

COMPETITION FOR TWO PERFECTLY SUBSTITUTABLE RESOURCES

EXPLOITATIVE COMPETITION IN THE CHEMOSTAT FOR TWO
PERFECTLY SUBSTITUTABLE RESOURCES

By

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Abstract

A model of the chemostat involving two populations of microorganisms competing for two perfectly substitutable, growth limiting nutrients is developed. To describe nutrient uptake, a general class of functions is used which allows for the effects that the consumption of one resource may have on the consumption of the other. It includes as a special case the model studied by Waltman, Hubbell and Hsu [21] in which they generalize Michaelis-Menten functional response for a single resource to two perfectly substitutable resources. It also generalizes the model studied by León and Tumpson [12] where the consumption of each resource is unaffected by the consumption of the other. Analytical methods are used to obtain information about the qualitative behaviour of the model. Interesting similarities are found between both the local and global behaviour in this model and in the model for perfectly complementary resources.

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Chapter 1

Introduction

1.1 The Chemostat

The chemostat is a laboratory apparatus used in the culturing of microorganisms. It was developed to provide a controlled environment in which the growth of microbial populations could be studied under nutrient limitation (see Novick and Sziliard [15]). This culturing technique, described below, is used in industry for the simulation of biological waste decomposition or water purification by microorganisms (see Yang and Humphrey [22]) as well as the economical production of useful microorganisms (see Herbert, Elsworth and Telling [7]).

The apparatus can be thought to consist of three chambers: a feed bottle, a culture vessel and a receptacle (see figure A.1).[†] The culture vessel, which is continuously stirred, contains a suspension of one or more populations of microorganisms. A steady stream of nutrient is pumped in from the feed bottle at a constant rate while medium is removed to the receptacle at the same rate, thus maintaining constant volume. As the contents of the culture vessel are continuously stirred, nutrients, microorganisms and byproducts are removed in proportion to their concentrations. The chemical composition of the nutrient in the feed bottle is controlled so that it contains near optimal concentrations of all required growth factors with the exception of those under investigation, the concentrations of which are controlled by the experimenter.

In contrast with the batch culture technique, in which an enriched mixture of

nutrients is added to a small sample of environmental medium in a closed culture vessel, the culturing method described above provides the microorganisms with a continuous supply of nutrient and is thus referred to as a continuous culture. The environment approximated by the chemostat is that of a simple lake, where resource densities are generally much lower than the high nutrient levels found in batch cultures. The properties which become important in mathematical modelling are that the concentration of nutrient in the feed bottle and the input flow rate are controlled by the investigator, the culture vessel has constant volume, its contents are well-stirred, and all external factors, such as temperature, are fixed.

In this thesis we will be focussing on two-species competition in the chemostat for two limiting resources. The competition is assumed to be exploitative, that is, the species compete only by consuming the common pool of nutrients.

1.2 Thesis Outline

In this thesis we examine exploitative competition for two resources under chemostat-like conditions. With two resources available it is important to consider how these nutrients, once consumed, are utilized by the individual competitors for growth. As will be seen, this leads to the classification of resources as perfectly complementary, perfectly substitutable and imperfectly substitutable. Restricting ourselves to the two-competitor situation, we will be focussing our attention primarily on the perfectly substitutable case.

León and Tumpson [12] appear to be the first to have modelled exploitative competition for perfectly substitutable resources. They assume that the consumption of one resource is independent of the concentration of the other resources and that each competitor's functional response is a strictly monotone increasing function of resource concentration. In the two resource, two competitor case, under the assumption of the existence of an interior equilibrium, they derive necessary and sufficient conditions for its local asymptotic stability and hence conditions for the coexistence of the competitors.

The content of this thesis is organized as follows. In chapter 2 we discuss the classical theory of ecological competition and briefly outline the more recent developments. In chapter 3 we describe a resource-based model of exploitative competition in the chemostat for two resources, focussing on functional responses which are strictly monotone functions of resource concentration. Further, we describe the classification of resources provided by León and Tumpson [12] and Rapport [16]. In chapter 4 we discuss the same model under the assumption that the resources are perfectly complementary. There we summarize the results of Butler and Wolkowicz [2] in the case of monotone kinetics. In chapter 5 we specify the model of chapter 3 in the case that the resources are perfectly substitutable. Under the assumptions of León and Tumpson [12], we give a complete global analysis of the three-dimensional subsystems as well as provide conditions which guarantee the existence of an interior equilibrium of the full four dimensional model and are necessary and sufficient for persistence. Also, we extend their model to a more general and realistic setting, incorporating the possible

inhibitory effects that the consumption of one resource may have on the consumption of the other. The model studied by Hsu, Hubbell and Waltman [21] is an example of this, as they specifically generalize Michaelis-Menten functional response for a single resource to two perfectly substitutable resources. For this extended model, we obtain sufficient conditions for the existence of an interior equilibrium and necessary conditions for its local asymptotic stability as well as conditions under which the three dimensional subsystems of interest are persistent. In chapter 6 we compare the local and global results obtained here in the case of perfectly substitutable resources to those obtained in the case of perfectly complementary resources. All figures and diagrams are given in appendix A and the background theory used in the analysis of chapter 5 is summarized in appendix B.

1.3 Notation

The following notation is used throughout this thesis.

\mathfrak{R} denotes the real numbers

$$\mathfrak{R}^n = \{(x_1, \dots, x_n) : x_i \in \mathfrak{R}, i = 1, \dots, n\}$$

$$\mathfrak{R}_+^n = \{(x_1, \dots, x_n) : x_i \geq 0, i = 1, \dots, n\}$$

C^1 denotes the class of continuously differentiable functions

$\overset{\circ}{A}$ denotes the interior of the set A

clA denotes the closure of the set A

$\mathcal{O}(X)$ denotes the entire orbit through the point X

$\Omega(X)$ denotes the omega limit set of the orbit through X

$M^+(E)$ denotes the stable manifold of the equilibrium point E

$M^-(E)$ denotes the unstable manifold of the equilibrium point E

All other notation is either standard or is defined independently for each chapter.

Chapter 2

The Classical Theory

The classical theory of ecological competition is attributed to Lotka [13] and Volterra [20] and is an extension of the basic logistic model for single-species growth due to Verhulst [19]. In accordance with this theory, the dynamical system for two competitors can be written:

$$\begin{aligned}x_1' &= r_1 x_1 \left(1 - \frac{x_1}{K_1} - \beta_1 x_2\right), \\x_2' &= r_2 x_2 \left(1 - \frac{x_2}{K_2} - \beta_2 x_1\right), \\x_1(0) &= x_{1o} > 0, \quad x_2(0) = x_{2o} > 0,\end{aligned}\tag{2.1}$$

where r_i , K_i , and β_i , $i = 1, 2$, are positive constants. Here, x_i is the size of the i^{th} population, r_i is the intrinsic rate of increase of population i , and K_i is the carrying capacity of the i^{th} species. The constants β_1 and β_2 are interaction coefficients, measuring the per capita effects of competitor two on one, and one on two respectively, in terms of the realized growth rate and carrying capacity of the rival species.

It is clear from (2.1) that extinction of both populations is impossible since in the absence of either species, the other species grows. Hence there are four distinct biological outcomes possible. Which outcome occurs depends on the carrying capacities and the interaction coefficients. Competitive instability (the initial numbers of

each competitor determine the sole survivor) occurs when $\beta_1 > \frac{1}{K_2}$ and $\beta_2 > \frac{1}{K_1}$. If exactly one of these inequalities is reversed we have competitive exclusion in which one or the other population survives independent of the initial numbers; if $\beta_1 > \frac{1}{K_2}$ and $\beta_2 \leq \frac{1}{K_1}$ then species two is the sole survivor and if $\beta_1 \leq \frac{1}{K_2}$ and $\beta_2 > \frac{1}{K_1}$ then species one is the sole survivor. Coexistence occurs when $\beta_1 < \frac{1}{K_2}$ and $\beta_2 < \frac{1}{K_1}$. A complete analysis of (2.1) can be found in Freedman [3], although it is treated in many textbooks on differential equations.

The appeal of the classical theory lies in its generality and simplicity. It seeks to describe how the numbers of competitors change without indicating the resources upon which competition is based or how these resources are utilized by the consumer. As it is difficult to estimate the interaction coefficients independent of actually growing the species together in competition, these models are often more phenomenological than predictive.

In response to these deficiencies, a more mechanistic, resource-based theory has developed over the last thirty years. The resources are incorporated into the models in order to capture consumer-resource interactions as well as competitive interactions. The resulting mathematical models may be less general and more difficult to analyze. However it should be noted that these models are often more predictive (for example, Hanson and Hubbell [6]) as the parameters can be measured on species grown alone, in advance of competition. The model that we will be considering is an example of this resource-based approach.

Chapter 3

Exploitative Competition in the Chemostat for Two Resources

3.1 The Model

We will be discussing exploitative competition in the chemostat for two nonreproducing resources. In the two-species case, the dynamical system may be written

$$\begin{aligned} S'(t) &= (S^o - S(t))D - \sum_{i=1}^2 x_i(t)\mathcal{U}_{S_i}(S(t), R(t)), \\ R'(t) &= (R^o - R(t))D - \sum_{i=1}^2 x_i(t)\mathcal{U}_{R_i}(S(t), R(t)), \\ x'_i(t) &= x_i(t)(-D_i + \mathcal{G}_i(S(t), R(t))), \quad i = 1, 2, \end{aligned} \tag{3.1}$$

$$S(0) = S_o \geq 0, \quad R(0) = R_o \geq 0, \quad x_i(0) = x_{io} > 0, \quad i = 1, 2.$$

In these equations, $x_i(t)$ is the concentration of the i^{th} population of microorganisms in the culture vessel at time t , $i = 1, 2$, while $S(t)$ and $R(t)$ represent the concentrations of the two nonreproducing resources in the culture vessel at time t . If only one feed bottle is used, S^o (resp. R^o) is the concentration of resource S (resp.

R) in the feed bottle, while D is the input rate from the feed bottle to the culture vessel as well as the washout rate from the culture vessel to the receptacle. Thus constant volume is maintained. We assume that there is perfect mixing in the culture vessel so that nutrients, microorganisms and byproducts are removed in proportion to their concentrations. The constants D_i denote the rate at which species i is removed from competition; that is, $D_i = D + \epsilon_i$, $\epsilon_i \geq 0$, where ϵ_i is the intrinsic death rate of population i .

The experimenter may wish to use two separate feed bottles, each containing only one limiting resource, and input from each feed bottle to the culture vessel at different rates, say D_S and D_R . In this case, the constants D , S^0 and R^0 of (3.1) are maintained by taking $D = D_S + D_R$, $S^0 = \frac{S^o D_S}{D_S + D_R}$ and $R^0 = \frac{R^o D_R}{D_S + D_R}$ where S^o and R^o represent the concentrations of S and R in each separate feed bottle. Here, D still represents the dilution and washout rates.

The function $\mathcal{U}_{S_i}(S(t), R(t))$ represents the rate of consumption of resource S per unit of population i as a function of the concentrations of $S(t)$ and $R(t)$ in the culture vessel. It is generally assumed that

$$\mathcal{U}_{S_i} : \mathfrak{R}_+^2 \longrightarrow \mathfrak{R}_+, \quad (3.2a)$$

$$\mathcal{U}_{S_i} \text{ is continuously differentiable.} \quad (3.3a)$$

It is natural to expect that if the concentration of resource S in the culture vessel is zero, there will be no consumption of resource S ; that is,

$$\mathcal{U}_{S_i}(0, R) = 0 \text{ for all } R \geq 0. \quad (3.4a)$$

Similarly, the function $\mathcal{U}_{R_i}(S(t), R(t))$ represents the rate of consumption of resource R per unit of population i as a function of the concentrations of $S(t)$ and $R(t)$ in the culture vessel. It is assumed that

$$\mathcal{U}_{R_i} : \mathfrak{R}_+^2 \longrightarrow \mathfrak{R}_+, \quad (3.2b)$$

$$\mathcal{U}_{R_i} \text{ is continuously differentiable.} \quad (3.3b)$$

Again, if the concentration of resource R in the culture vessel is zero, it is natural to expect that there will be no consumption of resource R ; that is,

$$\mathcal{U}_{Ri}(S, 0) = 0 \text{ for all } S \geq 0. \quad (3.4b)$$

In focussing on the consumer-resource interactions, we wish to describe each species' functional response; that is, how the consumption rate of each species changes in response to fluctuations in resource concentrations. In this thesis we will assume that the rate of consumption of one resource is a strictly monotone increasing function of the concentration of that same resource. In the one resource case, the three most common examples of monotone functional response are Lotka-Volterra kinetics, in which the rate of consumption increases linearly (figure A.2), Michaelis-Menten kinetics, where the consumption rate increases nonlinearly, decelerating smoothly to a maximum, resulting in a function which is concave down (figure A.3), and multiple saturation in which the rate of consumption increases slowly at low concentrations, faster at higher concentrations and decelerates smoothly to a maximum, forming an S-shaped curve (figure A.4). These prototypes of monotone kinetics are also referred to as Holling Type I, II and III respectively.

The hypothesis that the rate of consumption of resource S in (3.1) is a strictly monotone increasing function of the concentration of resource S is reflected in the assumption that

$$\frac{\partial}{\partial S} \mathcal{U}_{Si}(S, R) > 0 \text{ for all } (S, R) \in \mathfrak{R}_+^2. \quad (3.5a)$$

Similarly, for the consumption rate of resource R ,

$$\frac{\partial}{\partial R} \mathcal{U}_{Ri}(S, R) > 0 \text{ for all } (S, R) \in \mathfrak{R}_+^2. \quad (3.5b)$$

The function $\mathcal{G}_i(S(t), R(t))$ represents the growth rate of the i^{th} competitor per unit of species i as a function of the concentrations of resources S and R in the culture vessel. Here we assume that population growth is proportional to the amount of nutrient consumed. Thus, as the concentration of resource S increases, there is an increase in the consumption of resource S , which causes a proportional increase in population growth. This is reflected in the assumption that

$$\frac{\partial}{\partial S} \mathcal{G}_i(S, R) > 0 \text{ for all } (S, R) \in \mathring{\mathfrak{R}}_+^2; \quad (3.6a)$$

that is, $\mathcal{G}_i(S, R)$ is an increasing function of the concentration of resource S . Similarly, as the concentration of resource R increases, consumption of resource R increases, resulting in a proportional increase in population growth so that

$$\frac{\partial}{\partial R} \mathcal{G}_i(S, R) > 0 \text{ for all } (S, R) \in \mathring{\mathfrak{R}}_+^2. \quad (3.6b)$$

An important consideration which arises in the two resource case is how the resources, once consumed, are utilized by the individual competitors for growth. Rapport [16] and León and Tumpson [12] classify resources in terms of consumer needs. This classification yields a spectrum of resource types, and hence a continuum of competitive situations. On opposite extremes are the perfectly complementary and perfectly substitutable resources.

3.2 Perfectly Complementary and Perfectly Substitutable Resources

Suppose an individual of a particular species x consumes $g_1(S)$ and $g_2(R)$ units of resources S and R respectively per unit time. If the per capita growth rate of the consumer is given by $\frac{x'}{x} = \phi(g_1, g_2)$, then the curve $\phi(g_1, g_2) = K$ projected onto the (g_1, g_2) plane is a curve along which any combination of values of g_1 and g_2 gives the same per capita rate of growth K . In accordance with Rapport, we will call these curves indifference curves. They will be used in the classification of resources S and R .

Perfectly complementary resources are substances which fulfill different essential needs in terms of growth, and so must be taken together by the consumer. For example, a nitrogen source and a carbon source might be perfectly complementary for a bacterium. These resources must be used in fixed proportions in order to maintain a given per capita rate of growth. If a higher growth rate is to be attained, it is necessary to increase the consumption rate of both resources. Thus, perfectly complementary resources are characterized by indifference curves forming rectangular corners (see figure A.5).

Perfectly substitutable resources are alternate sources of the same essential nutrient. An example for a bacterium would be two carbon sources or two nitrogen sources. In this case, the rates of consumption of the different resources can be substituted in a fixed ratio in order to maintain a given per capita rate of growth. A higher growth rate can be attained by increasing the rate of consumption of either resource. Thus, perfectly substitutable resources are characterized by linear indifference curves in the (g_1, g_2) plane (see figure A.6).

In the intermediate case we have imperfectly substitutable resources. The consumer could survive on either one but if they are taken together the per capita growth rate could increase. These resources are characterized by indifference curves which are convex to the origin. The degree of convexity indicates the extent to which alternate resources can be considered perfectly substitutable or perfectly complementary (see figure A.7).

In the next chapter we discuss system (3.1) under the assumption that resources S and R are perfectly complementary. We describe the corresponding functions $\mathcal{U}_{S_i}(S, R)$, $\mathcal{U}_{R_i}(S, R)$ and $\mathcal{G}_i(S, R)$ and summarize the known results.

Chapter 4

Complementary Resources

In this chapter we assume that resources S and R of system (3.1) are perfectly complementary for species i , $i = 1, 2$. Before indicating the form of the functions $\mathcal{U}_{S_i}(S, R)$, $\mathcal{U}_{R_i}(S, R)$ and $\mathcal{G}_i(S, R)$ in this case, it will be necessary to describe the functional response of each species when only one of the resources is limiting; that is, when the other resource is assumed to be in abundant supply.

Suppose that, for species i , resource S alone is limiting. Let $p_i(S)$ denote the rate of growth of the i^{th} competitor per unit of species i . Assuming population growth is proportional to the amount of nutrient consumed, let ξ_i be the growth yield constant. Then $\frac{p_i(S)}{\xi_i}$ represents the consumption rate of resource S per unit of the i^{th} species. Similarly, if R is the only limiting resource, let $q_i(R)$ denote the rate of growth of the i^{th} competitor per unit of species i . Then $\frac{q_i(R)}{\eta_i}$ represents the rate of consumption of resource R per unit of the i^{th} competitor where η_i is the corresponding growth yield constant. Here it is assumed that

$$p_i, q_i : \mathcal{R}_+ \longrightarrow \mathcal{R}_+, \quad (4.1)$$

$$p_i, q_i \text{ are continuously differentiable.} \quad (4.2)$$

As in section 3.1 we assume that

$$p_i(0) = 0 \text{ and } q_i(0) = 0, \quad (4.3)$$

$$p'_i(S) > 0 \text{ for all } S > 0 \text{ and } q'_i(R) > 0 \text{ for all } R > 0, \quad (4.4)$$

We now define the breakeven concentrations for resources S and R . To do so, we assume that nutrient S (respectively R) is the only limiting resource.

