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INTERACTION IN A CHEMOSTAT: INTRODUCTION OF A COMPETITOR CAN PROMOTE GREATER DIVERSITY

GAIL S.K. WOLKOWICZ, MARY M. BALLYK AND SPIRO P. DAOUSSIS

ABSTRACT. It is well known that models of exploitative competition in a chemostat with constant input, by n populations of microorganisms for a single, essential, nonreproducing, growth-limiting resource predict competitive exclusion. That is, they predict that at most one population avoids extinction. In this paper we consider two scenarios based in a chemostat in which the introduction of a population that exploits common resource(s), actually promotes greater diversity. In the first example, feeding on more than one trophic level is allowed. In the second example, two perfectly substitutable resources are involved. In both examples, the extinction of a population is averted by the introduction of a population that interacts only by consuming common resource(s).

1. Introduction. It is well known (see, for example, [**1, 4, 9, 10, 16, 17, 20**]) that models of exploitative competition in a chemostat with constant input, by n populations of microorganisms for a single, essential, nonreproducing, growth-limiting resource predict competitive exclusion. That is, they predict that at most one population avoids extinction. Hence, exploitative competition is usually thought of as a factor that reduces the diversity of natural ecosystems. On the other hand, predation is usually assumed to be one of the factors that promotes diversity (see, for example, [**5, 12, 15, 18, 19**]). In fact, in Wolkowicz [**18**], a model of a food web in a chemostat

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is considered where an arbitrary number of competitor populations compete exploitatively for a single resource and an arbitrary number of predator populations predate on the competitor populations. The model predicts that *invasion* by a competitor population or *removal* of a predator population can cause a drastic reduction in the number of populations in the system.

In this paper we describe two different scenarios based in a chemostat in which the introduction of a population that exploits common resource(s) actually promotes *greater* diversity. In the first example, discussed in Section 2, we consider two populations competing exploitatively for the same resource. One of the populations also consumes the other and under certain conditions would consume his competitor population to extinction. The model predicts that invasion by a third population that interacts only by competing for the resource can prevent the predator from consuming the competitor population to extinction and that all three populations coexist.

In the second example, discussed in Section 3, we consider two populations that interact simply by consuming the same two perfectly substitutable resources. It is not surprising that competition for two resources can result in the coexistence of two competitor populations. What is surprising in the example considered is that one of the populations cannot survive in the absence of its apparent rival. However, survival is assured provided both populations are present initially, regardless of the initial concentrations. A similar situation occurs in Butler and Wolkowicz [**6**], where competition is for two perfectly complementary resources. Examples are given (see examples 3.9 and 3.11 in [**6**]) predicting that when both resources are limiting at low concentrations and at least one of the resources is inhibitory at high concentrations, two populations can coexist even though neither one can survive without the other.

These examples seem to indicate that exploitation of common resource(s) in some circumstances promotes diversity. For more complete analyses of the models discussed in Sections 2 and 3 of this paper, the reader is referred to Daoussis [**7**] and Ballyk and Wolkowicz [**2**].

2. Predator feeding on two different trophic levels.

2.1. *The model.* We consider a model of predator-mediated competition in the chemostat in which three competitor populations compete for a single, essential, nonreproducing, growth-limiting nutrient. The competitor population that requires the highest concentration of nutrient to maintain its concentration also predates on the competitor population that requires the lowest concentration of nutrient to maintain its concentration. Thus one population acts as both a competitor population as well as a predator population and feeds on two distinct trophic levels. For the purposes of this paper we restrict our attention to linear (Lotka-Volterra) response functions in this model. The model is given by the following system of differential equations:

$$\begin{aligned} S'(t) &= (S^0 - S(t))D - \frac{x_1(t)p_1(S(t))}{\eta_1} \\ &\qquad - \frac{x_2(t)p_2(S(t))}{\eta_2} - \frac{y(t)p_3(S(t))}{\eta_3} \\ x_1'(t) &= x_1(t)(-D + p_1(S(t))) - y(t)q(x_1(t))/z \\ x_2'(t) &= x_2(t)(-D + p_2(S(t))) \\ y'(t) &= y(t)(-D + p_3(S(t)) + q(x_1(t))) \end{aligned} \tag{2.1}$$

$$S(0) = S_0 \geq 0, \qquad x_i(0) = x_{i0} \geq 0, \quad i = 1, 2, \qquad y(0) = y_0 \geq 0.$$

The culture vessel is assumed to be well-stirred so that spatial variation need not be considered. We assume for convenience that the volume of the culture vessel is one cubic unit. $S(t)$ denotes the nutrient concentration and $x_1(t)$, $x_2(t)$ and $y(t)$ denote concentrations of microorganisms in the culture vessel at time t. All populations of microorganisms are assumed to compete for nutrient S. However, y is also a predator population, since besides consuming S, it predates on x_1. The functional response of each competitor population x_1, x_2 and y on nutrient S is given by $p_i(S) = DS/\lambda_i$, $i = 1, 2, 3$, respectively, and the rate of consumption of nutrient S for the respective populations is given by $p_i(S)/\eta_i$, $i = 1, 2, 3$. Thus, the constants η_i, $i = 1, 2, 3$, denote growth yield constants and we are assuming that consumption of nutrient by the microorganisms is proportional to conversion to biomass. Similarly, $q(x_1) = Dx_1/\delta$ denotes the functional response of predator y on prey x_1 and $q(x_1)/z$ is assumed to denote the prey-uptake function for the predator and so the constant z is the growth yield constant for the predator population feeding on the prey. The constants λ_i, $i = 1, 2, 3$, and δ denote the break-even concentrations of nutrient and prey, respectively. S^0 denotes the concentration of nutrient in the feed vessel and D denotes the dilution rate. The species specific death rates are assumed to be insignificant compared to the dilution rate.

The following substitutions help simplify the analysis of system (2.1):

$$\bar{t} = tD; \qquad \overline{S} = \frac{S}{S^0}; \qquad \bar{x}_i = \frac{x_i}{\eta_i S^0}, \quad i = 1, 2; \quad \bar{y} = \frac{y}{\eta_1 S^0 z}; \tag{2.2}$$

$$\bar{p}_i(\overline{S}) = \frac{p_i(S)}{D}, \quad i = 1, 2, 3; \qquad \bar{q}(\bar{x}_1) = \frac{q(x_1)}{D}; \qquad \gamma = \frac{\eta_2}{\eta_1 z}. \tag{2.3}$$

For technical reasons, we assume throughout that $\gamma = 1$. Omitting the bars, to simplify the notation, the scaled version of system (2.1) can be written as follows:

$$\begin{aligned} S'(t) &= (1 - S(t)) - x_1(t)S(t)/\lambda_1 - x_2(t)S(t)/\lambda_2 - y(t)S(t)/\lambda_3 \\ x_1'(t) &= x_1(t)(-1 + S(t)/\lambda_1) - y(t)x_1(t)/\delta \\ x_2'(t) &= x_2(t)(-1 + S(t)/\lambda_2) \\ y'(t) &= y(t)(-1 + S(t)/\lambda_3 + x_1(t)/\delta) \\ S_0 &\geq 0, \qquad x_{i0} \geq 0, \quad i = 1, 2, \qquad y_0 \geq 0. \end{aligned} \tag{2.4}$$

There is no loss of generality if we analyze system (2.4) instead of system (2.1). We identify (S, x_1, x_2, y)-space with $\mathbf{R}^4$. We assume that the break-even concentrations of the nutrient are ordered

$$\lambda_1 < \lambda_2 < \lambda_3, \tag{2.5}$$

so that population x_1 is the most efficient and population y the least efficient on nutrient S.

The critical points of system (2.4), when they exist, will be denoted by:

$$\begin{aligned} E_0 &= (1, 0, 0, 0), & E_{\lambda_1} &= (\lambda_1, 1 - \lambda_1, 0, 0), \\ E_{\lambda_2} &= (\lambda_2, 0, 1 - \lambda_2, 0), & E_{\lambda_3} &= (\lambda_3, 0, 0, (1 - \lambda_3)), \\ E_{S^*} &= (S^*, x_1^*, 0, y^*), & \widetilde{E}_{\lambda_2} &= (\lambda_2, \tilde{x}_1, \tilde{x}_2, \tilde{y}), \end{aligned}$$

where $S^* = \lambda_1\lambda_3/(\lambda_1\lambda_3 + \delta(\lambda_3 - \lambda_1))$, $x_1^* = \delta(1 - S^*/\lambda_3)$, $y^* = \delta(-1 + S^*/\lambda_1)$, $\tilde{x}_1 = \delta(1 - \lambda_2/\lambda_3)$, $\tilde{y} = \delta(-1 + \lambda_2/\lambda_1)$ and $\tilde{x}_2 = 1 - \lambda_2 - \delta(\lambda_2/\lambda_1 - \lambda_2/\lambda_3) > 0$.

We say that a critical point exists if and only if all of its components are nonnegative. Hence, E_{λ_i} exists provided that $\lambda_i \le 1$. E_{S^*} exists provided $\lambda_1 \le S^* \le \lambda_3$. $\widetilde{E}_{\lambda_2}$ exists provided that $1 - \lambda_2 - \delta(\lambda_2/\lambda_1 - \lambda_2/\lambda_3) > 0$ so that $\tilde{x}_2 > 0$.

For system (2.4), each coordinate face where any one of the species x_1, x_2 or y is absent is invariant, and if for some $\bar{t}$, $S(\bar{t}) = 0$, then $S'(\bar{t}) > 0$. From this, and the uniqueness of initial value problems, it follows that $\operatorname{int} \mathbf{R}_+^4$ is positively invariant for solutions of (2.4).

By adding the equations in system (2.4) and then solving the resulting first order linear ordinary differential equation in the dependent variable $S + \sum_{i=1}^2 x_i + y$, it follows that the simplex

$$\mathcal{S} = \left\{ (S, x_1, x_2, y) \in \mathbf{R}_+^4 : S + \sum_{i=1}^{2} x_i + y = 1 \right\}$$

is a global attractor for (2.4), and hence all solutions are bounded.

