

# 科技部補助專題研究計畫成果報告 期末報告

3 物種的捕食與被捕食模型，在不同的反應函數下的全域動態行為和分歧研究。

計畫類別：個別型計畫  
計畫編號：NSC 102-2115-M-032-004-  
執行期間：102年08月01日至103年07月31日  
執行單位：淡江大學數學系

計畫主持人：楊定揮

計畫參與人員：碩士班研究生-兼任助理人員：余金衛  
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報告附件：出席國際會議研究心得報告及發表論文

處理方式：

1. 公開資訊：本計畫涉及專利或其他智慧財產權，1年後可公開查詢
2. 「本研究」是否已有嚴重損及公共利益之發現：否
3. 「本報告」是否建議提供政府單位施政參考：否

中華民國 103 年 10 月 01 日

中文摘要：在這項工作中，我們考慮三個物種的 Lotka-Volterra 型食物鏈模型，且最頂端捕食者具有雜食特性。經過無維度變換，該系統實際上是一階微分方程三個方程模型與七個參數。經分析，我們將參數空間完整的分為三大類共含八種情況，其中五例發生滅絕，另外三例，我們驗證了系統的一致持續性。此外，在參數空間裡，系統維持一致持續性的區域中，通過 Hopf Bifurcation，我們證明了週期解的存在性，並給出了發生混沌動力行為的數值模擬。生物上來說，雜食性模組融合了幾種研究透徹的社區模塊，如食品鏈，剝削性的競爭，以及明顯的競爭的屬性。我們試圖指出這些模組定量之間的異同，並給予生物解釋。

中文關鍵詞：三個物種，均勻持久性，Hopf 分岔，混沌

英文摘要：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 system is actually a model of three equations of 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 parameter space where the system is uniform 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.

英文關鍵詞：three species, uniform persistence, Hopf bifurcation, chaos

# 行政院國家科學委員會補助專題研究計畫成果 報告

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計畫參與人員：碩士生：陳柏宇, 余金衛。

成果報告類型 (依經費核定清單規定繳交)：精簡報告

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中華民國 一百零三 年 十 月

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# 1 報告内容

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 between  $n$ -species that are all cooperative or competitive are well studied in the past three decades due to the theory of monotone dynamical systems [9]. However, for a non-monotone system whose interactions are blended at least one consumption (i.e. herbivory, predation and parasitism), most known results are constrained on two species cases since the classical Poincare-Bendixson Theorem can be applied. Hence the dynamics of a non-monotone ecosystem with at least 3-species are paid attentions recently.

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 (Figure 1 (a)), two predators competing for one prey (Figure 1 (b)), one predator acting on two preys (Figure 1 (c)), and loops (Figure 1 (d), (e)). We separate the case loop into two sub-cases, food chain with omnivory (Figure 1 (d)) and cycle (Figure 1 (e)). Because we observe that all species except for species  $z$  of case (d) with consumption in the above cases are the so-called the specialist predators which has 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.

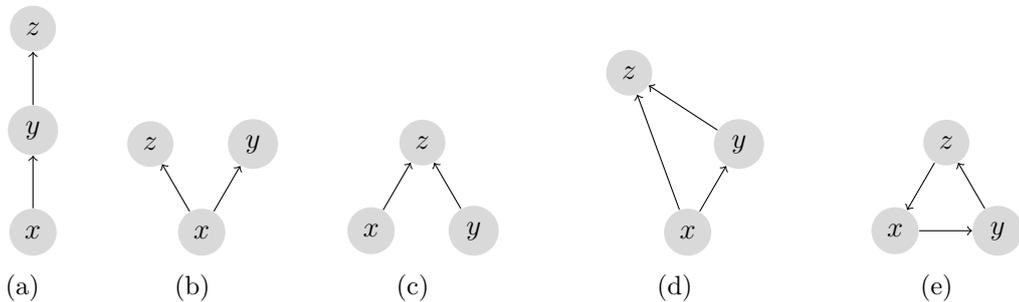


Figure 1: All possible schematic diagrams of the direct and indirect interactions among three species predator-prey systems. The arrows present the directions of biomass. (a) food chain; (b) two predators-one prey; (c) one predator-two preys; (d) food chain with omnivory; and (e) food chain with cycle.

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,

$$\begin{aligned}
 \frac{dN_1}{d\tau} &= N_1(B - a_{11}N_1 - a_{12}N_2 - a_{13}N_3), \\
 \frac{dN_2}{d\tau} &= N_2(-D_1 + a_{21}N_1 - a_{23}N_3), \\
 \frac{dN_3}{d\tau} &= N_3(-D_2 + a_{31}N_1 + a_{32}N_2), \\
 N_1(0) &\geq 0, \quad N_2(0) \geq 0, \quad N_3(0) \geq 0,
 \end{aligned} \tag{1}$$

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. The coefficient  $a_{11}$  denotes the intraspecific competition in the resource and  $a_{ij}(i < j)$  is the rate of consumption; and  $a_{ij}(i > j)$  measures the contribution of the victim (basal resource or intraguild prey) to the growth of the consumer.

System (4) 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 Figure 2). In this work, we would like to clarify the global dynamics and corresponding bi-

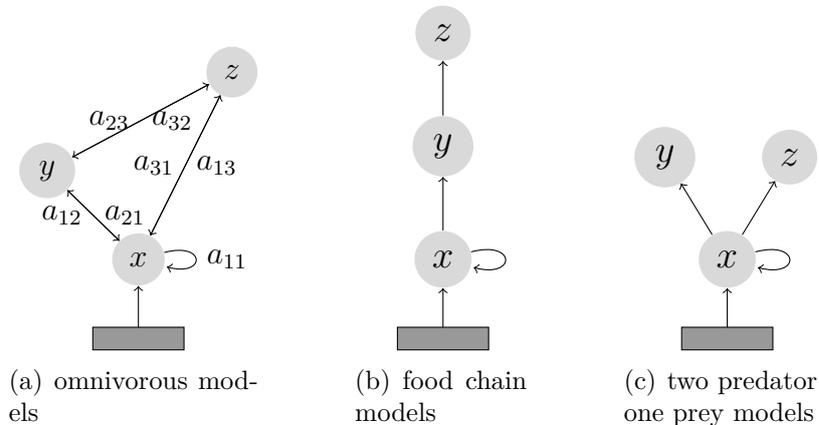


Figure 2: Three most simple interactions between three species with one renewable resource.

ological interpretations of (4). 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 model (4). From the mathematical point of views, we give the quantitative and biological interpretations in which some results are parallel to the compatible results of [10] and some results are new.

For mathematical simplification, we write the model (4) 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 (4) takes the form

$$\begin{aligned}
 \frac{dx}{dt} &= x(1 - x - y - \bar{\gamma}z), \\
 \frac{dy}{dt} &= y(-d_1 + \alpha x - \beta z), \\
 \frac{dz}{dt} &= z(-d_2 + \gamma x + \delta y),
 \end{aligned} \tag{2}$$

with initial conditions,  $x(0) \geq 0$ ,  $y(0) \geq 0$ ,  $z(0) \geq 0$ , where the parameters

are all positive with the rescaling:

$$\begin{aligned} d_1 &= D_1/B, & d_2 &= D_2/B, \\ \alpha &= a_{21}/a_{11}, & \beta &= a_{23}, \\ \gamma &= a_{31}/a_{11}, & \bar{\gamma} &= a_{13}, & \delta &= a_{32}/a_{12}. \end{aligned} \tag{3}$$

If we rewrite the first equation of (4) 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.

The rest of the paper is organized as follows. In Section 2, we show the boundedness of solutions of (5) 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.