Suppose species i is limited by S alone and set $\frac{x'_i}{x_i} = -D_i + \mathcal{G}_i(S, 0) = 0$. By (3.6a), $\frac{\partial}{\partial S} \mathcal{G}_i(S, 0) > 0$ for all $S > 0$. Thus, this equation has a unique solution, denoted λ_i , provided we assume that $\lambda_i = \infty$ if $\mathcal{G}_i(S, 0) < D_i$ for all $S \geq 0$. Therefore λ_i is the concentration of S at which the concentration of population i in the culture vessel is neither increasing nor decreasing. Similarly, if species i is limited by resource R alone, define μ_i to be the concentration of R at which the concentration of population i in the culture vessel is neither increasing nor decreasing. Therefore,

$$\mathcal{G}_i(\lambda_i, 0) = D_i \text{ and } \mathcal{G}_i(0, \mu_i) = D_i.$$

We now return to the case of two limiting resources. Recall that since resources S and R are perfectly complementary, they must be used in fixed proportions by each competitor in order to maintain a given growth rate. For given concentrations of resources S and R , say (\bar{S}, \bar{R}) , in fact only one resource is limiting, the one which is in relatively short supply. The other resource, in comparison, can be thought of as being in abundant supply. Thus, if resource S is limiting at (\bar{S}, \bar{R}) then the growth rate is given by $\mathcal{G}_i(\bar{S}, \bar{R}) = p_i(\bar{S})$. The consumption rate of the limiting resource S is given by $\mathcal{U}_{S_i}(\bar{S}, \bar{R}) = \frac{p_i(\bar{S})}{\xi_i}$ while the rate of consumption of the nonlimiting resource R is exactly that consumption rate which is proportional to a growth rate of $p_i(\bar{S})$, that is, $\mathcal{U}_{R_i}(\bar{S}, \bar{R}) = \frac{p_i(\bar{S})}{\eta_i}$. Note that $\mathcal{U}_{R_i}(\bar{S}, \bar{R}) = \frac{\xi_i}{\eta_i} \mathcal{U}_{S_i}(\bar{S}, \bar{R})$. Similarly, if resource R is limiting at (\bar{S}, \bar{R}) then the growth rate is given by $\mathcal{G}_i(\bar{S}, \bar{R}) = q_i(\bar{R})$. The rate of consumption of R is now the consumption rate when resource S is in abundant supply, that is, $\mathcal{U}_{R_i}(\bar{S}, \bar{R}) = \frac{q_i(\bar{R})}{\eta_i}$. The rate of consumption of the nonlimiting resource S is exactly that consumption rate which is proportional to a growth rate of $q_i(\bar{R})$, that is, $\mathcal{U}_{S_i}(\bar{S}, \bar{R}) = \frac{q_i(\bar{R})}{\xi_i}$. Note that $\mathcal{U}_{S_i}(\bar{S}, \bar{R}) = \frac{\eta_i}{\xi_i} \mathcal{U}_{R_i}(\bar{S}, \bar{R})$. Hence the consumption rate of the limiting resource is exactly the rate of consumption when the other nutrient is in abundant supply. The rate of consumption of the nonlimiting resource is proportional,

the constant of proportionality being the ratio of the growth yield constants ξ_i and η_i .

Thus, if the resources are perfectly complementary, the growth rate is given by $\mathcal{G}_i(S, R) = \min\{p_i(S), q_i(R)\}$ and the rate of consumption of S is $\mathcal{U}_{S_i}(S, R) = \frac{\mathcal{G}_i(S, R)}{\xi_i}$ while the rate of consumption of R is $\mathcal{U}_{R_i}(S, R) = \frac{\mathcal{G}_i(S, R)}{\eta_i}$. Hence system (3.1) becomes

$$\begin{aligned} S'(t) &= (S^o - S(t))D - \sum_{i=1}^2 \frac{x_i(t)}{\xi_i} \mathcal{G}_i(S(t), R(t)), \\ R'(t) &= (R^o - R(t))D - \sum_{i=1}^2 \frac{x_i(t)}{\eta_i} \mathcal{G}_i(S(t), R(t)), \\ x'_i(t) &= x_i(t)(-D_i + \mathcal{G}_i(S(t), R(t))), \quad i = 1, 2, \\ S(0) &= S_o \geq 0, \quad R(0) = R_o \geq 0, \quad x_i(0) = x_{io} > 0, \end{aligned} \tag{4.5}$$

where $\mathcal{G}_i(S, R) = \min\{p_i(S), q_i(R)\}$.

This is precisely Model III of León and Tumpson [12] adapted to the chemostat. If $D_i = D$, $i = 1, 2$, that is, the death rate of each species is assumed to be negligible compared to the dilution rate, then (4.5) is precisely the model studied by Butler and Wolkowicz [2] in the noninhibitory kinetics case. If we further assume that the p_i 's and q_i 's satisfy Michaelis-Menten dynamics, this is the model studied by Hsu, Cheng and Hubbell [9]. The results of Butler et al. [2] will be summarized here for later comparison.

Recall that the uptake rate of the nonlimiting resource is proportional to and determined by the rate of consumption of the limiting resource, the constant of proportionality being the ratio of the growth yield constants. Thus,

$$C_i = \frac{\xi_i}{\eta_i}, \quad i = 1, 2$$

is the invariant ratio in which S and R are consumed. The ratio in which S and R are externally regenerated under steady-state consumption pressure from population i in the absence of its competitor is given by

$$T_i = \frac{R^o - \mu_i}{S^o - \lambda_i}, \quad i = 1, 2.$$

As explained by Hsu et al. [9], one can determine if population i , in the absence of its rival, is S -limited or R -limited by comparing T_i and C_i . If $T_i > C_i$ then resource S is regenerating at a steady state rate slower than R with respect to the required consumption ratio of population i and so species i is S -limited. However, if $T_i < C_i$ then R is regenerating at a steady state rate slower than S with respect to the required consumption ratio of species i so that population i is R -limited. The constants

$$T^* = \frac{R^o - \mu_2}{S^o - \lambda_1} \text{ and } T_* = \frac{R^o - \mu_1}{S^o - \lambda_2}$$

represent the ratio of the steady state regeneration rate of R when x_2 (resp. x_1) is alone and that of S when x_1 (resp. x_2) is alone.

In this setting Butler et al. [2] show that the dynamics are always trivial in the sense that both species asymptotically approach some equilibrium concentration. By varying the parameters, each of the outcomes of the classical theory for two species competition described in chapter 2 is possible. Competition independent extinction, an impossibility in the classical model, can also occur. The criteria that guarantee each outcome are summarized in table 4.1 below which is adapted from Butler et al. [2].

Table 4.1: Complementary Resources: Monotone Kinetics

BIOLOGICAL OUTCOME	COMPETITION CRITERIA
Both species become extinct. ((a) \Rightarrow species 1 is the sole survivor) ((b) \Rightarrow species 2 is the sole survivor)	(a) $\lambda_1 > S^o$ or $\mu_1 > R^o$ and (b) $\lambda_2 > S^o$ or $\mu_2 > R^o$
Population 1 is the sole survivor.	$\lambda_1 < S^o$ and $\mu_1 < R^o$ and $\lambda_1 < \lambda_2$ and $\mu_1 < \mu_2$ or $\lambda_1 < \lambda_2$, $\mu_1 > \mu_2$ and $T_* > C_1, C_2$ or $\lambda_1 > \lambda_2$, $\mu_1 < \mu_2$ and $T^* < C_1, C_2$ or $\lambda_2 > S^o$ or $\mu_2 > R^o$
Population 2 is the sole survivor.	$\lambda_2 < S^o$ and $\mu_2 < R^o$ and $\lambda_1 > \lambda_2$ and $\mu_1 > \mu_2$ or $\lambda_1 < \lambda_2$, $\mu_1 > \mu_2$ and $T_* < C_1, C_2$ or $\lambda_1 > \lambda_2$, $\mu_1 < \mu_2$ and $T^* > C_1, C_2$ or $\lambda_1 > S^o$ or $\mu_1 > R^o$

Table 4.1: continued...

Table 4.1: Complementary Resources: Monotone Kinetics

BIOLOGICAL OUTCOME	COMPETITION CRITERIA
Populations 1 and 2 coexist at a positive equilibrium.	$\lambda_i < S^o$ and $\mu_i < R^o$, $i = 1, 2$ and $\lambda_1 < \lambda_2$, $\mu_1 > \mu_2$ and $C_1 > T_* > C_2$ or $\lambda_1 > \lambda_2$, $\mu_1 < \mu_2$ and $C_1 < T^* < C_2$
One population wins and the other dies out. Initial concentrations determine the outcome.	$\lambda_i < S^o$ and $\mu_i < R^o$, $i = 1, 2$ and $\lambda_1 < \lambda_2$, $\mu_1 > \mu_2$ and $C_1 < T_* < C_2$ or $\lambda_1 > \lambda_2$, $\mu_1 < \mu_2$ and $C_1 > T^* > C_2$

Chapter 5

Substitutable Resources

5.1 The Model

For the remainder of our discussion we assume that resources S and R of system (3.1) are perfectly substitutable for species i , $i = 1, 2$. Note again that we assume population growth is proportional to the amount of nutrient consumed. Thus the consumption rate of resource S per unit of competitor i is of the form

$$u_{Si}(S, R) = \frac{\mathcal{S}_i(S, R)}{\xi_i}$$

where $\mathcal{S}_i(S, R)$ is the growth rate of competitor i per unit of the i^{th} species due to the consumption of resource S and ξ_i is the corresponding growth yield constant. Similarly, the rate of consumption of resource R per unit of the i^{th} species is of the form

$$u_{Ri}(S, R) = \frac{\mathcal{R}_i(S, R)}{\eta_i}$$

where $\mathcal{R}_i(S, R)$ is the growth rate of the i^{th} species per unit of competitor i due to consumption of resource R and η_i is the corresponding growth yield constant.

We now determine the properties of the functions $\mathcal{S}_i(S, R)$, $\mathcal{R}_i(S, R)$ and $\mathcal{G}_i(S, R)$ in the case of perfectly substitutable resources S and R . Recall that perfectly substitutable resources are alternate sources of the same essential nutrient. As such, the growth rate of species i is made up of a contribution from the consumption

of resource S as well as a contribution from the consumption of resource R . Therefore, $\mathcal{G}_i(S, R) = \mathcal{S}_i(S, R) + \mathcal{R}_i(S, R)$. Note that this is consistent with Rapport's graphical description of perfectly substitutable resources, as projections of the function $\frac{x'_i}{x_i} = \mathcal{G}_i(S, R) - D_i$ into the $(\mathcal{S}_i, \mathcal{R}_i)$ plane are indeed linear.

It should be noted that with two resources available, both serving the same requisite need, it remains necessary to determine how changes in the concentration of one resource affect the consumption rate of the other. Suppose that the consumption of one resource does not affect the consumption of the other. In particular, suppose the consumption of resource S is independent of the concentration of resource R and depends only on the concentration of resource S . Then $\mathcal{S}_i(S, R) = p_i(S)$ where $p_i(S)$ is the rate of growth of species i per unit of population i due to consumption of resource S in the absence of resource R . Similarly, if the consumption of resource R is unaffected by the concentration of resource S , $\mathcal{R}_i(S, R) = q_i(R)$. This situation, however, is unlikely. It is more natural to assume that the consumption of one resource inhibits the consumption of the other resource. In Holling terminology, the handling time devoted to the processing of a unit of one resource is time no longer available for the processing of the other resource. One would expect, therefore, that as the concentration, and hence consumption, of resource R increases, the consumption of resource S decreases. This is reflected in the assumption that

$$\frac{\partial}{\partial R} \mathcal{S}_i(S, R) \leq 0 \text{ for all } (S, R) \in \mathfrak{R}_+^2.$$

Similarly, as the concentration, and hence consumption, of resource S increases, the consumption of resource R decreases; that is

$$\frac{\partial}{\partial S} \mathcal{R}_i(S, R) \leq 0 \text{ for all } (S, R) \in \mathfrak{R}_+^2.$$

We now specify system (3.1) in the case that resources S and R are perfectly substitutable, summarizing the assumptions made in section 3.1 for the purposes of self-containment. The model that will be considered is

$$\begin{aligned}
S'(t) &= (S^o - S(t))D - \sum_{i=1}^2 \frac{x_i(t)}{\xi_i} \mathcal{S}_i(S(t), R(t)), \\
R'(t) &= (R^o - R(t))D - \sum_{i=1}^2 \frac{x_i(t)}{\eta_i} \mathcal{R}_i(S(t), R(t)), \\
x'_i(t) &= x_i(t)(-D_i + \mathcal{G}_i(S(t), R(t))), \quad i = 1, 2,
\end{aligned} \tag{5.1}$$

$$S(0) = S_o \geq 0, \quad R(0) = R_o \geq 0, \quad x_i(0) = x_{io} > 0, \quad i = 1, 2,$$

where $\mathcal{G}_i(S(t), R(t)) = \mathcal{S}_i(S(t), R(t)) + \mathcal{R}_i(S(t), R(t))$. Here it is assumed that

$$\mathcal{S}_i, \mathcal{R}_i : \mathfrak{R}_+^2 \longrightarrow \mathfrak{R}_+, \tag{5.2}$$

$$\mathcal{S}_i, \mathcal{R}_i \text{ are continuously differentiable,} \tag{5.3}$$

$$\mathcal{S}_i(0, R) = 0 \text{ for all } R \geq 0 \tag{5.4}$$

$$\mathcal{R}_i(S, 0) = 0 \text{ for all } S \geq 0$$

That is, if one of the nutrients is absent, there is no consumption of that nutrient. Also,

$$\frac{\partial}{\partial S} \mathcal{S}_i(S, R) > 0 \text{ and } \frac{\partial}{\partial R} \mathcal{R}_i(S, R) > 0 \text{ for all } (S, R) \in \mathfrak{R}_+^2, \tag{5.5}$$

so that the rate of consumption of one resource is a strictly monotone increasing function of the concentration of that same resource. Moreover,

$$\frac{\partial}{\partial R} \mathcal{S}_i(S, R) \leq 0 \text{ and } \frac{\partial}{\partial S} \mathcal{R}_i(S, R) \leq 0 \text{ for all } (S, R) \in \mathfrak{R}_+^2. \tag{5.6}$$

That is, the consumption of one resource may inhibit the consumption of the other.

We define

$$\mathcal{S}_i(S, 0) = p_i(S) \text{ for all } S \geq 0, \tag{5.7}$$

$$\mathcal{R}_i(0, R) = q_i(R) \text{ for all } R \geq 0.$$

That is, $p_i(S)$ is the function describing the uptake of nutrient S in the absence of nutrient R . Similarly, $q_i(R)$ is the function describing the uptake of nutrient R in the absence of nutrient S .

Concerning the growth rate $\mathcal{G}_i(S, R) = \mathcal{S}_i(S, R) + \mathcal{R}_i(S, R)$ we assume

$$\frac{\partial}{\partial S}\mathcal{G}_i(S, R) > 0 \text{ and } \frac{\partial}{\partial R}\mathcal{G}_i(S, R) > 0 \text{ for all } (S, R) \in \mathfrak{R}_+^2. \quad (5.8)$$

Thus the growth rate of the i^{th} competitor is a strictly monotone increasing function of the concentration of each resource.

The breakeven concentrations for resources S and R are as defined in chapter 4; that is

$$\mathcal{G}_i(\lambda_i, 0) = p_i(\lambda_i) = D_i \text{ and } \mathcal{G}_i(0, \mu_i) = q_i(\mu_i) = D_i \quad (5.9)$$

By (5.8) and the Implicit Function Theorem (B1), there exists $\varphi_i \in C^1$ such that $\mathcal{G}_i(S, \varphi_i(S)) = D_i$ for all $0 < S < \lambda_i$ with $\varphi_i'(S) < 0$ for $0 < S < \lambda_i$. Also, by (5.9) and continuity, we define $\varphi_i(0) = \mu_i$ and $\varphi_i(\lambda_i) = 0$. Thus, φ_i is the subsistence curve in the (S, R) -plane giving the concentrations of S and R at which the concentration of population i in the culture vessel is neither increasing nor decreasing.

If $\mathcal{S}_i(S, R) = p_i(S)$ for all $R \geq 0$ and $\mathcal{R}_i(S, R) = q_i(R)$ for all $S \geq 0$, so that the consumption of each resource is unaffected by the consumption of the other, then model (5.1) reduces to Model I of León and Tumpson [12], adapted to the chemostat. Under the assumption of the existence of an interior equilibrium they show, by means of a linear analysis, that *the competitors coexist if at equilibrium each of them removes at a higher rate that resource which contributes more to its own rate of growth*. From our earlier discussion it follows that model (5.1) is more realistic than that of León and Tumpson [12], as it incorporates the possible inhibitory effects that the consumption of one resource has on the consumption of the other. Hsu, Hubbell and Waltman [21] give an example of uptake functions satisfying (5.2) through (5.9). There the functions $\mathcal{S}_i(S, R)$ and $\mathcal{R}_i(S, R)$ are given by

$$\frac{\mathcal{S}_i(S, R)}{\xi_i} = \frac{m_{S_i} S}{K_{S_i} \left(1 + \frac{S}{K_{S_i}} + \frac{R}{K_{R_i}}\right) \xi_i}$$

and

$$\frac{\mathcal{R}_i(S, R)}{\eta_i} = \frac{m_{R_i} R}{K_{R_i} \left(1 + \frac{S}{K_{S_i}} + \frac{R}{K_{R_i}}\right) \eta_i}$$

so that

$$\mathcal{G}_i(S, R) = \frac{\frac{m_{S_i}}{K_{S_i}} S + \frac{m_{R_i}}{K_{R_i}} R}{1 + \frac{S}{K_{S_i}} + \frac{R}{K_{R_i}}}.$$

Clearly this is a generalization of the familiar Michaelis-Menten prototype of functional response to a single resource.

5.2 The Scaled Version: Some Preliminary Results

Suppose that both S^o and R^o of (5.1) are zero. Then

$$S(t) \leq S(0)e^{-Dt} \text{ and } R(t) \leq R(0)e^{-Dt}.$$

Therefore, for t sufficiently large, system (5.1) behaves like

$$\begin{aligned} S'(t) &= 0, \\ R'(t) &= 0, \\ x'_i(t) &= -D_i x_i(t), \quad i = 1, 2, \end{aligned}$$

$$S(0) = 0, \quad R(0) = 0, \quad x_i(0) > 0, \quad i = 1, 2,$$

with solution

$$S(t) \equiv 0, \quad R(t) \equiv 0, \quad x_i(t) = x_i(0)e^{-D_i t}, \quad i = 1, 2.$$

That is, neither species survives.

If only one of S^o or R^o is zero, say $S^o = 0$ and $R^o \neq 0$, then, from (5.1),

$$S'(t) = -S(t)D - \sum_{i=1}^2 \frac{x_i(t)}{\xi_i} \mathcal{S}_i(S(t), R(t)) \leq -S(t)D.$$

This implies

$$S(t) \leq S(0)e^{-Dt}.$$

Therefore, for t sufficiently large, system (5.1) is approximated by

$$\begin{aligned} S'(t) &= 0, \\ R'(t) &= (R^o - R(t))D - \sum_{i=1}^2 \frac{x_i(t)}{\eta_i} q_i(R(t)), \\ x'_i(t) &= x_i(t)(-D_i + q_i(R(t))), \quad i = 1, 2, \end{aligned}$$

$$S(0) = 0, \quad R(0) = R_o \geq 0, \quad x_i(0) = x_{io} > 0, \quad i = 1, 2.$$

This is the model of exploitative competition in the chemostat for one limiting resource. If $D_i = D$ for $i = 1, 2$, we obtain the model studied by Butler and Wolkowicz [1] in the case of monotone kinetics. Under the further assumption that q_i assumes the form of Michaelis-Menten kinetics, we obtain the model examined by Hsu, Hubbell and Waltman [10] while Hsu [8] extended these results to the case of distinct D_i 's. For our purposes, we assume that neither S^o nor R^o is zero.

It will be more convenient to analyze the model after the following substitutions are performed:

$$\begin{aligned}\bar{t} &= tD, \quad \bar{S} = \frac{S}{S^o}, \quad \bar{R} = \frac{R}{R^o}, \\ \bar{\mathcal{S}}_i(\bar{S}, \bar{R}) &= \frac{\mathcal{S}_i(S, R)}{D}, \quad \bar{\mathcal{R}}_i(\bar{S}, \bar{R}) = \frac{\mathcal{R}_i(S, R)}{D}, \\ \bar{D}_i &= \frac{D_i}{D}, \quad \bar{\xi}_i = S^o \xi_i, \quad \bar{\eta}_i = R^o \eta_i.\end{aligned}\tag{5.10}$$

Note that by (5.10), $\bar{D} = 1$, $\bar{S}^o = 1$ and $\bar{D}_i = \frac{D_i + \epsilon_i}{D} = 1 + \bar{\epsilon}_i$. Removing the bars to simplify notation we obtain

$$\begin{aligned}S'(t) &= 1 - S(t) - \sum_{i=1}^2 \frac{x_i(t)}{\xi_i} \mathcal{S}_i(S(t), R(t)), \\ R'(t) &= 1 - R(t) - \sum_{i=1}^2 \frac{x_i(t)}{\eta_i} \mathcal{R}_i(S(t), R(t)), \\ x_i'(t) &= x_i(t)(-D_i + \mathcal{G}_i(S(t), R(t))), \quad i = 1, 2,\end{aligned}\tag{5.11}$$

$$S(0) = S_o \geq 0, \quad R(0) = R_o \geq 0, \quad x_i(0) = x_{io} > 0, \quad i = 1, 2.$$

All of assumptions (5.2) through (5.9) hold for this version of the model so there will be no loss of generality if we study (5.11) instead of (5.1). All of our results can be reinterpreted in terms of the unscaled variables using (5.10).