2.2. Competition responsible for diversity. In this section we show that if no population x_2 is present, it is possible for the predator population y to drive population x_1 to extinction, but that this can be prevented by the introduction of competitor x_2. Therefore, competition can be beneficial in the sense that it can promote greater diversity.

Theorem 2.1. (a) *If* $-1+\lambda_3/\lambda_1-(1-\lambda_3)/\delta < 0$, *then* E_{λ_3} *is globally asymptotically stable with respect to all solutions of* (2.4) *for which* $S_0 \ge 0$, $x_{10} \ge 0$, $x_{20} = 0$ *and* $y_0 > 0$, *and hence* $\lim_{t\to\infty} x_1(t) = 0$.

(b) *If* $1 - \lambda_2 - \delta(\lambda_2/\lambda_1 - \lambda_2/\lambda_3) > 0$, *so that* $\widetilde{E}_{\lambda_2}$ *lies in the positive cone, then* $\widetilde{E}_{\lambda_2}$ *is globally asymptotically stable with respect to all solutions of* (2.4) *for which* $S_0 \ge 0$, $x_{i0} > 0$, $i = 1, 2$, *and* $y_0 > 0$, *and hence* $\lim_{t\to\infty} x_1(t) > 0$.

Proof. (a) Since $x_{20} = 0$ implies that $x_2(t) \equiv 0$, there is no loss of generality if we restrict our attention to (S, x_1, y)-space. Using a standard linear analysis it is easy to show that $-1+\lambda_3/\lambda_1-(1-\lambda_3)/\delta<0$ implies that the equilibrium $(\lambda_3, 0, 1-\lambda_3)$ is locally asymptotically stable. Define the function $V : \operatorname{int}\mathbf{R}^3_+ \to \mathbf{R}$ by

$$\begin{aligned} V(S,x_1,y) = \{S-\lambda_3-\lambda_3\ln(S/\lambda_3)\} + x_1 \\ + \{y-(1-\lambda_3)-(1-\lambda_3)\ln(y/(1-\lambda_3))\}. \end{aligned}$$

The time derivative calculated along solutions of (2.4) is

$$\begin{aligned} \dot V(S,x_1,y) &= (1-\lambda_3/S)S' + x_1' + (1-(1-\lambda_3)/y)y' \\ &= ((S-\lambda_3)/S)(1-S) - (1-\lambda_3)(-1+S/\lambda_3) \\ &\quad + x_1(-1+\lambda_3/\lambda_1-(1-\lambda_3)/\delta) \\ &= -(S-\lambda_3)^2/(S\lambda_3) + x_1(-1+\lambda_3/\lambda_1-(1-\lambda_3)/\delta) \le 0. \end{aligned}$$

Since all solutions are positive and bounded, by an extension theorem of LaSalle, every solution of (2.4) for which $S_0>0$, $x_{10}>0$, and $x_2(t)\equiv 0$, approaches $\mathcal{M}$, where $\mathcal{M}$ is the largest invariant subset of

$$\mathcal{E} \equiv \{(S,x_1,y)\in\mathbf{R}^3_+ : \dot V(S,x_1,y)=0 \text{ and } x_2=0\}.$$

Since $-1+\lambda_3/\lambda_1-(1-\lambda_3)/\delta<0$, $\dot V(S,x_1,y)=0$ if and only if $S=\lambda_3$ and $x_1=0$. Since S is constant, $S'=0$ and so $y=(1-\lambda_3)$. Therefore, $\mathcal{E}=\mathcal{M}=\{(\lambda_3,0,1-\lambda_3)\}$, and the result follows.

(b) Define the function $V : \operatorname{int}\mathbf{R}^4_+ \to \mathbf{R}^4_+$ by

$$\begin{aligned} V(S,x_1,x_2,y) = S-\widetilde S-\widetilde S\ln(S/\widetilde S) + \{x_1-\tilde x_1-\tilde x_1\ln(x_1/\tilde x_1)\} \\ + \{x_2-\tilde x_2-\tilde x_2\ln(x_2/\tilde x_2)\} + \{y-\tilde y-\tilde y\ln(y/\tilde y)\}. \end{aligned}$$

Recalling that $\widetilde S=\lambda_2$, $\tilde x_1=\delta(1-\lambda_2/\lambda_3)$, $\tilde x_2=1-\lambda_2-\delta(\lambda_2/\lambda_1-\lambda_2/\lambda_3)>0$ and $\tilde y=\delta(-1+\lambda_2/\lambda_1)$, the time derivative calculated along solutions of system (2.4) is

$$\begin{aligned}
\dot{V}(S, x_1, x_2, y) &= (1 - \widetilde{S}/S)S' + (1 - \tilde{x}_1/x_1)x_1' + (1 - \tilde{x}_2/x_2)x_2' \\
&\quad + (1 - \tilde{y}/y)y' \\
&= ((S - \lambda_2)/S)(1 - S) + x_1(\lambda_2/\lambda_1 - 1 - \tilde{y}/\delta) \\
&\quad + y(\lambda_2/\lambda_3 - 1 + \tilde{x}_1/\delta) - \tilde{x}_1(-1 + S/\lambda_1) \\
&\quad - \tilde{x}_2(-1 + S/\lambda_2) - \tilde{y}(-1 + S/\lambda_3) \\
&= ((S - \lambda_2)/S)(1 - S) - \tilde{x}_1(-1 + S/\lambda_1) \\
&\quad - \tilde{x}_2(-1 + S/\lambda_2) - \tilde{y}(-1 + S/\lambda_3) \\
&= ((S - \lambda_2)/S)(1 - S) - \delta((\lambda_3 - \lambda_2)/\lambda_3)((S - \lambda_1)/\lambda_1) \\
&\quad - (1 - \lambda_2 - (\delta\lambda_2/(\lambda_1\lambda_3))(\lambda_3 - \lambda_1))((S - \lambda_2)/\lambda_2) \\
&\quad - \delta((\lambda_2 - \lambda_1)/\lambda_1)((S - \lambda_3)/\lambda_3) \\
&= ((S - \lambda_2)/S)(1 - S) - ((1 - \lambda_2)/\lambda_2)(S - \lambda_2) \\
&\quad - (\delta/(\lambda_1\lambda_3))\{(\lambda_3 - \lambda_2)(S - \lambda_1) - (\lambda_3 - \lambda_1)(S - \lambda_2) \\
&\qquad\qquad + (\lambda_2 - \lambda_1)(S - \lambda_3)\} \\
&= -(1/(S\lambda_2))(S - \lambda_2)^2 \le 0.
\end{aligned}$$

Since all solutions are positive and bounded, by an extension theorem of LaSalle, every solution of (2.4) for which $S_0 > 0$, $x_{i0} > 0$, $i = 1, 2$, and $y_0 > 0$, approaches $\mathcal{M}$, where $\mathcal{M}$ is the largest invariant subset of

$$\mathcal{E} \equiv \{(S, x_1, x_2, y) \in \operatorname{int} \mathbf{R}_+^4 : \dot{V}(S, x_1, x_2, y) = 0\}.$$

For any point in $\mathcal{E}$, $S = \lambda_2$ and so $S' = 0$ and $x_2' = 0$. This implies that x_2 is also constant, and so $S'(t) = (1 - \lambda_2) - x_1(t)(\lambda_2/\lambda_1) - x_2 - y(t)(\lambda_2/\lambda_3) = 0$. Solving for $y(t)$ we obtain

$$y(t) = (\lambda_3/\lambda_2)(1 - \lambda_2 - x_2) - x_1(t)(\lambda_3/\lambda_1).$$

Assume $x_1(t)$ is not a constant. Then differentiating the above expression it follows that

$$y'(t) = -x_1'(t)(\lambda_3/\lambda_1).$$

Substituting the above expressions for $y(t)$ and $y'(t)$ into the equations for $x_1'(t)$ and $y'(t)$ in (2.4) gives

$$x_1'(t) = x_1(t)\left(-1 + \frac{\lambda_2}{\lambda_1}\right) - \frac{\lambda_3 x_1(t)}{\delta}\left(\frac{1 - \lambda_2 - x_2}{\lambda_2} - \frac{x_1(t)}{\lambda_1}\right)$$

and

$$x_1'(t) = -\left(\frac{\lambda_1(1-\lambda_2-x_2)}{\lambda_2} - x_1(t)\right)\left(-1+\frac{\lambda_2}{\lambda_3}+\frac{x_1(t)}{\delta}\right).$$

Equating these two expressions for $x_1'(t)$ and solving yields a quadratic in $x_1(t)$:

$$x_1^2(t)\frac{(\lambda_3-\lambda_1)}{\lambda_1\delta} + x_1(t)(\lambda_3-\lambda_1)\left(\frac{\lambda_2}{\lambda_1\lambda_3} - \frac{1-\lambda_2-x_2}{\lambda_2\delta}\right) - \frac{\lambda_2(1-\lambda_2-x_2)}{\lambda_2\lambda_3}(\lambda_3-\lambda_2) = 0.$$

Therefore x_1 must be a constant, which implies y is also a constant. Therefore, $x_1' = 0$ and $y' = 0$. If $x_1 = 0$ and y is constant, by setting $y' = 0$ in (2.4) it follows that $y = 0$. By setting $S' = 0$ in (2.4), it follows that $x_2 = 1 - \lambda_2$. If $x_1 \neq 0$ and y is constant, then by setting $x_1' = 0$ we obtain $y = \delta(-1 + p_1(\lambda_2)) \equiv \tilde{y}$. By setting $y' = 0$, we obtain $x_1 = \delta(1 - p_3(\lambda_2)) \equiv \tilde{x}_1$. Together with $S' = 0$, this implies that $x_2 = 1 - \lambda_2 - \delta(p_1(\lambda_2) - p_3(\lambda_2)) \equiv \tilde{x}_2$. Hence, $\mathcal{E} = \{E_{\lambda_2}\} \cup \{\widetilde{E}_{\lambda_2}\}$. But E_{λ_2} is unstable and has stable manifold $\mathcal{W}^s(E_{\lambda_2}) = \{(S, x_1, x_2, y) : x_1 = 0, x_2 > 0, S, y \geq 0\}$. Since $\mathcal{W}^s(E_{\lambda_2})$ does not intersect $\operatorname{int}\mathbf{R}_+^4$ and the omega limit set of any solution of (2.4) is connected, it follows that all solutions approach $\widetilde{E}_{\lambda_2}$. $\square$

Recall that the components of E_{S^*} are nonnegative if and only if $\lambda_2 \leq S^* \leq \lambda_3$ where $S^* \equiv (\lambda_1\lambda_3)/(\lambda_1\lambda_3 + \delta(\lambda_3 - \lambda_1))$. The condition $1 - \lambda_2 - \delta(\lambda_2/\lambda_1 - \lambda_2/\lambda_3) > 0$ is equivalent to $S^* > \lambda_2$ and ensures that $\widetilde{E}_{\lambda_2}$ exists. The condition $-1 + \lambda_3/\lambda_1 - (1 - \lambda_3)/\delta < 0$ is equivalent to $S^* > \lambda_3$ and ensures that no equilibrium of the form E_{S^*} exists, but that one of the form $\widetilde{E}_{\lambda_2}$ does exist. It also ensures that E_{λ_1} is unstable.

