MATH581 - Project

Ming Hei Wong, Calvin

December 2022

Abstract

The paper that I am referencing is "Bistability in a system of two species interacting through mutualism as well as competition: Chemostat vs. Lotka-Volterra equations"[1]. This paper discussed the situation that in a chemostat, two species are having abiotic competition towards a substrate S_0 but at the same time, they produce nutrients that the opponent wants and can grow by intaking it. Analysis of this model is performed numerically. Also, this chemostat model is rewritten into a two-equation generalized Lotka-Volterra system under certain assumptions. Researchers have shown that under most circumstances, this simplified model has highly similar quantitative and qualitative behaviour, with the benefit that the two-equation Lotka Volterra is easier to analyse and the dynamics can be shown more intuitively on a 2D phase plane. Bifurcation from the parameters for both models are discussed numerically. In this work, I will analyse the given model to obtain stability results from Jacobian analysis instead of numerical simulations. Also, numerical simulations will be performed to see the long-term behaviour of the species via discretized schemes. Furthermore, the aforementioned numerical simulation will be repeated by randomly assigning the parameters and the prevalence of different kinds of monostability and bistability can be statistically investigated. Lastly, I will compare the two models numerically to see the similarity and difference both quantitatively and qualitatively. Unless otherwise specified, all the derivations, coding and simulations from section 2 to section 5 are my original work.

[1]The original paper can be found in `https://www.researchgate.net/publication/325609466_Bistability_in_a_system_of_two_species_interacting_through_mutualism_as_well_as_competition_Chemostat_vs_Lotka-Volterra_equations`.

Contents

An AI-generated photo of "Two species having competition and helping each other at the same time"

1 Summary of the Paper

Vet, Buyl, Faust, Danckaert, Gonze and Gelens have started the discussion from the original chemostat model for abiotic resource competition by Kot.

Abiotic Resource Competition Chemostat Model

$$\frac{dS}{dT} = D(S_i - S) - \frac{1}{Y_1}\frac{m_1 S N_1}{K_1 + S} - \frac{1}{Y_2}\frac{m_2 S N_2}{K_2 + S}, \tag{1a}$$

$$\frac{dN_1}{dT} = \frac{m_1 S N_1}{K_1 + S} - D N_1, \tag{1b}$$

$$\frac{dN_2}{dT} = \frac{m_2 S N_2}{K_2 + S} - D N_2, \tag{1c}$$

Although this model has already captured a lot of characteristics of abiotic resource competition, researchers are not satisfied. In a lot of microbial communities, both competition and mutualism mechanisms are observed and exist at the same time, but this classical model only models competitive behaviour towards the common nutrient/substrate. Human gut microbiota, or plants release carbon that allows the development of microbes in the rizosphere are great examples of this kind of environment. If the interaction of mutualism can be introduced to the classical model, this will bring additional realism. Mutualism can exist in the form of cross-feeding, that is, one species will produce carbon source that other species can take as nutrient. In this paper, only cross-feeding is introduced and studied.

Besides additional realism, this newly introduced model actually amend another even larger disadvantage of the original Abiotic Resource Competition Chemostat Model. The old model only consider "pairwise" interactions. In simple wording, "terms are added to the differential equations to represent interactions between two variables" (also called additivity assumption). The authors have quoted a recent researches, showing that although the community dynamics can be predicted to a certain extent from pairwise interaction, the additivity assumption and the neglect of the interaction mechanism are serious limitations of the Classic Lokta-Volterra competition model, and depending on the interaction mechanism, the model may fail[2]. In addition, researchers also quoted experimental evidence where pairwise interaction strengths do not add up in co-culture, while also theoretically the importance of higher order interactions, where there are multiple mediators, has been shown[3]. In view of this, simple Lokta-Volterra type model probably cannot do a good job on modelling situation where competition and mutualism take place at the same time.

1.1 First model: Competition-Mutualism Chemostat Model

From the above discussions, authors do not start with a Lokta-Volterra type model, but first proceed with a traditional chemostat model, but with mutualism considered. The model is as follows.

Competition-Mutualism Chemostat Model

$$\frac{dX_1}{dt} = (f_1(S_0, S_2) - \Phi)\, X_1, \tag{2a}$$

$$\frac{dX_2}{dt} = (f_2(S_0, S_1) - \Phi)\, X_2, \tag{2b}$$

$$\frac{dS_0}{dt} = \Phi\left(\tilde{S_0} - S_0\right) - \nu_{01} f_1 X_1 - \nu_{02} f_2 X_2 \tag{2c}$$

$$\frac{dS_1}{dt} = \Phi\left(\tilde{S_1} - S_1\right) + \nu_{11} f_1 X_1 - \nu_{12} f_2 X_2 \tag{2d}$$

$$\frac{dS_2}{dt} = \Phi\left(\tilde{S_2} - S_2\right) - \nu_{21} f_1 X_1 + \nu_{22} f_2 X_2 \tag{2e}$$

$$f_1\left(S_0, S_2\right) = \mu_1 \frac{S_0}{K_{10} + S_0} \frac{S_2}{K_{12} + S_2} \tag{2f}$$

$$f_2\left(S_0, S_1\right) = \mu_2 \frac{S_0}{K_{20} + S_0} \frac{S_1}{K_{21} + S_1} \tag{2g}$$

The meaning of the variables and the parameters and the units of them are as follows.

Quantity	**Symbol**	**Dimensions**
Bacterial Population Density	X	$\frac{\text{number}}{\text{volume}}$
Nutrient Concentration	S	$\frac{\text{mass}}{\text{volume}}$
Inflow of a nutrient	$\tilde{S}$	$\frac{\text{mass}}{\text{volume}}$
Growth Rate of the Bacteria	f	$\frac{1}{\text{time}}$
Flow Rate	Φ	$\frac{1}{\text{time}}$
Production/Consumption Constant	ν	$\frac{\text{mass}}{\text{number}}$
Maximum Growth Rate	μ	$\frac{1}{\text{time}}$
Half-Saturation Constant	K	$\frac{\text{mass}}{\text{volume}}$

This system of differential equations is trying to model the following: two bacteria with population density X_1 and X_2 respectively are in a chemostat with a baseline substrate S_0, which both bacteria can consume. During this process, bacteria 1 will release substance S_1, that bacteria 2 can take it as nutrient. Similarly, bacteria 2 will release substance S_2, that bacteria 1 can take it as nutrient.

The existence of the constant inflow of $\tilde{S_1}$ and $\tilde{S_2}$ may seem odd. But, authors state that a high inflow of S_0, combining with a low inflow of the nutrients S_1, S_2 strengthens the positive feedback between X_1, X_2.

We can see the following diagram for a more intuitive illustration.

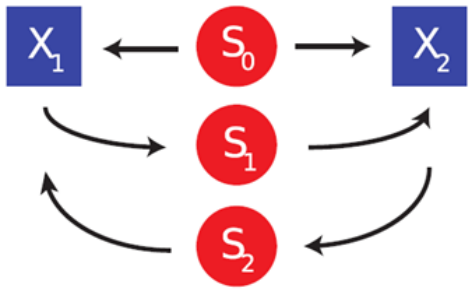

Figure 1: Dynamics of the proposed chemostat model [1]

From equation (2f) and (2g), we can see that the growth function for each bacteria is essentially the product of the Holling type II functional response of the two suitable nutrients respectively. Also, note $\nu_{01}, \nu_{02}, \nu_{12}, \nu_{21}$ are called consumption constants and ν_{11}, ν_{22} are called production constants. All of these 6 parameters are positive.

The authors of this paper have performed a big number of numerical simulations. This model will have the following 4 possible results, depending on the parameters and the initial conditions.

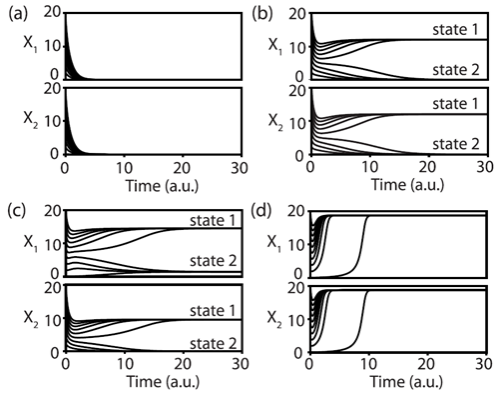

Figure 2: Different stability results for the first model [1]

In particular, we can observe the existence of monostability and bistability, depending on the set of parameters and the initial population densities. The topics that I will investigate on this model will be as follows.

1. Investigating the existence stability of some equilibrium points.
2. Plotting the solution curves for various parameter sets and show bistability.
3. In terms of probability, how likely will mutual extinction, exclusions, coexistence and bistability happen?

1.2 Second Model: Extended Lotka-Volterra Model

Under certain justifiable assumptions, the authors have derived an extended Lotka-Volterra Model that can estimate the behaviour of the Competition-Mutualism Chemostat Model, with the benefit of having only 2 variables and equations.

There are three main steps to derive the model.

