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Comparison of the global dynamics for two chemostat-like models: random temporal variation versus spatial heterogeneity.

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Abstract

This article is dedicated to the study and comparison of two chemostat-like 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 gradostat-like 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 globally very similar. We define for both model quantities called invasion rates which model the growth rate of a species when it is near to extinction. We show that the signs of these invasion rates essentially determine the long time behavior for both systems. In particular, we exhibit a new type of bistability with a stable coexistence steady state and a stable semi-trivial steady state.

1 Introduction

The model of chemostat is a standard model of competition of several species for a single resource in an open environment. Its studies as well as that of its many variants have been widely explored since fifty years. One can read Smith and Waltman's book [32] and recent survey [36] which give a view over 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.

In this article, we consider two species u and v competing for a single resource R.
The evolution of these different concentrations in a simple chemostat ε is given by the equations:

$$\begin{cases} \dot{R}(t) = \delta_r(R_0 - R(t)) - U(t)f_u(R(t)) - V(t)f_v(R(t)) \\ \dot{U}(t) = U(t)\left(f_u(R(t)) - \delta_u\right) \\ \dot{V}(t) = V(t)\left(f_v(R(t)) - \delta_v\right) \end{cases} \tag{1}$$

together with the initial conditions $U(0) > 0,\ V(0) > 0\ R(0) \geq 0$.

Here, we denote $U(t)$, $V(t)$ and $R(t)$ the concentrations of the species u, v and the resource R ; δ_r, δ_u and δ_v the dilution rates of R, u and v respectivly. R_0 is the constant input concentration of the resource in the vessel. For each species $w \in \{u, v\}$, the map $R \mapsto f_w(R)$ is the consumption function and verifies $f_w(0) = 0$. Thus, the *per capita* growth rate of the species w is $f_w(R) - \delta_w$. Note that according to the models, f_w can have different expressions. We assume here that f_w is increasing.
Under various assumptions on the dilution rates δ and the function f_w, the chemostat (1), is known to satisfy the *principle of exclusive competition (PEC)* which states that when several species compete for the same (single) resource, only one species survives, the one which makes 'best' use of the resource. The PEC has been first proven for equals dilution rates $\delta_r = \delta_u = \delta_v$ and Monod's consumption function (see (2)) in [19]. This has been generalized for different dilution rates and Monod's function in [19] and for any increasing function and same dilution rate in [1]. It is yet unknown if the CEP holds true for general increasing functions f_w if the assumption on the dilution rates is relaxed. See [38] for one of the last advance on this topic.

Though some natural observations and laboratory experiences support the principle of exclusive competition [15, 11], the observed population diversity within some natural ecosystems seems to exclude it [20, 30]. In order to take account of the biological complexity without excluding the specificity of the chemostat, various models has been introduced ([24, 27, 14] for more examples).

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 [9, 10]). Applied to the chemostat, this idea gave [33] 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 [3], 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 which consists in the concatenation of various chemostats where the adjacent vessels are connected in both directions, [25, 11]. 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 [21, 31]. See also [34, 13, 29, 16, 28] for more references on the general gradostat. The spatial heterogeneity has been also studies with partial differential equations models, see for instance [7, 8, 17]

Some other chemostat-like model has been introduced to take account of the temporal heterogeneity. See [23, 5, 33] with non autonomous deterministic model and in [6, 37] with stochastic models. In this article, we study the effect of heterogeneity through two different chemostat ε_1 and ε_2. For a given chemostat ε_i we take the most simple model of chemostat : $\delta_r = \delta_u = \delta_v := \delta$ is the common dilution rate for each species and the dilution rate of the resource and we choose the most common expression for f_w which is Monod's one:

$$f_w(R) = \frac{a_w R}{b_w + R}. \tag{2}$$

where a_w is the maximum growth rate for the species w and b_w is 'half-velocity constant' of the species w. .

The evolution of these different concentrations in the simple chemostat ε_i is then given by the equations:

$$\begin{cases} \dot{R}(t) = \delta(R_0 - R(t)) - U(t)f_u(R(t)) - V(t)f_v(R(t)) \\ \dot{U}(t) = U(t)\left(f_u(R(t)) - \delta\right) \\ \dot{V}(t) = V(t)\left(f_v(R(t)) - \delta\right) \end{cases} \tag{3}$$

The so-called 'break-even concentration'

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

is the concentration of resource satisfying $f_w(R_w) = \delta$ (if possible). The quantity R_w^* can be interpreted as the minimal concentration of resource 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 illustrates this statement (see [18, 19]).

Theorem 1.1 (Competitive Exclusion Principle (CEP)). *Suppose that $R_u^* < R_0$ (u is able to survive) and $R_u^* < R_v^*$ (u is the best competitor). The solutions of* (3) *satisfy:*

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

Remark 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 resource, it is easy to see that Σ satisfies the differential equation:

$$\dot{\Sigma}(t) = \delta(R_0 - \Sigma(t)).$$

It comes that $\Sigma(t) = R_0 + e^{-\delta t}(\Sigma(0) - R_0) \xrightarrow[t\to+\infty]{} R_0$.

Using that $\Sigma(t) \to R_0$, it is classical (see the appendix F in [32]) that the asymptotic dynamics of the system (3) *is given by the dynamics of the reducted system*

$$\begin{cases} \dot{U}(t) = U(t)\left(f_u(R_0 - U(t) - V(t)) - \delta\right) \\ \dot{V}(t) = V(t)\left(f_v(R_0 - U(t) - V(t)) - \delta\right) \end{cases} \tag{4}$$

Hence, the assumption that the dilution rates are the same for every species and the resource is a very strong hypothesis which allows to do the variable change $R(t) = R_0 - U(t) - V(t)$. This is the key ingredient in [1] to prove the CEP for general increasing consumption functions and same dilution rates.

In this paper, we consider two chemostats ε^1 and ε^2. For $j \in \{1, 2\}$, the parameters of the chemostat ε^j are denoted $(R_0^j, \delta^j, a_u^j, a_v^j, b_u^j, b_v^j)$. In all the article, the subscripts of a parameter or a variable make always reference to the species and the exponents make always reference to the environment. For a species $w \in \{u, v\}$, we set $\overline{w} \in \{u, v\} \setminus \{w\}$ 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 resource evolve is alternating randomly between ε^1 and ε^2. Assuming that the species and resource lives in ε^1 at $t = 0$, we wait a random exponential time of parameter λ^1 before switching the chemostat to 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 [3], 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 rate λ. Mathematically, this model is a system of 3×2 differential equations which modelizes spatial heterogeneity in a biosystem (see [25] for some mathematical results on the behavior of such system). The goal of this article is to compare the long time behavior of the dynamics of these two different systems. *For each model* we give a mathematical definition for what we will call *the invasion rate of the species*, denoted Λ_w for the species w in the probabilistic case[1]. Given the mathematical difference between the two models, the definition of these invasion rates is different for each model. However, we show that for each model, the signs of Λ_u and Λ_v essentially determine the state of the system at the equilibrium, and thus the long time dynamics. The precise results are stated in the section 2 for the probabilistic model and in the section 3 for the deterministic model.

We show (under an additional assumption for the probabilistic case) 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 exclusive bistability.
- If $\Lambda_u > 0$ and $\Lambda_v > 0$ there is persistence of both species (persistence means that $\liminf_{t \to +\infty} U(t) > 0$ and $\liminf_{t \to +\infty} V(t) > 0$).

In contrast, when $\Lambda_u \Lambda_v < 0$, the possibilities for the long time dynamics are not exactly the same for the two models. For instance, if $\Lambda_u > 0$ and $\Lambda_v < 0$. Then in the probabilistic model for any positive initial condition their is extinction of species v with probability 1, but for the deterministic model there is either

- Extinction of species v (for almost all positive initial condition).
- Extinction of species v or coexistence (depending on the initial condition). This situation is called the odd[2] bistability.

Consequently, comparing the two models will be essentially done by comparing the evolution of these invasion rates according to the parameter λ. An analytical and a numerical comparison of these invasion rates is done in section 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.

For a more fluid reading , the technical proofs are postponed to section 5.

2 Random temporal variation : model and main results.

2.1 The probabilistic model : a PDMP system

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

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[1] In the deterministic case the invasion rate of the species w is note Γ_w. However, we only refer to Λ_w in this introduction.

[2] We choose this term since this situation is ounter intuitive and is difficult to see in numerical simulations.

and its mathematical resolution has been introduced in [3]. In this previous article, the authors exhibit counter-intuitive 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:

$$\begin{cases} \dot{R}_t = \delta^{I_t}(R_0^{I_t} - R_t) - U_t f_u^{I_t}(R_t) - V_t f_v^{I_t}(R_t) \\ \dot{U}_t = U_t(f_u^{I_t}(R_t) - \delta^{I_t}) \\ \dot{V}_t = V_t(f_v^{I_t}(R_t) - \delta^{I_t}) \end{cases} \tag{5}$$

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 probability 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 [12].

Let us call:

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

and

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

According to remark 1.2, Z_t will reach M in finite time for any initial condition $Z_0 \in \mathbb{R}_+^3 \times \{1, 2\}$ and then stays in M. We can then assume that $Z_0 \in M$ and, as a consequence, M is 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:

$$M_0 = M_{0,u} \cup M_{0,v}$$

and the total extinction set:

$$M_{0,u,v} = M_{0,u} \cap M_{0,v}.$$

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

In order to describe the behavior of the process (Z_t) when $Z_0 \in M \setminus M_0$, [3] suggests to study the invasion rates of species w defined as:

$$\Lambda_w = \int \left(f_w^1(R) - \delta^1\right) d\mu_{\bar{w}}(R, 1) + \int \left(f_w^2(R) - \delta^2\right) d\mu_{\bar{w}}(R, 2),$$

where $\mu_{\bar{w}}$ is an invariant probability measure of (Z_t) on $M_{0,w} \setminus M_{0,u,v}$.

