

## A SURVEY OF CONSTRUCTING LYAPUNOV FUNCTIONS FOR MATHEMATICAL MODELS IN POPULATION BIOLOGY

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**Abstract.** In this paper we survey the construction of Lyapunov functions (or functionals) for various ecological models which take the form of ODE systems (or Reaction-Diffusion PDE systems). First we consider the resources-consumers type ecological models which study the competition of  $n$  microorganisms for a single limiting resource or two complementary resources in the chemostat. Next we consider the Gause-type predator-prey systems and the Leslie-type predator-prey systems. From the Lyapunov functions of the predator-prey system we construct new Lyapunov functions for three-level food chain models and one prey two predators models. Suppose a Lyapunov function is known for an ecological model which takes the form of an ODE system. Then we construct a Lyapunov functional for the corresponding reaction-diffusion PDE systems. Open problems are indicated when there is gap in the theory.

### 1. INTRODUCTION

In this paper we first survey various constructions of Lyapunov functions for the mathematical models (in the form of systems of ordinary differential equations) in population biology, especially in mathematical ecology. For a given mathematical model  $x' = f(x)$ ,  $x \in \mathbb{R}_+^n$  in population biology, if that  $E$  is the only locally asymptotically stable equilibrium then in most cases we may expect  $E$  to be globally stable in  $\mathbb{R}_+^n$ . However it is difficult to construct a Lyapunov function to establish the global stability of the equilibrium  $E$ . If we are able to construct a Lyapunov

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This paper is dedicated to Professor Hwai-Chuan Wang on his occasion of retirement.

function for the system then the global stability follows directly from the following modified LaSalle's invariant principle [12,27].

**Definition 1.1.** Consider the system of differential equations

$$(1.1) \quad \frac{dx}{dt} = f(x),$$

where  $f : \Omega \subseteq \mathbb{R}^n \rightarrow \mathbb{R}^n$  is continuous. We call  $V$  is a Lyapunov function on  $G \subseteq \Omega$  for system (1.1) if

- (a)  $V$  is continuous on  $G$ ,
- (b) If  $V$  is not continuous at  $\bar{x} \in \bar{G}$  (the closure of  $G$ ) then  $\lim_{\substack{x \rightarrow \bar{x} \\ x \in G}} V(x) = +\infty$ ,
- (c)  $\dot{V} = \text{grad } V \cdot f \leq 0$  on  $G$ .

**Theorem 1.1.** (LaSalle's Invariance principle) *Assume that  $V$  is a Lyapunov function of (1.1) on  $G$ . Define  $S = \{x \in \bar{G} \cap \Omega : \dot{V}(x) = 0\}$ . Let  $M$  be the largest invariant set in  $S$ . Then every bounded trajectory (for  $t \geq 0$ ) of (1.1) that remains in  $G$  approaches the set  $M$  as  $t \rightarrow +\infty$ .*

Actually, the first Lyapunov function in population biology was constructed by Vito Volterra ([3] p.414) in 1920. He considered the following predator-prey model which describes the fluctuation of predator species (selachians (sharks)) and prey species (the food fish) in the Mediterranean. Let  $x(t)$ ,  $y(t)$ , respectively, be the population densities of the prey and predator species at time  $t$ . The equations are

$$(1.2) \quad \begin{aligned} \frac{dx}{dt} &= ax - bxy, \\ \frac{dy}{dt} &= cxy - dy, \quad a, b, c, d > 0 \end{aligned}$$

$$(1.3) \quad x(0) > 0, \quad y(0) > 0$$

Let  $x^* = \frac{d}{c}$ ,  $y^* = \frac{a}{b}$ ,  $E = (x^*, y^*)$ . Then from (1.2) it follows that

$$\frac{dy}{dx} = \frac{\frac{dy}{dt}}{\frac{dx}{dt}} = \frac{cy(x - x^*)}{-bx(y - y^*)}.$$

By separation of variables, we have

$$\frac{x - x^*}{x} dx + \frac{b}{c} \frac{y - y^*}{y} dy = 0$$

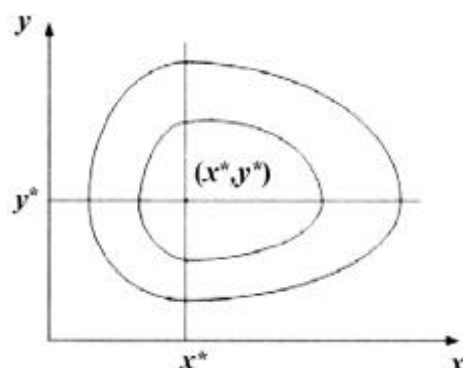


Fig. 1.

Introduce

$$(1.4) \quad V(x, y) = \int_{x^*}^x \frac{\eta - x^*}{\eta} d\eta + \frac{b}{c} \int_{y^*}^y \frac{\xi - y^*}{\xi} d\xi.$$

Then from (1.2) we have

$$\dot{V}(x, y) = \frac{dV}{dt} = \frac{x - x^*}{x} \frac{dx}{dt} + \frac{b}{c} \frac{y - y^*}{y} \frac{dy}{dt} \equiv 0.$$

Thus  $V(x(t), y(t)) \equiv V(x(0), y(0)) \equiv c$  and the solution  $(x(t), y(t))$  of I.V.P. (1.2) and (1.3) is a periodic solution of (1.2).

Thus we have a family of neutrally stable periodic solutions for system (1.2) (See Fig. 1). We note that B. S. Goh [11] used a Lyapunov function of the type (1.4) to establish the global stability of ecological models.

In Section 2, we shall construct several Lyapunov functions for the resources-consumers type ecological models. In Section 3, we discuss constructing Lyapunov functions for the predator-prey systems. In Section 4, we construct Lyapunov functionals for the corresponding reaction-diffusion systems to the ODE systems for which the Lyapunov functions are known. In section 2-4, open problems are indicated when there is a gap in the theory. Section 5 is the discussion section. Since Lyapunov functions and functionals are difficult to construct for the mathematical models in population biology, we survey several non-Lyapunov methods in the literature.

## 2. RESOURCE-CONSUMER TYPE ECOLOGICAL MODELS

In this section we first consider the exploitative competition of  $n$  microorganisms for a single-limited nutrient in a chemostat. The chemostat is a piece of laboratory apparatus that captures the essentials of exploitative competition in an open system. Basically, it consists of three vessels connected by pumps. The first is called the feed bottle and contains all of the nutrients essential for growth of microorganisms with one, hereafter called the nutrient, is in short supply. The contents of the feed bottle are pumped at a constant rate into the

second vessel, the reaction chamber which will be charged with microorganisms and is well mixed. The contents of the reaction vessel are pumped at the same constant rate into the final vessel, called the overflow vessel. Thus the volume of the reaction vessel is constant, an important assumption. Other names in use are continuous culture, CSTR (Continuously Stirred Tank Reactor) and bio-reactor. In ecology this is a laboratory model of a simple lake while in bio-technology this is the laboratory model of a commercial reactor, perhaps manufacturing a product with genetically altered organisms.