We first show that all solutions of (5.11) are positive and bounded. These are minimum requirements for a reasonable model of the chemostat.

Theorem 5.1 *All solutions $S(t), R(t), x_i(t), i = 1, 2$, of (5.11) are (a) positive and (b) bounded for $t > 0$.*

Proof of (a): Consider first $x_i(t), i = 1, 2$. From (5.11)

$$\frac{x_i'(t)}{x_i(t)} = -D_i + \mathcal{G}_i(S(t), R(t))$$

which implies

$$x_i(t) = x_i(0) \exp\left\{\int_0^t (-D_i + \mathcal{G}_i(S(\tau), R(\tau))) d\tau\right\} > 0.$$

Next consider $S(t)$. If $S(0) = 0$ then $S'(0) = 1 > 0$. Suppose there exists a first $T > 0$ with $S(T) = 0$; that is, $S(t) > 0$ for $0 < t < T$ and $S(T) = 0$. Then $S'(T) \leq 0$. However, by (5.11), $S'(T) = 1 > 0$, a contradiction.

Proof of (b): In general, define

$$z(t) = S(t) + R(t) + \frac{x_1(t)}{\max\{\xi_1, \eta_1\}} + \frac{x_2(t)}{\max\{\xi_2, \eta_2\}}.$$

For convenience, assume that $\xi_i \geq \eta_i$ for $i = 1, 2$ and consider

$$z(t) = S(t) + R(t) + \frac{x_1(t)}{\xi_1} + \frac{x_2(t)}{\xi_2}.$$

From (5.11) we have

$$\begin{aligned} z'(t) &= 2 - (S(t) + R(t)) - \sum_{i=1}^2 \frac{x_i(t)D_i}{\xi_i} + \sum_{i=1}^2 x_i(t)\mathcal{R}_i(S(t), R(t))\left(\frac{1}{\xi_i} - \frac{1}{\eta_i}\right) \\ &\leq 2 - (S(t) + R(t)) - \frac{x_1(t)D_1}{\xi_1} - \frac{x_2(t)D_2}{\xi_2} \end{aligned}$$

since $(\frac{1}{\xi_i} - \frac{1}{\eta_i}) \leq 0, i = 1, 2$. Also, since $D_i = 1 + \epsilon_i, \epsilon_i \geq 0, i = 1, 2$,

$$z'(t) \leq 2 - (S(t) + R(t)) - \frac{x_1(t)(1 + \epsilon_1)}{\xi_1} - \frac{x_2(t)(1 + \epsilon_2)}{\xi_2}.$$

Thus,

$$\begin{aligned} z'(t) &\leq 2 - (S(t) + R(t)) + \frac{x_1(t)}{\xi_1} + \frac{x_2(t)}{\xi_2} \\ &= 2 - z(t). \end{aligned}$$

This is a differential inequality for $z(t)$ with solution given by

$$z(t) \leq 2 + (z(0) - 2)e^{-t}.$$

Thus

$$S(t) + R(t) + \frac{x_1(t)}{\xi_1} + \frac{x_2(t)}{\xi_2} \leq 2 + (S(0) + R(0) + \frac{x_1(0)}{\xi_1} + \frac{x_2(0)}{\xi_2} - 2)e^{-t}$$

and so

$$S(t) + R(t) + \frac{x_1(t)}{\xi_1} + \frac{x_2(t)}{\xi_2} \leq \begin{cases} 2 & \text{if } S(0) + R(0) + \frac{x_1(0)}{\xi_1} + \frac{x_2(0)}{\xi_2} < 2, \\ S(0) + R(0) + \frac{x_1(0)}{\xi_1} + \frac{x_2(0)}{\xi_2} & \text{otherwise.} \end{cases}$$

Hence by (a) all solutions of (5.11) are bounded.

Proposition 5.1 *Given any $\delta > 0$, for all solutions $S(t)$, $R(t)$ of (5.11), $S(t) < 1 + \delta$ and $R(t) < 1 + \delta$ for all sufficiently large t .*

Proof: Consider $S(t)$. From (5.11)

$$S'(t) = 1 - S(t) - \sum_{i=1}^2 \frac{x_i(t)}{\xi_i} \mathcal{S}_i(S(t), R(t)) < 1 - S(t)$$

which implies

$$S(t) \leq 1 + (S(0) - 1)e^{-t}.$$

Proposition 5.2 *If there exists a $t_o \geq 0$ such that $S(t_o) < 1$ then $S(t) < 1$ for all $t \geq t_o$. A similar result holds for $R(t)$.*

Proof: Suppose there exists a first $T > t_o$ such that $S(T) = 1$ and $S(t) < 1$ for $t_o \leq t < T$. Then $S'(T) \geq 0$. However, by (5.11),

$$S'(T) = - \sum_{i=1}^2 \frac{x_i(T)}{\xi_i} \mathcal{S}_i(S(T), R(T)) < 0,$$

a contradiction.

In the next result we will use the following lemma due to Miller [14].

Lemma 5.1 Let $\omega(t) \in C^2(t_0, \infty)$, $\omega(t) \geq 0$ and $K > 0$.

(i) If $\omega'(t) \geq 0$, $\omega(t)$ is bounded and $\omega''(t) \leq K$ for all $t \geq t_0$ then $\omega'(t) \rightarrow 0$ as $t \rightarrow \infty$.

(ii) If $\omega'(t) \leq 0$, and $\omega''(t) \geq -K > -\infty$ for all $t \geq t_0$ then $\omega'(t) \rightarrow 0$ as $t \rightarrow \infty$.

Theorem 5.2 If $\mathcal{G}_i(1,1) < D_i$ for $i = 1, 2$ then E_0 is globally asymptotically stable for (5.11).

Proof: Suppose $S(t) > 1$ for all $t \geq 0$. Then $S'(t) < 0$ for all $t \geq 0$ which implies that $S(t) \searrow S^* \geq 1$ as $t \rightarrow \infty$. If $S^* > 1$ Then

$$S'(t) \leq 1 - S \leq 1 - S^*$$

which implies

$$S(t) \leq (1 - S^*)t + S(0) \rightarrow -\infty \text{ as } t \rightarrow \infty,$$

contradicting $S(t) > 1$ for all $t \geq 0$. Therefore $S(t) \searrow 1$ as $t \rightarrow \infty$. Similarly, if $R(t) > 1$ for all $t \geq 0$ then $R(t) \searrow 1$ as $t \rightarrow \infty$. By Proposition 5.2, if $S(\bar{t}) < 1$ for some $\bar{t} \geq 0$ then $S(t) < 1$ for all $t \geq \bar{t}$ and similarly if $R(\tilde{t}) < 1$ for some $\tilde{t} \geq 0$ then $R(t) < 1$ for all $t \geq \tilde{t}$. By the continuity of \mathcal{G}_i , there exists a $\delta > 0$ such that

$$\mathcal{G}_i(1 + \delta, 1 + \delta) < D_i.$$

From the above there exists a $T > 0$ such that

$$S(t) < 1 + \delta \text{ for all } t \geq T,$$

$$R(t) < 1 + \delta \text{ for all } t \geq T.$$

Then $x'_i(t) < 0$ for all $t \geq T$, which implies by the above lemma that $x'_i(t) \rightarrow 0$ as $t \rightarrow \infty$. However,

$$\limsup_{t \rightarrow \infty} \mathcal{G}_i(S(t), R(t)) \leq \mathcal{G}_i(1 + \delta, 1 + \delta) < D_i$$

and so $x_i(t) \rightarrow 0$ as $t \rightarrow \infty$. Let $Q \in \{(S, R, x_1, x_2) \in \mathfrak{R}_+^4 : x_1 > 0, x_2 > 0\}$. We have shown that for any $P = (\underline{S}, \underline{R}, \underline{x}_1, \underline{x}_2) \in \Omega(Q)$, $\underline{x}_1 = 0$ and $\underline{x}_2 = 0$, where

$\Omega(Q)$ denotes the omega limit set of the orbit through Q . On $\{(S, R, 0, 0) \in \mathfrak{R}_+^4\}$ the system reduces to

$$S'(t) = 1 - S$$

$$R'(t) = 1 - R$$

and hence $S(t) \rightarrow 1$, $R(t) \rightarrow 1$ so that $\{E_o\} \in \Omega(Q)$. Since E_o is locally asymptotically stable (see section 5.4), $\Omega(Q) = \{E_o\}$. Therefore, if $\mathcal{G}_i(1, 1) < D_i$ for $i = 1, 2$ then E_o is globally asymptotically stable for (5.11).

In the next section we examine the three dimensional subsystems of (5.11).

5.3 The Three Dimensional Subsystems

There are only two three dimensional subsystems of (5.11) of interest. Each involves one population of microorganisms consuming the two nonreproducing substitutable resources. Due to symmetry, both subsystems exhibit the same dynamics. To ascertain these dynamics, we examine the system

$$\begin{aligned}
 S'(t) &= 1 - S(t) - \frac{x(t)}{\xi} \mathcal{S}(S(t), R(t)), \\
 R'(t) &= 1 - R(t) - \frac{x(t)}{\eta} \mathcal{R}(S(t), R(t)), \\
 x'(t) &= x(t)(-d + \mathcal{G}(S(t), R(t))), \\
 S(0) &= S_o \geq 0, \quad R(0) = R_o \geq 0, \quad x(0) = x_o > 0,
 \end{aligned} \tag{5.12}$$

where the subscripts have been removed to simplify notation. Here, d still represents the rate of removal of the microbial population, that is, $d = 1 + \epsilon$, $\epsilon \geq 0$, where ϵ is the intrinsic death rate. The functions $\mathcal{S}(S(t), R(t))$, $\mathcal{R}(S(t), R(t))$ and $\mathcal{G}(S(t), R(t))$ are assumed to satisfy all of the assumptions (5.2) through (5.9). We first note

Proposition 5.3 *All solutions $S(t)$, $R(t)$, $x(t)$ of (5.12) are (a) positive and (b) bounded for $t > 0$.*

Proof: The method of proof is similar to that of Proposition 5.1. For (b), consider $z(t) = \xi S(t) + \eta R(t) + x(t)$.

Note that $E_o = (1, 1, 0)$ is a critical point of (5.12). If any other critical points exist, they must be interior equilibria, that is, equilibria in which S, R and x are all positive. An interior equilibrium of (5.12) is a solution $(\bar{S}, \bar{R}, \bar{x})$ of the system

$$\begin{aligned}
 x\mathcal{S}(S, R) &= \xi(1 - S) \\
 x\mathcal{R}(S, R) &= \eta(1 - R) \\
 \mathcal{G}(S, R) &= d
 \end{aligned} \tag{5.13}$$

with $(\bar{S}, \bar{R}, \bar{x}) \in \mathfrak{R}_+^3$. By (5.9) and the positivity constraint on \bar{x} , $0 < \bar{S} < \min\{1, \lambda\}$ and $0 < \bar{R} < \min\{1, \mu\}$.

Theorem 5.3 *There exists an interior equilibrium of (5.12) if and only if $\mathcal{G}(1, 1) > d$ and if one exists then it is unique.*

Proof: If there exists an interior equilibrium $(\bar{S}, \bar{R}, \bar{x})$ then $\mathcal{G}(\bar{S}, \bar{R}) = d$. But $0 < \bar{S} < 1$ and $0 < \bar{R} < 1$ and \mathcal{G} is an increasing function of both arguments, so $\mathcal{G}(1, 1) > d$.

To show the converse, suppose $\mathcal{G}(1, 1) > d$. Define

$$x_S(S) = \frac{\xi(1-S)}{\mathcal{S}(S, \varphi(S))} \text{ and } x_R(S) = \frac{\eta(1-\varphi(S))}{\mathcal{R}(S, \varphi(S))} \text{ for } S \in (0, \lambda).$$

Note that

$$\frac{d}{dS} x_S(S) = -\xi \frac{\mathcal{S}(S, \varphi(S)) + (1-S)(\frac{\partial}{\partial S} \mathcal{S}(S, \varphi(S)) + \frac{\partial}{\partial R} \mathcal{S}(S, \varphi(S))\varphi'(S))}{(\mathcal{S}(S, \varphi(S)))^2} < 0$$

for $S \leq 1$, while

$$\frac{d}{dS} x_R(S) = -\eta \frac{\mathcal{R}(S, \varphi(S))\varphi'(S) + (1-\varphi(S))(\frac{\partial}{\partial S} \mathcal{R}(S, \varphi(S)) + \frac{\partial}{\partial R} \mathcal{R}(S, \varphi(S))\varphi'(S))}{(\mathcal{R}(S, \varphi(S)))^2} < 0$$

for $\varphi(S) \leq 1$. Therefore $x_S(S)$ is an increasing function of S while $x_R(S)$ is a decreasing function of S . It suffices to show that $x_S(S)$ and $x_R(S)$ intersect on $(0, \lambda)$.

Case 1: $\lambda \leq 1$ and $\mu \leq 1$. In this case, we necessarily have $\mathcal{G}(1, 1) > d$. Now,

$$\lim_{S \rightarrow 0^+} x_S(S) = \lim_{S \rightarrow 0^+} \frac{\xi(1-S)}{\mathcal{S}(S, \varphi(S))} = \infty \text{ and } x_R(0) = \frac{\eta(1-\mu)}{d},$$

$$x_S(\lambda) = \frac{\xi(1-\lambda)}{d} \text{ and } \lim_{S \rightarrow \lambda^-} x_R(S) = \lim_{S \rightarrow \lambda^-} \frac{\eta(1-\varphi(S))}{\mathcal{R}(S, \varphi(S))} = \infty.$$

Therefore there exists a unique $\hat{S} \in (0, \lambda)$ such that $x_S(\hat{S}) = x_R(\hat{S})$ (see figure A.8) and hence a unique interior equilibrium.

Case 2: $\lambda > 1$ and $\mu > 1$. Here we use the assumption that $\mathcal{G}(1, 1) > d$. Since $\mathcal{G}(0, 1) < d$, there exists a unique $\tilde{S} \in (0, 1)$ such that $\mathcal{G}(\tilde{S}, 0) = d$ ($\varphi(\tilde{S}) = 1$). Since $\mathcal{G}(1, 0) < d$, there exists a unique $\tilde{R} \in (0, 1)$ such that $\mathcal{G}(1, \tilde{R}) = d$ ($\varphi(1) = \tilde{R}$). Now,

$$x_S(\tilde{S}) = \frac{\xi(1-\tilde{S})}{\mathcal{S}(\tilde{S}, 1)} > 0 \text{ and } x_R(\tilde{S}) = 0,$$

$$x_S(1) = 0 \text{ and } x_R(1) = \frac{\eta(1 - \tilde{R})}{\mathcal{R}(1, \tilde{R})} > 0.$$

Therefore there exists a unique $\hat{S} \in (\tilde{S}, 1)$ such that $x_S(\hat{S}) = x_R(\hat{S})$ (see figure A.9) and hence a unique interior equilibrium.

Case 3: $\lambda \geq 1$ and $\mu \leq 1$. Again, in this case, we necessarily have $\mathcal{G}(1, 1) > d$. Since $\mathcal{G}(1, \mu) > d$ and $\mathcal{G}(1, 0) < d$ there exists a unique $\tilde{R} \in (0, \mu)$ such that $\mathcal{G}(1, \tilde{R}) = d$ ($\varphi(1) = \tilde{R}$). Now,

$$\lim_{S \rightarrow 0^+} x_S(S) = \lim_{S \rightarrow 0^+} \frac{\xi(1 - S)}{\mathcal{S}(S, \varphi(S))} = \infty \text{ and } x_R(0) = \frac{\eta(1 - \mu)}{d},$$

$$x_S(1) = 0 \text{ and } x_R(1) = \frac{\eta(1 - \tilde{R})}{\mathcal{R}(1, \tilde{R})} = \infty \text{ if } \lambda = 1.$$

Therefore there exists a unique $\hat{S} \in (0, 1)$ such that $x_S(\hat{S}) = x_R(\hat{S})$ (see figure A.10) and hence a unique interior equilibrium.

Case 4: $\lambda \leq 1$ and $\mu \leq 1$. In this case, it again follows that $\mathcal{G}(1, 1) > d$. Since $\mathcal{G}(\lambda, 1) > d$ and $\mathcal{G}(0, 1) < d$, there exists a unique $\tilde{S} \in (0, \lambda)$ such that $\mathcal{G}(\tilde{S}, 1) = d$ ($\varphi(\tilde{S}) = 1$). Now,

$$x_S(\tilde{S}) = \frac{\xi(1 - \tilde{S})}{\mathcal{S}(\tilde{S}, 1)} \text{ and } x_R(\tilde{S}) = 0,$$

$$x_S(\lambda) = \frac{\xi(1 - \lambda)}{d} \text{ and } \lim_{S \rightarrow \lambda^-} x_R(S) = \lim_{S \rightarrow \lambda^-} \frac{\eta(1 - \varphi(S))}{\mathcal{R}(S, \varphi(S))} = \infty.$$

Therefore, there exists a unique $\hat{S} \in (\tilde{S}, \lambda)$ such that $x_S(\hat{S}) = x_R(\hat{S})$ (see figure A.11) and hence a unique interior equilibrium.

As the above exhausts all possible cases for the relative values of λ and μ , we have the existence of an interior equilibrium for (5.12) when $\mathcal{G}(1, 1) > d$ and when one exists it is unique.

Let us denote the interior equilibrium, when it exists, by $E = (\bar{S}, \bar{R}, \bar{x})$. Next we investigate the local stability properties of the equilibria.

The variational matrix of (5.12), denoted $V_3(S, R, x)$, is given by

$$V_3(S, R, x) = \begin{pmatrix} -1 - \frac{x}{\xi} \frac{\partial}{\partial S} \mathcal{S}(S, R) & -\frac{x}{\xi} \frac{\partial}{\partial R} \mathcal{S}(S, R) & -\frac{1}{\xi} \mathcal{S}(S, R) \\ -\frac{x}{\eta} \frac{\partial}{\partial S} \mathcal{R}(S, R) & 1 - \frac{x}{\eta} \frac{\partial}{\partial R} \mathcal{R}(S, R) & -\frac{1}{\eta} \mathcal{R}(S, R) \\ x \frac{\partial}{\partial S} \mathcal{G}(S, R) & x \frac{\partial}{\partial R} \mathcal{G}(S, R) & -d + \mathcal{G}(S, R) \end{pmatrix}$$

At E_o we have

$$V_3(1, 1, 0) = \begin{pmatrix} -1 & 0 & -\mathcal{S}(1, 1)/\xi \\ 0 & -1 & -\mathcal{R}(1, 1)/\eta \\ 0 & 0 & -d + \mathcal{G}(1, 1) \end{pmatrix}$$

with eigenvalues $\alpha_1 = \alpha_2 = -1$ and $\alpha_3 = \mathcal{G}(1, 1) - d$. Thus E_o is a locally asymptotically stable critical point if no interior equilibrium exists, that is, $\mathcal{G}(1, 1) \leq d$, and E_o is unstable if an interior equilibrium exists, that is, $\mathcal{G}(1, 1) > d$.

