J. Math. Anal. Appl. 426 (2015) 659–687

Contents lists available at ScienceDirect

Journal of Mathematical Analysis and Applications

www.elsevier.com/locate/jmaa

Analysis of three species Lotka–Volterra food web models with omnivory

Sze-Bi Hsu [a], Shigui Ruan [b], Ting-Hui Yang [c,*]

[a] Department of Mathematics and The National Center for Theoretical Science, National Tsing-Hua University, Hsinchu 30013, Taiwan, ROC
[b] Department of Mathematics, University of Miami, Coral Gables, FL 33124-4250, USA
[c] Department of Mathematics, Tamkang University, 151 Ying-chuan Road, New Taipei City 25137, Taiwan, ROC

ARTICLE INFO

Article history:
Received 27 August 2014
Available online 20 January 2015
Submitted by J.J. Nieto

Keywords:
Three species
Predator–prey
Omnivory
Generalist predator
Global dynamics
Uniform persistence

ABSTRACT

In this work, we consider a three species Lotka–Volterra food web model with omnivory which is defined as feeding on more than one trophic level. Based on a non-dimensional transformation, the model actually becomes a system of three first order ordinary differential equations with seven parameters. Analytically, we completely classify the parameter space into three categories containing eight cases, show the extinction results for five cases, and verify uniform persistence for the other three cases. Moreover, in the region of the parameter space where the system is uniformly persistent we prove the existence of periodic solutions via Hopf bifurcation and present the chaotic dynamics numerically. Biologically, the omnivory module blends the attributes of several well-studied community modules, such as food chains (food chain models), exploitative competition (two predators–one prey models), and apparent competition (one predator–two preys models). We try to point out the differences and similarities among these models quantitatively and give the biological interpretations.

1. Introduction

Three species food web models are fundamental building blocks of large scale ecosystems. To clarify the local or global and short-term or long-term behavior of ecosystems, it is essential to understand the interacting dynamics of three species food web models. A monotone ecosystem whose interactions among n-species are all cooperative or competitive ($n = 2$) have been well studied in the past three decades thanks to the theory of monotone dynamical systems [9]. However, for a non-monotone system whose interactions are blended at least with one consumption (i.e. herbivory, predation or parasitism), most known results

---

[*] Corresponding author.
E-mail addresses: sbhsu@math.nthu.edu.tw (S.-B. Hsu), ruan@math.miami.edu (S. Ruan), thyang@math.tku.edu.tw (T.-H. Yang).

http://dx.doi.org/10.1016/j.jmaa.2015.01.035

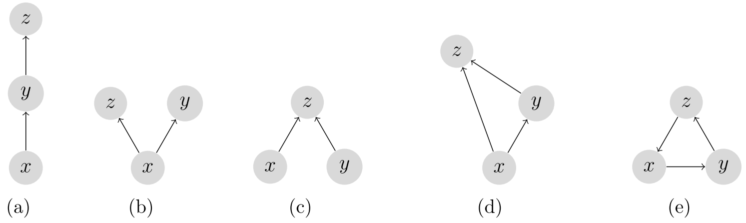


Fig. 1.1. All possible schematic diagrams of the direct and indirect interactions among three species predator–prey systems. The arrows present the directions of biomass. (a) Food chain; (b) two predators–one prey; (c) one predator–two preys; (d) food chain with omnivory; and (e) food chain with cycle.

are constrained on two species cases since the classical Poincaré–Bendixson Theorem can be applied. Hence recently attentions have been attracted to the dynamics of a non-monotone ecosystem with at least 3-species.

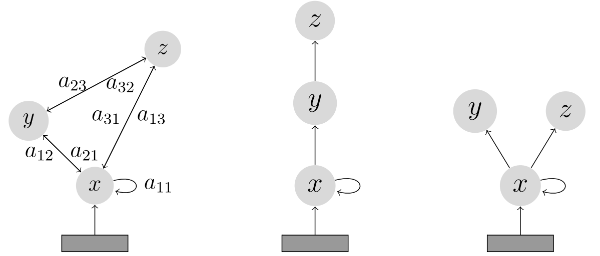
Since 1970's, there have been some interesting and impressive results on investigating the dynamics of three species predator–prey systems [7,8,11,12,15]. In particular, Krikorian [15] has classified all three-species food web Lotka–Volterra models into four types in all 34 cases: food chains (Fig. 1.1(a)), two predators competing for one prey (Fig. 1.1(b)), one predator acting on two preys (Fig. 1.1(c)), and loops (Fig. 1.1(d), (e)). We separate the case loop into two sub-cases, food chain with omnivory (Fig. 1.1(d)) and cycle (Fig. 1.1(e)). We observe that all species except for species z of case (d) with consumption in the above cases are the so-called specialist predators which have a limited diet. On the other hand, the species z of case (d) is called the generalist predator which can make use of a variety of different resources from two trophic levels.

In this paper, we will focus on three species food web models of predator–prey type with an omnivorous top predator which is defined as feeding on more than one trophic level. Actually, this is a general part of marine or terrestrial food web ecological systems. For example, species x are plants, species y are herbivores, and species z consume not only plants but also other herbivores. One can find more examples in the complex marine food web systems. This type of models has been reported in the past two decades [10,20,21,23,24]. This phenomenon has been variously called "trophic level omnivory", "intraguild predation", "higher order predation", or "hyperpredation". Moreover, Holt and Polis [10] point out that there is growing evidence for the importance of intraguild predation in many natural communities, yet little formal ecological theory addresses this particular blend of interactions, a mixture of competition and predation between two predators.

Motivated by the articles [4,10,13,15,17,27], we consider the following three species food web model with the Lotka–Volterra type interaction between populations,

$$\begin{aligned} \frac{dN_1}{d\tau} &= N_1(B - a_{11}N_1 - a_{12}N_2 - a_{13}N_3), \\ \frac{dN_2}{d\tau} &= N_2(-D_1 + a_{21}N_1 - a_{23}N_3), \\ \frac{dN_3}{d\tau} &= N_3(-D_2 + a_{31}N_1 + a_{32}N_2), \\ N_1(0) &\geq 0, \quad N_2(0) \geq 0, \quad N_3(0) \geq 0, \end{aligned} \tag{1.1}$$

where N_1, N_2, and N_3 denote the densities of a basal resource, an intermediate consumer (intraguild prey), and an omnivorous top predator (intraguild predator), respectively. The parameters are all positive and B, D_1, and D_2 are the intrinsic growth rate of the resource N_1, the death rate of the prey N_2, and the death rate of the predator N_3, respectively. In the absence of other species, species N_1 follows the traditional logistical growth model and the functional responses between different species are assumed to be Lotka–Volterra type. The coefficient a_{11} denotes the intraspecific competition in the resource and a_{ij} $(i < j)$ is the rate of



(a) omnivorous models (b) food chain models (c) two predator one prey models

Fig. 1.2. Three most simple interactions between three species with one renewable resource.

consumption; and a_{ij} $(i > j)$ measures the contribution of the victim (basal resource or intraguild prey) to the growth of the consumer.

System (1.1) can be regarded as a food-chain or two predators–one prey model when $a_{13} = a_{31} = 0$ or $a_{23} = a_{32} = 0$, respectively (see Fig. 1.2). In this work, we would like to clarify the global dynamics and corresponding biological interpretations of (1.1). But this task is non-trivial since it blends the attributes of several well-studied community modules, such as food chains, and exploitative competition (two predators–one prey). Actually, Holt and Polis [10] highlight similarities and differences among these modules and system (1.1). We provide detailed and completed mathematical analysis of model (1.1) with related biological implications. Our results provide us new insights in addition to some parallel results that have been discussed in [10].

The rest of the paper is organized as follows. In Section 2, we show the boundedness of solutions of (2.1) and recall some known local and global results for two-dimensional subsystems. Then some global behaviors of the boundary equilibria are investigated by the methods of Lyapunov and McGehee Lemma. In Section 3, we classify all parameters into six categories to investigate the existence of positive equilibria. Global dynamics are presented analytically for five cases including y die-out or z die-out, bi-stability phenomenon, and global stability of the coexistence state. In Section 4, two numerical results are given. One presents the existence of periodic solutions resulted from the Hopf bifurcation. The other presents complex behaviors routed by a period-doubling cascade. In Section 5, we give some discussions and remarks.

2. Preliminaries

In this section, first of all, we show that solutions of (2.1) are bounded. Then some well known two-dimensional results are recalled. Moreover, stabilities of all boundary equilibria in $\mathbb{R}^3$ are clarified. Finally, a necessary and sufficient condition which can reduce system (2.1) to the one- or two-dimensional subsystem is given.

For mathematical simplification, we write model (1.1) in non-dimensional forms. Let

$$\begin{aligned} t &= B\tau, & x &= a_{11}N_1/B, \\ y &= a_{12}N_2/B, & z &= N_3/B, \end{aligned}$$

then (1.1) takes the form

$$\begin{aligned} \frac{dx}{dt} &= x(1 - x - y - \bar{\gamma} z), \\ \frac{dy}{dt} &= y(-d_1 + \alpha x - \beta z), \\ \frac{dz}{dt} &= z(-d_2 + \gamma x + \delta y), \end{aligned} \tag{2.1}$$

with initial conditions, $x(0) \geq 0$, $y(0) \geq 0$, $z(0) \geq 0$, where the parameters are all positive with the rescaling:

$$\begin{aligned} d_1 &= D_1/B, & d_2 &= D_2/B, & & \\ \alpha &= a_{21}/a_{11}, & \beta &= a_{23}, & & \\ \gamma &= a_{31}/a_{11}, & \bar{\gamma} &= a_{13}, & \delta &= a_{32}/a_{12}. \end{aligned} \tag{2.2}$$

If we rewrite the first equation of (1.1) as the form,

$$\frac{dN_1}{d\tau} = BN_1\left(1 - \frac{a_{11}}{B}N_1 - \frac{a_{12}}{B}N_2 - \frac{a_{13}}{B}N_3\right),$$

then we can see that the traditional environmental carry capacity K of the logistic growth model is B/a_{11}. The parameters proportioned to K are $\alpha = a_{21}K/B$ and $\gamma = a_{31}K/B$ which are positive relative to the basal resource productivity. The parameter

$$\delta = \frac{a_{32}}{a_{12}} = \frac{a_{32}}{a_{23}}\frac{a_{23}}{a_{21}}\frac{a_{21}}{a_{12}}$$

measures the efficiency of biomass in the direction from x to y (a_{21}/a_{12}) and y to z (a_{32}/a_{23}), and the conversion rate for species y (a_{23}/a_{21}). The more biological details and implications will be discussed in the last section.

We can easily see that the solutions of (2.1) are positive (nonnegative) with positive (nonnegative) initial conditions. The following results on the boundedness of solutions of system (2.1) can be verified easily.

Proposition 2.1. *The system (2.1) is dissipative.*

Proof. From the first equation in system (2.1) we have

$$\frac{dx}{dt} \leq x(1-x),$$

so that the comparison principle implies that

$$\limsup_{t\to\infty} x(t) \leq 1.$$

Thus, for $\varepsilon > 0$ small, we have $x(t) \leq 1 + \varepsilon$ when t is sufficiently large. Denote $M = \max\{\alpha, \beta\gamma/(\bar{\gamma}\delta)\}$ and $D = \min\{d_1, d_2, 1\}$. From the equations in (2.1) we have

$$\begin{aligned} \frac{d}{dt}\big(Mx + y + (\beta/\delta)z\big) &= Mx(1 - x - y - \bar{\gamma}z) - d_1 y + \alpha xy - d_2(\beta/\delta)z + (\beta\gamma/\delta)xz \\ &\leq Mx - D\big(y + (\beta/\delta)z\big) \\ &\leq K - D\big(Mx + y + (\beta/\delta)z\big), \end{aligned}$$

where $K = (D+1)(1+\varepsilon)M$. Using the comparison principle a second time, we have

$$\limsup_{t\to\infty}\big(Mx + y + (\beta/\delta)z\big) \leq \frac{K}{D},$$

which implies that system (2.1) is dissipative. $\square$

2.1. Boundary equilibria and subsystems

By the previous result, it is easy to see that all solutions with nonnegative initial conditions will stay in a bounded region of the first octant with boundary. In this subsection, we will list all trivial and semi-trivial equilibria on the boundary of the first octant. It will help us to clarify the dynamics of all solutions on the boundary.

Based on biological meanings, we ask all equilibria to be nonnegative. Hence it is straightforward to calculate that there are one trivial equilibrium, $E_0 \equiv (0,0,0)$, and three semitrivial equilibria in system (2.1), $E_x \equiv (1,0,0)$, $E_{xy} \equiv (d_1/\alpha, 1-d_1/\alpha, 0)$, and $E_{xz} \equiv (d_2/\gamma, 0, (\gamma-d_2)/(\gamma\bar{\gamma}))$. It is obvious that the equilibria E_0 and E_x always exist without any restriction, the equilibrium E_{xy} exists if $\alpha > d_1$, and the equilibrium E_{xz} exists if $\gamma > d_2$. We recall some well-known one or two dimensional results.

Proposition 2.2. *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 (2.1) is reduced to the one-dimensional subsystem*

$$\frac{dx}{dt} = x(1-x). \tag{2.3}$$

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

(ii) *On H_2, system (2.1) is reduced to the two-dimensional subsystem*

$$\begin{aligned}\frac{dx}{dt} &= x(1-x-y),\\ \frac{dy}{dt} &= y(-d_1+\alpha x).\end{aligned} \tag{2.4}$$

If $\alpha \leq d_1$ then E_{xy} doest not exist and E_x is globally asymptotically stable; otherwise, if $\alpha > d_1$ then the equilibria E_0, E_x are saddles and E_{xy} is globally asymptotically stable.

