Commensalism and Syntrophy

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Sommaire

- Operating Diagram
- Self Inhibition
- Global results

Sommaire

TREASURE, for **Treatment and Sustainable Reuse of Effluents in semiarid climates**, is a scientific Euro-Mediterranean research network associating research labs and researchers from Southern Europe and Northern Africa countries about biological wastewater treatment plants and microbial ecosystems. At its origins, in 2006, the involved partners only consisted of academics from France, Algeria, Italy and Tunisia. Today the principal partners are located in Kenitra, Montpellier, Narbonne, Sfax, Tlemcen and Tunis.

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A MATHEMATICAL STUDY OF A SYNTROPHIC RELATIONSHIP OF A MODEL OF ANAEROBIC DIGESTION PROCESS

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THE MATHEMATICAL ANALYSIS OF A SYNTROPHIC RELATIONSHIP BETWEEN TWO MICROBIAL SPECIES IN A CHEMOSTAT

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Bifurcation and stability analysis of a two step model for monitoring anaerobic digestion processes☆

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Yessmine Daoud (Syntrophy)

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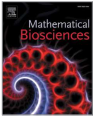

A model of a syntrophic relationship between two microbial species in a chemostat including maintenance

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STEADY STATE ANALYSIS OF A SYNTROPHIC MODEL: THE EFFECT OF A NEW INPUT SUBSTRATE CONCENTRATION

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Yessmine Daoud (Syntrophy)

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A Mathematical Model of Anaerobic Digestion with Syntrophic Relationship, Substrate Inhibition, and Distinct Removal Rates*

Radhouane Fekih-Salem†, Yessmine Daoud‡, Nahla Abdellatif§, and Tewfik Sari¶

Sommaire

Mathematical model

$$
\begin{aligned}
\dot{S}_1 &= D\left(S_1^{in} - S_1\right) - k_1\mu_1\left(S_1, S_2\right)X_1,\\
\dot{X}_1 &= \left(\mu_1\left(S_1, S_2\right) - D_1\right)X_1,\\
\dot{S}_2 &= D\left(S_2^{in} - S_2\right) + k_3\mu_1\left(S_1, S_2\right)X_1 - k_2\mu_2\left(S_1, S_2\right)X_2,\\
\dot{X}_2 &= \left(\mu_2\left(S_1, S_2\right) - D_2\right)X_2,
\end{aligned}
$$

- X_i: concentration of species $i = 1, 2$
- S_j: concentration of chemical $j = 1, 2$
- S_j^{in} : inlet concentration of chemical $j = 1, 2$
- k_i, $i = 1, 2, 3$ are yield factors
- $D = 1/HRT$ is the dilution rate (HRT is the hydraulic retention time)
- $D_i = \alpha_i D + a_i$: disappearance rate of species i
- a_i : death (or decay) rate parameters
- $\alpha_i \in [0, 1]$, $i = 1, 2$, represents the biomass proportion that leaves the bioreactor.

Hypotheses on growth functions

$$
\begin{aligned}
\dot{S}_1 &= D\left(S_1^{in} - S_1\right) - k_1\mu_1\left(S_1, S_2\right)X_1, \\
\dot{X}_1 &= \left(\mu_1\left(S_1, S_2\right) - D_1\right)X_1, \\
\dot{S}_2 &= D\left(S_2^{in} - S_2\right) + k_3\mu_1\left(S_1, S_2\right)X_1 - k_2\mu_2\left(S_1, S_2\right)X_2, \\
\dot{X}_2 &= \left(\mu_2\left(S_1, S_2\right) - D_2\right)X_2,
\end{aligned}
$$

- For $S_2 \geq 0$, we have $\mu_1(0, S_2) = 0$
- For $S_1 > 0$ and $S_2 \geq 0$, we have

$$\frac{\partial \mu_1}{\partial S_1}(S_1, S_2) > 0, \quad \frac{\partial \mu_1}{\partial S_2}(S_1, S_2) \leq 0$$

- For $S_1 \geq 0$, we have $\mu_2(S_1, 0) = 0$
- For $S_1 \geq 0$ and $S_2 > 0$, we have

$$\frac{\partial \mu_2}{\partial S_2}(S_1, S_2) > 0, \quad \frac{\partial \mu_2}{\partial S_1}(S_1, S_2) \leq 0$$

Hypotheses on growth functions

- $\mu_1(0, S_2) = 0, \quad \frac{\partial \mu_1}{\partial S_1}(S_1, S_2) > 0, \quad \frac{\partial \mu_1}{\partial S_2}(S_1, S_2) \leq 0$
- $\mu_2(S_1, 0) = 0, \quad \frac{\partial \mu_2}{\partial S_2}(S_1, S_2) > 0, \quad \frac{\partial \mu_2}{\partial S_1}(S_1, S_2) \leq 0$
- These Hypotheses signify that no growth takes place for species $i = 1, 2$ without substrate S_i, and the growth increases with S_i, while it is inhibited by the other substrate S_j, $j \neq i$
- the first organism is inhibited by its product S_2 (the food of the second organism)
- the second organism is inhibited by the food S_1 of the first organism
- Inhibition is not mandatory (because $\frac{\partial \mu_1}{\partial S_2}(S_1, S_2) \leq 0$ and $\frac{\partial \mu_2}{\partial S_1}(S_1, S_2) \leq 0$)

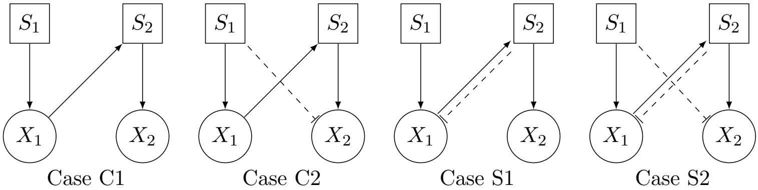
Examples of growth functions

$$
\begin{aligned}
\dot{S}_1 &= D\left(S_1^{in} - S_1\right) - k_1\mu_1\left(S_1, S_2\right)X_1,\\
\dot{X}_1 &= \left(\mu_1\left(S_1, S_2\right) - D_1\right)X_1,\\
\dot{S}_2 &= D\left(S_2^{in} - S_2\right) + k_3\mu_1\left(S_1, S_2\right)X_1 - k_2\mu_2\left(S_1, S_2\right)X_2,\\
\dot{X}_2 &= \left(\mu_2\left(S_1, S_2\right) - D_2\right)X_2,
\end{aligned}
$$

$$
\mu_1(S_1, S_2) = \frac{m_1 S_1}{K_1 + S_1}\frac{1}{1 + L_2 S_2} \qquad \mu_2(S_1, S_2) = \frac{m_2 S_2}{K_2 + S_2}\frac{1}{1 + L_1 S_1}
$$

- m_i is the maximum specific growth rate,
- K_i is the half saturation constant.
- L_j : strength of inhibition of species i by chemical j
- If $L_j = 0$, then there is no inhibition (μ_i depends only on S_i)

Microbial communities



Case	μ_1	μ_2
C1	$\mu_1(S_1) = \frac{m_1 S_1}{K_1+S_1}$	$\mu_2(S_2) = \frac{m_2 S_2}{K_2+S_2}$
C2	$\mu_1(S_1) = \frac{m_1 S_1}{K_1+S_1}$	$\mu_2(S_1, S_2) = \frac{m_2 S_2}{K_2+S_2} \frac{1}{1+L_1 S_1}$
S1	$\mu_1(S_1, S_2) = \frac{m_1 S_1}{K_1+S_1} \frac{1}{1+L_2 S_2}$	$\mu_2(S_2) = \frac{m_2 S_2}{K_2+S_2}$
S2	$\mu_1(S_1, S_2) = \frac{m_1 S_1}{K_1+S_1} \frac{1}{1+L_2 S_2}$	$\mu_2(S_1, S_2) = \frac{m_2 S_2}{K_2+S_2} \frac{1}{1+L_1 S_1}$

Commensalism and Syntrophy

- Case C1 ($L_1 = L_2 = 0$), is an example of pure commensalism, where the second population (the commensal population) depends for its growth on the first population (the host) and thus, benefits from its interaction, while the host population is not affected by the growth of the commensal population.
- Case C2 ($L_1 > 0$ and $L_2 = 0$), is also an example of commensalism, since the first population is not affected by the growth of the second population.
- Case S1 ($L_1 = 0$ and $L_2 > 0$) and Case S2 ($L_1 > 0$ and $L_2 > 0$), are not commensal, since the first population is affected by the growth of the second population.
- In S1, the first organism is inhibited by the substrate S_2. Hence, the growth of X_1 depends on the efficiency of the removal of the product S_2 by the bacteria X_2. Therefore, each population needs the other one for its growth (there is a syntrophic relationship between them).

Reduction $(k_1 = k_2 = k_3 = 1)$

We use the following change of variables :

$$s_1 = k_3 S_1/k_1,\ s_1^{in} = k_1 S_1^{in}/k_3,\ s_2 = S_2,\ s_2^{in} = S_2^{in},$$

$$x_1 = k_3 X_1,\ x_2 = k_2 X_2.$$

$$\begin{aligned}
\dot{s}_1 &= D\left(s_1^{in} - s_1\right) - f_1\left(s_1, s_2\right)x_1,\\
\dot{x}_1 &= \left(f_1\left(s_1, s_2\right) - D_1\right)x_1,\\
\dot{s}_2 &= D\left(s_2^{in} - s_2\right) + f_1\left(s_1, s_2\right)x_1 - f_2\left(s_1, s_2\right)x_2,\\
\dot{x}_2 &= \left(f_2\left(s_1, s_2\right) - D_2\right)x_2,
\end{aligned}$$

$$f_1(s_1, s_2) = \mu_1\left(k_3 s_1/k_1, s_2\right), \quad f_2(s_1, s_2) = \mu_2\left(k_3 s_1/k_1, s_2\right)$$

Sommaire

Graphical method

We use the graphical method of Tilman, complemented by Ballyk and Wolkowicz, to determine the outcome of competition between two species for two resources. Although our system is not a competition model, it appears that the concepts introduced by these authors are very useful to understand the existence and stability of equilibrium points in our commensalism and syntrophy models.

D. Tilman. Resources: a graphical-mechanistic approach to competition and predation. *American Naturalist* **116** (1980) 362-393.
D. Tilman. *Resource competition and community structure*. Princeton University Press, New Jersey (1982).
M.M. Ballyk, G.S.K. Wolkowicz, Classical and resource-based competition: a unifying graphical approach, *J. Math. Biol.* 62 (2011) 81–109.

Outline of the method

- Find the feasible set
- Find the FSBs (Feasable Set Boundaries)
- Find the ZNGIs (Zero Net Growth Isoclines)
- Find the equilibria
- Determine their stability conditions

The feasible set

- Definition: The *feasible set* $\mathcal{F}$ in (s_1, s_2)-space, is the set where the (s_1, s_2)-coordinate of any equilibrium point must be located.
- $\mathcal{F} = \{(s_1, s_2) \in \mathbb{R}^2 : 0 \le s_1 \le s_1^{in}, \quad 0 \le s_1 + s_2 \le s_1^{in} + s_2^{in}\}$
- Let (s_1, x_1, s_2, x_2) be an equilibrium point. We have

$$\begin{aligned}
0 = & \quad D\left(s_1^{in} - s_1\right) - f_1\left(s_1, s_2\right) x_1 \\
0 = & \quad \left(f_1\left(s_1, s_2\right) - D_1\right) x_1 \\
0 = & \quad D\left(s_2^{in} - s_2\right) + f_1\left(s_1, s_2\right) x_1 - f_2\left(s_1, s_2\right) x_2 \\
0 = & \quad \left(f_2\left(s_1, s_2\right) - D_2\right) x_2
\end{aligned}$$

- Exercise : prove that

$$x_1 = \frac{D}{D_1}\left(s_1^{in} - s_1\right), \quad x_2 = \frac{D}{D_2}\left(s_1^{in} + s_2^{in} - s_1 - s_2\right).$$

- Therefore, the equilibrium points concentrations x_i are positive if and only if

$$0 \le s_1 \le s_1^{in}, \qquad 0 \le s_1 + s_2 \le s_1^{in} + s_2^{in}$$

The feasible set boundary (FSB)

The boundary of $\mathcal{F}$ consists of two portions of the coordinate axes, together with two curves, namely the *feasible set boundary* for population i, FSB_i, $i = 1, 2$, defined as follows

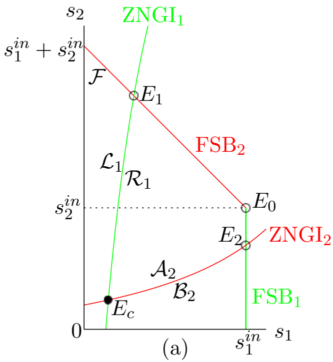
$$\mathrm{FSB}_1 = \{(s_1, s_2) \in \mathcal{C} : s_1 = s_1^{in}, 0 \leq s_2 \leq s_2^{in}\}$$
$$\mathrm{FSB}_2 = \{(s_1, s_2) \in \mathcal{C} : 0 \leq s_1 \leq s_1^{in}, s_1 + s_2 = s_1^{in} + s_2^{in}\}$$

$$x_1 = \tfrac{D}{D_1}\left(s_1^{in} - s_1\right), \quad x_2 = \tfrac{D}{D_2}\left(s_1^{in} + s_2^{in} - s_1 - s_2\right).$$

- If $(s_1, s_2) \in \mathrm{FSB}_1$ then $x_1 = 0$
- If $(s_1, s_2) \in \mathrm{FSB}_2$ then $x_2 = 0$

These curves are plotted in green and red respectively in the figure.

The feasible set and its boundary (FSB)



- $\mathcal{F} = \{(s_1, s_2) \in \mathcal{C} : 0 \leq s_1 \leq s_1^{in}, \quad 0 \leq s_1 + s_2 \leq s_1^{in} + s_2^{in}\}$
- $\mathrm{FSB}_1 = \{(s_1, s_2) \in \mathcal{C} : s_1 = s_1^{in}, 0 \leq s_2 \leq s_2^{in}\}$
- $\mathrm{FSB}_2 = \{(s_1, s_2) \in \mathcal{C} : 0 \leq s_1 \leq s_1^{in}, s_1 + s_2 = s_1^{in} + s_2^{in}\}$

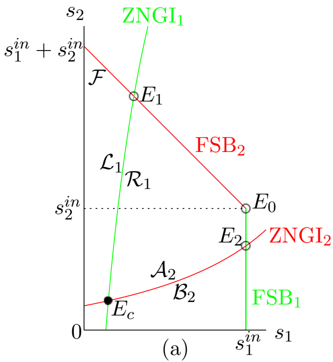
The zero net growth isocline (ZNGI)

- The ZNGI for population i (ZNGI_i) is the curve of substrate concentrations along which the decline in biomass density is balanced by its growth.

$$\mathrm{ZNGI}_1 = \{(s_1, s_2) \in \mathcal{C} : f_1(s_1, s_2) = D_1\}$$
$$\mathrm{ZNGI}_2 = \{(s_1, s_2) \in \mathcal{C} : f_2(s_1, s_2) = D_2\}$$

- If $(s_1, s_2) \in \mathrm{ZNGI}_1$ then $\dot{x}_1 = 0$
- If $(s_1, s_2) \in \mathrm{ZNGI}_2$ then $\dot{x}_2 = 0$
- We plot the ZNGI_i in $(s1, s_2)$-space using the same color used for population i as used for its FSB_i

The FSB and the ZNGIs



Each intersection of a green curve and a red curve in the feasible set corresponds to an equilibrium point, as depicted in the figure. More precisely, we have the following result.