Remark 2.1. *The idea behind the definition of the invasion rate Λ_u (same for Λ_v) is the following. From (5) 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 probability measure for the process (Z_t). If μ_v is an invariant probability measure of (Z_t) on $M_{0,u}$, we define $\Lambda_u = \int \mathcal{A}(z)d\mu_v(z)$. By Feller continuity (see [2]) it comes that Λ_u can be seen as the exponential growth rate of U_t when U_t is close to zero. Hence, if $\Lambda_u > 0$ the concentration of u tends to increase from low values and if $\Lambda_u < 0$ the concentration of u tends to decrease from low values.

2.2 Dynamics of the PDMP model

We are interested in the long time behavior of the concentration of the species u and v. In [3], 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 three following behavior for the concentration of the species u and v:

Definition 2.2. *(i) Species $w \in \{u, v\}$ goes to extinction if $W_t \to 0$ almost surely for any initial condition $Z_0 \in M \setminus M_0$.*

(ii) We have coexistence of the two species when neither of the two species goes to extinction for any initial condition $Z_0 \in M \setminus M_0$.

(iii) We have exclusive bistability if their is a probability one that one of the two species tends to zero for any initial condition $Z_0 \in M \setminus M_0$.

In the case (ii) above, as in [3], it is expected that the process (Z_t) restricted to $M \setminus M_0$ has an unique invariant probability measure Π supported by $M \setminus M_0$ and the empirical occupation measure[3] of (Z_t) converge weakly to Π.

The proof of this results use basically the fact that the process (Z_t) restricted to $M_{0,w}$ is a one dimensional process which has a unique positive measure on $M_{0,w} \setminus M_{0,u,v}$. However, their is a main difference between the Lotka-Volterra model of [3] and our chemostat model. Unlike than for the Lotka-Volterra model, it is not true here that the process restricted to $M_{0,w}$ is positively invariant because it is possible that $M_{0,u,v}$ is a global attractor of (Z_t) restricted to $M_{0,w}$ (the species w may not be able to survive, even without competition). In this case, the only invariant probability measure on $M_{0,w}$ will be supported by $M_{0,u,v}$.
Hence, we first study the single species cases, which will be use by using the fact that the process (Z_t) restricted to $M_{0,u,v}$ does posses a unique invariant probability measure μ_0, that can be use to discriminate between the case when the species w may survive or not *alone* (see theorem 2.3).

When the two species are able to survive, everything is similar to [3] and we may study the case of two species (see theorem 2.7). This precaution being taken, the proofs for theorem 2.3 and theorem 2.7 follow to a few details the same path as in [3] and are then omitted. Note that these proofs uses some renewal theory arguments coupled with the analytic properties of the invasion rates.

2.2.1 Long time behavior when only one species is introduced

Assume that species $\overline{w}$ is not in the system ($\overline{W_t} = 0$). Then (Z_t) belongs to $M_{0,\overline{w}}$ and we denote again $(Z_t) = (R_t, W_t, I_t)$. (Z_t) satisfies:

$$\begin{cases} \dot{R}_t = \delta^{I_t}(R_0^{I_t} - R_t) - W_t f_w^{I_t}(R_t) \\ \dot{W}_t = W_t(f_w^{I_t}(R_t) - \delta^{I_t}) \end{cases} \tag{6}$$

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

$$\Lambda_w^0 = \int \left(f_w^1(R) - \delta^1\right) d\mu_0(R, 1) + \int \left(f_w^2(R) - \delta^2\right) d\mu_0(R, 2),$$

where μ_0 is the unique invariant probability measure of the process (Z_t) restricted to $M_{0,u,v}$ (see theorem 4.1).

The following first result is similar to the main result in [3] but for only one species.

Theorem 2.3. *The sign of the invasion rate Λ_w^0 characterizes the evolution of the species w on $M_{0,\overline{w}}$:*

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[3] Let us recall that the empirical occupation measure of (Z_t) is the measure Π_t given by $\Pi_t = \frac{1}{t}\int_0^t \delta_{Z_s} ds$. Hence, for a borel set A, $\Pi_t(A)$ is the proportion of time spent by (Z_s) in A up to time t.

1. *If* $\Lambda^0_w < 0$ *species* w *goes to extinction:* $W_t \to 0$ *almost surely.*
   In that case, the only invariant probability measure of (Z_t) *restricted to* $M_{0,\overline{w}}$ *is* μ_0 *which is supported by* $M_{0,u,v}$*.*

2. *If* $\Lambda^0_w > 0$ *species* w *survives with probability one.*
   More precisely : there exists a unique invariant probabily measure μ_w *of* (Z_t) *restricted to* $M_{0,\overline{w}} \setminus M_{0,u,v}$ *and the empirical occupation measure of* (Z_t) *(restricted to* $M_{0,\overline{w}}$*) converges weakly to* μ_w*.*

2.2.2 Long time behavior when two species are introduced

Assume that that $\Lambda^0_{\overline{w}} > 0$. It follows that (Z_t) has an invariant probability measure $\mu_{\overline{w}}$ on $M_{0,w} \setminus M_{0,u,v}$.

The invasion rates are then defined by:

$$\Lambda_w = \int \left(f^1_w(R) - \delta^1\right) d\mu_{\overline{w}}(R,1) + \int \left(f^2_w(R) - \delta^2\right) d\mu_{\overline{w}}(R,2),$$

Now, we assume[4] that $R^1_0 = R^2_0 = R_0$. According to remark 1.2, the sum $\Sigma_t \to R_0$ as $t \to +\infty$. As a consequence, the long-time behavior of (Z_t) is obtained by assuming that $\Sigma_t = R_0$ in (5).

It follows that the study of the process (Z_t) can now be reduced to the study of the process $(\widetilde{Z_t}) = (U_t, V_t, I_t)$ where I_t is like before and U_t and V_t satisfy the following competition system :

$$\begin{cases} \dot{U_t} = U_t(f^{I_t}_u(R_0 - U_t - V_t) - \delta^{I_t}) \\ \dot{V_t} = V_t(f^{I_t}_v(R_0 - U_t - V_t) - \delta^{I_t}). \end{cases} \tag{7}$$

Note that if the consumption functions are linear (which is not the case here), this system is a lotka-volterra competition system. This similarity is the reason why we make the assumption $R^1_0 = R^2_0$. The strategy of the proofs for two species is then very similar to the strategy of [3].

In order to express our main theorem, we need the additional assumption 2.5 which refers to the averaged which is defined below.

Definition 2.4. *Formally, let* $\varepsilon_s = (1-s)\varepsilon^1 + s\varepsilon^2$ *the averaging of the two chemostats* ε^1 *and* ε^2*. The associated differential system modelizing the behavior of the different concentrations in* ε_s *is given by:*

$$\begin{cases} \dot{R} = \overline{\delta}(\overline{R_0} - R) - U\overline{f_u}(R) - V\overline{f_v}(R) \\ \dot{U} = U(\overline{f_w}(R) - \overline{\delta}) \\ \dot{V} = V(\overline{f_w}(R) - \overline{\delta}) \end{cases} \tag{8}$$

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

$$\overline{R_0} = \frac{(1-s)\delta^1 R^1_0 + s\delta^2 R^2_0}{\overline{\delta}}.$$

Despite the fact that the averaged consumption functions $\overline{f_w}$ *are not Monod functions in general, they are increasing functions verifying* $\overline{f_w}(0) = 0$*. Thus the PEC holds for* ε_s*. More precisly, we can then define the break even concentration for the averaged system :* $\overline{r_w} = \overline{f_w}^{-1}(\overline{\delta})$*. The best competitor in* ε_s*is the species with the lowest* $\overline{r_w}$*. The averaged chemostat* ε_s *is said to be unfavorable to a species* $w \in \{u, v\}$ *if* w *is not the best competitor in* ε_s*, that is if* $W(t) \to 0$ *as* $t \to +\infty$*.*

Assertion 2.5. *Denote* (H_w) *the assertion which is true if and only if one* $\exists s \in (0,1)$ *such that the averaged chemostat* ε_s *is unfavorable to the species* w *(see the definition 2.4 for a precise definition of the averaged chemostat).*

Remark 2.6. *The assertion* (H_w) *is needed for the points* 1 *and* 2 *of the theorem 2.7. The proofs of this points need to find an explicit trajectory such that the species* w *goes to zero.*

If the assertion (H_w) *is true then either :*

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[4] Under this assumption, one has (see section 5.1) the simple expression $d\mu_0(R,j) = (1-s)\Delta_{(R_0,1)} + s\Delta_{(R_0,2)}$ (where Δ_{R_0} is the dirac function at R_0) which yields the simple formula :

$$\Lambda^0_w = (1-s)f^1_w(R_0) - \delta^1) + s(f^2_w(R_0) - \delta^2).$$

(i) if $s \in (0,1)$, the species $\overline{w}$ is the best competitor at the limit $\lambda \to +\infty$ in a weighted average of the two chemostats $\varepsilon_s = (1-s)\varepsilon^1 + s\varepsilon^2$ (see the remark 2.4),

(ii) if $s \in \{0;1\}$, the species $\overline{w}$ is the best competitor in a given chemostat ε^{s+1} (here, the average chemostat is nothing but one of the two initial chemostats).

In the case (i), an explicit trajectory consists to switch very quickly between the two chemostat, obtaining in turn an average deterministic dynamics for which $W(t) \to 0$. In the case (ii), an explicit trajectory consists to follow the dynamics of the chemostat ε^{s+1} for which $W(t) \to 0$.
In both case, an easy an explicit an easy computation can insure that (H_w) holds.
Let us finish this remark by notice that if the maps $\lambda \to \Lambda_w(\lambda)$ are increasing then the assertion (H_w) can be dispensed, see the section 4. Unfortunately, we are not able to proof the monotony of these maps.