(iii) *On H_3, system (2.1) is reduced to the two-dimensional subsystem*

$$\begin{aligned}\frac{dx}{dt} &= x(1-x-\bar{\gamma}z),\\ \frac{dz}{dt} &= z(-d_2+\gamma x).\end{aligned} \tag{2.5}$$

If $\gamma \leq d_2$ then E_{xz} doest not exist and E_x is globally asymptotically stable; otherwise, if $\gamma > d_2$ then the equilibria E_0, E_x are saddles and E_{xz} is globally asymptotically stable.

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

2.2. Local stability and some global dynamics of boundary equilibria in $\mathbb{R}^3$

In this subsection, the dynamics of all solutions in $\mathbb{R}^3$ near the boundary equilibria will be addressed. It is easy to find the Jacobian matrix of system (2.1) by direct computation,

$$J(x,y,z) = \begin{bmatrix} 1-2x-y-\bar{\gamma}z & -x & -\bar{\gamma}x \\ \alpha y & -d_1+\alpha x-\beta z & -\beta y \\ \gamma z & \delta z & -d_2+\gamma x+\delta y \end{bmatrix}. \tag{2.6}$$

We now consider the local stability of equilibria on the boundaries, H_1–H_4.

(a) E_0: The trivial equilibrium E_0 is a saddle point, where H_1 is the unstable subspace and H_4 is the stable subspace.

(b) E_x: The semi-trivial equilibrium E_x with the Jacobian evaluated at E_x,

$$J(E_x) = \begin{bmatrix} -1 & -1 & -\bar{\gamma} \\ 0 & \alpha - d_1 & 0 \\ 0 & 0 & \gamma - d_2 \end{bmatrix}, \tag{2.7}$$

is asymptotically stable if $\alpha < d_1$ and $\gamma < d_2$. Otherwise, it is a saddle if $\alpha > d_1$ or $\gamma > d_2$.

(c) E_{xy}: The equilibrium E_{xy} exists if $\alpha > d_1$ and the Jacobian evaluated at E_{xy} is given by

$$J(E_{xy}) = \begin{bmatrix} -d_1/\alpha & -d_1/\alpha & -d_1\bar{\gamma}/\alpha \\ \alpha - d_1 & 0 & -\beta(1 - d_1/\alpha) \\ 0 & 0 & -d_2 + \gamma d_1/\alpha + \delta(1 - d_1/\alpha) \end{bmatrix}. \tag{2.8}$$

It easy to see that the top left 2×2 sub-matrix is exactly the Jacobian matrix for the subsystem (2.4) at the equilibrium E_{xy} and the third eigenvalue is given by $\lambda = -d_2 + \gamma d_1/\alpha + \delta(1 - d_1/\alpha)$. Thus the semi-trivial solution E_{xy} is asymptotically stable in $\mathbb{R}^3$ if and only if

$$-d_2 + \gamma \frac{d_1}{\alpha} + \delta\left(1 - \frac{d_1}{\alpha}\right) < 0.$$

(d) E_{xz}: Similarly, the equilibrium E_{xz} exists if $\gamma > d_2$ and the Jacobian evaluated at E_{xz} is given by

$$J(E_{xz}) = \begin{bmatrix} -d_2/\gamma & -d_2/\gamma & -d_2\bar{\gamma}/\gamma \\ 0 & -d_1 + \alpha d_2/\gamma - \beta(1 - d_2/\gamma)/\bar{\gamma} & 0 \\ (\gamma - d_2)/\bar{\gamma} & \delta(\gamma - d_2)/(\gamma\bar{\gamma}) & 0 \end{bmatrix}.$$

It is similar to case (c). We can get the 2×2 sub-matrix by erasing the second row and column of the Jacobian matrix $J(E_{xz})$ and it is exactly the Jacobian matrix for subsystem (2.5) at the equilibrium E_{xz}. The third eigenvalue is given by $\lambda = -d_1 + \alpha d_2/\gamma - \beta(1 - d_2/\gamma)/\bar{\gamma}$. Thus the equilibrium E_{xz} is asymptotically stable in $\mathbb{R}^3$ if and only if

$$-d_1 + \alpha \frac{d_2}{\gamma} - \frac{\beta}{\bar{\gamma}}\left(1 - \frac{d_2}{\gamma}\right) < 0.$$

Summarizing the above discuss, we have results on the local stability of boundary equilibria in $\mathbb{R}^3$.

Proposition 2.3. *For system (2.1), the following statements are true.*

(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_x is asymptotically stable if $\alpha \le d_1$ and $\gamma \le d_2$. Otherwise, it is a saddle.*
(iii) *If $\alpha > d_1$, then E_{xy} exists and is asymptotically stable in $\mathbb{R}^3$ if and only if*

$$-d_2 + \gamma \frac{d_1}{\alpha} + \delta\left(1 - \frac{d_1}{\alpha}\right) < 0. \tag{2.9}$$

(iv) *Similarly, if $\gamma > d_2$ then E_{xz} exists and is asymptotically stable in $\mathbb{R}^3$ if and only if*

$$-d_1 + \alpha \frac{d_2}{\gamma} - \frac{\beta}{\bar{\gamma}}\left(1 - \frac{d_2}{\gamma}\right) < 0. \tag{2.10}$$

To clarify the global behaviors of the semi-trivial equilibria of system (2.1) with the restriction $\alpha \leq d_1$, we have the following extinction results.

Proposition 2.4. *Let $(x(t), y(t), z(t))$ be a solution of system (2.1) with initial condition $\boldsymbol{p} = (x(0), y(0), z(0))$ where $x(0) > 0$, $y(0) > 0$, and $z(0) > 0$. Then the following statements are true.*

- (i) *If $\alpha < d_1$ and $\gamma < d_2$, then the semi-trivial equilibria E_{xy} and E_{xz} 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_x is globally asymptotically stable.*
- (ii) *If $\alpha < d_1$ and $\gamma > d_2$, then one semi-trivial equilibrium E_{xy} does not exist but the other semi-trivial equilibrium E_{xz} exists. Moreover, we have the limit $\lim_{t\to\infty} y(t) = 0$ and the equilibrium E_{xz} is globally asymptotically stable.*

Proof. (i) By the first equation of (2.1), for any positive number ε we have $x(t) < 1 + \varepsilon$ for enough large t. Take $\varepsilon = (d_1 - \alpha)/2\alpha > 0$, then for large t consider

$$\frac{\dot{y}}{y} = \alpha - d_1 + \alpha(x - 1) - \beta z < \frac{\alpha - d_1}{2} < 0.$$

Hence we have the limit $\lim_{t\to\infty} y(t) = 0$. Similarly, take $\varepsilon = (d_2 - \gamma)/4\gamma$ and t large enough such that $x(t) < 1 + \varepsilon$ and $y(t) \leq (d_2 - \gamma)/4\delta$. Consider

$$\frac{\dot{z}}{z} = \gamma - d_2 + \gamma(x - 1) + \delta y < \frac{\gamma - d_2}{2} < 0.$$

Hence we also have $\lim_{t\to\infty} z(t) = 0$. Therefore we can find a point $\boldsymbol{q} \in H_1 \cap \omega(\boldsymbol{p})$ where $\omega(\boldsymbol{p})$ is the ω-limit set of $\boldsymbol{p}$. Since the equilibrium E_x is globally asymptotically stable on H_1, by the property of invariance of the ω-limit set, $E_x \in \omega(\boldsymbol{p})$. The assumptions $\alpha < d_1$ and $\gamma < d_2$ guarantee that E_x is asymptotically stable in $\mathbb{R}^3$. Hence $\lim_{t\to\infty}(x(t), y(t), z(t)) = E_x$.

(ii) The assumptions $\alpha < d_1$ and $\gamma > d_2$ imply that E_{xy} does not exist and E_{xz} exists. And E_{xz} is asymptotically stable in $\mathbb{R}^3$ since the inequality

$$-d_1 + \alpha\frac{d_2}{\gamma} - \frac{\beta}{\bar{\gamma}}\left(1 - \frac{d_2}{\gamma}\right) < -d_1 + \alpha < 0$$

holds. Similar to case (i) by taking $\varepsilon = (d_1 - \alpha)/2\alpha > 0$, for large t consider

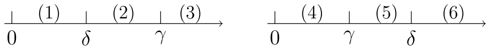
$$\frac{\dot{y}}{y} = -d_1 + \alpha x - \beta z \leq \frac{\alpha - d_1}{2} < 0.$$

So we have the limit $\lim_{t\to\infty} y(t) = 0$. The remaining arguments of the proof of this part are similar to case (i), so we omit it. The proof is complete. □

These results can be easily interpreted in the biological point of view. If the mortality rate d_1 of species y is greater than the conversion rate α, then y will die out eventually and system (2.1) is reduced to the one-dimensional x subsystem (2.3) or two-dimensional x–z subsystem (2.5). Thus classical two-dimensional results, Proposition 2.2, can be applied. Therefore, from now on, we generically make the assumption,

(A1) $\alpha > d_1$,

which will be used in the rest of this article. However, for species z the dynamics are more complicated due to the *omnivorous* effects. We consider this in the next section.



(a) $\gamma > \delta$ (b) $\gamma < \delta$

Fig. 3.1. All generic possibilities of classification of parameters with varied d_2 in regions (1)–(6) with $d_1 < \alpha$.

3. Existence, local stability and global dynamics of the equilibria in $\mathbb{R}^3$

By the results of the last section, we always assume that assumption **(A1)** holds. Logically, we have six generic cases of classification of parameters based on the relation of γ and δ respect to the death rate of species z, d_2. See Fig. 3.1. Biologically, if $\gamma > \delta$, then the top predator's conversion rate γ of x is larger than the conversion rate δ of y. It means that z will prefer to eat x because of the better efficiency. In this section, we will classify the dynamics of (2.1) according to d_2 within regions (1)–(6) by the following four categories,

(I) $d_2 > \max\{\gamma, \delta\}$ (in region (3) and (6) of Fig. 3.1);
(II) $\gamma > \max\{\delta, d_2\}$ (in region (1) and (2) of Fig. 3.1);
(III) $d_2 < \gamma < \delta$ (in region (4) of Fig. 3.1);
(IV) $\gamma < d_2 < \delta$ (in region (5) of Fig. 3.1).

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

3.1. Category (I): $d_2 > \max\{\gamma, \delta\}$

In this category, assumption **(A1)** and $d_2 > \max\{\gamma, \delta\}$ imply that one boundary equilibrium E_{xy} exists and the other boundary equilibrium E_{xz} does not exist. In order to complete the classification, we consider the possible existence of positive equilibria. To find the positive coexistence equilibrium $E_* = (x_*, y_*, z_*)$ is to find positive numbers x_*, y_* and z_* satisfying the following linear equations

$$\begin{aligned} 0 &= 1 - x - y - \bar{\gamma} z, \\ 0 &= -d_1 + \alpha x - \beta z, \\ 0 &= -d_2 + \gamma x + \delta y. \end{aligned} \tag{3.1}$$

With the substitution, $x = 1 - y - \bar{\gamma} z$, we obtain two straight lines, L_1 and L_2,

$$L_1 : \alpha y + (\alpha\bar{\gamma} + \beta)z = \alpha - d_1, \tag{3.2}$$

$$L_2 : (\gamma - \delta)y + \gamma\bar{\gamma} z = \gamma - d_2. \tag{3.3}$$

Hence the coexistence state 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 $\gamma < \delta$ and $\frac{d_2-\gamma}{\delta-\gamma} < \frac{\alpha-d_1}{\alpha}$. But, this is impossible since if $\gamma < \delta$ then $\frac{d_2-\gamma}{\delta-\gamma} > 1 > \frac{\alpha-d_1}{\alpha}$. 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 3.1.

Proposition 3.1. *Let assumption* **(A1)** *and $d_2 > \max\{\gamma, \delta\}$ hold. Then equilibria E_{xz} and E_* do not exist. Moreover, we have the limit $\lim_{t\to\infty} z(t) = 0$ and the equilibrium E_{xy} is globally asymptotically stable.*

Proof. We first claim that the semi-trivial equilibrium E_{xy} is asymptotically stable. Consider two subcases, $\gamma \geq \delta$ or $\gamma < \delta$. If $\gamma \geq \delta$ then

$$-d_2 + \gamma\frac{d_1}{\alpha} + \delta\left(1 - \frac{d_1}{\alpha}\right) \le -d_2 + \gamma\frac{d_1}{\alpha} + \gamma\left(1 - \frac{d_1}{\alpha}\right) = -d_2 + \gamma < 0$$

holds. On the other hand, if $\gamma < \delta$ then

$$-d_2 + \gamma\frac{d_1}{\alpha} + \delta\left(1 - \frac{d_1}{\alpha}\right) = \delta - d_2 + (\gamma - \delta)\frac{d_1}{\alpha} \le (\gamma - \delta)\frac{d_1}{\alpha} < 0$$

holds. Hence E_{xy} is locally asymptotically stable in $\mathbb{R}^3$ by Proposition 2.3.

Without loss of generality, we may assume that $x(t) \le 1$ for t large enough. Define $c = \max\{\gamma, \delta\}$ and consider

$$\begin{aligned}\frac{\dot z}{z} + c\frac{\dot x}{x} &= (-d_2 + \gamma x + \delta y) + c(1 - x - y - \bar\gamma z)\\ &= c - d_2 + (\gamma - c)x + (\delta - c)y - c\bar\gamma z\\ &\le c - d_2 < 0.\end{aligned}$$

Then we have $z(t)(x(t))^c$ approaches 0 as t approaches ∞. There are two possibilities that should be considered. The first one is that we can find a sequence of time $\{t_n\}$ such that t_n approaches ∞ and $x(t_n)$ approaches 0 as n approaches ∞. Another one is that there is a positive number ε such that $x(t) \ge \varepsilon$ for all time t.

