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ANALYSIS OF DYNAMICS IN A GENERAL INTRAGUILD PREDATION MODEL WITH INTRASPECIFIC COMPETITION*

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Abstract This paper is devoted to studying the dynamical properties of a general intraguild predation model with intraspecific competition. We first investigate the stability of all possible equilibria in relation to the ecological parameters, and then study the long time behavior of the solution. Moreover, we provide a detailed analysis of dynamics of a IGP model with linear functional response and intraspecific competition. Our results show that the impact of the intraspecific competition essentially increases the dynamical complexity of the system.

Keywords General IGP model, intraspecific competition, local and global stability, asymptotic behavior.

MSC(2010) 34A34, 34C11, 34D05, 34D20.

1. Introduction

Competition and predator-prey interaction are two of interspecies relations for ecological and social models [5]. The interaction among different species will exhibit the diversity and complexity, and generate the complex network of biological species [1,27,32]. Intraguild predation (IGP) is a typical type of interaction between three species, including top and intermediate predators termed as IG predator and IG prey, respectively, and a basal resource [26]. The IG predator and IG prey share the same resource while they are engaged in a predator-prey interaction.

A prototypical ODE system based on modeling framework for intraguild predation was made by Holt and Polis [13]. Their model was of form

$$\begin{cases} R'(t) = R(\phi(R) - a_1(R,N,P)N - a_2(R,N,P)P), \\ N'(t) = N(b_1 a_1(R,N,P)R - a_3(R,N,P)P - m_1), \\ P'(t) = P(b_2 a_2(R,N,P)R + b_3 a_3(R,N,P)N - m_2), \end{cases} \tag{1.1}$$

where $R(t)$, $N(t)$ and $P(t)$ are the densities at time t of the basal resource, IG prey, and IG predator, respectively. The functions $a_2(R,N,P)R$ and $a_3(R,N,P)N$ are

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functional responses of the IG predator to the resource and IG prey, respectively; $a_1(R, N, P)R$ is the functional response of the IG prey to the basal resource; and constants m_1 and m_2 are the death rates of the IG prey and predator, respectively. The parameters b_1 and b_2 convert resource consumption into reproduction for the IG prey and IG predator, respectively; the parameter b_3 scales the benefit enjoyed by the IG predator from its consumption of IG prey; $R\phi(R)$ is recruitment of the basal resource.

Usually $a_i(R, N, P)(i = 1, 2, 3)$ satisfy that

$$\frac{\partial[Ra_1(R,N,P)]}{\partial R} \geq 0, \frac{\partial[Ra_2(R,N,P)]}{\partial R} \geq 0, \frac{\partial[Na_3(R,N,P)]}{\partial N} \geq 0$$

for $R \geq 0, N \geq 0, P \geq 0$. $Ra_1(R, N, P) \to M_1, Ra_2(R, N, P) \to M_2$ for some $M_1, M_2 > 0$ as $R \to \infty$ and $Na_3(R, N, P) \to M_3$ for some $M_3 > 0$ as $N \to \infty$. When $\phi(R)$ is of a logistic growth, the dynamics of (1.1) has been considered in many articles, see for example [3,11,14–17,21,29–31]. For (1.1) with logistic growth on the basal resource and simplest linear functional response for the three predation terms, a rigorous dynamical analysis can be obtained (see Hsu et al. [17]). (1.1) with Holling type II functional response has been studied by Abrams and Fung [3]. (1.1) with Holling type II and ratio-dependent functional responses have been investigated by Verdy and Amarasekare [30] and Freeze et al. [11], respectively. And two models have been established by Kang and Wedekin [21], one of which is called IGP model with specialist predator and the other of which is called IGP model with generalist predator, and both models considered Holling type III functional response for predation on the IG prey by the IG predator. Many important phenomena have been observed, such as extinction scenarios, permenence effect of the populations in the IGP model (Freeze et al. [11]; Hsu et al. [17]; Kang and Wedekin [21]).

The role of intraspecific competition in shaping animal or plant communities has formed one of the major issues in ecology for decades. The effect of intraspecific competition within and between the larval instars of the yellow fever mosquito, Aedes aegypti, was investigated by Dye [8]. Hansen et al. [18] reported statistical results showing that both interspecific and intraspecific effects are important in the direct year-to-year density dependence. Kleunen et al. [22] presented the statistical results showing that intraspecific competition among clones of Ranunculus reptans is symmetric and increases the effective population size. Based on ecological theory and a series of experiments, Bolnick [4] provided that intraspecific competition drives disruptive selection and thus may be an important causal agent in the evolution of ecological variation.

We observe that the impact of intraspecific competition for the IG prey and IG predator has not been considered in (1.1) and other majority of works on IGP models except [2], which provides the coexistence of a intraguild predation model with intraspecific competition. In this paper, we shall consider the effect of intraspecific competition in the population growth rate of IG prey and IG predator.

In this paper, based on the model of Holt and Polis [13], taking account of the impact of intraspecific competition, we consider a general IGP model of the following form:

$$\begin{cases} R'(t) = R(\phi(R) - a_1(R)N - a_2(R)P), \\ N'(t) = N(b_1a_1(R)R - a_3(N)P - m_1 - d_1N), \\ P'(t) = P(b_2a_2(R)R + b_3a_3(N)N - m_2 - d_2P), \end{cases} \tag{1.2}$$

where $R(t)$, $N(t)$ and $P(t)$ are the densities at time t of the basal resource, IG prey, and IG predator, respectively. The functions $\phi(R), a_1(R), a_2(R), a_3(N) \in C^r(\mathbb{R}), r \geq 3$ and constants $b_i, m_j, d_j (i = 1, 2, 3; j = 1, 2)$ are interpreted as follows:

(a1) The function $\phi(R)$ describes the specific growth rate of the basal resource in the absence of IG prey and IG predator, and satisfies $\phi(0) > 0, \phi'(R) < 0$ for $R \geq 0$ and $\phi(K) = 0$, where $K > 0$ is the carrying capacity of the basal resource. A prototype is the logistic growth

$$\phi(R) = r\left(1 - \frac{R}{K}\right),$$

which satisfies above conditions.

(a2) The function $a_2(R)R$ and $a_3(N)N$ are functional responses of the IG predator to the resource and IG prey, respectively; $a_1(R)R$ is the functional response of the IG prey to the basal resource. We assume that $a_1(R), a_2(R)$ and $a_3(N)$ are positive, bounded and satisfy

$$\frac{\mathrm{d}[Ra_1(R)]}{\mathrm{d}R} \geq 0, \frac{\mathrm{d}[Ra_2(R)]}{\mathrm{d}R} \geq 0, \frac{\mathrm{d}[Na_3(N)]}{\mathrm{d}N} \geq 0$$

for $R \geq 0, N \geq 0, P \geq 0$.

(a3) The constants m_1 and m_2 are the death rates of the IG prey and predator, respectively. The parameters b_1 and b_2 convert resource consumption into reproduction for the IG prey and IG predator, respectively; the parameter b_3 scales the benefit enjoyed by the IG predator from its consumption of IG prey. And d_1 and d_2 represent the effect of intraspecific competition in the growth rate of IG prey and IG predator, respectively. All above parameters are assumed to be positive.

Our primary purpose is to analyze and demonstrate the complexity of population dynamics in the IGP model (1.2). We will show that the population function $(R(t), N(t), P(t))$ remains positive as long as the initial population $(R(0), N(0), P(0))$ is positive. We also give some results on the ultimate upper bounds of the basal resourse, IG prey and IG predator populations, as well as a extinction result when the initial population $R(0)$ is relatively smaller than $N(0)$ and $P(0)$. Sufficient conditions of permanence (existence of a positive global attractor) are also given for the model (1.2).

The rest of the paper is structured in the following way. In Section 2, we show the boundedness of solutions of (1.2) and present all possible nonnegative equilibria. In Section 3, we analyze the stabilities of trivial, semi-trivial and boundary equilibria. In Section 4, the long time behavior of the solution $(R(t), N(t), P(t))$ of (1.2) is investigated. Application to specific IGP model with simplest linear functional response and detailed biological discussions are given in Section 5. Some concluding remarks are given in Section 6.

2. Preliminaries

For (1.2), the domain of the phase space $\Omega = \{(R, N, P) \in \mathbb{R}^3 | R \geq 0, N \geq 0, P \geq 0\}$ is invariant. The following lemma guarantees that the system (1.2) is dissipative.

Lemma 2.1. *Suppose that $\phi(R), a_1(R), a_2(R)$ and $a_3(N)$ satisfy (a1)-(a2). Then any solution of (1.2) with positive initial value is positive and bounded.*

Proof. The first octant with boundary is an invariant region for (1.2) since $\{(R,N,P): R=0\}, \{(R,N,P) : N=0\}$ and $\{(R,N,P) : P=0\}$ are invariant manifolds of (1.2). Therefore the solutions of (1.2) with the initial values $R(0)>0, N(0)>0$ and $P(0)>0$ are positive.

For any $R(0)>K$, we have that $R' = R\,[\phi(R) - a_1(R)N - a_2(R)P] < 0$ as long as $R>K$; along $R=K, R' = -R[a_1(R)N + a_2(R)P] < 0$; and there is no any equilibrium point in the region $\{(R,N,P) : R>K, N\geq 0, P\geq 0\}$. Hence any positive solution satisfies

$$R(t) \leq \max\{R(0), K\} \triangleq J_1, \ \forall t \geq 0.$$

Then, we can see from (1.2) that

$$\begin{aligned}(b_1R+N)' &= b_1R[\phi(R) - a_2(R)P] - N[a_3(N)P + m_1 + d_1N] \\ &\leq b_1R\phi(R) - m_1N \\ &\leq b_1J_1\phi(0) + m_1b_1J_1 - m_1(b_1R+N), \ t\geq 0.\end{aligned}$$

From Gronwall's inequality, we obtain that

$$b_1R(t) + N(t) \leq (b_1R(0) + N(0))e^{-m_1t} + \frac{b_1J_1\phi(0) + m_1b_1J_1}{m_1}(1 - e^{-m_1t}).$$

Hence we have

$$N(t) \leq (R(0) + N(0)) + \frac{b_1J_1\phi(0) + m_1b_1J_1}{m_1} \triangleq J_2, \ \forall t \geq 0.$$

Let $\sigma_1 = \max\limits_{t\geq 0} a_1(R(t))$. Similarly, for $t \geq 0$, we have

$$\begin{aligned}(b_2R + b_3N + P)' =& b_2R[\phi(R) - a_1(R)N] + b_3N[b_1a_1(R)R - m_1 - d_1N] \\ &- P(m_2 + d_2P) \\ \leq& b_2J_1\phi(0) + \sigma_1b_1b_3J_1J_2 - b_3m_1N - m_2P \\ \leq& b_2J_1\phi(0) + \sigma_1b_1b_3J_1J_2 + \kappa b_2J_1 - \kappa(b_2R + b_3N + P),\end{aligned}$$

where $\kappa = \min\{m_1, m_2\}$. Using Gronwall's inequality again, we have that

$$b_2R(t) + b_3N(t) + P(t) \leq (b_2R(0) + b_3N(0) + P(0))e^{-\kappa t} + J_3(1 - e^{-\kappa t}),$$

where $J_3 = \frac{b_2J_1\phi(0)}{\kappa} + \frac{\sigma_1b_1b_3J_1J_2}{\kappa} + b_2J_1$. Hence $P(t)$ is also bounded. □

Then, we shall show the equilibria of system (1.2). There exist five possible non-negative equilibria as follows.

(i) System (1.2) always has trivial equilibrium $E_0 := (0,0,0)$ and semi-trivial equilibrium $E_1 := (K,0,0)$.

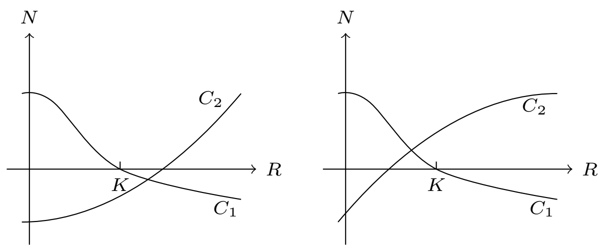
(ii) The IG prey-only equilibrium $E_{10} := (R_1, N_1, 0)$ is a boundary equilibrium of system (1.2) if and only if $b_1a_1(K)K > m_1$, where R_1, N_1 satisfy $\phi(R_1) - a_1(R_1)N_1 = b_1a_1(R_1)R_1 - m_1 - d_1N_1 = 0$ with $0 < R_1, N_1 < K$. In fact, the existence result of E_{10} follows from the two case for the intersection of two curves, $C_1 : \phi(R) - a_1(R)N = 0$ and $C_2 : b_1a_1(R)R - m_1 - d_1N = 0$ (see Fig. 1).

(iii) The IG predator-only equilibrium $E_{01} := (R_2, 0, P_2)$ is a boundary equilibrium of system (1.2) if and only if $b_2a_2(K)K > m_2$, where R_2, P_2 satisfy $\phi(R_2) - a_2(R_2)P_2 = b_2a_2(R_2)R_2 - m_2 - d_2P_2 = 0$ with $0 < R_2, P_2 < K$. Similarly, we can obtain the existence result of E_{01} from the two case for the intersection of two curves, $C_3 : \phi(R) - a_2(R)P = 0$ and $C_4 : b_2a_2(R)R - m_2 - d_2P = 0$ (see Fig. 2).

(iv) If (R^*, N^*, P^*) is the intersection point of

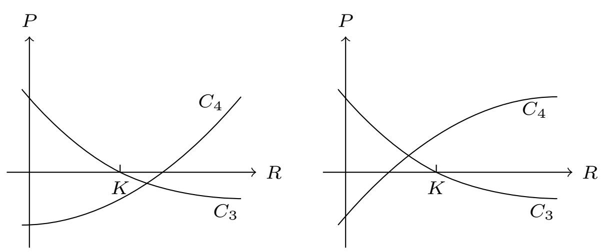
$$\begin{cases} \phi(R) - a_1(R)N - a_2(R)P = 0, \\ b_1a_1(R)R - a_3(N)P - m_1 - d_1N = 0, \\ b_2a_2(R)R + b_3a_3(N)N - m_2 - d_2P = 0, \end{cases}$$

with $0 < R^*, N^*, P^* < K$, then system (1.2) admits a positive equilibrium: $E^* := (R^*, N^*, P^*)$.



(a) $b_1a_1(K)K < m_1$ (b) $b_1a_1(K)K > m_1$

Figure 1. The two possible generic cases for the intersection of the two curves C_1 and C_2.



(a) $b_2a_2(K)K < m_2$ (b) $b_2a_2(K)K > m_2$

Figure 2. The two possible generic cases for the intersection of the two curves C_3 and C_4.

3. Stability of Trivial, Semi-Trivial and Boundary Equilibria

In this section, we provide some stability analyses for system (1.2) in the domain Ω. Without loss of generality, denote a non-negative equilibrium point of (1.2) as $E = (\hat{R}, \hat{N}, \hat{P})$ and define $X(t) = (R(t), N(t), P(t))^T$. Then the linearized equation of (1.2) at equilibrium E is described as

$$X'(t) = AX(t),$$

where A is a 3×3 matrix given by

$$A = \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix},$$

with

$$\begin{aligned}
&a_{11} = \phi(\hat{R}) - a_1(\hat{R})\hat{N} - a_2(\hat{R})\hat{P} + \hat{R}[\phi'(\hat{R}) - a_1'(\hat{R})\hat{N} - a_2'(\hat{R})\hat{P}],\\
&a_{12} = -\hat{R}a_1(\hat{R}),\ a_{13} = -\hat{R}a_2(\hat{R}),\ a_{21} = b_1\hat{N}[a_1'(\hat{R})\hat{R} + a_1(\hat{R})],\\
&a_{22} = b_1a_1(\hat{R})\hat{R} - a_3(\hat{N})\hat{P} - m_1 - d_1\hat{N} - \hat{N}[a_3'(\hat{N})\hat{P} + d_1],\ a_{23} = -\hat{N}a_3(\hat{N}),\\
&a_{31} = b_2\hat{P}[a_2'(\hat{R})\hat{R} + a_2(\hat{R})], a_{32} = b_3\hat{P}[a_3'(\hat{N})\hat{N} + a_3(\hat{N})],\\
&a_{33} = b_2a_2(\hat{R})\hat{R} + b_3a_3(\hat{N})\hat{N} - m_2 - 2d_2\hat{P}.
\end{aligned}$$

Thus, the characteristic equation of (1.2) at equilibrium E is given by

$$\triangle(E) \triangleq \det[\lambda I - A] = 0, \tag{3.1}$$

where I is an 3×3 unit matrix and λ denotes the characteristic root of Eq.(3.1).