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

Theorem 2.7. *Assume that $\Lambda_u^0 > 0$ and $\Lambda_v^0 > 0$. Assume also that $R_0^1 = R_0^2$. We refer to the definition 2.2 for a precise definition of the above vocabulary.*

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 there is a probability one that one of the species goes to extinction. We say that it is a situation of exclusive bistability.*
4. *If $\Lambda_u > 0$ and $\Lambda_v > 0$ then there is coexistence of both species.*

Remark 2.8. *The details of the proofs of theorems 2.3 and 2.7 are given in the last chapter of the phd thesis of the first autor: [22].*

See section 4 for a numerical investigation over the signs of these invasion rates. We show numerically that for any couple of signs $(x,y) \in \{+,-\}$ there exists pair of chemostats ε^1, ε^2 such that $(Sign(\Lambda_u), Sign(\Lambda_v)) = (x,y)$.

Moreover, ε^1 and ε^2 may be chosen both favorable to u ($R_u^j < R_v^j$ for $j = 1,2$) or both favorable to v ($R_u^j > R_v^j$ for $j = 1,2$) or one favorable to u and the other to v ($(R_u^1 - R_v^1)(R_u^2 - R_v^2) < 0$ for $j = 1,2$).

In particular, it is possible to pick chemostats ε^1 and ε^2 both favorable to the species u 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 (see figure 4-a).

3 Spatial heterogeneity : model and main results

3.1 The deterministic model : a gradostat-like system

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. 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 equations on the concentrations:

$$\begin{cases} \dot{U^1}(t) = -\dfrac{Q}{\mathcal{V}^1}U^1(t) + \dfrac{Q}{\mathcal{V}^1}U^2(t) \\ \dot{U^2}(t) = \dfrac{Q}{\mathcal{V}^2}U^1(t) - \dfrac{Q}{\mathcal{V}^2}U^2(t). \end{cases} \tag{9}$$

We will denote $\lambda^j = \frac{Q}{\mathcal{V}^j}$. Similarly, we denote $V^j(t)$ 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 denote $\{j, \overline{j}\} = \{1,2\}$.

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

$$\begin{cases} \dot{R^j}(t) = \delta^j(R_0^j - R^j(t)) - U^j(t)f_u^j(R^j(t)) - V^j(t)f_v^j(R^j(t)) & + \lambda^j(R^{\bar{j}}(t) - R^j(t)) \\ \dot{U^j}(t) = U^j(t)(f_u^j(R^j(t)) - \delta^j) & + \lambda^j(U^{\bar{j}}(t) - U^j(t)) \\ \dot{V^j}(t) = V^j(t)(f_v^j(R^j(t)) - \delta^j) & + \lambda^j(V^{\bar{j}}(t) - V^j(t)). \end{cases} \tag{10}$$

The part with λ^j in factor comes from the transfer equation (9) and the other part comes from the chemostat equation (3).

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, set $\lambda^1 = s\lambda$ and $\lambda^2 = (1-s)\lambda$ with $\lambda > 0$ and $s \in (0,1)$ and $K = \begin{pmatrix} -s & s \\ 1-s & s-1 \end{pmatrix}$. By convention $\begin{pmatrix} w \\ x \end{pmatrix} \begin{pmatrix} y \\ z \end{pmatrix} = \begin{pmatrix} wy \\ xz \end{pmatrix}$. With this notations, the system (10) reads shortly:

$$\begin{cases} \dot{R}(t) = \delta(R_0 - R(t)) - U(t)f_u(R(t)) - V(t)f_v(R(t)) + \lambda K R(t) \\ \dot{U}(t) = U(t)(f_u(R(t)) - \delta) \qquad + \lambda K U(t) \\ \dot{V}(t) = V(t)(f_v(R(t)) - \delta) \qquad + \lambda K V(t). \end{cases} \tag{11}$$

The initial value belongs to the set $(\mathbb{R}_+^* \times \mathbb{R}_+^*)^3$.

Set $\Sigma^j(t) = R^j(t) + U^j(t) + V^j(t)$. The vector $\Sigma(t) = \begin{pmatrix} \Sigma^1(t) \\ \Sigma^2(t) \end{pmatrix}$ satisfies the linear differential system:

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

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

The matrix $\Delta - \lambda K$ has two real positive eigenvalues. Hence we may set $\Sigma = \begin{pmatrix} \Sigma^1 \\ \Sigma^2 \end{pmatrix} := (\Delta - \lambda K)^{-1}(\delta R_0)$ and we have

$$\lim_{t \to +\infty} \Sigma(t) = \Sigma$$

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:

$$\begin{cases} \dot{U}(t) = U(t)(f_u(\Sigma - U(t) - V(t)) - \delta) + \lambda K U(t) \\ \dot{V}(t) = V(t)(f_v(\Sigma - U(t) - V(t)) - \delta) + \lambda K V(t). \end{cases} \tag{12}$$

With initial condition in the set $(\mathbb{R}_+^* \times \mathbb{R}_+^*)^2$. The appendix F of [32] shows that the long time dynamics of (10) is completely given by the dynamics of (12).

3.2 Dynamics of the gradostat like model

We are interested in the long time behavior of the solution of this differential system. It is proven in [32, 21], using strongly the monotonicity of the system, that any solution of (12) converges 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 results about monotone system due to Hirsch (see the appendix B and C in [32] and the references therein).

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 detailed in section 5. 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 (12).

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.

In section 5, it is show how the relative position of the four curves $R^2 = g_w(R^1)$ and $R^2 = F_w(R^1)$ ($w \in \{u, v\}$) give a graphical understanding of the existence of the steady states and their stability. See the figure 1.

3.2.1 Long time behavior when only one species is introduced

Assume that $\overline{w}$ is not in the system ($\overline{W}(t) = 0$). 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:

$$\dot{W}(t) = W(t)(f_w(\Sigma - W(t)) - \delta) + \lambda K W(t) \tag{13}$$

with initial condition $W(0) \in \mathbb{R}_+^* \times \mathbb{R}_+^*$.

It can be proven like in [32] that any trajectory of this previous differential equation goes to a stationary point. Let us call $E_0 = (0, 0)$, E_0 is the trivial stationary point of the system (13) and its linear stability characterizes the dynamics of (13):

Theorem 3.1 ([32] chapter 5 lemma 4.2 and 4.3 page 113)**.** *The global dynamics of the system* (13) *is as follows.*

- *If E_0 is linearly stable, 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 linearly unstable, then there exists a unique stationary point $E_w = (W^1, W^2) \in \mathbb{R}_+^* \times \mathbb{R}_+^*$. Moreover E_w is a global attractor for the system* (13) *in $\mathbb{R}_+^* \times \mathbb{R}_+^*$.*

Note that a stationary point for equation (13) satisfies the equation:

$$\mathcal{F}_w(W) = W(f_w(\Sigma - W) - \delta) + \lambda K W = 0.$$

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

$$A_w = \begin{pmatrix} f_w^1(\Sigma^1) - \delta^1 - \lambda^1 & \lambda^1 \\ \lambda^2 & f_w^2(\Sigma^2) - \delta^2 - \lambda^2 \end{pmatrix}. \tag{14}$$

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

$$\Gamma_w^0 = \frac{1}{2}\left(f_w^1(\Sigma^1) - \delta^1 + f_w^2(\Sigma^2) - \delta^2 - \lambda^1 - \lambda^2 + \sqrt{(f_w^1(\Sigma^1) - \delta^1 - f_w^2(\Sigma^2) + \delta^2)^2 + 4\lambda^1\lambda^2}\right) \tag{15}$$

Theorem 3.1 yields:

Corollary 3.2. *The sign of Γ_w^0 characterizes the behavior of the system* (13)*:*

- *If $\Gamma_w^0 < 0$ there is extinction of the species w: $\lim\limits_{t\to+\infty} W(t) = 0$.*
- *If $\Gamma_w^0 > 0$ there is persistence of the species w. More precisely: $\lim\limits_{t\to+\infty} W(t) = E_w \in \mathbb{R}_+^* \times \mathbb{R}_+^*$.*

3.2.2 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. The system (12) being strongly monotone (see proposition 3.7), the theorem C.9 from Hirsch [32] implies that for almost all initial condition, the solutions tends to a stationary point. Thus, the study of the existence and stability of the steady states is crucial in the understanding of the dynamics of (12).

From $R_0^1 = R_0^2 = R_0$, we have $\Sigma = \begin{pmatrix} R_0 \\ R_0 \end{pmatrix}$ and a stationary solution of (12) satisfyies:

$$H(U, V) = 0 \Leftrightarrow \begin{cases} U(f_u(R_0 - U - V) - \delta) + \lambda K U = 0 \\ V(f_v(R_0 - U - V) - \delta) + \lambda K V = 0. \end{cases} \tag{16}$$

$E_0 := (0,0,0,0)$ is the trivial stationary equilibrium. The Jacobian matrix of H at E_0 reads:

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

where A_w is defined in (14).

If both A_u and A_v have negative eigenvalues then E_0 is a locally attractive stationary point. with $w = u$ and $\sigma = (R_0, R_0)^T$. The consumption functions f_w^j being increasing, the solution (U, V) of (12) are controlled[5] by the solution $\widetilde{U}$ and $\widetilde{V}$ of the single species system (13). From corollary 3.2 we infer that $0 \leq W(t) \leq \widetilde{W}(t) \to 0$ if $\gamma_w < 0$. It follows that E_0 is a global attractor in $\mathbf{R}_+^4$ and in particular, their is no other non negative steady state.

If A_u has at least one positive eigenvalue, then E_0 is not locally attractive. As a consequence, theorem 3.1 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.

Moreover, arguments similar to the ones in [32] chapter 5 yield

Proposition 3.3.

- *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.

Define the following matrix:

$$M_w(R_{\overline{w}}) = \begin{pmatrix} f_w^1(R_{\overline{w}}^1) - \delta^1 - \lambda^1 & \lambda^1 \\ \lambda^2 & f_w^2(R_{\overline{w}}^2) - \delta^2 - \lambda^2 \end{pmatrix}. \tag{17}$$

We show in section 5.2.1 that the stability of the semi-trivial equilibrium $E_{\overline{w}}$ is given by the sign of the eigenvalues of $M_w(R_{\overline{w}})$.