Assume that there is a sequence $\{t_n\}$ such that $x(t_n)$ approaches zero as n approaches infinity. Since the solutions of (2.1) are bounded, there is a point $\boldsymbol{q} = (0, \bar y, \bar z) \in H_4 \cap \omega(\boldsymbol{p})$. By Proposition 2.2, the solution of (2.1) with initial condition $\boldsymbol{q} \in H_4$, $\phi(t, \boldsymbol{q})$, will approach E_0 when time goes to infinity. Hence $E_0 \in \omega(\boldsymbol{p})$. It is clear that $\omega(\boldsymbol{p}) \ne \{E_0\}$. Applying Butler–McGehee Lemma [6], there is a point $\boldsymbol{r} = (\bar x, 0, 0) \in H_1 \cap \omega(\boldsymbol{p})$. Clearly, $\boldsymbol{r} \ne E_0$ and $\phi(t; \boldsymbol{r})$ approaches E_x as time goes to infinity. Similarly, $\{E_x\} \subsetneq \omega(\boldsymbol{p})$ and applying Butler–McGehee Lemma again, we can find a point $\boldsymbol{s} \in \omega(\boldsymbol{p}) \cap H_2$ since the unstable manifold of E_x is contained in H_2. Again, $\phi(t; \boldsymbol{s})$ approaches E_{xy}, hence $E_{xy} \in \omega(\boldsymbol{p})$. Since E_{xy} is asymptotically stable in $\mathbb{R}^3$, we have the limit $\lim_{t\to\infty} \phi(t; \boldsymbol{p}) = E_{xy}$.

On the other hand, if $x(t) \ge \varepsilon > 0$ for all t then we have $z(t)$ approaches zero as t approaches infinity. Similar to the previous arguments, we can find a point $\boldsymbol{s}_1 \in H_2 \cap \omega(\boldsymbol{p})$. The remaining arguments of the proof are almost the same as the previous one, so we omit them. We complete the proof. □

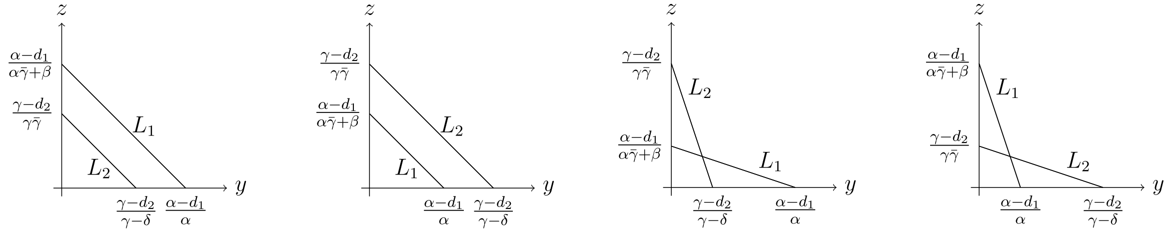
3.2. Category (II): $\gamma > \max\{\delta, d_2\}$

In this category, assumptions **(A1)** and $\gamma > d_2$ imply the existence of boundary equilibria E_{xy} and E_{xz}. Similarly, we solve (3.2) and (3.3) to find the positive equilibrium E_*. Note that all coefficients of these two straight lines, L_1 and L_2, are positive. Hence category (II) has four generic cases as shown in Fig. 3.2.

In Fig. 3.2(a), the two straight lines do not intersect in the first quadrant if $(\alpha - d_1)/\alpha > (\gamma - d_2)/(\gamma - \delta)$ and $(\alpha - d_1)/(\alpha\bar\gamma + \beta) > (\gamma - d_2)/(\gamma\bar\gamma)$. These two inequalities are equivalent to (2.9) and the reversed (2.10). Hence in this case E_{xy} is stable, E_{xz} 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 summarize the results of local stability of the boundary equilibria and existence of positive equilibrium of category (II) in Table 3.1.

From Eq. (2.6), if E_* exists then the Jacobian evaluated at E_* is given by

$$J(E_*) = \begin{bmatrix} -x_* & -x_* & -\bar\gamma x_* \\ \alpha y_* & 0 & -\beta y_* \\ \gamma z_* & \delta z_* & 0 \end{bmatrix}.$$



(a) (b) (c) (d)

Fig. 3.2. The four possible generic cases for the intersection of the two straight lines L_1 and L_2 for category (II).

Let λ be an eigenvalue. Then the characteristic equation is

$$\lambda^3 + x_*\lambda^2 + (\alpha x_* y_* + \gamma\bar{\gamma}x_* z_* + \beta\delta y_* z_*)\lambda + (\alpha\bar{\gamma}\delta + \beta\delta - \gamma\beta)x_* y_* z_* = 0. \tag{3.4}$$

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

$$\alpha\bar{\gamma}\delta + \beta\delta - \gamma\beta > 0 \tag{3.5}$$

and

$$\alpha x_* y_* + \gamma\bar{\gamma}x_* z_* > (\alpha\bar{\gamma}\delta - \gamma\beta)y_* z_*. \tag{3.6}$$

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

Proposition 3.2. *Let assumption* **(A1)** *hold and parameters be of category* (II). *Then the following statements are true.*

(i) *In case* (a) *of category (II), that is* $\frac{\alpha-d_1}{\alpha} > \frac{\gamma-d_2}{\gamma-\delta}$ *and* $\frac{\alpha-d_1}{\alpha\bar{\gamma}+\beta} > \frac{\gamma-d_2}{\gamma\bar{\gamma}}$, *if* (3.5) *holds, then the species* z *dies out eventually and the equilibrium* E_{xy} *is globally asymptotically stable.*

(ii) *In case* (b) *of category (II), that is* $\frac{\alpha-d_1}{\alpha} < \frac{\gamma-d_2}{\gamma-\delta}$ *and* $\frac{\alpha-d_1}{\alpha\bar{\gamma}+\beta} < \frac{\gamma-d_2}{\gamma\bar{\gamma}}$, *if* (3.5) *holds, then the species* y *dies out eventually and the equilibrium* E_{xz} *is globally asymptotically stable.*

(iii) *In case* (c) *of category (II), that is* $\frac{\alpha-d_1}{\alpha} > \frac{\gamma-d_2}{\gamma-\delta}$ *and* $\frac{\alpha-d_1}{\alpha\bar{\gamma}+\beta} < \frac{\gamma-d_2}{\gamma\bar{\gamma}}$, *the equilibrium* E_* *is a saddle point with one positive eigenvalue and two eigenvalues with negative real part, that is, there is a bistability phenomenon.*

Proof. (i) It is easy to see that the inequality of (3.5) is equivalent to the inequality $\frac{\gamma-\delta}{\alpha}\beta - \bar{\gamma}\delta < 0$. Let $\mu \equiv \frac{\gamma-\delta}{\alpha}(\alpha - d_1) - (\gamma - d_2) > 0$. Consider

$$\begin{aligned}\frac{\dot{z}}{z} + \delta\frac{\dot{x}}{x} - \frac{\gamma-\delta}{\alpha}\frac{\dot{y}}{y} &= -d_2 + \gamma x + \delta y + \delta(1 - x - y - \bar{\gamma}z) - \frac{\gamma-\delta}{\alpha}(-d_1 + \alpha x - \beta z)\\ &= (\gamma - d_2) - \gamma(1-x) + \delta(1-x) - \delta\bar{\gamma}z - \frac{\gamma-\delta}{\alpha}\big(\alpha - d_1 - \alpha(1-x) - \beta z\big)\\ &= (\gamma - d_2) - \frac{\gamma-\delta}{\alpha}(\alpha - d_1) + \left(\frac{\gamma-\delta}{\alpha}\beta - \delta\bar{\gamma}\right)z \le -\mu.\end{aligned}$$

Hence we have $z(t)(x(t))^{\delta}$ approaches zero as t approaches infinity. The remaining arguments are similar, so we omit them.

(ii) Similarly, (3.5) is equivalent to the inequality $\beta - \frac{\alpha\bar{\gamma}+\beta}{\gamma}\delta < 0$. Let us define $\mu \equiv (\alpha\bar{\gamma}+\beta)\frac{\gamma-d_2}{\gamma} - \bar{\gamma}(\alpha - d_1) > 0$ and consider

$$\begin{aligned}\bar{\gamma}\frac{\dot{y}}{y} - \beta\frac{\dot{x}}{x} - \frac{\alpha\bar{\gamma}+\beta}{\gamma}\frac{\dot{z}}{z} &= \bar{\gamma}(-d_1+\alpha x-\beta z) - \beta(1-x-y-\bar{\gamma}z) - \frac{\alpha\bar{\gamma}+\beta}{\gamma}(-d_2+\gamma x+\delta y)\\ &= \bar{\gamma}(\alpha-d_1) - \alpha\bar{\gamma}(1-x) - \beta(1-x) + \beta y - \frac{\alpha\bar{\gamma}+\beta}{\gamma}\big(\gamma-d_2-\gamma(1-x)+\delta y\big)\\ &= \bar{\gamma}(\alpha-d_1) - \frac{\alpha\bar{\gamma}+\beta}{\gamma}(\gamma-d_2) + \left(\beta - \frac{\alpha\bar{\gamma}+\beta}{\gamma}\delta\right)y \le -\mu.\end{aligned}$$

Hence $y(t)$ approaches zero as t approaches infinity. The remaining arguments are similar, so we omit them.

(iii) It is easy to see that the assumptions $\frac{\alpha-d_1}{\alpha} > \frac{\gamma-d_2}{\gamma-\delta}$ and $\frac{\alpha\bar{\gamma}+\beta}{\alpha-d_1} > \frac{\gamma\bar{\gamma}}{\gamma-d_2}$ imply the inequality,

$$\frac{\alpha\bar{\gamma}+\beta}{\alpha} > \frac{\gamma\bar{\gamma}}{\gamma-\delta}.$$

This inequality is in turn equivalent to $\alpha\bar{\gamma}\delta+\delta\beta-\gamma\beta < 0$. Hence the coexistence state E_* is unstable. By simple computing, the Routh array for (3.4) is

$$\begin{pmatrix} 1 & \alpha x_*y_* + \gamma\bar{\gamma}x_*z_* + \delta\beta y_*z_* & 0 & 0\\ x_* & (\alpha\bar{\gamma}\delta+\delta\beta-\gamma\beta)x_*y_*z_* & 0 & 0\\ b_1 & 0 & 0 & 0\\ c_1 & 0 & 0 & 0 \end{pmatrix},$$

where $b_1 = \alpha x_*y_* + \gamma\bar{\gamma}x_*z_* + (\gamma\beta-\alpha\bar{\gamma}\delta)y_*z_*$ and $c_1 = (\alpha\bar{\gamma}\delta+\delta\beta-\gamma\beta)x_*y_*z_* < 0$. We claim that (3.4) cannot have a purely imaginary root. If not let $\lambda = i\omega$, then we have

$$i\big(w-w^3\big) = x_*w^2 - (\alpha\bar{\gamma}\delta+\delta\beta-\gamma\beta)x_*y_*z_* < 0.$$

This is impossible for any $\omega \in \mathbb{R}$. So whenever b_1 is positive or negative, the signs of first column always change once. Hence the equilibrium E_* is a saddle point with one positive eigenvalue and two eigenvalues with negative real part. We complete the proof. □

3.3. Category (III): $d_2 < \gamma < \delta$

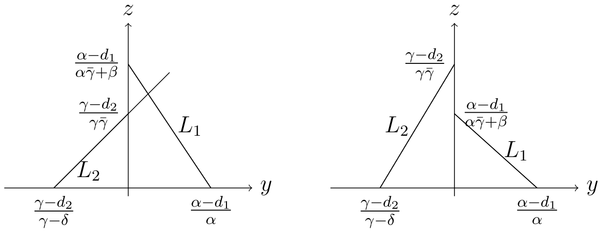
In this category, assumptions **(A1)** and $\gamma > d_2$ imply that the boundary equilibria E_{xy} and E_{xz} exist. Similarly, we solve (3.2) and (3.3) to find the positive equilibrium E_*. Note that all coefficients of these two straight lines, L_1 and L_2, are positive except for $\gamma-\delta$. Hence category (III) has two generic cases as shown in Fig. 3.3.

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

$$-d_2+\gamma\left(\frac{d_1}{\alpha}\right)+\delta\left(1-\frac{d_1}{\alpha}\right) = (\delta-\gamma)\left(1-\frac{d_1}{\alpha}\right)+\gamma-d_2 > 0.$$

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 a positive equilibrium of category (III) in Table 3.1. We obtain the following global extinction result.

Proposition 3.3. *Let assumption* **(A1)** *hold and parameters be of category* (III). *In case* (b) *of category* (III), *that is* $\frac{\alpha-d_1}{\alpha} > \frac{\gamma-d_2}{\gamma-\delta}$ *and* $\frac{\alpha-d_1}{\alpha\bar{\gamma}+\beta} < \frac{\gamma-d_2}{\gamma\bar{\gamma}}$, *the species y dies out eventually and the equilibrium* E_{xz} *is globally asymptotically stable.*



(a) (b)

Fig. 3.3. The two possible generic cases for the intersection of the two straight lines L_1 and L_2 for category (III).