A derivation of the chemostat equations can be found in almost any bioengineering text, for example in [33]. We give here a heuristic description and the reader is referred to one of the above references for a more detailed description. Let  $S(t)$  denote the concentration of the nutrient in the reaction vessel at time  $t$ ;  $S^{(0)}$ , the concentration of the nutrient in the feed bottle;  $F$ , the flow rate (determined by the pump speed);  $V$ , the volume of the reaction vessel; and define the parameter  $D$ , called the dilution rate, by  $D = \frac{F}{V}$ . If there were no microorganisms, the rate of change of the concentration of the nutrient in the reaction vessel would be given by

$$\frac{dS(t)}{dt} = (S^{(0)} - S(t)) D,$$

the simple statement that change in concentration is proportional to the difference between the incoming and the resident concentrations. If organisms are consuming the nutrient then this needs to be corrected and the consumed nutrient converted to growth is proportional to consumption. Nutrient uptake (consumption) is usually taken to be of the Monod (or Michaelis-Menten) form

$$\frac{m x S}{a + S},$$

where  $m$  is called the maximal growth rate and  $a$  is called the Michaelis-Menten constant. Thus, if  $x(t)$  denotes the concentration of a microorganism at time  $t$ , the equations take the form (suppressing the  $t$  dependence in the independent variables)

$$\begin{aligned} S' &= (S^{(0)} - S) D - \frac{x}{y} \frac{m S}{a + S}, \\ x' &= x \left( \frac{m S}{a + S} - D \right). \end{aligned}$$

The constant  $y$  is a yield constant and represents the conversion of nutrient to organisms.  $S^{(0)}$  and  $D$  are controlled by the experimenter and can be thought of as environmental variables while  $m$ ,  $a$ , and  $y$  are properties of the organism, to be measured in the laboratory. There is also an underlying assumption that all other effects are controlled and constant, such as temperature and pH, in particular.

With  $n$  competitors and the same assumptions, the equations become

$$(2.1) \quad \begin{aligned} S' &= (S^{(0)} - S) D - \sum_{i=1}^n \frac{x_i}{y_i} \frac{m_i S}{a_i + S}, \\ x'_i &= x_i \left( \frac{m_i S}{a_i + S} - D \right). \end{aligned}$$

Define  $\lambda_i$  as the solution of the following equation

$$(2.2) \quad \frac{m_i \lambda_i}{a_i + \lambda_i} = D.$$

The parameters  $\lambda_i$ ,  $i = 1, 2, \dots, n$  represent "break-even" concentrations, values of the nutrient where the derivatives of  $x_i$ ,  $i = 1, 2, \dots, n$  are zero. In [18], the authors used elementary mathematical methods to prove the following:

**Theorem 2.1.** ([18]) Let  $0 < \lambda_1 < \lambda_2 \leq \dots \leq \lambda_n \leq S^{(0)}$ . Then

$$\begin{aligned} \lim_{t \rightarrow \infty} S(t) &= \lambda_1, \\ \lim_{t \rightarrow \infty} x_1(t) &= S^{(0)} - \lambda_1 = x_1^* > 0, \\ \lim_{t \rightarrow \infty} x_i(t) &= 0, \quad i = 2, 3, \dots, n. \end{aligned}$$

Competitive exclusion holds and only one competitor survives.

In [2] Armstrong and McGehee consider the general monotone functional responses in the chemostat equation. Then (2.1) takes the form

$$\begin{aligned} (2.3) \quad S' &= (S^{(0)} - S) D - \sum_{i=1}^n f_i(S)x_i, \\ x_i' &= (f_i(S) - D) x_i, \\ S(0) &\geq 0, \quad x_i(0) > 0, \quad i = 1, 2, \dots, n, \end{aligned}$$

where the functional response  $f_i(S)$ ,  $i = 1, 2, \dots, n$ , satisfies

- (i)  $f_i(0) = 0$ ,
- (ii)  $f_i'(S) > 0$ ,  $S > 0$ .

We note that from the scaling we may assume the yield constants  $y_i = 1$  for all  $i = 1, 2, \dots, n$ .

Let the "break-even" concentration  $\lambda_i$  be defined as  $f_i(\lambda_i) = D$ . Then we have the following theorem.

**Theorem 2.2.** ([2,33]) Let  $0 < \lambda_1 < \lambda_2 \leq \dots \leq \lambda_n \leq S^{(0)}$ . Then

$$\begin{aligned} \lim_{t \rightarrow \infty} S(t) &= \lambda_1, \\ \lim_{t \rightarrow \infty} x_1(t) &= x_1^* = S^{(0)} - \lambda_1 > 0, \\ \lim_{t \rightarrow \infty} x_i(t) &= 0, \quad i = 2, 3, \dots, n. \end{aligned}$$

Competitive exclusion also holds for general monotone functional responses.

*Proof.* Set

$$\Phi = S + \sum_{j=1}^n x_j - S^{(0)},$$

and observe that in the variables  $\Phi, x_1, \dots, x_n$ , (2.3) takes the form

$$(2.4) \quad \begin{aligned} \Phi' &= -\Phi, \\ x_i' &= x_i \left[ f_i \left( S^{(0)} + \Phi - \sum_{j=1}^n x_j \right) - D \right], \\ i &= 1, 2, \dots, n. \end{aligned}$$

Obviously

$$(2.5) \quad \lim_{t \rightarrow \infty} \Phi(t) = 0,$$

and so it follows that the solutions of (2.3), (2.4) are positive and bounded. We are led to consider the limiting system of (2.4)

$$(2.6) \quad \begin{aligned} x_i' &= x_i \left[ f_i \left( S^{(0)} - \sum_{j=1}^n x_j \right) - D \right], \\ i &= 1, 2, \dots, n. \end{aligned}$$

The relevant domain for (2.6) is the set

$$\Omega = \left\{ x \in \mathbb{R}_+^n : \sum_{j=1}^n x_j \leq S^{(0)} \right\}.$$

It is easy to verify  $\Omega$  is positively invariant.

Let  $E_1 = (S^{(0)} - \lambda_1, 0, \dots, 0)$  be an equilibrium of (2.6). Define  $\Delta = \{x \in \Omega : \sum_j x_j = S^{(0)} - \lambda_1\}$ ,  $\mathcal{B} = \{x \in \Omega : \sum_j x_j < S^{(0)} - \lambda_1\}$ , and  $\mathcal{C} = \{x \in \Omega : \sum_j x_j > S^{(0)} - \lambda_1\}$ . It will be shown that a solution starting in  $\mathcal{C}$  either remains in  $\mathcal{C}$  and converges to  $E_1$ , or enters  $\mathcal{B}$  and remains there.

First, observe that

$$\left( \sum_{j=1}^n x_j \right)' = \sum_{j=1}^n x_j \left( f_j \left( S^{(0)} - \sum_k x_k \right) - D \right) < 0,$$

for all  $x \in (\mathcal{C} \cup \Delta) \setminus E_1$ , by the monotonicity of the  $f_j$  and the fact that  $S^{(0)} - \sum_{k=1}^n x_k \leq \lambda_1$ . It follows immediately that if  $x(t) \in \Delta \setminus E_1$  for some  $t$  then  $x(s) \in \mathcal{B}$  for  $s > t$ . In particular, once a solution enters  $\mathcal{B}$ , it can never get out.

Suppose the solution  $x(t)$  remains in  $\mathcal{C}$  for all  $t \geq 0$ . Introduce Lyapunov function  $V(x) = \sum_{j=1}^n x_j$  in  $\mathcal{C}$  then  $\dot{V}(x) < 0$ . It is easy to see that

$$\dot{V}(x) = 0 \text{ for } x \in \mathcal{C} \cup \Delta \text{ if and only if } x = E_1.$$

By the LaSalle's invariance principle  $x(t) \rightarrow E_1$  as  $t \rightarrow \infty$ .

