

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

BY

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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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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

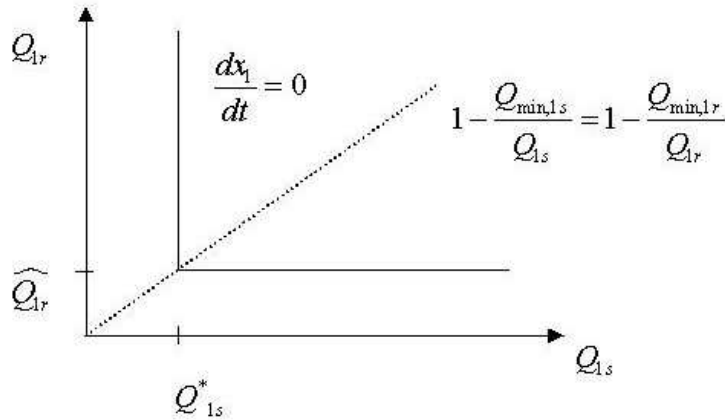


Figure 2.1.

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

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

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 $\hat{Q}_{1r} = \frac{Q_{min,1r}}{1 - \frac{d_1}{\mu_{1\infty}}}$, $f_{1r}(\lambda_{1r}) = d_1\hat{Q}_{1r} = \frac{d_1Q_{min,1r}}{1 - \frac{d_1}{\mu_{1\infty}}}$, $\hat{x}_{1r} = \frac{D_2(R^0 - \lambda_{1r})}{d_1\hat{Q}_{1r}} = \frac{D_2(R^0 - \lambda_{1r})}{f_{1r}(\lambda_{1r})}$, $(S^0 - \hat{S}_{1r})D_2 = f_{1s}(\hat{S}_{1r})\hat{x}_{1r}$, $\hat{Q}_{1s} = \frac{f_{1s}(\hat{S}_{1r})}{d_1}$. 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 equilibria 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 $1 - \frac{Q_{min,1r}}{\hat{Q}_{1r}} = \frac{d_1}{\mu_{1\infty}}$, 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 $d_1Q_{1r}^* = f_{1r}(R_{1s}^*)$ 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 . λ_{1s} and λ_{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

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

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 $\frac{R^0 - R_{1s}^*}{f_{1r}(R_{1s}^*)} = \frac{x_s^*}{D_2} = \frac{D_1(S^0 - \lambda_{1s})}{D_2 f_{1s}(\lambda_{1s})}$ 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

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

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

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:

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

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

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

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

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

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

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

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

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

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

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

By Cramer’s rule, it follows that

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

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

where

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

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

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

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:

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

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

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

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

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

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

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

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

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:

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

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

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

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

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

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

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

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

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

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

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

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

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 $\mu_{2s}(Q_{2s}^*) = \mu_{2\infty} \left(1 - \frac{Q_{min,2s}}{Q_{2s}^*}\right) = \frac{f_{2s}(\lambda_{1s})}{Q_{2s}^*} > 0$. 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 $\tilde{J}_1 =$

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

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 $A_1 > 0$, $A_3 > 0$ 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 $\frac{f_{1r}(\cdot)}{R^0 - (\cdot)}$ 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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