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Séminaire TREASURE au Hameau 2015

FEKIH SALEM Radhouane

Competition model of n species for a single resource and coexistence in the chemostat

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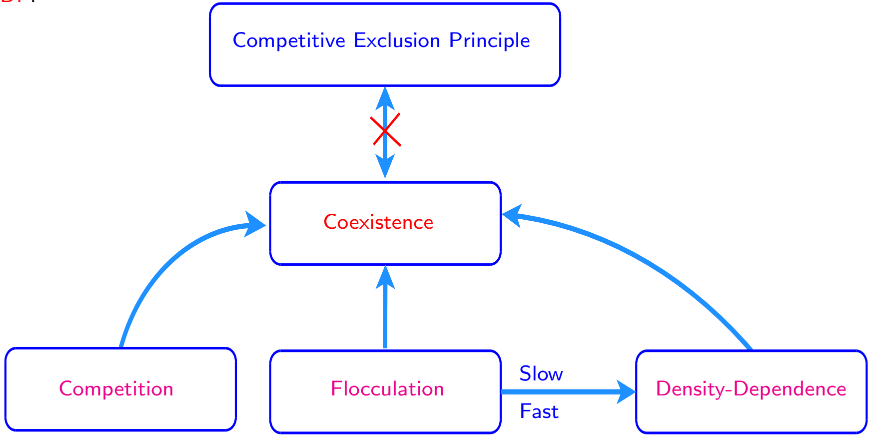
14 octobre 2015

Ph.D. :



Competitive Exclusion Principle

Coexistence

Competition

Flocculation

Slow

Fast

Density-Dependence

Three Step Model of Anaerobic Digestion

Postdoctoral :

Parameter Identification of the Fermentative Production of Fructo-oligosaccharides

Plan

Competitive Exclusion Principle

- At most, one species can survive to the competition : Experience of Hansen, Hubbel (1980).
- Classical chemostat model : Smith, Waltman, *The Theory of the Chemostat* (1995).

$$\left\{\begin{array}{lcl}\dot{S} & = & D(S_{in}-S)-\sum_{i=1}^{n}\frac{1}{y_i}f_i(S)x_i, \\ \dot{x}_i & = & [f_i(S)-D]x_i, \qquad\qquad\qquad i=1,\dots,n\end{array}\right.$$

- If $\lambda_1 < \lambda_j$, for $j \geqslant 2$ where $\lambda_i := f_i^{-1}(D)$ and $S_{in} > \lambda_1$

$$\Downarrow$$

Generically, all solutions converge toward the equilibrium Globally Asymptotically Stable

$$S = \lambda_1, \quad x_1 = y_1(S_{in}-\lambda_1), \quad x_j = 0, \; j \geqslant 2.$$

Coexistence

- Considering models with time-varying dilution rates, and or input nutrient concentration,

  G.S.K. Wolkowicz and X.Q. Zhao, n-Species Competition in a Periodic Chemostat, *Differential and Integral Equations* (1998).

  or with variable yields,

  T. Sari, A Lyapunov function for the chemostat with variable yields, *C. R. Acad. Sci. Paris Ser. I* (2010).

  T. Sari and F. Mazenc, Global dynamics of the chemostat with different removal rates and variable yields, *Math. Biosci. Eng.* (2011).

Density-Dependent Growth

- Lobry et al. have proposed growth functions depending on both the resource and the consumers.
- They introduce the concept of steady-state characteristic to give sufficient conditions for coexistence and to determine the asymptotic behavior of the system.

  C. Lobry and J. Harmand, A new hypothesis to explain the coexistence of n species in the presence of a single resource, *C. R. Biologies* (2006).

  C. Lobry and F. Mazenc, Effect on persistence of intra-specific competition in competition models, *Electron. J. Diff. Eqns.* (2007).

  C. Lobry and F. Mazenc and A. Rapaport, Persistence in ecological models of competition for a single resource, *C. R. Acad. Sci. Paris, Ser. I* (2005).

