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## **Global analysis of competition for perfectly substitutable resources with linear response**

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**Abstract.** We study a model of the chemostat with two species competing for two perfectly substitutable resources in the case of linear functional response. Lyapunov methods are used to provide sufficient conditions for the global asymptotic stability of the coexistence equilibrium. Then, using compound matrix techniques, we provide a global analysis in a subset of parameter space. In particular, we show that each solution converges to an equilibrium, even in the case that the coexistence equilibrium is a saddle. Finally, we provide a bifurcation analysis based on the dilution rate. In this context, we are able to provide a geometric interpretation that gives insight into the role of the other parameters in the bifurcation sequence.

### **1. Introduction**

The classical theory of ecological competition is attributed to Lotka [26] and Volterra [37] and is an extension of the basic logistic model of single-species growth due to Verhulst [36]. Models in this class describe how the biomass of each competitor changes without specifying the resources upon which competition is based or how these resources are used by the competitors. The lack of such considerations yields models that are more general than would otherwise be obtained. However, since the parameters governing the interactions cannot be measured without actually growing the species together in competition, the models are more phenomenological than predictive.

In response, a more mechanistic, resource-based theory of ecological competition has been developed (see, for example, [15, 21, 28, 31, 34]). Both consumer-

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resource interactions and competitive interactions are captured by incorporating the resources into the models. As a result, these models are often less general and more difficult to analyze (see, for example, [2, 3, 17]). However, they are predictive, since the parameters of the models can be measured on species grown alone in advance of competition (see, for example, [13]). The model that we will be considering is an example of this resource-based approach.

There are many articles devoted to such studies; as an incomplete sample, we mention [2, 3, 7, 10, 12, 14, 16–18, 21, 22, 32, 33, 35]. When considering the impact of supplying multiple resources in growth-limiting amounts, it becomes necessary to consider how the resources are used for growth by the individual competitors. Léon and Tumpson [21] and Rapport [30] classify resources in terms of consumer needs, and obtain a spectrum of resource types. At one extreme are the essential resources. These fulfill different requisite needs for growth, and they must be taken together by the consumer. For example, a nitrogen source and a carbon source might be classified as essential for a bacterium. Related studies include [7, 16, 18, 21, 22, 30, 38]. At the other extreme are the perfectly substitutable resources, which are alternative sources of the same requisite nutrient. Examples for a bacterium may include two carbon sources or two sources of nitrogen. Related studies include [3, 4, 29, 38]. Nutrients that fall into neither of these categories fill out the spectrum and are referred to as imperfectly substitutable.

In this paper we consider a model of competition between two species for two perfectly substitutable resources in a chemostat. The competition is assumed to be exploitative, so that the species compete only by consuming the common pool of resources. We focus on functional responses that are strictly monotone increasing functions of resource concentrations, and further assume that the amount of each resource consumed is independent of the concentration of the other resource. The resultant model corresponds to Model I of Léon and Tumpson [21] adapted to the chemostat and restricted to the case of non-reproducing resources. It is also a special case of the model studied in [3], where the possible inhibitory effects that the concentration of one resource may have on the consumption of the other resource were considered. Assuming the existence of an interior equilibrium, Léon and Tumpson [21] derive necessary and sufficient conditions for its local asymptotic stability. In the case of linear response functions, we complete the local analysis of the coexistence equilibrium by ruling out Hopf bifurcations (using compound matrices) and all other local bifurcations that do not involve interaction with the boundary of the positive cone. Though the assumption of linear uptake might appear to be restrictive, such a system is of interest to those studying adaptive dynamics [9]. We then provide sufficient conditions for global asymptotic stability of the coexistence equilibrium using Lyapunov methods. Further, recent advances in the theory of compound matrices combined with bifurcation theory have allowed us to provide a complete global analysis in a different subset of parameter space. This includes but is not limited to the case in which the coexistence equilibrium is a saddle. Finally, we provide a bifurcation analysis based on the dilution rate in the subset of parameter space dictated by the theory of compound matrices, and give a geometric interpretation.

## 2. The Model

The chemostat is a laboratory apparatus designed to provide a controlled environment in which to study the growth of microorganisms under nutrient limitation [28]. It can be thought to consist of three vessels: a feed vessel, a culture vessel, and a waste receptacle (though there are other possibilities, as described in the remark at the end of this section). The feed vessel contains all required nutrients at near-optimal amounts with the exception of those under investigation. These are maintained at growth-limiting amounts. The contents of the feed vessel are supplied to the culture vessel at a constant rate  $D$ , while the medium in the culture vessel is removed to the waste receptacle at the same rate. Thus, constant volume is maintained. The culture vessel, which has been inoculated with one or more populations of microorganisms, is continuously stirred. Thus, nutrients, microorganisms, and byproducts are removed in proportion to their concentrations.

To simplify notation, for the remainder of the paper we will assume that the flow rates have been scaled by the volume of the culture vessel. The concentration of resource  $S$  (respectively, resource  $R$ ) in the feed vessel is denoted  $S^0 > 0$  (respectively,  $R^0 > 0$ ). We will allow for the possibility that the resources in the culture vessel are depleted through some process additional to consumption or removal to the waste receptacle, with corresponding rates  $\alpha_S$  and  $\alpha_R$ . This is done for mathematical completeness, since it does not complicate the presentation. The rate at which resource  $S$  (respectively,  $R$ ) is removed from the culture vessel in the absence of microorganisms is then  $D_S = D + \alpha_S$  (respectively,  $D_R = D + \alpha_R$ ). Scaling  $S^0$  by  $\frac{D_S}{D}$  and  $R^0$  by  $\frac{D_R}{D}$ , the dynamical system in the two-competitor case can be written as

$$\begin{aligned} S' &= (S^0 - S)D_S - \frac{1}{\xi_1}x_1p_1(S) - \frac{1}{\xi_2}x_2p_2(S), \\ R' &= (R^0 - R)D_R - \frac{1}{\eta_1}x_1q_1(R) - \frac{1}{\eta_2}x_2q_2(R), \\ x_1' &= x_1(-D_1 + \mathcal{G}_1(S, R)), \\ x_2' &= x_2(-D_2 + \mathcal{G}_2(S, R)), \\ S(0), R(0), x_1(0), x_2(0) &\geq 0. \end{aligned} \tag{2.1}$$

We denote a solution to equation (2.1) by  $\varphi(t) = (S(t), R(t), x_1(t), x_2(t))$ . If one assumes that the volume of suspension in the culture vessel is one cubic unit, then the quantities in these equations are described as follows. The concentrations of resources  $S$  and  $R$  in the culture vessel at time  $t$  are represented by  $S(t)$  and  $R(t)$ , respectively, while  $x_i(t)$  is the biomass of the  $i$ th population of microorganisms in the culture vessel at time  $t$ ,  $i = 1, 2$ . Each species of microorganism has a natural individual death rate. Combined with the rate at which individuals are removed to the waste receptacle, the biomass of population  $i$  is removed from the dynamics at rate  $D_i x_i$  for  $i = 1, 2$ .

We have assumed that the conversion of nutrient to biomass is proportional to the amount of nutrient consumed. The function  $p_i(S)$  describes the rate of conversion of nutrient  $S$  to biomass of population  $i$  per unit of population  $i$ , with corresponding

growth yield constant  $\xi_i \neq 0$ . Similarly, the function  $q_i(R)$  describes the rate of conversion of nutrient  $R$  to biomass of population  $i$  per unit of population  $i$ , with corresponding growth yield constant  $\eta_i \neq 0$ . Since resources  $S$  and  $R$  are perfectly substitutable, the rate of consumption of nutrient to biomass is made up of a contribution from the consumption of resource  $S$  as well as a contribution from the consumption of resource  $R$ . Therefore,

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

Generally,  $p_i, q_i : \mathbb{R}_+ \rightarrow \mathbb{R}_+$  are assumed to be  $C^1$  with

$$\begin{aligned} p_i(0) &= 0, & p'_i(S) &> 0 \text{ for } S > 0, \\ q_i(0) &= 0, & q'_i(R) &> 0 \text{ for } R > 0, \end{aligned} \tag{2.2}$$

for  $i = 1, 2$ .

Define  $\lambda_i$  and  $\mu_i$  so that

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

Thus  $\lambda_i$  and  $\mu_i$  represent the breakeven concentrations for population  $i$  on resources  $S$  and  $R$ , respectively, when none of the other resource is available. By the monotonicity of  $p_i(S)$ ,  $\lambda_i$  is a uniquely defined extended positive real number provided we assume that  $\lambda_i = \infty$  if  $\mathcal{G}_i(S, 0) < D_i$  for all  $S \geq 0$ . A similar statement can be made for  $\mu_i$  and  $q_i(R)$ .

Under these assumptions, system (2.1) reduces to Model I of Léon and Tumpson [21] adapted to the chemostat and restricted to the case of non-reproducing resources. Model (2.1) also occurs as a special case of the model studied in [3], where the possible inhibitory effects that the concentration of one resource may have on the consumption of the other resource were considered. So as not to detract from the main results of the present paper, we summarize the relevant results in this general setting of monotone functional response in Section 3. In Section 4 we then further specify that the uptake functions  $p_i(S)$  and  $q_i(R)$  be linear. In this context we are able to obtain a complete understanding of the global dynamics of the model for a subset of the parameter space.

*Remark.* We note here that, as shown in [7], this model is also appropriate for the situation in which two feed vessels are used. Then,  $D$  is the sum of the flow rates from the two feed vessels, and  $S^0$  and  $R^0$  are the input concentrations of the two resources, measured in terms of the total input flow rate. □

### 3. General monotone response

Assuming the existence of an interior equilibrium, Léon and Tumpson [21] derive necessary and sufficient conditions for its local asymptotic stability and hence for coexistence of competitors. More specifically, they find that a coexistence equilibrium will be locally asymptotically stable if and only if

$$\left[ \left( \frac{\partial S'}{\partial x_1} \right) \left( \frac{\partial R'}{\partial x_2} \right) - \left( \frac{\partial S'}{\partial x_2} \right) \left( \frac{\partial R'}{\partial x_1} \right) \right] \left[ \left( \frac{\partial x'_1}{\partial S} \right) \left( \frac{\partial x'_2}{\partial R} \right) - \left( \frac{\partial x'_1}{\partial R} \right) \left( \frac{\partial x'_2}{\partial S} \right) \right] > 0 \tag{3.1}$$

when evaluated at the coexistence equilibrium. Physically, *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* [21].

Proceeding with our analysis, we note that all solutions of (2.1) are non-negative and bounded for positive time. These are minimum requirements for a reasonable model of the chemostat.

- Theorem 3.1.** (a) *All solutions of (2.1) for which  $x_i(0) > 0, i = 1, 2$ , are positive and bounded for  $t > 0$ .*  
 (b) *Given any  $\delta > 0$ , each solution of (2.1) satisfies  $S(t) < S^0 + \delta$  and  $R(t) < R^0 + \delta$  for all sufficiently large  $t$ .*  
 (c) *If there exists  $t_0 \geq 0$  such that  $S(t_0) < S^0$ , then  $S(t) < S^0$  for all  $t > t_0$ . A similar result holds for  $R(t)$ .*

Theorem 3.1 is adapted from Theorem 3.2 of [3]. The proof of (a) is similar to the proof given in [6]. The proofs of (b) and (c) are immediate from (2.1). In fact, letting

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

it can be shown that for  $t > 0$

$$z(t) \leq \begin{cases} (S^0 D_S + R^0 D_R)/D_0 & \text{if } z(0) < (S^0 D_S + R^0 D_R)/D_0, \\ z(0) & \text{otherwise,} \end{cases}$$

where  $D_0 = \min\{D_S, D_R, D_1, D_2\}$ . Let

$$\Delta = \left\{ (S, R, x_1, x_2) \in \text{int}(\mathbb{R}_+^4) : S < S^0, R < R^0, z < \frac{S^0 D_S + R^0 D_R}{D_0} \right\}. \tag{3.2}$$

**Proposition 3.2.** *Under the flow described by equation (2.1), each solution beginning in  $\Delta$ , remains in  $\Delta$  for all finite time.*

Three of the critical points of the full four-dimensional system are readily determined: the washout equilibrium  $E_0 = (S^0, R^0, 0, 0)$ , and the single-species equilibria  $E_1 = (\bar{S}_1, \bar{R}_1, \bar{x}_1, 0)$  and  $E_2 = (\bar{S}_2, \bar{R}_2, 0, \bar{x}_2)$ . If any other equilibria of (2.1) exist, they must be interior equilibria. We move now to the question of existence, uniqueness and stability of equilibria of each type. In what follows,  $\frac{\partial f}{\partial x}$  denotes the variational matrix of (2.1) evaluated at a general point  $(S, R, x_1, x_2)$ . It is given by

$$\frac{\partial f}{\partial x} = \begin{bmatrix} -D_S - \sum_{i=1}^2 \frac{1}{\xi_i} x_i p'_i(S) & 0 & -\frac{1}{\xi_1} p_1(S) & -\frac{1}{\xi_2} p_2(S) \\ 0 & -D_R - \sum_{i=1}^2 \frac{1}{\eta_i} x_i q'_i(R) & -\frac{1}{\eta_1} q_1(R) & -\frac{1}{\eta_2} q_2(R) \\ x_1 p'_1(S) & x_1 q'_1(R) & \mathcal{G}_1(S, R) - D_1 & 0 \\ x_2 p'_2(S) & x_2 q'_2(R) & 0 & \mathcal{G}_2(S, R) - D_2 \end{bmatrix}. \tag{3.3}$$

There are only two three-dimensional subsystems of (2.1) of interest. Each involves one population of microorganisms consuming the two non-reproducing, perfectly substitutable resources in the absence of the other population. Theorem 3.10 of [3] yields the following.

**Theorem 3.3.** Fix  $i, j \in \{1, 2\}$  with  $i \neq j$ .

- (a) If  $\mathcal{G}_i(S^0, R^0) \leq D_i$ , then  $E_0$  is globally asymptotically stable for (2.1) with respect to all solutions for which  $x_j(0) = 0$ .
- (b) If  $\mathcal{G}_i(S^0, R^0) > D_i$ , then the single-species equilibrium  $E_i$  exists and is unique. Furthermore,  $E_i$  is globally asymptotically stable for (2.1) with respect to all solutions for which  $x_i(0) > 0$ , and  $x_j(0) = 0$ .

The washout equilibrium  $E_0$  always exists and is clearly the only equilibrium for which  $x_1 = x_2 = 0$ . The eigenvalues of  $\frac{\partial f}{\partial x}(E_0)$  are  $-D_S, -D_R, \mathcal{G}_1(S^0, R^0) - D_1$ , and  $\mathcal{G}_2(S^0, R^0) - D_2$ . If  $\mathcal{G}_1(S^0, R^0) < D_1$  and  $\mathcal{G}_2(S^0, R^0) < D_2$ , then  $E_0$  is locally asymptotically stable. If either  $\mathcal{G}_1(S^0, R^0) > D_1$  or  $\mathcal{G}_2(S^0, R^0) > D_2$ , then  $E_0$  is unstable, and by Theorem 3.3(b) a unique single-species equilibrium exists in the corresponding three-dimensional subsystem.