1. Elimination of the nutrient variables which is possible since linear relations between S and X exist for $t >> \frac{1}{\Phi}$. However, the transient dynamics of the system is no longer accurately represented.
2. Simplification of the growth rates using a Taylor approximation when $K >> S$.
3. Elimination of higher order terms, so that it is easier to analyse the behaviour if we only want to investigate local behaviour.

After some heavy derivations, the following Extended Lotka-Volterra Model is proposed by the author.

Extended Lotka-Volterra Model

$$\frac{dX_1}{dt} = \left[r_1\left(a_1 - b_{11}X_1 + b_{12}X_2 - c_1X_2^2\right) - d\right]X_1, \tag{3a}$$

$$\frac{dX_2}{dt} = \left[r_2\left(a_2 - b_{22}X_2 + b_{21}X_1 - c_2X_1^2\right) - d\right]X_2. \tag{3b}$$

$$d = \Phi \tag{3c}$$

$$r_1 = \frac{\mu_1}{K_{01}K_{21}}, r_2 = \frac{\mu_2}{K_{02}K_{12}} \tag{3d}$$

$$a_1 = \tilde{S_0}\tilde{S_2}, a_2 = \tilde{S_0}\tilde{S_1} \tag{3e}$$

$$b_{11} = -\nu_{21}\tilde{S_0} - \nu_{01}\tilde{S_2}, b_{22} = -\nu_{12}\tilde{S_0} - \nu_{02}\tilde{S_1} \tag{3f}$$

$$b_{12} = +\nu_{22}\tilde{S_0} + \nu_{02}\tilde{S_2}, b_{21} = +\nu_{11}\tilde{S_0} + \nu_{01}\tilde{S_1} \tag{3g}$$

$$c_1 = -\nu_{22}\nu_{02}, c_2 = -\nu_{11}\nu_{01} \tag{3h}$$

From equation (3a) and (3b), we can see that the intersections of the two parabolas will be the equilibrium points. Solving the intersection of two parabolas with different orientation (since one of the are with variable X_1 and the other one is with variable X_2 on the $X_1 - X_2$ plane) will be very tedious and we have to split the discussion by considering having different number of intersection points. The authors have investigated this model by fixing the parameters, and find the equilibrium points via iterative methods and analyse the stability by phase diagram. We can see the following diagram.

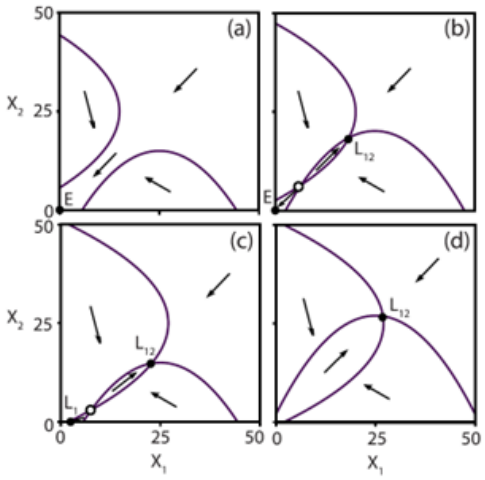

Figure 3: Different stability results for the second model [1]

The topics that I will investigate on this model will be as follows.

1. Plotting the solution curves for various parameter sets, and compare the quantitative and qualitative of the solution obtained from the cheomstat model.

2 Investigation on the First Model

2.1 Non-dimensionalization of the Model

To make the analysis easier, I first non-dimensionalize the system.
Define $s_0 = \frac{S_0}{\tilde{S_0}}, s_1 = \frac{S_1}{\tilde{S_1}}, s_2 = \frac{S_2}{\tilde{S_2}}$, and $x_1 = \frac{v_{01}X_1}{\tilde{S_0}}, x_2 = \frac{v_{02}X_2}{\tilde{S_0}}$, we can rewrite the chemostat model as follows.

$$\frac{dx_1}{dt} = (f_1(S_0, S_2) - \Phi)\, x_1, \tag{4a}$$

$$\frac{dx_2}{dt} = (f_2(S_0, S_1) - \Phi)\, x_2, \tag{4b}$$

$$\frac{ds_0}{dt} = \Phi\,(1 - s_0) - f_1 x_1 - f_2 x_2 \tag{4c}$$

$$\frac{ds_1}{dt} = \Phi\,(1 - s_1) + \alpha_{11} f_1 x_1 - \alpha_{12} f_2 x_2 \tag{4d}$$

$$\frac{ds_2}{dt} = \Phi\,(1 - s_2) - \alpha_{21} f_1 x_1 + \alpha_{22} f_2 x_2 \tag{4e}$$

$$f_1\,(s_0, s_2) = \mu_1 \frac{s_0\tilde{S_0}}{K_{10} + s_0\tilde{S_0}} \frac{s_2\tilde{S_2}}{K_{12} + s_2\tilde{S_2}} \tag{4f}$$

$$f_2\left(s_0, s_1\right) = \mu_2 \frac{s_0 \tilde{S_0}}{K_{20} + s_0 \tilde{S_0}} \frac{s_1 \tilde{S_1}}{K_{21} + s_1 \tilde{S_1}} \tag{4g}$$

where $\alpha_{11} = \dfrac{\tilde{S_0}\nu_{11}}{\tilde{S_1}\nu_{01}}, \alpha_{12} = \dfrac{\tilde{S_0}\nu_{12}}{\tilde{S_1}\nu_{02}}, \alpha_{21} = \dfrac{\tilde{S_0}\nu_{21}}{\tilde{S_2}\nu_{01}}, \alpha_{22} = \dfrac{\tilde{S_0}\nu_{22}}{\tilde{S_2}\nu_{02}}$.

Lastly, define $T = \Phi t$, we have the following non-dimensionalized system.

Non-dimensionalized Competition-Mutualism Chemostat Model

$$\frac{dx_1}{dT} = \left(g_1(s_0, s_2) - 1\right) x_1, \tag{5a}$$

$$\frac{dx_2}{dT} = \left(g_2(s_0, s_1) - 1\right) x_2, \tag{5b}$$

$$\frac{ds_0}{dT} = 1 - s_0 - g_1 x_1 - g_2 x_2 \tag{5c}$$

$$\frac{ds_1}{dT} = 1 - s_1 + \alpha_{11} g_1 x_1 - \alpha_{12} g_2 x_2 \tag{5d}$$

$$\frac{ds_2}{dT} = 1 - s_2 - \alpha_{21} g_1 x_1 + \alpha_{22} g_2 x_2 \tag{5e}$$

$$g_1\left(s_0, s_2\right) = A_1 \frac{s_0 \tilde{S_0}}{K_{10} + s_0 \tilde{S_0}} \frac{s_2 \tilde{S_2}}{K_{12} + s_2 \tilde{S_2}} \tag{5f}$$

$$g_2\left(s_0, s_1\right) = A_2 \frac{s_0 \tilde{S_0}}{K_{20} + s_0 \tilde{S_0}} \frac{s_1 \tilde{S_1}}{K_{21} + s_1 \tilde{S_1}} \tag{5g}$$

$$A_1 = \frac{\mu_1}{\Phi}, A_2 = \frac{\mu_2}{\Phi} \tag{5h}$$

2.2 Jacobian Matrix

We first find the Jacobian matrix J of the chemostat system. By the formula $[J]_{ij} = \dfrac{\partial F_i}{\partial x_j}$, the Jacobian matrix is as follows.

$$J = \begin{bmatrix} g_1 - 1 & 0 & x_1 \cdot \dfrac{\partial g_1}{\partial s_0} & 0 & x_1 \cdot \dfrac{\partial g_1}{\partial s_2} \\ 0 & g_2 - 1 & x_2 \cdot \dfrac{\partial g_2}{\partial s_0} & x_2 \cdot \dfrac{\partial g_2}{\partial s_1} & 0 \\ -g_1 & -g_2 & -1 - x_1 \cdot \dfrac{\partial g_1}{\partial s_0} - x_2 \cdot \dfrac{\partial g_2}{\partial s_0} & -x_2 \cdot \dfrac{\partial g_2}{\partial s_1} & -x_1 \cdot \dfrac{\partial g_1}{\partial s_2} \\ \alpha_{11} g_1 & -\alpha_{12} g_2 & \alpha_{11} x_1 \cdot \dfrac{\partial g_1}{\partial s_0} - \alpha_{12} x_2 \cdot \dfrac{\partial g_2}{\partial s_0} & -1 - \alpha_{12} x_2 \cdot \dfrac{\partial g_2}{\partial s_1} & \alpha_{11} x_1 \cdot \dfrac{\partial g_1}{\partial s_2} \\ -\alpha_{21} g_1 & \alpha_{22} g_2 & -\alpha_{21} x_1 \cdot \dfrac{\partial g_1}{\partial s_0} + \alpha_{22} x_2 \cdot \dfrac{\partial g_2}{\partial s_0} & \alpha_{22} x_2 \cdot \dfrac{\partial g_2}{\partial s_1} & -1 - \alpha_{21} x_1 \cdot \dfrac{\partial g_1}{\partial s_2} \end{bmatrix} \tag{6}$$

2.3 Stability at Mutual Extinction E_0

Now, we want to find the eigenvalue of the Jacobian matrix at the mutual extinction equilibrium $E_0 = (x_1, x_2, s_0, s_1, s_2) = (0, 0, 1, 1, 1)$.

