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遷徙的競爭種群之全局動態

Global Dynamics for Lotka-Volterra Competition Systems with Constant Dispersal

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中 華 民 國 一 百 零 一 年 六 月

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遷徙的競爭種群之全局動態

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摘 要

在這篇論文中，我們回顧了幾篇文獻資料是關於生態數學裡，Lotka - Volterra 模型以及有關物種的補丁模型(Patch model)的動態現象。關於多個物種互動的補丁模型，我們研究 S. A. Gourley 和 Y. Kuang 在 2005 年提出的兩個尚未解決的問題，這是探討遷徙率如何影響兩競爭物種的補丁模型的動態，與其物種的成長率分佈有關。據推測，在一個高度遷徙的環境中，物種的制勝策略取決於在某個單一補丁的成長率。也就是說，物種在其中一個補丁具有最大的成長率就獲勝。另一方面，在足夠小的遷徙率下可能會出現全局穩定的共存態。雖然我們還沒有解決這兩種全局動態的猜想，但在這些問題上已有更好的了解。

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Abstract

In this thesis, we review the investigations of dynamics for Lotka Volterra models and patch models in mathematical ecology. We study two open questions posed by Gourley and Kuang in 2005, which are concerned with how dispersal rates affect the competition in two-species patch model with various spatial distribution of their growth rate. It was conjectured that, in a high dispersal environment, the winning strategy for species depends on the growth rate in a single patch. That is, the species which has the greatest growth rate will win. On the other hand, the system may have a globally asymptotically stable positive equilibrium for a small enough dispersal rate. We have not solved the conjectures, but have better understanding on these issues.

Contents

1 Introduction

In this thesis, we mainly introduce some basic model in mathematical ecology and investigate their dynamics. In 1838, Verhulst, a Belgium mathematician, presented the logistic equation to describe the self-limiting growth of a biological population

$$\frac{dx}{dt} = rx(1 - \frac{x}{K}), \tag{1.1}$$

where the constant r is called the intrinsic growth rate and K is the carrying capacity due to the limited resource supply, such as food, nutrients, space, and so on. The biological meaning is that populations with interaction among individuals will control their reproduction. Lotka derived the equation again in 1925, calling it the law of population growth. The Lotka Volterra system, developed independently by Lotka (1925) and Volterra (1926), which be used to model the dynamics of ecological systems with predator-prey interactions.

$$\begin{aligned} \frac{dx}{dt} &= \alpha x - \beta xy, \\ \frac{dy}{dt} &= \gamma xy - \delta y, \end{aligned} \tag{1.2}$$

x is the population density of prey and y is the population density of predator. With the basic of logistic equation, the form is similar to the Lotka Volterra equations for predation is that equation for two similar species competing for a common limited resource. Assume that the population grew up logistically in the absence of the other, and reduce each others growth rates and saturation population by their competitive behavior. That is so-called Lotka Volterra competition system

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1 (1 - \frac{x_1}{K_1}) - \alpha x_1 x_2, \\ \frac{dx_2}{dt} &= r_2 x_2 (1 - \frac{x_2}{K_2}) - \beta x_1 x_2, \end{aligned} \tag{1.3}$$

where all parameters are positive, x_i is the population of i-th competing species. The ith species grows logistically with intrinsic rate r_i in the absence of the other, K_i is the carrying capacity of x_i and α, β are the interspecific competition coefficients.

In section 2, we will discuss the dynamics of the Lotka-Volterra competition system. The stability for the coexistence of system (1.3) can be determined by the conditions obtained by the graphical method (Rosenzweig and MacArthur 1963, MacArthur and Wilson 1967, Pielou 1969, Slobodkin 1962)[12, 14, 16]. The graphical analysis suggests that for two competing species, its local stability can imply the global dynamics. But this result is not necessarily true for more than two species and two species model under other interactions. In 1968, Levins, a mathematical ecologist, determined the local stability of the equilibrium for n species competition model by a necessary condition that the determinant of the matrix of competition coefficients is positive. Strobeck (1973) presented a necessary and sufficient condition for the local stability of coexistence of the n species competition model [17]. In 1975, May and Leonard studied the three competing species model, with a symmetric assumption of their competing parameters, which has a special class of periodic limit cycle solutions and a general class of non periodic oscillations of bounded amplitude but ever increasing cycle time [11]. And the proof of the general class had been modified by Schuster, Sigmund and Wolff (1979) [18]. Zhang and Chen (2000) discussed each cases of the assumption of parameters and presented some necessary and sufficient conditions for the global dynamics of the positive equilibrium, a family of limit cycle or a heteroclinic cycle [23]. It shows that, the systems with three or more dimensions must have much richer dynamical behaviors.

In addition to the competition model, we considered other types of model such as predator-prey or mutualism(cooperation), etc. And more, we want to know the global dynamics for n species Lotka-Volterra models. Consider the following system

$$\frac{dx_i}{dt} = x_i(b_i + \sum_{j=1}^{n} a_{ij}x_j), i = 1, \ldots, n, \tag{1.4}$$

In general, system (1.4) whose nontrivial equilibrium is locally stable may not be globally stable. By means of Lyapunov theory, we can guarantee the global dynamics for system (1.4). So far, most of results about the coexistence have been proposed. In 1977, Goh presented a sufficient condition to guarantee the global stability of positive equilibrium for the Lotka-Volterra model. Herein, the appropriate form of Lyapunov function as follows

$$V = \sum_{i=1}^{n} c_i \left[x_i - x_i^* - x_i^* \ln(\frac{x_i}{x_i^*}) \right]. \tag{1.5}$$

In particular, for two species interactions, the conditions can be reduced to its local stability and both species sustain the density-dependent mortalities due to intraspecific interactions, that is, $a_{11}, a_{22} < 0$. And for two species competition or mutualism system, the conditions of local stability implies directly $a_{11}, a_{22} < 0$. That is, the local dynamics of coexistence for two species competition or mutualism system guarantees their global dynamics. In the end of section 2, we introduced some interesting results between the competition and mutualism system which are proposed by Goh(1979) [3, 4, 5].

Biological dispersal refers to that species move from one habitat patch to another, the reasons leading to this phenomenon not only for individual fitness, but also for population dynamics, and species distribution. To understand dispersal and the evolutionary strategies, in section 3, we considered the dynamics of the Lotka-Volterra system with dispersal, for short, called patch model

$$\frac{du_i^k}{dt} = u_i^k(r_i + \sum_{j=1}^{n} a_{ij}u_j^k) + \sum_{l=1, l\neq k}^{m} (D_i^{kl}u_i^l - D_i^{lk}u_i^k), \tag{1.6}$$

$i = 1, \ldots, n, k = 1, \ldots, m$, where u_i^k is the population of species i in patch k, D_i^{kl} describes the dispersal coefficients from patch l to patch k. The forms like (1.6) have been studied by Levin (1974), Chewning (1975), Segel and Levin(1976). Hastings (1978) gave a sufficient conditions to the global stability of the coexistence for system (1.6). This result showed that the dynamics can not be changed for any dispersal rate if the coexistence always exists. In particular, in 1982, Hastings proved that the positive equilibrium for a single species patch model is locally stable under the sufficient large dispersal environment [7]. Dispersal is seem to have a stabilizing effect. Takeuchi (1989) had proposed such problem that whether the positive equilibrium, which the value can be changed by dispersal rate, continues to be positive and globally stable if we increasing the dispersal rates ? For two species cooperative patch model, Freedman, Rai and Waltman (1986) showed that there is a positive equilibrium for any dispersal rates, and which is globally stable if it is unique. Padron (2007) had proved the existence and uniqueness a positive equilibrium for single species patch model [15].

A coupled system of a nonlinear differential equations can be used to model a patch system with dispersal rates. Li and Shuai (2010) presented a systematic approach to construct Lyapunov function for coupled system. Assume that, when isolated, each vertex system has a globally stable equilibrium and a globally defined Lyapunov function $V_i, i = 1, \ldots, n$. Then, for the coupled system, a global Lyapunov function be constructed in this form

$$V = \sum_{i=1}^{n} c_i V_i, \tag{1.7}$$

where $c_i \geq 0$ are suitable constants chosen from some graph theory and matrix analysis. In their article, they re-proved the similar result about single species patch model [9].

Gourley and Kuang (2005) studied the competition in two-species patch model that have identical competing coefficients and with various spatial distribution of their growth rate. They studied the dynamics of ODE system largely through the linearized analysis, showing that the winning strategy for species with a large dispersal rate is that which has the greatest growth rate in a single patch. They hypothesized that this may be a possible explanation for the evolution of grouping behavior in many species. However, they only complete the result of local stability and left two conjectures about the global dynamics in the end of article [2].

This thesis is organized as follows. In section 2, we review the dynamics for Lotka-Volterra systems, such as competition, mutualism, and predator-prey system. In Section 3, we study the dynamics for Lotka-Volterra model with diffusion, such as single species patch model and two species competition in two patch model. In section 4, we give some numerically examples for two species competition in two patch model and for other similar models with different dispersal rates. In the end, we review some results about above subsections, we write it in appendices.

2 Dynamics for Lotka-Volterra systems

In this section, we introduce the dynamics of Lotka-Volterra competition system. First, consider the Lotka-Volterra system for two competitive species,

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1 (1 - \frac{x_1}{K_1}) - \alpha x_1 x_2, \\ \frac{dx_2}{dt} &= r_2 x_2 (1 - \frac{x_2}{K_2}) - \beta x_1 x_2, \end{aligned} \tag{2.1}$$

where all parameters are positive, x_i is the population of ith competing species. We consider only nonnegative initial values $x_1(0) \geq 0, x_2(0) \geq 0$. If system (2.1) has a positive equilibrium, then the stability for the coexistence can be determined by the conditions obtained by the graphical method [12, 14, 16]. The graphical analysis suggests that for two competing species, local stability implies global stability. This result is not necessarily true for more than two species and two species model under other interactions. Here the question is what conditions guarantee the local stability of the Lotka-Volterra competition model with more than two species ? Moreover, how would one conclude the the global dynamics for other types of models such as predator-prey, amensalism or mutualism ? Does the local stability can guarantee the global dynamics ? The answer is no. Here we give a simple example to demonstrate that a locally stable equilibrium for a two species Lotka-Volterra model may not be globally stable.

Example 2.0.1.

$$\begin{aligned} \frac{dx_1}{dt} &= x_1(-2 + x_1 + x_2) \\ \frac{dx_2}{dt} &= x_2(5 - 3x_1 - 2x_2) \end{aligned} \tag{2.2}$$

The system has a positive equilibrium at $(1, 1)$. For the linearized system corresponding to (2.2) , the variational matrix at $(x_1, x_2) = (1, 1)$ is

$$\begin{bmatrix} 1 & 1 \\ -3 & -2 \end{bmatrix}. \tag{2.3}$$

Its eigenvalues are $\frac{-1 \pm \sqrt{3}i}{2}$. Hence we concluded that the equilibrium $(1, 1)$ is locally stable for the model (2.2). But the trajectory through the initial data $(2, 1)$ tends to $(\infty, 0)$.

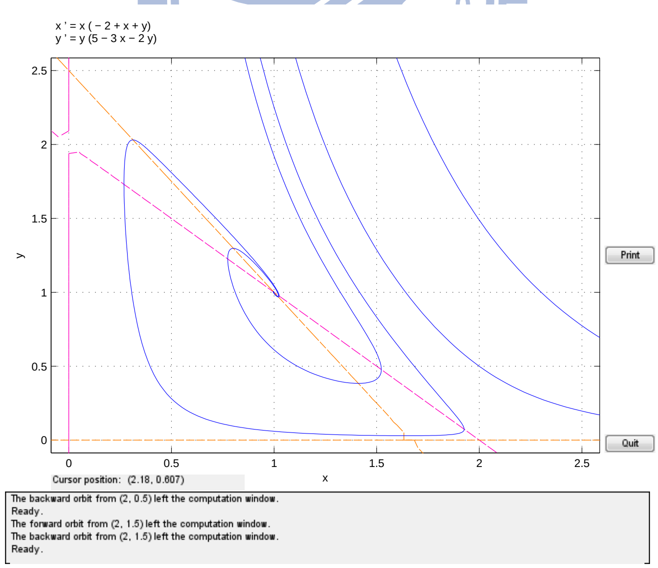

Figure 1: Illustrations for the dynamics of example 2.0.1.

In the following subsections, we review the results in the literature [3, 4, 5, 11, 17]. We review the local stability in n species competition system in subsection 2.1, three species competition system in subsection 2.2, global stability in two species under interaction in subsection 2.3, global stability in n species system in subsection 2.4, global stability in n species mutualism system in subsection 2.5.

2.1 n species competition systems - local stability

For $n > 2$, Strobeck (1973) derived the necessary and sufficient conditions to the local stability of coexistence for the following competition systems

$$\frac{dx_i}{dt} = \frac{r_i x_i}{K_i}(K_i - \alpha_{i1}x_i - \alpha_{i2}x_2 - \cdots - \alpha_{in}x_n), i = 1, \ldots, n, \tag{2.4}$$

where all parameters are positive, x_i is the population of i-th competing species, r_i is the intrinsic rate of growth, K_i is the carrying capacity of the i-th species and α_{ij} is the competition coefficients for j-th on i-th species, where $\alpha_{ii} = 1$ for all i. Assume that the system (2.4) has a positive equilibrium $E^* = (x_1^*, \ldots, x_n^*)$, which must be a solution of $\mathbf{A}(x_1^*, \ldots, x_n^*)^T = (K_1, \ldots, K_n)^T$,

$$\mathbf{A} = \begin{bmatrix} 1 & \alpha_{12} & \alpha_{13} & \ldots & \alpha_{1n} \\ \alpha_{21} & 1 & \alpha_{23} & \ldots & \alpha_{2n} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \alpha_{n1} & \alpha_{n2} & \alpha_{n3} & \ldots & 1 \end{bmatrix} \tag{2.5}$$

which has been called the community matrix by Levins (1968). The solution for $(x_1^*, \ldots, x_n^*)^T$ is given by Cramer's rule :

$$\begin{aligned} \tilde{x}_1 &= \det \begin{pmatrix} K_1 & \alpha_{12} & \alpha_{13} & \ldots & \alpha_{1n} \\ K_2 & 1 & \alpha_{23} & \ldots & \alpha_{2n} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ K_n & \alpha_{n2} & \alpha_{n3} & \ldots & 1 \end{pmatrix}, \ldots, \\ \tilde{x}_n &= \det \begin{pmatrix} K_1 & \alpha_{12} & \alpha_{13} & \ldots & K_1 \\ K_2 & 1 & \alpha_{23} & \ldots & K_2 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ K_n & \alpha_{n2} & \alpha_{n3} & \ldots & K_n \end{pmatrix} \end{aligned} \tag{2.6}$$

and $(x_1^*, \ldots, x_n^*)^T = \frac{1}{\det \mathbf{A}}(\tilde{x}_1, \ldots, \tilde{x}_n)^T$.

The following theorem give the necessary and sufficient condition for the local stability of E^* in system (2.4).

Theorem 2.1.1 (Strobeck, 1973). System (2.4) has a positive equilibrium which is stable if and only if $x_i^* > 0$ for all i and the corresponding linearized system satisfies the Routh-Hurwitz stability criterion.

Consider a linear system

$$\frac{d\mathbf{x}}{dt} = \mathbf{A}\mathbf{x}, \tag{2.7}$$

$\mathbf{A}$ is the Jacobian matrix about the equilibrium $\mathbf{x}^*$ and $\mathbf{x}(t_0) = \mathbf{x}_0$ is the initial data. By the theory of linearization for ordinary differential equation, the solution $\mathbf{x} = 0$ is linearly stable if and only if all eigenvalues of $\mathbf{A}$ have negative real part. Those eigenvalues are the roots of the characteristic polynomial of $\mathbf{A}$, which can be taken in this form

$$P(\lambda) = \lambda^n + a_1\lambda^{n-1} + a_2\lambda^{n-2} + \cdots + a_n, a_i \in \mathbb{R}, i = 1, \ldots, n. \tag{2.8}$$

Theorem 2.1.2 (Routh-Hurwitz stability criterion). The real part of each root for (2.8) is negative if and only if

$$\Delta_1 = a_1, \Delta_2 = \begin{vmatrix} a_1 & 1 \\ a_3 & a_2 \end{vmatrix}, \Delta_3 = \begin{vmatrix} a_1 & 1 & 0 \\ a_3 & a_2 & a_1 \\ a_5 & a_4 & a_3 \end{vmatrix}, \ldots,$$

and

$$\Delta_r = \begin{vmatrix} a_1 & 1 & 0 & 0 & \cdots & 0 \\ a_3 & a_2 & a_1 & 1 & \cdots & 0 \\ a_5 & a_4 & a_3 & a_2 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ a_{2r-1} & a_{2r-2} & a_{2r-3} & a_{2r-4} & \cdots & a_r \end{vmatrix}, r = 3, \ldots, n,$$

are all positive. If an element a_k appears in Δ_r with $k > r$, then it replaced by zero.

This theorem has many proofs, here we review the proof of Parks (1962)[13], the main idea of proof is to construct a matrix $\mathbf{B}$ such that $\mathbf{A}$ and $\mathbf{B}$ have the same characteristic polynomial and $\mathbf{B}$ satisfies the second method of Lyapunov.

Theorem 2.1.3. A necessary and sufficient condition for $\mathbf{x} = 0$ to be an asymptotically stable solution of (2.7) is that the matrix equation $\mathbf{PA} + \mathbf{A}^T\mathbf{P} = -\mathbf{Q}$ has a positive definite solution $\mathbf{P}$ for every positive definite matrix $\mathbf{Q}$.

That is, there is a positive definite matrix $\mathbf{P}$ such that $\mathbf{PB}+\mathbf{B}^T\mathbf{P}$ is negative definite. See [13] for the detail.

Example 2.1.4.

$$\begin{aligned}\frac{dx}{dt} &= x(1-x-ay)\\ \frac{dy}{dt} &= y(1-y-bx), a, b > 0.\end{aligned} \tag{2.9}$$

As $a, b < 1$, the system has a positive equilibrium $(x^*, y^*) = (\frac{1-a}{1-ab}, \frac{1-b}{1-ab})$. By the linearization theory, the variational matrix at $(x, y) = (x^*, y^*)$ is

$$\begin{bmatrix} 1-2x^*-ay^* & -ax^* \\ -by^* & 1-2y^*-bx^* \end{bmatrix}. \tag{2.10}$$

The characteristic polynomial of variational matrix at $(x^*, y^*) = (\frac{1-a}{1-ab}, \frac{1-b}{1-ab})$ is

$$P(\lambda) = \lambda^2 + (\frac{2-a-b}{1-ab})\lambda + \frac{(1-a)(1-b)}{1-ab}. \tag{2.11}$$

By the Routh-Hurwitz stability criterion,

$$\begin{aligned}\Delta_1 &= a_1 = \frac{2-a-b}{1-ab} > 0,\\ \Delta_2 &= \begin{vmatrix} a_1 & 1 \\ 0 & a_2 \end{vmatrix} = a_1a_2 = \frac{(2-a-b)(1-a)(1-b)}{(1-ab)^2} > 0,\end{aligned} \tag{2.12}$$

Hence, we can deduced that all eigenvalues of $\mathbf{A}(x^*, y^*)$ have negative real parts.

2.2 Three species competition systems

Consider model (2.4) with $n = 3$, we have

$$\begin{aligned}\frac{dx_1}{dt} &= \frac{r_1x_1}{K_1}(K_1 - x_1 - \alpha_{12}x_2 - \alpha_{13}x_3),\\ \frac{dx_2}{dt} &= \frac{r_2x_2}{K_2}(K_2 - \alpha_{21}x_1 - x_2 - \alpha_{23}x_3),\\ \frac{dx_3}{dt} &= \frac{r_3x_3}{K_3}(K_3 - \alpha_{31}x_1 - \alpha_{32}x_2 - x_3).\end{aligned} \tag{2.13}$$

Assume $r = r_i, K = K_i, i = 1, 2, 3$ and $\alpha_{12} = \alpha_{23} = \alpha_{31} = \alpha, \alpha_{21} = \alpha_{32} = \alpha_{13} = \beta$. We rescale the parameter by $\hat{x}_i = \frac{x_i}{K}, i = 1, 2, 3$ and $\hat{t} = rt$. Substituting into (2.13) and dropping the hat, we have

$$\begin{aligned}\frac{dx_1}{dt} &= x_1(1 - x_1 - \alpha x_2 - \beta x_3),\\ \frac{dx_2}{dt} &= x_2(1 - \beta x_1 - x_2 - \alpha x_3),\\ \frac{dx_3}{dt} &= x_3(1 - \alpha x_1 - \beta x_2 - x_3).\end{aligned} \tag{2.14}$$

In 1975, May and Leonard studied system (2.14) and focused on the system with a periodic limit cycle solution on the parameter setting $\alpha+\beta=2$, on the other hand, a nonperiodic population oscillations of bounded amplitude but ever increasing cycle time on parameter setting $\alpha+\beta>2$ and $\alpha<1$ [11]. (See Appendices)

System (2.14) has eight possible equilibria : $(0,0,0)$, $(1,0,0)$, $(0,1,0)$, $(0,0,1)$, $\frac{1}{1-\alpha\beta}(1-\alpha,1-\beta,0)$, $\frac{1}{1-\alpha\beta}(1-\beta,0,1-\alpha)$, $\frac{1}{1-\alpha\beta}(0,1-\alpha,1-\beta)$, $\frac{1}{1+\alpha+\beta}(1,1,1)$, denoted by $E_i, i=0,\ldots,7$.

Denote the corresponding linearized system for (2.14) by

$$\frac{d\mathbf{y}}{dt} = \mathbf{A}\mathbf{y}, \tag{2.15}$$

where the variational matrix $\mathbf{A}$ at (x_1^*, x_2^*, x_3^*) is given by

$$\begin{bmatrix} 1-2x_1^*-\alpha x_2^*-\beta x_3^* & -\alpha x_1^* & -\beta x_1^* \\ -\beta x_2^* & 1-\beta x_1^*-2x_2^*-\alpha x_3^* & -\alpha x_2^* \\ -\alpha x_3^* & -\beta x_3^* & 1-\alpha x_1^*-\beta x_2^*-2x_3^* \end{bmatrix} \tag{2.16}$$

In particular, the coexistence E_7 always exists and its local stability depends on the sign of real part of eigenvalues for

$$\mathbf{A}(E_7) = \frac{-1}{1+\alpha+\beta}\begin{bmatrix} 1 & \alpha & \beta \\ \beta & 1 & \alpha \\ \alpha & \beta & 1 \end{bmatrix}. \tag{2.17}$$

Then we can verify that the equilibrium E_7 is stable if and only if $\alpha+\beta<2$. We will see in section 2.3 that the local stability implies global stability in two species competition model. But it is not true for more than two species, just as this system (2.14), E_7 is not globally stable since $E_i, i=1,2,3$ are all saddle.

2.3 Global stability in two species under interaction

Consider this two species Lotka-Volterra system

$$\begin{aligned}\frac{dx_1}{dt} &= x_1(b_1 + a_{11}x_1 + a_{12}x_2),\\ \frac{dx_2}{dt} &= x_2(b_2 + a_{21}x_1 + a_{22}x_2).\end{aligned} \tag{2.18}$$

which the species under interaction may be the following types: (i) competition (ii) predator-prey (iii) mutualism (iv) amensalism, commensalism or others relation.

The positive equilibrium (x_1^*, x_2^*), if it exists, is the solution of

$$b_i + \sum_{j=1}^{2} a_{ij} x_j = 0, i = 1, 2. \tag{2.19}$$

Goh (1976) proposed a sufficient conditions for the global stability of positive equilibrium in two species model.

