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Interpretation of the Generalized Asymmetric May-Leonard Model of Three Species Competition as a Food Web in a Chemostat

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Abstract. Consider a simple model of a food web in a chemostat involving three species competing for a single, nonreproducing, growth-limiting nutrient in which one of the competitors also predates on one of the other competitors. If it is assumed that the response functions satisfy the law of mass action, it is shown that under certain assumptions on the parameters, this model is equivalent to a special case of the generalized asymmetric May-Leonard (Lotka-Volterra) model of three species competition or to a Lotka-Volterra model in which two of the species compete, and two are involved in predator-prey interaction. In both cases there is a repelling heteroclinic cycle connecting the three single species boundary equilibria, and a positive three species coexistence equilibrium that is globally asymptotically stable with respect to the interior of the positive cone.

1 Introduction

Consider the Gause-Lotka-Volterra model of three species competition:

$$\begin{aligned} x_1'(t) &= r_1x_1(t)(1-x_1(t)-\alpha_1x_2(t)-\beta_1x_3(t)),\\ x_2'(t) &= r_2x_2(t)(1-\beta_2x_1(t)-x_2(t)-\alpha_2x_3(t)),\\ x_3'(t) &= r_3x_3(t)(1-\alpha_3x_1(t)-\beta_3x_2(t)-x_3(t)),\\ &x_1(0)>0,\ x_2(0)>0,\ x_3(0)>0, \end{aligned} \tag{1.1}$$

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where r_i, α_i and β_i $i = 1, 2, 3$, are all positive constants. Under the additional assumption that

$$0 < \alpha_i < 1 < \beta_i, \quad i = 1, 2, 3, \tag{1.2}$$

we shall refer to this model as the *generalized* asymmetric May-Leonard model (GAML). In the case that $r_i = r$, $i = 1, 2, 3$, the model is referred to as the asymmetric May-Leonard model (AML) or the rock-paper-scissors game.

In model (1.1), t denotes time, and x_i, $i = 1, 2, 3$, denote some measure of the size of the ith competitor population at time t, e.g., density or concentration. The r_i, $i = 1, 2, 3$, denote the intrinsic growth rates of each population and the α_i and β_i, $i = 1, 2, 3$, denote the competition coefficients. Condition (1.2) implies that there exists a heteroclinic cycle connecting the single species equilibria on the boundary. In particular, let e_i, $i = 1, 2, 3$, denote the single species equilibrium on each x_i axis, with only species x_i present. Therefore, $e_1 = (1, 0, 0)$, $e_2 = (0, 1, 0)$, and $e_3 = (0, 0, 1)$. From results on two species competition (see for example Waltman [10]), it follows that (1.2) ensures that there is a heteroclinic orbit $\mathcal{O}_3$ on the the $x_1 - x_2$ plane from e_2 to e_1, a heteroclinic orbit $\mathcal{O}_2$ on the $x_1 - x_3$ plane from e_1 to e_3, and a heteroclinic orbit $\mathcal{O}_1$ on the the $x_2 - x_3$ plane from e_3 to e_2. Define

$$\bar{\mathcal{O}} \triangleq \text{ closure of } \cup_{i=1}^{3} \mathcal{O}_i. \tag{1.3}$$

That model (1.1) admits the heteroclinc cycle, $\bar{\mathcal{O}}$, when (1.2) holds was first proved by May and Leonard [7] in the so-called symmetric case, i.e., $\alpha_i = \alpha$, $\beta_i = \beta$, $i = 1, 2, 3$. In fact, they argued that in the case that $\alpha + \beta > 2$ and $0 < \alpha < 1 < \beta$, $\bar{\mathcal{O}}$ attracts all solutions with positive initial conditions, except the unique interior equilibrium point $P = \frac{1}{1+\alpha+\beta}(1, 1, 1)$ and its one dimensional stable manifold. In particular, they argued that and provided collaborating numerical simulations to show that asymptotically, solutions move in population space from a neigbourhood of e_1, to a neighbourhood of e_3, to a neigbourhood of e_2, back toward e_1, and so on, that the time spent in the vicinity of any one point is proportional to the total time elapsed up to that state, and that the total time spent in completing one cycle is proportional to the total length of time the system has been running.

