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A propos de quelques modèles à “compartiments”

Ecole-chercheur sur les modèles ressources-consommateurs

UMR MISTEA et UMR Eco&Sols

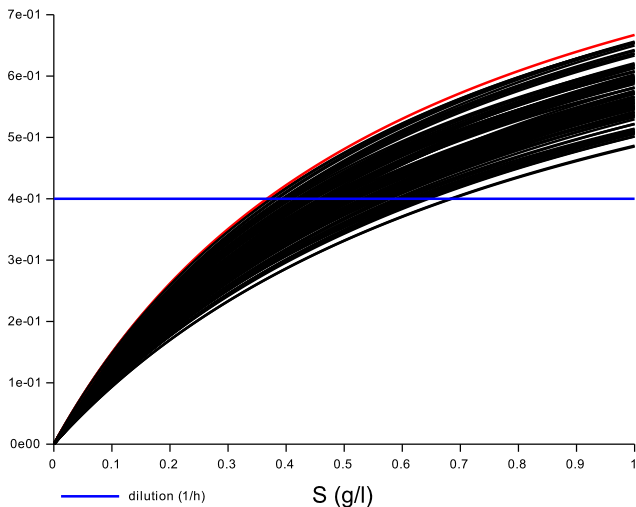
21–25 septembre 2015

Alain Rapaport

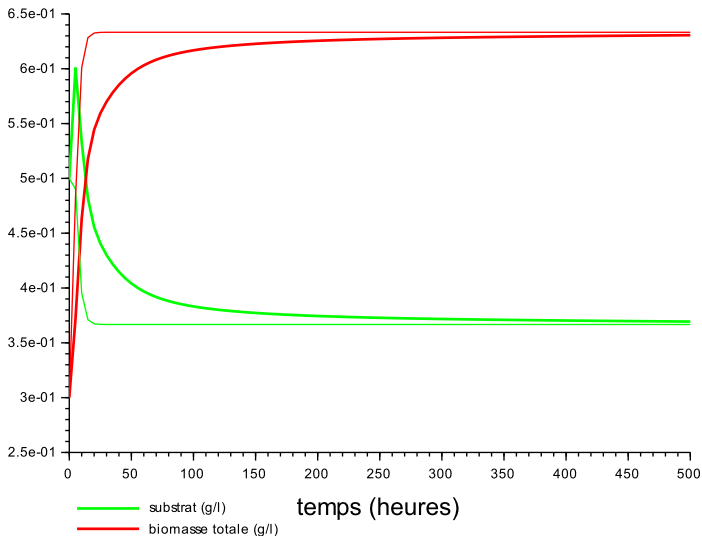
Le chémostat avec beaucoup d'espèces

$$D = 0.4h^{-1} \Rightarrow T_{dble} = \frac{\log 2}{D} \simeq 1.73h$$

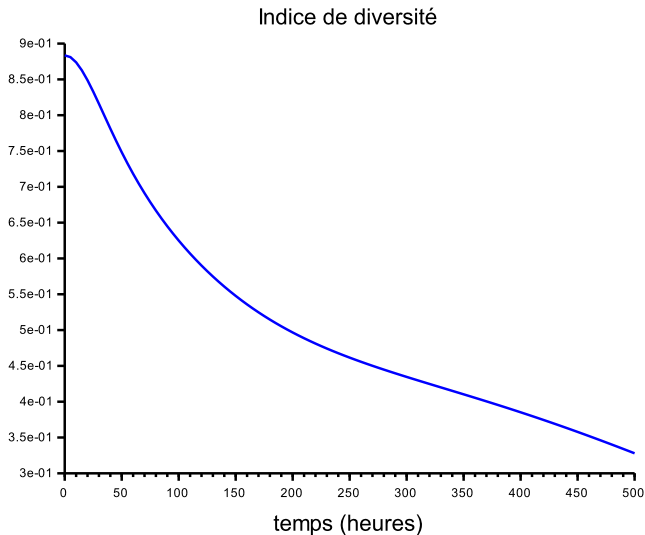
Courbes de croissance



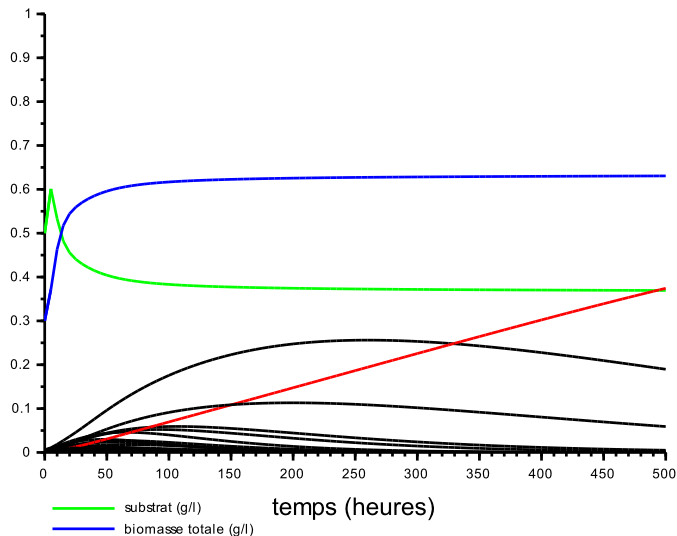
Le chémostat avec beaucoup d'espèces



Le chémostat avec beaucoup d'espèces



Le chémostat avec beaucoup d'espèces



Le chémostat avec beaucoup d'espèces

$$\dot{s} = - \sum_{j=1}^n \mu_j(s) x_j + D(s_{in} - s)$$

$$\dot{x}_i = \mu_i(s) x_i - D x_i \quad (i = 1 \cdots n)$$

Simulations numériques avec $n > 100$:

