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# MATHEMATICAL ANALYSIS OF TWO MICROBIAL SPECIES COMPETING FOR TWO COMPLEMENTARY RESOURCES WITH INTERNAL STORAGE AND DIFFERENT REMOVAL RATES

BY

SZE-BI HSU AND FENG-BIN WANG

The paper is dedicated to Professor M. Mimura on the occasion of his sixty-five birthday.

## Abstract

In the present paper, we consider a mathematical model of two microbial species competing for two complementary nutrients with internal storage and different removal rates. The competitive exclusion, coexistence, and bi-stability are predicted in this model as those in the two-species Lotka-Volterra competition model.

## 1. Introduction

The classical model of the chemostat is proposed by Monod [12,13] in 1950, it is assumed that the nutrient uptake rate is proportional to the reproductive rate. The constant of proportionality is called the yield constant. This classical model is called the “constant-yield” model, because the yield is assumed to be constant. In [2,3] Droop proposed a so-called “variable-yield” model for phytoplankton species. In this model, the yield is not constant and that it can vary depending on the growth rate. In this model, the nutrient uptake and growth are often decoupled. It assumes that phytoplankton cells

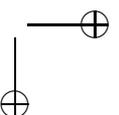
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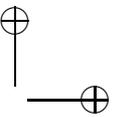
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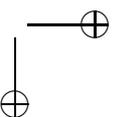
can store nutrient and that the growth rate depends on the stored nutrient. Nutrient uptake increases the internal stores of nutrients upon which growth depends [1,2].

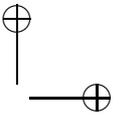
It has long been known that phytoplankton species require multiple nutrients for growth. Thus we need to include multiple potential limiting nutrients [10,17] in the mathematical model. Assume these nutrients are essential for the growth of a species, then the growth will depend on the internal storage of the most limiting nutrient. It is known as Liebig’s law of the minimum [4,14]. These thoughts has been accepted for at least 20 years. In 1997 Legovic and Cruzado [9] proposed a variable-yield model of a single species consuming multiple essential nutrients with Michaelis-Menten type functional response. In 2006, Leenheer et [8] established the global stability of the model in [9] by the method of monotone dynamical systems for general monotone functional responses. Recently, B. Li and H. L. Smith [11] consider a “variable-yield” model of two microbial species competing for two essential nutrients with Michaelis-Menten uptake, Droop’s growth rate and the same removal rates. They introduced similar concepts of “S-limited” and “R-limited” in [6] for the boundary and interior equilibrium. With the conservation property, by the method of monotone dynamical system, they showed that there are three possible outcomes, namely the competitive exclusion, coexistence, and bi-stability.

In this paper, we consider the above “variable -yield” model with different removal rates and dilution rates. In this model, we no longer have the conservation principle. Thus the method of monotone dynamical system does not work. We analyze the local stability of various equilibria. Although the globally results in this model can not be proved, our results are parallel to those established in [11]. The Lokta-Volterra like mechanism can be predicted successfully.

## 2. The Two Resources-One Specie Model

In this section, we introduce the notion of S-limited (or R-limited) in the model of single population consuming for multiple nutrients model. In the following model we consider a phytoplankton species consuming for two inorganic nutrients,  $S$  and  $R$ . Phytoplankton species is represented by three





variables: cellular quotas (amount of resource per cell) of nutrients  $Q_{1s}$  and  $Q_{1r}$  and biomass  $x_1$ . The model equations are:

$$\begin{aligned}
 S' &= (S^0 - S)D_1 - f_{1s}(S)x_1 \\
 R' &= (R^0 - R)D_2 - f_{1r}(R)x_1 \\
 Q'_{1s} &= f_{1s}(S) - \mu_{1\infty} \min\left(1 - \frac{Q_{min,1s}}{Q_{1s}}, 1 - \frac{Q_{min,1r}}{Q_{1r}}\right)Q_{1s} \\
 Q'_{1r} &= f_{1r}(R) - \mu_{1\infty} \min\left(1 - \frac{Q_{min,1s}}{Q_{1s}}, 1 - \frac{Q_{min,1r}}{Q_{1r}}\right)Q_{1r} \quad (2.1) \\
 x'_1 &= [\mu_{1\infty} \min\left(1 - \frac{Q_{min,1s}}{Q_{1s}}, 1 - \frac{Q_{min,1r}}{Q_{1r}}\right) - d_1]x_1 \\
 S(0) &\geq 0, \quad R(0) \geq 0, \quad Q_{1s}(0) \geq Q_{min,1s}, \\
 Q_{1r}(0) &\geq Q_{min,1r}, \quad x_1(0) \geq 0,
 \end{aligned}$$

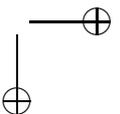
where  $S^0$  and  $R^0$  are input concentrations of resource  $S$  and  $R$ , respectively.  $D_1$  and  $D_2$  are the dilution rate of nutrients  $S$  and  $R$ , respectively.  $d_1$  is the death rate of specie  $x_1$ .  $\mu_{1\infty}$  is the growth rate at infinite quota.  $Q_{min,1s}$ ,  $Q_{min,1r}$  are the minimum quota of nutrients  $S$  and  $R$ , respectively at which growth ceases.  $f_{1s}(S) = \frac{V_{max,1s}S}{K_{1s}+S}$  and  $f_{1r}(R) = \frac{V_{max,1r}R}{K_{1r}+R}$  are the Michaelis-Menten functional response. The zero isocline for  $x_1$  is a pair of half-lines meeting at right angles at the point  $(Q_{1s}^*, \hat{Q}_{1r})$  in the  $Q_{1s} - Q_{1r}$  plane, where

$$Q_{1s}^* = \frac{Q_{min,1s}}{1 - \frac{d_1}{\mu_{1\infty}}}, \quad \hat{Q}_{1r} = \frac{Q_{min,1r}}{1 - \frac{d_1}{\mu_{1\infty}}}.$$

The lines are perpendicular because of the independence of the requirements for  $Q_{1s}$  and  $Q_{1r}$ . In this case, growth is limited at any given time either by  $Q_{1s}$  or  $Q_{1r}$ , but not by both  $Q_{1s}$  and  $Q_{1r}$  simultaneously except at the corner. The curving dashed line passing through the corner in the isocline represents the equation,

$$1 - \frac{Q_{min,1s}}{Q_{1s}} = 1 - \frac{Q_{min,1r}}{Q_{1r}}.$$

Above the dashed line in the  $Q_{1s} - Q_{1r}$  plane, specie  $x_1$  is S-limited, whereas below the dashed line, specie  $x_1$  is R-limited. When  $x_1$  is S-limited, no increase in  $Q_{1r}$  in the region above the dashed line will have any effect on increasing the growth rate of specie  $x_1$ ; only an increase in  $Q_{1s}$  will have this effect. The converse is true in the region below the dashed line. It should be noted



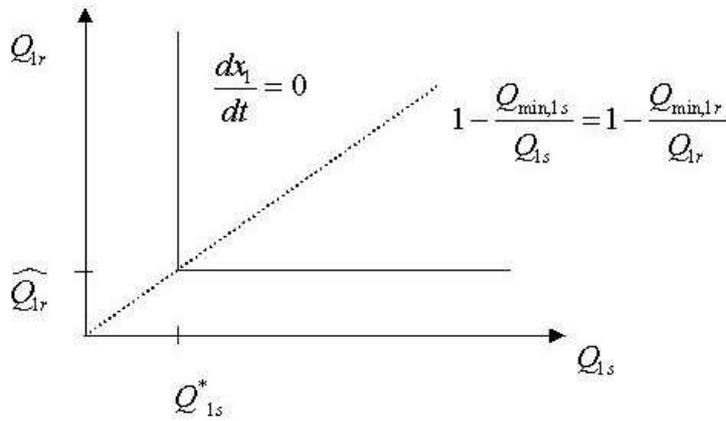
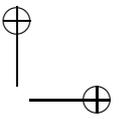


Figure 2.1.

that: when specie  $x_1$  is S-limited, the minimum of the functions  $\min(1 - \frac{Q_{min,1s}}{Q_{1s}}, 1 - \frac{Q_{min,1r}}{Q_{1r}})$  is independent of the concentration of  $Q_{1r}$ , whereas, when the species is R-limited, the minimum of the functions is independent of the concentration of  $Q_{1s}$ . Now, we want to know: “When is specie  $x_1$  S-limited ?” “When is specie  $x_1$  R-limited ?”

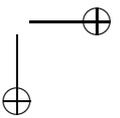
Assume that  $x_1$  is S-limited, model(2.1) becomes

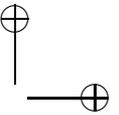
$$\begin{aligned}
 S' &= (S^0 - S)D_1 - f_{1s}(S)x_1 \\
 R' &= (R^0 - R)D_2 - f_{1r}(R)x_1 \\
 Q'_{1s} &= f_{1s}(S) - \mu_{1\infty}(1 - \frac{Q_{min,1s}}{Q_{1s}})Q_{1s} \\
 Q'_{1r} &= f_{1r}(R) - \mu_{1\infty}(1 - \frac{Q_{min,1s}}{Q_{1s}})Q_{1r} \\
 x'_1 &= [\mu_{1\infty}(1 - \frac{Q_{min,1s}}{Q_{1s}}) - d_1]x_1
 \end{aligned}
 \tag{2.2}$$

with the usual initial condition. The interior equilibrium of model (2.2) is in the form

$$E_{1s} = (\lambda_{1s}, R_{1s}^*, Q_{1s}^*, Q_{1r}^*, x_{1s}^*)$$

where  $Q_{1s}^* = \frac{Q_{min,1s}}{1 - \frac{d_1}{\mu_{1\infty}}}$ ,  $f_{1s}(\lambda_{1s}) = d_1 Q_{1s}^* = \frac{d_1 Q_{min,1s}}{1 - \frac{d_1}{\mu_{1\infty}}}$ ,  $x_{1s}^* = \frac{D_1(S^0 - \lambda_{1s})}{d_1 Q_{1s}^*}$ ,  $(R^0 - R_{1s}^*)D_2 - f_{1r}(R_{1s}^*)x_{1s}^* = 0$ ,  $Q_{1r}^* = \frac{f_{1r}(R_{1s}^*)}{d_1}$ .