Schuster, Sigmund and Wolf [8] considered the (AML) model and proved that if in addition to (1.2), one assumes that

$$\beta_i - 1 > 1 - \alpha_j, \quad 1 \le i, j \le 3, \tag{1.4}$$

then there exists an open set of orbits in the interior of $\mathbb{R}^3_+$ having $\bar{\mathcal{O}}_i$ as ω limit set. Hofbauer and Sigmund [5] provided conditions that allow one to decide whether the (GAML) model is permanent or the heteroclinic cycle is an attractor. In particular, defining $A_i = 1 - \alpha_i$ and $B_i = \beta_i - 1$ for $i = 1, 2, 3$, they proved that the (GAML) model is permanent if $A_1A_2A_3 > B_1B_2B_3$, but that the heteroclinic cycle is an attractor if $A_1A_2A_3 < B_1B_2B_3$. In Hofbauer and Sigmund ([6], section 15.3), the Volterra-Liapunov Theorem provides sufficient conditions for the global asymptotic stability of the interior equilibrium. They also proved in [5] that if one restricts $r_i = r$, $i = 1, 2, 3$, to obtain the (AML) model, there are no periodic orbits except in the case that $A_1A_2A_3 = B_1B_2B_3$, and that in this case there is a center, i.e., all orbits are periodic. Therefore, for the (AML) model either $A_1A_2A_3 > B_1B_2B_3$ and the interior equilibrium is globally asymptotically stable with respect to the interior of the positive cone, or $A_1A_2A_3 < B_1B_2B_3$ and the heteroclinic cycle on the boundary attracts almost all orbits, or $A_1A_2A_3 = B_1B_2B_3$, and there is a center. Chi, Hsu and Wu [3] also proved this result for the (AML) model using a different method.

Zeeman and Zeeman [13] proved that for competitive Lotka-Volterra systems (1.1), if an interior equilibrium P exists, and the carrying simplex of the system lies to one side of its tangent hyperplane at P, then there is no nontrivial recurrence and so the global dynamics are known. They also gave algebraic criteria for verifying this geometric condition and provided a computational algorithm.

Next, consider the following model of a food web in a chemostat:

$$\begin{aligned}
S'(t) &= (S^0 - S(t))D - \frac{x_1(t)p_1(S(t))}{\eta_1} - \frac{x_2(t)p_2(S(t))}{\eta_2} - \frac{x_3(t)p_3(S(t))}{\eta_3}, \\
x_1'(t) &= x_1(t)\left(-D + p_1(S(t)) - x_3(t)\frac{q(x_1(t))}{z}\right), \\
x_2'(t) &= x_2(t)\left(-D + p_2(S(t))\right), \\
x_3'(t) &= x_3(t)\left(-D + p_3(S(t)) + q(x_1(t))\right), \\
&\quad S(0) \geq 0,\ x_1(0) > 0,\ x_2(0) > 0,\ x_3(0) > 0, \\
&\quad S^0 > 0, D > 0, \eta_i > 0,\ i = 1,2,3,\ \text{and } z > 0.
\end{aligned} \tag{1.5}$$

As for model (1.1), in model (1.5), t denotes time, and x_i, $i = 1,2,3$, denote some measure of the size of the ith competitor population (in the culture vessel) at time t. However, in model (1.5), population $x_3(t)$ is also a predator, predating on population $x_1(t)$. Here $S(t)$ denotes the concentration of the nutrient in the culture vessel at time t. Parameter S^0 denotes the concentration of the 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 and are ignored. The culture vessel is assumed to be well-stirred and for convenience its volume is assumed to be one cubic unit. The functional response for each population $x_i(t)$ is assumed to satisfy the law of mass action and so we define $p_i(S) = m_i S$, $i = 1,2,3$, and $q(x_1) = nx_1$. In addition we assume that growth rate is proportional to the consumption rate and so the consumption rate of nutrient $S(t)$ by population i is given by $\frac{p_i(S(t))}{\eta_i}$ and the consumption rate of $x_1(t)$ by $x_3(t)$ is given by $\frac{q(x_1(t))}{z}$. The positive constants η_i, $i = 1,2,3$, and z are referred to as yield constants.

Model (1.5) is a special case of a more general model first studied in Daoussis [4], where a global analysis was given. In Wolkowicz, Ballyk, and Daoussis [11], this model was provided as an example of competitor-mediated competition, i.e. a scenario in which introduction of a population that exploits common resources promotes *greater* diversity.

