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ETUDE DU COMPORTEMENT EN TEMPS LONG DE PROCESSUS DE MARKOV DETERMINISTES PAR MORCEAUX

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Résumé

L'objectif de cette thèse est d'étudier le comportement en temps long de certains processus de Markov déterministes par morceaux (PDMP) dont le flot suivi par la composante spatiale commute aléatoirement entre plusieurs flots possédant un unique équilibre attractif (éventuellement le même pour chaque flot). Nous donnerons dans un premier temps un exemple d'étude d'un tel processus construit dans le plan à partir de flots associés à des équations différentielles linéaires stables où il est déjà possible d'observer des comportements contre-intuitifs. La deuxième partie de ce manuscrit est dédiée à l'étude et la comparaison de deux modèles de compétition pour une ressource dans un environnement hétérogène. Le premier modèle est un modèle alétoire simulant l'hétérogénéité temporelle d'un environnement sur les espèces en compétition à l'aide d'un PDMP. Son étude utilise des outils maintenant classiques sur l'étude des PDMP. Le deuxième modèle est un modèle déterministe (présentant sous forme d'un système d'équations différentielles) modélisant l'impact de l'hétérogénéité spatiale d'un environnement sur ces mêmes espèces. Nous verrons que malgré leur nature très différente, le comportement en temps long de ces deux systèmes est relativement similaire et est essentiellement déterminé par le signe des taux d'invasion de chacune des espèces qui sont des quantités dépendant exclusivement des paramètres du système et modélisant la vitesse de croissance (ou de décroissance) de ces espèces lorsqu'elles sont au bord de l'extinction.

Mots clés : Processus de Markov déterministes par morceaux ; Comportement en temps long ; Modèle de compétition ; Chemostat ; Gradostat

Abstract

The objective of this thesis is to study the long time behaviour of some piecewise deterministic Markov processes (PDMP). The flow followed by the spatial component of these processes switches randomly between several flow converging towards an equilibrium point (not necessarily the same for each flow). We will first give an example of such a process built in the plan from two linear stable differential equations and we will see that its stability depends strongly on the switching times. The second part of this thesis is dedicated to the study and comparison of two competition models in a heterogeneous environment. The first model is a probabilistic model where we build a PDMP simulating the effect of the temporal heterogeneity of an environment over the species in competition. Its study uses classical tools in this field. The second model is a deterministic model simulating the effect of the spatial heterogeneity of an environment over the same species. Despite the fact that the nature of the two models is very different, we will see that their long time behavior is very similar. We define for both model several quantities called invasion rates modelizing the growth (or decreasing) rate speed of a species when it is near to extinction and we will see that the signs of these invasion rates fully describes the long time behavior for both systems.

Keywords : Piecewise deterministic Markov processes ; Long time behaviour ; Competition model ; Chemostat ; Gradostat

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Introduction

Cette thèse porte sur l'étude du comportement en temps longs de processus de Markov déterministes par morceaux plus couramment appelés *piecewise deterministic Markov processes* dans la littérature et usuellement abrégé en PDMP. Cette classe de processus a été introduite en 1984 par Davis dans [Davis, 1984]. Les PDMP apparaissent naturellement dans la modélisation de nombreux phénomènes biologiques et écologiques mais également en informatique ou en finance ce qui a favorablement encouragé leur étude durant les dernières décennies.

Un PDMP est un processus suivant une dynamique déterministe (généralement associée à une équation différentielle) entre des temps de sauts aléatoires. A chaque de temps de saut, le processus change aléatoirement de position. Dans ce manuscrit, nous nous intéresserons plus particulièrement à une certaine sous-classe de ces PDMP. Les processus de cette sous-classe possèdent une composante spatiale continue et une autre composante discrète. La composante discrète détermine le flot déterministe suivi par la composante spatiale et c'est cette même composante discrète qui change aléatoirement à chaque temps de saut. Nous appellerons ces processus les SPDMP pour *switched PDMP*.

Dans ce manuscrit nous nous intéressons au comportement en temps long de certains SPDMP construits à partir de flots stables. Plus particulièrement, en supposant que plusieurs flots convergent vers le même et unique attracteur, est-ce que le SPDMP associé converge vers cet attracteur ? Il s'avère que la réponse est souvent négative et dépend fortement des champs de vecteurs mais aussi de la vitesse de commutation.

Ce manuscrit se divise en trois parties. Dans la première partie, nous reviendrons brièvement sur les définitions de processus de Markov et nous donnerons une définition mathématique des PDMP ainsi que quelques résultats qui seront largement utilisés dans la suite. Dans la deuxième partie, nous étudions de manière exhaustive un SPDMP planaire construit à partir d'équations linéaires stables mais pouvant exploser suivant le choix de la vitesse de commutation. La troisième partie consiste en l'étude et la comparaison de deux modèles construits à partir des équations du chemostat (voir [Hsu, 1978]) et modélisant à leur modeste échelle l'impact de l'environnement sur un système de compétition de deux espèces pour une ressource. Le premier modèle est un SPDMP dont la construction et l'étude ont été fortement inspirées de [Benaïm et Lobry, 2016] et qui simule les variations aléatoires de l'environnement. Le deuxième est un processus déterministe adapté des équations du gradostat (voir [Smith et Waltman, 1995] pour plus d'informations) simulant l'hétérogénéité d'un environnement.

Ce mémoire a été principalement écrit à partir des articles suivants :

- *A note on simple randomly switched linear systems*
- *Comparison of the global dynamics for two chemostat-like models : random temporal variation versus spatial heterogeneity.*

Chapitre 1

Introduction générale

L'objectif de ce chapitre est de donner les outils permettant de comprendre les études de processus effectuées dans les chapitres suivants. Nous donnerons tout d'abord une définition précise des PDMP avant de décrire les outils principaux permettant leurs études.

1.1 Processus de Markov

Les PDMP sont des cas particuliers de processus de Markov. Par conséquent, nous revenons brièvement sur leur définition dans cette partie (pour de plus amples détails, consulter [Ethier et Kurtz, 1986]). Soit (X_t) un processus aléatoire défini sur un espace probabilisé $(\Omega, \mathcal{F}, \mathbb{P})$ à valeurs dans $\mathbb{R}^d$. Notons $\mathcal{F}_t$ la tribu engendrée par la famille $(X_s)_{0\leq s\leq t}$. Alors (X_t) est un processus de Markov si :

$$\mathbb{E}(f(X_{t+s})|\mathcal{F}_t) = \mathbb{E}(f(X_{t+s})|X_t) \tag{1.1}$$

pour toute fonction mesurable bornée f et tout temps positifs s, t. On dit communément que l'évolution future d'un processus de Markov ne dépend du passé que par son état présent.

On associe au processus de Markov (X_t) son semi-groupe noté (P_t) qui est une famille d'opérateurs définie par :

$$P_t f(x) = \mathbb{E}(f(X_t)|X_0 = x)$$

pour tout x dans $\mathbb{R}^d$ et pour toutes fonctions borélienne et bornée f.

Remarque 1.1.1. *Le calcul suivant montre que (P_t) est un semi-groupe. Soit $x \in \mathbb{R}^d$ et f une fonction borélienne bornée, on a pour tout t, $s > 0$:*

$$\begin{aligned}
P_{t+s}f(x) &= \mathbb{E}(f(X_{t+s})|X_0 = x) \\
&= \mathbb{E}(\mathbb{E}(f(X_{t+s}|\mathcal{F}_s)|X_0 = x) \\
&= \mathbb{E}(\mathbb{E}(f(X_{t+s}|X_s)|X_0 = x) \\
&= \mathbb{E}(P_s f(X_t)|X_0 = x) \\
&= P_t \circ P_s f(x).
\end{aligned}$$

La relation $P_{t+s} = P_t \circ P_s$ est appelée la relation de Chapman-Kolmogorov.

Le semi-groupe caractérise la loi d'un processus de Markov en un temps t. Si μ est une mesure de probabilité, on notera :

$$\mu(f) = \int f d\mu \quad \text{et} \quad \mu P_t = \mathcal{L}(X_t | X_0 \sim \mu).$$

On a la relation suivante :

$$\mu(P_t f) = \mu P_t(f). \tag{1.2}$$

En effet :

$$\int f d\mu P_t = \mathbb{E}(f(X_t)) = \mathbb{E}(\mathbb{E}(f(X_t)|X_0)) = \mathbb{E}(P_t f(X_0)) = \int P_t f d\mu.$$

On dira qu'une mesure de probabilité μ est une mesure invariante pour un processus de Markov (X_t) si et seulement si pour tout temps t, X_t est distribué selon μ lorsque X_0 est distribué selon μ :

$$\forall t > 0, \quad \mu P_t = \mu.$$

Lorsqu'on étudie un processus de Markov, on s'intéresse toujours à l'éventuelle existence et unicité de sa mesure invariante ainsi qu'à sa convergence vers cette mesure invariante. En effet, lorsque ces propriétés sont vérifiées, cela permet de comprendre le comportement limite du processus ou de quantité lui étant reliées.

Le semi-groupe d'un processus de Markov est caractérisé par son générateur infinitésimal L qui est rigoureusement défini par :

$$Lf = \lim_{t \to 0} \frac{P_t f - f}{t}$$

où les fonctions f sont dans le domaine du générateur L noté $\mathcal{D}(L)$ qui contient l'ensemble des fonctions f pour lesquelles cette limite existe. Pour toutes fonctions f dans $\mathcal{D}(L)$, $P_t f$ est également dans $\mathcal{D}(L)$ et le générateur infinitésimal L vérifie les relations suivantes :

$$LP_t f = P_t L f, \quad P_t f = f + \int_0^t LP_t f ds.$$

Un processus de Markov est caractérisé par la donnée de son générateur infinitésimal. L'avantage de travailler avec ce dernier est que, contrairement au semi-groupe, il est généralement explicite et permet de faire des calculs. Nous utiliserons abondamment dans ce manuscrit la propriété suivante.

Proposition 1.1.2. *Soit (X_t) un processus de Markov de générateur infinitésimal L.*

$$\mu \text{ est une mesure invariante de } X_t \Leftrightarrow \forall f \in \mathcal{D}(L), \quad \int Lf d\mu = 0.$$

Démonstration. Si μ est une mesure invariante de (X_t), on a vu que $\forall t > 0$, $\mu P_t = \mu$. On a donc $\forall f \in \mathcal{D}(L)$:

$$\int f d(\mu P_t) = \int P_t f d\mu = \int f d\mu.$$

Donc :

$$\int \frac{1}{t}(Ptf - f)d\mu = 0.$$

Et donc par convergence dominée on a :

$$\int \frac{Ptf - f}{t} d\mu \underset{t\to 0}{\longrightarrow} \int Lf d\mu = 0.$$

Si $\int Lf d\mu = 0$, on écrit :

$$\int (P_t f - f)d\mu = \int \int_0^t LP_s f ds d\mu = \int_0^t \int LP_s f d\mu ds = 0.$$

□

Nous allons dans la prochaine section introduire les processus de Markov déterministes par morceaux qui sont au coeur de ce manuscrit.

1.2 Processus de Markov déterministes par morceaux

De manière générale, un PDMP est décrit par la donnée de trois objets :

- Un flot $\varphi : (\mathbb{R} \times \mathbb{R}^d) \to \mathbb{R}^d$ associé à un champ de vecteurs $F : \mathbb{R}^d \to \mathbb{R}^d$ donnant le comportement déterministe du PDMP entre les temps de saut,
- Un taux de saut $\lambda : \mathbb{R}^d \to \mathbb{R}_+$ qui permet de décrire la loi de la durée entre deux temps de sauts.
- Un noyau de transition $Q : \mathbb{R}^d \mapsto \mathcal{P}$ définissant la façon dont le PDMP saute lorqu'il arrive à un temps de saut.

Concrètement, la trajectoire d'un PDMP (X_t) de valeur initiale $X_0 = x$ est décrite de la manière suivante. Le premier temps de saut T_1 est défini par sa fonction de répartition :

$$\forall t \geq 0,\ \mathbb{P}(T_1 \leq t | X_0 = x) = 1 - \exp\left(- \int_0^t \lambda(\varphi(s, x))ds \right).$$

La trajectoire de (X_t) entre 0 et T_1 est donnée par :

$$\forall 0 \leq t \leq T_1,\ X_t = \begin{cases} \varphi(t, x) & \text{si } t < T_1 \\ Y_1 & \text{sinon} \end{cases}$$

où la variable aléatoire Y_1 est définie par :

$$\forall f \in \mathcal{B},\ \mathbb{E}(f(Y_1)|T_1,\ X_0 = x) = \int f(y) Q(\varphi(T_1, x), dy).$$

En partant de X_{T_1}, on définit de la même manière un nouveau temps de saut T_2 et la position Y_2 après le saut et ainsi de suite.

Remarque 1.2.1. *Lorsque le taux de saut λ est constant, les temps intersauts suivent des lois exponentielles.*

Dans tout le manuscrit, nous ferons l'hypothèse classique que quel que soit le temps t, le nombre de sauts entre 0 et t est fini ce qui assure que le processus n'explose pas. Cette hypothèse sera immédiatement vérifiée par les processus étudiés dans les Chapitres 2 et 3. Les PDMP ainsi définis sont des processus de Markov et vérifient la propriété forte de Markov.

Proposition 1.2.2. *Le générateur infinitésimal du PDMP (X_t) est donné par :*

$$Lf(x) = \langle F(x), \nabla f(x) \rangle + \lambda(x) \int (f(y) - f(x))Q(x, dy)$$

pour toutes fonctions $f : \mathbb{R}^d \to \mathbb{R}$ bornée de classe $\mathcal{C}^1$.

Dans ce manuscrit nous nous intéresserons exclusivement à une classe de PDMP de la forme (X_t, I_t). La première composante (X_t) est une composante spatiale évoluant dans $\mathbb{R}^d$ suivant le flot d'un champ de vecteur déterminé par la deuxième composante discrète (I_t). La trajectoire de (X_t) est alors continue et présente des "brisures" qui correspondent à un changement de flot lorsque (I_t) saute. Le générateur infinitésimal d'un tel PDMP est donné par :

$$Lf(x,i) = \langle F(x,i), \nabla_x f(x,i) \rangle + \lambda(x,i) \sum_{j \neq i} (f(x,j) - f(x,i))Q(x,i,j)$$

Nous appelerons ce type de processus *switched piecewise deterministic Markov processes* abrégé en SPDMP. Nous finirons cette partie en donnant divers exemples de SPDMP issus de la modélisation. Le lecteur intéressé pourra également consulter les articles [Malrieu, 2015] ainsi que [Cloez *et al.*, 2017] qui décrivent des exemples de tels processus et donnent les clés de leurs études.

Exemple 1.2.3. *Dans [Fontbona* et al.*, 2016], les auteurs modélisent la chimiotaxie d'une bactérie sur l'axe réel contenant des nutriments à son origine. En notant $X_t \in \mathbb{R}$ la position de la bactérie et $V_t \in \{-1, 1\}$ sa vitesse, on construit le SPDMP (X_t, V_t) par son générateur infinitésimal :*

$$Lf(x,v) = v.\frac{\partial f}{\partial x} + (a(x)\mathbb{1}_{xv>0} + b(x)\mathbb{1}_{xv<0})(f(x,-v) - f(x,v))$$

où a et b sont deux fonctions positives. Concrètement, le taux de saut dépend de la position de la particule mais également du fait qu'elle s'éloigne du nutriment ou qu'elle s'en rapproche.

Exemple 1.2.4. *Dans [Fetique, 2017], on s'intéresse également au déplacement d'une bactérie dans $\mathbb{R}^d$ en présence d'un nutriment placé à l'origine et agissant comme un attracteur. La bactérie se déplace de manière linéaire à la vitesse $v \in \overline{\mathcal{B}}(0,1)$ durant un temps aléatoire avant de changer de vitesse selon un noyau $Q(x, v, .)$. Le générateur du processus (X_t, V_t) modélisant le déplacement de cette bactérie est donné par :*

$$Lf(x,v) = \langle v, \nabla_x f(x,i) \rangle + \lambda(x,v) \int \big(f(x,v') - f(x,v)\big) Q(x,v,dv').$$

Exemple 1.2.5. *Dans [Costa, 2016] l'auteur s'intéresse à la dynamique d'une communauté de proies et prédateurs dans laquelle la population des prédateurs évolue plus vite que la population des proies. On note* $N_t \in \mathbb{N}^*$ *le nombre de proies au temps* t *et* $H_t \in \mathbb{R}$ *la densité de prédateurs au temps* t*. A un nombre* N *fixé de proies, la densité de prédateurs* H_t *suit la dnamique induite par l'équation différentielle suivante :*

$$\dot{H}_t = H_t(rB.N - D - C.H_t)$$

où r*,* B*,* D *et* C *sont des constantes propres à la communauté étudiée. La population des prédateurs évoluant plus vite que la population des proies, on modélise la dynamique de la communauté par un SPDMP* (H_t, N_t) *dont le générateur infinitésimal est donnée par :*

$$\begin{aligned}Lf(h,n) = \frac{\partial f}{\partial h}(h,n).h(rB.n - D - C.h) &+ b.n\left(f(h,n+1) - f(h,n)\right) \\ &n(d + c.n + B.h)\mathbb{1}_{n\geq 2}\left(f(n-1,h) - f(n,h)\right)\end{aligned}$$

où b*,* c *et* d *sont d'autres constantes propres à la communauté étudiée.*

1.3 Motivations et résultats

On considère un SPDMP construit à partir de champs de vecteurs F_i. En supposant que chaque champ de vecteurs F_i possède un unique équilibre stationnaire asymptotiquement stable, le SPDMP ainsi construit possède-t-il une mesure invariante ? Si oui est-elle unique et peut-on estimer la vitesse de convergence du processus vers celle-ci ? Supposons de plus que ces équilibres stationnaires soient le même pour chaque F_i, le processus converge-t-il presque sûrement vers cet équilibre ?

Dans [Benaïm *et al.*, 2012], les auteurs donnent une condition forte sur les champs de vecteurs F_i pour que le SPDMP associé possède une unique mesure invariante :

$$\langle x - x', F_i(x) - F_i(x')\rangle \leq \alpha_i \|x - x'\|^2. \tag{1.3}$$

En appelant φ^i le flot associé au champ de vecteurs F_i, (1.3) implique que :

$$\|\varphi_t^i(x) - \varphi_t^i(x')\| \leq e^{-\alpha_i t}\|x - x'\| \quad \forall x, x' \in \mathbb{R}^d \text{ et } \forall t > 0. \tag{1.4}$$

Par conséquent, en supposant que α_i ne dépend plus de i et que les champs de vecteurs F_i ont le même équilibre stationnaire x_{eq} alors (1.4) entraîne que le SPDMP converge vers x_{eq} presque sûrement.

Cependant ces conditions ne sont pas nécessaires et plusieurs articles ont depuis mis en évidence des SPDMP construits à partir de champs de vecteurs stables mais qui ne possèdent pas de mesure invariante. L'objectif initial de cette thèse est de construire et d'étudier de tels SPDMP afin de mettre en évidence la diversité des comportements en temps longs qu'il est possible d'obtenir en faisant commuter des champs de vecteurs stables.

1.3.1 Systèmes linéaires planaires aléatoirement commutés.

Soient A_0 et A_1 deux matrices Hurwitz de $\mathcal{M}_d(\mathbb{R})$ (leurs valeurs propres sont à parties réelles strictement négatives) et (I_t) une chaîne de Markov simple sur $E = \{0,1\}$ de taux de sauts λ_0, λ_1. On construit le SPDMP (X_t, I_t) en imposant que la composante spatiale (X_t) soit solution de l'équation différentielle :

$$\begin{cases} \dot{X}_t = A_{I_t} X_t \quad \forall t > 0 \\ X_0 = x_0 \in \mathbb{R}^d \end{cases} \tag{1.5}$$

Il est clair qu'en l'absence de commutation, les solutions à cette équation différentielle tendent vers 0 à une vitesse exponentielle. Cependant il a été montré dans divers articles (voir [Benaïm *et al.*, 2014] et [Lawley *et al.*, 2014]) qu'il était possible de bien choisir les matrices A_0 et A_1 afin que le SPDMP (X_t, I_t) explose presque sûrement pour certaines valeurs des taux de saut λ_0 et λ_1.

Dans [Lawley *et al.*, 2014], les auteurs construisent un tel SPDMP dont la composante spatiale X_t est dans $\mathbb{R}^{2n}$ dont le comportement en temps long alterne entre stable et explosif lorsque le taux de saut du processus de saut I_t augmente. Nous nous sommes alors demandé s'il était possible de faire de même mais pour un SPDMP à composante spatiale dans le plan $\mathbb{R}^2$.

Pour $a > 0$ and $b > 1$, On considère les matrices suivantes :

$$A_0 = \begin{pmatrix} -a & b \\ -\frac{1}{b} & -a \end{pmatrix} \quad \text{et} \quad A_1 = \begin{pmatrix} -a & \frac{1}{b} \\ -b & -a \end{pmatrix}.$$

Grâce à ces deux matrices, on peut définir le SPDMP (X_t, I_t) comme énoncé plus haut dans l'équation (1.5) où on rappelle que (I_t) est une chaîne de Markov sur $E = \{0,1\}$ de taux de saut λ_0, λ_1. On va poser $\lambda_0 = \beta u$ et $\lambda_1 = \beta(1-u)$ avec $\beta > 0$ et $u \in]0,1[$. La composante spatiale X_t suit une spirale dans le sens horaire durant un temps aléatoire de loi exponentielle avant de sauter vers une autre spirale comme décrit dans la figure 1.1.

Ce processus a un comportement très riche lorsque l'on suppose que I_t est une fonction déterministe périodique. En effet, il est assez facile de se convaincre au moins sur un schéma que lorsque la période de I_t augmente, le comportement limite de X_t alterne entre des phases stables et des phases explosives. Intuitivement, on pourrait s'attendre à observer le même comportement en supposant que (I_t) est une chaîne de Markov.

On définit :

$$\chi := \chi(a,b,\beta,u) = \lim_{t \to +\infty} \frac{1}{t} \log(\|X_t\|) \quad \text{p.s} \tag{1.6}$$

dont on prouvera l'existence dans le Chapitre 2. On peut constater que le signe de χ donne le comportement en temps long du processus. En effet, si χ est positif, la composante spatiale X_t explose presque sûrement alors que si χ est négatif, X_t tend vers 0 presque sûrement.

Le résultat principal du Chapitre 2 est le suivant.

Théorème 1.3.1. *Pour tout* $u \in]0,1[$,

(*i*) $\forall a, b > 0, \quad \chi(a,b,\beta,u) \longrightarrow -a$ *quand* $\beta \to 0$ *ou* $\beta \to +\infty$.

(*ii*) *Pour tout* $\beta, u > 0$ *il existe* $a > 0$ *et* $b > 1$ *tel que* $\chi(a,b,\beta,u) > 0$.

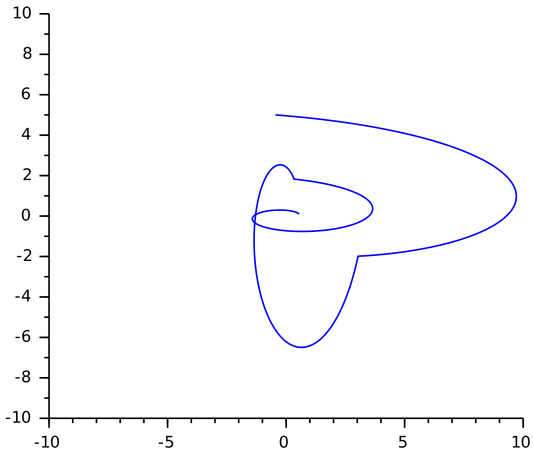


FIGURE 1.1 – Un exemple de trajectoire du processus (X_t, I_t).

On peut simuler numériquement le signe de χ comme on peut le voir sur la figure 1.2. On peut également donner le signe de χ dans le plan (β, u) comme on peut le voir sur la figure 1.3. Sur cette dernière, on peut voir que le signe de χ est positif dans un compact.

Ces graphiques combinés au Théorème 1.3.1 montrent que ce processus ne répond pas à nos attentes en terme de comportement alternatif. Il existe au maximum une unique zone connexe de paramètres pour le taux de saut de (I_t) pour laquelle le processus (X_t) explose alors que dans le cas où (I_t) est une fonction périodique, il peut y en avoir autant que l'on veut.

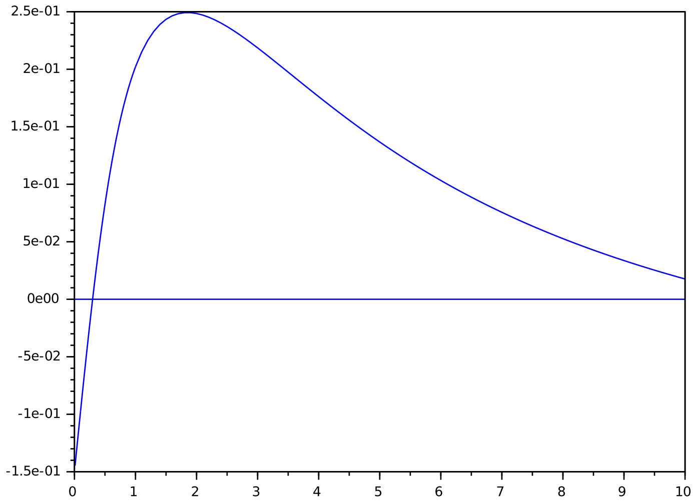


FIGURE 1.2 – La fonction $\beta \longmapsto \chi(0.15, 3, \beta, 0.5)$ où χ est donné par (1.6)

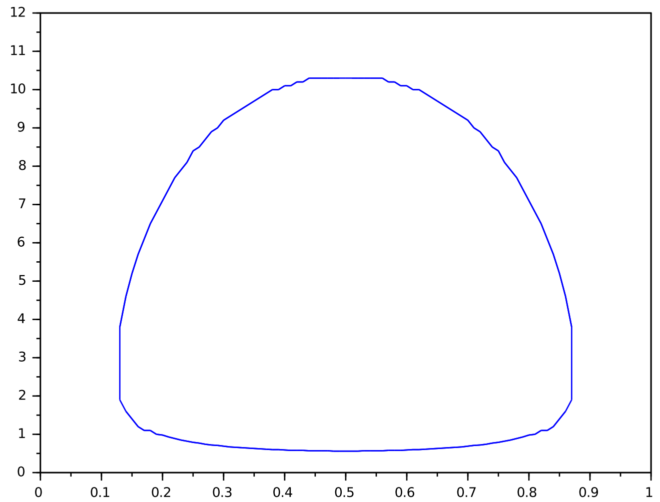


FIGURE 1.3 – Signe de $G : (\beta, u) \longmapsto \chi(0.1, 2.5, \beta, u)$. La courbe représente les point (β, u) pour lesquels $\chi(0.1, 2.5, \beta, u) = 0$. Le signe de G est positif à l'intérieur et négatif à l'extérieur.

1.3.2 Modèles de compétition aléatoirement commutés

En biologie, le principe d'exclusion compétitive stipule que deux espèces ayant les mêmes besoins écologiques ne peuvent pas coexister indéfiniment dans un environnement homogène. De nombreux modèles de compétition satisfont ce principe, l'un des plus connu est le modèle de compétition proie/prédateur de Lotka-Volterra. La biodiversité observée dans certains milieux ne pourrait donc s'expliquer que par leur hétérogéneité qu'elle soit spatiale ou temporelle. Afin de modéliser les fluctuations temporelles d'un environnement, on va commuter suffisamment vite les flots suivis par les densité des espèces pour observer de la coexistence ou au pire l'extinction de l'espèce qui a priori était meilleure compétitrice.

Dans [Benaïm et Lobry, 2016], les auteurs construisent et étudient un SPDMP (U_t, V_t, I_t) évoluant dans $\mathbb{R}_+ \times \mathbb{R}_+ \times \{0,1\}$ où (I_t) est une chaîne de Markov simple sur $\{0,1\}$ de taux de sauts λ_0, λ_1 et U_t, V_t (les tailles des populations u, v) suivent les flots de deux équations de Lotka-Volterra :

$$\begin{cases} \dot{U}_t = \alpha_{I_t} U_t \left(1 - a_{I_t} U_t - b_{I_t} V_t\right) \\ \dot{V}_t = \beta_{I_t} V_t \left(1 - c_{I_t} U_t - d_{I_t} V_t\right) \end{cases}$$

Ils montrent qu'il est possible de choisir deux systèmes de Lotka-Volterra favorables à l'espèce u et un bon taux de saut tel que le système commuté soit finalement défavorable à l'espèce u.

Nous avons voulu effectuer la même étude pour un modèle de compétition légèrement plus complexe, le modèle de compétition, avec une unique ressource, du chemostat. Le chemostat se présente sous la forme d'une cuve où deux espèces u et v sont en compétition pour une ressource R. Dans un chemostat ε, on note δ le taux de dilution commune des espèces u et v ainsi que celui de la ressource R. On note R_0 le taux de concentration de ressource entrant dans la cuve et pour toute espèce $w \in \{u, v\}$, f_w le taux de croissance de l'espèce w. Nous supposerons toujours que les fonctions f_w sont de la forme :

$$f_w(R) = \frac{a_w R}{b_w + R}.$$

où a_w est le taux de croissance maximale de l'espèce w et b_w est la constante de Michaelis-Menten de l'espèce w.

Notons $U(t)$, $V(t)$ et $R(t)$ les concentrations des espèces u, v et de la ressource R. L'évolution de ces différentes concentrations dans le chemostat ε est donnée par le système :

$$\begin{cases} \dot{R}(t) = \delta(R_0 - R(t)) - U(t) f_u(R(t)) - V(t) f_v(R(t)) \\ \dot{U}(t) = U(t) \left(f_u(R(t)) - \delta\right) \\ \dot{V}(t) = V(t) \left(f_v(R(t)) - \delta\right). \end{cases} \tag{1.7}$$

Notons :

$$R_w = \begin{cases} \frac{b_w \delta}{a_w - \delta} \text{ if } a_w > \delta \\ +\infty \text{ if } a_w \leq \delta, \end{cases}$$

la concentration de ressource satisfaisant $f_w(R) = \delta$ (si possible). Cette quantité R_w est interprétée comme étant la concentration minimale de ressource nécessaire à l'espèce w

pour survivre. L'espèce qui a le moins besoin de ressource pour survivre est la meilleure compétitrice au sein du chemostat.

Nous avons le théorème suivant ([Hsu, 1978],[Hsu *et al.*, 1977]) :

Théorème 1.3.2. *Supposons que $R_u < R_v$ et $R_u < R_0$ (l'espèce u est donc la meilleure compétitrice). Alors les solutions de 1.7 avec condition initiale $U(0) > 0$ satisfont :*

$$\begin{aligned}
&\lim_{t\to+\infty} R(t) = R_u,\\
&\lim_{t\to+\infty} U(t) = R_0 - R_u,\\
&\lim_{t\to+\infty} V(t) = 0.
\end{aligned}$$

Le chemostat satisfait donc le principe d'exclusion compétitive : si u est meilleur compétitrice que v, l'espèce v finira par s'éteindre.

Pour simuler l'hétérogénéité spatiale de l'environnement dans lequel évoluent nos deux espèces u et v ainsi que la ressource R on va commuter aléatoirement le chemostat dans lequel elles évoluent. Fixons deux chemostats ε^1 et ε^2. Les paramètres du chemostat ε^j seront notés $(R_0^j, \delta^j, a_u^j, a_v^j, b_u^j, b_v^j)$.

En appelant U_t, V_t les concentrations des espèces u, v et R_t est la concentration de la ressource, on construit le SPDMP (R_t, U_t, V_t, I_t) par le système suivant :

$$\begin{cases}
\dot{R}_t = \delta^{I_t}(R_0^{I_t} - R_t) - U_t f_u^{I_t}(R_t) - V_t f_v^{I_t}(R_t)\\
\dot{U}_t = U_t(f_u^{I_t}(R_t) - \delta^{I_t})\\
\dot{V}_t = V_t(f_v^{I_t}(R_t) - \delta^{I_t})
\end{cases} \tag{1.8}$$

où (I_t) est une chaîne de markov sur l'espace d'état $\{1, 2\}$ de taux de saut λ^1 et λ^2. Dorénavant nous appelerons (Z_t) le processus (R_t, U_t, V_t, I_t). En l'absence de spécification, on supposera toujours que les concentrations initiales U_0 et V_0 sont strictement positives.

On montrera qu'on pourra toujours supposer que le processus (Z_t) est inclus dans un compact M de $\mathbb{R}_+^3 \times \{1, 2\}$, et on notera les espaces d'extinction de l'espèce w :

$$M_w = \{(r, u, v, i) \in M | w = 0\}.$$

Afin de décrire le comportement du processus (Z_t) sur M, dans [Benaïm et Lobry, 2016], les auteurs suggèrent d'étudier les taux d'invasion des deux espèces u et v définis par :

$$\Lambda_w = \int \left(f_w^i(R) - \delta^i\right) d\mu_{\overline{w}},$$

où $\mu_{\overline{w}}$ est la mesure invariante du processus (Z_t) restreint à M_w. Le taux d'invasion Λ_w peut être vu comme le taux de croissance exponentiel de la concentration en espèce w lorsque celle-ci est très faible. En effet, d'après (1.8), on a au moins formellement que :

$$\begin{aligned}
&\frac{\dot{U}_t}{U_t} = f_u^{I_t}(R_t) - \delta^{I_t} = \mathcal{A}(Z_t)\\
&\int \frac{\dot{U}_t}{U_t} ds = \int \mathcal{A}(Z_s) ds\\
&\frac{1}{t}\log U_t = \frac{1}{t}\int \mathcal{A}(Z_s) ds.
\end{aligned}$$

D'après le théorème ergodique, il vient :

$$\frac{1}{t}\log U_t \to \int \mathcal{A}(z)d\mu(z),$$

où μ est une mesure invariante du processus (Z_t). On définit $\Lambda_u = \int \mathcal{A}(z)d\mu_u(z)$ où μ_u est la mesure invariante de (Z_t) restreint à M_u. Lorsque U_t est proche de 0, et étant donné que le processus (Z_t) est un processus de Feller, il vient que si $\Lambda_u < 0$, la concentration U_t diminue lorsqu'elle est basse et si $\Lambda_u > 0$, la concentration U_t augmente lorsqu'elle est basse.

Assertion 1.3.3. *Nous appelerons (H_w) l'assertion qui est vraie si et seulement si l'une des assertions suivante est vraie :*
- *(i) $\exists j \in \{1,2\}$ tel que ε^j est défavorable à l'espèce w.*
- *(ii) $\exists s \in (0,1)$ tel que le chemostat moyen ε_s est défavorable à l'espèce w (voir la remarque 3.2.7 pour une définition plus précise du chemostat moyen).*

Nous montrerons dans le chapitre 3 le théorème suivant qui donne le comportement en temps long du processus (Z_t).

Théorème 1.3.4. *Les signes des taux d'invasion Λ_u, Λ_v caractérisent l'évolution des concentrations des espèces u et v :*
- *Si $\Lambda_u > 0$, $\Lambda_v < 0$ et (H_v) est vraie alors on a extinction de l'espèce v : $V_t \to 0$ presque sûrement.*
- *Si $\Lambda_u < 0$, (H_u) est vraie et $\Lambda_v > 0$ alors on a extinction de l'espèce u : $U_t \to 0$ presque sûrement.*
- *Si $\Lambda_u < 0$ et $\Lambda_v < 0$ alors une des deux espèces disparaît presque sûrement. On dit qu'on est dans un état de bi-stabilité.*
- *Si $\Lambda_u > 0$ et $\Lambda_v > 0$ alors on a coexistence des deux espèces.*

Nous donnons sur la figure 1.5 un exemple numérique montrant qu'il est effectivement possible de choisir des chemostats ε^1, ε^2 ainsi que des taux de saut λ^1, λ^2 nous permettant d'observer chacuns des cas de ce théorème.

1.3.3 Modèle de compétition du gradostat général à deux espèces

Dans la partie précédente, nous avons proposé et étudié un modèle permettant de comprendre l'impact de l'hétérogénéité temporelle sur l'évolution de deux espèces en compétition dans un chemostat. Le gradostat, introduit par Lovitt et Wimpenny dans leur article [Lovitt et Wimpenny, 1981] est un modèle de compétition permettant de modéliser l'hétérogénéité spatiale d'un environnement sans perdre la spécificité des équations du chemostat. Il a depuis été largement étudié dans la littérature et on pourra consulter [Smith et Waltman, 1995] pour une première revue des divers résultats obtenus à leur sujet.

Nous construisons ici un modèle simple de gradostat. Prenons deux chemostats ε^1 et ε^2 dans lesquels deux espèces u et v sont en compétition pour une ressource R et autorisons les échanges de matière entre les deux cuves. Notons $\mathcal{V}^j$ le volume du chemostat j, Q le

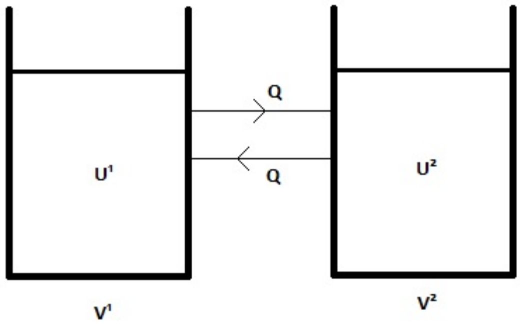


FIGURE 1.4 – Schéma représentant les échanges de matière entre deux cuves.

débit entre les deux cuves et $U^j(t)$ la concentration de l'espèce u dans la cuve j au temps t (voir figure 1.4). Il vient que :

$$\begin{cases} (U^1\mathcal{V}^1)'(t) = -QU^1(t) + QU^2(t) \\ (U^2\mathcal{V}^2)'(t) = QU^1(t) - QU^2(t). \end{cases}$$

En notant $\lambda^j = \frac{Q}{\mathcal{V}^j}$ on a alors :

$$\begin{cases} \dot{U}^1(t) = -\lambda^1 U^1(t) + \lambda^1 U^2(t) \\ \dot{U}^2(t) = \lambda^2 U^1(t) - \lambda^2 U^2(t). \end{cases} \tag{1.9}$$

On va noter $V^j(t)$ la concentration de l'espèce v dans la cuve j au temps t et $R^j(t)$ la concentration de la ressource dans la cuve j au temps t. On notera également $\{j, \bar{j}\} = \{1, 2\}$. Le système d'équation différentielles régissant l'évolution des différentes concentration au sein du chemostat est alors donné par :

$$\begin{cases} \dot{R}^j(t) = \delta^j(R_0^j - R^j(t)) - U^j(t)f_u^j(R^j(t)) - V^j(t)f_v^j(R^j(t)) \boldsymbol{-\lambda^j \mathbf{R}^{\mathbf{j}}(\mathbf{t}) + \lambda^j \mathbf{R}^{\bar{\mathbf{j}}}(\mathbf{t})} \\ \dot{U}^j(t) = U^j(t)(f_u^j(R^j(t)) - \delta^j) \boldsymbol{-\lambda^j \mathbf{U}^{\mathbf{j}}(\mathbf{t}) + \lambda^j \mathbf{U}^{\bar{\mathbf{j}}}(\mathbf{t})} \\ \dot{V}^j(t) = V^j(t)(f_v^j(R^j(t)) - \delta^j) \boldsymbol{-\lambda^j \mathbf{V}^{\mathbf{j}}(\mathbf{t}) + \lambda^j \mathbf{V}^{\bar{\mathbf{j}}}(\mathbf{t})}. \end{cases} \tag{1.10}$$

où la partie en gras est le terme de transfert donné par (1.9).

Pour s'affranchir des notations d'indices un peu lourdes nous allons noter $R(t) = \begin{pmatrix} R^1(t) \\ R^2(t) \end{pmatrix}$, $U(t) = \begin{pmatrix} U^1(t) \\ U^2(t) \end{pmatrix}$, $V(t) = \begin{pmatrix} V^1(t) \\ V^2(t) \end{pmatrix}$, $R_0 = \begin{pmatrix} R_0^1 \\ R_0^2 \end{pmatrix}$, $\delta = \begin{pmatrix} \delta^1 \\ \delta^2 \end{pmatrix}$ et $f_w(R) = \begin{pmatrix} f_w^1(R^1) \\ f_w^2(R^2) \end{pmatrix}$. De plus, en écrivant que $\lambda^1 = s\lambda$ et $\lambda^2 = (1-s)\lambda$ avec $\lambda > 0$ et $s \in]0, 1[$ on posera $K = \begin{pmatrix} -s & s \\ s-1 & s-1 \end{pmatrix}$. Par convention $\begin{pmatrix} w \\ x \end{pmatrix} \begin{pmatrix} y \\ z \end{pmatrix} = \begin{pmatrix} wy \\ xz \end{pmatrix}$. On a alors une écriture simplifiée du système d'équation différentielle :

$$\begin{cases} \dot{R}(t) = \delta(R_0 - R(t)) - U(t)f_u(R(t)) - V(t)f_v(R(t)) + \lambda K R(t) \\ \dot{U}(t) = U(t)(f_u(R(t)) - \delta) + \lambda K U(t) \\ \dot{V}(t) = V(t)(f_v(R(t)) - \delta) + \lambda K V(t). \end{cases} \tag{1.11}$$

Nous supposerons toujours que la condition initiale est dans $(\mathbb{R}^2_{+,*})^3$.

Il est aisé de montrer que la quantité $\Sigma(t) = R(t) + U(t) + V(t)$ tend vers un vecteur constant $\Sigma_0 \in (\mathbb{R}^*_+)^2$ lorsque t tend vers l'infini. Cette remarque permet de réduire le système différentiel ci-dessus en un nouveau système différentiel donné par :

$$\begin{cases} \dot{U}(t) = U(t)(f_u(\Sigma_0 - U(t) - V(t)) - \delta) + \lambda K U(t) \\ \dot{V}(t) = V(t)(f_v(\Sigma_0 - U(t) - V(t)) - \delta) + \lambda K V(t). \end{cases} \tag{1.12}$$

Ce nouveau système différentiel possède le même ensemble d'attracteurs (ou ensemble omega-limite) que le système différentiel (1.11).

De plus, le système dynamique (1.12) a pour autre propriété remarquable d'être fortement monotone selon un certain ordre (voir [Smith et Waltman, 1995] pour plus de précisions). Cette propriété conditionne fortement le comportement en temps long des solutions de (1.12), en particulier, pour presque toutes condition initiales, les solutions de (1.12) convergent vers un point stationnaire (le lecteur intéressé pourra regarder l'appendice C de [Smith et Waltman, 1995]).

Par conséquent, d'après les remarques précédentes, pour étudier le comportement en temps long de (1.11), on se concentre sur la recherche et l'étude de la stabilité asymptotique des solutions stationnaires de (1.12) c'est à dire de couples $(U, V) \in (\mathbb{R}^2_+)^2$ satisfaisant :

$$H(U,V) = 0 \Leftrightarrow \begin{cases} U(f_u(\Sigma_0 - U - V) - \delta) + \lambda K U = 0 \\ V(f_v(\Sigma_0 - U - V) - \delta) + \lambda K V = 0. \end{cases} \tag{1.13}$$

Une solution stationnaire (U, V) satisfaisant $U > 0$ et $V > 0$ sera appelée une solution de coexistence.