The following corollary asserts that if $\lambda_3 < 1$ and δ is sufficiently small, then without population x_2, population x_1 is driven to extinction by population y. However, the extinction of population x_1 is prevented by the introduction of population x_2. The condition $\delta < (\lambda_1(1 - \lambda_3))/(\lambda_3 - \lambda_1)$ is equivalent to $S^* > \lambda_3$.

Corollary 2.1. *Assume that* $0 < \delta < (\lambda_1(1 - \lambda_3))/(\lambda_3 - \lambda_1)$.

(a) *If* $x_{20} = 0$ *and* $y_0 > 0$*, then* $\lim_{t\to\infty} x_1(t) = 0$*.*

(b) *If* $x_{i0} > 0$*,* $i = 1, 2$*, and* $y_0 > 0$*, then* $\lim_{t\to\infty} x_1(t) > 0$*.*

Why should competition from population x_2 for resource S be helpful to population x_1? When competitor x_2 is not present, if the maximal growth rate of the predator population y on prey population x_1 is high enough (i.e., δ is sufficiently small), and $\lambda_3 < 1$ so that population y can survive on nutrient S alone, then population y can consume population x_1 to extinction. However, if population x_2 is introduced, this cannot occur since $\lambda_2 < \lambda_3$ and so population x_2 would outcompete population y for S once the concentration of population x_1 is sufficiently low. But $\lambda_1 < \lambda_2$, and so if the concentration of population y becomes sufficiently low, population x_1 would outcompete population x_2. This would allow the concentration of population x_1 to recover, and hence population x_1 would avoid extinction.

3. Competition for two perfectly substitutable resources. An important consideration that arises when competition is for more than one resource, is how the resources, once consumed, are utilized by the individual competitors for growth. Rapport [**13**] and León and Tumpson [**11**] classify resources in terms of consumer needs. This classification yields a spectrum of resource types, and hence a continuum of competitive situations. On opposite extremes are the perfectly complementary and perfectly substitutable resources.

Perfectly complementary resources are substances which fulfill different essential needs in terms of growth and so must be taken together by the consumer. For example, a nitrogen source and a carbon source might be perfectly complementary for a bacterium.

Perfectly substitutable resources are alternate sources of the same essential nutrient. In this case, the rates of consumption of the different resources can be substituted in a fixed ratio in order to maintain a given growth rate. An example for a bacterium would be two carbon sources or two nitrogen sources.

For the remainder of our discussion we assume that resources S and R are perfectly substitutable (in the above sense) for both populations x_1 and x_2. This terminology is different from that used by Tilman [**16**], who classifies resources based on the shape of the resource-dependent growth (reproduction) isoclines.

3.1. *The model.* We consider a model of exploitative competition in the chemostat in which two competitor populations compete for two nonreproducing, perfectly substitutable nutrients.

$$
\begin{aligned}
S'(t) &= (S^0 - S(t))D - \sum_{i=1}^{2} \frac{x_i(t)}{\xi_i} \mathcal{S}_i(S(t), R(t)),\\
R'(t) &= (R^0 - R(t))D - \sum_{i=1}^{2} \frac{x_i(t)}{\eta_i} \mathcal{R}_i(S(t), R(t)),\\
x_i'(t) &= x_i(t)(-D + \mathcal{G}_i(S(t), R(t))), \quad i = 1, 2,
\end{aligned}
\tag{3.1}
$$

$$S(0) = S_0 \geq 0, \qquad R(0) = R_0 \geq 0, \qquad x_i(0) = x_{i0} \geq 0, \quad i = 1, 2.$$

As in the previous model, we assume that the volume of suspension in the culture vessel is one cubic unit and that the culture vessel is well-stirred. $S(t)$ and $R(t)$ represent the concentrations of the two nonreproducing nutrients and $x_i(t)$, $i = 1, 2$, denote the biomass of the competing populations of microorganisms in the culture vessel at time t. Assuming only one feed bottle is used, S^0 and R^0 denote the concentrations of resource S and resource R, respectively, in the feed bottle. The constant D denotes the dilution rate and the specific death rates of the microorganisms are assumed to be insignificant compared to the dilution rate.

The function $\mathcal{S}_i(S, R)$ (respectively, $\mathcal{R}_i(S, R)$) represents the rate of conversion of nutrient S (R) to biomass of population x_i. Assuming that the conversion of nutrient to biomass is proportional to the amount of nutrient consumed, the consumption rate of resource S (R) per unit of competitor x_i is denoted $(\mathcal{S}_i(S, R)/\xi_i)$ $(\mathcal{R}_i(S, R)/\eta_i)$ where ξ_i (η_i) is the respective growth yield constant.

It is assumed that

$$\mathcal{S}_i, \mathcal{R}_i : \mathbf{R}_+^2 \to \mathbf{R}_+, \tag{3.2}$$

$$\mathcal{S}_i, \mathcal{R}_i \text{ are continuously differentiable.} \tag{3.3}$$

It is natural to expect that if the concentration of resource S in the culture vessel is zero, there will be no consumption or conversion of resource S. A similar statement holds for resource R. Therefore,

$$\mathcal{S}_i(0,R) = 0 \quad \text{for all } R \geq 0 \quad \text{and} \quad \mathcal{R}_i(S,0) = 0 \quad \text{for all } S \geq 0. \tag{3.4}$$

We will assume that the rate of consumption of each resource is a strictly monotone increasing function of the concentration of that resource.

$$\frac{\partial}{\partial S}\mathcal{S}_i(S,R) > 0 \quad \text{and} \quad \frac{\partial}{\partial R}\mathcal{R}_i(S,R) > 0 \quad \text{for all } (S,R) \in \operatorname{int}\mathbf{R}^2_+. \tag{3.5}$$

The function $\mathcal{G}_i(S,R)$ represents the rate of conversion of nutrient to biomass of population x_i as a function of the concentrations of resources S and R in the culture vessel. Since perfectly substitutable resources are alternate sources of the same essential nutrient, the rate of conversion of nutrient to biomass of population x_i is made up of a contribution from the consumption of resource S as well as a contribution from the consumption of resource R. Therefore,

$$\mathcal{G}_i(S,R) = \mathcal{S}_i(S,R) + \mathcal{R}_i(S,R). \tag{3.6}$$

It should be noted that with two resources available, both serving the same requisite need, it becomes necessary to determine how changes in the concentration of one resource affect the consumption rate of the other. It seems natural to assume that increasing the amount of one resource consumed might result in a reduction in the amount of the other resource consumed. In Holling terminology, the handling time devoted to the processing of a unit of one resource is time no longer available for the processing of the other resource. This is reflected in the assumption that

$$\frac{\partial}{\partial R}\mathcal{S}_i(S,R) \leq 0 \quad \text{and} \quad \frac{\partial}{\partial S}\mathcal{R}_i(S,R) \leq 0 \quad \text{for all } (S,R) \in \mathbf{R}^2_+. \tag{3.7}$$

Define

$$p_i(S) = \mathcal{S}_i(S,0) \quad \text{for all } S \geq 0 \tag{3.8 a}$$

and

$$q_i(R) = \mathcal{R}_i(0, R) \quad \text{for all } R \geq 0. \tag{3.8 b}$$

That is, $p_i(S)/\xi_i$ is the function describing the uptake of nutrient S in the absence of nutrient R. Similarly, $q_i(R)/\eta_i$ is the function describing the uptake of nutrient R in the absence of nutrient S. We assume that both $p_i(S)$ and $q_i(R)$ are strictly monotone increasing functions.

Further, define λ_i and μ_i so that

$$\mathcal{G}_i(\lambda_i, 0)(= p_i(\lambda_i)) = D \quad \text{and} \quad \mathcal{G}_i(0, \mu_i)(= q_i(\mu_i)) = D. \tag{3.9}$$

Thus λ_i (respectively, μ_i) represents the break-even concentration for resource S (R) when none of the other resource is available. By the monotonicity of $p_i(S)$ ($q_i(R)$), this concentration is a uniquely defined positive real number provided we assume that $\lambda_i = \infty$ if $\mathcal{G}_i(S, 0) < D$ for all $S \geq 0$ ($\mu_i = \infty$ if $\mathcal{G}_i(0, R) < D$ for all $R \geq 0$).

If the amount consumed of each resource is independent of the concentration of the other resource, i.e., if $\mathcal{S}_i(S, R) = p_i(S)$ and $\mathcal{R}_i(S, R) = q_i(R)$ for all $S \geq 0$ and $R \geq 0$, then model (3.1) reduces to Model I of León and Tumpson [**11**], adapted to the chemostat. However, model (3.1) allows for a more realistic selection of functions describing resource consumption, functions that take into consideration the possible effects that the consumption of one resource has on how much of the other resource is consumed.