The Jacobian matrix at E_0 is as follows.

$$J\Big|_{E_0} = \begin{bmatrix} g_1(1,1) - 1 & 0 & 0 & 0 & 0 \\ 0 & g_2(1,1) - 1 & 0 & 0 & 0 \\ -g_1(1,1) & -g_2(1,1) & -1 & 0 & 0 \\ \alpha_{11} g_1(1,1) & -\alpha_{12} g_2(1,1) & 0 & -1 & 0 \\ -\alpha_{21} g_1(1,1) & \alpha_{22} g_2(1,1) & 0 & 0 & -1 \end{bmatrix} \tag{7}$$

Note that $J\Big|_{E_0}$ is a lower triangular matrix. So, we have $\lambda_{3,4,5} = -1$. If we want the mutual extinction to occur, that is, E_0 is a stable node, then we require $g_1(1,1) < 1$ and $g_2(1,1) < 1$.

Now, note that $g_1(1,1) = A_1 \dfrac{\tilde{S_0}}{K_{10} + \tilde{S_0}} \dfrac{\tilde{S_2}}{K_{12} + \tilde{S_2}}$, if we have $A_1 = \dfrac{\mu_1}{\Phi} < 1$, then $g_1(1,1) < 1$ since both fractions must be smaller than 1. Similarly, if we set $A_2 = \dfrac{\mu_2}{\Phi} < 1$, then $g_2(1,1) < 1$. So, if $\mu_1, \mu_2 < \Phi$, the two bacteria will reach extinction together. In the context of the experiment, if the maximal growth rate of each bacteria is so slow (in particular, slower than the dilution rate), the effect of competition or mutualism does affect the long term result, and they just got flushed away from dilution. Both bacteria will extinct in such situation. In general, we require $A_1 \dfrac{\tilde{S_0}}{K_{10} + \tilde{S_0}} \dfrac{\tilde{S_2}}{K_{12} + \tilde{S_2}} < 1$ and $A_2 \dfrac{\tilde{S_0}}{K_{20} + \tilde{S_0}} \dfrac{\tilde{S_1}}{K_{21} + \tilde{S_1}} < 1$ as the sufficient and necessary condition for the mutual extinction to occur. Lastly, we can observe that these conditions are actually equivalent to $f_1(\tilde{S_0}, \tilde{S_2}) < \Phi$ and $f_2(\tilde{S_0}, \tilde{S_1}) < \Phi$, which means that given the fixed inflow of substrate with constant concentration $\tilde{S_0}, \tilde{S_1}, \tilde{S_2}$, the growth rate of the bacteria is less than the dilution rate. In view of this, we may want to make sure the concentration of the fixed inflow of substrate should be set to a high enough of level.

2.4 Condition of the Existence of L_1, and Uniqueness Result

Now, we are interested in the case that bacteria 1 excludes bacteria 2. We call this equilibrium point by $L_1 = (x_1^*, 0, s_0^*, s_1^*, s_2^*)$, that means "bacteria 1 lives only".

So, we assume $\lim\limits_{T \to \infty} x_1(T) = x_1^* > 0, \lim\limits_{T \to \infty} x_2(T) = 0$. Now, we add equation (5a) and (5c), and this yields

$$\frac{dx_1}{dT} + \frac{ds_0}{dT} = (g_1 - 1)x_1 + 1 - s_0 - g_1 x_1 - g_2 x_2 = 1 - (x_1 + s_0) - g_2 x_2 \tag{8}$$

Note that $g_2(s_0, s_2)$ is a bounded function. So, taking $T \to \infty$ and together with $\lim_{T\to\infty} x_2(T) = 0$ and squeeze theorem, we have

$$\lim_{T\to\infty} \left(\frac{dx_1}{dT} + \frac{ds_0}{dT} \right) = 0 = 1 - x_1^* - s_0^* - 0 \tag{9}$$

This yields $x_1^* + s_0^* = 1$. The derivative on left-hand-side converges to 0 due to the equilibrium assumption. Now, under the assumption of the chemostat being well-stirred and the experiment has continued for a sufficient long time, we can further assume a stronger condition that $x_1(T) + s_0(T) = 1$. Now, we want to solve for the equilibrium points $(x_1, x_2, s_0, s_1, s_2) = (x_1^*, 0, s_0^*, s_1^*, s_2^*)$ by setting the system 5 with all the derivatives as zero, and also substitute the auxiliary equation $x_1^* + s_0^* = 1$ into the model.

$$0 = (g_1(s_0^*, s_2^*) - 1)\, x_1^*, \tag{10a}$$

$$0 = 1 - s_0^* - g_1 x_1^* \tag{10b}$$

$$0 = 1 - s_1^* + \alpha_{11} g_1 x_1^* \tag{10c}$$

$$0 = 1 - s_2^* - \alpha_{21} g_1 x_1^* \tag{10d}$$

So, we have $g_1(s_0^*, s_2^*) = 1$ from (10a). That is,

$$g_1\left(s_0^*, s_2^*\right) = A_1 \frac{s_0^*}{\tilde{K_{10}} + s_0^*} \frac{s_2^*}{\tilde{K_{12}} + s_2^*} = 1 \tag{11}$$

where $\tilde{K_{10}} = \dfrac{K_{10}}{\tilde{S_0}}, \tilde{K_{12}} = \dfrac{K_{12}}{\tilde{S_0}}$.

Note $s_2^* = 1 - \alpha_{21} x_1^*$. Plugging this back into equation (11), we have

$$A_1 \frac{1 - x_1^*}{\tilde{K_{10}} + 1 - x_1^*} \frac{1 - \alpha_{21} x_1^*}{\tilde{K_{12}} + 1 - \alpha_{21} x_1^*} = 1 \tag{12}$$

which can be further simplified as the following quadratic equation.

$$p(x_1^*) = (A_1\alpha_{21} - 1)(x_1^*)^2 - [A_1(\alpha_{21} + 1) - \tilde{K_{10}} - \tilde{K_{12}} - 2]x_1^* + [A_1 - (\tilde{K_{10}} + 1)(\tilde{K_{12}} + 1)] = 0 \tag{13}$$

Here, we assume $\Delta \geq 0$ to guarantee the existence of real root(s). This is a horrible quadratic equation. However, we can still perform some analysis on it.

First of all, note that $A_1\alpha_{21} = \frac{\mu_1}{\Phi} \cdot \frac{\tilde{S}_0\nu_{21}}{\tilde{S}_2\nu_{01}}$. From the discussions on the last subsection, it is very reasonable to assume $A_1\alpha_{21} > 1$ so that dilution will not kill all of the species in the chemostat. Also, we have assumed $\tilde{S}_0 >> \tilde{S}_2$ from the biological standpoint. So from now on, $y = p(x_1^*)$ is a parabola opening upward.

Secondly, from the auxiliary condition $x_1^* + s_0^* = 1$ and the non-negativity of x_1^*, s_0^*, we know $x_1^* \in (0, 1)$. Thus, we need a set of conditions to check if we are given a quadratic equation having two distinct real roots or one double real root, when will both roots lie in $(0, 1)$? Fortunately, we can have some reference of the Jury condition, and have the Calvin Condition as follows.

Theorem 1 (Calvin Condition)

Consider the equation $P(x) = x^2 + bx + c = 0$. Then, the graph of $y = P(x)$ is an opening upward parabola. Furthermore suppose the discriminant is non-negative with roots α, β (they may not be distinct). Then, $\alpha, \beta \in (0, 1)$ if and only if the following conditions are all satisfied.

$$P(0) > 0 \tag{14a}$$

$$P(1) > 0 \tag{14b}$$

$$0 < \frac{sum\ of\ roots}{2} = -\frac{b}{2} < 1 \tag{14c}$$

$$0 < product\ of\ roots = c < 1 \tag{14d}$$

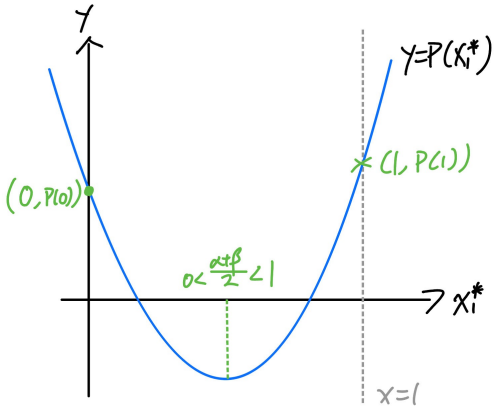

Figure 4: Geometrical understanding of the Calvin condition

Proof. ($\Rightarrow$) We first prove if the set of conditions are satisfied, then $\alpha, \beta \in (0, 1)$. The proof is essentially a case-splitting discussion.