Definition 3.4. *Let Γ_w be the maximum eigenvalue of the matrix $M_w(R_{\overline{w}})$. We call Γ_w the invasion rates of the species w.*

Remark 3.5. *Let us explain the designation "invasion rate" for Γ_u. If $\Gamma_u > 0$, it means that the semi-trivial equilibrium $E_u = (U^1, U^2, 0, 0)$ is unstable. Consequently, according to previous remark, it means that $(0,0)$ is un unstable equilibrium for the differential system:*

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

Hence, if $V(0)$ is small enough, then $t \mapsto V(t)$ is increasing on $(0, \tau)$ at an exponential speed Γ_u. In other words, v invade the environment. At the contrary, if $\Gamma_u < 0$, the semi-trivial equilibrium E_u is stable and from a small initial value $V(0)$, we have $\|V(t)\| \leq Ce^{t\Gamma_u}$ for some constant $C > 0$. In particular $V(t) \to (0,0)$.

The signs of the invasion rates Γ_w give the stability of the semi-trivial equilibrium $E_{\overline{w}}$ but determine also the existence and stability for coexistence stationary equilibrium. In section 5.2.1 we give a full characterization of the stationary solution and their stability.

Moreover, following [32] appendix B, we can show that the system (12) has a monotonic structure.

Definition 3.6. *Let $\leq_K$ be an order in $\mathbb{R}^4$ defined by $(x_1, x_2, x_3, x_4) \leq_K (y_1, y_2, y_3, y_4)$ if and only if $x_1 \leq y_1$, $x_2 \leq y_2$ and $x_3 \geq y_3$, $x_4 \geq y_4$. We defined $<_K$ by replacing all the signs $\leq$ by the sign $<$.*
Consider the smooth differential system in $\mathbb{R}^4$: (E) $x_i = f_i(x_1, x_2, x_3, x_4)$, $i = 1, 2, 3, 4$. recall that the flow $\phi_t : \mathbb{R}^4 \to \mathbb{R}^4$ of this system is defined by $\phi(x_0) = x(t)$ where $x(t) = (x_i(t))_i$ is the solution of (E) such that $x(0) = x_0$.
The system (E) is be monotone with respect to the order $\leq_K$ if $x \leq_k y$ implies $\phi_t(x) \leq_K \phi_t(y)$ for any $t \geq 0$.
It is strongly monotone with respect to $\leq_K$ if f $x \leq_k y$ and $x \neq y$ implies $\phi_t(x) <_K \phi_t(y)$ for any $t \geq 0$.

---

[5] For instance, let $\widetilde{U}$ verifying the system (13) we have $f_u(R_0 - \widetilde{U} - V) \leq f_u(R_0 - \widetilde{U})$ for any $V \in \mathbf{R}_+^2$. Let (U, V) be a solution of (12) with $\widetilde{U}(0) = U(0)$. By comparison, it follows that $U(t) \leq \widetilde{U}(t)$. From the corollary 3.2, we have $\widetilde{U}(t) \to 0$ and then $U(t) \to 0$. The same argument shows that $V(t) \to 0$.

It is classical that such a competition system is monotone.

Proposition 3.7 ([32] corollay B.5. p 265)**.** *The system* (12) *is strongly monotone with respect to* $\leq_K$*.*

Proof. for $\{i, j\} = \{1, 2\}$ and $w \in \{u, v\}$, define $F^i_w(u_1, u_2, v_1, v_2) = W^i(f_w(R_0 - u^i - v^i) - \delta^i) + \lambda^i(w^j - w^i)$. Following [32], the system is monotone because

$$\forall (i, j) \in \{1, 2\}^2 \text{ and } \{w, \bar{w}\} = \{u, v\}, \quad \frac{\partial F^i_w}{\partial \bar{w}^k} \leq 0$$

$$\forall \{i, j\} = \{1, 2\} \text{ and } w \in \{u, v\}, \quad \frac{\partial F^i_w}{\partial w^j} \geq 0.$$

The strong monotonicity is due to the fact that the Jacobian matrix at every point (U, V) is irreducible. □

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 (12) goes to a stationary equilibrium (see [32], appendix C). Hence, using the result from the section 5 and the same arguments that the ones stated in [32] page 143, we obtain theorem 3.8 which describes the possible dynamics of (12).

Theorem 3.8. *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* (12) *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* (12) *go either to E_u or 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. We say that it is a situation of exclusive bistability.*
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* (12) *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* (12) *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. We say that it is a situation of odd bistability.*

Remark 3.9. *As it is proven in [32], the cases 2. and 3.b are impossible if the consumption functions does not depend on the vessels ε^j. We show in figure 1 that every cases may happen in general.*

4 Comparison of the invasion rates between the two models

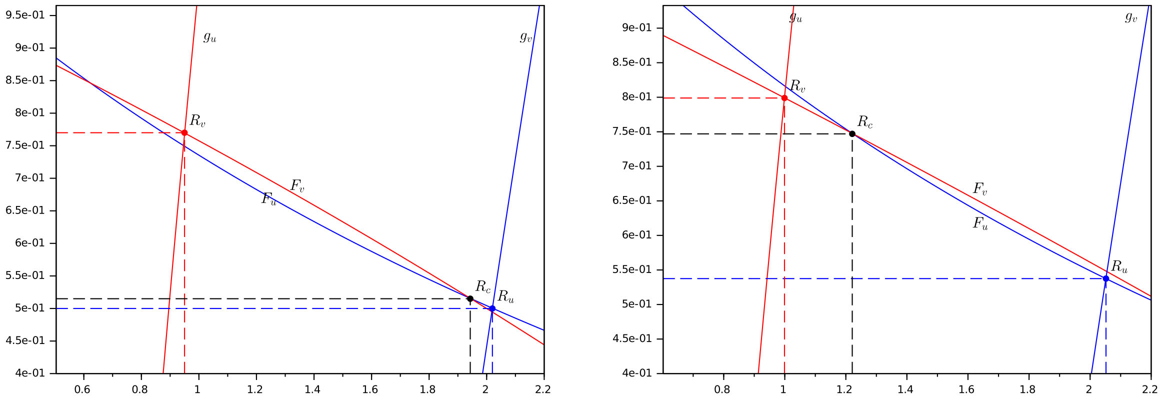
In section 2, a definition for the invasion rates in the probabilistic case is given and it is proven that the signs of the invasion rates characterize the long time behavior of the probabilistic model. Recall that in this case, we defined the invasion rates by :

$$\Lambda_w = \int \left(f^1_w(R) - \delta^1\right) d\mu_{\overline{w}}(R, 1) + \int \left(f^2_w(R) - \delta^2\right) d\mu_{\overline{w}}(R, 2),$$

where $\mu_{\overline{w}}$ is the invariant probability measure of (Z_t) on $M_{0,w} \setminus M_{0,u,v}$.

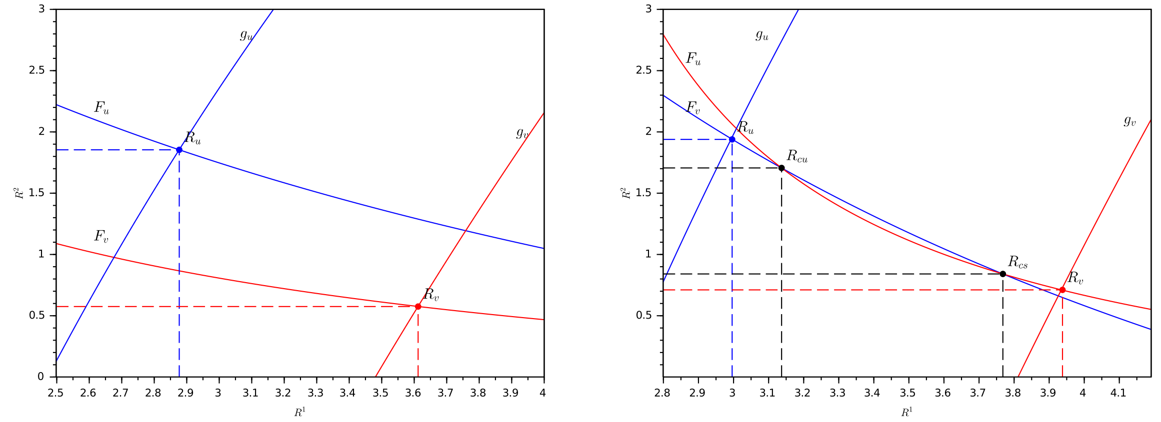
In section 3, the invasion rates Γ_w in the gradostat model are defined as the maximum eigenvalue of a two dimensional matrix and the theorem 3.8 shows that the sign of these invasion rates characterize (essentially) the behavior of the solutions of the gradostat model.

In this section, we aim to give a qualitative comparison of the two definition of the invasion rates in order to discuss the similarities and the differences of the two models we considered.



a - Typical coexistence case. R_c is associated to a globally stable coexistence stationary equilibrium. E_u and E_v are unstable.

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. E_v is stable, E_u is unstable and there is no coexistence steady state. 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 1: The graph of the functions F_w and g_w, $w \in \{u, v\}$ are sufficient to describe the global dynamics of (12). The precise definitions of the functions F_w and g_w a are given in section 5 as well than the proofs of their interpretations. A semitrivial solution $E_u = (R_u, U, 0) \in \mathbb{R}^2 \times \mathbb{R}^2 \times \mathbb{R}^2$ corresponds to an intersection $R_u^2 = F_u(R_u^1) = g_u(R_u^1)$ with $0 < R_u^j < R_0$ for $j = 1, 2$. Moreover, E_u is asymptotically stable if $F_u(R_u^1) < F_v(R_u^1)$. Similar conditions hold for $E_v = (R_v, 0, V)$. A coexistence solution $E_c = (R_c, U_c, V_c)$ corresponds to an intersection $R_c^2 = F_u(R_c^1) = F_v(R_c^1)$ which verifies the inequalities $R_w^1 < R_c^1 < R_{\overline{w}}^2$ and $R_{\overline{w}}^2 < R_c^2 < R_w^2$ for $\{w, \overline{w}\} = \{u, v\}$. Depending on the relative position of F_u and F_v, there may be zero coexistence steady state (figure (c)), one (figures (a) and (b)) or even two (figure d). If the (graph of the) function F_w are never tangent, the stability of the steady states switch when we count them starting from the top left to the upper right. For example on figure (a), E_u is unstable, E_c is stable and E_v is unstable.