Assume that  $x_1$  is R-limited, model (2.1) becomes

$$\begin{aligned}
 S' &= (S^0 - S)D_1 - f_{1s}(S)x_1 \\
 R' &= (R^0 - R)D_2 - f_{1r}(R)x_1 \\
 Q'_{1s} &= f_{1s}(S) - \mu_{1\infty}\left(1 - \frac{Q_{min,1r}}{Q_{1r}}\right)Q_{1s} \\
 Q'_{1r} &= f_{1r}(R) - \mu_{1\infty}\left(1 - \frac{Q_{min,1r}}{Q_{1r}}\right)Q_{1r} \\
 x'_1 &= [\mu_{1\infty}\left(1 - \frac{Q_{min,1r}}{Q_{1r}}\right) - d_1]x_1
 \end{aligned} \tag{2.3}$$

with the usual initial condition. We will have the interior equilibrium of model (2.3) in the form

$$E_{1r} = (\hat{S}_{1r}, \lambda_{1r}, \hat{Q}_{1s}, \hat{Q}_{1r}, \hat{x}_{1r})$$

where the parameters satisfy  $\hat{Q}_{1r} = \frac{Q_{min,1r}}{1 - \frac{d_1}{\mu_{1\infty}}}$ ,  $f_{1r}(\lambda_{1r}) = d_1\hat{Q}_{1r} = \frac{d_1 Q_{min,1r}}{1 - \frac{d_1}{\mu_{1\infty}}}$ ,  $\hat{x}_{1r} = \frac{D_2(R^0 - \lambda_{1r})}{d_1\hat{Q}_{1r}} = \frac{D_2(R^0 - \lambda_{1r})}{f_{1r}(\lambda_{1r})}$ ,  $(S^0 - \hat{S}_{1r})D_2 = f_{1s}(\hat{S}_{1r})\hat{x}_{1r}$ ,  $\hat{Q}_{1s} = \frac{f_{1s}(\hat{S}_{1r})}{d_1}$ . Since  $E_{1s} = (\lambda_{1s}, R_{1s}^*, Q_{1s}^*, Q_{1r}^*, x_{1s}^*)$ ,  $E_{1r} = (\hat{S}_{1r}, \lambda_{1r}, \hat{Q}_{1s}, \hat{Q}_{1r}, \hat{x}_{1r})$  are the interior equilibriums of model (2.2), (2.3) respectively, we should have the conditions:

$$1 - \frac{Q_{min,1s}}{Q_{1s}^*} < 1 - \frac{Q_{min,1r}}{Q_{1r}^*}, \tag{2.4}$$

$$1 - \frac{Q_{min,1r}}{\hat{Q}_{1r}} < 1 - \frac{Q_{min,1s}}{\hat{Q}_{1s}}. \tag{2.5}$$

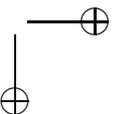
**Theorem 2.1.** *Suppose that  $\lambda_{1s} < S^0$  and  $\lambda_{1r} < R^0$ . Then*

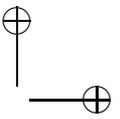
- (1) (2.4) is equivalent to  $\lambda_{1r} < R_{1s}^* < R^0$ ;
- (2) (2.5) is equivalent to  $\lambda_{1s} < \hat{S}_{1r} < S^0$ .

*Proof.*

- (1) Since  $\frac{R^0 - R_{1s}^*}{f_{1r}(R_{1s}^*)} = \frac{D_1(S^0 - \lambda_{1s})}{D_2 f_{1s}(\lambda_{1s})} > 0$ , it follows that  $R_{1s}^* < R^0$ .

From  $1 - \frac{Q_{min,1s}}{Q_{1s}^*} = \frac{d_1}{\mu_{1\infty}}$ , it follows that (2.4) is equivalent to  $\frac{d_1}{\mu_{1\infty}} < 1 - \frac{Q_{min,1r}}{Q_{1r}^*}$ , that is,  $\frac{Q_{min,1r}}{Q_{1r}^*} < 1 - \frac{d_1}{\mu_{1\infty}}$ . From  $1 - \frac{Q_{min,1r}}{Q_{1r}^*} = \frac{d_1}{\mu_{1\infty}}$ , it deduces that (2.4) is equivalent to  $\frac{Q_{min,1r}}{Q_{1r}^*} < \frac{Q_{min,1r}}{\hat{Q}_{1r}}$ , that is,  $Q_{1r}^* > \hat{Q}_{1r}$ . By the following relations  $d_1 Q_{1r}^* = f_{1r}(R_{1s}^*)$  and  $d_1 \hat{Q}_{1r} = f_{1r}(\lambda_{1r})$ , it





ensures that (2.4) is equivalent to  $f_{1r}(R_{1s}^*) > f_{1r}(\lambda_{1r})$ , that is,  $R_{1s}^* > \lambda_{1r}$  (Note that  $f_{1r}(\cdot)$  is strictly increasing). Thus part(1) is proved.

(2) It is similar to (1).

**Theorem 2.2.** *Suppose that  $\lambda_{1s} < S^0$  and  $\lambda_{1r} < R^0$ . Then*

(1) (2.4) is equivalent to

$$\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{1r})} < \frac{Q_{min,1s}}{Q_{min,1r}}; \tag{2.6}$$

(2) (2.5) is equivalent to

$$\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{1r})} > \frac{Q_{min,1s}}{Q_{min,1r}}. \tag{2.7}$$

*Proof.*

(1) By Theorem 2.1, (2.4) is equivalent to  $R^0 > R_{1s}^* > \lambda_{1r}$ . Since  $\frac{R^0 - R_{1s}^*}{f_{1r}(R_{1s}^*)} = \frac{D_1(S^0 - \lambda_{1s})}{D_2 f_{1s}(\lambda_{1s})}$  and  $\frac{R^0 - R}{f_{1r}(R)}$  is strictly decreasing. Hence, (2.4) is equivalent to  $\frac{R^0 - R_{1s}^*}{f_{1r}(R_{1s}^*)} < \frac{R^0 - \lambda_{1r}}{f_{1r}(\lambda_{1r})}$ , that is,  $\frac{D_1(S^0 - \lambda_{1s})}{D_2 f_{1s}(\lambda_{1s})} < \frac{R^0 - \lambda_{1r}}{f_{1r}(\lambda_{1r})}$  or  $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{1r})} < \frac{f_{1s}(\lambda_{1s})}{f_{1r}(\lambda_{1r})}$  or  $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{1r})} < \frac{Q_{min,1s}}{Q_{min,1r}}$ .

(2) It is similar to (1).

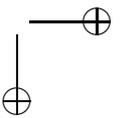
When specie  $x_1$  presents,  $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{1r})}$  represents the ratio of the steady-state nutrient regeneration rates at equilibrium under consumption by  $x_1$ .  $\lambda_{1s}$  and  $\lambda_{1r}$  are the equilibrium concentrations of resources S and R, respectively, under steady-state consumption by specie  $x_1$ .  $\frac{Q_{min,1s}}{Q_{min,1r}}$  represents the fixed yield ratio for specie  $x_1$  growing on resources S and R. We give the following definition:

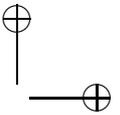
- (i) If  $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{1r})} < \frac{Q_{min,1s}}{Q_{min,1r}}$ , then we say that specie  $x_1$  is S-limited;
- (ii) If  $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{1r})} > \frac{Q_{min,1s}}{Q_{min,1r}}$ , then we say that specie  $x_1$  is R-limited.

It should be noted that

$$\frac{Q_{min,1s}}{Q_{min,1r}} = \frac{f_{1s}(\lambda_{1s})}{f_{1r}(\lambda_{1r})}. \tag{2.8}$$

By the definition and Theorem 2.2 above, it follows that: either  $x_1$  is S-limited or  $x_1$  is R-limited in model (2.1).





### 3. The Two-Resources, Two-Species Model

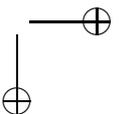
In this section, we consider two microbial populations, with densities  $x_1$  and  $x_2$ , competing for two nutrients of concentration  $S$  and  $R$  in the chemostat. The system of equations is

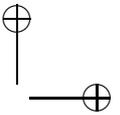
$$\begin{aligned}
 S' &= (S^0 - S)D_1 - f_{1s}(S)x_1 - f_{2s}(S)x_2 \\
 R' &= (R^0 - R)D_2 - f_{1r}(R)x_1 - f_{2r}(R)x_2 \\
 Q'_{1s} &= f_{1s}(S) - \mu_{1\infty} \min\left(1 - \frac{Q_{min,1s}}{Q_{1s}}, 1 - \frac{Q_{min,1r}}{Q_{1r}}\right) Q_{1s} \\
 Q'_{1r} &= f_{1r}(R) - \mu_{1\infty} \min\left(1 - \frac{Q_{min,1s}}{Q_{1s}}, 1 - \frac{Q_{min,1r}}{Q_{1r}}\right) Q_{1r} \\
 Q'_{2s} &= f_{2s}(S) - \mu_{2\infty} \min\left(1 - \frac{Q_{min,2s}}{Q_{2s}}, 1 - \frac{Q_{min,2r}}{Q_{2r}}\right) Q_{2s} \\
 Q'_{2r} &= f_{2r}(R) - \mu_{2\infty} \min\left(1 - \frac{Q_{min,2s}}{Q_{2s}}, 1 - \frac{Q_{min,2r}}{Q_{2r}}\right) Q_{2r} \\
 x'_1 &= [\mu_{1\infty} \min\left(1 - \frac{Q_{min,1s}}{Q_{1s}}, 1 - \frac{Q_{min,1r}}{Q_{1r}}\right) - d_1] x_1 \\
 x'_2 &= [\mu_{2\infty} \min\left(1 - \frac{Q_{min,2s}}{Q_{2s}}, 1 - \frac{Q_{min,2r}}{Q_{2r}}\right) - d_2] x_2 \\
 S(0) &\geq 0, R(0) \geq 0, Q_{is}(0) \geq Q_{min,is}, Q_{ir}(0) \geq Q_{min,ir}, \\
 x_i(0) &\geq 0, i = 1, 2,
 \end{aligned} \tag{3.1}$$

where  $S^0$  and  $R^0$  are input concentrations of resource  $S$  and  $R$ , respectively;  $D_1, D_2$  are the dilution rate of nutrients  $S$  and  $R$  respectively;  $d_1, d_2$  are the death rate of species  $x_1$  and  $x_2$  respectively;  $\mu_{i\infty}$  is the growth rate at infinite quota;  $Q_{min,is}, Q_{min,ir}$  are the minimum quota of nutrients  $S$  and  $R$  (respectively) at which growth ceases;  $f_{is}(S) = \frac{V_{max,is}S}{K_{is}+S}$ ,  $f_{ir}(R) = \frac{V_{max,ir}R}{K_{ir}+R}$  are Michaelis-Menten functional forms. In the “two-resources, one-species” case, we give a definition of “S-limited” and “R-limited”. Now, we give the following definitions about “S-limited” and R-limited for model (3.1).