Theorem 2.3.1 (Goh, 1976). If system (2.18) satisfies the following condition:
(i) there exists a positive equilibrium (x_1^*, x_2^*) which is locally asymptotically stable,
(ii) $a_{11}, a_{22} < 0$.
Then (x_1^*, x_2^*) is globally stable for system (2.18).

Note that the condition (ii) means the intraspecific interactions are all negative, each species must be self-regulating. By the linearization theory, the necessary and sufficient conditions for (x_1^*, x_2^*) to be locally asymptotically stable are

$$a_{11}x_1^* + a_{22}x_2^* < 0 \quad \text{and} \quad x_1^* x_2^*(a_{11}a_{22} - a_{12}a_{21}) > 0. \tag{2.20}$$

So it leads to the following result.

Corollary 2.3.2. For the cases of competition or mutualism, locally stability of the equilibrium implies $a_{11}, a_{22} < 0$. That is, local stability implies global stability.
proof: The variational matrix of (2.18) for (x_1^*, x_2^*) is

$$\begin{bmatrix} a_{11}x_1^* & a_{12}x_1^* \\ a_{21}x_2^* & a_{22}x_2^* \end{bmatrix}$$

For the case of competition or mutualism, $a_{12}a_{21} > 0$. From (2.20), it follows that $a_{11}a_{22} > 0$, thus $a_{11}, a_{22} < 0$. By Theorem 2.3.1, (x_1^*, x_2^*) is globally asymptotically stable.

Now, we give an example indicating that the argument in Theorem 2.3.1 may not true for more than two species model of interaction.

Example 2.3.3 (May, 1975).

$$\begin{aligned}\frac{dx_1}{dt} &= x_1(1 - x_1 - \alpha x_2 - \beta x_3)\\ \frac{dx_2}{dt} &= x_2(1 - \beta x_1 - x_2 - \alpha x_3)\\ \frac{dx_3}{dt} &= x_3(1 - \alpha x_1 - \beta x_2 - x_3), \alpha, \beta > 0.\end{aligned} \tag{2.21}$$

As $\alpha + \beta < 2$, the system has a positive equilibrium $E^* = \frac{1}{1+\alpha+\beta}(1, 1, 1)$ which is locally stable but not globally asymptotically stable. So, in next section, we will introduce a result proposed by Goh (1977), it is a sufficient conditions of the global stability of coexistence for the many-species model.

2.4 Global stability in n species systems

consider

$$\frac{dx_i}{dt} = x_i(b_i + \sum_{j=1}^{n} a_{ij}x_j), i = 1, \ldots, n, \tag{2.22}$$

The nontrivial equilibrium $(x_1^*, x_2^*, \ldots, x_n^*)$ for system (2.22) is the solution of the following system of equations

$$b_i + \sum_{j=1}^{n} a_{ij}x_j = 0, i = 1, 2, \ldots, n. \tag{2.23}$$

Denote

$$\mathbf{A} = [a_{ij}]. \tag{2.24}$$

Theorem 2.4.1 (Goh, 1977). If there is a positive equilibrium $(x_1^*, x_2^*, \ldots, x_n^*)$ and a constant positive diagonal matrix $\mathbf{C}$ such that $\mathbf{CA} + \mathbf{A}^T\mathbf{C}$ is negative definite, then $(x_1^*, x_2^*, \ldots, x_n^*)$ is globally asymptotically stable for system (2.22).

In particular, the theorem is true for $\mathbf{A}$ is symmetric and negative definite (May 1974) or $\mathbf{A}$ is not symmetric but $\mathbf{A} + \mathbf{A}^T$ is negative definite (Getz 1975). In the following example, $\mathbf{A}$ is not symmetric and $\mathbf{A} + \mathbf{A}^T$ is not negative definite, but the system also has a globally asymptotically stable equilibrium.

Example 2.4.2.

$$\begin{aligned}\frac{dx_1}{dt} &= x_1(1.1 - x_1 - 0.1x_2)\\ \frac{dx_2}{dt} &= x_2(4 - 3x_1 - x_2)\end{aligned} \tag{2.25}$$

The only one positive equilibrium $(1, 1)$ is globally asymptotically stable if we choose $c_1 = 1, c_2 = \frac{1}{30}$ in Theorem 2.4.1. Actually, we can also conclude the result by the argument of Theorem 2.3.1.

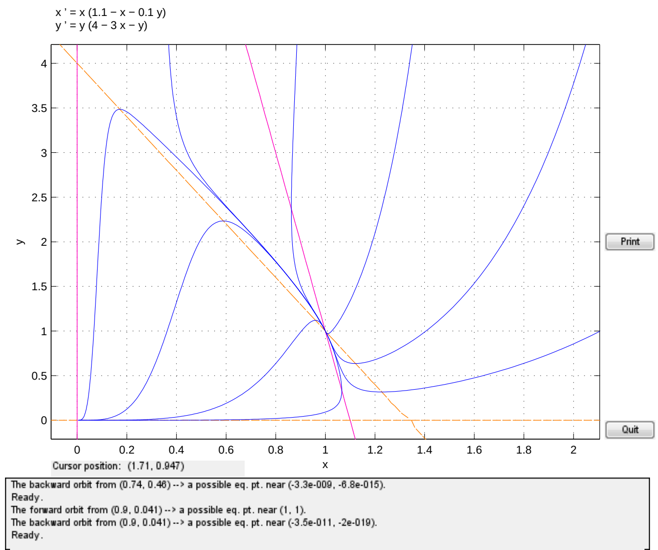

Figure 2: Illustrations for the dynamics of example 2.4.2.

The following example showed that the conditions in Theorem 2.4.1 is not necessary true for the global stability of system (2.22).

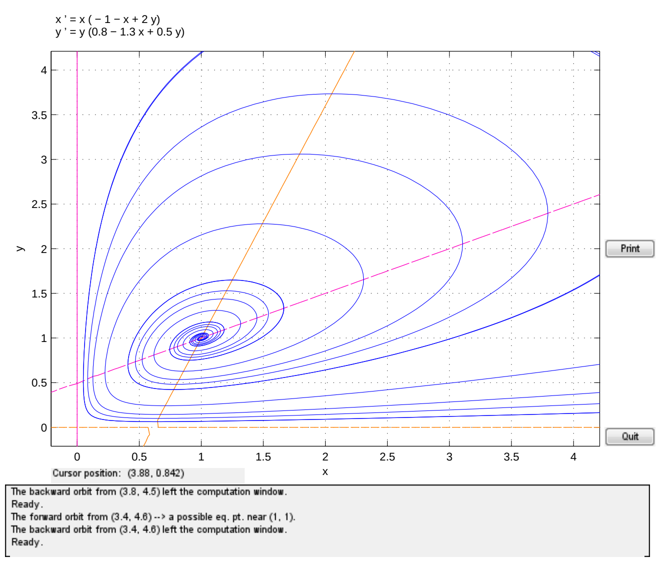

Figure 3: Illustrations for the dynamics of example 2.4.3.

Example 2.4.3.

$$\begin{aligned}\frac{dx_1}{dt} &= x_1(-1 - x_1 + 2x_2)\\ \frac{dx_2}{dt} &= x_2(0.8 - 1.3x_1 + 0.5x_2)\end{aligned} \tag{2.26}$$

The only one positive equilibrium $(1, 1)$ is globally asymptotically stable and we can verify that there is no suitable positive constants c_1, c_2 such that $\mathbf{CA} + \mathbf{A}^T\mathbf{C}$ is negative definite.

2.5 Global stability in n species mutualism system

Suppose that there exists a positive equilibrium $(x_1^*, x_2^*, \ldots, x_n^*)$ for system (2.22), then the model can be rewritten in this form

$$\frac{dx_i}{dt} = x_i \sum_{j=1}^{n} a_{ij}(x_j - x_j^*), i = 1, \ldots, n. \tag{2.27}$$

More generally to say, a mutualism (commensalism) between two species means that one species benefits (or not affected) from the interaction with the other. Each one species promotes the growth of every other species or unaffected under the interaction, that is, $a_{ij} \geq 0$ whenever $i \neq j$.

Denote

$$\mathbf{A} = [a_{ij}]. \tag{2.28}$$

Before studying the dynamics of system (2.27), we introduce the principal minors of a matrix. Let $\mathbf{M}$ be a $n \times n$ matrix, a minor of $\mathbf{M}$ is the determinant of some smaller square matrix obtained by deleting some numbers of rows and columns. A minor of order k is principal if it is obtained by deleting $n - k$ rows and the same $n - k$ columns. The leading principal minor of order k is a principal minor of order k obtained by deleting the last $n - k$ rows and the same $n - k$ columns.

Theorem 2.5.1 (Goh, 1979). The locally stable positive equilibrium of (2.27) in the case of mutualism is globally asymptotically stable if and only if all the leading principal minors of $-\mathbf{A}$ are positive.

Finally, we give an interesting result for the Lotka-Volterra systems, consider system (2.27), we assume $\mathbf{B} = [b_{ij}] = \mathbf{A}^{-1}$, if it exists. This gives a new system

$$\frac{dx_i}{dt} = x_i \sum_{j=1}^{n} b_{ij}(x_j - x_j^*), i = 1, \ldots, n, \tag{2.29}$$

Then the following result give a relationship between systems (2.27) and (2.29).

Let $\mathbf{Z}$ be the set of all real square matrices whose off-diagonal elements are all non-positive.

Theorem 2.5.2 (Goh, 1979). If (2.27) is a globally stable model of mutualism, then (2.29) is a globally stable model of competition.

Proof. Since $-\mathbf{A} \in \mathbf{Z}$ and from Theorem 2.5.1, we have all the leading principal minors of $-\mathbf{A}$ are positive. Equivalently, all real eigenvalues of $-\mathbf{A}$ are positive. This is equivalent to the inverse $(-\mathbf{A})^{-1}$ exists and all elements of $(-\mathbf{A})^{-1}$ are nonnegative. It follows that $(\mathbf{A})^{-1} = \mathbf{B}$ exists and all elements of $\mathbf{B}$ are non-positive. Such results had proved by Fiedler and Ptak (1962)[1]. Suppose that there exists a positive diagonal matrix $\mathbf{C}$ such that $\mathbf{CA} + \mathbf{A}^T\mathbf{C}$ is negative definite, then $(\mathbf{A}^{-1})^T(\mathbf{CA} + \mathbf{A}^T\mathbf{C})\mathbf{A}^{-1}$ is also negative definite. It follows that $\mathbf{B}^T\mathbf{C} + \mathbf{CB}$ is negative definite. Hence, the system (2.29) is a globally stable of competition.

Example 2.5.3. Consider the following model of mutualism among three species,

$$\begin{aligned}
\frac{dx_1}{dt} &= x_1(0.5 - 2x_1 + x_2 + 0.5x_3), \\
\frac{dx_2}{dt} &= x_2(-3 + 5x_1 - 4x_2 + 2x_3), \\
\frac{dx_3}{dt} &= x_3(4 + x_1 + 2x_2 - 7x_3).
\end{aligned} \tag{2.30}$$

The positive equilibrium $(1, 1, 1)$ is globally asymptotically stable if we choose $c_1 = 5, c_2 = 1$ and $c_3 = 1$ in Theorem 2.4.1. The inverse of the interaction matrix is given by

$$\mathbf{B} = \mathbf{A}^{-1} = \begin{bmatrix} -6 & -2 & -1 \\ -9.25 & -3.375 & -1.625 \\ -3.5 & -1.25 & -0.75 \end{bmatrix}$$

Hence, this is a model of competition as follows,

$$\begin{aligned}
\frac{dx_1}{dt} &= x_1(9 - 6x_1 - 2x_2 - 1x_3), \\
\frac{dx_2}{dt} &= x_2(14.25 - 9.25x_1 - 3.375x_2 - 1.625x_3), \\
\frac{dx_3}{dt} &= x_3(5.5 - 3.5x_1 - 1.25x_2 - 0.75x_3).
\end{aligned} \tag{2.31}$$

Again the equilibrium $(1, 1, 1)$ is also globally asymptotically stable by choosing $c_1 = 5, c_2 = 1$ and $c_3 = 1$ in Theorem 2.4.1.

But the converse of Theorem 2.5.2 is not necessarily true. It means that the inverse of the interaction matrix of a globally stable Lotka-Volterra model of competition may not be an interaction matrix for mutualism. This mathematical result suggested that in nature mutualism is less than competition and prey-predation [5].

3 Dynamics for Lotka-Volterra system with diffusion

Consider the following Lotka-Volterra system with n species under dispersal in m patches

$$\frac{du_i^k}{dt} = u_i^k(r_i + \sum_{j=1}^{n} a_{ij}u_j^k) + \sum_{l=1, l\neq k}^{m} (D_i^{kl}u_i^l - D_i^{lk}u_i^k), \tag{3.1}$$

where $i = 1, \ldots, n, k = 1, \ldots, m$, and u_i^k is the population of species i in patch k; D_i^{kl} describes the dispersal coefficients from patch l to patch k. System (3.1) or its similar form has been studied by Levin (1974), Chewning (1975), Segel and Levin(1976).

First, we recall the following result by Goh (1977), for the Lotka-Volterra system without diffusion,

$$\frac{du_i^k}{dt} = u_i^k(r_i + \sum_{j=1}^{n} a_{ij}u_j^k), i = 1, \ldots, n. \tag{3.2}$$

Theorem 3.1 (Goh, 1977). If there is a positive equilibrium E^* of (3.2) and a constant positive diagonal matrix $\mathbf{C}$ such that $\mathbf{CA} + \mathbf{A}^T\mathbf{C}$ is negative definite, then E^* is globally asymptotically stable for system (3.2).

We review the global stability for coexistence of species in subsection 3.1, Lyapunov functions for large-scaled coupled systems in subsection 3.2, single species Lotka-Volterra patch model in subsection 3.3. And the model of two species competition in two patches is studied in subsection 3.4, whose the results are proven in subsection 3.5.

3.1 Global stability for coexistence of species

Suppose that there also exists a positive equilibrium for system (3.1) with diffusion rate $D_i^{kl} \geq 0$, denoted by $\bar{E} = (\bar{u}^1, \bar{u}^2, \ldots, \bar{u}^m)$, where $\bar{u}^k = (\bar{u}_1^k, \bar{u}_2^k, \ldots, \bar{u}_n^k)$, and $\bar{u}_i^k > 0, i = 1, \ldots, n, k = 1, \ldots, m$. We will discuss the global stability for the coexistence $\bar{E}$ in system (3.1). In 1978, Hastings presented a sufficient conditions for the global stability of the coexistence $\bar{E}$ in system (3.1) as follows.

Theorem 3.1.1 (Hastings, 1978). Assume that (3.2) satisfies the hypotheses of Theorem 3.1 and $D_i^{kl} = D_i^{lk}, i = 1, \ldots, n, k, l = 1, \ldots, m$. Then the positive equilibrium $\bar{E}$ is also globally asymptotically stable in (3.1) for all initial conditions with $u_i^k(0) > 0$ for all i, k.

This result of Theorem 3.1.1 indicates that the global stability for the positive equilibrium is independent to the dispersal rates under the assumption. For single species, Takeuchi had proposed such problem that whether the positive equilibrium, which the value can be changed by dispersal rate, continues to be positive and globally stable if the dispersal rates are increased [21]? He showed that under some conditions, the single species patch model can have the unique globally asymptotically stable positive equilibrium [10]. Li and Shuai (2010) improved the result of [10] and proved by constructing a suitable Lyapunov function [9].

We give an example for a special case that the population of species are the same on each pathes,

$$\bar{u}_1^k = \bar{u}_2^k = \cdots = \bar{u}_n^k, \text{ for each } k,$$

by constructing a suitable Lyapunov function which the idea from [9].

Example 3.1.2. Consider the competitive patch model with three species and two patches,

$$\begin{aligned}
\frac{du_1^1}{dt} &= u_1^1(1 - u_1^1 - \alpha_1 u_2^1 - \beta_1 u_3^1) + d_1^{21}(u_1^2 - u_1^1), \\
\frac{du_2^1}{dt} &= u_2^1(1 - \beta_1 u_1^1 - u_2^1 - \alpha_1 u_3^1) + d_2^{21}(u_2^2 - u_2^1), \\
\frac{du_3^1}{dt} &= u_3^1(1 - \alpha_1 u_1^1 - \beta_1 u_2^1 - u_3^1) + d_3^{21}(u_3^2 - u_3^1),
\end{aligned} \tag{3.3}$$

and

$$\frac{du_1^2}{dt} = u_1^2(1 - u_1^2 - \alpha_2 u_2^2 - \beta_2 u_3^2) + d_1^{12}(u_1^1 - u_1^2),$$
$$\frac{du_2^2}{dt} = u_2^2(1 - \beta_2 u_1^1 - u_2^1 - \alpha_2 u_3^1) + d_2^{12}(u_2^1 - u_2^2), \tag{3.4}$$
$$\frac{du_3^2}{dt} = u_3^2(1 - \alpha_2 u_1^1 - \beta_2 u_2^1 - u_3^1) + d_3^{12}(u_3^1 - u_3^2).$$

Without all dispersal rates, we checked that if $0 < \alpha_i, \beta_i < 1, i = 1, 2$, models (3.3) and (3.4) have a globally asymptotically stable positive equilibria $(\bar{u}_1^1, \bar{u}_2^1, \bar{u}_3^1), (\bar{u}_1^2, \bar{u}_2^2, \bar{u}_3^2)$, respectively [23]. Note that $\bar{u}_1^1 = \bar{u}_2^1 = \bar{u}_3^1, \bar{u}_1^2 = \bar{u}_2^2 = \bar{u}_3^2$. Defined the Lyapunov functions $V_1 : \mathbb{R}_+^3 \to \mathbb{R}, V_2 : \mathbb{R}_+^3 \to \mathbb{R}$ for (3.3) and (3.4), respectively, by

$$V_1 = \sum_{i=1}^{3} c_i^1[u_i^1 - \bar{u}_i^1 - \bar{u}_i^1 \ln(\frac{u_i^1}{\bar{u}_i^1})] \tag{3.5}$$

and

$$V_2 = \sum_{i=1}^{3} c_i^2[u_i^2 - \bar{u}_i^2 - \bar{u}_i^2 \ln(\frac{u_i^2}{\bar{u}_i^2})]. \tag{3.6}$$

Denote

$$\mathbf{A} = \begin{bmatrix} -1 & -\alpha_1 & -\beta_1 \\ -\beta_1 & -1 & -\alpha_1 \\ -\alpha_1 & -\beta_1 & 1 \end{bmatrix}, \mathbf{B} = \begin{bmatrix} -1 & -\alpha_2 & -\beta_2 \\ -\beta_2 & -1 & -\alpha_2 \\ -\alpha_2 & -\beta_2 & 1 \end{bmatrix} \tag{3.7}$$

and choose $c_i^1, c_i^2 = 1, i = 1, 2, 3$, then

$$\dot{V}_1 = \frac{1}{2} \begin{pmatrix} u_1^1 - \bar{u}_1^1 \\ u_2^1 - \bar{u}_2^1 \\ u_3^1 - \bar{u}_3^1 \end{pmatrix}^T (\mathbf{A} + \mathbf{A}^T) \begin{pmatrix} u_1^1 - \bar{u}_1^1 \\ u_2^1 - \bar{u}_2^1 \\ u_3^1 - \bar{u}_3^1 \end{pmatrix} \leq 0, \tag{3.8}$$

and

$$\dot{V}_2 = \frac{1}{2} \begin{pmatrix} u_1^2 - \bar{u}_1^2 \\ u_2^2 - \bar{u}_2^2 \\ u_3^2 - \bar{u}_3^2 \end{pmatrix}^T (\mathbf{B} + \mathbf{B}^T) \begin{pmatrix} u_1^2 - \bar{u}_1^2 \\ u_2^2 - \bar{u}_2^2 \\ u_3^2 - \bar{u}_3^2 \end{pmatrix} \leq 0 \tag{3.9}$$

since $\mathbf{A} + \mathbf{A}^T$ and $\mathbf{B} + \mathbf{B}^T$ are all negative definite. Hence, the assumption holds in Theorem 3.1.

For $d_i^{kl} \geq 0, i = 1, 2, 3, k, l = 1, 2$, the coupled system has a positive equilibrium $(\bar{u}_1^1, \bar{u}_2^1, \bar{u}_3^1, \bar{u}_1^2, \bar{u}_2^2, \bar{u}_3^2)$, which the value can be changed by dispersal rates. Now, we claim that it is globally asymptotically stable by constructing the following Lyapunov function

$$V = b_1 V_1 + b_2 V_2. \tag{3.10}$$

Choosing $b_1 = \bar{u}_1^1 (= \bar{u}_2^1 = \bar{u}_3^1), b_2 = \bar{u}_1^2 (= \bar{u}_2^2 = \bar{u}_3^2)$, then

$$\begin{aligned}
\dot{V} &= b_1 \dot{V}_1 + b_2 \dot{V}_2 \\
&\le \bar{u}_1^1 d_1^{21} \bar{u}_1^2 (\frac{u_1^2}{\bar{u}_1^2} - \frac{u_1^1}{\bar{u}_1^1} + 1 - \frac{\bar{u}_1^1 u_1^2}{\bar{u}_1^2 u_1^1}) + \bar{u}_1^1 d_2^{21} \bar{u}_2^2 (\frac{u_2^2}{\bar{u}_2^2} - \frac{u_2^1}{\bar{u}_2^1} + 1 - \frac{\bar{u}_2^1 u_2^2}{\bar{u}_2^2 u_2^1}) \\
&+ \bar{u}_1^1 d_3^{21} \bar{u}_3^2 (\frac{u_2^2}{\bar{u}_3^2} - \frac{u_3^1}{\bar{u}_3^1} + 1 - \frac{\bar{u}_3^1 u_3^2}{\bar{u}_3^2 u_3^1}) + \bar{u}_1^2 d_1^{12} \bar{u}_1^1 (\frac{u_1^1}{\bar{u}_1^1} - \frac{u_1^2}{\bar{u}_1^2} + 1 - \frac{\bar{u}_1^2 u_1^1}{\bar{u}_1^1 u_1^2}) \\
&+ \bar{u}_1^2 d_2^{12} \bar{u}_2^1 (\frac{u_2^1}{\bar{u}_2^1} - \frac{u_2^2}{\bar{u}_2^2} + 1 - \frac{\bar{u}_2^2 u_2^1}{\bar{u}_2^1 u_2^2}) + \bar{u}_1^2 d_3^{12} \bar{u}_3^1 (\frac{u_3^1}{\bar{u}_3^1} - \frac{u_3^2}{\bar{u}_3^2} + 1 - \frac{\bar{u}_3^2 u_3^1}{\bar{u}_3^1 u_3^2}) \\
&\le 0.
\end{aligned}$$

And the equality holds for $(u_1^1, u_2^1, u_3^1, u_1^2, u_2^2, u_3^2) = (\bar{u}_1^1, \bar{u}_2^1, \bar{u}_3^1, \bar{u}_1^2, \bar{u}_2^2, \bar{u}_3^2)$. Hence, by the Lyapunov stability theory, the positive equilibrium $\bar{E} = (\bar{u}_1^1, \bar{u}_2^1, \bar{u}_3^1, \bar{u}_1^2, \bar{u}_2^2, \bar{u}_3^2)$ is globally asymptotically stable for the system (3.3) and (3.4).