Equilibria

- The intersection point $(s_1^{in}, s_2^{in}) = \mathrm{FSB}_1 \cap \mathrm{FSB}_2$ corresponds to the washout equilibrium $E_0 = (s_1^{in}, 0, s_2^{in}, 0)$ where both species are extinct.
- Any point $(\bar{s}_1, \bar{s}_2) \in \mathrm{ZNGI}_1 \cap \mathrm{FSB}_2$ corresponds to a boundary equilibrium $E_1 = (\bar{s}_1, \bar{x}_1, \bar{s}_2, 0)$, where species 2 is absent and species 1 is present.
- Any point where $(\tilde{s}_1, \tilde{s}_2) \in \mathrm{FSB}_1 \cap \mathrm{ZNGI}_2$ corresponds to a boundary equilibrium $E_2 = (\tilde{s}_1, 0, \tilde{s}_2, \tilde{x}_2)$, where species 1 is absent and species 2 is present.
- Any point $(s_1^*, s_2^*) \in \mathrm{ZNGI}_1 \cap \mathrm{ZNGI}_2$ lying in the interior $\mathcal{F}^{\mathrm{o}}$ of the feasible set $\mathcal{F}$ corresponds to a coexistence equilibrium $E_c = (s_1^*, x_1^*, s_2^*, x_2^*)$, where both species are present.

Proof

Let (s_1, x_1, s_2, x_2) be an equilibrium point. We have

$$0 = D\left(s_1^{in} - s_1\right) - f_1\left(s_1, s_2\right) x_1 \tag{1}$$

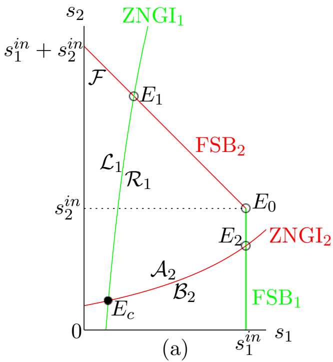
$$0 = \left(f_1\left(s_1, s_2\right) - D_1\right) x_1 \tag{2}$$

$$0 = D\left(s_2^{in} - s_2\right) + f_1\left(s_1, s_2\right) x_1 - f_2\left(s_1, s_2\right) x_2 \tag{3}$$

$$0 = \left(f_2\left(s_1, s_2\right) - D_2\right) x_2 \tag{4}$$

- Assume that $x_1 = 0$ and $x_2 > 0$ (a boundary equilibrium point E_2)
- From $x_1 = 0$ and (1) we deduce that $s_1 = s_1^{in}$.
- Using now $x_2 > 0$, from $x_2 = \frac{D}{D_2}\left(s_1^{in} + s_2^{in} - s_1 - s_2\right) = \frac{D}{D_2}\left(s_2^{in} - s_2\right)$ we deduce that $s_2 < s_2^{in}$. Since $\mathrm{FSB}_1 = \left\{(s_1, s_2) \in \mathcal{C} : s_1 = s_1^{in}, 0 \leq s_2 \leq s_2^{in}\right\}$ we have $(s_1, s_2) \in \mathrm{FSB}_1$.
- From $x_2 > 0$ and (4) we have $f_2(s_1, s_2) = D_2$. Therefore, using $\mathrm{ZNGI}_2 = \{(s_1, s_2) \in \mathcal{C} : f_2(s_1, s_2) = D_2\}$ we have $(s_1, s_2) \in \mathrm{ZNGI}_2$.
- Hence, $(s_1, s_2) \in \mathrm{FSB}_1 \cap \mathrm{ZNGI}_2$.
- Exercise : give the details of the proof in the other cases.

Existence and stability of equilibria



- Stable equilibria are plotted with a solid circle, and unstable ones with a circle.
- Panel (a): A unique stable coexistence equilibrium E_c
- Panel (b): Multiple positive equilibria E_c^1 and E_c^2 , exhibiting bistability of E_c^1 and E_1

Existence and stability of equilibria

- We need hypotheses on f_1 and f_2
- We use the notations $f_{ij} = \partial f_i / \partial s_j$, $i, j = 1, 2$.
- For all $s_1 > 0$, $s_2 \geq 0$ we have $f_1(0, s_2) = 0$, $f_{11}(s_1, s_2) > 0$ and $f_{12}(s_1, s_2) \leq 0$.
- For all $s_1 \geq 0$, $s_2 > 0$ we have $f_2(s_1, 0) = 0$, $f_{21}(s_1, s_2) \leq 0$ and $f_{22}(s_1, s_2) > 0$.
- Let $g_1(s_2) = f_1(+\infty, s_2) = \sup_{s_1 > 0} f_1(s_1, s_2)$.
- Let $g_2(s_1) = f_2(s_1, +\infty) = \sup_{s_2 > 0} f_2(s_1, s_2)$.

$$f_1(s_1, s_2) = \frac{m_1 s_1}{K_1 + s_1} \frac{1}{1 + L_2 s_2} \qquad f_2(s_1, s_2) = \frac{m_2 s_2}{K_2 + s_2} \frac{1}{1 + L_1 s_1}$$

$$g_1(s_2) = \frac{m_1}{1 + L_2 s_2} \qquad g_2(s_1) = \frac{m_2}{1 + L_1 s_1}$$

The break-even concentrations

- For $s_2 \geq 0$ and $D \in [0, g_1(s_2))$, the break-even concentration $s_1 = \lambda_1(D, s_2)$ is the unique solution of $f_1(s_1, s_2) = D$, i.e.

$$s_1 = \lambda_1(s_2, D) \iff f_1(s_1, s_2) = D.$$

- This solution exists and is unique since $f_{11}(s_1, s_2) > 0$
- We have $\mathrm{ZNGI}_1 = \{(s_1, s_2) \in \mathcal{C} : s_1 = \lambda_1(s_2, D_1)\}$
- For $s_1 \geq 0$ and $D \in [0, g_2(s_1))$, the break-even concentration $s_2 = \lambda_2(s_1, D)$ is the unique solution of $f_2(s_1, s_2) = D$, i.e.

$$s_2 = \lambda_2(s_1, D) \iff f_2(s_1, s_2) = D.$$

- This solution exists and is unique since $f_{22}(s_1, s_2) > 0$
- We have $\mathrm{ZNGI}_2 = \{(s_1, s_2) \in \mathcal{C} : s_2 = \lambda_2(s_1, D_2)\}$

The regions $\mathcal{L}_1$, $\mathcal{R}_1$, $\mathcal{A}_2$ and $\mathcal{B}_2$ of $\mathcal{F}$

- $\mathrm{ZNGI}_1 = \{(s_1, s_2) \in \mathcal{C} : f_1(s_1, s_2) = D_1\}$ divides the feasible set $\mathcal{F}$ into two connected possibly empty, regions

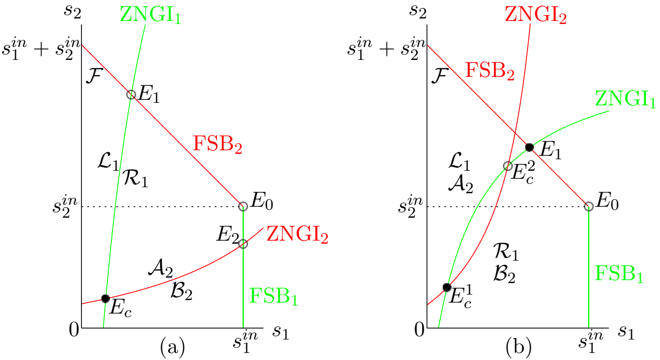
$$\mathcal{L}_1 = \{(s_1, s_2) \in \mathcal{F} : f_1(s_1, s_2) < D_1\},$$
$$\mathcal{R}_1 = \{(s_1, s_2) \in \mathcal{F} : f_1(s_1, s_2) > D_1\}$$

- $\mathrm{ZNGI}_2 = \{(s_1, s_2) \in \mathcal{C} : f_2(s_1, s_2) = D_2\}$ divides the feasible set $\mathcal{F}$ into two connected possibly empty, regions

$$\mathcal{B}_2 = \{(s_1, s_2) \in \mathcal{F} : f_2(s_1, s_2) < D_2\},$$
$$\mathcal{A}_2 = \{(s_1, s_2) \in \mathcal{F} : f_2(s_1, s_2) > D_2\}$$

- Exercise : give the details of the proof

Regions $\mathcal{L}_1$, $\mathcal{R}_1$, $\mathcal{A}_2$ and $\mathcal{B}_2$ of $\mathcal{F}$

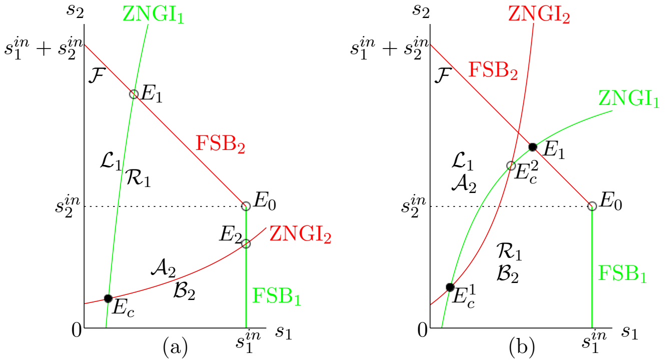


- Panel (a): A unique stable coexistence equilibrium E_c
- Panel (b): Multiple positive equilibria E_c^1 and E_c^2 , exhibiting bistability of E_c^1 and E_1

Theorem

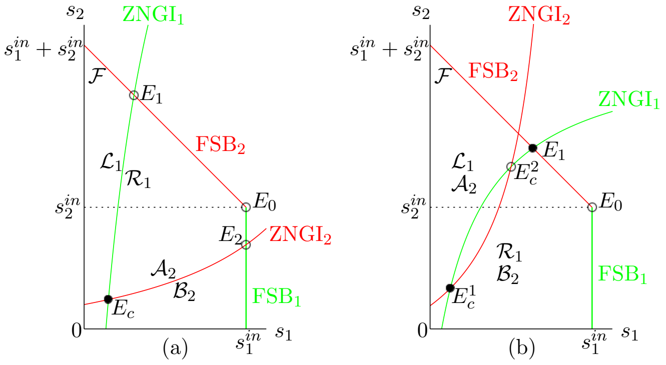
	Existence condition	Stability condition (local)
E_0	Always exists	$(s_1^{in}, s_2^{in}) \in \mathcal{L}_1 \cap \mathcal{B}_2$
E_1	$(s_1^{in}, s_2^{in}) \in \mathcal{R}_1$	$(\bar{s}_1, \bar{s}_2) \in \mathcal{B}_2$
E_2	$(s_1^{in}, s_2^{in}) \in \mathcal{A}_2$	$(\tilde{s}_1, \tilde{s}_2) \in \mathcal{L}_1$
E_c	$(s_1^*, s_2^*) \in \mathcal{F}^{\mathrm{o}}$	$(f_{11} f_{22} - f_{12} f_{21})(s_1^*, s_2^*) > 0$

Remark. The condition $(f_{11} f_{22} - f_{12} f_{21})(s_1^*, s_2^*) > 0$ means that the ZNGIs intersect transversally at (s_1^*, s_2^*) and ZNGI_2 crosses ZNGI_1 from the left to the right



On panel (a)

- E_0 is unstable since $(s_1^{in}, s_2^{in}) \notin \mathcal{L}_1 \cap \mathcal{B}_2$,
- E_1 exists since $(s_1^{in}, s_2^{in}) \notin \mathcal{R}_1$ and is unstable since $(\bar{s}_1, \bar{s}_2) \notin \mathcal{B}_2$,
- E_2 exists since $(s_1^{in}, s_2^{in}) \in \mathcal{A}_2$ and is unstable since $(s_1^{in}, \tilde{s}_2) \notin \mathcal{L}_1$
- E_c is stable since, ZNGI_2 crosses ZNGI_1 from the left to the right.



On panel (b)

- E_0 is unstable since $(s_1^{in}, s_2^{in}) \notin \mathcal{L}_1 \cap \mathcal{B}_2$,
- E_1 exists since $(s_1^{in}, s_2^{in}) \notin \mathcal{R}_1$ and is stable since $(\bar{s}_1, \bar{s}_2) \in \mathcal{B}_2$,
- E_2 does not exist since $(s_1^{in}, s_2^{in}) \notin \mathcal{A}_2$
- E_c^1 is stable since, ZNGI_2 crosses ZNGI_1 from the left to the right and E_c^2 is unstable since, ZNGI_2 crosses ZNGI_1 from the right to the left.

Existence and stability of equilibria

The system can have four types of equilibria:

- The washout equilibrium $E_0 = (s_1^{in}, 0, s_2^{in}, 0)$, which always exist. It is stable if and only if

  $$f_1(s_1^{in}, s_2^{in}) < D_1 \text{ and } f_1(s_1^{in}, s_2^{in}) < D_2 \text{ i.e. } (s_1^{in}, s_2^{in}) \in \mathcal{L}_1 \cap \mathcal{B}_2$$

- A boundary equilibrium $E_1 = (\bar{s}_1, \bar{x}_1, \bar{s}_2, 0)$, with $(\bar{s}_1, \bar{s}_2) = \mathrm{ZNGI}_1 \cap \mathrm{FSB}_2$, where $\bar{s}_1$ is a solution of equation

  $$f_1(s_1, s_1^{in} + s_2^{in} - s_1) = D_1 \tag{5}$$

  and

  $$\bar{s}_2 = s_1^{in} + s_2^{in} - \bar{s}_1, \quad \bar{x}_1 = \frac{D}{D_1}\left(s_1^{in} - \bar{s}_1\right). \tag{6}$$

  It is unique if it exists.
  It exists if and only if $f_1(s_1^{in}, s_2^{in}) > D_1$, i.e. $(s_1^{in}, s_2^{in}) \in \mathcal{R}_1$.
  It is stable if and only if $f_2(\bar{s}_1, \bar{s}_2) < D_2$, i.e. $(\bar{s}_1, \bar{s}_2) \in \mathcal{B}_2$.