1. From (14a), since $P(0) \neq 0$, we have $\alpha, \beta \neq 0$.
2. If both roots are negative, then $\alpha + \beta < 0$ which is a contradiction to (14c)
3. If the two roots are of different sign, then $\alpha\beta < 0$ which violates (14d).
4. So, from the above 2 results, both α, β must be positive.
5. From (14b), since $P(1) \neq 0$, we have $\alpha, \beta \neq 1$.
6. If both $\alpha, \beta > 1$, we will have $\dfrac{\alpha + \beta}{2} > 1$, and this is a violation to (14c).
7. If $\alpha \in (0, 1)$ and $\beta > 1$, then note $\alpha < 1 < \beta$ yields $P(1) < 0$. This is due to the graph being an opening upward parabola (one may also prove this algebraically, and this is left as an exercise for readers). This is a violation to (14b).
8. After rejecting all the above cases, the only possibility is that $\alpha, \beta \in (0, 1)$. We are done.

($\Leftarrow$) Now, we show if $\alpha, \beta \in (0, 1)$, then conditions (14a) to (14d) are satisfied. For easier communication, we first write $P(x) = (x - \alpha)(x - \beta)$.

1. Note $P(0) = (0 - \alpha)(0 - \beta) = \alpha\beta > 0$ since both α, β are positive.
2. Note $\alpha, \beta < 1$, so $1 - \alpha > 0$ and $1 - \beta > 0$. This yields $P(1) > 0$.
3. Obviously, $0 < \alpha, \beta < 1$ implies $0 < \dfrac{\alpha + \beta}{2} < 1$.
4. Trivially, $0 < \alpha, \beta < 1$ implies $0 < \alpha\beta < 1$.

Again, we are done. □

Now, we can actually show that in case of (13) having two real roots, a least one of them is not lying on $(0, 1)$, and furthermore we can show that the rejected solution is greater than 1. This shows that the equilibrium we are looking for is actually unique if exists.

By Calvin condition, if we need both roots for (13) to lie in $(0, 1)$, we need

$$A_1 > (\tilde{K_{10}} + 1)(\tilde{K_{12}} + 1) \tag{15a}$$

$$-\tilde{K_{10}}\tilde{K_{12}} > 0 \tag{15b}$$

$$0 < A_1(\alpha_{21} + 1) - \tilde{K_{10}} - \tilde{K_{12}} - 2 < 2(A_1\alpha_{21} - 1) \tag{15c}$$

$$0 < A_1 - (\tilde{K_{10}} + 1)(\tilde{K_{12}} + 1) < A_1\alpha_{21} - 1 \tag{15d}$$

Clearly, (15b) is impossible to be satisfied, since $\tilde{K_{10}}$ and $\tilde{K_{12}}$ are both positive parameters. This shows that we cannot have two distinct values of stable concentration of bacteria 1 when bacteria 2 dies eventually. In particular, $p(0) > 0$ and $p(1) < 0$ implies there is a root between 0 and 1, and $p(1) < 0$ for a opening up parabola implies that the other root is on the right hand side of 1.

Now, focusing on (15a). Recall $A_1 = \frac{\mu_1}{\Phi}$. So, if we want x_1^* to not be extinct, we need the maximal growth rate of bacteria 1 to satisfy $\mu_1 > \Phi(\tilde{K_{10}} + 1)(\tilde{K_{12}} + 1)$. Again, this is a very good insight when we try to perform numerical simulation on the model, or performing the experiment in real life.

In conclusion, the authors of the paper have shown that if both species do not go to extinction at the same time, bistability happens so that the populations of the two species may converge to different equilibrium depending on the initial conditions. Here, I proved that if one of the bacteria (bacteria 2 in this subsection) is going to extinct, there will only be one unique equilibrium value for x_1^* to approach. In fact, note that E_0 is unstable in this case, so this unique equilibrium point can only be stable.

2.5 Numerical Simulation

Now, we turn our focus on solving this model numerically. We will perform simulation on the original model (that is, not the non-dimensionalized one). In my work, I applied the second-order Taylor's Method for the system so that it is more accurate and sensitive than the first-order Euler's method. That is, we have using the following scheme.

Theorem 2 (Second-Order Taylor's Method for solving Competition-Mutualism Chemostat Model)
Let $X_1(t), X_2(t), S_0(t), S_1(t), S_2(t)$ be functions of t. Assume all of them are twice differentiable on $\mathbb{R}$. Define $F_1 = \frac{dX_1}{dt}, F_2 = \frac{dX_2}{dt}, F_3 = \frac{dS_0}{dt}, F_4 = \frac{dS_1}{dt}, F_5 = \frac{dS_2}{dt}$. Suppose $(x_{1n}), (x_{2n}), (s_{0n}), (s_{1n}), (s_{2n})$ are sequences of numerical approximation to the exact analytic solution to the function $X_1(t), X_2(t), S_0(t), S_1(t), S_2(t)$ respectively. Then, we have

$$x_{1(n+1)} = x_{1n} + \left[h \cdot F_1 + \frac{h^2}{2} \cdot \frac{dF_1}{dt}\right]\Big|_{(x_{1n}),(x_{2n}),(s_{0n}),(s_{1n}),(s_{2n})} \tag{16a}$$

$$x_{2(n+1)} = x_{2n} + \left[h \cdot F_2 + \frac{h^2}{2} \cdot \frac{dF_2}{dt}\right]\Big|_{(x_{1n}),(x_{2n}),(s_{0n}),(s_{1n}),(s_{2n})} \tag{16b}$$

$$s_{0(n+1)} = s_{0n} + \left[h \cdot F_3 + \frac{h^2}{2} \cdot \frac{dF_3}{dt}\right]\Big|_{(x_{1n}),(x_{2n}),(s_{0n}),(s_{1n}),(s_{2n})} \tag{16c}$$

$$s_{1(n+1)} = s_{1n} + \left[h \cdot F_4 + \frac{h^2}{2} \cdot \frac{dF_4}{dt}\right]\Big|_{(x_{1n}),(x_{2n}),(s_{0n}),(s_{1n}),(s_{2n})} \tag{16d}$$

$$s_{2(n+1)} = s_{2n} + \left[h \cdot F_5 + \frac{h^2}{2} \cdot \frac{dF_5}{dt}\right]\Big|_{(x_{1n}),(x_{2n}),(s_{0n}),(s_{1n}),(s_{2n})} \tag{16e}$$

for $n = 1, ..., T$ where $h \in \mathbb{R}^+$ is a small time step parameter.

After testing, the solutions obtained from this discretized scheme I coded out are essentially the same as solved by the MATLAB built in ODE45 solver. The non-zero equilibrium values agree to 1 decimal place for my sovler and ODE45 solver.

In all of the following simulations, we set $T = 10000$ and $h = 0.005$. Also, we will use the same set of parameters and initial value as follows.

$$\phi = 2 \tag{17a}$$

$$\tilde{\mathbf{S}} = \begin{bmatrix} \tilde{S_0} & \tilde{S_1} & \tilde{S_2} \end{bmatrix} = \begin{bmatrix} 50 & 1 & 1 \end{bmatrix} \tag{17b}$$

$$\mathbf{K} = \begin{bmatrix} K_{10} & K_{12} \\ K_{20} & K_{22} \end{bmatrix} = \begin{bmatrix} 200 & 200 \\ 200 & 200 \end{bmatrix} \tag{17c}$$

$$\mathbf{v} = \begin{bmatrix} \nu_{01} & \nu_{02} \\ \nu_{11} & \nu_{12} \\ \nu_{21} & \nu_{22} \end{bmatrix} = \begin{bmatrix} 1 & 1 \\ 0.2 & 0.1 \\ 0.1 & 0.2 \end{bmatrix} \tag{17d}$$

$$\mathbf{S}_{\text{initial}} = \begin{bmatrix} 50 & 1 & 1 \end{bmatrix} \tag{17e}$$

Since we want to demonstrate monostability/bistability results at different maximum growth rate and initial population density, μ_1, μ_2 and the initial value of X_1, X_2 will be specify in the below discussion case by case.

The code for the simulation is included in section 5.

2.5.1 Numerical Simulation - E_0 Situation

Recall that the sufficient for mutual extinction are $A_1 \dfrac{\tilde{S_0}}{K_{10} + \tilde{S_0}} \dfrac{\tilde{S_2}}{K_{12} + \tilde{S_2}} < 1$ and $A_2 \dfrac{\tilde{S_0}}{K_{20} + \tilde{S_0}} \dfrac{\tilde{S_1}}{K_{21} + \tilde{S_1}} < 1$.

Firstly, we set $\begin{bmatrix} \mu_1 & \mu_2 & X_{1_{\text{initial}}} & X_{2_{\text{initial}}} \end{bmatrix} = \begin{bmatrix} 1700 & 1600 & 5 & 4 \end{bmatrix}$ Then, we have

$$A_1 \frac{\tilde{S_0}}{K_{10} + \tilde{S_0}} \frac{\tilde{S_2}}{K_{12} + \tilde{S_2}} \approx 0.846 < 1, A_2 \frac{\tilde{S_0}}{K_{20} + \tilde{S_0}} \frac{\tilde{S_1}}{K_{21} + \tilde{S_1}} \approx 0.796 < 1.$$

After the simulation, we have $x_1(T) \approx 1.672 \cdot 10^{-5}$ and $x_2(T) \approx 5.786 \cdot 10^{-7}$. These two numbers are sufficiently close to zero that we can confidently conclude both bacteria extinct eventually. See figure 5.