We first give the stability conclusions of equilibria E_0 and E_1 as follows.

Theorem 3.1. *Consider system (1.2).*

(i) The trivial equilibrium E_0 is always unstable.

(ii) The semi-trivial equilibrium E_1 is locally asymptotically stable if and only if $b_1a_1(K)K < m_1$ and $b_2a_2(K)K < m_2$.

Proof. (i) Since

$$\triangle(E_0) = (\lambda - \phi(0))(\lambda + m_1)(\lambda + m_2) = 0,$$

the characteristic roots are given by $\lambda_1 = \phi(0), \lambda_2 = -m_1$ and $\lambda_3 = -m_2$. Thus, E_0 is unstable.

(ii) The characteristic equation about E_1 is given by

$$\triangle(E_1) = (\lambda - K\phi'(K))(\lambda + m_1 - b_1a_1(K)K)(\lambda + m_2 - b_2a_2(K)K) = 0,$$

which gives the eigenvalues $\lambda_1 = K\phi'(K)$, $\lambda_2 = b_1a_1(K)K - m_1$ and $\lambda_3 = b_2a_2(K)K - m_2$. Since $\phi'(K) < 0$, the conclusion is correct. □

Remark 3.1. If the trivial equilibrium E_1 is stable, then neither of the two boundary equilibria, E_{10} and E_{01} exist, and when E_1 loses its stability, one or both boundary equilibria emerge. In the case when either $m_1 = b_1a_1(K)K$ or $m_2 = b_2a_2(K)K$, the characteristic equation of E_1 has an eigenvalue $\lambda = 0$, and the remaining eigenvalues all have negative real parts. If $m_1 = b_1a_1(K)K$ and $m_2 = b_2a_2(K)K$, then system (1.2) has only two equilibria, E_0 and E_1.

Next, we study the stability of the IG prey-only equilibrium E_{10}. The characteristic equation corresponding to E_{10} will be

$$\triangle(E_{10}) \triangleq (\lambda^2 - T_1(d_1)\lambda + D_1(d_1))(\lambda - M_1) = 0, \tag{3.2}$$

where

$$\begin{aligned} T_1(d_1) &= R_1[\phi'(R_1) - a_1'(R_1)N_1] - N_1 d_1, \\ D_1(d_1) &= R_1 N_1[b_1 a_1(R_1)(a_1'(R_1)R_1 + a_1(R_1)) - d_1(\phi'(R_1) - a_1'(R_1)N_1)], \\ M_1 &= b_2 a_2(R_1)R_1 + b_3 a_3(N_1)N_1 - m_2. \end{aligned}$$

Theorem 3.2. *Consider system (1.2) with $b_1a_1(K)K > m_1$.*

(i) When $M_1 > 0$ or $T_1(d_1) > 0$ or $D_1(d_1) < 0$, the equilibrium E_{10} is unstable.

(ii) When $M_1 < 0$ and $\phi'(R_1) - a_1'(R_1)N_1 < 0$, the equilibrium E_{10} is locally asymptotically stable.

Proof. (i) From the above definitions, we have that Eq.(3.2) has at least one root with positive real part when $M_1 > 0$ or $T_1(d_1) > 0$ or $D_1(d_1) < 0$. Hence, the equilibrium E_{10} is unstable.

(ii) If $\phi'(R_1) - a_1'(R_1)N_1 < 0$, then $T_1(d_1) <$ and $D_1(d_1) > 0$. That is, when $M_1 < 0$ and $\phi'(R_1) - a_1'(R_1)N_1 < 0$, all roots of Eq.(3.2) has negative real part. Hence the conclusion is correct. □

For the IG predator-only equilibrium E_{01}, we have the following similar conclusion.

Theorem 3.3. *Consider system (1.2) with $b_2a_2(K)K > m_2$. Define*

$$\begin{aligned} T_2(d_2) &\triangleq R_2[\phi'(R_2) - a_2'(R_2)P_2] - P_2 d_2, \\ D_2(d_2) &= R_2 P_2[b_2 a_2(R_2)(a_2'(R_2)R_2 + a_2(R_2)) - d_2(\phi'(R_2) - a_2'(R_2)P_2)], \\ M_2 &= b_1 a_1(R_2)R_2 - a_3(0)P_2 - m_1. \end{aligned}$$

(i) When $M_2 > 0$ or $T_2(d_2) > 0$ or $D_2(d_2) < 0$, the equilibrium E_{01} is unstable.

(ii) When $M_2 < 0$ and $\phi'(R_2) - a_2'(R_2)P_2 < 0$, the equilibrium E_{01} is locally asymptotically stable.

The proof of Theorem 3.3 is similar to that of Theorem 3.2, hence we omit it here.

Remark 3.2. Given $b_2a_2(K)K > m_2$, we note that if $b_1a_1(K)K < m_1$ and $\phi'(R_2) - a_2'(R_2)P_2 < 0$, then the IG predator-only steady state, E_{01}, is always stable since in this case we can easily show that $M_2 < b_1a_1(K)K - m_1 < 0$.

We finally give the conditions for global asymptotic stability of the semi-trivial equilibrium E_1 and boundary equilibrium E_{01}.

Theorem 3.4.

(i) If $b_1a_1(K)K < m_1$ and $b_2a_2(K)K < m_2$, then the equilibrium E_1 is globally asymptotically stable.

(ii) If $b_1a_1(K)K < m_1, b_2a_2(K)K > m_2$ and $\phi'(R_2) - a_2'(R_2)P_2 < 0$, then the equilibrium E_{01} is globally asymptotically stable.

Proof. (i) It follows from the proof of Theorem 2.1 that $\limsup_{t\to+\infty} R(t) \le K$, which implies that for any $\varepsilon > 0$, there exists $T_1 > 0$ such that $R(t) < K + \varepsilon$ in $[T_1, +\infty)$. Then from the second equation of (1.2), we have

$$N'(t) \le N\left[b_1a_1(K+\varepsilon)(K+\varepsilon) - m_1\right], t \in [T_1, +\infty).$$

When $b_1a_1(K)K < m_1$, we can choose ε small enough such that $b_1a_1(K+\varepsilon)(K+\varepsilon) < m_1$ since $\frac{\mathrm{d}[Ra_1(R)]}{\mathrm{d}R} \geq 0$. This means that $0 \leq N(t) \to 0$ as $t \to +\infty$. For any given $\varepsilon > 0$, there exists $T_2 > T_1 > 0$, such that

$$0 \leq N(t) < \varepsilon, t \in [T_2, +\infty).$$

Similarly, if $b_2a_2(K)K < m_2$, then we can choose ε small enough such that $b_2a_2(K+\varepsilon)(K+\varepsilon) + b_3a_3(\varepsilon)\varepsilon < m_2$, which leads to $0 \leq P(t) \to 0$ as $t \to +\infty$. The equation of $R(t)$ is now asymptotically autonomous (see [24]), and its limit behavior is determined by the semiflow generated by the following equation:

$$R'(t) = R\phi(R). \tag{3.3}$$

It is well-known that every orbit of (3.3) converges to the unique positive constant solution $R = K$ (see [19]). Then from the theory of asymptotically autonomous system [24], we can see that the solution $((R(t), N(t), P(t))$ of (1.2) converges to $(K, 0, 0)$ as $t \to +\infty$. Since $b_1a_1(K)K < m_1$ and $b_2a_2(K)K < m_2$, it follows from Theorem 3.1(ii) that E_1 is locally asymptotically stable. Thus the equilibrium E_1 is globally asymptotically stable, which proves the part (i).

(ii) When $b_1a_1(K)K < m_1$, from the proof of part (i), we know that the equations of $(R(t), P(t))$ are now asymptotically autonomous (see [24]), and their limits behavior is determined by the semiflow generated by the following equations:

$$\begin{cases} R'(t) = R(\phi(R) - a_2(R)P), \\ P'(t) = P(b_2a_2(R)R - m_2 - d_2P). \end{cases} \tag{3.4}$$

If $b_2a_2(K)K > m_2$, then (R_2, P_2) is the unique positive constant solution to (3.4). We construct a well known Lyapunov functional as follows:

$$V(R(t), P(t)) = \int_{R_2}^{R} \frac{b_2a_2(\xi)\xi - m_2 - d_2P_2}{a_2(\xi)\xi}\mathrm{d}\xi + \int_{P_2}^{P} \frac{\eta - P_2}{\eta}\mathrm{d}\eta.$$

Then

$$\begin{aligned} V_t(u, w) &= \frac{b_2a_2(R)R - m_2 - d_2P_2}{a_2(R)R}R_t + \frac{P - P_2}{P}P_t \\ &= (b_2a_2(R)R - m_2 - d_2P_2)\left(\frac{\phi(R)}{a_2(R)} - P_2\right) - d_2(P - P_2)^2 \\ &= (b_2a_2(R)R - b_2a_2(R_2)R_2)\left(\frac{\phi(R)}{a_2(R)} - \frac{\phi(R_2)}{a_2(R_2)}\right) - d_2(P - P_2)^2. \end{aligned}$$

Therefore, the definitions of R_2, P_2 and (a1), (a2) imply that $V_t \leq 0$ along an orbit $(R(t), P(t))$ of subsystem (3.4) with any nonnegative initial condition $(R(0), P(0)) \neq (0, 0)$ or $(K, 0)$. And $V_t = 0$ if and only if $(R(t), P(t)) = (R_2, P_2)$, from which we obtain that $\lim_{t\to\infty}(R(t), P(t)) = (R_2, P_2)$. Similarly, it follows that the boundary equilibrium E_{01} is globally asymptotically stable, which completes the proof of part (ii). □

4. Dynamical Properties of the Solution

This section is devoted to investigating the long time behavior of the solution $(R(t), N(t), P(t))$ of (1.2). We first focus on finding the upper-bound functions for the basal resource, IG prey, and IG predator populations $R(t), N(t)$ and $P(t)$. These bounds will provide us with crucial information on extinction, co-existence, and exponential convergence of the species.

4.1. Exponential bounds and extinction scenarios

In this subsection, we study the ultimate bounds for the populations in model (1.2). The following theorem concerns the exponential bounds of the IG prey and IG predator, which leads to conditions for extinction of these populations.

Theorem 4.1. *Assume that $(R(t), N(t), P(t))$ is the solution of (1.2) with $R(0) > 0, N(0) > 0$ and $P(0) > 0$. Then $(R(t), N(t), P(t))$ satisfies*

$$\begin{cases} R(t) > 0 \text{ and } \limsup_{t\to\infty} R(t) \le K, \\ N(0)e^{-(\sigma_3 J_3 + m_1 + d_1 J_2)t} \le N(t) \le N(0)e^{(b_1\sigma_1 J_1 - m_1)t}, \\ P(0)e^{-(m_2 + d_2 J_3)t} \le P(t) \le P(0)e^{(b_2\sigma_2 J_1 + b_3\sigma_3 J_2 - m_2)t}, \end{cases} \tag{4.1}$$

where $\sigma_i = \max_{t\ge 0} a_i(R(t))(i = 1, 2), \sigma_3 = \max_{t\ge 0} a_3(N(t))$ and $J_i(i = 1, 2, 3)$ are defined in Lemma 2.1. Moreover,

(i) if $b_1\sigma_1 J_1 < m_1$, then the IG prey population $N(t)$ converges to 0 as $t \to \infty$;

(ii) if $b_2\sigma_2 J_1 + b_3\sigma_3 J_2 < m_2$, then the IG predator population $P(t)$ converges to 0 as $t \to \infty$.

Proof. Recall that the original equation for the basal resource population is

$$R'(t) = R(\phi(R) - a_1(R)N - a_2(R)P).$$

From Lemma 2.1, we can directly get that $R(t) > 0$ for $R(0) > 0$ and

$$\limsup_{t\to\infty} R(t) \le K.$$

Likewise, from the second and third equation in (1.2), we have

$$N(-\sigma_3 J_3 - m_1 - d_1 J_2) \le \frac{\mathrm{d}N}{\mathrm{d}t} \le N(b_1\sigma_1 J_1 - m_1),$$

and

$$P(-m_2 - d_2 J_3) \le \frac{\mathrm{d}P}{\mathrm{d}t} \le P(b_2\sigma_2 J_1 + b_3\sigma_3 J_2 - m_2).$$

The comparison argument also implies that $N(t)$ and $P(t)$ satisfy the inequalities in (4.1) and remain positive at any finite time. The upper bound $N(0)e^{(b_1\sigma_1 J_1 - m_1)t}$ for $N(t)$ converges to 0 as $t \to \infty$ when $b_1\sigma_1 J_1 < m_1$, and the upper bound $P(0)e^{(b_2\sigma_2 J_1 + b_3\sigma_3 J_2 - m_2)t}$ for $P(t)$ converges to 0 as $t \to \infty$ when $b_2\sigma_2 J_1 + b_3\sigma_3 J_2 < m_2$. □

We observe from the above proof that

$$R'(t) \ge R(\phi(R) - \sigma_1 J_2 - \sigma_2 J_3),$$

which implies that if $\sigma_1 J_2 + \sigma_2 J_3 < \phi(0)$, then the basal resource species is persistent with

$$\liminf_{t\to\infty} R(t) \ge c > 0,$$

where c is the unique root of $\phi(R) - \sigma_1 J_2 - \sigma_2 J_3 = 0$. The following theorem indicates that (1.2) is not persistent for larger $\sigma_1 J_2 + \sigma_2 J_3$.

Theorem 4.2. *If the following conditions hold:*

$$b_1\sigma_1 J_1 < m_1,\ b_2\sigma_2 J_1 + b_3\sigma_3 J_2 < m_2,\ \sigma_1 J_2 + \sigma_2 J_3 > \phi(0),$$
$$m_1 - \alpha b_1\sigma_1 J_2 > \max\{\sigma_3 J_3 + m_1 + d_1 J_2, m_2 + d_2 J_3\},$$

where $\alpha = \sigma_1 J_2 + \sigma_2 J_3 - \phi(0)$*, then there exist positive solutions* $(R(t), N(t), P(t))$ *of (1.2) with*

$$\lim_{t\to\infty}(R(t), N(t), P(t)) = (0, 0, 0).$$

Proof. Let $\nu = \min\{\sigma_3 J_3 + m_1 + d_1 J_2, m_2 + d_2 J_3\}$ and denote $F(t) = \max\left\{\frac{R(t)}{N(t)}, \frac{R(t)}{P(t)}\right\}$. Assume that $0 < \frac{R(0)}{N(0)}, \frac{R(0)}{P(0)} < \alpha$. We claim that $F(t) < \alpha$ and $\lim_{t\to\infty} R(t) = 0$ for all $t > 0$.

By contradiction, assume that $F(T) = \alpha$ and $F(t) < \alpha$ for $0 < t < T$. By standard comparison argument, then we have

$$\begin{aligned} R'(t) \le \alpha N'(t) &= \alpha N(b_1 a_1(R)R - a_3(N)P - m_1 - d_1 N) \\ &\le \alpha b_1\sigma_1 J_2 R - m_1\alpha N \\ &\le (\alpha b_1\sigma_1 J_2 - m_1)R \end{aligned}$$

for $0 \le t \le T$ and $R(t) \le R(0)e^{-(m_1-\alpha b_1\sigma_1 J_2)t}$ for $0 \le t \le T$. From Theorem 4.1, we also know that $N(t) \ge N(0)e^{-(\sigma_3 J_3 + m_1 + d_1 J_2)t}$ and $P(t) \ge P(0)e^{-(m_2+d_2 J_3)t}$. It follows that

$$\frac{R(t)}{N(t)} \le \frac{R(0)}{N(0)}\frac{e^{(\sigma_3 J_3 + m_1 + d_1 J_2)t}}{e^{(m_1-\alpha b_1\sigma_1 J_2)t}}$$

and

$$\frac{R(t)}{P(t)} \le \frac{R(0)}{P(0)}\frac{e^{(m_2+d_2 J_3)t}}{e^{(m_1-\alpha b_1\sigma_1 J_2)t}}$$

on the interval $0 \le t \le T$. Since $m_1 - \alpha b_1\sigma_1 J_2 > \nu$, we have that $F(t) < \alpha$ for $0 \le t \le T$, which contradicts with the assumption that $F(T) = \alpha$. It follows that $R(t) \le R(0)e^{-(m_1-\alpha b_1\sigma_1 J_2)t}$ for $0 \le t < \infty$, and we have $\lim_{t\to\infty} R(t) = 0$. From Theorem 4.1, we obtain $\lim_{t\to\infty} N(t) = 0$ and $\lim_{t\to\infty} P(t) = 0$. □

Remark 4.1. Under the assumption of Theorem 4.2 we have that $\lim_{t\to\infty}(R(t), N(t), P(t)) = (0, 0, 0)$ when the initial population $R(0)$ is relatively smaller than $N(0)$ and $P(0)$. However, the restrictions on the ratio of initial population sizes required in the proof of Theorem 4.2 do not allow us to obtain even local asymptotic stability for the trivial equilibrium E_0.