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### 3 計畫成果自評

在這項工作中，我們考慮三個物種的 Lotka-Volterra 型食物鏈模型，且最頂端捕食者具有雜食特性。方程如下，

$$\begin{aligned}
 \frac{dN_1}{d\tau} &= N_1(B - a_{11}N_1 - a_{12}N_2 - a_{13}N_3), \\
 \frac{dN_2}{d\tau} &= N_2(-D_1 + a_{21}N_1 - a_{23}N_3), \\
 \frac{dN_3}{d\tau} &= N_3(-D_2 + a_{31}N_1 + a_{32}N_2), \\
 N_1(0) &\geq 0, N_2(0) \geq 0, N_3(0) \geq 0,
 \end{aligned} \tag{4}$$

其中  $N_1$ ,  $N_2$ , and  $N_3$  分別代表底層食物，中間消費者 (intraguild prey) 及最上層掠食者 (intraguild predator) 的生物密度。所有的參數皆為正數，其中  $B$  為  $N_1$  的成長率， $D_1$  及  $D_2$  為  $N_2$  及  $N_3$  的死亡率。係數  $a_{ij}$  為物種  $i$  及  $j$  的交互作用係數。

經過無維度變換，

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

系統 (4) 可轉成下列型式

$$\begin{aligned}\frac{dx}{dt} &= x(1 - x - y - \bar{\gamma}z), \\ \frac{dy}{dt} &= y(-d_1 + \alpha x - \beta z), \\ \frac{dz}{dt} &= z(-d_2 + \gamma x + \delta y),\end{aligned}\tag{5}$$

其中係數,

$$\begin{aligned}d_1 &= D_1/B, & d_2 &= D_2/B, \\ \alpha &= a_{21}/a_{11}, & \beta &= a_{23}, \\ \gamma &= a_{31}/a_{11}, & \bar{\gamma} &= a_{13}, & \delta &= a_{32}/a_{12}.\end{aligned}\tag{6}$$

該系統實際上是一階微分方程三個方程模型與七個參數。經分析，我們將參數空間完整的分為三大類共含八種情況，其中五例發生滅絕 (extinction)，另外三例，我們驗證了系統的一致持續性 (uniform persistence)。此外，在參數空間裡，系統維持一致持續性的區域中，通過 Hopf Bifurcation，我們證明了週期解的存在性，並給出了發生混沌動力行為的數值模擬。生物上來說，雜食性模組融合了幾種研究透徹的社區模塊，如食物鏈 (food chain modules)，剝削性的競爭 (exploitative competition, two predators-one prey modules)，以及明顯的競爭 (apparent competition, one predator-two preys modules) 的屬性。我們試圖指出這些模組定量之間的異同，並給予生物解釋。我們這個工作的主要結果投稿到 *Journal of Mathematical Analysis and Applications*, 詳見附錄。

## 4 附錄

# Analysis of Three Species Lotka-Volterra Food Web Models with Omnivory

Sze-Bi Hsu\*, Shigui Ruan<sup>†</sup> and Ting-Hui Yang<sup>‡</sup>

August 12, 2014

## 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 system is actually a model of three equations of 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 parameter space where the system is uniform 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.

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# 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 between  $n$ -species that are all cooperative or competitive are well studied in the past three decades due to the theory of monotone dynamical systems [9]. However, for a non-monotone system whose interactions are blended at least one consumption (i.e. herbivory, predation and parasitism), most known results are constrained on two species cases since the classical Poincare-Bendixson Theorem can be applied. Hence the dynamics of a non-monotone ecosystem with at least 3-species are paid attentions recently.

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 (Figure 1.1 (a)), two predators competing for one prey (Figure 1.1 (b)), one predator acting on two preys (Figure 1.1 (c)), and loops (Figure 1.1 (d), (e)). We separate the case loop into two sub-cases, food chain with omnivory (Figure 1.1 (d)) and cycle (Figure 1.1 (e)). Because we observe that all species except for species  $z$  of case (d) with consumption in the above cases are the so-called the specialist predators which has 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.

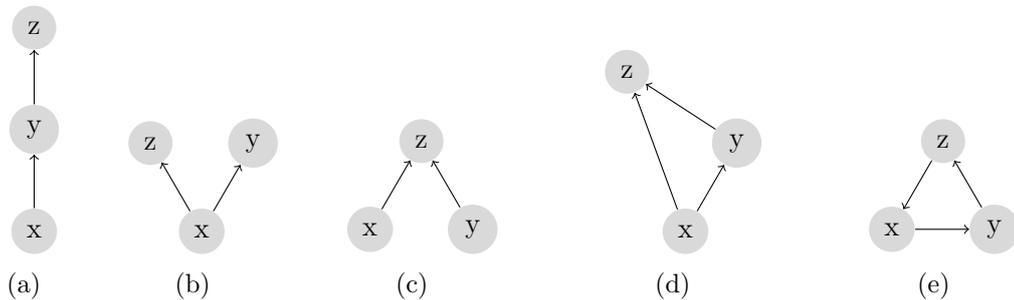


Figure 1.1: All possible schematic diagrams of the direct and indirect interactions among three species predator-prey systems. The arrows present the directions of biomass. (a) food chain; (b) two predators-one prey; (c) one predator-two prey; food chain with omnivory; and (d) food chain with cycle.

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,

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 \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. The coefficient  $a_{11}$  denotes the intraspecific competition in the resource and  $a_{ij}$  ( $i < j$ ) is the rate of 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 Figure 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

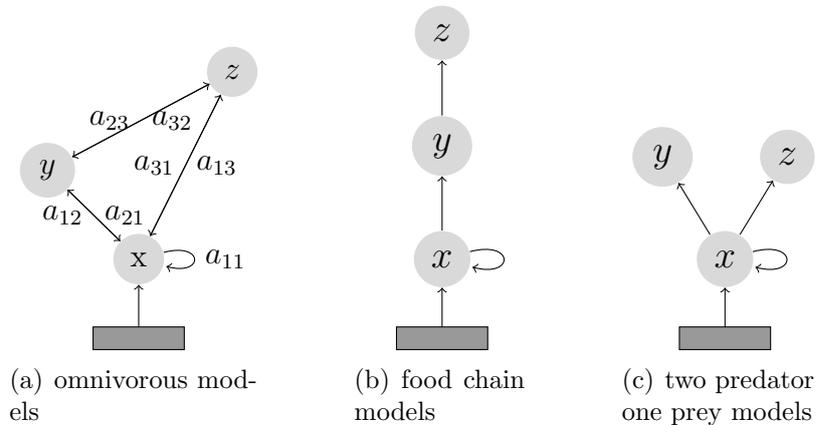


Figure 1.2: Three most simple interactions between three species with one renewable resource.

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 model (1.1). From the mathematical point of views, we give the quantitative and biological interpretations in which some results are parallel to the compatible results of [10] and some results are new.

For mathematical simplification, we write the 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

$$\begin{aligned} \frac{dx}{dt} &= x(1 - x - y - \bar{\gamma}z), \\ \frac{dy}{dt} &= y(-d_1 + \alpha x - \beta z), \\ \frac{dz}{dt} &= z(-d_2 + \gamma x + \delta y), \end{aligned} \tag{1.2}$$

with initial conditions,  $x(0) \geq 0$ ,  $y(0) \geq 0$ ,  $z(0) \geq 0$ , where the parameters

are all positive with the rescaling:

$$\begin{aligned} d_1 &= D_1/B, & d_2 &= D_2/B, \\ \alpha &= a_{21}/a_{11}, & \beta &= a_{23}, \\ \gamma &= a_{31}/a_{11}, & \bar{\gamma} &= a_{13}, & \delta &= a_{32}/a_{12}. \end{aligned} \tag{1.3}$$

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.

The rest of the paper is organized as follows. In Section 2, we show the boundedness of solutions of (1.2) 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 (1.2) 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 (1.2) to the one- or two-dimensional subsystem is given.

We can easily see that the solutions of (1.2) are positive (nonnegative) with positive (nonnegative) initial conditions. The following results on the boundedness of solutions of system (1.2) can be verified easily.