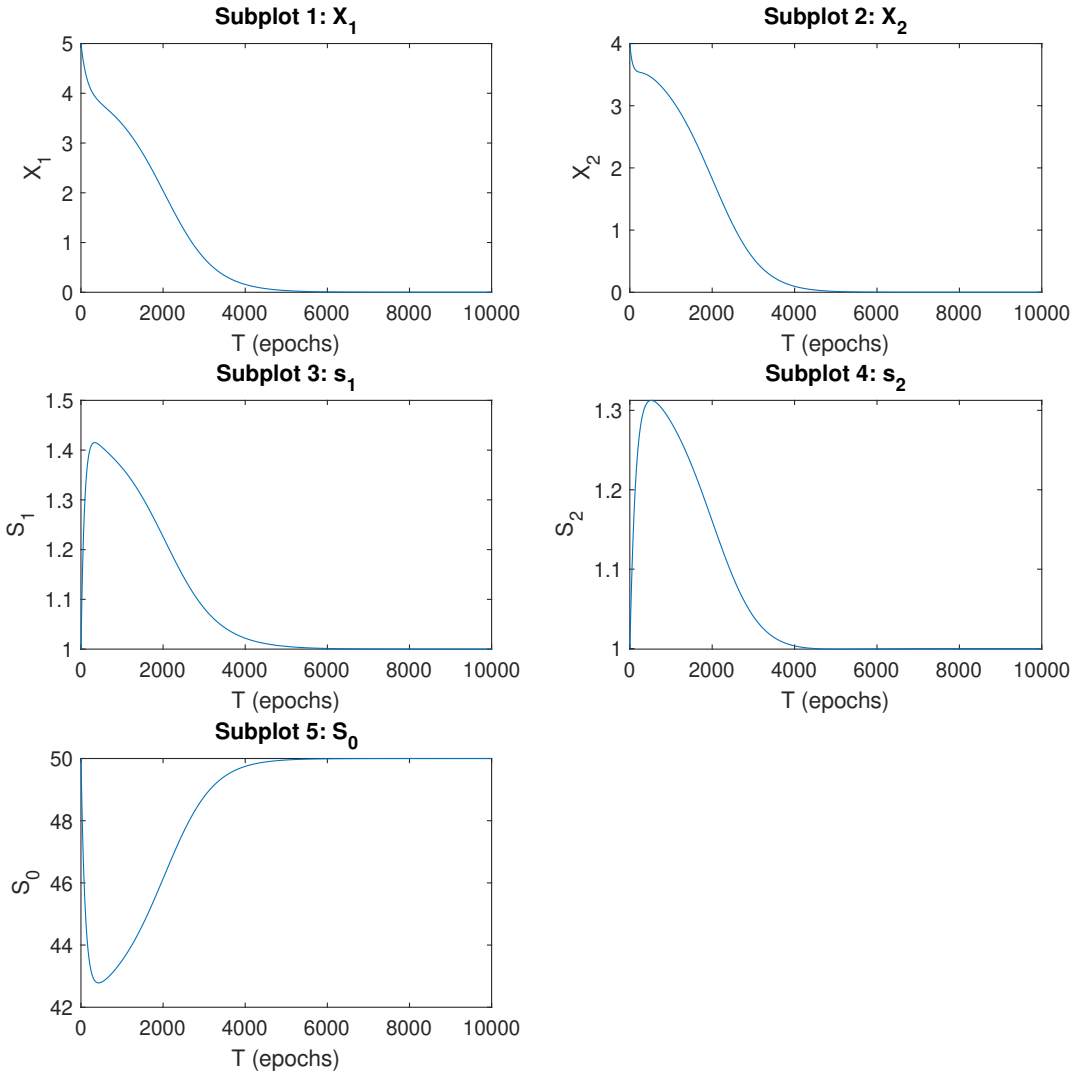

Figure 5: Under low maximum growth rate and low enough initial populations, both bacteria extinct. $\begin{bmatrix}\mu_1 & \mu_2 & X_{1_{\text{initial}}} & X_{2_{\text{initial}}}\end{bmatrix} = \begin{bmatrix}1700 & 1600 & 5 & 4\end{bmatrix}$

We can also see that the concentration level of the substrates are exactly equal to the inflow concentration respectively. Since the populations of both bacteria are going to extinction, so nothing is consuming the substrates. Hence, this is also a expected result.

Now, if we keep μ_1, μ_2 unchanged, but increase the initial value to $\begin{bmatrix}X_{1_{\text{initial}}} & X_{2_{\text{initial}}}\end{bmatrix} = \begin{bmatrix}6 & 5\end{bmatrix}$, both bacteria will survive at an equilibrium level. See figure 6.

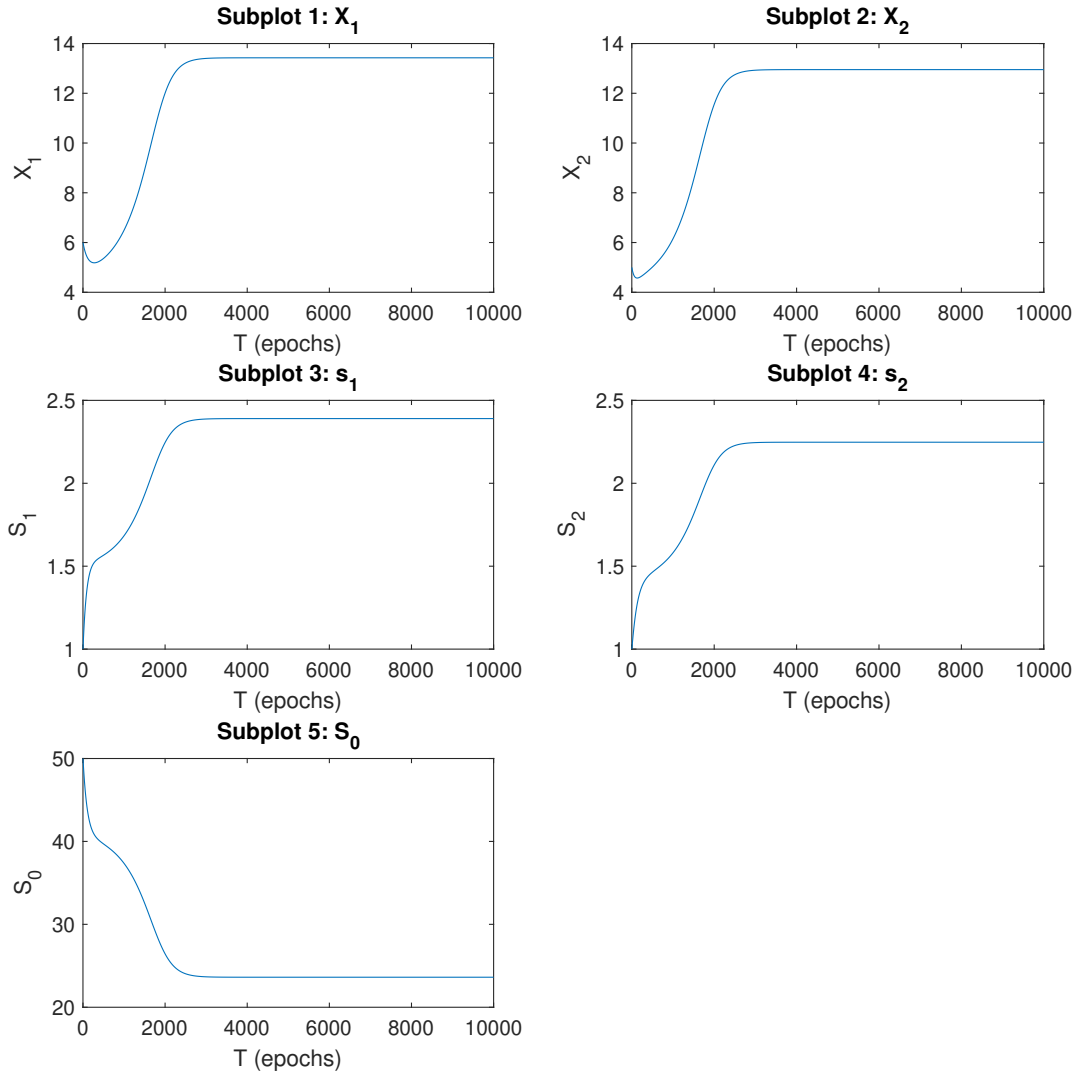

Figure 6: Under low maximum growth rate and higher initial populations, both bacteria survive.
$\begin{bmatrix}\mu_1 & \mu_2 & X_{1_{\text{initial}}} & X_{2_{\text{initial}}}\end{bmatrix} = \begin{bmatrix}1700 & 1600 & 6 & 5\end{bmatrix}$

After the simulation, we have $x_1(T) \approx 13.43$ and $x_2(T) \approx 12.95$. These two numbers are big enough that we are confident to conclude the two bacteria coexist in the chemostat.

This suggests the existence of bistability that there is a saddle point creating the separation with the unstable manifold. Note that this time, we can see that substrate 1 and 2 are at a relative high level, suggesting mutualisms are playing a very important role in the chemostat.