Next we consider a solution  $x(t)$  of (2.6) which belongs to  $\mathcal{B}$  for  $t \geq 0$  and for which  $x_1(0) > 0$ . For such a solution,

$$x_1'(t) = x_1(t) \left( f_1 \left( S^{(0)} - \sum_{j=1}^n x_j \right) - D \right) > x_1(t) (f_1(\lambda_1) - D) = 0,$$

so  $\lim_{t \rightarrow \infty} x_1(t)$  exists and exceeds  $x_1(0) > 0$ . Obviously if  $V(x) = -x_1$  in  $\mathcal{B}$  then  $\dot{V}(x) < 0$ . Further,  $\dot{V}(x) = 0$  for  $x \in \mathcal{B} \cup \Delta$  if and only if either  $x \in \Delta$  or  $x \in \mathcal{B}$  and  $x_1 = 0$ . By LaSalle's invariant principle and  $x'(t) > 0$ ,  $x_1(0) > 0$  for  $t \geq 0$ , we conclude that the  $w$ -limit set  $w(x(0)) \subset \Delta$  and  $x(t) \rightarrow E_1$  as  $t \rightarrow \infty$ . ■

Obviously, Theorem 2.2 is not only a generalization of Theorem 2.1 but also its proof is much shorter than that of Theorem 2.1 in [18]. In the following, we consider the chemostat equation with different removal rates

$$(2.7) \quad \begin{aligned} S' &= (S^{(0)} - S) D - \sum_{i=1}^n \frac{m_i S}{a_i + S} x_i, \\ x_i' &= x_i \left( \frac{m_i S}{a_i + S} - d_i \right), \\ S(0) &\geq 0, \quad x_i(0) > 0, \quad i = 1, 2, \dots, n. \end{aligned}$$

With different removal rate  $d_i$ ,  $i = 1, 2, \dots, n$ , the conservation property (2.5) no longer holds and the techniques used in Theorem 2.2 will not work for system (2.7). Define  $\lambda_i$ ,  $i = 1, 2, \dots, n$  as the solution of the following equation

$$\frac{m_i \lambda_i}{a_i + \lambda_i} = d_i.$$

Hsu in [16] constructs a Lyapunov function for system (2.7).

**Theorem 2.3.** ([16,33]) *Suppose that*

$$(H) \quad 0 < \lambda_1 < \lambda_2 \leq \lambda_3 \leq \dots \leq \lambda_n \text{ and } \lambda_1 < S^{(0)}.$$

*Then*

$$\begin{aligned} \lim_{t \rightarrow \infty} S(t) &= \lambda_1, \\ \lim_{t \rightarrow \infty} x_1(t) &= x_1^* = (S^{(0)} - \lambda_1) / d_1, \end{aligned}$$

*and*

$$\lim_{t \rightarrow \infty} x_i(t) = 0, \quad i = 2, 3, \dots, n.$$

*Proof.* On the set  $G = \{(S, x_1, \dots, x_n) \in \mathbb{R}_+^{n+1} : S > 0, x_1 > 0\}$ , define

$$(2.8) \quad V(S, x_1, \dots, x_n) = \int_{\lambda_1}^S \frac{\xi - \lambda_1}{\xi} d\xi + c_1 \int_{x_1^*}^{x_1} \frac{\eta - x_1^*}{\eta} d\eta + \sum_{i=2}^n c_i x_i,$$

where  $c_i = \frac{m_i}{m_i - d_i}$ . Then it follows that in  $G$

$$\begin{aligned} \frac{d}{dt} V(S(t), x_1(t), \dots, x_n(t)) &= \nabla V \cdot (S', x_1', \dots, x_n')^T \\ &= (S - \lambda_1) \left( \frac{S^{(0)} - S}{S} - \frac{m_1 x_1^*}{a_1 + S} \right) + \sum_{i=2}^n (\lambda_1 - \lambda_i) \frac{m_i x_i}{a_i + S}. \end{aligned}$$

The term  $x_1^*$  may be rewritten as

$$x_1^* = \frac{S^{(0)} - \lambda_1}{d_1} = \frac{(S^{(0)} - \lambda_1)(a_1 + \lambda_1)}{m_1 \lambda_1},$$

so that

$$\frac{S^{(0)} - S}{S} - \frac{m_1 x_1^*}{a_1 + S},$$

may be simplified to

$$-\frac{a_1(S - \lambda_1)}{\lambda_1 S(a_1 + S)}.$$

This in turn may be substituted into the expression for  $\frac{dV}{dt}$  to obtain

$$\frac{dV}{dt} = \frac{-(S - \lambda_1)^2 a_1}{(a_1 + S) S \lambda_1} + \sum_{i=2}^n m_i (\lambda_1 - \lambda_i) \frac{x_i}{a_i + S} \leq 0.$$

The set

$$E = \left\{ (S, x_1, \dots, x_n) : \frac{dV}{dt} = 0 \right\},$$

is given by

$$E = \{(\lambda_1, x_1, 0, \dots, 0) : x_1 > 0\}.$$

Since  $\lambda_1 < S^{(0)}$ , the only invariant set in  $E$  is

$$\begin{aligned} S &= \lambda_1, \\ x_1 &= (S^{(0)} - \lambda_1) / d_1, \\ x_i &= 0, \quad i = 2, \dots, n. \end{aligned}$$

An application of the LaSalle's invariance principle gives the desired result.  $\blacksquare$



We note that the Lyapunov function of the form (2.8) is not applicable to the following model with general monotone functional responses and different removable rates

$$(2.9) \quad \begin{aligned} S' &= (S^{(0)} - S) D - \sum_{i=1}^n f_i(S)x_i, \\ x_i' &= (f_i(S) - d_i) x_i, \\ S(0) &\geq 0, \quad x_i(0) > 0, \quad i = 1, 2, \dots, n. \end{aligned}$$

where  $f_i(S)$  is the general monotone functional response as in system (2.3).

Obviously,  $E_1 = (\lambda_1, x_1^*, 0, \dots, 0)$  be an equilibrium where  $x_1^* = \frac{(S^{(0)} - \lambda_1)D}{d_1}$ .

In [27] Wolkowicz and Lu introduced a Lyapunov function for system (2.9)

$$(2.10) \quad V(S, x_1, \dots, x_n) = \int_{\lambda_1}^S Q(\xi) d\xi + \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d + \sum_{i=2}^n c_i x_i,$$

where the function  $Q(S)$  and the positive constants  $c_i, i = 2, \dots, n$  will be determined according to the following computations. Differentiating both sides of (2.10) with respect to time  $t$  yields

$$(2.11) \quad \begin{aligned} \dot{V} &= \frac{dV}{dt} = Q(S) \left[ (S^{(0)} - S) D - \sum_{i=1}^n f_i(S)x_i \right] \\ &\quad + \frac{x_1 - x_1^*}{x_1} [f_1(S) - d_1] x_1 + \sum_{i=2}^n c_i (f_i(S) - d_i) x_i \\ &= \left[ Q(S) (S^{(0)} - S) D - x_1^* (f_1(S) - d_1) \right] \\ &\quad + x_1 (f_1(S) - d_1) \left[ 1 - \frac{Q(S)}{(f_1(S) - d_1)} f_1(S) \right] \\ &\quad + \sum_{i=2}^n x_i [-Q(S) f_i(S) + c_i (f_i(S) - d_i)]. \end{aligned}$$

Choose

$$Q(S) = \frac{x_1^* (f_1(S) - d_1)}{(S^{(0)} - S) D}.$$

Then from  $x^* = \frac{(S^{(0)} - \lambda_1)D}{d_1}$ , (2.11) becomes

$$(2.12) \quad \begin{aligned} \dot{V} &= x_1 (f_1(S) - d_1) \left( 1 - \frac{(S^{(0)} - \lambda_1) f_1(S)}{d_1 (S^{(0)} - S)} \right) \\ &\quad + \sum_{i=2}^n x_i \left[ c_i (f_i(S) - d_i) - \frac{f_i(S) (f_1(S) - d_1) (S^{(0)} - \lambda_1)}{(S^{(0)} - S) d_1} \right]. \end{aligned}$$