4.1 Comparison of the invasion rates in the one species case

Let us first look at the one species case. The following theorem deals with the probabilistic definition of the invasion rate of species w.

Theorem 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* *probability measure μ_0 when it is restricted to $M_{0,u,v}$. 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:

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

The uniqueness of the invariant probability measure is fairly obvious given the definition of the process (Z_t) restricted to $M_{0,u,v}$. Its explicit expression allows to obtain the announced expression for the invasion rate Λ_w^0. The computation of the invariant probability measure is postponed to the last section 5.1.1 of this article.

Recall that the jump rates of the Markov process (I_t) on the state space $\{1,2\}$ are given by: $\lambda^1 = s\lambda$ and $\lambda^2 = (1-s)\lambda$ with $\lambda \in \mathbb{R}$ and $s \in (0,1)$.

Proposition 4.2. *The invasion rate $\Lambda_w^0 = \left(\frac{s}{\delta^1}+\frac{1-s}{\delta^2}\right)\mathbb{E}\left[\Phi(B)\right]$ is monotone according to the variable λ.*

Once again the proof of this statement requires heavy computation and is postponed to section 5.1.2. This analytical property on the invasion rate is used in the proof of theorem 2.3.

An explicit expression of the invasion rate in the deterministic case is given in (15). We compute the limits as $\lambda \to 0$ and $\lambda \to +\infty$ of these invasion rates.

Proposition 4.3. *The behavior of the two model is the same when λ is large enough.*

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

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 not the same the same when λ is small enough.

$$\lim_{\lambda\to0}\Lambda_w^0 = (1-s)\left(f_w^1(R_0^1)-\delta^1\right)+s\left(f_w^2(R_0^2)-\delta^2\right),$$
$$\lim_{\lambda\to0}\Gamma_w^0 = \max\left(f_w^1(R_0^1)-\delta^1, f_w^2(R_0^2)-\delta^2\right).$$

Remark 4.4. *Though these results are easily obtained by a simple computation, the fact that the limits of the invasion rates are the same when λ goes to $+\infty$ is the consequence of some already known results on the averaging of vector fields. Under some condition over the switching vector fields, it is proven in [35] that a process built from switching between the different vector fields converges in law to the deterministic solution of the aggregated system of the vector fields defined in 2.4.*

We see that the behavior of the two models is very different for small λ and very similar for large λ.

- If $\lambda \to +\infty$, then in both model, the system is well mixed and can be approximate by the averaged chemostat which is homogeneous and satisfy the PEC (see definition 2.4). The invasion rate in the homogeneous case is easy to compute and is exactly the limit of both Λ_w^0 and Γ_w^0.
- If $\lambda = 0$ then the for both models, the system corresponds to two unconnected chemostats and the invasion rate in a chemosta ε^j is given by $f_w^j(R_0^j)-\delta^j$. But when $\lambda \to 0$, the limits of the invasion rates keep a trace of the way the two chemostats exchange information. It is then more accurate two think about the case of very small positive λ.
    - In the deterministic model, the essential of the dynamics occurs *simultaneously* in the two chemostat and there is a very small exchange between the two chemostat. It is enough that the species survive in one of the two chemostat to be presents in the domain (at a very small concentration in the other chemostat). It is why the limit is given by a max. In particular, for the species w to go to extinction, it is necessary that both chemostat are unfavorable to w.
    - By contrast, in the PDMP model the dynamics occurs in each chemostat *one after another* and stay a long time on each of them. Hence, there is then an average of the invasion rate in both chemostat weighted by the proportion of time s and $1-s$ the dynamics is given by ε_1 or by ε_2. This is why the limit is a weighted average. In particular, for the species w to go to extinction, it is sufficient that one of the two chemostat ε^j is unfavorable to w if the dynamics follows more likely ε^j.

Numerical simulations are presented in 2 for two sets of data Π_1 and Π_2 defined in the table 1.

Π_1	Π_2
$(a^1, a^2) = (1.1, 2)$	$(a^1, a^2) = (1.1, 2)$
$(b^1, b^2) = (0.4, 4)$	$(b^1, b^2) = (0.05, 2)$
$(\delta^1, \delta^2) = (1, 1)$	$(\delta^1, \delta^2) = (1, 1)$
$(R_0^1, R_0^2) = (10, 1)$	$(R_0^1, R_0^2) = (0.55, 2.1)$

Table 1: Set of data used in figure 2. The set Π_1 correspond to a case where ε^1 is favorable to the species ($\frac{a^1 R_0^1}{b^1+R_0^1} - \delta^1 > 0$) and ε^2 is unfavorable to the species ($\frac{a^2 R_0^2}{b^2+R_0^2} - \delta^2 < 0$). Π_2 correspond to a case where both ε^1 and ε^2 are favorable to the species.

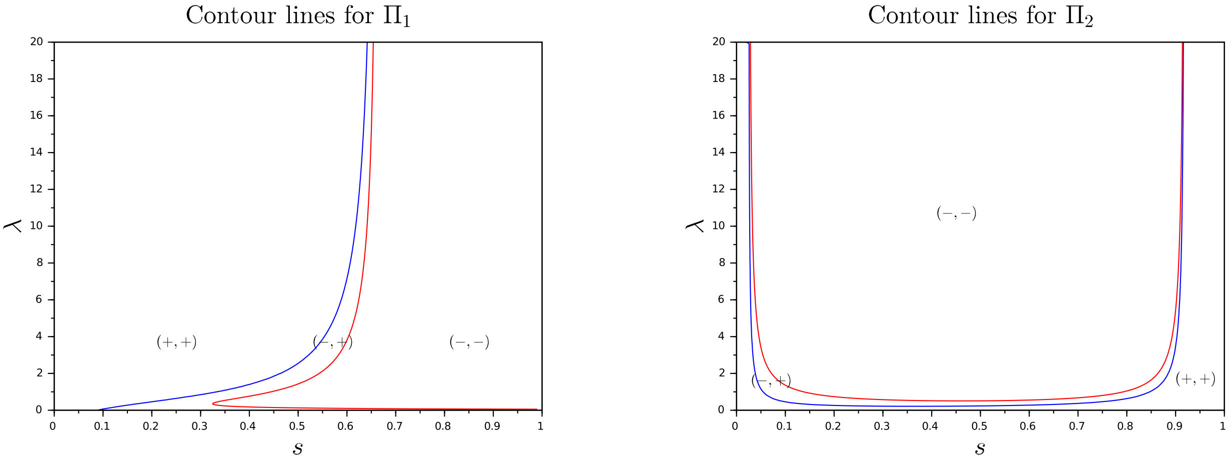


Figure 2: Comparisons of the zero level lines for Γ^0 and Λ^0 for the two sets of data Π_1 and Π_2. The color blue makes reference to Λ^0 (probabilistic invasion rate) and the red color makes reference to Γ^0 (deterministic invasion rate). In each zone of this figure, the sign of the pair (Λ^0, Γ^0) is constant and is plainly indicated by a pair of signs. Note that in the case Π_1, the map $\lambda \to \Gamma_w^0(\lambda, s)$ may not be monotonous. For $s = 0.5$ for instance, $\gamma_w^0(\lambda, 0)$ is positive for a small lambda, then positive for $\lambda \approx 1$ and then positive again for large λ. Such a phenomena is impossible for the probabilistic model for the invasion rate being monotonous. Note that in the case Π_2, both chemostat are favorable to the species but if s is neither to small nor to large, and λ large enough, then the species goes to extinction. Finally, note that in both case we have the embedding $\{(\lambda, s), \Gamma_w^0(\lambda, s) > 0\} \subset \{(\lambda, s), \Lambda_w^0(\lambda, s) > 0\}$. This seems to shows that the species survives more likely in the deterministic model than in the probabilistic one.

4.2 Comparison of the invasion rates in the two species case

We now have a qualitative discussion on the behavior of the invasion rates when two species are introduced in our models. Recall that it is assumed here that $R_0^1 = R_0^2$.

Theorem 4.5. *Let $w \in \{u, v\}$ and assume that $\Lambda_{\bar{w}}^0 > 0$. There exists a unique invariant probability measure $\mu_{\bar{w}}$ of (Z_t) restricted to $M_{0,w} \setminus M_{0,u,v}$.*
The invasion rates Λ_w is computable and its explicit expression 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:

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

$$g_{\bar{w}}(x) = \left(|f_{\bar{w}}^1(R_0 - x) - \delta^1| + |f_{\bar{w}}^2(R_0 - x) - \delta^2|\right) \frac{|f_{\bar{w}}^1(R_0 - x) - \delta^1||f_{\bar{w}}^2(R_0 - x) - \delta^2|}{x}$$

and

$$\begin{aligned} H_{\bar{w}}(x) = -(\nu_{\bar{w}}^1 \beta_{\bar{w}}^1 + \nu_{\bar{w}}^2 \beta_{\bar{w}}^2) \log(x) &+ \omega_{\bar{w}}^1 \alpha_{\bar{w}}^1 \log\left((b_{\bar{w}}^1 + R_0 - x)|f_{\bar{w}}^1(R_0 - x) - \delta^1|\right) \\ &+ \omega_{\bar{w}}^2 \alpha_{\bar{w}}^2 \log\left((b_{\bar{w}}^2 + R_0 - x)|f_{\bar{w}}^2(R_0 - x) - \delta^2|\right). \end{aligned}$$

The constants are defined by:

$$\alpha_{\bar{w}}^j = \frac{a_{\bar{w}}^j}{a_{\bar{w}}^j - \delta^j}, \; \beta_{\bar{w}}^j = 1 + \frac{R_0}{b_{\bar{w}}^j}, \; \nu_{\bar{w}}^1 = \frac{s}{\delta^1} \frac{R_{\bar{w}}^1}{R_0 - R_{\bar{w}}^1}, \; \nu_{\bar{w}}^2 = \frac{1-s}{\delta^2} \frac{R_{\bar{w}}^2}{R_0 - R_{\bar{w}}^2}.$$

The proof of this theorem is very computational and follows closely the proof of theorem 4.1. We will omit it. A complète proof may be find in [22]. This expression for the probabilistic invasion rate is rather heavy but allows us to do some simulations.

