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

Gail S. K. Wolkowicz

Department of Mathematics and Statistics

McMaster University

E-mail: wolkowic@mcmaster.ca

URL: www.math.mcmaster.ca/wolkowic/wolkowic.html

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Gause-Lotka-Volterra
Model of Three Species Competition

$$
\begin{aligned}
x_1'(t) &= r_1 x_1(t)(1 - x_1(t) - \alpha_1 x_2(t) - \beta_1 x_3(t)), \\
x_2'(t) &= r_2 x_2(t)(1 - \beta_2 x_1(t) - x_2(t) - \alpha_2 x_3(t)), \\
x_3'(t) &= r_3 x_3(t)(1 - \alpha_3 x_1(t) - \beta_3 x_2(t) - x_3(t)),
\end{aligned} \tag{1}
$$

$$x_1(0) > 0, x_2(0) > 0, x_3(0) > 0,$$

where r_i, α_i, β_i $i = 1, 2, 3$, are all positive constants.

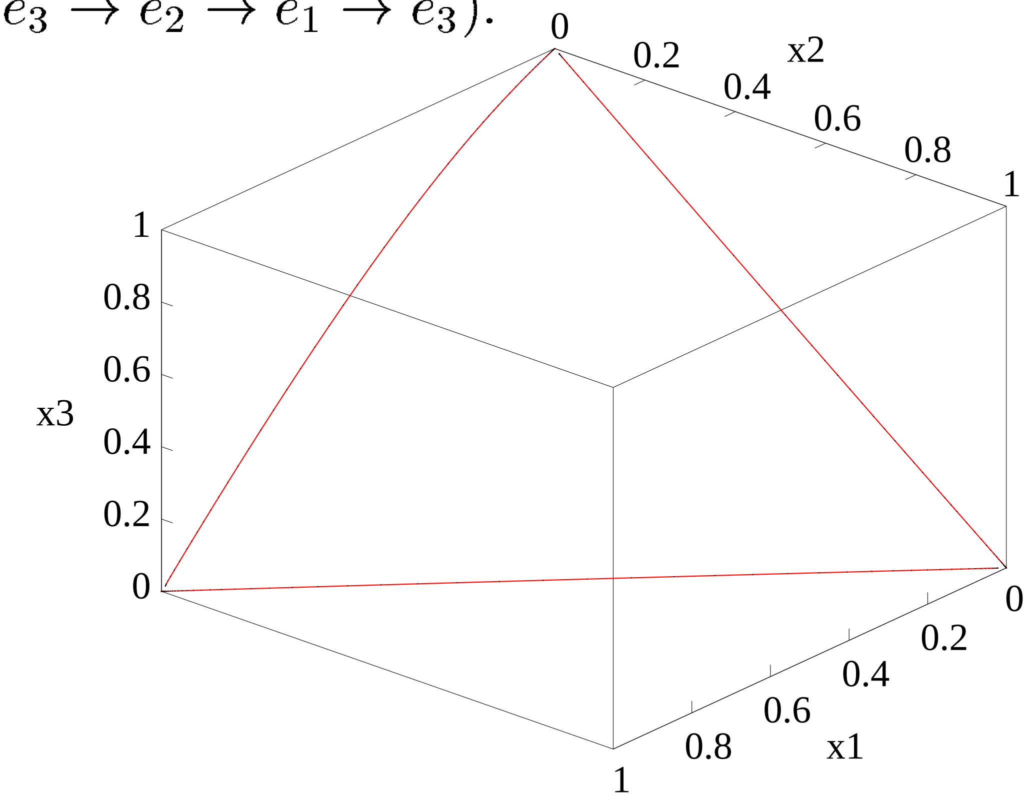
Under the additional assumption that

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

the model is referred to as the **asymmetric May-Leonard model.**

Heteroclinic Cycle

Under the assumption that $0 < \alpha_i < 1 < \beta_i, \quad i = 1, 2, 3$, there exists a **heterclinic cycle**, $\bar{\mathcal{O}}$, connecting the single species equilibria: $e_1 = (1, 0, 0,)$, $e_2 = (0, 1, 0)$, $e_3 = (0, 0, 1)$, on the boundary. $(e_3 \to e_2 \to e_1 \to e_3)$.