The first term in (2.12) is nonpositive and equals to zero when  $x_1 = 0$  or  $S = \lambda_1$ . If we can choose positive constants  $c_i$ ,  $i = 2, 3, \dots, n$  such that

$$(2.13) \quad h_i(S) = c_i (f_i(S) - d_i) - \frac{f_i(S) (f_1(S) - d_1) (S^{(0)} - \lambda_1)}{(S^{(0)} - S) d_1} \leq 0,$$

then from the LaSalle's invariance principle, it follows that  $(S(t), x_1(t), x_2(t), \dots, x_n(t)) \rightarrow (\lambda_1, x_1^*, 0, \dots, 0)$  as  $t \rightarrow \infty$ . From (2.13) and the assumption  $\lambda_1 < \lambda_2 \leq \lambda_3 \leq \dots \leq S^{(0)}$ , we note that

$$h_i(S) \leq 0 \quad \text{for } \lambda_1 \leq S \leq \lambda_i .$$

Hence we need to choose  $c_i > 0$  satisfying

$$c_i < \frac{f_i(S) (f_1(S) - d_1) (S^{(0)} - \lambda_1)}{(f_i(S) - d_i)} = w_i(S), \quad \text{for } \lambda_i \leq S \leq S^{(0)},$$

$$c_i > w_i(S), \quad \text{for } 0 < S < \lambda_1,$$

(See Fig. 2)  
or equivalently

$$(2.14) \quad \max_{0 \leq S \leq \lambda_1} w_i(S) < c_i < \min_{\lambda_i \leq S \leq S^{(0)}} w_i(S).$$

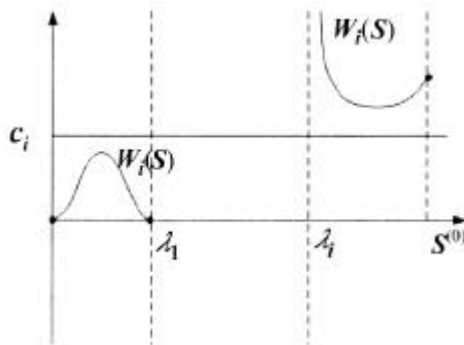


Fig. 2.

In [27] Wolkowicz and Lu verify that by symbolic computation, the Lyapunov function works for the sigmoidal-type functional responses

$$f_i(S) = \frac{m_i S^2}{(a_i + S)(b_i + S)}, \quad n \geq 1.$$

Hsu and Waltman [24] succeeded in applying the type of Lyapunov function (2.10) in their study of the two species competition in a chemostat when one competitor produces a toxin. We note that the type of Lyapunov function (2.8) does not work for the model in [24].

In [28] Bingtuan Li constructed a Lyapunov function  $V(S, x_1, \dots, x_n)$  for system (2.9) as follows

$$V = \int_{\lambda_1}^S \frac{(f_1(\xi) - d_1)(S^{(0)} - \lambda_1)}{d_1(S^{(0)} - \xi)} d\xi + \int_{x_1^*}^{x_1} \frac{\eta - x_1^*}{\eta} d\eta + C \left( \sum_{i=1}^n x_i \right) + \sum_{i=2}^n Mx_i,$$

where  $M$  is a constant to be determined and  $C(u)$  is a continuously differentiable function such that  $C'(u)$  is a piecewise linear function as shown in Fig. 3.

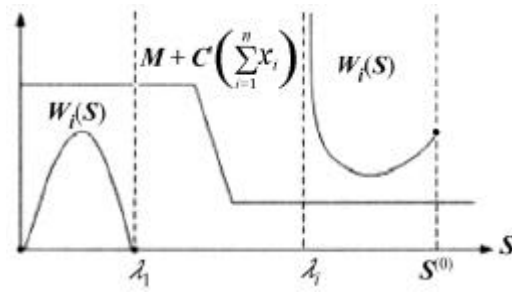


Fig. 3.

Let  $D_{max} = \max\{D, d_1, \dots, d_n\}$  and  $D_{min} = \min\{D, d_1, \dots, d_n\}$ .

In [28] the author showed that if  $\frac{DS^{(0)}}{D_{min}} - \frac{DS^{(0)}}{D_{max}} < \lambda_2 - \lambda_1$ , then  $\lim_{t \rightarrow \infty} (S(t), x_1(t), x_2(t), \dots, x_n(t)) = E_1$ .

Furthermore the method can also be applied to the case of nonmonotone functional responses, for example, the inhibited functional responses  $f_i(S) = \frac{mS}{(a+S)(b+S)}$ .

In the following we propose an open problem for the competition of  $n$  microorganisms for a single limited nutrient:

Open problem 1: Under assumption (H), prove competitive exclusion holds for system (2.9) with any general monotone functional responses and any different removable rates.

Next we consider the exploitative competition of  $n$  microorganisms for two complementary nutrients in a chemostat. The model takes the form [20]

$$(2.15) \quad \begin{aligned} S' &= (S^{(0)} - S) D - \frac{1}{y_{s1}} f_1(S, R)x_1 - \frac{1}{y_{s2}} f_2(S, R)x_2, \\ R' &= (R^{(0)} - R) D - \frac{1}{y_{r1}} f_1(S, R)x_1 - \frac{1}{y_{r2}} f_2(S, R)x_2, \\ x_1' &= (f_1(S, R) - D) x_1, \end{aligned}$$

$$x_2' = (f_2(S, R) - D) x_2,$$

$$S(0) \geq 0, \quad R(0) \geq 0, \quad x_1(0) > 0, \quad x_2(0) > 0,$$

where  $S^{(0)}, R^{(0)}$  are the input concentrations and  $y_{si}, y_{ri}$  are the yield constants of the  $i$ -th species, with respect to nutrient  $S$  and  $R$  respectively, and

$$f_i(S, R) = \min(p_i(S), q_i(R)),$$

$$p_i(S) = \frac{m_{si}S}{a_{si} + S}, \quad q_i(R) = \frac{m_{ri}R}{a_{ri} + R}.$$

Since  $S' + \frac{x_1'}{y_{s1}} + \frac{x_2'}{y_{s2}} = S^{(0)} - \left(S + \frac{x_1}{y_{s1}} + \frac{x_2}{y_{s2}}\right)$ , it follows that

$$(2.16) \quad S(t) + \frac{x_1(t)}{y_{s1}} + \frac{x_2(t)}{y_{s2}} = S^{(0)} + O(e^{-Dt}).$$

Similarly, we have

$$(2.17) \quad R(t) + \frac{x_1(t)}{y_{r1}} + \frac{x_2(t)}{y_{r2}} = R^{(0)} + O(e^{-Dt}).$$

From conservation properties (2.16) and (2.17), we reduce the system (2.15) to its limiting system

$$(2.18) \quad \begin{aligned} x_1' &= (f_1(S, R) - D) x_1, \\ x_2' &= (f_2(S, R) - D) x_2, \end{aligned}$$

where

$$\begin{aligned} S &= S^{(0)} - \frac{x_1}{y_{s1}} - \frac{x_2}{y_{s2}}, \\ R &= R^{(0)} - \frac{x_1}{y_{r1}} - \frac{x_2}{y_{r2}}. \end{aligned}$$

Let  $\lambda_{si}, \lambda_{ri}$  be the solutions of the equations

$$\frac{m_{si}\lambda_{si}}{a_{si} + \lambda_{si}} = D,$$

and

$$\frac{m_{ri}\lambda_{ri}}{a_{ri} + \lambda_{ri}} = D.$$

Biologically  $\lambda_{si}, \lambda_{ri}$  are the break-even concentrations of the  $i$ -th species with respect to nutrients  $S$  and  $R$ , respectively.

**Definition 2.1.** Let  $C_i = \frac{y_{si}}{y_{ri}}, T_i = \frac{R^{(0)} - \lambda_{ri}}{S^{(0)} - \lambda_{si}}$ . We say the  $i$ -th species is  $S$ -limited ( $R$ -limited) if  $T_i > C_i$  ( $T_i < C_i$ ).