Proof. We first show that inequality (3.5) holds in this case. Note that $d_2 < \gamma < \delta$ in the category. Hence inequalities

$$\frac{\alpha - d_1}{\alpha} > \frac{\gamma - d_2}{\gamma - \delta} \quad \text{and} \quad \frac{\alpha - d_1}{\alpha\bar{\gamma} + \beta} < \frac{\gamma - d_2}{\gamma\bar{\gamma}}$$

directly imply that

$$\frac{\alpha\bar{\gamma} + \beta}{\alpha} > \frac{\gamma\bar{\gamma}}{\gamma - \delta}$$

which is equivalent to (3.5). Moreover, it is also equivalent to $\beta < \frac{\alpha\bar{\gamma}+\beta}{\gamma}$. Moreover, the condition $\frac{\alpha-d_1}{\alpha\bar{\gamma}+\beta} < \frac{\gamma-d_2}{\gamma\bar{\gamma}}$ holds if and only if the inequality (2.10) holds, hence the equilibrium E_{xz} is asymptotically stable.

Take a positive number $\mu \equiv \frac{\alpha\bar{\gamma}+\beta}{\gamma}(\gamma - d_2) - \bar{\gamma}(\alpha - d_1)$. Consider

$$\begin{aligned}
\bar{\gamma}\frac{\dot{y}}{y} - \beta\frac{\dot{x}}{x} - \frac{\alpha\bar{\gamma}+\beta}{\gamma}\frac{\dot{z}}{z} &= \bar{\gamma}(-d_1 + \alpha x - \beta z) - \beta(1 - x - y - \bar{\gamma}z) - \frac{\alpha\bar{\gamma}+\beta}{\gamma}(-d_2 + \gamma x + \delta y) \\
&= \bar{\gamma}(\alpha - d_1) - \alpha\bar{\gamma}(1 - x) - \beta(1 - x) + \beta y - \frac{\alpha\bar{\gamma}+\beta}{\gamma}\big(\gamma - d_2 - \gamma(1 - x) + \delta y\big) \\
&= \bar{\gamma}(\alpha - d_1) - \frac{\alpha\bar{\gamma}+\beta}{\gamma}(\gamma - d_2) + \left(\beta - \frac{\alpha\bar{\gamma}+\beta}{\gamma}\delta\right)y \le -\mu.
\end{aligned}$$

Hence $y(t) \to 0$ as $t \to \infty$. The remaining arguments are similar, so we omit them. □

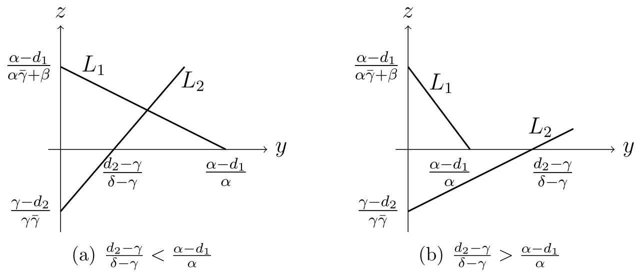
3.4. *Category (IV): $\gamma < d_2 < \delta$*

In this category, assumption **(A1)** and $\gamma < d_2 < \delta$ imply that one boundary equilibrium E_{xy} exists and the other boundary equilibrium E_{xz} does not exist. Similarly, we solve (3.2) and (3.3) to find the positive equilibrium E_* and there are two generic cases as shown in Fig. 3.4. In Fig. 3.4(b), the inequality $(\alpha - d_1)/\alpha < (d_2 - \gamma)/(\delta - \gamma)$ is equivalent to (2.9) hence E_{xy} is asymptotically stable. The other case of category (IV) is similar, so we summarize the results in Table 3.1. In this category, we show the extinction result in case (b) and the globally stability of the positive equilibrium in case (a) in the following.

Proposition 3.4. *Let assumption* **(A1)** *hold and parameters be in the case* (b) *of category* (IV). *Then we have the limit* $\lim_{t\to\infty} z(t) = 0$ *and the equilibrium* E_{xy} *is globally asymptotically stable.*

Proof. Inequality $\frac{\alpha-d_1}{\alpha} < \frac{d_2-\gamma}{\delta-\gamma}$ implies that E_{xy} is asymptotically stable and is equivalent to the following inequality,

$$d_2 - \gamma > \frac{\delta - \gamma}{\alpha}(\alpha - d_1).$$



(a) $\frac{d_2-\gamma}{\delta-\gamma} < \frac{\alpha-d_1}{\alpha}$ (b) $\frac{d_2-\gamma}{\delta-\gamma} > \frac{\alpha-d_1}{\alpha}$

Fig. 3.4. The two possible generic cases for the intersection of the two straight lines L_1 and L_2 for category (IV).

Let $\mu = d_2 - \gamma - \frac{\delta-\gamma}{\alpha}(\alpha - d_1) > 0$ and consider

$$\begin{aligned}\frac{\dot{z}}{z} + \delta\frac{\dot{x}}{x} + \frac{\delta-\gamma}{\alpha}\frac{\dot{y}}{y} &= (-d_2 + \gamma x + \delta y) + \delta(1 - x - y - z) + \frac{\delta-\gamma}{\alpha}(-d_1 + \alpha x - \beta z)\\ &= \gamma - d_2 - \gamma(1-x) + \delta(1-x) - \delta z + \frac{\delta-\gamma}{\alpha}\big(\alpha - d_1 - \alpha(1-x) - \beta z\big)\\ &\le \gamma - d_2 + \frac{\delta-\gamma}{\alpha}(\alpha - d_1) = -\mu.\end{aligned}$$

Hence we have $(x(t))^{\delta}(y(t))^{(\delta-\gamma)/\alpha}z(t)$ approaches zero as t approaches infinity. Similarly, we consider two possibilities. One is that we can find a sequence of time $\{t_n\}$ such that $x(t_n)$ approaches zero as n approaches infinity. The proof of this case is similar to previous one, we can obtain that E_{xy} is globally asymptotically stable. So we omit the details.

Another one is that $x(t) \ge \varepsilon$ for all time t. This implies that $(y(t))^{(\delta-\gamma)/\alpha}z(t)$ approaches zero as t approaches infinity. We still have two-subcases, that is, we can find a sequence of time $\{t_n\}$ such that $y(t_n)$ approaches zero as n approaches infinity or $y(t) \ge \varepsilon$ for all time t. If $y(t_n)$ approaches zero as n approaches infinity then by Butler–McGehee lemma again we can find a point $\boldsymbol{q} \in H_3 \cap \omega(\boldsymbol{p})$. By Proposition 2.2(iii), the solution $\phi(t; \boldsymbol{q})$ approaches E_x as t approaches infinity. Hence $E_x \in \omega(\boldsymbol{p})$. The remaining arguments are similar, so we omit them. However, if $y(t) \ge \varepsilon$ for all t then $z(t)$ approaches zero as t approaches ∞. Similar arguments are omitted. We complete the proof. □

Proposition 3.5. *Let assumption* **(A1)** *hold and parameters be in the case (a) of category* (IV)*, that is,* $\frac{\alpha-d_1}{\alpha} > \frac{\gamma-d_2}{\gamma-\delta}$ *and* $\frac{\alpha-d_1}{\alpha\bar{\gamma}+\beta} > \frac{\gamma-d_2}{\gamma\bar{\gamma}}$*. If* β *and* $\bar{\gamma}$ *are small enough, then the equilibrium* E_* *is globally asymptotically stable.*

Proof. First note that the condition $\frac{\alpha-d_1}{\alpha} > \frac{\gamma-d_2}{\gamma-\delta}$ implies that the reversed (2.9) holds, hence equilibrium E_{xy} is unstable. Moreover, it can be showed that E_* is asymptotically stable by checking the Routh–Hurwitz criteria (3.5) and (3.6) since $\delta > \gamma$ and $0 < \bar{\gamma}$, $\beta \ll 1$.

Consider a Lyapunov function

$$V(x, y, z) = -\ln\frac{x}{x_*} - \frac{1}{\alpha}\ln\frac{y}{y_*} - \frac{1}{\delta}\ln\frac{z}{z_*},$$

then

$$\begin{aligned}\frac{d}{dt}V &= -\frac{\dot{x}}{x} - \frac{1}{\alpha}\frac{\dot{y}}{y} - \frac{1}{\delta}\frac{\dot{z}}{z}\\ &= -(1 - x - y - \bar{\gamma}z) - \frac{1}{\alpha}(-d_1 + \alpha x - \beta z) - \frac{1}{\delta}(-d_2 + \gamma x + \delta y)\\ &= \left(-1 + \frac{d_1}{\alpha} + \frac{d_2}{\delta}\right) - \frac{\gamma}{\delta}x + \left(\bar{\gamma} + \frac{\beta}{\alpha}\right)z \le 0,\end{aligned}$$

if $\bar{\gamma}$ and β/α are small enough. Let

$$M = \left\{(x,y,z) : \left(-1+\frac{d_1}{\alpha}+\frac{d_2}{\delta}\right) - \frac{\gamma}{\delta}x + \left(\bar{\gamma}+\frac{\beta}{\alpha}\right)z = 0\right\}.$$

By tedious computations, we obtain

$$E_* = (x_*, y_*, z_*) = \left(\frac{\beta(\delta-d_2)+\bar{\gamma}\delta d_1}{\alpha\bar{\gamma}\delta+\beta\delta-\gamma\beta}, y_*, \frac{\alpha(\delta-d_2)-d_1(\delta-\gamma)}{\alpha\bar{\gamma}\delta+\beta\delta-\gamma\beta}\right) \in M.$$

We would like to clarify the maximal invariant set of M.

The set M is a two-dimensional plane whose projection on the x–z plane is the straight line

$$\left(\bar{\gamma}+\frac{\beta}{\alpha}\right)z = \frac{\gamma}{\delta}x + \left(1-\frac{d_1}{\alpha}-\frac{d_2}{\delta}\right)$$

or in this form

$$\left(\bar{\gamma}+\frac{\beta}{\alpha}\right)(z-z_*) = \frac{\gamma}{\delta}(x-x_*).$$

Hence the values $x - x_*$ and $z - z_*$ of orbits of (2.1) which are invariant in M must have the same sign or be zero simultaneously. M can be separated into nine disjoint parts as the forms,

$$M = M_1 \cup M_2 \cup M_3 \cup M_4 \cup N_1 \cup N_2 \cup N_3 \cup N_4 \cup \{E_*\},$$

where

$$\begin{aligned}
M_1 &= M \cap \{x > x_*, z > z_*, y > y_*\}, & M_2 &= M \cap \{x > x_*, z > z_*, y < y_*\},\\
M_3 &= M \cap \{x < x_*, z < z_*, y > y_*\}, & M_4 &= M \cap \{x < x_*, z < z_*, y < y_*\},\\
N_1 &= M \cap \{x = x_*, z = z_*, y > y_*\}, & N_2 &= M \cap \{x = x_*, z = z_*, y < y_*\},\\
N_3 &= M \cap \{x > x_*, z > z_*, y = y_*\}, & N_4 &= M \cap \{x < x_*, z < z_*, y = y_*\}.
\end{aligned}$$

Solutions which are invariant in M should have tangent vectors

$$\frac{dz}{dx} = \frac{z(-d_2+\gamma x+\delta y)}{x(1-x-y-\bar{\gamma}z)} = \frac{z(\gamma(x-x_*)+\delta(y-y_*))}{x((x_*-x)+(y_*-y)+\bar{\gamma}(z_*-z))} \geq 0 \tag{3.7}$$

if $(x_*-x)+(y_*-y)+\bar{\gamma}(z_*-z) \neq 0$, or

$$\frac{dx}{dz} = \frac{x(1-x-y-\bar{\gamma}z)}{z(-d_2+\gamma x+\delta y)} = \frac{x((x_*-x)+(y_*-y)+\bar{\gamma}(z_*-z))}{z(\gamma(x-x_*)+\delta(y-y_*))} \geq 0 \tag{3.8}$$

if $\gamma(x-x_*)+\delta(y-y_*) \neq 0$. It is clear that solutions of (2.1) cannot go into regions N_1–N_4, M_1 and M_4, since $\frac{dz}{dx} < 0$ if orbits are on these six regions.

Let solutions of (2.1) with initial conditions on M_2 be invariant in M_2. We consider two cases, $(x_* - x) + (y_* - y) + \bar{\gamma}(z_* - z) > 0$ or $(x_* - x) + (y_* - y) + \bar{\gamma}(z_* - z) \leq 0$. Let the first case hold, that is, $(x_* - x) + (y_* - y) + \bar{\gamma}(z_* - z) > 0$, then $\gamma(x - x_*) + \delta(y - y_*) < 0$. This contradicts to $\frac{dz}{dx} \geq 0$. Hence, we always have $(x_* - x) + (y_* - y) + \bar{\gamma}(z_* - z) \leq 0$ and $\gamma(x - x_*) + \delta(y - y_*) \leq 0$ on M_2. These two inequalities imply that the $x(t)$- and $z(t)$-coordinates of solution of (2.1) are decreasing for all time. But there is only

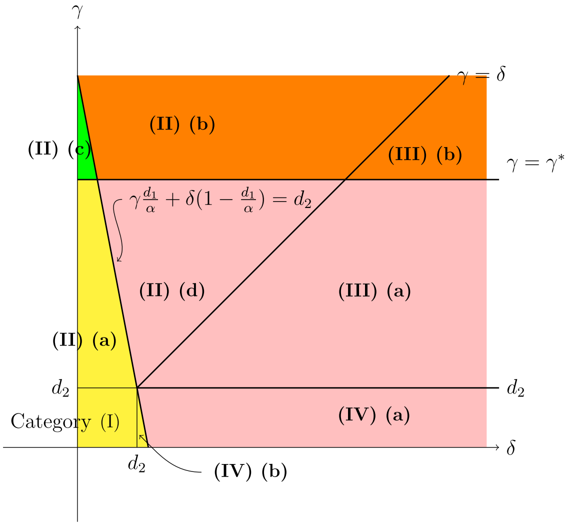


Fig. 3.5. A typical picture of the parameter space with varied γ, δ, and fixed d_1, d_2, m_1, m_2, α, β with $\alpha > d_1$. The dynamics in each region of the parameter space are indicated with different color. First, in the yellow regions species z dies out eventually because of results in Propositions 3.1, 3.2(i) and 3.4. In the orange region, species y dies out eventually (Propositions 3.2(ii) and 3.3). Moreover, in the green region, the bistability phenomenon occurs (Proposition 3.2(iii)). Finally, the coexistence state appears in the pink region and the model (2.1) is uniformly persistent (Proposition 3.6). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

one equilibrium E_* on M, solutions of (2.1) on M_2 approaches to E_* as time goes to infinity. It is similar to handle solutions with initial conditions on M_3, so we omit it.