Existence and stability of equilibria

- A boundary equilibrium $E_2 = (\tilde{s}_1, 0, \tilde{s}_2, \tilde{x}_2)$, with $(\tilde{s}_1, \tilde{s}_2) = \mathrm{FSB}_1 \cap \mathrm{ZNGI}_2$, where

$$\tilde{s}_1 = s_1^{in}, \quad \tilde{s}_2 = \lambda_2(s_1^{in}, D_2), \quad \tilde{x}_2 = \frac{D}{D_2}\left(s_2^{in} - \tilde{s}_2\right) \tag{7}$$

  It exists if and only if $f_2(s_1^{in}, s_2^{in}) > D_2$, i.e. $(s_1^{in}, s_2^{in}) \in \mathcal{A}_2$.
  It is stable if and only if $f_1(\tilde{s}_1, \tilde{s}_2) < D_1$, i.e. $(\tilde{s}_1, \tilde{s}_2) \in \mathcal{L}_1$.
- Coexistence equilibria $E_c = (s_1^*, x_1^*, s_2^*, x_2^*)$, with $(s_1^*, s_2^*) \in \mathrm{ZNGI}_1 \cap \mathrm{ZNGI}_2$, where (s_1^*, s_2^*) is a solution of the system of equations

$$f_1(s_1, s_2) = D_1, \quad f_2(s_1, s_2) = D_2. \tag{8}$$

  and

$$x_1^* = \frac{D}{D_1}\left(s_1^{in} - s_1^*\right), \quad x_2^* = \frac{D}{D_2}\left(s_1^{in} + s_2^{in} - s_1^* - x_2^*\right). \tag{9}$$

  It exists if and only if $(s_1^*, s_2^*) \in \mathcal{F}^{\mathrm{o}}$. It is stable if an only if

$$(f_{11}f_{22} - f_{12}f_{21})(s_1^*, s_2^*) > 0 \tag{10}$$

Proof for existence

- For $E_1 = (\bar{s}_1, \bar{x}_1, \bar{s}_2, 0)$ we have $(\bar{s}_1, \bar{s}_2) = \mathrm{ZNGI}_1 \cap \mathrm{FSB}_2$.
- This condition is equivalent to

$$f_1(\bar{s}_1, \bar{s}_2) = D_1 \quad \text{and} \quad \bar{s}_1 + \bar{s}_2 = s_1^{in} + s_2^{in} \tag{11}$$

- From the second formula in (11), we have $\bar{s}_2 = s_1^{in} + s_2^{in} - \bar{s}_1$ which proves (6).
- Replacing $\bar{s}_2$ in the first formula of (11) we have $f_1(\bar{s}_1, s_1^{in} + s_2^{in} - \bar{s}_1) = D_1$.
- Therefore $\bar{s}_1$ is solution of equation (5).
- The equation (5) is equivalent to $\psi_1(s_1) = D_1$, where $\psi_1(s_1)$ is defined by

$$\psi_1(s_1) = f_1(s_1, s_1^{in} + s_2^{in} - s_1)$$

- We have $\psi_1'(s_1) = (f_{11} - f_{12})(s_1, s_1^{in} + s_2^{in} - s_1) > 0$.
- Therefore equation (5) has at most one solution. Hence, if it exists, E_1 is unique.
- E_1 exists if an only if equation $\psi_1(s_1) = D_1$ has a solution in the interval $(0, s_1^{in})$. Since $\psi_1(0) = 0$ and $\psi_1(s_1^{in}) = f_1(s_1^{in}, s_2^{in})$, the solution exists if an only if $f_1(s_1^{in}, s_2^{in}) > D_1$.

Proof for stability

$$
\begin{aligned}
\dot{x}_1 &= \left(f_1\left(s_1, s_2\right) - D_1\right) x_1, \\
\dot{x}_2 &= \left(f_2\left(s_1, s_2\right) - D_2\right) x_2, \\
\dot{s}_1 &= D\left(s_1^{in} - s_1\right) - f_1\left(s_1, s_2\right) x_1, \\
\dot{s}_2 &= D\left(s_2^{in} - s_2\right) + f_1\left(s_1, s_2\right) x_1 - f_2\left(s_1, s_2\right) x_2.
\end{aligned}
$$

The local stability of an equilibrium point depends on the sign of the real parts of the eigenvalues of the corresponding Jacobian matrix for the system:

$$
J = \begin{bmatrix}
f_1 - D_1 & 0 & f_{11}x_1 & f_{12}x_1 \\
0 & f_2 - D_2 & f_{21}x_2 & f_{22}x_2 \\
-f_1 & 0 & -D - f_{11}x_1 & -f_{12}x_1 \\
f_1 & -f_2 & f_{11}x_1 - f_{21}x_2 & -D + f_{12}x_1 - f_{22}x_2
\end{bmatrix}
$$

where f_i and $f_{ij} = \frac{\partial f_i}{\partial s_j}$ are evaluated at the components (x_1, x_2, s_1, s_2) of the equilibrium point.

Sability of E_0

At E_0, $x_1 = 0$ and $x_1 = 0$. The Jacobian matrix becomes

$$J_0 = \begin{bmatrix} f_1\left(s_1^{in}, s_2^{in}\right) - D_1 & 0 & 0 & 0 \\ 0 & f_2\left(s_1^{in}, s_2^{in}\right) - D_2 & 0 & 0 \\ -f_1\left(s_1^{in}, s_2^{in}\right) & 0 & -D & 0 \\ f_1\left(s_1^{in}, s_2^{in}\right) & -f_2\left(s_1^{in}, s_2^{in}\right) & 0 & -D \end{bmatrix}$$

Its eigenvalues are $\lambda_1 = f_1\left(s_1^{in}, s_2^{in}\right) - D_1$, $\lambda_2 = f_2\left(s_1^{in}, s_2^{in}\right) - D_2$ and $\lambda_3 = \lambda_4 = -D$. Therefore E_0 is stable if and only if $\lambda_1 < 0$ and $\lambda_2 < 0$, that is to say

$$f_1\left(s_1^{in}, s_2^{in}\right) < D_1 \quad \text{and} \quad f_2\left(s_1^{in}, s_2^{in}\right) < D_2$$

Stability of E_1

At E_1, $x_2 = 0$ and $x_1 > 0$, so that $f_1 = D_1$. Evaluated at E_1, the Jacobian matrix becomes:

$$J_1 = \begin{bmatrix} 0 & 0 & f_{11}x_1 & f_{12}x_1 \\ 0 & f_2 - D_2 & 0 & 0 \\ -D_1 & 0 & -D - f_{11}x_1 & -f_{12}x_1 \\ D_1 & -f_2 & f_{11}x_1 & -D + f_{12}x_1 \end{bmatrix}$$

Its characteristic polynomial is:

$$P_1(\lambda) = (\lambda + D)(\lambda - f_2 + D_2)(\lambda^2 + c_1\lambda + c_2)$$

where $c_1 = D + (f_{11} - f_{12})x_1$ and $c_2 = D_1(f_{11} - f_{12})x_1$.

The eigenvalues of J_1 are $\lambda_1 = -D$, $\lambda_2 = f_2(\bar{s}_1, \bar{s}_2) - D_2$, together with λ_3 and λ_4, the roots of the quadratic polynomial in $P_1(\lambda)$.

Since $f_{11} > 0$ and $f_{12} \leq 0$, one has $c_1 > 0$ and $c_2 > 0$. Hence, λ_3 and λ_4 have negative real parts. Therefore E_1 is stable if and only if $\lambda_2 < 0$, that is to say

$$f_2(\bar{s}_1, \bar{s}_2) < D_1$$

Stability of E_2

At E_2, $x_1 = 0$ and $x_2 > 0$, so that $f_2 = D_2$. Evaluated at E_2, the Jacobian matrix becomes:

$$J_2 = \begin{bmatrix} f_1 - D_1 & 0 & 0 & 0 \\ 0 & 0 & f_{21}x_2 & f_{22}x_2 \\ -f_1 & 0 & -D & 0 \\ f_1 & -D_2 & -f_{21}x_2 & -D - f_{12}x_2 \end{bmatrix}$$

Its characteristic polynomial is:

$$P_2(\lambda) = (\lambda - f_1 + D_1)(\lambda + D)(\lambda^2 + c_1\lambda + c_2)$$

where $c_1 = D + f_{22}x_2$ and $c_2 = D_2 f_2 x_2$

The eigenvalues of J_2 are $\lambda_1 = f_1\left(\tilde{s}_1, \tilde{s}_2\right) - D_1$, $\lambda_2 = -D$, together with λ_3 and λ_4, the roots of the quadratic polynomial in $P_1(\lambda)$.

Since $f_{22} > 0$, one has $c_1 > 0$ and $c_2 > 0$. Hence, λ_3 and λ_4 have negative real parts. Therefore E_2 is stable if and only if $\lambda_1 < 0$, that is to say

$$f_1\left(\tilde{s}_1, \tilde{s}_2\right) < D_1$$

Stability of E_c

At E_c, $x_1 > 0$ and $x_2 > 0$, so that $f_1 = D_1$ and $f_2 = D_2$. Evaluated at E_c, the Jacobian matrix becomes:

$$J_c = \begin{bmatrix} 0 & 0 & f_{11}x_1 & f_{12}x_1 \\ 0 & 0 & f_{21}x_2 & f_{22}x_2 \\ -D_1 & 0 & -D - f_{11}x_1 & -f_{12}x_1 \\ D_1 & -D_2 & f_{11}x_1 - f_{21}x_2 & -D - f_{12}x_1 - f_{22}x_2 \end{bmatrix}$$

Its characteristic polynomial is:

$$P_c(\lambda) = \lambda^4 + c_1\lambda^3 + c_2\lambda^2 + c_3\lambda + c_4)$$

where

$$\begin{aligned} c_1 &= 2D + (f_{11} - f_{12})x_1 + f_{22}x_2 \\ c_2 &= D^2 + (D + D_1)(f_{11} - f_{12})x_1 + (D + D_2)f_{22}x_2 + (f_{11}f_{22} - f_{12}f_{21})x_1x_2 \\ c_3 &= DD_1(f_{11} - f_{12})x_1 + DD_2f_{22}x_2 + (D_1 + D_2)(f_{11}f_{22} - f_{12}f_{21})x_1x_2 \\ c_4 &= D_1D_2(f_{11}f_{22} - f_{12}f_{21})x_1x_2 \end{aligned}$$

The eigenvalues are of J_c have negative real parts if an only if the Routh-Hurwitz conditions are satisfied:

$$c_1 > 0, \quad c_3 > 0, \quad c_4 > 0 \quad \text{and} \quad r_1 = c_1c_2c_3 - c_1^2c_4 - c_3^2 > 0. \qquad (12)$$

Stability of E_c (continued)

- Since $f_{11} > 0$, $f_{12} \leq 0$ and $f_{22} > 0$ we see that $c_1 > 0$
- From $c_4 = D_1 D_2 (f_{11} f_{22} - f_{12} f_{21}) x_1 x_2$ we see that $c_4 > 0$ if and only if $f_{11} f_{22} - f_{12} f_{21} > 0$
- If $f_{11} f_{22} - f_{12} f_{21} > 0$ we deduce that $c_3 > 0$
- If $f_{11} f_{22} - f_{12} f_{21} > 0$ we can also prove that $r > 0$ (very technical and difficult !)
- Hence the conditions (12) are satisfied if and only if $f_{11} f_{22} - f_{12} f_{21} > 0$.

Sommaire

Operating parameters

- We consider the space of the operating parameters (SOP) defined by

$$\mathrm{SOP} := \left\{(D, s_1^{in}, s_2^{in}) \in \mathbb{R}^3 : D > 0, s_1^{in} \geq 0, s_2^{in} \geq 0\right\}$$

- We fix the biological parameters, i.e. the growth functions f_1 and f_2 and the parameters α_i and a_i, $i = 1, 2$.
- The operating diagram has the operating parameters as its coordinates and the various regions defined within it correspond to qualitatively different asymptotic behaviors.
- We begin with the simple cases C1, C2 and S1

Operating diagram

- Since the system has three operating parameters, and it is not easy to visualize regions in the three-dimensional operating parameter space, we fix the dilution rate D and we show the operating diagram in the operating plane (s_1^{in}, s_2^{in}). The effects of D can be shown in a series of operating diagrams.
- The curves

$$\Gamma_1 = \{(s_1^{in}, s_2^{in}) \in \mathrm{SOP} : f_1(s_1^{in}, s_2^{in}) = D_1 = \alpha_1 D + a_1\}$$
$$\Gamma_2 = \{(s_1^{in}, s_2^{in}) \in \mathrm{SOP} : f_2(s_1^{in}, s_2^{in}) = D_2 = \alpha_2 D + a_2\}$$

  play an essential role in the construction of the operating diagram
- Even though Γ_1 and Γ_2 are defined by the same equations as ZNGI_1 and ZNGI_2, it should be noted that the Γ_i are curves in SOP while for ZNGI_i, they are curves in $\mathcal{C}$

Outline of the method

- Find the feasible set
- Find the FSBs (Feasable Set Boundaries)
- Find the ZNGIs (Zero Net Growth Isoclines)
- Find the equilibria
- Determine their stability conditions

$\mathcal{F}$, FSB and ZNGI

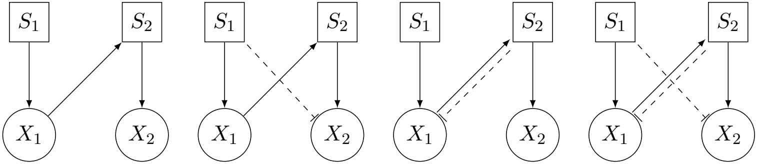
- $$\begin{cases} \dot{s}_1 &= D\left(s_1^{in} - s_1\right) - f_1\left(s_1, s_2\right)x_1, \\ \dot{x}_1 &= \left(f_1\left(s_1, s_2\right) - D_1\right)x_1, \\ \dot{s}_2 &= D\left(s_2^{in} - s_2\right) + f_1\left(s_1, s_2\right)x_1 - f_2\left(s_1, s_2\right)x_2, \\ \dot{x}_2 &= \left(f_2\left(s_1, s_2\right) - D_2\right)x_2, \end{cases}$$
- At equilibria : $\begin{cases} x_1 = \frac{D}{D_1}\left(s_1^{in} - s_1\right), \\ x_2 = \frac{D}{D_2}\left(s_1^{in} + s_2^{in} - s_1 - s_2\right). \end{cases}$
- $\mathcal{F} = \{(s_1, s_2) \in \mathbb{R}^2 : 0 \leq s_1 \leq s_1^{in}, \quad 0 \leq s_1 + s_2 \leq s_1^{in} + s_2^{in}\}$
- $\begin{cases} \mathrm{FSB}_1 = \{(s_1, s_2) \in \mathcal{C} : s_1 = s_1^{in}, 0 \leq s_2 \leq s_2^{in}\} \\ \mathrm{FSB}_2 = \{(s_1, s_2) \in \mathcal{C} : 0 \leq s_1 \leq s_1^{in}, s_1 + s_2 = s_1^{in} + s_2^{in}\} \end{cases}$
- $\begin{cases} \mathrm{ZNGI}_1 = \{(s_1, s_2) \in \mathcal{C} : f_1(s_1, s_2) = D_1\} \\ \mathrm{ZNGI}_2 = \{(s_1, s_2) \in \mathcal{C} : f_2(s_1, s_2) = D_2\} \end{cases}$
- $\begin{cases} \dot{x}_1 = 0 \iff (s_1, s_2) \in \mathrm{FSB}_1 \text{ or } (s_1, s_2) \in \mathrm{ZNGI}_1 \\ \dot{x}_2 = 0 \iff (s_1, s_2) \in \mathrm{FSB}_2 \text{ or } (s_1, s_2) \in \mathrm{ZNGI}_2 \end{cases}$