Now assume that  $\mathcal{G}_1(S^0, R^0) > D_1$  so that, by Theorem 3.3(b),  $E_1 = (\bar{S}_1, \bar{R}_1, \bar{x}_1, 0)$  exists and is unique. The characteristic polynomial of  $\frac{\partial f}{\partial x}(E_1)$  is given by

$$(\alpha - [\mathcal{G}_2(\bar{S}_1, \bar{R}_1) - D_2]) (\alpha^3 + A_1\alpha^2 + A_2\alpha + A_3),$$

where  $\alpha^3 + A_1\alpha^2 + A_2\alpha + A_3$  is the characteristic polynomial of the variational matrix for the three-dimensional subsystem corresponding to the absence of population  $x_2$  evaluated at  $(\bar{S}_1, \bar{R}_1, \bar{x}_1)$ . Since this equilibrium is globally asymptotically stable in this subsystem (again by Theorem 3.3(b)), the corresponding eigenvalues have non-positive real part. In fact, since the amount of each resource consumed is independent of the concentration of the other resource, the eigenvalues have negative real part. (See the relevant discussion on page 157 of [3].) Thus  $E_1$  is locally asymptotically stable with respect to the full four-dimensional system provided  $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2$  and unstable whenever  $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) > D_2$ . A similar results holds for  $E_2$ .

Theorems 3.4 and 3.5 pertain to competition-independent extinction of one or both populations (due to an inadequate supply of resource). The first follows from Theorem 3.4 of [3]. The second then follows from Theorems 3.3(b) and 3.4(a) of this work.

- Theorem 3.4.** (a) If  $\mathcal{G}_i(S^0, R^0) < D_i$  for some  $i \in \{1, 2\}$ , then  $x_i(t) \rightarrow 0$  as  $t \rightarrow \infty$ .  
 (b) If  $x_i(t) \rightarrow 0$  as  $t \rightarrow \infty$  for  $i = 1, 2$ , then  $E_0$  is globally asymptotically stable for (2.1).

**Theorem 3.5.** Fix  $i, j \in \{1, 2\}$  with  $i \neq j$ . Suppose  $\mathcal{G}_i(S^0, R^0) > D_i$  and  $\mathcal{G}_j(S^0, R^0) < D_j$ . Then  $E_i$  is globally asymptotically stable for (2.1) with respect to all solutions for which  $x_i(0) > 0$  and  $x_j(0) \geq 0$ .

Thus, the dynamics of system (2.1) can readily be determined when the resource supply is inadequate for one or both populations. We turn now to the more challenging problem in which  $\mathcal{G}_i(S^0, R^0) > D_i$  for  $i = 1, 2$ . Conditions for the existence of an interior (coexistence) equilibrium  $E^* = (S^*, R^*, x_1^*, x_2^*)$  will be outlined in the remainder of this section. The balance of the paper is then devoted to the global

dynamics of system (2.1) when the resource supply is adequate for each population in the absence of its competitor.

**Theorem 3.6.** *Suppose  $\mathcal{G}_i(S^0, R^0) > D_i$  for  $i = 1, 2$ . Then  $E_0$  is not an omega limit point of any solution to (2.1) for which  $x_i(0) > 0, i = 1, 2$ .*

*Proof.* Choose  $X = (S(0), R(0), x_1(0), x_2(0))$  with  $x_i(0) > 0, i = 1, 2$ . Since solutions to (2.1) are bounded in forward time, the omega limit set  $\Omega(X)$  is a non-empty compact set which is invariant with respect to system (2.1).

Suppose  $E_0 \in \Omega(X)$ . Since  $\mathcal{G}_i(S^0, R^0) > D_i$  for  $i = 1, 2, E_0$  is an unstable hyperbolic critical point. From (2.1) it is clear that  $E_0$  is globally attracting with respect to all solutions initiating in its stable manifold  $M^+(E_0) = \{(S, R, 0, 0) \in \mathbb{R}_+^4\}$ . Furthermore, each solution in  $M^+(E_0) \setminus \{E_0\}$  is unbounded for negative time. Since  $X \notin M^+(E_0), \Omega(X)$  contains more than just  $E_0$ . Therefore, by the Butler-McGehee Lemma (see Lemma A1 of [11]) there exists  $P \in (M^+(E_0) \setminus \{E_0\}) \cap \Omega(X)$  and hence  $\mathcal{O}(P) \subset \Omega(X)$  where  $\mathcal{O}(P)$  denotes the entire orbit through  $P$ . But then as  $t \rightarrow -\infty, \mathcal{O}(P)$  is unbounded, contradicting the fact that  $\Omega(X)$  is bounded. Therefore  $E_0 \notin \Omega(X)$ . □

**Corollary 3.7.** *Suppose  $\mathcal{G}_i(S^0, R^0) > D_i$  for  $i = 1, 2$ . Then any solution to equation (2.1) for which  $x_i(0) > 0, i = 1, 2$  satisfies  $\inf_{t \geq 0} \max\{x_1(t), x_2(t)\} > 0$ .*

Thus, we know that each solution for which  $x_i(0) > 0, i = 1, 2$  is bounded away from the set for which  $x_1 = x_2 = 0$ . The next theorem says that there is a uniform bound.

**Theorem 3.8.** *Suppose  $\mathcal{G}_i(S^0, R^0) > D_i$  for  $i = 1, 2$ . Then there exists  $\beta > 0$  such that any solution to equation (2.1) for which  $x_i(0) > 0, i = 1, 2$  satisfies  $\liminf_{t \rightarrow \infty} \max\{x_1(t), x_2(t)\} \geq \beta$ .*

The proof is similar to but simpler than the proof in [5] which uses compact isolating neighbourhoods to give conditions under which weak persistence implies uniform persistence.

An interior equilibrium  $E^*$  for (2.1) is not necessarily unique. Such an example need not involve complicated uptake functions. For instance, if

$$\mathcal{G}_1(S, R) = \frac{4S}{1.8 + S} + \frac{2R}{0.4 + R} \quad \text{and} \quad \mathcal{G}_2(S, R) = 2S + 3R,$$

with

$$\xi_1 = 200, \eta_1 = 1, \xi_2 = 3, \eta_2 = 20, \\ S^0 = R^0 = 1, \text{ and } D_S = D_R = D_1 = D_2 = 1,$$

then there exist precisely two interior equilibria. Note that in this example population 1 consumes both resources according to Michaelis-Menten dynamics, while population 2 consumes both resources linearly. If instead the functional response of both species to both resources is linear then, provided the breakeven concentrations are distinct (see (4.2)), there can be at most one interior equilibrium.

**4. Linear functional response: local analysis**

In this section we assume that the uptake functions are linear:

$$p_i(S) = c_i S, \quad q_i(R) = k_i R, \tag{4.1}$$

with  $c_i, k_i > 0, i = 1, 2$ . Note that for linear uptake functions, the breakeven concentrations are  $\lambda_i = \frac{D_i}{c_i}$  and  $\mu_i = \frac{D_i}{k_i}$ . The critical points are isolated if

$$(\lambda_1, \mu_1) \neq (\lambda_2, \mu_2), \tag{4.2}$$

as this ensures that the nullclines for  $x_1$  and  $x_2$  do not lie on top of each other. In fact, Theorem 3.15 of [3] provides the following.

**Theorem 4.1.** *Suppose (4.1) holds and that  $\mathcal{G}_i(S^0, R^0) > D_i$  for  $i = 1, 2$ .*

- (a) *If  $(\mathcal{G}_1(\bar{S}_2, \bar{R}_2) - D_1)(\mathcal{G}_2(\bar{S}_1, \bar{R}_1) - D_2) > 0$ , then  $E^*$  exists and is unique.*
- (b) *If  $(\mathcal{G}_1(\bar{S}_2, \bar{R}_2) - D_1)(\mathcal{G}_2(\bar{S}_1, \bar{R}_1) - D_2) < 0$ , then  $E^*$  does not exist.*

Moreover, we can determine the coordinates of the interior equilibrium  $E^* = (S^*, R^*, x_1^*, x_2^*)$ . The  $(S, R)$  coordinates of  $E^*$  come from solving

$$\begin{aligned} c_1 S + k_1 R &= D_1, \\ c_2 S + k_2 R &= D_2. \end{aligned}$$

This system will have at most one admissible solution whenever hypothesis (4.2) holds. Solving, we find

$$S^* = \frac{D_1 k_2 - D_2 k_1}{c_1 k_2 - c_2 k_1}$$

and

$$R^* = \frac{D_2 c_1 - D_1 c_2}{c_1 k_2 - c_2 k_1}.$$

The  $(x_1^*, x_2^*)$  coordinates of the coexistence equilibrium then come from solving

$$\begin{aligned} x_1 \frac{c_1}{\xi_1} S^* + x_2 \frac{c_2}{\xi_2} S^* &= (S^0 - S^*) D_S, \\ x_1 \frac{k_1}{\eta_1} R^* + x_2 \frac{k_2}{\eta_2} R^* &= (R^0 - R^*) D_R. \end{aligned}$$

Setting

$$\Gamma(S^*, R^*) = S^* R^* \left( \frac{c_1 k_2}{\xi_1 \eta_2} - \frac{c_2 k_1}{\xi_2 \eta_1} \right),$$

we find

$$x_1^* = \frac{1}{\Gamma(S^*, R^*)} \left( (S^0 - S^*) D_S \frac{k_2}{\eta_2} R^* - (R^0 - R^*) D_R \frac{c_2}{\xi_2} S^* \right)$$



and

$$x_2^* = \frac{1}{\Gamma(S^*, R^*)} \left( (R^0 - R^*) D_R \frac{c_1}{\xi_1} S^* - (S^0 - S^*) D_S \frac{k_1}{\eta_1} R^* \right).$$

Table 4.1 summarizes the existence and local stability results for the equilibria of system (2.1) when (4.1) holds (see Table 2 of [3]). With this additional information concerning the local stability of the equilibria, Theorem 4.1 states that for linear uptake functions, given the existence (and hyperbolicity) of  $E_1$  and  $E_2$ , the interior equilibrium exists (and is unique) if and only if the local asymptotic stability of  $E_1$  and  $E_2$  are the same (i.e. each is locally asymptotically stable or each is unstable). A consequence of the stated existence criterion for  $E^*$  is that

$$c_1 k_2 - c_2 k_1 \neq 0 \quad \text{and} \quad \frac{c_1 k_2}{\xi_1 \eta_2} - \frac{c_2 k_1}{\xi_2 \eta_1} \neq 0. \tag{4.3}$$

The condition for the local asymptotic stability of  $E^*$  given in Table 4.1 follows from the results of Léon and Tumpson [21]. We now complete the local stability analysis of  $E^*$  by ruling out Hopf bifurcations and other local bifurcations.

Following the formula given in [24], we can use equation (2.1) to write the second additive compound of the Jacobian matrix evaluated at the coexistence equilibrium as

**Table 4.1.** Summary of local stability results for (2.1) under assumption (4.1).

Critical Point	Existence Criteria	Criteria for Local Asymptotic Stability
$E_0 = (S^0, R^0, 0, 0)$	Always Exists	$\mathcal{G}_i(S^0, R^0) < D_i, i = 1, 2$
$E_1 = (\bar{S}_1, \bar{R}_1, \bar{x}_1, 0)$	$\mathcal{G}_1(S^0, R^0) > D_1$	$\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2$
$E_2 = (\bar{S}_2, \bar{R}_2, 0, \bar{x}_2)$	$\mathcal{G}_2(S^0, R^0) > D_2$	$\mathcal{G}_1(\bar{S}_2, \bar{R}_2) < D_1$
$E^* = (S^*, R^*, x_1^*, x_2^*)$	$\mathcal{G}_i(S^0, R^0) > D_i, \quad i = 1, 2$ and $(\mathcal{G}_1(\bar{S}_2, \bar{R}_2) - D_1) \times (\mathcal{G}_2(\bar{S}_1, \bar{R}_1) - D_2) > 0$	$\mathcal{G}_1(\bar{S}_2, \bar{R}_2) > D_1$ and $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) > D_2$

$$\frac{\partial f^{[2]}}{\partial x}(E^*) = \begin{bmatrix} -\left(\frac{D_S S^0}{S^*} + \frac{D_R R^0}{R^*}\right) - \frac{k_1}{\eta_1} R^* - \frac{k_2}{\eta_2} R^* & \frac{c_1}{\xi_1} S^* & \frac{c_2}{\xi_2} S^* & 0 \\ k_1 x_1^* & -\frac{D_S S^0}{S^*} & 0 & 0 & 0 & \frac{c_2}{\xi_2} S^* \\ k_2 x_2^* & 0 & -\frac{D_S S^0}{S^*} & 0 & 0 & -\frac{c_1}{\xi_1} S^* \\ -c_1 x_1^* & 0 & 0 & -\frac{D_R R^0}{R^*} & 0 & \frac{k_2}{\eta_2} R^* \\ -c_2 x_2^* & 0 & 0 & 0 & -\frac{D_R R^0}{R^*} & -\frac{k_1}{\eta_1} R^* \\ 0 & -c_2 x_2^* & c_1 x_1^* & -k_2 x_2^* & k_1 x_1^* & 0 \end{bmatrix}. \tag{4.4}$$

Suppose there is a Hopf bifurcation at the coexistence equilibrium. Then two of the eigenvalues of  $\frac{\partial f}{\partial x}$  are purely imaginary conjugates, adding to zero. Recalling that the eigenvalues of the second compound of a matrix are sums of pairs of eigenvalues of the original matrix [27], we see that when there is a Hopf bifurcation at  $E^*$ ,  $\frac{\partial f^{[2]}}{\partial x}(E^*)$  has zero as an eigenvalue, and so the determinant of  $\frac{\partial f^{[2]}}{\partial x}(E^*)$  must equal zero. Taking the determinant of  $\frac{\partial f^{[2]}}{\partial x}$  as it appears in equation (4.4) gives (omitting the superscript  $*$ )

$$\begin{aligned} \det\left(\frac{\partial f^{[2]}}{\partial x}\right) &= \frac{D^2 S^0 R^0}{SR\eta_1^2 \eta_2^2 \xi_1^2 \xi_2^2} \left( k_1^4 \xi_1^2 \xi_2^2 \eta_2^2 R^2 x_1^2 - 2k_1^2 c_2^2 \xi_1^2 \xi_2^2 \eta_1 \eta_2^2 SR x_1 x_2 \right. \\ &\quad \left. + c_2^4 \xi_1^2 \eta_1^2 \eta_2^2 S^2 x_2^2 + k_2^4 \xi_1^2 \xi_2^2 \eta_1^2 R^2 x_2^2 - 2k_2^2 c_1^2 \xi_1 \xi_2^2 \eta_1^2 \eta_2 SR x_1 x_2 \right. \\ &\quad \left. + c_1^4 \xi_2^2 \eta_1^2 \eta_2^2 S^2 x_1^2 + \text{other positive terms} \right) \\ &> \frac{D^2 S^0 R^0}{SR\eta_1^2 \eta_2^2 \xi_1^2 \xi_2^2} \left( \xi_1^2 \eta_2^2 (k_1^2 \xi_2 R x_1 - c_2^2 \eta_1 S x_2)^2 \right. \\ &\quad \left. + \xi_2^2 \eta_1^2 (k_2^2 \xi_1 R x_2 - c_1^2 \eta_2 S x_1)^2 \right) \\ &\geq 0. \end{aligned} \tag{4.5}$$

Thus, the determinant of  $\frac{\partial f^{[2]}}{\partial x}$  is never zero at  $E^*$  and therefore  $\frac{\partial f}{\partial x}(E^*)$  cannot have two purely imaginary eigenvalues. Hence, there cannot be a Hopf bifurcation at the coexistence equilibrium.