Nonlinear Aspects of Competition between Three Species
by Robert M. **May** and Warren J. **Leonard** (SIAM J Appl Math)

They considered the **symmetric case**:

$$\alpha_i = \alpha,\ \beta_i = \beta,\ r_i = r,\ \text{for all } i = 1, 2, 3.$$

They argue and provide collaborating numerical simulations in the case that $\alpha + \beta > 2$ and $0 < \alpha < 1 < \beta$, that

- $\bar{\mathcal{O}}$ attracts all solutions with positive initial conditions except the unique interior equilibrium point $\frac{1}{1+\alpha+\beta}(1, 1, 1)$, and its one dimensional unstable manifold.
- asymptotically, solutions move from a neighbourhood of e_1 to a neighbourhood of e_3 to a neighbourhood of e_2, back to e_1, and so on, and 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 length of time the system has been running.

On the Asymmetric May-Leonard Model of Three Competing Species

by C-W **Chi**, S-B **Hsu**, and L-I **Wu** (SIAM J Appl Math)

Assuming: $r_i = r, \;\; i = 1, 2, 3.$

Define $A_i = 1 - \alpha_i, \;\; B_i = \beta_i - 1, \;\; i = 1, 2, 3.$

- If $A_1 A_2 A_3 > B_1 B_2 B_3$, then the interior equilibrium is globally asymptotically stable with respect to the interior of R^3_+.
- If $A_1 A_2 A_3 < B_1 B_2 B_3$, then the heteroclinic cycle on the boundary attracts all orbits initiating in the interior of R^3_+ except the interior equilibrium and its one dimensional stable manifold.
- If $A_1 A_2 A_3 < B_1 B_2 B_3$, then there is a Hopf bifurcation resulting in a family of neutrally stable periodic orbits.

(Improved earlier results by Schuster, Sigmund and Wolf, and by Hofbauer and Sigmund.)

Intrinsic Growth Rates Not All Equal

i.e. r_i not all equal.

- J. Coste, J. Peyraud, and P. Coullet showed that nondegenerate Hopf bifurcation can occur.
- M.L. Zeeman also studied Hopf bifurcation.
- P. Van den Driessche and M.L. Zeeman - provide criteria for extinction of two species, as well as stable coexistence of at least two species.

Chemostat - Villefranche sur Mer

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Schematic Representation

Food Web in a Chemostat

Predator Feeding on Two Trophic Levels

with **Spiro Daoussis**

$$\begin{aligned} S'(t) &= (S^0 - S(t))D - \sum_{i=1}^{3} \frac{p_i(S(t))x_i(t)}{\eta_i} \\ x_1'(t) &= x_1(t)\,(-D + p_1(S(t))) - x_3(t)\frac{q(x_1(t))}{z} \\ x_2'(t) &= x_2(t)\,(-D + p_2(S(t))) \\ x_3'(t) &= x_3(t)\,(-D + p_3(S(t))) + x_3(t)q(x_1(t)) \end{aligned} \tag{3}$$

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

$$S^0 > 0, D > 0, \eta_i > 0,\ i = 1, 2, 3,\ \text{and } z > 0.$$

Notation

$x_1,\ x_2,\ x_3$ consume S.

x_3 also consumes x_1.

Mass action interactions: $p_i(S) = m_i S,\ i = 1,2,3,\ q(x_1) = n_1 x_1$.

Define break-even concentrations:

$$\lambda_i \ \ni\ p_i(\lambda_i) = D,\ i = 1,2,3,\ \text{and}\ \delta\ \ni\ q(\delta) = D.$$

i.e. $p_i(S) = \frac{D}{\lambda_i} S$ and $q(x_1) = \frac{D}{\delta} x_1$.

Perform a series of substitutions and transformations that convert model (3), the food web in a chemostat, into a model of the form (1)-(2), the asymetric May-Leonard model with a heteroclinic cycle on the boundary.

First, let

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

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

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

and assume that $\gamma = 1$.

To obtain (omitting the bars to simplify notation), the scaled version of the chemostat model (3):

$$\begin{aligned} S' &= (1-S) - x_1\frac{S}{\lambda_1} - x_2\frac{S}{\lambda_2} - x_3\frac{S}{\lambda_3}, \\ x_1' &= x_1(-1+\frac{S}{\lambda_1} - \frac{x_3}{\delta}), \\ x_2' &= x_2(-1+\frac{S}{\lambda_2}), \\ x_3' &= x_3(-1+\frac{S}{\lambda_3} + \frac{x_1}{\delta}), \\ & S(0) > 0, x_1(0) > 0, x_2(0) > 0, x_3(0) > 0. \end{aligned} \tag{4}$$

Globally Attracting Symplex

Adding the four equations in (4), it follows that

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

Therefore,

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

It is clear that for model (4), the positive cone is positively invariant, and so it follows that the simplex

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

is globally attracting.