La recherche de solutions de coexistence dans le gradostat (ou de ses modèles dérivés) n'est cependant jamais aisée et des arguments de degrés topologiques sont souvent utilisés dans la littérature pour, soit montrer leur existence, soit caractériser leur nombre. On pourra consulter [Smith et Waltman, 1995] dans le cas du gradostat simple ou encore [Castella et Madec, 2014] dans le cas d'un modèle avec diffusion.

Nous donnons cependant dans le chapitre 3 une méthode purement graphique permettant de connaître le comportement des solutions de (1.12) à partir des seules données des chemostats ε^j et de la matrice de transfert K. Cette méthode peut être essentiellement ramenée à l'étude du signe de deux quantités que l'on appelera encore les taux d'invasion des espèces u et v et que l'on notera Γ_u et Γ_v.

Définissons la matrice suivante :

$$M_w = \begin{pmatrix} f^1_w(\Sigma^1_0 - U^1 - V^1) - \delta^1 - \lambda^1 & \lambda^1 \\ \lambda^2 & f^2_w(\Sigma^2_0 - U^2 - V^2) - \delta^2 - \lambda^2 \end{pmatrix}$$

de sorte que :

$$H(U,V) = 0 \Leftrightarrow M_u(U,V).U = 0 \text{ et } M_v(U,V).V = 0.$$

On se placera toujours dans le cas où le système (1.13) possède au moins trois solutions. La première, $E_0 = (0,0)$ que l'on appellera la solution triviale, la seconde $E_u = (U,0)$ et la troisième $E_v = (0,V)$ que l'on appellera les solutions semi-triviales. On montrera que la stabilité des solutions semi-triviales caractérise le comportement des solutions de (1.11).

Proposition 1.3.5. *Soit $E_u = (U,0)$ une solution semi-triviale. Sa stabilité est donnée par le signe de la plus grande valeur propre de la matrice $M_v(\Sigma_0 - U, 0)$ que l'on notera Γ_v. Le même énoncé est valable pour la solution semi-triviale E_v.*

Remarque 1.3.6. *Si $\Gamma_v > 0$, E_u est instable (donc $V(t)$ s'éloigne toujours de 0). Si $\Gamma_v < 0$, alors E_u est stable (donc $V(t)$ est attiré par 0). C'est pour cela que l'on se permet d'appeler Γ_v le taux d'invasion de l'espèce v.*

On obtient un théorème ressemblant sensiblement au théorème obtenu pour le SPDMP construit dans la partie précédente mais avec une différence dans le cas ou les taux d'invasion n'ont pas le même signe.

Théorème 1.3.7. *Le signe des taux d'invasion caractérisent les solutions de l'équation* (1.11) *:*

- *Si $\Gamma_u > 0$ et $\Gamma_v > 0$, alors les solutions semi-triviales sont instables mais il existe une unique solution de coexistence et elle attire presque toutes les solutions de* (1.11).
- *Si $\Gamma_u < 0$ et $\Gamma_v < 0$, alors les solutions semi-triviales sont stables et il n'existe par de solutions de coexistence. Les solutions de* (1.11) *sont presque toutes attirées par l'une ou l'autre des solutions semi-triviales selon la position de la condition initiale. On est dans un cas de bi-stabilité*
- *Si $\Gamma_u > 0$ et $\Gamma_v < 0$, alors E_u est stable et E_v est instable. S'il n'existe pas de solutions de coexistence, alors E_u attire presque toutes les solutions de* (1.11). *Sinon, il existe deux solutions de coexistence, l'une est stable et l'autre est instable. Les solutions de* (1.11) *sont presque toutes attirées par E_u ou la solution de coexistence stable selon la position de la condition initiale (encore un cas de bi-stabilité)*
- *Si $\Gamma_u < 0$ et $\Gamma_v > 0$, alors E_u est instable et E_v est stable. S'il n'existe pas de solutions de coexistence, alors E_v attire presque toutes les solutions de* (1.11). *Sinon, il existe deux solutions de coexistence, l'une est stable et l'autre est instable. Les solutions de* (1.11) *sont presque toutes attirées par E_v ou la solution de coexistence stable selon la position de la condition initiale (encore un cas de bi-stabilité).*

On constate que dans le cas où les signes des taux d'invasion sont opposés, deux solutions de coexistence peuvent exister ce qui constitue une différence majeure avec le processus aléatoire. On verra qu'il est numériquement possible de faire apparaître ce cas de figure (voir figure 1.6). Nous donnons dans la figure 1.5 un exemple numérique montrant que tout les autres cas de figures donnés dans le théorème précédant peuvent survenir.

Nous proposons dans le chapitre 3 une investigation numérique afin de comparer le comportement des taux d'invasion probabilistes Λ_u et Λ_v avec le comportement des taux d'invasion déterministes Γ_u et Γ_v.

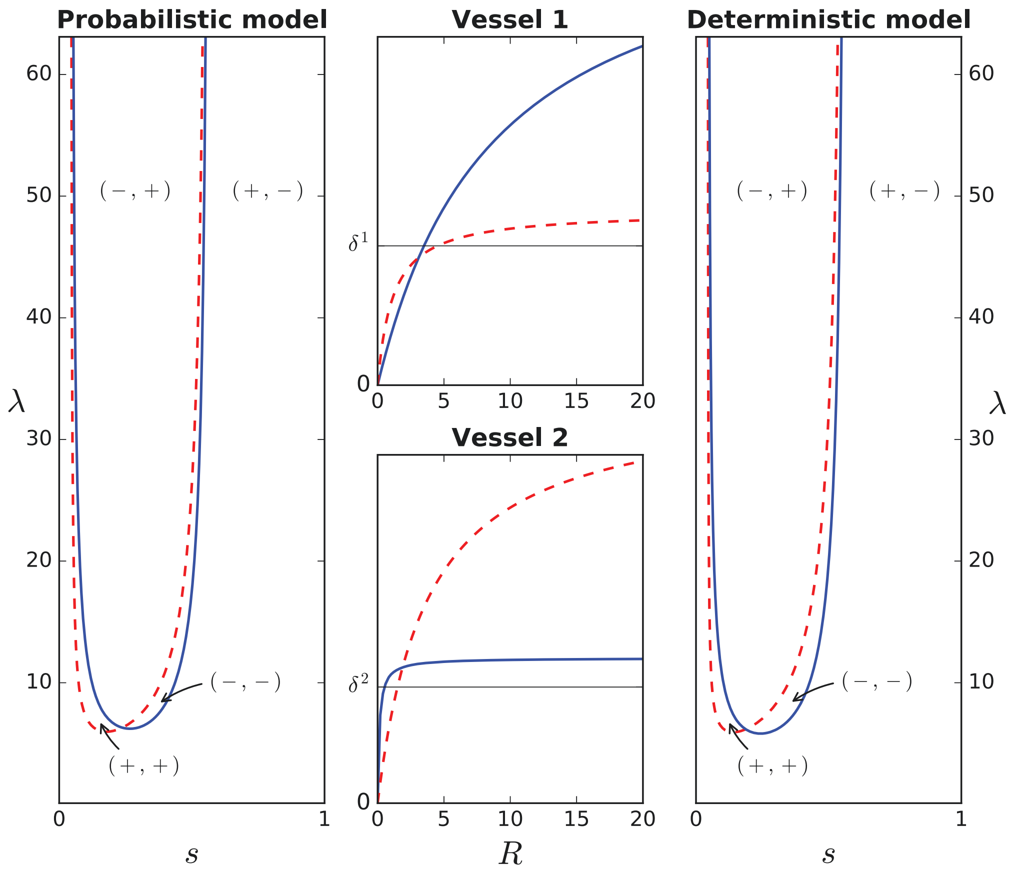


FIGURE 1.5 – Exemple numérique donnant le signe des taux d'invasion dans le cas probabiliste (à gauche) et le cas déterministe (à droite) dans le plan des paramètres de saut pour le modèle probabiliste et le plan des paramètres de diffusion pour le cas déterministe. Les courbes continues bleues (resp. pointillées rouges) sur les graphiques extrêmes correspondent aux lignes de niveau zéro des taux d'invasion de l'espèce u (resp. v). Dans chaque zone le signe des taux d'invasion est constant et est donné par un couple de signes. Le premier signe donne le signe du taux d'invasion de l'espèce u, le deuxième signe donne le signe du taux d'invasion de l'espèce v. Dans les graphiques centraux sont esquissés les fonctions de consommation de l'espèce u (resp. v) en couleur bleue (resp. rouge) dans les cuves ε^1 et ε^2.

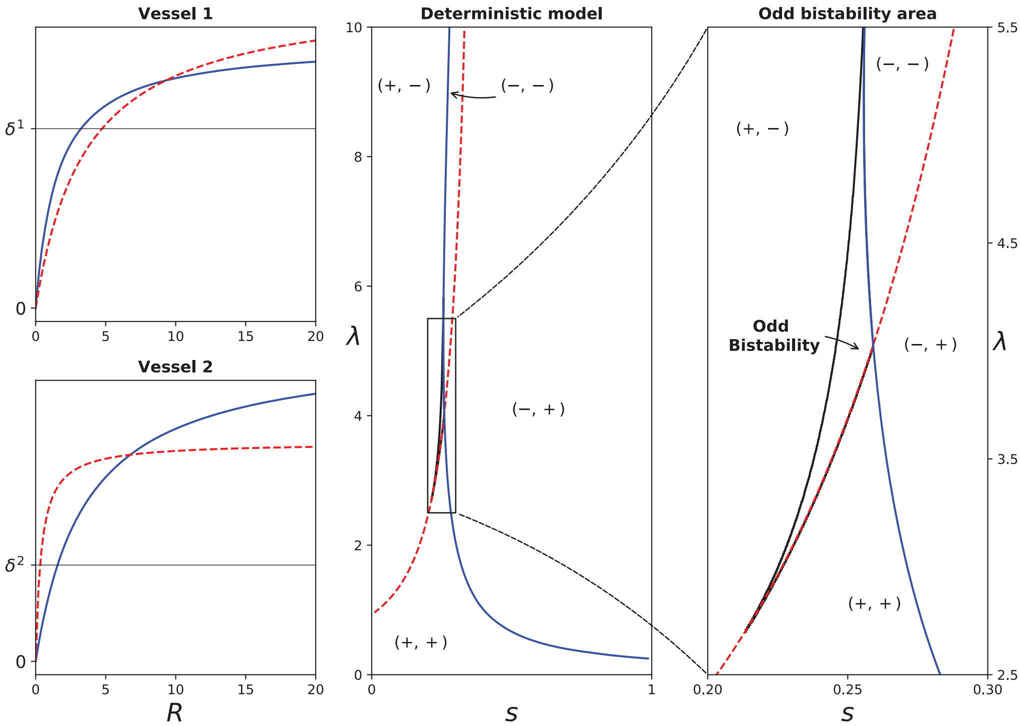


FIGURE 1.6 – Apparition d'une petite zone de bi-stabilité dans une zone où les taux d'invasion sont de signes opposés.

Et nous finirons ce manuscrit en donnant une condition suffisante sur les chemostats ε^1 et ε^2 pour qu'il puisse exister un état de bi-stabilité pour le système communiquant associé.

Chapitre 2

A note on simple randomly switched linear system

This chapter is taken from an article written in 2016 entitled /A note on simple randomly switched linear system.

2.1 Introduction

Let (I_t) be a continuous time Markov chain defined on the space of states $\{0,1\}$. We call λ_i the jump rate of the process (I_t) from state i to state $1-i$. The invariant measure of (I_t) is given by :

$$\frac{\lambda_1}{\lambda_0+\lambda_1}\delta_0 + \frac{\lambda_0}{\lambda_0+\lambda_1}\delta_1.$$

Set $F_0, F_1 : \mathbb{R}^d \to \mathbb{R}^d$ two smooth functions with $d \geq 1$.

We define $(X_t)_{t\geq 0}$ as the solution of the following differential equation :

$$\begin{cases} \dot{X}_t = F_{I_t}(X_t) \\ X_0 \in \mathbb{R}^d. \end{cases} \tag{2.1}$$

The process (X_t, I_t) belongs to the set of Piecewise Deterministic Markov Process (PDMP) which is a wide class of random processes introduced by Davis [Davis, 1984]. Processes defined by (2.1) play a role in the modelization of problems in various fields such as, molecular biology [Radulescu *et al.*, 2007] or population dynamics [Benaïm et Lobry, 2016] for example. Those processes are easy to define but the study of their behavior is never clear. More particularly, their stability is not clear even if the associated vector fields of F_0 and F_1 are stable. In [Benaïm *et al.*, 2012], the authors prove that if the vector fields F_i satisfies :

$$\exists \alpha(i) > 0, \quad \forall x, y \in \mathbb{R}^d \quad \langle F_i(x) - F_i(y), x-y\rangle \leq -\alpha(i)\|x-y\|^2, \tag{2.2}$$

then there exists a unique invariant measure μ for the process $(X_t, I_t)_{t\geq 0}$ and moreover the law of (X_t, I_t) converges at an exponential rate to μ for a given metric on the set of laws.

The goal of this note is to study simple systems which does not satisfy hypothesis (2.2). More precisely, we are here interested in the long time qualitative behaviour of the random switched process $(X_t, I_t)_{t\geq 0} \in \mathbb{R}^d \times \{0,1\}$ solving the equation

$$\begin{cases} \dot{X}_t = A_{I_t}(X_t - b_{I_t}) \\ X_0 = x_0, \end{cases} \tag{2.3}$$

where A_0, A_1 are $d\times d$ real Hurwitz matrices (the real part of their eigenvalues are negative), $b_0, b_1 \in \mathbb{R}^d$ and (I_t) is a Markov process on $E = \{0,1\}$ with constant jump rates λ_0, λ_1. The process $((X_t, I_t))_{t\geq 0}$ is a piecewise deterministic Markov process as defined in [Davis, 1984].

Without assumption (2.2), the process (X_t, I_t) can enventually explode if the parameters are well chosen. For example, in the two dimensional case where the constants b_0, b_1 are equal to zero and the switch rates λ_0, λ_1 are equal, the articles [Lawley *et al.*, 2014] or [Benaïm *et al.*, 2012] show that the behavior of the process (X_t, I_t) may be surprising : according to the value of the switching rate λ, the process can either blow up or go to zero.

When (I_t) is a function $I : \mathbb{R}_+ \to \{0,1\}$, (X_t) is deterministic and can be computated by solving (2.3). In this case, (I_t) is called a deterministic control. In Section 6, after showing a similar convergence as (2.20) for small jump rates, we will show that there is a connection between the existence of an explosive trajectory (with a deterministic control (I_t)) and the properties of the invariant measure, if it exists, in the random case ((I_t) is a Markov chain).

Let us call $T_0 = 0$, T_1, ..., T_n the jump times of the process (X_t) and τ_0, τ_1, ..., τ_n, the interjump times following an exponential law of parameters λ_0 and λ_1 alternatively. Let us define $Y_n = X_{T_{2n}}$. By simply solving Equation (2.3) between each jumping time we obtain :

$$Y_n = e^{\tau_{n+1}A_1} e^{\tau_n A_0} Y_{n-1} - e^{\tau_{n+1}} b_0 + b_1.$$

This kind of stochastic equation have been the object of numerous research. Applying Kesten's renewal theorem to the discrete process (Y_n) will give some informations about the tail of the invariant measure of (X_t) (see [Kesten, 1973] for the main article, see [Alsmeyer et Mentemeier, 2012], [De Saporta *et al.*, 2004] for different formulations of the same theorem). We will prove in Section 6 the following result.

Theorem 2.1.1. *If there is no deterministic control that makes the deterministic process associated to (Y_t) explodes, then there exists an invariant measure μ for the process (X_t, I_t) solution of (2.3) and the support of μ is necessarily bounded.*

In the other hand, we assume that the process (X_t, I_t) has an invariant measure and that there exists a deterministic control such that :

$$\exists k \in 2\mathbb{N}+1 \text{ such that } \forall x \in \mathbb{S}_{d-1}, \exists t_0, t_1, ..., t_k > 0 \text{ such that } \|e^{t_k A_{I_k}} ... e^{t_1 A_{I_1}} e^{t_0 A_{I_0}} x\| > \|x\|. \tag{2.4}$$

We call $B = e^{\tau_k A_{I_k}} ... e^{\tau_1 A_{I_1}} e^{\tau_0 A_{I_0}}$ and B_0, B_1, ..., B_n n random variables i.i.d following the law of B. We also assume that :

$$\max_{n\geq 0} \mathbb{P}\left(\frac{B_n ... B_0 x}{\|B_n ... B_0 x\|} \in U\right) > 0 \text{ for all } x \in \mathbb{S}_{d-1} \text{ and any open } \emptyset \neq U \subset \mathbb{S}_{d-1}. \tag{2.5}$$

$$\mathbb{P}(B_{n_0}\cdots B_0 \in \cdot) \geq \gamma_0 \mathbb{1}_{B_c(\Gamma_0)}\lambda \textit{ for some } \Gamma_0 \in GL_d(\mathbb{R}),\ n_0 \in \mathbb{N} \textit{ and } c, \gamma_0 > 0. \tag{2.6}$$

where λ is the Lebesgue measure on $\mathbb{R}^{n^2}$. Under these assumptions, there exists a unique invariant measure μ for the process (Y_n) and it has a heavy tails :

$$\exists p_1 > 0 \textit{ such that } \forall 0 \leq p < p_1 \quad \mathbb{E}_\mu[\|Y\|^p] < +\infty \textit{ and } \forall p > p_1 \quad \mathbb{E}_\mu[\|Y\|^p] = +\infty.$$

Before jumping into this theorem, we will first go back on the case with b_0 and b_1 equal to zero in (2.3). In the two dimensional case, the asymptotic behaviour of such processes when (I_t) is any deterministic function is now understood. Given two matrices in $\mathcal{M}_2(\mathbb{R})$, [Balde *et al.*, 2009] gives a necessary and sufficient condition for the existence of a deterministic function (I_t) that produces a blow up.

In [Lawley *et al.*, 2014], the authors build a randomly switched system living in the space $\mathbb{R}^{2n}$ which behaviour comes down to alternating blow up periods and stable periods a finite number of times as the jump rate grows. A question raised from this works is the existence of a planar randomly switched system which behaviour is also alternating between blow up periods and stable periods.

For $a > 0$ and $b > 1$, set the two real matrices :

$$A_0 = \begin{pmatrix} -a & b \\ -\frac{1}{b} & -a \end{pmatrix} \quad \text{and} \quad A_1 = \begin{pmatrix} -a & \frac{1}{b} \\ -b & -a \end{pmatrix}.$$

Thanks to these two matrices, we define the continuous process $((X_t, I_t))_{t\geq 0} \in \mathbb{R}^2 \times \{0,1\}$ solution of :

$$\begin{cases} \dot{X}_t = A_{I_t} X_t \\ X_0 = x_0, \end{cases} \tag{2.7}$$

where (I_t) is a Markov process on $E = \{0,1\}$ with constant jump rates λ_0, λ_1. Set $\lambda_0 = \beta u$ and $\lambda_1 = \beta(1-u)$ with $\beta > 0$ and $u \in (0,1)$. The path of X_t follows a spiral clockwisely during a random time with exponential law of parameter λ_i before switching on an other spiral as described in Figure 1.1.

This process has a richer behavior in the deterministic case than the processes studied in [Lawley *et al.*, 2014] and [Benaïm *et al.*, 2012]. If (I_t) is a periodic deterministic control function, we will see in Section 4 that the behavior of (X_t, I_t) is alternating between blow up periods and stable areas as the period of (I_t) increases. Intuitively, one can expect to have a similar behavior if (I_t) is a Markov chain.

We define :

$$\chi := \chi(a, b, \beta, u) = \lim_{t\to+\infty} \frac{1}{t} \log(\|X_t\|) \quad \text{a.s} \tag{2.8}$$

which sign gives the long time qualitative behaviour of the process. Indeed if χ is positive then the system explodes almost surely whereas if χ is negative the system is stable and goes to zero almost surely.

The main result of this note is the following which is similar to the main result in [Lawley *et al.*, 2014] except that here the jump rates can be different :

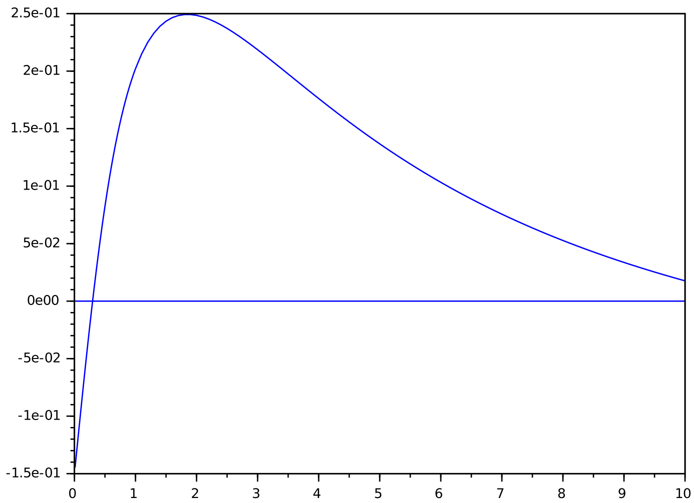


FIGURE 2.1 – The function $\beta \longmapsto \chi(0.15, 3, \beta, 0.5)$ where χ is given by (2.8)

Theorem 2.1.2. *For any $u \in (0, 1)$,*

(*i*) $\forall a, b > 0, \quad \chi(a, b, \beta, u) \longrightarrow -a$ *when* $\beta \to 0$ *or* $\beta \to +\infty$.

(*ii*) *For every* $\beta, u > 0$ *there exist* $a > 0$ *and* $b > 0$ *so that* $\chi(a, b, \beta, u) > 0$.

In Section 2, we establish an explicit expression of the function χ. In Section 3 we use it to prove Theorem 1.1.

The explicit expression of χ obtained in Proposition 2.2 allows us to compute numerically the function χ (See Figure 2.1). It is also interesting to show the sign of the function χ according to β and u as we can see in Figure 2.2. In this figure, we can see that for (β, u) in a compact, our system explodes when t goes to $+\infty$. We can see the same behaviour in the process studied in [Lawley *et al.*, 2014]. But this is different from what we can observe in [Benaïm et Lobry, 2016] and [Benaïm *et al.*, 2014] where the explosion happens for β large enough.

This graphics combined to Theorem 1.1 shows us that this process does not meet our expectations. There is a unique area of blow up whereas the deterministic periodic process has several blow up periods (see Section 4). It seems that, in the case of the random process, the variance of the waiting time in each state is too high to select precisely the good jump times that would allow it to have several blow up periods.

We will see in Section 5 a simple way to lower the variance of the waiting time without complicate too much the process, but first, in Section 4 we will give an interesting result about the deterministic process associated to our system.

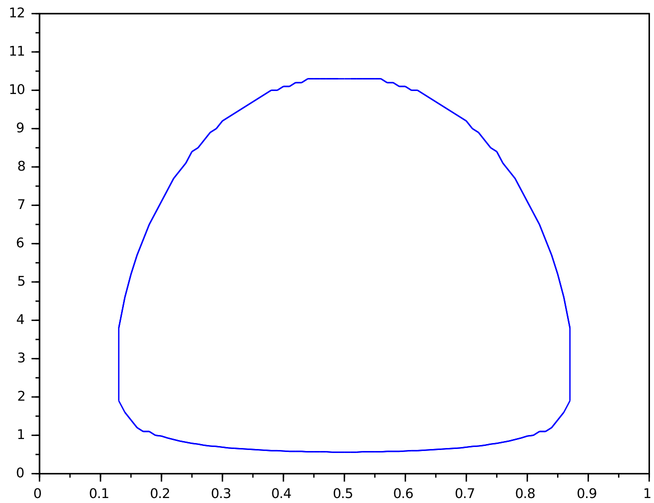


FIGURE 2.2 – Sign of the function $G : (\beta, u) \longmapsto \chi(0.1, 2.5, \beta, u)$. The curve is the set of points (β, u) such that $\chi(0.1, 2.5, \beta, u) = 0$. The sign of G is positive inside and negative outside.

2.2 Study of the angular process

In order to study our process $((X_t, I_t))_{t\geq 0}$ we use the polar coordinates for X_t. As a start, and as in [Lawley *et al.*, 2014], let us look at the case of the deterministic process. Let A be a 2-sized squared matrix and $x \in \mathbb{R}^2\backslash\{0\}$. We set $(x_t)_{t\geq 0}$ the solution of the ODE :

$$\begin{cases} \dot{x}_t = Ax_t & \text{for all } t > 0, \\ x_0 = x. \end{cases}$$

If x is nonzero, then it is also true for any x_t with t positive. So we can define the polar coordinates (r_t, θ_t) of x_t. We call e_θ the unitary vector $(\cos\theta, \sin\theta)$ and $u_t = e_{\theta_t}$. Then $x_t = r_t u_t$. As $r_t^2 = \langle x_t, x_t\rangle$, we obtain the relations :

$$r_t\dot{r}_t = \langle x_t, Ax_t\rangle$$

$$A(r_t u_t) = \dot{x}_t = \dot{r}_t u_t + r_t\dot{u}_t.$$

And then we have :

$$\dot{r}_t = r_t\langle u_t, Au_t\rangle \tag{2.9}$$

$$\dot{u}_t = Au_t - \langle u_t, Au_t\rangle u_t. \tag{2.10}$$

Let us write the equation (2) with the angle θ_t. As $\dot{u}_t = \dot{\theta}_t e_{\theta_t+\pi/2}$, by making the scalar product of (2) with $e_{\theta_t+\pi/2}$, we obtain :

$$\dot{\theta}_t = \left\langle Ae_{\theta_t}, e_{\theta_t+\pi/2}\right\rangle. \tag{2.11}$$

We use now the polar coordinates in order to study the process $((X_t, I_t))_{t\geq 0}$. Between the jumps, the process follows the flow determined by $A \in \{A_0, A_1\}$. From Equation (3), the development of θ is deterministic and does not depend on r. As a consequence, the processes $((\Theta_t, I_t))_{t\geq 0}$ and $((U_t, I_t))_{t\geq 0}$ are piecewise deterministic Markov processes on $\mathbb{R} \times \{0,1\}$ and $\mathbb{S}_1 \times \{0,1\}$ respectively. The principal interest of the study of these processes lies in the fact that the development of $(R_t)_{t\geq 0}$ is determined by that of the process $((\Theta_t, I_t))_{t\geq 0}$ as shown by Equation (1). Indeed, by solving (1) between the jumps and by calling $\mathcal{A}(\theta, i) = \langle A_i e_\theta, e_\theta \rangle$, we obtain :

$$R_t = R_0 \exp\left(\int_0^t \mathcal{A}(\Theta_s, I_s) ds \right). \tag{2.12}$$

So, as suggested by Equation (4), in order to study the behaviour of $(R_t)_{t\geq 0}$ we are going to study the process $((\Theta_t, I_t))_{t\geq 0}$ and particularly its invariant measure.

Lemma 2.2.1. *The invariant measure μ of the process $((\Theta_t, I_t))_{t\geq 0}$ is given by,*

$$\mu(d\theta, i) = \rho_i(\theta) d\theta$$

where

$$\rho_0 = \frac{\Phi}{d_0} \quad \textit{and} \quad \rho_1 = \frac{C - \rho_0 d_0}{d_1};$$

$$d_0(\theta) = -b \sin^2(\theta) - \frac{1}{b}\cos^2(\theta) \quad \textit{and} \quad d_1(\theta) = -\frac{1}{b}\sin^2(\theta) - b\cos^2(\theta);$$

$$\Phi(\theta) = \left(K + \int_0^\theta \beta C (1-u) \frac{1}{d_1(\alpha)} e^{-\beta v(\alpha)} d\alpha \right) e^{\beta v(\theta)};$$

v is the primitive null in zero of the function $-(\frac{u}{d_0} + \frac{1-u}{d_1})$;

K and C are two explicit constants.

Proof. We define, for $i \in \{0,1\}$,

$$d_i(\theta) = \left\langle A_i e_\theta, e_{\theta+\pi/2} \right\rangle.$$

Let (P_t) be the semigroup of the process $((\Theta_t, I_t))_{t\geq 0}$. Recall that :

$$P_t = E[f(\Theta_t, I_t) | \Theta_0 = \theta, I_0 = i].$$

Its infinitesimal generator L is defined by $Lf = \lim\limits_{t\to 0} \frac{P_t f - f}{t}$ for any smooth function f. L is given by :

$$Lf(\theta, i) = d_i(\theta) \frac{\partial f}{\partial \theta}(\theta, i) + \lambda_i \left(f(\theta, 1-i) - f(\theta, i) \right). \tag{2.13}$$

In our study case, the functions d_i are given by :

$$d_0(\theta) = -b \sin^2(\theta) - \frac{1}{b}\cos^2(\theta) \quad \text{and} \quad d_1(\theta) = -\frac{1}{b}\sin^2(\theta) - b\cos^2(\theta).$$

We notice that the functions d_i are negative and non constant. This implies that the process $((U_t, I_t))_{t\geq 0}$ is recurrent, irreducible and it has a unique invariant measure. We want to write it as follows :

$$\mu(d\theta, i) = \rho_i(\theta)d\theta. \tag{2.14}$$

where ρ_0 and ρ_1 are two 2π-periodical continuous functions.
In this case, for every good function f defined on $\mathbb{S}_1 \times \{0, 1\}$, we have :

$$\int_{\mathbb{S}_1\times\{0,1\}} Lf(\theta, i)d\mu(\theta, i) = 0.$$

Let f be a $\mathcal{C}^1$ function defined on $\mathbb{S}_1\times\{0, 1\}$. Injected in the previous formula, the expression (6) allows us to obtain :

$$\int_0^{2\pi} Lf(\theta, 0)\rho_0(\theta)d\theta + \int_0^{2\pi} L_\beta f(\theta, 1)\rho_1(\theta)d\theta = 0. \tag{2.15}$$

Assume initially that $\forall i,\ f(\theta, i) = f(\theta)$. So, by injecting in (6), and after integrating by parts, we obtain :

$$d_0\rho_0 + d_1\rho_1 = C \tag{2.16}$$

where C is a negative constant depending only of the parameters of the problem a, b, u and β.
Assume now that $f(\theta, 0) = f(\theta)$ and $f(\theta, 1) = 0$. The same way, we obtain the relation :

$$(d_0\rho_0)' = (1 - u)\beta\rho_1 - u\beta\rho_0.$$

Set $\Phi = d_0\rho_0$. By using the relation (7), we can write the last equation as a linear differential equation :

$$\Phi' = -\beta\Phi(\frac{u}{d_0} + \frac{1-u}{d_1}) + \frac{\beta C(1-u)}{d_1}. \tag{2.17}$$

This differential equation is easily solved, we obtain :

$$\Phi(\theta) = \left(K + \int_0^\theta \beta C(1-u)\frac{1}{d_1(\alpha)}e^{-\beta v(\alpha)}d\alpha\right)e^{\beta v(\theta)}$$

where K is an integration constant and v is the primitive null in zero of the function $-(\frac{u}{d_0} + \frac{1-u}{d_1})$. We can express v explicitly on the interval $(-\frac{\pi}{2}, \frac{\pi}{2})$:

$$v(\theta) = u\arctan(b\tan(\theta)) + (1-u)\arctan(\frac{1}{b}\tan(\theta)).$$

We extend v to $\mathbb{R}^+$ by continuity.
The constants C and K are left to calculate in such a way that μ is a probability measure. So :

$$\text{(i) } \rho_0 \text{ and } \rho_1 \text{ are non negative,} \quad \text{(ii) } \int_0^{2\pi}\rho_0(\theta)d\theta + \int_0^{2\pi}\rho_1(\theta)d\theta = 1.$$

The condition (i) gives us the following condition on Φ : $C < \Phi < 0$. By developping this inequality, we obtain :

$$\forall\theta\in\mathbb{R}^+,\ e^{-\beta v(\theta)} - \int_0^\theta \beta(1-u)\frac{1}{d_1(\alpha)}e^{-\beta v(\alpha)}d\alpha > \frac{K}{C} > -\int_0^\theta \beta(1-u)\frac{1}{d_1(\alpha)}e^{-\beta v(\alpha)}d\alpha.$$

As $\theta \longrightarrow +\infty$, we obtain :

$$\frac{K}{C} = -\beta(1-u)\int_0^\infty \frac{1}{d_1(\alpha)}e^{-\beta v(\alpha)}d\alpha.$$

In the sequel, we will call $\kappa = \frac{C}{K}$. In order to find K, we use the condition (ii) and we get easily :

$$\frac{1}{K} = \int_0^{2\pi}\left[e^{\beta v(\theta)}\left(1+\kappa\beta(1-u)\int_0^\theta \frac{1}{d_1(\alpha)}e^{-\beta v(\alpha)}d\alpha\right)\left(\frac{1}{d_0(\theta)}-\frac{1}{d_1(\theta)}\right)+\kappa\frac{1}{d_1(\theta)}\right]d\theta.$$

We finally get expressions of ρ_0 and ρ_1. Reciprocally, we check that the functions we obtained are solutions of our problem (one has to check the 2π-periodicity of these functions). □

We want now to describe the stability of our switched process according to the jump parameters u and β, and to the parameters of our matrices a and b. It appears thanks to Formula (4) that the following quantity :

$$\chi(\beta) = \lim_{t\to+\infty}\frac{1}{t}\log\left(\frac{R_t}{R_0}\right) = \lim_{t\to+\infty}\frac{1}{t}\left(\int_0^t \mathcal{A}(\Theta_s, I_s)ds\right)$$

is worth studying because not only its sign gives the behaviour in large time of our process but also, thanks to the Ergodic Theorem and the previous Lemma, we will obtain an explicit expression of χ.

Proposition 2.2.2. *The function χ can be calculated explicitly according to the data of the problem :*

$$\chi = -a-(1-u)\beta\kappa K\frac{(b-\frac{1}{b})}{2}\int_0^{2\pi}\sin(2\theta)\left(\frac{1}{d_0(\theta)}+\frac{1}{d_1(\theta)}\right)e^{\beta v(\theta)}\left(\int_\theta^\infty \frac{e^{-\beta v(\alpha)}}{d_1(\alpha)}d\alpha\right)d\theta.$$

Proof. Since we have :

$$\frac{1}{t}\log(\frac{R_t}{R_0}) = \frac{1}{t}\left(\int_0^t \mathcal{A}(\Theta_s, I_s)ds\right),$$

the Ergodic Theorem tells us that (we identify θ with e_θ) :

$$\frac{1}{t}\left(\int_0^t \mathcal{A}(\Theta_s, I_s)ds\right)\underset{t\longrightarrow\infty}{\longrightarrow}\int_0^{2\pi}\mathcal{A}(\theta,i)d\mu(\theta,i) = \chi.$$

Lemma 2.1 gives us the explicit formulation of the invariant measure of the process $((\Theta_t, I_t))_{t\geq 0}$ which allows us to obtain the claimed expression for χ. □

2.3 Stability of the switched process

In the previous section, we obtained the explicit expression of χ. We are now going to give some results on the asymptotic values of χ.

Theorem 2.3.1. *For any* $u \in (0,1)$*,*

(*i*) $\forall a, b > 0 \quad \chi(a,b,\beta,u) \longrightarrow -a$ *when* $\beta \to 0$ *or* $\beta \to +\infty$.

(*ii*) *For every* $\beta, u > 0$ *we can choose* $a > 0$ *and* $b > 0$ *so that* $\chi(a,b,\beta,u) > 0$.

Proof. (i) One can find an other way to prove this result in [Lawley *et al.*, 2014] in a more general way.
In order to study the limit of χ in 0, we study the limit of $-\frac{1}{\kappa} = \beta(1-u)\int_0^\infty \frac{e^{-\beta v(\alpha)}}{d_1(\alpha)}d\alpha$ in 0. We notice that :

$$\begin{aligned}\int_0^{+\infty} \frac{e^{-\beta v(\alpha)}}{d_1(\alpha)}d\alpha &= \sum_{i=0}^{+\infty} \int_{i\pi}^{(i+1)\pi} \frac{e^{-\beta v(\alpha)}}{d_1(\alpha)}d\alpha \\ &= \sum_{i=0}^{+\infty} e^{-\beta i\pi} \int_0^{\pi} \frac{e^{-\beta v(\alpha)}}{d_1(\alpha)}d\alpha \text{ because } v(\alpha+\pi) = v(\alpha)+\pi \\ &= \frac{1}{1-e^{-\beta\pi}} \int_0^{\pi} \frac{e^{-\beta v(\alpha)}}{d_1(\alpha)}d\alpha.\end{aligned}$$

Multiplicating by $\beta(1-u)$ and observing the presence of a rate of increase we get :

$$\beta(1-u)\int_0^\infty \frac{e^{-\beta v(\alpha)}}{d_1(\alpha)}d\alpha \longrightarrow \frac{1-u}{\pi}\int_0^\pi \frac{1}{d_1(\alpha)}d\alpha = l.$$

We finally can say that :

$$\forall\theta, \quad \left(\beta(1-u)\int_\theta^\infty \frac{e^{-\beta v(\alpha)}}{d_1(\alpha)}d\alpha\right) \underset{\beta\longrightarrow 0}{\longrightarrow} l.$$

Moreover, as :

$$\int_0^{2\pi} \sin(2\theta)\left(\frac{1}{d_0(\theta)} + \frac{1}{d_1(\theta)}\right)d\theta = 0$$

and the product κK is bounded as $\beta \to 0$, we deduce that $\chi(\beta) \longrightarrow 0$ when β goes to 0.
The limit of χ at $+\infty$ is obtained using the Laplace method :

$$\forall\theta,\ \beta(1-u)\int_\theta^\infty \frac{e^{-\beta v(\alpha)}}{d_1(\alpha)}d\alpha \underset{+\infty}{\sim} \frac{(1-u)e^{-\beta v(\theta)}}{d_1(\theta)v'(\theta)}.$$

From this relation, we obtain that κ and K converge when β goes to $+\infty$ and, by dominated convergence,

$$\int_0^{2\pi} \sin(2\theta)\left(\frac{1}{d_0(\theta)} + \frac{1}{d_1(\theta)}\right)e^{\beta v(\theta)}\beta(1-u)\left(\int_\theta^\infty \frac{e^{-\beta v(\alpha)}}{d_1(\alpha)}d\alpha\right)d\theta \underset{\beta\to+\infty}{\longrightarrow} 0.$$

So we finally conclude that χ goes to $-a$ when β goes to $+\infty$.
(ii) We will now show that for any parameter β, we can choose b large enough and a small enough so that the process goes to $+\infty$ almost surely (ie $\chi(\beta) > 0$). We can write the function χ as follows :

$$\chi(\beta) = -a + K\int_0^\pi f(\theta)g(\theta)d\theta$$

because the function under the integral is π-periodic and where :

$$f(\theta) = (b - \frac{1}{b}) \sin(2\theta) \left(\frac{1}{d_0(\theta)} + \frac{1}{d_1(\theta)} \right),$$

$$g(\theta) = e^{\beta v(\theta)} \frac{\int_\theta^{+\infty} \frac{e^{-\beta v(\alpha)}}{d_1(\alpha)} d\alpha}{\int_0^{+\infty} \frac{e^{-\beta v(\alpha)}}{d_1(\alpha)} d\alpha}.$$

Finally we write χ as follows :

$$\chi(\beta) = -a + K \int_0^{\frac{\pi}{2}} f(\theta) \left(g(\theta) - g(\pi - \theta) \right) d\theta$$

A straightforward computation leads to :

$$\int_0^{\frac{\pi}{2}} f(\theta) d\theta = \frac{4}{\gamma} \frac{b^2 - \frac{1}{b^2}}{(b - \frac{1}{b})^2} \log \left(\left| \frac{\gamma - 1}{\gamma + 1} \right| \right)$$

where $\gamma = \sqrt{1 + \frac{4}{(b - \frac{1}{b})^2}}$. We then conclude that :

$$\int_0^{\frac{\pi}{2}} f(\theta) d\theta \longrightarrow -\infty \text{ when } b \text{ goes to} + \infty.$$

In order to determine the limit of g when b goes to $+\infty$ we rewrite g as follows using the same method as before :

$$\begin{aligned} g(\theta) &= e^{\beta v(\theta)} \left(1 - (1 - e^{-\beta\pi}) \frac{\int_0^\theta \frac{1}{d_1(\alpha)} e^{-\beta v(\alpha)} d\alpha}{\int_0^\pi \frac{1}{d_1(\alpha)} e^{-\beta v(\alpha)} d\alpha} \right) \\ &= e^{\beta v(\theta)} \left(1 - (1 - e^{-\beta\pi}) \frac{\int_0^\theta \frac{1}{\cos^2(\alpha) + \frac{1}{b^2} \sin^2(\alpha)} e^{-\beta v(\alpha)} d\alpha}{\int_0^\pi \frac{1}{\cos^2(\alpha) + \frac{1}{b^2} \sin^2(\alpha)} e^{-\beta v(\alpha)} d\alpha} \right). \end{aligned}$$

Using the fact that :

$$\begin{aligned} v(\theta) &\underset{b \to +\infty}{\longrightarrow} \frac{\pi}{4} \text{ if } \theta \in (0, \frac{\pi}{2}) \\ v(\theta) &\underset{b \to +\infty}{\longrightarrow} \frac{3\pi}{4} \text{ if } \theta \in (0, \frac{\pi}{2}), \end{aligned}$$

it is now easy to see that :

$$\begin{aligned} g(\theta) &\underset{b \to +\infty}{\longrightarrow} e^{\beta \frac{\pi}{4}} \text{ if } \theta \in (0, \frac{\pi}{2}) \\ g(\pi - \theta) &\underset{b \to +\infty}{\longrightarrow} e^{-\beta \frac{\pi}{4}} \text{ if } \theta \in (0, \frac{\pi}{2}). \end{aligned}$$

Since $K < 0$, we can conclude that for b large enough,

$$K \int_0^{\frac{\pi}{2}} f(\theta) \left(g(\theta) - g(\pi - \theta)\right) d\theta > 0.$$

So for an appropriate choice of a, we see that $\chi(\beta) > 0$ inducing that the process explodes almost surely for this β and a with b large enough. $\square$

2.4 A quick look at the associated deterministic process

The deterministic switched system can be introduced as follows :

$$\begin{cases} x_0 \in \mathbb{R}^2 \backslash (0,0) \\ \dot{x_t} = A_{v_t} x_t \end{cases} \tag{2.18}$$

where $(v_t) \in \mathcal{F}(\mathbb{R}_+, \{0,1\})$ is the control function. The behaviour of these systems is well known, see [Balde *et al.*, 2009] for more details. Consequently, for our choice of matrices, we know that there exist a worst trajectory, that is to say, a choice of the control function v that makes the system explode, and this control is periodic.