For  $i = 1, 2$ , the isocline  $x'_i = 0$  of system (2.18) in the  $x_1x_2$  plane is of type either as in Fig. 4a or Fig. 4b.

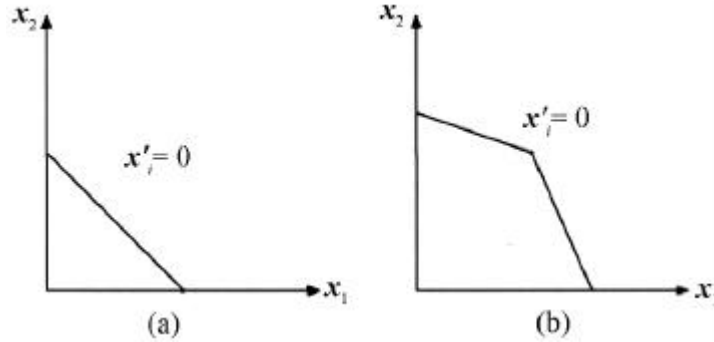


Fig. 4.

With the various combinations of the isoclines  $x'_1 = 0$ ,  $x'_2 = 0$ , it is easily seen that system (2.18) is similar to the classical two-dimensional Lotka-Volterra competition model. For details, the reader may consult [20]. In [29] Li and Smith extend the results in [20] to the case of  $n$  species competing for two complementary nutrient  $S$  and  $R$ . They completed the study for the  $n = 3$  case.

For the  $n > 3$  cases, there are still some open problems left. In [34] Huisman and Weissing did extensive numerical studies on the system of  $n$  species competing for  $k$  complementary nutrients. They found that for  $k = 3$  or  $k = 5$  there are some parameters ranges for the existence of periodic oscillations and “chaos”.

The above discussions are for the case of  $n$  species competing for  $k$  complementary nutrients with same dilution rates  $D$ . With this assumption on  $D$ , we are able to reduce the system of  $n + k$  equations to its limiting system of  $n$  equations. For the case of different removable rates, the problem is open. We also propose the following open problem.

Open problem 2: (i) Analyze the follow system of one species consuming two complementary nutrient  $S$  and  $R$

$$\begin{aligned}
 S' &= \left(S^{(0)} - S\right) D_s - \frac{1}{y_{s1}} f_1(S, R)x_1, \\
 R' &= \left(R^{(0)} - R\right) D_r - \frac{1}{y_{r1}} f_1(S, R)x_1, \\
 x'_1 &= (f_1(S, R) - d_1) x_1, \\
 S(0) &\geq 0, \quad R(0) \geq 0, \quad x_1(0) > 0.
 \end{aligned}$$

(ii) Analyze the following system of two species competing for the two complementary nutrient  $S$  and  $R$ :

$$S' = \left(S^{(0)} - S\right) D_s - \frac{1}{y_{s1}} f_1(S, R)x_1 - \frac{1}{y_{s2}} f_2(S, R)x_2,$$

$$\begin{aligned}
R' &= \left( R^{(0)} - R \right) D_r - \frac{1}{y_{r1}} f_1(S, R)x_1 - \frac{1}{y_{r2}} f_2(S, R)x_2, \\
x_1' &= (f_1(S, R) - d_1) x_1, \\
x_2' &= (f_2(S, R) - d_2) x_2, \\
S(0) &\geq 0, \quad R(0) \geq 0, \quad x_1(0) > 0, \quad x_2(0) > 0.
\end{aligned}$$

### 3. PREDATOR-PREY SYSTEM

Let  $x(t)$ ,  $y(t)$  be the population densities of prey and predator at time  $t$ , respectively. Consider the following Gause-type predator-prey system [17]

$$\begin{aligned}
(3.1) \quad & x' = xg(x) - cp(x)y, \\
& y' = (p(x) - d)y, \\
& x(0) > 0, \quad y(0) > 0,
\end{aligned}$$

where  $g(x)$  is the intrinsic growth rate of prey species,  $p(x)$  is the specific growth rate of predator species,  $c > 0$  is the conversion rate and  $d > 0$  is the death rate of predator species. We assume  $g(x)$  and  $p(x)$  satisfy the following:

**(H1)**  $g(0) > 0$  and there exists  $K > 0$  such that  $g(K) = 0$ ,  $g(x) > 0$  for  $0 \leq x < K$ . ( $K$  is called the carrying capacity of prey species)

**(H2)**  $p(0) = 0$ ,  $p'(x) > 0$  for  $0 \leq x \leq K$ .

From (3.1),  $x' = 0$  if and only if  $y = \frac{xg(x)}{cp(x)}$  and  $y' = 0$  if and only if  $x = x^*$  where  $x^*$  satisfies  $p(x^*) = d$ . We call the curve  $y = \frac{xg(x)}{cp(x)}$  the prey-isocline and the curve  $x = x^*$  predator isocline.

In [10], Freedman showed that the unique interior equilibrium  $(x^*, y^*)$  exists if  $x^* < K$  and  $(x^*, y^*)$  is locally asymptotically stable provided  $\frac{d}{dx} \left( \frac{xg(x)}{cp(x)} \right) \Big|_{x=x^*} < 0$ . To show that  $(x^*, y^*)$  is globally stable in the first quadrant of  $xy$ -plane, Hsu [17] introduced the following Lyapunov function

$$(3.2) \quad V(x, y) = \int_{x^*}^x \frac{p(\xi) - d}{p(\xi)} d\xi + c \int_{y^*}^y \frac{\eta - y^*}{\eta} d\eta.$$

Then it follows that

$$\begin{aligned}
(3.3) \quad \dot{V} &= \frac{dV}{dt} (x(t), y(t)) \\
&= \frac{p(x) - d}{p(x)} (xg(x) - cp(x)y) + c \frac{y - y^*}{y} (p(x) - d) y \\
&= \frac{p(x) - d}{p(x)} (xg(x) - cp(x)y^* - cp(x)(y - y^*)) + c(y - y^*)(p(x) - d) \\
&= c(p(x) - p(x^*)) \left( \frac{xg(x)}{cp(x)} - y^* \right) \leq 0,
\end{aligned}$$

provided the horizontal line  $y = y^*$  and the vertical line  $x = x^*$  separate the prey isocline  $y = \frac{xg(x)}{cp(x)}$  into two disjoint parts (See Fig. 5)

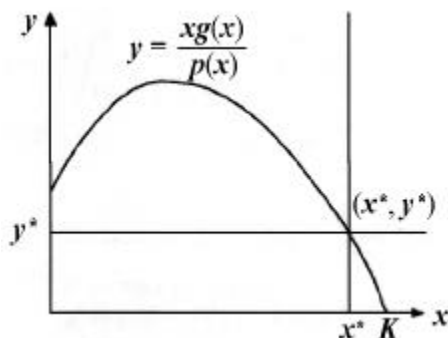


Fig. 5.

A. Ardito and P. Ricciardi [1] improve the above results by introducing the following mixed type Lyapunov function

$$(3.4) \quad V(x, y) = y^\theta \int_{x^*}^x \frac{p(\xi) - d}{p(\xi)} d\xi + \int_{y^*}^y \eta^{\theta-1} (\eta - y^*) d\eta.$$

Then it follows that

$$\dot{V}(x, y) = y^\theta (p(x) - d) \left[ \frac{xg(x)}{p(x)} - y^* + \theta \int_{x^*}^x \frac{p(\xi) - d}{p(\xi)} d\xi \right].$$

We note that if we choose  $\theta = 0$  in (3.4) then  $V(x, y)$  becomes (3.2). In [1] the authors show that with appropriate  $\theta > 0$ ,  $V(x, y) \leq 0$  in several important examples; e.g.,  $p(x) = \frac{mx}{a+x}$ ,  $g(x) = r \left(1 - \frac{x}{K}\right)$ .