**Proposition 2.1.** *The system (1.2) is dissipative.*

*Proof.* From the first equation in system (1.2) we have

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

so that the comparison principle implies that

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

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 (1.2) we have

$$\begin{aligned} & \frac{d}{dt}(Mx + y + (\beta/\delta)z) \\ &= Mx(1 - x - y - \bar{\gamma}z) - d_1y + \alpha xy - d_2(\beta/\delta)z + (\beta\gamma/\delta)xz \\ &\leq Mx - D(y + (\beta/\delta)z) \\ &\leq K - D(Mx + y + (\beta/\delta)z), \end{aligned}$$

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

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

which implies that system (1.2) 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 (1.2),  $E_x \equiv (1, 0, 0)$ ,  $E_{xy} \equiv (d_1/\alpha, 1 - d_1/\alpha, 0)$ , 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 (1.2) is reduced to the one-dimensional subsystem*

$$\frac{dx}{dt} = x(1 - x). \quad (2.1)$$

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

(ii) *On  $H_2$ , system (1.2) is reduced to the two-dimensional subsystem*

$$\begin{aligned} \frac{dx}{dt} &= x(1 - x - y), \\ \frac{dy}{dt} &= y(-d_1 + \alpha x). \end{aligned} \quad (2.2)$$

*If  $\alpha \leq d_1$  then  $E_{xy}$  does 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 (1.2) is reduced to the two-dimensional subsystem*

$$\begin{aligned} \frac{dx}{dt} &= x(1 - x - \bar{\gamma}z), \\ \frac{dz}{dt} &= z(-d_2 + \gamma x). \end{aligned} \quad (2.3)$$

*If  $\gamma \leq d_2$  then  $E_{xz}$  does 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 (1.2) by direct computation,

$$J(x, y, z) = \begin{bmatrix} 1 - 2x - y - \bar{\gamma}z & -x & -\bar{\gamma}x \\ \alpha y & -d_1 + \alpha x - \beta z & -\beta y \\ \gamma z & \delta z & -d_2 + \gamma x + \delta y \end{bmatrix}. \quad (2.4)$$

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  $E_x$ ,

$$J(E_x) = \begin{bmatrix} -1 & -1 & -\bar{\gamma} \\ 0 & \alpha - d_1 & 0 \\ 0 & 0 & \gamma - d_2 \end{bmatrix}, \quad (2.5)$$

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

$$J(E_{xy}) = \begin{bmatrix} -d_1/\alpha & -d_1/\alpha & -d_1\bar{\gamma}/\alpha \\ \alpha - d_1 & 0 & -\beta(1 - d_1/\alpha) \\ 0 & 0 & -d_2 + \gamma d_1/\alpha + \delta(1 - d_1/\alpha) \end{bmatrix}. \quad (2.6)$$

It is easy to see that the top left  $2 \times 2$  sub-matrix is exactly the Jacobian matrix for the subsystem (2.2) 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

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

It is similar to the case (c). We can get the  $2 \times 2$  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 (2.3) at the equilibrium  $E_{xz}$ . The third eigenvalue is given by  $\lambda = -d_1 + \alpha d_2/\gamma - \beta(1 - d_2/\gamma)$ . 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 (1.2), 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  $\alpha \leq d_1$  and  $\gamma \leq d_2$ . Otherwise, it is a saddle.*
- (iii) *If  $\alpha > d_1$  then  $E_{xy}$  exists and it is asymptotically stable in  $\mathbb{R}^3$  if and only if*

$$-d_2 + \gamma \frac{d_1}{\alpha} + \delta \left(1 - \frac{d_1}{\alpha}\right) < 0. \quad (2.7)$$

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

$$-d_1 + \alpha \frac{d_2}{\gamma} - \frac{\beta}{\bar{\gamma}} \left(1 - \frac{d_2}{\gamma}\right) < 0. \quad (2.8)$$

To clarify the dynamics of global behaviors of the semi-trivial equilibria of system (1.2) 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 (1.2) with initial condition  $\mathbf{p} = (x(0), y(0), z(0))$  where  $x(0) > 0$ ,  $y(0) > 0$ , and  $z(0) > 0$ . Then the following statements are true.*

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

*Proof.* (i) By the first equation of (1.2), for any positive number  $\varepsilon$  we have  $x(t) < 1 + \varepsilon$  for enough large  $t$ . Take  $\varepsilon = (d_1 - \alpha)/2\alpha > 0$ , then for large  $t$  consider

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

Hence we have the limit  $\lim_{t \rightarrow \infty} y(t) = 0$ . 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

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

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

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

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  $\alpha$ , then  $y$  will die out eventually and system (1.2) is reduced to the one-dimensional  $x$  subsystem (2.1) or two-dimensional  $x$ - $z$  subsystem (2.3). Thus classical two-dimensional results, Proposition 2.2, can be applied. Therefore, from now on, we 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 next section.

### 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  $\gamma$  and  $\delta$  respect to the death rate of species  $z$ ,  $d_2$ . See Figure 3.1. Biologically, if  $\gamma > \delta$  hold, then for the top predator's conversion rate  $\gamma$  of  $x$  is larger than the conversion rate  $\delta$  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 (1.2) 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 Figure 3.1.);
- (II)  $\gamma > \max\{\delta, d_2\}$  (in region (1) and (2) of Figure 3.1.);
- (III)  $d_2 < \gamma < \delta$  (in region (4) of Figure 3.1.);
- (IV)  $\gamma < d_2 < \delta$  (in region (5) of Figure 3.1.).

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

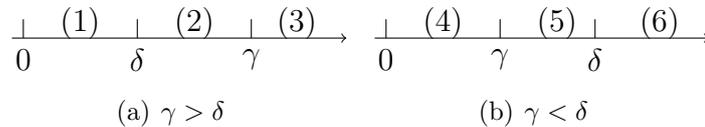


Figure 3.1: All generic possibilities of classification of parameters with varied  $d_2$  in regions (1)-(6) with  $d_1 > \alpha$ .

### 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 another 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 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 the 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  $\lim_{t \rightarrow \infty} z(t) = 0$  and the equilibrium  $E_{xy}$  is globally asymptotically stable.*

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

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

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

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

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

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

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

Then we have  $z(t)(x(t))^c$  approaches 0 as  $t$  approaches  $\infty$ . 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  $\infty$  and  $x(t_n)$  approaches 0 as  $n$  approaches  $\infty$ . Another one is that there is a positive number  $\varepsilon$  such that  $x(t) \geq \varepsilon$  for all time  $t$ .

Assume that there is a sequence  $\{t_n\}$  such that  $x(t_n)$  approaches zero as  $n$  approaches infinity. And since the solutions of (1.2) are bounded, there is a point  $\mathbf{q} = (0, \bar{y}, \bar{z}) \in H_4 \cap \omega(\mathbf{p})$ . By Proposition 2.2, the solution of (1.2) with initial condition  $\mathbf{q} \in H_4$ ,  $\phi(t, \mathbf{q})$ , will approach  $E_0$  when time goes to infinity. Hence  $E_0 \in \omega(\mathbf{p})$ . It is clear that  $\omega(\mathbf{p}) \neq \{E_0\}$ . Applying Butler-McGehee Lemma [6], there is a point  $\mathbf{r} = (\bar{x}, 0, 0) \in H_1 \cap \omega(\mathbf{p})$ . Clearly,  $\mathbf{r} \neq E_0$  and  $\phi(t; \mathbf{r})$  approaches  $E_x$  as time goes to infinity. Similarly,  $\{E_x\} \subsetneq \omega(\mathbf{p})$  and applying Butler-McGehee Lemma again, we can find a point  $\mathbf{s} \in \omega(\mathbf{p}) \cap H_2$  since the unstable manifold of  $E_x$  is contained in  $H_2$ . Again,  $\phi(t; \mathbf{s})$  approaches  $E_{xy}$ , hence  $E_{xy} \in \omega(\mathbf{p})$ . Since  $E_{xy}$  is asymptotically stable in  $\mathbb{R}^3$ , we have the limit  $\lim_{t \rightarrow \infty} \phi(t; \mathbf{p}) = E_{xy}$ .