Let us define (v_t) a $\frac{1}{u(1-u)\beta}$-periodical process satisfying :

$$\begin{aligned} &\forall t \in [0, \frac{1}{u\beta}), \quad v_t = 0 \\ &\forall t \in [\frac{1}{u\beta}, \frac{1}{u(1-u)\beta}), \quad v_t = 1. \end{aligned}$$

We denote $\chi^d(\beta) = \lim\limits_{t \longrightarrow \infty} \frac{1}{t} \log \left(\frac{\|x_t\|}{\|x_0\|} \right)$.
By simply solving the equation for the process (x_t) and calculating the matrices exponential we obtain :

$$x_t = e^{-at} B_{\xi_{N(t)+1}}(a_t) B_{\xi_{N(t)}}(\tau_{N(t)}) \cdots B_{\xi_1}(\tau_1)$$

where

$$B_0(t) = e^{tA_0} = \begin{pmatrix} \cos(t) & b\sin(t) \\ -\frac{1}{b}\sin(t) & \cos(t) \end{pmatrix} \quad \text{and} \quad B_1(t) = e^{tA_1} = \begin{pmatrix} \cos(t) & \frac{1}{b}\sin(t) \\ -b\sin(t) & \cos(t) \end{pmatrix},$$

$N(t)$ is the number of jumps of the deterministic process before t and τ_1, τ_2, ...,$\tau_{N(t)}$ the time spent in the states ξ_1, ξ_2, ..., $\xi_{N(t)}$, $\xi_{N(t)+1}$ by $v(t)$.
We have the surprising following result :

Proposition 2.4.1. *$\chi^d(\beta)$ almost surely does not depend on the initial value x_0.*

Proof. Although this result is true for any $u \in (0,1)$, for sake of simplicity, we will prove it only for the case $u = \frac{1}{2}$ where the computation is not heavy. In order to prove this result, we first notice that :

$$\frac{1}{2nt} \log \left(\frac{\|[B_0(\tau)B_1(\tau)]^n X_0\|}{\|X_0\|} \right) \underset{n \to +\infty}{\longrightarrow} \chi_d(\beta)$$

where $\tau = \frac{2}{\beta}$. Let us calculate the matrix :

$$B_0(\tau)B_1(\tau) = \begin{pmatrix} \cos^2(\tau) - b^2\sin^2(\tau) & C\sin(2\tau) \\ -C\sin(2\tau) & \cos^2(\tau) - \frac{1}{b^2}\sin^2(\tau) \end{pmatrix}$$

where $C = \frac{1}{2}(b + \frac{1}{b}) > 1$. We calculate the characteristic polynomial of this matrix and we obtain :

$$X^2 + X(4C^2\sin^2(\tau) - 2) + 1 = 0.$$

By a simple analysis of this polynomial, we can show that there exists two real eigenvalues if $2C^2\sin^2(\tau) - 1 > 0$ and two joint complex eigenvalues if $2C^2\sin^2(\tau) - 1 < 0$, concluding that our matrix is diagonalisable in $\mathbb{C}$. So there exists $P \in GL_2(\mathbb{C})$ such that :

$$(B_1(\tau)B_0(\tau))^n = P^{-1}\begin{pmatrix} \lambda_1^n & 0 \\ 0 & \lambda_2^n \end{pmatrix} P.$$

Let us now write :

$$\begin{aligned} \frac{1}{2n\tau}\log\left(\frac{\|[B_0(\tau)B_1(\tau)]^n X_0\|}{\|X_0\|}\right) &= \frac{1}{2nt}\log\left(\|\begin{pmatrix} \lambda_1^n & 0 \\ 0 & \lambda_2^n \end{pmatrix} PX_0\|\right) + o(1) \\ &= \frac{1}{2n\tau}\log\left(\|\begin{pmatrix} \lambda_1^n & 0 \\ 0 & \lambda_2^n \end{pmatrix}\begin{pmatrix} x \\ y \end{pmatrix}\|\right) + o(1). \end{aligned}$$

If the factor $4C^2\sin^2(\tau) - 2 \neq 0$ then one of the eigenvalues is superior to the other in absolute value, for example $|\lambda_1| > |\lambda_2|$. In this case, if $x \neq 0$ ie $X_0 \notin E_{\lambda_2}$ the characteristic space of the eigenvalue λ_2 :

$$\frac{1}{2n\tau}\log\left(\frac{\|[B_0(\tau)B_1(\tau)]^n X_0\|}{\|X_0\|}\right) = \frac{1}{2\tau}\log|\lambda_1| + o(1).$$

If $x = 0$ i.e. $X_0 \in E_{\lambda_2}$:

$$\frac{1}{2n\tau}\log\left(\frac{\|[B_0(\tau)B_1(\tau)]^n X_0\|}{\|X_0\|}\right) = \frac{1}{2\tau}\log|\lambda_2| + o(1).$$

If the factor $4C^2\sin^2(\tau) - 2 = 0$ then for every X_0 :

$$\frac{1}{2n\tau}\log\left(\frac{\|[B_0(\tau)B_1(\tau)]^n X_0\|}{\|X_0\|}\right) = \frac{1}{2\tau}\log|\lambda_1| + o(1).$$

□

Figure 2.3 illustrates Proposition 4.1.

2.5 A way to obtain several blow up areas

One of the expectations of this article was to get a planar linear switched system whose χ function admits several blow up areas. A quick look at the deterministic case (2.3) allowed

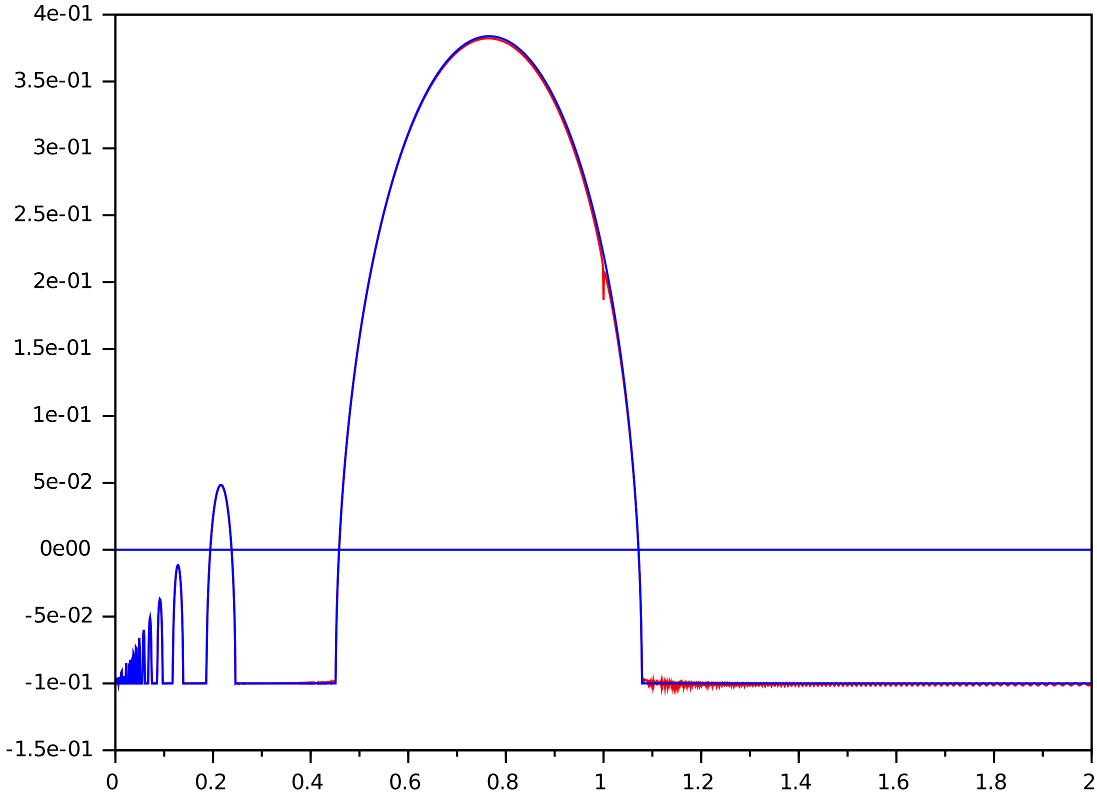


FIGURE 2.3 – In blue the general shape of χ^d for $a = 0.1$, $b = 2$ and $u = 0.5$. In red, x_0 is in E_{λ_2} for $\beta = 1$.

us to believe that it could be possible with our system. Unfortunately the simulation we can see in Figure 2.1 seems to show that we did not manage to succeed. We slightly modify the jump times in order to mimic the deterministic evolution (2.18).

Let $u = \frac{1}{2}$ (for sake of simplicity) and let n be a stricly positive integer. We now define the piecewise deterministic Markov process $((X_t^n, I_t^n))_{t\geq 0}$ as follows : $(I_t)_{t\geq 0}$ is a continuous time Markov process defined on the state space $\{0, 1, 2, ..., 2n-1\}$ with a constant jump rate $\frac{n\beta}{2}$ and a jump mesure :

$$\begin{aligned} &Q(i, .) = \delta_{i+1} \quad \text{if} \quad i < 2n-1, \\ &Q(2n-1, .) = \delta_0. \end{aligned}$$

And we define $(X_t^n)_{t\geq 0}$ as the solution of :

$$X_t = X_0^n + \int_0^t A_{\mathbb{1}_{I_t<n}} X_s^n ds.$$

This process looks like (2.3). The difference lies in the fact that, instead of waiting for an exponential time of parameter $\frac{\beta}{2}$ before jumping from a matrix to the other, the process waits for a time following a Gamma law of mean $\frac{2}{\beta}$ and variance $\frac{4}{n\beta^2}$.
The next result compares the stochastic process to the periodic one.

Lemma 2.5.1. *For every $T > 0$, the process $(X_t^n)_{0\leq t\leq T}$ uniformly converges to the deterministic process $(X_t)_{0\leq t\leq T}$ solution of* (2.18)*.*

Proof. Let us call $N^n(t)$ the number of jumps before t of the process (I_t^n), τ_1^n, τ_2^n, ...,$\tau_{N(t)}^n$ are the interjump times, they follow a gamma law of mean $\frac{1}{\beta}$ and variance $\frac{1}{n\beta^2}$. We denote $a_t^n = t - \sum_{k=1}^{N(t)} \tau_k^n$. We finally call ξ_1^n, ξ_2^n, ...,$\xi_{N(t)+1}^n \in \{0, 1\}$ the states.
By simply solving the equation for the process (X_t^n) and calculating the matrices exponential we obtain :

$$X_t^n = e^{-at} B_{\xi^n_{N^n(t)+1}}(a_t^n) B_{\xi^n_{N^n(t)}}(\tau^n_{N^n(t)}) \cdots B_{\xi_1^n}(\tau_1^n)$$

where

$$B_0(t) = \begin{pmatrix} \cos(t) & b\sin(t) \\ -\frac{1}{b}\sin(t) & \cos(t) \end{pmatrix} \quad \text{and} \quad B_1(t) = \begin{pmatrix} \cos(t) & \frac{1}{b}\sin(t) \\ -b\sin(t) & \cos(t) \end{pmatrix}.$$

Let us call $N(t)$ the number of jumps of the deterministic process. We have :

$$X_t = e^{-at} B_{\xi_{N(t)+1}}(a_t) B_{\xi_{N(t)}}(\frac{1}{\beta}) \cdots B_{\xi_1}(\frac{1}{\beta}).$$

We form the difference :

$$\begin{aligned} \|X_t^n - X_t\| \leq\ & \mathbb{1}_{N^n(t)=N(t)} \|B_{\xi^n_{N(t)+1}}(a_t^n) \cdots B_{\xi_1^n}(\tau_1^n) - B_{\xi_{N(t)+1}}(a_t) \cdots B_{\xi_1}(\frac{1}{\beta})\| \|X_0\| \\ & + \mathbb{1}_{N^n(t)\neq N(t)} \|B_{\xi^n_{N^n(t)+1}}(a_t^n) \cdots B_{\xi_1^n}(\tau_1^n) - B_{\xi_{N(t)+1}}(a_t) \cdots B_{\xi_1}(\frac{1}{\beta})\| \|X_0\|. \end{aligned}$$

We can prove by induction on $N(t)$ that :

$$\|B_{\xi^n_{N(t)+1}}(a^n_t)\cdots B_{\xi^n_1}(\tau^n_1) - B_{\xi_{N(t)+1}}(a_t)\cdots B_{\xi_1}(\frac{1}{\beta})\| \longrightarrow 0 \text{ in probability.}$$

The case $N(t) = 1$ shows us what happens :

$$\begin{aligned}\|B_{\xi_2}(t-\tau_1)B_{\xi_1}(\tau_1) - B_{\xi_2}(t-\frac{1}{\beta})B_{\xi_1}(\frac{1}{\beta})\| &\leq \|B_{\xi_2}(t-\tau_1)\|\|B_{\xi_1}(\tau_1) - B_{\xi_1}(\frac{1}{\beta})\| \\ &\quad + \|B_{\xi_2}(\frac{1}{\beta}) - B_{\xi_2}(\tau_2)\|\|B_{\xi_1}(\tau_1)\| \\ &\leq C_1|\tau_1 - \frac{1}{\beta}|.\end{aligned}$$

By using the inequality of Bienaymé-Tchebychev, we gain the claimed convergence. Moreover we can say that this convergence also holds in L^1 as the random variable is bounded because our process does not explode in a finite time.
We prove now that $\mathbb{P}[N^n(t) = N(t)] \longrightarrow 1$ when n goes to $+\infty$. First, let us write that $N(t) = p$ and $t = \frac{p}{\beta} + \eta$ where $0 \leq \eta < \frac{1}{\beta}$. We have :

$$\begin{aligned}\mathbb{P}[N^n(t) = p] &= \mathbb{P}\left[\tau_1 + \tau_2 + ... + \tau_p \leq t < \tau_1 + ... + \tau_p + \tau_{p+1}\right] \\ &= \mathbb{P}\left[0 \leq t - \sum_{i=1}^{p} \tau_i \text{ and } t < \sum_{i=1}^{p+1} \tau_i\right] \\ &= \mathbb{P}\left[\sum_{i=1}^{p} \tau_i - \frac{p}{\beta} < \eta\right] \mathbb{P}\left[t < \sum_{i=1}^{p+1} \tau_i \mid 0 \leq t - \sum_{i=1}^{p} \tau_i\right].\end{aligned}$$

The first probability goes to 1 when n goes to $+\infty$ thanks to the Bienaymé-Tchebychev inequality and the other probability is nonzero. This means that we have the claimed convergence : $\mathbb{P}[N^n(t) = N(t)] \longrightarrow 1$ when n goes to $+\infty$.
Back in the inequality, we take the expectation and using the previous results we prove that $\mathbb{E}[\|X^n_t - X_t\|]$ goes to 0 uniformly on $[0, T]$.

□

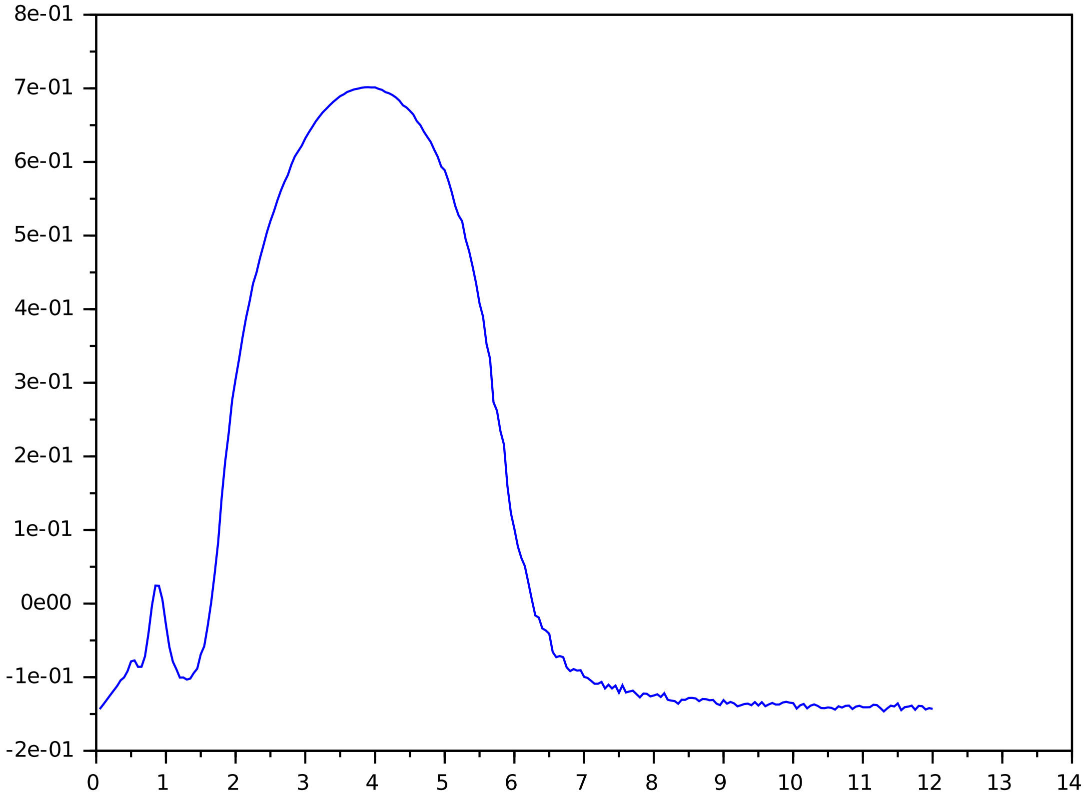


FIGURE 2.4 – For $a = 0.15$, $b = 3$ and $n = 50$, a second blow up area appears in χ.

2.6 Behaviour of the switched system with two centers of attraction

In this section we will have a discussion on the process (X_t, I_t) defined by the system (2.3) :

$$\begin{cases} \dot{X}_t = A_{I_t}(X_t - b_{I_t}) \\ X_0 = x_0, \end{cases} \tag{2.19}$$

where A_0, A_1 are $d \times d$ real Hurwitz matrices (the real part of their eigenvalues are negative), $b_0 \neq b_1 \in \mathbb{R}^d$ and (I_t) is a Markov process on $E = \{0, 1\}$ with constant jump rates λ_0, λ_1. Recall that $\lambda_0 = \beta u$ and $\lambda_1 = \beta(1-u)$ with $\beta > 0$ and $u \in (0,1)$.

For $i = 0, 1$ and $x \in \mathbb{R}^d$, let $t > 0 \mapsto \varphi_t^i(x)$ the solution of $\dot{x}_t = A_i(x_t - b_i)$ with $x_0 = x$.

Remark 2.6.1. *There exists $C \geq 1$ and $\eta > 0$ such that, for all $t \geq 0$,*

$$\left\|\varphi_t^i(x) - b_i\right\| \leq Ce^{-\eta t}\|x - b_i\|.$$

Recall that in [Benaïm *et al.*, 2012], the authors show that under assumption (2.2), the process (X_t, I_t) solution of (2.1) has a unique invariant measure μ and moreover, the following convergence holds for a certain distance made of a mixture of the Wasserstein distance and the total variation distance, $\mathcal{W}_p$:

$$\mathcal{W}_p(\mu_t, \mu) = \inf\left(\left(\mathbb{E}(|X - X'|^p)\right)^{\frac{1}{p}} + \mathbb{P}(I \neq I'),\ (X, I) \sim \mu_t \quad (X', I') \sim \mu\right) \underset{t \to +\infty}{\longrightarrow} 0 \tag{2.20}$$

for some $p \geq 1$ and where μ_t is the law of (X_t, I_t).

Recall that the Wasserstein distance W_p between two laws ν and ν' on $\mathbb{R}^d$ is defined by :

$$W_p(\nu, \nu') = \inf_{\Pi}\left(\int \|x - x'\|^p \Pi(dx, dx')\right)^{\frac{1}{p}}$$

where the infimum runs over all the probability measures Π with marginals ν and ν' (such measures are called couplings of ν and ν').

The total variation distance TV between two laws ν and ν' on $\mathbb{R}^d$ is defined by :

$$TV(\nu, \nu') = \min\left(\mathbb{P}(X \neq Y),\ X \sim \nu \quad Y \sim \nu'\right).$$

We first give a result similar to the one obtained in [Benaïm *et al.*, 2012] concerning the convergence in distance $\mathcal{W}_p$ (2.20) for the process (X_t, I_t) solution of (2.3) for small values of the parameter β.

Proposition 2.6.2. *Set ν_t, ν_t' the laws of the processes (X_t, I_t) and (X_t', I_t') with initial law ν_0 and ν_0'. For some β small enough and $p \geq 1$ we have the following convergence :*

$$\mathcal{W}_p(\nu_t, \nu_t') \underset{t \to +\infty}{\longrightarrow} 0.$$

Proof. We will proceed by coupling two paths (X_t, I_t) and (X'_t, I'_t) starting from (x, i) and (x', i) choosing the same jump times i.e. the same process $(I_t)_{t\geq 0}$. Then, the difference $D_t = X_t - X'_t$ is solution of :

$$\dot{D}_t = A_{I_t} D_t. \tag{2.21}$$

Note that the jump rates λ_0 and λ_1 do not depend on the position X_t. Hence, if the initial discrete components are different, one has to wait for a random time T following an exponential law of parameter $\lambda_0 + \lambda_1$ and then, they can be chosen equal for all $t \geq T$.

We assume that the initial discrete components are equal. Denote by N_t the number of jumps for $(I_t)_{t\geq 0}$ before time t. One can verify that $I_t = (-1)^{N_t} I_0$. As a consequence, since D_t is solution of (2.21), it comes :

$$D_t = \exp\Big((t - T_{N_t}) A_{T_{N_t}}\Big) \exp\Big((T_{N_t} - T_{N_t - 1}) A_{I_{N_t - 1}}\Big) \cdots \exp\Big((T_2 - T_1) A_{I_{T_1}}\Big) \exp(T_1 A_{I_0}) D_0.$$

Using Remark 2.6.1, one has

$$\|D_t\| \leq C^{N_t + 1} e^{-\eta t} \|D_0\|.$$

If the jump rates of I are equal, $(\lambda_0 = \lambda_1 = \lambda)$, then $(N_t)_{t\geq 0}$ is a simple Poisson process and

$$[\mathbb{E}(\|D_t\|^p)]^{1/p} \leq C \exp\left(-\left(\eta - \frac{\lambda(C^p - 1)}{p}\right) t\right) [\mathbb{E}(\|D_0\|^p)]^{1/p}.$$

This ensures that when λ and p are sufficiently small one can establish convergence in $\mathcal{W}_p$ distance (see [Bardet *et al.*, 2010],[Benaïm *et al.*, 2012]).

If the jump rates are not equal, $(N_t)_{t\geq 0}$ is not a Poisson process. For a fixed $c \in \mathbb{R}$, let us define $G_i(t) = \mathbb{E}_i(c^{N_t})$. Then, if T is the first jump time,

$$\begin{aligned} G_1(t) &= \mathbb{E}_1\left(c^{N_t} \mathbb{1}_{\{T \leq t\}}\right) + \mathbb{E}_1\left(c^{N_t} \mathbb{1}_{\{T > t\}}\right) \\ &= \int_0^t c G_0(t - s) \lambda_1 e^{-\lambda_1 s} ds + e^{-\lambda_1 t}. \end{aligned}$$

As a consequence, thanks to an integration by parts,

$$\begin{aligned} G'_1(t) &= c G_0(0) \lambda_1 e^{-\lambda_1 t} + c \int_0^t G'_0(t - s) \lambda_1 e^{-\lambda_1 s} ds - \lambda_1 e^{-\lambda_1 t} \\ &= c \lambda_1 e^{-\lambda_1 t} + c \Big[-G_0(t - s) \lambda_1 e^{-\lambda_1 t}\Big]_0^t - c \int_0^t G_0(t - s) \lambda_1^2 e^{-\lambda_1 s} ds - \lambda_1 e^{-\lambda_1 t} \\ &= -\lambda_1 G_1(t) + \lambda_1 c G_0(t). \end{aligned}$$

Notice that, if $\lambda_1 = \lambda_0$, one recovers that $G_0(t) = G_1(t) = \exp(\lambda t(c - 1))$. In the general case, G_0 and G_1 are solutions of

$$y'' + (\lambda_0 + \lambda_1) y' + \lambda_0 \lambda_1 (1 - c^2) y = 0$$

with respective initial conditions $G_i(0) = 1$, $G'_i(0) = \lambda_i(c - 1)$.

After solving this simple equation, it also comes that for λ and p small enough, we can establish convergence in Wasserstein distance. □

Corollary 2.6.3. *For β small enough, the process (X_t, I_t) admits a unique invariant measure ν.*

Remark 2.6.4. *By generalising the polar decomposition of section 2 for the dimension d, one can write $D_t = R_t U_t$ with $R_t > 0$ and $U_t \in S^{d-1}$. The same kind of computation will give :*

$$R_t = R_0 \exp\Big(\int_0^t \mathcal{A}(U_s, I_s)ds\Big).$$

Let us define :

$$\Psi_p(t) = \sup_{u \in S^1, i=0,1} \Big[\mathbb{E}_{(u,i)}\Big(\exp\Big(p\int_0^t \mathcal{A}(U_s, I_s)ds\Big)\Big)\Big]^{1/p}.$$

Thanks to Markov property, the function Ψ_p is under additive : $\Psi_p(t+s) \leq \Psi_p(t)\Psi_p(s)$. As a consequence, there exists χ_p such that

$$\chi_p = \lim_{t\to\infty} \frac{1}{t} \log \Psi_p(t).$$

Moreover, Jensen's inequality ensures that $\chi_p \geq \chi$. As a consequence, it is possible that $X_t \to 0$ a.s. with $\chi_p > 0$ for some $p > 0$.

Remark 2.6.5. *It is not easy to determine the sign of the Lyapunov exponent χ_p.*

We are now interested in the invariant measure, if it exists, of our process $(X_t)_{t\geq 0}$ solution of (2.3). Let us call $T_0 = 0$, T_1, ..., T_n the jumping times of the process (X_t) and τ_0, τ_1, ..., τ_n, the interjump times following an exponential law of parameters λ_0 and λ_1 alternatively. Let us define $Y_n = X_{T_{2n}}$. By simply solving the equation 2.3 between each jumping times we obtain :

$$Y_n = e^{\tau_{n+1}A_1} e^{\tau_n A_0} Y_{n-1} - e^{\tau_{n+1}} b_0 + b_1.$$

Applying Kesten's renewal theorem ([Kesten, 1973]) to the discrete process (Y_n) will give some informations about the tail of the invariant measure of (X_t).

Theorem 2.6.6. *If there is no deterministic control that makes the deterministic process associated to (Y_t) explodes, then there exists an invariant measure μ for our process and the support of μ is necessarily bounded.*

In the other hand, we assume that $\chi < 0$ and that there exists a deterministic control such as :

$$\exists k \in 2\mathbb{N}+1 \text{ such that } \forall x \in \mathbb{S}_{d-1}, \exists t_0, t_1, ..., t_k > 0 \text{ such that } \|e^{t_k A_{I_k}} ... e^{t_1 A_{I_1}} e^{t_0 A_{I_0}} x\| > \|x\|. \tag{2.22}$$

We call $B = e^{\tau_k A_{I_k}} ... e^{\tau_1 A_{I_1}} e^{\tau_0 A_{I_0}}$ and B_0, B_1, ..., B_n n random variables i.i.d following the law of B. We also assume that :

$$\max_{n\geq 0} \mathbb{P}\left(\frac{B_n...B_0 x}{\|B_n...B_0 x\|} \in U\right) > 0 \text{ for all } x \in \mathbb{S}_{d-1} \text{ and any open } \emptyset \neq U \subset \mathbb{S}_{d-1}. \tag{2.23}$$

$$\mathbb{P}(B_{n_0}...B_0 \in .) \geq \gamma_0 \mathbb{1}_{B_c(\Gamma_0)}\lambda \textit{ for some } \Gamma_0 \in GL_d(\mathbb{R}),\ n_0 \in \mathbb{N} \textit{ and } c, \gamma_0 > 0. \tag{2.24}$$

where λ is the Lebesgue measure on $\mathbb{R}^{n^2}$. Under these assumptions, there exists a unique invariant measure μ for the process (Y_t) and it has a heavy tails :

$$\exists p_1 > 0 \textit{ such that } \forall 0 \leq p < p_1 \quad \mathbb{E}_\mu[\|Y\|^p] < +\infty \textit{ and } \forall p > p_1 \quad \mathbb{E}_\mu[\|Y\|^p] = +\infty.$$

Proof. Let $x \in \mathbb{S}_{d-1}$. There exist t_0, t_1,... ,$t_k > 0$ such as :

$$\|e^{t_k A_{I_k}}...e^{t_1 A_{I_1}} e^{t_0 A_{I_0}} x\| > \|x\|.$$

Consequently, by continuity, there exist $\epsilon > 0$ and $\delta > 0$ such as :

$$\forall s_i \in J_i = (t_i - \delta, t_i + \delta), \quad \|e^{s_k A_{I_k}} \cdots e^{s_1 A_1} e^{s_0 A_0}\| \geq 1 + \epsilon.$$

Let us write $B = e^{\tau_k A_{I_k}}...e^{\tau_1 A_1} e^{\tau_0 A_0}$, where τ_0, τ_1,... ,τ_k are $k+1$ random exponential variables. We have :

$$\begin{aligned}\mathbb{E}\left[\|B\|^p\right] &\geq \mathbb{E}\left[\mathbb{1}_{\tau_k \in J_k} \cdots \mathbb{1}_{\tau_1 \in J_1} \mathbb{1}_{\tau_0 \in J_0} \|B\|^p\right] \\ &\geq \mathbb{P}(\tau_k \in J_k) \cdots \mathbb{P}(\tau_1 \in J_1) \mathbb{P}(\tau_0 \in J_0)(1+\epsilon)^p.\end{aligned}$$

As τ_0, τ_1,... ,τ_k are $k+1$ exponential random variables,

$$\mathbb{P}(\tau_k \in J_k) \cdots \mathbb{P}(\tau_1 \in J_1) \mathbb{P}(\tau_0 \in J_0) > 0.$$

Consequently :

$$\mathbb{E}\left[\|B\|^p\right] \underset{p \to +\infty}{\longrightarrow} +\infty,$$

meaning that there exists $x_1 > 0$ such as $\mathbb{E}\left[\|B\|^{x_1}\right] = 1$. Consequently, if the process (Y_t) does not explode, [Alsmeyer et Mentemeier, 2012] ensures that under the invariant measure μ :

$$\mathbb{P}(\|Y\| > r) \sim \frac{c}{r^{x_1}}.$$

It implies that μ has finite moments of order $p < x_1$. □

Remark 2.6.7. *In dimension 2, hypothesis (2.22) can be verified using the criteria in [Balde* et al.*, 2009] which gives the existence of an explosive control for the switched system. In higher dimension, no general result gives this information.*

Remark 2.6.8. *Hypotheses (2.23) and (2.24), directly extracted from a version of Kesten's renewal theorem in [Alsmeyer et Mentemeier, 2012], tell us, basically, that the process (Y_t) creates density according to the Lebesgue measure and its projection on the sphere $\mathbb{S}_{d-1}$ is a recurrent irreducible process. These hypotheses are not easy to check in the general case.*

Corollary 2.6.9. *If there exists a deterministic control that makes the system explode from one of the stable point b_0 or b_1, then, since A_0 and A_1 are Hurwitz, the invariant measure has a heavy tails.*

Example 2.6.10. *In dimension 3, it is possible to create an example satisfying Theorem 6.5 by picking the following matrices :*

$$A_0 = \begin{pmatrix} -a & b & 0 \\ -\frac{1}{b} & -a & 0 \\ 0 & 0 & -1 \end{pmatrix} \quad \textit{and} \quad A_1 = \begin{pmatrix} -1 & 0 & 0 \\ 0 & -a & b \\ 0 & -\frac{1}{b} & -a \end{pmatrix}.$$

When we consider each system $\dot{X}_t = A_i X_t$ separately, one can check that, when $a < 1$, the projection of (X_t) on the sphere tends to a different ecuador. Consequently, using results in [Bakhtin et Hurth, 2012], it is possible to show that the process (X_t) solution of (2.3) *satisfies hypothesis (2.23) and (2.24).*

Chapitre 3

Comparison of two chemostat-like models simulating environment heterogeneity

This chapter is the extended version of an article written in 2018 in collaboration with Sten Madec from the Tours University entitled *Comparison of the global dynamics for two chemostat-like models : random temporal variation versus spatial heterogeneity.*

3.1 Introduction

The chemostat is a standard model for the evolution and the competition of several species for a single resource in an open environment. Its studies as well as that of its many variants has been widely explored for fifty years. One can read Smith and Waltman's book ([Smith et Waltman, 1995]) which gives an overview of the complexity and variability of this research domain. There are numerous applications for the chemostat. For example, in population biology, the chemostat serves as a first approach for the study of natural systems. In industrial microbiology, the chemostat offers an economical production of micro-organisms.

The chemostat is known to satisfy the *principle of exclusive competition* which states that when several species compete for the same (single) resource, only one species survives, the one which makes the "best" use of the resource ([Hsu, 1978, Hsu *et al.*, 1977]). Though some natural observations and laboratory experiences support the principle of exclusive competition, the observed population diversity within some natural ecosystems seem to exclude it. In order to take account of the biological complexity without excluding the specificity of the chemostat, various models has been introduced ([Loreau *et al.*, 2003] for example).

The observed biodiversity could first be explained by the temporal fluctuations of the environment. This idea has been explored in the ecology literature (see for example [Chesson, 2000], [Chesson et Warner, 1981]). Applied to the gradostat, this idea gave the following article [Smith et Waltman, 2000] where the authors study the general gradostat with a periodic resource input. However, temporal fluctuations of an environment are most likely random. From this assumption comes the idea of studying an environment fluctuating randomly between a finite number of environments. In [Benaïm et Lobry, 2016], the authors gives a complete study for a two-species Lotka-Volterra model of competition where the species evolve in an environment changing randomly between two environments and prove that coexistence is possible.

In order to take account of the biological complexity without excluding the specificity of the chemostat, Lovitt and Wimpenny introduced the gradostat model (in their article [Lovitt et Wimpenny, 1981]) which consists in the concatenation of various chemostats where the adjacent vessels are connected in both directions. The resource output occurs in the first and last chemostats of the chain and those in between exchange their contents. The case where two species evolve in two interconnected chemostats is understood in various cases, one can read [Smith et Waltman, 1991], [Gaki *et al.*, 2009], [Rapaport, 2017] for more references. Some other chemostat-like partial differential equations has been introduced to take account of the environment heterogeneity (one can see [Castella et Madec, 2014],[Castella *et al.*, 2016] for example).

From now on, we will consider two species u and v competing for a resource R. In a chemostat ε, we will note δ the common dilution rate for each species and the dilution rate of the resource, R_0 the constant input concentration of the resource in the vessel and for each species $w \in \{u, v\}$, f_w the growth rate for the species w. The function f_w depends on the resource concentration R. Note that according to the models, f_w can have different expressions. We will pick here the most common expression for f_w which is Michaelis-Menten's one :

$$f_w(R) = \frac{a_w R}{b_w + R}.$$

where a_w is the maximum growth rate for the species w and b_w is the Michaelis-Menten constant of the species w.

Note $U(t)$, $V(t)$ and $R(t)$ the concentrations of the species u, v and the resource R. The evolution of these different concentrations in the simple chemostat ε is given by the equations :

$$\begin{cases} \dot{R}(t) = \delta(R_0 - R(t)) - U(t)f_u(R(t)) - V(t)f_v(R(t)) \\ \dot{U}(t) = U(t)\left(f_u(R(t)) - \delta\right) \\ \dot{V}(t) = V(t)\left(f_v(R(t)) - \delta\right). \end{cases} \tag{3.1}$$

Let us note :

$$R_w^* = \begin{cases} \frac{b_w\delta}{a_w-\delta} \text{ if } a_w > \delta \\ +\infty \text{ if } a_w \leq \delta, \end{cases}$$

the concentration of resource satisfying $f_w(R_w) = \delta$ (if possible). This quantity R_w can be interpreted as the minimal concentration rate needed by the species w to have its population growing. The species which needs the less resource to survive in the environment is the best competitor.

It is well known that the simple chemostat satisfies the principle of exclusive competition : only the best competitor survives. The following theorem [1] illustrates this statement

1. There exists various modifications of the theorem 3.1.1. In particular, the competitive exclusion

(see [Hsu, 1978, Hsu *et al.*, 1977]).

Theorem 3.1.1 (Competitive Exclusion)**.** *Suppose that $R_u < R_v$ and $R_u < R_0$ (u is the best competitor). The solutions of* (3.1) *satisfy :*

$$\lim_{t \to +\infty} (R(t), U(t), V(t)) = (R_u^*, R_0 - R_u^*, 0).$$

Remark 3.1.2. *Let us write :*

$$\Sigma(t) = R(t) + U(t) + V(t).$$

Considering that the dilution rate is the same for every species and the substrat, it is easy to see that Σ satisfies the following differential equation :

$$\dot{\Sigma}(t) = \delta(R^0 - \Sigma(t)).$$

It comes that $\Sigma(t) \underset{t \to +\infty}{\longrightarrow} R_0$. Hence, assuming that the dilutions rates are the same for every species and the resource is a strong hypothesis that allows us to do the variable change $R(t) = \Sigma(t) - U(t) - V(t)$.

In this paper, we consider two chemostats ε^1 and ε^2. The parameters of the chemostat ε^j will be noted $(R_0^j, \delta^j, a_u^j, a_v^j, b_u^j, b_v^j)$. Note that in all the article, the subscripts of a parameter or a variable will always make reference to the species and the exponent will always make reference to the environment. If $w \in \{u, v\}$ is a species we will note $\overline{w} \in \{u, v\}$ the other species. With these two chemostats, we build two competition models.

The first model is a probabilistic one. In this model the chemostat where the two species and the resouce evolve is alternating randomly between ε^1 and ε^2. Assuming that the species and resource live in ε^1 at t equal 0, we wait a random exponential time of parameter λ^1 before switching to the chemostat ε^2. Then, we wait an other independent random exponential time of parameter λ^2 before switching back to ε^1, and so on.

The goal here is to model time variations of the environment the species and resource evolve in. Mathematically, we build here a random process which study is totally different from the gradostat model. In [Benaïm et Lobry, 2016], the authors study a similar process for a Lotka-Volterra competition model and we claim that it is possible to adapt their techniques to the slightly more difficult chemostat switching competition model.

The second model is a gradostat-like model where the two chemostats ε^1 and ε^2 are connected and trade their content at a certain speed λ. Mathematically, this model is a differential equation system which models space heterogeneity in a biosystem (see [Lovitt et Wimpenny, 1981] for some mathematical results on the behavior of such system).

The goal of this chapter will be to compare the long time behavior of these two different systems. For each model we give a mathematical definition for what we will call the invasion rate of the species, noted Λ_w for the species w in the probabilistic [2]. Given the mathematical

principle holds true for general increasing consumption function f_w verifying $f_w(0) = 0$.

2. In the deterministic case the invasion rate of the species w will be noted Γ_w. However, we only refer to Λ_w in the introduction.

difference between the two models, the definition of these invasion rates will be different for each model. However, we will see that for each model, the signs of Λ_u and Λ_v essentially determine the state of the system at the equilibrium.

We show that, if $\Lambda_u\Lambda_v > 0$, then for any positive initial condition only the two following behavior can happen for the two models.

— If $\Lambda_u < 0$ and $\Lambda_v < 0$ there is extinction of either species u or species v This configuration will be called the bi-stability.
— If $\Lambda_u > 0$ and $\Lambda_v > 0$ there is coexistence of both species at any times.

In contrast, when $\Lambda_u\Lambda_v < 0$, the possibilities are not exactly the same for the two models. For instance, if $\Lambda_u > 0$ and $\Lambda_v < 0$. Then in the probabilistic model there is always extinction of species v but for the deterministic model there is either

— Extinction of species v (for all initial condition in the positive quarter plane).
— Extinction of species v or coexistence (depending on the initial condition in the positive quarter plane).

Consequently, comparing the two models will be essentially done by comparing the evolution of the two different definitions of these invasion rates according to the parameter λ. An analytical and a numerical comparison of these invasion rates is done in section 3.4. In particular, we show, for the two models, that even if the two environments are favorable to the same species, then the two species may coexist or, worse, the other species is the only survivor.

3.1.1 Random temporal variation : model and main results

3.1.1.1 The probabilistic model : a PDMP model

As stated before, we pick two environments ε^1 and ε^2 and we model the environmental variation of a biosystem by randomly switching the chemostat the two species and the resource evolve in. This idea and its mathematical resolution has been introduced in [Benaïm et Lobry, 2016]. In this previous article, the authors exhibit counterintuitive phenomenon on the behavior of a two-species Lotka-Volterra model of competition where the environment switches between two environments that are both favorable to the same species. Indeed, they show that coexistence of the two species or extinction of the species favored by the two environments can occur.

We consider the stochastic process (R_t, U_t, V_t) defined by the system of differential equations :

$$\begin{cases} \dot{R}_t = \delta^{I_t}(R_0^{I_t} - R_t) - U_t f_u^{I_t}(R_t) - V_t f_v^{I_t}(R_t) \\ \dot{U}_t = U_t(f_u^{I_t}(R_t) - \delta^{I_t}) \\ \dot{V}_t = V_t(f_v^{I_t}(R_t) - \delta^{I_t}) \end{cases} \tag{3.2}$$

where (I_t) is a continuous time Markov chain on the space of states $E = \{1, 2\}$. We note λ^1 and λ^2 the jump rates. Starting from the state j, we wait an exponential time of parameter λ^j before jumping to the state $\bar{j}$. The invariant measure of (I_t) is $\frac{\lambda^2}{\lambda^1+\lambda^2}\Delta^1 + \frac{\lambda^1}{\lambda^1+\lambda^2}\Delta^2$ (where Δ^j is the Dirac measure in j).

Let us note the jump rates : $\lambda^1 = s\lambda$ and $\lambda^2 = (1-s)\lambda$ with $s \in (0, 1)$ and $\lambda > 0$.

Parameter s (respectively $1-s$) can be seen as the proportion of time the jump process (I_t) spends in state 2 (respectively 1). The parameter λ will be seen as the global switch rate of (I_t).

The process $(Z_t) = (R_t, U_t, V_t, I_t)$ is what we call a Piecewise Deterministic Markov Process (PDMP) as introduced by Davis in [Davis, 1984].

Let us call :

$$K = \{(r,u,v) \in \mathbb{R}^3_+ \ , \quad \frac{\min(R_0^1, R_0^2)}{2} \leq r+u+v \leq 2\max(R_0^1, R_0^2)\},$$

and

$$M = K \times \{1,2\}.$$

According to remark 3.1.2, Z_t will reach M for any initial condition $Z_0 \in \mathbb{R}_+^{n+1} \times \{1,2\}$. We can then assume that $Z_0 \in M$ and, as a consequence, M will be seen as the state space of the process (Z_t).