  C. Lobry and A. Rapaport and F. Mazenc, Sur un modèle densité-dépendant de compétition pour une ressource, *C. R. Biologies* (2006).

Intra and inter-specific competition

- Two models : either intra-specific interferences or only inter-specific interactions.

  G.S.K. Wolkowicz and Z. Lu, Direct interference on competition in a chemostat, *J. Biomath* (1998).

- Both intra- and inter-specific interactions

  R. Fekih-Salem and T. Sari and N. Abdellatif, Sur un modèle de compétition et de coexistence dans le chémostat, *ARIMA J.* (2011).

- De Leenheer et al. have proposed a n species model by considering that mortality rates are due to the crowding effects.

  [1]. P. De Leenheer and D. Angeli and E.D. Sontag, Crowding effects promote coexistence in the chemostat, *J. Math. Anal. Appl.* (2006).

  - The authors were interested only in the positive equilibrium.
  - They require that all parameters of death rates are large enough to prove the existence of a positive equilibrium.
  - They use the theory of monotone dynamical systems for an interconnection of two input/output systems to prove an almost-global stability result of the positive equilibrium.

Objectives

1. To give a quite comprehensive analysis of the model of De Leenheer et al. [1] that takes into consideration regions of the parameters space.
2. Using the concept of steady-state characteristic introduced by Lobry et al., we present a geometric characterization that describes all equilibria of model and their stability.
3. Without the assumption that all parameters of death rates are large enough as in [1], we give necessary and sufficient conditions on the control parameters of the system to have a positive equilibrium.
4. We show that in the case of two species, even if one parameter of death rate is zero, the coexistence is still possible.

These results are surprising and new, compared to those in [1].

- Ruan et al. have raised a similar problem of the coexistence of two-competitors/one-prey when only one of the competitors exhibits a density-dependent mortality rate.

  S. Ruan and A. Ardito and P. Ricciardi and D. L. DeAngelis, Coexistence in competition models with density-dependent mortality, *C. R. Biologies* (2007).

- They have asserted that the majority of works assume that all competitors have a density-dependent mortality rate and that their contribution is to show how coexistence is possible even when only one competitor has a density-dependent mortality.

The chemostat model of n species competing for a single nutrient with intra-specific linear interactions, introduced by De Leenheer et al. [1]

$$\left\{\begin{array}{rcll} \dot{S} & = & D(S_{in}-S)-\sum_{i=1}^{n} f_i(S)x_i & \\ \dot{x}_i & = & [f_i(S)-a_i x_i - D_i]x_i, & i=1,\ldots,n \end{array}\right. \tag{1}$$

- D_i : removal rate of the species i which is the sum of the death rates of species i and the dilution rate D,
- a_i : a positive parameter giving rise to death rate $a_i x_i$ which is due to intra-specific interactions.

H1 : For $i = 1, \ldots, n$, $f_i(0) = 0$ and for all $S > 0$, $f_i'(S) > 0$.

Proposition 2.1

For any non-negative initial condition, the solution of (1) remains non-negative and is positively bounded. The set

$$\Omega = \left\{ (S, x_1, \ldots, x_n) \in \mathbb{R}_+^{n+1} : Z = S + \sum_{i=1}^{n} x_i \leqslant \max\left(Z(0), \frac{D}{D^*} S_{in} \right) \right\}$$

where $D^* = \min(D, D_1, \ldots, D_n)$, is positively invariant and a global attractor for (1).