With this in mind, we make the following assumptions regarding the functions that describe the rate of conversion of nutrient to biomass, $\mathcal{G}_i(S, R)$. Let

$$m_{S_i} = \lim_{S \to \infty} p_i(S), \qquad \left(m_{R_i} = \lim_{R \to \infty} q_i(R)\right) \tag{3.10}$$

denote the maximal growth rate of population x_i on resource S (R) when none of the other resource is available. Assume that one of the resources, say S, is superior in the sense that

$$m_{S_i} \geq m_{R_i}. \tag{3.11}$$

Then it seems reasonable to assume that the more of resource S that is consumed the better, that is,

$$\partial \mathcal{G}_i / \partial S > 0 \quad \text{for all } (S, R) \in \operatorname{int} \mathbf{R}_+^2. \tag{3.12}$$

However, if the inequality in (3.11) is strict, a critical concentration of S, say S_i^c, will exist such that

$$\begin{aligned} &\partial \mathcal{G}_i/\partial R > 0 \quad \text{for all } R > 0, 0 < S < S_i^c, \quad \text{and} \\ &\partial \mathcal{G}_i/\partial R < 0 \quad \text{for all } R > 0, S > S_i^c, \end{aligned} \tag{3.13}$$

where S_i^c is related to m_{R_i} in the following manner:

$$\mathcal{G}_i(S_i^c, R) = m_{R_i} \quad \text{for all } R \geq 0. \tag{3.14}$$

Thus, when both resources are in *relatively* short supply, increasing the concentration of either resource is beneficial. However, once resource S is plentiful enough that m_{R_i}, the maximal growth rate of population x_i on resource R when there is no resource S available, would be exceeded by consuming only resource S, the presence of resource R would actually become detrimental. In any case, the presence of resource R would never be detrimental enough to decrease $\mathcal{G}_i(S, R)$ below m_{R_i}.

$$\lim_{R\to\infty} \mathcal{G}_i(S, R) = \lim_{R\to\infty} q_i(R) = m_{R_i} \quad \text{for each fixed } S \geq 0. \tag{3.15}$$

It is also assumed that $\mathcal{G}_i(S, R)$ can never increase above m_{S_i}, the maximal growth rate of population x_i on resource S when there is no resource R available, since an abundance of S and no R would be optimal for the growth of population x_i.

$$\lim_{S\to\infty} \mathcal{G}_i(S, R) = \lim_{S\to\infty} p_i(S) = m_{S_i} \quad \text{for each fixed } R \geq 0. \tag{3.16}$$

If, instead, $m_{R_i} > m_{S_i}$, a critical concentration of R, say R_i^c, can be defined in an analogous manner, making the appropriate changes in assumptions (3.12)–(3.16). If $m_{R_i} = m_{S_i}$, define $R_i^c = S_i^c = \infty$.

The functions $\mathcal{S}_i(S, R)$ and $\mathcal{R}_i(S, R)$ in Waltman et al. [**17**] are a generalization of the familiar Michaelis-Menten prototype of functional response to a single resource. They are given by

$$\begin{aligned} \mathcal{S}_i(S, R) &= \frac{m_{S_i} S}{K_{S_i}(1 + S/K_{S_i} + R/K_{R_i}))} \quad \text{and} \\ \mathcal{R}_i(S, R) &= \frac{m_{R_i} R}{K_{R_i}(1 + S/K_{S_i} + R/K_{R_i})} \end{aligned} \tag{3.17}$$

where m_{S_i}, m_{R_i}, K_{S_i} and K_{R_i} are positive constants, so that

$$\mathcal{G}_i(S,R) = \frac{(m_{S_i}/K_{S_i})S + (m_{R_i}/K_{R_i})R}{1 + S/K_{S_i} + R/K_{R_i}}. \tag{3.18}$$

The functions $\mathcal{S}_i(S,R)$ and $\mathcal{R}_i(S,R)$ in (3.17) satisfy all assumptions (3.2)–(3.8) and $\mathcal{G}_i(S,R)$ in (3.18) satisfies all assumptions (3.6) and (3.9)–(3.16). In fact,

$$\lambda_i = \frac{DK_{S_i}}{m_{S_i} - D} \quad \text{and} \quad \mu_i = \frac{DK_{R_i}}{m_{R_i} - D}, \tag{3.19}$$

where $m_{S_i} \le D\,[m_{R_i} \le D]$ corresponds to $\lambda_i = \infty\,[\mu_i = \infty]$ in our earlier discussion, and

$$\begin{aligned} \frac{\partial \mathcal{G}_i}{\partial S} &= \frac{R(m_{S_i} - m_{R_i}) + m_{S_i}K_{R_i}}{K_{S_i}K_{R_i}(1 + S/K_{S_i} + R/K_{R_i})^2} \quad \text{and} \\ \frac{\partial \mathcal{G}_i}{\partial R} &= \frac{S(m_{R_i} - m_{S_i}) + m_{R_i}K_{S_i}}{K_{S_i}K_{R_i}(1 + S/K_{S_i} + R/K_{R_i})^2}. \end{aligned} \tag{3.20}$$

If $m_{S_i} > m_{R_i}$, then $S_i^c = (m_{R_i}K_{S_i})/(m_{S_i} - m_{R_i})$.

3.2. *Preliminary analysis.* As in the model in Section 2, one can show that int $\mathbf{R}_+^4$ is positively invariant for all solutions of (3.1) and that all solutions are bounded.

The washout equilibrium will be denoted $E_0 = (S^0, R^0, 0, 0)$. When they exist, the one-species survival equilibria will be denoted $E_1 = (\overline{S}_1, \overline{R}_1, \bar{x}_1, 0)$ and $E_2 = (\overline{S}_2, \overline{R}_2, 0, \bar{x}_2)$ and the coexistence equilibrium will be denoted $E^* = (S^*, R^*, x_1^*, x_2^*)$.

The following technical lemma summarizes some important consequences of assumptions (3.9)–(3.16). See Figure 1. An analogous result holds if $m_{R_i} > m_{S_i}$.

Lemma 3.1. 1. *If* $m_{S_i} \ge m_{R_i}$, *then*

(a) $\mathcal{G}_i(S,R) < m_{R_i}$ *if* $R \ge 0$ *and* $0 \le S < S_i^c$,

(b) $\mathcal{G}_i(S,R) > m_{R_i}$ *if* $R \ge 0$ *and* $S > S_i^c$,

(c) $\mathcal{G}_i(S,R) < m_{S_i}$ *if* $R \ge 0$ *and* $S \ge 0$.

2. *If* $m_{S_i} \ge m_{R_i}$ *and* μ_i *is finite, then*

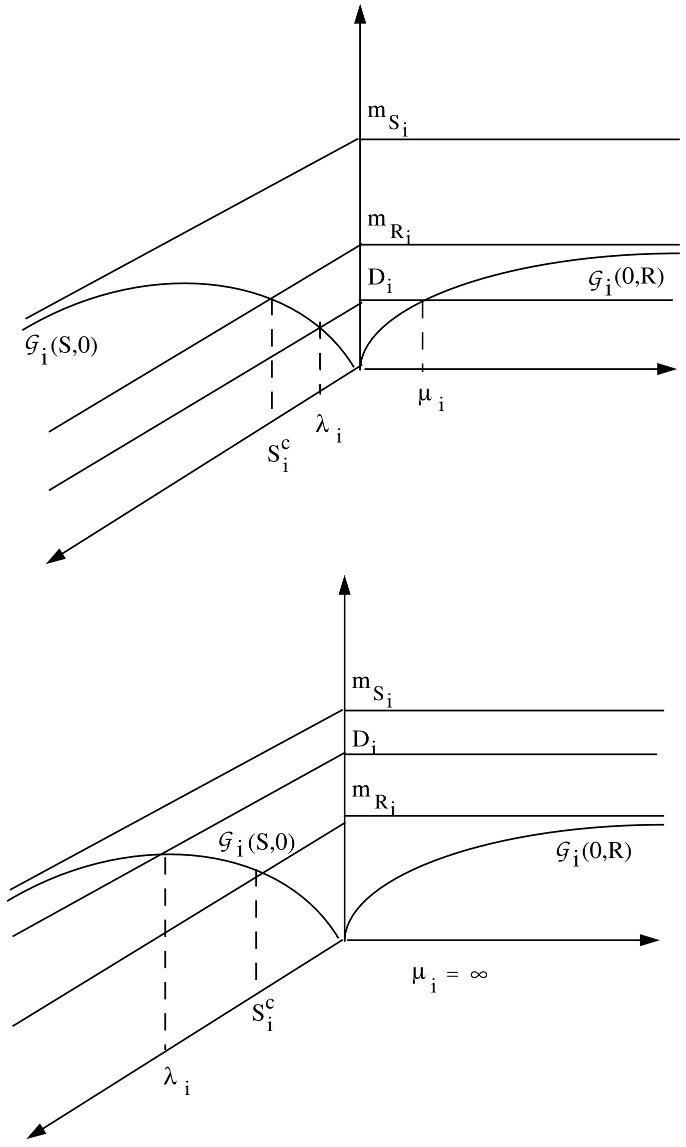

FIGURE 1. Schematic diagram for Lemma 3.1. Relative sizes of the parameters. (a) [Top Figure] $m_{S_i} > m_{R_i} > D_i$. (b) [Bottom Figure] $m_{S_i} > D_i > m_{R_i}$.