We will call the extinction set of species w the set :

$$M_{0,w} = \{(r,u,v,i) \in M \ , \quad w = 0\},$$

and the extinction set :

$$M_0 = \bigcup_w M_{0,w}.$$

It is clear that the process (Z_t) leaves invariant all the extinction set and the interior set $M \setminus M_0$.

In order to describe the behavior of the process (Z_t) when $Z_0 \in M \setminus M_0$, the article [Benaïm et Lobry, 2016] suggests to study the invasion rates of species w defined as :

$$\Lambda_w = \int \left(f_w^1(R) - \delta^1\right) d\mu(R,1) + \int \left(f_w^2(R) - \delta^2\right) d\mu(R,2),$$

where μ is an invariant probability measure of (Z_t) on $M_{0,w}$.

Remark 3.1.3. *The idea behind the definition of the invasion rate Λ_u (same for Λ_v) is the following. From (3.2) comes :*

$$\frac{\dot{U}_t}{U_t} = f_u^{I_t}(R_t) - \delta^{I_t} = \mathcal{A}(Z_t)$$
$$\int \frac{\dot{U}_t}{U_t} ds = \int \mathcal{A}(Z_s) ds$$
$$\frac{1}{t}\log U_t = \frac{1}{t}\int \mathcal{A}(Z_s) ds.$$

Formally, the ergodic theorem allows to write :

$$\frac{1}{t}\log U_t \to \int \mathcal{A}(z) d\mu(z),$$

where μ is an invariant measure for the process (Z_t). If μ is an invariant measure of (Z_t) on $M_{0,u}$, we define $\Lambda_u = \int \mathcal{A}(z) d\mu(z)$. By Feller continuity (see [Benaïm et al.*, 2014]) it comes that Λ_u can be seen as the exponential growth rate of U_t when U_t is close to zero.*

As stated in this previous remark, Λ_w can be seen as the exponential growth rate of the concentration of the species w when its concentration is close to zero. If $\Lambda_w > 0$, the concentration of w tends to increase from low values and if $\Lambda_w < 0$, the concentration of w tends to decrease from low values.

We are interested in the long time behavior of the concentration of the species u and v. In [Benaïm et Lobry, 2016], the authors show that the signs of the invasion rates characterizes the long time behavior of the randomly switched Lotka-Volterra model of competition. It is expected to have the same result in the chemostat case. We expect the two following behavior for the concentration of the species u and v :

— Species $w \in \{u, v\}$ goes to extinction if $W_t \to 0$ almost surely for any initial condition $Z_0 \in M \backslash M_0$.

— We have coexistence of the two species when the two species do not go to extinction for any initial condition $Z_0 \in M \backslash M_0$. In this case, any invariant measure of (Z_t) is supported by $M \backslash M_0$.

3.1.1.2 Long time behavior when only one species is introduced

Assume that species $\overline{w}$ is not in the system ($\overline{W_t} = 0$). Then, the process $Z_t = (R_t, W_t, I_t)$ satisfies :

$$\begin{cases} \dot{R}_t = \delta^{I_t}(R_0^{I_t} - R_t) - U_t f_u^{I_t}(R_t) \\ \dot{W}_t = W_t(f_w^{I_t}(R_t) - \delta^{I_t}) \end{cases} \tag{3.3}$$

In order to enphasize the fact that species $\overline{w}$ is absent of the system, let us define :

$$\Lambda_w^0 = \int \left(f_w^1(R) - \delta^1\right) d\mu_w^0(R, 1) + \int \left(f_w^2(R) - \delta^2\right) d\mu_w^0(R, 2),$$

where μ_w^0 will be proven (see Section 3.2) to be the unique invariant measure of the process (Z_t) restricted to $M_{0,w}$.

The first result which is similar to the main result in [Benaïm et Lobry, 2016] is :

Theorem 3.1.4. *The sign of the invasion rate Λ_w^0 characterizes the evolution of the species w :*

1. *If $\Lambda_w^0 < 0$ then species w goes to extinction : $W_t \to 0$ almost surely.*
2. *If $\Lambda_w^0 > 0$ then species w perpetuates.*

3.1.1.3 Long time behavior when two species are introduced

We will assume that $\underline{R_0^1 = R_0^2 = R_0}$. As a consequence, according to remark 3.1.2, the sum $\Sigma_t = R_t + U_t + V_t$ goes exponentially fast to R_0. Recall that the process $Z_t = (R_t, U_t, V_t, I_t)$ satisfies equation (3.2) and that :

$$\Lambda_w = \int \left(f_w^1(R) - \delta^1\right) d\mu_w(R, 1) + \int \left(f_w^2(R) - \delta^2\right) d\mu_w(R, 2),$$

where μ_w is an invariant measure of (Z_t) restricted to $M_{0,w}$.

We will also assume that the two species u and v can enter in competition in each vessel ε^1 and ε^2. Mathematically, this assumption means that for all $w \in \{u, v\}$ and for all $j \in \{1, 2\}$, the equation $f_w^j(r) = \delta^j$ has a unique positive solution noted R_w^j, and moreover $R_w^j < R_0^j$.

Assertion 3.1.5. *Let us note (H_w) the assertion which is true if and only if one of the following assertion is true :*
- *(i) $\exists j \in \{1, 2\}$ such that ε^j is unfavorable to the species w.*
- *(ii) $\exists s \in (0, 1)$ such that the averaged chemostat ε_s is unfavorable to the species w (see remark 3.2.7 for a precise definition of the averaged chemostat).*

Once again, the signs of the invasion rates Λ_u, Λ_v fully describe the long time behavior of the process :

Theorem 3.1.6. *The sign of the invasion rates Λ_u, Λ_v characterizes the evolution of the species :*
1. *If $\Lambda_u > 0$ and $\Lambda_v < 0$ and (H_v) is true then species v goes to extinction.*
2. *If $\Lambda_u < 0$ and (H_u) is true and $\Lambda_v > 0$ then species u goes to extinction.*
3. *If $\Lambda_u < 0$ and $\Lambda_v < 0$ then of one the species goes to extinction (bi-stability state).*
4. *If $\Lambda_u > 0$ and $\Lambda_v > 0$ then there is coexistence of both species.*

See section 3.4 for a numerical investigation over the signs of these invasion rates. We will show numerically that for any couple of signs $(x, y) \in \{+, -\}$ there exists pair of chemostats ε^1, ε^2 such that $(Sign(\Lambda_u), Sign(\Lambda_v)) = (x, y)$. Hence, it is possible to pick chemostats ε^1 and ε^2 such that for some values of the switching rate λ, $\Lambda_u < 0$: switching between two environments favorable to species u can surprisingly make it disappear.

3.1.2 Spatial heterogeneity : model and main results

3.1.2.1 The deterministic model : a gradostat-like model

The gradostat model is obtained by connecting the two chemostats ε^1 and ε^2 and allowing them to trade their content.

Note $\mathcal{V}^j$ the volume of the chemostat ε^j and Q the volumetric flow rate between the two vessels and $U^j(t)$ the concentration of the species u in the chemostat ε^j as shown in figure 3.1.

It comes :

$$\begin{cases} (U^1\dot{\mathcal{V}}^1)(t) = -QU^1(t) + QU^2(t) \\ (U^2\dot{\mathcal{V}}^2)(t) = QU^1(t) - QU^2(t). \end{cases}$$

Which implies the following differential equation on the concentrations :

$$\begin{cases} \dot{U^1}(t) = -\frac{Q}{\mathcal{V}^1}U^1(t) + \frac{Q}{\mathcal{V}^1}U^2(t) \\ \dot{U^2}(t) = \frac{Q}{\mathcal{V}^2}U^1(t) - \frac{Q}{\mathcal{V}^2}U^2(t). \end{cases} \tag{3.4}$$

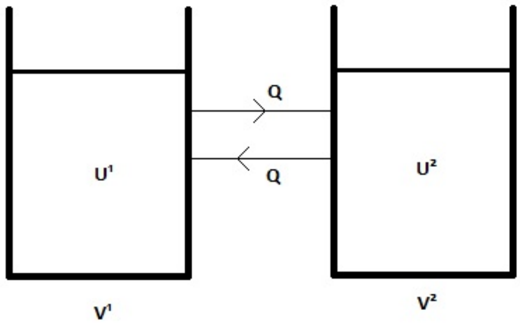


FIGURE 3.1 – Material flow between the two vessels.

We will note $\lambda^j = \frac{Q}{\mathcal{V}^j}$. Similarly, we note $V^j(t)$ the concentration of the species v in the chemostat j and $R^j(t)$ the concentration of the resource in the chemostat j. We will also note $\{j, \overline{j}\} = \{1, 2\}$.

The evolution of the gradostat is described by the following system of 6 differential equations :

$$\begin{cases} \dot{R}^j(t) = \delta^j(R^{0,j} - R^j(t)) - U^j(t) f_u^j(R^j(t)) - V^j(t) f_v^j(R^j(t)) & + \lambda^j(R^{\overline{j}}(t) - R^j(t)) \\ \dot{U}^j(t) = U^j(t)(f_u^j(R^j(t)) - \delta^j) & + \lambda^j(U^{\overline{j}}(t) - U^j(t)) \\ \dot{V}^j(t) = V^j(t)(f_v^j(R^j(t)) - \delta^j) & + \lambda^j(V^{\overline{j}}(t) - V^j(t)). \end{cases} \tag{3.5}$$

The part with λ^j in factor comes from the transfer equation (3.4) and the other part comes from the chemostat equation (3.1).

Notation 3.1.7. *Let us write* $R(t) = \begin{pmatrix} R^1(t) \\ R^2(t) \end{pmatrix}$, $U(t) = \begin{pmatrix} U^1(t) \\ U^2(t) \end{pmatrix}$, $V(t) = \begin{pmatrix} V^1(t) \\ V^2(t) \end{pmatrix}$, $R_0 = \begin{pmatrix} R_0^1 \\ R_0^2 \end{pmatrix}$, $\delta = \begin{pmatrix} \delta^1 \\ \delta^2 \end{pmatrix}$ *and* $f_w(R) = \begin{pmatrix} f_w^1(R^1) \\ f_w^2(R^2) \end{pmatrix}$. *Moreover, by noting* $\lambda^1 = s\lambda$ *and* $\lambda^2 = (1-s)\lambda$ *with* $\lambda > 0$ *and* $s \in (0,1)$ *we will call* $K = \begin{pmatrix} -s & 1-s \\ s & s-1 \end{pmatrix}$.

Moreover, by convention we have $\begin{pmatrix} w \\ x \end{pmatrix} \begin{pmatrix} y \\ z \end{pmatrix} = \begin{pmatrix} wy \\ xz \end{pmatrix}$.

Thanks to these notations, the system (3.5) reads :

$$\begin{cases} \dot{R}(t) = \delta(R_0 - R(t)) - U(t) f_u(R(t)) + \lambda K R(t) \\ \dot{U}(t) = U(t)(f_u(R(t)) - \delta) \qquad + \lambda K U(t) \\ \dot{V}(t) = V(t)(f_v(R(t)) - \delta) \qquad + \lambda K V(t). \end{cases} \tag{3.6}$$

The initial value will be taken in the set $(\mathbb{R}_+)^2 \times (\mathbb{R}_+^*)^2 \times (\mathbb{R}_+^*)^2$.

Remark 3.1.8. *Set $\Sigma^j(t) = R^j(t) + U^j(t) + V^j(t)$. It is easy to see that $\Sigma(t) = \begin{pmatrix}\Sigma^1(t)\\ \Sigma^2(t)\end{pmatrix}$ satisfies the linear differential equation :*

$$\dot{\Sigma}(t) = (\lambda K + \Delta)\,\Sigma(t) + \delta R_0,$$

where $\Delta = \begin{pmatrix}\delta^1 & 0\\ 0 & \delta^2\end{pmatrix}$.

The matrix $\lambda K + \Delta$ has two real negative eigenvalues. Hence $\Sigma(t)$ goes to an equilibrium Σ when t goes to to $+\infty$ where Σ is solution of the equation :

$$(\lambda K + \Delta)\,\Sigma + \delta R_0 = 0.$$

That is :

$$\Sigma = \begin{pmatrix}\Sigma^1\\ \Sigma^2\end{pmatrix}$$

where,

$$\Sigma^j = \frac{\lambda^2\delta^1 R_0^1 + \lambda^1\delta^2 R_0^2 + \delta^1\delta^2 R_0^j}{\lambda^1\delta^2 + \lambda^2\delta^1 + \delta^1\delta^2}.$$

Since every trajectory is asymptotic to its omega limit set, it is important to study the system on this set. As a consequence, in all the following our attention will be focused on the system reducted to this invariant set :

$$\begin{cases} \dot{U}(t) = U(t)(f_u(\Sigma - U(t) - V(t)) - \delta) + \lambda K U(t)\\ \dot{V}(t) = V(t)(f_v(\Sigma - U(t) - V(t)) - \delta) + \lambda K V(t). \end{cases} \tag{3.7}$$

With initial condition in the set $(\mathbb{R}_+^*)^2 \times (\mathbb{R}_+^*)^2$.

We are interested in the long time behavior of the solution of this differential system. It is proven in [Smith et Waltman, 1995], [Smith et Waltman, 1991], using strongly the monotonicity of the system, that any trajectory of (3.7) goes to a stationary equilibrium when the consumption functions f_w^j do not depend on the vessel ε^j. Their proofs are mainly based on the study of the existence and stability of stationary solutions and on general result about monotone system.

This strategy is still working in the case of vessel-dependent consumption function f_w^j, the main additional difficulty being that the structure of the stationary solutions is richer when the functions f_w^j do depend on j. We do a complete description of the stationary solution detailled in section 3.4. This description relies on the construction of different functions defined on the interval $[0, R_0^1]$ which intersections in a certain domain of the plane $[0, R_0^1] \times [0, R_0^2]$ gives the existence and stability of stationary solutions for (3.7).

The main idea of the construction of these functions is the following :

1. If the species w survives at the equilibrium, then 0 is the principal eigenvalue of the matrix $A_w(R) = f_w(R) - \delta + \lambda K$ which implies that $R = (R^1, R^2)$ belongs to the graph of a function F_w.
2. If the species w survives (without competition) then $W = R_0 - R$ is the principal eigenfunction of $A_w(R)$ and then $R = (R^1, R^2)$ belongs to the graph of a function g_w.

3.1.2.2 Long time behavior when only one species is introduced

Assume that $\overline{w}$ is not in the system ($\overline{W}(0) = 0$). In this particular case, it is possible to study the behavior of the system. Without competition, the differential equation describing the evolution of the system is :

$$\dot{U}(t) = U(t)(f_u(\Sigma - U(t)) - \delta) + \lambda K U(t) \tag{3.8}$$

with initial condition in $\mathbb{R}_+^{*,2}$.

An adaptation of the proof in [Smith et Waltman, 1995] shows that any trajectory of this previous differential equation goes to a stationary point. Let us call $E_0 = 0$. E_0 is the trivial stationary equilibrium of the system (3.8) and its linear stability gives the behavior of the solutions of (3.8) :

Theorem 3.1.9. *The stability of E_0 characterizes the behavior of (3.8) :*
- *If E_0 is a locally attractive equilibrium point, then it is the only stationary point and any trajectory is attracted by E_0 for any initial condition in $\mathbb{R}_+^{*,2}$.*
- *If E_0 is an unstable stationary point, then there exists a unique stationary point $E_w = W \in (\mathbb{R}_+^*)^2$. Moreover E_w is a global attractor in $(\mathbb{R}_+^*)^2$ for the system* (3.8).

Note that a stationary point for equation (3.8) satisfies the equation :

$$\mathcal{F}(U) = U(f_u(\Sigma - U) - \delta) + \lambda K U = 0.$$

The Jacobian matrix of $\mathcal{F}$ taken at E_0 is :

$$A_w = \begin{pmatrix} f_w^1(\Sigma^1) - \delta^1 - \lambda^1 & \lambda^1 \\ \lambda^2 & f_w^2(\Sigma^2) - \delta^2 - \lambda^2 \end{pmatrix}. \tag{3.9}$$

We define the invasion rate Γ_w^0 of the species w as the maximum eigenvalue of the matrix A_w :

$$\Gamma_w^0 = \frac{1}{2}\left(f_w^1(\Sigma^1) - \delta^1 + f_w^2(\Sigma^2) - \delta^2 - \lambda^1 - \lambda^2 + \sqrt{(f_w^1(\Sigma^1) - \delta^1 - f_w^2(\Sigma^2) + \delta^2)^2 + 4\lambda^1\lambda^2}\right) \tag{3.10}$$

From the previous theorem it comes :

Corollary 3.1.10. *The sign of Γ_w^0 characterizes the behavior of the system* (3.8) *:*
- *$\Gamma_w^0 < 0 \Rightarrow$ extinction of the species w for any initial condition in $\mathbb{R}_+^{*,2}$.*
- *$\Gamma_w^0 > 0 \Rightarrow$ persistence of the species w for any initial condition in $\mathbb{R}_+^{*,2}$.*

3.1.2.3 Long time behavior when two species are introduced

For sake of comparison with the probabilistic case, we set $R_0 = R_0^1 = R_0^2$ even if computations are possible when these two quantities are different. In the case where the consumption functions f_w^j does not depend on the vessel ε^j, it is proven in [Smith et Waltman, 1995] that any trajectory of (3.7) goes to a stationary point. We will see that this is also the case when the consumption functions depend on the vessel.

Since it is assumed that $R_0^1 = R_0^2$, according to remark 3.1.8, $\Sigma = R_0$. Hence, the stationary solutions of (3.7) satisfies the following equation :

$$\mathcal{H}(U,V) = 0 \Leftrightarrow \begin{cases} U(f_u(R_0 - U - V) - \delta) + \lambda K U = 0 \\ V(f_v(R_0 - U - V) - \delta) + \lambda K V = 0. \end{cases} \tag{3.11}$$

We will see that the study of the existence and stability of these solutions is crucial in the understanding of the long-time behavior of the solutions of (3.7).

Set $E_0 = (0,0)$. E_0 is the trivial stationary equilibrium. The jacobian matrix of $\mathcal{H}$ in E_0 is :

$$dH(E_0) = \begin{pmatrix} A_u & 0 \\ 0 & A_v \end{pmatrix}$$

where :

$$A_w = \begin{pmatrix} f_w^1(R_0) - \delta^1 - \lambda^1 & \lambda^1 \\ \lambda^2 & f_w^2(R_0) - \delta^2 - \lambda^2 \end{pmatrix}.$$

Remark 3.1.11. *Note that A_w is the jacobian computed in the single species case (see* (3.9)*) seen in the previous subsection and evaluated at the trivial stationary point.*

If both A_u and A_v have negative eigenvalues then E_0 is a locally attractive stationary point, and there are no other stationary equilibrium point.

If A_u has at least one positive eigenvalue, then E_0 is unstable. As a consequence, theorem 3.1.9 from the previous subsection gives the existence of a unique semi-trivial stationary equilibrium $E_u = (U,0)$. Likewise, if A_v has at least one positive eigenvalue, we define $E_v = (0,V)$ as the other semi-trivial stationary equilibrium.

Proposition 3.1.12. *According to [Smith et Waltman, 1995], we have :*

- *If E_u and E_v does not exists, then E_0 is a global attractor.*
- *Let $\{w,\overline{w}\} = \{u,v\}$. If E_w exists and $E_{\overline{w}}$ does not exists, then E_w is a global attractor.*

Hence, the most interesting case holds when both E_u and E_v exists. In that case, it is possible to have coexistence stationary solutions which may be stable or unstable.

We will take the following notations for the stationary equilibria of (3.7). Let $w \in \{u,v\}$. When the semi-trivial equilibrium E_w exists, the concentration of the species w at this equilibrium will be plainly noted W and the resource concentration will be noted R_w and satisfies $R_w = R_0 - W$. A stable (resp. unstable) coexistence stationary equilibrium will be noted $E_{cs} = (U_{cs}, V_{cs})$ (resp. $E_{cu} = (U_{cu}, V_{cu})$) and it satisfies $U_{cs} > 0$ and $V_{cs} > 0$ (resp. $U_{cu} > 0$ and $V_{cu} > 0$). The resource concentration at this equilibrium will be noted R_{cs} (resp. R_{cu}).

The stability of the semi-trivial stationary equilibrium can be given by a straightforward computation of the jacobian of $\mathcal{H}$ evaluated at E_u and E_v (for more explicit details, see Section 3.4). Define the following matrix :

$$M_{\overline{w}}(R_w) = \begin{pmatrix} f_{\overline{w}}^1(R_w^1) - \delta^1 - \lambda^1 & \lambda^1 \\ \lambda^2 & f_{\overline{w}}^2(R_w^2) - \delta^2 - \lambda^2 \end{pmatrix}.$$

It will be proven that the sign of the eigenvalues of $M_{\overline{w}}(R_w)$ gives the stability of the semi-trivial equilibrium E_w.

Definition 3.1.13. *Let us note Γ_w the maximum eigenvalue of the matrix $M_w(R_{\overline{w}})$. The quantities Γ_w will be called the invasion rates of the species w.*

Remark 3.1.14. *Let us explain the designation "invasion rate" for Γ_u. If $\Gamma_u > 0$, it means that the semi-trivial equilibrium $E_u = (U,0)$ is unstable. Consequently, according to previous remark, it means that 0 is un unstable equilibrium for the differential equation :*

$$\dot{V}(t) = V(t)\,(f_v(R_0 - U - V(t)) - \delta) + \lambda K V(t).$$

Hence, from a small initial value on V, V will increase (invade the environment). On the contrary, if $\Gamma_u < 0$, the semi-trivial equilibrium $E_u = (U,0)$ is stable. Hence, from a small initial value on V, V will go to 0 (disappear from the environment).

The signs of the invasion rates Γ_w give the stability of the semi-trivial equilibrium $E_{\overline{w}}$ but we will see that they also determine the existence and stability for coexistence stationary equilibrium. In section 3.3 we give a full characterization of the stationary solutions and their stability.

Moreover, the system (3.7) has a monotonic structure[3]. This monotonic structure is a very strong property which reduces the possibilities for the global dynamics of the system. In particular, for almost every initial condition, the trajectory of the solutions of (3.7) goes to a stationary equilibrium (see [Smith et Waltman, 1995], appendix C). Hence, using the result from the section 3.3 and the same arguments that the ones stated in [Smith et Waltman, 1995], we obtain theorem 3.1.15 which describes the possible dynamics of (3.7).

Theorem 3.1.15. *Assume that the two semi-trivial stationary equilibrium E_u and E_v exist.*

1. *If $\Gamma_v > 0$ and $\Gamma_u > 0$, then the solutions of (3.7) go to the unique coexistence equilibrium E^* which is linearly stable for almost every initial condition.*
2. *If $\Gamma_v < 0$ and $\Gamma_u < 0$, then there exists an unstable coexistence solution E_{cu}. Moreover, the solutions of (3.7) go either to E_u of to E_v (for almost every initial condition) depending on the location of the initial value according to the basin of attraction of the two semi-trivial equilibrium. The system is said to be in a bi-stable case.*
3. *Let $\{w, \overline{w}\} = \{u, v\}$ and suppose that $\Gamma_{\overline{w}} < 0$ and $\Gamma_w > 0$. Then either :*
   - *(a) There is not coexistence stationary equilibrium. In that case, any solution of (3.7) converges to E_w for almost every initial condition.*
   - *(b) There exist two coexistence stationary equilibrium : one stable E_{cs} and one unstable E_{cu}. Any trajectory of (3.7) go either to E_{cs} or to E_w (for almost every initial condition) depending on the location of the initial value according to the basin of attraction of the two stable equilibria. The system is said to be in a bi-stable case.*

Remark 3.1.16. *When the consumption functions do depend on the vessels ε^j, the case where both E_u and E_v are stable can happen which is not the case if they do not depend on the vessel (proven in [Smith et Waltman, 1995]).*

3. with respect to the order $(a_1, b_1) \leq_K (a_2, b_2)$ iff $a_1 \leq a_2$ and $b_1 \geq b_2$, see [Smith et Waltman, 1995]).

The proof of this theorem relies on the construction of four functions called F_u, F_v and g_u, g_v on the quarter plane (R^1, R^2) and depending only on the parameters of the system. The different intersections of these functions fully describe the existence and stability of the stationary equilibria for (3.7) according to the following criteria :

— The coordinates (R^1_w, R^2_w) of the only intersection between F_w and g_w matches the resource concentration for the semi-trivial equilbrium E_w.

— If $R^2_w < F_{\overline{w}}(R^1_w)$ then E_w is asymptotically stable. If $R^2_w > F_{\overline{w}}(R^1_w)$ then E_w is linearly unstable.

— Any intersection between F_u and F_v located between the curves of g_u and g_v is associated to an admissible stationary equilibrium. There can be at most two intersections between F_u and F_v.

— If we sort the abscissa of the previous intersections, then the following rule gives the linear stability of their associated stationary equilibrium. Let E be a linearly stable equilibrium (resp. unstable) and note R^1_E the abscissa of its associated intersection. Then the equilibria associated to the closest abscissa to R^1_E are linearly unstable (resp. stable).

We show in figure 3.2 that every case may happen.

3.2 Mathematical study of the probabilistic model

3.2.1 Computation and study of the invasion rates

Recall that we defined the invasion rates in the probabilistic model by :

$$\Lambda_w = \int \left(f^1_w(R) - \delta^1\right) d\mu(R,1) + \int \left(f^2_w(R) - \delta^2\right) d\mu(R,2),$$

where μ is an invariant probability measure of the process (Z_t) on $M_{0,w}$. The sign of the invasion rates will be proven to give the asymptotic behaviour of the probabilistic system. Hence a thorough study of these quantities is needed which will be the case in this section.

3.2.1.1 Only one species is introduced

Assume that species $\overline{w}$ is not in the system ($\overline{W_t} = 0$). Then, the process $Z_t = (R_t, W_t, I_t)$ satisfies :

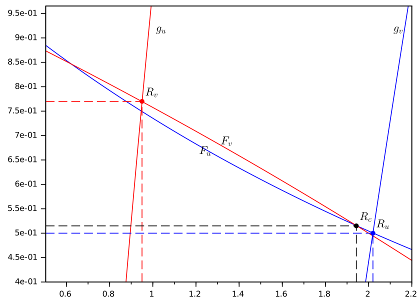
$$\begin{cases} \dot{R}_t = \delta^{I_t}(R^{I_t}_0 - R_t) - U_t f^{I_t}_u(R_t) \\ \dot{W}_t = W_t(f^{I_t}_w(R_t) - \delta^{I_t}) \end{cases} \tag{3.12}$$

In order to emphasize the fact that species $\overline{w}$ is absent of the system, let us define :

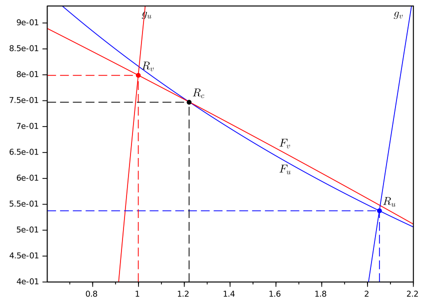
$$\Lambda^0_w = \int \left(f^1_w(R) - \delta^1\right) d\mu^0_w(R,1) + \int \left(f^2_w(R) - \delta^2\right) d\mu^0_w(R,2),$$

where μ^0_w is an invariant measure of the process (Z_t) restricted to $M_{0,w}$.

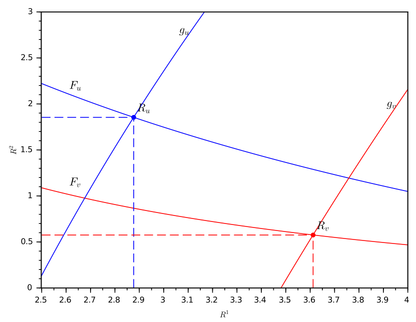
Theorem 3.2.1. *Let us assume that $R^1_0 < R^2_0$ and set $\gamma^j = \frac{\lambda^j}{\delta^j}$. The process (Z_t) has a unique invariant measure when it is restricted to $M_{0,w}$. The invasion rate of species w is* a - Typical coexistence case. R_c is associated to a globally stable coexistence stationary equilibrium.



b - Typical bi-stable case. R_c is associated to an unstable coexistence stationary equilibrium. E_u and E_v are stable.



c - Typical extinction case. Species u goes to extinction.



d - Rare bi-stable case. R_{cs} is associated to a stable equilibrium. R_{cu} is associated to an unstable equilibrium. E_u is stable, E_v is unstable.

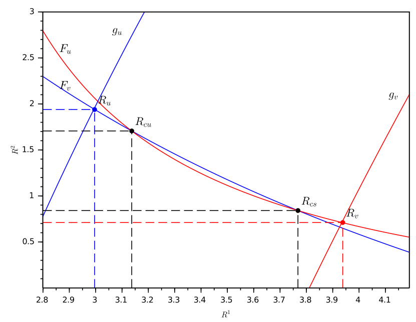


FIGURE 3.2 – The graph of the functions F_w and g_w, $w \in \{u, v\}$ are sufficient to describe the global dynamics of (3.7). The precise definition of the function F_w and g_w is given in section 3.3.

given by :

$$\Lambda_w^0 = \frac{\gamma^1+\gamma^2}{\lambda^1+\lambda^2}\mathbb{E}\left[\Phi(B)\right].$$

Where B is a random variable following a Beta law of parameters (γ^1,γ^2) and :

$$\Phi(x) = \delta^2(1-x)\left(f^1\left((R_0^2-R_0^1)x+R_0^1\right)-\delta^1\right)+\delta^1 x\left(f^2\left((R_0^2-R_0^1)x+R_0^1\right)-\delta^2\right).$$

Proof. Recall that only one species is introduced in our system. The invasion rate Λ_w^0 is defined by :

$$\Lambda_w^0 = \int \left(f_w^1(R)-\delta^1\right)d\mu_w^0(R,1)+\int\left(f_w^2(R)-\delta^2\right)d\mu_w^0(R,2)$$

where μ_w^0 is an invariant measure of the process (Z_t) restricted $M_{0,w}$. On $M_{0,w}$, $(Z_t) = (R_t,0)$ satisfies :

$$\dot{R}_t = \delta^{I_t}(R_0^{I_t}-R_t).$$

Its infinitesimal generator is given for any good functions f by :

$$Lf(r,i) = \delta^i(R_0^i-r)f'(r,i)+\lambda^1(f(r,\bar{i})-f(r,i)).$$

It is clear that for t large enough, (R_t) lives in $[R_0^1,R_0^2]$. By compacity, there exists an invariant measure for (R_t) and it is unique because the process is recurrent.

The unique invariant measure μ_w^0 satisfies :

$$\forall f\in\mathcal{C}([R_0^1,R_0^2]),\qquad \int Lf(r,i)d\mu_w^0 = 0. \tag{3.13}$$

We search μ_w^0 of the shape $\mu_w^0(dR,j) = \rho^j(R)\mathbb{1}_j dR$. It gives in 3.13 :

$$\begin{aligned}&\int_{R_0^1}^{R_0^2}\left(\delta^1(R_0^1-R)f'(R)+\lambda^1(f(R,2)-f(R,1))\right)\rho^1(R)dR+\\&\int_{R_0^1}^{R_0^2}\left(\delta^2(R_0^2-R)f'(R)+\lambda^2(f(R,1)-f(R,2))\right)\rho^2(R)dR=0.\end{aligned}\tag{3.14}$$

Assume that $f(x,j)=f(x)$. It gives in 3.14 :

$$\begin{aligned}&\int_{R_0^1}^{R_0^2}\left(\delta^1(R_0^1-R)f'(R)\right)\rho^1(R)dR+\\&\int_{R_0^1}^{R_0^2}\left(\delta^2(R_0^2-R)f'(R)\right)\rho^2(R)dR=0.\end{aligned}$$

An integration by parts gives :

$$\begin{aligned}&\left[\delta^1(R_0^1-R)f'(R)\rho^1(R)\right]_{R_0^1}^{R_0^2}+\left[\delta^2(R_0^2-R)f'(R)\rho^2(R)\right]_{R_0^1}^{R_0^2}\\&-\int_{R_0^1}^{R_0^2}f(x)\left((\delta^1(R_0^1-R)\rho^1(R))'+(\delta^2(R_0^2-R)\rho^2(R))'\right)dR=0.\end{aligned}$$

it seems "natural" that $\rho^j(R_0^{\bar{j}}) = 0$ according to the dynamics of the process (R_t, I_t). Assuming this, a classic density argument gives :

$$\delta^1(R_0^1 - R)\rho^1(R) + \delta^2(R^2 - R)\rho^2(R) = K.$$

And $K = 0$ since we assumed that $\rho^j(R_0^{\bar{j}}) = 0$ so :

$$\delta^1(R_0^1 - R)\rho^1(R) + \delta^2(R^2 - R)\rho^2(R) = 0. \tag{3.15}$$

Now, assume that $f(R,1) = f(R)$ et $f(R,2) = 0$. It gives in 3.14 :

$$\int_{R_0^1}^{R_0^2} \left(\delta^1(R_0^1 - R)f'(R) - \lambda^1 f(R)\right)\rho^1(R)dR + \int_{R_0^1}^{R_0^2} \lambda^2 f(R)\rho^2(R)dR = 0.$$

An integration by parts gives :

$$\int_{R_0^1}^{R_0^2} f(R)\left(-(\delta^1(R_0^1 - R)\rho^1(R))' - \lambda^1\rho^1(R) + \lambda^2\rho^2(R)\right)dR.$$

The same density argument as before gives :

$$-(\delta^1(R_0^1 - R)\rho^1(R))' - \lambda^1\rho^1(R) + \lambda^2\rho^2(R) = 0.$$

Hence :

$$-\delta^1(R_0^1 - R)\rho'^1(R) + \delta^1\rho^1(R) - \lambda^1\rho^1(R) + \lambda^2\rho^2(R) = 0.$$

Equation 3.15 gives :

$$\rho^2(R) = \frac{\delta^1(R - R_0^1)}{\delta^2(R^2 - R)}\rho^1(R).$$

As a consequence, ρ^1 satisfies the differential equation :

$$\rho'^1(R) + \rho^1(R)\left(\frac{1}{R - R_0^1} - \frac{\lambda^1}{\delta^1(R - R_0^1)} + \frac{\lambda^2}{\delta^2(R_0^2 - R)}\right) = 0. \tag{3.16}$$

Solving 3.16 gives the explicit expression for ρ^1 :

$$\rho^1(R) = C(R - R_0^1)^{\frac{\lambda^1}{\delta^1} - 1}(R_0^2 - R)^{\frac{\lambda^2}{\delta^2}}.$$

Hence,

$$\rho^2(R) = C\frac{\delta^1}{\delta^2}(R - R_0^1)^{\frac{\lambda^1}{\delta^1}}(R_0^2 - R)^{\frac{\lambda^2}{\delta^2} - 1},$$

where C is a constant. The value of C is determined by the fact that μ is a probability measure :

$$\int_{R_0^1}^{R_0^2} \rho^1(R)dR + \int_{R_0^1}^{R_0^2} \rho^2(R)dR = 1.$$

As a consequence :

$$C\int_{R_0^1}^{R_0^2}\left((R - R_0^1)^{\frac{\lambda^1}{\delta^1} - 1}(R_0^2 - R)^{\frac{\lambda^2}{\delta^2}} + \frac{\delta^1}{\delta^2}(R - R_0^1)^{\frac{\lambda^1}{\delta^1}}(R_0^2 - R)^{\frac{\lambda^2}{\delta^2} - 1}\right)dR = 1.$$

Now that μ_w^0 has an explicit expression we can compute Λ :

$$\begin{aligned}\Lambda = C\delta^2 \int_{R_0^1}^{R_0^2} (f_w^1(R) - \delta^1)(R - R_0^1)^{\frac{\lambda^1}{\delta^1}-1}(R_0^2 - R)^{\frac{\lambda^2}{\delta^2}} dR \\ + C\delta^1 \int_{R_0^1}^{R_0^2} (f_w^2(R) - \delta^2)(R - R_0^1)^{\frac{\lambda^1}{\delta^1}}(R_0^2 - R)^{\frac{\lambda^2}{\delta^2}-1} dR\end{aligned}$$

We do the variable change $x = \frac{R-R_0^1}{R_0^2-R_0^1}$. Set $\gamma^j = \frac{\lambda^j}{\delta^j}$ and $g_w^j(x) = f_w^j((R_0^2 - R_0^1)x + R_0^1)$:

$$\Lambda = C(R_0^2 - R_0^1)^{\gamma^1+\gamma^2} \int_0^1 \left[\delta^2(g_w^1(x) - \delta^1)(1-x) + \delta^1(g_w^2(x) - \delta^2)x\right] x^{\gamma^1-1}(1-x)^{\gamma^2-1}dx$$

One can recognize a part of the density of the Beta law of parameters (γ^1, γ^2). Using the same variable change for the expression of C and some classical properties of the beta function (like $B(x,y) = B(y,x)$ and $B(x, y+1) = \frac{y}{x+y}B(x,y)$), the expression of Λ becomes :

$$\Lambda = \frac{\gamma^1 + \gamma^2}{\lambda^1 + \lambda^2} \int_0^1 \left[\delta^2(g_w^1(x) - \delta^1)(1-x) + \delta^1(g_w^2(x) - \delta^2)x\right] \frac{x^{\gamma^1-1}(1-x)^{\gamma^2-1}}{B(\gamma^1, \gamma^2)}dx$$

Set $\Phi(x) = \delta^2(g_w^1(x) - \delta^1)(1-x) + \delta^1(g_w^2(x) - \delta^2)x$, then :

$$\Lambda_w^0 = \frac{\gamma^1 + \gamma^2}{\lambda^1 + \lambda^2}\mathbb{E}\left[\Phi(B)\right] \tag{3.17}$$

where B is a random variable following a Beta law of parameter (γ^1, γ^2). □

Remark 3.2.2. *If $R_0^1 = R_0^2 = R_0$ then one can easily check that (Δ_a is the Dirac measure on a) :*

$$d\mu_w^0(R, j) = (1-s)\Delta_{(R_0,1)} + s\Delta_{(R_0,2)}.$$

As a consequence, the invasion rate of the species is :

$$\Lambda_w^0 = (1-s)\left(f_w^1(R_0) - \delta^1\right) + s\left(f_w^2(R_0) - \delta^2\right).$$

Our expression of the invasion rate is similar to the one obtained in [Malrieu et Zitt, 2016] for the invasion rates defined in the Lotka-Volterra switching system introduced in the article [Benaïm et Lobry, 2016]. In order to study the invasion rate they use the following property :

Proposition 3.2.3. *(Convex order between Beta laws). Assume that X and X' are two random variables following Beta laws of parameters (a, b) and (a', b'). If $a < a'$, $b < b'$ and $\frac{a}{a+b} = \frac{a'}{a'+b'}$ then for any convex function ϕ :*

$$\mathbb{E}[\phi(X')] \leq \mathbb{E}[\phi(X)].$$

Proposition 3.2.4. *The invasion rate Λ_w^0 is monotonous acording to the variable λ.*

Proof. We proved that :

$$\Lambda_w^0 = \frac{\gamma^1+\gamma^2}{\lambda^1+\lambda^2}\mathbb{E}\left[\Phi(B)\right].$$

Recall that $\gamma^1(s,\lambda) = \frac{s\lambda}{\delta^1}$ and $\gamma^2(s,\lambda) = \frac{(1-s)\lambda}{\delta^2}$. It comes that :

$$\gamma^1+\gamma^2 = \lambda\left(\frac{s}{\delta^1}+\frac{1-s}{\delta^2}\right).$$

Hence, property 3.2.3 ensures that if B and B' are random variables following Beta laws of parameters $(\gamma^1(s,\lambda),\gamma^2(s,\lambda))$ and $(\gamma^1(s,\lambda'),\gamma^2(s,\lambda'))$ with $\lambda<\lambda'$ then for any convex function ϕ :

$$\mathbb{E}[\phi(B')] \leq \mathbb{E}[\phi(B)].$$

As a consequence, establishing the convexity (or concavity) of the function Φ can give the monotonicity of Λ according to the global switching rate λ.

Recall that :

$$\Phi(x) = \delta^2(1-x)\left(f_w^1\left((R_0^2-R_0^1)x+R_0^1\right)-\delta^1\right)+\delta^1 x\left(f_w^2\left((R_0^2-R_0^1)x+R_0^1\right)-\delta^2\right).$$

Here the convexity (or concavity) of Φ is not clear and will be checked by straight computation. Set $\alpha^j = \frac{a_w^j}{\delta^j}$, $\beta^j = \frac{b_w^j}{R_0^2-R_0^1}$ and $r = \frac{R_0^1}{R_0^2-R_0^1}$. It comes :

$$\Phi(x) = \delta^1\delta^2\left((1-x)\left(\frac{\alpha^1(x+r)}{\beta^1+x+r}-1\right)+x\left(\frac{\alpha^2(x+r)}{\beta^2+x+r}-1\right)\right).$$

Set $t=x+r$ ($t\in[r,1+r]$). It comes :

$$g(t) = \frac{\Phi(t)}{\delta^1\delta^2} = (1+r-t)\left(\frac{\alpha^1 t}{\beta^1+t}-1\right)+(t-r)\left(\frac{\alpha^2 t}{\beta^2+t}-1\right).$$

A straight forward computation gives the derivatives of g :

$$g'(t) = (1+r-t)\frac{\alpha^1\beta^1}{(t+\beta^1)^2}-\frac{\alpha^1 t}{\beta^1+t}+(t-r)\frac{\alpha^2\beta^2}{(t+\beta^2)^2}+\frac{\alpha^2 t}{\beta^2+t}$$

and

$$\frac{g''(t)}{2} = \frac{-\alpha^1\beta^1(1+r+\beta^1)(t+\beta^1)^3+\alpha^2\beta^2(r+\beta^2)(t+\beta^1)^3}{(t+\beta^1)^3(t+\beta^2)^3}.$$

Set $L^1=\alpha^1\beta^1(1+r+\beta^1)$ and $L^2=\alpha^2\beta^2$. It comes :

$$\begin{aligned}h(t) &= \frac{g''(t)}{2}(t+\beta^1)^3(t+\beta^2)^3\\ &= (L^2-L^1)t^3+3\left(\beta^1L^2-\beta^2L^1\right)t^2+3\left((\beta^1)^2L^2-(\beta^2)^2L^1\right)t+(\beta^1)^3L^2-(\beta^2)^3L^1.\end{aligned}$$

Set $L=\frac{L^2}{L^1}$ and $\beta=\frac{\beta^1}{\beta^2}$, it comes :

$$h(t) = (\beta^2)^3\left((L-1)\left(\frac{t}{\beta}\right)^3+3(L\beta-1)\left(\frac{t}{\beta}\right)^2+3(L(\beta)^2-1)\left(\frac{t}{\beta}\right)+L(\beta)^3-1\right).$$

The study of the polynomial $P=(L-1)X^3+3(L\beta-1)X^2+3(L(\beta)^2-1)X+L(\beta)^3-1$ will give the sign of the second derivative of Φ.

Lemma 3.2.5. *P has a unique root on $\mathbb{R}$ and its expression is :*

$$X_0 = \left|\frac{\beta-1}{L-1}\right| \left(-L^{\frac{1}{3}} - L^{\frac{2}{3}}\right) - \frac{L\beta-1}{L-1}.$$

Moreover, $X_0 < 0$.