In [8] Hsu and Chui consider the following three level food chain model

$$(3.5) \quad \begin{aligned} x' &= rx \left(1 - \frac{x}{K}\right) - \frac{m_1 x}{a_1 + x} y, \\ y' &= \left(\frac{m_1 x}{a_1 + x} - d_1\right) y - \frac{m_2 y}{a_2 + y} z, \\ z' &= \left(\frac{m_2 y}{a_2 + y} - d_2\right) z. \end{aligned}$$

In order to prove the extinction of top predator  $z$  in (3.5), they introduce the Lyapunov function of the following form

$$(3.6) \quad V(x, y, z) = \int_{y^*}^y \eta^{\theta-1} (\eta - y^*) d\eta + y^\theta \int_{x^*}^x \frac{p_1(\xi) - d_1}{p_1(\xi)} d\xi + cz.$$

Choosing appropriate  $\theta > 0$  and  $c > 0$  in (3.6) such that  $\dot{V}(x, y, z) \leq 0$ , they proved the global stability of the equilibrium  $(x^*, y^*, 0)$ .

In [7] Chui also applied the mixed type Lyapunov function to the following one prey-two predators model [19]

$$(3.7) \quad \begin{aligned} x' &= rx \left(1 - \frac{x}{K}\right) - \frac{m_1 x}{a_1 + x} y_1 - \frac{m_2 x}{a_2 + x} y_2, \\ y_1' &= \left(\frac{m_1 x}{a_1 + x} - d_1\right) y_1, \\ y_2' &= \left(\frac{m_2 x}{a_2 + x} - d_2\right) y_2. \end{aligned}$$

Let  $0 < \lambda_1 < \lambda_2$ ,  $K < a_1 + 2\lambda_1$ ,  $p_1(x) = \frac{m_1 x}{a_1 + x}$ . Construct the following Lyapunov function

$$(3.8) \quad V(x, y_1, y_2) = y_1^\theta \int_{\lambda_1}^{x_1} \frac{p_1(\xi) - d_1}{p_1(\xi)} d\xi + \int_{y_1^*}^{y_1} \eta^{\theta-1} (\eta - y_1^*) d\eta + c y_1^\theta y_2.$$

Choosing suitable  $c > 0$ ,  $\theta > 0$ , Chui is able to show  $\dot{V}(x, y_1, y_2) \leq 0$  for system (3.7).

Next we consider the Leslie-type predator-prey system ([22, 23])

$$(3.9) \quad \begin{aligned} x' &= xg(x) - p(x)y, \\ y' &= y \left(\delta - \beta \frac{y}{x}\right), \quad \delta, \beta > 0, \\ x(0) &> 0, \quad y(0) > 0. \end{aligned}$$

where  $g(x)$  and  $p(x)$  satisfy hypotheses (H1) and (H2).

In [22] Hsu and Hwang show that there exists a unique interior equilibrium  $(x^*, y^*)$  for system (3.9). The equilibrium  $(x^*, y^*)$  is locally asymptotically stable if  $h'(x^*) \leq 0$  where  $y = h(x) = \frac{xg(x)}{p(x)}$  is the prey isocline.

For system (3.9), we obtain the similar result as system (3.1) by constructing the following Lyapunov function

$$V(x, y) = \int_{x^*}^x \frac{\xi - x^*}{\xi p(\xi)} d\xi + c \int_{y^*}^y \frac{\eta - y^*}{\eta} d\eta,$$

where  $c = \frac{x^*}{\beta y^*}$ . Then

$$\dot{V} = \frac{(x - x^*)}{x} \left(\frac{xg(x)}{p(x)} - y^*\right) - c\beta \frac{(y - y^*)}{x} \leq 0,$$

provided

$$(3.10) \quad (x - x^*) \left(\frac{xg(x)}{p(x)} - y^*\right) < 0 \text{ for } 0 < x < K.$$

In particular if  $g(x) = r \left(1 - \frac{x}{K}\right)$  and  $p(x) = kx$  then (3.10) hold and  $(x^*, y^*)$  is globally stable.



4. REACTION DIFFUSION SYSTEMS

Let  $\Omega$  be a bounded domain in  $\mathbb{R}^N$  with smooth boundary,  $\alpha(x)$  and  $\beta(x)$  be continuous functions on  $\partial\Omega$ , and the matrix  $(a_{ij}(x))$  be symmetric and positive definite.

First we consider the scalar nonlinear PDE

$$(4.1) \quad \begin{aligned} u_t &= \sum_{i,j=1}^N \frac{\partial}{\partial x_i} \left( a_{ij}(x) \frac{\partial u}{\partial x_j} \right) + f(x, u) \quad \text{in } \Omega, \\ \alpha(x)u + (1 - \alpha(x)) \frac{\partial u}{\partial \nu} &= \beta(x) \quad \text{in } \partial\Omega. \end{aligned}$$

Take ([13,30])

$$(4.2) \quad \begin{aligned} V(u(t, \cdot, \phi)) &= \int_{\Omega} \left[ \frac{1}{2} \sum a_{ij}(x) \frac{\partial u}{\partial x_i} \frac{\partial u}{\partial x_j} - F(x, u) \right] dx \\ &+ \int_{\partial\Omega} a \left[ \frac{\alpha(x)}{2} u^2 + \frac{1 - \alpha(x)}{2} \left( \frac{\partial u}{\partial \nu} \right)^2 - \beta u \right] d\sigma \end{aligned}$$

where

$$a(y) = \left( \sum_i \left[ \sum_j a_{ij}(y) N_j(y) \right]^2 \right)^{\frac{1}{2}}, \quad F(x, u) = \int_0^u f(x, \xi) d\xi$$

and  $N(y)$  is the unit outer normal to  $\partial\Omega$  at  $y$ .

Then from (4.2) it follows that

$$\frac{d}{dt} V(u(t, \cdot, \phi)) = - \int_{\Omega} \left( \frac{\partial u}{\partial t} \right)^2 dx \leq 0.$$

Next we consider the following reaction-diffusion PDE system with Neumann boundary condition

$$(4.3) \quad \begin{aligned} \frac{\partial u}{\partial t} &= D\Delta u + f(u) \quad \text{in } \Omega \subseteq \mathbb{R}^N, \\ \frac{\partial u}{\partial \nu} &= 0 \quad \text{in } \partial\Omega, \end{aligned}$$

where  $u = u(x, t) \in \mathbb{R}^n$ ,  $D = \text{diag}(d_1, \dots, d_n)$ ,  $d_i > 0$ ,  $i = 1, \dots, n$ ,  $f : \mathbb{R}_+^n \rightarrow \mathbb{R}^n$  is continuously differentiable. We assume there exists a Lyapunov function  $V(u)$  for the corresponding ODE system

$$(4.4) \quad u' = f(u).$$

Then  $V(u)$  satisfies

$$(4.5) \quad \dot{V}(u) = \text{grad}_u V \cdot f(u) \leq 0 \quad \text{for all } u \in \mathbb{R}_+^n.$$

To study the global behavior of system (4.3), we introduce the following Lyapunov functional ([35, 36, 14])

$$(4.6) \quad W(t) = \int_{\Omega} V(u(x, t)) dx.$$

Then from (4.5), (4.6), we have

$$(4.7) \quad \begin{aligned} \frac{dW}{dt} &= \int_{\Omega} \text{grad}_u V \cdot \frac{\partial u}{\partial t} dx \\ &= \int_{\Omega} \text{grad}_u V \cdot (D\Delta u + f(u)) dx \\ &= \int_{\Omega} \left( \sum_{i=1}^n d_i \frac{\partial V}{\partial u_i} \Delta u_i \right) dx + \int_{\Omega} \dot{V} dx. \end{aligned}$$