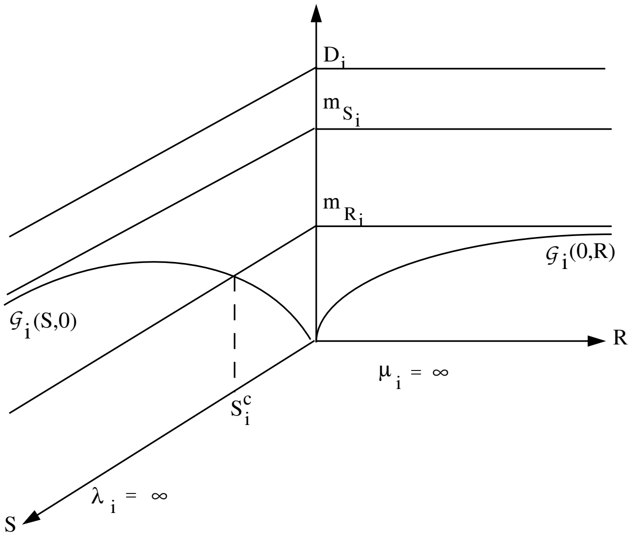

FIGURE 1. Schematic diagram for Lemma 3.1. Relative sizes of the parameters. (c) $D_i > m_{S_i} > m_{R_i}$.

(a) $m_{R_i} > D$, *and*

(b) λ_i *is finite and* $\lambda_i < S_i^c$.

3. *If* $m_{S_i} \geq m_{R_i}$ *and* $\mu_i = \infty$, *then either*

(a) $m_{R_i} < D$ *and* $\lambda_i > S_i^c$ *or* $\lambda_i = S_i^c = \infty$, *or*

(b) $m_{R_i} = D$ *and* $\lambda_i = S_i^c \leq \infty$.

Proof. Recall that $S_i^c = \infty$ if $m_{S_i} = m_{R_i}$.

1(a) and (b) follow from (3.12) and (3.14).

1(c). If $m_{S_i} = m_{R_i}$, then the result follows immediately from 1(a) (since $S_i^c = \infty$). Suppose that $m_{S_i} > m_{R_i}$. If $0 \leq S \leq S_i^c$, then by 1(a) and (3.14), $\mathcal{G}_i(S,R) \leq m_{R_i} < m_{S_i}$ for all $R \geq 0$. If $S > S_i^c$, then $\mathcal{G}_i(S,0) \geq \mathcal{G}_i(S,R)$ for all $R \geq 0$, and by (3.12), $\mathcal{G}_i(S,0) \leq \lim_{S\to\infty} \mathcal{G}_i(S,0) = m_{S_i}$.

2(a) $m_{R_i} = \mathcal{G}_i(S_i^c, \mu_i) > \mathcal{G}_i(0, \mu_i) = D$.

2(b) See Figure 1(a). Since, in 2(a), $m_{S_i} \geq m_{R_i} > D$, it follows that λ_i is finite. If $m_{S_i} = m_{R_i}$, then $S_i^c = \infty$. If $m_{S_i} > m_{R_i}$, then S_i^c is finite and $\mathcal{G}_i(S_i^c, 0) = m_{R_i} > D = \mathcal{G}_i(\lambda_i, 0)$.

3. See Figures 1(b) and (c). $\mu_i = \infty$ implies that $\mathcal{G}_i(0, R) < D$ for all $R \geq 0$. This implies that $m_{R_i} = \lim_{R\to\infty} \mathcal{G}_i(0, R) \leq D$. If $S_i^c = \infty$, then $\mathcal{G}_i(S, 0) < m_{R_i} \leq D$ for all $S \geq 0$ and so $\lambda_i = \infty$. If S_i^c is finite, then $\mathcal{G}_i(S_i^c, 0) = m_{R_i} \leq D = \mathcal{G}_i(\lambda_i, 0)$. □

Next we discuss subsistence curves, $\varphi_i(S)$ and $\sigma_i(R)$, in the (S, R)-plane. These are curves that give the concentrations of S and R at which the biomass of population x_i in the culture vessel is neither increasing nor decreasing.

Lemma 3.2. (a) *If λ_i and μ_i are both finite, then there exist C^1 functions $\varphi_i(S)$ and $\sigma_i(R)$ satisfying*

$$\begin{aligned} \varphi_i : [0, \lambda_i] \to [0, \mu_i], &\qquad \sigma_i : [0, \mu_i] \to [0, \lambda_i], \\ \mathcal{G}_i(S, \varphi_i(S)) = D, &\qquad \mathcal{G}_i(\sigma_i(R), R) = D, \\ \varphi_i'(S) < 0, &\qquad \sigma_i'(R) < 0. \end{aligned}$$

(b) *If $m_{S_i} > D > m_{R_i}$, and $0 < \lambda_i \leq S^0$, then there exist C^1 functions $\varphi_i(S)$ and $\sigma_i(R)$ satisfying*

$$\begin{aligned} \varphi_i : [\lambda_i, M_i^S] \to [0, R^0], &\qquad \sigma_i : [0, \varphi_i(M_i^S)] \to [\lambda_i, M_i^S], \\ \mathcal{G}_i(S, \varphi_i(S)) = D, &\qquad \mathcal{G}_i(\sigma_i(R), R) = D, \\ \varphi_i'(S) > 0, &\qquad \sigma_i'(R) > 0, \end{aligned}$$

where

$$M_i^S \equiv \max_{\substack{\lambda_i \leq S \leq S^0, \\ \mathcal{G}_i(S, R^0) \leq D}} S. \tag{3.21}$$

Proof. (a) By Lemma 3.1 and (3.9), $\mathcal{G}_i(S, 0) < D$ and $\mathcal{G}_i(S, \mu_i) > D$ for each $S \in (0, \lambda_i)$. Therefore, by (3.3), (3.12) and (3.13), to each fixed $S \in (0, \lambda_i)$, there corresponds a unique $R_S \in (0, \mu_i)$ such that $\mathcal{G}_i(S, R_S) = D$. Define $\varphi_i : [0, \lambda_i] \to [0, \mu_i]$ by setting $\varphi_i(S) = R_S$. Then $\mathcal{G}_i(S, \varphi_i(S)) = D$ for all $0 \leq S \leq \lambda_i$. In view of (3.12) and (3.13), by a straightforward application of the implicit function theorem, it follows that $\varphi_i \in C^1$ and $\varphi_i'(S) < 0$ for all $0 < S < \lambda_i$.

In a similar manner, one can define a function $\sigma_i : [0, \mu_i] \to [0, \lambda_i]$ such that $\mathcal{G}_i(\sigma_i(R), R) = D$ for all $0 \le R \le \mu_i$, with $\sigma_i \in C^1$ and $\sigma_i'(R) < 0$ for all $0 < R < \mu_i$.

(b) In this case, by Lemma 3.1 part 3, $\lambda_i > S_i^c$ and so $\mathcal{G}_i(\lambda_i, R^0) < D$. Thus, $\mathcal{G}_i(S, 0) > D$ and $\mathcal{G}_i(S, R^0) < D$ for each $S \in (\lambda_i, M_i^S)$. Therefore, by (3.3), (3.12) and (3.13), to each fixed $S \in [\lambda_i, M_i^S]$, there corresponds a unique $R_S \in [0, R^0]$ such that $\mathcal{G}_i(S, R_S) = D$. Define $\varphi_i : [\lambda_i, M_i^S] \to [0, R^0]$ by setting $\varphi_i(S) = R_S$. The rest of the proof is similar to the proof of (a). $\square$

For the functions (3.17) and (3.18), the subsistence curves

$$\begin{aligned} \varphi_i(S) &= \left(1 + S\left(\frac{D - m_{S_i}}{DK_{S_i}}\right)\right)\left(\frac{DK_{R_i}}{m_{R_i} - D}\right) \quad \text{and} \\ \sigma_i(R) &= \left(1 + R\left(\frac{D - m_{R_i}}{DK_{R_i}}\right)\right)\left(\frac{DK_{S_i}}{m_{S_i} - D}\right) \end{aligned} \tag{3.22}$$

are both linear functions.

In the rest of this section, we restrict our attention to the one-species growth model.

Lemma 3.3. *Let $j, k \in \{1, 2\}$ with $j \ne k$. The simplex $\mathcal{L} = \{(S, R, x_1, x_2) : x_k = 0, S, R, x_j \ge 0, \xi_j S + \eta_j R + x_j = \xi_j S^0 + \eta_j R^0\}$ is a global attractor for system* (3.1) *if $x_{k0} = 0$ and $x_{j0} \ge 0$.*

Proof. Define $z(t) = \xi_j S(t) + \eta_j R(t) + x_j(t)$. Then $z'(t) = ((\xi_j S^0 + \eta_j R^0) - z(t))D$, so that $z(t) = [z(0) - (\xi_j S^0 + \eta_j R^0)]e^{-Dt} + (\xi_j S^0 + \eta_j R^0)$. $\square$

Any one-species survival equilibrium E_j of system (3.1) must satisfy

$$\begin{aligned} x_j \mathcal{S}_j(S, R) &= \xi_j (S^0 - S) D \\ x_j \mathcal{R}_j(S, R) &= \eta_j (R^0 - R) D \\ \mathcal{G}_j(S, R) &= D \end{aligned} \tag{3.23}$$

with $\overline{S}_j$, $\overline{R}_j$, and $\bar{x}_j > 0$.

Lemma 3.4. *Assume that* $m_{S_j} \geq m_{R_j}$. *Suppose that a one-species survival equilibrium* E_j *of* (3.1) *exists.*

(a) *If* $m_{R_j} > D$, *then* $0 < \overline{S}_j < \min\{S^0, \lambda_j\}$ *and* $0 < \overline{R}_j < \min\{R^0, \mu_j\}$.

(b) *If* $m_{R_j} < D$ *and* $\lambda_j \leq S^0$, *then* $S_j^c < \lambda_j$ *and* $\lambda_j < \overline{S}_j < M_j^S \leq S^0$, $0 < \overline{R}_j < \varphi_j(M_j^S) \leq R^0$.

Proof. First, note that, from (3.23), $\bar{x}_j > 0$ implies that $0 < \overline{S}_j < S^0$ and $0 < \overline{R}_j < R^0$.