Proof. The existence and expression of X_0 is obtained by a straight forward computation using the classical method of resolution for third degrees polynomial equations.

We study the sign of X_0 by reviewing the different cases. One can check that :

$$X_0 = \left|\frac{\beta-1}{L-1}\right| \left(-L^{\frac{1}{3}} - L^{\frac{2}{3}}\right) - L\frac{\beta-1}{L-1} - 1.$$

If $L > 1$ and $\beta > 1$, $X_0 = \frac{\beta-1}{L-1}\left(-L^{\frac{1}{3}} - L^{\frac{2}{3}} - L\right) - 1 < 0$.

If $L < 1$ and $\beta < 1$, $X_0 = \frac{1-\beta}{1-L}\left(-L^{\frac{1}{3}} - L^{\frac{2}{3}} - L\right) - 1 < 0$.

If $L > 1$ and $\beta < 1$, $X_0 = \frac{1-\beta}{L-1}\left(-L^{\frac{1}{3}} - L^{\frac{2}{3}} + L\right) - 1 = (1-\beta)f(L) - 1$. One can check that for all $L > 1$, $f(L) < 1$ implying that $X_0 < -\beta < 0$.

If $L < 1$ and $\beta > 1$, $X_0 = \frac{\beta-1}{1-L}\left(-L^{\frac{1}{3}} - L^{\frac{2}{3}} + L\right) - 1 = (\beta-1)f(L) - 1$. One can check that for all $0 < L < 1$, $f(L) < 0$ implying that $X_0 < -1 < 0$. □

It comes from this previous lemma that the second derivative of Φ has a constant sign on $[0,1]$ implying that Φ is either convex or concave on $[0,1]$. So Λ_w^0 is monotonous according to 3.2.3. □

In Section 4, we will compare the behavior of the probabilistic definition of the invasion rate with the deterministic one. In order to have a discussion on the limits of these quantities, we compute here the limits of Λ_w^0.

Proposition 3.2.6. *The following limits are computable :*

$$\lim_{\lambda\to+\infty} \Lambda_w^0 = (1-s)\left(f_w^1(R^\infty) - \delta^1\right) + s\left(f_w^2(R^\infty) - \delta^2\right).$$

where $R^\infty = \frac{(1-s)\delta^1 R_0^1 + s\delta^2 R_0^2}{(1-s)\delta^1 + s\delta^2}$.

Moreover :

$$\lim_{\lambda\to 0} \Lambda_w^0 = (1-s)\left(f_w^1(R_0^1) - \delta^1\right) + s\left(f_w^2(R_0^2) - \delta^2\right).$$

Proof. Recall that we obtained an expression of Λ_w^0 depending on a Beta law :

$$\Lambda_w^0 = \frac{\gamma^1+\gamma^2}{\lambda^1+\lambda^2}\mathbb{E}\left[\Phi(B)\right]$$

where B is a Beta law of paramaters (γ^1, γ^2).

To obtain the limits of Λ_w^0, one has to recall that a Beta law of parameters $(ut,(1-u)t)$ converges in law to :

$$\begin{cases} (1-u)\Delta_0 + u\Delta_1 \text{ when } t \to 0 \\ \delta_u \text{ when } t \to +\infty \end{cases} \tag{3.18}$$

The announced limits immediatly come from this statement. □

Remark 3.2.7. *Let us note ε_s the averaging of the two chemostats ε^1 and ε^2. Formally $\varepsilon_s = (1-s)\varepsilon^1 + s\varepsilon^2$. The associated differential equation modelizing the behavior of the different concentrations in ε_s is given by :*

$$\begin{cases} \dot{R} = \overline{\delta}(\overline{R_0} - R) - U\overline{f_w}(R) \\ \dot{U} = U(\overline{f_w}(R) - \overline{\delta}). \end{cases} \tag{3.19}$$

Where $\overline{\delta} = (1-s)\delta^1 + s\delta^2$, $\overline{f_w} = (1-s)f_w^1 + sf_w^2$ and :

$$\overline{R_0} = \frac{(1-s)\delta^1 R_0^1 + s\delta^2 R_0^2}{\overline{\delta}}.$$

According to theorem 3.1.1, species w survives in ε_s if and only if $\overline{f_w}(\overline{R_0}) - \overline{\delta} > 0$. And it is easy to check that $\lim\limits_{\lambda \to +\infty} \Lambda_w^0 = \overline{f_w}(\overline{R_0}) - \overline{\delta}$.

Remark 3.2.8. *The fact that the limit of Λ_w^0 matches the condition given in theorem 3.1.1 is not an accident. Indeed, it is a known fact that the law of the solutions of a randomly switched differential equation converges towards the law of solutions of the averaging of these differential equations when the switching rate goes to infinity. One can check [Strickler et Benaïm, 2017] (Lemma 2.13) for a clean proof of this statement.*

3.2.1.2 Two species are introduced

Since we assume that $R_0^1 = R_0^2 = R_0$, according to remark 3.1.2, the quantity $\Sigma_t = R_t + U_t + V_t$ goes exponentially to R_0. As a consequence, for t large enough, the marginal law of (U_t, V_t, I_t) of the process $(Z_t) = (R_t, U_t, V_t, I_t)$ matches the law of the process $(\widetilde{Z}_t) = (U_t, V_t, I_t)$ solution of the following differential system :

$$\begin{cases} \dot{U}_t = U_t(f_u^{I_t}(R_0 - U_t - V_t) - \delta^{I_t}) \\ \dot{V}_t = V_t(f_v^{I_t}(R_0 - U_t - V_t) - \delta^{I_t}) \end{cases} \tag{3.20}$$

The process $(\widetilde{Z}_t)$ evolves on the space $\widetilde{M} = \{(u,v,i) \in \mathbb{R}_+^2 \times \{1,2\} \mid \exists r,\ (r,u,v,i) \in M\}$.

We will also assume that the two species u and v can enter in competition in each vessel ε^1 and ε^2. Mathematically, this assumption means that for all $w \in \{u,v\}$ and for all $j \in \{1,2\}$, the equation $f_w^j(r) = \delta^j$ has a unique positive solution noted R_w^j, and moreover $R_w^j < R_0^j$.

Theorem 3.2.9. *The invariant measure μ_w of $(\widetilde{Z}_t)$ restricted to $\widetilde{M}_{0,w}$ is unique. The invasion rates Λ_u and Λ_v are computable and their explicit expressions is given by :*

$$\Lambda_w = \frac{\int h_w(x) g_{\overline{w}}(x) e^{\lambda H_{\overline{w}}(x)} dx}{\int g_{\overline{w}}(x) e^{\lambda H_{\overline{w}}(x)} dx}.$$

Where :

$$h_w(x) = \frac{(f_w^2(R_0-x)-\delta^2)|f_{\overline{w}}^1(R_0-x)-\delta^1| + (f_w^1(R_0-x)-\delta^1)|f_{\overline{w}}^2(R_0-x)-\delta^2|}{|f_{\overline{w}}^1(R_0-x)-\delta^1| + |f_{\overline{w}}^2(R_0-x)-\delta^2|}$$

$$g_w(x) = \left(|f_w^1(R_0-x)-\delta^1| + |f_w^2(R_0-x)-\delta^2|\right) \frac{|f_w^1(R_0-x)-\delta^1||f_w^2(R_0-x)-\delta^2|}{x}$$

and

$$\begin{aligned} H_w(x) = &-(\omega_w^1\beta_w^1 + \omega_w^2\beta_w^2)\log(x) + \omega_w^1\alpha_w^1 \log\left((b_w^1 + R_0 - x)|f_w^1(R_0-x)-\delta^1|\right) \\ &+ \omega_w^2\alpha_w^2 \log\left((b_w^2 + R_0 - x)|f_w^2(R_0-x)-\delta^2|\right). \end{aligned}$$

The constants are defined by :

$$\begin{aligned} R_w^j &= \frac{b_w^j\delta^j}{a_w^j - \delta^j}, \\ \gamma_w^j &= \frac{\lambda^j}{\delta^j}\frac{R_w^j}{R_0 - R_w^j}, \\ \omega_w^1 &= \frac{s}{\delta^1}\frac{R_w^1}{R_0 - R_w^1}, \quad \omega_w^2 = \frac{1-s}{\delta^2}\frac{R_w^2}{R_0 - R_w^2}, \\ \alpha_w^j &= \frac{a_w^j}{a_w^j - \delta^j}, \\ \beta_w^j &= 1 + \frac{R_0}{b_w^j}. \end{aligned}$$

Proof. We will show how to compute Λ_v. The expression of Λ_u will come by interverting the species subscripts. The strategy of the proof is globally the same as in the case where only one species is introduced in the system. According to 3.20 :

$$\Lambda_v = \int \left(f_v^1(R_0 - U) - \delta^1\right) d\mu(U,1) + \int \left(f_v^2(R_0 - U) - \delta^2\right) d\mu(U,2).$$

Where μ is the invariant measure of the process (U_t, V_t, I_t) when $V_t = 0$ (where the unicity of μ comes from the previous one species case). Since $V_t = 0$, the process (U_t, I_t) is solution of the differential equation system :

$$\dot{U}_t = U_t(f_u^{I_t}(R_0 - U_t) - \delta^{I_t}). \tag{3.21}$$

The process (U_t, I_t) is a piecewise deterministic Markov process. Recall that R_u^j satisfies $f_u^j(R_u^j) - \delta^j = 0$. Set $U^j = R_0 - R_w^j$ and assume that $U^1 < U^2$. Since the functions f_u^j are growing, we can assume without loss of generality that the process (U_t, I_t) evolves on the state space $[U^1, U^2] \times \{0, 1\}$. Its infinitesimal generator is :

$$Lf(u,j) = u\left(f_u^j(R_0 - u) - \delta^j\right)\frac{\partial f}{\partial u}(u,j) + \lambda^j\left(f(u,\overline{j}) - f(u,j)\right).$$

The unique invariant measure μ of the process (U_t, I_t) satisfies :

$$\int Lf(U,j)\mu(dU,j) = 0. \tag{3.22}$$

Lemma 3.2.10. *The invariant measure is given by :*

$$\mu(dU, j) = \rho^j(U)\mathbb{1}_j dU$$

where :

$$\rho^1(U) = C\frac{(b_u^1 + R_0 - U)^{\gamma^1\alpha^1}(b_u^2 + R_0 - U)^{\gamma^2\alpha^2}}{U^{\gamma^1\beta^1+\gamma^2\beta^2+1}}|f_u^1(R_0-U)-\delta^1|^{\gamma^1\alpha^1-1}|f_u^2(R_0-U)-\delta^2|^{\gamma^2\alpha^2}$$

and

$$\rho^2(U) = C\frac{(b_u^1 + R_0 - U)^{\gamma^1\alpha^1}(b_u^2 + R_0 - U)^{\gamma^2\alpha^2}}{U^{\gamma^1\beta^1+\gamma^2\beta^2+1}}|f_u^1(R_0-U)-\delta^1|^{\gamma^1\alpha^1}|f_u^2(R_0-U)-\delta^2|^{\gamma^2\alpha^2-1}.$$

C is the normalization constant and :

$$\begin{aligned}\gamma^j &= \frac{\lambda^j}{\delta^j}\frac{R_u^j}{R_0 - R_u^j},\\ \alpha^j &= \frac{a_u^j}{a_u^j - \delta^j},\\ \beta^j &= 1 + \frac{R_0}{b_u^j}.\end{aligned}$$

The proof of this lemma is similar to the one for the case where only one species is introduced in the system except that the computation is slightly more dense. We define the following functions for $U \in (U^1, U^2)$:

$$g(U) = \left(|f_u^1(R_0 - U) - \delta^1| + |f_u^2(R_0 - U) - \delta^2|\right)\frac{|f_u^1(R_0 - U) - \delta^1||f_u^2(R_0 - U) - \delta^2|}{U}$$

$$\begin{aligned}H(U) = &-(\omega^1\beta^1 + \omega^2\beta^2)\log(U) + \omega^1\alpha^1\log\left((b_u^1 + R_0 - U)|f_u^1(R_0 - U) - \delta^1|\right)\\ &+ \omega^2\alpha^2\log\left((b_u^2 + R_0 - U)|f_u^2(R_0 - U) - \delta^2|\right)\end{aligned}$$

where :

$$\omega^1 = \frac{s}{\delta^j}\frac{R_u^1}{R_0 - R_u^1} \quad \omega^2 = \frac{1-s}{\delta^2}\frac{R_u^2}{R_0 - R_u^2}.$$

One can check that the normalization constant C can be written :

$$C = \frac{1}{\int_{U^1}^{U^2} g(U)e^{\lambda H(U)}dU}.$$

Moreover, if we define :

$$h(U) = \frac{(f_v^2(R_0 - U) - \delta^2)|f_u^1(R_0 - U) - \delta^1| + (f_v^1(R_0 - U) - \delta^1)|f_u^2(R_0 - U) - \delta^2|}{|f_u^1(R_0 - U) - \delta^1| + |f_u^2(R_0 - U) - \delta^2|}$$

We obtain the claimed expression for Λ_v :

$$\Lambda_v = \frac{\int_{U^1}^{U^2} h(U)g(U)e^{\lambda H(U)}dU}{\int_{U^1}^{U^2} g(U)e^{\lambda H(U)}dU}.$$

□

Once again we compute the limits of Λ_w.

Proposition 3.2.11. *The following limits are computable :*

$$\lim_{\lambda\to+\infty} \Lambda_w = (1-s)\left(f_w^1(R_w^\infty) - \delta^1\right) + s\left(f_w^2(R_w^\infty) - \delta^2\right)$$

where R_w^∞ is the unique positive solution of the equation :

$$(1-s)\left(f_{\overline{w}}^1(R) - \delta^1\right) + s\left(f_{\overline{w}}^2(R) - \delta^2\right) = 0.$$

Moreover :

$$\lim_{\lambda\to 0} \Lambda_w = (1-w)\left(f_w^1(R_{\overline{w}}^1) - \delta^1\right) + s\left(f_w^2(R_{\overline{w}}^2) - \delta^2\right).$$

where

$$R_w^j = \frac{b_w^j \delta^j}{a_w^j - \delta^j} \text{ is the solution of the equation } f_w^j(R) - \delta^j = 0.$$

Proof. The limit in $+\infty$ is again a consequence of the averaging phenomenon proved in [Strickler et Benaïm, 2017]. However, before taking notice of this strong result, we gave a pure computational proof of this limit which we give now.

Set $w = v$ and let us show that :

$$\lim_{\lambda\to+\infty} \Lambda_v = (1-s)\left(f_v^1(R_v^\infty) - \delta^1\right) + s\left(f_v^2(R_v^\infty) - \delta^2\right).$$

with R_v^∞ unique positive solution of :

$$(1-s)\left(f_u^1(R) - \delta^1\right) + s\left(f_u^2(R) - \delta^2\right) = 0.$$

The proof for Λ_u is the same after changing the subscripts. Recall the shape of the expression for Λ_v :

$$\Lambda_v = \frac{\int h_v(U) g_u(U) e^{\lambda H_u(U)} dU}{\int g_u(U) e^{\lambda H_u(U)} dU}.$$

A classic convergence result gives that if the function H_u admits a unique maximum on the integration domain,

$$\Lambda_v \underset{\lambda\to+\infty}{\longrightarrow} h_v(\arg\max(H_1)).$$

As a consequence we have to study the function H_u on the interval (U^1, U^2). Recall that :

$$\begin{aligned} H_u(U) = &-(\omega^1\beta^1 + \omega^2\beta^2)\log(U) + \omega^1\alpha^1 \log\left((b_u^1 + R_0 - U)|f_u^1(R_0 - U) - \delta^1|\right) \\ &+ \omega^2\alpha^2 \log\left((b_u^2 + R_0 - U)|f_u^2(R_0 - U) - \delta^2|\right) \end{aligned}$$

with :

$$\begin{aligned} \omega^1 &= \frac{s}{\delta^1}\frac{R_u^1}{R_0 - R_u^1}, \quad \omega^2 = \frac{1-s}{\delta^2}\frac{R_u^2}{R_0 - R_u^2}, \\ \alpha^j &= \frac{a_u^j}{a_u^j - \delta^j}, \\ \beta^j &= 1 + \frac{R_0}{b_u^j}. \end{aligned}$$

One can check that H_u can be written :

$$\begin{aligned} H_u(U) &= -(\omega_u^1\beta_u^1 + \omega_u^2\beta_u^2)\log(U) + \omega_u^1\alpha_u^1 \log\left((a_u^1-\delta^1)|R_0 - U - R_u^1|\right) \\ &+ \omega_u^2\alpha_u^2 \log\left((a_u^2-\delta^2)|R_0 - U - R_u^2|\right). \end{aligned}$$

Since $R = R_0 - U$,

$$\begin{aligned} H_u(R) &= -(\omega_u^1\beta_u^1 + \omega_u^2\beta_u^2)\log(R_0 - R) + \omega_u^1\alpha_u^1 \log\left((a_u^1-\delta^1)|R - R_u^1|\right) \\ &+ \omega_u^2\alpha_u^2 \log\left((a_u^2-\delta^2)|R - R_u^2|\right). \end{aligned}$$

Hence :

$$\begin{aligned} H_u'(R) &= \frac{\omega_u^1\beta_u^1 + \omega_u^2\beta_u^2}{R_0 - R} + \frac{\omega_u^1\alpha_u^1}{R - R_u^1} + \frac{\omega_u^2\alpha_u^2}{R - R_u^2} \\ &= \frac{\omega_u^1\beta_u^1}{R_0 - R} + \frac{\omega_u^1\alpha_u^1}{R - R_u^1} + \frac{\omega_u^2\beta_u^2}{R_0 - R} + \frac{\omega_u^2\alpha_u^2}{R - R_u^2}. \end{aligned}$$

A straightforward (but tricky) computation using the expressions for the constants ω_w^j, α_w^j and β_w^j shows that :

$$H_u'(R) = \frac{1}{(R_0 - R)}\left(\frac{s}{f_u^1(R) - \delta^1} + \frac{1-s}{f_u^2(R) - \delta^2}\right).$$

As a consequence :

$$\begin{aligned} H_u'(R) = 0 \text{ on the interval } [R_u^1, R_u^2] &\iff (1-s)(f_u^1(R) - \delta^1) = -s(f_u^2(R) + \delta^2) \\ &\iff (1-s)\left(f_u^1(R) - \delta^1\right) + s\left(f_u^2(R) - \delta^2\right) = 0 \\ &\iff R = R_v^\infty. \end{aligned}$$

Recall that :

$$h_v(U) = \frac{(f_v^2(R_0 - U) - \delta^2)|f_u^1(R_0 - U) - \delta^1| + (f_v^1(R_0 - U) - \delta^1)|f_u^2(R_0 - U) - \delta^2|}{|f_u^1(R_0 - U) - \delta^1| + |f_u^2(R_0 - U) - \delta^2|}.$$

It comes $h_v(R_0 - R_v^\infty) = (1-s)\left(f_v^1(R_v^\infty) - \delta^1\right) + s\left(f_v^2(R_v^\infty) - \delta^2\right)$.

□

3.2.2 Study of the long time behavior

We give in this subsection the idea of the proof of the theorems giving the long time behavior of the switched processes. The development of these proofs follow the same path as the one in the article [Benaïm et Lobry, 2016] and uses both the analytical properties of the invasion rates given in 3.2 and the following lemma 3.2.12.

Recall that the process $(Z_t) = (R_t, U_t, V_t, I_t)$ is defined by the following differential system :

$$\begin{cases} \dot{R}_t = \delta^{I_t}(R_0^{I_t} - R_t) - U_t f_u^{I_t}(R_t) - V_t f_v^{I_t}(R_t) \\ \dot{U}_t = U_t(f_u^{I_t}(R_t) - \delta^{I_t}) \\ \dot{V}_t = V_t(f_v^{I_t}(R_t) - \delta^{I_t}) \end{cases} \tag{3.23}$$

where (I_t) is a continuous time Markov chain on the state space $\{1,2\}$ and jump rates $\lambda^1 = s\lambda$, $\lambda^2 = (1-s)\lambda$ with $s \in (0,1)$ and $\lambda > 0$. The process (Z_t) evolves in a compact space M defined by :

$$M = K \times \{1,2\},$$

where

$$K = \{(r,u,v) \in \mathbb{R}_+^3 \ , \quad \frac{\min(R_0^1, R_0^2)}{2} \leq r + u + v \leq 2\max(R_0^1, R_0^2)\}.$$

We define the invasion rate of species $w \in \{u,v\}$ by :

$$\Lambda_w = \int \left(f_w^1(R) - \delta^1\right) d\mu(R,1) + \int \left(f_w^2(R) - \delta^2\right) d\mu(R,2),$$

where μ is an invariant measure of (Z_t) restricted to $M_{0,w}$.

Lemma 3.2.12. *Assume that $|\Lambda_w| > \alpha_w > 0$, then it exists $T_w > 0$, $\theta_w > 0$, $\varepsilon_w > 0$ and $0 \leq \rho_w < 1$ such that : $\forall z = (r,u,v,i) \in M_{0,w}^{\varepsilon} = \{(r,u,v,i) \in M, 0 < w \leq \varepsilon\}$,*

$$(i) \quad \frac{P_{T_w}F_w(z) - F_w(z)}{T_w} \leq -\alpha_w$$

$$(ii) \quad P_{T_w}(e^{\theta_w F})(z) \leq \rho_w e^{\theta_w F_w(z)}$$

where $F_w(z) = -sign(\Lambda_w)\log(w)$.

Proof. This proof is taken from [Benaïm et Lobry, 2016]. Let $w \in \{u,v\}$ and let W_t be the concentration of species w at time t. Assume that $\Lambda_w < -\alpha_w < 0$ (the proof is the same if $\Lambda_w > \alpha_w > 0$).

(*i*) $\forall Z_0 = z = (r,u,v,i) \in M$ with $w \neq 0$ on a :

$$\frac{\dot{W}_t}{W_t} = f_w^{I_t}(R_t) - \delta^{I_t}.$$

Hence :

$$F_w(Z_t) - F_w(z) = \int_0^t H(Z_s)ds, \tag{3.24}$$

where $H(r,u,v,i) = f_w^i(r) - \delta^i$.

Set $T > 0$. Taking the expectation of the previous equation and dividing by T leads to :

$$\frac{P_T F_w(z) - F_w(z)}{T} = \frac{1}{T}\int_0^T P_s H(z)ds.$$

Define $\mu_T^z(.) = \frac{1}{T}\int_0^T P_s(z,.)ds$, it comes :

$$\frac{P_T F_w(z) - F_w(z)}{T} = \int H d\mu_T^z.$$

This quantity is continuous according to z (by Feller continuity), as consequence it is enough to prove the announced inequality for $z \in M_{0,w}$ and show the existence of T_w and ε_w by continuity. The set $\{\mu_T^z\}$ (indexed by $z \in M_{0,w}$) is a compact set of measures. Any sub sequence of this set goes to the invariant measure of (Z_t) restricted to $M_{0,w}$ noted μ. As a consequence :

$$\lim_{T\to+\infty}\int H d\mu_T^z = \int H d\mu = \Lambda < -\alpha,$$

which proves inequality (i).

(ii) In 3.24, we apply the function $w \mapsto e^{\theta w}$ and it comes that :

$$e^{\theta F_w(Z_t)}e^{-\theta F_w(z)} = e^{\theta\int_0^t H(Z_s)ds}.$$

Taking the expectation leads to :

$$P_T(e^{\theta F_w})(z) = e^{\theta F_w(z)}e^{l(\theta,z)},$$

where $l(\theta,z) = \log\left(\mathbb{E}_z(e^{\theta\int_0^T H(Z_s)ds})\right)$.

Note that $\theta \mapsto l(\theta,z)$ is the logarithm of a laplace transformation. Hence, it is continuous, convex and satisfies :

$$l(0,z) = 0$$

and,

$$\frac{\partial l}{\partial\theta}(0,z) = \mathbb{E}_z\left(\int_0^T H(Z_s)ds\right) = P_T F_w(z) - F_w(z)$$

and finally,

$$0 \le \frac{\partial^2 l}{\partial^2\theta}(0,z) \le \mathbb{E}_z\left((\int_0^T H(Z_s)ds)^2\right) \le (T\|H\|_\infty)^2$$

where $\|H\|_\infty = \sup_{z\in M}|H(z)|$. Hence, thanks to Taylor-Lagrange inequality and the inequality (i) it comes that $\forall z = (r,u,v,i) \in M_{0,w}^\varepsilon$:

$$l(\theta,z) \le T\theta(-\alpha + \|H\|_\infty^2 T\frac{\theta}{2}),$$

which proves (ii) if we take $\theta_w = \frac{\alpha_w}{T_w\|H\|_\infty^2}$ and $\rho_w = \frac{-\alpha_w}{2\|H\|_\infty^2}$. ☐

3.2.2.1 Long time behavior when only one species in introduced

Assume that only species w is introduced in the system. The following theorem gives the long-time behavior of the process (Z_t) according to the sign of the invasion rate Λ_w^0.

Theorem 3.2.13. *The sign of the invasion rate Λ_w^0 characterizes the evolution of the species w :*

1. *If $\Lambda_w^0 < 0$ species w goes to extinction : $W_t \to 0$ almost surely.*
2. *If $\Lambda_w^0 > 0$ species w perpetuates.*

Proof. (i) If $\Lambda_w^0 > 0$, then according to [Strickler et Benaïm, 2017], the process is stochastically persistent implying that the species w do not disappear from the environment. (ii) Assume now that $\Lambda_w^0 < 0$. We want to prove that W_t goes to zero almost surely.

Recall that lemma 3.2.12 defines a function F_w, and the constants α_w, ε_w, θ_w, ρ_w and T_w. In all the proof, we will ignore the subscripts for the sake of simplicity. The proof is divided in three steps :

— First we prove that starting from any point of M, there is a positive probability such that (Z_t) enters $M_{0,w}^{\varepsilon/2}$.

— Note $\mathcal{A} = \{\limsup_{t \longrightarrow +\infty} \frac{F(Z_t)}{t} \leq -\alpha\}$. We prove that for any $z \in M_{0,w}^{\varepsilon_w/2}$, $\mathbb{P}_z(\mathcal{A}) \geq c_1 > 0$.

— Finally we show that $\mathbb{P}_z(\mathcal{A}) = 1$ which implies that W_t goes to zero almost surely.

In all the proof we consider the process $(Z_t) = (R_t, U_t, V_t, I_t)$ in order to treat the case where w is any of the species u or v. But recall that we assume that species $\overline{w}$ is not in the system. So $\overline{W_t} = 0$.

Step one. Let us show that for any $z \in M$:

$$\exists c > 0, \quad \mathbb{P}_z(\tau_{\varepsilon/2}^{in} < +\infty) \geq c,$$

where $\tau_{\varepsilon/2}^{in} = \min\{k \in \mathbb{N}, Z_{kT} \in M_{0,w}^{\varepsilon/2}\}$ and T, ε are defined in lemma 3.2.12. To prove this statement we need to be able to build a deterministic trajectory for (Z_t) (we pick manually the jumping times) such that (Z_n) is in $M_{0,w}^{\varepsilon/2}$ for any initial condition $z \in M$ and n large enough.

There are two cases : If the environment $i \in \{1, 2\}$ is unfavorable to species w, then if (Z_t) follows for enough time the dynamics of ε^i, then (Z_t) will land on $M_{0,w}^{\varepsilon/2}$ for any z.

Hence, by compacity there exists an integer k_0 such that :

$$\forall z \in M, \ \forall k \geq k_0, \quad \Phi_{kT}^{\varepsilon^i}(r, u, v) \in \{(r, u, v) \in \mathbb{R}_+^2, w < \frac{\varepsilon}{2}\},$$

where Φ^{ε^i} is the flow of the chemostat ε^i. As a consequence, for all $z \in M$,

$$\mathbb{P}(Z_{k_0T} \in M_{0,w}^{\varepsilon/2}) \geq \mathbb{P}(\forall t \leq k_0T, \quad I_t = i | I_0 = i) = e^{-\lambda^i k_0 T} \geq c > 0$$

which is what we wanted to prove.

In the other hand, if both environments are favorable to species w, then we use the monotonicity of Λ_w^0 to make the following statement. Since the two environments are favorable to species w, $\Lambda_w^0(\lambda = 0) > 0$. Moreover Λ_w^0 is monotonous according to λ and $\Lambda_w^0 < 0$. It comes that $\lim_{\lambda \to +\infty} \Lambda_w^0 < 0$. Hence according to remark 3.2.8, the average chemostat ε_s is unfavorable to species w.

As a consequence, by compacity, there exists an integer k_0 such that :

$$\forall z \in M, \ \forall k \geq k_0, \quad \Phi_{kT}^{\varepsilon_s}(r, u, v) \in \{(r, u, v) \in \mathbb{R}_+^2, w < \frac{\varepsilon}{2}\},$$

where Φ^{ε_s} is the flow of the average chemostat ε_s defined in 3.2.8.

Let us show that there exists a constant $c > 0$ such that :

$$\forall z \in M, \quad \mathbb{P}_z(Z_{k_0T} \in M_{0,w}^{\varepsilon/2}) \geq c.$$

Assume that this is not the case :

$$\forall c > 0, \ \exists z \in M, \quad \mathbb{P}_z(Z_{k_0T} \in M_{0,w}^{\varepsilon/2}) < c.$$

By taking $c = \frac{1}{n}$, we build a sequence (z_n) of M such that :

$$\mathbb{P}_{z_n}(Z_{k_0T} \in M_{0,w}^{\varepsilon/2}) \underset{+\infty}{\longrightarrow} 0.$$

The set M is compact, as a consequence, it exists a sub-sequence (z_m) of (z_n) converging towards a limit $z^* = (r^*, u^*, v^*, i^*)$ in M. According to Feller continuity, for any continuous function f :

$$\mathbb{E}(f(Z_{k_0T}|Z_0 = z_m) \to \mathbb{E}(f(Z_{k_0T}|Z_0 = z^*).$$

The law of Z_{k_0T} starting from z_m converges towards the law of Z_{k_0T} starting from z^*. The Portmanteau's theorem implies that :

$$\liminf_m \mathbb{P}_{z_m}(Z_{k_0T} \in M_{0,w}^{\varepsilon/2}) \geq \mathbb{P}_{z^*}(Z_{k_0T} \in M_{0,w}^{\varepsilon/2}).$$

Hence :

$$\mathbb{P}_{z^*}(Z_{k_0T} \in M_{0,w}^{\varepsilon/2}) = 0.$$

However, the set $\{\Phi_t^{\varepsilon_s}(r^*, u^*, v^*), t > 0\} \times \{1, 2\}$ is in the topological support of the law of (Z_t) (according to theorem 3.4 of [Benaïm *et al.*, 2015]) which leads to a contradiction.

Step two. Set $\mathcal{A}$ the event :

$$\mathcal{A} = \{\limsup_{t \longrightarrow +\infty} \frac{F(Z_t)}{t} \leq -\alpha\}.$$

Let us prove that for any $z \in M_{0,w}^{\varepsilon/2}$, $\mathbb{P}_z(\mathcal{A}) \geq c_1 > 0$.

Set $X_k = e^{\theta F(Z_{kT})}$. According to lemma 3.2.12 we have :

$$P_T(e^{\theta F})(z) \leq \rho e^{\theta F(z)}.$$

Hence :

$$\mathbb{E}(X_1|X_0) \leq \rho X_0.$$

Let us show that $X_{k \wedge \tau_\varepsilon^{out}}$ (where $x \wedge y = \min(x, y)$) is a super martingal. Because (Z_t) is a Markov process and thanks to lemma 3.2.12, it comes that if $k - 1 < \tau_\varepsilon^{out}$:

$$\mathbb{E}(X_k|\mathcal{F}_{k-1}) = P_T(e^{\theta F})(Z_{(k-1)T}) \leq \rho e^{\theta F(Z_{(k-1)T})} \leq X_{k-1}.$$

and if $k - 1 \geq \tau_\varepsilon^{out}$:

$$\mathbb{E}(X_{k \wedge \tau_\varepsilon^{out}}|\mathcal{F}_{k-1}) = \mathbb{E}(X_{\tau_\varepsilon^{out}}|\mathcal{F}_{k-1}) = X_{\tau_\varepsilon^{out}} = X_{(k-1)\wedge \tau_\varepsilon^{out}}.$$

As a consequence, for all $z \in K_{\varepsilon/2}$:

$$\mathbb{E}_z(X_{k \wedge \tau_\varepsilon^{out}} \mathbb{1}_{\tau_\varepsilon^{out} < \infty}) \leq X_0 = e^{\theta F(z)} \leq \left(\frac{\varepsilon}{2}\right)^\theta.$$

Let us take k to $+\infty$. Thanks to the dominated convergence theorem, it comes that :

$$\varepsilon^\theta \mathbb{P}_z(\tau_\varepsilon^{out} < \infty) \leq \mathbb{E}_z(X_{\tau_\varepsilon^{out}} \mathbb{1}_{\tau_\varepsilon^{out} < \infty}) \leq \left(\frac{\varepsilon}{2}\right)^\theta.$$

Hence :

$$\mathbb{P}_z(\tau_\varepsilon^{out} = \infty) \geq 1 - \frac{1}{2^\theta} = c_1 > 0.$$

Define :

$$M_n = \sum_{k=1}^{n} (F(Z_{kT}) - P_T F(Z_{(k-1)T})).$$

M_n is a martingale. It satisfies the hypothesis of the strong law of large numbers applied to the martingales, then $\frac{M_n}{n} \to 0$. We write :

$$\frac{M_n}{nT} = \frac{F(Z_{nT})}{nT} + \frac{1}{n} \sum_{k=1}^{n-1} \left(\frac{F(Z_{kT}) - P_T F(Z_{kT})}{T} \right) - \frac{P_T F(z)}{nT}.$$

Making n going to $+\infty$ and thanks to assertion (i) from lemma 3.2.12 and conditionnaly to the fact that (Z_t) does not leave $M_{0,w}^\varepsilon$, it comes :

$$\limsup_{n \to +\infty} \frac{F(Z_{nT})}{nT} \leq -\alpha.$$

Set $C = \sup\{f_w^i(r) - \delta^i, (r, u, v, i) \in M\}$, the mean value theorem gives :

$$F(Z_{kT+t}) - F(Z_{kT}) \leq Ct.$$

Hence :

$$\limsup_{t \to +\infty} \frac{F(Z_t)}{t} \leq -\alpha$$

almost surely on the event $\{\tau_\varepsilon^{out} = +\infty\}$. As a consequence,

$$\forall z \in M_{0,w}^{\varepsilon/2}, \quad \mathbb{P}_z(\mathcal{A}) \geq c_1 > 0.$$

Step three. From the two previous steps, it comes :

$$\forall z \in \{(r, u, v, i) \in M, w \neq 0\}, \quad \mathbb{P}_z(\mathcal{A}) \geq cc_1.$$

As a consequence :

$$\mathbb{1}_\mathcal{A} = \lim_{t \to +\infty} \mathbb{P}_z(\mathcal{A}|\mathcal{F}_t) = \lim_{t \to +\infty} \mathbb{P}_{Z_t}(\mathcal{A}) \geq cc_1$$

where the first equality is a consequence of Doob's Martingale convergence theorem and the second iequality comes from the Markov property. It finally comes that :

$$\forall z \in \{(r, u, v, i) \in M, w \neq 0\}, \quad \mathbb{P}_z(\mathcal{A}) = 1$$

which concludes the proof. □

Remark 3.2.14. *This theorem states that if both chemostats are favorable to species w but there exists $s \in (0, 1)$ such that the averaged chemostat ε_s is unfavorable to species w, then for some (λ, s) well chosen, species w might disappear from the switched system.*

3.2.2.2 Long time behavior when two species are introduced

Recall that we assumed that both species can enter in competition in each chemostat. We will now give the precise statements of the theorem 3.1.6 given in introduction.

Assertion 3.2.15. *We will call (H_w) the assertion which is true if and only if one of the following assertions are true :*
— *(i) $\exists j \in \{1, 2\}$ such that ε^j is unfavorable to the species w.*
— *(ii) $\exists s \in (0, 1)$ such that the averaged chemostat ε_s is unfavorable to the species w.*

Theorem 3.2.16. *The sign of the invasion rates Λ_u, Λ_v characterizes the evolution of the species :*

1. *$\Lambda_u > 0$ and $\Lambda_v < 0$ and (H_v) is true $\Rightarrow$ extinction of species v.*
2. *$\Lambda_u < 0$ and $\Lambda_v > 0$ and (H_u) is true $\Rightarrow$ extinction of species u.*
3. *$\Lambda_u < 0$ and $\Lambda_v < 0 \Rightarrow$ extinction of one species (bi-stability state).*
4. *$\Lambda_u > 0$ and $\Lambda_v > 0 \Rightarrow$ coexistence of both species.*

Proof. The point 4 is also a consequence of the fact that if $\Lambda_u > 0$ and $\Lambda_v > 0$, then the process $(\widetilde{Z}_t)$ is stochastically persistent.

Points 1 and 2 are the same after interchanging the species, hence, we just need to show how to prove point 1.

Note :

$$\tau^{in}_{w,\varepsilon} = \min\{k \in \mathbb{N}, \widetilde{Z}_{kT} \in \widetilde{M}^{\varepsilon}_{0,w}\}$$
$$\tau^{out}_{w,\varepsilon} = \min\{k \in \mathbb{N}, \widetilde{Z}_{kT} \in \widetilde{M} \setminus \widetilde{M}^{\varepsilon}_{0,w}\}$$

The prove almost follows the same path as the proof of the first assertion of 3.2.13 :
— First, we prove that $\mathbb{E}_z(\tau^{out}_{u,\varepsilon_u}) < +\infty$ for all $z \in \widetilde{M}^{\varepsilon_u}_{0,u} \setminus \widetilde{M}_0$.
— Then we prove that starting from any point of $\widetilde{M} \setminus \widetilde{M}_{0,u}$, there is a positive probability such that $(\widetilde{Z}_t)$ enters $\widetilde{M}^{\varepsilon_v/2}_{0,v}$.
— Note $\mathcal{A} = \{\limsup_{t \longrightarrow +\infty} \frac{F_v(Z_t)}{t} \leq -\alpha_v\}$. We prove that for any $z \in M^{\varepsilon_v/2}_{0,v}$, $\mathbb{P}_z(\mathcal{A}) \geq c_1 > 0$.
— Finally we show that $\mathbb{P}_z(\mathcal{A}) = 1$ which implies that V_t goes to zero almost surely.

Step one. Let us show that for all $z \in \widetilde{M}^{\varepsilon_u}_{0,u} \setminus \widetilde{M}_0$, $\mathbb{E}_z(\tau^{out}_{u,\varepsilon_u}) < +\infty$.

Set $L_k = F_u(\widetilde{Z}_{kT_u} + k\alpha_u T_u$. From lemma 3.2.12, one can show that $(L_{k\wedge\tau^{out}_{u,\varepsilon_u}})$ is a non-negative supermartingale. Hence, for all $z \in \widetilde{M}^{\varepsilon_u}_{u,0} \setminus \widetilde{M}_{0,u}$:

$$\alpha_u T_u \mathbb{E}_z(k \wedge \tau^{out}_{u,\varepsilon_u}) \leq \mathbb{E}_z(L_{k\wedge\tau^{out}_{u,\varepsilon_u}}) \leq L_0 = F_u(z).$$

As a consequence :

$$\mathbb{E}_z(\tau^{out}_{u,\varepsilon_u}) < \frac{F_u(z)}{\alpha_u T_u} < +\infty.$$

Step two. The fact that assertion (H_v) is true allows us to prove, exactly like in 3.2.13, that there exists $k_0 \in \mathbb{N}$ such that for all $z \in \widetilde{M} \setminus \widetilde{M}^{\varepsilon_u}_{u,0}$:

$$\mathbb{P}_z(\widetilde{Z}_{k_0 T_v} \in \widetilde{M}^{\varepsilon_v/2}_{v,0}) \geq c > 0.$$

Hence, thanks to the first step, it comes that previous inequality holds true for any $z \in \widetilde{M} \setminus \widetilde{M}_{u,0}$.

Step three and *four*. Exactly like in the proof of 3.2.13. □

Remark 3.2.17. *Hypothesis* (H_w) *states that it is possible to choose the jump times of the PDMP* $(\widetilde{Z}_t)$ *in such a way that* W_T *is as close to zero as we want for* T *large enough. We saw in the proof of theorem 3.2.13 and theorem 3.2.16 that when the invasion rate of the species* w *is negative, it is crucial to find such jump times in order to prove that* W_t *tends to zero.*

In the one species case, we proved that Λ_w^0 *is monotonous according to the switching rate* λ *implying that* H_w *is true. In the two species case, we were unable to prove that the invasion rates are monotonous according to* λ*. However, after various numerical simulations, it appears that this property might be true. As a consequence, it would imply that if* λ_w *is negative then* H_w *is true which would simplify theorem 3.2.16.*

3.3 Mathematical study of the deterministic model

In this section we study the behavior of the solutions of the differential system (3.6) modelizing the gradostat-like system :

$$\begin{cases} \dot{R}(t) = \delta(R_0 - R(t)) - U(t)f_u(R(t)) + \lambda K R(t) \\ \dot{U}(t) = U(t)(f_u(R(t)) - \delta) \qquad\qquad + \lambda K U(t) \\ \dot{V}(t) = V(t)(f_v(R(t)) - \delta) \qquad\qquad + \lambda K V(t), \end{cases} \tag{3.25}$$

where the initial value is taken in the set $(\mathbb{R}_+^*)^3$.

In [Smith et Waltman, 1995], it is proven that the solutions of the simple gradostat system of differential equations necessarily go to a stationnary equilibrium point. They use the fact that the system has a strong monotonous structure according to a certain order. It happens to be still the case for the gradostats-like model we introduced in this chapter.

Hence, in order to study the behavior of the solutions of (3.6), one has to study the existence and stability of the stationnary equilibria of this differential system.

Recall that, thanks to the variable change $\Sigma = R + U + V$, it is equivalent to the research of the stationnary equilibria of the system (3.7) :

$$\begin{cases} \dot{U}(t) = U(t)(f_u(\Sigma - U(t) - V(t)) - \delta) + \lambda K U(t) \\ \dot{V}(t) = V(t)(f_v(\Sigma - U(t) - V(t)) - \delta) + \lambda K V(t) \end{cases} \tag{3.26}$$

with initial condition in the set $(\mathbb{R}_+^{*;2})^2$.

We assumed that $R_0^1 = R_0^2$, hence, the stationnary equilibria of (3.7) satisfy the following equation (3.11) :

$$\mathcal{H}(U,V) = 0 \Leftrightarrow \begin{cases} U(f_u(R_0 - U - V) - \delta) + \lambda K U = 0 \\ V(f_v(R_0 - U - V) - \delta) + \lambda K V = 0. \end{cases} \tag{3.27}$$

We will give in this section a complete description of the stationnary solutions of (3.7) which will be synthetized in a graphics depending only on the parameters of the two chemostats ε^1 and ε^2.