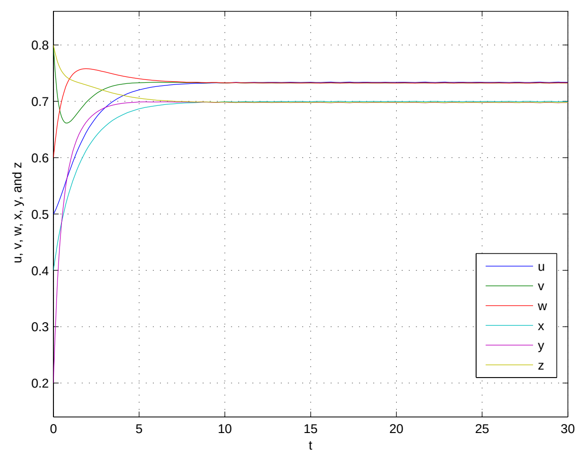

Figure 4: Illustrations for the dynamics of example 3.1.2 with $u = u_1^1$, $v = u_2^1$, $w = u_3^1$, $x = u_1^2$, $y = u_2^2$, $z = u_3^2$, and $\alpha_1 = 0.1, \beta_1 = 0.2, \alpha_2 = 0.2, \beta_2 = 0.3$, $d = 1$.

3.2 Lyapunov functions for large-scaled coupled systems

Summarizing the result in [9], its important assumption is that, when isolated, each vertex system has a globally stable equilibrium and a globally defined Lyapunov function $V_i, i = 1, \ldots, n$. Then, for coupled system, Li and Shuai constructed a global Lyapunov function in this form

$$V = \sum_{i=1}^{n} c_i V_i, \tag{3.11}$$

where $c_i \geq 0$ are suitable constants we will describe as follows.

Given a weighted digraph $\mathcal{G} = (V, E)$ with n vertices and a set of directed arcs (j, i) connected from vertex j to vertex i with weight a_{ij}. A spanning tree of $\mathcal{G}$ is a subgraph $\mathcal{H}$ has the same vertex and a set of arcs that contains no cycle. Here, $a_{ij} > 0$ if and only if there exists an arc from vertex j to vertex i. Denote $w(\mathcal{H})$ of $\mathcal{H}$ be the product of the weights on all its arcs. Define the weight matrix $\mathbf{A} = [a_{ij}]_{n\times n}$ whose entry a_{ij} equals the weight of arc (j, i) if it exists, and 0 otherwise. A diagraph $\mathcal{G}$ is strongly connected if there exists a directed path from one to the other for any two distinct vertices. A weighted diagraph $\mathcal{G}$ is strongly connected if and only if $\mathbf{A}$ is irreducible. We need only to consider $\mathbf{A}$ is irreducible since any reducible system can be separated into irreducible components. The Laplacian matrix of $\mathbf{A}$ is defined as

$$\mathbf{L} = \begin{bmatrix} \sum_{k\neq 1} a_{1k} & -a_{12} & \dots & -a_{1n} \\ -a_{21} & \sum_{k\neq 2} a_{2k} & \dots & -a_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ -a_{n1} & -a_{n2} & \dots & \sum_{k\neq n} a_{nk} \end{bmatrix}.$$

Then constants c_i in (3.11) is the cofactor of the i-th diagonal element of $\mathbf{L}$. As follows, we will introduce some results in graph theory.

Proposition 3.2.1 (Kirchhoff's matrix tree theorem). Assume $n \geq 2$. Then

$$c_i = \sum_{\mathcal{T}\in\mathbb{T}_i} w(\mathcal{T}), i = 1, \dots, n, \tag{3.12}$$

where $\mathbb{T}_i$ is the set of all spanning trees $\mathcal{T}$ of $\mathcal{G}$ that are rooted at vertex i, and $w(\mathcal{T})$ is the weight of $\mathcal{T}$.

The proof of Proposition 3.2.1 based on the following Lemma and induction :

Lemma 3.2.2. ([22]) Let G be a graph and $\tau(G)$ denote the number of spanning trees of graph G. If $e \in E(G)$, the set of edges of G, is not a loop, then

$$\tau(G) = \tau(G - e) + \tau(G \cdot e).$$

$\tau(G - e)$ denote the spanning trees do not contain e, $\tau(G \cdot e)$ denote the spanning trees contain e.

Lemma 3.2.3.

$$\begin{vmatrix} a_{11} + b_{11} & a_{12} & \dots & a_{1n} \\ a_{21} & a_{22} & \dots & a_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1} & a_{n2} & \dots & a_{nn} \end{vmatrix} = \begin{vmatrix} a_{11} & 0 & \dots & 0 \\ a_{21} & a_{22} & \dots & a_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1} & a_{n2} & \dots & a_{nn} \end{vmatrix} + \begin{vmatrix} b_{11} & a_{12} & \dots & a_{1n} \\ a_{21} & a_{22} & \dots & a_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1} & a_{n2} & \dots & a_{nn} \end{vmatrix}$$

Proposition 3.2.4 (Li and Shuai,2010). Assume $n \geq 2$. Let c_i be given in Proposition 3.2.1 Then the following identity holds

$$\sum_{i,j=1}^{n} c_i a_{ij} F_{ij}(x_i, x_j) = \sum_{\mathcal{Q} \in \mathbb{Q}} w(\mathcal{Q}) \sum_{(s,r) \in E(C_{\mathcal{Q}})} F_{rs}(x_r, x_s). \tag{3.13}$$

Here $F_{ij}(x_i, x_j), 1 \leq i, j \leq n$, are arbitrary functions, $\mathbb{Q}$ is the set all spanning unicyclic graphs of $\mathcal{G}$ that is defined by a disjoint union of rooted trees whose roots form a directed cycle. $w(\mathcal{Q})$ is the wight of $\mathcal{Q}$ and $C_{\mathcal{Q}}$ denotes the directed cycle of $\mathcal{Q}$.

Proposition 3.2.5 (Li and Shuai,2010). Assume $n \geq 2$. Let c_i be given in Proposition 3.2.1. Then the following identity holds

$$\sum_{i,j=1}^{n} c_i a_{ij} G_i(x_i) = \sum_{i,j=1}^{n} c_i a_{ij} G_j(x_j). \tag{3.14}$$

Here $G_i(x_i), 1 \leq i \leq n$, are arbitrary functions.

We consider a coupled system built on $\mathcal{G}$ by assigning each vertex has its own internal dynamics and coupling term based on directed arcs in $\mathcal{G}$. Then we obtain the following coupled system on $\mathcal{G}$

$$\frac{du_i}{dt} = f_i(u_i) + \sum_{j=1}^{n} g_{ij}(u_i, u_j), i = 1, \ldots, n. \tag{3.15}$$

We assume each vertex system has a globally stable equilibrium and a globally defined Lyapunov function $V_i, i = 1, \ldots, n$. Then, for the coupled system (3.15), the following result gives a general and systematic approach for constructing the equation (3.11).

Theorem 3.2.6 (Li and Shuai,2010). Assume the constants c_i are given in Proposition 3.2.1 and the following assumptions hold.

(i) There exist functions $V_i(u_i), F_{ij}(u_i, u_j)$, and constants $a_{ij} \geq 0$ such that

$$\dot{V}_i(u_i) \leq \sum_{j=1}^{n} a_{ij} F_{ij}(u_i, u_j), t > 0, i = 1, \ldots, n. \tag{3.16}$$

(ii) Along each directed cycle $\mathcal{C}$ of the weighted digraph $\mathcal{G}, \mathbf{A} = [a_{ij}]$,

$$\sum_{(s,r) \in E(C)} F_{rs}(u_r, u_s) \leq 0, t > 0. \tag{3.17}$$

Then the function V in (3.11) satisfies $\dot{V} \leq 0$ for $t > 0$. That is, V is a Lyapunov function for (3.15).

Conditions (3.17) of Theorem 3.2.5 can be replaced that if there exist functions $G_i(u_i), i = 1, \ldots, n$, such that

$$F_{ij}(u_i, u_j) \leq G_i(u_i) - G_j(u_j), 1 \leq i, j \leq n. \tag{3.18}$$

Next section, we will discuss the single species patch model with diffusion.

3.3 Single species Lotka-Volterra patch model

Consider two identical linear systems with the stable zero solution,

$$\begin{bmatrix} \dot{x}_i \\ \dot{y}_i \end{bmatrix} = \begin{bmatrix} -2 & 3 \\ -1 & 1 \end{bmatrix} \begin{bmatrix} x_i \\ y_i \end{bmatrix}, i = 1, 2. \tag{3.19}$$

For the following coupled system with only linear coupling term, then the zero solution is unstable.

$$\begin{bmatrix} \dot{x}_1 \\ \dot{y}_1 \\ \dot{x}_2 \\ \dot{y}_2 \end{bmatrix} = \begin{bmatrix} -2 & 3 & 1 & 0 \\ -1 & 1 & 0 & 0 \\ 1 & 0 & -3 & 3 \\ 0 & 0 & -1 & 1 \end{bmatrix} \begin{bmatrix} x_1 \\ y_1 \\ x_2 \\ y_2 \end{bmatrix} \tag{3.20}$$

Hence, the dispersal can lead the dynamics of coupled system to appear unstable. Here we also consider the question that whether the dispersal can lead each unstable equilibrium of isolated systems to a stable equilibrium for coupled system ? We use the two patch model as example, when isolated,

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1 (-\frac{1}{2} + \frac{3}{2} x_1 - x_1^2), \\ \frac{dx_2}{dt} &= r_2 x_2 (-2 + 3x_2 - x_2^2). \end{aligned} \tag{3.21}$$

There are two logistic equations of one dimensional, $x_1 = 1$ is a stable equilibrium in patch 1 and $x_2 = 1$ is an unstable equilibrium in patch 2. In the following coupled system,

$$\begin{aligned} \frac{dx_1}{dt} &= r_1 x_1 (-\frac{1}{2} + \frac{3}{2} x_1 - x_1^2) + d(x_2 - x_1), \\ \frac{dx_2}{dt} &= r_2 x_2 (-2 + 3x_2 - x_2^2) + d(x_1 - x_2). \end{aligned} \tag{3.22}$$

$(1,1)$ is an equilibrium of above system. We can verify that if $\frac{-r_1}{2} + r_2 < 0$ and d sufficient large, then $(1,1)$ is linearly stable for the coupled system. Therefore, we introduced a result proposed by Hastings (1982), he presented a model for a single species on patches, and showed that the coexistence of the model, if it exist, is locally stable for sufficient large diffusion. See the model

$$\frac{d\mathbf{x}}{dt} = f(\mathbf{x}) + \mathbf{D}\mathbf{x}, \tag{3.23}$$

where $\mathbf{D} = [d_{ij}]$ is a $n \times n$ matrix of diffusion coefficients with following assumptions (i) $\mathbf{D}$ is symmetric. (ii) All diagonal elements are negative and all off diagonal elements are nonnegative. (iii) Row sums and columns sums are all zero. (iv) $\mathbf{D}$ is irreducible.

Theorem 3.3.1 (Hastings,1982). If there exists an equilibrium $E^* = (x_1^*, \ldots, x_n^*)$ such that all the $\frac{d}{dx_i} f_i(x_i^*)$ are sufficiently small with respect to the entries in $\mathbf{D}$. Then E^* is locally asymptotically stable if

$$\sum_{i=1}^{n} \frac{df_i}{dx_i}(x_i^*) < 0$$

and unstable if

$$\sum_{i=1}^{n} \frac{df_i}{dx_i}(x_i^*) > 0.$$

The result shows that the sufficiently large dispersal rates have the powerful stabilizing role (den Boer, 1968). For the case $n = 3$, let $\mathbf{B} = [b_{ij}]$ be a diagonal matrix where $b_{ii} = \frac{df_i}{dx_i}(x_i^*)$ and $\varepsilon > 0$, claim that all eigenvalues of $\mathbf{D} + \varepsilon\mathbf{B}$ are negative if $\sum_{i=1}^{3} b_{ii} < 0$, and there is a positive eigenvalue if $\sum_{i=1}^{3} b_{ii} > 0$. Let

$$\mathbf{D} = \begin{bmatrix} -d_{12} - d_{13} & d_{12} & d_{13} \\ d_{12} & -d_{12} - d_{23} & d_{23} \\ d_{13} & d_{23} & -d_{23} - d_{23} \end{bmatrix}, \; d_{12}, d_{13}, d_{23} \geq 0 \tag{3.24}$$

and

$$\mathbf{B} = \begin{bmatrix} b_{11} & 0 & 0 \\ 0 & b_{22} & 0 \\ 0 & 0 & b_{33} \end{bmatrix}. \tag{3.25}$$

By the Gerschgorin's Theorem and that $\mathbf{D}$ has zero eigenvalue, 0 is the largest eigenvalue of $\mathbf{D}$. Since the characteristic polynomial $P(\lambda)$ of $\mathbf{D}+\varepsilon\mathbf{B}$ is given by

$$\begin{aligned}\det(\lambda\mathbf{I}-(\mathbf{D}+\varepsilon\mathbf{B})) &= \begin{vmatrix} \lambda-\varepsilon b_{11}+d_{12}+d_{13} & -d_{12} & -d_{13} \\ -d_{12} & \lambda-\varepsilon b_{22}+d_{12}+d_{23} & -d_{23} \\ -d_{13} & -d_{23} & \lambda-\varepsilon b_{33}+d_{23}+d_{23} \end{vmatrix} \\ &= \lambda^3 - trace(\mathbf{D}+\varepsilon\mathbf{B})\lambda^2+\cdots+(-1)^3\det(\mathbf{D}+\varepsilon\mathbf{B}).\end{aligned}$$

If $\sum_{i=1}^{3} b_{ii} < 0$, then

(i). $trace(\mathbf{D}+\varepsilon\mathbf{B}) = \varepsilon(b_{11}+b_{22}+b_{33}) - 2(d_{12}+d_{13}+d_{23}) < 0$ for ε small.

(ii).

$$\begin{aligned}\det(\mathbf{D}+\varepsilon\mathbf{B})) &= \begin{vmatrix} \varepsilon b_{11}+d_{12}+d_{13} & d_{12} & d_{13} \\ d_{12} & \varepsilon b_{22}+d_{12}+d_{23} & d_{23} \\ d_{13} & d_{23} & \varepsilon b_{33}+d_{23}+d_{23} \end{vmatrix} \\ &= \varepsilon(b_{11}+b_{22}+b_{33})(d_{12}d_{23}+d_{12}d_{13}+d_{23}d_{13}) + O(\varepsilon^2) \\ &< 0.\end{aligned}$$

Hence, we have $P(0) = (-1)^3\det(\mathbf{D}+\varepsilon\mathbf{B})) > 0$ and thus all eigenvalues of $(\mathbf{D}+\varepsilon\mathbf{B})$ are negative. Otherwise, if $\sum_{i=1}^{3} b_{ii} > 0$, we have $P(0) < 0$. It follows that there is an eigenvalue is positive. The proof for high dimensional system see appendix 5.4.

Consider the single species patch model among n patches $(n \geq 2)$,

$$\frac{dx_i}{dt} = x_i f_i(x_i) + \sum_{j=1}^{n} d_{ij}(x_j - x_i), i = 1, \ldots, n, \tag{3.26}$$

where x_i is the population of the species in patch i, $f_i \in C^1(\mathbb{R}_+, \mathbb{R})$ represents the density dependent growth rate in patch i, constant $d_{ij} \geq 0$ is the dispersal rate from patch j to patch i. In [9], the global stability of coexistence has been proved by Lyapunov function, this also improved the result in Takeuchi (1993)[10].

Theorem 3.3.2 (Li and Shuai,2010). Assume that the following assumptions hold,

(i) Dispersal matrix d_{ij} is irreducible,

(ii) $f_i'(x_i) \leq 0, x_i > 0, i = 1, \ldots, n$, and there exists k such that $f_k'(x_k) \neq 0$ in any open interval of $\mathbb{R}_+$,

(iii) system (3.26) is uniformly persistent,

(iv) solutions of (3.26) are uniformly ultimately bounded.

Then the system (3.26) has a globally asymptotically stable positive equilibrium E^* in $\mathbb{R}_+^n$.

3.4 Two species competition in two patches

The single species patch model has been studied extensively. We are interested to study the patch model with many species. Whether the results about single patch model can be extended for many species? In this subsection, we consider a model of two competing species in two patches:

$$\begin{aligned}\dot{u}_1 &= u_1(\alpha_1 - cu_1 - cv_1) + d(u_2 - u_1),\\ \dot{u}_2 &= u_2(\alpha_2 - cu_2 - cv_2) + d(u_1 - u_2),\\ \dot{v}_1 &= v_1(\beta_1 - cv_1 - cu_1) + d(v_2 - v_1),\\ \dot{v}_2 &= v_2(\beta_2 - cv_2 - cu_2) + d(v_1 - v_2).\end{aligned} \tag{3.27}$$

Herein, u_i and v_i are the populations of species u, v in patch $i, i = 1, 2$. The parameters $\alpha_i, \beta_i > 0$ are intrinsic growth rates of species u_i, v_i respectively; $d \geq 0$ is the dispersal rate between two patches. We assume that the competition coefficient c, in each patch is the same. Certainly we only consider nonnegative initial values $u_i(0) \geq 0$ and $v_i(0) \geq 0, i = 1, 2$.

After scaling, model (3.27) becomes the following system which is the one studied by Gourley and Kuang [2],

$$\begin{aligned}\frac{du_1}{dt} &= u_1(\alpha_1 - u_1 - v_1) + d(u_2 - u_1),\\ \frac{du_2}{dt} &= u_2(\alpha_2 - u_2 - v_2) + d(u_1 - u_2),\\ \frac{dv_1}{dt} &= v_1(\beta_1 - v_1 - u_1) + d(v_2 - v_1),\\ \frac{dv_2}{dt} &= v_2(\beta_2 - v_2 - u_2) + d(v_1 - v_2).\end{aligned} \tag{3.28}$$

First, let us present some basic properties about the positively invariant sets and boundedness of solutions for system (3.28). The proofs of this subsection are arranged in the next subsection.

Define

$$\begin{aligned}\bar{\mathbb{R}}_+^{2\times 2} &= \left\{(u_1, u_2, v_1, v_2) \in \mathbb{R}_+^{2\times 2} : u_1, u_2, v_1, v_2 \geq 0\right\},\\ \tilde{\mathbb{R}}_+^{2\times 0} &= \left\{(u_1, u_2, 0, 0) \in \bar{\mathbb{R}}_+^{2\times 2} : u_1 + u_2 > 0\right\},\\ \tilde{\mathbb{R}}_+^{0\times 2} &= \left\{(0, 0, v_1, v_2) \in \bar{\mathbb{R}}_+^{2\times 2} : v_1 + v_2 > 0\right\}.\end{aligned} \tag{3.29}$$

Proposition 3.4.1. $\bar{\mathbb{R}}_+^{2\times 2}, \tilde{\mathbb{R}}_+^{2\times 0}$ and $\tilde{\mathbb{R}}_+^{0\times 2}$ are all positively invariant under the solution flow generated by system (3.28).

Proposition 3.4.2. System (3.28) is dissipative. In fact,

$$\limsup_{t\to\infty}(u_1(t)+u_2(t)) \le 2\max\{\alpha_1,\alpha_2\}, \quad \limsup_{t\to\infty}(v_1(t)+v_2(t)) \le 2\max\{\beta_1,\beta_2\}.$$

Consider the subsystem obtained by setting $v_1, v_2 = 0$ in (3.28)

$$\begin{aligned} \frac{du_1}{dt} &= u_1(\alpha_1 - u_1) + d(u_2 - u_1), \\ \frac{du_2}{dt} &= u_2(\alpha_2 - u_2) + d(u_1 - u_2). \end{aligned} \tag{3.30}$$

System (3.30) can be seen as a single species patch model. It can be showed that there exists a positive equilibrium through direct computation. Padron (2007) showed the existence and uniqueness of a positive equilibrium for a high dimensional system [15]. Li and Shuai (2010) showed the positive equilibrium is globally asymptotically stable [9]. They constructed a Lyapunov function as follow

$$V(\mathbf{u}) = \sum_{i=1}^{n} c_i \left(u_i - u_i^* - u_1^* \ln(\frac{u_i}{u_i^*}) \right), \mathbf{u} = (u_1, \ldots, u_n), \tag{3.31}$$

the constants c_i can be chosen by a systematic approach that we introduced in Section 3.2. Hence, we have the following result.

Proposition 3.4.3. All solutions starting from initial data in $\tilde{\mathbb{R}}_+^{2\times 0}$ will converge to the semi-trivial equilibrium $(\bar{u}_1, \bar{u}_2, 0, 0)$ of system (3.28).

Similar setting for $u_1, u_2 = 0$ in (3.28), then we have

Proposition 3.4.4. All solutions starting from initial data in $\tilde{\mathbb{R}}_+^{0\times 2}$ will converge to the semi-trivial equilibrium $(0, 0, \bar{v}_1, \bar{v}_2)$ of system (3.28).

When $d = 0$(decoupled system), system (3.28) has a trivial equilibrium $E_0 = (0,0,0,0)$ and the following possible semi-trivial equilibria: single population solutions $E_1 = (\alpha_1, 0, 0, 0)$, $E_2 = (0, \alpha_2, 0, 0)$, $E_3 = (0, 0, \beta_1, 0)$, $E_4 = (0, 0, 0, \beta_2)$; two population solutions $E_5 = (\alpha_1, \alpha_2, 0, 0)$, $E_6 = (0, 0, \beta_1, \beta_2)$, $E_7 = (0, \alpha_2, \beta_1, 0)$ and $E_8 = (\alpha_1, 0, 0, \beta_2)$. And we can verify that the model has no positive equilibrium. Then the dynamics can deduced from the corresponding linearized system clearly. There has the following result and we can conclude that the species with larger growth rate in the same patch will preserve and drive the other to extinction.

Proposition 3.4.5. For the corresponding linearized system of (3.28) with $d = 0$,
(i). E_0, E_1, E_2, E_3 and E_4 are all unstable.
(ii). If $\alpha_1 < \beta_1$ and $\beta_2 < \alpha_2$, then only E_7 is stable.
(iii). If $\alpha_1 > \beta_1$ and $\beta_2 > \alpha_2$, then only E_8 is stable.
(iv). If $\alpha_1 > \beta_1$ and $\beta_2 < \alpha_2$, then only E_5 is stable.
(v). If $\alpha_1 < \beta_1$ and $\beta_2 > \alpha_2$, then only E_6 is stable.

When $d > 0$, we consider the following parameter setting: Assume u and v have the same total sum of growth rates,

$$\alpha_1 + \alpha_2 = \beta_1 + \beta_2. \tag{3.32}$$

How are the distribution of growth rates related to the species preservation or extinction ? Without loss of generality, we assumed

$$\beta_1 < \beta_2.$$

Gourley and Kuang (2005) studied the local stability under the distribution of growth rates as

$$0 < \beta_1 - \varepsilon = \alpha_1 < \beta_1 < \beta_2 < \alpha_2 = \beta_2 + \varepsilon. \tag{3.33}$$

Their study also largely through the linearized analysis. For each semi-trivial equilibria, the Jacobian matrix has a block diagonal structure. But it is not easy to compute and analyze the stability of coexistence equilibrium, here we study it using the Routh-Hurwitz stability criterion and mathematical computation software Maple. We have the following result.

Theorem 3.4.6. Under assumption (3.33), if there exists a positive equilibrium $\bar{E}$, then it is asymptotically stable in system (3.28).

Now, we introduced the main result about the local stability of two semi-trivial equilibria $(u_1^*, u_2^*, 0, 0)$ and $(0, 0, v_1^*, v_2^*)$ in [2].

Theorem 3.4.7 (Gourley and Kuang, 2005). If $\beta_2 > \beta_1$ and $\alpha_1 = \beta_1 - \varepsilon, \alpha_2 = \beta_2 + \varepsilon$ with $0 < \varepsilon < \beta_1$ and d is sufficiently large, then $(0, 0, v_1^*, v_2^*)$ is unstable and $(u_1^*, u_2^*, 0, 0)$ is stable.