Let us assume that the interior equilibrium $E = (\bar{S}, \bar{R}, \bar{x})$ exists and examine the local stability properties of E . At E we have

$$V_3(\bar{S}, \bar{R}, \bar{x}) = \begin{pmatrix} -1 - \frac{\bar{x}}{\xi} \frac{\partial}{\partial S} \mathcal{S}(\bar{S}, \bar{R}) & -\frac{\bar{x}}{\xi} \frac{\partial}{\partial R} \mathcal{S}(\bar{S}, \bar{R}) & -\frac{1}{\xi} \mathcal{S}(\bar{S}, \bar{R}) \\ -\frac{\bar{x}}{\eta} \frac{\partial}{\partial S} \mathcal{R}(\bar{S}, \bar{R}) & -1 - \frac{\bar{x}}{\eta} \frac{\partial}{\partial R} \mathcal{R}(\bar{S}, \bar{R}) & -\frac{1}{\eta} \mathcal{R}(\bar{S}, \bar{R}) \\ \bar{x} \frac{\partial}{\partial S} \mathcal{G}(\bar{S}, \bar{R}) & \bar{x} \frac{\partial}{\partial R} \mathcal{G}(\bar{S}, \bar{R}) & 0 \end{pmatrix}$$

with characteristic equation $\alpha^3 + A\alpha^2 + B\alpha + C$, where

$$A = 2 + \bar{x} \left(\frac{1}{\xi} \frac{\partial}{\partial S} \mathcal{S}(\bar{S}, \bar{R}) + \frac{1}{\eta} \frac{\partial}{\partial R} \mathcal{R}(\bar{S}, \bar{R}) \right) \quad (5.14a)$$

$$\begin{aligned}
B &= 1 + \bar{x}\left(\frac{1}{\xi}\frac{\partial}{\partial \bar{S}}\mathcal{S}(\bar{S}, \bar{R}) + \frac{1}{\eta}\frac{\partial}{\partial \bar{R}}\mathcal{R}(\bar{S}, \bar{R})\right) \\
&\quad + \bar{x}\left(\frac{1}{\xi}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial \bar{S}}\mathcal{G}(\bar{S}, \bar{R}) + \frac{1}{\eta}\mathcal{R}(\bar{S}, \bar{R})\frac{\partial}{\partial \bar{R}}\mathcal{G}(\bar{S}, \bar{R})\right) \\
&\quad + \frac{\bar{x}^2}{\xi\eta}\left(\frac{\partial}{\partial \bar{S}}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial \bar{R}}\mathcal{R}(\bar{S}, \bar{R}) - \frac{\partial}{\partial \bar{R}}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial \bar{S}}\mathcal{R}(\bar{S}, \bar{R})\right)
\end{aligned} \tag{5.14b}$$

$$\begin{aligned}
C &= \bar{x}\left(\frac{1}{\xi}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial \bar{S}}\mathcal{G}(\bar{S}, \bar{R}) + \frac{1}{\eta}\mathcal{R}(\bar{S}, \bar{R})\frac{\partial}{\partial \bar{R}}\mathcal{G}(\bar{S}, \bar{R})\right) \\
&\quad + \frac{\bar{x}^2}{\xi\eta}d\left(\frac{\partial}{\partial \bar{S}}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial \bar{R}}\mathcal{R}(\bar{S}, \bar{R}) - \frac{\partial}{\partial \bar{R}}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial \bar{S}}\mathcal{R}(\bar{S}, \bar{R})\right)
\end{aligned} \tag{5.14c}$$

By (5.2) through (5.8) it follows that A, B and C are all positive so that, by the Routh-Hurwitz Criterion (B2), to determine the stability of E it remains only to determine the sign of $AB - C$ where $AB - C$ is given by

$$\begin{aligned}
&2 + 3\bar{x}\left(\frac{1}{\xi}\frac{\partial}{\partial \bar{S}}\mathcal{S}(\bar{S}, \bar{R}) + \frac{1}{\eta}\frac{\partial}{\partial \bar{R}}\mathcal{R}(\bar{S}, \bar{R})\right) \\
&\quad + \bar{x}\left\{\frac{1}{\xi}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial \bar{S}}\mathcal{G}(\bar{S}, \bar{R}) + \frac{1}{\eta}\mathcal{R}(\bar{S}, \bar{R})\frac{\partial}{\partial \bar{R}}\mathcal{G}(\bar{S}, \bar{R})\right\} \\
&\quad + \bar{x}^2\left(\frac{1}{\xi}\frac{\partial}{\partial \bar{S}}\mathcal{S}(\bar{S}, \bar{R}) + \frac{1}{\eta}\frac{\partial}{\partial \bar{R}}\mathcal{R}(\bar{S}, \bar{R})\right)^2 \\
&\quad + \bar{x}^2\left(\frac{1}{\xi}\frac{\partial}{\partial \bar{S}}\mathcal{S}(\bar{S}, \bar{R}) + \frac{1}{\eta}\frac{\partial}{\partial \bar{R}}\mathcal{R}(\bar{S}, \bar{R})\right)\left(\frac{1}{\xi}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial \bar{S}}\mathcal{G}(\bar{S}, \bar{R}) + \frac{1}{\eta}\mathcal{R}(\bar{S}, \bar{R})\frac{\partial}{\partial \bar{R}}\mathcal{G}(\bar{S}, \bar{R})\right) \\
&\quad + \frac{\bar{x}^3}{\xi\eta}\frac{\partial}{\partial \bar{S}}\mathcal{S}(\bar{S}, \bar{R})\left(\frac{\partial}{\partial \bar{S}}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial \bar{R}}\mathcal{R}(\bar{S}, \bar{R}) - \frac{\partial}{\partial \bar{R}}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial \bar{S}}\mathcal{R}(\bar{S}, \bar{R})\right) \\
&\quad + \frac{\bar{x}^3}{\xi\eta}\frac{\partial}{\partial \bar{R}}\mathcal{R}(\bar{S}, \bar{R})\left(\frac{\partial}{\partial \bar{S}}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial \bar{R}}\mathcal{R}(\bar{S}, \bar{R}) - \frac{\partial}{\partial \bar{R}}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial \bar{S}}\mathcal{R}(\bar{S}, \bar{R})\right) \\
&\quad + \frac{\bar{x}^2}{\xi\eta}(2 - d)\left(\frac{\partial}{\partial \bar{S}}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial \bar{R}}\mathcal{R}(\bar{S}, \bar{R}) - \frac{\partial}{\partial \bar{R}}\mathcal{S}(\bar{S}, \bar{R})\frac{\partial}{\partial \bar{S}}\mathcal{R}(\bar{S}, \bar{R})\right)
\end{aligned} \tag{5.15}$$

A superficial examination of this expression yields a range of values of the intrinsic death rate ϵ for which $AB - C$ is positive and hence E is locally asymptotically stable. In particular, $d \leq 2$ (so that $\epsilon \leq 1$) is a sufficient condition for the local asymptotic stability of E . Moreover, by Lemma 5.1, below, if E can lose its stability, it can do so only by means of a Hopf bifurcation.

Lemma 5.1 *Given $p(\alpha) = \alpha^3 + A\alpha^2 + B\alpha + C$ with A, B and C positive, if $AB - C < 0$ then p has complex conjugate roots.*

Proof: Suppose p has three real roots, say θ, β and γ . By our hypothesis

$$A = -(\theta + \beta + \gamma) > 0$$

$$B = \theta\beta + \beta\gamma + \theta\gamma > 0$$

$$C = -\theta\beta\gamma > 0$$

Note that $C > 0$ implies that either all or exactly one of θ , β and γ is negative. But, by the Routh-Hurwitz Criterion (B2), $AB - C < 0$ rules out θ , β and γ all being negative. Suppose only γ is negative. A positive implies $-\gamma > \theta + \beta$ so that $-\gamma(\theta + \beta) > (\theta + \beta)^2$. B positive implies $\theta\beta > -\gamma(\theta + \beta)$. Hence $\theta\beta > -\gamma(\theta + \beta) > (\theta + \beta)^2$ which implies $0 > \theta^2 + \theta\beta + \beta^2$, a contradiction. Therefore p must have complex roots.

Since E exists only if $\mathcal{G}(1, 1) > d$, a Hopf bifurcation and hence a change in stability can only occur for $2 < d < \mathcal{G}(1, 1)$. Therefore if $\mathcal{G}(1, 1) > 2$ then no change in stability can occur. Although we have not ruled out the possibility of a Hopf bifurcation, this was not observed in any of the specific examples we studied.

For example, if we assume that $\mathcal{S}(S, R) = p(S)$ for all $R \geq 0$ and $\mathcal{R}(S, R) = q(R)$ for all $S \geq 0$, as long as E exists, it is locally asymptotically stable. In this case,

$$\begin{aligned} A &= 2 + \bar{x} \left(\frac{p'(\bar{S})}{\xi} + \frac{q'(\bar{R})}{\eta} \right), \\ B &= 1 + \bar{x} \left(\frac{p'(\bar{S})}{\xi} + \frac{q'(\bar{R})}{\eta} \right) + \bar{x} \left(\frac{p(\bar{S})p'(\bar{S})}{\xi} + \frac{q(\bar{R})q'(\bar{R})}{\eta} \right) + \frac{p'(\bar{S})q'(\bar{R})}{\xi\eta}, \\ C &= \bar{x} \left(\frac{p(\bar{S})p'(\bar{S})}{\xi} + \frac{q(\bar{R})q'(\bar{R})}{\eta} \right) + d\bar{x}^2 \frac{p'(\bar{S})q'(\bar{R})}{\xi\eta}. \end{aligned} \quad (5.16)$$

After replacing d by $p(\bar{S}) + q(\bar{R})$ and arranging $AB - C$ in increasing powers of \bar{x} , $AB - C$ is given by

$$\left\{ \begin{aligned} &2 + \bar{x} \left\{ 3 \left(\frac{p'(\bar{S})}{\xi} + \frac{q'(\bar{R})}{\eta} \right) + \frac{p(\bar{S})p'(\bar{S})}{\xi} + \frac{q(\bar{R})q'(\bar{R})}{\eta} \right\} + \bar{x}^2 \frac{2}{\xi\eta} p'(\bar{S})q'(\bar{R}) \\ &+ \bar{x}^2 \left\{ \left(\frac{p'(\bar{S})}{\xi} + \frac{q'(\bar{R})}{\eta} \right)^2 + p(\bar{S}) \left(\frac{p'(\bar{S})}{\xi} \right)^2 + q(\bar{R}) \left(\frac{q'(\bar{R})}{\eta} \right)^2 \right\} \\ &+ \bar{x}^3 \left(\frac{p'(\bar{S})}{\xi} + \frac{q'(\bar{R})}{\eta} \right) p'(\bar{S})q'(\bar{R}). \end{aligned} \right. \quad (5.17)$$

Clearly, $AB - C$ is positive and so, by the Routh-Hurwitz Criterion (B2), E is a locally asymptotically stable critical point, independent of the value of d .

We now turn to an examination of the global properties of (5.12).

Theorem 5.4 *Suppose $\mathcal{G}(1,1) > d$. Then system (5.12) is persistent (B3) with respect to all solutions for which $x(0) > 0$.*

Proof: Identify (S, R, x) -space with \mathfrak{R}_+^3 . Suppose for some solution $(S(t), R(t), x(t))$ of (5.12), $x(t) = 0$ for some $t > 0$. Then $x(t) \equiv 0$ since

$$x(t) = x(0)\exp\left\{\int_0^t (-d + \mathcal{G}(S(\tau), R(\tau)))d\tau\right\}.$$

In this case, system (5.12) reduces to

$$\begin{aligned} S'(t) &= 1 - S, \\ R'(t) &= 1 - R, \\ x'(t) &= 0, \end{aligned}$$

$$S(0) \geq 0, R(0) \geq 0, x(0) = 0.$$

This system has solution $S(t) = (S(0) - 1)e^{-t} + 1$, $R(t) = (R(0) - 1)e^{-t} + 1$, $x(t) \equiv 0$. Thus E_o is globally attracting with respect to solutions initiating in the set $\mathcal{J} = \{(S, R, 0) \in \mathfrak{R}_+^3\}$.

Choose $\underline{X} \in \mathfrak{R}_+^3$. By Proposition 5.3, $\Omega(\underline{X})$ is a nonempty, compact, invariant set with respect to (5.12). Suppose $\{E_o\} \in \Omega(\underline{X})$. Let $M^+(E_o)$ denote the stable manifold of E_o . Since $\mathcal{G}(1,1) > d$, E_o is unstable and therefore $\dim(M^+(E_o)) < 3$. Since $M^+(E_o) \supset \mathcal{J}$, $\dim(M^+(E_o)) \geq 2$. Therefore, $M^+(E_o) = \mathcal{J}$, and hence does not intersect \mathfrak{R}_+^3 . This implies that $\{E_o\} \neq \Omega(\underline{X})$. Therefore, by the Butler-McGehee Lemma (B4), there exists $P \in M^+(E_o)$ such that $P \in \Omega(\underline{X}) \setminus \{E_o\}$ and hence $cl\mathcal{O}(P) \subset \Omega(\underline{X})$ where $\mathcal{O}(P)$ denotes the entire orbit through P . However, since E_o is globally attracting, either $\mathcal{O}(P)$ becomes unbounded as or one of the S or R components becomes negative as $t \rightarrow -\infty$. In either case we have a contradiction and therefore $\{E_o\} \notin \Omega(\underline{X})$.

Since $x(t)$ is bounded by Theorem 5.1, $S'(t) > 0$ if $S(t)$ is sufficiently close to zero and $R'(t) > 0$ if $R(t)$ is sufficiently close to zero. It follows that any point in $\Omega(\underline{X})$ must satisfy $\underline{S} > 0$ and $\underline{R} > 0$. Suppose (5.12) is not persistent. Then

there exists a point $\tilde{P} \in \Omega(\underline{X})$ such that $\tilde{P} \in \mathcal{J}$ and hence $cl\mathcal{O}(\tilde{P}) \subset \Omega(\underline{X})$. But $\{E_o\} \in cl\mathcal{O}(\tilde{P})$ since E_o is globally attracting with respect to all solutions initiating in the set \mathcal{J} . This implies that $\{E_o\} \in \Omega(\underline{X})$, a contradiction. Therefore (5.12) is persistent.

If the functions $\mathcal{S}(S, R)$ and $\mathcal{R}(S, R)$ are assumed to be of the form studied by León and Tumpson [12], the above result can be significantly improved.

Theorem 5.5 *Assume $\mathcal{S}(S, R) = p(S)$ for all $R \geq 0$ and $\mathcal{R}(S, R) = q(R)$ for all $S \geq 0$.*

(a) *If $\mathcal{G}(1, 1) \leq d$ then E_o is globally asymptotically stable for (5.12) with respect to all solutions for which $S(0) \geq 0$, $R(0) \geq 0$ and $x(0) \geq 0$.*

(b) *If $\mathcal{G}(1, 1) > d$ then there exists a unique interior equilibrium E which is globally asymptotically stable for (5.12) with respect to all solutions for which $S(0) \geq 0$, $R(0) \geq 0$ and $x(0) > 0$.*

Proof of (a): Define $L : \mathfrak{R}_+^3 \rightarrow \mathfrak{R}$ by

$$L(S, R, x) = \xi \int_1^S \frac{-p(1) + p(\tau)}{p(\tau)} d\tau + \eta \int_1^R \frac{-q(1) + q(\tau)}{q(\tau)} d\tau + x$$

Since $p(S)$ and $q(R)$ are continuous on \mathfrak{R}_+^3 we have $L \in C^1(\mathfrak{R}_+^3)$. Also, $E_o = (1, 1, 0)$ is the global minimum of L on \mathfrak{R}_+^3 and $L(1, 1, 0) = 0$. To see this, consider $g(S) = S - 1 - p(1) \int_1^S \frac{d\tau}{p(\tau)}$. Then $g'(S) = (p(S) - p(1))/p(S) = 0$ if and only if $S = 1$ and $g''(S) = p'(S)p(1)/(p(S)^2)$ where $g''(1) = p'(1)/p(1) > 0$ by (5.5). The time derivative of L computed along solutions of (5.12) is

$$\begin{aligned} \dot{L}(S, R, x) &= \xi \left(\frac{p(S) - p(1)}{p(S)} \right) \cdot S' + \eta \left(\frac{q(R) - q(1)}{q(R)} \right) \cdot R' + x' \\ &= \xi \left(\frac{p(S) - p(1)}{p(S)} \right) \left(1 - S - \frac{xp(S)}{\xi} \right) \\ &\quad + \eta \left(\frac{q(R) - q(1)}{q(R)} \right) \left(1 - R - \frac{xq(R)}{\eta} \right) \\ &\quad + x(-d + \mathcal{G}(S, R)) \end{aligned}$$

$$\begin{aligned}
 &= \xi\left(\frac{p(S) - p(1)}{p(S)}\right)(1 - S) + \eta\left(\frac{q(R) - q(1)}{q(R)}\right)(1 - R) \\
 &\quad + x(-d + \mathcal{G}(S, R) - (p(S) - p(1)) - (q(R) - q(1))) \\
 &= \xi\left(\frac{p(S) - p(1)}{p(S)}\right)(1 - S) + \eta\left(\frac{q(R) - q(1)}{q(R)}\right)(1 - R) \\
 &\quad + x(\mathcal{G}(S, R) - d)
 \end{aligned}$$

Note that for $0 < S < 1$, $p(S) - p(1) < 0$ and if $S > 1$ $p(S) - p(1) > 0$. Therefore, since $\mathcal{G}(S, R) \leq d$, $\dot{L}(S, R, x) \leq 0$. If $\mathcal{G}(1, 1) < d$ then $\dot{L}(S, R, x) = 0$ if and only if $S = 1$, $R = 1$ and $x = 0$ and if $\mathcal{G}(1, 1) = d$ then $\dot{L}(S, R, x) = 0$ if and only if $S = 1$ and $R = 1$. In either case, L is a Lyapunov function (B5) for (5.12) in $\mathring{\mathfrak{R}}_+^3$. By Proposition 5.3 and LaSalle's Extension Theorem (B6) every solution of (5.12) for which $x(0) > 0$ approaches \mathcal{M} where \mathcal{M} is the largest invariant subset of $\mathcal{N} = \{(S, R, x) \in \mathring{\mathfrak{R}}_+^3 : \dot{L}(S, R, x) = 0\}$. If $\mathcal{G}(1, 1) < d$ then $\mathcal{N} = \{E_o\}$ and $\mathcal{M} = \{E_o\}$. If $\mathcal{G}(1, 1) = d$ then $\mathcal{N} = \{(S, R, x) \in \mathring{\mathfrak{R}}_+^3 : S = 1, R = 1, x \geq 0\}$. However, $S = 1$ and $R = 1$ imply $x = 0$ since, by (5.12), $S' = 0$ and $R' = 0$, and we again have $\mathcal{M} = \{E_o\}$.

Hence, if $\mathcal{S}(S, R) = p(S)$ for all $R \geq 0$, $\mathcal{R}(S, R) = q(R)$ for all $S \geq 0$ and $\mathcal{G}(1, 1) \leq d$, then E_o is globally asymptotically stable for (5.12) with respect to all solutions for which $S(0) \geq 0$, $R(0) \geq 0$ and $x(0) \geq 0$.