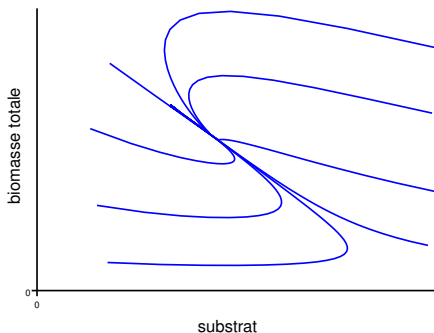
- ▶ tirage aléatoire des fonctions $\mu_i(\cdot)$ dans une famille de fonctions de Monod
- ▶ tirage aléatoire de la composition initiale en biomasse

Le chémostat avec beaucoup d'espèces

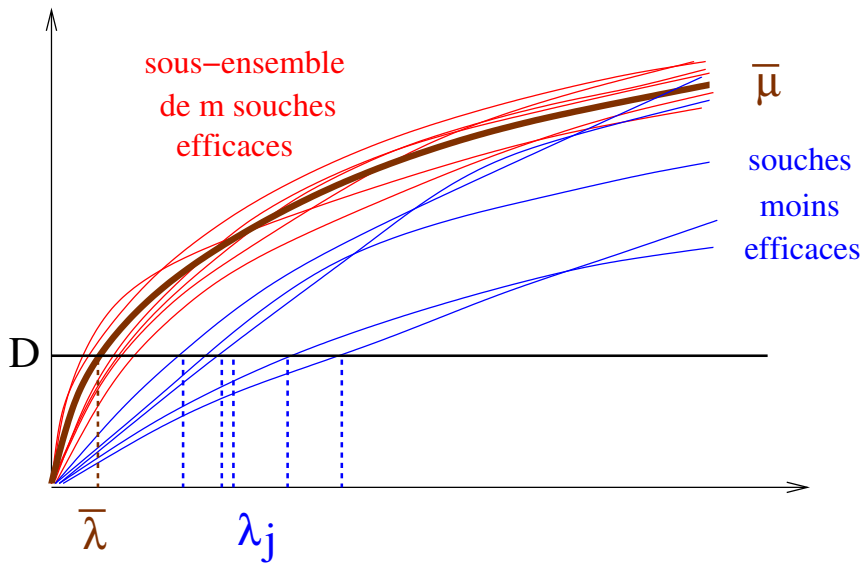
Soit $b = \sum_{i=1}^n x_i$ et $p_i = \frac{x_i}{b}$

$$\Rightarrow \begin{cases} \dot{s} &= -\tilde{\mu}(s, p)b + D(s_{in} - s) \\ \dot{b} &= \tilde{\mu}(s, p)b - Db \end{cases} \quad \text{with} \quad \tilde{\mu}(s, p) = \sum_{i=1}^n p_i \mu_i(s)$$

and $\dot{p}_i = (\mu_i(s) - \tilde{\mu}(s, p)) p_i$



Séparation en deux groupes



Dynamique “rapide”

$$\left\{ \begin{array}{l} \dot{s} = -\bar{\mu}(s)\bar{x} - \sum_{j=m+1}^n \mu_j(s)x_j + D(s_{in} - s) \\ \dot{\bar{x}} = \bar{\mu}(s)\bar{x} - D\bar{x} \\ \dot{x}_j = \mu_j(s)x_j - Dx_j \quad (j = m+1 \dots n) \end{array} \right.$$