This result showed that, for large dispersal rate, if the growth rates for the species v are unequal and if u increases the disparity between the birth rates but preserving the same mean, then u will win and drive v to extinction. But we found out that the proof in Theorem 3.4.7 seemed only true for ε small. If not, it can not guarantee the stability of the equilibrium $(0, 0, v_1^*, v_2^*)$. We leave the process of calculation in the end of this paper. In [2], the authors left two conjectures to be open problems. In conjecture 1, they supposed that the global stability for Theorem 3.4.7 is also true. On the other hand, in conjecture 2, if the dispersal rate is small enough, then system (3.28) has a positive equilibrium which is globally asymptotically stable. We state these conjectures in [2] as follows :

Conjecture 1 If $\beta_2 > \beta_1$ and $\alpha_1 = \beta_1 - \varepsilon, \alpha_2 = \beta_2 + \varepsilon$ with $0 < \varepsilon < \beta_1$ and d sufficient large. If initial point from $\bar{\mathbb{R}}_+^{2\times 2}$ with $u_1(0) + u_2(0) > 0$, then $\lim_{t\to\infty}(u_1(t), u_2(t), v_1(t), v_2(t)) = (u_1^*, u_2^*, 0, 0)$.

Conjecture 2 If $\beta_2 > \beta_1$ and $\alpha_1 = \beta_1 - \varepsilon, \alpha_2 = \beta_2 + \varepsilon$ with $0 < \varepsilon < \beta_1$. Assume d is small enough such that system (3.28) has a positive steady state E^*. If initial point from $\bar{\mathbb{R}}_+^{2\times 2}$ with $u_1(0) + u_2(0) > 0, v_1(0) + v_2(0) > 0$, then $\lim_{t\to\infty}(u_1(t), u_2(t), v_1(t), v_2(t)) = E^*$.

They said that if these conjectures are true, it suggest that species that can concentrate its growth in a single patch wins for the large dispersal rate. In short, the winning strategy is simply to focus as much growth in a single patch as possible.

First of all, we want to know how the dispersal rate d effects the existence of positive equilibrium for system (3.28) under assumption (3.33).

Theorem 3.4.8. Under assumption (3.33), system (3.28) has a positive equilibrium $(u_1^*, u_2^*, v_1^*, v_2^*)$ if and only if $d < \bar{d}$, where

$$\bar{d} := \frac{(\alpha_2^2 - \alpha_1^2) - \sqrt{(\alpha_2^2 - \alpha_1^2)^2 - 16\beta_1\beta_2\varepsilon(\beta_2 - \alpha_1)}}{8(\beta_2 - \alpha_1)}.$$

Moreover, if we set

$$0 < \beta_1 - \varepsilon_1 = \alpha_1 < \beta_1 < \beta_2 < \alpha_2 = \beta_2 + \varepsilon_2, \varepsilon_2 \geq \varepsilon_1 > 0, \qquad (3.34)$$

then the same assertion holds, and $\bar{d}$ can be estimated as

$$\frac{\alpha_1\alpha_2\varepsilon_1\varepsilon_2}{\alpha_2^2\varepsilon_2 - \alpha_1^2\varepsilon_1} < \bar{d} < \frac{\beta_1\beta_2\varepsilon_1\varepsilon_2}{\beta_2^2\varepsilon_2 - \beta_1^2\varepsilon_1}.$$

However, it is not easy to solve $\bar{d}$ under assumption (3.34). Using this result and Theorem 3.4.6, we can deduce that system (3.28) has a asymptotically stable equilibrium E^* if and only if $d < \bar{d}$. And Theorem 3.4.6 is true for the parameters setting (3.34). Next, we will show that the solution flow will go into a bounded region during a period of time. To formulate this result, we explain system (3.28) is a monotone dynamical system first. We introduce some definition as follows.

A $n \times n$ matrix $\mathbf{A}$ is called a cooperative matrix if all off-diagonal entries of $\mathbf{A}$ are nonnegative. $\mathbf{A}$ is called a type-K cooperative matrix if $\mathbf{A}$ has the form

$$\begin{bmatrix} A_1 & -A_2 \\ -A_3 & A_4 \end{bmatrix}, \tag{3.35}$$

where A_1, A_4 are $k \times k, (n-k) \times (n-k)$ cooperative matrix, respectively. A_2 and A_3 are nonnegative matrices. A system of differential equations $\dot{\mathbf{x}} = f(\mathbf{x})$ on $\mathbb{R}^n_+$ is called a type-K monotone system if the Jacobian matrix $\mathbf{D}f(\mathbf{x})$ of f is type-K cooperative at any $x \in \mathbb{R}^n_+$. We note that system (3.28) is a type-K monotone system since the Jacobian matrix is given by

$$\begin{bmatrix} \alpha_1 - 2u_1 - v_1 - d & d & -u_1 & 0 \\ d & \alpha_2 - 2u_2 - v_2 - d & 0 & -u_2 \\ -v_1 & 0 & \beta_1 - 2v_1 - u_1 - d & d \\ 0 & -v_2 & d & \beta_2 - 2v_2 - u_2 - d \end{bmatrix}.$$

Let

$$K = \{x \in \mathbb{R}^n : x_i \geq 0, 1 \leq i \leq k, x_j \leq 0, k+1 \leq j \leq n\} \tag{3.36}$$

be a closed cone. We define the order relation,

$$x \leq_K y \Leftrightarrow y - x \in K.$$

A semiflow ψ is said to be type-K monotone with respect to ordering $\leq_K$ if

$$\psi_t(x) \leq_K \psi_t(y) \text{ whenever } x \leq_K y \text{ and } t \geq 0. \tag{3.37}$$

Smith showed that the flow generated by a type-K monotone system is type-K monotone [20]. A vector function $f = (f_1, \ldots, f_n)$ of a vector variable $x = (x_1, \ldots, x_n)$ will be said to be of type K in a set S if for each $i = 1, \ldots, n$, $f_i(a) \leq f_i(b)$ for any two points $a = (a_1, \ldots, a_n), b = (b_1, \ldots, b_n)$ in S with $a_i = b_i$ and $a_k \leq b_k, k \neq i$.

Note that for an arbitrary scalar function is of type-K since the condition holds for $n = 1$ clearly. Herein, system (3.28) is also of type-K.

Let

$$\dot{\mathbf{x}} = f(t, \mathbf{x}) \tag{3.38}$$

Theorem 3.4.9 (Kamke, 1932)[8]. Let $f(t, \mathbf{x})$ be continuous in an open set $\mathbb{R}^+ \times D$ and of type-K for each fixed t. Let $x(t)$ be a solution of (3.38) on an interval $[a, b]$. If $y(t)$ is continuous on $[a, b]$ and satisfies $D_r y(t) \geq f(t, y)$ on (a, b) and $y(a) \geq x(a)$, then $y(t) \geq x(t)$ for $a \leq t \leq b$. If $z(t)$ is continuous on $[a, b]$ and satisfies $D_l z(t) \leq f(t, z)$ on (a, b) and $z(a) \leq x(a)$, then $z(t) \leq x(t)$ for $a \leq t \leq b$.

By Theorem 3.4.9, we construct the upper and lower systems for (3.28) under assumption (3.34). Let $u_1 + v_1 = \omega_1$ and $u_2 + v_2 = \omega_2$. From (3.28), we have

$$\begin{aligned} \frac{du_1}{dt} + \frac{dv_1}{dt} &= u_1(\alpha_1 - u_1 - v_1) + d(u_2 - u_1) + v_1(\beta_1 - u_1 + v_1) + d(v_2 - v_1) \\ &= (u_1 + v_1)(\beta_1 - u_1 - v_1) - \varepsilon_1 u_1 + d[(u_2 + v_2) - (u_1 + v_1)] \\ &\leq \omega_1(\beta_1 - \omega_1) + d(\omega_2 - \omega_1) \end{aligned}$$

and

$$\begin{aligned} \frac{du_2}{dt} + \frac{dv_2}{dt} &= u_2(\alpha_2 - u_2 - v_2) + d(u_1 - u_2) + v_2(\beta_2 - u_2 - v_2) + d(v_1 - v_2) \\ &= (u_2 + v_2)(\alpha_2 - u_2 - v_2) - \varepsilon_2 v_2 + d[(u_1 + v_1) - (u_2 + v_2)] \\ &\leq \omega_2(\alpha_2 - \omega_2) + d(\omega_1 - \omega_2). \end{aligned}$$

We define

$$\begin{aligned} \frac{d\hat{\omega}_1}{dt} &:= \hat{\omega}_1(\beta_1 - \hat{\omega}_1) + d(\hat{\omega}_2 - \hat{\omega}_1) \\ \frac{d\hat{\omega}_2}{dt} &:= \hat{\omega}_2(\alpha_2 - \hat{\omega}_2) + d(\hat{\omega}_1 - \hat{\omega}_2). \end{aligned} \tag{3.39}$$

Similarly, we have

$$\begin{aligned} \frac{du_1}{dt} + \frac{dv_1}{dt} &= u_1(\alpha_1 - u_1 - v_1) + d(u_2 - u_1) + v_1(\beta_1 - u_1 + v_1) + d(v_2 - v_1) \\ &= (u_1 + v_1)(\alpha_1 - u_1 + v_1) + \varepsilon_1 v_1 + d[(u_2 + v_2) - (u_1 + v_1)] \\ &\geq \omega_1(\alpha_1 - \omega_1) + d(\omega_2 - \omega_1) \end{aligned}$$

and

$$\begin{aligned} \frac{du_2}{dt} + \frac{dv_2}{dt} &= u_2(\alpha_2 - u_2 - v_2) + d(u_1 - u_2) + v_2(\beta_2 - u_2 - v_2) + d(v_1 - v_2) \\ &= (u_2 + v_2)(\beta_2 - u_2 + v_2) + \varepsilon_2 u_2 + d[(u_1 + v_1) - (u_2 + v_2)] \\ &\geq \omega_2(\beta_2 - \omega_2) + d(\omega_1 - \omega_2). \end{aligned}$$

We define

$$\begin{aligned}\frac{d\breve{w}_1}{dt} &:= \breve{w}_1(\alpha_1 - \breve{w}_1) + d(\breve{w}_2 - \breve{w}_1)\\ \frac{d\breve{w}_2}{dt} &:= \breve{w}_2(\beta_2 - \breve{w}_2) + d(\breve{w}_1 - \breve{w}_2).\end{aligned} \tag{3.40}$$

Here we study the behavior of two systems (3.39), (3.40) and give two results which have been proved by [9, 10, 15].

Theorem 3.4.10. The equilibrium $(\hat{\bar{\omega}}_1, \hat{\bar{\omega}}_2)$ of system (3.39) is globally asymptotically stable among all positive initial data.

Theorem 3.4.11. The equilibrium $(\check{\bar{\omega}}_1, \check{\bar{\omega}}_2)$ of system (3.40) is globally asymptotically stable among all positive initial data.

With the above results and Theorem 3.4.9, we have the following corollary to construct the invariant set $\bar{\Omega}$ for system (3.28).

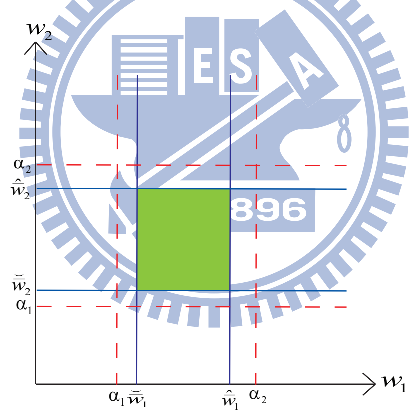

Figure 5: The bounded above and bounded below for ω_1 and ω_2.

Corollary 3.4.12. Under assumption (3.34), we have following properties

(i) $\check{\bar{\omega}}_1 \le \hat{\bar{\omega}}_1; \quad \check{\bar{\omega}}_2 \le \hat{\bar{\omega}}_2,$

(ii) $\beta_1 < \hat{\bar{\omega}}_1 < \hat{\bar{\omega}}_2 < \alpha_2; \alpha_1 < \check{\bar{\omega}}_1 < \check{\bar{\omega}}_2 < \beta_2,$

(iii) $\alpha_1 < \check{\bar{\omega}}_1, \hat{\bar{\omega}}_1, \check{\bar{\omega}}_2, \hat{\bar{\omega}}_2 < \alpha_2,$

(iv) $\hat{\bar{\omega}}_1, \hat{\bar{\omega}}_2 \to \dfrac{\alpha_2 + \beta_1}{2}$ and $\check{\bar{\omega}}_1, \check{\bar{\omega}}_2 \to \dfrac{\alpha_1 + \beta_2}{2}$ as $d \to \infty$.

Define

$$\bar{\Omega} = \left\{(u_1, u_2, v_1, v_2) \in \bar{\mathbb{R}}_+^{2\times 2} : \alpha_1 \leq u_1 + v_1 \leq \alpha_2, \alpha_1 \leq u_2 + v_2 \leq \alpha_2\right\}.$$

Theorem 3.4.13. Under the assumption (3.34), $\bar{\Omega}$ is positively invariant under the solution flow generated by system (3.28).

This result showed that all solutions of system (3.28) will enter the bounded region $\bar{\Omega}$ for a period of time. Next, we state the species synchronize in each patch with large dispersal rate.

Theorem 3.4.14. Under assumption (3.34), then

$$\begin{aligned} -\frac{\alpha_2(\alpha_2-\alpha_1)}{d} + \frac{\alpha_2(\alpha_2-\alpha_1)}{d}e^{-2dt} + (u_1(0)-u_2(0))e^{-2dt} \\ \leq u_1(t)-u_2(t) \leq (u_1(0)-u_2(0))e^{-2dt} \end{aligned}$$

$$\begin{aligned} -\frac{\beta_2(\beta_2-\beta_1+\varepsilon_2)}{d} + \frac{\beta_2(\beta_2-\beta_1+\varepsilon_2)}{d}e^{-2dt} + (v_1(0)-v_2(0))e^{-2dt} \\ \leq v_1(t)-v_2(t) \leq \frac{\varepsilon_2\beta_2}{d} - \frac{\varepsilon_2\beta_2}{d}e^{-2dt} + (v_1(0)-v_2(0))e^{-2dt} \end{aligned}$$

with initial point $(u_1(0)-u_2(0))$ and $(v_1(0)-v_2(0))$ start from the region $\bar{\Omega}$ at $t=0$. Then $u_1 - u_2$, $v_1 - v_2 \to O(\frac{1}{d})$ as $t \to \infty$.

We propose similar conjectures with an assumption weaker than [2].

Conjecture 3.4.15. Under the assumption (3.34),
(i) If initial point from $\bar{\Omega}$ with $u_1(0) + u_2(0) > 0$, and $d \geq \bar{d}$, then system (3.28) has no positive equilibrium and

$$\lim_{t\to\infty}(u_1(t), u_2(t), v_1(t), v_2(t)) = (u_1^*, u_2^*, 0, 0).$$

(ii) If initial point from $\bar{\Omega}$ with $u_1(0) + u_2(0) > 0$, $v_1(0) + v_2(0) > 0$ and $d < \bar{d}$, then system (3.28) has a positive equilibrium which is globally asymptotically stable.

Finally, we summarize an unsolved problem. We have shown that all solutions with initial point from $\mathbb{R}_+^{2\times 2}$ will enter a bounded region $\bar{\Omega}$ which is positive invariant. Next, we want to construct a Lyapunov function for system (3.28) with initial data starting from the positive invariant set except from $\tilde{\mathbb{R}}_+^{2\times 0}$ and $\tilde{\mathbb{R}}_+^{0\times 2}$. For the semi-trivial equilibrium $(u_1^*, u_2^*, 0, 0)$, we have tried

$$V_1 = u_1^* \left[u_1 + v_1 - u_1^* - u_1^* \ln\left(\frac{u_1}{u_1^*}\right)\right] + u_2^* \left[u_2 + v_2 - u_2^* - u_2^* \ln\left(\frac{u_2}{u_2^*}\right)\right], \quad (3.41)$$

and for the positive equilibrium $(u_1^*, u_2^*, v_1^*, v_2^*)$, we have tried

$$\begin{aligned} V_2 = {} & u_1^* \left[u_1 - u_1^* - u_1^* \ln\left(\frac{u_1}{u_1^*}\right) + v_1 - v_1^* - v_1^* \ln\left(\frac{v_1}{v_1^*}\right)\right] \\ & + u_2^* \left[u_2 - u_2^* - u_2^* \ln\left(\frac{u_2}{u_2^*}\right) + v_2 - v_2^* - v_2^* \ln\left(\frac{v_2}{v_2^*}\right)\right]. \end{aligned} \quad (3.42)$$

But it is difficult to check the time derivatives of V_1, V_2 are all non-positive. Whether this two Lyapunov functions does not work to verify the global dynamics of system (3.28) or there has more conditions in the positive invariant set we need to check to guarantee the process of computation of $\dot{V}$. It seems to need more mathematical analysis.

3.5 Proofs

Proof of Proposition 3.4.1. Let initial points start from $\tilde{\mathbb{R}}_+^{2\times 0}$ and $u_1(0) = 0$. Since $u_1(0) + u_2(0) > 0$, we have

$$\frac{du_1(0)}{dt} = du_2(0) > 0.$$

Then $\tilde{\mathbb{R}}_+^{2\times 0}$ is positively invariant. Similarly for $\tilde{\mathbb{R}}_+^{0\times 2}$. Clearly, $\tilde{\mathbb{R}}_+^{2\times 0} \subset \bar{\mathbb{R}}_+^{2\times 2}$ and $\tilde{\mathbb{R}}_+^{0\times 2} \subset \bar{\mathbb{R}}_+^{2\times 2}$. With initial point $(u_1(0), u_2(0), v_1(0), v_2(0)) \in \bar{\mathbb{R}}_+^{2\times 2}$,

$$\begin{aligned} &\text{if } u_1(0) = 0 \quad \text{then } \frac{du_1(0)}{dt} = du_2(0) \geq 0; \\ &\text{if } u_2(0) = 0 \quad \text{then } \frac{du_2(0)}{dt} = du_1(0) \geq 0; \\ &\text{if } v_1(0) = 0 \quad \text{then } \frac{dv_1(0)}{dt} = dv_2(0) \geq 0; \\ &\text{if } v_2(0) = 0 \quad \text{then } \frac{dv_2(0)}{dt} = dv_1(0) \geq 0. \end{aligned}$$

When $u_1(0) = 0$ and $\frac{du_1(0)}{dt} = du_2(0) = 0$, namely, $u_1(0) = u_2(0) = 0$, we have already proved that $\{(0, 0, v_1, v_2)\} \subset \bar{\mathbb{R}}_+^{0\times 2}$ is positively invariant and $\tilde{\mathbb{R}}_+^{2\times 0} \subset \bar{\mathbb{R}}_+^{2\times 2}$. Hence, $\bar{\mathbb{R}}_+^{2\times 2}$ is positively invariant.

Proof of Proposition 3.4.2.

$$\begin{aligned}\frac{d(u_1+u_2)}{dt} &= u_1(\alpha_1-u_1-v_1)+u_2(\alpha_2-u_2-v_2)\\ &= \alpha_1u_1+\alpha_2u_2-u_1^2-u_2^2-u_1v_1-u_2v_2\\ &\le \max\{\alpha_1,\alpha_2\}(u_1+u_2)-\frac{1}{2}(u_1+u_2)^2\\ &\le (u_1+u_2)\left\{\max\{\alpha_1,\alpha_2\}-\frac{1}{2}(u_1+u_2)\right\}.\end{aligned}$$

Similarly,

$$\frac{d(v_1+v_2)}{dt}\le (v_1+v_2)\left\{\max\{\beta_1,\beta_2\}-\frac{1}{2}(v_1+v_2)\right\}.$$

Thus,

$$\limsup_{t\to\infty}(u_1+u_2)\le 2\max\{\alpha_1,\alpha_2\},$$

and

$$\limsup_{t\to\infty}(v_1+v_2)\le 2\max\{\beta_1,\beta_2\}.$$

Proof of Proposition 3.4.3. Define the Lyapunov function $V:\tilde{\mathbb{R}}_+^{2\times 0}\to\mathbb{R}$ by

$$V(u_1,u_2,0,0)=u_1^*\left(u_1-u_1^*-u_1^*\ln\left(\frac{u_1}{u_1^*}\right)\right)+u_2^*\left(u_2-u_2^*-u_2^*\ln\left(\frac{u_2}{u_2^*}\right)\right). \quad (3.43)$$

With initial point $(u_1,u_2,0,0)\in\tilde{\mathbb{R}}_+^{2\times 0}$, then

$$\begin{aligned}\dot V(u_1,u_2,0,0) &= u_1^*\left[u_1(\alpha_1-u_1)+d(u_2-u_1)-u_1^*(\alpha_1-u_1)-du_1^*\left(\frac{u_2}{u_1}-1\right)\right]\\ &+ u_2^*\left[u_2(\alpha_2-u_2)+d(u_1-u_2)-u_2^*(\alpha_2-u_2)-du_2^*\left(\frac{u_1}{u_2}-1\right)\right]\\ &= u_1^*\left[(u_1-u_1^*)[-(u_1-u_1^*)+(\alpha_1-u_1^*)]+d(u_2-u_1)-du_1^*\left(\frac{u_2}{u_1}-1\right)\right]\\ &+ u_2^*\left[(u_2-u_2^*)[-(u_2-u_2^*)+(\alpha_2-u_2^*)]+d(u_1-u_2)-du_2^*\left(\frac{u_1}{u_2}-1\right)\right]\\ &= u_1^*\left[-(u_1-u_1^*)^2+(u_1-u_1^*)(\alpha_1-u_1^*)+d(u_2-u_1)-du_1^*\left(\frac{u_2}{u_1}-1\right)\right]\\ &+ u_2^*\left[-(u_2-u_2^*)^2+(u_2-u_2^*)(\alpha_2-u_2^*)+d(u_1-u_2)-du_2^*\left(\frac{u_1}{u_2}-1\right)\right]\\ &\le u_1^*\left[(u_1-u_1^*)(\alpha_1-u_1^*)+d(u_2-u_1)-du_1^*\left(\frac{u_2}{u_1}-1\right)\right]\\ &+ u_2^*\left[(u_2-u_2^*)(\alpha_2-u_2^*)+d(u_1-u_2)-du_2^*\left(\frac{u_1}{u_2}-1\right)\right].\end{aligned}$$

The equality holds if and only if $u_1 = u_1^*$ and $u_2 = u_2^*$. Since

$$\alpha_1 - u_1^* = -d\left(\frac{u_2}{u_1^*} - 1\right), \quad \alpha_2 - u_2^* = -d\left(\frac{u_1}{u_2^*} - 1\right), \tag{3.44}$$

we have

$$\begin{aligned}
\dot{V}(u_1, u_2, 0, 0) &\leq u_1^*\left[(u_1 - u_1^*)\left[-d\left(\frac{u_2^*}{u_1^*} - 1\right)\right] + d(u_2 - u_1) - du_1^*\left(\frac{u_2}{u_1} - 1\right)\right] \\
&+ u_2^*\left[(u_2 - u_2^*)\left[-d\left(\frac{u_1^*}{u_2^*} - 1\right)\right] + d(u_1 - u_2) - du_2^*\left(\frac{u_1}{u_2} - 1\right)\right] \\
&= u_1^* du_2^*\left(-\frac{u_1}{u_1^*} + 1 + \frac{u_2}{u_2^*} - \frac{u_1^* u_2}{u_1 u_2^*}\right) + u_2^* du_1^*\left(-\frac{u_2}{u_2^*} + 1 + \frac{u_1}{u_1^*} - \frac{u_1 u_2^*}{u_1^* u_2}\right) \\
&= du_1^* u_2^*\left[2 - \left(\frac{u_1^* u_2}{u_1 u_2^*} + \frac{u_1 u_2^*}{u_1^* u_2}\right)\right] \\
&\leq 0
\end{aligned}$$

since $a^2 + b^2 \geq 2ab$. The equality holds if and only if $u_1^* u_2 = u_1 u_2^*$. Hence, $\dot{V}(u_1, u_2, 0, 0) \leq 0$ and the equality holds if and only if $u_1 = \bar{u}_1$ and $u_2 = \bar{u}_2$. By the Lyapunov stability theory, the solutions starting from initial data in $\tilde{\mathbb{R}}_+^{2\times 0}$ will converge to the semi-trivial equilibrium $(u_1^*, u_2^*, 0, 0)$ of system (3.28).