In the next section we perform a series of substitutions and transformations on model (1.5) to show that under certain conditions it is equivalent to model (1.1)-(1.2). Hence, under these conditions, we provide a new interpretation of the May-Leonard three species competition model as a simple food web in a chemostat involving three species competing for a single, nonreproducing, growth-limiting nutrient in which one of the competitors also predates on one of the other competitors. The global dynamics of model (2.1) are completely understood. We summarize this in Section 3. However, the global dynamics of the (GAML) model are still not completely understood. Therefore, it is still useful to find new criteria that guarantee that the interior equilibrium P of (GAML) is globally asymptotically stable. We do this in Section 4. We also provide an example for which the criteria introduced here can be used to show that P is globally asymptotically stable, but both the Computational Theorem in [13] and the Volterra-Liapunov Theorem of [6] are inconclusive.

2 Transforming (1.5) into (1.1)-(1.2)

In this section we perform a series of substitutions and transformations that convert model (1.5) into a model of the form (1.1)-(1.2).

First let

$$\bar{t} = tD; \quad \bar{S}(\bar{t}) = \frac{S(t)}{S^0}; \quad \bar{x}_i(\bar{t}) = \frac{x_i(t)}{\eta_i S^0},\ i = 1,2; \quad \bar{x}_3(\bar{t}) = \frac{x_3(t)}{\eta_1 S^0 z};$$

$$\bar{p}_i(\bar{S}(\bar{t})) = \frac{p_i(S(t))}{D},\ i = 1,2,3; \quad \bar{q}(\bar{x}_1(\bar{t})) = \frac{q(x_1(t))}{D}; \quad \gamma = \frac{\eta_3}{\eta_1 z};$$

$$\lambda_i = \frac{D}{m_i},\ i = 1,2,3; \quad \delta = \frac{D}{n}.$$

and assume that $\gamma = 1$.

Then, omitting the bars to simplify notation, the scaled version of model (1.5) can be written as follows:

$$\begin{aligned} S'(t) &= (1 - S(t)) - x_1(t)\frac{S(t)}{\lambda_1} - x_2(t)\frac{S(t)}{\lambda_2} - x_3(t)\frac{S(t)}{\lambda_3}, \\ x_1'(t) &= x_1(t)\left(-1 + \frac{S(t)}{\lambda_1} - \frac{x_3(t)}{\delta}\right), \\ x_2'(t) &= x_2(t)\left(-1 + \frac{S(t)}{\lambda_2}\right), \\ x_3'(t) &= x_3(t)\left(-1 + \frac{S(t)}{\lambda_3} + \frac{x_1(t)}{\delta}\right), \\ &\quad S(0) \geq 0,\ x_1(0) > 0,\ x_2(0) > 0,\ x_3(0) > 0. \end{aligned} \tag{2.1}$$

Note that λ_i, $i = 1,2,3$, and δ are called the *break-even concentrations* of nutrient and prey, respectively.

Adding the four equations in (2.1), it follows that

$$\left(S'(t) + \sum_{i=1}^{3} x_i'(t)\right) = 1 - \left(S(t) + \sum_{i=1}^{3} x_i(t)\right).$$

Therefore,

$$\left(S(t) + \sum_{i=1}^{3} x_i(t)\right) = e^{-t}\left(-1 + S(0) + \sum_{i=1}^{3} x_i(0)\right) + 1.$$

It is clear that for model (2.1), the positive cone is positively invariant, and so it follows that the simplex

$$\mathcal{S} \triangleq \{(S, x_1, x_2, x_3) :\ S + \sum_{i=1}^{3} x_i = 1,\ x_i \geq 0,\ i = 1,2,3,\}$$

is globally attracting.

Remark 2.1 It is useful to note that the restriction that the initial concentration of the nutrient in model (2.1) must be nonnegative is only imposed for biological realism, and does not affect the asymptotic outcome of the solutions. If $S(0) < 0$ but $x_i(0) > 0,\ i = 1,2,3$, then it still follows that $x_i(t) > 0,\ i = 1,2,3$ for all positive time, and so if $S(0) < 0$, then $S(t)$ increases, $x_i(t),\ i = 1,2$ decrease, and $x_3(t)$ eventually decreases until at some finite time $T > 0,\ S(T) = 0$. Then $S(t)$ will be positive for all $t > T$.