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

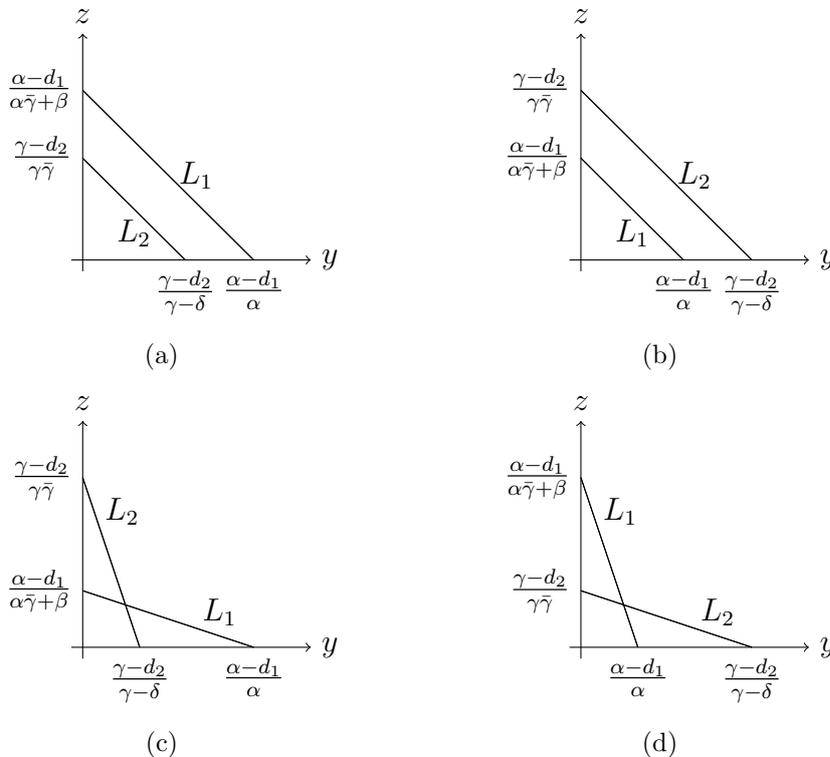


Figure 3.2: The four possible generic cases for the intersection of the two straight lines  $L_1$  and  $L_2$  for category (II).

### 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 Figure 3.2.

In Figure 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 (2.7) and reversed (2.8). 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 equation (2.4), if  $E_*$  exists then the Jacobian evaluated at  $E_*$  is given by

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

Let  $\lambda$  be an eigenvalue. Then the characteristic equation is

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

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

$$\alpha \bar{\gamma} \delta + \beta \delta - \gamma \beta > 0 \quad (3.5)$$

and

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

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

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

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

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

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 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

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

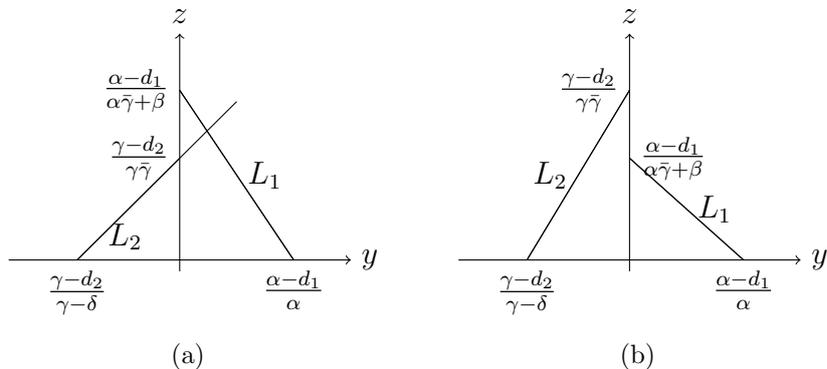


Figure 3.3: The two possible generic cases for the intersection of the two straight lines  $L_1$  and  $L_2$  for category (III).

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

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

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.  $\square$

### 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 Figure 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 equilibrium  $E_{xz}$  is globally asymptotically stable.*

*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 (2.8) 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

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

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

### 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 another boundary equilibrium  $E_{xz}$  does not exist. Similarly, we solve (3.2) and (3.3) to find the positive equilibrium  $E_*$  and

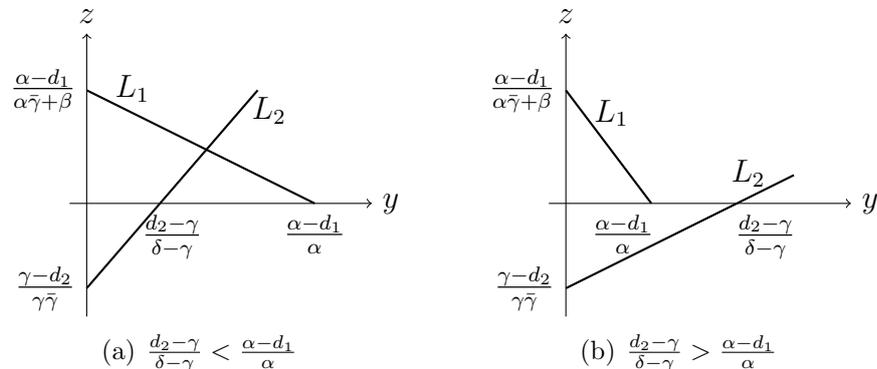


Figure 3.4: The two possible generic cases for the intersection of the two straight lines  $L_1$  and  $L_2$  for category (IV).

there are two generic cases as shown in Figure 3.4. In Figure 3.4(b), the inequality  $(\alpha - d_1)/\alpha < (d_2 - \gamma)/(\delta - \gamma)$  is equivalent to (2.7) hence  $E_{xy}$  is asymptotically stable. The other case of category (IV) is similar, so we summarize the results of stability of the boundary equilibria and the existence of a positive equilibrium of category (IV) 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  $\lim_{t \rightarrow \infty} z(t) = 0$  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,

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

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

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

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  $x(t) \geq \varepsilon$  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  $y(t) \geq \varepsilon$  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  $\mathbf{q} \in H_3 \cap \omega(\mathbf{p})$ . By Proposition 2.2 (iii), the solution  $\phi(t; \mathbf{q})$  approaches  $E_x$  as  $t$  approaches infinity. Hence  $E_x \in \omega(\mathbf{p})$ . The remaining arguments are similar, so we omit them. However, if  $y(t) \geq \varepsilon$  for all  $t$  then  $z(t)$  approaches zero as  $t$  approaches  $\infty$ . Similar arguments are omitted. We complete the proof.  $\square$

**Proposition 3.5.** *Let assumption (A1) hold and parameters be of category (IV). In case (a) of Table 4.2, that is,  $\frac{\alpha - d_1}{\alpha} > \frac{\gamma - d_2}{\gamma - \delta}$  and  $\frac{\alpha - d_1}{\alpha\gamma + \beta} > \frac{\gamma - d_2}{\gamma\bar{\gamma}}$ , if  $\beta$  and  $\bar{\gamma}$  are small enough, then the equilibrium  $E_*$  is globally asymptotically stable.*

*Proof.* Note that first the condition  $\frac{\alpha - d_1}{\alpha} > \frac{\gamma - d_2}{\gamma - \delta}$  implies that the reversed (2.7) 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 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

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

if  $\bar{\gamma}$  and  $\beta/\alpha$  are small enough. Let

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

By tedious computations, we obtain

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

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

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

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

or in this form

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

Hence the values  $x - x_*$  and  $z - z_*$  of orbits of (1.2) which are invariant in  $M$  must be the same sign or 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

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

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

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

if  $\gamma(x - x_*) + \delta(y - y_*) \neq 0$ . It is clear that solutions of (1.2) 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 (1.2) 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  $x(t)$  and  $z(t)$ -coordinates of solution of (1.2) are decreasing for all time. But there is only one equilibrium  $E_*$  on  $M$ , solutions of (1.2) 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.  $\square$

## 3.5 Dynamics of the Positive Equilibrium

Note that all global dynamics of (1.2) 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 (1.2) with parameters in these three regions. We show an analytical result in which system (1.2) is uniformly persistent and present some numerical simulations.