From Green's identity, it follows that

$$(4.8) \quad \begin{aligned} \int_{\Omega} \frac{\partial V}{\partial u_i} \Delta u_i dx &= \int_{\partial\Omega} \frac{\partial V}{\partial u_i} \frac{\partial u_i}{\partial \nu} - \int_{\Omega} \nabla_x \left( \frac{\partial V}{\partial u_i} \right) \cdot \nabla_x u_i dx \\ &= - \int_{\Omega} \left[ \sum_{j=1}^n \sum_{k=1}^n \frac{\partial^2 V}{\partial u_i \partial u_k} \frac{\partial u_i}{\partial x_j} \frac{\partial u_k}{\partial x_j} \right] dx \end{aligned}$$

Thus, in addition to the assumption (4.5), we assume that

$$(4.9) \quad \text{the matrix } \left( \frac{\partial^2 V}{\partial u_i \partial u_k} \right) \text{ is positive definite, for } i, k = 1, 2, \dots, n.$$

Then from (4.7), (4.8) we have

$$(4.10) \quad \frac{dW}{dt} \leq 0.$$

In particular if  $V(u)$  satisfies that

$$(4.11) \quad \text{(i) } V(u_1, \dots, u_n) = \sum_{i=1}^n h_i(u_i), \text{ i.e. } V(u) \text{ is of separable form,}$$

and

$$(4.12) \quad \text{(ii) } h_i''(u) \geq 0 \quad i = 1, 2, \dots, n,$$

then (4.9) holds.

For the diffusive predator-prey system corresponding to the ODE (3.1)

$$(4.13) \quad \begin{aligned} \frac{\partial u}{\partial t} &= d_1 \Delta u + (ug(u) - cvp(u)) && \text{in } \Omega, \\ \frac{\partial v}{\partial t} &= d_2 \Delta v + (p(u) - d)v && \text{in } \Omega, \\ \frac{\partial u}{\partial \nu} &= \frac{\partial v}{\partial \nu} = 0 && \text{in } \partial\Omega, \\ u(x, 0) &= u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0 && \text{in } \Omega. \end{aligned}$$

If we take the Lyapunov functional  $W$  as

$$(4.14) \quad W(t) = \int_{\Omega} V(u, v) dx,$$

where  $V(u, v)$  is (3.2). Then  $V(u, v)$  satisfies (4.11) and (4.12). Hence if (3.3) holds then equilibrium  $(u^*, v^*)$  is globally stable for system (4.13). Although the function  $V(u, v)$  introduced in (3.4) is a Lyapunov function for the corresponding ODE (3.1), the functional  $W$  defined in (4.14) does not necessarily satisfy (4.10) since  $V(u, v)$  defined in (3.4) does not satisfy (4.11) and (4.12). However in [21] we show that if  $\frac{d}{du} \left( \frac{ug(u)}{p(u)} \right) |_{u=u^*} < 0$  then the equilibrium  $(u^*, v^*)$  of the RD system (4.13) is locally asymptotically stable for any diffusion constants  $d_1 > 0, d_2 > 0$ . Hence we propose the following open problem.

Open Problem 3: Let  $\frac{d}{du} \left( \frac{ug(u)}{p(u)} \right) |_{u=u^*} < 0$ . Prove or disprove the global stability for the equilibrium  $(u^*, v^*)$  of system (4.13).

Next we consider the following diffusive predator-prey system with Lesile-type [9]

$$(4.15) \quad \begin{aligned} \frac{\partial u}{\partial t} &= d_1 \Delta u + u(\lambda - \alpha u - \beta v) && \text{in } \Omega, \\ \frac{\partial v}{\partial t} &= d_2 \Delta v + \mu v \left( 1 - \frac{v}{u} \right) && \text{in } \Omega, \\ \frac{\partial u}{\partial \nu} &= \frac{\partial v}{\partial \nu} = 0 && \text{in } \Omega, \\ u(x, 0) &= u_0(x), \quad v(x, 0) = v_0(x) && \text{in } \Omega. \end{aligned}$$

System (4.15) has a unique constant equilibrium  $(u^*, v^*)$  where  $u^* = v^* = \frac{\lambda}{\alpha + \beta}$ . In [9] the authors construct the following Lyapunov functional

$$W(t) = \int_{\Omega} V(u(x, t), v(x, t)) dx,$$

where

$$(4.16) \quad V(u, v) = \int_{u^*}^u \frac{\xi - u^*}{\xi^2} d\xi + \frac{\beta}{\mu} \int_{v^*}^v \frac{\eta - v^*}{\eta} d\eta.$$

Denote

$$f(u, v) = u(\lambda - \alpha u - \beta v), \quad g(u, v) = \mu v \left( 1 - \frac{v}{u} \right).$$

We have

$$(4.17) \quad \dot{V} = \frac{\partial V}{\partial u} f(u, v) + \frac{\partial V}{\partial v} g(u, v) = -\alpha \frac{(u - u^*)^2}{u} - \beta \frac{(v - v^*)^2}{u} \leq 0$$

and

$$(4.18) \quad \begin{aligned} W'(t) &= \int_{\Omega} \left( \frac{u - u^*}{u^2} d_1 \Delta u + c \frac{v - v^*}{v} d_2 \Delta v \right) dx + \int_{\Omega} \dot{V} dx \\ &= - \int_{\Omega} \left( d_1 \frac{2u^* - u}{u^3} |\nabla u|^2 + cd_2 \frac{v^*}{v^2} |\nabla v|^2 \right) dx + \int_{\Omega} \dot{V} dx \end{aligned}$$

If  $\alpha > \beta$  then  $2u^* = \frac{2\lambda}{\alpha+\beta} > \frac{\lambda}{\alpha}$ . From the first equation in (4.15), we have

$$\frac{\partial u}{\partial t} \leq d_1 \Delta u + u(\lambda - \alpha u).$$

Then  $u(x, t) < U(x, t)$  and  $U(x, t) \rightarrow \frac{\lambda}{\alpha}$  as  $t \rightarrow \infty$ . Hence  $2u^* - u(x, t) > 0$ . From (4.17), (4.18) we have  $W'(t) < 0$  and the following

**Theorem 4.1.** *When  $\alpha > \beta$ , the constant equilibrium  $(u^*, v^*)$  attracts every positive solution of (4.15).*

Next we show how the restriction  $\alpha > \beta$  can be relaxed by using a different Lyapunov function. Define

$$V^*(u, v) = \int_{u^*}^u \frac{\xi^2 - (u^*)^2}{\xi^2} d\xi + c \int_{v^*}^v \frac{\eta - v^*}{\eta} d\eta,$$

with  $c > 0$  to be determined. Let

$$W^*(t) = \int_{\Omega} V^*(u(x, t), v(x, t)) dx.$$

In [9] the authors proved the following theorem.

**Theorem 4.2.** *Suppose  $\frac{\alpha}{\beta} > s_0$ , where  $s_0 \in (\frac{1}{5}, \frac{1}{4})$  is the unique positive zero of*

$$h(s) = 32s^3 + 16s^2 - s - 1.$$

*Then  $(u^*, v^*)$  attracts every positive solution of (4.15).*

Open Problem 4: We conjecture the conclusion of Theorem 4.2 is valid for all  $\alpha, \beta > 0$ .

## 5. DISCUSSION

In the previous sections we presented the construction of Lyapunov functions for various mathematical models in population biology. However it is difficult to construct a suitable Lyapunov function to prove the global stability of a locally asymptotically stable equilibrium. In case when we do not succeed in constructing an appropriate Lyapunov, we need to use some non-Lyapunov approaches to complete the proof. In the following we shall review several non-Lyapunov methods.