Also, the determinant of the Jacobian at  $E^*$  can be shown to be

$$\det\left(\frac{\partial f}{\partial x}(E^*)\right) = S^* R^* x_1^* x_2^* (c_1 k_2 - c_2 k_1) \left( \frac{c_1}{\xi_1} \frac{k_2}{\eta_2} - \frac{c_2}{\xi_2} \frac{k_1}{\eta_1} \right). \tag{4.6}$$

Suppose parameters are varied so that an eigenvalue of  $E^*$  passes through zero. At the bifurcation point, either  $E^*$  is interacting with the boundary of the positive cone or  $E^*$  exists as an equilibrium in the interior of the positive cone, in which case (4.3) must hold. But, if (4.3) holds then the determinant of  $E^*$  cannot be zero, and so there is no bifurcation. Thus, if parameters are varied so that an eigenvalue of  $E^*$  passes through zero, then  $E^*$  must be interacting with the boundary of the positive cone. This can only happen at an equilibrium in the boundary. Hence such a bifurcation involves  $E^*$  coalescing with either  $E_1$  or  $E_2$  (or possibly  $E_0$  if there is a higher order bifurcation).

**5. Linear functional response: global analysis using Lyapunov functions**

We now give sufficient conditions for global asymptotic stability of the coexistence equilibrium using Lyapunov methods.

**Theorem 5.1.** *Consider system (2.1) and assume that (4.1) holds. Suppose that*

- (i)  $\mathcal{G}_1(S^0, R^0) > D_1$  and  $\mathcal{G}_2(S^0, R^0) > D_2$ ,
- (ii)  $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) > D_1$  and  $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2$ ,
- (iii)  $\frac{k_2 \bar{R}_1}{D_2 - c_2 \bar{S}_1} < \frac{\xi_1 \eta_2}{\xi_2 \eta_1} < \frac{D_2 - k_2 \bar{R}_1}{c_2 \bar{S}_1}$ .

Then  $E_1$  is globally asymptotically stable for system (2.1) with respect to all solutions for which  $x_1(0) > 0$  and  $x_2(0) \geq 0$ .

By simply interchanging the indices, the analogous result yields a global asymptotic stability condition for  $E_2$ .

Note that by Theorem 3.3 (b), condition (i) of Theorem 5.1 implies that  $E_1$  and  $E_2$  exist and are unique. From Table 4.1, condition (ii) implies that  $E_1$  is locally asymptotically stable and  $E_2$  is unstable. By Theorem 4.1(b),  $E^*$  does not exist. Condition (ii) implies there is an open interval of values in which  $\frac{\xi_1 \eta_2}{\xi_2 \eta_1}$  may lie so that condition (iii) is satisfied; furthermore, this interval contains 1.

*Proof.* Define  $L : \{(S, R, x_1, x_2) \in \mathbb{R}_+^4 : S, R, x_1 > 0\} \rightarrow \mathbb{R}$  by

$$L(S, R, x_1, x_2) = \xi_1 \int_{\bar{S}_1}^S \frac{\tau - \bar{S}_1}{\tau} d\tau + \eta_1 \int_{\bar{R}_1}^R \frac{\tau - \bar{R}_1}{\tau} d\tau + \int_{\bar{x}_1}^{x_1} \frac{\tau - \bar{x}_1}{\tau} d\tau + \sigma x_2$$

where  $\sigma = \min\{\frac{\xi_1}{\xi_2}, \frac{\eta_1}{\eta_2}\}$ . Then  $L$  is  $C^1$  on the interior of  $\mathbb{R}_+^4$ ,  $E_1$  is the global minimum of  $L$  on  $\mathbb{R}_+^4$ , and  $L(\bar{S}_1, \bar{R}_1, \bar{x}_1, 0) = 0$ . Using  $D_1 = c_1 \bar{S}_1 + k_1 \bar{R}_1$ , the time derivative of  $L$  computed along solutions of (2.1) is

$$\begin{aligned} L'(S, R, x_1, x_2) &= \xi_1 \frac{(S - \bar{S}_1)}{S} S' + \eta_1 \frac{(R - \bar{R}_1)}{R} R' + \frac{(x_1 - \bar{x}_1)}{x_1} x_1' + \sigma x_2' \\ &= \xi_1 \frac{(S - \bar{S}_1)}{S} \left( (S^0 - S) D_S - \frac{c_1}{\xi_1} \bar{x}_1 S \right) \\ &\quad + \eta_1 \frac{(R - \bar{R}_1)}{R} \left( (R^0 - R) D_R - \frac{k_1}{\eta_1} \bar{x}_1 R \right) \\ &\quad + x_2 \left( c_2 S \left( \sigma - \frac{\xi_1}{\xi_2} \right) + k_2 R \left( \sigma - \frac{\eta_1}{\eta_2} \right) \right) \\ &\quad + c_2 \bar{S}_1 \frac{\xi_1}{\xi_2} + k_2 \bar{R}_1 \frac{\eta_1}{\eta_2} - D_2 \sigma \end{aligned}$$

Let  $H$  denote the coefficient of  $x_2$ . Noting that  $(S^0 - S) D_S - \frac{c_1}{\xi_1} \bar{x}_1 S$  and  $(R^0 - R) D_R - \frac{k_1}{\eta_1} \bar{x}_1 R$  have the same signs as  $\bar{S}_1 - S$  and  $\bar{R}_1 - R$ , respectively,  $L' \leq 0$  whenever  $H \leq 0$  now show that (iii) ensures  $H < 0$ .

Consider  $\sigma = \frac{\xi_1}{\xi_2} \leq \frac{\eta_1}{\eta_2}$ . Hypothesis (ii) and (4.1) imply that  $D_2 - k_2 \bar{R}_1 > c_2 \bar{S}_1$ , so the right inequality of hypothesis (iii) holds automatically. Further,

$$\begin{aligned} H &= k_2 R \left( \frac{\xi_1}{\xi_2} - \frac{\eta_1}{\eta_2} \right) + c_2 \bar{S}_1 \frac{\xi_1}{\xi_2} + k_2 \bar{R}_1 \frac{\eta_1}{\eta_2} - D_2 \frac{\xi_1}{\xi_2} \\ &\leq c_2 \bar{S}_1 \frac{\xi_1}{\xi_2} + k_2 \bar{R}_1 \frac{\eta_1}{\eta_2} - D_2 \frac{\xi_1}{\xi_2} \end{aligned}$$

which is negative if and only if

$$\frac{k_2 \bar{R}_1}{D_2 - c_2 \bar{S}_1} < \frac{\xi_1 \eta_2}{\xi_2 \eta_1}.$$

If instead,  $\sigma = \frac{\eta_1}{\eta_2} \leq \frac{\xi_1}{\xi_2}$ , then the left inequality in hypothesis (iii) holds automatically and the requirement that  $H$  be negative yields

$$\frac{\xi_1 \eta_2}{\xi_2 \eta_1} < \frac{D_2 - k_2 \bar{R}_1}{c_2 \bar{S}_1}.$$

Thus,  $L'(S, R, x_1, x_2) \leq 0$ , and so  $L$  is a Lyapunov function for (2.1) in  $\text{int}(\mathbb{R}_+^4)$  in accordance with Definition 1.1 of [39]. Note that, since  $H < 0$ ,  $L'(S, R, x_1, x_2) = 0$  if and only if  $S = \bar{S}_1$ ,  $R = \bar{R}_1$ , and  $x_2 = 0$ . Hence, since all solutions are bounded in forward time (Theorem 3.1(a)), Theorem 1.2 of [39] implies every solution of (2.1) for which  $S(0), R(0), x_1(0) > 0$  approaches  $\mathcal{M}$ , where  $\mathcal{M}$  is the largest invariant subset of  $\{(S, R, x_1, x_2) \in \mathbb{R}_+^4 : S = \bar{S}_1, R = \bar{R}_1, x_1 \geq 0, x_2 = 0\}$ . But then  $\mathcal{M} = \{E_1\}$ , a single point, since by Theorem 3.3(b) the single-species survival equilibrium  $E_1$  is unique, and so  $x_1 \neq \bar{x}_1$  implies that  $S' \neq 0$  and  $R' \neq 0$ , violating the invariance of  $\mathcal{M}$ .  $\square$

The final result of this section pertains to the global stability of the coexistence equilibrium.

**Theorem 5.2.** *Consider system (2.1) and assume that (4.1) holds. Suppose*

- (i)  $\mathcal{G}_1(S^0, R^0) > D_1$  and  $\mathcal{G}_2(S^0, R^0) > D_2$ ,
- (ii)  $(\mathcal{G}_1(\bar{S}_2, \bar{R}_2) - D_1)(\mathcal{G}_2(\bar{S}_1, \bar{R}_1) - D_2) > 0$ ,
- (iii)  $\xi_1 \eta_2 = \xi_2 \eta_1$ .

*Then  $E^*$  is globally asymptotically stable for system (2.1) with respect to all solutions for which  $x_1(0) > 0$  and  $x_2(0) > 0$ .*

Note that by Theorem 3.3 (b), condition (i) of Theorem 5.2 implies that  $E_1$  and  $E_2$  exist, while condition (ii) and assumption (4.1) imply that the interior equilibrium  $E^*$  exists, is unique, and is locally asymptotically stable (see the remark at the end of this section).

*Proof.* Define  $L : \text{int}(\mathbb{R}_+^4) \rightarrow \mathbb{R}$  by

$$L(S, R, x_1, x_2) = \xi_1 \int_{S^*}^S \frac{\tau - S^*}{\tau} d\tau + \eta_1 \int_{R^*}^R \frac{\tau - R^*}{\tau} d\tau + \sum_{i=1}^2 \gamma_i \int_{x_i^*}^{x_i} \frac{\tau - x_i^*}{\tau} d\tau,$$

where  $\gamma_1 = 1$  and  $\gamma_2 = \xi_1/\xi_2$ . Then  $L \in C^1(\text{int}(\mathbb{R}_+^4))$ ,  $E^*$  is the global minimum of  $L$  on  $\mathbb{R}_+^4$ , and  $L(S^*, R^*, x_1^*, x_2^*) = 0$ . Note that under hypothesis (iii)

$$\gamma_i = \frac{\xi_1}{\xi_i} = \frac{\eta_1}{\eta_i}.$$

Using  $D_i = c_i S^* + k_i R^*$ , the time derivative of  $L$  computed along solutions of (2.1) is

$$\begin{aligned} L'(S, R, x_1, x_2) &= \xi_1 \left( \frac{S - S^*}{S} \right) \left( (S^0 - S)D_S - \frac{c_1}{\xi_1}x_1S - \frac{c_2}{\xi_2}x_2S \right) \\ &\quad + \eta_1 \left( \frac{R - R^*}{R} \right) \left( (R^0 - R)D_R - \frac{k_1}{\eta_1}x_1R - \frac{k_2}{\eta_2}x_2R \right) \\ &\quad + \sum_{i=1}^2 \gamma_i \left( \frac{x_i - x_i^*}{x_i} \right) x_i (c_i(S - S^*) + k_i(R - R^*)) \\ &= \sum_{i=1}^2 x_i \left( c_i(S - S^*) \left( \gamma_i - \frac{\xi_1}{\xi_i} \right) + k_i(R - R^*) \left( \gamma_i - \frac{\eta_1}{\eta_i} \right) \right) \\ &\quad + \xi_1 \frac{(S - S^*)}{S} \left( (S^0 - S)D_S - \sum_{i=1}^2 c_i x_i^* S \frac{\gamma_i}{\xi_i} \right) \\ &\quad + \eta_1 \frac{(R - R^*)}{R} \left( (R^0 - R)D_R - \sum_{i=1}^2 k_i x_i^* R \frac{\gamma_i}{\eta_i} \right) \\ &= \xi_1 \frac{(S - S^*)}{S} \left( (S^0 - S)D_S - \sum_{i=1}^2 \frac{c_i}{\xi_i} x_i^* S \right) \\ &\quad + \eta_1 \frac{(R - R^*)}{R} \left( (R^0 - R)D_R - \sum_{i=1}^2 \frac{k_i}{\eta_i} x_i^* R \right). \end{aligned}$$

Note that  $(S^0 - S)D_S > \sum_{i=1}^2 \frac{c_i}{\xi_i} x_i^* S$  for  $0 < S < S^*$ , while  $(S^0 - S)D_S < \sum_{i=1}^2 \frac{c_i}{\xi_i} x_i^* S$  for  $S > S^*$ . A similar statement holds for  $R$ . Thus,  $L'(S, R, x_1, x_2) \leq 0$ , and so  $L$  is a Lyapunov function for (2.1) in  $\text{int}(\mathbb{R}_+^4)$  in accordance with Definition 1.1 of [39]. Note that  $L'(S, R, x_1, x_2) = 0$  if and only if  $S = S^*$  and  $R = R^*$ . Hence by Theorem 3.1(a) and Theorem 1.2 of [39], every solution of (2.1) for which  $x_1(0) > 0$  and  $x_2(0) > 0$  approaches  $\mathcal{M}$ , where  $\mathcal{M}$  is the largest invariant subset of  $\{(S, R, x_1, x_2) \in \mathbb{R}_+^4 : S = S^*, R = R^*, x_1 \geq 0, x_2 \geq 0\}$ . But then  $\mathcal{M} = \{E^*\}$ , a single point, since (4.2) implies the only choice for  $x_1$  and  $x_2$  that ensures  $S' \equiv 0$  and  $R' \equiv 0$  is  $x_1 = x_1^*$  and  $x_2 = x_2^*$ .  $\square$

**Remark concerning Theorem 5.2:** Note that hypothesis (ii) implies the existence of the interior equilibrium  $E^*$ . It does not, in general, imply the local asymptotic stability of  $E^*$ . (See Table 4.1.) One might question if we have indeed proved that

$E^*$  can be an unstable equilibrium that is globally asymptotically stable! In fact, using hypothesis (iii) in the left hand side of (3.1) yields

$$\frac{1}{\xi_1 \eta_2} S^* R^* x_1^* x_2^* (c_1 k_2 - k_1 c_2)^2,$$

which is positive by (4.3). Therefore, if condition (iii) holds, then  $E^*$  is locally asymptotically stable (by the necessary and sufficient condition given in [21]) whenever it exists.