**Definition 3.1.** Suppose that the parameters  $\lambda_{1s}, \lambda_{1r}, \lambda_{2s}, \lambda_{2r}$  satisfy  $f_{is}(\lambda_{is}) = \frac{d_i Q_{min,is}}{1 - \frac{d_i}{\mu_{i\infty}}}$ , and  $f_{ir}(\lambda_{ir}) = \frac{d_i Q_{min,ir}}{1 - \frac{d_i}{\mu_{i\infty}}}$ ,  $i = 1, 2$ .

- (i) If  $\frac{D_1(S^0 - \lambda_{is})}{D_2(R^0 - \lambda_{ir})} < \frac{Q_{min,is}}{Q_{min,ir}}$ , we say that specie  $x_i$  is S-limited,  $i = 1, 2$ ;
- (ii) If  $\frac{D_1(S^0 - \lambda_{is})}{D_2(R^0 - \lambda_{ir})} > \frac{Q_{min,is}}{Q_{min,ir}}$ , we say that specie  $x_i$  is R-limited,  $i = 1, 2$ .





It should be noted that

$$\frac{Q_{min,is}}{Q_{min,ir}} = \frac{f_{is}(\lambda_{is})}{f_{ir}(\lambda_{ir})}, \quad i = 1, 2.$$

### 3.1. $x_1$ is S-limited, and $x_2$ is S-limited

If  $x_1$  is S-limited, and  $x_2$  is S-limited, (3.1) becomes the following:

$$S' = (S^0 - S)D_1 - f_{1s}(S)x_1 - f_{2s}(S)x_2 \tag{3.2a}$$

$$R' = (R^0 - R)D_2 - f_{1r}(R)x_1 - f_{2r}(R)x_2 \tag{3.2b}$$

$$Q'_{1s} = f_{1s}(S) - \mu_{1\infty} \left(1 - \frac{Q_{min,1s}}{Q_{1s}}\right) Q_{1s} \tag{3.2c}$$

$$Q'_{1r} = f_{1r}(R) - \mu_{1\infty} \left(1 - \frac{Q_{min,1s}}{Q_{1s}}\right) Q_{1r} \tag{3.2d}$$

$$Q'_{2s} = f_{2s}(S) - \mu_{2\infty} \left(1 - \frac{Q_{min,2s}}{Q_{2s}}\right) Q_{2s} \tag{3.2e}$$

$$Q'_{2r} = f_{2r}(R) - \mu_{2\infty} \left(1 - \frac{Q_{min,2s}}{Q_{2s}}\right) Q_{2r} \tag{3.2f}$$

$$x'_1 = \left[\mu_{1\infty} \left(1 - \frac{Q_{min,1s}}{Q_{1s}}\right) - d_1\right] x_1 \tag{3.2g}$$

$$x'_2 = \left[\mu_{2\infty} \left(1 - \frac{Q_{min,2s}}{Q_{2s}}\right) - d_2\right] x_2 \tag{3.2h}$$

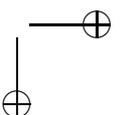
with the usual initial condition. Generically, (3.2) has at most three steady-state solutions. One of these, which we label  $E_0$ , corresponds to the absence of both competitors. It is given by

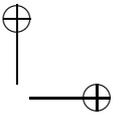
$$E_0 = (S, R, Q_{1s}, Q_{1r}, Q_{2s}, Q_{2r}, x_1, x_2) = (S^0, R^0, Q_{1s}^0, Q_{1r}^0, Q_{2s}^0, Q_{2r}^0, 0, 0),$$

where  $Q_{is}^0$  and  $Q_{ir}^0$  satisfy  $Q_{is}^0 = Q_{min,is} + \frac{f_{is}(S^0)}{\mu_{i\infty}}$  and  $Q_{ir}^0 = \frac{f_{ir}(R^0)Q_{is}^0}{f_{is}(S^0)}$ . We note that  $E_0$  always exists. The two other possible steady-states, labeled  $E_1$  and  $E_2$ , correspond to the presence of one population and the absence of the other. In the case that  $x_1$  and  $x_2$  are both S-limited,

$$E_1 = E_{1s} = (\lambda_{1s}, R_{1s}^*, Q_{1s}^*, Q_{1r}^*, Q_{2s}^*, Q_{2r}^*, x_{1s}^*, 0),$$

where  $Q_{1s}^* = \frac{Q_{min,1s}}{1 - \frac{d_1}{\mu_{1\infty}}}$ ,  $f_{1s}(\lambda_{1s}) = d_1 Q_{1s}^* = \frac{d_1 Q_{min,1s}}{1 - \frac{d_1}{\mu_{1\infty}}}$ ,  $x_{1s}^* = \frac{D_1(S^0 - \lambda_{1s})}{f_{1s}(\lambda_{1s})}$ ,  $(R^0 - R_{1s}^*)D_2 - f_{1r}(R_{1s}^*)x_{1s}^* = 0$ ,  $Q_{1r}^* = \frac{f_{1r}(R_{1s}^*)}{d_1}$ ,  $Q_{2s}^* = Q_{min,2s} + \frac{f_{2s}(\lambda_{1s})}{\mu_{2\infty}}$ ,  $f_{2r}(R_{1s}^*) - \frac{f_{2s}(\lambda_{1s})}{Q_{2s}^*} Q_{2r}^* = 0$ .





Since  $\frac{R^0 - R_{1s}^*}{f_{1r}(R_{1s}^*)} = \frac{x_{1s}^*}{D_2} = \frac{D_1(S^0 - \lambda_{1s})}{D_2 f_{1s}(\lambda_{1s})}$  and  $f_{1r}(R)$  is strictly increasing with  $f_{1r}(0) = 0$ , we have  $0 < R_{1s}^* < R^0$  when  $\lambda_{1s} < S^0$ . Hence, the steady-states  $E_1$  exists if and only if  $d_1 < \mu_{1\infty}$  and  $\lambda_{1s} < S^0$ . The above conditions state that the population  $x_1$  can achieve a steady-state population provided that: (a) the washout rate  $d_1$  is not too large; and (b) the reservoir contains sufficient nutrient, that is,  $\lambda_{1s} < S^0$ .

An analogous steady state in which only population  $x_2$  is present is given by

$$E_2 = E_{2s} = (\lambda_{2s}, R_{2r}^{**}, Q_{1s}^{**}, Q_{1r}^{**}, Q_{2s}^{**}, Q_{2r}^{**}, 0, x_{2s}^{**}),$$

where  $Q_{2s}^{**} = \frac{Q_{min,2s}}{1 - \frac{d_2}{\mu_{2\infty}}}$ ,  $f_{2s}(\lambda_{2s}) = d_2 Q_{2s}^{**} = \frac{d_2 Q_{min,2s}}{1 - \frac{d_2}{\mu_{2\infty}}}$ ,  $x_{2s}^{**} = \frac{D_1(S^0 - \lambda_{2s})}{f_{2s}(\lambda_{2s})}$ ,  $(R^0 - R_{2r}^{**})D_2 - f_{2r}(R_{2r}^{**})x_{2s}^{**} = 0$ ,  $Q_{2r}^{**} = \frac{f_{2r}(R_{2r}^{**})}{d_2}$ ,  $Q_{1s}^{**} = Q_{min,1s} + \frac{f_{1s}(\lambda_{2s})}{\mu_{1\infty}}$ ,  $f_{1r}(R_{2r}^{**}) - \frac{f_{1s}(\lambda_{2s})}{Q_{1s}^{**}} Q_{1r}^{**} = 0$ .

Use the same way, one can show that the steady-states  $E_2$  exists if and only if  $d_2 < \mu_{2\infty}$  and  $\lambda_{2s} < S^0$ . Now, we want to search the interior equilibrium. From (3.2.g) and (3.2.h), one has  $\mu_{1\infty}(1 - \frac{Q_{min,1s}}{Q_{1s}}) = d_1$  and  $\mu_{2\infty}(1 - \frac{Q_{min,2s}}{Q_{2s}}) = d_2$ , that is,  $Q_{1s} = \frac{Q_{min,1s}}{1 - \frac{d_1}{\mu_{1\infty}}}$  and  $Q_{2s} = \frac{Q_{min,2s}}{1 - \frac{d_2}{\mu_{2\infty}}}$ . From (3.2c) and (3.2e), one has  $f_{1s}(S) = \mu_{1\infty}(1 - \frac{Q_{min,1s}}{Q_{1s}})Q_{1s} = d_1 \frac{Q_{min,1s}}{1 - \frac{d_1}{\mu_{1\infty}}}$  and  $f_{2s}(S) = \mu_{2\infty}(1 - \frac{Q_{min,2s}}{Q_{2s}})Q_{2s} = d_2 \frac{Q_{min,2s}}{1 - \frac{d_2}{\mu_{2\infty}}}$ . Hence, one has  $S = \lambda_{1s}$  and  $S = \lambda_{2s}$ . It is possible that there exist steady states with both  $x_1$  and  $x_2$  present if  $\lambda_{1s} = \lambda_{2s}$ . Since this condition is highly unlikely, we ignore this case. Assume that  $x_1$  is S-limited and  $x_2$  is S-limited, we have the following theorems:

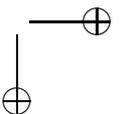
**Theorem 3.1.** *If  $\lambda_{1s} > S^0$  and  $\lambda_{2s} > S^0$ , then  $E_0 = (S^0, R^0, Q_{1s}^0, Q_{1r}^0, Q_{2s}^0, Q_{2r}^0, 0, 0)$  is locally asymptotically stable.*