Theorem

	Existence condition	Stability condition (local)
E_0	Always exists	$(s_1^{in}, s_2^{in}) \in \mathcal{L}_1 \cap \mathcal{B}_2$
E_1	$(s_1^{in}, s_2^{in}) \in \mathcal{R}_1$	$(\bar{s}_1, \bar{s}_2) \in \mathcal{B}_2$
E_2	$(s_1^{in}, s_2^{in}) \in \mathcal{A}_2$	$(\tilde{s}_1, \tilde{s}_2) \in \mathcal{L}_1$
E_c	$(s_1^*, s_2^*) \in \mathcal{F}^{\mathrm{o}}$	$(f_{11} f_{22} - f_{12} f_{21})(s_1^*, s_2^*) > 0$

Remark. The condition $(f_{11} f_{22} - f_{12} f_{21})(s_1^*, s_2^*) > 0$ means that the ZNGIs intersect transversally at (s_1^*, s_2^*) and ZNGI_2 crosses ZNGI_1 from the left to the right

The cases C1, C2, S1 and S2



Case	f_1	f_2
C1	$f_1'(s_1) > 0$	$f_2'(s_2) > 0$
C2	$f_1'(s_1) > 0$	$f_{22} > 0$ and $f_{21} \leq 0$
S1	$f_{11} > 0$ and $f_{12} \leq 0$	$f_2'(s_2) > 0$
S2	$f_{11} > 0$ and $f_{12} \leq 0$	$f_{22} > 0$ and $f_{21} \leq 0$

Cases C1, C2 and S1

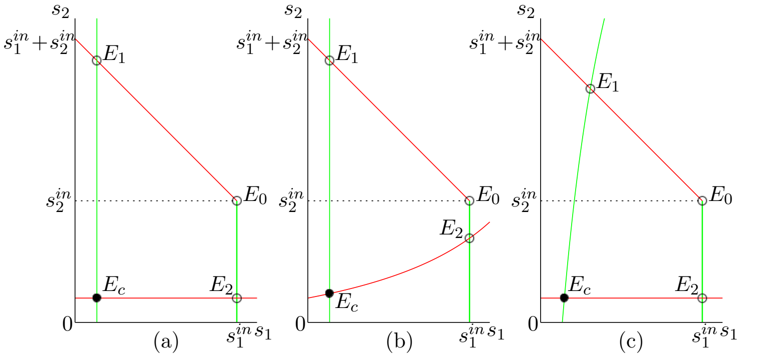
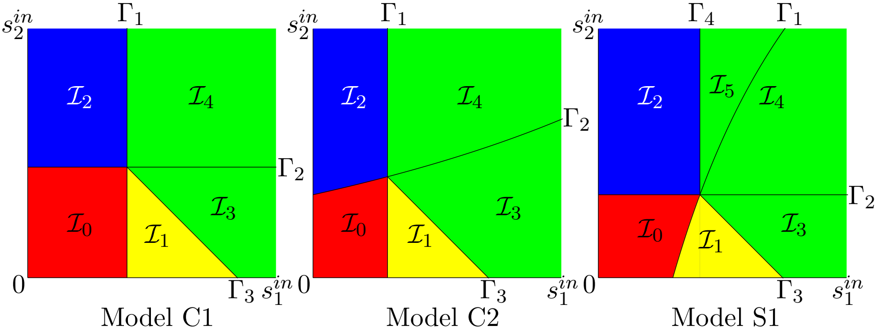


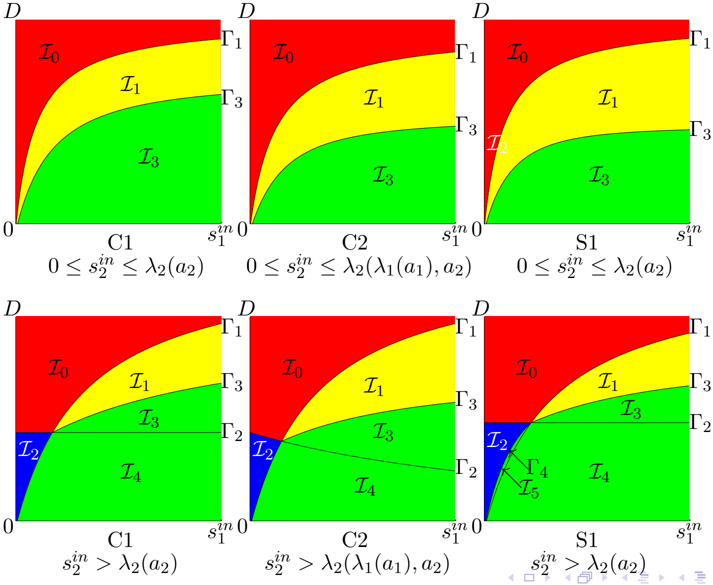
Figure: The feasible set and the ZNGIs for (a): C1 , (b): C2 and (c): S1.

Operating diagram (D constant)



	E_0	E_1	E_2	E_c^1	E_c^2	Color
$\mathcal{I}_0$	S					Red
$\mathcal{I}_1$	U	S				Yellow
$\mathcal{I}_2$	U		S			Blue
$\mathcal{I}_3$	U	U		S		Green
$\mathcal{I}_4$	U	U	U	S		Green
$\mathcal{I}_5$	U		U	S		Green

Operating diagram (s_2^{in} constant)



Pure commensalism

$$
\begin{aligned}
\dot{s}_1 &= D\left(s_1^{in} - s_1\right) - f_1\left(s_1\right)x_1, \\
\dot{x}_1 &= \left(f_1\left(s_1\right) - D_1\right)x_1, \\
\dot{s}_2 &= D\left(s_2^{in} - s_2\right) + f_1\left(s_1\right)x_1 - f_2\left(s_2\right)x_2, \\
\dot{x}_2 &= \left(f_2\left(s_2\right) - D_2\right)x_2,
\end{aligned}
$$

- $f_1(0) = 0$ and for $s_1 > 0$, $f_1'(s_1) > 0$
- $f_2(0) = 0$ and for $s_2 > 0$, $f_2'(s_2) > 0$

ZNGIs and equilibria

Table: Break-even concentrations and ZNGIs.

Break-even concentrations and ZNGIs
For $D \in [0, m_1)$ $s_1 = \lambda_1(D)$ is the unique solution of equation $f_1(s_1) = D$.
$\mathrm{ZNGI}_1 = \{(s_1, s_2) : s_1 = \lambda_1(D_1)\}$
For $D \in [0, m_2)$, $s_2 = \lambda_2(D)$ is the unique solution of equation $f_2(s_2) = D$.
$\mathrm{ZNGI}_2 = \{(s_1, s_2) : s_2 = \lambda_2(D_2)\}$

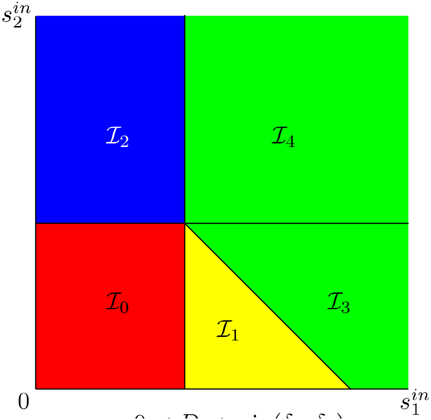
Table: Equilibria.

Components s_1 and s_2 of boundary and positive equilibria		
$E_1 = (\bar{s}_1, \bar{x}_1, \bar{s}_2, 0)$	$\bar{s}_1 = \lambda_1(D_1)$	$\bar{s}_2 = s_1^{in} + s_2^{in} - \bar{s}_1$
$E_2 = (\tilde{s}_1, 0, \tilde{s}_2, \tilde{x}_2)$	$\tilde{s}_1 = s_1^{in}$	$\tilde{s}_2 = \lambda_2(D_2)$
$E_c = (s_1^*, x_1^*, s_2^*, x_2^*)$	$s_1^* = \lambda_1(D_1)$	$s_2^* = \lambda_2(D_2)$

Existence and stability of equilibria

	Existence condition	Stability condition (local and global)
E_0	Always exists	$s_1^{in} < \lambda_1(D_1)$ and $s_2^{in} < \lambda_2(D_2)$
E_1	$s_1^{in} > \lambda_1(D_1)$	$s_1^{in} + s_2^{in} < \lambda_1(D_1) + \lambda_2(D_2)$
E_2	$s_2^{in} > \lambda_2(D_2)$	$s_1^{in} < \lambda_1(D_1)$
E_c	$\begin{cases} s_1^{in} > \lambda_1(D_1) \quad \text{and} \\ s_1^{in} + s_2^{in} > \lambda_1(D_1) + \lambda_2(D_2) \end{cases}$	Stable if it exists

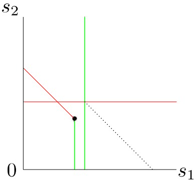
The Γ_k and the operating diagram



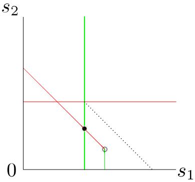
	E_0	E_1	E_2	E_c	Color
$\mathcal{I}_0$	S				Red
$\mathcal{I}_1$	U	S			Yellow
$\mathcal{I}_2$	U		S		Blue
$\mathcal{I}_3$	U	U		S	Green
$\mathcal{I}_4$	U	U	U	S	Green

$$\Gamma_1 = \{(D, s_1^{in}, s_2^{in}) : s_1^{in} = \lambda_1(D_1)\} = \{(D, s_1^{in}, s_2^{in}) : D_1 = f_1(s_1^{in})\}$$
$$\Gamma_2 = \{(D, s_1^{in}, s_2^{in}) : s_2^{in} = \lambda_2(D_2)\} = \{(D, s_1^{in}, s_2^{in}) : D_2 = f_2(s_2^{in})\}$$
$$\Gamma_3 = \{(D, s_1^{in}, s_2^{in}) : s_1^{in} + s_2^{in} = \lambda_1(D_1) + \lambda_2(D_2) \text{ and } s_2^{in} < \lambda_2(D_2)\}$$

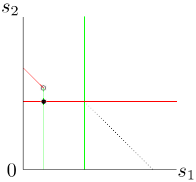
Proof



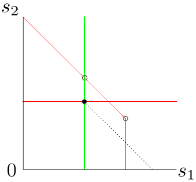
$(s_1^{in}, s_2^{in}) \in \mathcal{I}_0$



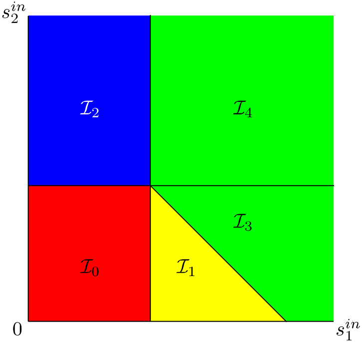
$(s_1^{in}, s_2^{in}) \in \mathcal{I}_1$

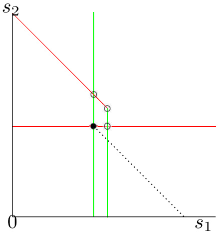


$(s_1^{in}, s_2^{in}) \in \mathcal{I}_2$



$(s_1^{in}, s_2^{in}) \in \mathcal{I}_3$





$(s_1^{in}, s_2^{in}) \in \mathcal{I}_4$

Commensalism with inhibition of x_2 by s_1

$$
\begin{aligned}
\dot{s}_1 &= D\left(s_1^{in} - s_1\right) - f_1\left(s_1\right)x_1,\\
\dot{x}_1 &= \left(f_1\left(s_1\right) - D_1\right)x_1,\\
\dot{s}_2 &= D\left(s_2^{in} - s_2\right) + f_1\left(s_1\right)x_1 - f_2\left(s_1, s_2\right)x_2,\\
\dot{x}_2 &= \left(f_2\left(s_1, s_2\right) - D_2\right)x_2,
\end{aligned}
$$

- $f_1(0) = 0$ and for $s_1 > 0$, $f_1'(s_1) > 0$
- $f_2(s_1, 0) = 0$ and for $s_1 \geq 0, s_2 > 0$ we have

$$f_{22}(s_1, s_2) > 0 \quad \text{and} \quad f_{12}(s_1, s_2) \leq 0$$

ZNGIs and equilibria

Table: Break-even concentrations and ZNGIs

Break-even concentrations and ZNGIs
For $D \in [0, m_1)$, $s_1 = \lambda_1(D)$ is the solution of equation $f_1(s_1) = D$.
$\mathrm{ZNGI}_1 = \{(s_1, s_2) : s_1 = \lambda_1(D_1)\}$
For $s_1 \geq 0$ and $D \in [0, m_2(s_1))$, $s_2 = \lambda_2(s_1, D)$ is the solution of $f_2(s_1, s_2) = D$.
$\mathrm{ZNGI}_2 = \{(s_1, s_2) : s_2 = \lambda_2(s_1, D_2)\}$

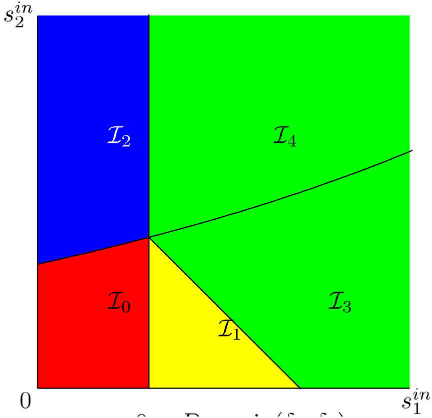
Table: Equilibria

Components s_1 and s_2 of boundary and positive equilibria		
$E_1 = (\bar{s}_1, \bar{x}_1, \bar{s}_2, 0)$	$\bar{s}_1 = \lambda_1(D_1)$	$\bar{s}_2 = s_1^{in} + s_2^{in} - \bar{s}_1$
$E_2 = (\tilde{s}_1, 0, \tilde{s}_2, \tilde{x}_2)$	$\tilde{s}_1 = s_1^{in}$	$\tilde{s}_2 = \lambda_2(s_1^{in}, D_2)$
$E_c = (s_1^*, x_1^*, s_2^*, x_2^*)$	$s_1^* = \lambda_1(D_1)$	$s_2^* = \lambda_2(\lambda_1(D_1), D_2)$