It is possible for system (2.1) to have an unstable interior equilibrium when hypothesis (iii) does not hold. Taking

$$\mathcal{G}_1(S, R) = 1.5S + 1.7R \quad \text{and} \quad \mathcal{G}_2(S, R) = 1.7S + 1.5R,$$

with

$$\begin{aligned} \xi_1 = 0.8, \eta_1 = 1, \xi_2 = 1, \eta_2 = 0.8, \\ S^0 = R^0 = 1, D_S = D_R = 0.97, \text{ and } D_1 = D_2 = 1.33, \end{aligned}$$

then there exists precisely one interior equilibrium, and the linearization about this equilibrium yields three eigenvalues with negative real part and one positive eigenvalue. □

### 6. Stability theory using compound matrices

We present here an application of the theory of Li and Muldowney to a situation which is frequently encountered in mathematical models related to biology and epidemiology. While the Li-Muldowney theory has generally been applied to demonstrate the global stability of an equilibrium, it is used here to show that the omega limit set of each orbit consists of a single equilibrium. This was also done in [1], but the method used here is more direct and more easily applied. An overview of compound matrices and their applications to global stability theory can be found in [23–25, 27].

Let  $B$  be the closed Euclidean unit ball in  $\mathbb{R}^2$  with boundary  $\partial B$ . Letting  $\text{Lip}(X \rightarrow Y)$  be the set of Lipschitzian functions from  $X$  to  $Y$ , a function  $\phi \in \text{Lip}(B \rightarrow \mathcal{D})$  is called a simply connected rectifiable surface in  $\mathcal{D}$ . We say  $\phi(\partial B)$  is the boundary of  $\phi$ . A function  $\psi \in \text{Lip}(\partial B \rightarrow \mathcal{D})$  is called a closed rectifiable curve in  $\mathcal{D}$  and is called simple if it is one-to-one. Let  $\Sigma(\psi, \mathcal{D}) = \{\phi \in \text{Lip}(B \rightarrow \mathcal{D}) : \phi|_{\partial B} = \psi\}$ . In [25], it is shown that if  $\psi$  is contained in a simply connected open subset of  $\mathcal{D}$ , then  $\Sigma(\psi, \mathcal{D})$  is non-empty.

Let  $\|\cdot\|$  be a norm on  $\mathbb{R}^{\binom{n}{2}}$ . Consider a functional  $\mathcal{S}$  on surfaces in  $\mathcal{D} \subseteq \mathbb{R}^n$  defined by

$$\mathcal{S}\phi = \int_B \left\| Q \cdot \left( \frac{\partial \phi}{\partial u_1} \wedge \frac{\partial \phi}{\partial u_2} \right) \right\| du \tag{6.1}$$

where  $u = (u_1, u_2)$ ,  $u \mapsto \phi(u)$  is in  $\text{Lip}(B \rightarrow \mathcal{D})$ , the wedge product  $\frac{\partial \phi}{\partial u_1} \wedge \frac{\partial \phi}{\partial u_2}$  is a vector in  $\mathbb{R}^{\binom{n}{2}}$  and  $Q$  is an  $\binom{n}{2} \times \binom{n}{2}$  matrix such that  $\|Q^{-1}\|$  is bounded on  $\phi(B)$ .

Functionals of this form give a measure of surface area. The next result, which follows from the development in [24] and [25], says that given a simple closed curve  $\psi$  in  $\mathbb{R}^n$  and a measure of surface area, all surfaces with boundary  $\psi$  have surface area uniformly bounded away from zero.

**Proposition 6.1.** *Suppose that  $\psi$  is a simple closed rectifiable curve in  $\mathbb{R}^n$ . Then there exists  $\delta > 0$  such that*

$$S\phi \geq \delta$$

for all  $\phi \in \Sigma(\psi, \mathbb{R}^n)$ .

Let  $f : \mathcal{D} \rightarrow \mathbb{R}^n$  be  $C^1$  where  $\mathcal{D} \subseteq \mathbb{R}^n$ . Consider the equation

$$\frac{dx}{dt} = f(x). \tag{6.2}$$

Let  $x(t; x_0)$  denote the solution to equation (6.2) which passes through  $x_0$  at time 0. For any surface  $\phi$ , we define the surface  $\phi_t$  by  $\phi_t(u) = x(t; \phi(u))$  for  $u \in B$ . Note that when viewed as a function of  $t$ ,  $\phi_t(u)$  gives the solution to (6.2) which passes through the point  $\phi(u)$  at time 0.

It follows from work done in [24] and [25] that

$$S\phi_t = \int_B \|z(t)\| du \tag{6.3}$$

where for each  $u \in B$ ,  $z(t) = z(t; \phi(u)) = Q(\phi_t(u)) \cdot \left( \frac{\partial \phi_t}{\partial u_1} \wedge \frac{\partial \phi_t}{\partial u_2} \right)$  is the solution to

$$\frac{dz}{dt} = M(\phi_t(u))z, \quad z(0) = Q(\phi(u)) \cdot \left( \frac{\partial \phi}{\partial u_1} \wedge \frac{\partial \phi}{\partial u_2} \right) \tag{6.4}$$

where  $M = Q_f Q^{-1} + Q \frac{\partial f}{\partial x} Q^{-1}$ . Here,  $Q_f$  is the directional derivative of  $Q$  in the direction of the vector field  $f$ , and  $\frac{\partial f}{\partial x}$  is the second additive compound of  $\frac{\partial f}{\partial x}$ .

Suppose there exist  $T, g > 0$  such that  $\|z(t)\| \leq \|z(0)\| e^{-gt}$  for all initial conditions and all  $t \geq T$ . Then equation (6.3) implies

$$S\phi_t \leq e^{-gt} S\phi \tag{6.5}$$

for  $t \geq T$ . As  $t$  becomes arbitrarily large, the right hand side of (6.5) goes to zero. Thus, by Proposition 6.1, for large  $t$  the boundary of  $\phi_t$  must be different from the boundary of  $\phi$ . In particular this means that the boundary of  $\phi$  could not have been an invariant closed curve under the flow (6.2), precluding the possibility of a periodic orbit, a homoclinic orbit or a heteroclinic cycle. In [24] this argument is extended, using Pugh’s Closing Lemma, to rule out non-constant non-wandering points. One consequence of this is that all omega limit points of solutions to (6.2) must be equilibria.

We give here a theorem that follows from the work of Li and Muldowney, which suits the present context. It is believed that this theorem will be relevant for many biological and epidemiological models.

**Theorem 6.2.** *Let  $\mathcal{D}$  be a simply connected open subset of  $\mathbb{R}^n$  such that solutions of equation (6.2) with  $x(0) = x_0 \in \mathcal{D}$ , remain in  $\mathcal{D}$  for all finite time. Let  $\|\cdot\|$  be a norm on  $\mathbb{R}^{\binom{n}{2}}$ , and let  $Q$  be an  $\binom{n}{2} \times \binom{n}{2}$  matrix-valued function on  $\mathcal{D}$  such that  $\|Q^{-1}\|$  is bounded on  $\mathcal{D}$ . Consider*

$$\frac{dz}{dt} = M(x(t; x_0))z \tag{6.6}$$

with  $M = Q_f Q^{-1} + Q \frac{\partial f}{\partial x} Q^{-1}$ . If for each compact set  $\mathcal{C} \subset \mathcal{D}$ , there exist  $T, g > 0$  such that  $\|z(t)\| \leq \|z(0)\| e^{-gt}$  for  $t \geq T$ , for all  $z(0) \in \mathbb{R}^{\binom{n}{2}}$  and all  $x_0 \in \mathcal{C}$ , then the omega limit set of any solution to (6.2) which is bounded away from the boundary of  $\mathcal{D}$  consists entirely of equilibria.

*Remark.* Although, in Theorem 6.2, a general compact set  $\mathcal{C} \subset \mathcal{D}$  is referred to, all that is necessary is that the condition be true when  $\mathcal{C}$  is a simply connected rectifiable surface in  $\mathcal{D}$ . □

If, in addition to the conditions of the above theorem, it can be shown that any solution to equation (6.2) which has a limit point on the boundary of  $\mathcal{D}$  in fact limits to an equilibrium in the boundary of  $\mathcal{D}$ , then each solution beginning in  $\mathcal{D}$  limits to a single equilibrium, either in the interior or on the boundary.

### 7. Linear functional response: global analysis using compound matrices

In this section we re-examine the global dynamics of system (2.1) under hypotheses (4.1) and (4.2), using the theoretical framework of compound matrices discussed in Section 6. Since the global dynamics have already been resolved in the case of competition-independent extinction, we will now apply Theorem 6.2 under the assumption that we do not have competition-independent extinction (so that  $G_i(S^0, R^0) > D_i$  for  $i = 1, 2$ ).

Take  $\mathcal{D} = \Delta$  where  $\Delta$  is given in equation (3.2). Note that  $\Delta$  is open, simply connected, and positively invariant for finite time, as required by Theorem 6.2.

For a non-zero constant  $v$  (to be specified later), define

$$Q = \frac{1}{x_1 x_2} \text{diag} \left( v \sqrt{\frac{x_1 x_2}{SR}}, \sqrt{\frac{\xi_2 x_2}{S}}, \sqrt{\frac{\xi_1 x_1}{S}}, \sqrt{\frac{\eta_2 x_2}{R}}, \sqrt{\frac{\eta_1 x_1}{R}}, 1 \right).$$

Then using any matrix norm,  $Q^{-1}$  is bounded on  $\Delta$ . We now demonstrate the necessary exponential decay of a functional of the form given in (6.1) when evaluated on surfaces in  $\Delta$  under the dynamics described by (2.1).

Following the formula given in [24], the second compound of the Jacobian matrix given in (3.3) is



$$\frac{\partial f^{[2]}}{\partial x} = \text{diag} \begin{pmatrix} -[D_S + D_R + \frac{c_1}{\xi_1}x_1 + \frac{c_2}{\xi_2}x_2 + \frac{k_1}{\eta_1}x_1 + \frac{k_2}{\eta_2}x_2] \\ c_1S + k_1R - [D_1 + D_S + \frac{c_1}{\xi_1}x_1 + \frac{c_2}{\xi_2}x_2] \\ c_2S + k_2R - [D_2 + D_S + \frac{c_1}{\xi_1}x_1 + \frac{c_2}{\xi_2}x_2] \\ c_1S + k_1R - [D_1 + D_R + \frac{k_1}{\eta_1}x_1 + \frac{k_2}{\eta_2}x_2] \\ c_2S + k_2R - [D_2 + D_R + \frac{k_1}{\eta_1}x_1 + \frac{k_2}{\eta_2}x_2] \\ c_1S + k_1R + c_2S + k_2R - [D_1 + D_2] \end{pmatrix} + \begin{bmatrix} 0 & -\frac{k_1}{\eta_1}R & -\frac{k_2}{\eta_2}R & \frac{c_1}{\xi_1}S & \frac{c_2}{\xi_2}S & 0 \\ k_1x_1 & 0 & 0 & 0 & 0 & \frac{c_2}{\xi_2}S \\ k_2x_2 & 0 & 0 & 0 & 0 & -\frac{c_1}{\xi_1}S \\ -c_1x_1 & 0 & 0 & 0 & 0 & \frac{k_2}{\eta_2}R \\ -c_2x_2 & 0 & 0 & 0 & 0 & -\frac{k_1}{\eta_1}R \\ 0 & -c_2x_2 & c_1x_1 & -k_2x_2 & k_1x_1 & 0 \end{bmatrix}. \tag{7.1}$$

Define  $M = Q_f Q^{-1} + Q \frac{\partial f^{[2]}}{\partial x} Q^{-1}$ ; then

$$M = \frac{1}{2} \text{diag} \begin{pmatrix} D_1 + D_2 - D_S(1 + \frac{S^0}{S}) - D_R(1 + \frac{R^0}{R}) \\ D_2 - D_S(1 + \frac{S^0}{S}) \\ D_1 - D_S(1 + \frac{S^0}{S}) \\ D_2 - D_R(1 + \frac{R^0}{R}) \\ D_1 - D_R(1 + \frac{R^0}{R}) \\ 0 \end{pmatrix} - \frac{1}{2} \text{diag} \begin{pmatrix} (c_1 + c_2)S + (k_1 + k_2)R + (\frac{c_1}{\xi_1} + \frac{k_1}{\eta_1})x_1 + (\frac{c_2}{\xi_2} + \frac{k_2}{\eta_2})x_2 \\ c_2S + k_2R + \frac{c_1}{\xi_1}x_1 + \frac{c_2}{\xi_2}x_2 \\ c_1S + k_1R + \frac{c_1}{\xi_1}x_1 + \frac{c_2}{\xi_2}x_2 \\ c_2S + k_2R + \frac{k_1}{\eta_1}x_1 + \frac{k_2}{\eta_2}x_2 \\ c_1S + k_1R + \frac{k_1}{\eta_1}x_1 + \frac{k_2}{\eta_2}x_2 \\ 0 \end{pmatrix} + \begin{bmatrix} 0 & -\frac{k_1v}{\eta_1\sqrt{\xi_2}}\sqrt{x_1R} - \frac{k_2v}{\eta_2\sqrt{\xi_1}}\sqrt{x_2R} & \frac{c_1v}{\xi_1\sqrt{\eta_2}}\sqrt{x_1S} & \frac{c_2v}{\xi_2\sqrt{\eta_1}}\sqrt{x_2S} & 0 & 0 \\ \frac{k_1\sqrt{\xi_2}}{v}\sqrt{x_1R} & 0 & 0 & 0 & 0 & c_2\sqrt{\frac{Sx_2}{\xi_2}} \\ \frac{k_2\sqrt{\xi_1}}{v}\sqrt{x_2R} & 0 & 0 & 0 & 0 & -c_1\sqrt{\frac{Sx_1}{\xi_1}} \\ -\frac{c_1\sqrt{\eta_2}}{v}\sqrt{x_1S} & 0 & 0 & 0 & 0 & k_2\sqrt{\frac{Rx_2}{\eta_2}} \\ -\frac{c_2\sqrt{\eta_1}}{v}\sqrt{x_2S} & 0 & 0 & 0 & 0 & -k_1\sqrt{\frac{Rx_1}{\eta_1}} \\ 0 & -c_2\sqrt{\frac{Sx_2}{\xi_2}} & c_1\sqrt{\frac{Sx_1}{\xi_1}} & -k_2\sqrt{\frac{Rx_2}{\eta_2}} & k_1\sqrt{\frac{Rx_1}{\eta_1}} & 0 \end{bmatrix}.$$

We are interested in the stability of the time-dependent linear systems

$$z' = M(\varphi(t)) z \tag{7.2}$$

where  $\varphi(t)$  is a solution to equation (2.1) with initial condition in  $\Delta$ . We wish to use  $V(z) = (z^T z)^{\frac{1}{2}}$  as a Lyapunov function for system (7.2). Note that

$$V'(z) = \frac{1}{V(z)} z^T \frac{1}{2} (M^T + M) z.$$

It has been established [8, p. 41] that  $z^T \frac{1}{2}(M^T + M)z \leq \rho V(z)^2$  where  $\rho$  is the largest eigenvalue of  $\tilde{M} = \frac{1}{2}(M^T + M)$ ; hence, we are motivated to examine the eigenvalues of  $\tilde{M}$ . In calculating  $\tilde{M}$ , we get a matrix for which the main diagonal is the same as that of  $M$ , and for which the only non-zero off-diagonal terms lie in the first row and the first column. Furthermore, there are two values of  $v$ ,  $v_1 = \sqrt{\xi_1 \eta_2}$  and  $v_2 = \sqrt{\xi_2 \eta_1}$ , that reduce the number of non-zero off-diagonal terms to four.