1. Introduction
2. Mathematical model
3. Analysis of the competition model with two species
4. Study of the competition model with several species
5. Operating diagram
6. Simulations
7. Conclusion

- For a better understanding of the qualitative behavior of solution of model (1), we begin by the case $n = 2$.

$$\left\{ \begin{array}{lcl} \dot{S} & = & D(S_{in} - S) - f_1(S)x_1 - f_2(S)x_2 \\ \dot{x}_1 & = & [f_1(S) - a_1 x_1 - D_1]x_1 \\ \dot{x}_2 & = & [f_2(S) - a_2 x_2 - D_2]x_2. \end{array} \right. \tag{2}$$

If equation $f_i(S) = D_i$ has a solution, we denote $\lambda_i = f_i^{-1}(D_i)$, for $i = 1, 2$. Otherwise, $\lambda_i = +\infty$. We assume that the populations x_i are labeled such that $\lambda_1 < \lambda_2$.

$$h_i(S) = \frac{f_i(S) - D_i}{a_i} f_i(S), \quad H_i(S) = D(S_{in} - S) - h_i(S), \quad i = 1, 2. \tag{3}$$

Let S_i be the solution of equation $H_i(S) = 0$ and let

$$\bar{x}_i = \frac{f_i(S_i) - D_i}{a_i}, \quad i = 1, 2. \tag{4}$$

Proposition 3.1

1. $E_1 = (S_1, \bar{x}_1, 0)$, *exists iff* $S_{in} > \lambda_1$.
2. $E_2 = (S_2, 0, \bar{x}_2)$, *exists iff* $S_{in} > \lambda_2$.

We define,

$$H(S) = D(S_{in} - S) - \sum_{i=1}^{2} h_i(S) \quad \text{and} \quad \bar{\lambda}_2 = \lambda_2 + \frac{h_1(\lambda_2)}{D}.$$

Proposition 3.2

The positive equilibrium $E^* = (S^*, x_1^*, x_2^*)$ *exists iff* $S_{in} > \bar{\lambda}_2$ *with* S^* *is solution of equation* $H(S) = 0$ *and*

$$x_i^* = \frac{f_i(S^*) - D_i}{a_i}, \quad i = 1, 2.$$

Equilibria	Existence condition	Stability condition
E_0	Always exists	$S_{in} < \lambda_i,\ i = 1, 2$
E_1	$S_{in} > \lambda_1$	$S_{in} < \bar{\lambda}_2$
E_2	$S_{in} > \lambda_2$	Unstable whenever it exists
E^*	$S_{in} > \bar{\lambda}_2$	Whenever it exists

TABLE : Existence and local stability of equilibria in system (2).

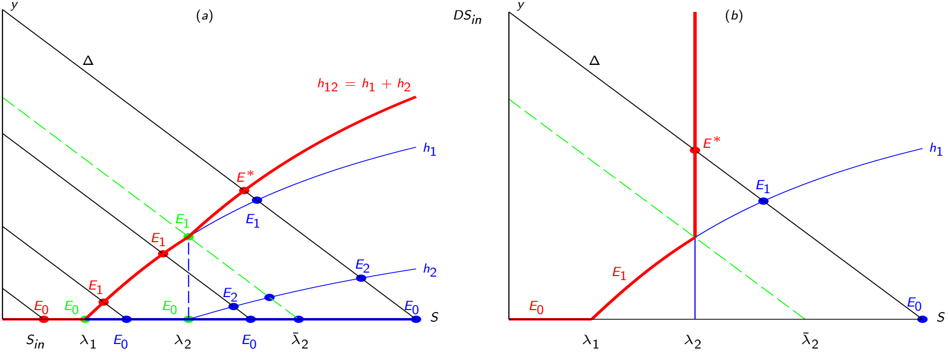


FIGURE : Steady-state characteristic : (a) equilibria of (2) according to S_{in} for $a_2 > 0$, (b) existence of E^* for $a_2 = 0$.