(a) Since μ_j is finite, then by Lemma 3.1 2(b), λ_j is finite and $\lambda_j < S_j^c$. Therefore, $\mathcal{G}_j(S, R) > \mathcal{G}_j(S, 0) > \mathcal{G}_j(\lambda_j, 0) = D$ for all $S > \lambda_j$, $R > 0$, and $\mathcal{G}_j(S, R) > \mathcal{G}_j(0, R) > \mathcal{G}_j(0, \mu_j) = D$ for all $S > 0$, $R > \mu_j$, and so $0 < \overline{S}_j < \min\{S^0, \lambda_j\}$ and $0 < \overline{R}_j < \min\{R^0, \mu_j\}$.

(b) In this case, Lemma 3.1 3(a), $S_j^c < \lambda_j$. Then $\mathcal{G}_j(S, R) \leq \mathcal{G}_j(S_j^c, R) = m_{R_j} < D$ for all $0 < S \leq S_j^c$, $R > 0$, $\mathcal{G}_j(S, R) \leq \mathcal{G}_j(\lambda_j, R) < \mathcal{G}_j(\lambda_j, 0) = D$ for all $S_j^c < S \leq \lambda_j$, $R > 0$, and $\mathcal{G}_j(S, R) \geq \mathcal{G}_j(M_j^S, R) > \mathcal{G}_j(M_j^S, \varphi_j(M_j^S)) = D$ for all $S \geq M_j^S$, $\varphi_j(M_j^S) > R > 0$, and so $\lambda_j < \overline{S}_j < M_j^S \leq S^0$ and $0 < \overline{R}_j < \varphi_j(M_j^S) \leq R^0$. ◻

Lemma 3.5. *Assume that* $m_{S_j} \geq m_{R_j}$. *If* μ_j *is finite, then a one-species survival equilibrium* E_j *of* (3.1) *exists if and only if* $\mathcal{G}_j(S^0, R^0) > D$ *and when a one-species survival equilibrium exists, then, for that species, it is unique. In particular, if* $\lambda_j < S^0$ *or if* $\mu_j < R^0$, *then* $\mathcal{G}_j(S^0, R^0) > D$.

Proof. First we show that if μ_j is finite and a one-species survival equilibrium E_j exists, then $\mathcal{G}_j(S^0, R^0) > D$. By Lemma 3.4(a), $0 < \overline{S}_j < \min\{\lambda_j, S^0\}$ and $0 < \overline{R}_j < \min\{\mu_j, R^0\}$. By Lemma 3.1 2(a,b), $m_{R_j} > D$ and $S_j^c > \lambda_j > \overline{S}_j$. If $S_j^c > S^0$, then $D = \mathcal{G}_j(\overline{S}_j, \overline{R}_j) < \mathcal{G}_j(S^0, \overline{R}_j) < \mathcal{G}_j(S^0, R^0)$. If $S_j^c \leq S^0$, then $D < m_{R_j} = \mathcal{G}_j(S_j^c, R^0) \leq \mathcal{G}_j(S^0, R^0)$.

Next, we show that if $\mathcal{G}_j(S^0, R^0) > D$, then a one-species survival equilibrium exists. For $S \in (0, \lambda_j)$, define

$$x_S(S) = \frac{\xi_j(S^0 - S)D}{\mathcal{S}_j(S, \varphi_j(S))} \quad \text{and}$$
$$x_R(S) = \frac{\eta_j(R^0 - \varphi_j(S))D}{\mathcal{R}_j(S, \varphi_j(S))}, \tag{3.24}$$

where, by Lemma 3.2, $\mathcal{G}_j(S, \varphi_j(S)) = D$ for all $0 \leq S \leq \lambda_j$. If $\mu_j > R^0$, then $\mathcal{G}_j(0, R^0) < D$, and since $\mathcal{G}_j(\lambda_j, R^0) > D$ and $\mathcal{G}_j(S^0, R^0) > D$, there exists a unique $\widetilde{S} \in (0, \min\{S^0, \lambda_j\})$ such that $\mathcal{G}_j(\widetilde{S}, R^0) = D$ and $\varphi_j(\widetilde{S}) = R^0$. By Lemma 3.2, $0 < \varphi_j(S) < \mu_j$ for $S \in (0, \min\{S^0, \lambda_j\})$ if $\mu_j \leq R^0$, and $0 < \varphi_j(S) < R^0$ for $S \in (\widetilde{S}, \min\{S^0, \lambda_j\})$ if $\mu_j > R^0$. In both cases, by (3.5), (3.7) and Lemma 3.2, $x_S(S)$ is a decreasing function, $x_R(S)$ is an increasing function, and both functions are continuous. There are four cases to consider.

Case 1. $\lambda_j \leq S^0$ and $\mu_j \leq R^0$.

$$x_S(0) = \infty \quad \text{and} \quad x_R(0) = \eta_j(R^0 - \mu_j),$$
$$x_S(\lambda_j) = \xi_j(S^0 - \lambda_j) \quad \text{and} \quad x_R(\lambda_j) = \infty.$$

Case 2. $\lambda_j > S^0$ and $\mu_j > R^0$.

$$x_S(\widetilde{S}) = \frac{\xi_j(S^0 - \widetilde{S})D}{\mathcal{S}_j(\widetilde{S}, R^0)} > 0 \quad \text{and} \quad x_R(\widetilde{S}) = 0,$$
$$x_S(S^0) = 0 \quad \text{and} \quad x_R(R^0) = \frac{\eta_j(R^0 - \varphi_j(S^0))D}{\mathcal{R}_j(S^0, \varphi_j(S^0))} > 0.$$

Case 3. $\lambda_j \leq S^0$ and $\mu_j \geq R^0$.

$$x_S(\widetilde{S}) = \frac{\xi_j(S^0 - \widetilde{S})D}{\mathcal{S}_j(\widetilde{S}, R^0)} > 0 \quad \text{and} \quad x_R(\widetilde{S}) = 0,$$
$$x_S(\lambda_j) = \xi_j(S^0 - \lambda_j) \quad \text{and} \quad x_R(\lambda_j) = \infty.$$

Case 4. $\lambda_j \geq S^0$ and $\mu_j \leq R^0$.

$$x_S(0) = \infty \quad \text{and} \quad x_R(0) = \eta_j(R^0 - \mu_j),$$
$$x_S(S^0) = 0 \quad \text{and} \quad x_R(R^0) = \frac{\eta_j(R^0 - \varphi_j(S^0))D}{\mathcal{R}_j(S^0, \varphi_j(S^0))}.$$

Therefore, in each case there exists a unique $\widehat{S} \in (0, \lambda_j)$ such that $x_S(\widehat{S}) = x_R(\widehat{S})$, and hence a unique one-species survival equilibrium, with $\overline{S}_j = \widehat{S}$, $\overline{R}_j = \varphi_j(\widehat{S})$, and $\bar{x}_j = x_S(\widehat{S}) = x_R(\widehat{S})$.

In particular, since $S_j^c > \lambda_j$, if $\lambda_j < S^0$, then $\mathcal{G}_j(S^0, R^0) > \mathcal{G}_j(\lambda_j, R^0) > D$, and if $\mu_j < R^0$, then $\mathcal{G}_j(S^0, R^0) > \mathcal{G}_j(0, R^0) > \mathcal{G}_j(0, \mu_j) = D$. $\square$

Lemma 3.6. *Consider system* (3.1). *Let* $j, k \in \{1, 2\}$ *with* $j \neq k$. *Assume* $x_{k0} = 0$ *and* $x_{j0} > 0$. *Suppose that* $\mathcal{G}_j(S^0, R^0) > D$. *Then* $\liminf_{t\to\infty} x_j(t) > 0$.

Proof. Identify (S, R, x_1, x_2)-space with $\mathbf{R}_+^4$. Choose $\underline{X} = (S_0, R_0, x_{10}, x_{20})$ where $x_{k0} = 0$ and $x_{j0} > 0$. Since all solutions of (3.1) are nonnegative and bounded, $\Omega(\underline{X})$ is a nonempty, compact invariant set.

Suppose $\{E_0\} \in \Omega(\underline{X})$. Since $\mathcal{G}_j(S^0, R^0) > D$, E_0 is an unstable, hyperbolic critical point. E_0 is globally attracting with respect to solutions initiating in its stable manifold, $M^s(E_0) = \{(S, R, 0, 0) \in \mathbf{R}_+^4\}$. Since $\underline{X} \notin M^s(E_0)$, $\{E_0\} \neq \Omega(\underline{X})$. Therefore, by the Butler-McGehee Lemma (see Lemma A1 of [**8**]), there exists $P \in (M^s(E_0)\backslash\{E_0\}) \cap \Omega(\underline{X})$ and hence $\operatorname{cl}\mathcal{O}(P) \subset \Omega(\underline{X})$ where $\operatorname{cl}\mathcal{O}(P)$ denotes the closure of the entire orbit through P. But then, as $t \to -\infty$, either $\mathcal{O}(P)$ becomes unbounded or one of the S or R components becomes negative. In either case we have a contradiction and therefore $\{E_0\} \notin \Omega(\underline{X})$.

Suppose $\liminf_{t\to\infty} x_j(t) = 0$. Then there exists a point $\widetilde{P} = (\underline{S}, \underline{R}, 0, 0) \in \Omega(\underline{X})$, which implies that $\operatorname{cl}\mathcal{O}(\widetilde{P}) \subset \Omega(\underline{X})$. But then $\{E_0\} \in \Omega(\underline{X})$, a contradiction. Thus, $\liminf_{t\to\infty} x_j(t) > 0$. $\square$

Lemma 3.7. *Consider system* (3.1). *Let* $j, k \in \{1, 2\}$ *with* $j \neq k$. *Assume that* $x_{k0} = 0$ *and* $x_{j0} > 0$. *Assume also that* $m_{S_j} > D$ *and* $m_{R_j} > D$. *If* $\mathcal{G}_j(S^0, R^0) > D$, *then there exists a unique one-species survival equilibrium* E_j *and* E_j *is globally asymptotically stable with respect to all solutions for which* $S_0 \geq 0$, $R_0 \geq 0$, $x_{j0} > 0$ *and* $x_{k0} = 0$.