First consider  $v_1 = \sqrt{\xi_1 \eta_2}$  and let  $M_1$  denote the matrix  $M$  evaluated with  $v = v_1$ . Then, letting

$$A = \frac{\xi_1 \eta_2}{\xi_2 \eta_1},$$

$\tilde{M}_1 = \frac{1}{2}(M_1 + M_1^T)$  is given by

$$\tilde{M}_1 = \begin{bmatrix} M_{11} & \frac{1}{2} \frac{(1-A)}{\sqrt{A}} k_1 \sqrt{\frac{x_1 R}{\eta_1}} & 0 & 0 & \frac{1}{2} \frac{(A-1)}{\sqrt{A}} c_2 \sqrt{\frac{x_2 S}{\xi_2}} & 0 \\ \frac{1}{2} \frac{(1-A)}{\sqrt{A}} k_1 \sqrt{\frac{x_1 R}{\eta_1}} & M_{22} & 0 & 0 & 0 & 0 \\ 0 & 0 & M_{33} & 0 & 0 & 0 \\ 0 & 0 & 0 & M_{44} & 0 & 0 \\ \frac{1}{2} \frac{(A-1)}{\sqrt{A}} c_2 \sqrt{\frac{x_2 S}{\xi_2}} & 0 & 0 & 0 & M_{55} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

where the  $M_{ii}$ 's represent the corresponding diagonal entries of  $M$  (which are independent of  $v$ ).

Noting that the last column of  $\tilde{M}_1$  consists entirely of zeroes it is clear that  $\tilde{M}_1$  has a zero eigenvalue. Nonetheless, we proceed to find conditions under which the five remaining eigenvalues of  $\tilde{M}_1$  have negative real part.

Since all off-diagonal entries in the third and fourth rows and columns of  $\tilde{M}_1$  are zero, the third and fourth diagonal entries of  $\tilde{M}_1$  are eigenvalues.

**Proposition 7.1.** *If*

$$D_1, D_2 < 2D_S, 2D_R, \tag{7.3}$$

*then the eigenvalues of  $\tilde{M}_1$  corresponding to its third and fourth diagonal entries will be negative on  $\Delta$ .*

*Proof.* Consider the third diagonal entry of  $\tilde{M}_1$ . We have

$$\begin{aligned} & \frac{1}{2} \left( D_1 - D_S \left( 1 + \frac{S^0}{S} \right) \right) - \frac{1}{2} \left( c_1 S + k_1 R + \frac{c_1}{\xi_1} x_1 + \frac{c_2}{\xi_2} x_2 \right) \\ & \leq \frac{1}{2} \left( D_1 - D_S \left( 1 + \frac{S^0}{S} \right) \right) \end{aligned}$$

which is negative in  $\Delta$  under assumption (7.3) since  $S < S^0$  in  $\Delta$ . The fourth diagonal entry of  $\tilde{M}_1$  is handled similarly. □

It follows from Proposition 7.1 that the only potentially positive eigenvalues of  $\tilde{M}_1$  are among the remaining three. Information about these eigenvalues can be obtained by considering  $\tilde{M}_1^\times$ , the  $3 \times 3$  minor of  $\tilde{M}_1$  that consists of the elements of the first, second and fifth rows and columns.

$$\tilde{M}_1^\times = \frac{1}{2} \begin{bmatrix} \begin{pmatrix} D_1 + D_2 - D_S(1 + \frac{S^0}{S}) \\ -D_R(1 + \frac{R^0}{R}) \\ -(c_1/\xi_1 + k_1/\eta_1)x_1 - (c_2/\xi_2 + k_2/\eta_2)x_2 \\ -(c_1 + c_2)S - (k_1 + k_2)R \end{pmatrix} & \frac{(1-A)}{\sqrt{A}}k_1\sqrt{\frac{x_1R}{\eta_1}} & \frac{(A-1)}{\sqrt{A}}c_2\sqrt{\frac{x_2S}{\xi_2}} \\ \frac{(1-A)}{\sqrt{A}}k_1\sqrt{\frac{x_1R}{\eta_1}} & \begin{pmatrix} D_2 - D_S(1 + \frac{S^0}{S}) \\ -c_1x_1 - c_2x_2 \\ -c_2S - k_2R \end{pmatrix} & 0 \\ \frac{(A-1)}{\sqrt{A}}c_2\sqrt{\frac{x_2S}{\xi_2}} & 0 & \begin{pmatrix} D_1 - D_R(1 + \frac{R^0}{R}) \\ -k_1x_1 - k_2x_2 \\ -c_1S - k_1R \end{pmatrix} \end{bmatrix}$$

Inequality (7.3) implies the diagonal entries of  $\tilde{M}_1^\times$  are negative. All of the off-diagonal entries of  $\tilde{M}_1^\times$  are zero if and only if  $A = 1$  (i.e.  $\xi_1\eta_2 = \xi_2\eta_1$ ). Therefore, inequality (7.3) and  $A = 1$  guarantee that the eigenvalues of  $\tilde{M}_1^\times$  are negative. The method of Gersgorin discs [19, Section 10.6] will be used to determine a more robust condition on the  $\xi_i$ 's and  $\eta_i$ 's that will ensure the eigenvalues of  $\tilde{M}_1^\times$  still have negative real part. Before determining the Gersgorin discs, we perform the similarity transformation  $P\tilde{M}_1^\times P^{-1}$  where

$$P = \text{diag} \left( \begin{matrix} 1 \\ \frac{(1-A)}{\sqrt{A}}k_1\sqrt{\frac{x_1R}{\eta_1}} / \left( \frac{c_1}{\xi_1}x_1 + \frac{c_2}{\xi_2}x_2 + c_2S + k_2R \right) \\ \frac{(A-1)}{\sqrt{A}}c_2\sqrt{\frac{x_2S}{\xi_2}} / \left( \frac{k_1}{\eta_1}x_1 + \frac{k_2}{\eta_2}x_2 + c_1S + k_1R \right) \end{matrix} \right)$$

and we denote the resultant matrix  $\tilde{M}_1^\square$ :

$$\tilde{M}_1^\square = \frac{1}{2} \begin{bmatrix} \begin{pmatrix} D_1 + D_2 - D_S(1 + \frac{S^0}{S}) \\ -D_R(1 + \frac{R^0}{R}) \\ -(c_1/\xi_1 + k_1/\eta_1)x_1 - (c_2/\xi_2 + k_2/\eta_2)x_2 \\ -(c_1 + c_2)S - (k_1 + k_2)R \end{pmatrix} & \begin{pmatrix} c_1x_1 + c_2x_2 \\ +c_2S + k_2R \end{pmatrix} & \begin{pmatrix} k_1x_1 + k_2x_2 \\ +c_1S + k_1R \end{pmatrix} \\ \frac{\bar{A} \frac{k_1^2}{\eta_1^2} x_1 R}{\left( \frac{c_1}{\xi_1}x_1 + \frac{c_2}{\xi_2}x_2 + c_2S + k_2R \right)} & \begin{pmatrix} D_2 - D_S(1 + \frac{S^0}{S}) \\ -c_1x_1 - c_2x_2 \\ -c_2S - k_2R \end{pmatrix} & 0 \\ \frac{\bar{A} \frac{c_2^2}{\xi_2^2} x_2 S}{\left( \frac{k_1}{\eta_1}x_1 + \frac{k_2}{\eta_2}x_2 + c_1S + k_1R \right)} & 0 & \begin{pmatrix} D_1 - D_R(1 + \frac{R^0}{R}) \\ -k_1x_1 - k_2x_2 \\ -c_1S - k_1R \end{pmatrix} \end{bmatrix}$$

where

$$\bar{A} = \frac{(A - 1)^2}{A} = \frac{(\xi_1\eta_2 - \xi_2\eta_1)^2}{\xi_1\xi_2\eta_1\eta_2}.$$

Similarly, by choosing  $\nu = \nu_2 = \sqrt{\xi_2 \eta_1}$ , one obtains the matrix

$$\tilde{M}_2^\square = \frac{1}{2} \begin{bmatrix} \begin{pmatrix} D_1 + D_2 - D_S(1 + \frac{S^0}{S}) \\ -D_R(1 + \frac{R^0}{R}) \\ -( \frac{c_1}{\xi_1} + \frac{k_1}{\eta_1} )x_1 - ( \frac{c_2}{\xi_2} + \frac{k_2}{\eta_2} )x_2 \\ -(c_1 + c_2)S - (k_1 + k_2)R \end{pmatrix} & \begin{pmatrix} \frac{c_1}{\xi_1}x_1 + \frac{c_2}{\xi_2}x_2 \\ +c_1S + k_1R \end{pmatrix} & \begin{pmatrix} \frac{k_1}{\eta_1}x_1 + \frac{k_2}{\eta_2}x_2 \\ +c_2S + k_2R \end{pmatrix} \\ \frac{\bar{A} \frac{k_2^2}{\eta_2^2} x_2 R}{( \frac{c_1}{\xi_1} x_1 + \frac{c_2}{\xi_2} x_2 + c_1 S + k_1 R )} & \begin{pmatrix} D_1 - D_S(1 + \frac{S^0}{S}) \\ -\frac{c_1}{\xi_1}x_1 - \frac{c_2}{\xi_2}x_2 \\ -c_1S - k_1R \end{pmatrix} & 0 \\ \frac{\bar{A} \frac{c_1^2}{\xi_1^2} x_1 S}{( \frac{k_1}{\eta_1} x_1 + \frac{k_2}{\eta_2} x_2 + c_2 S + k_2 R )} & 0 & \begin{pmatrix} D_2 - D_R(1 + \frac{R^0}{R}) \\ -\frac{k_1}{\eta_1}x_1 - \frac{k_2}{\eta_2}x_2 \\ -c_2S - k_2R \end{pmatrix} \end{bmatrix}$$

(where the matrices  $M_2, \tilde{M}_2, \tilde{M}_2^\times$  and  $\tilde{M}_2^\square$  are constructed in the same manner as  $M_1, \tilde{M}_1, \tilde{M}_1^\times$  and  $\tilde{M}_1^\square$ , respectively, but with  $\nu = \nu_2$  rather than  $\nu = \nu_1$ ). If the eigenvalues of  $\tilde{M}_1^\square$  (respectively,  $\tilde{M}_2^\square$ ) are bounded away from zero on the negative side in  $\Delta$ , then the same is true for all of the non-zero eigenvalues of  $\tilde{M}_1$  (respectively,  $\tilde{M}_2$ ). We now show that if (7.3) holds and

$$\bar{A} \leq 1, \quad \text{or equivalently} \quad (3 - \sqrt{5})/2 \leq A \leq (3 + \sqrt{5})/2, \tag{7.4}$$

then the Gersgorin discs (and therefore the eigenvalues) for at least one of  $\tilde{M}_1^\square$  or  $\tilde{M}_2^\square$  lie in the left half plane.

To determine a Gersgorin disc based on a column of a matrix, we sum the absolute values of the off-diagonal terms in that column and consider the circle in the complex plane with this radius, centred at the point on the real axis whose real part is given by the diagonal entry of that same column. All of the eigenvalues of a matrix are contained in the union of the Gersgorin discs. Thus, if all of the Gersgorin discs for a matrix are entirely in the left half plane, then all of the eigenvalues of the matrix have negative real part. To determine the right-most point of these discs, one simply adds the diagonal entry of a column to the sum of the absolute values of the off-diagonal entries of the same column. If the total is negative for each column, then each disc lies in the left half plane, and so the matrix is stable.

Suppose (7.3) and (7.4) hold. Then for each of  $\tilde{M}_1^\square$  and  $\tilde{M}_2^\square$ , the Gersgorin discs for columns two and three lie in the left half plane. A sufficient condition for the Gersgorin disc of the first column of  $\tilde{M}_1^\square$  to lie in the negative half plane is

$$\frac{\bar{A} \frac{k_1^2}{\eta_1^2} x_1 R}{( \frac{c_1}{\xi_1} x_1 + \frac{c_2}{\xi_2} x_2 + c_2 S + k_2 R )} + \frac{\bar{A} \frac{c_2^2}{\xi_2^2} x_2 S}{( \frac{k_1}{\eta_1} x_1 + \frac{k_2}{\eta_2} x_2 + c_1 S + k_1 R )} - \left( \frac{c_1}{\xi_1} + \frac{k_1}{\eta_1} \right) x_1 - \left( \frac{c_2}{\xi_2} + \frac{k_2}{\eta_2} \right) x_2 - (c_1 + c_2)S - (k_1 + k_2)R \leq 0. \tag{7.5}$$

Condition (7.5) holds whenever

$$\frac{\bar{A} \frac{k_1^2}{\eta_1^2} x_1 R}{( \frac{c_1}{\xi_1} x_1 + k_2 R )} \leq \left( \frac{c_1}{\xi_1} + \frac{k_1}{\eta_1} \right) x_1 + (k_1 + k_2)R$$

and

$$\frac{\bar{A} \frac{c_2^2}{\xi_2} x_2 S}{\left(\frac{k_2}{\eta_2} x_2 + c_1 S\right)} \leq \left(\frac{c_2}{\xi_2} + \frac{k_2}{\eta_2}\right) x_2 + (c_1 + c_2) S.$$

Multiplying each of these through by the denominators, and considering only the cross terms we see that (7.5) holds whenever

$$\bar{A} \frac{k_1^2}{\eta_1} \leq k_2 \left(\frac{c_1}{\xi_1} + \frac{k_1}{\eta_1}\right) + \frac{c_1}{\xi_1} (k_1 + k_2) \tag{7.6}$$

and

$$\bar{A} \frac{c_2^2}{\xi_2} \leq c_1 \left(\frac{c_2}{\xi_2} + \frac{k_2}{\eta_2}\right) + \frac{k_2}{\eta_2} (c_1 + c_2). \tag{7.7}$$

Since  $\bar{A}$  is assumed to be less than one, we see that in fact, (7.5) is satisfied whenever

$$k_1 \frac{k_1}{\eta_1} \leq k_2 \left(\frac{c_1}{\xi_1} + \frac{k_1}{\eta_1}\right) + \frac{c_1}{\xi_1} (k_1 + k_2) \tag{7.8}$$

and

$$c_2 \frac{c_2}{\xi_2} \leq c_1 \left(\frac{c_2}{\xi_2} + \frac{k_2}{\eta_2}\right) + \frac{k_2}{\eta_2} (c_1 + c_2). \tag{7.9}$$

Thus (7.8) and (7.9) are sufficient conditions for the Gersgorin discs based on column one of  $\tilde{M}_1^\square$  to be in the left half plane. Similarly, if

$$k_2 \frac{k_2}{\eta_2} \leq k_1 \left(\frac{c_2}{\xi_2} + \frac{k_2}{\eta_2}\right) + \frac{c_2}{\xi_2} (k_1 + k_2) \tag{7.10}$$

and

$$c_1 \frac{c_1}{\xi_1} \leq c_2 \left(\frac{c_1}{\xi_1} + \frac{k_1}{\eta_1}\right) + \frac{k_1}{\eta_1} (c_1 + c_2) \tag{7.11}$$

are satisfied then the Gersgorin disc based on column one of  $\tilde{M}_2^\square$  lies in the left half plane. We now show that either (7.8) and (7.9) are both satisfied or (7.10) and (7.11) are both satisfied.