4.2. Permanence

In order to investigate the permanence effect of the populations in the model (1.2) when $b_1\sigma_1 J_1 > m_1$ and $b_2\sigma_2 J_1 + b_3\sigma_3 J_2 > m_2$, we apply the approach of Pao in [25], defining a pair of upper-lower solutions $(\widetilde{R}, \widetilde{N}, \widetilde{P})$ and $(\widehat{R}, \widehat{N}, \widehat{P})$ for system (1.2) satisfying the following differential inequalities:

$$
\begin{aligned}
&\frac{\mathrm{d}\widetilde{R}}{\mathrm{d}t} \geq \widetilde{R}(\phi(\widetilde{R}) - a_1(\widetilde{R})\widehat{N} - a_2(\widetilde{R})\widehat{P}),\\
&\frac{\mathrm{d}\widetilde{N}}{\mathrm{d}t} \geq \widetilde{N}(b_1a_1(\widetilde{R})\widetilde{R} - a_3(\widetilde{N})\widehat{P} - m_1 - d_1\widetilde{N}),\\
&\frac{\mathrm{d}\widetilde{P}}{\mathrm{d}t} \geq \widetilde{P}(b_2a_2(\widetilde{R})\widetilde{R} + b_3a_3(\widetilde{N})\widetilde{N} - m_2 - d_2\widetilde{P}),\\
&\frac{\mathrm{d}\widehat{R}}{\mathrm{d}t} \leq \widehat{R}(\phi(\widehat{R}) - a_1(\widehat{R})\widetilde{N} - a_2(\widehat{R})\widetilde{P}),\\
&\frac{\mathrm{d}\widehat{N}}{\mathrm{d}t} \leq \widehat{N}(b_1a_1(\widehat{R})\widehat{R} - a_3(\widehat{N})\widetilde{P} - m_1 - d_1\widehat{N}),\\
&\frac{\mathrm{d}\widehat{P}}{\mathrm{d}t} \leq \widehat{P}(b_2a_2(\widehat{R})\widehat{R} + b_3a_3(\widehat{N})\widehat{N} - m_2 - d_2\widehat{P}),
\end{aligned}
\tag{4.2}
$$

with $(\widetilde{R}(t), \widetilde{N}(t), \widetilde{P}(t)) \geq (\widehat{R}(t), \widehat{N}(t), \widehat{P}(t))$ for all $t \geq 0$. It is well-known by comparison arguments in differential equation systems (see [25]) that if there exists a pair of upper-lower solutions, then the solution of model (1.2) satisfies

$$(\widetilde{R}(t), \widetilde{N}(t), \widetilde{P}(t)) \geq (R(t), N(t), P(t)) \geq (\widehat{R}(t), \widehat{N}(t), \widehat{P}(t))$$

for all $t > 0$ as long as

$$(\widetilde{R}(0), \widetilde{N}(0), \widetilde{P}(0)) \geq (R(0), N(0), P(0)) \geq (\widehat{R}(0), \widehat{N}(0), \widehat{P}(0)).$$

The three inequalities in (4.2) for lower solutions can be easily satisfied by setting

$$(\widehat{R}(t), \widehat{N}(t), \widehat{P}(t)) = (0, 0, 0),$$

which gives the nonnegativity of the populations. For ultimate upper bounds of the populations, it suffices to suitably construct upper solutions $(\widetilde{R}(t), \widetilde{N}(t), \widetilde{P}(t))$ with $(\widetilde{R}(0), \widetilde{N}(0), \widetilde{P}(0)) = (R(0), N(0), P(0))$.

Lemma 4.1. *Assume that* $b_1a_1(K)K > m_1$ *and* $b_2a_2(K)K + b_3a_3(J_4)J_4 > m_2$, *where* $J_4 = \frac{b_1a_1(K)K - m_1}{d_1}$. *If* $(R(0), N(0), P(0)) > (0, 0, 0)$, *then the population function* $(R(t), N(t), P(t))$ *as solution of (1.2) remains nonnegative and satisfies*

$$
\begin{cases}
\limsup\limits_{t\to\infty} R(t) \leq K,\\
\limsup\limits_{t\to\infty} N(t) \leq \dfrac{b_1a_1(K)K - m_1}{d_1},\\
\limsup\limits_{t\to\infty} P(t) \leq \dfrac{b_2a_2(K)K + b_3a_3(J_4)J_4 - m_2}{d_2}.
\end{cases}
\tag{4.3}
$$

Proof. By setting $(\widehat{R}(t), \widehat{N}(t), \widehat{P}(t)) = (0, 0, 0)$, we can find an upper solution $\widetilde{R}$ for $R(t)$ in model (1.2) that satisfies

$$\frac{\mathrm{d}\widetilde{R}}{\mathrm{d}t} = \widetilde{R}\phi(\widetilde{R}),\ \widetilde{R}(0) = R(0). \tag{4.4}$$

It is known through a simple stability analysis of (4.4) that

$$\limsup_{t\to\infty} R(t) \le \lim_{t\to\infty} \widetilde{R}(t) = K. \tag{4.5}$$

For any $\varepsilon > 0$, there exists a $T_3 > 0$ such that

$$\frac{\mathrm{d}N}{\mathrm{d}t} \le N(b_1a_1(K)K - m_1 - d_1N) + \varepsilon$$

in (T_3, ∞). From the arbitrariness of ε, we can find an upper solution $\widetilde{N}$ for $N(t)$ in (T_3, ∞),

$$\frac{\mathrm{d}\widetilde{N}}{\mathrm{d}t} = \widetilde{N}(b_1a_1(K)K - m_1 - d_1\widetilde{N}),\ \widetilde{N}(T_3) = N(T_3). \tag{4.6}$$

Seeing that for $b_1a_1(K)K > m_1$, the positive equilibrium $\frac{b_1a_1(K)K-m_1}{d_1}$ of (4.6) is globally asymptotically stable, we can also conclude that

$$\limsup_{t\to\infty} N(t) \le \lim_{t\to\infty} \widetilde{N}(t) = \frac{b_1a_1(K)K - m_1}{d_1} \triangleq J_4. \tag{4.7}$$

Finally, by the ultimate upper bounds for $R(t)$ and $N(t)$ given in (4.5) and (4.7), we see that for any $\varepsilon > 0$, there exists $T_4 > T_3 > 0$ such that

$$\frac{\mathrm{d}P}{\mathrm{d}t} \le P(b_2a_2(K)K + b_3a_3(J_4)J_4 - m_2 - d_2P) + \varepsilon$$

in (T_4, ∞). Again from the arbitrariness of ε, we can find an upper solution $\widetilde{P}$ for $P(t)$ in (T_4, ∞),

$$\frac{\mathrm{d}\widetilde{P}}{\mathrm{d}t} = \widetilde{P}(b_2a_2(K)K + b_3a_3(J_4)J_4 - m_2 - d_2\widetilde{P}),\ \widetilde{P}(T_4) = P(T_4). \tag{4.8}$$

When $b_1a_1(K)K > m_1$ and $b_2a_2(K)K + b_3a_3(J_4)J_4 > m_2$, the equation (4.8) has only one positive equilibrium $\frac{b_2a_2(K)K+b_3a_3(J_4)J_4-m_2}{d_2}$ which is globally asymptotically stable. This implies that

$$\limsup_{t\to\infty} P(t) \le \lim_{t\to\infty} \widetilde{P}(t) = \frac{b_2a_2(K)K + b_3a_3(J_4)J_4 - m_2}{d_2}. \qquad \square$$

We next show the sufficient conditions when the IGP model (1.2) is permanent with all populations ultimately bounded away from 0 provided that $\sigma_1J_2 + \sigma_2J_3 < \phi(0)$.

Lemma 4.2. *Assume that* $b_1a_1(c)c - a_3(J_4)J_5 > m_1, b_2a_2(c)c + b_3a_3(J_6)J_6 > m_2$ *and* $\sigma_1J_2 + \sigma_2J_3 < \phi(0)$, *where* $J_i (i = 4, 5, 6)$ *are defined in the proof of this lemma. If* $(R(0), N(0), P(0)) > (0, 0, 0)$, *then the population function* $(R(t), N(t), P(t))$ *as solution of (1.2) satisfies*

$$\begin{cases} \liminf\limits_{t\to\infty} R(t) \ge c, \\ \liminf\limits_{t\to\infty} N(t) \ge \dfrac{b_1a_1(c)c - a_3(J_4)J_5 - m_1}{d_1}, \\ \liminf\limits_{t\to\infty} P(t) \ge \dfrac{b_2a_2(c)c + b_3a_3(J_6)J_6 - m_2}{d_2}. \end{cases} \tag{4.9}$$

Proof. It is clear that the upper and lower solutions for model (1.2) are the upper and lower bounds of the populations $(R(t), N(t)P(t))$ in respective time intervals. From the nonnegativity of the populations, we see that a lower solution for $R(t)$ can be obtained by the equation

$$\frac{\mathrm{d}\widehat{R}}{\mathrm{d}t} = \widehat{R}(\phi(\widetilde{R}) - \sigma_1 J_2 - \sigma_2 J_3) \text{ in } (0,\infty),\ \widehat{R}(0) = R(0). \tag{4.10}$$

By the assumption that $\sigma_1 J_2 + \sigma_2 J_3 < \phi(0)$, we have

$$\liminf_{t\to\infty} R(t) \geq \lim_{t\to\infty} \widehat{R}(t) = c > 0. \tag{4.11}$$

Using the nonnegativity of $P(t)$, for any $\varepsilon > 0$, there exists a $T_5 > 0$ such that

$$\frac{\mathrm{d}N}{\mathrm{d}t} \geq N(b_1 a_1(c)c - a_3(J_4)J_5 - m_1 - d_1 N) - \varepsilon$$

in (T_5, ∞), where $J_4 = \frac{b_1 a_1(K)K - m_1}{d_1}$, $J_5 = \frac{b_2 a_2(K)K + b_3 a_3(J_4)J_4 - m_2}{d_2}$. From the arbitrariness of ε, we can find a lower solution $\widehat{N}$ for $N(t)$ in (T_5, ∞),

$$\frac{\mathrm{d}\widehat{N}}{\mathrm{d}t} = \widehat{N}(b_1 a_1(c)c - a_3(J_4)J_5 - m_1 - d_1\widehat{N}),\ \widehat{N}(T_5) = N(T_5). \tag{4.12}$$

Seeing that the nontrivial equilibrium $\frac{b_1 a_1(c)c - a_3(J_4)J_5 - m_1}{d_1} > 0$ of (4.12) is globally asymptotically stable when $b_1 a_1(c)c - a_3(J_4)J_5 > m_1$, we can also conclude that

$$\liminf_{t\to\infty} N(t) \geq \lim_{t\to\infty} \widehat{N}(t) = \frac{b_1 a_1(c)c - a_3(J_4)J_5 - m_1}{d_1} \triangleq J_6. \tag{4.13}$$

Finally, by the ultimate lower bounds for $R(t)$ and $N(t)$ given in (4.11) and (4.13), we obtain that for any $\varepsilon > 0$, there exists $T_6 > T_5 > 0$ such that

$$\frac{\mathrm{d}P}{\mathrm{d}t} \geq P(b_2 a_2(c)c + b_3 a_3(J_6)J_6 - m_2 - d_2 P) - \varepsilon$$

in (T_6, ∞), where $J_6 = \frac{b_1 a_1(c)c - a_3(J_4)J_5 - m_1}{d_1}$. From the arbitrariness of ε, we can also find a lower solution $\widehat{P}$ for $P(t)$ in (T_6, ∞),

$$\frac{\mathrm{d}\widehat{P}}{\mathrm{d}t} = \widehat{P}(b_2 a_2(c)c + b_3 a_3(J_6)J_6 - m_2 - d_2\widehat{P}),\ \widetilde{P}(T_6) = P(T_6). \tag{4.14}$$

When $b_1 a_1(c)c - a_3(J_4)J_5 > m_1$ and $b_2 a_2(c)c + b_3 a_3(J_6)J_6 > m_2$, the nonlinear equation (4.14) has only one positive equilibrium $\frac{b_2 a_2(c)c + b_3 a_3(J_6)J_6 - m_2}{d_2}$ which is globally asymptotically stable. This implies that

$$\liminf_{t\to\infty} P(t) \geq \lim_{t\to\infty} \widehat{P}(t) = \frac{b_2 a_2(c)c + b_3 a_3(J_6)J_6 - m_2}{d_2}.$$

The proof is completed. $\square$

Remark 4.2. It can be seen in Section 3 that when $b_2 a_2(R_1)R_1 + b_3 a_3(N_1)N_1 > m_2$ and $b_1 a_1(R_2)R_2 - a_3(0)P_2 > m_1$, both of the equilibria E_{10} and E_{01} are unstable. Notice that $\phi(R_1) - a_1(R_1)N_1 = b_1 a_1(R_1)R_1 - m_1 - d_1 N_1 = 0$ and $\phi(R_2) -$

$a_2(R_2)P_2 = b_2a_2(R_2)R_2 - m_2 - d_2P_2 = 0$, which implies $R_1, R_2 > c, J_5 > P_2$ and $J_4 > N_1 > J_6$. Then we have that $b_2a_2(R_1)R_1 + b_3a_3(N_1)N_1 > b_2a_2(c)c + b_3a_3(J_6)J_6$ and $b_1a_1(R_2)R_2 - a_3(0)P_2 > b_1a_1(c)c - a_3(J_4)J_5$. Therefore, the conditions in Lemma 4.2 also imply the instability of the semi-trivial and boundary equilibria discussed in Section 3.

Remark 4.3. Since $K > c$ and $J_4 > J_6$, we have that $b_1a_1(K)K > b_1a_1(c)c - a_3(J_4)J_5$ and $b_2a_2(K)K + b_3a_3(J_4)J_4 > b_2a_2(c)c + b_3a_3(J_6)J_6$. Therefore, the conditions in Lemma 4.2 guarantee the existence of ultimate upper and lower bounds of the populations $(R(t), N(t)P(t))$ of model (1.2).