Setting $S(t) = 1 - \sum_{i=1}^{3} x_i(t)$, we can eliminate the S' equation in (2.1) to obtain:

$$\begin{aligned}
x_1'(t) &= x_1(t)\left(\frac{1-\lambda_1}{\lambda_1} - \frac{x_1(t)}{\lambda_1} - \frac{x_2(t)}{\lambda_1} - \left(\frac{1}{\lambda_1} + \frac{1}{\delta}\right)x_3(t)\right),\\
x_2'(t) &= x_2(t)\left(\frac{1-\lambda_2}{\lambda_2} - \frac{x_1(t)}{\lambda_2} - \frac{x_2(t)}{\lambda_2} - \frac{x_3(t)}{\lambda_2}\right),\\
x_3'(t) &= x_3(t)\left(\frac{1-\lambda_3}{\lambda_3} - \left(\frac{1}{\lambda_3} - \frac{1}{\delta}\right)x_1(t) - \frac{x_2(t)}{\lambda_3} - \frac{x_3(t)}{\lambda_3}\right),\\
&x_1(0) > 0,\ x_2(0) > 0,\ x_3(0) > 0,\ S(t) = 1 - \sum_{i=1}^{3} x_i(t)
\end{aligned} \tag{2.2}$$

where, it follows from Remark 2.1 that there is no restriction on the sign of $S(t)$, and hence it is not necessary to assume that $\sum_{i=1}^{3} x_i(0) \le 1$. Even if $\sum_{i=1}^{3} x_i(0) > 1$, there exists $T > 0$ such that $\sum_{i=1}^{3} x_i(T) = 1$ and $\sum_{i=1}^{3} x_i(t) < 1$ for all $t > T$.

In order to obtain the same form as (1.1), we let

$$\hat{x}_i = \frac{x_i}{1-\lambda_i},\quad i = 1,2,3,$$

Omitting the hats for convenience of notation, and factoring

$$r_i \triangleq \frac{1-\lambda_i}{\lambda_i},\quad i = 1,2,3, \tag{2.3}$$

from the ith equation, the model can be rewritten:

$$\begin{aligned}
x_1'(t) &= r_1 x_1(t)\left(1 - x_1(t) - \frac{1-\lambda_2}{1-\lambda_1}x_2(t) - \frac{(1-\lambda_3)(\lambda_1+\delta)}{\delta(1-\lambda_1)}x_3(t)\right),\\
x_2'(t) &= r_2 x_2(t)\left(1 - \frac{1-\lambda_1}{1-\lambda_2}x_1(t) - x_2(t) - \frac{1-\lambda_3}{1-\lambda_2}x_3(t)\right),\\
x_3'(t) &= r_3 x_3(t)\left(1 - \frac{(1-\lambda_1)(\delta-\lambda_3)}{\delta(1-\lambda_3)}x_1(t) - \frac{1-\lambda_2}{1-\lambda_3}x_2(t) - x_3(t)\right),\\
&x_1(0) > 0,\ x_2(0) > 0,\ x_3(0) > 0,\ S(t) = 1 - \sum_{i=1}^{3}(1-\lambda_i)x_i(t).
\end{aligned} \tag{2.4}$$

Again we emphasize that there is no restriction on the sign of $S(0)$. This is a classical Lotka-Volterra model. For our analogy, we require more assumptions on the parameters in order to control the sign and relative magnitudes of the coefficients. Assume that the species are labelled so that

$$0 < \lambda_1 < \lambda_2 < \lambda_3 < 1. \tag{2.5}$$

Under this assumption, Butler and Wolkowicz, [1] proved that if x_3 does not consume x_1 (i.e., $n = 0$ or equivalently $\delta = \infty$), but instead consumes only S, then x_1 would be the sole survivor in a contest against x_2 or against both x_2 and x_3 and in the absence of x_1, x_2 would survive and drive x_3 to extinction. In this sense x_1 is the *strongest* competitor for resource S, and x_3 is the *weakest* competitor for resource S.

It follows from (2.5) that $r_i > 0$, $i = 1, 2, 3$, and so it makes sense to interpret each r_i as the intrinsic growth rate of the ith species.

If we now allow x_3 to consume both S and x_1, and in addition we assume that

$$\delta > \lambda_3, \tag{2.6}$$

so that $\alpha_3 > 0$, then model (2.2) has been transformed into the form of model (1.1), the Gause-Lotka-Volterra model of three species competition, with

$$\alpha_1 = \frac{1-\lambda_2}{1-\lambda_1}, \quad \alpha_2 = \frac{1-\lambda_3}{1-\lambda_2}, \quad \alpha_3 = \frac{(1-\lambda_1)(\delta-\lambda_3)}{\delta(1-\lambda_3)}, \tag{2.7}$$

$$\beta_1 = \frac{(1-\lambda_3)(\lambda_1+\delta)}{\delta(1-\lambda_1)}, \quad \beta_2 = \frac{1-\lambda_1}{1-\lambda_2}, \quad \beta_3 = \frac{1-\lambda_2}{1-\lambda_3}, \tag{2.8}$$

where $\alpha_i > 0$ and $\beta_i > 0$, $i = 1, 2, 3$.