Proof of (b): The existence and uniqueness of the interior equilibrium E is guaranteed by Theorem 5.3. To prove the global stability of this equilibrium, define $L : \mathring{\mathfrak{R}}_+^3 \rightarrow \mathfrak{R}$ by

$$L(S, R, x) = \xi \int_S^{\bar{S}} \frac{-p(\bar{S}) + p(\tau)}{p(\tau)} d\tau + \eta \int_R^{\bar{R}} \frac{-q(\bar{R}) + q(\tau)}{q(\tau)} d\tau + x - \bar{x} - \bar{x} \ln\left(\frac{x}{\bar{x}}\right)$$

Since $p(S)$ and $q(R)$ are continuous on $\mathring{\mathfrak{R}}_+^3$ we have $L \in C^1(\mathring{\mathfrak{R}}_+^3)$. Also, $E = (\bar{S}, \bar{R}, \bar{x})$ is the global minimum of L on $\mathring{\mathfrak{R}}_+^3$ and $L(\bar{S}, \bar{R}, \bar{x}) = 0$. To see this, consider $g(S) = S - \bar{S} - p(\bar{S}) \int_{\bar{S}}^S \frac{d\tau}{p(\tau)}$. Then $g'(S) = (p(S) - p(\bar{S}))/p(S) = 0$ if and only if $S = \bar{S}$ and $g''(S) = p'(S)p(\bar{S})/(p(S)^2)$ where $g''(\bar{S}) = p'(\bar{S})/p(\bar{S}) > 0$ by (5.5). The time derivative of L computed along solutions of (5.12) is

$$\begin{aligned}
\dot{L}(S, R, x) &= \xi\left(\frac{p(S) - p(\bar{S})}{p(S)}\right) \cdot S' + \eta\left(\frac{q(R) - q(\bar{R})}{q(R)}\right) \cdot R' + \left(\frac{x - \bar{x}}{x}\right) \cdot x' \\
&= \xi\left(\frac{p(S) - p(\bar{S})}{p(S)}\right)\left(1 - S - \frac{xp(S)}{\xi}\right) \\
&\quad + \eta\left(\frac{q(R) - q(\bar{R})}{q(R)}\right)\left(1 - R - \frac{xq(R)}{\eta}\right) \\
&\quad + \left(\frac{x - \bar{x}}{x}\right)x(-d + \mathcal{G}(S, R)) \\
&= \xi\left(\frac{p(S) - p(\bar{S})}{p(S)}\right)(1 - S) + \eta\left(\frac{q(R) - q(\bar{R})}{q(R)}\right)(1 - R) \\
&\quad - \bar{x}(-d + \mathcal{G}(S, R)) \\
&\quad + x(-d + \mathcal{G}(S, R) - (p(S) - p(\bar{S})) - (q(R) - q(\bar{R})))
\end{aligned}$$

Noting that $\bar{x} = \frac{\xi(1-\bar{S})}{p(\bar{S})} = \frac{\eta(1-\bar{R})}{q(\bar{R})}$ and $d = p(\bar{S}) + q(\bar{R})$, we have

$$\begin{aligned}
\dot{L}(S, R, x) &= \xi(p(S) - p(\bar{S})) \left(\frac{1-S}{p(S)} - \frac{1-\bar{S}}{p(\bar{S})} \right) \\
&\quad + \eta(q(R) - q(\bar{R})) \left(\frac{1-R}{q(R)} - \frac{1-\bar{R}}{q(\bar{R})} \right)
\end{aligned}$$

For $0 < S < \bar{S}$, $p(S) - p(\bar{S}) < 0$ and $\frac{1-S}{p(S)} - \frac{1-\bar{S}}{p(\bar{S})} > 0$ while for $S > \bar{S}$, $p(S) - p(\bar{S}) > 0$ and $\frac{1-S}{p(S)} - \frac{1-\bar{S}}{p(\bar{S})} < 0$. A similar result holds for R .

Thus, $\dot{L}(S, R, x) \leq 0$ and $\dot{L}(S, R, x) = 0$ if and only if $S = \bar{S}$ and $R = \bar{R}$ so that L is a Lyapunov function (B5) for (5.12) in \mathfrak{R}_+^3 . Hence, by Proposition 5.3 and LaSalle's Extension Theorem (B6) every solution of (5.12) for which $x(0) > 0$ approaches \mathcal{M} where \mathcal{M} is the largest invariant subset of $\{(S, R, x) \in \mathfrak{R}_+^3 : S = \bar{S}, R = \bar{R}, x > 0\}$. But then $\mathcal{M} = \{E\}$ as $S = \bar{S}$ and $R = \bar{R}$ imply that $x = \bar{x}$ since by (5.12) $x' = 0$ and by Theorem 5.3 the interior equilibrium is unique.

Hence, if $\mathcal{S}(R, S) = p(S)$ for all $R \geq 0$, $\mathcal{R}(S, R) = q(R)$ for all $S \geq 0$ and $\mathcal{G}(1, 1) > d$, there exists a unique interior equilibrium which is globally asymptotically stable for (5.12) with respect to all solutions for which $S(0) \geq 0$, $R(0) \geq 0$ and $x(0) > 0$.

In the next section we will use the information gathered here to ascertain existence and local stability properties of equilibria in the four dimensional system.

5.4 The Four Dimensional System

We now return to a study of the four dimensional system given in section 5.2; that is

$$\begin{aligned}
 S'(t) &= 1 - S(t) - \sum_{i=1}^2 \frac{x_i(t)}{\xi_i} \mathcal{S}_i(S(t), R(t)) \\
 R'(t) &= 1 - R(t) - \sum_{i=1}^2 \frac{x_i(t)}{\eta_i} \mathcal{R}_i(S(t), R(t)) \\
 x_i'(t) &= x_i(t)(-D_i + \mathcal{G}_i(S(t), R(t))), i = 1, 2
 \end{aligned} \tag{5.18}$$

$$S(0) = S_o \geq 0, R(0) = R_o \geq 0, x_i(0) = x_{io} > 0, i = 1, 2.$$

Three of the critical points of (5.18) are readily determined and will be denoted

$$E_o = (1, 1, 0, 0)$$

$$E_1 = (\bar{S}_1, \bar{R}_1, \bar{x}_1, 0)$$

$$E_2 = (\bar{S}_2, \bar{R}_2, 0, \bar{x}_2)$$

where by Theorem 5.3, an equilibrium of the form E_1 exists and is unique if and only if $\mathcal{G}_1(1, 1) > D_1$ and an equilibrium of the form E_2 exists and is unique if and only if $\mathcal{G}_2(1, 1) > D_2$. If any other critical points exist they must be interior equilibria in which S, R, x_1 and x_2 are all positive. An interior equilibrium of (5.18) is a solution (S^*, R^*, x_1^*, x_2^*) of the system

$$\begin{cases} \mathcal{G}_1(S, R) = D_1 \\ \mathcal{G}_2(S, R) = D_2 \end{cases} \tag{5.19a}$$

$$\begin{cases} \frac{x_1}{\xi_1} \mathcal{S}_1(S, R) + \frac{x_2}{\xi_2} \mathcal{S}_2(S, R) = 1 - S \\ \frac{x_1}{\eta_1} \mathcal{R}_1(S, R) + \frac{x_2}{\eta_2} \mathcal{R}_2(S, R) = 1 - R \end{cases} \tag{5.19b}$$

with $(S^*, R^*, x_1^*, x_2^*) \in \mathfrak{R}_+^4$ where by (5.9) and the positivity constraint on x_1^* and x_2^* , $0 < S^* < \min\{1, \lambda_1, \lambda_2\}$ and $0 < R^* < \min\{1, \mu_1, \mu_2\}$. We first examine system (5.19a), noting that it is independent of the values of x_1 and x_2 .

Theorem 5.6 *Suppose there exist $S_1, S_2 < \min\{1, \lambda_1, \lambda_2\}$, $S_1 \neq S_2$, such that either*

$$(a) \mathcal{G}_1(S_2, \varphi_2(S_2)) < D_1 \text{ and } \mathcal{G}_2(S_1, \varphi_1(S_1)) < D_2 \text{ or}$$

$$(b) \mathcal{G}_1(S_2, \varphi_2(S_2)) > D_1 \text{ and } \mathcal{G}_2(S_1, \varphi_1(S_1)) > D_2.$$

Then there exists a solution (S^, R^*) of (5.19a).*

Proof of (a): Recall that in section 5.1 we define $\varphi_i(S)$ such that $\mathcal{G}_i(S, \varphi_i(S)) = D_i$ for $0 < S < \lambda_i$. Under the hypotheses of the theorem, $\varphi_1(S_2) > \varphi_2(S_2)$ and $\varphi_2(S_1) > \varphi_1(S_1)$ since \mathcal{G}_i is an increasing function of its arguments. Without loss of generality, assume $S_1 < S_2$ and define $\psi(S) = \varphi_1(S) - \varphi_2(S)$ on $I = [S_1, S_2]$. Then ψ is continuous on I . Also,

$$\psi(S_1) = \varphi_1(S_1) - \varphi_2(S_1) < 0$$

$$\psi(S_2) = \varphi_1(S_2) - \varphi_2(S_2) > 0$$

Therefore, there exists $S^* \in \overset{\circ}{I}$ such that $\psi(S^*) = \varphi_1(S^*) - \varphi_2(S^*) = 0$, that is, $\mathcal{G}_1(S^*, R^*) = D_1$ and $\mathcal{G}_2(S^*, R^*) = D_2$ where $R^* = \varphi_1(S^*) = \varphi_2(S^*)$ (see figure A.12) so that we have a solution to (5.19a).

Proof of (b): Similar to part (a).

We will now examine system (5.19b), restricting our attention to $0 < S < \min\{1, \lambda_1, \lambda_2\}$ and $0 < R < \min\{1, \mu_1, \mu_2\}$. Define

$$\Delta(S, R) = \frac{S_1(S, R)}{\xi_1} \frac{\mathcal{R}_2(S, R)}{\eta_2} - \frac{S_2(S, R)}{\xi_2} \frac{\mathcal{R}_1(S, R)}{\eta_1}. \quad (5.20)$$

Then, from (5.19b), using Cramer's Rule it follows that

$$x_1 = \frac{\frac{1}{\eta_2} \mathcal{R}_2(S, R)(1 - S) - \frac{1}{\xi_2} S_2(S, R)(1 - R)}{\Delta(S, R)},$$

$$x_2 = \frac{\frac{1}{\xi_1} S_1(S, R)(1 - R) - \frac{1}{\eta_1} \mathcal{R}_1(S, R)(1 - S)}{\Delta(S, R)}. \quad (5.21)$$

As a solution with both x_1 and x_2 positive is required, we will first determine when this is possible. Suppose the numerators of both x_1 and x_2 are positive. Then

$$\frac{\mathcal{R}_2(S, R)}{\eta_2}(1 - S) > \frac{\mathcal{S}_2(S, R)}{\xi_2}(1 - R) \text{ and } \frac{\mathcal{S}_1(S, R)}{\xi_1}(1 - R) > \frac{\mathcal{R}_1(S, R)}{\eta_1}(1 - S).$$

Therefore, after rearranging,

$$\frac{\xi_2}{\mathcal{S}_2(S, R)} \frac{\mathcal{R}_2(S, R)}{\eta_2} > \frac{1 - R}{1 - S} \text{ and } \frac{1 - R}{1 - S} > \frac{\xi_1}{\mathcal{S}_1(S, R)} \frac{\mathcal{R}_1(S, R)}{\eta_1}$$

so that

$$\frac{\xi_2}{\mathcal{S}_2(S, R)} \frac{\mathcal{R}_2(S, R)}{\eta_2} > \frac{\xi_1}{\mathcal{S}_1(S, R)} \frac{\mathcal{R}_1(S, R)}{\eta_1},$$

that is,

$$\Delta(S, R) > 0.$$

Therefore, if the numerators of x_1 and x_2 are positive, both x_1 and x_2 are positive. Similarly, if the numerators of x_1 and x_2 are negative, then $\Delta(S, R) < 0$; that is, both x_1 and x_2 are positive. We have therefore proved the following result.

Theorem 5.7 *Let (x_1^*, x_2^*) be a solution of (5.19b). Then $x_1^* > 0$ and $x_2^* > 0$ if and only if the numerators of x_1^* and x_2^* as given in (5.21) are of the same sign.*

It remains to determine under what conditions this is possible, keeping in mind that we actually seek a solution to (5.19). Define

$$\mathcal{N}x_1(S) = \frac{\mathcal{R}_2(S, \varphi_2(S))}{\eta_2}(1 - S) - \frac{\mathcal{S}_2(S, \varphi_2(S))}{\xi_2}(1 - \varphi_2(S))$$

$$\mathcal{N}x_2(S) = \frac{\mathcal{S}_1(S, \varphi_1(S))}{\xi_1}(1 - \varphi_1(S)) - \frac{\mathcal{R}_1(S, \varphi_1(S))}{\eta_1}(1 - S)$$

$\mathcal{N}x_i(S)$ is the numerator of $x_i(S)$ as given in (5.21) with R replaced by $\varphi_j(S)$ where $i, j = 1, 2$ and $i \neq j$. Recall that at $E_2 = (\bar{S}_2, \bar{R}_2, 0, \bar{x}_2)$,

$$\bar{x}_2 = \frac{\xi_2(1 - \bar{S}_2)}{\mathcal{S}_2(\bar{S}_2, \varphi_2(\bar{S}_2))} = \frac{\eta_2(1 - \varphi_2(\bar{S}_2))}{\mathcal{R}_2(\bar{S}_2, \varphi_2(\bar{S}_2))}.$$

Therefore

$$\frac{\mathcal{R}_2(\bar{S}_2, \varphi_2(\bar{S}_2))}{\eta_2} (1 - \varphi_2(\bar{S}_2)) - \frac{\mathcal{S}_2(\bar{S}_2, \varphi_2(\bar{S}_2))}{\xi_2} (1 - \bar{S}_2) = \mathcal{N}x_1(\bar{S}_2) = 0.$$

By (5.9), $\varphi_2(\lambda_2) = 0$ and $\varphi_2(0) = \mu_2$ so that, by (5.4),

$$\mathcal{N}x_1(\lambda_2) = -\frac{D_2}{\xi_2} \text{ and } \mathcal{N}x_1(0) = \frac{D_2}{\eta_2}.$$

Also, at $E_1 = (\bar{S}_1, \bar{R}_1, \bar{x}_1, 0)$,

$$\bar{x}_1 = \frac{\xi_1(1 - \bar{S}_1)}{\mathcal{S}_1(\bar{S}_1, \varphi_1(\bar{S}_1))} = \frac{\eta_1(1 - \varphi_1(\bar{S}_1))}{\mathcal{R}_1(\bar{S}_1, \varphi_1(\bar{S}_1))}$$

and so, similarly

$$\mathcal{N}x_2(0) = -\frac{D_1}{\eta_1}, \mathcal{N}x_2(\bar{S}_1) = 0 \text{ and } \mathcal{N}x_2(\lambda_1) = \frac{D_1}{\xi_1}.$$

Moreover,

$$\begin{aligned} \frac{d}{dS} \mathcal{N}x_1(S) &= \frac{(1-S)}{\eta_2} \left\{ \frac{\partial}{\partial S} \mathcal{R}_2(S, \varphi_2(S)) + \frac{\partial}{\partial R} \mathcal{R}_2(S, \varphi_2(S)) \varphi_2'(S) \right\} \\ &\quad - \frac{(1-\varphi_2(S))}{\xi_2} \left\{ \frac{\partial}{\partial S} \mathcal{S}_2(S, \varphi_2(S)) + \frac{\partial}{\partial R} \mathcal{S}_2(S, \varphi_2(S)) \varphi_2'(S) \right\} \\ &\quad - \frac{\mathcal{R}_2(S, \varphi_2(S))}{\eta_2} + \varphi_2'(S) \frac{\mathcal{S}_2(S, \varphi_2(S))}{\xi_2}, \end{aligned}$$

and

$$\begin{aligned} \frac{d}{dS} \mathcal{N}x_2(S) &= \frac{(1-\varphi_1(S))}{\xi_1} \left\{ \frac{\partial}{\partial S} \mathcal{S}_1(S, \varphi_1(S)) + \frac{\partial}{\partial R} \mathcal{S}_1(S, \varphi_1(S)) \varphi_1'(S) \right\} \\ &\quad - \frac{(1-S)}{\eta_1} \left\{ \frac{\partial}{\partial S} \mathcal{R}_1(S, \varphi_1(S)) + \frac{\partial}{\partial R} \mathcal{R}_1(S, \varphi_1(S)) \varphi_1'(S) \right\} \\ &\quad - \varphi_1'(S) \frac{\mathcal{S}_1(S, \varphi_1(S))}{\xi_1} + \frac{\mathcal{R}_1(S, \varphi_1(S))}{\eta_1}. \end{aligned}$$

By (5.5) and (5.6) it follows that $\frac{d}{dS} \mathcal{N}x_1(S) < 0$ and $\frac{d}{dS} \mathcal{N}x_2(S) > 0$ provided $0 < S < 1$ and $0 < \varphi_1(S), \varphi_2(S) < 1$. See figure A.13. Note that if $\bar{S}_1 < \bar{S}_2$ then $\mathcal{N}x_1(S)$ and $\mathcal{N}x_2(S)$ are positive for all $\bar{S}_1 < S < \bar{S}_2$ and if $\bar{S}_2 < \bar{S}_1$ then $\mathcal{N}x_1$ and $\mathcal{N}x_2$ are negative for all $\bar{S}_2 < S < \bar{S}_1$.

Combining this with Theorem 5.7 we obtain the next result.

Theorem 5.8 *Suppose there exists a solution (S^*, R^*) of (5.19a). Then the corresponding solution (x_1^*, x_2^*) of (5.19b) satisfies $x_1^* > 0$ and $x_2^* > 0$ if and only if $\min\{\bar{S}_1, \bar{S}_2\} < S^* < \max\{\bar{S}_1, \bar{S}_2\}$.*

We now determine the local stability properties of the equilibria of (5.18) through an examination of the linearized system about each equilibrium point. The variational matrix, which will be denoted $V_4(S, R, x_1, x_2)$, is given by

$$\begin{pmatrix} -1 - \sum_{i=1}^2 \frac{x_i}{\xi_i} \frac{\partial}{\partial S} \mathcal{S}_i(S, R) & -\sum_{i=1}^2 \frac{x_i}{\xi_i} \frac{\partial}{\partial R} \mathcal{S}_i(S, R) & -\frac{\mathcal{S}_1(S, R)}{\xi_1} & -\frac{\mathcal{S}_2(S, R)}{\xi_2} \\ -\sum_{i=1}^2 \frac{x_i}{\eta_i} \frac{\partial}{\partial S} \mathcal{R}_i(S, R) & -1 - \sum_{i=1}^2 \frac{x_i}{\eta_i} \frac{\partial}{\partial R} \mathcal{R}_i(S, R) & -\frac{\mathcal{R}_1(S, R)}{\eta_1} & -\frac{\mathcal{R}_2(S, R)}{\eta_2} \\ x_1 \frac{\partial}{\partial S} \mathcal{G}_1(S, R) & x_1 \frac{\partial}{\partial R} \mathcal{G}_1(S, R) & -D_1 + \mathcal{G}_1(S, R) & 0 \\ x_2 \frac{\partial}{\partial S} \mathcal{G}_2(S, R) & x_2 \frac{\partial}{\partial R} \mathcal{G}_2(S, R) & 0 & -D_2 + \mathcal{G}_2(S, R) \end{pmatrix}$$

The variational matrix evaluated at E_o is

$$V_4(E_o) = \begin{pmatrix} -1 & 0 & -\mathcal{S}_1(1, 1)/\xi_1 & -\mathcal{S}_2(1, 1)/\xi_2 \\ 0 & -1 & -\mathcal{R}_1(1, 1)/\eta_1 & -\mathcal{R}_2(1, 1)/\eta_2 \\ 0 & 0 & -D_1 + \mathcal{G}_1(1, 1) & 0 \\ 0 & 0 & 0 & -D_2 + \mathcal{G}_2(1, 1) \end{pmatrix}$$

with eigenvalues $\alpha_1 = \alpha_2 = -1$, $\alpha_3 = \mathcal{G}_1(1, 1) - D_1$ and $\alpha_4 = \mathcal{G}_2(1, 1) - D_2$. Thus, E_o is a locally asymptotically stable critical point if $\mathcal{G}_1(1, 1) < D_1$ and $\mathcal{G}_2(1, 1) < D_2$, that is, if neither E_1 nor E_2 exist. The critical point E_o is unstable if either $\mathcal{G}_1(1, 1) > D_1$ or $\mathcal{G}_2(1, 1) > D_2$, that is, if either E_1 or E_2 exists.