Proposition 3.3

1. *If* $S_{in} < \lambda_1$*, there exists a unique equilibrium* $E_0 = (S_{in}, 0, 0)$ *which is GAS.*
2. *If* $\lambda_1 < S_{in} < \lambda_2$*, then there exists two equilibria :* E_0 *is unstable and* $E_1 = (S_1, \bar{x}_1, 0)$ *is GAS.*
3. *If* $\lambda_2 < S_{in} < \bar{\lambda}_2$*, then there exists three equilibria :* E_0 *and* $E_2 = (S_2, 0, \bar{x}_2)$ *are unstable while* E_1 *is LES. Moreover, if it exists a constant* $\alpha > 0$ *which satisfies :*

$$\max_{0<S<S_1} g(S) \leqslant \alpha \leqslant \min_{\lambda_2<S<S_{in}} g(S) \quad \textit{where} \quad g(S) = \frac{f_2(S)}{f_1(S_1)} \frac{f_1(S) - f_1(S_1)}{f_2(S) - D_2} \frac{S_{in} - S_1}{S_{in} - S},$$

   then E_1 *is GAS with respect to all solutions with* $x_1(0) > 0$*.*
4. *If* $S_{in} > \bar{\lambda}_2$*, then there exists four equilibria :* E_0*,* E_1 *and* E_2 *are unstable while* $E^* = (S^*, x_1^*, x_2^*)$ *is LES.*

The case $a_2 = 0$

$$\left\{ \begin{array}{lcl} \dot{S} & = & D(S_{in} - S) - f_1(S)x_1 - f_2(S)x_2 \\ \dot{x}_1 & = & [f_1(S) - a_1 x_1 - D_1]x_1 \\ \dot{x}_2 & = & [f_2(S) - D_2]x_2. \end{array} \right. \tag{5}$$

Proposition 3.4

The system (5) admits the following equilibria :

1. $E_0 = (S_{in}, 0, 0)$, *that always exists.*
2. $E_2 = (\lambda_2, 0, D(S_{in} - \lambda_2)/D_2)$, *that exists iff* $S_{in} > \lambda_2$.
3. $E_1 = (S_1, \bar{x}_1, 0)$, *with* S_1 *is solution of* $H_1(S) = 0$, *that exists iff* $S_{in} > \lambda_1$.
4. $E^* = (\lambda_2, x_1^*, x_2^*)$, *with* $x_1^* = (f_1(\lambda_2) - D_1)/a_1$, $x_2^* = H_1(\lambda_2)/D_2$, *that exists iff* $S_{in} > \bar{\lambda}_2$,

- If $\lambda_1 < \lambda_2$ then the first species has a competitive advantage over the second species and so this second species need not to inhibit its growth in order to coexist with the other species.
- The coexistence is due to the fact that the most efficient species sees its growth inhibited by the intra-specific competition even though the other species is not inhibited.

We assume that the populations x_i are labeled such that

$$\lambda_1 < \lambda_2 < \cdots < \lambda_n.$$

$$h_i(S) = \begin{cases} \frac{f_i(S)-D_i}{a_i} f_i(S) & \text{if } S > \lambda_i \\ 0, & \text{else} \end{cases} \qquad (6)$$

$$H(S) = D(S_{in} - S) - \sum_{i=1}^{n} h_i(S).$$

Proposition 4.1

The system (1) admits a unique positive equilibrium $E^* = (S^*, x_1^*, \ldots, x_n^*)$ *iff*

$$S_{in} > \bar{\lambda}_n \quad \textit{where} \quad \bar{\lambda}_n = \lambda_n + \frac{1}{D} \sum_{k=1}^{n-1} h_k(\lambda_n)$$

Définition 4.1

We define the steady-state characteristic by the set of the curves $y = 0$ *and* $y = h_J(S)$ *where*

$$h_J = \sum_{i \in J} h_i,$$

with J *is a subset of* $\{1, \ldots, n\}$, *defined for* $S \geqslant \max\{\lambda_j : j \in J\}$.