Set $S(t) = 1 - \sum_{i=1}^{3} x_i(t)$, to eliminate the S' equation in (4) to obtain:

$$\begin{aligned} x_1' &= x_1\left(\frac{1-\lambda_1}{\lambda_1} - \frac{x_1}{\lambda_1} - \frac{x_2}{\lambda_1} - \left(\frac{1}{\lambda_1} + \frac{1}{\delta}\right)x_3\right), \\ x_2' &= x_2\left(\frac{1-\lambda_2}{\lambda_2} - \frac{x_1}{\lambda_2} - \frac{x_2}{\lambda_2} - \frac{x_3}{\lambda_2}\right), \\ x_3' &= x_3\left(\frac{1-\lambda_3}{\lambda_3} - \left(\frac{1}{\lambda_3} - \frac{1}{\delta}\right)x_1 - \frac{x_2}{\lambda_3} - \frac{x_3}{\lambda_3}\right), \end{aligned} \tag{5}$$

$$x_1(0) > 0, x_2(0) > 0, x_3(0) > 0, S(t) = 1 - \sum_{i=1}^{3} x_i(t).$$

In order to obtain the same form as (1), let

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

Omit the hats for convenience of notation, and factor

$$r_i = \frac{1-\lambda_i}{\lambda_i} > 0, \quad i = 1, 2, 3, \tag{6}$$

from the ith equation, to obtain:

$$\begin{aligned} x_1' &= r_1 x_1 (1 - x_1 - \frac{1-\lambda_2}{1-\lambda_1} x_2 - \frac{(1-\lambda_3)(\lambda_1+\delta)}{\delta(1-\lambda_1)} x_3), \\ x_2' &= r_2 x_2 (1 - \frac{1-\lambda_1}{1-\lambda_2} x_1 - x_2 - \frac{1-\lambda_3}{1-\lambda_2} x_3), \\ x_3' &= r_3 x_3 (1 - \frac{(1-\lambda_1)(\delta-\lambda_3)}{\delta(1-\lambda_3)} x_1 - \frac{1-\lambda_2}{1-\lambda_3} x_2 - x_3), \end{aligned} \tag{7}$$

$$x_1(0) > 0, x_2(0) > 0, x_3(0) > 0, S(t) = 1 - \sum_{i=1}^{3} (1-\lambda_i) x_i(t).$$

This is a classical Lotka-Volterra model. However, we need more assumptions in order to control the sign and relative magnitudes of the coefficients. Assume that the species are labelled so that

$$0 < \lambda_1 < \lambda_2 < \lambda_3 < 1. \tag{8}$$

Under this assumption, Butler and Wolkowicz, prove that if x_3 does not consume x_1, 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. In this sense x_1 is the *strongest* competitor for resource S. In the absence of x_1, x_2 would survive and drive x_3 to extinction, and so x_3 is the *weakest* competitor for resource S.

If in addition, we assume that

$$\delta > \lambda_3, \tag{9}$$

so that $\alpha_3 > 0$, then model (5) is the asymmetric, Lotka-Volterra model of three species competition, model (1), where

$$\alpha_1 = \frac{1-\lambda_2}{1-\lambda_1}, \quad \alpha_2 = \frac{1-\lambda_3}{1-\lambda_2}, \quad \alpha_3 = \frac{(1-\lambda_1)(\delta-\lambda_3)}{\delta(1-\lambda_3)}, \tag{10}$$

$$\beta_1 = \frac{(1-\lambda_3)(\lambda_1+\delta)}{\delta(1-\lambda_1)}, \quad \beta_2 = \frac{1-\lambda_1}{1-\lambda_2}, \quad \beta_3 = \frac{1-\lambda_2}{1-\lambda_3}, \tag{11}$$

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

Since $\lambda_1 < \lambda_2 < \lambda_3 < 1$, clearly $\alpha_i < 1,\ i = 1, 2,\ \beta_i > 1, i = 2, 3.$