Without loss of generality, we can assume  $k_1 \leq k_2$ . This implies (7.8) holds. If  $c_2 \leq c_1$  or  $\frac{c_2}{\xi_2} \leq \frac{k_2}{\eta_2}$  then (7.9) holds and so the assertion is valid. Suppose instead that  $c_1 < c_2$  and  $\frac{k_2}{\eta_2} < \frac{c_2}{\xi_2}$ . Then it follows that (7.11) and (7.10), respectively, must hold. Therefore, if (7.3) and (7.4) hold, then the five non-zero eigenvalues of either  $\tilde{M}_1$  or  $\tilde{M}_2$  lie in the left half plane for all  $(S, R, x_1, x_2) \in \Delta$ .

*Remark.* While  $\bar{A} \leq 1$  is a sufficient condition for the Gersgorin discs to be in the left half plane, it is not necessary. On the other hand, it can be shown that for any  $\bar{A} > 1$ , it is possible to choose  $c_i, k_i, \xi_i$  and  $\eta_i$  such that one of (7.6) and (7.7) fails, as well as one of the analogous conditions for  $\tilde{M}_2^\square$ . This does not mean that  $\bar{A} \leq 1$  is optimal for every case, but it is always sufficient.  $\square$

We have now shown that it is possible to choose  $\nu$  such that the matrix  $\tilde{M}$  has zero as an eigenvalue, as well as five eigenvalues with negative real part. Furthermore, since (7.3) is a strict inequality, it follows that the five eigenvalues with negative real part are bounded away from real part zero on  $\Delta$ . Since  $\tilde{M}$  is symmetric, these eigenvalues are in fact real, and so we have eigenvalues  $\rho_6 \leq \dots \leq \rho_2 < 0 = \rho_1$ .

Thus,  $V(z) = (z^T z)^{\frac{1}{2}}$ , with derivative

$$V'(z) = \frac{1}{V(z)} z^T \tilde{M} z,$$

satisfies  $V'(z) \leq 0$  for all  $z$ , since the largest eigenvalue of  $\tilde{M}$  is zero, and so  $V(z)$  is a Lyapunov function for system (7.2).

We now show that along solutions to (7.2),  $V(z)$  decreases to zero. Let  $e_1, \dots, e_6$  be the standard basis vectors for  $\mathbb{R}^6$ . Then  $\mathcal{W} = \text{span}\{e_1, \dots, e_5\}$  is equal to the direct sum of the generalized eigenspaces of the eigenvalues of  $\tilde{M}$  with negative real part, and  $\mathcal{Y} = \text{span}\{e_6\}$  is the eigenspace associated with the zero eigenvalue of  $\tilde{M}$ . (Note that even though individual eigenvectors of  $\tilde{M}$  may vary over time, the corresponding eigenspaces align with the spaces  $\mathcal{W}$  and  $\mathcal{Y}$ , as described above, for all time.) Each  $z \in \mathbb{R}^6$  can be uniquely written as  $z = w + y$  where  $w = w(z) \in \mathcal{W}$  and  $y = y(z) \in \mathcal{Y}$ . For  $z \neq 0$ ,

$$\begin{aligned} V'(z) &= \frac{1}{V(z)} z^T \tilde{M} z \\ &= \frac{1}{V(z)} w^T \tilde{M} w. \end{aligned}$$

Choose  $\bar{\rho} > 0$  such that  $\rho_6, \dots, \rho_2 < -\bar{\rho}$  on  $\Delta$ . Since  $\tilde{M}$  is symmetric and  $w \in \mathcal{W}$ , we have  $w^T \tilde{M} w \leq -\bar{\rho} w^T w$  and so

$$\begin{aligned} V'(z) &\leq -\bar{\rho} \frac{1}{V(z)} w^T w \\ &= -\bar{\rho} \frac{w^T w}{z^T z} V(z). \end{aligned}$$

Thus  $V'(z)$  is zero if and only if  $w = 0$  or, equivalently,  $z \in \mathcal{Y}$ . Hence, by LaSalle’s Extension Theorem [20], the omega limit set of any solution to (7.2) lies in the largest invariant set  $\mathcal{B}$  contained in  $\mathcal{Y}$ . At a point  $z = \zeta e_6$ , we have  $z' = \zeta C_6$ , where  $C_6$  is the sixth column of  $M$ :

$$C_6 = \left( 0, c_2 \sqrt{\frac{Sx_2}{\xi_2}}, -c_1 \sqrt{\frac{Sx_1}{\xi_1}}, k_2 \sqrt{\frac{Rx_2}{\eta_2}}, -k_1 \sqrt{\frac{Rx_1}{\eta_1}}, 0 \right)^T.$$

**Proposition 7.2.** *Let  $\mathcal{C} \subset \Delta$  be a compact set.  $C_6$  is bounded away from zero for all solutions initiating in  $\mathcal{C}$ .*

*Proof.* By Theorem 3.8, there exists  $\beta > 0$  such that

$$\inf_{t \geq 0; x_0 \in \mathcal{C}} \max\{x_1(t), x_2(t)\} \geq \beta.$$

Also, for solutions starting in  $\mathcal{C}$ ,  $S(t)$  and  $R(t)$  are bounded away from zero for all  $t \geq 0$ . Thus, the magnitude of  $C_6$  is bounded away from zero.  $\square$

Noting that  $C_6$  is orthogonal to  $\mathcal{Y}$ , we see that if  $\zeta$  is non-zero, then the solution to (7.2) through  $z = \zeta e_6$  leaves  $\mathcal{Y}$ , contradicting the invariance of  $\mathcal{B}$ . Therefore,  $\mathcal{B}$  consists of exactly the origin, and so  $z$  goes to zero.

We now show that  $z$  goes to zero with exponential speed, uniformly for all initial conditions of (2.1) in compact  $\mathcal{C} \subset \Delta$  and all initial conditions of (7.2) in  $\mathbb{R}^6$ . For non-zero  $z$ , let  $\tilde{z} = z/\|z\|_2$  and  $\tilde{w} = w/\|z\|_2$ . Then

$$\begin{aligned} V'(z(t)) &\leq -\bar{\rho} \frac{\tilde{w}^T \tilde{w}}{\tilde{z}^T \tilde{z}} V(z(t)) \\ &= -\bar{\rho} \tilde{w}^T \tilde{w} V(z(t)), \end{aligned} \tag{7.12}$$

and so

$$V(z(t)) \leq V(z(0)) \exp\left(-\bar{\rho} \int_{\tau=0}^t \tilde{w}^T(z(\tau)) \tilde{w}(z(\tau)) d\tau\right). \tag{7.13}$$

Another consequence of  $C_6$  being bounded away from zero, while being orthogonal to  $\mathcal{Y}$  is that there exists  $\epsilon > 0$  and  $t_2 > t_1 > 0$  such that  $\|\tilde{w}(t_0)\|_2 < \epsilon$  implies  $\|\tilde{w}(t)\|_2 > \epsilon$  for  $t_1 < |t - t_0| < t_2$ . This follows since (7.2) is homogeneous. Thus, every time interval of length  $2t_2$  has a subset of measure at least  $2(t_2 - t_1)$  such that  $\tilde{w}^T \tilde{w} > \epsilon^2$  on that subset. For any  $t > 0$  let  $n_t$  be such that  $2n_t t_2 \leq t < 2(n_t + 1)t_2$ . Then

$$\begin{aligned} \int_{\tau=0}^t \tilde{w}^T \tilde{w} d\tau &\geq \int_{\tau=0}^{2n_t t_2} \tilde{w}^T \tilde{w} d\tau \\ &\geq 2n_t(t_2 - t_1)\epsilon^2 \\ &> 2n_t(t_2 - t_1)\epsilon^2 \frac{t}{2(n_t + 1)t_2} \\ &\geq \frac{(t_2 - t_1)}{2t_2} \epsilon^2 t \end{aligned}$$

where the last inequality only holds for  $t \geq 2t_2$  (since that makes  $\frac{2n_t}{n_t + 1} \geq 1$ ). Substituting into (7.13) gives,

$$V(z(t)) \leq V(z(0)) \exp\left(-\bar{\rho} \frac{(t_2 - t_1)}{2t_2} \epsilon^2 t\right)$$

for  $t \geq 2t_2$ , and so  $z$  goes to zero uniformly for all  $z(0) \in \mathbb{R}^6$  and all  $x(0) \in \mathcal{C}$ . Thus, by Theorem 6.2 the omega limit set of each orbit bounded away from the boundary of  $\Delta$  consists entirely of equilibria. If (4.2) holds, then the equilibria are isolated and so each omega limit set consists of a single equilibrium.

Since it has been shown that each solution of equation (2.1) having a limit point in the boundary of  $\Delta$  actually limits to an equilibrium in the boundary of  $\Delta$ , we have the following theorem.

**Theorem 7.3.** *Suppose (4.1), (4.2), (7.3) and (7.4) hold. Then the dynamics of (2.1) are trivial in the sense that each solution initiating in  $\Delta$  limits to an equilibrium.*

### 8. Bifurcation analysis

In the portion of parameter space dictated by the theory of compound matrices (i.e. when (7.3) and (7.4) hold), we offer the following bifurcation analysis based on decreasing the parameter  $D$ . We also assume (4.3) holds so that  $E^*$  can potentially exist. Let  $\epsilon_i$  denote the intrinsic death rate of population  $i$ . We will assume here that  $\mathcal{G}_i(S^0, R^0) > \epsilon_i, i = 1, 2$ . Otherwise, species  $i$  cannot consume enough resource to compensate for the rate at which it is dying, let alone the rate at which it is being removed. We will also assume that  $D_S = D_R = D$ .

Note that if  $c_i S + k_i R = D_i$ , then  $R = \frac{1}{k_i}(D_i - c_i S)$ . Also,  $\lambda_i = D_i/c_i$  and  $\mu_i = D_i/k_i$ . With this notation, define the subsistence curve  $\varphi_i(S)$  so that  $\mathcal{G}_i(S, \varphi_i(S)) = D_i$ :

$$\varphi_i(S) = \frac{1}{k_i}(D_i - c_i S) = \frac{\mu_i}{\lambda_i}(\lambda_i - S).$$

Its role in the bifurcation analysis is as follows. For each  $i = 1, 2$ , when  $D$  is large,  $(S^0, R^0)$  is contained in the triangular region bounded by the positive  $S$  and  $R$  axes and the subsistence curve  $\varphi_i(S)$  (see Figure 1, where the lines with negative slope are the  $\varphi_i$ ). Therefore,  $\mathcal{G}_i(S^0, R^0) < D_i$ , so  $E_i$  exists outside the nonnegative cone. As  $D$  is decreased, the subsistence curve maintains its slope, but moves closer to the origin (since  $\lambda_i$  and  $\mu_i$  decrease).  $E_i$  will then enter the positive cone through  $E^0$  as the subsistence curve passes through  $(S^0, R^0)$ . Furthermore, the  $S$  and  $R$  coordinates of  $E^*$  (when it exists) are given by the intersection of the subsistence curves, since it is only on these curves that  $x'_1$  and  $x'_2$  are zero for non-zero values of  $x_1$  and  $x_2$ , respectively.

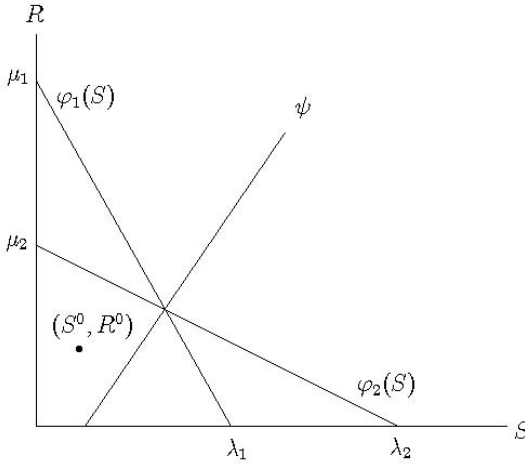
We now proceed with the bifurcation analysis. There are two cases to consider:

**Case 1:**  $(\lambda_1 - \lambda_2)(\mu_1 - \mu_2) > 0$

In this case, the subsistence curves do not intersect for any value of  $D$ , so that the coexistence equilibrium  $E^*$  cannot exist. Without loss of generality, suppose  $\lambda_1 < \lambda_2$ . Then  $\varphi_1$  lies below  $\varphi_2$ . Start with  $D$  large enough so that  $\mathcal{G}_i(S^0, R^0) < D_i, i = 1, 2$ . Then both  $E_i$  lie outside the nonnegative cone and the washout equilibrium  $E^0$  is globally asymptotically stable for (2.1) (Theorem 3.4). Now decrease  $D$  so that  $\mathcal{G}_1(S^0, R^0) = D_1$ , and hence  $E^0$  and  $E_1$  coalesce. As  $D$  decreases further,  $E_1$  bifurcates into the nonnegative cone, and  $E^0$  loses a degree of stability to  $E_1$ . Since  $\mathcal{G}_2(S^0, R^0) < D_2, E_1$  is globally asymptotically stable for (2.1) for all solutions for which  $x_1(0) > 0$  (Theorem 3.5). Now decrease  $D$  so that  $\mathcal{G}_2(S^0, R^0) = D_2$ , and hence  $E^0$  and  $E_2$  coalesce. As  $D$  decreases further,  $E_2$  bifurcates into the nonnegative cone and  $E^0$  loses another degree of stability to  $E_2$ . Since  $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) > D_1$  and  $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2$ , Theorem 7.3 can be applied to conclude that  $E_1$  is globally asymptotically stable for (2.1) whenever  $x_1(0) > 0$ . This remains the case as  $D$  is decreased further.