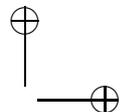
**Theorem 3.2.** *Assume that  $E_1$ , and  $E_2$  both exist (ie.  $\lambda_{1s} < S^0$ ,  $\lambda_{2s} < S^0$ , and  $d_i < \mu_{i\infty}$ ,  $i = 1, 2$ ). If  $\lambda_{1s} < \lambda_{2s}$ , then  $E_1 = (\lambda_{1s}, R_{1s}^*, Q_{1s}^*, Q_{1r}^*, Q_{2s}^*, Q_{2r}^*, x_{1s}^*, 0)$  is locally asymptotically stable and  $E_2 = (\lambda_{2s}, R_{2r}^{**}, Q_{1s}^{**}, Q_{1r}^{**}, Q_{2s}^{**}, Q_{2r}^{**}, 0, x_{2s}^{**})$  is unstable.*

### 3.2. $x_1$ is S-limited, and $x_2$ is R-limited

If  $x_1$  is S-limited, and  $x_2$  is R-limited, (3.1) becomes the following:

$$S' = (S^0 - S)D_1 - f_{1s}(S)x_1 - f_{2s}(S)x_2 \tag{3.3a}$$





$$R' = (R^0 - R)D_2 - f_{1r}(R)x_1 - f_{2r}(R)x_2 \tag{3.3b}$$

$$Q'_{1s} = f_{1s}(S) - \mu_{1\infty}(1 - \frac{Q_{min,1s}}{Q_{1s}})Q_{1s} \tag{3.3c}$$

$$Q'_{1r} = f_{1r}(R) - \mu_{1\infty}(1 - \frac{Q_{min,1s}}{Q_{1s}})Q_{1r} \tag{3.3d}$$

$$Q'_{2s} = f_{2s}(S) - \mu_{2\infty}(1 - \frac{Q_{min,2r}}{Q_{2r}})Q_{2s} \tag{3.3e}$$

$$Q'_{2r} = f_{2r}(R) - \mu_{2\infty}(1 - \frac{Q_{min,2r}}{Q_{2r}})Q_{2r} \tag{3.3f}$$

$$x'_1 = [\mu_{1\infty}(1 - \frac{Q_{min,1s}}{Q_{1s}}) - d_1]x_1 \tag{3.3g}$$

$$x'_2 = [\mu_{2\infty}(1 - \frac{Q_{min,2r}}{Q_{2r}}) - d_2]x_2 \tag{3.3h}$$

with the usual initial condition. Generically, (3.3) has at most four steady-state solutions. One of these, which we label  $E_0$ , corresponds to the absence of both competitors. It is given by

$$E_0 = (S, R, Q_{1s}, Q_{1r}, Q_{2s}, Q_{2r}, x_1, x_2) = (S^0, R^0, Q_{1s}^0, Q_{1r}^0, Q_{2s}^0, Q_{2r}^0, 0, 0),$$

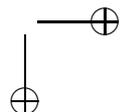
and it always exists. Here,  $Q_{1s}^0 = Q_{min,1s} + \frac{f_{1s}(S^0)}{\mu_{1\infty}}$ ,  $Q_{2r}^0 = Q_{min,2r} + \frac{f_{2r}(R^0)}{\mu_{2\infty}}$ ,  $Q_{1r}^0 = \frac{f_{1r}(R^0)Q_{1s}^0}{f_{1s}(S^0)}$ , and  $Q_{2s}^0 = \frac{f_{2s}(S^0)Q_{2r}^0}{f_{2r}(R^0)}$ . The steady-states, labeled  $E_1$  and  $E_2$ , correspond to the presence of one population and the absence of the other. In this case,

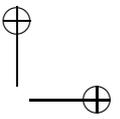
$$E_1 = E_{1s} = (\lambda_{1s}, R_{1s}^*, Q_{1s}^*, Q_{1r}^*, Q_{2s}^*, Q_{2r}^*, x_{1s}^*, 0)$$

where  $Q_{1s}^* = \frac{Q_{min,1s}}{1 - \frac{d_1}{\mu_{1\infty}}}$ ,  $f_{1s}(\lambda_{1s}) = d_1 Q_{1s}^* = \frac{d_1 Q_{min,1s}}{1 - \frac{d_1}{\mu_{1\infty}}}$ ,  $x_{1s}^* = \frac{D_1(S^0 - \lambda_{1s})}{f_{1s}(\lambda_{1s})}$ ,  $(R^0 - R_{1s}^*)D_2 - f_{1r}(R_{1s}^*)x_{1s}^* = 0$ ,  $Q_{1r}^* = \frac{f_{1r}(R_{1s}^*)}{d_1}$ ,  $Q_{2r}^* = Q_{min,2r} + \frac{f_{2r}(R_{1s}^*)}{\mu_{2\infty}}$ ,  $f_{2s}(\lambda_{1s}) - \frac{f_{2r}(R_{1s}^*)}{Q_{2r}^*}Q_{2s}^* = 0$ . It is obvious that  $E_1$  exists if and only if  $d_1 < \mu_{1\infty}$  and  $\lambda_{1s} < S^0$ . An analogous steady state in which only population  $x_2$  is present is given by

$$E_2 = E_{2R} = (S^{**}, \lambda_{2r}, Q_{1s}^{**}, Q_{1r}^{**}, Q_{2s}^{**}, Q_{2r}^{**}, 0, x_{2r}^{**}),$$

where  $Q_{2r}^{**} = \frac{Q_{min,2r}}{1 - \frac{d_2}{\mu_{2\infty}}}$ ,  $f_{2r}(\lambda_{2r}) = d_2 Q_{2r}^{**} = \frac{d_2 Q_{min,2r}}{1 - \frac{d_2}{\mu_{2\infty}}}$ ,  $x_{2r}^{**} = \frac{D_2(R^0 - \lambda_{2r})}{f_{2r}(\lambda_{2r})}$ ,  $(S^0 - S^{**})D_1 - f_{2s}(S^{**})x_{2r}^{**} = 0$ ,  $Q_{2s}^{**} = \frac{f_{2s}(S^{**})}{d_2}$ ,  $Q_{1s}^{**} = Q_{min,1s} + \frac{f_{1s}(S^{**})}{\mu_{1\infty}}$ ,  $f_{1r}(\lambda_{2r}) -$





$\frac{f_{1s}(S^{**})}{Q_{1s}^{**}}Q_{1r}^{**} = 0$ . It is obvious that  $E_2$  exists if and only if  $d_2 < \mu_{2\infty}$  and  $\lambda_{2r} < R^0$ . Next, the interior equilibrium takes the form:

$$E_c = E_c^{1S,2R} = (\lambda_{1s}, \lambda_{2r}, \hat{Q}_{1s}, \hat{Q}_{1r}, \hat{Q}_{2s}, \hat{Q}_{2r}, \hat{x}_{1s}, \hat{x}_{2r}),$$

where  $\hat{Q}_{1s} = \frac{Q_{min,1s}}{1 - \frac{d_1}{\mu_{1\infty}}}$ ,  $\hat{Q}_{2r} = \frac{Q_{min,2r}}{1 - \frac{d_2}{\mu_{2\infty}}}$ ,  $f_{1s}(\lambda_{1s}) = d_1 \hat{Q}_{1s} = d_1 \frac{Q_{min,1s}}{1 - \frac{d_1}{\mu_{1\infty}}}$ ,  $f_{2r}(\lambda_{2r}) = d_2 \hat{Q}_{2r} = d_2 \frac{Q_{min,2r}}{1 - \frac{d_2}{\mu_{2\infty}}}$ ,  $\hat{Q}_{1r} = \frac{f_{1r}(\lambda_{2r})}{d_1}$ ,  $\hat{Q}_{2s} = \frac{f_{2s}(\lambda_{1s})}{d_2}$ . Moreover,  $\hat{x}_{1s}$  and  $\hat{x}_{2r}$  satisfy

$$f_{1s}(\lambda_{1s})\hat{x}_{1s} + f_{2s}(\lambda_{1s})\hat{x}_{2r} = (S^0 - \lambda_{1s})D_1, \quad (3.4a)$$

$$f_{1r}(\lambda_{2r})\hat{x}_{1s} + f_{2r}(\lambda_{2r})\hat{x}_{2r} = (R^0 - \lambda_{2r})D_2. \quad (3.4b)$$

By Cramer’s rule, it follows that

$$\hat{x}_{1s} = \frac{\Delta_1}{\Delta}, \quad (3.5a)$$

$$\hat{x}_{2r} = \frac{\Delta_2}{\Delta}, \quad (3.5b)$$

where

$$\Delta = f_{1s}(\lambda_{1s})f_{2r}(\lambda_{2r}) - f_{1r}(\lambda_{2r})f_{2s}(\lambda_{1s}), \quad (3.6a)$$

$$\Delta_1 = D_1(S^0 - \lambda_{1s})f_{2r}(\lambda_{2r}) - D_2(R^0 - \lambda_{2r})f_{2s}(\lambda_{1s}), \quad (3.6b)$$

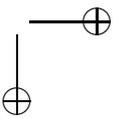
$$\Delta_2 = D_2(R^0 - \lambda_{2r})f_{1s}(\lambda_{1s}) - D_1(S^0 - \lambda_{1s})f_{1r}(\lambda_{2r}). \quad (3.6c)$$

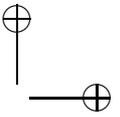
Assume that  $x_1$  is S-limited and  $x_2$  is R-limited, we have the following theorems:

**Theorem 3.3.** *If  $\lambda_{1s} > S^0$  and  $\lambda_{2r} > R^0$ , then  $E_0 = (S^0, R^0, Q_{1s}^0, Q_{1r}^0, Q_{2s}^0, Q_{2r}^0, 0, 0)$  is locally stable.*

**Proposition 3.1.** *The following statements hold*

- (1)  $E_1$  is locally stable if and only if  $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{2r})} > \frac{f_{1s}(\lambda_{1s})}{f_{1r}(\lambda_{2r})}$  if and only if  $\Delta_2 < 0$ ;
- (2)  $E_2$  is locally stable if and only if  $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{2r})} < \frac{f_{2s}(\lambda_{1s})}{f_{2r}(\lambda_{2r})}$  if and only if  $\Delta_1 < 0$ .