Proof of Proposition 3.4.4. The proof of Proposition 3.4.4 is similar to Proposition 3.4.3. By constructing the Lyapunov function $V : \tilde{\mathbb{R}}_+^{0\times 2} \to \mathbb{R}$,

$$V(0, 0, v_1, v_2) = v_1^*\left(v_1 - v_1^* - v_1^* \ln\left(\frac{v_1}{v_1^*}\right)\right) + v_2^*\left(v_2 - v_2^* - v_2^* \ln\left(\frac{v_2}{v_2^*}\right)\right). \tag{3.45}$$

Proof of Proposition 3.4.5. The variational matrix of corresponding linearized system of (3.28) with $d = 0$ is given by

$$\mathbf{A}(u_1, u_2, v_1, v_2) = \begin{bmatrix} \alpha_1 - 2u_1 - v_1 & 0 & -u_1 & 0 \\ 0 & \alpha_2 - 2u_2 - v_2 & 0 & -u_2 \\ -v_1 & 0 & \beta_1 - 2v_1 - u_1 & 0 \\ 0 & -v_2 & 0 & \beta_2 - 2v_2 - u_2 \end{bmatrix}$$

Then we have

$$\mathbf{A}(E_0) = \begin{bmatrix} \alpha_1 & 0 & 0 & 0 \\ 0 & \alpha_2 & 0 & 0 \\ 0 & 0 & \beta_1 & 0 \\ 0 & 0 & 0 & \beta_2 \end{bmatrix}, \ \mathbf{A}(E_1) = \begin{bmatrix} -\alpha_1 & 0 & -\alpha_1 & 0 \\ 0 & \alpha_2 & 0 & 0 \\ 0 & 0 & \beta_1 - \alpha_1 & 0 \\ 0 & 0 & 0 & \beta_2 \end{bmatrix},$$

$$\mathbf{A}(E_2) = \begin{bmatrix} \alpha_1 & 0 & 0 & 0 \\ 0 & -\alpha_2 & 0 & -\alpha_2 \\ 0 & 0 & \beta_1 & 0 \\ 0 & 0 & 0 & \beta_2-\alpha_2 \end{bmatrix}, \ \mathbf{A}(E_3) = \begin{bmatrix} \alpha_1-\beta_1 & 0 & 0 & 0 \\ 0 & \alpha_2 & 0 & 0 \\ -\beta_1 & 0 & -\beta_1 & 0 \\ 0 & 0 & 0 & \beta_2 \end{bmatrix},$$

$$\mathbf{A}(E_4) = \begin{bmatrix} \alpha_1 & 0 & 0 & 0 \\ 0 & \alpha_2-\beta_2 & 0 & 0 \\ 0 & 0 & \beta_1 & 0 \\ 0 & -\beta_2 & 0 & -\beta_2 \end{bmatrix}, \ \mathbf{A}(E_5) = \begin{bmatrix} -\alpha_1 & 0 & -\alpha_1 & 0 \\ 0 & -\alpha_2 & 0 & -\alpha_2 \\ 0 & 0 & \beta_1-\alpha_1 & 0 \\ 0 & 0 & 0 & \beta_2-\alpha_2 \end{bmatrix},$$

$$\mathbf{A}(E_6) = \begin{bmatrix} \alpha_1-\beta_1 & 0 & 0 & 0 \\ 0 & \alpha_2-\beta_2 & 0 & 0 \\ -\beta_1 & 0 & -\beta_1 & 0 \\ 0 & -\beta_2 & 0 & -\beta_2 \end{bmatrix}, \ \mathbf{A}(E_7) = \begin{bmatrix} \alpha_1-\beta_1 & 0 & 0 & 0 \\ 0 & -\alpha_2 & 0 & -\alpha_2 \\ -\beta_1 & 0 & -\beta_1 & 0 \\ 0 & 0 & 0 & \beta_2-\alpha_2 \end{bmatrix},$$

and

$$\mathbf{A}(E_8) = \begin{bmatrix} -\alpha_1 & 0 & -\alpha_1 & 0 \\ 0 & \alpha_2-\beta_2 & 0 & 0 \\ 0 & 0 & \beta_1-\alpha_1 & 0 \\ 0 & -\beta_2 & 0 & -\beta_2 \end{bmatrix},$$

We can find that the diagonal elements of each matrices are eigenvalues for the corresponding matrices. And all parameters $\alpha_i, \beta_i > 0$ and are different. Hence, we can deduced the following results (i). E_0, E_1, E_2, E_3 and E_4 are all unstable. (ii). If $\alpha_1 < \beta_1$ and $\beta_2 < \alpha_2$, then only E_7 is stable. (iii). If $\alpha_1 > \beta_1$ and $\beta_2 > \alpha_2$, then only E_8 is stable. (iv). If $\alpha_1 > \beta_1$ and $\beta_2 < \alpha_2$, then only E_5 is stable. (v). If $\alpha_1 < \beta_1$ and $\beta_2 > \alpha_2$, then only E_6 is stable.

Proof of Theorem 3.4.6. The system has a positive equilibrium $\bar{E} = (\bar{u}_1, \bar{u}_2, \bar{v}_1, \bar{v}_2)$ satisfying the following system of equations

$$\begin{aligned} &(\alpha_1 - \bar{u}_1 - \bar{v}_1) + d(\frac{\bar{u}_2}{\bar{u}_1} - 1) = 0, \quad (\alpha_2 - \bar{u}_2 - \bar{v}_2) + d(\frac{\bar{u}_1}{\bar{u}_2} - 1) = 0, \\ &(\beta_1 - \bar{v}_1 - \bar{u}_1) + d(\frac{\bar{v}_2}{\bar{v}_1} - 1) = 0, \quad (\beta_2 - \bar{v}_2 - \bar{u}_2) + d(\frac{\bar{v}_1}{\bar{v}_2} - 1) = 0. \end{aligned} \tag{3.46}$$

It follows that

$$\begin{aligned} \alpha_1 - \bar{u}_1 - \bar{v}_1 = d(1 - \frac{\bar{u}_2}{\bar{u}_1}), \quad \alpha_2 - \bar{u}_2 - \bar{v}_2 = d(1 - \frac{\bar{u}_1}{\bar{u}_2}), \\ \beta_1 - \bar{v}_1 - \bar{u}_1 = d(1 - \frac{\bar{v}_2}{\bar{v}_1}), \quad \beta_2 - \bar{v}_2 - \bar{u}_2 = d(1 - \frac{\bar{v}_1}{\bar{v}_2}). \end{aligned} \tag{3.47}$$

Now, form the linearized analysis, the variational matrix at $\bar{E}$ is

$$\mathbf{A}(\bar{E}) = \begin{bmatrix} \alpha_1 - 2\bar{u}_1 - \bar{v}_1 - d & d & -\bar{u}_1 & 0 \\ d & \alpha_2 - 2\bar{u}_2 - \bar{v}_2 - d & 0 & -\bar{u}_2 \\ -\bar{v}_1 & 0 & \beta_1 - 2\bar{v}_1 - \bar{u}_1 - d & d \\ 0 & -\bar{v}_2 & d & \beta_2 - 2\bar{v}_2 - \bar{u}_2 - d \end{bmatrix}$$

$$= \begin{bmatrix} -\bar{u}_1 - \frac{d\bar{u}_2}{\bar{u}_1} & d & -\bar{u}_1 & 0 \\ d & -\bar{u}_2 - \frac{d\bar{u}_1}{\bar{u}_2} & 0 & -\bar{u}_2 \\ -\bar{v}_1 & 0 & -\bar{v}_1 - \frac{d\bar{v}_2}{\bar{v}_1} & d \\ 0 & -\bar{v}_2 & d & -\bar{v}_2 - \frac{d\bar{v}_1}{\bar{v}_2} \end{bmatrix}$$

The corresponding characteristic polynomial is

$$P(\lambda) = \lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4, \tag{3.48}$$

where

$$\begin{aligned}
a_1 &= \bar{u}_1 + \bar{u}_2 + \bar{v}_1 + \bar{v}_2 + d(\frac{\bar{u}_2}{\bar{u}_1} + \frac{\bar{u}_1}{\bar{u}_2} + \frac{\bar{v}_2}{\bar{v}_1} + \frac{\bar{v}_1}{\bar{v}_2}), \\
a_2 &= \frac{1}{M}(\bar{u}_1\bar{u}_2\bar{v}_1^2\bar{v}_2^2 + \bar{u}_1^2\bar{u}_2\bar{v}_1\bar{v}_2^2 + \bar{u}_1\bar{u}_2^2\bar{v}_1^2\bar{v}_2 + \bar{u}_1^2\bar{u}_2^2\bar{v}_1\bar{v}_2 + d(\bar{u}_1\bar{u}_2\bar{v}_1^3 + \bar{u}_1\bar{u}_2\bar{v}_2^3 \\
&\quad + \bar{u}_1^3\bar{v}_1\bar{v}_2 + \bar{u}_2^3\bar{v}_1\bar{v}_2) + d(\bar{u}_1^2\bar{v}_1\bar{v}_2^2 + \bar{u}_2^2\bar{v}_1\bar{v}_2^2 + \bar{u}_1\bar{u}_2^2\bar{v}_1^2 + \bar{u}_1^2\bar{u}_2\bar{v}_1^2 \\
&\quad + \bar{u}_2^2\bar{v}_1\bar{v}_2^2 + \bar{u}_2\bar{v}_1^2\bar{v}_2 + \bar{u}_1\bar{u}_2^2\bar{v}_2^2 + \bar{u}_1^2\bar{u}_2\bar{v}_2^2) + d^2(\bar{u}_1^2 + \bar{u}_2^2)(\bar{v}_1^2 + \bar{v}_2^2), \\
a_3 &= \frac{d}{M}\{\bar{u}_1^2\bar{u}_2^2(\bar{v}_1^2 + \bar{v}_2^2) + \bar{v}_1^2\bar{v}_2^2(\bar{u}_1^2 + \bar{u}_2^2) + (\bar{u}_1\bar{v}_1 + \bar{u}_2\bar{v}_2)(\bar{u}_1^2 + \bar{v}_2^2 + \bar{u}_2^2 + \bar{v}_1^2) \\
&\quad + d[(\bar{u}_1^2 + \bar{u}_2^2)(\bar{v}_1^3 + \bar{v}_2^3) + (\bar{v}_1^2 + \bar{v}_2^2)(\bar{u}_1^3 + \bar{u}_2^3)]\}, \\
a_4 &= \frac{d^2}{M}(\bar{u}_1\bar{v}_2 + \bar{u}_2\bar{v}_1)(\bar{u}_1\bar{v}_2 - \bar{u}_2\bar{v}_1)^2, M = \bar{u}_1\bar{u}_2\bar{v}_1\bar{v}_2.
\end{aligned}$$

Hence, using mathematical computation software "Maple", we have

$$\Delta_1 = a_1 > 0, \Delta_2 = \begin{vmatrix} a_1 & 1 \\ a_3 & a_2 \end{vmatrix} = a_1 a_2 - a_3 > 0,$$

$$\Delta_3 = \begin{vmatrix} a_1 & 1 & 0 \\ a_3 & a_2 & a_1 \\ 0 & a_4 & a_3 \end{vmatrix} > 0, \Delta_4 = \begin{vmatrix} a_1 & 1 & 0 & 0 \\ a_3 & a_2 & a_1 & 1 \\ 0 & a_4 & a_3 & a_2 \\ 0 & 0 & 0 & a_4 \end{vmatrix} = a_4\Delta_3 > 0.$$

By the Routh-Hurwitz stability criterion, the real part of eigenvalues of $\mathbf{A}(\bar{E})$ are all negative. Hence, the equilibrium $\bar{E}$ is stable in system (3.28).

Review the Theorem 3.4.7. The proof in [2] is to check the local stability of two semi-trivial equilibria $(u_1^*, u_2^*, 0, 0)$ and $(0, 0, v_1^*, v_2^*)$. It satisfies the equations

$$\begin{aligned} u_1^*(\alpha_1 - u_1^*) + d(u_2^* - u_1^*) = 0, \\ u_2^*(\alpha_2 - u_2^*) + d(u_1^* - u_2^*) = 0, \end{aligned} \tag{3.49}$$

and

$$\begin{aligned} v_1^*(\beta_1 - v_1^*) + d(v_2^* - v_1^*) &= 0, \\ v_2^*(\beta_2 - v_2^*) + d(v_1^* - v_2^*) &= 0. \end{aligned} \tag{3.50}$$

respectively. From (3.49) and (3.50), we have

$$u_1^* = \frac{u_2^*}{d}(u_2^* - \alpha_2) + u_2^*, \tag{3.51}$$

and

$$v_1^* = \frac{v_2^*}{d}(v_2^* - \beta_2) + v_2^*. \tag{3.52}$$

Now, from the corresponding linearized system of (3.28), the variational matrices at this two equilibria are

$$\mathbf{A}(u_1^*, u_2^*, 0, 0) = \begin{bmatrix} \alpha_1 - 2u_1^* - d & d & -u_1^* & 0 \\ d & \alpha_2 - 2u_2^* - d & 0 & -u_2^* \\ 0 & 0 & \beta_1 - u_1^* - d & d \\ 0 & 0 & d & \beta_2 - u_2^* - d \end{bmatrix}$$

and

$$\mathbf{A}(0, 0, v_1^*, v_2^*) = \begin{bmatrix} \alpha_1 - v_1^* - d & d & 0 & 0 \\ d & \alpha_2 - v_2^* - d & 0 & 0 \\ -v_1^* & 0 & \beta_1 - 2v_1^* - d & d \\ 0 & -v_2^* & d & \beta_2 - 2v_2^* - d \end{bmatrix}.$$

Since those matrix have a block diagonal structure, we only need to check the signs of trace and determinant for their 2×2 diagonal blocks matrices. That is, for d large, we need to check

$$(\alpha_1 - 2u_1^*)(\alpha_2 - 2u_2^*) - d(\alpha_1 + \alpha_2 - 2u_1^* - 2u_2^*) > 0$$

and

$$(\beta_1 - u_1^*)(\beta_2 - u_2^*) - d(\beta_1 + \beta_2 - u_1^* - u_2^*) > 0.$$

On the other hand,

$$(\alpha_1 - v_1^*)(\alpha_2 - v_2^*) - d(\alpha_1 + \alpha_2 - v_1^* - v_2^*) < 0$$

or

$$(\beta_1 - 2v_1^*)(\beta_2 - 2v_2^*) - d(\beta_1 + \beta_2 - 2v_1^* - 2v_2^*) < 0.$$

Using (3.51) and setting $(\beta_1-u_1^*)(\beta_2-u_2^*)-d(\beta_1+\beta_2-u_1^*-u_2^*)=0$, from asymptotic analysis, we yield that

$$\begin{aligned} u_1^* &= \frac{\alpha_1+\alpha_2}{2}+\frac{1}{2d}[(\frac{\beta_2-\beta_1}{2})^2-(\frac{\beta_2+\beta_1}{2})(\varepsilon+\frac{\beta_2-\beta_1}{2})]+O(\frac{1}{d^2}),\\ u_2^* &= \frac{\alpha_1+\alpha_2}{2}+\frac{1}{2d}[(\frac{\beta_2-\beta_1}{2})^2+(\frac{\beta_2+\beta_1}{2})(\varepsilon+\frac{\beta_2-\beta_1}{2})]+O(\frac{1}{d^2}). \end{aligned} \tag{3.53}$$

Similarly, use (3.52) and set $(\alpha_1-v_1^*)(\alpha_2-v_2^*)-d(\alpha_1+\alpha_2-v_1^*-v_2^*)=0$, then we have

$$\begin{aligned} v_1^* &= \frac{\beta_1+\beta_2}{2}+\frac{1}{8d}[(\beta_2-\beta_1+2\varepsilon)^2+(\beta_1^2-\beta_2^2)]+O(\frac{1}{d^2}),\\ v_2^* &= \frac{\beta_1+\beta_2}{2}+\frac{1}{8d}[(\beta_2-\beta_1+2\varepsilon)^2-(\beta_1^2-\beta_2^2)]+O(\frac{1}{d^2}), \end{aligned} \tag{3.54}$$

It seems that we need ε is small enough in order that we can get the following formulas in [2],

$$\begin{aligned} u_1^* &= \frac{\alpha_1+\alpha_2}{2}-\frac{\alpha_1}{4d}(\alpha_2-\alpha_1)+O(\frac{1}{d^2}),\\ u_2^* &= \frac{\alpha_1+\alpha_2}{2}+\frac{\alpha_2}{4d}(\alpha_2-\alpha_1)+O(\frac{1}{d^2}). \end{aligned} \tag{3.55}$$

and

$$\begin{aligned} v_1^* &= \frac{\beta_1+\beta_2}{2}-\frac{\beta_1}{4d}(\beta_2-\beta_1)+O(\frac{1}{d^2}),\\ v_2^* &= \frac{\beta_1+\beta_2}{2}+\frac{\beta_2}{4d}(\beta_2-\beta_1)+O(\frac{1}{d^2}). \end{aligned} \tag{3.56}$$

Unfortunately, if ε not small, by (3.54), we get

$$\begin{aligned} &(\alpha_1-v_1^*)(\alpha_2-v_2^*)-d(\alpha_1+\alpha_2-v_1^*-v_2^*)\\ &\quad =-(\frac{\alpha_2-\alpha_1}{8d})(\beta_1^2-\beta_2^2)+O(\frac{1}{d^2})>0. \end{aligned} \tag{3.57}$$

and

$$\begin{aligned} &(\beta_1-2v_1^*)(\beta_2-2v_2^*)-d(\beta_1+\beta_2-2v_1^*-2v_2^*)\\ &\quad =d(\beta_1+\beta_2)+O(1)>0. \end{aligned} \tag{3.58}$$

Hence, we can not guarantee the equilibrium $(0,0,v_1^*,v_2^*)$ is unstable. Finally, the calculation about the asymptotic analysis for u_i^* and $v_i^*, i=1,2$ are as follows.

1. Let $u_1^*=f_0+\frac{1}{d}f_1+O(\frac{1}{d^2})$ and $u_2^*=g_0+\frac{1}{d}g_1+O(\frac{1}{d^2})$, where f_i, g_i are the functions

of parameters β_1, β_2. Substituting into the equation (3.51) and $(\beta_1 - u_1^*)(\beta_2 - u_2^*) - d(\beta_1 + \beta_2 - u_1^* - u_2^*) = 0$, and then comparing the coefficient of each order, we have

$$f_0 = g_0, f_1 = g_0(g_0 - \alpha_2) + g_1, f_0 + g_0 = \beta_1 + \beta_2 \text{ and } f_1 + g_1 = -(\beta_1 - f_0)(\beta_2 - g_0).$$

After some computation, we get

$$f_0 = g_0 = \frac{\beta_1 + \beta_2}{2} = \frac{\alpha_1 + \alpha_2}{2}$$

and

$$f_1 = \frac{1}{2}[(\frac{\beta_2 - \beta_1}{2})^2 - (\frac{\beta_2 + \beta_1}{2})(\varepsilon + \frac{\beta_2 - \beta_1}{2})], g_1 = \frac{1}{2}[(\frac{\beta_2 - \beta_1}{2})^2 + (\frac{\beta_2 + \beta_1}{2})(\varepsilon + \frac{\beta_2 - \beta_1}{2})].$$

Hence,

$$u_1^* = \frac{\alpha_1 + \alpha_2}{2} + \frac{1}{2d}[(\frac{\beta_2 - \beta_1}{2})^2 - (\frac{\beta_2 + \beta_1}{2})(\varepsilon + \frac{\beta_2 - \beta_1}{2})] + O(\frac{1}{d^2}),$$
$$u_2^* = \frac{\alpha_1 + \alpha_2}{2} + \frac{1}{2d}[(\frac{\beta_2 - \beta_1}{2})^2 + (\frac{\beta_2 + \beta_1}{2})(\varepsilon + \frac{\beta_2 - \beta_1}{2})] + O(\frac{1}{d^2}).$$

2. Let $v_1^* = f_0 + \frac{1}{d} f_1 + O(\frac{1}{d^2})$ and $v_2^* = g_0 + \frac{1}{d} g_1 + O(\frac{1}{d^2})$, where f_i, g_i are the functions of parameters β_1, β_2. Substituting into the equation (3.52) and $(\alpha_1 - v_1^*)(\alpha_2 - v_2^*) - d(\alpha_1 + \alpha_2 - v_1^* - v_2^*) = 0$, and then comparing the coefficient of each order, we have

$$f_0 = g_0, f_1 = g_0(g_0 - \beta_2) + g_1, f_0 + g_0 = \alpha + \alpha_2 \text{ and } f_1 + g_1 = -(\alpha_1 - f_0)(\alpha_2 - g_0).$$

After some computation, we get

$$f_0 = g_0 = \frac{\alpha_1 + \alpha_2}{2} = \frac{\beta_1 + \beta_2}{2}$$

and

$$f_1 = \frac{1}{8}[(\beta_2 - \beta_1 + 2\varepsilon)^2 + (\beta_1^2 - \beta_2^2)], g_1 = \frac{1}{8}[(\beta_2 - \beta_1 + 2\varepsilon)^2 - (\beta_1^2 - \beta_2^2)].$$

Hence,

$$v_1^* = \frac{\beta_1 + \beta_2}{2} + \frac{1}{8d}[(\beta_2 - \beta_1 + 2\varepsilon)^2 + (\beta_1^2 - \beta_2^2)] + O(\frac{1}{d^2}),$$
$$v_2^* = \frac{\beta_1 + \beta_2}{2} + \frac{1}{8d}[(\beta_2 - \beta_1 + 2\varepsilon)^2 - (\beta_1^2 - \beta_2^2)] + O(\frac{1}{d^2}),$$

Proof of Theorem 3.4.8. System (3.28) has a positive equilibrium $(u_1^*, u_2^*, v_1^*, v_2^*)$ if and only if

$$\begin{aligned}(\alpha_1 - u_1^* - v_1^*) + d(\frac{u_2^*}{u_1^*} - 1) = 0, \quad (\alpha_2 - u_2^* - v_2^*) + d(\frac{u_1^*}{u_2^*} - 1) = 0,\\ (\beta_1 - v_1^* - u_1^*) + d(\frac{v_2^*}{v_1^*} - 1) = 0, \quad (\beta_2 - v_2^* - u_2^*) + d(\frac{v_1^*}{v_2^*} - 1) = 0,\end{aligned} \tag{3.59}$$

is satisfied and $u_1^*, u_2^*, v_1^*, v_2^* > 0$. Simplifying each pair of these four equations, we get $-\varepsilon_1 + d(a-b) = 0$ and $\varepsilon_2 + d(\frac{1}{a} - \frac{1}{b}) = 0$, where $a = \frac{u_2^*}{u_1^*}, b = \frac{v_2^*}{v_1^*}$. Observe

$$ab = \frac{\varepsilon_1}{\varepsilon_2} \equiv k;$$

thus we obtain

$$a = \frac{\varepsilon_1 + \sqrt{\varepsilon_1^2 + 4kd^2}}{2d}, \; b = \frac{-\varepsilon_1 + \sqrt{\varepsilon_1^2 + 4kd^2}}{2d}.$$

Note that $a^2 > k > b^2$. Set $u_2^* = au_1^*, v_2^* = bv_1^*$, and substitute them back to (3.59), we obtain

(i) $(\alpha_1 - u_1^* - v_1^*) + d(a-1) = 0,$ (ii) $a(\alpha_2 - au_1^* - bv_1^*) + d(1-a) = 0,$