By (2.5), it is clear that $\alpha_i < 1$, $i = 1, 2$, and $\beta_i > 1, i = 2, 3$. However, $\beta_1 > 1$, if, and only if, we also assume that

$$0 < \delta < \frac{\lambda_1(1-\lambda_3)}{\lambda_3-\lambda_1}, \tag{2.9}$$

and $\alpha_3 < 1$, if, and only if, in addition to (2.5), we assume that

$$0 < \delta < \frac{\lambda_3(1-\lambda_1)}{\lambda_3-\lambda_1}. \tag{2.10}$$

Note that if (2.5) holds, then (2.9) implies (2.10).

Therefore, model (2.4) is in the form of model (1.1). If (2.5)-(2.9) hold, then (1.2) also holds and there is a heteroclinic cycle on the boundary, connecting the three singles species equilibria, e_1, e_2, and e_3. Thus we have shown that if $\gamma = \frac{\eta_3}{\eta_1 z} = 1$, then we have transformed model (1.5), a model of three species competition in a chemostat for a single, nonreproducing, growth-limiting nutrient in which one of the competitors, x_3, also predates on one of the other competitors, x_1, into the form of a generalized asymmetric May-Leonard model (1.1)-(1.2) of three species competition. On the other hand, if the inequality in (2.6) is reversed, then model (2.4) is of the same form as model (1.1), but α_3 is negative. The classical interpretation would be that instead of three species competition, x_1 and x_2 compete, but x_3 predates on x_1.

3 Dynamics of the chemostat model (2.1)

Let the equilibria of model (2.1) be denoted:

$$E_0 \triangleq (1,0,0,0); \quad E_{\lambda_1} \triangleq (\lambda_1, 1-\lambda_1, 0, 0); \quad E_{\lambda_2} \triangleq (\lambda_2, 0, 1-\lambda_2, 0);$$

$$E_{\lambda_3} \triangleq (\lambda_3, 0, 0, 1-\lambda_3); \quad E^* \triangleq (S^*, x_1^*, 0, x_3^*); \quad \tilde{E} \triangleq (\lambda_2, \tilde{x}_1, \tilde{x}_2, \tilde{x}_3),$$

where

$$S^* = \frac{\lambda_1\lambda_3}{\lambda_1\lambda_3 + \delta(\lambda_3-\lambda_1)}; \; x_1^* = \delta(1 - \frac{S^*}{\lambda_3}); \quad x_3^* = \delta(-1 + \frac{S^*}{\lambda_1});$$

$$\bar{x}_1 = \delta(1 - \frac{\lambda_2}{\lambda_3}); \quad \bar{x}_2 = 1 - \lambda_2 - \delta\lambda_2(\frac{\lambda_3 - \lambda_1}{\lambda_3\lambda_1}); \quad \bar{x}_3 = \delta(-1 + \frac{\lambda_2}{\lambda_1}).$$

Criteria for the existence and for the stability of the equilibria of model (2.1) are summarized in Table 3.1.

Table 3.1 Equilibria - Existence and Stability for (2.1)
(assuming $\lambda_1 < \lambda_j,\ j = 2, 3$)

	Existence†	Globally Asymptotically Stable‡ (assuming the equilibrium exists)
E_0	always	$\lambda_i \geq 1,\ i = 1, 2, 3$
E_{λ_1}	$\lambda_1 < 1$	$S^* < \lambda_1$
E_{λ_2}	$\lambda_2 < 1$	never
E_{λ_3}	$\lambda_3 < 1$	never
E^*	$\lambda_1 < S^* < \lambda_3$	$\lambda_1 < S^* < \lambda_2$
$\bar{E}$	$\lambda_1 < \lambda_2 < \lambda_3$ and $S^* > \lambda_2$	whenever it exists

† An equilibrium is assumed to exist if, and only if, all of its components are nonnegative.

‡ Global asymptotical stability is with respect to solutions initiating in the interior of the positive cone.

Note that under the assumption that $\lambda_1 < \lambda_j,\ j = 2, 3$, it follows that $0 < S^* < 1$, and that one of the equilibria, $E_0,\ E_{\lambda_1},\ E^*$, or $\bar{E}$ is globally asymptotically stable. This can be proved using the Liapunov functions summarized in Table 3.2 and the slightly modified version of the LaSalle Invariance Principle in Wolkowicz and Lu [12]. The proofs of the global asymptotic stability of the equilibria were first given in [4].