**Proposition 3.2.** *The following statements hold*

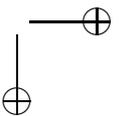
- (1) *If  $\Delta_1 > 0$  and  $\Delta_2 > 0$ , then  $\Delta > 0$ ;*
- (2) *If  $\Delta_1 < 0$  and  $\Delta_2 < 0$ , then  $\Delta < 0$ ;*
- (3) *If  $\lambda_{1s} < \lambda_{2s}$ , then  $\Delta_1 > 0$ ;*
- (4) *If  $\lambda_{2r} < \lambda_{1r}$ , then  $\Delta_2 > 0$ .*

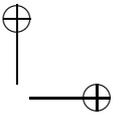
*Proof.*

- (1)  $\Delta_1 > 0$  and  $\Delta_2 > 0$  if and only if  $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{2r})} > \frac{f_{2s}(\lambda_{1s})}{f_{2r}(\lambda_{2r})}$  and  $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{2r})} < \frac{f_{1s}(\lambda_{1s})}{f_{1r}(\lambda_{2r})}$ . Hence,  $\frac{f_{1s}(\lambda_{1s})}{f_{1r}(\lambda_{2r})} > \frac{f_{2s}(\lambda_{1s})}{f_{2r}(\lambda_{2r})}$ , that is,  $\Delta > 0$ .
- (2) It is similar to (1).
- (3) Since  $x_2$  is R-limited, we have  $\frac{D_1(S^0 - \lambda_{2s})}{D_2(R^0 - \lambda_{2r})} > \frac{f_{2s}(\lambda_{2s})}{f_{2r}(\lambda_{2r})}$ . From  $\lambda_{1s} < \lambda_{2s}$ , we have  $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{2r})} > \frac{D_1(S^0 - \lambda_{2s})}{D_2(R^0 - \lambda_{2r})}$  and  $\frac{f_{2s}(\lambda_{2s})}{f_{2r}(\lambda_{2r})} > \frac{f_{2s}(\lambda_{1s})}{f_{2r}(\lambda_{2r})}$ . Hence,  $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{2r})} > \frac{f_{2s}(\lambda_{1s})}{f_{2r}(\lambda_{2r})}$ , that is,  $\Delta_1 > 0$ .
- (4) Since  $x_1$  is S-limited, we have  $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{1r})} < \frac{f_{1s}(\lambda_{1s})}{f_{1r}(\lambda_{1r})}$ . From  $\lambda_{2r} < \lambda_{1r}$ , we have  $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{2r})} < \frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{1r})}$  and  $\frac{f_{1s}(\lambda_{1s})}{f_{1r}(\lambda_{1r})} < \frac{f_{1s}(\lambda_{1s})}{f_{1r}(\lambda_{2r})}$ . Hence,  $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{2r})} < \frac{f_{1s}(\lambda_{1s})}{f_{1r}(\lambda_{2r})}$ , that is,  $\Delta_2 > 0$ .

**Theorem 3.4.** *Assume that  $E_1$ , and  $E_2$  both exist (ie.  $\lambda_{1s} < S^0$  and  $\lambda_{2r} < R^0$ , and  $d_i < \mu_{i\infty}$ ,  $i = 1, 2$ ).*

- (1) *Suppose  $\lambda_{1s} < \lambda_{2s}$  and  $\lambda_{1r} < \lambda_{2r}$ , then  $E_2$  is unstable. Moreover, we have the following outcomes:*
  - (a) *If  $E_1$  is locally asymptotically stable and  $E_2$  is unstable, then the interior equilibrium  $E_c$  doesn't exist.*
  - (b) *If  $E_1$  is unstable and  $E_2$  is unstable, then the interior equilibrium  $E_c$  exists and is unique.*
- (2) *Suppose  $\lambda_{1s} < \lambda_{2s}$  and  $\lambda_{2r} < \lambda_{1r}$ , then  $E_1$  and  $E_2$  are unstable, and the interior equilibrium  $E_c$  exists and is unique.*
- (3) *Suppose  $\lambda_{2s} < \lambda_{1s}$  and  $\lambda_{1r} < \lambda_{2r}$ , we have*
  - (a) *If  $E_1$  is locally asymptotically stable and  $E_2$  is unstable, or  $E_1$  is unstable and  $E_2$  is locally asymptotically stable, then the interior equilibrium  $E_c$  doesn't exist.*
  - (b) *If  $E_1$  and  $E_2$  are unstable or  $E_1$  and  $E_2$  are locally asymptotically stable, then the interior equilibrium  $E_c$  exists and is unique.*





(4) Suppose  $\lambda_{2s} < \lambda_{1s}$  and  $\lambda_{2r} < \lambda_{1r}$ , then  $E_1$  is unstable.

Moreover, we have the following outcomes:

- (a) If  $E_2$  is locally asymptotically stable and  $E_1$  is unstable, then the interior equilibrium  $E_c$  doesn't exist.
- (b) If  $E_2$  is unstable and  $E_1$  is unstable, then the interior equilibrium  $E_c$  exists and is unique.

*Proof.*

(1) Since  $\lambda_{1s} < \lambda_{2s}$ , from Proposition 3.2(3), we have  $E_2$  is unstable.

- (a) From Proposition 3.1:  $\Delta_1 > 0$  and  $\Delta_2 < 0$ . From (3.6),  $E_c$  doesn't exist.
- (b) From Proposition 3.1:  $\Delta_1 > 0$  and  $\Delta_2 > 0$ . From Proposition 3.2(1):  $\Delta > 0$ , that is,  $E_c$  exists and is unique.

(2) From Proposition 3.2 (3)(4), we have  $\Delta_1 > 0$  and  $\Delta_2 > 0$ . From Proposition 3.2 (1)(2), it follows that  $\Delta > 0$ . Hence,  $E_1$  and  $E_2$  are unstable, and the unique interior equilibrium  $E_c$  exists.

- (3) (a) Since either  $\Delta_1 < 0, \Delta_2 > 0$  or  $\Delta_1 > 0, \Delta_2 < 0$ ,  $E_c$  doesn't exist.
- (b) Obviously

$$\Delta_1 > 0, \Delta_2 > 0 \quad \text{imply} \quad \Delta > 0$$

and

$$\Delta_1 < 0, \Delta_2 < 0 \quad \text{imply} \quad \Delta < 0$$

thus  $E_c$  exists by (3.6).

(4) The proof is similar to (3).

### 3.3. $x_1$ is R-limited, and $x_2$ is S-limited model

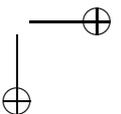
If  $x_1$  is R-limited, and  $x_2$  is S-limited, (3.1) becomes the following:

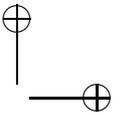
$$S' = (S^0 - S)D_1 - f_{1s}(S)x_1 - f_{2s}(S)x_2 \tag{3.7a}$$

$$R' = (R^0 - R)D_2 - f_{1r}(R)x_1 - f_{2r}(R)x_2 \tag{3.7b}$$

$$Q'_{1s} = f_{1s}(S) - \mu_{1\infty} \left(1 - \frac{Q_{min,1r}}{Q_{1r}}\right) Q_{1s} \tag{3.7c}$$

$$Q'_{1r} = f_{1r}(R) - \mu_{1\infty} \left(1 - \frac{Q_{min,1r}}{Q_{1r}}\right) Q_{1r} \tag{3.7d}$$





$$Q'_{2s} = f_{2s}(S) - \mu_{2\infty} \left(1 - \frac{Q_{min,2s}}{Q_{2s}}\right) Q_{2s} \tag{3.7e}$$

$$Q'_{2r} = f_{2r}(R) - \mu_{2\infty} \left(1 - \frac{Q_{min,2s}}{Q_{2s}}\right) Q_{2r} \tag{3.7f}$$

$$x'_1 = [\mu_{1\infty} \left(1 - \frac{Q_{min,1r}}{Q_{1r}}\right) - d_1] x_1 \tag{3.7g}$$

$$x'_2 = [\mu_{2\infty} \left(1 - \frac{Q_{min,2s}}{Q_{2s}}\right) - d_2] x_2 \tag{3.7h}$$

with the usual initial condition. This model is similar to model (3.3). Generically, (3.7) has at most four steady-state solutions. One of these, which we label  $E_0$ , corresponds to the absence of both competitors. It is given by

$$E_0 = (S, R, Q_{1s}, Q_{1r}, Q_{2s}, Q_{2r}, x_1, x_2) = (S^0, R^0, Q_{1s}^0, Q_{1r}^0, Q_{2s}^0, Q_{2r}^0, 0, 0)$$

and it always exists. The steady-states, labeled  $E_1$  and  $E_2$ , correspond to the presence of one population and the absence of the other. They take the form:  $E_1 = E_{1R} = (S_{1r}^*, \lambda_{1r}, Q_{1s}^*, Q_{1r}^*, Q_{2s}^*, Q_{2r}^*, x_{1r}^*, 0)$ ,  $E_2 = E_{2s} = (\lambda_{2s}, R^{**}, Q_{1s}^{**}, Q_{1r}^{**}, Q_{2s}^{**}, Q_{2r}^{**}, 0, x_{2s}^{**})$ . One can show that, the steady-states  $E_1$  exists if and only if  $d_1 < \mu_{1\infty}$  and  $\lambda_{1r} < R^0$ . In the same reason, the steady-states  $E_2$  exists if and only if  $d_2 < \mu_{2\infty}$  and  $\lambda_{2s} < S^0$ . Finally, the interior equilibrium takes the form  $E_c = E_c^{1R,2S} = (\lambda_{2s}, \lambda_{1r}, \hat{Q}_{1s}, \hat{Q}_{1r}, \hat{Q}_{2s}, \hat{Q}_{2r}, \hat{x}_{1r}, \hat{x}_{2s})$ . Assume that  $x_1$  is R-limited and  $x_2$  is S-limited, we have the following theorems:

**Theorem 3.5.** *If  $\lambda_{1r} > R^0$  and  $\lambda_{2s} > S^0$ , then  $E_0 = (S, R, Q_{1s}, Q_{1r}, Q_{2s}, Q_{2r}, x_1, x_2) = (S^0, R^0, Q_{1s}^0, Q_{1r}^0, Q_{2s}^0, Q_{2r}^0, 0, 0)$  is locally asymptotically stable.*

**Theorem 3.6.** *Assume that  $E_1$ , and  $E_2$  both exist (ie.  $\lambda_{1r} < R^0$  and  $\lambda_{2s} < S^0$ , and  $d_i < \mu_{i\infty}$ ,  $i = 1, 2$ )*

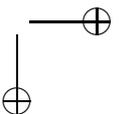
(1) *Suppose  $\lambda_{1r} < \lambda_{2r}$  and  $\lambda_{1s} < \lambda_{2s}$ , then  $E_2$  is unstable.*