Finally, by LaSalle's invariant principle, solutions with positive initial conditions will approach E_*. This completes the proof. □

3.5. Dynamics of the positive equilibrium

Note that all global dynamics of (2.1) 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 (2.1) with parameters in these three regions. We show an analytical result in which system (2.1) is uniformly persistent and present some numerical simulations.

3.5.1. Uniform persistence

First, we present a typical picture, Fig. 3.5, of the γ–δ parameter space with fixed α, β, d_1, d_2 and $\bar{\gamma}$ and the restriction $\alpha > d_1$ (see Proposition 2.4 and assumption **(A1)**). We use different colors to clarify the dynamics of solutions of (2.1) by the two inequalities of Table 3.1. One straight line, $\gamma \frac{d_1}{\alpha} + \delta(1 - \frac{d_1}{\alpha}) = d_2$, and one horizontal line,

$$\gamma = \gamma^* = \frac{(\alpha\bar{\gamma} + \beta)d_2}{\bar{\gamma}d_1 + \beta}, \tag{3.9}$$

are obtained to separate regions (II)–(IV) into two or four subregions by the inequalities of Table 3.1.

We indicate the dynamics in each region of the parameter space with different colors. First, in the yellow regions species z dies out eventually because of results in Propositions 3.1, 3.2(i) and 3.4. In the orange region, species y dies out eventually (Propositions 3.2(ii) and 3.3). Moreover, in the green region, the bistability phenomenon occurs (Proposition 3.2(iii)). Finally, the coexistence state appears in the pink region. The detailed biological interpretations will be discussed in the last section.

Table 3.1
Dynamics of equilibria of classifications categories (I)–(IV) (GAS means globally asymptotically stable).

	E_{xy}	E_{xz}	E_*
Category (I): $d_2 > \max\{\gamma, \delta\}$	GAS	does not exist	does not exist
Category (II): $\gamma > \max\{\delta, d_2\}$			
(a) $\frac{\alpha-d_1}{\alpha} > \frac{\gamma-d_2}{\gamma-\delta}$, $\frac{\alpha-d_1}{\alpha\bar{\gamma}+\beta} > \frac{\gamma-d_2}{\gamma\bar{\gamma}}$	GAS*	unstable	does not exist
(b) $\frac{\alpha-d_1}{\alpha} < \frac{\gamma-d_2}{\gamma-\delta}$, $\frac{\alpha-d_1}{\alpha\bar{\gamma}+\beta} < \frac{\gamma-d_2}{\gamma\bar{\gamma}}$	unstable	GAS*	does not exist
(c) $\frac{\alpha-d_1}{\alpha} > \frac{\gamma-d_2}{\gamma-\delta}$, $\frac{\alpha-d_1}{\alpha\bar{\gamma}+\beta} < \frac{\gamma-d_2}{\gamma\bar{\gamma}}$	stable	stable	exists (saddle)
(d) $\frac{\alpha-d_1}{\alpha} < \frac{\gamma-d_2}{\gamma-\delta}$, $\frac{\alpha-d_1}{\alpha\bar{\gamma}+\beta} > \frac{\gamma-d_2}{\gamma\bar{\gamma}}$	unstable	unstable	exists
Category (III): $d_2 < \gamma < \delta$			
(a) $\frac{\alpha-d_1}{\alpha} > \frac{\gamma-d_2}{\gamma-\delta}$, $\frac{\alpha-d_1}{\alpha\bar{\gamma}+\beta} > \frac{\gamma-d_2}{\gamma\bar{\gamma}}$	unstable	unstable	exists
(b) $\frac{\alpha-d_1}{\alpha} > \frac{\gamma-d_2}{\gamma-\delta}$, $\frac{\alpha-d_1}{\alpha\bar{\gamma}+\beta} < \frac{\gamma-d_2}{\gamma\bar{\gamma}}$	unstable	GAS	does not exist
Category (IV): $\gamma < d_2 < \delta$			
(a) $\frac{\alpha-d_1}{\alpha} > \frac{d_2-\gamma}{\delta-\gamma}$, $\frac{\alpha-d_1}{\alpha\bar{\gamma}+\beta} > \frac{\gamma-d_2}{\gamma\bar{\gamma}}$	unstable	does not exist	exists
(b) $\frac{\alpha-d_1}{\alpha} < \frac{d_2-\gamma}{\delta-\gamma}$, $\frac{\alpha-d_1}{\alpha\bar{\gamma}+\beta} > \frac{\gamma-d_2}{\gamma\bar{\gamma}}$	GAS	does not exist	does not exist

* With an extra inequality (3.5).

Now we are in the position to show that system (2.1) with parameters in the pink region is uniformly persistent. It is easy to check that system (2.1) is persistent by the results of [6]. Moreover, we now have the following results on the uniform persistence of system (2.1) (Bulter et al. [2], Freedman et al. [5]).

Proposition 3.6. *Let assumption* **(A1)** *hold and* $0 < \gamma < \gamma^*$ *defined in* (3.9)*. If* $\delta > \frac{\alpha d_2 - \gamma d_1}{\alpha - d_1}$ *then* (2.1) *is uniformly persistent.*

To show this proposition, we need the following results.

Lemma 3.7. *If assumption* **(A1)** *and* $\delta > \frac{\alpha d_2 - \gamma d_1}{\alpha - d_1}$ *hold, then the semi-trivial equilibrium* E_{xy} *exists and is a saddle with a two-dimensional stable manifold, the interior of the* x*–*y *plane, and a one-dimensional unstable manifold with tangent vectors which are non-zero in the* z *coordinate.*

Proof. It is easy to see that the inequality $\delta > \frac{\alpha d_2 - \gamma d_1}{\alpha - d_1}$ is equivalent to

$$-d_2 + \gamma \frac{d_1}{\alpha} + \delta\left(1 - \frac{d_1}{\alpha}\right) > 0.$$

By Proposition 2.3(iii), we only need to check that the z coordinate of a tangent vector of its unstable manifold is non-zero. To simplify the notation, let $E_{xy} = (d_1/\alpha, 1 - d_1/\alpha, 0) = (x_1, y_1, 0)$ and $p = -d_2 + \gamma \frac{d_1}{\alpha} + \delta(1 - \frac{d_1}{\alpha}) > 0$. Then the Jacobian of E_{xy} (2.8) can be simplified as

$$\begin{bmatrix} -x_1 & -x_1 & -\bar{\gamma} x_1 \\ \alpha y_1 & 0 & -\beta y_1 \\ 0 & 0 & p \end{bmatrix}.$$

To find a tangent vector (u, v, w) of the one-dimensional unstable manifold with respect to the positive eigenvalue p, we solve the linear equations

$$-x_1 u - x_1 v - \bar{\gamma} x_1 w = pu$$

$$\alpha y_1 u - \beta y_1 w = pv.$$

Rearrange the above equations, we have

$$\begin{bmatrix} -x_1 - p & -x_1 \\ \alpha y_1 & -p \end{bmatrix} \begin{bmatrix} u \\ v \end{bmatrix} = \begin{bmatrix} \bar{\gamma} x_1 w \\ \beta y_1 w \end{bmatrix}.$$

Since the determinant of the previous 2×2 matrix is positive, the existence of a non-zero eigenvector implies that the z coordinate of the eigenvector is non-zero. We complete the proof. □

Lemma 3.8. *If assumption* **(A1)** *and* $d_2 < \gamma < \gamma^*$ *hold, then the semi-trivial equilibrium* E_{xz} *exists and is a saddle with a two-dimensional stable manifold, the interior of the* x*–*z *plane, and a one-dimensional unstable manifold with tangent vectors which are non-zero in the* y *coordinate.*

Proof. We only would like to point out that the inequality $\gamma < \gamma^*$ is equivalent to

$$-d_1 + \alpha \frac{d_2}{\gamma} - \frac{\beta}{\bar{\gamma}} \left(1 - \frac{d_2}{\gamma} \right) > 0$$

which implies that equilibrium E_{xz} is a saddle by Proposition 2.3(iv). The rest of the proof is similar to the previous lemma, so we omit it. □

Lemma 3.9. *If assumption* **(A1)** *and* $0 < \gamma \leq d_2$ *hold, then the semi-trivial equilibrium* E_x *is a saddle with a two-dimensional stable manifold, the interior of the* x*–*z *plane, and a one-dimensional unstable manifold with tangent vectors on the* x*–*y *plane.*

Proof. In the case of $0 < \gamma \leq d_2$, the equilibrium E_{xz} does not exist. Assumption **(A1)** implies that E_{xy} exists and is globally asymptotical stable on the x–y plane. The Jacobian matrix evaluated at E_x is

$$\begin{bmatrix} -1 & -1 & -\bar{\gamma} \\ 0 & \alpha - d_1 & 0 \\ 0 & 0 & \gamma - d_2 \end{bmatrix}.$$

Whatever $\gamma < d_1$ or $\gamma = d_2$, it is easy to verify that the equilibrium E_x is a saddle with a two-dimensional stable manifold, the x–z plane, and a one-dimensional unstable manifold with tangent vectors on the x–y plane. □

Proof of Proposition 3.6. Our strategy is to use the main result in [5] to verify the uniform persistence of (2.1). It is sufficient to show that the boundary of the first octant for the solution of (2.1) is isolated and acyclic.

The parameters which satisfy the assumptions are exactly in the interior of the pink region of Fig. 3.5. We separate the pink region of the parameter space into two cases, $0 < \gamma \leq d_2$ or $\gamma > d_2$. It is clear that the isolated invariant sets of solutions on the boundary are $\{E_0, E_x, E_{xy}\}$ if $0 < \gamma \leq d_2$ or $\{E_0, E_x, E_{xy}, E_{xz}\}$ if $d_2 < \gamma < \gamma^*$. Showing that the set of equilibria on the boundary is acyclic is sufficient to complete the proof. This can be done by identifying the invariant manifolds of equilibria in each case. So we recall results of Proposition 2.2 and Proposition 2.3 on the dynamics of solutions on the boundary of the first octant.

1. The trivial equilibrium E_0 is always a saddle with a two-dimensional stable manifold, the y–z plane with boundaries, the y-axis and z-axis, and a one-dimensional unstable manifold, the x-axis.
2. By Proposition 2.3(iii), the semi-trivial equilibrium E_{xy} exists because of assumption **(A1)**. By Lemma 3.7, assumption $\delta > \frac{\alpha d_2 - \gamma d_1}{\alpha - d_1}$ implies that it is a saddle with a two-dimensional stable manifold, the interior of the x–y plane, and a one-dimensional unstable manifold with non-vanish z-coordinate tangent vectors.

3. Similarly, the interior of the x–z plane is the stable manifold of the semi-trivial equilibrium E_{xz}.
4. The whole x-axis is the stable manifold of the equilibrium E_x and the unstable manifold of E_0.

Summarize the above results, we can find a chain from E_0 to E_{xy},

$$E_0 \to E_x \to E_{xy},$$

if $0 < \gamma \leq d_2$, but E_{xy} cannot be chained to E_0 or E_x. Similarly, if $\gamma > d_2$ then there is either a chain from E_0 to E_{xy},

$$E_0 \to E_x \to E_{xy},$$

or a chain from E_0 to E_{xz},

$$E_0 \to E_x \to E_{xz}.$$

And neither E_{xy} nor E_{xz} can be chained to E_0 or E_x. Thus, the set of equilibria $\{E_0, E_x, E_{xy}, E_{xz}\}$ on the boundary is acyclic and the system is uniformly persistent. This completes the proof. □

3.5.2. Hopf bifurcation

In this part, we investigate the existence of periodic solutions via the Hopf bifurcation in the pink region of the parameter space. By the previous arguments, the coexistence state E_* is stable if and only if the inequalities (3.5) and (3.6) hold. Since condition (3.5) is always true in this region, we manipulate the inequality (3.6) and use similar arguments in Ruan [25] to establish the existence of periodic solutions bifurcated from the equilibrium E_*. Moreover, in this part we assume that the inequality

$$\alpha\bar{\gamma}\delta > \gamma\beta \tag{3.10}$$

holds. Otherwise, if $\alpha\bar{\gamma}\delta < \gamma\beta$ then the positive equilibrium E_* is always asymptotically stable.