**Principe d'Exclusion
Compétitive :**

$$\left\{ \begin{array}{l} \lim_{t \rightarrow +\infty} s(t) = s^* \\ \lim_{t \rightarrow +\infty} \bar{x}(t) = x^* = s_{in} - s^* \\ \lim_{t \rightarrow +\infty} x_j(t) = 0 \quad (j = m+1 \dots n) \end{array} \right.$$

La dynamique lente

Pour $i = 1 \cdots m$, on écrit $\mu_i(s) = \bar{\mu}(s) + \epsilon \nu_i(s)$

$$\Rightarrow \dot{p}_i = \epsilon \left(\nu_i(s^*) - \sum_{j=1}^m p_j \nu_j(s^*) \right) p_i$$

Solution explicite :

$$p_i(t) = \frac{p_i(0)e^{A_i \epsilon t}}{\sum_{j=1}^m p_j(0)e^{A_j \epsilon t}} \quad \text{avec} \quad A_j = \nu_j(s^*)$$

Propriétés de la dynamique lente

- ▶ Toute proportion $t \mapsto p_i(t)$ est
 - soit croissante jusqu'à un temps T_i puis décroissante,
 - soit croissante pour tout t ,
 - soit décroissante pour tout t .
- ▶ Lorsque $\varepsilon \rightarrow 0$ alors $T_i \rightarrow +\infty$ pour toutes les souches sauf une.
- ▶ L'entropie réactionnelle"

$$E(t) := \sum_j \mu_j(\bar{s}) p_j(t)$$

est croissante jusqu'à D .

see R. Dochain Harmand. *Long run coexistence in the chemostat with multiple species*, J. Theor. Bio. 2009

Remarque

Le Principe d'Exclusion Compétitive
est un résultat **asymptotique**.

About modelling flocculation and bacteria attachment at a macroscopic level

Results obtained in the ANR DISCO project - May 2013

Content

- ▶ Extensions of the classical chemostat model
- ▶ Dynamics with mono-specific flocs
- ▶ Dynamics with multi-specific flocs
- ▶ *Some results about overyielding*
- ▶ Concluding remarks and perspectives

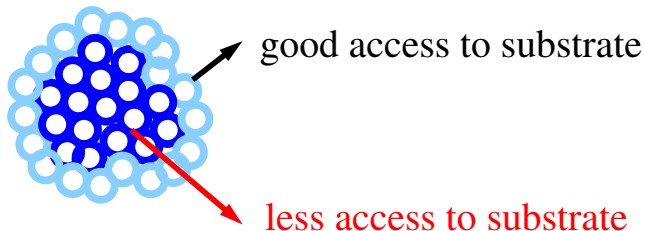
Main objective

Introduce in the simple chemostat model :

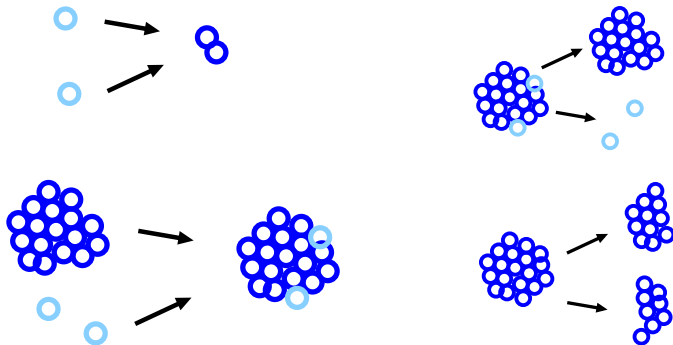
$$\dot{s} = -\mu(s)x + D(s_{in} - s) \quad (\text{substrate concentration})$$

$$\dot{x} = \mu(s)x - Dx \quad (\text{biomass concentration})$$

a consideration of planktonic bacteria and attached bacteria :