3.3.1 A graphical caracterisation of the equilibria and their stability

In this section, we construct a graphical approach in the plan (R^1, R^2) which contains all the information about the non negative stationary solution and their stability. This approach is based on the construction of four functions F_w and g_w, $w \in \{u, v\}$ described below.

For the sake of simplicity we will note :

$$X_w^j(R^j) = f_w^j(R^j) - \delta^j. \tag{3.28}$$

Any non-negative stationary equilibrium (U, V) of the differential equation (3.7) is solution of the system (3.11) which can be written :

$$\begin{cases} A_u(R)U = 0 \\ A_v(R)V = 0 \end{cases} \tag{3.29}$$

where, according to remark 3.1.2, we have $R = R_0 - U - V \in [0, R_0]$ and the matrices $A_w(R)$ are defined by :

$$A_w(R) = \begin{pmatrix} X_w^1(R) - \lambda^1 & \lambda^1 \\ \lambda^2 & X_w^2(R) - \lambda^2 \end{pmatrix}.$$

Recall that for any $w \in \{u, v\}$, we note $W \in \{U, V\}$ the concentration of the species w. Let (U, V) be a stationnary equilibrium of (3.29). If $W \neq 0$, it implies that $\det(A_w(R)) = 0$ which reads explicitly :

$$\left(X_w^1(R^1) - \lambda^1\right)\left(X_w^2(R^2) - \lambda^2\right) = \lambda^1\lambda^2. \tag{3.30}$$

Hence, if the species w survives at the equilibrium, it implies that the resource concentration at the equilibrium (R^1, R^2) is located on a one dimensional curve in the plane (R^1, R^2). It appears that this curve is the graph of a decreasing function F_w defined on a domain D_w :

$$(R^1, R^2) \text{ satisfies (3.30)} \ \Leftrightarrow \ R^1 \in D_w \text{ and } R^2 = F_w(R^1).$$

Moreover, these functions F_w may be explicitly computed as it is stated in the following proposition 3.3.1.

Proposition 3.3.1. *Let $w \in \{u, v\}$ and $g :\ x \mapsto g(x) = \lambda^2 + \frac{\lambda^1\lambda^2}{x - \lambda^1}$. Define :*

$$D_w = \{r \in [0, R_0],\ X_w^1(r) - \lambda^1 < 0\} \text{ and } F_w = \left(X_w^2\right)^{-1} \circ g \circ X_w^1.$$

Now, suppose that there exists a non-negative solution (U, V) of (3.29) such that the species concentration $W \in \{U, V\}$ is non zero. Then,

$$R^1 \in D_w \text{ and } R^2 = F_w(R^1)$$

Proof. First, assume that there exists a non-negative stationary equilibrium (U, V). The resource concentration is given by $R = R_0 - U - V$. Then, for $W \in \{U, V\}$ non zero we have :

$$A_w(R)W = 0. \tag{3.31}$$

With this notation, (3.31) reads

$$\begin{cases} \left(X_w^1(R^1) - \lambda^1\right) W^1 + \lambda^1 W^2 = 0 \\ \lambda^2 W^1 + \left(X_w^2(R^2) - \lambda^2\right) W^2 = 0. \end{cases} \tag{3.32}$$

Since $W^1 \geq 0$ and $W^2 \geq 0$, we obtain $W^1 > 0$ and $W^2 > 0$ which yields :

$$\left(X_w^1(R_u^1) - \lambda^1\right) < 0.$$

Moreover, (3.32) implies that 0 is an eigenvalue of $A_w(R)$ implying that $\det\left(A_w(R)\right) = 0$ which reads explicitly :

$$\left(X_w^1(R^1) - \lambda^1\right)\left(X_w^2(R^2) - \lambda^2\right) = \lambda^1\lambda^2 \tag{3.33}$$

Finally, we define

$$D_w = \{r > 0,\ X_w^1(r) - \lambda^1 < 0\}$$

and the function F_w such that :

$$\left(X_w^1(R^1) - \lambda^1\right)\left(X_w^2(F_w(R^1)) - \lambda^2\right) = \lambda^1\lambda^2$$

The function X_w^2 being injective, the function F_w reads shortly :

$$F_w = \left(X_w^2\right)^{-1} \circ g \circ X_w^1$$

wherein we have set the function g as :

$$g(x) = \lambda^2 + \frac{\lambda^1\lambda^2}{x - \lambda^1}.$$

□

Remark 3.3.2. *The functions X_w^j being increasing and the function g being decreasing, the identity $X_w^2 \circ F_w = g \circ X_w^1$ implies that the functions F_w are strictly decreasing on their definition set. Moreover it exists $(m_w^1, m_w^2, m_w^3, m_w^4) \in \mathbb{R}^4$ such that :*

$$F_w(x) = \frac{m_w^1 x + m_w^2}{m_w^3 x + m_w^4}.$$

The explicit formula of these parameters is useful in order to obtain numerical examples but it is not needed in the theoretical purpose, hence, we then omit it.

At this step, we see that it is necessary that the resource concentration at the equilibrium $R = (R^1, R^2)$ belongs to the graph $\mathcal{C}_w = \{(r, F_w(r)),\ r \in D_w\}$ for the species $w \in \{u, v\}$ to survive. But this is not a sufficient condition. Indeed, the definition of the functions F_w only matches the fact that 0 is an *eigenvalue*[4] of the matrix $A_w(R)$.

The analysis of the corresponding eigenvector (associated to the dominant eigenvalue 0) will give us a sufficient conditions for a point of the curve to be a semi-trivial equilibrium (proposition 3.3.4) or a coexistence equilibrium (proposition 3.3.6).

For instance, assume that (U, V) is a non-negative equilibrium of (3.29). If $W \in \{U, V\}$ is non zero, then $R = (R^1, R^2) \in \mathcal{C}_w$ and W is a positive eigenvector of the matrix $A_w(R)$ for the eigenvalue 0. It follows that there exists some scalar $\mu_w > 0$ such that :

$$W = \mu_w \begin{pmatrix} \lambda^1 \\ -(X^1_w(R^1) - \lambda^1) \end{pmatrix}. \tag{3.34}$$

If (U, V) is the semi-trivial solution associated to the species w, we have $\begin{pmatrix} R^1 \\ R^2 \end{pmatrix} = R = R_0 - W$ and it comes that :

$$R^2 = R_0 + \frac{1}{\lambda^1}(R_0 - R^1)\left(X^1_w(R^1) - \lambda^1\right).$$

This lead us to define, for $w \in \{u, v\}$, the functions g_w (defined on D_w) by :

$$g_w(r) = R_0 + \frac{1}{\lambda^1}(R_0 - r)\left(X^1_u(r) - \lambda^1\right).$$

Lemma 3.3.3. *Let $w \in \{u, v\}$. The function g_w is increasing on the set D_w. Moreover, if the semi-trivial stationary equilibrium E_w exists then the concentration $R_w = \begin{pmatrix} R^1_w \\ R^2_w \end{pmatrix}$ associated to E_w satisfies $g_w(R^1_w) = R^2_w$.*

Proof. The fact that $g_w(R^1_w) = R^2_w$ follows from the very definition of g_w. A direct computation gives

$$g'_w(r) = -\frac{X^1_w(r) - \lambda^1}{\lambda^1} + (R_0 - r)\frac{X^{1\prime}_w(r)}{\lambda^1}.$$

Since $X^1_w(R) - \lambda^1 < 0$ for $r \in D_w$, it comes that g_w is increasing on D_w. $\square$

We can now state the graphical characterization of the semi-trivial solution.

Proposition 3.3.4. *Let $w \in \{u, v\}$. The semi-trivial solution E_w exists if and only if there exists $r^1 \in D_w$ such that $F_w(r^1) = g_w(r^1) := r^2$. In that case E_w is unique and the resource concentration at E_w is $R_w = (R^1_w, R^2_w) = (r^1, r^2)$.*

Proof. The characterization of R_w is a direct consequence of the proposition 3.3.1 and the lemma 3.3.3. The uniqueness follows from the fact that $r \mapsto g_w - F_w$ is increasing on D_w. $\square$

4. Indeed, on D_w the eigenvalue 0 is the principal eigenvalue of $A_w(R)$, and by the Perron-Frobenius theorem, it is associated to a positive eigenvector which is nothing but U.

Previous proposition gives the complete graphical characterization of the semi-trivial equilibria of (3.29). Let us now study the case of the coexistence stationary equilibria. It follows immediately from the proposition 3.3.1 that if there exists a coexistence stationary equilibrium, that is a positive solution (U_c, V_c) to (3.29), then there exists $R_c^1 \in D_u \cap D_v$ such that :

$$F_u(R_c^1) = F_v(R_c^1) = R_c^2.$$

According to remark 3.3.2, the following lemma holds.

Lemma 3.3.5. *Suppose that $F_u \neq F_v$. Then there are at most two coexistence stationary equilibrium for the gradostat.*

There are at most two intersections between the curves of F_u and F_v but these intersections are not necessarily associated to a positive solution of (3.29). Indeed, if $F_u(R^1) = F_v(R^1)$ then the coefficients of the eigenvectors are not necessarily of the same signs.

The following proposition gives a good location for an intersection between the curves of F_u and F_v to be associated with an admissible stationary equilibrium solution of (3.29).

Proposition 3.3.6. *Let R_c be an intersection between the curves of F_u and F_v. R_c is associated to an admissible coexistence stationary equilibrium if and only if :*

$$\left(R_u^1 - R_v^1\right)\left(R_u^2 - R_v^2\right) < 0,$$

and R_c is in the rectangle K defined as :

$$K = [\min(R_u^1, R_v^2), \max(R_u^1, R_v^1)] \times [\min(R_u^2, R_v^1), \max(R_u^1, R_v^2)].$$

Proof. Let us define, for each semi-trivial equilibrium the following sets of $[0, R_0]^2$:

$$K_w = \{(R^1, R^2) \in [0, R_0]^2, \quad \left(R_w^1 - R^1\right)\left(R_w^2 - R^2\right) < 0\}.$$

A representation of K_w can be found in the following figure 3.3.

We first prove that any intersection R_c between the curves of F_u and F_v is in $K_u \cap K_v$. Recall that R_w is the associated resource concentration for the semi-trivial stationary equilibrium E_w. According to (3.31), R_c is associated to a stationary coexistence equilibrium only if $\det(A_u(R_c)) = 0$ and $\det(A_v(R_c)) = 0$. But we also know that $\det(A_u(R_u)) = 0$ and $\det(A_v(R_v)) = 0$ which finally implies that :

$$\begin{aligned}
\left(X_u^1(R_c^1) - \lambda^1\right)\left(X_u^2(R_c^2) - \lambda^2\right) &= \left(X_u^1(R_u^1) - \lambda^1\right)\left(X_u^2(R_u^2) - \lambda^2\right), \\
\left(X_v^1(R_c^1) - \lambda^1\right)\left(X_v^2(R_c^2) - \lambda^2\right) &= \left(X_v^1(R_v^1) - \lambda^1\right)\left(X_v^2(R_v^2) - \lambda^2\right).
\end{aligned}$$

The fact that the functions $X_w^j(R^j) - \lambda^j$ are increasing gives us that necessarily $R_c \in K_u \cap K_v$.

The concentration (U_c, V_c) associated to the concentration resource R_c are respectively eigenvalues of the matrices $A_u(R_c)$ and $A_v(R_v)$ for the eigenvalue zero. It is easy to check that the associated eigenvectors of these matrices are of the shape :

$$\overrightarrow{U} = \mu_u \begin{pmatrix} \lambda^1 \\ -(X_u^1(R_c^1) - \lambda^1) \end{pmatrix} \text{ and } \overrightarrow{V} = \mu_v \begin{pmatrix} \lambda^1 \\ -(X_v^1(R_c^1) - \lambda^1) \end{pmatrix}$$

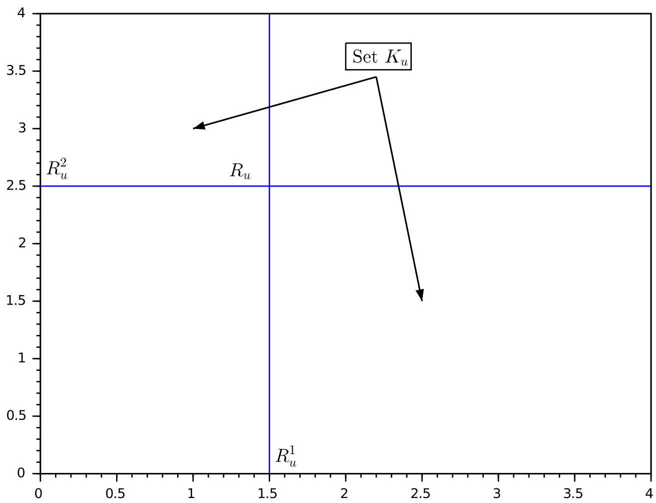


FIGURE 3.3 – Shape of the set K_u.

with $\mu_w \in \mathbb{R}$. Recall that according to remark 3.1.2, $U_c+V_c = R_0-R_c$. It comes immediately that the coefficients μ_u and μ_v are solution of an inversible system which gives :

$$U_c = \mu_u \begin{pmatrix} \lambda^1 \\ -(X_u^1(R_c^1) - \lambda^1) \end{pmatrix} \text{ and } V_c = \mu_v \begin{pmatrix} \lambda^1 \\ -(X_v^1(R_c^1) - \lambda^1) \end{pmatrix}$$

where the coefficients μ_u and μ_v are given by :

$$\mu_w = \frac{1}{X_{\overline{w}}^1(R_c^1) - X_w^1(R_c^1)} \left(g_{\overline{w}}(R_c^1) - R_c^2 \right).$$

We know that $X_w^1(R_c^1) - \lambda^1 < 0$ for each i. As a consequence, (U_c, V_c) is an admissible coexistence stationary equilibrium if and only if $\mu_u > 0$ and $\mu_v > 0$. Hence, if R_c is associated to an admissible coexistence stationary equilbrium, we have :

$$\min \left(g_u(R_c^1), g_v(R_c^1) \right) \leq R_c^2 \leq \max \left(g_u(R_c^1), g_v(R_c^1) \right).$$

Consequently, R_c is associated to an admissible equilibrium if and only if,

$$R_c \in \Theta = K_u \cap K_v \cap J \tag{3.35}$$

where,

$$J = \left\{ (R^1, R^2) \in [0, R_0]^2, \quad \min \left(g_u(R^1), g_v(R^1) \right) \leq R^2 \leq \max \left(g_u(R^1), g_v(R^1) \right) \right\}.$$

Recall that the functions g_w are defined by :

$$g_w(R) = R_0 + (R_0 - R) \frac{X_w^1(R) - \lambda^1}{\lambda^1}.$$

We just saw that if R_c is associated to an admissible coexistence stationary equilibrium, then $R_c \in \Theta$ (it is the condition (3.35)). Consequently, properties on the functions g_w allows the following statements :

If $\left(R_u^1 - R_v^1\right)\left(R_u^2 - R_v^2\right) > 0$, it can be checked that $\Theta = \varnothing$, implying that R_c does not exist. See figure 3.4 for an illustration of this case.

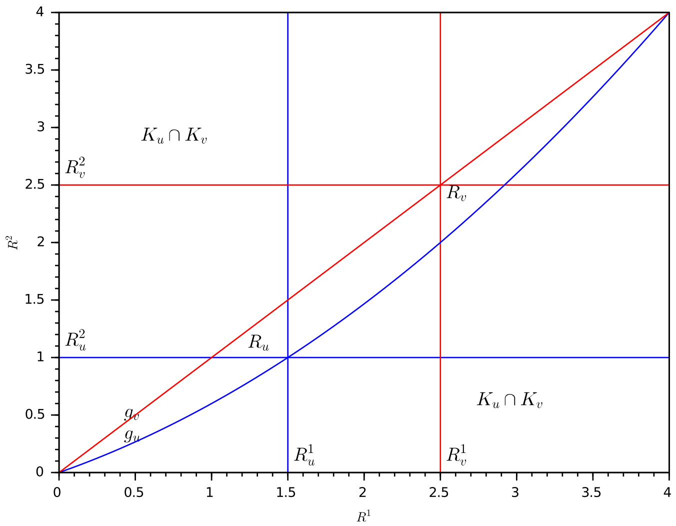


FIGURE 3.4 – $K_u \cap K_v$ is not between the curves of g_u and g_v.

If $\left(R_u^1 - R_v^1\right)\left(R_u^2 - R_v^2\right) < 0$, then $\Theta \subset K$ where K is the rectangle defined by :

$$K = [\min(R_u^1, R_v^2), \max(R_u^1, R_v^1)] \times [\min(R_u^2, R_v^1), \max(R_u^1, R_v^2)].$$

See figure 3.5 for an illustration of this case.

□

Corollary 3.3.7. *Assume that R_c is associated to an admissible coexistence stationary equilibrium. Then :*

$$R_u^1 < R_v^1 \Leftrightarrow X_u^1(R_c^1) > X_v^1(R_c^1).$$

Proof. Assume that $R_u^1 < R_v^2$. Proposition 3.3.6 implies that $R_u^2 > R_v^2$. The functions g_w are increasing on the set $[R_u^1, R_v^2]$ and $g_u(R_1^1) > g_v(R_2^1)$ because $g_w(R_w^1) = R_w^2$. As a consequence,

$$g_v(R_c^1) < R_c^2 < g_u(R_c^1).$$

In the proof of the proposition 3.3.6, we computated the coexistence stationary equilibrium associated to R_c and found out that U_c and V_c satisfy (3.34) where

$$\mu_w = \frac{1}{X_{\overline{w}}^1(R_c^1) - X_w^1(R_c^1)}\left(g_{\overline{w}}(R_c^1) - R_c^2\right).$$

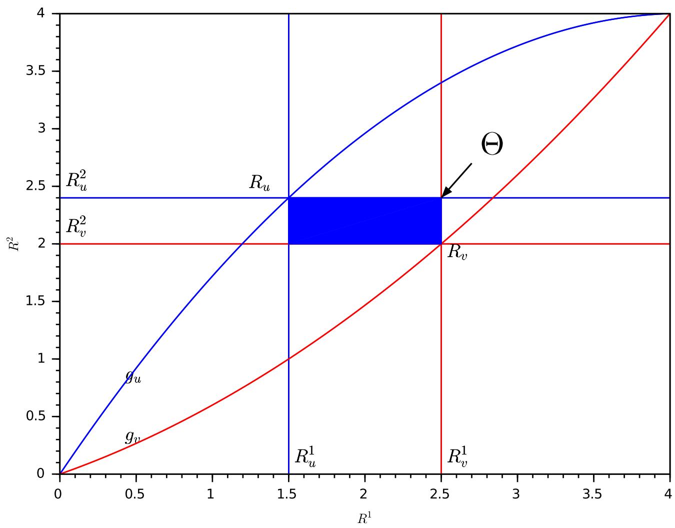


FIGURE 3.5 – Example of a non empty Θ.

Since $U_c > 0$ and $V_c > 0$, we have $\mu_u > 0$ and $\mu_v > 0$ which yields $X_u^1(R_c^1) > X_v^1(R_c^1)$. $\square$

To summarize, we can tell if an intersection R_c between the curves of F_u and F_v is associated to an admissible coexistence stationary equilibrium. We are now going to give criteria for the existence of coexistence stationary equilibrium according to the stability of the semi-trivial equilibria E_u and E_v.

Proposition 3.3.8. *The semi-trivial equilibrium E_w is stable if and only if $F_{\overline{w}}(R_w^1) > R_w^2$.*

Proof. The stability of E_w can be read on the Jacobian of $\mathcal{H}$ evaluated in E_w. For sake of simplicity we will do the proof for E_u. A straightforward computation gives :

$$DH(U,0) = \begin{pmatrix} A & B \\ 0 & C \end{pmatrix}$$

where,

$$A = \begin{pmatrix} X_u^1(R_u^1) - \lambda^1 - U^1 f_u^{1\prime}(R_u^1) & \lambda^1 \\ \lambda^2 & X_u^2(R_u^2) - \lambda^2 - U^2 f_u^{2\prime}(R_u^2) \end{pmatrix}$$

and

$$C = \begin{pmatrix} X_v^1(R_u^1) - \lambda^1 & \lambda^1 \\ \lambda^2 & X_v^2(R_u^2) - \lambda^2 \end{pmatrix}.$$

A simple computation using the fact that :

$$\left(X_u^1(R_u^1) - \lambda^1\right)\left(X_u^2(R_u^2) - \lambda^2\right) = \lambda^1\lambda^2,$$

and $X_u^i(R_u^i) - \lambda^i < 0$ allows us to state that the real parts of the eigenvectors of A are negative. As a consequence, E_u is stable if and only if the eigenvectors of C have negative real parts which gives the announced inequality (recall that $F_v = (X_v^2)^{-1} \circ g \circ X_v^1$ where $g(x) = \lambda^2 + \frac{\lambda^1\lambda^2 x}{x-\lambda^1}$). $\square$

Remark 3.3.9. *Let us note Γ_w the maximum eigenvalue of the following matrix :*

$$\begin{pmatrix} X_w^1(R_{\overline{w}}^1) - \lambda^1 & \lambda^1 \\ \lambda^2 & X_w^2(R_{\overline{w}}^2) - \lambda^2 \end{pmatrix}.$$

Then according to the previous proof, the sign of Γ_w determines the stability of the semi-trivial equilibrium $E_{\overline{w}}$:

— *If $\Gamma_w > 0$, then $E_{\overline{w}}$ is unstable.*
— *If $\Gamma_w < 0$, then $E_{\overline{w}}$ is stable.*

3.3.2 Proof of the theorem 3.1.15

We can now prove theorem 3.1.15 which can be written as follows according to remark 3.3.9 :

Theorem 3.3.10. *Assume that the two semi-trivial stationary equilibria E_u and E_v exist.*

1. *If E_u and E_v are unstable, then any solution of (3.7) goes to a unique coexistence equilibrium E_{cs} which is linearly stable.*
2. *If E_u and E_v are stable, then there exists an unstable coexistence solution E_{cu}. Moreover, the solutions of (3.7) with initial data different from E_{cu} goes either to E_u or to E_v depending on the location of the initial value according to the basin of attraction of the two semi-trivial equilibrium. The system is said to be in a bi-stable case.*
3. *Let $\{w, \overline{w}\} = \{u, v\}$ and suppose that E_w is stable and $E_{\overline{w}}$ is unstable. Then either :*
   (a) *There is not coexistence stationary equilibria. In that case, any solution of (3.7) converges to E_w.*
   (b) *There exist two coexistence stationary equilibrium : one stable E_{cs} and one unstable E_{cu}. Any trajectory of (3.7) with initial data different from E_{cu} goes either to E_{cs} or to E_w depending on the location of the initial value according to the basin of attraction of the two stable equilibria. The system is said to be in a bi-stable case.*

Proof. Let us assume that $R_u^1 < R_v^1$. The existence of a coexistence stationary equilibrium is a simple consequence of proposition 3.3.8 and the intermediate value theorem. Let us prove it if E_u and E_v are both stable, then according to proposition 3.3.8, $F_{\overline{w}}(R_w^1) > R_w^2$ for each i. Since $R_w^2 = F_w(R_w^1)$, it comes that :

$$F_u(R_v^1) - F_v(R_v^1) > 0 \text{ and } F_v(R_u^1) - F_u(R_u^1) > 0.$$

Hence, the intermediate value theorem implies that F_u and F_v have an odd number of intersections. According to proposition 3.3.5, there are at most two intersections between the curves of F_u and F_v. As a consequence there exists a unique $R_c^1 \in [R_u^1, R_v^1]$ such that $F_u(R_c^1) = F_v(R_c^1)$. Since the functions F_w are decreasing, one can check that $R_u^2 > R_v^2$ and

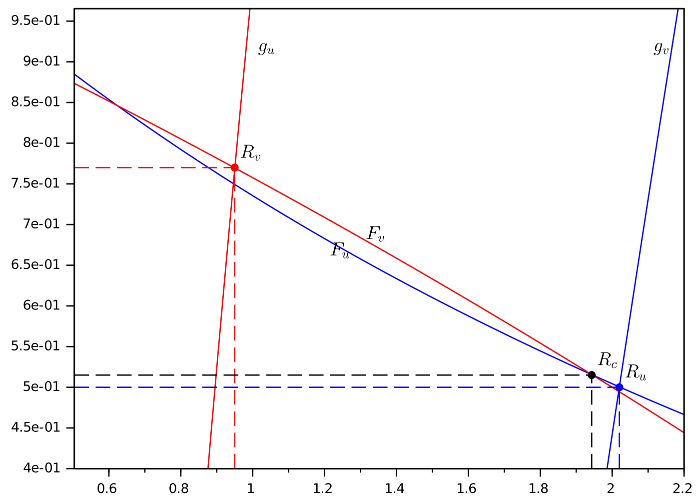


FIGURE 3.6 – R_c is associated to a stable coexistence stationary equilibrium.

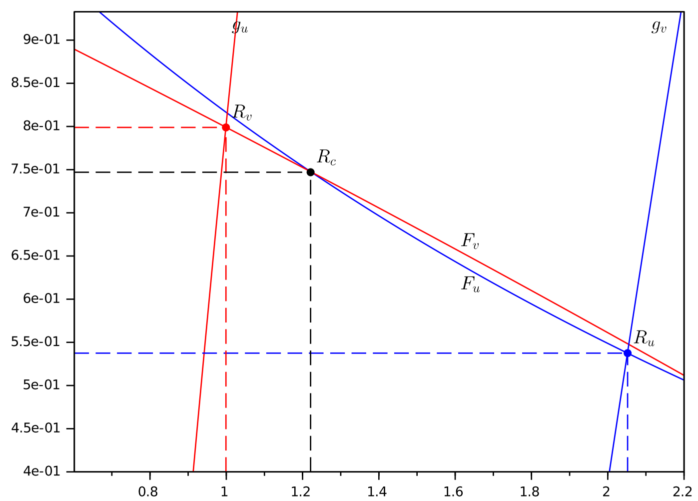


FIGURE 3.7 – R_c is associated to an unstable coexistence stationary equilibrium.

that $R_c^2 \in [R_v^2, R_u^2]$. Hence, proposition 3.3.6 implies that R_c is associated to an admissible coexistence stationary equilibrium. Figure 3.6 and figure 3.7 come as an illustration for this statement.

The stability of the coexistence stationary equilibrium is a bit more difficult to obtain and will have to be checked on the jacobian of $\mathcal{H}$ evaluated in (U_c, V_c). A straightforward computation gives :

$$D\mathcal{H}(U_c,V_c) = \begin{pmatrix} X_u^1-\lambda^1-\beta_u^1 & \lambda^1 & -\beta_u^1 & 0 \\ \lambda^2 & X_u^2-\lambda^2-\beta_u^2 & 0 & -\beta_u^2 \\ -\beta_v^1 & 0 & X_v^1-\lambda^1-\beta_v^1 & \lambda^1 \\ 0 & -\beta_v^2 & \lambda^2 & X_v^2-\lambda^2-\beta_v^2 \end{pmatrix}$$

where :

$$X_w^j = f_w^j(R_c^j) - \delta^j \text{ and } \beta_w^j = W_c^j f_w^{j\prime}(R_c^j).$$

First, note that :

$$\begin{aligned} & X_w^j - \lambda^j < 0 \\ & \beta_w^j > 0 \\ & \left(X_w^1 - \lambda^1\right)\left(X_w^2-\lambda^2\right) = \lambda^1\lambda^2 \end{aligned}$$

Also note that $D\mathcal{H}(U_c, V_c)$ is an irreducible matrix and it can be written :

$$D\mathcal{H}(U_c,V_c) = \begin{pmatrix} A & B \\ C & D \end{pmatrix},$$

where A and D are irreducible square matrices with nonnegative off diagonal elements and $B \leq 0$, $C \leq 0$ (in the sense that all of their coefficients are non positive).

Let us call $s(D\mathcal{H}(U_c, V_c))$ the maximum real part of the eigenvalues of $D\mathcal{H}(U_c, V_c)$. In [Smith et Waltman, 1995], the authors use the very strong following property dealing with these kind of matrices (that can be found in [Berman et J. Plemmons, 1994]) : we consider the following transformation of $D\mathcal{H}(U_c, V_c)$:

$$\overline{D\mathcal{H}(U_c,V_c)} = \begin{pmatrix} A & -B \\ -C & D \end{pmatrix}.$$

Then $s(D\mathcal{H}(U_c, V_c)) < 0$ if and only if $(-1)^k d_k > 0$ for $k \in \{1, 2, 3, 4\}$ where d_i is the i-th principal minor of $\overline{D\mathcal{H}(U_c, V_c)}$.

As a consequence, the signs of d_1, d_2, d_3 and d_4 will give us the stability of $D\mathcal{H}(U_c, V_c)$. We start with $d_1 = X_u^1 - \lambda^1 - \beta_u^1$ which is clearly negative. Next, it comes that :

$$\begin{aligned} d_2 &= \begin{vmatrix} X_u^1-\lambda^1-\beta_u^1 & \lambda^1 \\ \lambda^2 & X_u^2-\lambda^2-\beta_u^2 \end{vmatrix} \\ &= \beta_u^1(X_u^2-\lambda^2) - \beta_u^2(X_u^1-\lambda^1 + \beta_u^1\beta_u^2 > 0 \end{aligned}$$

An other straightforward computation gives :

$$\begin{aligned} d_3 &= \begin{vmatrix} X_u^1-\lambda^1-\beta_u^1 & \lambda^1 & \beta_u^1 \\ \lambda^2 & X_u^2-\lambda^2-\beta_u^2 & 0 \\ \beta_v^1 & 0 & X_v^1-\lambda^1-\beta_v^1 \end{vmatrix} \\ &= -\beta_u^1\beta_v^1(X_u^2-\lambda^2-\beta_u^2) + (X_v^1-\beta_v^1-\lambda^1)d_2 \\ &= -\beta_u^1(X_u^2-\lambda^2)(X_v^1-\lambda^1) - \beta_u^2(X_u^1-\lambda^1)(X_v^1-\lambda^1) \\ &+ \beta_u^1\beta_u^2(X_v^1-\lambda^1) + \beta_u^2\beta_v^1(X_u^1-\lambda^1) < 0. \end{aligned}$$

Obtaining the sign of d_4 requires heavy computations. As in [Smith et Waltman, 1995], we obtain an explicit expression for d_4 :

Lemma 3.3.11.

$$d_4 = \beta_u^1\beta_v^2\left[\left(X_u^2-\lambda^2\right)\left(X_v^1-\lambda^1\right)-\lambda^1\lambda^2\right]+\beta_u^2\beta_v^1\left[\left(X_u^1-\lambda^1\right)\left(X_v^2-\lambda^2\right)-\lambda^1\lambda^2\right].$$

Proof. A straightforward computation gives :

$$\begin{aligned} d_4 &= \begin{vmatrix} X_u^1-\lambda^1-\beta_u^1 & \lambda^1 & \beta_u^1 & 0 \\ \lambda^2 & X_u^2-\lambda^2-\beta_u^2 & 0 & \beta_u^2 \\ \beta_v^1 & 0 & X_v^1-\lambda^1-\beta_v^1 & \lambda^1 \\ 0 & \beta_v^2 & \lambda^2 & X_v^2-\lambda^2-\beta_v^2 \end{vmatrix} \\ &= \beta_v^2 D_1 - \lambda^2 D_2 + (X_v^2-\lambda^2-\beta_v^2)d_3 \end{aligned}$$

where,

$$\begin{aligned} D_1 &= \begin{vmatrix} X_u^1-\lambda^1-\beta_u^1 & \beta_u^1 & 0 \\ \lambda^2 & 0 & \beta_u^2 \\ \beta_v^1 & X_v^1-\lambda^1-\beta_v^1 & \lambda^1 \end{vmatrix} \\ &= -\beta_u^2(X_u^1-\lambda^1)(X_v^1-\lambda^1)+\beta_u^2\beta_u^1(X_v^1-\lambda^1)+\beta_u^2\beta_v^1(X_u^1-\lambda^1)-\beta 1^1\lambda^1\lambda^2 \end{aligned}$$

and,

$$\begin{aligned} D_2 &= \begin{vmatrix} X_u^1-\lambda^1-\beta_u^1 & \lambda^1 & 0 \\ \lambda^2 & X_u^2-\lambda^2-\beta_u^2 & \beta_u^2 \\ \beta_v^1 & 0 & \lambda^1 \end{vmatrix} \\ &= -\lambda^1\beta_u^1(X_u^2-\lambda^2)-\lambda^1\beta_u^2(X_u^1-\lambda^1)+\lambda^1\beta_u^1\beta_u^2+\lambda^1\beta_u^2\beta_v^1. \end{aligned}$$

By making good use of the relation $(X_w^1-\lambda^1)(X_w^2-\lambda^2)=\lambda^1\lambda^2$, one can check that :

$$d_4 = \beta_u^1\beta_v^2\left[\left(X_u^2-\lambda^2\right)\left(X_v^1-\lambda^1\right)-\lambda^1\lambda^2\right]+\beta_u^2\beta_v^1\left[\left(X_u^1-\lambda^1\right)\left(X_v^2-\lambda^2\right)-\lambda^1\lambda^2\right].$$

□

The sign of d_4 is not trivial at all and its study will require a transformation of its expression. Since $(X_w^1-\lambda^1)(X_w^2-\lambda^2)=\lambda^1\lambda^2$, one can write that :

$$\begin{aligned} d_4 = {} & \beta_u^1\beta_v^2\left[\left(X_u^2-\lambda^2\right)\left(X_v^1-\lambda^1\right)-\left(X_u^1-\lambda^1\right)\left(X_u^2-\lambda^2\right)\right] \\ & + \beta_u^2\beta_v^1\left[\left(X_u^1-\lambda^1\right)\left(X_v^2-\lambda^2\right)-\left(X_v^1-\lambda^1\right)\left(X_v^2-\lambda^2\right)\right] \end{aligned}$$

Implying that :

$$d_4 = -\left(X_u^1-X_v^1\right)\left(\beta_u^1\beta_v^2\left(X_u^2-\lambda^2\right)-\beta_u^2\beta_v^1\left(X_v^2-\lambda^2\right)\right)$$

Recall that $\beta_w^j = U_w^{j;c} f_w^{j\prime}(R_c^j)$. According to equation (3.34),

$$W_c = \mu_w \begin{pmatrix} \lambda^1 \\ -(X_w^1-\lambda^1) \end{pmatrix}.$$

and the coefficients μ_w are positive. From this relation comes that :

$$\beta_u^1\beta_v^2 = -\mu_u\mu_v(X_v^1-\lambda^1)f_u^{1\prime}(R_c^1)f_v^{2\prime}(R_c^2) \text{ and } \beta_u^2\beta_v^1 = -\mu_u\mu_v(X_u^1-\lambda^1)f_u^{2\prime}(R_c^2)f_v^{1\prime}(R_c^1).$$

For the sake of simplicity we will note $f_w^{j\prime}$ for $f_w^{j\prime}(R_c^j)$. It comes :

$$d_4 = \mu_u\mu_v(X_u^1-X_v^1)\left(f_u^{1\prime}f_v^{2\prime}\left(X_u^2-\lambda^2\right)\left(X_v^1-\lambda^1\right) - f_u^{2\prime}f_v^{1\prime}\left(X_u^1-\lambda^1\right)\left(X_v^2-\lambda^2\right)\right).$$

Using once again the relation $(X_w^1-\lambda^1)(X_w^2-\lambda^2)=\lambda^1\lambda^2$ gives :

$$d_4 = \mu_u\mu_v\lambda^1\lambda^2\frac{X_v^1-\lambda^1}{X_u^1-\lambda^1}f_u^{2\prime}f_v^{1\prime}\left(X_u^2-X_v^1\right)\left(\frac{f_u^{1\prime}f_v^{2\prime}}{f_u^{2\prime}f_v^{1\prime}} - \left(\frac{X_u^1-\lambda^1}{X_v^1-\lambda^1}\right)^2\right).$$

We are going to express the derivatives of the functions f_w^j using the functions F_w. It starts from a relation we already proved :

$$(X_w^1(R^1)-\lambda^1)(X_w^2(R^2)-\lambda^2) = \lambda^1\lambda^2 \Leftrightarrow R^2 = F_w(R^1).$$

It comes that :

$$(X_w^1(R^1)-\lambda^1)(X_w^2(F(R^1))-\lambda^2) = \lambda^1\lambda^2.$$

Derivating by R^1 gives :

$$\frac{f_w^{1\prime}(R^1)}{f_w^{j\prime}(F_w(R^1))} = -F_w'(R^1)\frac{X_w^1(R^1)-\lambda^1}{X_w^2(F_w(R^1))-\lambda^2}.$$

Since $R_c^2 = F_1(R_c^1) = F_2(R_c^1)$ it comes that :

$$\frac{f_u^{1\prime}f_v^{2\prime}}{f_u^{2\prime}f_v^{1\prime}} = \frac{F_1'(R_c^1)}{F_2'(R_c^1)}\left(\frac{X_u^1-\lambda^1}{X_v^1-\lambda^1}\right)^2.$$

Hence,

$$d_4 = \mu_u\mu_v\lambda^1\lambda^2 f_u^{2\prime}f_v^{1\prime}\frac{X_u^1-\lambda^1}{X_v^1-\lambda^1}\left(X_u^2-X_v^1\right)\left(\frac{F_u'(R_c^1)}{F_v'(R_c^1)}-1\right).$$

As a direct consequence, the sign of d_4 is given by the sign of the quantity :

$$\text{sign}(d_4) = \left(X_u^2-X_v^1\right)\left(\frac{F_u'(R_c^1)}{F_v'(R_c^1)}-1\right).$$

Moreover corollary 3.3.7 gives us a better understanding of this sign :

$$\text{sign}(d_4) = \left(R_v^1-R_u^1\right)\left(\frac{F_u'(R_c^1)}{F_v'(R_c^1)}-1\right).$$

Let us assume that $R_v^1-R_u^1>0$. We will now show how the stability of the semi-trivial equilibria E_u and E_v influence the stability of the coexistence stationary equilibrium when it exists.

If E_u and E_v are stable, then according to proposition 3.3.8, we have :

$$F_u(R_v^1)-F_v(R_v^1)>0 \text{ and } F_v(R_u^1)-F_u(R_u^1)>0.$$

And we already know that there exists a unique intersection between the curves of F_u and F_v in the interval $[R_u^1, R_v^1]$. A simple analytic consequence of these facts is that $F_v'(R_c^1) < F_u'(R_c^1)$ and since the functions F_w are decreasing it comes that :

$$\frac{F_u'(R_c^1)}{F_v'(R_c^1)} - 1 < 0.$$

Thus $d_4 < 0$ which implies that the unique coexistence equilibrium is unstable. (And the proof is the same if we suppose that $R_v^1 - R_u^1 < 0$. This reasoning also proves the stability property of the coexistence stationary equilibrium in the other cases which concludes the proof. □

3.4 Numerical comparison of the invasion rates

In this section, we want to discuss the similarities and the differences between the two models introduced in this chapter. According to section 3.2 and section 3.3 the sign of the invasion rates characterizes the long time behavior of these models. As a consequence, we compare the two models by comparing their invasion rates.

3.4.1 Comparison of the invasion rates when only one species in introduced

Assume that only species w is introduced in the systems. Let us recall the following propositions dealing with the invasion rates in the different models and their properties. First the probabilistic invasion rates :

Theorem 3.4.1. *Let us assume that $R_0^1 < R_0^2$ and set $\gamma^j = \frac{\lambda^j}{\delta^j}$. The process (Z_t) has a unique invariant measure when it is restricted to $M_{0,w}$. The invasion rate of species w is given by :*

$$\Lambda_w^0 = \frac{\gamma^1 + \gamma^2}{\lambda^1 + \lambda^2} \mathbb{E}\left[\Phi(B)\right].$$

Where B is a random variable following a Beta law of parameters (γ^1, γ^2) and :

$$\Phi(x) = \delta^2(1-x)\left(f^1\left((R_0^2 - R_0^1)x + R_0^1\right) - \delta^1\right) + \delta^1 x\left(f^2\left((R_0^2 - R_0^1)x + R_0^1\right) - \delta^2\right).$$

Proposition 3.4.2. *The invasion rate Λ_w^0 is monotonous acording to the variable λ.*

Recall that we gave an explicit expression for the invasion rate for the deterministic case in section 3.2.1 (see (3.10)).

Proposition 3.4.3. *The invasion rate of the only species w is given by :*

$$\Gamma_w^0 = \frac{1}{2}\left(f_w^1(\Sigma^1) - \delta^1 + f_w^2(\Sigma^2) - \delta^2 - \lambda^1 - \lambda^2 + \sqrt{(f_w^1(\Sigma^1) - \delta^1 - f_w^2(\Sigma^2) + \delta^2)^2 + 4\lambda^1\lambda^2}\right)$$

where Σ is given in remark 3.1.8 by :

$$\Sigma = \begin{pmatrix}\Sigma^1 \\ \Sigma^2\end{pmatrix} = \begin{pmatrix}\frac{\lambda^2\delta^1 R_0^1 + \lambda^1\delta^2 R_0^2 + \delta^1\delta^2 R_0^1}{\lambda^1\delta^2 + \lambda^2\delta^1 + \delta^1\delta^2} \\ \frac{\lambda^2\delta^1 R_0^1 + \lambda^1\delta^2 R_0^2 + \delta^1\delta^2 R_0^2}{\lambda^1\delta^2 + \lambda^2\delta^1 + \delta^1\delta^2}\end{pmatrix}$$

We give, in the following proposition, the limits behavior for the two invasion rates :

Proposition 3.4.4. *The following limits are computable :*

$$\lim_{\lambda\to+\infty}\Lambda_w^0 = \lim_{\lambda\to+\infty}\Gamma_w^0 = (1-s)\left(f_w^1(R^\infty)-\delta^1\right)+s\left(f_w^2(R^\infty)-\delta^2\right)$$

where $R^\infty = \frac{(1-s)\delta^1 R_0^1 + s\delta^2 R_0^2}{(1-s)\delta^1+s\delta^2}$. *The behavior of the two model is the same when* λ *is large enough.*

Moreover :

$$\lim_{\lambda\to 0}\Lambda_w^0 = (1-s)\left(f_w^1(R_0^1)-\delta^1\right)+s\left(f_w^2(R_0^2)-\delta^2\right),$$
$$\lim_{\lambda\to 0}\Gamma_w^0 = \max\left(f_w^1(R_0^1)-\delta^1, f_w^2(R_0^2)-\delta^2\right).$$

We now show numerical simulations of the functions Λ^0 and Γ^0 in order to compare their behavior for intermediate values of λ. We will see that both invasion rates is globally very similar. However, the behaviour for λ small can be completely different not only because the limits of Λ^0 and Γ^0 are not the same but also because Γ^0 is not necessarily monotonous for λ small.