Proof. The existence and uniqueness of the one-species survival equilibrium E_j is given by Lemma 3.5. By Lemma 3.3, if $j, k \in \{1, 2\}$ with $j \neq k$, and $x_{k0} = 0$ and $x_{j0} \geq 0$, the simplex $\mathcal{L} = \{(S, R, x_1, x_2) :$

$x_k = 0, S, R, x_j \geq 0, \xi_j S + \eta_j R + x_j = \xi_j S^0 + \eta_j R^0\}$ is a global attractor for system (3.1) and so first we restrict our attention to $\mathcal{L}$. Since $\mathcal{L}$ is positively invariant, let $x_j(t) = \xi_j(S^0 - S(t)) + \eta_j(R^0 - R(t))$ and consider the system

(3.25)

$$\begin{aligned} S'(t) &= (S^0 - S(t))D - (1/\xi_j)[\xi_j(S^0 - S(t)) + \eta_j(R^0 - R(t))] \\ &\quad \cdot \mathcal{S}_j(S(t), R(t)), \\ R'(t) &= (R^0 - R(t))D - (1/\eta_j)[\xi_j(S^0 - S(t)) + \eta_j(R^0 - R(t))] \\ &\quad \cdot \mathcal{R}_j(S(t), R(t)), \end{aligned}$$

$$S_0 \geq 0, \qquad R_0 \geq 0, \qquad \xi_j S^0 + \eta_j R^0 \geq \xi_j S_0 + \eta_j R_0.$$

From a local stability analysis, it follows that the equilibrium $\overline{E}_0 = (S^0, R^0)$ of (3.25) is unstable and noting that, if $m_{R_j} > D$ and $m_{S_j} > D$, then, by hypotheses (3.6), (3.5), (3.7), (3.12) and (3.13), it follows that

$$\begin{aligned} \frac{\partial}{\partial S}\mathcal{S}_j(\overline{S}_j, \overline{R}_j)\frac{\partial}{\partial R}\mathcal{R}_j(\overline{S}_j, \overline{R}_j) \\ - \frac{\partial}{\partial R}\mathcal{S}_j(\overline{S}_j, \overline{R}_j)\frac{\partial}{\partial S}\mathcal{R}_j(\overline{S}_j, \overline{R}_j) > 0, \end{aligned} \tag{3.26}$$

the equilibrium $\overline{E} = (\overline{S}, \overline{R}_j)$ of (3.25) (where $E_j = (\overline{S}_j, \overline{R}_j, \bar{x}_1, \bar{x}_2)$ is a one species survival equilibrium of (3.1) for species x_j), is locally asymptotically stable.

Fix $S(t) = S^0$ in (3.25), and define

$$F_1(R(t)) \equiv S'(t) = -(\eta_j/\xi_j)(R^0 - R(t))\mathcal{S}_j(S^0, R(t)).$$

Then $F_1(R_0) = 0$ and, by (3.2) and (3.7),

$$\frac{d}{dR}F_1(R) = -\frac{\eta_j}{\xi_j}(R^0 - R)\frac{\partial}{\partial R}\mathcal{S}_j(S^0, R) + \frac{\eta_j}{\xi_j}\mathcal{S}_j(S^0, R) > 0$$

for all $0 \leq R \leq R^0$. Therefore, $S'(t) < 0$ at all points (S^0, R) where $0 \leq R < R^0$.

Fix $S(t) = \overline{S}_j$ in (3.25) and define

$$\begin{aligned} F_2(R(t)) &\equiv S'(t) \\ &= (S^0 - \overline{S}_j)D - (1/\xi_j) \\ &\quad [\xi_j(S^0 - \overline{S}_j) + \eta_j(R^0 - R(t))]\mathcal{S}_j(\overline{S}_j, R(t)). \end{aligned}$$

Then $F_2(\overline{R}_j) = 0$, and by (3.2) and (3.7),

$$\begin{aligned}\frac{d}{dR}F_2(R) = -\frac{1}{\xi_j}[\xi_j(S^0 - \overline{S}_j) + \eta_j(R^0 - R)]& \\ \frac{\partial}{\partial R}\mathcal{S}_j(\overline{S}_j, R) + \frac{\eta_j}{\xi_j}\mathcal{S}_j(\overline{S}_j, R) > 0&\end{aligned}$$

for all $0 \leq R \leq R^0$. Therefore, $S'(t) < 0$ at all points $(\overline{S}_j, R)$ where $0 \leq R < \overline{R}_j$ and $S'(t) > 0$ at all points $(\overline{S}_j, R)$ where $\overline{R}_j < R \leq R^0$.

Similarly, fixing $R(t) = R^0$ and $R(t) = \overline{R}_j$, we obtain the partial vector field shown in Figure 2. It is clear that no periodic orbits exist in $\mathcal{L}$ and since by Lemma 3.6, $\liminf_{t\to\infty} x_j(t) > 0$, it follows from the Poincaré-Bendixson theorem that $\overline{E} = (\overline{S}_j, \overline{R}_j)$ is globally asymptotically stable for (3.25) with respect to all solutions for which $S_0 \geq 0$, $R_0 \geq 0$, $\xi_j S^0 + \eta_j R^0 > \xi_j S_0 + \eta_j R_0$. Since $\overline{E}$ corresponds to E_j which is locally asymptotically stable for (3.1) in the face where $x_{k0} = 0$, this and Lemma 3.6 imply that E_j is globally asymptotically stable for (3.1) with respect to all solutions satisfying $S_0 \geq 0$, $R_0 \geq 0$, $x_{k0} = 0$ and $x_{j0} > 0$. $\square$

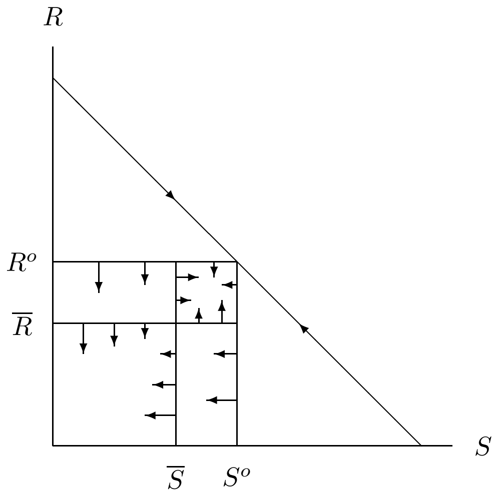

FIGURE 2. Partial vector field for Lemma 3.7. Vectors parallel to the S axis indicate the sign of $S'(t)$ along the indicated line. Vectors parallel to the R axis indicate the sign of $R'(t)$ along the indicated line.

Lemma 3.8. *Consider system* (3.1). *Let* $j, k \in \{1, 2\}$ *with* $j \neq k$. *If no one-species equilibrium* E_j *exists, then* E_0 *is globally asymptotically stable with respect to all solutions for which* $S_0 \geq 0$, $R_0 \geq 0$, $x_{j0} \geq 0$ *and* $x_{k0} = 0$.

Proof. Since all solutions are nonnegative and bounded, the result follows immediately from Lemma 3.3 and the Poincaré-Bendixson theorem. ☐

3.3. The main result—Again competition leads to diversity.

Theorem 3.1. *Consider system* (3.1). *Let* $j, k \in \{1, 2\}$ *with* $j \neq k$. *Assume that no one-species survival equilibrium of the form* E_j *exists. Assume also that there is a unique one-species survival equilibrium of the form* E_k *and that* E_k *is globally asymptotically stable with respect to the positive cone in* (S, R, x_k)*-space, but that it is unstable with respect to* (S, R, x_1, x_2)*-space.*

(a) *If* $x_{k0} = 0$, *then* $\lim_{t\to\infty} x_j(t) = 0$.

(b) *If* $x_{i0} > 0$, $i = 1, 2$, *then* $\liminf_{t\to\infty} x_i(t) > 0$.

Proof. (a) This follows immediately by Lemma 3.8.

(b) Define $X_0 = (S_0, R_0, x_{10}, x_{20})$ with $x_{i0} > 0$, $i = 1, 2$. Since all solutions of (3.1) are nonnegative and bounded, $\Omega(X_0)$ is a compact, invariant set contained in the nonnegative cone in (S, R, x_1, x_2)-space.

First we show that $E_0 \notin \Omega(X_0)$. Suppose $E_0 \in \Omega(X_0)$. Since $M^s(E_0) = \{(S, R, x_1, x_2) : S, R, x_j \geq 0, x_k = 0\}$ and $x_{k0} > 0$, $\Omega(X_0) \neq \{E_0\}$. By the Butler-McGehee Lemma, there exists $P^s \in (M^S(E_0)\backslash\{E_0\}) \cap \Omega(X_0)$. But, since $P^s \in \Omega(X_0)$, then the $\mathrm{cl}\,\mathcal{O}(P^s) \in \Omega(X_0)$. But since, by Lemma 3.3, $(M^s(E_0)\backslash\{E_0\})$ is two dimensional, and since no equilibrium of the form E_j exists, by the Poincaré-Bendixson theorem, $\mathrm{cl}\,\mathcal{O}(P^s)$ is either unbounded or leaves the nonnegative cone in (S, R, x_1, x_2)-space, a contradiction.

Next we show that $E_k \notin \Omega(X_0)$. Suppose $E_k \in \Omega(X_0)$. Since $M^s(E_k) = \{(S, R, x_1, x_2) : S, R \geq 0, x_j = 0, x_k > 0\}$, $\Omega(X_0) \neq \{E_k\}$. By the Butler-McGehee Lemma, there exists $Q^s \in (M^s(E^k)\backslash\{E_k\}) \cap \Omega(X_0)$. By Lemma 3.3 and the Poincaré-Bendixson theorem, $\mathrm{cl}\,\mathcal{O}(Q^s)$

either contains E_0, becomes unbounded, or leaves the nonnegative cone in (S, R, x_1, x_2)-space, a contradiction.