**Case 2:**  $(\lambda_1 - \lambda_2)(\mu_1 - \mu_2) < 0$





**Fig. 1.** Diagram showing the relative positions in the  $(S, R)$  plane of  $\varphi_1(S)$ ,  $\varphi_2(S)$ , and the line  $\psi$  describing the  $S$  and  $R$  coordinates of  $E^*$  (see equation (8.2)). As  $D$  is decreased, the slopes of  $\varphi_1$  and  $\varphi_2$  remain fixed, but their intersection moves along  $\psi$  so that  $\lambda_i$  and  $\mu_i$  move towards the origin. While the slope of  $\psi$  need not be positive,  $\psi$  need intersect one of the positive axes closer to the origin than each of  $\varphi_1$  and  $\varphi_2$

In this case, the subsistence curves  $\varphi_1(S)$  and  $\varphi_2(S)$  intersect uniquely in the positive cone. This intersection gives the  $(S, R)$  coordinates of the coexistence equilibrium

$$S^* = \frac{D_1 k_2 - D_2 k_1}{c_1 k_2 - c_2 k_1} = D \frac{k_2 - k_1}{c_1 k_2 - c_2 k_1} + \frac{\epsilon_1 k_2 - \epsilon_2 k_1}{c_1 k_2 - c_2 k_1} \tag{8.1}$$

and

$$R^* = \frac{D_2 c_1 - D_1 c_2}{c_1 k_2 - c_2 k_1} = D \frac{c_1 - c_2}{c_1 k_2 - c_2 k_1} + \frac{\epsilon_2 c_1 - \epsilon_1 c_2}{c_1 k_2 - c_2 k_1}.$$

As  $D$  is decreased, the point  $(S^*, R^*)$  remains on  $\psi(S)$ ,

the straight line through  $\left( \frac{\epsilon_1 k_2 - \epsilon_2 k_1}{c_1 k_2 - c_2 k_1}, \frac{\epsilon_2 c_1 - \epsilon_1 c_2}{c_1 k_2 - c_2 k_1} \right)$  with slope  $\frac{c_1 - c_2}{k_2 - k_1}$ .  $(8.2)$

Fix  $(S^0, R^0)$  in the plane with  $G_i(S^0, R^0) > \epsilon_i, i = 1, 2$ . There exists a unique  $\hat{D}$  such that

$$S^0 = \hat{D} \frac{k_2 - k_1}{c_1 k_2 - c_2 k_1} + \frac{\epsilon_1 k_2 - \epsilon_2 k_1}{c_1 k_2 - c_2 k_1}.$$

There are three possibilities.

(a) If

$$R^0 = \hat{D} \frac{c_1 - c_2}{c_1 k_2 - c_2 k_1} + \frac{\epsilon_2 c_1 - \epsilon_1 c_2}{c_1 k_2 - c_2 k_1}$$

then  $(S^0, R^0)$  lies on  $\psi(S)$ , the  $(S^*, R^*)$  line described in (8.2). In this case,  $E_1, E_2$ , and  $E^*$  coalesce with  $E^0$ , and then  $E_1$  and  $E_2$  enter the nonnegative cone and  $E^*$  enters the positive cone, simultaneously as  $D$  is decreased.

(b) If

$$R^0 > \hat{D} \frac{c_1 - c_2}{c_1 k_2 - c_2 k_1} + \frac{\epsilon_2 c_1 - \epsilon_1 c_2}{c_1 k_2 - c_2 k_1}$$

then  $(S^0, R^0)$  lies above  $\psi(S)$ . If  $\lambda_1 < \lambda_2$  then as  $D$  is decreased the  $E^0$ - $E_2$  transcritical bifurcation occurs first. If  $\lambda_2 < \lambda_1$  then the  $E^0$ - $E_1$  transcritical bifurcation occurs first. See Figure 1.

(c) If

$$R^0 < \hat{D} \frac{c_1 - c_2}{c_1 k_2 - c_2 k_1} + \frac{\epsilon_2 c_1 - \epsilon_1 c_2}{c_1 k_2 - c_2 k_1}$$

then  $(S^0, R^0)$  lies below  $\psi(S)$ . If  $\lambda_1 < \lambda_2$  then as  $D$  is decreased the  $E^0$ - $E_1$  transcritical bifurcation occurs first. If  $\lambda_2 < \lambda_1$  then the  $E^0$ - $E_2$  transcritical bifurcation occurs first.

Without loss of generality, assume  $\lambda_1 < \lambda_2$  and  $(S^0, R^0)$  is as in (b) above. Now decrease  $D$  so that  $\mathcal{G}_2(S^0, R^0) = D_2$ , and hence  $E^0$  and  $E_2$  coalesce. As  $D$  decreases further,  $E_2$  bifurcates into the nonnegative cone and  $E^0$  loses a degree of stability to  $E_2$ . Since  $\mathcal{G}_1(S^0, R^0) < D_1$ ,  $E_2$  is globally asymptotically stable for (2.1) for all solutions for which  $x_2(0) > 0$  (Theorem 3.5). Now decrease  $D$  so that  $\mathcal{G}_1(S^0, R^0) = D_1$ , and hence  $E^0$  and  $E_1$  coalesce. As  $D$  decreases further,  $E_1$  bifurcates into the nonnegative cone and  $E^0$  loses another degree of stability to  $E_1$ . We now have  $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) > D_2$  (so that  $E_1$  can be invaded) and  $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) < D_1$  (so that  $E_2$  cannot be invaded). Theorem 7.3 can be applied to conclude that  $E_2$  is globally asymptotically stable for (2.1) for all solutions for which  $x_2(0) > 0$ . The coexistence equilibrium  $E^*$  exists outside the nonnegative cone.

The passing of  $E^*$  through  $E_i$  is accompanied by a change in the stability of  $E_i$ , indicated by a change in the sign of  $\mathcal{G}_j(\bar{S}_i, \bar{R}_i) - D_j, i \neq j, i, j \in \{1, 2\}$ . One can express the  $S$ -coordinate of  $E_i$  in terms of  $D$  as follows: set  $x_j = 0$  and restrict the  $R$  coordinate to  $\varphi_i(S)$  (as dictated by  $x'_i = 0$ ). Then, solve  $S' = 0$  and  $R' = 0$  for  $x_i$ , set these expressions equal to each other, and solve the equation for  $S$  in terms of  $D$ . Denote by  $\Phi_i(D)$  the resulting curve in the  $(D, S)$ -plane. It can be shown that

$$D = \Phi_i^{-1}(S) = c_i S - \epsilon_i + \frac{k_i R^0 \eta_i c_i S}{\xi_i k_i (S^0 - S) + \eta_i c_i S}.$$

As  $E^*$  passes through  $E_i$ , the line described in (8.1) intersects  $\Phi_i$ . Clearly, the manner in which  $E^*$  passes through the positive cone is determined in part by the slope and intercepts of (8.1) together with the concavity of  $\Phi_1^{-1}$  and  $\Phi_2^{-1}$ . Note that  $\Phi_i^{-1}(S)$  is monotone increasing for  $S \in [0, S^0]$ , and its concavity is given by the sign of

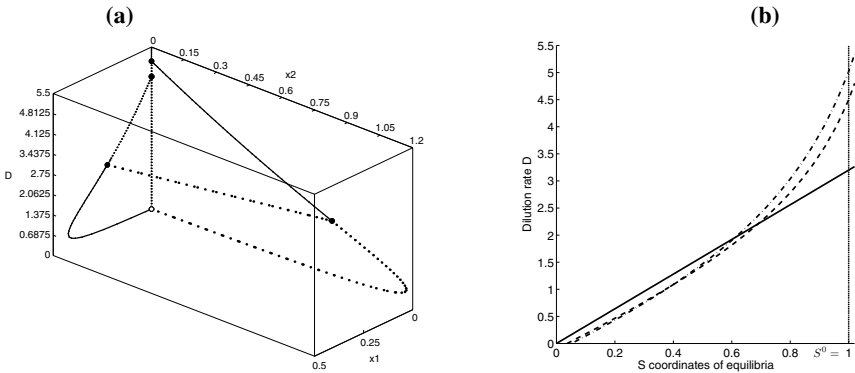
$$(\Phi_i^{-1})''(S) = -2 \frac{c_i k_i^2 \eta_i R^0 \xi_i S^0 (\eta_i c_i - \xi_i k_i)}{(\xi_i k_i (S^0 - S) + \eta_i c_i S)^3}.$$

On this same interval, the sign of  $(\Phi_i^{-1})''$  is fixed and so the concavity of  $\Phi_i^{-1}$  does not change. Thus, a straight line may intersect  $\Phi_i^{-1}$  at most twice. The balance between the parameters is quite delicate. Nonetheless, it is possible to produce various bifurcations of  $E^*$  into and out of the positive cone as  $D$  is decreased further. There are several possibilities, as illustrated in Figures 2 through 6.

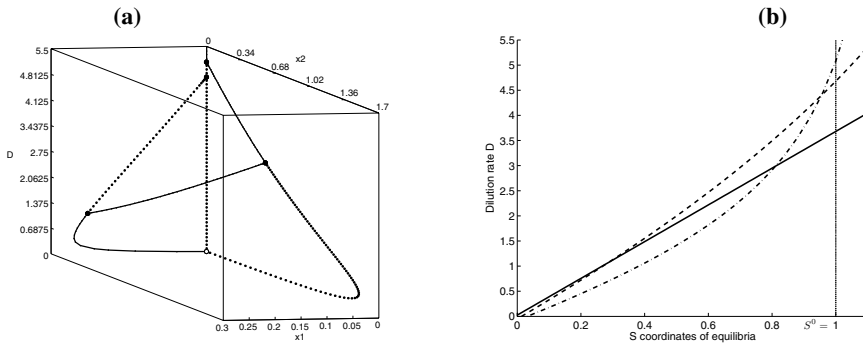
First, if there is no  $D > 0$  such that  $\mathcal{G}_j(\bar{S}_i, \bar{R}_i) = D_j$ , then  $E^*$  does not appear in the nonnegative cone as one decreases  $D$ .

Second, if there is a value of  $D$  at which  $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) = D_1$  and another at which  $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) = D_2$ , then  $E^*$  enters into the nonnegative cone through  $E_i$  and travels right through, leaving through  $E_j$ . If  $E^*$  enters through  $E_1$ , then Theorem 7.3 can be applied to show that  $E^*$  is a saddle. (See Figure 2. In (a), solid curves indicate stability while dotted curves indicate instability. In (b), the  $S$  coordinate of  $E_0$  is given by the vertical line at  $S^0 = 1$ , of  $E_1$  is given by  $- \cdot -$ , and of  $E_2$  is given by  $- \cdot \cdot -$ , and of  $E^*$  is given by the diagonal line. Bifurcations in (a) correspond to intersections in (b), but not vice versa. For instance, when the lines for the  $S$  coordinates of  $E_0$  and  $E^*$  cross, there is no bifurcation; the  $x_1$  and  $x_2$  coordinates of the equilibria differ.) If  $E^*$  enters through  $E_2$ , then Theorem 7.3 can be applied to show that  $E^*$  is globally asymptotically stable. (See Figure 3.)

Third, if there is precisely one value of  $D > 0$  at which  $\mathcal{G}_j(\bar{S}_i, \bar{R}_i) = D_j$ , but no value of  $D \geq 0$  at which  $\mathcal{G}_i(\bar{S}_j, \bar{R}_j) = D_i$ , then  $E^*$  enters the nonnegative cone through  $E_i$  and exits the nonnegative cone for  $D = 0$  as the  $x_1$  and  $x_2$  coordinates become negative. If  $E^*$  enters through  $E_2$ , then Theorem 7.3 can be applied to show that  $E^*$  is globally asymptotically stable. If  $E^*$  enters through  $E_1$ , then Theorem 7.3 can be applied to show that  $E^*$  is a saddle. Figure 4 shows an instance



**Fig. 2.** (a) Bifurcation diagram with  $E^*$  entering the nonnegative cone through  $E_1$  and leaving the nonnegative cone through  $E_2$ .  $D \in [0, 5.5]$  is the bifurcation parameter. Parameters used are:  $S^0 = 1.0$ ,  $R^0 = 1.2$ ,  $D_1 = D + \epsilon_1 = D + 0.1$ ,  $D_2 = D + \epsilon_2 = D + 0.14$ ,  $c_1 = 2.2$ ,  $c_2 = 1.8$ ,  $k_1 = 2$ ,  $k_2 = 2.8$ ,  $\xi_1 = 0.5$ ,  $\xi_2 = 1.2$ ,  $\eta_1 = 0.1$ ,  $\eta_2 = 0.5$ . The first transcritical bifurcation occurs at  $D = 5.02$  when  $E_2$  enters. The second transcritical bifurcation occurs at  $D = 4.5$  when  $E_1$  enters.  $E^*$  enters through  $E_1$  at  $D = 2.21$  and leaves through  $E_2$  at  $D = 1.96$ . Both single-species equilibria are locally stable and  $E^*$  is unstable when  $D \in (1.96, 2.21)$ . (b) Plot of the dilution rate  $D$  versus the  $S$  coordinate of each of the equilibria, using the same parameter values as were used for (a).



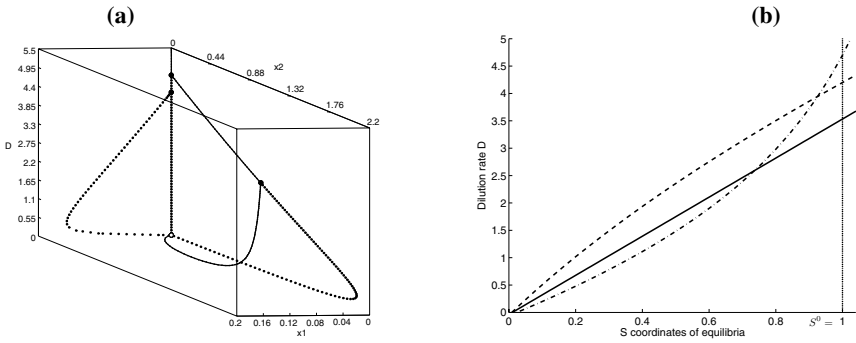
**Fig. 3.** (a) Bifurcation diagram with  $E^*$  entering the nonnegative cone through  $E_2$  and leaving the nonnegative cone through  $E_1$ .  $D \in [0, 5.5]$  is the bifurcation parameter. Parameters used are:  $S^0 = 1.0$ ,  $R^0 = 1.2$ ,  $D_1 = D + \epsilon_1 = D + 0.05$ ,  $D_2 = D + \epsilon_2 = D + 0.08$ ,  $c_1 = 2.33$ ,  $c_2 = 1.8$ ,  $k_1 = 2$ ,  $k_2 = 2.8$ ,  $\xi_1 = 0.2$ ,  $\xi_2 = 1.5$ ,  $\eta_1 = 0.1$ ,  $\eta_2 = 0.5$ . The first transcritical bifurcation occurs at  $D = 5.08$  when  $E_2$  enters. The second transcritical bifurcation occurs at  $D = 4.68$  when  $E_1$  enters.  $E^*$  enters through  $E_2$  at  $D = 2.99$  and leaves through  $E_1$  at  $D = 1.07$ . Both single-species equilibria are unstable and  $E^*$  is globally asymptotically stable when  $D \in (1.07, 2.99)$ . (b) Plot of the dilution rate  $D$  versus the  $S$  coordinate of each of the equilibria, using the same parameter values as were used for (a).

of the former. Note that for  $D = 0$ , any point satisfying  $x_1 = x_2 = 0$  is an equilibrium, so the passing of  $E_1$ ,  $E_2$ , and  $E^*$  out of the nonnegative cone represents a (degenerate) bifurcation. Also, note that as  $D$  approaches zero, condition (7.3) fails and the global behaviour becomes unknown.