When the conditions in Lemma 4.2 hold, the obtained ultimate lower bounds and the ultimate upper bounds given in Lemma 4.1 form a positive global attractor for the food-chain model (1.2) so that the ecological system is permanent. Define

$$\begin{cases} \underline{R}^{(0)} = c, \\ \overline{R}^{(0)} = K, \\ \underline{N}^{(0)} = \dfrac{b_1a_1(c)c - a_3(J_4)J_5 - m_1}{d_1}, \\ \overline{N}^{(0)} = \dfrac{b_1a_1(K)K - m_1}{d_1}, \\ \underline{P}^{(0)} = \dfrac{b_2a_2(c)c + b_3a_3(J_6)J_6 - m_2}{d_2}, \\ \overline{P}^{(0)} = \dfrac{b_2a_2(K)K + b_3a_3(J_4)J_4 - m_2}{d_2}, \end{cases} \tag{4.15}$$

where $J_4 = \frac{b_1a_1(K)K - m_1}{d_1}$, $J_5 = \frac{b_2a_2(K)K + b_3a_3(J_4)J_4 - m_2}{d_2}$ and $J_6 = \frac{b_1a_1(c)c - a_3(J_4)J_5 - m_1}{d_1}$. It is already proven that

$$\begin{aligned} (\underline{R}^{(0)}, \underline{N}^{(0)}, \underline{P}^{(0)}) &\le \liminf_{t\to\infty}(R(t), N(t), P(t)) \\ &\le \limsup_{t\to\infty}(R(t), N(t), P(t)) \le (\overline{R}^{(0)}, \overline{N}^{(0)}, \overline{P}^{(0)}). \end{aligned} \tag{4.16}$$

For any ε there exists a $T_\varepsilon > 0$ such that in (T_ε, ∞),

$$\begin{cases} \dfrac{\mathrm{d}R}{\mathrm{d}t} \le R(\phi(R) - a_1(R)\underline{N}^{(0)} - a_2(R)\underline{P}^{(0)}) + \varepsilon, \\ \dfrac{\mathrm{d}R}{\mathrm{d}t} \ge R(\phi(R) - a_1(R)\overline{N}^{(0)} - a_2(R)\overline{P}^{(0)}) - \varepsilon, \\ \dfrac{\mathrm{d}N}{\mathrm{d}t} \le N(b_1a_1(\overline{R}^{(0)})\overline{R}^{(0)} - a_3(N)\underline{P}^{(0)} - m_1 - d_1N) + \varepsilon, \\ \dfrac{\mathrm{d}N}{\mathrm{d}t} \ge N(b_1a_1(\underline{R}^{(0)})\underline{R}^{(0)} - a_3(N)\overline{P}^{(0)} - m_1 - d_1N) - \varepsilon, \\ \dfrac{\mathrm{d}P}{\mathrm{d}t} \le P(b_2a_2(\overline{R}^{(0)})\overline{R}^{(0)} + b_3a_3(\overline{N}^{(0)})\overline{N}^{(0)} - m_2 - d_2P) + \varepsilon, \\ \dfrac{\mathrm{d}P}{\mathrm{d}t} \ge P(b_2a_2(\underline{R}^{(0)})\underline{R}^{(0)} + b_3a_3(\underline{N}^{(0)})\underline{N}^{(0)} - m_2 - d_2P) - \varepsilon. \end{cases} \tag{4.17}$$

One can uniquely solve for the new values of ultimate bounds $(\underline{R}^{(1)}, \underline{N}^{(1)}, \underline{P}^{(1)})$ and

$(\overline{R}^{(1)}, \overline{N}^{(1)}, \overline{P}^{(1)})$ from the following system:

$$\begin{cases} \phi(\overline{R}^{(1)}) - a_1(\overline{R}^{(1)})\underline{N}^{(0)} - a_2(\overline{R}^{(1)})\underline{P}^{(0)} = 0, \\ \phi(\underline{R}^{(1)}) - a_1(\underline{R}^{(1)})\overline{N}^{(0)} - a_2(\underline{R}^{(1)})\overline{P}^{(0)} = 0, \\ b_1a_1(\overline{R}^{(0)})\overline{R}^{(0)} - a_3(\overline{N}^{(1)})\underline{P}^{(0)} - m_1 - d_1\overline{N}^{(1)} = 0, \\ b_1a_1(\underline{R}^{(0)})\underline{R}^{(0)} - a_3(\underline{N}^{(1)})\overline{P}^{(0)} - m_1 - d_1\underline{N}^{(1)} = 0, \\ b_2a_2(\overline{R}^{(0)})\overline{R}^{(0)} + b_3a_3(\overline{N}^{(0)})\overline{N}^{(0)} - m_2 - d_2\overline{P}^{(1)} = 0, \\ b_2a_2(\underline{R}^{(0)})\underline{R}^{(0)} + b_3a_3(\underline{N}^{(0)})\underline{N}^{(0)} - m_2 - d_2\underline{P}^{(1)} = 0. \end{cases} \tag{4.18}$$

By the arbitrariness of ε and the stability analysis of each single equation related to the inequalities in (4.17), we see that each of the unique positive steady-state value solved in (4.18) is globally asymptotically stable in the respective differential equation. The comparison argument implies that

$$\begin{aligned} (\underline{R}^{(0)}, \underline{N}^{(0)}, \underline{P}^{(0)}) &\le (\underline{R}^{(1)}, \underline{N}^{(1)}, \underline{P}^{(1)}) \\ &\le \liminf_{t\to\infty}(R(t), N(t), P(t)) \le \limsup_{t\to\infty}(R(t), N(t), P(t)) \\ &\le (\overline{R}^{(1)}, \overline{N}^{(1)}, \overline{P}^{(1)}) \le (\overline{R}^{(0)}, \overline{N}^{(0)}, \overline{P}^{(0)}). \end{aligned} \tag{4.19}$$

Through induction, it can be shown that two monotone sequences $(\underline{R}^{(n)}, \underline{N}^{(n)}, \underline{P}^{(n)})$ and $(\overline{R}^{(n)}, \overline{N}^{(n)}, \overline{P}^{(n)})$ will be generated by

$$\begin{cases} \phi(\overline{R}^{(n+1)}) - a_1(\overline{R}^{(n+1)})\underline{N}^{(n)} - a_2(\overline{R}^{(n+1)})\underline{P}^{(n)} = 0, \\ \phi(\underline{R}^{(n+1)}) - a_1(\underline{R}^{(n+1)})\overline{N}^{(n)} - a_2(\underline{R}^{(n+1)})\overline{P}^{(n)} = 0, \\ b_1a_1(\overline{R}^{(n)})\overline{R}^{(n)} - a_3(\overline{N}^{(n+1)})\underline{P}^{(n)} - m_1 - d_1\overline{N}^{(n+1)} = 0, \\ b_1a_1(\underline{R}^{(n)})\underline{R}^{(n)} - a_3(\underline{N}^{(n+1)})\overline{P}^{(n)} - m_1 - d_1\underline{N}^{(n+1)} = 0, \\ b_2a_2(\overline{R}^{(n)})\overline{R}^{(n)} + b_3a_3(\overline{N}^{(n)})\overline{N}^{(n)} - m_2 - d_2\overline{P}^{(n+1)} = 0, \\ b_2a_2(\underline{R}^{(n)})\underline{R}^{(n)} + b_3a_3(\underline{N}^{(n)})\underline{N}^{(n)} - m_2 - d_2\underline{P}^{(n+1)} = 0. \end{cases} \tag{4.20}$$

Moreover, they are ultimate upper and lower bounds for $(R(t), N(t), P(t))$ in model (1.2) and

$$\begin{aligned} (\underline{R}^{(n)}, \underline{N}^{(n)}, \underline{P}^{(n)}) &\le (\underline{R}^{(n+1)}, \underline{N}^{(n+1)}, \underline{P}^{(n+1)}) \\ &\le \liminf_{t\to\infty}(R(t), N(t), P(t)) \le \limsup_{t\to\infty}(R(t), N(t), P(t)) \\ &\le (\overline{R}^{(n+1)}, \overline{N}^{(n+1)}, \overline{P}^{(n+1)}) \le (\overline{R}^{(n)}, \overline{N}^{(n)}, \overline{P}^{(n)}). \end{aligned} \tag{4.21}$$

Since the non-decreasing sequence $(\underline{R}^{(n)}, \underline{N}^{(n)}, \underline{P}^{(n)})$ and non-increasing sequence $(\overline{R}^{(n)}, \overline{N}^{(n)}, \overline{P}^{(n)})$ are both bounded by $(\underline{R}^{(0)}, \underline{N}^{(0)}, \underline{P}^{(0)})$ and $(\overline{R}^{(0)}, \overline{N}^{(0)}, \overline{P}^{(0)})$, $(\underline{R}^{(n)}, \underline{N}^{(n)}, \underline{P}^{(n)})$ converges to $(\underline{R}, \underline{N}, \underline{P})$ and $(\overline{R}^{(n)}, \overline{N}^{(n)}, \overline{P}^{(n)})$ converges to $(\overline{R}, \overline{N}, \overline{P})$.

By setting $n \to \infty$ in 4.20 and (4.21) we can conclude that

$$\begin{cases} \phi(\overline{R}) - a_1(\overline{R})\underline{N} - a_2(\overline{R})\underline{P} = 0, \\ \phi(\underline{R}) - a_1(\underline{R})\overline{N} - a_2(\underline{R})\overline{P} = 0, \\ b_1 a_1(\overline{R})\overline{R} - a_3(\overline{N})\underline{P} - m_1 - d_1\overline{N} = 0, \\ b_1 a_1(\underline{R})\underline{R} - a_3(\underline{N})\overline{P} - m_1 - d_1\underline{N} = 0, \\ b_2 a_2(\overline{R})\overline{R} + b_3 a_3(\overline{N})\overline{N} - m_2 - d_2\overline{P} = 0, \\ b_2 a_2(\underline{R})\underline{R} + b_3 a_3(\underline{N})\underline{N} - m_2 - d_2\underline{P} = 0, \end{cases} \tag{4.22}$$

and

$$(\underline{R}, \underline{N}, \underline{P}) \leq \liminf_{t\to\infty}(R(t), N(t), P(t)) \leq \limsup_{t\to\infty}(R(t), N(t), P(t)) \leq (\overline{R}, \overline{N}, \overline{P}). \tag{4.23}$$

From the existence-comparison theory in [25], there exists a positive equilibrium bounded by $(\underline{R}, \underline{N}, \underline{P})$ and $(\overline{R}, \overline{N}, \overline{P})$. Thus, we have the following theorem on permanence.

Theorem 4.3. *Assume that* $b_1a_1(c)c - a_3(J_4)J_5 > m_1, b_2a_2(c)c + b_3a_3(J_6)J_6 > m_2$ *and* $\sigma_1 J_2 + \sigma_2 J_3 < \phi(0)$*, where* $J_i (i = 4, 5, 6)$ *are defined in the proof of Lemma 4.2. Let* $(\underline{R}, \underline{N}, \underline{P})$ *and* $(\overline{R}, \overline{N}, \overline{P})$ *be the respective limits of the monotone sequences* $(\underline{R}^{(n)}, \underline{N}^{(n)}, \underline{P}^{(n)})$ *and* $(\overline{R}^{(n)}, \overline{N}^{(n)}, \overline{P}^{(n)})$ *generated in (4.20). Then the IGP model (1.2) is permanent, with a global attractor* $[\underline{R}, \overline{R}] \times [\underline{N}, \overline{N}] \times [\underline{P}, \overline{P}]$ *which contains a positive equilibrium* (R^*, N^*, P^*)*. Moreover, if* $(\underline{R}, \underline{N}, \underline{P}) = (\overline{R}, \overline{N}, \overline{P})$*, then the positive equilibrium* (R^*, N^*, P^*) *is unique and globally asymptotically stable.*

Remark 4.4. We observe that positive equilibrium for model (1.2) need not be stable. And Theorem 4.3 also implies that there is no periodic solution of (1.2) if $(\underline{R}, \underline{N}, \underline{P}) = (\overline{R}, \overline{N}, \overline{P})$.

5. Model with the Linear Functional Response

In this section we apply the results obtained in Sections 3 and 4 to studying the IGP model with simplest functional and numerical responses as follows:

$$\begin{cases} R'(t) = R(r(1 - \frac{R}{K}) - a_1 N - a_2 P), \\ N'(t) = N(b_1 a_1 R - a_3 P - m_1 - d_1 N), \\ P'(t) = P(b_2 a_2 R + b_3 a_3 N - m_2 - d_2 P), \end{cases} \tag{5.1}$$

where basal resource is described as logistic growth with carrying capacity K. The parameters $a_i, i = 1, 2, 3$ represent the pradation rates for the three predator-prey interactions mentioned above. The parameters $b_i, i = 1, 2, 3$ represent the conversion rates of prey to predator for the three interactions, and the parameters m_1 and m_2 are the death rates of the IG prey and predator, respectively. And d_1 and d_2 scale the effect of intraspecific competition in the growth rate of IG prey and IG predator, respectively. We assume that all parameters are strictly positive.

For the convenience of mathematical analysis, we can use new dimensionless variables and parameters:

$$x = \frac{R}{K},\ y = \frac{a_1 N}{r},\ z = \frac{a_2 P}{R},\ \tilde{t} = rt,\ \gamma_1 = \frac{b_1 a_1 K}{r},\ \gamma_2 = \frac{b_2 a_2 K}{r},$$

and

$$c = \frac{a_3}{a_2},\ \gamma_3 = \frac{b_3 a_3}{a_1},\ e_1 = \frac{m_1}{r},\ e_2 = \frac{m_2}{r},\ \delta_1 = \frac{d_1}{a_1},\ \delta_2 = \frac{d_2}{a_2}.$$

But for simplicity, we keep the same notation for t. Then, we have

$$\begin{cases} x' = x(1 - x - y - z), \\ y' = y(\gamma_1 x - cz - e_1 - \delta_1 y), \\ z' = z(\gamma_2 x + \gamma_3 y - e_2 - \delta_2 z). \end{cases} \tag{5.2}$$

Obviously, Eq. (5.2) has five possible equilibria in the domain Ω, namely,

(i) trivial equilibrium: $E_0 := (0,0,0)$ and semi-trivial equilibrium: $E_1 := (1,0,0)$,

(ii) IG prey-only equilibrium: $E_{10} := \left(\frac{e_1+\delta_1}{\gamma_1+\delta_1}, \frac{\gamma_1-e_1}{\gamma_1+\delta_1}, 0\right)$ and IG predator-only equilibrium: $E_{01} := \left(\frac{e_2+\delta_2}{\gamma_2+\delta_2}, 0, \frac{\gamma_2-e_2}{\gamma_2+\delta_2}\right)$,

(iii) positive equilibrium: $E^* := (x^*, y^*, z^*) = \left(\frac{\Lambda_1}{\Lambda}, \frac{\Lambda_2}{\Lambda}, \frac{\Lambda_3}{\Lambda}\right)$,where

$$\begin{aligned} \Lambda &= \gamma_1\delta_2 + \gamma_2\delta_1 + \delta_1\delta_2 + \gamma_1\gamma_3 + c\gamma_3 - c\gamma_2, \\ \Lambda_1 &= e_1\delta_2 + e_2\delta_1 + \delta_1\delta_2 + \gamma_3 e_1 + c\gamma_3 - ce_2, \\ \Lambda_2 &= \gamma_1\delta_2 + \gamma_1 e_2 + ce_2 - e_1\delta_2 - \gamma_2 e_1 - c\gamma_2, \\ \Lambda_3 &= \gamma_1\gamma_3 + \gamma_2 e_1 + \gamma_2\delta_1 - \gamma_1 e_2 - \gamma_3 e_1 - e_2\delta_1. \end{aligned}$$

Proposition 5.1. *The conditions for the existence of equilibria of system (3.2) are following:*

(i) the trivial equilibrium E_0 and semi-trivial equilibrium E_1 always exist;

(ii) the IG prey-only equilibrium E_{10} exists if and only if $\gamma_1 > e_1$, and the IG predator-only equilibrium E_{01} exists if and only if $\gamma_2 > e_2$;

(iii) the unique positive equilibrium E^* exists if and only if $\Lambda \neq 0$ and $\frac{\Lambda_i}{\Lambda} > 0$, for $i = 1, 2, 3$.

Remark 5.1. It is easy to check that the positive equilibrium E^* exists but is unstable when $\Lambda < 0, \Lambda_i < 0, i = 1, 2, 3$.

5.1. Trivial, semi-trivial and boundary equilibria

We first recall some well-known one or two dimensional results.

Proposition 5.2 ([19]). *The subspaces $H_1 = \{(x,0,0) : x \geq 0\}, H_2 = \{(x,y,0) : x, y \geq 0\}, H_3 = \{(x,0,z) : x, z \geq 0\}$ and $H_4 = \{(0,y,z) : y, z \geq 0\}$ are invariant. Moreover, the following statements are true.*

(i) *On H_1, system (5.2) is reduced to the one-dimensional subsystem*

$$\frac{\mathrm{d}x}{\mathrm{d}t} = x(1-x). \tag{5.3}$$

Then the trivial equilibrium E_0 is unstable and E_1 is globally asymptotically stable.

(ii) *On H_2, system (5.2) is reduced to the two-dimensional subsystem*

$$\begin{aligned}\frac{\mathrm{d}x}{\mathrm{d}t} &= x(1-x-y),\\ \frac{\mathrm{d}y}{\mathrm{d}t} &= y(\gamma_1 x - e_1 - \delta_1 y).\end{aligned} \tag{5.4}$$

If $\gamma_1 < e_1$ then E_{10} doest not exist and E_1 is globally asymptotically stable; otherwise, if $\gamma_1 > e_1$ then the equilibria E_0, E_1 are saddles and E_{10} is globally asymptotically stable.

(iii) *On H_3, system (5.2) is reduced to the two-dimensional subsystem*

$$\begin{aligned}\frac{\mathrm{d}x}{\mathrm{d}t} &= x(1-x-z),\\ \frac{\mathrm{d}z}{\mathrm{d}t} &= z(\gamma_2 x - e_2 - \delta_2 z).\end{aligned} \tag{5.5}$$

If $\gamma_2 < e_2$ then E_{01} doest not exist and E_1 is globally asymptotically stable; otherwise, if $\gamma_2 > e_2$ then the equilibria E_0, E_1 are saddles and E_{01} is globally asymptotically stable.

(iv) *On H_4, the trivial equilibrium E_0 is globally asymptotically stable.*

We next analyze the dynamics of all solutions of (5.2) near the boundary equilibria. According to Theorems 3.1, 3.2 and 3.3, we get the stability conclusions of the trivial, semi-trivial and boundary equilibria.