Existence an stability of equilibria

	Existence condition	Stability condition (local and global)
E_0	Always exists	$s_1^{in} < \lambda_1(D_1)$ and $s_2^{in} < \lambda_2(s_1^{in}, D_2)$
E_1	$s_1^{in} > \lambda_1(D_1)$	$s_1^{in} + s_2^{in} < \lambda_1(D_1) + \lambda_2(\lambda_1(D_1), D_2)$
E_2	$s_2^{in} > \lambda_2(s_1^{in}, D_2)$	$s_1^{in} < \lambda_1(D_1)$
E_c	$\begin{cases} s_1^{in} > \lambda_1(D_1) \quad \text{and} \\ s_1^{in} + s_2^{in} > \lambda_1(D_1) + \lambda_2(\lambda_1(D_1), D_2) \end{cases}$	Stable if it exists

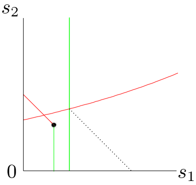
The Γ_k and the operating diagram



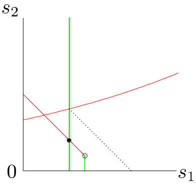
	E_0	E_1	E_2	E_c	Color
$\mathcal{I}_0$	S				Red
$\mathcal{I}_1$	U	S			Yellow
$\mathcal{I}_2$	U		S		Blue
$\mathcal{I}_3$	U	U		S	Green
$\mathcal{I}_4$	U	U	U	S	Green

$$\Gamma_1 = \left\{(D, s_1^{in}, s_2^{in}) : s_1^{in} = \lambda_1(D_1)\right\} = \left\{(D, s_1^{in}, s_2^{in}) : D_1 = f_1(s_1^{in})\right\}$$
$$\Gamma_2 = \left\{(D, s_1^{in}, s_2^{in}) : s_2^{in} = \lambda_2(s_1^{in}, D_2)\right\} = \left\{(D, s_1^{in}, s_2^{in}) : D_2 = f_2(s_1^{in}, s_2^{in})\right\}$$
$$\Gamma_3 = \left\{(D, s_1^{in}, s_2^{in}) : s_1^{in} + s_2^{in} = \lambda_1(D_1) + \lambda_2(\lambda_1(D_1), D_2) \text{ and } s_1^{in} > \lambda_1(D_1)\right\}$$

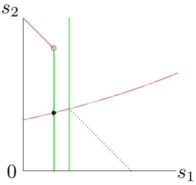
Proof



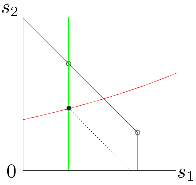
$(s_1^{in}, s_2^{in}) \in \mathcal{I}_0$



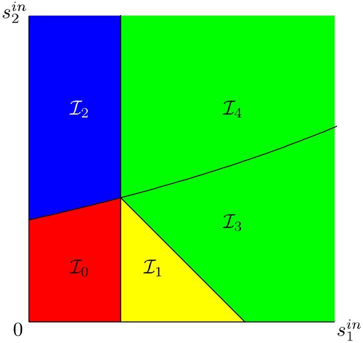
$(s_1^{in}, s_2^{in}) \in \mathcal{I}_1$

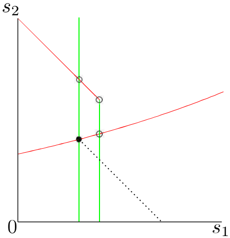


$(s_1^{in}, s_2^{in}) \in \mathcal{I}_2$



$(s_1^{in}, s_2^{in}) \in \mathcal{I}_3$





$(s_1^{in}, s_2^{in}) \in \mathcal{I}_4$

Pure syntrophy

$$
\begin{aligned}
\dot{s}_1 &= D\left(s_1^{in} - s_1\right) - f_1\left(s_1, s_2\right)x_1,\\
\dot{x}_1 &= \left(f_1\left(s_1, s_2\right) - D_1\right)x_1,\\
\dot{s}_2 &= D\left(s_2^{in} - s_2\right) + f_1\left(s_1, s_2\right)x_1 - f_2\left(s_2\right)x_2,\\
\dot{x}_2 &= \left(f_2\left(s_2\right) - D_2\right)x_2,
\end{aligned}
$$

- $f_1(0, s_2) = 0$ and for $s_1 > 0, s_2 \geq 0$ we have

$$f_{11}(s_1, s_2) > 0 \quad \text{and} \quad f_{12}(s_1, s_2) \leq 0$$

- $f_2(0) = 0$ and for $s_2 > 0$, $f_2'(s_2) > 0$

ZNGIs and equilibria

Table: Break-even concentrations and ZNGIs

Break-even concentrations and ZNGIs
For $s_2 \geq 0$ and $D \in [0, m_1(s_2))$, $s_1 = \lambda_1(s_2, D)$ is the solution of $f_1(s_1, s_2) = y$.
$\mathrm{ZNGI}_1 = \{(s_1, s_2) : s_1 = \lambda_1(s_2, D_1)\}$
For $D \in [0, m_2)$, $s_2 = \lambda_2(D)$ is the solution of $f_2(s_2) = D$.
$\mathrm{ZNGI}_2 = \{(s_1, s_2) : s_2 = \lambda_2(D_2)\}$

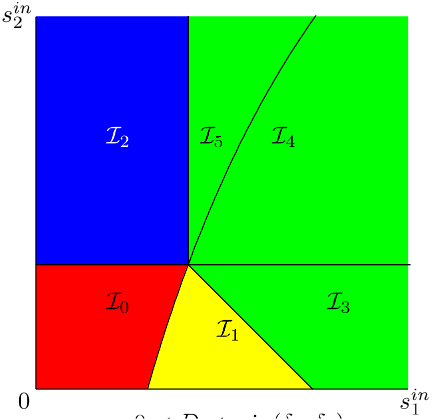
Table: Equilibria

Components s_1 and s_2 of boundary and positive equilibria		
$E_1 = (\bar{s}_1, \bar{x}_1, \bar{s}_2, 0)$	$\left\{ \begin{array}{l} s_1 \text{ is the unique solution of} \\ f_1(s_1, s_1^{in} + s_2^{in} - s_1) = 0 \end{array} \right.$	$\bar{s}_2 = s_1^{in} + s_2^{in} - \bar{s}_1$
$E_2 = (\tilde{s}_1, 0, \tilde{s}_2, \tilde{x}_2)$	$\tilde{s}_1 = s_1^{in}$	$\tilde{s}_2 = \lambda_2(D_2)$
$E_c = (s_1^*, x_1^*, s_2^*, x_2^*)$	$s_1^* = \lambda_1(\lambda_2(D_2), D_1)$	$s_2^* = \lambda_2(D_2)$

Existence an stability of equilibria

	Existence condition	Stability condition (local)
E_0	Always exists	$s_1^{in} < \lambda_1(s_2^{in}, D_1)$ and $s_2^{in} < \lambda_2(D_2)$
E_1	$s_1^{in} > \lambda_1(s_2^{in}, D_1)$	$s_1^{in} + s_2^{in} < \lambda_1(\lambda_2(D_2), D_1) + \lambda_2(D_2)$
E_2	$s_2^{in} > \lambda_2(D_2)$	$s_1^{in} < \lambda_1(\lambda_2(D_2), D_1)$
E_c	$\begin{cases} s_1^{in} > \lambda_1(\lambda_2(D_2), D_1) \quad \text{and} \\ s_1^{in} + s_2^{in} > \lambda_1(\lambda_2(D_2), D_1) + \lambda_2(D_2) \end{cases}$	Stable if it exists

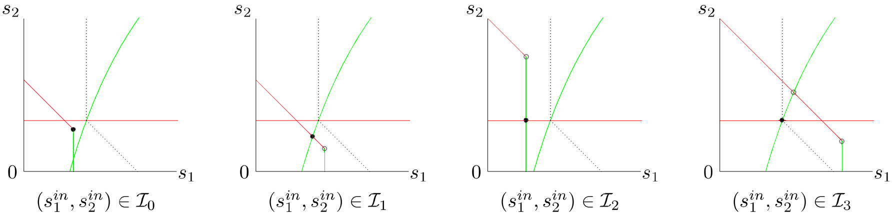
The Γ_k and the operating diagram



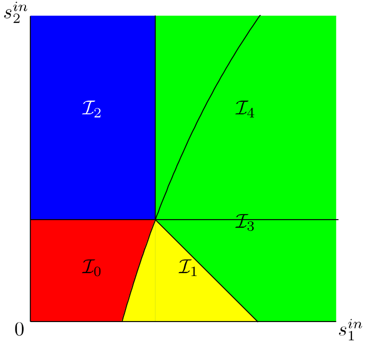
	E_0	E_1	E_2	E_c	Color
$\mathcal{I}_0$	S				Red
$\mathcal{I}_1$	U	S			Yellow
$\mathcal{I}_2$	U		S		Blue
$\mathcal{I}_3$	U	U		S	Green
$\mathcal{I}_4$	U	U	U	S	Green
$\mathcal{I}_5$	U		U	S	Green

$$\Gamma_1 = \left\{(D, s_1^{in}, s_2^{in}) : s_1^{in} = \lambda_1(s_2^{in}, D_1)\right\} = \left\{(D, s_1^{in}, s_2^{in}) : D_1 = f_1(s_1^{in}, s_2^{in})\right\}$$
$$\Gamma_2 = \left\{(D, s_1^{in}, s_2^{in}) : s_2^{in} = \lambda_2(D_2)\right\} = \left\{(D, s_1^{in}, s_2^{in}) : D_2 = f_2(s_2^{in})\right\}$$
$$\Gamma_3 = \left\{(D, s_1^{in}, s_2^{in}) : s_1^{in} + s_2^{in} = \lambda_1(\lambda_2(D_2), D_1) + \lambda_2(D_2) \text{ and } s_2^{in} < \lambda_2(D_2)\right\}$$
$$\Gamma_4 = \left\{(D, s_1^{in}, s_2^{in}) : s_1^{in} = \lambda_1(\lambda_2(D_2), D_1) \text{ and } s_2^{in} > \lambda_2(D_2)\right\}$$

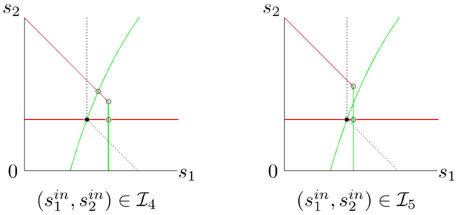
Proof



s_2
0
s_1
$(s_1^{in}, s_2^{in}) \in \mathcal{I}_0$
$(s_1^{in}, s_2^{in}) \in \mathcal{I}_1$
$(s_1^{in}, s_2^{in}) \in \mathcal{I}_2$
$(s_1^{in}, s_2^{in}) \in \mathcal{I}_3$

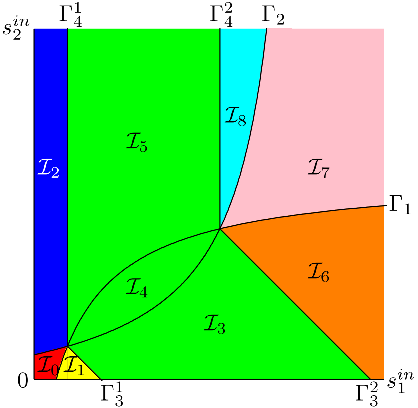


s_2^{in}
$\mathcal{I}_2$
$\mathcal{I}_4$
$\mathcal{I}_3$
$\mathcal{I}_0$
$\mathcal{I}_1$
0
s_1^{in}



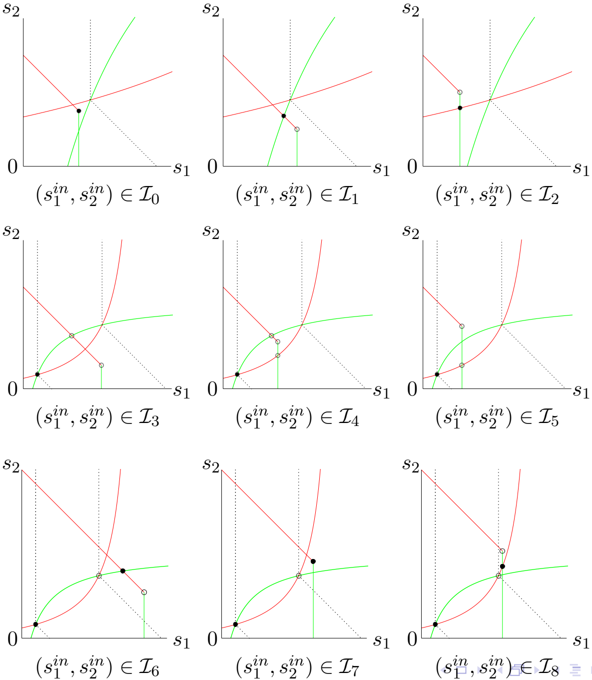
s_2
0
s_1
$(s_1^{in}, s_2^{in}) \in \mathcal{I}_4$
$(s_1^{in}, s_2^{in}) \in \mathcal{I}_5$

Operating diagram (S2)



	E_0	E_1	E_2	E_c^1	E_c^2	Color
$\mathcal{I}_0$	S					Red
$\mathcal{I}_1$	U	S				Yellow
$\mathcal{I}_2$	U		S			Blue
$\mathcal{I}_3$	U	U		S		Green
$\mathcal{I}_4$	U	U	U	S		Green
$\mathcal{I}_5$	U		U	S		Green
$\mathcal{I}_6$	U	S		S	U	Coral
$\mathcal{I}_7$	S			S	U	Pink
$\mathcal{I}_8$	U		S	S	U	Cyan

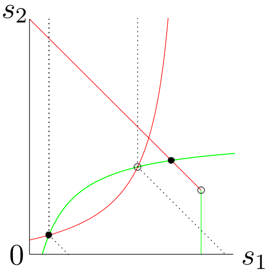
Figure: The Operating diagram of the system, in the (s_1^{in}, s_2^{in}) operating plane and $D \in (0, \delta_0)$ constant.