Assuming that $\mathcal{G}_1(1, 1) > D_1$ so that E_1 exists, we now evaluate $V_4(E_1)$, the variational matrix at E_1 , which is given by

$$\begin{pmatrix} -1 - \frac{\bar{x}_1}{\xi_1} \frac{\partial}{\partial S} \mathcal{S}_1(\bar{S}_1, \bar{R}_1) & -\frac{\bar{x}_1}{\xi_1} \frac{\partial}{\partial R} \mathcal{S}_1(\bar{S}_1, \bar{R}_1) & -\frac{\mathcal{S}_1(\bar{S}_1, \bar{R}_1)}{\xi_1} & -\frac{\mathcal{S}_2(\bar{S}_1, \bar{R}_1)}{\xi_2} \\ -\frac{\bar{x}_1}{\eta_1} \frac{\partial}{\partial S} \mathcal{R}_1(\bar{S}_1, \bar{R}_1) & -1 - \frac{\bar{x}_1}{\eta_1} \frac{\partial}{\partial R} \mathcal{R}_1(\bar{S}_1, \bar{R}_1) & -\frac{\mathcal{R}_1(\bar{S}_1, \bar{R}_1)}{\eta_1} & -\frac{\mathcal{R}_2(\bar{S}_1, \bar{R}_1)}{\eta_2} \\ \bar{x}_1 \frac{\partial}{\partial S} \mathcal{G}_1(\bar{S}_1, \bar{R}_1) & \bar{x}_1 \frac{\partial}{\partial R} \mathcal{G}_1(\bar{S}_1, \bar{R}_1) & 0 & 0 \\ 0 & 0 & 0 & -D_2 + \mathcal{G}_2(\bar{S}_1, \bar{R}_1) \end{pmatrix}$$

That is,

$$V_4(\bar{S}_1, \bar{R}_1, \bar{x}_1, 0) = \begin{pmatrix} V_3(\bar{S}_1, \bar{R}_1, \bar{x}_1) & F \\ 0 & -D_2 + \mathcal{G}_2(\bar{S}_1, \bar{R}_1) \end{pmatrix}$$

where $F = [-\mathcal{S}_2(\bar{S}_1, \bar{R}_1)/\xi_2 \quad -\mathcal{R}_2(\bar{S}_1, \bar{R}_1)/\eta_2 \quad 0]^T$. Therefore the characteristic polynomial of $V_4(\bar{S}_1, \bar{R}_1, \bar{x}_1, 0)$ is

$$(\alpha - (\mathcal{G}_2(\bar{S}_1, \bar{R}_1) - D_2))(\alpha^3 + A_1\alpha^2 + B_1\alpha + C_1)$$

where $\alpha^3 + A_1\alpha^2 + B_1\alpha + C_1$ is the characteristic polynomial of $V_3(\bar{S}_1, \bar{R}_1, \bar{x}_1)$ given in (5.14) and (5.15) with $\mathcal{S}(S, R) = \mathcal{S}_1(S, R)$, $\mathcal{R}(S, R) = \mathcal{R}_1(S, R)$, $\mathcal{G}(S, R) = \mathcal{G}_1(S, R)$ and $d = D_1$. Clearly, $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2$ is a necessary condition for the local asymptotic stability of E_1 .

In the special case that $\mathcal{S}_1(S, R) = p_1(S)$ for all $R \geq 0$ and $\mathcal{R}_1(S, R) = q_1(R)$ for all $S \geq 0$, then equations (5.16) and (5.17) imply that E_1 is locally asymptotically stable if and only if $\mathcal{G}_1(1, 1) > D_1$ and $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2$.

Assuming that $\mathcal{G}_2(1, 1) > D_2$ so that E_2 exists, a similar analysis of this critical point yields the characteristic polynomial of $V_4(\bar{S}_2, \bar{R}_2, 0, \bar{x}_2)$,

$$(\alpha - (\mathcal{G}_1(\bar{S}_2, \bar{R}_2) - D_1))(\alpha^3 + A_2\alpha^2 + B_2\alpha + C_2)$$

where $\alpha^3 + A_2\alpha^2 + B_2\alpha + C_2$ is the characteristic polynomial of $V_3(\bar{S}_2, \bar{R}_2, \bar{x}_2)$ given in (5.14) and (5.15) with $\mathcal{S}(S, R) = \mathcal{S}_2(S, R)$, $\mathcal{R}(S, R) = \mathcal{R}_2(S, R)$, $\mathcal{G}(S, R) = \mathcal{G}_2(S, R)$

and $d = D_2$. Clearly, $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) < D_1$ is a necessary condition for the local asymptotic stability of E_2 .

Again in the special case that $\mathcal{S}_2(S, R) = p_2(S)$ for all $R \geq 0$ and $\mathcal{R}_2(S, R) = q_2(R)$ for all $S \geq 0$, then equations (5.16) and (5.17) imply that E_2 is locally asymptotically stable if and only if $\mathcal{G}_2(1, 1) > D_2$ and $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) < D_1$.

Now, suppose there exists a solution $E_* = (S^*, R^*, x_1^*, x_2^*) \in \mathfrak{R}_+^4$ of (5.19). Evaluating $V_4(S^*, R^*, x_1^*, x_2^*)$ we have that the corresponding characteristic polynomial is given by

$$\begin{aligned} 0 = & \alpha^4 + (b_1 + b_4)\alpha^3 + (a_1 + a_4 + b_1b_4 - b_2b_3)\alpha^2 \\ & + (b_1a_4 + b_4a_1 - b_3a_2 - b_2a_3)\alpha + (a_1a_4 - a_2a_3) \end{aligned} \quad (5.22)$$

where

$$\begin{aligned} b_1 &= 1 + \frac{\partial}{\partial S}\mathcal{S}_1(S^*, R^*)\frac{x_1^*}{\xi_1} + \frac{\partial}{\partial S}\mathcal{S}_2(S^*, R^*)\frac{x_2^*}{\xi_2}, \\ b_2 &= \frac{\partial}{\partial R}\mathcal{S}_1(S^*, R^*)\frac{x_1^*}{\xi_1} + \frac{\partial}{\partial R}\mathcal{S}_2(S^*, R^*)\frac{x_2^*}{\xi_2}, \\ b_3 &= \frac{\partial}{\partial S}\mathcal{R}_1(S^*, R^*)\frac{x_1^*}{\eta_1} + \frac{\partial}{\partial S}\mathcal{R}_2(S^*, R^*)\frac{x_2^*}{\eta_2}, \\ b_4 &= 1 + \frac{\partial}{\partial R}\mathcal{R}_1(S^*, R^*)\frac{x_1^*}{\eta_1} + \frac{\partial}{\partial R}\mathcal{R}_2(S^*, R^*)\frac{x_2^*}{\eta_2}, \\ a_1 &= \frac{x_1^*}{\xi_1}\mathcal{S}_1(S^*, R^*)\frac{\partial}{\partial S}\mathcal{G}_1(S^*, R^*) + \frac{x_2^*}{\xi_2}\mathcal{S}_2(S^*, R^*)\frac{\partial}{\partial S}\mathcal{G}_2(S^*, R^*), \\ a_2 &= \frac{x_1^*}{\xi_1}\mathcal{S}_1(S^*, R^*)\frac{\partial}{\partial R}\mathcal{G}_1(S^*, R^*) + \frac{x_2^*}{\xi_2}\mathcal{S}_2(S^*, R^*)\frac{\partial}{\partial R}\mathcal{G}_2(S^*, R^*), \\ a_3 &= \frac{x_1^*}{\eta_1}\mathcal{R}_1(S^*, R^*)\frac{\partial}{\partial S}\mathcal{G}_1(S^*, R^*) + \frac{x_2^*}{\eta_2}\mathcal{R}_2(S^*, R^*)\frac{\partial}{\partial S}\mathcal{G}_2(S^*, R^*), \\ a_4 &= \frac{x_1^*}{\eta_1}\mathcal{R}_1(S^*, R^*)\frac{\partial}{\partial R}\mathcal{G}_1(S^*, R^*) + \frac{x_2^*}{\eta_2}\mathcal{R}_2(S^*, R^*)\frac{\partial}{\partial R}\mathcal{G}_2(S^*, R^*). \end{aligned}$$

First note that

$$\begin{aligned}
a_1 a_4 - a_2 a_3 &= \left(\frac{\partial}{\partial S} \mathcal{G}_1(S^*, R^*) \frac{\partial}{\partial R} \mathcal{G}_2(S^*, R^*) - \frac{\partial}{\partial R} \mathcal{G}_1(S^*, R^*) \frac{\partial}{\partial S} \mathcal{G}_2(S^*, R^*) \right) \cdot \\
&\quad \left(\frac{\mathcal{S}_1(S^*, R^*) \mathcal{R}_2(S^*, R^*)}{\xi_1 \eta_2} - \frac{\mathcal{S}_2(S^*, R^*) \mathcal{R}_1(S^*, R^*)}{\xi_2 \eta_1} \right) \\
&= \nabla(S^*, R^*) \cdot \Delta(S^*, R^*)
\end{aligned}$$

where $\Delta(S, R)$ is as in (5.20) and $\nabla(S, R)$ is given by

$$\nabla(S, R) = \frac{\partial}{\partial S} \mathcal{G}_1(S^*, R^*) \frac{\partial}{\partial R} \mathcal{G}_2(S^*, R^*) - \frac{\partial}{\partial R} \mathcal{G}_1(S^*, R^*) \frac{\partial}{\partial S} \mathcal{G}_2(S^*, R^*).$$

Therefore, by the Routh-Hurwitz Criterion (B2), a necessary condition for the local asymptotic stability of E_* is that $\nabla(S^*, R^*)$ and $\Delta(S^*, R^*)$ have the same sign.

Recall that $\varphi'_i(S) = -\frac{\frac{\partial}{\partial S} \mathcal{G}_i(S, R)}{\frac{\partial}{\partial R} \mathcal{G}_i(S, R)}$ for $i = 1, 2$. Suppose there exists a solution (S^*, R^*) of (5.19a) under the hypotheses of Theorem 5.6(a) with $\bar{S}_1 < S^* < \bar{S}_2$. Let $E^* = (S^*, R^*, x_1^*, x_2^*)$ denote the corresponding solution to (5.19) which exists by Theorem 5.8. Then

$$|\varphi'_1(S^*)| \leq |\varphi'_2(S^*)|,$$

that is,

$$\frac{\frac{\partial}{\partial S} \mathcal{G}_1(S^*, R^*)}{\frac{\partial}{\partial R} \mathcal{G}_1(S^*, R^*)} \leq \frac{\frac{\partial}{\partial S} \mathcal{G}_2(S^*, R^*)}{\frac{\partial}{\partial R} \mathcal{G}_2(S^*, R^*)}.$$

Therefore, after rearranging,

$$\nabla(S^*, R^*) = \frac{\partial}{\partial S} \mathcal{G}_1(S^*, R^*) \frac{\partial}{\partial R} \mathcal{G}_2(S^*, R^*) - \frac{\partial}{\partial R} \mathcal{G}_1(S^*, R^*) \frac{\partial}{\partial S} \mathcal{G}_2(S^*, R^*) \leq 0.$$

Since $\Delta(S^*, R^*) > 0$ if $\bar{S}_1 < S^* < \bar{S}_2$, $a_1 a_4 - a_2 a_3 \leq 0$ and E^* is unstable.

Similarly, if $\bar{S}_2 < S^* < \bar{S}_1$, then

$$|\varphi'_1(S^*)| \leq |\varphi'_2(S^*)|,$$

that is,

$$\nabla(S^*, R^*) \geq 0$$

and since $\Delta(S^*, R^*) < 0$, if $\bar{S}_2 < S^* < \bar{S}_1$, E^* is unstable.

Now, suppose that there exists a solution (S^*, R^*) of (5.19a) under the hypotheses of Theorem 5.6(b) with $\bar{S}_1 < S^* < \bar{S}_2$. Again, let $E^* = (S^*, R^*, x_1^*, x_2^*)$ denote the corresponding solution to (5.19) which exists by Theorem 5.8. Then

$$|\varphi'_1(S^*)| \geq |\varphi'_2(S^*)|, \quad (5.23)$$

that is,

$$\frac{\frac{\partial}{\partial S} \mathcal{G}_1(S^*, R^*)}{\frac{\partial}{\partial R} \mathcal{G}_1(S^*, R^*)} \geq \frac{\frac{\partial}{\partial S} \mathcal{G}_2(S^*, R^*)}{\frac{\partial}{\partial R} \mathcal{G}_2(S^*, R^*)}.$$

Therefore, after rearranging,

$$\nabla(S^*, R^*) = \frac{\partial}{\partial S} \mathcal{G}_1(S^*, R^*) \frac{\partial}{\partial R} \mathcal{G}_2(S^*, R^*) - \frac{\partial}{\partial R} \mathcal{G}_1(S^*, R^*) \frac{\partial}{\partial S} \mathcal{G}_2(S^*, R^*) \geq 0.$$

Since $\Delta(S^*, R^*) > 0$ if $\bar{S}_1 < S^* < \bar{S}_2$, $a_1 a_4 - a_2 a_3 > 0$ if strict inequality holds in (5.23).

Similarly, if $\bar{S}_2 < S^* < \bar{S}_1$, then

$$|\varphi'_1(S^*)| \leq |\varphi'_2(S^*)|, \quad (5.24)$$

so that

$$\nabla(S^*, R^*) \leq 0.$$

Since $\Delta(S^*, R^*) < 0$ if $\bar{S}_2 < S^* < \bar{S}_1$, $a_1 a_4 - a_2 a_3 > 0$ if strict inequality holds in (5.24).

If $\mathcal{S}_i(S, R) = p_i(S)$ for all $R \geq 0$ and $\mathcal{R}_i(S, R) = q_i(R)$ for all $S \geq 0$, then as shown by León and Tumpson [12], $a_1 a_4 - a_2 a_3 > 0$ is a necessary and sufficient condition for the local asymptotic stability of an interior equilibrium. This follows from the fact that, in this case, the characteristic equation of $V_4(E^*)$ satisfies all other conditions of the Routh Hurwicz Criterion (B2).

Finally we study a global property of the model. In the following result, identify (S, R, x_1, x_2) -space with \mathfrak{R}_+^4 .

Theorem 5.9 *Assume $\mathcal{G}_i(1, 1) > D_i$, $i = 1, 2$, $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) < D_1$ and $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2$. Assume also that E_1 is globally asymptotically stable with respect to all solutions initiating in*

$$\mathcal{J}_1 = \{(S, R, x_1, x_2) \in \mathfrak{R}_+^4 : x_1 > 0, x_2 = 0\}$$

and that E_2 is globally asymptotically stable with respect to all solutions initiating in

$$\mathcal{J}_2 = \{(S, R, x_1, x_2) \in \mathfrak{R}_+^4 : x_1 = 0, x_2 > 0\}.$$

Then system (5.18) is persistent (B3) with respect to all solutions for which $x_1(0) > 0$ and $x_2(0) > 0$.

Proof: If for some solution $(S(t), R(t), x_1(t), x_2(t))$ of (5.18)

$$x_i(t) = 0 \text{ for some } t \geq 0 \tag{5.25}$$

then $x_i(t) \equiv 0$ since

$$x_i(t) = x_i(0) \exp\left\{\int_0^t (-D_i + \mathcal{G}_i(S(\tau), R(\tau))) d\tau\right\}.$$

Suppose (5.25) holds for $i = 1, 2$. In this case, system (5.18) reduces to

$$\begin{aligned} S'(t) &= 1 - S(t), \\ R'(t) &= 1 - R(t), \\ x'_i(t) &= 0, \quad i = 1, 2, \end{aligned}$$

$$S(0) \geq 0, \quad R(0) \geq 0, \quad x_i(0) = 0, \quad i = 1, 2.$$

This system has solution $S(t) = (S(0) - 1)e^{-t} + 1$, $R(t) = (R(0) - 1)e^{-t} + 1$, $x_i(t) \equiv 0$, $i = 1, 2$. Thus E_o is globally attracting with respect to solutions initiating in the set

$$\mathcal{J}_o = \{(S, R, 0, 0) \in \mathfrak{R}_+^4\}.$$

Choose $\underline{X} \in \overset{\circ}{\mathfrak{R}}_+^4$. By Theorem 5.1, $\Omega(\underline{X})$ is a nonempty, compact, invariant set with respect to (5.18). Suppose $\{E_o\} \in \Omega(\underline{X})$. Let $M^+(E_o)$ denote the stable manifold of E_o . Since $\mathcal{G}_i(1, 1) > D_i$ for $i = 1, 2$, E_o is unstable and $V_4(E_o)$ has two positive real eigenvalues and two negative real eigenvalues. Therefore, since $M^+(E_o) \supset \mathcal{J}_o$, $M^+(E_o) = \mathcal{J}_o$ and hence does not intersect $\overset{\circ}{\mathfrak{R}}_+^4$. This implies that $\{E_o\} \neq \Omega(\underline{X})$. Therefore, by the Butler-McGehee Lemma (B4), there exists $P_o \in M^+(E_o)$ such

that $P_o \in \Omega(\underline{X}) \setminus \{E_o\}$ and hence $cl\mathcal{O}(P_o) \subset \Omega(\underline{X})$ where $\mathcal{O}(P_o)$ denotes the entire orbit through P_o . However, since E_o is globally attracting, either $\mathcal{O}(P_o)$ becomes unbounded or one of the S or R components becomes negative as $t \rightarrow -\infty$. In either case, we have a contradiction, and therefore $\{E_o\} \notin \Omega(\underline{X})$.

Suppose $\{E_1\} \in \Omega(\underline{X})$. Since $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2$, E_1 is unstable and therefore $\dim(M^+(E_1)) < 4$. Since $M^+(E_1) \supset \mathcal{J}_1$, $\dim(M^+(E_1)) \geq 3$. Therefore, $M^+(E_1) = \mathcal{J}_1$ and hence does not intersect \mathfrak{R}_+^4 . This implies that $\{E_1\} \neq \Omega(\underline{X})$. Therefore, by the Butler-McGehee Lemma, there exists $P_1 \in M^+(E_1)$ such that $P_1 \in \Omega(\underline{X}) \setminus \{E_1\}$ and hence $cl\mathcal{O}(P_1) \subset \Omega(\underline{X})$. However, since E_1 is globally attracting, either $\mathcal{O}(P_1)$ becomes unbounded as $t \rightarrow -\infty$ or $cl\mathcal{O}(P_1) \supset \{E_o\}$. In either case, we have a contradiction and therefore, $\{E_1\} \notin \Omega(\underline{X})$. Similarly, $\{E_2\} \notin \Omega(\underline{X})$.

Since, by Theorem 5.1 $x_i(t)$ is bounded for $i = 1, 2$, $S'(t) > 0$ if $S(t)$ is sufficiently close to zero and $R'(t) > 0$ if $R(t)$ is sufficiently close to zero. It follows that any point in $\Omega(\underline{X})$ must satisfy $\underline{S} > 0$ and $\underline{R} > 0$.

Suppose (5.18) is not persistent. Then there exists a point $\tilde{P} \in \Omega(\underline{X})$ such that $\tilde{P} \in \mathcal{J}_i$ for some $i \in \{0, 1, 2\}$ and so $cl\mathcal{O}(\tilde{P}) \subset \Omega(\underline{X})$. If $\tilde{P} \in \mathcal{J}_o$ then $\{E_o\} \in cl\mathcal{O}(\tilde{P})$ since E_o is globally attracting with respect to all solutions initiating in the set \mathcal{J}_o , implying that $\{E_o\} \in \Omega(\underline{X})$, a contradiction. If $\tilde{P} \in \mathcal{J}_1$ then $\{E_1\} \in cl\mathcal{O}(\tilde{P})$ since E_1 is globally attracting with respect to all solutions initiating in the set \mathcal{J}_1 , implying that $\{E_1\} \in \Omega(\underline{X})$, a contradiction. Similarly, if $\tilde{P} \in \mathcal{J}_2$ then $\{E_2\} \in cl\mathcal{O}(\tilde{P})$ since E_2 is globally attracting with respect to all solutions initiating in the set \mathcal{J}_2 , implying that $\{E_2\} \in \Omega(\underline{X})$, a contradiction. Therefore, (5.18) is persistent.

Note that if $\mathcal{S}_i(S, R) = p_i(S)$ for all $R \geq 0$ and $\mathcal{R}_i(S, R) = q_i(R)$ for all $S \geq 0$ for $i = 1, 2$ then for each i , by Theorem 5.5, E_i is globally asymptotically stable with respect to all solutions initiating in $\{(S, R, x_1, x_2) \in \mathfrak{R}_+^4 : x_i > 0, x_j = 0\}$ where $i \neq j \in \{1, 2\}$. Therefore, Theorem 5.9 gives necessary and sufficient conditions for persistence in this case.