### 3.5.1 Uniform Persistence

First, we present a typical picture, Figure 3.5, of  $\gamma$ - $\delta$  parameter space with fixed  $\alpha$ ,  $\beta$ ,  $d_1$ ,  $d_2$  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

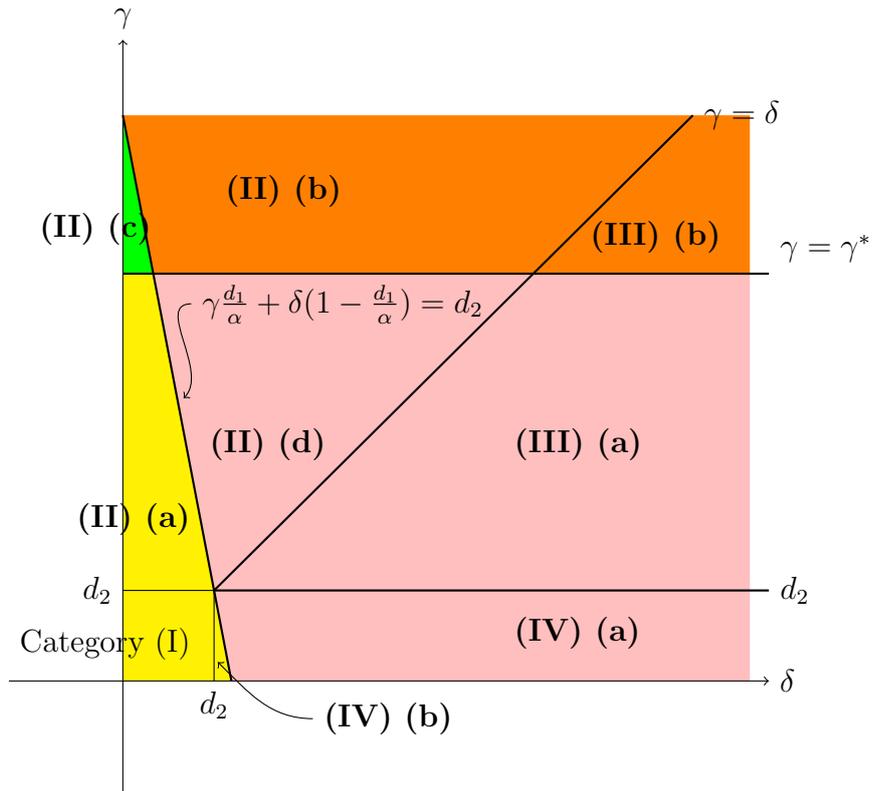


Figure 3.5: A typical picture of parameter space with various  $\gamma$ ,  $\delta$ , and fixed  $d_1$ ,  $d_2$ ,  $m_1$ ,  $m_2$ ,  $\alpha$ ,  $\beta$  with  $\alpha > d_1$ .

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).

solutions of (1.2) 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,

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

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

We indicate the dynamics of each region of parameter space with different color. First, in the gray region species  $y$  and  $z$  die out by Proposition 3.1; in the yellow regions species  $z$  dies out eventually because of results in Propositions 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.

Now we are the position to show that system (1.2) with parameters in the pink region is uniformly persistent. It is easy to check that system (1.2) is

persistent by the results of [6]. Moreover, we now have the following results on the uniform persistence of system (1.2) (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 (1.2) 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 it 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 the  $z$  coordinate of a tangent vector of its unstable manifold is non-zero. To simplify the notations, let  $E_{xy} = (d_1/\alpha, 1 - d_1/\alpha, 0) = (x_1, y_1, 0)$  and  $p = -d_2 + \gamma \frac{d_1}{\alpha} + \delta \left(1 - \frac{d_1}{\alpha}\right) > 0$ . Then the Jacobian of  $E_{xy}$  (2.6) 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 linear equations

$$\begin{aligned} -x_1 u - x_1 v - \bar{\gamma} x_1 w &= pu \\ \alpha y_1 u - \beta y_1 w &= pv. \end{aligned}$$

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  $2 \times 2$  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.  $\square$

**Lemma 3.8.** *If assumption (A1) and  $d_2 < \gamma < \gamma^*$  hold, then the semi-trivial equilibrium  $E_{xz}$  exists and it 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.  $\square$

**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. And 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.  $\square$

*Proof of Proposition 3.6.* Our strategy is to use the main result in [5] to verify the uniform persistence of (1.2). It is sufficient to show that the boundary of the first octant for the solution of (1.2) is isolated and acyclic.

The parameters which satisfy the assumptions are exactly in the interior of the pink region of Figure 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 stable 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  $E_{xy}$ ,

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

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  $E_{xy}$ ,

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

or a chain from  $E_0$  to  $E_{xz}$ ,

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

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.  $\square$

### 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

$$\alpha\bar{\gamma}\delta > \gamma\beta \quad (3.10)$$

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  $\lambda = a + bi$ ,

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

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

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

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

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

Hence we obtain one negative real eigenvalue and two purely imaginary eigenvalues. Let  $\mu$  be a parameter,  $x_*$ ,  $y_*$ , and  $z_*$  depend on  $\mu$ , 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  $\frac{da}{d\mu}\big|_{\mu=\bar{\mu}} \neq 0$ . Differentiating (3.12) with respect to  $\mu$  and solving linear system of  $\frac{da}{d\mu}\big|_{\mu=\bar{\mu}}$  and  $\frac{db}{d\mu}\big|_{\mu=\bar{\mu}}$ , we obtain

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

where the function

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

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 equations (3.2) and (3.3), we can find the positive equilibrium explicitly,

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

It is possible to set  $\mu$  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  $A y_* z_* - F(x_*(\bar{\delta}), y_*(\bar{\delta}), z_*(\bar{\delta})) = 0$  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 respect to parameter  $\delta$ . Choose parameter values as follows:

$\alpha$	$\beta$	$\gamma$	$\bar{\gamma}$	$d_1$	$d_2$
2.5	0.2	0.25	1.0	0.4	0.24

(3.16)

The graph of  $\bar{F}$ , Figure 3.6, can be obtained by vary  $\delta$  from 1.5 to 3.5 and calculating the value of the function  $\bar{F}$  in (3.14) with respect to  $\delta$ . Since the function  $\bar{F}$  is negative if and only if the inequality (3.6) holds, the

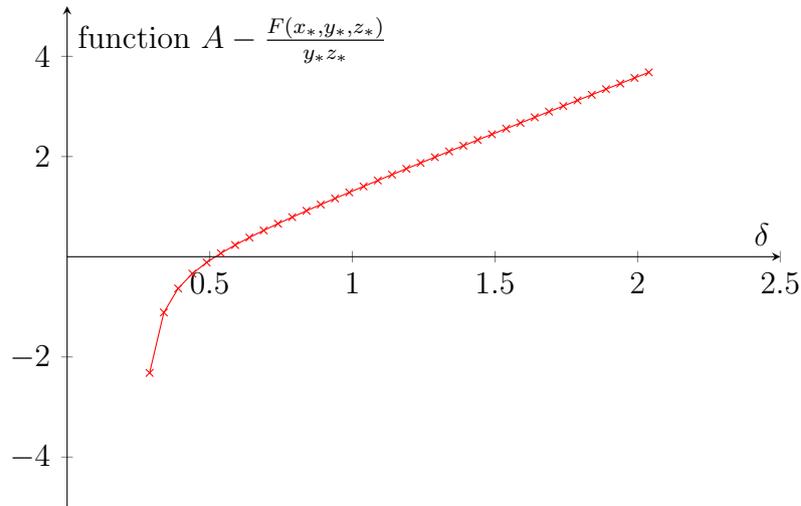


Figure 3.6: The graph of the function  $\bar{F}$  in terms of  $\delta$ .

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 (1.2) at  $\delta = 0.25, 1.0$  are performed and presented in the Figure 3.7 (a) and (b), respectively. We can see that the positive equilibrium is asymptotically stable (see Figure. 3.7 (a)) if  $\delta = 0.25$ . Now, using  $\delta$  as a bifurcation parameter, increase  $\delta$  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 Figure 3.7 (b)).

### 3.5.3 Chaos

In this section, some numerical simulations are presented to show the chaotic phenomena. 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  $\beta$  varies from 0.2 to 0.06 with stepsize -0.0001. **The parameters are in case (a) of Table ??**. We fix all parameters mentioned above and use  $\beta$  as the bifurcation parameter. A bifurcation diagram is drawn in Figure 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.