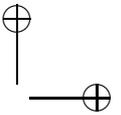
*Moreover, we have the following results:*

(a) *If  $E_1$  is locally asymptotically stable and  $E_2$  is unstable, then the interior equilibrium  $E_c$  doesn't exist.*

(b) *If  $E_1$  is unstable and  $E_2$  is unstable, then the unique interior equilibrium  $E_c$  exists.*

(2) *Suppose  $\lambda_{1r} < \lambda_{2r}$  and  $\lambda_{2s} < \lambda_{1s}$ , then  $E_1$  and  $E_2$  are unstable, and the unique interior equilibrium  $E_c$  exists.*





- (3) Suppose  $\lambda_{2r} < \lambda_{1r}$  and  $\lambda_{1s} < \lambda_{2s}$ , we have
- (a) If  $E_1$  is locally asymptotically stable and  $E_2$  is unstable (or  $E_1$  is unstable and  $E_2$  is locally asymptotically stable), then the interior equilibrium  $E_c$  doesn't exist.
  - (b) If  $E_1$  and  $E_2$  are unstable or  $E_1$  and  $E_2$  are locally asymptotically stable, then the unique interior equilibrium  $E_c$  exists.
- (4) Suppose  $\lambda_{2r} < \lambda_{1r}$  and  $\lambda_{2s} < \lambda_{1s}$ , then  $E_1$  is unstable. Moreover, we have the following results:
- (a) If  $E_2$  is locally asymptotically stable and  $E_1$  is unstable, then the interior equilibrium  $E_c$  doesn't exist.
  - (b) If  $E_2$  is unstable and  $E_1$  is unstable, then the unique interior equilibrium  $E_c$  exists.

### 3.4. $x_1$ is R-limited, and $x_2$ is R-limited

If  $x_1$  is R-limited, and  $x_2$  is R-limited, (3.1) becomes the following:

$$S' = (S^0 - S)D_1 - f_{1s}(S)x_1 - f_{2s}(S)x_2 \tag{3.8a}$$

$$R' = (R^0 - R)D_2 - f_{1r}(R)x_1 - f_{2r}(R)x_2 \tag{3.8b}$$

$$Q'_{1s} = f_{1s}(S) - \mu_{1\infty} \left(1 - \frac{Q_{min,1r}}{Q_{1r}}\right) Q_{1s} \tag{3.8c}$$

$$Q'_{1r} = f_{1r}(R) - \mu_{1\infty} \left(1 - \frac{Q_{min,1r}}{Q_{1r}}\right) Q_{1r} \tag{3.8d}$$

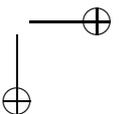
$$Q'_{2s} = f_{2s}(S) - \mu_{2\infty} \left(1 - \frac{Q_{min,2r}}{Q_{2r}}\right) Q_{2s} \tag{3.8e}$$

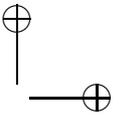
$$Q'_{2r} = f_{2r}(R) - \mu_{2\infty} \left(1 - \frac{Q_{min,2r}}{Q_{2r}}\right) Q_{2r} \tag{3.8f}$$

$$x'_1 = \left[\mu_{1\infty} \left(1 - \frac{Q_{min,1r}}{Q_{1r}}\right) - d_1\right] x_1 \tag{3.8g}$$

$$x'_2 = \left[\mu_{2\infty} \left(1 - \frac{Q_{min,2r}}{Q_{2r}}\right) - d_2\right] x_2 \tag{3.8h}$$

with the usual initial condition. This model is similar to (3.2). Generically, (3.8) has at most three steady-state solutions. One of these, which we label  $E_0$ , corresponds to the absence of both competitors. It is given by  $E_0 = (S, R, Q_{1s}, Q_{1r}, Q_{2s}, Q_{2r}, x_1, x_2) = (S^0, R^0, Q_{1s}^0, Q_{1r}^0, Q_{2s}^0, Q_{2r}^0, 0, 0)$  and it always exists. The two other possible steady-states, labeled  $E_1$  and  $E_2$ , correspond to the presence of one population and the absence of the other.





They take the forms:  $E_1 = E_{1R} = (S_{1r}^*, \lambda_{1r}, Q_{1s}^*, Q_{1r}^*, Q_{2s}^*, Q_{2r}^*, x_{1r}^*, 0)$  and  $E_2 = E_{2R} = (S_{2r}^{**}, \lambda_{2r}, Q_{1s}^{**}, Q_{1r}^{**}, Q_{2s}^{**}, Q_{2r}^{**}, 0, x_{2r}^{**})$ . Note that the steady-states  $E_1$  exists if and only if  $d_1 < \mu_{1\infty}$  and  $\lambda_{1r} < R^0$ .  $E_2$  exists if and only if  $d_2 < \mu_{2\infty}$  and  $\lambda_{2r} < R^0$ . There exist steady states with both  $x_1$  and  $x_2$  present if  $\lambda_{1r} = \lambda_{2r}$ . Since this condition is highly unlikely, we ignore this case. Assume that  $x_1$  is R-limited and  $x_2$  is R-limited, we have the following theorems:

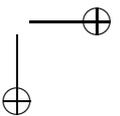
**Theorem 3.7.** *If  $\lambda_{1r} > R^0$  and  $\lambda_{2r} > R^0$ , then  $E_0 = (S^0, R^0, Q_{1s}^0, Q_{1r}^0, Q_{2s}^0, Q_{2r}^0, 0, 0)$  is locally asymptotically stable.*

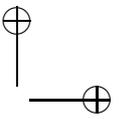
**Theorem 3.8.** *Assume that both of  $E_1$  and  $E_2$  exist (ie.  $\lambda_{1r} < R^0, \lambda_{2r} < R^0$ , and  $d_i < \mu_{i\infty}, i=1,2$ ). If  $\lambda_{1r} < \lambda_{2r}$ , then  $E_1 = (S_{1r}^*, \lambda_{1r}, Q_{1s}^*, Q_{1r}^*, Q_{2s}^*, Q_{2r}^*, x_{1r}^*, 0)$  is locally asymptotically stable and  $E_2 = (S_{2r}^{**}, \lambda_{2r}, Q_{1s}^{**}, Q_{1r}^{**}, Q_{2s}^{**}, Q_{2r}^{**}, 0, x_{2r}^{**})$  is unstable.*

From the above theorems, we summarize the results in Table 3.1, 3.2, and 3.3.

**Table 3.1.** Existence and stability of equilibria for a competition model based on storage with different removal rates.

Equilibrium	Existence condition	Stability condition
$E_0$	Always exists	$(\lambda_{1s} > S^0 \vee \lambda_{1r} > R^0)$ $\wedge (\lambda_{2s} > S^0 \vee \lambda_{2r} > R^0)$
$E_{1S}$	$\lambda_{1s} < S^0, \lambda_{1r} < R^0$ and $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{1r})} < \frac{f_{1s}(\lambda_{1s})}{f_{1r}(\lambda_{1r})}$	$\lambda_{1s} < \lambda_{2s}$ or $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{2r})} > \frac{f_{1s}(\lambda_{1s})}{f_{1r}(\lambda_{2r})}$
$E_{1R}$	$\lambda_{1s} < S^0, \lambda_{1r} < R^0$ and $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{1r})} > \frac{f_{1s}(\lambda_{1s})}{f_{1r}(\lambda_{1r})}$	$\lambda_{1r} < \lambda_{2r}$ or $\frac{D_1(S^0 - \lambda_{2s})}{D_2(R^0 - \lambda_{1r})} < \frac{f_{1s}(\lambda_{2s})}{f_{1r}(\lambda_{1r})}$
$E_{2S}$	$\lambda_{2s} < S^0, \lambda_{2r} < R^0$ and $\frac{D_1(S^0 - \lambda_{2s})}{D_2(R^0 - \lambda_{2r})} < \frac{f_{2s}(\lambda_{2s})}{f_{2r}(\lambda_{2r})}$	$\lambda_{2s} < \lambda_{1s}$ or $\frac{D_1(S^0 - \lambda_{2s})}{D_2(R^0 - \lambda_{1r})} > \frac{f_{2s}(\lambda_{2s})}{f_{2r}(\lambda_{1r})}$
$E_{2R}$	$\lambda_{2s} < S^0, \lambda_{2r} < R^0$ and $\frac{D_1(S^0 - \lambda_{2s})}{D_2(R^0 - \lambda_{2r})} > \frac{f_{2s}(\lambda_{2s})}{f_{2r}(\lambda_{2r})}$	$\lambda_{2r} < \lambda_{1r}$ or $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{2r})} < \frac{f_{2s}(\lambda_{1s})}{f_{2r}(\lambda_{2r})}$





**Table 3.2.** Existence of interior equilibria for a competition model based on storage with Different Removal Rates.

Equilibrium	Existence condition
$E_C^{1S,2R}$	$(\lambda_{1s} > \lambda_{2s}, \lambda_{1r} < \lambda_{2r},$ $\frac{f_{2s}(\lambda_{1s})}{f_{2r}(\lambda_{2r})} < \frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{2r})} < \frac{f_{1s}(\lambda_{1s})}{f_{1r}(\lambda_{2r})}) \vee (\frac{f_{1s}(\lambda_{1s})}{f_{1r}(\lambda_{2r})} < \frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{2r})} < \frac{f_{2s}(\lambda_{1s})}{f_{2r}(\lambda_{2r})})$
$E_C^{1R,2S}$	$(\lambda_{1s} < \lambda_{2s}, \lambda_{1r} > \lambda_{2r},$ $\frac{f_{1s}(\lambda_{2s})}{f_{1r}(\lambda_{1r})} < \frac{D_1(S^0 - \lambda_{2s})}{D_2(R^0 - \lambda_{1r})} < \frac{f_{2s}(\lambda_{2s})}{f_{2r}(\lambda_{1r})}) \vee (\frac{f_{2s}(\lambda_{2s})}{f_{2r}(\lambda_{1r})} < \frac{D_1(S^0 - \lambda_{2s})}{D_2(R^0 - \lambda_{1r})} < \frac{f_{1s}(\lambda_{2s})}{f_{1r}(\lambda_{1r})})$