Lastly, we increase μ_1, μ_2 so that E_0 becomes a saddle point. We simulate the case of parameters $\begin{bmatrix}\mu_1 & \mu_2 & X_{1_{\text{initial}}} & X_{2_{\text{initial}}}\end{bmatrix} = \begin{bmatrix}2500 & 2200 & 0.5 & 1\end{bmatrix}$. See figure 7.

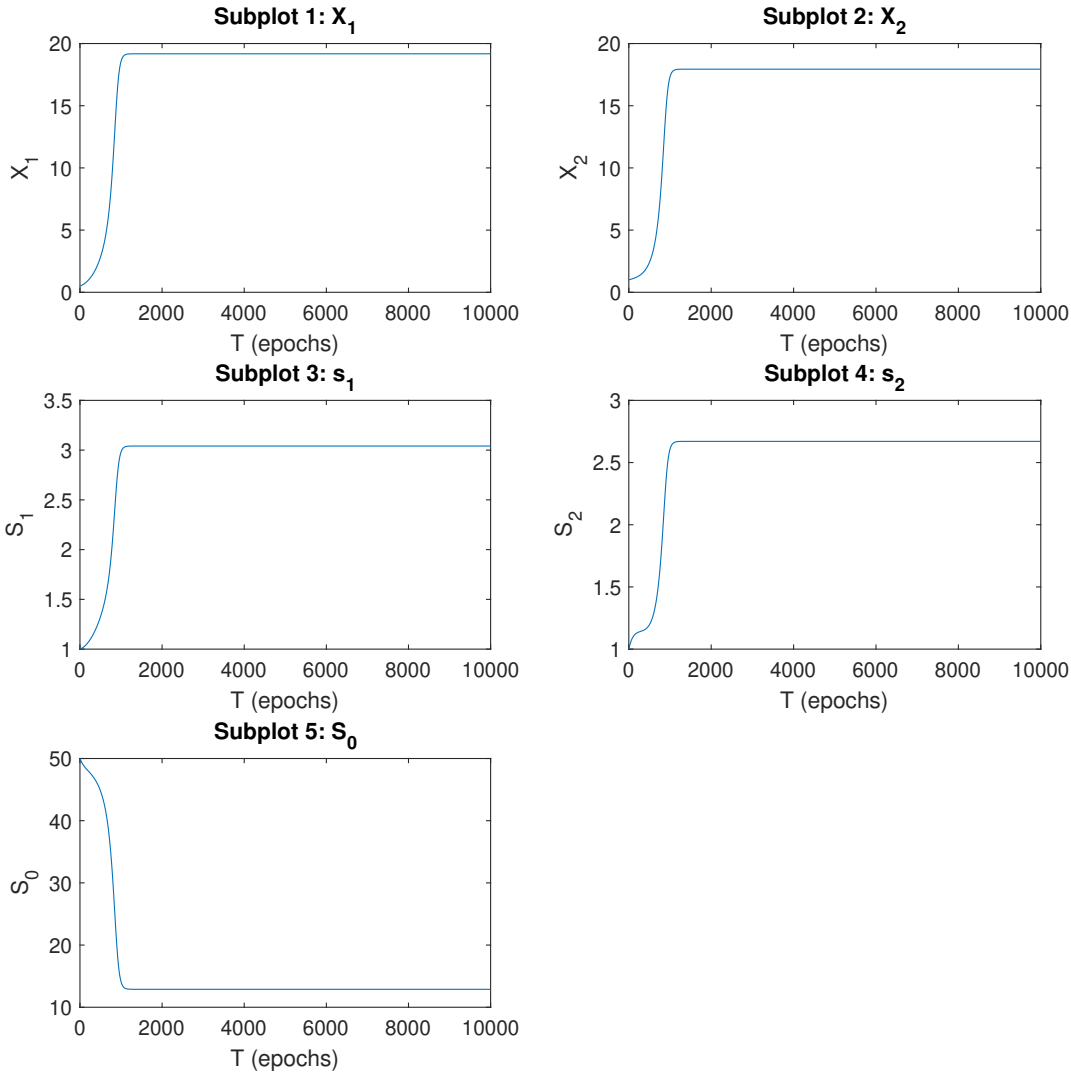

Figure 7: Under high enough maximum growth rate and low initial populations, both bacteria survive. $\begin{bmatrix}\mu_1 & \mu_2 & X_{1_{\text{initial}}} & X_{2_{\text{initial}}}\end{bmatrix} = \begin{bmatrix}2500 & 2200 & 0.5 & 1\end{bmatrix}$

These plots have supported my derivation of the threshold of mutual extinction numerically. If we are above the threshold, even with extremely low population density like 0.5 and 1 in this case, both bacteria can still survive.

2.5.2 Numerical Simulation - L_1 Situation

Although both the paper and me have not proposed a very clear threshold where one of the bacteria will exclude the other, we can still fine tune the parameters and initial values so that the exclusion is achieved. We set $\begin{bmatrix}\mu_1 & \mu_2 & X_{1_{\text{initial}}} & X_{2_{\text{initial}}}\end{bmatrix} = \begin{bmatrix}3000 & 600 & 20 & 20\end{bmatrix}$. See figure 8.

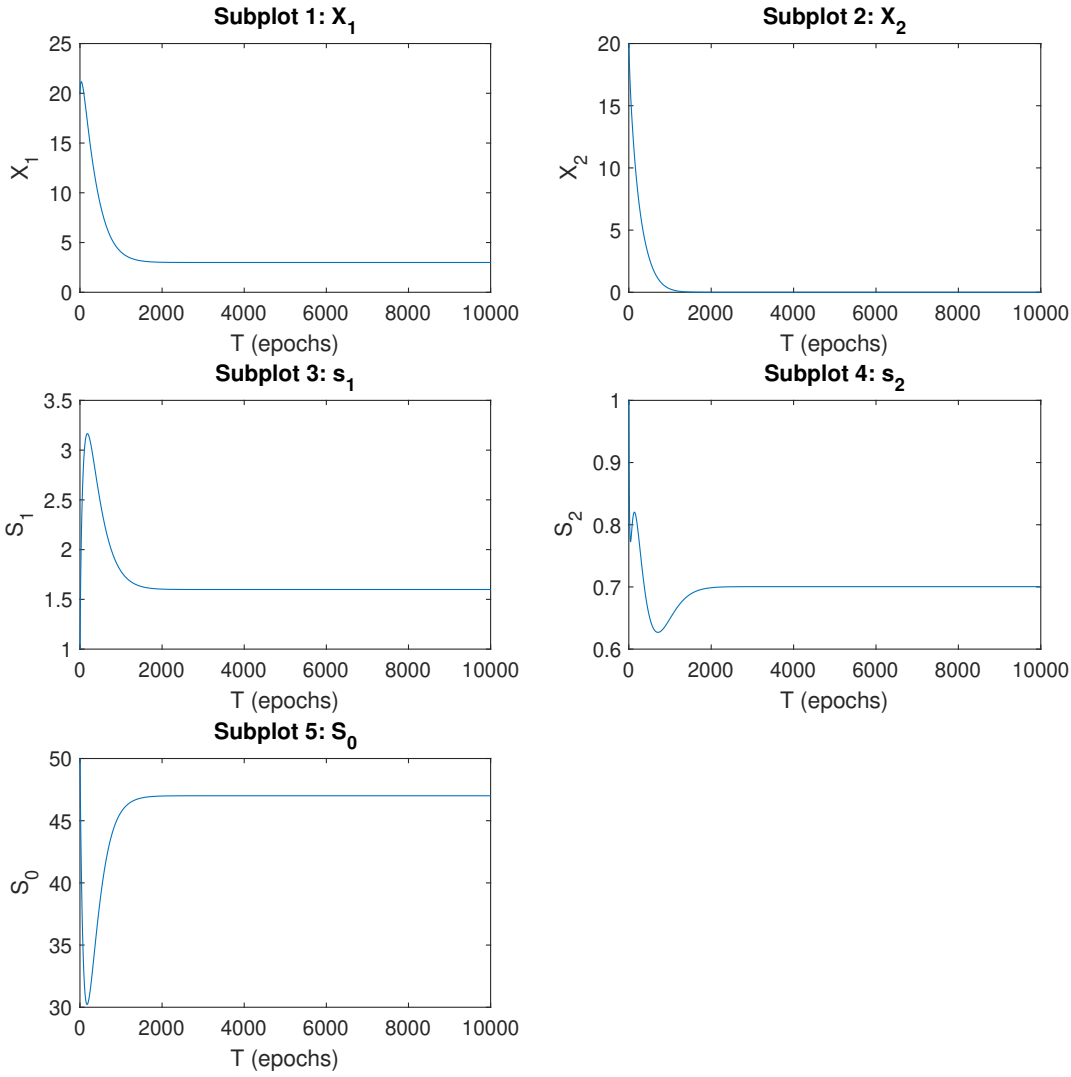

Figure 8: High difference between the maximum growth rate results in exclusion.
$\begin{bmatrix}\mu_1 & \mu_2 & X_{1_{\text{initial}}} & X_{2_{\text{initial}}}\end{bmatrix} = \begin{bmatrix}3000 & 600 & 20 & 20\end{bmatrix}$

2.6 Prevalence of E_0, L_1, L_2, L_{12}, B

Lastly, we are interested in the probability that mutual extinction (E_0), Exclusion of bacteria 2 by bacteria 1 (L_1), Exclusion of bacteria 1 by bacteria 2 (L_2), coexistence of the two bacteria (L_{12}) and bistability (B). The authors of the paper have performed numerical simulations to figure out the probabilities by randomly assigning the parameters drawn from a normal distribution. In particular, after we have fixed the set of parameters, if we want to check for monostability and bistability, we have to repeatedly run the model with different sets initial values and see if the equilibrium value changes.