(iii) $(\beta_1 - v_1^* - u_1^*) + d(b-1) = 0,$ (iv) $b(\beta_2 - bv_1^* - au_1^*) + d(1-b) = 0.$

Solving (i) and (ii), we have

$$u_1^* = \frac{a\alpha_2 + d - ad - k(\alpha_1 + ad - d)}{a^2 - k}$$

and

$$v_1^* = \alpha_1 - u_1^* + ad - d.$$

On the other hand, solving (iii) and (iv), we have

$$u_1^* = \frac{b\beta_2 + d - bd - b^2(\beta_1 + bd - d)}{k - b^2} \quad \text{and} \quad v_1^* = \beta_1 - u_1^* + bd - d.$$

We can verify the consistency; with $d(a-b) = \varepsilon_1$, we see that $\alpha_1 + ad - d = \beta_1 + bd - d$ and

$$\frac{a\alpha_2 + d - ad - k(\alpha_1 + ad - d)}{a^2 - k} = \frac{b\beta_2 + d - bd - b^2(\beta_1 + bd - d)}{k - b^2}.$$

Hence, the unique positive equilibrium exists for system (3.28) if and only if

$$\alpha_1 + ad - d > \frac{a\alpha_2 + d - ad - k(\alpha_1 + ad - d)}{a^2 - k} > 0, \tag{3.60}$$

or equivalently,

$$\beta_1 + bd - d > \frac{b\beta_2 + d - bd - b^2(\beta_1 + bd - d)}{k - b^2} > 0. \tag{3.61}$$

First, since $b < 1$, we have $\beta_2 - b\beta_1 > 0$, and

$$b\beta_2 + d - bd - b^2(\beta_1 + bd - d) = b(\beta_2 - b\beta_1) + d(1-b) + b^2 d(1-b) > 0, \text{ for all } d.$$

Next, we shall find the condition under which the left inequalities of (3.60) and (3.61) hold. These inequalities are equivalent to $G(d) > 0$ and $F(d) > 0$, where

$$\begin{aligned} F(d) &:= d(1+a^2)(a-1) + \alpha_1 a^2 - \alpha_2 a, \\ G(d) &:= k(\beta_1 + bd - d) + bd - d - \beta_2 b. \end{aligned} \tag{3.62}$$

Let us study the property for functions F and G. Note that

$$F(d) = \frac{a^2 - k}{k - b^2} G(d).$$

We claim that $G'(d) < 0$, for all $d > 0$. Indeed, since $b = \frac{-\varepsilon_1 + \sqrt{\varepsilon_1^2 + 4kd^2}}{2d}$, $k = \frac{\varepsilon_1}{\varepsilon_2}$, we have

$$b' = \frac{\varepsilon_1 b}{d\sqrt{\varepsilon_1^2 + 4kd^2}} > 0.$$

We then compute

$$\begin{aligned} G'(d) &= k(b'd + b - 1) + (b'd + b - 1) - \beta_2 b' \\ &= (k+1)(b'd + b - 1) - \beta_2 b' \\ &= (k+1)\left(\frac{\varepsilon_1 b}{\sqrt{\varepsilon_1^2 + 4kd^2}} + b - 1\right) - \beta_2 b' \\ &= (k+1)\left(\frac{2kd}{\sqrt{\varepsilon_1^2 + 4kd^2}} - 1\right) - \beta_2 b' \\ &< 0. \end{aligned}$$

Next, we show that

$$\begin{aligned} F(d) > 0, &\quad \text{for all} \quad d \le \frac{\alpha_1\alpha_2\varepsilon_1\varepsilon_2}{\alpha_2^2\varepsilon_2 - \alpha_1^2\varepsilon_1}, \\ G(d) < 0, &\quad \text{for all} \quad d \ge \frac{\beta_1\beta_2\varepsilon_1\varepsilon_2}{\beta_2^2\varepsilon_2 - \beta_1^2\varepsilon_1}. \end{aligned}$$

We set $b \le \frac{\alpha_1 k}{\alpha_2}$, then we have $a = \frac{k}{b} \ge \frac{\alpha_2}{\alpha_1} > 1$ and

$$\begin{aligned} F(d) &= d(1+a^2)(a-1) + \alpha_1 a^2 - \alpha_2 a \\ &= d(1+a^2)(a-1) + a(\alpha_1 a - \alpha_2) > 0. \end{aligned}$$

Moreover,

$$b = \frac{-\varepsilon_1 + \sqrt{\varepsilon_1^2 + 4kd^2}}{2d} \le \frac{\alpha_1 k}{\alpha_2}.$$

It follows that

$$\frac{\sqrt{\varepsilon_1^2 + 4kd^2}}{2d} \le \frac{\varepsilon_1}{2d} + \frac{\alpha_1 k}{\alpha_2}.$$

Squaring both sides and after some algebra, we have

$$d \le \frac{\alpha_1\alpha_2\varepsilon_1\varepsilon_2}{\alpha_2^2\varepsilon_2 - \alpha_1^2\varepsilon_1}.$$

On the other hand, We set $b \ge \frac{\beta_1 k}{\beta_2}$ and the fact that $b < 1$, then we have

$$\begin{aligned} G(d) &= k(\beta_1 + bd - d) + bd - d - \beta_2 b \\ &= kd(b-1) + d(b-1) + \beta_1 k - \beta_2 b < 0. \end{aligned}$$

Moreover,

$$b = \frac{-\varepsilon_1 + \sqrt{\varepsilon_1^2 + 4kd^2}}{2d} \ge \frac{\beta_1 k}{\beta_2}.$$

It follows that

$$\frac{\sqrt{\varepsilon_1^2 + 4kd^2}}{2d} \ge \frac{\varepsilon_1}{2d} + \frac{\beta_1 k}{\beta_2}.$$

Similarly, we square both sides and some algebra, then we get

$$d \ge \frac{\beta_1\beta_2\varepsilon_1\varepsilon_2}{\beta_2^2\varepsilon_2 - \beta_1^2\varepsilon_1}.$$

We thus conclude that the system must have a positive equilibrium when

$$d \le \frac{\alpha_1\alpha_2\varepsilon_1\varepsilon_2}{\alpha_2^2\varepsilon_2 - \alpha_1^2\varepsilon_1}$$

and has no positive equilibrium when

$$d \ge \frac{\beta_1\beta_2\varepsilon_1\varepsilon_2}{\beta_2^2\varepsilon_2 - \beta_1^2\varepsilon_1}.$$

Since we have $b' < 0$ for all $d > 0$, we can deduce that there is a unique point $\bar{d}$ with

$$\frac{\alpha_1\alpha_2\varepsilon_1\varepsilon_2}{\alpha_2^2\varepsilon_2 - \alpha_1^2\varepsilon_1} < \bar{d} < \frac{\beta_1\beta_2\varepsilon_1\varepsilon_2}{\beta_2^2\varepsilon_2 - \beta_1^2\varepsilon_1}$$

such that $F(\bar{d}) = G(\bar{d}) = 0$.

In particular, for the case $\varepsilon_1 = \varepsilon_2 = \varepsilon$, we have $ab = 1, a > 1 > b$ and

$$a = \frac{\varepsilon + \sqrt{\varepsilon^2 + 4d^2}}{2d}\ ,\ b = \frac{-\varepsilon + \sqrt{\varepsilon^2 + 4d^2}}{2d}.$$

Similarly argument as above, we have

$$u_1^* = \frac{a\alpha_2 + 2d - 2ad - \alpha_1}{a^2 - 1}, \quad v_1^* = \alpha_1 - u_1^* + ad - d.$$

or

$$u_1^* = \frac{b\beta_2 + d - bd - b^2(\beta_1 + bd - d)}{1 - b^2}, \quad v_1^* = \beta_1 - u_1^* + bd - d.$$

We can also verify the consistency,

$$\frac{a\alpha_2 + 2d - 2ad - \alpha_1}{a^2 - 1} = \frac{b\beta_2 + d - bd - b^2(\beta_1 + bd - d)}{1 - b^2}$$

and $\alpha_1 + ad - d = \beta_1 + bd - d$. Hence, the unique positive equilibrium exists for system (3.28) if and only if

$$\alpha_1 + ad - d > \frac{a\alpha_2 + 2d - 2ad - \alpha_1}{a^2 - 1} > 0. \tag{3.63}$$

or equivalently

$$\beta_1 + bd - d > \frac{b\beta_2 + d - bd - b^2(\beta_1 + bd - d)}{1 - b^2} > 0. \tag{3.64}$$

First, since $b < 1$, we have $\beta_2 - b\beta_1 < 1$ and

$$b\beta_2 + d - bd - b^2(\beta_1 + bd - d) = b(\beta_2 - b\beta_1) + d(1 - b) + b^2 d(1 - b) > 0, \text{ for all } d.$$

Next, we shall find the condition under which the left inequalities of (3.63) and (3.64) hold. These inequalities are equivalent to $G(d) > 0$ and $F(d) > 0$, where

$$F(d) := d(1 + a^2)(a - 1) + \alpha_1 a^2 - \alpha_2 a \quad \text{and} \quad G(d) := 2bd - 2d - \beta_2 b + \beta_1$$

Let us study the property for functions F and G. Note that

$$F(d) = \frac{a^2 - 1}{1 - b^2} G(d).$$

We claim that $G'(d) < 0$, for all $d > 0$. Indeed, since $b = \frac{-\varepsilon + \sqrt{\varepsilon^2 + 4d^2}}{2d}$, we have

$$b' = \frac{b\varepsilon}{d\sqrt{\varepsilon^2 + 4d^2}}.$$

We then compute

$$\begin{aligned} G'(d) &= 2(b'd + b - 1) - \beta_2 b' \\ &= 2\left(\frac{\varepsilon b}{\sqrt{\varepsilon^2 + 4d^2}} + b - 1\right) - \beta_2 b' \\ &= 2\left(\frac{2d}{\sqrt{\varepsilon^2 + 4d^2}} - 1\right) - \beta_2 b' \\ &< 0. \end{aligned}$$

Next, we show that $G(d) = 0$, where

$$d = \frac{(\alpha_2^2 - \alpha_1^2) - \sqrt{(\alpha_2^2 - \alpha_1^2)^2 - 16\beta_1\beta_2\varepsilon(\beta_2 - \alpha_1)}}{8(\beta_2 - \alpha_1)},$$

We set $G(d) = 0$, it follows that

$$2bd - 2d - b\beta_2 + \beta_1 = \frac{2d(-\varepsilon + \sqrt{\varepsilon^2 + 4d^2}) - 4d^2 - \beta_2(-\varepsilon + \sqrt{\varepsilon^2 + 4d^2}) + 2\beta_1 d}{2d} = 0.$$

Since $d > 0$, we let

$$2d(-\varepsilon + \sqrt{\varepsilon^2 + 4d^2}) - 4d^2 - \beta_2(-\varepsilon + \sqrt{\varepsilon^2 + 4d^2}) + 2\beta_1 d = 0.$$

It follows that

$$(-2d\varepsilon - 4d^2 + \beta_2\varepsilon + 2\beta_1 d)^2 = (\beta_2 - 2d)^2(\varepsilon^2 + 4d^2).$$

After some algebra, we have

$$4(\beta_2 - \alpha_1)d^2 + (\alpha_1^2 - \alpha_2^2)d + \beta_1\beta_2\varepsilon = 0.$$

Therefore, we have two roots

$$d_{\pm} = \frac{(\alpha_2^2 - \alpha_1^2) \pm \sqrt{(\alpha_2^2 - \alpha_1^2)^2 - 16\beta_1\beta_2\varepsilon(\beta_2 - \alpha_1)}}{8(\beta_2 - \alpha_1)}$$

But actually, the graph of $G(d)$ only intersect d-axis one time, we can check d_+ is not the root of $G(d) = 0$ by numerical computation. Hence, the only one root such that equation $G(d) = 0$ is

$$d_- = \frac{(\alpha_2^2 - \alpha_1^2) - \sqrt{(\alpha_2^2 - \alpha_1^2)^2 - 16\beta_1\beta_2\varepsilon(\beta_2 - \alpha_1)}}{8(\beta_2 - \alpha_1)},$$

denoted by $\bar{d}$. The proof of theorem is complete.

Proof of Theorem 3.4.10. We define a Lyapunov function $V : \mathbb{R}_+^2 \to \mathbb{R}$ by

$$V(\hat{\omega}_1, \hat{\omega}_2) = c_1\left(\hat{\omega}_1 - \hat{\bar{\omega}}_1 - \hat{\bar{\omega}}_1 \ln\left(\frac{\hat{\omega}_1}{\hat{\bar{\omega}}_1}\right)\right) + c_2\left(\hat{\omega}_2 - \hat{\bar{\omega}}_2 - \hat{\bar{\omega}}_2 \ln\left(\frac{\hat{\omega}_2}{\hat{\bar{\omega}}_2}\right)\right)$$

where $c_1 = \hat{\hat{\omega}}_1$ and $c_2 = \hat{\hat{\omega}}_2$. Then

$$
\begin{aligned}
\dot{V}(\hat{\omega}_1, \hat{\omega}_2) &= c_1 \left[\hat{\omega}_1(\beta_1 - \hat{\omega}_1) + d(\hat{\omega}_2 - \hat{\omega}_1) - \hat{\hat{\omega}}_1(\beta_1 - \hat{\omega}_1) - \hat{\hat{\omega}}_1 d \left(\frac{\hat{\omega}_2}{\hat{\omega}_1} - 1 \right) \right] \\
&+ c_2 \left[\hat{\omega}_2(\alpha_2 - \hat{\omega}_2) + d(\hat{\omega}_1 - \hat{\omega}_2) - \hat{\hat{\omega}}_2(\alpha_2 - \hat{\omega}_2) - \hat{\hat{\omega}}_2 d \left(\frac{\hat{\omega}_1}{\hat{\omega}_2} - 1 \right) \right] \\
&= c_1 \left[(\hat{\omega}_1 - \hat{\hat{\omega}}_1)[-(\hat{\omega}_1 - \hat{\hat{\omega}}_1) + (\beta_1 - \hat{\hat{\omega}}_1)] + d(\hat{\omega}_2 - \hat{\omega}_1) - \hat{\hat{\omega}}_1 d \left(\frac{\hat{\omega}_2}{\hat{\omega}_1} - 1 \right) \right] \\
&+ c_2 \left[(\hat{\omega}_2 - \hat{\hat{\omega}}_2)[-(\hat{\omega}_2 - \hat{\hat{\omega}}_2) + (\alpha_2 - \hat{\hat{\omega}}_2)] + d(\hat{\omega}_1 - \hat{\omega}_2) - \hat{\hat{\omega}}_2 d \left(\frac{\hat{\omega}_1}{\hat{\omega}_2} - 1 \right) \right] \\
&= c_1 \left[-(\hat{\omega}_1 - \hat{\hat{\omega}}_1)^2 + (\hat{\omega}_1 - \hat{\hat{\omega}}_1)(\beta_1 - \hat{\hat{\omega}}_1) + d(\hat{\omega}_2 - \hat{\omega}_1) - \hat{\hat{\omega}}_1 d \left(\frac{\hat{\omega}_2}{\hat{\omega}_1} - 1 \right) \right] \\
&+ c_2 \left[-(\hat{\omega}_2 - \hat{\hat{\omega}}_2)^2 + (\hat{\omega}_2 - \hat{\hat{\omega}}_2)(\alpha_2 - \hat{\hat{\omega}}_2) + d(\hat{\omega}_1 - \hat{\omega}_2) - \hat{\hat{\omega}}_2 d \left(\frac{\hat{\omega}_1}{\hat{\omega}_2} - 1 \right) \right] \\
&\leq c_1 \left[(\hat{\omega}_1 - \hat{\hat{\omega}}_1)(\beta_1 - \hat{\hat{\omega}}_1) + d(\hat{\omega}_2 - \hat{\omega}_1) - \hat{\hat{\omega}}_1 d \left(\frac{\hat{\omega}_2}{\hat{\omega}_1} - 1 \right) \right] \\
&+ c_2 \left[(\hat{\omega}_2 - \hat{\hat{\omega}}_2)(\alpha_2 - \hat{\hat{\omega}}_2) + d(\hat{\omega}_1 - \hat{\omega}_2) - \hat{\hat{\omega}}_2 d \left(\frac{\hat{\omega}_1}{\hat{\omega}_2} - 1 \right) \right]
\end{aligned}
$$

where equality holds if and only if $\hat{\omega}_1 = \hat{\hat{\omega}}_1$ and $\hat{\omega}_2 = \hat{\hat{\omega}}_2$. Then

$$
\begin{aligned}
\dot{V}(\hat{\omega}_1, \hat{\omega}_2) &\leq c_1 \left\{ (\hat{\omega}_1 - \hat{\hat{\omega}}_1) \left[-d \left(\frac{\hat{\hat{\omega}}_2}{\hat{\hat{\omega}}_1} - 1 \right) \right] + d(\hat{\omega}_2 - \hat{\omega}_1) - \hat{\hat{\omega}}_1 d \left(\frac{\hat{\omega}_2}{\hat{\omega}_1} - 1 \right) \right\} \\
&+ c_2 \left\{ (\hat{\omega}_2 - \hat{\hat{\omega}}_2) \left[-d \left(\frac{\hat{\hat{\omega}}_1}{\hat{\hat{\omega}}_2} - 1 \right) \right] + d(\hat{\omega}_1 - \hat{\omega}_2) - \hat{\hat{\omega}}_2 d \left(\frac{\hat{\omega}_1}{\hat{\omega}_2} - 1 \right) \right\} \\
&= c_1 d \hat{\hat{\omega}}_2 \left[-\frac{\hat{\omega}_1}{\hat{\hat{\omega}}_1} + 1 + \frac{\hat{\omega}_2}{\hat{\hat{\omega}}_2} - \frac{\hat{\hat{\omega}}_1 \hat{\omega}_2}{\hat{\omega}_1 \hat{\hat{\omega}}_2} \right] + c_2 d \hat{\hat{\omega}}_1 \left[-\frac{\hat{\omega}_2}{\hat{\hat{\omega}}_2} + 1 + \frac{\hat{\omega}_1}{\hat{\hat{\omega}}_1} - \frac{\hat{\omega}_1 \hat{\hat{\omega}}_2}{\hat{\hat{\omega}}_1 \hat{\omega}_2} \right] \\
&= d \hat{\hat{\omega}}_1 \hat{\hat{\omega}}_2 \left[2 - \left(\frac{\hat{\hat{\omega}}_1 \hat{\omega}_2}{\hat{\omega}_1 \hat{\hat{\omega}}_2} + \frac{\hat{\omega}_1 \hat{\hat{\omega}}_2}{\hat{\hat{\omega}}_1 \hat{\omega}_2} \right) \right] \\
&\leq 0
\end{aligned}
$$

since $a^2 + b^2 \geq 2ab$. The equality holds if and only if $\hat{\hat{\omega}}_1 \hat{\omega}_2 = \hat{\omega}_1 \hat{\hat{\omega}}_2$.

Therefore, we obtain $\dot{V}(\hat{\omega}_1, \hat{\omega}_2) = 0$ if and only if $\hat{\omega}_1 = \hat{\hat{\omega}}_1$, $\hat{\omega}_2 = \hat{\hat{\omega}}_2$ and $\hat{\hat{\omega}}_1 \hat{\omega}_2 = \hat{\omega}_1 \hat{\hat{\omega}}_2$. By the Lyapunov stability theory, The equilibrium $(\hat{\hat{\omega}}_1, \hat{\hat{\omega}}_2)$ of system (3.39) is globally asymptotically stable among all positive initial data.

Proof of Theorem 3.4.11. The proof of theorem 3.4.11 is similar to theorem 3.4.10. Defined the Lyapunov function $V : \mathbb{R}^2_+ \to \mathbb{R}$ by

$$
V(\breve{\omega}_1, \breve{\omega}_2) = c_1 \left(\breve{\omega}_1 - \breve{\breve{\omega}}_1 - \breve{\breve{\omega}}_1 \ln \left(\frac{\breve{w}_1}{\breve{\breve{\omega}}_1} \right) \right) + c_2 \left(\breve{w}_2 - \breve{\breve{\omega}}_2 - \breve{\breve{\omega}}_2 \ln \left(\frac{\breve{w}_2}{\breve{\breve{\omega}}_2} \right) \right)
$$

where $c_1 = \check{\check{\omega}}_1$ and $c_2 = \check{\check{\omega}}_2$.

Proof of Corollary 3.4.12. We only prove the upper boundedness. (i) Clearly by Theorem 3.4.10. (ii) The positive equilibrium $(\hat{\hat{\omega}}_1, \hat{\hat{\omega}}_2)$ satisfies

$$\begin{aligned} \hat{\hat{\omega}}_1(\beta_1 - \hat{\hat{\omega}}_1) + d(\hat{\hat{\omega}}_2 - \hat{\hat{\omega}}_1) &= 0 \\ \hat{\hat{\omega}}_2(\alpha_2 - \hat{\hat{\omega}}_2) + d(\hat{\hat{\omega}}_1 - \hat{\hat{\omega}}_2) &= 0. \end{aligned} \tag{3.65}$$

If $\hat{\hat{\omega}}_1 \geq \hat{\hat{\omega}}_2$, then $\hat{\hat{\omega}}_1 \leq \beta_1$ and $\alpha_2 \leq \hat{\hat{\omega}}_2$, namely, $\alpha_2 \leq \hat{\hat{\omega}}_2 \leq \hat{\hat{\omega}}_1 \leq \beta_1$. It contradicts with $\beta_1 < \alpha_2$. Thus, $\hat{\hat{\omega}}_1 < \hat{\hat{\omega}}_2$. Moreover, we obtain $\beta_1 < \hat{\hat{\omega}}_1$ and $\hat{\hat{\omega}}_2 < \alpha_2$ since $\hat{\hat{\omega}}_1 < \hat{\hat{\omega}}_2$. (iii) From (2), The results are true. (iv) Since

$$\hat{\hat{\omega}}_1 = \hat{\hat{\omega}}_2 + \frac{\hat{\hat{\omega}}_2}{d}(\hat{\hat{\omega}}_2 - \alpha_2), \tag{3.66}$$

we have $\hat{\hat{\omega}}_1 = \hat{\hat{\omega}}_2$, as $d \to \infty$. Then $\hat{\hat{\omega}}_1 = \hat{\hat{\omega}}_2 \to \frac{\alpha_2+\beta_1}{2}$. The same argument can proof the lower boundedness.

Proof of Theorem 3.4.13. With initial point from $\bar{\Omega}$, we claim the solution flow $\phi_t(u_1, u_2, v_1, v_2)$ stays in $\bar{\Omega}$.

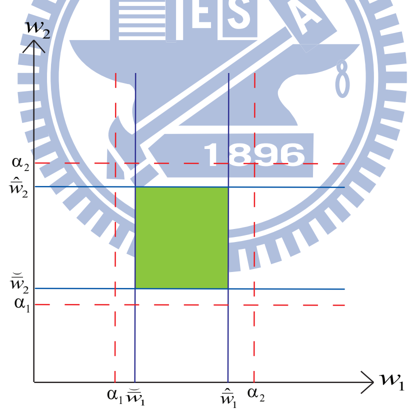

Figure 6: The bounded above and bounded below for ω_1 and ω_2.