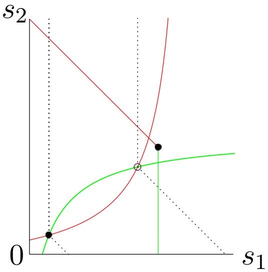
$(s_1^{in}, s_2^{in}) \in \mathcal{I}_0$ $(s_1^{in}, s_2^{in}) \in \mathcal{I}_1$ $(s_1^{in}, s_2^{in}) \in \mathcal{I}_2$

$(s_1^{in}, s_2^{in}) \in \mathcal{I}_3$ $(s_1^{in}, s_2^{in}) \in \mathcal{I}_4$ $(s_1^{in}, s_2^{in}) \in \mathcal{I}_5$

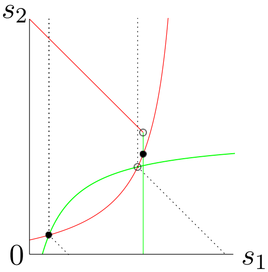
$(s_1^{in}, s_2^{in}) \in \mathcal{I}_6$ $(s_1^{in}, s_2^{in}) \in \mathcal{I}_7$ $(s_1^{in}, s_2^{in}) \in \mathcal{I}_8$



$(s_1^{in}, s_2^{in}) \in \mathcal{I}_6$

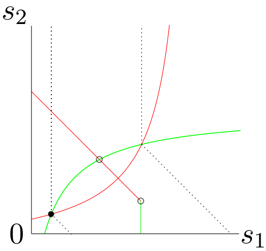


$(s_1^{in}, s_2^{in}) \in \mathcal{I}_7$

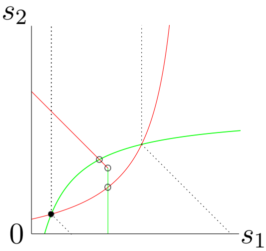


$(s_1^{in}, s_2^{in}) \in \mathcal{I}_8$

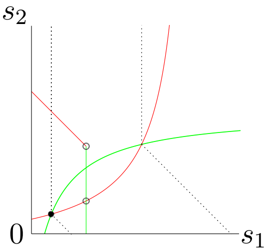
	E_0	E_1	E_2	E_c^1	E_c^2	Color
$\mathcal{I}_0$	S					Red
$\mathcal{I}_1$	U	S				Yellow
$\mathcal{I}_2$	U		S			Blue
$\mathcal{I}_3$	U	U		S		Green
$\mathcal{I}_4$	U	U	U	S		Green
$\mathcal{I}_5$	U		U	S		Green
$\mathcal{I}_6$	U	S		S	U	Coral
$\mathcal{I}_7$	S			S	U	Pink
$\mathcal{I}_8$	U		S	S	U	Cyan



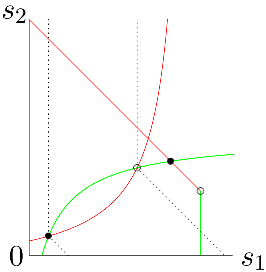
$(s_1^{in}, s_2^{in}) \in \mathcal{I}_3$



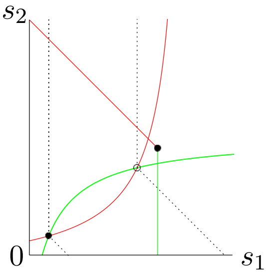
$(s_1^{in}, s_2^{in}) \in \mathcal{I}_4$



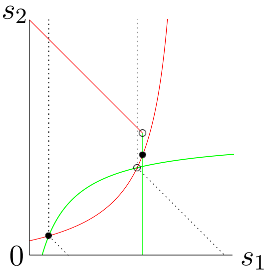
$(s_1^{in}, s_2^{in}) \in \mathcal{I}_5$



$(s_1^{in}, s_2^{in}) \in \mathcal{I}_6$

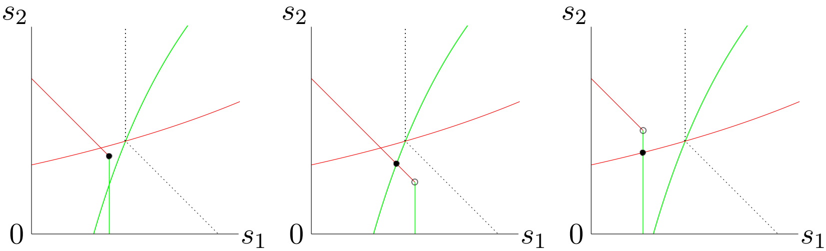


$(s_1^{in}, s_2^{in}) \in \mathcal{I}_7$



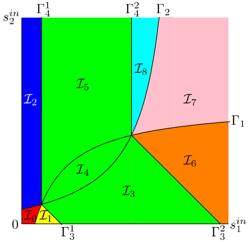
$(s_1^{in}, s_2^{in}) \in \mathcal{I}_8$

	E_0	E_1	E_2	E_c^1	E_c^2	Color
$\mathcal{I}_0$	S					Red
$\mathcal{I}_1$	U	S				Yellow
$\mathcal{I}_2$	U		S			Blue
$\mathcal{I}_3$	U	U		S		Green
$\mathcal{I}_4$	U	U	U	S		Green
$\mathcal{I}_5$	U		U	S		Green
$\mathcal{I}_6$	U	S		S	U	Coral
$\mathcal{I}_7$	S			S	U	Pink
$\mathcal{I}_8$	U		S	S	U	Cyan



$(s_1^{in}, s_2^{in}) \in \mathcal{I}_0$ $(s_1^{in}, s_2^{in}) \in \mathcal{I}_1$ $(s_1^{in}, s_2^{in}) \in \mathcal{I}_2$

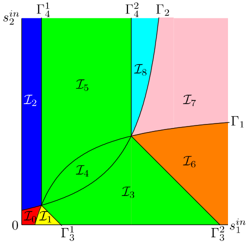
Asymptotic behaviors



	E_0	E_1	E_2	E_c^1	E_c^2	Color
$\mathcal{I}_0$	S					Red
$\mathcal{I}_1$	U	S				Yellow
$\mathcal{I}_2$	U		S			Blue
$\mathcal{I}_3$	U	U		S		Green
$\mathcal{I}_4$	U	U	U	S		Green
$\mathcal{I}_5$	U		U	S		Green
$\mathcal{I}_6$	U	S		S	U	Coral
$\mathcal{I}_7$	S			S	U	Pink
$\mathcal{I}_8$	U		S	S	U	Cyan

Table: Asymptotic behaviors).

Color	Asymptotic behavior	Regions
Red	Stability of E_0	$\mathcal{I}_0$
Yellow	Stability of E_1	$\mathcal{I}_1$
Blue	Stability of E_2	$\mathcal{I}_2$
Green	Stability of E_c^1	$\mathcal{I}_3$, $\mathcal{I}_4$, $\mathcal{I}_5$
Coral	Stability of E_1 and E_c^1	$\mathcal{I}_6$
Pink	Stability of E_0 and E_c^1	$\mathcal{I}_7$
Cyan	Stability of E_2 and E_c^1	$\mathcal{I}_8$



	E_0	E_1	E_2	E_c^1	E_c^2	Color
$\mathcal{I}_0$	S					Red
$\mathcal{I}_1$	U	S				Yellow
$\mathcal{I}_2$	U		S			Blue
$\mathcal{I}_3$	U	U		S		Green
$\mathcal{I}_4$	U	U	U	S		Green
$\mathcal{I}_5$	U		U	S		Green
$\mathcal{I}_6$	U	S		S	U	Coral
$\mathcal{I}_7$	S			S	U	Pink
$\mathcal{I}_8$	U		S	S	U	Cyan

Bifurcations

Subset of SOP	TB
$\partial\mathcal{I}_0 \cap \partial\mathcal{I}_1$	$E_0 = E_1$
$\partial\mathcal{I}_0 \cap \partial\mathcal{I}_2$	$E_0 = E_2$
$\partial\mathcal{I}_1 \cap \partial\mathcal{I}_3$	$E_1 = E_c^1$
$\partial\mathcal{I}_2 \cap \partial\mathcal{I}_5$	$E_2 = E_c^1$
$\partial\mathcal{I}_3 \cap \partial\mathcal{I}_4$	$E_0 = E_2$
$\partial\mathcal{I}_4 \cap \partial\mathcal{I}_5$	$E_0 = E_1$
$\partial\mathcal{I}_3 \cap \partial\mathcal{I}_6$	$E_1 = E_c^2$
$\partial\mathcal{I}_5 \cap \partial\mathcal{I}_8$	$E_2 = E_c^2$
$\partial\mathcal{I}_6 \cap \partial\mathcal{I}_7$	$E_0 = E_1$
$\partial\mathcal{I}_7 \cap \partial\mathcal{I}_8$	$E_0 = E_2$

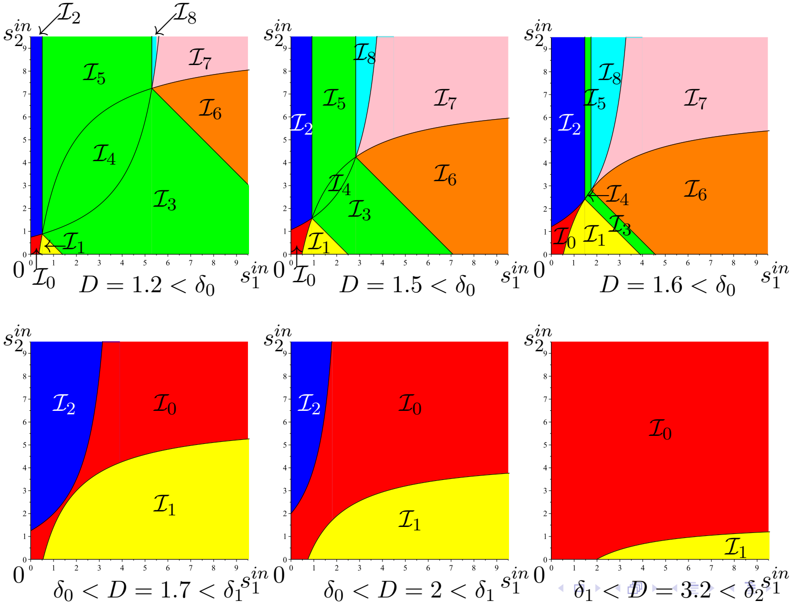
Illustrative example

$$
\begin{aligned}
\dot{s}_1 &= D\left(s_1^{in} - s_1\right) - f_1\left(s_1, s_2\right)x_1, \\
\dot{x}_1 &= \left(f_1\left(s_1, s_2\right) - D_1\right)x_1, \\
\dot{s}_2 &= D\left(s_2^{in} - s_2\right) + f_1\left(s_1, s_2\right)x_1 - f_2\left(s_1, s_2\right)x_2, \\
\dot{x}_2 &= \left(f_2\left(s_1, s_2\right) - D_2\right)x_2,
\end{aligned}
$$

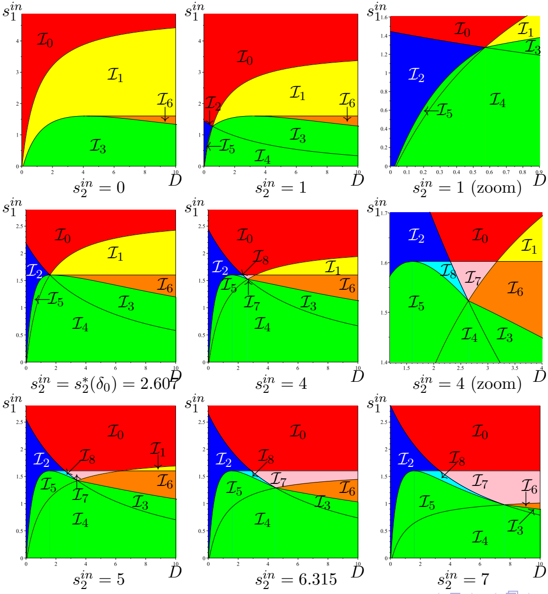
Table: Growth functions and parameters values

Growth functions and break-even concentrations									
$f_1(s_1, s_2) = \frac{m_1 s_1}{K_1 + s_1}\frac{1}{1+L_1 s_2} \Longleftrightarrow \lambda_1(s_2, D) = \frac{K_1 D(1+L_1 s_2)}{m1 - D(1+L_1 s_2)}$									
$f_2(s_1, s_2) = \frac{m_2 s_2}{K_2 + s_2}\frac{1}{1+L_2 s_1} \Longleftrightarrow \lambda_2(s_1, D) = \frac{K_2 D(1+L_2 s_1)}{m_2 - D(1+L_2 s_1)}$									
Parameters values									
m_1	K_1	L_1	m_2	K_2	L_2	α_1	a_1	α_2	a_2
4	1	0.3	3	1	0.2	0.8	0.1	0.9	0.2

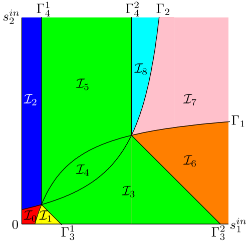
Operating diagrams with D constant



Operating diagrams with s_2^{in} constant



The surfaces Γ_k

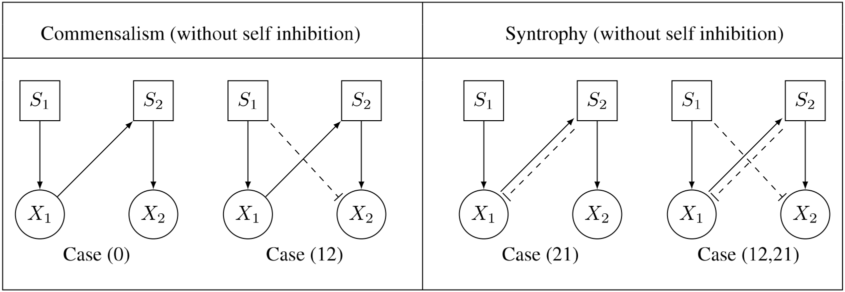


	E_0	E_1	E_2	E_c^1	E_c^2	Color
$\mathcal{I}_0$	S					Red
$\mathcal{I}_1$	U	S				Yellow
$\mathcal{I}_2$	U		S			Blue
$\mathcal{I}_3$	U	U		S		Green
$\mathcal{I}_4$	U	U	U	S		Green
$\mathcal{I}_5$	U		U	S		Green
$\mathcal{I}_6$	U	S		S	U	Coral
$\mathcal{I}_7$	S			S	U	Pink
$\mathcal{I}_8$	U		S	S	U	Cyan

$$\Gamma_1 = \left\{(D, s_1^{in}, s_2^{in}) \in \mathrm{SOP} : f_1(s_1^{in}, s_2^{in}) = D_1\right\}$$
$$\Gamma_2 = \left\{(D, s_1^{in}, s_2^{in}) \in \mathrm{SOP} : f_2(s_1^{in}, s_2^{in}) = D_2\right\}$$
$$\Gamma_3^1 = \left\{(D, s_1^{in}, s_2^{in}) \in \mathrm{SOP} : s_1^{in} + s_2^{in} = s_1^{*1}(D) + s_2^{*1}(D) \text{ and } f_2(s_1^{in}, s_2^{in}) < D_2\right\}$$
$$\Gamma_3^2 = \left\{(D, s_1^{in}, s_2^{in}) \in \mathrm{SOP} : s_1^{in} + s_2^{in} = s_1^{*2}(D) + s_2^{*2}(D) \text{ and } f_2(s_1^{in}, s_2^{in}) < D_2\right\}$$
$$\Gamma_4^1 = \left\{(D, s_1^{in}, s_2^{in}) \in \mathrm{SOP} : s_1^{in} = s_1^{*1}(D) \text{ and } f_1(s_1^{in}, s_2^{in}) < D_1\right\}$$
$$\Gamma_4^2 = \left\{(D, s_1^{in}, s_2^{in}) \in \mathrm{SOP} : s_1^{in} = s_1^{*2}(D) \text{ and } f_1(s_1^{in}, s_2^{in}) < D_1\right\}$$