Attachement and detachment processes



A simple modelling

The classical chemostat model :

$$\begin{aligned}\dot{s} &= -\mu(s)x + D(s_{in} - s) \\ \dot{x} &= \mu(s)x - Dx\end{aligned}$$

An extension with planktonic bacteria (of concentration v) and attached bacteria (of concentration w) with $x = v + w$:

$$\begin{aligned}\dot{s} &= -\mu_v(s)v - \mu_w(s)w + D(s_{in} - s) \\ \dot{v} &= \mu_v(s)v - D_v v - a(\cdot)v + b(\cdot)w \\ \dot{w} &= \mu_w(s)w - D_w w + a(\cdot)v - b(\cdot)w\end{aligned}$$

where $\left| \begin{array}{l} a(\cdot)v : \text{attachement} \\ b(\cdot)w : \text{detachment} \end{array} \right.$

Examples

- ▶ **adaptive nutrient uptake.** $a(\cdot) = a(s)$, $b(\cdot) = b(s)$
Tang Sitomer Jackson 97
- ▶ **wall attachment.** $a(\cdot) = a$, $b(\cdot) = b$
Pilyguin Waltman 99
- ▶ **intestine model.**
 $a(\cdot) = a \left(1 - \frac{v}{v_{\max}}\right)$, $b(\cdot) = b + \mu_v(s) \left(1 - G\left(\frac{v}{v_{\max}}\right)\right)$ with $G(\cdot) \searrow$
Freter 83
- ▶ **flocs.** $a(\cdot) = av$, $b(\cdot) = b$
Haegeman Rapaport 08

Main assumptions

$$\begin{aligned}\dot{s} &= -\mu_v(s)v - \mu_w(s)w + D(s_{in} - s) \\ \dot{v} &= \mu_v(s)v - D_v v - a(\cdot)v + b(\cdot)w \\ \dot{w} &= \mu_w(s)w - D_w w + a(\cdot)v - b(\cdot)w\end{aligned}$$

Assumption A1. $\mu_v(s) \geq \mu_w(s)$, $\forall s \geq 0$

Assumption A2. $a(\cdot) = \frac{1}{\varepsilon}\alpha(\cdot)$ and $b(\cdot) = \frac{1}{\varepsilon}\beta(\cdot)$ with ε **small**

\Rightarrow **quasi-stationary approximation :**

$$\begin{aligned}\alpha(s, v, w)v &= \beta(s, v, w)w \\ v + w &= x\end{aligned}$$

Reduced dynamics

Assumption A3. $\alpha(s, v, w)v = \beta(s, v, w)w$ can be solved as

$$\begin{aligned}v &= p(s, x)x \\w &= (1 - p(s, x))x\end{aligned}\quad \text{with } p(\cdot) \text{ smooth}$$

Define $\mu(s, x) = p(s, x)\mu_v(s) + (1 - p(s, x))\mu_w(s)$.

$$\Rightarrow \text{Model 1 : } \begin{cases} \dot{s} &= -\mu(s, x)x + D(s_{in} - s) \\ \dot{x} &= \mu(s, x)x - Dx \end{cases} \quad \text{if } D_v = D_w = D$$

$$\Rightarrow \text{Model 2 : } \begin{cases} \dot{s} &= -\mu(s, x)x + d(s, x)(s_{in} - s) \\ \dot{x} &= \mu(s, x)x - d(s, x)x \end{cases} \quad \text{if } D_v \neq D_w$$

with $d(s, x) = p(s, x)D_v + (1 - p(s, x))D_w$

Examples

- ▶ flocs of two individuals :

$$\alpha(\cdot) = av, \quad \beta(\cdot) = b$$

$$\Rightarrow p(x) = \frac{2}{1 + \sqrt{1 + 4a/bx}}$$

- ▶ undifferentiated flocs :

$$\alpha(\cdot) = a(v + w), \quad \beta(\cdot) = b$$

$$\Rightarrow p(x) = \frac{1}{1 + a/bx}$$

The Competitive Exclusion Principle

$$\begin{aligned}\dot{s} &= -\sum_{j=1}^n \mu_j(s)x_j + D(s_{in} - s) \\ \dot{x}_i &= \mu_i(s)x_i - Dx_i \quad i = 1 \cdots n\end{aligned}$$