(I) If exists some time $t_0 \geq 0$ such that $\omega_1(t_0) = \alpha_2$ and $\alpha_1 \leq \omega_2(t_0) \leq \alpha_2$, then

$$\begin{aligned} \frac{d(u_1+v_1)}{dt}(t_0) = \frac{d\omega_1(t_0)}{dt} &= \omega_1(t_0)(\beta_1 - \omega_1(t_0)) + d(\omega_2(t_0) - \omega_1(t_0)) - \varepsilon_1 u_1(t_0) \\ &\leq \omega_1(t_0)(\beta_1 - \omega_1(t_0)) + d(\omega_2(t_0) - \omega_1(t_0)) \\ &= \alpha_2(\beta_1 - \alpha_2) + d(\omega_2(t_0) - \alpha_2) \\ &\leq \alpha_2(\beta_1 - \alpha_2) + d(\alpha_2 - \alpha_2) < 0. \end{aligned}$$

(II) If exists some time $t_0 \geq 0$ such that $\omega_2(t_0) = \alpha_2$ and $\alpha_1 \leq \omega_1(t_0) < \alpha_2$, then

$$\begin{aligned} \frac{d(u_2+v_2)}{dt}(t_0) = \frac{d\omega_2(t_0)}{dt} &= \omega_2(t_0)(\alpha_2 - \omega_2(t_0)) + d(\omega_1(t_0) - \omega_2(t_0)) - \varepsilon_2 v_2(t_0) \\ &\leq \omega_2(t_0)(\alpha_2 - \omega_2(t_0)) + d(\omega_1(t_0) - \omega_2(t_0)) \\ &= \alpha_2(\alpha_2 - \alpha_2) + d(\omega_1(t_0) - \alpha_2) \\ &< \alpha_2(\alpha_2 - \alpha_2) + d(\alpha_2 - \alpha_2) = 0. \end{aligned}$$

(III) If exists some time $t_0 \geq 0$ such that $\omega_1(t_0) = \alpha_1$ and $\alpha_1 < \omega_2(t_0) \leq \alpha_2$, then

$$\begin{aligned} \frac{d(u_1+v_1)}{dt}(t_0) = \frac{d\omega_1(t_0)}{dt} &= \omega_1(t_0)(\alpha_1 - \omega_1(t_0)) + d(\omega_2(t_0) - \omega_1(t_0)) + \varepsilon_1 v_1(t_0) \\ &\geq \omega_1(t_0)(\alpha_1 - \omega_1(t_0)) + d(\omega_2(t_0) - \omega_1(t_0)) \\ &= \alpha_1(\alpha_1 - \alpha_1) + d(\omega_2(t_0) - \alpha_1) \\ &> \alpha_1(\alpha_1 - \alpha_1) + d(\alpha_1 - \alpha_1) = 0. \end{aligned}$$

(IV) If exists some time $t_0 \geq 0$ such that $\omega_2(t_0) = \alpha_1$ and $\alpha_1 \leq \omega_1(t_0) \leq \alpha_2$, then

$$\begin{aligned} \frac{d(u_2+v_2)}{dt}(t_0) = \frac{d\omega_2(t_0)}{dt} &= \omega_2(t_0)(\beta_2 - \omega_2(t_0)) + d(\omega_1(t_0) - \omega_2(t_0)) + \varepsilon_2 u_2(t_0) \\ &\geq \omega_2(t_0)(\beta_2 - \omega_2(t_0)) + d(\omega_1(t_0) - \omega_2(t_0)) \\ &= \alpha_1(\beta_2 - \alpha_1) + d(\omega_1(t_0) - \alpha_1) \\ &\geq \alpha_1(\beta_2 - \alpha_1) + d(\alpha_1 - \alpha_1) > 0. \end{aligned}$$

Secondly, we focus on the two points $\{w_1 = \alpha_2, w_2 = \alpha_2\}$ and $\{w_1 = \alpha_1, w_2 = \alpha_1\}$. Define

$$\begin{aligned} S_1 &= \left\{(u_1, v_1) \in \bar{\mathbb{R}}_+^2 : \alpha_1 \leq u_1 + v_1 \leq \alpha_2\right\}, \\ S_2 &= \left\{(u_2, v_2) \in \bar{\mathbb{R}}_+^2 : \alpha_1 \leq u_2 + v_2 \leq \alpha_2\right\}. \end{aligned}$$

(I). For $\{w_1 = \alpha_2, w_2 = \alpha_2\}$, it indicates $\{u_1 + v_1 = \alpha_2, u_2 + v_2 = \alpha_2\}$. Set $\mathbf{n} = (1, 1)$, then

$$\begin{aligned} \mathbf{n} \cdot \mathbf{f} &= [\omega_1(\beta_1 - \omega_1) + d(\omega_2 - \omega_1) - \varepsilon_1 u_1]|_{w_1=\alpha_2, w_2=\alpha_2} < 0, \\ \mathbf{n} \cdot \mathbf{g} &= [\omega_2(\alpha_2 - \omega_2) + d(\omega_1 - \omega_2) - \varepsilon_2 v_2]|_{w_1=\alpha_2, w_2=\alpha_2, v_2>0} < 0, \end{aligned}$$

where $\mathbf{f} = (f_1, f_2)$ and $\mathbf{f} = (f_1, f_2)$ are the vector field of u_1v_1-plane and u_2v_2-plane, respectively. It means that all initial point on the two line with $v_2 > 0$ will go inside the region $S_1 \times S_2$.

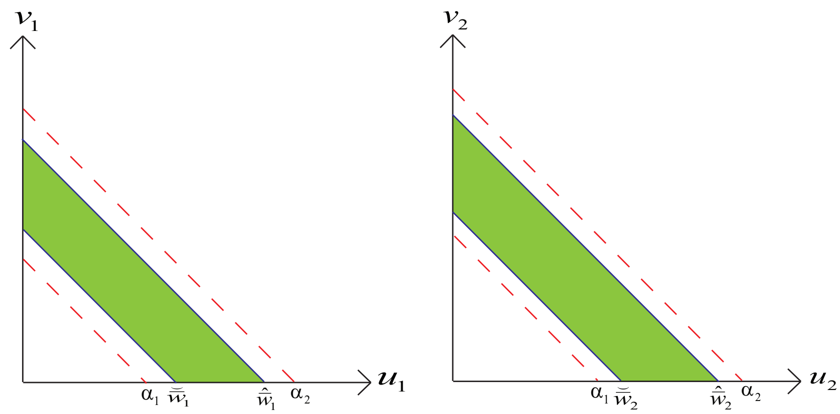

Figure 7: The bounded above and bounded below for (a) u_1 and v_1, (b) u_2 and v_2.

Finally, we check the point with $v_2 = 0$ as initial data :
(i) $(\alpha_2, \alpha_2, 0, 0)$, the solution always stays on u_1u_2-plane and tens to the semi-trivial equilibrium $(\bar{u}_1, \bar{u}_2, 0, 0)$ by Proposition 3.4.3.
(ii) With $(u_1, u_2, v_1, v_2) = (k, \alpha_2, \alpha_2 - k, 0)$ for some $k < \alpha_2$, then

$$\begin{aligned}
\dot{u}_2 &= \alpha_2(\alpha_2 - \alpha_2) + d(k - \alpha_2) = d(k - \alpha_2) < 0 \\
\dot{v}_2 &= d(\alpha_2 - k) > 0
\end{aligned}$$

Hence, the flow with $v_2 > 0$ alone the line $u_2 + v_2 = \alpha_2$ next time and satisfies the above argument. It means that all the solution will enter the positive region $S_1 \times S_2$.
(II) Similar argument for $\{w_1 = \alpha_1, w_2 = \alpha_1\}$, it means $\{u_1 + v_1 = \alpha_1, u_2 + v_2 = \alpha_1\}$. Set $\mathbf{n} = (1, 1)$, then

$$\begin{aligned}
\mathbf{n} \cdot \mathbf{f} &= [w_1(\alpha_1 - w_1) + d(w_2 - w_1) + \varepsilon_1 v_1]|_{w_1 = \alpha_1, w_2 = \alpha_1, v_1 > 0} > 0, \\
\mathbf{n} \cdot \mathbf{g} &= [w_2(\beta_2 - w_2) + d(w_1 - w_2) + \varepsilon_2 u_2]|_{w_1 = \alpha_1, w_2 = \alpha_1} > 0,
\end{aligned}$$

where $\mathbf{f} = (f_1, f_2)$ and $\mathbf{f} = (f_1, f_2)$ are the vector field of u_1v_1-plane and u_2v_2-plane, respectively. It means that all initial point on the two line with $v_1 > 0$ will go inside the region $S_1 \times S_2$. Finally, we check the point with $v_1 = 0$ as initial data :
(i) $(\alpha_1, \alpha_2, 0, 0)$, the solution always stays on u_1u_2-plane and tens to the semi-trivial equilibrium $(\bar{u}_1, \bar{u}_2, 0, 0)$ by Proposition 3.4.3.
(ii) With $(u_1, u_2, v_1, v_2) = (\alpha_1, k, 0, \alpha_1 - k)$ for some $k < \alpha_1$, then

$$\begin{aligned}
\dot{u}_1 &= \alpha_1(\alpha_1 - \alpha_1) + d(k - \alpha_1) = d(k - \alpha_1) < 0 \\
\dot{v}_1 &= d(\alpha_1 - k) > 0
\end{aligned}$$

Hence the flow with $v_1 > 0$ alone the line $u_2 + v_2 = \alpha_1$ next time and satisfies the above argument. It means that all the solution will enter the positive region $S_1 \times S_2$.

Hence, we conclude that all solution flow will enter the bounded region $\bar{\Omega}$ for a period of time. That is, $\bar{\Omega}$ is positively invariant.

Proof of theorem 3.4.14. With initial point $(u_1(0), u_2(0), v_1(0), v_2(0)) \in \bar{\Omega}$, by Corollary 3.4.13 (iii), we have

$$\begin{aligned}
\frac{d}{dt}(u_1 - u_2) &= u_1(\alpha_1 - u_1 - v_1) + d(u_2 - u_1) - u_2(\alpha_2 - u_2 - v_2) - d(u_1 - u_2) \\
&= \alpha_1 u_1 - u_1(u_1 + v_1) - \alpha_2 u_2 + u_2(u_2 + v_2) - 2d(u_1 - u_2) \\
&\leq \alpha_1 u_1 - \alpha_1 u_1 - \alpha_2 u_2 + \alpha_2 u_2 - 2d(u_1 - u_2) \\
&= -2d(u_1 - u_2).
\end{aligned}$$

Hence, fixed d sufficiently large, we have

$$u_1(t) - u_2(t) \leq (u_1(0) - u_2(0))e^{-2dt} \to 0 \quad \text{as } t \to \infty,$$

with initial point $(u_1(0) - u_2(0))$ from $\bar{\Omega}$ at $t = 0$.

$$\begin{aligned}
\frac{d}{dt}(u_1 - u_2) &= u_1(\alpha_1 - u_1 - v_1) + d(u_2 - u_1) - u_2(\alpha_2 - u_2 - v_2) - d(u_1 - u_2) \\
&= \alpha_1 u_1 - u_1(u_1 + v_1) - \alpha_2 u_2 + u_2(u_2 + v_2) - 2d(u_1 - u_2) \\
&\geq \alpha_1 u_1 - \alpha_2 u_1 - \alpha_2 u_2 + \alpha_1 u_2 - 2d(u_1 - u_2) \\
&= -(\alpha_2 - \alpha_1)(u_1 + u_2) - 2d(u_1 - u_2) \\
&\geq -2\alpha_2(\alpha_2 - \alpha_1) - 2d(u_1 - u_2)
\end{aligned}$$

Thus, fixed d sufficiently large, we have

$$\begin{aligned}
u_1(t) - u_2(t) &\geq -\frac{\alpha_2(\alpha_2 - \alpha_1)}{d}\left(1 - e^{-2dt}\right) + (u_1(0) - u_2(0))e^{-2dt} \\
&\to O(\frac{1}{d}) \quad \text{as } t \to \infty,
\end{aligned}$$

with initial point $(u_1(0) - u_2(0))$ from $\bar{\Omega}$ at $t = 0$. Therefore, we obtain

$$\begin{aligned}
-\frac{\alpha_2(\alpha_2 - \alpha_1)}{d} + \frac{\alpha_2(\alpha_2 - \alpha_1)}{d}e^{-2dt} + (u_1(0) - u_2(0))e^{-2dt} \\
\leq u_1 - u_2 \leq (u_1(0) - u_2(0))e^{-2dt}
\end{aligned}$$

with initial point $(u_1(0) - u_2(0))$ from the region $\bar{\Omega}$ at $t = 0$. Then $u_1 - u_2 \to O(\frac{1}{d})$ as $t \to \infty$. Similarly, we have

$$\begin{aligned}
\frac{d}{dt}(v_1 - v_2) &= v_1(\beta_1 - u_1 - v_1) + d(v_2 - v_1) - v_2(\beta_2 - u_2 - v_2) - d(v_1 - v_2) \\
&= \beta_1 v_1 - v_1(u_1 + v_1) - \beta_2 v_2 + v_2(u_2 + v_2) - 2d(v_1 - v_2) \\
&\leq \beta_1 v_1 - \alpha_1 v_1 - \beta_2 v_2 + \alpha_2 v_2 - 2d(v_1 - v_2) \\
&= (\beta_1 - \alpha_1)v_1 + (\alpha_2 - \beta_2)v_2 - 2d(v_1 - v_2) \\
&= \varepsilon_1 v_1 + \varepsilon_2 v_2 - 2d(v_1 - v_2) \\
&\leq \varepsilon_2(v_1 + v_2) - 2d(v_1 - v_2) \\
&\leq 2\varepsilon_2\beta_2 - 2d(v_1 - v_2)
\end{aligned}$$

Thus, fixed d sufficiently large,

$$v_1 - v_2 \leq \frac{\varepsilon_2\beta_2}{d} - \frac{\varepsilon_2\beta_2}{d}e^{-2dt} + (v_1(0) - v_2(0))e^{-2dt} \to O(\frac{1}{d}) \;\text{ as } t \to \infty,$$

with initial data $(v_1(0) - v_2(0))$ from the region $\bar{\Omega}$ at $t = 0$.

$$\begin{aligned}
\frac{d}{dt}(v_1 - v_2) &= v_1(\beta_1 - u_1 - v_1) + d(v_2 - v_1) - v_2(\beta_2 - u_2 - v_2) - d(v_1 - v_2) \\
&= \beta_1 v_1 - v_1(u_1 + v_1) - \beta_2 v_2 + v_2(u_2 + v_2) - 2d(v_1 - v_2) \\
&\geq \beta_1 v_1 - \alpha_2 v_1 - \beta_2 v_2 + \alpha_1 v_2 - 2d(v_1 - v_2) \\
&= -(\beta_2 - \beta_1 + \varepsilon_2)v_1 - (\beta_2 - \beta_1 + \varepsilon_1)v_2 - 2d(v_1 - v_2) \\
&\geq -(\beta_2 - \beta_1 + \varepsilon_2)(v_1 + v_2) - 2d(v_1 - v_2) \\
&\geq -2\beta_2(\beta_2 - \beta_1 + \varepsilon_2) - 2d(v_1 - v_2)
\end{aligned}$$

Hence, fixed d sufficiently large,

$$\begin{aligned}
v_1 - v_2 &\geq -\frac{\beta_2(\beta_2 - \beta_1 + \varepsilon_2)}{d} + \frac{\beta_2(\beta_2 - \beta_1 + \varepsilon_2)}{d}e^{-2dt} + (v_1(0) - v_2(0))e^{-2dt} \\
&\to O(\frac{1}{d}) \;\text{ as } t \to \infty,
\end{aligned}$$

with initial data $(v_1(0) - v_2(0))$ from the region $\bar{\Omega}$ at $t = 0$. Therefore, we obtain

$$\begin{aligned}
-\frac{\beta_2(\beta_2 - \beta_1 + \varepsilon_2)}{d} &+ \frac{\beta_2(\beta_2 - \beta_1 + \varepsilon_2)}{d}e^{-2dt} + (v_1(0) - v_2(0))e^{-2dt} \\
&\leq v_1 - v_2 \leq \frac{\varepsilon_2\beta_2}{d} - \frac{\varepsilon_2\beta_2}{d}e^{-2dt} + (v_1(0) - v_2(0))e^{-2dt}
\end{aligned}$$

with initial point $(v_1(0) - v_2(0))$ from the region $\bar{\Omega}$ at $t = 0$. Then $v_1 - v_2 \to O(\frac{1}{d})$ as $t \to \infty$.

4 Numerical examples

Example 1 : We present the example to illustrate our results. Set $\beta_1 = 1.5, \beta_1 = 2.5, \varepsilon_1 = \varepsilon_1 = 0.5$.

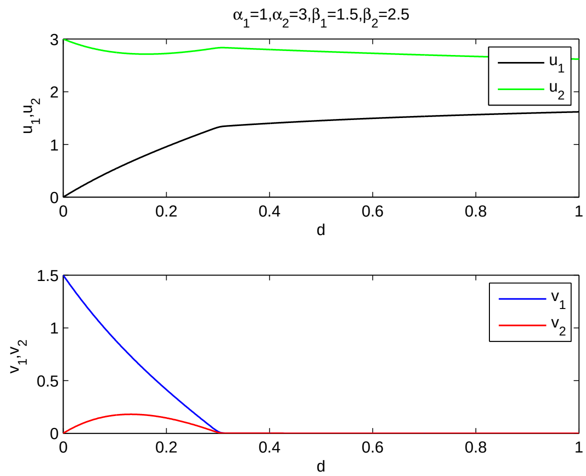

Figure 8: Illustrations for the dynamics $\beta_1 = 1.5, \beta_2 = 2.5, \varepsilon_1 = \varepsilon_2 = 0.5$.

Example 2 : We present the example to illustrate our results. Set $\beta_1 = 1.5, \beta_1 = 2.5, \varepsilon_1 = 0.3, \varepsilon_2 = 0.6$.

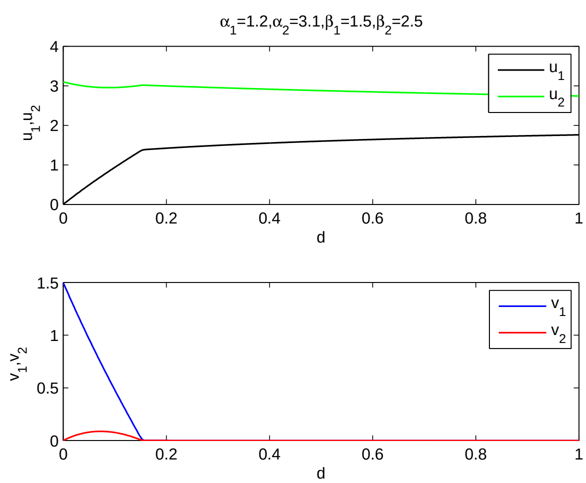

Figure 9: Illustrations for the dynamics $\beta_1 = 1.5, \beta_2 = 2.5, \varepsilon_1 = 0.3, \varepsilon_2 = 0.6$.

The form of model as (3.28) with different dispersal rates as follows.

$$\begin{aligned}\frac{du_1}{dt} &= u_1(\alpha_1 - u_1 - v_1) + du_2 - eu_1,\\ \frac{du_2}{dt} &= u_2(\alpha_2 - u_2 - v_2) + eu_1 - du_2,\\ \frac{dv_1}{dt} &= v_1(\beta_1 - v_1 - u_1) + dv_2 - ev_1,\\ \frac{dv_2}{dt} &= v_2(\beta_2 - v_2 - u_2) + ev_1 - dv_2,\end{aligned} \tag{4.1}$$

with the assumption of parameters

$$0 < \beta_1 - \varepsilon_1 = \alpha_1 < \beta_1 < \beta_2 < \alpha_2 = \beta_2 + \varepsilon_2, \varepsilon_2 \geq \varepsilon_1 > 0, e \geq d \geq 0. \tag{4.2}$$

We have the similar results:

Example 3 : We present the examples to illustrate our results. Set $\beta_1 = 1.5, \beta_1 = 2.5, \varepsilon_1 = \varepsilon_1 = 0.5, d = 0.1$.

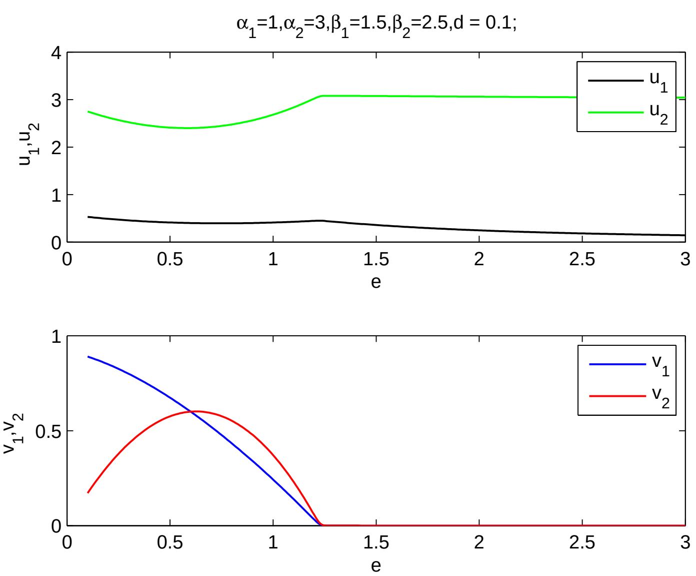

Figure 10: Illustrations for the dynamics $\beta_1 = 1.5, \beta_2 = 2.5, \varepsilon_1 = \varepsilon_2 = 0.5, d = 0.1$.

On the other hand, we let species with the different dispersal,

$$\begin{aligned}\frac{du_1}{dt} &= u_1(\alpha_1 - u_1 - v_1) + du_2 - du_1,\\ \frac{du_2}{dt} &= u_2(\alpha_2 - u_2 - v_2) + du_1 - du_2,\\ \frac{dv_1}{dt} &= v_1(\beta_1 - v_1 - u_1) + ev_2 - ev_1,\\ \frac{dv_2}{dt} &= v_2(\beta_2 - v_2 - u_2) + ev_1 - ev_2,\end{aligned} \tag{4.3}$$

with the assumption of parameters

$$0 < \beta_1 - \varepsilon_1 = \alpha_1 < \beta_1 < \beta_2 < \alpha_2 = \beta_2 + \varepsilon_2, \varepsilon_2 \geq \varepsilon_1 > 0, e \geq d \geq 0. \tag{4.4}$$

We have the following results:

Example 4 : We present the examples to illustrate our results. Set $\beta_1 = 1.5, \beta_1 = 2.5, \varepsilon_1 = \varepsilon_1 = 0.5, d = 0.1$.

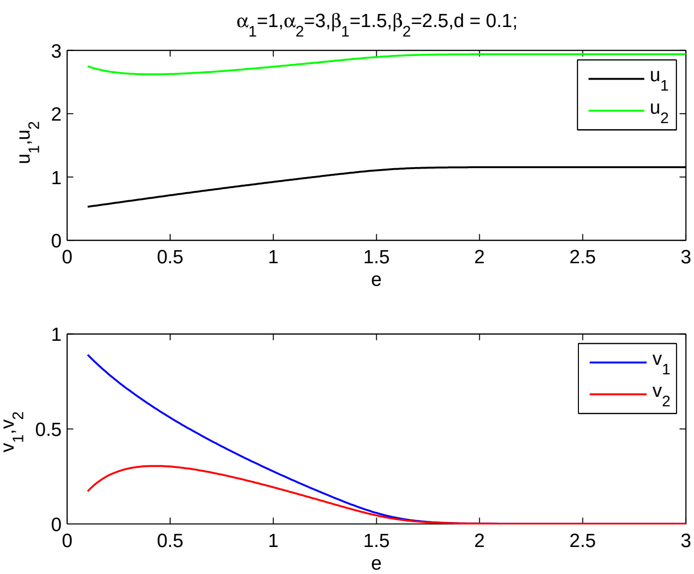

Figure 11: Illustrations for the dynamics $\beta_1 = 1.5, \beta_2 = 2.5, \varepsilon_1 = \varepsilon_2 = 0.5, d = 0.1$.