2.6.1 Proposed Methodology

The authors of the paper did not disclose the method they are using. I am now proposing the following methodology.

Theorem 3 (Numerical Method to check for Monostability and Bistability for the Competition-Mutualism Chemostat Model)

1. *The value of all the parameters are drawn randomly from a normal distribution in the range* $(0.1, 100)$*, except for* $\tilde{S_0}$ *which the range is set to be* $(5, 5000)$*.*

2. *For this set of parameters, we repeat the numerical simulation by* N_i *times with different initial values. The initial values of* X_1, X_2, S_1, S_2 *are drawn randomly from a normal distribution in the range* $(0.1, 100)$*, except for the initial value of* S_0 *which is drawn randomly from a normal distribution in the range* $(5, 5000)$*.*

3. *After repeating the experiments for* N_i *times, we observe these equilibrium points. If only one of* E_0, L_1, L_2, L_{12} *exists, this set of parameter possesses monostability. If more than one of those equilibrium states exist, this set of parameter possesses bistability.*

4. *We change the set of parameters by* N_p *times and count the possibilities.*

   In my work, I set $(N_p, N_i) = (20000, 100)$.

2.6.2 Result of Simulation

The researchers have set $N_p = 10000$. I set $N_p = 20000$ just for safety.

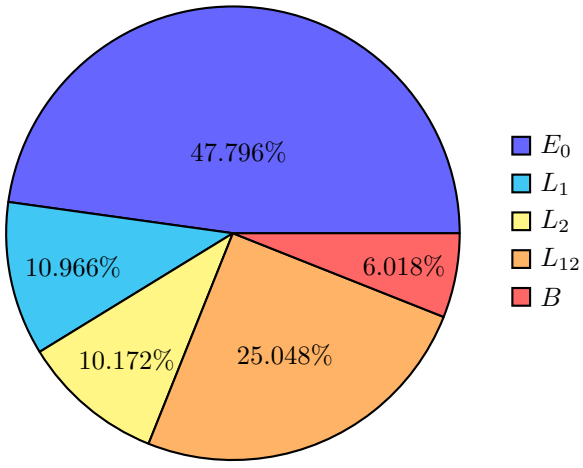

Figure 9: Results from the paper

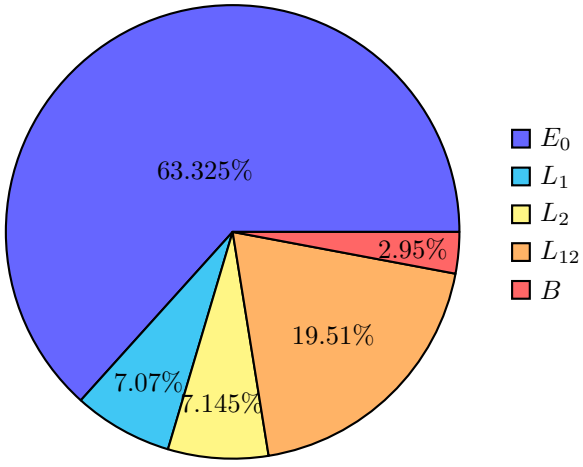

Figure 10: Results from my own simulation

Here is the frequency that I obtained.

State	E_0	L_1	L_2	L_{12}	B
Frequency	12665	1414	1429	3902	590

The distributions are significantly different. However, I have not investigated further to account for the difference.

2.7 Game Theory Extension: Freerider/Commensalism Situation

Lastly, I want to numerically simulate the situation that bacteria 1 is a freerider to the mutualism situation. That is, bacteria 1 is not actively producing substrate 1 for bacteria 2 to consume. We set $\nu_{11} = 0$ to represent this situation.

Again, using the same method of simulation stated in Theorem 3 in the last subsection, I obtain the following frequencies of different equilibrium states.

State	E_0	L_1	L_2	L_{12}	B
Frequency	13046	2205	1044	3102	3

Not surprisingly, we can see that it is more difficult for bacteria 2 to survive in this case. We can see that E_0 happens more frequently, and L_2, L_{12} happen less frequently. On the other hand, we can see that L_1 increases. This means in the absence of bacteria 2, bacteria 1 can still survive with the supply of S_0 and low constant inflow of S_2.

3 Investigation on the Second Model

The authors have proposed an extended Lokta-Volterra Model. They claim that this new model is easier to analyse and most of the quantitative and qualitative behaviour would be similar to the original Competition-Mutualism Chemostat model. Due to the limitation of length, I will not analyse the second model from scratch. Instead, I will use the same set of parameter used in subsection 2.5 and compare the two models both quantitatively and qualitatively.

The method to simulate the second model is extremely similar of that of the first model, so the details are omitted.

1. Parameter set $\begin{bmatrix} \mu_1 & \mu_2 & X_{1_{\text{initial}}} & X_{2_{\text{initial}}} \end{bmatrix} = \begin{bmatrix} 1700 & 1600 & 5 & 4 \end{bmatrix}$

Model\Result	x_1^*	x_2^*	Result
C-M Chemostat	0.0000167149	0.000000578570	E_0
Extended L-V	15.6021	15.2380	L_{12}

2. Parameter set $\begin{bmatrix} \mu_1 & \mu_2 & X_{1_{\text{initial}}} & X_{2_{\text{initial}}} \end{bmatrix} = \begin{bmatrix} 1700 & 1600 & 6 & 5 \end{bmatrix}$

Model\Result	x_1^*	x_2^*	Result
C-M Chemostat	13.4264	12.9515	L_{12}
Extended L-V	15.6021	15.2680	L_{12}

3. Parameter set $\begin{bmatrix} \mu_1 & \mu_2 & X_{1_{\text{initial}}} & X_{2_{\text{initial}}} \end{bmatrix} = \begin{bmatrix} 2500 & 2200 & 0.5 & 1 \end{bmatrix}$

Model\Result	x_1^*	x_2^*	Result
C-M Chemostat	19.1754	17.9393	L_{12}
Extended L-V	19.4085	18.8138	L_{12}

4. Parameter set $\begin{bmatrix} \mu_1 & \mu_2 & X_{1_{\text{initial}}} & X_{2_{\text{initial}}} \end{bmatrix} = \begin{bmatrix} 3000 & 600 & 20 & 20 \end{bmatrix}$

Model\Result	x_1^*	x_2^*	Result
C-M Chemostat	2.99544	0.000000	L_1
Extended L-V	3.87773	0.000000	L_1

As we can see, all of the 4 test cases exhibit quantitative difference. During the testing, I observed that the convergence rate for the extended L-V model is significantly slower than that of the chemostat model. However, for fairness, we fix the same step size and number of epochs during the comparison. Another bad news is that for the first set of parameter, we can see qualitative difference. The chemostat model predicts extinctions for both species, which coincides with my local Jacobian analysis in subsection 2.1. However, the extended L-V model predicts coexistence.

4 Conclusion and Discussion

In this paper, I have conducted Jacobian Analysis on the Competition-Mutualism Model, and performed numerical simulations to obtain numerical approximations of the concentration of the bacteria and substrates. The probabilities of each equilibrium states are shown, and the fact that mutual extinction is the most probable result tells us this ecological system is fragile and sensitive. Furthermore, I have compared the extended Lokta-Volterra Model numerically by several test cases, and the results are not as good as the researchers have claimed.

The Competition-Mutualism Chemostat Model is a very good generalization of the chemostat model only with competition. The dynamics of this system is richer, to the point that we cannot discuss a lot due to the restriction of length of the paper. For me, I would like to include game theory into this model. What if one of the bacteria is not creating nutrient for the opponent, but only accept nutrient from the opponent? Will this leads to mutual extinction or exclusion? Although I have explore a little bit of these via numerical simulations, a purely mathematical derivations will be very interesting that can be done in the future.