Proposition (Hsu Hubbell Waltman 77...) Under the conditions

$$\begin{aligned}0 < \mu_1^{-1}(D) < \mu_2^{-1}(D) \leq \cdots \mu_n^{-1}(D) \\ \mu_1^{-1}(D) < s_{in}\end{aligned}$$

any solution with $x_1(0) > 0$ satisfies

$$\lim_{t \rightarrow +\infty} (s(t), x_1(t), \cdots, x_n(t)) = (\mu_1^{-1}(D), s_{in} - \mu_1^{-1}(D), 0, \cdots, 0)$$

Chemostat model with density dependent growths

$$\begin{aligned}\dot{s} &= -\sum_{j=1}^n \mu_j(s, \mathbf{x}_j) x_j + D(s_{in} - s) \\ \dot{x}_i &= \mu_i(s, \mathbf{x}_i) x_i - D x_i \quad i = 1 \dots n\end{aligned}$$

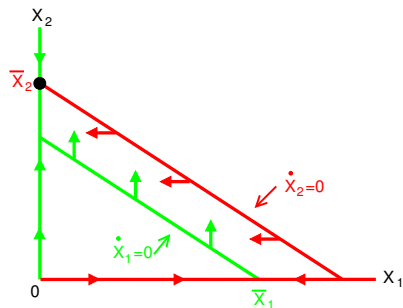
Proposition (Lobry Mazenc Rapaport 05...) Under the conditions

$$\begin{aligned}\mu_i(\cdot, \cdot) &\text{ increasing w.r.t. } s, \text{ decreasing w.r.t. } x_j \\ \mu_i(s_{in}, 0) &> D \\ \mu_i(s, +\infty) &= 0, \quad \forall s \geq 0\end{aligned}$$

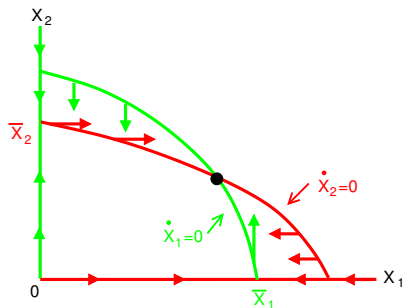
there exists an unique **positive equilibrium**, that is globally exponentially stable.

Sketch of proof in 2D

Example of two species on the attractive manifold $x_1 + x_2 = s_{in} - s$



without density dependency



with density dependency

Chemostat model with multi-specific flocs

$$\begin{aligned}\dot{s} &= -\sum_{j=1}^n \mu_j(s, x_1, \dots, x_n) x_j + D(s_{in} - s) \\ \dot{x}_i &= \mu_i(s, x_1, \dots, x_n) x_i - D x_i \quad i = 1 \dots n\end{aligned}$$

Typically $a_i(\cdot) = \frac{1}{\varepsilon} \sum_j \alpha_{ij} x_j$ and $b_i(\cdot) = \frac{1}{\varepsilon} \beta_i$

$$\Rightarrow p_i(x_1, \dots, x_n) = \frac{\beta_i}{\beta_i + \sum_j \alpha_{ij} x_j}$$

Lobry Harmand 06 : Under the conditions

$\mu_i(\cdot)$ increasing in s , decreasing in each x_j

$x_i = 0 \Rightarrow \mu_i(s_{in}, \dots) > D$

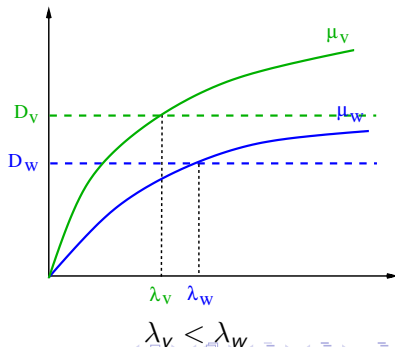
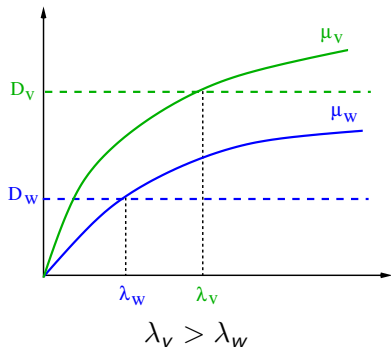
$x_i = +\infty \Rightarrow \mu_i(\cdot) = 0$

simulations show the existence of asymptotically stable **positive equilibrium**, but the *theory* is not ready at the moment...