5 Appendices

5.1 Note of Section 2.2

1. Special case $\alpha + \beta = 2$.

$$\frac{dx_1}{dt} = x_1(1 - x_1 - \alpha x_2 - \beta x_3), \tag{5.1}$$
$$\frac{dx_2}{dt} = x_2(1 - \beta x_1 - x_2 - \alpha x_3), \tag{5.2}$$
$$\frac{dx_3}{dt} = x_3(1 - \alpha x_1 - \beta x_2 - x_3). \tag{5.3}$$

Define

$$x_T(t) = x_1(t) + x_2(t) + x_3(t).$$

Summing (5.1), (5.2) and (5.3), we have

$$\begin{aligned} \frac{dx_T}{dt} &= (x_1 + x_2 + x_3) - \big(x_1^2 + x_2^2 + x_3^2 + (\alpha + \beta)(x_1x_2 + x_2x_3 + x_3x_1)\big) \\ &= x_T - x_T^2. \end{aligned} \tag{5.4}$$

Hence,

$$x_T(t) = \frac{x_T(0)}{x_T(0) + (1 - x_T(0))e^{-t}}$$

with some initial value $x_T(0) = x_1(t) + x_2(t) + x_3(t)$. Clear, $x_T(t) \to 1$ as $t \to \infty$. That is, the solutions of the system (2.14) approach to the plane $x_1(t) + x_2(t) + x_3(t) = 1$. Define

$$P(t) = x_1(t)x_2(t)x_3(t).$$

Then,

$$\begin{aligned} \frac{d(\ln P)}{dt} = \frac{d(\ln x_1x_2x_3)}{dt} &= \frac{d(\ln x_1 + \ln x_2 + \ln x_3)}{dt} \\ &= \frac{1}{x_1}\frac{dx_1}{dt} + \frac{1}{x_2}\frac{dx_2}{dt} + \frac{1}{x_3}\frac{dx_3}{dt} \\ &= (1 - x_1 - \alpha x_2 - \beta x_3) + (1 - \beta x_1 - x_2 - \alpha x_3) + (1 - \alpha x_1 - \beta x_2 - x_3) \\ &= 3(1 - x_T) = \frac{3}{x_T}(x_T - x_T^2) \\ &= \frac{3}{x_T}(\frac{dx_T}{dt}) \\ &= \frac{d(\ln x_T^3)}{dt}. \end{aligned} \tag{5.5}$$

Integrating both side, we have

$$\ln P(t) - \ln P(0) = \ln x_T^3(t) - \ln x_T^3(0)$$

with some initial value $P(0) = x_1(0)x_2(0)x_3(0) > 0$. Hence,

$$P(t) = P(0)(\frac{x_T^3(t)}{x_T^3(0)}).$$

Since $x_T(t) \to 1$, we have

$$P(t) \to P(0)(\frac{1}{x_T^3(0)}) \text{ as } t \to \infty.$$

That is, the solutions of the system (2.14) approaches a hyperboloid $x_1x_2x_3 = C$, where $C = \frac{P(0)}{x_T^3(0)}$. Combining these results, the solution of (2.14) for $\alpha + \beta = 2$ tends to a periodic limit cycle in the 3-dimensional population space. These periodic cycles constitute a one-dimensional family, specified by the constant C depends on all initial values.

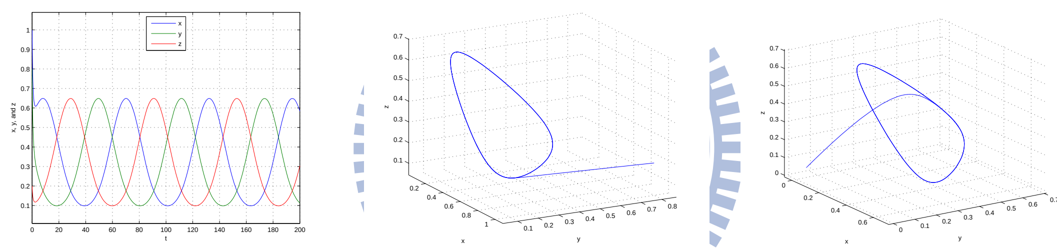

Figure 12: Illustrations for the dynamics $\alpha = 0.8, \beta = 1.2$. (a) time plot (b) initial point (1,0.8,0.2) (c) initial point (0.01,0.04,0.05).

2. General case $\alpha + \beta > 2$ and $\alpha < 1$. Let F denote the union of the three orbit closures,

$$F = \bigcup_{i=1}^{3} o_i,$$

where o_1 is the orbit in the x_2x_3-plane form $(0,0,1)$ to $(0,1,0), o_2$ is the orbit in the x_1x_3-plane form $(1,0,0)$ to $(0,0,1)$ and o_3 is the orbit in the x_1x_2-plane form $(0,1,0)$ to $(1,0,0)$.

Theorem (Schuster, Sigmund and Wolff, 1979). With the exception of the fixed point E_7 and one orbit whose w-limit is E_7, every orbit in the interior of $\mathbb{R}_+^3$ has F as w-limit.

Note that E_7 is the positive equilibrium for system (2.14). And it is a saddle for $\alpha+\beta>2$ and $\alpha<1$ since some eigenvalues for the corresponding linearized matrix have negative real part.

Proof: Let $V = x_1 + x_2 + x_3$ be a Lyapunov function, then

$$\frac{dV}{dt} = (x_1 + x_2 + x_3) - (x_1^2 + x_2^2 + x_3^2 + (\alpha+\beta)(x_1x_2 + x_2x_3 + x_3x_1)), \tag{5.6}$$

which is a quadric form of a two-sheeted hyperboloid with center $\frac{1}{1+\alpha+\beta}(\frac{1}{2},\frac{1}{2},\frac{1}{2})$. The sheet through E_7 and also contains $(1,0,0),(0,1,0)$ and $(0,0,1)$.

For every points on the sheet has $V \geq \frac{3}{1+\alpha+\beta}$ and the equality holds for $(x_1,x_2,x_3) = E_7$. For $x_1+x_2+x_3 = 1$, we have $V = 1$ and

$$\begin{aligned}\frac{dV}{dt} &= (x_1 + x_2 + x_3) - (x_1^2 + x_2^2 + x_3^2 + (\alpha+\beta)(x_1x_2 + x_2x_3 + x_3x_1)) \\ &= (x_1 + x_2 + x_3) - ((x_1 + x_2 + x_3)^2 + (\alpha+\beta-2)(x_1x_2 + x_2x_3 + x_3x_1)) \\ &= 1 - 1 - (\alpha+\beta-2)(x_1x_2 + x_2x_3 + x_3x_1)) \\ &= (\alpha+\beta-2)(x_1x_2 + x_2x_3 + x_3x_1)) < 0,\end{aligned}$$

Hence, the solution will into the bounded region

$$Q_1 = \{(x_1,x_2,x_3) \in \mathbb{R}^3_+ : \frac{3}{1+\alpha+\beta} \leq V \leq 1\}.$$

Define $P = x_1x_2x_3$ be the second Lyapunov function, then

$$\begin{aligned}\dot{P} &= \dot{x}_1x_2x_3 + x_1\dot{x}_2x_3 + x_1x_2\dot{x}_3 \\ &= x_1x_2x_3(1 - x_1 - \alpha x_2 - \beta x_3) + x_1x_2x_3(1 - \beta x_1 - x_2 - \alpha x_3) + x_1x_2x_3(1 - \alpha x_1 - \beta x_2 - x_3) \\ &= x_1x_2x_3(3 - (1+\alpha+\beta)(x_1 + x_2 + x_3)) \\ &= P(3 - (1+\alpha+\beta)V) \\ &\leq 0\end{aligned}$$

for all initial values start from Q_1 and the equality holds for $V = \frac{3}{1+\alpha+\beta}$ or $P = 0$. $V = \frac{3}{1+\alpha+\beta}$ means the solution is an orbit whose w-limit is E_7. With the exception of those orbit, all other orbits start form Q_1 approaches the set $P = 0$, that is, the boundary of $\mathbb{R}^3_+$. It shows that the orbits of almost all points in $\mathbb{R}^3_+$. approaches the set $Q_1 \cap bd\mathbb{R}^3_+$. Moreover, E_1, E_2 and E_3 are all unstable because of $1-\alpha > 0$. Hence, the only remaining invariant set in $Q_1 \cap bd\mathbb{R}^3_+$ is F, which must be the w-limit.

Similarly for the parameter assumption $\alpha+\beta > 2$ and $\beta < 1$.

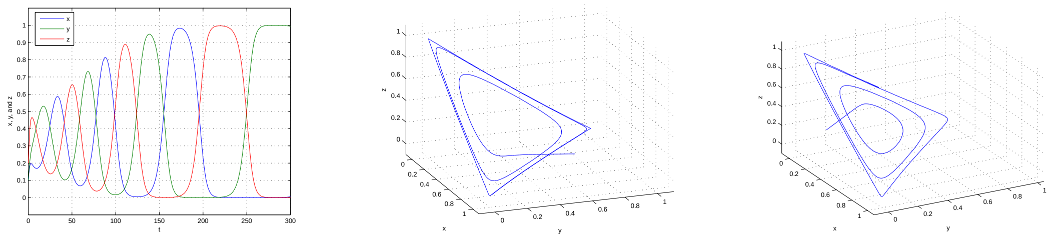

Figure 13: Illustrations for the dynamics $\alpha = 0.8, \beta = 1.3$. (a) time plot (b) initial point (0.8,0.6,0.2) (c) initial point (0.1,0.08,0.2).

5.2 Proof of Theorem 2.3.1.

Proof: Let $V : \mathbb{R}^2_+ \to \mathbb{R}$ be a Lyapunov function for system (2.18), $c_1, c_2 > 0$,

$$V(x_1, x_2) = c_1 \left(x_1 - x_1^* - x_1^* \ln(\frac{x_1}{x_1^*}) \right) + c_2 \left(x_2 - x_2^* - x_2^* \ln(\frac{x_2}{x_2^*}) \right). \tag{5.7}$$

Then,

$$\begin{aligned}\dot{V} &= c_1(x_1 - x_1^*)(b_1 + a_{11}x_1 + a_{12}x_2) + c_2(x_2 - x_2^*)(b_2 + a_{21}x_1 + a_{22}x_2) \\ &= c_1(x_1 - x_1^*)[a_{11}(x_1 - x_1^*) + a_{12}(x_2 - x_2^*)] + c_2(x_2 - x_2^*)[a_{21}(x_1 - x_1^*) + a_{22}(x_2 - x_2^*)] \\ &= c_1 a_{11}(x_1 - x_1^*)^2 + (c_1 a_{12} + c_2 a_{21})(x_1 - x_1^*)(x_2 - x_2^*) + c_2 a_{22}(x_2 - x_2^*)^2\end{aligned}$$

Choosing the suitable positive constants to verify that the quadric from is a ellipse. That is, claim that

$$(c_1 a_{12} + c_2 a_{21})^2 - 4c_1 c_2 a_{11} a_{22} < 0. \tag{5.8}$$

For the following cases: (i) $a_{12}a_{21} = 0$, (ii) $a_{12}a_{21} > 0$, (iii) $a_{12}a_{21} < 0$,

(i). W.L.O.G., assume $a_{12} = 0, a_{21} \neq 0$, then choosing $c_1 = 1, c_2 < \frac{4a_{11}a_{22}}{a_{21}^2}$ such that

$$(c_1 a_{12} + c_2 a_{21})^2 - 4c_1 c_2 a_{11} a_{22} = c_2(c_2 a_{21}^2 - 4a_{11}a_{22}) < 0.$$

(ii). (5.8) can be written to

$$(c_1 a_{12} - c_2 a_{21})^2 - 4c_1 c_2 (a_{11}a_{22} - a_{12}a_{21}) < 0,$$

and holds for choosing $c_1 = 1, c_2 = \frac{a_{12}}{a_{21}}$. Note that $a_{11}a_{22} - a_{12}a_{21} > 0$ by the local stability of positive equilibrium, which is the assumption of Theorem 2.3.1.

(iii). Choosing $c_1 = 1, c_2 = -\frac{a_{12}}{a_{21}}$, then

$$(c_1 a_{12} + c_2 a_{21})^2 - 4c_1 c_2 a_{11} a_{22} < 0.$$

Hence, the quadric from is always a ellipse and it can be rewritten to be the normal form of an ellipse

$$a_{11}X_1^2 + a_{22}X_2^2.$$

Since $a_{11} < 0, a_{22} < 0$, we have

$$\dot{V} \leq 0,$$

and the equality holds for $x_1 = x_1^*, x_2 = x_2^*$.

Recall the computation in $\dot{V}$, we have

$$\begin{aligned}
\dot{V} &= c_1a_{11}(x_1 - x_1^*)^2 + (c_1a_{12} + c_2a_{21})(x_1 - x_1^*)(x_2 - x_2^*) + c_2a_{22}(x_2 - x_2^*)^2 \\
&= \frac{1}{2} \begin{bmatrix} x_1 - x_1^* \\ x_2 - x_2^* \end{bmatrix}^T \begin{bmatrix} 2c_1a_{11} & c_1a_{12} + c_2a_{21} \\ c_1a_{12} + c_2a_{21} & 2c_2a_{22} \end{bmatrix} \begin{bmatrix} x_1 - x_1^* \\ x_2 - x_2^* \end{bmatrix}.
\end{aligned}$$

And

$$\begin{bmatrix} 2c_1a_{11} & c_1a_{12} + c_2a_{21} \\ c_1a_{12} + c_2a_{21} & 2c_2a_{22} \end{bmatrix} = (\mathbf{CA} + \mathbf{A}^T\mathbf{C}).$$

Hence the proof is equivalent to claim that whether $\mathbf{CA} + \mathbf{A}^T\mathbf{C}$ is negative definite for suitable positive constants c_1, c_2. This argument also applicable for many species model, see Theorem 2.4.1.

5.3 Proof of Theorem 2.4.1.

Proof: Let $V : \mathbb{R}_+^n \to \mathbb{R}$ be the Lyapunov function for model (2.22) by

$$V(x_1, \ldots, x_n) = \sum_{i=1}^n c_i \left(x_i - x_i^* - x_i^* \ln(\frac{x_i}{x_i^*}) \right). \tag{5.9}$$

Then,

$$\begin{aligned}
\dot{V} &= \sum_{i=1}^n c_i(x_i - x_i^*)(b_i + \sum_{j=1}^n a_{ij}x_j) \\
&= \sum_{i=1}^n c_i(x_i - x_i^*)(\sum_{j=1}^n a_{ij}(x_j - x_j^*)) \\
&= \sum_{i=1}^n \sum_{j=1}^n c_ia_{ij}(x_i - x_i^*)(x_j - x_j^*) \\
&= \frac{1}{2} \left(\mathbf{x} - \mathbf{x}^* \right)^T (\mathbf{CA} + \mathbf{A}^T\mathbf{C}) \left(\mathbf{x} - \mathbf{x}^* \right),
\end{aligned}$$

where $\mathbf{x} = (x_1, \ldots, x_n), \mathbf{x}^* = (x_1^*, \ldots, x_n^*)$. Since $\mathbf{CA} + \mathbf{A}^T\mathbf{C}$ is negative definite, we have

$$\dot{V} \le 0,$$

and the equality holds for $(x_1, \ldots, x_n) = (x_1^*, \ldots, x_n^*)$. By the Lyapunov theory, $(x_1^*, \ldots, x_n^*)$ is globally asymptotically stable for system (2.22)

5.4 Proof of Theorem 3.3.1.

Proof: In general,
(1). n is odd. Since we have

$$\begin{aligned} P(\lambda) &= \det(\lambda \mathbf{I} - (\mathbf{D} + \varepsilon \mathbf{B})) \\ &= \lambda^n - trace(\mathbf{D} + \varepsilon \mathbf{B})\lambda^{n-1} + \cdots + (-1)^n \det(\mathbf{D} + \varepsilon \mathbf{B}). \end{aligned}$$

If $\sum_{i=1}^n b_{ii} < 0$, then
(i). $trace(\mathbf{D} + \varepsilon \mathbf{B}) = \varepsilon(\sum_{i=1}^n b_{ii}) - 2(\sum_{i<j}^n d_{ij}) < 0$ for ε small.
(ii).

$$\det(\mathbf{D} + \varepsilon \mathbf{B})) = \varepsilon(\sum_{i=1}^n b_{ii})(-1)^{n-1} M,$$

where M is the $(n-1)$ principal minors of $-\mathbf{D}$ and $M > 0$. (Fiedler and Ptak, 1962) So we have $\det(\lambda \mathbf{I} - (\mathbf{D} + \varepsilon \mathbf{B})) < 0$. It follows that $P(0) = (-1)^n \det(\lambda \mathbf{I} - (\mathbf{D} + \varepsilon \mathbf{B})) > 0$. Otherwise, if $\sum_{i=1}^n b_{ii} > 0$, we have $P(0) < 0$.
(2). n is even.
Similar argument as above, then we also have $P(0) = (-1)^n \det(\lambda \mathbf{I} - (\mathbf{D} + \varepsilon \mathbf{B})) > 0$ for $\sum_{i=1}^n b_{ii} < 0$. And $P(0) < 0$ for $\sum_{i=1}^n b_{ii} > 0$.

5.5 Proof of Theorem 3.3.2.

Proof: The assumptions (iii) and (iv) implies that the system (3.26) has at least one positive equilibrium, Padron have proved the existence and uniqueness of positive steady state for the system (3.26)[15].

Let $E^* = (x_1^*, \ldots, x_n^*), x_i^* > 0$ be the positive equilibrium for system (3.26), then x_i^* satisfies the equation

$$f_i(x_i^*) + \sum_{j=1}^n (\frac{x_j^*}{x_i^*} - 1) = 0.$$

The defined Lyapunov function $V : \mathbb{R}^+ \to \mathbb{R}$ for patch i is given by

$$V_i(x_i) = x_i - x_i^* - x_i^* \ln(\frac{x_i}{x_i^*}).$$

We can verify that $V_i(x_i) > 0$ for all $x_i > 0$ and $V_i(x_i) = 0$ if and only if $x_i = x_i^*$. Hence,

$$\begin{aligned}
\frac{dV}{dt} &= (1 - \frac{x_i^*}{x_i})[x_i f_i(x_i) + \sum_{j=1}^{n} d_{ij}(x_j - x_i)] \\
&= (x_i - x_i^*)[f_i(x_i) + \sum_{j=1}^{n} d_{ij}(\frac{x_j}{x_i} - 1) - f_i(x_i^*) - \sum_{j=1}^{n} d_{ij}(\frac{x_j^*}{x_i^*} - 1)] \\
&= (x_i - x_i^*)(f_i(x_i) - f_i(x_i^*)) + \sum_{j=1}^{n} d_{ij} x_j^* (\frac{x_j}{x_j^*} - \frac{x_i}{x_i^*} + 1 - \frac{x_i^* x_j}{x_j^* x_i})
\end{aligned}$$

By assumption (ii), since $f_i'(x_i) \leq 0$, we have $(x_i - x_i^*)(f_i(x_i) - f_i(x_i^*)) \leq 0$. Let $a_{ij} = d_{ij} x_j^*, F_{ij}(x_i, x_j) = \frac{x_j}{x_j^*} - \frac{x_i}{x_i^*} + 1 - \frac{x_i^* x_j}{x_j^* x_i}$ and $G_i(x_i) = -\frac{x_i}{x_i^*} + \ln(\frac{x_i^* x_j}{x_j^* x_i})$. Then we have

$$\frac{dV}{dt} \leq a_{ij}(G_i(x_i) - G_j(x_j)), \tag{5.10}$$

and the equality holds for $x_i = x_i^*, i = 1, \ldots, n$. Now, set

$$V = \sum_{i=1}^{n} c_i V_i.$$

By Theorem 3.2.6 and (3.18), c_i is the cofactor of i-th diagonal element of Laplacian matrix corresponding to $[a_{ij}]$, then V is a Lyapunov function for coupled system (3.26). And thus,

$$\frac{dV}{dt} \leq 0$$

and the equality holds for $x_i = x_i^*, i = 1, \ldots, n$. By the Lyapunov stability theory, E^* is globally asymptotically stable in $\mathbf{R}_+^n$.

References

[1] Fiedler, Ptak, *On matrices with non-positive off-diagonal elements and positive principal minors*, Czechoslovak Mathematical Journal, Vol. 12, No. 3, (1962), pp. 382-400.

[2] S. A. Gourley, Y. Kuang, *Two-species competition with high dispersal: the winning strategy*, Mathematical Bioscineces and Engineering , Vol. 2, No. 2, (2005), pp. 345-362.

[3] B. S. Goh, *Global stability in two species interactions*, Journal of Mathematical Biology, Vol. 3, No. 3-4, (1976), pp. 313-318.

[4] B. S. Goh, *Global stability in many-species systems*, The American Naturalist Vol. 111, No. 977, (1977), pp. 135-143.

[5] B. S. Goh, *Stability in model of mutualism*, The American Naturalist Vol. 113, No. 2, (1979), pp. 261-275.

[6] A. Hastings, *Global stability in Lotka-Volterra systems with diffusion*, Journal of Mathematical Biology, Vol. 6, No. 2, (1978), pp. 163-168.

[7] A. Hastings, *Dynamics of a single species in a spatially varying environment:The stabilizing role of high dispersal rates*, Journal of Mathematical Biology, Vol. 16, No. 1, (1982), pp. 49-55.

[8] S. B. Hsu, *Ordinary differential equations with applications*, Series on Applied Mathematics, Vol. 16, (2006).

[9] M. Y. Li, Z. Shuai, *Global-stability problem for coupled system of differential equations on networks*, Journal of Differential Equations, 248 (2010), pp. 1-20.

[10] Z. Lu, Y. Takeuchi, *Global asymptotic behavior in single-species discrete diffusion systems*, Journal of Mathematical Biology, Vol. 32, No. 1 (1993), pp. 67-77.

[11] R. M. May, W.J. Leonard, *Nonlinear aspects of competition between three species*, SIAM Journal on Applied Mathematics, Vol. 29, No. 2, (1975), pp. 243-253.

[12] R. H. MacArthur, E.O. Wilson, *The Theory of island biogeography*, Princeton Univ. Press, (1967), pp. 203.

[13] P. C. Parks, *A new proof of the Routh-Hurwitz stability criterion using the second method of Lyapunov*, Mathematical Proceedings of the Cambridge Philosophical Society, Vol. 58, Issue 04, (1962), pp. 694-702.

[14] E. C. Pielou, *An Introduction to mathematical ecology*, John Wiley and Sons, New York, (1969), pp. 286.

[15] V. Padron, *Existence and uniqueness of a positive steady state solution for a logistic system of differential difference equations*, Rev. Colombiana Mat. 41 (2007), pp. 189-195.

[16] Rosenzweig, MacArthur, *Graphical representation and stability conditions of predator-prey interactions*, The American Naturalist, Vol. 97, No. 895 ,(1963), pp. 209-223.

[17] C. Strobeck, *N Species Competition*, Ecological society of America, Vol. 54, No. 3, (1973), pp. 650-654.

[18] Schuster, Sigmund, Wolff, *On w-limits for competition between three species*, SIAM Journal on Applied Mathematics, Vol. 37, No. 1, (1979), pp. 49-54.

[19] H. L. Smith, *Competing subcommunities of mutualists and a generalized Kamke Theorem*, SIAM Journal on Applied Mathematics, Vol. 46, No. 5,(1986).

[20] H. L. Smith, *Monotone Dynamical Systems: an introduction to the theory of competitive and cooperative systems*, Mathematical Surveys and Monographs, Amer. Math. Soc., Vol.41 (1995).

[21] Y. Takeuchi, *Cooperative systems theory and global stability of diffusion models*, Acta Applicandae Mathematicae, Vol. 14, No. 1-2, (1989), pp. 49-57.

[22] D. B. West, *Introduction to Graph Theory, Second Edition*, Prentice Hall, (2000), pp. 84 .

[23] X.-a. Zhang, L.-S. Chen, *The Global dynamic behavior of the competition model of three species*, Journal of Mathematical Analysis and Applications, Vol. 245, Issue 1, (2000), pp. 124-141.