Let us reconsider the characteristic function (3.4) at E_* with a complex eigenvalue $\lambda = a + bi$,

$$(a+bi)^3 + x_*(a+bi)^2 + F(x_*, y_*, z_*)(a+bi) + Ax_*y_*z_* = 0, \tag{3.11}$$

where $A = \alpha\bar{\gamma}\delta + \beta\delta - \gamma\beta$ and

$$F(x, y, z) = \alpha xy + \gamma\bar{\gamma}xz + \beta\delta yz.$$

Solving (3.11), we have

$$\begin{aligned} &a^3 - 3ab^2 + x_*\left(a^2 - b^2\right) + F(x_*, y_*, z_*)a + Ax_*y_*z_* = 0, \\ &3a^2b - b^3 + 2abx_* + F(x_*, y_*, z_*)b = 0. \end{aligned} \tag{3.12}$$

If $a = 0$, then we obtain

$$F(x_*, y_*, z_*) = Ay_*z_*$$

and the coexistence state E_* loses its stability. Moreover, this is equivalent to failure of the inequality (3.6). Simultaneously, the characteristic equation (3.4) can be factored as the form

$$(\lambda + x_*)\left(\lambda^2 + (\alpha x_*y_* + \gamma\bar{\gamma}x_*z_* + \beta\delta y_*z_*)\right) = 0.$$

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 $\bar{\mu}$ be the value such that $a(\bar{\mu}) = 0$. Hence to verify the existence of periodic solutions bifurcated from E_*, we only need to establish the transversality condition $\frac{da}{d\mu}|_{\mu=\bar{\mu}} \neq 0$. Differentiating (3.12) with respect to μ and solving linear system of $\frac{da}{d\mu}|_{\mu=\bar{\mu}}$ and $\frac{db}{d\mu}|_{\mu=\bar{\mu}}$, we obtain

$$\begin{aligned}\left.\frac{da}{d\mu}\right|_{\mu=\bar{\mu}} &= \left(\frac{x_*}{2b^2+2x_*^2}\right)\frac{d}{d\mu}\left(Ay_*z_* - F(x_*,y_*,z_*)\right)\Big|_{\mu=\bar{\mu}} \\ &= \left(\frac{x_*}{2b^2+2x_*^2}\right)\frac{d}{d\mu}\left(y_*z_*\left(A - \frac{F(x_*,y_*,z_*)}{y_*z_*}\right)\right)\Big|_{\mu=\bar{\mu}} \\ &= \left(\frac{x_*y_*z_*}{2b^2+2x_*^2}\right)\frac{d\bar{F}}{d\mu}(\bar{\mu}),\end{aligned} \tag{3.13}$$

where the function

$$\bar{F}(\mu) \equiv A - \frac{F(x_*,y_*,z_*)}{y_*z_*} = (\alpha\bar{\gamma}\delta - \gamma\beta)y_*z_* - \alpha x_*y_* - \gamma\bar{\gamma}x_*z_*. \tag{3.14}$$

Note that the inequality (3.6) holds if and only if $\bar{F} < 0$. Therefore we have the following conclusion on the Hopf bifurcation at the coexistence state E_*.

Proposition 3.10. *Assume that (3.10), $\bar{F}(\bar{\mu}) = 0$ and $d\bar{F}/d\mu(\bar{\mu}) > 0$ hold. Then the positive equilibrium E_* is locally 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_*.*

Straight forward to solve Eqs. (3.2) and (3.3), we can find the positive equilibrium explicitly,

$$\begin{aligned}E_* &= (x_*, y_*, z_*) \\ &= \left(1 - y_* - \bar{\gamma}z_*, \frac{((\alpha - d_1)\bar{\gamma}\gamma - (\gamma - d_2)(\alpha\bar{\gamma} + \beta))}{\alpha\bar{\gamma}\delta + \beta\delta - \gamma\beta}, \frac{(\alpha(\gamma - d_2) - (\alpha - d_1)(\gamma - \delta))}{\alpha\bar{\gamma}\delta + \beta\delta - \gamma\beta}\right).\end{aligned} \tag{3.15}$$

It is possible to set μ in any one of the seven parameters, $\{\alpha, \beta, \gamma, \bar{\gamma}, \delta, d_1, d_2\}$ to cause the existence of periodic solutions bifurcated from the instability of coexistence E_*. For example, if we take $\mu = \delta$ and $\bar{\delta}$ is the value such that $Ay_*z_* - F(x_*(\bar{\delta}), y_*(\bar{\delta}), z_*(\bar{\delta})) = 0$ then the transversality condition is

$$\frac{\partial}{\partial\delta}\left(A - \frac{F(x_*,y_*,z_*)}{y_*z_*}\right)\Big|_{\delta=\bar{\delta}} > 0.$$

We present some numerical simulations of the function $A - F(x_*,y_*,z_*)/(y_*z_*)$ and Hopf bifurcation with respective to parameter δ. Choose parameter values as follows:

α	β	γ	$\bar{\gamma}$	d_1	d_2
2.5	0.2	0.25	1.0	0.4	0.24

. (3.16)

The graph of $\bar{F}$, Fig. 3.6, can be obtained by varying δ from 1.5 to 3.5 and calculating the value of the function $\bar{F}$ in (3.14) with respective to δ. Since the function $\bar{F}$ is negative if and only if the inequality (3.6) holds, the positive equilibrium E_* is unstable if $\bar{F}(\delta) > 0$. Hence there is a periodic solution bifurcated from the positive equilibrium E_*. Furthermore, numerical simulations of (2.1) at $\delta = 0.25, 1.0$ are performed and presented in Fig. 3.7(a) and (b), respectively. We can see that the positive equilibrium is asymptotically stable (see Fig. 3.7(a)) if $\delta = 0.25$. Now, using δ as a bifurcation parameter, increase δ will destabilize the positive equilibrium and Hopf bifurcation will occur. When $\delta = 1.0$, the positive equilibrium loses its stability and a periodic solution bifurcates from it (see Fig. 3.7(b)).

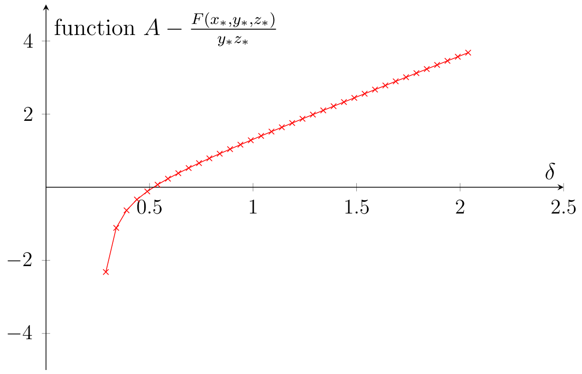
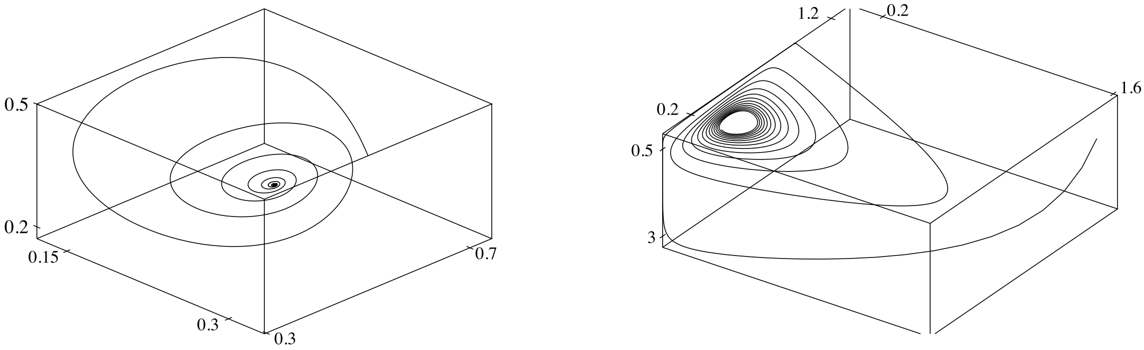


Fig. 3.6. The graph of the function $\bar{F}$ in terms of δ.



(a) $\delta = 0.25$

(b) $\delta = 1.0$

Fig. 3.7. (a) The coexistence state is asymptotically stable when $\delta = 0.25$. (b) A periodic solution bifurcates from the coexistence state via Hopf bifurcation when $\delta = 1.0$.

3.5.3. Chaos

In this section, some numerical simulations are presented to show the chaotic phenomenon. Tanabe and Namba [27] have numerically presented a bifurcation diagram of system (1.1) with parameters $B = 5$, $D_1 = 1$, $D_2 = 1.2$, $a_{11} = 0.4$, $a_{12} = 1$, $a_{21} = 1$, $a_{23} = 1$, $a_{32} = 1$, and $a_{31} = 0.1$. And the parameter a_{13} varies from 0 to 20. They found that chaotic dynamics appear via a period-doubling cascade. We take the same parameter values as in [27] after the nondimensional scaling, $d_1 = D_1/B = 0.2$, $d_2 = D_2/B = 0.24$, $\alpha = a_{21}/a_{11} = 2.5$, $\gamma = a_{31}/a_{11} = 0.25$, and $\delta = a_{32}/a_{12} = 1$. The parameter β varies from 0.2 to 0.06 with stepsize -0.0001. We fix all parameters mentioned above and use β as the bifurcation parameter. A bifurcation diagram is drawn in Fig. 3.8. The vertical axis is the population density of the top predator z on the section of which y is fixed at the equilibrium value. It is easy to see that the period-doubling cascade occurs numerically.

4. Comparison of omnivory models to food chain and two predators–one prey models

In this section, we rewrite system (2.1) in the following form

$$\begin{aligned}\frac{dx}{dt} &= x\big(1 - x - y - (s\gamma)z\big),\\ \frac{dy}{dt} &= y\big(-d_1 + \alpha x - (\mu\delta)z\big),\\ \frac{dz}{dt} &= z(-d_2 + \gamma x + \delta y),\end{aligned} \tag{4.1}$$

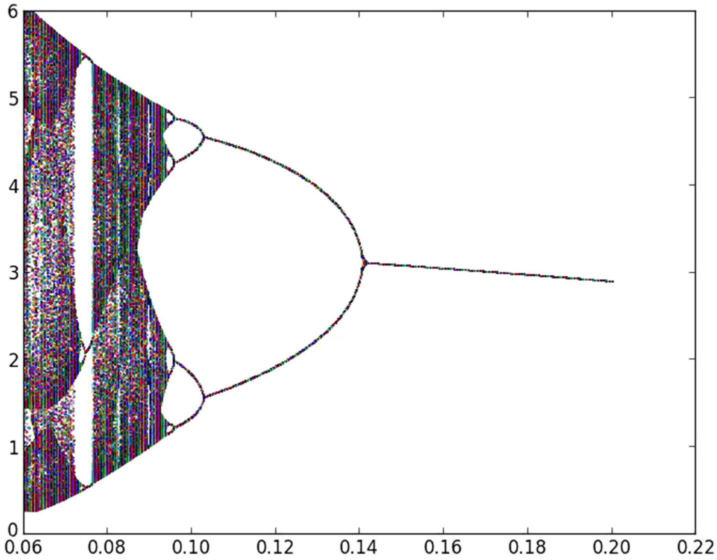


Fig. 3.8. The numerical simulation of a period-doubling cascade when the bifurcation parameter β varies from 0.2 to 0.06.

where s and μ are scaling parameters of $\bar{\gamma}$, γ and β, δ, respectively. It is clear that if $\gamma = 0$ then system (4.1) takes the following form,

$$\begin{aligned}\frac{dx}{dt} &= x(1 - x - y),\\ \frac{dy}{dt} &= y(-d_1 + \alpha x - \mu\delta z),\\ \frac{dz}{dt} &= z(-d_2 + \delta y).\end{aligned} \tag{4.2}$$

It is actually a *Lotka–Volterra food chain model*. Similarly, if $\delta = 0$ then system (4.1) becomes the following form,

$$\begin{aligned}\frac{dx}{dt} &= x(1 - x - y - s\gamma z),\\ \frac{dy}{dt} &= y(-d_1 + \alpha x),\\ \frac{dz}{dt} &= z(-d_2 + \gamma x).\end{aligned} \tag{4.3}$$

It is actually a *Lotka–Volterra two predators–one prey model*. If we take system (4.1) as a general three species food web model with the "specialist predator" y and the "generalist predator" z, then the parameters γ and δ are taken as the factors of the species z how general it is. Since the species z is actually a specialist predator when either γ or δ is equal to zero.

Before comparing the dynamics of these three models, we clarify the dynamics of the food chain model (4.2) and the two predators–one prey model (4.3) in the following two subsections.

4.1. Dynamics of food chain models (4.2)

It is straightforward to calculate that $E_0 \equiv (0, 0, 0)$, $E_x \equiv (1, 0, 0)$, and $\bar{E}_{xy} \equiv (d_1/\alpha, 1 - d_1/\alpha, 0)$ are equilibria of system (4.2). The equilibria E_0 and E_x always exist without any restriction and the equilibrium E_{xy} exists if $\alpha > d_1$. The following extinction results also can be easily obtained in $\mathbb{R}^3$.

Proposition 4.1. *If* $d_1 \geq \alpha$ *then* $\lim_{t\to\infty} y(t) = 0$ *and* $\lim_{t\to\infty} z(t) = 0$*. Moreover, system* (4.2) *can be reduced to the one-dimensional subsystem with* E_x *as its global attractor.*

By previous proposition we always assume that the inequality $\alpha > d_1$ holds for (4.2) in this subsection and it clearly implies the existence of E_{xy}. The local stability of the equilibrium E_{xy} can be obtained easily by linearization since the Jacobian matrix evaluated at E_{xy} is given by

$$J(E_{xy}) = \begin{bmatrix} -d_1/\alpha & -d_1/\alpha & 0 \\ \alpha - d_1 & 0 & -\beta(1-d_1/\alpha) \\ 0 & 0 & -d_2 + \delta(1-d_1/\alpha) \end{bmatrix}.$$

Hence E_{xy} is asymptotically stable if and only if $1 - d_1/\alpha < d_2/\delta$. Actually, we can show the following global results.