First for the two-dimensional ODE system

$$(5.1) \quad \begin{aligned} x' &= f(x, y), \\ y' &= g(x, y), \end{aligned}$$

if we are able to eliminate the possibility of the existence of periodic orbits then from the Poincaré-Bendixson Theorem [12] we establish the global stability of the local stable equilibrium. To exclude the existence of periodic solutions of (5.1), we may apply Dulac's criterion, i.e. to find  $h(x, y) \in C^1$  such that

$$\frac{\partial(hf)}{\partial x} + \frac{\partial(hg)}{\partial y}$$

has same sign. Interested readers may consult the papers [19], [22], [26]. The another approach combined with Poincaré-Bendixson Theorem is to show

$$\int_{\Gamma} \frac{\partial f}{\partial x} + \frac{\partial g}{\partial y} dt < 0$$

for any periodic orbit  $\Gamma$  of (5.1). Then the periodic orbit  $\Gamma$  is orbitally stable. Since equilibrium  $(x^*, y^*)$  is asymptotically stable, it is impossible to have a stable limit cycle enclosing a stable equilibrium. Hence there exists no periodic solution. The readers may consult [33](p.54), [5].

For three-dimensional irreducible competition systems, Hirsch and Smith [15], [32] showed that the Poincaré-Bendixson Theorem holds. To rule out the possibility of the existence of periodic solutions, Chih et al [6] constructed a surface and a vector field to obtain a contradiction to Stoke's Theorem. In [25], Hsu and Waltman apply the uniform persistence theorem to obtain global stability of a local stable equilibrium for a three-dimensional competitive system from a mathematical model of two species competing for a single limit resource in the chemostat with external inhibitor. For  $n > 3$ , Mallet-Paret and Smith [31] establish Poincaré-Bendixson Theorem for a monotone feedback system.

#### REFERENCES

1. A. Ardito, P. Ricciardi, Lyapunov functions for a generalized Gause-type model, *J. Math. Biology*, **33** (1995), 816-828.
2. R. A. Armstrong and R. McGehee, Competitive exclusion American Naturalist, **115** (1980), 151.
3. M. Braun, *Differential Equations and Their Application*, Springer-Verlag, 1975.
4. G. Butler, S. B. Hsu and P. Waltman, Coexistence of competing predator in a chemostat, *J. Math. Biology*, **17** (1983), 133-151.
5. K. Cheng, S. B. Hsu and S. S. Lin, Some results on global stability of a predator-prey system, *J. Math. Biology*, **12** (1981), 115-126
6. C. W. Chi, S. B. Hsu and L. I. Wu, On the asymmetric May-Leonard model of three competing species SIAM, *J. Appl. Math.*, **58(1)** (1998), 211-226.
7. C. H. Chiu, Lyapunov functions for the global stability of competing predators, *J. Math. Anal. Appl.*, **230(1)** (1999), 232-241.
8. C. H. Chiu and S. B. Hsu, Extinction of top predator in a three-level food-chain model, *J. Math. Biology*, **37** (1998), 372-380.
9. Y. Du and S. B. Hsu, A diffusive predator-prey model: in heterogeneous environment, *J. Differential Equations*, **203** (2004), no. 2, 331-364.
10. H. I. Freedman, Graphical stability, enrichment, and pestcontrol by a natural enemy, *Math. Biosci.*, **31** (1976), 207-225.

11. B. S. Goh, Global stability in many species system, *Amer. Naturalist*, **111** (1977), 135-143.
12. J. Hale, *Ordinary Differential Equations*, Wiley-Interscience, 1969.
13. J. Hale, *Asymptotic Behavior of Dissipative Systems*, AMS Monographs Number 25, 1988.
14. A. Hasting, Global stability in Lotka-Volterra systems with diffusion, *J. Math. Biology*, **6** (1978), 163-168.
15. M. Hirsch, Systems of differential equations which are competitive or cooperative I: limitsets, *SIAM J. Math. Analysis*, **13** (1982), 167-179.
16. S. B. Hsu, Limiting behavior for competing species, *SIAM J. Appl. Math.*, **34** (1978), 760-763.
17. S. B. Hsu, On global stability of a predator-prey systems, *Math. Biosci.*, **39** (1978), 1-10.
18. S. B. Hsu, S. P. Hubbell and P. Waltman, A mathematical theory for single nutrient competition in continuous cultures of micro-organisms, *SIAM J. Appl. Math.*, **32** (1977), 366-383.
19. S. B. Hsu, S. P. Hubbell and P. Waltman, Competing predator, *SIAM J. Appl. Math.*, **135(4)** (1978), 617-625.
20. S. B. Hsu, K. S. Cheng and S. P. Hubbell, Exploitative competition of microorganisms for two complementary nutrients in continuous culture, *SIAM J. Appl. Math.*, **41** (1981), 422-444.
21. R. T. Gong and S. B. Hsu, Stability analysis for a class of diffusive coupled system with application to population biology, *Can. Appl. Math. Quart.*, **8** (2000), 79-96.
22. S. B. Hsu and T. W. Hwang, Global stability for a class of predator-prey system, *SIAM J. Appl. Math.*, **55(3)** (1995), 763-783.
23. S. B. Hsu and T. W. Hwang, Hopf bifurcation analysis for a predator-prey system of Holling and Lesile type, *Taiwanese J. Math.*, **1** (1999), 35-53.
24. S. B. Hsu and P. Waltman, Competition in chemostat when one competitor produces toxin, *Japan J. Industrial and Applied Math.*, **15(3)** (1998), 471-490.
25. S. B. Hsu and P. Waltman, Analysis of a model of two competitors in a chemostat with an external inhibitor, *SIAM J. Appl. Math.*, **52(2)** (1992), 528-540.
26. S. B. Hsu, P. Waltman and G. Wolkowicz, Global analysis of a model of plasmid-bearing, plasmid-free competition in a chemostat, *J. Math. Biol.*, **32** (1994), 731-742.
27. Z. Lu and G. Wolkowicz, Global dynamics of a mathematical model of competition in the chemostat: general response functions and different death rates, *SIAM J. Appl. Math.*, **52(1)** (1992), 222-233.
28. B. Li, Global asymptotic behavior of the chemostat: general response function and different death rates, *SIAM J. Appl. Math.*, **59** (1999), 411-422.

29. B. Li and Hal Smith, How many species can two essential resources support? *SIAM J. Appl. Math.*, **62(1)** (2001), 333-366.
30. H. Matano, Convergence of solutions of one-dimensional semilinear parabolic equation, *J. Math. Kyoto Univ.*, **18** (1978), 224-243.
31. J. Mallet-Paret and Hal Smith, The Poincaré-Bendixson theorem for monotone cyclic feedback systems, *J. Dynam. Differential Equations*, **2** (1990), 367-421.
32. H. Smith, *Monotone Dynamical Systems, An introduction to the theory of competitive and cooperative systems*, AMS Monographs Vol. 41, 1995.
33. H. Smith and P. Waltman, *Theory of Chemostat*, Cambridge Press, 1995.
34. F. J. Weissing and J. Huisman, Biodiversity of plankton by species oscillations and chaos, *Nature*, **402** (1999), 407-410.
35. N. Alikakos, An application of the invariance principle to reaction-diffusion equations. *J. Diff. Eqns.*, **33** (1979), 201-225.
36. N. Alikakos, A Liapunov functional for a class of reaction-diffusion systems. *Modelling and Differential Equation in Biology*, (Conf. Southern Illinois Univ., Carbon-dale, Ill. 1978), pp. 153-170, Lecture Notes in Pure and Applied Math., 58, Dekker, New York, 1980.

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