42 (2018) 691–709.
- [17] D. Ryan, R.S. Cantrell, Avoidance behavior in intraguild predation communities: a cross-diffusion model, *Discrete Contin. Dyn. Syst.* 35 (2015) 1641–1663.
- [18] H. Shu, X. Hu, L. Wang, J. Watmough, Delay induced stability switch, multitype bistability and chaos in an intraguild predation model, *J. Math. Biol.* 71 (2015) 1269–1298.
- [19] H.-C. Wei, A mathematical model of intraguild predation with prey switching, *Math. Comput. Simulation* 165 (2019) 107–118.
- [20] D. Zhang, B. Dai, A free boundary problem for the diffusive intraguild predation model with intraspecific competition, *J. Math. Anal. Appl.* 474 (2019) 381–412.
- [21] G. Zhang, X. Wang, Extinction and coexistence of species for a diffusive intraguild predation model with B-D functional response, *Discrete Contin. Dyn. Syst. Ser. B* 23 (2018) 3755–3786.
- [22] L. Berec, E. Angulo, F. Courchamp, Multiple Allee effects and population management, *Trends Ecol. Evol.* 22 (2006) 185–191.
- [23] F. Courchamp, L. Berec, J. Gascoigne, *Allee Effects in Ecology and Conservation*, Oxford University Press, Oxford, 2008.
- [24] M.S. Mooring, T.A. Fitzpatrick, T.T. Nishihira, D.D. Reising, Vigilance, predation risk, and the Allee effect in desert bighorn sheep, *J. Wildl. Manag.* 68 (2004) 519–532.

- [25] D.J. Rinella, M.S. Wipfli, C.A. Stricker, R.A. Heintz, M.J. Rinella, Pacific Salmon (*Oncorhynchus* sp.) runs and consumer fitness: growth and energy storage in stream-dwelling salmonids increase with salmon spawner density, *Can. J. Fish. Aquat. Sci.* 69 (2012) 73–84.
- [26] P.A. Stephens, W.J. Sutherland, Consequences of the Allee effect for behaviour, ecology and conservation, *Trends Ecol. Evol.* 14 (1999) 401–405.
- [27] P.A. Stephens, W.J. Sutherland, R.P. Freckleton, What is the Allee effect? *Oikos* 87 (1999) 185–190.
- [28] W. Allee, Studies in animal aggregations: mass protection against colloidal silver among goldfishes, *J. Exp. Zool.* 61 (1932) 185–207.
- [29] B. Dennis, Allee effects: population growth, critical density, and the chance of extinction, *Nat. Resour. Model.* 3 (1989) 481–538.
- [30] Y. Kang, O. Udiani, Dynamics of a single species evolutionary model with Allee effects, *J. Math. Anal. Appl.* 418 (2014) 492–515.
- [31] M.A. Lewis, P. Kareiva, Allee dynamics and the spread of invading organisms, *Theor. Popul. Biol.* 43 (1993) 141–158.
- [32] D. Manna, A. Maiti, G.P. Samanta, A Michaelis–Menten type food chain model with strong Allee effect on the prey, *Appl. Math. Comput.* 311 (2017) 390–409.
- [33] E. González-Olivares, et al., Multiple stability and uniqueness of the limit cycle in a Gause-type predator–prey model considering the Allee effect on prey, *Nonlinear Anal. RWA* 12 (2011) 2931–2942.
- [34] Md.S. Rahman, S. Chakravarty, An eco-epidemiological model of competitive interacting species with Allee effect, *Int. J. Dyn. Control* 3 (2015) 239–252.
- [35] G.A.K. van Voorn, L. Hemerik, M.P. Boer, B.W. Kooi, Heteroclinic orbits indicate overexploitation in predator–prey systems with a strong Allee effect, *Math. Biosci.* 209 (2007) 451–469.
- [36] M.H. Wang, M. Kot, Speeds of invasion in a model with strong or weak Allee effects, *Math. Biosci.* 171 (2001) 83–97.
- [37] J. Wang, J. Shi, J. Wei, Predator–prey system with strong Allee effect in prey, *J. Math. Biol.* 62 (2011) 291–331.
- [38] P.J. Pal, T. Saha, Qualitative analysis of a predator–prey system with double Allee effect in prey, *Chaos Solitons Fractals* 73 (2015) 36–63.
- [39] L. Berec, V. Bernhauerová, B. Boldin, Evolution of mate-finding Allee effect in prey, *J. Theoret. Biol.* 441 (2018) 9–18.
- [40] S.R.J. Jang, Allee effects in a discrete-time host–parasitoid model, *J. Difference Equ. Appl.* 12 (2006) 165–181.
- [41] Y. Kang, Scramble competitions can rescue endangered species subject to strong Allee effects, *Math. Biosci.* 241 (2013) 75–87.
- [42] Y. Kang, A.-A. Yakubu, Weak Allee effects and species coexistence, *Nonlinear Anal. RWA* 12 (2011) 3329–3345.
- [43] S.J. Schreiber, Allee effects, extinctions, and chaotic transients in simple population models, *Theor. Popul. Biol.* 64 (2003) 201–209.
- [44] M. Sen, M. Banerjee, Y. Takeuchi, Influence of Allee effect in prey populations on the dynamics of two-prey-one-predator model, *Math. Biosci. Eng.* 15 (4) (2018) 883–904.
- [45] D. Sen, S. Ghorai, M. Banerjee, Allee effect in prey versus hunting cooperation on predator-enhancement of stable coexistence, *Internat. J. Bifur. Chaos* 29 (6) (2019) 1950081.
- [46] W. Wang, Population dispersal and Allee effect, *Ric. Mat.* 65 (2016) 535–548.
- [47] S.R. Zhou, C.Z. Liu, G. Wang, The competitive dynamics of metapopulation subject to the Allee-like effect, *Theor. Popul. Biol.* 65 (2004) 29–37.
- [48] V. Makler-Pick, M.R. Hipsey, T. Zohary, Y. Carmel, G. Gal, Intraguild predation dynamics in a lake ecosystem based on a coupled hydrodynamic-ecological model: the example of Lake Kinneret (Israel), *Biology* 6 (2017) 22.
- [49] O. Sarnelle, R.A. Knapp, Zooplankton recovery after fish removal: limitations of the egg bank, *Limnol. Oceanogr.* 49 (4, part 2) (2004) 1382–1392.
- [50] S. Wiggins, Introduction to Applied Nonlinear Dynamical Systems and Chaos, in: *Texts in Applied Mathematics*, vol. 2, Springer, New York, 1990.
- [51] J. Guckenheimer, P. Holmes, *Nonlinear Oscillations, Dynamical Systems, and Bifurcations of Vector Fields*, Springer-Verlag, 1983.
- [52] M. Sieber, F.M. Hilker, The hydra effect in predator–prey models, *J. Math. Biol.* 64 (2012) 341–360.
- [53] Y. Kang, S.K. Sasmal, A.R. Bhowmick, J. Chattopadhyay, Dynamics of a predator–prey system with prey subject to Allee effects and disease, *Math. Biosci. Eng.* 11 (4) (2014) 877–918.
- [54] T. Revilla, Effects of intraguild predation on resource competition, *J. Theoret. Biol.* 214 (2002) 49–62.