The case of density-dependent dilution rate

$$\begin{cases} \mu(s^*, x^*)x^* = D(s_{in} - s^*) \\ \mu(s^*, x^*) = d(x^*) \end{cases} \implies \begin{cases} s^* = g(x^*) := s_{in} - x^* \frac{d(x^*)}{D} \quad \downarrow \\ s^* = f(x^*) \quad \uparrow \text{ or } \downarrow \quad ? \end{cases}$$

$$s^* = f(x^*) : \boxed{p(x^*) \underbrace{[\mu_v(s^*) - D_v]}_{= 0 \text{ for } s^* = \lambda_v} + (1 - p(x^*)) \underbrace{[\mu_w(s^*) - D_w]}_{= 0 \text{ for } s^* = \lambda_w} = 0}$$



Multiplicity of equilibria

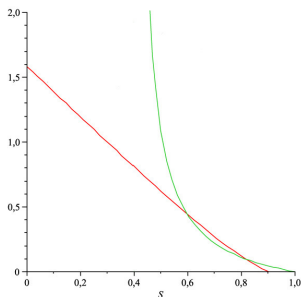
Proposition (Fekih-Salem Harmand Lobry Rapaport Sari 12)

$\lambda_v < \lambda_w$ ($f \nearrow$)		$\lambda_v > \lambda_w$ ($f \searrow$)	
$\lambda_v < s_{in}$	$\lambda_v > s_{in}$	$\lambda_v < s_{in}$	$\lambda_v > s_{in}$
$\exists!(s^*, x^*)$ G.A.S.	no positive equ.	even nb. of equ. alter. stab. and unstab.	uneven nb. of equ. alter. stab. and unstab.
		wash-out eq. repulsive	wash-out eq. attractive

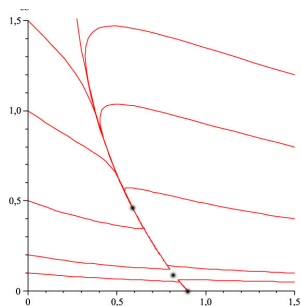
Example

$$\mu_v(s) = \frac{2s}{1+s}, \quad \mu_w(s) = \frac{1.5s}{0.8+s}$$

$$D_u = D = E, \quad D_1 = 0.5, \quad \alpha = 4, \quad \beta = 1, \quad s_{in} = 0.9$$



intersection of the null-clines



phase portrait

The multiple species case

$$\begin{aligned}\dot{s} &= -\sum_{j=1}^n \mu_j(s, x) x_j + D(s_{in} - s) \\ \dot{x}_i &= \mu_i(s, x) x_i - d_i(x) x_i \quad i = 1 \cdots n\end{aligned}$$

Define $\bar{\lambda}_v = \max_i \lambda_{v,i}$ and $\underline{\lambda}_w = \min_i \lambda_{w,i}$.

Assumptions. $\lambda_{v,i} < \lambda_{w,i}$,
 $d'_i(x_i) > \partial_{x_i} \mu_i(s, x_i)$,
 $\bar{\lambda}_v < \min(\underline{\lambda}_w, s_{in})$.

Proposition (Fekih-Salem Harmand Lobry Rapaport Sari 12)
Dynamics admits an unique positive equilibrium E^* if and only if

$$\sum_i \mu_i(\bar{\lambda}_v, g_i^{-1}(\bar{\lambda}_v)) g_i^{-1}(\bar{\lambda}_v) < D(s_{in} - \bar{\lambda}_v)$$

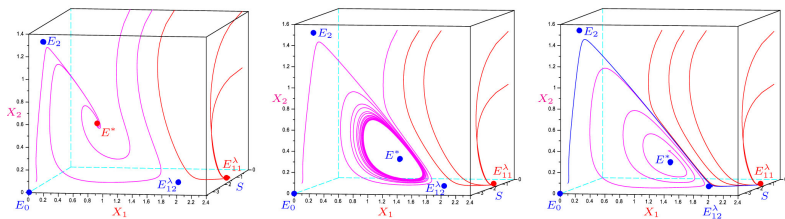
When E^* exists, it is locally exponentially stable.