$\beta_1 > 1$, if, and only if, we also assume that

$$0 < \delta < \frac{\lambda_1(1 - \lambda_3)}{\lambda_3 - \lambda_1}, \tag{12}$$

$\alpha_3 < 1$, if, and only if, in addition to $\lambda_1 < \lambda_2 < \lambda_3 < 1$, we assume

$$0 < \delta < \frac{\lambda_3(1 - \lambda_1)}{\lambda_3 - \lambda_1}. \tag{13}$$

Note that if $\lambda_1 < \lambda_2 < \lambda_3 < 1$ holds, then (12) implies (13).

Therefore, model (7) is precisely model (1) and if (8)-(12) hold, then (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 the foodweb in a chemostat model (3) into the asymmetric May-Leonard model (1)-(2) of three species competition.

On the other hand, if the inequality in (9) is reversed, then model (7) is of the same form as model (1), but β_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.

Dynamics of the Model of a Foodweb in a Chemostat

Let the equilibria of model (4) be denoted:

$$E_0 \equiv (1, 0, 0, 0);$$

$$E_{\lambda_1} \equiv (\lambda_1, 1-\lambda_1, 0, 0); \;\; E_{\lambda_2} \equiv (\lambda_2, 0, 1-\lambda_2, 0); \;\; E_{\lambda_3} \equiv (\lambda_3, 0, 0, 1-\lambda_3);$$

$$E^* \equiv (S^*, x_1^*, 0, x_3^*); \quad \tilde{E} \equiv (\lambda_2, \tilde{x}_1, \tilde{x}_2, \tilde{x}_3),$$

where

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

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

Table 1: Equilibria - Existence and Stability
(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^*	$\lambda_1 < S^* < \lambda_3$	$\lambda_1 < S^* < \lambda_2$
$\tilde{E}$	$\lambda_1 < \lambda_2 < \lambda_3$ and $S^* > \lambda_2$	whenever it exists

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

Note that under the assumption that $\lambda_1 < \lambda_j,\ j = 1, 2$, that $0 < S^* < 1$, and one of the equilibria, $E_0,\ E_{\lambda_1},\ E^*$, or $\tilde{E}$ is globally asymptotically stable. This can be proved using the Liapunov functions summarized in Table 2 and the slightly modified version of the LaSalle Extension theorem.

Table 2: Summary of Liapunov functions for (4)

$V = V(S, x_1, x_2, x_3)$

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^*	$V = S - S^* - S^* \ln(\frac{S}{S^*}) + \sum_{i=1,3}(x_i - x_i^* - x_i^* \ln(\frac{x_i}{x_i^*})) + x_2$ $\dot{V} = -\frac{(S-S^*)^2}{SS^*} + x_2(\frac{S^*-\lambda_2}{\lambda_2})$
$\tilde{E}$	$V = S - \lambda_2 - \lambda_2 \ln(\frac{S}{\lambda_2}) + \sum_{i=1}^{3}(x_i - \tilde{x}_i - \tilde{x}_i \ln(\frac{x_i}{\tilde{x}_i}))$ $\dot{V} = -\frac{1}{S\lambda_2}(S-\lambda_2)^2$

REMARK: 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 (4) 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.

Solving (10)-(11) for the $\lambda_i, \ i = 1, 2, 3$, and δ in terms of $\alpha_i, i = 1, 2, 3$ and β_1, we obtain the unique solution:

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

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

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

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

Provided α_i, and β_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 analysis in the previous section applies, and so model (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 1 and the Remark at the end of the previous section, and note that E_{λ_i} in (4) corresponds to the single species survival equilibria, e_i, $i = 1, 2, 3$, for system (1), E_0 corresponds to the washout equilibrium, $e_0 \equiv (0, 0, 0)$, E^* corresponds to the two species survival equilibrium $e^* \equiv (x_1^*, 0, x_2^*)$, and $\tilde{E}$ corresponds to the equilibrium with all three components positive, $\tilde{e} \equiv (\tilde{x}_1, \tilde{x}_2, \tilde{x}_3)$.