Proposition 5.3. *Consider system (5.2).*

(i) *The trivial equilibrium E_0 is always a saddle with the unstable subspace H_1 and the stable subspace H_4.*

(ii) *The semi-trivial equilibrium E_1 is locally asymptotically stable if and only if $\gamma_1 < e_1$ and $\gamma_2 < e_2$.*

(iii) *If $\gamma_1 > e_1$, then E_{10} exists and is locally asymptotically stable if and only if*

$$-e_2 + \frac{\gamma_2(e_1+\delta_1)}{\gamma_1+\delta_1} + \frac{\gamma_3(\gamma_1-e_1)}{\gamma_1+\delta_1} < 0. \tag{5.6}$$

(iv) *If $\gamma_2 > e_2$, then E_{01} exists and is locally asymptotically stable if and only if*

$$-e_1 + \frac{\gamma_1(e_2+\delta_2)}{\gamma_2+\delta_2} - \frac{c(\gamma_2-e_2)}{\gamma_2+\delta_2} < 0. \tag{5.7}$$

From Theorem 3.4, we have the following extinction results.

Proposition 5.4. *Let $(x(t), y(t), z(t))$ be a solution of system (5.2) with initial condition $(x(0), y(0), z(0))$ where $x(0) > 0, y(0) > 0$ and $z(0) > 0$. Then the following statements are true.*

(i) *If $\gamma_1 < e_1$ and $\gamma_2 < e_2$, then the boundary equilibria E_{10} and E_{01} do not exist and we have the limits $\lim_{t\to\infty} y(t) = 0$ and $\lim_{t\to\infty} z(t) = 0$. Furthermore, E_1 is globally asymptotically stable.*

(ii) *If $\gamma_1 < e_1$ and $\gamma_2 > e_2$, then one boundary equilibrium E_{10} does not exist but the other boundary equilibrium E_{01} exists. Moreover, we have the limit $\lim_{t\to\infty} y(t) = 0$ and the equilibrium E_{01} is globally asymptotically stable.*

These results can be easily interpreted in the biological point of view. If the death rate e_1 of species y is greater than the conversion rate γ_1, then y will die out eventually and system (5.2) is reduced to the one-dimensional x subsystem (5.3) or two-dimensional x–z subsystem (5.5). Thus classical two-dimensional results, Proposition 5.2, can be applied. Therefore, from now on, we make the generic assumption,

(L_1) $\quad \gamma_1 > e_1$,

which will be used in the rest of this section. However, for species z the dynamics are more complicated. We consider this in the next subsection.

5.2. Existence, local stability and global dynamics of the equilibria of system (5.2)

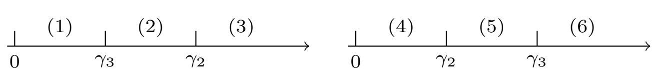
In this section, we always assume that assumption (L_1) holds. Seeing Fig. 3, we have six generic cases of classification of parameters based on the relation of γ_2 and γ_3 respect to the death rate, e_2, of species z. Similar to [17], we will classify the dynamics of (5.2) according to e_2 within regions (1)–(6) by the following four categories,

(I) $e_2 > \max\{\gamma_2, \gamma_3\}$ (in region (3) and (6) of Fig. 3);

(II) $\gamma_2 > \max\{e_2, \gamma_3\}$ (in region (1) and (2) of Fig. 3);

(III) $e_2 < \gamma_2 < \gamma_3$ (in region (4) of Fig. 3);

(IV) $\gamma_2 < e_2 < \gamma_3$ (in region (5) of Fig. 3).



(a) $\gamma_2 > \gamma_3$ (b) $\gamma_2 < \gamma_3$

Figure 3. All generic possibilities of classification of parameters with varied e_2 in regions (1)–(6) with $\gamma_1 > e_1$.

We will discuss the dynamics of each category in the following subsections.

5.2.1. Category (I): $e_2 > \max\{\gamma_2, \gamma_3\}$

In this category, since assumption (L_1) and $e_2 > \max\{\gamma_2, \gamma_3\}$ hold, the boundary equilibrium E_{10} exists but the other boundary equilibrium E_{01} does not exist. Then we consider the possible existence of positive equilibria. To find the positive positive equilibrium $E^* = (x^*, y^*, z^*)$ is to find the positive solution of the following equations

$$1 - x - y - z = 0,$$
$$\gamma_1 x - cz - e_1 - \delta_1 y = 0,$$
$$\gamma_2 x + \gamma_3 y - e_2 - \delta_2 z = 0.$$

With the substitution, $x = 1 - y - z$, we obtain two straight lines, L_1 and L_2,

$$L_1 : (\gamma_1 + \delta_1)y + (\gamma_1 + c)z = \gamma_1 - e_1, \tag{5.8}$$
$$L_2 : (\gamma_2 - \gamma_3)y + (\gamma_2 + \delta_2)z = \gamma_2 - e_2. \tag{5.9}$$

Hence the positive equilibrium exists if and only if these two straight lines L_1 and L_2 intersect in the interior of the first quadrant of the yz-plane. The only possibility of existence of a positive equilibrium is that parameters satisfy inequalities $\gamma_2 < \gamma_3$ and $\frac{e_2-\gamma_2}{\gamma_3-\gamma_2} < \frac{\gamma_1-e_1}{\gamma_1+\delta_1}$. But, this is impossible since if $\gamma_2 < \gamma_3$ then $\frac{e_2-\gamma_2}{\gamma_3-\gamma_2} > 1 > \frac{\gamma_1-e_1}{\gamma_1+\delta_1}$. Hence there is no positive equilibrium in category (I). However, we have the following extinction and globally stability results and the dynamics of category (I) are summarized in Table 1.

Proposition 5.5. *Let assumption (L_1) and $e_2 > \max\{\gamma_2, \gamma_3\}$ hold. Then equilibria E_{01} and E^* do not exist. Moreover, we have that $\lim_{t\to\infty} z(t) = 0$ and the equilibrium E_{10} is globally asymptotically stable.*

Proof. We first proof that the boundary equilibrium E_{10} is asymptotically stable. Consider two subcases, $\gamma_2 \geq \gamma_3$ or $\gamma_2 < \gamma_3$. If $\gamma_2 \geq \gamma_3$ then

$$-e_2 + \frac{\gamma_2(e_1+\delta_1)}{\gamma_1+\delta_1} + \frac{\gamma_3(\gamma_1-e_1)}{\gamma_1+\delta_1} \leq -e_2 + \frac{\gamma_2(e_1+\delta_1)}{\gamma_1+\delta_1} + \frac{\gamma_2(\gamma_1-e_1)}{\gamma_1+\delta_1} = \gamma_2 - e_2 < 0$$

holds. On the other hand, if $\gamma_2 < \gamma_3$ then

$$-e_2 + \frac{\gamma_2(e_1+\delta_1)}{\gamma_1+\delta_1} + \frac{\gamma_3(\gamma_1-e_1)}{\gamma_1+\delta_1} = \gamma_3 - e_2 + \frac{(\gamma_2-\gamma_3)(e_1+\delta_1)}{\gamma_1+\delta_1} < 0$$

holds. Hence E_{10} is locally asymptotically stable in $\mathbb{R}^3$ by Proposition 5.3.

Without loss of generality, we assume that $x(t) \leq 1$ for t large enough. Define $\nu = \max\{\gamma_2, \gamma_3\}$ and consider

$$\begin{aligned}\frac{z'}{z} + \nu\frac{x'}{x} &= (\gamma_2 x + \gamma_3 y - e_2 - \delta_2 z) + \nu(1 - x - y - z)\\ &= \nu - e_2 + (\gamma_2 - \nu)x + (\gamma_3 - \nu)y - (\delta_2 + \nu)z\\ &\leq \nu - e_2 < 0,\end{aligned}$$

which implies $z(t)(x(t))^\nu \to 0$ as $t \to \infty$. Then we should consider two possibilities, one of which is that there exists a sequence of time $\{t_n\}$ such that $t_n \to \infty$ and $x(t_n) \to 0$ as $n \to \infty$, the other of which is that there exists $\varepsilon >$ such that $x(t) > \varepsilon$ for all time t.

Assume that there is a sequence $\{t_n\}$ such that $x(t_n) \to 0$ as $n \to \infty$. Since the solutions of (5.2) are bounded, there is a point $\boldsymbol{q} = (0, \bar{y}, \bar{z}) \in H_4 \cap \omega(\boldsymbol{p})$. By Proposition 5.2, the solutions of (5.2) with initial condition $\boldsymbol{q} \in H_4$, $\phi(t, \boldsymbol{q})$, will approach E_0 when $t \to \infty$. Hence $E_0 \in \omega(\boldsymbol{p})$. It is clear that $\omega(\boldsymbol{p}) \neq \{E_0\}$. Applying

Butler-McGehee Lemma [6, 9], there is a point $\boldsymbol{r} = (\bar{x}, 0, 0) \in H_1 \cap \omega(\boldsymbol{p})$. Clearly, $\boldsymbol{r} \neq E_0$ and $\phi(t, \boldsymbol{r})$ approaches E_1 as $t \to \infty$. Similarly, $E_1 \subsetneq \omega(\boldsymbol{p})$ and applying Butler-McGehee Lemma again, we can find a point $\boldsymbol{s} \in H_2 \cap \omega(\boldsymbol{p})$ since the unstable manifold of E_1 is contained in H_2. Again, $\phi(t, \boldsymbol{s})$ approaches E_{10}, hence $E_{10} \in \omega(\boldsymbol{p})$. Since E_{10} is asymptotically stable in $\mathbb{R}^3$, we have the limit $\lim_{t\to\infty} \phi(t, \boldsymbol{p}) = E_{10}$.

On the other hand, if $x(t) > \varepsilon > 0$ for all t then we have $z(t) \to 0$ as $t \to \infty$. Similar to the previous arguments, we can find a point $s_1 \in H_2 \cap \omega(\boldsymbol{p})$. The rest of the proof is almost the same as the previous one, so we omit it. We complete the proof. □

5.2.2. Category (II): $\gamma_2 > \max\{e_2, \gamma_3\}$

In this category, since assumption (L_1) and $\gamma_2 > e_2$ hold, the boundary equilibria E_{10} and E_{01} exist. Similarly, we solve (5.8) and (5.9) to find the positive equilibrium E^*. There are four generic cases of Category (II) as shown in Fig. 4.

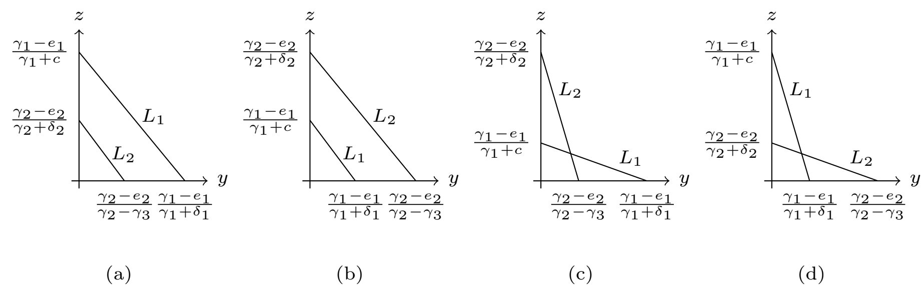


Figure 4. The four possible generic cases for the intersection of the two straight lines L_1 and L_2 for category (II).

In Fig. 4(a), the two straight lines do not intersect in the first quadrant if $\frac{\gamma_1-e_1}{\gamma_1+\delta_1} > \frac{\gamma_2-e_2}{\gamma_2-\gamma_3}$ and $\frac{\gamma_1-e_1}{\gamma_1+c} > \frac{\gamma_2-e_2}{\gamma_2+\delta_2}$. These two inequalities are equivalent to (5.6) and the reversed (5.7). Hence in this case E_{10} is stable, E_{01} is unstable and E^* does not exist. The arguments of local dynamics in other three cases of category (II) are similar, so we omit them. And the results of local stability of the boundary equilibria and existence of positive equilibrium of category (II) are summarized in Table 1.

If E^* exists then the the characteristic equation at E^* is given by

$$\triangle(E^*) = \lambda^3 + A_2\lambda^2 + A_1\lambda + A_0 = 0, \tag{5.10}$$

where

$$\begin{aligned} A_2 &= x^* + \delta_1 y^* + \delta_2 z^*, \quad A_0 = x^* y^* z^* \Lambda, \\ A_1 &= x^* y^* (\delta_1 + \gamma_1) + x^* z^* (\delta_2 + \gamma_2) + y^* z^* (\delta_1\delta_2 + c\gamma_3). \end{aligned}$$

By Routh-Hurwitz criterion, the real parts of three roots of the characteristic equation are all negative if and only if

$$\Lambda = \gamma_1\delta_2 + \gamma_2\delta_1 + \delta_1\delta_2 + \gamma_1\gamma_3 + c\gamma_3 - c\gamma_2 > 0 \tag{5.11}$$

and

$$A_2A_1 - A_0 = {x^*}^2 y^* (\delta_1 + \gamma_1) + {x^*}^2 z^* (\delta_2 + \gamma_2) + x^* {y^*}^2 (\delta_1^2 + \delta_1\gamma_1)$$

$$
\begin{aligned}
&+ {y^*}^2 z^*(\delta_1^2\delta_2 + c\gamma_3\delta_1) + x^* {z^*}^2(\delta_2^2 + \delta_2\gamma_2)\\
&+ y^* {z^*}^2(\delta_1\delta_2^2 + c\gamma_3\delta_2) + x^*y^*z^*(2\delta_1\delta_2 + c\gamma_2 - \gamma_1\gamma_3)\\
>&0. \qquad (5.12)
\end{aligned}
$$

In this category, we obtain two extinction results and one bistability phenomenon.

Proposition 5.6. *Let assumption* (L_1) *and* $\gamma_2 > \max\{e_2, \gamma_3\}$ *hold. Then the following statements are true.*

(i) In case (a) of Category (II), that is $\frac{\gamma_1-e_1}{\gamma_1+\delta_1} > \frac{\gamma_2-e_2}{\gamma_2-\gamma_3}$ *and* $\frac{\gamma_1-e_1}{\gamma_1+c} > \frac{\gamma_2-e_2}{\gamma_2+\delta_2}$, *if (5.11) holds, then the species* z *dies out eventually and the equilibrium* E_{10} *is globally asymptotically stable.*

(ii) In case (b) of Category (II), that is $\frac{\gamma_1-e_1}{\gamma_1+\delta_1} < \frac{\gamma_2-e_2}{\gamma_2-\gamma_3}$ *and* $\frac{\gamma_1-e_1}{\gamma_1+c} < \frac{\gamma_2-e_2}{\gamma_2+\delta_2}$, *if (5.11) holds, then the species* y *dies out eventually and the equilibrium* E_{01} *is globally asymptotically stable.*

(iii) In case (c) of Category (II), that is $\frac{\gamma_1-e_1}{\gamma_1+\delta_1} > \frac{\gamma_2-e_2}{\gamma_2-\gamma_3}$ *and* $\frac{\gamma_1-e_1}{\gamma_1+c} < \frac{\gamma_2-e_2}{\gamma_2+\delta_2}$, *the equilibrium* E^* *is a saddle point. Meanwhile, a bistability phenomenon occurs.*

Proof. (i) Consider

$$
\begin{aligned}
\frac{z'}{z} + \frac{\gamma_1\gamma_3+\delta_1\gamma_2}{\gamma_1+\delta_1}\frac{x'}{x} - \frac{\gamma_2-\gamma_3}{\gamma_1+\delta_1}\frac{y'}{y} =&(\gamma_2 x + \gamma_3 y - e_2 - \delta_2 z) + \frac{\gamma_1\gamma_3+\delta_1\gamma_2}{\gamma_1+\delta_1}(1-x\\
&- y - z) - \frac{\gamma_2-\gamma_3}{\gamma_1+\delta_1}(\gamma_1 x - cz - e_1 - \delta_1 y)\\
=& - e_2 + \frac{\gamma_1\gamma_3+\delta_1\gamma_2}{\gamma_1+\delta_1} + \frac{e_1(\gamma_2-\gamma_3)}{\gamma_1+\delta_1} - \frac{\Lambda}{\gamma_1+\delta_1}z\\
\le& - e_2 + \frac{\gamma_1\gamma_3+\delta_1\gamma_2}{\gamma_1+\delta_1} + \frac{e_1(\gamma_2-\gamma_3)}{\gamma_1+\delta_1} < 0.
\end{aligned}
$$

Hence we have $z(t)(x(t))^{\frac{\gamma_1\gamma_3+\delta_1\gamma_2}{\gamma_1+\delta_1}} \to 0$ as $t\to\infty$. The remaining arguments are similar, so we omit them.