Ongoing work

Consider a species with $\left\{ \begin{array}{l} \mu_v(\cdot) \text{ non monotonic (Haldane)} \\ \mu_w(\cdot) \text{ monotonic (Monod)} \end{array} \right.$

- Possible behaviors :
- i. no positive equilibrium
 - ii. one positive equilibrium (L.A.S)
 - iii. bi-stability

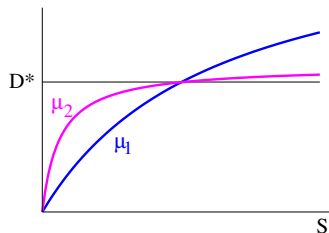
Add a species with monotonic growth, that does not aggregate :



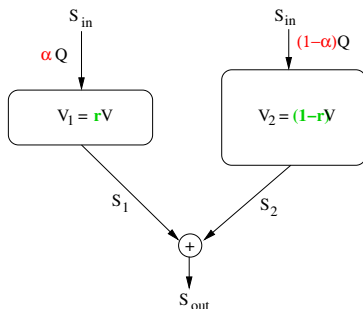
Hopf bifurcation

About niches and overyielding

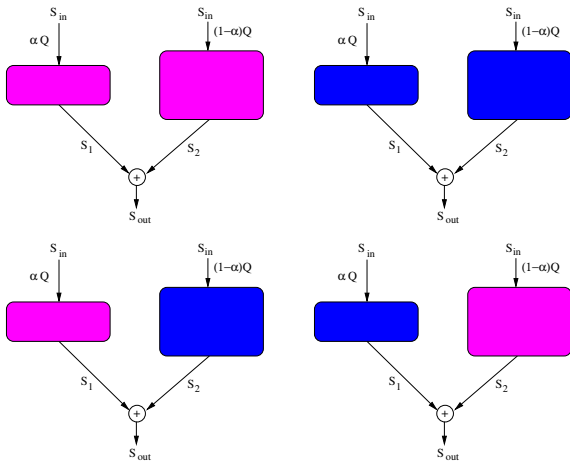
Consider two species



and a spatial structure



Bioconversion overyielding



Which is the best configuration ?

Steady state overyielding

Assumption : $\mu(\cdot)$ is increasing.

$$\text{Let } \lambda(D) = \begin{cases} \mu^{-1}(D) & \text{if } D \leq \mu(s_{in}) \\ s_{in} & \text{if } D > \mu(s_{in}) \end{cases}$$

Define $F(\alpha, r) := \alpha \lambda\left(\frac{\alpha}{r} D\right) + (1 - \alpha) \lambda\left(\frac{1 - \alpha}{1 - r} D\right)$

Definition : There is **overyielding** exactly when

$$G(\alpha, r) := \alpha \lambda_1\left(\frac{\alpha}{r} D\right) + (1 - \alpha) \lambda_2\left(\frac{1 - \alpha}{1 - r} D\right) < \min(F_1(\alpha, r), F_2(\alpha, r))$$

Steady state overyielding

$$C = \{(\alpha, r) \in [0, 1]^2 \mid (\alpha/r)D \leq \mu(s_{in}) \text{ and } ((1 - \alpha)/(1 - r))D \leq \mu(s_{in})\}$$

$$T_1 = \{(\alpha, r) \in [0, 1]^2 \mid (\alpha/r)D > \mu(s_{in})\}$$

$$T_2 = \{(\alpha, r) \in [0, 1]^2 \mid ((1 - \alpha)/(1 - r))D > \mu(s_{in})\}$$

Proposition. If $\mu(\cdot)$ is concave then the restriction of F on C is convex.

Proposition. Define $T^{in}(D) = \lambda(D) + D\lambda'(D)$. One has

$$\min_{[0,1]^2} F = \begin{cases} \lambda(D) = F(\alpha, \alpha), \forall \alpha \in [0, 1], \text{ for } s_{in} \geq T^{in}(D) \\ \min_{\alpha} F(\alpha, 0) < \lambda(D), \text{ for } s_{in} < T^{in}(D) \end{cases}$$

Steady state overyielding

Assume that there exists D^* such that $\lambda_1(D^*) = \lambda_2(D^*)$.