5.5 Summary of Results

In this section we summarize the results of sections 5.2 through 5.4 in terms of the original unscaled model.

We obtained our most complete results in the case that the consumption of one resource does not affect the consumption of the other, that is, for the model of León and Tumpson [12]. First we showed that if $\mathcal{G}_i(S^\circ, R^\circ) < D_i$ for $i = 1, 2$ then E_o is globally asymptotically stable, that is, both species become extinct. In analyzing the (S, R, x_i) subsystems of (5.1) for $i \in \{1, 2\}$, we found that there exists a unique interior equilibrium $(\bar{S}_i, \bar{R}_i, \bar{x}_i)$ which is globally asymptotically stable provided $\mathcal{G}_i(S^\circ, R^\circ) > D_i$. We also found that a necessary and sufficient condition for solutions of the full four dimensional model to persist is that $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) > D_1$ and $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) > D_2$. In table 5.2 we summarize the criteria that ensure the existence of equilibria in the nonnegative cone as well as criteria that guarantee local asymptotic stability of these critical points.

Next we extended this model to a more realistic setting, incorporating the possibility that the consumption of one resource inhibits the consumption of the other. Again, if $\mathcal{G}_i(S^\circ, R^\circ) < D_i$ for $i = 1, 2$ then both species become extinct. Here we found that for each $i \in \{1, 2\}$, a necessary and sufficient condition for solutions of the (S, R, x_i) subsystem to persist is that $\mathcal{G}_i(S^\circ, R^\circ) > D_i$. The criteria ensuring the existence of equilibria in the nonnegative cone and the local asymptotic stability of E_o are identical to those found in table 5.2. For each $i \in \{1, 2\}$, we have only shown the criteria for the local asymptotic stability of the E_i given in table 5.2 to apply under the further assumption that $\mathcal{G}_i(S^\circ, R^\circ) > 2D$. Also, the condition for the local asymptotic stability of E_* is only a necessary condition in this case, ensuring that the constant term in the characteristic equation of $V_4(E_*)$ is positive. Under the above restrictions and in the case that the consumption of one resource does not affect the consumption of the other, the local stability results are consistent with those of Waltman, Hubbell and Hsu [21].

Assuming that, for $i = 1, 2$, either $\mathcal{S}_i(S, R) = p_i(S)$ for all $R \geq 0$ and

$\mathcal{R}_i(S, R) = q_i(R)$ for all $S \geq 0$ or $\mathcal{G}_i(S^\circ, R^\circ) > 2D$ we give the following bifurcation analysis of our results based on the parameters D_1 and D_2 . If D_1 and D_2 are too large for the species to subsist, that is, $\mathcal{G}_i(S^\circ, R^\circ) < D_i$ for $i = 1, 2$, then none of E_1 , E_2 or E_* can exist in the non-negative cone. The critical point E_o , corresponding to total washout, is globally asymptotically stable. If D_1 is decreased so that $\mathcal{G}_1(S^\circ, R^\circ) = D_1$, then critical points E_o and E_1 corresponding to the sole survival of species one, coalesce. If D_1 is slightly reduced, E_1 bifurcates into $\{(S, R, x_1, x_2) \in \mathfrak{R}_+^4 : x_1 > 0, x_2 = 0\}$ and E_o loses its stability to E_1 . Consider $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) < D_1 < \mathcal{G}_1(S^\circ, R^\circ)$. If D_2 is now decreased so that $\mathcal{G}_2(S^\circ, R^\circ) = D_2$, the critical points E_o and E_2 corresponding to the sole survival of species two, coalesce. As D_2 is decreased slightly, E_2 bifurcates into $\{(S, R, x_1, x_2) \in \mathfrak{R}_+^4 : x_1 = 0, x_2 > 0\}$ and E_o loses another dimension of stability to E_2 . For $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2 < \mathcal{G}_2(S^\circ, R^\circ)$, both E_1 and E_2 are locally asymptotically stable. If D_1 is now decreased, and E_2 loses its stability for $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) > D_1$. As D_2 is now decreased, the critical points E_1 and E_* coalesce when $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) = D_2$. When $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) > D_1$, E_1 loses its stability and E_* bifurcates into $\{(S, R, x_1, x_2) \in \mathfrak{R}_+^4 : x_1 > 0, x_2 > 0\}$. In the case that the consumption of neither resource reduces the consumption of the other, solutions of the model persist, that is, neither species becomes extinct.

We have found that by varying the parameters each of the outcomes of the classical theory for two species competition described in chapter 2 are possible at least locally. In contrast with the classical model, the interior equilibrium need not be unique. Coexistence in the classical model corresponds to persistence when the consumption of each resource is independent of the consumption of the other. Competitive independent extinction, an impossibility in the classical model, can also occur. Each outcome depends on the species' abilities to subsist at the given equilibrium concentrations of the resources.

It is interesting to note that regardless of the assumptions imposed on the uptake functions, the analysis of the two competitor, two resource model depends heavily on the three dimensional subsystems involving one species and the two non-reproducing substitutable resources. In the more general model, this is apparent in the analysis of the local stability of equilibria. For the model of León and Tumpson

[12] it is still more apparent. In this case, the condition guaranteeing that the model is persistent is minimal in the sense that it is precisely the condition that ensures that the critical points in the three dimensional subsystems exist and are unstable, repelling into the interior.

One shortcoming of the model is that certain simplifying assumptions were made. For example, it is assumed that the conversion of nutrient to biomass is instantaneous, whereas there is experimental evidence indicating that there is a time delay between absorption of nutrient and production of biomass. Also, it may be the case that the growth rate due to the consumption of one resource is not proportional to the rate of consumption of that same resource. Furthermore, we have not admitted uptake functions which describe inhibition by the substrates at high concentrations.

It would be interesting to consider the "Principle of Competitive Exclusion" in this context to determine whether or not it is possible for more than two competitors to survive if limited by only two resources. A more complete analysis of the model considered here would likely be useful.

Table 5.2: Summary of Local Stability Analysis of (5.1)

$$\begin{aligned} \mathcal{S}_i(S, R) &= p_i(S) \text{ for all } R \geq 0 \\ \mathcal{R}_i(S, R) &= q_i(R) \text{ for all } S \geq 0 \end{aligned}$$

CRITICAL POINT	EXISTENCE CRITERIA	CRITERIA FOR ASYMPTOTIC STABILITY
E_o	always exists	$\mathcal{G}_1(S^o, R^o) < D_1$ and $\mathcal{G}_2(S^o, R^o) < D_2$
E_1	$\mathcal{G}_1(S^o, R^o) > D_1$	$\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2$
E_2	$\mathcal{G}_2(S^o, R^o) > D_2$	$\mathcal{G}_1(\bar{S}_2, \bar{R}_2) < D_1$
E_* (not necessarily unique)	(i) $\mathcal{G}_1(\bar{S}_2, \varphi_2(\bar{S}_2)) < D_1$ and $\mathcal{G}_2(\bar{S}_1, \varphi_1(\bar{S}_1)) < D_2$ or (ii) $\mathcal{G}_1(\bar{S}_2, \varphi_2(\bar{S}_2)) > D_1$ and $\mathcal{G}_2(\bar{S}_1, \varphi_1(\bar{S}_1)) > D_2$	(ii) holds and either $ \varphi'_1(S^*) > \varphi'_2(S^*) $ and $\bar{S}_1 < \bar{S}_2$ or $ \varphi'_1(S^*) < \varphi'_2(S^*) $ and $\bar{S}_1 > \bar{S}_2$

Chapter 6

Discussion

In this section we compare the results of Butler and Wolkowicz [2] in the noninhibitory kinetics case to those found here. To this end, we assume that $D_i = D$, $i = 1, 2$, that is, the death rate of each species is negligible in comparison to the dilution rate. The notation for the critical points of model (4.5) in the complementary case, adapted from Butler et al. [2], are given in table 6.3. In table 6.4 we compare the criterion for the existence of equilibria in the nonnegative cone. Note that in the substitutable case we have shown that in the (S, R, x_i) subsystems the critical point E_i exists if and only if $\mathcal{G}_i(S^\circ, R^\circ) > D$ and if E_i exists then it is unique. In the complementary case, one of two equilibria in each of the (S, R, x_i) subsystems exists. The criterion $\mathcal{G}_i(S^\circ, R^\circ)$ is sufficient to guarantee the existence of an equilibrium. Which one exists depends on whether species i is S -limited or R -limited. Thus, the criteria for the existence of equilibria appear to differ in each case. However, it is interesting to note that the criteria given by Bulter et al. [2] for the existence and local asymptotic stability of the equilibria in the perfectly complementary case have the same form as those found here in the perfectly substitutable case. In table 6.5 we compare the criteria for the local asymptotic stability of the equilibria when they exist. Recall that we have only shown the criteria for the local asymptotic stability of E_* to be a necessary condition, ensuring that the constant term in the characteristic equation of $V_4(E_*)$ is positive. Also, the interior equilibrium in the substitutable case need not be unique. In the case that the uptake functions assume the form of those studied by

Waltman, Hubbell and Hsu [21], E_* , when it exists, is unique and the constant term in the characteristic equation of $V_4(E_*)$ will be positive if and only if $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) > D$ and $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) > D$, one of the other conditions being satisfied immediately. The same is true in the complementary case where the form of the subsistence curves ensure that the interior equilibrium, when it exists, is unique.

Consider first the critical points E_1 , $E_{\lambda_1^*}$ and $E_{*\mu_1}$. For substitutable resources, the critical point E_1 exists if and only if $\mathcal{G}_1(S^\circ, R^\circ) > D$ and is locally asymptotically stable if and only if it exists and $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D$. In the complementary case, the critical point $E_{\lambda_1^*}$ exists if and only if $\lambda_1 < S^\circ$ and $T_1 > C_1$ and is locally asymptotically stable if and only if it exists and $\lambda_1 < \lambda_2$ or $T^* < C_1$. Now, $\lambda_1 < S^\circ$ and $T_1 > C_1 > 0$ imply $\mu_1 < R^\circ$ so that $\mathcal{G}_1(S^\circ, R^\circ) = \min\{p_1(S^\circ), q_1(R^\circ)\} > D$. The condition $\mathcal{G}_1(S^\circ, R^\circ) > D$ alone does not imply that $E_{\lambda_1^*}$ exists since population one must further be S -limited. Also, if $\mathcal{G}_2(\lambda_1, R^\circ - C_1(S^\circ - \lambda_1)) = \min\{p_2(\lambda_1), q_2(R^\circ - C_1(S^\circ - \lambda_1))\} < D$ then either $\lambda_1 < \lambda_2$ or $R^\circ - C_1(S^\circ - \lambda_1) < \mu_2$, that is, either $\lambda_1 < \lambda_2$ or $\frac{R^\circ - \mu_2}{S^\circ - \lambda_1} < C_1$. Similarly, if either $\lambda_1 < \lambda_2$ or $T^* < C_1$ then $\mathcal{G}_2(\lambda_1, R^\circ - C_1(S^\circ - \lambda_1)) = \min\{p_2(\lambda_1), q_2(R^\circ - C_1(S^\circ - \lambda_1))\} < D$. A similar argument shows that $E_{*\mu_1}$ exists if and only if $\mathcal{G}_1(S^\circ, R^\circ) > D$ and $T_1 < C_1$ and is locally asymptotically stable if and only if it exists and $\mathcal{G}_2(S^\circ - \frac{1}{C_1}(R^\circ - \mu_1), \mu_1) = \min\{p_2(S^\circ - \frac{1}{C_1}(R^\circ - \mu_1)), q_2(\mu_1)\} < D$ where $\lambda_2 < S^\circ$ if $p_2(S^\circ - \frac{1}{C_1}(R^\circ - \mu_1)) \leq q_2(\mu_1)$.

Next consider the critical point $E_{\lambda_1\mu_2}$ and suppose $\lambda_1 > \lambda_2$, $\mu_1 < \mu_2$, $C_1 < T^* < C_2$ and $\lambda_1 < S^\circ$. Now, $\lambda_1 < S^\circ$, $C_1 < T^*$ and $\mu_1 < \mu_2$ imply $T_1 > T^* > C_1$ so that $E_{\lambda_1^*}$ exists and $\lambda_1 < S^\circ$, $0 < T^* < C_2$ and $\lambda_1 > \lambda_2$ imply $\lambda_2 < S^\circ$, $\mu_2 < R^\circ$ and $T_2 < T^* < C_2$ so that $E_{*\mu_2}$ exists. Also, $C_1 < T^*$ is equivalent to $\mu_2 < R^\circ - C_1(S^\circ - \lambda_1)$ and since $\lambda_2 < \lambda_1$, $\mathcal{G}_2(\lambda_1, R^\circ - C_1(S^\circ - \lambda_1)) = \min\{p_2(\lambda_1), q_2(R^\circ - C_1(S^\circ - \lambda_1))\} > D$. Similarly, $T^* < C_2$ is equivalent to $\lambda_1 < S^\circ - \frac{1}{C_2}(R^\circ - \mu_2)$ and since $\mu_1 < \mu_2$, $\mathcal{G}_1(S^\circ - \frac{1}{C_2}(R^\circ - \mu_2), \mu_2) = \min\{p_1(S^\circ - \frac{1}{C_2}(R^\circ - \mu_2)), q_1(\mu_2)\} > D$. Conversely, if $\lambda_1 < S^\circ$ then $\mathcal{G}_1(S^\circ - \frac{1}{C_2}(R^\circ - \mu_2), \mu_2) > D$ implies $\mu_1 < \mu_2$ and $\lambda_1 < S^\circ - \frac{1}{C_2}(R^\circ - \mu_2)$ so that $T^* > C_2$, and $\mathcal{G}_2(\lambda_1, R^\circ - C_1(S^\circ - \lambda_1)) > D$ implies $\lambda_1 > \lambda_2$ and $R^\circ - C_1(S^\circ - \lambda_1) > \mu_2$ so that $C_1 < T^*$. Therefore the condition $\lambda_1 > \lambda_2$, $\mu_1 < \mu_2$, $C_1 < T^* < C_2$ and $\lambda_1 < S^\circ$ is equivalent to $\lambda_1 < S^\circ$, $\mathcal{G}_1(S^\circ - \frac{1}{C_2}(R^\circ - \mu_2), \mu_2) > D$ and $\mathcal{G}_2(\lambda_1, R^\circ - C_1(S^\circ - \lambda_1)) > D$. Similarly, for $E_{\lambda_2\mu_1}$ the condition $\lambda_1 < \lambda_2$, $\mu_1 > \mu_2$,

$C_1 > T_* > C_2$ and $\lambda_2 < S^\circ$ is equivalent to $\lambda_2 < S^\circ$, $\mathcal{G}_1(\lambda_2, R^\circ - C_2(S^\circ - \lambda_2)) > D$ and $\mathcal{G}_2(S^\circ - \frac{1}{C_1}(R^\circ - \mu_1), \mu_1) > D$.

By varying the parameters in the model for perfectly substitutable resources, each of the outcomes for perfectly complementary resources are possible at least locally. In contrast to the perfectly complementary case, the interior equilibrium need not be unique. Coexistence in the perfectly complementary case corresponds to persistence when the consumption of each resource is independent of the consumption of the other. Competition independent extinction can occur for perfectly substitutable and perfectly complementary resources. The similarities in the criteria for the existence and local asymptotic stability of equilibria would indicate that in both cases the outcome is determined by the species' abilities to subsist at the given equilibrium concentrations of the resources. This possible correlation is consistent with the analysis of Tilman [18]. Using graphical techniques to examine the local stability properties of two species competition for two resources, he conjectures that *the type of resources for which competition occurs will not lead to major, qualitative differences in the ecological patterns that can result from competition between two species for two resources.*

Table 6.3: Notation for the Critical Points of Model (4.5)

NOTATION	CRITICAL POINT (provided it lies in \mathbb{R}_+^4)
E_o	$(S^o, R^o, 0, 0)$
$E_{\lambda_1^*}$	$(\lambda_1, R^o - C_1(S^o - \lambda_1), \xi_1(S^o - \lambda_1), 0)$
$E_{*\mu_1}$	$(S^o - (R^o - \mu_1)/C_1, \mu_1, \eta_1(R^o - \mu_1), 0)$
$E_{\lambda_2^*}$	$(\lambda_2, R^o - C_2(S^o - \lambda_2), 0, \xi_2(R^o - \lambda_2))$
$E_{*\mu_2}$	$(S^o - (R^o - \mu_2)/C_2, \mu_2, 0, \eta_2(R^o - \mu_2))$
$E_{\lambda_1\mu_2}$	$(\lambda_1, \mu_2, \tilde{x}_1, \tilde{x}_2)$ where $\tilde{x}_1 = \xi_1\eta_1 \left(\frac{\xi_2(S^o - \lambda_1) - \eta_2(R^o - \mu_2)}{\eta_1\xi_2 - \xi_1\eta_2} \right)$ and $\tilde{x}_2 = \xi_2\eta_2 \left(\frac{\eta_1(R^o - \mu_2) - \xi_1(S^o - \lambda_1)}{\eta_1\xi_2 - \xi_1\eta_2} \right)$
$E_{\lambda_2\mu_1}$	$(\mu_1, \lambda_2, \hat{x}_1, \hat{x}_2)$ where $\hat{x}_1 = \xi_1\eta_1 \left(\frac{\xi_2(S^o - \lambda_2) - \eta_2(R^o - \mu_1)}{\eta_1\xi_2 - \xi_1\eta_2} \right)$ and $\hat{x}_2 = \xi_2\eta_2 \left(\frac{\eta_1(R^o - \mu_1) - \xi_1(S^o - \lambda_2)}{\eta_1\xi_2 - \xi_1\eta_2} \right)$

Table 6.4: Criteria for Existence Of Equilibria
Substitutable vs Complementary

SUBSTITUTABLE RESOURCES		COMPLEMENTARY RESOURCES	
CRITICAL POINT	EXISTENCE CRITERIA $\mathcal{G}_i = \mathcal{S}_i + \mathcal{R}_i$	CRITICAL POINT	EXISTENCE CRITERIA $\mathcal{G}_i = \min\{p_i, q_i\}$
E_o	always exists	E_o	always exists
E_1	$\mathcal{G}_1(S^o, R^o) > D$	$E_{\lambda_1^*}$	$\mathcal{G}_1(S^o, R^o) > D$ and $T_1 > C_1$
		$E_{*\mu_1}$	$\mathcal{G}_1(S^o, R^o) > D$ and $T_1 < C_1$
E_2	$\mathcal{G}_2(S^o, R^o) > D$	$E_{\lambda_2^*}$	$\mathcal{G}_2(S^o, R^o) > D$ and $T_2 > C_2$
		$E_{*\mu_2}$	$\mathcal{G}_2(S^o, R^o) > D$ and $T_2 < C_2$
E_* (not necessarily unique)	(i) $\mathcal{G}_1(\bar{S}_2, \varphi_2(\bar{S}_2)) < D$ and $\mathcal{G}_2(\bar{S}_1, \varphi_1(\bar{S}_1)) < D$ or (ii) $\mathcal{G}_1(\bar{S}_2, \varphi_2(\bar{S}_2)) > D$ and $\mathcal{G}_2(\bar{S}_1, \varphi_1(\bar{S}_1)) > D$	$E_{\lambda_1\mu_2}$	(i) $\lambda_1 > \lambda_2$ and $\mu_1 < \mu_2$ and $C_1 > T^* > C_2$ and $\lambda_1 < S^o$ or (ii) $\lambda_1 < S^o$ and $\mathcal{G}_1(S^o - \frac{1}{C_2}(R^o - \mu_2), \mu_2) > D$ $\mathcal{G}_2(\lambda_1, R^o - C_1(S^o - \lambda_1)) > D$
		$E_{\lambda_2\mu_1}$	(i) $\lambda_1 < \lambda_2$ and $\mu_1 > \mu_2$ and $C_1 < T_* < C_2$ and $\lambda_2 < S^o$ or (ii) $\lambda_2 < S^o$ and $\mathcal{G}_1(\lambda_2, R^o - C_2(S^o - \lambda_2)) > D$ $\mathcal{G}_2(S^o - \frac{1}{C_1}(R^o - \mu_1), \mu_1) > D$