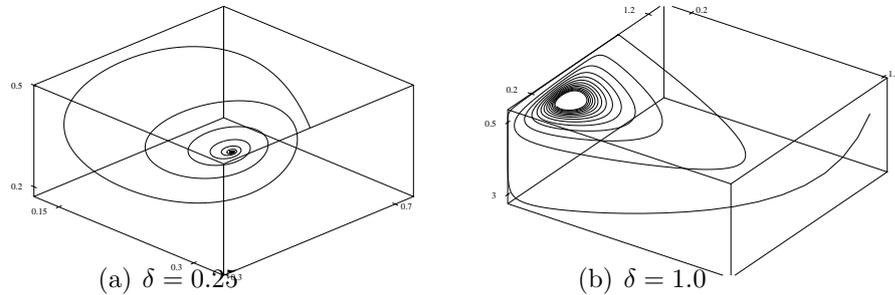


Figure 3.7: (a) The coexistence state is asymptotically stable when  $\delta = 0.25$ . (b) A periodic solution bifurcates from the coexistence state via Hopf bifurcation when  $\delta = 1.0$ .

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.

## 4 Comparison of Omnivory Models to Food Chain and Two Predators-One Prey Models

In this section, we rewrite system (1.2) in the following form

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

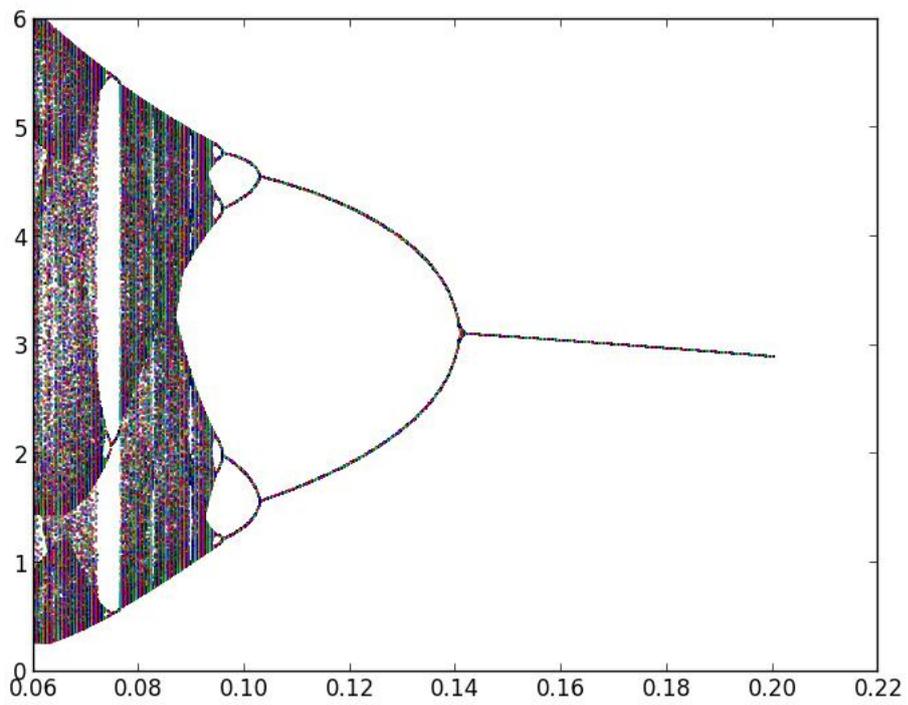


Figure 3.8: The numerical simulation of a period-doubling cascade when the bifurcation parameter  $\beta$  varies from 0.2 to 0.06.

where  $s$  and  $\mu$  are scaling parameters of  $\bar{\gamma}$ ,  $\gamma$  and  $\beta$ ,  $\delta$ , respectively. It is clear that if set  $\gamma = 0$  then system (4.1) is 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 set  $\delta = 0$  then system (4.1) is 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  $\gamma$  and  $\delta$  are taken as the factors of the species  $z$  how general it is. Since the species  $z$  is actually a specialist predator when either  $\gamma$  or  $\delta$  is equal to zero.

Before comparing the dynamics of 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  $\bar{E}_{xy}$  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  $\lim_{t \rightarrow \infty} y(t) = 0$  and  $\lim_{t \rightarrow \infty} z(t) = 0$ . 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 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  $\lim_{t \rightarrow \infty} z(t) = 0$ . Moreover, the equilibrium  $E_{xy}$  is globally asymptotically stable.*

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

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

Hence  $z(t)^{1/\delta} y(t)^{1/\alpha} x(t) \rightarrow 0$  as  $t \rightarrow \infty$ . Applying McGehee Lemma and similar arguments in Proposition 2.4, we can show that  $\lim_{t \rightarrow \infty} z(t) = 0$ . 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.  $\square$

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 equation (4.4) is equivalent to

$$1 > \frac{d_1}{\alpha} + \frac{d_2}{\delta} \quad (4.4)$$

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 Lyapunov function

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

Along the trajectories of system (4.2) we have

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

Then  $dV/dt \leq 0$  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.  $\square$

We summarize the results on the dynamics of (4.2) in Table 4.2 and a picture of the parameter space of (4.2) with various  $\alpha$ ,  $\delta$  and fixed  $d_1$ ,  $d_2$ ,  $\beta$  is presented in Figure 4.1.

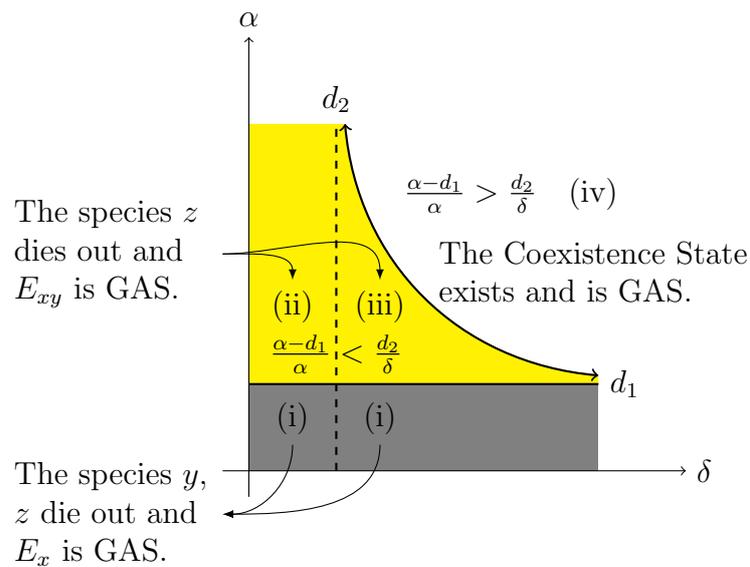
## 4.2 Dynamics of Two Predators-One Prey Model (4.3)

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

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

cases	$\bar{E}_{xy}$	$\bar{E}_*$	global dynamics
FI : $\alpha \leq d_1$	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.

Figure 4.1: The parameter space and its corresponding dynamics of (4.2) with various  $\alpha, \delta$  and fixed  $d_1, d_2, \beta$ .

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

**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.  $\square$

We summarize the results of dynamics of (4.3) in the Table 4.2 and a picture of parameter space of (4.2) with various  $\alpha$ ,  $\gamma$  and fixed  $d_1$ ,  $d_2$ ,  $\beta$  is presented in Figure 4.1.

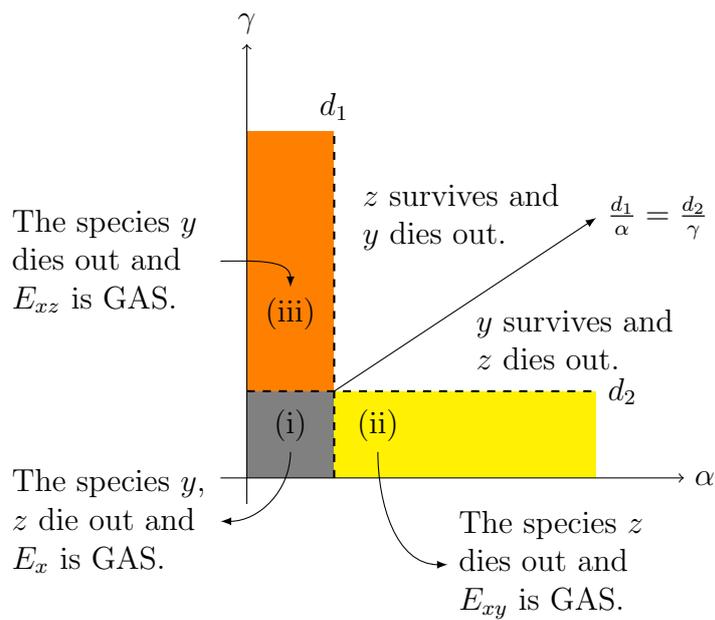
### 4.3 Food Chain, Two Predators-One Prey and Omnivory Models

Now we are in the position to compare these three models.