5 Code

5.1 Code for Solving the Competition-Mutualism Chemostat Model

The following is the code for the second-order Taylor's Method scheme to solve the Competition-Mutualism Chemostat Model.

```
clc;
clear all;
%We introduce the parameter here.
phi=2;
mu1=2200;
mu2=1600;
S0=50;
S1=1;
S2=1;
K10=200;
K12=200;
```

```
K20=200;
K21=200;
v01=1;
v02=1;
v11=0.2;
v12=0.1;
v21=0.1;
v22=0.2;
%We introduce the initial variable here.
x_1=10;
x_2=20;
s_0=50;
s_1=1;
s_2=1;
%We introduce the duration of the simulation.
T=10000;
%Creating array to store the function value
x_1a=[x_1 zeros(1,T)];
x_2a=[x_2 zeros(1,T)];
s_0a=[s_0 zeros(1,T)];
s_1a=[s_1 zeros(1,T)];
s_2a=[s_2 zeros(1,T)];
%Iteration
h=0.005; %this is step size

for i=1:T
    currentvalue=[x_1a(i) x_2a(i) s_0a(i) s_1a(i) s_2a(i)];
    p=currentvalue(1);
    q=currentvalue(2);
    r=currentvalue(3);
    s=currentvalue(4);
    t=currentvalue(5);
```

```
    ef1=mu1*(r/(K10+r)*t/(K12+t));
    ef2=mu2*(r/(K20+r)*s/(K21+s));

    F1=(ef1-phi)*p;
    F2=(ef2-phi)*q;
    F3=(phi*(S0-r)-v01*ef1*p-v02*ef2*q);
    F4=(phi*(S1-s)+v11*ef1*p-v12*ef2*q);
    F5=(phi*(S2-t)-v21*ef1*p+v22*ef2*q);

    edf1=mu1*K10/(K10+S0)^2*S2/(K12+S2)+mu1*S0/(K10+S0)*K12/(K12+S2)^2;
    edf2=mu2*K20/(K20+S0)^2*S1/(K21+S1)+mu2*S0/(K20+S0)*K21/(K21+S1)^2;

    DF1=(ef1-phi)*F1+p*edf1;
    DF2=(ef2-phi)*F2+q*edf2;
    DF3=-phi*F3-v01*(ef1*F1+p*edf1)-v02*(ef2*F2+q*edf2);
    DF4=-phi*F4+v11*(ef1*F1+p*edf1)-v12*(ef2*F2+q*edf2);
    DF5=-phi*F5-v21*(ef1*F1+p*edf1)+v22*(ef2*F2+q*edf2);

    newx_1=p+h*F1+h^2/2*DF1;
    newx_2=q+h*F2+h^2/2*DF2;
    news_0=r+h*F3+h^2/2*DF3;
    news_1=s+h*F4+h^2/2*DF4;
    news_2=t+h*F5+h^2/2*DF5;

    x_1a(i+1)=newx_1;
    x_2a(i+1)=newx_2;
    s_0a(i+1)=news_0;
    s_1a(i+1)=news_1;
    s_2a(i+1)=news_2;
end
```

```
fig=figure;
subplot(3,2,1)
plot(x_1a)
xlim([0,T])
xlabel('T (epochs)')
ylabel('X_1')
title('Subplot 1: X_1')
subplot(3,2,2)
plot(x_2a)
xlim([0,T])
xlabel('T (epochs)')
ylabel('X_2')
title('Subplot 2: X_2')
subplot(3,2,3)
plot(s_1a)
xlim([0,T])
xlabel('T (epochs)')
ylabel('S_1')
title('Subplot 3: s_1')
subplot(3,2,4)
plot(s_2a)
xlim([0,T])
xlabel('T (epochs)')
ylabel('S_2')
title('Subplot 4: s_2')
subplot(3,2,5)
plot(s_0a)
xlim([0,T])
xlabel('T (epochs)')
ylabel('S_0')
title('Subplot 5: S_0')
```

5.2 Code for Counting the Frequencies of the Equilibrium States

The following is the code for counting the frequencies of the equilibrium states used in subsection 2.6 and 2.7.

```
clc
clear all
E0=0;
L1=0;
L2=0;
L12=0;
B=0;
epsilon=0.00000001; %Floating point zero
Etime=50; %N_p%
%I make a progress bar so that users can know the progress
stroke=0;
fprintf('Progress: [                    ]\n')
stroke=0;
for count=1:Etime
    if count>=(stroke+1)*Etime/20;
        stroke=stroke+1;
        str='';
        for jjj=1:stroke
            str=[str '-'];
        end
        for jjj=1:20-stroke
            str=[str ' '];
        end
        clc
        str=['Progress: [' str ']\n'];
        fprintf(str);
    end
phi=99.9*rand(1)+0.1;
```

```
mu1=99.9*rand(1)+0.1;
mu2=99.9*rand(1)+0.1;
S0=4995*rand(1)+5;
S1=99.9*rand(1)+0.1;
S2=99.9*rand(1)+0.1;
K10=99.9*rand(1)+0.1;
K12=99.9*rand(1)+0.1;
K20=99.9*rand(1)+0.1;
K21=99.9*rand(1)+0.1;
v01=99.9*rand(1)+0.1;
v02=99.9*rand(1)+0.1;
v11=99.9*rand(1)+0.1; %change it to 0 for the game theory simulation.
v12=99.9*rand(1)+0.1;
v21=99.9*rand(1)+0.1;
v22=99.9*rand(1)+0.1;

%We introduce the duration of the simulation.
T=15000;

E0i=0;
L1i=0;
L2i=0;
L12i=0;

inner=0;
needinner=100; %N_i
while inner<needinner
%We introduce the initial variable here.
x_1=99.9*rand(1)+0.1;
x_2=99.9*rand(1)+0.1;
s_0=4995*rand(1)+5;
s_1=99.9*rand(1)+0.1;
```

```
s_2=99.9*rand(1)+0.1;
%Creating array to store the function value
x_1a=[x_1 zeros(1,T)];
x_2a=[x_2 zeros(1,T)];
s_0a=[s_0 zeros(1,T)];
s_1a=[s_1 zeros(1,T)];
s_2a=[s_2 zeros(1,T)];

%Iteration
h=0.005; %this is step size
for i=1:T
    currentvalue=[x_1a(i) x_2a(i) s_0a(i) s_1a(i) s_2a(i)];
    p=currentvalue(1);
    q=currentvalue(2);
    r=currentvalue(3);
    s=currentvalue(4);
    t=currentvalue(5);

    ef1=mu1*(r/(K10+r)*t/(K12+t));
    ef2=mu2*(r/(K20+r)*s/(K21+s));

    F1=(ef1-phi)*p;
    F2=(ef2-phi)*q;
    F3=(phi*(S0-r)-v01*ef1*p-v02*ef2*q);
    F4=(phi*(S1-s)+v11*ef1*p-v12*ef2*q);
    F5=(phi*(S2-t)-v21*ef1*p+v22*ef2*q);

    edf1=mu1*K10/(K10+S0)^2*S2/(K12+S2)+mu1*S0/(K10+S0)*K12/(K12+S2)^2;
    edf2=mu2*K20/(K20+S0)^2*S1/(K21+S1)+mu2*S0/(K20+S0)*K21/(K21+S1)^2;

    DF1=(ef1-phi)*F1+p*edf1;
    DF2=(ef2-phi)*F2+q*edf2;
```

```
    DF3=-phi*F3-v01*(ef1*F1+p*edf1)-v02*(ef2*F2+q*edf2);
    DF4=-phi*F4+v11*(ef1*F1+p*edf1)-v12*(ef2*F2+q*edf2);
    DF5=-phi*F5-v21*(ef1*F1+p*edf1)+v22*(ef2*F2+q*edf2);

    newx_1=max(p+h*F1+h^2/2*DF1,0);
    newx_2=max(q+h*F2+h^2/2*DF2,0);
    news_0=max(r+h*F3+h^2/2*DF3,0);
    news_1=max(s+h*F4+h^2/2*DF4,0);
    news_2=max(t+h*F5+h^2/2*DF5,0);

    x_1a(i+1)=newx_1;
    x_2a(i+1)=newx_2;
    s_0a(i+1)=news_0;
    s_1a(i+1)=news_1;
    s_2a(i+1)=news_2;
end

inner=inner+1;

if (newx_1<=epsilon)&&(newx_2<=epsilon)
    E0i=E0i+1;
end
if (newx_1>=epsilon)&&(newx_2<=epsilon)
    L1i=L1i+1;
end
if (newx_1<=epsilon)&&(newx_2>=epsilon)
    L2i=L2i+1;
end
if (newx_1>=epsilon)&&(newx_2>=epsilon)
    L12i=L12i+1;
end
```

```
end
v=[E0i L1i L2i L12i];
v=sort(v);
if v(3)~=0
    B=B+1;
    continue;
end
    if E0i==max(v)
        E0=E0+1;
    end
    if L1i==max(v)
        L1=L1+1;
    end
    if L2i==max(v)
        L2=L2+1;
    end
    if L12i==max(v)
        L12=L12+1;
    end
end
fprintf('The results are as follows.\n')
fprintf('E0 L1 L2 L12 B\n');
[E0 L1 L2 L12 B]
```

6 References

[1] Vet S, de Buyl S, Faust K, Danckaert J, Gonze D, Gelens L (2018) Bistability in a system of two species interacting through mutualism as well as competition: Chemostat vs. Lotka-Volterra equations. PLoS ONE 13(6): e0197462. https://doi.org/10.1371/journal.pone.0197462

[2] Momeni B, Xie L, Shou W. Lotka-Volterra pairwise modeling fails to capture diverse pairwise microbial interactions. eLife. 2017; 6. https://doi.org/10.7554/eLife.25051 PMID: 28350295

[3] Bairey E, Kelsic ED, Kishony R. High-order species interactions shape ecosystem diversity. Nature Communications. 2016; 7:12285. https://doi.org/10.1038/ncomms12285 PMID: 27481625