Table 6.5: Criteria for the Local Asymptotic Stability of Equilibria
Substitutable vs Complementary

SUBSTITUTABLE RESOURCES		COMPLEMENTARY RESOURCES	
CRITICAL POINT	CRITERIA FOR ASYMPTOTIC STABILITY $\mathcal{G}_i = \mathcal{S}_i + \mathcal{R}_i$	CRITICAL POINT	CRITERIA FOR ASYMPTOTIC STABILITY $\mathcal{G}_i = \min\{p_i, q_i\}$
E_o	$\mathcal{G}_1(S^o, R^o) > D$ and $\mathcal{G}_2(S^o, R^o) > D$	E_o	$\mathcal{G}_1(S^o, R^o) < D$ and $\mathcal{G}_2(S^o, R^o) < D$
E_1	$\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D$	$E_{\lambda_1^*}$	$\mathcal{G}_2(\lambda_1, R^o - C_1(S^o - \lambda_1)) < D$ and $\lambda_2 < S^o$ if $p_2(S^o - \frac{1}{c_1}(R^o - \mu_1)) \leq q_2(\mu_1)$
		$E_{*\mu_1}$	$\mathcal{G}_2(S^o - \frac{1}{c_1}(R^o - \mu_1), \mu_1) < D$
E_2	$\mathcal{G}_1(\bar{S}_2, \bar{R}_2) < D$	$E_{\lambda_2^*}$	$\mathcal{G}_1(\lambda_2, R^o - C_2(S^o - \lambda_2)) < D$
		$E_{*\mu_2}$	$\mathcal{G}_1(S^o - \frac{1}{c_2}(R^o - \mu_2), \mu_2) < D$ and $\lambda_1 < S^o$ if $p_1(S^o - \frac{1}{c_2}(R^o - \mu_2)) \leq q_1(\mu_2)$
E_* (not necessarily unique)	(ii) holds and either $ \varphi'_1(S^*) > \varphi'_2(S^*) $ and $\bar{S}_1 < \bar{S}_2$ or $ \varphi'_1(S^*) < \varphi'_2(S^*) $ and $\bar{S}_1 > \bar{S}_2$	$E_{\lambda_1\mu_2}$	(ii) holds
		$E_{\lambda_2\mu_1}$	(ii) holds

Appendix A

Figures

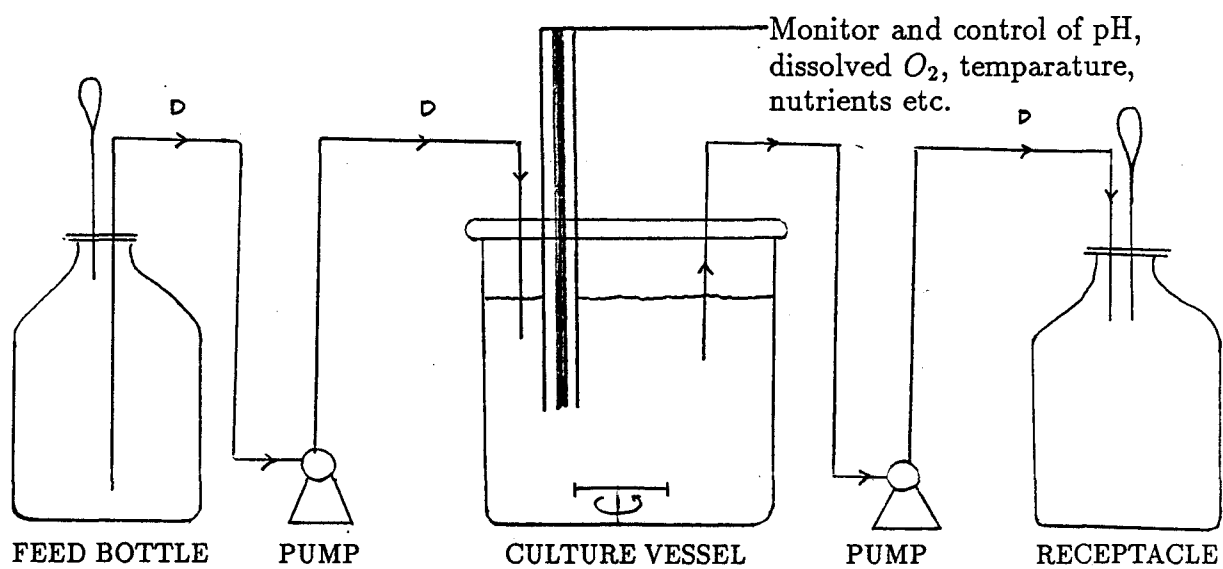


Figure A.1: Schematic Diagram of the Chemostat

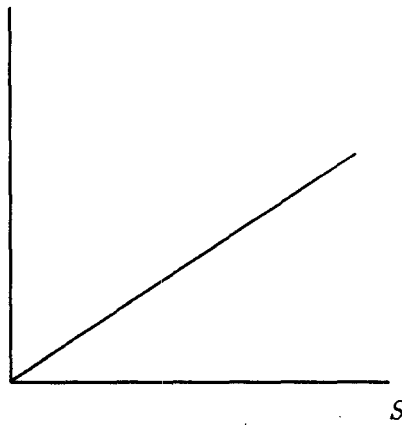


Figure A.2: Holling Type I Functional Response: $\frac{x'}{x} = rS$

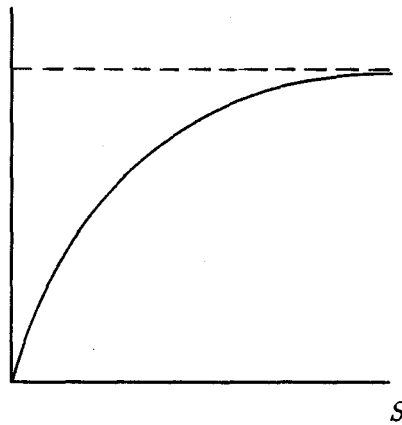


Figure A.3: Holling Type II Functional Response: $\frac{x'}{x} = \frac{mS}{K+S}$

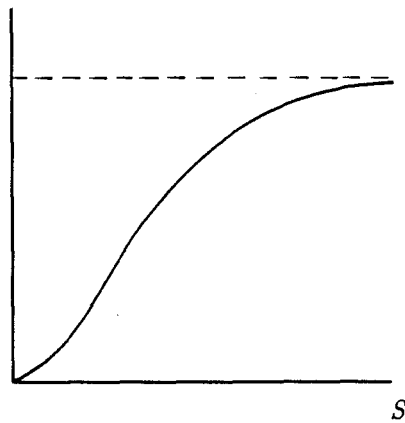


Figure A.4: Holling Type III Functional Response: $\frac{x'}{x} = \frac{mS^2}{S^2 + KS + L}$

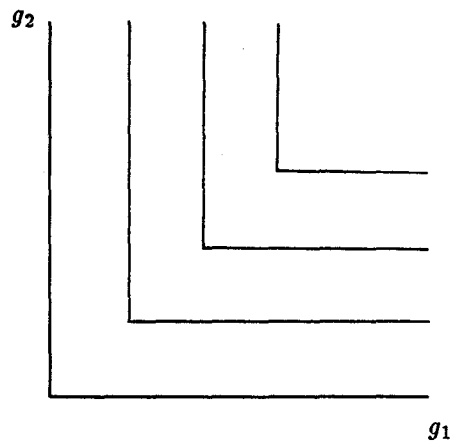


Figure A.5: Indifference Curves for Perfectly Complementary Resources

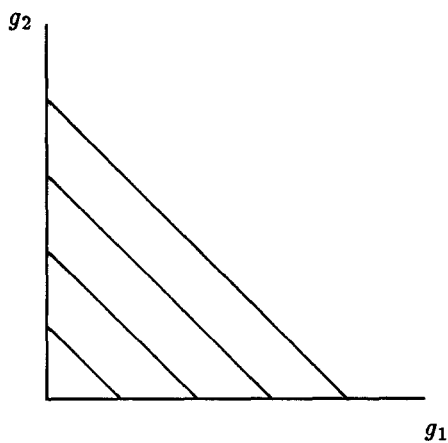


Figure A.6: Indifference Curves for Perfectly Substitutable Resources

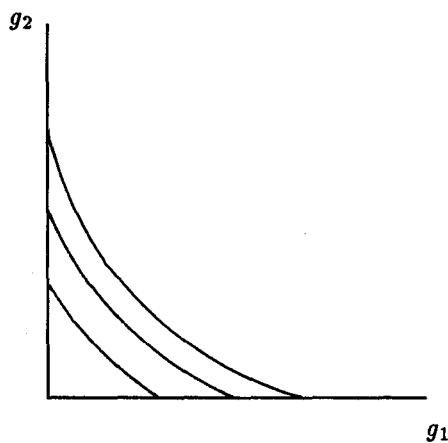


Figure A.7: Indifference Curves for Imperfectly Substitutable Resources

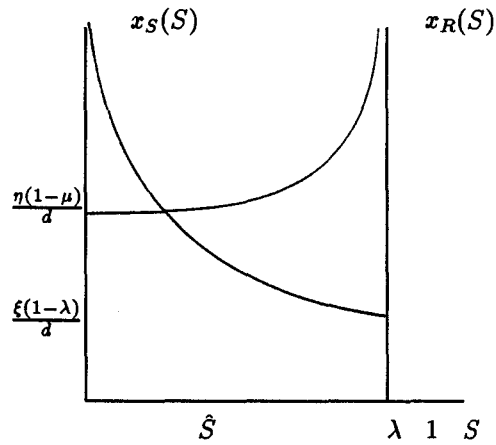


Figure A.8: Schematic Diagram Theorem 5.3 Case 1: $\lambda \leq 1$ and $\mu \leq 1$

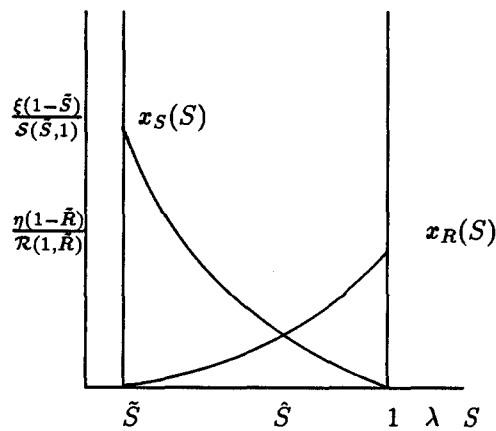


Figure A.9: Schematic Diagram Theorem 5.3 Case 2: $\lambda > 1$ and $\mu > 1$

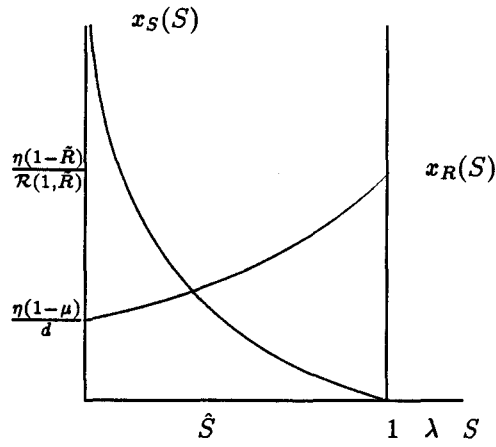


Figure A.10: Schematic Diagram Theorem 5.3 Case 3: $\lambda \geq 1$ and $\mu \leq 1$

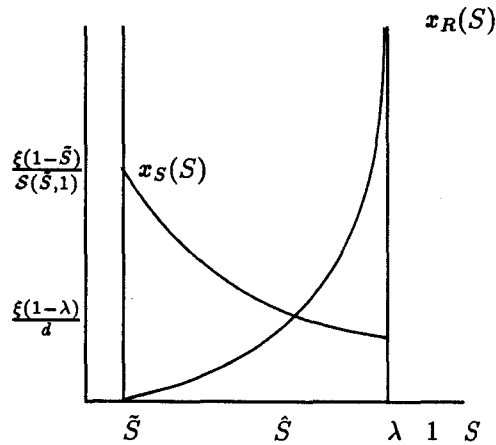


Figure A.11: Schematic Diagram Theorem 5.3 Case 4: $\lambda \leq 1$ and $\mu \geq 1$

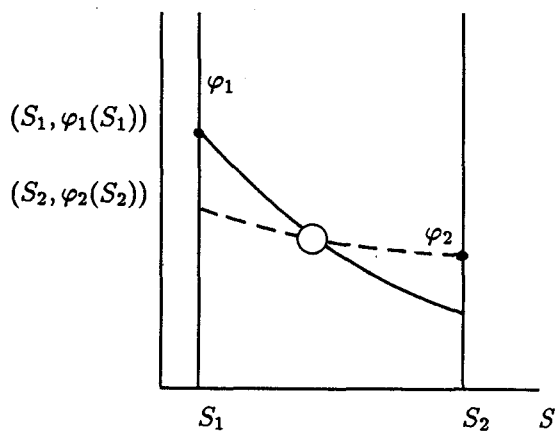
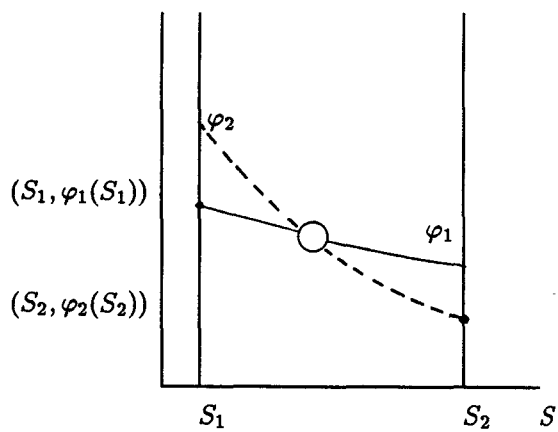


Figure A.12: Schematic Diagram Theorem 5.6 (a) and (b)

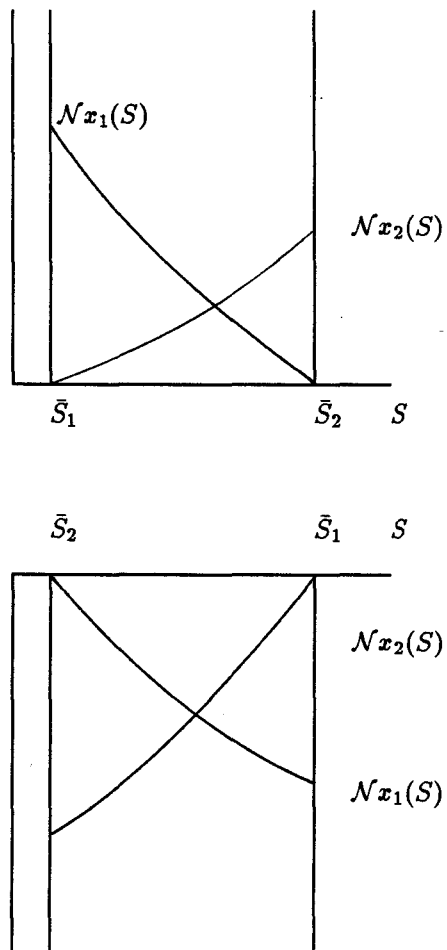


Figure A.13: Schematic Diagram Theorem 5.8

Appendix B

Background Theory

B1: The Implicit Function Theorem [17]

Let $F(x_1, \dots, x_n, z)$ be defined on an $(n + 1)$ -dimensional neighborhood of the point (a_1, \dots, a_n, c) . Suppose that F has continuous partial derivatives in this neighborhood, and furthermore, assume that

$$F(a_1, \dots, a_n, c) = 0, \quad \frac{\partial}{\partial x_{n+1}} F(a_1, \dots, a_n, c) \neq 0.$$

Under these conditions there exists a box-like region defined by certain inequalities

$$|x_1 - a_1| < A_1, \dots, |x_n - a_n| < A_n, \quad |z - c| < C,$$

lying in the above neighborhood, and such that the following assertions are true:

Let R be the n -dimensional region

$$|x_1 - a_1| < A_1, \dots, |x_n - a_n| < A_n$$

in the space of the variables x_1, \dots, x_n . Then

1. For any (x_1, \dots, x_n) in R there is a unique z such that

$$|z - c| < C \text{ and } F(x_1, \dots, x_n, z) = 0.$$

Let us express this dependence of z on (x_1, \dots, x_n) by writing

$$z = f(x_1, \dots, x_n).$$

2. The function f is continuous in R .
3. The function f has continuous first partials given by

$$\frac{\partial}{\partial x_i} f(x_1, \dots, x_n) = -\frac{\frac{\partial}{\partial x_i} F(x_1, \dots, x_n, z)}{\frac{\partial}{\partial x_{n+1}} F(x_1, \dots, x_n, z)}, \quad i = 1, \dots, n,$$

where $z = f(x_1, \dots, x_n)$.

B2: Routh-Hurwitz Criterion [5]

Consider

$$p(\alpha) = A_0 \alpha^n + A_1 \alpha^{n-1} + \dots + A_{n-1} \alpha + A_n \text{ with } A_0 > 0$$

Define

$$\Delta_1 = A_1, \quad \Delta_2 = \begin{vmatrix} A_1 & A_0 \\ A_3 & A_2 \end{vmatrix}, \quad \Delta_3 = \begin{vmatrix} A_1 & A_0 & 0 \\ A_3 & A_2 & A_1 \\ A_5 & A_4 & A_3 \end{vmatrix}.$$

In general, define

$$\Delta_n = \begin{vmatrix} A_1 & A_0 & 0 & 0 & 0 & 0 & 0 & \dots & 0 \\ A_3 & A_2 & A_1 & A_0 & 0 & 0 & 0 & \dots & 0 \\ A_5 & A_4 & A_3 & A_2 & A_1 & A_0 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \dots & \vdots \\ A_{2n-1} & A_{2n-2} & A_{2n-3} & A_{2n-4} & A_{2n-5} & A_{2n-6} & A_{2n-7} & \dots & A_n \end{vmatrix},$$

where $A_j = 0$ for $j > n$. In particular, $\Delta_n \equiv A_n \Delta_{n-1}$.

A necessary and sufficient condition for all of the roots of $p(\alpha)$ to have their real parts negative is that all the determinants Δ_i , $i = 1, \dots, n$, be positive.

B3: Persistence [4]

A population $\rho(t)$ is said to persist if $\rho(0) > 0$ and $\liminf_{t \rightarrow \infty} \rho(t) > 0$. A system is said to be persistent if each component population persists. In the language of dynamical systems, a solution with initial conditions in the interior will persist if there are no Ω -limit points on the boundary.

B4: The Butler-McGehee Lemma [4]

Let E be an isolated equilibrium with nonzero eigenvalues in the omega limit set $\Omega(X)$ of an orbit $\mathcal{O}(X)$. Then either $\Omega(X) = \{E\}$ or there exist points P^+ , P^- in $\Omega(X)$ with $P^+ \in M^+(E)$ and $P^- \in M^-(E)$.

B5: Lyapunov Function [11]

Consider the general system of differential equations

$$(*) \quad x' = f(x) \quad f(x_0) = 0$$

Here $f(x)$ is a vector-valued function, continuous in x for $x \in clG$ where G is an open subset of \mathfrak{R}^n . The function V mapping \mathfrak{R}^n to \mathfrak{R} is said to be a *Lyapunov Function* in G for $(*)$ if it satisfies the following properties:

1. $V(x)$ is continuous together with its first partial derivatives in G .
2. $V(x) \geq 0$ with equality only when $x = x_0$.
3. $\dot{V} = (gradV) \cdot f \leq 0$ in G .

B6: La Salle's Extension Theorem [11]

Let V be a Lyapunov function in G for $(*)$. Then each bounded orbit approaches M where M is the largest invariant subset of $\{x \in clG : \dot{V} = 0\}$.

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