Table 3.2 Summary of Liapunov functions for (2.1)
$V = V(S, x_1, x_2, x_3)$

E_0	$V = S - 1 - \ln(S) + x_1 + x_2 + x_3$ $\dot{V} = -\frac{(S-1)^2}{S} + \sum_{i=1}^{3} x_i(\frac{1-\lambda_i}{\lambda_i})$
E_{λ_1}	$V = S - \lambda_1 - \lambda_1 \ln(\frac{S}{\lambda_1}) + x_1 - (1 - \lambda_1) - (1 - \lambda_1)\ln\frac{x_1}{1-\lambda_1}$ $\dot{V} = -\frac{(S-\lambda_1)^2}{\lambda_1 S} - x_2(\frac{\lambda_2-\lambda_1}{\lambda_2}) + x_3(-1 + \frac{\lambda_1}{\lambda_3} + \frac{1-\lambda_1}{\delta})$
E^*	$V = S - S^* - S^* \ln(\frac{S}{S^*}) + \sum_{i=1,3}(x_i - x_i^* - x_i^* \ln(\frac{x_i}{x_i^*})) + x_2$ $\dot{V} = -\frac{(S-S^*)^2}{SS^*} + x_2(\frac{S^*-\lambda_2}{\lambda_2})$
$\bar{E}$	$V = S - \lambda_2 - \lambda_2 \ln(\frac{S}{\lambda_2}) + \sum_{i=1}^{3}(x_i - \bar{x}_i - \bar{x}_i \ln(\frac{x_i}{\bar{x}_i}))$ $\dot{V} = -\frac{1}{S\lambda_2}(S - \lambda_2)^2$

Remark 3.1 In fact, one can also prove that if instead, we assume that $\lambda_2 < \lambda_j,\ j = 1, 3$ and $\lambda_2 < 1$, then E_{λ_2} is globally asymptotically stable, or that if $\lambda_3 < \lambda_j,\ j = 1, 2$ and $\lambda_3 < 1$, then E_{λ_3} is globally asymptotically stable. Hence, model (2.1) only admits very simple dynamics. In particular, there is always a single, globally asymptotically stable equilibrium point that attracts all solutions with positive initial conditions.

4 Implications for the dynamics of model (1.1)

Solving (2.7)-(2.8) for the $\lambda_i,\ i=1,2,3$, and δ in terms of $\alpha_i, i=1,2,3$ and β_1, is equivalent to solving the linear system of equations:

$$\begin{bmatrix} -\alpha_1 & 1 & 0 & 0 \\ 0 & -\alpha_2 & 1 & 0 \\ 0 & 0 & 1 & \alpha_1\alpha_2\alpha_3 - 1 \\ -\alpha_1\alpha_2 & 0 & 0 & \beta_1 - \alpha_1\alpha_2 \end{bmatrix} \begin{bmatrix} \lambda_1 \\ \lambda_2 \\ \lambda_3 \\ \delta \end{bmatrix} = \begin{bmatrix} 1-\alpha_1 \\ 1-\alpha_2 \\ 0 \\ 0 \end{bmatrix}$$

We obtain the unique solution:

$$\lambda_1 = \frac{(\beta_1 - \alpha_1\alpha_2)(1-\alpha_1\alpha_2)}{\alpha_1\alpha_2(1-\beta_1-\alpha_1\alpha_2\alpha_3+\alpha_1\alpha_2)},$$

$$\lambda_2 = \frac{\beta_1 - 2\alpha_1\alpha_2 - \alpha_1\alpha_2^2\alpha_3 + \alpha_2 - \alpha_2\beta_1 + \alpha_1\alpha_2^2 + \alpha_1^2\alpha_2^2\alpha_3}{\alpha_2(1-\beta_1-\alpha_1\alpha_2\alpha_3+\alpha_1\alpha_2)},$$

$$\lambda_3 = \frac{(1-\alpha_1\alpha_2\alpha_3)(1-\alpha_1\alpha_2)}{1-\beta_1-\alpha_1\alpha_2\alpha_3+\alpha_1\alpha_2},$$

$$\delta = \frac{1-\alpha_1\alpha_2}{1-\beta_1-\alpha_1\alpha_2\alpha_3+\alpha_1\alpha_2}.$$

Provided α_i, and $\beta_i,\ i=1,2,3$, are chosen so that $\beta_2 = \frac{1}{\alpha_1},\ \beta_3 = \frac{1}{\alpha_2}$, $\lambda_i > 0,\ i=1,2,3$, and $\delta > 0$, the results in the previous section hold, and so model (1.1) has simple dynamics, i.e. there is always a globally asymptotically stable equilibrium that attracts all solutions with positive initial conditions. This is true, even if some or all of the r_i, α_i, β_i are negative.