The interesting case when only one species is introduced in our systems is when the agregated chemostat ε_s is unfavorable to the introduced species whereas one of the chemostats ε^1 and ε^2 is favorable to it. Indeed, in this configuration, the sign of the invasion rates may change according to λ. We will give two sets of numerical simulations for two sets of data Π_1 and Π_2 defined by :

Π_1	Π_2
$(a^1,a^2)=(1.1,2)$	$(a^1,a^2)=(1.1,2)$
$(b^1,b^2)=(0.4,4)$	$(b^1,b^2)=(0.05,2)$
$(\delta^1,\delta^2)=(1,1)$	$(\delta^1,\delta^2)=(1,1)$
$(R_0^1,R_0^2)=(10,1)$	$(R_0^1,R_0^2)=(0.55,2.1)$

Remark 3.4.5. *Note that in all the following figures, the blue color will make reference to the probabilistic system and the red color will make reference to the deterministic system.*

One can check in figure 3.8 that for the set of data Π_1, ε^1 is favorable to the introduced species and ε^2 is not. For the set of data Π_2, both chemostats are favorable to the introduced species.

Figure 3.9 shows that for $s=0.5$, the agregated system ε_s is favorable to the species for the set of data Π_1 but it is unfavorable to the species for Π_2 :

Figure 3.10 gives the shape of the functions Λ^0 and Γ^0 for $s=0.5$. Evolution of both curves seem very similar althought the behavior for λ small can be totally different implying that the nature of the probabilistic system is different from the deterministic system.

We can plot in the plane (s,λ) the zero contour lines of the invasion rates for the deterministic model and the probabilistic model as shown in figure 3.11. In each zone of this figure, the sign of the pair (Λ^0,Γ^0) is constant and is plainly indicated by a pair of signs.

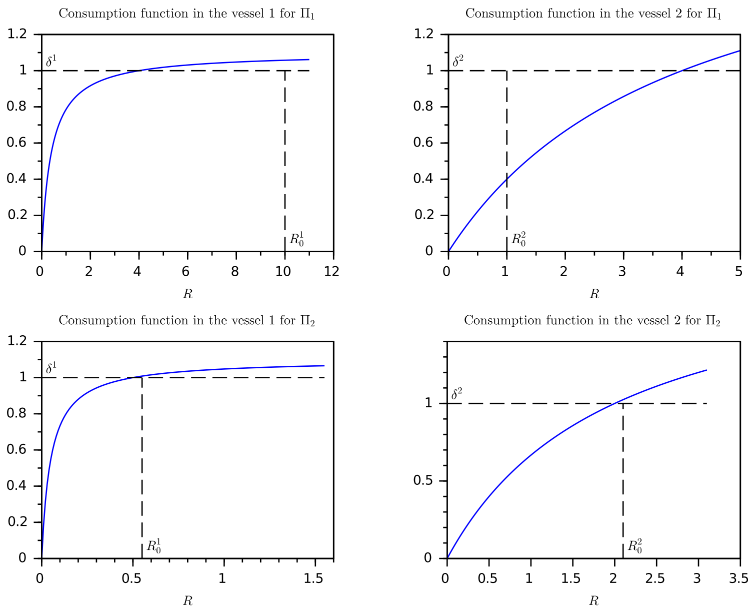


FIGURE 3.8 – The consumption functions in the different vessels for Π_1 and Π_2.

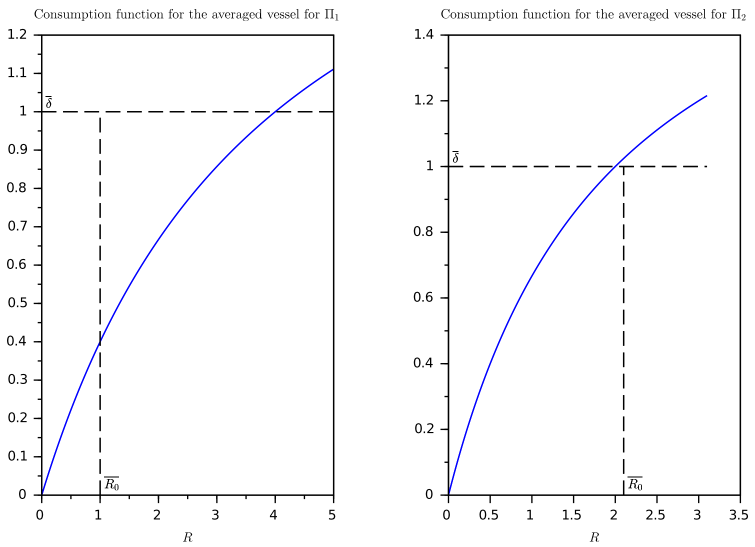


FIGURE 3.9 – The averaged consumption functions for Π_1 and Π_2.

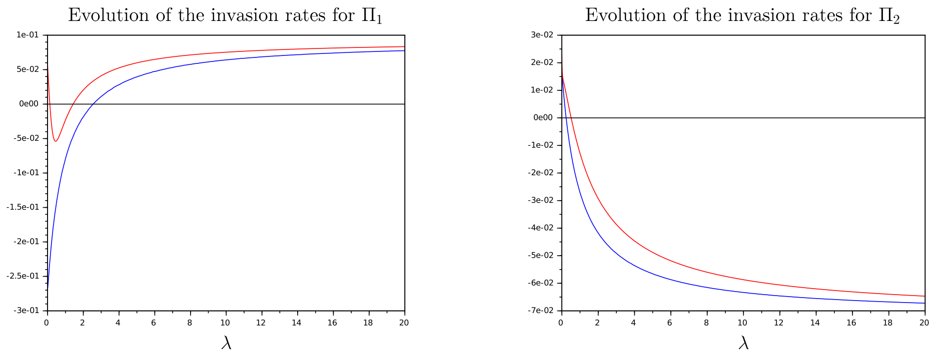


FIGURE 3.10 – Evolution of the invasion rates for Π_1 and Π_2.

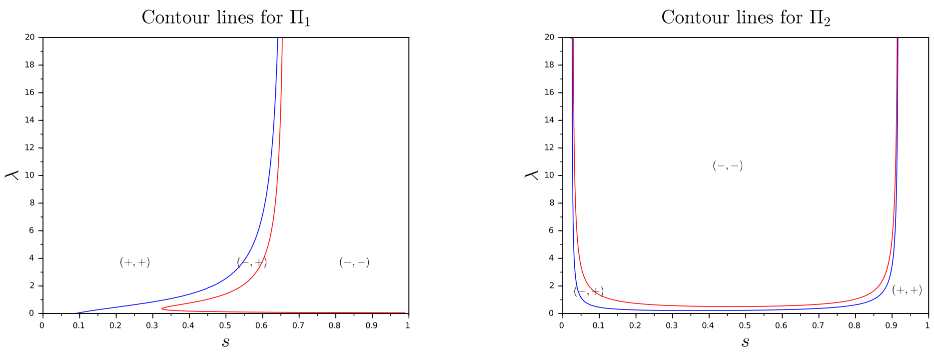


FIGURE 3.11 – Contour lines of the invasion rates for Π_1 and Π_2.

Remark 3.4.6. *These numerical simulations show that the long time behavior of our two models is globally the same. The transitions between the survival areas and the exctinction areas are very similar except for λ close to zero where there can be a huge difference between the two models (see Π_1 typically). This difference if mostly due to the fact that the limits of the probabilistic and deterministic invasion rates as λ goes to zero are not the same.*

3.4.2 Comparison of the invasion rates in the two species case

We can now have a qualitative discussion on the behavior of the invasion rates when two species are introduced in our models. Once again, we recall their expressions and properties. Recall that we assumed that $R_0^1 = R_0^2$. First the probabilistic case :

Theorem 3.4.7. *The invariant measure μ_w of (Z_t) restricted to $M_{0,w}$ is unique. The invasion rates Λ_u and Λ_v are computable and their explicit expressions is given by :*

$$\Lambda_w = \frac{\int h_w(x) g_{\overline{w}}(x) e^{\lambda H_{\overline{w}}(x)} dx}{\int g_{\overline{w}}(x) e^{\lambda H_{\overline{w}}(x)} dx}.$$

Where :

$$h_w(x) = \frac{(f_w^2(R_0 - x) - \delta^2)|f_{\overline{w}}^1(R_0 - x) - \delta^1| + (f_w^1(R_0 - x) - \delta^1)|f_{\overline{w}}^2(R_0 - x) - \delta^2|}{|f_{\overline{w}}^1(R_0 - x) - \delta^1| + |f_{\overline{w}}^2(R_0 - x) - \delta^2|}$$

$$g_w(x) = \left(|f_w^1(R_0 - x) - \delta^1| + |f_w^2(R_0 - x) - \delta^2|\right) \frac{|f_w^1(R_0 - x) - \delta^1||f_w^2(R_0 - x) - \delta^2|}{x}$$

and

$$\begin{aligned} H_w(x) = &-(\omega_w^1 \beta_w^1 + \omega_w^2 \beta_w^2) \log(x) + \omega_w^1 \alpha_w^1 \log\left((b_w^1 + R_0 - x)|f_w^1(R_0 - x) - \delta^1|\right) \\ &+ \omega_w^2 \alpha_w^2 \log\left((b_w^2 + R_0 - x)|f_w^2(R_0 - x) - \delta^2|\right). \end{aligned}$$

The constants are defined by :

$$\begin{aligned} R_w^j &= \frac{b_w^j \delta^j}{a_w^j - \delta^j}, \\ \gamma_w^j &= \frac{\lambda^j}{\delta^j} \frac{R_w^j}{R_0 - R_w^j}, \\ \omega_w^1 &= \frac{s}{\delta^1} \frac{R_w^1}{R_0 - R_w^1}, \quad \omega_w^2 = \frac{1-s}{\delta^2} \frac{R_w^2}{R_0 - R_w^2}, \\ \alpha_w^j &= \frac{a_w^j}{a_w^j - \delta^j}, \\ \beta_w^j &= 1 + \frac{R_0}{b_w^j}. \end{aligned}$$

Recall that we gave a definition of the invasion rates Γ_w in section 3.2.2.

Proposition 3.4.8. *Note R_w the resource concentration for the semi-trivial stationary equilibrium E_w. By definition Γ_w is the maximum eigenvalue of the matrix :*

$$M_{\overline{w}}(R_w) = \begin{pmatrix} f^1_{\overline{w}}(R^1_w) - \delta^1 - \lambda^1 & \lambda^1 \\ \lambda^2 & f^2_{\overline{w}}(R^2_w) - \delta^2 - \lambda^2 \end{pmatrix}.$$

Though it is possible to compute R_w, the complexity of its expressions does not make it interesting to give it formally. However its explicit expressions is used in the numerical simulations. Once again we give the limits of the invasion rates :

Proposition 3.4.9. *The following limits are computable :*

$$\lim_{\lambda\to+\infty} \Lambda_w = \lim_{\lambda\to+\infty} \Gamma_w = (1-s)\left(f^1_w(R^\infty_w) - \delta^1\right) + s\left(f^2_w(R^\infty_w) - \delta^2\right).$$

where R^∞_w is the unique positive solution of the equation :

$$(1-s)\left(f^1_{\overline{w}}(R) - \delta^1\right) + s\left(f^2_{\overline{w}}(R) - \delta^2\right) = 0.$$

Once again the behavior of the two models is the same for λ large enough. Moreover :

$$\begin{aligned} \lim_{\lambda\to 0} \Lambda_w &= (1-s)\left(f^1_w(R^1_{\overline{w},0}) - \delta^1\right) + s\left(f^2_w(R^2_{\overline{w},0}) - \delta^2\right), \\ \lim_{\lambda\to 0} \Gamma_w &= \max\left(f^1_w(R^1_{\overline{w},0}) - \delta^1, f^2_w(R^2_{\overline{w},0}) - \delta^2\right). \end{aligned}$$

where

$$R^j_{w,0} = \frac{b^j_w \delta^j}{a^j_w - \delta^j} \text{ is the solution of the equation } f^j_w(R) - \delta^j = 0.$$

Let us now compare the probabilistic and the deterministic dependance of the invasion rates with respect to λ and s within the two models on particular example. In all the following figures, the blue color is associated to the species u whereas the red color is associated to the species v. The different couple of signs give the couple of signs of the invasion rates (Λ_u, Λ_v) in the probabilistic case and (Γ_u, Γ_v) in the determinisctic case. Recall that according to theorem 3.2.16 and theorem 3.1.15 the sign of the invasion rates gives information on the long time behavior of each model.

The huge difference between theorem 3.2.16 and theorem 3.1.15 lies in the case where the invasion rates do not have the same sign. In the probabilistic case, it is an extinction case where the disappearing species is the one with the negative invasion rate. However, in the deterministic case, it is possible to have bi-stability or extinction when the invasion rates are of opposite signs. We show in the following figure 3.14 that in the area of the plane (s, λ) where the invasion rates are of opposite signs, a little area of bi-stability may appear.

a - Typical coexistence situation. b - Typical bistability sitation.

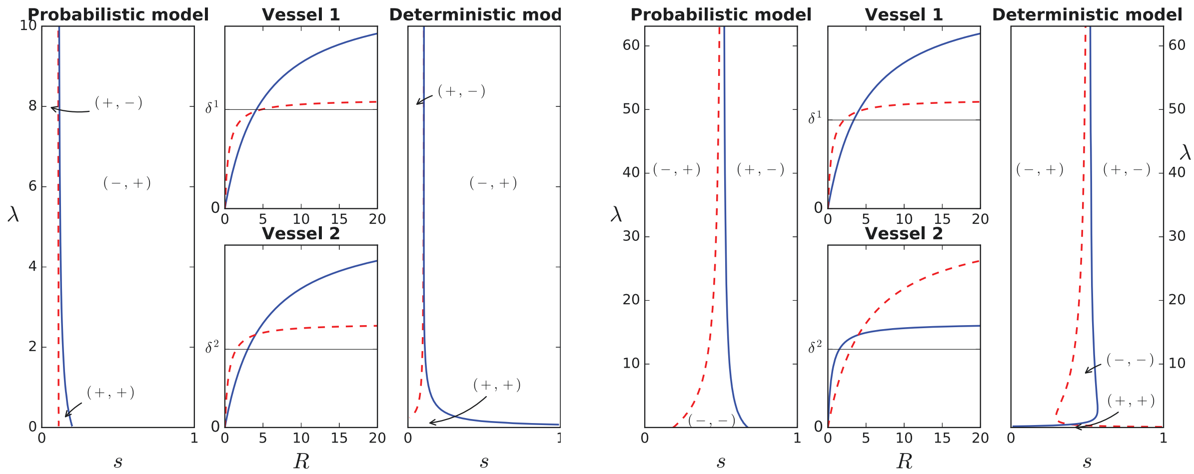


FIGURE 3.12 – a - $(a_u^1, a_u^2, a_v^1, a_v^2) = (4.2, 4, 2.1, 2)$, $(b_u^1, b_u^2, b_v^1, b_v^2) = (5, 5, 0.5, 0.5)$, $(\delta^1, \delta^2) = (1.9, 1.5)$ and $R_0 = 8$. b - The role of species are reversed between the vessels. $(a_u^1, a_u^2, a_v^1, a_v^2) = (4.2, 2, 2.1, 4)$, $(b_u^1, b_u^2, b_v^1, b_v^2) = (5, 0.5, 0.5, 5)$, $(\delta^1, \delta^2) = (1.7, 1.5)$ and $R_0 = 8$.

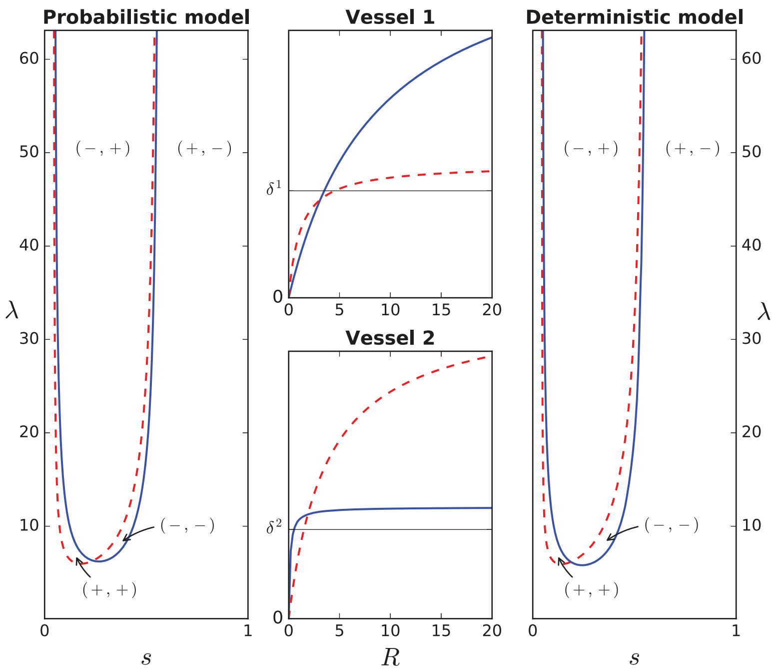


FIGURE 3.13 – Zero contour lines when the two vessels are favorable to the same species. $(a_u^1, a_u^2, a_v^1, a_v^2) = (3.5, 2.5, 1.25, 7)$, $(b_u^1, b_u^2, b_v^1, b_v^2) = (8.75, 0.125, 1.125, 3.75)$, $(\delta^1, \delta^2) = (1, 2)$ and $R_0 = 7$.

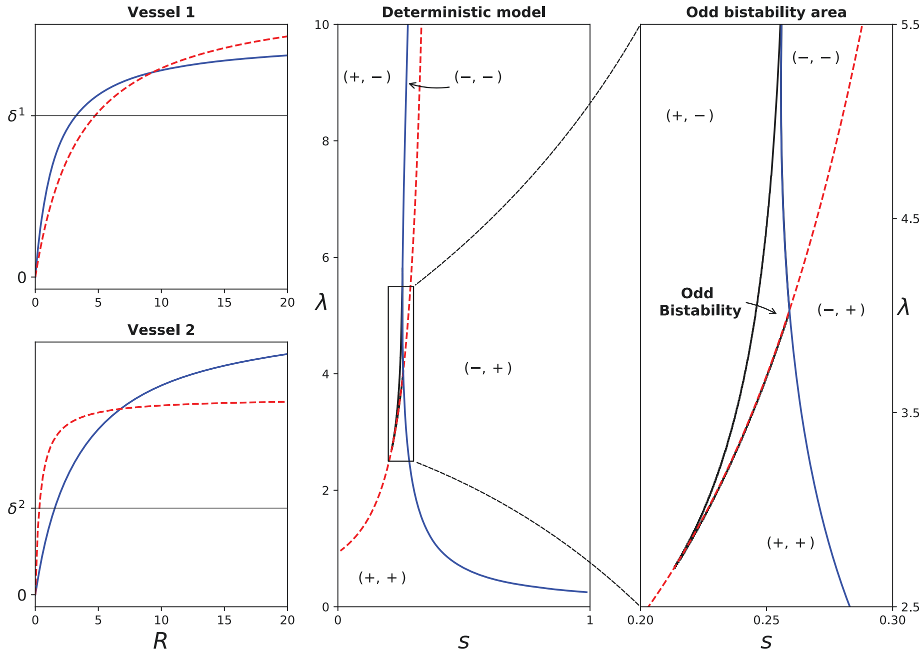


FIGURE 3.14 – Zoom on the odd bistable area in a $(+,-)$ area for the deterministic model. $(a_u^1, a_u^2, a_v^1, a_v^2) = (3.7, 3.6, 4.4, 2.5)$, $(b_u^1, b_u^2, b_v^1, b_v^2) = (1.55, 3.55, 3.6, 0.4)$, $(\delta^1, \delta^2) = (2.5, 1.1)$ and $R_0 = 20$.

3.4.3 Concluding remarks

Let us conclude on the similarities and differencies between the two models we studied in this chapter. For each models we gave a definition of the invasion rates of the introduced species which depend only on the parameters of the systems. Despite the differences of their mathematical nature, theorem 3.2.16 and 3.1.15 show that the long-time behavior of the two models only depend on the signs of the invasion rates. Hence, we decided to compare the two models by comparing the behavior of the invasion rates according to the parameters (s, λ) (where $\lambda^1 = s\lambda$ and $\lambda^2 = (1-s)\lambda$). In the probabilistic case, (λ^1, λ^2) are the parameters of the Markov chain governing the switching between the environments whereas in the deterministic case, (λ^1, λ^2) are the exchange parameters between the two vessels.

From the previous theorems and numerical simulations come the following similarities between the two models :

— When the invasion rates are positive (resp. negative) for u and v, the probabilistic system and the deterministic system are in a coexistence state (resp. bistable state). Moreover, we proved numerically that it is possible to have bistability with two introduced species and two vessels. This numerical result is similar to the result of [Hofbauer et So, 1994] where they proved in their particular case (dilutions rates and consumption functions not depending on the vessel, two introduced species) that at least three vessels are needed for the existence of an unstable coexistence equilbrium.

— The limits of the invasion rates when λ goes to infinity are the same for both models. We saw that the reason behind this result is the averaging phenomenon occuring when λ is large enough implying that both systems behave like the averaged chemostat ε_s. Graphically, we see that the zero contour lines of the invasion rates are really alike for λ large enough and have the same asymptote when λ goes to infinity.

The main differences between our competition models are the following :

— In the probabilistic model, when the invasion rates have opposite signs, only one species survives, the one with the positive invasion rate. However, in the deterministic model, when the invasion rates have opposite signs, it is possible for the system to be in an "odd" bistable state where one of the stable stationary equilibrium is a coexistence equilibrium.

— The most important difference between the two models occurs when λ is close to zero because the limits of the invasion rates when λ goes to zero are different. We can interpret this difference by the difference of nature of the two models when λ is very small. For the probabilistic model, λ very small implies that the process follows for a very long time the flow of each chemostat ε^1 and ε^2 and the invasion rates measures the averaging of the behavior of each flows. But in the deterministic case, when λ is very small, there are almost no exchanges between the two vessels implying that the system almost behaves like two isolated chemostats.

We give here a little discussion over the parameter restrictions we did on our models. First, note that the most important parameters involved in the heterogenity of our two models are the quantities R_w^j which are the minimum resource quantities needed by species

w to survive in the vessel j (when the vessels are isolated). Recall that R_w^j is solution of the equation :

$$f_w^j(R) - \delta_w^j = 0$$

where f_w^j are the consumption functions and δ_w^j the dilution rates. As a consequence, allowing the consumption functions or the dilution rates to depend on w and j is the easiest way to allow the parameters R_w^j to be different according to w and j.

Note that in the probabilistic model we had to assume that the ressource entries R_0^j are equal in order to reduce the system and do some computations. But this hypothesis is not necessary in the deterministic model where we claim that the computations are still possible. In fact, in [Smith et Waltman, 1995], the authors model the environment heterogeneity with a different resource input for each vessel, and thanks to this heterogeneity, a coexistence stationary equilibrium may appear. In our case, we model the environment heterogeneity by taking vessel dependant consumption functions and dilution rates.

In all the chapter, we decided that only the consumption functions will depend on w and j while the dilution rates only depend on the vessel j. This hypothesis is crucial because it allows us to reduce the systems of differential equations (thanks to the variable Σ) into a monotonous system, ultimately leading to the long-time behavior theorems. However, it was not a natural choice in the deterministic model because in the gradostat applications, the consumption functions do not depend on the vessels but only on the species. As a consequence, this hypothesis took us away from the gradostat context (and its application in the industry for example) to bring us in a more theoretical ecological study of the spatial heterogeneity.

Nonetheless, the approach with the functions F_w and g_w might lead to the obtention of the existence and stability of the stationary equilibria of the gradostat-like model when the dilution rates also depend on the species and can be the subject of some future work.

3.5 A sufficient condition for the existence of the bi-stability in the deterministic model

The numerical simulations showed that is is possible to pick wisely the chemostats ε^1, ε^2 and the rates λ^1, λ^2 such that the systems (probabilistic or deterministic) are in a bi-stable state. In the deterministic case, the question of the existence of bi-stable state is a hard question, only few articles shows that it is numerically possible and in complicated cases (see [Hofbauer et So, 1994] for example). We will give in this section a surprisingly computational proof of the existence of the bi-stability for the gradostat-like system introduced in section 3.1.2.

Set c_u and c_v in $\mathbb{R}_+$ the bifurcation parameters. We are interested in the stationary equilibrium of the following equation :

$$\begin{cases} \dot{U}(t) = U(t)(c_u f_u(R_0 - U(t) - V(t)) - \delta) + \lambda K U(t) \\ \dot{V}(t) = V(t)(c_v f_v(R_0 - U(t) - V(t)) - \delta) + \lambda K V(t), \end{cases} \tag{3.36}$$

We will still call $E_0 = (0, 0)$ the trivial stationary equilibrium. We will note $E_u(c_u)$ and

$E_v(c_v)$ the semi-trivial stationary equilibrium and $E_c(c_u, c_v)$ a coexistence stationary equilibrium.

In [Castella et Madec, 2014] bifurcation techniques are used to construct coexistence solutions in a chemostat-like model with species dependent diffusion rates. But the results of these article are extended to our simple gradostat system (3.36) (see [Madec, 2011]). The following theorem holds.

Theorem 3.5.1. *It exists c_u^0 such that $E_u(c_u)$ exists if and only if $c_u > c_u^0$.*

It exists c_v^0 such that $E_v(c_v)$ exists if and only if $c_v > c_v^0$.

Remark 3.5.2. *According to theorem 3.1.9, c_w^0 is the smallest value of c_w for which the following matrix has zero for eigenvalue :*

$$M_w = \begin{pmatrix} f_w^1(R_0) - \delta^1 - \lambda^1 & \lambda^1 \\ \lambda^2 & f_w^2(R_0) - \delta^2 - \lambda^2 \end{pmatrix}.$$

Let us note $\mathcal{C}_w = \{(c_w, E_w(c_w)),\ c_w > c_w^0\}$ the subsets of semi-trivial solutions. Next theorem gives the existence of coexistence stationary equilibrium.

Theorem 3.5.3. *(Coexistence solutions)*

— *Set $c_u > c_u^0$. It exists $c_v^* = c_v^*(c_u) > c_v^0$ and $c_v^{**} = c_v^{**}(c_u) > c_v^0$ such that, if we note $\overline{c_v} = \max(c_v^*, c_v^{**})$ and $\underline{c_v} = \min(c_v^*, c_v^{**})$ it exists a function :*

$$B_{c_u} : c_v \in (\underline{c_v}, \overline{c_v}) \mapsto E_c(c_u, c_v).$$

Moreover $B_{c_u}(c_v^*) \in \mathcal{C}_1$, $B_{c_u}(c_v^{**}) \in \mathcal{C}_2$.

— *Set $c_v > c_v^0$. It exists $c_u^* = c_u^*(c_v) > c_u^0$ and $c_u^{**} = c_u^{**}(c_v) > c_u^0$ such that, if we note $\overline{c_u} = \max(c_u^*, c_u^{**})$ and $\underline{c_u} = \min(c_u^*, c_u^{**})$ it exists a function :*

$$B_{c_v} : c_u \in (\underline{c_u}, \overline{c_u}) \mapsto E_c(c_u, c_v).$$

Moreover $B_{c_v}(c_u^*) \in \mathcal{C}_v$, $B_{c_v}(c_u^{**}) \in \mathcal{C}_u$.

Remark 3.5.4. *It comes that in this simple case, c_w^* is the smallest value of c_w for which the invasion rate $\Gamma_w = 0$ (and c_w^{**} is the maximum value). Recall that Γ_w is the smallest eigenvalue of the matrix :*

$$M_w(R_{\overline{w}}^*) = \begin{pmatrix} c_w f_w^1(R_{\overline{w}}^1) - \delta^1 - \lambda^1 & \lambda^1 \\ \lambda^2 & c_w f_w^2(R_{\overline{w}}^2) - \delta^2 - \lambda^2 \end{pmatrix}.$$

where $R_{\overline{w}}$ is the resource concentration associated to the semi equilibrium $E_{\overline{w}}(c_{\overline{w}})$.

Let us call Θ the domain of the plane (c_u, c_v) where previous theorem gives the existence of at least one coexistence stationary equilibrium. The following theorem gives us more informations on the shape of this domain Θ.

Theorem 3.5.5. *The following properties holds :*

— *$c_v^{**}(c_u)$ (resp. $c_u^{**}(c_v)$) satisfies $c_u^*(c_v^{**}(c_u)) = c_u$ (resp. $c_v^*(c_u^{**}(c_v)) = c_v$).*

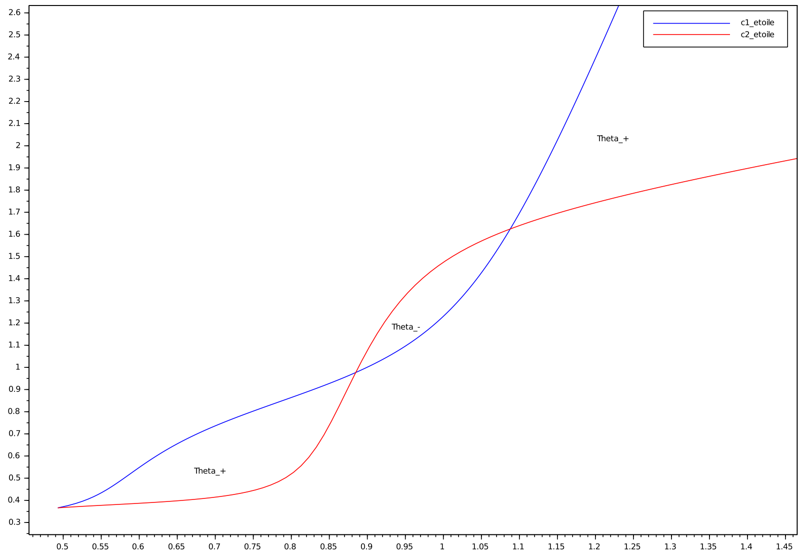


FIGURE 3.15 – Example of shape of the domain Θ.

— *The functions* $c_v \in (c_v^0, +\infty) \mapsto c_u^*(c_v)$ *and* $c_u \in (c_u^0, +\infty) \mapsto c_v^*(c_u)$ *are continuous and increasing. Moreover*

$$\lim_{c_v \to c_v^0} c_u^*(c_v) = c_u^0, \quad \lim_{c_v \to +\infty} c_u^*(c_v) = +\infty, \quad \lim_{c_u \to c_u^0} c_v^*(c_u) = c_v^0, \quad \lim_{c_u \to +\infty} c_v^*(c_u) = +\infty$$

— *Call* $\Theta_- = \{(c_u, c_v),\ c_u < c_u^*(c_v)$ *et* $c_v < c_v^*(c_u)\}$, $\Theta_+ = \{(c_u, c_v),\ c_u > c_u^*(c_v)$ *and* $c_v > c_v^*(c_u)\}$ *and* $\Theta = \Theta_- \cup \Theta_+$. *Then* $\overline{\Theta}$ *is a connected set and for all* $(c_u, c_v) \in \Theta$, *there exists at least one coexistence stationary equilibrium.*

Remark 3.5.6. *According to theorem 3.1.15 in the area* Θ *there exists a unique coexistence stationary equilibrium. Moreover, in* Θ_-, *this equilibrium is unstable and in* Θ_+, *this equilbrium is stable (indeed, the semi-trivial equilibrium* $E_{\overline{w}}(c_{\overline{w}})$ *is unstable if and only if* $c_w > c_w^*(c_{\overline{w}})$*).*

The diagram of bifurcation of the system is the graphic representation of c_u^* and c_v^* in the plane (c_u, c_v) (see figure 3.15).

We will see in the following that it is possible to define the quantities c_w^0 and c_w^* for λ equal 0. Moreover c_u and c_v are proven to be regular in $\lambda = 0$ in [Madec, 2011]. Hence, the relative positioning of the curves of c_u^* and c_v^* for λ equal 0 determines the relative positioning of the curves of c_u^* and c_v^* for λ small enough.

In this section, we claim that if the curves of c_u^* and c_v^* for λ equal 0 cross themselves in a good area of the quarter plane $\mathbb{R}_+^2$ then $\Theta_- \neq \emptyset$ for λ small enough.

Set λ equal 0. Since there are no transfer of material between the two vessels, the study of the system limits itself at the study of the evolution of two simple chemostat. The species w enters in competition in the chemostat j if and only if $R_w^j < R_0$ where,

$$R_w^j = \frac{b_w^j \delta^j}{c_w a_w^j - \delta^j}.$$

This condition defines two constants $c_w^{0,1}$ and $c_w^{0,2}$ such that species w enters in competition in the chemostat j if and only if $c_w > c_w^{0,j}$. Calling $c_w^0 = \min(c_w^{0,1}, c_w^{0,2})$ and $c_w^{0\prime} = \max(c_w^{0,1}, c_w^{0,2})$, it comes that the semi-trivial stationary equilibrium E_w exists if and only if $c_w > c_w^0$.

Define $P = (c_u^{0\prime}, +\infty) \times (c_v^{0\prime}, +\infty)$.

The following theorem gives a sufficient condition over the curves of c_u^* and c_v^* (taken at $\lambda = 0$) for which the system can be in a bi-stable state for λ small enough for some good values of (c_u, c_v).

Theorem 3.5.7. *If the curves of c_u^* and c_v^* for $\lambda = 0$ admit a unique intersection (c_u^+, c_v^+) in the quarter plan P defined previously, then for any rate λ small enough, the area $\Theta_- \neq \emptyset$ and appears from the intersection (c_u^+, c_v^+).*

We give here a numerical example in order to illustrate this theorem. Set $(a_w^j)_{1\leq j\leq 2} = \begin{pmatrix} 3.5 & 2.5 \\ 1.25 & 7 \end{pmatrix}$, $(b_w^j)_{1\leq i,j\leq 2} = \begin{pmatrix} 8.75 & 0.125 \\ 1.125 & 3.75 \end{pmatrix}$, $(\delta^1, \delta^2) = (1, 2)$ and $R_0 = 7$. Figure 3.16 shows the bifurcation diagram for $\lambda = 0$. Figure 3.17 shows the bifurcation diagram for $\lambda = 1$ where we can see a small area of bi-stability.

The two following subsections are dedicated to the proof of this theorem.

3.5.1 Full description of the system without exchanges

According to theorem 3.1.1, the expressions for c_u^* and c_v^* are :

$$\begin{aligned} \forall c_u > c_u^0 \quad & c_u^*(c_v, 0) = \inf\{c_u, \exists j \text{ such that } R_1^j(c_u) < R_2^j(c_v)\} \\ \forall c_v > c_v^0 \quad & c_v^*(c_u, 0) = \inf\{c_v, \exists j \text{ such that } R_2^j(c_v) < R_1^j(c_u)\}, \end{aligned}$$

with :

$$\begin{aligned} c_u^0 &= \inf\{c_u, \exists j \text{ such that } R_1^j(c_u) < R_0\} \\ c_v^0 &= \inf\{c_v, \exists j \text{ such that } R_2^j(c_u) < R_0\}. \end{aligned}$$

A simple computation show that :

$$\begin{aligned} c_u^0 &= \min\left(\frac{\delta^1}{f_u^1(R_0)}, \frac{\delta^2}{f_u^2(R_0)}\right) = \min\left(c_u^{0,1}, c_u^{0,2}\right) \\ c_v^0 &= \min\left(\frac{\delta^1}{f_v^1(R_0)}, \frac{\delta^2}{f_v^2(R_0)}\right) = \min\left(c_v^{0,1}, c_v^{0,2}\right). \end{aligned}$$

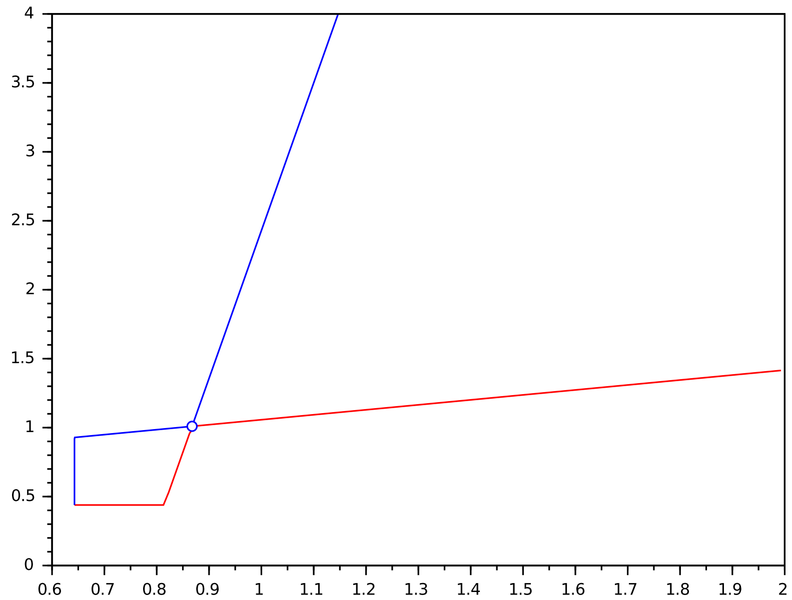


FIGURE 3.16 – for $\lambda = 0$ in blue c_u^* and in red c_v^*, in abscissa c_u and in ordinate c_v.

We will note :

$$c_u^{0\prime} = \max\left(\frac{\delta^1}{f_u^1(R_0)}, \frac{\delta^2}{f_u^2(R_0)}\right)$$
$$c_v^{0\prime} = \max\left(\frac{\delta^1}{f_v^1(R_0)}, \frac{\delta^2}{f_v^2(R_0)}\right)$$

In order to compute $c_u^*(c_v, 0)$ and $c_v^*(c_u, 0)$, we have to look closely to the curves $\mathcal{C}^j$ corresponding to the set of points (c_u, c_v) satisfying $R_1^j(c_u) = R_2^j(c_v)$. It appears that in this case, they are straight lines of equation :

$$\mathcal{C}^j : c_v = \frac{\delta^j}{f_v^j(R_1^j)} = \frac{a_u^j b_v^j}{b_u^j a_v^j} c_u + \delta^j \frac{b_u^j - b_v^j}{b_u^j a_v^j},$$

and equivalently :

$$\mathcal{C}^j : c_u = \frac{\delta^j}{f_u^j(R_2^j)} = \frac{a_v^j b_u^j}{b_v^j a_u^j} c_u + \delta^j \frac{b_v^j - b_u^j}{b_v^j a_u^j}.$$

Note that $\mathcal{C}^j$ is well defined only for $c_u > c_u^{0,j}$ and $c_v > c_v^{0,j}$.

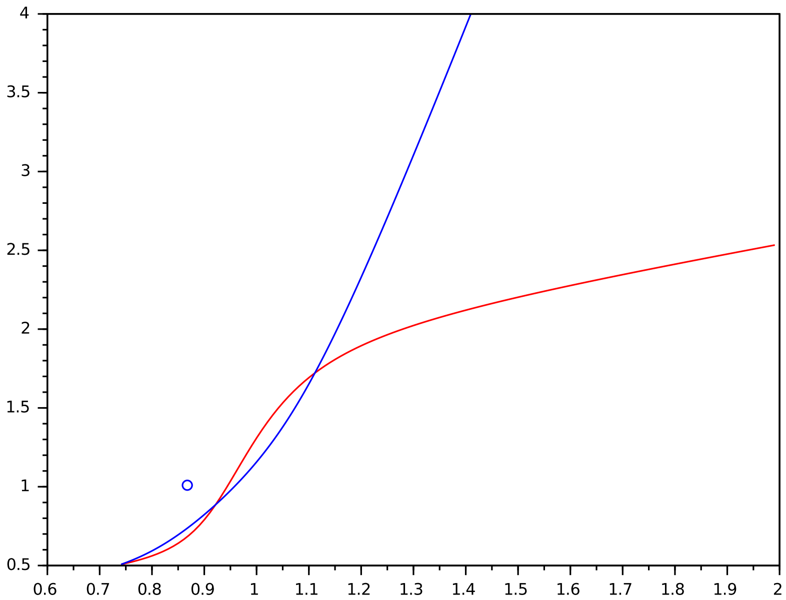


FIGURE 3.17 – for $\lambda = 1$ in blue c_u^* and in red c_v^*, in abscissa c_u and in ordinate c_v (The point shows the intersection between the curves of c_u^* and c_v^* for $\lambda = 0$).

We will call u^j the slope of $\mathcal{C}^j$:

$$u^j = \frac{a_v^j b_u^j}{b_v^j a_u^j} = \frac{f_v^{j\prime}(0)}{f_u^{j\prime}(0)}.$$

The curve $\mathcal{C}^j$ marks, for the chemostats j, the border between the set of parameters for which species u survives and species v goes to extinction and the set of parameters for which species v survives and species u goes to extinction.

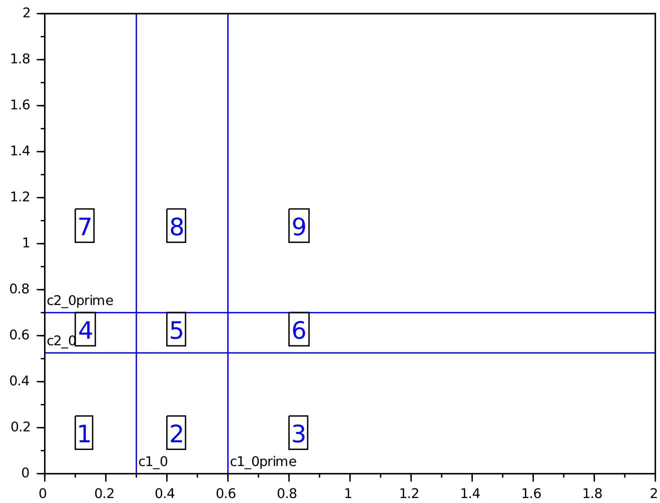
Remark 3.5.8. *If $u^1 \neq u^2$, $\mathcal{C}^1$ and $\mathcal{C}^2$ admit a unique intersection point which coordinates (c_u^+, c_v^+) are :*

$$c_u^+ = \frac{\delta^1 \frac{b_u^2 - b_v^2}{a_v^2 b_u^2} - \delta^2 \frac{b_u^1 - b_v^1}{a_v^1 b_u^1}}{\frac{a_u^1 b_v^1}{a_v^1 b_u^1} - \frac{a_u^2 b_v^2}{a_v^2 b_u^2}}$$

and

$$c_v^+ = \frac{\delta^1 \frac{b_v^2 - b_u^2}{a_u^2 b_v^2} - \delta^2 \frac{b_v^1 - b_u^1}{a_u^1 b_v^1}}{\frac{a_v^1 b_u^1}{a_u^1 b_v^1} - \frac{a_v^2 b_u^2}{a_u^2 b_v^2}}.$$

Note that at the intersection, $R_1^1(c_u^+) = R_2^1(c_v^+)$ and $R_1^2(c_u^+) = R_2^2(c_v^+)$.



We divide the plane (c_u, c_v) in nine areas like in figure 3.5.1.