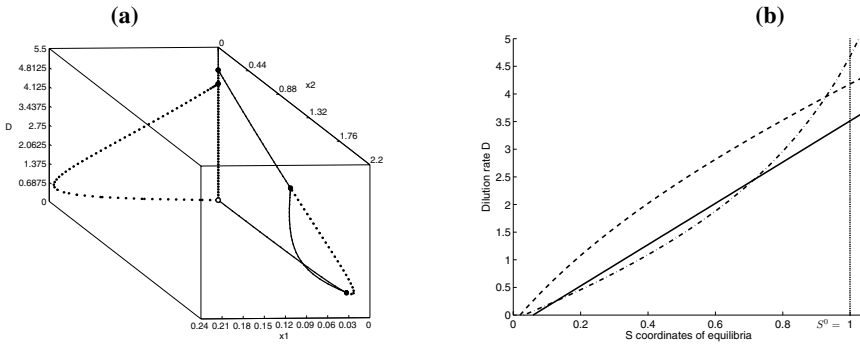
There are at most two values of  $D$  at which  $\mathcal{G}_j(\bar{S}_i, \bar{R}_i) = D_j$ , since this represents the intersection of the  $S^*$  line with  $\Phi_i(D)$ . If there are two values of  $D > 0$  at which  $\mathcal{G}_j(\bar{S}_i, \bar{R}_i) = D_j$  but no value of  $D \geq 0$  at which  $\mathcal{G}_i(\bar{S}_j, \bar{R}_j) = D_i$ , then  $E^*$  enters the nonnegative cone through  $E_i$ , passes into the interior, and then leaves again through  $E_i$ . Again, if  $E^*$  enters through  $E_2$ , then Theorem 7.3 can be applied to show that  $E^*$  is globally asymptotically stable (see Figure 5). If  $E^*$  enters through  $E_1$ , then it is a saddle and Theorem 7.3 can be applied to show that there is global bistability.

Figure 6 illustrates what is, in some sense, the most interesting scenario – one in which the line described in (8.1) intersects both  $\Phi_1$  and  $\Phi_2$  twice. In this particular case,  $E^*$  enters through  $E_2$  and exits through  $E_1$ , then reenters through  $E_1$  and exits again through  $E_2$ . As one can see from the associated plot in  $(S, D)$ -space, there are certainly other possibilities that can be obtained by delicately balancing the parameters governing the concavity of  $\Phi_1$  and  $\Phi_2$ , the slope in (8.1), etc. None will result in more than two crossings of  $E^*$  through the interior.

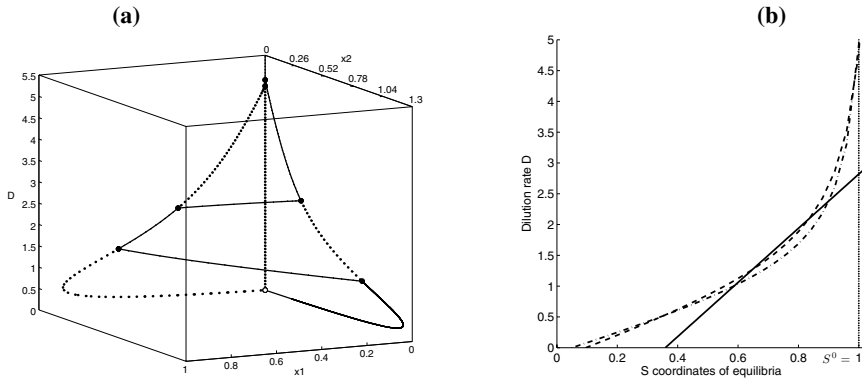
Now, consider *any* fixed set of parameter values at which  $E^*$  is globally asymptotically stable and choose *any* curve in parameter space that passes through this particular set of parameter values. In Section 4 we showed that  $E^*$  cannot undergo a Hopf bifurcation, and that the only local bifurcations of  $E^*$  occur when  $E^*$  passes out of the positive cone through one of the faces. Therefore, if the parameters are varied in such a way that  $E^*$  remains in the interior of the positive cone, then  $E^*$  remains globally asymptotically stable unless there is a non-local bifurcation.



**Fig. 4.** (a) Bifurcation diagram with  $E^*$  entering the nonnegative cone through  $E_2$  and leaving the nonnegative cone for  $D = 0$  as the  $x_1$  and  $x_2$  coordinates become negative.  $D \in [0, 5]$  is the bifurcation parameter. Parameters used are:  $S^0 = 1.0$ ,  $R^0 = 1.2$ ,  $D_1 = D + \epsilon_1 = D + 0.05$ ,  $D_2 = D + \epsilon_2 = D + 0.06$ ,  $c_1 = 2.33$ ,  $c_2 = 1.4$ ,  $k_1 = 1.6$ ,  $k_2 = 2.8$ ,  $\xi_1 = 0.08$ ,  $\xi_2 = 1.5$ ,  $\eta_1 = 0.1$ ,  $\eta_2 = 1.0$ . The first transcritical bifurcation occurs at  $D = 4.70$  when  $E_2$  enters. The second transcritical bifurcation occurs at  $D = 4.20$  when  $E_1$  enters.  $E^*$  enters through  $E_2$  at  $D = 2.59$ . All three equilibria leave through  $(S, R, 0, 0)$  when  $D = 0$ , but with different values of  $S$  and  $R$ . Both single-species equilibria are unstable and  $E^*$  is stable when  $D \in (0, 2.59)$ . (b) Plot of the dilution rate  $D$  versus the  $S$  coordinate of each of the equilibria, using the same parameter values as were used for (a).



**Fig. 5.** (a) Bifurcation diagram with  $E^*$  entering and exiting the nonnegative cone through  $E_2$ .  $D \in [0, 5]$  is the bifurcation parameter. Parameters used are:  $S^0 = 1.0$ ,  $R^0 = 1.2$ ,  $D_1 = D + \epsilon_1 = D + 0.14$ ,  $D_2 = D + \epsilon_2 = D + 0.08$ ,  $c_1 = 2.4$ ,  $c_2 = 1.4$ ,  $k_1 = 1.6$ ,  $k_2 = 2.8$ ,  $\xi_1 = 0.12$ ,  $\xi_2 = 1.5$ ,  $\eta_1 = 0.2$ ,  $\eta_2 = 1.0$ . The first transcritical bifurcation occurs at  $D = 4.68$  when  $E_2$  enters. The second transcritical bifurcation occurs at  $D = 4.18$  when  $E_1$  enters.  $E^*$  enters through  $E_2$  at  $D = 2.45$  and leaves through  $E_2$  at  $D = 0.25$ . Both single-species equilibria are unstable and  $E^*$  is globally asymptotically stable when  $D \in (0.25, 2.45)$ . (b) Plot of the dilution rate  $D$  versus the  $S$  coordinate of each of the equilibria, using the same parameter values as were used for (a).



**Fig. 6.** (a) Bifurcation diagram with  $E^*$  entering and exiting the nonnegative cone through  $E_2$ .  $D \in [0, 5]$  is the bifurcation parameter. Parameters used are:  $S^0 = 1.0$ ,  $R^0 = 1.2$ ,  $D_1 = D + \epsilon_1 = D + 0.18$ ,  $D_2 = D + \epsilon_2 = D + 0.08$ ,  $c_1 = 1.6$ ,  $c_2 = 1.4$ ,  $k_1 = 2.8$ ,  $k_2 = 3.0$ ,  $\xi_1 = 1.5$ ,  $\xi_2 = 1.7$ ,  $\eta_1 = 0.2$ ,  $\eta_2 = 0.2$ . The first transcritical bifurcation occurs at  $D = 4.92$  when  $E_2$  enters. The second transcritical bifurcation occurs at  $D = 4.78$  when  $E_1$  enters.  $E^*$  enters through  $E_2$  at  $D = 2.39$  and leaves through  $E_1$  at  $D = 2.1$ .  $E^*$  enters once more, this time through  $E_1$  at  $D = 1.26$  and leaves through  $E_2$  at  $D = 1.0$ . Both single-species equilibria are unstable and  $E^*$  is globally asymptotically stable when  $D \in (2.1, 2.39)$  and when  $D \in (1.0, 1.26)$ . (b) Plot of the dilution rate  $D$  versus the  $S$  coordinate of each of the equilibria, using the same parameter values as were used for (a).

Now suppose  $E^*$  exists and is a saddle. Then Theorem 5.2 implies  $A = \frac{\xi_1 \eta_2}{\xi_2 \eta_1}$  is not equal to 1. If  $A$  is varied to be made equal to 1, then Theorem 5.2 says that if  $E^*$  exists, then it is stable. Since local bifurcations at  $E^*$  can only occur when  $E^*$  coalesces with  $E_1$  or  $E_2$ , such a transcritical bifurcation must occur before  $A = 1$ .

### 9. Discussion

In this paper we consider a resource-based model of two-species competition in the chemostat for two growth-limiting, non-reproducing, non-inhibitory, perfectly substitutable resources  $S$  and  $R$ . The competition is exploitative, so that the members of the microbial populations compete only by reducing the common pool of resources. We assume that the amount of each resource consumed is a monotone increasing function of the abundance of that resource and is independent of the concentration of the other resource. The resultant model corresponds to Model I of Léon and Tumpson [21] adapted to the chemostat and restricted to the case of non-reproducing resources. It is also a special case of the model studied in [3, 29], where the possible inhibitory effects that the concentration of one resource may have on the consumption of the other resource were considered.

In the single-species growth submodel  $(S, R, x_1, 0)$ , species  $x_1$  avoids extinction if and only if  $\mathcal{G}_1(S^0, R^0) > D_1$ . In other words, if species 1 cannot consume enough resource to more than compensate for the rate  $D_1$  at which it is being removed, even if the growth vessel is maintained at the input concentrations  $S^0$  and  $R^0$ , then species 1 will become extinct. Otherwise, there exists a unique one-spe-

cies survival equilibrium that is globally asymptotically stable for all solutions for which  $x_1(0) > 0, x_2(0) = 0$ . A similar result holds for the  $(S, R, 0, x_2)$  submodel.

For the two-species competition model, first we consider the case in which one or both species are eliminated due to an inadequate resource supply (competition-independent extinction). If  $\mathcal{G}_i(S^0, R^0) < D_i$  for  $i = 1$  and 2, so that the resource supply is inadequate for each species, then the washout equilibrium  $E_0$  is globally asymptotically stable. If  $\mathcal{G}_1(S^0, R^0) > D_1$  and  $\mathcal{G}_2(S^0, R^0) < D_2$ , so that the resource supply is inadequate only for population two, then the unique single-species equilibrium  $E_1 = (\bar{S}_1, \bar{R}_1, \bar{x}_1, 0)$  exists and is globally asymptotically stable with respect to all solutions with  $x_1(0) > 0$ . A similar result holds when the resource supply is inadequate only for population one.

We then move to the more challenging problem of determining the asymptotic behaviour of solutions when the resource supply is adequate for each species, so that  $\mathcal{G}_i(S^0, R^0) > D_i$  for  $i = 1$  and 2. Note that both of the equilibria  $E_1$  and  $E_2$  exist, and their local stability is determined by the standard invasion criterion:  $E_1$  is unstable whenever  $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) > D_2$  (and so can be invaded by species two) and  $E_2$  is unstable whenever  $\mathcal{G}_1(\bar{S}_2, \bar{R}_2) > D_1$  (and so can be invaded by species one). When each species' functional response to each resource is linear,  $(\mathcal{G}_2(\bar{S}_1, \bar{R}_1) - D_2)(\mathcal{G}_1(\bar{S}_2, \bar{R}_2) - D_1) < 0$  ensures that no coexistence equilibrium exists, whereas  $(\mathcal{G}_2(\bar{S}_1, \bar{R}_1) - D_2)(\mathcal{G}_1(\bar{S}_2, \bar{R}_2) - D_1) > 0$  implies the existence of a unique interior equilibrium.

Next, two techniques are used to examine the global dynamics under the assumption of linear uptake functions. First we employ Lyapunov function arguments to determine the global behaviour of the system. We show that  $E_1$  is globally asymptotically stable with respect to all solutions with  $x_1(0) > 0$  provided  $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) < D_2, \mathcal{G}_1(\bar{S}_2, \bar{R}_2) > D_1$ , and  $\frac{k_2 \bar{R}_1}{D_2 - c_2 \bar{S}_1} < \frac{\xi_1 \eta_2}{\xi_2 \eta_1} < \frac{D_2 - k_2 \bar{R}_1}{c_2 \bar{S}_1}$ . (Of course, the first two conditions ensure that there is no coexistence equilibrium.) It is then shown that there exists a unique coexistence equilibrium that is globally asymptotically stable with respect to all solutions with  $x_i(0) > 0, i = 1$  and 2 provided  $\mathcal{G}_2(\bar{S}_1, \bar{R}_1) > D_2, \mathcal{G}_1(\bar{S}_2, \bar{R}_2) > D_1$ , and  $\xi_1 \eta_2 = \xi_2 \eta_1$ . (Note that the first two conditions ensure that both of the single-species equilibria can be invaded.)

Our most complete results are obtained in the theoretical framework of compound matrices. Here we impose two conditions on the parameters of the model:  $D_1, D_2 < 2D_S, 2D_R$ , so that the intrinsic death rates are not too large, and  $(3 - \sqrt{5})/2 \leq \frac{\xi_1 \eta_2}{\xi_2 \eta_1} \leq (3 + \sqrt{5})/2$ , so that the ratios of the growth yields cannot differ greatly between the two species. We find that the dynamics of the competition model are trivial in the sense that each solution initiating in the feasible region of  $(S, R, x_1, x_2)$ -space approaches an equilibrium in the limit. In particular, the global behaviour can be resolved here even when the coexistence equilibrium is a saddle.

Finally, using the dilution rate  $D$  as a bifurcation parameter we describe the different possible sequences of bifurcations. Ecologists often think of the chemostat as a lake in a laboratory. This analysis seems to warn us that the diversity of populations in a lake system might be sensitive to the changes in the dilution rate that could result from, for example, dams used to control the water levels, or changes in the weather, and that it might not be obvious whether increasing or

decreasing the dilution rate is better, if one wishes to protect diversity. This is most dramatically illustrated in the example given in Figure 6. We see that as the dilution rate is decreased, there is a transfer of global asymptotic stability from  $E_0$  to  $\bar{E}_2$  to  $E^*$  to  $\bar{E}_1$  to  $E^*$  to  $\bar{E}_2$ . Thus, if both species coexist at a given dilution rate, then depending on which branch  $E^*$  lies on, a particular species may be eliminated either by an increase or by a decrease in the dilution rate.

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