To determine which equilibrium is globally asymptotically stable, use Table 3.1 and Remark 3.1 at the end of the previous section, and note that E_{λ_i} in (2.1) corresponds to the single species survival equilibria, $e_i,\ i=1,2,3$, for system (1.1), E_0 corresponds to the washout equilibrium, $e_0 \triangleq (0,0,0)$, E^* corresponds to the two species survival equilibrium $e^* \triangleq (x_1^*, 0, x_2^*)$, and $\tilde{E}$ corresponds to the equilibrium with all three components positive, $\tilde{e} \triangleq (\tilde{x}_1, \tilde{x}_2, \tilde{x}_3)$.

In order to have a globally attracting equilibrium in the interior of the positive cone with a repelling heteroclinic cycle on the boundary of the positive cone, select $0 < \alpha_i < 1,\ i=1,2,3$. Then, provided that in addition,

$$\beta_1 < 1 + \alpha_1\alpha_2(1-\alpha_3) \triangleq \beta_M, \tag{4.1}$$

so that the denominators are all positive, it follows that $\lambda_1 > 0$ and $0 < \lambda_3 < \delta$. For $\lambda_2 > 0$, one must also assume that the numerator in the expression for λ_2 above is also positive, i.e.,

$$\beta_1 > \frac{\alpha_2(2\alpha_1 + \alpha_1\alpha_2\alpha_3 - 1 - \alpha_1\alpha_2 - \alpha_1^2\alpha_2\alpha_3)}{1-\alpha_2} \triangleq \beta_m. \tag{4.2}$$

Note that,

$$\beta_M > 1 \ \text{ and } \ \beta_M - \beta_m = (1-\alpha_1\alpha_2)(1-\alpha_1\alpha_2\alpha_3) > 0,$$

since $0 < \alpha_i < 1,\ i=1,2,3$. Therefore, it is always possible to select $\beta_i,\ i=1,2,3$, so that $\beta_2 = \frac{1}{\alpha_1}$, $\beta_3 = \frac{1}{\alpha_2}$, and $\max(1,\beta_m) < \beta_1 < \beta_M$, and hence (1.2) holds.

If

$$\beta_1 = \alpha_1\alpha_2(2 - \alpha_1\alpha_2\alpha_3) \triangleq \beta_{crit},$$

then

$$\lambda_1 = \lambda_2 = \lambda_3 = S^* = 1,$$

and if

$$\beta_1 < \beta_{crit},$$

then

$$\lambda_1 < \lambda_2 < \lambda_3 < S^* < 1.$$

Note that,

$$\beta_{crit} - \beta_m = \alpha_2 \frac{(1-\alpha_1\alpha_2)(1-\alpha_1\alpha_2\alpha_3)}{1-\alpha_2} > 0,$$

Also,

$$\beta_M - \beta_{crit} = (1-\alpha_1\alpha_2)(1-\alpha_2\alpha_2\alpha_3) > 0,$$

so that

$$\beta_m < \beta_{crit} < \beta_M.$$

Note also, that if

$$\frac{1}{\alpha_1\alpha_2} + \alpha_1\alpha_2\alpha_3 < 2,$$

then

$$\beta_{crit} > 1.$$

Therefore, we have just proved,

Theorem 4.1 *In model (1.1)-(1.2), if*

$$0 < \alpha_i < 1,\ i = 1,2,3, \quad \frac{1}{\alpha_1\alpha_2} + \alpha_1\alpha_2\alpha_3 < 2, \quad \textit{and} \quad \max(1,\beta_m) < \beta_1 < \beta_{crit},$$

then there is a a repelling heteroclinic cycle on the boundary of the positive cone and a unique positive equilibrium that is globally asymptotically stable with respect to all orbits initiating in the interior of the positive cone.