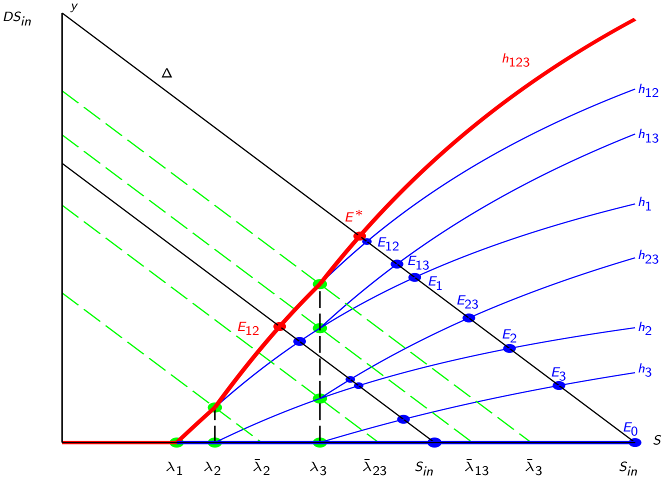


FIGURE : Steady-state characteristic for $n = 3$.

Proposition 4.2

For any value of S_{in}, there is only one LES equilibrium. All other equilibria are unstable.

Proposition 4.3

Assume that $\lambda_1 < S_{in} < \bar{\lambda}_2$ *and that there exist constants* $\alpha_i > 0$, *for each* $i \geqslant 2$ *satisfying* $\lambda_i < S_{in}$ *such that*

$$\max_{0<S<\lambda_1} g_i(S) \leqslant \alpha_i \leqslant \min_{\lambda_i<S<S_{in}} g_i(S) \tag{7}$$

where

$$g_i(S) = \frac{f_i(S)}{f_1(S_1)} \frac{f_1(S) - f_1(S_1)}{f_i(S) - D_i} \frac{S_{in} - S_1}{S_{in} - S}.$$

Then, $E_1 = (S_1, \bar{x}_1, 0, \ldots, 0)$ *is GAS for system (1) with respect to all solutions with* $x_1(0) > 0$.

Condition	E_0	E_1	E_2	E_{12}	E_3	E_{23}	E_{13}	E^*
$S_{in} < \lambda_1$	S							
$\lambda_1 < S_{in} < \lambda_2$	U	S						
$\lambda_2 < S_{in} < \bar{\lambda}_2$	U	S	U					
$\bar{\lambda}_2 < S_{in} < \lambda_3$	U	U	U	S				
$\lambda_3 < S_{in} < \bar{\lambda}_{23}$	U	U	U	S	U			
$\bar{\lambda}_{23} < S_{in} < \bar{\lambda}_{13}$	U	U	U	S	U	U		
$\bar{\lambda}_{13} < S_{in} < \bar{\lambda}_3$	U	U	U	S	U	U	U	
$S_{in} > \bar{\lambda}_3$	U	U	U	U	U	U	U	S

Each parameter D_i, can be written as $D_i = D + A_i$, $A_i \geqslant 0$ where A_i can be interpreted as the specific natural death rate of species i. Denote

$$\bar{m}_i = \sup_{S \geqslant 0} f_i(S) - A_i, \quad i = 1, 2, 3,$$

and we assume that $\bar{m}_i > 0$. We define the inverse function F_i of the increasing functions f_i :

$$S = F_i(D) \Leftrightarrow f_i(S) = D + A_i, \text{ for all } S \in [0, +\infty[\text{ and } D \in [0, \bar{m}_i[.$$

Let Γ_i be the curve of equation $S_{in} = F_i(D)$. We assume

$$F_1(D) < F_2(D) < F_3(D), \quad \text{for all} \quad D \in]0, \bar{m}_3[. \tag{8}$$

$$\begin{array}{rcl} F_{ij} :]0, \quad \bar{m}_j[& \longrightarrow &]0, +\infty[\\ D & \longrightarrow & F_j(D) + \frac{h_i(F_j(D))}{D}, \quad \text{for all} \quad i, j = 1, 2, 3 \quad \text{with} \quad i < j \end{array}$$

and

$$\begin{array}{rcl} F_{123} :]0, \quad \bar{m}_3[& \longrightarrow &]0, +\infty[\\ D & \longrightarrow & F_3(D) + \frac{1}{D} \sum_{i=1}^{2} h_i(F_3(D)). \end{array}$$