Proposition 4.2. *If inequalities* $\alpha > d_1$ *and*

$$1 - \frac{d_1}{\alpha} < \frac{d_2}{\delta}$$

hold, then $\lim_{t\to\infty} z(t) = 0$*. Moreover, the equilibrium* E_{xy} *is globally asymptotically stable.*

Proof. Let $\mu = 1 - d_1/\alpha - \delta_2/\delta < 0$. Consider

$$\begin{aligned} \frac{1}{\delta}\frac{\dot z(t)}{z(t)} + \frac{1}{\alpha}\frac{\dot y(t)}{z(t)} + \frac{\dot x(t)}{x(t)} &= \frac{1}{\delta}(-d_2 + \delta y) + \frac{1}{\alpha}(-d_1 + \alpha x - \beta z) + (1 - x - y) \\ &\leq 1 - \frac{d_2}{\delta} - \frac{d_1}{\alpha} = \mu. \end{aligned}$$

Hence $z(t)^{1/\delta} y(t)^{1/\alpha} x(t) \to 0$ as $t \to \infty$. Applying Butler–McGehee Lemma and similar arguments in Proposition 2.4, we can show that $\lim_{t\to\infty} z(t) = 0$. Finally, system (4.2) can be reduced to a two-dimensional subsystem with only species x and y eventually, hence E_{xy} is globally asymptotical stable. We complete the proof. □

The coexistence state of (4.2) $\bar E_* = (\bar x_*, \bar y_*, \bar z_*) = (1 - \frac{d_2}{\delta}, \frac{d_2}{\delta}, \frac{1}{\alpha\beta}(\frac{\alpha - d_1}{\alpha} - \frac{d_2}{\delta}))$ exists if and only if the inequality,

$$\frac{\alpha - d_1}{\alpha} > \frac{d_2}{\delta},$$

holds. Since Eq. (4.4) is equivalent to

$$1 > \frac{d_1}{\alpha} + \frac{d_2}{\delta} \tag{4.4}$$

and implies $\alpha > d_1$ and $\delta > d_2$. The following global result of $\bar E_*$ can be obtained by the Lyapunov method.

Proposition 4.3. *If inequality* (4.4) *holds then the coexistence state* $\bar E_*$ *exists and is globally asymptotically stable.*

Proof. Define a Lyapunov function

$$V\big(x(t), y(t), z(t)\big) = \int\limits_{x(0)}^{x(t)} \frac{\eta - \bar x^*}{\eta} d\eta + \frac{1}{\alpha} \int\limits_{y(0)}^{y(t)} \frac{\eta - \bar y^*}{\eta} d\eta + \frac{\beta}{\alpha\delta} \int\limits_{z(0)}^{z(t)} \frac{\eta - \bar z^*}{\eta} d\eta.$$

Table 4.1
Classification of equilibria and global dynamics of system (4.2).

Cases	$\bar{E}_{xy}$	$\bar{E}_*$	Global dynamics
FI: $\alpha \le d_1$	does not exist	does not exist	y, z die out E_x is GAS.
FII: $\alpha > d_1$			
(a) $1 < \frac{d_1}{\alpha} + \frac{d_2}{\delta}$	stable	does not exist	z dies out E_{xy} is GAS.
(b) $1 > \frac{d_1}{\alpha} + \frac{d_2}{\delta}$	unstable	exists	$\bar{E}_*$ is GAS.

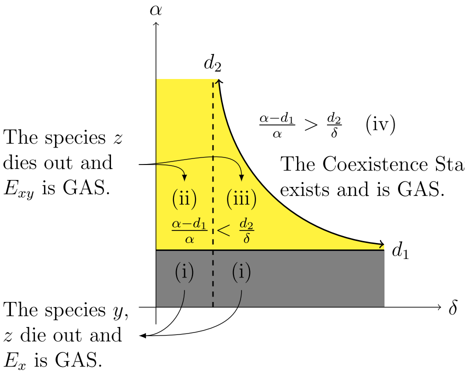


Fig. 4.1. The δ–α parameter space and its corresponding dynamics of (4.2) with varied α, δ and fixed d_1, d_2, β. The species y will die out by the reason of the high mortality d_1 in the gray region (i). And the species z dies out too, since it is a specialist predator with food y only (Proposition 4.1). In the yellow regions (ii) and (iii), the species z dies out due to the high mortality d_2 and low conversion rate δ of species z (Proposition 4.2). Finally, the species can coexist if inequality (4.4) holds, since the flow of biomass can sustain exploitation of species z. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Along the trajectories of system (4.2) we have

$$\begin{aligned}\frac{dV}{dt} &= (x-\bar{x}_*)\frac{\dot{x}}{x} + \frac{1}{\alpha}(y-\bar{y}_*)\frac{\dot{y}}{y} + \frac{\beta}{\alpha\delta}(z-\bar{z}_*)\frac{\dot{z}}{z} \\ &= -(x-\bar{x}_*)^2 \le 0.\end{aligned}$$

Then $dV/dt \le 0$ and $dV/dt = 0$ if and only if $x = \bar{x}_*$. The largest invariant set of $\{dV/dt = 0\}$ is $\{(\bar{x}_*, \bar{y}_*, \bar{z}_*)\}$. Therefore, LaSalle's Invariant Principle implies that $\bar{E}_* = (\bar{x}_*, \bar{y}_*, \bar{z}_*)$ is globally stable. This completes the proof. □

We summarize the results on the dynamics of (4.2) in Table 4.1 and a picture of the parameter space of (4.2) with varied α, δ and fixed d_1, d_2, β is presented in Fig. 4.1. Detailed biological interpretations will be given in Section 4.3 and Section 5.

4.2. Dynamics of two predators–one prey model (4.3)

Similarly, it is straightforward to calculate that $E_0 \equiv (0,0,0)$, $E_x \equiv (1,0,0)$, $\tilde{E}_{xy} \equiv (\frac{d_1}{\alpha}, 1-\frac{d_1}{\alpha}, 0)$, $\tilde{E}_{xz} \equiv (\frac{d_2}{\gamma}, \frac{\gamma-d_2}{s\gamma^2}, 0)$ are equilibria of system (4.3). The equilibria $\tilde{E}_{xy}$, $\tilde{E}_{xz}$ exist if $\alpha > d_1$, $\gamma > d_2$, respectively. Actually, the following extinction results can be easily obtained in $\mathbb{R}^3$.

Proposition 4.4.

(i) *If* $d_1 \ge \alpha$ *and* $d_2 \ge \gamma$, *then* $\lim_{t\to\infty} y(t) = 0$ *and* $\lim_{t\to\infty} z(t) = 0$. *Moreover, system (4.3) can be reduced to a one-dimensional subsystem with* E_x *as its global attractor.*

Table 4.2
Classification of equilibria and global dynamics of system (4.3).

Cases	$\tilde{E}_{xy}$	$\tilde{E}_{xz}$	Global dynamics
TI: $\alpha \le d_1$, $\gamma \le d_2$	does not exist	does not exist	y, z die out E_x is GAS.
TII: $\alpha > d_1$, $\gamma \le d_2$	stable	does not exist	z die out E_{xy} is GAS.
TIII: $\alpha \le d_1$, $\gamma > d_2$	does not exist	stable	y die out E_{xz} is GAS.
TIV: $\alpha > d_1$, $\gamma > d_2$, $\frac{d_1}{\alpha} > \frac{d_2}{\gamma}$	unstable	stable	y dies out E_{xz} is GAS.

(ii) *If $d_1 < \alpha$ and $d_2 \ge \gamma$, then $\lim_{t\to\infty} z(t) = 0$. Moreover, system (4.3) can be reduced to a two-dimensional subsystem with E_{xy} as its global attractor.*

(iii) *If $d_1 \ge \alpha$ and $d_2 < \delta$, then $\lim_{t\to\infty} y(t) = 0$. Moreover, system (4.3) can be reduced to a two-dimensional subsystem with E_{xz} as its global attractor.*

By previous proposition we always assume that the inequalities $\alpha > d_1$ and $\gamma > d_2$ hold for (4.3) in this subsection and it clearly implies the existence of $\tilde{E}_{xy}$ and $\tilde{E}_{xz}$.

It is well known that the coexistence state of (4.3) does not exist generically by the reason of Competitive Exclusion Principle. Considering the linearization of (4.3), it is easy to see that equilibrium E_{xz} is asymptotically stable if and only if $\frac{d_1}{\alpha} > \frac{d_2}{\gamma}$. Moreover, we can show the following global result which says that the species z wins the exploitative competition because of the lower death rate d_2 or the better conversion rate γ.

Proposition 4.5. *Let $\alpha > d_1$ and $\gamma > d_2$. If $\frac{d_1}{\alpha} > \frac{d_2}{\gamma}$ then the species y will die out eventually. Moreover, the equilibrium E_{xz} is globally asymptotically stable.*

Proof. Consider

$$\frac{1}{\alpha}\frac{\dot{y}}{y} - \frac{1}{\gamma}\frac{\dot{z}}{z} = -\frac{d_1}{\alpha} + \frac{d_2}{\gamma} < 0.$$

Similarly, we can easily verify that species y will die out eventually. This completes the proof. □

We summarize the results of dynamics of (4.3) in Table 4.2 and a picture of the parameter space of (4.2) with various α, γ and fixed d_1, d_2, β is presented in Fig. 4.2. Detailed biological interpretations will be given in Section 4.3 and Section 5.

4.3. Food chain, two predators–one prey and omnivory models

Now we are in the position to compare these three models. First, let us re-examine the biological meanings of model (4.2) in the graph of the α–δ parameter space, Fig. 4.1. The species y will die out by the reason of the high mortality d_1 in the gray region (i). And the species z dies out too, since it is a specialist predator with food y only (Proposition 4.1). In the yellow regions (ii) and (iii), the species z dies out due to the high mortality d_2 and low conversion rate δ of species z (Proposition 4.2). Finally, the species can coexist if inequality (4.4) holds, since the flow of biomass can sustain exploitation of species z.

Similarly, we re-examine the biological meanings of model (4.3) in the graph of the α–γ parameter space, Fig. 4.2. In the gray region (i), yellow region (ii), and orange region (iii), the death rates of species y and z dominate the dynamics of (4.3). However, in the two white regions separated by the line $\frac{d_1}{\alpha} = \frac{d_2}{c}$, the positive equilibrium cannot exist due to the Competitive Exclusion Principle. Furthermore, those with lower death rate or higher conversion rate win the exploitation competition and survive.

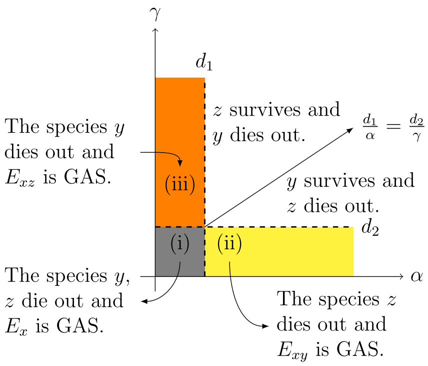


Fig. 4.2. The α–γ parameter space and its corresponding dynamics of (4.3) with varied α, δ and fixed d_1, d_2, β. In the gray region (i), yellow region (ii), and orange region (iii), the death rates of species y and z dominate the dynamics of (4.3). In the two white regions separated by the line $\frac{d_1}{\alpha} = \frac{d_2}{c}$, the positive equilibrium cannot exist due to the Competitive Exclusion Principle. Those who have lower death rate or higher conversion rate can win the exploitation competition and survive. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

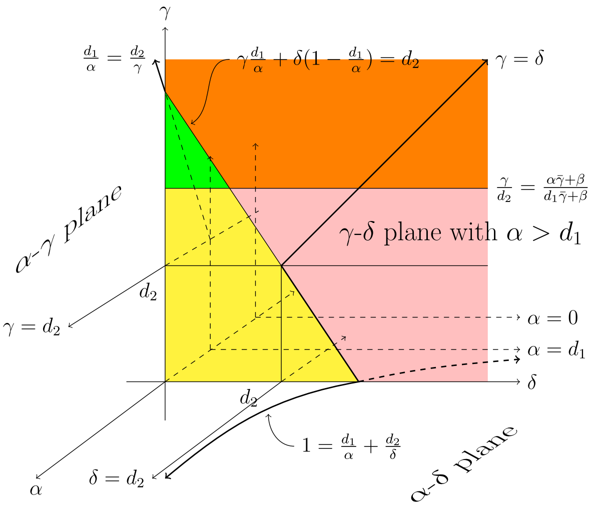


Fig. 4.3. The α–γ–δ-parameter space and its corresponding dynamics of model (2.1). Fig. 4.2 is put on the left two-dimensional plane which presents the dynamics of model (4.3) and is denoted by "α–γ plane". Similarly, Fig. 4.1 is put on the under two-dimensional plane which is denoted by "α–δ plane". Finally, we put Fig. 3.5 on the γ–δ plane with $\alpha > d_1$. The biological meanings and quantitative properties of these pictures and models will be given in the final section. (For interpretation of the colors in this figure, the reader is referred to the web version of this article.)

We note that there are more rich dynamics of (2.1) than the other two models, (4.2) and (4.3). A fundamental difference between the omnivory model (2.1) and food chain model (4.2), two predators–one prey models (4.3) is that the omnivory model contains a generalist predator z. It is well known that the existence of a positive equilibrium implies the globally asymptotically stability in two species predator–prey systems with Lotka–Volterra functional response and there is no periodic solution in this kind of models for any parameters. Similar results without any periodic solutions are obtained in the models of (4.2) and (4.3). However, the coexistence of (2.1) can be found in the state of a positive equilibrium or in the state of periodic solutions. Moreover, the phenomenon of bistability also are found in the omnivory model.

Finally, we present a picture, Fig. 4.3, of the α–γ–δ-parameter space to interpret the relations of these three models. Fig. 4.2 is put on the left two-dimensional plane of Fig. 4.3 which presents the dynamics of model (4.3) and is denoted by "α–γ plane". Similarly, Fig. 4.1 is put on the under two-dimensional plane of Fig. 4.3 which is denoted by "α–δ plane". Finally, we put Fig. 3.5 on the γ–δ plane with $\alpha > d_1$. The biological meanings and quantitative properties of these pictures and models will be given in the final section.