(ii) Similarly, we consider

$$
\begin{aligned}
\frac{y'}{y} - \frac{c\gamma_2-\gamma_1\delta_2}{\gamma_2+\delta_2}\frac{x'}{x} - \frac{\gamma_1+c}{\gamma_2+\delta_2}\frac{z'}{z} =&(\gamma_1 x - cz - e_1 - \delta_1 y) - \frac{c\gamma_2-\gamma_1\delta_2}{\gamma_2+\delta_2}(1-x\\
&- y - z) - \frac{\gamma_1+c}{\gamma_2+\delta_2}(\gamma_2 x + \gamma_3 y - e_2 - \delta_2 z)\\
=& - e_1 - \frac{c\gamma_2-\gamma_1\delta_2}{\gamma_2+\delta_2} + \frac{e_2(\gamma_1+c)}{\gamma_2+\delta_2} - \frac{\Lambda}{\gamma_2+\delta_2}y\\
\le& - e_1 - \frac{c\gamma_2-\gamma_1\delta_2}{\gamma_2+\delta_2} + \frac{e_2(\gamma_1+c)}{\gamma_2+\delta_2} < 0.
\end{aligned}
$$

If $c\gamma_2-\gamma_1\delta_2 \ge 0$ then $y(t)\to 0$ as $t\to\infty$; if $c\gamma_2-\gamma_1\delta_2 < 0$, then $y(t)(x(t))^{\frac{\gamma_1\delta_2-c\gamma_2}{\gamma_2+\delta_2}} \to 0$ as $t\to\infty$. The remaining arguments are similar, so we omit them.

(iii) It is easy to see that the assumptions $\frac{\gamma_1-e_1}{\gamma_1+\delta_1} > \frac{\gamma_2-e_2}{\gamma_2-\gamma_3}$ and $\frac{\gamma_1-e_1}{\gamma_1+c} < \frac{\gamma_2-e_2}{\gamma_2+\delta_2}$ imply the inequality,

$$\frac{\gamma_1+c}{\gamma_1+\delta_1} > \frac{\gamma_2+\delta_2}{\gamma_2-\gamma_3}.$$

This inequality is equivalent to $\Lambda < 0$. Hence the positive equilibrium E^* is unstable. Since $A_2 > 0$ and $A_0 < 0$, the sum of all roots of (5.10) is less than 0 and the product of all roots of (5.10) is large than 0, which implies the equilibrium E^* is a saddle point. Since $\frac{\gamma_1-e_1}{\gamma_1+\delta_1} > \frac{\gamma_2-e_2}{\gamma_2-\gamma_3}$ and $\frac{\gamma_1-e_1}{\gamma_1+c} < \frac{\gamma_2-e_2}{\gamma_2+\delta_2}$ are equivalent to the inequalities (5.6) and (5.7), respectively, it follows from Proposition 5.2 that E_{10} and E_{01} are both locally asymptotically stable. That is, a bistability phenomenon occurs. We complete the proof. □

5.2.3. Category (III): $e_2 < \gamma_2 < \gamma_3$

In this category, since assumption (L_1) and $\gamma_2 > e_2$ hold, the boundary equilibria E_{10} and E_{01} exist. Similarly, we solve (5.8) and (5.9) to find the positive equilibrium E^*. There are two generic cases of Category (III) as shown in Fig. 5.

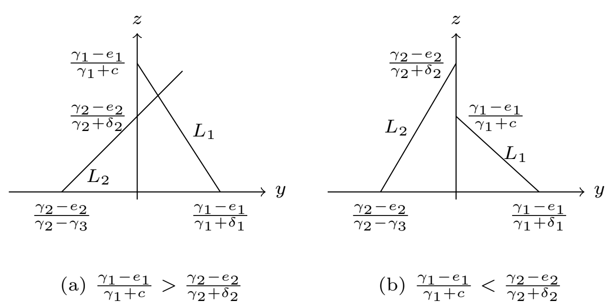


Figure 5. The two possible generic cases for the intersection of the two straight lines L_1 and L_2 for category (III).

For category (III), it is obvious that E_{10} is unstable, since

$$-e_2 + \frac{\gamma_2(e_1+\delta_1)}{\gamma_1+\delta_1} + \frac{\gamma_3(\gamma_1-e_1)}{\gamma_1+\delta_1} = \gamma_2 - e_2 + \frac{(\gamma_3-\gamma_2)(\gamma_1-e_1)}{\gamma_1+\delta_1} > 0.$$

Remaining arguments of local dynamics of category (III) are similar to the previous category, so we omit them and summarize the results on the local stability of boundary equilibria and the existence of positive equilibrium of category (III) in Table 1. We then have the following extinction result.

Proposition 5.7. *Let assumption (L_1) and $e_2 < \gamma_2 < \gamma_3$ hold. In case (b) of category (III), that is $\frac{\gamma_1-e_1}{\gamma_1+\delta_1} > \frac{\gamma_2-e_2}{\gamma_2-\gamma_3}$ and $\frac{\gamma_1-e_1}{\gamma_1+c} < \frac{\gamma_2-e_2}{\gamma_2+\delta_2}$, the species y dies out eventually and the equilibrium E_{01} is globally asymptotically stable.*

Proof. We first show that inequality (5.11) holds in this case. Since $\frac{\gamma_1-e_1}{\gamma_1+\delta_1} > \frac{\gamma_2-e_2}{\gamma_2-\gamma_3}$, $\frac{\gamma_1-e_1}{\gamma_1+c} < \frac{\gamma_2-e_2}{\gamma_2+\delta_2}$ and $e_2 < \gamma_2 < \gamma_3$, we have that

$$\frac{\gamma_1+c}{\gamma_1+\delta_1} > \frac{\gamma_2+\delta_2}{\gamma_2-\gamma_3},$$

which is equivalent to (5.11). Moreover, the condition $\frac{\gamma_1-e_1}{\gamma_1+c} < \frac{\gamma_2-e_2}{\gamma_2+\delta_2}$ holds if and only if the inequality (5.7) holds, hence the equilibrium E_{01} is asymptotically stable.

Consider

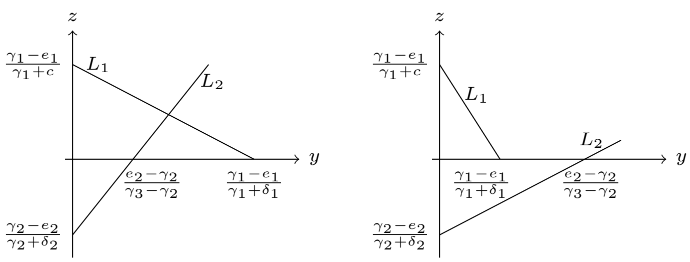
$$\frac{y'}{y} - \frac{c\gamma_2-\gamma_1\delta_2}{\gamma_2+\delta_2}\frac{x'}{x} - \frac{\gamma_1+c}{\gamma_2+\delta_2}\frac{z'}{z} = (\gamma_1 x - cz - e_1 - \delta_1 y) - \frac{c\gamma_2-\gamma_1\delta_2}{\gamma_2+\delta_2}(1-x-y-z)$$

$$
\begin{aligned}
&- \frac{\gamma_1 + c}{\gamma_2 + \delta_2}(\gamma_2 x + \gamma_3 y - e_2 - \delta_2 z) \\
&= - e_1 - \frac{c\gamma_2 - \gamma_1\delta_2}{\gamma_2 + \delta_2} + \frac{e_2(\gamma_1 + c)}{\gamma_2 + \delta_2} - \frac{\Lambda}{\gamma_2 + \delta_2} y \\
&\leq - e_1 - \frac{c\gamma_2 - \gamma_1\delta_2}{\gamma_2 + \delta_2} + \frac{e_2(\gamma_1 + c)}{\gamma_2 + \delta_2} < 0.
\end{aligned}
$$

If $c\gamma_2 - \gamma_1\delta_2 \geq 0$ then $y(t) \to 0$ as $t \to \infty$; if $c\gamma_2 - \gamma_1\delta_2 < 0$ then $y(t)(x(t))^{\frac{\gamma_1\delta_2 - c\gamma_2}{\gamma_2 + \delta_2}} \to 0$ as $t \to \infty$. The remaining arguments are similar, so we omit them. □

5.2.4. Category (IV): $\gamma_2 < e_2 < \gamma_3$

In this category, since assumption (L_1) and $\gamma_2 < e_2$ hold, the boundary equilibrium E_{10} exist but the other boundary equilibrium E_{01} does not exist. Similarly, we solve (5.8) and (5.9) to find the positive equilibrium E^*. There are two generic cases of Category (IV) as shown in Fig. 6.



(a) $\frac{\gamma_1 - e_1}{\gamma_1 + \delta_1} > \frac{e_2 - \gamma_2}{\gamma_3 - \gamma_2}$ (b) $\frac{\gamma_1 - e_1}{\gamma_1 + \delta_1} < \frac{e_2 - \gamma_2}{\gamma_3 - \gamma_2}$

Figure 6. The two possible generic cases for the intersection of the two straight lines L_1 and L_2 for category (IV).

In Fig. 6(b), the inequality $\frac{\gamma_1 - e_1}{\gamma_1 + \delta_1} < \frac{e_2 - \gamma_2}{\gamma_3 - \gamma_2}$ is equivalent to (5.6) hence E_{10} is asymptotically stable. The other case of category (IV) is similar, so we summarize the results in Table 1. The following theorem gives the extinction result in case (b).

Proposition 5.8. *Let assumption (L_1) hold and parameters be in the case (b) of category (IV). Then we have that $\lim_{t\to\infty} z(t) = 0$ and the equilibrium E_{10} is globally asymptotically stable.*

Proof. Inequality $\frac{\gamma_1 - e_1}{\gamma_1 + \delta_1} < \frac{e_2 - \gamma_2}{\gamma_3 - \gamma_2}$ implies that E_{10} is asymptotically stable and is equivalent to the following inequality,

$$-e_2 + \frac{\gamma_1\gamma_3 + \delta_1\gamma_2}{\gamma_1 + \delta_1} + \frac{e_1(\gamma_2 - \gamma_3)}{\gamma_1 + \delta_1} < 0.$$

Consider

$$
\begin{aligned}
\frac{z'}{z} + \frac{\gamma_1\gamma_3 + \delta_1\gamma_2}{\gamma_1 + \delta_1}\frac{x'}{x} + \frac{\gamma_3 - \gamma_2}{\gamma_1 + \delta_1}\frac{y'}{y} =& (\gamma_2 x + \gamma_3 y - e_2 - \delta_2 z) + \frac{\gamma_1\gamma_3 + \delta_1\gamma_2}{\gamma_1 + \delta_1}(1 - x \\
& - y - z) - \frac{\gamma_2 - \gamma_3}{\gamma_1 + \delta_1}(\gamma_1 x - cz - e_1 - \delta_1 y)
\end{aligned}
$$

$$= - e_2 + \frac{\gamma_1\gamma_3 + \delta_1\gamma_2}{\gamma_1 + \delta_1} + \frac{e_1(\gamma_2 - \gamma_3)}{\gamma_1 + \delta_1} - \frac{\Lambda}{\gamma_1 + \delta_1} z$$
$$\leq - e_2 + \frac{\gamma_1\gamma_3 + \delta_1\gamma_2}{\gamma_1 + \delta_1} + \frac{e_1(\gamma_2 - \gamma_3)}{\gamma_1 + \delta_1} < 0.$$

Hence we have $(x(t))^{\frac{\gamma_1\gamma_3+\delta_1\gamma_2}{\gamma_1+\delta_1}}(y(t))^{\frac{\gamma_3-\gamma_2}{\gamma_1+\delta_1}}z(t) \to 0$ as $t \to \infty$. Similarly, we consider two possibilities. One is that there exists a sequence of time t_n such that $x(t_n) \to 0$ as $n \to \infty$. The proof of this case is similar to the previous one, we can obtain that E_{10} is globally asymptotically stable. So we omit the details.

Another one is that $x(t) \geq \varepsilon$ for all time t. This implies that $(y(t))^{\frac{\gamma_3-\gamma_2}{\gamma_1+\delta_1}}z(t) \to 0$ as $t \to \infty$. We also have two subcases, one of which is that there is a sequence of time t_n such that $y(t_n) \to 0$ as $n \to \infty$, the other of which is that $y(t) \geq \varepsilon$ for all time t. The remaining arguments of these two subcases are similar, so we omit them. We complete the proof. □

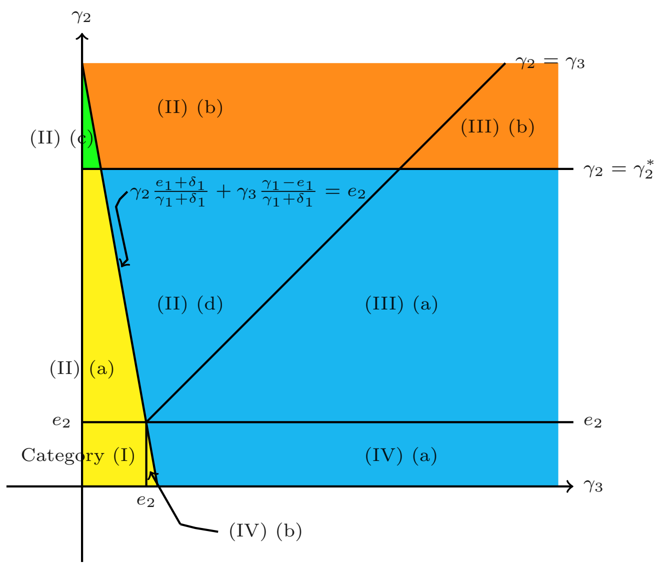


Figure 7. A typical picture of the parameter space with varied γ_2, γ_3 and fixed $e_1, e_2, \delta_1, \delta_2, \gamma_1, c$ with $\gamma_1 > e_1$. The dynamics in each region of the parameter space are indicated with different color. First, in the yellow regions species z dies out eventually because of results in Propositions 5.5, 5.6(i) and 5.8. In the orange region, species y dies out eventually (Propositions 5.6(ii) and 5.7). Moreover, in the green region, the bistability phenomenon occurs (Proposition 5.6(iii)). Finally, the positive equilibrium appears in the cyan region and the permanence effect of the populations of the model (5.2) follows (Proposition 5.11).

In the end of this subsection, we present a typical picture, Fig. 7, of the γ_2, γ_3 parameter space with fixed $e_1, e_2, \delta_1, \delta_2, \gamma_1$ and c and the restriction $\gamma_1 > e_1$ (see Proposition 5.4 and assumption (L_1)). We use different colors to clarify the dynamics of solutions of (5.2) by the two inequalities of Table 1. One straight line, $\gamma_2 \frac{e_1+\delta_1}{\gamma_1+\delta_1} + \gamma_3 \frac{\gamma_1-e_1}{\gamma_1+\delta_1} = e_2$, and one horizontal line,

$$\gamma_2 = \gamma_2^* = \frac{e_2(\gamma_1 + c) + \delta_2(\gamma_1 - e_1)}{c + e_1},$$

are obtained to separate regions (II)–(IV) into two or four subregions by the inequalities of Table 1.

Table 1. Dynamics of equilibria of classifications categories (I)–(IV) (GAS means globally asymptotically stable).

	E_{10}	E_{01}	E^*
Category (I): $e_2 > \max\{\gamma_2, \gamma_3\}$	GAS	does not exist	does not exist
Category (II): $\gamma_2 > \max\{e_2, \gamma_3\}$			
(a) $\frac{\gamma_1-e_1}{\gamma_1+\delta_1} > \frac{\gamma_2-e_2}{\gamma_2-\gamma_3}, \frac{\gamma_1-e_1}{\gamma_1+c} > \frac{\gamma_2-e_2}{\gamma_2+\delta_2}$	GAS*	unstable	does not exist
(b) $\frac{\gamma_1-e_1}{\gamma_1+\delta_1} < \frac{\gamma_2-e_2}{\gamma_2-\gamma_3}, \frac{\gamma_1-e_1}{\gamma_1+c} < \frac{\gamma_2-e_2}{\gamma_2+\delta_2}$	unstable	GAS*	does not exist
(c) $\frac{\gamma_1-e_1}{\gamma_1+\delta_1} > \frac{\gamma_2-e_2}{\gamma_2-\gamma_3}, \frac{\gamma_1-e_1}{\gamma_1+c} < \frac{\gamma_2-e_2}{\gamma_2+\delta_2}$	stable	stable	exists (saddle)
(d) $\frac{\gamma_1-e_1}{\gamma_1+\delta_1} < \frac{\gamma_2-e_2}{\gamma_2-\gamma_3}, \frac{\gamma_1-e_1}{\gamma_1+c} > \frac{\gamma_2-e_2}{\gamma_2+\delta_2}$	unstable	unstable	exists
Category (III): $e_2 < \gamma_2 < \gamma_3$			
(a) $\frac{\gamma_1-e_1}{\gamma_1+\delta_1} > \frac{\gamma_2-e_2}{\gamma_2-\gamma_3}, \frac{\gamma_1-e_1}{\gamma_1+c} > \frac{\gamma_2-e_2}{\gamma_2+\delta_2},$	unstable	unstable	exists
(b) $\frac{\gamma_1-e_1}{\gamma_1+\delta_1} > \frac{\gamma_2-e_2}{\gamma_2-\gamma_3}, \frac{\gamma_1-e_1}{\gamma_1+c} < \frac{\gamma_2-e_2}{\gamma_2+\delta_2},$	unstable	GAS	does not exist
Category (IV): $\gamma_2 < e_2 < \gamma_3$			
(a) $\frac{\gamma_1-e_1}{\gamma_1+\delta_1} > \frac{e_2-\gamma_2}{\gamma_3-\gamma_2}, \frac{\gamma_1-e_1}{\gamma_1+c} > \frac{\gamma_2-e_2}{\gamma_2+\delta_2},$	unstable	does not exist	exists
(b) $\frac{\gamma_1-e_1}{\gamma_1+\delta_1} < \frac{e_2-\gamma_2}{\gamma_3-\gamma_2}, \frac{\gamma_1-e_1}{\gamma_1+c} > \frac{\gamma_2-e_2}{\gamma_2+\delta_2},$	GAS	unstable	does not exist

*With an extra inequality (5.11).