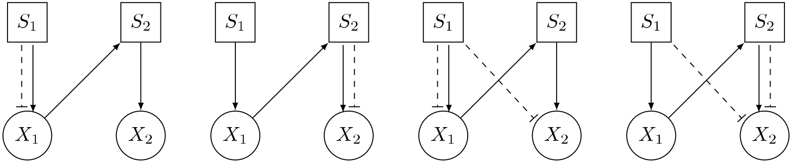
Sommaire

Microbial communities (without self-inhibition)



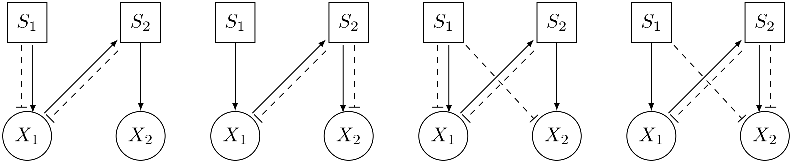
One self inhibition

Commensalism (with one self inhibition)



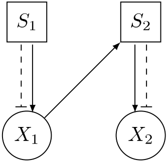
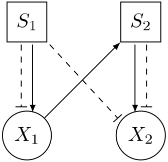
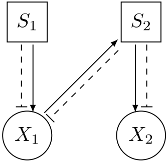
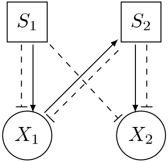
Case (11) Case (22) Case (11,12) Case (12,22)

Syntrophy (with one self inhibition)



Case (11,21) Case (21,22) Case (11,12,21) Case (12,21,22)

Two self inhibitions

Commensalism (with two self inhibitions)		Syntrophy (with two self inhibitions)	
 Case (11,22)	 Case (11,12,22)	 Case (11,21,22)	 Case (11,12,21,22)

Commensalism

μ_1	μ_2	S_2^{in}	D_i	Year Ref.
Monod	Monod	0	D	1974 Reilly
M-function	M-function	0	D	1981 Stephanopoulos
Monod	Monod	0	$D + a_i$	2003 Simeonov and Stoyanov
Monod	Monod	0	D	2019 Di and Yang
Monod	I-Monod	0	D	2019 Di and Yang
M-function	I-M-function	0	D	2019 Ben Ali

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Syntrophy

μ_1	μ_2	S_2^{in}	D_i	Year Ref.
Monod-I	Monod	0	D	1974 Wilkinson et al.
KB1	Monod	0	D	1986 Kreikenbohm and Bohl
M-I-function	M-function	0	D	1994 Burchard
Monod-I	Monod	0	$D + a_i$	2011 Xu et al.
M-I-function	M-function	0	D	2010 El Hajji et al.
M-I-function	I-M-function	0	D	2012 Sari et al.
M-I-function	M-function	0	$D + a_i$	2016 Sari and Harmand
M-I-function	M-function	≥ 0	$D + a_i$	2018 Daoud et al.
Monod-I	Monod	0	D	2019 Di and Yang
Monod-I	I-Monod	0	D	2019 Di and Yang

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Growth functions

Function	Defintion
Monod	$\mu_i(S_i) = \frac{m_i S_i}{K_i + S_i}$
Monod-I	$\mu_1(S_1, S_2) = \frac{m_1 S_1}{K_1 + S_1} \frac{1}{1 + L_2 S_2}$
I-Monod	$\mu_2(S_1, S_2) = \frac{m_2 S_2}{K_2 + S_2} \frac{1}{1 + L_1 S_1}$
KB1	$\mu_1(S_1, S_2) = \begin{cases} \frac{m_1(S_1 - S_2/K_1)}{K_2 + S_1 + K_3 S_2} & \text{if } S_1 - S_2/K_1 > 0 \\ 0 & \text{otherwise} \end{cases}$
M-function	$\mu(0) = 0$ and for $S > 0$, $\mu'(S) > 0$
M-I function	$\mu_1(0, S_2) = 0$ and, for $S_1, S_2 > 0$, $\frac{\partial \mu_1}{\partial S_1}(S_i, S_2) > 0$, $\frac{\partial \mu_1}{\partial S_2}(S_i, S_2) \leq 0$
I-M function	$\mu_2(S_1, 0) = 0$ and, for $S_1, S_2 > 0$, $\frac{\partial \mu_2}{\partial S_2}(S_i, S_2) > 0$, $\frac{\partial \mu_2}{\partial S_1}(S_i, S_2) \leq 0$

Commensalism with self inhibition

μ_1	μ_2	S_2^{in}	D_i	Year Ref.
H-function	H-function	0	D	1981 Stephanopoulos
Monod	Haldane	≥ 0	αD	2001 Bernard et al.
Monod	Haldane	≥ 0	D	2010 Simeonov and Diop
M-function	H-function	0	D	2010 Sbarciog et al.
M-function	H-function	≥ 0	αD	2012 Benyahia et al.
M-function	H-function	0	D	2012 Weedermann
M-function	H-function	≥ 0	αD	2018 Bayen and Gajardo
M-function	H-function	≥ 0	αD	2021 Sari and Benyahia
M-function	H-function	≥ 0	$\alpha_i D + a_i$	2022 Sari

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Syntrophy with self inhibition

μ_1	μ_2	S_2^{in}	D_i	Year Ref.
KB2	I-Monod	0	D	1988 Kreikenbohm and Bohl
HGG	H-function	0	D	2014 Harvey et al.
M-I function	H function	≥ 0	$D + a_i$	2017 Fekih Salem et al.
M-I function	H function	≥ 0	$\alpha_i D + a_i$	2020 Fekih Salem et al.

- R. Kreikenbohm, E. Bohl (1988). Bistability in the Chemostat. *Ecological Modelling* 43, 287-301.
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Growth functions

Function	Defintion
Haldane	$\mu_2(S_2) = \frac{m_2 S_2}{K_2+S_2+S_2^2/K_I}$
KB2	$\mu_1(S_1,S_2) = \begin{cases} \frac{m_1(S_1-S_2/K_1)}{K_2+S_1+K_3S_2+S_1^2/K_4} & \text{if } S_1 - S_2/K_1 > 0 \\ 0 & \text{otherwise} \end{cases}$
H-function	$\mu(0)=0$ and there is an $S^m \in (0,+\infty]$ such that $\mu'(S)>0$ if $S<S^m$ and $\mu'(S)<0$ if $S>S^m$ (If $S^m=+\infty$ we have an M-function)
HHG	$\mu_1(S_1,S_2)=f(S_1)I(S_2)$ with $f(0)=0$ and for $S_1>0$, $f'(S_1)>0$, for $S_2>0$, $I'(S_2)<0$

Sommaire

Di and Yang paper

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Analysis of productivity and stability of synthetic microbial communities

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Bioreactors that employ a synthetic microbial community hold potential to overcome limitations of those based on a single species, which embrace a higher level of complexity due to the inter-species interactions. In this work, a number of generic system structures involving two cross-feeding species and various types of inhibition have been studied, together with two three-species cases where a third species is introduced to fulfil a specific function. These cases are represented by mathematical models and inspected through bifurcation analysis and numerical simulation to reveal how the system

Base System = our model C1 or (0)

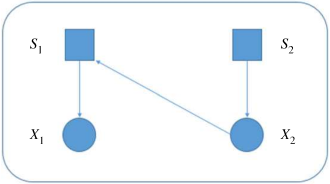
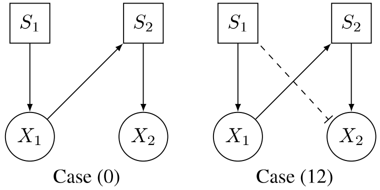
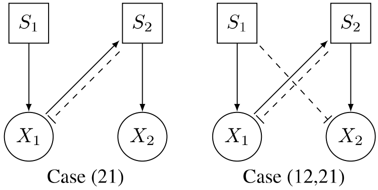


Figure 1. The base system. (Online version in colour.)

Commensalism (without self inhibition)	Syntrophy (without self inhibition)
	

Single inhibition (Di and Yang)

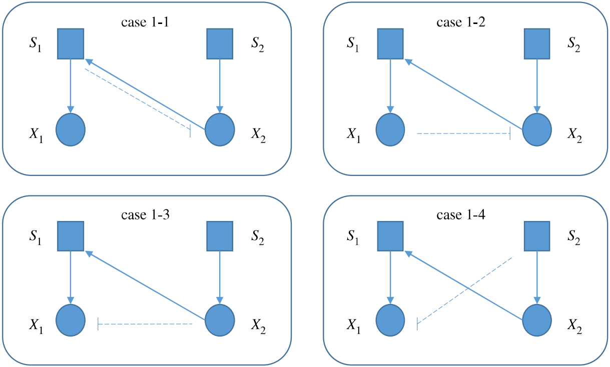


Figure 2. Two-species systems with a single inhibition (layer-1 cases). (Online version in colour.)

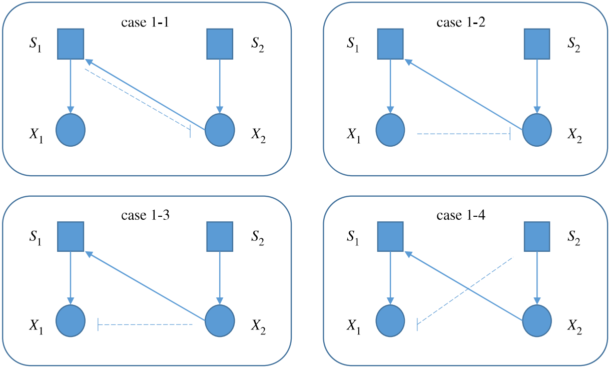
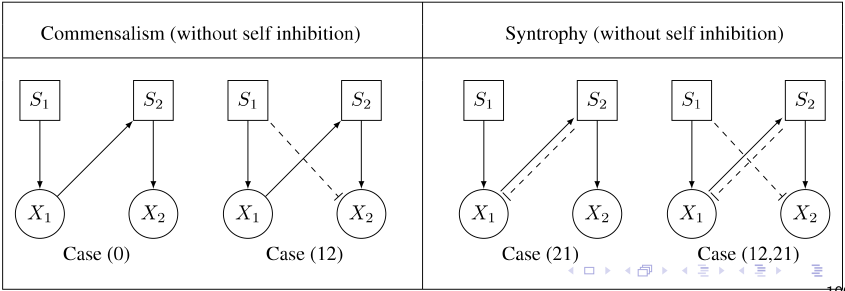


Figure 2. Two-species systems with a single inhibition (layer-1 cases). (Online version in colour.)



Double inhibitions (Di and Yang)

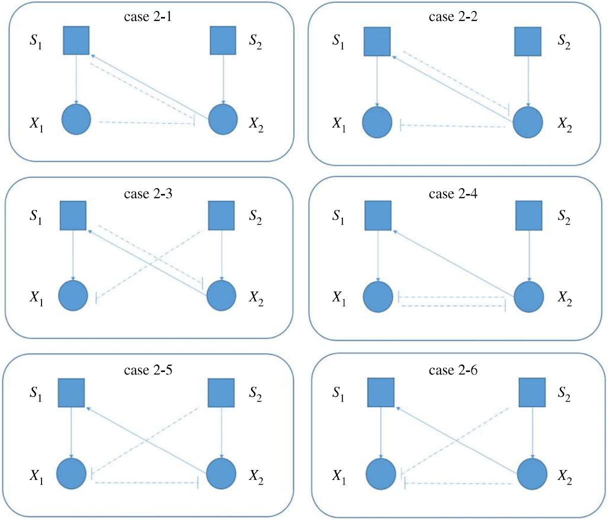


Figure 3. Two-species systems with double inhibitions (layer-2 cases). (Online version in colour.)

Inhibition of x_i by x_j, with $i \neq j$

- x_1 is inhibited by x_2 means that

$$f_1(s_1, x_2) = \frac{m_1 s_1}{K_1 + s_1} \frac{1}{1 + L_2 x_2}$$

- x_1 is inhibited by s_2 and x_2 means that

$$f_1(s_1, s_2, x_2) = \frac{m_1 s_1}{K_1 + s_1} \frac{1}{1 + L_2 x_2} \frac{1}{1 + M_2 s_2}$$

- These growth functions are density dependent.
- Our theory does not apply.
- However, it can be extended (work in progress)

Self inhibition or not ?

On top of this base system, we construct its variations with three layers of complexity. In layer 1 (figure 2), four two-species cases (numbered as cases 1-1 to 1-4) are considered, each of which contains an inhibition between a chemical and a species or between the two species. In reality, an inter-species inhibition may still be mediated by a certain chemical, which is however not explicitly represented in the system structure. Note that, an inhibition between S_1 and X_1 and that between S_2 and X_2 are not considered, as they will not affect the interactions between the two species and are therefore not relevant to this study.

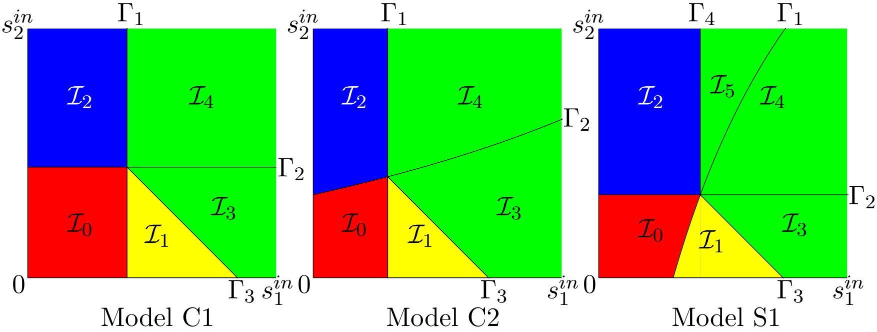
In the next step, single inhibitions from layer 1 are combined, leading to six cases (numbered as cases 2-1 to 2-6), each of which includes two different inhibitions; these cases are referred as those of layer 2 (figure 3 and table 2). The layer-2 cases are considered in order to investigate the compound effects of multiple inhibitions that may exist in a two-species system.