Remark 3.5.9. *Assume that* $c_v^0 = c_v^{0,1}$. *Then in the areas* 2, 5 *and* 8, *species* u *can survive only in the chemostat* 1. *In the areas* 4, 5 *and* 6, *species* v *can survive only in the chemostat* 1. *The graphic representation of the quantities* c_u^* *and* c_v^* *looks like 3.18.*

Remark 3.5.10. *Assume that* $c_v^0 = c_v^{0,2}$. *Then in the areas* 2, 5 *and* 8, *species* u *can survive only in the chemostat* 1. *In the areas* 4, 5 *and* 6, *species* v *can survive only in the chemostat* 2. *Therefore, area* 5 *is a coexistence area for the globallity of our system. The graphic representation of the quantities* c_u^* *and* c_v^* *looks like 3.19.*

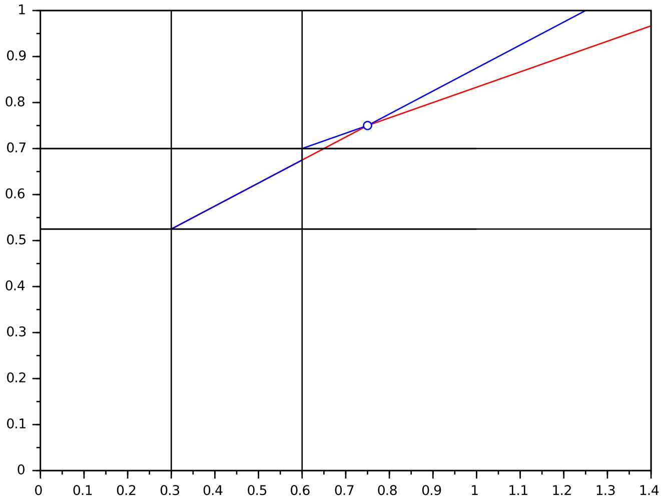


FIGURE 3.18 – For $\lambda = 0$, in blue c_u^* and in red c_v^*, in abscissa c_u and in ordinate c_v

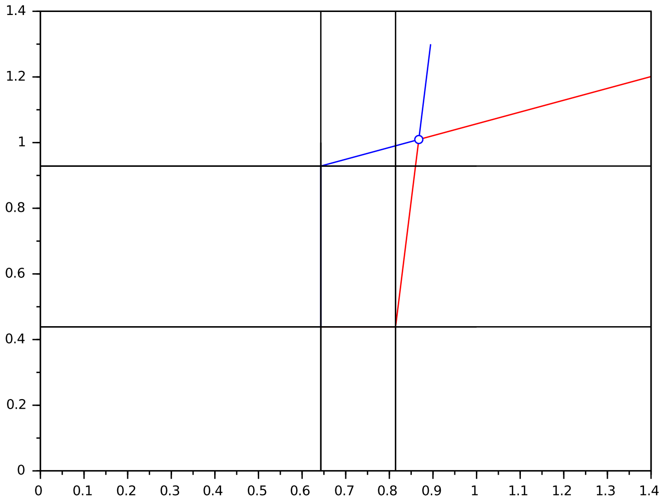


FIGURE 3.19 – for $\lambda = 0$ in blue c_u^* and in red c_v^*, in abscissa c_u and in ordinate c_v

3.5.2 Bi-stability for small exchanges

Here is another formulation for theorem 3.5.7 using the quantities defined in previous subsection.

Theorem 3.5.11. *Assume that $u^1 \neq u^2$. If the intersection point (c_u^+, c_v^+) is in area 9 then for λ smal enough, it exists parameters (c_u, c_v) for which the system is bistable.*

Proof. The proof is totally computational. For the sake of readability we will cut it in three parts. A point (c_u, c_v) satisfying for $\lambda > 0$:

$$c_u^*(c_v, \lambda) > c_u \quad \text{and} \quad c_v^*(c_u, \lambda) > c_v,$$

is in a bi-stable area. We are going to search $(\alpha_u, \alpha_v) \in \mathbb{R}^2$ such that if :

$$\begin{pmatrix} c_u \\ c_v \end{pmatrix} = \begin{pmatrix} c_u^+ \\ c_v^+ \end{pmatrix} + \lambda \begin{pmatrix} \alpha_u \\ \alpha_v \end{pmatrix},$$

then :

$$c_u^*(c_v, \lambda) > c_u \quad \text{and} \quad c_v^*(c_u, \lambda) > c_v.$$

First step :

We are going to develop $c_u^*(c_v, \lambda)$ and $c_v^*(c_u, \lambda)$ at $\lambda = 0$.

In order to compute c_v^* (same way for c_u^*), we linearize the system around the semi-trivial equilibrium point $(R_u, U, 0)$ and we look at the eingenvalues of the matrix :

$$M(\lambda) = \begin{pmatrix} c_v f_v^1(R^1) - \delta^1 - \lambda & \lambda \\ \lambda & c_v f_v^2(R^2) - \delta^2 - \lambda \end{pmatrix}.$$

Where U is the non zero solution of the equation $U(c_u f_u(R) - \delta) + \lambda K U = 0$ and $R = R_0 - U)$.

For $\lambda > 0$, $c_v^*(c_u, \lambda)$ is the smallest value of c_v for which this matrix is not reversal (admits 0 as eigenvalue). As a consequence, the limited development of R is required. Since $R = R_0 - U$, the development of U in $\lambda = 0$ will be computated.

U is solution of $F_1(\lambda, U) = U(c_u f_u(R) - \delta) + \lambda K U = 0$. More precisely, U is solution of :

$$F_1(\lambda, U) = \begin{pmatrix} U^1(c_u f_u^1(R_0 - U^1) - \delta^1) + \lambda(U^2 - U^1) \\ U^2(c_u f_u^2(R_0 - U^2) - \delta^2) + \lambda(U^1 - U^2) \end{pmatrix} = 0$$

in order to use the implicit function theorem, one has to compute the jacobian of F_1 in regards with U :

$$dF_1(\lambda, U) = \begin{pmatrix} c_u f_u^1(R_0 - U^1) - \delta^1 - U^1 c_u f_u^{1\prime}(R_0 - U^1) - \lambda & \lambda \\ \lambda & c_u f_u^2(R_0 - U^2) - \delta^2 - U^2 c_u f_u^{2\prime}(R_0 - U^2) - \lambda \end{pmatrix}.$$

Therefore :

$$dF_1(0, U) = \begin{pmatrix} -U^1 c_u f_u^{1\prime}(R_u^1) & 0 \\ 0 & -U^2 c_u f_u^{2\prime}(R_u^2) \end{pmatrix}$$

which is reversal (where $R_u^j = R_u^j(0) = \frac{b_u^j \delta^j}{c_u a_u^j - \delta^j}$). As a consequence, it exists a neighborhood X of $(0, U(0))$, a neighborhood Y of 0 and $g : Y \to \mathbb{R}^2$ such that :

$$\forall (\lambda, U) \in X, \quad F_1(\lambda, U) = 0 \Leftrightarrow U = g(\lambda),$$

and since $h(\lambda) = F_1(\lambda, g(\lambda)) = 0$, $h'(0) = 0$ which gives :

$$\begin{pmatrix} U^2 - U^1 \\ U^1 - U^2 \end{pmatrix} + \begin{pmatrix} -U^1 c_u f_u^{1\prime}(R_0 - U^1) & 0 \\ 0 & -U^2 c_u f_u^{2\prime}(R_0 - U^2) \end{pmatrix} g'(0) = 0.$$

As a consequence :

$$g'(0) = \begin{pmatrix} \frac{U^2 - U^1}{U^1 c_u f_u^{1\prime}(R_0 - U^1)} \\ \frac{U^1 - U^2}{U^2 c_u f_u^{2\prime}(R_0 - U^2)} \end{pmatrix} = \begin{pmatrix} p^1 \\ p^2 \end{pmatrix}.$$

And obviously $U(\lambda) = U + \lambda g'(0) + o(\lambda)$. Now we can look at the matrix :

$$M(\lambda) = \begin{pmatrix} c_v f_v^1(R_0 - U^1(\lambda)) - \delta^1 - \lambda & \lambda \\ \lambda & c_v f_v^2(R_0 - U^2(\lambda)) - \delta^2 - \lambda \end{pmatrix}.$$

Let us write $U^j(\lambda) = U^j + p^j \lambda + q^j \lambda^2 + o(\lambda^2)$, the development of this previous matrix at the second order gives (remind that $R_0 - U^j = R_u^j$) :

$$M(\lambda) = \begin{pmatrix} f^1 - \lambda C_v^1 - \lambda^2 D^1 + o(\lambda^2) & \lambda \\ \lambda & f^2 - \lambda C_v^2 - \lambda^2 D^2 + o(\lambda^2) \end{pmatrix},$$

where $C_v^j = p^j c_v f_v^{j\prime}(R_1^j) + 1 = \frac{U^{\bar{j}} - U^j}{U^j} \frac{c_v^+ f_v^{1\prime}(R_1^j)}{c_u^+ f_u^{1\prime}(R_1^j)} + 1$. This constant depends on c_u. We will see later that it will be factor of a order 1 term which makes it pointless to develop. Hence, set :

$$C_w^j = \frac{U_{\overline{w}}^{\bar{j}} - U_{\overline{w}}^j}{U_{\overline{w}}^j} \frac{c_w^+ f_w^{j\prime}(R_{\overline{w}}^j)}{c_{\overline{w}}^+ f_{\overline{w}}^{j\prime}(R_{\overline{w}}^j)} + 1$$

where U_w and R_w^* are taken for $c_w = c_w^+$.

The characteristic polynomial of the matrix $M(\lambda)$ is (we ignore the subscripts in the constants C_v^j as an attempt to lighten up the computations) :

$$P = \det(M(\lambda) - XI_2) = \begin{vmatrix} f^1 - \lambda C^1 - \lambda^2 D^1 + o(\lambda^2) - X & \lambda \\ \lambda & f^2 - \lambda C^2 - \lambda^2 D^2 + o(\lambda^2) - X \end{vmatrix}$$

After straight computation, one can get that :

$$\begin{aligned} P =& X^2 + X(\lambda(C^1 + C^2) + \lambda^2(D^1 + D^2) - f^1 - f^2) + f^1 f^2 - \lambda(C^1 f^2 + C^2 f^1) \\ & - \lambda^2(D^1 f^2 + D^2 f^1) + \lambda^2 C^1 C^2 - \lambda^2 + o(\lambda^2). \end{aligned}$$

The discriminant equals :

$$\Delta = (f^1 - f^2)\left((f^1 - f^2) - 2\lambda(C^1 - C^2) - 2\lambda^2(D^1 - D^2)\right) + \lambda^2(C^1 - C^2)^2 + 4\lambda^2 + o(\lambda^2).$$

Recall that we search the development of $c_v^*(c_u, \lambda)$ where $c_u = c_u^+ + \lambda\alpha_u$. Let us write :

$$c_v = c_v^*(c_u, \lambda) = c_v^+ + h_v(\lambda) + o(\lambda).$$

Recall that $f^1 = c_v f_v^1(R_u^1) - \delta^1$. Moreover $R_u^1 = R_u^1(c_u) = R_u^1(c_u^+ + \lambda\alpha_u)$. Hence :

$$f^1 = c_v\left(f_v^1(R_u^1(c_u^+)) + \lambda\alpha_u m_v^1\right) - \delta^1 + o(\lambda),$$

where m_v^1 comes from the development of $f_v^1(R_u^1(c_u))$ with respect to λ. Straight computation gives :

$$\begin{aligned} f^1 &= c_v^+ f_v^1(R_v^1(c_v^+)) - \delta^1 + \lambda\alpha_u m_v^1 c_v^+ + h_v(\lambda) f_v^1(R_u^1(c_u^+)) + o(\lambda) \\ &= \lambda\alpha_u m_v^1 c_v^+ + \frac{h_v(\lambda)}{c_v^+}\delta^1 + o(\lambda) \end{aligned}$$

Hence :

$$f^1 - f^2 = \lambda\alpha_u c_v^+(m_v^1 - m_v^2) + \frac{h_v(\lambda)}{c_v^+}(\delta^1 - \delta^2) + o(\lambda)$$

$$f^1 + f^2 = \lambda\alpha_u c_v^+(m_v^1 + m_v^2) + \frac{h_v(\lambda)}{c_v^+}(\delta^1 + \delta^2) + o(\lambda)$$

Using these results allows to compute the development of Δ at the second order :

$$\Delta = \left(\lambda\alpha_u c_v^+(m_v^1 - m_v^2) + \frac{h_v(\lambda)}{c_v^+}(\delta^1 - \delta^2) - \lambda(C_v^1 - C_v^2)\right)^2 + 4\lambda^2 + o(\lambda^2).$$

As a consequence the eigenvalues of $M(\lambda)$ at the first order are :

$$X = \frac{1}{2}\left(-\lambda(C_v^1 + C_v^2) + \lambda\alpha_u c_v^+(m_v^1 + m_v^2) + \frac{h_v(\lambda)}{c_v^+}(\delta^1 + \delta^2) \pm \sqrt{\Delta}\right) + o(\lambda).$$

Writing $X = 0$ gives us a second order equation for $h_v(\lambda)$:

$$\begin{aligned} \delta^1\delta^2\left(\frac{h_v(\lambda)}{c_v^+}\right)^2 &+ \frac{h_v(\lambda)}{c_v^+}\left(\lambda\alpha_u c_v^+(\delta^1 m_v^2 + \delta^2 m_v^1) - \lambda(\delta^1 C_v^2 + \delta^2 C_v^1)\right) \\ &+ m_v^1 m_v^2(\lambda\alpha_u c_v^+)^2 + C_v^1 C_v^1\lambda^2 - \lambda^2 - \lambda^2\alpha_u c_v^+(m_v^1 C_v^2 + m_v^2 C_v^1) = 0. \end{aligned}$$

A straight computation gives the discriminant of this new equation :

$$\Delta = \left(\lambda\alpha_u c_v^+(\delta^1 m_v^2 - \delta^2 m_v^1) - \lambda(\delta^1 C_v^2 - \delta^2 C_v^1)\right)^2 + 4\delta^1\delta^2\lambda^2.$$

$h_v(\lambda)$ is the smallest solution of this equation :

$$\begin{aligned} h_v(\lambda) = &\frac{c_v^+}{2\delta^1\delta^2}\Big(-\lambda\alpha_u c_v^+(\delta^1 m_v^2 + \delta^2 m_v^1) + \lambda(\delta^1 C_v^2 + \delta^2 C_v^1) \\ &- \sqrt{\left(\lambda\alpha_u c_v^+(\delta^1 m_v^2 - \delta^2 m_v^1) - \lambda(\delta^1 C_v^2 - \delta^2 C_v^1)\right)^2 + 4\delta^1\delta^2\lambda^2} \Big). \end{aligned}$$

Symetrically, $c_u^*(c_v^+ + \lambda\alpha_v, \lambda) = c_u^+ + h_u(\lambda) + o(\lambda)$ with :

$$\begin{aligned} h_u(\lambda) = & \frac{c_u^+}{2\delta^1\delta^2}\Big(-\lambda\alpha_v c_u^+(\delta^1 m_u^2 + \delta^2 m_u^1) + \lambda(\delta^1 C_u^2 + \delta^2 C_u^1) \\ & - \sqrt{\left(\lambda\alpha_v c_u^+(\delta^1 m_u^2 - \delta^2 m_u^1) - \lambda(\delta^1 C_u^2 - \delta^2 C_u^1)\right)^2 + 4\delta^1\delta^2\lambda^2} \quad \Big). \end{aligned}$$

Let us now compute the explicit value of m_w^j. Recall that $f_w^j(R_{\overline{w}}^j(c_{\overline{w}})) = f_w^j(R_{\overline{w}}^j(c_w)) + \lambda\alpha_{\overline{w}} m_w^j + o(\lambda)$. For sake of simplicity, we compute the value of m_v^1 and we will deduce from it the general value of m_w^j. Let us first develop $R_u^1(c_u) = R_u^1(c_u^+ + \lambda\alpha_u)$:

$$\begin{aligned} R_u^1(c_u^+ + x\alpha_u) &= \frac{b_u^1\delta^1}{(c_u^+ + \lambda\alpha_u + o(\lambda))a_u^1 - \delta^1} \\ &= \frac{b_u^1\delta^1}{c_u^+ a_u^1 + \lambda\alpha_u a_u^1 - \delta^1 + o(\lambda)} \\ &= \frac{b_u\delta^1}{c_u^+ a_u^1 - \delta^1} \times \frac{1}{1 + \frac{\lambda\alpha_u a_u^1}{c_u^+ a_u^1 - \delta^1} + o(\lambda)} \\ &= R_u^1\left(1 - \lambda\alpha_u \frac{a_u^1}{c_u^+ a_u^1 - \delta^1} + o(\lambda)\right) \\ &= R_u^1 - \lambda\alpha_u R_u^1 \frac{b_u^1\delta^1}{c_u^+ a_u^1 - \delta^1} \times \frac{a_u^1}{b_u^1\delta^1} + o(\lambda) \\ &= R_u^1 - \lambda\alpha_u (R_u^1)^2 \frac{f_u^{1\prime}(0)}{\delta^1} + o(\lambda) \end{aligned}$$

Hence :

$$\begin{aligned} f_v^1(R_u^1(c_1)) &= f_v^1\left(R_u^1 - \lambda\alpha_u (R_u^1)^2 \frac{f_u^{1\prime}(0)}{\delta^1} + o(\lambda)\right) \\ &= f_v^1(R_u^1) - \lambda\alpha_u (R_u^1)^2 \frac{f_u^{1\prime}(0)}{\delta^1} f_v^{1\prime}(R_u^1) + o(\lambda). \end{aligned}$$

We note that :

$$\begin{aligned} f_v^{1\prime}(R_u^1) &= f_v^{1\prime}(R_v^1) \\ &= \frac{1}{c_v^+} \times \frac{c_v^+ a_v^1 b_v^1}{(b_v^1 + R_v^1)^2} \\ &= \frac{1}{c_v^+} \times \frac{c_v^+ a_v^1 R_v^1}{b_v^1 + R_v^1} \times \frac{1}{R_v^1} \times \frac{b_v^1}{b_v^1 + R_v^1} \\ &= \frac{1}{c_v^+} \times \delta^1 \times \frac{1}{R_v^1} \times b_v^1 \times \frac{c_v^+ a_v^1 R_v^1}{b_v^1 + R_v^1} \times \frac{1}{c_v^+ a_v^1 R_v^1} \\ &= \frac{1}{c_v^+} \times \left(\frac{\delta^1}{R_v^1}\right)^2 \times \frac{b_v^1}{c_v^+ a_v^1} \\ &= \left(\frac{\delta^1}{R_v^1}\right)^2 \frac{1}{(c_v^+)^2 f_v^{1\prime}(0)}. \end{aligned}$$

After simple computations (using $R^1_v = R^1_u$) :

$$m^1_v = -\frac{\delta^1}{(c^+_v)^2}\frac{f^{1\prime}_u(0)}{f^{1\prime}_v(0)}.$$

As a consequence m^j_w :

$$m^j_w = -\frac{\delta^j}{(c^+_w)^2}\frac{f^{j\prime}_{\overline{w}}(0)}{f^{j\prime}_w(0)}.$$

We can give fresh expressions for $h_u(\lambda)$ and $h_v(\lambda)$:

$$\begin{aligned} h_1(\lambda) = \frac{\lambda}{2}(\quad & -\alpha_v(c^+_u)^2\left(\frac{m^2_u}{\delta^2}+\frac{m^1_u}{\delta^1}\right)+c^+_u\left(\frac{C^2_u}{\delta^2}+\frac{C^1_u}{\delta^1}\right) \\ & -\sqrt{\left(-\alpha_v(c^+_u)^2\left(\frac{m^2_u}{\delta^2}-\frac{m^1_u}{\delta^1}\right)+c^+_u\left(\frac{C^2_u}{\delta^2}-\frac{C^1_u}{\delta^1}\right)\right)^2+4(c^+_u)^2\frac{1}{\delta^1\delta^2}} \quad). \end{aligned}$$

$$\begin{aligned} h_2(\lambda) = \frac{\lambda}{2}(\quad & -\alpha_u(c^+_v)^2\left(\frac{m^2_v}{\delta^2}+\frac{m^1_v}{\delta^1}\right)+c^+_v\left(\frac{C^2_v}{\delta^2}+\frac{C^1_v}{\delta^1}\right) \\ & -\sqrt{\left(-\alpha_u(c^+_v)^2\left(\frac{m^2_v}{\delta^2}-\frac{m^1_v}{\delta^1}\right)+c^+_v\left(\frac{C^2_v}{\delta^2}-\frac{C^1_v}{\delta^1}\right)\right)^2+4(c^+_v)^2\frac{1}{\delta^1\delta^2}} \quad). \end{aligned}$$

Recall that $u^j = \frac{a^j_v b^j_u}{b^j_v a^j_u} = \frac{f^{j\prime}_v(0)}{f^{j\prime}_u(0)}$, we have :

$$\begin{aligned} h_1(\lambda) = \frac{\lambda}{2}(\quad & \alpha_v\left(u^2+u^1\right)+c^+_u\left(\frac{C^2_u}{\delta^2}+\frac{C^1_u}{\delta^1}\right) \\ & -\sqrt{\left(\alpha_v\left(u^2-u^1\right)+c^+_u\left(\frac{C^2_u}{\delta^2}-\frac{C^1_u}{\delta^1}\right)\right)^2+4(c^+_u)^2\frac{1}{\delta^1\delta^2}} \quad). \end{aligned}$$

$$\begin{aligned} h_2(\lambda) = \frac{\lambda}{2}(\quad & \alpha_u\left(\frac{1}{u^2}+\frac{1}{u^1}\right)+c^+_v\left(\frac{C^2_v}{\delta^2}+\frac{C^1_v}{\delta^1}\right) \\ & -\sqrt{\left(\alpha_u\left(\frac{1}{u^2}-\frac{1}{u^1}\right)+c^+_v\left(\frac{C^2_v}{\delta^2}-\frac{C^1_v}{\delta^1}\right)\right)^2+4(c^+_v)^2\frac{1}{\delta^1\delta^2}} \quad). \end{aligned}$$

Recall that

$$C^j_w = \frac{U^{\overline{j}}_{\overline{w}}-U^j_{\overline{w}}}{U^j_{\overline{w}}}\frac{c^+_{\overline{w}}f^{j\prime}_w(R^j_{\overline{w}})}{c^+_{\overline{w}}f^{j\prime}_{\overline{w}}(R^j_{\overline{w}})}+1.$$

Using the fact that $f^{j\prime}_w(R^1_{\overline{w}}) = \left(\frac{\delta^j}{R^j_w}\right)^2\frac{1}{(c^+_w)^2 f^{j\prime}_w(0)}$ we obtain :

$$C^j_w = \frac{U^{\overline{j}}_{\overline{w}}-U^j_{\overline{w}}}{U^j_{\overline{w}}}\frac{c^+_{\overline{w}}f^{j\prime}_{\overline{w}}(0)}{c^+_i f^{j\prime}_i(0)}+1.$$

Set $\gamma^j = \frac{U_1^{\bar{j}} - U_1^j}{U_1^j}$, we have :

$$C_u^j = \gamma^j u^j \frac{c_v^+}{c_u^+} + 1 \quad \text{and} \quad C_v^j = \gamma^j \frac{1}{u^j} \frac{c_u^+}{c_v^+} + 1.$$

Second step : Recall that we search $(\alpha_u, \alpha_v) \in \mathbb{R}^2$ such that for λ small :

$$c_u^*(c_v^+ + \lambda\alpha_v, \lambda) > c_u^+ + \lambda\alpha_u \quad \text{and} \quad c_v^*(c_u^+ + \lambda\alpha_u, \lambda) > c_v^+ + \lambda\alpha_v,$$

which means :

$$h_1(\lambda) + o(\lambda) > \lambda\alpha_u \quad \text{and} \quad h_2(\lambda) + o(\lambda) > \lambda\alpha_v.$$

Hence, we seek $(\alpha_u, \alpha_v) \in \mathbb{R}^2$ such that :

$$\begin{aligned} g_1(\alpha_u, \alpha_v) &= \alpha_v(u^2 + u^1) - 2\alpha_u + c_u^+ \left(\frac{C_u^2}{\delta^2} + \frac{C_u^1}{\delta^1} \right) \\ &\quad - \sqrt{\left(\alpha_v \left(u^2 - u^1\right) + c_u^+ \left(\frac{C_u^2}{\delta^2} - \frac{C_u^1}{\delta^1} \right) \right)^2 + 4(c_u^+)^2 \frac{1}{\delta^1 \delta^2}} > 0, \end{aligned}$$

and,

$$\begin{aligned} g_2(\alpha_u, \alpha_v) &= \alpha_u \left(\frac{1}{u^2} + \frac{1}{u^1} \right) - 2\alpha_v + c_v^+ \left(\frac{C_v^2}{\delta^2} + \frac{C_v^1}{\delta^1} \right) \\ &\quad - \sqrt{\left(\alpha_u \left(\frac{1}{u^2} - \frac{1}{u^1} \right) + c_v^+ \left(\frac{C_v^2}{\delta^2} - \frac{C_v^1}{\delta^1} \right) \right)^2 + 4(c_v^+)^2 \frac{1}{\delta^1 \delta^2}} > 0. \end{aligned}$$

It is clear that for any α_u, the function $\alpha_v \mapsto g_1(\alpha_u, \alpha_v)$ is increasing and the function $\alpha_v \mapsto g_2(\alpha_u, \alpha_v)$ is decreasing. Moreover :

$$\begin{aligned} &\lim_{\alpha_v \to -\infty} g_1(\alpha_u, \alpha_v) = -\infty \quad && \lim_{\alpha_v \to +\infty} g_1(\alpha_u, \alpha_v) = +\infty \\ &\lim_{\alpha_v \to -\infty} g_2(\alpha_u, \alpha_v) = +\infty \quad && \lim_{\alpha_v \to +\infty} g_2(\alpha_u, \alpha_v) = -\infty \end{aligned}$$

Thus, by continuity, this proves the existence of $X_u(\alpha_u)$ and $X_v(\alpha_u)$ satisfying :

$$g_1(\alpha_u, X_u(\alpha_u)) = 0 \quad \text{and} \quad g_2(\alpha_u, X_v(\alpha_u)) = 0.$$

It comes that if $X_u(\alpha_u) < X_v(\alpha_u)$, then for any α_v in the interval $(X_u(\alpha_u), X_v(\alpha_u))$, our system of inequations is satisfied et the proof of the theorem is complete. Hence, we have to prove that there exists values of α_u such that $X_u(\alpha_u) < X_v(\alpha_u)$.

Third step : First let us compute $X_u(\alpha_u)$ (the explicit value of $X_v(\alpha_u)$ is clear).

$$\begin{aligned} g_1(\alpha_u, \alpha_v) = 0 \Leftrightarrow \alpha_v(u^2 + u^1) - 2\alpha_u + c_u^+ \left(\frac{C_u^2}{\delta^2} + \frac{C_u^1}{\delta^1} \right) = \\ \sqrt{\left(\alpha_v \left(u^2 - u^1\right) + c_u^+ \left(\frac{C_u^2}{\delta^2} - \frac{C_u^1}{\delta^1} \right) \right)^2 + 4(c_u^+)^2 \frac{1}{\delta^1 \delta^2}}. \end{aligned}$$

In order to solve this equation, we square the equation and we solve the appearing second order equation. We obtain two solutions :

$$\begin{aligned} X^{\pm}(\alpha_u) = \frac{1}{2u^1u^2} & \left(\alpha_u(u^2+u^1) - c_u^+ \left(u^2 \frac{C_u^1}{\delta^1} + u^1 \frac{C_u^2}{\delta^2} \right) \right) \\ & \pm \sqrt{ \left(\alpha_u(u^2-u^1) - c_u^+ \left(u^2 \frac{C_u^1}{\delta^1} - u^1 \frac{C_u^2}{\delta^2} \right) \right)^2 + 4u^1u^2(c_u^+)^2 \frac{1}{\delta^1\delta^2} }. \end{aligned}$$

It is clear that $X^+ > X^-$ and one can check that $X_u = X^+$:

$$\begin{aligned} X_u(\alpha_u) = \frac{1}{2u^1u^2} & \left(\alpha_u(u^2+u^1) - c_u^+ \left(u^2 \frac{C_u^1}{\delta^1} + u^1 \frac{C_u^2}{\delta^2} \right) \right) \\ & + \sqrt{ \left(\alpha_u(u^2-u^1) - c_u^+ \left(u^2 \frac{C_u^1}{\delta^1} - u^1 \frac{C_u^2}{\delta^2} \right) \right)^2 + 4u^1u^2(c_u^+)^2 \frac{1}{\delta^1\delta^2} }. \end{aligned}$$

$X_v(\alpha_u)$ is given by :

$$\begin{aligned} X_v(\alpha_u) = \frac{1}{2u^1u^2} & \left(\alpha_u(u^2+u^1) + u^1u^2c_v^+ \left(\frac{C_v^2}{\delta^2} + \frac{C_v^1}{\delta^1} \right) \right) \\ & - \sqrt{ \left(\alpha_u(u^2-u^1) - u^1u^2c_v^+ \left(\frac{C_v^2}{\delta^2} - \frac{C_v^1}{\delta^1} \right) \right)^2 + 4(u^1u^2c_v^+)^2 \frac{1}{\delta^1\delta^2} }. \end{aligned}$$

We want to prove that there exists values of α_u such that $X_u < X_v$. We form the difference :

$$\begin{aligned} \mathcal{H}(\alpha_u) &= 2u^1u^2(X_v(\alpha_u) - X_u(\alpha_u)) \\ &= u^1u^2c_v^+ \left(\frac{C_v^2}{\delta^2} + \frac{C_v^1}{\delta^1} \right) + c_u^+ \left(u^2 \frac{C_u^1}{\delta^1} + u^1 \frac{C_u^2}{\delta^2} \right) \\ &\quad - \sqrt{ \left(\alpha_u(u^2-u^1) - u^1u^2c_v^+ \left(\frac{C_v^2}{\delta^2} - \frac{C_v^1}{\delta^1} \right) \right)^2 + 4(u^1u^2c_v^+)^2 \frac{1}{\delta^1\delta^2} } \\ &\quad - \sqrt{ \left(\alpha_u(u^2-u^1) - c_u^+ \left(u^2 \frac{C_u^1}{\delta^1} - u^1 \frac{C_u^2}{\delta^2} \right) \right)^2 + 4u^1u^2(c_u^+)^2 \frac{1}{\delta^1\delta^2} }. \end{aligned}$$

Studying this function will prove that its maximum is positive. Let us note arbitrarily :

$$\begin{aligned} a &= c_u^+ u^2 \frac{C_1^1}{\delta^1} \quad & c &= u^1u^2c_v^+ \frac{C_2^1}{\delta^1}, \\ b &= c_u^+ u^1 \frac{C_1^2}{\delta^2} \quad & d &= u^1u^2c_v^+ \frac{C_2^2}{\delta^2}, \\ A &= 2c_u^+ \sqrt{\frac{u^1u^2}{\delta^1\delta^2}} \quad & B &= 2u^1u^2c_v^+ \frac{1}{\sqrt{\delta^1\delta^2}}, \end{aligned}$$

So that if $x = \alpha_u(u^2 - u^1)$:

$$\mathcal{H}(x) = a + b + c + d - \sqrt{(x - (a-b))^2 + A^2} - \sqrt{(x - (d-c))^2 + B^2}.$$

Simple computation show that this function admits a unique maximum achieved in :

$$x_M = \frac{a(d-c) + B(a-b)}{A+B}.$$

This maximum is :

$$\mathcal{H}(x_M) = a+b+c+d - \sqrt{(A+B)^2 + (d-c-a+b)^2}.$$

Notice that :

$$a+b+c+d = u^1u^2c_v^+\frac{\gamma^1+1}{\delta^1} + u^1u^2c_v^+\frac{\gamma^2+1}{\delta^2} + u^2c_u^+\frac{\gamma^1+1}{\delta^1} + u^1c_u^+\frac{\gamma^2+1}{\delta^2}.$$

But :

$$\gamma^j + 1 = \frac{U_u^{\bar{j}} - U_u^j}{U_1^j} + 1 = \frac{U_u^{\bar{j}}}{U_u^j} > 0.$$

So $a+b+c+d > 0$. We can write :

$$\begin{aligned}\mathcal{H}(x_M) > 0 &\Leftrightarrow (a+b+c+d)^2 > (A+B)^2 + (d-c-a-b)^2 \\ &\Leftrightarrow 4(b+d)(a+c) > (A+B)^2.\end{aligned}$$

Notice that :

$$b+d = \frac{u^1}{\delta^2}(\gamma^2+1)(u^2c_v^+ + c_u^+) \quad \text{and} \quad a+c = \frac{u^2}{\delta^1}(\gamma^1+1)(u^1c_v^+ + c_u^+).$$

Hence :

$$\mathcal{H}(x_M) > 0 \Leftrightarrow 4\frac{u^1u^2}{\delta^1\delta^2}(\gamma^1+1)(\gamma^2+1)(u^2c_v^+ + c_u^+)(u^1c_v^+ + c_u^+) > (2c_u^+\sqrt{\frac{u^1u^2}{\delta^1\delta^2}} + 2u^1u^2c_v^+\frac{1}{\sqrt{\delta^1\delta^2}})^2.$$

Since $(\gamma^1+1)(\gamma^2+1) = 1$, computation shows that :

$$\mathcal{H}(x_M) > 0 \Leftrightarrow c_u^+c_v^+(\sqrt{u^2} - \sqrt{u^1})^2 > 0.$$

which is true and conclude the proof.

$\square$

Bibliographie

[Alsmeyer et Mentemeier, 2012] Alsmeyer, G. et Mentemeier, S. (2012). Tail behaviour of stationary solutions of random difference equations : the case of regular matrices. *Journal of Difference Equations and Applications*, pages 1305–1332.

[Bakhtin et Hurth, 2012] Bakhtin, Y. et Hurth, T. (2012). Invariant densities for dynamical systems with random switching. *Nonlinearity*, 25:2937–2952.

[Balde *et al.*, 2009] Balde, M., Boscain, U. et Mason, P. (2009). A note on stability conditions for planar switched systems. *International Journal of Control*, pages 1882–1888.

[Bardet *et al.*, 2010] Bardet, J.-B., Guérin, H. et Malrieu, F. (2010). Long time behavior of diffusions with markov switching. *ALEA Latin American Journal of Probability and Mathematical Statistics*, pages 151–170.

[Benaïm *et al.*, 2012] Benaïm, M., Le Borgne, S., Malrieu, F. et Zitt, P.-A. (2012). Quantitative ergodicity for some switched dynamical systems. *Electronic Communications in Probability*, pages no. 56, 14.

[Benaïm *et al.*, 2014] Benaïm, M., Le Borgne, S., Malrieu, F. et Zitt, P.-A. (2014). On the stability of planar randomly switched systems. *The Annals of Applied Probability*, pages 292–311.

[Benaïm *et al.*, 2015] Benaïm, M., Le Borgne, S., Malrieu, F. et Zitt, P.-A. (2015). Qualitative properties of certain piecewise deterministic markov processes. *Annales de l'Institut Henri Poincaré, Probabilités et Statistiques*, pages 1040–1075.

[Benaïm et Lobry, 2016] Benaïm, M. et Lobry, C. (2016). Lotka-Volterra with randomly fluctuating environments or “How switching between beneficial environments can make survival harder”. *The Annals of Applied Probability*, pages 3754–3785.

[Berman et J. Plemmons, 1994] Berman, A. et J. Plemmons, R. (1994). *Nonnegative Matrices in the Mathematical Sciences.*

[Castella et Madec, 2014] Castella, F. et Madec, S. (2014). Coexistence phenomena and global bifurcation structure in a chemostat-like model with species-dependent diffusion rates. *Journal of Mathematical Biology*, pages 377–415.

[Castella *et al.*, 2016] Castella, F., Madec, S. et Lagadeuc, Y. (2016). Global behavior of n competing species with strong diffusion : diffusion leads to exclusion. *Applicable Analysis*, pages 341–372.

[Chesson, 2000] Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, pages 343–366.

[Chesson et Warner, 1981] Chesson, P. L. et Warner, R. R. (1981). Environmental variability promotes coexistence in lottery competitive systems. *The American Naturalist*, pages 923–943.

[Cloez *et al.*, 2017] Cloez, B., Dessalles, R., Genadot, A., Malrieu, F., Marguet, A. et Yvinec, R. (2017). Probabilistic and piecewise deterministic models in biology. *ESAIM : Procs*, pages 225–245.

[Costa, 2016] Costa, M. (2016). A piecewise deterministic model for a prey-predator community. *The Annals of Applied Probability*, pages 3491–3530.

[Davis, 1984] Davis, M. H. A. (1984). Piecewise-deterministic markov processes : A general class of non-diffusion stochastic models. *Journal of the Royal Statistical Society. Series B (Methodological)*, pages 353–388.

[De Saporta *et al.*, 2004] De Saporta, B., Guivarc'H, Y. et Le Page, E. (2004). On the multidimensional stochastic equation Y(n+1)=a(n)Y(n)+b(n). *Comptes rendus de l'Académie des sciences. Série I, Mathématique*, pages 499–502.

[Ethier et Kurtz, 1986] Ethier, S. et Kurtz, T. (1986). *Markov processes : characterization and convergence*. Wiley.

[Fetique, 2017] Fetique, N. (2017). Long-time behaviour of generalised zig-zag process.

[Fontbona *et al.*, 2016] Fontbona, J., Guérin, H. et Malrieu, F. (2016). Long time behavior of telegraph processes under convex potentials. *Stochastic Processes and their Applications*, pages 3077–3101.

[Gaki *et al.*, 2009] Gaki, A., Theodorou, A., Vayenas, D. V. et Pavlou, S. (2009). Complex dynamics of microbial competition in the gradostat. *Journal of Biotechnology*, pages 38–46.

[Hofbauer et So, 1994] Hofbauer, J. et So, J. W.-H. (1994). Competition in the gradostat : the global stability problem. *Nonlinear Analysis : Theory, Methods & Applications*, pages 1017–1031.

[Hsu, 1978] Hsu, S. B. (1978). Limiting behavior for competing species. *SIAM Journal on Applied Mathematics*, pages 760–763.

[Hsu *et al.*, 1977] Hsu, S. B., Hubbell, S. et Waltman, P. (1977). A mathematical theory for single-nutrient competition in continuous cultures of micro-organisms. *SIAM Journal on Applied Mathematics*, pages 366–383.

[Kesten, 1973] Kesten, H. (1973). Random difference equations and renewal theory for products of random matrices. *Acta Mathematica*, pages 207–248.

[Lawley *et al.*, 2014] Lawley, S. D., Mattingly, J. C. et Reed, M. C. (2014). Sensitivity to switching rates in stochastically switched ODEs. *Communications in Mathematical Sciences*, pages 1343–1352.

[Loreau *et al.*, 2003] Loreau, M., Mouquet, N. et Gonzalez, A. (2003). Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences*, pages 12765–12770.

[Lovitt et Wimpenny, 1981] Lovitt, R. et Wimpenny, J. (1981). The gradostat : a bidirectional compound chemostat and its application in microbiological research. *J Gen Microbiol.*

[Madec, 2011] Madec, S. (2011). *Spatial heterogeneity in population dynamics.* Theses, Université Rennes 1.

[Malrieu, 2015] Malrieu, F. (2015). Some simple but challenging Markov processes. *Annales de la Faculté des Sciences de Toulouse. Mathématiques. Série 6*, pages 857–883.

[Malrieu et Zitt, 2016] Malrieu, F. et Zitt, P.-A. (2016). On the persistence regime for lotka-volterra in randomly fluctuating environments. *Preprint.*

[Radulescu *et al.*, 2007] Radulescu, O., Muller, A. et Crudu, A. (2007). Théorèmes limites pour des processus de markov à sauts. synthèse des résultats et applications en biologie moleculaire. *TSI (Revue Technique et Science Informatiques)*, pages 443–469.

[Rapaport, 2017] Rapaport, A. (2017). Some non-intuitive properties of simple extensions of the chemostat model. *Ecological Complexity.*

[Smith et Waltman, 1991] Smith, H. et Waltman, P. (1991). The gradostat : A model of competition along a nutrient gradient. *Microb Ecol.*

[Smith et Waltman, 1995] Smith, H. et Waltman, P. (1995). *The Theory of the Chemostat Dynamics of Microbial Competition.*

[Smith et Waltman, 2000] Smith, H. et Waltman, P. (2000). Competition in the periodic gradostat. *Nonlinear Analysis : Real World Applications*, pages 177–188.

[Strickler et Benaïm, 2017] Strickler, E. et Benaïm, M. (2017). Random switching between vector fields having a common zero. *Preprint.*

Résumé :

L'objectif de cette thèse est d'étudier le comportement en temps long de certains processus de Markov déterministes par morceaux (PDMP) dont le flot suivi par la composante spatiale commute aléatoirement entre plusieurs flots possédant un unique équilibre attractif (éventuellement le même pour chaque flot). Nous donnerons dans un premier temps un exemple d'étude d'un tel processus construit dans le plan à partir de flots associés à des équations différentielles linéaires stables où il est déjà possible d'observer des comportements contre-intuitifs. La deuxième partie de ce manuscrit est dédiée à l'étude et la comparaison de deux modèles de compétition pour une ressource dans un environnement hétérogène. Le premier modèle est un modèle alétoire simulant l'hétérogénéité temporelle d'un environnement sur les espèces en compétition à l'aide d'un PDMP. Son étude utilise des outils maintenant classiques sur l'étude des PDMP. Le deuxième modèle est un modèle déterministe (présentant sous forme d'un système d'équations différentielles) modélisant l'impact de l'hétérogénéité spatiale d'un environnement sur ces mêmes espèces. Nous verrons que malgré leur nature très différente, le comportement en temps long de ces deux systèmes est relativement similaire et est essentiellement déterminé par le signe des taux d'invasion de chacune des espèces qui sont des quantités dépendant exclusivement des paramètres du système et modélisant la vitesse de croissance (ou de décroissance) de ces espèces lorsqu'elles sont au bord de l'extinction.

Mots clés :

Processus de Markov déterministes par morceaux ; Comportement en temps long ; Modèle de compétition ; Chemostat ; Gradostat

Abstract :

The objective of this thesis is to study the long time behaviour of some piecewise deterministic Markov processes (PDMP). The flow followed by the spatial component of these processes switches randomly between several flow converging towards an equilibrium point (not necessarily the same for each flow). We will first give an example of such a process built in the plan from two linear stable differential equations and we will see that its stability depends strongly on the switching times. The second part of this thesis is dedicated to the study and comparison of two competition models in a heterogeneous environment. The first model is a probabilistic model where we build a PDMP simulating the effect of the temporal heterogeneity of an environment over the species in competition. Its study uses classical tools in this field. The second model is a deterministic model simulating the effect of the spatial heterogeneity of an environment over the same species. Despite the fact that the nature of the two models is very different, we will see that their long time behavior is very similar. We define for both model several quantities called invasion rates modelizing the growth (or decreasing) rate speed of a species when it is near to extinction and we will see that the signs of these invasion rates fully describes the long time behavior for both systems.

Keywords :

Piecewise deterministic Markov processes ; Long time behaviour ; Competition model ; Chemostat ; Gradostat