We indicate the dynamics in each region of the parameter space with different colors of Fig. 7. Firstly, in the yellow regions species z dies out eventually because of results in Propositions 5.5, 5.6(i) and 5.8. In the orange region, species y dies out eventually (Propositions 5.6(ii) and 5.7). Moreover, in the green region, the bistability phenomenon occurs (Proposition 5.6(iii)). Finally, the positive equilibrium appears in the cyan region.

5.3. Dynamics of the positive equilibrium

Note that all global dynamics of (5.2) are clarified analytically except for cases of parameters in (II)(d), (III)(a), and part of (IV)(a). Hence, in this subsection, we would like to discuss the dynamics of (5.2) with parameters in these three regions. We show an analytical result in which system (5.2) is permanence and present some numerical simulations.

5.3.1. Permanence

For investigating the permanence phenomenon of system (5.2), we apply the result of Section 4. In fact we can use the conditions of Theorem 4.3 to have the following results.

Proposition 5.9. *Assume that* $\gamma_1 > e_1$ *and* $\gamma_2 + \gamma_3 J_4 > e_2$*, where* $J_4 = \frac{\gamma_1-e_1}{\delta_1}$*. If* $(x(0), y(0), z(0)) > (0, 0, 0)$*, then the population function* $(x(t), y(t), z(t))$ *as solution* *of (5.2) remains nonnegative and satisfies*

$$\begin{cases} \limsup_{t\to\infty} x(t) \le 1, \\ \limsup_{t\to\infty} y(t) \le \dfrac{\gamma_1 - e_1}{\delta_1}, \\ \limsup_{t\to\infty} z(t) \le \dfrac{\gamma_2 + \gamma_3 J_4 - e_2}{\delta_2}. \end{cases}$$

Proposition 5.10. *Let*

$$J_4 = \frac{\gamma_1 - e_1}{\delta_1},\ J_5 = \frac{\gamma_2 + \gamma_3 J_4 - e_2}{\delta_2},\ \sigma = 1 - J_4 - J_5,\ J_6 = \frac{\gamma_1\sigma - cJ_5 - e_1}{\delta_1}.$$

Assume that $\gamma_1\sigma - cJ_5 > e_1, \gamma_2\sigma + \gamma_3 J_6 > e_2$ *and* $J_4 + J_5 < 1$*. If* $(x(0), y(0), z(0)) > (0, 0, 0)$*, then the population function* $(x(t), y(t), z(t))$ *as solution of (5.2) satisfies*

$$\begin{cases} \liminf_{t\to\infty} x(t) \ge 1 - J_4 - J_5, \\ \liminf_{t\to\infty} y(t) \ge \dfrac{\gamma_1\sigma - cJ_5 - e_1}{\delta_1}, \\ \liminf_{t\to\infty} z(t) \ge \dfrac{\gamma_2\sigma + \gamma_3 J_6 - e_2}{\delta_2}. \end{cases}$$

The proofs of Propositions 5.9 and 5.10 are similar to Lemmas 4.1 and 4.2, respectively, hence we omit them here. When the conditions of Proposition 5.10 hold, the obtained ultimate lower bounds and the ultimate upper bounds given in Proposition 5.9 form a positive global attractor for the food-chain model (5.2) such that the ecological system is permanent. Define

$$\begin{cases} \underline{x}^{(0)} = 1 - J_4 - J_5,\ \underline{y}^{(0)} = \dfrac{\gamma_1\sigma - cJ_5 - e_1}{\delta_1},\ \underline{z}^{(0)} = \dfrac{\gamma_2\sigma + \gamma_3 J_6 - e_2}{\delta_2}, \\ \overline{x}^{(0)} = 1,\ \overline{y}^{(0)} = \dfrac{\gamma_1 - e_1}{\delta_1},\ \overline{z}^{(0)} = \dfrac{\gamma_2 + \gamma_3 J_4 - e_2}{\delta_2}, \end{cases}$$

where $J_4 = \frac{\gamma_1 - e_1}{\delta_1}, J_5 = \frac{\gamma_2 + \gamma_3 J_4 - e_2}{\delta_2}$ and $J_6 = \frac{\gamma_1\sigma - cJ_5 - e_1}{\delta_1}$.

It is easy to verify that $(\underline{x}^{(0)}, \underline{y}^{(0)}, \underline{z}^{(0)})$ and $(\overline{x}^{(0)}, \overline{y}^{(0)}, \overline{z}^{(0)})$ are also coupled lower and upper solution of system (5.2) according to the conditions of Proposition 5.10. Thus we can define iterated sequences $(\underline{x}^{(n)}, \underline{y}^{(n)}, \underline{z}^{(n)})$ and $(\overline{x}^{(n)}, \overline{y}^{(n)}, \overline{z}^{(n)})$ satisfying

$$\begin{cases} 1 - \overline{x}^{(n+1)} - \underline{y}^{(n)} - \underline{z}^{(n)} = 0, \\ 1 - \underline{x}^{(n+1)} - \overline{y}^{(n)} - \overline{z}^{(n)} = 0, \\ \gamma_1\overline{x}^{(n)} - c\underline{z}^{(n)} - e_1 - \delta_1\overline{y}^{(n+1)} = 0, \\ \gamma_1\underline{x}^{(n)} - c\overline{z}^{(n)} - e_1 - \delta_1\underline{y}^{(n+1)} = 0, \\ \gamma_2\overline{x}^{(n)} + \gamma_3\overline{y}^{(n)} - e_2 - \delta_2\overline{z}^{(n+1)} = 0, \\ \gamma_2\underline{x}^{(n)} + \gamma_3\underline{y}^{(n)} - e_2 - \delta_2\underline{z}^{(n+1)} = 0. \end{cases} \tag{5.13}$$

Similarly, we can deduce from the induction method that

$$(\underline{x}^{(0)}, \underline{y}^{(0)}, \underline{z}^{(0)}) \le (\underline{x}^{(n)}, \underline{y}^{(n)}, \underline{z}^{(n)}) \le (\overline{x}^{(n)}, \overline{y}^{(n)}, \overline{z}^{(n)}) \le (\overline{x}^{(0)}, \overline{y}^{(0)}, \overline{z}^{(0)}),$$

and that the limits

$$\lim_{n\to\infty}(\underline{x}^{(n)}, \underline{y}^{(n)}, \underline{z}^{(n)}) = (\underline{x}, \underline{y}, \underline{z}), \quad \lim_{n\to\infty}(\overline{x}^{(n)}, \overline{y}^{(n)}, \overline{z}^{(n)}) = (\overline{x}, \overline{y}, \overline{z})$$

exist and satisfy the following equations

$$\begin{cases} 1 - \overline{x} - \underline{y} - \underline{z} = 0, \\ 1 - \underline{x} - \overline{y} - \overline{z} = 0, \\ \gamma_1\overline{x} - c\underline{z} - e_1 - \delta_1\overline{y} = 0, \\ \gamma_1\underline{x} - c\overline{z} - e_1 - \delta_1\underline{y} = 0, \\ \gamma_2\overline{x} + \gamma_3\overline{y} - e_2 - \delta_2\overline{z} = 0, \\ \gamma_2\underline{x} + \gamma_3\underline{y} - e_2 - \delta_2\underline{z} = 0. \end{cases} \tag{5.14}$$

Thus, we have the following conclusions on permanence.

Proposition 5.11. *Assume that $\gamma_1\sigma - cJ_5 > e_1, \gamma_2\sigma + \gamma_3 J_6 > e_2$ and $J_4 + J_5 < 1$, where $J_i (i = 4, 5, 6)$ are defined in the proof of Proposition 5.10. Let $(\underline{x}, \underline{y}, \underline{z})$ and $(\overline{x}, \overline{y}, \overline{z})$ be the respective limits of the monotone sequences $(\underline{x}^{(n)}, \underline{y}^{(n)}, \underline{z}^{(n)})$ and $(\overline{x}^{(n)}, \overline{y}^{(n)}, \overline{z}^{(n)})$ generated in (5.13). Then the system (5.2) is permanent, with a global attractor $[\underline{x}, \overline{x}] \times [\underline{y}, \overline{y}] \times [\underline{z}, \overline{z}]$ which contains a positive equilibrium (x^*, y^*, z^*). If $(\underline{x}, \underline{y}, \underline{z}) = (\overline{x}, \overline{y}, \overline{z})$, then the positive equilibrium (x^*, y^*, z^*) is unique and globally asymptotically stable.*

Next, we investigate on a sufficient condition for $(\underline{x}, \underline{y}, \underline{z}) = (\overline{x}, \overline{y}, \overline{z})$, which ensures the uniqueness and global stability of the positive equilibrium (x^*, y^*, z^*).

Proposition 5.12. *Assume that $\gamma_1\sigma - cJ_5 > e_1, \gamma_2\sigma + \gamma_3 J_6 > e_2$ and $J_4 + J_5 < 1$, where $J_i (i = 4, 5, 6)$ are defined in the proof of Proposition5.10. Denote*

$$D = \begin{pmatrix} 1 & -1 & -1 \\ \gamma_1 & -\delta_1 & c \\ \gamma_2 & \gamma_3 & -\delta_2 \end{pmatrix}.$$

If $\det D \neq 0$, then the IGP model (5.2) has a unique positive equilibrium (x^*, y^*, z^*). When $(x(0), y(0), z(0)) > (0, 0, 0)$, the solution $(x(t), y(t), z(t))$ of (5.2) satisfies

$$\lim_{t\to\infty}(x(t), y(t), z(t)) = (x^*, y^*, z^*).$$

Proof. From Eq. (5.14) we see that

$$\begin{cases} (\overline{x} - \underline{x}) - (\overline{y} - \underline{y}) - (\overline{z} - \underline{z}) = 0, \\ \gamma_1(\overline{x} - \underline{x}) - \delta_1(\overline{y} - \underline{y}) + c(\overline{z} - \underline{z}) = 0, \\ \gamma_2(\overline{x} - \underline{x}) + \gamma_3(\overline{y} - \underline{y}) - \delta_2(\overline{z} - \underline{z}) = 0. \end{cases}$$

If $\det D \neq 0$, then we have $(\underline{x}, \underline{y}, \underline{z}) = (\overline{x}, \overline{y}, \overline{z})$. This completes the proof. $\square$

5.3.2. Global stability of positive equilibrium

In the Subsection 5.2.2, we have shown that the positive equilibrium E^* is locally asymptotically stable if (5.11) and (5.12) hold. From the pervious subsection, we know that the conditions of Theorem 5.11 can guarantee the permanence phenomenon of the system (5.2). But these conditions are too strong according to the discussion in Remark 4.2. Now we shall find some weaker conditions under which the positive equilibrium E^* is globally asymptotically stable.

Proposition 5.13. *Assume that $\Lambda \neq 0$ and $\frac{\Lambda_i}{\Lambda} > 0$, for $i = 1, 2, 3$. Then the positive equilibrium E^* is globally asymptotically stable if*

$$4c\gamma_2\gamma_3\delta_1 > (\gamma_1\gamma_3 - c\gamma_2)^2. \tag{5.15}$$

Proof. The proof of the global stability of the positive equilibrium $E^*(x^*, y^*, z^*)$ can be reached by constructing a Lyapunov function V as follows:

$$\begin{aligned} V(t) = {} & l_1\left(x(t) - x^* - x^* \ln\frac{x(t)}{x^*}\right) + l_2\left(y(t) - y^* - y^* \ln\frac{y(t)}{y^*}\right) \\ & + l_3\left(z(t) - z^* - z^* \ln\frac{z(t)}{z^*}\right), \end{aligned}$$

where $l_i (i = 1, 2, 3)$ are positive constants to be determined.

Calculating the derivative of $V(t)$ along positive solutions to (5.2), it follows that

$$\begin{aligned} V'(t) &= l_1(x(t) - x^*)\frac{x'(t)}{x(t)} + l_2(y(t) - y^*)\frac{y'(t)}{y(t)} + l_3(z(t) - z^*)\frac{z'(t)}{z(t)} \\ &= l_1(x_1(t) - x_1^*)[-(x(t) - x^*) - (y(t) - y^*) - (z(t) - z^*)] \\ &\quad + l_2(y(t) - y^*)[\gamma_1(x(t) - x^*) - c(z(t) - z^*) - \delta_1(y(t) - y^*)] \\ &\quad + l_3(z(t) - z^*)[\gamma_2(x(t) - x^*) + \gamma_3(y(t) - y^*) - \delta_2(z(t) - z^*)]. \end{aligned}$$

Setting $l_1 = \gamma_2, l_2 = \gamma_3/c, c_3 = 1$, then it is derived from above equation that

$$\begin{aligned} V'(t) = {} & -\frac{\gamma_3\delta_1}{c}\left[\frac{\gamma_1\gamma_3 - c\gamma_2}{2\gamma_3\delta_1}(x(t) - x^*) - (y(t) - y^*)\right]^2 \\ & - \left[\gamma_2 - \frac{(\gamma_1\gamma_3 - c\gamma_2)^2}{4c\gamma_3\delta_1}\right](x(t) - x^*)^2 - \delta_2(z(t) - z^*)^2. \end{aligned}$$

Denote

$$\mathcal{G} = \{(x, y, z) \in \mathbb{R}^3; 0 < x \leq J_1, 0 < y \leq J_2, 0 < z \leq J_3\}$$

where $J_i (i = 1, 2, 3)$ are defined in Lemma 2.1. If (5.15) holds, for any $(x(t), y(t), z(t)) \in \mathcal{G}$, we have $V'(t) \leq 0$, with equality if and only if $x(t) = z_1^*, y(t) = z_2^*, z(t) = z_3^*$.

Then we look for the invariant subset M within the set

$$M = \{(x(t), y(t), z(t)) : V'(t) = 0\}.$$

Clearly, the only invariant set in M is $M = \{(x^*, y^*, z^*)\}$. Using the LaSalle invariant principle, the global asymptotic stability of E^* follows. $\square$

5.3.3. Hopf bifurcation

In this part, we investigate the existence of periodic solutions via the Hopf bifurcation in the cyan region of the parameter space. By the previous arguments, the positive equilibrium E^* is stable if and only if the inequalities (5.11) and (5.12) hold. Since condition (5.11) is always true in this region, we manipulate the inequality (5.12) and use similar arguments in Ruan [28] to establish the existence of periodic solutions bifurcated from the equilibrium E^*. Moreover, in this part we assume that the inequality

$$\gamma_1\gamma_3 + c\gamma_3 > c\gamma_2$$

holds, which implies $\Lambda > 0$.

Let us reconsider the characteristic equation (5.10) at E^* with a complex eigenvalue $a + b\mathrm{i}$,

$$(a + b\mathrm{i})^3 + A_2(a + b\mathrm{i})^2 + A_1(a + b\mathrm{i}) + A_0 = 0, \tag{5.16}$$

where

$$\begin{aligned}
&A_2 = x^* + \delta_1 y^* + \delta_2 z^*, \quad A_0 = x^* y^* z^* \Lambda,\\
&A_1 = x^* y^*(\delta_1 + \gamma_1) + x^* z^*(\delta_2 + \gamma_2) + y^* z^*(\delta_1\delta_2 + c\gamma_3).
\end{aligned}$$

Solving (5.16), we have

$$\begin{aligned}
&a^3 - 3ab^2 + A_2(a^2 - b^2) + A_1 a + A_0 = 0,\\
&3a^2 b - b^3 + 2abA_2 + A_1 b = 0.
\end{aligned} \tag{5.17}$$

If $a = 0$, then we get $A_2 A_1 = A_0$ and E^* loses its stability. Moreover, this is equivalent to the reversed (5.12). Simultaneously, the characteristic equation (5.10) can be rewritten as

$$(\lambda + A_2)(\lambda^2 + A_1) = 0.$$

Hence we obtain one negative real eigenvalue and two purely imaginary eigenvalues.