For the deterministic case, the invasion rates Γ_w is defined in 3.4 as the maximal eigenvalue of the matrix $M_w(R_{\overline{w}})$ which is defined in (17) and where $R_{\overline{w}}$ is the resource concentration at $E_{\overline{w}}$. Though $R_{\overline{w}}$ verifies a second degree polynomial, and can be explicitly expressed (see section 5.2.1), the complexity of its expressions does not make it interesting to give it formally. However its explicit expressions is used in the numerical simulations.

Proposition 4.6. *The behavior of the two models is the same for λ large enough.*

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

where $R_{\overline{w}}^\infty$ is the unique positive solution of the equation:

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

The behavior of the two models is not the same for λ small enough:

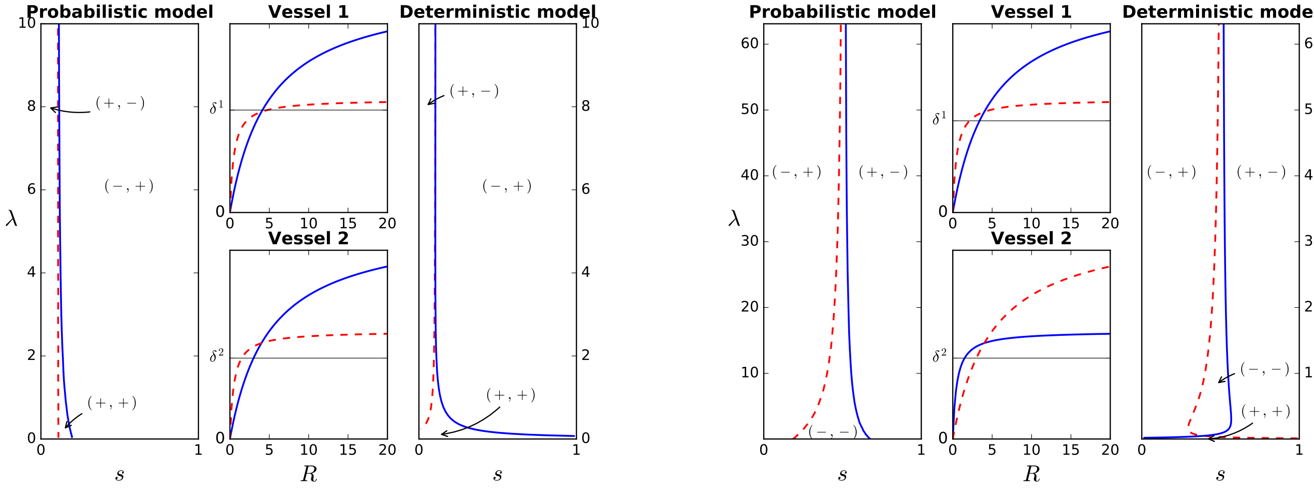
$$\begin{aligned} \lim_{\lambda \to 0} \Lambda_w &= (1-s)\left(f_w^1(R_{\overline{w}}^{1,*}) - \delta^1\right) + s\left(f_w^2(R_{\overline{w}}^{2,*}) - \delta^2\right), \\ \lim_{\lambda \to 0} \Gamma_w &= \max\left(f_w^1(R_{\overline{w}}^{1,*}) - \delta^1, f_w^2(R_{\overline{w}}^{2,*}) - \delta^2\right). \end{aligned}$$

where

$$R_{\overline{w}}^{j,*} = \frac{b_{\overline{w}}^j \delta^j}{a_{\overline{w}}^j - \delta^j} \text{ is the solution of the equation } f_{\overline{w}}^j(R) - \delta^j = 0,$$

that is the break even concentration of the species $\overline{w}$ on the chemostat j.

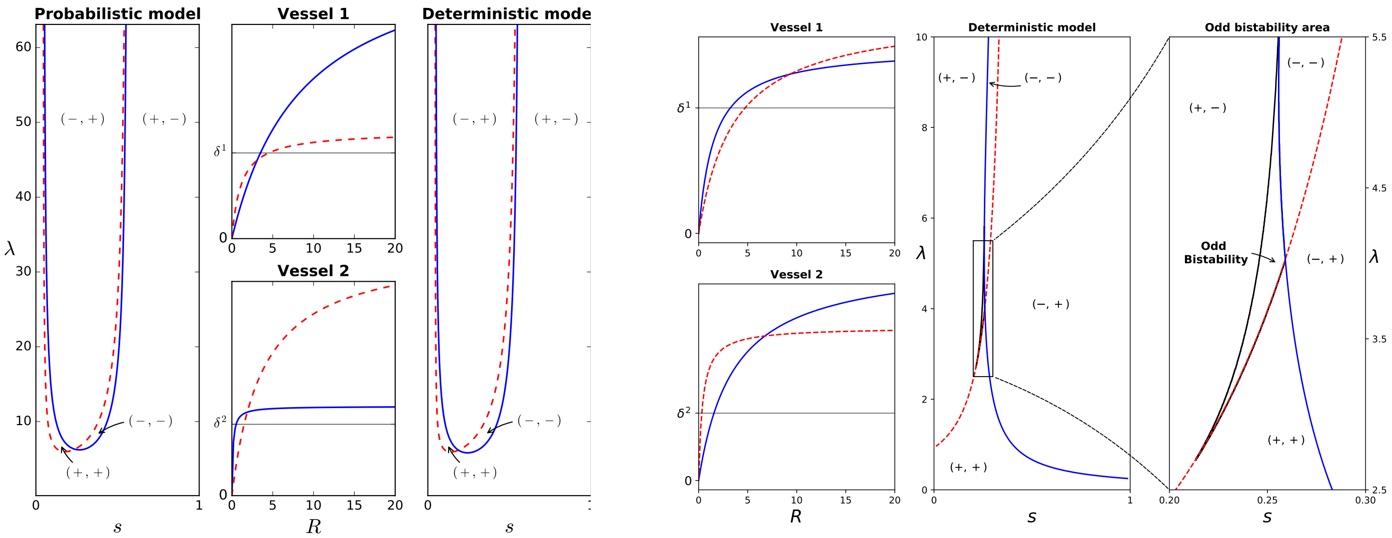
Let us now compare the probabilistic and the deterministic dependance of the invasion rates with respect to λ and s within the two models on particular example. In all the following figures, the blue color is associated to the species u whereas the red color is associated to the species v. The different 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 deterministic case.



a - Typical coexistence situation.

b - Typical bistability sitation.

Figure 3: Both species is the best competor in one vessels. The middle plots represents f_w in both vessels. a - An appropriate averaged ratio between the vessels leads coexistence $(a_u^1, a_u^2, a_v^1, a_v^2) = (4.2, 4, 2.1, 2)$, $(b_u^1, b_u^2, b_v^1, b_v^2) = (5, 5, 0.5, 0.5)$, $(\delta^1, \delta^2) = (1.9, 1.5)$ and $R_0 = 8$. b - The role of species are reversed between the vessels. For the probabilistic model, there is either exclusion or bistability. The same holds for the deterministic case, exept that small diffusion permits coexistence. $(a_u^1, a_u^2, a_v^1, a_v^2) = (4.2, 2, 2.1, 4)$, $(b_u^1, b_u^2, b_v^1, b_v^2) = (5, 0.5, 0.5, 5)$, $(\delta^1, \delta^2) = (1.7, 1.5)$ and $R_0 = 8$.



a - Two vessels favorable to the species u.

b -Odd bistability in the deterministic model.

Figure 4: Two interesting situations. a - The two vessels are favorable to the same species. The middle plots represents f_w in both vessels. Depending on λ and s, each situation may occurs for both models (extinction of u or v, exclusive bistability or coexistence). $(a_u^1, a_u^2, a_v^1, a_v^2) = (3.5, 2.5, 1.25, 7)$, $(b_u^1, b_u^2, b_v^1, b_v^2) = (8.75, 0.125, 1.125, 3.75)$, $(\delta^1, \delta^2) = (1, 2)$ and $R_0 = 7$. b - A situation like in figure 3-a with an odd bistable area in the deterministic model (the probabilistic model behaves like the one figure 3-a). The left plots represents f_w in both vessels. We show only the deterministic model and make a zoom on the odd bistable area in a $(+,-)$ area. This zone corresponds to the case 3-(b) in the theorem 3.8. $(a_u^1, a_u^2, a_v^1, a_v^2) = (3.7, 3.6, 4.4, 2.5)$, $(b_u^1, b_u^2, b_v^1, b_v^2) = (1.55, 3.55, 3.6, 0.4)$, $(\delta^1, \delta^2) = (2.5, 1.1)$ and $R_0 = 20$.

Remark 4.7. *In all the figure, the zeros level sets of* Γ_u, Γ_v, Λ_u *and* λ_v *have the same vertical asymptotes since the two models are described by the* same *averaged chemostat* ε_s *as* $\lambda \to +\infty$ *and that* ε_s *satisfy the PEC.*

Remark 4.8. *Numerically, the invasion rates Λ_w seem to have a monotonous behavior according to λ just like in the case $n = 1$. Sadly the complexity of their expressions does not allow us to prove it. We will conjecture it. Under this conjecture, we do not need the assumption H_w in the theorem 2.7.*
Ours numerical examples shows that this is not the cases for the deterministic model, even for $n = 1$ (see figure 2-a, 3-b and 4-b).

4.3 Concluding remarks

Let us conclude on the similarities and differences 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 2.7 and 3.8 show that the long-time behaviors of the two models essentially depend on the signs of the invasion rates. Hence, we compared 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 [16] 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 equilibrium.
- 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 occurring 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 an the other a semi-trivial solution.
- 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 between 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 with a very small diffusion between them.