EXAMPLE Selecting

$$\alpha_1 = \frac{9}{10},\ \alpha_2 = \frac{8}{9},\ \alpha_3 = \frac{5}{12},$$

$$\beta_1 = \frac{6}{5},\ \beta_2 = \frac{10}{9},\ \beta_3 = \frac{9}{8},$$

$$r_1 = \frac{5}{3},\ r_2 = \frac{9}{7},\ r_3 = 1,$$

in model (1.1)-(1.2) corresponds to taking

$$\lambda_1 = \frac{3}{8},\ \lambda_2 = \frac{7}{16},\ \lambda_3 = \frac{1}{2},\ \delta = \frac{3}{4},\ S^* = \frac{2}{3}$$

in model (2.1). For these parameters, it follows from Theorem 4.1 that both models (1.1) and (2.1) have a repelling heteroclinic cycle on the boundary and a globally attracting equilibrium in the interior of the positive cone. It is interesting to note that neither the Zeeman Computational Theorem (see [13] for more details and proof), nor the Volterra-Lyapunov Stability Theorem (see ([6], Section 15.3) for more details and a proof) can be used to show the global stability of the interior equilibrium in this example. We provide the statements of both results here for the readers' convenience and demonstrate that a hypothesis fails in each case.

We first introduce notation similar to that used in [13]. Model (1.1) and (2.1) can be written in the form $x' = \chi(b - Ax) = \chi A(p - x)$, where

$$x = \begin{bmatrix} x_1 \\ x_2 \\ x_3 \end{bmatrix}, \quad b = \begin{bmatrix} r_1 \\ r_2 \\ r_3 \end{bmatrix}, \quad p = A^{-1}b,$$

$$\chi = diag(x) = \begin{pmatrix} x_1 & 0 & 0 \\ 0 & x_2 & 0 \\ 0 & 0 & x_3 \end{pmatrix}, \quad A = \begin{pmatrix} r_1 & r_1\alpha_1 & r_1\beta_1 \\ r_2\beta_2 & r_2 & r_2\alpha_2 \\ r_3 & r_3\alpha_3 & r_3 \end{pmatrix}.$$

For an arbitrary $n \times n$ matrix M define the symetric matrix

$$M^S \triangleq \frac{1}{2}(M + M^T),$$

and

$$M^R \triangleq M_{nn} + M_{11} - M_{n1} - M_{1n},$$

where M_{ij} denotes the $(n-1) \times (n-1)$ submtrix of M obtained by deleting row i and column j from M.

Then,

$$M^{SR} \triangleq (M^S)^R.$$

Theorem 4.2 *(Computational Theorem ([13], Theorem 6.7)) Given the competitive system $x' = \chi A(p - x)$, with a unique interior equilibrium point $P = p = A^{-1}b \in int\mathbb{R}^n_+$. Let h^T be a strictly positive left eigenvector of $\mathcal{P}A$ and let $\mathcal{H} = diag(h)$. If all the eigenvalues of $(A\mathcal{H}^{-1})^{SR}$ are negative (positive), then P is a global repellor (attractor).*

Verifying the hypotheses of the Computational Theorem using Maple, we find (to 4 decimal places) that

$$b = \begin{bmatrix} \frac{5}{3} \\ \frac{9}{7} \\ 1 \end{bmatrix}, \quad A = \begin{pmatrix} \frac{5}{3} & \frac{3}{2} & 2 \\ \frac{10}{7} & \frac{9}{7} & \frac{8}{7} \\ \frac{5}{12} & \frac{9}{8} & 1 \end{pmatrix}, \quad p = A^{-1}b = \begin{pmatrix} \frac{3}{20} \\ \frac{11}{18} \\ \frac{1}{4} \end{pmatrix}, \quad h = \begin{pmatrix} 0.9889 \\ 1.0375 \\ 1.0 \end{pmatrix},$$

$$(A\mathcal{H}^{-1})^S = \begin{pmatrix} 1.6667 & 1.429 & 1.1972 \\ 1.4292 & 1.2255 & 1.1012 \\ 1.1972 & 1.1012 & 0.9889 \end{pmatrix}, \quad (A\mathcal{H}^{-1})^{SR} = \begin{pmatrix} 0.0338 & 0.1077 \\ 0.1077 & 0.0119 \end{pmatrix}.$$

$(A\mathcal{H}^{-1})^{SR}$ has a positive and a negative eigenvalue and hence is neither positive nor negative definite, and so the Computational Theorem is inconclusive.

Theorem 4.3 *(Volterra-Liapunov Theorem [6]) If there exists a diagonal matrix D with positive diagonal entries such that $(DA)^S$ is positive definite, then $P = p$ is a globally asymptotically stable equilibrium point of the competitive system $x' = \chi A(p - x)$.*

Recalling that the principal minors of a positive definite matrix must all be strictly positive, since $\det A_{33} = 0$, by a similar argument to that given in Lemma 7.2 and 7.3 of [13], no diagonal matrix D with positive diagonal entries exists such that $(DA)^S$ is positive definite, and so the Volterra-Liapunov Theorem cannot be used to show the global stability of this interior equilibrium point.

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