**Table 3.3.** Biological Classification of the Outcomes for Two Complementary Resources with Internal Storage and Different Removal rates;

$$T_i = \frac{D_1(S^0 - \lambda_{is})}{D_2(R^0 - \lambda_{ir})}, C_i = \frac{f_{is}(\lambda_{is})}{f_{ir}(\lambda_{ir})}, i=1,2.$$

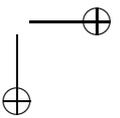
Biological Case	Competition Criteria
Species 1 always wins, regardless of initial density; species 2 die out	(a) $\lambda_{1r} < \lambda_{2r}, T_1 > C_1, T_2 > C_2$ (b) $\lambda_{1s} < \lambda_{2s}, T_1 < C_1, T_2 < C_2$
Species 2 always wins, regardless of initial density; species 1 die out	(a) $\lambda_{1s} > \lambda_{2s}, T_1 < C_1, T_2 < C_2$ (b) $\lambda_{1r} > \lambda_{2r}, T_1 > C_1, T_2 > C_2$
Species 1 and 2 persist in a stable coexistence	(a) $\lambda_{1s} < \lambda_{2s}, \lambda_{1r} > \lambda_{2r}, T_1 < C_1, T_2 > C_2$ (b) $\lambda_{1s} > \lambda_{2s}, \lambda_{1r} < \lambda_{2r}, T_1 > C_1, T_2 < C_2$
Species 1 always wins, or Species 2 wins, while rival Species dies out; initial densities determine eventual winner	(a) $\lambda_{1s} < \lambda_{2s}, \lambda_{1r} > \lambda_{2r}, T_1 > C_1, T_2 < C_2$ (b) $\lambda_{1s} > \lambda_{2s}, \lambda_{1r} < \lambda_{2r}, T_1 < C_1, T_2 > C_2$

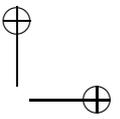
### 4. Appendix: The proof

#### 1. The local stability of equilibrium of system (3.2)

The local stability of equilibrium of system(3.2) is determined by the Jacobian matrix of (3.2), denoted by  $J(S, R, Q_{1s}, Q_{1r}, Q_{2s}, Q_{2r}, x_1, x_2) =$

$$\begin{bmatrix} a_{11} & 0 & 0 & 0 & 0 & 0 & -f_{1s}(S) & -f_{2s}(S) \\ 0 & a_{22} & 0 & 0 & 0 & 0 & -f_{1r}(R) & -f_{2r}(R) \\ f'_{1s}(S) & 0 & -\mu_{1\infty} & 0 & 0 & 0 & 0 & 0 \\ 0 & f'_{1r}(R) & a_{43} & -\mu_{1s}(Q_{1s}) & 0 & 0 & 0 & 0 \\ f'_{2s}(S) & 0 & 0 & 0 & -\mu_{2\infty} & 0 & 0 & 0 \\ 0 & f'_{2r}(R) & 0 & 0 & a_{65} & -\mu_{2s}(Q_{2s}) & 0 & 0 \\ 0 & 0 & a_{73} & 0 & 0 & 0 & a_{77} & 0 \\ 0 & 0 & 0 & 0 & a_{85} & 0 & 0 & a_{88} \end{bmatrix}$$





where  $a_{11} = -D_1 - f'_{1s}(S)x_1 - f'_{2s}(S)x_2$ ,  $a_{22} = -D_2 - f'_{1r}(R)x_1 - f'_{2r}(R)x_2$ ,  $a_{43} = -\mu'_{1s}(Q_{1s})Q_{1r}$ ,  $a_{65} = -\mu'_{2s}(Q_{2s})Q_{2r}$ ,  $a_{73} = \mu'_{1s}(Q_{1s})x_1$ ,  $a_{77} = \mu_{1s}(Q_{1s}) - d_1$ ,  $a_{85} = \mu'_{2s}(Q_{2s})x_2$ ,  $a_{88} = \mu_{2s}(Q_{2s}) - d_2$ .

**(Proof of Theorem 3.1)**  $J_0 = J(E_0) =$

$$\begin{bmatrix} -D_1 & 0 & 0 & 0 & 0 & 0 & -f_{1s}(S^0) & -f_{2s}(S^0) \\ 0 & -D_2 & 0 & 0 & 0 & 0 & -f_{1r}(R^0) & -f_{2r}(R^0) \\ f'_{1s}(S^0) & 0 & -\mu_{1\infty} & 0 & 0 & 0 & 0 & 0 \\ 0 & f'_{1r}(R^0) & \bar{a}_{43} & -\mu_{1s}(Q_{1s}^0) & 0 & 0 & 0 & 0 \\ f'_{2s}(S^0) & 0 & 0 & 0 & -\mu_{2\infty} & 0 & 0 & 0 \\ 0 & f'_{2r}(R^0) & 0 & 0 & \bar{a}_{65} & -\mu_{2s}(Q_{2s}^0) & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \bar{a}_{77} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \bar{a}_{88} \end{bmatrix}$$

where  $\bar{a}_{43} = -\mu'_{1s}(Q_{1s}^0)Q_{1r}$ ,  $\bar{a}_{65} = -\mu'_{2s}(Q_{2s}^0)Q_{2r}$ ,  $\bar{a}_{77} = \mu_{1s}(Q_{1s}^0) - d_1$ ,  $\bar{a}_{88} = \mu_{2s}(Q_{2s}^0) - d_2$ . The eigenvalues of  $J_0$  are

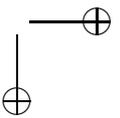
$$-D_1, -D_2, -\mu_{1\infty}, -\mu_{2\infty}, -\mu_{1s}(Q_{1s}^0), -\mu_{2s}(Q_{2s}^0), \mu_{1s}(Q_{1s}^0) - d_1, \mu_{2s}(Q_{2s}^0) - d_2.$$

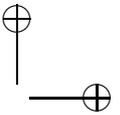
Since  $\mu_{is}(Q_{is}^0) = \mu_{i\infty}(1 - \frac{Q_{min,is}}{Q_{is}^0}) = \frac{f_{is}(S^0)}{Q_{is}^0} > 0, i = 1, 2$ . Hence,  $E_0$  is locally asymptotically stable if and only if  $\mu_{is}(Q_{is}^0) < d_i, i = 1, 2$ . if and only if  $\mu_{i\infty}(1 - \frac{Q_{min,is}}{Q_{is}^0}) < d_i$  if and only if  $Q_{is}^0 < \frac{Q_{min,is}}{1 - \frac{d_i}{\mu_{i\infty}}}$  if and only if  $Q_{min,is} + \frac{f_{is}(S^0)}{\mu_{i\infty}} < \frac{Q_{min,is}}{1 - \frac{d_i}{\mu_{i\infty}}}$  if and only if  $f_{is}(S^0) < \frac{d_i Q_{min,is}}{1 - \frac{d_i}{\mu_{i\infty}}} \equiv f_{is}(\lambda_{is})$  if and only if  $S^0 < \lambda_{is}, i = 1, 2$ .

**(Proof of Theorem 3.2)**  $J_1 = J(E_1) =$

$$\begin{bmatrix} a_{11}^* & 0 & 0 & 0 & 0 & 0 & -f_{1s}(\lambda_{1s}) & -f_{2s}(\lambda_{1s}) \\ 0 & a_{22}^* & 0 & 0 & 0 & 0 & -f_{1r}(R_{1s}^*) & -f_{2r}(R_{1s}^*) \\ f'_{1s}(\lambda_{1s}) & 0 & -\mu_{1\infty} & 0 & 0 & 0 & 0 & 0 \\ 0 & f'_{1r}(R_{1s}^*) & a_{43}^* & -d_1 & 0 & 0 & 0 & 0 \\ f'_{2s}(\lambda_{1s}) & 0 & 0 & 0 & -\mu_{2\infty} & 0 & 0 & 0 \\ 0 & f'_{2r}(R_{1s}^*) & 0 & 0 & a_{65}^* & -\mu_{2s}(Q_{2s}^*) & 0 & 0 \\ 0 & 0 & a_{73}^* & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & a_{88}^* \end{bmatrix}$$

where  $a_{11}^* = -D_1 - f'_{1s}(\lambda_{1s})x_{1s}^*$ ,  $a_{22}^* = -D_2 - f'_{1r}(R_{1s}^*)x_{1s}^*$ ,  $a_{43}^* = -\mu'_{1s}(Q_{1s}^*)Q_{1r}$ ,





$a_{65}^* = -\mu_{2s}'(Q_{2s}^*)Q_{2r}^*$ ,  $a_{73}^* = \mu_{1s}'(Q_{1s}^*)x_{1s}^*$ ,  $a_{88}^* = \mu_{2s}(Q_{2s}^*) - d_2$ . The eigenvalues of  $J_1$  are

$$-\mu_{2s}(Q_{2s}^*), -\mu_{2\infty}, a_{88}^*, -d_1, a_{22}^*$$

and the eigenvalues of  $\tilde{J}_1 =$

$$\begin{bmatrix} a_{11}^* & 0 & -f_{1s}(\lambda_{1s}) \\ f_{1s}'(\lambda_{1s}) & -\mu_{1\infty} & 0 \\ 0 & a_{73}^* & 0 \end{bmatrix}.$$

The characteristic polynomial of  $\tilde{J}_1$  is  $\det(zI - \tilde{J}_1) = z^3 + A_1z^2 + A_2z + A_3$  where  $A_1 = -(a_{11}^* - \mu_{1\infty}) > 0$ ,  $A_2 = -\mu_{1\infty}a_{11}^*$ ,  $A_3 = f_{1s}'(\lambda_{1s})a_{73}^*f_{1s}(\lambda_{1s}) > 0$ . Since  $\mu_{1s}'(Q_{1s}^*) = \mu_{1\infty} \frac{Q_{min,1s}}{(Q_{1s}^*)^2}$ , and  $f_{1s}(\lambda_{1s}) = d_1Q_{1s}^*$ . Hence,

$$\begin{aligned} & A_1A_2 - A_3 \\ &= \mu_{1\infty}(D_1 + f_{1s}'(\lambda_{1s})x_{1s}^* + \mu_{1\infty})(D_1 + f_{1s}'(\lambda_{1s})x_{1s}^*) - f_{1s}'(\lambda_{1s})\mu_{1s}'(Q_{1s}^*)x_{1s}^*f_{1s}(\lambda_{1s}) \\ &= \mu_{1\infty}(D_1 + f_{1s}'(\lambda_{1s})x_{1s}^* + \mu_{1\infty})(D_1 + f_{1s}'(\lambda_{1s})x_{1s}^*) - f_{1s}'(\lambda_{1s})\mu_{1\infty} \frac{Q_{min,1s}}{Q_{1s}^*}d_1x_{1s}^* \\ &= \mu_{1\infty}(D_1 + f_{1s}'(\lambda_{1s})x_{1s}^* + \mu_{1\infty})(D_1 + f_{1s}'(\lambda_{1s})x_{1s}^*) - f_{1s}'(\lambda_{1s})\mu_{1\infty}(1 - \frac{d_1}{\mu_{1\infty}})d_1x_{1s}^*. \end{aligned}$$