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 heterogeneity of our two models are the quantities R^j_w which are the minimum resource quantities needed by species w to survive in the vessel j (when the vessels are isolated). Recall that R^j_w is solution of the equation:

$$f^j_w(R) - \delta^j_w = 0$$

where f^j_w are the consumption functions and δ^j_w 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^j_w to be different according to w and j.

Note that in the probabilistic model we had to assume that the resource entries R^j_0 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 [32], 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 dependent consumption functions and dilution rates.

In this paper, 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 monotone 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 proof 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.

5 Mathematical proofs

5.1 Computation of the invariant probability measures in the probabilistic case

We show in this subsection how to compute the invariant probability measures announced in theorem 4.1 and 4.5.

5.1.1 Proof of the theorem 4.1

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

$$\Lambda_w^0 = \int \left(f_w^1(R) - \delta^1\right) d\mu_0(R,1) + \int \left(f_w^2(R) - \delta^2\right) d\mu_0(R,2)$$

where μ_0 is an invariant probability measure of the process (Z_t) restricted $M_{0,u,v}$. On $M_{0,u,v}$, $(Z_t) = (R_t, 0)$ satisfies:

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

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

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

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

The unique invariant probability measure μ_0 satisfies:

$$\forall\phi, \qquad \int L\phi(r,i)d\mu_0 = 0. \tag{18}$$

We search μ_0 of the shape $\mu_0(dR,j) = \rho^j(R)\mathbb{1}_j dR$. It gives in (18):

$$\begin{aligned}
&\int_{R_0^1}^{R_0^2} \left(\delta^1(R_0^1 - R)\phi'(R) + \lambda^1(\phi(R,2) - \phi(R,1))\right)\rho^1(R)dR + \\
&\int_{R_0^1}^{R_0^2} \left(\delta^2(R_0^2 - R)\phi'(R) + \lambda^2(\phi(R,1) - \phi(R,2))\right)\rho^2(R)dR = 0.
\end{aligned} \tag{19}$$

Assume that $\phi(x,j) = \phi(x)$. It gives in (19):

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

An integration by parts gives:

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

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:

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

From $\rho^j(R_0^{\bar{j}}) = 0$ we have $K = 0$ which yields:

$$\delta^1(R_0^1 - R)\rho^1(R) + \delta^2(R^2 - R)\rho^2(R) = 0. \tag{20}$$

Now, assume that $\phi(R, 1) = \phi(R)$ and $\phi(R, 2) = 0$. Plugging this in (19) and integrate by parts yields

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

By the same density argument as before, we obtain

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

that is

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

Equation (20) 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:

$$\rho'^1(R) + \rho^1(R)\left(\frac{1}{R - R_0^1} - \frac{\lambda^1}{\delta^1(R - R_0^1)} + \frac{\lambda^2}{\delta^2(R_0^2 - R)}\right) = 0. \tag{21}$$

Solving (21) 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_0 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:

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

This explicit expression of μ_0 allows us to compute Λ_w^0:

$$\Lambda_w^0 = C\delta^2 \int_{R_0^1}^{R_0^2} (f_w^1(R) - \delta^1)(R - R_0^1)^{\frac{\lambda^1}{\delta^1} - 1}(R_0^2 - R)^{\frac{\lambda^2}{\delta^2}} dR + C\delta^1 \int_{R_0^1}^{R_0^2} (f_w^2(R) - \delta^2)(R - R_0^1)^{\frac{\lambda^1}{\delta^1}}(R_0^2 - R)^{\frac{\lambda^2}{\delta^2} - 1} dR$$

Set $x = \frac{R - R_0^1}{R_0^2 - R_0^1}$, $\gamma^j = \frac{\lambda^j}{\delta^j}$ and $g_w^j(x) = f_w^j((R_0^2 - R_0^1)x + R_0^1)$, we obtain

$$\Lambda_w^0 = C(R_0^2 - R_0^1)^{\gamma^1 + \gamma^2} \int_0^1 \left[\delta^2(g_w^1(x) - \delta^1)(1 - x) + \delta^1(g_w^2(x) - \delta^2)x\right] x^{\gamma^1 - 1}(1 - x)^{\gamma^2 - 1} dx$$

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:

$$\Lambda_w^0 = \frac{\gamma^1 + \gamma^2}{\lambda^1 + \lambda^2} \int_0^1 \left[\delta^2(g_w^1(x) - \delta^1)(1 - x) + \delta^1(g_w^2(x) - \delta^2)x\right] \frac{x^{\gamma^1 - 1}(1 - x)^{\gamma^2 - 1}}{B(\gamma^1, \gamma^2)} dx$$

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

$$\Lambda^0_w = \frac{\gamma^1 + \gamma^2}{\lambda^1 + \lambda^2}\mathbb{E}\left[\Phi(B)\right] \tag{22}$$

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

Remark 5.1. *The proof for theorem 4.5 uses the same idea except that it requires more heavy computations. We omit it for the sake of readability of this article. See [22] chapter 3 for details.*

5.1.2 Proof of the proposition 4.2

Our expression of the invasion rate is similar to the one the authors of [26] obtained for the invasion rates defined in the Lotka-Volterra switching system introduced in [3]. In order to study the invasion rate they use the following property:

Proposition 5.2. *(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:*

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

We will use this proposition in order to prove the following proposition:

Proposition 5.3. *The invasion rate Λ^0_w is monotone according to the variable λ.*

Proof. We proved that:

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

Recall that $\gamma^1(s,\lambda) = \frac{s\lambda}{\delta^1}$ and $\gamma^2(s,\lambda) = \frac{(1-s)\lambda}{\delta^2}$. Proposition 5.2 ensures that if B and B' are random variables following Beta law 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:

$$\Phi(x) = \delta^2(1-x)\left(f^1_w\left((R^2_0 - R^1_0)x + R^1_0\right) - \delta^1\right) + \delta^1 x\left(f^2_w\left((R^2_0 - R^1_0)x + R^1_0\right) - \delta^2\right).$$

Here the convexity (or concavity) of Φ is not clear and will be checked by straight computation. Set $\alpha^j = \frac{a^j_w}{\delta^j}$, $\beta^j = \frac{b^j_w}{R^2_0 - R^1_0}$ and $r = \frac{R^1_0}{R^2_0 - R^1_0}$. 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:

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

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 5.4. *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. This result is proven by a computation of the roots of the polynomial P. It comes that P has a unique root and it is negative. □

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^0_w is monotonous according to 5.2. □

5.2 Proof of the results for the deterministic model

5.2.1 A graphical characterization 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 set

$$X^j_w(R^j) = f^j_w(R^j) - \delta^j. \tag{23}$$

Any non-negative stationary equilibrium (U, V) of the differential equation (12) are solution of the system (16):

$$\begin{cases} A_u(R)U = 0 \\ A_v(R)V = 0 \end{cases} \tag{24}$$

where, according to remark 1.2, we have $R = R_0 - U - V \in [0, R_0]$ and the matrices $A_w(R)$ are defined by

$$A_w(R) = \begin{pmatrix} X^1_w(R) - \lambda^1 & \lambda^1 \\ \lambda^2 & X^2_w(R) - \lambda^2 \end{pmatrix}.$$

Recall that for any $w \in \{u, v\}$, we denote $W \in \{U, V\}$ the concentration of the species w. If $W \neq \begin{pmatrix} 0 \\ 0 \end{pmatrix}$ in (24), it implies that $\det(A_w(R)) = 0$ which reads explicitly:

$$\left(X^1_w(R^1) - \lambda^1\right)\left(X^2_w(R^2) - \lambda^2\right) = \lambda^1\lambda^2. \tag{25}$$

It follows that the set of points (R^1, R^2) for which the species w may survive is a one dimensional curve. It appears that this curve is the graph of a decreasing function F_w defined on a domain D_w:

$$(R^1, R^2) \text{ verifies (25)} \Leftrightarrow R^1 \in D_w \text{ and } R^2 = F_w(R^1).$$

Moreover, these functions F_w may be explicitly computed as it is stated in the proposition 5.5.

Proposition 5.5. *Let $w \in \{u, v\}$ and $g: x \mapsto g(x) = \lambda^2 + \frac{\lambda^1\lambda^2}{x - \lambda^1}$. Define:*

$$D_w = \{r \in [0, R_0],\ X^1_w(r) - \lambda^1 < 0\} \text{ and } F_w = \left(X^2_w\right)^{-1} \circ g \circ X^1_w.$$

Now, suppose that there exists a non-negative solution (U, V) of (24) such that $W \in \{U, V\}$ is non zero. Then

$$R^1 \in D_w \text{ and } R^2 = F_w(R^1)$$

Remark 5.6. *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.

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:

$$A_w(R)W = 0. \tag{26}$$

With this notation, (26) reads

$$\begin{cases} \left(X_w^1(R^1) - \lambda^1\right) W^1 + \lambda^1 W^2 = 0 \\ \lambda^2 W^1 + \left(X_w^2(R^2) - \lambda^2\right) W^2 = 0. \end{cases} \tag{27}$$

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, (27) implies that 0 is an eigenvalue of $A_w(R)$ implying that $\det\left(A_w(R)\right) = 0$ which reads explicitly:

$$\left(X_w^1(R^1) - \lambda^1\right)\left(X_w^2(R^2) - \lambda^2\right) = \lambda^1 \lambda^2 \tag{28}$$

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:

$$g(x) = \lambda^2 + \frac{\lambda^1 \lambda^2}{x - \lambda^1}.$$

□

At this step, we see that it is necessary that $R = (R^1, R^2)$ 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 correspond to the fact that 0 is an *eigenvalue*[6] of the matrix $A_w(R)$.

The analysis of the corresponding eigenvector will give us sufficient conditions for a point of the curve to be a semi-trivial equilibrium (proposition 5.8) or a coexistence equilibrium (proposition 5.10).

For instance, assume that (U, V) is a non-negative equilibrium of (24). 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:

$$W = \mu_w \begin{pmatrix} \lambda^1 \\ -(X_w^1(R^1) - \lambda^1) \end{pmatrix}. \tag{29}$$

---

[6] 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 W.