5. Discussion

In this work, we considered a three-species food web model with omnivory (intraguild predation) which are the species feed at more than one tropic level. Using a non-dimensional scaling model with seven parameters, all possible dynamics of (2.1) are clarified and classified theorically and numerically. We not only analyzed the model (2.1) but also found the connections of the three basic models (2.1), (4.2), (4.3) by two factors s and μ.

Recall that the parameters proportioned to K are $\alpha = a_{21}K/B$ and $\gamma = a_{31}K/B$ which are positive relative to the basal resource productivity. Parameter

$$\delta = \frac{a_{32}}{a_{12}} = \frac{a_{32}}{a_{23}}\frac{a_{23}}{a_{21}}\frac{a_{21}}{a_{12}}$$

measures the efficiency of biomass in the direction from x to y (a_{21}/a_{12}) and from y to z (a_{32}/a_{23}), and conversion rate for species y (a_{23}/a_{21}).

First, for the two predators–one prey model (4.3), exploitative competition occurs between the two predators, because both predators share the same basal resources. Let the ratio $\frac{\alpha}{d_1}$ and $\frac{\gamma}{d_2}$ be defined the index of resource exploitation of species y and z, respectively. The inequality $\frac{\alpha}{d_1} < (>) \frac{\gamma}{d_2}$ means that the species y is inferior (superior) at resource exploitation to species z. So Proposition 4.5 says that in model (4.3) species y loses and dies out since it is inferior at resource exploitation to species z. This result is the so-called Competitive Exclusion Principle. On the other hand, for the food chain model (4.2), if species y and z overcome their mortalities, i.e. $\alpha > d_1$ and $\delta > d_2$, then they coexist if the resource exploitation (d_1/α) is good for y and the conversion efficiency (d_2/δ) is excellent for z. Hence the inequality (4.4) guarantees the existence and globally asymptotical stability of the positive equilibrium.

Next, let us look at the omnivory model (2.1) and the γ–δ plane of Fig. 4.3 carefully. The straight line

$$\frac{d_1}{\alpha} + \frac{\delta}{\gamma}\left(1 - \frac{d_1}{\alpha}\right) = \frac{d_2}{\gamma} \tag{5.1}$$

of the γ–δ plane which connects the straight line $d_1/\alpha = d_2/\gamma$ of the left α–γ plane and the curve $1 = \frac{d_1}{\alpha} + \frac{d_2}{\delta}$ of the bottom α–δ plane separates the whole γ–δ plane into two parts. This straight line implies that the ability of persistence of species z is depend on two factors, the resource exploitation of y and the conversion efficiency of z. If the resource exploitation of y is inferior (d_1/α is large) and the conversion efficiency of z is excellent (δ is large), then parameters fall into the right hand side. So the dynamics of model (2.1) are that z will persist (the orange and pink regions). The horizontal line

$$\frac{\gamma}{d_2} = \frac{\alpha\bar{\gamma} + \beta}{d_1\bar{\gamma} + \beta} \tag{5.2}$$

indicates that the borderline of the real resource exploitation of y, $\frac{\alpha\bar{\gamma}+\beta}{d_1\bar{\gamma}+\beta}$, with a positive predation factor β by species z. Hence in the orange regions, species z wins and y dies out since $\frac{\gamma}{d_2} > \frac{\alpha\bar{\gamma}+\beta}{d_1\bar{\gamma}+\beta}$, i.e. the resource exploitation of z is superior to y. On the contrary, all species coexist in the pink regions. This result has been indicated in [10] which states that model (2.1) can coexist and suggests that coexistence requires that the species y be superior at exploiting shared resources. Since the inferior competitor z can gain sufficiently from predation on the species y to offset competitive inferiority on the shared resource.

For the left hand side of the straight line (5.1), if $\frac{\gamma}{d_2} < \frac{\alpha\bar{\gamma}+\beta}{d_1\bar{\gamma}+\beta}$ then species z cannot persist. Since it is neither superior at exploiting shared resources nor efficient in converting species y. But, there is a different story in the green region. Mathematically, we obtain a bistability phenomenon here (Proposition 3.2(iii)), hence the final dynamics is depend on the initial condition. Biologically, species z is superior just a little bit in resource exploitation to y. So the advance in this point can be eliminated by the large amount of species y. Therefore, the solution will approach E_{xy} eventually if the population of species z is rare. The other symmetric case can be argued similarly. This mathematical result and its biological interpretations have not been reported in the literature so far in our best knowledge.

Moreover, we would like to mention the recent works by Kang and Wedekin [13]. They consider an IGP model with a specialist predator:

$$\begin{cases} x' = x(1 - x - y - z) \\ y' = \gamma_1 y\left(x - \dfrac{a_1 yz}{y^2 + \beta^2} - d_1\right) \\ z' = \gamma_2 z\left(x + \dfrac{a_2 y^2}{y^2 + \beta^2} - d_2\right), \end{cases}$$

and an IGP model with a generalist predator:

$$\begin{cases} x' = x(1 - x - y - z) \\ y' = \gamma_1 y\left(x - \dfrac{a_1 yz}{y^2 + \beta^2} - d_1\right) \\ z' = \gamma_2 z\left(a_3 - a_4 z + x + \dfrac{a_2 y^2}{y^2 + \beta^2}\right). \end{cases} \tag{5.3}$$

They call species z of model (5.3) the generalist predators since they feed on the basal resource x, IG-prey y, and other diet resources described by the logistic growth $\gamma_2 z(a_3 - a_4 z)$. By theoretical analysis and numerical simulations, they obtain the following implications:

1. IGP with generalist predator can have potential “top down” regulation.
2. The persistence of species y requires it being superior competitor to IG predator [10].
3. The IGP model with a generalist predator is prone to have coexistence of three species.
4. Holling-Type III functional response between IG-prey and IG-predator in IGP models lead to much more complicate dynamics than IGP models with only Holling-Type I functional response.

Not only the functional response but also the nonlinear interactions of our model (1.1) are much simpler than Kang’s. Even though model (1.1) only consists of Lotka–Volterra type functional responses but the model has very rich dynamics, such as extinction, coexistence, bistability, periodic solutions, and chaos.

Finally, we would like to discuss a longstanding debate in ecology [14]: Does omnivory *destabilize* [19,18] or *stabilize* [16,28,20,3,22,26,1] the food web system? Based on our analytical and simulation results, we try to answer this question by transferring it to the following: How does the omnivorous effect γ affect the stability of the positive equilibrium of an omnivory model? Before answer this question, we should do some numerical works.

By the persistent result of (2.1) Proposition 3.6, if parameters are in the pink region of Fig. 3.5 then all solutions of (2.1) with positive initial conditions are in a bounded set of first octant and ε-away from xy-, yz-, and xz-planes for some positive number ε. We have showed global stability of E_* for some parameters in the pink region near the region of parameters of the food chain model (Proposition 3.5). However, it is difficulty to determine the global dynamics of a system with dimension large than two. So we numerically check the conditions (3.5) and (3.6) for the local stability of E_* with a particular set of parameters, $\alpha = 2.5$, $\beta = 1.0$, $d_1 = 0.8$, $d_2 = 0.9$, $s = 1.0$ and discretized parameters γ and δ in the pink region of Fig. 3.5.

It is straightforward to see that the first condition (3.5) of Routh–Hurwitz criterion is always true if parameters are in the pink regions because of the inequalities

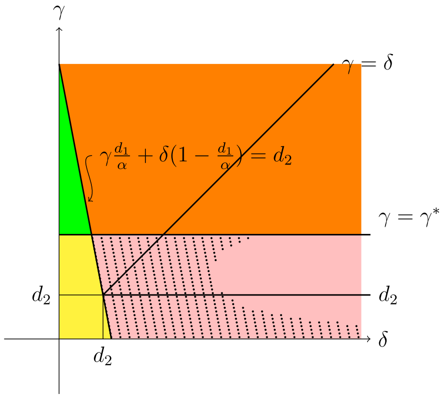


Fig. 5.1. A typical picture of the parameter space with variously γ, δ, and fixed d_1, d_2, m_1, m_2, α, β with $\alpha > d_1$. Numerically, we verify that the coexistence equilibrium E_* is stable with parameters γ, δ in the shadow region and $\alpha = 2.5$, $\beta = 1.0$, $d_1 = 0.8$, $d_2 = 0.9$, $s = 1.0$. (For interpretation of the colors in this figure, the reader is referred to the web version of this article.)

$$\gamma < \gamma^* \quad \text{and} \quad \gamma \frac{d_1}{\alpha} + \delta\left(1 - \frac{d_1}{\alpha}\right) > d_2.$$

Based on the explicit form of y^* and z^* in (3.15), the second condition (3.6) of Routh–Hurwitz criterion can be checked numerically for the previous setting parameters. We find numerically that inequality (3.6) is true in the shadow region of Fig. 5.1.

Now we are on the position to answer the question. Our answer is that it is depend on the values of γ and δ. For medium values of δ, the equilibrium E_* is stable if $0 < \gamma < \gamma^*$ or unstable if $\gamma > \gamma^*$. For larger δ, the equilibrium E_* will be stable, unstable, stable or unstable when γ increases from 0 to the orange region of Fig. 5.1. Finally, the equilibrium E_* is stable only for large δ and small γ.

References

[1] M. Arim, P.A. Marquet, Intraguild predation: a widespread interaction related to species biology, Ecol. Lett. 7 (7) (July 2004) 557–564.
[2] G. Butler, H.I. Freedman, P. Waltman, Uniformly persistent systems, Proc. Amer. Math. Soc. 96 (3) (1986) 425–430.
[3] S. Diehl, Relative consumer sizes and the strengths of direct and indirect interactions in omnivorous feeding relationships, Oikos 68 (1) (Oct. 1993) 151–157.
[4] S. Diehl, M. Feißel, Effects of enrichment on three-level food chains with omnivory, Amer. Nat. 155 (2) (2000) 200–218.
[5] H.I. Freedman, S. Ruan, M. Tang, Uniform persistence and flows near a closed positively invariant set, J. Dynam. Differential Equations 6 (4) (1994) 583–600.
[6] H.I. Freedman, P. Waltman, Persistence in models of three interacting predator–prey populations, Math. Biosci. 68 (2) (1984) 213–231.
[7] M.E. Gilpin, Spiral chaos in a predator–prey model, Amer. Nat. 113 (2) (1979) 306–308.
[8] A. Hastings, T. Powell, Chaos in a three-species food chain, Ecology 72 (3) (1991) 896–903.
[9] M.W. Hirsch, H. Smith, Monotone dynamical systems, in: Handbook of Differential Equations: Ordinary Differential Equations. Vol. II, 2005, pp. 239–357.
[10] R.D. Holt, G.A. Polis, A theoretical framework for intraguild predation, Amer. Nat. 149 (1997) 745–764.
[11] S.B. Hsu, S.P. Hubbell, P. Waltman, A contribution to the theory of competing predators, Ecol. Monogr. 48 (3) (1978) 337–349.
[12] S.B. Hsu, S.P. Hubbell, P. Waltman, Competing predators, SIAM J. Appl. Math. 35 (4) (1978) 617–625.
[13] Y. Kang, L. Wedekin, Dynamics of a intraguild predation model with generalist or specialist predator, J. Math. Biol. 67 (5) (2013) 1227–1259.
[14] P. Kratina, R.M. LeCraw, T. Ingram, B.R. Anholt, Stability and persistence of food webs with omnivory: is there a general pattern?, Ecosphere 3 (6) (June 2012), art50.
[15] N. Krikorian, The Volterra model for three species predator–prey systems: boundedness and stability, J. Math. Biol. 7 (2) (1979) 117–132.
[16] B.A. Menge, J.P. Sutherland, Community regulation–variation in disturbance, competition, and predation in relation to environmental-stress and recruitment, Amer. Nat. 130 (5) (Nov. 1987) 730–757.
[17] T. Namba, K. Tanabe, Omnivory and stability of food webs, Ecol. Complexity 5 (2008) 73–85.
[18] S.L. Pimm, Properties of food webs, Ecology 61 (2) (Apr. 1980) 219–225.
[19] S.L. Pimm, J.H. Lawton, On feeding on more than one trophic level, Nature 275 (5680) (Oct. 1978) 542–544.

[20] G.A. Polis, Complex trophic interactions in deserts: an empirical critique of food-web theory, Amer. Nat. 138 (1) (July 1991) 123–155.
[21] G.A. Polis, C.A. Myers, R.D. Holt, The ecology and evolution of intraguild predation – potential competitors that eat each other, Ann. Rev. Ecol. Syst. 20 (1989) 297–330.
[22] S. Ponsard, R. Arditi, What can stable isotopes (delta N-15 and delta C-13) tell about the food web of soil macro-invertebrates?, Ecology 81 (3) (Mar. 2000) 852–864.
[23] J.A. Rosenheim, Higher-order predators and the regulation of insect herbivore populations, Entomology 43 (1997) 421–447.
[24] J.A. Rosenheim, H.K. Kaya, L.E. Ehler, J.J. Marois, B.A. Jaffee, Intraguild predation among biological-control agents: theory and evidence, Biol. Control 5 (1995) 303–335.
[25] S. Ruan, Oscillations in plankton models with nutrient recycling, J. Theoret. Biol. 208 (1) (2001) 15–26.
[26] S. Scheu, M. Falca, The soil food web of two beech forests (Fagus sylvatica) of contrasting humus type: stable isotope analysis of a macro- and a mesofauna-dominated community, Oecologia 123 (2) (May 2000) 285–296.
[27] K. Tanabe, T. Namba, Omnivory creates chaos in simple food web models, Ecology 86 (12) (Dec. 2005) 3411–3414.
[28] D.E. Walter, Trophic behavior of mycophagous microarthropods, Ecology 68 (1) (Feb. 1987) 226–229.