First, we note that there are more rich dynamics of (1.2) than the other two models, (4.2) and (4.3). Let us re-examine the biological meaning of

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

cases	$\tilde{E}_{xy}$	$\tilde{E}_{xz}$	global dynamics
T I : $\alpha \leq d_1, \gamma \leq d_2$	does not exist	does not exist	$y, z$ die out $E_x$ is GAS.
T II : $\alpha > d_1, \gamma \leq d_2$	stable	does not exist	$z$ die out $E_{xy}$ is GAS.
T III : $\alpha \leq d_1, \gamma > d_2$	does not exist	stable	$y$ die out $E_{xz}$ is GAS.
T IV : $\alpha > d_1, \gamma > d_2$ $\frac{d_1}{\alpha} > \frac{d_2}{\gamma}$	unstable	stable	$y$ dies out $E_{xz}$ is GAS.

Figure 4.2: The parameter space and its corresponding dynamics of (4.2) with various  $\alpha, \delta$  and fixed  $d_1, d_2, \beta$ .

model (4.2) in the parameter space, Figure 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 region (ii) and (iii), the species  $z$  dies out due to the high mortality  $d_2$  and low conversion rate  $\delta$  of species  $z$ , respectively (Proposition 4.2). Finally, the species can coexist if inequality (4.4) holds. Similarly, we re-examine the parameter space of the model (4.3), Figure 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 who with lower death rate or higher conversion rate can win and survive.

A fundamental difference between the omnivory model (1.2) 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 (1.2) can be found in the state of 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, Figure 4.3, of  $\alpha$ - $\gamma$ - $\delta$ -parameter space to interpret the relations of these three models. Figure 4.2 is put on the left two-dimensional plane of Figure 4.3 which is presented the dynamics of model (4.3) and denoted by “ $\alpha$ - $\gamma$  plane”. Similarly, Figure 4.1 is put on the under two-dimensional plane of Figure 4.3 which denoted by “ $\alpha$ - $\delta$  plane”. Finally, we put Figure 3.5 on the  $\gamma$ - $\delta$  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 trophic level. Using a non-dimensional scaling model with seven parameters, all possible dynamics of (1.2) are clarified and classified theoretically and numerically. We

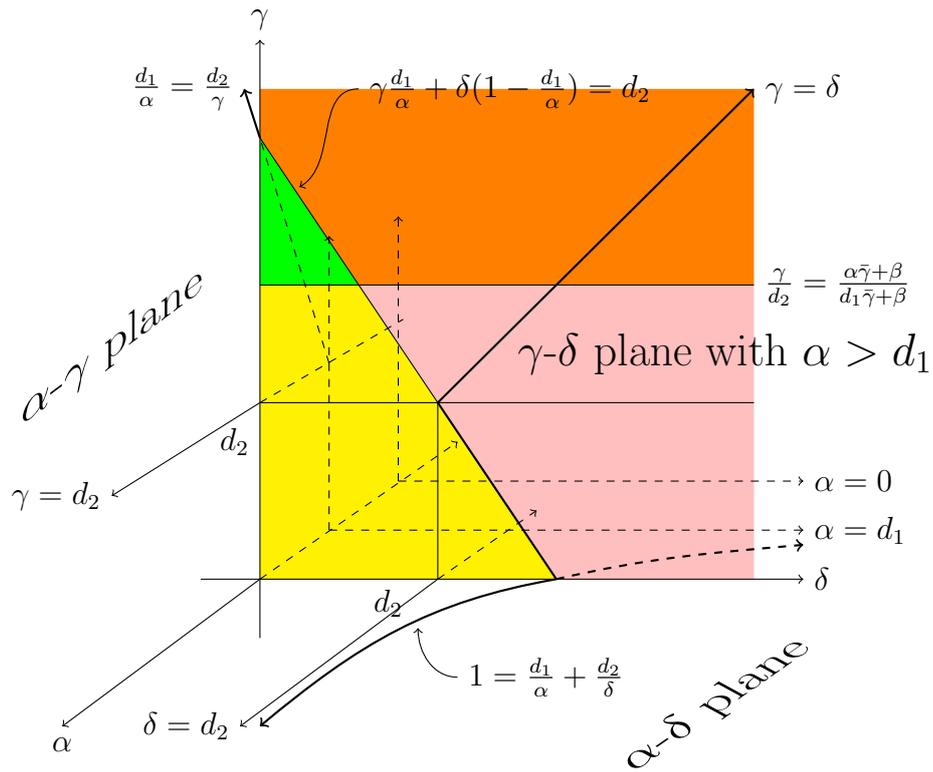


Figure 4.3: Relations of the these food chain.

not only analyze the model (1.2) but also find the connections of three basic models (1.2), (4.2), (4.3) by two factors  $s$  and  $\mu$ .

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

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

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 conversion rate for species  $y$  ( $a_{23}/a_{21}$ ).

First, for the two predators-one prey model (4.3), it happens exploitative competition between 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 than 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 than 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 the mortality, i.e.  $\alpha > d_1$  and  $\delta > d_2$ , then they coexist if the resource exploitation ( $d_1/\alpha$ ) is good for  $y$  and the conversion efficiency ( $d_2/\delta$ ) is excellent for  $z$ . Hence the inequality (4.4) guarantees the existence and globally asymptotical stability of positive equilibrium.

Next, let us look at the omnivory model (1.2) and  $\gamma$ - $\delta$  plane of Figure 4.3 carefully. The straight line

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

of the  $\gamma$ - $\delta$  plane which connects the straight line  $d_1/\alpha = d_2/\gamma$  of left  $\alpha$ - $\gamma$  plane and the curve  $1 = \frac{d_1}{\alpha} + \frac{d_2}{\delta}$  of the bottom  $\alpha$ - $\delta$  plane separates the whole  $\gamma$ - $\delta$  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 conversion efficiency of  $z$ . If the resource exploitation of  $y$  is inferior ( $d_1/\alpha$  is large) and the conversion efficiency of  $z$  is excellent ( $\delta$  is large), then parameters fall into the right hand side. So the dynamics of model (1.2) is that  $z$  will persist (the orange and pink regions). The horizontal line

$$\frac{\gamma}{d_2} = \frac{\alpha\bar{\gamma} + \beta}{d_1\bar{\gamma} + \beta} \quad (5.2)$$

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  $\beta$  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 than  $y$ . On the contrary, all species coexist in the pink regions. This result has been indicated in [10] which states that model (1.2) 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 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 in 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 than  $y$ . So the advance in this point can be eliminated by large amount of species  $y$ . Therefore, the solution will approaches to  $E_{xy}$  eventually if the population of species  $z$  is rare. And the other symmetric case can be argued similarly. This mathematical result and biological interpretations has not been reported so far in our best knowledge.

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

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

and an IGP model with generalist predator :

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

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 the theoretical analysis and numerical simulations, they will get 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 [R. Holt & G. Polis Am. Nat. 1997].
3. The IGP model with 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 in functional response but also nonlinear interactions of our model (1.1) are more simple than Kang's. But we still obtain a periodic solution and very complex dynamics. We suggest that the complex dynamics are due to the impact of presentation of a generalist predator rather than the complexity of functional response II/III.

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  $\gamma$  effect 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 (1.2) Proposition 3.6, if parameters are in the pink region of Figure 3.5 then all solutions of (1.2) with positive initial conditions are in a bounded set of first octant and  $\varepsilon$ -away from  $xy$ ,  $yz$ , and  $xz$ -planes for some positive number  $\varepsilon$ . We have showed global stability of  $E_*$  for some parameters in 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  $\gamma$  and  $\delta$  in the pink region of Figure 3.5.