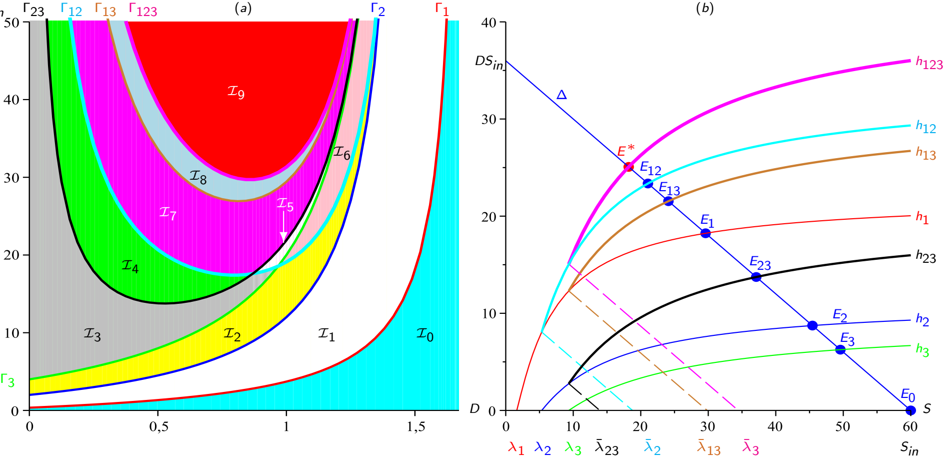


FIGURE : (a) Operating diagram of (1) with $n = 3$. (b) Steady-state characteristic for $(D, S_{in}) \in \mathcal{I}_9$ with $D < D_1^*$.

- If there are two zeros parameters a_i then the positive equilibrium E^* does not exist.

  E^* can be stable if all the species are inhibited except the least competitive species.

- Making the parameter a_3 varying, the regions of operating diagram are identical

$$F_i(\cdot), \quad F_{ij}(\cdot), \quad i,j = 1,2,3; \quad i<j \quad and \quad F_{123}(\cdot) \text{ are independent of } a_3.$$

Hence, the intra-specific competition of the least competitive species has no effect on the region of coexistence.

Region	E_0	E_1	E_2	E_3	E_{23}	E_{12}	E_{13}	E^*
$(D, S_{in}) \in \mathcal{I}_0$	S							
$(D, S_{in}) \in \mathcal{I}_1$	U	S						
$(D, S_{in}) \in \mathcal{I}_2$	U	S	U					
$(D, S_{in}) \in \mathcal{I}_3$	U	S	U	U				
$(D, S_{in}) \in \mathcal{I}_4$	U	S	U	U	U			
$(D, S_{in}) \in \mathcal{I}_5$	U	U	U	U		S		
$(D, S_{in}) \in \mathcal{I}_6$	U	U	U			S		
$(D, S_{in}) \in \mathcal{I}_7$	U	U	U	U	U	S		
$(D, S_{in}) \in \mathcal{I}_8$	U	U	U	U	U	S	U	
$(D, S_{in}) \in \mathcal{I}_9$	U	U	U	U	U	U	U	S

TABLE : Existence and local stability of steady states of three species model.