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,

$$\beta_1 < 1 + \alpha_1 \alpha_2 (1 - \alpha_3) \equiv \beta_M, \tag{14}$$

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.,

$$\beta_1 > \frac{\alpha_2(2\alpha_1 + \alpha_1\alpha_2\alpha_3 - 1 - \alpha_1\alpha_2 - \alpha_1^2\alpha_2\alpha_3)}{1 - \alpha_2} \equiv \beta_m. \tag{15}$$

Note that,

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

provided $\alpha_i > 0,\ i = 1,2,3$. In this case it is always possible to select $\beta_i,\ i = 1,2,3,$ so that $\beta_2 = \frac{1}{\alpha_1},\quad \beta_3 = \frac{1}{\alpha_2},$ and $\max(1,\beta_m) < \beta_1 < \beta_M,$ so that (2) holds.

If $\beta_1 = \alpha_1\alpha_2(2 - \alpha_1\alpha_2\alpha_3) \equiv \beta_{crit}$,
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, if we select $0 < \alpha_i < 1,\ i = 1, 2, 3,\ \ \frac{1}{\alpha_1\alpha_2} - \alpha_1\alpha_2\alpha_3 < 2$, and $\max(1, \beta_m) < \beta_1 < \beta_{crit}$, both the May-Leonard model (1)-(2) and the chemostat model (4), have a globally attracting equilibrium in the interior of the positive cone with a repelling heteroclinic cycle on the boundary of the positive cone.

Example

Taking

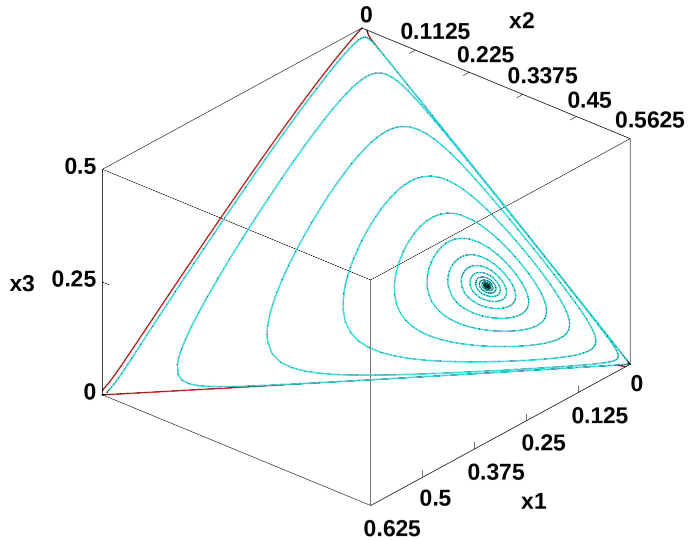
$$\alpha_1 = \frac{9}{10},\ \alpha_2 = \frac{8}{9},\ \alpha_3 = \frac{5}{12},\ \beta_1 = \frac{6}{5},\ \beta_2 = \frac{10}{9},\ \beta_3 = \frac{9}{8},$$

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

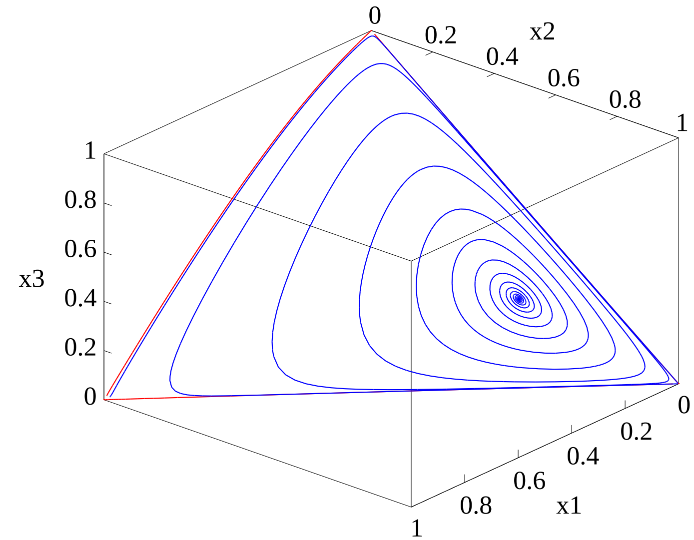
corresponds to taking

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

Both models have a repelling heteroclinic cycle on the boundary and a globally attracting equilibrium in the interior of the positive cone.



(a)



(b)

Figure 1: (a) Foodweb in a chemostat; (b) Lotka-Volterra competition.