In the case of the semi-trivial solution, we have $\begin{pmatrix} R^1 \\ R^2 \end{pmatrix} = R = R_0 - W$ and it comes that:

$$R^2 = R_0 + \frac{1}{\lambda^1}(R_0 - R^1)\left(X_w^1(R^1) - \lambda^1\right).$$

This lead us to define, for $w \in \{u, v\}$, the functions g_w (defined on D_w) by:

$$g_w(r) = R_0 + \frac{1}{\lambda^1}(R_0 - r)\left(X_u^1(r) - \lambda^1\right).$$

Lemma 5.7. *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 resource concentration $R_w = \begin{pmatrix} R_w^1 \\ R_w^2 \end{pmatrix}$ associated to E_w satisfies $g_w(R_w^1) = R_w^2$.*

Proof. The fact that $g_w(R_w^1) = R_w^2$ follows from the very definition of g_w. A direct computation gives

$$g_w'(r) = -\frac{X_w^1(r) - \lambda^1}{\lambda^1} + (R_0 - r)\frac{X_w^{1\prime}(r)}{\lambda^1}.$$

Since $X_w^1(r) - \lambda^1 < 0$ for $r \in D_w$, it comes that g_w is increasing on D_w. ☐

We can now state the graphical characterization of the semi-trivial solution.

Proposition 5.8. *Let $w \in \{u, v\}$. The semi-trivial solution E_w exists if and only if there exists $R_w^1 \in D_w$ such that $F_w(R_w^1) = g_w(R_w^1) := R_w^2$. In that case E_w is unique and the resource concentration at E_w is $R_w = (R_w^1, R_w^2)$.*

Proof. The characterization of R_w is a direct consequence of the proposition 5.5 and the lemma 5.7. The uniqueness follows from the fact that $r \mapsto g_w - F_w$ is increasing on D_w. ☐

Now, let us study the case of the coexistence stationary equilibrium. From the proposition 5.5, if there exists a coexistence solution, that is a positive solution (U_c, V_c) to (24), 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 5.6, we obtain the following lemma.

Lemma 5.9. *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_1 and F_2 but these intersections are not necessarily associated to a positive solution of (24). 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 (24).

Proposition 5.10. *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 $[0, R_0]^2$:

$$K_w = \{(R^1, R^2) \in [0, R_0]^2, \quad \left(R_w^1 - R^1\right)\left(R_w^2 - R^2\right) < 0\}.$$

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 stationary equilibrium E_w. According to (26), 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 $R_c \in K_u \cap K_v$.

From the equation (29) coupled to the fact that $R_c = R_0 - U_c - V_c$, it comes that the values of the concentration (U_c, V_c) associated to R_c are given by:

$$U_c = \mu_u \left(\frac{\lambda^1}{-(X_u^1(R_c^1) - \lambda^1)}\right) \text{ and } V_c = \mu_v \left(\frac{\lambda^1}{-(X_v^1(R_c^1) - \lambda^1)}\right) \tag{30}$$

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:

$$\min\left(g_u(R_c^1), g_v(R_c^1)\right) \le R_c^2 \le \max\left(g_u(R_c^1), g_v(R_c^1)\right).$$

Consequently, R_c is associated to an admissible equilibrium if and only if,

$$R_c \in \Theta = K_u \cap K_v \cap \left\{(R^1, R^2) \in [0, R_0]^2, \quad \min\left(g_u(R^1), g_v(R^1)\right) \le R^2 \le \max\left(g_u(R^1), g_v(R^1)\right)\right\} \tag{31}$$

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 (31)). 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.

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:

$$K = [\min(R_u^1, R_v^2), \max(R_u^1, R_v^1)] \times [\min(R_u^2, R_v^1), \max(R_u^1, R_v^2)].$$

□

Corollary 5.11. *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 5.10 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 5.10, we calculated the coexistence stationary equilibrium associated to R_c and found out that U_c and V_c satisfy (29) where

$$\mu_w = \frac{1}{X_{\overline{w}}^1(R_c^1) - X_w^1(R_c^1)}\left(g_{\overline{w}}(R_c^1) - R_c^2\right).$$

Since $U_c > 0$ and $V_c > 0$, we have $\mu_u > 0$ and $\mu_v > 0$ which yields $X_u^1(R_c^1) > X_v^1(R_c^1)$. □

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. Now, we state a criteria for the existence of coexistence stationary equilibrium according to the stability of the semi-trivial equilibrium E_u and E_v.

Proposition 5.12. *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 H evaluated in E_w. For sake of simplicity we give 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

$$C = \begin{pmatrix} X_v^1(R_u^1) - \lambda^1 & \lambda^1 \\ \lambda^2 & X_v^2(R_u^2) - \lambda^2 \end{pmatrix}.$$

Using the facts 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 $X_u^i(R_u^i) - \lambda^i < 0$, a simple computation shows that the real part 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 part which gives the announced inequality (recall that $F_v = (X_v^2)^{-1} \circ g \circ X_v^1$ and $g(x) = \lambda^2 + \frac{\lambda^1\lambda^2 x}{x - \lambda^1}$). ☐

5.2.2 Proof of the theorem 3.8

Proof. Let us assume that $R_u^1 < R_v^1$. The existence of coexistence stationary equilibrium is a simple consequence of proposition 5.12 and the intermediate value theorem. Let us prove it if E_u and E_v are both stable, then according to proposition 5.12, $F_{\overline{w}}(R_w^1) > R_w^2$ 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 5.9, 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 that $R_c^2 \in [R_v^2, R_u^2]$. Hence, proposition 5.10 implies that R_c is associated to an admissible coexistence stationary equilibrium. Figure 1 comes as an illustration for this statement.

The stability of the coexistence stationary equilibrium is more difficult to obtain. The Jacobian matrix of H evaluated in (U_c, V_c) reads:

$$DH(U_c, V_c) = \begin{pmatrix} X_u^1 - \lambda^1 - \beta_u^1 & \lambda^1 & -\beta_u^1 & 0 \\ \lambda^2 & X_u^2 - \lambda^2 - \beta_u^2 & 0 & -\beta_u^2 \\ -\beta_v^1 & 0 & X_v^1 - \lambda^1 - \beta_v^1 & \lambda^1 \\ 0 & -\beta_v^2 & \lambda^2 & X_v^2 - \lambda^2 - \beta_v^2 \end{pmatrix}$$

where:

$$X_w^j = f_w^j(R_c^j) - \delta^j < 0 \text{ and } \beta_w^j = U_w^{j,c} f_w^{j\prime}(R_c^j) > 0.$$

Note that $DH(U_c, V_c)$ is an irreducible matrix and it can be written:

$$DH(U_c, V_c) = \begin{pmatrix} A & B \\ C & D \end{pmatrix},$$

where A and D are irreducible square matrices with positive off diagonal elements and B and C are diagonal matrix with negative diagonal elements.

Let $s(DH(U_c, V_c))$ be the maximum real part of the eigenvalues of $DH(U_c, V_c)$. Following [32], we now use a very strong following property dealing with these kind of matrices (which can be found in [4]): Defined

$$\overline{DH(U_c, V_c)} = \begin{pmatrix} A & -B \\ -C & D \end{pmatrix}.$$

Then $s(DH(U_c, V_c)) < 0$ 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 $\overline{DH(U_c, V_c)}$.

As a consequence, the signs of d_1, d_2, d_3 and d_4 characterize the stability of $DH(U_c, V_c)$. Firstly, we have $d_1 = X_u^1 - \lambda^1 - \beta_u^1 < 0$. Next, we have:

$$d_2 = \begin{vmatrix} X_u^1 - \lambda^1 - \beta_u^1 & \lambda^1 \\ \lambda^2 & X_u^2 - \lambda^2 - \beta_u^2 \end{vmatrix} = -\beta_u^1(X_u^2 - \lambda^2) - \beta_u^2(X_u^1 - \lambda^1) + \beta_u^1\beta_u^2 > 0.$$

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. A straight computation, similar to the one in [32] gives:

Lemma 5.13.

$$d_4 = \mu_u\mu_v\lambda^1\lambda^2 f_u^{2\prime} f_v^{1\prime} \frac{X_u^1 - \lambda^1}{X_v^1 - \lambda^1}\left(X_u^2 - X_v^1\right)\left(\frac{F_u'(R_c^1)}{F_v'(R_c^1)} - 1\right).$$

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:

$$d_4 = \beta_u^1\beta_v^2\left[\left(X_u^2 - \lambda^2\right)\left(X_v^1 - \lambda^1\right) - \lambda^1\lambda^2\right] + \beta_u^2\beta_v^1\left[\left(X_u^1 - \lambda^1\right)\left(X_v^2 - \lambda^2\right) - \lambda^1\lambda^2\right].$$

From $(X_w^1 - \lambda^1)(X_w^2 - \lambda^2) = \lambda^1\lambda^2$, we infer

$$d_4 = \left(X_v^1 - X_u^1\right)\left(\beta_u^1\beta_v^2\left(X_u^2 - \lambda^2\right) - \beta_u^2\beta_v^1\left(X_v^2 - \lambda^2\right)\right).$$

Recall that $\beta_w^j = U_w^{j;c} f_w^{j\prime}(R_c^j)$. According to proposition 30,

$$W_c = \mu_w \begin{pmatrix} \lambda^1 \\ -(X_w^1 - \lambda^1) \end{pmatrix}.$$

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 realtion 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:

$$\operatorname{sign}(d_4)=\left(X_u^2-X_v^1\right)\left(\frac{F_u'(R_c^1)}{F_v'(R_c^1)}-1\right).$$

Moreover corollary 5.11 gives us a better understanding of this sign:

$$\operatorname{sign}(d_4)=\left(R_v^1-R_u^1\right)\left(\frac{F_u'(R_c^1)}{F_v'(R_c^1)}-1\right).$$

Let us assume that $R_v^1-R_u^1>0$ (the proof is the same if we suppose that $R_v^1-R_u^1<0$). We will now show how the stability of the semi-trivial equilibrium 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 5.12, 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.

This reasoning also proves the stability property of the coexistence stationary equilibrium in the other cases which concludes the proof. □

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