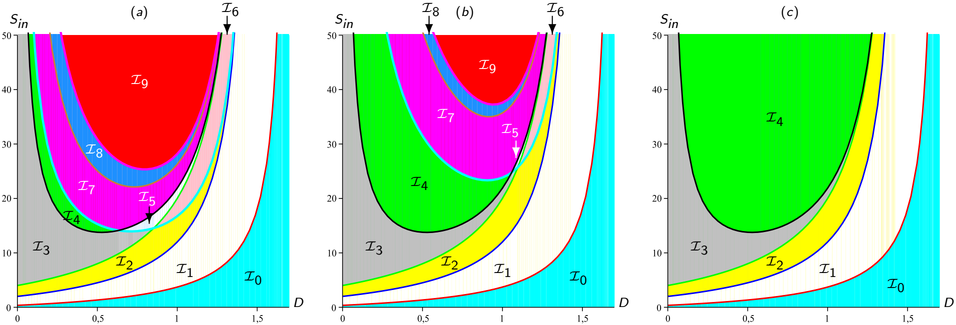


FIGURE : Reduction and disappearance of the coexistence region $\mathcal{I}_9$ as a_1 decreases : (a) $a_1 = 0.15$, (b) $a_1 = 0.06$ and (c) $a_1 = 0.015$.

- Decreasing a_1 reduces the coexistence region $\mathcal{I}_9$ and increases the region $\mathcal{I}_4$ of competitive exclusion of the second and third species (see Fig. 4(a-b)).
- The coexistence region $\mathcal{I}_9$ tends to disappear as a_1 tends to zero (see Fig. 4(c)).

Thus, the intra-specific competition of the most competitive species leads to changes in the size and presence of coexistence regions.

The functions $f_i(\cdot)$ are of Monod type, defined by :

$$f_i(S) = \frac{m_i S}{K_i + S}, \quad i = 1, 2, 3, \tag{9}$$

where m_i is the maximum specific growth rate and K_i is the Michaelis-Menten constant. Straightforward calculation shows that

$$F_i(D) = \frac{K_i(D + A_i)}{m_i - D - A_i}, \quad i = 1, 2, 3.$$

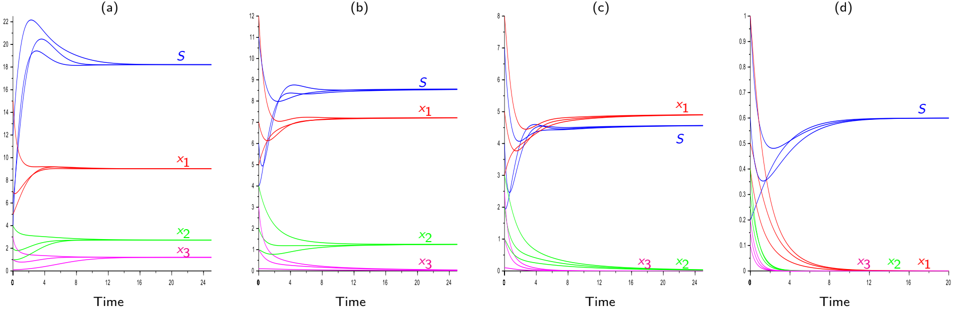


FIGURE : (a) Coexistence of the three species for $(D, S_{in}) \in \mathcal{I}_9$. (b) Competitive exclusion of the third species for $(D, S_{in}) \in \mathcal{I}_8$. (c) Competitive exclusion of the third and the second species for $(D, S_{in}) \in \mathcal{I}_4$. (d) Washout of all species for $(D, S_{in}) \in \mathcal{I}_0$.

Novelty / originality

1. Using the concept of steady-state characteristic, we present a geometric characterization of the existence and stability of all equilibria.
2. We give necessary and sufficient conditions on the control parameters of the system to have a positive equilibrium.
3. Using a Lyapunov function, we give a global asymptotic stability result for the competition model of several species.
4. The operating diagram depicts regions in the (D, S_{in}) plane in which the various outcomes occur and illustrates the effect of the intra-specific competition on the region of coexistence.

$$\Downarrow$$

- The intra-specific competition of the $n-1$ most efficient species introduces a region of coexistence of n species while the least competitive species has no reason to be inhibited in order to coexist with all other species.
- The importance of the main control parameters D and S_{in} on the maintenance of species coexistence and the protection of the least relevant species among microbial ecosystems.

Thank you for your attention

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