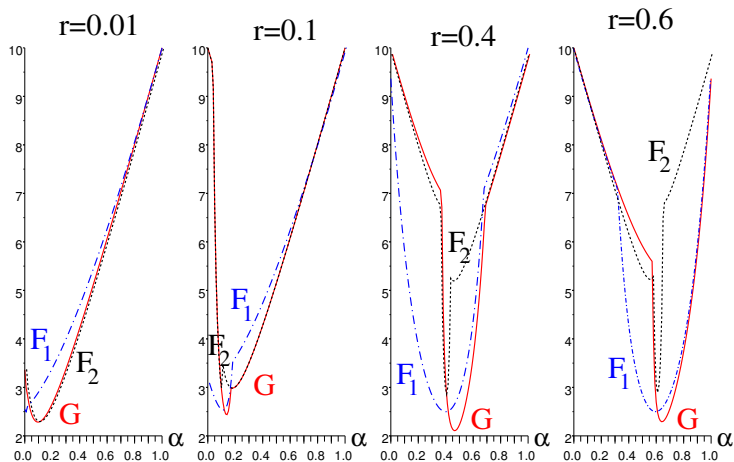
Proposition. When $D = D^*$ and $\alpha \in (0, 1)$, there exist configurations close to (α, α) that present overyielding.

Proposition. When $D \neq D^*$, there exists (α, r) with

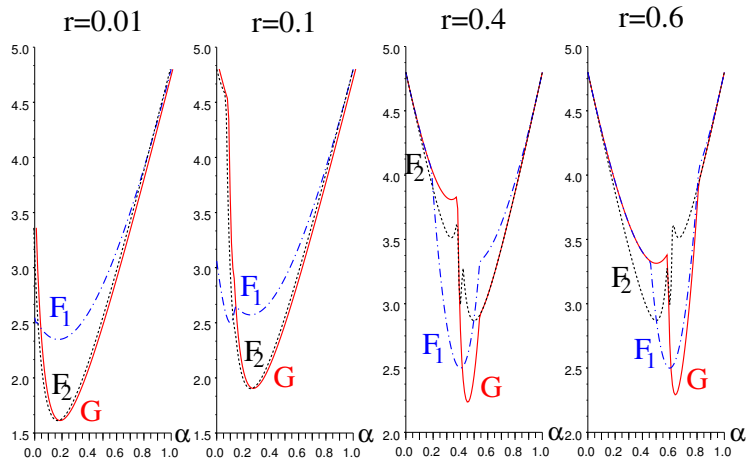
$$\frac{\alpha}{r}D < D^* < \frac{1-\alpha}{1-r}D < \min(\mu_1(s_{in}), \mu_2(s_{in}))$$

that corresponds to overyielding.

Example (large s_{in})



Example (small s_{in})



Concluding remarks and perspectives

- ▶ Macroscopic models of flocs with same dilution rate lead to **density-dependent growth rate** for the overall biomass.
- ▶ Macroscopic models of flocs with different dilution rate lead in addition to **density-dependent dilution rate** for the overall biomass.
- ▶ Richness of possible behaviors with possibly multiple positive equilibria, bi-stability, limit cycle... **How to infer the right attachment and detachment terms?**
- ▶ We would like to see if all these predictions could occur on more realistic (and more complex) models as well as in real flocs or biofilms...

References

- ▶ Haegeman, B., C. Lobry and J. Harmand (2007) *Modeling bacteria flocculation as density-dependent growth*, AIChE Journal, Vol. 53(2) , pp. 535-539.
- ▶ Haegeman, B. and Rapaport, A. (2008) *How flocculation can explain coexistence in the chemostat*, Journal of Biological Dynamics, Vol. 2, No. 1, pp. 1-13.
- ▶ Fekih-Salem R., Harmand J., Lobry C., Rapaport, A. and Sari T. (2012) *Extensions of the chemostat model with flocculation*, J. of Mathematical Analysis and Applications, Vol. 397, pp. 292-306.
- ▶ Fekih-Salem R., Rapaport, A. and Sari T. (2013) *Effect of the flocculation on the coexistence of microbial species and apparition of limit cycles with non monotonic growth rates*, submitted.