And 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

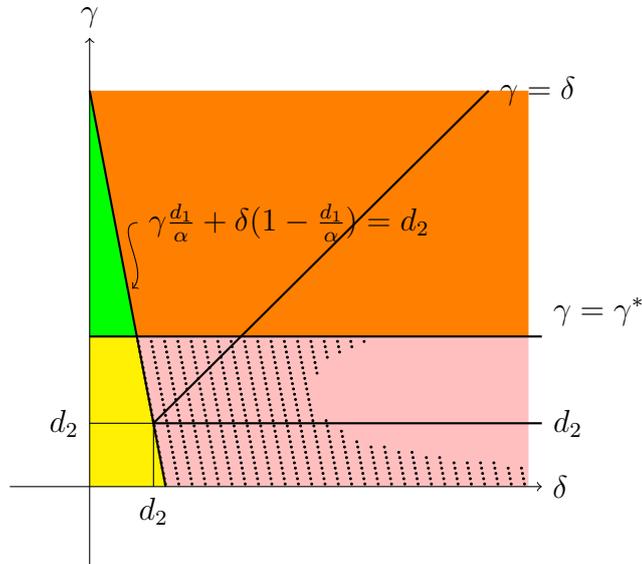


Figure 5.1: A typical picture of parameter space with variously  $\gamma$ ,  $\delta$ , and fixed  $d_1$ ,  $d_2$ ,  $m_1$ ,  $m_2$ ,  $\alpha$ ,  $\beta$  with  $\alpha > d_1$ .

of the inequalities

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

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

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

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## 國科會補助專題研究計畫出席國際學術會議心得報告

日期：102 年 9 月 2 日

計畫編號	NSC 102-2115-M-032 -004 -		
計畫名稱	三物種的捕食與被捕食模型, 在不同的反應函數下的全域動態行為和分歧研究。		
出國人員姓名	楊定揮	服務機構及職稱	淡江大學數學系
會議時間	102 年 8 月 26 日至 102 年 8 月 29 日	會議地點	德國 Osnabruck
會議名稱	(中文) 2013 動物數量及生態模型國際會議 (英文) International Conference MPDE'13 Models in Population Dynamics and Ecology		
發表題目	(中文) 三物種雜食性 L-V 類食物網模型的動態行為及為什麼須要雜食性? (英文) Dynamics of Three Species Lotka-Volterra Food Web Models with Omnivory and Why Omnivory ?		

## 一、參加會議經過：

此會議是由 Ecological Society of Europe 所舉辦的每年一次的生態會議，。

## 二、與會心得：

這是一個由歐洲生物數學協會每年舉辦一次的大型國際生態及數學建模會議，每年都吸引了不少國際知名學者參與，例如今年會議參與人員有，日本明治大學的 Prof. Mimura (日本生物數學協會主席)，U. C. Davis 大學的 Prof. Alan Hasting，主要都是正在 Mathematical Biology 領域非常活躍，而且與我領域高度相關的研究者，尤其是這一次認識了台灣的一位學者在德國 Dresden 的 Max Planck Institute for the Physics of Complex Systems 的博士後研究 Dr. Lin, Yen-Ting，與他深入討論許多有趣的 Predator-prey 生態模型。

在台灣年輕的數學家在國際科學社群，與其他領域的人應該要有更多的交流與參與，以擴大他們的觀點和知識。因此，我出席這次國際生態及數學建模會議，有很大的科學價值，並且與許多學者的深入討論，給我許多深刻的印象，啟發許多的靈感及想法。

最後，我要感謝國家科學基金委員會的慷慨支持，讓我能出席本次會議。

### 三、發表論文全文或摘要：

標題：Dynamics of Three Species Lotka-Volterra Food Web Models with Omnivory and Why Omnivory ?

摘要：In this work, we consider a three species Lotka-Volterra food web model with omnivory. Based on a non-dimensional transformation, the system is a model of three equations of first order ordinary differential equations with seven parameters. The model with some suitable parameters can be seen as a food chain model or a two predator-one prey model.

The difficulties are that a predator-prey ecological model is not monotonic and the classical Poincare-Bendixson Theorem cannot be applied. However, we completely classify the parameter space into eight cases of four categories and determine global dynamics analytically for six cases. For some particular parameters, we show that the Hopf bifurcation occurs and some chaotic phenomena are presented numerically. Finally, we interpret the biological meanings of our numerical results. Moreover, we compare three predator-prey models, omnivory models, food chain models and two predator-one prey models, with a omnivorous effect.

### 四、建議：

### 五、攜回資料名稱及內容

### 六、其他

# 科技部補助計畫衍生研發成果推廣資料表

日期:2014/09/25

科技部補助計畫	計畫名稱: 3物種的捕食與被捕食模型, 在不同的反應函數下的全域動態行為和分歧研究。
	計畫主持人: 楊定揮
	計畫編號: 102-2115-M-032-004- 學門領域: 常微分方程
無研發成果推廣資料	

102 年度專題研究計畫研究成果彙整表

計畫主持人：楊定揮		計畫編號：102-2115-M-032-004-				計畫名稱：3 物種的捕食與被捕食模型，在不同的反應函數下的全域動態行為和分歧研究。	
成果項目		量化			單位	備註（質化說明：如數個計畫共同成果、成果列為該期刊之封面故事...等）	
		實際已達成數（被接受或已發表）	預期總達成數（含實際已達成數）	本計畫實際貢獻百分比			
國內	論文著作	期刊論文	0	0	100%	篇	
		研究報告/技術報告	0	0	100%		
		研討會論文	0	0	100%		
		專書	0	0	100%		
	專利	申請中件數	0	0	100%	件	
		已獲得件數	0	0	100%		
	技術移轉	件數	0	0	100%	件	
		權利金	0	0	100%	千元	
	參與計畫人力（本國籍）	碩士生	0	0	100%	人次	
		博士生	0	0	100%		
博士後研究員		0	0	100%			
專任助理		0	0	100%			
國外	論文著作	期刊論文	1	1	100%	篇	
		研究報告/技術報告	0	0	100%		
		研討會論文	0	0	100%		
		專書	0	0	100%	章/本	
	專利	申請中件數	0	0	100%	件	
		已獲得件數	0	0	100%		
	技術移轉	件數	0	0	100%	件	
		權利金	0	0	100%	千元	
	參與計畫人力（外國籍）	碩士生	2	2	100%	人次	
		博士生	0	0	100%		
博士後研究員		0	0	100%			
專任助理		0	0	100%			

<p style="text-align: center;">其他成果</p> <p>(無法以量化表達之成果如辦理學術活動、獲得獎項、重要國際合作、研究成果國際影響力及其他協助產業技術發展之具體效益事項等，請以文字敘述填列。)</p>	<p style="text-align: center;">無</p>
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	成果項目	量化	名稱或內容性質簡述
科 教 處 計 畫 加 填 項 目	測驗工具(含質性與量性)	0	
	課程/模組	0	
	電腦及網路系統或工具	0	
	教材	0	
	舉辦之活動/競賽	0	
	研討會/工作坊	0	
	電子報、網站	0	
	計畫成果推廣之參與(閱聽)人數	0	

# 科技部補助專題研究計畫成果報告自評表

請就研究內容與原計畫相符程度、達成預期目標情況、研究成果之學術或應用價值（簡要敘述成果所代表之意義、價值、影響或進一步發展之可能性）、是否適合在學術期刊發表或申請專利、主要發現或其他有關價值等，作一綜合評估。

1. 請就研究內容與原計畫相符程度、達成預期目標情況作一綜合評估

達成目標

未達成目標（請說明，以 100 字為限）

實驗失敗

因故實驗中斷

其他原因

說明：

2. 研究成果在學術期刊發表或申請專利等情形：

論文： 已發表  未發表之文稿  撰寫中  無

專利： 已獲得  申請中  無

技轉： 已技轉  洽談中  無

其他：（以 100 字為限）

3. 請依學術成就、技術創新、社會影響等方面，評估研究成果之學術或應用價值（簡要敘述成果所代表之意義、價值、影響或進一步發展之可能性）（以 500 字為限）