Let μ be a parameter, x^*, y^* and z^* depend on μ, and $\bar{\mu}$ satisfies $a(\bar{\mu}) = 0$. We then establish the transversality condition which guarantees the existence of periodic solutions bifurcated from E^*. Differentiating (5.17) with respect to μ and solving linear system of $\frac{\mathrm{d}a}{\mathrm{d}\mu}|_{\mu=\bar{\mu}}$ and $\frac{\mathrm{d}b}{\mathrm{d}\mu}|_{\mu=\bar{\mu}}$, we obtain

$$\begin{aligned}
\left.\frac{\mathrm{d}a}{\mathrm{d}\mu}\right|_{\mu=\bar{\mu}} &= -\left.\frac{(-3b^2 + A_1)(-b^2\frac{\mathrm{d}A_2}{\mathrm{d}\mu} + \frac{\mathrm{d}A_0}{\mathrm{d}\mu}) + 2b^2 A_2 \frac{\mathrm{d}A_1}{\mathrm{d}\mu}}{(-3b^2 + A_1)^2 + 4b^2 A_2^2}\right|_{\mu=\bar{\mu}}\\
&= \left.\frac{1}{2b^2 + 2A_2^2}\frac{\mathrm{d}(A_0 - A_1 A_2)}{\mathrm{d}\mu}\right|_{\mu=\bar{\mu}}\\
&= -\frac{1}{2b^2 + 2A_2^2}\frac{\mathrm{d}F}{\mathrm{d}\mu}(\bar{\mu}),
\end{aligned} \tag{5.18}$$

where the function

$$F(\mu) = A_1 A_2 - A_0.$$

Note that the inequality (5.12) holds if and only if $F > 0$. Therefore we have the following conclusion on the Hopf bifurcation at the positive equilibrium E^*.

Proposition 5.14. *Assume that* $\Lambda_i > 0 (i = 1, 2, 3), \gamma_1\gamma_3 + c\gamma_3 > c\gamma_2, F(\bar{\mu}) = 0$ *and* $\frac{\mathrm{d}F}{\mathrm{d}\mu}(\bar{\mu}) > 0$ *hold. Then the positive equilibrium* E^* *is locally asymptotically stable when* $\mu > \bar{\mu}$ *and loses its stability when* $\mu = \bar{\mu}$. *When* $\mu < \bar{\mu}$, E^* *becomes unstable and a family of periodic solutions bifurcates from* E^*.

From the biological point of view, we should consider the influence of intraspecies competition on the dynamic behavior of the positive equilibrium E^*. Then we take δ_1, δ_2 as the bifurcation parameter to cause the existence of periodic solutions bifurcated from the instability of positive equilibrium E^*.

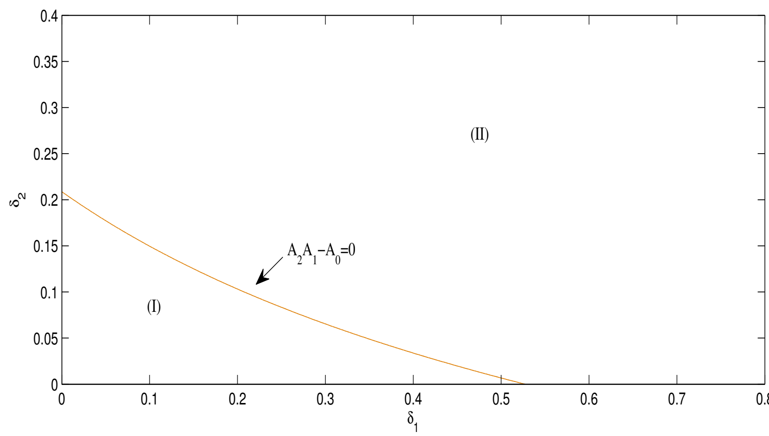


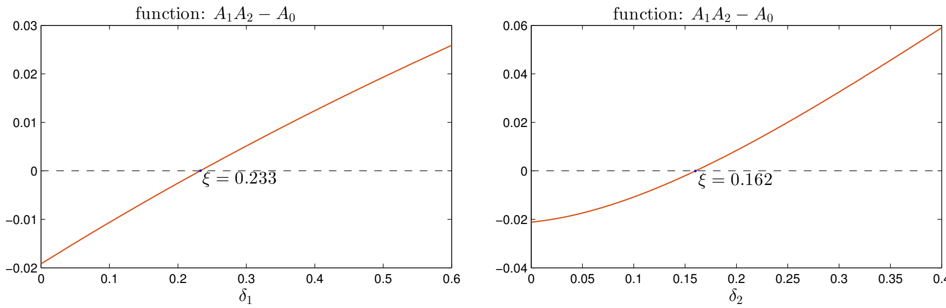
Figure 8. Hopf bifurcation curve of system (5.2) with parameter condition C_1. When $(\delta_1, \delta_2) \in$ (I), $F(\delta_1, \delta_2) = A_2A_1 - A_0 < 0$. When $(\delta_1, \delta_2) \in$ (II), $F(\delta_1, \delta_2) = A_2A_1 - A_0 > 0$.

By the previous arguments, the positive equilibrium E^* is stable if and only if $\Lambda > 0, \Lambda_i(i = 1, 2, 3) > 0$ and $F > 0$. Referring to Li and Dai [23], we take parameter values as follows:

$$(C_1): \quad \gamma_1 = 6, \gamma_2 = 3.5, \gamma_3 = 2, e_1 = 0.10, e_2 = 0.7, c = 1.$$

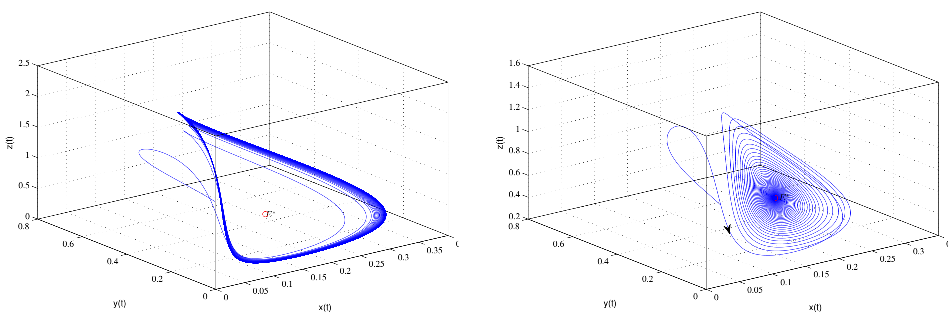
Then the Hopf bifurcation curve $F(\delta_1, \delta_2) \triangleq A_2A_1 - A_0 = 0$ of system (5.2) with respect to δ_1, δ_2 is depicted in Fig. 8. When $(\delta_1, \delta_2) \in$ (I) in Fig. 8, $F(\delta_1, \delta_2) < 0$, which means E^* is unstable and indicates the existence of periodic solution. When $(\delta_1, \delta_2) \in$ (II) in Fig. 8, $F(\delta_1, \delta_2) > 0$, which means E^* is locally asymptotically stable.

We first fix the parameter δ_2 as 0.09 and the graph of F, Fig. 9(a), can be obtained by varying δ_1 from 0 to 0.6 and calculating the value of the function F with respective to δ_1. Since the positive equilibrium E^* is unstable if $F < 0$, there is a periodic solution bifurcated from the positive equilibrium E^*. Numerical simulations of (5.2) at $\delta_1 = 0.08, 0.4$ are performed and presented in Fig. 10(a) and (b), respectively. We can see that the positive equilibrium E^* is locally asymptotically stable when $\delta_1 = 0.4$ (see Fig. 10(b)) and Hopf bifurcation will occur as the bifurcation parameter δ_1 decreases. When $\delta_1 = 0.08$, the positive equilibrium E^* loses its stability and a periodic solution bifurcates from it (see Fig. 10(a)). Next, we fix the parameter δ_1 as 0.08 and the graph of F, Fig. 9(b), can be obtained by varying δ_2 from 0 to 0.6 and calculating the value of the function F with respective to δ_2. Then, similar results of numerical simulations about δ_2 can be obtained and we omit them here.



(a) (b)

Figure 9. (a) The graph of F in terms of δ_1. (b) The graph of F in terms of δ_2



(a) $\delta_1 = 0.08$ (b) $\delta_1 = 0.4$

Figure 10. Two numerical solutions of system (5.2) with parameter condition (C_1). (a) A periodic solution bifurcates from the positive equilibrium via Hopf bifurcation when $\delta_1 = 0.08$. (b) The positive equilibrium E^* is locally asymptotically stable when $\delta_1 = 0.4$. The initial condition is: $(x_0, y_0, z_0) = (0.19, 0.5, 0.3)$.

6. Conclusion

In this paper, we study a general intraguild predation (IGP) model (1.2), which contains intraspecific competition in the growth of IG prey and IG predator, and give a rigorous analysis for a special IGP model (5.1) with linear functional response.

For the general IGP model, we have obtained some conditions about stability for trivial, semi-trivial and boundary equilibria. The long time behavior of the solution $(R(t), N(t), P(t))$ of (1.2) is investigated. Under the assumption of Theorem 4.2 we get the extinction result of three species when the initial population $R(0)$ is relatively smaller than $N(0)$ and $P(0)$. Under the assumption of Theorem 4.3 the IGP model (1.2) is permanent, with a global attractor $[\underline{R}, \overline{R}] \times [\underline{N}, \overline{N}] \times [\underline{P}, \overline{P}]$ which contains a positive equilibrium (R^*, N^*, P^*). It is a pity that we can not find some relatively weak conditions to ensure the permanence result.

For the case with the linear functional response, the conditions for local stability and global stability of trivial, semi-trivial and boundary equilibria are rigorously divided into four classes (see Fig. 7 and Table 1), which is similar to the results of [17]. In the cyan region of Fig. 7, the positive equilibrium exists and the permanence effect of the population of model (5.2) follows (Proposition 5.11). Compared with the model in [17], the parameters δ_1, δ_2, that are the intraspecific competition coefficients among the populations of IG prey and IG predator, respectively, can promote complex dynamical behavior. Numerical simulations are conducted to show the potential role that intraspecific competition can play in the model (5.2). By using δ_1 and δ_2 as the bifurcation parameters, we numerically sketch the Hopf bifurcation curves of system (5.2) with parameter condition C_1. Our results show that intraspecific competition has a stabilizing effect and eliminates oscillations. If the positive equilibrium is unstable and oscillations are observed in model (5.2), then the intraspecific competition can have a stabilizing role, and as δ_1 or δ_2 increases, the oscillations disappear and the positive equilibrium gains its stability (see Proposition 5.14 and Figs. 8, 9 and 10).

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References

[1] A. Atabaigi, *Bifurcation and chaos in a discrete time predator-prey system of Leslie type with generalized Holling type III functional response*, J. Appl. Anal. Comput., 2017, 7(2), 411–426.

[2] P. Amarasekare, *Coexistence of intraguild predators and prey in resource-rich environments*, Ecol., 2008, 89(10), 2786–2797.

[3] P. Abrams, S. Fung, *Prey persistence and abundance in systems with intraguild predation and type-2 functional response*, J. Theor. Biol., 2010, 264, 1033–1042.

[4] D. Bolnick, *Can intraspecific competition drive disruptive selection? an experimental test in natural populations of sticklebacks*, Evol., 2004, 58(3), 608–618.

[5] F. Brauer, C. Castillo Chavez, *Mathematical Models in Population Biology and Epidemiology (Second Edition)*, Springer, New York, 2012.

[6] G. Butler, H. Freedman, P. Waltman, *Uniformly persistent systems*, Proc. Amer. Math. Soc., 1986, 96(3), 425–430.

[7] S. Chow, C. Li, D. Wang, *Normal Forms and Bifurcation of Planar Vector Fields*, Cambridge University Press, Cambridge, 1994.

[8] C. Dye, *Intraspecific competition amongst larval Aedes aegypti food exploitation or chemical interference*, Ecol. Entomol., 1982, 7, 39–46.

[9] H. Freedman, P. Waltman, *Persistence in models of three interacting predator-prey populations*, Math. Biosci., 1984, 68(2), 213–231.

[10] H. Freedman, S. Ruan, M. Tang, *Uniform persistence and flows near a closed positively invariant set*, J. Dynam. Diff. Eqs., 1994, 6(4), 583–600.

[11] M. Freeze, Y. Chang, W. Feng, *Analysis of dynamics in a complex food chain with ratio-dependent functional response*, JAAC, 2014, 4(1), 69–87.

[12] C. Holling, *The components of predation as revealed by a study of small mammal predation of the European Pine Sawfly*, Can. Entomol., 1959, 91, 293–320.

[13] R. Holt, G. Polis, *A theoretical framework for intraguild predation*, Am. Nat., 1997, 149, 745–764.

[14] R. Han, B. Dai, *Spatiotemporal dynamics and Hopf bifurcation in a delayed diffusive intraguild predation model with Holling II functional response*, Int. J. Bifurcat. Chaos, 2016, 26(12), 1–31.

[15] R. Han, B. Dai, *Spatiotemporal dynamics and spatial pattern in a diffusive intraguild predation model with delay effect*, Appl. Math. Comput., 2017, 312, 177–201.

[16] R. Han, B. Dai, L. Wang, *Delay induced spatiotemporal patterns in a diffusive intraguild predation model with Beddington-DeAngelis functional response*, Math. Biosci. Eng., 2018, 15(3), 595–627.

[17] S. Hsu, S. Ruan, T. Yang, *Analysis of three species Lotka-Volterra food web models with omnivory*, J. Math. Anal. Appl., 2015, 426(2), 659–687.

[18] T. Hanse, N. Stenseth, H. Henttonen, J. Tast, *Interspecific and intraspecific competition as causes of direct and delayed density dependence in a fluctuating vole population*, Proc. Natl. Acad. Sci., 1999, 96, 986–991.

[19] A. Korobeinikov, *Stability of ecosystem: global properties of a general predator-prey model*, Math. Medic. Biol., 2009, 26, 309–321.

[20] Y. Kuznetsov, *Elements of Applied Bifurcation Theory (Third Edition)*, Springer, New York, 2004.

[21] Y. Kang, L. Wedekin, *Dynamics of a intraguild predation model with generalist or specialist predator*, J. Math. Biol., 2013, 67(5), 1227–1259.

[22] M. Van Kleunen, M. Fischer, B. Schmid, *Effects of intraspecific competition on size variation and reproductive allocation in a clonal plant*, OIKOS, 2001, 94, 515–524.

[23] Z. Li, B. Dai, *Global dynamics of delayed intraguild predation model with intraspecific competition*, Int. J. Biomath., 2018, 11(8), 1–39.

[24] K. Mischaikow, H. Smith, H. Thieme, *Asymptotically autonomous semiflows: chain recurrence and Lyapunov functions*, Trans. Amer. Math. Soc., 1995, 347(5), 1669–1685.

[25] C. Pao, *Nonlinear parabolic and elliptic equations*, Plenum Press, New York and London, 1992.

[26] G. Polis, R. Holt, *Intraguild predation: the dynamics of complex trophic interactions*, Trends Ecol. Evol., 1992, 7, 151–154.

[27] M. Peng, Z. Zhang, X. Wang, X. Liu, *Hopf bifurcation analysis for a delayed predator-prey system with a prey refuge and selective harvesting*, J. Appl. Anal. Comput., 2018, 8(3), 982–997.

[28] S. Ruan, *Oscillations in plankton models with nutrient recycling*, J. Theor. Biol., 2001, 208(1), 15–26.

[29] H. Shu, X. Hu, L. Wang, J. Watmough, *Delay induced stability switch, multitype bistability and chaos in an intraguild predation model*, J. Math. Biol., 2015, 71, 1269–1298.

[30] A. Verdy, P. Amarasekare, *Alternative stable states in communities with intraguild predation*, J. Theor. Biol., 2010, 262(1), 116–128.

[31] Y. Wang, D. DeAngelis, *Stability of an intraguild predation system with mutual predation*, Commun. Nonl. Sci. Numer. Simul., 2016, 33, 141–159.

[32] Y. Wang, W. Jiang, *Bifurcations in a delayed differential-algebraic plankton economic system*, J. Appl. Anal. Comput., 2017, 7(4), 1431–1447.