Suppose there exists a point $\underline{X} = (\underline{S}, \underline{R}, \underline{x}_1, \underline{x}_2) \in \Omega(X_0)$. If $\underline{x}_k = 0$ and $\underline{x}_j \geq 0$ then since $\operatorname{cl} \mathcal{O}(\underline{X}) \subset \Omega(X_0)$, $E_0 \in \Omega(X_0)$, a contradiction, and if $\underline{x}_j = 0$ and $\underline{x}_k > 0$, then $E_k \in \Omega(X_0)$, again a contradiction. □

Corollary 3.1. *Consider system* (3.1). *Let* $j, k \in \{1, 2\}$ *with* $j \neq k$. *Assume*

$$\frac{R^0 - \widehat{R}}{S^0 - \widehat{S}} > \frac{(1/\eta_j)\mathcal{R}_j(\widehat{S}, \widehat{R})}{(1/\xi_j)\mathcal{S}_j(\widehat{S}, \widehat{R})} \tag{3.27}$$

for all $\widehat{S} \in (0, S^0)$, $\widehat{R} \in (0, R^0)$ *satisfying* $\mathcal{G}_j(\widehat{S}, \widehat{R}) = D$. *Assume also that* $m_{R_k} > D$, $m_{S_k} > D$, $\mathcal{G}_k(S^0, R^0) > D$, *and* $\mathcal{G}_j(\overline{S}_k, \overline{R}_k) > D$.

(a) *If* $x_{k0} = 0$, *then* $\lim_{t\to\infty} x_j(t) = 0$.

(b) *If* $x_{i0} > 0$, $i = 1, 2$, *then* $\liminf_{t\to\infty} x_i(t) > 0$.

Proof. Condition (3.27) implies that no one-species survival equilibrium of the form E_j exists. By Lemma 3.7, conditions $m_{R_k} > D$, $m_{S_k} > D$, and $\mathcal{G}_k(S^0, R^0) > D$ imply that E_k exists and is globally asymptotically stable with respect to the positive cone in (S, R, x_k)-space. By a standard linear analysis, $\mathcal{G}_j(\overline{S}_k, \overline{R}_k) > D$ implies that E_k is unstable with respect to (S, R, x_1, x_2)-space. The result now follows immediately from Theorem 3.1. □

Remark 1. It can be shown that in order to satisfy hypotheses (3.27) and $\mathcal{G}_j(\overline{S}_k, \overline{R}_k) > D$, in Corollary 3.1, $\mathcal{G}_j(S^0, R^0) \leq D$ and $m_{S_j} > D > m_{R_j}$ must hold.

2. Under the hypotheses of Corollary 3.1, it follows easily from the main result of Butler et al. [**3**] that system (3.1) is uniformly persistent. This guarantees that at least one coexistence equilibrium E^* exists. In fact, there is exactly one coexistence equilibrium in this case, since from (3.1), $\mathcal{G}_i(S^*, R^*) = D$ for $i = 1, 2$. By Lemma 3.2(a), $\varphi_k'(S) < 0$ for all $S \in (0, \lambda_k)$ and by Lemma 3.2(b), $\varphi_j'(S) > 0$ for all $S \in (\lambda_j, M_j^S)$.

3. It can be shown that under the hypotheses of Corollary 3.1, the nutrient concentrations S^*, R^* of the unique coexistence equilibrium

E^* must satisfy the inequality

$$\frac{(1/\eta_k)\mathcal{R}_k(S^*,R^*)}{(1/\xi_k)\mathcal{S}_k(S^*,R^*)} > \frac{R^0-R^*}{S^0-S^*}. \tag{3.28}$$

Why should exploitation of resources S and R by population x_k help population x_j? Under the hypotheses of Corollary 3.1, $m_{S_j} > D > m_{R_j}$ (Remark 1). Therefore, the rate at which population x_j is removed from competition by dilution exceeds its maximal growth rate on resource R. As well, there exists a critical concentration S_j^c of resource S beyond which the presence of resource R becomes detrimental to population x_j. Since $\widehat{S} > (\lambda_j >) S_j^c$ for all $(\widehat{S},\widehat{R})$ satisfying $\mathcal{G}_j(\widehat{S},\widehat{R}) = D$, when the concentration of resource S is close to any such concentration $\widehat{S}$, the presence of resource R is detrimental to population x_j. One would expect that the faster resource R is depleted, the better. But (3.27) implies that the ratio of the net supply of resource R to that of resource S exceeds the ratio of the consumption rate of resource R by population x_j to that of resource S close to any subsistence concentrations $(\widehat{S},\widehat{R})$. Therefore, population x_j cannot deplete resource R quickly enough and so no one-species survival equilibrium of the form E_j exists. In the absence of population x_k, the washout equilibrium E_0 is globally attracting and population x_j dies out.

On the other hand, for population x_k, $m_{S_k} > D$ and $m_{R_k} > D$. Since $\mathcal{G}_k(S^0,R^0) > D$, E_0 is unstable, and in the absence of population x_j, population x_k would survive at a globally asymptotically stable one-species survival equilibrium $E_k = (\overline{S}_k,\overline{R}_k,\bar{x}_1,\bar{x}_2)$, where $\bar{x}_j = 0$. At the resource concentrations of this one-species survival equilibrium E_k, $\mathcal{G}_j(\overline{S}_k,\overline{R}_k) > D$, and so population x_j would be able to compensate for the rate at which it was being removed from competition by dilution and so E_k is unstable with respect to (S,R,x_1,x_2)-space. Also, $\lambda_j < \overline{S}_k < \lambda_k$, and so population x_j would outcompete population x_k driving it to extinction if no resource R were available. Under these conditions, a unique coexistence equilibrium E^* exists. From (3.28), we see that at resource concentrations near (S^*,R^*), the ratio of the consumption of resource R by population x_k to that of resource S would exceed the ratio of the net supply rate of resource R to that of resource S. Thus, population x_k would deplete resource R quickly enough so that coexistence is possible.

That the hypotheses of Corollary 3.1 can be easily satisfied is shown in the following example:

$$\begin{aligned} S' &= 1 - S - \frac{x_1}{\xi_1}\left(\frac{2.25S}{1+S+R}\right) - \frac{x_2}{\xi_2}\left(\frac{2.1S}{1+S+R}\right) \\ R' &= 1 - R - \frac{x_1}{\eta_1}\left(\frac{0.5R}{1+S+R}\right) - \frac{x_2}{\eta_2}\left(\frac{2.1R}{1+S_R}\right) \\ x_1' &= x_1\left(-1 + \frac{2.25S+0.5R}{1+S+R}\right) \\ x_2' &= x_2\left(-1 + \frac{2.1S+2.1R}{1+S+R}\right). \end{aligned}$$

In Corollary 3.1, $j = 1$, $k = 2$, $S^0 = R^0 = D = 1$, $m_{S_1} = 2.25 > 1 > 0.5 = m_{R_1}$, $m_{S_2} = 2.1 = m_{R_2} > 1$, $\lambda_1 = 4/5$, $\mu_1 = \infty$, $\lambda_2 = \mu_2 = 10/11$, $\mathcal{G}_1(1,1) = 11/12 < 1$, $\mathcal{G}_2(1,1) = 1.4 > 1$, $S_1^c = 2/7$, $R_1^c = S_2^c = R_2^c = \infty$. Provided that ξ_i and η_i, $i = 1,2$, are chosen so that (3.27) holds, i.e., $\xi_1/\eta_1 < 9(20 - 11\sqrt{10})/(40 - 13\sqrt{10}) \approx 119.9210$, and (3.28) holds, i.e., $\xi_2/\eta_2 > 2272/39 \approx 58.2564$, then the hypotheses of Corollary 3.1 are all satisfied by this example. The coexistence equilibrium, $E^* = (64/77, 6/77, x_1^*, x_2^*)$ where $x_1^* = 7\xi_1\eta_1(2272\eta_2 - 39\xi_2)/(176(2\xi_1\eta_2 - 9\eta_1\xi_2))$ and $x_2^* = 5\xi_2\eta_2(-3408\eta_1 + 13\xi_1)/(176(2\xi_1\eta_2 - 9\eta_1\xi_2))$, can be shown to be locally asymptotically stable and is probably globally asymptotically stable. In the absence of population x_2, population x_1 dies out. However, if at some time, both populations x_1 and x_2 are present in any amount, then both populations persist.

Note that resource R is not inherently detrimental to population x_1. If nothing were changed in the above example except that the dilution rate D were reduced so that $D < m_{R_1}$, then it would not be possible to satisfy the hypotheses of the corollary. In the absence of population x_2, population x_1 would survive at a globally stable one-species survival equilibrium. In fact, if D is sufficiently small and no x_2 is present, even if resource S is eliminated, x_1 could survive by consuming resource R exclusively. With this in mind, the following scenario is possible. If D is sufficiently small, x_1 could survive with or without x_2. If D is suddenly increased (e.g., the dilution rate often changes significantly due to spring run off) x_1 could be forced to extinction unless some x_2 is present.

The above example also provides support for the so-called *paradox of enrichment* introduced by Rosenzweig [**14**]—"Man must be careful in attempting to enrich ecosystems in order to increase its food yield. There is a real chance that such activity may result in a decimation of the food species that are wanted in greater abundance." One could imagine the following scenario. In the above example, fix $\xi_1/\eta_1 < 45/2$ and take $x_{20} = 0$. If $S^0 = 1$ and $R^0 = 0$, then the model predicts that x_1 approaches a positive equilibrium concentration. However, if the environment is enriched by increasing R^0 above a critical value $R_c^0 \in (0,1)$, x_1 is no longer able to avoid extinction.

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Department of Mathematics and Statistics, McMaster University, Hamilton, Ontario, Canada L8S 4K1