One of the conclusions of Di & Yang

reduction in stability. Inhibitions were also shown to be able to reduce the productive operating window that corresponds to the coexistence region of the operating space. Complex behaviours such as stable oscillation and bi-stability may occur with certain structural features such as feedback loops, combined with a suitable range of parameter values. It was also learned

Les mathématiques peuvent (et doivent ?) aider
à clarifier
les concepts
mis en avant par les biologistes

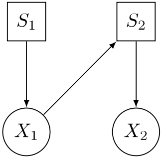
Operating diagram (C1, C2 and S1



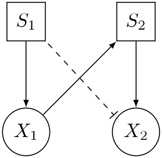
	E_0	E_1	E_2	E_c	Color
$\mathcal{I}_0$	S				Red
$\mathcal{I}_1$	U	S			Yellow
$\mathcal{I}_2$	U		S		Blue
$\mathcal{I}_3$	U	U		S	Green
$\mathcal{I}_4$	U	U	U	S	Green
$\mathcal{I}_5$	U		U	S	Green

Inhibition of X_2 by S_2

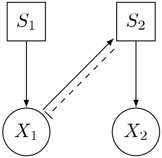
Commensalism (without self inhibition)	Syntrophy (without self inhibition)



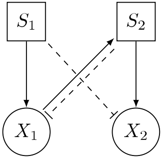
Case (0)



Case (12)

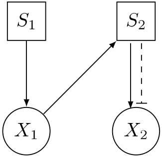


Case (21)

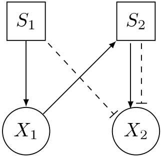


Case (12,21)

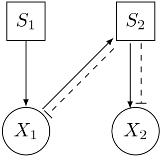
Commensalism (without inhibition of S_2 on X_2)	Syntrophy (with inhibition of S_2 on X_2)



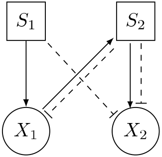
Case (22)



Case (12,22)



Case (21,22)



Case (12,21,22)

Commensalism and Inhibition of X_2 by S_2

$$
\begin{aligned}
\dot{s}_1 &= D\left(s_1^{in} - s_1\right) - f_1\left(s_1\right)x_1, \\
\dot{x}_1 &= \left(f_1\left(s_1\right) - D_1\right)x_1, \\
\dot{s}_2 &= D\left(s_2^{in} - s_2\right) + f_1\left(s_1\right)x_1 - f_2\left(s_2\right)x_2, \\
\dot{x}_2 &= \left(f_2\left(s_2\right) - D_2\right)x_2,
\end{aligned}
$$

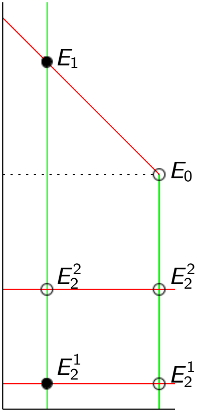
- $f_1(0) = 0$ and for $s_1 > 0$, $f'(s_2) > 0$
- $f_2(0) = 0$ and there exists s_2^m such that, for $0 < s_2 < s_2^m$, $f_2'(s_2) > 0$ and for $s_2 > s_2^m$, $f_2'(s_2) < 0$

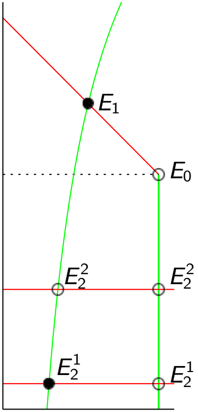
Syntrophy and Inhibition of X_2 by S_2

$$
\begin{aligned}
\dot{s}_1 &= D\left(s_1^{in} - s_1\right) - f_1\left(s_1; s_2\right)x_1, \\
\dot{x}_1 &= \left(f_1\left(s_1, s_2\right) - D_1\right)x_1, \\
\dot{s}_2 &= D\left(s_2^{in} - s_2\right) + f_1\left(s_1, s_2\right)x_1 - f_2\left(s_2\right)x_2, \\
\dot{x}_2 &= \left(f_2\left(s_2\right) - D_2\right)x_2,
\end{aligned}
$$

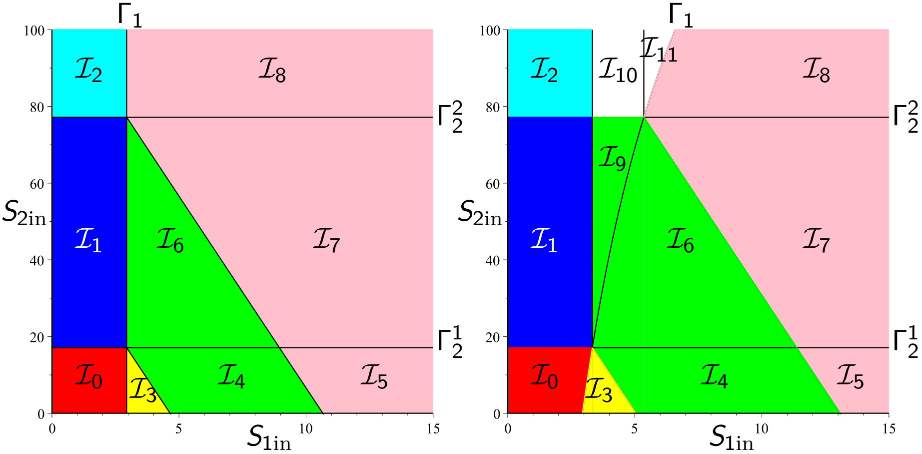
- $f_1(0, s_2) = 0$ and for $s_1 > 0, s_2 \geq 0$, $f_{11}(s_1, s_2) > 0$ and $f_{12}(s_1, s_2) \leq 0$
- $f_2(0) = 0$ and there exists s_2^m such that, for $0 < s_2 < s_2^m$, $f_2'(s_2) > 0$ and for $s_2 > s_2^m$, $f_2'(s_2) < 0$

Break-even concentrations and ZNGIs
For $s_2 \geq 0$ and $D \in [0, m_1(s_2))$, $s_1 = \lambda_1(s_2, D)$ is the solution of $f_1(s_1, s_2) = D$.
$\mathrm{ZNGI}_1 = \{(s_1, s_2) : s_1 = \lambda_1(s_2, D_1)\}$
For $D \in [0, m_2)$, $s_2^1 = \lambda_2^1(D)$ and $s_2^2 = \lambda_2^1(D)$ are the solutions of $f_2(s_2) = D$.
$\mathrm{ZNGI}_2^1 = \left\{(s_1, s_2) : s_2 = \lambda_2^1(D_2)\right\}$ $\quad$ $\mathrm{ZNGI}_2^2 = \left\{(s_1, s_2) : s_2 = \lambda_2^2(D_2)\right\}$





(22) and (21,22)



(22)

(21,22)

Existence and stability of equilibria of (22)

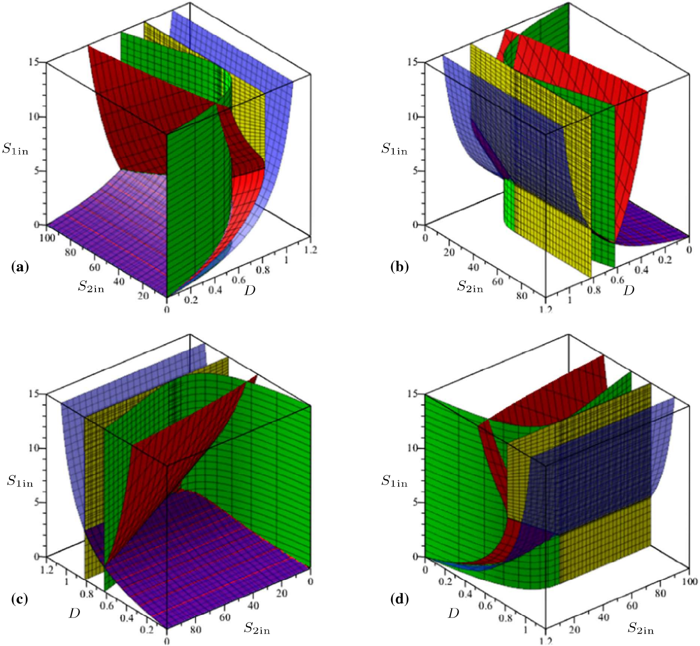
	E_0	E_2^1	E_2^2	E_1	E_c^1	E_c^2	Color
$\mathcal{I}_0$	GAS						Red
$\mathcal{I}_1$	U	GAS					Blue
$\mathcal{I}_2$	S	S	U				Cyan
$\mathcal{I}_3$	U			GAS			Yellow
$\mathcal{I}_4$	U			U	GAS		Green
$\mathcal{I}_5$	U			S	S	U	Pink
$\mathcal{I}_6$	U	U		U	GAS		Green
$\mathcal{I}_7$	U	U		S	S	U	Pink
$\mathcal{I}_8$	U	U	U	S	S	U	Pink

Existence and stability of equilibria of (21,22)

	E_0	E_2^1	E_2^2	E_1	E_c^1	E_c^2	Color
$\mathcal{I}_0$	S						Red
$\mathcal{I}_1$	U	S					Blue
$\mathcal{I}_2$	S	S	U				Cyan
$\mathcal{I}_3$	U			S			Yellow
$\mathcal{I}_4$	U			U	S		Green
$\mathcal{I}_5$	U			S	S	U	Pink
$\mathcal{I}_6$	U	U		U	S		Green
$\mathcal{I}_7$	U	U		S	S	U	Pink
$\mathcal{I}_8$	U	U	U	S	S	U	Pink
$\mathcal{I}_9$	U	U			S		Green
$\mathcal{I}_{10}$	S	U	U		S		White
$\mathcal{I}_{11}$	S	U	U		S	U	White

Asymptotic behaviors

Color	Asymptotic behavior	Regions
Red	Stability of E_0	$\mathcal{I}_0$
Yellow	Stability of E_1	$\mathcal{I}_3$
Blue	Stability of E_2^1	$\mathcal{I}_1$
Green	Stability of E_c^1	$\mathcal{I}_4$, $\mathcal{I}_6$, $\mathcal{I}_{10}$
Cyan	Stability of E_0 and E_2^1	$\mathcal{I}_2$
Pink	Stability of E_1 and E_c^1	$\mathcal{I}_5$, $\mathcal{I}_7$
White	Stability of E_0 and E_c^1	$\mathcal{I}_{10}$, $\mathcal{I}_{11}$


(a)
(b)
(c)
(d)
$S_{1\mathrm{in}}$
$S_{2\mathrm{in}}$
D
0 5 10 15
0 20 40 60 80 100
0 0.2 0.4 0.6 0.8 1 1.2

Sommaire

Commensalism

$$\begin{cases} \dot{s}_1 & = & D\left(s_1^{in}-s_1\right)-f_1\left(s_1\right)x_1, \\ \dot{x}_1 & = & \left(f_1\left(s_1\right)-D_1\right)x_1, \\ \dot{s}_2 & = & D\left(s_2^{in}-s_2\right)+f_1\left(s_1\right)x_1-f_2\left(s_1,s_2\right)x_2, \\ \dot{x}_2 & = & \left(f_2\left(s_1,s_2\right)-D_2\right)x_2, \end{cases}$$

- Let $(s_1(t), x_1(t), s_2(t), x_2(t))$ be a solution of this system
- Then $(s_1(t), x_1(t))$ is a solution of the 2D system

$$\begin{cases} \dot{s}_1 & = & D\left(s_1^{in}-s_1\right)-f_1\left(s_1\right)x_1, \\ \dot{x}_1 & = & \left(f_1\left(s_1\right)-D_1\right)x_1, \end{cases}$$

- and $(s_2(t), x_2(t))$ is a solution of the non autonomous 2D system

$$\begin{cases} \dot{s}_2 & = & D\left(s_2^{in}-s_2\right)+f_1\left(s_1(t)\right)x_1(t)-f_2\left(s_1(t),s_2\right)x_2, \\ \dot{x}_2 & = & \left(f_2\left(s_1(t),s_2\right)-D_2\right)x_2, \end{cases}$$

Asymptoticaly autonomous systems

- The first system $\begin{cases} \dot{s}_1 &= D\left(s_1^{in} - s_1\right) - f_1\left(s_1\right)x_1, \\ \dot{x}_1 &= \left(f_1\left(s_1\right) - D_1\right)x_1, \end{cases}$ is a classical chemostat system. Every solution (except for a set of initial conditions of measure 0) converges toward an equilibrium (s_1^*, x_1^*)
- Therefore the second system is asymptotically autonomous system and converges toward the autonomous system

$$\begin{cases} \dot{s}_2 &= D\left(s_2^{in} - s_2\right) + f_1\left(s_1^*\right)x_1^* - f_2\left(s_1^*, s_2\right)x_2, \\ \dot{x}_2 &= \left(f_2\left(s_1^*, s_2\right) - D_2\right)x_2, \end{cases}$$

- This system is also a classical chemostat system. Its solutions (except for a set of initial conditions of measure 0) converge toward an equilibrium (s_2^*, x_2^*).
- Use Thieme theory to conclude.

Reduction to a 2 dimensional system

- We assume that $D_1 = D_2 = D$
- The system becomes

$$\begin{aligned}
\dot{s}_1 &= D\left(s_1^{in} - s_1\right) - f_1\left(s_1, s_2\right) x_1, \\
\dot{x}_1 &= \left(f_1\left(s_1, s_2\right) - D\right) x_1, \\
\dot{s}_2 &= D\left(s_2^{in} - s_2\right) + f_1\left(s_1, s_2\right) x_1 - f_2\left(s_1, s_2\right) x_2, \\
\dot{x}_2 &= \left(f_2\left(s_1, s_2\right) - D\right) x_2,
\end{aligned}$$

- We use the variables (z_1, z_2, x_1, x_2), where z_1 and z_2 are defined by

$$z_1 = s_1 + x_1, \quad z_2 = s_2 - x_1 + x_2.$$

- The system becomes

$$\begin{aligned}
\dot{x}_1 &= \left(f_1\left(z_1 - x_1, z_2 + x_1 - x_2\right) - D\right) x_1, \\
\dot{x}_2 &= \left(f_2\left(z_1 - x_1, z_2 + x_1 - x_2\right) - D\right) x_2, \\
\dot{z}_1 &= D\left(s_1^{in} - z_1\right), \\
\dot{z}_2 &= D\left(s_2^{in} - z_2\right),
\end{aligned}$$

- Since $\dot{z}_1 = D\left(s_1^{in} - z_1\right)$ and $\dot{z}_2 = D\left(s_2^{in} - z_2\right)$, we have

$$z_1(t) = s_1^{in} + (z_1(0) - s_1^{in})e^{-Dt}, \quad z_2(t) = s_2^{in} + (z_2(0) - s_2^{in})e^{-Dt}$$

- $x_1(t)$ and $x_2(t)$ are the solutions of the non autonomous 2D system

$$\begin{array}{rcl} \dot{x}_1 & = & \left(f_1\left(z_1(t) - x_1, z_2(t) + x_1 - x_2\right) - D\right)x_1, \\ \dot{x}_2 & = & \left(f_2\left(z_1(t) - x_1, z_2(t) + x_1 - x_2\right) - D\right)x_2 \end{array}$$

- This is an asymptotically autonomous system, whose limiting system is

$$\begin{array}{rcl} \dot{x}_1 & = & \left(f_1\left(s_1^{in} - x_1, s_2^{in} + x_1 - x_2\right) - D\right)x_1, \\ \dot{x}_2 & = & \left(f_2\left(s_1^{in} - x_1, s_2^{in} + x_1 - x_2\right) - D\right)x_2 \end{array}$$

- Thanks to Thieme's results theory, the asymptotic behaviour of the solutions of the reduced model is informative for the complete system.

Thank you for your attention