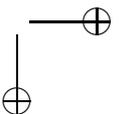
Since  $\mu_{1\infty} > d_1$ , we have

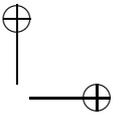
$$\begin{aligned} & A_1A_2 - A_3 \\ &> d_1(D_1 + f_{1s}'(\lambda_{1s})x_{1s}^* + \mu_{1\infty})(D_1 + f_{1s}'(\lambda_{1s})x_{1s}^*) - f_{1s}'(\lambda_{1s})\mu_{1\infty}(1 - \frac{d_1}{\mu_{1\infty}})d_1x_{1s}^* \\ &> 0. \end{aligned}$$

The Routh-Hurwitz criterion [5] shows that the real part of the eigenvalues of  $\tilde{J}_1$  are negative. Hence  $E_1$  is locally asymptotically stable if and only if

$$0 < \mu_{2s}(Q_{2s}^*) < d_2.$$

Notice that  $\mu_{2s}(Q_{2s}^*) = \mu_{2\infty}(1 - \frac{Q_{min,2s}}{Q_{2s}^*}) = \frac{f_{2s}(\lambda_{1s})}{Q_{2s}^*} > 0$ . Hence,  $E_1$  is locally asymptotically stable if and only if  $\mu_{2s}(Q_{2s}^*) < d_2$  if and only if  $Q_{2s}^* < \frac{Q_{min,2s}}{1 - \frac{d_2}{\mu_{2\infty}}}$  if and only if  $Q_{min,2s} + \frac{f_{2s}(\lambda_{1s})}{\mu_{2\infty}} < \frac{Q_{min,2s}}{1 - \frac{d_2}{\mu_{2\infty}}}$  if and only if  $f_{2s}(\lambda_{1s}) < Q_{min,2s} \cdot \frac{d_2}{1 - \frac{d_2}{\mu_{2\infty}}} = f_{2s}(\lambda_{2s})$  if and only if  $\lambda_{1s} < \lambda_{2s}$ . The stability analysis for  $E_2$  is similar to  $E_1$  and we omit it.





**2. The local stability of equilibrium of system (3.3)**

The proof of Theorem 3.3 is similar to Theorem 3.1 and we omit it. The proof of Proposition 3.1(2) is similar to Proposition 3.1(1) thus and we only prove Proposition 3.1(1). The local stability of equilibrium of system (3.3) is determined by the Jacobian matrix of (3.3), denoted by

$$J(S, R, Q_{1s}, Q_{1r}, Q_{2s}, Q_{2r}, x_1, x_2) = \begin{bmatrix} a_{11} & 0 & 0 & 0 & 0 & 0 & -f_{1s}(S) & -f_{2s}(S) \\ 0 & a_{22} & 0 & 0 & 0 & 0 & -f_{1r}(R) & -f_{2r}(R) \\ f'_{1s}(S) & 0 & -\mu_{1\infty} & 0 & 0 & 0 & 0 & 0 \\ 0 & f'_{1r}(R) & a_{43} & -\mu_{1s}(Q_{1s}) & 0 & 0 & 0 & 0 \\ f'_{2s}(S) & 0 & 0 & 0 & -\mu_{2r}(Q_{2r}) & a_{56} & 0 & 0 \\ 0 & f'_{2r}(R) & 0 & 0 & 0 & -\mu_{2\infty} & 0 & 0 \\ 0 & 0 & a_{73} & 0 & 0 & 0 & a_{77} & 0 \\ 0 & 0 & 0 & 0 & 0 & a_{86} & 0 & a_{88} \end{bmatrix}$$

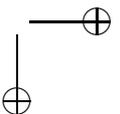
where  $a_{11} = -D_1 - f'_{1s}(S)x_1 - f'_{2s}(S)x_2$ ,  $a_{22} = -D_2 - f'_{1r}(R)x_1 - f'_{2r}(R)x_2$ ,  $a_{43} = -\mu'_{1s}(Q_{1s})Q_{1r}$ ,  $a_{56} = -\mu'_{2r}(Q_{2r})Q_{2s}$ ,  $a_{73} = \mu'_{1s}(Q_{1s})x_1$ ,  $a_{77} = \mu_{1s}(Q_{1s}) - d_1$ ,  $a_{86} = \mu'_{2r}(Q_{2r})x_2$ ,  $a_{88} = \mu_{2r}(Q_{2r}) - d_2$ .

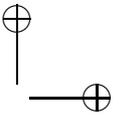
**(Proof of Proposition 3.1(1))**  $J_1 = J(E_1) =$

$$\begin{bmatrix} a^*_{11} & 0 & 0 & 0 & 0 & 0 & -f_{1s}(\lambda_{1s}) & -f_{2s}(\lambda_{1s}) \\ 0 & a^*_{22} & 0 & 0 & 0 & 0 & -f_{1r}(R^*_{1s}) & -f_{2r}(R^*_{1s}) \\ f'_{1s}(\lambda_{1s}) & 0 & -\mu_{1\infty} & 0 & 0 & 0 & 0 & 0 \\ 0 & f'_{1r}(R^*_{1s}) & a^*_{43} & -d_1 & 0 & 0 & 0 & 0 \\ f'_{2s}(\lambda_{1s}) & 0 & 0 & 0 & -\mu_{2r}(Q^*_{2r}) & a^*_{56} & 0 & 0 \\ 0 & f'_{2r}(R^*_{1s}) & 0 & 0 & 0 & -\mu_{2\infty} & 0 & 0 \\ 0 & 0 & a^*_{73} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & a^*_{88} \end{bmatrix}$$

where  $a^*_{11} = -D_1 - f'_{1s}(\lambda_{1s})x^*_{1s}$ ,  $a^*_{22} = -D_2 - f'_{1r}(R^*_{1s})x^*_{1s}$ ,  $a^*_{43} = -\mu'_{1s}(Q^*_{1s})Q^*_{1r}$ ,  $a^*_{56} = -\mu'_{2r}(Q^*_{2r})Q^*_{2s}$ ,  $a^*_{73} = \mu'_{1s}(Q^*_{1s})x^*_{1s}$ ,  $a^*_{88} = \mu_{2r}(Q^*_{2r}) - d_2$ . The eigenvalues of  $J_1$  are

$$-\mu_{2r}(Q^*_{2r}), -\mu_{2\infty}, a^*_{88}, -d_1, a^*_{22}$$





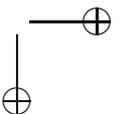
and the eigenvalues of  $\tilde{J}_1 =$

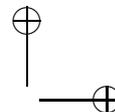
$$\begin{bmatrix} a_{11}^* & 0 & -f_{1s}(\lambda_{1s}) \\ f'_{1s}(\lambda_{1s}) - \mu_{1\infty} & 0 & 0 \\ 0 & a_{73}^* & 0 \end{bmatrix}.$$

The characteristic polynomial of  $\tilde{J}_1$  is  $\det(zI - \tilde{J}_1) = z^3 + A_1z^2 + A_2z + A_3$ , where  $A_1 = -(a_{11}^* - \mu_{1\infty}) > 0$ ,  $A_2 = -\mu_{1\infty}a_{73}^*$ ,  $A_3 = f'_{1s}(\lambda_{1s})a_{73}^*f_{1s}(\lambda_{1s}) > 0$ . Since  $A_1 > 0$ ,  $A_3 > 0$  and  $A_1A_2 - A_3 > 0$ , the Routh-Hurwitz criterion shows that the real part of the eigenvalues of  $\tilde{J}_1$  are negative. Hence  $E_1$  is locally asymptotically stable if and only if  $0 < \mu_{2r}(Q_{2r}^*) < d_2$ . Notice that  $\mu_{2r}(Q_{2r}^*) = \mu_{2\infty}(1 - \frac{Q_{min,2r}}{Q_{2r}^*}) = \frac{f_{2r}(R_{1s}^*)}{Q_{2r}^*} > 0$ . Hence,  $E_1$  is locally asymptotically stable if and only if  $\mu_{2r}(Q_{2r}^*) < d_2$ , that is,  $Q_{2r}^* < \frac{Q_{min,2r}}{1 - \frac{d_2}{\mu_{2\infty}}}$ , that is,  $Q_{min,2r} + \frac{f_{2r}(R_{1s}^*)}{\mu_{2\infty}} < \frac{Q_{min,2r}}{1 - \frac{d_2}{\mu_{2\infty}}}$ , that is,  $f_{2r}(R_{1s}^*) < Q_{min,2r} \frac{d_2}{1 - \frac{d_2}{\mu_{2\infty}}} = f_{2r}(\lambda_{2r})$ , that is,  $R_{1s}^* < \lambda_{2r}$ , that is,  $\frac{f_{1r}(R_{1s}^*)}{R^0 - R_{1s}^*} < \frac{f_{1r}(\lambda_{2r})}{R^0 - \lambda_{2r}}$  (Note that  $\frac{f_{1r}(\star)}{R^0 - (\star)}$  is increasing), that is,  $\frac{D_2 f_{1s}(\lambda_{1s})}{D_1(S^0 - \lambda_{1s})} < \frac{f_{1r}(\lambda_{2r})}{R^0 - \lambda_{2r}}$  (Note that  $\frac{f_{1r}(R_{1s}^*)}{R^0 - R_{1s}^*} = \frac{D_2 f_{1s}(\lambda_{1s})}{D_1(S^0 - \lambda_{1s})}$ ), that is,  $\frac{D_1(S^0 - \lambda_{1s})}{D_2(R^0 - \lambda_{2r})} > \frac{f_{1s}(\lambda_{1s})}{f_{1r}(\lambda_{2r})}$ , that is,  $\Delta_2 < 0$ .

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